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RESEARCH

Seasonal shape variations, ontogenetic shape changes, and sexual dimorphism in a population of land isopod *Porcellionides pruinosus*: a geometric morphometric study

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Abstract

Background: Isopods shape features are sensitive and respond to several selective pressures which may result in variations of these features. These pressures might reflect the heterogeneity of the environment where an animal lives. Land isopods *Porcellionides pruinosus* were collected from an agricultural field. Landmarks geometric morphometrics was applied to evaluate its shape changes during two different seasons. The present work aims to (i) assess and characterize morphological changes in body shape of *P. pruinosus* as a response to seasonal variations, (ii) determine differences in the body shape during ontogeny, (iii) examine the effect of intraspecific allometry to interpret the observed variations in the species, and (iv) clarify whether the body shape of *P. pruinosus* can be used as a sexual differentiating trait.

Results: Juveniles showed no seasonal variations in the body shape, which were detected among adults, females and males as shown by PCA, DFA, and MANOVA.

The adult winter forms have large bodies, small heads, broad pereons, and short but wide telsons. The adult summer forms have small slender bodies, slightly stretched heads, and relatively long telsons. Juveniles' growth to adulthood showed body shape changes in the head and pereon, that include shrank of the head in the anteroposterior direction and its level became slightly lower than the body. The pereon becomes broader and the two anterolateral projections of the first pereonite extend anteriorly, reaching a little beyond the posterior margin of the eyes. Present species showed a shape sexual dimorphism which includes the broader body and more convex pereon in females and a small waist between the second and third pleonites in males. Shape sexual dimorphism was attributed to reproductive activity. Both allometric trajectories of juveniles and adults (ontogenetic allometry) and of sexes (static allometry) were parallel.

Conclusions: The landmark geometric morphometric technique was able to reveal the seasonal shape variations in terrestrial isopod *P. pruinosus*. Also, this method provides information about shape variations between juveniles and adults, as well as about shape sexual dimorphism.

Keywords: Isopoda, Body shape variations, Geometric morphometric, Seasonal effects, Ontogeny, Sexual dimorphism

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Background

Body shape plays a critical role in the life of terrestrial isopods by affecting some traits as locomotion, feeding, reproduction, and facing challenges of desiccation, respiration, and risk of predation, consequently, affecting their abundance and vertical distribution (Baliga & Mehta, 2016; Broly, Devigne, & Deneubourg, 2015; Csonka, Halasy, Buczko, & Hornung, 2018; Dias et al., 2013; Hornung, 2011). Furthermore, morphology still has an essential role in their taxonomy.

Heterogeneity of the environment, where an animal lives, results in selective pressures that lead to some phenotypic differences among individuals of the same species (Fusco & Minelli, 2010; Kawecki & Ebert, 2004). Phenotypic differences may appear as a result of direct interaction between the organism's genetic structure and the environment where it lives, as well as in sometimes, with the lagged components that come indirectly from the environmental effects on its parents and transmitted to the offspring (Hepp, Fornel, Restello, Trevisan, & Santos, 2012; Rieseberg, Widmer, Arntz, & Burke, 2002). Thus, morphological variations may rely on phenotypic response to the selective environmental pressures functioning on populations and give a better chance for individuals' adaptations to their environment (Ismail, 2018; Klingenberg, Duttke, Whelan, & Kim, 2012). Phenotypic differences act during ontogenetic development (occurred by differentiation of certain tagmata during growth from juvenile to adult stage) (Hartnoll, 2001; Shreeves & Field, 2008) or in adults which is a major focus of evolutionary ecology (Moczek, 2010; Monaghan, 2008).

The association of the shape change of a particular part of an organism's body with the body size change is known as morphological allometry. Allometry may account for part of the morphological variability found between sexes or among all individuals. There are three types of allometry, namely, ontogenetic allometry (changes in the shape associated with size change during development), static allometry (covariation between size and shape at the same developmental stage of the same population), and evolutionary allometry (covariation between size and shape across populations) (Klingenberg et al., 2012; Pélabon et al., 2013). In isopods, the growing from juveniles to adult stage revealed changes in size and shape producing specific patterns of ontogenetic allometry (Dangerfield & Telford, 1990; Diawol, Giri, & Collins, 2015; Klingenberg, 2016; Montesanto, Pizzo, Caruso, & Lombardo, 2012).

Shape and size sexual dimorphism present among many animals due to reproductive selective pressures on females and males (Eberhard, 2009). It includes characteristics other than the differences in the sexual organs as secondary sexual characteristics, size, shape, color, and sexual and foraging behavior. In some animals, reproductive success is linked to one or more of those characteristics. Shape sexual dimorphism is important for many animals because different body parts can do multiple functions and subject to distinct selective mechanisms (Berns, 2013).

In some crustacean, the shape of body parts that related to reproduction as the carapace, chelipeds, gnathopods, oostegites, and antennae (Briffa & Dallaway, 2007; Rufino, Abelló, & Yule, 2004; Tsoi & Chu, 2005; Wada, Yasuda, & McLay, 2014) showed evident morphological differentiation which attributed to varied reproductive roles and investments of females and males. Therefore, the shape of these body parts may subject to differential selection between the sexes and use to produce more offspring (Eberhard, 2009). On the other hand, in other crustaceans, these secondary sexual traits being subtle and required quantitative analyses based on comparative morphometric techniques as in relative growth (Bertin, David, Cézilly, & Alibert, 2002; Hartnoll, 2001; Moraes et al., 2018). Geometric morphometrics approach is applied in the quantitative analysis of shape variation and sexual dimorphism (Idaszkin, Márquez, & Nocera, 2013; Trevisan, Marochi, Costa, Santos, & Masunari, 2012). Its importance lies in obtaining geometric information of an object under study and preserving it throughout the analysis (Bookstein, 1997). It is a suitable tool for discriminating shapes within a population and hence detecting unclear morphological variations (Zelditch, Swiderski, & Sheets, 2012).

Porcellionides pruinosus (Brandt, 1833) is a widely distributed terrestrial isopod (Lefebvre & Marcadé, 2005) and found above ground hiding under stones, decayed leaves, and logs; the two latter items utilized as food and shelter. *Porcellionides pruinosus* individuals produce two or more generations per year (Achouri, Charfi-Cheikhrouha, & Marques, 2002) and have limited dispersal abilities; therefore, they may respond to environmental changes behaviourally (Morgado, Ferreira, Cardoso, Soares, & Loureiro, 2015) or morphologically (Csonka et al., 2018). Phenotypic reproductive variations have been reported among some population of this species (Achouri & Charfi-Cheikhrouha, 2005) and considered to be forms of resistance to the environmental conditions (Vandel, 1962). In the same context, several examples of environmental influence on the phenotype of *P. pruinosus* and other isopods were reported (Dangerfield & Telford, 1990; Eroukhmanoff & Svensson, 2009; Winkler & Wallin, 1987); however, none of these studies used geometric morphometrics.

In the present study, the landmark geometric morphometrics approach was used to provided information on the geometry of *P. pruinosus* shape that can aid in understanding its shape variations which may reflect the developmental plasticity of individuals to produce the necessary phenotype that adapts with the environment to avoid the selective pressures against them and to increase their fitness (Conde-Padín, Grahame, & Rolán-Alvarez, 2007; Herrel, Joachim, Vanhooydonck, & Irschick, 2006; Loy, Mariani, Bertelletti, & Tunesi, 1998; Nettle & Bateson, 2015; Yusseppone et al., 2018).

Therefore, the present work aims to (i) assess and characterize morphological changes in body shape of *Porcellionides pruinosus* as a response to seasonal variations, (ii) determine differences in the body shape during ontogeny, (iii) examine the effect of intraspecific allometry to interpret the observed variations in the species, and (iv) clarify whether the body shape of *P. pruinosus* can be used as a sexual differentiating trait (i.e., sexually dimorphic trait).

Methods

Site of collection and sampling

Sohag is one of the Upper Egypt governorates, characterized by a desert climate and the year showed two distinct periods: a cool winter (November to April) and a hot summer (May to October) (Ouda & Zohry, 2016). During this work, the winter averages of the temperature and relative humidity were 20 °C and 32% (maxima were 24 °C and 36%), while those in summer were 37 °C and 47% (maxima were 51 °C and 59%) (obtained from Shandaweel Agricultural Research Station, Sohag).

Individuals of land isopods *Porcellionides pruinosus* were collected from an agricultural field (specimens were collected with a permission from the owner) situated about 6.86 km south of Sohag City, Egypt (26° 31′ 20″ N; 31° 43′ 52′′ E) (Fig. 1). Sampling was carried out on two different occasions: during winter (January) and summer (July) 2018. The agricultural field is surrounded by a few willow trees (*Salix safsaf*), where their canopies create significant shading, reducing the amount of sunlight, and thus aiding in the presence of many macroinvertebrates including isopods. The present isopod specimens were collected from areas around the willow trees to avoid the effects of crop rotation, soil tillage, and the use of agricultural pesticides, leaving the effect of seasonal changes on isopod body shape variation to be the prominent effect (Souty-Grosset & Faberi, 2018).

Isopod specimens were sampled by two methods; first, specimens were hand collected from fallen and decayed leaves, logs, and under stones that were located around willow trees. Second, from the same places, soil samples were taken using a soil core sampler (8 cm diameter) that inserted to a depth of 5 cm in the soil. All samples were kept in plastic containers.

