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RESEARCH ARTICLE

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Effect of temperature on specific dynamic action in the common octopus, *Octopus vulgaris* (Cephalopoda)

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Abstract Feeding causes an increase of metabolic rate, which initially escalates rapidly, reaches a peak value and then gradually declines to the pre-feeding rate. This phenomenon, termed "specific dynamic action" (SDA), reflects the energy requirements of the behavioral, physiological and biochemical processes that constitute feeding. The effect of temperature on SDA of the common octopus, *Octopus vulgaris*, was evaluated, by measuring the temporal pattern of the oxygen consumption rates of octopuses, after feeding, at two constant temperatures, 20°C and 28°C. At 20°C, the relative increase in the oxygen consumption rate after feeding (relative SDA) was significantly greater than at 28°C. The peak of the relative SDA occurred 1 h after feeding, and it was 64% at 20°C and 42% at 28°C. However, the SDA absolute peak, SDA duration (9.5 h) and SDA magnitude (the integrated postprandial increase in oxygen uptake) did not differ significantly between the two temperatures, indicating that the energetic cost of feeding was the same at both temperatures. The SDA response in *O. vulgaris* was much faster than it was in polar species, which have extended SDA responses due to low temperatures, and was also relatively fast in relation to the response in other temperate species, which is probably connected to the remarkably high growth rates of the species. A possible explanation of the observed summer migration of large octopuses from shallow to deeper areas is given, based on the effect of temperature on the energetic requirements of octopuses.

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Introduction

The effect of feeding on the oxygen consumption rate (R) of aquatic poikilotherms has been documented in several studies. R increases rapidly after a single meal and then gradual declines back to pre-feeding values over a period of several hours or days. This phenomenon is known as the "specific dynamic action" of food (SDA) (Brody1964) and reflects the energy requirements of the behavioral, physiological and biochemical processes that constitute feeding, including capture, handling, ingestion, digestion, the assimilation of prey and the increased synthesis of proteins and lipids associated with growth (Jobling1981, 1993; Wells et al. 1983).

The parameters that are usually used to describe SDA include the overall magnitude (the integrated postprandial increase in oxygen uptake), peak levels and duration (Jobling1981; Whiteley et al. 2001). These parameters, together with the exact temporal pattern of the SDA, depend on the species and on several other factors such as diet composition (Du and Niu2002; Thor et al. 2002), feeding rate (Jobling1981; Forsberg1997) and feeding frequency (De la Gándara et al. 2002). Among the exogenous and endogenous factors that influence metabolic rates, temperature is one of the most important (Rao and Bullock 1954; Kinne1970). Postprandial increases in the oxygen consumption rate have been studied in fish (Jobling1981), but only a limited number of studies have dealt with aquatic invertebrates, mainly crustaceans (Robertson et al. 2001a, 2001b, 2002; Whiteley et al. 2001).

The aim of the present study was to evaluate the temperature effect on the SDA of the common octopus, *Octopus vulgaris*. The common octopus is a temporal

species of great scientific and commercial importance, and its culture is becoming an area of increasing interest. It is a coastal and sedentary species, living between 0 and 200 m depth, with a decreasing abundance with depth (Guerra1981). It was thought to have a world-wide distribution in tropical, subtropical and temperate waters (Atlantic, Indian Ocean, western Pacific), but recent papers indicate that *O.vulgaris* is restricted to the Mediterranean and eastern Atlantic coasts (Mangold1998; Söller et al. 2000). Routine metabolic rates of *O.vulgaris* in relation to temperature and body mass have been studied by Katsanevakis et al. (2004), and SDA peak levels and duration for one individual at a constant temperature have been reported by Wells et al. (1983).

