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Infection by gymnophallid metacercariae enhances predation mortality of SW Atlantic stout razor clam *Tagelus plebeius*

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ABSTRACT

Parasite life cycles are frequently completed in different hosts, thus the parasites have its life cycle overlapped to natural trophic webs. The family Gymnophallidae (Class: Trematoda; Subclass: Digenea) includes digenetic parasites whose larval stages occur on bivalves and may affect bivalve predation by the final host of these parasites. In this work we evaluated: (a) if individuals of the razor clam *Tagelus plebeius* with higher parasite intensity suffer higher predation by the oystercatcher *Haematopus palliatus* and, (b) if there is any effect of parasite intensity on burrowing and escape behaviours of these razor clams which may enhance exposure to predators. Field experiments (oystercatcher exclusion vs. open access) showed that clams with higher parasite intensity support higher predation by oystercatchers, which suggests a higher consumption of more parasitized clams and thus, a more successful reproduction of parasites linked to the intensity of infection. However, clam burrowing and escape behaviours did not show differences related to different parasite intensity, suggesting that the commonly believed mechanisms are not responsible in this case.

1. Introduction

Trophic relationships are some of the most important interactions among organisms (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). Within trophic interactions, parasitism is an intimate and continuous association between two individuals of different species that involves a certain degree of metabolic dependence (Smith, 1994). Frequently, parasite life cycles are completed in different hosts, thus the parasite life cycle may be overlapped to the natural trophic webs (Bush et al., 2001). Moreover, many parasites change the behaviour of the parasitized animal facilitating the parasite transmission to the next host (Moore, 2002).

Digenetic trematodes (Class: Trematoda; Subclass: Digenea) can use bivalves as intermediate as well as definitive hosts (Lauckner, 1983). The Gymnophallidae family includes digenetics whose larval stages (i.e., sporocyst and metacercariae) occur in marine coastal bivalves (Lauckner, 1983). Gymnophallid metacercariae can cause different pathologies such as gaping, valve asymmetry, castration and pearls (Ching, 1995). Moreover, there are evidences of parasites producing a negative effect on the host energy stored (Edelaar et al., 2003). As well as pathological effects, gymnophallids may change some host behaviours, such as what happens with the orientation of infected clams *Venerupis aurea* (Bartoli, 1965) or the "crawling behaviour" of the clam *Macoma balthica* (Swennen, 1969). These behavioural changes may increase the availability of the bivalve hosts to predators having consequences in the host mortality (Zwarts and Wanink, 1989).

The stout razor clam *Tagelus plebeius* is a euryhaline filter feeder 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 (41° S, Argentina) (Olivier et al., 1972). It is a deep-burrowing species that inhabits permanent burrows of up to 70 cm depth (Holland and Dean, 1977).

For most gymnophallids, marine birds are the final hosts (Lauckner, 1983). In the SW Atlantic, the final host of the gymnophallids present in *T. plebeius* is likely to be the American oystercatcher *Haematopus palliatus*, since it preys mainly on this bivalve (prey size range: 29.77–74.64 mm; Bachmann and Martínez, 1999) and it is their only predator (Iribarne et al., 1997; Mariano-Jelicich et al., 2008; Martinetto et al., 2005). Oystercatchers are cosmopolitan shorebirds, with a long and compressed bill (mean large = 80 mm, SD = 3.54 Nol and Humphrey, 1994) well adapted for capturing and handling intertidal shellfish (del Hoyo et al., 1996). When searching for *T. plebeius*, oystercatchers made superficial pecks and deep probes to capture it, visually determining where to peck (Bachmann and Martínez, 1999) probably using the filtration activity in the clams' siphon holes as indication of their

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presence (pers. obs.). As expected, in benthic habitats, predation risk from surface predators is maximal for infauna living near the surface (Zwarts and Wanink, 1989). Within a species, individuals living at greater depth experience lower risk of being eaten by surface predators (Richardson, 1985). However, although *T. plebeius* dig deep burrows and make vertical movements, they feed near the sediment surface (Holland and Dean, 1977) within the reach of the bill of oystercatchers (Iribarne et al., 1998).

