Zooplankton metabolic activity (respiration and ETS) from three stages of the MALASPINA 2010 campaign

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Zooplankton metabolic activity (respiration and ETS) from three stages of the MALASPINA 2010 campaign

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Abstract

During the MALASPINA 2010 campaign three ocean transects were sampled for ETS activity and respiration, two from the Indian Ocean and one from the Atlantic Ocean. Zooplankton samples are captured from the upper 150 m with a WP2 100µm mesh net. Respiration (R), biomass and potential respiration (Φ) were measured on three size fractions of mixed populations of crustaceans from these samples. In addition, experiments of the effect of starvation on R and Φ were conducted on mixed crustaceans. In the Great Australian Bight the protein-specific R and Φ were 1.58 ± 0.81 and 1.98 ± 0.68 µmol $O_2 \cdot h^{-1} \cdot mg^{-1}$, in the southern Indian Ocean they were 1.49 ± 0.62 and 1.60 ± 0.62 µmol $O_2 \cdot h^{-1} \cdot mg^{-1}$, and during the Atlantic crossing they were 1.24 ± 0.82 and 1.06 ± 0.64 µmol $O_2 \cdot h^{-1} \cdot mg^{-1}$. Challenging Kleiber's law, we found that the Kleiber exponent, b, for the southern Indian Ocean zooplankton was 0.70, approaching Rubner's surface law with a b of 0.66, but the values of b for the Great Australian Bight were 0.93 and for the Atlantic crossing, 1.03, closer to the isometric theory of Glazier (2005).

Starvation results showed that there was no significant difference ($p>0.05$) in either R/Φ or log R / log biomass after 24 hours of starvation

Keywords: *Malaspina 2010, Respiration, ETS activity, Zooplankton*

Resumen

Durante la campaña de circunnavegación MALASPINA 2010 se muestrearon tres transectos, para determinar la respiración (R) y la actividad del sistema de transporte de electrones (ETS); dos de estos transectos se llevaron a cabo en el Océano Índico y el otro en el Océano Atlántico. Las muestras de zooplancton de los primeros 150m de la columna de agua, se obtuvieron con una red WP2, equipada con malla de 100 µm. La respiración (R), biomasa y respiración potencial (Φ), se midieron en tres fracciones de talla. Así mismo se desarrollaron experimentos sobre los efectos de la inanición en la R y Φ. En el Leg correspondiente a la costa sur Australiana (Leg4), los valores de R y Φ específicos por proteina fueron de 1.58 ± 0.81 y 1.98 ± 0.68 µmol $O_2 \cdot h^{-1} \cdot mg^{-1}$ en el Océano Índico Sur de 1.49 ± 0.62 y 1.60 ± 0.62 µmol $O_2 \cdot h^{-1} \cdot mg^{-1}$, durante el cruce del Atlántico fueron de 1.24 ± 0.82 y 1.06 ± 0.64 µmol $O_2 \cdot h^{-1} \cdot mg^{-1}$. Desafiando la ley de Kleiber, hemos encontrado, que el exponente de Kleiber (b) para el zooplancton del Océano Índico Sur fue de 0.70, acercándose más al valor de la teoría de superficie de Rubner (0.66). El exponente encontrado para la región sur de la costa Australiana fue de 0.93 y para el Atlántico de 1.03 aproximándose más a la teoría isométrica de Glazier (2005).

Los resultados de inanición muestran que no existen diferencias estadísticamente significativas ($p>0.05$) tanto para las relaciones R/Φ como log R / log biomasa después de 24 horas en inanición.

Palabras clave: *Malaspina 2010, Respiración, Actividad ETS, Zooplancton*

Introduction

The interdisciplinary project of the circumnavigation MALASPINA 2010 expedition has, as one of its main objectives, generated a large inventory of samples and a plethora of information on ocean global change impacts and diversity in the deep ocean. On this expedition we had the chance to acquire data, from some of the least explored oceanic regions in the world. We sampled the southern Indian Ocean and the tropical and subtropical North Atlantic during three different transects, taking surface zooplankton samples. From this pool of samples our group measured ammonium excretion, intracellular concentration of respiration substrates, respiration, and potential respiration. Here we present the respiration and potential respiration observations.

Key to the understanding of how ocean ecosystems work, is learning how the environment affects zooplankton respiration. One approach towards this end is through the metabolic theory of ecology (Allan and Gillooly, 2007; Brown *et al*, 2004) and Kleiber's law (Kleiber, 1932, 1961; Glazier, 2005, 2006) that argue the significance of biomass in respiration and growth. Another is through the enzymology that controls the chemistry of respiration. Here we explore the latter approach.

