

VARIATION IN THE LIFE HISTORY AND ABUNDANCE OF THREE POPULATIONS OF BRUNEAU HOT SPRINGSNAILS (*PYRGULOPSIS BRUNEAUENSIS*)

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ABSTRACT.—Bruneau hot springsnail density, size class structure, recruitment, and mortality were measured monthly over approximately 2 years and compared to environmental variables at 3 hot spring sites in southwestern Idaho. Food resources (attached algae) and water chemistry were similar among sites, but temperature, population density, and size structure differed significantly. Density was highest at a warm, fairly constant temperature site. A cooler, highly variable temperature site and a site where temperatures frequently approached or exceeded thermal maxima tolerance limits had lower densities. Size class structure varied seasonally and distinctly among sites, with recruitment occurring year-round at temperatures <36°C. Mortality affected different size classes at different sites, with smaller snails incurring greatest mortality at site 3 (highest temperature variability). Growth rates were positively correlated with temperatures up to 36°C. Mean snail size differed among sites and also appeared to be related to temperature, with the variable temperature sites having larger snails. Although these snail populations are found in a range of water temperatures, they appear best adapted to springs with mean temperatures between 32° and 33°C and low thermal variance.

Key words: *Pyrgulopsis bruneauensis*, *Bruneau Hot Springs*, *hydrobiid*, *snail*, *thermal springs*, *life history*, *endangered species*.

Hydrobiid snails are one of the most common Prosobranch families occupying marine, brackish, and freshwater habitats worldwide. Thirty-one genera containing more than 200 species are known from North America (Burch 1982, Hershler 1998). Certain hydrobiid genera are well studied (van der Schalie and Davis 1965, 1968, Gore 1967, Liang and van der Schalie 1975, French 1977, Lassen and Clark 1979, Forbes and Lopez 1990). Hydrobiids inhabiting mound springs in South Australia were investigated by Ponder et al. (1989). A recent systematic review of *Pyrgulopsis* in the Great Basin region of the western USA was conducted by Hershler (1998). O'Brien and Blinn (1999) examined distribution of *Pyrgulopsis montezumensis* in relation to a CO₂ gradient in a thermal spring outflow in Arizona; however, little else is known of the life histories of hydrobiid snails in the arid North American West.

The Bruneau hot springsnail (*Pyrgulopsis bruneauensis* Hershler 1990) is an endemic, endangered species inhabiting hot springs adjacent to the Bruneau River south of Mountain Home, Idaho. *Pyrgulopsis bruneauensis* occupies flowing thermal waters in both rheocrene

(a spring originating from the ground as a flowing stream) and madicolous habitats (thin sheets of water flowing over rock faces [Ward 1992]). The species is confined to these thermal systems (Mladenka 1992). Taylor (1982) gave a brief physiological and biological description of the snail, and Fritchman (1985) studied its reproduction under laboratory conditions, but no other studies of its biology are known. This study addresses aspects of life history variation in the hydrobiid *Pyrgulopsis bruneauensis* inhabiting 3 distinct thermal sites in a localized area of southwestern Idaho. We examined recruitment, growth, mortality, and density of *P. bruneauensis* in relation to key environmental factors, especially temperature.

STUDY SITES

We found *Pyrgulopsis bruneauensis* in more than 100 small warm springs and seeps along 8 km of the lower Bruneau River. However, all springs derive from a single geothermal aquifer consisting of fractured volcanic rock (Berenbrock 1993). The surrounding area is high desert that receives <25 cm of precipitation yearly, predominantly during winter months.

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During this study air temperatures varied from -7°C in January 1990 to 39°C in June and August 1991. Mean annual temperature was 29.4°C ($s = 7.2$), with a mean low temperature of 4.5°C ($s = 5.9$).

