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Environmental variability influences the relationship between prawn host size and ectoparasite body size: insights from a long-term stream study

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Abstract Larger host body size can lead to larger parasites, as more energy is available for parasite growth. However, this size-matching correlation can also be influenced by additional host and environmental factors. Here, we utilized a long-term dataset of cymothoid isopods parasitizing palaemonid prawns to investigate whether there is evidence supporting a relationship between host and parasite body traits (i.e., length, sex, weight), while accounting for the effects of season (i.e., dry and wet) and year. We also tested whether prawn body condition (i.e., Scaled Mass Index—SMI) is affected by parasitism. We compared parasitized and non-parasitized prawns by sex. Prawns were sampled seasonally over 4 years in a tropical stream in southeastern Brazil. Our analysis showed that isopod body length and weight were positively associated with host length and weight. This relationship was independent of host sex and seasonal variation, but was influenced by interannual variability. Host length and weight explained most of the variation, while environmental variability accounted for the remainder. We also showed that the SMI was reduced in parasitized individuals of both sexes, compared to non-parasitized prawns. Moreover, we found a significant difference in SMI between sexes and years, but not between seasons, when considering only parasitized hosts. The findings suggest that interannual variability and parasitism may jointly affect host energetics, shaping the dynamics of the 'host-parasite-environment' triad. Future research should consider interannual variability as a potentially key driver of host-parasite interactions in freshwater ecosystems.

Keywords Environmental variability · Harrison's rule · *Macrobrachium brasiliense* · Ectoparasitism · Seasonal variation · *Telotha henselii*

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Introduction

Host-parasite dynamics are influenced by host traits such as body size, sex, and mass, which affect susceptibility to infection and ultimately shape parasite evolution (Poulin 2007; Johnson and Hoverman

2014; Stewart Merrill et al. 2021; Leung 2022). Across diverse host-parasite taxa, a well-documented positive relationship exists between host and parasite body size, known as Harrison´s rule (Harrison 1915; Clayton et al. 2016; Ni et al. 2021; Schmid-Hempel 2021). This pattern has been observed across multiple parasite groups, including crustaceans, fleas, ticks, mites, and helminths (Johnson et al. 2005; Clayton et al. 2016; Harnos et al. 2017; Villa et al. 2018; Welicky et al. 2019; Rózsa et al. 2024). However, within individual host-parasite systems, additional variation may arise due to ecological and physiological factors (Poulin 2007; Maestri et al. 2020; Patra et al. 2024; Melo et al. 2024; Sánchez-Hernández et al. 2025).

Larger hosts offer more space and energy resources, enabling parasites to grow larger, which may increase their fitness through greater fecundity (Sasal et al. 1999; Lisnerová et al. 2022). It seems much more likely that parasite size and biomass within a single population increase with host body size due to host energetics (Hechinger 2013). Larger host has higher resource intake and a larger pool of assimilated resources that can be used by the parasites to growth, enhancing their fitness through increased body size and fecundity (e.g., larger offspring—Poulin 2007; Ni et al. 2021; Rózsa et al. 2024). In some cases, host behavior, immunity, or environmental conditions may distort this size-matching pattern, resulting in correlations that are not directly driven by host traits (Johnson and Hoverman 2014) or environmental changes (e.g., seasonality and temperature), which can create spurious correlations in this pattern, where no intrinsic properties of the host directly affect the parasite's body size (Maestri et al. 2020; Ni and de Dutra Angeli 2023). Therefore, changes in this pattern can occur depending on the host-parasite system and also due to ecological forces that act to shape this pattern (Poulin 2007; Johnson and Hoverman 2014; Clayton et al. 2016; Lim et al. 2022).

Environmental variability and temperature changes can influence parasite growth rates and body size, potentially altering the correlation between host and parasite body traits (Johnson et al. 2005; Poulin 2007; Clayton et al. 2016; Poulin 2021; Lim et al. 2022; Lisnerová et al. 2022). Temperature and precipitation can also disrupt host-parasite size relationships, as shown in flea-rodent assemblages (Maestri et al. 2020). Although this pattern has been reported in several taxa (Poulin 2007; Harnos et al. 2017; Ni et al. 2021), the combined effects of host traits and seasonal variation on parasite size have yet to be explored on a large temporal scale. Ni and de Dutra Angeli (2023) also identified a significant proportion of variance in cymothoid isopod size that cannot be attributed solely to host size, suggesting that the relationship between parasites and host sizes can be determined by environmental variability. Therefore, conducting long-term studies is crucial to investigate how interannual variability in abiotic conditions, such as temperature, pollution, and habitat fragmentation, influences parasite dynamics (Altizer et al. 2006; Cable et al. 2017; Davenport et al. 2024). Moreover, models that include this interannual variability in abiotic conditions will help us better predict the fluctuations in parasite infections and dynamics in freshwater systems (Cable et al. 2017; Wunderlich et al. 2024).

