

This discussion paper is/has been under review for the journal Biogeosciences (BG).
Please refer to the corresponding final paper in BG if available.

Ammonium excretion and oxygen respiration of tropical copepods and euphausiids exposed to oxygen minimum zone conditions

R. Kiko¹, H. Hauss¹, F. Buchholz², and F. Melzner¹

¹GEOMAR Helmholtz Centre for Ocean Research Kiel, Wischhofstr. 1–3, 24105 Kiel, Germany

²Alfred-Wegener-Institute, Am Handelshafen 12, 27570 Bremerhaven, Germany

Received: 27 August 2015 – Accepted: 9 October 2015 – Published: 28 October 2015

Correspondence to: R. Kiko (rkiko@geomar.de)

Published by Copernicus Publications on behalf of the European Geosciences Union.

BGD

12, 17329–17366, 2015

Ammonium excretion
and oxygen
respiration of tropical
copepods

R. Kiko et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Abstract

Calanoid copepods and euphausiids are key components of marine zooplankton communities worldwide. Most euphausiids and several copepod species perform diel vertical migrations (DVMs) that contribute to the export of particulate and dissolved matter to midwater depths. In vast areas of the global ocean, and in particular in the eastern tropical Atlantic and Pacific, the daytime distribution depth of many migrating organisms corresponds to the core of the oxygen minimum zone (OMZ). At depth, the animals experience reduced temperature and oxygen partial pressure (pO_2) and an increased carbon dioxide partial pressure (pCO_2) compared to their near-surface nighttime habitat. Although it is well known that low oxygen levels can inhibit respiratory activity, the respiration response of tropical copepods and euphausiids to relevant pCO_2 , pO_2 and temperature conditions remains poorly parameterized. Further, the regulation of ammonium excretion at OMZ conditions is generally not well understood. It was recently estimated that DVM-mediated ammonium supply considerably fuels bacterial anaerobic ammonium oxidation – a major loss process for fixed nitrogen in the ocean. These estimates were based on the implicit assumption that hypoxia or anoxia in combination with hypercapnia (elevated pCO_2) does not result in a downregulation of ammonium excretion. Here we show that exposure to OMZ conditions can result in strong depression of respiration and ammonium excretion in calanoid copepods and euphausiids from the Eastern Tropical North Atlantic and the Eastern Tropical South Pacific. These physiological responses need to be taken into account when estimating DVM-mediated fluxes of carbon and nitrogen into OMZs.

1 Introduction

Many zooplankton and nekton organisms feed in the ocean's surface layer during the night and migrate to beneath the photic zone during daytime, mainly to avoid visual predation (Lampert, 1989). These so-called diel vertical migrations (DVMs) mediate

BGD

12, 17329–17366, 2015

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



5 Escribano et al., 2009). The ETSP OMZ features severely hypoxic to anoxic conditions, anoxia being detected at about 100 to 300 m depth and oxygen levels between 0 and $5 \mu\text{mol kg}^{-1}$ (~ 0 to about 0.4 kPa) at about 30 to 100 m depth and 300 to 400 m depth (Thamdrup et al., 2012). In contrast, oxygen concentrations in the Eastern Tropical
10 North Atlantic (ETNA) seldom fall below $40 \mu\text{mol kg}^{-1}$ (~ 3.4 kPa at 12°C , Karstensen et al., 2008), but transient severely hypoxic to anoxic conditions have been observed in mesoscale eddies (Karstensen et al., 2015). OMZs expanded in the recent past and a further expansion, mainly due to global warming, is expected (Stramma et al., 2008; Keeling et al., 2010). A possible expansion of OMZs will have far-reaching consequences for marine tropical ecosystems, as for example it results in the compression of
15 the habitat of billfishes (Stramma et al., 2012), but also in the extension of areas where fixed nitrogen is lost from the ocean (Kalvelage et al., 2011).

Many organisms have developed special adaptations like an enhanced oxygen uptake capacity to thrive at particularly low oxygen levels of less than 5 kPa ($\sim 40 \mu\text{mol kg}^{-1}$) oxygen (Childress and Seibel, 1998, 2011). The abundance and biomass of zooplankton and nekton permanently inhabiting extreme OMZs is rather low (e.g. Wishner et al., 1998; Auel and Verheye, 2007; Escribano et al., 2009), but the migrating zooplankton and nekton biomass can be very high even in these regions. Most zooplankton and nekton organisms can regulate their oxygen uptake rate over
20 a wide range of oxygen concentrations, but this regulatory ability breaks down at a certain critical oxygen concentration. The point at which the aerobic metabolism can no longer be maintained independent of the environmental oxygen partial pressure ($p\text{O}_2$) is called the critical oxygen partial pressure p_{crit} (e.g. Seibel, 2011). The p_{crit} is species specific and varies with habitat oxygen concentrations (e.g. Childress and Seibel, 1998; Richards, 2011) and temperature (Deutsch et al., 2015). Many OMZ inhabiting species
25 have evolved significantly lower p_{crit} values than non-OMZ inhabiting species (Childress and Seibel, 1998) and can survive extended periods of time at oxygen levels below their p_{crit} or even at anoxia (Childress, 1975; Kiko et al., 2015). Migrations into waters with oxygen levels below the p_{crit} should result in a metabolic suppression that

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

of the migrating zooplankton community of the tropical Atlantic (Steinberg et al., 2000; Auel and Verheye, 2007), whereas *Undinula vulgaris* is an ubiquitous non-migrating epipelagic calanoid copepod of the tropical oceans (Chahsarvar-Archard and Razouls, 1982; Razouls et al., 2005–2015). *Euphausia gibboides* is found regularly at low latitudes in the Atlantic and Pacific (Siegel, 2015), and *E. mucronata* is the dominant euphausiid in the ETSP (Antezana, 2009, 2010). Both euphausiid species conduct diel vertical migrations into the OMZ. Our work should help to better parameterize ammonium excretion and respiration rates of crustacean zooplankton and nekton in OMZ regions and aims to provide a base for revising model formulations of DVM-mediated export in OMZ regions.

