

Zooplankton biomass variability off Angola and Namibia investigated by a lowered ADCP and net sampling

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Abstract

Variability in horizontal and vertical zooplankton biomass distribution was investigated down to a maximum depth of 1250 m off Angola/Namibia in August/September 2000 using a combination of net samples and backscatter profiles. The latter were measured by a 300-kHz ADCP mounted on the CTD frame. Thus, we obtained a near constant signal to noise ratio over the entire water column. This approach allowed both, a large spatial coverage and a relative high resolution in horizontal and vertical plane. The volume-backscattering coefficient was calibrated against biomass concentration of size fractionated net samples. In this way differences in shape and scatter properties of organisms were considered in a first approximation. Potential occasional larger signals were smoothed by averaging backscatter intensity over net sampling layers prior to the statistical comparison. The agreement in biomass concentration ranges and in horizontal distribution patterns derived by both methods was used as an additional quality factor. The biomass-rich zone spread deeper in the regions south of the Angola Benguela Frontal Zone (ABFZ) than north of it as a response to coastal upwelling. The diel vertical migration (DVM) caused “centres of the populations” (weighted mean depths) in 122 m (night), 303 m (day), 135 m (dawn), and 154 m (dusk). The average biomass at night within the upper 200 m exceeded those at day by a factor of 3.5. The phenomenon was more pronounced north and seaward of the ABFZ than south and shoreward of it. Minimum oxygen concentrations of about 0.2 ml/l were no barrier for migrating organisms passing the intermediate oxygen minimum zone (OMZ), which is a characteristic feature in the region.

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1. Introduction

Zooplankton net sampling and particularly the sample analysis is time consuming. Ship time restrictions often limit the vertical coverage during deep-sea studies. This may result in sampling effects due to insufficient measuring length and/or measuring inter-

vals. For example, short-term influences, like the diel vertical migration, may produce false large-scale horizontal distribution patterns if sampling continues round the clock (cf., Platt and Denman, 1975). These particular limitations were evident when examining the zooplankton biomass patterns by net sampling near the Angola–Benguela Frontal Zone (ABFZ) during the interdisciplinary r/v “Meteor” Cruise 48-3, in August/September 2000. We tried to overcome this problem by complementing the data with the backscatter signal of an

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ADCP. The 300-kHz broadband ADCP was originally applied for current measurements. Mounted on a CTD frame, it produced vertical profiles with a nearly constant noise level through the entire water column up to 1250 m on many more stations than net sampling positions.

Principally there are two ways to make the backscattering signal available for quantitative zooplankton studies, (1) the comparison between acoustic backscatter and plankton concentration (used in this study) and (2) the so-called forward problem approach (cf., Foote and Stanton, 2000; Wiebe and Benfield, 2003; Holliday and Stanton, 2005; Jaffe, *in press*). Since the acoustic scattering varies with size, shape, orientation, and physiology of organisms (Chu et al., 1992; Stanton et al., 1994; McGehee et al., 1998), a direct comparison between mean volume–backscattering strength and zooplankton biomass is difficult for a diverse zooplankton community (Fielding et al., 2004; Brierley et al., 2005). Fielding et al. (2004) additionally called attention to the mismatch between sampling volumes of the net and acoustic instrument. However, this aspect concerns both methods. Solving the forward problem, one adjusts the observed backscatter intensity with the expected intensity calculated using taxon-specific backscatter models and their observed abundance obtained by net samples (Pieper and Holliday, 1984, Holliday and Pieper, 1995). This method adequately considers rare but strong scatterers like pteropods, but it generally depends on the quality of the used models. The initial models were based on empirical measurements under controlled laboratory conditions (Greene et al., 1991; Stanton et al., 1994) and were improved by Stanton et al. (1998a,b), Chu and Stanton (1998), and Chu et al. (2000). LeBourges-Dhaussy and Ballé-Béganton (2004) and Mair et al. (2005) used the so-called “inverse method” for the *in situ* prediction of the shape and size of the dominant scatterers from multifrequency backscattering. But still there remain potential sources of inconsistencies, like the difficulty in determining *in situ* animal orientation (Foote and Stanton, 2000), the limited amount of published data on the subject of density and sound–speed contrast in zooplankton and the geographically restricted validity of the model parameters (Mair et al., 2005).

Flagg and Smith (1989), Heywood et al. (1991) and Smith et al. (1994) were the first to demonstrate the successful use of ADCPs for zooplankton studies. Heywood et al. (1991) even used acoustic backscatter signals without any of the special ADCP modifications and considerations as proposed by Flagg and Smith (1989). Since then, between two and five papers were

published annually according to *Aquatic Science and Fisheries Abstracts*. Frequencies of 150 kHz were used in nearly 70% of cases, somewhat over 20% used 300 kHz and a 614-kHz ADCP has been applied in a fresh water environment (Lorke et al., 2004). More than 50% of the published results were derived from vessel-mounted ADCPs, another 25% from bottom-mounted equipment, and the remainder from devices fixed on moorings or towed vehicles. To date, studies on zooplankton in the water column above hydrothermal vents are the only published approaches using a profiling ADCP/sampling package (Thomson et al., 1989, 1991, 1992; Burd and Thomson, 1994), while the cast mode use of more sophisticated acoustic instrumentation is quite common (cf., the abovementioned review papers).

In contrast to lowered ADCPs, vessel or bottom-mounted devices have a restricted vertical coverage because absorption of sound by seawater causes an unfavourable signal to noise ratio with increasing distance from the transducer. Consequently, comparison of vessel-mounted ADCP backscattering data with those of regularly calibrated scientific echo-sounders revealed good correlation of both methods only at near distances and poor correlation at far distances (Brierley et al., 1998). This problem intensifies with higher frequencies because the degree of acoustical absorption is proportional, and the shortest resolvable pulse length is inversely proportional, to the acoustic carrier frequency. “The key to using high-frequency sound in the study of zooplankton ... is to deploy the acoustical transducer in a manner that gets it sufficiently close to the animals of interest” (Greene and Wiebe, 1990). In this respect, the use of a lowered broadband ADCP (L-ADCP) as described here is the best way to achieve this. The configuration provides the backscatter signal from a sonified volume at a fixed short distance from the acoustic transmitters from the surface to large depths or even to the ocean bottom.

We correlated the measured volume backscatter coefficients and zooplankton biomass concentrations as derived from parallel net samples considering the relative proportion of five size classes. Since size and taxonomic composition are related (Sieburth et al., 1978), we indirectly included the shape and the material properties of organisms.

The agreement in the biomass concentration ranges and in horizontal distribution patterns derived by both, the classical biomass determination and the acoustically computed biomass, based on data from the same stations, was used as an additional quality factor for the acceptance of our attempt.

Finally, we examined the derived patterns concerning their reliability as proposed by Lyons et al. (1994). In this context, we focussed on biomass patterns in the vicinity of the Angola–Benguela Frontal Zone (ABFZ), and on aspects of diel vertical migration, especially in relation to the intermediate oxygen minimum zone (OMZ), which are common features in Namibian and Angolan waters (Lass et al., 2000; Levin, 2003; Loick et al., 2005).

The ABFZ is known to be a barrier for certain zooplankton populations in upper water layers in terms of abundance and taxonomic composition (Macpherson, 1991; Barangé et al., 1992; Verheye et al., 2001; Da Silva et al., submitted for publication). The first large-scale investigation in this region was performed by Hentschel (1936) during the famous r/v “Meteor I” Cruise between 1925 and 1927. The abundance distribution mirrored the main feature and the average position of the ABFZ in the upper 50 m with higher biomass concentrations south- and shoreward the front. Detailed quantitative research on biomass patterns, which is important for food web studies is mostly missing in the region. They are restricted to the Northern Benguela system south of 17°30'N, which allows a small overlap with our area. The results of Fearon et al. (1986), Olivar and Barangé (1990) from the upper 50 m and 200 m respectively were compiled and compared with those of the Southern Benguela region by Hutchings et al. (1991). Investigations of Timonin et al. (1992) touched our region also in a large-scale manner and covered the pelagic zone up to 1500 m depth. Their results stem from net sampling (180- μ m mesh size) with all the abovementioned restrictions of low frequent sampling intervals. Until now, the only acoustic zooplankton observations off Southwest Africa with higher sampling frequency were done by Brierley et al. (2001, 2005) in order to evaluate the amount of jellyfishes and to estimate the abundance of mesozooplankton co-occurring with layers of jellyfish medusae respectively. The specific goal of the latter work was to estimate the possible contribution of mesozooplankton backscatter to the total volume density recorded for jellyfish, i.e., potential bias by zooplankton, which was found to be negligible. Postel (1990) and Postel et al. (1995) performed the only studies with a high degree of spatial and temporal resolution by net sampling at 20°S. However, these studies needed to be restricted to the upper 75 m. Hence, our current mesozooplankton biomass approach became the first one for this group of organisms in the region, which contains both, a large coverage and a relative high resolution in horizontal and vertical plane.

2. Material and methods

Six transects were carried out between the Angolan/Namibian coast and 8°E and from 9°S to 20°19'S during the r/v “Meteor” Cruise M 48-3 from 30 August to 13 September, 2000 (Fig. 1a).

2.1. Collecting Zooplankton and sample analysis

Zooplankton samples were collected on 17 stations by Multinet oblique hauls (Hydrobios GmbH, Kiel, Germany) just after the deployment of the CTD/L-ADCP system. The equipment consisted of a net frame with an opening area of 0.25 m², a pressure protected motor unit (3000 dbar) with an external battery housing, 5 nets ($L=2.5$ m, diameter at the end=0.11 m) with zip fasteners, 5 plastic net buckets with side windows covered with sieve gauze, a V-fin depressor, and a deck unit. Depth was recorded in real-time by a pressure

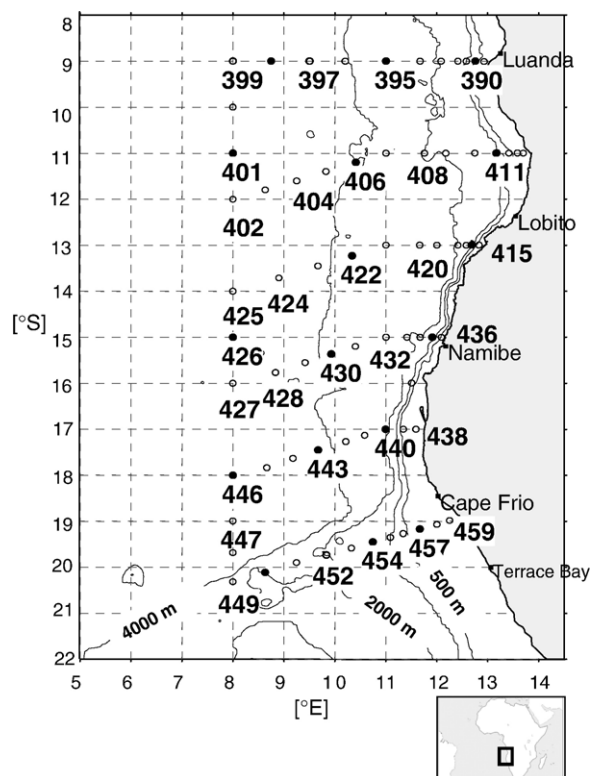


Fig. 1. 71 CTD/L-ADCP stations (all dots) and 17 parallel Multinet sampling sites (bold dots) processed on Meteor cruise M48-3 off Angola/Namibia from August 26th to September 16th, 2000. Net sampling was carried out at three depth levels (0–25 m, 25–75 m, 75–200 m) with exception of stations 398, 426, and 450 on which additional sampling took place between 200 and 500 m.

sensor. Flow velocities and the amount of water filtered were measured by two flowmeters, mounted in and on the outside of the frame. The data were collected and visualized by OCEAN LAB Software. At the same time, the r/v “Meteor” central data collection and distribution system made it possible to follow in real-time both the ship’s speed through the water (1 to 1.5 kn) and the winch velocity. Winch speeds were adjusted to ship speed in order to achieve an average tow velocity of about 0.5 m/s (for more details, cf., Lass et al., 2001). The opening device enabled the collection of plankton at different depth levels during a single deployment from 200 to 75 m, 75 to 25 m and 25 m to the sea surface. An additional level was introduced from 500 to 200 m at three stations to the north and south of the ABFZ, and at one station within the transition area. The sampler was used twice at every station, alternatively equipped with two net sets with mesh sizes of 55 μm and 200 μm . Therefore, we received two samples per depth layer. For the preparation of the smaller size fractions, we used the 55- μm sample, for the fractions $>200 \mu\text{m}$ the second one from the 200- μm set. This approach ensured the quantitative sampling of plankton in the size range between 55 μm and about 10 mm.

