Life History and Secondary Production of *Goniobasis proxima* (Prosobranchia: Pleuroceridae) from Four Appalachian Headwater Streams in Western North Carolina

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Abstract

I investigated life history traits and secondary production of populations of *Goniobasis proxima* in four streams from July 2005 to June 2006. Measurements of canopy cover, conductivity, alkalinity, temperature, and nitrate-nitrogen (NO_3-N), as well as snail size, density, and occupied substrate were taken monthly for each stream. Snail growth rates were determined in an aquarium for 10 size classes and secondary production was estimated as the summed product of size class growth rates and field biomass measurements. Size class production estimates tracked biomass with intermediate to larger sized snails dominating production, despite smaller snails growing faster. Production estimates across streams ranged from 1,400 mg m^{-2} yr^{-1} to 22,183 mg m^{-2} yr^{-1} with noticeable summer highs and winter lows. Annual turnover was slow (0.43-0.49) owing to slow growth and long development time. Snails preferred leaves/wood as a substrate to occupy over rock and sand and showed no appreciable grazing effect on the epilithon community.

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Introduction

Molluscs occupy all habitats. They are among the most successful taxa having more than twice as many species as vertebrates and only arthropods are more numerous and successful (Russell-Hunter, 1983). Many marine and freshwater mollusc species constitute the dominant members of their communities in both biomass and production making them very important ecologically (Aldridge, 1983: Russell-Hunter, 1983). In particular, gastropod biomass may dominate lower trophic levels (Habdija et al. 1995; Stone et al. 2005; Hall et al. 2006) significantly contributing to, and potentially altering, the structure and function of the aquatic systems they inhabit. Using secondary production as a response variable, I examined four populations of the freshwater prosobranch gastropod, *Goniobasis proxima*, in four Appalachian streams to gain insight into their life history, population dynamics and structure.

Goniobasis proxima is a widespread native freshwater snail found on both sides of the eastern continental divide in the mountains and piedmont of the southeastern United States (Dillon, 1988a; Dillon and Keferl, 1999). Populations are scattered across Virginia (south of the Roanoke River) to western Georgia and are isolated from each other by mountains and large rivers. Density tends to increase as stream order decreases resulting in populations restricted to small headwaters and tributaries no more than a few meters wide (Dillon and Keferl, 1999; Dillon and Frankis, 2004). This restriction leads to tributaries having discreet populations with high inter-population genetic variation and unusually low intra-population genetic variation (Dillon, 1988a; Dillon and Reed, 2002). However, population transplant experiments and artificial introductions demonstrated no evidence supporting reproductive isolation (Dillon, 1986 & 1988a). Isolation of

populations will likely increase as suitable habitat is reduced by land use change from forested to urban and agricultural development.

G. proxima is specialized to graze on solid substrates. However, they may also graze on unconsolidated substrates if the surface is firm enough to allow accumulation of algae and detritus (Dillon and Keferl, 1999). Individuals tend to orient and move upstream at a maximum upstream migration rate of 15-20 m yr^{-1} but only 5-10 m yr^{-1} downstream (Dillon, 1988b).

Populations are perennial with a fairly restricted egg-laying season. Egg laying begins as early as March and usually ends by July. Eggs hatch after two weeks and have a sex ratio of 50:50 although females occasionally outnumber males (Dillon, 1988a; Dillon and Frankis, 2004). *G. proxima* is iteroparous and dioecious; females mate mostly once per year and may store sperm for long periods (Dillon, 1988a). Populations of *G. proxima* are known to have high infestation rates of trematode parasites. The parasites congregate in the gonads and may result in castration of the snail with implications for reproduction and growth.

The objectives of this study were to investigate aspects of the ecology of select *G. proxima* populations located in four headwater streams. Specifically, I studied substrate selection, grazing effect, population dynamics, and secondary production. Several species of *Goniobasis* have been re-classified as *Elimia* sp. I have retained the use of *Goniobasis* for this study because the majority of literature cited uses this nomenclature.

Methods and Materials

Site Description

I collected snails monthly from July 2005 to June 2006 in four 1st order headwater streams in the Nantahala National Forest, Macon County in western North Carolina. The stream names were RB R, RB 30m, RB 10m, and RB 0m to reflect a riparian cut project (RCP) conducted to establish streamside buffer strips of 30 meters, 10 meters, and 0 meters. RB R was the reference stream where no logging was conducted. At the start of sampling, no watershed logging had begun and at the conclusion, only the RB 10m cut was completed. Although logging was not an integral part of our study, I retained the names used for these streams to maintain consistency with others who worked on this RCP.

All streams drained forests dominated by Tulip Poplar (*Liriodendron tulipifera*), Maple (*Acer spp.*), Oak (*Quercus spp.*), Eastern Hemlock (*Tsuga canadensis*), White Pine (*Pinus strobis.*) with an under-story of Rhododendron (*Rhododendron maxima*.), and Mountain Laurel (*Kalmia latifolia*). Streambed morphology consisted of alternating riffles and pools with runs providing substrate habitat composed of sand, cobble, exposed bedrock, leaf packs and log jams.

Snail Populations and Substrate Preference

Study reaches were 100 meters long partitioned into 10m sub-reaches. Snails were sampled quantitatively using a 1/4m^2 PVC frame. Three random samples were taken every 10m totaling 30 samples per reach per month. The area within the PVC frame was carefully examined to ensure all snails were counted and measured for a total of 360 samples per stream over the course of the study. Snail size was determined by measuring

shell width to the nearest 0.05 mm using calipers (Stiven and Walton, 1967). Width was measured rather than length because shell apices typically were substantially eroded.

Substrate from which each snail was removed, including rock, sand, and leaves/wood, was recorded. I determined snails were removed from sand, as opposed to rock, when the operculum and foot were covered with sandy material. When snails were removed from rock (gravel, pebbles, cobbles, and bedrock), or leaves/wood the operculum and foot were clean. Percentages of substrates within grid samples were estimated by observation.

Prior to the first month of sampling, 129 snails were randomly collected downstream of study reach RB 10m and brought to the lab to develop a width-mass regression curve. Snails were dried for 48 hours at 60° C and weighed, with shell, to 0.0001 g. The width-mass regression for *G. proxima* was mass = $0.01w^{3.18}$ ($r^2 = 0.99$) where w is shell width in millimeters. All snails subsequently collected were measured on site and returned to the stream. Measured widths were then applied to the regression equation to determine biomass in dry weight.

In July 2007, I collected 161 snails ranging in size from 1.5 – 5.8 mm from one m^2 of the RB 10m stream bed and examined them for parasite burden. Snail shells were cracked with pliers and parasite burden was determined under low magnification by the presence of trematodes throughout the gonads and body cavity.

Environmental Variables

Canopy cover was measured every 10 meters using a spherical densiometer. Conductivity and temperature were measured every 10 meters with a YSI model EC300 conductivity meter and discharge was estimated using the slug injection technique

(Gordon et al., 2004). Three 125ml water samples were collected mid reach for alkalinity and NO_3-N analysis. Water samples were kept on ice until returning to the lab where they were either analyzed or frozen. Standard methods (APHA, 1998) were applied for determining alkalinity and NO_3-N concentrations. All variables were measured monthly in each stream. Table 1 contains summary values for these various physical and chemical variables.

