

Research Article

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Temporal dynamics of parasite community in the three-spot cichlid *Amphilophus trimaculatus* from Tres Palos Lagoon, Guerrero, Mexico

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Abstract: The temporal dynamics of parasite communities of the Three-spot cichlid *Amphilophus trimaculatus* Günther 1867 was examined during an annual cycle. A total of 770 fishes were collected between March 2019 and February 2020 from a tropical coastal lagoon. Thirteen taxa of metazoan parasites were identified, two of monoxenous and 11 of heteroxenous parasites. No significant changes were observed in the species composition of parasite communities in *A. trimaculatus* during a 12-yr period (2008–2020). The prevalence of infection of six heteroxenous parasites *Austrodiplostomum ostrowskiae* Dronen, 2009, *Cladocystis* cf. *trifolium* Poche, 1926, *Clinostomum* cf. *tataxumui* Sereno-Uribe, Pinacho-Pinacho, García-Varela et Pérez-Ponce de León, 2013, *Crassicutis cichlasomae* Manter, 1936, *Southwellina* cf. *hispida* Witenberg, 1932 and *Contracaecum* sp. varied between sampling months, and/or climatic seasons. Some species were more prevalent during some months of the dry season, while others during the rainy season, suggesting that these parasite populations respond differently to environmental changes. The environmental changes generated by the dry/rainy cycle may have affected the availability of intermediate host populations, and the feeding and reproductive behaviour of the host. Temporal variations in the infection levels of some parasite species generated important changes in the structure of the component communities over time. This study allows us to appreciate the sensitivity of parasite-host systems to environmental variability, and suggests that alterations to hydrological regimes could have significant consequences on parasite biodiversity in tropical brackish water environments.

Key words: Cichlidae, digeneans, temporal variation, component community, tropical Pacific.

In tropical coastal lagoons, the environmental changes generated by the seasonal dry-rainy cycle affect the recruitment process of many endoparasite species (Violante-González et al. 2008a, Carpio-Hernández et al. 2024a). These variations can be reflected in the infection levels of parasite populations, and the composition and structure of the entire parasite community over time (Zander et al. 1999, Violante-González et al. 2008a, 2009, Carpio-Hernández et al. 2024a,b). In highly eutrophic lagoons these changes can be even more extreme. For example, the increase in eutrophication can alter the dynamics of parasitic infections due to changes in the density and distribution of hosts, as well as in their resistance to diseases, due to increased stress (Diamant et al. 1999, Dzikowski et al. 2003, Carpio-Hernández et al. 2024b).

The high productivity also favours the growth of large populations of herbivorous snails and benthic and pelagic micro-crustaceans that act as intermediate hosts for many species of endoparasites (Valtonen et al. 1997, Zander 1998,

Violante-González et al. 2008a). Some studies conducted on the temporal variation of parasite communities in the Mexican Pacific indicate that significant changes can occur in the structure and species composition of these communities, mainly over periods of several years, due to the replacement or alternation of dominant parasite species (Violante-González et al. 2009, Carpio-Hernández et al. 2024b).

Cichlids (Cichlidae) are a species-rich monophyletic group of freshwater and brackish water fish. In Mexico, 57 species belonging to 11 genera have been reported to date (Chakrabarty 2004, Paredes-Trujillo et al. 2020). Most of the cichlid species are opportunistic carnivores or piscivores, but some species may have a more diverse diet, feeding on crustaceans, mollusks, larvae of aquatic insects', plankton or plant material (Shalloof et al. 2020).

In coastal lagoons of the Mexican southern Pacific only two species of cichlids have been reported: a native species *Amphilophus trimaculatus*, and an introduced species *Oreochromis* sp. (Violante-González et al. 2008b). The three-

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spot *A. trimaculatus* is a territorial and aggressive monogamous cichlid which exhibits biparental care of eggs, larvae and fry (Violante-González 1995). This cichlid is of great economic value locally due to its prized meat. However, its populations have declined considerably in recent years due to overfishing and habitat loss, as it is typically found among the submerged vegetation and roots of mangroves, where it finds refuge.

The parasite fauna of *A. trimaculatus* has been studied in two coastal lagoons in the Guerrero state (Violante-González and Aguirre-Macedo 2007, Violante-González et al. 2007, 2008b), and the seasonal variation of their parasite community was studied in the Tres Palos lagoon, but more than 10 years ago (Violante-González et al. 2008b). This is a highly eutrophic coastal lagoon and there are currently no studies that allow us to know, if the infection levels of the parasites that infect *A. trimaculatus* populations have increased or decreased due to the increase in eutrophication in recent years.

Therefore, the objectives of the present study were: 1) to examine the temporal dynamics of *A. trimaculatus* parasite community during an annual cycle and, 2) to determine whether the infection levels of its parasite species have increased or remained stable over time. We hypothesised that parasite populations infecting *A. trimaculatus* would respond differently to environmental changes generated by the dry and rainy seasons in Tres Palos lagoon, due to their different lifestyles.

MATERIALS AND METHODS

Study area

Tres Palos lagoon (16.7833N, 99.6500W) is predominantly oligohaline, with salinity ranges of 2 to 4 Practical Salinity Unit (psu) year-round. Located on the Mexican Pacific coast, 25 km east of Acapulco, it covers an area of 55 km² (5,500 ha) and its depth varies from 0.5 to 8 m (De la Lanza-Espino et al. 2008, Carpio-Hernández et al. 2024a). The region experiences two distinct climatic seasons during the year, a rainy period from June to November (total precipitation \approx 980 mm), and a dry season from December to May (total precipitation < 70 mm) (Carpio-Hernández et al. 2024a). Temperature and precipitation data for the study area were obtained from the local meteorological station (No. 12002). Possible differences in these environmental parameters were assessed using a Student's *t*-test.

Fish collection and biometric data

A total of 770 *Amphilophus trimaculatus* specimens (total length 10.6–21.3 cm) were obtained from commercial catches between March 2019 and February 2020. Fish were measured (total length), weighed, and sexed at the time of collection, and later pooled into three size-classes: immature (< 13 cm), pre-adults (13–15 cm), and adults (> 15 cm). The Fulton's condition factor (CF) was calculated using the equation: $CF = W_t/L_t^3$, where W_t is total weight, and L_t = total length. The stomach and gonads were weighed to the nearest gram (g), and the data used to calculate some physiological indices. The gastric repletion index (GRI) was calculated with the equation: $GRI = W_s/W_t * 100$, where W_s = stomach weight, and W_t = total weight. The gonadosomatic

index (GSI) was calculated only in females: $GSI = W_g/W_t * 100$, where W_g is gonad weight, and W_t is total weight of an individual. Possible differences in the body size of fish between sampling months were evaluated using a One-way ANOVA.

