

# The effect of the SW Atlantic burrowing crab *Chasmagnathus granulatus* on the intertidal razor clam *Tagelus plebeius*

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## Abstract

The deposit feeding burrowing crab *Chasmagnathus granulatus* and the suspension feeding burrowing clam *Tagelus plebeius* occur sympatrically in the intertidal flats of the south western Atlantic estuarine environments. Common ecological theory predicts negative effects of deposit feeder bioturbation on co-occurring suspension feeders up to complete exclusion of the latter. By means of descriptive and experimental approaches performed at the Mar Chiquita coastal lagoon (37°32'S–57°19'W; Argentina) we show that within beds of *C. granulatus* (i) frequency of clam shell damage is higher, (ii) shell geometry shows proportionally shorter shells, (iii) clam condition is lower and, (iv) shell growth rates are lower. The negative effect of crabs increases towards lower tidal level. Changes in shell geometry are only detectable in damaged shells, suggesting that this pattern results from direct physical effects by crabs. The negative effect of crabs on clam condition and growth is mediated by indirect mechanisms. Burrowing and migrating of crabs may disrupt clam feeding and/or may force clams to invest more energy into escape movements and burrow rebuilding, thus leaving less energy for growth. Our study indicates that the adaptation of *T. plebeius* to a highly dynamic intertidal environment enables the clam to coexist with this strong bioturbator, too. The additional stress inflicted by *C. granulatus* does affect the clam negatively, but is not sufficiently high to eliminate it from the system.

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## 1. Introduction

Trophic relations are the most important interaction between organisms in most ecosystems (e.g., De Ruiter et al., 2005), giving rise to a research field of its own that focused on aquatic trophic interactions and food web dynamics (Belgrano et al., 2005). Non-trophic interactions appear to be comparatively less significant (but see Jones et al., 1994), albeit both positive and negative non-trophic interactions can be a major structuring force

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under certain conditions (e.g. Dunstan and Johnson, 2003; Nugues et al., 2004).

In marine benthic habitats, bioturbation (i.e., the physical disturbance of the sediment by an organism) is an important non-trophic interaction. Bioturbators modify physical as well as chemical characteristics of the sediment (e.g., Bertness, 1985; Levinton, 1989; Reise, 2002) and thus can affect other organisms sharing this habitat in various ways (Brenchley, 1981; Posey, 1986, 1987; Posey et al., 1991). Large burrowing organisms such as shrimps, crabs and polychaetes are of particular significance, especially if they occur at high densities and/or construct extensive semi-permanent galleries (e.g., Peterson, 1977; Montague, 1980; Brenchley, 1981; Hoffman et al., 1984; Bertness, 1985; Brey, 1991). Under such circumstances they may alter the physico-chemical characteristics and dynamics of the sediment dramatically and at large scales, thus severely affecting sympatric plant and animal populations (Weinberg, 1984; Murphy, 1985; Brey, 1991).

The burrowing grapsid crab *Chasmagnathus granulatus* occurs at high densities in estuaries and embayments of the SW Atlantic (southern Brazil to northern Patagonia in Argentina; Boschi, 1964; Spivak et al., 1994; Iribarne et al., 1997, 2005). This species (up to 4 cm carapace width) inhabits tidal flats and salt marshes dominated by *Spartina* spp. and *Sarcocornia* spp., with densities up to 60 crabs m<sup>-2</sup> (Iribarne et al., 1997; Bortolus and Iribarne, 1999). The crab excavates and maintains semi-permanent open burrows (Spivak et al., 1994; Iribarne et al., 1997). In salt marshes these burrows are straight tunnels (entrance diameter up to 10 cm) that may extend down to 1 m depth (Iribarne et al., 1997; Bortolus and Iribarne, 1999; Bortolus et al., 2004; Botto et al., 2005). In mud flats, tidal creeks and channels, where crabs are mainly deposit feeding, burrows are shallow (down to 30 cm depth) and with funnel-shaped entrances (diameter up to 20 cm; Iribarne et al., 1997; Botto and Iribarne, 2000; Botto et al., 2005). Due to the high crab digging activity, single burrows move laterally by up to 3.2 cm d<sup>-1</sup> and overall sediment excavation rates may be up to 5.9 kg m<sup>-2</sup> d<sup>-1</sup> (Iribarne et al., 1997). At the same time, the large semi-permanent funnel-shaped burrow entrances act as detritus traps and cause an increase in sediment organic matter content (Botto et al., 2006). Consequently, there are distinct changes in sediment chemistry (Gutiérrez et al., 2006), composition and transport (e.g., Botto and Iribarne, 2000; Palomo et al., 2004) and in bottom topography (Escapa et al., 2004; Perillo and Iribarne, 2004) within crab beds. These changes directly affect

abundances of nematodes, polychaetes, juvenile crabs (Botto and Iribarne, 2000; Palomo et al., 2004; Escapa et al., 2004), the fiddler crab *Uca uruguayensis* (Daleo et al., 2003), the mud crab *Cyrtograpsus angulatus* (Iribarne et al., 2003), the cordgrass *Spartina densiflora* (Bortolus and Iribarne, 1999; Bortolus et al., 2002, 2004), the pickleweed *Sarcocornia perennis* (formerly known as *Salicornia ambigua*; Perillo and Iribarne, 2004) and indirectly habitat use and foraging rates of migratory shorebirds (Botto et al., 1998, 2000; Palomo et al., 2003; Iribarne et al., 2005).