Epilithon Biomass

Ten cobbles were randomly sampled along each 100m stream reach each month to assess epilithic bio-film biomass and chlorophyll *a* using standard rock scrubbing techniques (Hauer and Lamberti, 1996). Epilithon biomass was determined as ash-free dry mass (AFDM) (APHA, 1998). Chlorophyll *a* was extracted following Sartory and Grobbelaar (1984) and determined with spectrophotometry (APHA, 1998).

Secondary Production and Growth Rates

Population size distributions were bell-shaped making cohort estimates of secondary production impossible. Consequently, I reared 83 snails in the lab for three months to determine size-specific growth rates. Snails were collected randomly from site RB 10m, brought to the lab, and placed in a 10-gallon aquarium to monitor growth. Prior to introduction, snails were individually color-coded with nail polish and their widths measured. The aquarium was filled with approximately 5 cm of sand, 10-12 rocks, and approximately 8 liters of water all from the collection stream. Four air stones were dispersed in the aquarium for stream water circulation and oxygenation. Water temperature mimicked summer stream temperatures (17-20° C) with ceiling lights and natural sunlight providing insolation.

Snails were allowed to graze for one-month after which they were removed, blotted dry, and their widths re-measured. Shell widths were applied to the width-mass regression curve I established earlier to estimate individual biomass. These biomass estimates were then used to calculate instantaneous snail growth rates according to Hall et al. (2006) using: $\ln(M_f) - \ln(M_i)/t$

where: ln = natural log

M_f = final snail mass (mg)

M_i = initial snail mass (mg)

t = time interval (d)

Snails were distributed over 10 size classes, chosen arbitrarily, with size class growth rates determined by summing the instantaneous growth of all individual snails in each size class divided by the number of snails in that size class. These rates were then multiplied by the corresponding size class biomass from monthly field data and summed across size classes to estimate monthly and annual secondary production (Benke, 1993). Growth rates for sizes <1.0 mm and >5.45 mm were not directly calculated from the aquarium experiment due to a lack of these sized snails. However, growth rate for snails 5.5 - 5.95 mm (size class 10) was calculated from the regression equation ($g = 0.012e^{-0.33x}$, where g = growth, x = chosen size class, 1-10 (Figure 6)) and multiplied with field biomass data due to a large number of these sized snails measured in the field. Growth rate was not calculated for snails below 1.0 mm due to very low numbers observed in the field.

I did not incorporate slower growth rates, such as those that would be observed in winter months, resulting in maximum annual production estimates. Maximum production

estimates would then in turn lead to an over estimation of snail P/B. Additionally, my biomass estimates are presented as dry weight and include shell mass. This approach would present higher secondary production estimates when comparing to other snail production estimates presented as AFDM.

Measured shell width differences over the 30-d trial were also used to calculate an age approximation using an assumed size of 0.5 mm at birth (Richardson et al., 1988) and by dividing individual snail width by the mean shell width increase observed for all snails over the 30-d trial

Snails demonstrated burrowing behavior in the aquarium study and up to 31% of snails were completely buried in sediment prior to removal for measurement. Assuming these snails exhibit this behavior in the field, my not having sampled them would cause an underestimation of production.

Statistical Analysis

Paired t-test and one-way ANOVA were used to test for significant differences across and within streams regarding percent substrate type available and percent snails found on substrate types. Tukey's or Holm-Sidak were used as multiple comparison procedures.

Chi-square was used to measure how much the observed proportion of snails found on substrate types diverged from the expected proportion of snails on those substrates. Data from Table 4 were used as the observed proportion and data from Table 3 were used as the expected proportion.

Pearson's Product Moment and Linear Regression were used to address the relationship strength between snail density in the four streams to the environmental

variables measured to include temperature, conductivity, canopy cover, nitrate concentration, chlorophyll a and epilithon AFDM. One way ANOVA was used to test for differences in environmental variables across streams. All analysis were run using SigmaStat 3.1 software.

Results

Snail Populations and Environmental Variables

A total of 11,668 snails were counted in the four streams from July 2005 to June 2006 and the populations were dominated by mid to larger sized snails (Figure 1). Snail density across streams paralleled each other and varied seasonally. Highest numbers occurred in warmer months and lowest in the colder months (Figure 2). Linear regression analysis demonstrated positive significant relationships ($p > 0.05$) between snail density and temperature ($r^2 = 0.58$, $p = 0.006$), conductivity ($r^2 = 0.55$, $p = 0.009$), and NO_3-N ($r^2 = 0.43$, $p = 0.04$) in RB 0m and with canopy cover ($r^2 = 0.43$, $p = 0.03$), epilithon AFDM ($r^2 = 0.58$, $p = 0.006$), and NO_3-N ($r^2 = 0.40$, $p = 0.05$) in RB 30m. No relationship was found between snail density and any of the environmental variables in either RB10m or RB R.

There were no significant differences across streams in temperature, canopy cover, alkalinity, chlorophyll a, and epilithon AFDM ($\alpha = 0.05$). The RB 30m stream differed in conductivity and NO_3-N to RB R ($p = 0.005$, $p = 0.002$, respectively) and in NO_3-N to RB 10m ($p = 0.02$).

Mean annual snail width and weight across streams was 3.81 mm (range: 0.9-6.4 mm) and 50.14 mg (range: 0.40-218 mg). Lowest annual mean density was in RB 0m

(5.3 snails m^{-2}) and highest was in RB 10m (73.1 snails m^{-2}) (Table 2). Approximately 29% of the 161 snails sampled for parasite burden were infested with trematodes. Of those, only three snails smaller than 4.0mm were infested, the smallest being 3.6mm.

Substrate Preference

Across streams, mean available substrate was 43.30% rock, 40.24% sand and 16.47% leaves/wood. The percent available substrate was lowest for leaves/wood across all streams yet some of the highest percentage of snails were found on this substrate; the opposite of this was true for sand (Figure 3). Chi-square results indicate a significant difference (critical value: 12.59, $df = 6$, $\alpha = 0.05$) between the observed and expected proportion of snails on both sand and leaves/wood across all streams (Table 5) suggesting snails prefer leaves/wood. A summary of the percent substrate type available within and across streams can be seen in Table 3 and a summary of the percent snails on certain substrate types can been seen in Table 4.

There was a significant shift (paired t-test, $p = 0.002$) in snail location towards leaves across all streams with the onset of leaf-fall in October and November (Figure 4). In the summer months prior to leaf fall (July - Sept.), mean percentage of snails found on leaves across streams was 25.3%. During October and November, mean percentage of snails occupying leaves was 63.34%. Comparison of leaf percentages between July and August to October and November was not possible because substrate grid observations in July and August did not take into account percent leaves available, only the number of snails found on leaves.

After logging of the RB 10m watershed was complete in December 2005, a significant shift in snail location from other substrates to wood was observed over the

remainder of the study in this stream (Figure 5), (paired t-test, $p = 0.037$). In the months prior to completion of logging (July 2005 – Dec. 2005), there were no significant differences across all streams in percent snails found on wood (ANOVA, $p = 0.274$). Post logging, (Jan 2006 – June 2006) there was a significant difference between RB 10m from both RB R and RB 30m (ANOVA, $p = 0.01$). There was no significant difference ($p = 0.073$) post logging between RB 10m and RB 0m.

