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An energy budget for the subtidal bivalve *Modiolus barbatus* (Mollusca) at different temperatures

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ABSTRACT

Clearance rates, respiration rates and food absorption efficiencies of the commercially interesting subtidal bivalve *Modiolus barbatus* were measured at different temperatures under laboratory conditions and scope for growth calculated. Clearance rates were highest at temperatures from 20 °C to 28 °C, whereas respiration rate was maximal at 9 °C and minimal at 26 °C. Highest mean values of absorbed energy occurred at 20 °C and 26 °C. Scope for growth trend had negative values at 9 °C, 15 °C and 28 °C and positive values at temperatures 20 °C and 26 °C. The profitable thermal window for *M. barbatus* to have energy sufficient for growth and reproduction corresponded to <5 months per year. Seawater temperature increases will potentially impact the eco-physiological responses of subtidal *M. barbatus* causing life history traits to change with important repercussions for subtidal biodiversity in the Mediterranean.

1. Introduction

Temperature is a main factor that have influence on animals physiological responses (Gillooly et al., 2001; Kearney et al., in press; Sarà et al., in press) and is, therefore, one of the most important factors determining the fundamental niche of a species (Chase and Leibold, 2003; Schoener, 1986). Most marine organisms, including bivalves, are ectotherms and many aspects of their energy budgets like, for instance, the lifetime amount of energy invested and/or the proportion of consumed energy allocated to growth are particularly sensitive to external temperature changes (Kooijman, 2010). While we recognize the potentially key roles of successful fertilization, embryonic development and larval recruitment in determining the distribution of marine organisms, the ultimate amount of energy available to build gonads and abundant gametes in organisms with "indeterminate growth" (*sensu* Charnov, 1993) may represent the proximate insurance to form stable populations that guarantee a species' persistence over time (*sensu* Kearney et al., in press; Sarà et al., in press).

Many studies on the effects of temperature on energy budgets are concerned with intertidal organisms (e.g. Helmuth, 2009; Helmuth et al., 2010; Kearney et al., in press; Sarà et al., 2008, in press; Wilbur and Hilbish, 1989) as they represent a reliable model to: (i),investigate adaptations to highly fluctuating environmental variance (*sensu* Burrows et al., 2009; Davenport and Davenport, 2005; Davenport et al., 2005) and (ii), forecast the distribution and abundance of intertidal biodiversity in the context of climate change (Helmuth et al., 2010). Deeper marine conditions are usually considered more stable than intertidal ones (Southward, 1958). Hence, subtidal bivalves assume the same body temperatures of the waters they live in and should oscillate less sharply than in the intertidal, primarily as a function of water mass seasonality (Margalef, 1985). Thus, the stability of subtidal conditions should lead to a longer life-expectancy and an adaptive consequence of this will be a reduced plasticity in eco-physiological responses to environmental changes (Somero, 2010). It is expected, as a consequence, that small fluctuations in the environmentally variable water column (e.g., temperature, salinity, food availability) may have large impacts on ecological performance. Although several studies have analyzed the energy budgets of subtidal bivalves (e.g. Navarro and Thompson, 1996; Sarà and Pusceddu, 2008; Sukhotin et al., 2003; Wong and Cheung, 2003), there is limited information available

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for certain commercially important species, including *Modiolus barbatus*.

Modiolus barbatus generally occurs from depths of a few meters to several dozens of meters in the western Mediterranean and the Adriatic Sea and represents an important ecosystem engineer (*sensu* Jones et al., 1994) in marine coastal habitats. Together with another bivalve, *Arca noae, M. barbatus* serves as an attachment substratum for conspecifics (Hrs-Brenko, 1980) and several subtidal phyto- and zoo-biofoulers (Peharda, pers. obs.). Natural populations are harvested and it is also considered to be a potential aquaculture candidate (Peharda et al., 2007). Despite its importance, no information is available on the energy budget of *M. barbatus* apart from some indirect metabolic data obtained on responses along the higher side (from 24 °C to 30 °C) of a thermal tolerance curve (Anestis et al., 2008).

