



Oxygen Consumption of Nauplii of Marine Planktonic Copepods



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Submission: 📅 February 13, 2018; Published: 📅 February 20, 2018

Abstract

The objective of our study was to determine the oxygen consumption rates of nauplii of two small calanoid species, *Paracalanus quasimodo* and *Temora turbinata*, and compare their rates with those of three other planktonic species. The comparisons reveal that motion results in higher oxygen consumption i.e. higher energy expenditure than little or no motion. In addition, the type of motion results in different oxygen consumption rates, and therefore different energy expenditures. Our findings also show that nauplii consume more energy per unit body weight than their copepodids. This implies that small calanoid nauplii, having few energy reserves, are at a disadvantage in relation to copepodid stages as they require continuous food supply and continuous feeding which here is accompanied by continuous motion. That leaves them vulnerable to predators. Thus, not only predation but also discontinuous/intermittent feeding activity could result in increased mortality of calanoid nauplii.

Keywords: Copepod nauplii; Oxygen consumption; Metabolism

Introduction

Marine planktonic copepods are the most abundant metazoa on our planet [1]. Within this taxon the early juveniles, the nauplii, are the most abundant. So far, the vast majority of research on planktonic copepods has been on late juveniles and adult stages i.e. nauplii were rarely included [2]. In his *Biology of Calanoid Copepods* of 710 pages devoted about 1% (less than 10 pages) to nauplii. More than four decades ago the significance of copepod nauplii was addressed within process studies on calanoid copepods: [3-7] since nauplii of planktonic copepods usually do not accumulate energy reserves as copepodid stages and adults do [8] they most likely will not survive food shortages over longer periods of time. Yet our knowledge on their food requirements and energy needs is limited [9,10]. Studies in temperate waters revealed that in situ mortality of nauplii and older stages is related to invertebrate and vertebrate predators [11,12]. We know from laboratory studies that survival of nauplii and older stages of calanoid is also a function of food abundance [5]. So far, our knowledge of nauplius mortality in relation to food abundance in warmer waters is scarce. We know that energy consumption per unit body weight decreases from younger to older stages of copepods [10,13]. The goal of this study was to quantify the oxygen consumption rate of two species of small calanoid copepods, *Paracalanus quasimodo* and *Temora turbinata* which often occur abundantly on the U.S. southeastern continental shelf [14] and compare their rates to those of other planktonic copepod species, and with older stages. We calculated their daily

energy requirements by transforming oxygen consumption into energy units and compared this with their food intake assuming 93% assimilation efficiency [9].

Material and Methods

Rearing of nauplii

Late copepodid stages and adult females were collected from the U.S. southeastern continental shelf during summer of 2007 and late winter 2008 (*Temora turbinata*), and January/February 2015 and March 2016 (*Paracalanus quasimodo*). The copepodid stages moulted to adults followed by egg production. Eggs were also obtained from the collected females (age unknown) which had a short reproductive period (age unknown). Rearing occurred at 19.5 to 20.1 °C during 12h dim light/12h darkness in glass vessels of 960 to 1,900ml volume on a plankton wheel rotating at 0.5rpm. The nauplii were offered simultaneously the flagellates *Isochrysis galbana* and *Rhodomonas sp.* and the diatom *Thalassiosira weissflogii* at total average food concentrations of near 60µg C L⁻¹. This approach provided food levels close to frequently 60µg C L⁻¹ occurring phytoplankton abundances on the middle to outer shelf. The jars were inspected daily and the concentrations of each of the three food species were determined by using a Beckman-Coulter Multisizer IV. At the beginning of each experiment additional food particles were added to reach food levels of near 20-30% higher than the average food concentration (Table 1).

Table 1: O₂ Consumption rates, weight-specific respiration and ingestion of different planktonic copepods. *Rho Rhodomonas sp.*, *Thw Thalassiosira weissflogii*.

Species	Stage	Weight	Temperature	Average Food		O ₂ -Consumption	Weight-Specific		References
				concentration	Food species		respiration	respiration	
		(ng C)	°c	(µg CL ⁻¹)			(nl O ₂ d ⁻¹)		
<i>Oithona davisae</i>	N III/N IV	55	20	no food		21	16.4	n.d.	
						46	36	n.d.	Almeda et al. [8]
<i>Eucalanus pileatus</i>	N IV-N VI	480-990	21.5	61		430-720	29.7	17.7	Köster et al. [7]
<i>Paracalanus quasimodo</i>	N IV-N VI	40-71	21.5	22.3	<i>Rho</i>	95	71.1	67.6	This study
<i>Temora turbinata</i>	N III-N VI	67-157	21.5	9.1	<i>Thw</i>	91	33	24.1	This study

Fluorescence-based oxygen quantification

The oxygen consumption of nauplii of the calanoid copepods *P. quasimodo* and *T. turbinata* was quantified using optical fluorescence-based oxygen respirometry [15]. A 24-channel Sensor Dish Reader (SDR, Presens, Regensburg, Germany) was used to quantify oxygen consumption in 8ml and 10.5ml respiration chambers containing nauplii and food. Changes in oxygen concentrations were recorded continuously at 5-minute intervals over 4 to 6h i.e. in time-series. All oxygen measurements were performed in darkness. For further information [9]. All experiments were run at 21.5 to 21.8 °C.