We studied *P. bruneauensis* at 3 noncontiguous sites having different temperature and flow regimes. Water chemistry was relatively constant within sites during this study and similar among sites (Table 1). Mean pH was 8.6 for all sites. Hardness ranged from 21.8 to $26.7 \text{ mg} \cdot \text{L}^{-1}$ and total alkalinity from 91 to $102 \text{ mg} \cdot \text{L}^{-1}$ (both as CaCO_3). Mean conductivity ranged from 267 to $287 \mu\text{S} \cdot \text{cm}^{-1}$. Total phosphorus ranged from 0.028 to $0.047 \text{ mg} \cdot \text{L}^{-1}$ and nitrate nitrogen from 0.40 to $0.60 \text{ mg} \cdot \text{L}^{-1}$. Site 2 maintained the most constant temperature (measured monthly) of the 3 sites (range = $25.0\text{--}34.5^{\circ}\text{C}$), whereas site 3 had the widest temperature range ($8.0\text{--}32.0^{\circ}\text{C}$). Site 1 had the highest temperatures ($\bar{x} = 34.9^{\circ}\text{C}$, $s = 1.1$, max. = 37°C).

Sites ranged in size and habitat type from a nearly vertical 1.5-m-high \times 1.3-m-wide rock face and its 1.0-m-wide \times 2.0-m-long outflow (site 2) to a 1-m-wide \times 10-m-long stream segment (site 1). Study sites were typical of other springs containing Bruneau hot springsnails. The study sites are located near the Bruneau River tributary Hot Creek, just downstream of Bruneau Canyon (NE 1/4 Sec 3, T8S, R6E).

Site 1, on Hot Creek, had a mean discharge of $0.016 \text{ m}^3 \cdot \text{s}^{-1}$ during the study. In general, higher flows occurred from late autumn through spring, while lower flows, corresponding to the irrigation season, occurred during the remainder of the year. Water temperature ranged from 25° to 37°C (except during a rainstorm runoff event in September 1991 when it decreased to 14.5°C ; Fig. 1). Cobbles, gravel, and sand comprised the streambed, and sedge (*Juncus*) grew along the stream banks. Sand and silt accumulated in the study reach from December 1990 through the study's conclusion, with most cobble substrate becoming completely buried by June 1991. Sites 2 and 3 are east-facing madicolous habitats with associated outflows over gravel and cobble substrate bordering the west side of Bruneau River downstream of its confluence with Hot Creek.

METHODS

We measured temperature monthly with maximum-minimum recording thermometers.

Alkalinity (as CaCO_3), pH, hardness, and specific conductance at 25°C were determined monthly. We performed tests to determine specific conductance and pH in the field using an electronic meter (Orion Instruments model 26). Other analyses were done at the Idaho State University Stream Ecology Center according to standard methods (APHA 1989). Samples were analyzed for total phosphorus and nitrogen quarterly for 1 year. Nitrogen and phosphorus analyses were conducted at Desert Research Institute Water Laboratory, Reno, NV. Dissolved oxygen was measured 3 times during spring and summer 1990 using an oxygen probe (Orion Instruments O_2 electrode, model 97-08).

Food abundance was measured monthly at each site. A known area of periphyton was scraped from rocks and transferred to a preashed filter of known mass as described in Cushing et al. (1983). Samples were analyzed for biomass and chlorophyll *a* (APHA 1989).

We determined temperature tolerance by placing 5 snails in 11-cm-diameter \times 6-cm-high plastic dishes, all receiving water via a submersible pump in a 15-L plastic bucket containing a submersible heater. Water was continuously aerated and filtered. Complete flow-through time for the system was 40 minutes. Periphyton from field sites was provided in all dishes as a food source. Snails were acclimated to the dishes for 2 days at 30°C . During the high-temperature tolerance experiment, water temperature remained at 30°C for a control group, while temperature in the experimental group was raised 1°C per 24-hour period. At the end of each 24-hour period, locations of all snails were recorded (in or out of water). Water temperature was increased until all snails (in the experimental group) exited the water. We conducted a parallel experiment to determine low-temperature tolerance. Temperature in this experimental group was lowered 1°C per 24-hour period, at which point snails were checked for their ability to right themselves after being inverted. Water temperature was lowered until $<50\%$ snails could right themselves in 1 minute. Using a different apparatus, we conducted another high-temperature tolerance experiment following the procedures previously described. In this 2nd experiment, 20 snails were placed in each of four 1-L beakers. Water was heated and aerated independently in each beaker.