2 Material and methods

2.1 Animal collection and maintenance

Sampling was conducted during RV *Maria S. Merian* cruise MSM22 (ETNA; 24 October 2012 to 23 November 2012) and RV *Meteor* cruises M93 (ETSP; 6 February 2013 to 4 March 2013) and M97 (ETNA; 25 May 2013 to 28 June 2013; Fig. 1). Zooplankton was collected using a Hydrobios Multinet Midi (0.25 m² mouth opening, 200 µm mesh size, 5 nets), a Hydrobios Multinet Maxi (0.5 m² mouth opening, 330 µm mesh size, 9 nets), a WP-2 net (0.26 m² mouth opening, 200 µm mesh size), a MOCNESS (1 m² mouth opening, 2 mm mesh size) or a CalCOFI-Net (0.78 m² mouth opening, 500 µm mesh size). All specimens used for experiments were caught in the upper 400 m of the water column and only animals appearing unharmed and fit were used for experiments. Specimens were sorted, identified and transferred into aquaria with filtered, well-oxygenated seawater immediately after the catch and maintained for 1 to 13 h prior to physiological experiments at the respective experimental temperature. Only adult euphausiids and adult female copepods were used for the experiments. OMZ temperatures during MSM22 and M97 ranged from 5.5 to 13.6 °C at 300 to 600 m

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



depth and from 13 to 29 °C in the upper 100 m. Temperature at 200 to 300 m depth during M93 ranged from 10.2 to 13.3 °C. Maintenance and physiological experiments were therefore conducted in darkness in temperature-controlled incubators at 11, 13 or 23 °C ($\pm 1^\circ$). Before and during experiments, animals were not fed.

5 Stomach fullness and coloration of the mid gut gland were routinely categorized in *E. gibboides*. Possible scores of the mid gut gland coloration were 0–5, indicating transparent through green to dark brown coloration (Morris et al., 1983).

2.2 Incubation conditions

Respiration and ammonium excretion rate measurements (both in $\mu\text{mol h}^{-1} \text{gDW}^{-1}$) at
10 varying oxygen concentrations were conducted in 12 to 60 mL gas-tight glass bottles. These were equipped with oxygen microsensors (\varnothing 3 mm, PreSens Precision Sensing GmbH, Regensburg, Germany) attached to the inner wall of the bottles to monitor oxygen concentrations non-invasively. Read-out of oxygen concentrations was conducted using multi-channel fiber optic oxygen transmitters (Oxy-4 and Oxy-10 mini, PreSens Precision Sensing GmbH, Regensburg, Germany) that were connected via optical
15 fibers to the outside of the bottles directly above the oxygen microsensor spots. Calibration of the oxygen microsensors was conducted at the beginning of each cruise or when a different incubation temperature was set with a Na_2SO_3 -solution (0% oxygen) and aerated seawater (100% air saturation) at the respective measurement temperature. Oxygen concentration was calculated from air saturation according to the PreSens manual. All other oxygen unit conversions were conducted using the R-package AquaEnv (Hofmann et al., 2010) and R scripts obtained from Andreas F. Hofmann. Measurements were started at pre-adjusted oxygen and carbon dioxide levels. For this, seawater stocks with adjusted $p\text{O}_2$ and $p\text{CO}_2$ were prepared by equilibrating 3 to 4 L
20 of filtered (0.2 μm filter Whatman GFF filter) and UV – sterilized (Aqua Cristal UV C 5 Watt, JBL GmbH & Co. KG, Neuhofen, Germany) water with premixed gases (certified gas mixtures from Air Liquide) for 4 h at the respective experimental temperature. $p\text{CO}_2$ levels were chosen to mimic the environmental $p\text{CO}_2$ in the ETSP OMZ or the ETNA

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



OMZ. $p\text{CO}_2$ levels for the respective area were calculated from data published by the World Ocean Circulation Experiment (WOCE, 2002; ETSP: data from the upper 150 m between 14.74 to 16.38° S and 75.25 to 76.93° W; ETNA: data from the upper 400 m between 4.5° S to 11° N and 7 to 26° W) using CO2sys_v2.1 (Pierrot et al., 2006). Furthermore, gas mixes with different levels of oxygen, but without CO₂ were used to test the effects of this experimental manipulation. The detailed composition of the premixed gases used is described in Table 1. After equilibration, the stocks were supplemented with antibiotics (25 mgL⁻¹ ampicillin and 25 mgL⁻¹ streptomycin) to inhibit microbial activity.

The salinity and pH of the prepared water was measured immediately on board with a handheld multiparameter meter Multi 350i equipped with a Sentix 41 pH and a ConOx conductivity probe (WTW). Calibration of the pH-probe was conducted daily prior to the measurements using 7.000 and 10.012 pH IUPAC standard buffers (Radiometer analytical) and the conductivity probe was calibrated at the beginning of each cruise using 0.01 molL⁻¹ KCl. 250 mL of the prepared water were collected in gas-tight glass bottles and fixed with 100 μL saturated mercury chloride solution for later measurements of total alkalinity (A_T) and dissolved inorganic carbon (C_T). C_T was measured using an AIRICA system (Marianda, Kiel, Germany) via a LI-COR 7000 infrared CO₂/H₂O analyser. A_T was measured in duplicates via potentiometric titration with an automated titrator (Titroline 7000, SI Analytics, Germany) using 50 mL of sample and 0.05 M HCl. C_T was measured for samples from cruise MSM22, whereas A_T was measured for samples from cruises M93 and M97, due to a breakdown of the C_T measurement system. A_T and C_T were measured against certified reference material provided by Andrew Dickson of Scripps Institution of Oceanography. The $p\text{CO}_2$ established in the different incubation trials was calculated with CO2sys_v2.1, using experimental temperature, water salinity, pH_{NBS} and C_T or A_T as input.

ration. No excretion rate measurements were conducted in this case, but the oxygen level at which the animal died was noted.

