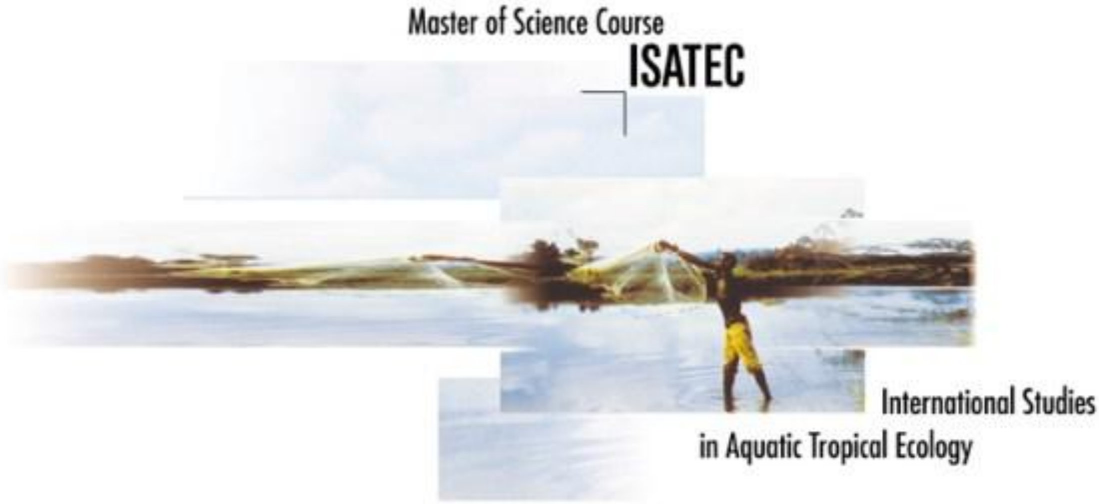

Zooplankton Distribution in the Namibian Upwelling Region:

A comparison of net catches with ADCP measurements

by

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Statement according to § 6 (8) of:

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for the

Master Degree in International Studies in Aquatic Tropical Ecology

I (*Richard R Horaeb*) hereby confirm that I have elaborated my Masters' thesis titled:

Zooplankton Distribution in the Namibian Upwelling Region:

A comparison of net catches with ADCP measurements

single-handed and without using (re)sources other than mentioned therein.

Place and Date

Signature

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List of Acronyms

ABF	Angola-Benguela Front
ABSC	Acoustic Backscatter Cross-section
AWI	Alfred -Wegener - Institute for Polar and Marine Research
BCLME	Benguela Current Large Marine Ecosystem
CTD	Conductivity, Temperature, Depth sensors
DVM	Diel Vertical Migration
OMZ	Oxygen Minimum Zone
MOCNESS	Multiple Opening and Closing Net and Environmental Sensing System
RMT	Rectangular Mid-water Trawl
S_v	Mean Volume Backscattering Strength
TS	Target Strength
(VM) -ADCP	(Vessel Mounted) –Acoustic Doppler Current Profiler

List of Table and Figures

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Dedication

Mona-Lisa and Dantago

Abstract

The distribution of zooplankton biomass and species abundance in relation to biological and physical factors is important in understanding the structure and functioning of marine plankton communities. Zooplankton samples from the Northern Benguela Upwelling region, off Walvis Bay were collected in September 2010 with a 1 m^2 double Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS) and a 150 kHz broadband vessel mounted Acoustic Doppler Current Profiler (VM-ADCP) to examine the temporal distribution and taxonomic composition of mesozooplankton during an upwelling season. The results of the samples collected at discrete depths from the station located at the shelf break during daytime and night-time are presented. Generally, mesozooplankton displayed a bimodal vertical distribution of biomass and abundance, with concentrations in the surface layer (0-80 m) and greater depths (>200 m). This mode of distribution was interpreted to be an apparent attempt to avoid the thermocline and the oxygen minimum zone. The scarcity of zooplankton within the thermocline and the oxygen minimum zone seemed to indicate that the layers act as an effective barrier to zooplankton migrations. The calanoid copepods were the numerically most abundant mesozooplankton. The net catches and ADCP measurements both showed that the zooplankton community performed diel vertical migrations (DVM) that conformed to the classical pattern of ascent at dusk and descent at dawn. Diel vertical migration was one of the factors that were attributed more to the observed distributional patterns of mesozooplankton. Not all mesozooplankton performed vertical migrations, but mesozooplankton in the size range 0.5-2 mm, which composed mainly of calanoid copepods, were responsible for most of the vertical migrations. The net catches and ADCP measurements were compared. The acoustic backscatter cross-section (ABSC) as a measure for biomass generally did not gave significant correlations to mesozooplankton and krill biomass. Although more variation in net catches and ADCP measurements could be account for, the night-time relationship was inverse. This resulted from the mismatch of measurements depths by the instruments, notably in the surface layer. The results from both the net catches and ADCP measurements proved to be a useful combination in providing more insight into the distribution patterns of mesozooplankton on a temporal scale, despite the limitations of the ADCP.

1 Introduction

1 Introduction

Zooplankton are diverse assemblages of animals that drift the waters of the world's oceans. They do not have the ability to move horizontally against the ocean currents and therefore must "go with the flow" (Gibbons 1997). These organisms play a key role in the pelagic food web by controlling phytoplankton production, thus shaping the pelagic ecosystem (Ayon *et al.* 2008).

Zooplankton transfer organic material and energy to higher trophic levels such as the pelagic fish stocks, which are commercially exploited. Since zooplankton organisms play a critical role as a food source for larval and juvenile fish, the dynamics of zooplankton populations, their reproductive cycles, growth, reproduction and survival are all important factors influencing recruitment of fish stocks (Ayon *et al.* 2008). Moreover, the availability of zooplankton of the right size, at the right place and time during the first feeding period of the fish larvae constitute Cushing's (1990) famous match/mismatch hypothesis. The availability of zooplankton, apart from predation is regarded as the most important environmental factor controlling the year class strength of a large number of commercial fish known to be subject to strong environmental fluctuations (Lenz 2000). Therefore, studying zooplankton abundance is important, as it gives important information on the potential feeding conditions and since marine food webs are size based, a slight but sustained change in zooplankton may lead to an alternation of the balance between species of fish or results in subsequent declines (Gibbons 1997).

Zooplankton grazing also determines the amount and composition of the vertical particle flux (Al-Mutairi & Landry 2001, Longhurst *et al.* 1990, Lenz 2000). This contributes to the removal of surplus anthropogenic CO_2 from the atmosphere through sedimentation and burial of organic and inorganic carbon compounds (Hays *et al.* 2001, Lenz 2000).

Zooplankton are classified by a number of ways, among them life-cycle strategy and trophic guild, however they are usually classified by size. This is primarily because organisms of a particular size have common physiological rates irrespective of taxon and marine pelagic food webs are essentially size base, whereby by big organisms normally eat smaller organisms (Gibbons 1997). Furthermore, size determines the sampling methodology of zooplankton. The four metazooplankton size classes according to Sieburth *et al.* (1978) are: micro-zooplankton (2-200µm), meso-zooplankton (200µm-2mm), macro-zooplankton (2-20mm) and mega-zooplankton (>20mm).

The distribution of planktonic organisms is largely controlled by the physical and chemical regimes of the oceans, whereas other ecological factors, such as trophic status may be important as well; the diversity, behaviour, ecological significance and interaction of zooplankton with other organisms will also determine their distribution (Lalli & Parsons 2002). However, the biological and oceanographic features associated with zooplankton dynamics occur over a continuum of time and space scales, and various processes are interlinked, thus it is not possible to know the actual distribution of zooplankton. Therefore, limitations in understanding and predicting plankton distributions in highly dynamic regions, such as the Benguela, arise from a mismatch between the scales at which the biological and physical measurements are routinely made (Skjoldal *et al.* 2000, Albaina & Irigoien 2007). Most of the information on zooplankton is derived from sampling by conventional net catches, notwithstanding the low spatial and temporal resolution of most sampling programs. Therefore, studies on zooplankton dynamics need a collaborative efforts from physical, biological, chemical and fisheries disciplines (Lenz 2000).

1.1 Zooplankton patchiness

Zooplankton biomass in the oceans is not evenly distributed, as distinct horizontal and vertical gradients exist in the water column (Dower & Brodeur 2004). Patches, density gradients, aggregations, swarms and layers all refer to zooplankton distribution. Patches are loosely described as regions of higher zooplankton abundance often composed of several taxa (Folt & Burns 1999). Zooplankton patch dynamics require an understanding of the way in which physical and biological drivers influence aggregations on a spatial scale. The four often most cited biological drivers of zooplankton patchiness are: diel vertical migration (DVM), predator avoidance, finding food and mating, with evidence suggesting that these drivers alone or in combination drive spatial heterogeneity in numerous situations (Folt & Burns 1999).

Zooplankton patchiness is further important as it has important implications in zooplankton experimental design and sampling in open oceans. For example, the key design issue concerns the temporal and spatial scales at which the dominant processes are operating and the subsequent interactions between processes occurring at different scales, which may bias or alter the direct effects being studied (Skjoldal *et al.* 2000).

1.2 Diel vertical migration (DVM)

Diel vertical migration is a well observed and studied phenomenon of zooplankton dynamics. It is the tendency of plankton to swim upwards and downwards at certain times during the 24 hour day. It is one of the widespread and powerful biological causes of patchiness. Advective processes together with DVM control large-scale spatial and temporal dynamics of many zooplankton species in marine systems (Folt & Burns 1999). The various causes of vertical migration of zooplankton and the effect of the governing biotic and abiotic factors have been proposed but no single theory explains all migrations.

Light is regarded as an important trigger, however, trophic relations must also be considered. The search for food, predator avoidance and metabolic advantages are all considered to play a role in DVM of many zooplankton (Buchholz 1995, Cornet & Gili 1993).

Other studies have demonstrated that physical and chemical characteristics of the water column may influence the behavior of migratory species. Buchholz *et al.* (1995) found that krill did not cross a temperature barrier of 14 °C, although rich food sources were situated beyond it, whereas salinity did not have an influence. Auel and Verheye (2007) raised the question of whether the oxygen minimum zone (OMZ) represents an effective barrier for zooplankton migration. They found that abundances of calanoid copepods were higher at the surface and below 300 m than in the centre of OMZ. Therefore, seasonal, as well as vertical changes in temperature, salinity and oxygen also affect migrations and distribution of zooplankton (Cornet & Gili 1993, Auel & Verheye 2007).

DVM is assumed to be important in the rapid export of carbon and nitrogen by “active” diel migrant zooplankton from the surface layers to deeper layers (Al-mutairi & Landry 2001), though assessing the contribution of migrating zooplankton to export fluxes from the upper ocean involves many assumptions about capture efficiencies, depth distribution and feeding habits of migrant population (Zhang & Dam 1997).

Since zooplankton constitute a central component of marine ecosystems, the knowledge of variability in zooplankton biomass is important for understanding the effects climate change may have on marine ecosystems (Jiang *et al.* 2007). High resolution measurements of zooplankton biomass on diel, seasonal and inter-annual time scales can help to constrain both the effects of climate change and shorter term physical effects on zooplankton communities and the influence of zooplankton on carbon and nutrient cycling in the sea (Jiang *et al.* 2007).

However, zooplankton net sampling and the analysis of the samples is a time consuming task and ship time restrictions often limit the vertical coverage during deep sea studies, and this may subsequently result in sampling effects (Postel *et al*. 2007).

Conventional net sampling represents a compromise and pose a methodological problem due to the patchy distribution of plankton, therefore integration of different approaches in ecological studies characterizes current efforts to understand the structure and dynamics of zooplankton population in world's oceans (Skjoldal *et al.* 2000). Furthermore, various methods of sampling and analyzing zooplankton have different strengths and weaknesses, thus it seems appropriate to combine the different methods to obtain a broader and more representative results.

Hence, different methods and approaches have been developed over the years to study zooplankton and analyze samples from net catches. The visible light optical contrast is employed, apart from light microscopy, in silhouette photography, optical counting and video recording of plankton organisms, both *in situ* and *ex situ* (Benfield *et al.* 1998, Foote 2000, Baumgartner 2003). More recently, automatic identification methods of plankton have been developed. The so-called image analysis technique use by ZOOSCAN and the software ZooImage, is used to analyze large samples of net zooplankton samples, extracting biomass, abundance and size spectra data in the process (Grosjean *et al*. 2004, Teuber 2009).

1.3 Fisheries acoustics

Another approach used in zooplankton studies is fisheries acoustics. Fisheries acoustics is a potential significant application in zooplankton studies, but has a limited history of application partly due to its relative newness and the complexity of the sampling tool (Foote & Stanton 2000). Furthermore, data reduction and analysis are complex, making acoustical studies expensive and difficult to carry out, while the nature of the acoustical data sometimes precludes dynamical analyses of ecological interest (Flagg & Smith 1989), meaning that processes such as feeding, growth, respiration and predator-prey interactions cannot be studied.

1.3.1 Acoustic Doppler Current Profilers (ADCPs)

The development of the Acoustic Doppler Current Profilers (ADCPs) has provided a new window of opportunity for estimating zooplankton biomass. ADCPs are being used for physical current measurements and thus provide enhanced opportunities to study zooplankton via the recording of acoustic backscatter data (Jiang *et al.* 2007). The vertical and temporal resolution of the ADCPs is excellent and provides biological oceanographers with data on the same time and space scales as the physical data and enables climatic studies with continuous measurements. Therefore, the relationship between acoustic backscatter intensity derived from ADCPs and zooplankton biomass from net-collected zooplankton samples provide a powerful tool to describe variability in the distribution of zooplankton biomass and zooplankton migration (Jiang *et al.* 2007).

ADCPs have been deployed in a number of ways: mounted on a mooring (bottom mounted or on floating platforms), vessel mounted or lowered along with other sampling packages such as the CTD probe system. Mounted on moorings, ADCPs can be deployed and left untended for long periods of time on moorings, thus it is possible to obtain time series data on zooplankton dynamics without constant attendance, tedious net hauls and without invading and destructive sampling in the water column (Roe & Griffiths 1993). In shipboard application, ADCPs can guide sampling schemes through real-time data display of zooplankton abundance, thus the exact location of zooplankton patches would facilitate direct net sampling (Flagg & Smith 1989). ADCPs have also enabled to study other important features such as DVM (Buchholz *et al.* 1995, Heywood 1996, Cisewski *et al.* 2010) and biomass estimation (Ressler 2002, Postel *et al.* 2007).

An ADCP is essentially an echo sounder that uses the Doppler effect by transmitting sound at a fixed frequency and “listening” to the echoes returning from the sound scatterers in the water column (Foote & Stanton 2000, RD Instruments 2006). The scatterers are small particles or plankton that reflect the sound (i.e. Doppler shifted sound) back to the ADCP. In the open ocean, these particles will be mainly zooplankton and micronekton. The key assumption is that the scatterers float or move at the same average horizontal velocity as the water currents (RD Instruments 2006), thus ADCPs are able to deduce current speed. The measure of the signal strength of the echo returning from the ADCP transmit pulse, called the echo intensity is used to estimate the concentration of zooplankton abundance.

However, there are some important factors that need careful consideration and interpretation when using the backscatter data. Relating the intensity of an echo to the scatterers in the water requires knowledge of several variables: the power transmitted into the water, the acoustic characteristics of the transducer and the resulting acoustic beam, the power attenuation caused by propagating losses (including absorption and beam spreading), and the properties of the receivers (Deines 1999). Acoustic properties varies with size, shape, orientation and physiology of an organism (Chu *et al.* 1992). Scattering by organisms is often empirically derived through measurements and physics-mathematics based models (Foote and Stanton 2000). However, the description of scattering is quite difficult as the body of each animal does not resemble a simple shape like a sphere but rather a complex shape that cannot be easily described by a mathematical function (Chu *et al.* 1992). Moreover, vessel or bottom mounted ADCPs have a restricted vertical coverage because absorption of sound by seawater causes an unfavorable signal to noise ratio with increasing distance from the transducer (Postel *et al.* 2007).

In view of the above, a direct comparison between the commonly used acoustical scattering quantities (Maclennan 2002), such as the mean volume backscattering strength (S_v) or the relative acoustic backscatter cross-section (ABSC), derived from a known target strength (TS) and net collected zooplankton biomass is difficult for a diverse zooplankton community (Fielding *et al.* 2004). However, the S_v and ABSC from the ADCP data has been well correlated with bulk zooplankton biomass in a number of studies (Flagg & Smith 1989, Roe & Griffiths 1993, Buchholz *et al.* 1995, Ressler 2002, Postel *et al.* 2007). For details on the calculation of S_v, see Deines (1999), Postel *et al.* (2007) and Jiang *et al.* (2007).

The acoustic estimates of zooplankton biomass rely on the assumption that S_v or ABSC measured in the ocean at frequencies on the order of 10^2 kHz are primarily due to zooplankton and micro-nekton targets. The size of the animals that will contribute most to the backscatter will depend on the frequency used. For example, a frequency of 150 kHz has a wavelength of 10 mm and animals which will most likely contribute to backscatter at this frequency will be euphausids, amphipods and possibly large copepods (Roe & Griffiths 1993). The latter authors also called attention to the differences in sampling volumes of the net and the ADCP. Therefore, knowing the dominant biological scatterers in the water column is useful in interpreting mean volume backscattering strength or the relative acoustic backscatter cross-section measurements.

It should be noted that the S_v or ABSC measurements from ADCPs do not represent the state of the art of zooplankton acoustics technology (Ressler 2002), but with careful consideration of relevant aspects and supported by careful calibration procedures, ADCPs are capable of collecting data on zooplankton in a way that was previously difficult, if not impossible to obtain.

1.4 Purpose of the study

The main purpose of this study was to examine the temporal variability of mesozooplankton distribution in the Upwelling region off Namibia through the comparison of net catches with acoustic measurements. This would provide a more informed and potentially more insightful interpretation of the distributional patterns of mesozooplankton on a temporal scale.