Here, we tested if different temperatures set the thermal limits of energetic functioning by *M. barbatus*. In particular, we measured, under mesocosm conditions, the effects of temperature over a range from 9 °C to 28 °C on: (i), clearance rate as an expression of food intake; (ii) oxygen consumption rates as an expression of metabolic requirements to lastly depict (iii), scope for growth as an expression of energy available for growth and reproduction. Such data are crucial for the management of natural populations of commercially exploited bivalves, the initiation and sustainability of bivalve aquaculture and are potentially useful as predictive indicators of changes in Mediterranean subtidal biodiversity caused by temperature increases.

2. Material and methods

2.1. Sample collection and experimental set-up

Individuals of *Modiolus barbatus* were collected in November 2009 from Mali Ston Bay (Croatia; 42°51′29″N and 17°41′44″E) using SCUBA at depths of between 2 and 4 m and were brushed to remove epibionts. At this location, seawater temperature generally varies from 9 °C in January–February to 25 °C in July–August (Mladineo et al., 2007). Collected individuals were acclimated in the sea at the Institute of Oceanography and Fisheries in Split for two weeks at an ambient seawater temperature of 17 °C. After acclimation, individuals were transported to the Laboratory of Experimental Ecology and Behaviour (Palermo, Italy), where they were further acclimated for another two weeks at the original ambient temperature to reduce possible stress deriving from transportation. They were divided randomly into 5 groups of 20 individuals of shell length 5.4 ± 0.5 cm. Each group of *M. barbatus* was maintained under the same salinity (38 psu), and at one of five different experimental temperatures (9 °C, 15 °C, 20 °C, 26 °C, 28 °C) maintained by means of isothermal aquaria. This acclimation period, for each temperature prior to experimentation, was for seven days as based on earlier studies with *Mytilus edulis* and *Brachidontes pharaonis*; indeed, if there is to be significant physiological adaptation to temperature it should occur rapidly and largely within the first seven days (Sarà et al., 2008; Widdows and Bayne, 1971). The bivalves were fed daily with a monoalgal culture of *Isochrysis galbana* (25,000 cells ml^{-1}) and aquaria water was aerated continuously. Before the start of experiments at each temperature, animals were standardisingly fasted for 24 h (Widdows and Staff, 2006). Clearance rate, respiration rate and food absorption efficiency were measured for each group at each temperature according to procedures reported upon by Widdows and Staff (2006) and later successfully used by Sarà et al. (2008). To measure the physiological responses of *M. barbatus*, eight individuals were used from each temperature group. Clearance rate was measured in a closed system by placing one individual each in a beaker containing 1 L of filtered thermo-regulated seawater. To do this, beakers were positioned on heated stirring base plates, also used to maintain temperatures at constant values and to keep the water mixed and oxygenated throughout the experimental sessions. After a period of 20 min, as the bivalves started to filter, algal cells (*Isochrysis galbana*) were added to each beaker at an initial concentration of 25,000 cells ml^{-1}. We used *Isochrysis galbana* as it is the microalga of choice in most other similar experiments, as evidenced by the ample literature on this topic (e.g., Flye-Sainte-Marie, 2006; Pouvreau et al., 2006; Sarà et al., 2008; Van Haren and Kooijman, 1993; Widdows and Staff, 2006).

