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The effect of temperature on the inhalant siphon regeneration of *Amiantis purpurata* (Lamarck, 1818) (Bivalvia; Veneridae)

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ORIGINAL ARTICLE

The effect of temperature on the inhalant siphon regeneration of *Amiantis purpurata* (Lamarck, 1818) (Bivalvia; Veneridae)

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Abstract

The purple clam *Amiantis purpurata* inhabits intertidal and shallow subtidal platforms from San Matías Gulf, Argentina to Santa Catarina, Brazil. This edible bivalve is an important component of the marine trophic webs due to siphon nipping. The present study investigates the influence of temperature on the regeneration of the inhalant siphon tentacle crown of *A. purpurata*. Under laboratory conditions 140 purple clams were exposed to four different temperatures (12, 15, 20 and 22°C). At each temperature, the distal 0.5 cm of the inhalant siphon was removed from each clam. The length of long tentacles from each group was measured on different days until the tentacles had reached asymptotic growth. Four candidate models were used for each tentacle data set for growth at the four experimental temperatures. The data were fitted to size-increments for the long siphon at different temperatures using maximum likelihood. The von Bertalanffy model was the one that best fitted the data at most experimental temperatures. To evaluate differences in tentacle regeneration in each treatment, the growth parameters were compared using a likelihood ratio test. The two interdependent parameters affecting the regeneration process k (growth constant) and t_{ip} (inflection point), were clearly influenced by temperature. In the case of k , increasing temperature produces acceleration in the regeneration process while t_{ip} is not dependent on temperature. Regeneration was slower than in any other species previously reported in the literature and decreasing temperature slowed down the process.

Key words: Purple clam, siphon cropping, south-western Atlantic, regeneration, inhalant siphon

Introduction

Recent findings have demonstrated the importance of temperature in the physiology and ecology of some organisms (e.g. Somero 2002; Dahlhoff 2004; Hofmann 2005). Temperature is one of the main factors affecting growth. This effect is more evident in aquatic organisms than in terrestrial ones due to the large thermal capacity of water (Clarke & Johnston 1999). For example, it has been reported for zooplankton (Van As et al. 1980), fish (e.g. Cox & Coutant 1981; Zdanovich 1999; Konstantinov et al. 2003), shrimps (e.g. Miao & Tu 1993, 1996) and starfish (Sanford 2002) that within low temperature ranges, small temperature increments have

a positive effect on growth, while at high temperatures, it has a negative effect.

In the case of marine infauna, growth rates and the abiotic variables that modulate them, such as temperature, can be very important as regeneration due to predation or defensive autotomy (i.e. cropping or nipping) (e.g. Pekkarinen 1984; Riera 1995; Luzzatto & Penchaszadeh 2001) can be temperature-dependent. Examples of these are found in the siphons of clams (Edwards & Steele 1968; Peterson & Quammen 1982; De Vlas 1985; Ansel et al. 1999), arms of brittlestars (Bowmer & Keegan 1983; Stancyk et al. 1994), and tentacles and tails of worms (De Vlas 1979a,b; Woodin 1982; Clavier 1984; Zajac 1985). However, the regeneration

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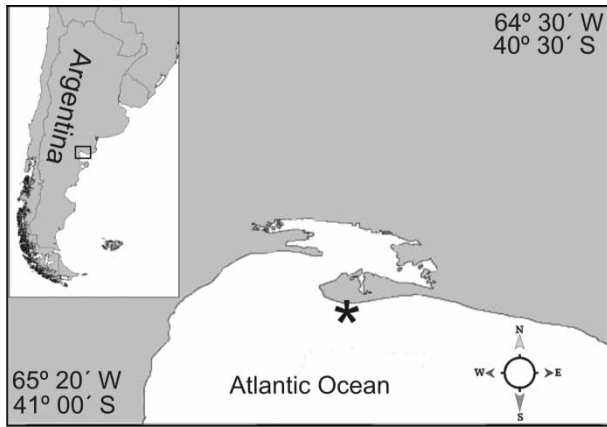


Figure 1. Map of Argentina showing the sampling site (black star).

processes occur at the expense of a reduction in somatic growth and reproduction, which in turn affects fitness (Peterson & Quammen 1982; Kamermans & Huitema 1994; Irlandi & Mehlich 1996).