Throughout its geographical range *C. granulatus* can be encountered sympatrically with the stout razor clam *Tagelus plebeius*. This euryhaline suspension feeder (Holland and Dean, 1977a; Arruda et al., 2003) inhabits intertidal flats with cohesive sandy-silty sediments along the American Atlantic coast from Cape Cod, Massachusetts (42° N, USA; Leal, 2002) to the northern Argentinean Patagonia (San Matías Gulf, 41° S, Argentina; Olivier et al., 1972a,b). Their shells are ubiquitous in Holocene estuarine deposits of central South America (1340 to 3850 year b.p.; Fasano et al., 1982; Schnack et al., 1982) and are often used as an indicator of palaeoenvironmental conditions (see Goffieri et al., 1998; Iribarne and Botto, 1998; Iribarne et al., 1998; Aguirre and Farinati, 1999). The clam *T. plebeius* constructs a deep permanent burrow (up to 70 cm deep) in which the clam moves up and down in a rhythm coupled to the tidal cycle (personal observation). When feeding during high tide, clams are positioned close to the sediment surface (10 to 15 cm deep; Holland and Dean, 1977a,b; Arruda et al., 2003; B. Lomovasky personal observation).

Field observations indicate that *C. granulatus* may negatively affect *T. plebeius* in several ways: (i) juvenile crabs settle inside the holes of clams inhalant siphons, where they start constructing their burrows as they grow (Gutiérrez and Iribarne, 1998); (ii) larger crabs prefer to feed on organic matter deposited in the depression generated by the clam siphon activity (Gutiérrez and Iribarne, 2004); and (iii) crab burrows are spatially mobile, thus they can disrupt the clam burrows (Lomovasky et al., 2005). The first two mechanisms are likely to disturb the clam during feeding, whereas the latter may force it to invest more time and effort into burrow rebuilding and is even assumed to be the major cause of clam shell damage (see Lomovasky et al., 2005). However, the crabs may positively affect clams (as found between the polychaete *Clymenella torquata* and the bivalve *Gemma gemma*; Weinberg, 1984), given that their funnel shape burrows are passive traps for sediment and detritus (Botto and Iribarne, 2000; Botto et

al., 2006) which could also enhance food availability for the clams.

Crab effects on clam behaviour, shell damage and body condition have been reported, but the overall picture is rather contradictory as such effects appear to be site specific (Gutiérrez and Iribarne, 2003; Lomovasky et al., 2005). However, we suspect that such site effects may actually be a combination of tidal level and crab effects, and therefore this study evaluates by means of descriptive and experimental approaches the effects of *C. granulatus* on frequency of shell damage, morphometric relationships and growth rates of *T. plebeius*, and whether these effects depend on tidal level.

## 2. Materials and methods

### 2.1. Study area

The study was performed between January 2003 and March 2004 in the Mar Chiquita Coastal Lagoon (37° 32'S; 57° 19'W; Argentina). This is a brackish water area of about 46 km<sup>2</sup> with muddy sediments and low tidal amplitude (<1 m, Fasano et al., 1982). Both the stout razor clam *Tagelus plebeius* (Olivier et al., 1972a, b) and discrete high-density patches (=“crab beds”) of the burrowing crab *Chasmagnathus granulatus* (Iribarne et al., 1997) can be found on most intertidal flats. Within the lagoon, three sites at which crabs were present and four sites without crabs (Fig. 1) were selected. Samples for the analysis of morphometric relationships and frequency of repaired shell damage (RSD) in *T. plebeius* were collected at three tidal levels at each site parallel to the shore with similar exposition time as follows: Low=0.40 m above mean low tide (amlt; LTL), Medium=0.55 m amlt (MTL), and High=0.75 m amlt (HTL). Exclusion/inclusion experiments to determine crab effects on frequency of RSD and shell growth were carried out at one of the sites at medium tidal level (Fig. 1, site A).

### 2.2. Sediment characteristics

Five sediment samples (cores of 5 cm diameter and 35 cm depth) were collected at each site and tidal level in January 2004. Organic matter content (OMC) of approximately 10 g subsamples was determined as the difference between dry weight (80 °C to constant weight) and the ash weight (450 °C for 8 h). Grain size frequency distribution was obtained by sieving a dried 400 g subsample through a series of five screens (screen sizes: 2000, 500, 250, 125, 62 µm). Crab/tidal level

