

# Siphon nipping facilitates lethal predation in the clam *Mesodesma mactroides* (Reeve, 1854) (Mollusca: Bivalva)

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**Abstract** In soft sediment marine communities, fishes frequently bite off extended siphons of buried clams; the consequential shortening of the siphon is known to reduce burial depth of the clams, secondarily increasing their vulnerability to lethal excavating predators. In this study, siphon nipping on the yellow clam, *Mesodesma mactroides*, was simulated by removing the top 6.6–30% of siphons. This caused a burrow reduction in 25–75%, respectively, compared to control individuals with intact siphons, in field and laboratory trials. To examine subsequent consequences of reduced burial depth, we exposed nipped and intact clams to potential predators in the laboratory simulating the observed natural clam abundance. Artificially nipped clams were consumed twice as much as control clams. The present results suggest that sympatric croppers contribute to the stock recovery failure by facilitation of lethal predation and that re-seeding to increase the local abundance of *M. mactroides* should be an essential aspect of conservation efforts in South America.

## Introduction

Sublethal predation on bivalves occurs when fish or crabs cut a piece of the prey tissue without killing them (de Vlas 1979; Peterson and Quammen 1982; Kamermans and Huitema 1994; Smith et al. 1999; Sasaki et al. 2002). Such processes function as secondary production in food webs (Tomiya and Omori 2007). But sublethal predation negatively affects growth and reproduction of prey animals (Peterson and Quammen 1982; Zajac 1985, 1995; Coen and Heck 1991; Irlandi and Mehlich 1996; Nilsson 1999; Hentschel and Harper 2006). Some animal taxa are able to regenerate body parts after non-lethal predation (de Vlas 1979; Bowmer and Keegan 1983; Dial and Fitzpatrick 1984; Lindsay and Woodin 1992; Lindsay et al. 1996; Sasaki et al. 2002). Despite the regenerative potential of these organisms, studies on the clam *Venerupis* sp. demonstrated that partial predation significantly reduces survivorship of the individuals due to indirect facilitation for lethal predators (Meyer and Byers 2005). This effect is ecologically relevant and impacts population dynamics of prey animals (Nakaoka 2000).

The principal defence of clams against lethal predation is to burrow into the sediment, hindering the detection and manipulation by predators (Virnstein 1977; Blundon and Kennedy 1982; Zaklan and Ydenberg 1997; Smith et al. 1999; Seitz et al. 2001). The deeper the prey burrows, the lower its probability to be caught (Haddon et al. 1987; Smith et al. 1999; Whitlow et al. 2003). In the case of species with limited mobility, their vulnerability to predators may change by altering burial depth in the sediment. Therefore, the predation risk enhancement occurs when a sublethal predation event induces a behaviour change on the prey exposing it to lethal predators (Kotler et al. 1993; Soluk 1993).

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Depth of burrowing can be affected by habitat characteristics (Seitz et al. 2001, 2003; Tallqvist 2001; Byers 2002), but its maximum limit is generally set by the length and biomass of the siphons (Zwarts and Wanink 1989; Zwarts et al. 1994; de Goeij et al. 2001).

The yellow clam *Mesodesma mactroides* is an endemic infaunal inhabitant of sandy beaches that ranges from Santos Bay in southern Brazil to the mouth of the Río Negro river in Argentina (de Castellanos 1970). Its distribution and abundance are primarily linked to the abiotic factors such as temperature and sediment grain size (Defeo et al. 1986). The yellow clam was formerly among the most common bivalves at the South American beaches (Defeo 1989) and an important economic resource in Argentina (Coscarón 1959). A dramatic population decline led to an extraction ban in 1958 (Olivier and Penchaszadeh 1968).

Harvest prohibition is still in force today, but the stock has never recovered. Continuing illegal extraction and the impact of tourism are probably the main factors of this recovery failure (Bastida et al. 1991). Additional mass mortality events have prolonged the stock recovering problems. The *M. mactroides* populations have crashed repeatedly, in March 1993 (red tide incident: Odebrecht et al. 1995), November 1995 (undetermined cause: Fiori and Cazzaniga 1999) and September 2004 (undetermined cause: Thompson and Sánchez de Bock 2007).