Materials and methods

Octopuses (*Octopus vulgaris*), ranging in mass from 186 to 874 g, were collected by SCUBA and free diving in the Saronicos Gulf (37°30′N–37°55′N; 23°E–24°E). Immediately after collection the animals were placed into 40-l plastic holding tanks, with sufficient aeration by portable air pumps; within 2 h they were transferred to the laboratory. The specimens were collected during June and July 2003, from areas with temperatures ranging between 20.5°C and 28.1°C. The experiment was conducted in a closed seawater system, described in detail in Katsanevakis et al. (2004). Before the experiments, the octopuses were subjected to a 1-month acclimatization period, during which they were adapted to their new environment and to feeding on frozen anchovy (*Engraulisencrasicolus*). Preliminary experiments showed that octopuses need approximately 1 week to get accustomed to captivity, to eat regularly, to start gaining weight and to stabilize their metabolic rates; thus a 1-month acclimatization appears to be sufficient.

Salinity and pH were monitored daily and regulated. The increase in salinity due to evaporation was corrected with the addition of deionized water, and remained at $38.5 \pm 0.2‰$ throughout the experiment. There was a trend toward a decline in pH, mainly due to respiration and nitrification; this was corrected regularly with the addition of sodium bicarbonate (Spotte1992). The pH ranged between 7.7 and 8.1 during the experiment. Ammonia, nitrite, nitrate and phosphate concentrations were monitored twice weekly. In the closed system, mean and maximum values were, respectively, for ammonia, 2.4 and 5.5 μmol l^{-1}, for nitrite, 0.9 and 1.4 μmol l^{-1}, for nitrate, 5.0 and 7.1 mmol l^{-1}, and for phosphate, 0.15 and 0.25 mmol l^{-1}. There was a photoperiod of 12 h light:12 h darkness, with the light period between 0800 and 2000 hours.

To minimize stress, a plastic pot was placed in all holding tanks to be used by the octopus as a den, and the ratio of the volume of the holding tank to the weight of the animal was in every case > 50 l kg^{-1}. The experiments were conducted in the holding tanks; no separate respiration chamber was used, to allow the octopuses to adapt well to their artificial environment and to avoid stress due to transfer to another chamber just before measurements. The sides of the holding tanks were covered with a black self-adhesive blind to avoid stress or excess activity due to people moving around in the laboratory.

The oxygen consumption rate of each octopus was measured for a 24-h period, during 1-h-long measurements starting at 0900 hours. The octopuses were fed on frozen anchovy flesh (*E.encrasicolus*), at a rate of 3% of body weight, just after the first measurement, at 1000 hours. Seven such 1-h oxygen consumption rate measurements were conducted, starting at the following times: 0900, 1030, 1200, 1330, 1500, 1630 and at 0900 hours on the next day. As controls, some octopuses were measured following the same procedure, but without being fed. Controls were used in order to exclude variation in R due to reasons other than feeding (diurnal variation of activity, response to experimental procedure, etc.). Animals used in the "feeding measurements" and animals used as controls had been fed for the last time at 1000 hours on the previous day.

During every measurement, the holding tank of the octopus being measured was isolated from the closed system by closing the inflow valve, while aeration was also turned off. One 500-ml water sample was taken via a 5-mm rubber tube from the experimental tank every 5 min and for a period of 1 h. Dissolved oxygen of the samples was measured with a WTW (Wissenschaftlich-TechnischeWerkstatten) polarographic oxygen probe (Cellox 325) connected to a WTW (MultiLine P4) meter, while stirring the samples gently with a magnetic stirrer. After measuring the oxygen content, the water sample was returned gently through a 5-mm rubber tube to the experimental tank. If the oxygen concentration in the experimental tank fell below 3.0 mg l^{-1}, the measurement was terminated earlier than 1 h, as below 2 mg l^{-1} octopuses begin to show signs of distress and oxygen consumption declines (Maginniss and Wells 1969). Immediately after the end of each 1-h measurement, the experimental tank was reconnected to the closed system and aeration was turned on again, till the next measurement. For each 1-h measurement, a time series of the oxygen content of the tank was calculated from the product of oxygen concentration measurements and the tank volume. R (in mg h^{-1}) was estimated as the declining rate of the tank oxygen content, which was calculated as the slope of the least squares line that fitted the time series. This oxygen consumption rate corresponds to the central point of the respective 1-h time interval. The feeding time (1000 hours) was given the value $t = 0$. Measurements in the same tanks with a similar procedure, but without animals (blanks), showed that the background rate of oxygen uptake due to microbial action or diffusion was statistically zero and may be ignored.

