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Original Article

Baseline growth of the Trinidad freshwater crab *Poppiana dentata* (Randall, 1840) under laboratory conditions

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(With 2 figures)

Abstract

Poppiana dentata (Randall, 1840) is widely distributed throughout riverine habitats in Trinidad. However, there is a scarcity of information on the biology of this species. This study provides the first baseline examination that describes growth aspects for *P. dentata*. Juvenile crabs were obtained from berried females collected in northwest Trinidad. Carapace width (CW), length (CL), moult incident, intermoult period and qualitative aspects were recorded for crabs ($N = 23$) over 9 months. CW, CL and intermoult period were used to derive percentage size increment, specific growth rate (SGR) and size at structural maturity for both sexes. Growth curves and logistic equations were also generated for each sex. Hatched crabs (< 5 mm CW) underwent rapid hardening after their first moult, indicating a fast turnover of moult cycles. SGR and CW percent increment were also the highest for this initial moult ($P < 0.05$). CW, CL, intermoult period, size increment and SGR did not differ between sexes ($P > 0.05$), with logistic equations expressed as $CW = 32.81\ (1+\exp\ (1.481-0.031t))^{-1}$ for males and $CW = 34.07\ (1+\exp\ (1.516-0.027t))^{-1}$ for females. Yet, breakpoint analyses indicated dissimilar sizes for structural maturity (male: 28.40 mm CW; female: 16.84 mm CW). These patterns reflect a shorter life span for this species in comparison to what has been reported for other trichodactylid relatives. This can have implications for *P. dentata* populations residing in anthropogenically disturbed habitats; thus, highlighting the need for conservation strategies to ensure preservation of native wild stock.

Keywords: freshwater Trichodactylid, growth rate, *Poppiana dentata*, structural maturity.

Crescimento do caranguejo de água doce de Trinidad, *Poppiana dentata* (Randall, 1840), em condições laboratoriais

Resumo

O *Poppiana dentata* (Randall, 1840) está amplamente distribuído nos habitats fluviais de Trinidad. Existem, porém, poucas informações sobre a biologia dessa espécie. Este estudo fornece a primeira análise de referência que descreve aspectos do crescimento do *P. dentata*. Caranguejos jovens foram obtidos a partir de fêmeas em desova na região noroeste de Trinidad. A largura da carapaça (LC), o comprimento da carapaça (CC), a incidência de muda, o período de intermuda e aspectos qualitativos foram registrados para caranguejos ($N = 23$) ao longo de mais de nove meses. A LC, o CC e o período de intermuda foram utilizados para obter o aumento porcentual, a taxa específica de crescimento (TEC), e o tamanho na maturidade estrutural para os dois sexos. Curvas de crescimento e equações logísticas foram também geradas para cada sexo. Os caranguejos que nasceram (com largura de carapaça < 5 mm) apresentaram um endurecimento rápido depois de sua primeira muda, o que indica uma rápida rotação dos ciclos de muda. A TEC e o aumento da porcentual da LC foram também os mais altos para esta muda inicial ($P < 0{,}05$). Não houve variação da LC, CC, do período de intermuda, aumento do tamanho e da TEC entre os sexos ($P > 0{,}05$), e as equações logísticas foram expressas como: $LC = 32{,}81\ (1+\exp\ (1{,}481-0{,}031t))^{-1}$ para machos, e $LC = 34{,}07\ (1+\exp\ (1{,}516-0{,}027t))^{-1}$ para fêmeas. Porém, as análises de quebra indicaram tamanhos diferentes para maturidade estrutural (LC para macho: 28,40; para fêmea: 16,84 mm). Esses padrões refletem um período de vida mais curto para esta espécie em comparação com o que tem sido registrado para outras famílias de Trichodactylidae. Isso pode ter implicações para as populações de *P. dentata* que residem em habitats modificados antropogenicamente; destaca-se, assim, a necessidade de estratégias de conservação para assegurar a preservação das populações selvagens nativas.

Palavras-chave: Trichodactylidae de água doce, taxa de crescimento, *Poppiana dentata*, maturidade estrutural.

1. Introduction

Trichodactylids occupy key functional feeding roles in aquatic food webs, serving as efficient nutrient processors of allochthonous and autochthonous materials associated with their riverine habitats. The family Trichodactylidae consists of 51 species that are endemic to the Neotropical region (Silva et al., 2014), with *Poppiana dentata* (Randall, 1840) having a wide distribution throughout freshwater habitats of northern South America and Trinidad (Cumberlidge, 2008). Most brachyurans, such as *P. dentata*, undergo discontinuous growth whereby increase in size takes place when their rigid, calcified shell is shed during ecdysis or moulting. The crab will then rapidly absorb water, resulting in an increase in size. Hardening of the new exoskeleton takes place through mineralization (Warner, 1977; McLay, 2015), whereby calcium is sourced from the surrounding environment and/or endogenous deposits such as gastroliths (Hartnoll, 1988; Luquet, 2012).