Respiration is a key physiological process in all marine organisms, which along with primary productivity, is paramount to metabolic balance in the ocean. Furthermore, from respiration one can calculate new production and carbon flux in different oceanic ecosystems. Accordingly, it is essential to understand and predict respiration in all the different regions and depths of the ocean. But, for all its utility it is rarely measured in an oceanographic sense because it is difficult to impossible to measure except in eutrophic surface waters. With regard to zooplankton, one of the difficulties in measuring respiration is that during capture by nets, zooplankton are injured and crowded in extreme conditions. As a result, physiological measurements reflect these extreme conditions and not real *in situ* conditions. Even after appropriate dilution and acclimatization the measurements

are likely to be distorted. That is why the ETS method was developed (Packard *et al*., 1971; Packard *et al*., 1974). ETS activity measures potential respiration. This enzyme activity is a reaction rate, but a biological reaction rate and as such depends on the physiological state of the organism. If the organism is nutrient-limited or starved the *in vivo* enzyme activity in its living cells may be low. If these organisms are nutrient-sufficient or well-fed the *in vivo* enzyme activity may be high. However, measuring *in vivo* enzyme activities is extremely difficult. Normally, enzymes are extracted from the cells and their activities measured *in vitro* by supplying unlimited amounts of all reactants (substrates). This *in vitro* activity is the V_{max} (sensu Michaelis-Menten). Relating this in vitro respiration capacity to the true *in vivo* rate (respiration) is a challenge that is usually met by seeking a statistical relationship between the *two processes.* This was one of the objectives of our Malaspina research. We measured *in situ* respiration and potential respiration in an effort to calibrate the ETS method for zooplankton and further our understanding of the metabolic state of zooplankton in different zones of the world.

Here we examine some of these relations between *in vivo* respiration, potential respiration, biomass and the effects of 24h starvation in zooplankton from around the world.

Methods

The oceanographic cruise MALASPINA 2010 had a total of seven legs, but our research group participated in only three. We took zooplankton samples and conducted physiological experiments on Leg 3 (Cape Town-Perth), Leg 4 (Perth-Sydney) and Leg 7 (Cartagena de Indias – Cartagena) (Figure 1).

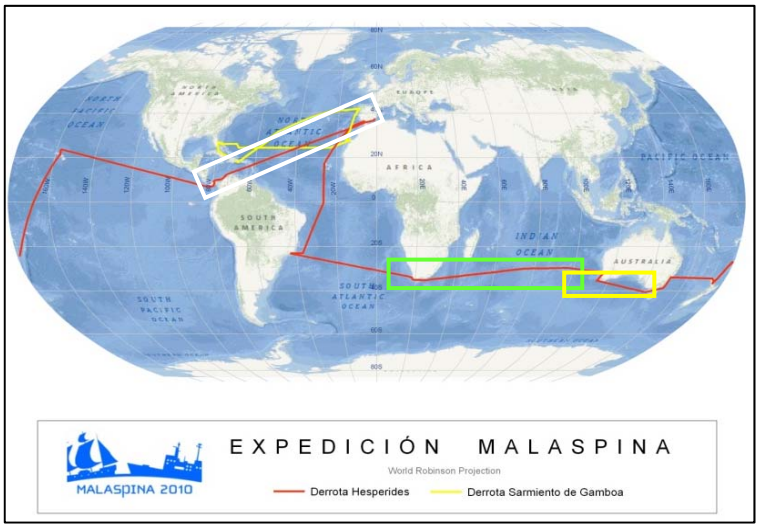

Figure 1. Description of the cruise tracks made for the complete MALASPINA campaign. Data used correspond to Leg 3 (February 12 to March 13, 2011) from Cape Town to Perth (green box), Leg 4 (17-30 March, 2011) from Perth to Sydney (yellow box), and Leg 7 (June 20 to July 14, 2011) from Cartagena de Indias to Cartagena (white box).

Samples were collected with a WP2 100 µm mesh size, with a physiological purposes collector as describe by UNESCO (1968). Vertical hauls were made from 150 m to surface. Samples were immediately fractionated into three size classes (100-500 µm, 500-1000 µm and >1000 µm). Each one of these was placed individually in half litter plastic vessel with filtered sea water (2 µm) with the average temperature of the water column of the net haul. Then with extreme care gelatinous organisms were taking out, the remaining zooplankton, in good health and shape, were removed one by one, for the bigger sizes or by siphoning, in the smaller ones and put in bottles with filtered sea water to measure the oxygen consumption with O_2 electrodes (Strathkelvin Instrument Oxygen Interface 928) for an hour. Each bottle had an individual steering mechanism, isolated from the organisms to assure no damage and to ensure homogenous distribution of oxygen. The temperature of the experiments was controlled all the time by a thermostatic bath, maintaining the temperature at which the animals were accustomed, assuring less stress and a more realistic data. At the end of the measurement the

sample was immediately frozen in liquid nitrogen and stored at -80 ℃ to preserve enzymatic activity (Gómez *et al*., 1996).

