Temporal and spatial variability in a copepod community off St Helena Bay in 2000/1

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ABSTRACT

The driving forces behind changes in copepod community structure in the Benguela upwelling region are examined. For this study, monthly changes in copepod size structure and species composition were examined at St Helena Bay in 2000/1 in relation to upwelling, phytoplankton and fish. The copepod assemblage was dominated by large species categories in the early period of recruitment (April) and smaller species categories in the late period of recruitment (August). The reappearance of large species categories and increase in copepod biomass is observed in summer months. This is attributed to both predation and upwelling intensity. Arguments are developed to suggest that the copepod size structure is consistent with 'wasp-waist' control and 'bottom-up' control was responsible for the copepod increase.

INTRODUCTION

The Benguela Current system off the west coast of southern Africa is one of four regions globally that are characterized by coastal upwelling systems. Coastal upwelling in the southern Benguela results from strong winds along the west coast during September – May (Shannon *et al.* 1992). These winds blow the surface water northwestward and cause cold, nutrient-rich water to upwell to the surface. Phytoplankton use the nutrients to grow and multiply. Phytoplankton are eaten by zooplankton, which in turn are food for pelagic fish. Upwelling intensity has increased in the past five decades in the Benguela region, and yields of pelagic fish have shown large fluctuations during this period (Bakun 1990, Shannon *et al.* 1992).

In most eastern boundary current systems studied to date, it was found that zooplankton have declined in terms of biomass over the past five decades (Verheye 2000). In the Benguela region, zooplankton have increased 100-fold in terms of numbers (Verheye 2000). In previous studies (Cury *et al.* 2001, Verheye 2000), it was proposed that there are a number of upwelling-associated, "bottom-up" processes that could have contributed to the increase in zooplankton:

- Intensified coastal upwelling, leading to an increase in zooplankton production through an increase in phytoplankton biomass.

- Increased southerly winds, which could intensify equatorward transport of phytoplankton populations from upwelling waters further south in the region, thereby leading to an increase in zooplankton production.

Verheye (2000) supported the hypothesis that the decadal scale increase in zooplankton is a long-term biological reaction to stronger coastal upwelling, which leads to nutrient enrichment and increased phytoplankton production and biomass.

Cury *et al.* (2001) hypothesized three controls that may play a role in changing the marine food chain (Figure. 1). The first hypothesis was that the abundance of small pelagic fish controls the abundance of their predators and their zooplankton prey. A decrease in prey fish abundance has a negative effect on predators. The same decline in abundance of the prey fish reduces predation on zooplankton, which increases their abundance. Abundant zooplankton increases grazing pressure on phytoplankton and leads to a decline in phytoplankton; this hypothesis is called wasp-waist control (Cury *et al.* 2000).

In top-down control (Figure 1), there is a cascading trophic effect of predator-prey interactions, whereby organisms of a higher trophic level (predator) exert profound effects on the levels of abundance and on the community structure of the prey. A decrease in top predators will cause

small pelagic fish abundance to increase, which in turn causes a decrease in zooplankton and an increase in phytoplankton. Bottom-up control is associated with a decrease in phytoplankton production, which leads to a decrease in zooplankton abundance and that of all subsequent trophic levels (Figure 1).

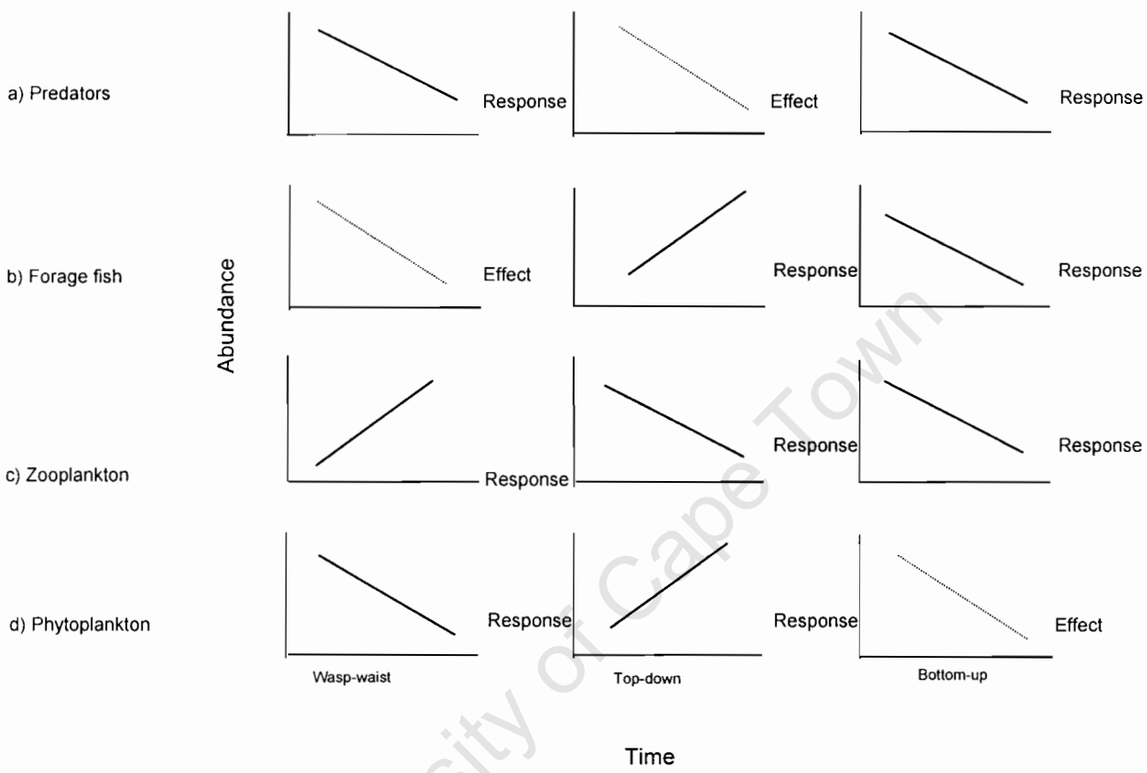

Fig. 1: Wasp-waist, Top-down and bottom-up control in a pelagic ecosystem, showing the response in terms of abundance of (a) predators (c) zooplankton and (d) phytoplankton upon changing one component of a marine food chain (after Cury *et al.* 2000).

