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AUTUMNAL TISSUE DEGROWTH IN *PHYSELLA GYRINA* (GASTROPODA, PULMONATA)

David A. Smith
Wabash College
Department of Biology
Crawfordsville, Indiana 47933

Abstract: Adult *Physella gyrina* (Say, 1821) were sampled from Sugar Creek in west-central Indiana between October and December, 1987. Baseline analysis, in August, showed that tissue dry weight (TDW) related to shell dry weight (SDW) as TDW = 0.23·SDW+0.373 mg. This relationship was used as a predictor of TDW, and differences between actual and predicted TDWs, from October to December, were used as estimates of tissue metabolism. Significant levels of tissue degrowth were found in autumnal natural populations of *Physella*. Tissue losses during this period averaged 27.6% of predicted tissue biomass

INTRODUCTION

Several laboratory and field studies have demonstrated that gastropod molluscs experience tissue loss overwinter (Russell-Hunter and Eversole, 1976; Russell-Hunter, *et al.*, 1984; Russell-Hunter, 1985). One of the first reports of direct field evidence for such tissue "degrowth" (Russell-Hunter, 1985) in molluscs was for natural populations of *Helisoma trivolvis* and *Lymnaea palustris* in central New York (Russell-Hunter, *et al.*, 1984). Tissue degrowth in molluscs had also been studied using nearly concurrent assessments of oxygen consumption and of nitrogen excretion (Russell-Hunter, *et al.*, 1983). These bioenergetic analyses showed a clearly controlled differential catabolism of protein resources overwinter.

The present investigation quantified tissue losses for a field population of *Physella gyrina* in west-central Indiana. This study provides new information on molluscan tissue degrowth: first, by quantifying patterns of tissue metabolism during the approach to winter rather than in early spring; and second, by assessing these patterns across a range of adult and juvenile sizes. It is this differential degrowth among size cohorts which should ultimately be considered in any analysis of the growth and demography of natural populations of freshwater gastropod mollusca.

MATERIALS AND METHODS

Physella gyrina is one of the more common pulmonate snails of central Indiana. This euryoecic gastropod is found mostly in eutrophic environments, including ponds and streams. Animals used in the present study were taken from Sugar Creek in Montgomery County (86°56.78'W, 40°2.46'N).

In August 1987, approximately 350 individuals were collected. Maximum shell lengths (SL, ± 0.1 mm) were determined and individuals were divided into four size classes (< 3.0, 3.0-4.9, 5.0-6.9 and > 7.0 mm). Note that size classes here differ from those used for data analysis. To better interpret size-dependent patterns of metabolism, it was necessary to (1) divide the smallest class (< 3.0 mm) into two classes (< 2.0 and 2.0-2.9 mm), to (2) divide the second class (3.0-4.9 mm) into two classes (3.0-3.9 and 4.0-4.9 mm), and to (3) combine the last two classes (5.0-6.9 and > 7.0 mm) into one (SL > 5.0 mm).

Sixty snails from each of four size classes were placed in tared aluminum-foil boats, dried to constant weight (60°C), weighed (± 0.1 mg), and then placed in a muffle furnace for 6 hours at 500°C. Tissue dry weight (TDW, including shell periostracum) was obtained by subtracting ash dry weight (SDW, as $CaCO_3$) from initial dry weight. Regression analysis was used to associate TDW with SDW.

Weekly sampling to quantify natural patterns of tissue metabolism began in early October and ended in mid-December, 1987. Each collection consisted of 60 animals (55 for week 9). Snails were placed in tared aluminum-foil boats, dried to constant weight, weighed, and then placed in a muffle furnace as above. Tissue dry weights were determined, and the difference between these and expected values (determined by regression) were used as a measures of tissue metabolism (positive values indicating growth, and negative values indicating degrowth). Note that while all tissue degrowth should be quantifiable by actual and expected tissue weights, not all tissue growth need be since concurrent shell growth may accompany at least part of the tissue growth process. Therefore, estimates of tissue growth reported here are minimum values.

