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Causal relationships among the body-related and egg-related traits in crayfish: A case study on Turkish freshwater crayfish *Pontastacus leptodactylus* (Astacidae: Decapoda)

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Abstract

In this study, the direct and indirect causal relationships among the length, weight, egg diameter, egg weight, and egg quantity of female *Pontastacus leptodactylus* were analyzed using a path analysis. A total of 79 egg-bearing female crayfish with a total weight (WT; 39.1 ± 16 g) and total length (TL; 109.6 ± 18.1 mm), were sampled from Eğirdir Lake, Türkiye, in 2022 and 2023. Significant direct effects were observed several traits, such as crayfish length and weight, weight and egg diameter, length and egg quantity, egg diameter and egg quantity, weight and egg quantity, length and egg weight, and egg quantity and egg weight (p<0.05). These relationships indicate that larger females tend to produce a higher number of eggs and have greater overall reproductive potential. In contrast, no significant relationships were found between length and egg diameter, weight and egg weight, and egg diameter and egg weight (p>0.05), suggesting that body size may not directly influence egg size in this species. Regarding indirect effects, crayfish length was found to significantly influence egg weight through egg quantity (p<0.05). This suggests that larger females indirectly affect egg weight by producing more eggs. Although the direct effect of egg diameter on egg weight was not significant (p>0.05), its indirect effect of egg diameter on egg weight through egg quantity was significant (p<0.05), indicating that egg diameter plays a role in reproductive output through its influence on egg numbers. The findings of this study contribute to a better understanding of the direct and indirect causal relationships between growth-related traits and egg-related traits in freshwater crayfish. These insights can be utilized in sustainable fisheries management and aquaculture practices by informing selective breeding programs to enhance reproductive success or guiding conservation strategies that protect larger females in natural populations.

Keywords: Freshwater crayfish, Fecundity, Path analysis, Modelling, Morphometry

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1. Introduction

The number and size of eggs produced by crustaceans vary depending on factors such as reproductive period, temperature, photoperiod, age, nutrition, body size, body weight, molting, and claw loss (Pinheiro et al., 2003; Veríssimo et al., 2011; Mazlum & Eversole, 2005; Czerniejewski & de Giosa, 2013; Sheppard et al., 2024). Although egg productivity is generally proportional to body size (Hamasaki & Kawai, 2023), variations in egg size can also affect the number of eggs. For example, in crayfish, as in fish, larger females typically produce larger eggs (Mason, 1977). Penaeid shrimp can lay between 200,000 and 1,000,000 eggs, freshwater shrimp (*Macrobrachium rosenbergii*) can produce between 20,000 and 80,000 eggs, and lobsters (*Homarus* spp.) can produce between 5,000 and 80,000 eggs. Freshwater crayfish produce various numbers of eggs under natural and controlled conditions. For example, the cambarid crayfish species *Procambarus acutus acutus* produces 106-556 eggs (Eversole & Mazlum, 2002), *Procambarus zonangulus* produces 189-764 eggs (Eversole & Mazlum, 2002; Mazlum, 2003), *Procambarus clarkii* produces 100-700 eggs (Mazlum & Eversole, 2004), and *Orconectus* sp. produces approximately 500 eggs (Graczyk et al., 2019). Among astacid crayfish, *Austropotamobius pallipes* produces 20 eggs (Sáez-Royuela et al., 2006), while *Pontastacus leptodactylus* produces about 137-400 eggs (Köksal, 1988; Berber et al., 2006; Berber & Mazlum, 2009; Berber et al., 2011; Boyalik & Berber, 2020). Among parastacid crayfish, *Cherax quadricarinatus* can produce 150-600 eggs (Yeh & Rouse, 1994), *Cherax destructor* can produce 124-960 eggs, and *Cherax tenuimanus* can produce 200-600 eggs (Austin, 1998), reflecting the influence of reproductive season, temperature, age, and nutritional conditions.