Here, cymothoid isopods parasitizing freshwater prawns were used as a model system to investigate seasonal and interannual variation in host-parasite body size relationships. It was hypothesized that parasite body traits would scale with host size and mass, independent of host sex or seasonal changes. This pattern was also expected to remain consistent across dry and wet seasons and over multiple years, suggesting that host traits primarily drive isopod body size, rather than environmental fluctuations. In addition, a scaled mass index (SMI) was calculated for each prawn as a proxy for body condition to test whether parasitism affects host energy balance. Differences in SMI were evaluated between parasitized and non-parasitized individuals, as well as across sexes, seasons, and years, considering only parasitized hosts.

Material and methods

Study area and sampling

Over four years (1995–1998), we collected palaemonid prawns (*Macrobrachium brasiliense*) in a stream (Águas Claras) located in the Pardo River basin, southeastern Brazil (Fig. 1a, b). Sampling was conducted bimonthly at fixed sites for 2 hours during the day. At each site, prawns were manually collected using sweeping sieves (50 cm in diameter, 4 mm mesh size) near marginal aquatic vegetation. After the collection, we verify the sweeping sieves for potential detached isopods. The specimens were kept in

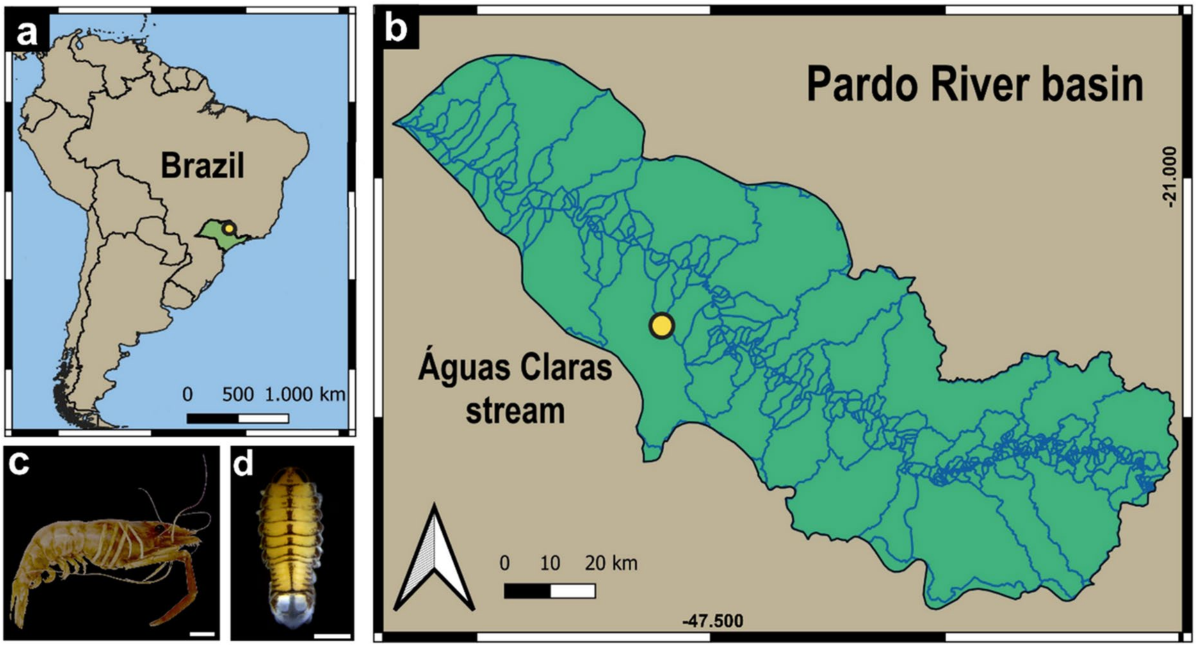

Fig. 1 Geographic location of the Rio Pardo basin (**a**), highlighting the Águas Claras stream (**b**), where palaemonid prawns (*Macrobrachium brasiliense*) (**c**) and the cymothoid isopods (*Telotha henselii*) (**d**) were collected. Scale bar: (c) = 4 mm; and (d) = 1 mm

thermal plastic containers and transported to the laboratory, where they were euthanized by thermal shock (3 °C for 30 min), then fixed and preserved in 70% ethanol. The material was subsequently deposited in the Museum of Zoology at the University of São Paulo (MZUSP), with accession numbers for prawns (MZUSP 47525) and isopods (MZUSP 47526).

Measures of host-related traits

In the laboratory, prawn specimens underwent biometric analysis, including body measurements and weight. Carapace length (CL) was measured from the base of the rostral spine to the posterior margin of the carapace, and total length (TL) from the base of the rostral spine to the tip of the telson. Measurements were taken using a caliper with a precision of 0.05 mm. Wet weight (W) was recorded in grams using a digital scale with a precision of 0.01 g. Sex was determined by the presence or absence of the appendix masculina on the endopod of the second pair of pleopods (Nogueira et al. 2020). Subsequently, prawns were examined externally for cymothoid isopods (Fig. 1c, d).