Euphausia mucronata survived exposure to anoxia, enabling the measurement of ammonium excretion rates under severely hypoxic to anoxic conditions. These measurements were started after 2–5 h when animals had respired all oxygen from the incubation bottles. Thereafter, a 1 mL water sample was taken from the 12–13 mL bottles used to determine the ammonium concentration at the onset of the trial. The withdrawn water was replaced with 0% oxygen water prepared using pure nitrogen gas. Oxygen levels slightly increased during this procedure, but never rose above ~3% air saturation. This small amount of oxygen was in most cases respired after about 30 min, but in some cases anoxia was not reached until the end of the trial. After an incubation period of 2.5 h at severe hypoxia to anoxia, a second sample for the ammonium concentration measurement was taken. The ammonium excretion rate was calculated as the difference of the first and second measurement and the oxygen concentration was calculated as the mean of the start and stop oxygen levels. All individuals used in the described experiments were subsequently frozen at -80°C and dried at 50°C for 72 h and weighed to determine their dry weight. Oxygen consumption and ammonium excretion rates (R , $\mu\text{mol h}^{-1} \text{gDW}^{-1}$) were standardized to an average dry weight (DW in mg) of 0.1 g applying a scaling coefficient b of -0.25 (Moloney and Field, 1989) as

$$R_{\text{std}} = R \times \left(\frac{0.1}{\text{weight}} \right)^{-0.25} \quad (1)$$

The rates presented should be considered routine metabolic rates, as activity was not monitored and animals were not fed (Prosser, 1961).

2.4 Statistical analysis

General linear models (GLM) with $p\text{O}_2$ as continuous variable and $p\text{CO}_2$ (two levels) and temperature (for all except *E. mucronata*, two levels) as categorical predictor were

BGD

12, 17329–17366, 2015

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



used on log-transformed respiration and excretion rate data for each species separately to explore the overall effect of experimental conditions on the metabolic response.

To directly compare the respiration and excretion rate at the two $p\text{CO}_2$ -treatments at otherwise same experimental conditions (temperature and $p\text{O}_2$), pairwise t tests were employed. For these tests, the mean respiration rate obtained at a given experimental condition (starting $p\text{O}_2$ value and experimental temperature) for a replicate was determined. E.g. if an experimental run with an animal was started at 50 % airsaturation, stopped at 20 % airsaturation and lasted 8 h, four determinations of the respiration rate were available for this replicate and the mean of these respiration rates was determined.

Where possible, metabolic rates were modelled as a function of $p\text{O}_2$ using nonlinear regressions with the python module `lmfit`. If hypoxia was found to have lethal effects at a given temperature, the metabolic data was transformed prior to fitting the power function by subtracting the lowest observed lethal $p\text{O}_2$ from the abscissa data. A power function with a y-intercept of zero

$$R_{\text{std}, \text{O}_2} = a \times p\text{O}_2^b \quad (2)$$

was fitted to the standardized (according to Eq. 1) and transformed respiration rate data as the respiration rate at 0 kPa oxygen or that of dead individuals is zero by definition. A power function with y-intercept

$$R_{\text{std}, \text{NH}_4} = a \times p\text{O}_2^b + c \quad (3)$$

was fitted to the standardized and transformed ammonium excretion rate data.

To calculate the p_{crit} , the standardized and transformed respiration or excretion rates were normalized by dividing each respiration or excretion rate by the highest observed respiration or excretion rate, respectively. Power functions as described above were fitted to these standardized, transformed and normalized rates. The respiration or ex-

BGD

12, 17329–17366, 2015

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



pared to the respiratory p_{crit} in all species observed and ammonium excretion at anoxia was drastically downregulated in *E. mucronata*. Mean (\pm SD) standardized ammonium excretion at severe hypoxia ($pO_2 < 0.5$ kPa) was significantly reduced by a factor of 5.9 compared to ammonium excretion (0.65 ± 0.33 vs. $3.82 \pm 2.54 \mu\text{mol h}^{-1} \text{gDW}^{-1}$) under normoxia ($15\text{--}22$ kPa pO_2 , t test, $p < 0.01$) in *E. mucronata*.

Ammonium excretion rates calculated according to Ikeda (2014) for 0.1 g copepods or euphausiids coincided well with the excretion rates observed at normoxia in almost all species (Figs. 5 and 6). Only the excretion rates observed in *E. gibboides* were lower than predicted. Stomachs of *E. gibboides* were mostly half-full and midgut coloration ranged between 1 and 2 in this species.

4 Discussion

Empirical models exist to predict copepod (Ikeda, 2014) and euphausiid (Tremblay et al., 2014; Ikeda, 2014) respiration and excretion rates, but these models do not include pO_2 or pCO_2 as environmental factors. We here developed an approach to determine copepod and euphausiid respiration and excretion rates at temperatures, oxygen and carbon dioxide levels consistent with those found in the ETNA and ETSP OMZ. We furthermore tested whether respiration and excretion rates are altered when the oxygen, but not the carbon dioxide level is experimentally adjusted to represent OMZ conditions compared to the scenario when both levels are adjusted according to OMZ conditions.

4.1 Impact of pCO_2 -levels on respiration and excretion

As expected, the use of CO_2 -minus gas mixes resulted in a removal of CO_2 from the incubation water, mirrored in a pH increase and a pCO_2 decrease. The use of CO_2 -plus gas mixes allowed a more realistic simulation of OMZ conditions. pH, A_T and C_T data were available for the Peruvian OMZ (WOCE 2002) and we calculated the CO_2 -

BGD

12, 17329–17366, 2015

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



phausia gibboides and *Pleuromamma abdominalis*. The Q_{10} was below 2 in *Undinula vulgaris*, but this might be related to the fact that this surface dwelling species is seldom exposed to 11 °C and the Q_{10} therefore might not be representative for the normal thermal range of this species. An increase in temperature furthermore impaired hypoxia tolerance as indicated by a higher lethal pO_2 , respiration p_{crit} and ammonium excretion p_{crit} in all species tested. That elevated temperatures impair hypoxia tolerance has been found for numerous other marine species and quantitative estimates of the p_{crit} can help to understand distribution patterns of marine organisms (e.g. Deutsch et al., 2015). Consistent with previous studies (e.g. Childress and Seibel, 1998), respiratory p_{crit} values of *E. mucronata* from the ETSP were found to be lower than in species from weak- (*E. gibboides*, *P. abdominalis* and *U. vulgaris*) or non-OMZ regions (Childress and Seibel, 1998). No large differences in respiratory p_{crit} could be observed when comparing the tropical Atlantic copepod and krill species. In general, our findings support the hypothesis that the critical oxygen partial pressure evolved to largely match the minimum oxygen level to which a species is regularly exposed (Seibel, 2011; Richards, 2011).

