



ELSEVIER



In Collaboration with the
Royal Netherlands Institute
for Sea Research

Journal of Sea Research 54 (2005) 163–175

JOURNAL OF
SEA RESEARCH

www.elsevier.com/locate/seares

Identifying repaired shell damage and abnormal calcification in the stout razor clam *Tagelus plebeius* as a tool to investigate its ecological interactions

Betina J. Lomovasky^{a,*}, Jorge L. Gutiérrez^{a,b}, Oscar O. Iribarne^{a,c}

^aDepartamento de Biología, FCEyN, Universidad Nacional de Mar del Plata, CC 573 Correo Central, B7600WAG, Mar del Plata, Argentina

^bInstitute of Ecosystem Studies, Millbrook, NY, USA

^cConsejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

Received 5 May 2004; received in revised form 18 January 2005; accepted 18 January 2005

Available online 3 June 2005

Abstract

Analysis of acetate peels of shell sections of the stout razor clam *Tagelus plebeius* from the Mar Chiquita coastal lagoon (37° 32'S, 57° 19'W, Argentina) revealed the presence of a series of repaired shell margin breaks and different types of abnormal calcifications on the inner surface of their valves. Shell damage and subsequent repair was observed in 73% of the specimens analysed (70.3% of them with scars in both valves around the shell margin, 54.5% with the posterior shell area damaged in one or both valves, 30% with more than one damage). There were only few sediment grains incorporated in the shell matrix when scars occurred around the shell margin. A field experiment suggests that this pattern of shell damage results from natural re-burrowing (vertical movement) activities. However, 10% of the individuals showed an inner shell alteration forming a blister full of sediment grains in the area of the shell pallial sinus. These blisters were associated with repaired shell breaks in the posterior part of the valve, which was confirmed with a field experiment. The development of such blisters could be an indirect consequence of sub-lethal predatory attacks by the American oystercatcher *Haematopus palliatus*, given that this species breaks the posterior part of the shells of stout razor clams when extracting them from the sediments. The third type of shell alteration (94.3% of the shells) was an orange to brown coloration on the inner shell surface concurrently with irregular carbonate deposition that, in some cases, results in the formation of localised calcium carbonate concretions. This pattern is associated with the presence of metacercariae of gymnophallid parasites. In conclusion, *Tagelus plebeius* is able to repair its shell after damage produced by different agents. These repairs are very distinctive and, thus, they can be used as evidence of interactions between this clam and its environment (e.g. sediment characteristics) and the associated community (e.g., predators, parasites). © 2005 Elsevier B.V. All rights reserved.

Keywords: *Tagelus plebeius*; Shell damage; Abnormal calcifications; Acetate peels; Predator; Parasitism; Re-burrowing activity; Mar Chiquita Coastal Lagoon

* Corresponding author.

E-mail address: lomovask@mdp.edu.ar (B.J. Lomovasky).

1. Introduction

Shell damage and abnormal calcifications are common phenomena in bivalve molluscs and can result from a series of interactions or disturbances that often lead to different, distinctive marks. For example, natural burrowing activities in the bivalves *Ensis siliqua*, *Lutraria lutraria*, *Mya arenaria* and *Solecurtus strigilatus* cause damage and chipping of the shell edge (Checa, 1993). Predatory attacks by crabs increase the number of scars in the shell of *Glycymeris glycymeris* (Ramsay et al., 2001), and *Geukensia demissa* (Hughes and Seed, 1981). Birds break the posterior margins of the valve in *Tagelus plebeius* (Holland and Dean, 1977b; Bachmann, 1995; Bachmann and Martínez, 1999) and fragment the shells of *Cerastoderma edule*, *Mytilus edulis* and *Ensis directus* (Cadée, 1994, 1995, 2000) leaving recognisable marks. The gastropod *Sinistrofulgur sinistrum* uses its shell lip to chip open the shell of its prey *Mercenaria mercenaria*, often resulting in breakage to its own shell (Dietl, 2003). Moreover, disturbances such as commercial dredging increase the incidence of scars in the shells of *Artica islandica* (Witbaard and Klein, 1994), *Glycymeris glycymeris* (Ramsay et al., 2000), *Ensis arcuatus* (Robinson and Richardson, 1998) and *E. siliqua* (Gaspar et al., 1994, 1998). Calcareous depositions on the inner shell surface such as pearls, calcium carbonate concretions, crests, ridges (Goater, 1993; Cremonte, 1999; Cremonte and Ituarte, 2003) and igloo-like structures (Campbell, 1985; Ituarte et al., 2001) often occur in response to parasites. If properly evaluated, all these marks can provide useful information on the life activity and death of recent and fossil populations (e.g., Carter, 1968; Vermeij et al., 1981; Cadée, 1994; Cadée et al., 1997; Golfieri et al., 1998; Iribarne et al., 1998; Alexander and Dietl, 2001; Dietl, 2003). Thus, recognising them can be useful to understand palaeoecological processes and the relative importance of different sources of disturbance in extant and extinct populations.

The stout razor clam *Tagelus plebeius* is a euryhaline species that inhabits tidal flats with cohesive sandy silt 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; Iribarne and Botto, 1998). Their shells are ubiquitous in Holocene

estuarine deposits of central South America (1340 to 3850 y BP; Fasano et al., 1982; Schnack et al., 1982) and are often used as an indicator of palaeoenvironmental conditions (see Golfieri et al., 1998; Iribarne and Botto, 1998; Iribarne et al., 1998; Aguirre and Farinati, 1999). The extant population is the main food source of the American oystercatcher *Haematopus palliatus* (Bachmann, 1995; Bachmann and Martínez, 1999), which consumes up to 18.8 clams $m^{-2} y^{-1}$ — a remarkably high consumption in relation to a clam density of up to 200 ind m^{-2} (Iribarne et al., 1998). *T. plebeius* also supports a small-scale artisanal fishery along the Argentinean coast. Its maximum age is 14 years and it produces annual growth lines (Lomovasky et al., in prep.). It is a deep-burrowing species that inhabits permanent burrows (up to 0.70 m depth) and shows vertical movements during each semidiurnal tidal cycle. It is a suspension feeder (Holland and Dean, 1977a; Arruda et al., 2003), whose siphons are separated and not visible under field conditions (i.e. no groping behaviour). Despite its deep burrows, it feeds near the sediment surface (0.10 to 0.15 m deep; Holland and Dean, 1977a,b; Arruda et al., 2003; pers. obs.) within reach of long-billed shorebirds such as the American oystercatcher *Haematopus palliatus* (male bill length: mean=70.9 mm, SD=3.96, female bill length: mean=78.8 mm, SD=5.23; Nol and Humphrey, 1994).

A series of shell alterations have previously been observed in *T. plebeius*. These include breakage of the anterior, ventral and posterior margin of the valves (Alexander and Dietl, 2001), the latter being attributed to failed predation attempts by oystercatchers (Bachmann and Martínez, 1999), and an inner calcareous alteration associated with the presence of metacercariae of gymnophallid (Trematoda: Digenea) parasites (morph-type 4; Cremonte, 1999). However, the microstructure of this damage is unknown. Given the past and present importance of this species, the identification and description of the microstructure of repaired shell damages in extant populations may be useful to understand the repair mechanisms and infer ecological processes in extinct and extant populations. Here, we first identify and describe the microstructure of different kinds of repaired shell damage and abnormal calcifications found in an extant population of *Tagelus plebeius*. Then, we examine the contribution of shell repair and alteration to overall

shell mass and experimentally investigate the relationship between damage to the posterior part of the valve and the incorporation of sediments in the shell matrix.

