



Potential respiration estimated by electron transport system activity in deep-sea suprabenthic crustaceans off Balearic Islands (Western Mediterranean)



A. Herrera^{a,*}, M. Gómez^a, T.T. Packard^a, P. Reglero^b, E. Blanco^b, C. Barberá-Cebrián^b

^a Plankton Ecophysiology Group, Instituto de Oceanografía y Cambio Global, Universidad de Las Palmas de Gran Canaria, Campus Universitario de Tafira 35017, Las Palmas De G.C., Canary Islands, Spain

^b Instituto Español de Oceanografía, Centre Oceanogràfic de les Balears, Moll de Ponent s/n, Apdo. 291, 07015 Palma, Spain

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ABSTRACT

ETS is an acronym for the activity of the respiratory electron transport system; the ETS assay is a biochemical method for estimating the “potential” respiration (Φ). We apply this technique to suprabenthic species captured at three depths (250 m, 650 m and 850 m) in two different locations: Cabrera (Algerian subbasin) and Sóller (Balearic subbasin) during the IDEADOS survey during summer 2010. The aim of this study was to compare specific Φ between areas and between three depths to identify differences in the suprabenthos physiological state related to nutritional conditions. Specific Φ , expressed in unit of $\mu\text{l O}_2 \text{ h}^{-1} \text{ mg prot}^{-1}$ was not significantly different between species. Mean values were for the decapods: *Plesionika heterocarpus*, 8.4 ± 7.9 ; *Gennadas elegans*, 8.3 ± 2.9 ; and *Sergestes arcticus* 7.3 ± 4.6 . Within the euphausiids specific Φ averaged 6.5 ± 4.2 for *Thysanopoda aequalis* and 9.8 ± 5.1 for *Meganycitiphanes norvegica*; while for the mysids it ranged from 7.7 ± 4.4 for *Boreomysis arctica* and 2.1 ± 0.6 for *Eucopeia unguiculata*. The comparison of specific potential respiration (Φ), with the pooling of the data of all the species, showed differences between the two locations, being higher in Cabrera. However, no significant differences between the different depths of each locality were found. The slope of the log Φ –log biomass plot was 0.93 ± 0.09 for Cabrera and 0.64 ± 0.11 in Sóller. We interpret these differences as indicating that the suprabenthos in the Cabrera area, as compared to the Sóller area, has been well-nourished.

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1. Introduction

Respiration rates are fundamental measures of biological activity and especially of its energy production process. In metazoans these rates are limited by their mitochondria and the biochemical mechanisms that control them.

Historically, biomass has served as an easily measured proxy for respiration (Ikeda, 1970; Prosser and Brown, 1961) even though it was well known that the function of the biomass was to package the mitochondria (Fرتون and Simmonds, 1958; Nelson and Cox, 2005; Packard and Gómez, 2008). The role of temperature in modulating respiration has been recognized, at least since the time of Arrhenius (1915), but has its own history in oceanography (Ikeda, 1985; Packard et al., 1975; Seiwel, 1937). From these studies it was clear that respiration increased with the weight and size associated with biomass and with the warmth of a temperature increase. Respiratory rates are also

related to swimming activity, when zooplankton are slowly maintaining their position in the water column their respiration is low, when they swim rapidly to escape predators or capture prey their respiration speeds up. Cowles and Childress (1988) observed this respiratory shift in mysids. In addition, respiration is stimulated during feeding and mating (Bohrer and Lampert, 1988; Hernández-León and Gómez, 1996; Kiorboe et al., 1985; Lampert, 1986; Thor, 2003). All these factors modulate respiration and should be considered when using respiration to make ecological or oceanographic calculations.

The direct measurement of respiration rates in the oceanic environment is difficult because the rates are so low. Furthermore, they cannot be made by using incubations in the laboratory because the conditions cannot exactly reproduce the natural conditions. The ETS technique was developed by Packard (Packard, 1971; Packard et al., 1971, 1974) and then has been applied to estimate respiration in zooplankton (Bämsted, 1980; Hirsch et al., 2009; King and Packard, 1975; King et al., 1978; Minutoli and Guglielmo, 2009; Owens and King, 1975; Packard et al., 1974; Schalk, 1988), phytoplankton (Kenner and Ahmed, 1975; Packard, 1971) and bacteria (Aristegui and Montero, 1995; Packard et al., 1983; Packard et al., 1996). Since its inception the ETS method has been investigated and improved to provide increasingly reliable

* Corresponding author at: Universidad de Las Palmas de Gran Canaria, Campus Universitario de Tafira 35010, Las Palmas de Gran Canaria, Canary Islands, Spain. Tel.: +34 928454546.

E-mail address: alicia.herrera102@alu.ulpgc.es (A. Herrera).

estimates of respiration (Gómez et al., 1996; Hernández-León and Gómez, 1996; Maldonado et al., 2012; Packard and Gómez, 2008). The basis of this technique is that the ETS is the biochemical origin of respiration and controls energy production via oxidative phosphorylation. This technique uses the reduction of an artificial electron acceptor, a tetrazolium-salt (INT), to stoichiometrically measure the capacity of the mitochondria to consume O_2 . This can be done because the reduction of 2 mol of INT by the ETS is equivalent of the ETS-driven reduction of 2 atoms of oxygen (or 1 molecule of O_2) (Packard, 1971). The respiratory enzymatic system is saturated with substrates (NADH, NADPH and succinate) to obtain the “potential” activity or maximum activity of the electron transport system (Φ), as demonstrated in a recent study by Maldonado et al. (2012). ETS, as an ecological measure of respiration, is as reliable as any other proxy or index used in aquatic ecology or ocean geochemistry (Del Giorgio and Williams, 2005).

