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GROWTH, LENGTH-WEIGHT RELATIONSHIPS, AND CONDITION ASSOCIATED WITH GENDER AND SEXUAL STAGE IN THE INVASIVE NORTHERN CRAYFISH, *ORCONECTES VIRILIS* HAGEN, 1870 (DECAPODA, CAMBARIDAE)

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ABSTRACT. The northern crayfish, *Orconectes virilis* Hagen 1870, is an invasive species in North America and Europe and is currently expanding its range and influence ecologically and globally. Growth patterns and relationships of body morphometrics were evaluated to understand basic life history relationships. Growth and size relationships are provided for gender, sexual phase distributions for adults and juveniles, and chelae length and width relationships to interpret information on sexual dimorphism. The length-weight relationship for the male form I ($y = 3.048x - 3.659$, $r^2 = 0.945$, $F = 839.2$, $p = <0.001$), and male form II ($y = 3.228x - 3.950$, $r^2 = 0.958$, $F = 1008.6$, $p = <0.001$) sexual reproductive phases; and female ($y = 3.071x - 3.734$, $r^2 = 0.948$, $F = 1848.8$, $p = <0.001$), showed positive Fulton Condition Index allometric rates of change with increasing length, while juveniles ($y = 1.137x - 1.544$, $r^2 = 0.784$, $F = 345.1$, $p = <0.001$) showed negative allometric change. Carapace width ($y = 0.4902x - 0.3973$, $r^2 = 0.971$, $F = 4.039$, $p = <0.001$), carapace depth ($y = 0.4767x - 0.1899$, $r^2 = 0.980$, $F = 4.311$, $p = <0.001$), abdomen width ($y = 0.4244x - 0.4099$, $r^2 = 0.956$, $F = 5.308$, $p = <0.001$), chelae width ($y = 0.3011x - 1.0863$, $r^2 = 0.787$, $F = 8.675$, $p = <0.001$), and chelae length ($y = 0.705x - 2.1319$, $r^2 = 0.880$, $F = 1.770$, $p = <0.001$) all grew allometrically with respect to carapace length. Based on northern crayfish rapid growth and large size, a competitive advantage during invasion is attained by adults based on larger CL sizes and sexual dimorphism in male chelae size.

Keywords: morphometrics, Fulton Condition index, growth, length-weight relationships

INTRODUCTION

The native distribution of the northern crayfish, *Orconectes virilis* Hagen, 1870, includes the northern USA and Canada (Hobbs 1989). It is native to the Great Lakes, the southern Arctic Ocean, and northern Mississippi drainages from northern Arkansas, Mississippi, and Tennessee to Alberta and southeastern Quebec, with populations extending west in the Mississippi drainage to Montana and Colorado (Hagen 1870; Faxon 1914; Holthuis 1962). It has been introduced to other regions in North America and into at least nine other states and the District of Columbia (Schwartz et al. 1963), including California (Riegel 1959), Utah (Johnson 1986), Washington (Larson et al. 2010), Arizona, Pennsylvania, New Jersey (Crocker 1979; Smith 1979), Maryland (Meredith & Schwartz 1960; Schwartz et al., 1963), Virginia, West Virginia (Loughman & Welsh 2010; Loughman & Simon 2011), and North Carolina (Bouchard 1976). It has also been introduced into New Brunswick, Canada (McAlpine et al. 2007), Chihuahua, Mexico (Campos & Contreras-Balderas 1985; Hamr 2002), North London, England (Ahern et al. 2008), and the Netherlands (Ahern et al. 2008).

