Diel vertical migration behaviour in Euphausiids of the northern Benguela current: seasonal adaptations to food availability and strong gradients of temperature and oxygen

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In the highly productive northern Benguela upwelling system, euphausiids can dominate the mesozooplankton community and may contribute substantially to the vertical flux of organic carbon. The diurnal vertical distribution of four euphausiid species was observed over three seasons from different years. The most abundant, *Euphausia hanseni*, showed pronounced diel vertical migration (DVM), regularly crossing the thermocline and retreating again to the oxygen minimum zone (OMZ). *Nematoscelis megalops* was a weak migrant, persisting in the OMZ throughout 24 h. *Euphausia recurva* showed vertical migration into the OMZ but may have avoided oxygen concentrations below $1 \, mL \, O_2 \, L^{-1}$, *Euphausia americana* remained in the upper water layers above the OMZ. Thus, euphausiids were divided into different ecological groups using or avoiding the OMZ and were vertically separated, thus avoiding interspecific competition. However, DVM behaviour was adjusted to seasonal variations in water temperature, oxygen and food availability. A conceptual model, combining DVM patterns, environmental parameters such as temperature and food availability and physiological constraints such as species-specific respiration rates, was used to assess the carbon demand of the seasonal DVM behaviours. Energetic considerations based on the DVM model

showed that temperature acted as the controlling and limiting factor with food abundance further modifying vertical positioning of euphausiid species.

KEYWORDS: carbon demand; krill; oxygen minimum zone; physiological constraints; vertical migration model

INTRODUCTION

The northern Benguela upwelling system located at the west-coast off Namibia is one of the four major upwelling regions and the second most productive coastal upwelling system of the world oceans (Hutchings, 1992). It is characterized by strong temperature and oxygen gradients in the water column and a high seasonal and interannual variability in atmospheric forcing and water mass characteristics (Hutchings et al., 2009). Euphausiids and copepods can dominate the mesozooplankton communities in this region and are an important trophic link between primary producers and higher trophic levels throughout the world oceans (Ekau et al., 2010). Eight different euphausiid species regularly occur in the northern Benguela upwelling system with Euphausia hanseni and Nematoscelis megalops showing highest biomass and abundance (Barange, 1990). Due to different diel vertical migration (DVM) behaviour, different euphausiid species occupy divergent vertical strata (Barange, 1990) and in this way, krill can substantially contribute to the vertical flux of organic carbon to deeper layers (Tarling and Johnson, 2006). During their ascent and descent, euphausiid species in the northern Benguela upwelling system encounter various water masses and have thus to deal with a wide range of temperatures, dissolved oxygen concentrations and different trophic environments. Euphausiids, or in general zooplankton, have to adapt to these variations to some extent or have to avoid conditions which are not suitable for them.

The typical pattern of the DVM of zooplankton consists of an ascent during dusk and descent during dawn with shallow residence at night and deep residence by day (Andersen and Sardou, 1992; Timonin, 1997; Taki, 2008). However, also several observations of a "reversed" migration have been reported (Ohman et al., 1983). To explain the benefits of vertical migration, competing hypotheses like metabolic and demographic advantages, energy conservation, resource-related hypotheses and light-related mortality have been proposed (Lampert, 1989). Predator avoidance, food availability and metabolic capacity modify patterns of DVM in many zooplankton taxa (Buchholz et al., 1995). Trade-offs between these different aspects, e.g. maximum energy input versus maximum protection, have to be considered. A general concept or unifying theory is still lacking (Lampert, 1989). However, the possibility of building such a unifying theory is doubtful because of the high adaptive flexibility in behaviour and physiology of species. The DVM of euphausiids, in particular, has been the subject of several studies (Brinton, 1967; Barange, 1990; Buchholz et al., 1995; Tarling et al., 2000; Yoon et al., 2007; Taki, 2008). Some krill species migrate intensively, while others migrate only to a small extent and in euphausiids, such as N. megalops, the migration behaviour seems to be irregular (Yoon et al., 2007). In the current study, the DVM behaviour of four different krill species: Euphausia americana, E. hanseni, Euphausia recurva and N. megalops, was examined. Stratified net catches were conducted during three different cruises in summer 2004, autumn 2008 and winter 2010 at three locations over a period of 36 h. The data were related to the concurrent temperature profiles and the oxygen content of the water column. Furthermore, metabolic rates at different temperatures measured during shipboard experiments (Werner et al., 2012) were used to assess the energy demand of krill and the trophic environment was observed to investigate possible food-induced changes in the DVM behaviour of these species. These parameters were implemented in a conceptual model developed to estimate the carbon demand of different DVM behaviours and to allow comparison between cruises/seasons.

The aim of this work was to investigate the DVM behaviours of various, co-occurring euphausiids and to relate these DVM behaviours to seasonal differences of vertical gradients of food availability, temperature and oxygen constraints. Furthermore, energetic calculations were conducted in order to evaluate possible trade-offs between different proximate factors. The vertical migration studies performed at three seasons during different years were evaluated within the GENUS project (Geochemistry and Ecology of the Namibian Upwelling System), over a period of 6 years, with concurrent data on hydrographic and trophic conditions and subsequent calculation of energetic trade-offs in krill.

METHOD

Vertical distribution and migration behaviour of juvenile and adult euphausiids were investigated over a time

period of 36 h during three different cruises in the northern Benguela upwelling system during (late) Austral summer, autumn and (late) winter. Sampling was carried out at three different locations from RV *Alexander von Humboldt* in 2004 [Cruise AHAB02, Kunene-Transect at T2.2 (a); 03.–04. February 2004], RV *Maria S. Merian* in 2008 (Cruise MSM07/3, Kunene-Transect at T 2.2; 01.–02. April 2008) and RSS *Discovery* in 2010 [Cruise D356, Walvis Bay-Transect at T8.4 (a); 07.–08. October 2010; Fig. 1].

Net catches targeting euphausiids were conducted using a 1 m^2 MOCNESS (Multiple Opening and Closing Net and Environmental Sensor System, Wiebe *et al.*, 1985) with a large mesh size of 2000 μm and a soft cloth cod-end to increase the catchability of the net and to decrease damage to specimens at the same time. The MOCNESS was deployed every 6 h close to the bottom then hauled obliquely to the surface while opening and closing nets in a pre-set sequence (Table I). Zooplankton samples for description of the trophic environment were further taken with a double MOCNESS (mesh size 330 μm) during autumn 2008 and winter 2010. Sampling was done day and night at different strata in the water column: 350–300; 300–250; 250–200; 200–150; 150–100; 100–50; 50–25; 25–0 m during winter 2010 and 600–400; 400–200;

200–150; 150–100; 100–50; 50–25; 25–0 m during autumn 2008. The towing speed for both nets was 3.7 km h^{-1} and the samples were preserved in 4% buffered formalin and shipped to the laboratories in Bremerhaven, Germany. Before the nets were deployed, the hydrographic conditions, i.e. temperature (°C), salinity, oxygen (mL O$_2$ L^{-1}) and fluorescence (Chl *a*; mg m^{-3}), were recorded with a CTD-probe (Sea-Bird).

In the laboratory, juvenile and adult euphausiids were separated, counted and their lengths were measured between the front of the eyes to the tip of the telson using a millimetre scale under a stereomicroscope. The wet weight (WW) was determined on a microbalance (Sartorius LA 230 S). The relation between length and weight was characterized by regression analysis (Table II). Biomass of each species was calculated using species-specific weight to body length correlations. The abundances of the krill species were standardized to a volume of 1000 m^3 (ind. 1000 m^{-3}). In order to describe the vertical migration behaviour, the weighted mean depths (WMD) were estimated for each tow after Barange (Barange, 1990):

$$\text{WMD} = \frac{\sum(\text{ni} \times \text{di})}{\mathcal{N}} \qquad (1)$$

where di corresponds to the mean depth of the sample stratum; ni corresponds to the number of individuals at that depth and $\mathcal{N}$ is the sum of individuals over all sampling depths. WMD estimation was done for each species and for five different size classes (5–10, 11–15, 16–20, 21–25 and ≥26 mm) in order to reveal possible differences between these size classes. In parallel to the 36 h stations, except for summer 2004, the vertical distribution and abundance of the zooplankton community was investigated. These zooplankton samples were divided into four size classes: <0.5; 0.5–1; 1–2 and 2–5 mm. Copepod biomass was determined in order to further describe the vertical trophic environment during the cruise in winter 2010 (Karolin Bohata, IHF Hamburg, personal communication). These data sets were related to the DVM of krill species. Furthermore, the abundance of five dominant copepod species during winter 2010 was calculated: *Calanoides carinatus*, *Eucalanus hyalinus*, *Metridia lucens*, *Pleuromamma* sp. and *Rhincalanus nasutus*.

Chl *a* data (mg Chl *a* m^{-3}) were taken from CTD casts and converted into carbon content (*C*, mg C m^{-3}) using the conversion factor *F* [Equation (2)]. In the literature, the conversion factor *F* varies between 10 and 150 in general, and between 10 and 130 in the Benguela region (Pitcher, 1988).

$$F = C \times (\text{Chl } a)^{-1} \qquad (2)$$
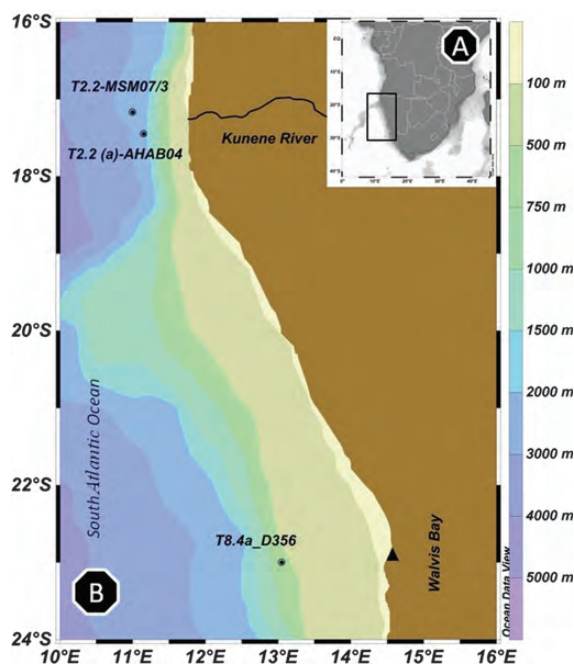
Fig. 1. Location of the northern Benguela upwelling system in the Southwest Atlantic Ocean (inset **A**) and the station positions sampled (**B**). Circles denote locations of sample stations, triangles geographic landmarks.