Suprabenthos or hyperbenthos, characterized by their swimming capacity, occupy the 2 m nephloid layer immediately above the seabed (Mees and Jones, 1997). Permanent suprabenthos consist of peracaridan crustaceans such as amphipods, cumacean, isopods and mysids; and eucaridan crustaceans as euphausiids and decapods (Sainte-Marie and Brunel, 1985). Other groups, defined as not permanent and more likely to zooplankton community, are also abundant and frequent, as copepods, chaetognaths, fish larvae, etc. As free swimming metazoans, the suprabenthos are an important community in coastal ecosystems exploiting a diversity of food resources near the bottom. They consume organic particles, detritus, phytoplankton and zooplankton (Cartes et al., 2001; Cunha et al., 1999) and have great importance in the transfer of organic matter and energy due their particular population dynamics related to their swarming behavior, their high activity level, and their tendency to make vertical and horizontal migrations (Mees and Jones, 1997). Their presence supports many demersal fish and epibenthic

crustaceans, such as *Merluccius merluccius* (Bozzano et al., 1997; Cartes et al., 2004), and the red shrimp *Aristeus antennatus* (Cartes, 1994).

In the deep waters around the Balearic Islands, suprabenthic assemblages and some aspects of their trophic relationships have been described (Cartes et al., 2001; Cartes et al., 2008; Madurell et al., 2008; Maynou and Cartes, 2000; Polunin et al., 2001). These deep waters are located on the continental slopes of two subbasins in the western Mediterranean Sea off the NE Spanish coast (Fig. 1). The subbasins (Algerian and Balearic) have different geomorphological and oceanographic characteristics and their boundaries are influenced by both seasonal and mesoscale processes in the adjacent areas (López-Jurado et al., 2008; Pinot et al., 2002). The Balearic Islands are the natural boundary between two subbasins, the topographic conditions and channels between islands influence the regional circulation water (Lüdmann et al., 2012). The Algerian subbasin is characterized by a smooth slope, receives warmer and less saline water from the Atlantic Ocean and the circulation is mainly driven by density gradients. In the Balearic subbasin the abrupt slope is irregular, with numerous small canyons, more influenced by atmospheric forcing and Mediterranean waters, which are colder and more saline (Hopkins, 1978; López-Jurado et al., 2008; Pinot et al., 2002). The processes mentioned above mark the differences between the two locations, which are reflected in the water column structure. Both temperature and salinity show more variability in the north than in the south (López-Jurado et al., 2008). In addition, the northwest location is affected by colder and more productive waters of the Gulf of Lion (Monserat et al., 2008), that can act as an external fertilization mechanism that influences productivity (Fernández de Puelles et al., 2004).

Previous studies have demonstrated differences in trophic web structure between the subbasins (Cartes et al., 2001; Maynou and Cartes, 2000). Suprabenthos assemblages and abundance seem to be a

