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Original Article

Fecundity selection depends on local environmental conditions among sympatric populations of two Amazonian stream-shrimp species

Elmo Pereira da Silva[1,*], Pedro A.C.L. Pequeno[2], William E. Magnusson[1,3]

[1]Graduate Program in Ecology, National Institute for Amazonian Research, André Araújo Avenue, 2936, Petrópolis, Manaus, AM, 69067-375, Brazil
[2]National Institute of Sciences and Technology for Synthesis of Amazonian Biodiversity, André Araújo Avenue, 2936, Petrópolis, Manaus, AM, 69067-375, Brazil
[3]Biodiversity Coordination, National Institute for Amazonian Research, André Araújo Avenue, 2936, Petrópolis, Manaus, AM, 69067-375, Brazil

[*]Corresponding author. Graduate Program in Ecology, National Institute for Amazonian Research, André Araújo Avenue, 2936, Petrópolis, Manaus, AM 69067-375, Brazil. E-mail: elmopereira1317@gmail.com

ABSTRACT

In most ectotherms, females are larger than males. Darwin suggested that this was because larger females have a fitness advantage: they had more space and resources to bear more offspring, an idea known as fecundity selection. However, evidence for a strong fecundity-size relationship among populations is contradictory and may depend strongly on local environmental conditions. Here, we tested for divergence in the fecundity-size relationship in shrimp reproductive females along small-scale environmental gradients in a tropical rainforest. We sampled 235 reproductive females of two endemic shrimp species (*Macrobrachium inpa* and *Macrobrachium amazonensis*) in 50-m stream reaches across a 64-km^2 area in Central Amazonia. Total body size of individuals was measured and all eggs were counted. Our results showed that *M. inpa* reproductive-female body length was significantly different between stream catchments, while *M. amazonensis* body length was significantly associated with a stream-area gradient. Furthermore, the fecundity-size relationship for *M. inpa* varied along a water-velocity gradient, while that of *M. amazonensis* varied along a substrate-type gradient. These patterns could be explained by either local adaptation, plasticity, or both. Regardless, they show that the expression of fecundity selection varies even across relatively small spatial extents and along subtle environmental gradients within a tropical rainforest.

Keywords: local adaptation; environmental gradients; body length; fecundity traits; plasticity

INTRODUCTION

Evolution is dependent on processes that guarantee an organism's reproduction and viability over time. Survival, mating success, and fecundity are some of the processes that define the trajectories of adaptations (Darwin 1859, Bell 2008). These processes are the basis for three selection mechanisms: natural, sexual, and fecundity. In contrast to natural and sexual selection, fecundity selection studies remain lacking despite its major role in species life-history processes (Shine 1988, Roff 2002). The term 'fecundity selection' was originally derived from Darwin's fecundity-advantage hypothesis (Darwin 1874), to explain the sexual dimorphism when females are larger than males across animal species. The primary causes for these body-size differences between sexes are that larger females can accommodate a greater number of eggs and allocate more energy for reproductive events (i.e. energy reserve hypothesis) (Williams 1966, Calder 1984).

Despite Darwin's assumptions, fecundity selection is not always related to female-biased sexual size dimorphism (SSD) (Pincheira-Donoso and Tregenza 2011, Soulsbury *et al.* 2014). Female-biased SSD can also be a result of sexual selection, particularly for smaller male body size and not necessarily acting on female size (Pincheira-Donoso and Hunt 2017). Fecundity selection can vary within species through natural selection by ecological divergence (Roff 2002), as selective mechanisms can interact spatially and temporally (Badyaev and Ghalambor 2001, Hoekstra *et al.* 2001). Many studies have shown the effect of environment on fecundity at a large scale (i.e. hundreds to thousands of kilometres), and a strong positive relationship between fecundity and size (Nali *et al.* 2014, Dick *et al.* 2017). However, this relationship can change across environments, even at local scales, but most evidence comes from bird populations (Pincheira-Donoso and Hunt 2017). Therefore, larger females do not always have higher

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fecundity and more research is needed to investigate this relationship in other taxa.

Historically, fecundity selection was treated as a function of fecundity traits, since this type of selection favours traits that increase the reproductive output (Roff 2001). Instead, most studies use body size as a proxy of fitness traits in fecundity selection studies since fecundity is usually a function of body size (Pincheira-Donoso and Hunt 2017, Ahti *et al.* 2020, Common *et al.* 2020). The correlation between body size and fecundity may result from several mechanisms, where either small or large sizes can display higher fecundity (Gergely and Tökölyi 2023). For instance, in limited conditions, larger individuals may allocate more energy for tissue maintenance than reproduction (i.e. energy demand hypothesis) (Reim *et al.* 2006). Conversely, smaller individuals require less energy for tissue maintenance and may reproduce sooner and with better effort (Blanckenhorn 2000). Nevertheless, larger females often reproduce unequally more than smaller females (Barneche *et al.* 2018), both intra- and inter-specifically (Hayward and Gillooly 2011, Dick *et al.* 2017), although that correlation depends greatly on the species and the environment.

Fecundity selection has been reported for many taxa, mostly ectotherms and some endotherms (crustaceans: Hirst and Kiorboe 2014, Nguyen and Nguyen 2018; insects: Afaq and Afaq 2012, Hu *et al.* 2015; fish: Winkler *et al.* 2012, Horne *et al.* 2020; amphibians: Juarez *et al.* 2023; reptiles: Meiri *et al.* 2012; birds: Lislevand *et al.* 2009, Caron and Pie 2024; mammals: Cassini 2017), and has been found to operate primarily towards female size. However, fecundity selection may also act on male size if males play a significant role in reproductive success or for selective pressures acting independently in both sexes (Pincheira-Donoso and Hunt 2017). For example, in Syngnathidae fish, larger males can enhance female reproductive output as male brood pouches and female abdomens are selected to guarantee fecundity and offspring viability (Wilson 2009, Winkler *et al.* 2012).