In the laboratory, specimens were sorted from the leaf litter under a stereomicroscope and sexed based on the presence of gonopores (on the 6th thoracic segment) and oostegites for females, and gonopores (on the 8th thoracic segment), and copulatory pleopods for males. If

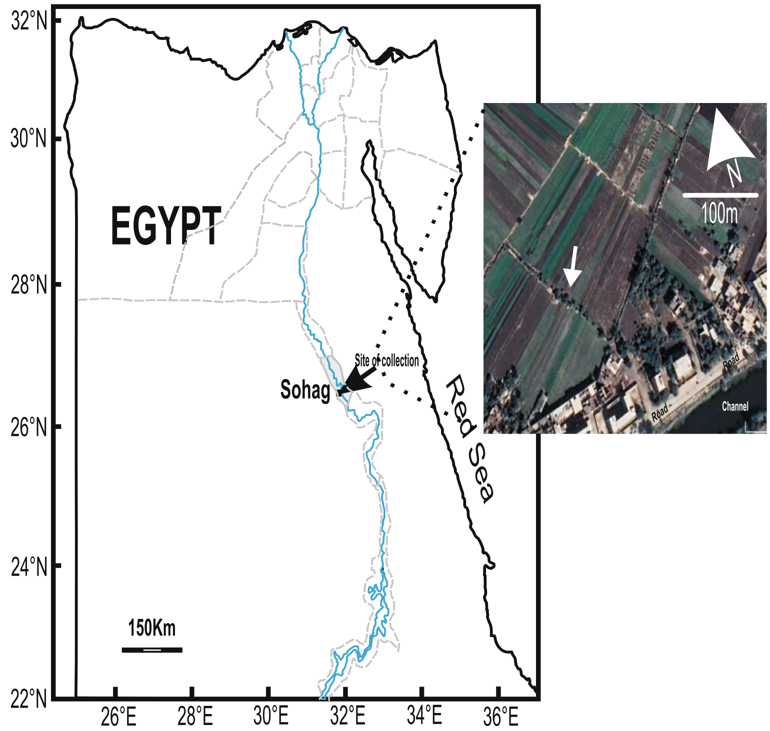

Fig. 1 Map of Egypt showing the location of Sohag Governorate and site of collection. To the right a Google earth map showing the agricultural field and willow trees (arrow), where the specimens were collected

these structures were not observed, the specimens were considered juveniles. The study species were identified according to the guidelines of Shultz (2018).

A total of 216 individuals were chosen for the analysis, of which 91 were non-ovigerous females (38 in winter and 53 in summer), 73 males (33 in winter and 40 in summer), and 52 juveniles (26 in winter and 26 in summer). The minimum, maximum, and mean ± standard deviation of the total body length ranged between 4.42 and 11.10 mm (6.12 ± 1.43) for females, 4.47 and 13.88 mm (6.49 ± 2.04) for males, and 1.24 and 3.27 mm (2.27 ± 0.39) for juveniles. The cuticle of juveniles often had a white appearance, while that of adults was dark-brown. Herein, the specimens captured in winter will be named winter forms, while those captured in summer will be named summer forms.

Geomorphic morphometric analysis

Data acquisition

Digital images for the dorsal view of the whole undamaged individuals were taken using a Canon digital camera (power shot A590) attached to a binocular zoom stereo microscope. Before images were captured, all pereopods and pleopods had been removed, then, specimens were fixed between two slides to ensure that specimens were laid flat and avoid any bending in segments. Thirty-three anatomical landmarks, describing the left half-body of the isopod (to avoid redundancy in information), were digitized on each individual using the tpsDig. 2.22 software (Rohlf, 2015). The used landmarks were 1-5 for cephalothorax, 6-21 for pereon, and 22-33 for pleotelson (Fig. 2).

Two datasets were analyzed to cover the aims of the present investigation. The first dataset included landmark coordinates of juveniles and adults (containing both females and males) and referred to as “age.” The second dataset included landmark coordinates of females and males and referred to as “sex.” Both datasets were further divided into winter and summer individuals.

Image and digitizing errors were assessed by the author for a subsample of 60 randomly selected specimens (20 for each of females, males, and juveniles) on three different sessions. Each specimen was photographed twice, and each photo was digitized twice.

Size analysis

The configuration size was represented by the centroid size (CS). In geometric morphometrics, the centroid size (the square root of the sum of the squared distances between each landmark and body centroid) is generally used as the measure of the overall size of an object and its importance comes from its mathematical independence from the shape (Zelditch et al., 2012).

In the present work, CS was log-transformed to avoid any deviation from linearity and to scale all values in the comparisons (Bookstein, 1997). Seasonal variations in the size of adults and juveniles as well as between sexes were investigated using one-way ANOVA.

Shape analysis

Landmarks of all the specimens of each dataset were entered into a generalized Procrustes analysis (GPA). GPA superimposes all configurations to remove variations (non-shape effects) of orientation, scale, and location and compute the Procrustes average shape. This was followed by checking outliers’ mistakes in the landmarking and correcting them. After removing non-shape effects, only geometric information of shape remained and are known as shape variables (shape effects).

Principal Components Analysis (PCA) and Discriminant Function Analysis (DFA) were used to explore the shape variations between the two seasons for age and sex datasets. PCA was performed on a variance-covariance matrix of the two datasets to reduce data and produce new shape variables (PC scores) that allowed exploration of the relative relationships between individual shapes. DFA was applied to maximize separation between seasons for age group and between sexes (shape sexual dimorphism). DFA displayed the accuracy of age and sex classification using Mahalanobis distances in conjunction with a permutation test (10,000 randomizations). The results of the classification were cross-validated using the Jackknife method to test the success of assigning the specimens to their groups.

A multivariate analysis of variance (MANOVA) was performed on PC scores of each dataset to determine whether there were differences in isopod body shapes between seasons, as well as between sexes. PC cores that explained more than 90% of the total variance were used as dependent variables, while seasons and sexes were used as the independent variables.

Allometric trajectories

Allometric trajectories were examined for the two datasets (age and sex) for analyzing ontogenetic and static allometries. Thus, multivariate regression analyses of shape (using Procrustes coordinates as the dependent variables) on size (using log centroid size as the independent variable was performed (Klingenberg, 2011)). The independence between shape and size was examined using the permutation test with 10,000 runs (Good, 2000; Klingenberg, 2011). Then, a multivariate analysis of covariance (MANCOVA) was used to compare allometric trends among datasets (age and sex) using the TPSRegI 1.45 software (Rohlf, 2016). The slopes of allometric trends were compared using the test for common slopes that determined the significance of “age X size” and “sex X size” interaction (Roggero, Giachino, & Palestrini, 2013). Significance of this interaction implies that allometric trends among two datasets have different

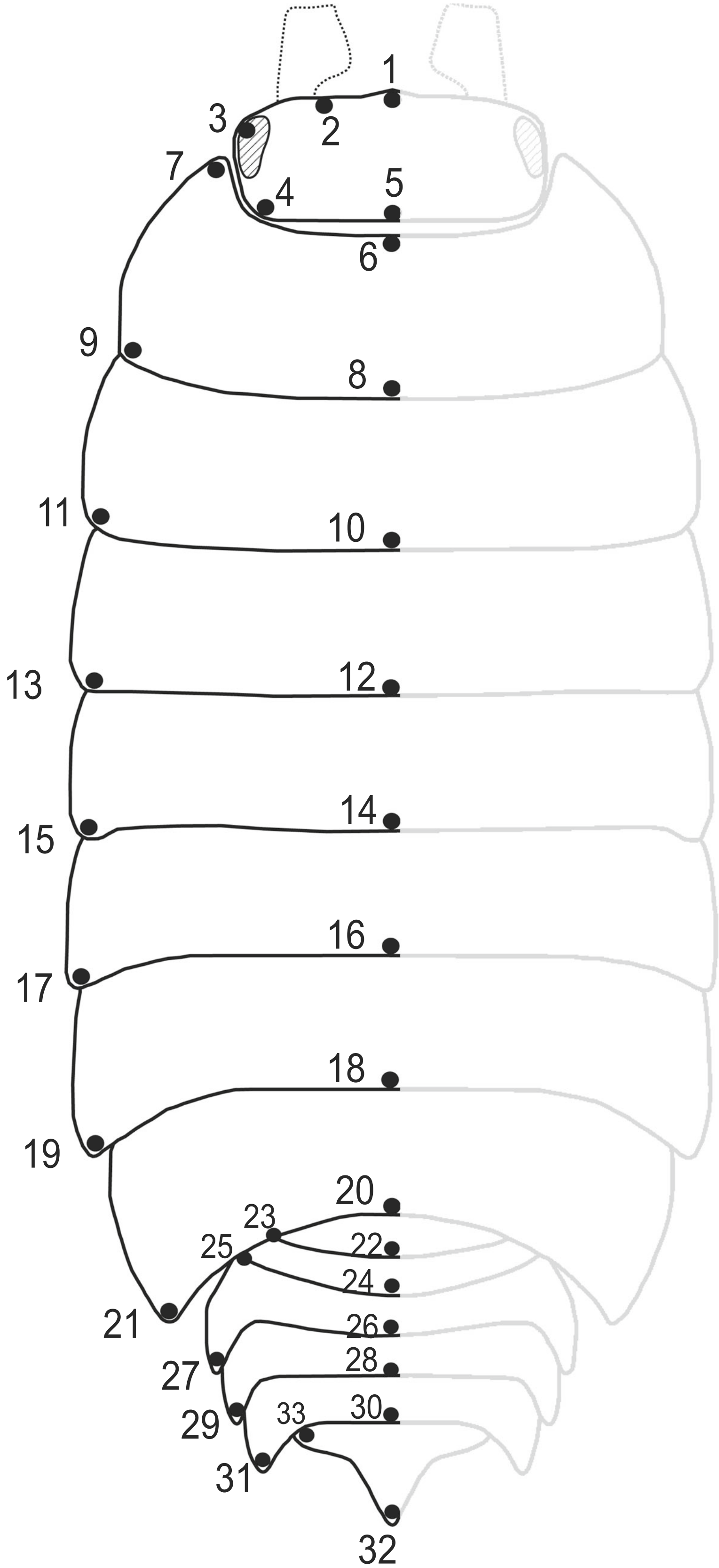

Fig. 2 (See legend on next page.)