Epilithon Biomass

Mean annual epilithon biomass AFDM and chlorophyll *a* values did not differ significantly over the year across streams (ANOVA: AFDM: $p = 0.65$; Chlorophyll *a*: $p = 0.4$). Epilithon biomass values ranged from 7.9 – 9.3 g AFDM m^{-2} and chlorophyll *a* ranged from 0.033 - 0.050 mg m^{-2} (Table 6). No significant relationship, other than that seen in RB 30m between snail density and AFDM ($p = 0.006$), was observed.

Secondary Production and Growth Rates

Mean snail width increased from 3.12 mm to 3.20 mm and mean snail mass increased from 30.67 mg to 32.36 mg in the aquarium study. Maximum observed snail width was 6.4 mm in the field and using an assumed width of 0.5 mm at birth and a mean shell growth rate of 0.075 mm $month^{-1}$, I estimated that 6.5 years were required to achieve maximum observed size.

Growth rate was fastest in the two smallest size classes (0.0079 and 0.0091 day^{-1}, respectively). A strong drop in growth rate occurred between the second and third size class followed by a gradual decline through the remaining eight size classes (Figure 6).

Total biomass ranged from 3,265 mg dry weight m^{-2} in RB 0m to 45,382 mg dry weight m^{-2} in RB 10m. Annual production estimates varied from 1,400 mg dry weight m^{-}

^{2} yr^{-1} in RB 0m to 22,183 mg dry weight m^{-2} yr^{-1} in RB 10m. Biomass and production estimates tracked each other through size classes and over time in all streams. Highest values for both biomass and production were observed in larger size classes and in April and May, respectively (Figures 7 & 8). Estimated turnover rates (P/B) ranged from 0.43 yr^{-1} in RB 0m to 0.49 yr^{-1} in RB 10m. For specific size class and monthly biomass and production estimates, see Appendix 1.

Discussion

Snail Populations

Population distributions favoring intermediate sizes, as observed in this study (Figure 1), are anticipated for long-lived species that are fairly constant in population size (Butler, 1982; Krebs, 1985). Richardson et al. (1988) found similar population distributions in two closely related *Elimia* species in an Alabama stream. Maxima and minima in snail density and biomass occurred in summer and winter months, respectively (Figure 2); a pattern also observed by Hall et al. (2006). A 60% reduction in snail density was observed from December 2005 to February 2006 when compared to the remaining months of sampling. I attribute this winter minima to burial/hibernation, a behavior validated in my aquarium experiment. However, efforts to find snails in sandy areas within the streambed and along the banks were unsuccessful. It is unlikely that snail mortality would explain the observed decrease in density and biomass because snail development time and estimated turnover rates for these populations would not allow for recovery to the numbers observed during the following spring and summer.

I observed less than 10 empty snail shells over the course of my study leading me to speculate non-predatory snail mortality is low. This contention further supports the conclusion these snail populations are stable and comprised of long living individuals. Low mortality may also be attributed to a general lack of predators in accordance with the notion that these streams maybe considered two-level trophic systems with snails representing the top level, similar to a model suggested by Rosemond et al. (1993) for Walker Branch, Tennessee. As such, in-stream predation would be non-existent. If snails were being preyed upon, shells must have been broken apart during feeding with resulting degradation too rapid to gain an accurate estimate of snail mortality by observing empty shells every month. However, no fish were observed and density of crayfish appeared to be very low and did not seem to regulate snail density. I did observe scavenging on snails by limnephilid and glossosomatid caddisfly larvae, though very infrequent and no birds were seen foraging in the stream.

Variation in snail density across streams may best be explained based on physical barriers (Dillon, 2000) restricting migration, especially since regression analysis of measured environmental variables showed very inconsistent relationships to snail density. Low density in RB 0m may be due to dry zones downstream of my study site present at certain times of year. RB R and RB 30m were in adjacent watersheds as tributaries to the same stream, yet density in RB R was notably lower. This may be explained by the presence of a large sliding waterfall and a longer upstream distance from the confluence to the RB R study reach. Snail populations in these four streams may be in the process of either expanding or shrinking, all at different rates, and observed density may represent populations in different stages of that process.

Snail density was very low compared to the findings of Rosemond et al. (1993) who reported densities of *Elimia claeveformis* over 1,000 individuals m^{-2} year round in Walker Branch, a 1st order stream in Tennessee. However, snail density in my study streams was similar to findings by Richardson et al. (1988) for *Elimia cahawbensis* and *E. clara* (~200 - 550 and ~60 - 275 snails m^{-2}, respectively) in Little Schultz Creek; a 2nd order, spring-fed stream in Alabama. Ross and Ultsch (1980) observed combined density for *E. cahawbensis* and *E. carinifera* of 19.2 - 532.8 snails m^{-2} in Big Sandy Creek, a tributary of the Black Warrior River, also in Alabama.

My estimated life span of ca. 6.5 years for *G. proxima* represents a shorter duration than the snails may actually live because I only used the fastest estimated growth rates derived from my aquarium study to project life span. My estimate is lower than those estimated by Richardson et al. (1988) for two similar species: 11 years for *E. clara* and 10 years for *E. cahawbensis*. On the other hand, my estimate is 2-3 years longer than that reported for *G. proxima* by Dillon (2000). Huryn et al. (1994) predicted minimum cohort duration ranging from ~2^+ to 6^+ years for various *Elimia* species while Miller-Way and Way (1989) reported the lifespan of another prosobranch snail (*Leptoxis dilatata*) from the Laurel Fork River in West Virginia to have a mean life span of around two years. Several factors may contribute to the disparity in life span estimates such as environmental variation across snail habitats, duration of sampling, type of measurement techniques, and inherent differences in the species, despite being closely related.

Substrate Preference

I observed a large proportion of snails on leaves/wood despite a low expected proportion and a small proportion of snails on sand despite a large expected proportion

(Figure 3). This may be explained by considering the ability of these substrates to provide a high quality, nutritious food along with providing a stable platform on which to graze. Haley (1997) concluded the nutritional value of fresh leaves/wood entering streams might be greater when compared to well-decayed pieces that have been in streams several months while Golladay and Sinsabaugh (1991) noted microbial biomass on leaves in streams peaked within 30 days of exposure while ATP and Chlorophyll *a* on wood peaked within 30-70 days. The subsequent shift of snails to leaves across all study streams during the fall months and to wood in RB 10m post-logging (Figures 4 & 5) support the notion that leaves and wood may provide a more nutritious and favorable food source (Haley, 1997; Hicklen et al., 2006).

Snails may graze on wood preferentially over leaves because leaf surfaces are more prone to softening and fragmentation thus limiting bio-film development. In contrast, the fragmentation and scouring of wood exposes fresh surfaces for microbial colonization (Golladay and Sinsabaugh, 1991) and microbes are known to increase the nutritional value of resources by lowering the C:N ratio (Aldridge, 1983). Additionally, highly nitrogenous foods have been shown to increase snail growth and fecundity (Aldridge, 1983). Benke et al. (1985) found snags (wood) supported 60% of total invertebrate biomass and 16% of production for a stretch of the Satilla River in southeastern Georgia despite providing only 4% habitat surface. These findings present a similar trend observed in the present study concerning substrate selection.