Table I: Sampling stations, sampling strata and sampling astronomic times for dusk and dawn (LT, local time) at different stations done with a MOCNESS (2000 μm) in the northern Benguela system during three cruises in 2004, 2008 and 2010

	D356	MSM07/3	AHAB02
Station/time	T8.4a/36 h	T2.2/36 h	T2.2(a)/24 h
Dates	07.10.2010–08.10.2010	01.04.2008–02.04.2008	03.02.2004–04.02.2004
Season	Winter	Autumn	Summer
Location	23°00 S; 13°02 E	17°46 S; 11°00 E	17°10 S; 11°18 E
Dusk/dawn (LT)	20:04/05:47	18:28/06:09	20:35/07:36
Dusk 1 (LT)	18:32–19:33	18:06–19:51	19:33–21:29
Midnight (LT)	01:05–01:54	00:00–01:26	00:12–01:51
Dawn (LT)	06:44–07:34	06:01–07:24	07:06–08:55
Noon (LT)	12:41–13:39	12:02–13:35	11:24–13:11
Dusk 2 (LT)	18:38–19:39	18:05–19:26	—
Strata sampled (m)	380–350; 350–300; 300–200; 200–100; 100–50; 50–25; 25–0	600–400; 400–300; 300–200; 200–150; 150–100; 100–50; 50–25; 25–0	600–400; 400–300; 300–200; 200–120; 120–80; 80–40; 40–0

Table II: Species-specific length (mm) to WW (mg) regressions for different krill species in the Northern Benguela upwelling system

Species	Regression	R^2	n
E. hanseni	$y = 0.0084 \times {}^{2.9447}$	0.939	110
N. megalops	$y = 0.0103 \times {}^{2.847}$	0.929	58

Fig. 2. Multi-beam acoustic backscatter profile (120 kHz) during a cruise with the RV Dr F. Nansen in March 2007 (BENEFIT Survey, 23/07, 7.2.—23 March 2007; Jens-Otto Krakstad, with permission).

However, an intermediate conversion factor of $F = 70$ was used for diatoms which dominated between Walvis Bay and Kunene River (N. Wasmund, IOW Warnemünde, personal communication).

Temperature-dependent oxygen consumption rates of *E. hanseni* and *N. megalops* given by Werner *et al.* (Werner *et al.*, 2012) were used to calculate the oxygen consumption at a depth-specific temperature. It was assumed that during migration, euphausiids had a 2.7 times higher respiration rate than at rest (non-migrating) (Torres and Childress, 1983). Multi-beam acoustic data (Jens-Otto Krakstad, IMR—Bergen, RV Dr F. Nansen, cruise report) showed a clear diurnal pattern most probably due to the vertical migration of *E. hanseni* as indicated by control net catches. *Euphausia hanseni* descended within 1 h from 30 m depth to 170 m depth at dawn (Fig. 2, used with permission). From the migration pattern recorded at the krill-relevant frequency, 120 kHz, descent and ascent speeds were assessed at 2.3 bl s^{-1}, assuming an average body length (bl) of 22 mm, taken from the length–frequency diagram (Fig. 3). As euphausiid swimming speed is ∼0–10 bl s^{-1}, with most of the observations at the lower end of this range (de Robertis *et al.*, 2003), these assumptions seem reasonable.

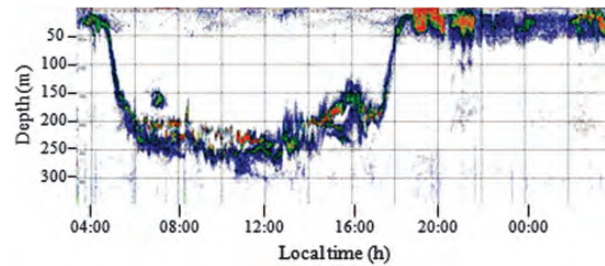We developed a conceptual model to investigate the effect of temperature and food availability on the migration behaviour of *E. hanseni* and *N. megalops*, accordingly. Temperature has a strong impact on metabolic rates and thus influences the DVM behaviour of krill species (Lampert, 1989), due to different thermal adaptations of species, different energy expenditures (Werner *et al.*, 2012), e.g. swimming costs, and a variety of other physiological processes, e.g. moult activities. Accordingly, the specific temperature profiles at the sampling stations had to be considered to calculate the energy demand or more specifically the oxygen uptake of euphausiids during DVM. Using the respiration rates, O:N ratios and estimated minimum food requirements, from Werner *et al.* (Werner *et al.*, 2012), we assessed the costs of DVM in *E. hanseni* and *N. megalops*. The temperature profiles at the sampling stations were used as a reference for calculating the carbon demand of different DVM behaviours. It was assumed that krill species migrated with a swimming speed of 2.3 bl s^{-1} in one "step" between their shallowest and deepest residence depths. Furthermore, a swimming speed of ∼1 bl s^{-1} was assumed to represent the routine metabolism of each species (Torres and Childress, 1983) and that a swimming speed of ∼1 bl s^{-1} was fast enough to perform their regular
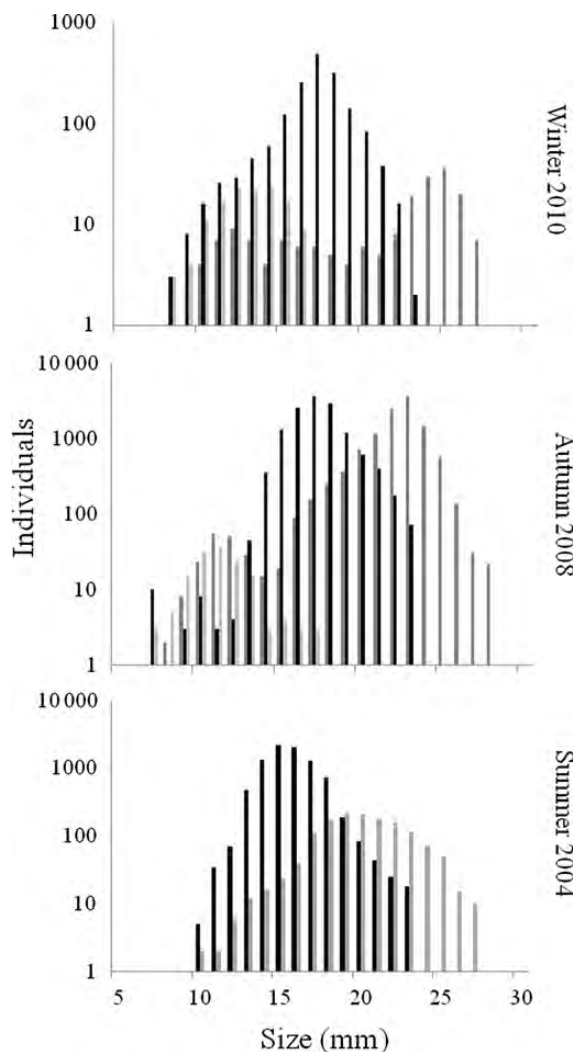
Fig. 3. Length–frequency distribution of *E. hanseni* (grey), *N. megalops* (black), *E. recurva* (light grey) and *E. americana* (light grey) at station T8.4a, Walvis Bay-Transect winter 2010, at station T2.2, Kunene-Transect autumn 2008 and at station T2.2a, Kunene-Transect summer 2004.

feeding activities. "Migration time" was estimated by dividing the differences between WMD at time 1 (shallowest distribution) and time 2 (deepest distribution) by a swimming speed of 2.3 bl s^{-1} (Fig. 4). The oxygen uptake and carbon demand was calculated over 24 h in order to estimate the energetic costs of a whole vertical migration cycle (in μmol O$_2$ g$_{ww}^{-1}$). The calculation was based on the following equation:

$$R_{DVM} = R_{Temp} \times h (\times 2.7) \tag{3}$$

where R_{Temp} (in μmol O$_2$ h^{-1} g$_{ww}^{-1}$) corresponds to the oxygen demand at a specific temperature, where "h" is the amount of time spent at that temperature/depth

(Fig. 4) and 2.7 corresponds to the behaviour whether the animals showed "normal" swimming speed (1 bl s^{-1}; routine metabolism) or "increased" swimming speed (2.3 bl s^{-1}; active metabolism). These calculations were repeated until a whole migration cycle was completed (24 h) and then the different R_{DVM} (μmol O$_2$ g$_{ww}^{-1}$ day^{-1}) were summed up. These results were converted from micromole to millilitre and then the carbon demands (CA$_{adj}$, mg C g$_{ww}^{-1}$ day^{-1}), as indices for minimum food requirements, were calculated using the following equation:

$$CA_{adj} = R_{DVM} \times RQ \times \frac{12}{22.4} \tag{4}$$

where RQ represents the "Respiratory Quotient", the molar ratio of carbon dioxide produced to oxygen consumed (0.97 for *E. hanseni* and 0.72 for *N. megalops*; see Werner *et al.*, 2012) and where 12/22.4 is the weight of carbon in 1 mol (22.4 L) of carbon dioxide. Assuming a dry weight (DW) of 25% WW and a carbon content of 40.4% DW in *E. hanseni* and 41.8% DW in *N. megalops* (Werner *et al.*, 2012), we calculated the daily ratio of the carbon demand (due to vertical migration) expressed in % body C day^{-1}.

The minimum food requirements, necessary to cover metabolic energy demands, were related to the trophic environment at the different stations in order to assess energetic trade-offs between temperature and food availability. To assess possible (dis-)advantages, e.g. energetic trade-offs, from the oxygen demand during different DVM behaviour and different temperature profiles, the minimum carbon uptake was calculated according to the assumption that assimilation efficiency is similar to that of *Euphausia pacifica*, thus 0.8 for phytoplankton and 0.9 for carnivorous diets (Ross, 1982). Due to the high variability of filtration rates for euphausiids given in the literature (Morris, 1984) and the uncertainty of (maximum) ingestion rates in krill (Pakhomov *et al.*, 1997; Atkinson *et al.*, 2006), filtration rates of a standardized *E. hanseni* individual (100 mg WW^{-1}) were assessed, assuming phytoplankton feeding to meet 75 and 50% of the daily metabolic requirements during nighttime. One calculation was based on the average amount of Chl *a* in the upper 50 m of the water column during winter 2010. Another approach used highest concentration of Chl *a* found in the upper 50 m during winter 2010, which was applied assuming that euphausiids were capable of detecting rich algal patches (Price, 1989). Filtration rates were estimated using the equation:

$$F = CA_{adj} \times 0.75 \times (h \times C_{Phyto} \times 0.8)^{-1} \tag{5}$$
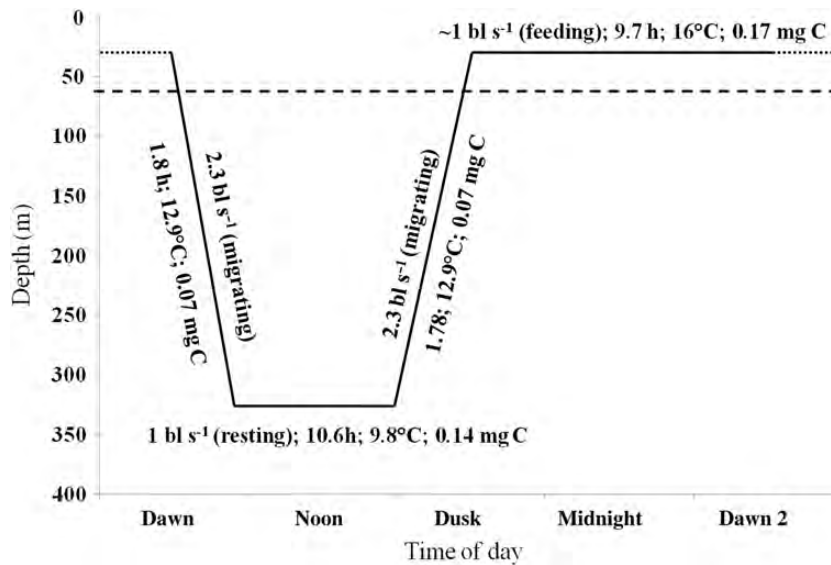
Fig. 4. Migration behaviour of *E. hanseni* (100 mg WW) depicted as a migration model. Shown are the assumed swimming speeds (bl s^{-1}), residence time (h), temperatures (°C), according to CTD data from the D356 cruise, and calculated carbon demands (mg C). Broken line indicates the position of the oxycline during the 36 h station T8.4a, Walvis Bay-Transect winter 2010.