Using field size histograms and laboratory rearing, we estimated growth rates. Snails were kept in 40-L glass aquaria half filled with hot spring water and equipped with air stones placed inside 20-cm lengths of 3-cm-diameter clear plastic tubing to create a slight current. Periphyton from the field was maintained in the aquaria at levels exceeding snail food requirements. Distilled water was added, when required, to maintain water levels and dissolved solute concentrations. Twenty-five juvenile snails were placed in each of 3 aquaria maintained at temperatures of 15°, 30°, and 34°C. Shell heights were determined at approximately 20-day intervals for 87 days using a dissection microscope equipped with an ocular micrometer. A statistical comparison employing analysis of variance was done after 39 days to ensure adequate sample sizes, since some mortality occurred.

Snail density was estimated employing random quadrat counts in the area of a ring ($A = 60.8 \text{ cm}^2$). We made visual counts of all encircled *Pyrgulopsis bruneauensis* in 20 locations at each site. An inverted petri dish of the same size as the inside diameter of the ring eliminated water turbulence and allowed clear viewing of substrate and snails at site 1 and deeper outflow areas at site 2 (site 3 was entirely madicolous and did not require this technique). From February 1990 through November 1991, we monitored density monthly.

Snails for size-structure analysis were collected at each site from at least 5 rocks. After gently removing rocks from the water, we rinsed the snails with a 500-mL hypodermic syringe into a 10-cm-diameter petri dish. After thorough mixing, the sample was viewed under a dissection microscope with an ocular micrometer. Each month (from 16 February 1990 through 15 December 1991), we measured shell heights of the first 100 snails from each site to the nearest 0.14 mm at 40X magnification. Snails were then returned to their habitat. During March 1991 (site 3) and August 1991 (sites 1, 2), 49, 36, and 36 snails >1.4 mm long were also sexed and enumerated at sites 1, 2, and 3, respectively. Male genitalia were extruded and clearly evident as snails attempted to right themselves after being inverted.

We did not determine reproduction or fecundity directly, to avoid sacrificing the

snails. Newly hatched *P. bruneauensis* were about 0.3 mm long, but some growth occurs before sexual maturity is reached. We arbitrarily considered snails ≤ 0.57 mm long to be juveniles. We feel this is a conservative estimate as male genitalia were not evident at shell heights <1.4 mm. A rough estimate of the number of juveniles produced per female was calculated by dividing the number of juveniles by 0.5 of the snails ≥ 1.4 mm present in the previous month's sample (sex ratios were determined to be 1:1). Therefore, in this paper recruitment refers to the presence of snails ≤ 0.57 mm long.

To assess broad, cumulative differences in mortality among sites, we collected shells of dead individuals ($n = 56, 103,$ and 102 at sites 1, 2, and 3, respectively) on 3 October 1990 from the substrate at each site using a strainer (7.5-cm-diameter) and measured them as in live snails.

Site-specific size differences between male and female snails were analyzed with *t* tests. Comparisons among site density and structure were done using analysis of variance. Water chemistry was analyzed in the laboratory using standard methods (APHA 1989). An analysis of variance was performed on each water chemistry parameter (questionable alkalinity and hardness data from the first 3 months' samples were excluded from analysis). When analysis of variance revealed significant differences, we employed Tukey's test to determine significant differences among means. Sex ratios were compared to a 1:1 ratio using a chi-square test. Relationships between density and food abundance (biomass), temperature, and flow were analyzed using 1st-order regressions.

