DOI:10.2478/s11686-013-0184-0
© W. Stefański Institute of Parasitology, PAS
Acta Parasitologica, 2013, 58(4), 577–584; ISSN 1230-2821

Can the studies at a spatial scale of 100s meters detect the spatiotemporal fluctuations of a parasite assemblage?

Manuela Parietti[1]*, Matías Javier Merlo[1] and Jorge Alejandro Etchegoin[1]

Laboratorio de Parasitología, Instituto de Investigaciones Marinas y Costeras (IIMyC). Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata. Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). Funes 3350, 7600 Mar del Plata, Argentina. [1]CONICET

Abstract

The importance of small-scale heterogeneity in local factors which overrides that of larger-scales factors, suggest that local factors play a major role in determining the richness and prevalence of larval digeneans in intertidal gastropods. The restricted distribution of the snail *Heleobia australis* along a 500 m transect in Cangrejo creek (Mar Chiquita, Argentina) provides a good opportunity to test the assumption that a study at spatial scale of 100s meters can detect spatiotemporal fluctuations of a larval digenean assemblage. To analyze that, 3600 specimens of *H. australis* were collected seasonally during the year 2011. A quantitative variation and a space-time interaction between sampling points and seasons of the year for the total prevalence of larval digeneans and snail's densities were found, as well as a positive correlation with abiotic factors. These results revealed that the fluctuations in the community of larval digeneans of the snail *H. australis* can be detected at small spatial scale, using its natural distribution of 500 m. This study also highlights the importance of seasonality as a factor that must be considered in studies focused on the search for patterns structuring the communities of larval digeneans, at medium and large scales.

Keywords

Heleobia australis, digenean, small spatial scale

Introduction

In the latest years, parasitological studies regarding different aspects of the host-parasite relationships have placed special emphasis on the spatial scale at which those relationships are examined (Poulin and Mouritsen 2003; Byers *et al*. 2008). In general, infection processes are proximately driven by local factors (environmental conditions, resources or biotic interactions) which ultimately may be correlated over large regional scale (Byers *et al.* 2008). For this reason, studies conducted at large, nested spatial scales are considered as particularly informative (Byers *et al*. 2008). Nevertheless, in the case of the larval digeneans parasitizing snail hosts, Poulin and Mouritsen (2003) stressed the importance of small-scale heterogeneity in local factors which overrides that of larger-scales factors, suggesting that local factors play a major role in determining the richness and prevalence of larval digeneans in intertidal gastropods.

The digenean life cycles are typically complex and require at least one intermediate snail host (Hasseb and Fried 1997). The completion and the spatial distribution of the these life cycles depends of a variety of factors such as the coincidence in the distribution of both intermediate and definitive hosts, and the characteristics of the environmental factors that can favor or limit the transmission of free-living stages (Galaktionov and Dobrovolskij 2003). All these factors that act interdependently (Faltýnková *et al.* 2008) determine the spatiotemporal variability, in terms of species richness and prevalence, commonly observed in the larval digenean communities in snail hosts.

In general, studies dealing with the spatiotemporal variability of larval digenean assemblages in the same snail species are based on samples collected on a scale of kilometers (e.g. Granovitch *et al.* 2000; Eschweiler *et al.* 2009). However, Poulin and Mouritsen (2003) suggested that local factors, operating on a scale of 10s to 100s of m, can also determine how many digenean species are present or how many snails are infected.

The gastropod *Heleobia australis* (d´Orbigny, 1835) (Cochliopidae) is one of the most abundant species of invertebrates inhabiting the Mar Chiquita coastal lagoon (Buenos Aires province, Argentina) (37º46´S, 57º27´W). This species of small size (usually <7mm total shell length) has a life span of 12 months (De Francesco and Isla 2004) and may reach densities over 11 individual/cm^3 (De Francesco and Isla 2003).

*Corresponding author: manuelaparietti@hotmail.com

With reference to parasitological studies, Etchegoin (1997, 2001) reported a total of 13 species of larval digeneans parasitizing *H. australis.* Some of these species were described by Martorelli (1986, 1989, 1990); Martorelli and Etchegoin (1996) and by Etchegoin and Martorelli (1998).

In previous investigations (Etchegoin 1997, 2001), the Cangrejo creek was not included as study area. In this creek, connected with the estuarine zone of the lagoon which communicates with the open sea, *H. australis* presents a distribution of only 500 m. Taking into account that studies related to the detection of spatiotemporal variations in parasite/invertebrate relationships at small spatial-scale are scanty, the restricted distribution of *H. australis* in the Cangrejo creek provides a good opportunity to test the supposition that local factors play a major role in determining the richness and prevalence of larval digeneans in gastropods. As a first approach to the study of the local factors influencing larval digenean assemblages in the area, the objective of this study was to determine if a study at small spatial scale operating on a scale of 100s meters can detect the spatiotemporal fluctuations, related to species richness and prevalence, of a larval digenean assemblage in a snail host.