The narrow-clawed crayfish, *Pontastacus leptodactylus*, is Türkiye's only native crayfish species, with increasing demand due to its high economic value and export potential (Mazlum et al., 2021; Alvanou et al., 2024). P. *leptodactylus,* whose reproductive cycle consists of specific stages (Mazlum & Yılmaz, 2006), mates in October-November when the water temperature is 7-12°C, and spawning occurs 4-6 weeks later when the temperature is 6-11°C. Therefore, the egg incubation period continues throughout winter and spring. *P. leptodactylus* can carry its eggs for 5-6 months in temperate climates and 6-7 months or more in colder climates. Under natural conditions, the development period of *P. leptodactylus* eggs can last 150-210 days or more (Aydın & Dilek, 2004; Köksal, 1988), and they reproduce only once a year (Köksal, 1988).

Egg productivity in crayfish is expressed in two ways: "Ovarian-eggs" represent the reproductive potential of crayfish, while "Pleopod-eggs" represent actual reproduction (Corey, 1987; Eversole & Mazlum, 2002; Eversole et al., 2002; Mazlum & Eversole, 2004; Berber & Mazlum, 2009). Pleopod-eggs, which indicate eggs laid by the crayfish, are influenced by many factors under natural conditions, resulting in significant variations in egg numbers among crayfish species (Corey, 1987; Eversole et al., 2002).

It is known that crayfish morphological characteristics are influenced by both genetic and environmental factors (Li et al., 2024). Therefore, individuals of the same species may exhibit phenotypic diversity depending on changing environmental conditions (Li et al., 2024). Morphometric relationships provide information on growth and reproductive potential characteristics of individuals in relation to environmental conditions (Hossain et al., 2019; Berber et al., 2020; Gören & Karayücel, 2022; Garabaghi et al., 2022; Benzer & Benzer, 2022; Gültepe et al., 2024; Boyalık et al., 2023; Alvanou et al., 2024; Roljić et al., 2024). For example, claws, an important morphometric structure used for survival, show variability rates of 38.67 and 66.74 in female and male individuals, respectively (Mazlum et al., 2007; Li et al., 2024). Additionally, larger claws in crayfish are advantageous during agonistic encounters, particularly for males during the mating season. In females, larger claws are beneficial for defending their eggs or rejecting unwanted male suitors during the breeding period (Bovbjerg, 1956; Buřič et al., 2010).

It is known that the relationship between morphometry and egg productivity varies depending on the species and habitats of crayfish (Hossain et al., 2019). This study aims to elucidate the causal relationships between body-related and egg-related traits of the *P. leptodactylus* population in Türkiye to support sustainable fishing policies, and aquaculture practices.

2. Material and Methods

2.1. Sampling

Seventy-nine egg-bearing female crayfish were collected from Eğirdir Lake, Türkiye, on May 9, 2022, and May 15, 2023, using fyke nets with a 16 mm mesh size. The crayfish had an average weight (WT) of 39.1 ± 16 g and a total length (TL) of 109.6 ± 18.1 mm. The crayfish were transported live and on ice in a styrofoam box by bus to the Faculty of Marine Sciences and Technology at Iskenderun Technical University. Measurements were conducted at the Marine Sciences Application and Research Unit.

2.2. Measurements and statistical analysis

It has been reported that crayfish length affects crayfish weight, egg diameter, egg number, and egg weight; crayfish weight affects egg diameter, egg weight, and egg number; egg diameter affects egg number and egg weight; and egg number affects egg weight (Berber, 2005; Hubenova et al., 2002; Eversole & Mazlum, 2002). Therefore, measurements of length, weight, egg diameter, egg weight, and egg number for the sampled female crayfish individuals were used in the study. The total length (TL) of female crayfish was measured to the nearest millimeter, and wet weight (WW) was measured to the nearest 0.01 g. Pleopod eggs were removed from each crayfish using watch markers forceps and counted. Egg subsamples (n=75) were removed from each ovigerous female, and egg diameters were measured with a dissection microscope equipped with a calibrated ocular micrometer. Egg weight was calculated from the mean weight of 75 eggs, weighed using a digital scale (0.0001 g) after wiping the eggs with a paper towel.