Besides female size, other conditions can limit the number of offspring that a female can bare (Yampolsky and Scheiner 1996, Kolding and Fenchel 1981, Dani and Kodandaramaiah 2017). Resource availability and seasonality can affect species reproductive processes, as resources can change spatially and temporally (Castiglioni *et al.* 2018, Kürschner *et al.* 2021). Consequently, divergent relationships between fitness traits and ecological resources may arise among contrasting environments (Silvestro *et al.* 2023). This is the main premise of ecological divergence. Therefore, divergent selection could indicate local adaptation by populations that experience different resource availability. Habitat and food availability were reported as key drivers affecting reproduction and survival of species (Thomas *et al.* 2001, Durant *et al.* 2007), once the quantity and quality of those resources affects species energetic demands, which depends on organism size (Blanckenhorn 2000).

Environmental gradients are suggested as the main drivers of biological diversification in freshwater systems, even at microgeographic scales (Loomis *et al.* 2020). Among those gradients, system size has been widely associated with ecological divergence for increasing habitat availability and niche partitioning (Chavarie *et al.* 2018, Tiddy *et al.* 2024), although those are more related to fish populations in temperate and glacial regions. Populations restricted to freshwater environments are also limited by dispersal barriers between river catchments (e.g. plateaus separating waterbodies) (McGlashan and Hughes 2000, Hughes 2007), in which a population's selective regimes depend on direct or temporary connections between catchments (Bilton *et al.* 2001). In this way, populations that occupy different catchments are characterized by unique selective aspects (Avise 1994, Cook *et al.* 2002), possibly leading to strong selection at catchment level.

Crustaceans, such as shrimps and crabs, were the first animals used by evolutionists to investigate natural selection and adaptation in the field (Weldon 1890). Variation in their egg number has been linked to female size and environmental variation (e.g. temperature, dissolved oxygen) (Reid and Corey 1991, Pantaleão *et al.* 2018, Limberger *et al.* 2024). However, the potential role of spatial and temporal variation in fecundity selection is still poorly understood, and most studies focus only on the effects of season on egg number (Castiglioni *et al.* 2018). Shrimp species commonly present strong patterns of fecundity selection (Tamburus *et al.* 2012, Herrera-Correal *et al.* 2013) and their distribution is often related to environmental changes (Silva *et al.* 2020). However, the role of local environmental gradients on selection for size-specific fecundity is unclear.

In Amazonian small streams, shrimp species distributions are mainly affected by environmental factors (Kemenes *et al.* 2010, Silva *et al.* 2020). For the same species, populations were found to be size-structured, where small individuals shared minimal habitat resources with large ones (Silva and Magnusson 2023). However, the extent to which Amazonian shrimp species are under divergent fecundity selection is unknown. Here, we collected comprehensive data on two abundant Amazonian shrimp species (*Macrobrachium inpa* Kensley & Walker, 1982 and *Macrobrachium amazonensis* Ramos-Porto, 1979) to test if (i) reproductive female size has diverged between sites with contrasting local environmental conditions; and (ii) whether such divergence can be explained by differential fecundity selection (i.e. different relationships between number of eggs and body length) in sympatric populations of Amazonian small-stream shrimps.

MATERIAL AND METHODS

Study area and environmental sampling

The study was undertaken in Amazonian small streams within a 64-km^2 trail system in Ducke Forest Reserve (DFR) (2°56′ S; 59°54′ W). DFR covers an area of 10 000 ha of *terra-firme* tropical rainforest (i.e. non-flooded) (Fig. 1). Average air temperature is around 26°C and annual precipitation between 1966 and 2018 was 2570 mm (Costa *et al.* 2020). Vegetation cover is predominantly old-growth *terra-firme* rainforest and soils are mainly clayey, becoming sandier at low elevations (Chauvel *et al.* 1987, Guillaumet 1987). DFR streams drain to different catchments in the East and West. Eastern streams drain to the Amazon River and western streams drain to the Negro River.

Twenty-four first- and second-order stream reaches (50-m) were sampled between September 2021 and January 2024. Sampling sites corresponded to 10 stream reaches in the eastern catchment and 14 in the western catchment. Sites were chosen to coincide with some of the 38 permanent study plots established by the National Institute for Amazonian Research (INPA) Graduate Program in Ecology