We calculated a scaled mass index (SMI) for each prawn as a proxy for its body condition between parasitized and non-parasitized hosts. First, we log-transformed the prawn body weight and length to estimate the β coefficient of the regression for each sex across seasons and years. Then, we used the formula:

$$SMI = Wi\left(L_0/L_i\right)^{bSMA}$$

where W_i and L_i are the weight and length of each prawn specimen, respectively; L_0 is the average length of the population for each sex, season, and year; and *bSMA* is the β coefficient (Peig and Green 2009; Maceda-Veiga et al. 2016).

Parasitological screening and measurements

Ectoparasites found on each animal were collected and measured under a stereomicroscope (Zeiss® Stemi® SV-6), and their weight was recorded. They were then fixed in 70% ethanol and identified based on the descriptions provided by Lemos de Castro (1985), Wunderlich et al. (2011), and Andrade et al. (2020). Identification was based on standard taxonomic keys and comparative morphology. The

Table 1 Total length (mm) and weight (g) of *Macrobrachium brasiliense* prawns and *Telotha henselii* cymothoid isopods across seasons and years. Values are presented as mean ± standard error (Mean ± SE)

Season/Year	*Macrobrachium brasiliense*						*Telotha henseliii*		
	n	Male length Mean ± SE	Male weight Mean ± SE	n	Female length Mean ± SE	Female weight Mean ± SE	n	Parasite length Mean ± SE	Parasite weight Mean ± SE
1995									
Winter	13	24.2 ± 1.33	0.177 ± 0.019	34	20.6 ± 0.64	0.117 ± 0.009	47	4.4 ± 0.16	0.005 ± 0.0004
Spring	10	26.3 ± 0.61	0.214 ± 0.030	14	23.6 ± 0.97	0.169 ± 0.014	24	5.3 ± 0.31	0.007 ± 0.0008
Summer	7	21.1 ± 2.02	0.129 ± 0.028	9	17.2 ± 1.14	0.079 ± 0.013	16	3.2 ± 0.24	0.002 ± 0.0005
Autumn	9	20.3 ± 0.65	0.102 ± 0.009	24	21.3 ± 1.96	0.126 ± 0.027	33	3.8 ± 0.14	0.003 ± 0.0003
Total	39	23.7 ± 0.97	0.170 ± 0.015	81	20.7 ± 0.43	0.117 ± 0.006	120	4.3 ± 0.11	0.004 ± 0.0003
1996									
Winter	–	–	–	–	–	–	–	–	–
Spring	–	–	–	–	–	–	–	–	–
Summer	10	21.2 ± 1.42	0.143 ± 0.027	13	19.1 ± 1.06	0.102 ± 0.019	23	3.4 ± 0.17	0.003 ± 0.0004
Autumn	–	–	–	–	–	–	–	–	–
Total	10	21.2 ± 1.42	0.143 ± 0.027	13	19.1 ± 1.06	0.102 ± 0.019	23	3.4 ± 0.17	0.003 ± 0.0004
1997									
Winter	11	27.6 ± 0.98	0.222 ± 0.023	16	25.4 ± 0.72	0.188 ± 0.014	27	5.2 ± 0.18	0.005 ± 0.0005
Spring	–	–	–	–	–	–	–	–	–
Summer	11	20.7 ± 1.34	0.130 ± 0.025	14	18.9 ± 0.89	0.099 ± 0.014	25	3.3 ± 0.30	0.003 ± 0.0008
Autumn	–	–	–	–	–	–	–	–	–
Total	22	24.1 ± 1.11	0.176 ± 0.020	30	22.4 ± 0.82	0.146 ± 0.013	52	4.3 ± 0.21	0.004 ± 0.0005
1998									
Winter	–	–	–		–	–		–	–
Spring	–	–	–		–	–		–	–
Summer	6	24.9 ± 0.42	0.200 ± 0.005	25	17.5 ± 0.63	0.081 ± 0.010	31	3.1 ± 0.15	0.002 ± 0.0003
Autumn	12	25.7 ± 0.58	0.225 ± 0.017	25	23.3 ± 0.47	0.143 ± 0.008	37	3.7 ± 0.12	0.003 ± 0.0003
Total	18	25.4 ± 0.42	0.217 ± 0.012	50	19.1 ± 0.45	0.103 ± 0.008	68	3.4 ± 0.11	0.002 ± 0.0002
TOTAL	89	23.8 ± 0.51	0.176 ± 0.009	174	20.4 ± 0.30	0.120 ± 0.005	263	3.9 ± 0.08	0.004 ± 0.0002

cymothoid isopods were identified using morphological traits, including the second pereopod with five spines on the inner margin of the propodus and the sixth pereopod with four spines on the propodus and one on the merus.