In order to measure the effects of starvation, samples were collected every other day. When time and weather conditions permitted, each day. When there was sufficient quality biomass, samples were split in two. One part was used immediately for the T = 0 assays (0h), the other was kept in 2l bottles with filtered sea water with continuous oxygenation and controlled temperature, for 24 hours. Storage and respiration were as described above.

In the laboratory, the determination of the potential respiration (Φ) by measuring the ETS activity was done according to Owens and King (1975). Protein was determined as a measure of biomass by the method of Lowry *et al*. (1951) modified by Rutter (1967).

Statistical analysis

Data was analyzed using R Development Core Team 2010 (R Foundation for Statistical Computing, Vienna, Austria). To confirm normality, ETS activity (Φ), specific ETS activity, respiration and specific respiration, data was treated by Shapiro Wilk test (Shapiro and Wilk, 1965) and the homoscedasticity of the residuals was assessed graphically. All results were tested by the Shapiro-Wilk test (Shapiro and Wilk, 1965) for normality. The results showed that none of the data was normally distributed. Consequently, the non-parametric Kruskal-Wallis test was used to test differences in the R, Φ, biomass, specific R and specific Φ data between the different cruise leg's and different size classes. The correlation between biomass, Φ and R was estimated with the Pearson test, at a confidence level of 95%. For the starvation data a non-parametric statistical hypothesis test (Mann–Whitney *U test)* for assessing whether one of two samples of independent observations tends to have larger values than the other was used.

Results

Crossing the southern Indian Ocean on Leg 3, there were a total of seven stations at which we took samples. Crossing the Great Australian Bight on Leg 4, there were four stations and on Leg 7, the final Atlantic crossing from Cartagena de Indias to Cartagena, Spain, there were twelve stations sampled. The differences in the number of samples (Table 1) taken in each transect was due to the length of the transect, the priorities on board, and the weather conditions. For example during the crossing of the southern Indian Ocean, the weather was often too terrible for samples to be taken. Also, for consideration of the >1000 μm size class only the crustacean zooplankton were taken into account, all selectable salps, jellyfishes, chaetognaths and fish larvae were eliminated.

Tables 1 and 2 summarize the original ETS and respiration measurements. Table 3 summarizes the relationships between the respiration and the ETS activity and well as the relationships between these two indices of metabolism and their biomass base (protein). Table 4 present the biomass specific respiration and ETS activities. For the entire cruise the protein specific ETS activity ranged from 1-2 μmol $O_2 \cdot h^{-1} \cdot mg^{-1}$ and the protein specific respiration ranged from 1.2-1.6 μmol $O_2 \cdot h^{-1} \cdot mg^{-1}$.

Table 1. Means and standard deviation of total biomass, respiration (R) and potential respiration (Φ), listed here to compare variability due to geography (cruise leg), size class, and nutrient-limitation (starvation). For the starvation experiments, all data were integrated by treatment. The minimum and maximal values are given inside the parenthesis. In Leg 3 seven stations, Leg 4 four stations and Leg 7 twelve stations where sampled.

	Biomass (mg)	R (µmol $O_2 \cdot h^{-1}$)	Φ (µmol $O_2 \cdot h^{-1}$)
LEG			
3	0.33 ± 0.21 (0.009; 0.73)	0.50 ± 0.32 (0.009; 0.73)	0.52 ± 0.36 (0.026; 1.25)
4	0.72 ± 0.65 (0.11; 1.82)	0.91 ± 0.77 (0.18; 2.66)	1.34 ± 1.11 (0.17; 3.47)
7	0.64 ± 0.64 (0.17; 3.53)	0.86 ± 0.84 (0.004; 3.72)	0.76 ± 1 (0.09; 4.67)
Size Class			
100-500 µm	0.77 ± 0.77 (0.035; 3.53)	1.15 ± 0.95 (0.004; 3.72)	1.20 ± 1.23 (0.04; 4.67)
500-1000 µm	0.54 ± 0.47 (0.075; 2.61)	0.66 ± 0.46 (0.103; 1.74)	0.63 ± 0.68 (0.082; 3.47)
>1000 µm	0.35 ± 0.19 (0.009; 0.84)	0.34 ± 0.24 (0.05; 1.07)	0.34 ± 0.29 (0.026; 1.29)
Treatment			
0 h	0.59 ± 0.59 (0.009;3.53)	0.79 ± 0.75 (0.003; 3.72)	0.79 ± 0.95 (0.026; 4.67)
24 h	0.49 ± 0.46 (0.06; 1.79)	1.05 ± 0.99 (0.05; 3.81)	0.88 ± 1.16 (0.06; 1.79)