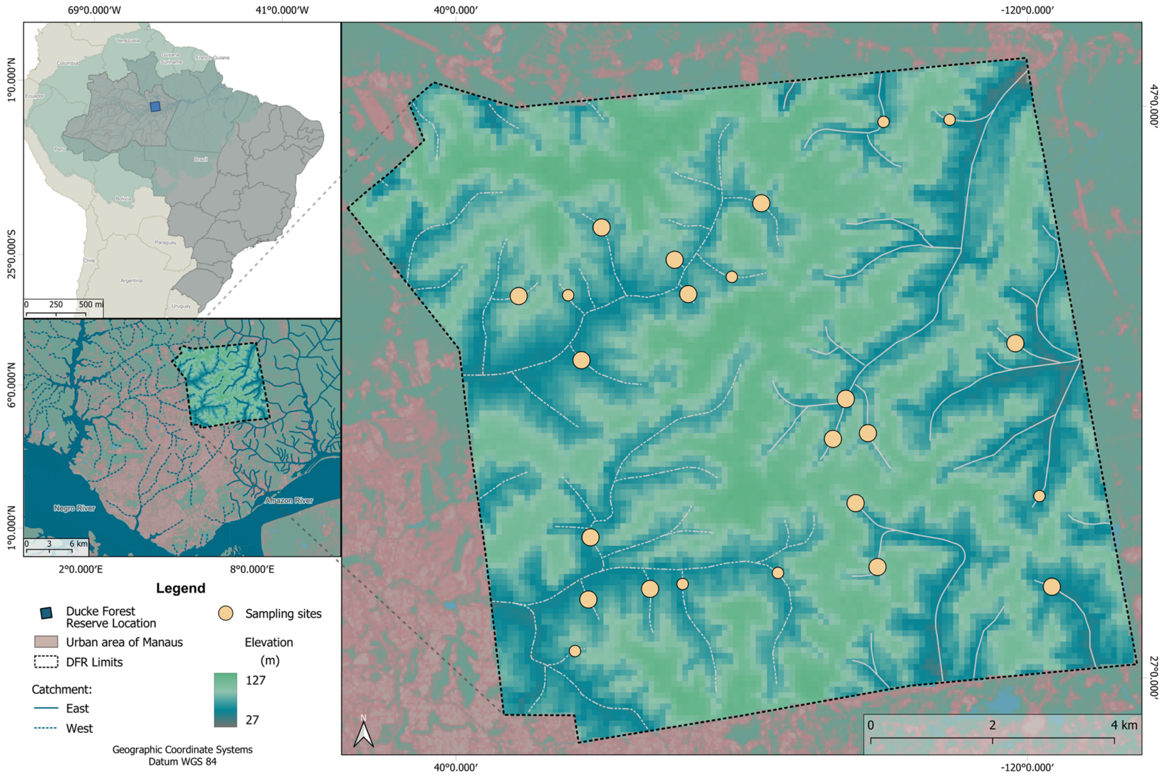

Figure 1. Location of Ducke Forest Reserve (DFR) showing the distribution of 24 sampling sites in streams divided between two catchments, East (streams shown as continuous lines) and West (streams shown as dashed lines). Larger circles represent sites where both species were sampled, and smaller circles represent sites where one or the other species was sampled.

and coordinated by the Biodiversity Research Program of Western Amazonia (PPBio-AmOc). Data collection followed an adaptation of the standard PPBio protocol for fish (Mendonça *et al.* 2005). Specimens and environmental variables were collected on the same day and by the same researchers in each plot.

Environmental variables were measured before shrimp sampling to avoid changes in habitat structure caused by researcher movement. Stream hydraulic features were measured in four transects across streams spaced 16-m apart along the sample reach. Channel morphometry at the position of each of the four transects was represented by total channel width and by average depth, measured at nine equidistant points across the channel in each transect. Stream surface velocity at the centre of the channel was estimated using the time that a floating low-density object took to travel a 1-m distance (i.e. distance divided by the travel time). Substrate type was registered at each of the nine depth-measurement points and was categorized as sand, clay, pebble, coarse litter, fine litter, root, trunk, or macrophyte.

Shrimp species

Shrimp individuals were captured through active sampling using fine-mesh hand nets manipulated by two researchers moving in a downstream-upstream direction. Sampling was carried out in the daytime and at night (only for the first five samples) by the same collectors for 2 hours in each stream reach. Shrimps could not be reliably identified in the field, so they were kept in well-aerated buckets with stream water and later killed by anaesthesia in alcohol diluted in stream water and in cold water with ice and stored in 70% ethanol. Individuals were identified to species level using specialized guides (Kensley and Walker 1982, Melo 2003). Sex was determined for each specimen by the presence (male) or absence (female) of an appendix masculina on the second pleopod. Total length (TL: from the tip of the rostrum to the end of the telson) was measured using a manual caliper (0.05 mm) and for ovigerous females all eggs were counted. Here, TL (cm) was used to represent body length for statistical analysis and fecundity refers to the number of eggs in a single clutch (i.e. single reproductive episode), also known as transient fecundity (Pincheira-Donoso and Hunt 2017). For most reproductive females analysed here, eggs were in a similar embryonic development stage, which was the transition between no apparent embryo formation to the visualization of developing eyes (i.e. eggs change colour to whitish with a black spot), although no apparent hatching was observed. Ovigerous females in very early embryonic development stages were not considered, since early-fertilized eggs popped before counting, as well as females in late stages with apparent egg hatching or loss.

At least four species of shrimps are found in DFR (Fonseca *et al.* 2009, Silva *et al.* 2020, Carvalho *et al.* 2025), but only two (*Macrobrachium inpa* and *Macrobrachium amazonensis*) were sufficiently common for analysis. Both species are endemic to the Amazonian region with more records in the Amazon state of Brazil (Kensley and Walker 1982, Melo 2003). *Macrobrachium inpa* occurs mainly on submerged leaf litter and stream-margin roots, feeding generally on terrestrial and aquatic invertebrates, including young stages of shrimp (Kensley and Walker 1982). For this species, males are larger than females, with ovigerous females average total body length (TL) of 27 mm and clutches consisting of 8 to 19 elliptical, yolk-rich, dark-red eggs (Magalhães 2016).

For analyses, this species was represented by 171 adult females collected in 24 stream reaches.

Macrobrachium amazonensis occurs mainly in open waters with sandy substrate and floating roots, feeding on invertebrates, especially annelids and insects (Kensley and Walker 1982). For this species, females are larger than males, ovigerous females have a mean TL of 36.5 mm and clutches consisting of 13 to 19 elliptical, yolk-rich, dark-green eggs (Magalhães and Medeiros 1998). For analyses, this species was represented by 64 adult females collected in 16 stream reaches.

