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JOURNAL OF CRUSTACEAN BIOLOGY, 33(1), 15-24, 2013

Journal of Crustacean Biology

LIFE HISTORIES OF TWO POPULATIONS OF THE IMPERILED CRAYFISH *ORCONECTES* (*PROCERICAMBARUS*) *WILLIAMSI* (DECAPODA: CAMBARIDAE) IN SOUTHWESTERN MISSOURI, U.S.A.

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ABSTRACT

The imperiled Williams' Crayfish, *Orconectes williamsi* Fitzpatrick, 1966 is endemic to southwestern Missouri and northwestern Arkansas, U.S.A., an area experiencing rapid urbanization and other land use changes. Populations of *O. williamsi* in two small streams were studied for 26 months to describe annual reproductive cycles, and gather information about fecundity, sex ratio, size at maturity, size-class structure, and growth. We captured a monthly average of more than 120 *O. williamsi* from each of the two study populations. The life history of *O. williamsi* appeared generally similar to what has been reported for several other stream-dwelling species of *Orconectes*. Breeding season occurred in mid to late autumn and perhaps into early winter. Egg brooding occurred during late winter and early spring, although it was difficult to locate females carrying eggs or hatchlings. Young of year first appeared in samples during May and June. We estimated that these populations of *O. williamsi* contained 3 or 4 size-classes; smaller *O. williamsi* grew faster than larger individuals and the mean specific growth rate was about 2% per day during summer. Life history information presented herein will be important if expected future conservation efforts are required.

KEY WORDS: crayfish, life history, *Orconectes williamsi*

DOI: 10.1163/1937240X-00002109

INTRODUCTION

Biologists require knowledge of life histories to effectively manage and conserve species of concern and those that play pivotal roles in ecosystems. Freshwater crayfishes are the third-most imperiled terrestrial or aquatic faunal group (after freshwater mussels and snails) in North America (NatureServe, 2010) with 48% of the United States (U.S.) and Canadian fauna imperiled (Taylor et al., 2007). Crayfish are also well documented as "keystone" organisms or "ecological dominants" in North American freshwater systems (Momot et al., 1978; Creed, 1994; Momot, 1995; Rabeni et al., 1995; Simberloff, 1998). Despite their ecological importance and level of imperilment, life history studies have been conducted on only about 12% (M. Moore and R. DiStefano, Missouri Department of Conservation and E. Larson, University of Tennessee, unpublished data) of the 347 U.S. and Canadian crayfish species (Taylor et al., 2007).

Orconectes williamsi Fitzpatrick, 1966 (common name, Williams' Crayfish) is a "small" crayfish (Pflieger, 1996), endemic to the upper White River drainage of southwestern Missouri and the upper White, Mulberry and Elk River drainages of northwestern Arkansas. The species is known from only 18 streams in Missouri (Westhoff et al., 2005; Westhoff et al., 2006; Missouri Natural Heritage Program, 2012) where it is listed as "imperiled" (Missouri Natural Heritage Program, 2012), and 26 streams in Arkansas where it is also listed as state "imperiled" and "globally rare" (Wagner et al., 2007; Wagner et al., 2010). There are long-term conservation concerns for this species. Construction of several major impoundments (Beaver Reservoir, Table Rock Reservoir, Lake Taneycomo, Bull Shoals Reservoir) on the upper White River fragmented populations of *O. williamsi* (Westhoff et al., 2006), restricting gene flow and source populations for recolonization (Fetzner and DiStefano, 2008). Past or current land use practices have deposited excess fine sediments in several streams in the drainage, leading to unstable and shifting substrate (Bayless and Vitello, 2002; Jacobson, 2004). Rapid urbanization in the surrounding region (Center on Urban and Metropolitan Policy, 2002), livestock pasturing, and a large number of concentrated animal feeding operations (swine and poultry) present water quality challenges such as increased inputs of fine sediments and elevated nutrient concentrations (Bayless and Vitello, 2002).

Effective conservation strategies for *O. williamsi* will require knowledge of its distribution, habitat requirements, population genetics, and life history. Biologists have recently completed studies on this species' distribution (Westhoff et al., 2006; Wagner et al., 2007; Wagner et al., 2010),

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DOI:10.1163/1937240X-00002109

habitat associations (Westhoff et al., 2006), and population genetics (Fetzner and DiStefano, 2008), but no information exists concerning life history (Pflieger, 1996; Wagner et al., 2010). Our goal was to examine life history characteristics of *O. williamsi* populations in two streams to account for possible variation due to local environmental conditions. Specifically, we aimed to describe these two populations' annual life cycles, and to gather additional information about population size structure and growth.

Materials and Methods

Study Sites

We conducted our study in two streams, Emory Creek and Roark Creek, in the upper White River drainage of Taney County, Missouri (Fig. 1). Emory Creek is a second order tributary to Bull Creek (which flows directly into Lake Taneycomo). The Emory Creek site (X-UTM coordinate 480574, Y-UTM coordinate 4064442, Zone 15 N) was located 7.7 km north of Branson, Missouri. The Roark Creek site (X-UTM 474403, Y-UTM 4059615, Zone 15 N) was located on a second order (Strahler, 1957) stream reach in Ruth and Paul Henning Conservation Area, 1 km east of Garber, Missouri. These two stream sites were each approximately 0.7 km in length, had alternating riffles and pools, and were about 3-9 m wide (wetted channel width) and <0.5 m in water depth (Emory Creek), and about 4-11 m wide and <1.0 m deep (Roark Creek) during June flows, although both ceased flowing at least once during the study. Despite increasing urbanization in the surrounding region, both of these watersheds had well-forested riparian corridors. Both stream sites also included *Orconectes ozarkae* Williams, 1952, and *Orconectes neglectus chaenodactylus* Williams, 1952, in their crayfish communities. Unless otherwise stated, study sampling occurred over the 26-month period from July 2004-August 2006.

Life Cycle Field Sampling

Sampling typically occurred during the middle of every month. Diel seining throughout all major habitats (i.e., riffles, runs, pools, stream margins, root wads) was the primary method used to sample crayfish, but it was supplemented with hand collections and occasionally with overnight baited trapping. Seining and hand collections were typically conducted for about 3 hours at each site with a goal of collecting at least 100 *O. williamsi*. Low numbers of crayfish (about 12 per site per month) were collected at both sites during December 2005-February 2006 due to low flows and ice covering the streams, and also during September 2004 (0 crayfish at Emory Creek, 6 crayfish at Roark Creek) when both stream sites were completely dry. Water temperature was recorded continuously at both stream sites using remote Tidbit_v2 temperature loggers (Onset Computer Corporation, Cape Cod, MA, U.S.A.) as an additional means to evaluate life cycle patterns. Furthermore, we collected additional data during June through August of 2007 and 2008 to assess growth for both populations.

