

Hypoxia tolerance in the copepod *Calanoides carinatus* and the effect of an intermediate oxygen minimum layer on copepod vertical distribution in the northern Benguela Current upwelling system and the Angola–Benguela Front

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Abstract

There is a growing concern that hypoxic and anoxic areas in the sea spread in extent and intensity, posing a severe risk to marine ecosystems and fisheries. Hypoxia may affect fish stocks directly or via detrimental effects on important prey species, such as zooplankton. A unique feature of the northern Benguela Current upwelling region and Angola–Benguela frontal system is a pronounced intermediate oxygen minimum layer (IOML) at 60–500 m depth with oxygen concentrations $\leq 1.4 \text{ mg O}_2 \text{ l}^{-1}$ (minimum $< 0.7 \text{ mg O}_2 \text{ l}^{-1}$). Field studies during February–March 2002 demonstrated that the abundance of calanoid copepods and the biomass of mesozooplankton in general were severely reduced within the IOML. The dominant copepod *Calanoides carinatus* showed a bimodal vertical distribution with parts of the population either comprising all developmental stages concentrated in the surface layer (0–60 m), or copepodids C5 diapausing below 400 m depth apparently avoiding the IOML. Accordingly, abundances of other calanoid copepods were higher at the surface and below 300 m than in the centre of the IOML. The scarcity of planktonic life within the IOML raises the question whether this layer represents an effective barrier for zooplankton vertical migrations. Especially in *C. carinatus*, ontogenetic vertical migration plays a key role in the retention of the population within the productive upwelling region and for the rapid re-colonisation of plumes of newly upwelled water. To address this issue, the hypoxia tolerance of *C. carinatus* was determined in a series of laboratory-based, closed-bottle experiments in January 2005. Copepods were kept in gas-tight bottles and the decreasing oxygen concentrations were monitored to establish their minimum oxygen demands. Although copepodids survived apparently unharmed at surprisingly low oxygen concentrations of ca. $1.5 \text{ mg O}_2 \text{ l}^{-1}$, they could not tolerate oxygen levels $< 1.1 \text{ mg O}_2 \text{ l}^{-1}$, implying that the core of the IOML, where O_2 concentrations are below this threshold, is uninhabitable for *C. carinatus*. In contrast, the IOML may represent a refuge from competition and predation for other copepod species specifically adapted to hypoxic environments.

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1. Introduction

The spreading of hypoxic and anoxic conditions in the ocean is a burning issue of growing global concern. At least partly caused by anthropogenic impacts such as global warming and eutrophication, oxygen depletion is expected to affect large areas of coastal and marginal seas as well as low-latitude open oceans in the forthcoming decades. The United Nations Environment Programme (UNEP, 2004a,b) recently identified oxygen depletion as the most eminent future threat to global fishery resources and marine ecosystems. Consequently, in 2005 the Scientific Committee on Oceanic Research (SCOR) established a new Working Group on Natural and Human-Induced Hypoxia and Consequences for Coastal Areas.

Extended regions with hypoxic conditions occur naturally in the Benguela Current, a productive upwelling system off the west coast of southern Africa. On the northern Benguela shelf off Namibia, there is an almost permanent hypoxic layer above the seafloor with occasional outbreaks of toxic hydrogen sulphide in the near-bottom water (Weeks et al., 2002). In addition, very low oxygen concentrations of $<1.4 \text{ mg O}_2 \text{ l}^{-1}$ are found at 60–500 m depth (the so-called intermediate oxygen minimum layer, IOML, Verheye and Ekau, 2005). The effects of oxygen depletion can be studied at all trophic levels of the Benguela ecosystem. Via biogeochemical interactions, oxygen depletion contributes to a horizontal zonation of phytoplankton groups (i.e. diatoms and dinoflagellates vs. cyanobacteria) across upwelling regions (Schiebel et al., 2004, Rixen et al., 2006). When remineralisation of organic matter in the water column occurs under anoxic conditions, nitrate is reduced to molecular nitrogen N_2 , which is not available for most primary producers (Kuypers et al., 2005, Rixen et al., 2005, 2006). Besides denitrification, anaerobic ammonia oxidation (Anammox) also contributes to the nitrogen deficiency for phytoplankton (Kuypers et al., 2005). Only cyanobacteria, which are able to utilise molecular nitrogen, flourish under these circumstances and replace diatoms and dinoflagellates in later stages of maturing upwelling plumes (Schiebel et al., 2004, Rixen et al., 2006).