Twenty ml aliquots were sampled from every beaker at 30 min intervals over a period of 2 h. The decline in *Isochrysis galbana* cell concentration was monitored using a Coulter Counter (Beckman Coulter© Model Z2). Two control beakers, without *M. barbatus*, showed no significant decline in cell concentration over the entire experimental period. Clearance rate was calculated using the following equation: $\mathrm{CR}\ (\mathrm{l\ h^{-1}}) = 1\ \mathrm{L}\ (\log_e \mathrm{C}_1 - \log_e \mathrm{C}_2)/\text{time interval}$ (h): where C_1 and C_2 were the cell concentrations at the beginning and end of each time increment (i.e., every 30 min). Clearance rates were used to calculate ingestion rates, i.e., the amount of ingested food per hour (IR, mg food l h^{-1}) ($\mathrm{IR} = \mathrm{CR} \times \text{mg Algae l}^{-1}$). Respiration rate was determined by placing another eight individuals of *M. barbatus* in glass respirometers (2 L) containing air-saturated pre-filtered (0.45 µm; GF/F Whatman) seawater, agitated by a magnetic stirrer bar. These individuals were different from those used for clearance rate measurements in order to meet the assumption of independence (*sensu* Underwood, 1997). The respirometer was sealed and the decline in oxygen concentration measured for at least 40–60 min by means of a Stratkelvin electrode (Model 282). Food absorption efficiency (AE) was measured according to Conover (1966) by comparing the proportion of organic matter in the algal cells and faeces identified as dark brown strings in contrast to the lighter-coloured pseudofaeces, which were not collected. Algal food and faecal pellets were collected on GF/C Whatman filters (washed, ashed and pre-weighed). The filters were dried at 90 °C and weighed before ashing in a furnace at 450 °C for 4 h and weighed again with a Mettler balance (accuracy: 1 mg). Faeces were collected from the acclimation beaker after the timing of respiration measurements. Food Absorption Efficiency $(\mathrm{AE}) = (\mathrm{F} - E)/[(1 - E) * \mathrm{F}]$ where F = ash-free dry weight: dry weight ratio of food, and E = ash-free dry weight: dry weight ratio of the faeces. After physiological measurements, the tissues of *M. barbatus* were removed from their shells and dried at 80 °C to obtain shell and tissue dry weights. The individual clearance rates (L h^{-1}) and oxygen consumption rates (micromoles O_2 h^{-1}) were converted to mass specific rates for a ‘standard *M. barbatus*’ of 1g dry weight using the standard weight exponent ($b = 0.67$; Widdows and Staff, 2006). In order to calculate the energy budget and scope for growth (SFG), each physiological rate was then converted into energy equivalents (J h^{-1} g^{-1}). Specifically, the Maximal Consumed/Ingested Energy (C, J g^{-1} h^{-1}) was obtained by converting IR values into energy equivalents using the coefficient 18.5 (J mg POM; Brown, 1991; Whyte, 1987); the Energy Absorbed (AR, J g^{-1} h^{-1}) was obtained by multiplying the Ingested Energy (C) by the Food Absorption Efficiency (AE), while the Energy Respired (RR, J g^{-1} h^{-1}) was obtained from consumed oxygen as expressed in micromoles O_2 (h^{-1}) multiplied by 0.456 where the heat equivalent of oxygen uptake was 0.456 J µmol^{-1} O_2 according to Gnaiger (1983). Scope for Growth (SFG) represented the difference between the energy absorbed (AR) and the energy loss via respiration (RR).

2.2. Statistical analyse

An analysis of variance (ANOVA; Underwood, 1997) was carried out to test the effect of temperature (5 levels, fixed) on physiological variables respiration and scope for growth and for these variables the heterogeneity of variances was tested using Cochran's C test prior to the analysis of variance, and a Student-Newman-Keuls (SNK) test allowed comparison of the appropriate means. Clearance and absorption rates were tested them by using the Kruskal–Wallis one-way analysis of variance. A posteriori pairwise tests were performed within the PERANOVA test (Anderson, 2001) with ln $(y + 1)$ transformation, Euclidean distance and 9999 permutations (Sweeting et al., 2009).

3. Results

Significant differences in physiological rates were observed for *Modiolus barbatus* kept at different temperatures (Tables 1 and 2). Clearance rates of *M. barbatus* individuals acclimated to a temperature of 20 °C and over were higher (from about 0.17 l h^{-1} g^{-1} to over 0.23 l h^{-1} g^{-1}) than those of conspecifics maintained at lower temperatures (9 and 15 °C), which had values < 0.1 l h^{-1} g^{-1} (Fig. 1). Clearance rate was determined to be stable between 9 °C and 15 °C ($p > 0.05$; Fig. 1) and also between 20 °C, 26 °C and 28 °C ($p > 0.05$; Fig. 1). Values recorded at temperatures >20 °C differed significantly from those recorded at lower ones. Respiration rate (Fig. 2) was highest at 9 °C (20.89 μmol h^{-1} g^{-1}) and lowest at 26 °C (9.83 μmol h^{-1} g^{-1}). Significant difference (Fig. 2; $p > 0.05$) in this parameter was observed only between individuals kept at 26 °C and those kept at other temperatures. The highest mean values of absorbed energy were reached at 20 °C and 26 °C (about 2.5–3.0 J h^{-1} g^{-1}; Fig. 3). In contrast, *M. barbatus* individuals kept at 9 °C, 15 °C and 28 °C absorbed significantly less energy (about 0.5–1.5 J h^{-1} g^{-1}; Fig. 3). Absorption efficiency was lowest at 28 °C (0.41) while at other temperatures it ranged from 0.69 to 0.81 (Fig. 4). The scope for growth of *M. barbatus* had a significantly lower values at 9 °C, 15 °C and 28 °C ($p < 0.05$) than values at 20 °C and 26 °C (Fig. 5).

