

Oxygen consumption in relation to motion of marine planktonic copepods

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ABSTRACT: The goal of these studies was to quantify the energy consumption of abundant marine planktonic copepods with different motion behaviors but similar body weight by determining their oxygen consumption under conditions approaching those encountered in their natural environment. The motion behaviors of adult females of the 3 copepod taxa studied ranged from the continuously fast-moving *Clausocalanus furcatus* to the continuously slow-moving and feeding current-producing *Paracalanus aculeatus* to the occasionally moving *Oncaea* spp. At 20°C, the daily oxygen consumption per unit body weight decreased significantly with decreasing activity, i.e. *C. furcatus* > *P. aculeatus* > *Oncaea* spp. Expressed as percent of body carbon metabolized per day, the average values were 23.4% for *C. furcatus*, 15.1% for *P. aculeatus*, and 10.5% for *Oncaea* spp. Oxygen consumption of *P. aculeatus* and *Oncaea* spp. was significantly higher at 23°C than at 20°C. It is concluded that not only body weight and temperature, but also the extent of motion will affect energy expenditures of planktonic copepods.

KEY WORDS: Oxygen · Motion · Copepods

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INTRODUCTION

The activities of marine planktonic copepods range from occasional motion to continuous rapid swimming (e.g. Gauld 1966, Paffenhöfer et al. 1996, Mazzocchi & Paffenhöfer 1999). According to modeling studies, increased motion results in increased metabolic expenditures (e.g. Klyashtorin & Yarzombek 1973). To date, oxygen consumption of copepods has been related to body mass and temperature (e.g. Ikeda 1985, Hiromi et al. 1988, Castellani et al. 2005), to general feeding behavior (Klekowski et al. 1977), and to diel cycles (Pavlova 1994). In the subtropical to tropical open ocean, abundances of potential food organisms for planktonic copepods are usually low compared to neritic regions (Paffenhöfer et al. 2003), which implies that metabolic and growth demands may not always be met (e.g. Dam et al. 1995, Roman & Gauzens 1996). The goal of this study was to quantify the oxygen consumption of 3 taxa of abundant subtropical/tropical planktonic copepods with different motion behaviors, and determine to what extent 2 of the 3 were able to

meet their metabolic needs at environmental food concentrations found at 3 different locations of the subtropical to tropical western Atlantic Ocean.

MATERIALS AND METHODS

The copepods in the present study were adult females of the calanoids *Clausocalanus furcatus* and *Paracalanus aculeatus*, and the poecilostomatoid *Oncaea* spp. *C. furcatus* and *P. aculeatus* occur abundantly from the middle southeastern continental shelf to the open ocean off the USA (Bowman 1971) and in the tropical Caribbean (Webber & Roff 1995), as does the genus *Oncaea* (Paffenhöfer et al. 1984, Webber & Roff 1995). *C. furcatus* and *Oncaea* spp. were collected on the middle and outer shelf (30 to 50 m isobath) off the southeastern USA at surface temperatures ranging from about 18 to 24°C, using oblique tows from near the sea floor to the surface with open-mouth nets of 200 µm mesh equipped with codends of 4 l capacity. They were immediately placed in 2 l glass

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jars filled with unfiltered seawater collected with Niskin bottles at mid-depth at the same location, and kept at temperatures near 20 to 23°C until arrival at the laboratory. There they were transferred into jars of unfiltered seawater collected at the location of copepod collection. The dinoflagellate *Gymnodinium nelsoni* was added at a concentration of about 15 µgC l⁻¹ to the *C. furcatus* jars, and at about 65 µgC l⁻¹ to the *Oncaea* jars, each of which had a capacity of 1900 to 3800 ml. These jars were mounted on a plankton wheel which rotated at about 0.3 rpm. Maintenance temperature was 20 to 21°C with a 12:12 h light:dark cycle. These females were used for experiments within 1 to 3 d of collection. The *P. aculeatus* females had been reared in the laboratory at 20°C on a plankton wheel, feeding on the flagellates *Isochrysis galbana* (4.5 µm equivalent spherical diameter, ESD) and *Rhodomonas* sp. (8.2 µm ESD), each at approximate average concentrations of 15 to 30 µgC l⁻¹. They originated from females collected on the outer shelf using the methods described above. As the copepodids approached copepodid stage V, they received only *Rhodomonas* sp. at near 10 to 15 µgC l⁻¹ average food concentration in order to acclimate them to food levels close to those found in the upper 75 m of the open subtropical ocean (Paffenhöfer et al. 2003). Only fertilized females that had molted to adult less than 10 d prior to an experiment were used.