RESULTS

Temperature and water chemistry data are presented in Table 1. Sites had very similar water chemistry with the exception of higher alkalinity at site 1 ($F = 49.51, P < 0.0005$) and higher N at site 3 ($F = 8.12, P < 0.01$). Water temperature varied seasonally at all sites (Fig. 1); however, mean maximum water temperature differed significantly among sites ($F = 109.4, P < 0.0005$). Site 1 reached the highest maximum temperature (37°C), while site 3 had the most variable regime and lowest mean high temperature (26.8°C, $s = 3.7$). Site 2 water temperature fluctuated least among sites, with

TABLE 1. Physicochemical variables for the Bruneau Hot Springs study sites. Means and standard deviations (in parentheses) for pH, hardness, conductivity, and alkalinity are for 18 March 1990–16 November 1991.

Site	Temperature (C°)		pH	Hardness (mg CaCO ₃)	Conductivity (μS @ 25°C)	Alkalinity (mg · L ⁻¹)	Oxygen (mg · L ⁻¹ dissolved)	Phosphorus (mg · L ⁻¹ as P)	Nitrogen (mg · L ⁻¹ as N)
	Max.	Min.							
1	34.9 (1.1)	30.5 (3.7)	8.6 (0.2)	26.7 (6.2)	287 (13)	102 (3)	6.6 (0.3)	0.034 (0.015)	0.60 (0.01)
2	33.3 (0.8)	30.8 (2.3)	8.6 (0.2)	23.7 (9.3)	267 (42)	91 (4)	6.3 (0.7)	0.028 (0.025)	0.60 (0.01)
3	26.8 (3.7)	17.4 (3.8)	8.6 (0.3)	21.8 (5.2)	276 (29)	92 (4)	6.9 (0.4)	0.047 (0.010)	0.40 (0.12)