4. Discussion

The amount of energy available for ectotherms generally varies as a function of environmental variance and, in particular, with the temperature that is able to consistently affect the magnitude of allocation to growth and reproduction (Brown et al., 2004). Ecophysiological information arising from the present experiment focussing on the role of temperature on the energy budget of *Modiolus barbatus*, integrates well with previous information on growth (Peharda et al., 2007) and reproduction (Mladineo et al., 2007) of this species and metabolic data obtained by Anestis et al. (2008). This further supports the view that temperature represents an important driver able to influence the energy budget, growth and reproduction allocation in *M. barbatus*. In addition to direct effects on the metabolic rate of bivalves, temperature also influences food availability, which, in turn, has effects on gonadal and somatic development (Gosling, 2003).

According to previous growth experiments conducted on *M. barbatus* by Peharda et al. (2007), which included an analysis of seasonal growth of marked individuals in Mali Ston Bay, this species grows fastest during the warmest part of the year (from May to August) when seawater temperatures in the bay have an average range from 20 °C to 25 °C (Mladineo et al., 2007). In contrast, during other periods of the year, when seawater temperatures are lower (∼15 °C with a minimum of 9.9 °C; from November to May; Mladineo et al., 2007), growth rates of *M. barbatus* were significantly lower (Peharda et al., 2007). A similar seasonal growth pattern is also seen in the Aegean Sea (Marsin Bay, Turkey; Lok et al., 2006). In the latter case, a slight temporal shift coincided with the different pattern of temperatures typically observed in that part of the Mediterranean Sea. That is, the highest monthly specific growth rate of *M. barbatus* was from June to September, while growth rates were significantly reduced during other times of the year (Lok et al., 2006). In both locations, however, this species seems to attain a maximum growth rate when the water temperature is between 20 °C and 26 °C. That range would also coincide with the maximum potential reproductive output (Mladineo et al., 2007) and the lowest mortality rate (Anestis et al., 2008) reported upon for this species. Mladineo et al. (2007) obtained a significantly positive correlation between gonad index and temperature in Mali Ston Bay, with the maximum occurrence of spawning events being recorded during the warmest months of the year. Conversely, Anestis et al. (2008) showed an increase in mortality with temperature according to the following scheme: no mortality occurred in individuals acclimated to 24 °C, whereas ~3% died at 26 °C, 10% at 28 °C, and 20% at 30 °C after a 30-day experiment. It is interesting to note that spawning periodicity coincided with maximal shell growth rates, indicating that this species has enough energy available to conduct both activities simultaneously.

Table 1
PERANOVA testing the effect of temperature on *M. barbatus* clearance (CR, l h^{-1} g^{-1} = standardized clearance rate) and absorption rates (ABS, J h^{-1} g^{-1} = absorbed energy) [* = $P \le 0.05$; ** = $P \le 0.01$; *** = $P \le 0.001$; ns = no significant difference ($p > 0.05$)].

Source	CR				ABS		
	df	MS	Pseudo-F	P	MS	Pseudo-F	P
Temperature (TEMP)	4	3.86E-02	5.1	**	1.03	6.04	**
Residuals	35	7.61E-03			0.17		

Table 2
ANOVA testing the effect of temperature on *M. barbatus* respiration rate (RR, μmol h^{-1} g^{-1} = standardized respiration rate) and Scope for Growth (SFG, J h^{-1} g^{-1} = scope for growth) [* = $P \le 0.05$; ** = $P \le 0.01$; *** = $P \le 0.001$; ns = no significant difference ($p > 0.05$)].