Hutchings *et al.* (2002) showed some evidence supporting the "wasp-waist" hypothesis. They looked at seasonal biomass of zooplankton off St Helena Bay from 2000 and 2001 and compared these values with those from 1977/8. They found that in 2000 and 2001 there was a seasonal pattern in the biomass of zooplankton, which showed a pronounced increase in summer, compared with uniform biomass year-round in 1977/78. The peak summer values in 2000/1 were approximately ten times the mean biomass in 1977/78. This increase was attributed to increased upwelling intensity and retention in St Helena Bay (Verheye *et al.* 1998). The decrease in winter zooplankton biomass was attributed to predation by pelagic fish rather than a decrease in upwelling and phytoplankton. These findings indicate the important role that the pelagic fish may play in the marine food web.

Zooplankton heterogeneity in community structure at a range of spatial and temporal scales is an important focus of aquatic ecological research. Zooplankton serves a key role in marine food chains as they transfer energy from primary productivity to higher trophic levels (Clark *et al.* 2001, Timonin 1990).

This study examines the temporal and spatial variability in the copepod community in St Helena Bay, the same study area as for Hutchings *et al.* (2002). St Helena Bay is a recruitment area for important South African

pelagic fish, anchovy *Engraulis encrasicolus* and pilchard or sardine *Sardinops sagax* (Crawford *et al.* 1987). Recruitment to the West Coast is at a maximum during the period of February - June /July (Cochrane and Hutchings 1995, Timonin 1990). Recruits of anchovy and sardine feed on zooplankton of different sizes. Sardine recruits feed on small zooplankton (modal size class approximately 300 μm) with anchovy consuming size-classes approximately between 600-900 μm, with little competition between the two species (Louw *et al.* 1998). The survival rate of pelagic fish depends to some extent on sufficient food being available in the critical early stages of their life history. Therefore, it is essential to monitor plankton abundance and community structure changes, spatially and temporally, on a regular basis, particularly in this fishing area. Monitoring and understanding variability of copepod community structure in St Helena Bay is of general ecological interest as well as being of relevance to growth rates of pre-recruit and juvenile fish, which can affect biomass yields to the fishery and energy reserves for spawning later in the year.

In 1999/2000 and 2000/1 the high recruitment success of anchovy resulted in an extraordinary large biomass of planktivorous pelagic fish along the West Coast during the winter months (van der Lingen 2002a). The recruitment success has been attributed to unusual oceanographic events that occurred during the 1999 - 2000 summer season off the West

Coast of South Africa (Roy *et al.* 2001). The first event was a strong and sustained warming that occurred in mid-December and lasted for two weeks. The second event was an enhanced cooling that lasted from mid to late summer. These events resulted from fluctuations in wind-induced upwelling. The upwelling regime recorded during the mid and late summer season might have enhanced food availability to the larvae that had previously reached the West Coast nursery area during the December 1999 relaxed upwelling event. Improved food availability probably reduced mortality of anchovy larvae and young juveniles. The high recruitment could have resulted in a decrease in zooplankton biomass, which showed a strong seasonal signal in 2000/1, with summer values five times bigger than winter values, when pelagic fish recruits are feeding in the inshore region on the west coast (Hutchings *et al.* 2002).

This study aims to build on the study of Hutchings *et al.* (2002) by:

1.) Examining the structure of the copepod community during summer and winter 2000/1.
2.) Establishing whether the "wasp-waist" hypothesis is supported by the data.

Pelagic fish are size-selective feeders and this study aims to see whether the size classes of their preferred prey are missing in the winter months, because this will support the grazing pressure hypothesis. The

hypothesis for this study is that pelagic fish impact the copepod community not only in terms of biomass, as shown by Hutchings *et al.* (2002), but also in terms of species composition because of size-selective feeding. An alternative hypothesis is that bottom-up control exists and zooplankton was affected by changes in phytoplankton variability and so controlled fish growth.

MATERIALS AND METHODS

Zooplankton samples selected for this study have been collected since April 2000 in the St Helena Bay Monitoring Line sampling programme by staff of Marine and Coastal Management. Figure 2 shows the stations that were sampled across the shelf on a monthly basis for this study. The sampling gear that was used was a vertical bongo net, which has a 200 μm mesh size. The sampling was done from 20 m depth in the inshore stations up to 200 m in the offshore stations.

The criterion used for the selection of the samples analysed specifically by me for this study was taking one year of samples, in this case from

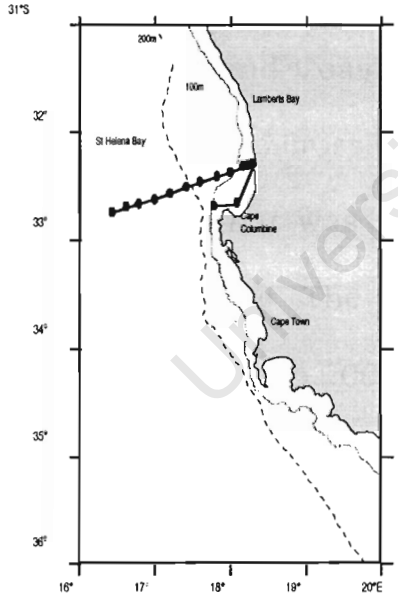

Fig. 2: The study area showing the St Helena Bay Monitoring line with the positions of the 14 stations sampled.

April 2000 to February 2001, selecting alternate months. A total of 84 samples was analysed from April, June, August, October, December 2000 and February 2001.

