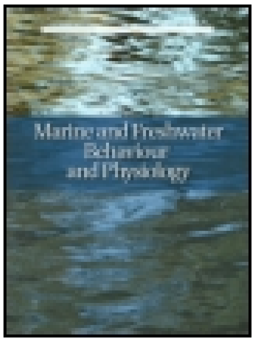

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Field evaluation of oxygen consumption by two freshwater decapod morphotypes (Trichodactylidae and Aeglidae); the effect of different times of the day, body weight and sex

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ABSTRACT

We report an analysis of the effect of two different times of day (noon and dusk), body weight and sex on the oxygen consumption rate (OCR) of the freshwater crabs *Trichodactylus kensleyi* (Trichodactylidae), *Aegla singularis* and *A. platensis* (Aeglidae) in their natural environment. Both families are sympatric in the studied locations, with a co-occurrence found between *T. kensleyi* and *A. singularis* or *T. kensleyi* and *A. platensis*. The mean OCR was highest in *A. singularis* and lowest in *A. platensis*. The OCR was higher in *Aegla* species at noon, and *Trichodactylus* consumed more oxygen at dusk. In aeglids, there was no difference in oxygen consumption between noon and dusk. *T. kensleyi* exhibited statistically significant differences in the OCR between noon and dusk. The oxygen uptake of all three species analysed was not influenced by the sex of the individual but varied according to the animals' weight. The families evaluated share some biological and ecological characteristics, such as diet and habitats, but the strategies used in the regulation of gas exchange at different times of the day were different. Environmental factors may be influencing the oxygen consumption of each morphotype differently.

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Aegla; *Trichodactylus*; freshwater crustaceans; crabs; oxygen consumption rate

Introduction

Several studies on oxygen consumption in crustaceans have been carried out (Waterman 1960). However, few have examined groups such as the freshwater brachyurans and anomuran aeglids, even though these groups comprise the majority of the Neotropical freshwater decapod diversity (Dalosto & Santos 2011).

Decapods are a diverse group found in a wide range of habitats, from deep sea to fresh water and land. Differing conditions and sites (e.g. heights and latitudes) influence the variability of the abiotic conditions across environments, as well as patterns of variation throughout the day and seasons. The occurrence of decapods in varying environments suggests the development of adaptive responses to the variability within these habitats (Miranda-Anaya 2004; Williner et al. 2009). Among these organisms, one such ecophysiological strategy

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is the adjustment of metabolic rate in response to changing abiotic conditions (Díaz & Latournerié 1980).

Two different freshwater crab morphotypes are found throughout South America: the crabs from the Trichodactylidae and Pseudothelphusidae families and those from the Aeglidae family (Collins et al. 2007; Giri et al. 2011). Species of the Trichodactylidae and Aeglidae taxonomic groups are similarly distributed in some regions of South America and are sympatric (Morrone & Lopretto 1994). This occurs in the trichodactylid *Trichodactylus kensleyi* (Rodríguez 1992) and the aeglids *Aegla singularis* (Ringuelet 1948) or *A. platensis* (Schmitt 1942). Both families share biological and ecological traits, such as diet and habitats (Melo 2003) as they are generalists and opportunists with a broad trophic spectrum (Burress & Gangloff 2013). The diet of these decapods is mainly omnivorous and occurs at different trophic levels. They are able to hunt and/or also shred different foods (plant remains, algae, zooplankton, insect larvae, and oligochaetans, among others). They simultaneously constitute a source of food for terrestrial and aquatic animals (Collins et al. 2007; Bond-Buckup et al. 2008; Caldart et al. 2011; Cogo & Santos 2013; Williner et al. 2014). These dual roles and an intermediate position in the food web emphasize their importance in matter and energy exchange between terrestrial and aquatic environments (Collins et al. 2006; Teodósio & Masunari 2009; Williner et al. 2009). These freshwater decapods live under rocks, plant debris, aquatic vegetation and submerged trunks in shallow lakes, ponds, riversides and main channels (Melo 2003). They survive by adjusting their metabolism to variations in abiotic environmental conditions, including those associated with hydrologic, thermal and light–dark cycles (Lopretto 1995; Collins et al. 2004). Despite these similarities, these animals represent different evolutionary lineages (Cumberlidge & Peter 2009) so that one might expect different physiological adaptations in response to the same environmental conditions (Evans 2009).

