

Burrowing behavior of an infaunal clam species after siphon nipping



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ABSTRACT

Burial depth plays an important role in the life of many infaunal clam species. For these organisms, the most effective defense against predation is to bury into the sediment, which hinders the detection and manipulation of predators. In laboratory conditions, we examined *Mesodesma mactroides* normal burial depth recovery after two artificial siphon nipping levels (1 cm and 5 cm). The 1 cm siphon nipping experiment was repeated in winter and spring to evaluate if burial depth recovery differs between seasons. The data of normal burial depth (uncut clams) were fitted using linear mixed-effects models, and the data of burial depth recovery (cut clams) were analyzed using non-linear mixed-effects models. In the latter case, three candidate models were tested with each depth data set to explain the normal burial depth recovery at the two cut levels and seasons. The logistic model best explained the recovery of normal burial depth after siphon nipping in *M. mactroides*. The normal burial depth (uncut clams) did not vary among the studied seasons (winter and spring). On the other hand, there was a synergic effect between seasonality and siphon nipping on clam normal burial depth recovery, being faster in spring than in winter. Lastly, the clams with 5 cm siphon nipping had a delay in recovering the normal burial depth in comparison to clams with 1 cm siphon nipping. Thus, our results show that the temporal window of lethal predation risk could increase according to the level of siphon nipping and the season in which occurs.

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1. Introduction

Burial depth plays an important role in many infaunal clam species. Although these organisms have hard shells, their most effective defense against predation is to bury into the sediment, which hinders the detection and manipulation by predators (e.g., Mouritsen, 2004; Pape-Lindstrom et al., 1997; Seitz et al., 2001). Thus, the deeper the clam burrows, the lower its probability to be caught by predators (e.g., Meyer and Byers, 2005; Seitz et al., 2001; Whitlow et al., 2003).

Several factors may constrain the capability of clams to bury into the sediment (Byers, 2002; Seitz et al., 2001, 2003; Tallqvist, 2001). For instance, habitat characteristics (e.g., water temperature, algal mats, and sand grain) may determine the depth of burrowing in several clam species (e.g., Auffrey et al., 2004; Lardies et al., 2001; Tallqvist, 2001). However, burial depth in clam individuals is primarily limited by the length of the clam's siphons (Meyer and Byers, 2005). Siphons must reach the sediment surface to obtain oxygen and suspended particles from the water; thus, their length ultimately determines the depth that clam attain inside the sediment (de Goeij et al., 2001; Zwartz et al., 1994).

The yellow clam, *Mesodesma mactroides*, is an endemic infaunal species of sandy beaches from Santos Bay in southern Brazil to the mouth of Río Negro in Argentina (de Castellanos, 1970). This species was formerly considered among the most common bivalves at the South American beaches (Defeo, 1989) and an important economic

resource in Argentina (Coscarón, 1959). However, a dramatic population decline led to an extraction ban in 1958 (Olivier and Penchaszadeh, 1968). Currently, *M. mactroides* is considered an endangered species (Fiori and Cazzaniga, 1999), and although harvest prohibition is still in force today, the stock has never recovered. In addition to tourism (Bastida et al., 1991) and illegal extraction by fishermen (Ortega et al., 2012), *M. mactroides* have suffered massive mortality events (Fiori and Cazzaniga, 1999; Fiori et al., 2004; Odebrecht et al., 1995; Thompson and Sánchez de Bock, 2007). These would be related to climatological anomalies (Ortega et al., 2012), which modified the abundance of this species and consequently accentuate the stock recovering problems (Fiori et al., 2004; Ortega et al., 2012).