In some parts of its introduced range, *O. virilis* has been reported to displace native crayfish species and disrupt reproductive success of native fish species (Dorn & Mittlebach 2004). The competitive advantage of *O. virilis* is speculated to be based on its large size compared to sympatric native species (Loughman & Simon 2011). This advantage may be based on size and weight differences caused by unequal growth of body parts (Lockwood et al. 2013). Change in growth of select structures, which might be sexually dependent, may be observed as either allometric or isometric rate change (Mazlum et al. 2007). The Fulton Condition Index (Nielson & Johnson 1983) is a measure of growth rate, such that it is a measure of the slope (b). Growth is isometric (equal) when

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b = 3, and when b < 3 or b > 3, growth is allometric. This suggests that positive allometric growth occurs when organism weight increases more than length (b > 3) and negative allometric growth occurs when length increases more than weight (b < 3). Allometry may change during growth and sexual stage. We propose that these growth rate changes can result in differential expression based on sex or sexual maturation phase, which may not provide a competitive advantage for females and juveniles.

Basic life history information is generally lacking for most crayfish species (Moore et al. 2013), while patterns in growth and length-weight relationships are limited (Stein 1976; Romaire et al. 1977; Rhodes & Holdich 1984; Garvey & Stein 1993), other than for commercial aquaculture species (Mazlum et al. 2007; Wang et al. 2011). The current study evaluates the relationships between growth, gender, and body morphology, which could enhance competitive advantage for the invasive northern crayfish. We investigate length and weight, carapace, chelae, and abdomen relationships among male form I and II, female, and juvenile individuals of *O. virilis*. This information will contribute to baseline information needs for evaluating invasive species life history attributes.

METHODS

All specimens (n = 298) used for measurement of *O. virilis* morphometry were collected from ambient natural streams (n = 183), lakes (n = 32), and drowned river mouth coastal wetland (n = 53) environments associated with either the Laurentian Great Lakes (n = 132) or Ohio River (n = 166) basins, USA. Surveys were conducted in the Midwestern United States from Indiana, Michigan, Ohio, Wisconsin, and Minnesota from May 1999 until September 2005. Sampling was restricted to daylight hours and all available habitats within a reach (defined as a linear distance of 15 times the wetted stream width or minimum distance of 150 m of shoreline margin in lakes and wetlands). Crayfish were collected using standard operating procedures described in Simon (2004) based on a variety of gear types appropriate for each waterbody type. Collection methods included electrofishing (i.e., backpack, tow-barges, and boat-mounted), collection by hand by flipping rocks, and excavation methods. We have pooled data over the native range of this species in order to examine the relationships between growth, gender, sexual stage, and size.

A total of 104 females, 97 males (n = 51 form I and n = 46 form II), and 97 juveniles were measured using digital calipers to the nearest 0.1 mm. Individuals were segregated by gender and sexual stage groups. To avoid bias due to measuring procedures, the same individual completed all morphological measurements (CS). A second individual (TPS) measured 5% of the total individuals to ensure measurement precision and accuracy was within 5% using standard quality assurance procedures. All measured individuals had a full complement of chelae and walking legs and no visible body deformation. Damaged and regenerated chelae were not used. All individuals were measured for morphometric variables and for weight. Weight (W_{WT}) was measured by placing the individual on paper towel to remove excess water, and then weighed with a Mettler AT20 digital balance with an accuracy of 0.001 g. The following seven morphometric characteristics were measured for each specimen (Fig. 1) – carapace length (CL); postorbital carapace length (POCL) [from the anterior margin of postorbital spine to the posterior margin of the carapace]; carapace width (CW); carapace depth (CD) [distance from the sternum to the dorsal surface]; chelae length (ChL); chelae width (ChW); chelae depth (ChD) [vertical measure from the dorsal to ventral margins of the chelae at the thickest depth]; and abdomen width (ABW). Based on similar studies of other *Procambarus* crayfish species (Mazlum et al. 2007; Wang et al. 2011), these morphological characters are related to sexual dimorphism and are controlled by environmental and food resources.