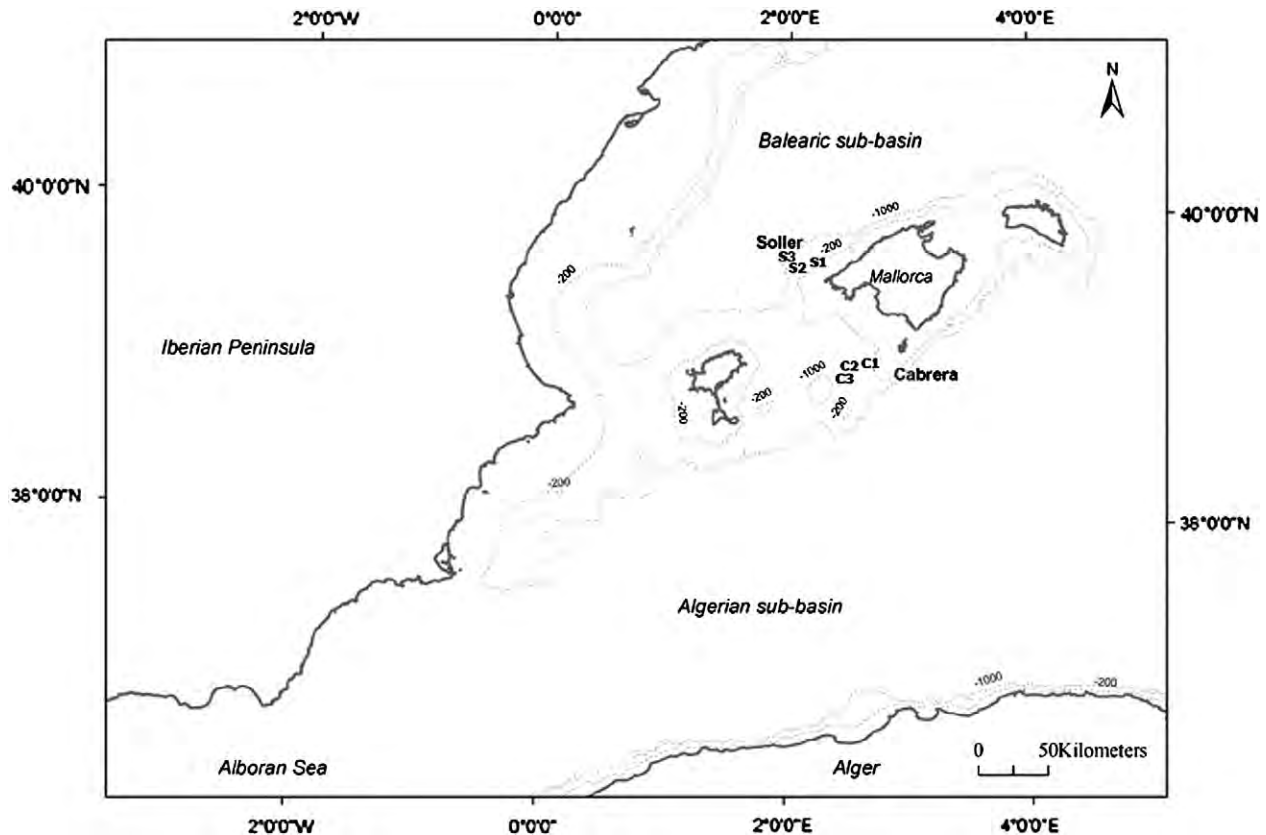


Fig. 1. Map of study area, indicating the locations of the suprabenthos sampling areas: Soller (Balearic subbasin) and Cabrera (Algerian subbasin); and stations: S1. Soller 250 m, S2. Soller 650 m, and S3. Soller 850 m, C1. Cabrera 250 m, C2. Cabrera 650 m and C3. Cabrera 850 m.

function of depth gradients and are related to the nature of the sediment (e.g. grain size) and its trophic condition (e.g. total organic matter content (%OM) and potential REDOX) in both subbasins (Cartes et al., 2008). Other authors found, in studies of zooplankton, that specific changes between areas, or decreases with depth, are related to the temperature and paucity of food in deep waters (Hirsch et al., 2009; Schalk, 1988). In deeper suprabenthos food availability may increase at greater depths, depending on the nature of the sediments and their trophic conditions (%OM, potential REDOX). This is in contrast to the zooplankton that depend almost exclusively on phytoplankton from the surface (Cartes et al., 2008). Studies in the area show that the percent of OM increases with depth from the shelf-slope break stations (1.6–4.5%) to bathyal stations (2.5–9%), and that increment generally paralleled the increase in the proportion of mud in the sediments (Cartes et al., 2008).

The objective of this study was to apply the ETS technique in three representative groups of permanent suprabenthos (decapoda, mysidacea and euphausiacea) in order to: (i) Estimate potential respiration in selected species of these groups and to test the hypothesis of interspecific variations, (ii) detect spatial variations in potential respiration between Algerian and Balearic subbasins, and (iii) assess how potential respiration varies with depth at each location.

2. Material and methods

2.1. Study area and sampling methods

The study was performed in two established fishing areas situated in the northwestern and southern waters off Mallorca (Balearic Islands, western Mediterranean) within the framework of the multidisciplinary project IDEADOS (<http://www.ba.iao.es/ideados>). The suprabenthos samples were collected during a summer survey in July 2010 at three depths (250 m, 650 m and 850 m) in two different locations (Cabrera and Sóller), separated by a distance of ca. 60 nm. The northwest location was close to the harbor of Sóller, in the Balearic subbasin. The Southern location was close to the Cabrera Archipelago, in the Algerian subbasin (Fig. 1). The samples were collected with a rectangular net rigged in a beam-trawl used to catch megabenthic fauna within 0.6 m above the bottom. The dimensions of net were 1.25 m by 0.3 m. At each location and depth three samples of suprabenthos were collected, covering a sampling unit area that oscillated between 600 and 2000 m². At each of 18 samples, a number of individuals (between 3 and 5) of different selected species were caught and immediately frozen on board at –196 °C in liquid nitrogen. Previous studies in the area (Cartes et al., 2008, 2011) facilitated the selection of the most abundant species: the decapods *Gennadas elegans* (Smith, 1884), *Plesionika heterocarpus* (Costa, 1871) and *Sergestes arcticus* (Krøyer, 1855); the mysids *Boreomysis arctica* (Krøyer, 1855) and *Eucopeia unguiculata* (Willemoes-Suhm, 1875); and the euphausiids *Meganyctiphanes norvegica* (M. Sars, 1857) and *Thysanopoda aequalis* (Hansen, 1905). For ETS assay we selected only adult males to avoid confounding factors as life history stage or sex. Although high abundances of these species were found, the number of collected individuals depended on the availability of live specimens in the samples. Only in the case of *B. arctica* was it possible to obtain samples at different depths and locations. In the laboratory, samples were stored at –80 °C until measurements of ETS activity and protein biomass could be made.

The rest of the sample was fixed in buffered formaldehyde (4%). Samples were processed at the laboratory, sorting and counting all the individuals of the target taxonomic group (decapods, mysids and euphausiids) under a stereomicroscope. The abundance of selected taxa was estimated as individuals 100 m² in order to characterize the sampling stations. Temperature (°C), salinity (PSU) and depth (m) were recorded by a CTD on transects with a SB39 profiler mounted on the beam-trawl. At each profile, the measurements were made at 1 m above the bottom. Data on dissolved oxygen (ml l⁻¹) and fluorescence

were obtained from the IDEADOS database. These data were made with a fluorometer and an oxygen electrode mounted on the CTD simultaneously where suprabenthos were collected. The oxygen electrode for the dissolved oxygen was a SBE43 with a Clark polarographic membrane. Fluorescence was measured with a WetLab Ecoview sensor and calculated as equivalent mg Chl-a m⁻³. More detailed information about this sampling can be found in Massutí et al. (2014). Dissolved oxygen concentration is a good water mass tracer (Balbín et al., 2014) which can influence respiration rates and production.