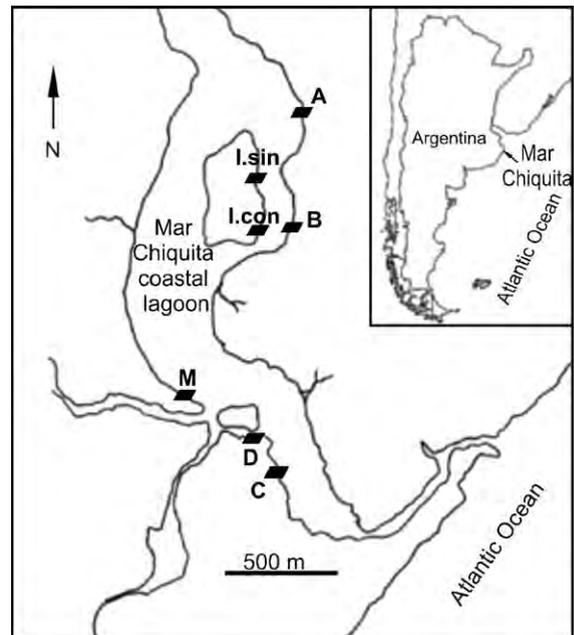


Fig. 1. Sampling sites in the Mar Chiquita Coastal Lagoon with areas inhabited by the burrowing crab *Chasmagnathus granulatus* (areas B, D and I.cgn) and areas without crabs (A, C, I.sin and M). The stout razor clam *Tagelus plebeius* is present at all sites.

effects were examined by two-way analysis of variance (ANOVA, dependent variable vs. crab × tidal level). All data sets were tested for normality and homogeneity of variances and proportional data were arcsinus transformed prior to ANOVA to comply with the parametric assumptions (Zar, 1999; Sokal and Rohlf, 1995). Pairwise differences between crabs × tidal level data sets were identified by post-hoc comparisons of means using Tukey's multiple comparison test (Tukey's HSD; Zar, 1999).

### 2.3. Shell damage frequency and shell morphometrics of *T. plebeius*

One hundred to one hundred thirty specimens of *T. plebeius* were collected at each site and tidal level in January 2003 and between January 2004 and March 2004 by excavating the sediment with a shovel. For all individuals ( $N=2491$ ) shell height ( $H$ ) from the umbo to the ventral margin; shell length ( $L$ ) along the anterior–posterior axis and shell width ( $W$ ) (precision  $\pm 0.1$  mm) were measured. Total mass (TM), shell mass (SM), shell free wet mass (SFWM) and shell free dry mass (SFDM; dried at 80 °C to constant weight; precision of  $\pm 0.01$  g) were determined. Signs of repair can be found in almost all parts of the shell of *T. plebeius*, but only damage around the shell margins is likely to be caused by *C.*

*granulatus* (following Lomovasky et al., 2005; Fig. 2). All shells collected at the seven sites were inspected visually and sorted into “repaired shell damage” (RSD) or “non-damaged”.

In order to enhance overall data set homogeneity, the statistical analysis was restricted to the size range  $\geq 11$  mm to  $<25$  mm height, as no shells  $<11$  mm height were damaged and shells  $\geq 25$  mm were rare and not present at all sites. Subsequently, multivariate outliers in the sample space [ $\log(H)$ ,  $\log(L)$ ,  $\log(W)$ ,  $\log(\text{SFDM})$ ,  $\log(\text{SM})$ ,  $\log(\text{TM})$ ] were identified by Mahalanobis Jackknife distances (Barnett and Price, 1995). Eight outliers (Jackknife distance  $\geq 6.0$ ) were identified and excluded, thus reducing the number of data to  $N=2182$ .

Differences in RSD rate were assessed by contingency table analysis (Zar, 1999) coupled with the Cochran–Mantel–Haenszel test (e.g., Hall et al., 2000) which checks whether the response is conditionally independent of the explanatory variable when adjusting for a third classification (i.e., if the effect of crab presence on shell damage may be due to tidal level).

In addition to field sampling, shell damage was investigated by a crab–clam exclusion/inclusion experiment (January 4th 2004 to January 11th 2005 at sampling site “A” at MTL; Fig. 1). Eighteen plastic cages (50 cm  $\times$  50 cm area and 50 cm height with a mesh size of 5 mm) were randomly located in the clam bed matching a local density of 10 clams per cage. Then, 6 individuals of *C. granulatus* (3 males and 3 females, 25 to 36 mm carapace width, “inclusion” setup) were added to each of 9 cages, whereas the other 9 cages received no crabs (“exclusion” setup). This density of crabs is about the one reported for the same area previously (Iribarne et al., 1997, 2000). At the end of the experiment, all living

clams were recovered from each cage. Each clam was measured and shells were examined for signs of damage as described above. Differences in RSD rate between “inclusion” and “exclusion” setups were assessed by contingency table analysis (Zar, 1999).

Shell damage may have other causes than *C. granulatus*, and the presence of RSD may obscure other effects of *C. granulatus* on shell morphometrics. Therefore damaged and undamaged shells were analyzed separately. A full interaction ANCOVA model (dependent variable vs. covariate  $\times$  crab  $\times$  tidal level) with subsequent Tukey’s HSD test on differences between means was used to evaluate effects on (i) the relation between shell height ( $H$ ), length ( $L$ ), width ( $W$ ); and on (ii) the relation between shell volume and shell mass (SM) and shell free dry mass (SFDM), respectively, which are equivalent to condition factors (Ricker, 1975). Shell volume ( $V$ ) was approximated from shell size by

$$V = (H * L * W)$$

#### 2.4. Growth rate of *Tageelus plebeius*

To evaluate the effect of crab presence on the growth rate of *T. plebeius*, an exclusion/inclusion experiment was carried out between January 16th 2004 and May 14th 2004 at sampling site “A” at MTL (Fig. 1). Forty *T. plebeius* were collected, measured in  $H$  and  $L$  as previously described (in Section 2.3; 11.35 to 23.8 mm  $H$ ) and marked with numbered plastic labels adhered to the surface of the periostracum. Ten wire cages (as described before in Section 2.3) were positioned in areas without clams and to each, 4 marked *T. plebeius* were

