Zooplankton spatial distribution along the South African coast studied by multifrequency acoustics, and its relationships with environmental parameters and anchovy distribution

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Lebourges-Dhaussy, A., Coetzee, J., Hutchings, L., Roudaut, G., and Nieuwenhuys, C. 2009. Zooplankton spatial distribution along the South African coast studied by multifrequency acoustics, and its relationships with environmental parameters and anchovy distribution. – ICES Journal of Marine Science, 66: 1055–1062.

The Central Agulhas Bank (CAB) is an important component of the southern Benguela ecosystem. Despite relatively low primary production, secondary production supports large populations of mid-trophic-level pelagic fish. Exhaustive sampling of the Agulhas Bank ecosystem was performed during a routine acoustic biomass survey in November 2006. A TAPS-6 was deployed with near-simultaneous, plankton-net sampling. Concurrent collections of fish-school and environmental data permitted a detailed study of the water column. Zooplankton was classified by equivalent spherical diameter (ESD; mm): 0.0–0.35 (Class I), 0.35–0.8 (Class II), 0.8–2 (Class III), and >2.0 mm (Class IV). Clear relationships with environmental parameters were only evident at night on the CAB (west of 23°E) for Classes II and III. Class III exhibited pronounced diel vertical migrations, whereas Class I exhibited a reverse pattern. Also observed were the effects of anchovy predation on small zooplankton aggregated in areas of high chlorophyll *a*.

Keywords: Agulhas, anchovy, Benguela, multifrequency, TAPS-6, zooplankton.

Received 1 August 2008; accepted 20 February 2009; advance access publication 8 May 2009.

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Introduction

The Benguela Current ecosystem is one of the four major, eastern-boundary current upwelling systems (Humboldt, Canary, California) in the world (Parrish *et al.*, 1983; Shillington *et al.*, 2006). They are all characterized by intense upwelling of cold, nutrient-rich waters along the coast because of Ekman offshore divergence in response to equatorward windstress (Shannon and Nelson, 1996; Shillington *et al.*, 2006). They are important centres of plankton production and support large biomasses of mid-trophic-level fish, such as sardine and anchovy, as well as seabirds and marine mammals (Koné *et al.*, 2005; Van der Lingen *et al.*, 2006b). The Benguela ecosystem is bordered in the south by the warm waters of the Agulhas Current, resulting in a highly dynamic and unique system (Shannon and Nelson, 1996; Figure 1b). The Agulhas Bank (Figure 1a) has a very wide shelf region and a highly stratified water column in summer, which becomes well mixed in winter (Shillington *et al.*, 2006). Coastal upwelling, especially during summer, and the presence of a seasonal, subsurface, cold tongue stretching across the bank in autumn to early winter (Boyd and Shillington, 1994) ensure a nutrient-rich environment for most of the year. Sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicholus*) are abundant pelagic species that spawn and feed in the area, but recruit to the South African west coast in winter.

A high-frequency, acoustic profiler TAPS-6 ("Tracor Acoustic Profiling System"; Holliday and Pieper, 1980) permits high-resolution assessment of the micro- and mesozooplankton community structure at the same temporal and spatial scales of physical measurements. Such data were used to investigate the distributions of zooplankton in the Benguela ecosystem and their relationships with physical parameters and anchovy schools.

Methods

Equipment and survey protocol

Acoustic data were collected with a calibrated echosounder (Simrad EK60 operating at 18, 38, 120, and 200 kHz) during an annual, pelagic-fish assessment survey along parallel transects off the coast of South Africa aboard the FRS "Africana" in November 2006. Additional sampling was conducted along some designated "plankton transects", using a combination of CTD (SBE-9), rosette, TAPS-6, and vertical bongo net (200 μm mesh), and along Transect 38 using a Hydrobios multinet (0.25 m^2 opening, five 200 μm mesh closing nets; Figure 1a). In all, 94 profiles were acquired at stations spaced 10 nautical miles apart, along 14 transects from ~19°30′E to 29°E.

The TAPS-6 was mounted on the CTD rosette cage, deployed at 0.5 m s^{-1} to a maximum depth of 200 m, then retrieved to sample the water column at designated depths. The vertical bongo net was then towed at a maximum depth of 200 m. Along Transect 38, the TAPS-6 was mounted perpendicular to the towing direction on the Hydrobios multinet (Figure 1c). Samples were recorded during a