Statistical analysis

We used generalized linear mixed models (GLMM) to examine the relationship between prawn body traits (i.e., host length and weight) and cymothoid body traits (i.e., parasite length and weight), and to assess whether this relationship varied with host sex (male vs. female), season (dry vs. wet), and year (1995–1998). Host and parasite traits, season, year, and their interactions were treated as fixed effects, while month and year were included as random intercepts (random effects). Only individuals parasitized by a single cymothoid isopod were used in the analysis. We used a generalized additive model ("gam") as a smoothing method to visualize the relationship between parasite and host length and weight. To test the effect of cymothoid isopods on prawn body condition (i.e., scaled mass index), we used a generalized linear mixed model and compared the scaled mass index (SMI) of parasitized and non-parasitized hosts.

Generalized linear mixed models (GLMMs) using a gamma distribution with a log link function were used for continuous response variables (Zuur et al. 2013). We also calculated the marginal R^2 values (R^2_m, fixed effects only) and conditional R^2 (R^2_c, fixed plus random effects) for each model (Nakagawa and

Table 2 Results of generalized linear mixed models describing the relationship between parasite length (Length model) and parasite weight (Weight model) as a function of host length, host weight, host sex (male vs. female), seasons (i.e. wet vs. dry), and years (i.e. 1995, 1996, 1997, 1998)

Model	Parameter estimate	SE	Wald $z-$value	$P-$value	95% CI		R^2_c	R^2_m	IC (%)
					Lower	Upper			
Length model							0.79	0.72	
Intercept	0.384	0.082	4.674	**0.001**	**0.212**	**0.554**			
Host length	0.048	0.002	18.752	**0.001**	**0.043**	**0.053**			67.4
Host sex (male)	− 0.0004	0.021	− 0.022	0.982	− 0.042	0.043			2.4
Season (wet)	− 0.048	0.068	− 0.707	0.479	− 0.183	0.086			4.8
Year (1996)	− 0.139	0.114	− 1.218	0.223	− 0.363	0.084			25.4
Year (1997)	− 0.042	0.100	− 0.426	0.670	− 0.239	0.153			
Year (1998)	− 0.245	0.075	− 3.267	**0.001**	**− 0.392**	**− 0.098**			
Weight model							0.82	0.74	
Intercept	− 6.590	0.193	− 33.991	**0.001**	**− 7.042**	**− 6.253**			
Host weight	8.193	0.456	17.958	**0.001**	**7.300**	**9.089**			60.6
Host sex (male)	− 0.057	0.058	− 0.976	0.329	− 0.057	0.172			3.2
Season (wet)	− 0.354	0.217	− 1.629	0.103	− 0.777	0.069			7.1
Year (1996)	− 0.438	0.368	− 1.190	0.234	− 1.162	0.268			29.1
Year (1997)	− 0.233	0.313	− 0.745	0.456	− 0.859	0.357			
Year (1998)	− 1.072	0.239	− 4.479	**0.001**	**− 1.538**	**− 0.607**			

Parameter estimates, standard error (SE), Wald z-values, *P*-value, 95% confidence interval, total marginal (R^2_m), conditional (R^2_c), and individual contribution percentage (IC%) are provided for each predictor and model. Bold values and the confidence intervals (CI) that exclude zero indicate significant variables (n = 263).

Schielzeth 2013). Multicollinearity among predictors was assessed using a variance inflation factor (VIF) from the *performance* R package (Lüdecke et al. 2021). Predictors with VIFs greater than five were excluded (Zuur et al. 2013). Diagnostic plots from the *DHARMA* R package (Hartig 2024) were used to verify normality and homoscedasticity.

Model selection was performed using the Akaike Information Criterion (AIC) with the *performance* package (Lüdecke et al. 2021), and predictor importance was evaluated using the *glmm.hp* package (Lai et al. 2022). All GLMM analyses were conducted in R version 4.4.1 (R Development Core Team 2024), using the *lme4* (Bates et al. 2015) and *glmmTMB* (Magnusson et al. 2020) packages. Generalized additive models (GAMs) were performed with the *mgcv* package (Wood 2011). We have also adopted the recent recommendations on good research practices and reporting on statistical ecology (Popovic et al. 2024). Maps were created using QGIS version 3.34.3 (Team QD 2024), and graphics were generated with the *ggplot2* package (Wickham 2011).

Results

Overall, we observed slight differences in average length and weight between male and female prawns across seasons and years. Males were, on average, 2–3 mm longer than females, except in 1998, when the difference was more pronounced (approximately 6 mm; Table 1). Similar trends were observed for weight, with males consistently heavier than females (Table 1). Parasite length and weight varied in relation to host body traits across seasons and years (Table 1).