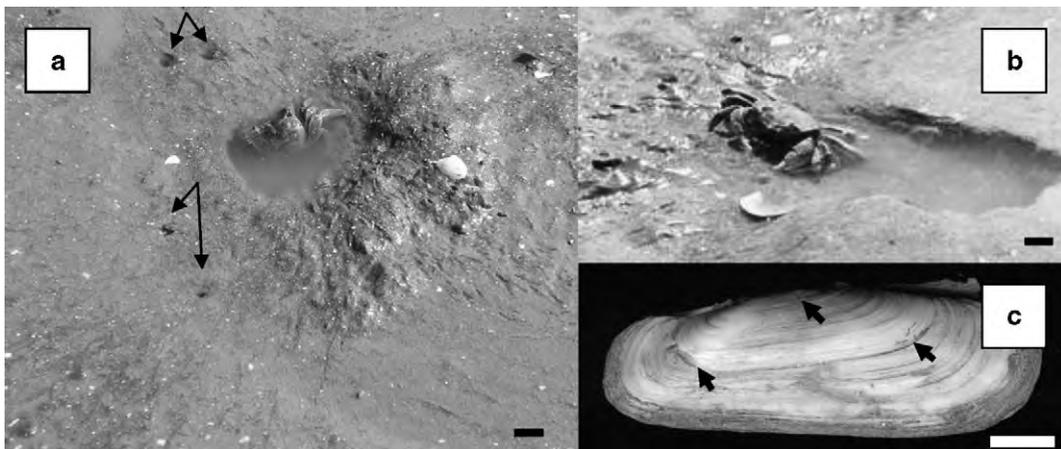


Fig. 2. (a) Photograph of siphon holes (black arrows) of *T. plebeius* close to the burrow entrance of the crab *C. granulatus*; (b) Male *C. granulatus* outside his burrow; (c) right valve of *T. plebeius* showing scars (black arrows) around the shell margin. Scale bar=10 mm.

added. To 5 of the cages, 6 individuals of *C. granulatus* (3 males and 3 females, 26 to 35 mm carapace width) were added (“crab inclusion” treatment) and the other five cages remained without crabs (“crab exclusion” treatment). After four months clams were recovered. Individuals were measured and for each one was determined the difference between the clam height ( $dH$ , mm) and length ( $dL$ , mm) at start and end of the experiment respectively. A full interaction ANCOVA model (size increment vs. initial size  $\times$  crab) with subsequent Tukey’s HSD test on differences between means was used to evaluate effects on growth rates (Zar, 1999).

2.5. Displacement of crab burrow at different tidal levels

To evaluate the displacement of crab burrow across the intertidal area a field experiment was carried out between December 12th and 22nd 2005 at sampling site “B” (Fig. 1). At each tidal level, twelve inhabited crab burrows were selected. Four sticks were positioned in a circle with 15 cm radius around each burrow entrance at positions 0°, 90°, 180° and 270° as reference marks for the entrance position. During the course of the experiment burrow entrance position relative to the fixed points as well as the largest ( $d_1$ ) and the smallest diameter ( $d_2$ ) of the ellipsoid entrance were measured daily. Burrow displacement ( $\text{cm day}^{-1}$ ) from the original position and entrance area ( $=\pi * d_1/2 * d_2/2$ )

were calculated accordingly. When burrows were abandoned by crabs, new burrows were immediately selected as described above to continue the experiment. Burrow abandonment rate was calculated daily as the difference in the number of burrows between two consecutive days. The null hypothesis of no difference in the mean displacement rate, entrance area and burrow abandonment rate between tidal levels was tested by ANOVA with subsequent Tukey’s HSD test (Zar, 1999). When assumptions of normality and homogeneity of variances were rejected, a non parametric test was used (Kruskal–Wallis test: K–W, Zar, 1999).

3. Results

3.1. Sediment characteristics

Sediment organic matter content (OMC) was affected by both crab presence/absence and tidal level. OMC was higher in areas inhabited by the crab *C. granulatus* than areas without them (3.73%, SD=0.90 and 3.11%, SD=0.88 respectively;  $p<0.05$ ), and higher at LTL compared to MTL and HTL (3.94%, SD=0.99 compared to 3.13%, SD=0.82 and 3.04%, SD=0.73 respectively,  $p<0.05$ ). There were no significant interactions between crab presence/absence and tidal level. The silt and clay sediment fraction  $<62 \mu\text{m}$  showed the same pattern as OMC ( $p<0.05$ ). The share of the 125–250  $\mu\text{m}$  grain size fractions was lower inside crab beds ( $p<0.01$ ) and at LTL ( $p<0.05$ ). The share of the coarser

Table 1  
Effects of crab absence/presence (0, 1) and tidal level (LTL, MTL, HTL) on morphometric relationships in *T. plebeius* shells that show repaired shell damage (RSD)