2.2. ETS analysis

Potential respiration (Φ) was estimated according to the ETS method (Packard, 1971) with modifications (Gómez et al., 1996; Kenner and Ahmed, 1975; Owens and King, 1975; Packard and Christensen, 2004). Samples were homogenized with ultrasound for 45 s in 1.5 ml of Milli-Q double-distilled water, and then centrifuged for 10 min at 4000 rpm at 0 °C. A 0.5 ml aliquot of the supernatant was added to 1.5 ml of solution containing the substrates (0.2% (v/v) Triton X-100, 50 mM sodium phosphate buffer pH 8, 0.133 M disodium succinate, 0.835 mM of 0.24 mM NADH and NADPH) and 0.5 ml of 4 mM INT (Sigma Lab). Each sample was controlled by a blank without substrates. Samples were incubated at 18 °C for 20 min after which the reaction was stopped with a quench solution consisting of 50% phosphoric acid 0.1 M and 50% formaldehyde to 36%. The absorbance reading was performed in a spectrophotometer (Beckman DU 650, USA) at 490 nm and 750 nm to correct for turbidity. Φ was calculated according to the following equation:

$$\Phi = \text{COD} \cdot 60 \cdot H \cdot \text{AS} / (1.42 \cdot t \cdot L \cdot F) \quad (1)$$

where COD is the absorbance of the sample at 490 nm corrected for blank and reagents, H is the homogenate volume in ml, AS is the volume of the reaction mixture in ml, the factor 60 converts min to h, 1.42 is the conversion factor of INT-formazan into O₂ as μl , L is the cuvette length (1 cm), F is the volume of the homogenate in the assay in ml and t is the incubation time in min. Φ was corrected for in situ temperature using Arrhenius equation and activation energy (E_a) of 15 kcal mol⁻¹ (Packard et al., 1975).

$$\Phi_{\text{assay}} = \Phi_{\text{insitu}} \cdot e^{(E_a/R) \cdot (1/T_{\text{assay}} - 1/T_{\text{insitu}})} \quad (2)$$

where R is the gas constant, T_{assay} is the temperature of the assay and T_{insitu} is the in situ temperature where the sample was taken. The specific Φ indicates oxygen consumption per unit biomass and it is an indicator of the physiological activity of living biomass. Biomass was estimated in mg of protein by the method of Lowry et al. (1951), as amended by Rutter (1967).

2.3. Statistical analysis

The variability of environmental parameters (temperature, salinity, oxygen and fluorescence) and abundance of selected groups of suprabenthos were tested by a two way ANOVA test. The test included two nested factors: location (Cabrera/Sóller) and depth into location (250 m, 650 m and 850 m), with 3 replicates for treatment. Specific Φ per unit biomass was used in order to test spatial changes in respiration rates, by pooling the data of all the species for location and depth. Previously we verified by one-way ANOVA no significant differences between species ($p > 0.05$). We apply two-way ANOVA test with two nested factors: location; and depth into location in the pooled data to detect spatial differences. To confirm normality of the residuals, specific Φ data were analyzed by the Shapiro–Wilk test and the homoscedasticity of the data was confirmed with Levene's test. Relationships between Φ and protein biomass from different locations and depths were obtained by the regression equations, using confidence limits of 95% and the

Pearson correlation coefficient. We applied ANCOVA to determine statistical differences between slopes and ordinates in the regression lines. Normality of residuals was confirmed by the Shapiro–Wilk test. Data were analyzed using the program R Development Core Team 2010 (R Foundation for Statistical Computing, Vienna, Austria).

3. Results

3.1. Characterization of the sampling area

Mean environmental parameters and suprabenthos abundance at sampling stations are shown in Table 1. Environmental parameters changed between depths, but not between locations according to ANOVA test (Table 2). This analysis did not detect any differences between locations in the case of temperature, although it was slightly higher in Cabrera at three depth levels. At both locations it was statistically higher at 250 m ($p < 0.01$). Oxygen also significantly differed between depths ($p < 0.001$), being higher at 250 m in both locations. Although no differences were detected, the mean value was higher in Söller, largely because the value at 250 m (4.54 ml l^{-1}) was so high (Table 2). The differences in concentration of oxygen between depths (0.05 in Cabrera and 0.20 ml l^{-1} in Söller) and temperature between depths ($0.15 \text{ }^\circ\text{C}$ in Cabrera and $0.17 \text{ }^\circ\text{C}$ in Söller) were very small, thus not affecting the respiration rates. Decapod abundance was not statistically different between locations and depths. Euphausiid abundance was higher at 250 m in Söller. Mysid abundance was higher at 650 m than at 850 and 250 m ($p < 0.001$; Table 2).

3.2. Biomass, potential respiration (Φ) and specific potential respiration (ϕ)

Decapods had the highest Φ . The mean values were $17.4 \mu\text{l O}_2 \text{ h}^{-1} \text{ ind}^{-1}$ for *P. heterocarpus*, $54.7 \mu\text{l O}_2 \text{ h}^{-1} \text{ ind}^{-1}$ for *G. elegans* and $102.0 \mu\text{l O}_2 \text{ h}^{-1} \text{ ind}^{-1}$ for *S. arcticus*. These activities correlate with higher protein biomass, between 5 and 14 mg ind^{-1} (Table 3). Euphausiids showed intermediate values of Φ , $18.4 \mu\text{l O}_2 \text{ h}^{-1} \text{ ind}^{-1}$ for *M. norvegica* and $16.2 \mu\text{l O}_2 \text{ h}^{-1} \text{ ind}^{-1}$ for *T. aequalis*, with the corresponding range of protein biomass ranging from 1 to 4 mg ind^{-1} (Table 3). Mysids showed lower values of Φ : $7.8 \mu\text{l O}_2 \text{ h}^{-1} \text{ ind}^{-1}$ for *B. arctica* and $7.9 \mu\text{l O}_2 \text{ h}^{-1} \text{ ind}^{-1}$ for *E. unguiculata*. The mysid protein biomass range was: $1\text{--}4 \text{ mg ind}^{-1}$ (Table 3).