Our models indicated that isopod body length (Length model) and weight (Weight model) were positively associated with host length ($R^2_c = 0.79$; $R^2_m = 0.72$; Table 2, Fig. 2a) and host weight ($R^2_c = 0.82$; $R^2_m = 0.74$; Table 2, Fig. 3a). No significant effects were detected for host sex (Table 2, Figs. 2b, 3b) or season (Table 2, Figs. 2c, 3c). However, a significant year effect was observed for both parasite length (Fig. 2d) and weight (Fig. 3d). Among fixed predictors, host length (67.4%) and year (25.4%) contributed most to the variation in parasite length,

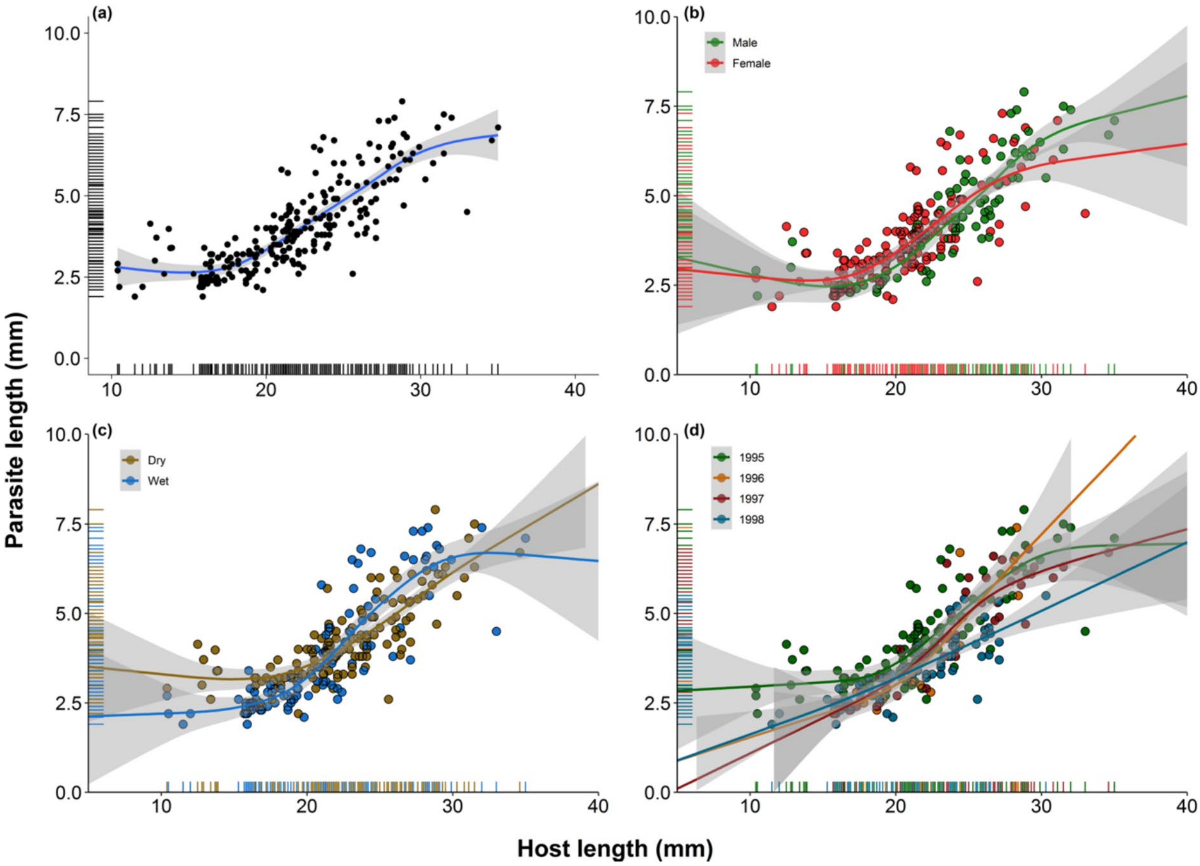

Fig. 2 Relationships between host length and parasite length modeled using a generalized linear mixed model (**a**), with comparisons by sex (**b**), season (**c**), and year (**d**). Tick marks along the axes represent individual data points. The generalized additive model (GAM) was applied as a smoothing function

while host weight (60.6%) and year (29.1%) were the primary contributors in the weight model (Table 2).

We found a lower significant difference of the scaled mass index (SMI) in parasitized prawns compared to non-parasitized individuals (GLMM estimate ± SE: 0.094 ± 0.044, $p = 0.033$; Fig. 4), and also differed between sexes (GLMM estimate ± SE: −0.309 ± 0.031, $p < 0.001$; Fig. 4). In parasitized prawns only, SMI also varied by sex (estimate ± se: −0.388 ± 0.021, $p < 0.001$; Fig. 5a), and by year (estimate ± SE: 0.226 ± 0.077, $p = 0.003$; Fig. 5c), but not by season (estimate ± SE: 0.073 ± 0.070, $p = 0.297$; Fig. 5b).

Discussion

We found strong evidence that larger prawns support larger cymothoid isopods, consistent with Harrison's rule (HR), through a positive relationship between parasite length and host length, as well as parasite weight and host weight. However, no influence of host sex or season (dry or wet) was detected. Contrary to our expectations, we observed significant interannual variation in the relationships between host and parasite sizes. These findings reinforce the scaling relationship between host and parasite body size, as proposed by Harrison´s rule, and extend its applicability to cymothoid isopods infecting invertebrates (Clayton et al. 2016; Ni et al. 2021; Poulin 2021; Leung 2022; Ni and de Angeli Dutra 2023).

