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DENSITY, DEMOGRAPHY, AND MICROHABITAT OF CAMPELOMA DECAMPI (GASTROPODA: VIVIPARIDAE)

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ABSTRACT

Campeloma decampi, the Slender Campeloma, is a federally endangered snail endemic to the Tennessee River drainage in Alabama, U.S.A. We studied a population in Round Island Creek, Limestone County, in July, 2010, to obtain information about density, microhabitat, and demography. The overall mean density at the site was 49.2/m² (\pm 14.4 SE), but the distribution was highly clumped. We used generalized linear models and multi-model inference to examine the response of snail density to seven microhabitat explanatory variables. The greatest densities were associated with shallow, low-flow areas with silt and clay near the stream margin. Shell heights ranged from 4.3–34.7 mm, and the size distribution appeared to be composed of three cohorts possibly representing age 0+ recruits, age 1+ individuals, and individuals \geq 2 years of age. The population was dominated by small individuals (4–12 mm; modal size class = 6 mm), and individuals >20 mm made up only 7% of the population. This size distribution suggests that parturition occurs over a protracted period from late winter to summer and that most individuals produce only one or two broods in their lifetime; however, additional sampling and information about life span are needed to more conclusively describe the reproductive strategy.

KEY WORDS *Campeloma decampi*, Freshwater Gastropod, Endangered Species, Microhabitat, Density, Demography, Slender Campeloma

INTRODUCTION

Understanding the life history and ecological requirements of imperiled freshwater snails is a high priority for their conservation (Lysne et al., 2008; Strong et al., 2008; Johnson et al., 2013). *Campeloma decampi* (Binney, 1865) (Slender Campeloma, Viviparidae) is a freshwater snail endemic to a small portion of the Tennessee River drainage in northern Alabama (Haggerty & Garner, 2008; U.S. Fish and Wildlife Service, 2012). In 2000, *C. decampi* was listed as endangered under the U.S. Endangered Species Act (Federal Register, 2000; Johnson et al., 2013). Rapid urban and industrial growth within the species' range threatens its survival, and ecological data are needed to effectively monitor and manage remaining populations.

Little is known about the life history and ecology of *C. decampi*. It reaches about 35 mm in size (shell height), and like other members of the Viviparidae, it is ovoviparous and is most likely a detritivore (Garner, 2004; Haggerty & Garner, 2008). Preliminary observations suggest that *C. decampi* has a highly clumped spatial distribution and occurs primarily in shallow habitats with little current near stream margins and emergent vegetation, and it burrows into fine substrates or detritus (Garner, 2004; Haggerty & Garner, 2008). Other *Campeloma* species are found in similar habitats, and they give birth to live young in winter or spring, and in some cases into the summer (Allison, 1942; Bovbjerg, 1952; Vail, 1978; Imlay et al., 1981; Brown et al., 1989).

These specialized habitats appear necessary for feeding and reproduction.

The goals of this study were to 1) quantitatively describe the spatial distribution of *C. decampi* and the microhabitat characteristics associated with the species, and 2) provide information about demography and reproduction in our study population.

METHODS

The study was conducted in Round Island Creek, Limestone Co., Alabama, U.S.A., which supports high densities of *C. decampi* (Haggerty & Garner, 2008). Round Island Creek is a third-order stream approximately 25 km long with a drainage area of 135 km². It lies within the Tennessee Valley District of the Interior Low Plateau Physiographic Province (Sapp & Emplainscourt, 1975) and flows into Wheeler Reservoir at Tennessee River mile 298. The underlying geology of Round Island Creek is Fort Payne Chert and Tusculumbia Limestone (Osborne et al., 1988; Szabo et al., 1988). The drainage is primarily agricultural or forested, riparian zones are generally intact and banks are stable, and the stream is extensively canopied. Stream habitats include riffles, runs, and pools, and the substrate of the runs and riffles is mostly gravel with interstitial sand and silt. Pools and marginal areas often have deposits of mud and beds of Waterwillow, *Justicia americana* (Linnaeus) Vahl. Exposed bedrock occurs at some sites, but outcrops are generally not extensive. In June 2007, average physico-chemical measurements from three sites on Round Island Creek where *C. decampi* occurred were: temperature (27.4°C), dissolved oxygen (4.30 mg/l), dissolved oxygen percent saturation (51.6%), pH (8.4), specific

conductance (138.7 µS/cm), total hardness (69.3 ppm), calcium hardness (45.3 ppm), and magnesium hardness (24 ppm) (Haggerty & Garner, 2007).