(See figure on previous page.)
Fig. 2 Diagrammatic drawing of the dorsal view of *P. pruinosus* showing the location of 33 morphological landmarks on the left-body half, which used in the geometric morphometric analysis

directions (not parallel). In the case of insignificant interaction, a second multivariate analysis was performed after removing the interaction (i.e., controlling the effect of allometry). Significance of the variables (age or sex) means that age and/or sex have parallel allometric trajectories (same slopes) and share a common allometric trajectory which may explain size-related shape differences (Cardini & Thorington Jr, 2006). Also, angles between regression vectors of juveniles and adults and between sexes were compared. Sexual dimorphism was illustrated as the difference between the average half-body shape of females and males.

The statistical analyses were performed using the PAST (V. 3.26) software (Hammer, Harper, & Ryan, 2001) and the SPSS software (IBM Corp, N, 2013), while other geometric morphometric analyses (GPA, outlier detection, Procrustes ANOVA, PCA, DFA, and multivariate regression analysis) were performed with the help of MorphoJ integrated package (V. 1.07a) (Klingenberg, 2011). The Corel Draw software was used to redraw figures for the better visualization.

Results

Measurement errors

The results of Procrustes ANOVA showed that photographing and digitizing measurement errors led to small and negligible shape variation (0.89%), compared with individual variations (99.11%) (Table 1).

Seasonal size variations

The present data showed that the winter and summer forms of juveniles, adults, females, and males were differed significantly in means of log CS, reflecting seasonal variations in their body size (juveniles, ANOVA, $F_{1,51} = 4.78$, $P = 0.03$; adults, ANOVA, $F_{1,163} = 24.31$, $P < 0.0001$; females, ANOVA, $F_{1,90} = 13.7$, $P = 0.001$; males, ANOVA, $F = {}_{1,72}12.4$, $P = 0.001$) (Additional file 1: Fig. A1).

Effect of seasonal variations on body shape

PCA of the dataset "age" showed that the first two PC axes explained 50.62% of the total variation (Additional file 3: Table A1, Fig. 3). The analysis showed an overlap among individuals of two seasons for each of juveniles and adults. MANOVA and DFA analyses demonstrated that the average body shape for the winter individuals did not differ from that of the summer individuals for juveniles, but differed for adults (Table 2, Fig. 4a, b). Based on the body shape, DFA correctly classified 100% of juveniles and 87.2% of adults to the correct season. This percentage dropped after cross-validation analysis to become 57.5% and 70.1% for juveniles and adults, respectively (Additional file 4: Table A2).

Figure 4b illustrates the seasonal shape differences of adults. These differences were contraction of side landmarks at the head region (landmarks 3, 4) and widening of landmarks around the pereon region for winter forms. Compared with summer forms, the first three pleonites were broader, while telson was slightly shorter and narrower in winter forms. The posterior margin of the last pereonite of the summer forms was somewhat longer and more concave compared with the winter forms.

As for the females' and males' seasonal variations, both follow the same trajectory of the adults, i.e., females and males of the winter season were significantly varied in their shape from summer ones (Table 2).

Ontogenetic trajectories

The multivariate regression analysis showed a significant effect for size on the shape revealing ontogenetic allometry. The variance explained by the two MANCOVA models ranged from 13.6% (separate lines; Wilks'λ = 0.01, $F_{62,153} = 3.9$, $P = 3.28 \times 10^{-40}$; Goodall's F test = 6.6, df = 310,13020, $P < 0.0001$) to 13.0% (single line; Wilks'λ = 0.03, $F_{62,153} = 5.51$, $P = 6.67 \times 10^{-50}$; Goodall's F test = 10.34, df = 186, 13144, $P < 0.0001$).

The interaction between age dataset (juveniles and adults) and log CS (allometric patterns) was insignificant revealing that the allometric trajectories are parallel, i.e., had the same directions (MANCOVA, test for common slopes; Wilks'λ = 0.47, $F_{62,150} = 1.1$, $P = 0.26$). The interaction was removed and the MANCOVA was repeated, where the adults group showed a significant difference between adults and juveniles (test for intercept; Wilks'λ = 0.04, $F_{62,152} = 3.11$, $P = 1.26 \times 10^{-29}$; Goodall's F test = 8.32, df = 26,13268, $P < 0.001$). Also, regression analysis showed that ontogenetic allometry was entirely related to PC2 ($r = 0.67$, $P < 0.01$), but not PC1 ($r =$

Table 1 Analysis of measurement errors for shape of *P. pruinosus*

Shape (Procrustes ANOVA)	% Explained variance	SS	MS	df	F	P
Individuals	99.11	0.526702	0.54952	1798	32.12	< 0.0001
Image error	0.886	0.024418	0.000271	1860	2.85	< 0.0001
Digit. error	0.0031	0.017228	0.000119	3720		

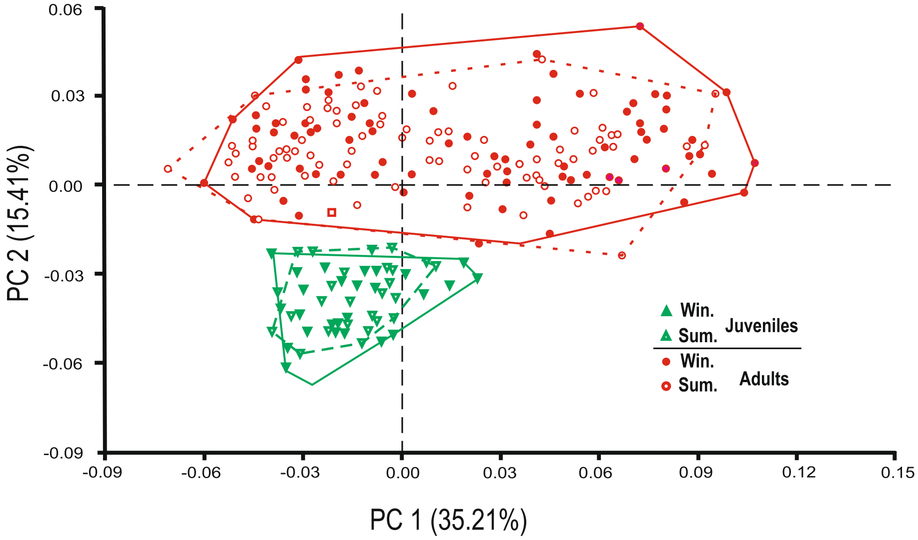

Fig. 3 Scatter plot of PC1 and PC2 for left body-half of *P. pruinosus*. The plot reflects the overlap between winter and summer individuals for adults and juveniles

0.28, $P > 0.05$). Figure 5a reflected the results of MANCOVA and showed that ontogenetic trajectories of juveniles and adults are similar and in the same direction. The angle between juveniles' and adults' ontogenetic trajectory was 47.1° which differed significantly ($P < 0.0001$) from an excepted angle (90°) of random vectors. The size explained about 1.42% of shape change in adults, while it explained about 3.8% of shape change in juveniles.

The exploration of the thin plate spline deformation grids of *P. pruinosus* resulted from multivariate regression showed that the shapes of juveniles and adults differ in two main regions, the head and pereon (Fig. 5b). The head region in the juveniles laid somewhat in a higher level than the rest of the body and its surface was more towering at the middle part than the surrounding parts with gradual sliding toward the front edge. The pereon of the juvenile was slim and the anterolateral projections of the first pereonite somewhat parallel the posterior margin of the head. All pereon segments show gradual sliding from the middle line toward the lateral sides. During development to the adult stage, the head shrank anteroposteriorly, narrowed and its level became slightly lower than that of the body. The pereon became broader, with the two anterolateral projections of the first pereonite extending anteriorly and reaching a little beyond the posterior margin of the eyes. The pleon was laterally compressed, with a slight concavity along its mid-dorsal line, which diminished toward the end. The telson of adults became wider and shorter than that of juveniles.