Several studies investigated the life history and population dynamics of *Mesodesma mactroides*, examining growth, mortality and recruitment (e.g. Defeo et al. 1992a, b 1993; Defeo 1998; Fiori et al. 2004a, b; Bastida et al. 1991) and distribution density and size (Coscarón 1959; Fiori et al. 2004a, b). But little work has been done on the interaction of this species and its predators (Rocha-Barreira de Almeida 2002). This work reports for the first time the changes in burrowing depth and reduction in survival to predation of the yellow clam in different conditions as additional factors contributing to the understanding of the interaction of this species with its community.

## Materials and methods

Individuals of *M. mactroides* were hand collected at Punta Mogotes beach, Argentina (37°59'S, 57°33'W). Local density of clams was recorded and simulated in laboratory treatments.

### Allometric relationships

To establish the percentage of nipped siphon and maximum burrowing depth, it was necessary to estimate the maximum length of the siphon. The relationships between clam shell length, maximum length of the inhalant siphon and

siphon biomass were studied. The maximum siphon length was obtained by inducing 50 clams to extend their siphons through placing them into low oxygen sea water and relaxing them with a solution of MgCl<sub>2</sub> following the procedure of Miloslavich et al. (2004). The length of the siphon and shell length were measured to the nearest 1 mm. Then, to analyse the relationship of siphon dry weight with clam size, the clams were frozen at -20°C for 24 h prior to dissection. Clams were thawed, the whole tissue was removed from the shell using a scalpel, and siphons were separated from the rest of the body. The siphon and remaining soft parts were placed into two pre-weighed aluminium pans, dried for 12 h at 75°C, and weighed to the nearest 0.1 mg.

The following variables were analysed with linear regression: shell size (logT), dry weight of the siphon (logPS) and logarithm of siphon length (logLS). To estimate the contribution of the siphon to the food web, the dry weight of cut siphons at 1 cm and 5 cm was recorded.

### Experimental design

In order to maintain clams in the laboratory, systems with open water flux were built. They received unfiltered sea water directly from the sea through a pump. Within this system, we placed three aquaria (10 L) for each treatment, each filled with sand. In order to simulate the photoperiod characteristic of the season in which experiments were conducted, artificial illumination was controlled with a timer. The water temperature was measured with an alcohol thermometer to the nearest 1°C and salinity with a Bio-Marine Aquafauna refractometer to the nearest 1 ppm.

Only adult clams with shell length between 35 and 65 mm were used to avoid deviations due to differential burrowing behaviour of juvenile clams (Narchi 1981). The clams were placed into the aquaria simulating the observed field densities of 186 individual/m<sup>2</sup> in the sampled zone. Before starting the experiments, the animals were kept in the aquaria system for acclimation during 2 days.

For siphon nipping, the clams were relaxed following the above-mentioned procedure (Miloslavich et al. 2004), and then the siphons were cut using surgical scissors.

A 25-cm-long nylon thread of (0.25 mm diameter) was glued to the posterior end of the left valve of each individual, to measure the depth of burrowing. Different thread colours were used to distinguish separate individuals.

### Impact of laboratory conditions

Exposed sandy beaches (i.e. field condition) are one of the most dynamic environments, where sediment is constantly moved by waves, winds and tides (McLachlan and Brown 2006). These characteristics were not replicated in the laboratory experiment. Therefore, we evaluated the effect of

**Table 1** *Mesodesma mactroides*

Location	Group	Cut of the siphon	Number of exemplars
Laboratory	SC	Not cut	20 × 3
	S1	Cut 1 cm	20 × 3
	S5	Cut 5 cm	20 × 3 (2)
Field	FC	Not cut	20 × 3
	F1	Cut 1 cm	20 × 3(3)

Detail of different treatment: Control in laboratory conditions (SC), individuals with the 1 cm tip of the inhalant siphon removed and maintained in the laboratory (S1), individuals with the 5 cm tip of the inhalant siphon removed and maintained in the laboratory (S5), control in field conditions (FC), individuals with the 1 cm tip of the inhalant siphon removed and maintained in the field (F1)

Numerals in parentheses show numbers of dead individuals. Individuals that escaped from cages were removed from the results. The number that multiplies at the number of clam is the number of replicate for each treatment

laboratory conditions by carrying out the same experiment simultaneously in the field and in the laboratory. The same size aquaria were used for field and laboratory experiments.