Infection parameters and classification of parasite taxa

A complete necropsy was carried out on all specimens, and all parasites were collected from the external and internal organs. The parasites were morphologically identified to the lowest possible taxonomic level using specialised literature. Vouchers of the most abundant and best preserved parasite specimens were deposited in the Colección Nacional de Helmintos (CNHE), Universidad Nacional Autónoma de México, México City (voucher numbers 12501–12514). Autogenic species of parasites were defined as those which reach maturity in aquatic hosts and thus have a limited ability to colonise new locations. Allogenic species were those with birds or mammals as definitive hosts and whose natural migrations favour helminth dispersion, providing them a wide geographic distribution (Esch et al. 1988).

Parasite species were further classified based on traits of their life cycle as monoxenous (single-host life cycle) and heteroxenous (multi-host life cycle) parasites (Sures et al. 2017). Infection levels for each species of parasite were described according to Bush et al. (1997), using prevalence, mean abundance, mean number of parasites and intensity expressed as a range (minimum-maximum). Possible differences in infection levels between sampling months, and climatic seasons were identified using likelihood ratio *G*-tests, and Factorial Anovas (General Linear Model, GLM) for abundance.

Negative binomial Generalised Additive Models (MvGLM) were used to examine the effects of biotic or abiotic factors (predictor variables) on abundance (response variable) of component parasite species (prevalence >10%, *sensu* Bush et al. 1990). In addition, *post hoc* univariate tests were applied to determine the response of these parasite species. To determine the possible collinearity between the included variables in the models, variance inflation factors (VIF) and tolerance (T) were calculated using the check collinearity function of the performance package in R, prior to the analysis. The best model was selected based on the average Akaike information criterion (AICc). Spearman's correlation coefficient (r_s) was used to determine possible relationships between the fish total length and abundance of each component parasite species, or the infracommunity parameters.

Study levels

Analyses were made at the levels of component community and infracommunity (Bush et al. 1997). Component community parameters included: total species richness (helminth and crustaceans), the total number of individual parasites, the ratio of monoxenous to heteroxenous species of parasite (TM/TH), the helminth diversity (1D = exponential of Shannon's entropy index), and the Berger-Parker Index (BPI) as a measure of numerical dominance of a helminth species.

Similarity analysis, based on Bray-Curtis similarity coefficients (square root transformed abundance data), were used to evaluate similarity and difference in parasite community species composition between sampling months. Non-metric multidimensional scaling (nMDS) based on the Bray-Curtis similarity index was used to rank the component parasite communities according to their relative similarities and visualise possible differences in species com-

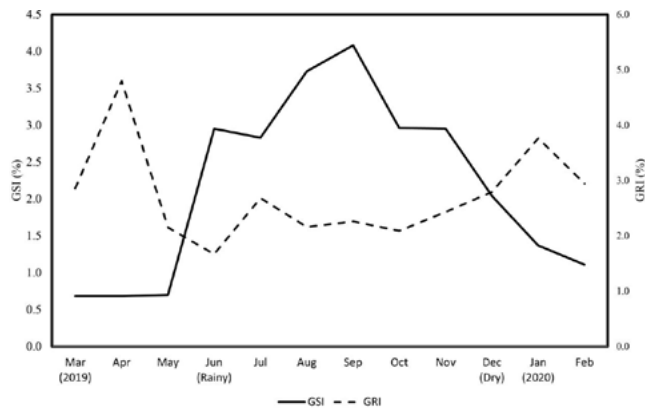


Fig. 1. Relationship between the gonadosomatic index (GSI) and gastric repletion index (GRI) in the cichlid *Amphilophus trimaculatus* from Tres Palos lagoon.

position. Differences between component community parameters were identified using the non-parametric Kruskal-Wallis H-test, considering the total number of fish that were examined on each sampling month as a component community.

To evaluate if the sample size of the examined hosts were sufficient to recover all or most of the parasite taxa in each sampling month, non-parametric rarefaction and extrapolation curves of diversity species were constructed (R package iNEXT), based on the Hill number $q = 0$; which estimates the expected parasite species richness (Chao et al. 2016). Sample size-based completeness curves through the sample coverage estimator (\hat{C}_n), were used to estimate the sample size needed to achieve a fixed degree of sampling completeness (Chao et al. 2014).

Infracommunities were described in terms of the mean number of species of parasite per host, mean number of individuals of each species of parasites, and the mean Brillouin diversity index (H') value per host. The multivariate general linear model (GLM) was used to evaluate changes in the infracommunity parameters (dependent variables) between sampling months, and climatic seasons (predictor variables). Principal Component Analysis (PCA) was applied to identify biotic or abiotic factors that influenced parasite infracommunity species richness and diversity. The statistical packages SPSS (IBM SPSS Statistics for Windows, Ver. 20.0), R package “vegan” Ver. 2.5–7 (Oksanen et al. 2020), and PRIMER v6. Software (Clarke and Gorley 2006), were used for statistical analyses.

RESULTS

Abiotic factors

The water temperature in Tres Palos Lagoon varied significantly from 24.2°C (January 2020) to 26.7°C (April 2019) (t -test = 6.35, $p < 0.01$) during the sampling period. The highest rainfall was recorded during September 2019 (300.7 mm).

Host's physiological indices

A total of 770 (312 males, 429 females, and 29 juvenile) specimens of *Amphilophus trimaculatus* were examined during the 1-yr study period (March 2019 to February 2020) (Table 2). Mean total length (TL) of fish varied significantly (One-way Anova, $F_{11,758} = 8.30$, $p < 0.01$) from 13.9 ± 1.5

cm (July) to 15.9 ± 1.5 cm (October) (Table 2), without registering significant differences between male and female fish (One-way Anova, $F_{1,740} = 0.843$, $p > 0.05$). CF values indicated that the fishes were in good health (CF > 1.9, Table 2). The GSI values identified one spawning peak, between August and September (Fig. 1). The GRI values indicated that feeding behaviour of fish decreased significantly during these months (Fig. 1). Both indices were negatively correlated during the study period ($r_s = -0.596$, $p < 0.05$).