The study site was a 125 m stream reach at Ripley Road, Limestone County, Alabama (34.75290° N, 87.08437° W). Average channel width in the study reach was 10.6 m (± 1.1 SE, n = 8 cross sections). We sampled at this site from July 16-22, 2010, a time when stream conditions were relatively constant and accurate sampling could be conducted. Data were collected along eight transects placed perpendicular to stream flow at approximately 10-15 m intervals. Transects were placed to encompass a range of suitable and unsuitable habitats for *C. decampi* based on previous qualitative observations (Haggerty & Garner, 2008). We sampled four 0.25 m² quadrats along each transect; one adjacent to each stream bank, and two at equidistant points between the banks. We excavated and removed the substrate within each quadrat to a depth of approximately 6 cm, washed the sediments with creek water across 10 and 2 mm mesh nested sieves, and then examined this material for *C. decampi*. We counted all individuals and measured shell height to the nearest 0.1 mm using digital calipers; the spires were not eroded, which allowed accurate shell height measurements of all individuals. No attempt was made to sex individuals, and all snails were returned to the area from which they were collected.

Seven environmental variables were measured at each quadrat location (Table 1): distance from stream bank (BD), distance to nearest emergent vegetation (DEV), water depth (WD), surface current velocity (CV), mean sediment grain size (φ), percentage of silt and clay (SC), and percentage of organic matter (OM).

TABLE 1

Average values (± SE) for microhabitat variables associated with quadrats having high density (>12 individuals/m²) and low density (≤12 individuals/m²) of *Campeloma decampi* in Round Island Creek, Limestone County, Alabama. Asterisks (P<0.05) and NS (not significant) report results of individual t-test or Wilcoxon test for each variable between high- and low-density quadrats.

Variables	High density (N = 12)	Low Density (N = 19)
Distance to bank (m)*	0.70 ± 0.21	2.73 ± 0.35
Distance to emergent vegetation (m) ^{NS}	2.71 ± 1.08	2.28 ± 0.56
Current velocity (cm/s)*	0.78 ± 0.58	3.46 ± 0.77
Water depth (cm)*	13.80 ± 2.50	31.51 ± 4.28
Sediment grain size (φ) ^{NS}	0.91 ± 0.16	0.64 ± 0.06
% Organic matter ^{NS}	5.76 ± 1.18	4.42 ± 0.21
% Silt and Clay ^{NS}	0.006 ± 0.001	0.003 ± 0.001

Distance to bank and emergent vegetation were measured with a measuring tape. Water depth was measured with a pole marked in 1 cm increments. Surface current velocity was measured with a measuring tape, standardized float, and stopwatch. Substrate characteristics (ϕ , SC, OM) were estimated from sediment cores collected near the upstream edge of each quadrat with a 7.6 cm diameter, 1.2 m long galvanized metal pipe, which was forced into the substrate as far as possible and capped with a rubber stopper. A sturdy, flat piece of metal was positioned over the opening of the pipe as it was removed from the substrate. The pipe was then quickly raised and emptied into a 3.8 L zippered plastic bag. Samples were transported to the laboratory in a cooler of ice, and then frozen.

In the laboratory, frozen sediment samples were thawed, allowed to settle, decanted, and oven-dried for 24 hours at a minimum of 70°C. The dried samples were sieved across the following mesh sizes: 63mm, 8mm, 4mm, 2mm, 1mm, 500 μ m, 250 μ m, 125 μ m, and 63 μ m (Buchanan, 1984), and the fraction retained on each sieve was weighed. The program GRADISTAT and the Folk and Ward method were then used to obtain a logarithmic mean grain size (ϕ) for each sample (Blott & Pye, 2001). Silt and clay estimates were obtained from the percentage by weight of sediments that passed through the 63 μ m sieve. Prior to sieving, a subsample of approximately 20 ml of material was taken from each core sample and ashed for two hours at or above 550°C to estimate percent organic matter.

We computed the variance-to-mean ratio for snail densities across all quadrats to evaluate the spatial dispersion of the population (Ludwig & Reynolds, 1988). A size frequency histogram of the shell height measurements was used to depict population demography during the sample period.