Zooplankton sampling in the northern Benguela current region off Namibia has been conducted on semi-routine basis, almost exclusively by net catches since the 1950’s, with varying spatio-temporal coverage (Hansen *et al.* 2005). It is the objective of this study to:

- Describe temporal (day/night) zooplankton distribution through net catches and VM-ADCP measurements
- Examine temporal variability of acoustically estimated zooplankton biomass and compare with net sampling
- Describe diel vertical migration of different mesozooplankton groups

2 Materials and Methods

2 Materials and Methods

2.1 Study area

The Benguela Upwelling region is situated along the coast of south western Africa from the east of the Cape of Good Hope in the south, to northwards into the Angolan waters, encompassing the full extent of Namibia’s marine environment (*Fig. 2.1*). It extends from 34°S 26°E (near Port Elizabeth) to 5°S 12°E of Cabinda in Angola (Hutchings *et al*. 2009). Together with the Humboldt, California and Canary upwelling systems, the Benguela upwelling system belongs to the four major upwelling systems located in the eastern boundary current zones of the oceans, which are important centers of marine biodiversity and marine food production. It is one of the major upwelling systems of the world which lie at the eastern boundaries of the world. It comprises of cool upwelled water induced by strong south-easterly trade winds that cause a strong offshore Ekman transport of surface water masses, resulting in a north to north-westward flow of the current along the coast (Nelson & Hutchings 1983).

Its distinctive bathymetry, hydrogaphy, chemistry and trophodynamics combined, make it to one of the most productive ocean areas in the world, with a mean annual primary productivity of 1.25 kg Cm^2 yr^{-1}, approximately six times higher than the North Sea ecosystem (Shannon & O'Toole 2003, Wasmund *et al.* 2005). The Benguela upwelling is unique in the global context that it is bounded in the north and south by warm currents, namely the equatorial eastern Atlantic and the Indian Ocean’s Agulhas current and its retroflection. The principal and perennial upwelling centre which is located near Lüderitz (27°) is the most intense found in any upwelling regime (Duncombe Rae 2005), and forms a natural internal barrier within the Benguela, with domains to the north and south functioning differently (Shannon & O'Toole 2003).

The southern Benguela is demarcated from the vicinity of the Orange river mouth (ca. 29°S) southwards along the west coast and eastward to 28°E (around East London), whereas the northern Benguela (focus of this study) extends from the vicinity of the Orange river mouth to the northern boundary of Angola (Nelson & Hutchings 1983). The northern Benguela shelf is a typical upwelling system with equator-ward winds, cool water, high plankton biomass and moderate to high fish biomass. The southern Benguela region is characterized by pulsed, seasonal and wind driven upwelling events at discrete centers and warm Agulhas water offshore. High primary productivity forms a belt of enrichment along the coast, constraint by a front (Hutchings *et al*. 2009).

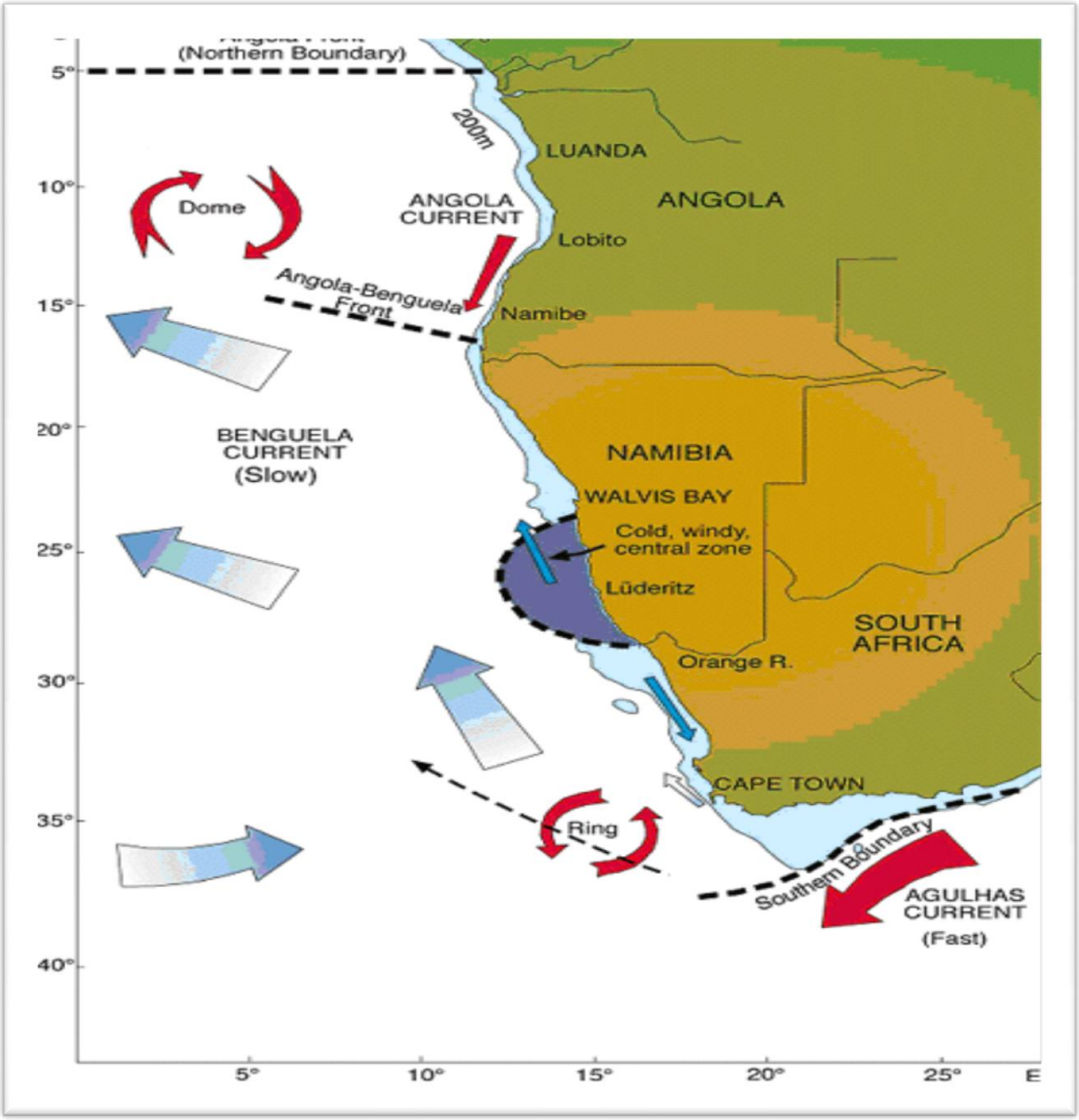


Fig. 2.1 The external and internal boundaries of the Benguela large marine ecosystem, bathymetric features and surface currents (Adapted from www.bclme.org)

Pronounced fronts exist at the boundaries of the Benguela upwelling system. The Agulhas current front at the southern boundary between 32°-37° S and the Angola-Benguela Front (ABF) zone in the north. The ABF convergence zone is formed when the cool equator-ward flowing Benguela current meets the warm tropical pole-ward flowing Angola current (Shillington *et al.* 2006). The fronts display a substantial spatial and temporal variability, depending on the strength of the two adjacent current systems, whereas the frontal zones are characterized by marked changes in temperature and salinity due to the character of the different water masses (Mohrholz *et al.* 2008).

The Benguela Current Large Marine Ecosystem (BCLME) also interacts with adjacent water systems over a large scale. There are tele-connections between the Benguela and the processes in the North Atlantic and Indo-Pacific (Shannon & O'Toole 2003). Moreover, episodic events in the northern Benguela system exist, whereby warm and highly saline nutrient poor waters from Angola intrude deep into the northern Benguela, resulting in a decrease of upwelling intensities and a south-ward shift of the ABF. The waters become anomalously warm as a consequence of a sudden relaxation of the trade winds, the thermocline deepens and the heat loss from the ocean to the atmosphere is reduced (Shannon & O'Toole 2003, Shillington *et al.* 2006).

These episodic events in the Benguela have been dubbed “*Benguela Niño’s*” as an analogue to the Pacific event, the *El Niño* and have a strong effect on the variability of the system and the regional fisheries (Shillington *et al.* 2006). Overall, the Benguela upwelling system is a highly variable ecosystem, therefore understanding the variability of plankton over time scales ranging from meso-scale upwelling events of a few days duration to decadal scale changes is important in the forecasting and modeling of the region’s dynamics (Hutchings *et al.* 2006)

2.2 Sampling

During the second leg of *RRS Discovery* cruise (D356) from the 10th September to 13th October 2010, a 36 hour study was undertaken at 23° S 13° E (marked by a cross) in the vicinity of the Walvis Bay monitoring transect (Fig 2.2). Two hauls were taken at this station, one during the day and one during the night, down to a maximum depth of 350 m, just about 40 m above bottom.

Fig. 2.2 Map of the Namibian coast, showing the monitoring line at 23 °S off Walvis Bay and the sampling station, marked with a cross (modified after Hansen *et al*. 2005).

2.3 Mesozooplankton sampling and sample analysis

Mesozooplankton were sampled by oblique hauls, at an average ship's speed of two knots, with the use of 1 m^2 Double Multiple Opening and Closing Net and Environmental Sensing System, MOCNESS (Wiebe *et al.* 1985). The MOCNESS was equipped with 18 nets (9×9, side by side) of 333 µm mesh aperture, thus two samples per depth layer were obtained in a single deployment. The nets are opened and closed sequentially by commands transmitted from the surface deck unit through a single conducting cable to the underwater unit, enabling the sampling of zooplankton at discrete depths interval during a single deployment from 0-25, 25-50, 50-100, 100-150, 150-200, 200-250, 250-300 m. During daytime, the 300-350 m layer was additionally sampled (Table 2.1). The procedure was to lower the MOCNESS down to the maximum sampling depth, and then the nets were opened one at a time as the MOCNESS was hauled toward the surface. The mean depths of the sampling intervals were used in the computations.

The flow velocities and the volume of water filtered per the net were measured by a flow-meter mounted at the frame (Table 2.1). The device carries CTD (Conductivity, Temperature, and Depth) sensors to collect the environmental data at the same time. The central data collection and distribution system of the ship enable it to follow both the ships speed (~ 2 knots) and winch velocity (~ 0.5 m^{-1}) through the water column in real time.

Upon the recovery of MOCNESS onboard the ship, the nets were carefully rinsed with seawater to ensure all contents were moved into the cod-end. The nets were raised vertically and hold in position while washing with seawater from the outside of the net. Then the cod-end was detached to pass the sample into an appropriate sample container for further treatment. Half of the samples (9) were preserved in 4% formaldehyde-seawater solution buffered with sodium tetraborate (Steedman 1976, Gifford & Caron 2000) for biomass and taxonomic analysis for this study and the other half were deep frozen for other studies.

The first net sample, usually the integrated sample over the depth was discarded. All the samples were properly labeled, recorded and stored away for land based laboratory analysis.

Table 1.1 Station data for the sampling period. The local time (UTC +2) denotes the opening time of the nets.

Date	**Lat. (°S)**	**Long. (°E)**	**Day/ Night**	**Local time**	**Haul**	**Bucket**	**Sampled depth(m)**	**Volume (m^3)**
07.10.10	23°00‘10	13°03‘17	**Night**	23:10	MOC-D-24	L2	300-250	303.5
07.10.10	23°00‘16	13°03‘20	**Night**	23:13	MOC-D-24	L3	250-200	194.3
07.10.10	23°00‘19	13°03‘21	**Night**	23:15	MOC-D-24	L4	200-150	130.9
07.10.10	23°00‘24	13°03‘23	**Night**	23:16	MOC-D-24	L5	150-100	118.4
07.10.10	23°00‘35	13°03‘29	**Night**	23:22	MOC-D-24	L6	100-50	381.9
07.10.10	23°00‘37	13°03‘30	**Night**	23:24	MOC-D-24	L7	50-25	65.5
07.10.10	23°00‘40	13°03‘31	**Night**	23:26	MOC-D-24	L8	25-0	131.2
08.10.10	23°00‘37	13°03‘16	Day	11:17	MOC-D-25	L2	350-300	197.3
08.10.10	23°00‘43	13°03‘19	Day	11:20	MOC-D-25	L3	300-250	179.3
08.10.10	23°00‘48	13°03‘22	Day	11:22	MOC-D-25	L4	250-200	164
08.10.10	23°00‘54	13°03‘24	Day	11:25	MOC-D-25	L5	200-150	152.8
08.10.10	23°01‘00	13°03‘27	Day	11:28	MOC-D-25	L6	150-100	218
08.10.10	23°01‘07	13°03‘30	Day	11:32	MOC-D-25	L7	100-50	211.7
08.10.10	23°01‘09	13°03‘31	Day	11:33	MOC-D-25	L8	50-25	65.1
08.10.10	23°01‘13	13°03‘33	Day	11:36	MOC-D-25	L9	25-0	150.3

2.4 Biomass and taxonomic analysis

2.4.1 Biomass determination

In the land-based laboratory, the preserved zooplankton samples were sieved in size fractions of <0.5, 0.5-1, 1-2, 2-5 and >5 mm. After placing each size class fraction in 70% ethanol (ethanol is volatile and aid in the removal of excess and interstitial water in the sample) for about 30 seconds and drying it on a tissue paper, each sample was weighed on a analytical balance to obtain the wet mass. Wet mass was used as a measure of biomass rather than the precise dry mass to allow further taxonomic analysis of the whole sample. After measuring the wet mass, the samples were preserved in a sorting fluid, which is composed of 0.5% propylene-phenoxetol, 5.0% propylene-glycol and 94.5% freshwater (Steedman 1976).

Since the mesh size of 330 µm of the MOCNESS is known to quantitatively sample plankton in the size range of <5 mm (Wiebe *et al.*1985), the size class fraction >5 mm was very variable and generally excluded from the calculations of biomass and abundance values, however, where it is included will be stated.

2.4.2 Taxonomic analysis

After the biomass determination, the fractionated zooplankton size classes were sorted into taxonomic groups and counted under a stereomicroscope. Bogorov trays of suitable sizes were used during the counting. Samples that were highly concentrated and rich in plankton often required sub-sampling and splitting in the whirling vessel sub-sampler (Zo 1977). The sample was emptied into the apparatus and mixed by spinning the cylinder by hand gently and allowing it to settle in the aliquot compartments (10) at the bottom of the cylinder. The sample was split into ten equal parts and 1 to 4 sub-samples, but mostly 2 sub-samples were taken for effective enumeration. Taxonomic determination was performed down to the main groups, usually order, whereas the order Copepoda was further sorted into sub-orders:

Calanoida, Cyclopoida and Harpacticoida. The exuviae and carcasses discriminated according to Wheeler (1967) and Weikert (1977) were enumerated but were not included in the final count. Although, Siphonophores and Chaetognaths are suppose to belong to the size class fraction >5 mm, they often ended up in smaller size class fractions due to the morphology, thus they were included in the count of those size class fractions. Identification was carried out using mainly literature from the Benguela region (Gibbons 1997) and South Atlantic in general (Boltovskoy 1999).

2.5 Vessel Mounted Acoustic Doppler Current Profiler (VM-ADCP)

The vessel mounted 150 kHz broadband ADCP (RD Instruments) mounted on the ship's hull in a downward looking position was used to obtain a full-depth current and acoustic backscatter signal from the 4-9th October 2010, with an acoustic backscattering average of 60 seconds. The vertical resolutions of the measurements were 16 m, which corresponded to the one vertical depth cell or "bin". The primary interest was the acoustic backscatter signal from the ADCP for estimating zooplankton biomass. The data output from the VM-ADCP was recorded by the central collection system of the ship and later process by the physical oceanographers. For the purpose of this study, the relative Acoustic Backscatter Cross-Section (ABCS), which is derived from known target strength (TS) and thought to be equivalent to zooplankton biomass was used in conjunction with parallel net catches to study the distribution patterns of zooplankton biomass and abundance, without going into details of ADCP data processing.

Parallel net catches with the MOCNESS were done on the 7th and 8th October, while ADCP measurements were recorded continuously during the same period. The ADCP measurements started only from 37 m since the upper surface layers are often affected by anomalous high backscatter signal due to turbulence created by the ship and the possibility of the ADCP not being able to detect the scatterers in the surface layers due to the depth at which the ADCP is mounted and the blank after transmit range (Heywood 1996, Postel *et al.* 2007).

2.6 Krill biomass estimate

Since krill are greater than 5 mm in length and slightly larger, they are capable of avoiding the MOCNESS, thus very few are retained in the net. They are also known to be strong scatterers to the 150 kHz ADCP. As they are not the focus of this study, their onboard biomass estimate is used to correlate with relative ABSC from the ADCP. The target species were *Euphausia hanseni* and *Nematosclesis megalops*, which display different migratory behavior. *Euphausia hanseni* is known to display extensive well defined migrations, whereas *N. megalops* does not display much migration and remain mostly deeper depths (Prof. Buchholz, AWI, pers. comm.).

The krill were sampled with a 1 m^2 single-MOCNESS, with a mesh size aperture of 2 mm and 9 nets. Sampling followed standard MOCNESS protocol described for mesozooplankton. Sampling depths and intervals were the same as for the double MOCNESS. Onboard the vessel, an estimate count of each species was obtained (courtesy of Prof. Buchholz). Sampling was done every six hours, starting at dusk on the 7th Oct' and ending at dusk 8th Oct'2011.