where F represents the filtration rate (L h^{-1}), CA$_{adj}$ the daily carbon demand (mg C day^{-1}) [Equation (4)], the value 0.75 describes the fraction of phytoplankton feeding when this meets 75% of the daily metabolic requirements. This value is set at 0.5 when phytoplankton feeding meets 50%. Where h depicts the amount of time between astronomical dusk and dawn, C_{Phyto} reflects the average or maximum carbon concentration (mg C m^{-3}) due to phytoplankton in the upper 50 m of the water column and 0.8 is the assumed assimilation efficiency. Accordingly, zooplankton ingestion rates, e.g. copepod ingestion rates, were calculated by the equation given in Tarling *et al.* (Tarling *et al.*, 2000) for *Meganyctiphanes norvegica*:

$$\log_{10}G = 0.746 \times \log_{10}C + 1.092 \qquad (6)$$

where G is the ingestion rate of copepods and C the copepod/zooplankton biomass (>5 mm) around WMD during day (noon) and nighttime (midnight). The calculated time to cover the carbon demand by a carnivorous diet was then divided by 0.9, because an assimilation efficiency of 0.9 was assumed (see above). *Euphausia hanseni* is known as a filter-feeding omnivorous species, whereas *N. megalops* does not have a feeding basket adapted to filter feeding (Mauchline, 1980). All euphausiid species are omnivores, but *N. megalops* adults show a high degree of carnivory (Gurney *et al.*, 2001, 2002). Feeding in *E. hanseni* was presumed to take place during nighttime, whereas *N. megalops* fed throughout a 24 h cycle, as was suggested by Barange *et al.* (Barange *et al.*,

1991). In *E. hanseni*, feeding time, to cover carbon demand over 24 h, was calculated using different ratios of herbivorous and carnivorous diets (100/0%; 66/33%; 33/66% and 0/100%). The calculated feeding time in both species was used as an index for "optimal" migration behaviour in terms of food availability and temperature. An overview of the presumed residence times, temperatures and migration amplitudes of *E. hanseni* and *N. megalops* during the three different cruises are given in Table III.

Data analysis

The canonical correspondence analysis (CCA) applied is an appropriate multivariate method for analyzing the relationship between abundance of (marine) species and (seasonal) environmental variables (ter Braak and Verdonschot, 1995). Before application, VIF (variance inflation factor) values were calculated to test for co-linearity between environmental factors. VIF values larger than 30 were assumed to indicate co-linearity between environmental variables (explanatory variables) and such variables were then removed. Vertical distribution data (response variables) were square root transformed (Zuur *et al.*, 2007). CCA for the winter situation was applied using zooplankton (mg C m^{-3}) and Chl *a* (mg Chl *a* m^{-3}) concentrations and temperature (°C) as explanatory variables and species abundance (ind. 1000 m^{-3}) of *E. hanseni*, *E. recurva* and *N. megalops* as response variables. For the autumn situation zooplankton, Chl *a*

Table III: Estimated WMD (m), migration amplitudes (m), temperatures (°C), residence times (h), time for migration (h) and mean temperatures (°C) during migration of E. hanseni *and* N. megalops *used to calculate oxygen uptake (carbon demand) under different hydrographic conditions*

	Time of day (night/day)	WMD (m)	Migration amplitude (m)	Temperature (°C)	Residence time at depth time spend at depth (h)	Time for migration (h)	Mean temperature during migration (°C)
E. hanseni winter 2010	Night	25		16.0	9.7	3.7	12.9
	Day	325	300	9.8	10.6		
E. hanseni autumn 2008	Night	123		15.0	11.7	2.3	12.9
	Day	325	202	10.8	10.0		
E. hanseni summer 2004	Night	29		16.5	11	2.6	13.9
	Day	249	220	11.2	10.4		
N. megalops winter 2010	Night	163		12.2	9.7	1.9	11
	Day	289	126	9.8	12.4		
N. megalops autumn 2008	Night	234		12.7	11.7	1	13.5
	Day	168	66	14.2	11.3		
N. megalops summer 2004	Night	198		11.9	11	2.4	10.9
	Day	348	150	9.8	10.6		

and dissolved oxygen (mL O_2 L^{-1}) concentrations and temperature as explanatory variables and species abundance of *E. americana*, *E. hanseni* and *N. megalops* as response variables were included in the final run. Chl *a* and dissolved oxygen concentrations and temperature were chosen as explanatory variables for the CCA of the summer distribution and the distribution in general (all seasons pooled). Abundances of *E. hanseni* and *N. megalops* were defined as response variables in the last case. For multivariate analyses, the free software package R and the statistical package Brodgar (Version 2.6.6) were used.

RESULTS

During the three vertical migration studies, six euphausiid species were caught: *E. americana*; *Euphausia gibboides*; *E. hanseni*; *E. recurva*; *Nyctiphanes capensis* and *N. megalops* where *E. hanseni* and *N. megalops* showed by far the highest biomass and abundance. An overview of the biomass at different times and depths during autumn 2008 and winter 2010 are given in Fig. 5. Length−frequency distribution for the most abundant species during each cruise is given in Fig. 3.

Hydrographic and trophic conditions

The sea surface temperature (SST) and salinity were highest during autumn 2008, followed by summer 2004. During both seasons, the SST was well above 20°C and salinity close to 36. In contrast, during winter 2010, SST data and salinity were significantly lower, with 16.4°C and 35.57, respectively (Fig. 6). In summer and autumn, a 20−30 m thick surface layer was

bordered by a strong thermocline. During autumn, the thermocline ranged from 30 to 60 m (gradient: $0.25°C\ m^{-1}$) where temperature decreased to 16.5°C. In summer, a more intense thermocline (gradient: $0.5°C\ m^{-1}$) prevailed between 22 and 33 m where temperature decreased to 16.3°C and salinity to 35.57. In winter 2010, no thermocline could be detected and the hydrographic data showed a steady decline in temperature and salinity from the surface to a depth of ∼280 m. Below 280 m, salinity and temperature were constant near 34.87 and 10°C. During all seasons, moderate-to-strong oxyclines were detected (Fig. 6). Detailed descriptions of the different physical parameters during winter 2010, autumn 2008 and summer 2004 are given in the corresponding cruise reports (Ekau *et al.*, 2004, 2008; Buchholz 2010).

During winter 2010, the phytoplankton community in the upper 20 m at station T8.4a (Walvis Bay-Transect) was dominated by dinoflagellates with a WW of 117.9 mg m^{-3} corresponding to 15.5 mg C m^{-3} and diatoms showed a WW of 33.9 mg m^{-3} or 1.8 mg C m^{-3} (N. Wasmund, IOW Warnemünde, Germany, personal communication). CTD data showed highest Chl *a* concentration between 20 and 48 m with a maximum of 0.46 mg Chl *a* m^{-3} at 44 m depth. In autumn 2008, highest Chl *a* and phycoerythrin concentrations were found at around 20 m depth (CTD data; Fig. 6), with a Chl *a* maximum of 0.98 mg Chl *a* m^{-3} at 24 m. Chl *a* concentrations above 0.2 were found till 60 m depth. In summer 2004, highest Chl *a* concentrations were observed between the surface and 38 m where values were always above 0.2 mg Chl *a* m^{-3}, with a peak at 15 m showing a Chl *a* content of 0.69 mg m^{-3}. Chl *a* concentrations above 0.1 mg Chl *a* m^{-3} were observed down to 46 m depth.
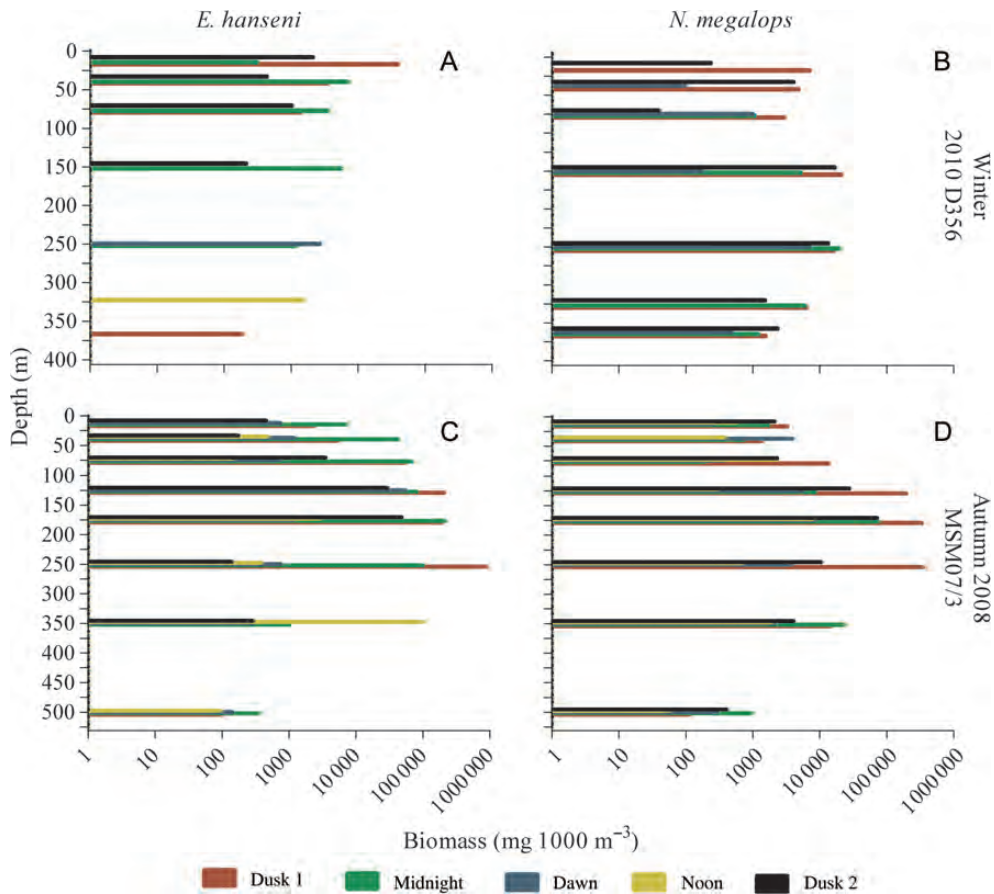
Fig. 5. Biomass/depth plots of *E. hanseni* (**A** and **C**) and *N. megalops* (**B** and **D**) during the D356 cruise in winter 2010 (A and B) and the MSM07/3 cruise in autumn 2008 (C and D). Data were standardized to a volume of 1000 m³.