In the beach, six aquaria were buried to the top in the sand and covered with a plastic net of 1 cm mesh size in order to prevent the clams from escaping.

The treatment group was composed of 60 clams with the distal 1 cm of the inhalant siphon removed (following the laboratory experiment procedure) while those in the control group (60 clams) were left intact (Table 1). Both groups of clams were placed into the six aquaria (20 clams per aquarium). The burrowing depth of all clams was measured 2 days after siphon nipping.

The data obtained were analysed by two-way analysis of covariance (ANCOVA) to assess the effects of field conditions on the burial depth (dependent variable) of the control individuals (laboratory conditions, SC; and field conditions, FC) and the nipped individuals (laboratory conditions, S1; and field conditions, F1). The replicate (group 1, 2 and 3) and conditions (SC vs. FC and S1 vs. F1, respectively) were used as fixed factors and clam shell length as the covariate.

The result showed no laboratory effect, since in both cases, the condition factors (SC vs. FC and S1 vs. F1, respectively) did not present significant differences in the burial depth (Table 2). The replicate comparison showed a similar non-significant result (Table 2). Therefore, no within-treatments effect was observed. On the other hand, the covariate shell length presented a significant difference in the burial depth (Table 2, Fig. 1).

#### Effect of siphon nipping at different lengths

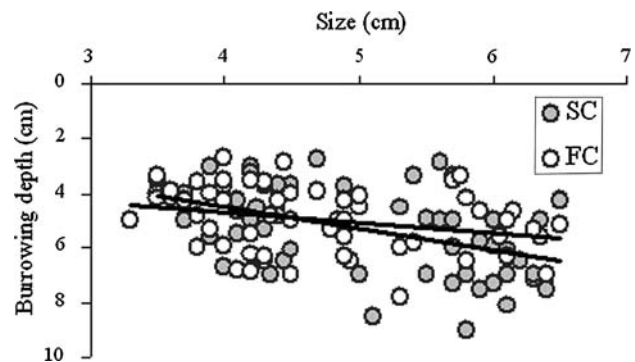
As we determined there was no laboratory effect, we experimentally examined the effect of different level of cut on the

**Table 2** *Mesodesma mactroides*

Source of variation	df	F	P
Control			
Size	1	10.179	<b>&lt;0.001</b>
Conditions	1	1.251	0.266
Replicate	2	1.308	0.275
Conditions × replicate	2	3.892	<b>0.023</b>
Cut			
Size	1	25.245	<b>&lt;0.001</b>
Conditions	1	1.714	0.193
Replicate	2	1.986	0.142
Conditions × replicate	2	0.817	0.444

Results of the two-way analysis of covariance (ANCOVA) using as dependent variables the burial depth (depth cm) and as independent variables the conditions (laboratory conditions or field conditions) and replicate (three replicate for each conditions)

The covariate was the size of clams. Bold letters show the *P* values that are significant, all *P* values are less than 0.05



**Fig. 1** Burrowing depth (cm) of *M. mactroides* after different treatments: Control in laboratory conditions (SC) and control in field conditions (FC)

burrowing deep in the laboratory conditions. A set of 180 clams were divided into three treatment groups. The distal 1 cm of the inhalant siphon was removed to one group, the distal 5 cm to the other and a control group was left uncut (Table 1). After surgery, the clams were returned to the aquaria, and the burial depth was measured after 2 days in order to let the clams recover from the stress of the treatment.

The data obtained were analysed by two-way analysis of covariance (ANCOVA) to assess the effects of cut condition (different size of excision) on the burial depth (dependent variable) of the individuals in laboratory (SC, S1 and S5) and in the field (FC and F1). The replicates (group 1, 2 and 3) and conditions (SC vs. S1 vs. S5 and FC vs. F1, respectively) were used as fixed factors and clam shell length as the covariate. Homogeneity of variance and homogeneity of regression slopes were checked as described in Huitema (1980). *Post hoc* comparisons for the

detection of a significant interaction were done using a Tukey test.

### Lethal predation experiment

Meyer and Byers (2005) indicated that sublethal predation on infaunal bivalves would facilitate detection by predators. After the loss of a part of the siphons due to siphon nipping, the depth of burrowing diminishes, which increases the potential exposure to lethal predators with the ability to dig into the sediment. In order to test whether the assertions of Meyer and Byers (2005) apply in the case of *M. mactroides*, laboratory experiments were performed where the nipped clams were exposed to potential predators.