The experiments were conducted at two different temperatures: 20°C and 28°C. At 20°C, ten octopuses were measured after feeding and another six as controls; at 28°C, nine different octopuses were measured after feeding and another nine as controls. The specimens

were of both sexes, either immature or mature, according to the classification of Mangold-Wirz (1963). No juveniles, females near spawning, or spent females were measured.

Aerobic metabolism may be separated into three components: $R = R_s + R_f + R_a$, where R represents the total metabolism, R_s is standard metabolism, R_f is the specific dynamic action and R_a is the active metabolic rate associated with movement and locomotion. During experiments conducted for measuring the absolute SDA, R is measured before (superscript i) and after (superscript t) feeding, and absolute SDA, expressed as R_f^t is calculated from the difference D of the two rates:

$$D = R^t - R^i = \left(R_s^t - R_s^i\right) + \left(R_f^t - R_f^i\right) + \left(R_a^t - R_a^i\right) \Rightarrow \quad R_f^t = D - \left(R_s^t - R_s^i\right) - \left(R_a^t - R_a^i\right) + R_f^i \tag{1}$$

For the control (without feeding), the difference D_c of the two measurements, for the same time periods as for D, is:

$$D_c = {}^cR^t - {}^cR^i = \left({}^cR_s^t - {}^cR_s^i\right) + \left({}^cR_a^t - {}^cR_a^i\right) \tag{2}$$

We assume that the expected value of the difference $\left({}^cR_a^t - {}^cR_a^i\right) - \left(R_a^t - R_a^i\right)$ is zero. This assumption may be considered realistic because: (1) octopus activity that is related to experimental handling was common in both cases (“fed” and “control”); (2) the “fed” and the “control” octopuses were measured at corresponding times of the day; thus, any variation in activity metabolism related to the diurnal rhythm of the octopuses cancels out; (3) the extra activity related to feeding is a constituent of SDA (as SDA has been defined as the excess energy requirements of the behavioral, physiological and biochemical processes that constitute feeding, including capture, handling of prey and all relevant activity); thus, it is not included in the R_a terms; (4) activity during the experiments was minimal, and, if an individual showed excessive activity, it was excluded; thus, even if there was some difference in activity between the feeding experiment and the control, it would be insignificant. Thus, $\left({}^cR_a^t - {}^cR_a^i\right) = \left(R_a^t - R_a^i\right)$ and Eq. 2 becomes $D_c = \left({}^cR_s^t - {}^cR_s^i\right) + \left({}^cR_a^t - {}^cR_a^i\right) = \left({}^cR_s^t - {}^cR_s^i\right) + \left(R_a^t - R_a^i\right) \Rightarrow \left(R_a^t - R_a^i\right) = D_c - \left({}^cR_s^t - {}^cR_s^i\right)$.

Replacing $\left(R_a^t - R_a^i\right)$ from the above equation to Eq. 1, we have $R_f^t = D - \left(R_s^t - R_s^i\right) - \left[D_c - \left({}^cR_s^t - {}^cR_s^i\right)\right] + R_f^i = D - D_c + \left[\left({}^cR_s^t - R_s^t\right) + \left(R_s^i - {}^cR_s^i\right) + R_f^i\right]$.