Juvenile and adult specimens were distinguished using a size threshold of 25 mm CL, which corresponds to the smallest female with ripe gonads. This threshold was established for females by dissecting the oviduct aperture and evaluating ovarian development based on early maturing ova presence. We evaluated only females, but considered the size threshold for both sexes, since all individuals below this size belong to the first age group, and male gonopodia identification was not possible (Hobbs 1989). Any possible relationship between smaller (CL < 25 mm) and larger (CL > 25 mm) specimens were determined by

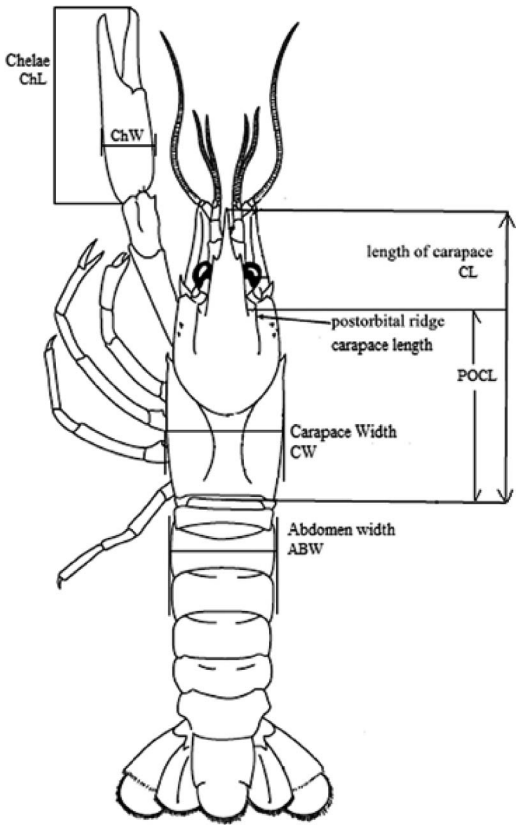

Figure 1.—Morphometric measurements taken for *Orconectes virilis* Hagen 1870 individuals (n = 298). CL = carapace length, POCL = Postorbital carapace length, CD = carapace depth, CW = carapace width, ChL = chelae length, ChW = chelae width, ABW = abdomen width. [Line art modified from Loughman & Simon (2011)].

comparing the ratios between the means of above measurements and mean carapace length (CL/ABW, CL/POCL, CL/CW, CL/CD, CL/ChL, CL/ChW) of all individuals in each group.

Carapace length was considered as the independent variable for all relationships performed as it appears to be minimally affected by growth variations and sexual maturation among decapod crustaceans (Lovett & Felder 1989). Regression analyses to determine the relationship between all measurements versus CL was investigated for each sex separately using the multiplicative model: $Y = aX^b$, where Y and X are the morphological dimensions and a and b are the regression constants. The relationships obtained were log transformed to the form $\log_{10} Y = \log_{10} a + b \log_{10} X$. The log transformation is preferred to better satisfy the assumptions of regression analysis (Sokal & Rohlf 1981) and allows the derivation of a single value from the analysis for the scaling relationship between the two-morphometric parameters. The allometry pattern for each parameter was established by testing the slope (b) of the regression equations against isometry (H_o: $b = 3$) applying the Student's t-test.

Fulton's condition factors for male (form I and form II), female, and the general population were calculated using the relationship between W_{WT} and CL of each individual (Nielson & Johnson 1983). Weight was plotted by CL for all individuals within each sex or sexual phase and a trend line was applied to best fit each scatter plot graph, with the b value of each line equation representing the Fulton's condition factor. The b value represents the type of allometric growth (Nielson & Johnson 1983).

Analysis of Covariance (ANCOVA) was used to compare the slopes b and carapace length between sexes, sizes, and sampling period (Zar 1984). The Kruskall–Wallis test (Zar 1984) was used to identify possible differences in time, area, and size, at the 95.0% confidence level with Mann–Whitney tests used to compare independent samples, at the 95.0% confidence level (Sokal & Rohlf 1981), while a simple regression analysis was used to examine the relationship between *O. virilis* morphological characters with sex as a covariate.