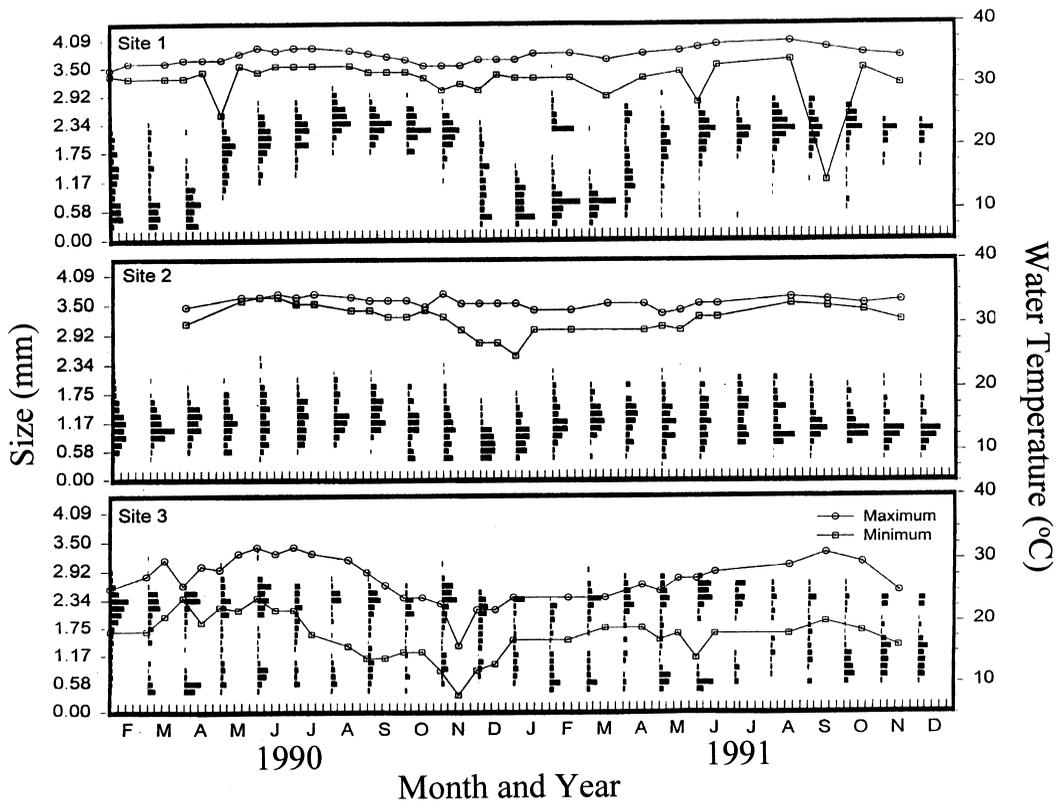


Fig. 1. Size histograms and maximum and minimum water temperatures for the Bruneau hot springsnail study sites versus time. X-axis tick marks represent 10 snails per unit. Horizontal tick marks represent 0.14-mm size classes ($n = 100 \cdot \text{sample}^{-1}$). Circles and squares represent maximum and minimum water temperatures, respectively.

a mean maximum temperature of 33.3°C ($s = 0.8$).

Periphyton biomass varied widely within and among sites (Fig. 2), with site 1 showing greatest variation (range = 2.24–74.13 mg · m⁻² ash-free dry weight). Mean biomass at sites 1, 2, and 3 was 14.31 ($s = 15.96$), 16.34 ($s = 8.82$), and 21.97 g · m⁻² ($s = 10.65$), respectively. Chlorophyll *a* concentrations paralleled

biomass. There were no significant differences in biomass or chlorophyll *a* among sites.

We determined the maximum tolerable temperature to be 36°C in the laboratory. When water temperatures approached or exceeded this temperature at site 1, snails became concentrated along spring margins, on algal mats, and in areas of upwelling water, where water temperature was 1–7°C lower

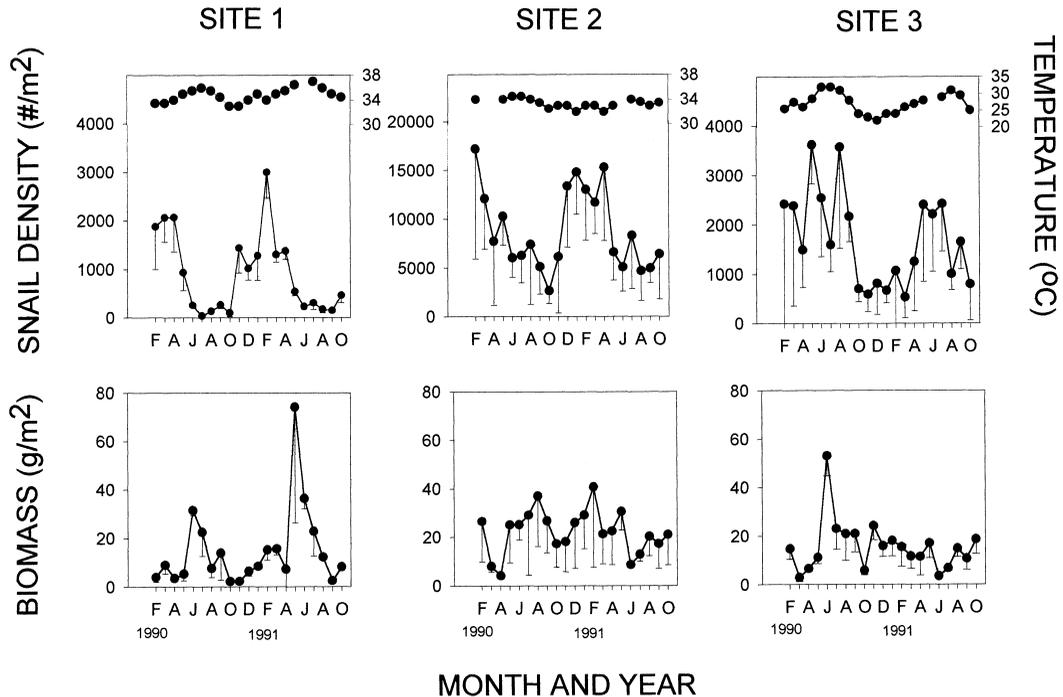


Fig. 2. Mean snail density, maximum water temperature, and periphyton biomass (ash-free dry weight) versus time for the Bruneau hot springsnail study sites. Note differences in scale on y-axes. Error bars represent $\pm 1 s$ for the mean of 3 density estimates.

than recorded in the main flow. The low-temperature tolerance limit was not as distinct; however, >50% snails failed to right themselves within 1 minute when temperatures were below 10°C.