Sexual dimorphism

Winter and summer specimens were pooled within each gender to study the sexual dimorphism. The mean (± SD) log centroid size was almost equal for females and males (females = 7.01 ± 0.13, males = 6.98 ± 0.16), and consequently, univariate analysis (ANOVA) revealed no evidence for size sexual dimorphism ($F = 1.31$, $P = 0.21$). The first two PC axes accounted for 59% of the total shape variation between sexes (Additional file 2: Fig. A2) and reflected a clear overlap between them. However,

Table 2 The effect of seasons on the body shape of *P. pruinosus* tested by multivariate analysis (MANOVA) and discrimination functional analysis (DFA)

	MANOVA					DFA					
	Wilks'λ	df1	df2	F	*P*					*P* permut. test	
						Proc. d.	D^2	T^2	*P*	Proc.d.	T^2 *P*
Juveniles	0.42	18	26	2.02	0.081	0.017	2.98	99.47	0.98	0.21	0.11
Adults	0.78	17	147	2.44	0.002	0.023	2.94	350.5	0.02	0.01	0.02
Females	0.45	20	28	2.85	0.001	0.021	4.67	482.8	0.01	0.01	0.01
Males	0.64	20	51	4.27	0.008	0.016	8.81	140.3	0.02	0.01	0.02

df degrees of freedom; *Proc.d.* Procrustes distance; D^2 Mahalanobis distance; T^2 Hotteling's T^2 test; P permut. test *P* values after permutation test (10,000 runs) for Procrustes distance and Hotteling's T^2 test

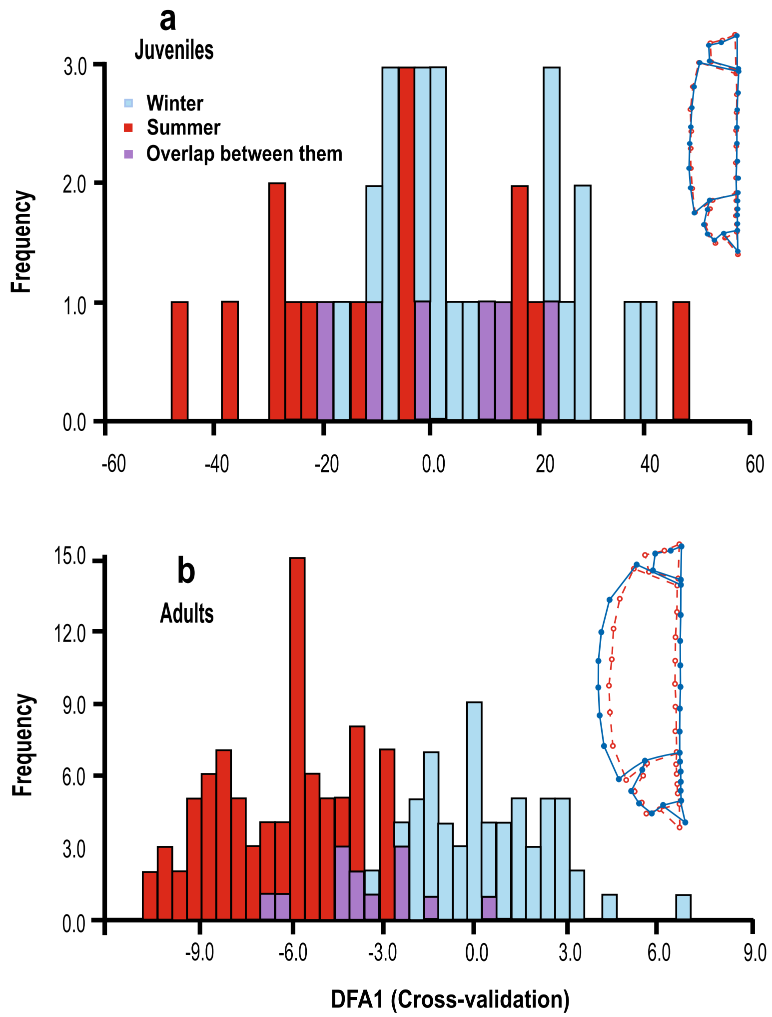

Fig. 4 Frequency histograms of discriminant analysis showing the effect of seasons on the body shape of *P. pruinosus* for juveniles (**a**) and adults (**b**). Note the body shape overlaps between two studied seasons for juveniles and adults. The wireframe drawings beside each histogram represent the mean shape deformation for the winter and summer individuals

body shape varied significantly according to sex (Hotelling's T^2 test = 420.4, $P < 0.001$). Furthermore, Mahalanobis distance (measure the distance between shapes of the female and male relative to average shape) between sexes was significant (D^2 = 3.22, $P < 0.001$), suggesting the presence of a shape variation between the sexes. Nevertheless, this variation was small (Procrustes distance = 0.014, R^2 = 0.02), where none of the sexes formed a notable cluster. Level of sex classification accuracy revealed that 95.1% of the individuals of the whole specimens were correctly assigned to their sex, whereas cross-validation yield 93.3% correct classification (Additional file 5: Table A3).

Deformation grids for the average shapes of females and males illustrated shape variations between them (Fig. 6). The heads of the females were somewhat quadratic, wider than that in males, and its posterior part was more elevated than the surrounding areas and gently descended to the front and sides. The males' heads were towered at the middle part and slide forward, backwards, and laterally. Also, males' head showed a forward protrude fronting at midline more than females that may be due to large labrium and clypus. Females possessed a broader pereon region than males, with the posterior margin covered large part of the lateral sides of the first two pleonites. Furthermore, the pleon region was wider in females than in males, elevated along the middle line, and slightly descended to the sides (i.e, showing convexity). In males, the first two pleonites were more elevated than the rest of pleonites and gradually descended backwardly, while a small waist was observed between the second and third pleonites. The telson was broader in females than in males.

Allometric trajectories of females and males were parallel (test for common slope, Wilks'λ = 0.86, $F_{62,89}$ =

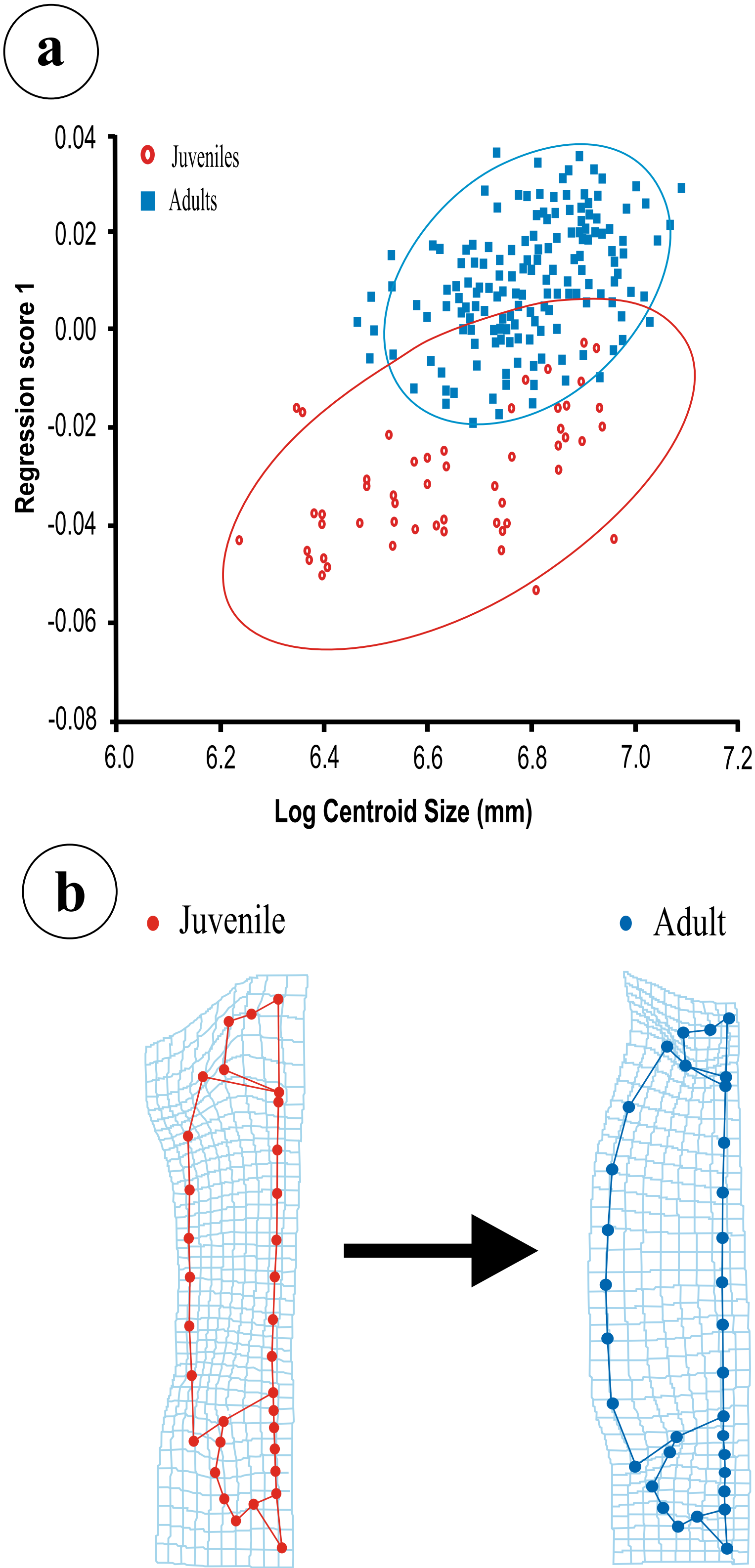

Fig. 5 a Scatterplot of multivariate regression of shape variables onto log CS showing ontogenetic allometry of *P. pruinosus*. **b**Thin plate spline deformation grids showing shape changes from the average shape predicted by multivariate regression analysis for juvenile and adult of *P. pruinosus* at 6.3 and 7.1 units of log CS

