

Spatial variability of larval parasites harboured by two crab species in an estuarine environment in Argentina

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Soft bottom intertidals of the Atlantic SW are dominated by the semi-terrestrial crab Neohelice granulata and the grapsid crab Cyrtograpsus angulatus. They are similar in size but C. angulatus is mainly a subtidal species, while N. granulata inhabits the intertidal zones, thus the two species overlap only during high tides in this area. Since these distribution differences between crab species across the Mar Chiquita Coastal lagoon may affect digenean infection success, the objective of this work is to describe the spatial differences in parasite infection levels and their selectivity on the host. To determine possible spatial differences in parasitism levels between sites and crab species across the lagoon, three areas dominated by N. granulata were selected and adult crabs of N. granulata and C. angulatus were collected. Both crab species harboured metacercariae of the digeneans Microphallus szidati and Maritrema bonaerensis (Microphallidae), and cystacanths of the acanthocephalan Profilicollis chasmagnathi (Profilicollidae). Digenean species showed preferences between the two crabs. Maritrema bonaerensis mean intensity was higher in N. granulata than in C. angulatus, while the opposite trend was found for M. szidati and could indicate some level of specificity. These results, nevertheless, depended on the study site. For P. chasmagnathi the highest values of mean intensity depended more on the site than on the crab species. The values found here, compared with previous works from both crab species, suggest that besides the spatial heterogeneity, interspecific competition between parasites could explain the differences observed.

Keywords: Parasites, crabs, estuaries

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INTRODUCTION

Most parasites with complex life cycles require the use of one or more intermediate hosts (those harbouring the larval stages) and a definitive host (harbouring the adults) to complete their life cycle. Reproduction occurs in the definitive host (which usually eats the intermediate host), and the parasite's eggs are then released into the environment with the host's faeces. The selection of these hosts in a predator–prey system could be critical in determining parasite success.

Optimal foraging models assume that natural selection favours the strategy that maximizes reproductive success (Stephens & Krebs, 1986). A suboptimal foraging decision is potentially more risky for parasites than for free-living animals, given that a mistake in choosing the host could lead to no potential offspring. However, rejecting a potential host could lead to a similar outcome (Lewis *et al.*, 2002). Nevertheless, it is common that at any stage of their life cycle, parasites use several sympatric host species belonging to either the same taxonomic group or ecological guild. Moreover, several co-existing parasite species with the same definitive hosts can potentially use the same intermediate host species (see Koehler & Poulin, 2010). The abundance

and distribution of alternative host species as well as non-hosts (e.g. predators of infective larval stage) may affect infection levels in second intermediate hosts (Thieltges *et al.*, 2008). The resulting flow will depend on a variety of biotic (availability of hosts) and/or abiotic (salinity, temperature, tidal amplitude) factors and to interspecific interactions among parasite species (e.g. Kuris, 1991; Skirnisson *et al.*, 2004; Byers *et al.*, 2008; Faltýnková *et al.*, 2008).

Soft bottom intertidals (and salt marshes) of the Mar Chiquita Coastal lagoon (Argentina: 37°32'–37°45'S 57°19'–57°26'W) are dominated by the semi-terrestrial crab *Neohelice granulata* (Dana, 1851; Grapsidae) (Iribarne *et al.*, 2003). They are mainly deposit feeders in intertidal mud flats (creeks and channels) but herbivorous in salt marshes (Iribarne *et al.*, 1997; Bortolus & Iribarne, 1999). The crab *Cyrtograpsus angulatus* (Dana, 1851; Grapsidae) is similar in size (Boschi, 2000) but is mainly a subtidal species, while *N. granulata* inhabits the intertidal zones, and the two species overlap only during high tides in this area (Martinetto *et al.*, 2007). *Neohelice granulata* is extremely well adapted to exposure to atmospheric air, whereas *C. angulatus* shows a high degree of osmoregulatory capability (Spivak *et al.*, 1994). Due to these physiological differences, *C. angulatus* is able to inhabit areas of the lagoon with salinities varying from fresh to seawater, whereas *N. granulata* is able to occupy the uppermost parts of the intertidal zone of brackish waters (Spivak *et al.*, 1994). One particular difference between the

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distributions of these two crab species is that *N. granulata* is found in discrete high-density patches (Crab beds) across the lagoon, while *C. angulatus* stability through time is less predictable because of their high mobility.