After sampling, the nets were rinsed from the outside with seawater. Samples were stored at 4 °C until processing. Then they were split by the beaker technique (Guelpen et al., 1982) using 1000-cm³ or 500-cm³ measuring cups according to requirements. Each part was fractionated into the following size categories: $>1000 \mu\text{m}$, 1000–500 μm , 500–200 μm , 200–100 μm and 100–55 μm . This was achieved by successive rinsing with a seawater hose equipped with a 55- μm gauze attachment through a set of filters. Finally, half of the sample was frozen on pre-weighed glass fibre filters (Whatman GF/C) at –20 °C for biomass determination; the other was stored in buffered formaldehyde (4% final concentration) for taxonomic analysis.

In the land-based laboratory we determined the ash-free dry mass (AFDM) by combustion in a muffle furnace at 500 °C for at least 12 h (cf., Postel et al., 2000).

The species analysis of the larger zooplankton required a stereomicroscope (Leica, MZ 8) with a magnification between 16 and 80. The smaller size classes were analysed by an inverted microscope (Labovert FS, Leitz) usually with a 50 times magnification. In both cases, Bogorov trays of suitable sizes were used for counting. The total samples were first surveyed for rare specimens. High sample concentrations often required the analysis of sub-samples. The entire procedure and the discussion of errors have been

described in detail in Postel et al. (2000). Taxonomic determinations were performed to different levels, often down to genera, using literature for the Angolan–South African region (Gibbons, 1997), the South Atlantic in general (Boltovskoy, 1999), the northern hemisphere (ICES, 1939–2001) and the Mediterranean (Trégouboff and Rose, 1978; Riedl, 1983). Results were summarized within categories of similar scatter properties such as crustaceans, siphonophora, thaliaceans, chaetognaths, foraminifera, etc. and compared as relative abundances, i.e., individual dominance (%).

2.2. Lowered Acoustic Doppler Current Profiler (L-ADCP)

The L-ADCP system was used to obtain full depth volume-backscattering coefficient profiles at each CTD station. The system consisted of two broadband ADCPs WH-300 (RD Instruments, San Diego, CA, USA) attached to the frame of the CTD-probe, one in a downward and the other in the upward looking mode. They were equipped with an external battery case in order to avoid magnetic disturbances, which may occur if internal power supply packs are used. The L-ADCP/CTD system was run at 71 stations down to a maximum depth of 1250 m. The maximum depth was reached in 53 cases. Thirty-three stations (34 profiles) were carried out during the night, 31 stations (32 profiles) during the day, and 7 stations (profiles) during the twilight respectively. Prior to deployment the deck unit PC-clock of the ADCP was synchronised with the CTD deck unit PC clock in order to assign the depth from the CTD probe to the ADCP by time. The vertical bin size was 8 m. Measurements were performed continuously during both the downcast and the upcast of the CTD. Data from the first depth bin were not used since they are often affected by anomalous high backscatter signals due to the turbulent wake of the vertical moving CTD-Rosette system. With increasing distance from the transducer the signal to noise ratio is decreasing. The uncertainty of the applied corrections for sound attenuation and beam widening also increases with distance. Taking this into account and the fact that only on short ranges the correlation between scientific echo sounders and ADCP backscatter is good (Brierley et al., 1998), the acoustic backscatter data were used only from the 2nd to the 4th bin of both ADCPs. Due to a blank after transmit range of 4 m and ignoring the 1st bin, raw target strength (E) was used in the range between 12 and 36 m distance from each of the transmitters.

Volume-backscattering strength S_V (dB) was calculated from the recorded target strength E (counts) after Deines (1999) according to the following formula

$$S_V = C + 10\log_{10}((T_X + 273.16)R^2) - L_{DBM} - P_{DBW} + 2\alpha R + K_C(E - E_r)$$

where S_V is the volume-backscattering strength in dB, L_{DBM} is the $10\log_{10}$ (transmit pulse length/meter), P_{DBW} is the $10\log_{10}$ (transmit power/Watt), T_X is the temperature of the transducer ($^{\circ}\text{C}$), R is the range along the beam to the scatterers (m), α is the absorption coefficient of seawater (dB/m), K_C is the device specific coefficient transferring raw target strength E (counts) into dB and E_r (counts) is the beam specific reference level in the absence of scatterers (noise level). For the use of definitions and symbols we followed MacLennan et al., 2002.

E_r was estimated for each of the 8 individual beams from measurements of E in the most distant bin at 1250 m depth at the most distant station from the coast. Outliers of relative target strength $E - E_r$ in each single depth cell were identified and rejected by the fish rejection algorithm. Thereby a value was classified as outlier if it differed more than 10 db from the median.

Since the target strength is proportional to $\log(\sigma_{bs}/4\pi)$, where σ_{bs} is the backscattering cross section of the target, one would expect as a first approximation that the total zooplankton cross section would depend on the volume-backscattering strength S_V as $\text{AFDM} \propto 10^{S_V/10}$. We refer the term $10^{S_V/10}$ in the further discussion as the ‘volume backscatter coefficient’ s_v which is specific for the used instrument. K_C was adjusted between the downward and upward looking ADCP by comparing the depth adjusted profiles of $E - E_r$ of both instruments. The S_V was calculated for the downward and upward looking ADCP for the bins 2 to 4 taking into account the local α as function of temperature, salinity and pressure. Then the volume backscatter coefficient s_v was calculated and averaged over the four beams in each depth bin. All s_v were assigned to a single depth profile with 8 m depth steps. In each depth level, the standard deviation was calculated. Data, which were outside a range of three times the standard deviation from the mean value were classified as outliers and rejected (“standard deviation threshold”). The remaining data were averaged in each depth bin.

Finally, data were rejected in depth cells affected by reflections of both the main beams and the side lobes at the surface and the bottom. As result, reliable data of volume backscatter coefficients were usually obtained from 16 m below the surface down to 16 m above the bottom.

2.3. L-ADCP derived volume backscatter coefficient versus zooplankton biomass concentration

At first, the s_v results were averaged for the net sampling depth layers. According to the 8-m bin length, approximately two s_v estimates were available in the upper layer from the 16 m to 24 m depths. Six data points existed between 25 and 75 m, sixteen from 75 to 200 m and thirty-seven from the layer up to the 500 m depth per station.

Next, the correlation was tested stepwise between volume backscatter coefficient s_v and zooplankton biomass, first by separating in size classes, and second by checking the influence of depth using the sum of all size classes ($\text{AFDM}_{\text{total}}$) in order to find the most appropriate way for the comparison. The statistical agreement between s_v and biomass should be stronger in the larger size classes. Objects with a spherical diameter in the order of 5 mm length are the ideal reflectors for the signals of the 300-kHz L-ADCP system according to $\lambda = c/f$, where λ is the wave length (m), c the sound velocity (in water approximately 1500 m/s) and f is the L-ADCP frequency [Hz]. Finally, we expected a varying AFDM proportion of different size fractions to the total due to potential size-dependent variations in the community structure in relation to the ABFZ and to the different behaviour during DVM. Therefore, we searched for sample groups of similar size class proportions in order to perform the $s_v - \text{AFDM}_{\text{total}}$ comparison separately within homogenous conditions. For this purpose, we conducted similarity and cluster analyses of the 54 AFDM proportions (14 stations with 3 depth levels down to 200 m, 3 stations with 4 depths up to 500 m) using PRIMER software applying Bray Curtis similarity, square root transformation and complete linkage as the cluster mode (cf., Clarke and Warwick, 1994). Next, we characterized the clusters obtained in terms of average AFDM percentage per size class and by taxonomic categories with similar acoustic properties. Finally, the correlations between s_v and the $\text{AFDM}_{\text{Total}}$ concentration and the conversion formulas within the chosen cluster were determined.

In all cases, we used the linear regression model $y = a * x$, with s_v as the independent term and biomass concentration as the dependent one, and calculated the particular coefficients of determination r^2 . Tests of significance of the random sample correlation coefficients r were performed using the test parameter of the Student distribution for the appropriate degree of freedom.

For the application of the conversion formulas of the cluster approach, we needed to solve the problem of

assigning the L-ADCP stations to the clusters, which were originally based on Multinet stations only. If L-ADCP stations were located between Multinet stations of the same cluster, we included them. In case of uncertainty, we allocated the L-ADCP stations according to water mass characteristics in terms of temperature, salinity, nutrient and phytoplankton properties after Wasmund et al. (2005).

Our net sampling did not cover the entire water column, as the L-ADCP measurements did. It was mainly carried out in the upper 200 m and three times up to 500 m, making an extrapolation of the comparison between net samples and acoustic results below these depths necessary. This is only possible if the zooplankton community structure becomes more ideal in relation to the 300 kHz in terms of size and scatter properties of the organisms. The data allowed investigating these aspects down to 500 m.

Finally, we examined the agreement in the biomass concentration ranges and in horizontal distribution patterns derived by both the classical biomass determination and the acoustically computed biomass in three depth levels on the same stations as an additional quality factor for our attempt. For this purpose we averaged the L-ADCP AFDM_{Total} within the depth intervals of net samples.

2.4. Patterns of L-ADCP AFDM concentration in relation to the ABFZ, diel vertical migration and the oxygen minimum zone (OMZ)

Horizontal and vertical biomass patterns were visualized using Surfer Software (v.8.02 by Golden Software, Inc.). Diel vertical migration patterns were investigated by vertical scatter plots of L-ADCP AFDM_{Total} (mg/m³) in relation to the daily light phases day, night, dawn, and dusk based on local times and by the estimation of the distribution centres of the populations. For the latter we computed the so-called weighted mean depths (Z_x) following Hassett and Boehlert (1999): $Z_x = \frac{\sum (\text{average depth of tow } Z_{\text{AVG}} [\text{m}] * \text{depth interval of tow } \Delta_Z [\text{m}] * \text{AFDM} [\text{mg}/\text{m}^3])}{\sum (\text{depth interval of tow } \Delta_Z [\text{m}] * \text{AFDM} [\text{mg}/\text{m}^3])}$, where ash-free dry mass (AFDM) stands for L-ADCP AFDM_{Total}. We choose the following depth layers 0–25 m, 25–75 m, 75–200 m, 200–500 m, 500–800 m, 800–1250 m for this purpose, which result in the average towing depths Z_{AVG} of 12.5, 37.5, 62.5, 350, 650, 1025 m, and depth intervals Δ_Z of 25, 50, 125, 300, 300, 450 m respectively.

