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Life in the sea of plenty: Seasonal and regional comparison of physiological performance of *Euphausia hanseni* in the northern Benguela upwelling system

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ABSTRACT

Variability in upwelling events may lead to periods of constrained food availability in the northern Benguela upwelling system (NBUS), thereby affecting the physiological state and metabolic activity of euphausiids. Most attention has so far been paid to seasonal effects but little is known about regional variability. Metabolic activity (expressed by respiration and excretion rates) and physiological state (expressed by reproductive effort and moult activity) in *Euphausia hanseni* were examined at different stations during austral summer (minimum upwelling) and austral winter (maximum upwelling). Overall, regional differences in physiological state, influencing metabolic activity, were greater than seasonal ones, indicating favourable conditions for growth and reproduction year-round. Higher respiration rates were found for females in more advanced stages of sexual development. Moult stage did not affect oxygen consumption rates, however. The physiological state of *E. hanseni* at the time of capture may serve as a meaningful indicator of the associated hydrographic conditions in the NBUS, to be further used in eco-system analysis on seasonal or long-term time scales. A latitudinal comparison of species highlights the extraordinary physiological plasticity of euphausiids.

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1. Introduction

One of the four major Eastern Boundary upwelling systems, the northern Benguela upwelling system (NBUS), is located off the west-coast of Namibia. It is bordered in the north by the Angola-Benguela front (~17°S) and in the south by the strong upwelling cell at Lüderitz (26°S). The NBUS is characterized by perennial upwelling, with a maximum during austral winter/spring and a minimum during austral summer/autumn. Influenced by several atmospheric and oceanographic processes, the NBUS is a complex and highly variable ecosystem (Shannon and Nelson, 1996). In addition, wind-driven coastal upwelling makes this area one of the most productive ecosystems in the world's oceans. Fluctuations in upwelling intensity correlate with variations in the magnitude and direction of winds. Timing and duration of upwelling events influence the physical and biological properties of coastal seas, including the population biology of krill (Dorman et al., 2005). In the NBUS the biomass and distribution of mesozooplankton are spatially and temporally highly variable and upwelling intensity shows a clear seasonal signal (Martin et al., 2014). Upwelling events favour phytoplankton growth through nutrient input and subsequent zooplankton blooms, thereby supporting omnivorous species like *Euphausia hanseni*, the dominant krill species in the NBUS. Consequently, *E. hanseni* may show physiological adaptations to these poly-pulsed, upwelling-mediated, plankton blooms. The adjustment of metabolic rates in krill to (seasonal) differences in abiotic (e.g., temperature, oxygen) and biotic (e.g., food availability) factors has been the target of several studies (e.g., Buchholz and Saborowski, 2000; Kim et al., 2010; Meyer et al., 2009, 2010; Saborowski et al., 2002). However, the effects of regional variability in the physical and biological environment on euphausiid physiology are largely unknown.

Physiological processes such as growth and reproduction are influenced by food availability. Accordingly, euphausiids adapt their reproductive cycles to local feeding conditions (Tarling and Cuzin-Roudy, 2003); both egg production and length of the reproductive period are controlled by temperature and trophic conditions (Cuzin-Roudy and Buchholz, 1999). Furthermore, the recruitment success of krill species depends both on adequate condition of the females prior to spawning and favourable trophic conditions during larval development (Tarling and Cuzin-Roudy, 2003). Growth in euphausiids is controlled mainly by temperature and food supply (Huntley and Boyd, 1984) and moulting accelerates both respiration and excretion rates (Ikeda and Mitchell, 1982). Furthermore, seasonal changes in food availability can alter the chemical composition of zooplankton, which in turn affects respiration and excretion rates (Conover and Corner, 1968). The Northern Krill (*Meganyctiphanes norvegica*) for instance, tunes metabolic activity to both thermal and trophic conditions: In the naturally oligotrophic Ligurian Sea growth and reproduction in *M. norvegica* are

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maximized during the short productive season (Buchholz and Saborowski, 2000). The spatial and temporal availability of food constrains the physiological state of zooplankton. To better understand the consequences of this variability for *E. hanseni*, seasonal comparisons of the physiology of krill species are necessary. Such investigations are aimed at assessing the potential effects of krill's physiological performance on lower and higher trophic levels (e.g., the commercially important horse mackerel *Trachurus trachurus capensis*) and the food web structure in the NBUS as a whole.

In the present paper, seasonal (austral winter/summer) and regional (mesoscale) differences in metabolic activity (respiration and excretion) and physiological states (moult activity and reproductive effort) of *E. hanseni* were examined and are discussed in relation to upwelling intensity/trophic conditions and to seasonal adaptations of other euphausiid species such as Antarctic *Euphausia superba* and boreal *M. norvegica*. Furthermore, the impact of growth, depicted by moult stages and the influence of reproductive activity, depicted by sexual developmental stages (SDSs), on the oxygen uptake in *E. hanseni* were determined.

2. Materials and methods

2.1. Field sampling

Juvenile and adult Euphausiids were collected on board the RRS *Discovery* in austral winter 2010 (10.09.–13.10.2010, cruise D356) and on board the RV *Maria S. Merian* in late austral summer 2011 (30.01.–07.03.2011, cruise MSM17/3 (Werner et al., 2012)). Specimens were collected between Walvis Bay (23° S) and Kunene (17°25 S) in the northern Benguela upwelling system off Namibia. Krill were caught at different stations (8 stations during austral winter 2010; 5 Stations during austral summer 2011, Fig. 1) during nighttime with a 1-m^2 Multiple Opening and Closing Net with Environmental Sensing System (MOCNESS, Wiebe et al., 1985). Nighttime sampling ensured comparable catch depths, oriented at vertical migration in *E. hanseni* (see Werner and Buchholz, 2013) and prevented deep hauls causing stress on experimental individuals. A large mesh size (2000 μm) and a large soft closed cod-end bucket were used to further decrease stress on the experimental animals.