Specific ϕ or ϕ per unit of biomass expressed in units of $\mu\text{l O}_2 \text{ h}^{-1} \text{ mg prot}^{-1}$, was not significantly different between species (Table 5), with mean values that ranged between $2.1 \mu\text{l O}_2 \text{ h}^{-1} \text{ mg prot}^{-1}$ for *E. unguiculata* and $9.8 \mu\text{l O}_2 \text{ h}^{-1} \text{ mg prot}^{-1}$ for *M. norvegica* (Table 4). Overall, the specific ϕ was significantly higher in Cabrera than in Söller (Table 5, $p < 0.05$; Fig. 2). However, the specific ϕ was not significant different between depths (Table 5).

Table 2

Results of 2-way ANOVA testing for differences in environmental parameters between locations and depths. Lo = location; De = depth; Ca = Cabrera; So = Söller.

	df	MS	F	P	SNK test
<i>Temperature</i>					
Lo	1	0.0075	0.34	0.5923	
De (Lo)	4	0.0222	33.73	***	Ca: 250 > 650 = 850**
Residual	12	0.0007	0		So: 250 > 650 = 850**
<i>Salinity</i>					
Lo	1	0.0002	0.54	0.5045	
De (Lo)	4	0.0003	1.72	0.2108	
Residual	12	0.0002			
<i>Oxygen</i>					
Lo	1	0.3793	3.04	0.1562	
De (Lo)	4	0.1247	30.24	***	Ca: 250 > 650*; 250 > 850*
Residual	12	0.0041			So: 250 > 650 > 850**
<i>Chl fluorescence</i>					
Lo	1	0.0002	0.64	0.4674	
De (Lo)	4	0.0003	12.5	***	
Residual	12	0			
<i>Decapods</i>					
Lo	1	8.3985	0.83	0.4136	
De (Lo)	4	10.1069	1.56	0.2476	
Residual	12	6.4807			
<i>Euphausiids</i>					
Lo	1	1.5808	0.5	0.5186	
De (Lo)	4	3.1621	3.73	*	Ca: n.s.
Residuals	12	0.8489			So: 250 > 650 = 850***
<i>Mysids</i>					
Lo	1	0.2539	0.01	0.9451	
De (Lo)	4	47.3406	8.61	**	Ca: 650 > 850 = 250***
Residuals	12	5.4986			So: 650 > 850 = 250***

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

3.3. Relationship between potential respiration (Φ) and protein biomass

The relationship between Φ ($\mu\text{l O}_2 \text{ h}^{-1} \text{ ind}^{-1}$) and biomass ($\text{mg protein ind}^{-1}$) on an individual basis, expressed in logarithmic terms, is represented by the equation:

$$\log \Phi = b \log W + \log a \tag{3}$$

or

$$\Phi = aW^b \tag{4}$$

Fig. 3 represents the relationship between biomass and Φ at the two different locations, the coefficients of regression and determination

Table 1

Summary of environmental characteristics and suprabenthos abundance in individual 100 m^{-2} (mean \pm SD) of sampling stations in Algerian subbasin (Cabrera) and Balearic subbasin (Söller), at three depth levels (250 m, 650 m and 850 m). n = number of samples.

	Cabrera				Söller			
	Total n = 9	250 n = 3	650 n = 3	850 n = 3	Total n = 9	250 n = 3	650 n = 3	850 n = 3
Temperature (C)	13.15 \pm 0.07	13.24 \pm 0.04	13.11 \pm 0.02	13.09 \pm 0.01	13.11 \pm 0.09	13.21 \pm 0.04	13.07 \pm 0.02	13.04 \pm 0.01
Salinity (PSU)	38.49 \pm 0.01	38.50 \pm 0.01	38.49 \pm 0.00	38.48 \pm 0.00	38.49 \pm 0.02	38.50 \pm 0.03	38.49 \pm 0.00	38.48 \pm 0.00
Oxygen (ml l ⁻¹)	4.20 \pm 0.08	4.26 \pm 0.01	4.14 \pm 0.02	4.21 \pm 0.03	4.37 \pm 0.14	4.54 \pm 0.09	4.23 \pm 0.05	4.34 \pm 0.04
Chl fluor. (mg m ⁻³)	0.024 \pm 0.008	0.017 \pm 0.005	0.024 \pm 0.005	0.032 \pm 0.006	0.021 \pm 0.004	0.018 \pm 0.003	0.019 \pm 0.004	0.023 \pm 0.004
Decapods	1.98 \pm 3.76	0.03 \pm 0.04	4.85 \pm 6.08	1.07 \pm 0.32	0.61 \pm 0.81	0.05 \pm 0.04	0.69 \pm 0.81	1.10 \pm 1.06
Euphausiids	5.12 \pm 6.03	10.34 \pm 8.95	3.35 \pm 1.25	1.67 \pm 0.77	22.48 \pm 45.02	60.61 \pm 69.43	4.47 \pm 4.00	2.36 \pm 1.99
Mysids	3.21 \pm 4.28	0.05 \pm 0.08	8.25 \pm 3.87	1.34 \pm 0.22	3.45 \pm 3.69	0.44 \pm 0.75	7.26 \pm 3.33	2.65 \pm 2.51

Table 3

Average biomass and potential respiration (ϕ) in representative species of suprabenthos caught in deeper bottoms (–250 m, –650 m and –850 m) of Sóller and Cabrera (Balearic Islands). Values are mean \pm SD, n = number of analyzed individuals.

