

Effects of parasitism and environment on shell size of the South American intertidal mud snail *Heleobia australis* (Gastropoda)

Pilar Alda^{a,*}, Nicolás Bonel^b, Néstor J. Cazzaniga^c, Sergio R. Martorelli^a

^a Centro de Estudios Parasitológicos y Vectores, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de La Plata (CCT-La Plata-CONICET-UNLP), Calle 2 No. 584, 1900, La Plata, Buenos Aires, Argentina

^b División Zoología Invertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, CONICET. Paseo del Bosque s/NO, 1900, La Plata, Buenos Aires, Argentina

^c Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur. San Juan No. 670, 8000, Bahía Blanca, Buenos Aires, Argentina

ARTICLE INFO

Article history:

Received 24 August 2009

Accepted 14 January 2010

Available online 22 January 2010

Keywords:

Marine molluscs

hydrobiid snail

shell size

parasitism

trematoda

Microphallus simillimus

environmental factors

Argentina, Buenos Aires, Bahía Blanca

estuary

ABSTRACT

The aim of this work was to evaluate the effects of parasitism and certain environmental factors on the shell size of *Heleobia australis* (Hydrobiidae, Cochliopinae). We report sporocysts and metacercariae of *Microphallus simillimus* (Microphallidae, Trematoda) parasitizing the gonad and digestive gland of *H. australis* specimens from two sites of Bahía Blanca estuary, Argentina. The prevalence of infection was significantly higher (34.17% in winter and 68.14% in late spring) in snails from the outer estuary at Site 2 than in those from the inner estuary at Site 1 (5.88% and 4.71% respectively). The only known definitive host for this digenean is the white-backed stilt *Himantopus melanurus* (Recurvirostridae, Aves), most abundant in the estuary during winter. Parasitism by *M. simillimus* causes variations in the shell dimensions of *H. australis*, the shells of infected snails being narrower than those of uninfected snails. Snails from Site 2 were found in general to be significantly smaller than those at Site 1, possibly as a result of differences in environmental factors such as the degree of exposure to wave energy, the allocation of energy to reproduction rather than growth (induced by predation and/or parasitic castrators) and anthropogenic stressors.

© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

Morphological variations among populations or generations of a mollusc species may be caused by genetic differences, environmental factors acting on ecophenotypic plasticity (Kemp and Bertness, 1984) or parasitism altering shell shape or size (Rohde, 1993; Levri and Fisher, 2000; Levri et al., 2005, 2007). Effects induced by parasites are extremely variable, ranging from gigantism (Probst and Kube, 1999; Miura et al., 2006) to reduced growth rate in infected snails (Fernandez and Esch, 1991). Moreover, Hechinger et al. (2009) found that different trematode species affect body mass differently in a single snail species. Figueiredo-Barros et al. (2006) reported some shell size differences in populations of the South American intertidal mud snail *Heleobia australis* (d'Orbigny 1835) from sites with different abiotic conditions in a Brazilian coastal environment, but no mention was made of parasites infecting the studied snails.

Heleobia australis is a common benthic component of the coastal ecosystem in Bahía Blanca estuary, Argentina (Fig. 1), where it is frequently parasitized by the digenean *Microphallus simillimus* Travassos 1920 (Fig. 2). *Microphallus simillimus* has an abbreviated life cycle involving two hosts. The entire larval portion of the life cycle takes place in the gonad and digestive gland of the infected intermediate snail host. In infected *H. australis*, sporocysts produce modified blastocercariae which develop into metacercariae that encyst within the sporocyst. The adult stage of *M. simillimus* is known to occur in the white-backed stilt, *Himantopus melanurus* Vieillot 1817, at the Mar Chiquita Lagoon, Buenos Aires, Argentina (Martorelli, 1991). *Himantopus melanurus* is the most abundant resident bird in Bahía Blanca estuary and reaches its highest densities of up to 160 birds km⁻² in winter (Delhey and Petracci, 2004).

Here we test the hypothesis that different microhabitats within Bahía Blanca estuary and parasitism by *Microphallus simillimus* affect the shell size of *Heleobia australis*. We further examine ecological aspects of this snail–parasite relationship by comparing snail sex with prevalence of infection at studied sites and explore the possibility that parasite infection increases with the greater abundance of a known definitive host.

* Corresponding author.

E-mail addresses: pilaralda@fncym.unlp.edu.ar (P. Alda), nbonel@fncym.unlp.edu.ar (N. Bonel), ficazzan@criba.edu.ar (N.J. Cazzaniga), sergio@cepave.edu.ar (S.R. Martorelli).

