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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 hinder 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.

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; Zwarts 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/m^2 (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 $MgCl_2$ 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 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.

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

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 m_1–m_2–m_3, 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, er is the random effect error.

Model	Equations	Model/source
m_1	$BD = IBD^{*}e^{CIR^{*}day} + er$	Exponential I
m_2	$BD = IBD^{*}CIR^{*}e^{day} + er$	Exponential II
m_3	$BD = IBD / (1 + e^{-CIR^{*}(day-IP)}) + er$	Logistic