Oxygen consumption was quantified in Plexiglas chambers of 230 to 460 ml capacity, rotating at about 0.3 rpm on a plankton wheel, using the microWinkler method (Jahnke & Craven 1994). Each chamber had 2 narrow stoppered openings allowing simultaneous withdrawal and addition of seawater. Experiments were run at 20 and 23°C over periods of 20 to 24 h. The larger chambers (460 ml) were always used for *Clausocalanus furcatus*, which moved at velocities of up to 10 mm s⁻¹, in order to limit wall encounters, and also for some experiments with *Paracalanus aculeatus*. The smaller chambers (230 ml) were used for *Oncaea* spp., which only moved occasionally, and for *P. aculeatus*, which moved at velocities of about 0.4 mm s⁻¹ while creating a feeding current, and were not affected in their feeding activities when they occasionally encountered walls. Copepod concentrations in the experimental chambers ranged from 12 to 25 per 100 ml for *C. furcatus*, from 20 to 40 per 100 ml for *Oncaea* spp., and from 17 to 35 per 100 ml for *P. aculeatus*. One to 3 control chambers were run simultaneously. Oxygen concentrations in the experimental chambers at the end of experiments were never below 70% of the initial concentration. To provide food during the experimental periods, *Gymnodinium nelsoni* was added at about 15 µgC l⁻¹ to the jars containing *Oncaea* spp. and *C. furcatus*, and *Rhodomonas* sp. at 15 µgC l⁻¹ to those containing *P. aculeatus*.

At the beginning and end of each experiment, each of the chambers was slowly turned top over bottom to achieve gentle mixing prior to drawing 10.0 ml with a glass syringe. At the same time, 10.0 ml of filtered seawater, identical with that in the chambers, was sucked into the respective chamber from an identical glass syringe. This method ascertained that the water in the control and experimental chambers had no intermittent contact with air prior to being analyzed. Replicate 4.0 ml samples were taken from this 10 ml and used to determine oxygen content using a micro-burette with an accuracy of ±1 µl of sodiumthiosulfate, which was repeatedly calibrated (Jahnke & Craven 1994). The oxygen consumption data and copepod body weights were converted into units of calories (1 ml oxygen respired equaled 4.86 cal at a respiratory quotient of 1.0; 1 mg ash-free dry weight equaled 5.0 cal, Winberg 1971, Omori & Ikeda 1984). Ikeda (1985) developed regressions relating oxygen uptake of zooplankton to their body weight. To compare his results with those of this study his equation will be applied:

$$\ln y = a_0 + a_1 \ln X_1 + a_2 X_2$$

where y is oxygen respired (µl ind.⁻¹ h⁻¹); X_1 is the body mass of an individual (mg dry weight); X_2 is temperature; and a_0 , a_1 and a_2 are constants.

To obtain ingestion rates of *Paracalanus aculeatus* females at near oligotrophic conditions, laboratory feeding experiments were conducted with just fertilized females which had been reared on several species of phytoplankton at levels close to oligotrophic conditions. At 20°C, 4 different phytoplankton species, including *Isochrysis galbana* (4.5 µm ESD), *Rhodomonas* sp. (8.2 µm ESD), *Thalassiosira weissflogii* (11.5 µm ESD) and *T. eccentrica* (32 µm ESD), were offered alone or in pairs at total concentrations ranging from 5 to 15 µgC l⁻¹, i.e. close to those found in the subtropical to tropical Atlantic in the nanoplankton range (Paffenhöfer et al. 2003). Methodology included a 12:12 h light:dark cycle, 960 ml glass jars, 0.3 rpm on plankton wheels, 18 to 22 h experimental periods, and particle quantification using an inverted microscope and a Coulter Multisizer with a 140 µm diameter orifice tube. These experiments were used to calculate the clearance rates (Frost 1972) to be applied to natural food abundances (Paffenhöfer et al. 2003) in order to determine their food intake (Table 1). Clearance rates for *Clausocalanus furcatus* originated from *in situ* studies in the subtropical open ocean (Table 1, Paffenhöfer et al. 2006).