Table 2. Means and standard deviation of biomass, respiration (R), potential respiration (Φ), of each size by Leg. The minimum and maximal value are giving inside the parenthesis.

	Biomass (mg)	R (µmol $O_2 \cdot h^{-1}$)	Φ (µmol $O_2 \cdot h^{-1}$)
LEG 3			
100-500 µm	0.34 ±0.24(0.036; 0.73)	0.62 ±0.43 (0.16; 1.33)	0.57 ±0.45 (0.037; 1.25)
500-1000 µm	0.29 ±0.16 (0.075; 0.53)	0.42 ±0.21 (0.16; 0.63)	0.53 ±0.25 (0.09; 0.76)
>1000 µm	0.35 ±0.22 (0.009; 0.67)	0.41 ±0.13 (0.26; 0.63)	0.43 ±0.28 (0.026; 0.86)
LEG 4			
100-500 µm	0.92 ±0.88 (0.11; 2.35)	1.25 ±1.09 (0.52; 2.66)	1.55 ±1.19 (0.17; 2.8)
500-1000 µm	0.79 ±0.68 (0.16; 1.82)	0.91 ±0.59 (0.22; 1.25)	1.72 ±1.32 (0.34; 3.47)
>1000 µm	0.44 ±0.28 (0.22; 0.84)	0.57 ±0.36 (0.19; 1.07)	0.65 ±0.40 (0.26; 1.29)
LEG 7			
100-500 µm	0.90 ±0.84 (0.12; 3.53)	1.32 ±1.01 (0.003; 3.7)	1.38 ±1.36 (0.09; 4.04)
500-1000 µm	0.54 ±0.45 (0.11; 2.61)	0.69 ± 0.48 (0.10; 1.74)	0.45 ±0.34 (0.08; 1.41)
>1000 µm	0.31 ±0.15 (0.12; 0.64)	0.21 ±0.11 (0.049; 0.43)	0.19 ±0.12 (0.035; 0.33)

Kleiber's law

The relationships between log biomass and log R, between the different legs of the cruise yielded ratios around 0.75 for samples from the Indian Ocean and slightly higher for the Atlantic (1.03, see Table 3). The relationship between R and Φ versus biomass is consistent with the hypothesis that the higher the biomass, the higher the metabolic activity (Figure 2 and 3). However, the stability of the ETS measurements is reflected in the high correlation (r^2) with biomass (Table 3). In fact, the relationship is close enough to 1 that a logarithmic transformation is not needed. In the case of respiration, given the difficulty in making good respiration measurements with the oxygen electrode in field, few precise measurements were made (Table 3). Even so there is no statistical difference ($p>0.05$) between all ratios.

Table 3. Relationships between log biomass, potential respiration (Φ) and respiration (R). They are presented here to compare with Kleiber's law and to determine the impact of variability of the metabolic state on the R/Φ ratio. Part of this variability consisted of geography (cruise leg), part consisted of size class, and part consisted of nutrient-limitation (starvation). For the starvation experiments, all data were integrated by treatment. The coefficient of determination and the number of measurements are given in parentheses (r^2; n).

	Log Φ / log biomass	Log R / log biomass	R /Φ
LEG			
3	0.98 (0.85; 25)	0.70 (0.62; 20)	0.85 (0.82; 20)
4	0.93 (0.84; 16)	0.93 (0.77; 14)	0.85 (0.90; 14)
7	1.18 (0.77; 78)	1.03 (0.65; 50)	0.78 (0.82; 50)
Size Class			
100-500 µm	1.07 (0.89; 46)	0.88 (0.79; 34)	0.81 (0.88; 35)
500-1000 µm	0.95 (0.62;46)	0.94 (0.52; 26)	0.81 (0.31; 26)
>1000 µm	0.82 (0.63;27)	0.64 (0.42; 24)	0.75 (0.88; 24)
Treatment			
0 h	1.04 (0.73; 119)	0.81 (0.53; 84)	0.77 (0.81; 84)
24 h	1.76 (0.91; 25)	0.83 (0.47; 19)	0.73 (0.80; 19)

Indian Ocean (Legs 3 and 4 same value). The samples from the Atlantic crossing, Leg 7, were slightly lower (0.78) (Figure 4), but considering all the data, there is no significant differences between the ratios from the different oceanic zones ($p>0.05$). From the size point of view, the R/Φ ratio in the 100-500 and 500-1000 µm fraction was the highest (0.81), followed by the >1000 µm fraction (0.75) (Figure 4).

