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High resolution vertical distribution of the copepod *Calanus chilensis* in relation to the shallow oxygen minimum zone off northern Peru using LOKI, a new plankton imaging system

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ABSTRACT

The vertical distribution of copepodite stage V and adult *Calanus chilensis* was studied on two transects across the Humboldt Current System off northern Peru using the LOKI system. LOKI is an optical plankton recorder, which simultaneously collects images of zooplankton and environmental data such as temperature, salinity, oxygen, and fluorescence. Image quality allowed determination of CV, females and males and identification of *C. chilensis* from 3 co-occurring Calanid copepods. *C. chilensis* was inhabiting the upper 250 m. Highest abundances with a maximum of ca. 44.000 Ind. m^{-2} were observed in a narrow band within Cold Coastal Water at stations closest to the coast, coinciding with the Poleward Undercurrent. This raises questions for the life cycle closure within the Humboldt Current system. In contrast to observations in the southern part of the Humboldt Current System, the three stages studied were most abundant in hypoxic waters at oxygen concentrations between 5 and 50 μM. Thus *C. chilensis* seems to be the only species of the family *Calanidae* where not only a resting stage can tolerate hypoxia, but also both adult stages. This impacts availability to predators, as despite a locally high biomass only part of the population is available to anchovy and other important fish species which are restricted to waters with higher oxygen concentrations.

1. Introduction

At low latitudes, the eastern Pacific Ocean is characterized by a permanent, often shallow, intermediate oxygen minimum zone (OMZ) (Karstensen et al., 2008; Stramma et al., 2010). This zone is thickest, comes closest to the surface, and is most depleted of oxygen within two tongue-like projections lying north and south of the equator (Wyrtki, 1967). In regions of coastal upwelling, nearly anoxic water from this OMZ can be found within a few meters of the surface. Biogeographical studies suggest that the OMZ may act as a barrier to dial vertical migration and limit diel and ontogenetic migration. Ekau et al., 2010 and Gilly et al. (2013) reviewed the literature describing the impacts of oxygen deficiency on pelagic communities.

In the Humboldt current system (HCS) the most important parameter shaping the zooplankton communities is the OMZ (e.g. Judkins, 1980; Bertrand et al., 2008; Escribano et al., 2009), which divides the water column into completely different habitats. Compression of the vertical ranges of most zooplankton species into the uppermost layer by shoaling of the oxygen minimum may have an important effect on the trophodynamics of the ecosystem. Increased near-surface concentrations of zooplankton also may enhance feeding rates in planktivores, such as the Peruvian anchovy (Judkins, 1980). A recent study (Stramma et al., 2008) documents that the oxygen concentrations in tropical oceans at a depth of 300 to 700 m seem to have declined during the past 50 years. The expected strengthening of the OMZ by global climate change scenarios may have substantial biological and economical consequences. To understand and predict future changes a better understanding is required of the interactions between the OMZ and the pelagic ecosystem.

Due to their high abundance and outstanding importance for the nutrition of many fish species, copepods of the order *Calanoida* are a key component in the highly productive upwelling systems of the world oceans, e.g. *Calanus helgolandicus* off NW Africa (Postel et al., 1995; Ceballos et al., 2004), *Calanus agulhensis* in

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the Benguela system (Huggett, 2001), *Calanoides carinatus* off NW Africa (Binet and Suisse de Sainte-Claire, 1975; Postel et al., 1995), in the Benguela system (Verheye, 1991), off Somalia and in the Arabian Sea (Smith 1984), *Calanus pacificus californiensis* in the California current system (Alldredge et al., 1984), and *Calanus marshallae* (Peterson, 1998) off Oregon. In the HCS *Cyathea australis* and *Calanus chilensis* are among the most numerous and important species. Unfortunately they were often not distinguished as their taxonomic status is unclear (Geynrikh, 1973; Semenova et al., 1982; Marín et al., 1994; Morales et al., 2010). There are controversial observations as to their vertical distribution and tolerance to low dissolved oxygen concentrations (DOs) (e.g. Quiñones et al., 2006; Judkins, 1980). However, understanding the vertical habitat partitioning is crucial to understand the functioning of the highly productive HCS, where the most important planktivorous fish, *Engraulis ringens* and *Sardinops sagax*, have only limited tolerance to low oxygen concentrations (Jarre et al., 1991).

During METEOR cruise 77/4 we deployed LOKI (Lightframe On-sight Keyspecies Investigation), a new system for high resolution zooplankton sampling (Schulz et al., 2010) on transects along 6°S and 3°35′S off the Peruvian coast. LOKI was used to sample the distribution of *C. chilensis* in relation to its ambient environment like temperature, salinity, oxygen, and chlorophyll a concentrations with a resolution in the one-meter scale.