RESULTS

Regressions showed that tissue dry weights related to shell dry weights, in August, as TDW = 0.234·SDW+0.373 mg (r = 0.97, N = 160, P < 0.001). Snails in each of the 10 weekly samples (beginning in October) of *Physella* showed tissue losses based on this regression (Figure 1). During the first week, 70% of individuals showed tissue gains averaging +21.8% of predicted tissue dry weight (TDWp, range of 0.01% to 53.4%). During the same period, 30% of individuals showed biomass losses averaging -34.9% (range of -1.3 to -72.8%). These averages correspond to raw values of 0.41 ± 0.065 mg for the gains, and -0.19 ± 0.021 mg for the losses. During week 5, 18% of individuals showed biomass increases averaging +21.8% of TDWp (range of 0.5 to 75.9%). During the same period, 82% of individuals experienced biomass losses averaging -39.8% (range of -2.0 to -64.5%). These averages correspond to raw values of 0.41 ± 0.164 mg for the gains, and -0.23 ± 0.010 mg for the losses. Finally, during week 10, 93% of individuals sampled showed tissue losses averaging -54.7% (range of -11.1 to -84.6%), and only 7% of individuals experienced any weight gain, averaging +17.3% of TDWp (range of 1.2 to 33.3%). These values correspond to -0.33 ± 0.009 mg tissue for the losses, and 0.29 ± 0.119 mg tissue for the gains.

Individual size was an excellent indicator of individual tissue loss. Smaller individuals always experienced greater losses than did larger ones. For example, during week one, the smallest individuals (SL < 2 mm) experienced tissue losses averaging -63.9% (N = 4), while their larger counterparts (SL > 5 mm) exceeded