Vertical oxygen patterns were taken from Lass et al. (2001).

3. Results

3.1. L-ADCP derived volume-backscattering coefficients versus zooplankton biomass concentration

Generally, the larger biomass concentrations and s_v signals originated from night samples and registrations in the near surface waters.

Considering size fractions, the correlation became increasingly significant with growing size of the individuals due to the increasing favourable scattering properties of the larger groups in relation to the 300-kHz ADCP properties. The coefficients of determination r^2 reached 0.3738 in the 55–100 μm size class, 0.3871 in 100–200 μm ; 0.4751 in 200–500 μm ; 0.4960 in 500–1000 μm ; and 0.4188 in the >1000 μm size class. The number of observations was always 49, the significance of the correlations reached a probability level of <0.001 in all cases. When separating the data into different depth levels significant correlation was only found in the 25–75 m depth range ($r^2=0.7194$, $P<0.001$).

Similarity and cluster analyses of the 54 AFDM size class proportions resulted in four categories with a similarity level between 75 and 80% (Fig. 2a). The derived patterns were particularly related to the position of the Angola–Benguela Frontal Zone (Fig. 2b). Cluster 4 dominated in the two levels between 25 and 200 m north of the ABFZ situated at approximately 16°S (Lass et al., 2001). Clusters 1 to 3 characterized the conditions to the south of it. In the upper 25 m, the patterns were more irregular.

The average differences between the clusters were more apparent in the relative biomass proportions of size classes than in taxonomic composition (Table 1). All size classes contributed similar percentages to the AFDM_{Total} concentration in cluster 1 (Table 1, upper panel). Fractions smaller than 200 μm dominated cluster 2 by 65%, while zooplankton larger than 500 μm characterized clusters 3 and 4 by percentages of 71 and 80%, respectively. The results on the relative abundance (individual dominance) of two analysed size fractions are included in the lower panel of Table 1. In both cases the crustaceans were predominant in the 200 to 500 μm fraction as compared to the fraction >1000 μm . In the latter gelatinous organisms and chaetognaths, fish and other eggs and fish larvae were also present. This implies that since cluster 4 dominated the water body north of the ABFZ and between 25 and 200 m, there was dominance of organisms larger than 500 μm mainly made up of crustaceans and a minor proportion of gelatinous organisms, chaetognaths, and protozoans. South of

the ABFZ, smaller crustaceans dominated together with a larger percentage of protozoans at the same depth levels. In the upper layer the situation was more

variable in terms of size and species composition probably due to DVM. However, all the principal differences were considered by determining the cluster-

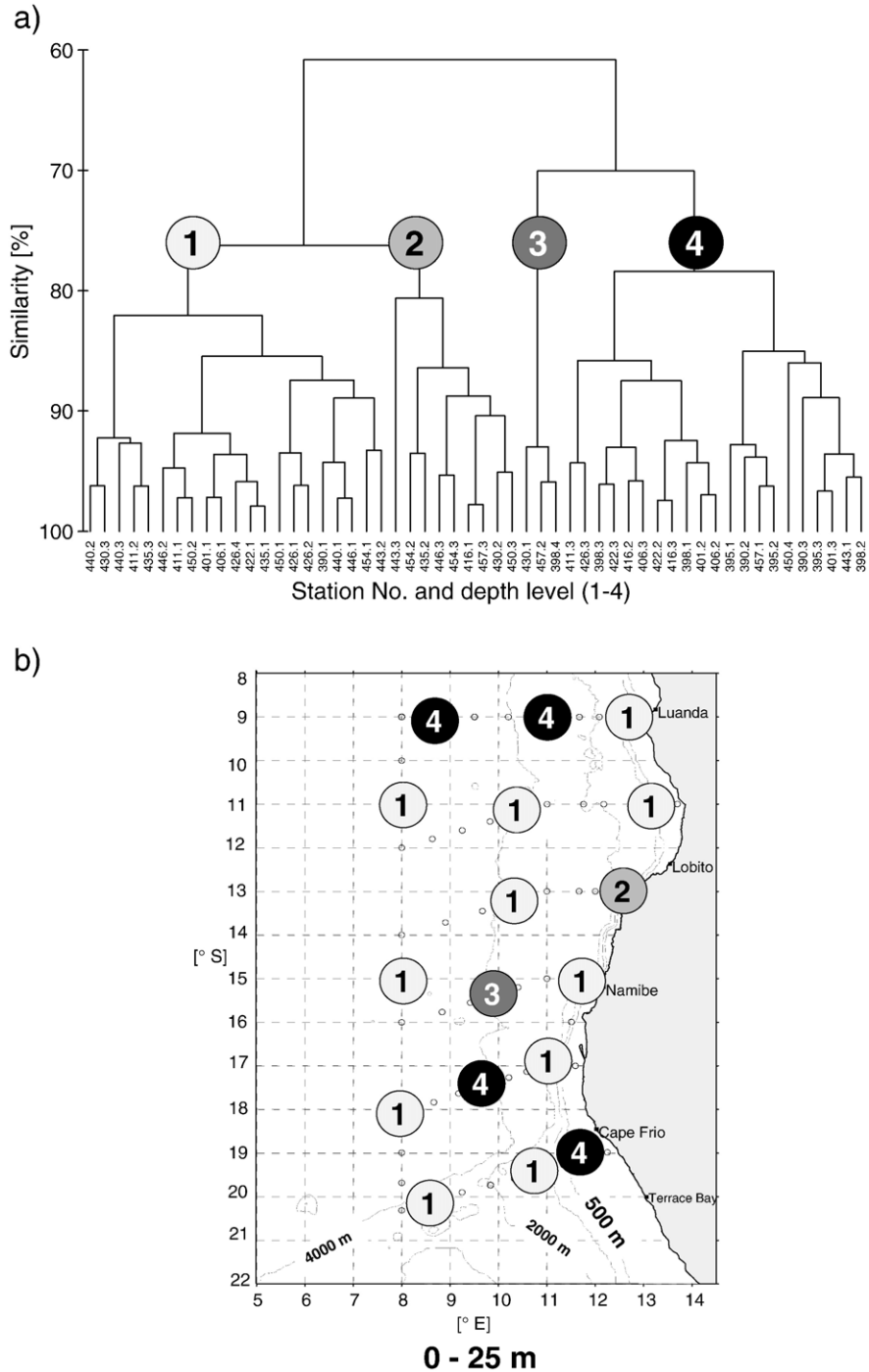


Fig. 2. (a) Dendrogram for hierarchical clustering (complete linkage) computed for AFDM proportion of different size fractions of the AFDM_{Total} within the various depth levels (station number plus index 1=0–25 m, 2=25–75 m, 3=75–200 m, 4=200–500 m) using results of the Bray Curtis similarity of square root transformed data and (b) geographical patterns in three depth levels in the area under investigations created by four categories (1), (2), (3), (4) at a similarity level between 75 and 80%.

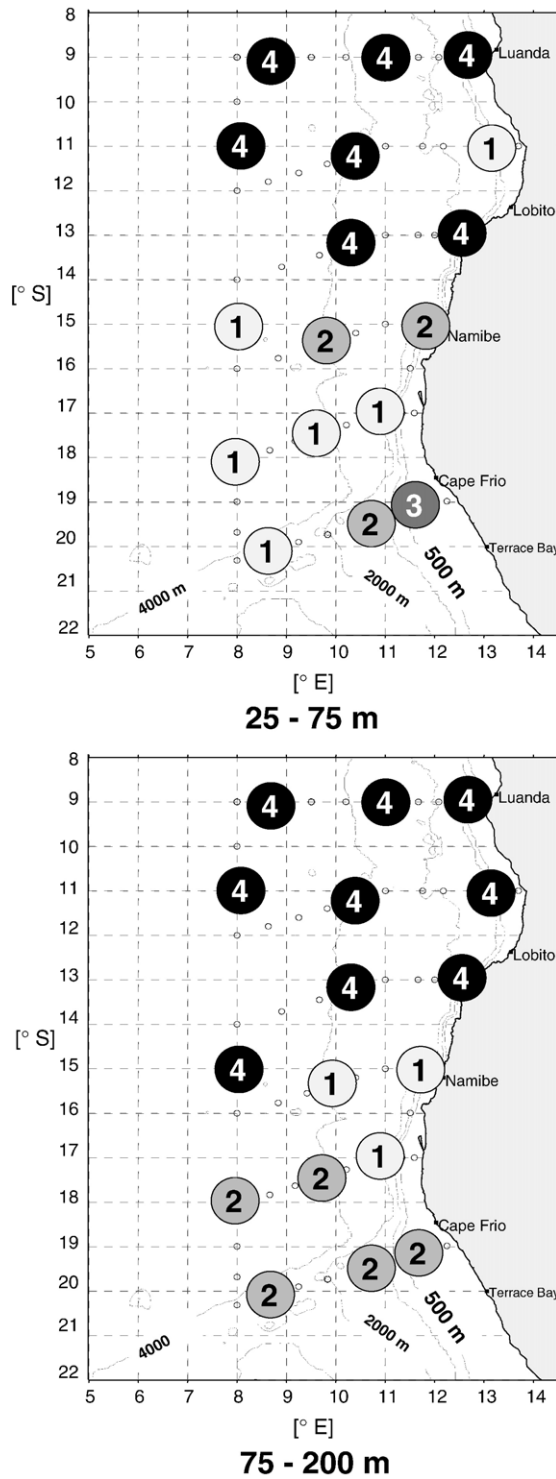


Fig. 2 (continued).

specific relationships between the volume-backscattering coefficient (s_v) and zooplankton biomass ($AFDM_{Total}$).

Clusters 3 and 4 were combined due to the low number of observations in cluster 3 and we neglected three outliers in cluster 1 and one outlier in clusters 3+4.

Table 1

Characteristics of the used sample cluster in terms of both the average AFDM percentage per size class at AFDM_{Total} and in acoustically relevant taxonomic categories (cf. text)

Cluster	Size class AFDM [%] of total AFDM				
	>1000 μm	500–1000 μm	200–500 μm	100–200 μm	55–100 μm
1	22	13	21	29	15
2	12	6	17	38	27
3	57	6	8	18	11
4	30	22	28	13	7

Cluster	Taxonomic categories [%]							
	>1000 μm							
	Crustaceans	Gelatinous and similar	Siphonophora	Elastic shelled	Thaliaceans	Other eggs, fish eggs and larvae	Protozoans	Other
1	46	18	2	0	2	22	10	0
2	35	18	2	0	1	23	20	1
3	42	20	1	1	1	22	12	1
4	57	12	5	1	2	11	11	1

200–500 μm								
1	78	3	0	0	0	5	14	0
2	69	3	0	0	0	0	28	0
3	69	0	1	0	0	0	29	1
4	83	2	0	0	0	6	8	0

These concerned data pairs with high s_v but relative low biomass concentrations and they exclusively stem from the upper 25 m, which were not fully covered by acceptable acoustic data in contrast to the biomass measurements, which were always performed up to the surface.