Respiration, or oxygen consumption, is a measurement that indicates the metabolic level of the organism. Values of oxygen consumption are commonly used in the description of the respiratory capacity and the estimation of the metabolic rate. This rate reflects metabolic energy and can be utilized as a precise indicator of the physiological health of the organism (Díaz-Iglesias et al. 2004; Daoud et al. 2007; Dalosto & Santos 2011). Oxygen consumption is influenced by internal and external variables, including body weight, sex, the light–dark cycle, exposure to chemical contaminants, temperature, among others (Newman & Unger 2003; Radford et al. 2004; Momo & Doyle 2009). Most of the work on oxygen consumption in crustaceans involves laboratory studies (Gutiérrez-Yurrita et al. 1994; Oberlin & Blinn 1997; Díaz-Iglesias et al. 2004; Re et al. 2004; Montagna & Collins 2008; Valdez et al. 2008; Momo & Doyle 2009; Dalosto & Santos 2011; Negro et al. 2012). Studies carried out under controlled conditions are important because they provide a basis for the development of these research areas. Laboratory studies do not, however, answer important questions about how these organisms behave in their natural habitat. This is largely due to the stress of transport and maintenance under laboratory conditions.

Despite the importance of these two crustacean morphotypes in aquatic ecosystems, there is little information about their oxygen consumption or about oxygen consumption in freshwater decapods in their natural environment. Investigating this issue is important because not only does it inform us about the metabolic requirements of the given species, it also demonstrates how different species interact with their environment. Considering this background, the aim of this work was to analyse the effect of three variables, the time of

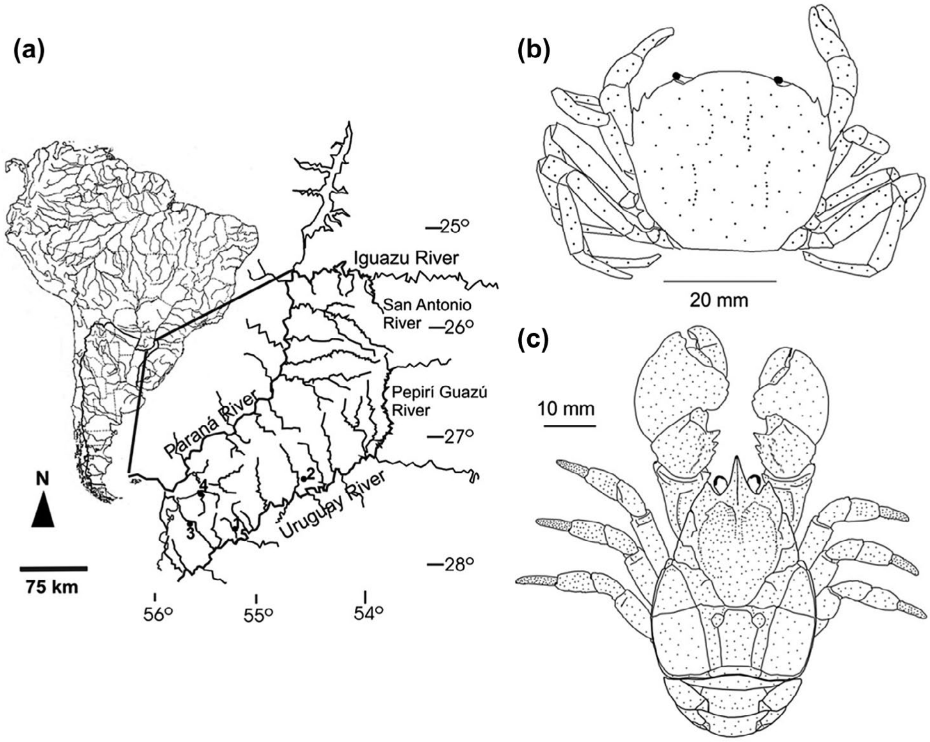

Figure 1. (a) Schematic map of the streams where specimens of trichodactylus and aeglids were captured. (1) Itacuararué, (2) Santa Rita, (3) Anchico, and (4) Isabel; and the two taxonomic groups analyzed. (b) Trichodactylidae crabs and (c) Aeglidae crabs.

the day (noon and dusk), body weight and sex, on the rate of oxygen consumption of the crabs *T. kensleyi, A. singularis* and *A. platensis* in their natural environment.