Snails raised in laboratory aquaria at 15°, 30°, and 34°C grew at 0.020, 0.029, and 0.034 mm · d⁻¹, respectively. Snails attained different sizes at 15° (\bar{x} = 0.792 mm, s = 0.069) and 34°C (\bar{x} = 1.32 mm, s = 0.260; F = 26.93, P < 0.05). Size increases estimated from field size histograms (Fig. 1) were 0.022, 0.010, and 0.024 mm · d⁻¹ for sites 1, 2, and 3, respectively.

Snail density varied among sites and seasonally within sites (Fig. 2). Although high densities (2997 · m⁻², March 1991) were found seasonally at site 1 (\bar{x} = 909 · m⁻², s = 795), the greatest mean density (8900 · m⁻², s = 3936) occurred at site 2 (F = 17.79, P < 0.0005). Site 3 had a mean density of 1782 · m⁻² (s = 953).

Mean snail size differed among sites (F = 597.03, P < 0.0001; Table 2), with the largest snails and mean size at site 1. Juveniles were

noticeably absent on a number of sampling dates at site 1 (Fig. 1), with the highest proportion of juveniles recorded from November through April. As a result, distinct cohorts of snails are clearly evident. In contrast, juveniles were present in nearly all samples at the other sites. Site 2 exhibited the most stable size structure; however, mature snails were the smallest among the sites. Site 3 exhibited bimodal distribution for nearly all samples, while other sites did not.

Shells of dead snails were bimodally distributed at site 1, but large size classes predominated among composite samples of live snails prior to and during this time (Fig. 3). Size distribution of dead snails at site 2 was similar to size distribution among living snails, whereas at site 3 there was a greater proportion of dead snails in smaller size classes compared to size distribution of living snails.

Newly hatched, *Pyrgulopsis bruneauensis* are nearly transparent and have a mean shell height of 0.3 mm. When snails reach approximately 0.7 mm, they become nearly black. Male genitalia are clearly evident in snails

TABLE 2. Mean snail size and standard deviation for the Bruneau Hot Springs study sites.

Site	Mean	Standard deviation	F-value	P
1	1.57	0.72	194.15	<0.0001
2	1.11	0.39	20.92	<0.0001
3	1.51	0.71	10.85	<0.0001

exceeding a shell height of 1.4 mm. Snails lacking male genitalia at that size and greater were considered female. The percentage of males at all sites did not significantly differ from 50%. Mean male and female sizes were significantly different only at site 1 ($P < 0.05$), with females being slightly larger ($\bar{x} = 2.25$ mm, $s = 0.371$) than males ($\bar{x} = 2.02$ mm, $s = 0.230$).

The estimated number of juveniles produced per female ranged from 0 to $18.5 \cdot \text{month}^{-1}$ for the sites. The approximate number of juveniles per female ranged from a mean of 1.24 ($s = 2.79$) at site 1 to 0.80 ($s = 1.56$) at site 2. Site 3 had a mean of 1.19 ($s = 3.89$); however, differences among sites were not statistically significant.

DISCUSSION

Marked differences in recruitment patterns and densities of *P. bruneauensis* among study sites were especially correlated with differences in thermal regimes. Snail density at site 1 (a site which occasionally exceeded 36°C) was inversely related to temperature ($P < 0.02$), whereas the relationship for site 3 (always $<36^{\circ}\text{C}$) was positive ($P < 0.005$; Fig. 4). At site 3 highest densities were reached during periods of continually warm ambient air temperature when discharge was observed to be low (not directly measured).