Taxon	Species	n	Biomass (mg protein ind ⁻¹)	ϕ ($\mu\text{O}_2 \text{ h}^{-1} \text{ ind}^{-1}$)
DEC	<i>G. elegans</i>	7	6.6 \pm 2.9	54.7 \pm 29.8
DEC	<i>P. heterocarpus</i>	3	5.1 \pm 5.8	17.4 \pm 14.0
DEC	<i>S. arcticus</i>	5	14.2 \pm 4.4	102.0 \pm 70.2
EUPH	<i>M. norvegica</i>	11	2.6 \pm 1.4	18.4 \pm 5.9
EUPH	<i>T. aequalis</i>	3	2.0 \pm 1.2	16.2 \pm 15.2
MYS	<i>B. arctica</i>	15	1.3 \pm 0.9	7.8 \pm 4.0
MYS	<i>E. unguiculata</i>	2	4.0 \pm 0.9	7.9 \pm 0.7

coefficients are shown in Table 6. ϕ increased with increasing body mass, but the slope of the regression was higher in Cabrera (Table 6).

4. Discussion

This study provides comparative data on respiratory metabolism of three representative groups of suprabenthos crustaceans in nephroid layer over the continental slope off the Balearic Islands. Calculation of ϕ based in the ETS method, used here, has broadly been reported for natural zooplankton communities (Bämsted, 1980; Hirsch et al., 2009; King and Packard, 1975; King et al., 1978; Minutoli and Guglielmo, 2009; Owens and King, 1975; Schalk, 1988), but rarely on suprabenthos assemblages. All of these reports and observations demonstrate the utility of this approach in estimating oxygen consumption, in providing an index of physiological state of organisms, in detecting spatial changes due to different environmental conditions, and in demonstrating the possible implications in carbon flux research (Hernández-León et al., 2001; Hirsch et al., 2009; Minutoli and Guglielmo, 2009; Schalk, 1988).

Respiration rates are related to body size, so one can deduce that differences in ϕ per individual among species or groups depend on their average size (Ikeda, 1985; Ivleva, 1980). The widely studied decapod *G. elegans* and *S. arcticus* had an average adult body length of 40 mm and 45 mm, respectively (Zariquiey Alvarez, 1968) and one would predict that they would have high levels of ETS activity. Indeed, we found that these shrimp showed the highest values of ϕ , consistent, not only with their large size, but also with their high protein biomass. *Pleisonika* sp. is a decapod genus which can grow as large as 50–70 mm (Zariquiey

Table 4

Mean specific potential respiration (ϕ) in $\mu\text{O}_2 \text{ h}^{-1} \text{ mg prot}^{-1}$ (values \pm SD) in suprabenthos at each location and depth. n = number of live analyzed individuals at each station.

		Cabrera		Sóller		Total	
		n	sp. ϕ	n	sp. ϕ	n	sp. ϕ
<i>G. elegans</i>	650	3	11.1 \pm 0.9	2	5.5 \pm 0.1	5	8.9 \pm 3.1
	850			2	7.0 \pm 2.4	2	7.0 \pm 2.4
	Total	3	11.1 \pm 0.9	4	6.3 \pm 1.6	7	8.3 \pm 2.9
<i>P. heterocarpus</i>	250	3	8.4 \pm 7.9			3	8.4 \pm 7.9
	850	3	10.4 \pm 2.0	2	2.6 \pm 2.8	5	7.3 \pm 4.6
<i>M. norvegica</i>	250	1	6.9	3	10.0 \pm 4.9	4	9.3 \pm 4.3
	650			3	11.5 \pm 8.5	3	11.5 \pm 8.5
	850	1	13.9	3	7.3 \pm 2.5	4	8.9 \pm 3.9
Total	2	10.4 \pm 4.9	9	9.6 \pm 5.4	11	9.8 \pm 5.1	
<i>T. aequalis</i>	250	1	1.9			1	1.9
	650	2	8.9 \pm 1.8			2	8.9 \pm 1.8
	Total	3	6.5 \pm 4.2			3	6.5 \pm 4.2
<i>B. arctica</i>	250	2	9.6 \pm 2.6	1	4.3	3	7.8 \pm 3.6
	650	3	9.2 \pm 6.3	3	4.4 \pm 0.4	6	6.8 \pm 4.8
	850	3	11.3 \pm 5.2	3	5.8 \pm 3.3	6	8.6 \pm 4.9
	Total	8	10.1 \pm 4.6	7	5.0 \pm 2.1	15	7.7 \pm 4.4
<i>E. unguiculata</i>	850			2	2.1 \pm 0.6	2	2.1 \pm 0.6
	Overall	250	7	7.6 \pm 5.4	4	8.6 \pm 4.9	11
Overall	650	8	9.8 \pm 3.6	8	7.3 \pm 5.8	16	8.6 \pm 4.8
	850	7	11.3 \pm 3.4	12	5.2 \pm 3.0	19	7.5 \pm 4.3
	Total	22	9.6 \pm 4.3	24	6.5 \pm 4.4	46	8.0 \pm 4.6

Table 5

Results of 1-way ANOVA testing for differences in specific potential respiration (ϕ) between species; and 2-way ANOVA testing differences between locations and depths. Lo = location; De (Lo) = depth nested into location; Ca = Cabrera; So = Sóller.

	df	MS	F	P	
sp. ϕ					
Specie	6	0.68054	1.9154	0.1026	
Residual	39	0.35530			
sp. ϕ Pairwise test					
Lo	1	2.34306	7.0872	*	Ca > So*
De (Lo)	4	0.59321	1.7943	0.14901	
Residual	40	0.33061			

* $p < 0.05$.

