Re-examining extreme longevity of the cave crayfish *Orconectes australis* using new mark–recapture data: a lesson on the limitations of iterative size-at-age models

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SUMMARY

1. Centenarian species, defined as those taxa with life spans that frequently exceed 100 years, have long been of interest to ecologists because they represent an extreme end point in a continuum of life history strategies. One frequently reported example of a freshwater centenarian is the obligate cave crayfish *Orconectes australis*, with a maximum longevity reported to exceed 176 years. As a consequence of its reported longevity, *O. australis* has been used as a textbook example of life history adaptation to the organic-carbon limitation that characterises many cave-stream food webs.

2. Despite being widely reported, uncertainties surround the original estimates of longevity for *O. australis*, which were based on a single study dating from the mid-1970s. In the present study, we re-evaluated the growth rate, time-to-maturity, female age-at-first-reproduction and longevity of *O. australis* using a mark–recapture study of more than 5 years based upon more than 3800 free-ranging individuals from three isolated cave streams in the south-eastern United States.

3. The results of our study indicate that accurate estimates of the longevity of *O. australis* are ≤22 years, with only a small proportion of individuals (<5%) exceeding this age. Our estimates for female time-to-maturity (4–5 years) and age-at-first-reproduction (5–6 years) are also substantially lower than earlier estimates.

4. These new data indicate that the age thresholds for life history events of *O. australis* are comparable to other estimates for a modest assemblage of cave and surface species of crayfish for which credible age estimate exists, suggesting that a cave environment *per se* is not required for the evolution of extreme longevity in crayfish.

Keywords: crayfish, growth rate, life history, longevity, time-to-maturity

Introduction

A select group of aquatic animals exhibit remarkable longevity. The ocean quahog clam [*Arctica islandica* (L.)], for example, has been reported to live for more than 400 years (Wanamaker *et al.*, 2008), while marine tube-worms surrounding hydrocarbon seeps can live for over 200 years (Bergquist, Williams & Fisher, 2000). Among vertebrates, several species of deep-sea fishes have life spans in excess of 100 years (see Koslow *et al.*, 2000; Finch, 2009). Such 'centenarian taxa' have long been of interest to biologists because they represent an extreme end point on the life history continuum and provide insights into the

physiological processes (e.g. genome maintenance and reduced oxidative stress) that produce exceptionally long life spans (Bodnar, 2009; Voituron *et al.*, 2011). Not surprisingly, the population dynamics of such long-lived species also pose unique challenges for management and conservation.

Among freshwater taxa, cave-adapted organisms offer some excellent examples of extreme longevity. In cave ecosystems, resources are limited owing to the absence of light, which prevents primary production (except in chemolithoautotrophy-based systems; Engel *et al.*, 2004), and by reduced surface connectivity, which limits inputs of allochthonous organic matter (Poulson & Lavoie, 2001).

In response, many obligate cave species have evolved K-selected life history characteristics, such as long life span, slow growth rate and reduced fecundity (Hüppop, 2001). One frequently reported example of longevity in a cave organism is the extreme life span estimated for the obligate cave crayfish *Orconectes australis* (Rhoades). Cooper (1975) used a mark–recapture approach to study the population size, age structure and growth of *O. australis* in Shelta Cave, Alabama, U.S.A. Using models based on growth rates from free-roaming individuals, he predicted that it would take 37–176 years for *O. australis* to reach a carapace length of 47 mm. Using Cooper's (1975) data, Culver (1982) further estimated female time-to-maturity to range from 16 to 35 years, while female age-at-first-reproduction was predicted to range from 29 to 105 years.

Given the astonishing longevity suggested by his data, Cooper (1975; p. 314) expressed some doubts about his analytical approach, stating 'This apparently extraordinary finding requires further comment. Two alternative approaches are open: (i) consideration of factors which could actually confer ''immortality'' on these populations, and (2) further search for the flies which are undoubtedly lurking in the ointment of growth records (based on carapace lengths) and rates inferred from them.' Despite this plea for caution, these longevity estimates have been referred to in comparative life history studies (Hobbs, Hobbs & Daniel, 1977; Weingartner, 1977; Streever, 1996; Cooper & Cooper, 2004; Vogt, 2012) and toxicology studies (Dickson, Briese & Giesy, 1979). References to these estimates can also be found in books, popular magazines, journal newsletters and websites, which discuss life history evolution in cave species, cave conservation issues and the uniqueness of cave ecosystems (Culver, 1982; Anonymous, 1999; Hüppop, 2001; Krajick, 2001; Poulson & Lavoie, 2001; Culver, 2005; Krajick, 2007; web search: *O. australis* life span; 100-year-old cave crayfish, 17 July 2011).