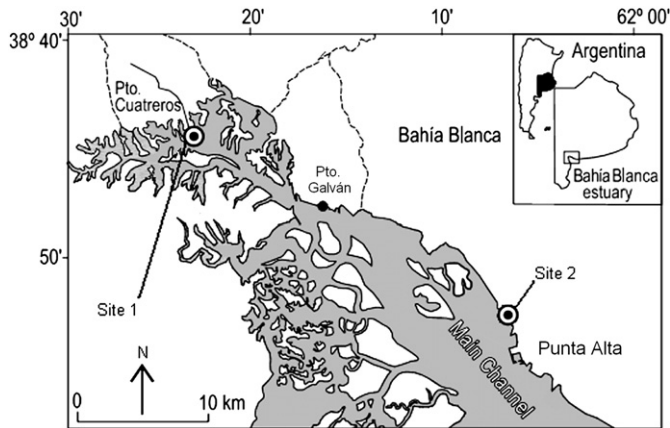


Fig. 1. Map of Bahía Blanca estuary, Buenos Aires province, Argentina (modified from Beigt et al., 2008). Site 1: Puerto Cuatros, Site 2: Villa del Mar.

1.1. Study area

The Bahía Blanca estuary in the southwest of Buenos Aires province is the second largest estuary in Argentina after the Río de la Plata estuary. Its two main cities, Bahía Blanca and Punta Alta, are located close to the north shore of the estuary. Both cities release non-treated domestic sewage effluents directly into the estuary. Several port terminals exporting agricultural crops, petroleum derivatives and chemical fertilizers operate along the same shore and the main navigation channel is periodically dredged from the mouth to Puerto Galván. The northern end of the estuary is narrow and consists of a complex system of anastomosing channels separated by extensive tidal flats, patches of low marshes, and islands. The mouth of the estuary is wider and opens to the Atlantic Ocean. There are strong semidiurnal tides whose average range

increases from the mouth (2.2 m) to the northern end (3.5 m) (Perillo and Piccolo, 1991).

A few minor rivers contribute freshwater to the estuary, producing localized spots of lower salinity, but marine conditions prevail overall. Salinity concentrations fluctuate throughout the year and are most pronounced at the northern end, ranging from a minimum of 22.8 to a maximum of 41.0 in summer at Puerto Cuatros (Gayoso, 1998). The annual mean surface water temperature is 13 °C, varying from 21.6 °C in summer to 8.5 °C in winter (Perillo et al., 2001). A distinctive annual biological feature of the estuary is a winter phytoplankton bloom consisting mainly of centric diatoms, predominantly *Thalassiosira curviseriata* Takano, which comprises about 90% of the algal biomass (Gayoso, 1998; Popovich and Gayoso, 1999). Chlorophyll a reaches 54 $\mu\text{g L}^{-1}$ during bloom, with maximum productivity at 200 $\text{mg C m}^{-3} \text{h}^{-1}$ (Perillo et al., 2001). Nutrient availability (NO_3^- , NO_2^- , NH_4^+ , PO_4^{3-} , SiO_4^{4-}) is therefore minimal in winter (July–August) and maximum availability coincides with the absence of algal blooms in late spring (November) and autumn (May–June). The highest level of primary productivity was found in the inner estuary, e.g. at Puerto Cuatros (Gayoso, 1998). The physical and biological characteristics of the Bahía Blanca estuary have been thoroughly reviewed by Perillo et al. (2001).

In the present study we examined snails from two sites in Bahía Blanca estuary: Site 1, at Puerto Cuatros (38° 44' S – 62° 22' W), located at the innermost part of the estuary; and Site 2, at Villa del Mar (38° 51' S – 62° 07' W), lying closer to the mouth (Fig. 1). Salinity fluctuation, wave exposure, current speed, dredging activities, sediments and benthic composition, and the amount of anthropogenic organic matter as well as other stressors differ greatly between the two sites. Site 1 is characterized by clayish mud sediments and a depauperate macrobenthic fauna dominated by polychaetes; Site 2 has a higher proportion of silt-sand sediment and a richer macrobenthic faunal assemblage dominated by crustaceans, molluscs, and polychaetes (Elías, 1985). Site 2 is close to a sewage discharge point source.

1.2. The snail

Heleobia australis is the only hydrobiid snail inhabiting the Bahía Blanca estuary (Elías et al., 2004). This species has a broad geographic distribution, ranging from Rio de Janeiro, Brazil, to San Antonio Oeste, Argentina (Gaillard and Castellanos, 1976), and is cited as a main component of benthic communities in the Atlantic coast of South America (De Francesco and Isla, 2003). This snail is a known intermediate host for several larval digeneans including: *Maritrema bonaerense* Etchegoin & Martorelli 1997 (Microphallidae) at Mar Chiquita lagoon, Argentina (Etchegoin and Martorelli, 1997); *Ascocotyle (Phagicola) longa* Ransom 1920 (Heterophyidae) in Uruguay (Carnevia et al., 2004); and *Pygidiopsis macrostomum* Travassos 1928 (Heterophyidae) and *Acanthocollari-trema umbilicatum* Travassos, Freitas and Bührnheim 1965 (Cryptogonimidae) in Brazil (Simões et al., 2008, 2009). *Heleobia australis* also hosts unknown cercariae resembling those of *M. bonaerense*, *Levinseniella cruzi* Travassos 1920 (Microphallidae), and *Himasthla escamosa* Diaz and Cremona 2004 (Echinostomidae) in Bahía Blanca estuary (La Sala et al., 2009).