In particular, clam siphon nipping can have deleterious effects, as behavioural modifications (Cledón & Nuñez 2010) such as weight loss and reduction in overall health may increase the risk of subsequent lethal predation of clams (e.g. Skilleter & Peterson 1994; Zwarts et al. 1994; De Goeij & Luttikhuisen 1998). Thus, the time period needed by the clam to regenerate the siphon can be important for its survival, and temperature could be an important abiotic factor modulating the speed of those processes. One study on the effect of temperature on bivalve siphon regeneration is by Tomiyama & Ito (2006), but no study has been carried out on its effect on siphon tentacle regeneration. Tentacles are structures that play important roles in nutrition, reproduction and defence (Zwarts & Wanink 1989; Jeffrey et al. 1999).

An example of clams subjected to siphon nipping is the purple clam *Amiantis purpurata* (Lamarck, 1818). This clam inhabits intertidal and shallow subtidal sandy bottoms along the Atlantic coast of South America, from 20°S to 41°S (i.e. the biogeographic province of Argentina; Scarabino 1977; Ríos 1994). It is known to be a long-lived (more than 40 years old) and slow-growing species (Morsan & Orensanz 2004). In the northwestern San Matías Gulf, the southernmost boundary of its geographic distribution, the purple clam has an unusually abundant population, located at 4–10 m depth (Morsan 2003) and is economically important because it supports an artisanal fishery. *A. purpurata* is subjected to sub-lethal predation (i.e. siphon nipping) by the electric ray *Discopyge tschudii* (Arrighetti et al. 2005) and probably by other benthic fishes.

In this context, the aim of the present work is to investigate the process of siphon regeneration of

A. purpurata and its relationship to temperature. To achieve this, the inhalant siphons were artificially cropped and the regeneration process was followed at different temperatures.

Materials and methods

The clams were collected at the intertidal zone of La Conchilla (40°49'51"S–64°51'54"W), a sandy beach located in the proximity of San Antonio Bay (NW of San Matías Gulf, Argentina; Figure 1). The average tidal amplitude at the sampling site is 7.62 m (maximum 9.2 m), which results in a beach 450–600 m wide during low tides, facilitating sampling. Sediment is predominantly fine sand, with patches of shell hash. The water temperature ranges, on average, from 10°C in August (winter) to 18.2°C in January (summer) at 20 m depth (Morsan et al. 2010).

Regeneration descriptions

Individuals of *Amiantis purpurata* were collected by hand during low tide in March 2009 and transported to the laboratory in an icebox filled with fresh wet sand collected at the same time to minimize stress. In order to standardize the clam size, only individuals with shell length ranging between 60 and 70 mm were used. Moreover, only the clams with black tentacle tips were collected because the presence of pigment indicates that tentacles are complete. Before starting the experiments, 10 randomly chosen clams were used to study the external structure of the filtering tentacles crown of the inhalant siphon. The clams were sacrificed and the siphons were removed and fixed in 5% formaldehyde. The number and disposition of long and short tentacles were observed under stereomicroscope. The structure determination allowed us to establish the relevant morphological characters in which we based the experiments before artificial nipping.

In order to evaluate the effect of temperature on siphon regeneration rates, four treatments were carried out in the laboratory (Table I). Four groups consisting of 35 clams each (total $n = 140$) were

Table I. *Amiantis purpurata* experimental design.

Group	Temperature (°C)	Conditions		N	Mortality
		(treated or control)			
G1	22	Cut (treated)	30	5	
		Not cut (control)	5	0	
G2	20	Cut (treated)	30	1	
		Not cut (control)	5	0	
G3	15	Cut (treated)	30	0	
		Not cut (control)	5	0	
G4	12	Cut (treated)	30	4	
		Not cut (control)	5	1	

placed separately in aquaria of (60 l) with half of the volume filled with sand at 22, 20, 15 and 12°C, respectively, and half with aerated seawater (extracted by an electric pump directly from the sea).

During the experimentation the individuals were fed ad libitum with a mixed phytoplankton culture (*Nannochloropsis oculata* and *Tetraselmis suecica*). Before starting the experiments the clams were maintained for acclimation under these conditions for 2 days. Water temperature was measured with an alcohol thermometer to the nearest 1°C, and salinity with a refractometer to the nearest 1 ppm.