The effect of parasitism by gymnophallids on bivalves on predation mortality by shorebirds was indirectly evaluated, comparing predation on surfacing or crawler bivalves and burrower bivalves, showing that crawler bivalves increased their risk of being eaten by birds (Hulscher, 1982; Mouritsen, 2004). However crawling behaviour may not be the consequence of larger parasite intensity, but instead it may be caused by other factors like reproductive needs or food supply (Mouritsen, 1997; Edelaar et al., 2003). Hence, at least in deposit feeder bivalves (Mouritsen, 1997; Edelaar et al., 2003), these burrowing behaviours could be the cause rather than the consequence of greater parasite intensity. Moreover, the pattern of differential predation mortality between crawler and burrower bivalves may not be due to parasites, although the parasite may have a benefit from that behaviour (Mouritsen, 2004). In fact no studies evaluating if infaunal bivalves more parasitized by gymnophallids are actually more consumed than less or non parasitized ones have been carried out up to now.

Given the high prevalence of gymnophallid metacercariae in *T. plebeius* at the Mar Chiquita coastal lagoon (Argentina, 37° 32′S, 57° 19′W), we hypothesize that clams with a higher parasite load are more consumed by the oystercatcher *H. palliatus* and this effect is mediated by (a) the shallower burrowing depth and/or (b) a lower burrowing speed and/or (c) the higher reaction time of more parasitized clams when preyed by oystercatcher. These processes would facilitate the transmission of parasites to the final host. In this context, we evaluate if (1) clams with higher parasite intensity suffer higher predation mortality by oystercatchers, and (2) parasite intensity affects burrowing depth, burrowing speed and reaction time of clams under the attack of oystercatchers.

2. Materials and methods

2.1. Study area

Samplings and field experiments with *T. plebeius* were made at Mar Chiquita coastal lagoon (in a site named CELPA; Fig. 1), between January 2006 and December 2008. The lagoon is a brackish water area of 46 km^2 with soft muddy sediments and low tidal amplitudes (<1 m; Fasano et al., 1982). Clams used in samplings and experiments (see Sections 2.2, 2.3 and 2.4) were collected by excavating with a hand shovel.

2.2. Effect of parasite intensity of T. plebeius on predation mortality by the oystercatcher H. palliatus

In order to establish the mean parasite intensity in the population, a random sampling of clams was made (initial conditions, $n = 77$) at the medium intertidal level (0.55 m above mean low tidal level) in