As a dissipative beach bivalve species, *M. mactroides* present features like large size, low densities, and relative fast burrowing rate that correspond to an environment of low swash pressure (McLachlan et al., 1995). Furthermore, the yellow clam is a seasonal migratory species (Coscarón, 1959; McLachlan et al., 1996); at the end of the austral spring clam, individuals colonize the intertidal zone of the sand beaches where lives until the end of the autumn. Then clams return to the shallow subtidal, staying there during the austral winter and spring (McLachlan et al., 1996). During the period in the shallow subtidal, fishes and crabs crop the siphon tips that clams expose to the bottom surface when feed on suspended particles (Cledón and Nuñez, 2010). After siphon cropping, clams regenerate the siphons during a period that vary according to the level of cut (Nuñez et al., 2010). However, until regeneration process was done, siphon-cut clams are forced to inhabit shallow depths, which dramatically increase the chances of a

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secondary attack by predators (Cledón and Nuñez, 2010). Therefore, the regeneration of the cropped siphons and the recuperation of the normal burial depth in *M. mactroides* would be critic to avoid further lethal predation.

The aim of the present study was to explore the recuperation of the normal burial depth of *M. mactroides* after siphon nipping. To accomplish this goal, we first conducted an experiment during the austral winter to analyze the recovery of the burial depth in *M. mactroides* after artificial siphon nipping at two cut levels (1 and 5 cm from the tip). Then the 1 cm level cut experiment was repeated in spring to determine whether the studied seasons (i.e., winter and spring) influence the recovery of burial depth after siphon nipping.

2. Materials and methods

2.1. Collection and maintenance of *M. mactroides*

Specimens of *M. mactroides* were collected at Punta Mogotes beach (37°59'S, 57°33'W), Mar del Plata, Argentina. Punta Mogotes is a dissipative beach characterized by relative fine sand ($\phi = 0.93$) and high wave energy (Bértola, 2006). Clams were captured by hand after dig holes in the sand during low tides. Clams were transported to the laboratory in an icebox with wet sand and then maintained in open water flux systems, where they received unfiltered seawater extracted directly from the sea through a pump. The water drained through aquaria (30 × 30 × 30 cm), which were almost full of sand, where the individuals were placed (Nuñez et al., 2010). Only adult clams with shell length between 50 and 55 mm were used in experiments to avoid deviations in burrowing behavior due to different body size (Cledón and Nuñez, 2010; Narchi, 1981). The aquaria of the experimental systems contained sand taken at Punta Mogotes beach. Water salinity, temperature and pH were daily measured with a Bio-Marine Aquafauna refractometer and a pH meter Adwa AD12, respectively. The water temperature was 9.6 ± 1.26 °C in winter and 15.08 ± 1.45 °C in spring. The salinity and pH ranged from 34 to 36 and from 8.4 to 8.8, respectively, at both seasons.

To avoid a potential dense-dependent influence on clams burrowing behavior, all experimental systems simulated approximately the field densities observed in the sampling zone, which was 186 individuals/m² (J.D. Nuñez, personal observation). A 25 cm long nylon thread of 0.25 mm in diameter was glued to the posterior end of the left valve of each individual to register the depth of burrowing (see Cledón and Nuñez, 2010). Different colors of thread were used for each group to facilitate treatment identification. Before starting the experiment, clam individuals were kept in the systems during 48 h for acclimation.

2.2. Effect of siphon nipping degree on the burial depth recovery

We analyzed the recuperation of the normal burial depth in *M. mactroides* after two levels of artificial siphon nipping during winter. For this purpose, clams were induced to extend the siphons with an MgCl₂ solution following the procedure of Miloslavich et al. (2004). Then the distal 1 cm and 5 cm of the inhalant and exhalant siphon tips were cutoff with surgery scissors, allowing to differentiate two different groups of clams (cut 1 and cut 5). After artificial nipping, individuals were returned to the experimental tanks. We used a third group of uncut clams as control. The three groups of clams (control, cut 1 and cut 5) consisting in 21 individuals per group were distributed in nine aquaria (7 clams per aquarium) (see Table 1). The nylon thread length was measured firstly 2 days after siphon nipping and then every 2 days until all treated clams recovered the expected burial depth according to the control clams.

2.3. Influence of the studied seasons on the depth recovery

To study the effect of the seasons in the recuperation of the normal burial depth of nipped clams, the 1 cm level cut experiment was

Table 1

Detail of the performed treatments: Control in spring (CS) and in winter (CW), 1 cm of the siphons tip removed in spring (S1) and winter (W1), 5 cm of the siphons tip removed in winter (W5). The number that multiplies the number of clams is the number of aquaria replicate per treatment.