2. Material and methods

2.1. Sample collection and laboratory procedure

Snails were collected from both study sites in November 2007 (late spring) during a period of low primary productivity, when white-backed stilt abundance was at its lowest, and in July 2008



Fig. 2. *Microphallus simillimus* (Digenea: Microphallidae).

(winter) during the winter phytoplankton bloom, when white-backed stilt abundance was at its maximum. Snails were removed during low tide from mud at the intertidal fringe of each location using a 1 mm-mesh sieve, transported to the laboratory in La Plata, and kept live in aquaria for 15 days until examined. Photos were taken from a random sub-sample of snails using a dissecting microscope. Snails were dissected and observed for the presence of parasites. To facilitate metacercarial excystment, encysted metacercariae were placed in small Petri dishes containing saline solution at 39–40 °C for 48 h. Cysts and excysted metacercariae were fixed in 10% formalin. A voucher specimen of the metacercaria of *Microphallus simillimus* was deposited in the Museo de La Plata Helminth Collection, Argentina, 5987.

The total length (LT) of each snail shell from the apex to the base of the aperture and the width of the last whorl on a perpendicular axis (WT) were measured using ImageTool software and the photos mentioned above. The sex and infection status of the snails was recorded and specimens with infections other than *Microphallus simillimus* were excluded from the analysis.

2.2. Statistical analysis

Sex- and time-related prevalence data were analyzed using chi-square (χ^2) tests. The effects of parasitism and study site on shell dimensions [length (LT) and width (WT)] for both sampling dates were evaluated using ANCOVA, with LT data as covariate and WT as the dependent variable (Kemp and Bertness, 1984; Levri et al., 2005). Shell measurements were transformed to $\ln(x + 1)$ for normalizing and stabilizing variances. Levene's test for homogeneity of variance was performed before each comparison to test for violations of assumptions of ANCOVA. Classes were compared on shell dimension by testing for significant differences between slopes and vertical shift of linear regressions. Differences in shape were evaluated by comparing data on study site, date, sex, and uninfected or infected individuals. Pair-wise comparison of slopes and vertical shifts was performed using multiple Student's *t*-tests, estimating individual error by applying the Dunn–Šidák correction with a global error of 5%:

$$\alpha_i = 1 - (1 - \alpha_g)^{1/K}$$

where α_i is the individual α ; α_g is the global α ; and k is the number of independent tests.

Shell size differences were also compared by study site, date, and uninfected or infected individuals by one-tailed Student's *t*-test.

3. Results

The sex ratio of the sampled snails did not differ significantly from 1:1 ($\chi^2 = 3.17$, d.f. = 3, $p = 0.366$). Out of 537 measured and dissected specimens of *Heleobia australis* from the two sites, 157 snails were infected with *Microphallus simillimus* (Total prevalence = 29.24%). From 34.17% to 68.14% of individuals were found to be infected at Site 2, whereas snails from Site 1 showed a significantly lower percentage of infestation on both sampling dates (5.88% in winter and 4.71% in late spring) (Table 1). The low number of infected snails at Site 1 prevented further analysis of sex-related prevalence or the effects of parasitism on shell size and form at this site.

Prevalence values did not differ significantly between males and females at Site 2: $\chi^2 = 2.54$, d.f. = 3, $p = 0.467$, but were significantly higher in late spring than in winter: $\chi^2 = 33.50$, d.f. = 3, $p < 0.0001$.

Descriptive statistics of the sampled material are shown in Table 2 and ANCOVA results are presented in Table 3.

Table 1

Prevalence of *Microphallus simillimus* sporocysts and metacercariae on mud snails, *Heleobia australis*, at Puerto Cuatrerros (Site 1) and Villa del Mar (Site 2) in Spring (November 2007) and Winter (July 2008).

		Spring		Winter		Total
		Female	Male	Female	Male	
Site 1	Infected	1	4	6	1	12
	Uninfected	58	43	52	60	213
	Prevalence	1.69%	8.51%	10.34%	1.64%	5.33%
Site 2	Infected	48	29	42	26	145
	Uninfected	20	16	69	62	167
	Prevalence	70.59%	64.44%	37.84%	29.55%	46.47%
Total		127	92	169	149	537

There was no sexual dimorphism in the shell WT/LT ratio between males and females of the same condition (uninfected Site 1; uninfected or infected Site 2) in spring. Uninfected spring snails were significantly longer ($t = 1.656$, $p < 0.0001$, d.f. = 135) and wider ($t = 1.656$, $p < 0.0001$, d.f. = 135) and had a significantly higher shell WT/LT ratio (i.e. fatter shells) in Site 1 than in Site 2. Multiple Student's *t*-test showed significant differences between the adjusted means of individuals from Site 1 and Site 2 ($\alpha_i = 0.008$, after Dunn–Šidák correction). The linear regression slope and adjusted means of infected individuals of both sexes from Site 2 did not differ significantly from those of uninfected individuals (Table 3). However, uninfected males and females at Site 2 were significantly wider ($t = 1.659$, $p < 0.01$, d.f. = 111) in spring than infected males and females (Table 2).