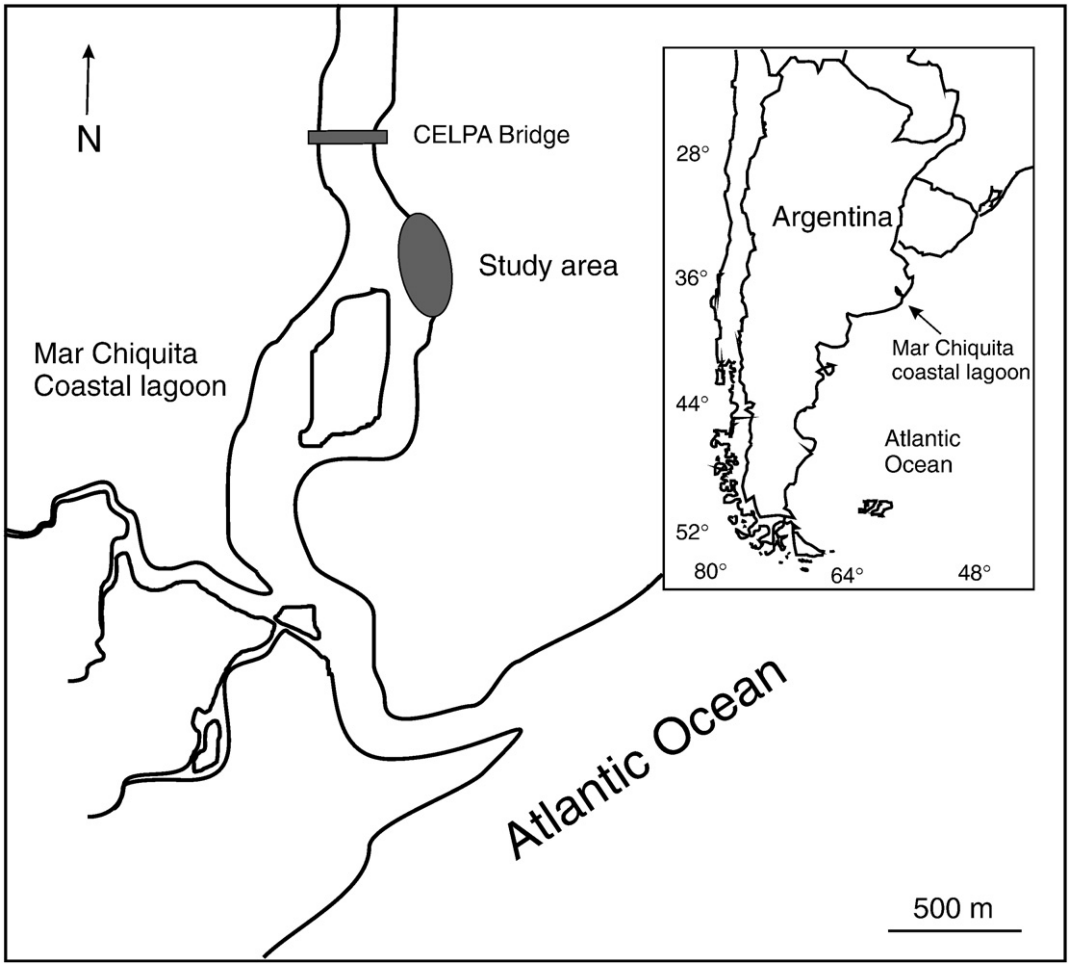

Fig. 1. Mar Chiquita coastal lagoon channel zone. Study areas used for the different samplings and experiments.

June 2006. All individuals were measured in shell length (anterior–posterior axis; precision ± 0.1 mm). To establish the parasite intensity of each clam, the number of metacercariae per clam were quantified by examination under a 20× binocular microscope (following Bush et al., 1997). Individuals were classified into three categories of parasite intensity: low (L)<300; medium (M): 300 to 900 and high (H)>900 metacercariae per clam, and the proportion distribution of these three categories in the population was established.

An exclusion experiment was performed from June to October 2006 at the medium intertidal level to determine possible differences in the predation by oystercatchers on *T. plebeius* with different parasite intensity. This period corresponds to the higher predation season (see Bachmann and Martínez, 1999). Thirty square areas of 40 cm side were delimitated randomly in an area of 500 m^2. Fifteen of them were covered with a plastic net (1 cm mesh size) 15 cm above sediment surface to avoid oystercatcher access (Exclusion treatment), the others (without the net) allowed oystercatcher access (Predation treatment). In October 2006, 5 months later, 27 squares could be recovered and all clams ($n = 80$) present in those square areas were extracted. Parasite intensity and length were determined for all individuals. In order to perform a more powerful analysis, we looked for differences between replicates into each treatment and as no differences were found (see Results), the data into each treatment were pooled.

Relationships between length and parasite intensity for clams at each treatment were analyzed given that they are expected to have a size effect on parasite load. Also, the null hypothesis of equal mean length between Initial condition, treatments Exclusion and Predation was tested with ANOVA. The null hypothesis of no differences for mean density as well as mean parasite intensity between Initial condition, treatments Exclusion and Predation was tested by ANOVA; the assumptions of normality and homogeneity of variances were tested. To evaluate predation effect by oystercatchers on parasite intensity categories proportion distribution contingency table analysis was performed (Zar, 1999).