Animals for metabolic measurements were randomly chosen and transferred to aerated plastic aquaria filled with filtered seawater. All adult *E. hanseni* used for experiments were actively swimming, appeared healthy without obvious damage. The remaining animals from each haul, or a representative subsample, were used to assess the physiological state of *E. hanseni* in the field.

2.2. Hydrographic conditions

For seasonal comparison of sea surface temperatures (SST) and Chl *a* concentrations Moderate-Resolution Imaging Spectroradiometer (MODIS)-Aqua data, processed by the Ocean Biology Processing Group (OBPG) at Goddard Space Flight Center, were used. Ferrybox data (an automated monitoring system, especially for biological–chemical parameters, where water is pumped from subsurface layers into the measuring circuit of multiple sensors) provided by N. Lahajnar (University of Hamburg, Germany) were employed to determine small-scale differences in temperature (°C) and salinity at the different sampling stations during austral winter.

2.3. Metabolic measurements

Respiration measurements were conducted using a closed respirometry system with Oxygen-Microsensors (PreSens, Germany) and a 4-channel micro-fibre optic oxygen transmitter (Oxy-4-micro, PreSens, Germany) on board the research vessels. Specially designed small tube-shaped chambers (volume 20 mL) were used as respiration chambers optimized for krill (cf. Werner et al., 2012). As *E. hanseni* is a strong diel vertical migrator (Barange, 1990; Werner and Buchholz, 2013) respiration measurements were conducted in a temperature-controlled water bath at three different temperatures (5, 10 and 15 °C) reflecting the water temperatures around Walvis Bay (23°S) between 50, 300 and deep water layers and around 700 m respectively. Regional comparisons of metabolic rates were conducted at 10 °C only. All experiments were performed within 24 h of capture in order to minimize confounding effects due to starvation (Huenerlage and Buchholz, 2013). *E. hanseni* adults were first acclimated for approximately 12 h at 8–10 °C and then further acclimated to the experimental temperatures in the respiration chamber for 1 to 4 h. The oxygen uptake was monitored in the dark over a period of 3 to 6 h. Each temperature experiment was run in triplicate with an additional empty chamber to serve as the control. The respiration chambers were placed in a water bath, which was controlled by a lab cooler (±0.5 °C; Julabo F25, Germany). Filtered seawater (0.2 μm Acropak™ 1000 Capsule, Pall Filtersystems GmbH, Germany) was used to minimize bacterial oxygen consumption. Since the metabolic rate of animals is known to vary both interspecifically and intraspecifically with body mass, respiration rates (RR_{O2}) were standardized to units of comparison of μmol O_2 h^{-1} $g_{ww}{}^{-1}$ (g_{ww}: grammes wet weight). After each experiment animals were sexed by identification of the thelycum (copulatory structure on underside of thorax of female euphausiids) or the petasma (modified endopodite of the first pair of pleopods of male

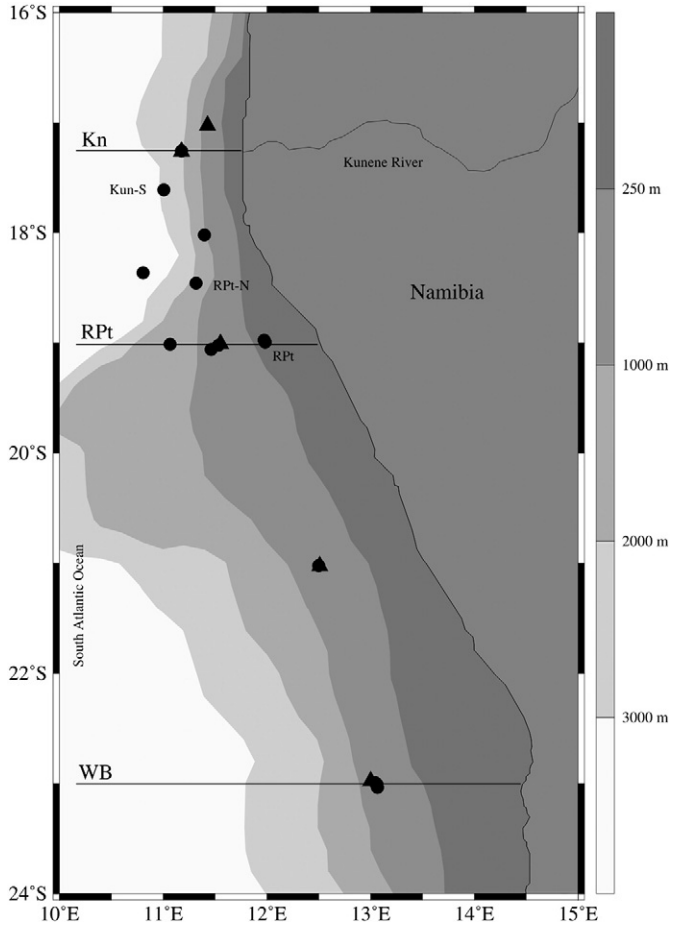

Fig. 1. Location of the northern Benguela upwelling system and stations sampled during austral winter 2010 (dots) and austral summer 2011 (triangles). Lines represent positions of transects: Walvis Bay (WB, 23°S), Rocky Point (RPt, 19°S) and Kunene (Kn, 17.25°S). Stations used for regional comparison during austral winter 2010 are highlighted by acronyms (see text). This map was created using the ODV4 software (Schlitzer, 2015).

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