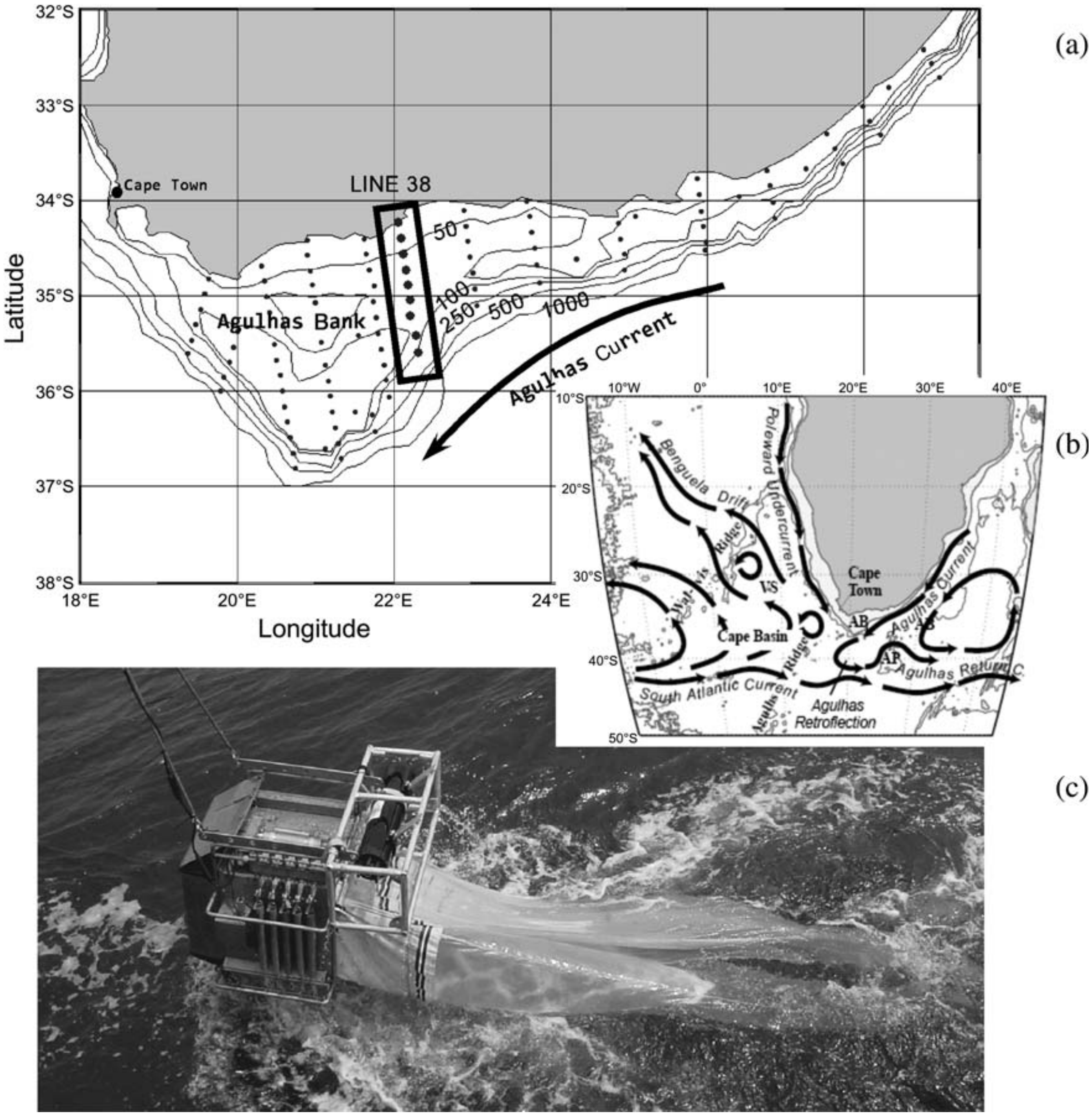

Figure 1. (a) MCM small pelagic survey (November 2006), plankton transects with the Hydrobios transect (Line 38) specified. (b) Illustration of the oceanography south of Africa. Source Boebel *et al.* (2003). (c) Mounting of the TAPS-6 on the Hydrobios.

slow (0.1–0.3 m s^{-1}) oblique ascent through the water column. The five nets discretely sampled the deep-homogenous layer, the thermocline, the upper mixed layer, and close to the surface. The CTD profile and water sampling were carried out separately.

The TAPS-6 system and its data-acquisition procedures are described in Pieper *et al.* (2001) and Roman *et al.* (2001). Measurements of volume-backscattering strength (S_v) at 265, 420, 700, 1100, 1850, and 3000 kHz were averaged over 2-m vertical bins and 50–125 measurements. TAPS-6 was calibrated at BAE Systems in November 2005.

Fish-school data were extracted from the 38-kHz daytime acoustic transects with the Sonardata Echoview schools module according to the following criteria: minimum length = 12 m, minimum height = 1.5 m, S_v threshold = − 65 dB, minimum candidate length = 1 m, minimum candidate height = 1 m, maximum vertical linking distance = 1 m, and maximum horizontal linking distance = 20 m. The resulting estimates of school depth, height, mean S_v, and geographical position were exported for further analyses.

Plankton processing

From the samples collected on the eight Hydrobios multinet tows along Transect 38, salps and jellies were first removed by a 1600-μm sieve, then four subsamples of the plankton collected in each net were analysed for species composition and size by microscope. Conversions of lengths to equivalent biovolumes, and subsequently to equivalent spherical diameter (ESD), were performed according to equations from Beers (1966), Omori (1969), Holland (1978), Stuart (1986), James (1987), Heron *et al.* (1988), Chisholm and Roff (1990), and Van der Lingen (2002).