The growth patterns and characteristics associated with sexual maturity of Neotropical freshwater brachyurans have been investigated in species such as *Sylviocarcinus australis* Magalhães and Türkay, 1996 and *Dilocarcinus pagei* (Mansur et al., 2005; Pinheiro and Taddei, 2005; Taddei and Herrera, 2010; Herrera et al., 2013) Stimpson, 1861, as well as *Trichodactylus* sp (Lima et al., 2013; Silva et al., 2014; Williner et al., 2014) Latreille, 1828. For these trichodactylids, differential growth patterns were commonly noted across life stages and sexes with respect to dimensions of the carapace, abdomen and propodus, as well as the gonopods (Williner et al., 2014). In most cases, these trends, defined by isometric and/or allometric growth of dimensional structures, reflected the transition from juvenile to adult, ontogenic energy requirements and the reproductive strategies of the species (Herrera et al., 2013; Lima et al., 2013; Silva et al., 2014; Williner et al., 2014). Variations in size increment, female abdominal width and some aspects of the major propodus were also observed for the local Neotropical species, *Rodriguezus garmani* (Rostant et al., 2008) Rathbun, 1898. Growth aspects for other freshwater brachyuran groups of the Eastern world were also noted to grow inconsistently and were described by different levels of allometry (Gherardi and Micheli, 1989; Micheli et al., 1990; Tao et al., 1994; Araki and Matsuura, 1995; Stemmer and Schubart, 2013).

While growth remains a well-studied aspect that can provide insight into a species adaptation to habitats, and indirectly, population fitness (Gibertini et al., 2008), there is still a lack of growth information for some freshwater species such as *P. dentata*. The latter is a widely distributed trichodactylid residing in freshwater habitats, some of which are anthropogenically impacted in Trinidad. Longevity has been examined for one South American trichodactylid species, *D. pagei*, from populations in São José do Rio Preto in São Paulo (Brazil), with a reported life span of 2.4 and 2.7 years for males and females respectively (Pinheiro and Taddei, 2005). More recent work on populations from Barra Mansa Dam, Mendonça, São Paulo indicated an extended longevity of 4.4 and 4.1 years for males and females respectively (Taddei and Herrera, 2010). Field observations and local collections of different life stage sizes of *P. dentata*, over a year, alludes to the possibility that this trichodactylid may have a short life span in comparison to its close relatives (personal observations). This can have consequences for indigenous populations of *P. dentata*, since its life span and reproductive maturity can reflect environmental pressures, such as anthropogenic impacts. This warrants the need for further research to evaluate the species growth, and by extension, provide baseline data for estimating its longevity and maturity. However, no examination of growth aspects has been made for *P. dentata*, to date. This study, therefore, sought to address this information gap by describing the baseline growth of *P. dentata*; namely, through examining its growth patterns using specific growth rate (SGR), growth curves and morphological maturity. The use of size, measured as carapace width (CW) and carapace length (CL), and intermoult period were the main components used to determine these characteristics. An account of juvenile moult behaviour was also used to qualitatively describe growth for *P. dentata* during this early life stage.

2. Material and Methods

2.1. Acquisition of crabs and experimental design

For some species of freshwater crabs, such as the indigenous *P. dentata* and *R. garmani*, epimorphic development is characteristic, whereby offspring hatch directly into small crabs or hatchlings. Hence, this study's cohort comprised of juvenile crabs obtained from berried wild stock females collected in Bamboo, northwest Trinidad (10°37'49.2" N; 61°25'51.2" W). This collection site entailed 2 freshwater waterways that drain into the Caroni River. Berried females were collected from mesh traps that were deployed at 4 different accessible points, approximately 50 metres apart along these waterways. The species of the collected female crabs was confirmed using the diagnostic characteristics and species key described by Magalhães and Türkay (2008). Further verification of the species was done using pleopod characteristics (Magalhães and Türkay, 2008) for male counterparts collected at the same site as the females.

The growth period was selected for 9 months since monitoring beyond this point could have yielded inconsistent growth rates, due to reproductive influences. This was confirmed from an earlier 12-month experiment, comprising a cohort of wild stock juvenile crabs ($N = 12$, CW ≥ 5 mm) collected from the aforementioned site. Live specimens were qualitatively collected via dip-netting with a D-frame net, at the same access points as those of the current study's site. During this trial, adult crabs at 10 months old and beyond were observed to exhibit longer intermoult periods (> 70 days) and abnormal feeding rates, indicating reproductive investment being favoured over growth. On this assumption, male and female crabs at 10 months or older were placed together in chambers and copulation was observed with pairs. This further suggested the reproductive status of the species at this age.