2.7 Data Analysis

2.7.1 Biomass

The biomass data for each size class fraction were standardized to volume (1000 m^3) by applying the following formula:

$$\textbf{Biomass (mg. 1000 m}^{-3}\textbf{)} = \frac{\text{Biomass} \times 1000}{\text{Volume filtered}}$$

The biomass of the total sample was not weighed but only the biomass of the different size class fractions. The standing stock biomass for each depth layer was then calculated by using the formula below:

$$\textbf{\textit{Biomass (mg. m}}^{-2}\textbf{\textit{)}} = \frac{\textit{Biomass} \times \textit{depth interval}}{\textit{Volume filtered}}$$

2.7.2 Abundance determination

The abundance data for the main taxonomic groups were calculated by applying the following formula:

$$\textbf{\textit{Abundance (Ind.1000m}}^{-3}\textbf{\textit{)}} = \frac{\textit{(No. of Individuals} \times \textit{Splitting factor) 1000}}{\textit{Volume filtered}}$$

The multiplication by 1000 was applied to standardize to volume of 1000 m^3. The term “Splitting factor” was only included for those rich samples that were sub-sampled. If the sample was split into ten equal parts and only two sub-samples of the ten were used in the enumeration, then the number of individuals counted in the two sub-samples was multiplied by the splitting factor (8/10, i.e. multiplied by five in this case).

The standing stock abundance per depth layer was calculated using the formula:

$$\textbf{\textit{Abundance (Ind. m}}^{-2}\textbf{\textit{)}} = \frac{\textit{Abundance} \times \textit{depth interval}}{\textit{Volume filtered}}$$

2.7.3 Vessel mounted – Acoustic Doppler Current Profiler biomass estimate

The relative backscattering cross-section in m^2 was calculated from the recorded target strength after Maclennan (2002) according to the following formula:

$$\boldsymbol{\sigma_{bs}} = [r^2 I_{bs}(r)\, 10^{\alpha r/10} / I_{inc}]$$

where σ_{bs} is the backscattering cross-section (m^2), r is the distance of the measurement position from a small target, $I_{bs}(r)$ is the intensity of the backscattered wave, α is the acoustic absorption coefficient and I_{inc} is the intensity of the transmitted or incident wave at the target.

2.7.4 VM-ADCP derived relative ABSC vs. net mesozooplankton concentration

The biomass values were calculated as relative ABSC in m^2 m^{-3}. Only the relative ABSC data that cover the time period of net deployment were used. The ABCS data were average for each ADCP depth measurement from (37 - 325 m). Each depth layer had seven and eight data point measurements during the day and night respectively. Then the ADCP results were average for the net sampling depth layers (25-50, 50-100, 100-150, 150-200, 200-250, 250-300 and 300-350m).

Next a correlation was carried out between relative ABSC and biomass of each size class. Then the standing stock biomass from 0 to 300 m in m^2 was used to correlate with the relative ABSC during the day and night. In each correlation, a linear regression model with relative ABSC as an independent variable and net biomass as a dependent variable was used and the coefficient of determination (r^2) determined.

2.7.5 VM-ADCP vs. onboard Krill biomass estimates

Since biomass was of interest to the study, the length-mass relationship was used to convert the number of krill to biomass values by applying the formula below:

$$Y = 7.08 * \exp^{(0.1102*X)}$$

The mean length used for *E. hanseni* was 18.7 mm ±1.3 mm and for *N. megalops* was 24.7 mm ±4.1 mm (Prof. Buchholz, AWI).

Next, a correlation between relative ABSC and biomass estimates at different sampling times for each species was carried out. In each correlation, a linear regression model with relative ABSC as an independent variable and net biomass as a dependent variable was used and the coefficient of determination (r^2) determined.

3 Results

3 Results

3.1 Hydrography

The hydrographical data show a triple layered stratified water column both in temperature and salinity distribution (Fig 3.1 and 3.2). The surface layer extends from the surface to ca. 75 m, with a maximum temperature of 15.5 °C and salinity of 35.2 psu during the day. There seems to be no substantial change in temperature and salinity profiles during day and night-time, though the night-time profiles are slightly higher. The surface temperature during the day extends a little deeper to about 60 m before it starts to decline, whereas night temperatures start to decrease from about 20 m. The second intermediary layer extends from about 70 m down to about 240 m, where temperature decreases to about 10 °C, accompanied by salinity decrease to 34.85 psu. In the deeper layer below 240 m, temperature and salinity were constantly near 9.5 °C and 34.8 psu respectively. Salinity seems to stabilize from 240 m downwards.

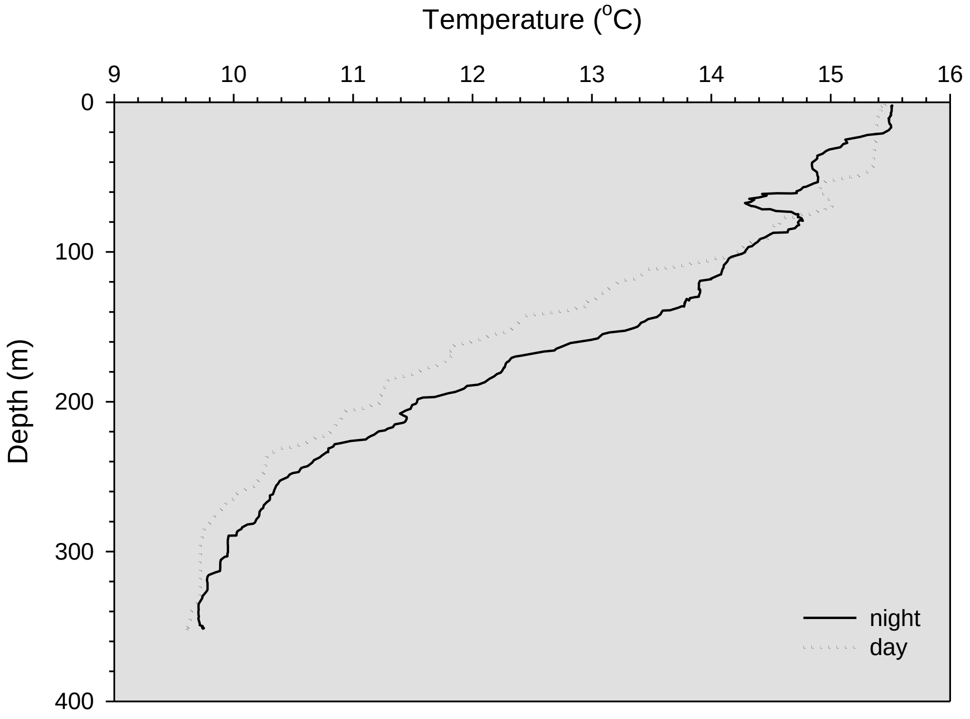


Fig. 3.1 Vertical distribution of temperature at the sampling site

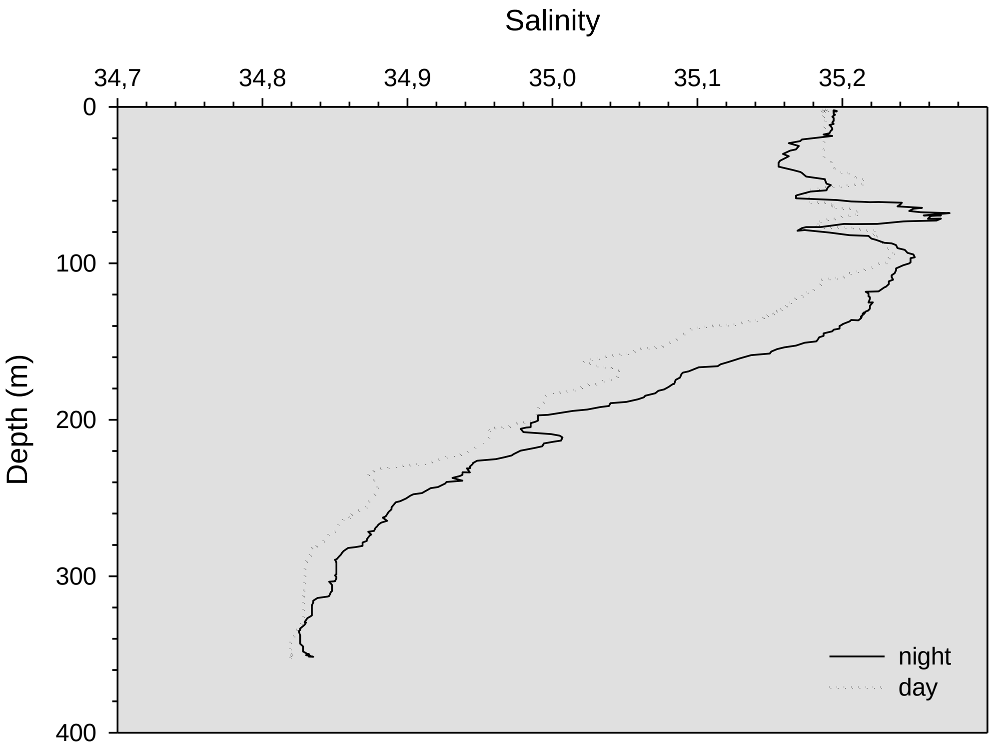


Fig. 3.2 Vertical distribution of salinity at the sampling site

3.2 Mesozooplankton biomass and abundance

Generally, total biomass and abundance seem to be highly concentrated in two layers, both during the day and night, although biomass and abundance are higher during the night by an order of a magnitude. The same patterns are exhibited by the different size class fractions. For biomass (Fig. 3.3) at the surface layer (ca. 0-80 m), the total biomass values range from a maximum of 53 056 mg.1000 m^{-3} (night at 12.5 m) and 36 373 mg.1000 m^{-3} (day at 12.5 m) to 27 437 (night, 37.5 m) and 9 839 mg.1000 m^{-3} (75 m). Between 50 and 200 m, the total biomass values are at lowest. Below 200 m, the total biomass values increase again, reaching a maximum of 126 142 mg.1000 m^{-3} during the day at the deepest depth (325 m) and 26 283 mg.1000 m^{-3} (275 m) during the night.

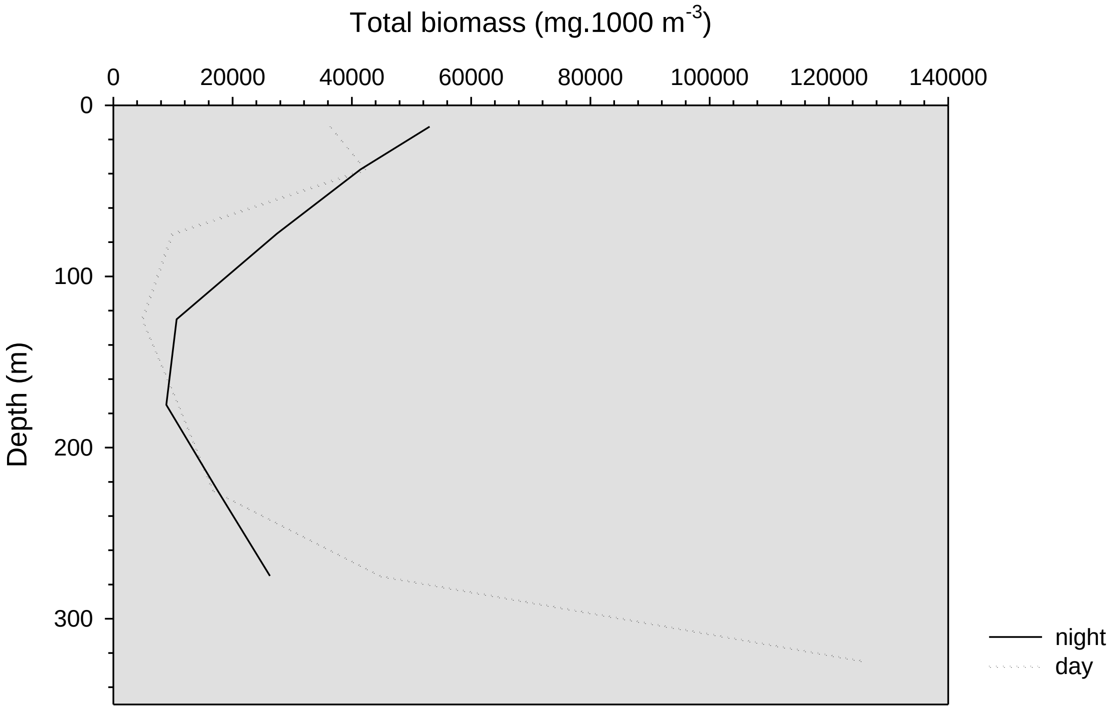


Fig. 3.3 Vertical distribution of total biomass over the water column

The different size classes (Fig. 3.4), exhibit the same pattern as described above, whereby the biomass is generally concentrated in the surface layer and the deeper layer below the intermediate layer. The smallest size fraction is the only size class fraction that seem to show a constantly low biomass values throughout the water column both during day and night-time. During the day, the size class 2-5 mm reached a much higher value (24 593 mg.1000 m^{-3}) than during the night (4 870 mg.1000 m^{-3}) at the depth of 37.5 m. The size class 1-2 mm recorded the highest biomass of 36 501 mg.1000 m^{-3} during the night. Generally, the biomass is much higher in the deeper layers (>200 m) during the day, whereas the biomass increases in the surface layers (0-80 m), during the night.

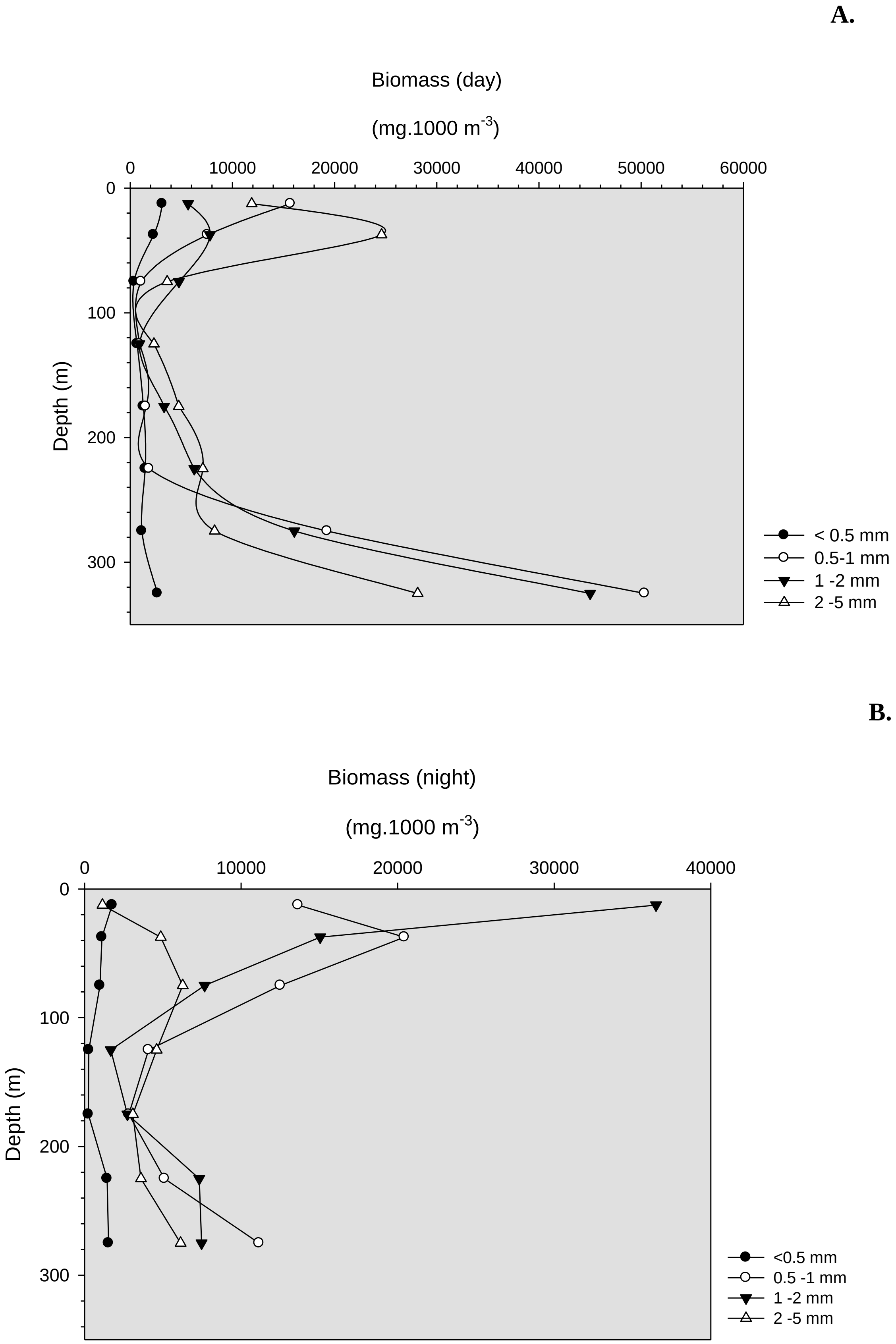
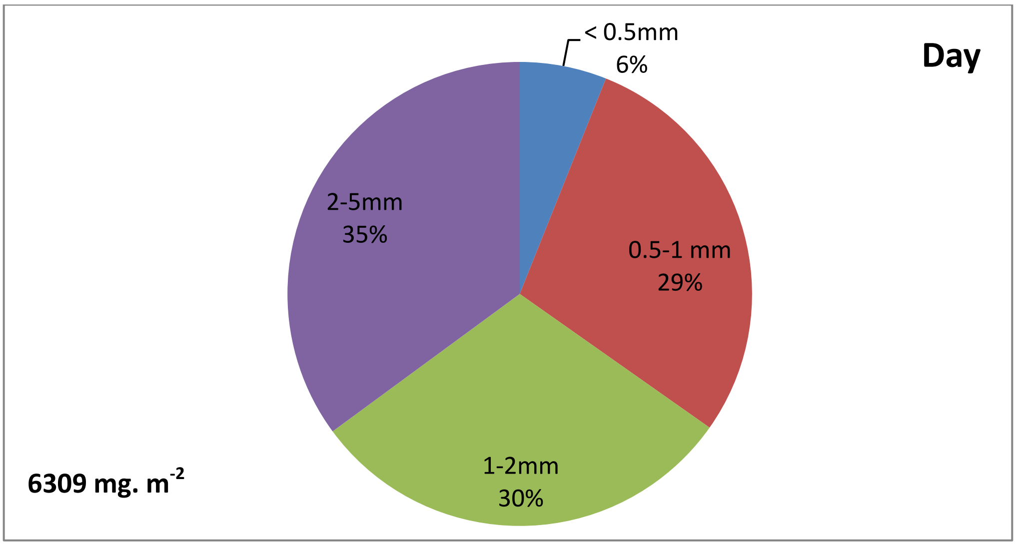


Fig. 3.4 Vertical biomass size class distribution, day (**A**) and night (**B**)

Looking at the biomass standing stock of different size classes integrated over the 300 m water column (Fig. 3.5 A-B), size class <0.5 mm made up 6% of the total standing stock during the day and 4% during the night. The relative abundances of size the classes 0.5-1 and 1-2 mm are high during the night (~38%) and low during daytime (30%). During daytime the 2-5 mm fraction is more abundant.