ANCOVA results for individuals sampled in winter (July 2008) show no significant differences in linear regression slopes among classes. The vertical shifts on the other hand do differ significantly, infected snails of both sexes being significantly narrower ($t = 1.653$, $p < 0.05$, d.f. = 197) than uninfected individuals. Multiple Student's *t*-test shows significant differences in adjusted means between individuals from Site 1 and Site 2 (i.e. snails from Site 1 are larger than snails from Site 2; Fig. 3); and between uninfected and infected snails from Site 2 ($\alpha_i = 0.008$, after Dunn–Šidák correction).

Adjusted means of the allometric curves of shell length to shell width of uninfected snails from Site 1 and uninfected and infected snails from Site 2 (Fig. 4) were all significantly different ($F_{2,524} = 126.93$; $p < 0.0001$).

4. Discussion

Prior to the present study, the hydrobiid snail *Heleobia conexa* (Gaillard 1974) was the only known intermediate host for

Table 2

Mean shell length (LT) and mean shell width (WT) in millimeters \pm standard deviation of *Heleobia australis* infected with *Microphallus simillimus* and uninfected, at Puerto Cuatrerros (Site 1) and Villa del Mar (Site 2) in Spring (November 2007: Date 1) and Winter (July 2008: Date 2).

		Spring			
		LT	WL	WL \times 100/LT	<i>n</i>
Site 1	Infected	5.94 \pm 0.53	3.69 \pm 0.29	62.12 \pm 2.51	5
	Uninfected	6.25 \pm 0.60	3.93 \pm 0.30	63.18 \pm 3.23	101
Site 2	Infected	4.70 \pm 0.51	2.25 \pm 0.21	48.17 \pm 2.79	77
	Uninfected	4.88 \pm 0.40	2.37 \pm 0.19	48.60 \pm 3.02	36
		Winter			
		LT	WL	WL \times 100/LT	<i>n</i>
Site 1	Infected	6.57 \pm 0.61	3.17 \pm 0.26	48.25 \pm 1.47	7
	Uninfected	5.97 \pm 1.18	2.95 \pm 0.47	50.01 \pm 4.20	112
Site 2	Infected	4.71 \pm 0.50	2.27 \pm 0.22	48.41 \pm 3.42	68
	Uninfected	4.67 \pm 0.90	2.37 \pm 0.36	51.68 \pm 4.86	131

Table 3
ANCOVA of two linear dimensions of *Heleobia australis*, uninfected at Puerto Cuatrerros (Site 1), infected with *Microphallus simillimus* and uninfected at Villa del Mar (Site 2) in Spring (November 2007: Date 1) and Winter (July 2008: Date 2). Equal letters mean non-significant differences.

Spring	Compared classes	Slopes	Slope equality	Common slope	Slope nullity	Vertical shift	Adjusted means
Site 1	Uninfected females	0.666a	$F_{5,202} = 0.47$ $P = 0.80$	0.616	$F_{1,207} = 425.83$ $P < 0.000$	$F_{5,207} = 16.22$ $P < 0.000$	1.331a
	Uninfected males	0.583a					1.322a
Site 2	Uninfected females	0.541a					1.260b
	Infected females	0.578a					1.249b
	Uninfected males	0.685a					1.272b
	Infected males	0.644a					1.256b
Winter	Compared classes	Slopes	Slope equality	Common slope	Slope nullity	Vertical shift	Adjusted means
Site 1	Uninfected females	0.642a	$F_{5,299} = 1.92$ $P = 0.09$	0.604	$F_{1,304} = 2063.65$ $P < 0.000$	$F_{5,304} = 24.90$ $P < 0.000$	1.290a
	Uninfected males	0.637a					1.286a
Site 2	Uninfected females	0.591a					1.260b
	Infected females	0.547a					1.220c
	Uninfected males	0.520a					1.253b
	Infected males	0.668a					1.215c

Microphallus simillimus. Martorelli (1991) reported that *H. conexa* was parasitized by *M. simillimus* at Mar Chiquita lagoon, Argentina. *Heleobia conexa* lives in brackish ecosystems from Mar Chiquita lagoon to Valdés Peninsula (Cazzaniga, 1982), but does not thrive in marine habitats (De Francesco and Isla, 2003). The species is entirely absent from the Bahía Blanca estuary, where marine conditions prevail. This study represents the first report of *M. simillimus* parasitizing *Heleobia australis*.

There are no published studies on the population dynamics or life history of *Heleobia australis* in Bahía Blanca estuary. However, in Brazil, recruitment of *H. australis* occurs in autumn (May–June) (Figueiredo-Barros et al., 2006). Recruitment of *H. australis* in Mar Chiquita lagoon, Argentina, occurs in summer, from January to March, depending on local conditions (De Francesco and Isla, 2004). The new Mar Chiquita lagoon cohort grows to sub-adult size in about three months and the mean size of snails does not change significantly throughout the rest of the year. De Francesco and Isla (2004) determined the life span of *H. australis* at Mar Chiquita lagoon to be one year, and our study assumes a similar life span for *H. australis* in Bahía Blanca estuary. Snails collected in the Bahía Blanca estuary in winter are therefore taken to be young

4–6-month-old sub-adults and snails collected in spring, full adult specimens 8–10 months old.