The preliminary work also assisted in validating the growth conditions that were selected for this study's experiment, involving temperature, dissolved oxygen (DO), photoperiod, feeding regime and diet for *P. dentata.* For the trial experiment, each wild stock crab was observed under conditions of 26.0 °C, a DO concentration of 5.9 ± 0.2 mg/L and a light regime of 12 h light:12 h darkness. These physicochemical conditions were considered suitable for growth, since previous monitoring at the same collection site revealed a similar temperature (26.1 ± 0.3 °C) and DO concentration (6.1 ± 0.9 mg/L). The photoperiodic exposure of 12 h light:12 h darkness was selected because this was fairly comparable to the light-dark diurnal cycles that generally occur in Trinidad, throughout most of the year. A feeding regime akin to that of this study's experiment, was also applied, whereby crabs were fed daily using a varied diet of Hikari crab cuisine pellets (Kyorin Food Industries Co., Ltd.) and segments of *Egeria densa* Planchon, 1849. Additionally, the overall behaviour of the trial crabs were observed, to ensure that the laboratory conditions did not impair feeding, locomotion and other general activities. This was done on a qualitative basis whereby personal observations were made on each crab, involving its response to food input (whether most, or none, of the food was eaten when administered), moulting incidents and daily locomotion of walking, climbing and grooming.

2.2. Experimental conditions and growth measurements

After being released from the abdomen of the collected female crabs, each hatchling was then reared in a glass aquarium (length 8 inches × width 6 inches × height 6 inches) containing 1600 mL of laboratory prepared, de-chlorinated water. DO was kept at > 5.0 mg/L (6.1 ± 0.3 mg/L) and a photoperiod of 12 h light:12 h darkness and temperature of 26.0 ± 0.5 °C were also maintained. Crabs were fed every day with the mixed diet involving Hikari crab cuisine pellets and *E. densa* plant segments. The quantity of daily food administered was modified to accommodate the intake of growing crabs. Hence, the regime followed as such; crabs of CW < 5 mm were fed 2 g of pellets and 2 g of *E. densa* segments, CW ≥ 5 - 15 mm fed 5 g of the pellets and 4 g of *E. densa* segments, CW > 15 - 25 mm fed 10 g of pellets and 6 g of *E. densa* plant segments, CW > 25 mm fed 24 g of pellets and 6 g of *E. densa* segments. Removal of uneaten food and water exchange took place every other day.

It should be noted that crabs that experienced loss of appendages at any time during the monitoring period were removed from the study cohort, resulting in a final dataset for individuals, $N = 23$. Observations were also made of crabs after their moulting, in relation to when they consumed their exuvia and the appearance of their exoskeletons. These observations were taken during their early growth and served as qualitative indications of how fast juvenile crabs hardened and advanced through their moult cycles. Based on these observations, carapace width (CW) and carapace length (CL) were carefully measured from moulted crabs, only after their exoskeletons had hardened. A digital caliper (VINCA DCLA) was used to perform these measurements to the nearest hundredth of a millimeter. CW was measured as the maximum width of the carapace and CL as the distance between the median notch of the frontal margin and the posterior margin of the carapace.

Size increase or increment and intermoult period served as discrete parameters of growth. The size increase was computed as the difference between the CW or CL measurements (mm) between 2 consecutive moults. Each size increment was then expressed as a percentage of the corresponding premoult CW or CL. This represented the percent size increment, or the extent to which the CW or CL postmoult exceeded that of the respective premoult (Hartnoll, 1982). The intermoult period was recorded as the number of days between 2 successive moults, with the actual day of ecdysis not included in this period. Specific growth rate (SGR) was calculated for each moult from the relevant CW or CL size increment and intermoult period, using the method from Romano and Zeng (2006). Monthly SGR was also calculated using the same procedure. The mean size class (in terms of CW), intermoult period and SGR were also derived for each moult. Mean CW and intermoult periods were then used to plot separate growth curves for the male and female datasets, with the mean intermoult periods plotted cumulatively. The change in CW size (mm) over time (cumulative intermoult period) was also fitted to the standard logistic equation, similar to that used by Jin et al. (2001). Moreover, variation in CW served as the dimensional change used to estimate structural maturity for this study. As such, breakpoint analysis of CW differences was used to estimate structural maturity for each sex, using scatter plots created in R (R Development Core Team, 2016) and the package 'strucchange' (Zeileis et al., 2002).