Materials and methods

Sampling of individuals

Field trials were carried out in the subtropical rainforest of southern South America (Misiones Province, Argentina) in four streams with drainage to the Uruguay and Paraná Rivers: Santa Rita (27°29′9.75″S, 54°41′0.62″W), Anchico (27°39′876″S, 55°36′5.60″W), Itacaruaré (27°52′26″S, 55°16′64.5″W), and Isabel (27°31′0.54″S, 55°27′0.15″W). The altitude of the sampled streams ranged from 88 to 137 masl. This area covers the sub region of the Paranaense forest and is characterized by great biological diversity, which is unique in southern South America (Myers et al. 2000). It is located in the upper zone of the Paraná basin. In the west, it is limited by the Paraná River, in the east by the Uruguay, San Antonio and Pepirí Guazú Rivers, and in the north by the Iguazú River (Figure 1). The so-called gallery forest borders the stream shorelines with dominance of hydrophilic vegetation. The streams of sampling are shallow, have high transparency, water velocity, and have barely submerged vegetation. The river bottoms are composed of clay, sand and rocks.

Table 1. Species collected in each stream, and their respective sub-basin.

Streams	Tributary of:	Species
Santa Rita	Río Uruguay	*Aegla platensis Trichodactylus kensleyi*
Itacararué	Río Uruguay	*Aegla platensis Trichodactylus kensleyi*
Isabel	Río Paraná	*Aegla singularis Trichodactylus kensleyi*
Anchico	Río Uruguay	*Aegla singularis Trichodactylus kensleyi*

Individuals of *A. singularis* ($n = 16$), *A. platensis* ($n = 33$) and *T. kensleyi* ($n = 20$) were collected from the bottom and below rocks manually and/or with a hand net (Figure 1; Table 1). The capture technique was adjusted according to the accessibility of each environment. All selected individuals were in the intermoult period (Diawol & Collins 2012), exhibited no physical damage and females were non-ovigerous. To study the pattern of daily respiratory activity (over a period of light–dark), samples were taken at two different times of the day; at noon (11–13 h) and dusk (17–19 h).

Field trial procedures

After capture, animals were placed in individual respirometric chambers and acclimated for 30 min. These respirometers consisted of cylindrical transparent plastic chambers with a 400-ml capacity. Environmental parameters (conductivity, temperature and pH) were measured with digital sensors (HANNA instruments, Woonsocket, RI, USA) before the field trial procedure. In each sampling site, control trials were performed without animals. The resulting values were considered to reflect the basal consumption of the microbial community and were subtracted from values with trial animals in each chamber. Each respirometric chamber was filled to capacity with water from the sampling site prior to the introduction of the crab. The initial dissolved oxygen (DO) was then measured with a digital oximeter (Hanna HI 98,129) and the chambers submerged in the streams for 60 min. Oxygen concentration was subsequently measured and each organism was extracted from the respirometric chamber. The water retained between the pleopods and other appendages was removed by absorbing it onto filter paper. The wet weight (Ww; ± 0.001 g) of each crab was obtained with a portable balance. The carapace length (CL) for aeglids and carapace width (CW) for trichodactylids (according to the convention for their respective morphologies) were recorded with a digital calliper (0.01 mm precision). The sex was determined by the presence of the masculine appendix and abdominal characteristics (Lopretto 1976; Martin & Abele 1988). Finally, they were released back into the environment at their collection sites.

Calculation of the oxygen consumption rate

The oxygen consumption rate (OCR) was expressed in mg O_2 g^{-1} h^{-1} and was calculated for each individual in separate respirometric chambers using the following formula:

$$\text{OCR} = \frac{DO_f - DO_i}{W.T}$$

where DO_f and DO_i are the final and initial DO of each respirometric chamber after one hour. W is the wet weight (Ww) of the individual and T is the time that the individual was

Table 2. Mean values and standard deviation of environmental variables at each time of day.