Sample analysis

Each sample was put into a glass cylinder for 24 hours to allow it to settle. Large gelatinous zooplankton were removed from the sample and not considered further, because most of them were badly damaged. After taking the measurements of the settled volume of zooplankton, the sample was diluted to ten times the settled volume. The sample was agitated with a tube to obtain a homogeneous distribution of the zooplankton. Aliquots of 2 ml were drawn from the sample using a modified wide-bore Stempel pipette (Verheye and Richardson 1998) and placed in a Bogorov tray (Gibbons 1999). All zooplankton organisms were counted and identified under a dissecting microscope using 10x – 40x magnifications. *Calanoides carinatus* and *Calanus agulhensis* were classified according to their copepodite stages (C1-C6). Young stages (C1-C3) of both species are difficult to identify and their body shape is almost identical (*Calanus* is slightly larger and fuller than *Calanoides*). In these stages the dominating species for the adult stages was assigned to the small stages in that sample. The identifying features for these stages are as follows:

C3 = 4 pairs of legs

C2 = 3 pairs of legs

C1 = 2 pairs of legs

Other dominant copepod species (*Centropages brachiatus* and *Metridia lucens)* were subdivided by sex and juvenile stages. Small copepods (*Paracalanus, Ctenocalanus* and *Clausocalanus)* were not identified to species level but pooled as small copepods. All counts were standardized to number.m-^{2} using equation (1) below:

$$\text{No.m}^{-2} = \frac{\text{No. of individuals}}{\text{Sub - sample (ml)}} \times \frac{\text{Total diluted volume (ml)}}{\text{Volume filtered (m}^3\text{)}} \times \text{Depth (m)} \qquad (1)$$

All the stations with missing data were deleted, so as to comply with the PRIMER software requirements. All rare species categories were deleted; the criterion used for the removal of these species categories was that those that occurred less than 30 times in total samples were removed from the analysis. In total, for the PRIMER analyses, the abundances of 22 species categories were used from 84 samples, which represented 14 stations at six alternate months. The final data set was classified into size classes in terms of total length; those that were <1000μm were classified as being small, 1000μm -2000μm as being medium and those >2000μm as being large.

Data Analysis: community composition

The PRIMER package (Clarke and Gorley 2001) was used for analysis of these data. In the analyses, similarities between the samples were

calculated using the Bray Curtis similarity measure (Clarke and Gorley 2001) after transforming the data using a root-root transformation, which is recommended for data with very large and very small values (Clarke and Gorley 2001). Similarity matrices are the basis of many multivariate methods (Field *et al.* 1982). In this case, the similarity matrix was used to discriminate samples from each other by using hierarchical cluster analysis and clustering these samples in groups that have similar species compositions. Similarities within each group of samples are greater than those between groups.

Ordination is a graphical representation of the data in two dimensions, which may be obtained through a method known as multi-dimensional scaling, MDS (Clarke and Gorley 2001). Ordination plots place samples close together if they have similar communities, and far apart if they have few species in common or the same species at different levels of abundance. Thus ordination allows a gradation among samples to be represented graphically.

"Simper" analysis was carried out in PRIMER to look at the percentage contributions of different species categories to the groups identified from the dendrogram and ordination plots. Mean abundance of species categories in all groups was also calculated. Species contributions were represented in a pie chart for each group. Abundance and size classes of

different species categories were represented in the form of bar graphs. Abundance of each species was converted into biomass using dry weight measurements of each species from Richardson *et al.* (2001) using equation (2):

$$\text{Biomass}\left(\mu g.m^{-2}\right) = \text{Abundance}\left(No.m^{-2}\right) \times \text{Dry weight}\left(\mu g\right) \quad (2)$$

Data analysis: Environmental data

Environmental data used were obtained from the previous study by Hutchings *et al.* (2002) for the same area. These data include temperature and chlorophyll *a* profiles.

RESULTS

The species categories that were identified and counted in this study are summarized in Table 1. A total of 39 species categories was counted and identified; of the 39, 22 were used in further analyses. These final 22 species categories were classified according to size estimates obtained from Richardson *et al.* (2001) and Stuart and Huggett (1992). Out of the 22 species categories eight were classified as small, six species categories were classified as medium and eight species categories were classified as large. Small copepods and *Oithona* spp were most commonly found in the samples when species categories are considered. However, in terms of single species, *Calanus agulhensis, Calanoides carinatus, Centropages brachiatus* and *Metridia lucens* contributed greater frequencies than the other species and species groups (Table 1). *Pleuromamma borealis* was least common among all the species categories.

Table 1: Zooplankton species categories from St Helena Bay that were identified and counted and the number of samples in which they occurred. Those categories that were used for the PRIMER analysis are shown together with abbreviations used and their size estimates. (Richrdson *et. al.* 2001, Stuart and Huggett 1992)

Species	Stages	Frequency	Size estimate	Total Length µm
Calanus agulhensis	CI	9	Small	780
	C2	14	Small	950
	C3	20	Medium	1350
	C4	28	Medium	1700
	C5	11	Large	2300
	Females (C6)	29	Large	2760
	Males (C6)	25	Large	2720
Calanus agulhensis(Ca)	Total	37		
Calanoides carinatus	C1	8	Small	788
	C2	11	Medium	1010
	C3	17	Medium	1253
	C4	25	Medium	1653
	C5	8	Large	2095
Cl Fe	Females (C6)	33	Large	2498
	Males (C6)	24	Large	2460
Calanoides carinatus(Cl)	Total	32		
Centropages brachiautus (Ce Fe)	Females	29	Medium	1790
	Males	33	Medium	
Ce Ju	Juveniles	33	Small	
Centropages brachiautus (Ce)	Total	32		
Small copepods (Small Cop)		55	Small	
Phueromamma	Females	1		
	Males	1		
	Juveniles	0		
Phueromamma borealis	Total	1		
Metridia F	Females	32	Large	2294
	Males	35	Large	2264
Metridia J	Juveniles	29	Medium	
Metridia lucens	Total	33		
Copepod Nauplii		27		
Chaetognaths		22		
Oithona spp		52	Small	710
Bivalves		19		
Decapods		10		
Euphausiids		17		
Tunicates		16		
Cirripedes		14		
Amphipods		3		
Cladocerans		18		
Polychaetes		8		
Other calanoids		8		
Rhincalanus nasutus		6		
Oncacea spp		7		
Gastropods		10		
Corycaeus/ Corycella spp		8		

The groups that were identified during classification analysis are shown in Figure. 3. The horizontal axis represents the stations sampled and the vertical axis represents the similarity level at which the groups are formed. From the resulting dendrogram four groups of stations were selected and were labelled Groups A, B1, B2 and C. Obvious outliers were labelled O. There were five obvious outliers, representing stations that were very dissimilar to the other stations.