Statistical tests included the Kruskal-Wallis non-parametric analysis of variance by ranks, which was followed by a multiple comparison test if the null hypothesis was not rejected (Conover 1980).

Table 1. *Paracalanus aculeatus* and *Clausocalanus furcatus*. Clearance rates ($\text{ml ind.}^{-1} \text{d}^{-1}$) of *P. aculeatus* females at 20°C at various particle size ranges feeding on different phytoplankton species at total concentrations ranging from 5 to 15 $\mu\text{gC l}^{-1}$ and comparative data for *C. furcatus* females at 23°C, feeding on *in situ* particles (Paffenhöfer et al. 2006). ESD: equivalent spherical diameter

Size range (μm , ESD)	<i>P. aculeatus</i>	<i>C. furcatus</i>
2–4	–	28
4–6	31	40
6–8	58	55
8–10	106	78
10–20	195	99
20–40	320	237

RESULTS

Mortality during the oxygen consumption experiments was zero for *Paracalanus aculeatus*, less than 2% for *Oncaea* spp., and between 0 and 5% for *Clausocalanus furcatus*. At the end of each experiment, most *C. furcatus* females were moving slower than at the beginning, indicating that the encroaching conditions or food limitation affected their motion. However, within several hours after being returned to a 3800 ml jar on the plankton wheel containing *Gymnodinium nelsoni* at concentrations of $\sim 10 \mu\text{gC l}^{-1}$, *C. furcatus* had regained most of their initial motion activity. Also, *P. aculeatus* and *Oncaea* spp. escaped less effectively at the end than at the beginning of an experiment. *Oncaea* spp. and *C. furcatus* consumed all food particles in their chambers, while food concentrations in the *P. aculeatus* chambers diminished to close to $1 \mu\text{gC l}^{-1}$.

The individual data indicate that *Oncaea* spp. had the lowest, and *Clausocalanus furcatus* the highest, oxygen consumption rate in relation to their ash-free dry weight at both 20 (Fig. 1) and 23°C (Table 2). *Oncaea* spp. were the lightest and *Paracalanus aculeatus* the heaviest (Fig. 1, Table 2). The results reveal that on average *Oncaea* spp. consumed $4.74 \mu\text{l oxygen mg}^{-1} \text{h}^{-1}$, *P. aculeatus* $6.56 \mu\text{l mg}^{-1} \text{h}^{-1}$, and *C. furcatus* $11.32 \mu\text{l mg}^{-1} \text{h}^{-1}$ at 20°C (Table 2). These data were significantly different from each other ($p < 0.05$, Kruskal-Wallis test with ensuing multiple comparison test, Conover 1980). The respective average values at 23°C were 6.52, 9.63 and $13.81 \mu\text{l mg}^{-1} \text{h}^{-1}$ (Table 2). For *Oncaea* spp. and *P. aculeatus*, the values measured at 20°C were significantly lower than those at 23°C ($p < 0.05$, Kruskal-Wallis test). At 20°C, the occasionally moving *Oncaea* spp. females (inactive 74.4% of the time, Paffenhöfer et al. 2006) metabolized on average 10.5% of their body weight per day, the continuously but slowly moving and feeding current-creating *P. aculeatus* females (0.33 mm s^{-1} , Paffenhöfer et al. 1996)

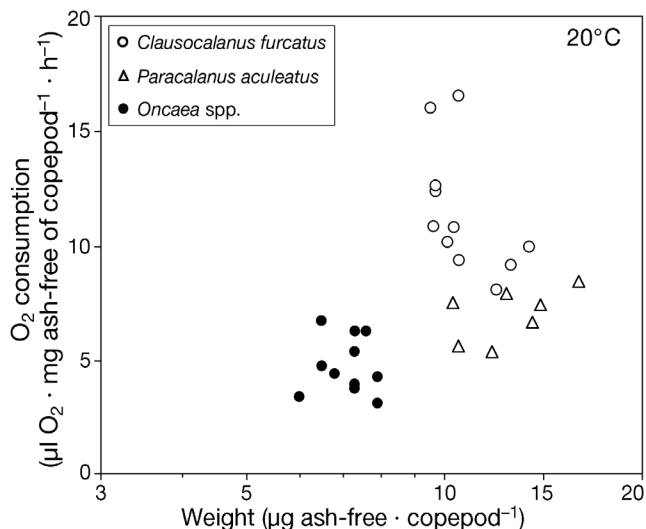


Fig. 1. *Oncaea* spp., *Paracalanus aculeatus* and *Clausocalanus furcatus*. Oxygen consumption of females in relation to their body weight at 20°C

metabolized 15.1%, and the continuously fast-moving *C. furcatus* females (6 to 10 mm s^{-1} , Mazzocchi & Paffenhöfer 1999) metabolized 23.4%. At 23°C, the respective data were 15.2, 22.4, and 32.2%.