Nauplii experiments

The oxygen consumption experiments with nauplii of *T. turbinata* were run in September 2007 and March 2008, and those with nauplii of *P. quasimodo* in March 2015 and September 2016, all at a temperature of 21.5 °C. The *T. turbinata* studies occurred in standing vials of 10.5ml volume with the number of nauplii ranging from 39 to 65 per vial; stages ranged from N III to N VI, weighing 67 to 157ng C. We decided to offer food at environmental abundances because the absence of food would result in an underestimation of metabolic rates of copepods [10]. The food species was *T. weissflogii* (1,000 to 1,200µm³ cell volume). The more recent studies with nauplii of *P. quasimodo* were conducted in 8.0ml vessels being on a plankton wheel rotating at 0.5rpm. The number of nauplii per vial ranged from 39 to 64 weighing on average 40 to 71ng C Nauplius⁻¹ (N IV to N VI). Here the food was *Rhodomonas sp.* (300 to 350µm³ cell volume); and later *Isochrysis galbana* (40µm³ cell volume). Four vials, serving as controls, were always run simultaneously. The control vessels had the same phytoplankton species and concentration as were offered to the nauplii. The oxygen consumption by the nauplii in each vessel was quantified from the linear part of the time-series oxygen concentration data by linear regression. The nauplius' individual respiration rate was quantified by subtracting the average rates in the control vials from the individual respiration rates in order to eliminate the net oxygen consumption or production by bacteria and phytoplankton. The

daily metabolic expenditures per Nauplius were calculated as 1nl oxygen respired = 0.43ng C respired [4].

After the oxygen time-series experiments the nauplii's morphology and motion behavior were inspected under a dissecting microscope. The contents of each vial were placed in a settling chamber, preserved with 2% Lugol's solution to count the remaining phytoplankton cells. Initial and final phytoplankton concentrations served to calculate clearance and ingestion rates of all nauplius experiments [16]. Each nauplius' body length was measured to obtain an average weight (ng C) from a previously obtained regression of Nauplius length vs. weight for each of the two copepod species: *P. quasimodo* log y = 2.088 log x - 2.921; *T. turbinata* log y = 3.195 log x - 5.446.

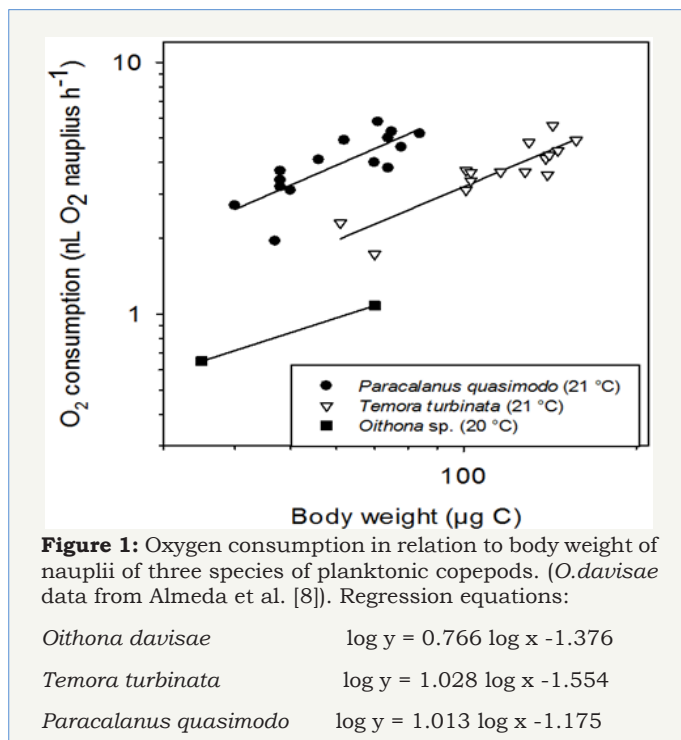
Statistics

We calculated linear regressions of Nauplius weight (ng C Nauplius⁻¹) vs. oxygen consumption (nl oxygen respired Nauplius⁻¹ h⁻¹), and then compared slopes and elevations [17].