TAPS-6 data processing

Noise removal followed the manufacturer's recommended method, i.e. the lowest values of S_v logged at each frequency

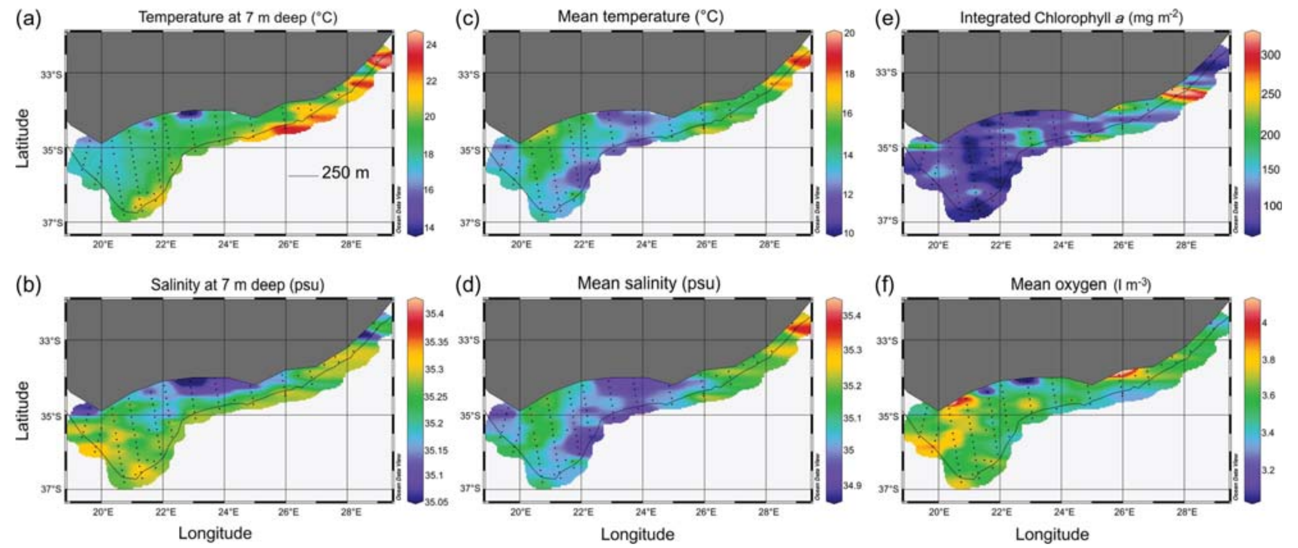

Figure 2. Physical oceanography during the survey. (a) Temperature at 7 m; (b) salinity at 7 m; (c) mean temperature; (d) mean salinity; (e) integrated chlorophyll *a*; and (f) mean oxygen. Means and integration are over the water column. Visualization performed in Ocean Data View software (Schlitzer, 2008).

were subtracted from measured values. In addition, data collected at 265 kHz were not processed, given concerns about their quality. Zooplankton abundance was estimated from the measurements of S_v at the five remaining frequencies, using an inversion algorithm that employs the non-negative, least-squares method (Greenlaw and Johnson, 1983; Holliday and Pieper, 1995). The truncated-fluid-sphere model (Holliday, 1992) with $g = 1.12$ and $h = 1.09$ (Greenlaw and Johnson, 1982) was used to derive estimates of zooplankton biovolume (mm^3 m^{-3}) by size class, expressed for ESD. The validity of this method has been demonstrated (Costello *et al.*, 1989; Holliday *et al.*, 1989). This model was chosen for two reasons: (i) samples from concurrent net sampling revealed that cladocerans and copepods are by far the dominant organisms within the volume sampled by the TAPS-6, and (ii) comparative biovolume estimates are obtained from the TAPS-6 and the net samples. The following four broad ESD (mm) classes were defined: 0.0–0.35 (I), 0.35–0.8 (II), 0.8–2.0 (III), and >2.0 (IV).

Vertical migrations

Because no stations were sampled repeatedly by day and night, the relative contributions to the total integrated biovolume of a subsurface (20–60 m) and deeper layer (60–200 m) were calculated for all stations. From the mean day and night biovolume profiles (not presented), 60 m appeared a sensible depth to delineate these two regions.

Relationships between zooplankton and the environment

Relationships were investigated with correlations (Pearson; r) between the measurements of environmental parameters, temperature (TMP), salinity (SAL), density (DEN), chlorophyll *a* (FLO), turbidity (TUR), oxygen (OXY), and zooplankton biovolumes (BVL) for the various size classes (BVL_I, BVL_II, . . ., BVL_T for the total). To detect trends, the dataset was split at 23°E into western and eastern components and daytime and night-time data were evaluated independently. Measurements of biovolume and environmental parameters were log-transformed and mean-centred. A principal component analysis (PCA) was conducted on each of the four datasets. A varimax-normalized rotation was applied to the data to maximize the variance explained by the PCA.