DISCUSSION

Oxygen consumption and copepod motion

To date, no empirical data are available directly comparing oxygen consumption or metabolic expenditures of planktonic copepods with their motion. So far, evaluations of metabolic expenditures in relation to motion have been based on fluid dynamics theory. The

Table 2. Oxygen consumption of marine planktonic copepods ($\mu\text{l mg}^{-1} \text{ ash-free dry weight h}^{-1}$), average ash-free dry weight, and number of observations (± 1 SE)

Species	Ash-free dry weight (μg)	n	Oxygen $\mu\text{l O}_2 \text{ mg}^{-1} \text{ h}^{-1}$
20°C			
<i>Clausocalanus furcatus</i>	10.7 ± 0.47	11	11.32 ± 0.84
<i>Paracalanus aculeatus</i>	12.6 ± 0.67	8	6.56 ± 0.53
<i>Oncaea</i> spp.	7.1 ± 0.18	11	4.74 ± 0.37
23°C			
<i>Clausocalanus furcatus</i>	9.6 ± 0.32	5	13.81 ± 1.36
<i>Paracalanus aculeatus</i>	12.5 ± 1.08	8	9.63 ± 0.80
<i>Oncaea</i> spp.	7.4 ± 0.17	11	6.52 ± 0.62

most advanced modeling effort for copepod swimming expenditures was made by Morris et al. (1985). They included variables such as mechanical energy required for appendage movement, kinetic energy dissipation in the fluid, and metabolic costs of swimming in their assessment. Their model is in agreement with empirical observations of larger crustaceans (e.g. shrimps), which indicate that swimming should be energetically expensive. This disagrees with earlier calculations using fewer variables, which concluded that copepod swimming would require little energy (e.g. Klyashtorin & Yarzombek 1973).

Quantifications of oxygen consumption by nauplii and copepodid stages of the cyclopoid *Mesocyclops brasiliensis* revealed major differences between nauplii and post-nauplii (Epp & Lewis 1979). Specifically, while nauplius stage VI (NVI, 0.22 µg dry weight), which rarely moves, respired 13.9×10^{-4} µl oxygen h⁻¹ at 24°C, copepodid stage I (CI, 0.23 µg dry weight), which moves frequently, respired 34.4×10^{-4} µl oxygen h⁻¹. While the body mass had hardly changed, the motion had increased sharply, and with it oxygen consumption by a factor of about 2.5. Which variables could be responsible for such differences in oxygen consumption? The mechanical energy costs of appendage movement and the metabolic costs of swimming described by Morris et al. (1985) may play a role. While a nauplius has 3 pairs of appendages, a CI has 6 pairs of cephalic appendages and 2 pairs of swimming feet. Thus, not only the energy for body propulsion but also that for motion of the different number and morphologies of appendages should contribute to the overall energy costs.

Concerning the 3 copepod taxa studied here, *Paracalanus aculeatus* late copepodids and females move continuously at 0.33 mm s⁻¹, creating a feeding current at a mouthpart frequency of 80 Hz (Paffenhöfer et al. 1996). The similarly sized *Clausocalanus furcatus* females also move continuously, but at 6 to 10 mm s⁻¹; the mouthpart frequency is unknown (Mazzocchi & Paffenhöfer 1999). *Oncaea* spp. females are motionless/sinking for 74.4 ± 8.3 % (SE) of the time during light hours at 20°C (Paffenhöfer et al. 2006). Morris et al. (1985) calculated that at a swimming speed of 5.2 body lengths s⁻¹ the metabolism of the copepod *Pleuromamma xiphias* (6 mm prosome length) was 3.1. times higher than its standard (non-moving) metabolism. If one takes the weight-specific energy expenditure of a female *Oithona similis* at 20°C (10.5%, Castellani et al. 2005, Table 3), being slightly smaller than *C.*

furcatus, as an approximate non-moving metabolic expenditure, the metabolism of *C. furcatus* (23.4%) moving at 6 to 10 body lengths s⁻¹, i.e. about 2.2 times that of a rarely moving copepod, would be in the range of that of the moving *P. xiphias*.