Mesozooplankton in general and dominant herbivorous copepods, such as *Calanoides carinatus*, in particular play an important role in the Benguela upwelling ecosystem forming a trophic link between primary production and small pelagic fish (anchovy and sardine) and higher trophic levels (Loick et al., 2005, Verheye et al., 2005). In the southern Benguela system off South Africa, annual secondary production by copepods alone

is about $100 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Richardson et al., 2001). Highest zooplankton biomass values are usually recorded at some distance offshore, “downstream” from the coastal band of high phytoplankton biomass. These areas of high zooplankton biomass constitute important feeding grounds and habitats for juvenile anchovy and sardine (Ekau et al., 2001, Ekau and Verheye, 2005). Studies on mesozooplankton vertical distribution during field expeditions in 2002 and 2004 showed a bimodal distribution with high abundances of *C. carinatus* in the upper 30 m layer or below 400 m depth, but almost none in the intermediate layer coinciding with the IOML (Auel et al., 2005, Verheye et al., 2005).

Moreover, many key zooplankton species including copepods and krill (Euphausiacea) perform vertical migrations, either on a diel basis or ontogenetically based. For instance, *C. carinatus* survives periods of food limitation during the cessation of upwelling as sub-adult copepodite stage C5 in a dormant state at 400–700 m depth (Auel et al., 2005, Verheye et al., 2005). Plumes of newly upwelled water are quickly re-colonised by copepods advected with the upwelled water onto the shelf from this quasi-permanent reservoir. The copepods moult to the adult stage, mate and utilise the high productivity following the new upwelling event for reproduction and growth. They are transported offshore within the wind-driven upwelling plume (Peterson, 1998). When the productivity of the plume decreases following nutrient depletion and the mixing with the surrounding oligotrophic offshore waters, pre-adult C5 copepodids, having stored large lipid reserves (Verheye et al., 2005), descend and enter diapause. The triggers for this behaviour and whether the descent is an active migration or the consequence of passive sinking are still unknown. It is likely that the extended IOML acts as a barrier preventing the completion of life cycles of ontogenetic vertical migrators and interfering with vertical feeding migrations of daily ascending zooplankton such as krill. Thus, in addition to the effects on the distribution of zooplankton, the IOML may also negatively affect zooplankton secondary production and, hence, food availability for pelagic fish.

Because the majority of the vertical flux of particulate organic matter (POM) to the deep sea is achieved by fast sinking large particles, such as copepod faecal pellets (Honjo, 1980, Urrère and Knauer, 1981, Turner, 2002), mesopelagic zooplankton considerably contributes to and accelerates the export of photosynthetically fixed carbon from the euphotic zone to deeper layers. Via feeding and faecal pellet production as well as vertical migrations (“biological pump”, Longhurst and Harrison, 1989, Longhurst, 1991), zooplankton changes

POM properties in terms of particle abundance, size and shape as well as biochemical composition and sinking speed (González and Smetacek, 1994, Wassmann, 1998). Thus, a reduced abundance of mesopelagic zooplankton due to the IOML may also affect pelago–benthic coupling processes and even result in a shift towards a more retention-oriented system.

The large-scale regime shifts and species replacements in the Benguela upwelling system have attracted considerable interest in recent years (Moloney et al., 1991, Jarre-Teichmann et al., 1998, Verheye et al., 1998, Shannon and Jarre-Teichmann, 1999, Shannon and O'Toole, 1999, Verheye, 2000, Shannon et al., 2003, Hutchings et al., 2006). Hypoxia has been suggested to play as critical a role as other environmental factors in limiting pelagic species and processes (Ekau and Verheye, 2005, Verheye and Ekau, 2005). Besides marine upwelling regions, this issue has also been studied in freshwater lakes (Beadle, 1963) focusing on hypoxia effects on copepods and rotifers (Ruttner-Kolisko, 1980, Esparcia et al., 1989, Kizito and Nauwerck, 2005, Žurek, 2006). However, empirical data on the hypoxia tolerance of marine pelagic species are rather scant.

Therefore, the two main objectives of the present study were (i) to collect detailed information on the vertical distribution of key zooplankton species, in particular copepods, in relation to the IOML and (ii) to experimentally determine the hypoxia tolerance of the dominant copepod *C. carinatus* under controlled laboratory conditions. This two-pronged approach allows discussion of the ecological implications of physiological limits with regard to the vertical distribution and migration of zooplankton in the northern Benguela upwelling system.

2. Materials and methods

2.1. Field study: Vertical distribution of copepods in relation to the IOML

Stratified day and night zooplankton samples were collected using multiple opening/closing net hauls (Hydro-Bios MultiNet Type Midi, 0.25 m² mouth opening, 200 µm mesh size) in the upper 700 m at three stations (T2-7, T4-1 and T4-5) across the Angola–Benguela frontal system (Fig. 1) during a BENEFIT (Benguela Environment Fisheries Interaction and Training) cruise in February–March 2002 aboard the South African FRS “Africana” (see Verheye and Ekau, 2005 and Verheye et al., 2005 for full details). These samples provided quantitative data on the vertical distribution of dominant zooplankton taxa, in particular calanoid cope-

pods, relative to the IOML. Zooplankton samples were preserved on board in a 4% formalin seawater solution and analysed in the laboratory under a dissecting microscope. Environmental data, including vertical profiles of water temperature, salinity and oxygen concentration, were collected from CTDO₂ casts down to 1000 m depth at the same stations.