2. Material and methods

2.1. Study site and sampling procedure

Specimens of the stout razor clam *Tagelus plebeius* (n=610) were collected between January and March 2003 in the Mar Chiquita Coastal Lagoon (Argentina, 37° 32'S, 57° 19'W). This is a brackish water area of about 46 km² with muddy sediments and low tidal amplitude (<1 m, Fasano et al., 1982). Sampling was conducted in a tidal flat area along 600 m of shoreline ca. 3 km from the lagoon inlet. Clams were collected by excavating the sediment with a shovel. Shell height (H; from the umbo to the ventral margin), length (L; the anterior-posterior axis) and shell mass (SM) were determined for all the individuals (H and L: precision ± 0.1 mm; SM: precision ± 0.01 g) and their length-frequency distribution was analysed.

2.2. Examination of shell damage

The frequency of shell damage was estimated by visual examination of the valves of all the specimens collected. Damage was classified according its position in the shell (i.e., around the shell margins, anterior, posterior and inner shell) and as to whether it occurred in one or both valves.

To investigate growth disturbance, shell scars and abnormal calcifications, left valves (n=100) were embedded in epoxy resin and sectioned along the axis containing the portion of repaired shell damage using a diamond saw. The cross-sections were polished on a grinding machine using grits of 180, 400, 600, 1200 and 2400 grade, and etched for 10 min using 0.5% DE-CAL agent. Acetate peel replicates (recommended by Gaspar et al., 1994; Ramsay and Richardson, 2000) were made of the cross-sectioned surfaces to allow microscopic examination (see Rhoads and Lutz, 1980). These peels were examined using 100 and 200 × magnifications.

The abnormal calcareous structures and shell damages identified by direct visual observation were

also examined in X-ray photographs. X-ray photographs allowing the identification of higher density structures were taken with a Hewlett Packard Faxitron 43855 mammograph with fixed anode, using AGFA-Strukturix D4 FW film and the following parameter setting: focal film distances 45 cm, voltage 30 to 45 KV, exposure time 90 to 120 s.

2.3. Changes in shell mass due to damage

Differences in shell mass between animals with different loads of parasitism (n=98; 54.72 to 70.36 mm L) were evaluated. Although the prevalence of gymnophallid parasites in *T. plebeius* (i.e. the percentage of the sampled clams that are hosts to these parasites) is 100%, the intensity of infection ranges between less than 200 to more than 800 parasites per clam (Cremonte, 1999). Variation in the intensity of infection is related to the intensity of coloration in the inner surface of the shell (Cremonte, 1999). Using inner shell coloration as a surrogate of parasitic load, we tested for differences in shell mass between clams showing high and low intensity of infection (extreme cases). High parasitism (>800 parasites per clam) was attributed to shells with 90 to 95% of the inner surface coloured dark reddish-brown, while low parasitism (<200 parasites per clam) was attributed to shells that had less than 5% of the inner surface with such coloration (Cremonte, 1999; pers. obs.). Although there were intermediate degrees of inner shell coloration, they were excluded from our statistical analyses because they cannot be unequivocally related to a given level of parasitic load based on current knowledge. Parallelism tests (Zar, 1984) were used to compare the slope of relationship between shell mass (SM) and shell length (L) between shells of clams with high and low parasitic load. Given that the slope of the relationship between shell mass (SM) and shell length (L) differed significantly between shells from specimens with low and high parasitism (see Results), we were unable to use ANCOVA (see Zar, 1984). Consequently, the following index (hereafter 'Shell mass condition index', CI) was calculated to test for differences in shell mass associated with variations in the incidence of parasitism:

$$CI = \text{Shell Mass}/\text{Length}^b \quad (1)$$

Where b is the slope of the linear relationship between shell mass and shell length after log-transformation of both variables:

$$\text{Log (Shell Mass)} = a + b \cdot (\text{log (Length)}). \quad (2)$$

To evaluate the null hypothesis of no difference in the shell mass condition index between shells from clams with low and high parasitism we performed a t test. The assumptions of normality and homogeneity of variances were tested using the Kolmogorov-Smir-

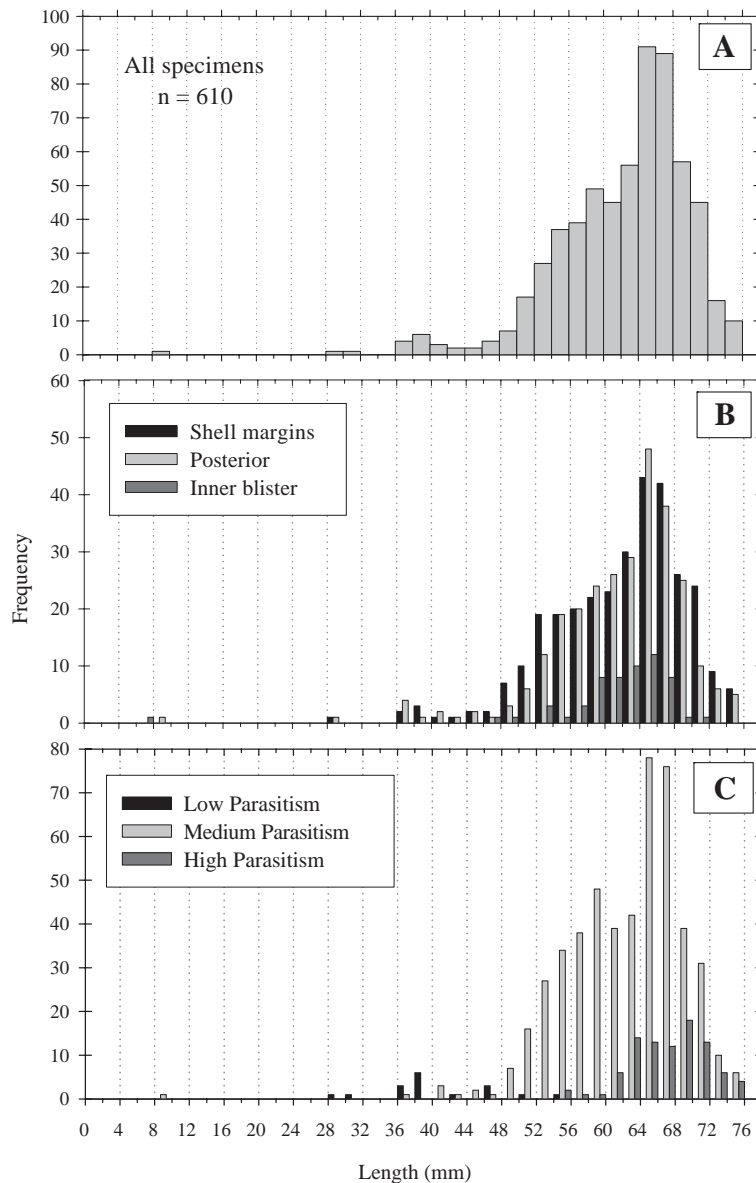


Fig. 1. (A) Size frequency distribution of anterior-posterior length of 610 specimens of *Tagelus plebeius* sampled from Mar Chiquita Coastal Lagoon; (B) size frequency distribution of specimens with different types of damage; (C) and with different intensity of coloration in the inner surface of the valve (load of parasitism low:<200 parasites per bivalve, medium:>200 to 800 parasites per bivalve, high:>800 parasites per bivalve, see [Cremonte, 1999](#)).

nov test and the Levene's test, respectively (Zar, 1984; Sokal and Rohlf, 1995).