This approach clearly improved the correlation between s_v and AFDM_{Total}. The coefficients of determination r^2 were high in all cases in spite of the small sample numbers (Fig. 3). The random sample correlation coefficients r varied between 0.82 and 0.88. They were significant with a probability of less than 0.001 (clusters 1 and 3+4) and 0.01 (cluster 2) as determined by the Student test.

The agreement between the biomass concentration ranges and the horizontal AFDM_{Total} distribution of different depth layers, derived by both the classical biomass determination and the acoustically computed biomass is shown in Fig. 4. There are similarities in the magnitude and in shape of the distribution patterns, taking the 20 mg/m³ isolines in the uppermost layer and the 10 and the 1 mg/m³ isolines in the next two deeper layers for orientation. There are regions of higher AFDM_{Total} concentrations in the north and in the south with a minimum area between them in both cases. The correspondence was best in the 75–200 m layer. The deviations in the layer <25 m may be explained by

missing acoustic data in the 0–16 m layer and by one missing L-ADCP data point at the near coastal station on the northernmost section.

The comparison between s_v and L-ADCP AFDM_{Total} was mainly limited to the upper 200 m (in three cases up to 500 m). In spite of this restriction, there was a need to apply the regression formulas used in the 75 to 200 m layer down to the particular maximum depths. This seems to be appropriate due to the increasing proportion of organisms of nearly optimal scatter properties (relative to the used 300-kHz frequency) with increasing depth. According to Fig. 5a, the percentage of the organisms >1000 μm successively increased from 19% of total AFDM in the uppermost layer to up to 52% between 200 and 500 m depth. Likewise, the plankton community became more homogenous in composition, i.e., in scatter properties. The proportion of crustaceans increased from 58% to 78% (Fig. 5b). Both trends led to the conclusion that the correlation between s_v and AFDM_{Total} applied for the 75 to 200 m layer also holds at least in depths larger than 200 and 500 m. Finally, we restricted vertical contour plots to 800 m in order to avoid near bottom disturbances potentially produced by turbidity due to dispersed sediment in shelf edge vicinities as observed by Zhu et al. (2000) in Beppu Bay (Japan).

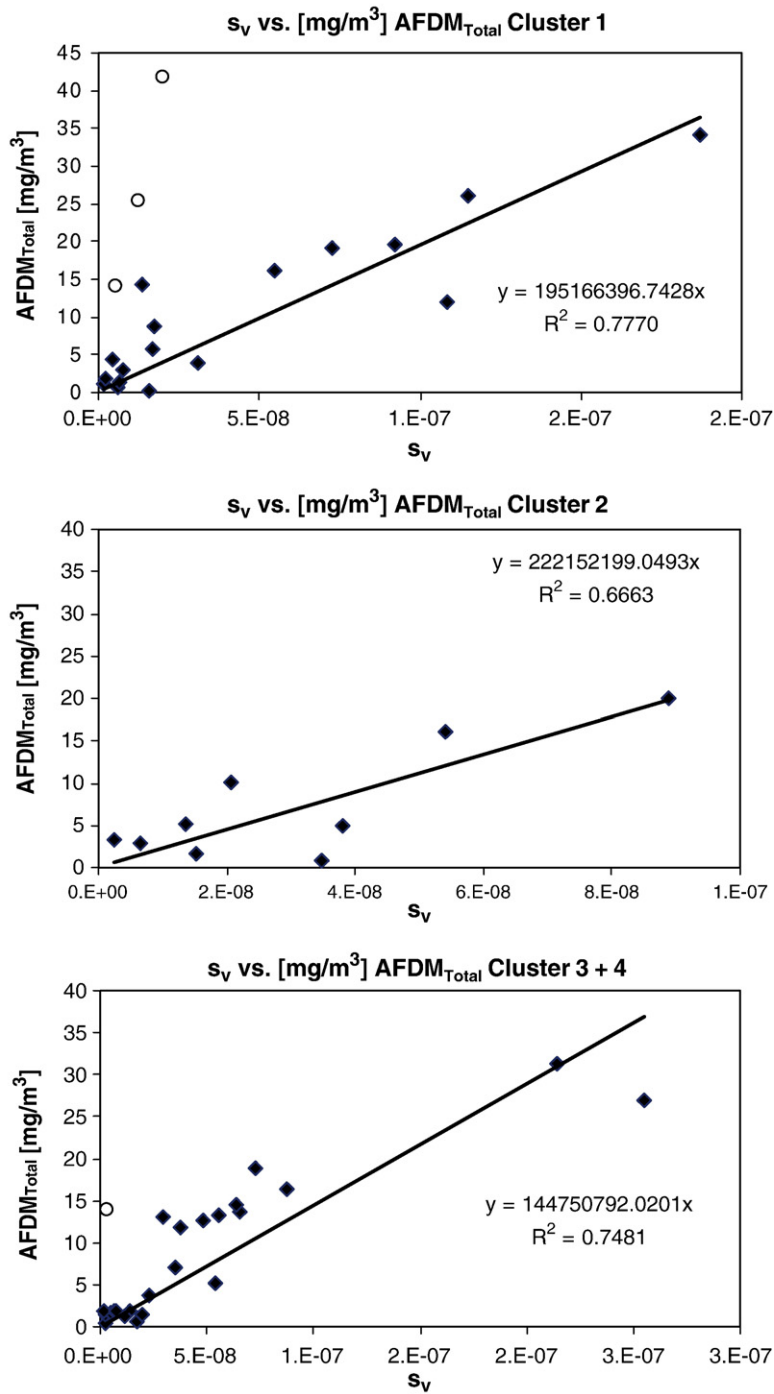


Fig. 3. Volume-backscattering coefficient s_v versus AFDM_{Total} within the clusters 1 ($N=12$), 2 ($N=9$), and 3+4 ($N=23$) including regression equations and coefficients of determination r^2 . Three outliers (circles) in cluster 1 and one in clusters 3+4 were neglected.

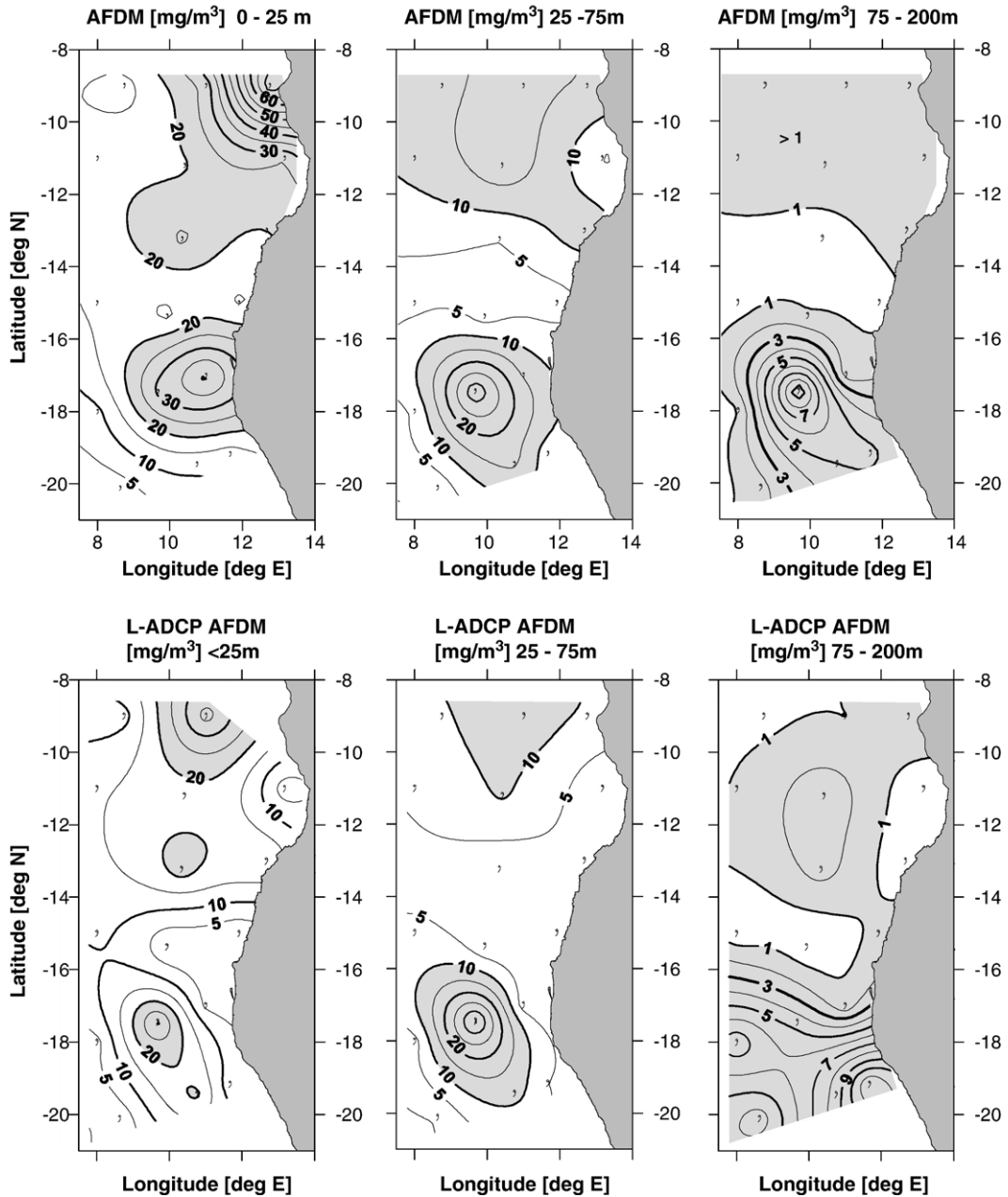


Fig. 4. Horizontal AFDM_{Total} patterns in three depth levels in the investigated area based on direct measurements (upper panel) in comparison with those based on L-ADCP calculations (lower panel) at 17 Multinet stations (negative latitudes *N* were used for software reasons, they are equal to positive latitudes *S*).