Sartori et al. (2008) pointed out the importance of relaxation before treatment to avoid siphon shape change. In order to avoid tentacle retraction and prior to the removal of the siphon tip, the purple clams were relaxed in low-oxygen seawater with a solution of MgCl₂ (see Miloslavich et al. 2004). Taking into consideration that long tentacles grow until regeneration is completed, their length was used as an indicator of siphon regeneration (Nuñez et al. 2010). In each treatment, the distal 0.5 cm of the inhalant siphons of 30 individuals was removed using surgical scissors while 5 individuals were kept as controls.

A detailed observation and description of inhalant siphon sequence regeneration in all temperature was made under a stereomicroscope. We chose the lowest temperature (12°C) treatment to illustrate the regeneration process due to the fact that at this temperature the main events of the process are markedly separated, making them easy to observe. This was done by scanning electron microscopy (SEM). Samples were fixed in 2.5% glutaraldehyde solution for up to 24 h. Then they were preserved in buffer cacodylate (Na 0.1 M, pH 7.2) at 4°C until processing. Tissue dehydration was carried out by transfer through a series of ethyl alcohol solutions of increasing concentration. From 30% to 60% alcohol, tissues were dehydrated in increasing concentrations of 10% and were left in each solution for 10 min. In 70%, 80%, 90% and 95% alcohol the tissues were left for 15 min and lastly were transferred into two changes of absolute alcohol (100%). Then the samples were metallized with Ag/Pd in a Denton Vacuum Desk II metallizer. The analyses were carried out with a Jeol JSM 6460LV microscope in the Electronic Microscopy Laboratory at the Universidad Nacional de Mar del Plata, Argentina.

Long tentacles growth

The length of five tentacles of three individuals from each experimental group was measured under stereomicroscope every 2 days until the 18th day at 22 and 20°C, and 22 days at 15°C, when the tentacles reached asymptotic growth. In the case of

Table II. Alternative growth models fitted to size-at-day regeneration data of *Amiantis purpurata*. L_s is the tentacle siphon length (mm) at time t , L_m the mean asymptotic long tentacle size (mm), k is a growth constant (day⁻¹), t_{ip} is the time when the tentacle size reaches the half of asymptotic size and represents the inflexion point of the model. d is the shape parameter for the Richards model.

Model	Equations	Model/source
m_1	$L_s = L_m * (1 - e^{-k*(day-t_{ip})})$	von Bertalanffy (1938)
m_2	$L_s = L_m / (1 + e^{-k*(day-t_{ip})})$	Logistic (Ricker 1975)
m_3	$L_s = L_m * \exp(-e^{-k*(day-t_{ip})})$	Gompertz (1825)
m_4	$L_s = L_m / (1 + e^{k*(day-t_{ip})})^{1/d}$	Richards (1959)

the 12°C treatment, the measurement days were 2, 4, 8, 14, 16, 20, 22, 28, 34 and 36, because for this temperature the regeneration process was slower than for the other experiment temperatures. The five tentacle measurements of each individual were averaged and used to fit a growth model. To avoid autocorrelation of data, each individual was used for only one event measurement.

To identify a growth model that best fitted the data, a set of four candidate models was used for each data set of tentacle growth at the four experimental temperatures (i.e. von Bertalanffy 1938; Gompertz 1825; Richards 1959; and Logistic (Ricker 1975), referred to as m_1 – m_4 , respectively; Table II). These models were fitted to regeneration data at different temperatures using maximum likelihood. Statistical analyses were conducted in R 2.13.0 (R Development Core Team 2011). We used the library bbmle (Bolker 2011) to find parameter values maximizing the likelihood and the profile likelihood to generate 95% confidence intervals or regions to each estimated parameter. The Akaike information criterion (AIC; Akaike 1973) was used to assess model performance. The model with the smallest AIC value was chosen as the model that ‘best’ represented the growth pattern observed in the regeneration data. In addition, we computed Akaike’s weight (w) (Franklin et al. 2001). The weights ranged between 0 and 1 and are interpreted as the weight of evidence in favours of model i as the best model among the set of all candidate models examined (Burnham & Anderson 2002). The von Bertalanffy model (m_1) was the one that best fitted the data except for 12°C (Table III), where the logistic model was the one better supported. Nonetheless, we use von Bertalanffy for all temperatures taking into consideration that differences between AIC weights were minimal, and it allowed comparison between them. Then, in order to evaluate differences in tentacles regeneration rate at each temperature, the growth parameters of von Bertalanffy were compared using likelihood ratio test (Kimura 1980; Cerrato 1990). This method allows

Table III. *Amiantis purpurata*. Results of model selection for the respective long tentacles regeneration in each temperature. No. par_i, number of parameters, Akaike's information criterion (AIC_i), Akaike differences (Δ_i), normalized weights of AIC (w_i %).