RESULTS

Mean carapace length (CL ± SD), mean weight (W_{WT} ± SD), and the range for the general population (n = 298) were 23.55 ± 12.78 mm (range = 2.61–54.13 mm), 6.21 ± 7.59 g (range = 0.05–35.28 g) (Table 1). Mean carapace length (CL ± SD), mean weight (W_{WT} ± SD), and the range were calculated for male and female sex as: CL_{male} = 31.28 ± 8.49 mm (range = 16.92–51.29 mm), W_{WT} = 9.76 ± 7.94 g (range = 1.01–34.84 g), and CL_{female} = 29.12 ± 9.26 (range = 13.0–54.13 mm), $W_{WT\ female}$ = 7.83 ± 7.52 g (range = 0.51–35.28 g), respectively. The normalized ($\log_{10}$) length-weight relationship for the general population was y = 2.1285x - 5.4489, r^2 = 0.907, F = 2979, p = <0.001 (Figure 2). The normalized $\log_{10}$ length-weight relationship for male and female was: y_{male} = 3.169x - 3.851,

Table 1.—Descriptive statistics, estimated parameters ($\log_{10}$), and growth type of length-weight relationships for 298 individual *Orconectes virilis*. SE = standard error of *b*; CL = confidence limits of *b*; n = number of crayfish; +A = positive allometric growth, -A = negative allometric growth.

		Carapace length (mm)			Wetted weight (g)			Parameters of relationships					
Sex and sexual form	n	Mean (SD)	Min	Max	Mean (SD)	Min	Max	*a*	*b*	SE	CL (*b*)	r^2	Type of growth
Male	97	31.28 (8.49)	16.92	51.29	9.76 (7.94)	1.01	34.84	3.169	3.85	0.010	3.55-4.04	0.952	+A
Male form I	51	31.07 (7.05)	17.22	51.29	9.28 (6.99)	1.24	32.42	3.048	3.66	0.011	3.55-3.77	0.945	+A
Male form II	46	30.79 (9.75)	16.92	49.60	9.69 (8.96)	1.01	34.84	3.228	3.95	0.009	3.86-4.04	0.958	+A
Female	104	29.12 (9.26)	13.00	54.13	7.83 (7.52)	0.51	35.28	3.071	3.73	0.007	3.64-3.80	0.948	+A
Juvenile	97	8.73 (4.96)	2.61	22.13	0.38 (0.35)	0.05	2.13	1.137	1.54	0.037	1.50-1.58	0.815	-A
Total	298	23.55 (12.78)	2.61	54.13	6.21 (7.59)	0.05	35.28	2.129	5.44	0.008	3.12-4.00	0.910	+A

$r^2 = 0.952$, $F = 1894$, $p = <0.00$ and $y_{female} = 3.071x - 3.7342$, $r^2 = 0.9477$, $F = 1848$, $p = <0.001$, respectively.

Mean carapace length (CL ± SD), mean weight (W_{WT} ± SD), and range were calculated for male form I and male form II sex phase: $CL_{form\ I} = 31.07 \pm 7.05$ mm (range = 17.22–51.29 mm), $W_{WT\ form\ I} = 9.28 \pm 6.99$ g (range = 1.24–32.42 g), $CL_{form\ II} = 30.79 \pm 9.75$ mm (range = 16.92–49.6 mm), $W_{WT\ form\ II} = 9.69 \pm 8.96$ g (range = 1.01–34.84 g), respectively (Figure 2). The normalized ($\log_{10}$) length-weight relationship for male form I was explained by the linear equation $y = 3.048x - 3.659$, $r^2 = 0.945$, $F = 839.2$, $p = <0.001$; male form II was explained by the linear equation $y = 3.228x - 3.950$, $r^2 = 0.958$, $F = 1008.6$, $p = <0.001$; female length and weight was explained by the linear equation $y = 3.071x - 3.734$, $r^2 = 0.948$, $F = 1848.8$, $p = <0.001$; and juveniles by the equation, $y = 1.137x - 1.544$, $r^2 = 0.815$, $F = 345.1$, $p = <0.001$) (Figure 2). All adult sexual phases showed positive allometric rates of weight change with increasing length, while juvenile growth was at a negative allometric rate.