Relationships between anchovy-school locations and their environment

It was necessary to estimate physical parameters and zooplankton biovolumes at the exact locations of the schools. Because these parameters were only collected from stations spaced 10 nautical miles apart on selected transects, a kriged-variable surface was generated for each parameter, at a vertical resolution of five metres. A PCA, as described above, was used to detect differences in the relationship between variables when schools were present and absent. This analysis was confined to anchovy schools detected during the day because very few sardine schools were encountered, and pelagic-fish schools disperse at night-time. Additionally, because most anchovy schools were detected west of 23°E, it was not feasible to conduct a separate PCA for each region.

Results

Oceanography and *in situ* chlorophyll biomass

Surface temperatures (7-m depth) illustrate the influence of the warm Agulhas Current along the shelf edge (Figure 2a). The narrow, eastern part of the shelf is characterized by saline, warm, surface water (Figure 2b), whereas pockets of fresher, cool, inshore water between 21 and 24°E result from coastal upwelling. The inshore area around 23°E often has elevated quantities of cool water, indicative of upwelling following easterly winds (Boyd and Shillington, 1994; Lutjeharms *et al.*, 2000). This cool ridge is a prominent feature during many of these south-coast surveys.

Mean values of temperature and salinity (Figure 2c and d) are similar to the surface values in the east, but relatively higher than those on the western part, ~20–21°E, of the Central Agulhas Bank (CAB) where cold water is absent, especially close inshore. Integrated chlorophyll *a* peaks in the eastern part and towards the shelf edge on the CAB (Figure 2e). The mean oxygen is relatively high over the entire area, except in the upwelled pockets (Figure 2f).

Nets–TAPS-6 comparisons

This section provides a synopsis of biovolume comparisons for validation purposes only and considers the eight stations sampled from 3803 (inshore) to 3817 (offshore, Figure 1). The mean biovolumes obtained per station are similar (Figure 3). The largest difference is observed for station 3811. Salps were numerous along this line, especially from the mid-shelf to offshore, and allied with the presence of surface bubbles resulted in the extensive removal of large values from TAPS-6 samples in the upper layers. For station 3811, it may have caused the removal of part of the actual biovolume, although the results of the net samples for this station are especially variable. The correlation coefficient (r) between the two series is 0.58, and it increases to 0.83 if station 3811 is removed from the dataset.

TAPS-6 zooplankton assessments

Horizontal distribution

The mean densities of zooplankton are low across the widest part of the shelf and west of 23°E, but increase towards the coastal areas of the south and east coast. The highest concentration is found close inshore in association with the cool upwelled water on the south coast (Figure 4a). Integrated biovolume is highest towards the shelf edge on the east coast, but is also elevated in most offshore areas farther to the west (Figure 4b).

Vertical distributions

Apportioning the biovolume into size classes allowed vertical migratory patterns for different-sized organisms to be identified (Table 1). Clear, upward, night-time migrations are observed for