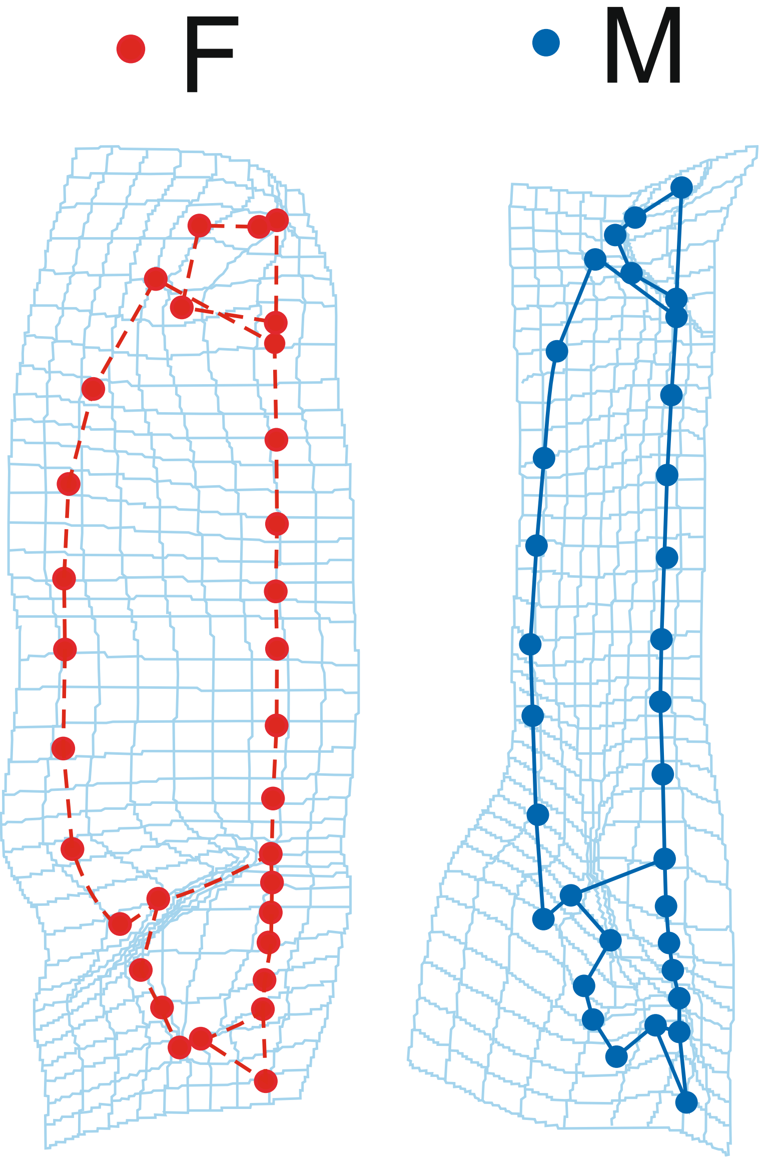

Fig. 6 Wireframe drawing of sexual dimorphism in body shape of isopod *P. pruinosus*. Deformation-based on discrimination functional analysis between two sexes. The graph visualizes how the average body shape of female differs concerning that of male. F, female; M, male

3.81, P = 0.28; Goodall's test F = 0.36, P = 0.36). After removing the interaction, MANCOVA showed a significant difference (test for intercept; Wilks'λ = 0.57, $F_{62,89}$ = 5.38, P < 0.0001; Goodall's test F = 81.68, P = 0.000). Females and males showed a 25.9° angle between their allometric trajectories that significantly (P < 0.0001) differed from an excepted angle (90°) of random vectors. The previous result revealed that the shape of the body was affected by size in females and males but in a different manner, where the shape of females was more affected (6.6% of variance explained by allometry) than males (5.7% of variance explained by allometry).

Discussion

Effect of seasonal variations on body shape

In the present work, juveniles of *P. pruinosus* showed no seasonal variations in the body shape. Regarding the adults (females and males) shape, the winter forms significantly differed from those of the summer. The winter forms have large bodies with small heads, broad pereons, and short narrow telsons. The summer forms have somewhat small slender body shape with slightly stretched heads in the anterior direction and relatively long and wide telsons. Although the phenotypic variations between winter and summer forms of *P. pruinosus* adults were small and may not be detectable by eye, the geometric morphometric analyses significantly detected these morphological differences. Seasonal variations in biotic and abiotic factors result in selective pressures and the evolutionary response to this appeared as phenotypic plasticity (Williams et al., 2017). Some species that produce two or more generations per year and subject to an annual climatic fluctuation as *Bicyclus* butterflies, may show different phenotypes that are repeated year after year (Roskam & Brakefield, 1999). Different phenotypes between generations were interpreted as across-generations plasticity and attributed to epigenetic variations (Fusco & Minelli, 2010). This is agreed with the case of *P. pruinosus* (produce two or more generations per year, Achouri et al., 2002); therefore, genetic analysis for individuals of *P. pruinosus* in winter and summer seasons is needed.

For most terrestrial isopods, temperature, air humidity, and soil moisture are the main factors controlling their vertical distribution (Hassall & Tuck, 2007; Morgado, Ferreira, Cardoso, Soares, & Loureiro, 2015). Under these environmental conditions, isopod individuals can respond eco-morphologically and behaviorally (Sfenthourakis & Hornung, 2018) and the selection of plasticity emerges as an essential strategy and can be a significant source of phenotypic variations within a population (Xue & Leibler, 2018). Generally, phenotypic plasticity showed three forms, neutral, adaptive, and maladaptive based on abiotic and biotic factors and their interactions (Nettle & Bateson, 2015). In this context, an organism may have one phenotype for a particular environmental condition below a threshold and another phenotype for the same environmental condition but above that threshold (Stearns, 1989).

Summer climate in Upper Egypt is characterized by high temperatures (average 35-47 °C) all the season. Also, agricultural fields are irrigated by surface irrigation methods (Strelkoff, Clemmens, El-Ansary, & Awad, 1999). Consequently, the high temperatures in summer lead to the quick evaporation (the potential evapotranspiration of about 9.2 mm/day) of irrigating water and speed the drought of the soil surface, which cracks upon drying (Ouda & Taha, 2018; Ouda & Zohry, 2016; Paris, 1963). It is worth mentioning that the rate of plant litter decomposition is accelerated with the increase of temperature in summer (Krishna & Mohan, 2017; Thongjoo, Miyagawa, & Kawakubo, 2005), and thus the soil contained less organic matter.

Therefore, the results of the present study suggested that the shape of adult summer forms of *P. pruinosus* seem quite suitable to summer conditions, where the stretched head and slender body may indicate their plasticity for vertical migrations or burrowing into the deep moist ground avoiding decrease water loss in the drier air at the soil surface, as was reported for some isopod species (Warburg, Linsenmair, & Bercovitz, 1984). Besides, their slender body decreased body surface area, which in turn minimized exposure to desiccation at the soil surface as shown in other isopods (Broly, Devigne, & Deneubourg, 2015; Dias et al., 2013). It is also suitable for some isopods that have to stay under the fallen and decayed leaves at the soil surface for foraging as a result of the low content of organic matter in deep soil layers.

In the winter, irrigation causes waterlogging of the surface and in deep soil layers and even during winter closure in Egypt (about 3 weeks in January and February, where the irrigation system is shut down for maintenance) the deep soil layers are still moist (because water potential evapotranspiration rate is low, about 3.6 mm/day) which this leads to slow the rates of litter decomposition resulting in increased organic matter and nutrient stocks in the soil (Isaac & Nair, 2005; Ouda & Zohry, 2016). Accordingly, isopod individuals tend to avoid the presence in areas that contains excess of water and/or overly humid soils, in which, they absorb water through the cuticle of the ventral region of pleon resulting in osmoregulation problems or drowning (Wright & Machin, 1990). Experimentally, *P. pruinosus* showed high mortality rate in high moisture conditions (Ferreira et al., 2016). It can be suggested that the present adult winter forms of *P. pruinosus* may motivate to burrow and distribute deep into the soil in winter searching for less moisture areas. This could be achieved with help of their body shape (wide body, compressed head, and the two lateral projections of the first pereonite) through pushing wet soil particles away and moving into deeper burrows. Usually, terrestrial isopods, by themselves, do not dig burrows, but usually, use other burrows or cracks and enter first their head into the soil (Taylor & Moore, 1995). The same pattern was found in isopod *Ligidium japonicum* (Warburg, Linsenmair, & Bercovitz, 1984).

Ontogenetic allometry was found in *P. pruinosus*, although the shape features that discriminate juveniles and adults were not simply allometric because the amount of variation explained by size was small and dropped to become 1.42% in the adult stage. This can be attributed to crustacean relative growth (Hartnoll, 2001), where more molts occur in the early stages of life. Also, the small effect of size on shape change in adults indicated that the size is not a key factor in the adult morphology. The shape variations between juveniles and adults of *P. pruinosus* were closely linked to some body features and may appear as a result of some factors such as sexual maturity, as adaptive plasticity to the differential occupied habitats and type of diet, in addition to others (Bravi & Benítez, 2013).

Previous studies showed that isopod juveniles preferred to hide under small stones and wet decayed leaves and logs above ground near the trees, while adults found more in subsurface layers of the soil (Alikhan, 1995). The present results proposed that the slim shape of juveniles' body may give them a relative agility and flexibility to move over decaying leaves and small stones and facilitate their entry to tight and confined areas on logs. Also, the light colored bodies of juveniles fit and resemble above ground microhabitats provided by leaf litter and other decayed materials.