Group	Cut of the siphon	Number of exemplars	Season
CS	Uncut	7 × 3	Spring
CW	Uncut	7 × 3	Winter
W1	1 cm	7 × 3	Winter
W5	5 cm	7 × 3	Winter
S1	1 cm	7 × 3	Spring

repeated in spring using other group of clam individuals in which the distal 1 cm of the inhalant and exhalant siphon tips was removed. As before, we used a group of uncut clams as control. In this case, the rationale of this control was twofold. First, the burial depth of uncut clams served to compare with treated clams in spring and thereby determine the effect of cut on the burial of clams. Second, the control also permitted to determine if the burial depth of uncut clams varies between spring and winter. The two groups of clams (control and cut 1) consisting in 21 individuals per group were distributed in six aquaria (7 clams per aquarium) (see Table 1). The nylon thread length was measured firstly 2 days after siphon nipping and then every 2 days until all treated clams recovered the normal burial depth of the control clams.

2.4. Data analysis

Our experimental data were obtained from individuals that were measured repeatedly through time. Linear and non-linear mixed-effect models are particularly useful when there is temporal pseudo-replication (repeated measurement) (Pinheiro and Bates, 2000). Therefore, we used mixed-effect models in order to include "individuals" as a random effect and thus accounting for within-individual correlation in all models (Littell et al., 2000).

A linear mixed-effect model was performed to determine if the normal burial depth of uncut clams (dependent variable) varies due to days of experimentation, experimental aquaria and the studied seasons (independent variables). On the other hand, the recovery of the burial depth showed a non-linear behavior. Thus, in order to find a model that best describe it, a set of three candidate non-linear mixed-effects models were fitted to the artificial siphon nipping data. For each data set belonging to the experimental groups (see Table 1), Exponential I, Exponential II and logistic models were tested using maximum likelihood. From here on, those models are referred as m₁–m₂–m₃, respectively (see Table 2). In all cases, the Akaike information criterion [AIC (Akaike, 1973)] was used to assess models performance. In addition, we computed Akaike's weight (w_i) (Franklin et al., 2001). The weights range between 0 and 1 and are interpreted as the weights of evidence in favor of model i as the best model among the set of all candidate models examined (Burnham and Anderson, 2002). Thus, the model with the smallest AIC and the highest w_i values was chosen as the model that "best" represented the data. To supplement parameter likelihood evidence, we also calculated 95% confidence intervals for all parameters estimated in each analyzed model.

Table 2

Alternative non-linear models fitted to burial-per-day data of *Mesodesma mactroides*. BD is the burial depth (cm) at time t , IBD is the infinite burial depth parameter (cm), CIR is a curve increment rate (day⁻¹), IP (cm) is the time when the burial depth reaches the half of asymptotic depth and represents the inflexion point of the model. In all cases, ϵ_r is the random effect error.

Model	Equations	Model/source
m ₁	$BD = IBD \cdot e^{CIR \cdot \text{day}} + \epsilon_r$	Exponential I
m ₂	$BD = IBD \cdot CIR \cdot e^{\text{day}} + \epsilon_r$	Exponential II
m ₃	$BD = IBD / (1 + e^{-CIR \cdot (\text{day} - IP)}) + \epsilon_r$	Logistic

Table 3

Non-linear mixed-effects models selection for burial depth data variation in each treatment (W1: 1 cm siphon cut in winter; W5: 5 cm siphon cut in winter; S1: 1 cm siphon cut in spring). Number of parameters (N° par_i), Akaike's information criterion (AIC_i), Akaike differences (Δi) and normalized weights of AIC (w_i). The best models are in bold.