Recruitment was evident throughout the study at site 3 except in December 1990 and August 1991, and occurred at sites 1 and 2 when not inhibited by excessive water temperatures (Fig. 1). Recruitment at site 1 was seasonal, and the highest proportion of juveniles was recorded from November through April. Because sites had different temperature regimes, seasonality of recruitment depended upon when or if the thermal limit was exceeded. At sites 1 and 2 increased density followed increased recruitment during periods of optimal temperatures. For example, many juve-

niles were present in site 1 December 1990 samples following decreased maximum water temperatures that had been apparent since September (Fig. 1). Site 1 abundance peaked in March, apparently a result of increased recruitment. Generally, thermal stability resulted in higher snail density, with site 2 consistently having highest abundance (Fig. 2). Size distribution histograms of *P. bruneauensis* at site 3 were bimodal for nearly every sample during the study (Fig. 1). This suggests continuous low recruitment into larger size classes.

Comparisons of mortality histograms (Fig. 3) indicated differences in size-specific mortality among sites. Mortality at site 1, which was generally warmer than and intermediate in temperature variability compared to sites 2 and 3, tended toward a bimodal distribution, indicating increased mortality in both small and large size classes. The histogram from site 3 (cooler, more variable temperature) indicates increased mortality among juveniles. Given that the sites were otherwise relatively similar, slower growth at site 3 may be a prominent mechanism preventing recruitment into larger size classes. This could be a result of lower minimum temperatures or large temperature fluctuations.

We feel that collection and measurement of empty shells followed by comparison with a living population give insights into general differences in age-specific mortality among sites even though smaller size classes may have been underrepresented in the samples because of possible shorter shell disintegration times. Although hydrobiid snails are relatively dense and soon settle out of the current (T. Frest personal communication), different-sized shells may have drifted differentially after the animals decomposed. However, numerous low-velocity areas were available for shell entrainment, and juvenile shells were found in each sample. While shells do accumulate and decompose over time, they should accumulate and decompose similarly at sites with similar water chemistry (as in our sites), and comparisons among sites give a general indication of how age classes are affected by mortality. Our conclusions relative to temperature effects could be affected by our method of temperature measurement. Hourly temperature data obtained after this study from the same sites indicate occasional, short-duration temperature fluctuations. We could not distinguish