Source		RR			SFG		
	df	MS	F	P	MS	F	P
Temperature (TEMP)	4	15.51	3.43	*	20.55	9.64	***
Residuals	35	4.52			2.14		
Cochran's test	39			ns			ns

Clearance rate measured in the present paper reached a maximum at 20 °C and did not drop significantly at 28 °C, suggesting a food energy intake dependence on temperature. Below

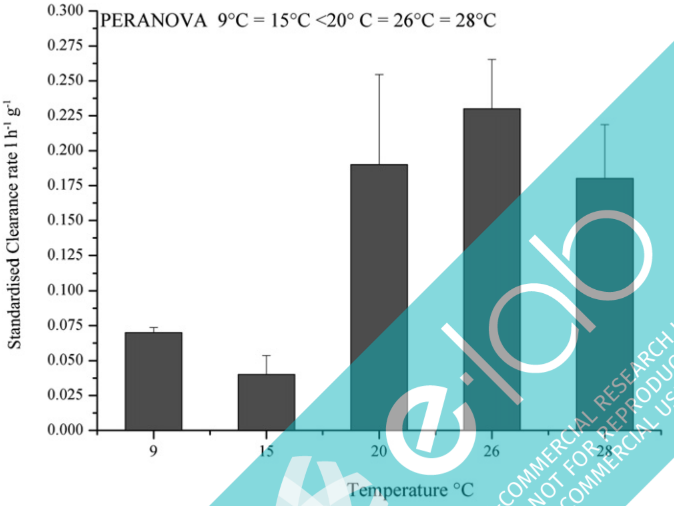

Fig. 1. Effect of temperature on the clearance rate (l h^{-1} g^{-1}) of *Modiolus barbatus*. Values are mean ± SEM, $N = 8$.

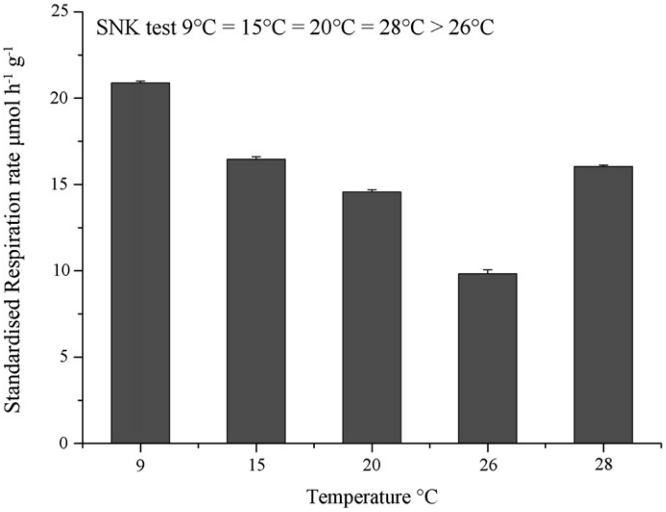

Fig. 2. Effect of temperature on the standardized respiration rate (µmol h^{-1} g^{-1}) of *Modiolus barbatus*. Values are mean ± SEM, $N = 8$.

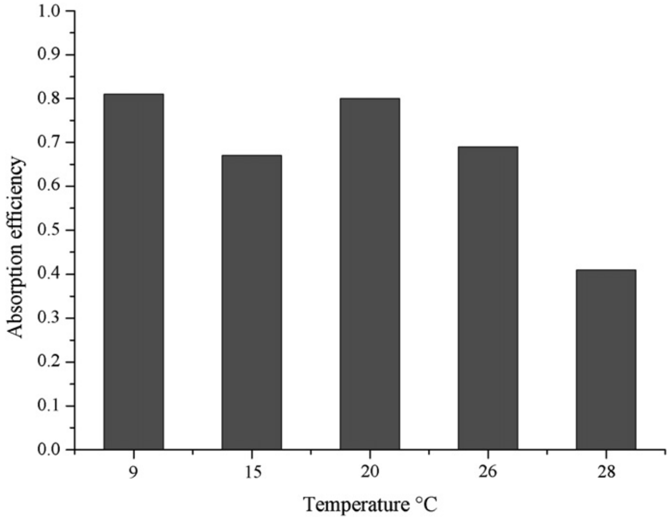

Fig. 4. Effect of temperature on the absorption efficiency of *Modiolus barbatus*.