2.3. Statistical analyses

All statistical analyses and graphical depictions were done using R version 3.3.1 (R Development Core Team, 2016). An alpha level of 0.05 was used for all statistical tests. A number of statistical procedures require datasets to come from normal populations, with homogeneity of variances (Zar, 1999). Hence, normality checks were performed on the growth dataset using the Shapiro-Wilk test, coupled with the Levene's test for assessing equality of variances. The data was found to be non-normal from the Shapiro-Wilk test ($P < 0.05$), with unequal variances (heteroscedasticity) detected by the Levene's test ($P < 0.05$). Accordingly, non-parametric tests were used instead, since these types of tests are recommended for datasets that deviate from conditions of normality and homogeneity of variances (Zar, 1999). The Spearman rank correlation coefficient was used to explore the relationship between carapace dimension and intermoult period. The Mann-Whitney U statistical test was used to further detect differences between sexes, in terms of CL, CW, intermoult period, size increment and SGR. CW, CL and SGR of these dimensions were also statistically assessed for differences across moults and months using the Kruskal-Wallis test. The post hoc Dunn's test was used for pairwise comparisons of SGR of different moults and the same was done for SGR associated with different months. The package 'dunn.test' (Dinno, 2014) was used for both the Kruskal-Wallis and the Dunn's test, since this package performs both statistical applications and reports on the statistical values for these.

3. Results

3.1. Qualitative aspects: moult behaviour of crabs

Berried females released hatchlings in captivity that averaged 3.09 ± 0.47 mm CW and 3.01 ± 0.45 mm CL in size. The majority of hatchlings underwent moulting within a few days of being released from their mother's abdomen (intermoult period: 2 ± 2 days). *P. dentata* crabs at this size (< 5 mm CW) were observed to consume their moulted exuvia within a few hours of their ecdysis, along with a subsequent transition from transparent to opaque exoskeletons within 24 to 48 hours. This postmoult consumption behaviour and fast transitioning of the shell appearance indicated a rapid hardening of the exoskeleton. Alternatively, this changed as crabs grew older (> 15 mm CW), whereby consumption of exuvia and opacity of the exoskeletons took place 1 to 3 days after moulting.

3.2. Absolute growth

Within this study period, 23 *P. dentata* crabs experienced 239 moults, each having undergone 9 to 12 moult incidences. Overall, as CW increased intermoult period also increased (see Figure 1a and 1c). This was also reflected in the size class distributions for both female and male crabs (see Figure 1b and 1d), where mean intermoult period increased with mean CW size class. Initially, size increase of juvenile crabs was substantial with percent moult increment being the highest for CW for the first moult and CL for the second moult. Coupled with the prominent size increase after the first moult, was the brief intermoult period, which was just a few days for this moult (intermoult period: 2 ± 2 days; CW: 4.46 ± 0.72 mm; CL: 3.88 ± 0.74 mm) and subsequent 3 moults (intermoult period: 6 ± 2 days; CW: 7.95 ± 2.32 mm; CL: 7.02 ± 2.00 mm). Consequently, as crabs grew older, dimensional growth slowed down and the intermoult period became longer toward the end of 9 months (mean: 58 ± 5 days).

Growth of dimensions for male and female crabs followed a similar pattern. CW, CL, intermoult period and CW size increment for each moult did not differ significantly between female and male crabs (CW: $W = 7213, P > 0.05$; CL: $W = 7096, P > 0.05$; intermoult period: $W = 7450, P > 0.05$; CW size increment: $W = 7872, P > 0.05$). However, adult female crabs did show a sign of slight decrease in intermoult period for the largest size class (CW: 37.21 ± 1.90 mm; intermoult period: 43 ± 6 days) (see Figure 1b). Both male and female crabs' CW increments were the highest for the first moult (female: 46%; male: 47%) but the CL increments were the highest for the second moult (female: 45%; male: 44%) (as shown in Table 1). Minimum percent increments of 16% for CW and 14% for CL were associated with the twelfth or last moult recorded