A.



B.

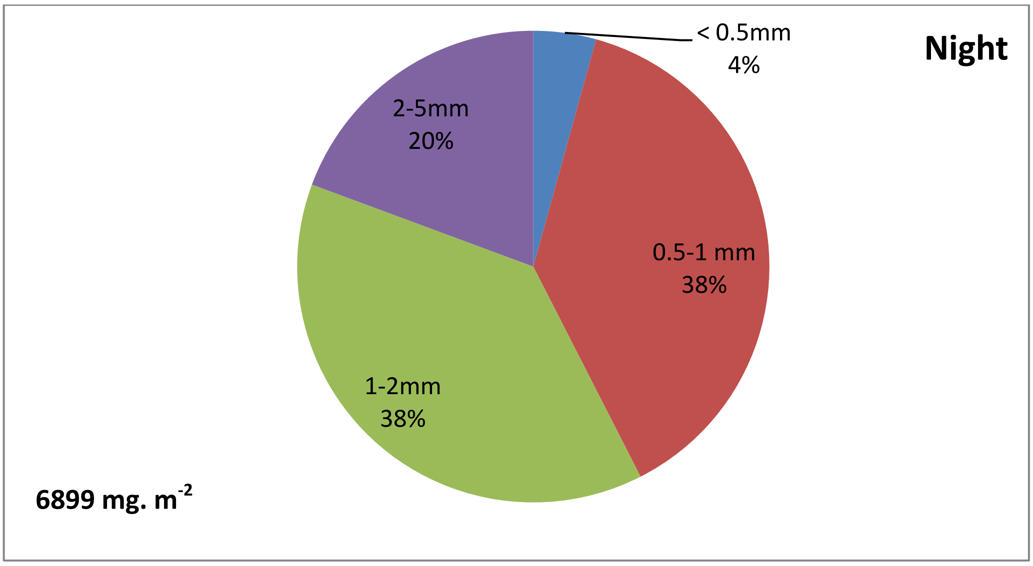


Fig. 3.5 Standing stock biomass of mesozooplankton size classes (0-300 m), day (**A**) and night (**B**)

In terms of the total mesozooplankton abundance distribution (Fig 3.6), maxima appeared in two layers, one above and one below the thermocline. Mesozooplankton abundance is much higher at the surface layers during the night (292 721 Ind.1000 m^{-3} at 12.5 m) than during the day (17 013 Ind.1000 m^{-3} at 12.5 m). The abundance in the discontinuity layer (ca. 50-200 m) drops below 30 000 Ind.1000 m^{-3} both during the day and night. Below the thermocline, the abundance increases again, recording 172 895 Ind.1000 m^{-3} (275 m, day) and 16 233 Ind.1000 m^{-3} (275 m, night). At greater depths, the abundance continues to increase up to 320 705 Ind. 1000 m^{-3} during the daytime.

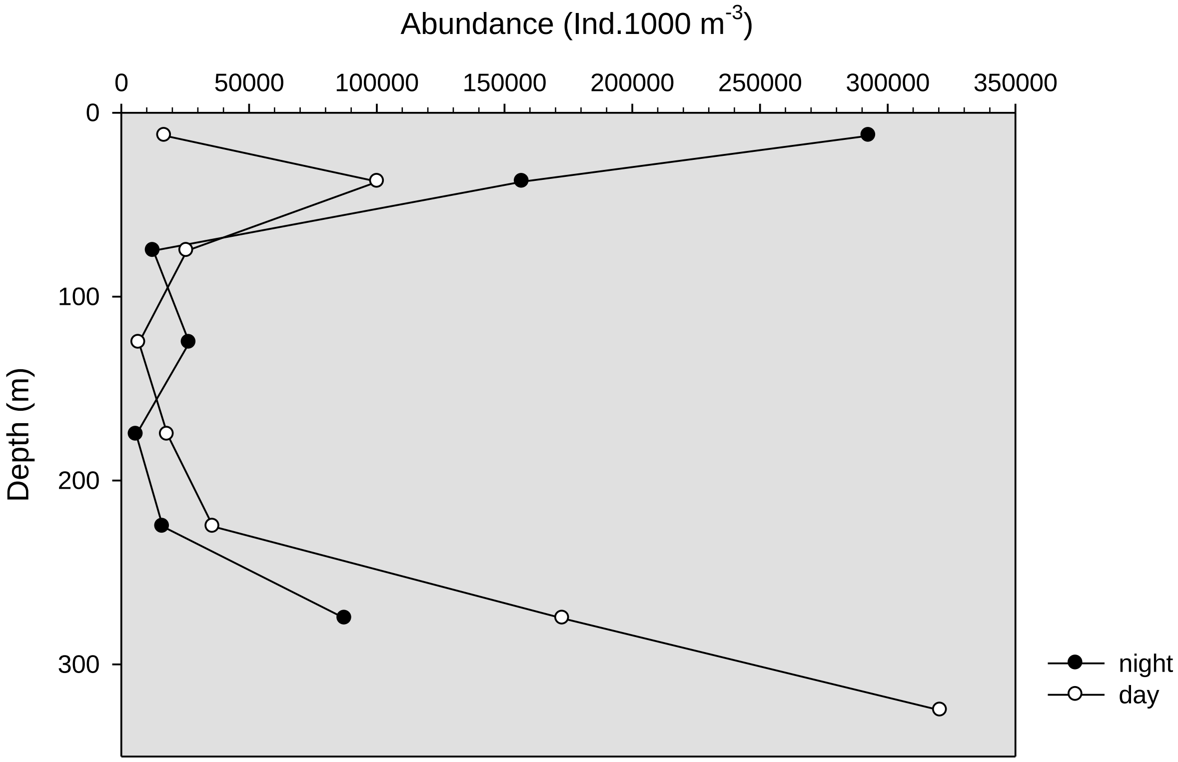
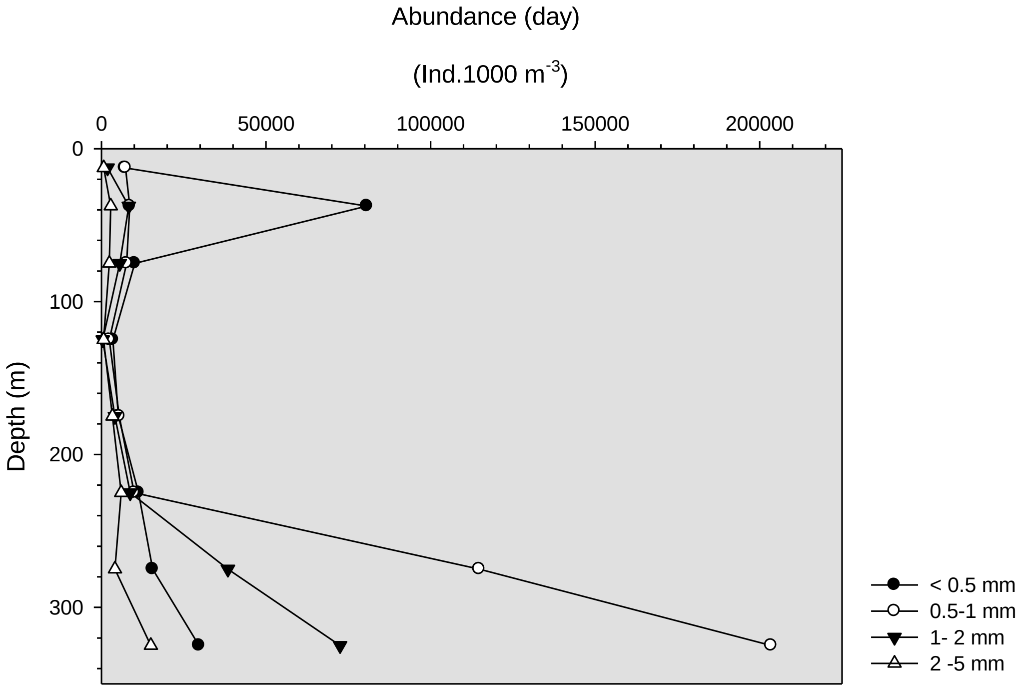


Fig. 3.6 Mesozooplankton abundance distribution

The vertical distribution of mesozooplankton abundance of different size classes (Fig. 3.7 A-B), reveals similar distributional patterns than the biomass (Fig 3.6), albeit striking differences in the size classes. During the day (Fig. 3.7 A), all the size classes are less abundant (<10 000 Ind.1000 m $^{-3}$) in the surface and intermediate layers, except the size class <0.5 mm that show a marked increase of 80 645 Ind.1000 m^{-3}. The abundance of all size classes then start to increase in the deeper layer.

The night samples show a different pattern for the size class fractions of zooplankton (Fig. 3.7 B). The size class fraction 2-5 mm remained less abundant during the day throughout the entire water column, even showing a slight increase in the deeper layer. The size class fraction 1-2 mm showed a biggest increase in abundance from a mere 1 896 Ind.1000 m^{-3} (at 12.5 m, day) to 145 046 Ind.1000 m^{-3} at night (12.5 m). The other two size classes also increase in abundance, with size class 0.5-1 mm reaching 108 079 Ind.1000 m^{-3} at night (12.5 m) and size class <0.5 mm reaching 37 500 Ind.1000 m^{-3} at night (12.5 m). For all the size classes, abundance is less in the deeper layer at night, than during the day.

A.



B.

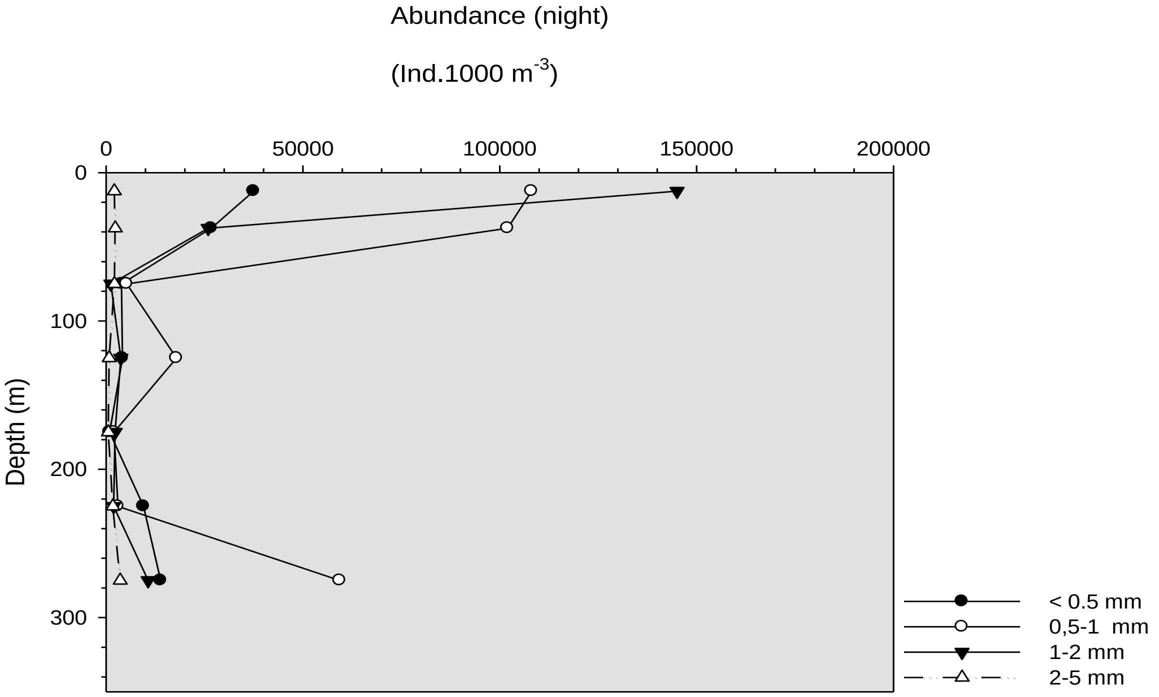
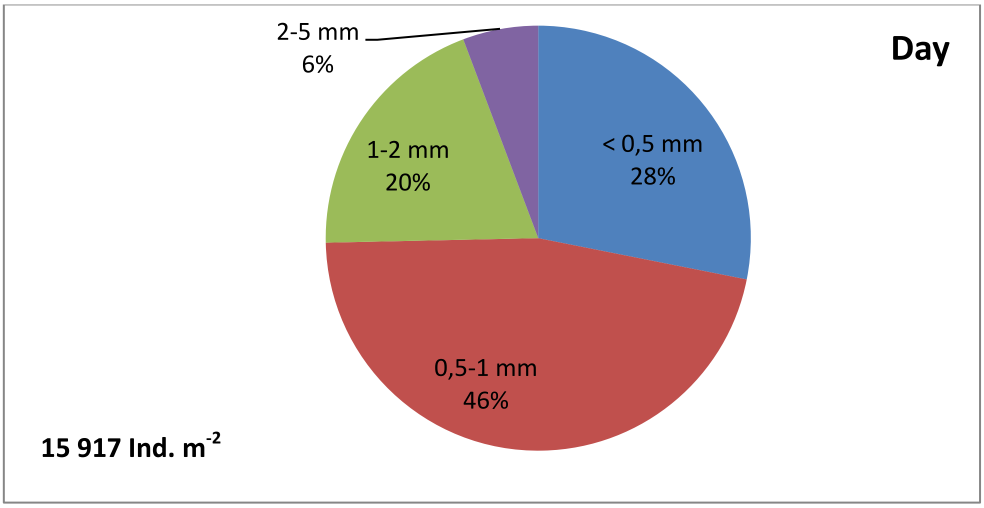


Fig. 3.7 Vertical abundance size class distribution, day (**A**) and night (**B**)

The contribution of different size classes to the standing stock integrated over the 300 m water column during the day and night is shown in Fig. 3.8 A-B. The size class 0.5-1 mm was the most numerically abundant, making up around 50% of the total mesozooplankton sampled. The size class 1-2 mm increased by 8% from day (20%) to night (28%). The size class 2-5 mm decrease by 3% from day to night. The size class fraction <0.5 mm also showed a decrease of 11% from day to night.

A.



B.

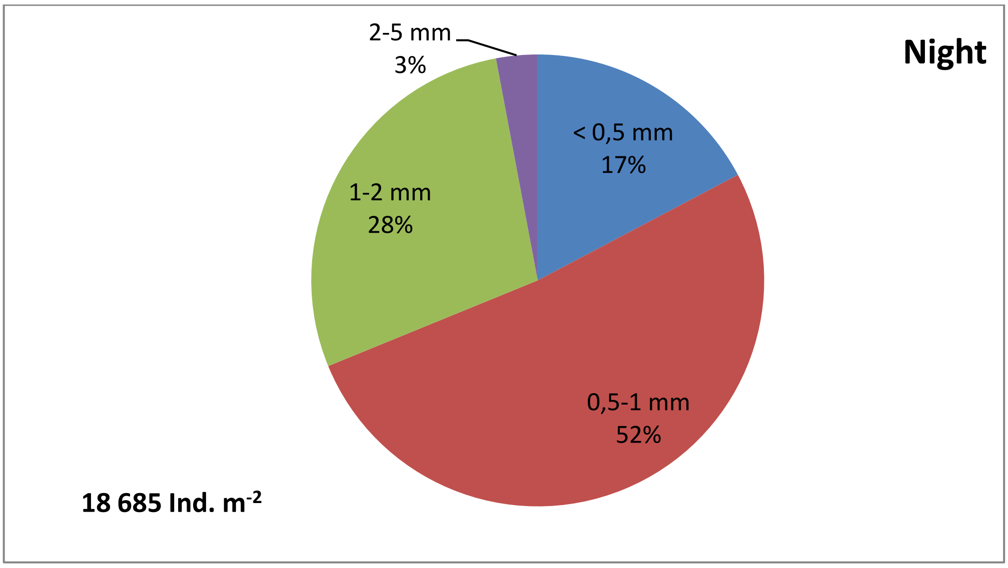
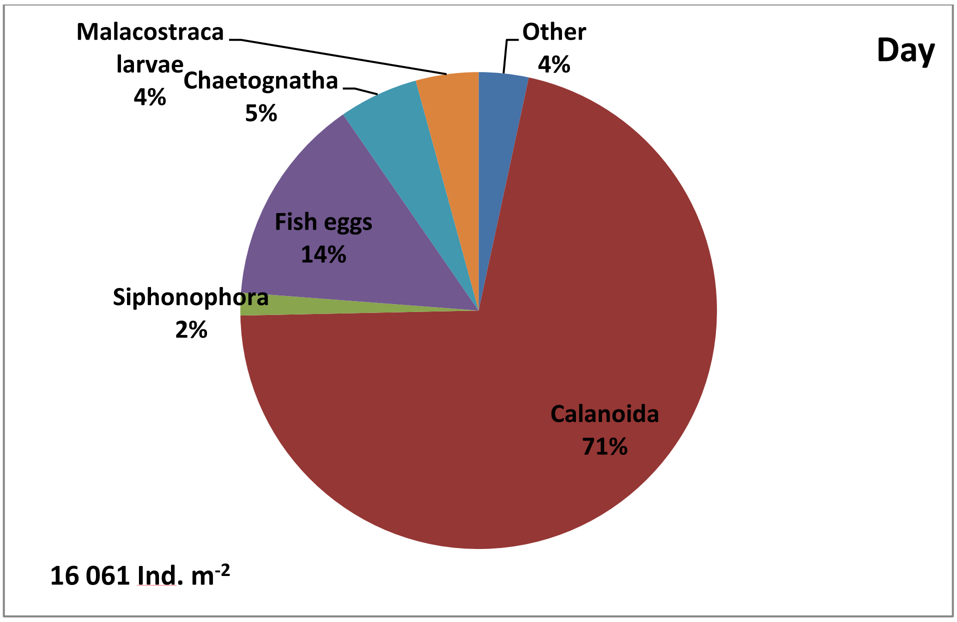


Fig. 3.8 Standing stock abundance of mesozooplankton size classes (0-300 m), day (**A**) and night (**B**)

In terms of the standing stock abundance composition of the main orders and suborders (Fig. 3.9 A-B), the Calanoid copepods were numerically most abundant during the day (71%) and night (74%). The Cyclopoid copepods formed less than 2% during the day and were included in the grouped labeled “Other” but during the night they form 5% of the sampled mesozooplankton. The Ostracods were also included in the group labeled other as it formed less than 2% of sampled mesozooplankton during the day. However, during the night their numbers increased and it formed 4% of the sample. Chaetognaths were slightly more abundant during the day (5%) than during the night (2%). The Malacostraca larvae formed 4% of the abundance during both the day and night. Siphonophora formed 2 % during the day but a negligible percentage during the night, thus part of the group “Other”. The group labeled “Others” include the following orders during the day: Amphipoda, Polychaeta, Mollusca (other), Fish/larvae, diverse gelatinous jelly, Ctenophora, Cnidaria, Pteropoda, Cyclopoida, Mysidacea, larvae (other), Euphausiaceae, Salpida and Siphonophora and during the night it included all except, Cyclopoida, Decapoda, Siphonophora and Ostracoda. They were less abundant (<2%), thus pooled together in one group. Among them, when pooled together, they only represented 4% (day) and 2% (night) of the total zooplankton composition. Although, fish eggs do not form part of the mesozooplankton (they belong to ichthyoplankton), they are represented here to illustrate their abundance in the water column in relation to other zooplankton orders.