When preferable food sources are lacking, snails may graze on less desirable food sources, such as detritus, found on less preferable substrates, such as sand. The physical stability of the substrate strongly influences bio-film development and shifting sand in

lotic systems may limit microbial colonization. However, Ross and Ultsch (1980) collected just over 50% of *E. cahawbensis* and 43% of *E. carinifera* from substrates of sand or with a combination of sand during their study in Big Sandy Creek, Alabama. Yet, those findings may be due to sand comprising the majority of substrate available or perhaps being firm enough to promote bio-film development and subsequent grazing.

Rock substrate provides a firm, stable platform on which snails may attach themselves to graze and lay eggs (Dillon, 2000). Assuming rock is more stable than leaves and wood in these study streams, the low chi-square value for rock substrate would support the notion snails preferentially choose substrates for food availability over substrate stability.

Epilithon Biomass

When taking a top-down point of view of trophic levels, substantial evidence exists supporting the profound impact herbivore grazing may have on algal biomass and primary production (Rosemond, 1994; Feminella et al., 1989; Power et al., 1988; Hill and Knight, 1987; Lamberti and Resh, 1983). However, due to low snail density in my streams, top-down negative grazing effects were not observed (Table 6) potentially leaving the epilithon community composition unaltered (Huntly, 1991). By comparison, Rosemond et al. (1993) reported changes in algal community composition and reduced algal biomass and primary production due to snail grazing. In that study, prostrate forms of algae dominated grazed communities while un-grazed communities had mostly filamentous forms. Chlorophyll *a* was 10x more abundant after three weeks in un-grazed enclosures with nutrient additions than enclosures with nutrient additions and snails (Rosemond et al. 1993).

From a bottom-up point of view, evidence suggests primary production may limit the productivity of higher trophic levels (Hunter & Price, 1992; Power, 1992b). Hill et al. (1995) implicated bottom-up limitations on snail growth through enhancement of primary production by increasing available sunlight and nutrients resulting in increases in snail growth and density. Additionally, Hill et al. (2001) showed that growth rates of *E. claeveformis* decreased substantially with modeled decreases in the productivity of their food resource. Because nutrient concentrations in headwater streams are typically low and my study streams are heavily shaded for much of the year, primary production may be nutrient and/or light limited. This in turn may affect the growth of the resident snail populations that, as primary consumers, are dependent upon primary production as their food source (Grubaugh and Wallace 1995; Rosemond et al. 1993).

S*econdary Production and Growth*

My production estimates, though overestimated, are comparable to studies by Huryn et al. (1995) and Richardson et al. (1988). Huryn et al. (1995) estimated mean production for two *Elimia* species of 1,565 and 2,990 mg AFDM m^{-2} yr^{-1} in the Piedmont and Valley/Ridge regions of Alabama, respectively. Richardson et al. (1988), also working in Alabama streams, estimated production from laboratory and field experiments to be 803 – 1,594 mg AFDM m^{-2} yr^{-1} for *E. clara* and 609 – 700 mg AFDM m^{-2} yr^{-1} for *E. cahawbensis*.

Smaller snails exhibited faster growth rates relative to larger snails in my aquarium experiment (Figure 6); a trend similar to that found by Hall et al. (2006), Richardson et al. (1998) and Noda (1997). Whether fast or slow, growth for any organism is dependent on food availability and quality. Low nutrient concentrations and sunlight

may limit primary production in these study streams but may not be the only abiotic factors affecting *G. proxima* production and growth. Temperature largely determines the growth of freshwater snails (McMahon, 1983) either indirectly by altering the quantity or quality of their food source, or directly by influencing behavior or metabolism (Cummins and Klug, 1979; Benke, 1984; Sweeney, 1984). I attribute the low snail production in my study streams observed during the winter months (Figures 8 & 9) to lower stream temperatures. Huryn et al. (1995) and Miller-Way & Way (1989) also observed a near cessation of growth during the winter months in their studies of freshwater snails.

Stream water chemistry has been positively correlated to secondary production estimates in aquatic systems. Krueger and Waters (1983) found invertebrate production in three Minnesota streams to be positively correlated with alkalinity and nitrate concentration. Aldridge (1983) suggested nitrogen-rich food availability to be a limiting factor in most environments and low ratios of carbon to nitrogen in foods favor higher growth rates and fecundity. Both alkalinity and NO_3-N values in these study streams are low (Table 1) and may be a limiting factor in snail growth and production.

Calcium is one of the more important ions for freshwater molluscs because it is sequestered for shell growth and comprises a significant portion of the shell as $CaCO_3$ (Burky, 1983). These study streams have low Ca^{2+} concentrations (Table 1) making them less than ideal for shell growth. However, Aldridge (1983) noted there is high interspecific variation among molluscs for tolerance to low calcium in stream water and *G. proxima* appears to be a tolerant species.

Parasitism

These snails are known to harbor trematode parasites that may alter growth and reproduction through gonadal castration. A review of over 41 publications and 100 field and lab experiments by Sorensen and Minchella (2001) revealed that trematode infestation commonly castrated snails leading to reduction in or complete inhibition of reproductive activity. Assuming these populations of *G. proxima* to be stable, host growth rates would be low with substantial energy expenditure toward maintenance and growth rather than reproduction. As such, castration would not free up much energy from reproductive efforts to be allocated towards growth (Sorensen and Minchella 2001). The consequence would be, in addition to lowered fecundity, stunted snail growth due to trematode parasitism.

Parasitism, nutrient-poor water, and low primary production may help to explain the slow growth of these *G. proxima* populations. Low P/B reflects the fact these populations are dominated by slower growing, older snails and have low recruitment of faster growing young snails. Additionally, headwater streams in which these snails live are typically viewed as stable environments that in turn would promote slow growth, iteroparity, late maturation, and longevity (Gonzalez-Solis and Ruiz, 1996; Sorensen and Minchella, 2001).

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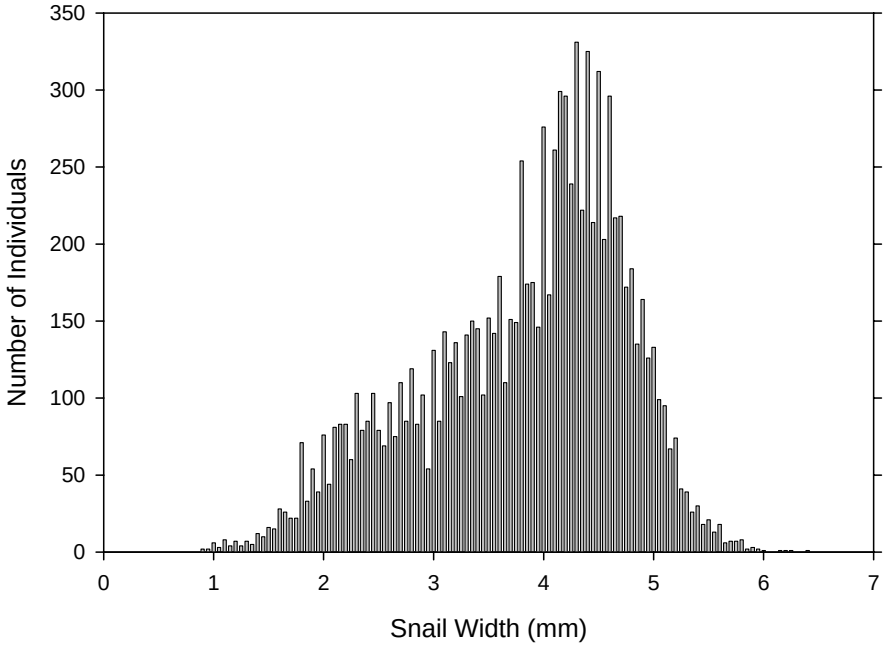

Figure 1. Snail size distribution for 11,668 snails measured from July 2005 – June 2006 among the four study streams.