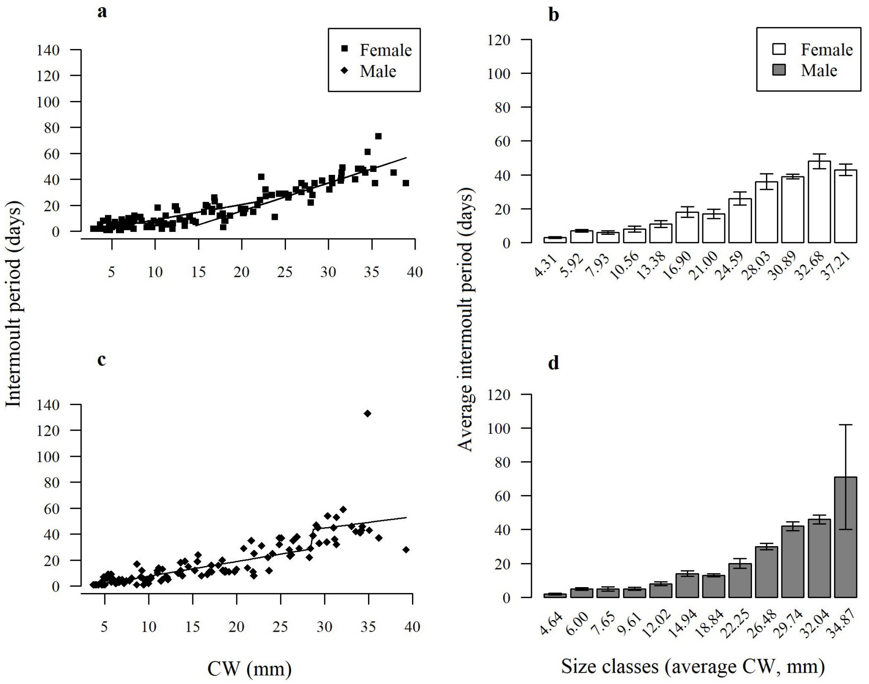

Figure 1. Growth aspects for *Poppiana dentata* with respect to: intermoult period and carapace width (CW) for female (a) and male (c) crabs over 9 months; average intermoult period for CW size classes of female (b) and male (d) crabs. Error bars in (b) and (d) represent the standard errors for the intermoult periods.

Table 1. Mean carapace width (CW) and carapace length (CL) size increase with standard deviations (SD), along with percentage size increments, for male and female *Poppiana dentata* crabs.

Moult no.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Female												
CW size increase (mm ± SD)	1.31 ± 0.77	1.61 ± 0.80	1.87 ± 1.54	2.59 ± 1.11	2.82 ± 1.47	3.52 ± 1.57	4.10 ± 1.63	3.59 ± 1.32	5.06 ± 2.26	5.74 ± 1.13	4.33 ± 0.88	5.14 ± 0.72
CW percent increment (%)	46	39	31	33	28	27	25	17	22	23	16	16
CL size increase (mm ± SD)	0.69 ± 0.47	1.65 ± 0.70	1.69 ± 1.10	2.38 ± 1.08	2.40 ± 1.42	2.99 ± 1.76	3.96 ± 1.53	3.60 ± 1.36	4.11 ± 1.57	3.77 ± 1.22	4.38 ± 0.94	3.68 ± 2.77
CL percent increment (%)	24	45	32	35	28	25	29	19	20	16	18	14
Male												
CW size increase (mm ± SD)	1.44 ± 0.85	1.36 ± 0.64	1.66 ± 1.08	1.96 ± 1.06	2.40 ± 1.16	2.92 ± 0.93	3.90 ± 1.36	3.41 ± 0.65	4.22 ± 1.06	4.02 ± 0.85	3.65 ± 1.58	4.95 ± 0.38
CW percent increment (%)	47	30	28	27	25	25	26	19	19	16	13	17
CL size increase (mm ± SD)	1.05 ± 0.81	1.42 ± 0.59	1.53 ± 1.12	1.49 ± 0.72	2.09 ± 1.24	3.00 ± 1.20	3.53 ± 1.27	2.95 ± 0.77	3.70 ± 1.02	3.07 ± 1.27	3.60 ± 0.80	2.70 ± 1.63
CL percent increment (%)	36	44	29	25	25	30	27	18	19	15	14	10

for the female crabs within the monitoring period. Even lower percentage increments were associated with males' CW (13%) after the eleventh moult and CL (10%) after the twelfth moult (as shown in Table 1).

3.3. Specific Growth Rate (SGR) and growth curves

SGR for *P. dentata* was highest for the first moult and within the first month. Within this initial month of the crabs being released from the female abdomens, 3 to 6 moult events occurred within short intervals. Maximum SGR (CW: 0.25 mm/day; CL: 0.86 mm/day) was noted for the initial moult and this rate was considerably higher than that of the second moult (females: $V = 68$, $P < 0.05$; males: $V = 60$, $P < 0.05$), as well as successive moults (see Figure 2a and 2c). CW SGR generally declined as crabs grew older, differing substantially across moults ($\chi^2 = 175.21$, $P < 0.05$) and months ($\chi^2 = 151.84$, $P < 0.05$). However, CL SGR did not follow the same trend as CW SGR, despite a strong correlation between CL and CW dimensions (male: $rho = 0.98$, $P < 0.05$; female: $rho = 0.99$, $P < 0.05$). Growth rate of this dimension (CL) was similar across the initial and second moults (males: $V = 53$, $P > 0.05$; females: $V = 56$, $P > 0.05$) and this was also reflected by the marginal changes in rate between the first and subsequent 6 moults (females: $Z = 2.37$, $P > 0.05$; males: $Z = 2.70$, $P > 0.05$).