Host diet composition

The alimentary spectrum of *A. trimaculatus* included 13 prey items, of which small fishes (32%), ostracods (30%), and insect larvae (11%) represented the largest proportions. Additional prey items accounted for 27% of the diet and included: algae, shrimps, crabs, snails, amphipods, isopods, and juvenile frogs, among others. The diet composition variable between climatic seasons, being more varied during the rainy season (13 and 9 items, respectively) although in both seasons fish were the main prey item. Feeding habits also changed with fish body size: adult individuals (> 15 cm) exhibited a more specialised diet consisting mainly of fish (60%), while pre-adults (13–15 cm) and immature fish (< 13 cm) had a more varied diet that included higher percentages of ostracods and insect larvae.

Parasite species composition

Thirteen taxa of metazoan parasites (11 helminths and two crustaceans) were identified, and 53,678 individual parasites recovered. These taxa included: six species of Digenea (one adult and five metacercariae), three of Acanthocephala (two juvenile, and one cystacanth), two of Nematoda (larvae), and two of Crustacea (Table 1). Seven of the taxa found as larvae stages were classified as allogenic parasites, since they mature in ichthyophagous aquatic birds living in the lagoon. The autogenic species included the digenean *Crassicutis cichlasomae* Manter, 1936, the acanthocephalans *Pseudoleptorhynchoides lamothiei* Salgado-Maldonado, 1976 and *Neoechinorhynchus brentnickoli* Monks, Pulido-Flores et Violante-González, 2011, the nematode *Hysterothylacium perezii* Gopar-Merino, Osorio-Sarabia et Garcia-Prieto, 2005, and the crustaceans *Argulus* sp. and *Ergasilus* cf. *davidi* Suárez-Morales et Santana-Pineros, 2008 (Table 1). All species of parasite were further classified based on the characteristics of their life cycle as monoxenous (single-host life cycle), and heteroxenous (multi-host life cycle) parasites (Table 1).

Variation in the infection levels

The prevalence values of six helminth species varied significantly between the sampling months. The digeneans *Clinostomum* cf. *tataxumui* Sereno-Urbe, Pinacho-Pinacho, García-Varela et Pérez-Ponce de León, 2013 ($G = 32.3$, $p < 0.05$) and *Austrodiplostomum ostrowskiae* Dronen, 2009 ($G = 23.5$, $p < 0.05$), as well as the acanthocephalan *Southwellina* cf. *hispidula* Witenberg, 1932 ($G = 77.9$, $p < 0.05$), and the nematode *Contracaecum* sp., ($G = 70.6$, $p < 0.05$) were more prevalent during some months of the dry season (December to May, Table 1). In contrast, the

Table 1. Monthly parameters of parasite infection in *Amphilophus trimaculatus* from Tres Palos lagoon. Colonization strategy: Au – autogenic species, Al – allogenic species. Traits of life cycle: M – monoxenous, H – heteroxenous. P – prevalence, (A) – mean number of parasites per infected fish, T – total number of individual parasites collected, IR – intensity range. Significantly different measurements of prevalence (*G*-test) and abundance (Factorial Anova) ($p < 0.05$), are in bold.

Parasite taxa	Mar 2019	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan 2020	Feb
Digenea (Adult)	P(A)/ T[IR]	P(A)/ T[IR]	P(A)/ T[IR]	P(A)/ T[IR]	P(A)/ T[IR]	P(A)/ T[IR]	P(A)/ T[IR]	P(A)/ T[IR]	P(A)/ T[IR]	P(A)/ T[IR]	P(A)/ T[IR]	P(A)/ T[IR]
<i>Crassicuttis cichlasomae</i> ^{Au, H}	19 (1.2)	8 (0.8)	14 (0.5)	22 (1.5)	2 (0.1)	40 (3.5)	17.4 (0.5)	39 (3.6)	21.0 (0.6)	23 (1.58)	12 (0.75)	15 (1.63)
	80 [1–34]	58 [2–39]	21 [1–14]	81 [1–30]	4 [1–3]	232 [1–61]	25 [1–7]	229 [1–87]	53 [1–22]	68 [1–38]	51 [1–26]	145 [1–54]
Digenea (Larvae)												
<i>Austrodiplostomum ostrowskiae</i> ^{Al, H}	39 (0.70)	51 (1.1)	57 (1.5)	37 (1.1)	30 (0.8)	48 (0.9)	33 (0.8)	48 (1.2)	27 (0.4)	35 (0.8)	35 (0.5)	36 (0.5)
	47 [1–6]	81 [1–8]	65 [1–18]	59 [1–15]	74 [1–25]	59 [1–7]	35 [1–7]	80 [1–10]	32 [1–3]	33 [1–11]	37 [1–4]	41 [1–4]
<i>Ascocotyle (Phagicola) longa</i> ^{Al, H}				7 (0.5)	3 (0.1)			3 (0.7)	1 (0.1)		3 (0.1)	
				26 [3–9]	4 [1–2]			43 [7–36]	2 [0–2]		9 [1–8]	
<i>Cladocystis cf. trifolium</i> ^{Al, H}	7 (0.2)	10 (0.3)	5 (0.4)	35 (3.3)	15 (1.7)	36 (3.7)	24 (1.6)	41 (14.3)	30 (4)	14 (1.3)	16 (4.3)	24 (1.4)
	14 [1–9]	19 [1–7]	16 [4–12]	180 [1–42]	157 [1–90]	248 [1–50]	74 [1–23]	913 [1–456]	327 [1–60]	54 [1–38]	296 [1–200]	124 [1–24]
<i>Clinostomum cf. tataxumui</i> ^{Al, H}	30 (2.03)	55 (2.9)	29 (0.9)	46 (1.7)	21 (1.0)	33 (1.3)	35 (2)	28 (1.1)	27 (0.8)	23 (0.4)	25 (0.6)	37 (1.6)
	136 [1–64]	211 [1–27]	36 [1–9]	92 [1–31]	96 [1–32]	89 [1–15]	94 [1–32]	70 [1–23]	69 [1–12]	16 [1–5]	42 [1–9]	140 [1–17]
<i>Posthodiplostomum sp.</i> ^{Al, H}				1.8 (0.1)								
				1 [0–1]								
Acanthocephala												
<i>Neoechinorhynchus brentnickoli</i> ^{Au, H}	4 (0.1)		14 (0.9)	7 (0.1)	3 (0.1)	3 (0.1)			1 (0.1)	5 (0.1)		1 (0.1)
(Juvenile)	3 [0–1]		38 [1–30]	4 [0–1]	5 [1–3]	2 [0–1]			3 [0–3]	4 [0–2]		1 [0–1]
<i>Pseudoleptorhynchoides lamothei</i> ^{Au, H}				2 (0.1)					1 (0.1)		3 (0.1)	1 (0.1)
(Juvenile)				1 [0–1]					1 [0–1]		2 [0–1]	1 [0–1]
<i>Southwellina cf. hispida</i> ^{Al, H}	34 (1.5)	12 (0.4)	29 (0.7)	28 (1.8)	56 (2.4)	37 (0.9)	61 (1.4)	17 (0.4)	42 (2.4)	49 (1.8)	66 (3.7)	46 (2.2)
(Larvae)	100 [1–18]	27 [1–12]	29 [1–12]	98 [1–30]	222 [1–22]	59 [1–12]	64 [1–7]	29 [1–7]	192 [1–41]	76 [1–17]	255 [1–38]	193 [1–43]
Nematoda												
<i>Contracaecum sp.</i> ^{Al, H}	39 (1.4)	16 (0.3)	29 (0.5)	52 (1.9)	19 (0.3)	27 (0.4)	22 (0.3)	34 (0.9)	41 (1.1)	56 (1.4)	54 (1.6)	62 (1.21)
(Larvae)	95 [1–14]	24 [1–5]	20 [1–4]	101 [1–26]	30 [1–5]	30 [1–4]	14 [1–3]	55 [1–10]	88 [1–8]	60 [1–20]	112 [1–16]	108 [1–7]
<i>Hysterothylacium perezii</i> ^{Au, H}	1 (0.1)					6 (0.1)	2 (0.1)	3 (0.1)		5 (0.1)	3 (0.1)	
(Larvae)	1 [0–1]					4 [0–1]	3 [0–3]	2 [0–1]		3 [1–2]	4 [1–3]	
Crustacea												
<i>Argulus sp.</i> ^{Au, M}						10 (0.1)		6 (0.1)				3 (0.1)
						7 [0–1]		5 [1–2]				4 [1–2]
<i>Ergasilus cf. davidi</i> ^{Au, M}	95 (49.7)	94 (158.7)	100 (50.8)	96 (48.2)	93 (20.8)	92 (28.7)	91 (66.2)	100 (67.1)	100 (69.3)	95 (63.3)	98 (47.9)	94 (42.31)
	3327 [2–267]	11583 [4–450]	2132 [2–208]	2603 [1–201]	1938 [3–184]	1924 [1–169]	3045 [2–393]	4293 [4–250]	5617 [1–300]	2724 [12–335]	3259 [15–185]	3766 [2–275]