The contribution of blister-like alterations to shell mass was analysed by comparing the weight of individual valves in specimens showing an intact and an altered valve ($n=11$). The null hypothesis of no difference in the shell mass between valves with blisters and without them was evaluated using a paired t test (Zar, 1984).

2.4. Relationship between damage in the posterior edge and blister formation

A mark-recapture experiment was carried out from 14 May 2003 to 16 May 2004 to investigate whether the presence of sediment in the shell matrix and the development of blisters is a consequence of damage in the posterior part of the valve. Sixty individuals of different sizes (12.25 to 27.75 mm H, average 19.96 mm H) were collected, measured and marked with numbered plastic labels adhered to the surface of the periostracum. Thirty-two of these

individuals were experimentally damaged in the posterior part of the valve (mimicking the damage produced by the local oystercatcher) while the remaining individuals were left intact (treatments were randomly assigned). We used a larger number of damaged than intact individuals because previous observations had shown a higher mortality of damaged individuals during the experimental period. Each animal was then returned to the intertidal area and allowed to burrow in individual PVC tubes (10 cm diameter and 50 cm long) vertically buried with their upper border flush with the surface of the surrounding substratum. The walls of these tubes were perforated to permit the horizontal flow of water. The animals were recovered after one year and their shells were examined by visual analysis and the acetate peel technique as described above. A chi-square test (Zar, 1984) was used to investigate whether the frequency of sediment intrusions in the inner surface of the shell differed between intact and experimentally damaged clams. Clam mortality occurred during the experimental period leading to

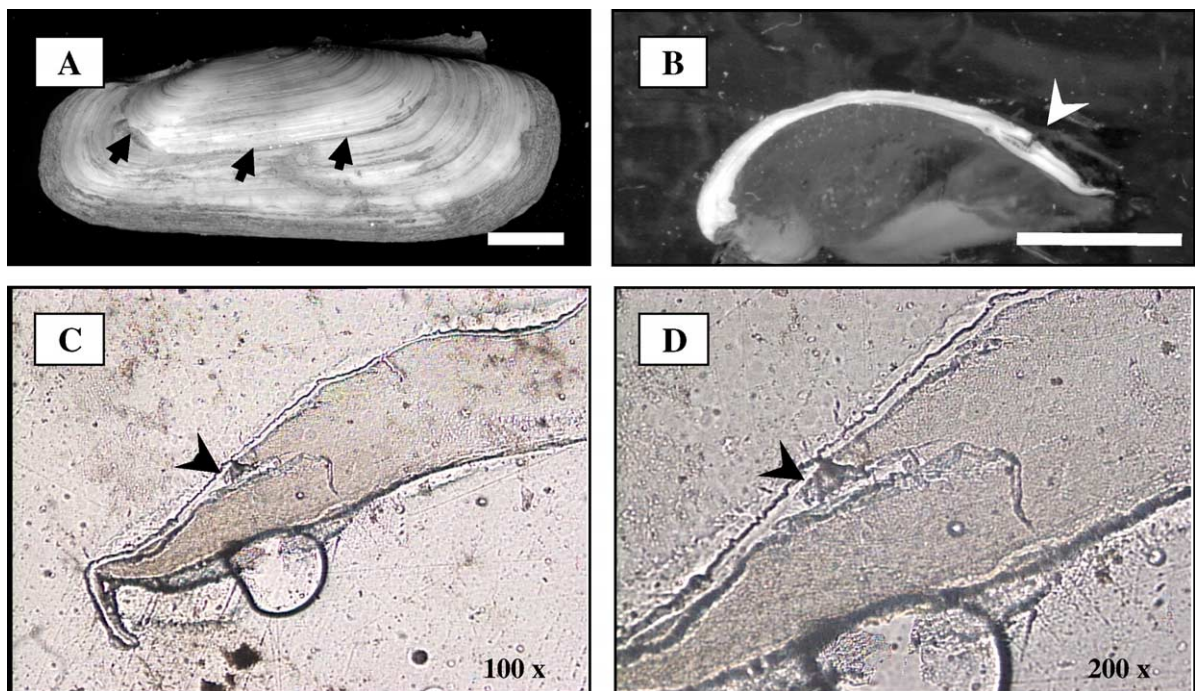


Fig. 2. Scars around the shell margin in valves of *Tagelus plebeius*: (A) photograph of the right valve; (B) shell section showing the shell break (white arrow); (C, D) photomicrographs of acetate peel replicates of shell sections showing shell breaks with some sediment grains (black arrows). Scale bar=10 mm.