Materials and Methods

Sampling site

The Mar Chiquita coastal lagoon, designated a Man and Biosphere Reserve by UNESCO, can be divided into a freshwater zone, characterized by continental water discharge, and an estuarine zone which communicates with the open sea. The estuarine zone is characterized by mixo-euryhaline waters and is greatly influenced by marine water. Cangrejo creek, where this

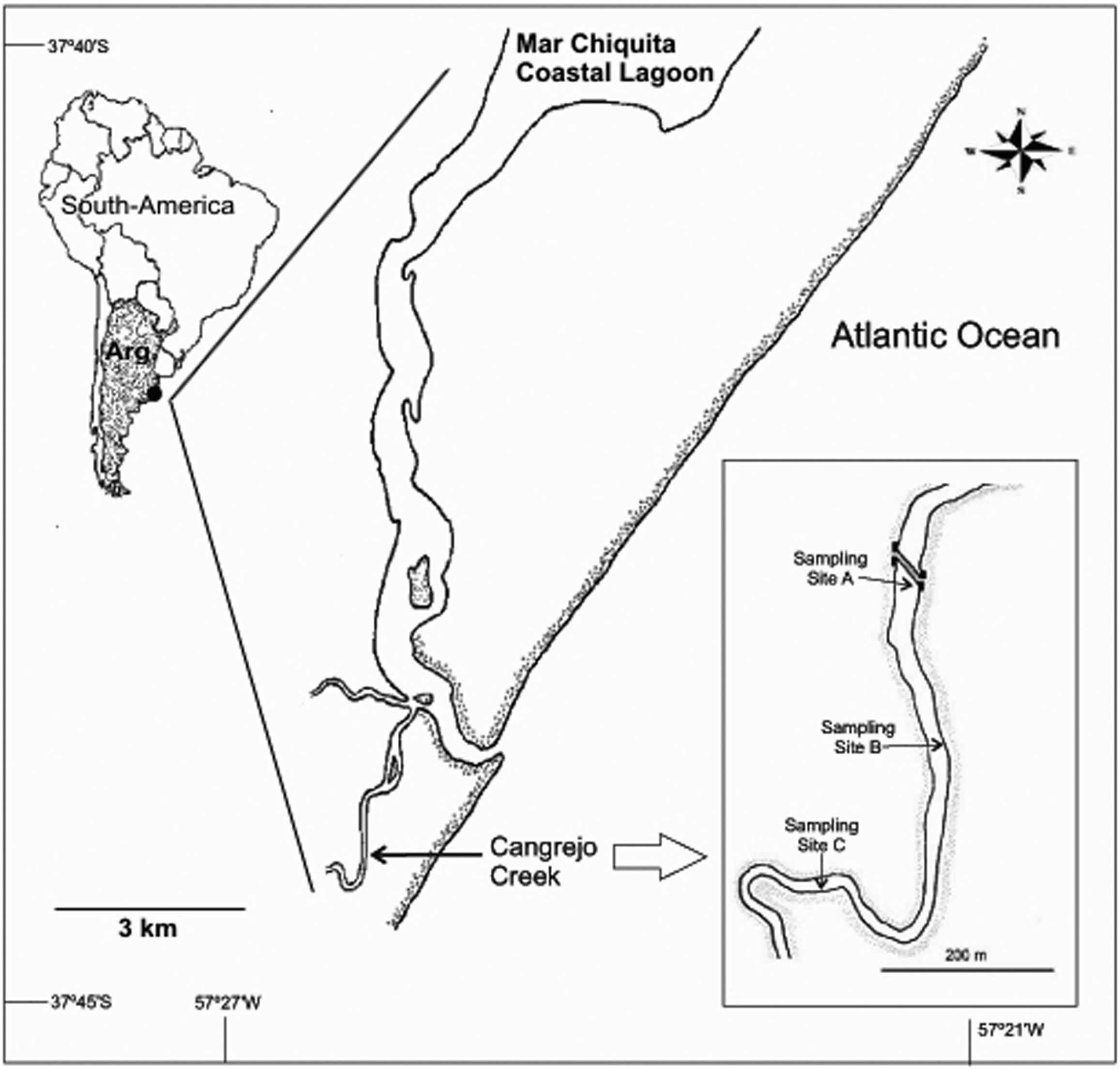

Fig.1. Map of Mar Chiquita Coastal Lagoon, Argentina (Arg.) showing the location of sampling points

Table I. Seasonal values of prevalence (mean ± standard deviation) and detailed list of species or morphological types of larval digeneans parasitizing *Heleobia australis* (Mollusca, Gasteropoda) in Cangrejo creek (Mar Chiquita Coastal Lagoon, Argentina)