Alvarez, 1968), however, the individuals caught in the study were small, had correspondingly lower amounts of protein, and lower ETS activities. The species of euphausiids and mysids analyzed here were similar in size (20–40 mm) (Brinton et al., 2000; Tattersall and Tattersall, 1951), but both groups were smaller than *G. elegans* and *S. arcticus*. Consequently, their levels of ϕ were correspondingly lower.

The specific ϕ ($\mu\text{O}_2 \text{ h}^{-1} \text{ mg prot}^{-1}$) is really the parameter that enables one to compare potential respiration rates in organisms of different sizes. However, in this study inter-specific differences were not detected in specific ϕ . Probably, the analyzed species have similar life habits and swimming activities, that are known to be important factors affecting variability in respiration rates (Cowles and Childress, 1988; Ikeda, 1985; Torres and Childress, 1983). The studied species have similar feeding habits. They are omnivorous, actively filtering out phytoplankton, zooplankton, and detritus. For example, *B. arctica* is a voracious copepod feeder (Polunin et al., 2001). The diet of *G. elegans* includes a high proportion of green detritus, probably originating from radiolaria, whereas *E. unguiculata*'s food seems to consist of mainly small copepods and coelenterates, at least in the North East Atlantic (Roe, 1984).

Comparing respiration rates with literature data is difficult, because of the differences in methodologies and environmental conditions. For example, Herrera et al. (2011) measured ϕ rates, normalized by protein biomass under laboratory condition at 20.5 °C for the mysid *Leptomysis lingvura*, and found that they ranged from 30.1 to 42.6 $\mu\text{O}_2 \text{ h}^{-1} \text{ mg prot}^{-1}$. ϕ in epipelagic zooplankton collected around Mallorca averaged 17.45 \pm 1.64 $\mu\text{O}_2 \text{ h}^{-1} \text{ mg prot}^{-1}$ (Herrera, 2014); and Minutoli and Guglielmo (2009) found that ϕ in Western Mediterranean region averaged 0.026 \pm 0.001 $\mu\text{O}_2 \text{ h}^{-1} \text{ mg wet weight}^{-1}$. For sure, because of the temperature difference, ϕ here will be lower compared to the measurements made by Herrera et al. (2011) but specific respiration in the mesopelagic oceans is always lower than in the epipelagic ocean (Childress, 1975; Cowles and Childress, 1988; Mahaut et al., 1995; Torres et al., 1979). Nevertheless, the value of ϕ obtained in the current study is in the range of values predicted from zooplankton studies in the region by Herrera (2014) and Minutoli and Guglielmo (2009).

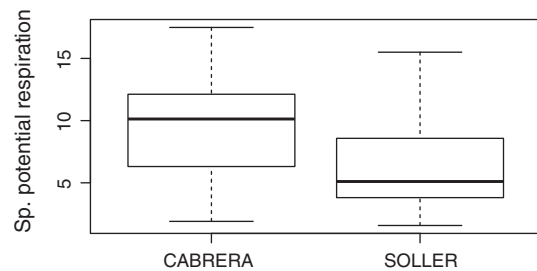


Fig. 2. Overall specific potential respiration (ϕ) ($\mu\text{O}_2 \text{ h}^{-1} \text{ mg prot}^{-1}$) by location. The box limits indicate the upper and lower quartiles, the line into the box indicates the median and the whiskers indicate the lowest and highest data points.

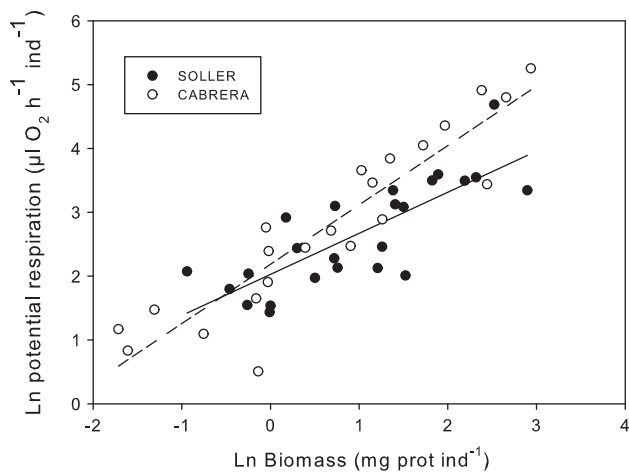


Fig. 3. Relationship between potential respiration (ϕ) ($\mu\text{l O}_2 \text{ h}^{-1} \text{ ind}^{-1}$) and biomass (mg protein) at two locations: Cabrera and S oller, on a natural logarithmic scale.

Spatial differences were found in specific ϕ between the two locations, S oller and Cabrera, however, no significant difference was found between depths. Cabrera and S oller are separated by only 60 km but are located in different subbasins with different oceanographic conditions (EUROMODEL Group, 1995). S oller is more influenced by atmospheric forcing and by cold, saline Mediterranean waters, while Cabrera is more influenced by forcing due to the density gradients and receives warmer and less saline Atlantic waters (Pinot et al., 2002). Neither the difference in O_2 (0.17 ml l^{-1}) nor the difference in temperature ($0.04 \text{ }^\circ\text{C}$) can explain the difference in specific ϕ between the two areas.