Sampling times	Conductivity (μs cm^{-1})	Temperature (°C)	pH	Dissolved oxygen (mg O_2^{-1})
Noon	85 ± 7.07	20.75 ± 3.04	7.36 ± 1.36	6.32 ± 1.17
Dusk	85 ± 49.49	22.9 ± 1.55	8.19 ± 0.26	6.33 ± 1.32

in the respirometric chamber (Montagna & Collins 2008). The values were corrected by subtracting the control values without animals.

Statistical analysis

The homogeneity and normality of the data were determined by Shapiro–Wilk and Levene test exploratory analyses. Crabs of each species belonging to different streams but of the same sampling time were pooled for the statistical analysis. The environmental conditions between sampling times (noon and dusk) were compared with a *t*-test. The weights of each species between sampling times were tested with Mann–Whitney and among species with Kruskal–Wallis (H) non-parametric tests. The OCR between sexes and sampling times within each species (independently of the time of day) were also tested with a Mann–Whitney non-parametric test. The OCR among species was tested with a Kruskal–Wallis (H) non-parametric test. Then this variable was tested between species in a pairwise manner with a Mann–Whitney non-parametric test.

A linear regression analysis with log–log basis was applied to analyse the OCR in response to the wet weight at each time for each species. The comparison of slopes and intercepts of these regressions between sampling times on each species were tested by ANCOVA using time of day as a covariate.

The variation of OCR relative to animal weight for each species (without separation into different time measurement groups) was analysed with a logarithmic regression.

The statistical analysis was carried out with the software R (R Development CoreTeam 2008). In all cases, a p value of <0.05 was utilized as the criteria for statistical significance (Zar 1996).

Results

Environmental conditions were similar at noon and dusk ($p > 0.05$; Table 2). The populations of each species had similar weight frequency at sampling times (Figure 2). Additionally, the weights of the individuals sampled from each species did not show significant differences between noon and dusk; the mean value for *A. platensis* was 0.93 ± 0.54 g (H: 117.0, $p = 0.51$) and for *A. singularis* was 0.79 ± 0.34 g (H: 36.0, $p = 0.55$). The species *T. kensleyi* weighed 1.03 ± 0.80 g (H: 53.0, $p = 0.82$). Finally, the weights for the three species were similar (H: 0.88, $p = 0.6436$). The CL of *A. singularis* ranged between 8.46 and 15.82 mm, *A. platensis* 6.18 and 18.18 mm, and the CW of *T. kensleyi* ranged between 6.02 and 20.94 mm (Table 3).

Description of the OCR between sexes and sampling times within and between species

There were no statistically significant differences between the OCR of males and females in each species ($p > 0.05$). A comparison of the OCR between species showed that it was higher

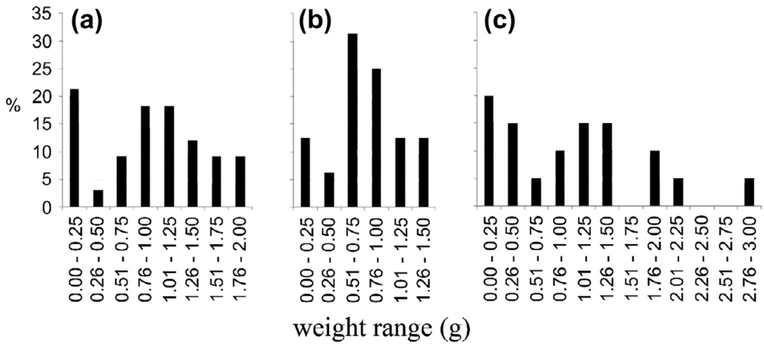

Figure 2. Frequency of weights in percentage for: (a) *Aegla platensis*; (b) *Aegla singularis* and (c) *Trichodactylus kensleyi*.

Table 3. Values of mean and standard deviation (SD), minimum and maximum of the CL (mm) of the aeglids and CW (mm) of trichodactylids.