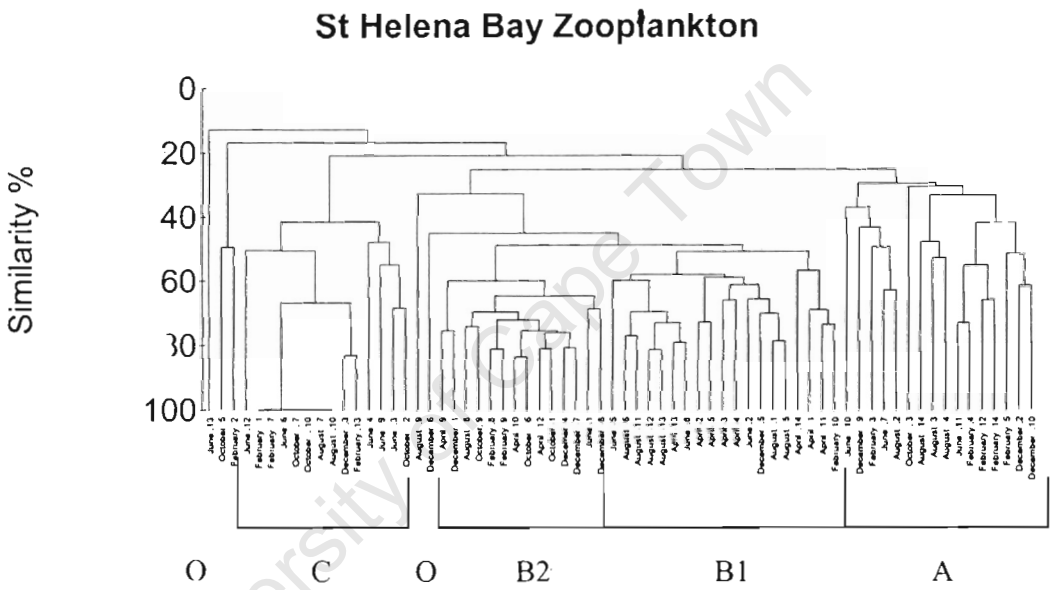

Fig 3: St Helena Bay stations (indicated by numbers) grouped in a dendrogram, using hierarchical clustering. Group-average linking of Bray-Curtis similarities was used, based on √√-transformed abundance data for the copepod species categories.

The ordination plot (Fig. 4) displays the relationships among the four groups (A, B1, B2 and C) and obvious outliers represented by O from Figure 3. The adequacy of the MDS is measured in terms of stress levels,

with the smaller the value the better the representation. The stress value given in Figure 4 is 0.16, which indicates a potentially useful two-dimensional picture (Clarke and Gorley 2001).

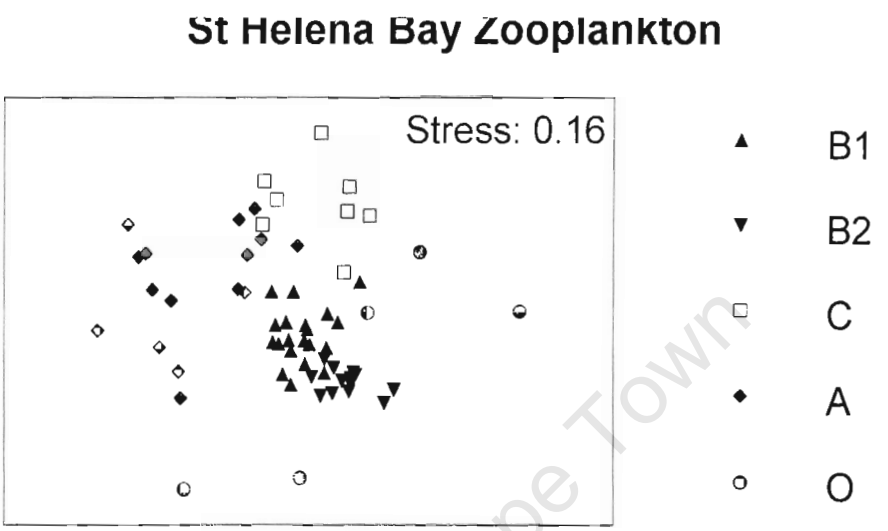

Fig. 4: MDS ordination of all the stations based on √√-transformed abundances of the copepod species categories and Bray-Curtis similarities (stress= 0.16).

Ordination plots in Figure 4 indicate that groups B1 and B2 are very similar because they are close to each other. Group A is more similar to group C judging by their distance apart. Outliers are far from the other groups.

The results from the Simper analysis give the species contributions to each group (Fig. 5). Small copepods and *Oithona* spp contributed substantially to most of the groups, but they were abundant only in groups A, B1 and B2 (Fig. 6). Contributions varied, with groups B1 and

B2 having a greater diversity of species categories than A and C. Although small copepods contribute to groups B1 and B2 (Fig. 5), other small and large copepods are also important. In group B1, the large copepods are represented by *Metridia lucens* females and juveniles, whereas in group B2 there are contributions from females of *Centropages brachiatus* and *Calanoides carinatus*.