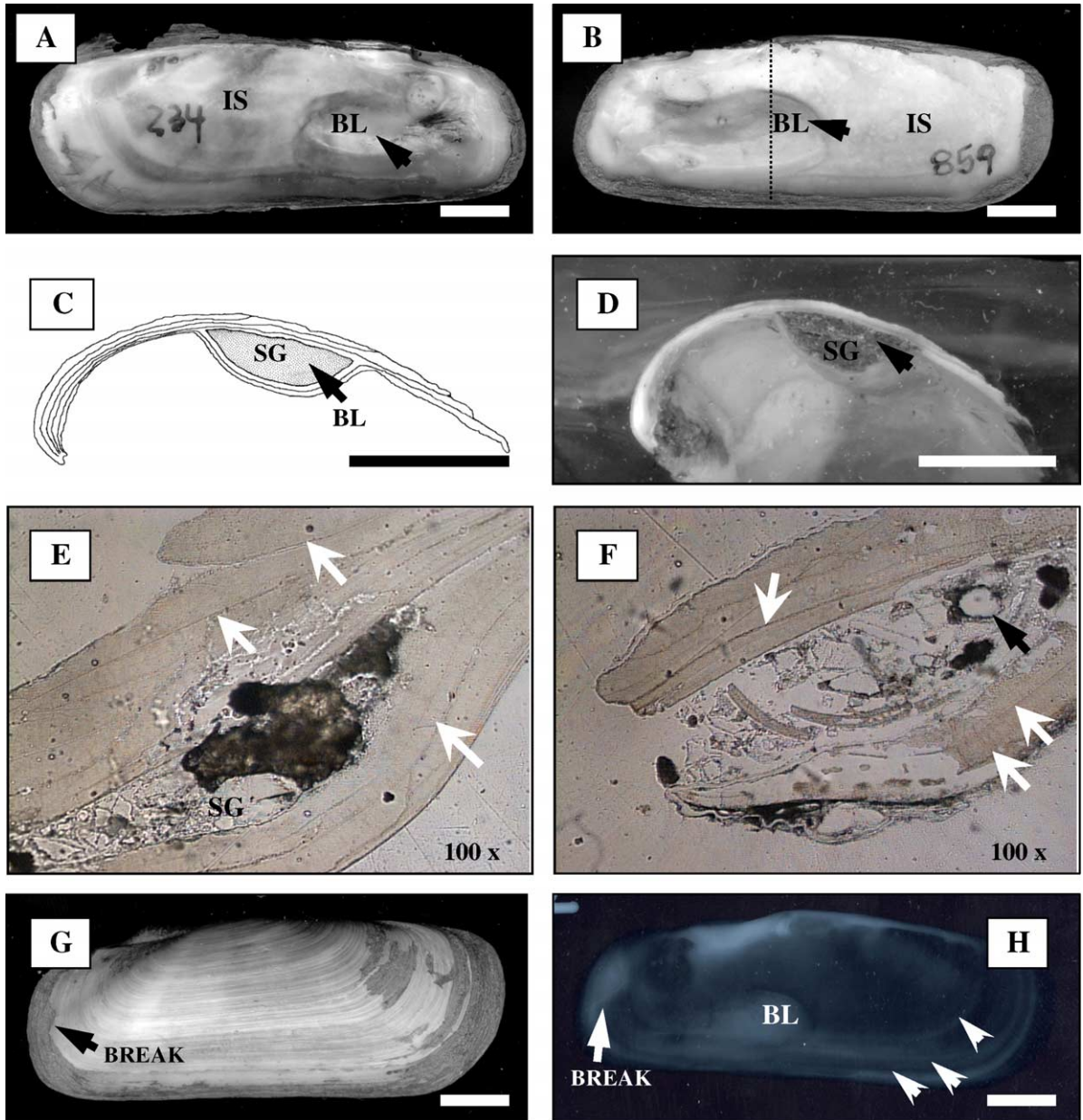


Fig. 3. (A, B) Inner alteration on the shell pallial sinus developing a blister (pocket-like structure) of a right and left valve, respectively (dotted line: cut axis); (C) scheme of the shell cross-section showing the blister; (D) photograph of the shell section showing the blister full of sediment grains; (E, F) acetate peels showing the grains incorporated between the old and newly accreted shell developing a blister; (G) association between blister-like alterations and repaired shell damage at posterior part of the valve; (H) X-ray photomicrography showing the posterior shell damage and the different calcareous density. BL: blister; IS: inner surface; SG: sediment grains; white arrows: translucent growth bands. Scale bar=10 mm.

an unbalanced design with sample sizes of 17 and 14 for intact and experimentally damaged clams, respectively. The number of replicates was re-balanced by randomly discarding three intact clams.

3. Results

The sizes of *Tagelus plebeius* used in this study (n=610) were between 6.57 and 73.78 mm L with a mean length of 60.24 mm and median of 62.09 mm L (Fig. 1A). Repaired shell damage was evident in 73% of the sampled specimens and 30% of them showed more than one repair in different parts of the valve. Most (70.3%) of the shells had scars in both valves around the shell margin, and 54.5% had a repaired damage at the posterior part of the valve. In general, sediment particles were observed in the damaged area between the old and newly accreted shell.

Acetate peels of shell sections allowed us to distinguish the microscopic characteristics of the different types of shell repair. Scars around the shell margin

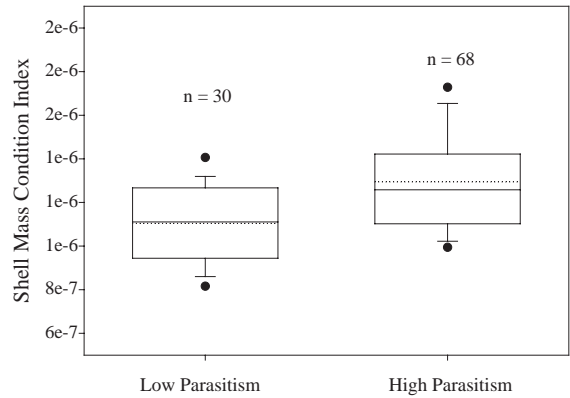


Fig. 5. Shell Mass Condition Index in *Tagelus plebeius* with low and high parasitism. Box plots are constructed with limits of boxes being the 75th and 25th percentile and vertical bars represent 5th and 95th percentile. Solid lines inside boxes indicate means, dotted lines indicate medians and circles represent outliers.

were common in all length size classes (Figs. 1B, 2A), and all of them occurred in both valves at the same time. They showed only few sediment grains embedded in the shell matrix. Cross-sections of

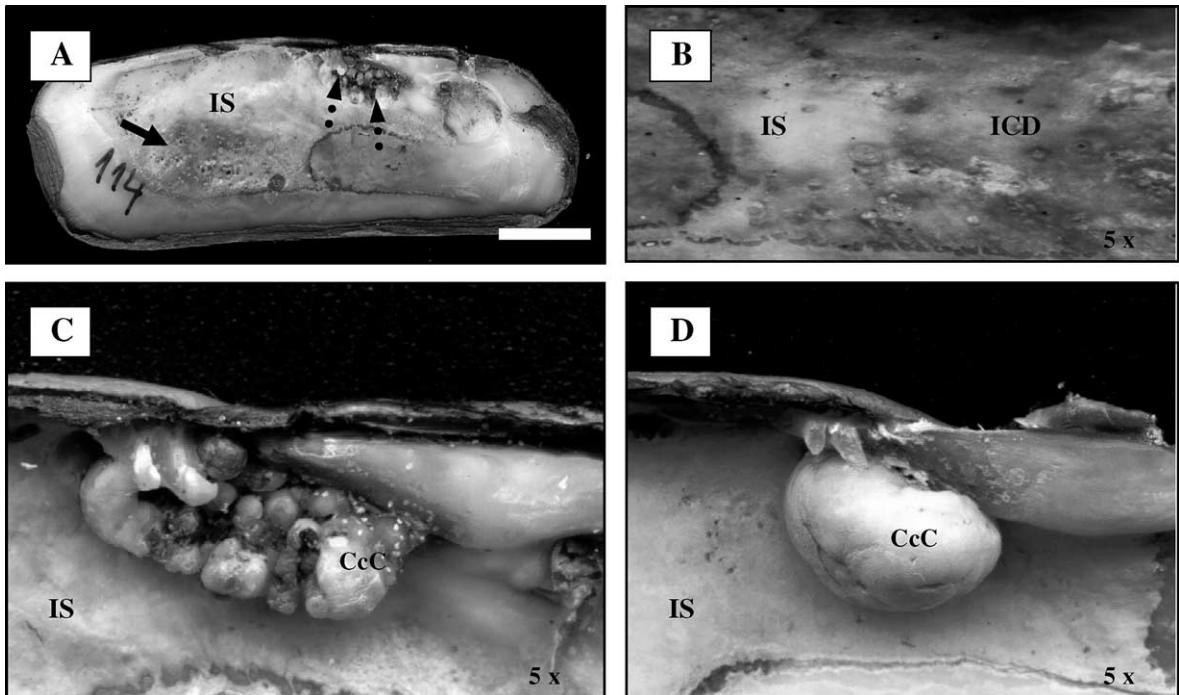


Fig. 4. (A) Inner shell alterations in valves of *Tagelus plebeius* elicited by digenean parasites; (B) irregular carbonate depositions on the inner shell surface; (C, D) calcium carbonate concretions observed on the inner area of the valve in some specimens. CcC: calcium carbonate concretions; ICD: irregular carbonate depositions; IS: inner surface. Scale bar=10 mm.

these shells showed the interruption of shell growth (Fig. 2B) and photomicrographs of acetate peels (Fig. 2C, 2D) showed the incorporation of sediment grains between the internal growth bands.