Highest copepod abundance (73%) in winter 2010 was found close to the surface between 0 and 50 m during nighttime. However, ∼10% of the entire copepod community was found between 250 and 300 m. During the day, most of the copepods (90%) were found at depths between 250 and 350 m. The copepod community consisted of 94.5 ± 0.5% Calanoidea and 5.5 ± 0.5 Cyclopoida (Harpacticoida were not considered). The size classes between 0.5 and 2 mm made up to 91% of the copepods investigated both during day and night (Fig. 7). The most abundant copepod species at all depths was *M. lucens* (69.5 ± 14.5%; Fig. 7), followed by *C. carinatus* (20.0 ± 18.5%) and *Pleuromamma* sp. (7.0 ± 5.9%). In autumn, the highest zooplankton biomass occurred at ∼300 m during daytime (65 mg ww m⁻³) and 500 m during nighttime (159 mg ww m⁻³) (Fig. 8) (B. Martin, IHF Hamburg, personal communication). No zooplankton sampling was done in parallel to the 24-h station in summer 2004.

Zooplankton vertical distribution

In winter 2010 and summer 2004, *E. hanseni* displayed a "normal" migration pattern with an ascent at dusk and

a descent at dawn (Fig. 9). During daytime, the animals resided in the oxygen depleted waters ∼250–325 m (<1 mL O_2 L^{-1}). At night, *E. hanseni* entered the upper layers of the water column during both seasons. *Euphausia hanseni* showed pronounced migration amplitude of up to 300 m (winter 2010). In contrast, during autumn 2008, most of the animals did not enter the upper water layers above 100 m and the migration amplitude of ∼200 m was comparably small. Furthermore, between dusk and dawn, a reversed migration pattern was observed. In winter, *E. hanseni* migrated out of the OMZ during night, whereas during summer 2004 and autumn 2008, it appeared to stay in the OMZ throughout the whole diel cycle and did not migrate above the oxy- and thermocline. CCA plots indicated that the species optima differed between seasons. *Euphausia hanseni* abundance was positively correlated with temperature, dissolved oxygen concentrations and the trophic environment (Chl *a* and zooplankton) during winter 2010 and summer 2004. No such correlation was found during autumn 2008 (Fig. 10). However, in general, *E. hanseni* showed intense
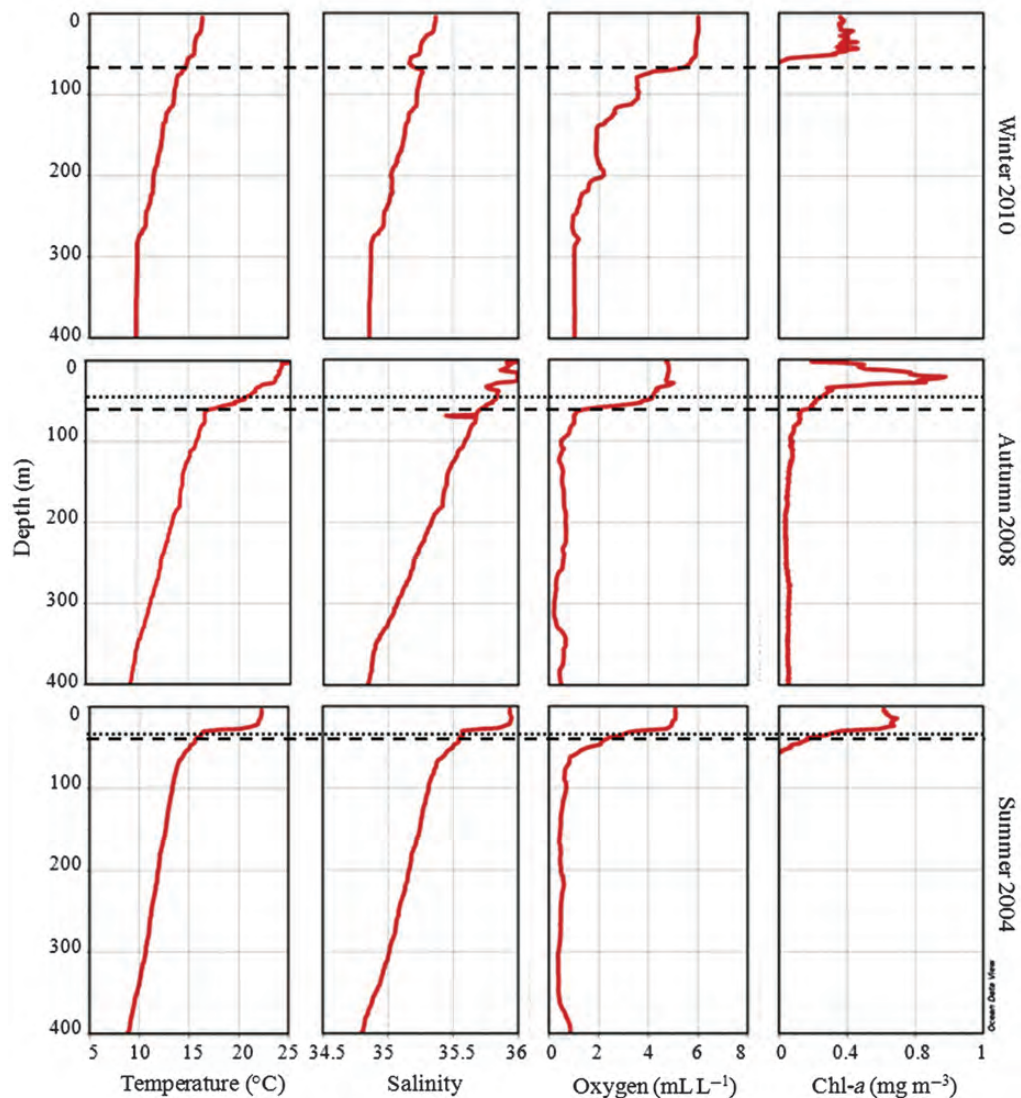
Fig. 6. Hydrographic conditions [temperature (°C), salinity, dissolved oxygen concentration (mL O_2 L^{-1}) and Chl a (mg Chl a m^{-3})] at station T8.4a, Walvis Bay-Transect winter 2010, at station T2.2, Kunene-Transect autumn 2008 and at station T2.2a, Kunene-Transect summer 2004. Broken line indicates the position of the oxycline. Dotted line indicates the position of the thermocline.

DVM, stayed in the OMZ during most time of the day and migrated into severely oxygen depleted waters (<0.3 mL O_2 L^{-1}, summer 2004, Fig. 9) during daylight. A similar DVM pattern was observed in *N. megalops* during winter 2010, with deeper residence depths during dusk and shallower residence depth during the day compared with *E. hanseni*. *Nematoscelis megalops* stayed in the OMZ throughout the entire day and showed a moderate migration amplitude of up to 126 m during winter 2010. During autumn 2008, a different DVM behaviour was observed. Here, the animals stayed in deeper waters throughout 24 h and small differences of ~60 m between day (noon) and night (midnight) were

noted in vertical distributions (Fig. 9). During summer 2004, the migration amplitude of *N. megalops* (150 m) was comparable to the winter situation. However, during summer, the animals reached their shallowest residence depth at midnight, whereas during winter 2010, they already arrived there at dusk. *Nematoscelis megalops* avoided the thermocline during all seasons and stayed in the OMZ throughout the whole diel cycle. Its vertical migration appeared to be irregular. Biplots of CCA indicated that the abundance of *N. megalops* was negatively correlated with temperature and dissolved oxygen concentrations during all seasons. During winter 2010 and autumn 2008, *N. megalops* vertical positioning
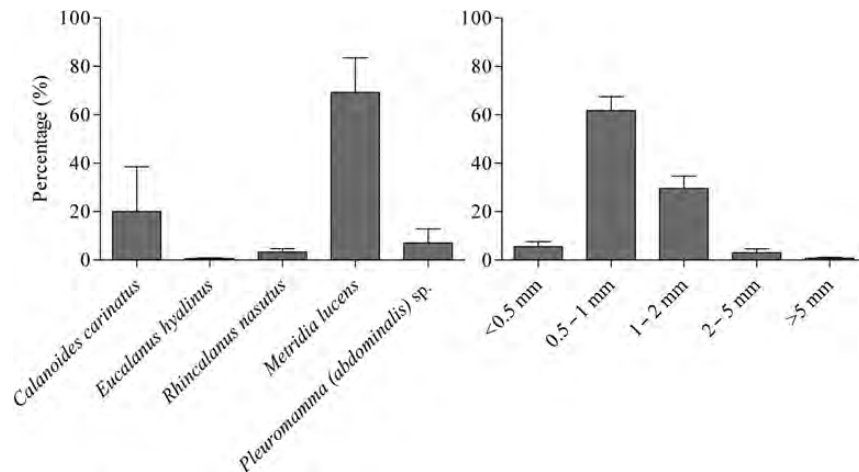
Fig. 7. Copepod species abundance (left) and size class abundance (right) at the 36 h station T8.4a, Walvis Bay-Transect winter 2010.

always overlapped with the "average" vertical distribution range of zooplankton (Fig. 8). DVM behaviour in *E. recurva* could only be investigated during winter 2010, because during the other seasons, insufficient animals were caught to allow estimation. *Euphausia recurva* resided in deeper waters during the day and shallower waters during the night (Fig. 9). This species showed intense vertical migration with persistence in or close to the oxycline during nighttime but entered the OMZ during dawn. Multivariate analysis showed that the abundance of *E. recurva* was negatively correlated with Chl *a* and zooplankton. No differences in the daytime versus nighttime vertical distribution of the species *E. americana* were found during autumn 2008. In *E. americana*, the highest abundance occurred in the upper 25 m of the water column and smaller proportions were detected down to 100 m depth during nighttime. Daytime distribution showed a peak between 0 and 50 m; some animals were also caught at a depth of 150–350 m. The animals appeared to mainly avoid the OMZ but crossed the thermo- and oxycline during dusk (2). The highest vertical abundance of *E. americana* coincided with high water temperatures, high dissolved oxygen and high Chl *a* concentrations as indicated by CCA. Due to insufficient animals caught during winter 2010 and summer 2004, no data for the DVM pattern of this species could be shown for these seasons.