Temperature	Models	No. par _i	AIC _i	Δ_i	w_i (%)
22	m_1	3	-26.40	0	34
	m_2	3	-26.09	0.308	29
	m_3	3	-26.13	0.263	29
	m_4	4	-23.24	3.168	0.7
20	m_1	3	-27.15	0	31
	m_2	3	-27.15	0.003	30
	m_3	3	-27.05	0.099	3
	m_4	4	-24.14	3.001	0.7
15	m_1	3	-34.70	0	70
	m_2	3	-31.57	3.125	14
	m_3	3	-31.13	3.564	11
	m_4	4	-28.36	6.339	0.3
12	m_1	3	-27.95	0.391	28
	m_2	3	-28.34	0	34
	m_3	3	-28.08	0.267	30
	m_4	4	-25.26	3.081	0.7

the testing of several hypotheses to compare two curves by analysing one or more growth parameters simultaneously as detailed in the results section.

Results

Regeneration descriptions

The siphons of purple clams are fused along their entire length. They are white with a distinctive dark tentacular crown on the tip. The aperture of the inhalant siphon is flanked by around 30 short tentacles and interspersed with 20 long tentacles (Figure 2).

After removal of the distal end of the siphon, the first rudiments of the long tentacles began developing on the second day in all experiments. Short tentacles start developing at the sixth day of regen-

eration at 22°C and 20°C, the eighth day at 15°C and the twelfth day at 12°C (Figure 3).

Long tentacles growth

The von Bertalanffy models of all treatments are shown in Figure 4 and the estimated parameters are summarized in Table IV. The 95% confidence intervals were determined by a one-dimensional likelihood profile for all parameters. The confidence intervals (CI) of infinite length of the long tentacle (Lm) confidence levels did not overlap in any experimental temperatures, and the likelihood ratio test (LRT) comparisons did not show significant differences (Table V). In the case of inflexion points of the models (t_{ip}), they were highly variable between temperatures (Table IV). The CI of 15°C did not show overlap with 20°C and 12°C, and this did not show overlap with 22°C. The CI of other temperatures overlapped. The LRT comparisons were concordant with CI estimation (Table V). Here we found significant differences between 20–15 and 15–12°C. Therefore, the t_{ip} did not show a dependent relation with temperature (Figure 5).

In the case of k , only the CI at 12°C did not show overlap with all other temperatures. The LRT comparisons were concordant with CI estimations (Table V). Significant differences between experiments at 12°C and all other temperatures were found. The k showed a negative relation with temperature (Figure 6). This last relationship shows that at high temperature, the regeneration process is more accelerated and, therefore, tentacles grow faster.

Estimated growth curves were significantly different for the hypothesis of three identical parameters at all temperatures (Ho4, $p < 0.01$, Table V).

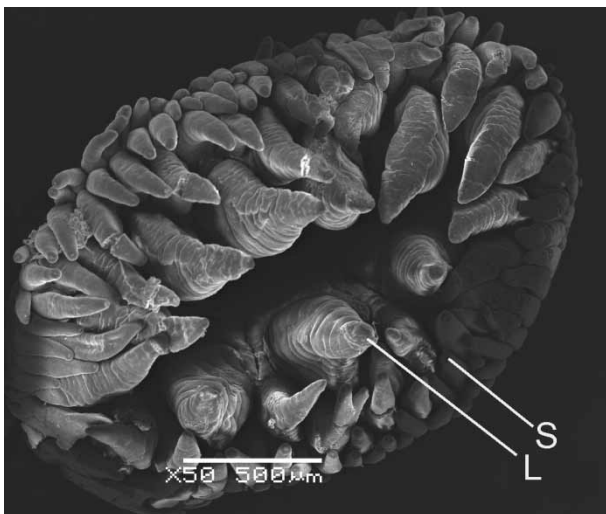


Figure 2. *Amiantis purpurata*. Crown of tentacles at the tip of the inhalant siphon. L, long tentacles and S, short tentacles.