An information-theoretic approach was used to examine associations among microhabitat variables and *Campeloma decampi* density (Burnham & Anderson, 2001, 2002; Burnham et al., 2011). We formulated 12 *a priori* candidate models based on previous observations of habitat (e.g., Haggerty & Garner, 2008) and published accounts of congeners (Medcof, 1940; Allison, 1942; Bovbjerg, 1952; Chamberlain, 1958; Imlay et al., 1981; Brown et al., 1989). Only models of interest and empirical support were included in the analysis (Table 2; Burnham & Anderson, 2001). Poisson regression in log linear models (i.e., generalized linear models), maximum likelihood estimations, and Akaike's information criterion corrected for small sample size (AIC_c) were used to compare the fit and explanatory power of each model. Because of an error in the collection of sediment from one of the quadrats, all the data from that sample were excluded from analysis. When modeling count data, an important preliminary step is testing the fit of the global model including all variables ($\phi + DB + DEV + CV + WD + SC + OM$). The global model provided a significantly greater fit to the snail density data than the null model (Whole Model Test: $\chi^2 = 640.98$; $P < 0.0001$), but it fit the data poorly (Goodness-of-Fit Test: $\chi^2 = 254.95$; $P < 0.0001$). Therefore, the calculated

TABLE 2

Ranked candidate models used to evaluate the influence of microhabitat variables on *Campeloma decampi* density at Round Island Creek, Limestone Co., Alabama. Models are ranked in ascending order by their QAIC_c differences (Δ QAIC_c) relative to the best model in the set. Variables are distance to bank (DB), % silt and clay (SC), water depth (WD), current velocity (CV), % organic matter (OM), distance to emergent vegetation (DEV), and sediment grain size (ϕ).

Rank	Model	-Log Likelihood	K ^a	QAIC _c	Δ QAIC _c	w_i ^b
1	DB + SC + WD + CV	166.50	6	45.54	0.00	0.56
2	DB + SC	209.08	4	47.26	1.72	0.24
3	DB + CV + SC	208.16	5	49.96	4.42	0.06
4	DB + OM	225.13	4	50.16	4.62	0.06
5	DB + ϕ	225.22	4	50.17	4.63	0.06
6	SC + WD + CV	217.27	5	51.60	6.06	0.03
7	WD + SC	247.85	4	54.26	8.72	0.01
8	DEV + SC + CV	349.25	5	75.41	29.87	0.00
9	DEV + SC	384.78	4	78.96	33.42	0.00
10	CV + OM	388.69	4	79.67	34.13	0.00
11	CV + ϕ	388.58	4	79.65	34.11	0.00
12	SC	410.79	3	81.00	35.46	0.00

^a number of parameters in model

^b probability that model is best in model set

variance inflation factor for the global model ($\hat{c} = 11.08$) was used for each candidate model to obtain a quasi-likelihood and a modified AIC_c (i.e., $QAIC_c$) (Burnham & Anderson, 2002). Variables based on percentages (SC, OM) were arcsine square root transformed before analysis. All analyses were conducted with JMP 9.02 (SAS Institute Inc., Cary, NC) and Microsoft Excel.

To provide a quantitative description of habitat that supported *C. decampi*, we categorized quadrats as high snail density (> 12 individuals/m²) or low density (≤ 12 individuals/m²), and calculated mean values of each habitat variable for both categories.

RESULTS

A total of 395 *C. decampi* were captured from 19 (61%) of the 32 quadrats (Fig. 1). Most individuals were buried in the substrate. The overall mean density at the site was 49.2/m² (± 14.4 SE), but the distribution was highly clumped (Fig. 1A; variance-to-mean ratio 33.7) and the highest recorded density was 284/m².

The best supported model for explaining variation in snail density included four variables (DB, SC, WD, CV; Table 2), but other models had varying degrees of support. The difference in w_i between the best and the second best supported model (DB, SC) was small