This pattern has been widely confirmed across multiple host-parasite systems, including myxozoans in elasmobranchs (Lisnerová et al. 2022), digeneans in fish (Sasal et al. 1999), nematodes in mammals (Morand and Poulin 2002), lice and ticks in birds (Johnson et al. 2005), fleas in rodents (Maestri et al.

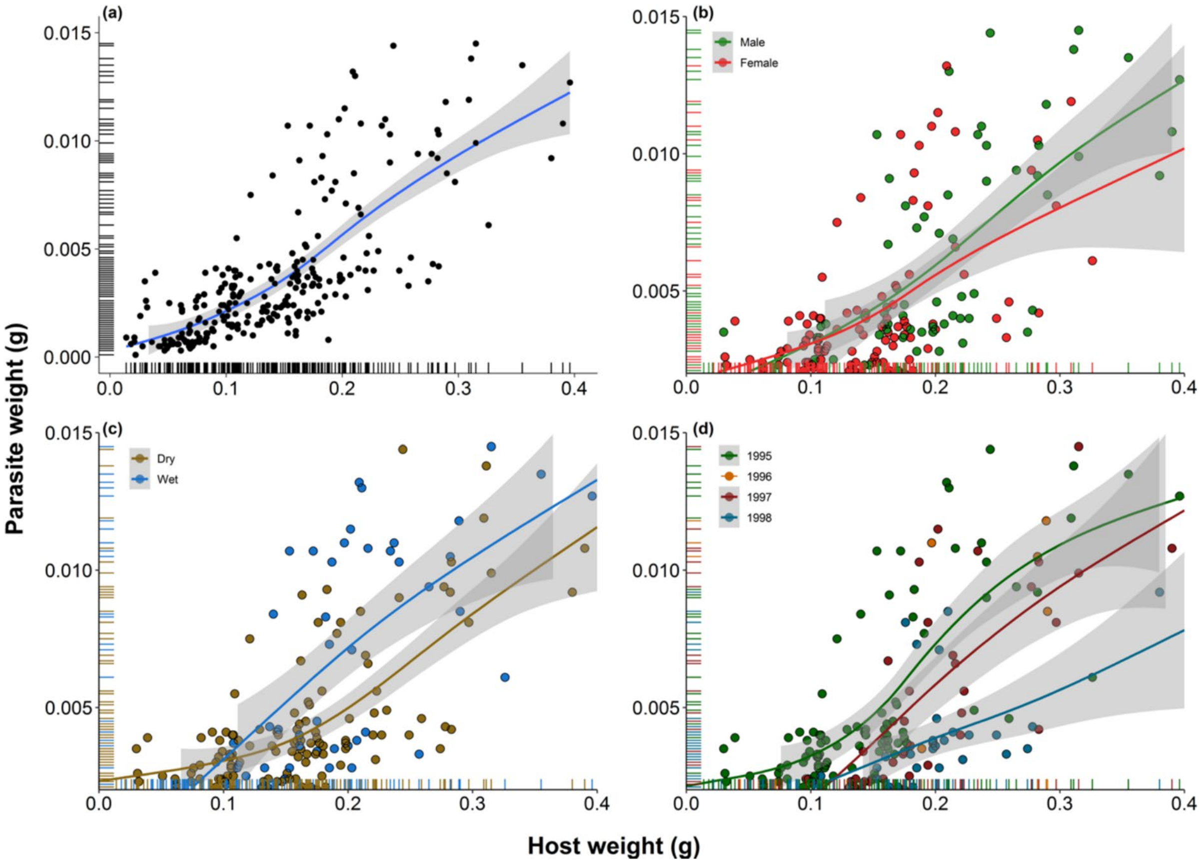

Fig. 3 Relationship between host weight and parasite weight modeled using a generalized linear mixed model (**a**), with comparisons by sex (**b**), season (**c**), and year (**d**). Short lines along the Y and X axes represent each data point. The generalized additive model (GAM) was applied as a smoothing function

2020), and rhizocephalans in amphipods (Poulin and Hamilton 1997). Most studies on cymothoids have focused on fish hosts (Welicky et al. 2019; Ni and Dutra 2023), and few have investigated this pattern in arthropod hosts (see Ni et al. 2021; Lim et al. 2022). Our findings add to this gap by providing strong support for a size-scaling pattern in cymothoid isopods parasitizing a freshwater decapod, that have an alignment with similar studies involving cymothoid-fish systems (see Welicky et al. 2019 and Kottarathil et al. 2019).