3.2. Patterns of L-ADCP AFDM concentration in relation to the ABFZ, diel vertical migration and the oxygen minimum zone (OMZ)

The vertical structure of calculated L-ADCP AFDM_{Total} concentrations perpendicular to the coast from 9°S to 19/20°S (Fig. 6) and a latitudinal section at 8/9°E

(Fig. 7) demonstrated several interesting features. Firstly, significant differences were found between day and night stations with higher near surface concentrations during night. Secondly, maximum concentrations during night partly occurred in the upper layer of the oceanic regions north of the Angola–Benguela Frontal Zone (stations 396, 400, 403, 404, 424, 425) and not as

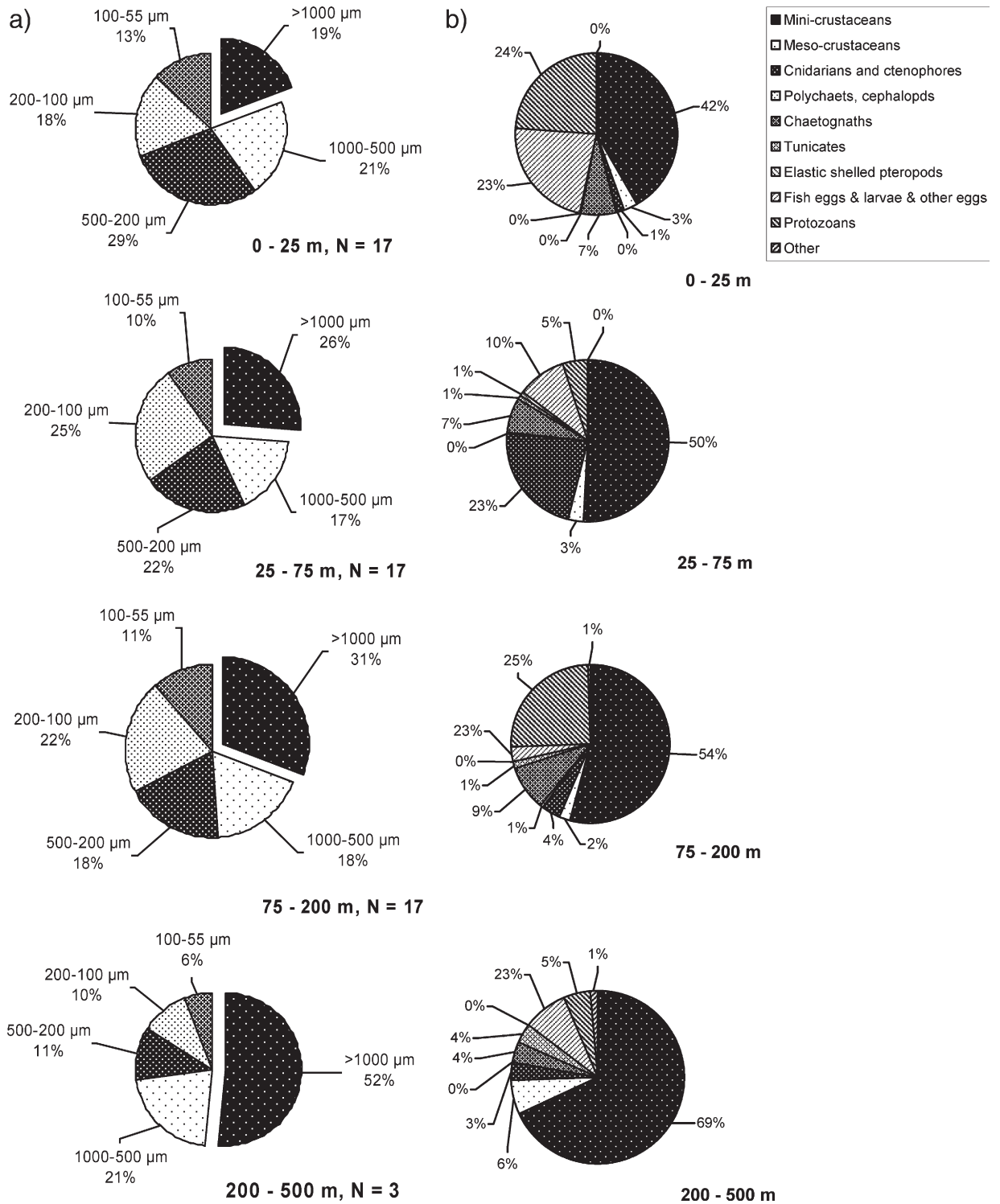


Fig. 5. Average AFDM proportions of different size classes of all Multinet samples (*N*) in four depth levels (a) and the numerical proportion of main taxonomic groups within the size class >1000 µm of the oceanic station 398 (b). The following groups were distinguished: *mini-crustaceans* (calanoid copepods, oithonids, oncaeids, sapphirinids, coryceids, harpacticoids, nauplia, ostracods and the cladoceran *Evadne* sp.), *meso-crustaceans* (adult euphausiids and larvae, amphipods, penaeids and other malacostraca larvae), *cnidarians* (adult siphonophora and larvae, hydromedusae, trachymedusae) and *ctenophores*, *polychaets and cephalopods*, *chaetognaths*, *tunicates* (appendicularians, thaliaceans), *elastic shelled pteropods*, *fish eggs and larvae and other eggs*, *protozoans* (radiolarians, foraminifera, tintinnids) and *other* (unidentified mesozooplankton).

expected on the shelf. Thirdly, oxygen concentrations of less than 0.5 ml/l and with a minimum of 0.2 ml/l did not act as barrier for migrating organisms. Fourthly, the biomass-rich zone spread deeper in the regions affected by near coastal upwelling south of the Angola–Benguela Frontal Zone at approximately 16°S, than north of it.

Horizontally, the ABFZ should dominate the patterns in the area of investigation. Following [Lass et al. \(2001\)](#), the front separates upwelling water, with a lower sea surface temperature and salinity in combination with higher plant pigment concentrations of the upper 60 m in the south and in a near coastal band, from an oceanic area with opposite properties ([Fig. 8](#)). In the comparable horizontal distribution of L-ADCP AFDM_{Total} ([Fig. 9](#)), we expected an upwelling influence south and shoreward of the front with higher concentrations. This was not the case in the upper 200 m although we distinguished between night and day sampling positions avoiding a biased picture produced by DVM. This phenomenon dominated the conditions in the upper layers especially in the oceanic waters. Only at depths below 200 m, the L-ADCP AFDM_{Total} concentration formed expected patterns taking the 1 and 2 mg/m³ isolines during night and the 3 mg/m³ isoline during day for orientation.

The comparison of vertical profiles of L-ADCP based AFDM concentrations for day and night as well as dawn and dusk showed the two principally different conditions with maxima in about 300 m depth during day and at less than 100 m during night and transition states at dawn and dusk ([Fig. 10a, b](#)). Although there is a wide scatter, the influence of DVM is noticeable, and will become clearer by determination of “distribution centres of the populations” computed by weighted mean depths (Z_x). We found them at 122 m during the night and 303 m during the day ([Fig. 10c](#)). The preferred depths at dawn and dusk are in between at 135 and 154 m, respectively. The basic data for the computation of Z_x (depth layers, average biomass concentrations as mg/m³ and mg/m²) are included in [Table 2](#). It also contains the percentages of the integrated averages in relation to the entire water column, separated into dawn, day, dusk, and night phases. The AFDM concentration amounted to 0.919 g/m² in the upper 200 m during the day and 3.185 g/m² at night. Consequently, about 38% of the biomass was concentrated in the upper 200 m during the day and 84% during the night. The largest percentage shifted from the 200–500 m depth layer during the day to the 25–75 m layer during the night. Therefore, the 75–200 m depth level seems to act as a major transient layer. Below 500 m, about 8% remained

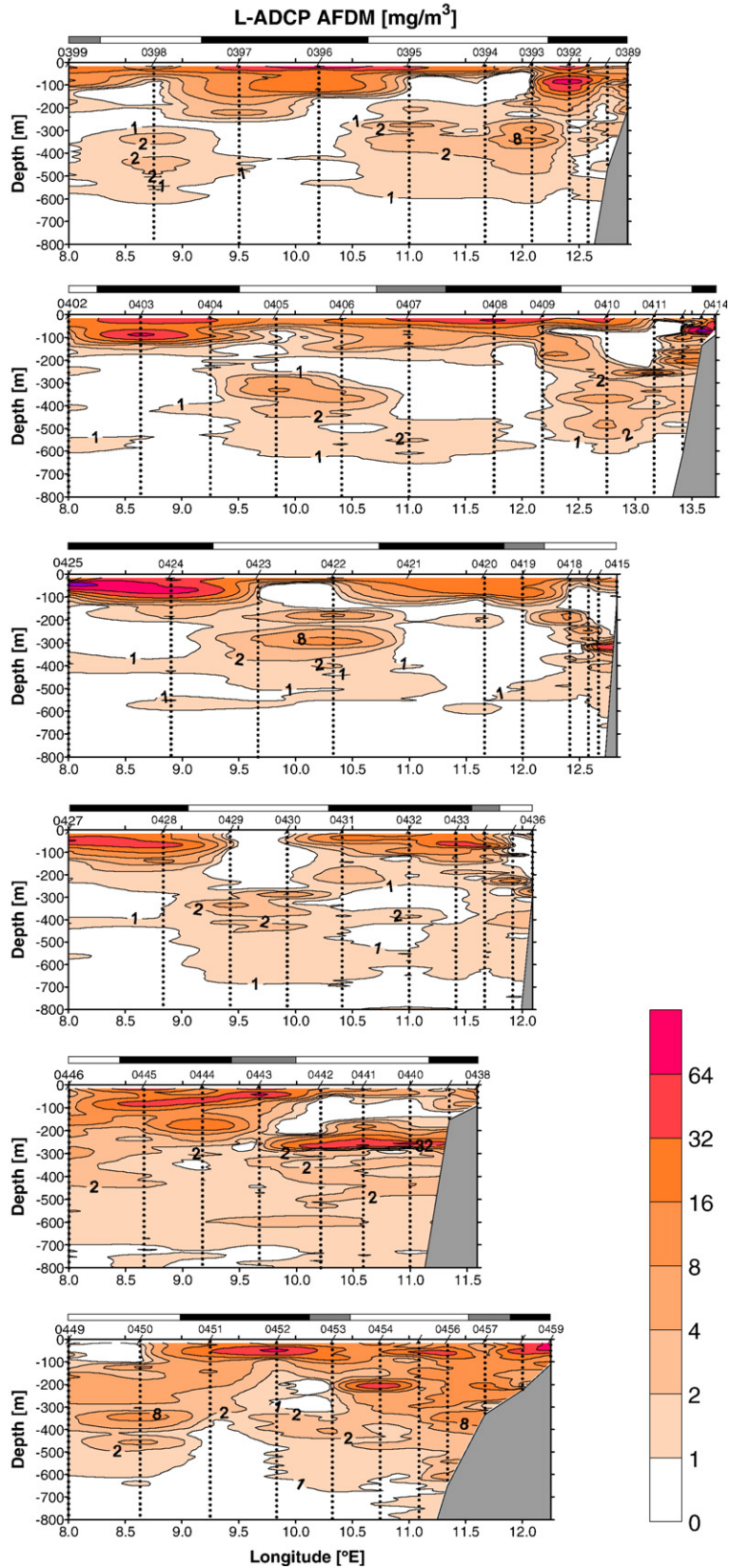
there during the night and this fraction increased by a factor of >2 during the day.

4. Discussion and conclusions

4.1. Methodological aspects

As stated in the Introduction, the acoustic properties of zooplankton vary with the size, shape, orientation, and the physiology of the organisms. Therefore, a direct comparison between mean volume-backscattering strength and zooplankton biomass is a complex task. The higher the diversity of scattering types, the more difficult it is to interpret the data. Solving the forward problem was recently recommended e.g. by [Fielding et al. \(2004\)](#), [Brierley et al. \(2005\)](#), and [Mair et al. \(2005\)](#) in order to consider single strong scatters which may be small in biomass. This technique depends much on the quality of the models used. On the other hand, there are examples of specific empirical relationships which directly relate the integrated energy to animal abundance or biomass concentration. Their validity is determined via ancillary methods such as net tows ([Jaffe, in press](#)). Moreover, zooplankton is known as the particle fraction in the ocean, which contributes most to scatter signals obtained by ADCP measurements. Consequently, some authors have used the acoustic backscatter data as a zooplankton proxy for the detection of diel vertical migration patterns (e.g., [Fischer and Visbeck, 1993](#); [Roe and Griffiths, 1993](#), [Zhu et al., 2000](#)), whereas [Flagg and Smith \(1989\)](#) cautioned against the use of unmodified ADCP equipment. [Heywood et al. \(1991\)](#) underlined that data derived from commercially available devices are worth investigating. They used a vessel-mounted 150-kHz ADCP and compared the acoustic backscatter signal summed from the surface to a depth of 200 m with zooplankton biomass concentrations collected by a net haul over the same vertical range at the same stations in the Indian Ocean and found significant correlations.