If Cooper's (1975) models are correct, *O. australis* belongs to a small group of animals known to have life spans of 100+ years (see Ziuganov *et al.*, 2000; Finch, 2009). However, extraordinary life span estimates must be informed by extraordinary data. In the light of Cooper's (1975) uncertainties regarding his longevity models, we sought to re-evaluate the life history of *O. australis*. Access to Shelta Cave is now restricted, and the site has also been affected by groundwater pollution (Burnett *et al.*, 2004). Consequently, we measured growth rate, time-to-maturity, female age-at-first-reproduction and maximum longevity of *O. australis* inhabiting three hydrologically isolated cave systems in Alabama, U.S.A. that are close to Shelta Cave and that share genetically similar populations.

Methods

Study sites

Hering, Limrock and Tony Sinks caves. Three caves containing streams in north-eastern Alabama (Jackson County, U.S.A.) were chosen for study: Hering, Limrock and Tony Sinks caves. These caves contained large populations of *O. australis* and had similar macrofaunal assemblages, which included the facultative cave crayfish *Cambarus tenebrosus* Hay and the obligate cave salamander *Gyrinophilus palleucus* (McCrady). The southern cavefish [*Typhlichthys subterraneus* (Girard)] and the mottled sculpin [*Cottus bairdi* (Girard)] also occurred in Limrock and Hering caves.

Shelta Cave. Cooper's (1975) study site, Shelta Cave, is located 20–42 km west of our study sites. Shelta Cave consists of three large rooms measuring about 610 m long (Cooper, 1975, p. 22; fig. 3), with only a small portion of the cave containing water perennially (∼150 m; Cooper, 1975, p. 106; fig. 19). Macrofaunal assemblages in Shelta Cave during Cooper's (1975, p. 57) study were similar to those at our study sites and consisted of three species of cave crayfish (including *O. australis*) in addition to *C. tenebrosus*, *G. palleucus* and *T. subterraneus*. Water temperature in Shelta Cave averaged 15.5 °C (Cooper, 1975, p. 115). Since Cooper's (1975) study, the population of crayfish has decreased to <10% of its initial size owing to decreased water quality and possibly the loss of a resident bat colony (Elliott, 2001).

A phylogeographic study by Buhay & Crandall (2005) showed that the populations of *O. australis* in Limrock, Hering and Shelta caves shared common mtDNA 16S haplotypes, indicating that at least these three populations share a common evolutionary history. While Tony Sinks Cave was not included in Buhay and Crandall's study, its close geographical proximity to the other caves (10–42 km) suggests that its crayfish population falls within the same well-defined clade, supporting their recognition as a single species.

Life history sampling and growth modelling in the present study

A study reach ranging from 327 to 1202 m containing a series of riffle and pool habitats with sand, gravel and bedrock substrata was designated in each cave. Sampling began in November 2005 in Hering, January 2006 in Limrock and July 2006 in Tony Sinks caves and was conducted semi-monthly (conditions permitting) to August 2011. On each visit, study reaches were surveyed

on foot, and all crayfish encountered were collected using dip-nets. Captured crayfish were marked using both internal tags [visible implant alpha tags (VIAT), Northwest Marine Technology, Shaw Island, WA, U.S.A.] and visible implant elastomer (VIE; Northwest Marine Technology). VIATs are small (1.0×2.5 mm), fluorescent, uniquely numbered tags that were placed beneath the abdominal cuticle. The VIE was injected directly posterior to the VIATs and was used to assess tag loss, which was infrequent. Once marked, the total carapace length (TCL) and ocular carapace length (OCL; posterior margin of ocular cavity to posterior centre-margin of carapace) of each crayfish were measured (± 0.1 mm) with dial callipers, its reproductive status (form I or II for males; presence of cement glands, ova or young for females) was recorded, and it was released at the point of capture. OCL was used rather than TCL to avoid errors owing to damage to the acumen following release. Water temperature was recorded every 30 min using a Solinst Barologger model 3001 (Solinst, Georgetown, ON, Canada) from June 2007 to July 2011. Temperature data are not available for Tony Sinks Cave from March 2009 to January 2010 owing to instrument loss.

Crayfish growth rates were estimated as the difference between OCL at initial marking and the OCL upon recapture divided by days elapsed. This rate was then multiplied by 365 to acquire an annual growth increment. Since growth increments are 'episodic' owing to the moulting cycle, annual growth increments were only calculated for individuals recaptured over intervals of 350 days or longer. Negative annual growth increments were attributed to measuring error and were excluded from analyses. For crayfish recaptured multiple times, the annual growth increment was calculated using the recapture date closest to the 350-day minimum. Annual growth increments were regressed against average OCL to estimate the size-specific annual growth rate. To estimate size-at-age, the size-specific annual growth rate was first seeded with a 3-mm-OCL individual, the size of juveniles attached to the pleopods of a single female collected from Hering Cave. This process was then iterated at annual intervals, and growth trajectories bounded by 95% confidence limits were then constructed using a bootstrap technique (Whitmore & Huryn, 1999). A significant difference in growth trajectories among caves was assumed when 95% confidence intervals did not overlap.