During all seasons, *E. hanseni* showed significant differences between day and night vertical distributions. During the night, the animals appeared to have spread farther than during the day (Fig. 8). No differences in the daytime versus nighttime vertical distribution of *N. megalops* were found. During winter 2010 and summer 2004, a clear vertical separation between *E. hanseni* and

N. megalops during night appeared, where *E. hanseni* stayed in the upper water layers, whereas *N. megalops* resided in deeper waters (Fig. 8). In contrast, the vertical distributions of *E. hanseni* and *N. megalops* during autumn 2008 partly overlapped during nighttime (Fig. 8). During the day, vertical segregation between these species was evident during all seasons but less marked than during the night. In winter 2010, the vertical distribution of *E. hanseni* and *E. recurva* largely overlapped during night. Both species occupied the upper layers of the water column (25–75 m), whereas *N. megalops* persisted between 50 and 380 m (Fig. 8). In autumn 2008, there was a clear vertical separation of *E. americana*, *E. hanseni* and *N. megalops* during the day (Fig. 8). *Euphausia americana* occupied the upper layers of the water column (0–50 m), *N. megalops* persisted between 125 and 250 m and *E. hanseni* spent the day at a depth between 250 and 500 m. During night, the vertical separation was blurred. Vertical distribution of *N. megalops* and *E. hanseni* partly overlapped, but *E. hanseni* showed its highest abundance ∼150 m, whereas *N. megalops* occurred mainly at a depth of 250 m. *Euphausia americana* still persisted in the upper water layers (0–75 m).

Size class distribution

Due to the 2 mm mesh size used, our data sets did not provide enough data to determine the residence depth of smaller size classes <5 mm during daytime. However, in *E. hanseni*, smaller size classes showed narrower migration amplitudes compared with larger ones during winter 2010 and autumn 2008 (Fig. 11). In summer 2004, the largest size class (≥26 mm) migrated into shallower waters during the night and into deeper
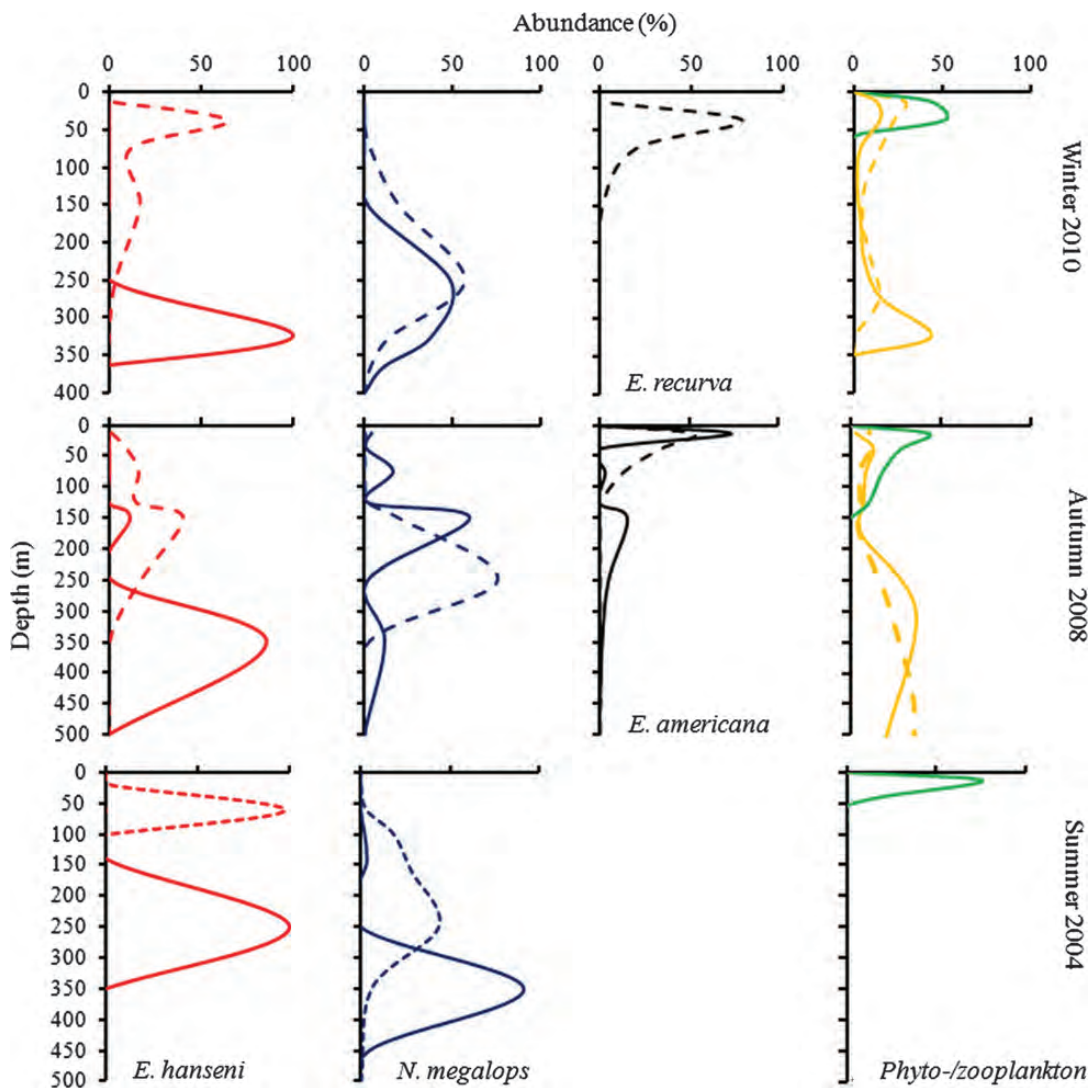
Fig. 8. Day (solid line) and night (broken line) distribution of *E. hanseni* (red line), *N. megalops* (blue line), *E. americana* (black line), phytoplankton (green line) and zooplankton (orange line) at the 36 h station T8.4a, Walvis Bay-Transect winter 2010, at station T2.2, Kunene-Transect autumn 2008 and at station T2.2a, Kunene-Transect summer 2004.

waters at dawn compared with the other size classes (11−25 mm). Therefore, its vertical migration range was slightly wider, i.e. 350 m compared with 317 ± 2 m (Fig. 11). In winter 2010, *N. megalops* individuals of size classes 5−15 and 21−25 mm showed comparable migration amplitudes (144 ± 13 m). The vertical migration range of the 16−20 mm size class was limited to 93 m. The 11−20 mm size class showed a shallow residence at night (dusk: 153 ± 9 m) and deep residence by day (dawn: 237 ± 3 m). After reaching their shallowest distribution at dusk (127 m), the 21−25 mm size class descended to 270 m depth (midnight) and then ascended again up to 140 m during dawn (Fig. 11). In autumn 2008, larger *N. megalops* migrated deeper than smaller ones, but only animals between 11 and 25 mm were

found at a depth of 500 m. In summer 2004, all three size classes showed similar depth distributions during dusk, dawn and noon, but a clear separation was observed at midnight, where smaller animals were found ∼167 m and bigger animals ∼282 m (Fig. 11). In *E. americana*, the smallest size class (5−10 mm) conducted the most extensive migration down to 274 m in autumn 2008. However, no migration pattern was found for this size class. Animals of 11−15 mm size showed a small migration amplitude of 60 ± 3 m. A "reversed" pattern was noted in animals between 16 and 20 mm. They resided in the upper water layers (13 ± 0 m) during dawn and noon. During dusk and midnight, the animals were located deeper at 38 and 75 m, respectively. No differences in the vertical
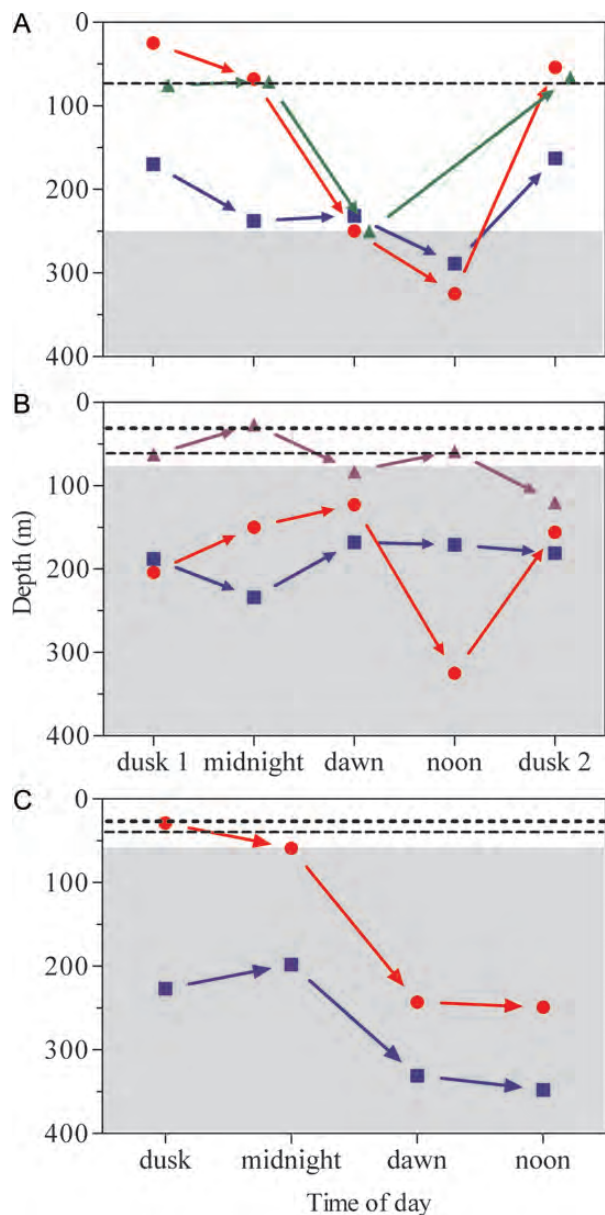
Fig. 9. WMD of *E. hanseni* (red line, grey in print, dots), *N. megalops* (blue line, black in print, squares), *E. recurva* (green line, light grey in print, triangles) and *E. americana* (purple line, light grey in print, triangles) at the 36 h station T8.4a, Walvis Bay-Transect winter 2010 (**A**), at station T2.2, Kunene-Transect autumn 2008 (**B**) and at station T2.2a, Kunene-Transect summer 2004 (**C**). Broken line indicates the position of the oxycline. Dotted line indicates the position of the thermocline. Shaded grey area indicates dissolved oxygen concentration below $1\,mL\ O_2\ L^{-1}$. For colour version, refer the online version of this figure.

distribution between size classes were observed in *E. recurva* during winter 2010 (Fig. 11).

### Energy demand and DVM behaviour

Filtration rates in *E. hanseni* were assessed at $0.9-1.1\,L\,h^{-1}$ ($1\,L\,h^{-1}$), assuming phytoplankton feeding to

meet 50% of the daily metabolic requirements and $1.3-1.6\,L\,h^{-1}$ ($1.45\,L\,h^{-1}$), assuming phytoplankton feeding to meet 75%. Carbon demands over 24 h of a standardized *E. hanseni* (100 mg WW) and standardized *N. megalops* (50 mg WW) over 24 h are given in Table IV.