In order to standardise and present data on the vertical distribution of different copepod species collected at the different stations over varying depth intervals and at different times of day, and to allow comparison, preferred depth layers were calculated assuming a random distribution of individuals within each sampled depth interval. These data are presented in the form of box plots, where each box represents 50% of the population and the bars encompass the 5th to the 95th percentiles.

2.2. Laboratory experiments: Hypoxia tolerance of *C. carinatus*

In order to experimentally determine the hypoxia tolerance of *C. carinatus*, one of the dominant species in the Benguela Current region (Verheye, 1991), individuals were collected during short tows (5–10 min) with a drift net (300 µm mesh size, mouth opening 0.25 m²), usually from an inflatable boat, within 1 km distance from the coast off Sea Point (Cape Town, South Africa) and on one occasion from the end of the Cape Town harbour mole, between January 11th and 24th 2005. At the time of sampling, strong upwelling conditions prevailed with sea-surface temperatures along the coast of 11–12 °C. The net was fitted with an extra-large cod-end bucket so as not to harm the copepods. Samples were gently transferred into buckets with ambient seawater and transported to a temperature-controlled room (11–12 °C) at the Marine Research Aquarium in Sea Point for subsequent experimental studies. Specimens of copepodite stage C5 as well as adult females were sorted from the samples under a dissecting microscope and kept in the room in buckets filled with 0.2 µm filtered seawater for 1–2 days of acclimation prior to the start of the experiments.

Usually, 10 adults or 20 copepodids were transferred into gas-tight glass bottles filled with ca. 110 ml of 0.2 µm filtered and oxygenated seawater. In total, 15 experiments were conducted and the animals were incubated for 9–20 h under *in situ* conditions of 11–12 °C and a 12:12 h light:dark cycle. Initially, it was intended to conduct separate series of experiments with adults and copepodids C5. However, this proved to be impractical because many copepodids moulted during the incubation period.