SGR for dimensions followed a similar pattern for both sexes (CW SGR: $W = 7089$, $P > 0.05$; CL SGR: $W = 7050$, $P > 0.05$) and followed an analogous decrease over successive moults (see Figure 2a and 2c). This similarity was also noted for monthly SGR (CW SGR: $W = 5511$, $P > 0.05$; CL SGR: $W = 5455$, $P > 0.05$). Male and female crabs grew rapidly in their first month in terms of CW, with the SGR for this dimension being significantly higher than that of the second month (males: $V = 66$, $P < 0.05$; females: $V = 78$, $P < 0.05$). This corresponded with the early moults in the first month being associated with the highest CW percent increments (> 30%). Growth curves for both sexes also reflected a similar trend for CW variation over time. Faster growth of CW was noted for both sexes at an earlier period but this slowed down after 150 days or approximately 5 months (see Figure 2b and 2d). Accordingly, similar components were noted for the fitted logistic equations, expressed as $CW = 32.81\ (1+\exp\ (1.481 - 0.031t))^{-1}$ for males and $CW = 34.07\ (1+\exp\ (1.516 - 0.027t))^{-1}$ for females. Monthly CL SGR did not vary like this, since the rates for the first and subsequent 5 months were alike for males ($Z = 2.50$, $P > 0.05$) and similarly for the first and subsequent 6 months, for the females ($Z = 2.02$, $P > 0.05$).

3.4. Structural maturity

CW was noted to be significantly correlated with intermoult period for both male ($rho = 0.92$, $P < 0.05$) and female ($rho = 0.89$, $P < 0.05$) *P. dentata* crabs. However, breakpoint determination and scatter plots revealed a segmented relationship between CW and intermoult

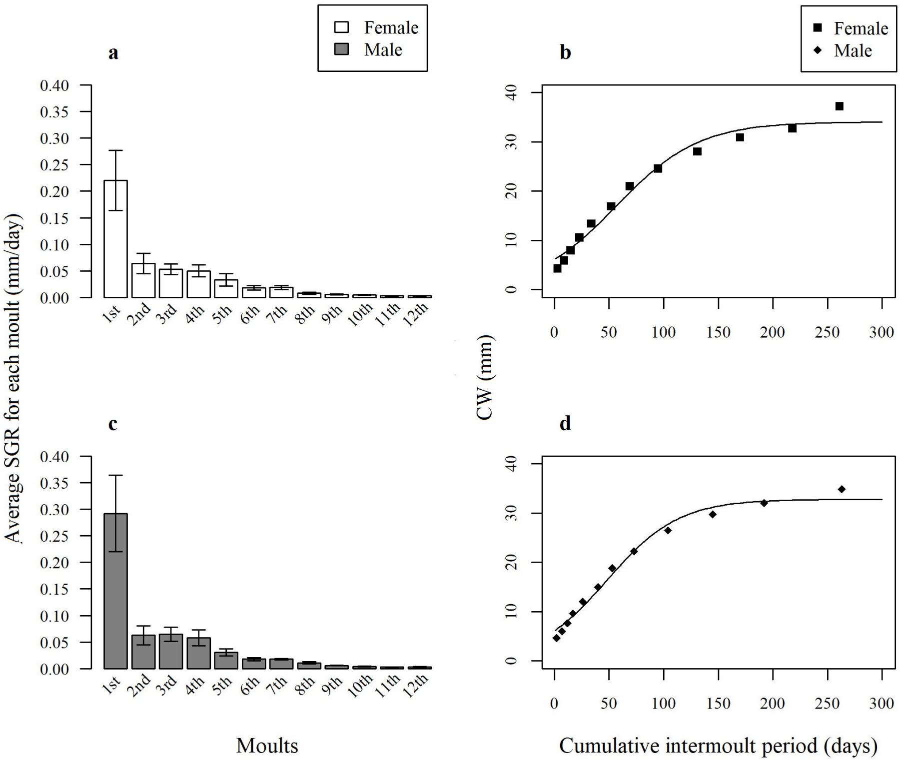

Figure 2. Growth rate aspects for *Poppiana dentata* with respect to: average Specific Growth Rate (SGR) in female (a) and male (c) crabs for successive moults, over 9 months; growth curves for female (b) and male (d) carapace width (CW) reared over the same time period. Error bars in (a) and (c) represent the standard errors for SGR.

period. Breakpoints identified were 16.84 mm CW with an intermoult period of 26 days for the female crabs (see Figure 1a) and 28.40 mm CW with an intermoult period of 35 days for the male crabs (see Figure 1c). For the former sex, an overlap in slopes occurred within the CW range of 14.70 to 22.77 mm whereas the slope for the males showed an inflection from the respective breakpoint.