Data recorded for each crayfish captured included sex, carapace length (CL, from tip of rostrum to the posterior border of the thoracic region,

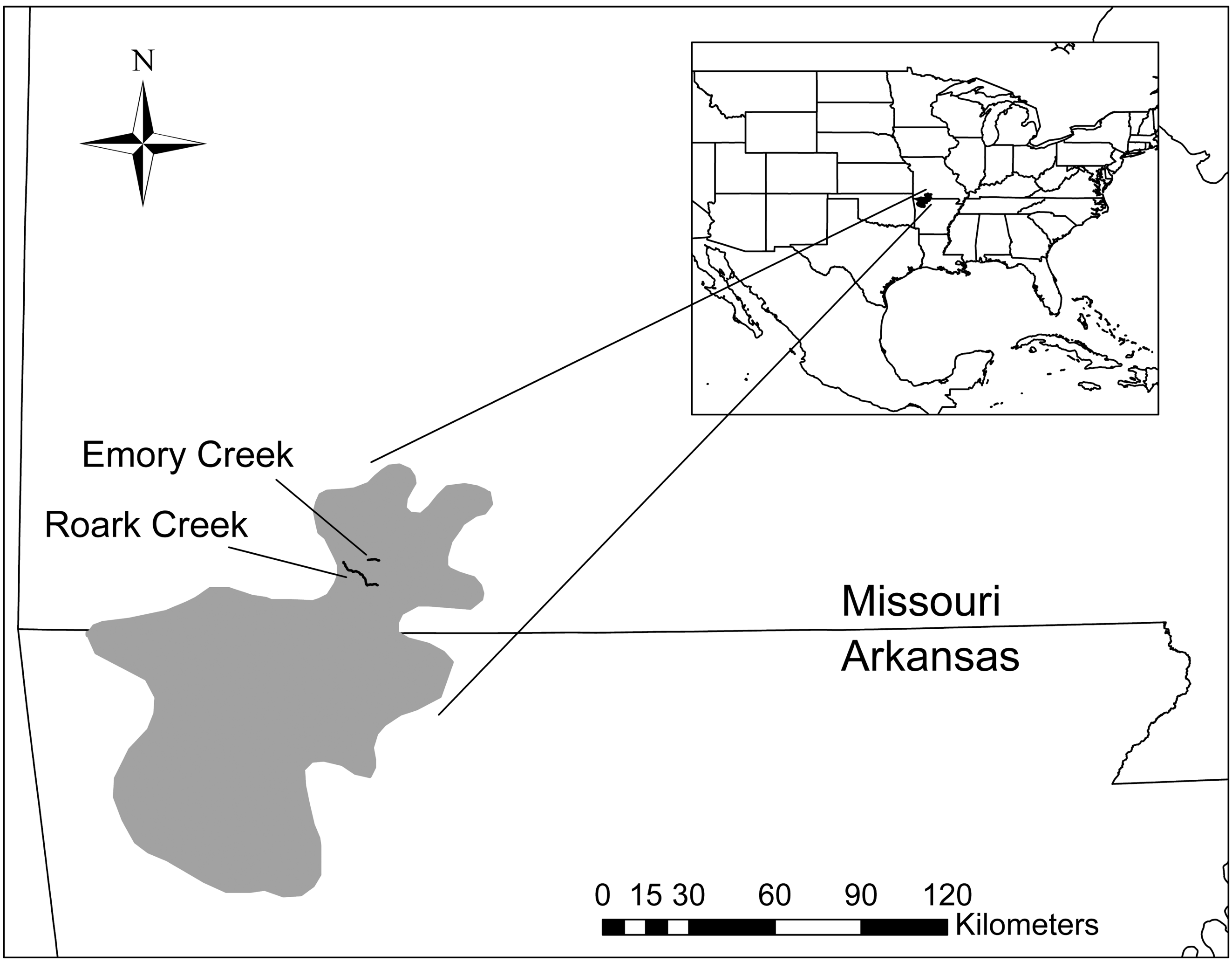

Fig. 1. Geographic range (gray shading) of *Orconectes williamsi* (from Westhoff et al., 2006; Wagner et al., 2007), and location of Emory Creek and Roark Creek study streams in Missouri, U.S.A.

to nearest 0.1 mm), evidence of recent molting (judged by softness of exoskeleton or very clean and slippery exoskeleton; Muck et al., 2002a, 2002b), male reproductive form (Form I = reproductively active, Form II = reproductively inactive or immature; Riggert et al., 1999), and indications of female reproductive activity. Reproductive indications included the presence of eggs, hatchlings, visible active glair glands around the base of pleopods and/or on uropods (Stephens, 1952), and mucilaginous sperm plugs in the annulus ventralis indicating successful mating (Andrews, 1904; Fielder, 1972). Realized fecundity (Corey, 1987b; Stechey and Somers, 1995) was estimated by recording numbers of abdominal (external) eggs in the field for nine ovigerous females (7 and 2 from Emory and Roark creeks) whose clutches appeared to be intact (not damaged during our collection); those females were transported to the laboratory where eggs were removed, counted again, and mean egg diameters (to nearest 0.1 mm) were estimated (Muck et al., 2002a) based on 10 eggs.

We employed two approaches to document the growth of *O. williamsi* during the supplemental 2007-2008 data collection. First, we assessed growth rate *in situ* by tagging individuals with visible implant elastomer (VIE) tags (Northwest Marine Technologies, Inc., Shaw Island, WA, U.S.A.). Second, we developed CL-weight models for males and females separately in each population.

We selected three stream reaches for mark-recapture, averaging 30 m in length, nested within each Emory Creek and Roark Creek study site. We used only riffle-run reaches (no pools) as *O. williamsi* has a strong affinity for riffle habitats (Westhoff et al., 2006). We initially captured, tagged, and released 306 crayfish during July-August 2007 and then conducted monthly recapture sampling the following summer in June-August 2008, i.e., three sampling periods. During summer 2008 we captured, tagged, and released an additional 1438 new crayfish. Initial captures were conducted primarily during daylight hours using timed (30 s/m^2) hand-net searches, but supplemental collections were made using diurnal seining, nocturnal hand-net searches, and overnight baited trapping. In total, during 2007-2008 we tagged and released 1744 *O. williamsi*: 722 in Emory Creek (364 male, 358 female); and 1022 in Roark Creek (505 male, 517 female).