Contrary to our expectations, maximum values of infection did not coincide with the peak of abundance of the anticipated bird host, *Himantopus melanurus*. Though this is the most abundant resident bird in the Bahía Blanca estuary, it reaches highest density during the peak of primary productivity, i.e. in winter, and is seldom seen in spring (Delhey and Petracci, 2004). Assuming a one-year life span, the infected spring snails could not have survived until the next abundance peak of *H. melanurus*. Some species of *Microphallus* take time to develop (pre-patent period) inside hydrobiids, the parasite penetrating the host and eventually filling the snail with metacercariae in well-established infections (Krist and Lively, 1998). The relatively low prevalence in winter snails could be due to a delay in development of the trematode in the snail, with the high values in late spring signifying the final phase of the infection process in adults destined to reproduce and die during the following 1–3 months. If this time lag is short in *Microphallus simillimus*, the high prevalence of *M. simillimus* metacercariae in spring suggests there are other definitive hosts that are more abundant in this ecosystem in spring. Delhey and Petracci (2004) reported 59 bird species within the study area, which is an important site for transient migratory birds. Furthermore, numerous trophically transmitted parasites have been shown to alter the behaviour of their intermediate hosts in such a way as to increase their vulnerability to predatory definitive hosts (Thomas et al., 2005). If birds preferentially feed on infected snails, the prevalence of *M. simillimus* could be lower in winter during the abundance peak of *H. melanurus*.

The presence of larval stages of trematodes in first intermediate hosts is a good indicator of habitat diversity and trophic interactions (Hechinger et al., 2008). The highest prevalence of *Microphallus simillimus* in Site 2 is therefore most likely related to the presence of higher levels of organic matter and greater abundance of the final host.

If there had been a reproductive time gap between snails at Site 1 and Site 2, the larger size of the snails at the former could have been attributed to age differences. However, even the largest snails at Site 2 (late spring) did not attain the size of young sub-adults at Site 1 in winter, from which it may be concluded that the size of uninfected *Heleobia australis* within the estuary varies significantly.

The smaller shell dimensions of the snails at Villa del Mar (Site 2) may be due to a combination of the following abiotic and biotic factors:

- (1) Snails living on exposed shores differ strikingly from closely related gastropods living on sheltered shores in a number of

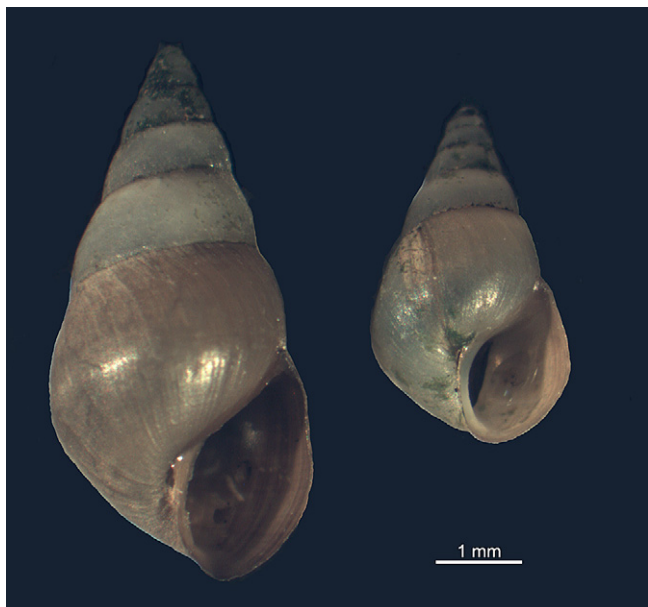


Fig. 3. Uninfected winter snails from Site 1 (left) and Site 2 (right).