Both crab species harbour metacercariae of the digeneans *Microphallus szidati* (Martorelli, 1986) and *Maritrema bonaerensis* (Etchegoin & Martorelli 1997; Microphallidae), and cystacanths of the acanthocephalan *Proflicollis chasmagnathi* (Holcman-Spector, Mañé-Garzón & Del-Cas, 1977; Proflicollidae) (Etchegoin, 1997). The three species are parasitic in birds as adults (seagulls of the genus *Larus* and the white-backed stilt *Himantopus melanurus* (Viellot, 1817) for *P. chasmagnathi* and *M. szidati*). Crabs become infected by digeneans when the cercariae, after leaving the snail first intermediate hosts (*Heleobia australis* d'Orbigny, 1835 and *H. conexa* Gaillard, 1974), encyst as metacercariae in the body cavity (*M. bonaerensis*) or in the hepatopancreas (*M. szidati*). In the case of *P. chasmagnathi*, crabs ingest the parasite eggs (containing the acanthor stage) deposited in bird faeces. After ingestion, the eggs hatch and the larval worms reach the crab body cavity where they develop to the acanthella stage and, finally, to the cystacanth stage. Metacercariae and cystacanths need to be eaten by a suitable definitive host to complete their life cycles (Etchegoin, 1997, 2001; Alda, 2011; Alda et al., 2011).

Given the distribution differences between crab species across the lagoon, and that local factors may affect digenean infection success, the objective of this work is to describe the spatial differences in parasite infection levels and their preference on the host.

MATERIALS AND METHODS

Study site

The Mar Chiquita coastal lagoon (Figure 1) can be divided into a freshwater zone, characterized by continental water

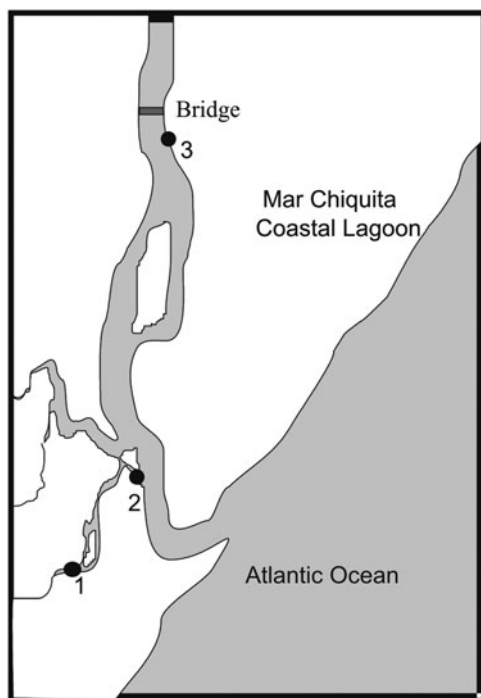


Fig. 1. Mar Chiquita Coastal Lagoon map showing the sampling places.

discharge without tidal effects, and an estuarine zone that communicates with the open sea. The estuarine zone is characterized by mixo-euryhaline waters and is greatly influenced by marine water (Reta et al., 2001) while the freshwater zone receives fresh water and sediment from a drainage basin of approximately 10,000 km² (Fasano et al., 1982). Nevertheless, the limits between the two zones and the levels of salinity are extremely variable (Reta et al., 2001). The sampling areas (Figure 1) were selected in the estuarine zone where crab beds are more stable in time. Site 1 is a very shallow creek, while site 2 and 3 show deeper and extensive intertidals. In this area only *H. australis* is present (Parietti, 2011). These zones vary in salinity from the mouth of the lagoon to the inner part, and both species of crabs are present.

Sampling procedures

To determine possible spatial differences in parasitism levels between sites and crab species across the lagoon, three areas dominated by *Neohelice granulata* were selected and adult specimens (considering same proportion of males and females) of *N. granulata* and *C. angulatus* were collected randomly by hand during summer (January–February) of 2012. These sites were selected based on the *N. granulata* crab presence stability across time (Lomovasky et al., 2006; Botto et al., 2008). All sampling sites are practically devoid of humans: Site 1 is a shallow creek with private access to people; Site 2 is a deep creek surrounded by a crab bed which makes people avoid this area (see Botto et al., 2008) and site 3 is accessible only by boats.