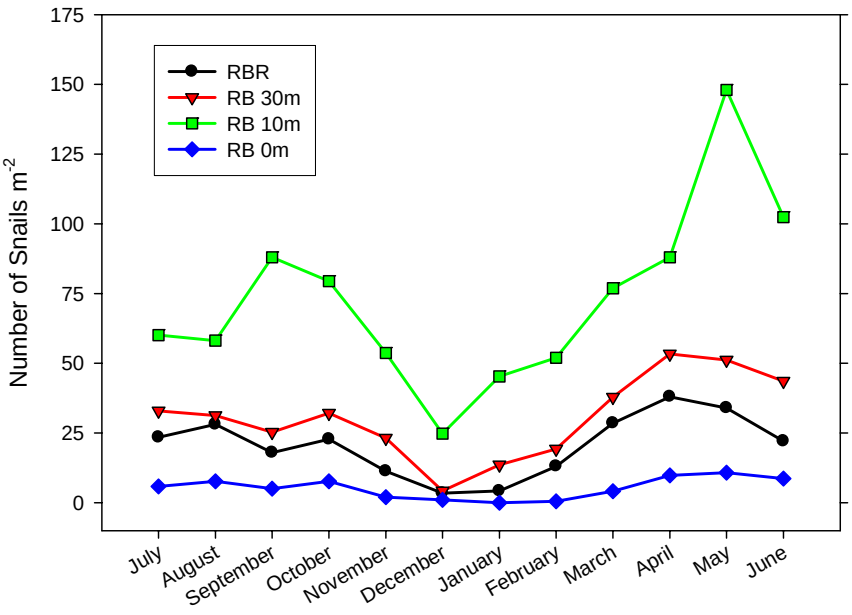

Figure 2. Mean monthly snail density for each stream. n=30 samples per stream per month.

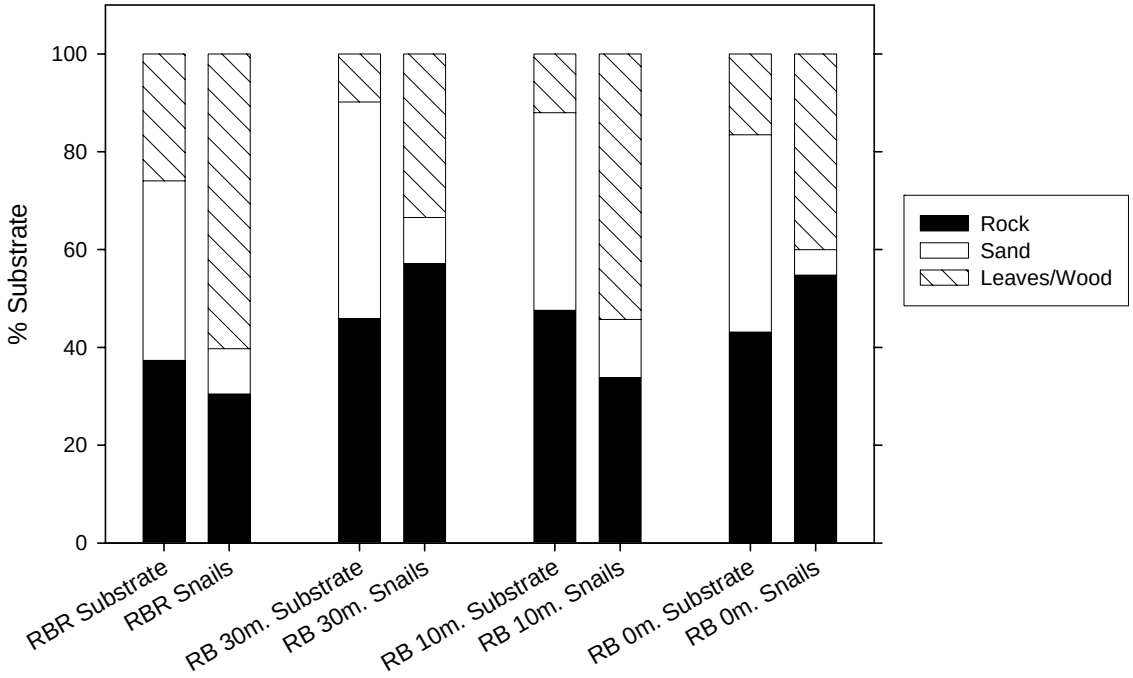

Figure 3. Comparison of mean annual percent substrate available to mean annual percent snails found on substrates from all grid square samples taken; n=30 samples per stream per month.

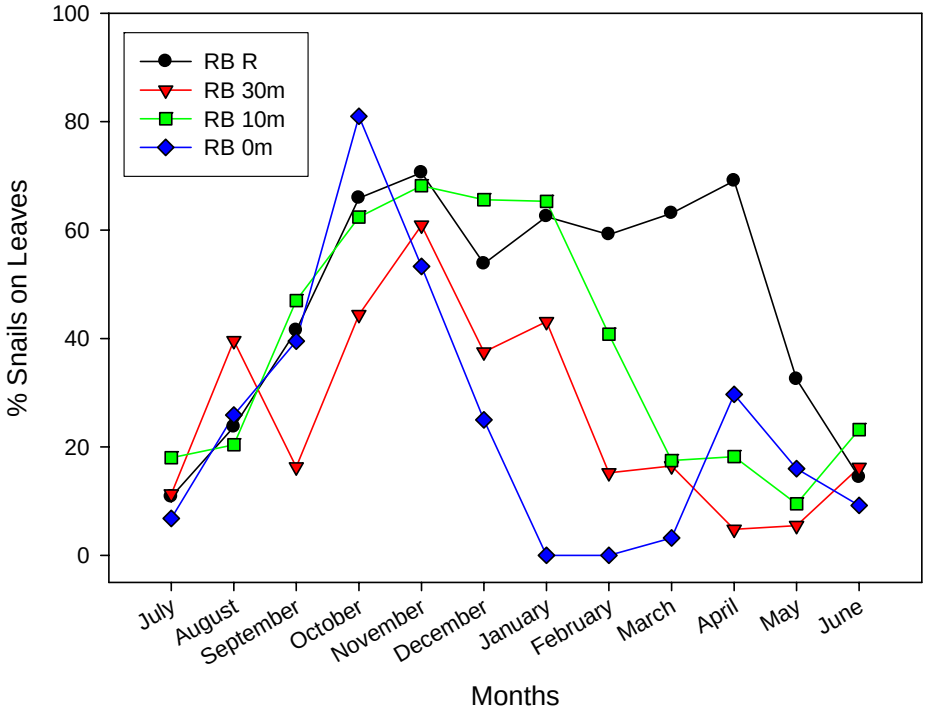

Figure 4. Mean monthly percent snails observed on leaves for each stream. n=30 samples per stream per month.