In the initial evaluation of these variables, significant correlations were found between the variables, supporting previous literature (Figure 1). Therefore, considering these relationships between variables, a path model was tested to evaluate both direct and indirect effects together (Figure 2).

Since the variables had different scales of measurement (Table 1), each variable was standardized using Z-transformation prior to performing the path analysis.

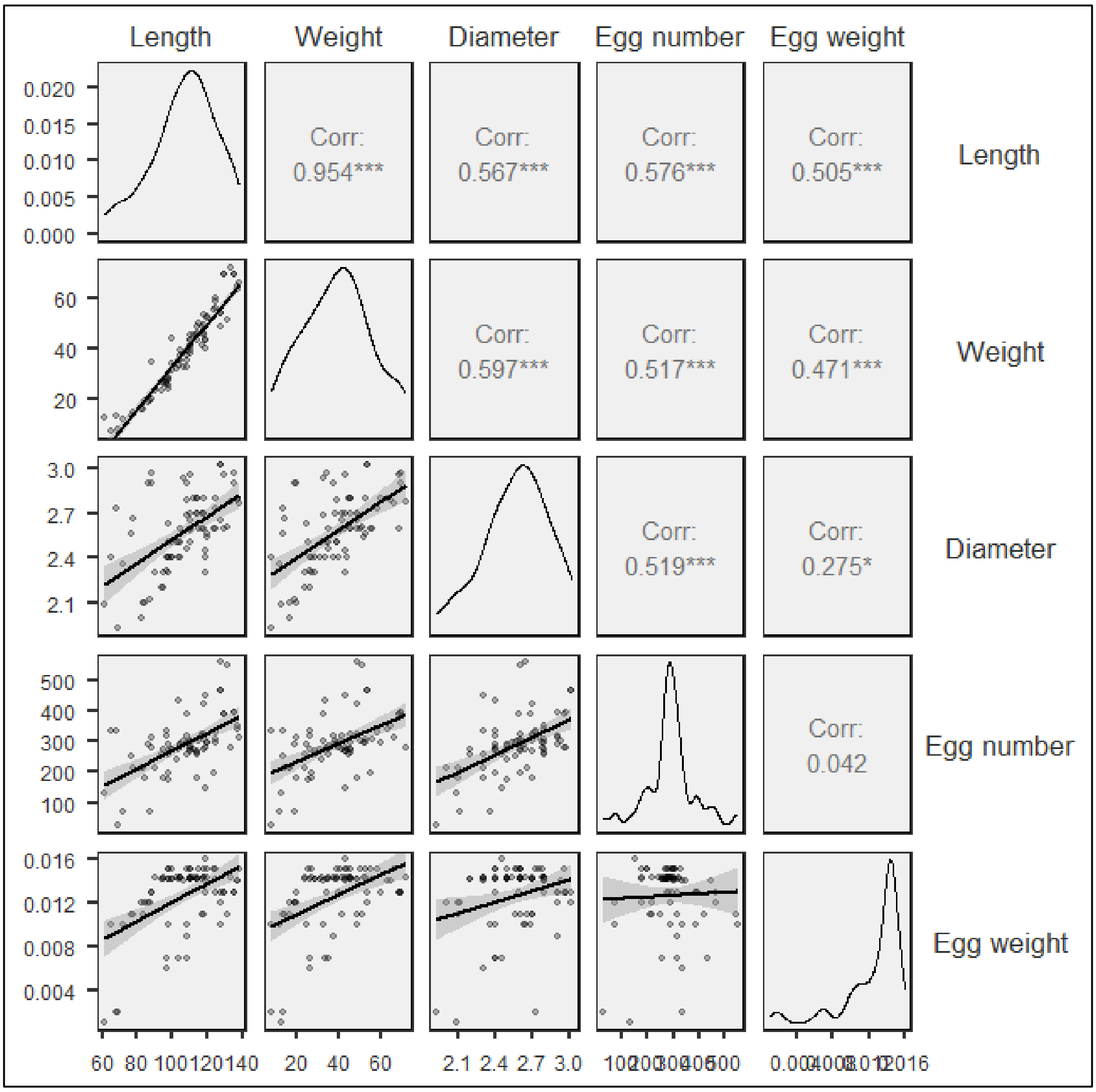

Figure 1. Linear relationships, correlations, and distributions of variables

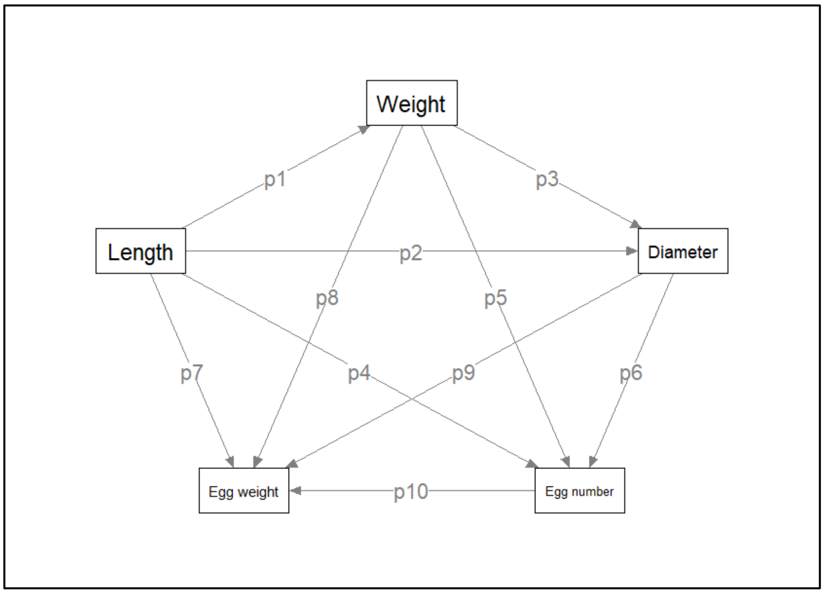

Figure 2. Path coefficients (parameters) in the tested conceptual model

Table 1. Descriptive statistics for the sampled 79 individuals

	Length (mm)	Weight (g)	Diameter (mm)	Egg number	Egg weight (mg)
N	79	79	79	79	79
Mean	107	39.1	2.58	290	0.0127
Median	110	39.7	2.60	289	0.0142
Standard deviation	18.1	16.0	0.250	90.8	0.00309
Minimum	61	7.70	1.93	27.0	0.00100
Maximum	138	71.9	3.02	556	0.0160

Path analysis provides an estimate of the significance and importance levels of hypothetical cause-effect relationships among a set of variables. Therefore, this analysis method is preferred in determining the direct, indirect, and total effects in causality among variables, especially when indirect relationships are significant (Rutherford & Choe, 1993; Webley, 1997; Sarwono, 2007).

In this study, five estimation methods were considered: "Maximum Likelihood," "Generalized Least Squares (GLS)," "Weighted Least Squares (WLS)," "Diagonally Weighted Least Squares (DWLS)," and "Unweighted Least Squares (ULS)." Among these, the Weighted Least Squares (WLS) method provided the best results in estimating the path analysis parameters.

As seen in the conceptual model (Figure 2), the hypotheses to be tested in the study in terms of direct and indirect effects are summarized as follows.

Direct Effects:
• The direct effect of body length on body weight (p1), egg diameter (p2), egg number (p4), and egg weight (p7).
• The direct effect of body weight on egg diameter (p3), egg number (p5), and egg weight (p8).
• The direct effect of egg diameter on egg number (p6) and egg weight (p9).
• The direct effect of egg number on egg weight (p10).

Indirect Effects:
The 11 hypotheses to be tested in terms of indirect effects are given in Table 2.

Statistical analyses were performed using the JAMOVI program, which utilizes the R ecosystem (R Core Team, 2022; The Jamovi Project, 2023).