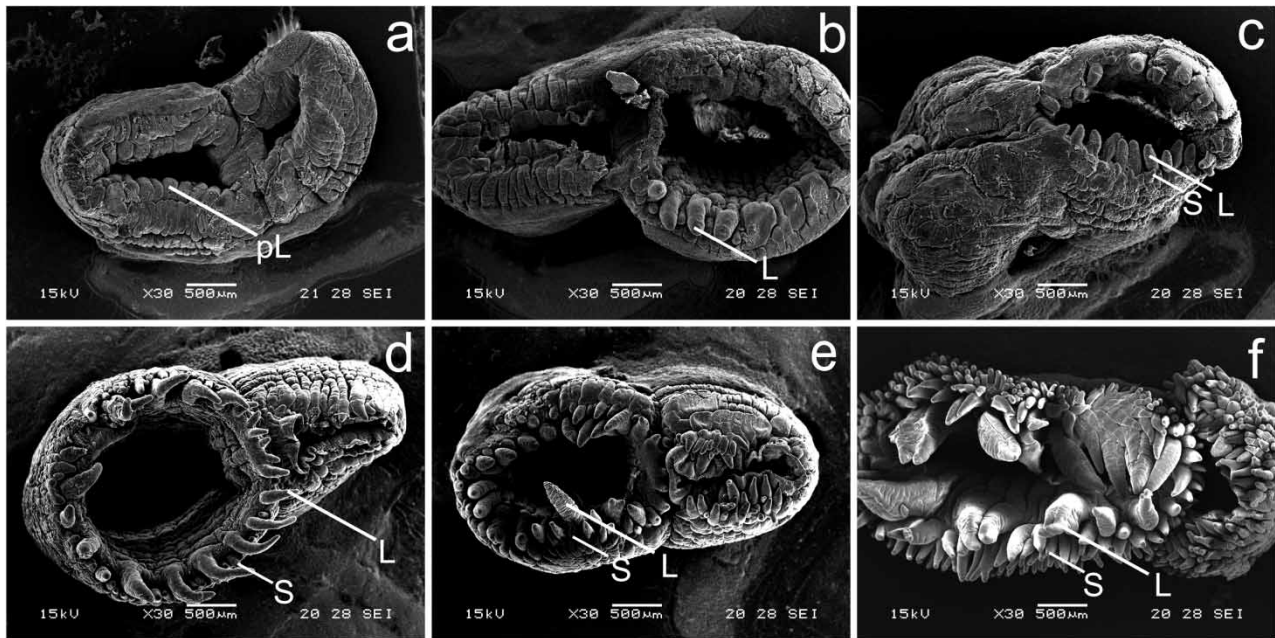


Figure 3. *Amiantis purpurata*. Schematic sequence of regeneration of the tentacle crown at 12°C. (a) Two days after amputation, (b) 8 days after amputation, (c) 12 days after amputation, (d) 18 days after amputation, (e) 28 days after amputation, (f) 36 days after amputation. Long tentacle primordium (pL), long tentacles (L), short tentacles (S).

In relation to time of regeneration, at 22, 20 and 15°C, clams completed the regeneration approximately within 22 days, but at 12°C it took longer (i.e. 36 days approximately).

Discussion

Regeneration descriptions

The time that *Amiantis purpurata* needed to complete the regeneration process was longer than

reported for other bivalve species. For example, *Donax hanleyanus* at 21±1°C needed 10 days to complete siphon regeneration (Luzzatto & Penchaszadeh 2001), while *A. purpurata* at 20 and 22°C needed 20–22 days. *Donax denticulatus* at 23°C needed 5 days (Miloslavich et al. 2004), while *A. purpurata* at 22°C needed 22 days. *Mesodesma macroides* at 10±3°C needed between 16 and 18 days while *A. purpurata* 36 days, and at 16±3°C needed 10–12 days (Nuñez et al. 2010), while *A.*

Table IV. *Amiantis purpurata*. Maximum likelihood parameter estimates and 95% confidence limits corresponding to von Bertalanffy function model, into the brackets the lower and upper interval of confidence.