Family	Species/Morphological type	*	Summer			Autumn			Winter			Spring		
			Sampling point A	Sampling point B	Sampling point C	Sampling point A	Sampling point B	Sampling point C	Sampling point A	Sampling point B	Sampling point C	Sampling point A	Sampling point B	Sampling point C
Heterophyidae (Definitive host: birds and mammals)	Pleurolophocercaria VI	d	–	0.32(±0.55)	–	–1.33(±1.82)	–0.67(±0.91)	0.33(±0.75)	–	–	–	–	–0.33(±0.75)	–0.67(±0.91)
	Pleurolophocercaria IV	d	–	1.90(±1.65)	0.63(±0.55)	–	–	1.33(±1.39)	1.33(±1.39)	0.67(±1.49)	–	–	0.33(±0.75)	–
	Pleurolophocercaria V	d	–	0.32(±0.55)	–	1.00(±1.49)	0.67(±0.75)	–	–	–	–	–	0.33(±0.75)	–
	Pleurolophocercaria III	d	–	0.32(±0.55)	1.27(±1.46)	–	–	0.33(±0.75)	0.33(±0.75)	0.33(±0.75)	–	–	–	–
	Cercaria magnacauda I	d	–	–	–	1.67(±2.04)	0.67(±0.75)	0.33(±0.75)	–	–	–	–	0.33(±0.75)	2.00(±1.39)
	Cercaria Heterophyidae sp.8	g	0.32(±0.55)	–	0.32(±0.55)	–	–	3.33(±3.53)	1.00(±0.91)	1.67(±1.67)	1.00(±0.91)	0.33(±0.75)	–	–
Acanthostomidae (Defenitive host: Fishes, reptiles and amphibians)	Pleurolophocercaria I	d	0.63(±0.55)	–	–	–	–	0.33(±0.75)	–	0.67(±0.91)	0.33(±0.75)	–	2.00(±2.74)	–
Microphallidae (Defenitive host: birds and mammals)	*Microphallus simillimus*	e	–	–	–	0.33(±0.75)	0.67(±0.75)	0.33(±0.75)	0.33(±0.75)	0.33(±0.75)	–	–	–	–
	Matitrema bonaerensis	e	42.86(±7.79)	19.68(±6.75)	17.14(±4.15)	6.42(±5.19)	13.33(±8.09)	17.33(±7.41)	10.33(±5.19)	11.02(±3.84)	11.00(±4.8)	6.67(±5.27)	10.67(±3.84)	12.00(±5.94)
	Microphallus szidati	a; e	9.84(±3.06)	4.76(±1.65)	1.59(±1.1)	1.59(±1.42)	4.00(±3.46)	5.8(±8.39)	2.67(±2.53)	3.33(±2.64)	2.00(±0.74)	1.67(±2.04)	5.33(±3.98)	8.00(±2.98)
Echinostomatidae (Definitive host: birds, mammals and fishes)	Cercaria heleobicola V	c	0.32(±0.55)	1.27(±1.10)	0.95(±0.96)	–	–	–	–	–	0.33(±0.75)	0.33(±0.75)	0.33(±0.75)	–
	Echinocercaria sp. 1	e	0.32(±0.55)	–	–	–	–	–	–	–	–	–	0.33(±0.75)	–
Haploporidae (Definitive host: fishes)	Cercaria Haploporidae sp.1	f	–	–	–	0.33(±0.75)	–	–	0.33(±0.75)	–	–	–	–	–
	Cercaria Haploporidae sp. 2	f	17.78 (±12.06)	6.67(±1.65)	9.84(±7.15)	55.92 (±19.53)	6.00(±4.00)	19.67 (±18.87)	4.58(±3.7)	5.33(±5.05)	9.33(±5.08)	0.33(±0.75)	3.00(±2.74)	11.33(±13.46)
	Cercaria heleobicola III	b	0.32(±0)	–	–	–	–	–	–	–	–	–	–	–
	Cercarria Haploporidae sp. 3	g	–	–	0.32(±0.55)	–	–	0.33(±0.75)	–	–	–	–	–	–
Notocotylidae (Definitive host: birds and mammals)	Notocotylidae sp. 1	f	–	0.32(±0.55)	0.32(±0.55)	–	–	0.33(±0.75)	–	–	1.00(±1.49)	–	0.67(±0.91)	0.33(±0.75)
Cyatocothylidae (Definitive host: birds and mammals)	Furcocercaria sp. 1	f	–	–	–	1.33(±2.17)	0.33(±0.75)	–	–	–	–	–	–	–
Homalometridae (Definitive host: fishes)	Cercaria heleobicola II	f	–	–	–	–	–	–	–	–	–	–	0.33(±0.75)	–
Ochetosomatidae (Definitive host: reptiles)	Xiphidiocercaria sp. 2	f	–	0.32(±0.55)	–	–	–	–	–	–	–	–	–	–
Psilostomatidae (Definitive host: birds and mammals)	Cercaria aff. Psilochasmus oxyurus (Creplin, 1835)	f	–	–	–	0.33(±0.75)	0.33(±0.75)	0.33(±0.75)	–	–	0.33(±0.75)		–	0.33(±0.75)
Aporocotylidae (Definitive host: fishes)	Cercaria Aporocotylidae sp. 1	g	–	–	–	–	–	–	–	–	–	–	–	0.33(±0.75)
	Overall Prevalence		68.89 (±7.21)	35.51 (±10.27)	31.11 (±8.21)	62.55 (±15.65)	25.33 (±15.06)	46.66 (±22.42)	19.33 (±5.35)	23.33 (±6.56)	25.67 (±5.06)	9.33 (±8.30)	23.33 (±7.17)	37.33 (±17.1)

*References: a. Martorelli (1986); b. Martorelli (1989); c. Martorelli (1990); d. Martorelli & Etchegoin (1996); e. Etchegoin (1997); f. Etchegoin & Martorelli (1998); g. Parietti (2011).

study was conducted, is connected with the main body of the lagoon in the outer estuarine zone which communicates with the open sea (Fig. 1).

Sampling procedures

Specimens of *H. australis* were collected from 1 sampling trips per season during the year 2011, along a 500 m transect which coincide with the entire distribution of *H. australis* in the creek. Along this transect, three sampling point were selected: one in the south end of the transect (point A) and the other two at 250 m and 500 m of the point A (points B and C, respectively) (Fig. 1). At each sampling point, five replicates samples per sampling trip were taken and water temperature and salinity were measured, using a Digital Multi-Thermometer range –50, 150°C and a Portable Refractometer FG-211 Salinity/ATC 0~100 °/oo, respectively. Snails were collected using random cores (8 cm diameter × 3 cm depth) and the content of each core was placed into plastic cups filled with water from the lagoon for transportation. In the laboratory, snails were removed from mud, quantified and measured for total length with a Vernier caliper (precision 0.1 mm). Density of *H. australis* at each core was calculated as the number of snails by cm^3. The sample size was calculated according to the methodology developed in Merlo *et al.* (2010), and a total of 3600 randomly selected snails were isolated individually and exposed to a 100 W incandescent lamp for 48 h to stimulate shedding of cercariae. Finally, all gastropods were dissected under a stereomicroscope in order to detect the presence of sporocysts, rediae and developing cercariae (prepatent infections; Curtis and Hubbard, 1990). Developing or completely developed cercariae, sporocysts and rediae were identified using previous studies dealing with larval digeneans parasitizing snails of the genus *Heleobia* from Mar Chiquita coastal lagoon (Martorelli 1986, 1989, 1990; Martorelli and Etchegoin 1996; Etchegoin 1997; Etchegoin and Martorelli 1998).