A.



B.

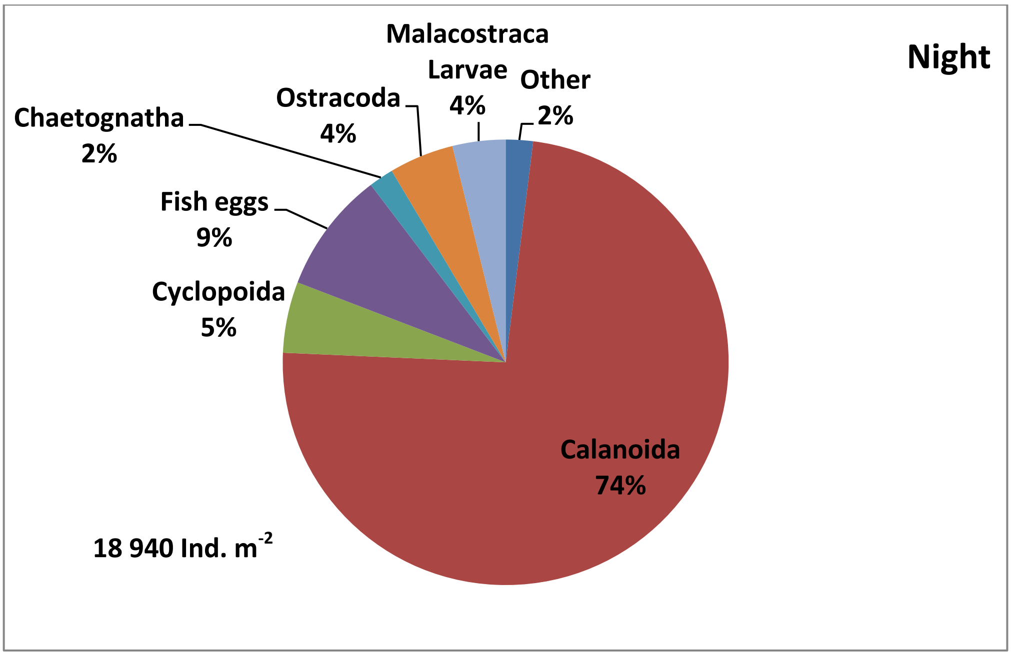


Fig. 3.9 Composition of different mesozooplankton orders (0-300 m), **A** (day), **B** (night)

Looking at the vertical distribution of the key taxa or the numerically most abundant taxa in the water column, calanoid copepods (Fig. 3.10) reflect the same distribution pattern as described for total biomass. Their abundance at the surface (12.5 m) reaches almost to 250 000 Ind.1000 m^{-3} during the night, compared to a small number of 7 884 Ind.1000 m^{-3} during the day at the same depth. Abundance at the intermediate depth is relatively low, whereas at deeper depths (325 m) the abundance increases above 250 000 Ind.1000 m^{-3} during the day.

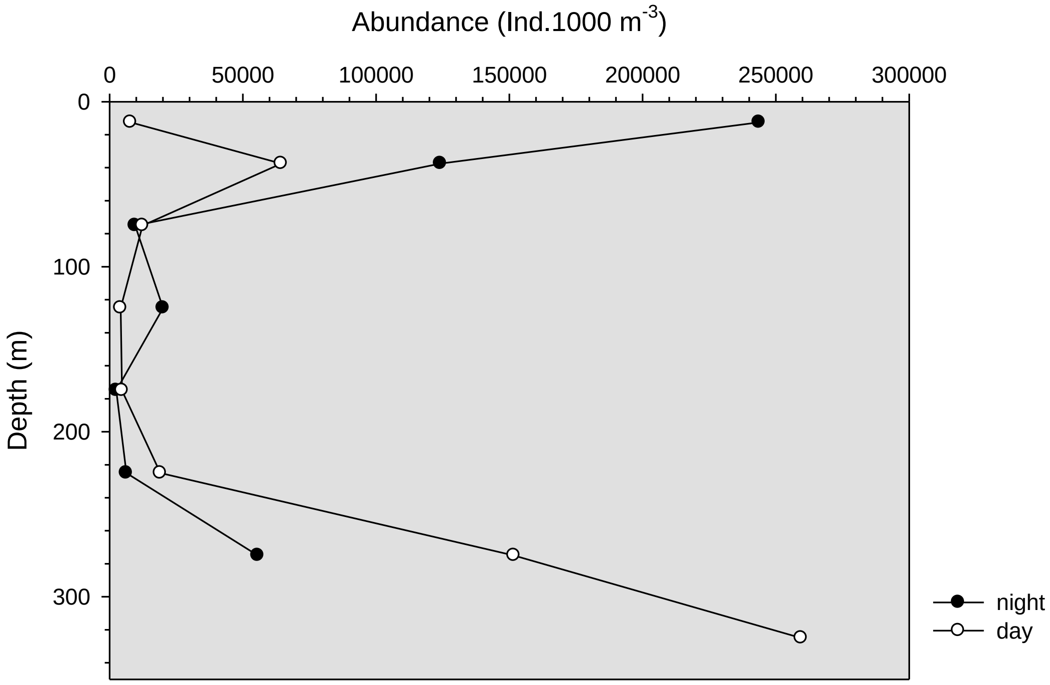


Fig. 3.10 Vertical distribution of calanoid copepods

Cyclopoid copepods also show a similar pattern of abundance distribution (Fig. 3.11), whereby their abundance reach close to 20 000 Ind.1000 m^{-3} at the surface during the night, but only 160 Ind.1000 m^{-3} during daytime. The abundance values are considerably low during the day at the surface and intermediary layers, but increase sharply below 300 m.

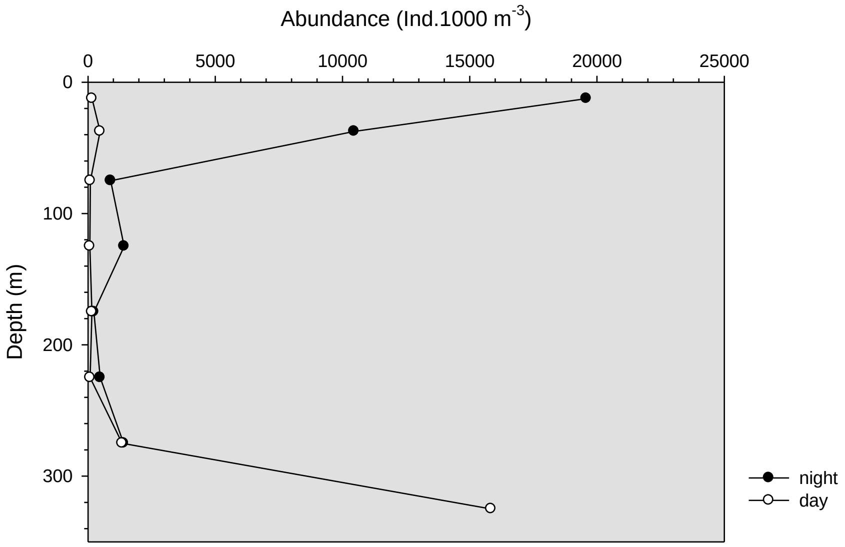


Fig. 3.11 Vertical distribution of cyclopoid copepods

Chaetognaths show a very unusual pattern of abundance distribution from the rest of the mesozooplankton (Fig. 3.12). They seem to be more abundant during the day then during the night. The night abundance reflects the pattern of distribution of other zooplankton, whereas the day distribution looks distorted. The pattern of Chaetognath abundance distribution is thus questionable.

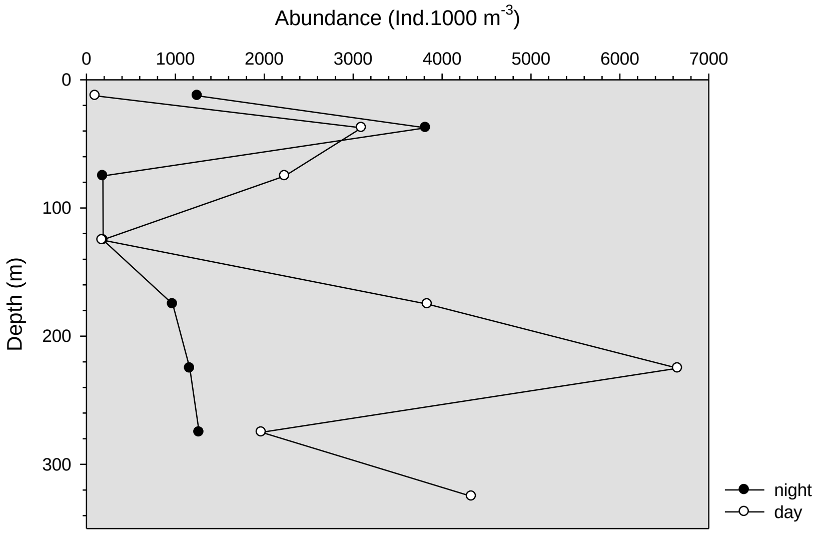


Fig. 3.12 Chaetognath abundance distribution

The Malacostraca larvae abundance distribution is similar to the distributional patterns of other zooplankton , showing a clear day-night variation in the surface layers above and below the thermocline (Fig. 3.13).

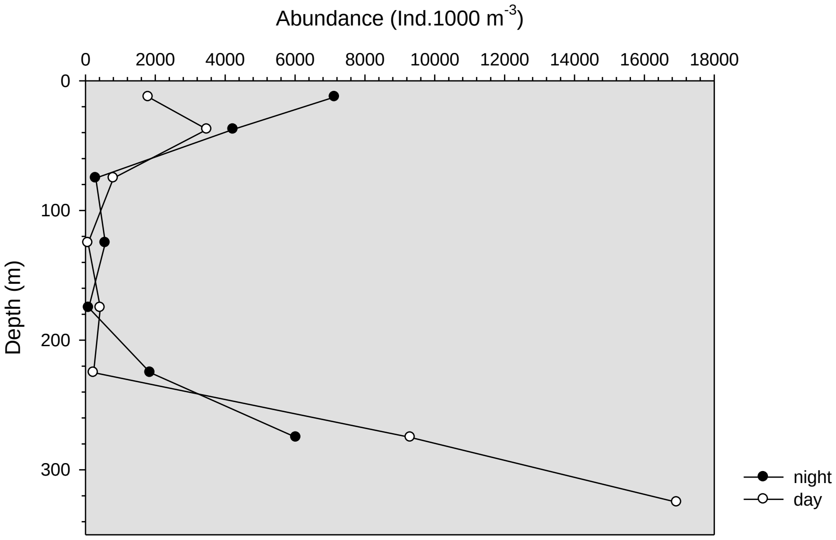


Fig. 3.13 Malacostraca larvae abundance distribution

The Ostracods show little variation in their abundance distributional patterns in the surface layer and the layer below the thermocline. The abundance values are quite low both during the day and night, and only start to show a slight increase below 220 m (Fig. 3.14).

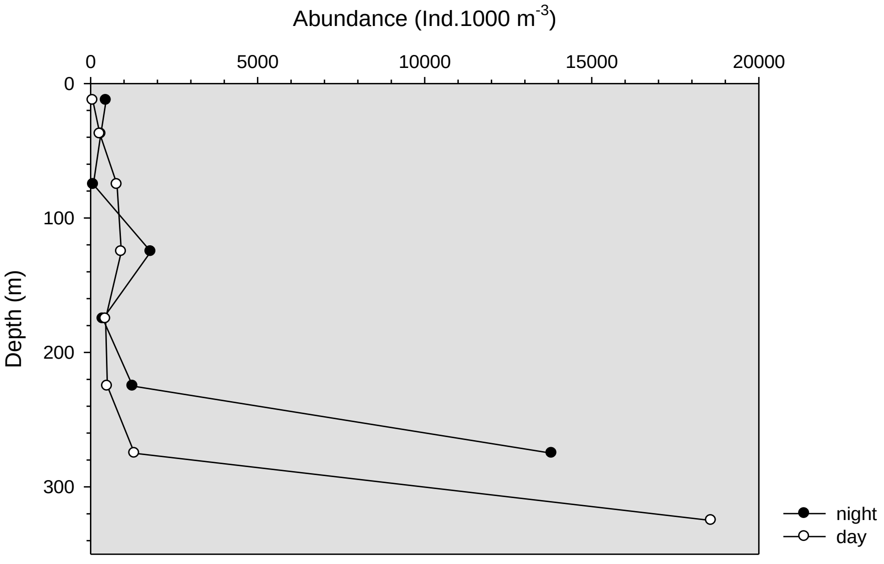


Fig. 3.14 Ostracoda abundance distribution

3.3 ADCP zooplankton biomass estimate

The measurements of the relative acoustic backscatter intensity during the sampling period show a distinct pattern of zooplankton distribution (Fig. 3.15). The 20 to 25th hour's falls within the time of the night haul (7th Oct'10). The intensity of the backscatter is much higher in the 75-150 m layer, indicating large numbers of zooplankton presence during the night time period. Very few zooplankton are responsible for the backscatter at depths >300 m. The day haul falls between 30th and 40th hours (8th Oct'10). The backscatter intensity decreases rapidly. At the dawn of the day time period (around the 30th hour), the relative backscatter shows a different pattern. The zooplankton seem to have disappeared from the surface layers as evident from the little backscatter, however deeper layers (300-350 m) seem to register a relatively higher acoustic backscatter. Also, at the surface there seems to be a film of consistent but little backscatter activity. The relative acoustic backscatter cross-section show a distinct day-night zooplankton variation in terms of distribution.

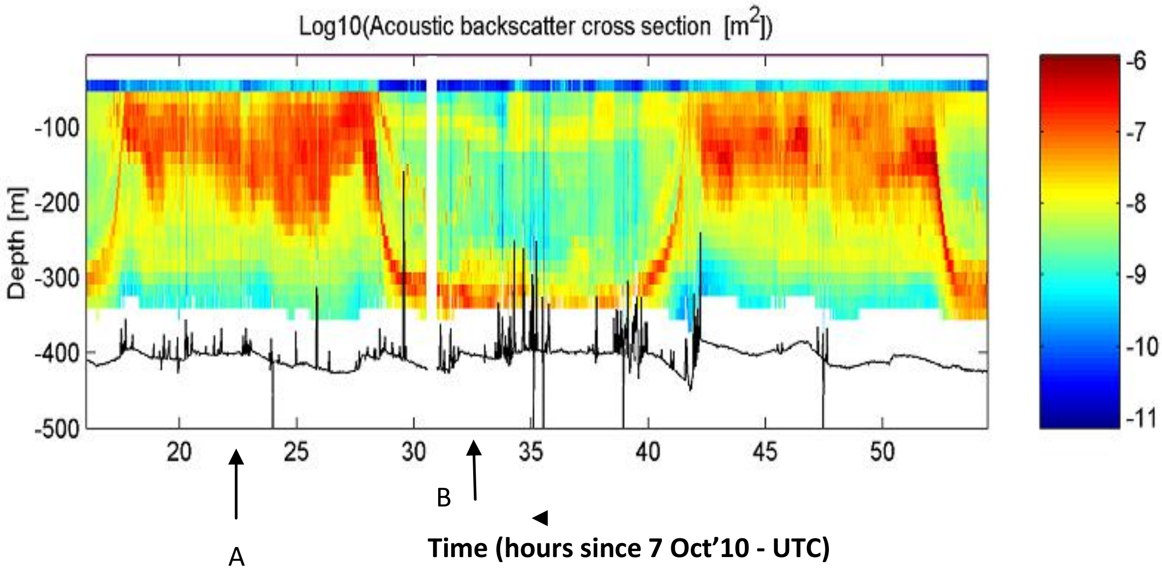
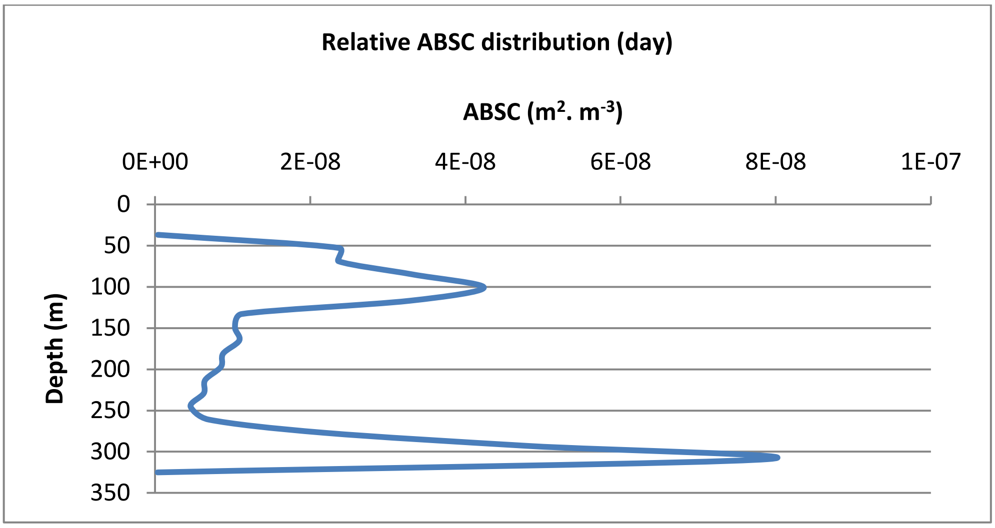


Fig. 3.15 The acoustic backscatter cross-section plot covering the sampling period (arrows A and B show approximate sampling times during the night and day respectively)

Figure 3.16 A-B shows the acoustic backscatter cross-section distribution at the time covering the net sampling period. Figure 3.16 A shows the backscatter between 10:09 and 11:59 local time on the 8th October 2010, whereas, Fig. 3.16 B shows the recorded backscatter distribution between 22:09 and 23:19, local time on the 7th October 2010. The distribution follows the pattern described above for Fig. 3.15.