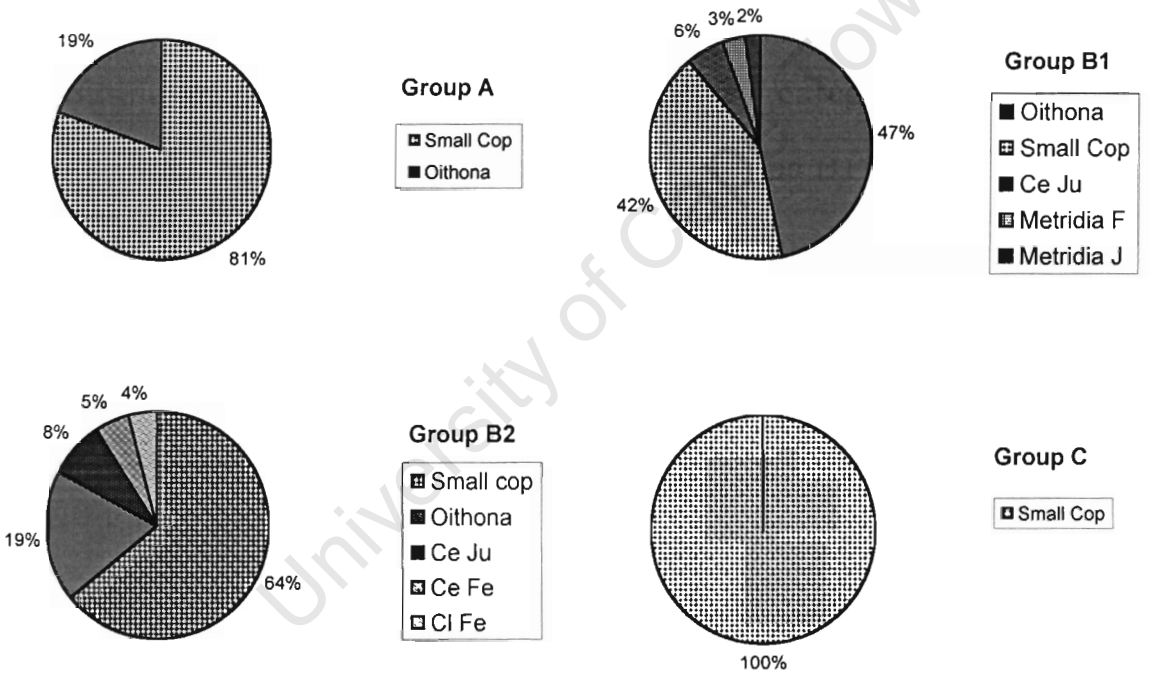

Fig. 5: Results of the Simper analysis in PRIMER, showing the contributions by different species categories to the four groups that were identified in the cluster analysis. Note that these contributions are not equivalent to relative abundance.

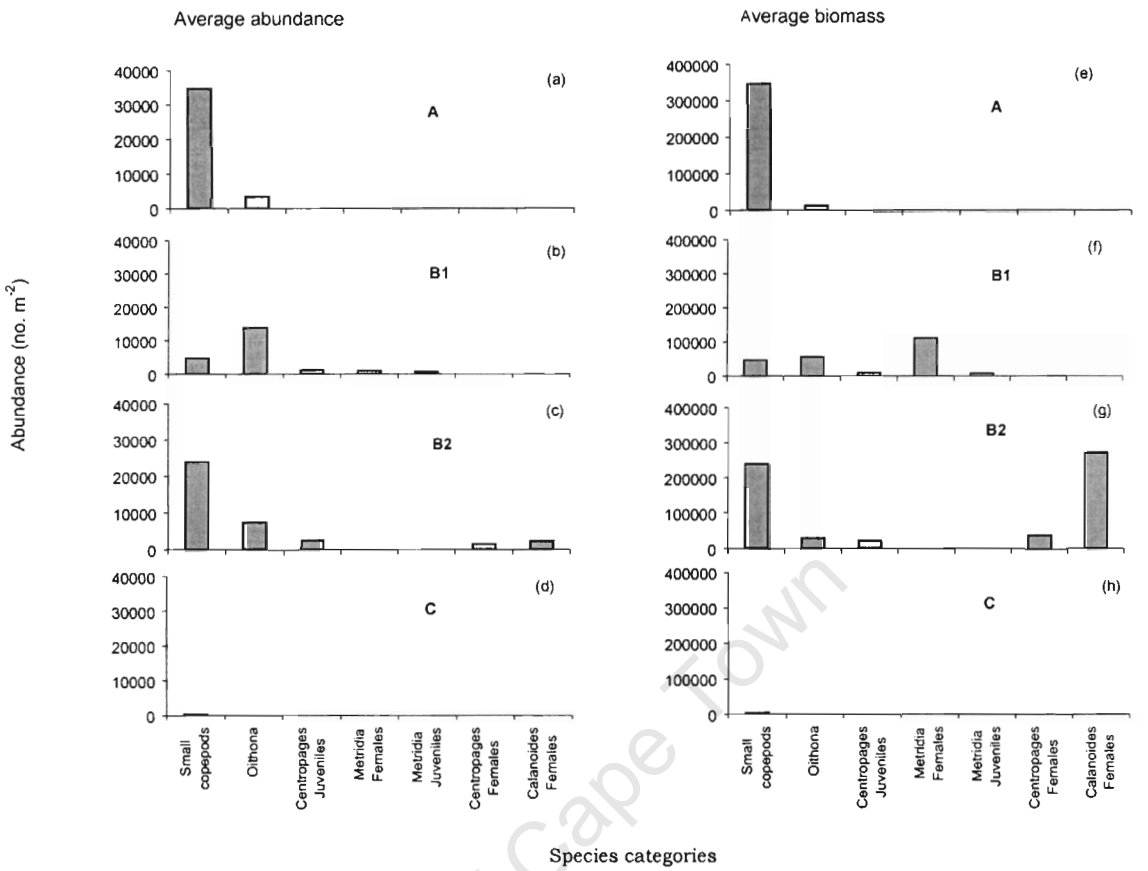

Fig. 6: Results of the Simper analysis in PRIMER. (a-d) Average abundance of main species categories in the identified groups. (e-h) Average biomass of the different species categories in the groups identified.

Average abundance and biomass of species categories in the different groups is shown in Figure. 6. In group A small copepods are abundant and they also have the largest biomass. In group B2, the small copepod abundance was five times larger than in group B1. The difference between B1 and B2 is that B1 has *Metridia* juveniles and females, whereas B2 has *Centropages* and *Calanoides* females. This difference is more apparent in the biomass plots where *Centropages* and *Calanoides*

females contributed large biomass in group B2 and *Metridia* females contributed largest biomass in group B1. Although *Oithona* spp were abundant in group B1, their biomass was almost the same as small copepods. Group C had relatively low numbers of small copepods, which was the only species category represented in this group

Size classification (Fig. 7) in group A shows that there are only small size class species present. In group B1 there are three size classes: small, medium and large. In group B2 there are two size classes (small and large), and in Group C there were only small size classes present.