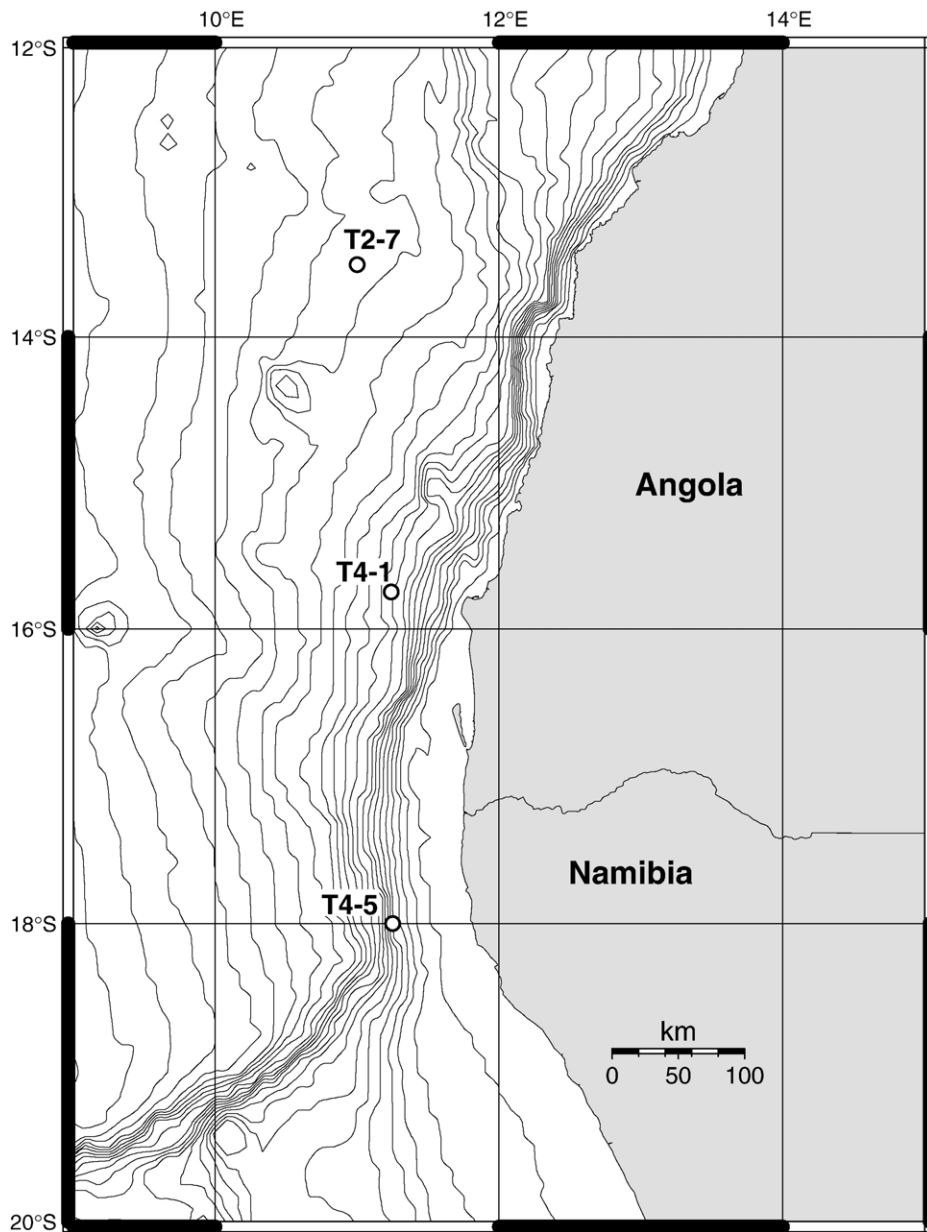


Fig. 1. Map of the study area with three representative stations of zooplankton sampling during the BENEFIT 2002 cruise: T2-7 in the southern Angola Current, T4-1 in the Angola–Benguela Front and T4-5 in the northern Benguela Current.

Therefore, the results of all 15 bottle incubations were combined to form one set of experiments.

During the first phase of the experiment when mortality was expected to be low due to high oxygen levels, the number of copepods still alive was recorded at regular time intervals and each time the oxygen concentration in one of the bottles was measured by a Winkler titration (Ikeda, 2000, precision: $0.08 \text{ mg O}_2\text{l}^{-1}$). During the second phase, as mortality increased with decreasing oxygen concentration, experiments

were terminated at certain rates of survivorship, i.e. 70%, 60%, 20%, 5% and 0%, and oxygen concentrations were again determined by Winkler titration.

3. Results

3.1. Hydrographic regimes and environmental data

The area of investigation during the cruise in late summer 2002 was located off the coasts of southern

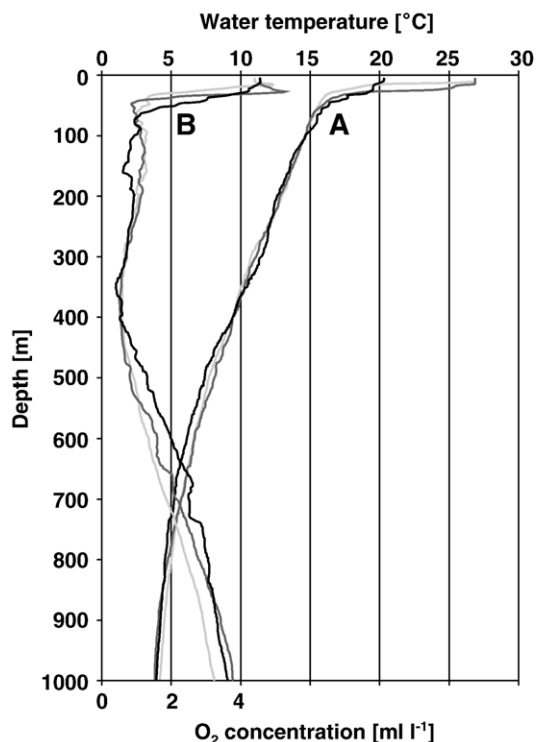


Fig. 2. Profiles of water temperature (A) and oxygen concentration (B) at the stations T2-7 (light grey), T4-1 (dark grey) and T4-5 (black).

Angola and northern Namibia, across the Angola–Benguela frontal system (13.5–18°S, Fig. 1). A detailed description of the environmental conditions and the distribution of surface chlorophyll *a* concentration can be found in Ekau and Verheye (2005) and Verheye et al. (2005).

The three zooplankton sampling stations were located in three different hydrographic regimes. Profiles of temperature and dissolved oxygen at the three stations, which were representative of these three regimes (Verheye et al., 2005), are shown in Fig. 2. The northernmost station (T2-7 at 13.5°S 11°E) was situated in the warm southern Angola Current, the central station (T4-1 at 15.7°S 11.25°E) in close proximity of the strongest gradient in sea-surface temperature within the Angola–Benguela Front (ABF), and the southern station (T4-5 at 18°S 11.25°E) in waters strongly influenced by upwelling of cold water of the Benguela Current.

The influence of the different currents is evident from the sea-surface temperature, with high values of 26.9 °C at T2-7 and T4-1 (Fig. 2) and a lower temperature of 20.3 °C at T4-5. Despite the strong differences at the surface, sub-surface temperature profiles were rather similar at all three stations with deviations of less than 0.5 °C between the stations at any given depth below

55 m. Below the thermocline, temperature decreased linearly with depth from ca. 16 °C at 50 m to 6 °C at 600 m (Fig. 2). From there onwards, the decline was weaker, reaching 4 °C at 1000 m depth.