2.3. Effect of parasite intensity on T. plebeius burrowing depth

In order to analyze the parasite infection in relation with intertidal levels, 97 randomly selected clams from 37.4 mm to 68.7 mm in length were collected in three intertidal levels: High = 0.75 m above mean low tidal level, Medium (described in Section 2.2) and Low = 0.40 m above mean low tidal level. Shell length and the parasite intensity were determined for all individuals (according to Section 2.2.) and the existence of linear relationships between these variables was evaluated. Then, the null hypothesis of equal mean parasite intensity between intertidal levels was analyzed using ANCOVA. The corresponding assumptions were tested before the analysis (following Zar (1999)).

To determine the effect of parasite intensity on burrowing depth of clams, a field experiment was performed in two sets, of 1 month each one, at the three intertidal levels described above in order to assure the use of clams from all the ranges of parasite intensities. Data from the two experimental sets are presented together. Depth was measured when sediment surface was immersed. Seventy-five clams, from 32.9 mm to 65.6 mm in length, were collected on each intertidal level ($n = 225$, two experimental sets), measured in length (according to Section 2.2.) and a known size nylon cord (0.30 mm diameter and 1 m length) was adhered to the periostracum surface with synthetic glue (Zwarts, 1986). Each individual was immediately relocated on a 4 cm diameter and 30 cm deep hole made in the sediment surface, allowing each clam to construct a new burrow (according to Lomovasky et al. (2005)). To relocate each individual a fine wire rod was inserted approximately 10 cm behind each hole. After 7 days in which clams had enough time to construct the new burrow, the burrowing depth was estimated by measuring the remaining nylon cord left on the surface. One measure of burrowing depth of each clam was taken each of 3 days; an average of these 3 measures was used for further analysis. At the end of each experimental set all surviving clams ($n = 86$, two sets) were recovered and taken to the laboratory where the parasite intensity was determined for each one (according to Section 2.2.).

Relationships between length and depth were evaluated at the three intertidal levels. In addition, the null hypothesis of equal mean length between intertidal levels was tested with Kruskal–Wallis analysis. To look for differences between mean depths between intertidal levels an ANOVA analysis was performed (Zar, 1999). Since depth was no different between intertidal levels (see Results), this variable was not taken into account here and thereafter. To test the null hypothesis of equal depth between clams from the three parasite intensity categories (H, M and L) we performed an ANOVA analysis. The assumptions of normality and homogeneity of variances were tested before the analysis and when the assumptions were not fulfilled the data were log transformed (Zar, 1999).

2.4. Effect of parasite intensity on clam reaction time and burrowing speed regarding predator presence

To evaluate the effect of parasite intensity on reaction time of clams under the presence of its predator, a field experiment was performed at the medium intertidal level, between May and September 2007. To measure clam reaction time, 83 clams from 46.9 to 71.1 mm in length were used. The disturbance caused by an oystercatcher when looking for prey (according to Bachmann and Martínez (1999)) was simulated using a red 8 cm length rod, similar to the oystercatcher bill. The burrowing depth of clams was measured using the procedure described in Section 2.3, and the clam movements were registered by the movement of the fragment of nylon adhered to the periostracum (described in Section 2.3). The time spent between the beginning of the disturbance and the beginning of clam movement (clam reaction time) was measured using a chronometer (precision 0.01 s). After the experiment, 81 clams were recovered and the parasite intensity was determined following Section 2.2.

Thirty-one clams out of the 81 recovered reacted to the disturbance, and these were used in further analysis. To evaluate if reaction time changes with the initial burrowing depth of clams, the relationship between those variables was analyzed for clams from H and M parasite intensity categories (defined in Section 2.2). The same relationship was evaluated between length and reaction time. In addition, length of clams was compared between clams from H and M parasite intensity categories with t-test analysis. Given that reaction time did not change with the length of individual (see Results), the reaction time between clams from different parasite intensity categories (H and M) was compared with t-test analysis. The assumptions of normality and homogeneity of variances were tested before the analysis (Zar, 1999).