Standard metabolism is by definition independent of feeding and the related physiological and biochemical processes. It may, however, present diurnal or seasonal variations. As R_s^t and ${}^cR_s^t$ or R_s^i and ${}^cR_s^i$, respectively, referred to the same time of the day and all measurements at the same temperature were conducted with a time lag of less than a month, it is reasonable to accept that $\left({}^cR_s^t - R_s^t\right) + \left(R_s^i - {}^cR_s^i\right) = 0$. R_f^i is zero, since the specimens were fasted for 24 h before the experiment. We thus conclude that absolute SDA expressed by R_f^t is accurately estimated by the difference $D - D_c$. All R and absolute SDA values in this study are in milligrams per hour. In this study we have also used relative SDA values, according to the relationship:

$$R_f^t = D - D_c \Rightarrow \frac{R_f^t}{R^i} = \frac{\left(R^t - R^i\right) - \left({}^cR^t - {}^cR^i\right)}{R^i} = \frac{R^t}{R^i} - \frac{{}^cR^t}{R^i} \quad \Rightarrow \quad \text{relative SDA} = \left(\frac{R^t}{R^i}\right)_{\text{fed}} - \left(\frac{R^t}{R^i}\right)_{\text{control}} \tag{3}$$

Results

At each temperature, the ratio of the R^t value of each 1-h measurement to the initial R^ibefore feeding (at $t = -0.5$ h) was calculated for each specimen. The mean of all replicate ratios at each temperature was calculated, and the same was done for the corresponding control measurements. The temporal pattern of the relative SDA was estimated as the difference of the two R^t/R^i time series (fed octopuses minus control), according to Eq. 3 (Fig. 1). At both temperatures, the peak of the SDA response occurred during the first hour after feeding, and then the increase in R gradually declined. At 20°C, the curve of the R increase was always higher than the curve of the R increase at 28°C, for a 7-h period after feeding (Fig. 2). A paired t-test was conducted between the relative SDA estimated during the 7-h period after feeding at 20°C and the corresponding relative SDA at 28°C. The relative SDA at 20°C was found to be significantly greater than that at 28°C ($n = 5, t = 4.75$, $P = 0.0045$). The peak relative SDA was 64% at 20°C and 42% at 28°C.

Least squares linear regression equations were calculated for the portion of the SDA response curves from just after feeding ($t = 1$ h) till $t = 7$ h, and the lines were

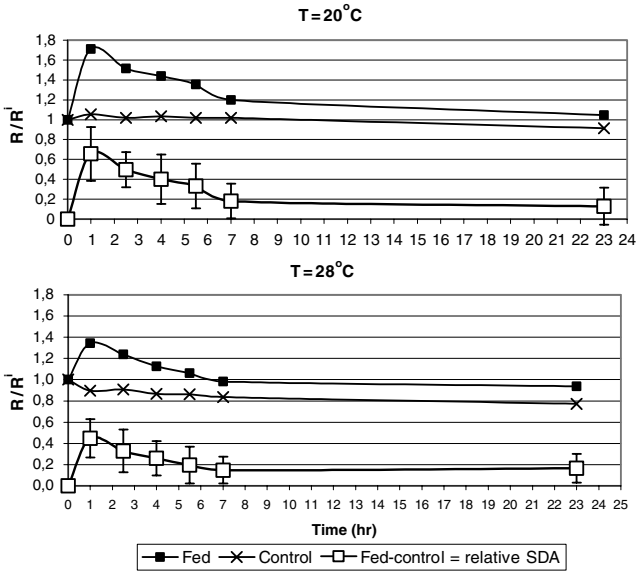

Fig. 1 *Octopus vulgaris*. Mean temporal pattern of the relative specific dynamic action (*SDA*) calculated as the difference of the R/R^i time series of “fed” and “control” animals, at the two temperatures (T, 20°C and 28°C). The error bars indicate 95% confidence intervals and for reasons of clarity are given only for the relative SDA time series