Separate growth trajectories were produced for male and female crayfish to assess sex-specific patterns. Time-to-maturity was estimated by plotting the smallest reproductive (form I) male and female (using the presence of cement glands) onto the resulting growth trajectories. The largest male and female and the smallest female with ova or young were used to estimate minimum life span and age-at-first-reproduction, respectively. Ages constrained by 95% confidence limits represented the estimated range. Cumulative size-frequency distributions were constructed for each cave, including Shelta Cave, and then compared to examine for differences in size-structure among populations using pairwise Kolmogorov–Smirnov (K-S) tests. K-S tests were performed in program R version 2.14.0 (R Development Core Team, 2008).

Cooper's (1975) growth models

Growth rates reported by Cooper (1975) were estimated as the difference between TCL at initial marking and upon recapture divided by months elapsed. Cooper (1975) calculated monthly growth rates for a total of 56 individuals (Cooper, 1975, pp. 273–280; Tables 36 and 37) ranging in size from 10 to 47 mm TCL. Only 10 of these were <23 mm TCL, however. Cooper (1975) constructed his mean and maximum growth models by placing the 56 individuals for which he calculated monthly growth rates into six size-classes. The mean and maximum monthly growth rate for each size-class was then used to estimate the number of months required for an individual to grow through each size-class. Essentially, Cooper (1975) constructed a series of linear growth models that approximated an exponential growth model.

To compare the results of our study with those of Cooper (1975), we first reconstructed Cooper's (1975) original growth models (Cooper, 1975, p. 312; Table 43). Annual growth rates were then calculated from the crayfish that Cooper (1975) had marked for at least 11 months ($n = 26$; Cooper, 1975, pp. 273-280; Tables 36 and 37), and growth models were constructed using the methods described in this study. We chose to use a subset of Cooper's (1975) data because it better reflected the rationale (e.g. crayfish moult cycle) and methods (e.g. annual growth rates) used to construct growth models for our three study populations. A size-frequency histogram for the Shelta Cave population was also recreated (Cooper, 1975, p. 158; fig. 26) by digitising the original figure (DigitizeIt version 1.5.8b; Bormann, 2010). Cooper's (1975) TCL was converted to OCL using a conversion factor that allowed size-classes and cumulative size-frequency distributions to be compared among studies. Crayfish from Hering Cave were used to generate the conversion factor by regressing OCL against TCL ($n = 925$, $r^2 = 0.98$; OCL = 0.79(TCL) – 0.40).

Results

Hering, Limrock and Tony Sinks caves

A total of 3812 crayfish were marked in Hering (919 individuals), Limrock (943) and Tony Sinks (1950) caves. The longest period between a mark and recapture date for a single crayfish was more than 5 years (1920 days). Growth models were constructed using 78 (37 males and 41 females) crayfish in Hering Cave, 112 (47 males and 65 females) in Limrock Cave and 97 (46 males and 51 females) in Tony Sinks Cave (Fig. 1). The 95% confidence intervals for male and female growth models overlapped within each cave, indicating sex-specific growth rates were similar (data not shown). Growth trajectories were generally similar among caves, with the 95% confidence intervals estimated for the Tony Sinks Cave overlapping those estimated for Hering and Limrock caves (Fig. 2). The models for Hering and Limrock caves overlapped little during model years 1–4, suggesting growth rates were only marginally similar during this peak growth period. Average daily water temperature in all caves was approximately 13.0 °C and showed little annual variation (standard deviation of average daily water temperature was ±1 °C).