4. Discussion

P. dentata crabs released from their female parents were < 5 mm in size (3.09 ± 0.47 mm CW; 3.01 ± 0.45 mm CL) but this is similar to that of other freshwater species such as *D. pagei* (2.63 ± 0.18 mm CW) (Sant'Anna et al., 2015), *Kingsleya latifrons* Randall, 1840 (3.9 ± 0.28 mm CW) and *Potamon fluviatile lanfrancoi* Capolongo and Cilia, 1990 (~ 3.5 mm CW) (Wehrtmann et al., 2010). These juvenile *P. dentata* crabs moulted quickly within a few days of being released (intermoult period: 2 ± 2 days) and consumed their exuvia within a few hours of their ecdysis. Once a crab has moulted, previously stored organic and mineral reserves would be utilized for cuticle secretion since the new, soft exoskeleton would not facilitate feeding (Warner, 1977). However, juvenile *P. dentata* appeared to have undergone rapid hardening of their exoskeletons (metaecdysis) within 24 to 48 hours of their initial moults; as evident by their prompt feeding on the moulted shells and relatively fast transition from transparent to opaque, mineralized exoskeletons. This can be advantageous since it accommodates a rapid turnover of moult cycles, allowing immature crabs to grow quickly into adults within a few months. Furthermore, a rapid hardening of the soft, post-ecdysis shell can also reduce juvenile vulnerability to predators and intraspecific cannibalism. Cannibalism is not unusual for freshwater crabs (Yeo et al., 2008) and has been reported for *Sesarma fossarum* (Anger, 2005) Schubart et al., 1997, *R. garmani* (Rostant et al., 2008) and *P. dentata* (personal observations).

In addition to an increase in size (CW and CL) with successive moults, the intermoult period became longer. This agrees with Rostant et al. (2008) in which CW size class increased with intermoult period for another indigenous freshwater crab, *R. garmani*. This trend is expected since an isometric growth pattern is plausible for dimensions such as CW and CL (Warner, 1977). Furthermore, most crustaceans generally have a longer intermoult period being associated with size increase (Hartnoll, 1982). This is because an extended intermoult period allows accumulation of sufficient resources needed for the next size increase in ecdysis and also accommodates for offspring bearing by the females during intermoult (Hartnoll, 1982).

Maximum percent increment (> 40%) for dimensions was associated with juvenile crabs, with a general decrease as crabs grew older. Kobayashi (2012) reported a similar trend of decline in percent CW size increment with increase in size for the brachyuran, *Eriocheir japonica* De Haan, 1835. This decline in growth increment with increasing size is typical for crustaceans and is hardly ever constant for decapods (Warner, 1977). The growth curves and CW SGR for both sexes also reflected this decline. The flattening of slopes for both sexes showed a deceleration in CW growth as crabs matured and both moult and monthly CW SGR showed a decrease, further into the 9-month period. The fast, initial growth of *P. dentata* juvenile crabs, followed by a reduction in growth rate as these crabs matured, can be attributable to energetic investments being shifted from growth to reproduction (Wolcott, 1988; McLay, 2015). These ontogenic changes are typical for brachyurans, whereby growth is characterized as consecutive phases, with each phase associated with its specific growth rate (Hartnoll, 1974, 1982).

The SGR for the length of the carapace was different from the width for *P. dentata*. Variations in CL were not as significant as those for CW, despite these 2 dimensions being strongly correlated. Growth of the carapace length for brachyurans would generally undergo minimum variation (Tao et al., 1994). It is also likely for different anatomical features of brachyurans to have distinct growth patterns, given the different structural functions of morphologies in reproduction (Hartnoll, 1982). It is possible that energy investment favoured the growth of the carapace width over the length, at least for growing female crabs, since the former would facilitate the successive widening of the abdomen for reproduction, rather than an increase in the length. A negative allometric relationship has been described for CW and abdomen width of juvenile trichodactylids (Herrera et al., 2013; Williner et al., 2014), thus inferring an early, rapid growth and investment in the CW.

Interestingly, similar patterns in growth of dimensions were noted for both sexes. Corresponding growth patterns can allow males and females to maintain similar sizes in a population; as shown by the logistic growth equations reflecting comparable maximum sizes for *P. dentata* (males: 32.81 mm CW; females: 34.07 mm CW). This is useful for pair formation in a population and has also been reported for another trichodactylid species, *T. borellianus* (Williner et al., 2014). Additionally, increase in the width of the carapace can accommodate development of reproductive organs (males and females) and can also be conducive to the widening of the abdominal chamber space for incubating young (females). A slight decrease in intermoult period was observed for females of the largest CW size class and this possibly coincided with the onset of functional sexual maturity for this sex; such that female crabs at this point needed to increase in size faster, in order to accommodate gonadal development. Further histological investigation of the gonads is needed to confirm this for *P. dentata*, considering the onset of structural maturity for females was noted at a much smaller CW size.