Temperature (°C)	Parameters		
	L_m	k	t_{ip}
22	1.05 (0.98–1.16)	0.07 (0.058–0.079)	–0.05 (–0.36 to 0.24)
20	1.04 (1.00–1.08)	0.065 (0.061–0.070)	0.22 (0.09–0.36)
15	1.04 (0.96–1.16)	0.054 (0.045–0.064)	–0.7 (–1.11 to –0.31)
12	0.97 (0.95–0.99)	0.036 (0.035–0.037)	0.42 (0.32–0.52)

Table V. *Amiantis purpurata*. Comparison of growth parameters estimated from size-increment long siphon data at each temperature by likelihood ratio test. (θ), L_m , k , t_{ip}

Comparison	Temperature (°C)	H_{o1}	H_{o2}	H_{o5}	H_{o4}
		$L_{m1} = L_{m2}$	$k_1 = k_2$	$t_{ip1} = t_{ip2}$	$\theta_1 = \theta_2$
Likelihood ratio test	22–20	n.s.	n.s.	n.s.	< 0.001
	22–15	n.s.	n.s.	n.s.	< 0.001
	22–12	n.s.	< 0.05	< 0.05	< 0.001
	20–15	n.s.	n.s.	< 0.05	< 0.001
	20–12	n.s.	< 0.001	n.s.	< 0.001
	15–12	n.s.	< 0.05	< 0.05	< 0.001

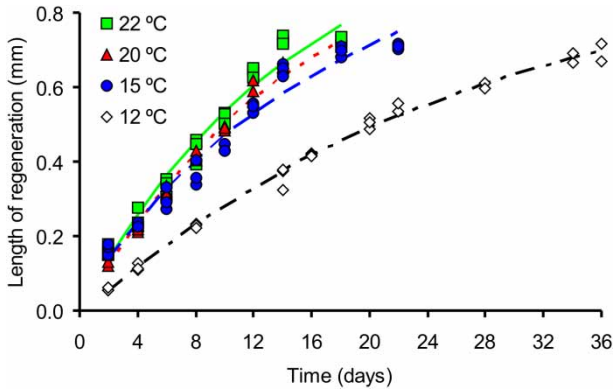


Figure 4. *Amiantis purpurata*. Regeneration rate of the long tentacles of the inhalant siphon. The line corresponds to adjusted von Bertalanffy growth function, different type line correspond to different temperatures.

purpurata for the same temperature range needed between 16 and 20 days. Moreover, we also observed that although *A. purpurata* tentacles initiated their development one day after ablation, the same as other bivalves such as *D. haleyamus* (Luzzatto & Penchaszadeh 2001), *D. denticulatus* (Miloslavich et al. 2004) and *M. mactroides* (Nuñez et al. 2010), the initial regeneration of short tentacles occurs between 3 and 5 days later than the latter-mentioned species. Thus, *A. purpurata* should need longer time periods in order to normalize the functioning of its siphon and the processes related to it.

The siphons of bivalves are responsible for important activities such as breathing, feeding, and defecation, while the tentacular crown is responsible for filtering large particles. Therefore, its ablation can have a direct impact on these activities. In fact, low regeneration rates during the initial days after ablation is the cause of physiological adequation needed to repair the tissue, since the regeneration itself is an energy consuming process (Hodgson 1982). Moreover, there is also evidence that the

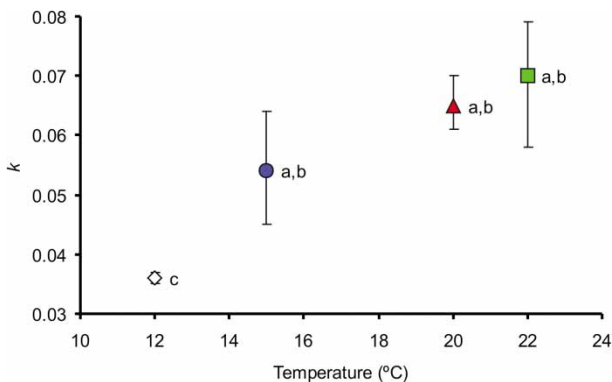


Figure 5. *Amiantis purpurata*. Maximum likelihood estimate of k (growth constant) at different temperatures. The bars indicate 95% confidence intervals. Different letters indicate significant differences.