A



B

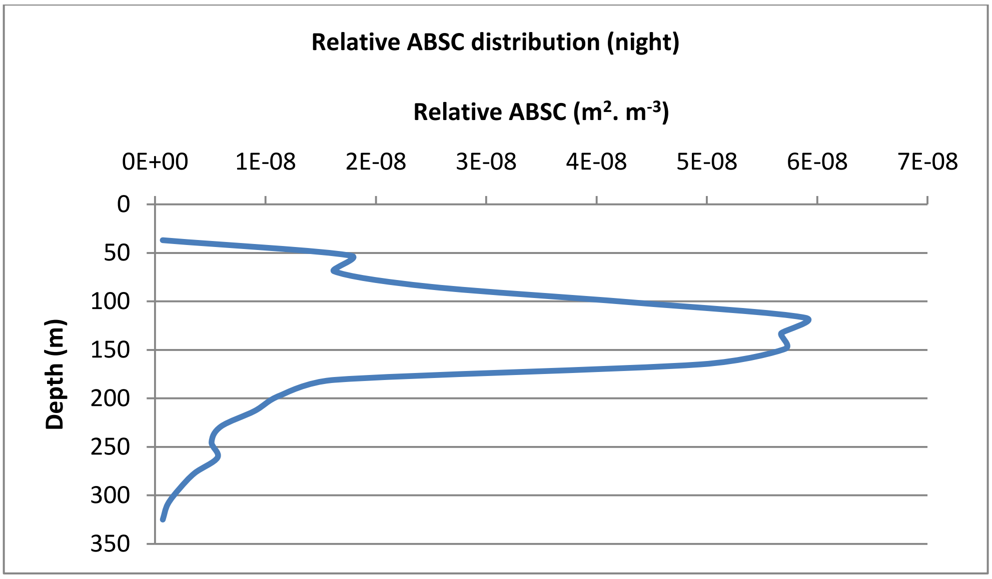
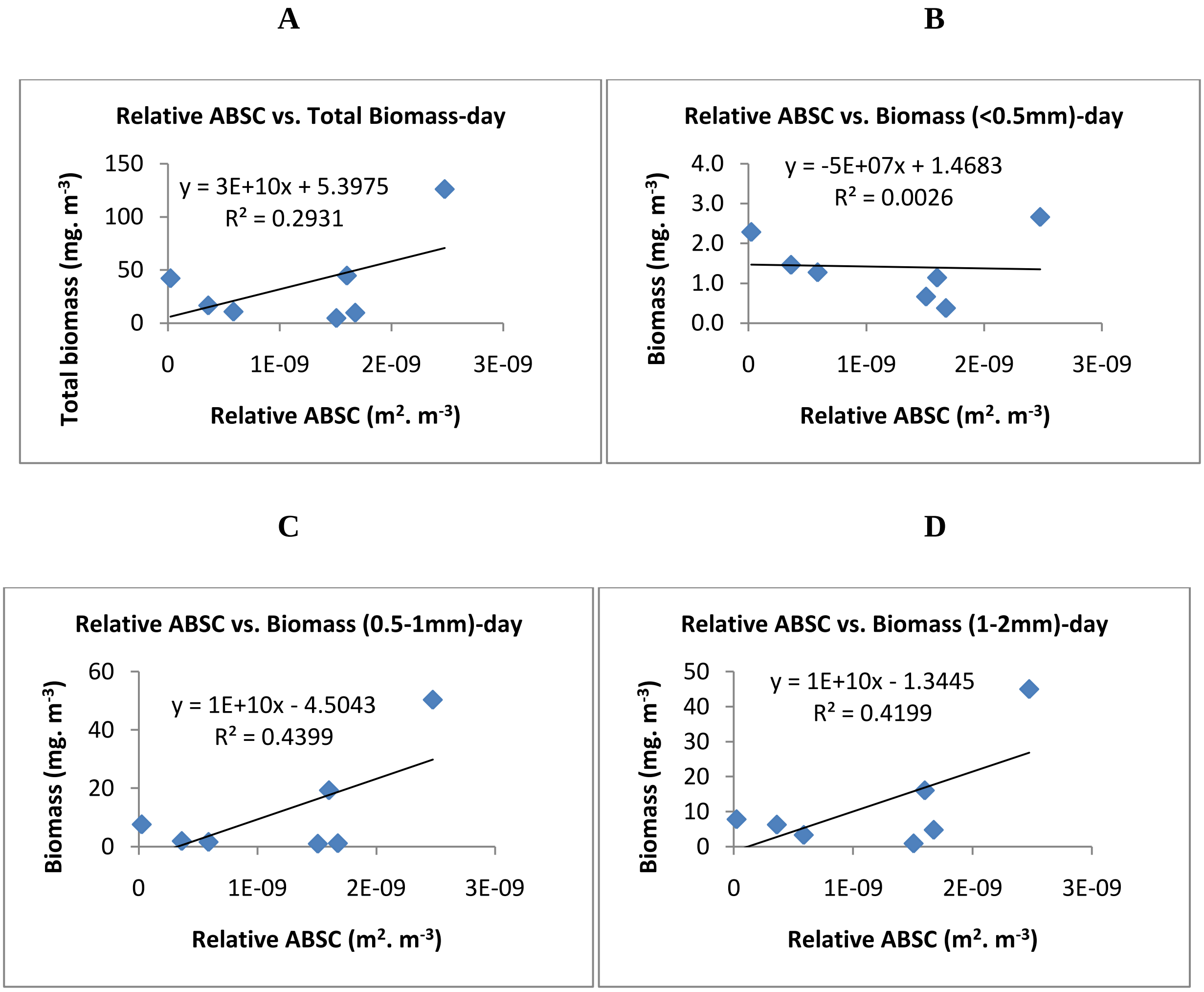


Fig. 3.16 The acoustic backscatter cross-section distribution during the sampling period the sampling period, day (**A**) and night (**B**)

3.4 ADCP and net zooplankton concentration

The relationship between the relative acoustic backscatter cross-section and biomass from net catches during the day and night show varied results (Fig 3.17 A-K). None of the correlations for biomass catches during the day showed any significance (P>0.05), although much of the variability could be accounted for by slightly higher coefficients of determination, r^2 by different size class fractions (Fig 3.17 A-F). The r^2 reached 0.29, 0.44 and 0.42 for total biomass, size class fractions 0.5-1 and 1-2 mm respectively (Fig.17 A,C-D). The night biomass catch correlations showed a strong significant (P<0.05) but negative relationships, at least for some size class fractions (Fig 3.17 G-K). The total biomass, size class fractions <0.5 and 1-2 mm reach r^2 of 0.73, 0.83 and 0.72 respectively (Fig.317 H,J). The other two size class fractions showed no significant correlations (P>0.05), Fig.3.17 I,K.



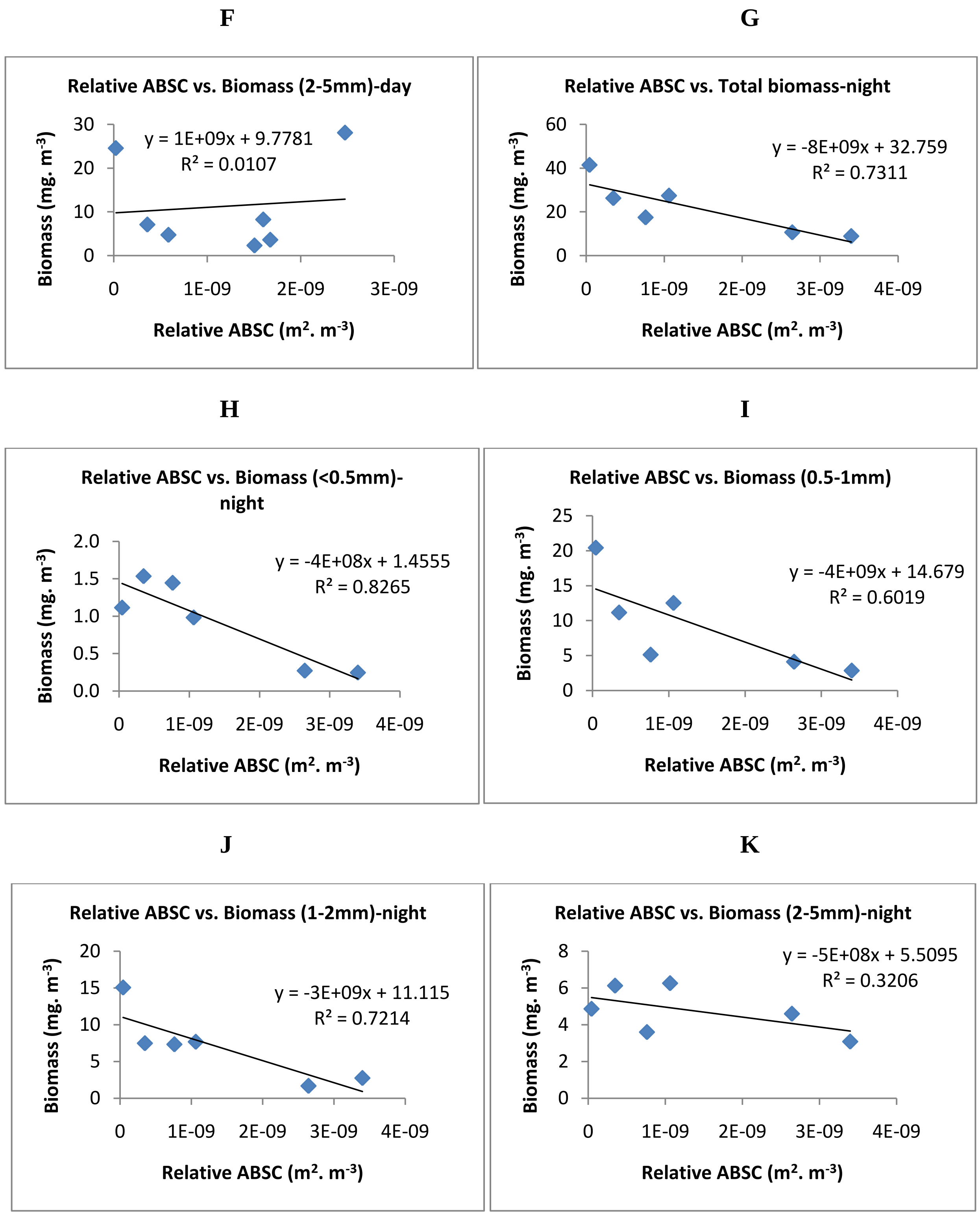
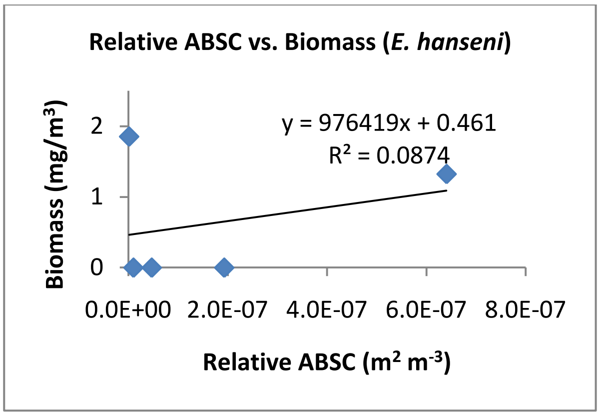


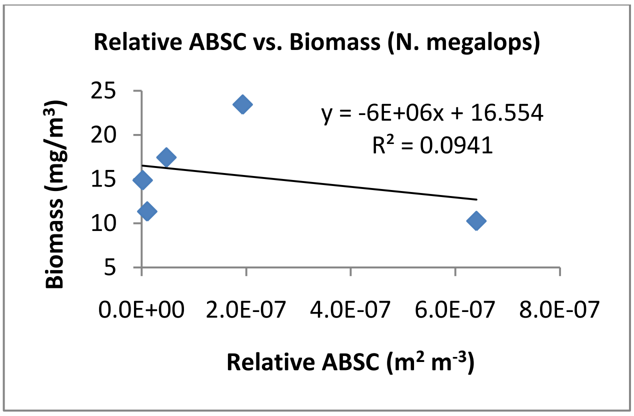
Fig. 3.17 A-K Acoustic backscatter cross-section and net zooplankton biomass, including regression equations and coefficients of determination, r^2

3.5 VM- ADCP and Krill biomass estimate

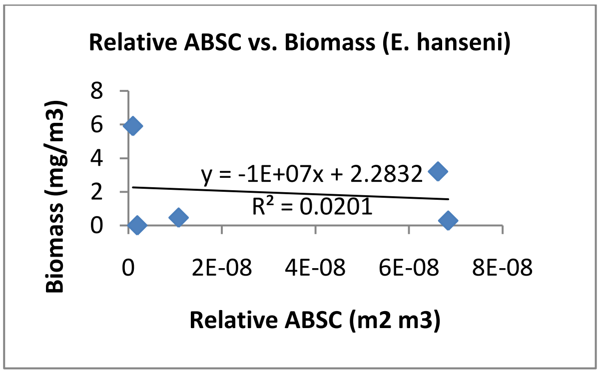
The relationship between the relative ABSC and the onboard biomass estimates for the two krill species (*E. hanseni* and *N. megalops*), Fig. 3.18 A-D, appears weak and non-significant ($P>0.05$) over the entire sampling period. Though not significant, the coefficient of determination, r^2 for *N. megalops* at dawn (0.40) and dusk 2 (0.46) is much higher than at dusk 1 (0.09) and midnight (0.07). For *E. hanseni*, the coefficient of determination is much lower over the entire sampling period (<0.09).