To avoid differences in prevalence and mean intensity with size (Etchegoin, 1997) only adult crabs (carapace width [CW] >22 mm) were sampled. The prevalence represents the number of parasitized crabs/number of collected crabs × 100, and the mean Intensity represents the total number of parasites of a particular species found in a sample divided by the number of hosts infected with that parasite (Bush et al., 1997). Once collected, crabs were transported to the laboratory and maintained in aerated water. Tetra Min Pro Tropical Crisps was provided as food.

In the laboratory, CW of each crab was measured with a Vernier caliper (precision: 0.1 mm). Later, crabs were dissected under a stereo-microscope in order to detect the presence of parasites, and each species of parasite was identified and quantified. Some metacercariae released spontaneously from their cysts and others were helped to release from their cyst through use of dissecting needles. Larval digeneans were identified according to Martorelli (1986) and Etchegoin & Martorelli (1997) and cystacanths were identified according to Vizcaino (1989).

Data analysis

To rule out the influence of the size range of crabs selected on parasitism levels, correlation analysis between CW and prevalence, and intensity values were performed. For prevalence values, correlation was performed between ranges of 2 mm. For each sample (N range = 20–70) prevalence and mean intensity was calculated for the three parasites best represented. Prevalences were compared with proportion z-tests after angular transformation (Zar, 1999). For each parasite species, differences in mean intensity between zones and

crab species were performed with a two-way ANOVA after log transformation to meet the assumptions. When differences were detected, a Fisher LSD a posteriori test was performed.

RESULTS

Both crab species harboured metacercariae of the digeneans *Microphallus szidati* and *Maritrema bonaerensis* (Microphallidae), and cystacanths of the acanthocephalan *Proflicollis chasmagnathi* (Proflicollidae). Sex ratios (m:h) were 0.6:0.4 for *N. granulata* and 0.53:0.47 for *C. angulatus*. No differences in mean intensity were found between sexes so they were pooled in the subsequent analysis. The correlation analysis for *N. granulata* showed no effect of the sizes selected and prevalences for *M. bonaerensis* ($r = 0.35$, $F_{(1,11)} = 1.56$, $P = 0.23$), *P. chasmagnathi* ($r = 0.17$, $F_{(1,11)} = 0.33$, $P = 0.57$) and *M. szidati* ($r = 0.59$, $F_{(1,11)} = 1.56$, $P = 0.23$). There were no correlations between crab size and intensity values for *P. chasmagnathi* ($r = 0.2$, $F_{(7,1)} = 2.76$, $P = 0.1$), *M. bonaerensis* ($r = 0.05$, $F_{(160)} = 0.42$, $P = 0.5$) or *M. szidati* ($r = 0.363$, $F_{(27)} = 3.98$, $P = 0.56$).

Correlation analysis for *Cyrtograpsus angulatus* showed no effect of size for prevalence values for each parasite species (*M. bonaerensis*: $r = 0.36$, $F_{(7)} = 1.07$, $P = 0.33$; *P. chasmagnathi*: $r = 0.44$, $F_{(7)} = 1.72$, $P = 0.23$; *M. szidati*: $r = 0.5$, $F_{(7)} = 3$, $P = 0.13$). Intensity values showed no correlation for *P. chasmagnathi* ($r = 0.06$, $F_{(56)} = 0.19$, $P = 0.65$) and *M. bonaerensis* ($r = 0.22$, $F_{(34)} = 1.79$, $P = 0.19$). For *M. szidati*, there was a significant correlation ($r = 0.5$, $F_{(82)} = 29.9$, $P < 0.01$). So, in order to detect possible differences in crab sizes between samples a one-way ANOVA was performed between mean sizes collected at the different sites. No differences between sizes of crabs was detected ($F_{(2,85)} = 1.02$, $P = 0.36$).

Prevalence values of *M. bonaerensis* showed differences between sites only for *N. granulata*, and were higher in *N. granulata* than in *C. angulatus* (Table 1). The comparisons between mean intensity values in the three sites and crab species showed no interaction for *M. bonaerensis* ($F_{(2,154)} = 0.38$; $P = 0.68$), but there were differences between sites ($F_{(2,154)} = 4.35$; $P = 0.01$) and between crab species: *N. granulata* had higher mean intensity values than *C. angulatus* ($F_{(2,154)} = 13.8$; $P = 0.0003$; Figure 2A).