these threshold values and presumably beyond 28 °C (unfortunately we do not have data for temperatures higher than 28 °C), food acquisition should decline to almost complete cessation (only some ml h^{-1} g^{-1}) between 15 °C and 9 °C. This suggests that for several months of the year, food intake is minimal. A dependence of clearance rate on temperature has been previously described for many other species including *Ostrea edulis* (Buxton et al., 1981), *Ruditapes decussatus* (Sobral and Widdows, 1997), *Pinctada margaritifera* and *P. maxima* (Yukihira et al., 2000), *Spisula subtruncata* (Rueda and Smaal, 2004) and *Brachiodontes pharaonis* (Sarà et al., 2008). Clearance rates recorded for *M. barbatus* in this study were remarkably lower. For instance, clearance rate of *R. decussatus* fed with a culture of *Phaeodactylum tricornutum* was 7.33 l h^{-1} g^{-1} at 20 °C, 6.17 l h^{-1} g^{-1} at 27 °C and 4.66 l h^{-1} g^{-1} at 32 °C (Sobral and Widdows, 1997). Similarly, *Mytilus edulis* kept at 9 °C had a clearance rate of 3.02 l h^{-1} g^{-1} (Widdows and Johnson, 1988) while the Lessepsian bivalve *Brachidontes pharaonis* kept at 37 psu and fed with *Isochrysis galbana* had one of 0.75 l h^{-1} g^{-1} at 11 °C and >5.0 l h^{-1} g^{-1} at 15 °C and 20 °C (Sarà et al., 2008). The clearance rates of tropical pearl oysters, *P. margaritifera* and *P. maxima*, fed with same the species of phytoplankton also varied with respect to experimental temperatures - from ~5–7.5 l h^{-1} for individuals kept at 19 °C to ~11–13 l h^{-1} for those kept at 28 °C (Yukihira et al., 2000).

Differences in CR can occur not only between species but between conspecifics from different habitats. This was confirmed by the great differences in clearance rates detected between *Mytilus galloprovincialis* collected from the Atlantic coast of Spain and from the Mediterranean coast of France, and both fed with *I. galbana*. The clearance rate of Atlantic *M. galloprovincialis* of 53 mm shell length was 17.5 l h^{-1} g^{-1} (Maire et al., 2007) whereas the clearance rate of Mediterranean conspecifics were 2.02, 2.93 and 2.61 l h^{-1} g^{-1}, respectively, for individuals of 61.6 mm, 73.0 mm and 88.9 mm shell length (Perez Camacho et al., 2000; data standardized according to Widdows and Staff, 2006).

Although *M. barbatus* CR values were significantly lower from those described above, we must consider that body size and age could significantly affect pumping rate. For example, *M. edulis* pumping rate decreases in individuals older than six years (Sukhotin et al., 2003). Hence, the reason for the relatively low filtration rate recorded for *M. barbatus* might be ascribed to the fact that the shell lengths of the individuals used in this experiment had matching ages of >8 years (Peharda et al., 2007).

Moreover, previous literature data deal with faster-growing and shorter-lived species than *M. barbatus* (Peharda et al., 2007), which would explain the obtained higher clearance rate values.

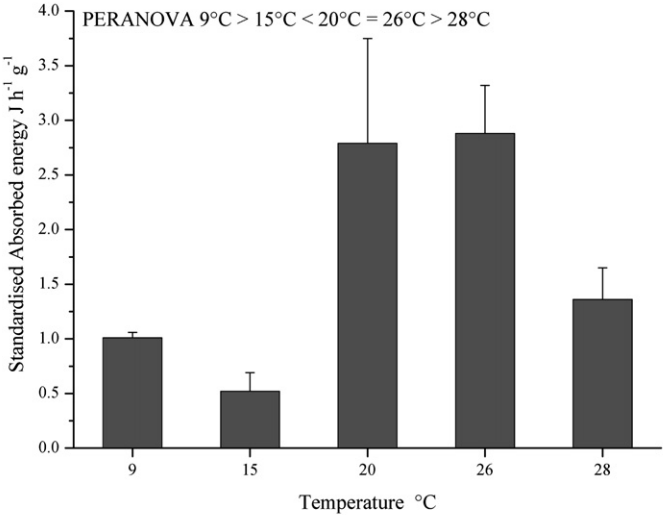

Fig. 3. Effect of temperature on the absorbed energy (J h^{-1} g^{-1}) of *Modiolus barbatus*. Values are mean ± SEM, $N = 8$.