Data analysis

To analyse and compare the community of larval digeneans in *H. australis* over time and space, the following indices were used: (a) Species richness (S) which represents the total number of species in a sample (Ludwig and Reynolds 1988, Magurran 1988); (b) Overall prevalence = the number of parasitized snails/the number of collected snails × 100 (Lafferty *et al.* 1994); (c) Prevalence of a species = the number of snails parasitized by that species/the number of collected snails × 100.

Similarities in the composition of the larval digenean community were analyzed with the Anosim and Simper tests, where the factors analyzed were the sampling points (A, B and C) and the different seasons of the year (summer, autumn, winter and spring), Anosim and Simper tests were implemented in PRIMER 6 (Clarke and Green 1988). Two-way ANCOVA test was used for comparisons between overall prevalence, using the snail's sizes as covariable. Two-way ANOVA test was used to analyze species richness and snail's densities. In both tests, the factors analyzed were the sampling points (A, B and C) and the different seasons of the year (summer, autumn, winter and spring) and Tukey test (Zar 2009) was used for post-hoc comparisons. Furthermore, to establish possible relationships between the seasonal overall prevalence vs. snail's densities, Spearman correlation index was applied. Finally, to establish possible relationships between the seasonal overall prevalence and abiotic factors (temperature and salinity), Pearson correlation index was applied in both cases. All analyses were done using the statistical programming language R, version 2.15.2. (R Development Core Team 2005) and InfoStat/L (FCA-UNC, 2012).

Results

A total of 22 digenean species, belonging to 11 families, were observed in the community of larval digeneans parasitizing *H. australis* (Table I). The means of species richness recorded in each season, fluctuated between 2.2 and 6.33 (Table II). Similarities in the composition of the larval digenean community between three points were not significantly different (ANOSIM R value = 0.11; p = 0.227) as well as between four seasons of the year (ANOSIM R value = 0.25; p = 0.077). SIMPER analysis found that >50% of this similarities were due to the relative greater occurrence in three sampling points of *Maritrema bonaerensis*, *Microphallus szidati* and the cercariae of Haploporidae sp. 2. The number of species found at each point and at each season revealed no significant differences (Two-Way Anova Factor: Point: $F_{2;42}$ = 1.556, P = 0.223; Season: $F_{3;42}$ = 2.782, P = 0.053; Point × Season: $F_{6;42}$ =2.16; P = 0.066).

The overall prevalence and prevalence of species for each sampling point and for each season of the year are showed in Table I. Analysis of the overall prevalence revealed a significant snail's size effect ($F_{6;42}$ = 11.96; P = 0.0013), and an interaction between sampling points and seasons of the year ($F_{6;42}$ = 8.72; P<0.0001) was found after correction carried out from the effect due to the snail's size. This means that the differences found between sampling point varied according to the season of the year under study. Moreover, the overall prevalence showed different seasonal patterns at each point. In sampling point A overall prevalence showed higher values in summer (S) and autumn (A) than in winter (W) and spring (Sp) (S vs Sp; S vs W; A vs Sp and A vs W P<0.05; in all other cases P>0.05). Sampling points B and C showed constant overall prevalence values throughout the year (in all cases P>0.05). Regarding to the differences between sampling sites for each season of the year, only the sampling point A was significantly different from sampling points B and C during the summer (A vs B and A vs C P<0.05) and from sampling point C during the autumn (P<0.05) (Fig. 2a).

Table II. Summary of seasonal data for snail's length, snail's densities, overall prevalence, species richness, temperature and salinity. All values are expressed as range (mean)

Sample point	Season of the year	Nº snail examinated	Snails length (mm)	Snail's density (snails/cm³)	Prevalence (%)	Species richness	Temperatue (ºC)	Salinity (PPM)
A	Winter	300	3.90–8.42 (6.23)	0.5–1.20 (0.80)	15–26.66 (19.33)	2–6 (4.2)	7.8–9.4 (8.8)	14
	Spring	300	3.74–9.20 (6.59)	0.45–1.54 (1.03)	3.3–23.33 (9.33)	1–4 (2.2)	18.8–20.5 (19.60)	15
	Summer	300	4.68–8.26 (6.40)	0.64–1.22 (0.95)	64.76–78.09 (68.89)	3–7 (5)	25.4–26.5 (25.96)	27–28 (27.5)
	Autumn	300	4.36–9.36 (6.80)	0.01–0.45 (0.146)	46.15–81.91 (62.55)	3–9 (6.25)	17–18.1 (17.6)	27–29 (27.8)
B	Winter	300	4.21–7.33 (6.29)	0.38–0.74 (0.58)	16.66–33.33 (23.33)	3–6 (4.4)	10.9–13.1 (11.88)	10–16 (14.2)
	Spring	300	3.90–7.80 (6.49)	0.57–1.02 (0.71)	16.66–28.33 (23.33)	3–7 (5)	20.1–21.4 (20.98)	15
	Summer	300	5.14–7.95 (6.29)	1.2–1.49 (1.37)	24.76–42.85 (35.51)	5–7 (6.33)	29.7–30.5 (30.03)	28–29 (28.5)
	Autumn	300	4.52–7.95 (6.08)	0.88–1.55 (1.12)	10–48.33 (25.33)	2–8 (4.8)	19.4–20.5 (20)	26–30 (28.4)
C	Winter	300	4.99–8.42 (7.31)	0.2–0.75 (0.45)	16.66–31.66 (25.67)	4–7 (4.8)	10.7–11.9 (11.5)	15–16 (16.8)
	Spring	300	5.46–8.11 (6.98)	0.37–1.22 (0.79)	23.33–65 (37.33)	4–6 (5.4)	19.3–20 (19.66)	14–15 (14.4)
	Summer	300	4.99–9.51 (7.21)	1.19–1.63 (1.43)	23.80–40.95 (31.11)	6	24–30 (28.31)	29–30 (29.66)
	Autumn	300	4.99–9.36 (7.42)	0.2–0.94 (0.54)	25–73.33 (46.66)	3–7 (5)	19.2–19.5 (19.38)	21-30 (22.8)