Mean carapace width (CW ± SD), mean carapace depth (CD ± SD), and the range for male and female were $CW_{males} = 15.07 \pm 4.51$ mm (range = 6.89–24.83 mm), $CD_{male} = 14.51 \pm 4.40$ mm (range = 7.22–24.60 mm), and $CW_{females} = 14.08 \pm 4.79$ mm (range = 5.72–24.52 mm), $CD_{female} = 13.98 \pm 4.494$ mm (range = 5.72–26.97 mm), respectively. Abdomen width (ABW ± SD), and the range for form I male, form II male, and female were $ABW_{form\ I} = 12.54 \pm 2.69$ mm (range = 6.87–18.543 mm), $ABW_{form\ II} = 12.13 \pm 3.98$ mm (range = 5.65–20.19 mm), and $ABW_{females} = 12.76 \pm 4.69$ mm (range = 4.89–25.01 mm), respectively.

The relationship between carapace length with carapace width ($y = 0.4902x - 0.3973$, $r^2 = 0.971$, $F = 4.039$, $p = <0.001$), carapace depth ($y = 0.4767x - 0.1899$, $r^2 = 0.980$, $F = 4.311$, $p = <0.001$), abdomen width ($y = 0.4244x - 0.4099$, $r^2 = 0.956$, $F = 5.308$, $p = <0.001$), chelae width ($y = 0.3011x - 1.0863$, $r^2 = 0.787$, $F = 8.675$, $p = <0.001$), and chelae length ($y = 0.705x - 2.1319$, $r^2 = 0.880$, $F = 1.770$, $p = <0.001$) all grew at a positive allometric rate. Mean carapace width (CW ± SD), mean carapace depth (CD ± SD), and the range were calculated for form I male, form II male,