Treatment	Models	N° par _i	AIC _i	Δi	w_i
W1	m ₁	2	1278.7	43	<0.001
	m ₂	2	1368.23	132.5	<0.001
	m₃	3	1235.72	0	1
W5	m ₁	2	1206.79	18.9	<0.001
	m ₂	2	1374.34	186.4	<0.001
	m₃	3	1187.92	0	1
S1	m ₁	2	1245.84	51.9	<0.001
	m ₂	2	1289.96	96	<0.001
	m₃	3	1193.94	0	1

The logistic model (m₃) fitted the data best at most experimental treatment (Table 3); therefore, it was used to make the comparison between treatments. This model has three parameters that represent the behavior of the curve estimated through the fitted data. In order to use this model to describe and compare the burrowing behavior after siphon nipping in the current and futures works, we did a biological interpretation of these parameters. Thus, the inflexion point parameter (IP) is the time when the burial depth reaches the half of the asymptotic depth, and it is interpreted as the time in which the clams start to recover the burial depth. The curve increment rate parameter (CIR) is the curve growth constant that is interpreted as the velocity of the recovery process. Finally, the infinite burial depth parameter (IBD) is the mean model curve asymptote that is interpreted as normal burial depth that each clam could reach after recovery burial depth process.

Therefore, in order to evaluate differences in depth recovery due to siphon cut level and the season, the parameters of the Logistic model were compared using the Akaike information criterion (AIC) and Akaike's weight (w_i) (Franklin et al., 2001). The null model (without any of the independent variables) and the full model (with all independent variables) were also included in the comparison procedure. In this way, models with all possible combinations of variables were considered.

All statistical analyses were conducted in R 2.13.0 (R Development Core Team, 2011). Linear and non-linear mixed-effect models were fitted using maximum likelihood with "nlme" package (Pinheiro and Bates, 2000). We used the library "bbmle" (Bolker and R Development Core Team, 2011) to find parameter values maximizing the likelihood and to generate 95% confidence intervals or regions to each estimated parameter.

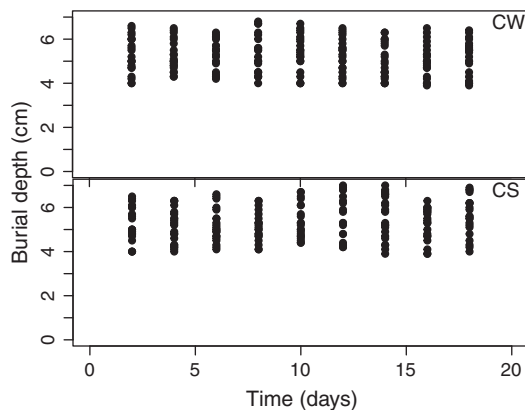


Fig. 1. Graph of burial depth related to days at different studied season of untreated individuals. CS: control spring; CW: control winter.

Table 4

Linear mixed-effect model selection for normal burial depth variation at both studied seasons (winter and spring). Number of parameters (N° par_i), Akaike's information criterion (AIC_i), Akaike differences (Δi) and normalized weights of AIC (w_i). S: season; D: days of experimentation; R: replicate. The best models are in bold.

Model i	N° par _i	AIC _i	Δi	w_i
D + S + R + S:R + S:D	10	908.3	11.5	<0.001
D + S + R + R:S	9	907.5	10.7	<0.001
S + R + D + S:D	9	906.3	9.5	<0.001
D + S + R	7	903.3	6.5	0.001
D	4	898.4	1.6	0.17
S	4	898.1	1.3	0.13
Null	3	896.8	0.0	0.38

3. Results

The relation between normal burial depth and days of experimentation at the studied seasons for each control individual is shown in the Fig. 1. Based on the ranking of AIC differences (Δi), the minimal adequate model describing normal burial depth did not incorporate any term (see Table 4). This indicates that the analyzed factors (days of experimentation, the replicates aquaria and season) have no effects on burial depth of control clams.