Dependent variable		Length ( <i>L</i> )	Width ( <i>W</i> )	Length ( <i>L</i> )	Shell Mass (SM)	Shell Free Dry Mass (SFDM)
Covariate		Height ( <i>H</i> )	Height ( <i>H</i> )	Width ( <i>W</i> )	Volume ( <i>V</i> )	Volume ( <i>V</i> )
<i>Independent variable</i>						
Crab	<i>P</i> -value	<0.001	0.011	<0.001	<0.001	0.001
	Crab effect	Negative	Positive	Negative	Negative	Negative
Tidal level	<i>P</i> -value	<0.001	ns	<0.001	<0.001	<0.001
	Tukey’s HSD					
	LTL	A –	–	A –	– B	A – –
	MTL	A –	–	A –	A –	– B –
HTL	– B	–	– B	A –	– – C	
Crab $\times$ TL	<i>P</i> -value	0.001	0.024	<0.001	0.026	ns
	Tukey’s HSD					
	0 $\times$ LTL	A – –	– B	A – – –	– B C	–
	0 $\times$ MTL	A – –	A B	A – – –	A – –	–
	0 $\times$ HTL	– – C	– B	– B C –	A – –	–
	1 $\times$ LTL	– B C	A –	– – C D	– – C	–
	1 $\times$ MTL	– B –	A B	– B – –	– B C	–
	1 $\times$ HTL	– – C	A B	– – – D	A B –	–

Full interaction ANCOVA model (dependent vs. covariate  $\times$  crab  $\times$  tidal level) with subsequent Tukey’s HSD test. Equal letters indicate no significant differences at  $\alpha=0.05$ . The average ratio of dependent variable to covariate decreases in alphabetical sequence. *P*-values for covariates are always  $<0.001$ . ns=not significant ( $p>0.05$ ).

fractions 250–500, 500–2000, and >2000  $\mu\text{m}$  was lower inside crab beds (all  $p < 0.05$ ).

No differences in sediment structure could be detected between inclusion treatments and exclusion treatments at the end of the exclusion/inclusion shell damage experiment at site “A” (one-way ANOVA,  $p > 0.05$ ).

3.2. Shell damage frequency

Overall repaired shell damage (RSD) frequency was 52.4% (1144 of 2182 individuals) in the shell height range between 11 and 25 mm. Contingency analysis indicated a higher RSD ratio in crab beds (57.2% vs. 48.1%,  $p < 0.001$ ), whereas with respect to tidal level

RSD ratio was lower at HTL (45.4%) compared to the pooled data from MTL and LTL (56.1%,  $p < 0.001$ ). In clams recovered after the one-year exclusion/inclusion field experiment (inclusion  $N = 53$ , exclusion  $N = 45$ ) we found a higher percentage of damaged individuals in crab inclusion treatments (75%) than in crab exclusion treatments (49%,  $p < 0.01$ ).

3.3. Shell morphometrics

In shells showing repaired shell damage the presence of *C. granulatus* has a significant negative effect on *T. plebeius*  $L/H$  and  $L/W$  ratios, with lower values inside crab beds at low (LTL) and medium tidal level (MTL) than outside, and a positive effect on  $W/H$  at LTL (Table