[Fielding et al. \(2004\)](#) indicated the net avoidance by the more mobile scatterers as a source of error and even the mismatch between sampling volume of the net and acoustic instrument. Already [Lyons et al. \(1994\)](#) recommended the simultaneously insonification and net sampling in the same volume of water as the preferred field method for calibrating purposes. However, the comparison should cover large spatial scales, for example cross-shelf gradients, to diminish errors caused by small-scale variability, which is difficult to measure simultaneously by both methods. In our case the parallel handling of both methods was impossible



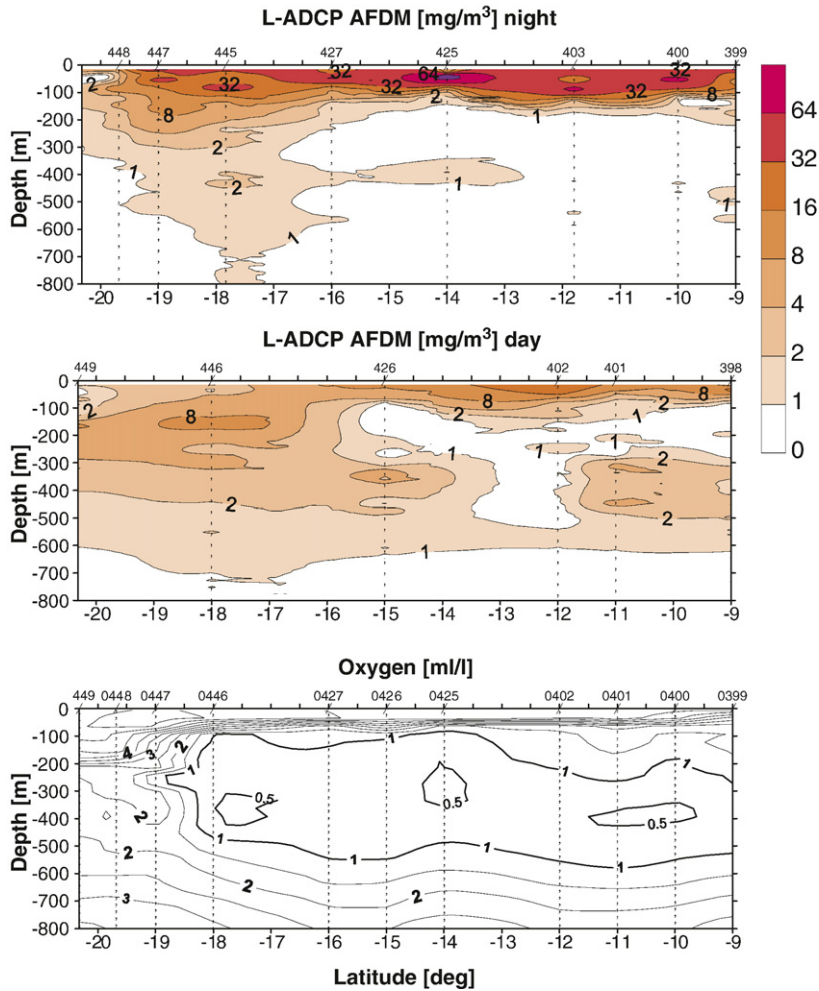


Fig. 7. Vertical L-ADCP AFDM_{Total} patterns on a latitudinal section at 8 and 9°E separated in night or day stations in comparison with oxygen concentration at 8°E (Lass et al., 2001). Station numbers on top of each section refer to Fig. 1 (for negative latitudes *N*, cf. caption of Fig. 4).

for logistic reasons, but most likely the influence of occasionally larger signals was reduced by averaging backscatter activity over the net sampling depth prior to the statistical comparison with AFDM_{Total}. The aspect of large-scale coverage was considered in our study. Additionally, we used the advantages of a lowered ADCP with a nearly constant noise level through the entire water column. This excluded the negative effect of the dependency of the sonified volume on the distance between the object and the transducer in the case of vessel-mounted ADCPs as discussed by Brierley et al. (1998). We also took into account the various percentages of size fractions to the total biomass

concentrations within groups differentiated at the same similarity level. This approach considered the size of organisms, and to a certain extent the taxonomic composition (Sieburth et al., 1978).

4.2. L-ADCP derived volume-backscattering coefficient versus zooplankton biomass concentration

In general, the statistical agreement between s_v and biomass concentration considering size fractions became increasingly significant with growing individual size. It should be stronger in the larger size classes because objects with a spherical diameter in the order of

Fig. 6. Vertical L-ADCP AFDM_{Total} patterns perpendicular to the coast between 8°S and approximately 19°S. The black (night), hatched (twilight) and white (day) bar in top of the patterns indicate the local dark/light phase. Station numbers on top of each section refer to Fig. 1.

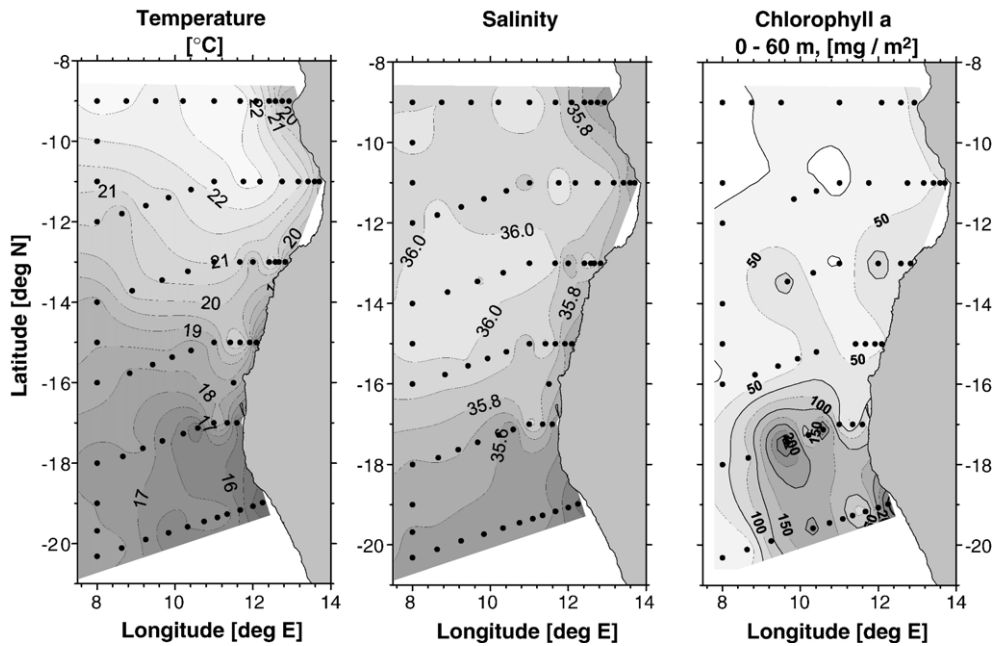


Fig. 8. Horizontal patterns of sea surface temperature and salinity as well as chlorophyll-a concentration integrated over the upper 60 m (Lass et al., 2001) (for negative latitudes N , cf. caption of Fig. 4).

5 mm length are the ideal reflectors for the signals of the 300-kHz L-ADCP system. However, the correlation was not the best in the size class $>1000 \mu\text{m}$. We interpreted this result as an effect of the more diverse species composition within this group in the epipelagic layer (Fig. 5b). In fact, it was generally more variable than in the smaller size classes. While the fraction of 200–500 μm consisted on average of 86% of copepods and ostracods in the upper 200 m, there were only 47% in the $>1000 \mu\text{m}$ group (Da Silva, 2004). The remaining part in the largest group consisted of chaetognaths (20%), fish larvae and fish eggs (16%), and foraminifera (8%). The significant correlations between s_v and AFDM of smaller organisms were expected due to trophical interactions of different size classes as previously observed. For example, Buchholz et al. (1995) found a close correlation not only between backscatter intensity and dry mass concentration of the larger Nordic krill *Meganictyphanus norvegica* but also between backscatter intensity and dry mass concentration of the smaller zooplankton which was actually not anticipated in the case of the used 153-kHz ADCP.

When separating data into different depth levels, the correspondence was clearly restricted to depths between 25 and 75 m. We mentioned the missing correlation in the layer <25 m because of the missing acoustic data in depths <16 m in contrast to net sampling data which originate from the entire upper 25 m layer. Even the

outliers in Fig. 3 stem exclusively from this affected layer. The reasons could be more complex for the missing correlation in the 75–200 m layer. This depth range seemed to act as a transition zone between the maximum night concentration of AFDM_{Total} in the 25 to 75 m layer and the maximum day concentration between 200 and 500 m (Fig. 10). The migration process could have produced a varying incident angle between scattering organisms and transducer, which is mentioned as being an important factor at higher frequencies by McGehee et al. (1998). If anisotropic individuals are orientated in a manner that energy is scattered from broadside, s_v will be highest in contrast to the situation where the energy is scattered from cranial or distal ends. Deviations of $\pm 25\%$ from average should be common. Consequently, the importance of the incident angle for the missing correspondence between s_v and AFDM_{Total} in this layer may be a reasonable explanation.

Finally, we used three different relationships between s_v and AFDM_{Total} by the cluster related approach. The relationships were statistically significant with an error probability of less than 0.01 and 0.001 respectively. This attempt considered both the varying proportion of the size classes of the AFDM_{Total} in relation to the position of the Angola–Benguela Frontal Zone below of 25 m (Fig. 2b) and to DVM which was an important signal in our data.