Oxygen consumption of small copepods

Oxygen consumption rates of small planktonic copepods were normalized to daily metabolic expenditures as percent of their body weight, applying conversion factors of Omori & Ikeda (1984, shown in 'Materials and methods'). These rates had been obtained at different temporal and spatial conditions, ranging from microrespirometers where a copepod was placed in less than 1 ml (Klekowski 1977), through vessels of 60 ml capacity (Nakamura & Turner 1997, Castellani et al. 2005), to this study's 230 and 460 ml chambers. The daily metabolic expenditures measured by the different authors for each of the genera *Oithona* and *Oncaea* varied by a factor of about 2 (Table 3). Since *Oithona* and *Oncaea* only move occasionally, one could expect similar expenditures for both, as was found in the most recent quantifications (Castellani et al. 2005 and this study). The variability of rates observed for each of the 2 genera (Table 3) is most likely due to differing methodology, including vessel volume, pre-experimental treatment, geographical location, different behavior among species within a genus, and the age of the experimental adult females. Even though identical methods were applied, the individual data of this study (Fig. 1) show an approximately 2-fold difference between the lowest and highest values for each of the

Table 3. Daily metabolic expenditures calculated from oxygen consumption quantifications, expressed as % of each copepod's body weight

Genus/Species	Temperature (°C)	Daily metabolic expenditures (% of body weight)	Source
<i>Oncaea</i>	20	55	Klekowski et al. (1977)
<i>Calocalanus</i>	20	10.7	
<i>Oithona</i>	20	19.1	
<i>Paracalanus</i>	20	24.7	
<i>Clausocalanus</i>	20	28.0	
<i>Oncaea venusta</i>	20	9.8	Gaudy & Boucher (1983)
<i>Oithona davisae</i>	20	20.9	Hiroimi et al. (1988)
<i>Oithona similis</i>	19	20.3	Nakamura & Turner (1997)
<i>Oithona similis</i>	20	10.5	Castellani et al. (2005)
<i>Oncaea</i> spp.	20	10.5	This study
<i>Paracalanus aculeatus</i>	20	15.1	
<i>Clausocalanus furcatus</i>	20	23.4	

3 copepods. In essence, a general comparison of all data in Table 3 reveals that the rarely moving copepods had the lowest metabolic rates and the fastest moving ones had the highest.

Applying Ikeda's (1985) equation for oxygen uptake in relation to a temperature of 20°C and a body mass of 10 µg (0.010 mg) dry weight, such a small copepod would metabolize 12.8% of its body weight daily. Such a value would be relatively close to those obtained for *Oncaea* spp. and *Paracalanus aculeatus* in our experiments, but far lower than the results for *Clausocalanus furcatus*. Although a generalization like Ikeda's (1985) reveals overall relationships between temperature, body mass and metabolic rates, quantifications of individual rates in relation to a species' behavior are needed as they reveal part of that organism's means to operate and exist.

A comparison between our respiration rates at 20 and 23°C indicated metabolic increases of 22.0% for *Clausocalanus furcatus*, 46.8% for *Paracalanus aculeatus*, and 37.6% for *Oncaea* spp. (Table 2). What could such different increases imply? Again applying Ikeda's (1985) regression for oxygen consumption, an increase from 20 to 23°C for a small copepod of 4 µg carbon (10 µg ash-free dry weight) should result in an increase in oxygen consumption of 19.8%. This would imply that *C. furcatus* would be less affected metabolically by such a temperature increase than the other 2 copepods. This could partly explain why this species has been found regularly near temperatures of 25°C and even above in the warm open ocean, in contrast to the genus *Oncaea*, which usually increases in abundance with depth and decreasing temperatures below 40 m, and reaches highest concentrations near 100 m depth (Paffenhöfer & Mazzocchi 2003).