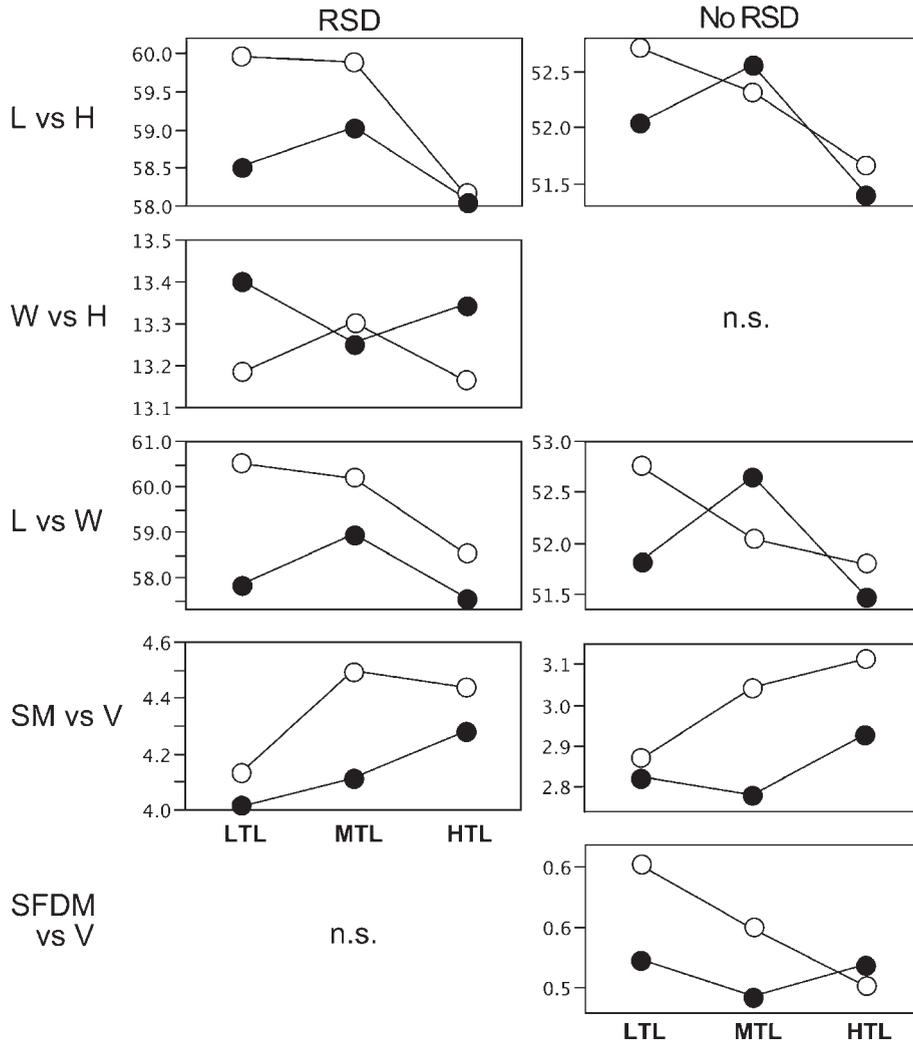


Fig. 3. Least Squares Means (LSMeans) plots of combined effects of crab presence and tidal level on shell morphometrics of *T. plebeius* according to ANCOVA results presented in Tables 1 and 2. Note that LSMeans are not identical to the true means of the independent variable. LTL, MTL, HTL: low, medium, high tidal level; RSD: repaired shell damage.

1, Fig. 3). In undamaged shells, crab effects were detectable only in the interaction crab × tidal level (Table 2). Tidal level affected both *L/H* and *L/W* ratio negatively (lower at HTL), but did not affect *W/H* (Table 2, Fig. 3).

SM-to-volume and SFDM-to-volume ratios were negatively affected by crab presence in both damaged (Table 1) and undamaged shells (Table 2). SM-to-volume ratio increases with tidal level, whereas SFDM-to-volume decreases with tidal level with lower values at LTL and MTL inside crab beds (Tables 1 and 2, Fig. 3).

### 3.4. Growth rate of *Tagelus plebeius*

The exclusion/inclusion experiment showed that shells grew significantly ( $p < 0.05$ ) less both in height and in length in the presence of crabs (Fig. 4).

### 3.5. Displacement of crab burrow at different tidal levels

Mean lateral movement of crab burrows was lowest at HTL ( $0.37 \text{ cm d}^{-1}$ ;  $SD=0.72$ ). It was significantly higher at MTL and at LTL, averaging  $1.55 \text{ cm d}^{-1}$  ( $SD=1.67$ ) and  $3.59 \text{ cm d}^{-1}$  ( $SD=2.39$ ) respectively ( $K-W$ ,  $H=62.36$ ,  $p < 0.05$ ; Fig. 5). Accordingly, mean burrow entrance area was lower at HTL ( $21.67 \text{ cm}^2$ ;  $SD=13.45$ ) than at MTL ( $47.02 \text{ cm}^2$ ;  $SD=25.40$ ) and at LTL ( $48.41 \text{ cm}^2$ ;  $SD=29.70$ ;  $F=23.92$ ,  $p < 0.05$ ). The burrow abandonment rate was significantly higher at

LTL ( $0.54 \text{ d}^{-1}$ ) than at MTL and HTL ( $0.19 \text{ d}^{-1}$  and  $0.01 \text{ d}^{-1}$  respectively;  $K-W$ ,  $H=9.43$ ,  $p < 0.05$ ).

## 4. Discussion

Our study demonstrated significant effects of both the burrowing crab *Chasmagnathus granulatus* and the tidal level on shell geometry, condition index, rate of repaired shell damage (RSD) and growth rate of the stout razor clam *Tagelus plebeius*. While tidal level effects increase from low to high tidal level, crab effects become more distinct in the opposite direction.

We observed tidal level effects on RSD, shell geometry and condition index. With regard to RSD, however, an original tidal level effect is questionable. As we were not able to test crab and tidal level effects on RSD simultaneously, the lower RSD rate at HTL may be related to tidal level effects on crab activity (see below). This is different in shell geometry and bivalve condition: with increasing tidal level, shells become comparatively shorter and heavier, whereas soft body mass proportion decreases. This trend exists in both damaged (Table 1) and undamaged shells (Table 2), as well as inside and outside crab beds (Fig. 3), and could be a consequence of lower shell growth rate at HTL. There is evidence that growth rates of intertidal bivalves decrease with decreasing immersion time (Gillmor, 1982; Peterson and Black, 1988; this study), owing to less time for feeding as well as higher temperature and desiccation stress during low tide (Marsden and Weatherhead, 1999)

Table 2  
Effects of crab absence/presence (0, 1) and tidal level (LTL, MTL, HTL) on morphometric relationships in undamaged *T. plebeius* shells