2. Methods

2.1. Sampling

The vertical distribution of *C. chilensis* was studied at 11 stations (Fig. 1a, Table 1) on transects along 6°S and 3°35′S off Peru during RV METEOR cruise 77/4 between February 2 and 4, 2009. Our two zonal transects extended over 215 km (3°35′S) and 275 km (6°S), respectively, from the deep basin to the very narrow Peruvian shelf. Samples were taken with LOKI, a new optical system for high-resolution plankton investigations (Schulz et al., 2010). LOKI was towed vertically at a speed of 25 cm s^{-1} from 500 m or close to the sea floor to the surface. Due to winch problems the tows were generally not continuous. Therefore a continuous haul was reconstructed using depth information for each image. Organisms were concentrated with a plankton net (0.3 × 0.3 m mouth opening, 200 μm mesh) mounted on the front of the frame (Schulz et al., 2010, their Fig. 1g) and imaged during the passage through a cuvette. After the passage they were collected in a net (200 μm mesh) mounted on the outlet of the sampling head. Samples were preserved in 4% formalin buffered with borax.

2.2. Imaging and environmental parameters

The dimension of the imaged object plane, perpendicular to the cross section was 18 mm × 13 mm. Images were recorded by a 2/3″ Sony ICX285 chip of a Prosilica GigE camera (1.3 megapixel; 1 pixel equals 13.4 μm in the object plane). Imaging takes place with 15 frames s^{-1} at full resolution. Exposure triggered a high power LED flash allowing exposure times of > 90 μs to avoid motion blurring. Each image frame was processed in real time and Areas Of Interest (AOI) were extracted in the underwater unit. Time stamps were assigned to every AOI and allowed association with recorded environmental parameters. Final data handling was managed by a SQL database backend.

Temperature and salinity were measured concurrently with a CTD (SBE 37-SI MicroCAT) mounted on the LOKI frame. Oxygen data were collected by the IFM-Geomar group, Kiel, with an Anderaa oxygen optode 3830. After calibration these oxygen data were merged with the LOKI data in the browser, where environmental parameters are assigned to each image. For calibration of the optode, oxygen from bottle samples was determined by Winkler titration with an rms difference of the CTD oxygen sensor of ± 1.3 μM (Stramma, personal communication). The LOKI haul usually followed immediately the CTD cast, resulting in a time lag of 1 to 1.5 h between the two casts; only at station 18 it was 3.5 h (Table 1). Temperature profiles from the hydrographic CTD and LOKI CTD were checked for potential shifts of thermocline depth as indicator for changes in oxycline depth (Table 1). For better comparison, all DOs (dissolved oxygen concentration) are presented in μM, literature data will be converted using the relationship 1 ml l^{-1} = 44.7 μM.

Fluorescence was measured with a Backscat in-situ Fluorometer (Dr. Haardt, Kiel). The probe was calibrated with chlorophyll measurements of water samples taken from the CTD rosette system on several stations and depths during the transects (GF/F filter, 0.5 to 1 l). Concentrations of chlorophyll a were determined on a Turner Design fluorometer after grinding and extracting (90% acetone) filtered samples from water casts (Evans and O'Reilly, 1966). Pure chlorophyll a in 90% acetone (Sigma) was used for calibration.

2.3. Species and stage identification

Four species of the family *Calanidae* were found in the samples: *Nannocalanus minor, Mesocalanus tenuicornis, Cosmocalanus darwinii* and *C. chilensis*. The latter is the most abundant and the largest species. We used prosome length to identify *C. chilensis*. Measurements were conducted under the microscope at 20 × magnification to the nearest 0.05 mm. The morphological separation of *C. chilensis* and another south eastern Pacific copepod, *C. australis*, is extremely difficult (e.g. Geynrikh, 1973; Marín et al., 1994). Both species have been found previously in coastal and oceanic waters off Chile (e.g., Brodsky, 1959; Arcos, 1975). However, Marín et al. (1994) found only *C. chilensis* in the Pacific Coastal waters of South America between 10°S and 4°S. In contrast, Morales et al. (2010) found both *C. chilensis* and *C. australis* to inhabit the sea off central Chile. It seems that *C. australis* tends to decrease in abundance between 34° and 37°S, whereas both species have similar proportions in the oceanic and coastal areas between 37° and 39°S. Therefore various morphometric measurements of exopodites and endopodites of the 5th leg together with length/width ratios of the cephalon as proposed by Marín et al. (1994) and Arcos (1975) were conducted on approximately 200 males and females from different stations.

LOKI images were analysed manually. Image quality allowed a clear separation of *Calanidae* from co-occurring families and distinction between copepodite stage V (CV), males (AM) and females (AF; Fig. 2) in about 70% of the images. In the other images the abdomen with the genital segment and the base of the first antennae, the characters used for distinction, were not in an appropriate position. Prosome length of all *Calanus*-type objects in the respective size range was measured on-screen with a built-in tool in the LOKI software and used for separation of other *Calanidae*. As we could not distinguish younger copepodids on the images, they were not considered. Specimens in the uppermost 1 m were excluded from analysis due to uncharted wave action at recovery.

3. Results

3.1. Hydrographic environment

The distribution of temperature, salinity, and oxygen along the transects is shown in Fig. 1b–g). Six major water masses were