Statistical analysis

Sample units corresponded to the reproductive females (i.e. individuals with presence of eggs) collected in all sampling sites and months. Due to relatively high collinearity, depth and width ($r^2 = 0.77$; $t = 38.6$; $p < 0.0001$) were summarized into a principal component axis (PCA) as a proxy of channel morphometry using the *prcomp* function from the *stats* package. Substrate proportions were summarized into the first three principal component axes, representing 66 (for *M. inpa*) to 78% (for *M. amazonensis*) of the variation among all eight substrate types (Supporting Information, Table S1). Catchment identity (East or West) was used as a categorical variable to test for stream-basin effect on dependent variables. To account for autocorrelation among individuals from the same site and month, we used those as random factors in our models (see below). First, we compared models using different random factors (i.e. site or month) but the same fixed factors assuming Maximum Likelihood (ML). Second, we ran models again using Restricted Maximum Likelihood (REML) to estimate better variance for random-factor coefficients. This method is more likely to avoid type I error bias by fixed factor estimation without overloading models (Patterson and Thompson 1971, Clifford *et al.* 1989, Rameez *et al.* 2022). Finally, we used Akaike information criterion (ΔAIC) to select the best fitted model, considering the random factors and avoiding type I and II errors (Barnett *et al.* 2010). As sites and months produced similar effects in our analyses (Supporting Information, Table S2), we chose sampling sites to represent the autocorrelation component in our tests due to lower ΔAIC in most of the models. All statistical analyses were performed in R statistical software v.4.3.1 (R Core Team 2025).

Body-size and fecundity-selection-divergence models

Dependent variables corresponded to reproductive-female size for body-size models and to the number of eggs for those same females for fecundity-selection models. Generalized linear mixed models (GLMM) were used to test for possible relationships between reproductive-female size and number of eggs (each separately) with environmental gradients. GLMMs were constructed with log-transformed dependent variables and assuming residuals with normal distribution. The following predictors were included: catchment identity (East or West), channel morphometry (principal component), substrate type (principal components), water velocity (m/s), and sampling sites (random factor). Predictors were selected based on their variation among stream reaches, their independent effect (i.e. Pearson correlation coefficients < 0.6), and their importance for shrimp distribution in tropical streams. To test for divergent-fecundity selection, the model for number of eggs included interactions between body length and each environmental predictor. For the purpose of this study, the independent effect of size on egg number, considering the fecundity-selection-divergence models without interactions, will be referred as habitat-independent selection. All models were constructed using the *gam* function in the *mgcv* package (Wood *et al.* 2016).

RESULTS

Body-size divergence

Macrobrachium inpa reproductive-female size showed a significant relationship only with catchment identity ($t = 2.324$; $p = 0.001$) (Table 1; Fig. 2A). *Macrobrachium amazonensis* reproductive-female size showed a significant relationship only with channel morphometry ($t = -2.723$; $p = 0.009$) (Table 1; Fig. 2B), which represents depth and width measurements.

Fecundity-selection divergence

Macrobrachium inpa presented a statistically significant relationship between number of eggs and body length independent of environmental predictors (i.e. habitat-independent fecundity selection) ($t = 2.982$; $p = 0.003$) (Table 2; Fig. 3A). Water velocity and substrate gradient-PC3, which represent proportions of fine litter and macrophytes (Supporting Information, Table S1), were correlated with egg number (WV: $t = -2.460$, $p = 0.01$; PC3: $t = 2.491$, $p = 0.01$)

Table 1. Generalized linear mixed models (GLMM) of reproductive-female size on environmental gradients (fixed components) and sampling sites (random component). The number of replicates (reproductive females) was at least 64 for each analysis.

	Generalized Linear Mixed Models				
		Statistics			
	Fixed components	***t-value***	***p***	***edf***	***R²***
Macrobrachium inpa					
	Catchment (East/West)	2.324	**0.001**	-	-
	Channel morphometry (PC)	0.344	0.73	-	-
	Substrate (PC1)	-1.114	0.92	-	-
	Substrate (PC2)	-0.102	0.75	-	-
	Substrate (PC3)	0.782	0.43	-	-
	Water velocity (m/s)	0.630	0.53	-	-
	Random component				
	Sampling sites	-	**0.01**	6.56	0.23
Macrobrachium amazonensis					
	Catchment (East/West)	-0.074	0.94	-	-
	Channel morphometry (PC)	-2.273	**0.03**	-	-
	Substrate (PC1)	-1.189	0.24	-	-
	Substrate (PC2)	0.156	0.88	-	-
	Substrate (PC3)	-0.167	0.87	-	-
	Water velocity (m/s)	-0.261	0.8	-	-
	Random component				
	Sampling sites	-	**0.01**	5.86	0.52

Bold values indicate low probability associated with null hypothesis.