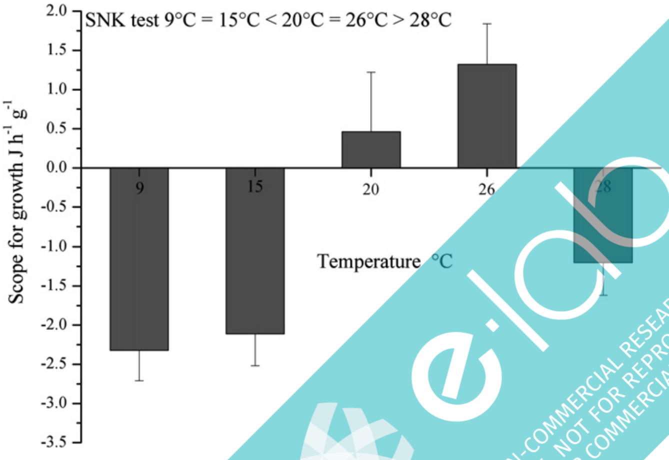

Fig. 5. Effect of temperature on scope for growth (J h^{-1} g^{-1}) of *Modiolus barbatus*. Values are mean ± SEM, $N = 8$.

Differences in filtration rate between fast-growing and slower-growing oysters (*Saccostrea glomerata*) were commented upon by Bayne (2004) who showed that faster-growing individuals had higher filtration rates. Hence, if fast growth is the result of higher feeding rates and reduced metabolic expenditure (Bayne, 2004), slow growth of *M. barbatus* could be a result of low CR values and higher RR.

Indeed, a wider ability to modulate clearance rates may be an adaptive strategy in some species having a short life-expectancy such as those living in highly variable habitats, for example, most intertidal and shallow-water species. Such organisms should seize an immediate advantage from every profitable environmental situation allowing them to acquire energy to be allocated to growth and reproduction (Krebs and Davies, 1993). In contrast, *M. barbatus* showed a low rate of food acquisition per unit time and weight which would equate more reasonably with a species living under more constant conditions both of temperature and food availability as typically occurs in subtidal Mediterranean habitats. This hypothesis is supported by a study of Charles and Newell (1997) who reported that ribbed mussel, *Geukensia demmissa*, individuals held under subtidal conditions showed lower feeding rates than intertidal conspecific. In addition, intertidal *Geukensia demissa* acquired energy more efficiently from food than subtidal *conspecifics* (Kreeger et al., 1990).

The lower amount of absorbed energy in *M. barbatus* with respect to, for instance, *Mytilus edulis* (Widdows and Johnson, 1988) would further seem to confirm its subtidal nature. Anestis et al. (2008) analyzed metabolic and molecular stress responses of *M. barbatus* to increasing seawater temperatures. According to their results, *M. barbatus* should reach optimal metabolic and molecular responses at temperatures of ~24 °C, while higher temperatures would probably induce a detrimental response. This coincides with our scope for growth results showing that large adults of this species had a positive amount of energy over the thermal range between 20 °C and 26 °C, peaking at 26 °C. In contrast, Mladineo et al. (2007) observed that the active development of gametes in *M. barbatus* from the same region (Mali Ston Bay) started in March, when temperatures are usually <20 °C and when scope for growth should be negative according to herein presented results. Such an apparent contradiction deserves investigation.