3.1. Effect of siphon nipping degree on the burial depth recovery

The relation between the burial depth recovery and days of experimentation at different siphon nipping level for each individual during winter (W1 and W5) is shown in the Fig. 2. The estimated parameters of the Logistic models for the two treatments (i.e., W1, W5) are summarized in Table 5. The minimal adequate model based on the ranking of AIC differences (Δi) incorporated the cut factor in all estimated parameters, which indicates that the level of cut affects the normal burial depth recovery in *M. mactroides* (Table 6). The inflexion points of the models (IP) were lower in W1 (about 1 day) than W5 (about 8 days) (Table 5, Fig. 2). Thus, *M. mactroides* clams with a deeper siphon nipping (5 cm from the siphon tip) have a higher delay in start the recovery of

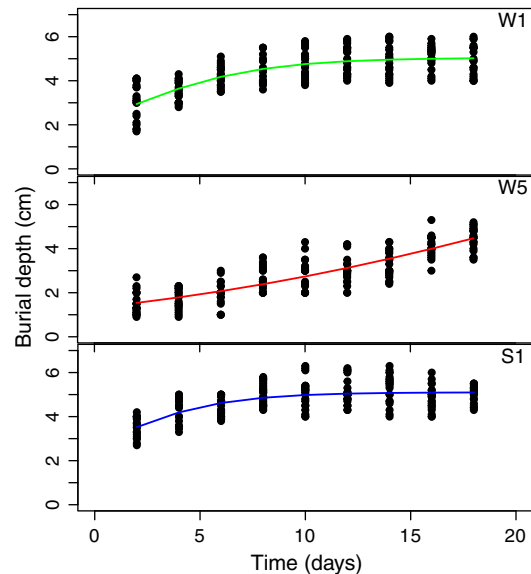


Fig. 2. Graph of burial depth recovery related to days at different treatments: level cut and studied seasons. W1: individuals with the 1 cm tip of the siphons removed in winter; W5: individuals with the 5 cm tip of the siphons removed in winter; S1: individuals with the 1 cm tip of the siphons removed in spring. The lines in each graph indicate the estimated mean of non-linear mixed-effect logistic model. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

Table 5

Non-linear mixed-effects models parameter estimates and 95% confidence limits corresponding to the logistic function model. The values in parentheses are the lower and upper confidence intervals.

Treatment	Parameters		
	AS	CIR	IP
W5	8.84 (3.39 to 14.28)	0.1 (0.06 to 0.13)	7.8 (0.083 to 15.52)
W1	5.04 (4.86 to 5.22)	0.27 (0.18 to 0.34)	0.91 (0.078 to 1.75)
S1	5.12 (4.96 to 5.24)	0.36 (0.24 to 0.48)	−0.2 (−1.15 to 0.75)

the normal burial depth than clams with a less deep siphon cut (1 cm from the tip). The curve increment rate parameter (CIR) was higher in W1 than in W5 level cut (Table 5; Fig. 2), indicating that W5 showed less acceleration in the recovery. Finally, while the infinite burial depth parameter (IBD) seems to be affected by siphon nipping level, the confidence intervals (CI) were overlapped between treatments, indicating no differences in the burial depth reached by clams after the regeneration process between siphon cut levels (Table 5; Fig. 2).

3.2. Influence of the studied seasons on the depth recovery

The relation between the burial depth recovery and days of experimentation at different seasons for each individual is shown in the Fig. 2. The estimated parameters of the logistic models for all treatments are summarized in Table 5. The minimal adequate Logistic model based on the ranking of AIC differences (Δ_i) incorporated the season factor only in the curve increment rate parameter (CIR) (Table 6). Since this parameter (CIR) was lower in W1 than S1, the results indicate that burial depth recovery presented a less acceleration in winter (Table 5; Fig. 2). The inflexion point of the model (IP: the time in which the clams start to recover the burial depth) and the infinite burial depth parameter (IBD: the mean normal burial depth that each clam could reach after recovery burial depth process) seems not to be affected by the studied seasons.

4. Discussion

The recuperation of the burial depth in clams of *M. mactroides* depends on the siphon cut level. During the austral spring, clams with the cut at 1 cm recovered the normal depth faster than those clams with 5 cm siphon nipping. Moreover, the burial depth of *M. mactroides* did not vary between winter and spring. However, there was observed a synergic effect between seasons and siphon nipping on burial depth recovery.