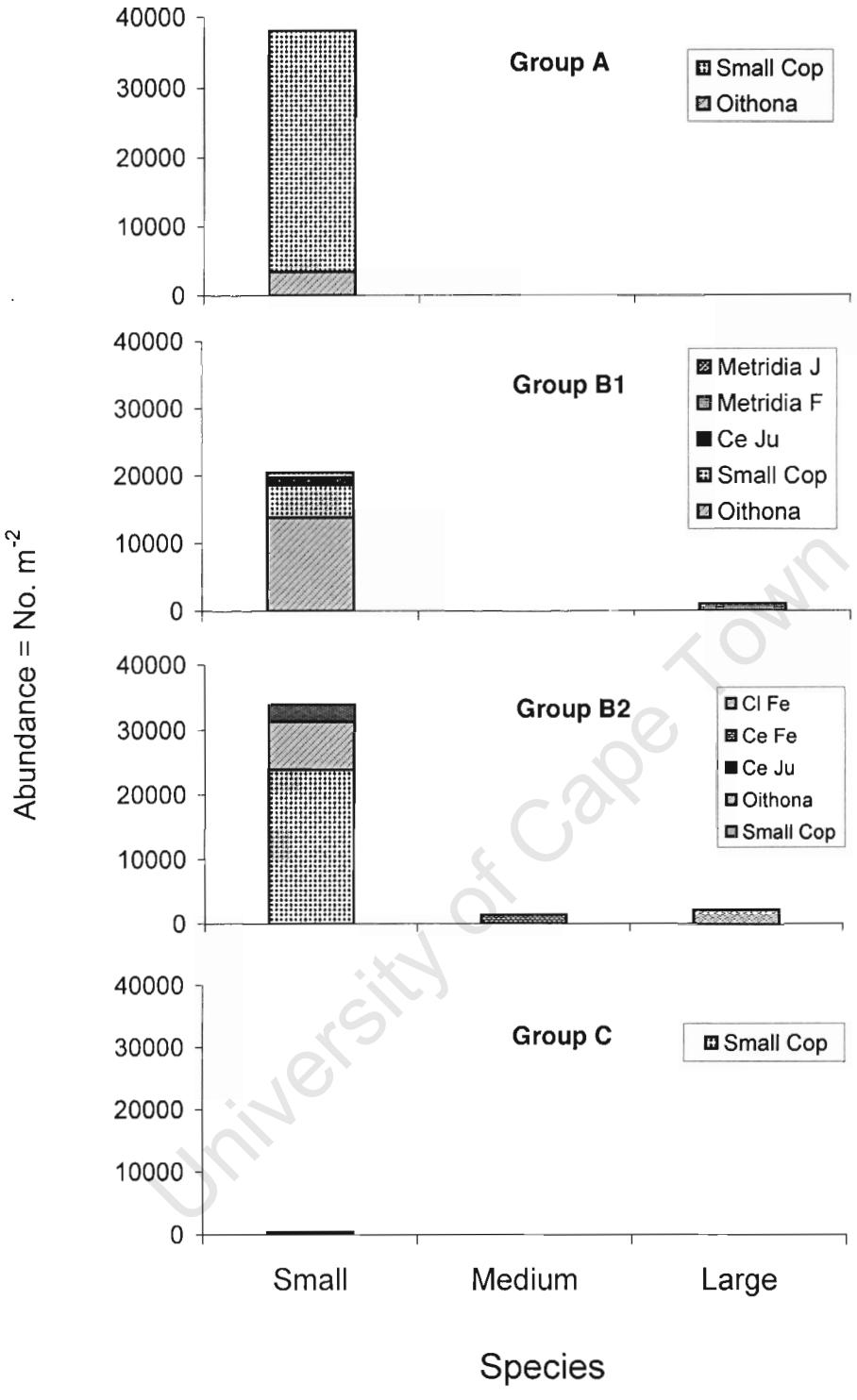

Fig. 7: The abundance of different size classes and the contributions of the different species categories to the size classes for the four groups (A, B1, B2 and C).

The spatial and temporal distributions of the groups identified in this study are showed in Figure 8 and Table. 2. In the inshore stations <100m depth, (where there is 100 % anchovy (Hutchings *et al.* 2002)), the following pattern is observed:

In April only B1 is dominating at the inshore stations. In June B1, which is represented by all size classes, is found at two stations. B2, which is represented by all size classes and C, which is represented by small size classes, has replaced other B1 stations. In August group A, which is also represented by small size classes, dominates at the five inshore stations and B1 is found at two stations. In October there is no clear trend, with one station unsampled and all the other groups except B1 present. In December groups B1 and B2 are found at most stations, with group A at one station. In February groups A and C are found at most stations, with one unsampled station.

Station	April	June	August	October	December	February
1						
2						X
3						
4				X		
5						
6	X					X
7	X					
8	X			X		
9						
10					X	
11				X	X	X
12				X	X	
13				X	X	
14		X		X	X	

KEY

Group	
A	
B1	
B2	
C	
O	
none	X

Table 2: Spatial and temporal patterns shown by the species groups along the entire transect, with stations 1-4 being the inshore stations and the rest offshore.