Additionally, to measure the clam burrowing speed, the initial and final burrowing depth of clams before and after the disturbance was registered respectively and the time spent between the beginning and the end of their movement (precision 0.01 s) was measured. The burrowing speed of clams was determined as follows:

$$\frac{\text{final burrowing depth–initial burrowing depth (cm)}}{\text{time spent between the beginning and the end of the movement (s)}}$$

Relationship between length and burrowing speed was analyzed. Burrowing speeds between clams from different parasite intensity categories (H and M) were compared with t-test. Finally, mean parasite intensity between those clams that responded to the disturbance ($n = 31$) and those that did not respond ($n = 50$) was compared with t-test. The assumptions of normality and homogeneity of variances

were tested before the analysis and when the assumptions were not fulfilled the data were log transformed (Zar, 1999).

3. Results

3.1. Effect of parasite intensity of T. plebeius on predation mortality by the oystercatcher H. palliatus

Mean parasite intensity was not different between replicates into each treatment (ANOVA, $df = 24$ and 25, $F = 0.43$ and 0.74, $p = 0.92$ and 0.70; Exclusion and Predation respectively), thus data into each treatment were pooled.

There were no relationships between length and parasite intensity for the Initial condition and the two treatments (Table 1). Mean length was smaller at treatment Exclusion [mean length (95% confidence interval) = 54.2 (53, 55.4) mm] than at Initial condition and Predation treatment [56.5 (55.6, 57.4) mm] (ANOVA, $df = 156$, $F = 4.02$, $p = 0.02$; Tukey HSD, $p < 0.05$). However, we could not relate this difference to any difference in parasite intensity (see below). Mean density was higher in Initial conditions [mean density (95% confidence interval) = 36 (31, 41) ind m^{-2}] than treatments Exclusion and Predation [22 (13, 31) and 15 (11, 20) ind m^{-2}; respectively] (ANOVA, $df = 41$, $F = 13.48$, $p = 0.00035$; Tukey HSD, $p < 0.05$), also showing a tendency to lower values at Predation treatment (Minimum–Maximum values: Exclusion = 6–56 and Predation = 6–31 clams m^{-2}). Mean parasite intensity was smaller in treatment Predation [561 (436, 686) metacercaria per clam] than Initial condition and treatment Exclusion [784 (711, 857)] (ANOVA, $df = 156$, $F = 5.18$, $p < 0.007$; Tukey HSD, $p < 0.05$). The proportion of individuals in the parasite intensity category *H* was smaller in treatment Predation compared to Initial condition and treatment Exclusion (Predation − Initial condition: $X^2 = 7.74$, $p = 0.02$; Predation and Exclusion: $X^2 = 6.57$, $p = 0.04$). Parasite intensity category (*L*, *M* and *H*) proportion distribution did not show differences between Initial condition and treatment Exclusion ($X^2 = 0.19$, $p = 0.9$; Fig. 2).

3.2. Effect of parasite intensity on T. plebeius burrowing depth

Linear relationships between length and parasite intensity of individuals were found at the intertidal levels High and Low but were not found at level Medium (High and Low: $df = 42$ and 19 $p < 0.0001$ and $p = 0.002$ respectively; Medium: $df = 35$, $p = 0.26$). Mean parasite intensity was lower at intertidal level High [mean parasite intensity (95% confidence interval) = 594 (495, 693) metacercariae per clam] than at the other two levels [950 (796, 1103)] (ANCOVA, $df = 87$, $F = 7.44$, $p = 0.001$; Tukey HSD, $p < 0.05$).

Clams did not show a linear relationship between length and burrowing depth at the three intertidal levels (High, Medium and Low: $df = 28$, 36, and 20; $p = 0.52$, 0.1 and 0.6 respectively). Length did not show differences between intertidal levels (Kruskal–Wallis, $n = 86$, $H = 3.47$, $p = 0.18$). Depth of clams did not show differences between intertidal levels (ANOVA, $df = 85$, $F = 2.42$, $p = 0.09$). Moreover, no differences were found on depth of clams between individuals from the three parasite intensity categories [*H*, *M* and *L*; mean depth (95% confidence interval) = 18.6 (17.7, 19.6) cm; ANOVA, $df = 85$, $F = 1.89$, $p = 0.16$; Fig. 3].