In addition to the positive relationship, we found a positive association between parasite and host weight. However, this relationship was unaffected by host sex, despite the pronounced sexual dimorphism observed in *M. brasiliense* (Mantelatto and Barbosa 2005; Taddei et al. 2017; Nogueira et al. 2019, 2022). The lack of a sex effect may reflect overlapping spatial distributions and behaviors between males and females (Nogueira et al. 2019), which in turn influence parasite exposure (see Wunderlich et al. 2024). Additionally, *Telotha henselii* may have an evolved capacity to parasitize both sexes in proportion to their size (Beck 1979; Rasch and Bauer 2015). Alternatively, dominant factors such as host size or environmental variability may have masked any sex-related effects.

In contrast, our results showed that the scaled mass index (SMI) was significantly reduced in parasitized prawns, particularly among females. Parasites are known to affect host energy reserves and body condition (Peig and Green 2009; Lagrue and Poulin 2015; Maceda-Veiga et al. 2016). The SMI is considered the most robust body condition index for assessing the impact of parasites on host condition (Maceda-Veiga

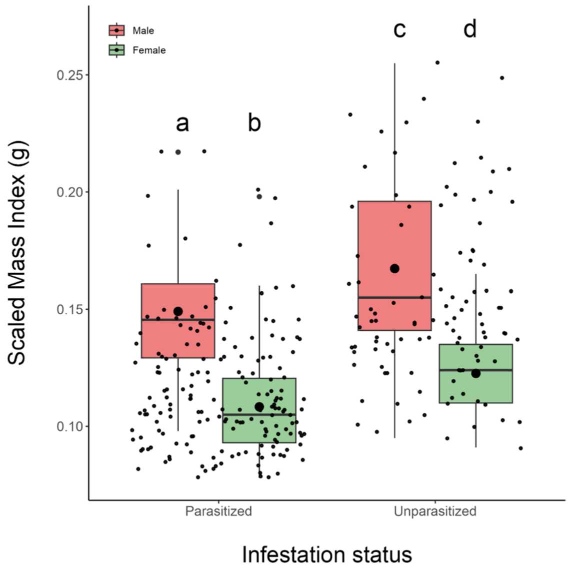

Fig. 4 Comparison of the scaled mass index (SMI) between parasitized and unparasitized prawns by sex. Box-and-whisker plots represent the mean, median, interquartile range, and minimum and maximum values

et al. 2014; Maceda-Veiga et al. 2016; Msoffe et al. 2025). The substantial reduction in SMI among females may indicate greater physiological costs of parasitism in this sex, potentially related to reproductive investment or size-energy scaling. Similar associations have been reported in studies of fleas and mites in rodents, with effects varying by sex and locality (Msoffe et al. 2025). In addition to parasitism, anthropogenic stressors such as water quality and habitat degradation have also been linked to variation in SMI (Maceda-Veiga et al. 2014; Maceda-Veiga et al. 2016; Msoffe et al. 2025), although no seasonal differences were observed in this study.

From an evolutionary perspective, parasite body often scales with host traits to maintain attachment and functional efficiency (Clayton et al. 2016). In our system, it is reasonable to expect that cymothoids adjust their size to match host growth and maintain their position on the host's carapace. However, this covariation does not apply universally, even when controlling for phylogenetic constraints (Morand et al. 2000; Poulin 2007). Host-parasite size relationships may fluctuate due to temporal (Maestri et al. 2020) and environmental variation (Johnson et al. 2005; Poulin 2021; Lisnerová et al. 2022), and such variation was evident in our data.

The interannual variation observed, particularly in 1998, likely reflects climatic fluctuations (e.g., rainfall, dry periods, temperature) that can disrupt this relationship, resulting in misleading correlations between body sizes of parasites and their hosts across assemblages (Maestri et al. 2020; Rózsa et al. 2024). These factors are known to influence benthic macroinvertebrate communities (Herbst et al. 2019; Bae and Park 2019), and also affect the demographics and structure of prawn populations, with hydrological regime changes directly impacting parasitism rates in freshwater prawns (Wunderlich et al. 2024). Temperature has also been a factor affecting host-parasite interactions by modulating host metabolic processes, thereby enhancing parasite feeding rates at the individual host level (Hechinger 2013; Byers 2021). These effects can also scale allometrically across the ecosystems, influencing broader host-parasite dynamics (Grunberg and Anderson 2021). However, recent findings suggest that temperature shifts may have only weak effects on infection outcomes in first intermediate hosts, indicating that seasonal variation in parasitism may be species- or system-specific (Paterson et al. 2024). Taken together, our results suggest that host-parasite size relationships are not solely driven by host size or energetics. Instead, they may be constrained by interannual environmental variability, which affects host condition and parasite development over time. A recent study has shown that the host body size (i.e. the HR test between parasites and birds) is usually constrained by environmental effects and phylogenetic constraints, while the parasite body size tends to follow the variation of the host body size (Rózsa et al. 2024).