The smallest mature male (form I; 12–13 mm OCL), female (obvious cement glands; ~16 mm OCL) and ovigerous female (ova or young present; 19–21 mm OCL) were similar in size among caves (Fig. 3). Males in Tony Sinks Cave reached maturity earlier (~2.5 years) than those of Hering and Limrock caves (~3.5 years; Fig. 3, Table 1). Females matured earliest in Hering Cave (3.5 years) and latest in Limrock Cave (5.1 years). Age-at-first-reproduction was also earliest in Hering (4.6 years) and latest in Limrock (6.4 years). The largest male (35.7 mm OCL) and female (33.3 mm OCL) crayfish were collected from Hering Cave, while the largest males and females in Tony Sinks Cave were 25 and 29 mm OCL, respectively, and were 33 and 29 mm OCL in Limrock Cave. Because of the asymptote produced by the growth models, only minimum life span could be estimated (Fig. 3, Table 1). Minimum male life span was shortest in Tony Sinks Cave (11+ years) and longest in Hering Cave (22+ years). Minimum female life span was shortest in Limrock Cave (15.5 years) and longest in Hering and Tony Sinks caves (22+ years). Minimum life span could not be confidently estimated in all caves because the growth models reached an asymptote before they intersected with the size of the largest male and female.
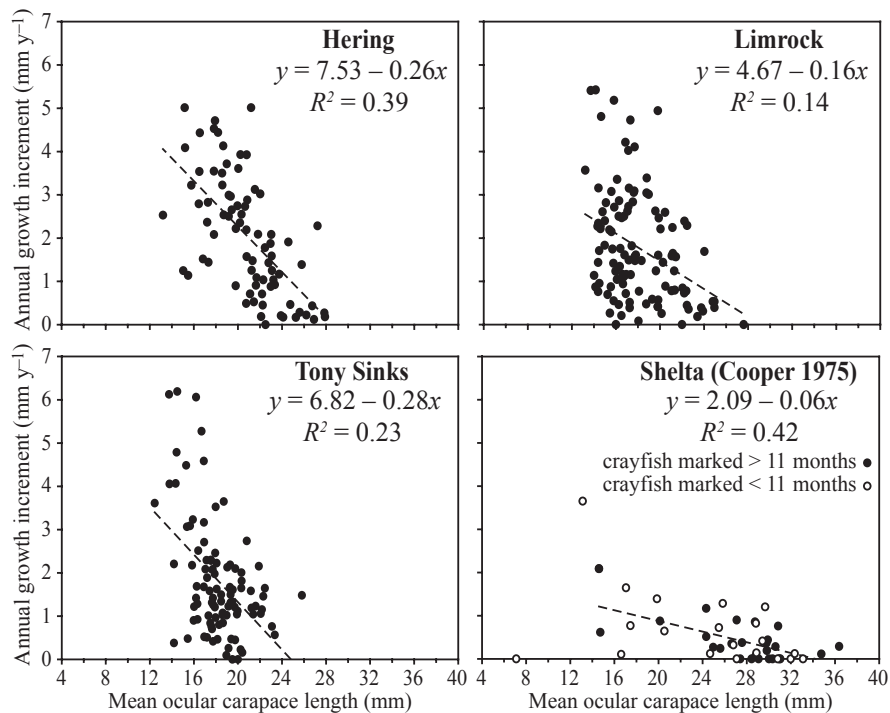

Fig. 1 Annual growth increment (mm y^{-1}) vs. mean ocular carapace length (mm) for *Orconectes australis* crayfish in Hering, Limrock, Tony Sinks and Shelta (Cooper, 1975) caves. Dashed lines are results of least-squared regression. For the Shelta Cave data, only crayfish that were marked for ≥11 months were included in the reconstruction of Cooper's growth models [see *Methods: Cooper's (1975) growth models*] and in the least-squared regression line.
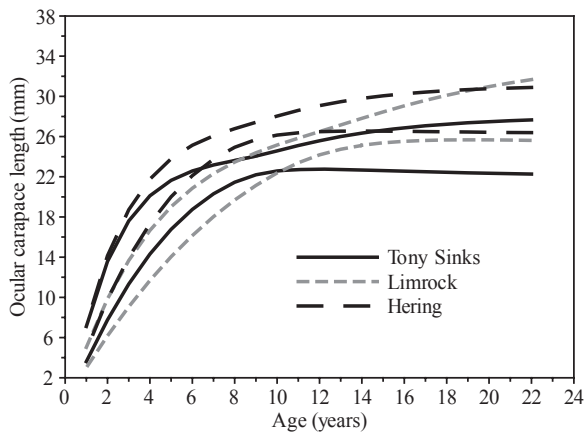
Fig. 2 Growth models for *Orconectes australis* from Hering, Limrock and Tony Sinks caves. Lines indicate the upper and lower 95% confidence intervals for each model.

Size-frequency distributions were constructed for crayfish populations in each cave using data pooled from 2005 to 2011. Pairwise comparisons revealed no significant differences in size-structure among Hering, Limrock and Tony Sinks caves (K-S test, $P > 0.05$; differences between Hering and Tony Sinks caves were marginally significant, $P = 0.05$, Fig. 3). More than 70% of males and 50% of females from all caves were mature (Fig. 3, Table 1). The male/female ratio indicated a positive bias towards females in all caves (Table 1; male/female = 0.76–0.89). Ninety-five percentage of the individuals comprising populations in Hering and Limrock caves were estimated to be ≤13 years old. In Tony Sinks Cave, 95% of the population was ≤8 years old (Fig. 3). Twenty-five percentage of the population was ≤4 years old in Tony Sinks Cave, ≤6 years old in Limrock Cave and ≤4 years old in Hering Cave.