Oxygen concentration dropped from high surface levels of 4.4–5.0 ml O₂l⁻¹ at all three stations to hypoxic conditions below the thermocline (Fig. 2). This decline was more pronounced at T4-1, where levels of <1 ml O₂l⁻¹ were reached already at 44 m depth, whereas the same threshold was surpassed at 66 and 71 m at T2-7 and T4-5, respectively. Lowest oxygen concentrations of 0.50 and 0.41 ml O₂l⁻¹ were recorded at 370 m depth at T4-1 and at 350 m at T4-5, respectively (Fig. 2). Oxygen levels remained low down to approx. 420 m; from there onwards they steadily increased again reaching 2 ml O₂l⁻¹ between 600 and 720 m and between 3.2 and 3.8 ml O₂l⁻¹ at 1000 m depth. This increase was more rapid at T4-5 with considerably higher oxygen concentrations between 420 and 830 m depth in the northern Benguela upwelling region compared with the southern Angola Current or the ABF (Fig. 2).

3.2. Copepod vertical distribution

The vertical distribution of the dominant herbivorous copepod *C. carinatus* was bimodal. In the northern Benguela upwelling region (T4-5), the population was concentrated in the surface layer (0–60 m) and consisted of all ontogenetic stages, whereas diapausing copepods C5 below 400 m depth comprised the bulk of the population in the southern Angola Current (T2-7) and the ABF (T4-1) (for more details see Verheye et al., 2005).

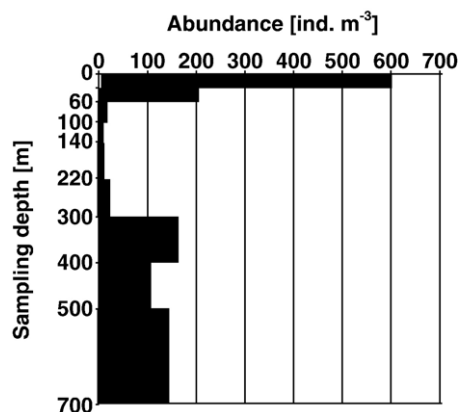


Fig. 3. Vertical distribution of mean total abundance [ind. m⁻³] of calanoid copepods (excluding *C. carinatus*) at the stations T2-7, T4-1 and T4-5 during the BENEFIT 2002 cruise (for data on *C. carinatus* see Verheye et al., 2005).

Accordingly, the vertical distribution of other calanoid copepods (all species combined) showed a similar, bimodal pattern with maximum abundances of $>600 \text{ ind. m}^{-3}$ in the surface layer (0–30 m), sharply decreasing to 207 ind. m^{-3} between 30 and 60 m and to $<23 \text{ ind. m}^{-3}$ from 60 to 300 m depth, and increasing again to 105–162 ind. m^{-3} below 300 m depth (Fig. 3). Thus, the depth of minimum abundance of both *C. carinatus* and other calanoid copepods coincided with the IOML. According to preliminary results, a very similar vertical distribution pattern with severely reduced abundances of calanoid copepods within the IOML was observed in January/February 2004 during the AHAB expedition onboard of RV “A. v. Humboldt” in the same region.

Species-specific information on the vertical distribution and total abundance of several characteristic copepod species is given in Fig. 4. Most species inhabited discrete depth ranges. *Centropages brachiatus* and *Temora* sp. (Fig. 4a), *Nannocalanus minor* (Fig. 4b) and *Scolecithrix* sp. (Fig. 4c) mainly inhabited the surface layer (0–50 m). The major population fractions of *Euchaeta* cf. *marina* and *Neocalanus gracilis* also occurred in the upper 100 m, while *Rhincalanus nasutus*, *Pleuromamma robusta*, *Heterorhabdus* sp., *Aetideopsis carinata* and *Metridia lucens* showed a more mesopelagic distribution between 100 and 700 m depth (Fig. 4a). Among these mesopelagic species, a vertical succession or partitioning of the water column was