In our laboratory experiments, uncut (control) clams of *M. mactroides* burrow 5–6 cm deep in the sand, similar than previously reported in this species during field and laboratory measurements (Cledón and Nuñez, 2010). Other studies reported that *M. mactroides* is found at 20–30 cm deep (Coscarón, 1959; Olivier et al., 1971). Differences in methods used to determine burial depth might explain the notable discrepancy

between our results and previous reports. In our experiments, we estimated the burial depth by measuring the longitude of nylon threads glued to the posterior margin of the shell, as employed before in other infaunal clam species (e.g., *Mya arenaria*, Auffrey et al., 2004; *Macoma balthica* Long et al., 2008). This method does not disturb the sediment above of burrowed clams, thus minimizing the error in depth measurements. In contrast, authors reporting a deeper burial depth in *M. mactroides* (see Olivier et al., 1971) employed shovels or rakes to dig holes in the sediment and then caught borrowed clams. Since these methods entail a disturbance to these organisms, the depths recorded by these authors might indeed represent a “safe burial depth” that clams attain to avoid being caught. However, differences in environmental factors among the present study area and those examined in previous studies might also explain the different estimated burial depth.

4.1. Effect of siphon nipping degree on the burial depth recovery

Our results showed that non-linear mixed-effects approach introduced here provides a simple method to evaluate the recovery of the burial depth using individual measures repeated through time. In *M. mactroides*, the Logistic model better explained the recovery of the normal burial depth after siphon nipping. Additional experiments in other infaunal clam species are needed to determine whether the logistic equation can be considered a general approach model in the recovery of the normal burial depth after siphon nipping.

Nipping sublethal predation events can negatively affect the survival chances of clam individuals (de Goeij et al., 2001; Meyer and Byers, 2005). Although this harm does not cause mortality, cropped clams must confront further costs. First, shorter siphons constrain the burial depths that, in turn, facilitate the lethal attacks by other predators (Meyer and Byers, 2005). Clams that lost siphon mass are forced to burrow shallower than in normal conditions, and the rate of successful predation attacks is compressively increase. For instance, in a previous study in *M. mactroides*, clam individuals with siphons cut at 1 cm and exposed to predators 48 h later were consumed 2-fold than control clams (Cledón and Nuñez, 2010). Moreover, if sufficient siphon mass is lost to force clams to burial shallower than a critical burial depth threshold, they will be as good as dead (Meyer and Byers, 2005). On the other hand, to regain the capacity to burial deeper, clams must regenerate the cropped siphon, which is an energetically expensive process and may ultimately affect other costly processes, i.e., growth and reproduction (Coen and Heck, 1991; Irlandi and Mehlich, 1996; Kamermans and Huitema, 1994).

Yellow clams, like many other clam species, respond to siphon nipping through the regeneration of their siphons (Nuñez et al., 2010) and thus return to their normal burial depth. In this study, we observed that the level of the siphon cut significantly influenced the period of time that clams need to re-establish the normal burial depth. The difference in that period implies more or less time being vulnerable to lethal predators. Clams with 5-cm siphon nipping (ca. 1/3 of siphon) are 2-fold

Table 6

Non-linear mixed-effects models selection for burial depth variation in each treatment: cut level and season. Number of parameters (N° par_i), Akaike's information criterion (AIC_i), Akaike differences (Δ_i) and normalized weights of AIC (w_i). fac: type of analyzed factor. The best models are in bold.

Treatment	Models	N ^o par _i	Level cut effect fac = cut			Season effect fac = season		
			AIC _i	Δ_i	w_i %	AIC _i	Δ_i	w_i %
IBD ~ fac, CIR ~ fac, IP ~ fac	IBD ~ 1, CIR ~ fac, IP ~ fac	11	677.5	0.0	0.954	687.6	2.6	0.10
	IBD ~ fac, CIR ~ 1, IP ~ fac	10	683.9	6.4	0.039	685.63	0.6	0.271
	IBD ~ fac, CIR ~ 1, IP ~ fac	10	690.6	13.1	<0.001	686.74	1.7	0.156
	IBD ~ fac, CIR ~ fac, IP ~ 1	10	715.8	38.3	<0.001	688.76	3.7	0.056
	IBD ~ fac, CIR ~ 1, IP ~ 1	9	810.9	133.4	<0.001	696.36	11.3	<0.001
	IBD ~ 1, CIR ~ fac, IP ~ 1	9	761.3	83.7	<0.001	685.01	0.0	0.370
	IBD ~ 1, CIR ~ 1, IP ~ fac	9	688.2	10.6	0.004	689.31	4.3	0.043
	IBD ~ 1, CIR ~ 1, IP ~ 1	8	775.6	98.0	<0.001	703.00	18.0	<0.001