Table 2. Hypotheses tested for indirect effects using path analysis

Hypothesis	Path	Parameter
Body length has an indirect effect on egg weight through body weight, egg diameter, and egg number.	Length ⇒ Weight ⇒ Egg Diameter ⇒ Egg Number ⇒ Egg Weight	p1*p3*p6*p10
Body length has an indirect effect on egg weight through body weight and egg diameter.	Length ⇒ Weight ⇒ Egg Diameter ⇒ Egg Weight	p1*p3*p9
Body length has an indirect effect on egg weight through body weight and egg number.	Length ⇒ Weight ⇒ Egg Number ⇒ Egg Weight	p1*p5*p10
Body length has an indirect effect on egg weight through body weight.	Length ⇒ Weight ⇒ Egg Weight	p1*p8
Body length has an indirect effect on egg weight through egg diameter and egg number.	Length ⇒ Egg Diameter ⇒ Egg Number ⇒ Egg Weight	p2*p6*p10
Body length has an indirect effect on egg weight through egg diameter.	Length ⇒ Egg Diameter ⇒ Egg Weight	p2*p9
Body length has an indirect effect on egg weight through egg number.	Length ⇒ Egg Number ⇒ Egg Weight	p4*p10
Body weight has an indirect effect on egg weight through egg diameter and egg number.	Weight ⇒ Egg Diameter ⇒ Egg Number ⇒ Egg Weight	p3*p6*p10
Body weight has an indirect effect on egg weight through egg diameter.	Weight ⇒ Egg Diameter ⇒ Egg Weight	p3*p9
Body weight has an indirect effect on egg weight through egg number.	Weight ⇒ Egg Number ⇒ Egg Weight	p5*p10
Egg diameter has an indirect effect on egg weight through egg number.	Egg Diameter ⇒ Egg Number ⇒ Egg Weight	p6*p10

3. Results

It was determined that the conceptual model tested was significant as a whole (Chi-square = 303, df = 10, $p<0.001$) and that all endogenous variables in the model were also significant for the model ($p<0.05$) (Table 3). Accordingly, the most important exogenous variables in the model were, in order, weight, number of eggs, egg weight, and egg diameter. Results for direct and indirect effects are provided in Figure 3, Table 4, and Table 5.

Table 4 shows that the relationships between length-weight (β=0.95), weight-egg diameter (β=0.63), length-number of eggs (β=0.94), egg diameter-number of eggs (β=0.33), weight-number of eggs (β=-0.57), length-egg weight (β=1.04), and number of eggs-egg weight (β=-0.42) are significant ($p<0.05$), while the relationships between length-egg diameter (β=-0.04), weight-egg weight (β=-0.38), and egg diameter-egg weight (β=0.14) were not significant ($p>0.05$).

From the tested path model, it is observed that the dependent variable for all variables was egg weight. Among the independent variables with respect to egg weight, it is seen that the variable with the greatest impact on egg weight was the length of the organism. An increase of one unit in the organism's length increases the egg weight by 1.0378 units, while a one-unit increase in the number of eggs decreases the egg weight by -0.4228 units (Table 4). It was interesting that the effects of organism weight and egg diameter on egg weight were not significant ($p>0.05$).

Regarding indirect effects (Table 5), the effect of crayfish length on egg weight through the number of eggs was significant (p4*p10, $p<0.05$). Although the effect of egg diameter on egg weight was not significant ($p>0.05$, Table 4), the effect of egg diameter on egg weight through the number of eggs was significant (p6*p10, $p<0.05$).

Table 3. Some statistics and significance levels for the dependent variables

Variable	R^2	95% Confidence Intervals		Wald X^2	df	p
		Lower	Upper			
Weight	0.910	0.862	0.942	797.6	1	< 0.001
Egg Diameter	0.353	0.184	0.519	43.1	2	< 0.001
Egg Number	0.414	0.242	0.573	55.8	3	< 0.001
Egg Weight	0.368	0.198	0.532	46.0	4	< 0.001