digeneans *C. cichlasomae* ($G = 141.4$, $p < 0.05$) and *Cladocystis cf. trifolium* Poche, 1926 ($G = 74.1$, $p < 0.05$) exhibited higher prevalence values in some months of the rainy season (August and October, Table 1).

With the exception of *C. cf. trifolium*, the other five species of parasites also showed significant variation in their mean abundance between sampling months (GLM: $p < 0.01$). Host body size correlated positively with the abundance values of the nematode *Contracaecum sp.* ($r_s = 0.138$, $p < 0.01$), and the copepod *E. cf. davidi* ($r_s = 0.110$, $p < 0.01$). A weak and non-significant negative correlation was observed between fish length and the abundance of *S. cf. hispida*.

The mvabund deviance analysis models indicated that abundance of some component parasite species was strongly influenced by local environmental factors over time. The best model (AICc = 2757.69), included one biotic (body size), and 2 abiotic parameters (temperature and

precipitation) as predictor variables (Table 3). The parasite species that were most influenced were *E. cf. davidi*, *C. cf. trifolium* and *Contracaecum sp.* (Table 4).

Component communities

The rarefaction and extrapolation diversity species curves (Fig. 2) supported the hypothesis that the majority of parasite taxa of each component community had been collected. According to the sample coverage estimator \hat{C}_n and interpolation-extrapolation curves, the sample sizes used were high enough to register most (>93%) of the parasite species in each monthly sample.

No significant correlation was observed between sample size and the component community parameters at this level ($p > 0.05$), indicating that the different sample sizes used in the analyses had no effect on the results. Total species richness of parasites at this level (Table 2) varied significantly from seven (April) to 11 species (June) (H-test = 34.4,

Table 2. Characteristics of the parasite component communities in *Amphilophus trimaculatus* from Tres Palos lagoon, Guerrero, Mexico (March 2019-February 2020). CF – condition Factor, GRI – gastric repletion index, GSI – gonadosomatic index, TM/TH – ratio of total Monoxenous to Heteroxenous parasites. BPI – Berger-Parker index, ¹D – exponential of Shannon-Wiener diversity index, Aust – *Austrodiplostomum ostrowskiae*, Clad – *Cladocystis cf. trifolium*, Clin – *Clinostomum cf. tataxumui*, Sout – *Southwellina cf. hispida*. Significant values are in bold.

Month/Season	No. of fish	Length (cm)	Host's physiological indices					Helminth communities				
			CF	GRI	GSI	Species richness	TM/TH	No. of parasites	BPI	Dominant species	¹ D	
Mar (Dry)	67	14.6 ± 1.4	2.13	2.86	0.68	9	6.99	3803	0.286	Clin	16.39	
Apr	69	15.4 ± 1.4	1.97	4.80	0.68	7	27.58	12003	0.502	Clin	11.14	
May	42	15.3 ± 2.0	2.10	2.15	0.70	8	9.48	2357	0.289	Aust	20.54	
Jun (Rainy)	54	15.3 ± 2.4	1.98	1.67	2.95	11	4.05	3246	0.28	Clad	21.53	
Jul	87	13.9 ± 1.5	2.01	2.68	2.83	9	3.27	2530	0.375	Sout	13.19	
Aug	67	15.7 ± 1.4	2.11	2.16	3.73	10	2.67	2654	0.343	Clad	14.01	
Sep	42	15.3 ± 1.5	2.12	2.26	4.08	8	9.85	3354	0.304	Clad	15.95	
Oct	64	15.9 ± 1.5	2.06	2.09	2.96	10	3.02	5719	0.643	Clad	10.26	
Nov	81	15.1 ± 1.4	1.98	2.43	2.95	10	7.32	6384	0.426	Clad	13.27	
Dec (Dry)	43	15.4 ± 1.6	2.14	2.79	2.04	9	8.68	3038	0.242	Sout	18.87	
Jan	65	15.1 ± 1.3	1.99	3.76	1.37	10	4.03	4067	0.366	Clad	13.82	
Feb	89	15.5 ± 1.6	1.97	2.94	1.11	10	5.01	4523	0.256	Sout	17.52	