Analysis of Cooper's (1975) data from Shelta Cave

When our modelling technique was applied to Cooper's (1975) data, it produced results similar to those of his original mean and maximum growth models (Fig. 4). The smallest mature male (form I) reported by Cooper (1975) in Shelta Cave had a TCL of 21 mm (Cooper, 1975, pp. 157 and 205). Time-to-maturity for this individual was estimated at 4–8 years using Cooper's models and 6–21 years using our models (Fig. 4). The smallest mature (cement glands) and ovigerous (presence of ova or young) females reported in Cooper (1975) were 31 mm (Cooper, 1975, p. 236) and 37 mm (Cooper, 1975, p. 244) TCL, respectively. Time-to-maturity estimated using Cooper's models for a 31-mm-TCL female was 11–19 years, while estimates using our models ranged from 11 to 34 years (Fig. 4). Age-at-first-reproduction estimated using Cooper's mod-

els for a 37-mm-TCL female was 14–31 years, while an age of 16+ years was estimated by our model (Fig. 4). The largest specimen of *O. australis* reported for Shelta Cave (Cooper, 1975, p. 157) was 47 mm TCL. While this specimen exceeded the upper 95% confidence limit of our model, Cooper's (1975) models estimated an age of 38+ years (Fig. 4).

The majority of individuals that Cooper (1975) used to estimate monthly growth rates were substantially larger than those from Limrock, Hering and Tony Sinks caves (Fig. 1). The size-frequency distribution in Shelta Cave was similar to Hering (K-S test, $P > 0.05$), but different from Limrock and Tony Sinks (K-S test, $P = 0.03$). This was probably caused by the disproportionate representation of larger size-classes in Shelta Cave (Figs 3 and 4). The modal TCL of *O. australis* in Shelta Cave was 38 mm (Fig. 4), while the modal TCL for Limrock, Hering and Tony Sinks caves ranged from 21 to 26 mm (16 to 20 mm OCL, Fig. 3).

Ninety-five percent of the population in Shelta Cave was estimated to be ≤32 years old using Cooper's (1975) mean model and ≤24 years in age using Cooper's (1975) maximum model and the upper 95% confidence interval in our model (Fig. 4). Cooper's (1975) models predicted that 25% of the population was ≤10 years in age, while our model predicted that 25% of the population would be ≤20 years in age.

Discussion

A re-evaluation of the life history of Orconectes australis

Our estimates of life span for *O. australis* are substantially lower than Cooper's (1975) estimate of 37–176 years, indicating that his trepidation regarding these estimates was warranted. We suggest that a more accurate estimate of the life span for *O. australis* is ≤22 years, with only a few percent of the individuals of a given population exceeding this age. Our estimates for female time-to-maturity (4–5 years) and age-at-first-reproduction (5–6 years) are also substantially lower than the estimates of 16–35 and 29–105 years, respectively, reported by Culver (1982) using Cooper's (1975) data.