Two predators of the surf clams are known from Brazilian beaches, *Olivancillaria vesica auricularia* (Rocha-Barreira de Almeida 2002) and the American oystercatcher *Haematopus palliatus* (Vooren and Chiaradia 1990). This last was observed feeding on *M. mactroides* in Mar Chiquita beach near the sampling area during summer and spring. But, during autumn and winter, when *M. mactroides* migrates to the subtidal, bottom trawling sampling commonly show, the octopus *Octopus tehuelchus* and the crab *Platyxanthus crenulatus* together, so these species were also considered as potential predators of *M. mactroides* and used for the experimentations on this study.

To test survival rate after siphon nipping, we placed a mix of treatment and control clams (size class 50–55 mm in shell length) in experimental 40 aquaria. Ten yellow clams with the distal 1 cm of siphon removed and 10 control clams (simulating field density) were exposed to one predator in each aquarium. To allow clams to burrow and start regeneration, they were left with no predator for 48 h (following normal protocol), ensuring that no haemolymph trace would attract the predators, which could induce false results. The only cause of death to clams during the whole experimentation was predation, since no dead clams were recorded during the previous experiments or in the 48 h of acclimation prior to predator exposure. The following predators were used: twenty cephalopods *O. tehuelchus* (mantle length 43–56 mm) and twenty crabs *P. crenulatus* (carapace width 54–57 mm).

To differentiate residual valves (post-predation) from control or treated individuals, each group of clams was painted with a different colour of epoxy paint.

Table 1 shows that clams with the siphon cut at 1 cm present no mortality. We use this result as control (with no predator) for the predation experiment. Clams used for the predation experiment were also with siphon cut at 1 cm, so mortality is exclusively due to predation.

A chi-square test was applied to the results to investigate whether the predators preferred the treated (shallower) clams.

## Results

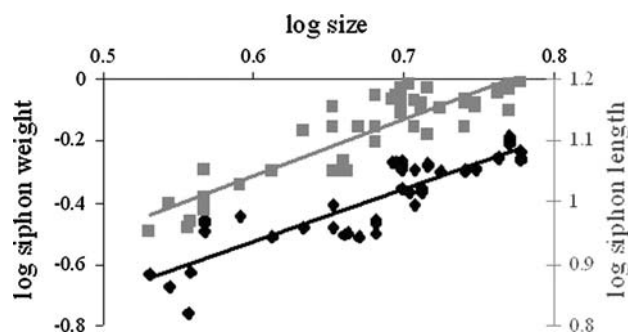
### Allometric relationship

Dry weight of the siphon (logPS) and shell size (logT) adjusted to a linear regression  $\log PS = 1.7029 \log T - 1.5461$  ( $r^2 = 0.7659$ ;  $N = 50$ ). Siphon length (logSL) and shell size (logT) of *M. mactroides*, for size class 35–60 mm adjusted to a linear regression  $\log SL = 0.9134 \log T + 0.4955$ ; ( $r^2 = 0.7967$   $N = 50$ ; Fig. 2).

Maximum siphon length in all size classes was about three times as long as the shell length.

### Effect of siphon nipping at different lengths

The effects of shell length (covariate), treatment (SC, S1 and S5), replicate (group 1, 2 or 3) and the interaction of both (replicate  $\times$  treatment) are shown in Table 3 for each shell length. The two-way ANCOVA showed that size



**Fig. 2** *Mesodesma mactroides*. Correlations of logarithm of clam size with logarithm of dry mass of inhalant siphon and with logarithm of length of inhalant siphon

**Table 3** *Mesodesma mactroides*

Source of variation	<i>df</i>	<i>F</i>	<i>P</i>
<b>System</b>			
Size	1	14.196	<b>&lt;0.001</b>
Treatment	2	173.469	<b>&lt;0.001</b>
Replicate	2	1.308	0.082
Treatment $\times$ replicate	4	2.717	<b>0.032</b>
<b>Field</b>			
Size	1	9.904	<b>&lt;0.001</b>
Treatment	1	29.20	<b>&lt;0.001</b>
Replicate	2	0.989	0.375
Treatment $\times$ replicate	2	0.82	0.443