An inner shell alteration that develops a blister (pocket-like structure) on the shell pallial sinus (Fig. 3A, 3B) was found in 10% of the shells and was present in all size classes (Fig. 1B). Shell cross-sections showed (Fig. 3C, 3D) that these structures were full of sediment grains. The incorporation of sediment grains increased the shell mass of each valve $11.83\% \pm 7.26\%$ (Paired sample t-test: $t = -4.45$, $df = 10$, $p < 0.01$). Acetate peels showed the grains incorporated between the old and newly accreted growth bands (Fig. 3E, 3F). All these alterations

were associated with repaired shell damage of the posterior part of the valve (Figs. 1B, 3G, 3H).

Most (94.3%) of the clams (Fig. 1C) were orange to brown in the inner part of the valve and had irregular carbonate depositions (Fig. 4A, 4B) earlier associated with the presence of gymnophallid metacercariae parasites (Cremonte, 1999). Concretions of calcium carbonate associated with an intense coloration on the inner surface of the shell were observed in 5.9% of the individuals (Fig. 4C, 4D). Irregular carbonate depositions and concretions (high parasitism) significantly increased the shell mass ($t_{0.05,96} = -3.94$; $p < 0.05$; Fig. 5). Photomicrographs of acetate peels taken from these shells (Fig. 6) showed alteration in the deposition of growth bands, and abnormal calcifi-

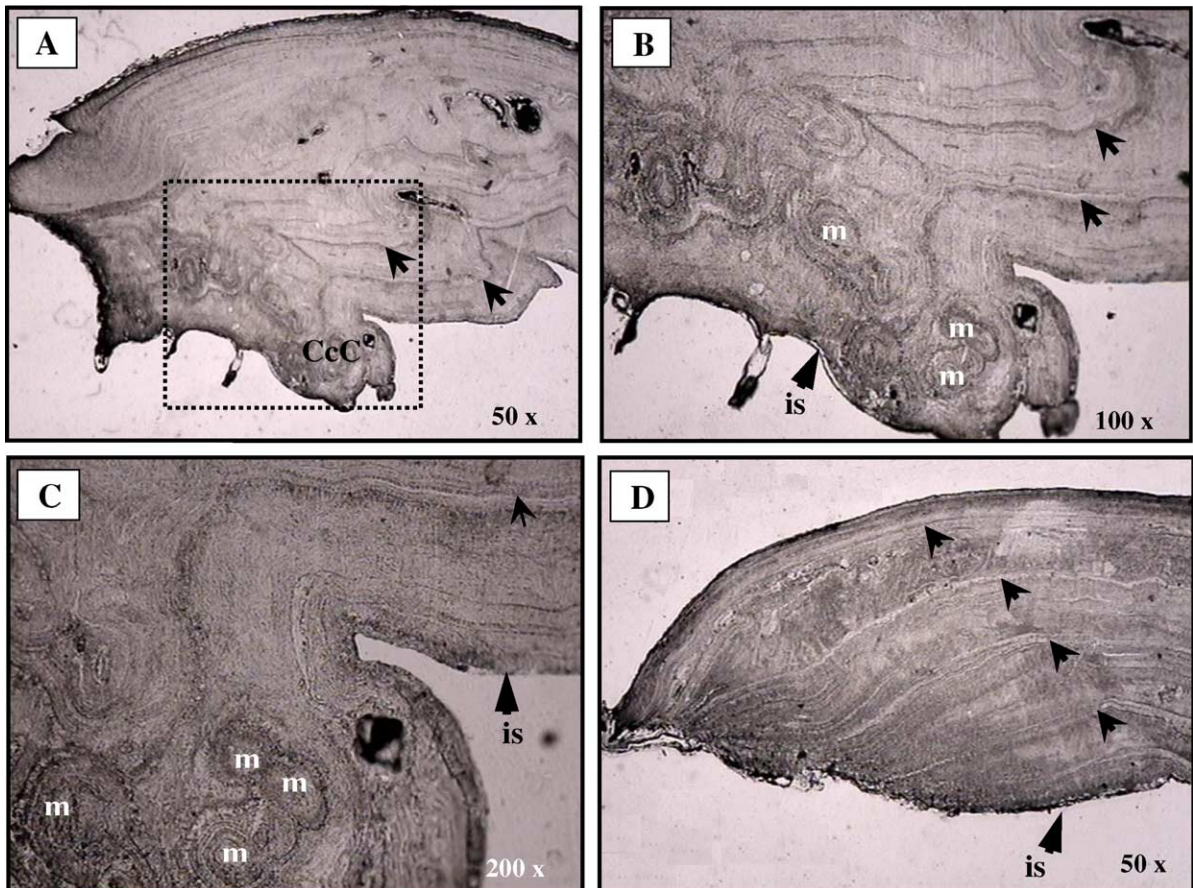


Fig. 6. Photomicrographs of acetate peels showing alteration of the inner shell surface elicited by parasites. (A) Umbo with calcium carbonate concretions; (B, C) enlargement of the area depicted in (A) with calcium carbonate concretions showing metacercariae with multiple concentric layers and alterations in the deposition of growth bands; (D) umbo with normal growth bands and inner shell surface. CcC: calcium carbonate concretions; IS: inner surface; m: metacercariae; black arrows: translucent growth bands.

cations with multiple concentric layers in the inner shell surface. The lower levels of parasitism were in smaller individuals while larger individuals showed the higher levels (Fig. 1C).

Of the 60 individuals introduced in the mark-recapture experiment, only 31 survived after one year. Eleven out of the 14 clams that survived the transplant after the experimental damage of the posterior part of their valves showed inner shell alterations consisting of a blister with sediment grains similar to those described above. No inner shell alterations were observed in intact animals. A chi-square test conducted with balanced sample sizes of 14 (i.e. after eliminating three of the zero data from intact clams) indicated that sediment blisters occur at a significantly higher density in damaged than intact clams ($\chi^2=35$, $df=2$, $p<0.01$). Scars around the shell margin were observed in all the surviving animals coinciding with the size that shells had at the beginning of the experiment.

4. Discussion

The shells of *Tagelus plebeius* exhibit a number of surface marks, including growth rings, repaired shell margin breaks and abnormal calcifications. Damage and repair around the shell margin is associated with the inclusion of sediment grains into the shell matrix (Fig. 2). Damage and chipping of the shell edge was observed in the bivalves *Ensis siliqua*, *Lutraria lutraria* and *Mya arenaria* as a consequence of their natural burrowing movements (Checa, 1993). A similar pattern of repaired shell damage in the razor clam *Ensis siliqua* from Barrinha, Southern Portugal, is attributed to dredge operations (Gaspar et al., 1994). However, it was not investigated whether the damage was caused by the dredge itself or by the re-burrowing activity of the discarded bivalves. In the present study, we found that all the individuals that survived our mark-recapture experiment showed scars in the margin of their shells, irrespective of whether their posterior part was experimentally damaged or not. Considering that re-burrowing is a necessary part of the mark-recapture procedure, the damage observed around the edge of *T. plebeius* shells could be the consequence of the re-burrowing activity and the vertical movements of the clams after being removed

from the sediments, as proposed for *Solecurtus strigilatus* (Checa, 1993), *Ensis directus*, *Mya arenaria* and dead specimens of *Tagelus plebeius* from New Jersey (Alexander and Dietl, 2001). Indeed, *T. plebeius* inhabit permanent deep burrows. This clam maintains compact burrow walls in stable structures exerting continual pressure against the burrow walls by gaping during slower-growing adult stages and by a continuous vertical movement in the burrow (Holland and Dean, 1977a). Disturbances of the sediment could destroy their burrows and vertical movements are necessary for burrow reconstruction, with concomitant shell damage.