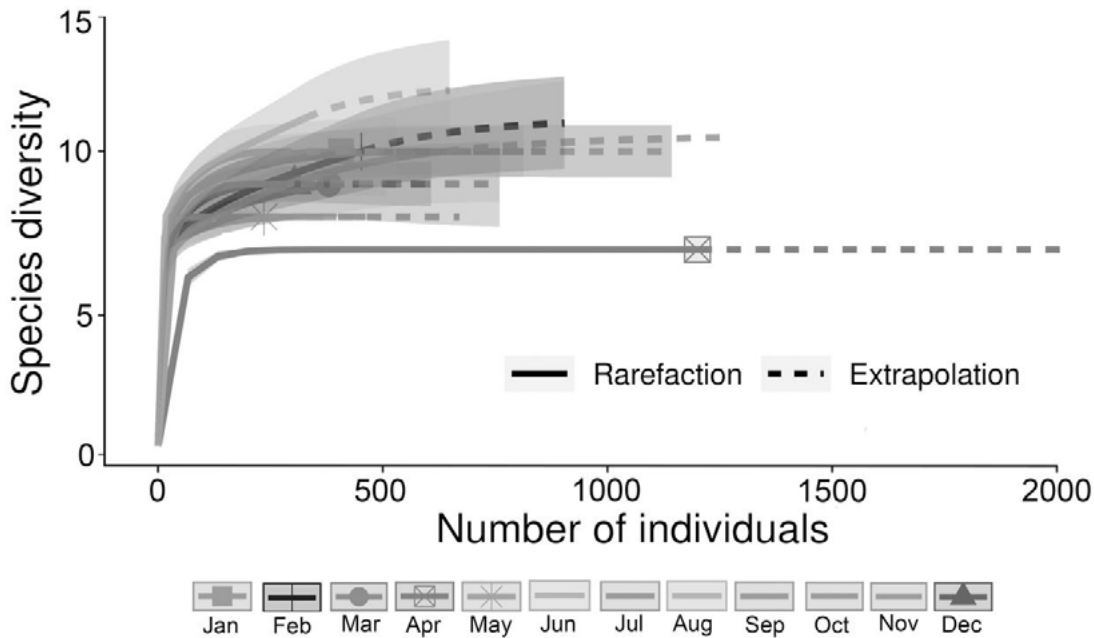


Fig. 2. Rarefaction, and extrapolation curves of diversity species for component communities of *Amphilophus trimaculatus* from Tres Palos lagoon.

Table 3. Summary of the fitted negative binomial Generalised Linear Models (MvGLM), on biotic and abiotic factors that explain variation in the abundance of component parasite species in *Amphilophus trimaculatus*, from Tres Palos lagoon. e.d.f. – effective degrees of freedom; Dev – explained deviance, Pr (>Dev) – significance, AICc – average Akaike information criterion, Δi – difference in the AICc, ωi – Akaike weights.

Predictor	e.d.f.	Model 1		Model 2	
		Dev	Pr (>Dev)	Dev	Pr (>Dev)
Size	768	30.7	0.001	30.7	0.001
Temperature	767			92.5	0.001
Month	754	557.7	0.001	465.1	0.001
AICc			2757.69		2759.77
Δi			0.0001		2.0803
ωi			73.88		26.11

Table 4. Factors that explain variation in the abundance (mva-bund analysis of deviance) of component parasite species in *Amphilophus trimaculatus* from Tres Palos lagoon. Erga – *Ergasilus cf. davidi*, Clad – *Cladocystis cf. trifolium*, Aust – *Austrodiplostomum ostrowskiae*, Clin – *Clinostomum cf. tataxumui*, Cras – *Crassicutis cichlasomae*, Sout – *Southwellina cf. hispida*, Cont – *Contracaecum sp.*

Predictor variable	Erga	Clad	Aust	Clin	Cras	Sout	Cont
Significant deviation values							
Univariate test							
Size	11.76	6.91					9.80
Month	229.59	56.41	38.06	31.99	50.82	70.15	80.64

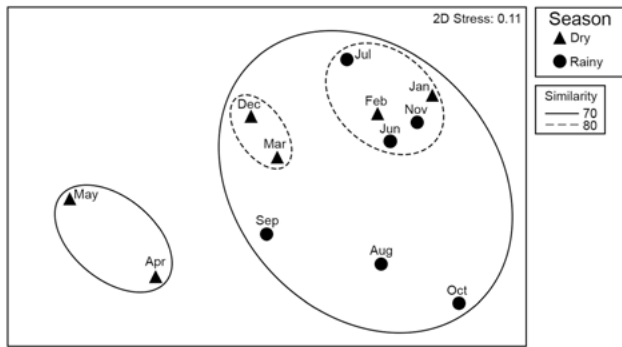


Fig. 3. Non-metric multidimensional scaling (nMDS) plot for parasite communities in *Amphilophus trimaculatus* from Tres Palos lagoon. Ellipses represent similarity levels between sampling months.