Our re-evaluation of the longevity of *O. australis* indicates that it is comparable to other estimates for both cave and surface species of crayfish (Table 2). Weingartner (1977), for example, reported that the life span and time-to-maturity for the obligate cave crayfish *Orconectes inermis* (Cope) ranged from 9 to 10 years and 2 to 3 years, respectively, while Streever (1996) estimated a life span of 16+ years for the obligate cave crayfish *Procambarus*
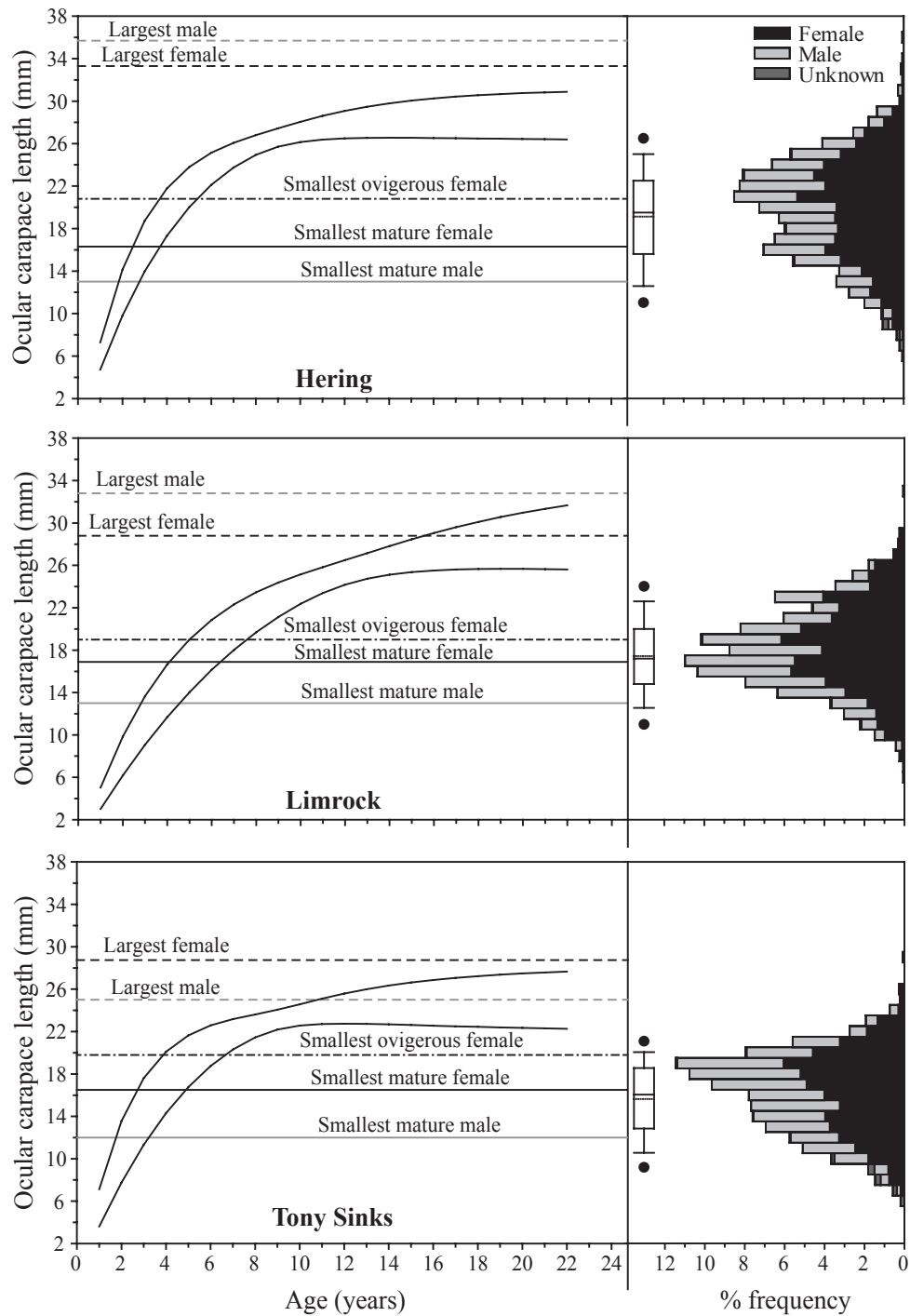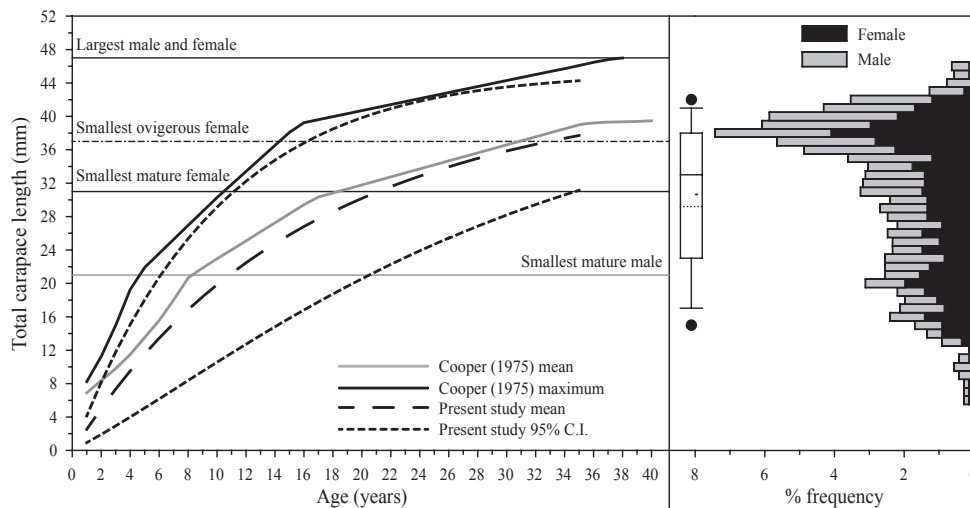
Fig. 3 Growth models for *Orconectes australis* from Hering, Limrock and Tony Sinks caves. Curved solid lines are upper and lower 95% confidence intervals. The pooled size-frequency distribution for each population is plotted to the right of each growth model. To the left of the size-frequency distribution are box and whisker plots. The boxes are the 25th and 75th percentile containing the mean (dashed line) and median (solid line); whiskers are error bars; dots are the 5th and 95th percentiles.

erythrops (Relyea & Sutton). Hobbs & Lodge (2010) recently suggested *O. inermis* has a 60-year life span. This estimate, however, is not supported by the citations provided by the authors (e.g. Cooper & Cooper, 1978; Hobbs, 1978; Streever, 1996), indicating that Weingartner's (1977)

estimates for *O. inermis* are the most credible for this species. Estimates of life span and time-to-maturity in surface crayfish also vary widely, ranging from 1 to 60 years and 6 months to 14 years, respectively (see Vogt, 2012). In other species of *Orconectes*, life span ranges from 1