While various disturbances may affect the structure of tidal flat sediments, only a few go deep enough to disrupt the stout razor clam burrows (see Hall, 1994). These include the disturbances associated with the harvesting of infaunal organisms and the burrowing activity of large bioturbators. The harvesting of stout razor clams to be used as bait was a small-scale activity in the region before 1999 (Gutiérrez and Valero, 2000; Gutiérrez et al., 2004), but is currently forbidden. Local fishermen dug for clams during low tide using hand shovels (Gutiérrez et al., 2004). However, our study site remained unexploited because of its inaccessibility (see Gutiérrez et al., 2004). In contrast, the study area showed fluctuating densities of the burrowing crab *Chasmagnathus granulatus* (up to 20.3 ind m^{-2} ; Botto and Iribarne, 1999, 2000). This species constructs large (up to 2 l volume and 40 cm depth) semi-permanent burrows in tidal flat sediments with remarkably high rates of sediment excavation (up to 5.9 kg $m^{-2} d^{-1}$; Iribarne et al., 1997). Moreover, their burrows show lateral displacement (3.2 cm d^{-1} ; Iribarne et al., 1997), which may cause considerable disruption of clam burrows even when crabs are scarce. This suggests that crab bioturbation is the major source of disruption for clam burrows.

Damage in the posterior margin of shells of *Tagelus plebeius* is often (18.35%) associated with a blister full of sediment grains in the inner part of each valve (Fig. 3) and is likely to be the consequence of a sublethal attack by the American oystercatcher *Haematopus palliatus* (Bachmann, 1995; Bachmann and Martínez, 1999). This is the most important predator of *T. plebeius* in our study site (Bachmann, 1995; Iribarne et al., 1998; Bachmann and Martínez, 1999). Oystercatchers use the ‘single

probe' technique when searching for clams (Bachmann and Martínez, 1999), which are relatively close to the sediment surface when pumping and feeding (0.10 to 0.15 m deep; Holland and Dean, 1977a; pers. obs.). They use their long bill to extract the clams from their burrows, grasping the posterior portion of a valve and in 65% of cases chipping the posterior margin of the shells (Fig. 7; Holland and Dean, 1977b; Iribarne et al., 1998; Bachmann and Martínez, 1999). The damage found in the posterior margin of shells of many living clams (this study) is similar to that resulting from a successful predatory attack by the oystercatcher (see Fig. 7).

Specimens of *T. plebeius* collected from death assemblages in New Jersey showed the same type of damage at the posterior end as observed here. That damage was attributed to siphon nipping (Alexander

and Dietl, 2001). However, stout razor clams rarely regenerated siphons in our study area (pers. obs.). This suggests that the damage of the posterior end of the shell is the consequence of failed predation attempts by oystercatchers. There is evidence in other bivalves that attacks by birds result in the production of fragments and distinctive marks (Carter, 1968; Cadée, 1994, 1995, 2000, 2001).

Our field experiment showed that when individuals are damaged at the posterior end of their valves, mimicking the damage produced by oystercatchers, they have a high probability (75%) of developing a blister with sediment grains. The incorporation of small amounts of sediment grains into the shell matrix has been reported for other bivalves such as *Ensis siliqua* (Gaspar et al., 1994) and *Arctica islandica* (Witbaard and Klein, 1994). In *Lutraria lutraria*, *L. magna*, *Panopea glycymeris*, *Ensis siliqua* and *Solen vagina*, a similar sediment intrusion between the inner shell surface and mantle was observed and attributed to unsuccessful predatory attacks (Checa, 1993). The development of blisters in *Tagelus plebeius* is likely to be the consequence of, (a) the incorporation of large quantities of sediment into the extrapallial space when the posterior part of the valve is damaged and, (b) subsequent growth increments that cover the incorporated sediments. A shell break is likely to separate the shell-secreting epithelium of the mantle from the shell margin allowing sediments to penetrate into the extrapallial space. Then, newly accreting shell develops as a blister that excludes the foreign particles from the animal's internal part (Fig. 8). The acetate peel confirmed this deposition pattern (Fig. 3E, 3F).

Other types of shell alteration found in *T. plebeius* are those associated with the presence of metacercariae of gymnophallid parasites (see Cremonte, 1999; Fig. 4). Abnormal calcifications with multiple concentric layers in the inner shell surface were observed in photomicrographs of acetate peels of *T. plebeius* (Fig. 6). The intensity of parasitism is positively correlated with the development of calcium carbonate concretions and the intensity of the coloration on the inner shell surface of *T. plebeius* (Cremonte, 1999). As described by Cremonte (1999), parasitic load increased with clam size (Fig. 1C). Shell alterations were observed in the clam *Darina solenoides* (5 to



Fig. 7. Photographs of the shell damage produced by the American oystercatcher *Haematopus palliatus* in the posterior part of the valve of *Tagelus plebeius* after a successful attack. Scale bar=10 mm.

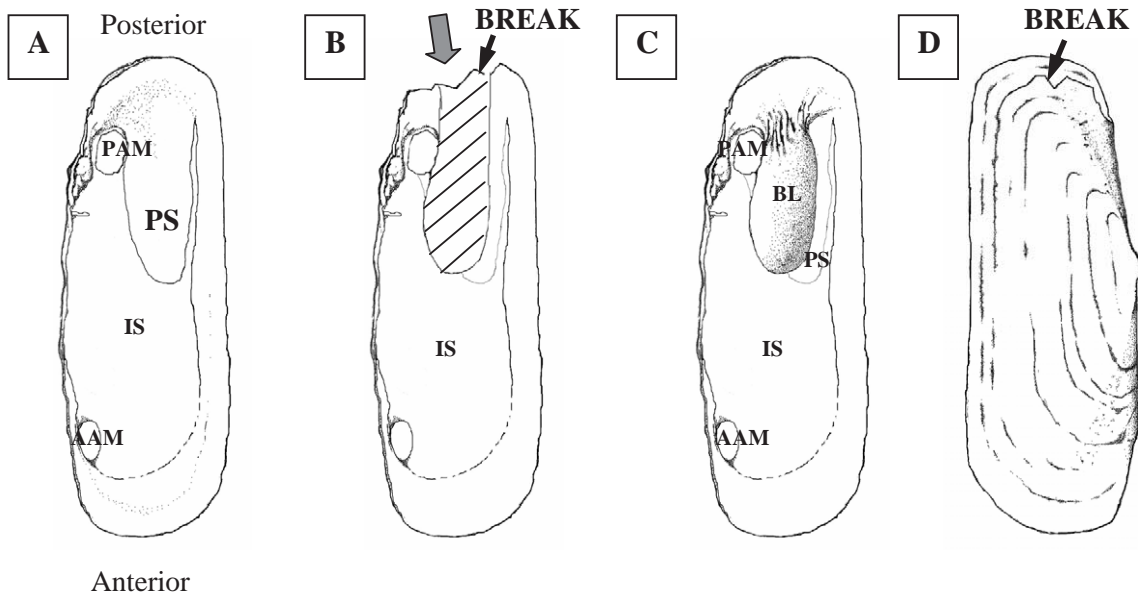


Fig. 8. Hypothesised process of incorporation of sediment grains. (A, B) Major damage in the posterior part of the valve occurs, large quantities of sediment are incorporated into the extrapallial space; (C) subsequent growth increments cover the sediment incorporated in the extrapallial space forming a blister; (D) view of external shell surface with repaired shell damage in the posterior part of the valve. AAM: anterior adductor muscle; BL: blister; IS: inner surface; PAM: posterior adductor muscle; PS: pallial sinus.