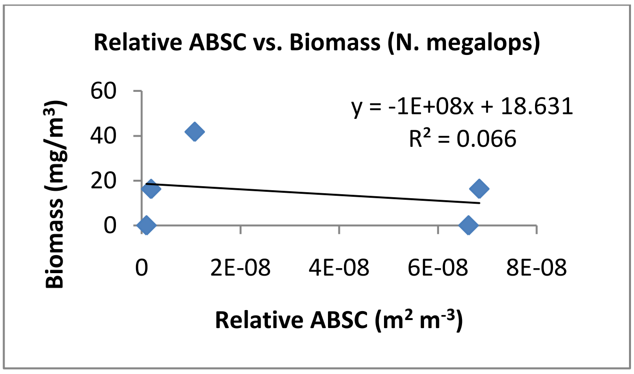
A. Dusk 1



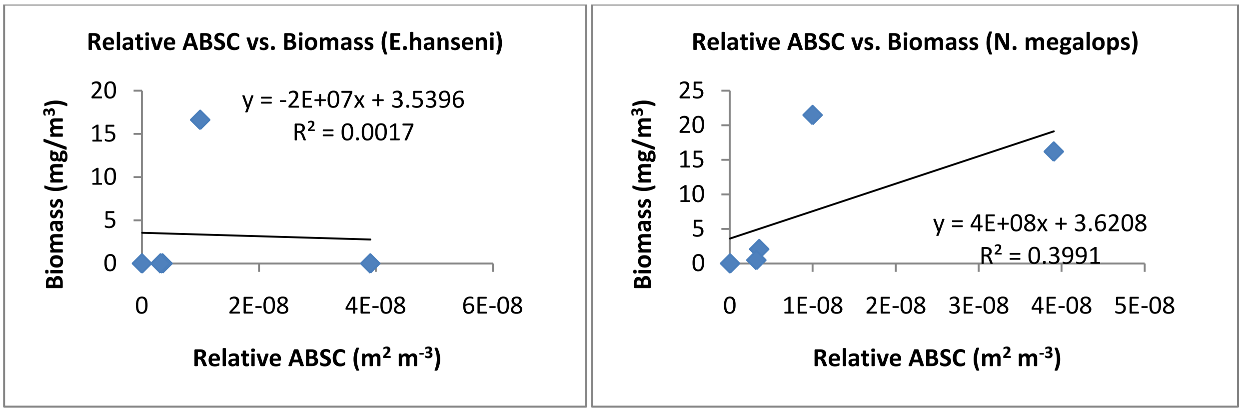


B. Midnight





C. Dawn



D. Dusk 2

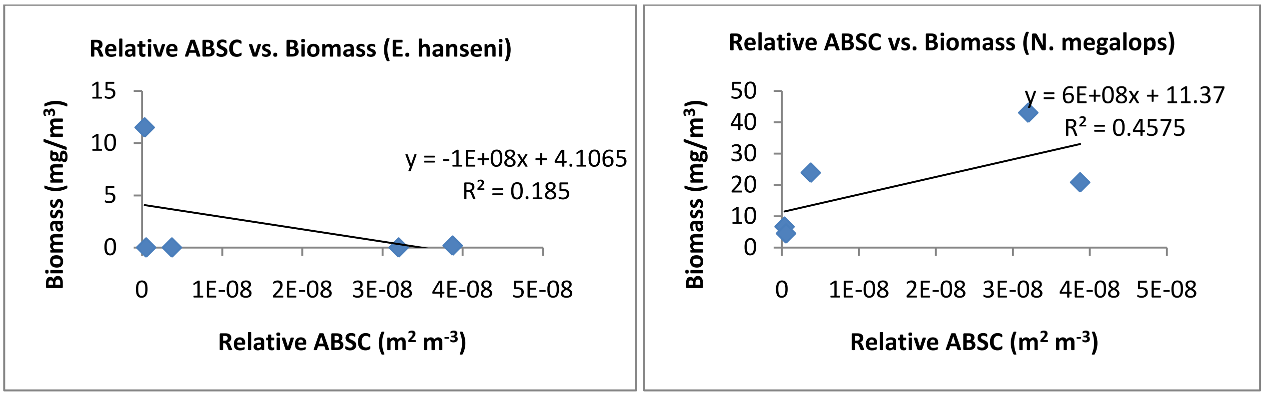


Fig. 3.18 A-D Acoustic backscatter cross-section and krill biomass estimates, including regression equations and coefficients of determination, r^2

4 Discussion

4 Discussion

4.1 Hydrography

The study was undertaken during the annual upwelling season in the Northern Benguela. September is particularly characterized by active coastal upwelling, with maximum upwelling reported to occur during this month (Hansen *et al*. 2005). During the study, upwelling filaments were also observed, but outside the range of the sampling station. They were visible as a water body with lower temperature and salinity than the ambient water in the upper layer. The upwelling front off Namibia appears diffused and is constantly crossed by plumes and filaments (Shannon & Nelson 1996). The general annual cycle of upwelling in the Northern Benguela is characterized by hydrographically distinct periods: February to April is characterized by warmer surface water, resulting in a stratified water column, whereas May to December is characterized by active coastal upwelling, with cold upwelled surface waters (Hansen *et al.* 2005).

There is also a change in the flow of the wind fields seasonally, however, predominant winds blow from south-south east parallel to the coast, resulting in a north-westward flow of the Benguela Current and coastal upwelling through Ekman pumping (Shannon 2006).

The sampling station was located on the shelf edge and the preliminary oceanographic data showed a clear indication of the presence of internal waves. In the bottom layer, the vertical structure changed between well mixed and stratified conditions. During the well mixed phases, the mixed bottom layer had a vertical extend up to 100 m. Since turbidity was enhanced in the bottom layer it may have pointed to the breaking event of internal waves.

4.1.1 Mesoscale structures and zooplankton distribution

Mesoscale hydrographic phenomena were observed throughout the region and the region is reported to be composed of a series of anticyclonic eddies responsible for the irregularity and instability of the upwelling region (Hart & Currie 1960, Salat *et al.* 1988, cited in Olivar & Barangé 1990). Internal waves were present during the sampling period and it is useful to consider the effect that it may have had on the distribution and composition of zooplankton on a temporal scale. It is cannot be said with certainty that internal waves had an effect on the biomass and abundance distribution of mesozooplankton during this study. However, several studies have shown that mesoscale structures do influence zooplankton distribution and species composition (Davis *et al.* 2004, Genin 2004) . Albaina and Irigoien (2007) found that apart from other mesoscale other structures such as river plumes, fronts and eddies, internal waves generated over the shelf break determined the composition and abundance of zooplankton assemblages on a fine scale. Olivar and Barangé (1990) observed a common pattern of influence on all zooplankton groups, when zooplankton seemed to be trapped and transported to deeper layers by an eddy that was located off Walvis Bay during their study, though they could not draw firm conclusions. If mesoscale structures are recurrent and predictable, then it indicates a progress in operational oceanography and this will in turn influence the biology of zooplankton organisms with some measure of certainty. Zooplankton patches are long considered to be a product of large scale physical processes (Folt & Burns, 1999), but the extent to which mesoscale structures such as the internal waves and eddies contribute to the formation and break up of these patches need a further consideration. Studies on how different mesoscale structures contribute to shape zooplankton communities over a large area are scarce because of the difficulties of fine scale sampling over a large area with high taxonomic resolution (Albaina & Irigoien 2007).

4.2 Mesozooplankton biomass and abundance

Mesozooplankton distribution (Fig. 3.3 and 3.6) showed a very clear pronounced distribution pattern during the day and night-time over the water column as observed by ADCP measurements and parallel net catches. Both abundance and biomass are concentrated in two layers, the uppermost surface layer and the layer below 200 m (i.e. bimodal distribution). During the day, the surface biomass and abundance values were much lower, whereas the values increase at greater depths (>200 m). At night the opposite happens, the values at the surface increase dramatically and values in greater depths decline. This is true for both biomass and abundance. The observations are consistent with those of Olivar & Barangé (1990), Timonin *et al.* (1992) and Postel *et al*. (2007). Timonin (1992) observed up to 2-2.5 times higher zooplankton (in the Walvis Bay area) in the upper 100 m layer during the night-time than during the day-time, collected by a net with 180 μm mesh size. There is no doubt that the biomass and distribution patterns are reflective of the active diel vertical migration by zooplankton (Hays *et al.* 2001), as outlined in the Introduction. Diel vertical migration cannot be solely attributed to the said distribution patterns, as not all zooplankton display DVM. Therefore, physical characteristics of the water, particularly temperature and oxygen need to be taken into consideration.

Water column structures, in particular, the existence of a strong thermocline and a oxygen minimum zone (OMZ) affects zooplankton migration and vertical distribution (Auel & Verheye, 2007). The unique feature of the Northern Benguela Current upwelling region is the presence pronounced OMZ at 60-500 m depth with oxygen concentrations of ≤ 1.4 mg $O_2 l^{-1}$ (Auel & Verheye 2007). The latter authors observed that the dominant copepod *Calanoides carinatus* and other calanoid copepods showed a bimodal vertical distribution (similar findings to this study), in an apparent attempt to avoid the OMZ. It was further observed that the oxygen minimum layer near the bottom in the southern Benguela limited the diel vertical migrations of *C. carinatus* to the overlying water (Verheye 1991). Loick *et al.* (2005) also observed that the occurrence of a well defined pelagic OMZ in the ABF region had a similar effect on the vertical distribution of copepod populations. It is likely that the extended OMZ acts as a barrier preventing the completion of life cycles of ontogenetic vertical migrators' and interfere with vertical feeding migrations of daily ascending zooplankton such as krill (Auel & Verheye 2007).

Judging from the hydrography prevailing during the time of sampling (Fig. 3.1-2), the thermocline at the intermediate depth may have act as a barrier to non-migranting zooplankton, whereas it did not certainly act as a barrier to actively migrating zooplankton. The need to cross the thermocline represents a major energy expenditure for many zooplankton, therefore, vertical migration across the thermocline carries a fitness cost and not a benefit (Ohman 1990). The non-migratory zooplankton during daytime are clearly visible with the ADCP measurements (Fig. 3.15). Off Namibia, three groups of zooplankton are often observed: non-migrating, slightly migrating and actively migrating, depending on their ecological preferences and physiological stage (Postel *et al.* 2007).

Since not all zooplankton display active DVM, which ones do or better, which size classes display pronounced DVM? The younger stages of copepods and euphausiids in the Benguela do not migrate and tend to dwell in the surface layers, whereas juveniles and adults carry out vertical migration (Olivar & Barangé 1990), and this is clearly reflected on the ADCP measurements during the daytime. The size classes 0.5-1 and 1-2 mm display pronounced DVM, based on the biomass and abundance distribution (Fig. 3.4 and 3.7). These two size classes were mainly composed of calanoid copepods, both during day and night. Between them, these size classes made up 59% of the standing stock biomass during the day-time and 76% during night-time (Fig.3.5). In terms of the standing stock abundance, the size class 0.5-1 mm made up around 50% of the total standing stock abundance (Fig. 3.8). These two size classes must therefore comprise predominantly calanoid copepods since they are numerically most abundant (Fig. 3.9). Although this study did not attempt to identify the mesozooplankton to species level, various studies have found that the region off Walvis Bay is dominated by four calanoid copepods: *Metridia lucens*, *Calanoides carinatus*, *Rhincalanus nasutus* and *Centropages* spp. (mainly *C. brachiatus*), and each displays a particular spatial and temporal distribution pattern. There is often a marked inshore-offshore shift in the dominance of these species and their seasonal abundance (Olivar & Barangé 1990, Timonin e*t al.* 1992, Hansen *et al.* 2005).

Hansen *et al.* (2005) observed that *C. carinatus* was more prominent inshore, whereas *M. lucens* was far outnumbered by all the three other copepods in the offshore zone. The authors also generally recorded low abundances close inshore, increasing in the mid-shelf and peaking at offshore stations. The multiple peaks are often attributed to the pulse and dynamic nature of the Benguela upwelling system.

The tropho-ecological characteristics of zooplankton species, in addition to the hydrographical features, are also important in determining species distribution. For example, *M. lucens*, an omnivorous species, became more prominent during upwelling and when conditions became more stable, whereas *C. brachiatus*, also an omnivorous species, has a more restricted, nearshore distribution. However, *C. carinatus* and *R. nasutus*, both herbivorous species, increase rapidly in response to intense upwelling (Timonin 1992, Hansen *et al*. 2005). Calanoid copepods display extensive DVM (Fig. 3.7). *C. carinatus* is especially known to display ontogenetic vertical migration, which play a key role in the retention of the population within the productive upwelling region and for rapid re-colonization of plumes of newly upwelled water (Auel &Verheye 2007). In regions of high biological productivity such as the Benguela, high zooplankton concentrations increase competitive interactions, thus biological interactions may exert an influence on the distribution and composition of zooplankton communities, as important as environmental factors (Cornet & Gili 1993, Folt & Burns, 1999).

The biomass of the bigger size class 2-5 mm was 15% higher during the day than during the night (Fig. 3.5), whereas its abundance was generally lower and around 3% (Fig. 3.8). It is not clear why this class exhibit this type of distribution. Diel vertical migration cannot be attributed to this distributional pattern but probably a combination of physical and/or biological factors. Some species undergo so-called “reverse migration”, where zooplankton ascend at dawn and descend at night. Although this is a less common type of migration, there is little quantitative information to substantiate this claim (Heywood 1996). One plausible explanation might be the net avoidance by zooplankton during the day. Several studies have shown that fast moving species can use vision to detect net approach and are able to avoid it (Wiebe *et al.* 1981, Wiebe and Benfield 2003, Benoit *et al.* 2010). The size class 2-5 mm was composed mainly of bigger copepods, Chaetognaths and a few salps.

The size class <0.5 mm, which comprised predominantly of cyclopoid copepods, Malacostraca larvae and large number of fish eggs did not show much variation in biomass and abundance distribution. It only made up on average 5% of the standing stock biomass during the sampling period, although it was slightly more abundant during the day-time. The Malacostraca larvae formed 4% of the standing stock abundance, whereas cyclopoid copepods only become prominent during the day (Fig. 3.9). Both cyclopoid copepods and Malacostraca larvae displayed strong gradient in vertical distribution (Figs. 3.11 and 3.13).

Although some studies have shown that copepods in the Benguela do not generally migrate over great distances (Verheye & Hutchings 1988), this study has shown that even relatively smaller zooplankton display extensive diel vertical migration, at least on a temporal scale.

Chaetognaths were mostly represented in the size classes 1-2 and 2-5 mm, although it should ideally belong to the size class fraction >5 mm. Due to their morphology, they often ended up in the former size classes during size fractionation using sieves. Chaetognaths were slightly more abundant during the daytime than the night-time (Fig. 3.9). Their abundance and distribution, however, yielded a distorted pattern, which may suggest that they were not adequately sampled by the net. Weak osmo-regulatory abilities constrain Chaetognath species within a narrow salinity ranges, forcing them to occupy niches within specific oceanic zones and water masses. Chaetognath distribution and species composition vary from inshore to offshore waters and among the different water masses (Coston-Clements *et al.* 2009), whereas they also have been shown not to exhibit a conspicuous gap nor high densities in the Benguela region (Olivar & Barangé 1990).

Ostracods only become more prominent during the night (Fig. 3.9) and their distribution pattern indicates that they do not perform vertical migrations but remain mostly between 200 and 325 m depths both during daytime and night-time (Fig. 3.14).

The other zooplankton caught did not form any significant part of the total zooplankton standing stock. Maybe their abundance distribution is seasonal or they reside outside the range of the sampling area, or they were simply not sampled adequately by the net. For example, Cornet & Gilli (1993) studied the vertical distribution of Hyperiid amphipods using a rectangular mid-water trawl (RMT) multiple opening and closing net with 200 µm mesh size at an oceanic station during a major intrusion by Angola Current waters in the northern-most Benguela. They found most species to be concentrated in the uppermost 40 m of the water column. They also noted that only few species were able to migrate through the thermocline. Most amphipods in the Benguela belong to the family Hyperidae. Amphipods have a tendency to be associated with Medusae or Ctenophores (Olivar & Barangé 1990), though there are several free-living forms. Since neither Medusae nor Ctenophore were hardly caught during the sampling period, it can only be assumed that their distribution may have been affected by such tendency.

Gelatinous zooplankton, cnidarians and salps were poorly represented in the net catches. The inherent difficulty of obtaining quantitative estimates of gelatinous zooplankton biomass and abundance result from their fragility and incomplete capture by the nets (Sameoto *et al.* 2000). Many salps, cnidarians and other gelatinous zooplankton were destroyed during the collection and since their abundance was generally low, their distributional patterns could not be determined.

4.3 ADCP biomass estimate and net zooplankton biomass

The ABSC showed a clear diel migratory behavior of zooplankton (Fig. 3.15). The backscatter distribution was bimodal during the day-time and unimodal during the night-time (Fig.3.16). The bimodal distribution of ABSC signal suggest that there are zooplankton that do not migrate and reside in the upper 100 m of the water column, and there are those that reside at greater depths during the daytime and perform daily vertical migrations during night-time (Fig. 3.16 B).

The DVM patterns matched well as determined parallel by ADCP measurements and net catches and this is consistent with observations from a number of studies (Heywood 1996, Buchholz *et al.* 1995, Ressler 2002, Postel *et al.* 2007). However, the backscatter signal as a measure of biomass generally did not gave good correlations to wet mass of mesozooplankton from net catches (Fig. 3.17). Almost all the correlations were not significant and this is attributed to the low sampling power since the data originate from one station only. Despite the insignificance of the correlations, there are some important insights that can be drawn.

It should be noted that acoustic properties of zooplankton differ and therefore a direct comparison between acoustic backscatter signal and zooplankton biomass is a complex task.

The higher the diversity of scattering types, the more difficult it is to interpret the data (Postel *et al*. 2007). Since certain components of zooplankton biomass may contribute more to the acoustic backscatter signal than others, it was useful to separate them into size class fractions.

Correlation during the day was relatively higher, particularly in size classes 0.5-1 and 1-2 mm. This size classes were dominated by calanoid copepods and therefore these group must have accounted for close to 42% of the acoustic backscatter signal (Figs. 3.17 C-D). The total mesozooplankton biomass accounted for about 30% of the backscatter signal (Fig. 3.17 A), showing a distortion of the signal when the mesozooplankton are considered as a whole relative to the backscatter. Weak correlations in size classes <0.5 and 2-5 mm are interpreted as resulting from the effect of more diverse species composition generally within the water column. The possibility of strong but rare scatterers such as pteropods cannot also be ruled out.

On the contrary, the correlations during the night-time show a very strong negative relationship and thus should be interpreted with caution. During the night-time, the bulk of net biomass were recorded in the uppermost 50 m of the water column, whereas the ADCP measurements only started from 37.5 m. The maximum backscatter was at close to 100 m during the night-time, whereas the maximum zooplankton biomass from the net catches was recorded in the upper 50 m of the water column. The peak backscatter at 100 m was not reflected in the net catches. The resulting discrepancy and inverse relationship between the ADCP measurements and net catches is thus interpreted to be coming from this mismatch in measurements depths. Furthermore, the discrepant quantitative values also may be due to possible errors in net sampling and to interference of animals other than mesozooplankton in ADCP measurements (Buchholz *et al.* 1995). The ADCP also covers a large cross-section of measurement than the nets. Diel vertical migration could have produced a varying incident angle between the scattering organisms and the transducer (McGehee *et al.*1998). Therefore, for better interpretation of the ABSC during the night-time, the missing acoustic data in uppermost water column above 37.5 m should have been considered but this was not possible as explained in the Material and Methods section.

Also, the 150 kHz ADCP has been shown to be more suitable for larger zooplankton (>5 mm) (Heywood 1996, Liljebladh & Thomasson 2001, Jiang *et al.* 2007), though other studies have found a close correlation between backscatter intensity and dry mass of smaller zooplankton using the ADCP of the same frequency (Buchholz *et al.* 1995).

The precise magnitude of the net avoidance by mobile scatterers is generally not known, so no simple correction for this problem could be applied. If net avoidance was indeed a significant but constant factor, it may have bias the estimates for larger zooplankton such as the krill, which the net may not have sampled quantitatively.