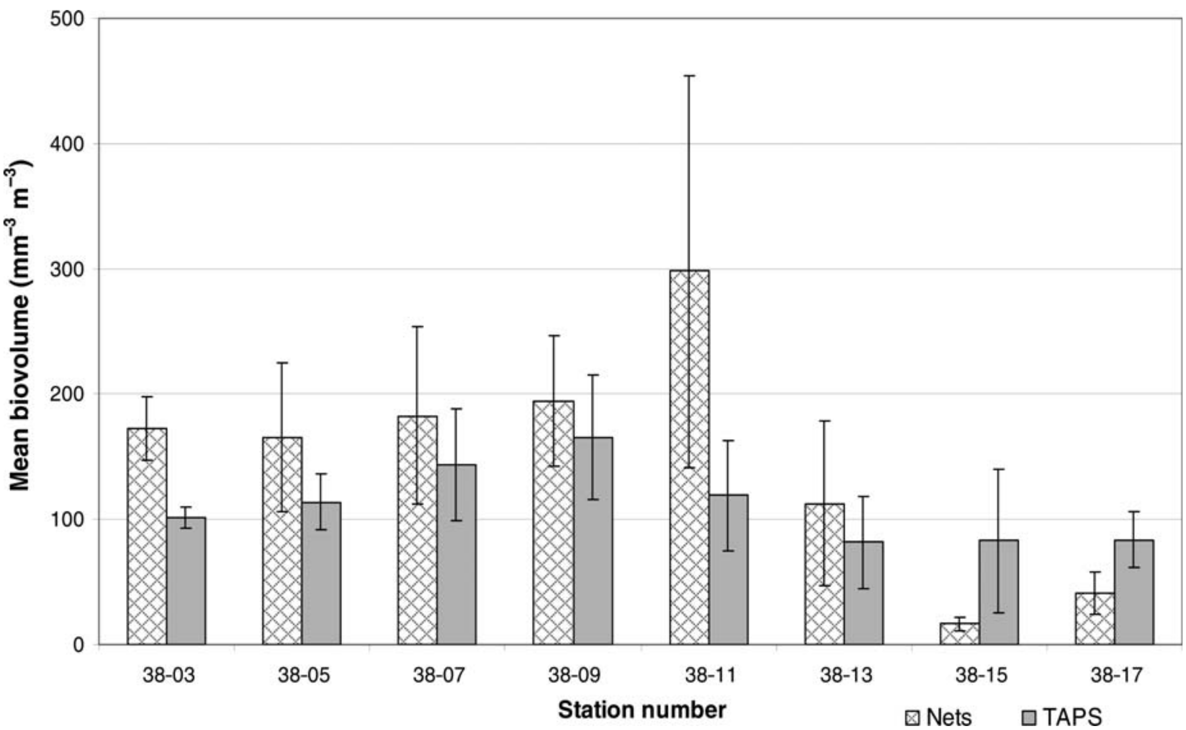

Figure 3. Mean biovolumes (mm^3 m^{-3}) calculated for the eight stations of Line 38. Nets and TAPS results. A full error bar equals 1 s.d.

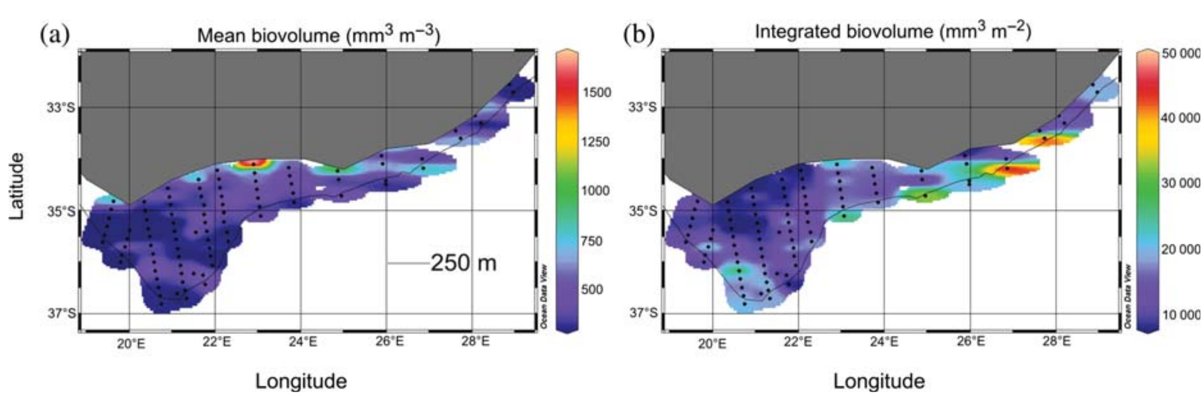

Figure 4. Horizontal distribution of the global zooplankton. (a) Mean biovolume (mm^3 m^{-3}); (b) integrated biovolume (mm^3 m^{-2}).

Table 1. Contributions of the 20–60 and 60–200 m layers to the integrated zooplankton biovolume, by day and night, calculated from TAPS-6 data processing: comparison by size class.

	Percentage of the 20–200-m integrated biovolume per ESD (mm) class				
Layer	**Total**	**0–0.35**	**0.35–0.8**	**0.8–2**	**>2**
20–60 m day	38	31	39	35	32
60–200 m day	62	69	61	65	68
20–60 m night	36	25	55	72	50
60–200 m night	64	75	45	28	50

Table 2. Correspondence between ESD classes and zooplankton.

Size class ESD range (mm)	CL I 0–0.35	CL II 0.35–0.8	CL III 0.8–2	CL IV >2
Species	Cladocerans	*Calanus*	*Calanus*	Fish eggs
	Copepod nauplii	*Calocalanus*	*Calocalanus*	Euphausiids
	Oithona	*Candacia*	*Candacia*	Amphipods
	Oncaea	*Centropages*	*Centropages*	Fish larvae
	Mussel larvae	*Nannocalanus*	*Nannocalanus*	
		Small copepods	*Pleuromamma*	
		Oncaea	Oikopleuridae	
		Oikopleuridae	Fish eggs	
		Harpacticoida	Euphausiids	
		Chaetognaths		
		Copepod nauplii		

Classes II, III, and IV (ESD from 0.35 to >2 mm), being most pronounced for Class III (0.8–2 mm ESD), which includes the bulk of the calanoid copepods (Table 2). Class II includes the smaller copepods and small stages of calanoid copepods; Class IV includes sporadically occurring large animals, such as euphausiids and fish larvae. Class I organisms, which include most of the cladocerans, the smaller of the copepod nauplii, *Oithona*, and small stages of *Oncaea*, exhibit contrasting downward migrations at night.