13% of examined specimens) similar to those caused by metacercariae of the gymnophallid *Bartolius pierrei* (Cremonte and Ituarte, 2003). Such alterations are likely to result from the encapsulation of digenean metacercariae by the bivalve host in the extrapallial space (i.e. a cellular defence mechanism against foreign particles; see Cremonte and Ituarte, 2003). The reaction starts in the extrapallial space leading to the formation of a sac consisting of a one-cell-thick layer originated in an invagination of the mantle epithelium that contains the metacercariae. Then, this sac loses the connection with the extrapallial space and mantle tissues and generates a wall formed by multiple layers of aragonite (Cremonte, 1999). Such abnormal calcification, which is associated with relatively old infections (Cremonte and Ituarte, 2003), leads to a significant increase in the shell mass of the host (Fig. 4).

The increased shell mass observed in the present study as a possible consequence of both failed predation attempts (i.e. incorporation of sediment grains and development of blisters) and parasitism (i.e. calcium carbonate concretions) suggests that stout razor clams make a major energetic investment in repairing

their shells, which is likely to affect their growth rate. Thus, the activity of predators and parasites could have important non-lethal effects on stout razor clam populations, with potential implications for secondary production in their estuarine ecosystems. Moreover, increases in shell calcification after repair can enhance shell hardness and, thus, their persistence in the fossil record. Consequently, recognising the different types, sources and characteristics of repaired shell damage and abnormal calcifications in *T. plebeius* is useful not only to understand the interaction between this clam and its environment (sediment characteristics) and community (predator-prey interactions; parasitism) in extant and extinct populations, but also to identify biases in the fossil record that could affect palaeoecological analysis.

Acknowledgements

We thank Agustina Méndez Casariego, Martín Bruschetti, Paulina Martinetto and Gabriela Palomo for field assistance and Florencia Cremonte for her guidance in the analysis of parasitism. *J. Sea Res.*

Editor G.C. Cadée and three anonymous referees provided valuable suggestions that greatly improved the manuscript. This project was supported by a grant from the British Ecological Society (SEPG No. 2218) to B.J. Lomovasky; and grants from Universidad Nacional de Mar del Plata, International Foundation for Science (Sweden; No. A2501-2F), Fundación Antorchas (Argentina; No. A013672 and No. 13900-13) and CONICET (Argentina; PIP No. 2851) to O.O. Iribarne. B.J. Lomovasky and J.L. Gutiérrez were supported by fellowships from CONICET (Argentina).

References

- Aguirre, M.L., Farinati, E.A., 1999. Taphonomic processes affecting late Quaternary molluscs along the coastal area of Buenos Aires Province (Argentina; Southwestern Atlantic). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 149, 283–304.
- Alexander, R., Dietl, G.P., 2001. Shell repair frequencies in New Jersey bivalves: a recent baseline for tests of escalation with Tertiary, Mid-Atlantic congeners. *Palaios* 16, 354–371.
- Arruda, E.P., Domaneschi, O., Amaral, A.C.Z., 2003. Mollusc feeding guilds on sandy beaches in Sao Paulo State, Brazil. *Mar. Biol.* 143, 691–701.
- Bachmann, S., 1995. Ecología alimentaria del ostrero pardo, *Haematopus palliatus*, en la Albufera de Mar Chiquita. Licenciado degree thesis, Universidad Nacional de Mar del Plata, Argentina. 41 pp.
- Bachmann, S., Martínez, M.M., 1999. Feeding tactics of the American oystercatcher (*Haematopus palliatus*) in Mar Chiquita Coastal Lagoon, Argentina. *Ornit. Neotrop.* 10, 81–84.
- Botto, F., Iribarne, O., 1999. Effect of the burrowing crab *Chasmagnathus granulata* (Dana) on the benthic community of a SW Atlantic coastal lagoon. *J. Exp. Mar. Biol. Ecol.* 241, 263–284.
- Botto, F., Iribarne, O., 2000. Contrasting effects of two burrowing crabs (*Chasmagnathus granulata* and *Uca uruguayensis*) on sediment composition and transport in estuarine environments. *Est. Coast. Shelf Sci.* 51, 141–151.
- Cadée, G.C., 1994. Eider, shelduck, and other predators, the main producers of shell fragments in the Wadden Sea: palaeoecological implications. *Palaeontology* 37, 181–202.
- Cadée, G.C., 1995. Birds as producers of shell fragments in the Wadden Sea, in particular the role of the Herring gull. *Geobios* 18, 77–85.
- Cadée, G.C., 2000. Herring gulls feeding on a recent invader in the Wadden Sea, *Ensis directus*. In: Harper, E.M., Taylor, J.D., Cramer, J.A. (Eds.), *The Evolutionary Biology of the Bivalvia*, Spec. Publ. Geol. Soc. London, vol. 177, pp. 459–464.
- Cadée, G.C., 2001. Herring gulls learn to feed on a recent invader in the Dutch Wadden Sea, the Pacific oyster *Crassostrea gigas*. *Basteria* 65, 33–42.
- Cadée, G.C., Walker, S.E., Flessa, K.W., 1997. Gastropod shell repair in the intertidal of Bahía la Choya (N. Gulf of California). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 136, 67–78.
- Campbell, D., 1985. The life cycle of *Gymnophallus rebecqui* (Digenea: Gymnophallidae) and the response of the bivalve *Abra tenuis* to its metacercariae. *J. Mar. Biol. Ass. UK* 65, 589–601.
- Carter, R.M., 1968. On the biology and palaeontology of some predators of bivalve molluscs. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 4, 29–65.
- Checa, A., 1993. Non-predatory shell damage in recent deep-endobenthic bivalves from Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 100, 309–331.
- Cremonte, F., 1999. Estudio parasitológico de bivalvos que habitan ambientes marinos y mixohalinos en Argentina. Ph.D. Thesis, Universidad Nacional de La Plata, Argentina. 194 pp.
- Cremonte, F., Ituarte, C., 2003. Pathologies elicited by the Gymnophallid metacercariae of *Bartolius pierrei* in the clam *Darina solenoides*. *J. Mar. Biol. Ass. UK* 83, 311–318.
- Dietl, G.P., 2003. Interaction strength between a predator and dangerous prey: *Sinistrofulgur* predation on *Mercenaria*. *J. Exp. Mar. Biol. Ecol.* 289, 287–301.
- Fasano, J.L., Hernández, M.A., Isla, F.I., Schnack, J.E., 1982. Aspectos evolutivos y ambientales de la Laguna Mar Chiquita (provincia de Buenos Aires, Argentina). *Oceanol. Acta (Suppl. A)*, 285–292.
- Gaspar, M.B., Richardson, C.A., Monteiro, C.C., 1994. The effects of dredging on shell formation in the razor clam *Ensis siliqua* from Barrinha, Southern Portugal. *J. Mar. Biol. Ass. UK* 74, 927–938.
- Gaspar, M.B., Castro, M., Monteiro, C.C., 1998. Influence of tow duration and tooth length on the number of damaged razor clams *Ensis siliqua*. *Mar. Ecol. Prog. Ser.* 169, 303–305.
- Goater, C.P., 1993. Population biology of *Meiogympophallus minutus* (Trematoda: Gymnophallidae) in cockles from the Exe Estuary. *J. Mar. Biol. Ass. UK* 73, 163–177.
- Golfieri, G.A., Ferrero, L., Zárate, M., 1998. Tafonomía y paleoecología de *Tagelus plebeius* (Lightfoot, 1786) (Mollusca, Bivalvia) en sedimentos Holocenos del Río Quequén Grande, Provincia de Buenos Aires, Argentina. *Ameghiniana* 35, 255–264.
- Gutiérrez, J., Valero, J., 2000. La almeja navaja *Tagelus plebeius* y su participación en mecanismos ecológicos de comunidades intermareales mediante la producción de valvas. In: Iribarne, O. (Ed.), *Reserva de la Biósfera Mar Chiquita: Características Físicas, Biológicas y Ecológicas*. Editorial Martín, Mar del Plata, pp. 121–128.
- Gutiérrez, J., Palomo, M.G., Iribarne, O., 2004. Environmental heterogeneity and species responses to fishing disturbance: are the effects of clam harvesting spatially consistent? *Fish Res.* 67, 55–70.
- Hall, S.J., 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanogr. Mar. Biol. Ann. Rev.* 32, 179–239.
- Holland, A.F., Dean, J., 1977a. The biology of the stout razor clam *Tagelus plebeius*. I. Animal-sediment relationships, feeding mechanism and community biology. *Chesapeake Sci.* 18, 58–66.