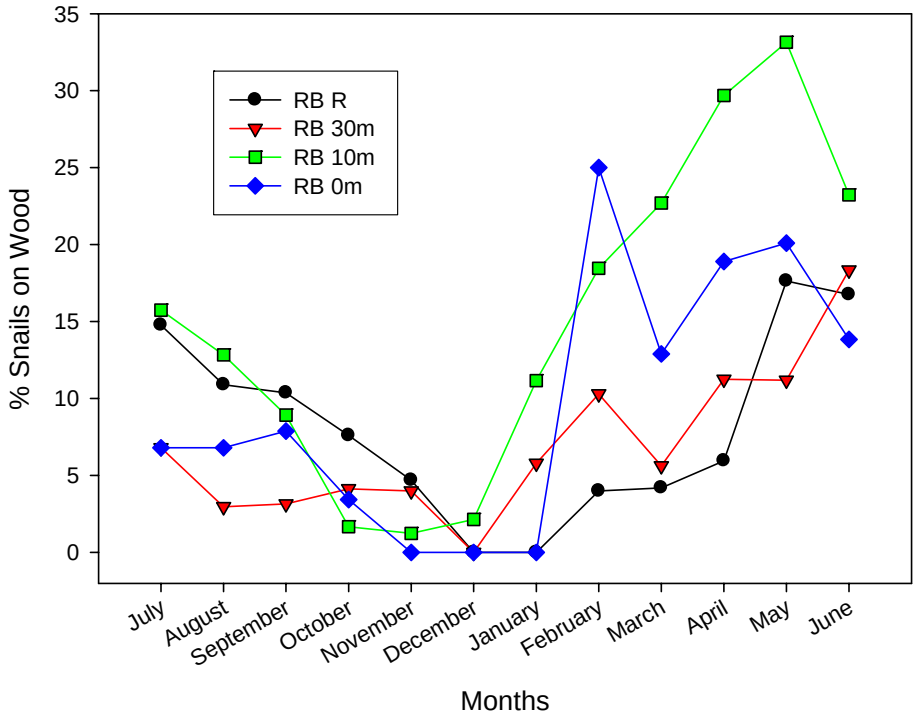

Figure 5. Mean monthly percent snails observed on wood for each stream. n=30 samples per stream per month.

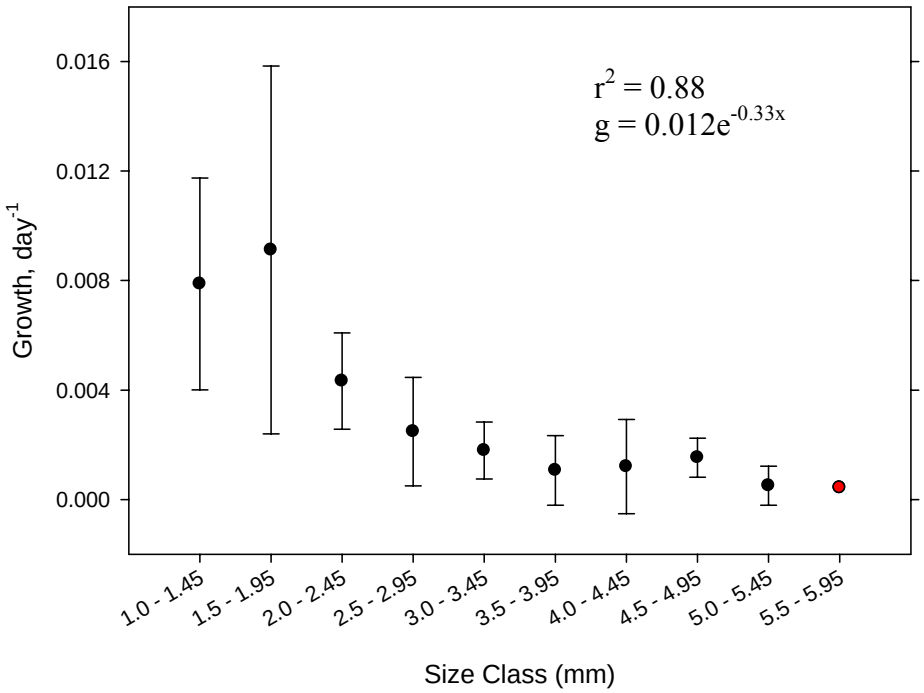

Figure 6. Growth rates, day^{-1}, for each size class (n = 83). Size class 5.5-5.95 mm growth rate calculated from the regression equation. Error bars (sd).

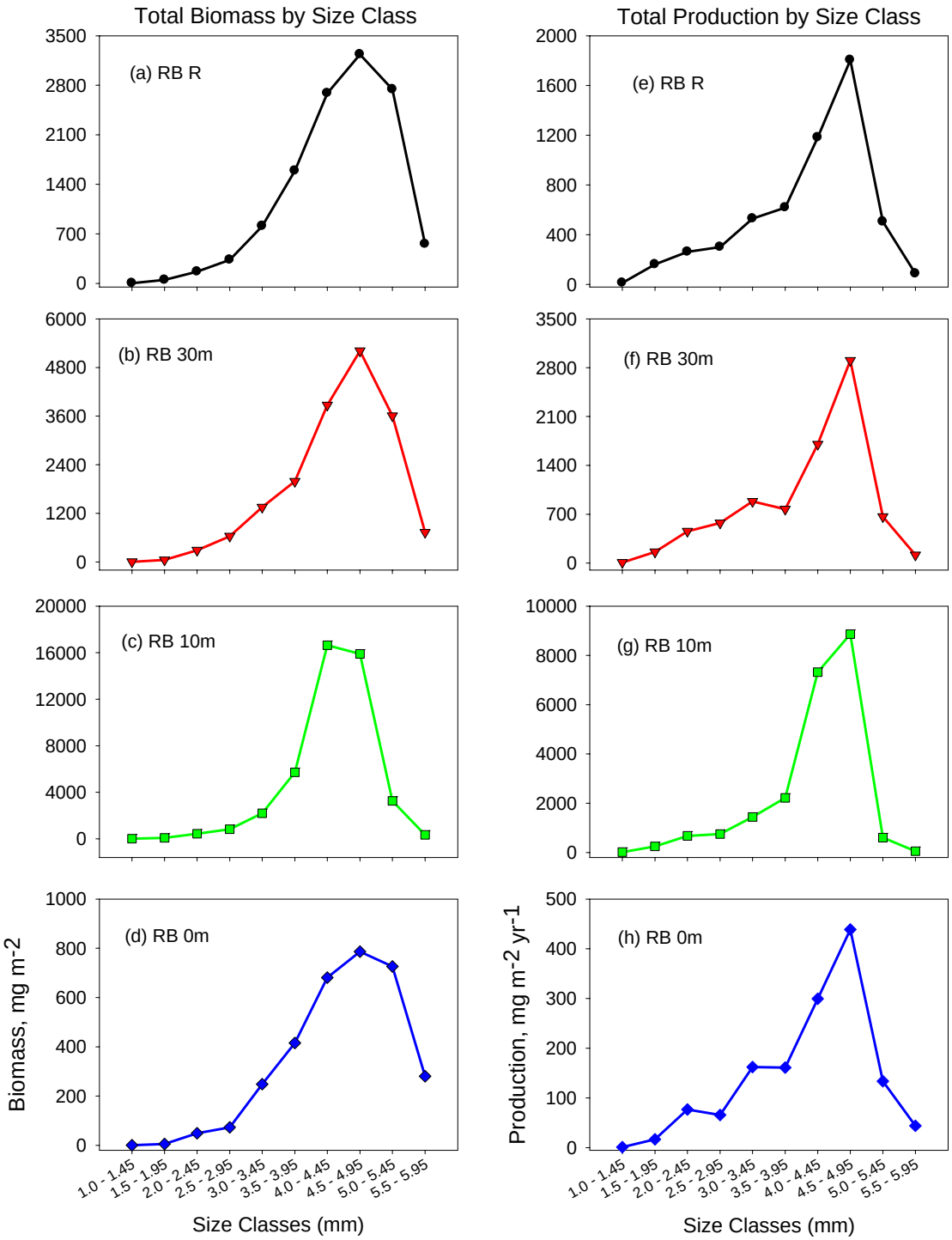

Figure 7. Total biomass, mg m^{-2}, by size class (a-d) and production, mg m^{-2} $year^{-1}$ by size class (e-h) from July 2005 - June 2006. Note different y-axis