With regard to the snail's densities (Table II and Fig. 2b), the statistical analysis indicated significant interaction between sampling points and seasons of the year (Two-way ANOVA; $F_{6; 42} = 6.84$; P<0.001). The Tukey test revealed differences between the seasons of the year for each sampling point. In the sampling point A, autumn was significantly different from the other seasons of the year (A vs S; A vs W and A vs Sp P<0.05; in all other cases P>0.05). In the sampling point B, the summer was significantly different compared with spring and winter (S vs Sp; S vs W P<0.05), and autumn presented higher values than winter (P<0.05). Finally, in the sampling point C, the values of summer were significantly higher than the values calculated for the other seasons (S vs Sp; S vs W and S vs A P<0.05; in all other cases P>0.05). The analyses of the differences between sampling points for each season of the year revealed that, only during the autumn, the sampling point B evidenced lower values than sampling points A and C (B vs A and B vs C P<0.05; in all other cases, P>0.05).

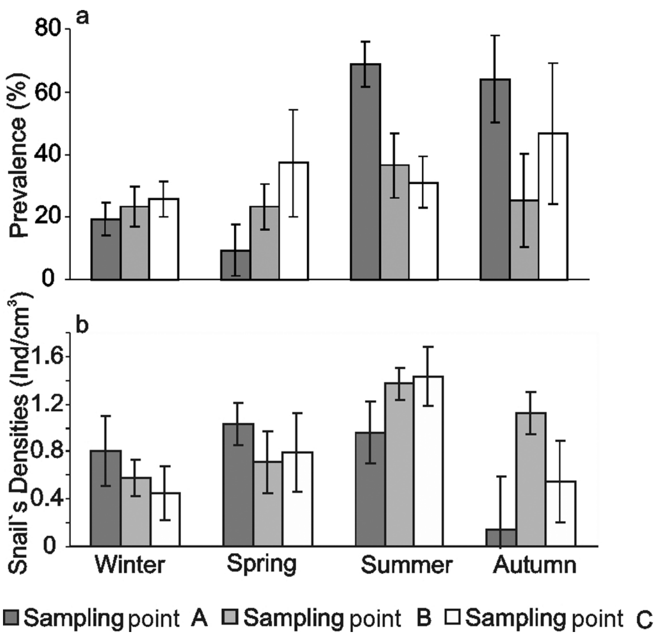

Fig. 2. Seasonal variation in the three sampling point (A, B, C) located in Cangrejo creek for: **a.** Overall prevalence (± S.D) of larval digeneans parasitizing *Heleobia australis*; **b.** *Heleobia australis'* densities (± S.D)

Spearman correlation index revealed significant negative correlations between seasonal overall prevalence and densities in autumn ($rs_{autumn} = -0.85$; P<0.001), however in the other seasons of the year no correlations were found ($rs_{summer} = -0.6$; $rs_{winter} = -0.08$; $rs_{spring} = -0.5$; in all cases P>0.05).

Regarding to the abiotic factors measured in Cangrejo creek, the maximum values of water temperature were recorded in the summer and the minimum values in winter (Table II). The values of salinity were typical of an estuarine lagoon to which Cangrejo creek is associated, where the maximum values were registered in summer and autumn and the minimum values in winter and spring (Table II). In both cases, Pearson's correlation index revealed significant positive correlations between overall prevalence with salinity ($R^2 = 0.22$; $P<0.05$) and with temperature ($R^2 = 0.10$; $P<0.05$).

Discussion

In Cangrejo Creek, the community of larval digeneans in *Heleobia australis* species comprised a total of 22 morphological types. The species richness and the composition of morphological types (or species) of larval digeneans in Cangrejo creek was homogeneous between the three sampling points and during the four seasons of the year. This spatial homogeneity in species richness and the composition of morphological types (or species) could be mainly due to a homogeneous distribution of species of the definitive host (mainly birds) in the 500 m of the snail distribution in the creek (Parietti 2011). In addition, gastropods have the ability to float and move along water bodies (Armonies and Hartke 1995), and this behaviour could also contribute, in the case of *H. australis*, to the homogeneity in species richness. For example, due to the mobility of *H. australis*, a snail that was infected in the sampling point A could float to point B, transporting a parasite originally absent in point B and contributing to the homogeneity in species richness of the larval digenean community, observed in the different sampling points.

In general, ecological factors that determine parasite prevalence include the distribution of hosts, the biological interaction among them and the abiotic factors. The strength of these three factors can be scale dependent (Thieltges and Reise 2007; Thieltges *et al.* 2009). Changes in habitat features over large and small spatial scales can directly or indirectly influence transmission dynamics, and thus, the recruitment of parasites to their hosts (Sousa and Grosholz 1991). The overall prevalence in the population of *H. australis* in Cangrejo creek showed spatial variations, but these variations should be studied taking into account the seasons of the year.