Table 1
Linear regressions between length and parasite intensity for Initial condition and treatments Exclusion and Predation.

Treatment	*p*-value	R^2	*df*	Mean length	SD
Initial condition	0.6	NS	61	55.8	2.4
Exclusion	0.5	NS	38	55.4	2.5
Predation	0.7	NS	27	56.3	2.1

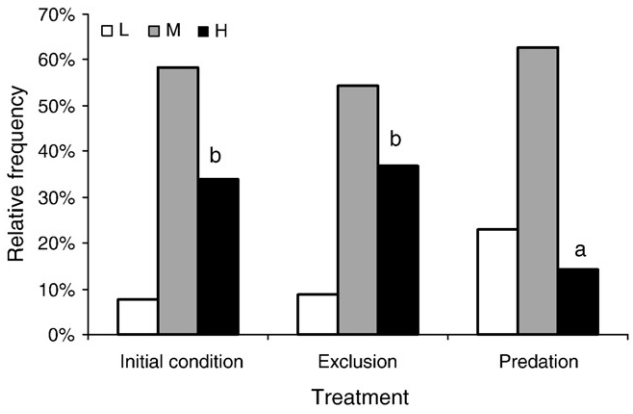

Fig. 2. Proportion distributions of the three parasite intensity categories at the Initial condition and the two treatments of exclusion experiment. *L*, *M* and *H* denote parasite intensity categories Low, Medium and High respectively ($n = 77$, 46 and 34; Initial condition, Exclusion and Predation respectively). Letters above vertical bars represent contingency table analysis results in ascendant order.

3.3. Effect of parasite intensity on clam reaction time and burrowing speed regarding predator presence

No linear relationships were found between initial burrowing depth and reaction time of clams from both parasite intensity categories (*H* and *M*: $df = 19$ and 7, $p = 0.86$ and 0.81 respectively)). The same was interpreted for the relationship between length and reaction time since the linear regressions showed a low fit (*H* and *M*: $df = 19$ and 7, $r = 0.009$ and 0.06 respectively). Length of clams did not show differences between parasite intensity categories (*t*-test, $df = 27$, $t = 2.02$, $p = 0.054$). Reaction time of clams did not show differences between individuals from both parasite intensity categories [*H* and *M*; mean reaction time (95% confidence interval): 7.87 (6.87, 8.87) s; *t*-test, $df = 28$, $t = -0.98$, $p = 0.34$; Fig. 4a].

No linear relationship was found between length and burrowing speed for both parasite intensity categories (*H* and *M*: $df = 19$ and 7, $p = 0.72$ and 0.66 respectively). Burrowing speed of clams did not show differences between parasite intensity categories [mean burrowing speed (95% confidence interval): 1.48 (1.11, 1.85) cm s^{-1}; $df = 28$, *t*-test, $t = -0.72$, $p = 0.48$; Fig. 4b]. Mean parasite intensity did not show differences between those clams that responded to the disturbance (see Section 2.4.) and those that did not respond to the

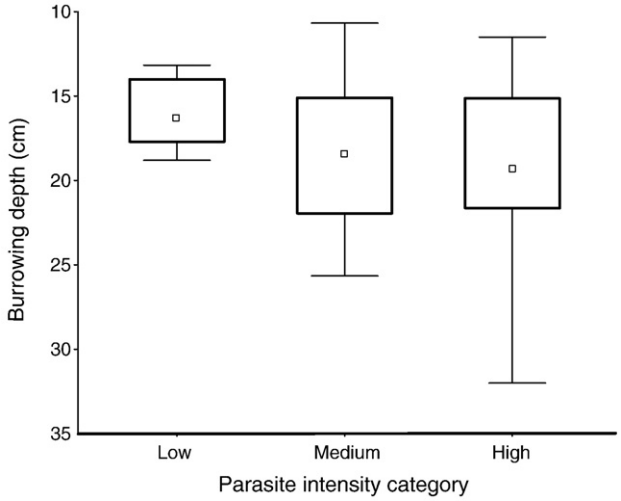

Fig. 3. Depth of clams from the three parasite intensity categories ($n = 17$, 48 and 37; Low, Medium and High respectively). Limits of boxes represent 25 and 75% percentiles, points inside represent median and vertical bars represent minimal and maximal values.