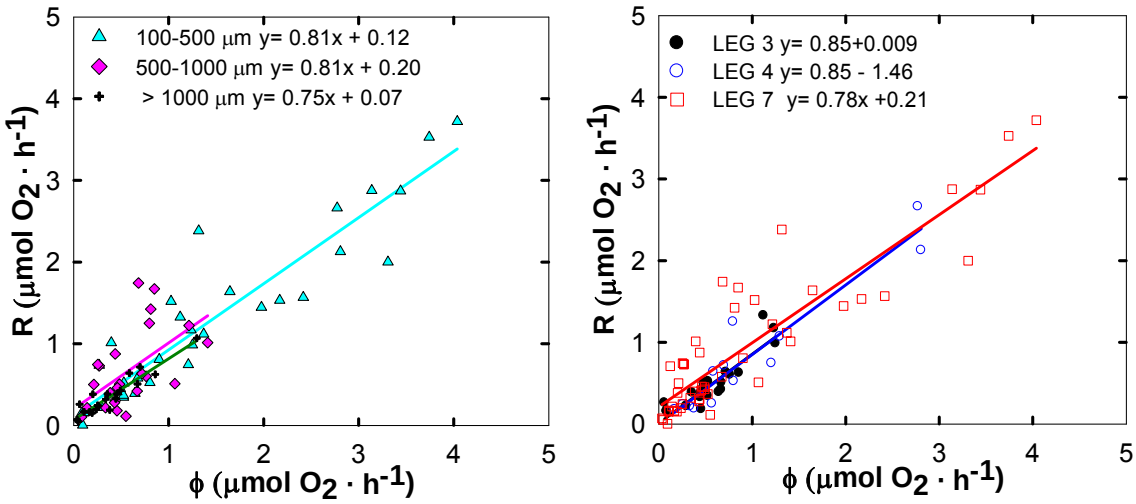

Figure 4. Relation between respiration and ETS activity. Upper plot data compared by Leg; bottom plot by the contribution of each size.

Specific activities

R and Φ specific activity reveals that Indic Ocean data have the higher activities, in the Leg 4, 1.49 and 1.60 µmol $O_2 \cdot h^{-1} \cdot$ mg $prot^{-1}$ respectively, follow by Leg 3, 1.49 and 1.60 µmol $O_2 \cdot h^{-1} \cdot$ mg $prot^{-1}$. Leg 7 have lower values (1.24 and 1.06 µmol $O_2 \cdot h^{-1} \cdot$ mg $prot^{-1}$) (Table 4). We also observed that the specific activity decrease with size (Table 4), same behavior was found by Hernandez-León and Gómez (1996).

Table 4. Specific activity of respiration (R) and potential respiration (Φ), to compare this variability of geography (cruise leg), size class, and part consisted of nutrient-limitation (starvation). For the starvation experiments, all data were integrated by treatment. The minimum and maximal values are giving inside the parenthesis. In Leg 3 seven stations, Leg 4 four stations and Leg 7 twelve stations where sampled.

	R (µmol $O_2 \cdot h^{-1} \cdot mg\ prot^{-1}$)	Φ (µmol $O_2 \cdot h^{-1} \cdot mg\ prot^{-1}$)
LEG		
3	1.49 ± 0.62 (0.69; 2.56)	1.60 ± 0.62 (0.42; 2.88)
4	1.58 ± 0.81 (0.81; 3.52)	1.98 ± 0.68 (0.84; 3.43)
7	1.24 ± 0.82 (0.03; 3.18)	1.06 ± 0.64 (0.17; 3.12)
Size Class		
100-500 µm	1.50 ± 0.72 (0.03; 2.88)	1.55 ± 0.65 (0.62; 3.12)
500-1000 µm	1.47 ± 0.89 (0.39; 3.52)	1.20 ± 0.74 (0.37; 3.43)
>1000 µm	0.98 ± 0.61 (0.25; 2.94)	1.04 ± 0.72 (0.17; 2.88)
Treatment		
0 h	1.48 ± 0.88 (0.028; 4.14)	1.31 ± 0.73 (0.17; 3.43)
24 h	1.89 ± 1.44 (0.25; 6.26)	1.24 ± 0.87 (0.12; 2.81)