One factor that could contribute to differences in prevalences found in sampling point A could be the presence of the exotic polychaete *Ficopomatus enigmaticus* (Serpulidae) that serve as shelter and preference habitat of invertebrates (Schwindt *et al.* 2001; Obenat *et al.* 2006; Bruschetti *et al.* 2009) and as a site of resting and feeding areas for birds (Bruschetti *et al.* 2009). Also, *F. enigmaticus* have an important role in facilitating the transmission of larval digeneans in the lagoon. The reefs like aggregates builder by this polychaete may act as foci of parasite transmission mainly when they are present in a given area during a long time, and when they become the unique or preferred habitat for the snail host species Etchegoin *et al.* (2012).

Although the diversity and distribution of the definitive host species is homogeneous along the creek as mention above, the abundance of definitive host is higher in the sampling point A (Parietti 2011). The presence of invertebrates and vertebrates associated with the aggregates, increases the chances of contact between potential intermediate and definitive hosts (Etchegoin *et al*. 2012), contributing to the higher values of prevalence observed at sampling point A. In fact, prevalences were higher in the months of onset of migratory birds in sampling point A where these vertebrates are more abundant. Positive relationship between bird abundance and the presence of larval digenean parasitizing snail hosts on small to medium spatial scales were found by several studies (e.g. Curtis and Hurd 1983; Hechinger and Lafferty 2005; Koprivnikar *et al.* 2007; Merlo and Etchegoin 2011). In addition, Prinz *et al.* (2010) observed that the temperature increase coincides with a large number of definitive hosts and with a consequent increase in parasite prevalence in the mollusc hosts. The same pattern could apply to the community of larval digeneans in *H. australis* because during the warmer months (September to April), the Mar Chiquita lagoon becomes an important site for migratory birds as well as a breeding area for native species (Botto *et al.* 1998; Ferrero 2001).

Spatial and temporal variability in prevalence of larval digenean communities has been related to the density of the snail hosts (Kube *et al*. 2002; Faltýnkova *et al*. 2008). According to our results, only a negative association between prevalence of larval digeneans and snail's density was detected during the autumn. This observation agrees with the miracidial limitation hypothesis of Kuris and Lafferty (2005) who suggested that, at a small scale view of transmission, increasing snail density reduces prevalence. Due to snail's density does not appear to be a major factor influencing spatial and temporal variability in prevalence of larval digenean communities, other factors should be taken into account for future studies, such as snail's habitat preference, vagility, snail's sizes and life-history dynamics (Fernandez and Esch 1991; Sousa 1993; Jokela and Lively 1995).

In the case of digeneans, abiotic factors such as temperature and salinity have a quite crucial effect on the transmission cycles (Poulin 2006; Koprivnikar and Poulin 2009). Indeed, in Cangrejo creek, the values recorded for both water temperature and salinity coincides with the typical annual range of the lagoon, and the overall prevalence showed significant correlations with temperature and salinity. Nevertheless, the values of the Pearson's correlation index, despite being significant, were very low. For this reason, the increase in prevalence could be considered indirectly related to the seasonal increase in the water temperature values, and directly influenced by the seasonal presence of definitive hosts. As mentioned earlier, during the spring and summer, a notorious increment in the presence of migratory birds can be observed in the lagoon (Botto *et al*. 1998; Ferrero 2001), which may determine an increment in the digenean´s transmission. The importance of the positive correlation between prevalence and salinity may be considered as not determinant, because salinity fluctuates daily in the lagoon. In addition, most of the species of digeneans in *H. australis* have a high tolerance to changes in the levels of salinity (a typical adaptation of organisms living in estuarine environment) (Zander 2005).

In summary, the results obtained during this study revealed that the fluctuations in the community of larval digeneans of the snail *H. australis* can be detected at small spatial scale, using its natural distribution of 500 m. Given that local factors play an important role in determining the richness and abundance of larval digeneans in their snail host (Poulin and Mouritsen 2003; Byers *et al.* 2008), therefore, differences in the spatio-temporal distribution of the community of larval digeneans in *H. australis* should not be attributed to the effect of only a limited number of factors. This study also highlights the importance of seasonality as a factor that must be considered in studies focused on the search for patterns structuring the communities of larval digeneans, at medium and large scales.

Acknowledgements. The authors gratefully thank Dr. Lawrence Curtis for his critical comments and valuable suggestions on an earlier version of the manuscript. M. Parietti, M. J. Merlo and J. A. Etchegoin are members of Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). This work was supported by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) (J.A.E., grant number PIP 114-200801-00001); and Universidad Nacional de Mar del Plata (J.A.E., grant number EXA 583/12 15/E531).

References

Armonies W., Hartke D. 1995. Floating of mud snails Hyrdoboia ulvae in tidal waters of the Wadden sea, and its implications in distribution patterns. *Helgolander Meeresunters*, 49, 529–538.

Botto F., Iribarne O.O., Martínez M.M. 1998. The effect of migratory shorebirds on the benthic species of three southwestern Atlantic Argentinean Estuaries. *Estuaries*, 21, 700–709. DOI: org/10.2307/1353274.

Bruschetti M., Bazterrica C., Luppi T., Iribarne O.O. 2009. An invasive intertidal reef-forming polychaete affect habitat use and feeding behavior of migratory and locals birds in a SW Atlantic coastal lagoon. *Journal of Experimental Marine Biology Ecology*, 375, 76–93. DOI: org/10.1016/j.jembe.2009.05.008.

