

**INFLUENCE OF *MICROPHALLUS SZIDATI* MARTORELLI, 1986 (TREMATODA)  
ON THE FECUNDITY OF THE SECOND INTERMEDIATE HOST,  
*PALAEONETES ARGENTINUS* NOBILI, 1901 (DECAPODA: NATANTIA)**

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A B S T R A C T

Parasites usually have strong negative effects on the fitness of their hosts, as in the reduction of host fecundity. We evaluated the female fecundity of *Palaemonetes argentinus* Nobili, 1901 from two populations with contrasting levels of parasitism: the population from Nahuel Rucá (NR), Argentina that was fully parasitized by a larval digenean (*Microphallus szidati* Martorelli, 1986) and the population from El Burro (EB) that was completely free of parasites. Realized and actual fecundity (i.e., number of newly spawned embryos and number of embryos ready to hatch, respectively) were higher in the parasitized females from NR. Moreover, infected females from NR produced heavier eggs than uninfected ones from EB. Egg loss (estimated as difference between realized and actual fecundity), however, was higher in the parasitized population (18.6 versus 10%). Higher egg loss is likely a negative effect of parasitism; however, the differences in fecundity between the two *P. argentinus* populations may be explained by differences in local ecological conditions. Future studies under controlled experimental conditions should compare realized and actual fecundity between parasitized and non-parasitized *P. argentinus* from a same population. Our results highlight the importance of parasitism as a biotic factor to be considered in analyzing life history traits in shrimp populations.

**KEY WORDS:** Argentina, crustacean hosts, digenean larvae, palaemonid shrimps, parasitism

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INTRODUCTION

Parasites may affect host characteristics of demographic importance such as birth and death rates because they can directly or indirectly cause the death of their hosts and/or influence their reproduction by the reduction or even inhibition of their reproductive processes (e.g., Galaktionov, 1993; Zohar and Holmes, 1998; McCurdy et al., 1999; Ferreira et al., 2005; Baldauf et al., 2007; Vale and Little, 2012; Cézilly et al., 2013). The two fitness components that are typically considered with regard to parasitism are host fecundity and survival (Ebert, 2005), and most studies on the influence of parasites on host fitness generally conclude that parasites have a strong negative effect on their hosts (e.g., Sorensen and Minchella, 1998; Bollasche et al., 2002; Decaestecker et al., 2005). Parasitism is therefore recognized as a factor that influences the composition and structure of populations and communities (Minchella and Scott, 1991; Combes, 1996; Hudson and Greenman, 1998; Poulin, 1999; Chadwick and Little, 2005; Adamo, 2013).

Parasitic flatworms (Platyhelminthes) belonging to the subclass Digenea usually requires three hosts to complete their life cycles: a definitive host (generally a vertebrate), a first intermediate host (almost always a mollusc), and a sec-

ond intermediate host that can be an invertebrate or vertebrate (e.g., molluscs, annelids, crustaceans, fishes, amphibians). The second intermediate host carries the metacercaria stage, which when ingested by or in contact with the definitive host, completes the life cycle. Digeneans have significant effects on the fitness on their intermediate hosts (first and second), since they are known to cause a decrease in the competitive ability of males, a diminished attractiveness to another mate, the prevention of females from attaining sexual maturity, castration, the decrease of the female fecundity, and a reduction of the reproductive output (e.g., Minchella and Loverde, 1981; Thomas et al., 1995, 1996a, b; Fredensborg and Poulin, 2006; Bartoli and Boudouresque, 2007; Zbikowska, 2011).

The natantian shrimp *Palaemonetes argentinus* Nobili, 1901 occurs in limnic inland habitats such as lakes and streams and also in brackish coastal lagoons connected to the sea, geographically ranging from Uruguay and southern Brazil to central eastern Argentina (Spivak, 1997; Ituarte, 2008). Because of its high abundance, this species plays a key role as predator of zooplankton and as prey of fishes and birds in coastal lagoons and freshwater environments of eastern South America (Collins, 1999; López et al., 2001; González Sagrario, 2004; González Sagrario et al., 2009).