Species	Mean ± SD	Minimum	Maximum
A. singularis	13.52 ± 1.90	8.46	15.82
A. platensis	14.36 ± 3.11	6.18	18.18
T. kensleyi	11.89 ± 4.71	6.02	20.94

Table 4. Mean and standard deviation (SD) of the OCR (mg O_2 g^{-1} h^{-1}) of each species (total OCR) and at different sampling times.

Species	Sampling time	Oxygen consumption rate (mean ± SD)	Total oxygen consumption rate (mean ± SD)
A. singularis	Noon	5.26 ± 7.23	3.63 ± 4.15
	Dusk	2.65 ± 0.81	
A. platensis	Noon	1.23 ± 2.17	0.77 ± 1.56
	Dusk	0.33 ± 0.42	
T. kensleyi	Noon	1.28 ± 0.91	3.11 ± 4.55
	Dusk	4.79 ± 5.61	

in *Aegla* species at noon, whereas *T. kensleyi* consumed more oxygen at dusk (Table 4). There were not however significant differences in the OCR between sampling times within each species ($p > 0.05$). The OCR was statistically significant among species (H: 26.71, $p = 1.57 \times 10^{-6}$) and was significantly greater in *A. singularis* than *A. platensis* (U: 35; $p = 1.92 \times 10$; Table 4). *T. kensleyi* has a higher OCR than *A. platensis* (Table 4) (U: 138; $p = 0.00$; Table 4). The results indicate that the OCR is greater in *A. singularis* than in the other species under study.

OCR in response relative to wet weight

In *A. singularis*, there was a statistically significant negative relationship between the OCR and wet weight (Ww) at noon and dusk (Table 5; Figure 3(a)). Neither the slopes nor the intercepts of these variables between noon and dusk were significantly different (Table 6,

Table 5. Values of the linear regression analysis with log–log basis of the oxygen consumption rate in response to the wet weight in each species and time.

Species	Sampling time	F	p-value	r^2
A. singularis	Noon	8.55	0.0043	0.68
	Dusk	132	$2.99.10^{-6}$	0.94
A. platensis	Noon	15.26	0.0016	0.52
	Dusk	3.18	0.095	0.17
T. kensleyi	Noon	172.9	3.52×10^{-7}	0.95
	Dusk	3.26	0.17	0.52

Figure 3(a)). The negative relationship of the OCR with the wet weight of *A. platensis* was statistically significant at noon (Table 5; Figure 3(b)). However, at dusk, though the relationship was negative (Figure 3(b)), it was not statistically significant (Table 5). There were no statistically significant differences between the slopes or the intercepts between noon and dusk (Table 6; Figure 3(b)). In *T. kensleyi*, the negative relationship between OCR and Ww (Figure 3(c)) was significant at noon, but it was not statistically significant at dusk (Table 5). These moments of the day showed statistical significance between their slopes and their intercepts according to the relationship between OCR and Ww in this crab (Table 6; Figure 3(c)).

OCR relative to the animals' weight

The OCR decreased with increasing wet weight in all three species (Figure 4). This decrease was significant ($p < 0.0001$) in the two aeglids with high r-values (0.76 in *A. platensis*, 0.82 in *A. singularis*) when both sampling times are considered together. In the crab *T. kensleyi*, however, the r-value was a low 0.31 and not significant ($p < 0.1780$) as was the slope and intersection to the axis (F: 1.97; $p = 0.178$, Figure 4).

Discussion

The time of day, body weight and sex may all affect the oxygen consumption in the taxa studied in different ways. Although the two taxonomic groups studied share biological characteristics, the strategies for regulation of gas exchange were different. The oxygen-consumption data show that the crab *T. kensleyi* exhibits daily variation in oxygen metabolism, with the period of highest oxygen consumption being at dusk or night. In contrast, aeglids did not present differences on the OCR during the times evaluated. The findings in this study are consistent with observations in other crustaceans, which describe similar OCRs between times of day, and other species, which show clear differences (Rosas et al. 1992; Radford et al. 2004; Cerezo Valverde et al. 2009; Dalosto & Santos 2011).