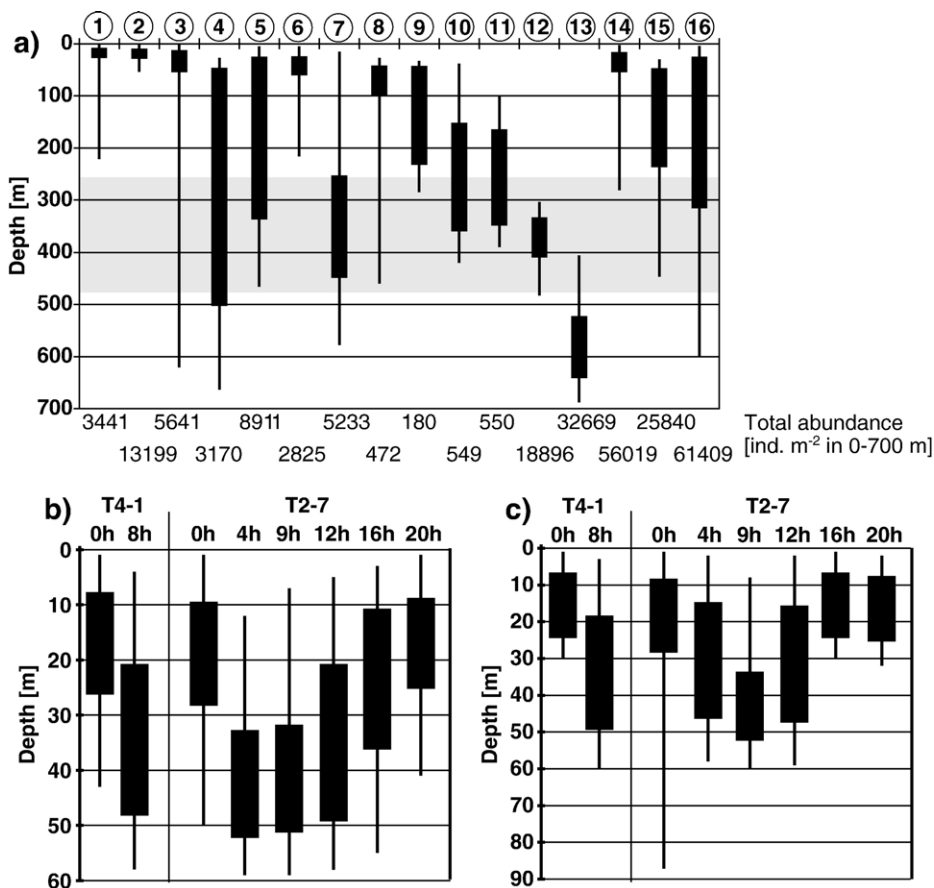


Fig. 4. a) Vertical distribution and abundance [ind. m⁻²] in the upper 700 m of different copepod species in the study area during the BENEFIT 2002 cruise. 1. *Centropages brachiatus* (means of T4-1 and T4-5), 2. *Temora* sp. (T4-1), 3. *Eu-/Subeu-/Pareucalanus* spp. (mean of T2-7 at 12 h, 16 h, 20 h), 4. *Eu-/Subeu-/Pareucalanus* spp. (mean of T2-7 at 0 h, 4 h, 9 h), 5. *Eu-/Subeu-/Pareucalanus* spp. (T4-1), 6. *Euchaeta* cf. *marina* (T2-7), 7. *Euchaeta* sp. (T4-1), 8. *Neocalanus gracilis* (T2-7, diel mean), 9. *Rhincalanus nasutus* (T4-1 at 8 h), 10. *Pleuromamma robusta* (means of T2-7, T4-1 and T4-5), 11. *Heterorhabdus* sp. (T4-1 at 8 h), 12. *Aetideopsis carinata* (T4-5), 13. *Metridia lucens* (means of T4-1 and T4-5), 14. Cyclopoida, mainly *Oithona* spp. (mean of T2-7 at 12 h and 20 h), 15. Cyclopoida, mainly *Oithona* spp. (mean of T2-7 at 0 h and 4 h), and 16. Poecilostomatata, mainly *Oncaea* spp. (means of T2-7, T4-1 and T4-5). Boxes contain 50% of the populations, while the bars include the 5th to the 95th percentiles. Superimposed in light grey is the vertical extent of the centre of the IOML with oxygen concentrations of $<0.8 \text{ ml O}_2 \text{ l}^{-1}$. b) Diel vertical migration of *Nannocalanus minor* at stations T4-1 and T2-7. c) Diel vertical migration of *Scolecithrix* sp. at stations T4-1 and T2-7. Boxes contain 50% of the populations, while the bars include the 5th to the 95th percentiles.

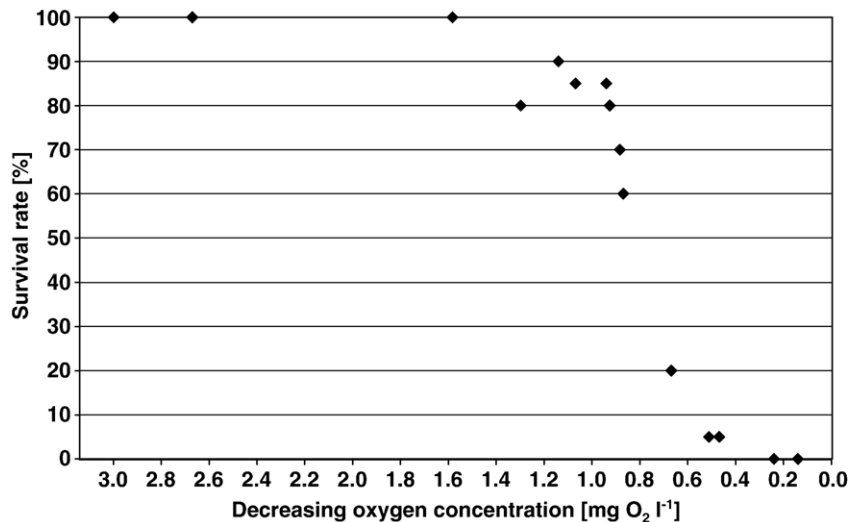


Fig. 5. Hypoxia tolerance of *C. carinatus* presented as survival rate [%] at decreasing oxygen concentrations [mg O₂ l⁻¹] derived from incubation experiments.