Relationships between zooplankton and its environment

Considering the entire dataset, several significant, but weak correlations were found: the highest ($r > 0.3$) correlations were between BVL_II, BVL_III, and BVL_T with density (negative) and chlorophyll *a* (positive), as well as between BVL_T and turbidity (positive). Stronger correlations ($r > 0.5$) were observed for the dataset comprising only observations west of 23°E at night (Table 3). Highest positive correlations were between BVL_II and temperature, salinity, oxygen, and chlorophyll *a*, and between BVL_III, temperature, and oxygen, whereas density was negatively correlated with BVL_II and BVL_III. Correlations between BVL and the environmental variables for the other three datasets (west of 23°E, day; east of 23°E, day and night) were very low.

The proportion of the variance explained by the first three factors of the PCA ranged from 69.5% (west of 23°E, day) to 76.3% (west of 23°E, night). In all but the fourth set (east of 23°E, night), the first factor, which explained most of the variance, was correlated with variables related to the physical environment, whereas the second and third factors were correlated with turbidity and zooplankton biovolume to various degrees. The loadings of the first three factors allow structure to emerge (Figure 5), and this is described later. West of 23°E, the variables form two separate groups during the day: those related to the environment and those related to biovolume (except BVL_I) and turbidity. At night, however, only one group of variables is apparent. Variables related to the biovolume move closer to or merge into the grouping of environmental variables, indicating a stronger association between the environment and biovolume of all but the smallest zooplankton at night. For both day and night, BVL_I is isolated. East of 23°E, no clear groupings of variables are evident by day, although it appears that chlorophyll *a*, oxygen, and turbidity may have a positive association with a higher level of BVL_II to BVL_IV, and a negative association with BVL_I and BVL_T. At night, a clear grouping of some environmental variables (TUR, FLO, and OXY), allied with those associated with BVL_II, BVL_III, BVL_IV, and BVL_T, is evident, although temperature, salinity, and BVL_I are isolated.

The zooplankton variables that are most structured by the environmental parameters are BVL_II and BVL_III by night, west of 23°E. Histograms of environmental parameters corresponding to their highest values were calculated. The temperature mode is 18°C, and the oxygen mode is 4.3 ml l^{-1} for both classes; the salinity has two peaks for Class II (35.15 and 35.25 psu), but one dominates (35.25 psu) for Class III. Chlorophyll *a* peaks at 1.4 mg m^{-3} for both classes.

Comparisons with fish-school locations

Anchovy schools are generally located in areas where oxygen is >3 ml l^{-1}, and chlorophyll *a* levels and the biovolumes of small zooplankton (BVL_I) are high. Some schools are also associated with high biovolumes of larger zooplankton. These observations are supported by the results from the PCA conducted between variables when anchovy schools were present vs. absent (Figure 6). The first and second principal components account for 55.4% of the variance, whereas the third factor explains an additional 13%. The first factor is highly loaded by variables related to the physical environment. The second is positively correlated with BVL_II, BVL_III, and BVL_T, and to a lesser extent

Table 3. Pearson correlation coefficients (r), emboldened where $|r| > 0.5$, between environmental parameters and zooplankton biovolumes for the various size classes.

Location	Night or day	Biovolume	TMP	SAL	OXY	FLO	DEN	TUR
West of 23°E	Night	BVL_I	−0.19	−0.16	−0.18	−0.06	0.22	0.22
		BVL_II	**0.62**	**0.55**	**0.55**	**0.54**	**−0.63**	0.11
		BVL_III	**0.59**	0.48	**0.53**	0.5	**−0.61**	0.09
		BVL_IV	0.31	0.29	0.24	0.14	−0.32	−0.16
		BVL_T	0.46	0.38	0.38	0.43	−0.47	0.27
	Day	BVL_I	0.11	0.08	0.10	0.12	−0.10	0.18
		BVL_II	0.05	−0.02	−0.17	0.08	−0.14	0.31
		BVL_III	0.16	0.08	−0.01	0.22	−0.25	0.27
		BVL_IV	0.04	0.00	0.07	−0.01	−0.08	−0.07
		BVL_T	0.24	0.13	0.07	0.29	−0.33	0.38
East of 23°E	Night	BVL_I	−0.03	−0.09	−0.09	0.01	−0.03	0.22
		BVL_II	0.22	−0.01	0.37	0.43	−0.31	0.35
		BVL_III	0.1	−0.19	0.34	0.41	−0.27	0.36
		BVL_IV	0.19	−0.07	0.26	0.38	−0.31	0.20
		BVL_T	0.16	−0.19	0.3	0.41	−0.35	0.44
	Day	BVL_I	0.17	0.18	0.15	0.12	−0.12	−0.05
		BVL_II	0.20	0.05	0.30	0.41	−0.28	**0.53**
		BVL_III	0.00	−0.16	0.16	0.23	−0.12	0.46
		BVL_IV	−0.03	−0.18	0.18	0.11	−0.13	0.08
		BVL_T	0.17	−0.02	0.36	0.38	−0.29	0.43