In summary, we observed significant interannual variation in the relationship between host and parasite traits, alongside the expected positive correlations between isopod and prawn size. These correlations were consistent across seasons (dry and wet) and sexes, but not across years. We also demonstrated that parasitism can negatively affect the scaled mass index (SMI), indicating a reduction in host body condition can be influenced by parasitism. These findings support the idea that both interannual variability and parasitism influence the host's energy balance, thereby shaping the dynamics of 'host-parasite-environment' interactions. Future studies should investigate environmental variability across spatial and temporal scales to

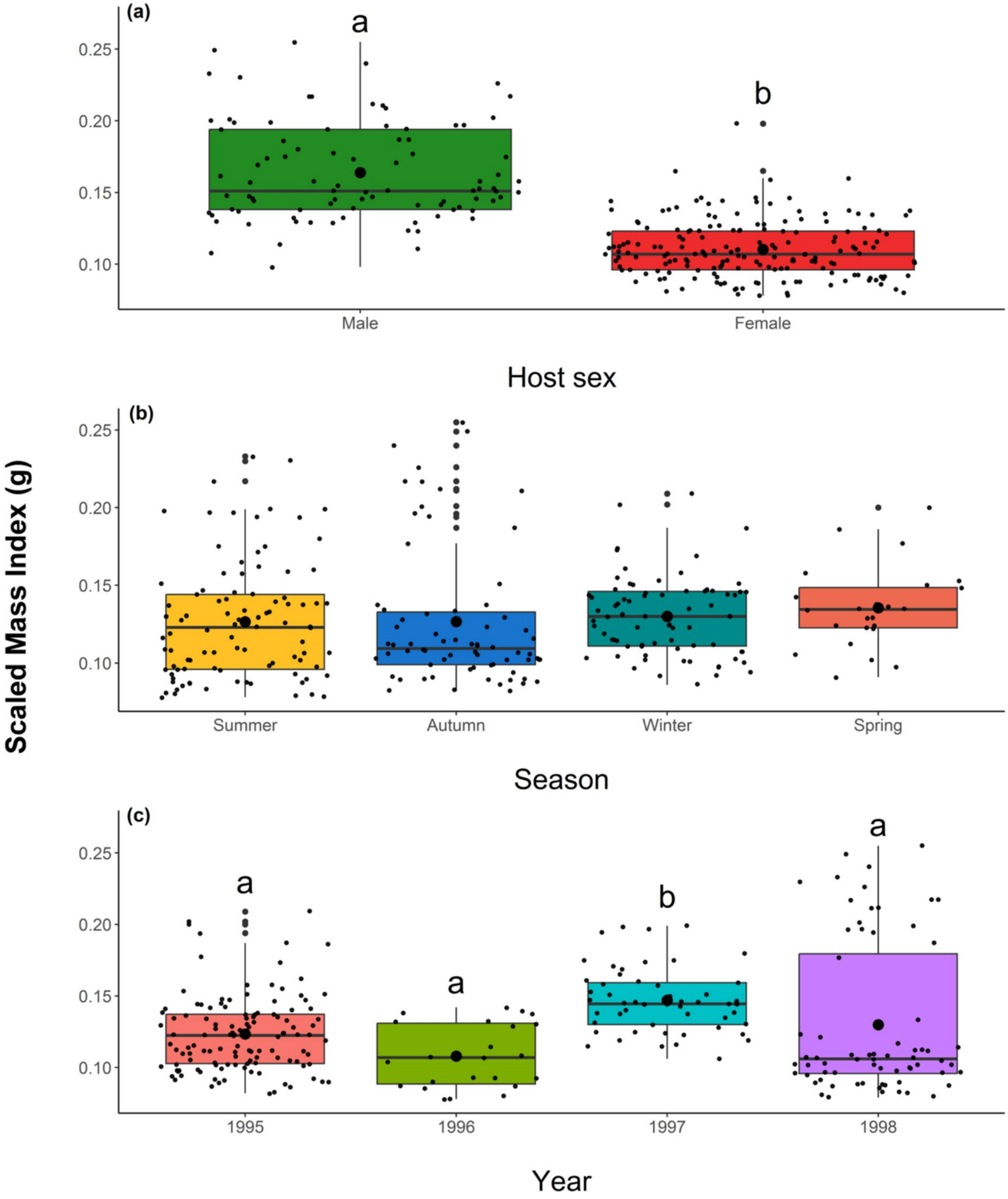

Fig. 5 Variation of the scaled mass index (SMI) for each parasitized prawn by sex (**a**), season (**b**), and year (**c**). Box-and-whisker plots represent the mean, median, interquartile range, and minimum and maximum values

understand better whether the observed patterns are consistent across ecosystems and to assess the generality of host-parasite size relationships in other aquatic systems.

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Author contributions A.C.W. and M.A.A.P. conceived and designed study. A.C.W. analyzed the data and wrote the first draft of the manuscript. E.E.D.M. and M.A.A.P. provided critical input and made substantial contribution to improve the map and manuscript editing. All authors read and approved the final manuscript.

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Data availability No datasets were generated or analysed during the current study.

Code availability R code will be made available from the corresponding author on reasonable request.

Declarations

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