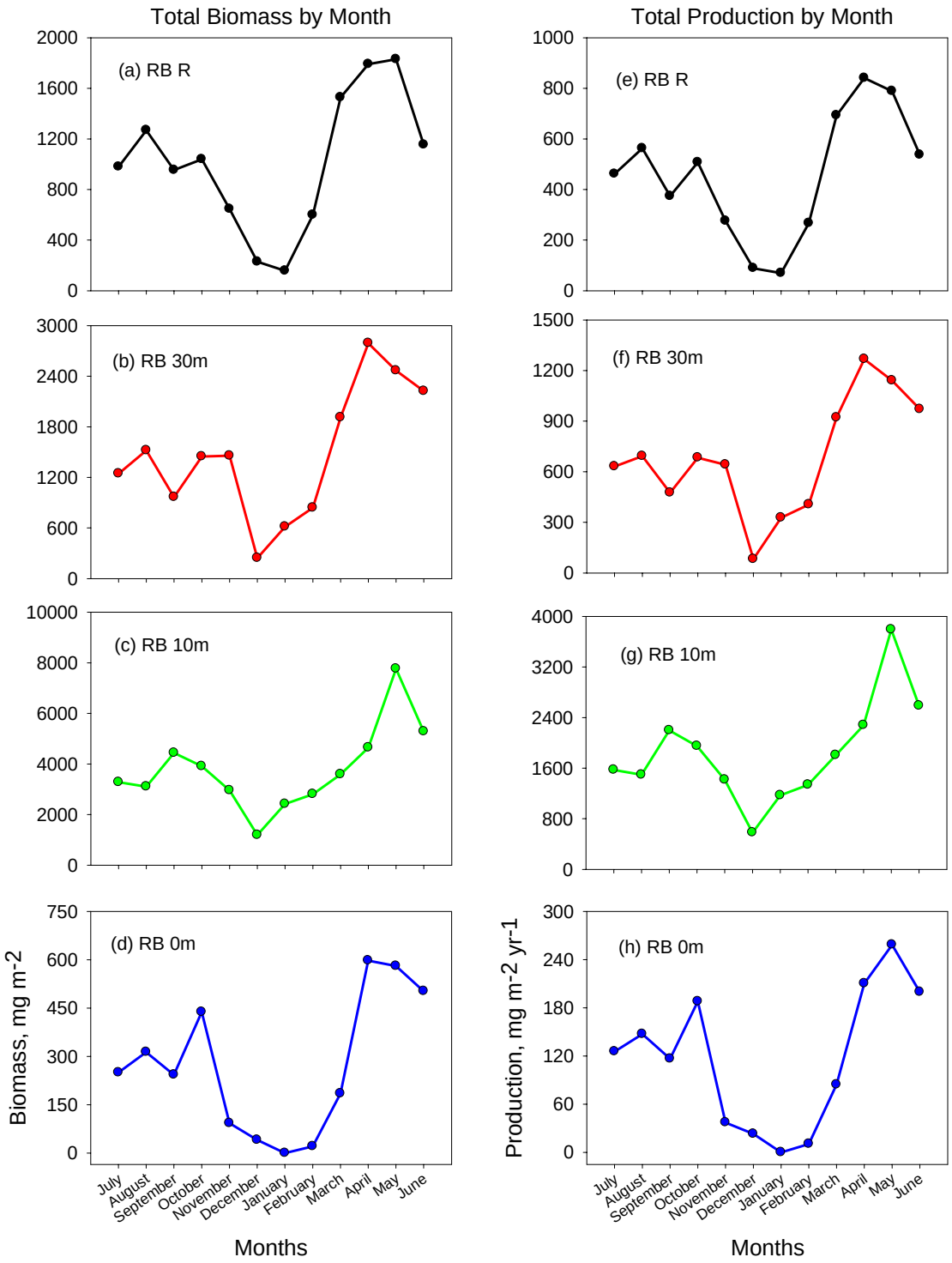

Figure 8. Total biomass, mg m^{-2}, by month (a-d) and production, mg m^{-2} $month^{-1}$ (e-h), July 2005 - June 2006. Note different y-axis.

Table 1. Annual means of selected physical and chemical variables for the four streams. Mean temperature followed by minimum/maximum recorded. All others followed by ±1 SE (sample size). *RB 10m watershed was logged Fall 2005. **Calcium data provided by the Coweeta Hydrological Laboratory.

Variable/Stream	RB R	RB 30m	RB 10m	RB 0m
Coordinates	35° 11' 22.0" N 083° 29' 28.7" W	35° 11' 28.6" N 083° 29' 58.7" W	35° 12' 04.6" N 083° 32' 39.2" W	35° 11' 54.5" N 083° 29' 01.7" W
Meters ASL	909	857	863	835
Canopy, %	91.6 ±1.9 (120)	93.5 ±1.5 (120)	81.1* ±4.0 (120)	94.8 ±1.3 (120)
Discharge, L/s	3.6 ±0.9 (12)	12.5 ±2.4 (12)	6.9 ±1.2 (12)	5.2 ±1.2 (12)
Temperature, °C	10.9 (5.8/ 16.3)	11.0 (5.2/ 16.3)	11.6 (5.3/ 17.9)	11.7 (3.7/ 19.3)
Conductivity, µS	18.8 ±0.7 (100)	14.9 ±1.0 (100)	16.9 ±0.8 (100)	16.2 ±1.2 (100)
NO_3-N, µg/L	81.4 ±13.5 (30)	21.5 ±5.0 (30)	63.3 ±15.9 (30)	49.6 ±7.0 (30)
Alkalinity, mg/L	11.3 ±0.4 (19)	10.0 ±0.3 (21)	11.0 ±0.3 (21)	10.6 ±0.4 (20)
Calcium, mg/L**	1.04 ±0.03 (12)	0.85 ±0.04(12)	1.03 ±0.05(12)	1.10 ±0.04(12)
Lithology	Biotite Gneiss	Biotite Gneiss	Biotite Gneiss	Biotite Gneiss

Table 2. Mean annual snail density and biomass (range). Significant differences (a-d) (p = 0.001).

Variable/Stream	RB R	RB 30m	RB 10m	RB 0m
Density, m^2	20.6^{abd} (0 – 276)	30.7^{bc} (0 – 332)	73.1^{bc} (0 – 784))	5.3^{ad} (0 – 56)
Biomass, mg/m^2	1014.5^{abd} (0 - 1791)	1477.5^{bc} (0 - 2791)	3781.9^{bc} (0 - 7763)	272.1^{ad} (0 - 597)

Table 3. Mean annual percent substrate available (sd). Significant differences (a,b,c) are **within** each stream. Significant differences (A,B,C,D) are **across** streams. Mean substrate values were used in the chi-square analysis as the expected proportion of snails to be observed. n=30 samples per stream per month.