Food limitation (starvation experiments)

It was expected that the respiration would fall and the ETS activity would maintain its original level during these experiments. The results showed otherwise, both metabolic indices maintained their original levels. The experiments were hampered by the paucity of biomass in the open ocean samples. This problem might have been obviated with a larger net to sample more seawater, but that was not the case. Because of the low biomass there were many occasions when we could only manage to measure respiration in the initial sample. That is why in Table 3 there are nearly 5 times the number of initial measurements (T = 0) as they are measurements after 24 hours (24h). Furthermore, the problem was compounded by the high mortality rate of the zooplankters during the first 24 h after capture. For these reasons these starvation experiments were conducted on pooled samples rather than on individual size classes.

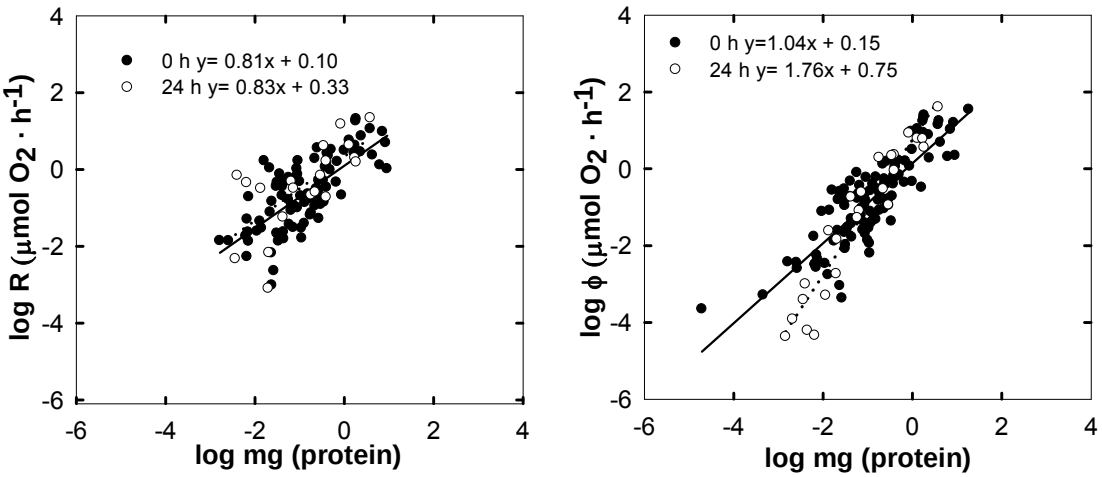

Figure 5. Relation between log of respiration (R) (left) and potential respiration (Φ) (right) with log biomass. Note the difference in the number of data points of Φ compared to R. This is due to the difficulty in making good quality *in situ* measurements at sea with oxygen electrodes. In both cases there is no significant differences (p>0,05) between 0 h (natural oceanic conditions) and 24 h treatments (nutrient limited conditions).

Even so, the relationships between log biomass and log R are almost equal (Table 3; Figure 5) also reflected in the specific activity of each state (Table 4). In the case for the log Φ, the ratio to log biomass for 24h is higher than the 0h (1.76 over 1.04) even if there is no statistical difference (p> 0.05). Also the R/Φ rates were not different between the two treatments (Figure 6).

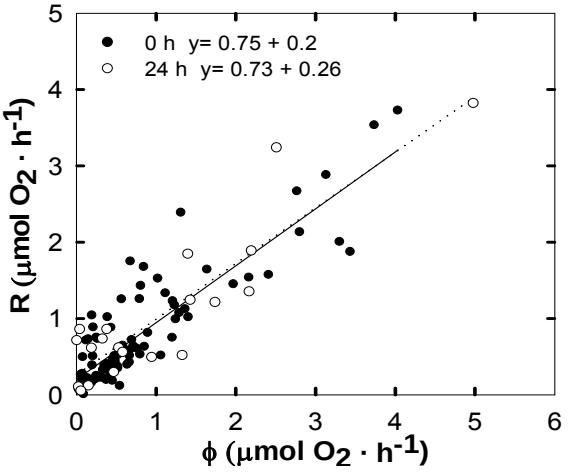

Figure 6. Relation between respiration (R) and potential respiration (Φ) for all the data from the two treatments 0h and 24 h. There is no significant differences (p>0,05) between the two both treatments.