The daily ratio of the carbon demands in *E. hanseni* varied between 4.5% body C day^{-1} during winter 2010 and summer 2004 and 4.2% body C day^{-1} during autumn 2008. In *N. megalops*, the daily ratio of carbon demand was 3.1% body C day^{-1} during winter, 3.6% body C day^{-1} during autumn and 3.3% body C day^{-1} during summer. Due to the differences in the migration amplitudes observed, the percentage of migration of the daily carbon demand increased. Accordingly, the percentage of migration of the daily carbon demand in *E. hanseni* was 32% during winter, 21% during autumn and 25% during summer. In *N. megalops*, this fraction was 18% during winter, 10% during autumn and 22% during summer (Table IV). In all three cases (summer 2004, autumn 2008 and winter 2010), both species were able to cover their daily minimum food requirements within 24 h. In *E. hanseni*, the calculated feeding time, to cover its carbon demand, varied between 16.6 h during winter ($F = 1\,L\,h^{-1}$; 100% phytoplankton) and 6.2 h during summer ($F = 1.45\,L\,h^{-1}$; 100% phytoplankton). Although the vertical distribution of *E. hanseni* during autumn 2008 prevented feeding on living phytoplankton, it would have been able to cover its carbon demand by daytime feeding within 9 h, exclusively feeding on copepods. However, 19.9 h were necessary assuming nighttime feeding. *Nematoscelis megalops* needed to feed between $8.3\,h \pm 3.8$ during winter 2010 and $9.7\,h \pm 9.3$ during autumn 2008. If *E. hanseni* would have shown a migration behaviour like that during winter 2010 and summer 2004, entering the upper water layers, assuming hydrographic and trophic conditions like those observed during autumn 2008, its carbon demand would have increased to 0.53 mg C day^{-1} (18% higher compared with winter and summer), corresponding to 5.3% body C day^{-1}. The estimated feeding time for such a scenario would vary between 5.3 h ($F = 1.45\,L\,h^{-1}$; 100% phytoplankton) and 14.6 h ($F = 1\,L\,h^{-1}$; 100% phytoplankton). The same scenario in *N. megalops* showed a 25% higher carbon demand compared with winter 2010 with a daily ratio of 3.9% body C day^{-1}. The estimated feeding time would be $7.1\,h \pm 2.5$.

Canonical correspondence analyses

An estimated 51.7% of the observed variance in the data set of the winter distribution in 2010 was explained by axis 1 and 7% by axis 2, as indicated by CCA (Table V). In autumn 2008, 67.4% of the inertia found
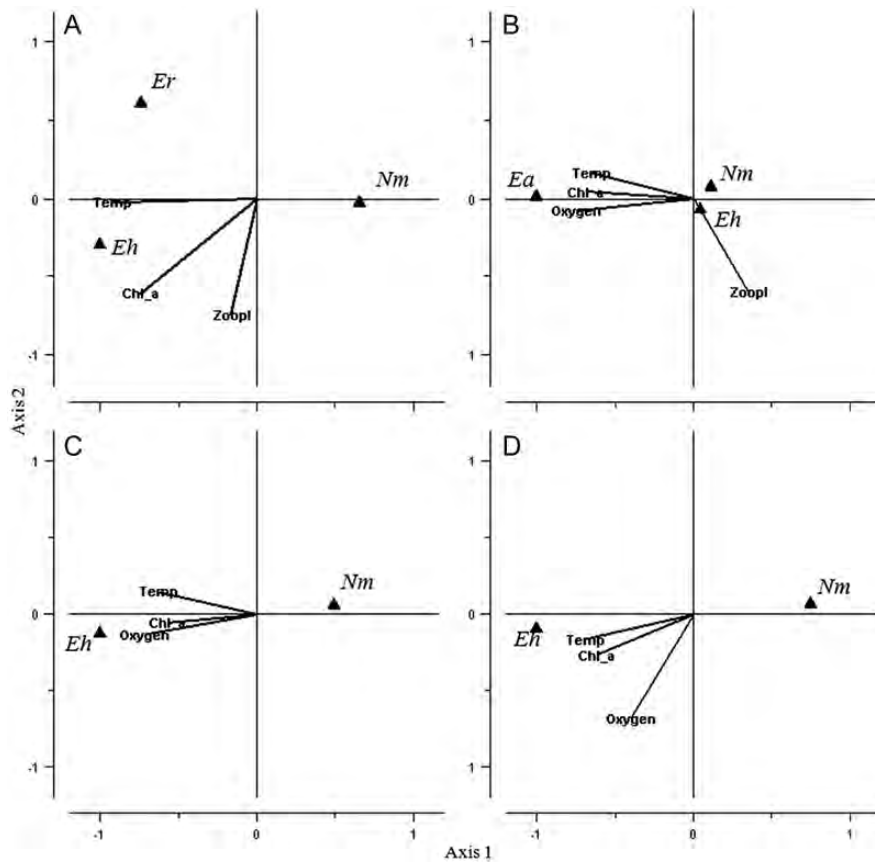
Fig. 10. CCA ordination biplots of species (*Ea*, *E. americana*; *Eh*, *E. hanseni*; *Er*, *E. recurva*; *Nm*, *N. megalops*) vertical distribution as response variables and environmental factors (Chl *a*, chlorophyll *a* concentration; Temp, temperature; Oxygen, dissolved oxygen concentration; Zoopl, zooplankton biomass) as explanatory variables based on CCA. Arrow length and arrow head indicate correlation between environmental variables and the CCA axes, triangles depict species composition. For a detailed description of the total inertia explained and the eigenvalues of the axis refer to Table V. (**A**) Winter 2010, (**B**) autumn 2008, (**C**) summer 2004 and (**D**) all seasons.

was explained by axis 1 and 4.5% by axis 2. 75.3% of the variance observed during summer 2004 could be explained by axis 1 and <0.01 by axis 2. In general, 26.9% of the variance in the DVM behaviour of krill as a function of environmental parameters (pooled data) could be explained by axis 1 and <0.01% by axis 2. The percentage of the total variation (inertia) in the vertical distribution of species that was explained by the chosen environmental variables was high. This clearly indicates that these parameters strongly influence the vertical position of euphausiid species in the northern Benguela upwelling system. An overview of correlations of each environmental variable (explanatory variable) with each axis is given in Table VI.

DISCUSSION

Each euphausiid species occupies different vertical strata as a result of DVM in the northern Benguela

upwelling system (Barange, 1990). In the current study, the vertical migration behaviour of four euphausiid species, *E. hanseni*, *E. americana*, *E. recurva* and *N. megalops* and their susceptibility to being constrained by water temperature, oxygen and food availability, was compared. The results will be discussed in the following sequence: (i) species-specific DVM in relation to hydrographic and trophic conditions, (ii) vertical segregation among species and (iii) DVM energy demand.

Species-specific DVM in relation to hydrographic and trophic conditions

Animals perform DVM to exploit the food-rich upper water layers during night and to reduce mortality from visual predators during the day. Differences in the day and night distributions, as well as the observed migration patterns as a whole, indicated that light, changes in light intensity (dusk/dawn), was the proximate cue initiating up and downward migration. However,
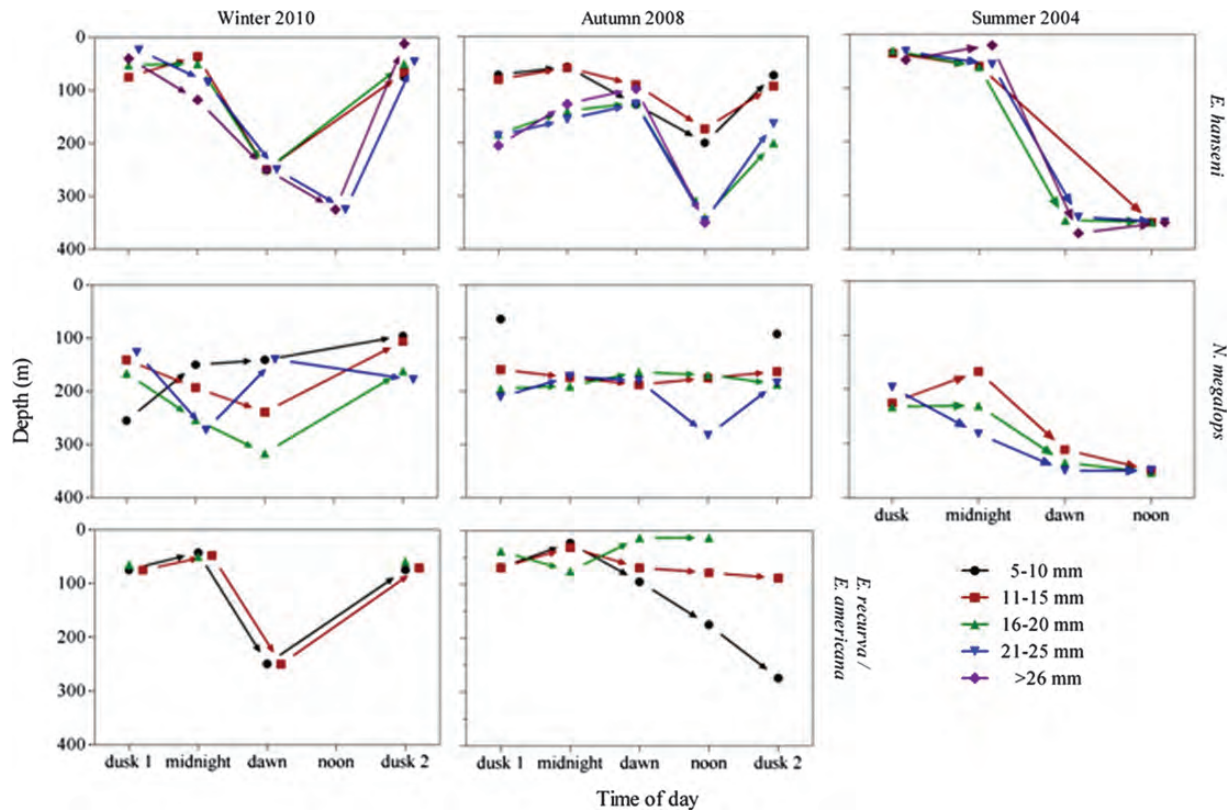
Fig. 11. WMD of different size classes of *E. hanseni*, *N. megalops*, *E. recurva* and *E. americana* at the 36 h station T8.4a, Walvis Bay-Transect winter 2010, at station T2.2, Kunene-Transect autumn 2008 and at station T2.2a, Kunene-Transect summer 2004.

pronounced migration leads to higher energy consumption, due to exposure to higher temperatures, low oxygen concentrations and increased swimming speeds during upward and downward migration (Torres and Childress, 1983 Lampert, 1989). In contrast, persistence in the cold deep during daytime may lead to low growth and reproduction rates (Lampert, 1989). Furthermore, abiotic factors like temperature and dissolved oxygen concentration are known to influence the vertical distribution of euphausiids (Buchholz *et al.*, 1995; Antezana, 2009; Escribano *et al.*, 2009). A comparison of the hydrographic conditions found at the sampling stations during the cruises in summer, autumn and winter is given in Table VII.