The agreements in the biomass concentration ranges and in the horizontal patterns in the different depths

derived by both the classical biomass determination and the acoustically computed biomass were taken as a quality criterion for our attempt. Using the Multinet stations only, we found a good visual correlation between patterns derived from classical biomass determination on one hand and those of L-ADCP

based AFDM_{Total} patterns on the other hand (Fig. 4). There were high biomass concentrations in the north and higher ones in the south separated by a minimum area. Again, the deviation in the upper layer might be the result of missing acoustic data in depths <16 m in contrast to net sampling data which originate from the

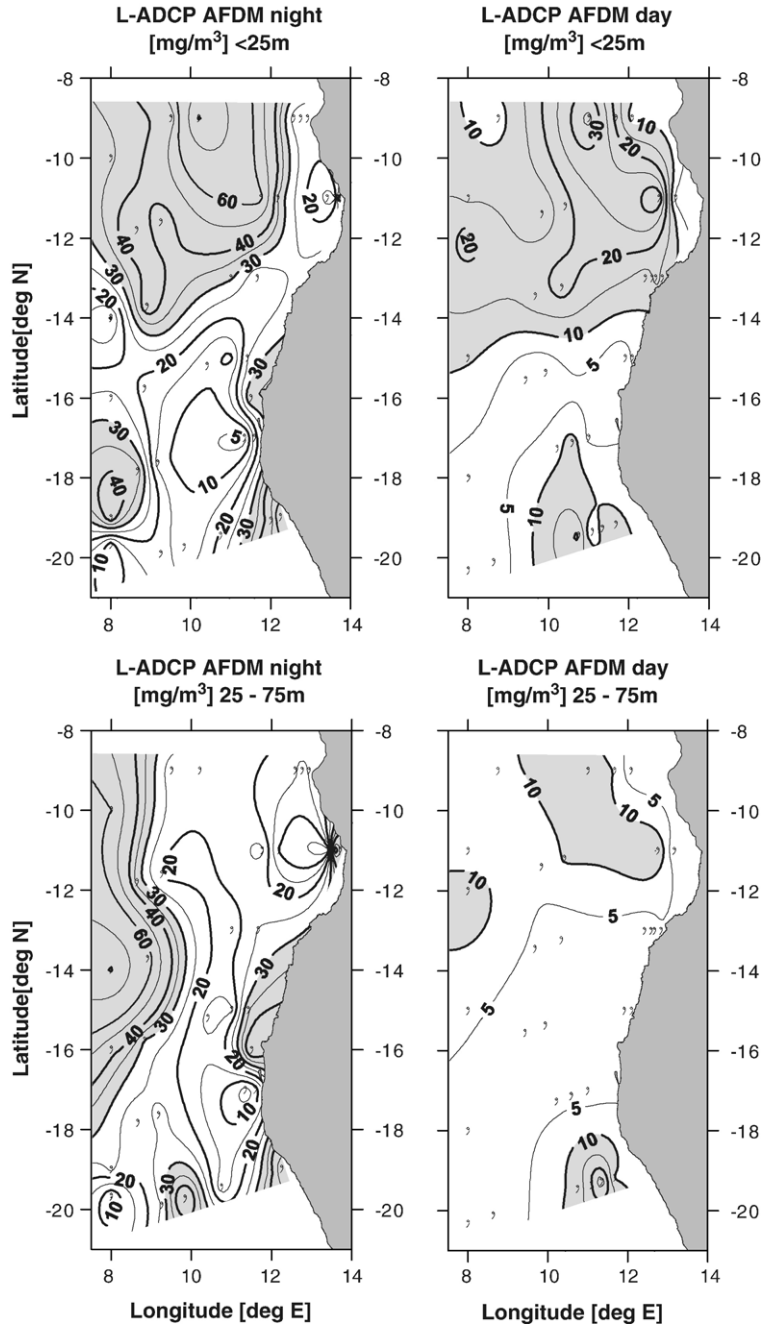


Fig. 9. Horizontal L-ADCP AFDM_{Total} patterns in four successive depth levels in the study area separated into stations during the night and daytime (for negative latitudes N, cf. caption of Fig. 4).

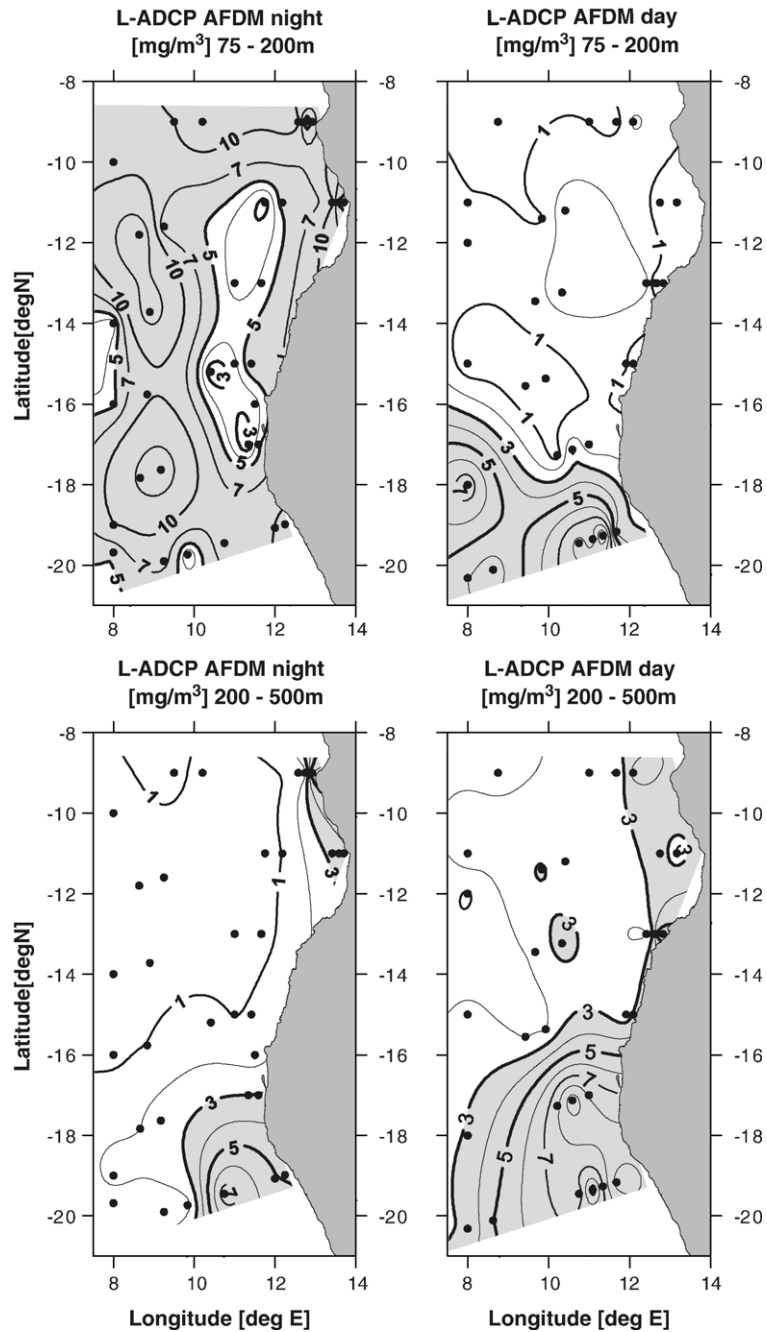


Fig. 9 (continued).

entire upper 25 m layer. The derived magnitudes of $AFDM_{Total}$ agreed well (with a slight exception in the northern part of the 25–75 m layer: 5 mg/m^3 instead of the expected 10 mg/m^3).

There are not many data of mesozooplankton biomass concentrations available for regional comparisons in the investigated area. All of them originate from the

Northern Benguela system south of $17^{\circ}30'N$, a region that has some overlap with our area. They are exclusively based on net sampling with mesh sizes varying between 180 and $300 \mu\text{m}$, and cover all seasons. Sampling was mainly restricted to the upper 200 m, except in the study of [Timonin et al. \(1992\)](#) with depths up to 1500 m. The data ranged between 0.240 and 22.400 g/m^2 . They were

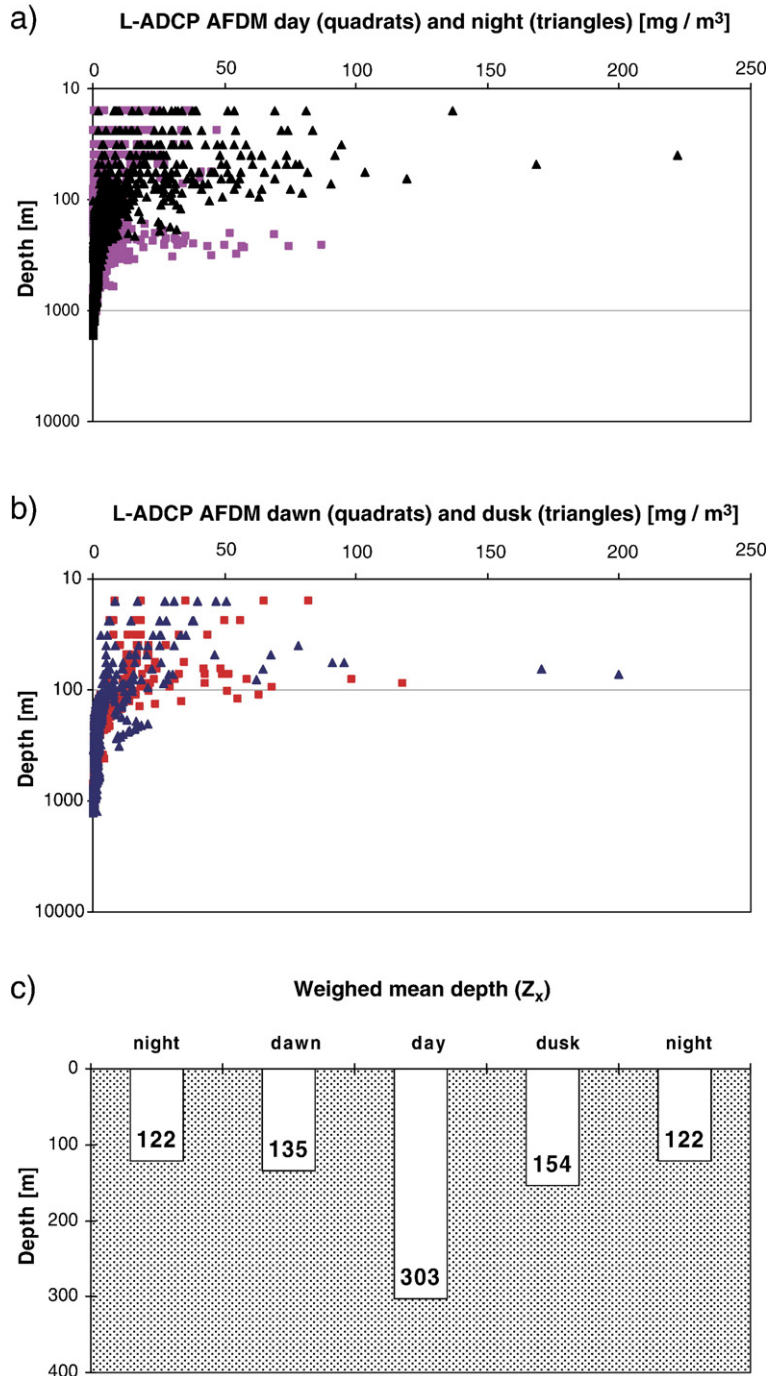


Fig. 10. Vertical profiles of L-ADCP AFDM_{Total} during day and night (a), dawn and dusk (b) and the estimated average distribution centres of the populations computed by weighted mean depths (Z_x) during the different periods of day (c). For the background of data, cf. Table 3.

mostly in the magnitude of 1 to 2 mg/m² (Table 3). The upper ranges were larger in the second half of the year. This is an effect of the seasonality in the upwelling system, which has its northern most position and the highest activity in austral spring (Berrit, 1962, cited by

Cushing, 1971). The conditions of net sampling during October 1990 (Timonin et al., 1992) were very similar to ours in terms of mesh size and depth range. Our data ranged between 2.439 and 4.522 g AFDM/m² and the mesozooplankton maximum of Timonin et al. (1992)

Table 2

Average L-ADCP AFDM_{Total} concentration (AVG) with amount of data (*N*) and standard deviation (STD) in (mg/m³) for various depth layers, supplemented by the integrated averages (mg/m³) and their percentages in relation to the entire water column, separated in dawn, day, dusk, and night using 6, 32, 7, and 28 L-ADCP profiles, respectively