When an individual of *O. williamsi* was captured, it was measured/processed as previously described, but also wet-weighed to the nearest 0.01 g. Crayfish $\geqslant$ 10 mm CL were injected with a VIE tag into the abdominal tissue as this location provides high retention rates in crayfish, e.g., $\geqslant$92% for *Cherax destructor* Clark, 1936 (Jerry et al., 2001) and 100% for *Orconectes obscurus* (Hagen, 1870) (Clark and Kershner, 2006). Crayfish were tagged using the method outlined by Hollows (1998) which allows 255 animals to be tagged per VIE color, and crayfish were released along a transect perpendicular to stream flow at the center of the riffle/run from which crayfish were originally captured.

Recapture efforts in 2008 began at the downstream periphery of each riffle-run reach and were conducted by operating seines and hand-nets in a zigzag upstream pattern to increase the area covered. All crayfish were placed in a bucket containing fresh water until they could be identified to species and examined for VIE tag presence. Unmarked *O. williamsi* ($\geqslant$10 mm CL) were then tagged and released as previously described.

Data Analysis

Life cycle analyses largely concerned adult *O. williamsi*; therefore, adult CL "thresholds" were established for the smallest crayfish exhibiting sexual maturity (females indicating reproductive activity and Form I males) within each population (Payne and Price, 1983). Descriptive statistics and frequency histograms summarized temporal life cycle changes. We used CL-frequency histograms to examine seasonal changes in size-class structure. Separation between size classes was agreed upon by two independent observers and assessed as the lowest point between two parabolic shapes; a method providing at least 80% accuracy for *Orconectes* spp. (Momot, 1967). We determined that interannual variation in size structure was small, and thus months were pooled across years to facilitate visual delineation of size classes. Final analysis relied primarily on data from April and July, although data from other months were used secondarily to confirm apparent trends. April and July were selected because young-of-year (YOY, age 0) were generally not susceptible to our sampling until after April, and July represented the first month in which large numbers of YOY were readily collected in our samples for both sites in most years. Thus April and July provided the strongest contrast in size classes. In addition, Pearson correlation and linear regression were used to explore relationships between CL and field/laboratory enumeration of external abdominal eggs (CORR and REG procedures; SAS Institute, 2008).

We measured growth rate using specific growth rate (SGR), the "parameter of choice" for evaluating freshwater crayfish growth, especially when young crayfish are included in the analysis (Evans and Jussila, 1997). We measured summertime growth for crayfish recaptured at least 3 d and up to 329 d after being tagged, with most being recaptured in the 2-4 week range (median time from tagging to recapture = 15 d). Recapture rate was low, and we had only 36 recaptures available for SGR analysis: 27 from Roark Creek and 9 from Emory Creek. Specific growth rate as % weight increase per d was calculated using the following formula:

$$\mathrm{SGR} = \frac{\ln(W_f) - \ln(W_i)}{\text{Number of days}} \times 100,$$

where W_i = initial wet body weight and W_f = final wet body weight (Wurtsbaugh and Cech, 1983; Laha and Mattingly, 2007). Linear regression models were fitted using program R (R Development Core Team, 2011) to assess the relationship between SGR (% per d) and CL (mm) at initial marking. The effect of site was not examined because of uneven sample sizes between sites. The preliminary model included CL, sex, and their interaction in order to examine differences in SGR between sexes. However, the main effect of sex and the interaction term were not statistically significant, and therefore we report a simple regression model with both sexes pooled.

Finally, Program R was used to develop a CL-wet weight regression model for each sex at each site, using the CL-weight data collected during 2007-2008. Both CL and wet weight were log-transformed prior to analysis, and the following model was fitted to account for nonlinearity:

$$\log(\text{wet weight}) = a + b(\log(\mathrm{CL})).$$

Statistical significance was $\alpha = 0.05$ throughout.

RESULTS

Fitzpatrick (1966) described *O. williamsi* as having a "ground color which is light brown or tan" with dark brown or black mottling over the entire body, whereas Pflieger (1996) described an "olive-brown" or "reddish-tan" uniform color with a "pale, vase-shaped zone" present along the carapace midline. We noted that most *O. williamsi* in the Emory Creek and Roark Creek populations were olive-brown or tan in color, but about 3-7% of both adults and YOY were bright reddish or orange in color. The vast majority, but not all specimens possessed the "vase-shaped" pattern described by Pflieger (1996).

Reproductive Cycle

We collected monthly means of 136 (SE = 14) and 122 (SE = 12) *O. williamsi* at Emory and Roark creeks. Most males in both creeks were reproductively inactive (Form II) throughout much of the year, but we observed multiple peaks annually in the relative proportion of reproductively active (Form I) males (Fig. 2). The peak in proportion of Form I males occurred in late autumn through winter (December-March) for both study years, although data from December 2005-February 2006 should be interpreted with caution due to previously stated small sample sizes. Males in both populations began molting to Form I in increasing numbers in September or October, and relative percentages of adult (Table 1) Form I males (out of all males) peaked in January and February at 54-75% in Emory Creek and at 64-82% in Roark Creek. Males that were not sexually mature when the relative proportion of Form I males peaked averaged 14.8 mm CL (SE = 0.3) and 14.3 mm CL (SE = 0.3) for Emory and Roark creeks, and appeared to be mostly YOY.

The onset of visible glair development in females varied among years but was generally first observed in summer

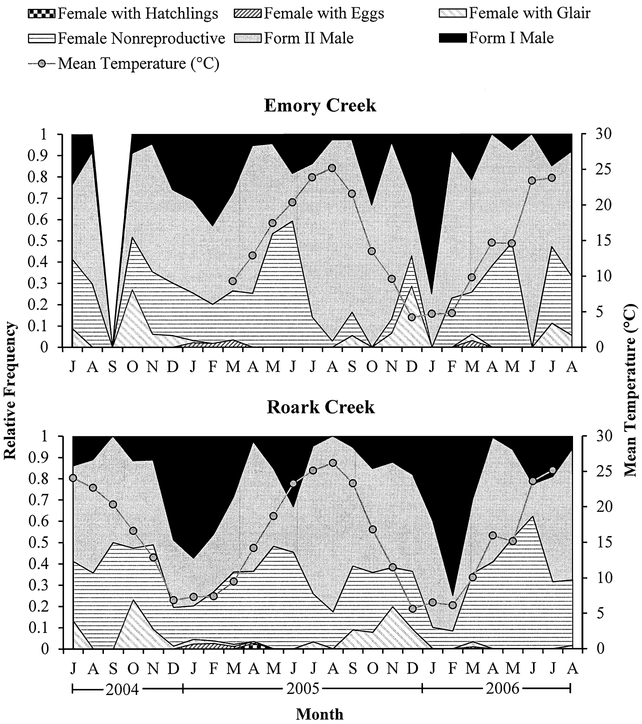

Fig. 2. Reproductive state of mature male and female *Orconectes williamsi*. Percentage occurrence is the percentage of crayfish in a reproductive state from July 2004-August 2006 in Emory and Roark creeks relative to all mature individuals found in that sampling period. Mature *O. williamsi* were all crayfish that had reached the minimum size of sexual maturity (see Table 1).