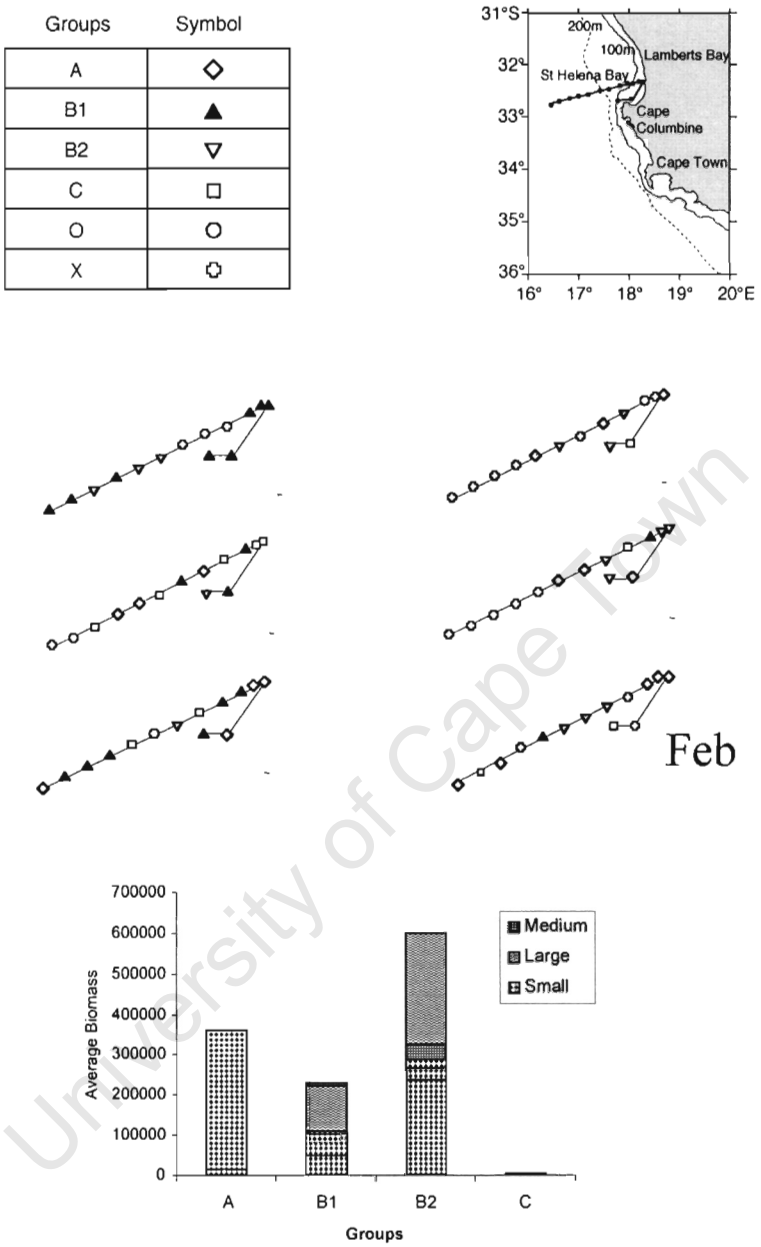

Fig. 8: St Helena Bay monitoring line showing the distribution of groups (A, B1, B2, C, and outliers) that were identified by the classification and MDS analyses. Samples are plotted for each of the months analysed. Average biomass is shown in terms of size classes for different groups.

Hydrography

Chlorophyll *a* is an index of phytoplankton abundance, which is an indication of the amount of autotrophic food available to zooplankton. Chlorophyll values were greatest inshore (Fig. 9).

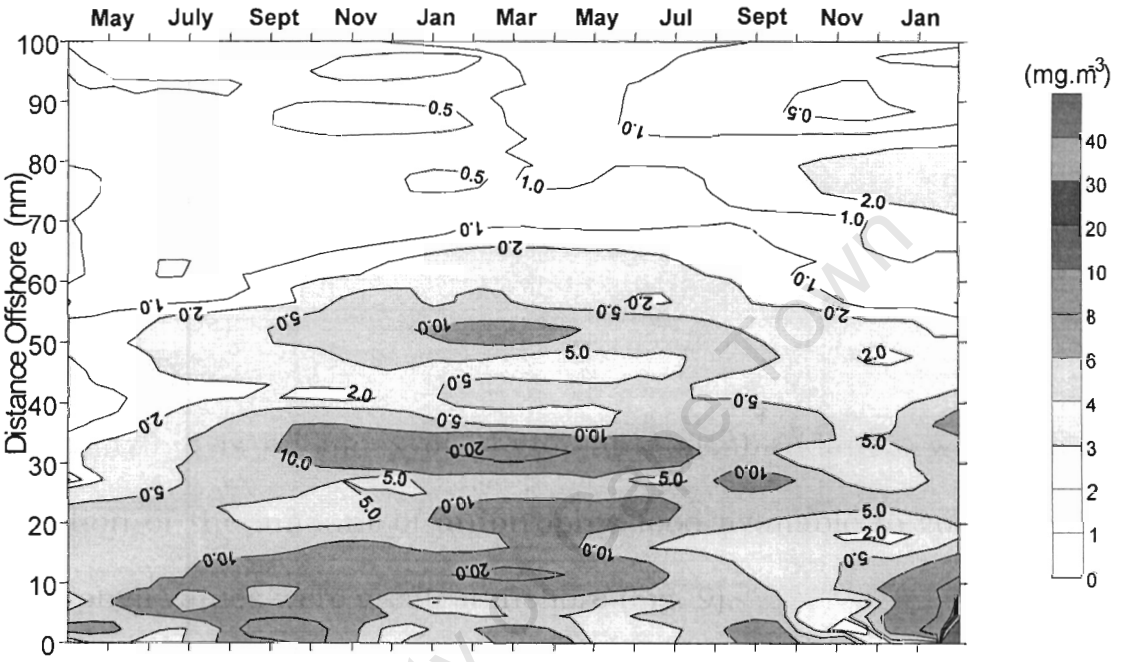

Fig 9: Surface chlorophyll values from the St Helena Bay Monitoring Line from April 2000 to February 2002, indicating low chlorophyll values offshore, where there is warm water (Hutchings *et al.* 2002).

Newly upwelled water is cold, nutrient-rich, and phytoplankton poor, and therefore shows lowest chlorophyll values. In Figure 10, it is observed that in December, when there is intensified upwelling, there are low chlorophyll concentrations because phytoplankton has not yet grown,

and in the offshore stations, where there is warm water, low chlorophyll concentrations are a result of nutrient depletion.