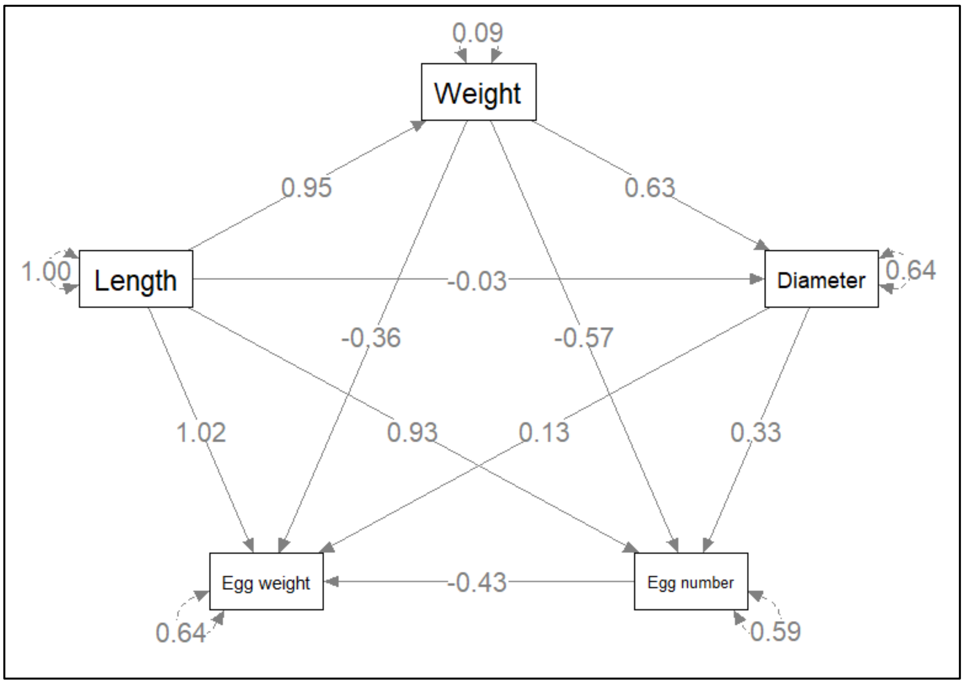

Figure 3. Regression coefficients (β) for causal relationships between variables (direct effects) and variance estimates for the variables

Table 4. Path analysis results for direct effects

Dependent	Independent	Estimate	SE	Z	*p*
Weight	Length	0.9539	0.0338	28.242	< 0.001
Egg Diameter	Length	-0.0358	0.3015	-0.119	0.906
Egg Diameter	Weight	0.6280	0.3015	2.083	0.037
Egg Number	Length	0.9364	0.2869	3.263	0.001
Egg Number	Weight	-0.5713	0.2947	-1.939	0.053
Egg Number	Egg Diameter	0.3283	0.1071	3.066	0.002
Egg Weight	Length	1.0378	0.3175	3.269	0.001
Egg Weight	Weight	-0.3812	0.3133	-1.217	0.224
Egg Weight	Egg Diameter	0.1432	0.1176	1.218	0.223
Egg Weight	Egg Number	-0.4228	0.1169	-3.618	< 0.001

Table 5. Path analysis results for indirect effects

Path	Parameter	Estimate	SE	Z	*p*
Length ⇒ Weight ⇒ Egg Diameter ⇒ Egg Number ⇒ Egg Weight	p1*p3*p6*p10	-0.083	0.054	-1.553	0.120
Length ⇒ Weight ⇒ Egg Diameter ⇒ Egg Weight	p1*p3*p9	0.086	0.082	1.050	0.294
Length ⇒ Weight ⇒ Egg Number ⇒ Egg Weight	p1*p5*p10	0.230	0.135	1.706	0.088
Length ⇒ Weight ⇒ Egg Weight	p1*p8	-0.364	0.299	-1.216	0.224
Length ⇒ Egg Diameter ⇒ Egg Number ⇒ Egg Weight	p2*p6*p10	0.005	0.042	0.118	0.906
Length ⇒ Egg Diameter ⇒ Egg Weight	p2*p9	-0.005	0.043	-0.118	0.906
Length ⇒ Egg Number ⇒ Egg Weight	p4*p10	-0.396	0.163	-2.423	0.015
Weight ⇒ Egg Diameter ⇒ Egg Number ⇒ Egg Weight	p3*p6*p10	-0.087	0.056	-1.556	0.120
Weight ⇒ Egg Diameter ⇒ Egg Weight	p3*p9	0.090	0.086	1.051	0.293
Weight ⇒ Egg Number ⇒ Egg Weight	p5*p10	0.242	0.141	1.709	0.087
Egg Diameter ⇒ Egg Number ⇒ Egg Weight	p6*p10	-0.139	0.059	-2.339	0.019