more vulnerable to further lethal predation than clams with 1-cm siphon nipping (Cledón and Nuñez, 2010). Therefore, the larger the siphon mass the clam must regenerate, the longer the period to recover the burial depth and thereby the longer the period exposed to predators. In the natural environment, differential degrees of siphon nipping and consequently the different predation risks would depend on the sublethal predator species that browse the prey. Additional experiments using lethal and sublethal natural predators should be carried out in future works to test it.

4.2. Influence of the studied seasons on the depth recovery

Like many other daily activities (e.g., migration, filtration, among others), burial depth may vary with seasonality (e.g., de Goeij and Honkoop, 2003; de Goeij and Luttkhuizen, 1998; Lardies et al., 2001). In clams, changes in the burial depth due to seasonality have mainly been associated with the feeding habit. The deposit feeders *Macoma balthica* and *Scrobicularia plana* burrow deeper in winter than in summer, whereas suspension feeders such as *Cerastoderma edule* and *Mya arenaria* do not change their burial depth at different seasons (Zwarts and Wanink, 1989). *M. mactroides* seem to fit to the latter case; this clam mostly feed on suspended particles (Cledón and Nuñez, 2010; Narchi, 1981; Olivier et al., 1971), and uncut clams do not vary its burial depth at different studied seasons (i.e., winter and spring), as indicate by our results. Therefore, although unknown the mechanism(s) that underlay the differences in the burial depth between deposit and suspension feeders related to seasonality, the results of the present study reinforce the existence of a generalized pattern.

During winter, 1-cm siphon nipped clams experienced a delay in recovering the normal burial depth compared to 1-cm siphon nipped clams in spring. Previous studies have reported that both the seasonality and the sublethal predation may affect, as independent factors, the burial depth in some clam species (e.g., Cledón and Nuñez, 2010; de Goeij and Honkoop, 2003; Meyer and Byers, 2005). However, up to now, these two factors were never analyzed concurrently. Differences in the period that clams need to recover the normal burial depth in winter and spring suggest that these factors (siphon nipping and season) act synergistically in *M. mactroides*. Despite season do not influence the normal burial depth in uncut clams, a season effect is observed when clam siphons are artificial cropped. This observed difference in the recuperation kinetic of the normal burial depth could be associated with differences in the water temperature and/or phytoplankton biomass between winter and spring. In this sense, the rate at which clams regenerate the lost siphon tissues is lower in winter than spring, as previously reported in this species (Nuñez et al., 2010) and in other infaunal clam species (e.g., *Amiantis purpurata*, Nuñez et al., 2013; *Nuttallia olivacea*, Tomiyama and Ito, 2006). Therefore, higher temperatures of spring, which accelerates the physiological process of tissue regeneration (Nuñez et al., 2010), might ultimately accelerate the recovery in the burial depth. Furthermore, the faster recovery in the burial depth might also be a consequence of a higher food intake due to spring algal blooms in the area (Carreto et al., 1995; Lutz et al., 2006), which could improve the energy available to face the cost related to tissue regeneration (Nuñez et al., 2010).

The ecological implications of our experimental results are relevant. Considering that clams exhibit a delay in recovering the normal burial depth in winter, sublethal predation that occurs during this season might increase the rate at which clams die by further lethal attacks. Siphon nipping in winter, therefore, increase the temporal window in which clams are more exposed to crabs, fishes and other potential lethal predators in the shallow subtidal.

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