Discussion

Kleiber's law

The relationship between metabolic rate, sensu respiration (R), and body mass (M), the exponent b in the equation $R = aM^b$, is accepted by many authors to be 0.75 (Hemmingsen, 1960; Kleiber, 1932, 1961; Savage *et al*., 2004). However, Glazier (2005, 2006), cautions that this value is only a statistical mean and should not be considered invariant. He found that many pelagic organisms have a metabolic scaling exponent (b) around 1 and that for pelagic crustacea it is 0.88. Our values range from 0.64 for the larger zooplankton (> 1000 μm) to 0.94 for the mid size (500-1000 μm) and 0.70 for the southern Indian Ocean to 1.03 in for the central Atlantic Ocean (Table 3). However, the variability in our measurements is so great that these differences are not statistically significant. Nevertheless, for the sake of argument one might say that the larger zooplankton follow the surface law of Sarrus and Rameaux (1938) where the rate of oxygen consumption (metabolic rate) increases with increases in body weight to the 0.66 power (b). In other word respiration increases as the square of the organisn's size (area) while the biomass increases as the cube of the organism's size (volume). Variations of b are well documented, but not understood. It is likely that evolutionary, ecological, physiological, and biochemical factors need to be considered before this variability can be explained Ikeda (1970), Martínez *et al*. (2010), Herrera *et al*. (2011). These authors have pointed out that elevated departures from b = 0.75 may indicate healthy and well-fed organisms while values of b < 0.75 may indicate starved or otherwise unhealthy organisms.

Again for the sake of argument, our metabolic activity measurements fit the pattern in which the smallest zooplankton have higher metabolic rates in proportion to their body mass (Kleiber 1932; Gillooly *et al*., 2001; Glazier, 2006; Kolokotrones *et al*., 2010). The same pattern is found in the ratio log Φ/log biomass ratio. This type of relationship is also found in other poikilothermal

animals (Weymouth *et al*., 1944) as well as to bacteria and big mammals (Zeuthen, 1953).

Our results are not precise enough to establish which power law of biomass-metabolism applies to the zooplankton captured on our legs of the Malaspina cruise. Nevertheless, they do establish the range of the exponent, b (0.64-1.03) for zooplankton metabolism in these waters and they demonstrate the difficulty in making physiological measurements on oceanographic expeditions.

R/Φ

The ratio R/Φ is an index of physiological state as stated by Christensen *et al*. (1980). It is believed that when this ratio is low (< 0.5) organisms are nutrient-limited and visceversa (Christensen *et al*., 1980; Packard *et al*., 1996). Hernández-León and Gómez (1996) found that for zooplankton, temperature, diet, physiological state, and age could determine the variability of the ratio.

Following this idea, because the R/Φ ratio in all size fractions of our zooplankton samples was greater than 0.5, we conclude that the zooplankton in our samples were in good physiological state. Apparently, even in oligothophic environments the zooplankton manage to maintain their good health. Even when there is no statistical difference ($p>0.05$) between the rates of the middle-sized fraction (500-1000 μm) where the physiology is characterized by a high ratio (0.81) with a very low correlation ($r^2=0.31$, Table 3). One reason for this low value is that in these waters the gelatinous animals were quite abundant (personal observation) and in the higher sizes gelatinous organisms can be easily separated, in the smallest they are not expected to be present, but in the mid size they are present and difficult to remove. Consequently, they may have contributed to the variability and low correlation of the data of this class size. This can partially explain by the idea proposed by Glazier (2005), where some of these animals are kind of neutrally buoyant, decreasing locomotors activity, but this mechanism requires some other mechanism unexplored that need testing (Glazzier 2006; Bidigare and

Biggs, 1980). In one way or another the values here present matches with the ones found by Arístegui and Montero (1995), where they find for the microbial community (<225μm) in different oceanic regions a ratio of 0.75.

Even that there is no statistical difference ($p>0.05$) between the Leg's, the Indic Ocean transects (3 and 4), show high values of R/Φ ratio, as explain above. But the Leg 7 is quite peculiar since have a relative low value, pointing the different conditions present in the two oceans.

Food limitation (starvation)

As shown there is no difference between the measurements either R or Φ. Theory argues that the R/Φ ratio should be lower with time, as starvation reduces the levels of Krebs cycle intermediates and other essential donors to the ETS (NADH and NADPH). This in turn will reduce respiration. However, in our experiments, the time elapsed between capture (0h) and the measurement after 24h may not have been long enough to alter the respiration. Herrera *et al*. (2011) found the same phenomena in cultured mysids. Under normal conditions R/Φ and R/biomass ratios are > 0.75 are thought to indicate well-fed organism. Since, our values fall into this category, perhaps R does not decay in 24h because the organisms need more time to feel stress. Or, perhaps they are adapted in some way to maintain normal metabolic activity in spite of a scarse food supply.