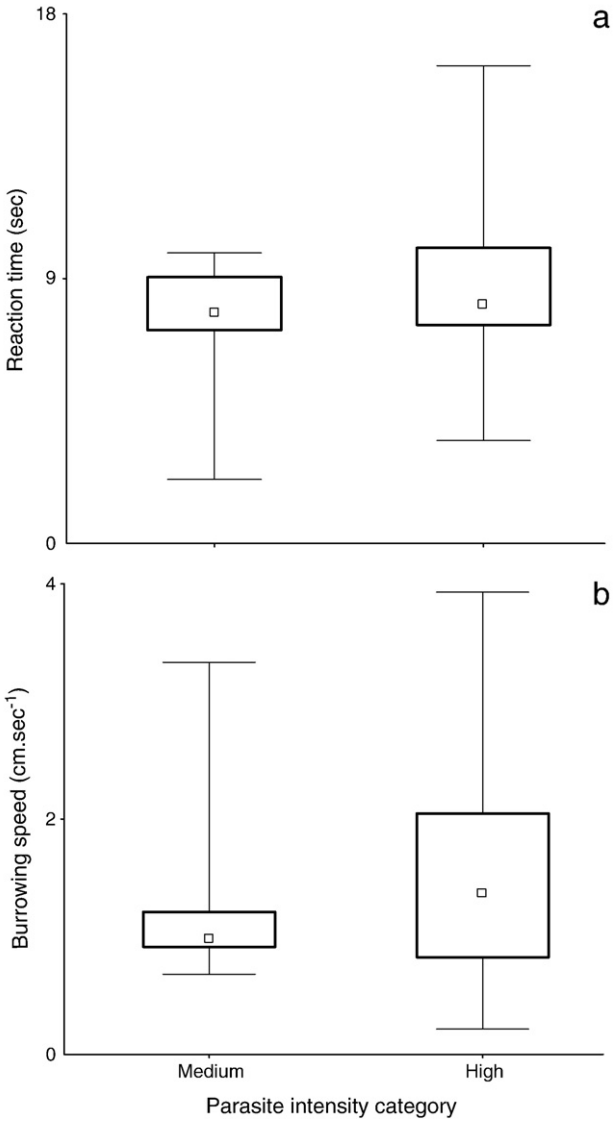

Fig. 4. (a) Reaction time and (b) burrowing speed of clams from different parasite intensity categories ($n = 9$ and 21, Medium and High respectively). Limits of boxes represent 25 and 75% percentiles, points inside represent median and vertical bars represent minimal and maximal values.

disturbance [1099 (968, 1229) metacercariae per clam; $df = 79$, t-test, $t = 0.75$, $p = 0.45$].

4. Discussion

T. plebeius with higher parasite infection by gymnophallid metacercariae suffered greater predation mortality by oystercatchers, the final host of those parasites, in their major predation area (medium intertidal level). However, burrowing depth as well as reaction time and burrowing speed of clams under a stress similar to the attack of an oystercatcher did not show differences depending on their parasite intensity, indicating that changes in these burrowing characteristics are not responsible for the larger predation mortality suffered by more parasitized clams.

Similar results concerning predation mortality in relation to parasites had been shown in other taxa such as ants and copepods (i.e. Moore, 1995; Johnson et al., 2006). Unlike the present study, those findings could be related to a conspicuous abnormal behaviour of the prey, such as lower flaying ability in ants, and/or different body characteristics (e.g. rare body colours) of parasitized individuals in comparison with non parasitized ones. In all cases, an increase in parasite infection results in enhanced chances of completing the parasite life cycle, since it increments predation mortality.