The growth of the juvenile to an adult form causes narrowing and shortening of the head, lowering its level than the rest of the body, and widening of the pereon and shortening of the telson. Adults shape may show adaptation to burrowing behavior down into the ground by working as a wedge and helping by securing burrow walls (Faulkes, 2013). This is accompanied with anterior extending of anterolateral projections of the first pereonite which help in pushing soil particles away while moving downward. Also, the wide and darkly colored bodies of adults fit and resemble deep soil burrows and color of soil particles and decomposed litter (Lovei & Sunderland, 1996). Thus, morphological patterns and background matching minimize predation risk in both stages.

Difference in diet between juveniles and adults generally reflects ontogenetic changes. Head shape variation in adults may be attributed to development of mouthparts, especially mandibles and their corresponding attached muscles (Loureiro, Sampaio, Brandão, Nogueira, & Soares, 2006). Generally, food preference varied among terrestrial isopods; however, the soft leaves with low polyphenolic concentrations and high nitrogen content were considered the best for majority of isopods including *P. pruinosus* (Lavy, Van Rijn, Zoomer, & Verhoef, 2001; Loureiro et al., 2006). Juveniles of *Armadillidium vulgare*, *Oniscus asellus*, and *Porcellio scaber* showed high growth rates associated with high-quality diet that is rich in nitrogen content, while diets with low nitrogen content was found to increase mortality rate among juveniles (Faberi, Lopez, Clemente, & Manetti, 2011; Rushton & Hassall, 1983). Based on the results presented here, changes in the head size and shape and consequently mandible force are important morphological characters helping in litter decomposition through mechanical and chemical breakdown soil (Krishna & Mohan, 2017).

Moreover, the widening of pereon and pleon in adults of *P. pruinosus* reflected internal growth (as alimentary canal, muscles, and gonads) and agonistic behavior (mostly during feeding of adults) (Diawol, Giri, & Collins, 2015). Furthermore, widening of pleon region may be explained by the requirements of large gills-surface area for ventilation and respiration (Faulkes, 2013), where the adults live in a deep soil layer wherever low oxygen level are found.

Another explanation for the changes in the morphology of juveniles and/or adults may be as a response to presence of some crustacean predators or their kairomones (as *Daphnia* sp. and *Chthamalus anisopoma* barnacles), while in the absence of the predators, they developed to a typical form (Ghadouani & Pinel-Alloul, 2002; Lively, 1986; Maurone, Suppa, & Rossi, 2018).

Sexual dimorphism

The present results showed no size sexual dimorphism for *P. pruinosus*. This may result from the similar size of collected specimens. Generally, sexual dimorphism of isopods and other crustaceans, mainly lies in size variation between sexes that has been attributed to sexual selection (Bertin et al., 2002) and to reproduction or reproductive strategy (Anastasiadou, Liasko, & Leonardos, 2009).

On the other hand, the present results demonstrated the existence of a shape sexual dimorphism in *P. pruinosus*, although it was relatively small. Geometric morphometrics determined the shape of sexual dimorphism in females of *P. pruinosus* as widening of pereon and pleon regions. The allometric growth of females appeared to affect more the pereon region (because of the pereon widening). The wide and convex pereon of the present females may reflect the role of this region in reproductive activity and sex selection as reported in other crustaceans (Shinozaki-Mendes & Lessa, 2019), where the wide pereon is positively associated with enlargement of paired ovaries and the relative space allocated for the distended marsupium to fit the incubated eggs (Appel, Quadros, & Araujo, 2011; Rufino, Abelló, & Yule, 2004) and increase the fecundity (Ismail, 2018; Moraes et al., 2018; Shinozaki-Mendes & Lessa, 2019). Also, the growth of pereon in females creates a biomechanical reply to support body weight increase during egg incubation (Marochi, Costa, Leite, Da Cruz, & Masunari, 2019).

The similar allometric pattern between present females and males of *P. pruinosus* considered as an evolutionary limitation that lessens the extent of shape variation that subjected to evolutionary change. However, as an advantage, it may reduce the risk of selective predation, if present. Although the allometric trajectory of juveniles and adults, as well as that of females and males, showed similar directions, the angle of trajectory in the first case (47.1°) was larger than in the second one (25.9°). This indicates that allometric trajectories are more divergent between juveniles and adults, as previously mentioned because of more molts occur in the early stages of life.

Conclusion

A landmarks geometric morphometric approach was applied on *P. pruinosus* to investigate both size and shape variations. Seasonal variations and habitat preferences could be responsible for patterning phenotypic variation in adults. Data revealed that juveniles undergo shape change during development into adulthood. Shape sexual dimorphism was not found for juveniles. Adult shape sexual dimorphism could be related to reproductive activity, sex selection, allometry, and/or using of habitats differently.

All the previous information about *P. pruinosus* reflects the animal's phenotypic plasticity, its relation to the habitat during life span and would be helpful in future population studies.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s41936-021-00209-y.

Additional file 1: Fig. A1 Seasonal size variations, using mean of log centroid size distribution, for juveniles, adults, females and males. The plot displays the mean and standard error of log CS.

Additional file 2: Fig. A2 Scatter plot of PC1 and PC2 for left body-half of *P. pruinosus* for sexes, illustrating the overlap between them.

Additional file 3: Table A1. Summary of principal component analysis for *P. pruinosus* among shapes of adults and juveniles regarding seasons variations and between individuals of two sexes. Analysis showing the PCs that explained more than 90% of the total variance.

Additional file 4: Table A2. Classification of the groups (juveniles and adults) of *P. pruinosus* between two seasons according to DFA analysis.

Additional file 5: Table A3. Classification of the sexes of *P. pruinosus* according to DFA analysis.

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Author's contributions

Idea and all steps in the article made by a single author. The author read and approved the final manuscript.

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Availability of data and materials

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Competing interests

The author declares no competing interests.

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References

Achouri, M. S., & Charfi-Cheikhrouha, F. (2005). Variabilité morphologique et reproductive de *Porcellionides pruinosus* (Brandt, 1833) en Tunisie (isopoda, Oniscidea) morphological and reproductive variability in *Porcellionides pruinosus* (Brandt, 1833) from Tunisia (isopoda, Oniscidea). *Crustaceana*, *78*(8), 897–916. https://doi.org/10.2307/20107562.

Achouri, M. S., Charfi-Cheikhrouha, F., & Marques, J. (2002). Biology, population structure, and field-growth rates of *Porcellionides pruinosus* (Brandt, 1833) (isopoda, Oniscidea) at Garat Nâam (Kasserine, Tunisia). *Crustaceana*, *75*(10), 1241–1262. https://doi.org/10.1163/156854002321518171.

Alikhan, M. (1995). *Terrestrial isopod biology*. Boca Raton: CRC Press.

Anastasiadou, C., Liasko, R., & Leonardos, I. D. (2009). Biometric analysis of lacustrine and riverine populations of *Palemonetes antennarius* (H. Milne-Edwards, 1837) (Crustacea, Decapoda, Palaemonidae) from North-Western Greece. *Limnologica*, *39*(3), 244–254.

Appel, C., Quadros, A. F., & Araujo, P. B. (2011). Marsupial extension in terrestrial isopods (Crustacea, isopoda, Oniscidea). *Nauplius*, *19*(2), 123–128. https://doi.org/10.1590/S0104-64972011000200003.

Baliga, V. B., & Mehta, R. S. (2016). Ontogenetic allometry in shape and flexibility underlies life history patterns of labrid cleaning behavior. *Integrative and Comparative Biology*, *56*(3), 416–427. https://doi.org/10.1093/icb/icw028.

Berns, C. M. (2013). The evolution of sexual dimorphism: Understanding mechanisms of sexual shape differences. In H. Moriyama (Ed.), *Sexual dimorphism (p. 1-16)*IntechOpen. https://doi.org/10.5772/55154.

Bertin, A., David, B., Cézilly, F., & Alibert, P. (2002). Quantification of sexual dimorphism in *Asellus aquaticus* (Crustacea: Isopoda) using outline approaches. *Biological Journal of the Linnean Society*, *77*(4), 523–533. https://doi.org/10.1046/j.1095-8312.2002.00125.x.

Bookstein, F. L. (1997). *Morphometric tools for landmark data: Geometry and biology*. Cambridge University Press, New York.

Bravi, R., & Benítez, H. A. (2013). Left–right asymmetries and shape analysis on *Ceroglossus chilensis* (Coleoptera: Carabidae). *Acta Ooecologica*, *52*, 57–62. https://doi.org/10.1016/j.actao.2013.07.007.

Briffa, M., & Dallaway, D. (2007). Inter-sexual contests in the hermit crab *Pagurus bernhardus*: Females fight harder but males win more encounters. *Behavioral Ecology and Sociobiology*, *61*(11), 1781–1787. https://doi.org/10.1007/s00265-007-0411-5.

Broly, P., Devigne, C., & Deneubourg, J. L. (2015). Body shape in terrestrial isopods: A morphological mechanism to resist desiccation? *Journal of Morphology*, *276*(11), 1283–1289. https://doi.org/10.1002/jmor.

Cardini, A., & Thorington Jr., R. W. (2006). Postnatal ontogeny of marmot (Rodentia, Sciuridae) crania: Allometric trajectories and species divergence. *Journal of Mammalogy*, *87*(2), 201–215. https://doi.org/10.1644/05-MAMM-A-242R1.1.