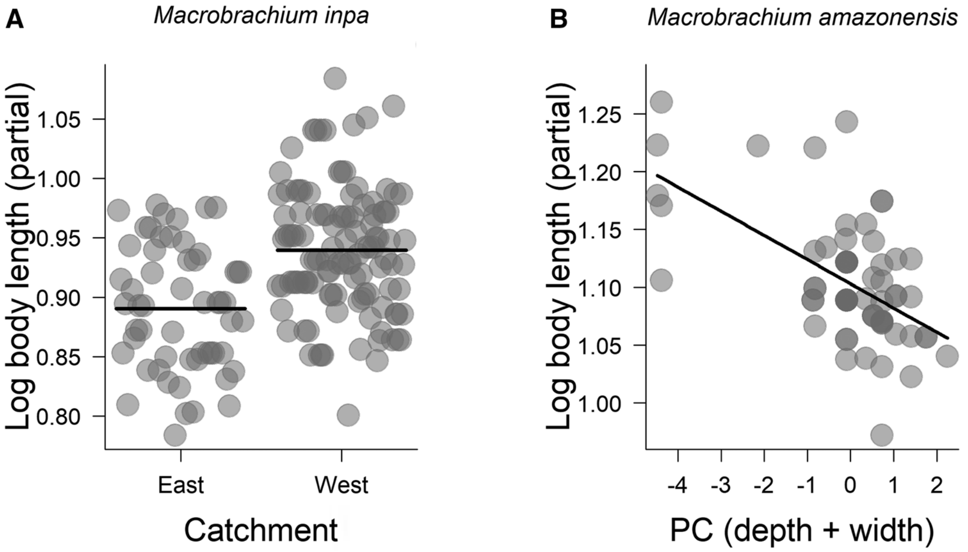

Figure 2. Partial-regression plots (fixed + random components) for a generalized linear mixed model (GLMM) illustrating the relationship between the log of body length (cm) with catchment identity (East or West) for *Macrobrachium inpa* (A) and with stream area (depth + width) for *Macrobrachium amazonensis* (B).

Table 2. Generalized linear mixed models (GLMM) of size-specific fecundity on environmental gradients (fixed components) and sampling sites (random component). The number of replicates (reproductive females) was at least 64 for each analysis.

	Generalized Linear Mixed Models				
		Statistics			
	Fixed components	***t-value***	***p***	***edf***	***R^2***
Macrobrachium inpa					
	Habitat-independent body length (cm)	2.982	**0.003**	-	-
	Body length (cm)	-0.806	0.42	-	-
	Catchment (East/West)	1.048	0.3	-	-
	Channel morphometry (PC)	-0.797	0.43	-	-
	Substrate (PC1)	-0.568	0.57	-	-
	Substrate (PC2)	-0.955	0.34	-	-
	Substrate (PC3)	2.491	**0.01**	-	-
	Water velocity (m/s)	-2.460	**0.01**	-	-
	Body length: Water velocity	2.392	**0.02**	-	-
	Body length: PC3	-1.376	0.17	-	-
	Random component				
	Sampling sites	-	0.1	4.15	0.14
Macrobrachium amazonensis					
	Habitat-independent body length (cm)	3.150	**0.002**	-	-
	Body length (cm)	3.579	**0.0007**	-	-
	Catchment (East/West)	-0.454	0.65	-	-
	Channel morphometry (PC)	0.07	0.94	-	-
	Substrate (PC1)	2.016	**0.05**	-	-
	Substrate (PC2)	-0.849	0.4	-	-
	Substrate (PC3)	-1.751	0.09	-	-
	Water velocity (m/s)	-0.653	0.52	-	-
	Body length: PC1	-1.981	**0.05**	-	-
	Random component				
	Sampling sites	-	0.84	<0.0001	0.24

Bold values indicate low probability associated with null hypothesis.

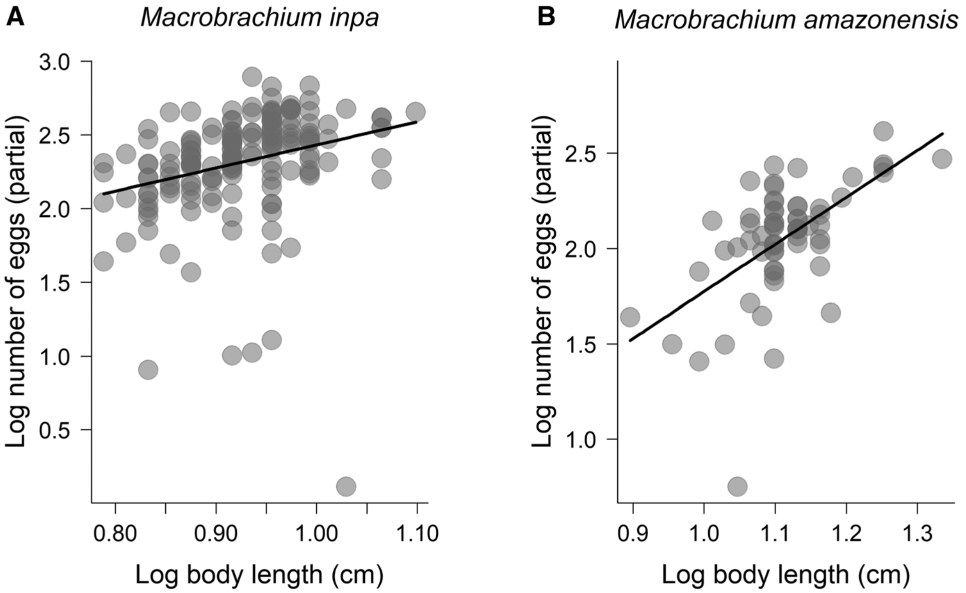

Figure 3. Partial-regression plots (fixed + random components) for a generalized linear mixed model (GLMM) illustrating the habitat-independent relationship between the log of number of eggs (partial) and the log of body length (cm) for *Macrobrachium inpa* (A) and for *Macrobrachium amazonensis* (B).