evident with *R. nasutus* occupying the interval from 40 to 230 m, *P. robusta* and *Heterorhabdus* sp. mainly inhabiting 155–360 m, while *A. carinata* was most abundant from 330 to 410 m and *M. lucens* dominated between 520 and 640 m. Thus, despite the general scarcity of calanoid copepods within the IOML (60–500 m, Fig. 3), certain species, such as *R. nasutus*, *P. robusta*, *Heterorhabdus* sp. and *A. carinata*, apparently flourished under hypoxic conditions and actually preferred the IOML as habitat.

The observation that Poekilostomata, mainly *Oncaea* spp., and *Eu-/Subeu-/Pareucalanus* spp. were distributed over wider depth ranges, might at least partly be explained by the presence of different species, which were not distinguished in the sample analysis.

N. minor and *Scolecithrix* sp. performed diel vertical migrations within the uppermost 60 m of the water column at stations T4-1 and T2-7 (Fig. 4b, c). Pronounced differences in the daytime and night-time distributions over more extended depth ranges were recorded for Cyclopoida, mainly *Oithona* spp., and *Eu-/Subeu-/Pareucalanus* spp. at T2-7 (Fig. 4a).

3.3. Hypoxia tolerance of *C. carinatus*

In total, 15 incubations with individuals of *C. carinatus* were conducted to establish minimum oxygen tolerance levels. Survivorship remained at 100% down to surprisingly low oxygen concentrations of 1.5 mg O₂ l⁻¹, whereas 80% of the copepods still survived hypoxic conditions of 0.93 mg O₂ l⁻¹ (Fig. 5). Towards lower oxygen concentrations, the mortality rate strongly in-

creased with survival rates of only 60% and 20% at oxygen concentrations of 0.87 and 0.67 mg O₂ l⁻¹ respectively. All individuals died at hypoxic conditions of <0.3 mg O₂ l⁻¹. These experimental results correspond to a mortality of 50% at an interpolated oxygen concentration of 0.83 mg O₂ l⁻¹.

4. Discussion

In coastal upwelling areas, benthic boundary layers are often subject to hypoxic or anoxic conditions since the enhanced primary production in the surface layer leads to increased sedimentation of organic matter and oxygen-consuming remineralisation of organic matter on the sea floor. A unique feature of the Benguela coastal upwelling system of Southwest Africa is the development of an intermediate oxygen minimum layer in 60–500 m depth, which extends far offshore beyond the continental shelf (Ekau and Verheye, 2005) and may affect the distribution, behaviour, and productivity of pelagic species.

The experimental part of the present study demonstrates that *C. carinatus* is surprisingly tolerant with regard to hypoxic conditions. The species is able to survive apparently unharmed at oxygen concentrations as low as 1.4 mg O₂ l⁻¹. Obviously, our short-term experiments do not allow assessing chronic effects of long-term exposure to hypoxic conditions such as decreases in egg production and population growth (Richmond et al., 2006 for *Acartia tonsa*). However, there is an empirical evidence from field studies in the southern Benguela upwelling region that 1.4 mg O₂ l⁻¹ (=1 ml O₂ l⁻¹) is in fact a relevant threshold for the

vertical distribution of *C. carinatus*, supporting our experimental results and their relevance for *in situ* distribution. During a 27-day anchor station study in St Helena Bay (32°S) in March–April 1987, the weighted mean depth of *C. carinatus* copepodids C4 and C5 as well as adults followed the depth of the 1 ml O₂ l⁻¹ isopleth at the upper margin of the oxygen-deficient bottom layer (see Fig. 4 in Verheye, 1991).

Publications of other empirical studies on the hypoxia tolerance of zooplankton for comparison with results of the present study are rather scarce. Individuals of the marine cladoceran *Moina micrura* not acclimated to oxygen deficiency showed a severely reduced scope of activity (62.5-fold reduction over the range of 10–0.3 mg O₂ l⁻¹), when subjected to hypoxic conditions (Svetlichny and Hubareva, 2002). They stopped filtration and increased the time spent swimming at concentrations of 0.7–0.8 mg O₂ l⁻¹, similar to the minimum tolerable oxygen concentration determined for *C. carinatus* in this study. However, individuals that had been acclimated to hypoxic conditions via the accumulation of haemoglobin were less affected. They showed no response at this oxygen concentration and survived apparently unharmed at levels as low as 0.2 mg O₂ l⁻¹, maintaining their filtering activity (Svetlichny and Hubareva, 2002).