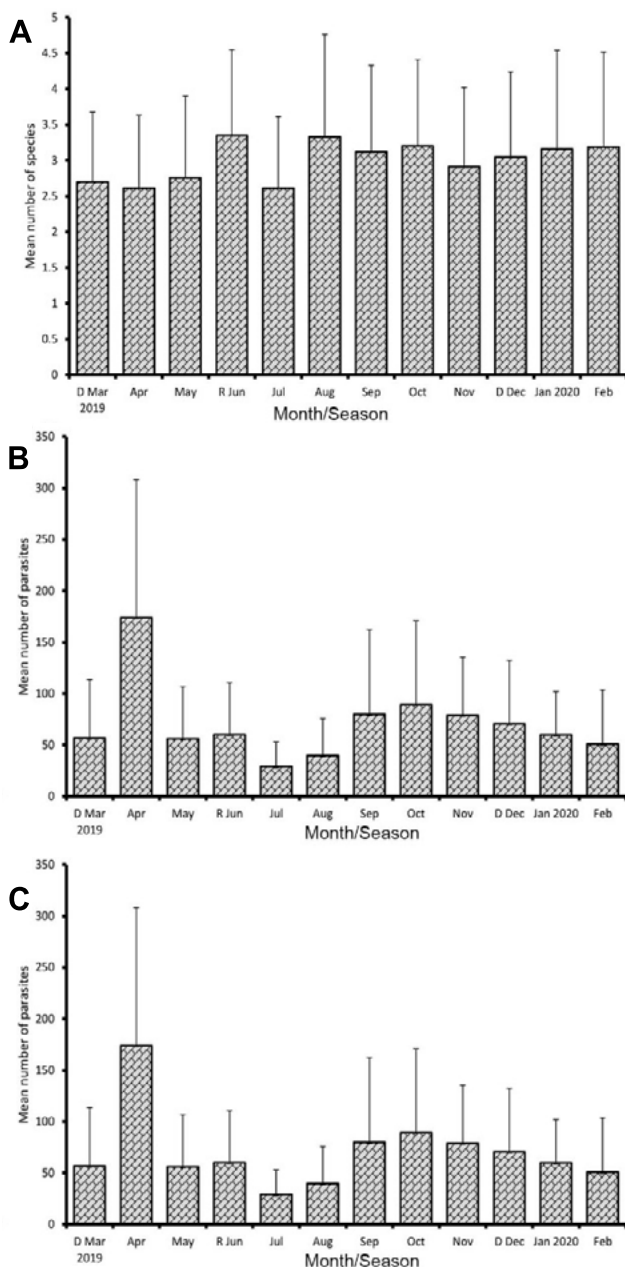


Fig. 4. Mean values of the infracommunity parameters (\pm standard deviation) in *Amphilophus trimaculatus* from Tres Palos lagoon. **A** – mean number of species; **B** – mean number of parasites; **C** – mean diversity; **D** – dry season; **R** – rainy season.

$p < 0.01$). The ratio of total monoxenous to heteroxenous parasites (TM/TH) varied from 2.67 to 27.58 and favoured to the monoxenous parasites throughout the sampling period. The total number of individual parasites ranged from 2,357 (May) to 12,003 (April) (H-test = 172.62, $p < 0.01$), and the copepod *E. cf. davidi* numerically dominated the global communities during all the sampling period (BPI > 0.70). Because the high and constant dominance of one parasite species can obscure some structuring patterns in parasite communities, subsequent analyses at this level considered only helminth populations.

Diversity index values for helminth communities varied from 8.26 (October) to 21.53 (June) (H-test = 80.64, $p < 0.01$). Only the parasite load (higher in dry season), and diversity values (rainy season) varied between climatic seasons (H-test = 7.76; 15.8, $p < 0.01$, respectively). Three digeneans and one acanthocephalan dominated the helminth communities: the digenean *C. cf. trifolium* dominated in up to six of the sampling months (Table 2).

Similarity in the species composition of helminth communities was generally high during the study period (mean = 73.2%). However, the nMDS ranking of the helminth communities showed a strong clustering of ten sampling months at a similarity level of 70% (Fig. 3). In general, similarity was higher within a single season and over short periods of time (e.g., March–December, and April–May, Fig. 3).

Infracommunities

All infracommunity parameters varied significantly between sampling months. Mean species richness of parasites varied from 2.61 ± 1.0 to 3.35 ± 1.2 (GLM: Anova $F_{10,769} = 3.23$, $p < 0.01$), the mean number of individual parasites from 29.1 ± 24.1 to 174.0 ± 134.1 (GLM: Anova $F_{10,769} = 21.84$, $p < 0.01$), and the Brillouin diversity index (H') values varied from 0.27 ± 0.32 to 0.75 ± 0.47 (GLM: Anova $F_{10,618} = 6.10$, $p < 0.01$). Mean values of species richness and diversity were lower during the first three months of 2019 (dry season), but not during the dry season months of 2020 (Fig. 4), indicating that structure of infracommunities can change from one year to the next for the same climatic season. Considering all sampling months, mean species richness ($r_s = 0.087$, $p < 0.05$), and mean number of individual parasites ($r_s = 0.117$, $p < 0.01$) exhibited positive correlations with host body size.

In the PCA used to identify the possible influence of biotic and abiotic factors on parasite infracommunity structure (Fig. 5), the first two principal component axes explained 46% of total variance: they contributed 27% (eigenvalue = 3.56) and 19% (eigenvalue = 2.49), respectively. The first component variable indicated that the richest and most diverse parasite infracommunities were also more uniform in their parasite abundances. Infracommunities with these characteristics were registered mainly during the rainy season months (Table 2). The second variable associated the parasite load with the host body size and the climatic season. According to this variable, larger fish had a higher parasite load mainly during the dry season (Table 2).

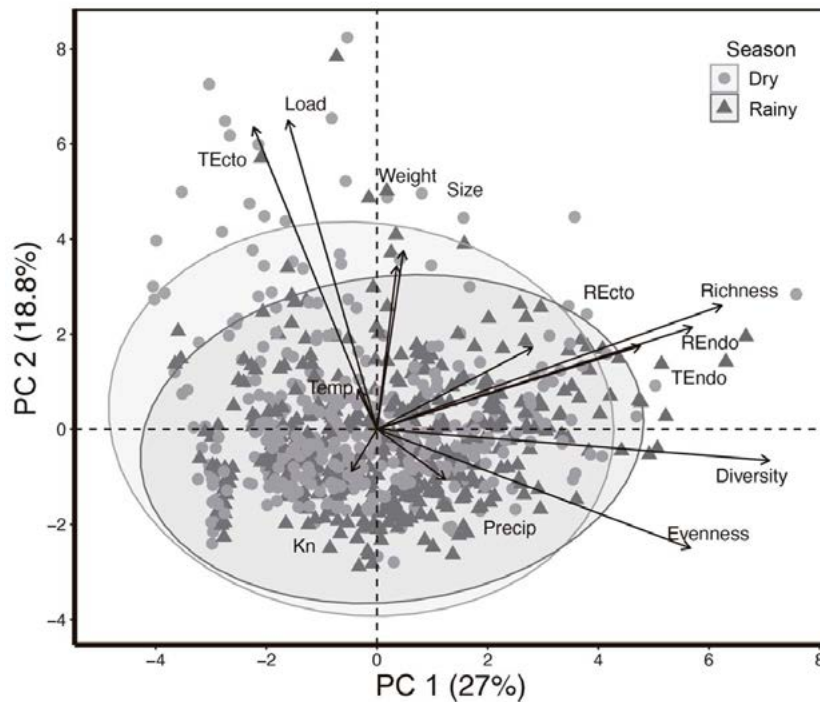


Fig. 5. Scatter plot of Principal Component Analysis (PCA) of factors that influence the species richness and diversity of the parasite infracommunities of *Amphilophus trimaculatus*, from Tres Palos lagoon. “Predictor variables”: Month – sampling month, Temp – surface temperature, Precip – precipitation volume, CF – condition factor, Size – host body size (total length), Weight – total weight. Infracommunity parameters: Richness – number of parasite species per host, Diversity – Brillouin diversity index values, Load – total number of parasites per infracommunity, Evenness – species evenness, REndo – number of endoparasite species, REcto – number of ectoparasite species, TEndo – total number of endoparasites, TEcto – total number of ectoparasites. Ellipses represent climatic seasons.