(Fig. 2). The presence of visible active glair glands peaked in Emory Creek in October 2004 and December 2005, when the percentage of mature-sized females with glair (relative to all females) was 52% and 67%; visible glair peaked in Roark Creek in October 2004 (49% of mature-sized females) and November 2005 (52%). No sperm plugs were observed on any female *O. williamsi*. Only 10 and 9 ovigerous females (carrying external eggs on the pleon) were observed in Emory and Roark creeks. Ovigerous females were observed in Emory Creek from January-March in 2005 (Fig. 2). Three ovigerous females were also observed in Emory Creek in March 2006 (monthly mean water temperature of 9.8°C). Ovigerous females were observed in Roark Creek during January-April (all four months) of 2005 (7-14°C), and only in March of 2006 (9-10°C). Only 3 females bearing hatchlings were collected in our study (April 2005).

Young-of-year *O. williamsi* (CLs of about 5 or 6 mm) were first observed in May at both sites. May 2005 samples contained many YOY, whereas May 2006 samples contained relatively fewer YOY perhaps suggesting a later hatch that year. Recruitment of YOY was largely completed in both populations by July 2004 and 2005 and in Roark Creek by July 2006 when fewer than 2% of all *O. williamsi* collected were <7 mm CL. Recruitment of YOY in Emory Creek in 2006 did not appear to be completed until August. *Orconectes williamsi* YOY appeared in our samples before YOY of sympatric *O. ozarkae* and *O. n. chaenodactylus*.

We observed only 94 and 21 recently molted *O. williamsi* in Emory and Roark creeks (61 males, 54 females), over the study, making it difficult to discern temporal patterns (Fig. 3). Molting was observed primarily in late winter through summer at both sites in both years. A late winter synchronous molting period peaked during March 2005 (mean monthly water temperatures of 9-10°C) and April 2006 (14-15°C) at both sites when all males molted to Form II. We observed 50% (27 individuals) of all female molts during spring. Molting activity in summer appeared to be associated almost entirely with YOY incremental growth, with little indication of molting to a reproductive state. None of the 54 recently molted males we recorded had molted to Form I. Yet, during summer 2008 sampling we observed that 8 of 9 recently molted males > 18.0 mm CL were Form I. Little evidence of molting was noted in Emory Creek during autumn and early winter of both years, except for 4 crayfish (out of 119 collected) in November 2004 and 3 crayfish (out of 167 collected) in August 2005. This period of little observed molting corresponded with water temperatures decreasing from 26°C in August to around 5.5-6.5°C in winter (2005-2006). We observed little evidence of molting in Roark Creek during autumn and early winter of both years when water temperatures were decreasing from 23°C to a low of ≈7°C.

Fecundity

Ovigerous *O. williamsi* females ranged in size from 17.5-25.7 mm CL (Table 1), and laboratory counts indicated they carried between 28 and 132 abdominal eggs ($\bar{x} = 70$, $N = 9$; Fig. 4). A positive linear relationship existed between the total number of eggs and CL (Eggs = −238.0 + 14.7 [CL]; $P = 0.0001$, $R^2 = 0.89$). There was also a significant positive relationship between field and laboratory egg counts (Laboratory egg count = 0.90 + 1.08 [Field egg count]; $P < 0.0001$, $R^2 = 0.99$). Mean egg diameter ranged from 1.9-2.7 mm, and was positively related with female's CL (Egg diameter = 0.78 + 0.07 [CL]; $P = 0.0251$, $R^2 = 0.54$).

Sex Ratios

Sex ratios of *O. williamsi* were skewed toward males with total male : female sex ratios of 2.03 and 1.59 for Emory and Roark creeks. Spring was the only season where male:female sex ratios approached 1.00 or an even ratio. Highest ratios were in winter; 3.15 and 2.45 for Emory and Roark creeks, and May (0.93 in Emory Creek, 0.97 in Roark Creek) and June (0.96 in Emory Creek, 0.78 in Roark Creek) were the only months when females outnumbered males.

Size at Maturity

Orconectes williamsi had the potential to reproduce in their first year. The smallest sexually mature crayfish were 15.1 and 11.9 mm CL for females and 11.6 and 9.9 mm CL for males in Emory and Roark creeks (Table 1). Both sexes at both sites had typically matured by a size of 15 mm CL, and perhaps at a smaller size in Roark Creek (Fig. 5).

Size-class Structure

The CL of *O. williamsi* ranged from 3.6-25.7 mm and 4.1-26.4 mm in Emory and Roark creeks (Table 1, Fig. 5). The April CL-frequency distributions (Fig. 5), prior to recruitment of YOY, indicated much variation in growth of the previous year's YOY, with the peak of that first size

Table 1. Carapace lengths and chela widths at widest point (right chelae, none regenerated) of various life history stages for *Orconectes williamsi* in Emory and Roark creeks. Adult females were designated as those larger than the smallest to show signs of reproductive activity; Emory Creek ⩾ 15.0 mm CL[1]; Roark Creek ⩾ 11.9 mm CL[1]. Adult males were designated as those larger than the smallest Form I; Emory Creek ⩾ 11.6 mm CL[1]; Roark Creek ⩾ 9.9 mm CL[1]. [1]Some "juveniles" are reported to have CLs greater than the smallest size to show signs of sexual maturity because they were measured in spring, prior to recruitment of the next YOY-class; [2]Nonreproductive females were all females showing no signs of active glair glands, no eggs, nor any hatchlings.