The specificity of the response of each species was particularly notable between the two aeglids species where the mean OCR was highest in *A. singulari* lowest in s *A. platensis*. Each species showed a specific metabolic demand that was independent of its family of origin. *Aegla singularis* had a higher metabolic rate than *T. kensleyi*, confirming reports by other researchers (Dalosto & Santos 2011) which evaluated the oxygen consumption of *A. longirostris*, *T. panoplus* and *Parastacus brasiliensis* in laboratory experiments under conditions of limited and constant oxygen availability. This study described less variation in oxygen consumption in aeglids than in trichodactylids and was able to characterize

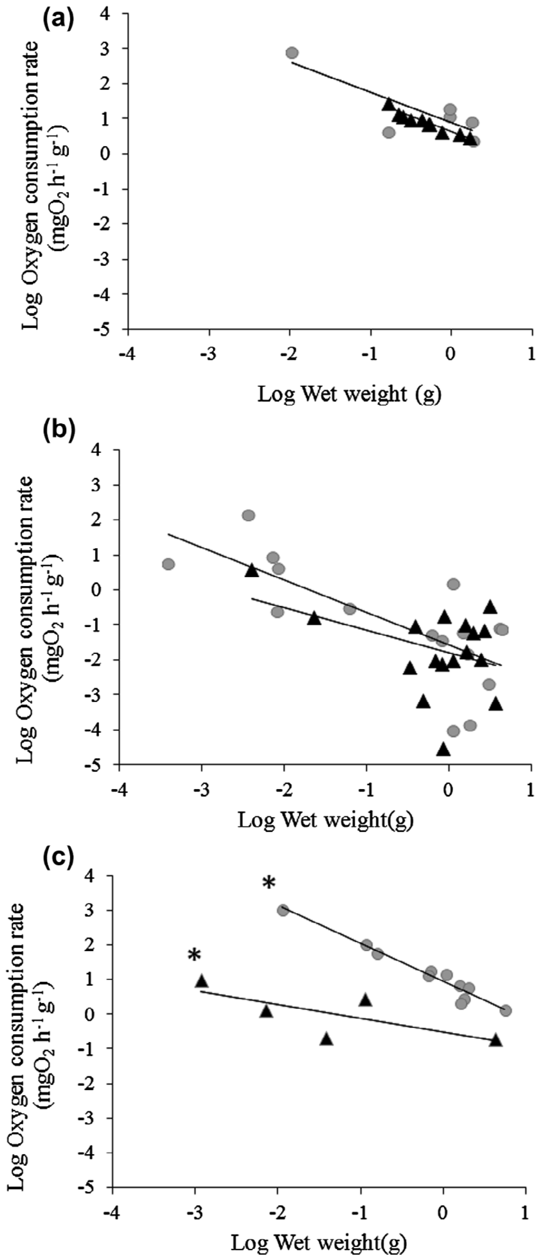

Figure 3. The relationship between OCR and the wet weight (Ww) of the three species of decapod studied. (a) *Aegla singularis*; grey circle (noon): LogOCR = −0.86LogWw + Log0.89, and black triangle (dusk): LogOCR = −0.89LogWw + Log0.64. (b) *Aegla platensis*; grey circle (noon) LogOCR = −0.94LogWw-Log1.56, and black triangle (dusk): LogOCR = −0.65LogWw-Log1.8. (c) *Trichodactylus kensleyi*, grey circle (noon): LogOCR = −1.09LogWw + Log0.95, and black triangle (dusk): LogOCR = −0.39LogWw-Log0.50.

these species as strongly oxygen-independent and oxygen-dependent, respectively (Dejours 1975). Oxygen independence would allow crabs to cope with unfavourable environmental conditions and a reduction in metabolic rate would permit survival in environments not

Table 6. Values of slopes and intercepts of OCR in response to the wet weight between sampling times (noon and dusk) on each species; through ANCOVA, using time of day as a covariate.