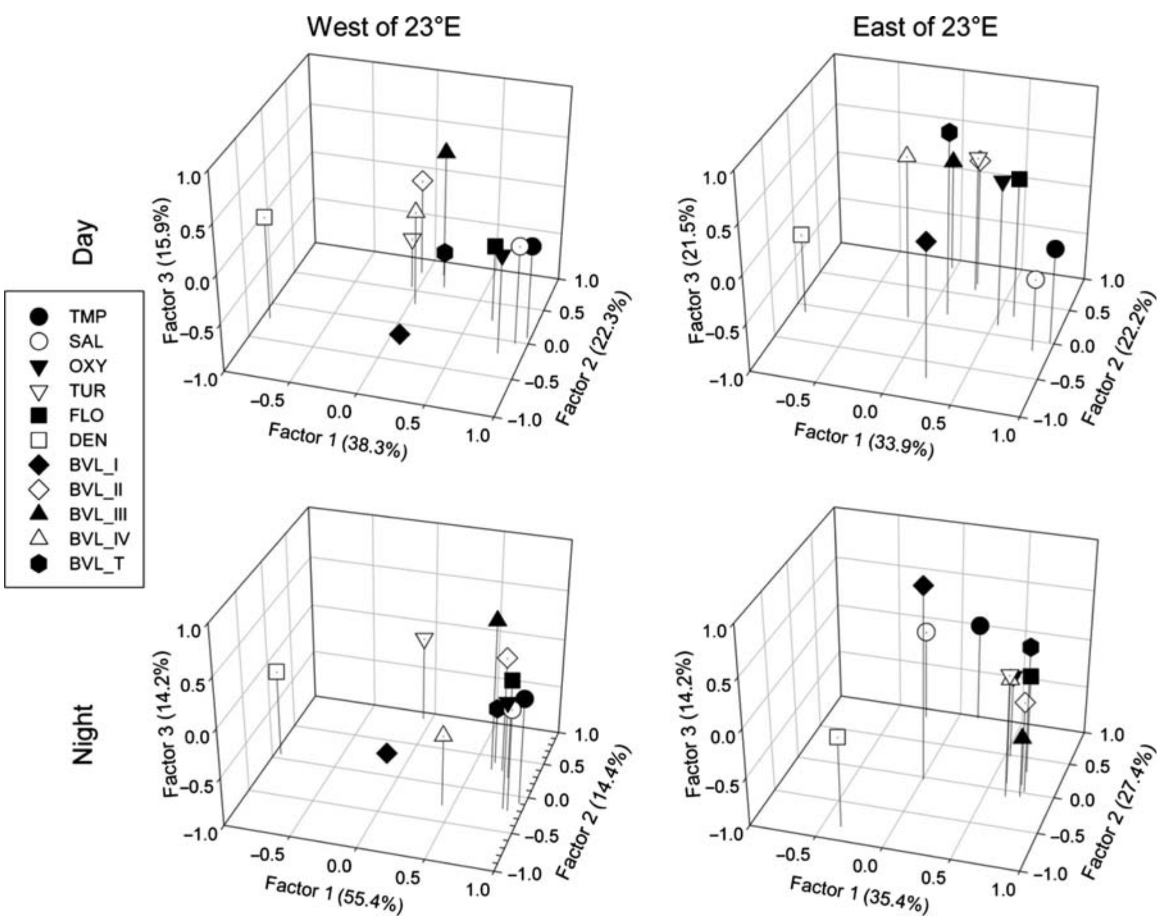

Figure 5. Results of the PCA analysis between environmental parameters and the size classes of zooplankton.

BVL_IV, and negatively correlated with BVL_I. The third factor had the highest correlations with BVL_I, followed by BVL_T and BVL_III. Plots of the first vs. second principal components reveal a strong association between anchovy-school location and variables related to physical parameters (i.e. elevated levels of chlorophyll *a*, temperature, oxygen, and salinity) because of the