Stream/Substrate	% available Rock	% available Sand	% available Leaves/Wood
RB R	$37.43^{a\ ABD}$ (7.77)	$36.68^{a\ ABCD}$ (12.46)	$25.88^{a\ ACD}$ (17.99)
RB 30m	$45.90^{a\ ABCD}$ (8.38)	$44.27^{a\ ABCD}$ (5.25)	$9.83^{b\ BCD}$ (8.45)
RB 10m	$47.55^{a\ BCD}$ (6.92)	$40.41^{b\ ABCD}$ (5.46)	$12.05^{c\ ABCD}$ (6.57)
RB 0m	$43.22^{a\ ABCD}$ (7.12)	$40.13^{a\ ABCD}$ (6.33)	$16.64^{b\ ABCD}$ (11.09)
Mean	43.53 (4.84)	40.37 (3.43)	16.10 (8.27)

Table 4. Mean annual percent snails found on substrates (sd). Significant differences (a,b,c) are **within** each stream. Significant differences (A,B,C,D) are **across** streams. Mean snail values were used in the chi-square analysis as the observed proportion of snails. n=30 samples per stream per month.

Stream/Snails	% snails on Rock	% snails on Sand	% snails on Leaves/Wood
RB R	$30.13^{a\ ACD}$ (12.13)	$9.13^{b\ ABCD}$ (4.20)	$60.74^{c\ AC}$ (13.93)
RB 30m	$61.56^{a\ BD}$ (15.68)	$9.04^{b\ ABCD}$ (5.89)	$29.40^{a\ BCD}$ (15.67)
RB 10m	$38.29^{a\ ACD}$ (14.10)	$11.43^{b\ ABCD}$ (6.23)	$50.28^{c\ ABCD}$ (16.42)
RB 0m	$50.53^{a\ ABCD}$ (27.19)	$5.61^{b\ ABCD}$ (5.55)	$43.85^{a\ BCD}$ (23.67)
Mean	45.13 (13.84)	8.80 (2.75)	46.07 (12.41)

Table 5. Chi-square values for (observed snails - expected snails)^2/expected snails. Observed values taken from Table 4, expected values taken from Table 3. Critical value = 12.59, 6 df, $\alpha = 0.05$.

Streams/Substrate	Rock	Sand	Leaves/Wood
RB R	1.14	19.96	40.13
RB 30m	5.35	28.07	39.12
RB 10m	1.82	20.83	123.12
RB 0m	1.28	29.83	44.73
Mean	2.39	24.67	61.78

Table 6. Correlation coefficients between mean annual snail density, m^{-2}, to mean annual chlorophyll *a*, mg m^{-2}, and mean annual epilithon, mg AFDM m^{-2}. Only RB 30m epilithon presented a significant correlation ($p > 0.05$). Annual chloro *a* and epilithon values derived from monthly means of 10 rock samples for each stream.

	Snail Density	Correlation (p values)		Annual Mean (se)	
		Chloro *a*	Epilithon	Chloro *a*	Epilithon
RB R	20.6	-0.42 (0.13)	0.39 (0.15)	0.036 (0.007)	9250 (786)
RB 30m	30.7	0.64 (0.06)	**0.76 (0.006)**	0.050 (0.004)	8750 (768)
RB 10m	73.1	0.44 (0.20)	0.35 (0.32)	0.038 (0.004)	9220 (1020)
RB 0m	5.3	0.07 (0.85)	-0.02 (0.96)	0.033 (0.009)	7890 (857)

Appendix A

Table 1. Mean growth rates, day^{-1}, per size class. Size class 5.5-5.95 mm was calculated from Figure 6.

Size class, mm	1.0-1.45	1.5-1.95	2.0-2.45	2.5-2.95	3.0-3.45	3.5-3.95	4.0-4.45	4.5-4.95	5.0-5.45	5.5-5.95
Mean Growth	0.0079	0.0091	0.0043	0.0025	0.0018	0.0011	0.0012	0.0015	0.0005	0.0004

Table 2. Total annual biomass, mg dry weight m^{-2}, for each size class per stream.

Streams/Size Class	1.0-1.45	1.5-1.95	2.0-2.45	2.5-2.95	3.0-3.45	3.5-3.95	4.0-4.45	4.5-4.95	5.0-5.45	5.5-5.95	Total
RB R	4.63	48.65	166.3	332.4	810.2	1592	2687	3236	2743	554.2	**12174**
RB 30m	2.93	48.20	288.9	633.7	1352	1990	3869	5208	3606	730.3	**17730**
RB 10m	5.48	74.47	426.5	826.3	2200	5716	16643	15899	3256	335.9	**45382**
RB 0m	0.42	5.09	48.66	72.67	248.4	415.2	680.9	786.7	726.2	280.4	**3265**

Table 3. Snail production estimates, mg dry weight m^{-2} year^{-1}, for each size class per stream.

Streams/ Size Class	1.0-1.45	1.5-1.95	2.0-2.45	2.5-2.95	3.0-3.45	3.5-3.95	4.0-4.45	4.5-4.95	5.0-5.45	5.5-5.95	Total	P/B
RB R	13.31	161.9	262.5	301.1	529.3	617.7	1182	1805	505.3	87.23	**5465**	0.45
RB 30m	8.41	160.4	456.2	574.0	883.3	772.2	1703	2905	664.4	114.9	**8241**	0.46
RB 10m	15.75	247.8	673.5	748.4	1437	2218	7324	8866	599.9	52.87	**22183**	0.49
RB 0m	1.20	16.94	76.84	65.82	162.3	161.1	299.7	438.7	133.8	44.14	**1400**	0.43

Table 4. Total snail biomass, mg dry weight m^{-2}, for each month per stream.

Streams/Months	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	June	Total
RB R	978.7	1268	953.5	1038	646.0	229.1	157.3	599.0	1528	1791	1830	1153	**12174**
RB 30m	1246	1521	966.2	1448	1458	243.1	614.3	840.8	1911	2791	2466	2224	**17730**
RB10m	3282	3104	4436	3912	2957	1194	2417	2806	3590	4644	7763	5277	**45382**
RB 0m	250.3	313.2	243.0	438.0	92.94	40.95	0.00	20.74	185.0	597.4	580.8	502.5	**3265**

Table 5. Snail production estimates, mg dry weight m^{-2} month^{-1} for each stream. Low annual P/B year^{-1} indicate long snail development times.

Streams/Months	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	June	Total	P/B
RB R	461.6	562.7	373.8	507.1	276.1	88.78	69.63	266.7	692.8	840.4	788.6	536.9	**5465**	0.45
RB 30m	631.1	693.2	475.2	683.2	642.0	81.84	327.5	406.1	921.9	1267	1141	971.0	**8241**	0.46
RB 10m	1571	1496	2198	1951	1416	581.9	1169	1336	1804	2279	3792	2588	**22183**	0.49
RB 0m	125.5	147.3	116.5	188.0	37.22	22.98	0.00	10.43	84.31	210.2	258.5	199.6	**1400**	0.43