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The shrimp has been reported in Argentina as second intermediate host for two digenean species belonging to the family Microphallidae: *Microphallus szidati* Martorelli, 1986 and *Levinseniella cruzi* Travassos, 1920 (Martorelli, 1986, 1988; Parietti et al., 2015). The previous studies involving these flatworms have been focused on their descriptions, the elucidation of their life cycle and their seasonal variation (Martorelli, 1988; Martorelli and Schuldt, 1990; Martorelli et al., 2006; Parietti et al., 2015). Metacercariae of microphalliid parasites usually develop in crustaceans as secondary intermediate hosts and several species of this family show high host specificity (Galaktionov and Drobrovskij, 2003). Despite the ecological significance of *P. argentinus* in aquatic environments in eastern South America, there is so far no information on the effects of metacercariae on the fitness of the shrimp.

As a part of ongoing studies on the population dynamics of digenean species from Nahuel Rucá Lake (Buenos Aires Province, Argentina), we found that *P. argentinus* was nearly always heavily parasitized (Merlo, 2014; Parietti et al., 2015). In contrast, we had no record of such levels of parasitism for individuals coming from northernmost populations (RBI, pers. obs.). Since microphalliid metacercariae have been mainly located in abdominal muscles of *P. argentinus* (Parietti et al., 2015), we hypothesized that fecundity is negatively affected in parasitized females. We evaluated female fecundity in *P. argentinus* from two geographically isolated populations, one of them heavily parasitized by one species of digenean larvae and the other completely free of parasites. We measured realized and actual fecundity, brood loss, and dry mass of eggs in parasitized and non-parasitized females.

## MATERIALS AND METHODS

### Sampling Sites

The study sites are located in Buenos Aires Province, Argentina (Fig. 1). Nahuel Rucá Lake (NR: 37°37'S, 57°25'W) is a shallow-water lake located in a large wetland area belonging to the Mar Chiquita Coastal Lagoon Basin, a UNESCO Man and the Biosphere Reserve since 1996. It has a surface area of about 400 ha and a mean depth of 1.5 m. El Burro Lake (EB: 35°41'S, 57°57'W) is a shallow eutrophic lake that belongs to a system of

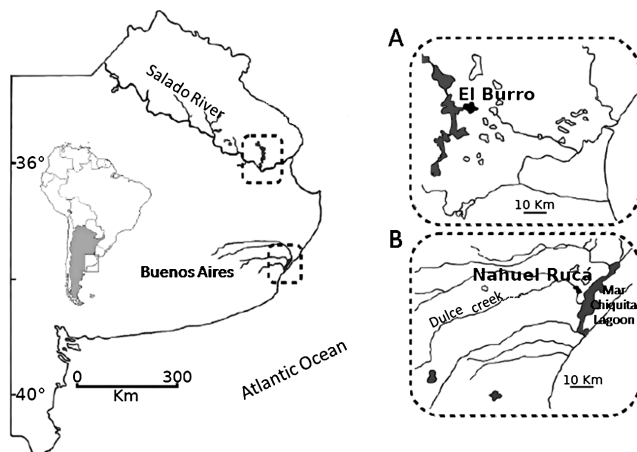


Fig. 1. Location of the *Palaemonetes argentinus* population studied in Buenos Aires Province, Argentina. A, “Las Encadenadas de Chascomús” shallow lakes, El Burro Lake in black; B, Mar Chiquita Coastal lagoon basin, Nahuel Rucá Lake in black.

shallow lakes interconnected by creeks (“Las Encadenadas de Chascomús”) that are connected to the Salado River (Giovagnoli et al., 2014). It has a surface area of about 1200 ha and a mean depth of 2 m (Fig. 1).