It seems reasonable to also transfer this concept to the impact of oxygen levels on ammonium excretion rates. A reduction of ammonium excretion under severely hypoxic or anoxic conditions was observed in *E. mucronata* and is consistent with similar observations from the squat lobster *Pleuroncodes monodon* (Kiko et al., 2015) and from several calanoid copepods (Cass and Daily, 2014). It follows that both respiration and ammonium excretion are drastically reduced when crustacean zooplankton organisms are exposed to severe hypoxia or anoxia. The characterization of metabolic rates across the entire tolerated oxygen level spectrum (including, if possible, anoxia) is key to properly estimate effects of hypoxia and anoxia on species distribution and activity, as well as related biogeochemical fluxes.

BGD

12, 17329–17366, 2015

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



4.3 Implications for the calculation of biogeochemical fluxes of oxygen, carbon and nitrogen

Several studies assessed the active DVM-mediated fluxes and the passive particle-mediated fluxes of carbon and nitrogen in regions that mostly do not feature severe hypoxia ($pO_2 < 1$ kPa) or anoxia at midwater depths (Longhurst et al., 1990; Zhang and Dam, 1997; Hidaka et al., 2001; Steinberg et al., 2002; Davison et al., 2013). Excretion rates used in these studies to calculate the active flux were obtained at mild hypoxia ($pO_2 > 1$ kPa) to normoxia (e.g. Donnelly and Torres, 1988; Dagg et al., 1980; Steinberg et al., 2002). For mild OMZs like the ETNA OMZ, this approach seems reasonable. The respiration and ammonium excretion p_{crit} of *Pleuromamma abdominalis* were found to be 0.6 and 1.8 kPa at 11 °C, respectively. The respiratory p_{crit} of *Euphausia gibboides* was found to be 2.4 kPa at 13 °C and no significant reduction of ammonium excretion was observed at a mean pO_2 of 5.1 kPa for *E. gibboides* at this temperature. *P. abdominalis* and *E. gibboides* normally do not encounter extremely low oxygen levels in their natural habitat. Oxygen concentrations in the ETNA seldom fall below 40 $\mu\text{mol kg}^{-1}$ (~ 3.4 kPa at 12 °C, Karstensen et al., 2008). It follows that zooplankton respiration and excretion rates for biogeochemical flux calculations in the ETNA can be calculated from published empirical models of zooplankton respiration and excretion (Ikeda, 2014), if oxygen levels above ~ 2.4 kPa are encountered. However, food conditions should also be taken into account. Excretion rates of *E. gibboides* at normoxia were lower than predicted via the empirical model by Ikeda (2014), possibly due to low food availability as indicated by low midgut coloration scores.

Estimates of DVM-mediated fluxes to midwater depth with drastically reduced oxygen levels in the Pacific (e.g. Longhurst et al., 1990; Escribano et al., 2009; Bianchi et al., 2014) are likely too high. *E. mucronata* migrates to the core of the ETSP OMZ that features oxygen concentrations below 4 $\mu\text{mol O}_2 \text{ kg}^{-1}$ (~ 0.34 kPa) (Antezana, 2009). Later work by Thamdrup et al. (2012) showed that the core of the ETSP OMZ is often anoxic. Antezana (2002) tested the dependence of respiration on oxygen concentration

BGD

12, 17329–17366, 2015

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



References

- Antezana, T.: Adaptive behavior of *Euphausia mucronata* in relation to the oxygen minimum layer of the Humboldt Current, in: Oceanography of the Eastern Pacific, Vol II, edited by: Färber-Lorda, J., Editorial CICESE, Ensenada, 29–40, 2002.
- 5 Antezana, T.: Species-specific patterns of diel migration into the Oxygen Minimum Zone by euphausiids in the Humboldt Current Ecosystem, *Progr. Oceanogr.*, 83, 228–236, 2009.
- Antezana, T.: *Euphausia mucronata*: a keystone herbivore and prey of the Humboldt Current System, *Deep-Sea Res. Pt. II*, 57, 652–662, 2010.
- Auel, H. and Verheye, H. M.: 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, *J. Exp. Mar. Biol. Ecol.*, 352, 234–243, 2007.
- 10 Bianchi, D., Dunne, J., Sarmiento, J., and Galbraith, E.: Data-based estimates of suboxia, denitrification and N₂O production in the ocean, and their sensitivities to change, *Global Biogeochem. Cy.*, 26, 6550–6555, 2012.
- Bianchi, D., Babbín, A. R., and Galbraith, E. D.: Enhancement of anammox by the excretion of diel vertical migrators, *P. Natl. Acad. Sci. USA*, 111, 15653–15658, 2014.
- Bograd, S. J., Castro, C. G., Di Lorenzo, E., Palacios, D. M., Bailey, H., Gilly, W., and Chavez, F. P.: Oxygen declines and the shoaling of the hypoxic boundary in the California Current, *Geophys. Res. Lett.*, 35, L12607, doi:10.1029/2008GL034185, 2008.
- 20 Bopp, L., Resplandy, L., Orr, J. C., Doney, S. C., Dunne, J. P., Gehlen, M., Halloran, P., Heinze, C., Ilyina, T., Séférián, R., Tjiputra, J., and Vichi, M.: Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models, *Biogeosciences*, 10, 6225–6245, doi:10.5194/bg-10-6225-2013, 2013.
- 25 Brandt, P., Bange, H. W., Banyte, D., Dengler, M., Didwischus, S.-H., Fischer, T., Greatbatch, R. J., Hahn, J., Kanzow, T., Karstensen, J., Körtzinger, A., Krahnmann, G., Schmidtko, S., Stramma, L., Tanhua, T., and Visbeck, M.: On the role of circulation and mixing in the ventilation of oxygen minimum zones with a focus on the eastern tropical North Atlantic, *Biogeosciences*, 12, 489–512, doi:10.5194/bg-12-489-2015, 2015.
- 30 Cass, C. J. and Daly, K. L.: Eucalanoid copepod metabolic rates in the oxygen minimum zone of the eastern tropical north Pacific: effects of oxygen and temperature, *Deep-Sea Res. Pt. I*, 94, 137–149, 2014.