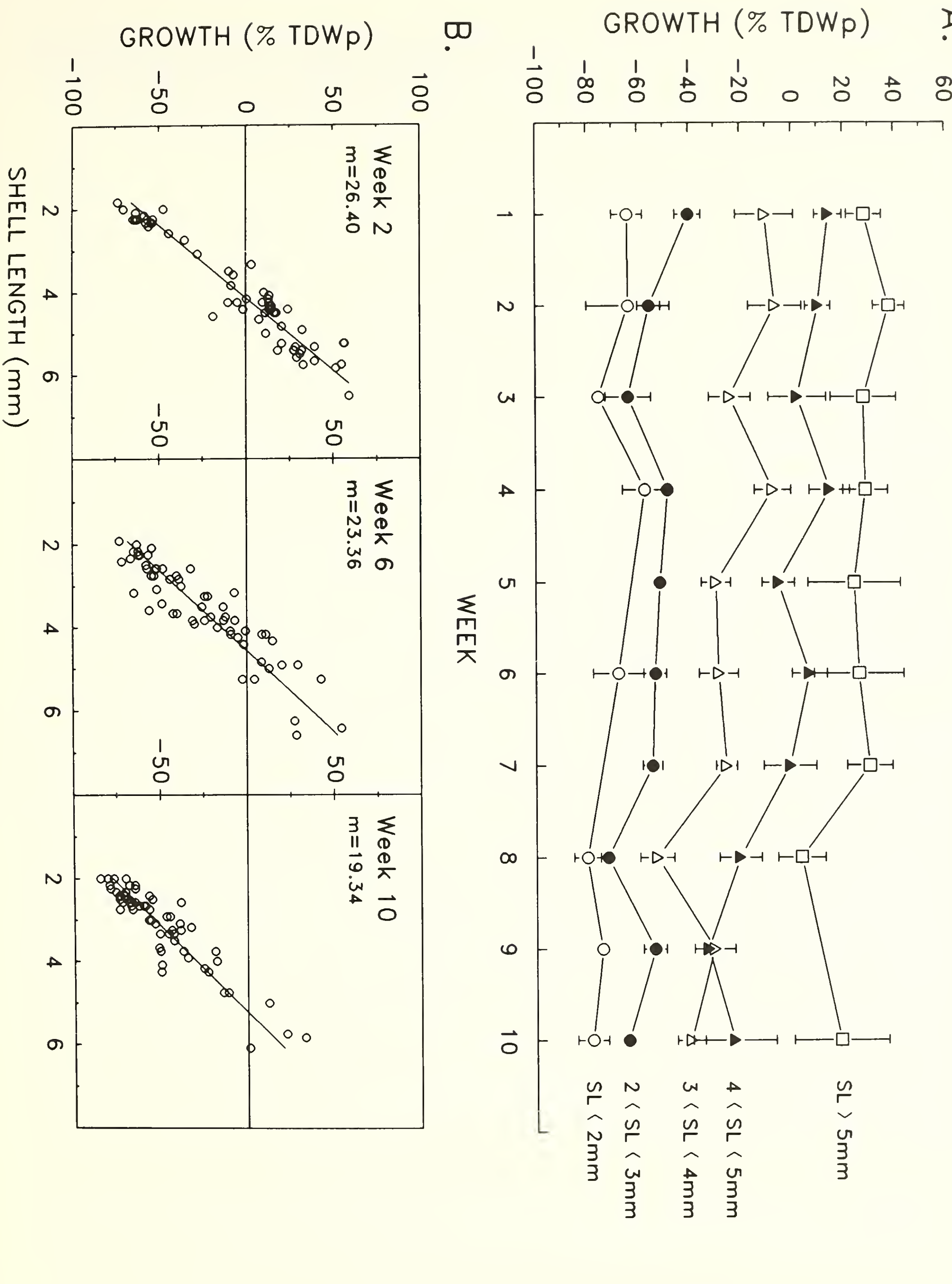

Figure 1. Patterns of tissue condition in a natural population of *Physella gyrina*. Plot A shows pattern of tissue loss for individuals belonging to five size classes of *Physella*. Values are means and standard errors. TDWp is tissue dry weigh predicted from regression analysis. Plot B shows the pattern of tissue metabolism across size classes. Values (m) represent slopes of least-squares regressions.

Table 1. Patterns of tissue metabolism in *Physella gyrina*. Analysis is a two-way ANOVA of tissue degrowth as (TDW-TDWp)/TDWp across time and size. Note that all P < 0.001.

Source*				
Model	SS	d.f.	MS	F
Time	25368.10	9	1426.13	17.79
Size	299811.97	4	633.84	473.01
Time x size	16054.40	33	5229.16	3.07
Error	86835.67	548	158.46	

* Analysis was performed on data subject to arcsine transformation.

TDWp by an average of 28.5% (N = 21). This pattern continued and the gap between size classes widened during week 6. Here, small individuals experienced degrowth averaging -67.8% of TDWp (N = 2), while the largest individuals exceeded TDWp by 26.0% (N = 6). Finally, during week 10 the small individuals showed tissue losses averaging -78.0% (N = 4), and large ones exceeded TDWp by 19.0% (N = 3).

Regression analysis at week 2 showed the relationship between shell length and tissue condition (as % TDWp) to be TDWp = 26.403·SL-105.732 (r = 0.943, N = 60). At week 6, the relationship was Y = 23.356·X-106.894 (r = 0.904, N = 60), and at week 10, it was Y = 19.336·X-103.636 (r = 0.905, N = 60). From inspection of Figure 1B and from analysis of Table 1, it is clear that two concurrent phenomena occurred in these demographically-representative samples. First, as the season proceeded, an increasing fraction of the population accumulated negative metabolic equity; and second, smaller individuals comprised an increasing proportion of this losing population with time. Results from two-way ANOVA (Table 1) showed significant size and time effects and, more importantly, a significant interaction between these variables. While smaller individuals made up an increasing proportion of the losing population, mid-sized animals (4.0-4.9 mm) were the most dramatic losers, going from positive growth (14.5% TDWp in week 1) to degrowth in week 10 (-20.3% TDWp). In contrast, animals from other classes showed average declines of just 19.2% over this same period.

DISCUSSION

Several studies have demonstrated that seasonal changes in the patterns of metabolism in natural populations of freshwater mollusca may be reflected in modifications of tissue C:N ratios (Russell-Hunter and Eversole, 1976). Both field and laboratory investigations have shown, specifically, that freshwater snails undergo a decline in mass of structural protein while overwintering. This study demonstrates that snails sampled from natural populations of *Physella gyrina* experience autumnal tissue degrowth. Although no data showing reductions in algal biomass during the approach to winter have been presented here, qualitative observations plainly revealed declines in the availability of pasturage for these animals.

Previous accounts of molluscan degrowth have quantified tissue losses "after the fact" in early spring (Russell-Hunter, *et al.*, 1984; Smith and Russell-Hunter, 1990). The present study not only demonstrates that degrowth accelerates with declining water temperatures but also that small to mid-sized individuals are more severely influenced by these declines. The latter observation is of significance to studies of life-cycle patterns and bioenergetics. Indiana populations of *Physella gyrina* studied here show a bivoltine life cycle similar to that discussed by Brown (1979) for Iowa *P. gyrina*. The largest individuals collected here are part of a spring generation (G1) which mature in late summer and oviposit members of a G2 generation in the fall. G2 individuals overwinter to oviposit the next spring generation. Such an annual life-cycle pattern is very common among pulmonates living in temperate fresh waters (Russell-Hunter, 1961, 1978; Calow, 1978, 1983) and is clearly correlated with the large temperature and trophic changes occurring seasonally in such habitats. However, many molluscan populations do not reproduce throughout the summer (Russell-Hunter, 1961; Calow, 1978) but limit egg-laying to late spring (or early summer). As winter conditions begin, size-related mortality brings about an increase in the average size of survivors. The present investigation demonstrates that such differential mortality is paralleled in smaller individuals by proportionately greater tissue degrowth. For snails like *Physella*, being born in late summer may not enhance fitness

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