Dependent variable		Length ( <i>L</i> )	Width ( <i>W</i> )	Length ( <i>L</i> )	Shell Mass (SM)	Shell Free Dry Mass (SFDM)
Covariate		Height ( <i>H</i> )	Height ( <i>H</i> )	Width ( <i>W</i> )	Volume ( <i>V</i> )	Volume ( <i>V</i> )
<i>Independent variable</i>						
Crab	<i>P</i> -value	ns	ns	ns	<0.001	<0.001
	Crab effect	–	–	–	Negative	Negative
TL	<i>P</i> -value	<0.001	ns	0.001	<0.001	<0.001
	Tukey's HSD					
	LTL	A –	–	A –	– B	A –
	MTL	A –	–	A –	– B	– B
HTL	– B	–	– B	A –	– B	
Crab × TL	<i>P</i> -value	0.045	ns	0.003	0.041	0.001
	Tukey's HSD					
	0 × LTL	A – –	–	A – –	– B C	A – –
	0 × MTL	A B –	–	A B C	A B – –	– B –
	0 × HTL	– B C	–	– – C	A – – –	– – C
	1 × LTL	A B C	–	– B C	– – C	– B C
	1 × MTL	A – –	–	A B –	– – C	– – C
	1 × HTL	– – C	–	– – C	– B C	– B C

Full interaction ANCOVA model (dependent vs. covariate × crab × tidal level) with subsequent Tukey's HSD test on differences between means. Equal letters indicate no significant differences at  $\alpha=0.05$ . The average ratio of dependent variable to covariate decreases in alphabetical sequence. *P*-values for covariates are always <0.001. ns=not significant ( $P > 0.05$ ).

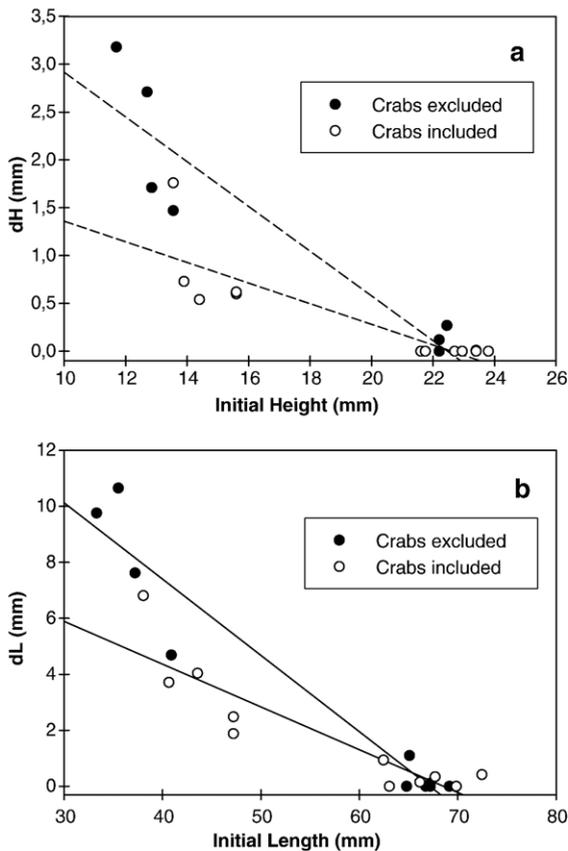


Fig. 4. Effect of crab presence on the growth rate of *T. plebeius* in the crab exclusion/inclusion field experiment. (a) Relationship between height increment ( $dH$ , mm) during the experimental time and initial height (mm); and (b) between length increment ( $dL$ , mm) and initial length (mm).

such as observed to *T. plebeius* from South Carolina (North Inlet estuary,  $33^{\circ} 20' N$ , Holland and Dean, 1977b). However, the tidal level effect on shell geometry and condition (SFDM/ $V$ ) was stronger outside crab beds than inside (tidal level–crabs interaction, see below).

Crab effects are present in all clam parameters investigated, but the underlying mechanisms may differ. The crab *C. granulatus* generates strong environmental heterogeneity by affecting the physical–chemical characteristics of the sediment (e.g., Botto and Iribarne, 2000; Palomo et al., 2004; Gutiérrez et al., 2006). Sediments within crab beds are more humid, softer, and homogeneous at all tidal levels as well as through the whole tidal cycle (Escapa et al., 2004). At our study sites, sediments were finer and had a higher organic matter content (OMC) at LTL compared to MTL and HTL. Nevertheless, the presence of crabs shifted sediment characteristics to yet finer grain size and

higher OMC at all tidal levels (Botto and Iribarne, 2000; this study). Higher OMC and finer sediment indicate higher sediment stability (Grant and Daborn, 1994), and less sediment transport by tides within *C. granulatus* crab beds (see Botto and Iribarne, 2000; Botto et al., 2006). Such conditions should facilitate suspension feeding clams in terms of growth and body condition (Holland and Dean, 1977a; Murphy, 1985; Botto and Iribarne, 2000). Our findings indicate, however, that these potentially positive effects of *C. granulatus* on *T. plebeius* are outweighed by negative effects most likely related to crab mobility and bioturbation activity.