Vertical migration in *E. americana* was not pronounced in this study, in contrast to James (James, 1987), who reported extensive DVM in this species in the north-east Atlantic (over ~200 m). Since *E. americana* may avoid nets (James, 1987), the abundance estimated in the upper layers during the day may be underestimated. In the current study, most of the population stayed in the upper 150 m of the water column both during day and night and only a small part was found between 150 and 350 m during the day. Smaller animals migrated deeper than bigger ones which is in accordance with James (James, 1987), who showed that juveniles were found deeper than adults. Irrespective of the weak vertical migration amplitude, *E. americana* crossed the thermocline twice during nighttime but remained in or close to the thermocline during the day. *Euphausia americana* appeared to avoid low oxygen concentrations and only briefly entered the OMZ. In the north-east Atlantic, severe low oxygen concentrations occur in deeper layers (300−600 m) compared with the northern Benguela upwelling system (Fig. 6). Accordingly, avoidance of low oxygen concentrations may be the reason for the observed differences between this study and James (James, 1987). In the northern Benguela upwelling system, *E. americana* resided in well-oxygenated surface waters and showed no DVM.

In *E. recurva*, differences in vertical distribution between dusk and dawn were distinct, suggesting pronounced DVM. This contrasts with Griffiths (Griffiths, 1979) who found only little migration in *E. recurva* from the Coral and Tasmanian Seas during May 1972. However, Griffiths noted that most of the animals

Table IV: Estimated carbon demands (mg C day⁻¹) of a standardized E. hanseni *(100 mg WW) and* N. megalops *(50 mg WW), carbon demand due to migration (mg C day⁻¹), assumed food ratios and calculated feeding time (h) depending on the average and maximum Chl* a *concentration in the upper 50 m of the water column, assuming a filtration rate of 1.45 L h⁻¹ of* E. hanseni *and* N. megalops *during the 36 h studies in summer 2004, autumn 2008 and winter 2010*

	Carbon demand (mg C day^{-1})	Carbon demand for migrating (mg C day^{-1})	Food ratio (phytoplankton/zooplankton)	Calculated feeding time min−max (h)
E. hanseni winter	0.45	0.15 (32%)	100/0	9.3–11.4
			66/33	10.3–11.6
			33/66	11.3–11.9
			0/100	12.5 (night)
E. hanseni autumn	0.42	0.09 (21%)	0/100	9 (day)
			0/100	19.9 (night)
E. hanseni summer	0.45	0.11 (25%)	100/0	6.2–9.8
N. megalops winter	0.16	0.029 (18%)	0/100	5 (day)
			0/100	11.8 (night)
N. megalops autumn	0.19	0.019 (10%)	0/100	16.3 (day)
			0/100	3.1 (night)
N. megalops summer	0.17	0.037 (22%)	–	–

Table V: Eigenvalues, total inertia (variation), total inertia explained by the first two axes and the amount of inertia explained by the two axes as a fraction of the total explainable inertia in CCA

	Eigenvalue axe 1	Eigenvalue axe 2	Total inertia	Total inertia explained by axes 1 + 2 (%)	Variance of species−environment relation explained by axes 1 + 2 (%)
Winter 2010	0.14	0.019	0.27	58.7	77.8
Autumn 2008	0.131	0.009	0.19	71.9	21.2
Summer 2004	0.276	<0.01	0.37	75.3	27.0
All seasons	0.038	<0.01	0.14	26.9	15.4

Table VI: Correlation of environmental parameters (explanatory variables) with each axis tested by CCA

	Winter 2010		Autumn 2008		Summer 2004		All seasons	
	axis 1	axis 2	axis 1	axis 2	axis 1	axis 2	axis 1	axis 2
Chl *a* (mg Chl *a* m^{-3})	−0.75	−0.61	−0.69	0.04	−0.57	−0.06	−0.62	−0.27
Zooplankton (mg C m^{-3})	−0.16	−0.75	0.36	−0.60	n.t.	n.t.	n.t.	n.t.
Oxygen (mL O$_2$ L^{-1})	n.t.	n.t.	−0.75	−0.08	−0.72	−0.14	−0.40	−0.69
Temperature (°C)	−0.92	−0.03	−0.65	0.16	−0.63	0.15	−0.69	−0.17

n.t., not tested.

caught were in a reproductive state, with females carrying spermatophores and most of the males having spermatophores in their ejaculatory duct. Sex-dependent differences in the migration amplitude, with females migrating closer to the surface and using the energy supplement for reproduction, have also been shown for *M. norvegica* (Tarling, 2003). Accordingly, the differences between Griffiths (Griffiths, 1979) and our study could be explained by the divergent reproductive status which was not analysed here. Furthermore, water temperature in the upper water layers was higher off the east Australian coast compared with the winter situation in

the northern Benguela upwelling system. Thus, the temperature profile of the water column may have further influenced DVM behaviour in this species. Brinton (Brinton, 1967) showed that *E. recurva* individuals in the California Current, with hydrographic conditions comparable to our study, migrated intensively from 300–600 m during the day to 0–100 m during the night. Unfortunately, *E. recurva* was caught only during winter 2010, when no thermocline was found, thus the vertical distribution of this species in relation to the thermocline could not be observed. However, *E. recurva* showed long-range vertical migration during winter and was capable

Table VII: Comparison of hydrographic and trophic conditions during winter 2010, autumn 2008 and summer 2004

	Winter 2010	Autumn 2008	Summer 2004
Temperature			
SST (°C)	16.4	24.7	22.3
At 400 m depth (°C)	9.8[a]	9.3	8.9
Depth of thermocline (m)	n.d.	30–60	22–33
Thermocline (°C m^{-1})	n.d.	0.25	0.50
Oxygen level			
Min (mL O$_2$ L^{-1})	0.98	0.21	0.37
Max (mL O$_2$ L^{-1})	6.01	4.80	5.10
Depth of oxycline (m)	66–79	50–70	22–62
Oxycline (mL O$_2$ L^{-1} m^{-1})	0.15	0.15	0.10
Phytoplankton			
Min (0–50 m; Chl a mg m^{-3})	0.32	0.19	0.10
Max (0–50 m; Chl a mg m^{-3})	0.46	0.98	0.69
Average (0–50 m; Chl a mg m^{-3})	0.38 ± 0.03	0.52 ± 0.25	0.45 ± 0.24
Zooplankton			
Min (0–500 m; mg dw m^{-3})	1.2[b]	1.4	n.d.a.
Max (0–500 m; mg dw m^{-3})	31.6[b]	39.8	n.d.a.
Average (0–500 m; mg dw m^{-3})	8.0 ± 7.6[b]	10.6 ± 10.5	n.d.a.
Euphausiid species			
E. americana	+	+	+
E. gibboides	−	+	+
E. hanseni	+	+	+
E. recurva	+	−	−
N. capensis	−	+	−
N. megalops	+	+	+

[a]Bottom depth was 390 m. Therefore, temperature at 350 m depth was used.
[b]Bottom depth was 390 m. Therefore, data are given for 0–300 m depth.
n.d., not detectable; n.d.a., no data available.

of using the OMZ as a refuge during the day, but avoided severe low dissolved oxygen concentrations (below 1 mL O$_2$ L^{-1}).

In *E. hanseni*, a clear day/night difference was observed during all cruises, indicative of intensive migration with a migration amplitude of more than 300 m. Regular DVM was observed where animals ascended to the upper layers during nighttime and descended to deeper layers during the day. WMD plots suggested some degree of midnight sinking (cf. Tarling *et al.*, 1999a). *Euphausia hanseni* reached its shallowest distribution at dusk and deepest distribution at noon. During autumn 2008, the observed DVM pattern of *E. hanseni* was distinctly different in that the animals did not migrate into the upper water layers and reached their shallowest distribution already at dawn. *Euphausia hanseni* dispersed below the thermocline, thus avoiding higher water temperatures in the uppermost water layers which may lead to lower oxygen (carbon) demand over 24 h. These findings are partly in accordance with Barange (Barange, 1990) who found that *E.*

hanseni remained above and within the thermocline during nighttime. The need to cross the thermocline (Ohman, 1990) represents a major energy expenditure and thus carries a fitness cost and not a benefit. Accordingly, we presume that crossing the thermocline and entering warm waters above the thermocline may take place only for short (feeding) excursions or for re-productively active females (Tarling *et al.*, 1999a; Tarling, 2003). In contrast, during winter 2010, when no thermocline was detectable, *E. hanseni* entered the upper 20 m of the water column. However, the autumn distribution below the thermocline may exclude the om-nivorous species *E. hanseni* from the food-rich upper water layers. Thus, *E. hanseni* may not be able to feed, or only to a small extent, on living phytoplankton, as the phytoplankton community (Chl a content above 0.1 mg m^{-3}) was restricted to the upper 80 m. Accordingly, a mismatch between adequate food conditions and a higher energy expenditure, due to elevated water temperatures in the upper water layers, was assumed at least during autumn 2008 (see below). In autumn 2008, *E. hanseni* did not enter the upper water layers and overlap with the vertical distribution of prey items was low. However, zooplankton abundance between 200 and 500 m depth was very high and the persistence in the vicinity of prey maxima may have been sufficient to cover their daily carbon demands. Accordingly, the necessity to migrate was only poor. A match in vertical distribution of euphausiids and of their prey were investigated by Sameoto *et al.* (Sameoto *et al.*, 1987) who suggested that prey concentration may be more important than temperature in determining the vertical positioning of krill. In contrast, a re-evaluation of field data on DVM in *Daphnia* by Loose and Dawidowicz (Loose and Dawidowicz, 1994) suggested that vertical temperature gradients were more important than food gradients. Gibbons (Gibbons, 1993) suggested that *Euphausia lucens* in the southern Benguela reacts to food concentrations in two different ways. He stated that the vertical distribution of food determines the depth of *E. lucens* during nighttime and the amount of food affects the strength of the DVM response. For *Meganyctiphanes norvegica* in the Danish Läsö-Deep, Buchholz *et al.* (Buchholz *et al.*, 1995) showed that the upper temperature limit excluded this species from rich food sources (copepods and phyto-plankton) near the surface. However, with abundant food, other constraints, like water column structure, may act as controlling factors (Barange, 1990). Multivariate analyses showed that during autumn 2008, the least percentage of the vertical distribution variation could be explained by the environmental parameters, indicating that other factors should be considered. Nakagawa *et al.*

(Nakagawa *et al.*, 2001, 2002) showed that *Euphausia pacifica* may switch their feeding preferences from phytoplankton to zooplankton during DVM. Accordingly, *E. hanseni* may be able to cover its carbon demand in the deep, if food conditions were appropriate and water column structure may have prevented immigration into the upper water layers. This was further supported by the positive correlation between zooplankton biomass and the vertical positioning of *E. hanseni* during winter 2010 and autumn 2008 (Fig. 10). As a consequence, vertical migration may have been suspended for an unknown number of diurnal cycles. Differences in the migration behaviour between different size classes were not distinct, but migration amplitude of size classes 5–15 mm was less pronounced compared with the bigger size classes >16 mm. This may have reflected the ability of larger animals to swim faster and more efficiently. Additionally, smaller animals may attain higher survival rates when avoiding larger individuals, i.e. as "predator" avoidance, since cannibalism has been observed in several euphausiid species (Buchholz, 2003 and personal observation). Different swimming performance would explain why smaller animals reached their shallowest distribution at midnight, whereas bigger individuals already arrived there at dusk (Fig. 11). However, prey-size spectra differ with euphausiid size (Barange *et al.*, 1991). Accordingly, vertical segregation between different krill species, as a matter of competition avoidance and optimized foraging, may also play a role between different size classes. In general, *E. hanseni* is a pronounced long-range vertical migrator, entering the oxygen minimum zone (OMZ) and may adjust its migration behaviour to the prevailing trophic conditions.