Oxygen consumption

Nauplii of *T. turbinata* which create a feeding current and move slowly at 0.5mms⁻¹ [18] consumed 2.15µl h⁻¹ while those of *P. quasimodo* of the same weight (70ng C), moving continuously at 1.34mms⁻¹ consumed 4.5nl h⁻¹ i.e. over 100% more than *T. turbinatanauplii*. Nauplii of *Oithonadavisae* of the same weight but without food consumed only 1.1nl O₂⁻¹h⁻¹ at 20 °C [10]. It appears that oxygen consumption increased with increased motion as shown earlier for adult female copepods [19]. The fast-moving females of *Clausocalanus furcatus* consumed about 65% more oxygen than the slowly-moving and feeding current-producing *Paracalanus aculeatus* females [10]. Also determined oxygen consumption of *O. davisae* nauplii at the extraordinarily high food concentration of 2.75mg C L⁻¹ resulting in an O₂ consumption increase by factor 2.3 i.e. 2.5nl O₂h⁻¹ of a 70ng C Nauplius. Such an increase in oxygen consumption is thought to be associated with Specific Dynamic Action (SDA) which has been related to the expense associated with biosynthesis of new tissue from recent ingestion [20]. They

showed that respiration of the copepod *Acartia tonsa* increased with markedly increasing ingestion. We intentionally offered food near environmental levels in our experiments because of our generally environmentally-oriented research. This implies that no experiments were conducted without food. We are also comparing our findings with those of [21] on non-feeding copepods because the taxa we used in our experiments were part in their metabolic rate quantifications (*Temora turbinata* and the genus *Paracalanus*). Their equation of oxygen consumption vs. body carbon at 21.5 °C gives a value of 3.0nl O₂h⁻¹ for a copepod of 70ngC, ranging between our values of *T.turbinata* and *P. quasimodo*. Would there be no food shortage effects of oxygen consumption by starving copepods? At 20 °C *O.davisae* nauplii without food are lowering their oxygen consumption rate 10h after starting the experiment, implying that immediate effects of food absence were not observed (Figure 1). It appears that oxygen consumption rates of copepods measured for several hours just after they were removed from their food are close to those or even identical as when they were feeding.



Significance of metabolic expenditures and behaviors for copepod nauplii and older stages

When comparing metabolic expenditures of the various juvenile stages of planktonic copepods it became apparent that expenditures per unit body weight decrease with increasing stage [10]. Nauplii of many calanoid species are at an evolutionary disadvantage because they not only have a higher metabolic demand than their older brethren but also have to find food by moving continuously, thus leaving them exposed to predators. In addition, their mechanosensory performance is inferior to that of the copepodid stages as shown by results from [22] late nauplii of the genera *Paracalanus* and *Acartia* were more heavily preyed upon than early copepodids of the same species by the females of

the carnivorous calanoid *Labidocera trispinosa*. While the nauplii of *T. turbinata* and *P. quasimodo* are moving all their appendages and setae continuously their copepodid stages possess the non-moving first antennae with 3-D oriented setae at their tips which perceive oncoming predators, and thus avoid heavy predation. While we observe a major change in morphology from Nauplius VI (N VI) to copepodid stage I (C I), particularly for the first antennae (A1), there can be no change in motion behavior, e.g. the genus *Temora* producing continuously feeding currents, which should be accompanied by hardly any change in oxygen consumption from N VI to C I (as their weights hardly differ). Or, a major change is observed as for the genus *Paracalanus* where the nauplii move hop-wise continuously fast whereas the copepodid stages produce a feeding current and moving slowly [18] which should result in less energy expenditure.

The opposite is observed for the cyclopoid *Mesocyclops brasiliensis*: Here the nauplii hardly move; right after moulting the C I moves continuously consuming 250% more oxygen than the N VI of about the same weight [18]. Are there any *in situ* indications that nauplii may suffer higher mortality than their older stages in continental shelf waters? Time-series observations during summer of 1978 were made possible by following a drogoue in up welled water over 10 days sampling each vertical layer (warm upper mixed layer=UML, thermocline=TH, and intruding cold up welled water mass=IN) with 100 and 30 micron mesh. This allowed quantitative sampling of nauplii and older stages of abundant copepods [24]. The average concentrations of nauplii of *T. turbinata* of 7 stations was 6067, 3903 and 3244 m⁻³ in the UML, TH and IN, respectively. The average concentrations of copepodids and adults of the same species were only 641, 1042, and 1873 m⁻³, respectively. At each depth range of each of the 7 stations the concentrations of the nauplii surpassed those of the older stages clearly. From those data the probability of substantial mortality of nauplii cannot be excluded, as compared to the post naupliar stages. The question then would remain whether food and/or predators were the cause. During autumn the omnivorous calanoid *Centropages velificatus* intermittently dominates on the southeastern middle shelf while the often dominant mainly herbivorous *P. quasimodo* hardly occurs (unpubl. results). It is assumed that the strongly carnivorous omnivore [25] affects the *P. quasimodo* assemblage by consuming its nauplii.