Byers J.E., Blakeslee A.M.H., Linder E., Cooper A.B., Maguire T.J. 2008. Control of spatial variation in the prevalence of trematode parasites infecting marine snail. *Ecology*, 89, 439–451. DOI: org/10.1890/06-1036.1.

Clarke K.R., Green R.H. 1988. Statistical design and analysis for a ''biological efects'' study. *Marine Ecology Progress Serial*, 46, 213–226.

Curtis L.A., Hurd L.E. 1983. Age, sex, and parasites: spatial heterogeneity in a sandflat population of Ilyanassa Obsoleta. *Ecology*, 64, 819–828. DOI: org/10.2307/1937205.

Curtis L.A., Hubbard K.M. 1990. Trematode infections in a gastropod host misrepresented by observing shed cercariae. *Journal Experimental Marine Biology Ecology*, 143, 131–137. DOI: org/10.1016/0022-0981(90)90115-S.

De Francesco C.G., Isla F. I. 2003. Distribution and abundance of hydrobiid snails in a mixed estuary and a coastal lagoon, Argentina. *Estuaries Coasts*, 26, 790–797. DOI: org/10.1007/BF 02711989.

De Francesco C.G., Isla F.I. 2004. The life cycle and growth of *Heleobia australis* (D'Orbigny, 1835) and *H. conexa* (Gaillard, 1974) (Gastropoda: Rissooidea) in Mar Chiquita Coastal Lagoon (Argentina). *Journal of Molluscan Studies*, 70, 173–178. DOI: org/10.1093/mollus/70.2.173.

Eschweiler N., Molis M., Buschbaum C. 2009. Habitat-specific size structure variations in periwinkle populations (*Littorina littorea*) caused by biotic factors. *Helgol Marine Research*, 63, 119–127. DOI: org/10.1007/s10152-008-0131-x.

Etchegoin J.A. 1997. Sistemas parasitarios presentes en la albufera Mar Chiquita. PhD Thesis. Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata.

Etchegoin J.A. 2001. Dinámica de los sistemas parasitarios. In: (Eds. Iribarne, O.O.) Reserva de Biósfera Mar Chiquita: Características Físicas, Biológicas y Ecológicas. Editorial Martín, Mar del Plata, Argentina, 171–185.

Etchegoin J.A., Martorelli S.R. 1998. Nuevos estadios larvales de digeneos parásitos de *Heleobia conexa* (Mollusca: Hydrobiidae) en Mar Chiquita (Buenos Aires, Argenina). *Neotrópica*, 44, 41–50.

Etchegoin J.A., Merlo M.J., Parietti M. 2012. The role of the invasive polychaete *Ficopomatus enigmaticus* (Fauvel, 1923) (Serpulidae) as facilitator of parasite transmission in Mar Chiquita coastal lagoon (Buenos Aires, Argentina). *Parasitology*, 139, 1506–1512. DOI: org/10.1017/S0031182012000820.

Faltýnková A., Valtonen E.T., Karvonen A. 2008. Spatial and temporal structure of the trematode component community in *Valvata macrostoma* (Gastropoda: Psobranchia). *Parasitology*, 135, 1691–1699. Doi.org/10.1017/S0031182008005027.

Fernandez J.C., Esch G.W. 1991. Effect of parasitism on the growth rate of the pulmonate snail Helisoma anceps. Journal of Parasitology. 77. 937–944. DOI: org/10.2307/3282746.

Ferrero L. 2001. La avifauna de Mar Chiquita. Síntesis de la tesis Doctoral de M.M. Martínez. In: (Eds. Iribarne, O.O.) Reserva de Biósfera Mar Chiquita: Características Físicas, Biológicas y Ecológicas. Editorial Martín, Mar del Plata, Argentina. 227–250.

Galaktionov K.V., Dobrovolskij A.A. 2003. Specific traits of populations formed by trematodes. In: (Eds. Galaktionov, K.V. & Dobrovolskij, A.A.) The biology and evolution of trematodes. An essay on the biology, morphology, life cycles, transmission, and evolution of digenetic trematodes. Kluwer Academic Publishers, Dordrecht, 349–405.

Granovitch A.I., Sergievsky S.O., Sokolova I.M. 2000. Spatial and temporal variation of trematode infection in coexisting populatios of intertidal gastropods *Littorina saxatilis* and *L. obtusata*. *Disease of Aquatic Organism*, 41, 53–64.

Hasseb M.A., Fried B. 1997. Modes of transmission of trematode infections and their control. In: (Eds. Fried, B. & Graczyk, T.K.) Advances in trematode biology. CRC Press, New York, 31–56.

Hechinger R.F., Lafferty K.D. 2005. Host diversity begets parasite diversity: bird final host and trematodes in snail intermediate hosts. *Procedures of the Royal Society of London*, 272, 1059–1066.

Jokela J., Lively C.M. 1995. Spatial variation in infection by digenetic trematodes in a population of freshwater snails (*Potamopyrgus antipodarum*). *Oecologia*, 103, 509–517. DOI: org/10.1007/BF00328690.

Koprivnikar J., Poulin R. 2009. Effects of temperature, salinity, and water level on the emergence of marine cercarie. *Parasitology Research*, 105, 957–965. DOI: org/10.1007/s00436-009-1477-y.

Koprivnikar J., Baker R.L., Forbes M.R. 2007. Environmental factors influencing community composition of gastropods and their trematode parasites in Southern Ontario. *Journal of Parasitology*, 93, 992–998. DOI: org/10.1645/GE-1144R.1.