Ingestion rates and metabolic needs

Are previously quantified ingestion rates (Paffenhöfer et al. 2006) sufficient to support the metabolic expenditures presented in this study? Using particle concentrations (µgC l⁻¹) quantified for the range from 2 to 40 µm ESD at 3 different stations at 2 different depths in the western tropical and subtropical Atlantic Ocean (Paffenhöfer et al. 2003) where *Clausocalanus* spp. is dominant and *Paracalanus aculeatus* common to abundant (Webber & Roff 1995), ingestion rates were calculated for females of both species by applying previously quantified clearance rates for the different particle size ranges for *C. furcatus* (Paffenhöfer et al. 2006), and clearance rates from experiments described earlier for *P. aculeatus* (Table 1). The ingestion rates of particles in the abovementioned range are thought to be a function of their volume (Bartram 1981, Paffenhöfer et al. 2006). Applying an assimilation effi-

ciency of 90% (Conover 1979, Paffenhöfer & Köster 2005) and the abovementioned daily metabolic expenditures in % of body carbon at 23°C (32.2% for *C. furcatus*, and 22.4% for *P. aculeatus*), ingestion rates of *C. furcatus* and *P. aculeatus* met metabolic needs in 3 and 4 out of 6 cases, respectively (Table 4). In the case of *P. aculeatus*, part of the ingested food would be available for reproduction. At Stns 19 and 35, the food concentrations appeared to be quite sufficient to support the metabolic needs of both copepods, while at Stn 11a at both depths, neither copepod could obtain sufficient amounts of food. As abundance of these copepods is continually very low in oligotrophic waters (e.g. Webber & Roff 1995) and ingestion rates of adult females barely meet or exceed metabolic needs, one could speculate that reproduction rates at *in situ* food abundances are severely limited. No meaningful calculations could be made for *Oncaea* spp. for which credible ingestion rates for the subtropical/tropical open ocean are not yet available.

Almost all previously obtained oxygen consumption measurements of planktonic copepods were made without offering food to the experimental animals. Thus, these quantifications should not be identical with rates in their natural environment, as the results from Kjørboe et al. (1985) for an estuarine copepod indicate. They found an increase in oxygen consumption rates with increasing food concentrations. The experiments in this paper used food abundances resembling the regularly found low environmental abundances at the beginning of each period as an attempt to simulate the natural environment of the copepods. Furthermore, the limited space in experiments could have an effect on oxygen consumption. It

Table 4. *Clausocalanus furcatus* and *Paracalanus aculeatus*. Ingestion rates (ng C female⁻¹ d⁻¹) at 23°C at environmental concentrations of combined phyto- and protozooplankton from 2 to 40 µm ESD from 3 different stations in the western Atlantic (Paffenhöfer et al. 2003), and daily assimilation as percentage of body C (at 90% assimilation efficiency). Clearance rates of *P. aculeatus* obtained at 20°C were assumed to be similar to those at 23°C. Ingestion rates of *C. furcatus* from Paffenhöfer et al. (2006). *: copepods met metabolic requirements

Stn	15 m Ingestion	Assimilation	45 m Ingestion	Assimilation
<i>C. furcatus</i>				
11a	680	20.8	784	23.8
19	1102	36.3*	1187	39.0*
35	1299	42.6*	972	31.9
<i>P. aculeatus</i>				
11a	829	16.6	1045	20.7
19	1446	28.6*	1695	33.5*
35	1809	35.7*	1329	26.3*

was attempted to improve on this in the present study by utilizing larger vessel volumes. Yet, the concentrations of copepods required to obtain significant oxygen reductions are such that vessels with volumes large enough to have little effect on copepod motion (>2000 ml, judging from their motion) would require extraordinary abundances of copepods. This means that the methods applied so far ought to be improved upon.

In conclusion, the data from this study reveal more than 2-fold differences in oxygen consumption between planktonic copepods with different motion behaviors. Such energy consumption could be roughly seen as a function of the motion activity of the respective taxon. These results may also give rise to thoughts about the means of operation of the different taxa, which allow them to persist in a narrower or wider range of environments, ranging from the coastal to the oligotrophic open ocean.

Acknowledgements. This research was supported by a grant from the National Science Foundation (OCE 99 11513). R. and D. Jahnke provided equipment and valuable advice for the microWinkler quantifications. J. Williams skillfully built the oxygen consumption chambers. The captain and crew of the RVs 'Blue Fin' and 'Savannah' cooperated dependably and competently. Their support is gratefully acknowledged.

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