The extent to which other zooplankton such as salps, cnidarians, polychaetes, ampipods etc. contributed to the backscatter is unknown as these zooplankton were poorly represented in the net catches. Apart from being recorded in low numbers in the water column, it is difficult to estimate the contribution of the gelatinous zooplankton to the backscatter signal. The gelatinous plankton seem to be on the acoustical detection limit of the zooplankton, as its density contrast is low because of the large percentage of water (~96%) inside the body (Pugh 1984). The frequency used will determine the contribution of an organism to the backscatter, as outlined before. For example, although salps have been more easily detected with a 200 kHz acoustic system, experiments have shown that salps are generally inefficient scatterers of sound (Stanton *et al.* 1994).

4.4 ADCP measures and krill biomass estimates

Since krill species would have been ideal scatterers of the 150 kHz ADCP, it was useful to consider the krill biomass estimates in relation to the ADCP measurements (Fig. 3.18). It should be noted that this were only estimates and it may not give the actual contribution of the krill to the total backscatter signal. The two species of krill are known to have different migratory behaviours and are thought to contribute differently to the backscatter signal (Prof. Buchholz, AWI, pers. comm.).

For krill species *E. hanseni*, the contribution to the ABSC was very weak throughout the sampling period. The same reasons for a lack of correlation, as explained for the mesozooplankton are applicable. For *N. megalops*, the first dusk and midnight period showed a weak correlation, however, dawn and the second dusk period indicate that *N. megalops* contributed about 43% to the backscatter signal. This variation in correlation in relation to the different sampling periods suggest that vertical migrations may play an important role in the acoustic properties of the water column. Low backscatter strength in the upper surface layers of the water column at dawn, which is typically a downward migration phase, may suggest that krill body angles are steeper at dawn than during ascent or upward migration at dusk.

The change in krill body angle during ascend and descend presents a smaller dorsal surface to the acoustical signal (Tarling *et al.* 2001). The orientation of the krill at different times of the day may be one factor among many responsible for variations in the backscatter signal intensity and thus biomass estimates (Fig. 3.18). The backscatter strength varies with the time of the day (Cochrane & Sameoto 1994, Liljebladh & Thomasson 2001, Tarling *et al.* 2001) and periods of active migration (Buchholz *et al*. 1995) as observed in this study as well. Therefore, it would be speculative to say exactly the contribution of the krill species to the total backscatter, as the backscatter varies throughout the entire sampling period. The possibility that other krill species, such as *Nyctiphanes capensis,* also typical of Northern Benguela, may also have contributed to the backscatter cannot be ruled out, although the species were not identified in the biomass estimates.

5 Conclusions and Outlook

5 Conclusions and outlook

Much of the research on zooplankton variability has been carried out on a large scale, thereby overlooking much of the small-scale variability in zooplankton distribution in highly dynamic ecosystems. Mesoscale structures may influence the composition and abundance of zooplankton communities. The vertical distribution of zooplankton biomass and species abundance in relation to biophysical interactions are an important aspect of the structure and function of marine plankton communities.

Most mesozooplankton displayed a bimodal vertical distribution in biomass and abundance, and this was interpreted as an attempt to avoid the thermocline and the oxygen minimum layer. Diel vertical migration has been attributed to the bimodal distribution pattern, although other factors also need to be taken into account. Not all mesozooplankton displayed diel vertical migration, however, actively migrating zooplankton were mainly found in the size range 0.5-2 mm, which was comprised of calanoid copepods.

The acoustic Doppler current profiler measurements showed a clear diel migratory behaviour of zooplankton, however, the acoustic backscatter signal did not gave a good correlation to the wet mass of mesozooplankton and krill from net catches.

The data set presented in this study is small but provides a good snapshot of zooplankton variability on a temporal scale and the potential use of ADCPs on a parallel routine zooplankton studies. Since the data originated only from one station, it cannot be generalized for the whole Benguela upwelling region, but it may be a relative reflection of the Northern Benguela, particularly the vicinity of Walvis Bay.

Long term *in situ* studies on zooplankton distribution in relation to environmental parameters, with acoustic methods is recommended. Future studies should focus on the offshore-inshore and the frontal zones. Such studies should consider using ADCPs relative to the target organism or use high resolution multiple frequency acoustics. Future studies should also be able to determine and predict the regularity of mesoscale events and the response of plankton communities to these events. Therefore, these studies should ask some key questions:

- To what extent do mesoscale structures shape plankton communities
- Which species (also male and female) and developmental stage perform diel vertical migration
- How are different developmental stages of zooplankton organisms distributed
- How do seasonal changes in zooplankton biomass, abundance and composition affect the food web structure and fish stocks
- How are different plankton organisms physiologically adapted to the oxygen minimums and the thermocline

Answers to these and other questions will fill the necessary gaps in understanding the Benguela ecosystem as a whole and may eventually lead to the adoption of better management practices in the region.

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Appendix

Station data: Night – 07 September 2010

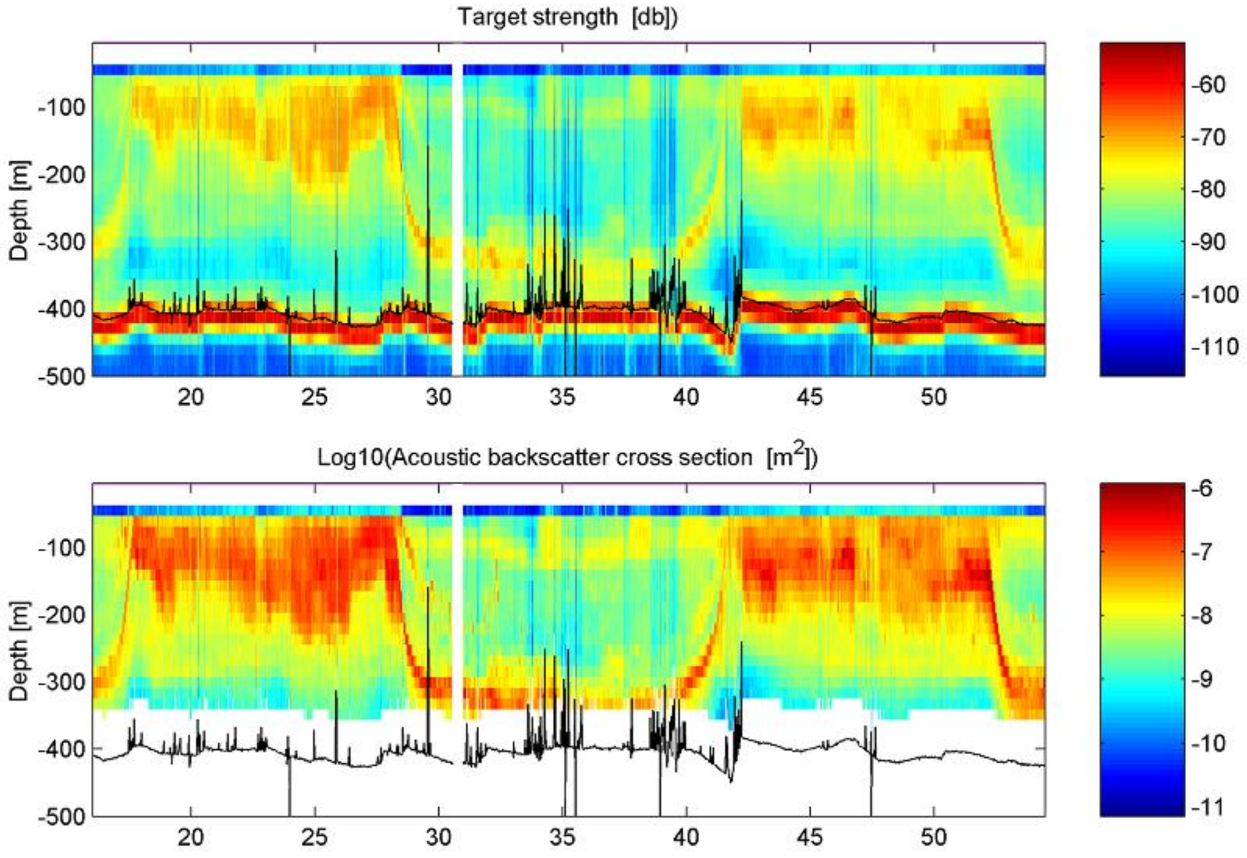
Haul	Bucket	Depth (m)	Mean depth (m)	Interval (m)	Lat.	Long.	Volume (m^3)	Bottom depth (m)	Winch Speed (ms^{-})	Rope Length (m)
MOC-D-24	L2	250-300	275	50	23°00‘37	13°03‘16	303.5	396	2.1	404
MOC-D-24	L3	200-250	225	50	23°00‘43	13°03‘19	194.3	395	2.5	314
MOC-D-24	L4	150-200	175	50	23°00‘48	13°03‘22	130.9	396	2.6	265
MOC-D-24	L5	100-150	125	50	23°00‘54	13°03‘24	118.4	396	2.4	210
MOC-D-24	L6	50-100	75	50	23°01‘00	13°03‘27	381.9	396	2.0	75
MOC-D-24	L7	25-50	37.5	25	23°01‘07	13°03‘30	65.5	396	1.9	37
MOC-D-24	L8	0-25	12.5	25	23°01‘09	13°03‘31	131.2	396	2.0	<15

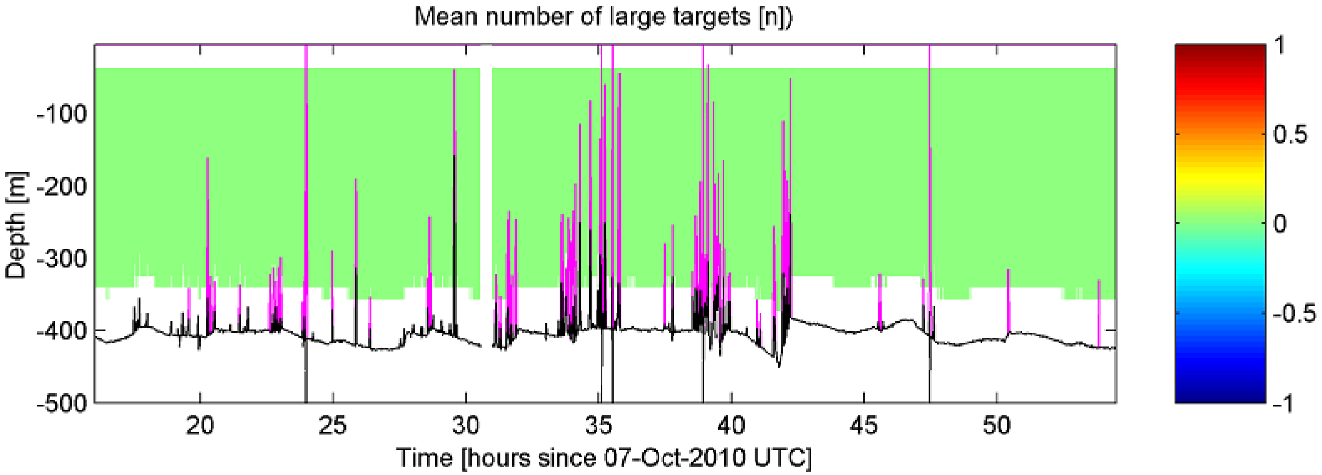
Station data: Day – 08 September 2010

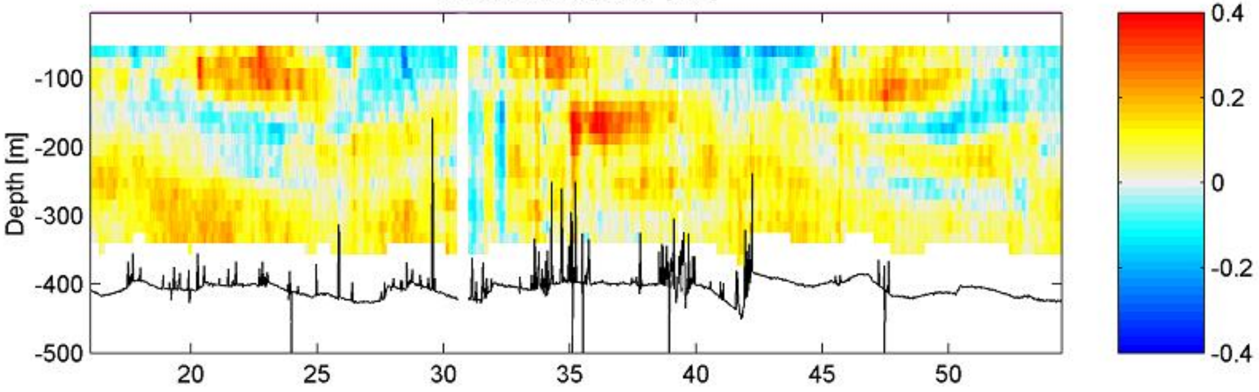
Haul	Bucket	Depth (m)	Mean depth (m)	Interval (m)	Lat.	Long.	Volume (m^3)	Bottom depth (m)	Winch Speed (ms^-)	Rope Length (m)
MOC-D-25	L2	300-350	375	50	23°00'‘10	13°03'‘17	197.3	403	1.5	522
MOC-D-25	L3	250-300	275	50	23°00'‘16	13°03'‘20	179.3	403	2.1	441
MOC-D-25	L4	200-250	225	50	23°00'‘03	13°03'‘16	164	403	3.6	361
MOC-D-25	L5	150-200	175	50	23°00'‘19	13°03'‘21	152.8	403	2.3	288
MOC-D-25	L6	100-150	125	50	23°00'‘24	13°03'‘23	218	404	1.5	188

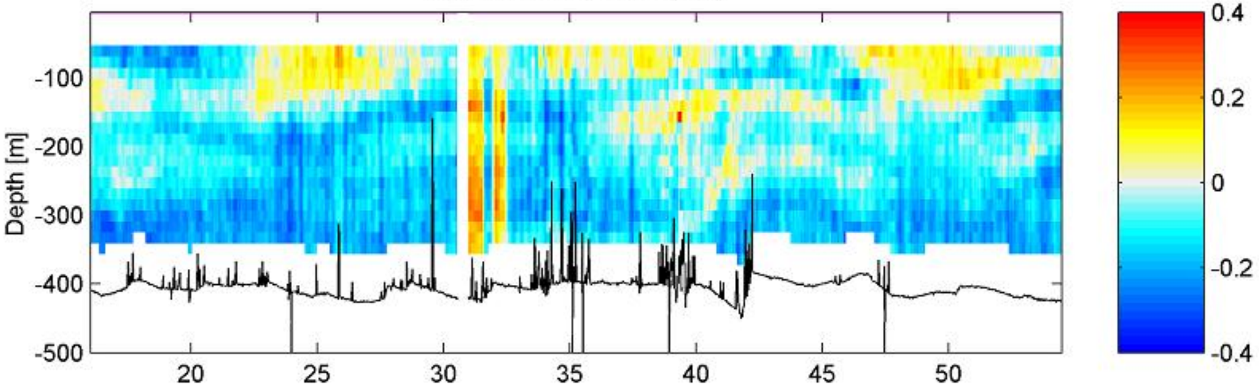
MOC-D-25	L7	50-100	75	50	23°00‘35	13°03‘29	211.7	404	2.3	90
MOC-D-25	L8	25-50	37.5	25	23°00‘37	13°03‘30	65.1	404	3.2	53
MOC-D-25	L9	0-25	12.5	25	23°00‘40	13°03‘31	150.3	404	1.8	<15

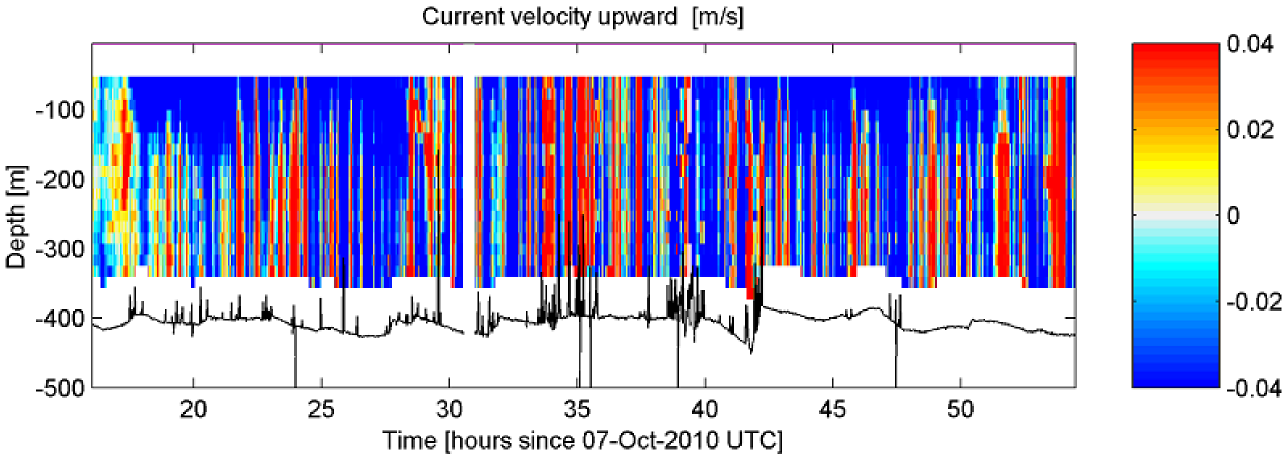
Vessel Mounted ADCP time series **Start**: 07 Oct' 2010 16:00:18 **End**: 09 Oct' 2010 06:29:13 Acoustic backscattering over: 60 sec




Mean number of large targets [n])
Depth [m]
-100
-200
-300
-400
-500
20
25
30
35
40
45
50
Time [hours since 07-Oct-2010 UTC]
1
0.5
0
-0.5
-1


Current velocity east [m/s]


Current velocity north [m/s]


Current velocity upward [m/s]
Depth [m]
-100
-200
-300
-400
-500
20
25
30
35
40
45
50
Time [hours since 07-Oct-2010 UTC]
0.04
0.02
0
-0.02
-0.04