Depth range (m)	<i>N</i>	AVG [mg/m ³]	STD [mg/m ³]	AVG [mg/m ²]	AVG [%]
<i>L-ADCP AFDM, dawn</i>					
<25	11	33.05	26.31	826	18.3
25–75	36	23.48	12.02	1174	26.0
75–200	96	13.60	19.48	1700	37.6
200–500	222	1.50	0.89	450	9.9
500–800	228	0.80	0.38	239	5.3
>800	360	0.29	0.23	132	2.9
<i>L-ADCP AFDM, day</i>					
<25	61	12.16	10.08	304	12.5
25–75	192	5.86	8.34	293	12.0
75–200	499	2.58	4.19	322	13.2
200–500	1093	3.68	6.53	1104	45.3
500–800	1060	0.97	0.67	292	12.0
>800	1513	0.28	0.30	124	5.1
<i>L-ADCP AFDM, dusk</i>					
<25	14	26.96	14.82	674	16.7
25–75	42	32.33	41.70	1617	40.2
75–200	102	6.50	8.12	813	20.2
200–500	200	1.66	2.75	498	12.4
500–800	190	0.96	0.63	289	7.2
>800	292	0.30	0.30	133	3.3
<i>L-ADCP AFDM, night</i>					
<25	51	30.78	25.41	770	20.2
25–75	157	30.78	29.70	1539	40.3
75–200	401	7.01	10.41	876	23.0
200–500	814	1.13	1.08	339	8.9
500–800	798	0.68	0.38	204	5.3
>800	1220	0.20	0.20	89	2.3

amounted to 5.600 g AFDM/m². Taking their northern most section at 17°S only (Timonin et al., 1992, Fig. 2, converted to AFDM, as described in caption of Table 3), the concentrations varied between 0.4 and 3.2 g/m² in October which is close to values reported in this study. Furthermore, our 0.293 g/m² for day time and the 1.539 g/m² for night-time sampling in the 25–75 m layer fit into the average concentration range from 1.080 to 2.628 g AFDM/m² of the 30–70 m layer between the upwelling centre and the maximum concentration downstream of it in October 1979 (Postel, 1990).

These agreements should encourage us to consider the L-ADCP as a reliable tool in zooplankton research. Actual comparison by net sampling, averaging the backscatter intensity for the depth levels accordingly

and taking the variations of species composition by similarity and cluster analysis into account, are necessary preconditions for consistent results.

4.3. Patterns of L-ADCP AFDM concentration in relation to the ABFZ, diel vertical migration and the oxygen minimum zone (OMZ)

During September 2000, the ABFZ was situated at approximately 16°S in the oceanic region separating water masses of the Benguela Current (south) and of the Angola Current (north). In the near shore vicinity, it turned northward and delimited upwelling water from the oceanic region in the euphotic zone (Lass et al., 2001, Wasmund et al., 2005). Sea surface temperature and salinity fields, as well as the horizontal chlorophyll-*a* patterns in the upper 60 m characterized the Benguela region and coastal upwelling area as a cold, low saline water region rich on plant pigments in contrast to the Angola Current water (Fig. 8). At the same time, we expected an upwelling response of zooplankton by higher L-ADCP AFDM_{Total} south and shoreward the front. This was not observed due to the dominant influence of DVM in the upper 200 m although we distinguished between night and day sampling positions (Fig. 9). Only at depths below 200 m, the L-ADCP AFDM_{Total} concentration formed patterns that corresponded with the environmental properties at the surface and the epipelagic layer in Fig. 8 taking the 1 and 2 mg/m³ isolines during night and the 3 mg/m³ isoline during day time into account. The higher biomass in these layers is a sign of coupling between the euphotic zone and deeper layers in coastal upwelling regions as described by Margalef (1978). While temperature and salinity indicate upwelling phenomena at sea surface, successive effects in phytoplankton (i.e., deep chlorophyll maximum), zooplankton biomass concentration and degradation processes (cf. OMZ) are typical consequences below the so-called EKMAN layer. The vertical distribution of L-ADCP AFDM_{Total} in Figs. 6 and 7 included both the deepening of higher concentrations south and shoreward the ABFZ due to the response to coastal upwelling and the signal of DVM. The upwelling effect seems to reach depths of 700–800 m while the lower border of the DVM visually varied between 700 m during day and about 150 m at night. Successively migrating layers of organisms in this range are typically found in the deep ocean (Vinogradov and Tseitlin, 1983).

The diel vertical migration (DVM) was the predominant process in producing the vertical patterns (Fig. 10a, b). It allowed checking the plausibility of our L-

ADCP results in this respect. First, we observed maximum biomass concentrations in about 300 m depth during daytime and at less than 100 m during the night. Above and below, there were vertically shifting scatters. This means, that DVM seems to be a variable phenomenon as currently described for the Irish Sea (Irigoin et al., 2004) and as observed off Namibia by Timonin (1997). Off Namibia, three groups of zooplankton were determined: not migrating, slightly migrating, and actively migrating depending on their ecological preferences and physiological stages. The regionally dominant calanoid copepod species *Calanoides carinatus* belonged to the active group. Their population medians of 300–320 m during the daytime and 150–300 m during night-time fitted quite well in the extreme values of Fig. 10a, b. The medians of another active genus (*Pleuromamma*) ranged between 280 m during daytime and 15 m at night.

Timonin (1995) observed up to 2–2.5 times higher zooplankton biomass in the upper 100 m layer during night-time than during daytime collected by net with 180 μm mesh size. He found this number in correspondence with the typical ratio of 1.3–2 times or maximum

ratios of 1.1–4 times in the tropical zone of the ocean according to Vinogradov (1968, cited by Timonin, 1997). Taking our averages (Table 2) we obtained a factor of 3.9 for the upper 75 m, and 3.5 for the upper 200 m respectively, which is in the range of the maximum ratio.

The opinions and results concerning migration velocities are also quite variable. Mauchline (1998) compiled upward and downward rates of calanoid copepods, which differ not much, because they ascended and descended by active movements. Heywood (1996) used an ADCP for the detection of DVM patterns in the Northeast Atlantic. She mentioned in her introductory part that most studies found migration to be symmetrical. However Smith et al. (1989, cited by Heywood, 1996) found about two times slower migration rates during descent than during ascent. According to the more general overview by Raymond (1983), combination of active movements and sinking should be possible. Our differences between the distribution centres of the populations at night and dawn on one hand and between day and dusk on the other hand (Fig. 10c) could be an indication for a more

Table 3

Estimates of AFDM concentrations of meso- and macrozooplankton in the Northern Benguela ecosystem (modified following Hutchings et al., 1991)

AFDM estimates of meso- and macrozooplankton in the Northern Benguela ecosystem [g/m^2]					
Area	Gear and mesh size [μm]	Depth sampled [m]	Sampling date	Meso-zooplankton	Reference, comments
17°30′–23°30′S	Oblique Bongo 300	Upper 50	Jan. 1985	0.784	Fearon et al., 1986 (night time only)
17°30′–26°30′S	RMT-1 \times 6 200	Upper 200	Apr. 1986	0.956 1.948 1.128	Olivar and Barangé, 1990 (inshore, shelf, slope)
23°00′–29°30′S	Oblique Bongo 300	Upper 200	Jul. 1983 Jul. 1984	1.096 0.282	Barangé, 1989 (shelf break, shelf)
20–21° S	WP-2, 200	0–30 30–75	Oct. 16th to Nov. 11th, 1979	1.032–2.112 1.080–2.628	Postel, 1990 (inshore, shelf, slope, averages over time)
17°–25° S	J-OM net, 180 Juday net, 180	0–1500	May 1985, Jan. 1986, Jan. 1988, Oct. 1990	0.240–22.400 (Oct.-Max.: 5.600)	Timonin et al., 1992
9°–20°19′S	L-ADCP AFDM, calibrated by Multinet (200, 55)	0–1250	Sept. 2000	2.439–4.522	This paper, Table 3) (Min.–max. averages of the water column)
9°–20°19′S	L-ADCP AFDM, calibrated by Multinet (200, 55)	Upper 200	Sept. 2000	0.919 3.185	This paper, Table 3 day averages night averages

Carbon biomass was converted to AFDM by factor 2, wet mass to dry mass by factor 0.1 (Hutchings et al., 1991), AFDM=0.8 * DM (Postel et al., 2000).

rapid upward than downward migration. Summarizing, DVM of mesozooplankton is a predominant phenomenon of the upper 300 m with minor effects down to 700 m (Figs. 6, 7, 10). The process is a non-uniform one, as indicated by the scatter in Fig. 10a, b and considering the discussion in the literature. The oceanic regions seem to be mostly affected (Fig. 9).

Interestingly, the intermediate oxygen minimum zone (OMZ) with an oxygen content of less than 0.5 ml/l between 200 and 400 m (Fig. 7), with a minimum of up to 0.252 ml/l, is no limitation for diel vertical migration. DMV through the OMZ would indicate that the involved organisms are alive. Significant quantities of zooplankton in OMZs have already been described in the past. Longhurst (1967) found numerous individuals at oxygen concentrations as low as 0.2 ml/l in the California Current. Kinzer (1969) detected zooplankton concentrations in oxygen-deficient deep scattering layers with oxygen contents between 0.1 and 0.04 ml/l, which amounted to one-third of those in surface hauls in the Arabian Sea, confirming the results of Vinogradov and Voronina (1961). Recently, Luo et al. (2000) reported the diel migrations of fish and zooplankton despite the year round presence of an oxygen minimum of <0.2 ml/l at 125–150 m in the Arabian Sea during the intermonsoon (April/May) and monsoon (August) period. Wishner et al. (1998) also found significant zooplankton concentrations in OMZs of the Arabian Sea at oxygen concentrations between 0.1 and 0.05 ml/l. Stalder and Marcus (1997) reported differences in copepod species and developmental stages in response to hypoxia. While adult *Acartia tonsa* could tolerate dissolved oxygen at 1 ml/l but were killed at 0.5 ml/l, their nauplia were more resistant. *Centropages hamatus* survived only above 1 ml/l. They also found that copepods are not able to escape from hypoxic layers. Devol (1981) studied the vertical zooplankton distribution and respiration in British Columbia Fjords, and found 5 µg atom O₂/l which is equal to 0.06 ml/l, as the limiting concentration for living zooplankton. Loick et al. (2005) investigated water-body preferences of dominant calanoid copepod species in the ABFZ with minimum concentrations up to 0.64 ml/l. *Calanus carinatus* CV stages were regularly found in the OMZ of the oceanic region between 300 and 500 m depth. The authors interpreted the occurrence as resting stages in combination with a certain hypoxic tolerance. Other species of the same community like *Metridia lucens* (females) and *Aetideopsis carinata* (females) seemed to be only physiologically adapted. The authors discussed adaptations to low oxygen conditions as an opportunity to extend the inhabitable volume by involving the OMZ during diel vertical

migration. These results from the literature are in agreement with our observations.

Organisms may suffer in OMZ, but zooplankton is able to tolerate concentrations of nearly 0 ml/l at least over short periods of the DVM through such layers. Here we recommend using acoustic techniques as a tool for long-term *in situ* studies of zooplankton distribution in relation to the dynamics of hypoxic layers off Namibia supported by parallel net sampling for the consideration of species composition.

Acknowledgements

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