Vertical migration in *N. megalops* is quite flexible, often irregular and strong net avoidance has been observed in this species (Wiebe *et al.*, 1982; Roe *et al.*, 1984; Barange, 1990). However, its migration amplitude is in any case smaller than in *E. hanseni* (Barange *et al.*, 1991). These findings agree with our study, where day/night differences in *N. megalops* were less marked than in *E. hanseni* and their migration amplitude was comparably small. During summer 2004, *N. megalops* migrated within a layer of ~60 m, whereas during autumn 2008, the animals showed enhanced vertical migration of up to 150 m. In winter 2010, a migration amplitude of 126 m was observed. As stated by Mauchline (Mauchline, 1980) and Barange (Barange, 1990), the upper limit of its vertical distribution is related to the position of the thermocline. Although Wiebe *et al.* (Wiebe *et al.*, 1982) argued that day/night differences were due to net avoidance in *N. megalops* and Roe *et al.* (Roe *et al.*, 1984) suggested that these differences resulted either from net avoidance, patchiness, vertical

migration or a combination of all three, we suggest a regular migration pattern with persistence in the upper layers during night and persistence in deeper layers during the day, however, typically without crossing the thermocline. Werner *et al.* (Werner *et al.*, 2012) showed that *N. megalops* is adapted to low water temperatures reflected by a Q_{10} of 1.9 between 5°C and 10°C. During all seasons, its vertical distribution ranged between 150 and 350 m depth, where temperature was below 15°C. A concentration of animals below the thermocline, as reported by Barange (Barange, 1990), was not supported by our observations. Vertical distribution of *N. megalops* during winter 2010 coincided with maximum copepod distribution during the day but not during the night. In autumn 2008, *N. megalops* showed no accordance with the zooplankton distribution by night and also during the day, only a small proportion was found at the same depth as the maximum zooplankton abundance. Accordingly, during winter in 2010, temperature and the maximum prey concentration may have regulated the vertical distribution of this krill species. *Nematoscelis megalops* stayed at a specific depth and may have exploited the migrating copepod community, as suggested by Barange *et al*. (Barange *et al.*, 1991) and further supported by multivariate analyses (Fig. 10). Size-dependent differences in DVM were obvious, where small animals (5–10 mm) stayed above the rest of the population or even showed a reversed migration pattern. Again, larger animals showed more pronounced vertical migration. Accordingly, different swimming performance could explain why small animals showed less pronounced migration amplitudes compared with larger ones. Furthermore, different size-dependent prey-size spectra (Barange *et al.*, 1991) and possible dietary shifts from omnivory to carnivory with an increase in size could lead to different strata being occupied, depending on the vertical distribution of varying prey sizes. In summary, *N. megalops* showed a weak migration pattern, avoided higher water temperatures and prevailed in the OMZ throughout 24 h.

Vertical segregation among species

Barange (Barange, 1990) showed that the euphausiid community in the northern Benguela upwelling system, regardless of migrating or non-migrating species, is segregated in space during night. Water column structure and reproductive strategies of particular species were responsible for this pattern. Vertical space partitioning was suggested to be a strategy of sharing highly productive areas, like the northern Benguela shelf/slope region, thus avoiding intraspecific competition (Barange *et al.*, 1991). Vertical separation among *E. americana, E. hanseni*

and *N. megalops* was evident in this study, both during day and night and during all seasons. However, vertical distribution among *E. hanseni* and *N. megalops* partly overlapped, but *N. megalops* was distributed over a wider range between ∼50 and 400 m, whereas *E. hanseni* was restricted to more narrowly defined strata. In the case of *E. hanseni* and *E. recurva*, their vertical distributions largely overlapped, at least during nighttime. *Euphausia hanseni* (Barange *et al.*, 1991) and *E. recurva* (Suh and Choi, 1998) feed omnivorously and therefore, competition for food sources is likely. However, *E. recurva* is a small species (max. length in this study was 17 mm, average 12.7 mm), whereas *E. hanseni* is comparably large (max. length 27 mm, average 20 mm). Assuming size-dependent prey-size spectra, this competition may be diminished and co-occurrence in the food-rich top layers may not result in food limitation in these species. As *E. hanseni* descended to deeper layers by day and the position of *E. recurva* during daytime (noon) is still unknown, food competition at least during the day may not take place. As different feeding patterns, and thus diel periodicity in feeding activity, could not be excluded, competition for food resources may have been further dampened. The highly productive northern Benguela upwelling system may provide favourable feeding conditions for both species at the same time. In conclusion, our results support the observation of a highly structured euphausiid community, in this way avoiding interspecific competition.

DVM energy demand

According to Torres and Childress (Torres and Childress, 1983), DVM is energetically expensive. Staying in the cold deep during the day is associated with low food concentrations, low growth, low fecundity rates and prolongation of the developmental time of eggs (Lampert, 1989).

The influence of temperature on the metabolism of both species differs significantly (Werner *et al.*, 2012). Accordingly, variations in the DVM behaviour, thus facing different temperatures over a diel cycle, lead to divergent carbon demands. In addition, a protein-oriented metabolism in *E. hanseni* and a lipid-oriented metabolism in *N. megalops*, with differing RQs, accounted for ∼33% higher carbon demand and thus minimum food requirements in *E. hanseni*. The proportion needed for swimming up and down of the total daily carbon demand was $26 \pm 5\%$ in *E. hanseni* and only $17 \pm 5\%$ in *N. megalops*. Thus, "swimming costs" were 53% higher in *E. hanseni* than in *N. megalops*. During autumn 2008, with highest water temperatures, both species avoided the upper water layers, and this observation is indicative of temperature as a controlling and limiting factor. Despite great behavioural and temperature variations, the carbon demands calculated for both species showed only small differences between seasons, with $4.4\% \pm 0.1$ body C day^{-1} in *E. hanseni* and $3.3\% \pm 0.2$ body C day^{-1} in *N. megalops*, indicative of a species-specific energy (carbon) expenditure. Food concentrations during the different seasons were high enough to cover their daily carbon demands within a reasonable amount of time. However, during autumn 2008, food concentrations for *E. hanseni* during nighttime were comparably low and the calculated feeding time would have been too long. If *E. hanseni* were able to switch their nighttime feeding activity from phytoplankton near the surface to daytime feeding of copepods in deeper layers, as shown for *E. lucens* (Stuart and Pillar, 1990) and *E. pacifica* (Nakagawa *et al.*, 2002), feeding time would be comparably short. If *E. hanseni* had migrated into the warm upper water layers during autumn 2008, its carbon demand would have been 23% higher. However, Chl *a* concentrations in the upper 50 m were ∼37% higher, counterbalancing the higher carbon demand due to higher water temperatures (Table VII). If we use the estimated feeding times as indices for "favourable" migration behaviour in terms of food availability and temperature, we should expect that *E. hanseni* migrated into the food-rich upper layers during each season and should preferentially have fed on phytoplankton. However, our observations during autumn 2008 showed that *E. hanseni* did not enter the food-rich upper water layers and may have switched to other food sources. A possible explanation may be the differences in calorific content between metazoan food sources and phytoplankton and the suggested species-specific energy (carbon) expenditure. An individual feeding carnivorously may need to ingest less material than one feeding on phytoplankton. Additionally, metazoan material may be digested more readily and the carbon ratio based on weight may be underestimated (Gurney *et al.*, 2002). This behaviour may change if individuals of different physiological states require higher water temperature, e.g. egg-bearing females. Day and night distributions of *E. hanseni* indicated that only part of the population was vertically migrating. Accordingly, differences in the DVM behaviour of individuals were an active behavioural response to internal physiological processes and external intraspecific stimuli, as suggested for *M. norvegica* by Tarling *et al.* (Tarling *et al.*, 1999a). Furthermore, suspended vertical migration with convenient food supply in deeper water layers may diminish both the daily carbon demand and the predation risk. Energy budgets for *N. megalops* indicated that persistence in the deep lead to low carbon demands which can easily be satisfied by exploiting

the migrating zooplankton community while staying constantly in the deep.

In general, the energetic considerations for both species showed that temperature acted as a controlling and limiting factor but could not be used alone to explain the vertical positioning and DVM behaviour of krill species in the northern Benguela upwelling system. Food abundance influenced the DVM behaviour of krill species, but the vertical distribution of krill did not always coincide with highest food concentrations. However, trade-offs between food abundance and temperature constraints suggested that different migration behaviours were energetically feasible. In the highly productive poly-pulsed northern Benguela upwelling system, where food abundance is seldom a limiting factor over longer periods, vertical distribution may result primarily from competition and predator avoidance. In other (mono-pulsed, i.e. with only one spring bloom) systems, with sometimes limiting food sources, trade-offs between temperature and food may result in different behaviours. However, the current study did not consider sex-dependent differences or predator abundance and net avoidance during the day, as a common capability in large euphausiids, which may have biased observations to a certain extent.

CONCLUSIONS

Our study showed seasonal differences in the DVM behaviour of *E. hanseni* and *N. megalops*, due to different water temperatures, dissolved oxygen concentrations, food availability and energetic trade-offs. Due to different thermal constraints, temperature acted as a controlling factor in *E. hanseni*, and as a limiting factor in *N. megalops*, influencing the vertical position of both krill species, as illustrated by energetic calculations. Most euphausiids in the northern Benguela upwelling system were capable of entering low dissolved oxygen concentrations, thus the active utilization of the OMZ. However, others were restricted to the upper water layers mainly avoiding the OMZ. Despite behavioural differences between seasons, *E. hanseni* is a pronounced long-range vertical migrant, regularly crossing the thermocline and retreating again to the OMZ, whereas *N. megalops* is a weak migrant, avoiding the thermocline and persisting in the OMZ throughout 24 h. *Euphausia recurva* performs intense DVM entering the OMZ but was not found at dissolved oxygen concentrations below $1 \, \mathrm{mL} \, O_2 \, L^{-1}$, whereas *E. americana* is restricted to the upper water layers not entering the OMZ. Accordingly, the euphausiid community is vertically separated, thus avoiding interspecific competition. The link between the observed migration patterns, hydrographic and trophic conditions and physiological constraints in *E. hanseni* and *N. megalops* indicated that different DVM behaviours were energetically feasible. Predator and competition avoidance were ultimate cues which may determine the DVM behaviour of euphausiids in the northern Benguela upwelling system. The relative change of light (day/night) was the principal proximate cue controlling the timing of upward and downward migration. Temperature profiles, position and intensity of the OMZ and food availability were further proximate factors which influenced the DVM behaviour. The conceptual model based on physiological considerations allowed us to identify which environmental parameter substantially modified the DVM behaviour of krill during different seasons and may be considered as a suitable tool to enhance understanding of the simultaneous effects of a suite of proximate factors on the DVM behaviour of zooplankton and may be used as a framework for further (numerical) DVM models.

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