DISCUSSION

Although species composition and parasite species richness varied little during the study period, some component parasite species exhibited temporal changes in their infection dynamics. Environmental changes in Tres Palos lagoon caused by the seasonal dry/rainy cycle possibly influenced the availability of intermediate hosts, and the feeding and reproductive behaviour of *Amphilophus trimaculatus*, which in turn affected the recruitment processes of some heteroxenous parasite species.

Species composition

No significant changes were observed in the species composition of parasite communities in *A. trimaculatus*, since most of the reported parasite species previously reported by Violante-González et al. (2008b) were also recorded in this study. The digeneans (one adult and five metacercariae) were the best represented parasite group in this cichlid, which is similar to the pattern reported for other fish species in Mexico (Jiménez-García 1993, Salgado-Maldonado and Kennedy 1997, Paredes-Trujillo et al. 2020). The greater richness of digenean species in coastal lagoons may be linked to the high temperatures, shallow depth, and high productivity of these aquatic systems.

These environmental factors favour the development of large populations of herbivorous snails, and benthic and pelagic crustaceans, which act as intermediate hosts for heteroxenous parasites such as digeneans, acanthocephalans and nematodes (Valtonen et al. 1997, Zander et al.

1999, Carpio-Hernández et al. 2024a). Acanthocephalans are considered to be quite rare parasites among freshwater fish in Mexico (Salgado-Maldonado et al. 2004). The occurrence as many as three species of acanthocephalans in *A. trimaculatus* (Table 1) may be related to its diet, which according to the results includes high percentages of benthic crustaceans (ostracods and amphipods), which act as intermediate hosts for these parasites (Kennedy 2006).

Southwellina cf. *hispidia* is a generalist acanthocephalan considered as one of the most abundant species of polymorphids associated with piscivorous birds in Mexico (García-Varela et al. 2023). In Tres Palos lagoon, adults of *S. cf. hispidia* has been reported in *Ardea alba* Linnaeus, *Nyctanassa violacea* (Linnaeus), and *Phalacrocorax brasilianus* (Gmelin) (Violante-González et al. 2015), and its cystacanth (larvae) in seven species of fish (Violante-González et al. 2007, Carpio-Hernández et al. 2024b). The infection levels of this acanthocephalan (Table 1) were higher than those reported for this same cichlid species in Tres Palos lagoon several years ago (Violante-González et al. 2007, 2008b), which is possibly related to the increase in the populations of its intermediate hosts in recent years.

On the other hand, many species of tropical cichlids are infected with monogeneans of the genera *Gussevina* Kohn et Paperna, 1964, *Sciadicoleithrum* Kritsky, Thatcher et Boeger, 1989 and *Trinidactylus* Hanek, Molnár et Fernando, 1974 (Mendoza-Franco and Vidal-Martínez 2005, Tavares-Dias et al. 2017, Santos et al. 2018, Oliveira et al. 2019); however, no monogenean species were recorded in *A. trimaculatus*.

In Mexico, four species of *Sciadicleithrum* (*S. bravohollisae* Kritsky, Vidal-Martínez et Rodríguez-Canul, 1994, *S. meeki* Mendoza-Franco, Scholz et Vidal-Martínez, 1997, *S. mexicanum* Kritsky, Vidal-Martínez et Rodríguez-Canul, 1994, and *S. splendida* Kritsky, Vidal-Martínez et Rodríguez-Canul, 1994) have been identified in endemic cichlids (Mendoza-Franco et al. 1999). Although *S. mexicanum* has been identified in cultured *A. trimaculatus*, as well as in wild populations from the Papagayo River (Violante-González et al. 2008b), this monogenean was not found in Tres Palos Lagoon. Its absence may be attributed to the fact that it is a freshwater species, which generally lives in rivers, and may not thrive in the coastal lagoons of Guerrero, which are unstable and highly polluted brackish environments (Violante-González et al. 2008b).

Variation in infection levels

Temporal variations in the infection parameters of some heteroxenous parasites (Table 1), suggest that transmission process of these parasites can experience temporal fluctuations, due to variations in the availability of suitable intermediate hosts, and differences in their infection strategies (Moravec et al. 2002, Violante-González et al. 2008a, 2009). Temperature and salinity are important abiotic factors that affect the survival and performance of benthic invertebrates and set limits on their spatial and temporal distribution within brackish and freshwater systems (Pörtner and Farrell 2008, Vereshchagina et al. 2016).

Snail populations experience high mortality due to dehydration during the dry season, when water volumes decrease. However, their mortality rates vary depending on the species, habitat, and the depth at which they aestivate (Chaiyasaeng et al. 2019). At least five species of snails have been recorded in some lagoons in the Guerrero state: *Bithynia* cf. *tentaculata* (Linnaeus), *Biomphalaria* cf. *havanensis* (Pfeiffer), *Littoridinops tenuipes* Couper, *Clypeolum* cf. *latissimus* (Broderip) and the invasive snail *Melanoides tuberculata* (Müller), which apparently has a high susceptibility to infections, because it can harbour several types of cercariae (unpublished data).

MvGLM models and PCA analysis indicated that year-round variations in water temperature and precipitation volume significantly influenced the abundance of some component parasite species (Table 3, Fig. 5). It points out that a moderate increase in water temperature can enhance transmission of the majority of parasitic species, e.g., by increasing the rate and lengthening the period of larval production, increasing parasites' infectivity, and changing the global distribution of parasites (Löhmus and Björklund 2015, Mouritsen et al. 2018, Gopko et al. 2020). In addition, increased temperature causes multiple shifts in biology of the definitive and intermediate host (e.g., growth rate, feeding and reproductive behaviour, abundance, diversity, etc.) (Löhmus and Björklund 2015, Gopko et al. 2020).