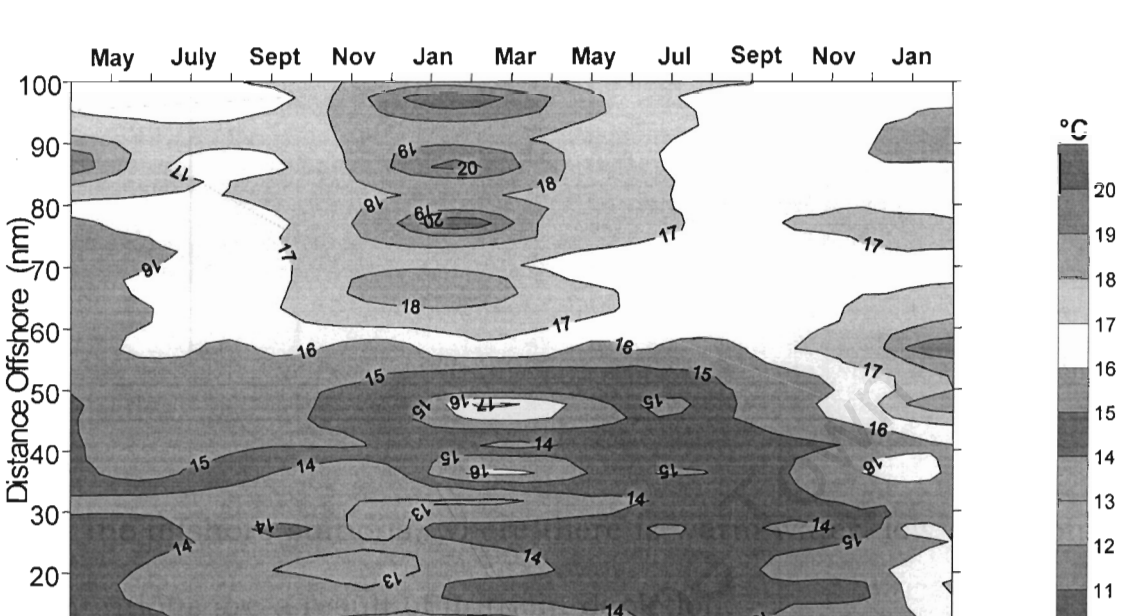

Fig 10:Sea surface temperature plots from the St Helena Bay Monitoring Line from April 2000 to February 2002. In summer 2000 there is evidence of cooler waters (Hutchings *et al* 2002).

Temperature distributions in Figure 10 indicate the presence of cooler waters inshore in summer for this study from October 2000 to February 2001. Hydrographic data showed that the usual driving forces were operating normally (Hutchings *et al.* 2002), judging from the temperature fluctuations. There were cooler temperatures in summer than winter indicating upwelling.

DISCUSSION

The results of this study suggest that pelagic fish might exert a control on the community structure of copepods. This supports the findings of Hutchings *et al.* (2002) that the zooplankton in St Helena Bay is affected by grazing. This control however, is found in many productive ecosystems of the world and particularly in upwelling ecosystems: Canary, California, Humboldt and Benguela (Cury *et al.* 2000). The size of animals within observed species categories (zooplankton communities) can reveal driving forces that may have shaped marine ecosystems (Shiomoto *et al.* 1997). In this case, the presence of large species categories during the early recruitment period of pelagic fish (April), which were replaced over time by smaller species categories, indicates that the presence of pelagic fish may have resulted in the observed zooplankton community structure. Micheli (1999) discovered that inter-annual fluctuations in zooplankton biomass were negatively correlated with those of planktivorous fish, indicating that fish predation can control zooplankton biomass.

The biomass of all zooplankton declines in the winter months (Hutchings *et al.* 2002) and distributions of the four groups (A, B1, B2 and C) changed temporally with the presence of pelagic fish in the inshore area. In less than 100 m depth (inshore) groups B1 and B2, which were dominating in April to August, were characterized by the presence of

large and medium species categories and were displaced by the groups A and C, which were characterized by small species categories. April to August is part of the recruitment period of anchovy, which normally runs through winter and spring.

Taking size groups into consideration, B1 and B2 species categories include those that were roughly estimated as being large and medium species. The decrease in zooplankton biomass in the winter months (Hutchings *et al* 2002), which is a period of recruitment, indicates the presence of recruits in the area, which were feeding on small zooplankton. The recruits are found in different stages of their life cycles depending on the time of arrival at the recruitment grounds. Therefore those that had arrived in the early period of recruitment (February) may have already started feeding on large copepods in June, when there is a displacement inshore by groups A and C. In a study conducted by Clark *et al.* (2001), it was found that where there is a high abundance of planktivorous fish, size-selective predation (fish selectively consuming larger prey) can lead to a dominance of small-sized zooplankton species and as a consequence, there may be less intense zooplankton grazing and hence an increase in phytoplankton productivity. Particulate feeding anchovy are more likely to ingest large particles (Louw *et al.* 1998), which may result in size variation in zooplankton community structure. In a study conducted by van der Lingen (2002b) on the diet of sardine he

found that, of the zooplankton component, calanoid copepods were the dominant prey category, accounting for 35% of the ingested carbon, and cyclopoid copepods were the second most important prey category, accounting for 24.3% of the ingested carbon. Fish eggs were the third largest contributor to ingested carbon (27.7%) and none of the other zooplankton prey categories accounted for more than 6% of the ingested carbon. It is said that phytoplankton contribute high volumes in the diet of sardine, but zooplankton contributes most of their ingested carbon (Miller *et al.* 2000, Timonin 1992).

Taking the whole transect, spatial distribution patterns of the four groups from August to February (except December) indicate that groups A and C were found mainly in the inshore stations. The reason for the presence of these two groups in this particular area is because large pre-recruits are primarily found inshore (van der Lingen 2002a) and they will feed on larger zooplankton inshore. The acoustic surveys done in the area by Hutchings *et al.* (2002) to look at changes in forage fish abundance using echograms, indicated 100% anchovy dominance in the pelagic fish layer inshore. In summer (December and February), group B1, which had disappeared in October, is found in one of the inshore stations and an increase in the presence of B2 as well is seen.

In the previous study in the same area conducted by Hutchings *et al.* (2002) they discovered a seasonal signal in the annual cycle of zooplankton biomass during 2000/1. The chlorophyll *a* results indicate large concentrations in summer (Hutchings *et al.* 2002). In Figure 10, the intensified upwelling in December 2000 may have resulted in increased availability of food for zooplankton, which may have led to the recovery of zooplankton biomass that had decreased during the year. In the absence of upwelling (winter) and with a correspondingly limited development of phytoplankton, which is a principal food for most of the zooplankton, the zooplankton biomass in winter was low compared with the summer zooplankton. At the time of intensified upwelling, which causes phytoplankton development in the inshore waters, the conditions for most of the zooplankton improved and its quantitative distribution changed.

It is difficult to compare offshore distributions with the inshore ones because most of the offshore summer stations were removed during the analysis.

The inshore copepod community shifted spatio-temporally from a community dominated by large copepods (in April) to a community dominated by small copepods (in August). It is suggested that the presence of pelagic fish in the area played a role in the attained copepod

community structure. The visible changes in copepod community structure are more observed in the inshore zone than in the offshore.

These analyses were based on one annual cycle of data, limited to a year when there was abnormally large recruitment. To evaluate to what extent the pelagic fish affect the annual zooplankton community structure, the distribution of pelagic fish recruits should be studied together with zooplankton community structure during a number of years.

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