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Hagerman, L., Søndergard, T., Weile, K., Hosie, D., and Uglow, R. F.: Aspects of blood physiology and ammonia excretion in *Nephrops norvegicus* under hypoxia, *Comp. Biochem. Physiol.*, 97, 51–55, 1990.

Hauss, H., Franz, J. M. S., and Sommer, U.: Changes in N : P stoichiometry influence taxonomic composition and nutritional quality of phytoplankton in the Peruvian upwelling, *J. Sea Res.*, 73, 74–85, 2012.

Heywood, K. J.: Diel vertical migration of zooplankton in the Northeast Atlantic, *J. Plankton Res.*, 18, 163–184, 1996.

Hidaka, K., Kawaguchi, K., Murakami, M., and Takahashi, M.: Downward transport of organic carbon by diel migratory micronekton in the western equatorial Pacific: its quantitative and qualitative importance, *Deep-Sea Res. Pt. I*, 48, 1923–1939, 2001.

Hofmann, A. F., Soetaert, K., Middelburg, J. J., and Meysman, F. J. R.: AquaEnv: an aquatic acid-base modelling environment in R, *Aquat. Geochem.*, 16, 507–546, 2010.

Holmes, R. M., Aminot, A., K erouel, R., Hooker, B. A., and Peterson, B. J.: A simple and precise method for measuring ammonium in marine and freshwater ecosystems, *Can. J. Fish. Aquat. Sci.*, 56, 1801–1808, 1999.

Ikeda, T.: Respiration and ammonia excretion by marine metazooplankton taxa: synthesis toward a global-bathymetric model, *Mar. Biol.*, 161, 2753–2766, 2014.

Isari, S., Zervoudaki, S., Saiz, E., Pelejero, C., and Peters, J.: Copepod vital rates under CO₂-induced acidification: a calanoid species and a cyclopoid species under short-term exposures, *J. Plankton Res.*, 37, 912–922, doi:10.1093/plankt/fbv057, 2015.

Kalvelage, T., Jensen, M. M., Contreras, S., Revsbeck, N. P., Lam, P., G nter, M., LaRoche, J., Lavik, G., and Kuypers, M. M. M.: Oxygen sensitivity of anammox and coupled N-cycle processes in oxygen minimum zones, *PLoS ONE*, 6, e29299, doi:10.1371/journal.pone.0029299, 2011.

Karstensen, J., Stramma, L., and Visbeck, M.: Oxygen minimum zones in the eastern tropical Atlantic and Pacific oceans, *Prog. Oceanogr.*, 77, 331–350, 2008.

Karstensen, J., Fiedler, B., Sch tte, F., Brandt, P., K rtzinger, A., Fischer, G., Zantopp, R., Hahn, J., Visbeck, M., and Wallace, D.: Open ocean dead zones in the tropical North Atlantic Ocean, *Biogeosciences*, 12, 2597–2605, doi:10.5194/bg-12-2597-2015, 2015.

Keeling, R. F., K rtzinger, A., and Gruber, N.: Ocean deoxygenation in a warming world, *Ann. Rev. Mar. Sci.*, 2, 199–229, 2010.

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)




[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


Kiko, R., Hauss, H., Dengler, M., Sommer, S., and Melzner, F.: The squat lobster *Pleuroncodes monodon* tolerates anoxic “dead zone” conditions off Peru, *Mar. Biol.*, 162, 1913–1921, doi:10.1007/s00227-015-2709-6, 2015.

Kroeker, K. J., Kordas, R. L., Crim, R. N., and Singh, G. G.: Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms, *Ecol. Lett.*, 13, 1419–1434, 2010.

Lampert, W.: The adaptive significance of diel vertical migration of zooplankton, *Funct. Ecol.*, 3, 21–27, 1989.

Longhurst, A. R., Bedo, A. W., Harrison, W. G., Head, E. J. H., and Sameoto, D. D.: Vertical flux of respiratory carbon by oceanic diel migrant biota, *Deep-Sea Res. Pt. I*, 37, 685–694, 1990.

Maas, A. E., Wishner, K. F., and Seibel, B. A.: The metabolic response of pteropods to acidification reflects natural CO₂-exposure in oxygen minimum zones, *Biogeosciences*, 9, 747–757, doi:10.5194/bg-9-747-2012, 2012a.

Maas, A. E., Wishner, K. F., and Seibel, B. A.: Metabolic suppression in thecosomatous pteropods as an effect of low temperature and hypoxia in the eastern tropical North Pacific, *Mar. Biol.*, 159, 1955–1967, 2012b.

Marshall, D. J., Bode, M., and White, C. R.: Estimating physiological tolerances – a comparison of traditional approaches to nonlinear regression techniques, *J. Exp. Biol.*, 216, 2176–2182, 2013.

Melzner, F., Thomsen, J., Koeve, W., Oschlies, A., Gutowska, M., Bange, H. W., Hansen, H. P., and Körtzinger A.: Future ocean acidification will be amplified by hypoxia in coastal habitats, *Mar. Biol.*, 160, 1875–1888, 2013.

Meyer, J., Löscher, C. R., Neulinger, S. C., Reichel, A. F., Loginova, A., Borchard, C., Schmitz, R. A., Hauss, H., Kiko, R., and Riebesell, U.: Changing nutrient stoichiometry affects phytoplankton production, DOP build up and dinitrogen fixation – a mesocosm experiment in the eastern tropical North Atlantic, *Biogeosciences Discuss.*, 12, 9991–10029, doi:10.5194/bgd-12-9991-2015, 2015.

Moloney, C. L. and Field, J. G.: General allometric equations for rates of nutrient uptake, ingestion, and respiration in plankton organisms, *Limnol. Oceanogr.*, 34, 1290–1299, 1989.

Morris, D. J., Ward, P., and Clarke, A.: Some aspects of feeding in the Antarctic krill, *Euphausia superba*, *Polar Biol.*, 2, 21–26, 1983.