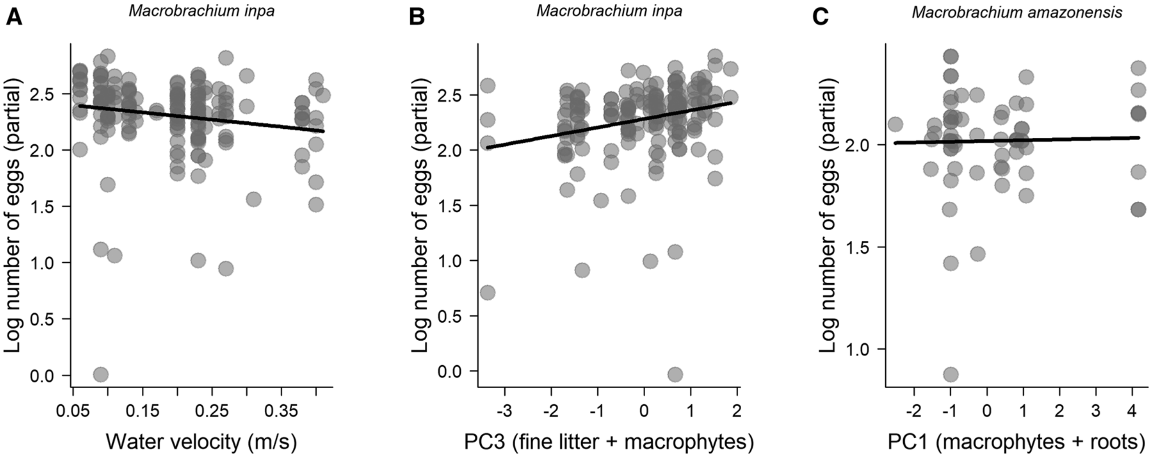

Figure 4. Partial-regression plots (fixed + random components) for a generalized linear mixed model (GLMM) illustrating the relationship between the log of number of eggs with water velocity (m/s) for *Macrobrachium inpa* (A), with substrate type (fine litter + macrophytes) for *Macrobrachium inpa* (B), and with substrate type (macrophytes + roots) for *Macrobrachium amazonensis* (C).

(Table 2; Fig. 4A, B). For this species, size-specific fecundity showed divergent relationships only along the water-velocity gradient ($t = 2.392$; $p = 0.02$) (Table 2; Fig. 5). *Macrobrachium amazonensis* also showed significant habitat-independent fecundity selection ($t = 3.150$; $p = 0.002$) (Table 2; Fig. 3B). Substrate gradient-PC1, which represents proportions of macrophytes and roots (Supporting Information, Table S1), was correlated with egg number ($t = 2.016$, $p = 0.05$) (Table 2; Fig. 4C). For this species, size-specific fecundity was only related to the substrate gradient-PC1 ($t = -1.981$, $p = 0.05$) (Table 2; Fig. 6).

DISCUSSION

Here, we showed that fine geographical scales can promote ecological divergence through differences in the fecundity-size relationship along subtle environmental gradients in Amazonian small-stream shrimps. Size of reproductive females for *M. inpa* varied among different catchments, although none of the measured environmental predictors were related to such variation. This pattern in reproductive-female-size variation between catchments could be a result of non-measured environmental gradients or genetic differences accumulated among individual trait values (Raffard *et al.* 2024). Differences among river catchments are the main drivers of divergence for freshwater populations (Hughes *et al.* 2009), and environmental gradients are related to freshwater shrimp species divergence within and between catchments (Rahman *et al.* 2020). Variation in reproductive-female size was also observed for *M. amazonensis*, but this was more related to changes in channel morphometry. Habitat complexity associated with system-area and depth gradients promote intra- and inter-specific divergence through selection in freshwater environments (Skoglund *et al.* 2015, Recknagel *et al.* 2017), as different strata are subject to distinct biotic and