Results of the two-way analysis of covariance (ANCOVA) using as dependent variables the burial depth (depth cm) and as independent variables the treatment (cut or control) and replicate (three replicate for each conditions)

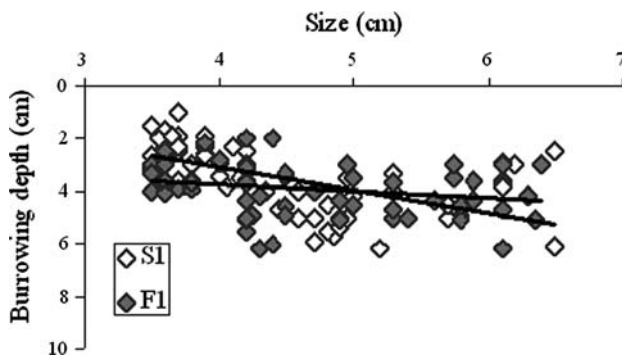
The covariate was the size of clams. Bold letters show the *P* values that are significant, all *P* values are less than 0.05

(shell length) had a significant effect on monitored parameters ( $P < 0.05$ ). There was also a significant effect of siphon nipping on the burial depth ( $P < 0.05$ ). The Tukey test showed significant differences between the three treatments (SC, S1 and S5). There was no aquarium effect since no significant differences were observed in burrowing depth among the three replicates of each treatment (SC, S1 and S5;  $P < 0.05$ ).

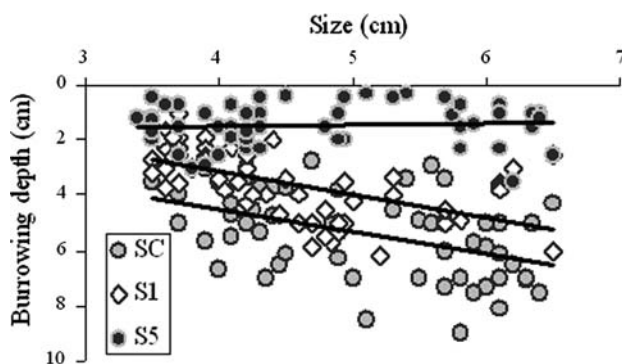
The results of the field experiment were similar to those in the laboratory. The effects of shell length (covariate), treatment (FC and F1), replicate (group 1, 2 or 3) and the interaction of both (replicate  $\times$  treatment) are shown in Table 3 for each shell length. In both cases (field and laboratory conditions), we saw that the burial depth is strongly influenced by the shell length (Figs. 1, 3, 4 and 5).

### Lethal predation experiment

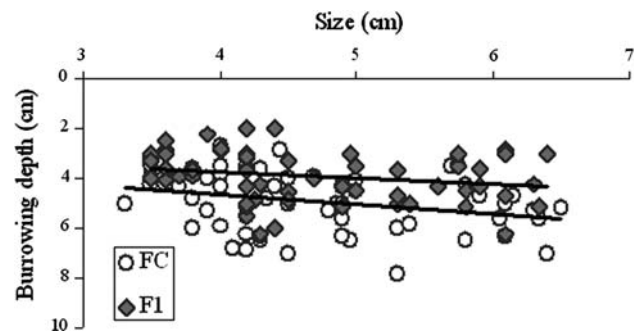
Mortality of the yellow clams due to predation was significant after siphon nipping by both *O. tehueltchus* (Pearson's chi-square = 22.5  $P < 0.05$ ), and *P. crenulatus* (Pearson's chi-square = 10  $P < 0.05$ ). The main mortality rate of clams



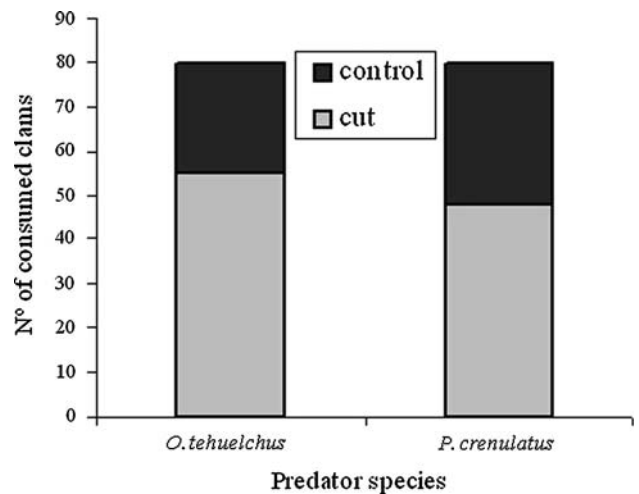
**Fig. 3** Burrowing depth (cm) of *M. macroides* after different treatments: Cut in laboratory conditions (S1) and cut in field conditions (F1)