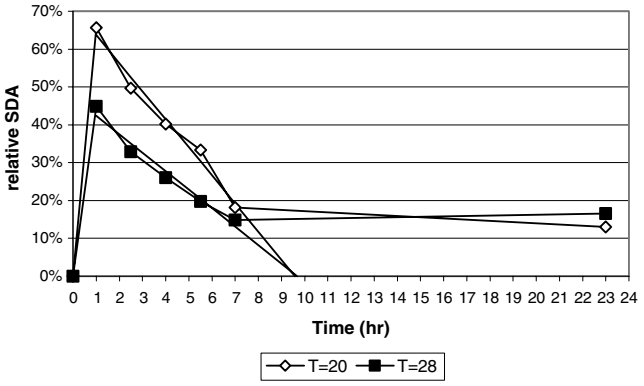

Fig. 2 *Octopus vulgaris*. Mean temporal pattern of the relative specific dynamic action (*SDA*) at the two temperatures (*T*, 20°C and 28°C), where least squares regression lines have been fitted to the data from just after feeding ($t = 1$ h) up to $t = 7$ h and extrapolated till they cut the time axis, to estimate SDA duration

extrapolated till they cut the time axis (Fig. 2). At 20°C the regression line was $y = 0.711–0.0741t$ ($R^2 = 0.98$) and at 28°C it was $y = 0.472–0.0487t$ ($R^2 = 0.97$). The regression was highly significant both at 20°C ($F = 155$, $P = 0.0011$) and at 28°C ($F = 92$, $P = 0.0024$). The slopes of the two regression lines were compared with ANOVA and differed significantly ($F = 10.5$, $P = 0.018$). At approximately $t = 9.5$ h both regression lines cut the time axis; thus, the duration of the SDA response was 9.5 h and did not differ with temperature. The 9.5-h SDA duration estimated validates the assumption made that the 24-h fasting period of the specimens is sufficient for the zeroing of $R^{\mathrm{i}}_{\mathrm{f}}$.

Defining $f_{20}(t)$ and $f_{28}(t)$ as the functions that give the relative SDA at 20°C and 28°C, respectively, we have:

$$f_{20}(t) = \begin{cases} 0.637t, & 0 < t \leqslant 1.0 \\ 0.711 - 0.0741t, & 1.0 < t \leqslant 9.6 \end{cases}$$
$$f_{28}(t) = \begin{cases} 0.423t, & 0 < t \leqslant 1.0 \\ 0.472 - 0.0487t, & 1.0 < t \leqslant 9.7 \end{cases} \quad (4)$$

Consequently, the mass-scaled SDA magnitude (I_T, at temperature T) is calculated at each temperature and for each individual as:

$$\begin{aligned} I_{20+}(\mathrm{mg}) &= \int_0^{9.6} (\text{mass - scaled absolute SDA})\mathrm{d}t \\ &= \int_0^{9.6} R^{i(0)} \cdot f_{20}(t) \cdot \mathrm{d}t \\ &= R^{i(0)} \cdot \left[\int_0^{1.0} 0.637t\mathrm{d}t + \int_{1.0}^{9.6} (0.711 - 0.0741t)\mathrm{d}t \right] \\ &= 3.06 \cdot R^{i(0)} \end{aligned} \quad (5)$$

and

$$\begin{aligned} I_{28}(\mathrm{mg}) &= \int_0^{9.7} (\text{mass - scaled absolute SDA})\mathrm{d}t \\ &= \int_0^{9.7} R^{i(0)} \cdot f_{28}(t) \cdot \mathrm{d}t \\ &= R^{i(0)} \cdot \left[\int_0^{1.0} 0.423t\mathrm{d}t + \int_{1.0}^{9.7} (0.472 - 0.0487t)\mathrm{d}t \right] \\ &= 2.05 \cdot R^{i(0)} \end{aligned} \quad (6)$$

where $R^{i(0)} = R^i / M^{0.901}$ is the mass-scaled R^{i}, using the value $b = 0.901$ as the scaling factor (Katsanevakis et al. 2004). The mean I_{20} and the mean I_{28} were compared (*t*-test), and they did not differ significantly ($t = 1.67$, $P = 0.11$).