Life cycle stage	Carapace length (mm) mean ± SE (range)	*N*	Chela width (mm) mean ± SE (range)	*N*
Emory Creek				
All crayfish	13.1 ± 0.1 (3.6-25.7)	3508	–	–
All adult females	18.3 ± 0.1 (15.1-25.7)	527	2.4 ± 0.1 (0.7-7.9)	202
[2]Nonreproductive females	18.1 ± 0.1 (15.1-25.2)	459	4.3 ± 0.2 (2.9-6.4)	14
Females with glair	19.2 ± 0.2 (15.1-24.8)	58	–	–
Ovigerous females	21.5 ± 0.6 (20.0-25.7)	10	–	–
Females with hatchlings	–	0	–	–
All males	16.1 ± 0.1 (11.6-25.6)	1072	3.7 ± 0.2 (1.6-7.9)	33
Form I males	19.6 ± 0.1 (11.6-25.6)	228	6.4 ± 0.5 (5.4-7.9)	4
Form II males	15.1 ± 0.1 (11.6-24.2)	844	3.3 ± 0.2 (1.6-4.9)	29
All juveniles[1]	10.1 ± 0.1 (3.6-15.0)	1909	2.0 ± 0.0 (0.7-3.8)	155
Roark Creek				
All crayfish	13.8 ± 0.1 (4.1-26.4)	3129	3.4 ± 0.2 (0.7-8.4)	100
All adult females	15.9 ± 0.1 (11.9-24.6)	875	3.7 ± 0.2 (1.7-7.3)	29
[2]Nonreproductive females	15.7 ± 0.1 (11.9-24.6)	777	3.7 ± 0.2 (1.7-7.3)	29
Females with glair	17.9 ± 0.3 (11.9-23.2)	88	–	–
Ovigerous females	19.4 ± 0.6 (17.5-21.3)	9	–	–
Females with hatchlings	19.3 ± 1.4 (17.4-22.1)	3	–	–
All males	15.4 ± 0.1 (9.9-26.4)	1389	3.8 ± 0.2 (1.5-8.4)	52
Form I males	18.3 ± 0.1 (9.9-26.4)	413	6.6 ± 0.4 (4.4-8.4)	9
Form II males	14.1 ± 0.1 (9.9-23.8)	976	3.2 ± 0.2 (1.5-6.9)	43
All juveniles[1]	9.2 ± 0.1 (4.1-11.8)	865	2.1 ± 0.1 (0.7-3.0)	19

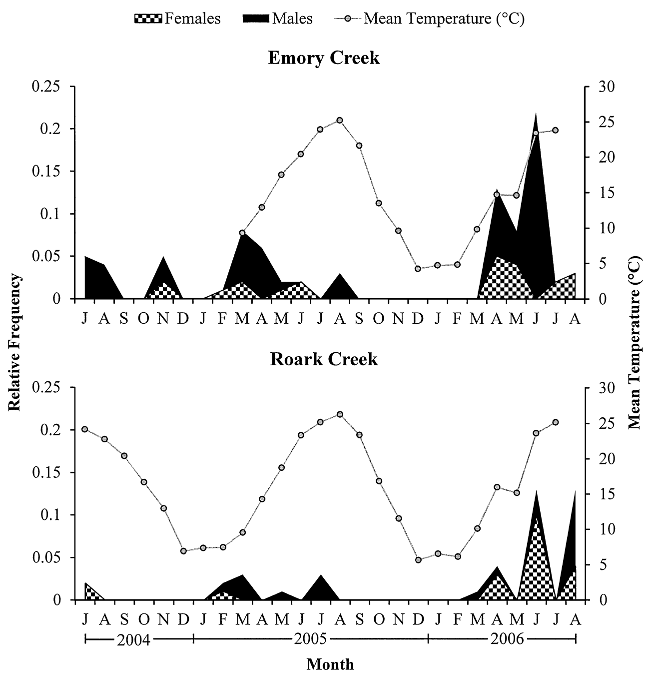

Fig. 3. Monthly molting activity of *Orconectes williamsi* in Emory (top) and Roark (bottom) creeks, with super-imposed mean monthly water temperatures (°C). Data points represent proportion of recently molted crayfish collected relative to all crayfish collected for each sex during that sampling period.

class measuring about 14-17 mm CL at both sites. July CL-frequency distributions were different than those in April. July CL distributions (with confirmation from other months) suggested the presence of three to four size classes. The peak of the second size class at that time was 12-17 mm CL, and the peak of the third size class in July was 19-22 mm CL.

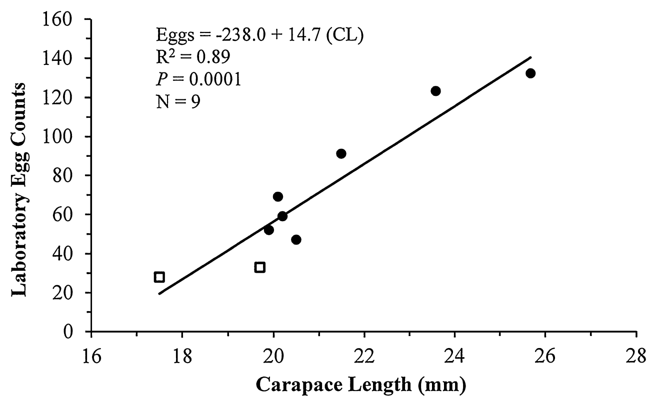

Fig. 4. Relationship between *Orconectes williamsi* carapace length (mm) and fecundity (number of external abdominal eggs counted in laboratory). $N = 9$ female crayfish: 7 from Emory Creek (solid circles); 2 from Roark Creek (open squares).