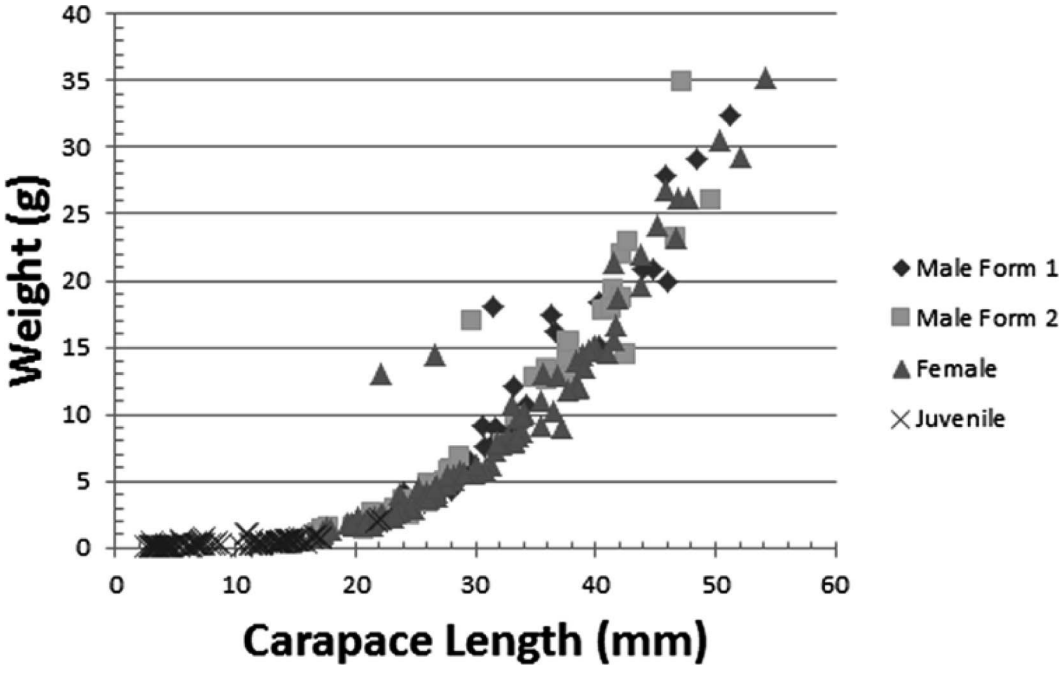

Figure 2.—Length-weight relationships for *Orconectes virilis* Hagen 1870 sexual phases. Diamonds (form I males), boxes (form II males), triangles (females), and x's (juveniles).

female, and juveniles respectively: $CW_{form\ I}$ = 15.27 ± 3.74 mm (range = 7.49–24.38 mm), $CD_{form\ I}$ = 14.44 ± 3.89 mm (range = 7.22–24.60 mm), $CW_{form\ II}$ = 14.85 ± 5.27 mm (range = 6.89–24.83 mm), $CD_{form\ II}$ = 14.59 ± 4.95 mm (range = 7.38–23.66 mm), CW_{female} = 14.08 ± 4.79 mm (range = 5.72–26.97 mm), CD_{female} = 13.98 ± 4.94 mm (range = 5.72–26.97 mm), and CW_{juv} = 4.08 ± 2.17 mm (range = 1.23–9.91 mm), and CW_{juv} = 4.41 ± 2.41 mm (range = 1.20–10.90 mm), respectively.

Carapace width (CW) growth rate increased at a negative allometric rate with weight for juveniles, while form I and form II male, female, and the general population grew with a positive allometric rate. ANCOVA tests showed that length-weight regression slopes and intercepts were significantly different among sexes and sexual stage ($p < 0.0001$). In addition, our results showed that form II male were 1.04 times heavier than form I male and 1.18 times heavier than females. Form I males were 1.95 mm larger than females and form II males were 1.67 mm larger than females. Mean total length and weight did not differ between males and females ($p > 0.060$); the only significant differences were detected among sexual stages ($p < 0.0001$).

Relationships among chelae length and width measurements for the population were evaluated for gender and sexual stage (Table 2). Mean chelae length (ChL ± SD), mean chelae width (ChW ± SD), and their range were calculated for form I, form II, and females, respectively, as $ChL_{form\ I}$ = 21.56 ± 8.47 mm (5.7-41.2 mm), $ChW_{form\ I}$ = 8.37 ± 3.61 mm (1.5-18.1 mm), $ChL_{form\ II}$ = 20.60 ± 9.26 mm (5.2-47.7 mm), $ChW_{form\ II}$ = 8.60 ± 4.12 mm (1.3-18.0 mm), and ChL_{female} = 17.05 ± 7.42 mm (4.5-36.9 mm), ChW_{female} = 7.31 ± 4.21 mm (1.1-30.5 mm).

No statistically significant difference was observed in mean ChL between form I and form II males (t-test, $p > 0.05$), but significant differences were detected in mean ChL form I male and females (t-test, $p < 0.05$) and form II male and females (t-test, $p < 0.05$). Form I male had longer ChL than either form II male or females. A similar trend was observed in mean ChW for form I and form II males, but a significant difference was observed between form II male and females ($p < 0.05$). Chela

Table 2.—*Orconectes virilis* mean and standard deviation (SD) for chelae length (ChL) and chelae width (ChW) characteristics and parameters of the relationship between ChL and ChW of each sex and sexual forms. SE = standard errors of *b*; CL = confidence limits of *b*; n = number of crayfish; r^2 = coefficient of determination.