4. Discussion

Despite the negative correlations predicted between live weight and both egg weight and egg number, these relationships were not statistically significant ($p>0.05$). Similar results have been reported in previous studies, where a negative correlation between total egg number and average egg weight was observed (Berber & Mazlum, 2009; Gören et al., 2019; Cilbiz, 2020). It has been reported that females of the same size might show differences in developmental stages due to slowing or stopping growth rate at later ontogenetic stages, which could affect egg number (Longshaw & Stebbing, 2016; Hamasaki et al., 2022). However, a significant positive correlation was found between live weight and egg diameter ($p<0.05$), highlighting that egg diameter (size) affects both the condition and survival rates of the offspring (Huner, & Lindqvist, 2020). The relationship between egg size and female weight reflects the effects of energy allocation (Eversole & Mazlum, 2002; Bernardo, 1996). Larger eggs contain more yolk and have longer incubation period, as larger females tend to invest more energy into reproduction rather than growth (Mazlum & Eversole, 2004; Mazlum & Eversole, 2005; Rey et al., 2017). Conversely, no significant relationship was found between body size and egg diameter ($p>0.05$). A study by Mazlum & Eversole (2004) on *Procambarus clarkii* reported that smaller females had lower fecundity (200 eggs/female) compared to larger females (700 eggs/female) with a positive linear correlation between egg number and total length. This differs from our findings, as we observed significant positive relationships between size and both egg number and egg weight ($p<0.05$). As body size increases, both individual egg weight and total egg number rise. However, despite a positive relationship between the body size and weight, the relationships between egg diameter, egg number, and egg weight differ (Table 4). This likely reflects significant variability in live weight among organisms of the same age (Berber & Mazlum, 2009), suggesting that body size is a more reliable criterion than weight in breeding, cultivation, and stock management studies. Genetic structure and biotic/abiotic factors also play a role (Skurdal et al., 2011), as crayfish in warmer climates reach sexual maturity earlier than those in colder climates. Genetic structure leads to greater egg production in larger and older crayfish compared to younger ones. A positive relationship between crayfish size and egg number has been reported in many crayfish species (Yeh & Rouse, 1994; Reynolds, 2002; Cilbiz, 2020). In our study, we found a significant positive correlation between egg diameter and egg number ($p<0.05$); however, egg diameter had no significant effect on egg weight($p>0.05$). Notably, as egg number increased, individual egg weight decreased significantly ($p<0.05$), suggesting a trade-off between the number of eggs and the resources allocated to each egg (Table 4). This negative relationship likely reflects energy limitations, where a greater number of eggs results in smaller energy reserves for each individual egg.

In terms of indirect effects, the effect of crayfish size on egg weight through egg number (p4*p10: -0.396) was found to be significant ($p<0.05$) (Table 5). The direct effect of crayfish size on egg weight was also significant and positive (1.0378), while the direct effect of egg number on egg weight was significant but negative (-0.4228). Considering the coefficients of direct effects, a one-unit increase in crayfish size leads to a 1.0378-unit increase in egg weight, while a one-unit increase in egg number reduces egg weight by 0.4228 units. When considering the coefficient of the indirect effect (p4*p10: -0.396), it is observed that egg number has a greater impact on egg weight than crayfish size itself. This suggests that an increase in the number of eggs leads to smaller individual egg weights due to energy trade-offs. It is known that genetic structure and biotic and abiotic factors in the ecosystem also affect these relationships (Cilbiz, 2021; Skurdal et al., 2011). A positive relationship between crayfish size and egg number has been reported in many crayfish species (Reynolds, 2002; Cilbiz, 2020).