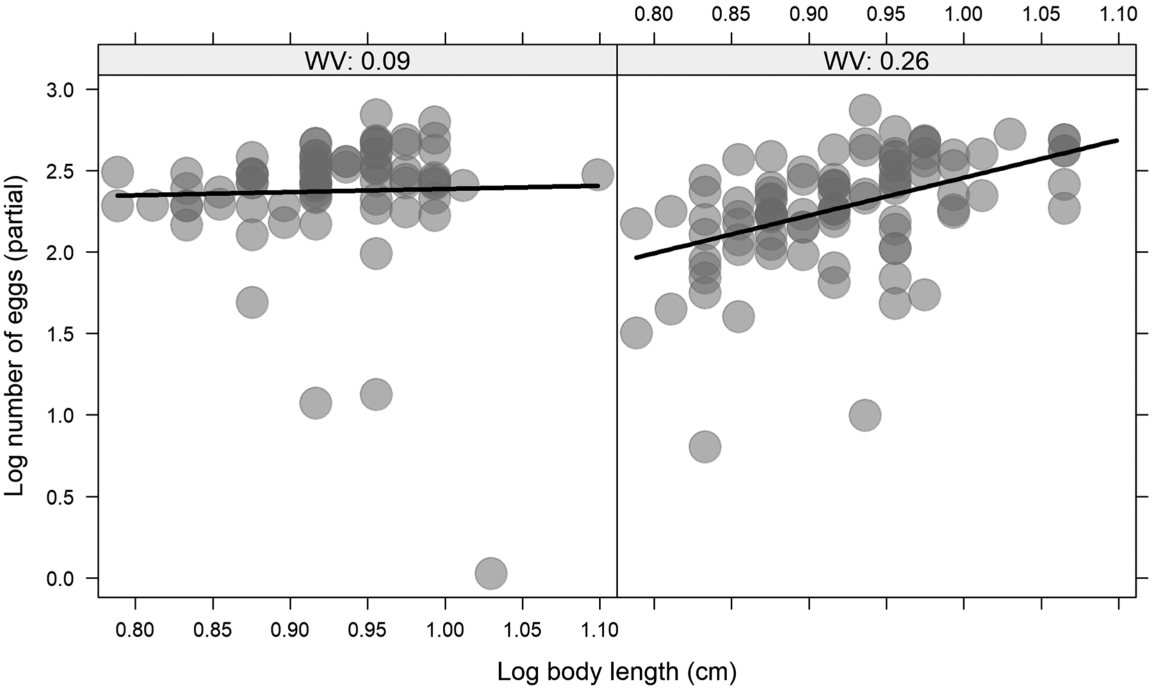

Figure 5. Partial-regression plot (fixed + random components) for a generalized linear mixed model (GLMM) illustrating the habitat-dependent fecundity selection divergence for the relationship between the log of number of eggs and the log of body length along the water-velocity gradient (WV; m/s) for *Macrobrachium inpa*.

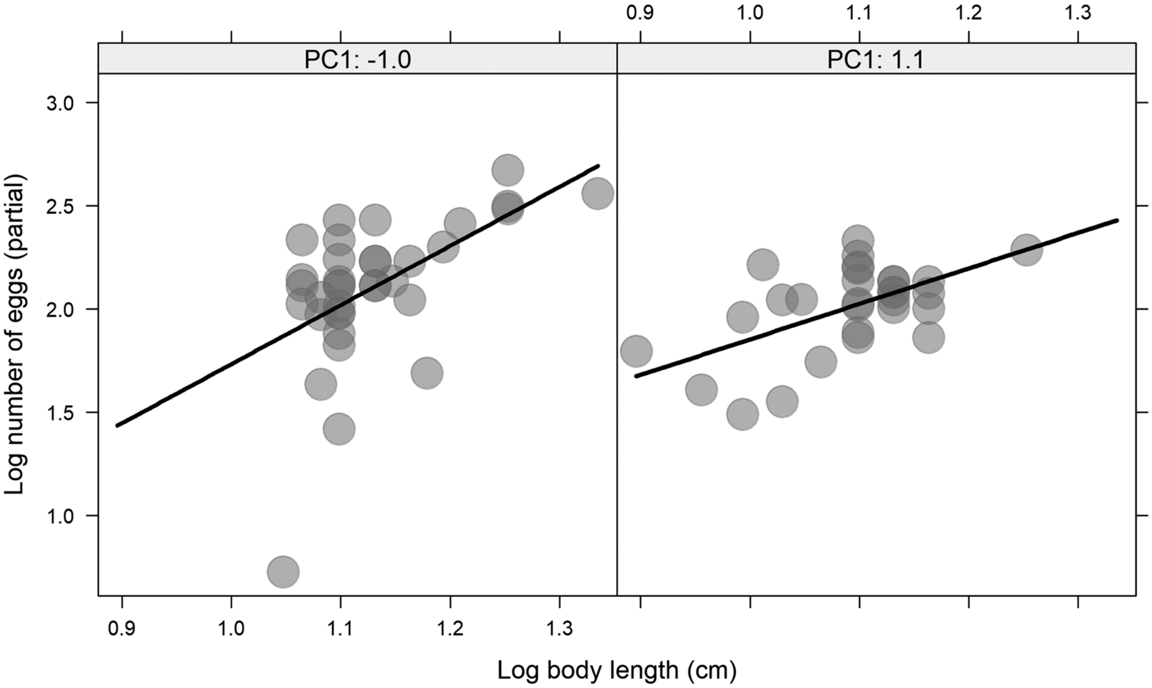

Figure 6. Partial-regression plot (fixed + random components) for a generalized linear mixed model (GLMM) illustrating the habitat-dependent fecundity selection divergence for the relationship between the log of number of eggs and the log of body length along the substrate gradient-PC1 (macrophytes + roots) for *Macrobrachium amazonensis*.

abiotic conditions. In this study, only populations of *M. amazonensis* showed evidence of reproductive-size selection along environmental gradients, with stream area being the most important selective component. Morphological divergence for sympatric populations could be a result of genotypically plastic responses to environmental variation or genotype related habitat preference (Pequeno *et al.* 2021).

Macrobrachium inpa showed evidence of habitat-independent fecundity selection, and that is inconsistent with species whose males are larger than females, as fecundity selection usually results in female-biased SSD (Darwin 1874, Williams 1966, Calder 1984). However, strong fecundity selection not related to female-biased SSD had already been recorded for other taxa (Monroe *et al.* 2015). This outcome suggests that other selective mechanisms could interact with fecundity selection, as sexual selection can also affect SSD and fecundity (Badyaev and Ghalambor 2001, Hoekstra *et al.* 2001, Pincheira-Donoso and Hunt 2017). Sexual selection usually favours larger males than females as a result of territoriality and male-male competition (Slatkin 1984, Simpson *et al.* 2016), common behaviours for *Macrobrachium* species. In the species studied, variation in size-specific fecundity was consistent with divergent selection for contrasting stream-water-velocity environments. Processes that occur strongly in fast-flowing streams (e.g. intra- and inter-specific competition, predation risk, reduced food availability) may exert a direct effect of size on egg number, where larger females produce more eggs, which could be a result of fecundity selection mediated through environmental variation (Stahlschmidt *et al.* 2020). Conversely, reproductive-female size seems to be a neutral trait in slow-flowing streams, where the number of eggs produced does not depend on size, although more eggs are produced in those environments.