The overlap of slopes for females in the scatterplot highlighted the CW size range (14.70 to 22.77 mm) within which the puberty moult could have occurred, while the inflected slope for the males depicted discontinuity in CW growth (see Figure 1a and 1c). Most of the male crabs would have undergone their puberty moult at this inflection point or breakpoint size of 28.40 mm CW, or greater. This was almost 2 times the size of that for the female crabs (CW = 16.84 mm), inferring a much larger size and longer time span at which structural maturity occur for male *P. dentata* crabs. These breakpoint differences between sexes of *P. dentata* can be attributed to a transitional phase, such as a 'sub-adult' stage that the crabs experience before adulthood. Growth and longevity examined for *D. pagei* revealed a similar trend, in which the puberty moult for males occurred later, at a greater age (1.2 years) than for females (0.9 years) (Pinheiro and Taddei, 2005). Herrera et al. (2013) also similarly found that females of *D. pagei* matured at smaller sizes than the males because of differential reproductive requirements.

However, similar sizes have been noted in male and female crabs for onset of sexual maturity; such as 18 mm CW for both sexes of *T. fluviatilis* reported by Lima et al. (2013), similar sizes (female: 9.03 mm CW; male: 8.35 mm CW) for the same species noted by Silva et al. (2014) and similar sizes (female: 19 mm CW; male: 18 mm CW) for the puberty moult of *Geothelphusa dehaani* White, 1847, highlighted by Araki and Matsuura (1995). Yet, some of these estimations would have included functional (gonadal) as well as determinate measurements of collected specimens at discrete times and did not include the growth component of intermoult period. The latter represents a key element in modelling crustacean growth (Chang et al., 2012) and can be used to determine growth patterns and growth curves for crustacean species (Hartnoll, 1982). Intermoult period has been useful for assessing maturity of other freshwater species, such as for *R. garmani* (Rostant et al., 2008) and *E. japonica* (Kobayashi, 2012).

It is also not uncommon for male and female brachyurans to have different sizes signifying morphological sexual maturity (Herrera et al., 2013). This allows for the reproductive advantage of males achieving structural maturity at larger sizes, conveying benefit for intra-species competition for potential mates. For marine brachyurans, the larger size of males is useful for rivalry with other male counterparts, acquiring mates and facilitating control over females (Jivoff, 1997). Furthermore, the size disproportion between sexes can be warranted by female crabs' investing relatively more in reproduction over somatic growth (Herrera et al., 2013; Silva et al., 2014). Females have also been known to be smaller in size than males for brachyurans (Wolcott, 1988; Silva et al., 2014) and this has been noted in other freshwater species such as *P. potamios palestinensis* (Gherardi and Micheli, 1989) Bott, 1967, *Potamon fluviatile* (Micheli et al., 1990) Herbst, 1785, *Sinopotamon yangtsekiense* (Tao et al., 1994) Bott, 1967 and *D. pagei* (Pinheiro and Taddei, 2005). This concurs with the CW breakpoint of female *P. dentata* crabs being considerably smaller than that of the males. Female *P. dentata* possibly undergo their puberty moult at an earlier age, becoming structurally mature at a smaller size but not necessarily reaching functional maturity (development of ovaries/oogenesis), simultaneously. Given the fast growth rate for *P. dentata* from juvenile to adult in just 9 months, structural maturity at an early onset can favour reproduction. This conveys a benefit whereby pubescent females could still engage in mating with mature males, when opportunistic encounters occur, and subsequently store sperm in their spermathecae or seminal receptacles until functional maturity is reached (Gherardi and Micheli, 1989; Micheli et al., 1990; Liu and Li, 2000; Chua et al., 2014).

This baseline growth information can serve as a comparative reference for future toxicological experiments, involving chronic effects of environmental contaminants on development. Moreover, these findings can be used in conjunction with functional organ maturity, to assist in determination of age at sexual maturity for *P. dentata*. Other sexual characteristics, such as abdominal width and propodus length for females and males respectively, represent dimensions that can also assist in determining the onset of sexual maturity. Sexual maturity and longevity for this species are worth investigating further since a much shorter life span could be plausible for this local trichodactylid, in comparison to other reported relatives. Its life span and age at maturity can reflect environmental pressures that influence these, thus warranting conservation attention for long term preservation of indigenous populations.

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