The relatively high metabolic rates of the nauplii (near 33% of body C for *T. turbinata*, and 69% for *P. quasimodo*) require near continuous food supply because these nauplii have hardly any energy reserves which older stages have [8]. Will there be a continuously sufficient food supply on the SE shelf during much of the year? Since the range of perception and ingestion is limited for those small nauplii, mainly in the range of 4 to 11 microns (pers. obs.), and competition is provided by heterotrophic dinoflagellates and mixotrophs, sufficient food concentrations may not always be found [26]. Analyzed the effects of starvation on nauplii of *Calanus pacificus*: when initial feeding was delayed for about 10h after moulting to N III survivorship was reduced. For well-feeding stages

of N III to N VI survival was reduced when starving for more than 6h. However, complete starvation may not often occur, as abundances of phytoplankton will never be below $0.04\mu\text{g}$ chlorophyll L^{-1} [19] i.e. about $2\mu\text{g}$ C L^{-1} . However, major reductions of small phytoplankton will occur on the SE shelf as e.g. abundances of more than 5,000 *P. quasimodo* copepodids/adult females were intermittently encountered which would substantially reduce cells in the range of 5 to $12\mu\text{m}$ ESD (Equivalent Spherical Diameter and Paffenhöfer, unpubl. results).

At which food concentrations will nauplii of *T. turbinata* and *P. quasimodo* meet their metabolic expenditure? In our oxygen consumption experiments the weight-specific ingestion rate of *T. turbinata* nauplii was 24.1% at an average food concentration of $9.1\mu\text{g}$ C L^{-1} of *T. weissflogii* while the respiration expenditure was 33% of its body carbon. In jars of 480 and 960 ml capacity *T. turbinata* nauplii ingested daily 36% of their body carbon at $10\mu\text{g}$ C L^{-1} of *T. weissflogii* (unpubl. results). It appears that the small oxygen consumption vessels of 10.5ml capacity, and the not-moving, could have affected the nauplii's ingestion rates. Nauplii of *P. quasimodo*, being smaller, were studied in vessels of 8.0ml capacity, starting at higher food concentrations (flagellate *Rhodomonas* sp.) than for *T. turbinata*, being mounted on a slowly-moving plankton wheel. At an average food concentration of $22.3\mu\text{g}$ C L^{-1} those nauplii ingested *Rhodomonas* at a rate of 71% of their body carbon d^{-1} while respiring 69% daily at 21.6°C . When feeding on *T. weissflogii* at 20°C at about $8\mu\text{g}$ C L^{-1} a N VI of *Paracalanus* sp. ingested daily near 70% and at $24\mu\text{g}$ C L^{-1} near 105% of its body carbon. That occurred in vessels of 960ml [28] where hardly any wall effects should be encountered. Post naupliar stages spend far less energy per unit body weight than nauplii despite being able to compete with the nauplii for part of the same food: Adult females of *Paracalanus aculeatus* expend only 15% of their body carbon per day at 20°C [19]. At the same time copepodid stages can accumulate energy reserves; they also are able to vertically explore food reserves more readily than nauplii.

Outlook

For future studies we plan to record the motion, and feeding of various stages of calanoid copepod species in 100ml respiration chambers using a sensitive infrared digital camera, and monitor simultaneously the oxygen consumption at environmental food levels (including food limitation) in extended time-series experiments (more than 12h).

Conclusion

Survival of its nauplii is essential for the persistence of a species. How could we determine survival and associated variables, and find out whether Nauplius losses are caused by predation and/or food shortage? [29] obtained in Australian river estuaries *in situ* evidence that the calanoid *Gladioferens imparipesis* replaced by the omnivorous calanoid *Sulcanus conflictus* because the latter preys heavily on the nauplii of the former. It appears that on a continental shelf a closely spaced time-series, building on earlier data, would be needed to track a defined body of water in vertical layers over time. Nauplii, copepodid stages and potential predators and

associated needed variables would be collected quantitatively [30]. The respective prey species would require to be staged [31-35]. This would be readily possible for each of the two *Temora* species on the SE shelf [36-40].

Financial Support

This research was supported by NSF Grant OCE 1031263.

Acknowledgement

Captain and crew of the R/V Savannah always supported us with competence and can-do attitude. We gratefully acknowledge their support.

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