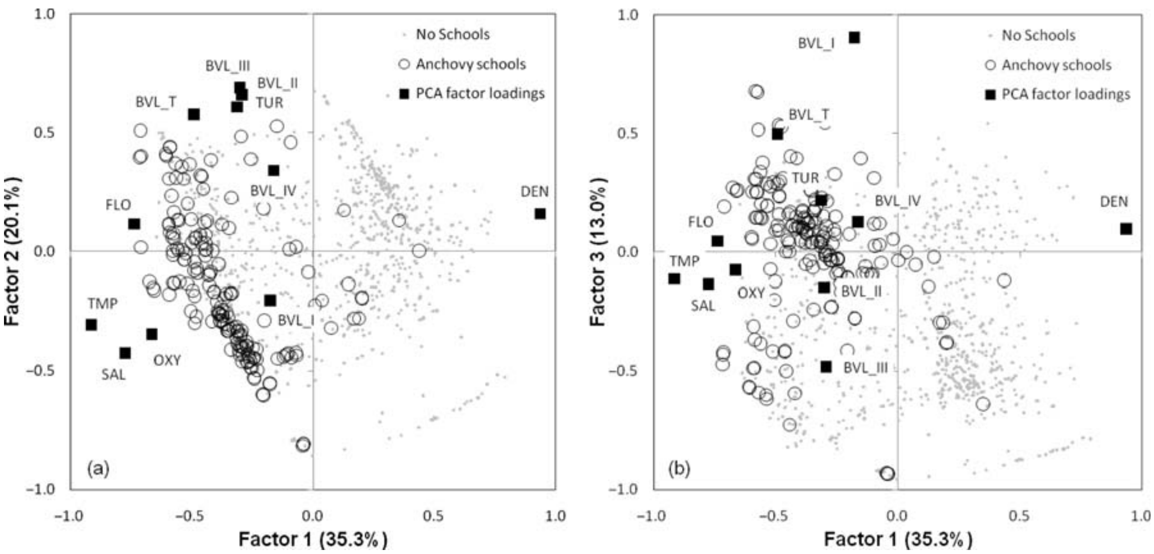

Figure 6. Loadings of the first vs. second (a) and first vs. third (b) factors extracted by the PCA in the presence and absence of anchovy schools for the entire region during daylight.

first factor, and a weak association with BVL_II and BVL_III, and to a lesser extent with BVL_T. A strong association with BVL_I, and to a lesser extent BVL_III, emerges when the third factor is plotted against the first.

Discussion

Horizontal distributions

The food environment on the CAB, west of 23°E, was poor compared with that farther east. Exceptions include a few areas close inshore where upwelling was evident and zooplankton concentrations peaked, despite low levels of chlorophyll *a*.

Relationships with the environment

Strong relationships only emerged once the shelf was split into western and eastern regions. These are clearer on the western side of the CAB. There are marked differences in the thermal structure between these two regions (Boyd and Shillington, 1994), with a deep thermocline, common isothermal conditions, and low productivity in the west, and a consistently strong and shallow thermocline farther east (Barange *et al*., 2005). The eastern part, which has a narrow shelf, is greatly influenced by the very strong Agulhas Current (Boebel *et al*., 2003). For productivity, Koné *et al*. (2005) distinguish enrichment by the shear-edge eddy on the eastern side of the Agulhas Bank (Lutjeharms *et al*., 2003) from a regenerated regime farther to the west.

It is not surprising that correlations between zooplankton and the environment were only found at night, especially when considering chlorophyll *a*, because the daily migrations allow copepods to aggregate in chlorophyll-rich layers. The two ESD classes 0.35–0.8 (II) and 0.8–2 mm (III) are strongly related to the environmental parameters. They exhibit strong diel vertical migratory (DVM) behaviour, which also explains why correlations are not found by day. DVMs are well known, although they are not a uniform phenomenon. Their range depends on the ecological preferences and physiological stages of the organisms (Postel *et al*., 2007); larger animals usually perform greater migrations (Verheye and Field, 1992). Reverse migration patterns were also observed in the southern Benguela (Barange *et al*., 2005), involving copepods descending at night. Cladocerans have also been observed performing erratic or reverse daily migrations (Saito and Hattori, 2000). This type of behaviour may help to explain the downward migration of the smallest size class at night. Consequently, this class appears isolated in the PCA of relationships between zooplankton and environmental parameters.

Fish-school locations vs. zooplankton sizes

Anchovy are size-selective omnivores, capable of ingesting both phytoplankton and zooplankton. They choose the sizes that provide them the highest amount of carbon and, therefore, large zooplankton (>1 mm), i.e. calanoid copepods and euphausiids, are selected if present. However, the smallest particle that can be filtered by anchovy is 200–250 μm, and they switch from filter- to particulate-feeding at a prey-size threshold of 700 μm (Van der Lingen *et al*., 2006a). Based on the current data, anchovy schools are associated with areas of high levels of chlorophyll *a* and usually high concentrations of zooplankton. Strong correlations were observed between schools and Class I, although correlations with Classes II and III were also evident. Stomach contents of anchovy analysed during the survey contained mostly small copepods (*Oithona* and *Oncaea* in particular), even for large anchovy. Because *Calanus* exhibit extensive DVMs, they are less available to anchovy during the daytime, whereas the smaller zooplankton, which have the highest biovolumes, are well-dispersed. The fish may, therefore, effectively be balancing their relatively poor feeding environment during the spawning season against the fact that their location might improve the transport of their eggs and larvae to the west coast nursery area (Huggett *et al*., 2003).

Acknowledgements

The officers and crew of the FRS "Africana" and its management agency (Smit Marine) are acknowledged for their assistance during the survey and for facilitating the import and export of the TAPS-6 to South Africa. We also thank the anonymous reviewers and D. Demer for exhaustive advice, and E. Machu and P. Penven for checking the last version.

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doi:10.1093/icesjms/fsp129