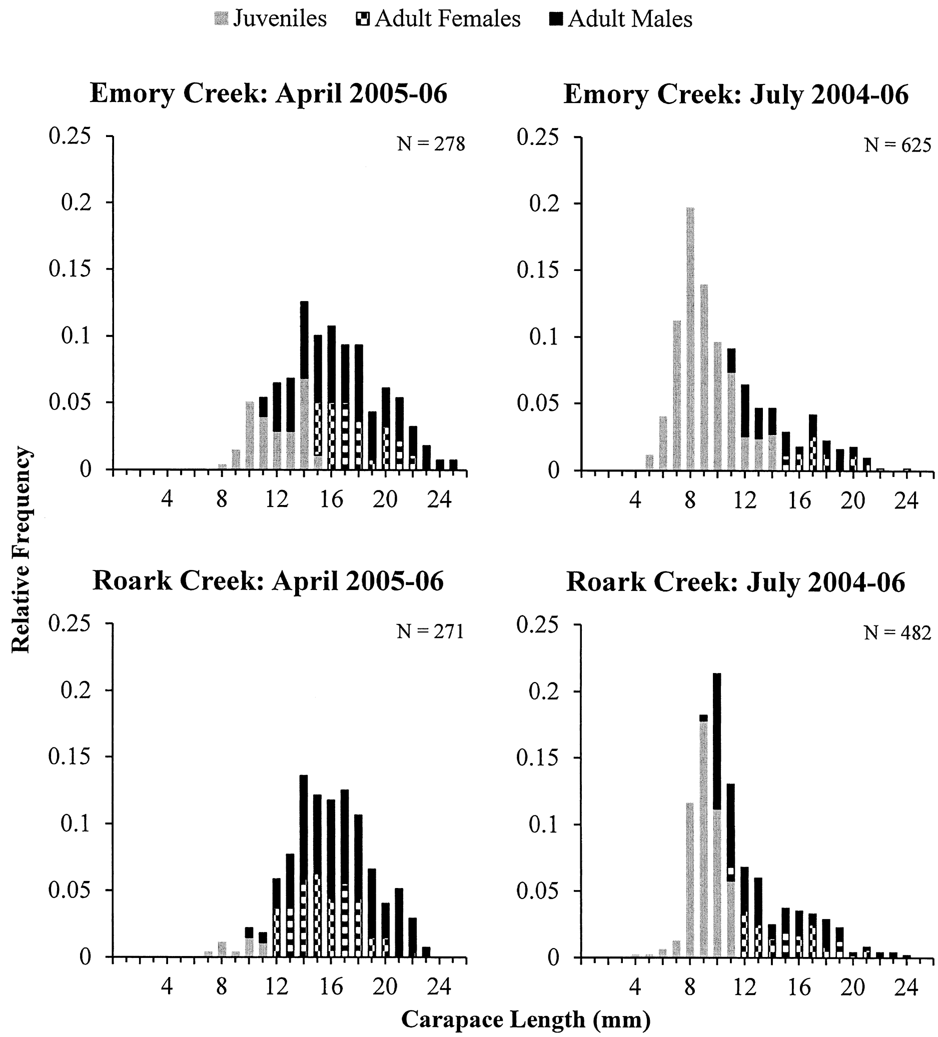

Fig. 5. An example of Emory Creek (top panel) and Roark Creek (bottom panel) *Orconectes williamsi* population size structure as depicted by carapace length-frequency distribution histograms from April 2005 and 2006, and July 2004, 2005, and 2006 (years pooled). $N = 278$ and $N = 625$ in Emory Creek in April and July. $N = 271$ and $N = 482$ in Roark Creek in April and July.

Growth Analyses

Smaller crayfish exhibited higher SGRs than larger crayfish (Fig. 6). The effect of CL at time of initial tagging was significant ($P = 0.004$; $R^2 = 0.23$) and is given by the linear model, SGR = 5.294-0.231(CL). Thirty-five of 36 individuals exhibited SGRs of <5% per d, but a 12-mm-CL male recaptured only 3 days after initial tagging in Emory Creek had molted, grown > 9% per day and was removed from the analysis as an outlier (Fig. 6). Mean (± SD) SGR was 1.96 ± 0.97% per d for all 35 crayfish (outlier excluded). Mean SGRs were 2.44 ± 1.08, 1.88 ± 0.57, and 1.10 ± 0.50% per d for the smallest (<14 mm CL; $N = 16$), intermediate (14-16 mm CL; $N = 11$), and largest crayfish (>16 mm CL; $N = 8$).

Carapace length-wet weight relationships followed non-linear trends (Fig. 7). Log-log regressions were nearly identical between males and between females at both sites (Fig. 7). Slope coefficients were 3.46 (SE = 0.03) and 3.43 (SE = 0.03) for males, and 3.20 (SE = 0.03) and 3.22 (SE = 0.02) for females in Emory and Roark creeks, indicating males grew heavier than females of the same size.

Discussion

Life Cycle

The timing of *O. williamsi* reproductive life cycle events appeared generally similar among study years and between sites. However, the slight interannual variation in some parameters likely resulted from both an artifact of monthly sampling frequency (versus more frequent) and natural variation in environmental factors, e.g., hydrologic patterns and water temperature regimes. For example, egg maturation and oviposition are partially regulated by temperature regimes (Aiken, 1969) that vary among years. The variation we observed underscores the importance of selecting appropriate sampling frequency and study duration when planning crayfish life history investigations.

Muck et al. (2002a, 2002b) and Larson and Magoulick (2008) observed few intra-specific differences in the timing of reproductive events in *Orconectes* spp. among multiple

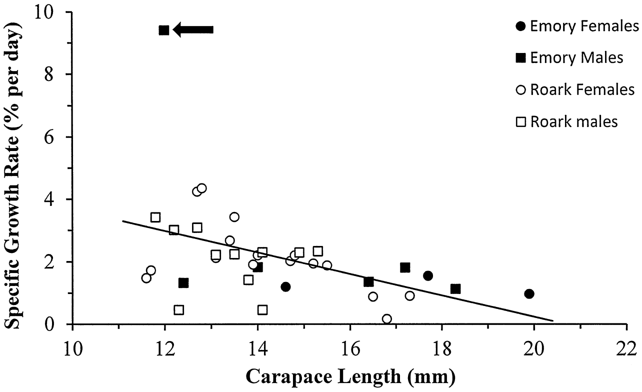

Fig. 6. Relationship between carapace length at first marking (mm) and specific growth rate (SGR, % increase in weight per d) for *Orconectes williamsi* from Emory (denoted with solid squares for males and solid circles for females) and Roark (denoted with open squares for males and open circles for females) creeks collected in 2007 and 2008. The observation denoted by an arrow was not included in any analysis as it represents an Emory Creek male that molted just prior to tagging and was recaptured three days later, resulting in an unusually high SGR.

sites in a single stream. However, our study and others that simultaneously examined populations in multiple streams (Corey, 1988; DiStefano et al., 2002) recorded variation in the timing of several reproductive events, suggesting the importance of simultaneously collecting data at multiple streams to obtain more robust estimates of crayfish species' life histories.

Peaks in relative numbers of males molting to Form I and females with active glair glands suggest that the breeding season of *O. williamsi* occurred in mid-to-late autumn, perhaps extending into early winter. This general pattern was similar to reports for several other stream-dwelling species of *Orconectes*, although males of *O. williamsi* molted to Form I slightly later than recorded for some species (Van Deventer, 1937; Boyd and Page, 1978; DiStefano et al., 2002) and females showed active glair glands slightly earlier than some species (Boyd and Page, 1978; Payne and Price, 1983; Muck et al., 2002a).

Female *O. williamsi* never showed the mucilaginous sperm plugs that are used to help confirm the timing of breeding season for other *Orconectes* (Andrews, 1904; Prins, 1968; Fielder, 1972; Riggert et al., 1999). However, several studies involving *Orconectes* (Pippitt, 1977; DiStefano et al., 2002; Muck et al., 2002a, 2002b) reported infrequent or no sperm plugs, even when females without such plugs later oviposited (Larson and Magoulick, 2008). Failure to observe sperm plugs might be explained by their erosion over time (Crocker and Barr, 1968; Berrill and Arsenault, 1982) or by a tendency for a population's fertilized females (with sperm plugs) to sequester themselves when laying or brooding eggs (Prins, 1968).