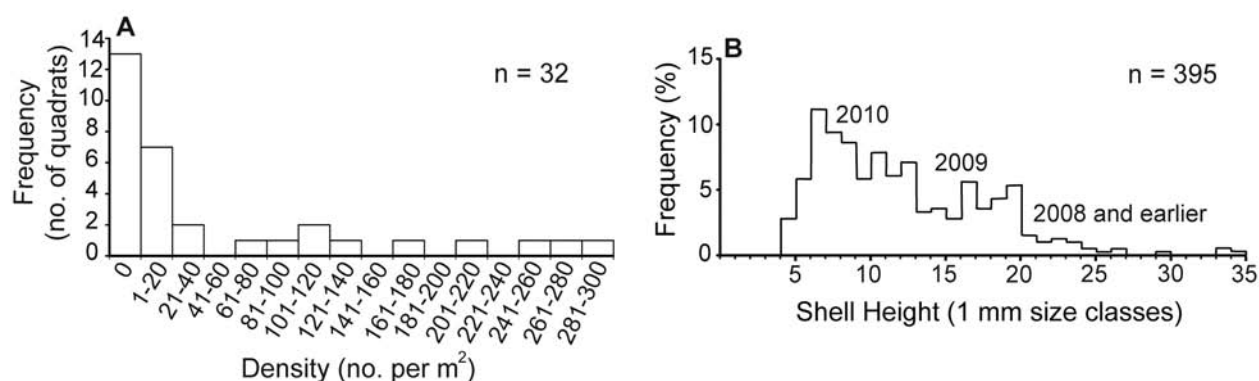


FIGURE 1

A) Density-frequency distribution of *Campeloma decampi* in 0.25 m² quadrats in Round Island Creek, Limestone County, Alabama. B) Size-frequency distribution for *C. decampi* in July, 2010. Dates indicate suspected year of recruitment for apparent size cohorts.

(evidence ratio = 2.3) indicating that the second model was also plausible. Models 3-7 also had some empirical support ($\Delta QAIC_c < 10$), but they all had low probabilities of being the best model; the remaining models were not supported ($\Delta QAIC_c > 10$; Table 2). No variable occurred in all plausible models, but distance from the bank (DB) and % silt and clay (SC) occurred in over half of plausible models, including both of the top two models. Distance to emergent vegetation (DEV) did not appear in any plausible model.

Because our results indicated model uncertainty, a *post hoc* confidence set from the first five models ($\Sigma w_i > 0.95$) was used to obtain model averages, unconditional SE values, 95% CI, and relative importance values for the variables shared among the models (Burnham & Anderson, 2002). Of the confidence set, distance from the bank (DB), % silt and clay (SC), and current velocity (CV) all had an effect on snail density (i.e., confidence interval excluded 0), but sediment grain size (ϕ) and % organic matter (OM) did not (Table 3); water depth had

a relatively high importance weight, but the 95% CI for this effect included zero. Parameter estimates indicated that density was inversely related to distance from bank and current velocity, but positively related to % silt and clay (Table 3). Among the confidence set, distance from the bank was the most important variable for explaining variation in snail density ($\Sigma w_i = 1$), but % silt and clay and current velocity also had high relative importance weights (Table 3).

There were clear univariate differences in some microhabitat variables between quadrats with high and low densities of *C. decampi* (Table 1), and these patterns generally reflected results of the information-theoretic analysis. High density quadrats were closer to the bank and had significantly lower depths and current velocities than low density quadrats. There were no significant differences in sediment characteristics or proximity to emergent vegetation between high and low density quadrats.

TABLE 3

Model-averaged parameter estimates (\pm unconditional SE), 95% CI for estimates, and relative importance for variables explaining variation in *Campeloma decampi* density in Round Island Creek, Limestone County, Alabama.

Parameter	Model-averaged estimate \pm unconditional SE	95% CI	Relative Importance (Δw_i)
Distance to bank	-1.24 \pm 0.32	- 1.88 to -0.59	1.00
% silt and clay	10.43 \pm 1.80	6.74 to 14.11	0.89
Current velocity	-0.06 \pm 0.02	-0.11 to -0.01	0.64
Water depth	-0.05 \pm 0.03	-0.11 to 0.02	0.58
Sediment grain size (ϕ)	-0.18 \pm 1.96	-0.41 to 0.05	0.06
% organic matter	-1.27 \pm 80.78	-2.86 to 0.032	0.06

The distribution of snail size was non-normal (Goodness-of-fit test, $p < 0.0001$; $n = 395$) and strongly right-skewed, and the population was dominated by small individuals (Fig. 1B). Shell height ranged from 4.3-34.7 mm, but the mean was 12.0 ± 0.3 (SE), the modal size class was 6 mm, and over 75% of the population was < 17 mm (Fig. 1B). The size frequency distribution showed evidence of at least three size cohorts, one centered on about 8 mm (about 4-12 mm), another centered on about 16 mm (about 13-19 mm), and another composed of individuals > 20 mm; these largest individuals made up only 7% of the population.