**Fig. 4** Burrowing depth (cm) of *M. macroides* after different treatments: Control in laboratory conditions (SC), individuals with the 1 cm tip of the inhalant siphon removed and maintained in the laboratory (S1) and individuals with the 5 cm tip of the inhalant siphon removed and maintained in the laboratory (S5)



**Fig. 5** Burrowing depth (cm) of *M. macroides* after different treatments: Control in field conditions (FC) and individuals with the 1 cm tip of the inhalant siphon removed and maintained in the field (F1)



**Fig. 6** *Mesodesma macroides* number of clams predated by two different predator species (20 crabs and 20 octopuses). For each predator species, clams with the tip of the inhalant siphon removed in black and control clams in grey

exposed to *P. crenulatus* was  $0.40 \pm 0.055$  when the siphons were intact and  $0.60 \pm 0.055$  with cropped siphon. Mean lethal predation on individuals exposed to *O. tehueltchus* was  $0.31 \pm 0.06$  for clams with intact siphons and  $0.68 \pm 0.06$  for siphon-cropped individuals (Fig. 6). These results indicate that predation success on the yellow clam increases significantly when a previous event of siphon nipping occurred in the recent past.

### Discussion

The field and laboratory controls showed similar results (Fig. 1 and 3), so the experimental systems do not influence the behaviour of the clams, and the laboratory result reflects the natural conditions.

The length of the siphon (LS) and the mass of the siphon (PS) generally set the maximum burrowing depth of any

clam (Zwarts and Wanink 1989; Zwarts et al. 1994; de Goeij et al. 2001). For example, the maximum burrowing depths of the suspension-feeding clams *Mya arenaria* and *Ceratoderma edule* depend on the maximum length of the siphons (Zwarts and Wanink 1989). The yellow clam *M. mactroides* is described as a suspension feeder (Coscarón 1959; Olivier et al. 1971; Narchi 1981; Gianuca 1983; Defeo 1985), but laboratory and field observations have demonstrated that it also uses a deposit-feeding behaviour (Defeo and Scarabino 1990). In the present study, no deposit-feeding behaviour was observed. The specimens of *M. mactroides* we studied extended their siphons almost three times the shell length, confirming the observations of Narchi (1981). The clams could therefore maintain filtering activity at a depth where shell crushing predators have limited access due to the energy investment needed to reach the clam capture through the sediment.

Since the maximum burrowing depth is dependent on the siphon length, and siphon length is related to the size of the clam, the length of the shell is a good predictor of maximum burrowing depth. Siphon extensibility provides the clams with a useful tool to maintain filtration at different depths given different environmental conditions, but limits the maximum burial depth where filtration can be achieved. This situation increases survival under predation for larger individuals since they have the ability to maintain filtration deeper in the substrate than smaller individuals. *M. mactroides* does not use the maximum length of siphon in normal life conditions: the measurement of burrowing depth control individuals in the field were about 60% less than the maximum length of the siphons measured in laboratory conditions and reported by Narchi (1981). An explanation for this observation can be based on Poiseuille's equation, which demonstrates that the increase in tube length implies a decrease in flow rate in direct proportion. The deeper the clams live the lower the filtering rate (Vogel 1981). So, these clams preferentially live as shallow as the environmental conditions and community composition allow, and use the capacity of burrowing and siphon extension to escape in the presence of predators.

The increased depth of burrowing is an effective defence against predation because it increases the manipulation time by the predator (Seitz et al. 2001) and rate of unsuccessful tries (Smith et al. 1999), so it influences the decision of the predator and consequently reduces the predation rate. For example, other clams, *Venerupis* sp. and *Protothaca* sp. also reduced the burrowing depth after siphon nipping (Meyer and Byers 2005). In our work, the same effect was observed for the yellow clam (Fig. 4 and 5). When 33% of the siphon weight was removed in each individual, they reduced their burrowing depth to 25% of that in the controls, while a siphon nipping of 66.6% induced a burrowing depth reduction of 75% compared to the controls.