Absolute SDA peaks (the absolute difference between peak R after feeding and R^{i}) have been calculated for each individual, control corrected, and divided by $M^{0.901}$ to remove the effect of mass. The means at the different temperature levels of these mass-standardized absolute SDA peaks (± standard deviation) were 0.108 ± 0.054 mg h^{-1} at 20°C and 0.118 ± 0.048 mg h^{-1} at 28°C, and there was no significant difference ($t = 0.41$, $P = 0.69$).

Discussion

Even short-term starvation for a couple of days induces a decline in the R of *Octopus vulgaris* (Boucher-Rodoni and Mangold1985). Therefore, the decline in the control time-series, at both temperatures, on $t = 23$ h is mainly due to the ~2-day starvation period of the octopuses (since the previous morning, before the start of the experimental procedure). Thus, the values of the relative SDA on $t = 23$ h were probably biased, and the values of Ron $t = 23$ h are not expected to be significantly higher than those of R^{i}. For this reason, the regression lines were considered more reliable in describing the SDA temporal pattern after the peak and up to full recovery of the initial oxygen consumption rate on $t \approx 9.5$ h; thus, the SDA magnitude was calculated using the regression lines.

The absolute SDA peak, the time to reach this peak and the magnitude and duration of the SDA response did not differ significantly between the two temperatures, 20°C and 28°C. The magnitude of the SDA reflects the energy requirement of all the behavioral, physiological and biochemical processes involved in feeding. As there is no difference in SDA magnitude between 20°C and 28°C, it is deduced that at both temperatures, octopuses spent the same amount of energy to capture, handle, ingest, digest and assimilate their prey. Independence of the SDA magnitude on temperature has also been reported for other

ectotherms, such as the Burmese python *Python molurus* (Wang et al. 2003), the marine toad *Bufomarinus* (Secor and Faulkner 2002), the toad *Ceratophryscranwelli* (Powell et al. 1999) and the plaice*Pleuronectesplatessa* (Jobling and Davies 1980). In contrast a dependence of the SDA magnitude on temperature has been reported for several ectotherm species, like the snake *Boa constrictor amarali* (Toledo et al. 2003), the Baltic isopod*Saduriaentomon* (Robertson et al. 2001a) and the shore crab*Carcinusmaenas* (Robertson et al. 2002). Octopuses not only spend the same amount of energy at the experimental temperatures, but they do it at the same speed (equal SDA durations) and with the same intensity (equal absolute SDA peaks). Thus, the efficiency of digestion was the same at both temperatures.

When temperature falls from 28°C to 20°C, the routine oxygen consumption rate of octopus is reduced by 37% (Katsanevakis et al. 2004). Consequently, for the same absolute increase in R, there has to be a greater relative increase in R at 20°C than at 28°C. Thus, the greater relative SDA values, found for 20°C compared to 28°C, are logical in view of the constant SDA magnitude and duration.

The energy balance equation representing the energy flow through the octopus (Wells and Clarke1996) is $C = P + G + E + U + F$, where C is the total energy content of the food consumed,$P$and G are the energy equivalents of somatic and gonadal growth, respectively, E is the energy utilized in respiration, U is the energy lost as nitrogenous and other waste compounds excreted in the urine and F is the unabsorbed energy released with the feces. As $E = E_s + E_f + E_a$ (total energy for respiration = energy for standard metabolism + SDA magnitude + energy associated with movement and locomotion), the energy equation becomes $(P + G) = C - E_s - E_f - E_a - U - F$, where the sum $P + G$ represents the energy available for growth. Comparing $P + G$ for the two temperature levels of this study and taking into account that: (1) C was standardized (3% of weight in every case), (2) it was found that E_f does not differ significantly between the two temperatures, (3)U is $< 2\%$ of the ingested energy for a growing octopus (Wells and Clarke 1996) and, for a first approximation, may be ignored, and (4) it can be reasonably assumed that F is not largely affected by temperature, then $(P + G)_{20} - (P + G)_{28} = -(E_s + E_a)_{20} + (E_s + E_a)_{28}$.