The existence of gymnophallid parasite adaptations to manipulate their intermediate host to facilitate their transmission to the final host has been indirectly sustained in bivalves by observations of certain unusual burrowing behaviours attributed to parasitized individuals (Swennen, 1969; Bartoli, 1965), but without taking into account that non parasitized ones also present these behaviours (Mouritsen, 1997). Thus, at least for gymnophallids there is questionable direct evidence of unusual burrowing behaviours in bivalves to be generated by parasites. Furthermore, we have not found any burrowing behavioural change related to the parasite intensity in *T. plebeius* that could explain the larger consumption of more parasitized clams. Unlike gymnophallids, there is evidence for other trematode parasites that they generate some burying changes associated with a greater consumption by birds, such as the case of the cockle *Austrovenus stutchburyi* infected with a parasite of the family Echinostomatidae (Thomas and Poulin, 1998).

Burrowing depth has been reported to present different kinds of relationship with size of individuals and for different bivalve species. A negative correlation between these variables was first described for *M. balthica* at the Wadden Sea (Hulscher, 1973), and further, positive functions were found for *M. balthica*, *Scrobicularia plana*, *Mya arenaria* and *Cerastoderma edule* in the same site (Zwarts and Wanink, 1993). We did not find any relationship between size and burrowing depth in *T. plebeius*. The burrowing depth may be a determinant variable in the accessibility of oystercatchers to a bivalve prey, given that the effective capture depends on preys being within the scope of bird beak (see Zwarts and Wanink, 1993). In our case, burrowing depth takes more extreme values when parasite intensity increases, indicating some effect of parasitism on this variable. However, mean burrowing depth of *T. plebeius* does not differ between individuals with different parasite intensity. *M. balthica* shows similar results (Hulscher, 1973). Thus, higher predation mortality on more infected clams would not be directly mediated by burrowing depth of clams.

Additionally, evidences from other taxa (e.g. cockroach) shows that escape behaviours in front of a predator are different (abnormal) in parasitized individuals than in those not parasitized, facilitating parasite transmission to the predator that is also the final host (i.e. Libersat and Moore, 2000; Seppälä et al., 2004). However, the escape behaviour represented by reaction time and burrowing speed regarding predator presence was not different between *T. plebeius* with different parasite intensity. Moreover, the comparison of parasite intensity between clams that responded to the similar-predator stimuli and those that did not respond was not different. Thus, our results suggest that reaction time and burrowing speed do not constitute the mechanisms resulting in higher predation mortality of more parasitized clams.

The negative effect of gymnophallid parasites on the host energy stored (Edelaar et al., 2003) may result in an enhanced feeding activity of the bivalve host. Frequently, filtration activity of *T. plebeius* is visible in the field by water currents on the inhalant and exhalent siphon holes (Holland and Dean, 1977) and also by the expulsion of water spurts from the siphon holes (personal observations), which may be detected by oystercatchers searching for *T. plebeius* given that they determine visually the site where to peck (Bachmann and Martínez, 1999). In this scenario, if filtration activity is enhanced by parasites, this is likely to be the key in the mechanism resulting in this pattern of predation. A larger circulation of water through the siphon holes may increase clam visibility to oystercatchers. On the contrary, there is a case of *M. balthica* where those individuals more parasitized present a higher body weight (Zwarts, 1991). Even if there is not such a negative effect of parasites on host energy stored or if the effect is the inversed one, as in the case of *M. balthica*, clams require an extra feeding to sustain/enhance their body condition. In these cases, parasites would

be responsible for higher predation mortality of clams enhancing their own reproduction indirectly by higher exposure of the host to predators. Further studies are necessary to test this hypothesis.

This is the first direct evaluation of the effect of the intensity of gymnophallid parasites of a bivalve prey, such as *T. plebeius*, on predation mortality by a shorebird that constitutes the final host of those parasites. Our results show higher consumption of more parasitized clams and thus, a more successful reproduction of parasites linked to the intensity of infection. However, neither burrowing and escape behaviour were implicated, thus we propose that filtration activity may be the alternative in the mechanism involved in obtaining this pattern of predation.

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