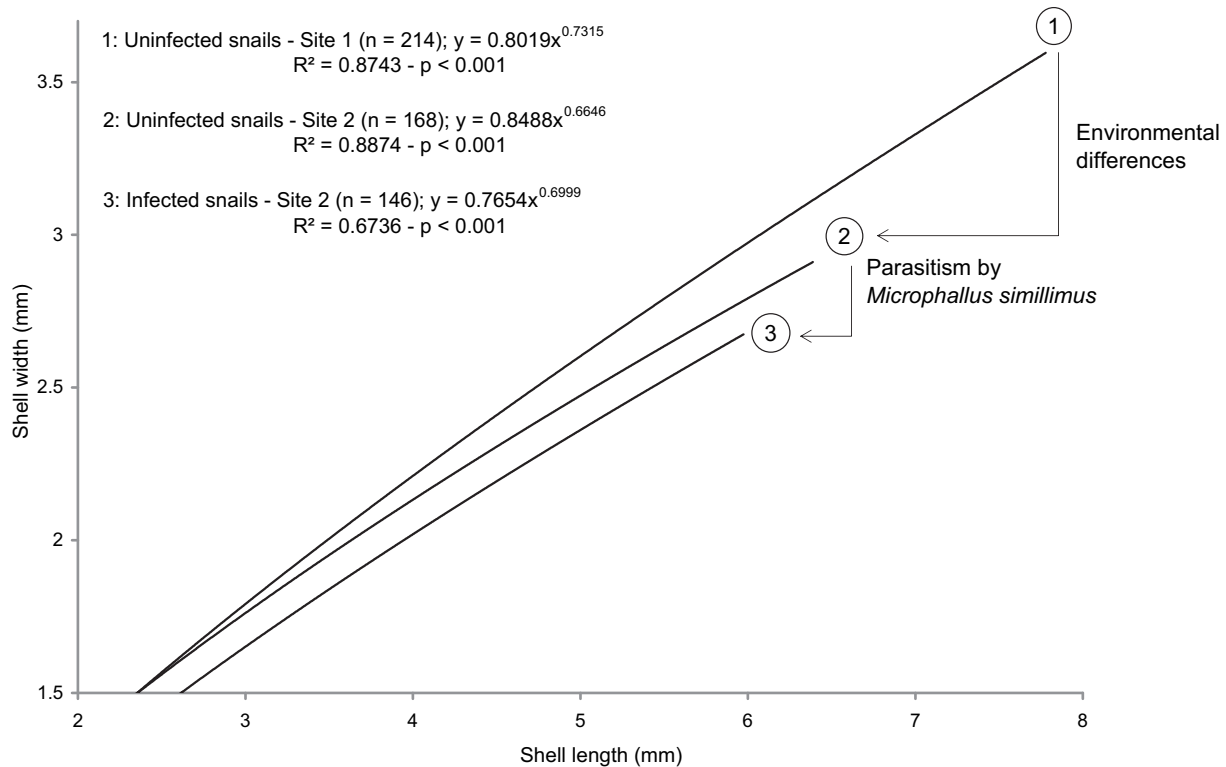


Fig. 4. Allometric curves of shell length to shell width for uninfected snails from Site 1 and Site 2, and infected snails at Site 2.

morphological and life history traits (Boulding, 1990). Exposure to waves is often associated with differences in the nature and quantity of available food (Kitching and Lockwood, 1974) and Boulding (1990) proposed that marine prosobranchs on shores exposed to heavy surf tend to be smaller than prosobranchs from sheltered areas. Roberts and Hughes (1980) demonstrated that individuals of the common name *Littorina rudis* Maton 1797 living on a sheltered boulder shore in Wales, U.K., grew faster than those living on an exposed cliff, mainly owing to environmental differences (e.g. reduced foraging time in exposed habitats). In the Bahía Blanca estuary, Villa del Mar (Site 2) has greater wave energy than Puerto Cuatreros (Site 1) (G.M.E. Perillo, pers.comm., August 2009), this higher exposure to waves coinciding with a smaller shell size in *Heleobia australis*.

- (2) Extrinsic mortality or the probability of being killed by predators (Crowl and Covich, 1990) or castrated by parasites (Lafferty, 1993) influences a snail's energy allocation between growth and reproduction. Under conditions of increased extrinsic mortality, snails may reach maturity at a smaller size. The greater abundance of predators (*Himantopus melanurus*) and the parasitic castrator *Microphallus simillimus* at Site 2 could explain the size distribution of *Heleobia australis* at Bahía Blanca estuary.
- 3) Anthropogenic stressors such as dredging activities, sewage discharges, and large commercial vessels are also more common at Site 2. At least some of these stressors could increase eutrophication, leading to higher snail densities (Lillebø et al., 1999).

The absence of the above-mentioned stressors – and possibly others – at Site 1 may help to explain the larger size of snails at this location.

Some species of *Microphallus* are known to cause gigantism in short-lived snails (Levri et al., 2005). Trematodes that invade the digestive gland cause an increase in shell growth by destroying

digestive gland cells, thus releasing ionic calcium which eventually becomes amalgamated in the shell (Cheng, 1971). Our results show to the contrary that infected snails from Bahía Blanca have narrower shells than uninfected snails. *Microphallus simillimus* parasitizing gonad and digestive gland of *Heleobia australis* may induce the allocation of energy to reproduction rather than growth in infected snails.

5. Conclusions

This is the first report of *Microphallus simillimus* parasitizing gonad and digestive gland tissue in *Heleobia australis*. The higher prevalence of the parasite observed at Site 2 (Villa del Mar, in the outer estuary) could be due to a higher abundance of the definitive host of this parasite. The lack of a concomitant peak in abundance of the predator *Himantopus melanurus* and higher prevalence of the castrating parasite *M. simillimus* in *H. australis* shows that the parasite's development is probably delayed in the snail or that other definitive hosts of this parasite are present in Bahía Blanca estuary. The size of uninfected *H. australis* individuals varies significantly within the estuary. The smaller snail size recorded at Site 2 (Villa del Mar) may be a consequence of greater wave strength, allocation of energy to reproduction induced by predators or parasitic castrators, anthropogenic stressors, or perhaps a combination of these factors.

It may therefore be concluded that the shell size of *Heleobia australis* in Bahía Blanca estuary is affected by *Microphallus simillimus* and a variety of abiotic and biotic environmental factors.