Standard metabolism at 28°C is approximately 37% greater than that at 20°C (Katsanevakis et al. 2004). Furthermore, octopuses are more active at 28°C than at 20°C. Thus, $(E_s + E_a)_{28} > (E_s + E_a)_{20}$and, consequently, $(P + G)_{20} > (P + G)_{28}$. Even if the assumption of approximately constant F is not true, it does not affect the result, as F is $< 8\%$ of ingested energy, while E_s accounts for approximately 21% of ingested energy for a growing octopus (2% body mass per day) and for approximately 70% of ingested energy for an octopus maintaining its weight (Wells and Clarke1996).

Thus, when octopuses consume a constant ration, a temperature of 20°C favors growth in relation to a temperature of 28°C. Put differently, in order to achieve the same growth rate at 28°C, an octopus has to consume larger quantities of food than at 20°C. Within the normal range of its temperature adaptation, *O.vulgaris* eats more at high than at low temperatures (Mangold1983). Such increased demand for food at high temperatures is not always easily satisfied, especially in soft sediment areas where the food availability is a significant constraint on the distribution of *O.vulgaris* (Katsanevakis2004) and especially for large octopuses that have greater energy requirements. In the summer, large octopuses in soft sediment areas migrate from shallow areas (with temperatures of approximately 28°C) to deeper areas (with temperatures < 25°C), and remain there until the breakdown of the thermocline in autumn (Katsanevakis and Verriopoulos 2004). This migration of large octopuses during the hot season might be due to the lower energy requirements at lower temperatures.

The fact that a temperature of 20°C favors growth in relation to a temperature of 28°C, when the available food is restricted, is largely because of the equity of the SDA magnitude between the two temperatures. In certain cases, higher temperatures are an advantage; for example, in *Boa constrictor amarali* the energy allocated to SDA was greater at 25°C compared to 30°C, indicating that a postprandial thermophilic response could be an advantage for the species, by improving digestive efficiency (Toledo et al. 2003).

The 1-h time interval to reach the peak SDA and the 9.5-h SDA duration that were found for *O. vulgaris* belong to the lower end of the range for temperate species. Wells et al. (1983) estimated a similar short SDA duration for one *O.vulgaris* specimen. In fish, the peak usually occurs within 12 h after feeding, with a duration of 24–36 h (Jobling1981). In the crab*Carcinusmaenas*, the peak occurred 3 h after a meal, and the SDA duration was < 24 h (Houlihan et al. 1990).*Cancer pagurus* reached the peak in R 6–9 h after feeding and returned to its pre-fed value after 24 h. The southern rock lobster*Jasusedwardsii*reached its peak SDA after 10–13 h and needed 42 h to return to the pre-feeding levels (Crear and Forteath2000). Species living at the permanently low temperatures of polar regions experience very extended SDA responses, with durations of 18–20 days being common (Peck 1998; Whiteley et al. 2001). The short SDA response of *O.vulgaris* is an indicator of its ability to digest and assimilate food rapidly and efficiently. Indeed, the growth rates of cephalopods, and octopuses in particular, are remarkably high. The daily relative growth rates of *O.vulgaris* exceeded 10% just after settlement (Itami et al. 1963) and, for the mass range of 100–1000 g at 20°C, were 1.14–5.08% (Mangold and vonBoletzky1973). These growth rates would not be possible with a lengthy and/or inefficient digestion process. On the contrary, polar species with lower activity, lower rates of oxygen uptake, lower growth rates and relative longevity have extended SDA responses (Whiteley et al. 2001).

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