- Holland, A.F., Dean, J., 1977b. The biology of the stout razor clam *Tagelus plebeius*. 2. Some aspects of the population dynamics. Chesapeake Sci. 18, 188–196.
- Hughes, R.N., Seed, R., 1981. Size selection of mussels by the blue crab *Callinectes sapidus*: Energy maximizer to time minimizer? Mar. Ecol. Prog. Ser. 6, 83–89.
- Iribarne, O., Botto, F., 1998. Orientation of the extant stout razor clam *Tagelus plebeius* in relation to current direction: its paleoecologic implications. J. Shellfish Res. 17, 165–168.
- Iribarne, O., Bortolus, A., Botto, F., 1997. Between-habitat differences in burrow characteristics and trophic modes in the southwestern Atlantic burrowing crab *Chasmagnathus granulata*. Mar. Ecol. Prog. Ser. 155, 132–145.
- Iribarne, O., Valero, J., Martínez, M.M., Lucifora, L., Bachmann, S., 1998. Shorebird predation may explain the origin of Holocene beds of stout razor clams in life position. Mar. Ecol. Prog. Ser. 167, 301–306.
- Iuarte, C.F., Cremonte, F., Deferrari, G., 2001. Mantle-shell complex reactions elicited by digenean metacercariae in *Gaimardia trapesina* (Bivalvia: Gaimardiidae) from the Southwestern Atlantic Ocean and Magellan Strait. Dis. Aquat. Org. 48, 47–56.
- Leal, J.H., 2002. Bivalvia. In: Carpenter, K.E. (Ed.), The Living Marine Resources of the Western Central Atlantic. I: Introduction, Mollusks, Crustaceans, Hagfishes, Sharks, Batoid Fishes and Chimaeras. FAO Identification Guide for Fishery Purposes. FAO, Rome, pp. 25–98.
- Nol, E., Humphrey, R.C., 1994. American oystercatcher (*Haematopus palliatus*). In: Poole, A., Stettenheim, P., Gill, F. (Eds.), The Birds of North America, N° 82. Philadelphia: Acad. Nat. Sci., Washington DC. Amer. Ornithol. Un., pp. 9–24.
- Olivier, S.R., Escofet, A., Penchaszadeh, P., Orensanz, J.M., 1972a. Estudios ecológicos de la region estuarial de Mar Chiquita (Buenos Aires, Argentina). I: Las comunidades bentónicas. An. Soc. Cient. Argentina 193, 237–262.
- Olivier, S.R., Escofet, A., Penchaszadeh, P., Orensanz, J.M., 1972b. Estudios ecológicos de la region estuarial de Mar Chiquita (Buenos Aires, Argentina). II: Relaciones tróficas. An. Soc. Cient. Argentina 194, 84–104.
- Ramsay, K., Richardson, C.A., 2000. Techniques for assessing repaired shell damage in dog cockles *Glycymeris glycymeris* L. J. Shellfish Res. 19, 927–931.
- Ramsay, K., Kaiser, M.J., Richardson, C.A., Veale, L.O., Brand, A.R., 2000. Can shell scars on dog cockles (*Glycymeris glycymeris* L) be used as an indicator of fishing disturbance? J. Sea Res. 43, 167–176.
- Ramsay, K., Richardson, C.A., Kaiser, M.J., 2001. Causes of shell scarring in dog cockles *Glycymeris glycymeris* L. J. Sea Res. 45, 131–139.
- Rhoads, D.C., Lutz, R.A. (Eds.), 1980. Skeletal Growth of Aquatic Organisms. Plenum Press, New York, p. 750.
- Robinson, R.F., Richardson, C.A., 1998. The direct and indirect effects of suction dredging on a razor clam (*Ensis arcuatus*) population. ICES J. Mar. Sci. 55, 970–977.
- Schnack, J.E., Fasano, J.L., Isla, F.I., 1982. The evolution of Mar Chiquita lagoon, Province of Buenos Aires, Argentina. In: Colquhoun, D.J. (Ed.), Holocene Sea-Level Fluctuations: Magnitudes and Causes, IGCP, vol. 61. Univ. South Carolina, Columbia, pp. 143–155.
- Sokal, R.R., Rohlf, F.J., 1995. Biometry: The Principles and Practice of Statistics in Biological Research. W.H. Freeman and Company, New York. 887 pp.
- Vermeij, G.J., Schindel, D.E., Zipser, E., 1981. Predation through geological time: Evidence from gastropod shell repair. Science 214, 1024–1026.
- Witbaard, R., Klein, R., 1994. Long-term trends on the effects of southern North Sea beam trawl fishery on the bivalve mollusc *Artica islandica* L. (Mollusca Bivalvia). ICES J. Mar. Sci. 51, 99–105.
- Zar, J.H., 1984. Biostatistical Analysis. Prentice-Hall Inc. Englewood Cliffs, New Jersey. 718 pp.