Acknowledgements

We thank S. S. Curran and anonymous reviewers for their critical review of the manuscript. We also thank R. F. Hechinger and V. Negrín for providing useful bibliography. PA and NB are doctoral

fellows of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). NJC is a staff researcher of the Comisión de Investigaciones Científicas de la Provincia de Buenos Aires (CIC). This work was partially funded by a research grant from the Agencia Nacional de Promoción Científica y Técnica (PICT 34412/05) to SRM.

References

- Beigt, D., Piccolo, M.C., Perillo, G.M.E., 2008. Surface heat exchanges in an estuarine tidal flat (Bahía Blanca estuary, Argentina). *Ciencias Marinas* 34, 1–15.
- Boulding, E.G., 1990. Are the opposing selection pressures on exposed and sheltered shores sufficient to maintain genetic differentiation between gastropod populations with high intermigration rates? *Hydrobiologia* 193, 41–52.
- Carnevia, D., Perreta, A., Venzal, J.M., Castro, O., 2004. *Heleobia australis* (Mollusca, Hydrobiidae) y *Mugil platanus* (Pisces, Mugilidae), primer y segundo hospedador intermediario de *Ascocotyle* (Phagocota) *longa* (Digenea, Heterophyidae) en Uruguay. *Revista Brasileira de Parasitologia Veterinária* 13, 283.
- Cazzaniga, N.J., 1982. Notas sobre hidróbidos argentinos II. Una Littoridina del “grupo parchappii” en Península Valdés (Chubut). *Revista del Museo de La Plata, Sección Zoología* 129, 11–16.
- Cheng, T.C., 1971. Enhanced growth as manifestation of parasitism and shell depositing in parasitized molluscs. In: Cheng, T.C. (Ed.), *Aspects of the Biology of Symbiosis*. University Park Press, Baltimore, pp. 103–137.
- Crowl, T.A., Covich, A.P., 1990. Predator-induced life-history shifts in a freshwater snail. *Science* 247, 949–951.
- De Francesco, C.G., Isla, F., 2003. Distribution and abundance of hydrobiid snails in mixed estuary and a coastal lagoon, Argentina. *Estuaries and Coasts* 26, 790–797.
- De Francesco, C.G., Isla, F., 2004. The life cycle and growth of *Heleobia australis* (d’Orbigny, 1835) and *H. conxa* (Gaillard, 1974) (Gastropoda: Rissosoidea) in Mar Chiquita coastal lagoon (Argentina). *Journal of Molluscan Studies* 70, 173–178.
- Delhey, K., Petracci, P., 2004. Aves marinas y costeras. In: Piccolo, M.C., Hoffmeyer, M.S. (Eds.), *Ecosistema del estuario de Bahía Blanca*. Instituto Argentino de Oceanografía, Bahía Blanca, Argentina, pp. 203–220.
- Elías, R., 1985. Macrobentos del estuario de la Bahía Blanca (Argentina). I. Mesolitoral. *Spheniscus* 1, 1–33.
- Elías, R., Iribarne, O., Bremec, C.S., Martínez, D.E., 2004. Comunidades bentónicas de fondos blandos. In: Piccolo, M.C., Hoffmeyer, M.S. (Eds.), *Ecosistema del estuario de Bahía Blanca*. Instituto Argentino de Oceanografía, Bahía Blanca, Argentina, pp. 179–190.
- Etchegoin, J.A., Martorelli, S.R., 1997. Description of a new species of *Maritrema* (Digenea: Microphallidae) from Mar Chiquita coastal lagoon (Buenos Aires, Argentina) with notes on its life cycle. *Journal of Parasitology* 83, 709–713.
- Fernandez, J., Esch, G.W., 1991. Effect of parasitism on the growth rate of the pulmonate snail *Helisoma anceps*. *Journal of Parasitology* 77, 937–944.
- Figueiredo-Barros, M.P., Leal, J.J.F., Esteves, F.A., Rocha, A.M., Bozelli, R.L., 2006. Life cycle, secondary production and nutrient stock in *Heleobia australis* (d’Orbigny 1835) (Gastropoda: Hydrobiidae) in a tropical coastal lagoon. *Estuarine, Coastal and Shelf Science* 69, 87–95.
- Gaillard, M.C., Castellanos, Z.J.A.de, 1976. Moluscos Gasterópodos, Hydrobiidae. In: Ringuet, R.A. (Ed.), *Fauna de agua dulce de la República Argentina*, vol. 15. Fundación para la Educación, la Ciencia y la Cultura (FECIC), Buenos Aires, Argentina, pp. 1–39.
- Gayoso, A.M., 1998. Long-term phytoplankton studies in the Bahía Blanca estuary, Argentina. *ICES Journal of Marine Science* 55, 655–660.
- Hechinger, R.F., Lafferty, K.D., Kuris, A.M., 2008. Trematodes indicate animal biodiversity in the Chilean intertidal and lake Tanganyika. *Journal of Parasitology* 94, 966–968.