### Sampling Procedures

Collections were made in October and December 2012. Shrimps were collected using a hand net at randomly chosen spots. In the laboratory, ovigerous females were sorted in two groups according to the degree of development of their embryos. The two stages of embryonic development used correspond to those described by Ituarte et al. (2007): newly spawned embryos (SI) and embryos ready to hatch (SIII). Realized fecundity ( $N_{SI}$ ) was defined as the number of SI embryos per female and actual fecundity ( $N_{SIII}$ ) as the number of SIII embryos per female (Ituarte et al., 2007). Dry weight (W) of SI embryos was determined on a H54 Mettler AR balance to the nearest 0.01 mg. Embryos were transferred to pre-weighed capsules of aluminum foil and dried at 90°C to constant weight (at least 24 h). The size of females was estimated as the carapace length (CL, mm), from the posterior orbital margin to the dorso-posterior border of the carapace, using an Olympus SZ40 stereomicroscopy.

Females from both populations were kept alive in individual plastic beakers (100 ml) until dissection, usually within 24 h of collection. All parts of the female body were checked for parasites, including the appendages. After dissection, parasites were identified and the number of metacercarial cysts was counted.

### Statistical Analysis

Three quantitative descriptors of parasite populations were used: 1) prevalence (number of parasitized grass shrimp/number of collected grass shrimp  $\times$  100), 2) intensity of infection (number of individuals of a particular parasite species in a single infected host), and 3) mean intensity (total number of parasites of a particular species/the number of host infected with that parasites) (Bush et al., 1997). Difference in mean intensities between embryonic stages (SI vs. SIII) was tested by Student *t*-tests.

Least-square regression models were fitted to describe the relationships between CL and egg production (both  $N_{SI}$  and  $N_{SIII}$ ) in each of the populations. All variables were logarithmically transformed to satisfy the assumptions of normality and homogeneity of variances. Either  $N_{SI}$  or  $N_{SIII}$  were compared between populations with analysis of covariance (ANCOVA) using CL as the covariate. The equality of regression lines was tested using a Parallelism test (Zar, 2009) for all ANCOVA analyses. When the slopes were equal (homogeneous), ANCOVA was performed to test differences in mean *Y* adjusted for differences in *X*. The Tukey HSD test was used to test differences among individual *Y*-intercepts.

Difference between  $N_{SI}$  and  $N_{SIII}$  was tested within each population using ANCOVA with CL as covariate. The brood loss was calculated in both populations as the difference between *Y*-intercepts using the following equation (modified from Ituarte et al., 2007):  $100(1 - \exp(a_{SIII} - a_{SI}))$ . Difference in dry weight (W) of SI embryos between populations was tested by a Mann-Whitney *U*-test.

## RESULTS

A total of 299 bearing females ( $n = 199$  from NR) and ( $n = 100$  from EB) was examined. In NR, 99 females had newly spawned embryos (SI) and 100 females had their embryos in an advanced developmental stage (SIII). In EB, 50 females had SI embryos and 50 females had their embryos in SIII.

All ovigerous females of *P. argentinus* from NR were parasitized with *Microphallus szidati* (Microphallidae). The prevalence of *M. szidati* metacercariae was 100% in females carrying both embryonic stages (SI and SIII). The mean intensity was higher in females with advanced (SIII) than newly spawned embryos (SI) (Student's *t*-test:  $t = 6.97$ ,  $df = -0.66$ ,  $P < 0.0001$ ). The intensity of infection ranged from 6 to 231 cysts in shrimps with SI embryos (mean value 35.95 cysts per host,  $n = 99$ ,  $SD = 30.78$ ) and from 10 to 225 cysts in shrimps with SIII embryos (mean value 69.44 cysts per host,  $n = 100$ ,  $SD = 50.57$ ). We never found metacercarial cysts in shrimps from EB during the collections.

Table 1. Regression equations describing fecundity in *Palaemonetes argentinus* originating from two geographically separated populations: the parasitized population of Nahuel Rucá (NR) and the non-parasitized population from El Burro (EB), Argentina. Realized fecundity (number of stage-I embryos, SI) and actual fecundity (number of stage-III embryos, SIII) are as functions of female body size (CL, mm; logarithmically transformed data).