Table 1 Estimated minimum life span (years), mean time-to-maturity (years), age-at-first-reproduction (years), proportions of males and females that were mature and male/female ratio for *Orconectes australis* in Hering, Limrock and Tony Sinks caves. Ranges are in parentheses

| | Life span | | Time-to-maturity | | Age-at-first-reproduction | % of gender mature | | |
	Male	Female	Male	Female	(ovigerous female)	Male	Female	Male/Female
Hering	22+	22+	3.3 (2.75–3.75)	3.5 (3–4)	4.6 (3.75–5.5)	72	63	0.78
Limrock	22+	15.5+	3.9 (3–4.75)	5.1 (4–6.25)	6.4 (5–7.75)	88	58	0.76
Tony Sinks	11+	22+	2.5 (1.75–3.25)	3.9 (2.75–5)	5.5 (4–7)	83	50	0.89

Fig. 4 Growth models for *Orconectes australis* from Shelta Cave. Black and grey solid lines are a reconstruction of Cooper's (1975) maximum and mean growth models. The black dotted lines are the upper and lower 95% confidence intervals, and the black dashed line is the mean for the growth model that was constructed using a subset of Cooper's (1975) data and our modelling technique [see *Methods: Cooper's (1975) growth models*]. The pooled size-frequency distribution for the population is plotted to the right of the growth model. To the left of the size-frequency distribution is a box and whisker plot. The box represents the 25th and 75th percentile with the mean (dashed line) and median (solid line); whiskers are error bars; dots are the 5th and 95th percentiles.

to 5 years and time-to-maturity from 6 months to 2 years (Table 2). Regardless of our shorter life span estimate for *O. australis*, its estimated longevity (~22 years) is relatively great compared with surface species in the same genus, indicating a K-selected life history and a high degree of specialisation to cave habitats (Table 2).

What explains the large discrepancy between the estimates of Cooper (1975), Culver (1982) and our study? Since the general approach and methods in the two studies were similar, the differences between conclusions must be related to the data used to drive the size-at-age models. Below, we discuss potential factors related to the data, particularly with respect to (i) the size distribution of crayfish used to estimate growth rates; (ii) the size thresholds used to define life history stages (e.g. size-at-maturity, age-at-first-reproduction) and (iii) the general limitations of using iterative growth models to estimate size-at-age.

Differences in the size distribution of crayfish used to estimate growth rates

The morphology of a growth model is influenced by the distribution of size-classes included in its construction. In many species, smaller size-classes show greater mass-specific growth per unit time than larger size-classes. Growth models that include a wide range of size-classes will typically show an early period of exponential growth, followed by an abrupt plateau. However, growth models become more protracted and almost linear when smaller size-classes are underrepresented, which can ultimately cause inaccurate estimates (i.e. overestimates) of life span, time-to-maturity and age-at-first-reproduction.

In Cooper's (1975) original size-at-age models, only 12 of the 56 individuals were <30 mm TCL, and only two of the 26 individuals we used to produce size-at-age models based on Cooper's (1975) data were <30 mm TCL (23 mm

Table 2 Estimated life span (years, shortest to longest) and time-to-maturity (years) of selected surface (S) and cave (C) crayfish with the method utilized for approximation

Habitat	Species	Life span	Time-to-maturity	Method	Author
S	*Procambarus clarkii* Girard	1–12		SF, VBGF	Scalici *et al.*, 2010; Fidalgo *et al.*, 2001
S	*Orconectes* spp.	1–5	1–2	MR, SF, GM	Momot, 1984; Price & Payne, 1984; Muck *et al.*, 2002
S	*Cambarus halli* (Hobbs)	2+		SF	Dennard *et al.*, 2009
S	*Fallicambarus gordoni* Fitzpatrick	2–3		SF	Johnston & Figiel, 1997
S	*Cambarus hubbsi* Creaser	3		SF	Larson & Magoulick, 2011
S	*Procambarus suttkusi* Hobbs	3		SF	Baker *et al.*, 2008
S	*Paranephrops planifrons* (White)	3–4	1–2	MR, SF	Parkyn *et al.*, 2002
S	*Cambarus elkensis* Jezerinac and Stocker	5	2.5–3	SF	Jones & Eversole, 2011
S	*Fallicambarus fodiens* (Cottle)	6		MR, SF	Norrocky, 1991
S	*Cambarus dubius* Faxon	7	1	SF, GM	Loughman, 2010
S	*Astacus leptodactylus* (Eschscholtz)	7		SF, VBGF	Deval *et al.*, 2007
C	*Orconectes inermis* Cope	9–10	2–3	MR, GM	Weingartner, 1977
S	*Parastacoides tasmanicus tasmanicus* Clark	10	3–5	MR	Hamr & Richardson, 1994
S	*Cambaroides japonicus* (Haan)	10–11	5–6	SF, VBGF	Kawai *et al.*, 1997
S	*Pacifastacus leniusculus* (Dana)	11	3–4	MR, GM	Flint, 1975
S	*Cambarus bartonii* (Fabricius)	13	5	MR, GM	Huryn & Wallace, 1987
S	*Paranephrops zealandicus* (White)	16+	6	MR, GM	Whitmore & Huryn, 1999
C	*Procambarus erythrops* Relyea & Sutton	16+		MR	Streever, 1996
S	*Astacoides betsileoensis* Petit	20		MR, VBGF	Jones *et al.*, 2007
C	*Orconectes australis* Rhoades	22+	4–6	MR, GM	This study*
S	*Astacoides granulimanus* Monod and Petit	25+	7	MR, VBGF	Jones & Coulson, 2006