Summary

1. In the Great Australian Bight the protein-specific R and Φ were 1.58 ± 0.81 and 1.98 ± 0.68 μmol $O_2 \cdot h^{-1} \cdot mg^{-1}$, in the southern Indian Ocean they were 1.49 ± 0.62 and 1.60 ± 0.62 μmol $O_2 \cdot h^{-1} \cdot mg^{-1}$, and during the Atlantic crossing they were 1.24 ± 0.82 and 1.06 ± 0.64 μmol $O_2 \cdot h^{-1} \cdot mg^{-1}$.

2. Values of metabolic scaling and R/Φ points to a zooplankton community in good conditions.

3. There is no effect of the starvation in the metabolic behavior of the zooplankton collected, pointing for a well adapted condition to the environment or insufficient time to see any changes in the decrease of respiration.

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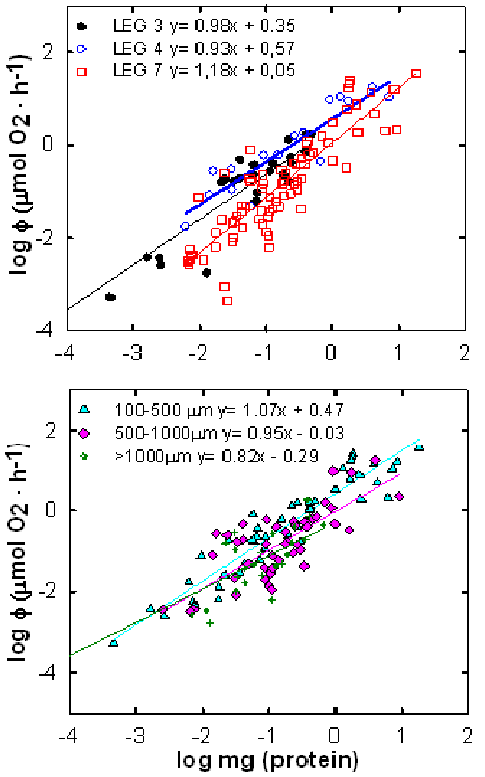

Figure 2. Relation between log potential respiration (Φ) and log total protein (biomass). Upper plot compared by Leg; bottom plot by the contribution of each size.

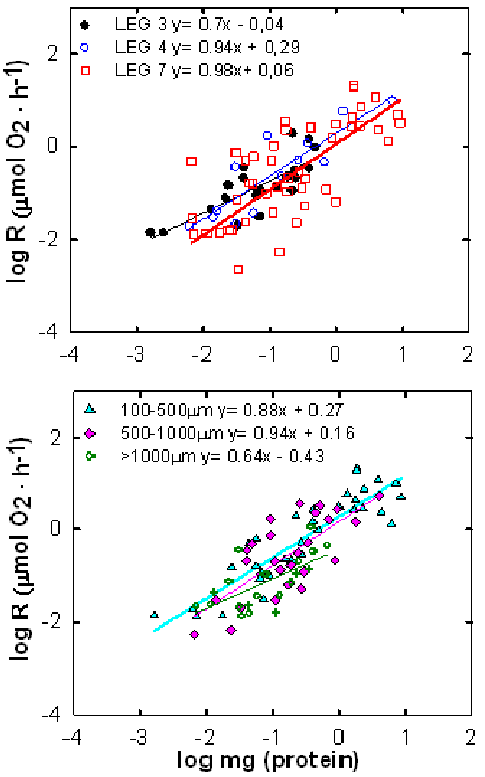

Figure 3. Relation between log oxygen consumption (R) and log total protein (biomass). Upper plot data compared by Leg; bottom plot by the contribution of each size.

R/Φ

The ratio of R/Φ is an index of the amount of respiratory capacity used. If R/Φ = 1 the zooplankton are using all their respiratory capacity to live and have no reserve. If R/Φ < 1 the zooplankton have a reserve with which they can respond to some biological stress. Ratios higher than 1 indicate either a flaw in the theory, the presence of unknown biochemistry operating, or errors in the measurements (underestimating ETS or over estimating R). Here the R/Φ ranged from 0.78 to 0.85. The higher ratios of R/Φ (0.85) (Table 3) characterized the transects of the