Our experimental results imply that *C. carinatus* is not able to survive in the core of the IOML in the northern Benguela upwelling region and Angola–Benguela Front where oxygen concentrations were <0.8 ml O₂ l⁻¹ (<1.1 mg O₂ l⁻¹) at 350–400 m depth (Ekau and Verheye, 2005). Thus, the experimental results can explain the observed bimodal vertical distribution of this species with markedly reduced abundances in the IOML (Verheye et al., 2005). Our field observations indicate that other dominant copepod species apparently also avoided the IOML (Fig. 3), possibly for physiological reasons. Among those species that avoided the IOML were, for instance, *N. minor* and *Scolecithrix* sp., whose diel vertical migrations were confined to the upper 60 m, above the IOML (Fig. 4). *M. lucens*, which is usually considered a mesopelagic species and omnivorous eurybiont with a preference for cold, deep waters and which exhibits extensive diel vertical migrations in the Benguela region (Unterückerbächer, 1964, Timonin, 1997), generally occurs between the euphotic zone and 300 m depth even in the core and upper part of the IOML (e.g. Loick et al., 2005 for winter 1999). However, *M. lucens* was exclusively found at depths below the IOML during the present study (Fig. 4).

In contrast, there are other copepod species that inhabited the IOML and, thus, must be able to tolerate

lower oxygen levels. This group of species includes *P. robusta*, *Heterorhabdus* sp., *A. carinata* and, to a lesser extent, *R. nasutus*. Their adaptation to life at hypoxic conditions allows them to seek refuge from competition and risk of predation by the majority of less tolerant copepods, other zooplankton and pelagic fish. Future work will focus on the measurement of the hypoxia tolerance levels and metabolic rates of these “refugee” species and on an investigation of the biochemical, physiological and behavioural adaptations that enable them to cope with such hypoxic conditions.

Recent studies in the northern Benguela Current upwelling region and Angola–Benguela Front (this study, Auel et al., 2005, Ekau and Verheye, 2005, Loick et al., 2005, Verheye and Ekau, 2005, Verheye et al., 2005) emphasise the important role of hypoxia and, in particular, the IOML in structuring pelagic communities and ecosystems. Hypoxia may influence pelagic species via several mechanisms and on different levels, ranging from the biochemical and cellular level to the community scale (Hochachka and Mustafa, 1972, Marcus, 2001, Richmond et al., 2006). Effects include changes in community composition (extending to regime shifts), vertical distribution of zooplankton abundance and biomass, biodiversity, and life-cycle adaptations of pelagic species. Evidence for the important role that IOMLs play in structuring pelagic ecosystems is also provided by studies on other tropical and subtropical seas as well as upwelling regions (Wishner et al., 1998, 2000, Koppelman and Weikert, 2005 and references therein, Escubano, 2006).

In the Arabian Sea, for instance, the lower interface of the oxygen minimum zone (OMZ) was characterised by a sub-surface maximum of zooplankton biomass and high biological activity (Wishner et al., 2000). Similarly to *A. carinata* in our study, another deep-sea copepod, *Lucicutia grandis*, was identified as a typical specialist associated with the OMZ in the Arabian Sea (Wishner et al., 2000, Koppelman and Weikert, 2005). Wishner et al. (2000) concluded that animals of the oceanic OMZ must be uniquely adapted to the very low oxygen and strong spatial gradients in this widespread suboxic environment.

There is a growing concern that the spreading and intensification of hypoxic areas in the ocean poses a serious threat to global fishery resources (UNEP 2004a,b). In the Benguela region, the more frequent and intensified occurrence of hypoxic conditions has been identified as a potential cause for the collapse and subsequent non-recovery of pelagic fish stocks. The increase of the pelagic goby (*Sufflogobius bibarbatus*) has been attributed to the assumption that gobies, as descendants of benthic ancestors, should be more

tolerant to oxygen depletion than pelagic fish such as sardine and anchovy (Cury and Shannon, 2004, Gibbons and Gro Veá Salvanes, 2004). Accordingly, the perceived ‘outbreak’ of jellyfish in coastal waters off Namibia in recent years (Brierley et al., 2005, Lynam et al., 2006) may be supported by increasingly hypoxic conditions favouring gelatinous zooplankton with their low metabolic rates and oxygen demands and, hence, a greater tolerance against oxygen deficiency (Parsons and Lalli, 2002). Thus, there is an accumulating evidence that oxygen concentration and, in particular, hypoxia play a critical role in shaping pelagic communities and food webs. Additional studies on the effects of hypoxia on zooplankton, their ecophysiology, recruitment, migrations and distribution patterns represent an urgent research need. Experimental results on hypoxia tolerance can be used to model and map potential habitats of key species and forecast the consequences of future environmental and anthropogenic changes on pelagic communities and, hence, commercially valuable fish stocks.

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