- Paulmier, A., Ruiz-Pino, D., and Garçon, V.: CO₂ maximum in the oxygen minimum zone (OMZ), *Biogeosciences*, 8, 239–252, doi:10.5194/bg-8-239-2011, 2011.
- Pierrot, D., Lewis, E., and Wallace, D. W. R.: MS Excel Program Developed for CO₂ System Calculations, ORNL/CDIAC-105a, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U. S. Department of Energy, Oak Ridge, Tennessee, doi:10.3334/CDIAC/otg.CO2SYS_XLS_CDIAC105a, 2006.
- Prosser, C. L.: Oxygen: respiration and metabolism, in: *Comparative Animal Physiology*, edited by: Prosser, C. L. and Brown, F. A., Saunders, Philadelphia, 165–211, 1961.
- Putzeys, S.: Carbon active fluxes in the Northeast Atlantic subtropical gyre, PhD Thesis, Univ. de Las Palmas de Gran Canaria, available at: <http://hdl.handle.net/10553/11069> (last access: 9 July 2015), 2013.
- Razouls, C., de Bovée, F., Kouwenberg, J., and Desreumaux, N.: Diversity and Geographic Distribution of Marine Planktonic Copepods, available at: <http://copepodes.obs-banyuls.fr/en> (last access: 4 August 2015), 2005–2015.
- Richards, J. G.: Physiological, behavioral and biochemical adaptations of intertidal fishes to hypoxia, *J. Exp. Biol.*, 214, 191–199, 2011.
- Rosa, R. and Seibel, B. A.: Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator, *P. Natl. Acad. Sci. USA*, 105, 20776–20780, 2008.
- Rosas, C., Martinez, E., Gaxiola, G., Brito, R., Sánchez, A., and Soto, L. A.: The effect of dissolved oxygen and salinity on oxygen consumption, ammonia excretion and osmotic pressure of *Penaeus setiferus* (Linnaeus) juveniles, *J. Exp. Mar. Biol. Ecol.* 234, 41–57, 1999.
- Saba, G. K., Schofield, O., Torres, J. J., Ombres, E. H., and Steinberg, D. K.: Increased feeding and nutrient excretion of adult Antarctic krill, *Euphausia superba*, exposed to enhanced carbon dioxide (CO₂), *PLoS ONE*, 7, e52224, doi:10.1371/journal.pone.0052224, 2012.
- Seibel, B. A.: Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones, *J. Exp. Biol.* 214, 326–336, 2011.
- Semenova, T. N., Timonin, A. G., and Flint, M. V.: Characteristic features of the lateral and vertical distributions of abundant zooplankton species near the Peruvian coast, *Oceanology*, 22, 216–220, 1982.
- Siegel, V.: *Euphausia gibboides* Ortmann, 1893, in: *World Euphausiacea Database*, 2015, edited by: Siegel, V., accessed through: *World Register of Marine Species*, available at: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=110684>, last access: 9 July 2015.

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



- Steinberg, D. K., Carlson, C. A., Bates, N. R., Goldthwait, S. A., Madin, L. P., and Michaels, A. F.: Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea, *Deep-Sea Res. Pt. I*, 47, 137–158, 2000.
- Steinberg, D. K., Goldthwait, S. A., and Hansell, D. A.: Zooplankton vertical migration and the active transport of dissolved organic and inorganic nitrogen in the Sargasso Sea, *Deep-Sea Res. Pt. I*, 49, 1445–1461, 2002.
- Stramma, L., Johnson, G. C., Sprintall, J., and Mohrholz, V.: Expanding oxygen-minimum zones in the tropical oceans, *Science*, 320, 655–658, 2008.
- Stramma, L., Prince, E. D., Schmidtko, S., Luo, J., Hoolihan, J. P., Visbeck, M., Wallace, D. W. R., Brandt, P., and Körtzinger, A.: Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes, *Nature Climate Change*, 2, 33–37, 2012.
- Svetlichny, L., Hubareva, E., and Arashkevich, E.: Physiological and behavioural response to hypoxia in active and diapausing stage V copepodites of *Calanus euxinus*, *Arch. Hydrobiol. Spec. Issues Adv. Limnol.*, 52, 507–519, 1998.
- Teal, J. M. and Carey, F. G.: Respiration of a *Euphausiid* from the oxygen minimum layer, *Limnol. Oceanogr.*, 12, 548–550, 1967.
- Thamdrup, B., Dalsgaard, T., and Revsbech, N. P.: Widespread functional anoxia in the oxygen minimum zone of the Eastern South Pacific, *Deep-Sea Res. Pt. I*, 65, 36–45, 2012.
- Thomsen, J. and Melzner, F.: Moderate seawater acidification does not elicit long-term metabolic depression in the blue mussel *Mytilus edulis*, *Mar. Biol.*, 157, 2667–2676, 2010.
- Thor, P. and Dupont, S.: Transgenerational effects alleviate severe fecundity loss during ocean acidification in a ubiquitous planktonic copepod, *Glob. Change Biol.*, 21, 2261–2271, 2015.
- Thor, P. and Oliva, E. O.: Ocean acidification elicits different energetic responses in an Arctic and a boreal population of the copepod *Pseudocalanus acuspes*, *Mar. Biol.*, 162, 799–807, 2015.
- Tremblay, N., Werner, T., Huenerlage, K., Buchholz, F., Abele, D., Meyer, B., and Brey, T.: Euphausiid respiration model revamped: latitudinal and seasonal shaping effects on krill respiration rates, *Ecol. Model.*, 291, 233–241, 2014.
- Trübenbach, K., Pegado, M. R., Seibel, B. A., and Rosa, R.: Ventilation rates and activity levels of juvenile jumbo squid under metabolic suppression in the oxygen minimum zone, *J. Exp. Biol.*, 216, 359–368, 2013.
- WOCE Data Products Committee: WOCE Global Data, Version 3.0, WOCE International Project Office, WOCE Report No. 180/02, Southampton, UK, November, 2002.

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

Wishner, K. F., Gowing, M. M., and Gelfman, C.: Mesozooplankton biomass in the upper 1000 m in the Arabian Sea: overall seasonal and geographic patterns, and relationship to oxygen gradients, Deep-Sea Res. Pt. II, 45, 2405–2432, 1998.

5 Zhang, X. S. and Dam, H. G.: Downward export of carbon by diel migrant mesozooplankton in the central equatorial Pacific, Deep-Sea Res. Pt. II, 44, 2191–2202, 1997.

BGD

12, 17329–17366, 2015

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Table 1. Volumetric composition of used premixed gases.