Female *O. williamsi* reproductive activity during late winter and early spring generally coincides with other stream-dwelling species of *Orconectes* (Van Deventer, 1937; Boyd and Page, 1968; Prins, 1968; Weagle and Ozburn, 1972; Payne and Price, 1983; Corey, 1988; Mitchell and Smock, 1991; Muck, 1996; Riggert et al., 1999; DiStefano et al., 2002; Muck et al., 2002a, 2002b; Larson and Magoulick, 2008). Some notable intraspecific temporal differences have been reported; *Orconectes virilis* (Hagen, 1870) in northern Ontario (Weagle and Ozburn, 1972) brooded later than *O. virilis* in Virginia (Mitchell and Smock, 1991), and multiple populations of *Orconectes propinquus* (Girard, 1852) within southwestern Ontario showed temporal differences of several weeks (Corey, 1988). Such differences might be attributable to differences in water temperature. However, recruitment of YOY *O. williamsi* preceded recruitment of sympatric *O. ozarkae* and *O. n. chaenodactylus* at the same sites by several weeks, and suggests possible interspecific temporal differences in oviposition and brooding among these congeners. Such interspecific differences were previously reported from an Ozark stream where patterns in *O. ozarkae* and *Orconectes luteus* (Creaser, 1933) differed from those of sympatric *Orconectes punctimanus* (Creaser, 1933) (Muck, 1996).

We observed only 19 female *O. williamsi* carrying eggs and only three carrying hatchlings in our study, despite considerable efforts to locate them. Ovigerous females constituted only 11% (Emory Creek) and 5% (Roark Creek) of all females collected. Eight other studies of stream-dwelling species of *Orconectes* reported that ovigerous females made up 2-90% of females collected in their spring samples, but also that at least 30% of the female population was berried at some time during spring (Van Deventer, 1937; Prins, 1968; Corey, 1988; Mitchell and Smock, 1991; Riggert et al., 1999; Muck et al., 2002a; Larson and Magoulick, 2008). The studies of the life history of few stream-dwelling *Orconectes* reporting females bearing hatchlings, recorded only a few such females and suggested they were highly reclusive during that life stage (Van Deventer, 1937; Prins, 1968).

Brooding habitat observations on 11 of the 19 ovigerous *O. williamsi* indicated that 8 were collected in low current velocity margins of riffle or run habitats, 2 were in high-velocity riffle habitats, and 1 was collected from a plunge pool. Five of those 11 females were found under individual pieces of cobble or boulder (>65 mm diameter). Two of the 3 hatchling-bearing females were found under cobble/boulder in high-velocity riffles. Similarly, a subsequent study of this species' habitat use during "reproductive seclusion" failed to locate ovigerous or hatchling-bearing females, although several adult females were observed without eggs or young during the spring brooding period (Black, 2011). The few occasions when equal sex ratios were observed coincided with non-reproductive months, whereas sex ratios were highly skewed toward males during most months. The difficulty locating mature females of this species in the field may be due to its ability to burrow deeply (30 cm or deeper) into stream substrates (DiStefano et al., 2009). Habitat preferences of females of this life stage warrant future study. This reproductive seclusion appears rather unique for this species: previous studies of stream-dwelling species of *Orconectes* typically reported large numbers of berried females (Van Deventer, 1937; Mitchell and Smock, 1991; Riggert et al., 1999; Muck et al., 2002a; Larson and Magoulick, 2008).

The observed size range of ovigerous *O. williamsi* was within that observed for several other species of *Orconectes*,

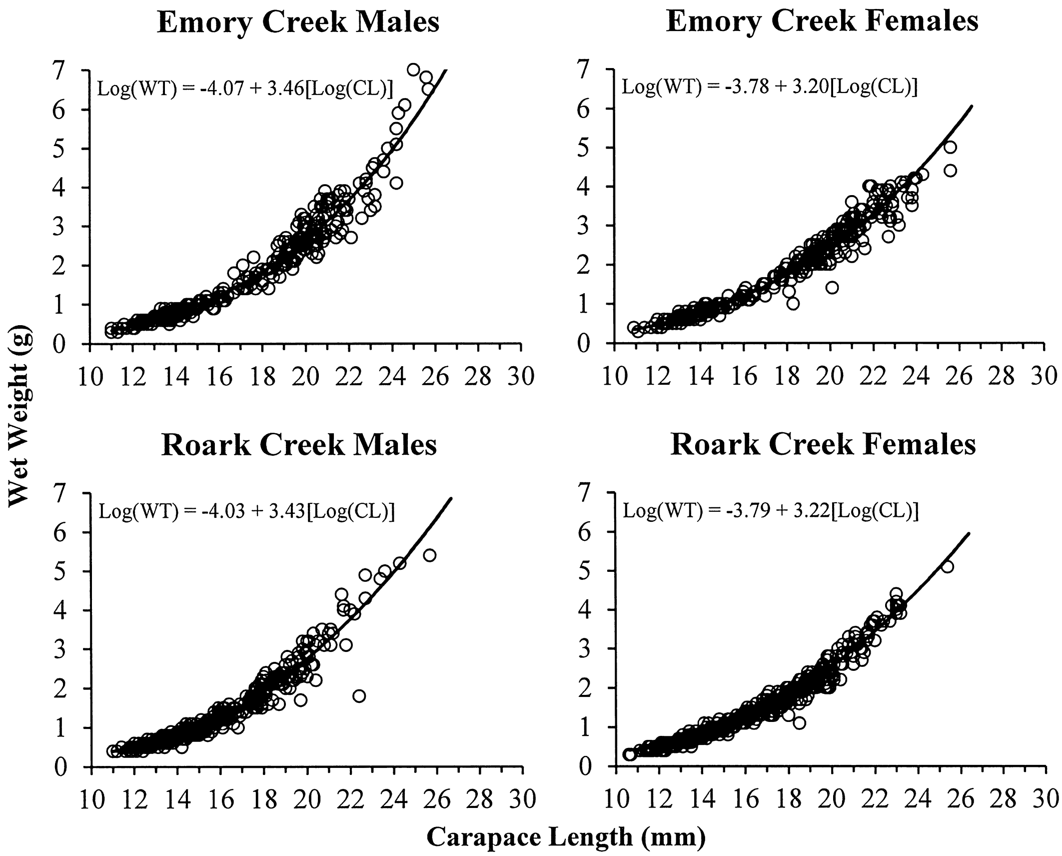

Fig. 7. Log-transformed carapace length-wet weight regressions for male and female *Orconectes williamsi* from Emory and Roark creeks during 2007 and 2008.