	Slopes comparison		Intercepts comparison	
Species	*t*	*p*-value	*t*	*p*-value
A. singularis	0.94	0.0770	1.138	0.2700
A. platensis	0.62	0.5400	−0.54	0.5900
T. kensleyi	3.68	0.0031	5.71	9.68×10^{-5}

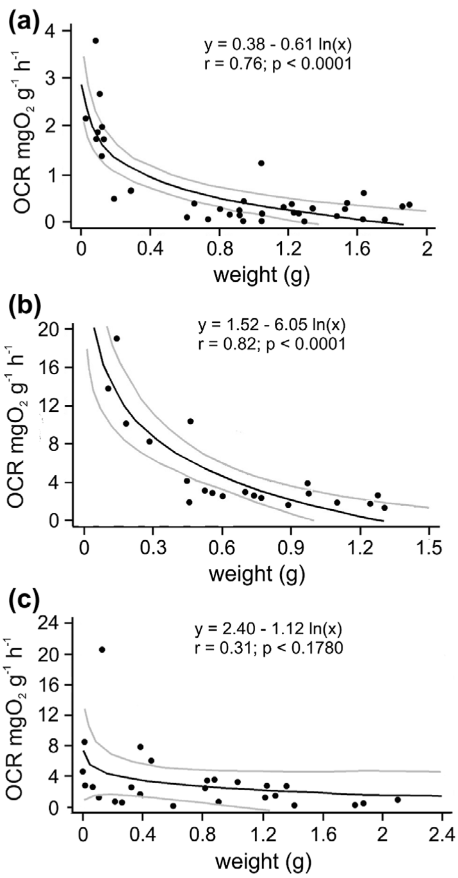

Figure 4. OCR relative to the animals' weight: (a) *Aegla platensis*, (b) *Aegla singularis* and (c) *Trichodactylus kensleyi*, considering both sampling periods together.

normally available to aeglids (Dalosto & Santos 2011). According to Bond-Buckup and Buckup (1994) and Melo (2003) the aeglids are known to inhabit clear and well-oxygenated waters but thus far no study has verified a similar requirement for highly oxygenated waters (Dalosto & Santos 2011).

The findings in this study regarding the variation in oxygen consumption between males and females are consistent with observations in other crustaceans, which describe similar OCRs by both sexes (Gutiérrez-Yurrita et al. 1994; Senkman et al. 2014). According to

Table 7. Marine and freshwater species of crustacean in which has been observed decreased metabolic rate associated with weight gain.

Species	Authors	Year
Callinectes sapidus	Laird & Haefner	1976
Pagurus bernhardus	Shumway	1978
Procambarus clarkii	Gutiérrez-Yurrita et al.	1994
Hyalella montezuma	Oberlin & Blinn	1997
Palaemonetes argentinus	Collins & Capello	2006
T. borellianus	Montagna & Collins	2008
Maja brachydactyla	Valverde et al.	2009
A. longirostris T. panoplus Parastacus brasiliensis	Dalosto & Santos	2011

other authors (Laird & Haefner 1976; Villarreal 1990), a difference in oxygen consumption between the sexes is not common in crustaceans. Cerezo Valverde et al. (2009), however, found differences in the oxygen uptake between males and females of *Maja brachydactyla*, acknowledging that the variations could have been due to different patterns of activity or specialized physiology in both sexes. Although the majority of studies have not discriminated between the sexes, this variable could be significant, especially during the reproductive season.

Decreases in the metabolic rate associated with weight gain were registered in *A. platensis*, *A. singularis* and *T. kensleyi*. This relationship has been noted over several decades in a variety of marine species and, more recently, in freshwater species (Table 7).

From an ecophysiological viewpoint the relationship between oxygen consumption and body weight as observed in *A. singularis*, *A. platensis* and *T. kensleyi* would allow organisms with higher body weights to live in parts of the environment with less stable oxygen levels. The response of an organism to environmental variations differs according to a variety of factors (e.g. nutritional condition, ecdysis and reproductive season) that can act synergistically or separately (Hill 1976; Prosser 1978).

The techniques and procedures used in this study allowed us to analyse the oxygen consumption in two decapod morphotypes in their natural environment. This alternative approach to the study of oxygen consumption broadens the scope of the study to include natural environmental sampling in geographically distant sites. It also eliminates the need to transport animals to the laboratory and allows the animals to be released back to the environment once the studies are complete. This is a particularly important consideration in aeglids which are subject to stress during transportation when many die due because of overheating and/or anoxia.

Disclosure statement

No potential conflict of interest was reported by the authors.

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