Prevalences of *M. szidati* were always higher in *C. angulatus*, and showed no differences between sites (Table 1). Mean intensity values for *M. szidati* showed no interaction between sites and crab species ($F_{(2,110)} = 0.6$; $P = 0.56$). No differences

Table 1. Prevalence values for *Neohelice granulata* and *Cyrtograpsus angulatus* in the different sampled zones. Same letters indicate no differences for prevalence values between sites. Asterisks show differences between crab species from the same site.

Site (N)	<i>M. bonaerensis</i>	<i>P. chasmagnathi</i>	<i>M. szidati</i>
<i>N. granulata</i>			
1 (70)	91% a*	43%	20%*
2 (33)	67% b*	60%	13%*
3 (52)	71% b*	65%	27%*
<i>C. angulatus</i>			
1 (30)	53%*	60%	87%*
2 (21)	33%*	62%	95%*
3 (37)	32%*	68%	97%*

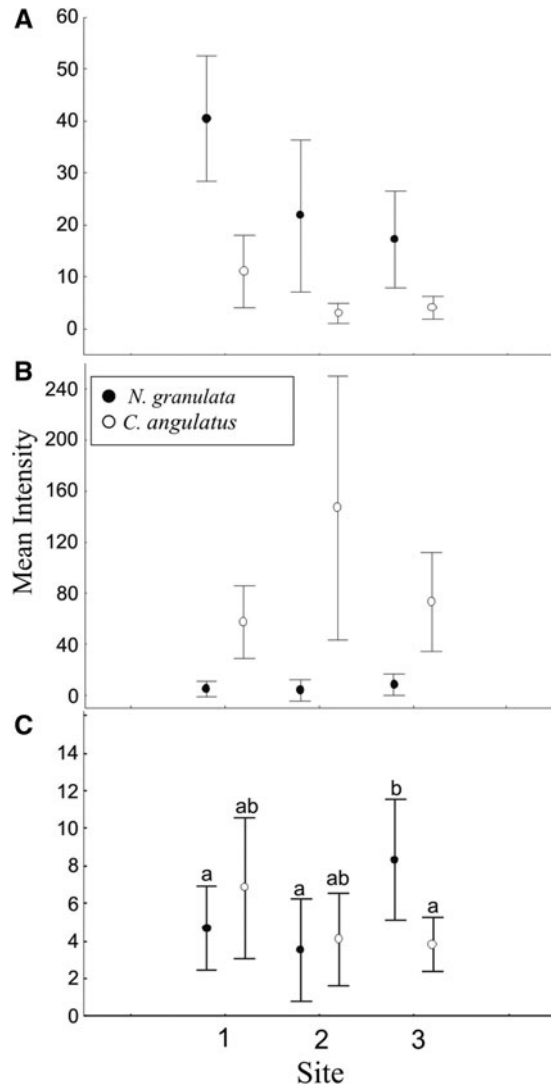


Fig. 2. LSD results comparing mean intensity between crab species and sites for *Maritrema bonaerensis* (A), *Microphallus szidati* (B), and *Proflicollis chasmagnathi* (C). Points represent means and vertical bars denote 0.95 confidence intervals. Same letters indicate no differences between intensity values.

were found between sites ($F_{(2,110)} = 0.5$; $P = 0.6$), but there were higher levels for *C. angulatus* ($F_{(2,110)} = 54.5$; $P < 0.0001$; Figure 2B).

Prevalence values for the acanthocephalan *P. chasmagnathi* showed differences between sites only for *N. granulata*, and no differences were found on prevalence values between crab species (*C. angulatus* and *N. granulata*; Table 1). Mean intensity values for *P. chasmagnathi* showed interaction between crab species and sites ($F_{(2,132)} = 3$; $P = 0.05$; Figure 2C). There were differences in sites for *N. granulata* (site 3), and there were also differences between crab species at different sites (Figure 2C).