with other species carrying eggs at both smaller sizes, e.g., *O. luteus* (in Muck et al., 2002a), and larger sizes, e.g., *Orconectes hylas* (Faxon, 1890) (in DiStefano et al., 2002). *Orconectes williamsi* realized fecundity was notably lower than that reported for several (Boyd and Page, 1968; Prins, 1968; Weagle and Ozburn, 1972; Mitchell and Smock, 1991; Muck, 1996; DiStefano et al., 2002; Muck et al., 2002a, 2002b) but not all (Larson and Magoulick, 2008) other stream-dwelling species of *Orconectes*. Egg diameter was similar to that reported for other species of *Orconectes*, although larger than that of *O. luteus* (Muck et al., 2002a). However, it is important to note that our estimates of *O. williamsi* size range of berried females, fecundity, and egg size are based upon a small sample size. Fecundity data also indicated that field counts of external abdominal eggs only slightly underestimated (by 9%) laboratory counts, suggesting that field counts might be relied upon to approximate *O. williamsi* realized fecundity.

The positive correlation we observed between *O. williamsi* CL and egg counts was previously observed for 9 other species of *Orconectes* (Boyd and Page, 1968; Prins, 1968; Weagle and Ozburn, 1972; Corey, 1987a, 1988; Muck, 1996; DiStefano et al., 2002; Muck et al., 2002a, 2002b). The positive correlation we noted between *O. williamsi* CL and egg size was reported for two other species of *Orconectes* (Muck et al., 2002a, 2002b).

Size-class Structure

Both *O. williamsi* populations had total average CLs (Emory = 13.1 mm, Roark = 13.8 mm; Table 1) slightly lower than Arkansas *O. williamsi* reported by Wagner et al. (2010; 16.5 mm); maximum CLs for both populations were fairly similar to Arkansas populations (Wagner et al., 2010; 27 mm).

Our estimate of 3-4 *O. williamsi* size classes conforms to 10 of the 12 studies that estimated stream-dwelling species of *Orconectes* to have 3-4 age classes. Populations of *O. virilis* and *O. n. chaenodactylus* were reported to have 2-3 age classes (Mitchell and Smock, 1991), and 4-5 classes (Price and Payne, 1984a), respectively. Accurate determination of crayfish population size- or age-class structure requires sampling the available stream habitat types proportionately, because each size (or age) class is not distributed equally throughout all habitats (Muck et al., 2002a). Although we made an effort to sample in all major habitat types proportionately, we did not quantify these attempts, thus potentially reducing the accuracy of our size-class structure results.

Growth

Several environmental factors influence crayfish growth (Reynolds, 2002; Seiler and Turner, 2004), in particular water temperature which has a strong effect on aquatic ectotherms (Brett, 1979). In our study, mean monthly summer water temperatures typically ranged between 20-25°C in Emory and Roark creeks in 2004-2006 (Fig. 3). The summer-based SGRs averaged 2% per d in 2007-2008, similar to those reported by Tropea et al. (2010) for *Cherax quadricarinatus* (von Martens, 1868) after a year of culture at 27-30°C, where SGR decreased over time from approximately 6% to 2% per d. We expect *O. williamsi* SGRs would be lower than 2% per d during colder seasons of the year.

Orconectes williamsi CL-weight relationships were remarkably consistent between sites, indicating very similar growth patterns for these two populations. We noted differences in CL-weight relation slope coefficients between sexes that might be partly attributable to the larger size (and thus weight) of male (particularly Form I) chelae (Table 1), although we did not weigh chelae. Males (Riggert et al., 1999; Larson and Magoulick, 2008) or particularly Form I males (DiStefano et al., 2002) of some species of *Orconectes* weighed more than females when adjusted for CL, but one study reported no differences (Price and Payne, 1984b).

Molting

We observed relatively little molting, but the general pattern displayed by *O. williamsi* males was similar to that of other stream-dwelling species of *Orconectes* (Van Deventer, 1937; Boyd and Page, 1978; Riggert et al., 1999; DiStefano et al., 2002). Specifically, mature males molted synchronously from the reproductive form (Form I) to the non-reproductive state (Form II) in late winter through early spring. Summer molts appeared dominated by YOY, but mature males molted back to Form I in late summer, presumably in preparation for autumn mating. The one synchronous spring molt that we observed in female *O. williamsi* coincides with some other species of *Orconectes* (Van Deventer, 1937; Boyd and Page, 1978). Adults of some species of *Orconectes* molt only once or twice annually (Van Deventer, 1937; Prins, 1968; Weagle and Ozburn, 1972; St. John, 1976; Muck et al., 2002b), and others up to four times annually (Price and Payne, 1984b). Unfortunately, we were unable to observe enough molting to estimate the number of annual molts for adult *O. williamsi*.

In conclusion, Wagner et al. (2010) noted the lack of existing biological information for *O. williamsi* and recommended life history work; our study contributes significantly to such knowledge for this species. The life history of *O. williamsi* as observed from populations in Emory and Roark creeks appears generally similar to what has been reported for several other stream-dwelling species of *Orconectes*. However, this species appears to differ from several others in that the females use habitats that are less accessible to conventional crayfish sampling methods, especially when they are ovigerous or carrying hatchlings. Given the recently identified factors of potential concern with regard to this imperiled species' conservation including ongoing gravel mining and the rapid urbanization of the surrounding area, we believe that the conservation status of *O. williamsi* will require periodic assessment for stability or possible declines. The life history information presented herein will be important for future conservation efforts. In anticipation of such efforts, we suggest additional work to determine the habitat use by female *O. williamsi*, but particularly females during the critical life cycle period when they are carrying eggs and hatchlings.

Acknowledgements

Missouri Department of Conservation and Tennessee Technological University provided funding. Thanks to T. Boersig, L. Cole, M. Culler, I. Dasho, P. Horner, E. Imhoff, V. Jones, A. Meyer, E. Rahm, J. Rice, C. Riggert, J. Schisler, K. Walker, and J. Westhoff for assistance with data collection, data entry and data management. E. Imhoff constructed the map. Taxonomic verifications were provided by C. A. Taylor (Illinois Natural History Survey). Manuscript reviews were provided by two anonymous reviewers.

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RECEIVED: 17 April 2012.
ACCEPTED: 24 August 2012.
AVAILABLE ONLINE: 27 September 2012.