		50 % air sat.	33 % air sat.	10 % air sat
ETNA CO ₂ -plus	Nitrogen	89.58	93.02	97.85
	Oxygen	10.36	6.91	2.07
	Carbon Dioxide	0.06	0.07	0.08
ETSP CO ₂ -plus	Nitrogen	89.53	92.96	97.77
	Oxygen	10.36	6.91	2.07
	Carbon Dioxide	0.11	0.13	0.16
CO ₂ -minus	Nitrogen	89.64	93.09	97.93
	Oxygen	10.36	6.91	2.07
	Carbon Dioxide	0.00	0.00	0.00

BGD

12, 17329–17366, 2015

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)

[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


Table 2. Recommended volumetric composition for premixed gases for the ETSP OMZ.

		50 % air sat.	33 % air sat.	10 % air sat
ETSP CO ₂ -plus	Nitrogen	89.56	93.00	97.81
	Oxygen	10.36	6.91	2.07
	Carbon Dioxide	0.08	0.09	0.11

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

Table 3. Lethal pO_2 , parameter estimates (a , b) of fitted power functions, p_{crit} and Q_{10} values for respiration and excretion rate data.

Species	Target Temp. (°C)	mean lethal pO_2 (kPa), (SD, n)	minimum lethal pO_2 (kPa)	a_{resp}	b_{resp}	$p_{crit, resp}$ (kPa)	a_{NH_4-excr}	b_{NH_4-excr}	p_{crit, NH_4-excr} (kPa)	$Q_{10, resp}$	Q_{10, NH_4-excr}
<i>Undinula vulgaris</i>	11	2.7 (0.3, 6)	2.3	15.48	0.20	2.4	2.29	0.13	2.9	1.4	1.6
<i>Pleuromamma abdominalis</i>	23	6.6 (0.7, 6)	5.5	27.55	0.17	6.2	n/a	n/a	n/a		
<i>Euphausia gibboides</i>	11	n/a	n/a	9.62	0.33	0.6	1.51	0.30	1.8	2.0	2.3
<i>Euphausia mucronata</i>	23	6.3 (1.0, 2)	5.3	31.31	0.25	6.5	6.37	0.13	6.5		
<i>Euphausia mucronata</i>	13	2.5 (1.4, 20)	1.1	19.70	0.22	2.4	n/a	n/a	n/a	2.0	2.3
<i>Euphausia mucronata</i>	23	7.5 (1.9, 20)	4.5	27.12	0.33	6.2	n/a	n/a	n/a		
<i>Euphausia mucronata</i>	13	n/a	n/a	10.00	0.39	0.6	1.27	0.36	0.73	n/a	n/a
<i>Euphausia mucronata</i>	20	n/a	n/a	n/a	n/a	2 to 4*	n/a	n/a	n/a	n/a	n/a

* approximate p_{crit} deduced from Fig. 2 in Teal and Carey (1967). n/a = not applicable.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



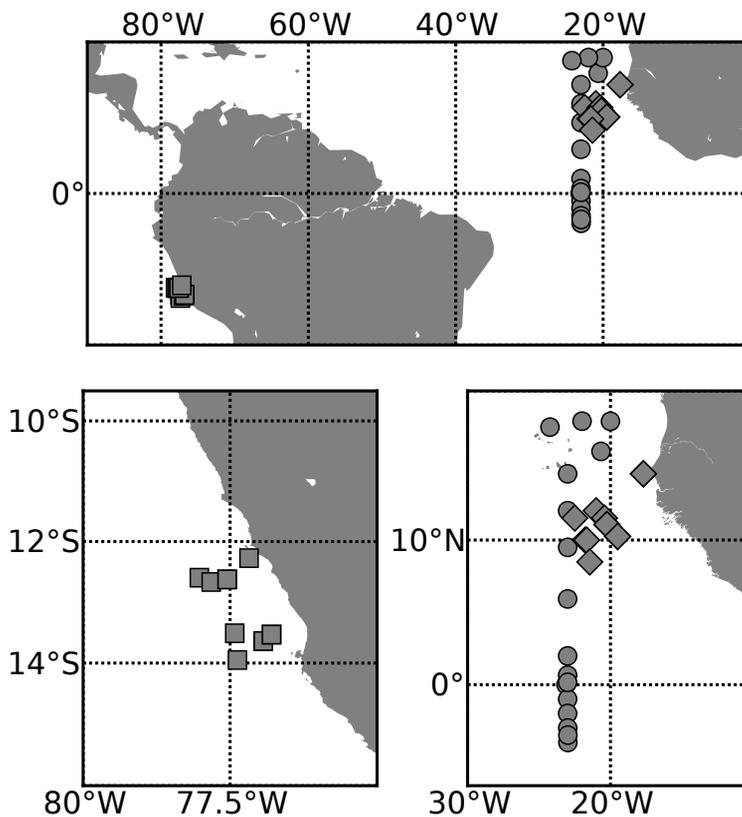


Figure 1. Sampling locations of specimens for respiration and excretion measurements. Circles: *Pleuromamma abdominalis* and *Undinula vulgaris* during cruise MSM22 (October/November 2012); squares: *Euphausia mucronata* during cruise M93 (February 2013); diamonds: *Euphausia gibboides* during cruise M97 (May 2013).

Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

[Title Page](#)

[Abstract](#) | [Introduction](#)

[Conclusions](#) | [References](#)

[Tables](#) | [Figures](#)

[◀](#) | [▶](#)

[◀](#) | [▶](#)