- Hechinger, R.F., Lafferty, K.D., Mancini III, F.T., Warner, R.R., Kuris, A.M., 2009. How large is the hand in the puppet? Ecological and evolutionary factors affecting body mass of 15 in their snail host. *Evolutionary Ecology* 23, 651–667.
- Kemp, P., Bertness, M.D., 1984. Snail shape and growth rates: evidence for plastic shell allometry in *Littorina littorea*. *Proceedings of the National Academy of Sciences of the United States of America* 81, 811–813.
- Kitching, J.A., Lockwood, J., 1974. Observations on shell form and its ecological significance in thaisid gastropods of the genus *Lepsiella* in New Zealand. *Marine Biology* 28, 131–144.
- Krist, A.C., Lively, C.M., 1998. Experimental exposure of juvenile snails (*Potamopyrgus antipodarum*) to infection by trematode larvae (*Microphallus* sp.): infectivity, fecundity compensation and growth. *Oecologia* 116, 575–582.
- La Sala, L.F., Martorelli, S.R., Alda, P., Marcotequi, P., 2009. Some digeneans from Olrog’s gull *Larus atlanticus* Olrog, 1958 (Aves: Laridae) from the Bahía Blanca Estuary, Argentina. *Comparative Parasitology* 76, 113–116.
- Lafferty, K.D., 1993. The marine snail, *Cerithidea californica*, matures at smaller sizes where parasitism is high. *Oikos* 68, 3–11.
- Levri, E.P., Fisher, L., 2000. The effect of a trematode (*Microphallus* sp.) on the response of the freshwater snail, *Potamopyrgus antipodarum* to light and gravity. *Behaviour* 137, 1141–1151.
- Levri, E.P., Dillard, J., Martin, T., 2005. Trematode infection correlates with shell shape and defence morphology in a freshwater snail. *Parasitology* 130, 699–708.
- Levri, E.P., Lunnen, S.J., Itle, C.T., Mosquea, L., Kinkade, B.V., Martin, T.G., Delisser, M.A., 2007. Parasite-induced alteration of diurnal rhythms in a freshwater snail. *Journal of Parasitology* 93, 231–237.
- Lillebø, A.I., Pardal, M.A., Marques, J.C., 1999. Population structure, dynamics and production of *Hydrobia ulvae* (Pennant) (Mollusca: Prosobranchia) along an eutrophication gradient in the Mondego estuary (Portugal). *Acta Oecológica* 20, 289–304.
- Martorelli, S.R., 1991. El ciclo biológico abreviado de *Microphallus similimus* (Travassos, 1920), comb. n. (Digenea: Microphallidae), parásito de *Heleobia conxa* (Mollusca, Hydrobiidae) y de *Himantopus melanurus* (Aves, Recurvirostridae) en Argentina. *Iheringia, Série Zoología* 71, 91–98.
- Miura, O., Kuris, A.M., Torchin, M.E., Hechinger, R.F., Chiba, S., 2006. Parasites alter host phenotype and may create a new ecological niche for snail hosts. *Proceedings of the Royal Society B* 273, 1323–1328.
- Perillo, G.M.E., Piccolo, M.C., 1991. Tidal response in the Bahía Blanca Estuary. *Journal of Coastal Research* 7, 437–449.
- Perillo, G.M.E., Piccolo, M.C., Parodi, E., Freije, R.H., 2001. The Bahía Blanca estuary, Argentina. In: U. Seeliger, U., Kjerfve, B. (Ed.), *Coastal Marine Ecosystems of Latin America*. Ecological Studies, vol. 144, pp. 205–217.
- Popovich, C.A., Gayoso, A.M., 1999. Effect of irradiance and temperature on the growth rate of *Thalassiosira curviseriata* Takano (Bacillariophyceae), a bloom diatom in Bahía Blanca estuary (Argentina). *Journal of Plankton Research* 21, 1101–1110.
- Probst, S., Kube, J., 1999. Histopathological effects of larval trematode infections in mudsnails and their impact on host growth: what causes gigantism in *Hydrobia ventrosa* (Gastropoda: Prosobranchia)? *Journal of Experimental Marine Biology and Ecology* 238, 49–68.
- Rohde, K., 1993. *Ecology of Marine Parasites*, second ed. CAB International, Wallingford, UK, 298 pp.
- Roberts, D.J., Hughes, R.N., 1980. Growth and reproductive rates of *Littorina rudis* from three contrasted shores in North Wales. *Marine Biology* 58, 47–54.
- Simões, S.B.E., Barbosa, H.S., Santos, C.P., 2009. The life history of *Pygidiopsis macrostomum* Travassos, 1928 (Digenea: Heterophyidae). *Memórias do Instituto Oswaldo Cruz* 104, 106–111.
- Simões, S.B.E., Neves, R.F.C., Santos, C.P., 2008. Life history of *Acanthocollaritrema umbilicatum* Travassos, Freitas and Bührnheim, 1965 (Digenea: Cryptogonimidae). *Parasitology Research* 103, 523–528.
- Thomas, F., Adamo, S., Moore, J., 2005. Parasitic manipulation: where are we and where should we go? *Behavioural Processes* 68, 185–199.