DISCUSSION

Digenean species showed differences between the two crabs. *Maritrema bonaerensis* mean intensity and prevalence was higher in *N. granulata* than in *C. angulatus*, while the opposite trend was found for *M. szidati*. These results, nevertheless,

depended on the study site. For *P. chasmagnathi* the highest values of mean intensity depended more on the site than on the crab species. These variations could be the result of several variables such as the availability of previous and final hosts (Etchegoin *et al.*, 2012), the particular microhabitat of the crabs (Lei & Poulin, 2011), and the type of intertidal of each site. The particular microhabitat occupied by a potential host can affect their susceptibility to parasitism. For example, salinity influences the number of larvae stages produced, the time they need to encyst, how many succeed at encysting and how long encysted metacercariae survive (Lei & Poulin, 2011). Differences in temperature among sites may be also important because the rate at which larvae are produced (and released) is affected by temperature (Fredensborg *et al.*, 2005; Thieltges & Rick, 2006; Poulin, 2006). This also may be important at each site as well at a micro-scale level. Both crabs differ in their behaviour and in the frequency and abundance of the three species of parasites they share. Even though both crab species come into contact with water inhabited by *Heleobia conexa* and *Heleobia australis* (Cochliopidae), the snail first intermediate hosts of the trematodes, *C. angulatus* is more a subtidal species, changing, in consequence, the probability of being infected by cercariae. *Neohelice granulata* is extremely well adapted to exposure to atmospheric air, whereas *C. angulatus* shows a high degree of osmoregulatory capability. Due to these physiological differences, *C. angulatus* is able to inhabit areas of the lagoon with salinities varying from fresh to seawater, whereas *N. granulata* is able to occupy the uppermost parts of the intertidal zone of brackish waters (Spivak *et al.*, 1994). Site 1 is a very shallow creek where differences in habitat use by both crabs across the intertidal could be less important, while site 2 and 3 show deeper and extensive intertidals. Therefore, these physiological differences seem to become less important in areas where the intertidal zone is narrow, with lower slopes and depths. This also changes the probability of becoming infected by *P. chasmagnathi*, since the more time spent in the intertidal, the more chances to acquire acanthocephalan eggs (they lie on the mud with the faeces of the bird definitive host). Moreover, these differences in habitat use of the intertidal by crabs, and the particular differences that may affect the presence and habitat use by the final hosts (birds) can change the infection levels of both intermediate hosts.

We compared our results with the data obtained by Etchegoin (1997). The crabs were collected from the mouth of the lagoon to site 1. Mean intensities for *C. angulatus* showed similar trends but lower values: presenting maximum values in *M. szidati* (44 vs 139 founded here) and lower values for *M. bonaerensis* and *P. chasmagnathi* (2.7 and 9.7 respectively vs 5.9 and 4.1 in this work). Nevertheless, for *N. granulata* the maximum values were recorded also for *M. szidati* (7.5) differing from the values presented here (2.4) and *M. bonaerensis* showed very low intensity (2.9) compared with the maximum values obtained here (38.3). These differences could be due to differences in sampling sites, either in the physical conditions or the availability of first intermediate and/or final host. Even though three sites were sampled here and in all of them values in *N. granulata* were higher for *M. bonaerensis* than for *M. szidati*, and could indicate some level of preference (resulting from some level of specificity with the host, or by the physical factors within or surrounding the host). These contrasting data could be showing that either that preference switched, or most likely depends on the study site.

In the Bahia Blanca estuary, no presence of *M. szidati* was found in either *N. granulata* or *C. angulatus* (Alda *et al.*, 2011). In this zone, the prevalence of *M. bonaerensis* in *C. angulatus* is more than double (94%) the values found here (35%) and for *N. granulata* 100 vs 74% found here. The values found here compared with Bahia Blanca values (Alda, 2011, Alda *et al.*, 2011), suggesting that besides the spatial heterogeneity, interspecific competition between parasites could explain differences observed. The fact that *M. szidati* is not found in Bahia Blanca seems to favour *M. bonaerensis* being hosted in *C. angulatus*, since the highest intensity and prevalence values were found in this crab. For *N. granulata*, the prevalences and mean intensities of *M. szidati* found here seem to be too low to affect values of *M. bonaerensis*. The values obtained in this work for the acanthocephalan *P. chasmagnathi*, showed the opposite trend for *C. angulatus* (71 vs 20% in Bahia Blanca), and in *N. granulata* 68 vs 47%. As we have shown here, this contrast seems to be the result of differences in sampling sites.

The data presented in this work gives another example of the benefit of studying how parasites use available hosts within their community. This improves the knowledge of ecological interactions, such as degrees of host specificity, which can be overlooked when looking only at a single host or parasite species.

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