Regarding egg productivity, previous studies have shown that *P. leptodactylus* produces different numbers of eggs across different populations. For example, the average egg production per female is reported as 211 eggs in Lake Eğirdir (Köksal, 1988), 240 eggs in Lake İznik (Aydın et al., 2015), and 276 eggs on the northern coast of the Caspian Sea (Kolmykov, 2001). In the Divzak Lake population in Poland, egg production ranges from 210 to 410 eggs, while in the Mazurian Lake population, the average is 374 eggs (Stypinskaya, 1978). Similarly, females in lakes in Norway, Finland, and Lithuania produce 204, 210, and 139 eggs, respectively (Karimpour & Taghavi, 2002). These differences in egg productivity can be attributed to variations in genotypes, environmental conditions, and food availability across the different various *P. leptodactylus* populations (Mirheydari et al., 2013; Gitau et al., 2024). Genetic factors can influence reproductive traits, with larger and older crayfish typically producing more eggs. Environmental conditions, such as water temperature and food availability, also play a key role, with warmer climates and richer food sources potentially leading to higher egg production.

The effect of egg number also shows itself in the indirect effect, where the direct effect of crayfish egg diameter on egg weight (0.1432) is not significant ($p>0.05$), but the effect of egg diameter on egg weight through egg number (p6*p10) is negative and significant ($p<0.05$). It is thought that as egg number increases, egg diameters decrease and smaller females mating with large males produce more eggs. Similar results have been found in (*Astacus astacus*) (Abrahamsson, 1971), *A. leptodactylus* (Berber & Mazlum, 2009), and signal crayfish (*Pacifastacus leniusculus*) (Math et al., 2004). Additionally, besides crayfish size, food availability in the environment affects crayfish productivity. A similar explanation was proposed by Matthews & Reynolds (1992) for *Austropotamobius pallipes*. Crayfish require food and optimal temperatures for rapid growth of offspring. Increased fecundity also depends on food and temperature parameters (Momot, 1984). For long-lived species with low fecundity (*Pacifastacus*, *Austropotamobius*, and *Astacus* species) living in low-energy and low-nutrient environments, it is suggested to form larger adult populations and to eutrophize the environment to increase fecundity (Eversole & Mazlum, 2002). Short-lived species or those with short hatching times (*Cherax*) show high fecundity (Morrissy, 1975), while some species reproduce almost continuously (*Procambarus*) (Huner, 1978). *Cherax* and *Procambarus* exhibit the highest numbers in terms of production, biomass, and yield per unit area (Morrissy, 1980; Huner & Romaire, 1981; Huner, 1978). Variations in average yields of crayfish in high-nutrient, high-energy environments show about five times the fluctuation compared to the approximately two-fold variation observed for *Orconectes virilis* in low-nutrient, low-energy environments (Momot, 1984).

With increasing egg number, egg diameters decrease. In crayfish, eggs are attached to the mother's pleopods throughout the development period and hatching occurs there. Mazlum & Eversole (2004) noted that some crayfish (*Procambarus acutus acutus*) do not release all their eggs but keep them in the ovary within the body. Some crayfish have also been found to have eggs in their stomachs. Previous studies have shown that smaller-sized females mating with large males produce more eggs (Galeotti et al., 2006). This situation suggests that larger crayfish will emerge from larger eggs and will provide an advantage in the population. It has been reported that the adaptation period and natural habitat of crayfish can affect egg productivity (Gören et al., 2019).

5. Conclusion

In conclusion, for the species *P. leptodactylus*, size of the crayfish appears to be the most important factor affecting both directly and indirectly egg number and egg weight for aquaculture, breeding, and sustainable fishing management.

Conflict of interest

The authors declare that they have no known competing financial or non-financial, professional, or personal conflicts that could have appeared to influence the work reported in this paper.

Ethical Approval

The paper is not currently being considered for publication elsewhere, and it reflects the author's' own research and analysis in a truthful and complete manner.

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