|                    | Regression equation                     | $r$  | $n$ | $P$    |
|--------------------|---|------|-----|--------|
| Realized fecundity | $\ln_{SI} = 1.68 \cdot \ln CL + 1.82$   | 0.55 | 99  | <0.001 |
|                    | $\ln_{SI} = 1.45 \cdot \ln CL + 1.96$   | 0.55 | 50  | <0.001 |
| Actual fecundity   | $\ln_{SIII} = 1.68 \cdot \ln CL + 1.82$ | 0.32 | 100 | 0.001  |
|                    | $\ln_{SIII} = 1.77 \cdot \ln CL + 1.28$ | 0.57 | 50  | <0.001 |

The number of newly spawned embryos ( $N_{SI}$ , realized fecundity) and the number of embryos ready to hatch ( $N_{SIII}$ , actual fecundity) increased in both populations linearly and positively with female CL (Table 1). The  $N_{SI}$  differed between populations (ANCOVA:  $F_{1,146} = 30.7$ ,  $P < 0.001$ ). At equal CL,  $N_{SI}$  was higher in females from the parasitized population (NR, Fig. 2). Similarly, the number of embryos near to hatch differed also between populations (ANCOVA:  $F_{1,147} = 19.2$ ,  $P < 0.001$ ) being also higher in females from the parasitized population (NR, Fig. 2).

Realized and actual fecundity differed within each population (ANCOVA NR:  $F_{1,107} = 5.6$ ,  $P = 0.02$ ; EB:  $F_{1,97} = 4.7$ ,  $P = 0.03$ ; Fig. 2) indicating a significant egg loss during embryonic development. The percentage of embryonic loss was higher in the parasitized population (18.6 vs. 10%).

Dry weight of early embryos (SI) differed between populations (Mann-Whitney  $U = 1900$ ,  $P = 0.021$ ). Parasitized

females from NR produced heavier eggs (0.087 mg W per embryo,  $n = 99$ ,  $SD = 0.008$ ) than those from uninfected females from EB (0.081 mg,  $n = 50$ ,  $SD = 0.01$ ).

## DISCUSSION

The impact of parasitism on the host can be assessed with respect to the probability of contacting the parasite in the environment, considering its potential effect on host reproductive success, and the relative cost of host resistance (Minchella, 1985). Here we report that ovigerous females from NR were 100% parasitized by a single species of digenetic trematode, whereas all gravid females from EB were uninfected. The maximum values of prevalence and intensity for *M. szidati* in *P. argentinus* in NR are coincident with the values of prevalence recorded in the first intermediate host, the snail *Heleobia parchappii* (Merlo, 2014). The abundance of *M. szidati* metacercariae in the second intermediate host is therefore influenced in part by the abundance of the cercaria stages in the environment. We never found during samplings in EB neither the snail *H. parchappii* nor other *Heleobia* species, as also reported by Tiezte (2011), suggesting that infections of shrimps were prevented by the absence of the first intermediate host.

Most studies support a negative relationship between host fitness and infection levels (e.g., Minchella, 1985; Sorensen and Minchella, 1998; Bollasche et al., 2002; Decaestecker et al., 2005). In contrast, we found that parasitized *P. argentinus* females laid more eggs and have more embryos ready to hatch than uninfected ones of the same size, in spite of parasitized shrimps lost more embryos through development. High realized and actual fecundity from parasitized females from NR can be explained to a large extent by intraspecific variability of life-history trait in *P. argentinus* populations (Ituarte et al., 2007). The fact that the snail *H. parchappii* was present in NR but absent in ER indicates that local ecological conditions differ between sites, which could exert differential selection pressures in the evolution of the life history of this shrimp (Ituarte et al., 2007). Shells of *H. parchappii* can be for instance fouled with marine diatoms belonging to the genus *Hyalodiscus*, and epibiosis levels increase with salinity concentration when environmental salinity ranging from 3 to 7 psu (Cazanniga, 2011). The higher the level of epibiosis, the smaller the snail size and the higher the difficulty of female snails to attach egg capsules to other snail shells (Cazanniga, 2011). Impairment in the fitness of fouled snails suggests that epibiosis affects the population dynamics of *H. parchappii* in mesohaline habitats (e.g., Cazanniga, 2011). Whether parasitism, salinity, or both factors can account for differences in fecundity between the two *P. argentinus* populations should be tested under experimentally controlled conditions.