DISCUSSION

Campeloma decampi has a highly clumped distribution, which is apparently related to its specific microhabitat requirements. It primarily occupies shallow, slow-current areas along the stream margin where the substrate contains silt and clay. The highest densities of the species were found almost exclusively in this habitat type.

Observations from other sites in Round Island Creek and elsewhere in its range suggest that this habitat preference is a general characteristic of the species (Haggerty & Garner, 2008). Indeed, this type of habitat appears to be required by most species in the Viviparidae. Most viviparids feed on mud, detritus, and decaying organic matter, and high snail densities and growth are often associated with habitats rich in these materials (Allison, 1942; Chamberlain, 1958; Imlay et al., 1981; Richardson & Brown, 1989). Consequently, the low relative importance value for organic matter, sediment grain size, and the low ranking of the silt and clay

model in our study were surprising. We did not remove surface litter (e.g., sticks and intact leaves) from our substrate samples before processing, and inconsistency in the presence of these larger organic materials among samples may have obscured patterns related to finer, buried organic matter that serve as a food source for snails. Oxygen concentration in organic sediments also may influence the distribution of *C. decampi*. Some of our sample locations had relatively high percentages of silt, clay, and organic material but had the smell of hydrogen sulfide suggesting that they were hypoxic; such habitats can be inhabited by *Viviparus georgianus*, but they rarely contain *C. decampi*. It is also likely that concentrations of organic matter vary in these depositional habitats seasonally and among years.

Alternatively, the lack of strong relationships regarding potential food availability and fine substrates may indicate that other factors are equally important in determining habitat selection by *C. decampi*. The low flow, near-shore habitats that supported high densities of *C. decampi* may represent refuges from scouring flows (Bovbjerg, 1952); this may be especially important for large, globose species like *Campeloma* compared with more hydrodynamically streamlined species that occur in main channel habitats (e.g., pleurocerids). Shallow, near-shore areas also may be refuges from fish predation, which can be important in limiting snail density (Medcof, 1940). Regardless of the mechanism responsible for habitat selection, these shallow shoreline habitats clearly are critical for survival of this species and a better understanding of their characteristics and temporal stability is needed.

Our demographic data offer some insights into the life history of *C. decampi*. Assuming that *C. decampi* has a birth size (approximately 3–4 mm) and juvenile growth rate (1.7–2 mm/month during the first year) similar to other *Campeloma* (Van Cleave & Altringer, 1937; Chamberlain, 1958; Vail, 1978; Brown & Richardson, 1992), the smallest size cohort in our population (about 4–12 mm) may represent individuals that were born over a protracted period from late winter to mid-summer, 2010. This growth estimate also suggests that *C. decampi* reaches a minimum brood-bearing size during their first year (i.e., 15.0–21 mm; Van Cleave & Altringer, 1937; Medcof, 1940; Chamberlain, 1958; Brown & Richardson, 1992) and could give birth early the following year. This has been reported for some other species of *Campeloma* (Van Cleave & Altringer, 1937; Medcof, 1940; Chamberlain, 1958; Brown & Richardson, 1992).

The size cohort centered around 16 mm (about 13–19 mm) may have been made up of individuals born in 2009, while those larger than 20 mm represent individuals born in 2008 and earlier. Life span ranges from two to five years for some congeners (Van Cleave & Altringer, 1937; Medcof, 1940; Chamberlain, 1958; Brown & Richardson, 1992). Few of the *C. decampi* in our population appear to live three years or longer. The rarity of large individuals suggests that few produce more than one or two broods in their lifetime; this life cycle is more similar to subtropical populations than those in north temperate areas (Van Cleave & Altringer, 1937; Medcof, 1940; Brown & Richardson, 1992). It is unknown whether the Round Island Creek *C. decampi* population is sexual or parthenogenetic. Additional research is needed to better understand the life cycle of *C. decampi* and how it may be influenced by environmental conditions (see Crummett et al., 2013).

The high density of *C. decampi* and the preponderance of small individuals indicate that the population at our study site is healthy and reproducing. Qualitative observations from other Round Island Creek sites suggest that similarly robust populations exist throughout the lower and middle reaches of the stream (Haggerty & Garner, 2008). Nevertheless, the restricted distribution of this species makes it highly vulnerable and warrants additional research on its life history and demography.

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