The crab effects on the size ratios  $L/H$ ,  $L/W$  and  $W/H$  in damaged (RSD) but not in undamaged individuals (Tables 1 and 2) indicate that the differences in morphometric relations are related to the damage observed at the ventral shell margin. This damage results from direct physical impact (i.e., digging crab damages those shells that come across; Lomovasky et al., 2005). This damage and repair may cause a change in shell geometry (shells becomes shorter and wider). The frequently observed incorporation of sediment grains into the shell matrix during repair growth (see Lomovasky et al., 2005) does not increase shell mass substantially (Table 1). The question remains, however, what are the causes for shell damage outside crab beds (48% RSD compared to 57% at nearby sites with crabs). RSD outside crab beds is of a different type as it is not accompanied by changes in shell geometry (Table 1) and thus may have different origin. We can only speculate here, but the shell of *T. plebeius* is very fragile and therefore they may be easily damaged by a variety of causes. One possible cause may be shell damage by

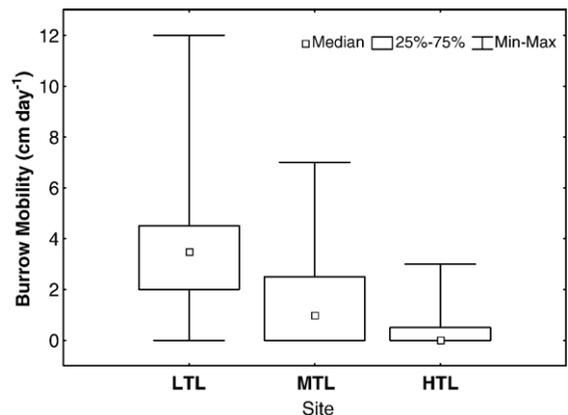


Fig. 5. Effects of tidal level (LTL, MTL, HTL) on displacement of crab burrow. Box plots are constructed with limits of boxes being the 75th and 25th percentiles and vertical bars represent maximum and minimum values; points inside boxes indicate medians. All significant differences with  $p < 0.05$ .

rapid burrowing during escape from predatory attacks, e.g. by the American oystercatcher *Haematopus palliatus* (Bachmann, 1995; Bachmann and Martínez, 1999), an abundant clam predator in this area. Damage by wandering burrowing crabs, which are common during high tide, offer another explanation: they leave digging pits in area not defined as crab beds (Gutiérrez et al., 2004).

The distinct negative effect of crab presence on SM/V and on SFDM/V in both damaged and undamaged shells (Tables 1 and 2) suggests indirect mechanisms are at work. Lower body conditions (mass per volume) as well as lower shell growth rates (Fig. 4) indicate that less energy is available for shell and soft body growth. This may be due to (i) lower energy intake and/or (ii) to higher energy investment in other activities. The crab *C. granulatus* may affect both parts of the clam energy budget. Lower energy intake may result from frequent disruption of feeding during high tide, which is the time of intense suspension feeding (Arruda et al., 2003; personal observation) as well as the time when the crabs roam outside their burrows (see Iribarne et al., 1997). Contact between crabs and siphons will cause siphon retraction and thus a disruption of the water pumping and filtration process. Juvenile crabs settling inside the holes of clam inhalant siphons, where they start constructing their burrows as they grow (Gutiérrez and Iribarne, 1998) and feeding of larger crabs on organic matter accumulated in the depression generated by the clam siphon activity (Gutiérrez and Iribarne, 2004) may also disrupt clam feeding. On the other hand, energy expenditure and allocation of *T. plebeius* may be affected by the burrowing activity of *C. granulatus*, too. Crab burrows are highly mobile in space and time; they can move laterally at rates of up to several centimeters per day (Iribarne et al., 1997; this study). Therefore a clam burrow is likely to be damaged or destroyed frequently when situated within a crab bed, and consequently the clam has to invest more energy in burrow reconstruction (see Lomovasky et al., 2005) and in repair of collateral shell damage (see above).

Crabs and tidal level effects on *T. plebeius* display distinct interactions (Tables 1 and 2). Crab effects on shell geometry and clam soft body condition are most pronounced at low tidal level (LTL) and weakest or even not detectable at high tidal levels (HTL; Fig. 3). This is in line with the increase in the displacement of crab burrows (Fig. 5), higher burrow entrance areas as well as individual activity of crabs (e.g., higher burrow abandonment rate with posterior construction of new burrows) towards LTL, indicating that crabs are adding an additional effect on the typical intertidal physiologi-

cal stress (see above). SM/V of undamaged shells is of particular interest, as here the difference between unaffected and crab-affected shells is highest at MTL and HTL (Fig. 3). This seemingly contradictory pattern results from the strong increase of SM/V with tidal level and the simultaneous decrease in crab impact.

In summary, our findings suggest that the indirect and direct effects of mobility and burrow construction and maintenance of *C. granulatus* are a major constraint for *T. plebeius*, with likely negative implications for population secondary production. Common concepts dealing with the functioning of soft bottoms communities predict that high density of deposit feeders will exclude suspension feeders from the system owing to direct and indirect disturbance caused by the deposit feeder (i.e., functional group hypotheses; Rhoads and Young, 1970; Woodin, 1981; Brenchley, 1981, 1982). Our study indicates, together with a few others (Weinberg, 1984; Murphy, 1985; Gutiérrez and Iribarne, 2003), that such causal relations do not establish deterministic rules but rather propensities (*sensu* Ulanowicz, 1999) which may become a reality conditional upon the actual circumstances. Thus, all evidence suggests that the adaptations of *T. plebeius* to the life in intertidal environments allow them to coexist with this strong bioturbator. The additional stress inflicted by *C. granulatus* does affect the clam negatively, but is not sufficiently high to eliminate it from the system.

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