It is widely known that parasites can influence the genetics of populations, and thus can affect the selection pressures acting on the parasites themselves (Webster et al., 2001). The importance of parasites as agents of natural selection becomes evident when their number reaches levels at which can visibly affect the abundance of a host (Poulin and Morand, 2004). Mutual selection triggers coevolution between parasites and hosts. The parasite reduces life ex-

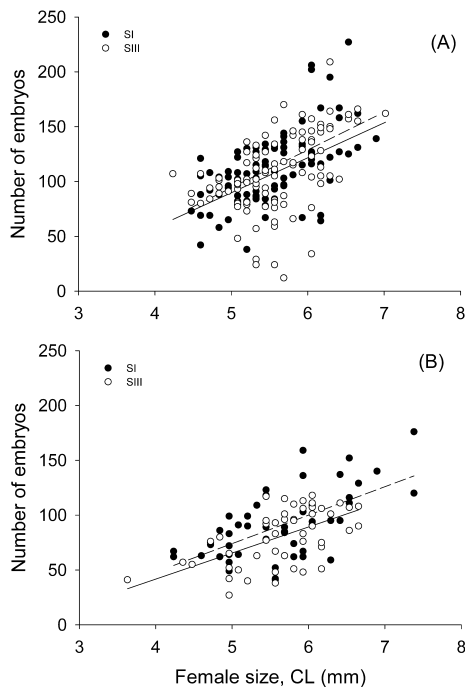


Fig. 2. Comparison of realized (number of stage-I embryos, SI) and actual fecundity (number of stage-III embryos, SIII) within populations, with female size (CL; mm) as covariable. A, Parasitized females from Nahuel Rucá; B, non-parasitized females from El Burro. Embryonic loss is the difference between Y-intercept within each population. Dashed and entire lines: regression lines for realized and actual fecundity, respectively.

pectancy or host's fertility trying to maximize the exploitation thereof and, in turn, the host tries to minimize the loss of fitness by the parasite. This leads to what has been called "The Red Queen Hypothesis," in which the species involved in an antagonistic coevolution should "run" (evolutionarily) as fast as they can to avoid extinction (van Valen, 1973; Hamilton, 1980). The high realized and actual fecundity of parasitized females from NR could therefore be partly explained as a coevolutionary process between the parasite and the host. The higher number and weight of the eggs could be an evolutionary response to an increased predation rate caused by digeneans (e.g., Lafferty and Shaw, 2013).

The higher egg loss throughout embryonic development in parasitized *P. argentinus* females is most likely a negative effect of infections. Metacercarial cysts of the parasite *M. szidati* usually encyst in shrimp abdominal muscles (Martorelli et al., 2006; Parietti et al., 2015). Larger number of metacercariae in the abdominal muscles could interfere with care activities of ovigerous females, preventing enough ventilation and/or cleaning of embryos. Decreasing care activity that provides protection against hypoxia and pathogens could therefore be related to higher egg loss during embryonic development. Moreover, care activities in most decapods increase through the end of the embryonic development (e.g., Baeza and Fernández, 2002; Giovagnoli et al., 2014). The higher number of cysts in females with advanced embryos compared to those with newly spawned eggs indicates that shrimp females were actively infected by *M. szidatis* throughout the time of host embryonic development, which could contribute to a physical disability to effectively care their embryos.

In addition to a possible physical disability, trophically transmitted parasites that infected invertebrates are more likely to increase the host contact with predators by manipulating the behavior of their hosts (Lafferty and Shaw, 2013). The metacercariae in abdominal muscle along with the egg mass could increase the predation of *P. argentinus*, possibly affecting the swimming stamina and predator avoidance response of the shrimp, as it has also been suggested by other similar host-parasite system (*P. pugio* – *M. turgidus*; Kunz and Pung, 2004). The level of parasites can thus increase the chances of shrimps to be eaten by a potential predator through a physical impairment and/or the manipulation of shrimp behavior. It seems that parasitism can be an important factor in the reproduction of *P. argentinus* and should be considered in studies that analyze variations in the life history of other palaemonid shrimps.

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