Conde-Padín, P., Grahame, J., & Rolán-Alvarez, E. (2007). Detecting shape differences in species of the *Littorina saxatilis* complex by morphometric analysis. *Journal of Molluscan Studies*, *73*(2), 147–154. https://doi.org/10.1093/mollus/eym009.

Csonka, D., Halasy, K., Buczko, K., & Hornung, E. (2018). Morphological traits – Desiccation resistance – Habitat characteristics: A possible key for distribution in woodlice (isopoda, Oniscidea). *ZooKeys*, *801*, 481–499. https://doi.org/10.3897/zookeys.801.23088.

Dangerfield, J., & Telford, S. (1990). Breeding phenology, variation in reproductive effort and offspring size in a tropical population of the woodlouse *Porcellionides pruinosus*. *Oecologia*, *82*(2), 251–258. https://doi.org/10.1007/BF00323542.

Dias, A. T., Krab, E. J., Mariën, J., Zimmer, M., Cornelissen, J. H., Ellers, J., & Berg, M. P. (2013). Traits underpinning desiccation resistance explain distribution patterns of terrestrial isopods. *Oecologia*, *172*(3), 667–677. https://doi.org/10.1007/s00442-012-2541-3.

Diawol, V. P., Giri, F., & Collins, P. A. (2015). Shape and size variations of *Aegla uruguayana* (Anomura, Aeglidae) under laboratory conditions: A geometric morphometric approach to the growth. *Iheringia. Série Zoologia*, *105*(1), 76–83. https://doi.org/10.1590/1678-4766201510517683.

Eberhard, W. G. (2009). Static allometry and animal genitalia. *Evolution: International Journal of Organic Evolution*, *63*(1), 48–66. https://doi.org/10.1111/j.1558-5646.2008.00528.x.

Eroukhmanoff, F., & Svensson, E. I. (2009). Contemporary parallel diversification, antipredator adaptations and phenotypic integration in an aquatic isopod. *PLoS One*, *4*(7), e6173. https://doi.org/10.1371/journal.pone.0006173.

Faberi, A. J., Lopez, A. N., Clemente, N. L., & Manetti, P. L. (2011). Importance of diet in the growth, survivorship and reproduction of the no-tillage pest *Armadillidium vulgare* (Crustacea: Isopoda). *Revista Chilena de Historia Natural*, *84*(3), 407–417.

Faulkes, Z. (2013). Morphological adaptations for digging and burrowing. *Functional Morphology and Diversity*, 276–295. https://doi.org/10.1093/acprof:osobl/9780195398038.003.0010.

Ferreira, N. G., Morgado, R. G., Amaro, A., Machado, A. L., Soares, A. M., & Loureiro, S. (2016). The effects of temperature, soil moisture and UV radiation on biomarkers and energy reserves of the isopod *Porcellionides pruinosus*. *Applied Soil Ecology*, *107*, 224–236. https://doi.org/10.1016/j.apsoil.2016.06.007.

Fusco, G., & Minelli, A. (2010). Phenotypic plasticity in development and evolution: Facts and concepts. *Philosophical Transactions of the Royal Society B*, *365*, 547–556. https://doi.org/10.1098/rstb.2009.0267.

Ghadouani, A., & Pinel-Alloul, B. (2002). Phenotypic plasticity in *Daphnia pulicaria* as an adaptation to high biomass of colonial and filamentous cyanobacteria: Experimental evidence. *Journal of Plankton Research*, *24*(10), 1047–1056. https://doi.org/10.1093/plankt/24.10.1047.

Good, P. (2000). *Permutation tests: A practical guide to resampling methods for testing hypotheses*. Springer Science & Business Media, New York.

Hammer, Ø., Harper, D. A., & Ryan, P. D. (2001). *PAST: Paleontological statistics software package for education and data analysis*.

Hartnoll, R. G. (2001). *Growth in Crustacea—Twenty years on*. In *Advances in decapod crustacean research*, (pp. 111–122). Springer Science+Business Media, Springer, Dordrecht.

Hassall, M., & Tuck, J. M. (2007). Sheltering behavior of terrestrial isopods in grasslands. *Invertebrate Biology*, *126*(1), 46–56. https://doi.org/10.1111/j.1744-7410.2007.00075.x.

Hepp, L. U., Fornel, R., Restello, R. M., Trevisan, A., & Santos, S. (2012). Intraspecific morphological variation in a freshwater crustacean *Aegla plana* in southern Brazil: Effects of geographical isolation on carapace shape. *Journal of Crustacean Biology*, *32*(4), 511–518. https://doi.org/10.1163/193724012X630660.

Herrel, A., Joachim, R., Vanhooydonck, B., & Irschick, D. J. (2006). Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard *Anolis lineatopus*. *Biological Journal of the Linnean Society*, *89*(3), 443–454. https://doi.org/10.1111/j.1095-8312.2006.00685.x.

Hornung, E. (2011). Evolutionary adaptation of oniscidean isopods to terrestrial life: Structure, physiology and behavior. *Terrestrial Arthropod Reviews*, *4*(2), 95.

IBM Corp, N (2013). *IBM SPSS statistics for windows. Version 22.0*.

Idaszkin, Y. L., Márquez, F., & Nocera, A. (2013). Habitat-specific shape variation in the carapace of the crab *Cyrtograpsus angulatus*. *Journal of Zoology*, *290*(2), 117–126.

Isaac, S. R., & Nair, M. A. (2005). Biodegradation of leaf litter in the warm humid tropics of Kerala, India. *Soil Biology and Biochemistry*, *37*(9), 1656–1664. https://doi.org/10.1016/j.soilbio.2005.02.002.

Ismail, T. G. (2018). Effect of geographic location and sexual dimorphism on shield shape of the Red Sea hermit crab *Clibanarius signatus* using the geometric morphometric approach. *Canadian Journal of Zoology*, *96*(7), 667–679. https://doi.org/10.1139/cjz-2017-0050.

Kawecki, T. J., & Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters*, *7*(12), 1225–1241. https://doi.org/10.1111/j.1461-0248.2004.00684.x.

Klingenberg, C., Duttke, S., Whelan, S., & Kim, M. (2012). Developmental plasticity, morphological variation and evolvability: A multilevel analysis of morphometric integration in the shape of compound leaves. *Journal of Evolutionary Biology*, *25*(1), 115–129. https://doi.org/10.1111/j.1420-9101.2011.02410.x.

Klingenberg, C. P. (2011). MorphoJ: An integrated software package for geometric morphometrics. *Molecular Ecology Resources*, *11*(2), 353–357. https://doi.org/10.1111/j.1755-0998.2010.02924.x.

Klingenberg, C. P. (2016). Size, shape, and form: Concepts of allometry in geometric morphometrics. *Development Genes and Evolution*, *226*(3), 113–137. https://doi.org/10.1007/s00427-016-0539-2.

Krishna, M., & Mohan, M. (2017). Litter decomposition in forest ecosystems: A review. *Energy, Ecology and Environment*, *2*(4), 236–249. https://doi.org/10.1007/s40974-017-0064-9.

Lavy, D., Van Rijn, M. J., Zoomer, H. R., & Verhoef, H. A. (2001). Dietary effects on growth, reproduction, body composition and stress resistance in the terrestrial isopods *Oniscus asellus* and *Porcellio scaber*. *Physiological Entomology*, *26*(1), 18–25. https://doi.org/10.1111/j.1365-3032.2001.00211.x.

Lefebvre, F., & Marcadé, I. (2005). New insights in the *Porcellionides pruinosus* complex (isopoda, Oniscidea): Biological, behavioural, and morphological approaches. *Crustaceana*, *78*, 465–480. https://doi.org/10.1163/1568540054473512.

Lively, C. M. (1986). Predator-induced shell dimorphism in the acorn barnacle *Chthamalus anisopoma*. *Evolution*, *40*(2), 232–242. https://doi.org/10.1111/j.1558-5646.1986.tb00466.x.

Loureiro, S., Sampaio, A., Brandão, A., Nogueira, A. J., & Soares, A. M. (2006). Feeding behaviour of the terrestrial isopod *Porcellionides pruinosus* Brandt, 1833 (Crustacea, isopoda) in response to changes in food quality and contamination. *Science of the Total Environment*, *369*(1-3), 119–128. https://doi.org/10.1016/j.scitotenv.2006.05.023.

Lovei, G. L., & Sunderland, K. D. (1996). Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, *41*(1), 231–256. https://doi.org/10.1146/annurev.en.41.010196.001311.

Loy, A., Mariani, L., Bertelletti, M., & Tunesi, L. (1998). Visualizing allometry: Geometric morphometrics in the study of shape changes in the early stages of the two-banded sea bream, *Diplodus vulgaris* (Perciformes, Sparidae). *Journal of Morphology*, *237*(2), 137–146. https://doi.org/10.1002/(SICI)1097-4687(199808)237:2<137:AID-JMOR5>3.0.

Marochi, M. Z., Costa, M., Leite, R. D., Da Cruz, I. D. C., & Masunari, S. (2019). To grow or to reproduce? Sexual dimorphism and ontogenetic allometry in two Sesarmidae species (Crustacea: Brachyura). *Journal of the Marine Biological Association of the United Kingdom*, *99*(2), 473–486. https://doi.org/10.1017/S0025315418000048.