During the dry season (December–May) the environment of Tres Palos lagoon is relatively stable (Violante-González et al. 2008a, 2009). This can favour the active transmission process of some parasites, such as *Austrodiplotomum ostrowskiae* and *Clinostomum* cf.

tataxumui because of higher availability of snail populations more resistant to dehydration that act as intermediate hosts. On the other hand, the GRI and GSI values indicated that feeding activity of *A. trimaculatus* increased before the reproductive period (dry season), and decreased during the rainy season when its reproduction occurred (August to September, Fig. 1).

These changes in feeding behaviour, together with the greater or lesser availability of pelagic and benthic microcrustacean populations (copepods, ostracods and amphipods) during some months of the year, possibly generated variations in the infection levels of some parasites with trophic transmission, such as the nematode *Contraecum* sp. and as well as the acanthocephalans *Neoechinorhynchus brentnickoli* and *S. cf. hispida* (Table 1). Indeed, several studies have shown that seasonal variation in the diet and quantity of food ingested by the hosts affect the infection dynamics of intestinal parasites, and the parasite community structure (Carpio-Hernández et al. 2004a, Violante-González et al. 2008a, 2009, 2010).

Component communities

Total component communities (helminth and crustaceans) were characterised by low species richness (7 to 11 species), low diversity (${}^1D = 1.93$ to 6.40; data not shown) and a high dominance of one copepod species (*Ergasilus* cf. *davidi*). Parasite communities intensely dominated by a single parasite species can mask or hide important structuring patterns (Neves et al. 2013). When the species diversity analysis considered only helminth species, diversity values were quite high (${}^1D = 10.26$ –21.53) and up to 4 helminth species (3 digeneans and 1 acanthocephalan) dominated the communities during some of the two climatic seasons (Table 2).

The copepod *E. cf. davidi* numerically dominate the global parasite community during all sampling period, with infection levels very similar to those recorded more than 10 years ago in Tres Palos lagoon (Violante-González et al. 2008b). Monoxenous parasites such as *E. cf. davidi* can predominate in highly eutrophic environments (Johnson and Carpenter 2008, Hoshino and Tavares-Dias 2019), due to their high tolerance to altered habitats and short life cycle (< one month, Alekseev et al. 2021, Velázquez-Ornelas and Suárez-Morales 2022).

Ergasilid copepods infect at least 12 other fish species of freshwater, marine, and brackish origin in Tres Palos lagoon; however, *A. trimaculatus* exhibits the highest infection levels compared to the other fish species (prevalence = 100%, and mean abundance = 230 copepods per infected fish) (Violante-González et al. 2007). In this study, its infection levels were very similar (100% and 159, Table 1). The shallow depth of the lagoon and the benthic and territorial behaviour of *A. trimaculatus*, as well as its preference for living among the roots of mangroves and submerged vegetation (Violante-González 1995), exposes it to greater infection of free-living stages (copepodids and cercariae) of ergasilids and helminths as *C. cf. tataxumui*, *A. ostrowskiae* and *Cladocystis* cf. *trifolium* which also exhibit higher levels of infection in this cichlid (Violante-González et al. 2007).

The similarity of helminth communities was generally high and did not show differences between climatic seasons (dry = 75.5%, rainy = 72.4%). However, the nMDS analysis showed higher levels of similarity mainly during consecutive months in the same climatic season (Fig. 2). Some parasitological studies carried out over long time periods, have concluded that parasite communities may be more stable in species composition during short time periods, but not during longer periods (Villalba-Vasquez et al. 2022, Violante-González et al. 2023).

In tropical estuarine parasite communities, changes in structure and species composition have been linked to environmental alterations generated by the dry-rainy cycle, which affects the species' recruitment process of parasites (Violante-González et al. 2008a, 2009, Hoshino and Tavares-Dias 2019, Carpio-Hernández et al. 2024a). However, rainfall can vary between years because it can be affected by large-scale natural phenomena such as El Niño or La Niña (Bravo-Cabrera et al. 2017). Therefore, the environmental changes generated by the dry-rainy cycle do not occur with the same duration and intensity over the years, so they can alter the structure of parasite communities differently, making them quite unpredictable.

Infracommunities

Some parasite infracommunities in cichlid fish are characterised by low diversity, species richness, and number of parasite individuals (Paredes-Trujillo et al. 2020). The infracommunities of *A. trimaculatus* showed this pattern, although they exhibited a richness (mean = 3.0 ± 1.2), diversity (0.54 ± 0.41) and mean parasite load (70 ± 61) slightly higher than those recorded for other cichlids such as *Chiapaheros grammodes* (Taylor et Miller), *Vieja breidohri* (Werner et Stawikowski) and *V. hartwegi* (Taylor et Miller) (Paredes-Trujillo et al. 2020). Several biotic and abiotic factors have been identified as important determinants of species richness and diversity in parasite communities (Luque et al. 2004, Villalba-Vasquez et al. 2018, Carpio-Hernández et al. 2024a).

The results of multivariate analyses (MvGLM and PCA) indicated that the structure of parasite infracommunities in *A. trimaculatus* depends to some extent on the body size and physical condition of this fish. Larger fish with better physical condition were collected mainly during the dry season

(Table 2), when their feeding activity was higher. A large body size can facilitate parasite colonisation, because larger individuals tend to ingest greater quantities of food and they are older, and thus they have had more time to accumulate parasites than smaller individuals (Luque et al. 2004, Tavares and Luque 2008, Villalba-Vasquez et al. 2018).

Non-parametric correlation tests also confirmed the existence of positive associations between two infracommunity parameters (mean species richness and number of parasites) and the body size. However, these correlations were weak, as evidenced by the low correlation values ($r_s = 0.087$, and 0.117). This indicates that factors other than host body size may be more important determinants of the structuring of *A. trimaculatus* parasite infracommunities (Neves et al. 2013, Tavares-Dias et al. 2017); i.e., host habitat, feeding and reproductive behaviour, variation in the abundance of intermediate host populations, and differences in the infection strategies of its parasites.

Several species of component parasites that infected *A. trimaculatus* in the Tres Palos lagoon, showed temporal variations in their infection levels throughout the year, or during different climatic seasons. These results suggest that these parasite populations respond differently to environmental changes generated by the dry/rainy cycle. Temporal variations in the infection dynamics were possibly caused by a combination of biotic and abiotic factors, influenced by the seasonal dry/rainy cycle, which can affect the availability of intermediate host populations, as well as the feeding and reproductive behaviour of the host.

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