Kube J., Kube S., Dieschke V. 2002. Spatial and temporal variations in the trematode component community of the mudsnail *Hydrobia ventrosa* in relation to the occurrence of waterfowl as definitive hosts. *Journal of Parasitology*, 88, 1075–1086. DOI: org/10.2307/3285475.

Kuris A.M., Lafferty K.D. 2005. Population and communities ecology of larval trematodes in molluscan first intermediate host. In: (Eds. Rohde, K.) *Marine Parasitology*. CSIRO PUBLISHING, 321–325.

Lafferty K.D., Sammond D.T., Kuris A.M. 1994. Analysis of larval trematode communities. *Ecology*, 75, 2275–2285. DOI: org/10.2307/1940883.

Ludgwing J.A., Reynolds J.F. (Ed.). 1988. Statistical Ecology. John Wiley and Sons, Inc. New York, USA, 337 pp.

Magurran A.E. (Ed.). 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, NJ, USA, 192 pp.

Martorelli S.R. 1986. Estudio sistemático y biológico de un digeneo perteneciente a la familia Microphallidae Travassos, 1920. I: *Microphallus szidati* sp. nov. parásito intestinal de *Rallus sanguinolentus sanguinolentus* (Aves: Rallidae) e *Himantopus melanurus* (Aves: Recurvirostridae). *Revista Iberica de Parasitologia*, 46, 373–378.

Martorelli S.R. 1989. Estudios parasitológicos en la albufera Mar Chiquita, provincia de Buenos Aires, República Argentina. II. Cercarias (Digenea) parásitas de *Heleobia conexa* (Mollusca: Hydrobiidae), pertenecientes a las familias Schistosomatidae, Haploporidae y Homalometridae. *Neotrópica*, 35, 81–90.

Martorelli S.R. 1990. Estudios parasitológicos en la albufera Mar Chiquita, provincia de Buenos Aires, República Argentina. III: Sobre dos cercarias parásitas de *Heleobia conexa* (Mollusca: Hydrobiidae) pertenecientes a la superfamilia Echinostomatoidea. *Neotrópica*, 36, 55–63.

Martorelli S.R., Etchegoin J.A. 1996. Cercarias de la superfamilia Opistorchioidea en *Heleobia conexa* (Mollusca: Hydrobiidae) de la albufera de Mar Chiquita. *Neotrópica*, 42. 61–67.

Merlo M.J., Parietti M., Etchegoin J.A. 2010. Evaluation of species richness estimators in studies of diversity involving two larval digenean communities parasitizing snail hosts. *Parasitology Research*, 107, 1093–1102. DOI: org/10.1007/s00436-010-1977-9.

Merlo M.J., Etchegoin J.A. 2011. Testing temporal stability of the larval digenean community in *Heleobia conexa* (Mollusca: Cochliopidae) and its possible use as an indicator of environmental fluctuations. *Parasitology*, 138, 249–256. DOI: org/10.1017/S0031182010001150.

Obenat S., Spivak E., Garrido L. 2006. Life history and reproductive biology of the invasive amphipod *Melita palmata* (Amphipoda: Melitidae) in the Mar Chiquita coastal lagoon, Argentina. *Journal of Marine Biological Association U.K.*, 86, 1381–1387. DOI: org/10.1017/S002531540601441X.

Parietti M. 2011. Distribución especial y estabilidad temporal de la comunidad de digeneos larvales que parasitan a *Heleobia australis* (Mollusca: Cochiliopidae) en la laguna de Mar Chiquita. Thesis. Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata.

Poulin R. 2006. Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. *Parasitology*, 132, 143–151. DOI: org/10.1017/S0031182005008693.

Poulin R., Mouritsen K.N. 2003. Large-scale determinants of trematode infections in intertidial gastropods. *Marine Ecology Progress Series*, 254, 187–198. DOI: org/10.3354/meps254187.

Prinz K., Kelly T.C., O'Riordan R.M., Culloty S.C. 2010. Temporal variation in prevalence and cercarial development of *Echinostephilla patellae* (Digenea, Philophthalmidae) in the intertidal gastropod *Patella vulgata*. *Acta Parasitologica*, 55, 39–44. DOI: org/10.2478/s11686-010-0002-x.

R Development Core Team. 2005. R: A language and environment for statistical computing, reference index version 2.2.1. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Schwindt E., Bortolus A., Iribarne O.O. 2001. Invasion of a reef-builder polychaete: direct and indirect impacts on the native benthic community structure. *Biological Invasions*, 3, 137–149. DOI: 10.1023/A:1014571916818.

Sousa W.P. 1993. Interspecific antagonism and species coexistence in a diverse guild of larval trematode parasites. *Ecology Monographers*, 63, 103–128.

Sousa W.P., Grosholz E.D. 1991. The influence of habitat structure on the transmission of parasites. *Population Community Biological Series*, 300–324. DOI: org/10.1007/978-94-011-3076-9_15.

Thieltges D.W., Reise K. 2007. Spatial heterogeneity in parasite infections at different spatial scales in an intertidal bivalve. *Oecologia*, 150, 569–581. DOI: org/10.1007/s00442-006-0557-2.

?Thieltges D.W., Fredensborg B.L., Poulin R. 2009. Geographical variation in metacercarial infection levels in marine invertebrate hosts: parasite species character versus local factors. *Marine Biology*, 156, 983–990. DOI: org/10.1007/s00227-009-1142-0.

Zander C.D. 2005. Parasites in brackish waters. In: (Ed. Rhode, K.) Marine Parasitology. 1 ed. CSIRO PUBLISHING, 298–302.

Zar J.H. (Eds.) 2009. Biostatistical Analysis. Pearson Education Inc, New Jersey, USA. 944 pp.

(Accepted: October 14, 2013)