Maurone, C., Suppa, A., & Rossi, V. (2018). Polymorphisms in predator induced defences of coexisting *Daphnia pulex* and *D. longispina*. *Hydrobiologia*, *823*(1), 121–133. https://doi.org/10.1007/s10750-018-3701-1.

Moczek, A. P. (2010). Phenotypic plasticity and diversity in insects. *Philosophical transactions of the Royal Society of London. Series B, Biological science*, *365*(1540), 593–603. https://doi.org/10.1098/rstb.2009.0263.

Monaghan, P. (2008). Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1497), 1635–1645.

Montesanto, G., Pizzo, G. M., Caruso, D., & Lombardo, B. M. (2012). The postmarsupial development of *Porcellio siculoccidentalis*, with some data on reproductive biology (Crustacea, isopoda, Oniscidea). *ZooKeys*, *176*, 87–101. https://doi.org/10.3897/zookeys.176.2369.

Moraes, S., Alencar, C., Fransozo, A., Costa, R., Castilho, A., & Freire, F. (2018). Sexual and ontogenetic morphometric variation in *Xiphopenaeus kroyeri* (Crustacea, Decapoda, Penaeidae): A new approach with linear and angular morphometric data. *Invertebrate Reproduction & Development*, *62*(3), 143–153.

Morgado, R., Ferreira, N. G., Cardoso, D. N., Soares, A. M., & Loureiro, S. (2015). Abiotic factors affect the performance of the terrestrial isopod *Porcellionides pruinosus*. *Applied Soil Ecology*, *95*, 161–170. https://doi.org/10.1016/j.apsoil.2015.06.012.

Nettle, D., & Bateson, M. (2015). Adaptive developmental plasticity: What is it, how can we recognize it and when can it evolve? *Proceedings of the Royal Society B: Biological Sciences*, *282*(1812), 20151005. https://doi.org/10.1098/rspb.2015.1005.

Ouda, S. A., & Taha, A. (2018). Required interval of weather data for proper irrigation scheduling. *Egyptian Journal of Agronomy*, *40*The15th International Conference on Crop Science, 105–114.

Ouda, S. A., & Zohry, A. E. H. (2016). *Management of climate induced drought and water scarcity in Egypt: Unconventional solutions*. Springer Briefs in Environmental Science, Springer Nature

Paris, O. H. (1963). The ecology of *Armadillidium vulgare* (isopoda: Oniscoidea) in California grassland: Food, enemies and weather. *Ecological Monographs*, *33*(1), 1–22.

Pélabon, C., Bolstad, G. H., Egset, C. K., Cheverud, J. M., Pavlicev, M., & Rosenqvist, G. (2013). On the relationship between ontogenetic and static allometry. *The American Naturalist*, *181*(2), 195–212. https://doi.org/10.1086/668820.

Rieseberg, L. H., Widmer, A., Arntz, A. M., & Burke, J. M. (2002). Directional selection is the primary cause of phenotypic diversification. *Proceedings of the National Academy of Sciences*, *99*(19), 12242–12245. https://doi.org/10.1073/pnas.192360899.

Roggero, A., Giachino, P. M., & Palestrini, C. (2013). A new cryptic ground beetle species from the *Alps characterised* via geometric morphometrics. *Contributions to Zoology*, *82*(4), 171–183. https://doi.org/10.1163/18759866-08204002.

Rohlf, F. J. (2015). *tpsDig2, version 2.22. Digitize coordinates of landmarks and capture outlines (version 2.22)*. Stony Brook: Department of Ecology and Evolution, State University of New York.

Rohlf, F. J. (2016). *tpsRegl, version 1.45. Software*. Stony Brook: Department of Ecology and Evolution, State University of New York.

Roskam, J., & Brakefield, P. (1999). Seasonal polyphenism in *Bicyclus* (Lepidoptera: Satyridae) butterflies: Different climates need different cues. *Biological Journal of the Linnean Society*, *66*(3), 345–356. https://doi.org/10.1111/j.1095-8312.1999.tb01895.x.

Rufino, M., Abelló, P., & Yule, A. B. (2004). Male and female carapace shape differences in *Liocarcinus depurator* (Decapoda, Brachyura): An application of geometric morphometric analysis to crustaceans. *Italian Journal of Zoology*, *71*(1), 79–83. https://doi.org/10.1080/11250000409356554.

Rushton, S. P., & Hassall, M. (1983). The effects of food quality on the life history parameters of the terrestrial isopod (*Armadillidium vulgare* (Latreille)). *Oecologia*, *57*(1-2), 257–261. https://doi.org/10.1007/BF00379587.

Sfenthourakis, S., & Hornung, E. (2018). Isopod distribution and climate change. *ZooKeys*, *801*, 25–61. https://doi.org/10.3897/zookeys.801.23533.

Shinozaki-Mendes, R., & Lessa, R. (2019). Ontogenetic trajectories in *Callinectes danae* (Crustacea: Brachyura): Sex and age polymorphism. *Journal of the*

Marine Biological Association of the United Kingdom, *99*(1), 111–118. https://doi.org/10.1017/S0025315417001758.

Shreeves, G., & Field, J. (2008). Parental care and sexual size dimorphism in wasps and bees. *Behavioral Ecology and Sociobiology*, *62*(5), 843–852. https://doi.org/10.1007/s00265-007-0510-3.

Shultz, J. W. (2018). A guide to the identification of the terrestrial isopoda of Maryland, USA (Crustacea). *ZooKeys*, *801*, 207–228. https://doi.org/10.3897/zookeys.801.24146.

Souty-Grosset, C., & Faberi, A. (2018). Effect of agricultural practices on terrestrial isopods: A review. *ZooKeys*, *801*, 63–96. https://doi.org/10.3897/zookeys.801.24680.

Stearns, S. C. (1989). The evolutionary significance of phenotypic plasticity. *Bioscience*, *39*(7), 436–445. https://doi.org/10.2307/1311135.

Strelkoff, T. S., Clemmens, A. J., El-Ansary, M., & Awad, M. (1999). Surface-irrigation evaluation models: Application to level basins in Egypt. *American Society of Agricultural Engineers.*, *42*(4), 1027–1036.

Taylor, A., & Moore, P. (1995). The burrows and physiological adaptations to a burrowing lifestyle of *Natatolana borealis* (isopoda: Cirolanidae). *Marine Biology*, *123*(4), 805–814. https://doi.org/10.1007/BF00349124.

Thongjoo, C., Miyagawa, S., & Kawakubo, N. (2005). Effects of soil moisture and temperature on decomposition rates of some waste materials from agriculture and agro-industry. *Plant Production Science*, *8*(4), 475–481. https://doi.org/10.1626/pps.8.475.

Trevisan, A., Marochi, M. Z., Costa, M., Santos, S., & Masunari, S. (2012). Sexual dimorphism in *Aegla marginata* (Decapoda: Anomura). *Nauplius*, *20*(1), 75–86. https://doi.org/10.1590/S0104-64972012000100008.

Tsoi, K.-H., & Chu, K.-H. (2005). Sexual dimorphism and reproduction of the amphipod *Hyale crassicornis* Haswell (Gammaridea: Hyalidae). *Zoological Studies -TAIPEI*, *44*(3), 382–392.

Vandel, A. (1962). Isopodes terrestres (2eme partie). *Faune de France*, *66*, 1–416 Ed. P. Lechevalier, Paris.

Wada, S., Yasuda, C. I., & McLay, C. (2014). Sexual size dimorphism in two endemic hermit crabs, *Pagurus traversi* and *P. novizealandiae*, in New Zealand. *Bulletin of Fisheries Sciences, Hokkaido University*, *64*(2), 31–35. https://doi.org/10.1080/00288330.1985.9516099.

Warburg, M., Linsenmair, K. E., & Bercovitz, K. (1984). The effect of climate on the distribution and abundance of isopods. In *Symposia of the Zoological Society of London, 53*, 339-367. Cambridge University Press.

Williams, C. M., Ragland, G. J., Betini, G., Buckley, L. B., Cheviron, Z. A., Donohue, K., & Marshall, K. E. (2017). Understanding evolutionary impacts of seasonality: An introduction to the symposium. *Integrative and Comparative Biology*, *57*(5), 921–933. https://doi.org/10.1093/icb/icx122.

Winkler, D. W., & Wallin, K. (1987). Offspring size and number: A life history model linking effort per offspring and total effort. *The American Naturalist*, *129*(5), 708–720.

Wright, J. C., & Machin, J. (1990). Water vapour absorption in terrestrial isopods. *The Journal of Experimental Biology*, *154*(1), 13–30.

Xue, B., & Leibler, S. (2018). Benefits of phenotypic plasticity for population growth in varying environments. *Proceedings of the National Academy of Sciences*, *115*(50), 12745–12750. https://doi.org/10.1073/pnas.1813447115.

Yusseppone, M. S., Márquez, F., Luquet, C. M., Brey, T., Ríos de Molina, M. C., & Rocchetta, I. (2018). Does shell shape variation play a role in conservation of the long-lived freshwater bivalve *Diplodon chilensis* (Bivalvia, Hyriidae)? *Ecohydrology*, *11*(2), e1931. https://doi.org/10.1002/eco.1931.

Zelditch, M. L., Swiderski, D. L., & Sheets, H. D. (2012). *Geometric Morphometrics for biologists: A primer*, (2nd ed.,). New York (NY): Elsevier Academic Press. https://doi.org/10.1016/B978-012778460-1/50007-7.

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