SF, Size-frequency; MR, mark–recapture; GM, growth model; VBGF, von Bertalanffy growth function.
*Vogt (2012) contains a reference to a preliminary agency report by Huryn *et al.* (2008) that suggests that the life span of *O. australis* may approach 50 years. While the growth models used to estimate longevity in both Huryn *et al.* (2008) and this study are methodologically identical and share some data (1650 marked crayfish that were recaptured during 2005 to 2008), the data conclusions presented in this study are more robust owing to a much larger data set (3812 marked crayfish that were recaptured during 2005–2011).

OCL). When comparing the distribution of individuals used to estimate growth rates (Fig. 1) with the actual size distribution of *O. australis* sampled from Shelta Cave (Fig. 4), it is clear that there was a strong bias to large individuals in Cooper's full set of recapture data, even though smaller individuals (e.g. 12–30 mm TCL) were well represented in the population. Unlike the growth models for Shelta Cave, all available size-classes were well represented in our models from the three new Alabama cave sites, which produced distinct periods of exponential growth in each model.

Differences in size thresholds used to define life history stages

While methods used to distinguish ovigerous females were consistent among studies (presence of ova or attached young), those used to set thresholds for female size-at-maturity differed significantly. Cooper (1975, p. 202) conservatively identified mature female crayfish as those displaying 'late stage (3–4) oocytes and, usually, cement glands'. We identified mature females using the presence of cement glands alone, which is a reliable indicator of maturity in female surface crayfish (see Reynolds, 2002). Applying our definition to Cooper's (1975) data for Shelta Cave resulted in a reduction in female time-to-maturity by 5–16 years.

Limitations of iterative growth models

The asymptotic relationship between size and age is an inherent limitation to size-at-age estimates made using iterative growth models. If the models are interpreted literally, the largest individuals in a population are not significantly different from an infinitely old crayfish, such as in the model for Hering Cave (Fig. 3). In such cases, size is no longer an accurate predictor of age because annual growth increments become vanishingly small or stop altogether. Additionally, iterative models do not account for anomalies, such as individuals that are much larger than average at birth or those that have exceptionally fast growth rates (Weingartner, 1977, p. 208). Presumably, it is factors such as these that are the 'flies lurking in the ointment of growth records' to which Cooper was referring (1975, p. 314). To avoid such drawbacks, iterative models must be interpreted within the context of popula-

tion structure and dynamics. For example, Hering Cave's growth model cannot estimate the age of the largest male or female. When examining the frequency histogram for Hering Cave, however, it is immediately apparent that the largest size-classes account for a very small percentage (~5%) of the total population. Thus, from both an ecological and a conservation perspective, the majority of population dynamics (e.g. production, reproduction and mortality) occurred within the smaller size-classes and on much shorter time scales than would be expected from only the largest size-classes (Fig. 3).

The longevity of Orconectes australis: a new perspective

Single species are often used as benchmarks to illustrate biological theories or define a particular ecosystem. Examples include the use of Galápagos finches to illustrate evolution via natural selection or the status of the red-eyed tree frog [*Agalychnis callidryas* (Cope)] as a 'poster-species' for conservation of Central American rainforests. Previously, the life span of 100+ years of *O. australis* was used to illustrate how evolution can shape extreme life histories in obligate cave species and to focus conservation efforts on cave ecosystems. However, our re-examination of Cooper's (1975) data, coupled with new life history information, strongly suggest that *O. australis* is not a 'centenarian' species. While our new estimates are substantially lower than Cooper's (1975), they remain impressive, however. The life span of *O. australis* is 4 to 20× longer than any other crayfish within the same genus, which continues to provide an excellent example of potential K-selected life history evolution in an obligate cave species. Our study also emphasises the importance of interpreting the life history information of long-lived species within the context of both population structure and methodological limitations. Using a minority (e.g. the largest or oldest individuals) to interpret the dynamics of an entire population will misrepresent the timescale over which important life history events (e.g. reproduction) occur and potentially influence the development of species-specific management strategies.

Acknowledgments

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