These results show that the size of the sectioned portion of the siphon may determine the survival of the individual.

Clams that lose siphon mass are often as good as dead, but only if sufficient mass is lost to force them to feed at a shallower depth than a critical threshold burial depth (Meyer and Byers 2005). In the predation experiment carried out in the present study, yellow clams with siphons cut at 1 cm from the tip were consumed twice as often as control clams by the predators *O. tehuilchus* and *P. crenulatus* (Fig. 6). These results indicate that a sublethal nipping event can strongly reduce the survival chances of the individuals making them vulnerable to lethal predation. This effect of sublethal predation is a striking example of predator facilitation. The predators *O. tehuilchus* and *P. crenulatus* share habitats with this clam species in winter, when clams migrate to the subtidal and their siphons are found in croaker stomach content. In the months of summer and spring, when *M. mactroides* inhabit the intertidal zone, we observed the oystercatcher *H. ostralegus* consuming yellow clams. Similar predator-prey relationships between seabirds and surf clams were observed at Chilean beaches where *H. ostralegus pitanay* feeds on *Mesodesma donacium* (Googall et al. 1951). In this context, the yellow clam experiences different predation pressures depending on the time of year.

The experimental design used in the present work probably underestimates the natural occurrence of this facilitation effect of lethal predation, since the lethal predators benefit not only from reduced burial depths of clam prey, but also from olfactory cues that are likely to be released from the wound when siphons are cropped. Predators in our experiment had no such benefit since they were introduced in the experiments 2 days after cropping, providing time for open wounds to be healed and odours from cut tissue to dissipate (Nuñez et al. 2009).

The estimated predation rates indicated that *O. tehuilchus* consumed two times more than the crabs (mean = 1.10 SD = 0.76 and mean = 0.69 SD = 0.52, respectively). Such differences would be explained by the different predatory strategies used to locate and manipulate the prey. On one hand, octopuses have been reported to be major predators of motile species in several marine communities (Onuf 1972; Fotheringham 1974; Wells 1980; Schnitt 1982; Ambrose and Nelson 1983; Fawcett 1984). *Octopus bimaculatus*, for example, can be effective in reducing prey abundance, and are selective predators (Ambrose 1984), while crabs are opportunists (Taylor 2000). Therefore, the superior rate of predation of *O. tehuilchus* compared to the crabs may be explained by their selective preference. On the other hand, the crabs, as opportunistic generalist predators, are not so specialised in hunting motile prey. Even if these clams represent a preferred prey type, the claw of durophagous crabs have evolved due to multiple uses, the

primary activity crushing strong material may be incompatible with nimble requirements (Smith et al. 1999; Taylor 2000).

Surf clams can contribute in up to 95% to the total biomass of sandy beach communities (McLachlan et al. 1981; Arntz and Fahrbach 1991; Ieno and Bastida 1998). In this context, it is expected that most predator species of the community may be specialized for catching clams. Since the mean dry siphon mass of an adult is 0.09 g, this represents a siphon biomass of 16.74 g/m<sup>2</sup> for Punta Mogotes beach (186 individuals/m<sup>2</sup>, JD Nuñez unpublished data). Siphons of this clam represent an important source of food in this community. Interestingly, there is information indicating that the croaker *Micropogonias fuernierii* off Uruguay is commonly found to have such siphons in its stomach contents (Defeo, personal communication). Surf clams, given their whole body mass, can contribute in up to 95% to the total biomass of sandy beach communities (McLachlan et al. 1981; Arntz and Fahrbach 1991; Ieno and Bastida 1998). In this context, it is expected that most predator species of the community may be specialized for catching clams.

Life history evolution may select for the appropriate species-specific balance of the growth-mortality trade-off that burial depth largely controls (Meyer and Byers 2005), but when the balance is broken by any cause the sympatric predators may contribute to the stock recovery failure. In this sense, the observed responses to siphon nipping suggest that *M. mactroides* abundance will correlate negatively with predator abundance until the population balance is reached again. Such balance was not achieved in the last several decades in South America and the species remains protected and the present situation will persist or worsen. To prevent this, we advise the initiation of new plans for re-seeding projects.

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