Possible indicators of food availability for suprabenthos can be the percentage, content and quality of organic matter, and the availability of phytoplankton and zooplankton in the water column. Cartes et al. (2008) showed that the percent of OM increased with depth, however in our study, at each location the specific potential respiration does not show any difference between depths, indicating that the organisms are in similar physiological state. In this sense, the % OM was similar in both areas (Cartes et al., 2011), but at S oller, the more energetic environment may induce higher settling velocity of particles and thus lower degradation of OM (Pasqual et al., Personal communication). Therefore, higher nutritional value of OM associated with fresh marine organic matter inputs was found in this area, where primary production may be induced by the occurrence of stronger frontal systems linked to Northern and Balearic currents flowing along the slope (L opez-Jurado et al., 2008). However, the sediments in Cabrera showed higher contents of lipids and carbohydrates, whereas the proportion of protein was lower (indicative of higher degradation of organic matter) (Pasqual et al., Personal communication).

The Algerian basin is subject to more unpredictable events such as eddies generated by entry of Atlantic waters through the Straits of Gibraltar (L opez-Jurado et al., 2008). Punctual inputs of fresh marine organic matter during phytoplankton blooms during spring can explain the better condition of suprabenthos in summer in Cabrera. In the upper water column, differences in the mesozooplankton biomass and carbon and nitrogen content has been observed between the water

masses in S oller and Cabrera affecting the trophic pattern in fish larvae (Laiz-Carri on et al., 2013). Herrera et al., 2014 found higher zooplankton biomass in Cabrera than in S oller in studies carried out in summer 2010. Also, high productivity events (Bosc et al., 2004; Estrada, 1996) induced by oceanographic or current events may contribute to increased zooplankton biomass (Cartes et al., 2008). Cartes et al. (2011) concluded that secondary production for overall suprabenthos was similar in both areas, but on the upper slope at S oller (350–450 m), the increase of natural disturbances in the area, increased P/B and the diversity of suprabenthic peracarids. Moreover, the production may depend more on the trophic levels under analysis and the proximity of target taxa to the primary food sources that they exploit, than on the scale adopted. Diverse studies revealed better conditions for top predators inhabiting the Balearic subbasin (S oller), as indicated by higher food consumption, by energy content of diets, and by fecundity (i.e. *M. merluccius* (Cartes et al., 2008; Hidalgo et al., 2008); *A. antennatus* (Cartes et al., 2009; Gujjarro et al., 2008)). However, no conclusive evidence at present has indicated increased nutrient availability in either the Algerian or the Balearic subbasin.

Respiration rates are generally expressed as power functions of body size according to the equation (Prosser and Brown, 1961):

$$R = a W^b.$$

This so called Kleiber's law (Kleiber, 1961) established a value of 0.75 for the b exponent in this equation. However, other authors found that this value of 0.75 is highly variable (Glazier, 2005; Glazier, 2006). For example, in fish larvae b values can range from 0.65 to 1.69 (Giguere et al., 1988). Herrera et al. (2011) found that in mysids this is related to feeding conditions. G omez et al. (2008) suggested that this exponent is less than 0.75 in oligotrophic regions and greater than or equal to 0.75 in regions with higher food availability such as coastal or upwelling regions. Other authors have found similar relationships related to food availability in culture conditions (Herrera et al., 2011; Mart nez et al., 2010). This sensitivity of the exponent in Kleiber's law suggests that the ϕ -biomass relationship could be used as an indicator of physiological state of individual organisms and ecological communities, or in other words, an index of what proportion of an organism's biomass is being used for the production of energy.

The ETS activity measure ϕ (the maximum oxygen consumption under substrate saturating conditions) is not directly related to food intake or associated processes that increase respiration rates like SDA (Specific Dynamic Action) (Kiorboe et al., 1985; Thor, 2003). ETS, being a constituent part of the mitochondria, should not change rapidly with environmental conditions or with the amount of metabolizable substrate, as does respiration (Cammen et al., 1990; Herrera et al., 2011). Changes in ϕ have more to do with long-term processes such as the production of structural proteins and more respiratory complexes related to metabolic process. In our results, the exponent b was 0.93 ± 0.09 in Cabrera and 0.63 ± 0.11 in S oller. This difference in the relationship between biomass and ϕ suggests that the organisms in Cabrera are in a better physiological state than those from S oller. Other authors suggested that this may be due to greater food availability (G omez et al., 2008; Herrera et al., 2011; Mart nez et al., 2010), unfortunately, as mentioned above, more data from this region will be needed to corroborate this hypothesis.

Table 6

Parameters of the regression equation $\log \phi = b \log W + \log a$ (\pm SE) in different areas. ϕ = potential respiration ($\mu\text{l O}_2 \text{ h}^{-1} \text{ ind}^{-1}$), W = biomass (mg prot ind^{-1}).

[0.3 mm] Location	a	b ^a	r ²	n	p value
Cabrera	2.18 ± 0.14	0.93 ± 0.09	0.84	22	<0.01
S�oller	2.03 ± 0.15	0.64 ± 0.11	0.63	24	<0.01

^a Indicate significant differences between Cabrera and S oller coefficients (ANCOVA, $p < 0.05$).

5. Conclusions

1. The ETS technique facilitated estimations of the suprabenthos respiratory activity and the detection of the physiological changes in the organisms from the two areas.
2. Specific potential respiration in mysids, decapods and euphausiids shows no differences.

3. The ETS–biomass ratio showed significant differences between Cabrera and Sóller suggesting that organisms are in a better physiological state in Cabrera than in Sóller.
4. Within each locality, specific potential respiration showed no significant differences between 250 m, 650 m and 850 m depths.

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