Similarly, negative SFG values were also recorded for *M. edulis* during periods of increased gamete development. Such individuals were collected from areas with a lower temperature range (from 9 °C to 17 °C) than those reported upon herein, and showed negative SFG values of −0.76 and −0.40 J h^{-1} in March (~9 °C) and October (~14 °C), respectively. A positive SFG value was recorded in June (1.23 J h^{-1}) during the spawning period when temperature was ~13 °C. There are no data, however, on SFG at the highest temperatures in this region and it is thus not possible to identify a profitable thermal window for *M. eduils* (Hawkins et al., 1985). SFG of *M. edulis* from Norway had a positive value at 9 °C which is in sharp contrast to *M. barbatus* which had a negative SFG value at that temperature (Widdows and Johnson, 1988). Such results are not surprising if we consider that *M. barbatus* occurs in warm, temperate, waters and *M. edulis* is a boreal species: both are best adapted to the conditions of their geographic ranges. Bivalves are, however, able to make some metabolic compensations to maintain their biological functions at relatively constant values, although under conditions of year-round negative SFG they cannot survive in certain areas. This was confirmed by SFG comparison of *M. galloprovincialis* from two areas: one with a naturally high abundance of individuals and another into which individuals were translocated for experimental purposes but where no natural population existed. SFG was negative during summer and winter (temperatures were ~16 and ~11 °C, respectively) in the area with low concentrations of organic matter possibly explaining why a natural population does not exist there. In the area with a higher concentration of organic matter and high *M. galloprovincialis* abundance, SGF values were >80 J g^{-1} for both seasons (Gardner, 2000). A short period of the year with positive SFG values was recorded for the sub-Arctic mussel *Modiolus modiolus* although smaller individuals had a longer period of the year with positive SFG values. Larger individuals had negative SFG values during the major part of year with positive values recorded only in spring when the temperature was around 0 °C (Navarro and Thompson, 1996). Despite this, *M. modiolus* is abundant in cold seas, leading to the conclusion that the species gains energy requirement for maintenance over a short frame. Only Anestis et al. (2008) have performed some physiological tests on *M. barbatus* but, unfortunately, these were conducted over a temperature range of between 20 °C and 28–30 °C, so that we cannot draw an overlapping curve between their and our results obtained from a wider range of experimental temperatures (9°–28 °C). However, if we correlate our and their results obtained over the temperature range from 20 °C to 28 °C, a similar trend is obtained and which approximates the centre of the experimentally derived thermal curve peaking at 26 °C.

Anestis et al. (2008) evidenced a metabolic depression and a shift from aerobic to anaerobic metabolism at the lower and finer observation scales of cellular and molecular. Such results are not coincident with our respiration data probably because respiration rates depict a metabolic response at a different level of organization (i.e., organism). Respiration rates at the extremes of the lower region of the *M. barbatus* experimental thermal curve were higher than those obtained for *Mytilus edulis* (10.1 μm h^{-1} g^{-1}; Widdows and Johnson, 1988) and *Brachidontes pharaonis* (~1.5 μm h^{-1} g^{-1}; Sarà et al., 2008). The significant difference in respiration rate was obtained between 26 °C (the minimum) and all other temperatures. *M. barbatus* exhibited a higher respiration rate during acclimation at the lowest temperature (9 °C) and which, therefore, seems to be an adaptive mechanism. This finding is in agreement with the activities of key intermediate metabolic enzymes in the congeneric, *Modiolus modiolus* (Lesser and Kruse, 2004). That is, the higher respiration rate could be due to mitochondrial compensation, as discussed by other investigators (Lurman et al., 2010; Sommer and Pörtner, 2002). However, as has also been shown, summer-collected *Modiolus modiolus* exhibited higher respiration rates than conspecifics collected during winter (Lesser and Kruse, 2004).

In conclusion, although the present experiment has limitations in terms of the *M. barbatus* size classes it investigated, as well as other factors that can have a strong influence on energy gain and expenditure (e.g. food availability, seasonal physiological variation), it provides a valuable insight into the energy budget of a commercially important bivalve species. Although at present only natural populations are harvested, *M. barbatus* is considered a potential species for introduction into bivalve aquaculture (Peharda et al., 2007) and data on its energy budget and its, in turn, dependence on temperature, could be crucial for selecting potential aquaculture sites and optimal culture depths. The most profitable thermal window for large adult individuals of *M. barbatus* seems to be ~4–6 °C. During the period over which such temperatures occur, individuals should have energy sufficient for growth and reproduction for ~5–6 months of the year.

Thus, in the situation of temperature increases in the near future due to climate change (IPCC, 2007), and a slight shift of temperature extremes towards the lower and higher side of curve are anticipated scenario, we expect that such a scenario would restrict slightly optimal performance of *M. barbatus,* pushing it closer to its eco-physiological limits. This shift could impact *Modiolus* fitness as the temporal scheme of its life history strategy would significantly deviate from the common natural pattern with the expectation of important repercussions on marine biodiversity.

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Appendix. Supplementary data

Supplementary data related to this article can be found online, at doi:10.1016/j.marenvres.2010.10.005.

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