[Back](#) | [Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



Ammonium excretion and oxygen respiration of tropical copepods

R. Kiko et al.

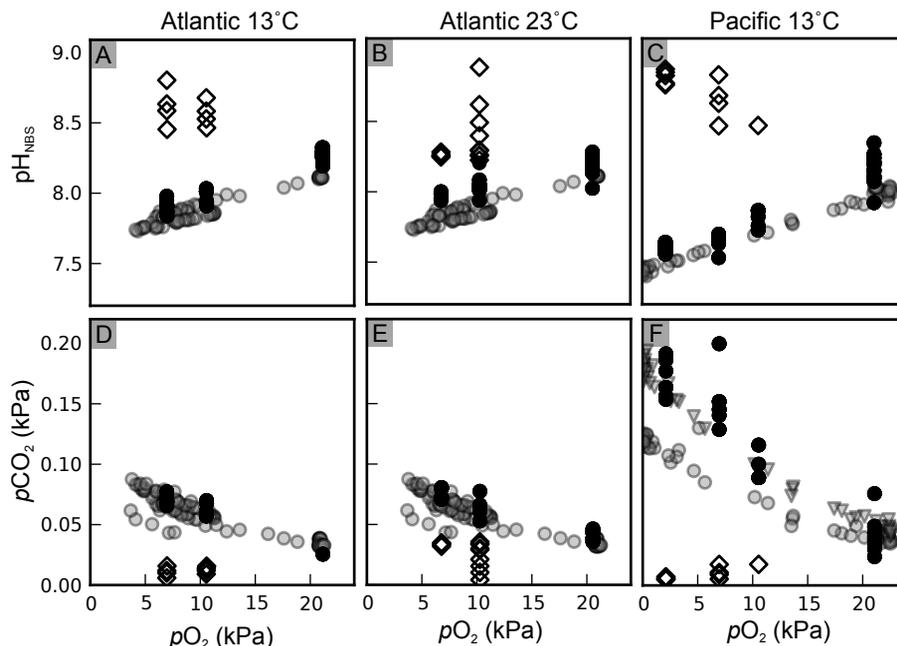


Figure 2. pH_{NBS} and pCO₂ in incubation water (black symbols), compared to environmental levels (grey symbols) for the ETNA OMZ and the ETSP OMZ. Black circles: CO₂-plus treatment. Open diamonds: CO₂-minus treatment. Grey circles: environmental pH or pCO₂ data, pCO₂ calculated from A_T and C_T. Grey triangles in (f): pCO₂ calculated from pH and A_T.

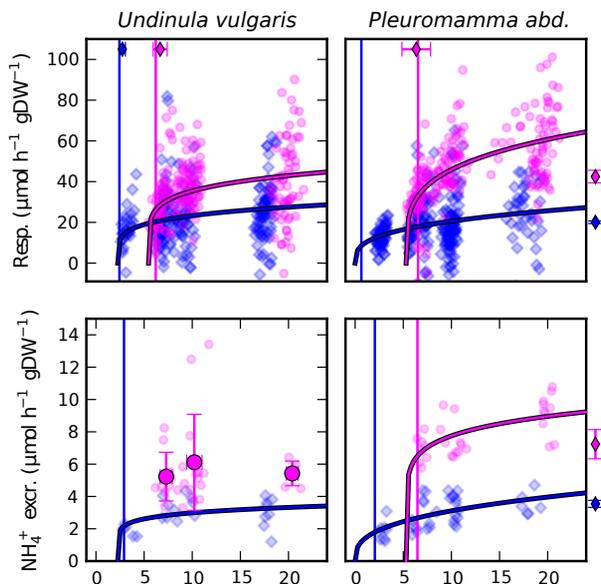


Figure 5. Weight-specific respiration and ammonium excretion rates of *Undinula vulgaris* and *Pleuromamma abdominalis* at different oxygen partial pressures and temperatures (CO₂-plus and CO₂-minus treatments combined). Magenta symbols = 23 °C, Blue symbols = 11 °C. Transparent dots represent individual measurements. Solid curves indicate the power function fits to the data. Regression coefficients are given in Table 3. Solid vertical lines indicate the respective p_{crit} . Horizontal error bars in the upper panels indicate the mean (\pm SD) lethal pO_2 at the respective temperature. A power function could not be fitted to the ammonium excretion data for *U. vulgaris* at 23 °C, therefore the mean (\pm SD) excretion rates for the three pre-set oxygen levels (100 % air saturation, 50 and 33 %) are plotted with vertical errorbars. Respiration and excretion rates were standardized to a mean dry mass of 0.1 g. Error bars right beside the plots indicate the respiration or ammonium excretion rate (\pm SE) calculated according to Ikeda (2014) for calanoid copepods (0.1 gDW) at the respective temperature.

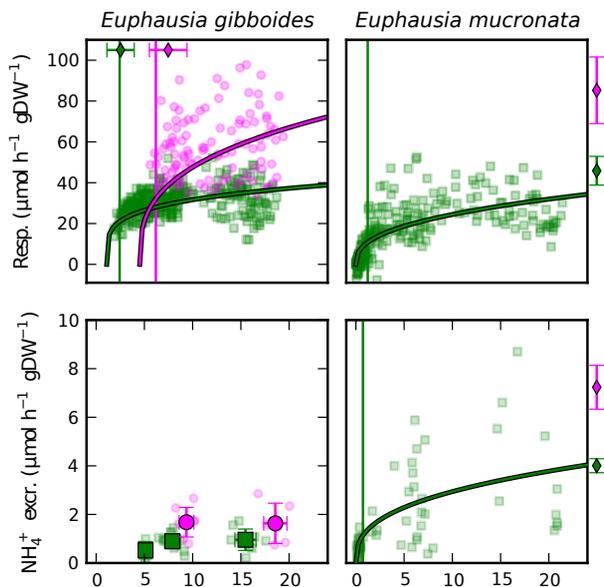


Figure 6. Weight-specific respiration and ammonium excretion rates of *Euphausia gibboides* and *Euphausia mucronata* at different oxygen partial pressures and temperatures (CO₂-plus and CO₂-minus treatments combined). Magenta symbols = 23 °C, Green symbols = 13 °C. Transparent dots represent single measurements. Solid curves indicate the power function fits to the data. Regression coefficients are given in Table 3. Solid vertical lines indicate the respective p_{crit} for respiration and ammonium excretion. Horizontal error bars indicate the mean (\pm SD) lethal pO_2 at the given temperature for *E. gibboides*. A power function could not be fitted to the ammonium excretion data for *E. gibboides*, therefore the mean (\pm SD) excretion rates for the three pre-set oxygen levels (100 % air saturation, 50 and 33 %) are plotted with vertical errorbars. Respiration and excretion rates were standardized to a mean dry mass of 0.1 g. Error bars right beside the plots indicate the respiration or ammonium excretion rate (\pm SE) calculated according to Ikeda (2014) for euphausiids (0.1 gDW) at the respective temperature.