		Chelae length			Chelae width			Parameters of relationships					
Sex and sexual form	n	Mean (SD)	Min	Max	Mean (SD)	Min	Max	*a*	*b*	SE (*b*)	CL (*b*)	r^2	*Type of growth*
Male form I	51	21.56 (8.47)	5.70	41.20	8.37 (3.61)	1.50	18.10	1.902	0.538	0.043	0.50-0.58	0.946	+A
Male form II	46	20.60 (9.26)	5.20	47.70	8.60 (4.12)	1.30	18.00	1.109	0.528	0.052	0.48-0.58	0.950	+A
Female	104	17.05 (7.42)	4.50	36.90	7.83 (7.52)	0.51	35.28	1.202	0.631	0.078	0.55-0.71	0.903	+A
Juveniles	97	5.07 (2.76)	1.34	12.64	2.14 (1.15)	0.56	5.62	0.980	0.361	0.033	0.33-0.39	0.984	-A
Total	298	11.15 (6.36)	1.23	24.97	11.04 (6.16)	1.20	26.97	1.235	0.389	0.010	0.38-0.40	0.970	+A

lengths and width increased in a positive allometric rate with CL for both adult genders and sexual stages (Table 2). In addition, chelae length-weight relationships were positively correlated with gender and sexual states (Table 2). Although the slope and intercepts of regressions for ChL and ChW were similar for form I and form II males, the slope and intercepts of regression of females were not significantly different from form I male and form II male (ANCOVA, $P > 0.05$).

DISCUSSION

The relative growth between the sexes differs only slightly as indicated by morphometric relationships. A positive allometry of all body relationships observed in both sexes and sexual phases reflects the decreasing growth rate of these morphological characters in relation to CL.

Studies focused on length-weight relationships in captive held individuals show that sexual dimorphism is common in freshwater crayfish species (Lindqvist & Lahti 1983; Holdich 2001; Mazlum et al. 2007; Wang et al. 2011). Differences in sexual dimorphism are a function of the rapid disproportionate growth of chelae in male compared to female genders. Differences in body size among sex and sexual stage was consistent with those reported in other studies (Stein 1976; Romaire et al. 1977; Rhodes & Holdich 1984; Garvey & Stein 1993; Mazlum et al. 2007; Wang et al. 2011). Juvenile crayfish grew at a negative allometric rate and rapidly attained adult sizes.

The relative growth rate of the abdomen in males form I and form II was not statistically significant; however, females were significantly different from males (ANCOVA $p > 0.001$). This is attributed to a sex-related variation (Wetzel 2002). Variation in abdomen width is commonly found in freshwater crayfish, but is always related to sex, sexual maturity, and size (Wetzel 2002). Widening of female abdomen width (ABW) reflects a sexually active female that is correlated with either swollen or white glair, dependent offspring, or remnants of egg stalks attached to pleopods (Wetzel 2002). Wetzel (2002) found that only form I females mated with form I males and reinforced the view that wide abdomens are a reflection of the act of mating and rearing offspring. Reasons for female variation may include presence of ovigerous stages of ova development, instar development during the prolonged period of

recruitment, and larval growth (Wetzel 2002). Only a small portion of the *O. virilis* females are reproductively active and exhibit the widened ABW.

In this study, the length-weight relationships showed that the largest individual females were heavier than individual males of the same length (Figure 2). The largest male (51.29 mm CL) was shorter and lighter (34.84 g) than the longest female (54.13 mm) weighing 35.28 g. No statistical difference in mean weight was observed; however, this is attributed to the accelerated development of the chelae in sexually mature form I males, whereas chelae of females grow slowly throughout life. The relatively longer chelae of form I and form II males are due to sexually dimorphic change. In summary, *O. virilis* exhibits chelae dimorphism typical of many crayfish species with form I male attaining the largest size, but differs from other crayfish by attaining large body size and weight. With this baseline understanding, further comparative studies of native crayfish species that experience displacement by *O. virilis* may be undertaken and potential competitive advantages elucidated in native and introduced range.

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