Selection tends to favour individuals that reduce the costs for reproduction, which may be associated with ecology (van Noordwijk and de Jong 1986, Brommer 2000, Harshman and Zera 2007). Environments with fast-flowing water may increase intra- and inter-specific competition, leading to greater acquisition of food items and a better direct competitive performance by larger females. Meanwhile, slow-flowing environments seem to be more stable, with less competitive pressures and/or more resource availability, as egg number is independent of size, where all females produce a similar number of eggs and in a larger amount than those from fast-flowing environments. These results suggest that either local adaptation or phenotypic plasticity to distinct local water-velocity environments could be related to such divergence in *M. inpa* populations, where intraspecific competition may be more intense in one environment than in the other, then traits with fewer competitors present a greater fitness (Slatkin 1979, Abrams *et al.* 1993).

Habitat-independent fecundity selection was also evident for *M. amazonensis* populations, where larger females bore more eggs. A recent review updated this species status, where the previous genus (i.e. *Pseudopalaemon*) was considered a junior synonym of *Macrobrachium* (Mota *et al.* 2025). For all species from the previous *Pseudopalaemon* genus, females are larger than males. As fecundity selection usually favours species with larger females than males (Darwin 1874, Williams 1966, Calder 1984), the observed outcome was expected for such populations. For this species, variation in size-specific fecundity was consistent with selection associated with macrophyte and root proportions. Selection varied along the substrate gradient, but the fecundity-size relationship remained positive, although the slope varied significantly. Phenotypic variability can be affected by some adaptative processes, such as directional and stabilizing selection (Haller and Hendry 2014), and those depend greatly on environmental conditions. Streams with lower proportions of macrophytes and roots sustain larger individuals with more eggs, and that could be related to niche shifts in substrate use among individuals of different sizes or lower competition/predation risk in those environments. For this species, size-related niche partitioning has already been recorded, although sex-specific effects were not considered and reference was only made to changes in stream depth (Silva and Magnusson 2023). In our study location, streams vary largely in substrate composition and hydraulic features, and those often follow changes in habitat/food availability and in susceptibility to predation, which could affect size at sexual maturity and egg production (Blanckenhorn 2000, Dani and Kodandaramaiah 2017, Pantaleão *et al.* 2018, Paschoal and Zara 2020).

Palaemonidae shrimps usually display a direct effect of size on egg number (Tamburus *et al.* 2012, Bertini *et al.* 2013, Lima *et al.* 2014, Carnevali *et al.* 2016, De Oliveira *et al.* 2019), although average size, size at sexual maturity, and fecundity depend greatly on environmental variation (Mashiko 2000, Pantaleão *et al.* 2012, Pantaleão *et al.* 2018, Paschoal and Zara 2020). Both species tested here are common in non-seasonally-flooded streams in the Amazonia region. They complete their entire life cycle in freshwater environments, have advanced abbreviated larval development (i.e. larvae hatch at an advanced stage), and low fecundity, but with large yolk-rich eggs (Magalhães and Walker 1988, Magalhães and Medeiros 1998, Magalhães 2016). However, species vary mainly in average egg number and metamorphosis duration (Magalhães and Medeiros 1998, Magalhães 2016). The different patterns observed between the species may be related to distinct selection mechanisms acting on populations as well as ecological differences, since habitat-related niche partitioning (i.e. along water velocity and pH gradients) has already been recorded between these species for the same environments (Silva *et al.* 2020).

Fecundity selection originally implied the selection of fitness components that grant higher fecundity, usually expressed as a positive directional relationship (Darwin 1874). However, the expression of this type of selection depends mostly on natural selection through offspring viability (Pincheira-Donoso and Hunt 2017). Lack's (1947) and Williams' (1966) principles predict that fecundity is displayed as a stabilizing selection (i.e. intermediate traits being favoured), considering offspring viability and parental energy allocation, respectively. Habitat-dependent fecundity selection was expressed only as positive directional selection for *M. amazonensis* along the macrophytes and roots gradient and as divergent selection for *M. inpa* along the water-velocity gradient, and that possibly reflects differences in the species' ecological fitness, which is affected by a single trait in one species and by multiple traits in the other.

CONCLUSION

Our results highlight that phylogenetically related, and to a lesser extent, ecologically related (Silva *et al.* 2020, Silva and Magnusson 2023, Mota *et al.* 2025), tropical shrimp populations can display divergent natural selection to local environmental gradients for the fecundity-size relationship, which may be a result of local adaptation, plasticity to contrasting environments, or both. Although genetic processes were not tested here, effects of selection on different fitness traits caused by ecological variation could be sufficient to isolate local populations (Richardson *et al.* 2014), as ecological divergence usually implies genetic divergence (Nosil 2012). Habitat isolation is frequently cited as a major mechanism behind sympatric population divergence, once genotypes are habitat-specific, enabling local adaptation and possibly speciation (Rice 1984, Edelaar *et al.* 2008).

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AUTHOR CONTRIBUTIONS

Elmo Pereira da Silva (Conceptualization, Investigation, Data curation, Conducting the research, Methodology, Formal analysis, Data interpretation, Preparation of figures and tables, Funding acquisition, Writing—original draft preparation, Writing—review and editing), Pedro A.C.L. Pequeno (Conceptualization, Investigation, Data curation, Methodology, Formal analysis, Data interpretation, Writing—review and editing), William E. Magnusson (Methodology, Funding acquisition, Writing—review and editing).

SUPPORTING INFORMATION

Supplementary data is available at *Biological Journal of the Linnean Society* online.

CONFLICT OF INTEREST

The authors of this manuscript have no conflicts of interest to declare.

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DATA AVAILABILITY STATEMENT

The authors declare that the dataset used in this manuscript is not publicly available yet but is available from the corresponding author on reasonable request.

ETHICAL APPROVAL

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