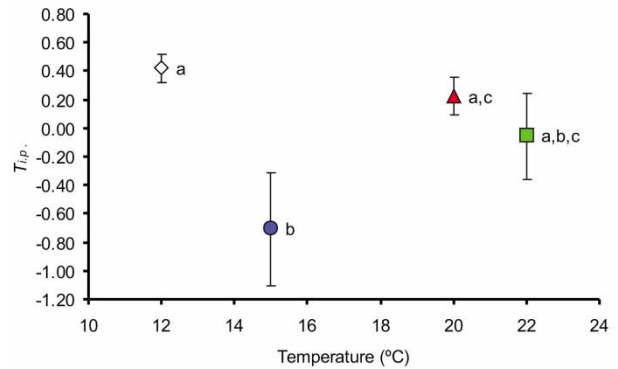


Figure 6. *Amiantis purpurata*. Maximum likelihood estimate of t_{ip} (inflexion point) at different temperatures. The bars indicate 95% confidence intervals. Different letters indicate significant differences.

regeneration of lost body parts requires the allocation of resources than otherwise would have gone to other physiological processes (Maginnis 2006). In that sense, there is much evidence of bivalve siphons malfunctioning after amputation. For example in *D. denticulatus* large particles (700 μm) were found in the mantle cavity after siphon amputation (Wade 1969). This forced the organism to invest effort in extracting the particles from the mantle, and in turn caused the temporary suspension of feeding activity (Wade 1969). In a case in *Macoma balthica*, siphon muscles contracted to close the wound just after amputation, preventing the loss of haemolymph, as well as the water flowing through the siphons (Pekkarinen 1984). In this context, the regeneration process and siphon malfunctioning of *A. purpurata* could also imply a physiological cost and have negative effects on physiological characters such as somatic growth, feeding and defecation. This could be exacerbated by the fact that this clam needs longer time periods than other species to regenerate the siphon. These issues should be evaluated in future works, through the study of filtration rates and growth of normal and siphon-clipped individuals.

Long tentacles growth

In this study, we found that at high temperatures the regeneration process is more accelerated than at low temperatures, and in turn the tentacles grow faster. In general terms there have been few studies evaluating the abiotic and biotic variable effects on regeneration speed. For example, Tremblay (1740, cited in Emmel 1905) reported that hydra heads could regenerate faster in warmer weather, and Spallanzani (1768, cited in Dinsmore 1996) showed that nutrient limitation could alter rates of regeneration. To our knowledge, there is only one previous work dealing with the regeneration of siphons at

different temperatures. In that work, a similar temperature effect on the siphon regeneration process as in our work was reported for the bivalve *Nuttallia olivacea* (Tomiyama & Ito 2006).

As mentioned before, the purple clams regenerated the tentacles more slowly than other studied bivalve species. This could be related to the fact that the purple clam is a slow-growing, long-lived organism (Morsan & Orensanz 2004). In fact, considering the von Bertalanffy size–age growth function, k , as an indicator of a physiological response to growth, its range of values was estimated between 0.09 and 0.2 year⁻¹ (Morsan & Orensanz 2004), being much lower than that estimated for donacids (k among 0.4–0.9 year⁻¹; Vélez et al. 1985; Defeo 1996; Cardoso & Veloso 2003; Herrman et al. 2009), *M. mactroides* (k among 0.3–0.9 year⁻¹; Defeo et al. 1992a,b; Fiori & Morsan 2004) and *M. balthica* (k among 0.37–0.4 year⁻¹; Caddy 2010). Thus, the siphon regeneration rate could be related to the low somatic growth rate.

Exposure to suboptimal environmental conditions may induce physiological changes in an organism that increase its ‘cost of living’ (Somero 2002). In a natural context, at the sampling site, the surface seawater temperature goes below 15°C from autumn to spring, reaching 8°C in winter. Taking into consideration low winter temperatures, siphon regeneration should slow down during this season. The latter could cause important physiological impairment, exacerbated even more by the fact that during winter, siphon nipping occurs at higher rates by the fish *Discopyge tschudii* (Spath 2010)

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