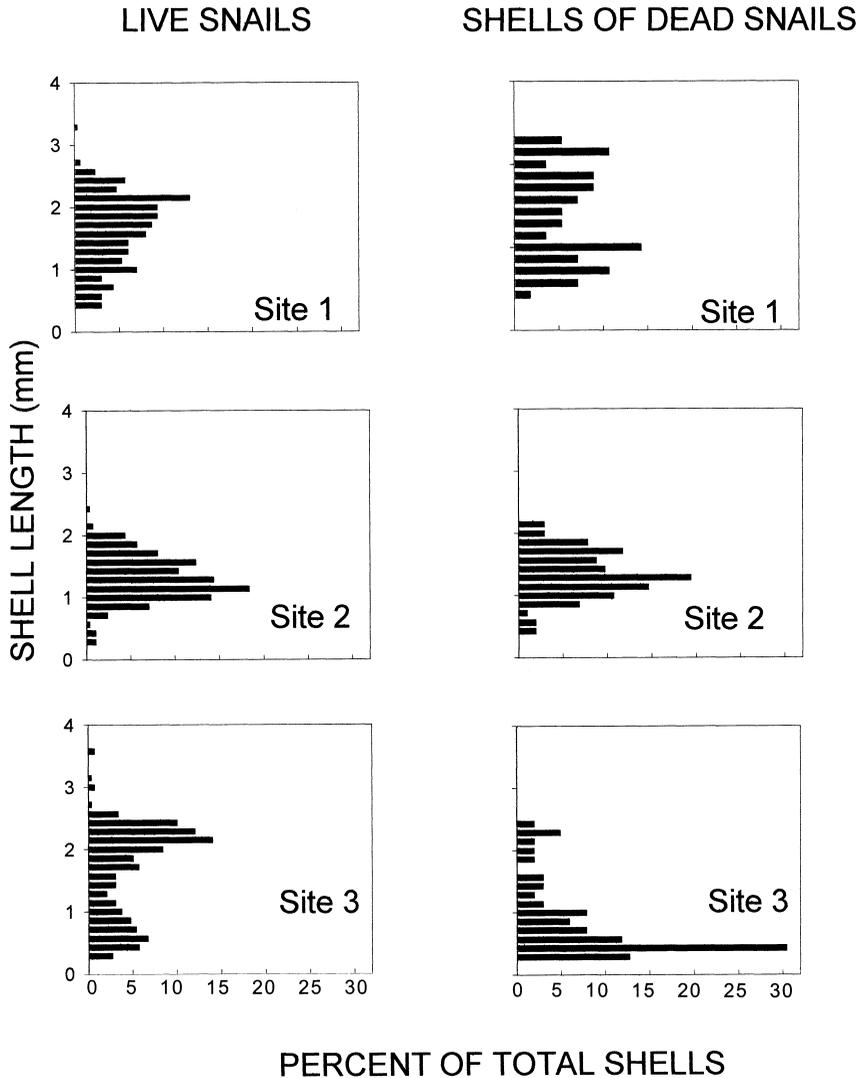


Fig. 3. Histograms illustrating percentage of mean live snail shell heights (mean of live samples taken over a 3-month period leading into and including the dead shell sampling) and shell heights of dead snails for the Bruneau hot springsnail study sites.

short-duration (1–2 hours) from longer-duration changes. Since hydrobiid hatching times can be as short as 8 days (Otori et al. 1956, Chi and Wagner 1957, Liang and van der Schalie 1975, Lassen and Clark 1979), a short-duration temperature increase or decrease could mask a period of optimal temperature for reproduction. Reproduction could occur and be reflected in size and density data, while our temperature data would not indicate optimal conditions existed during that period.

When we compared discharge to density at site 1 (discharge could not be measured at

other sites because of shallow, dispersed flows), we found a strong correlation ($r^2 = 0.70$, $P < 0.001$, $y = -1912.24 + 174109.82x$). Discharge and temperature were inversely correlated ($r^2 = 0.39$, $P < 0.01$, $y = 37.48 - 160.64x$); however, discharge measurements reflected rather steadily changing flows and were not impacted by discrete, short-term events. Given such a high correlation with density and the fact that we did not measure flow during May 1990 and September 1991 flood events, it may be that in this case these measurements give a better indication of general

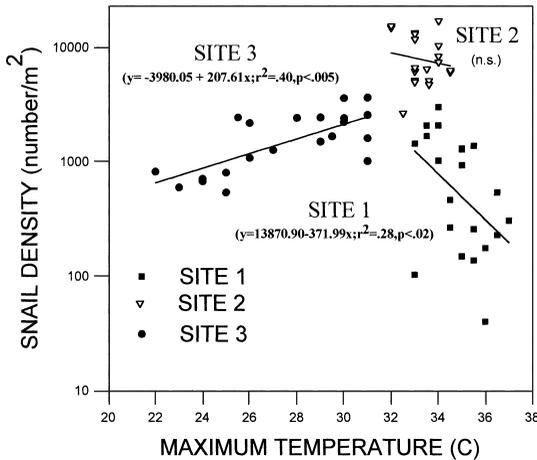


Fig. 4. Linear regressions of snail density versus maximum temperature for Bruneau hot springsnailed study sites. Note logarithmic scale on y-axis.

trends (including temperature) than our actual temperature measurements.

Of the other environmental factors we measured, water chemistry remained fairly constant throughout the study. Chlorophyll *a* was not significantly correlated with recruitment or density. Biomass correlated with density only at site 2, and only when densities at mid-range temperatures (i.e., excluding outliers) were compared ($r^2 = 0.47$, $y = 8009.74 + 229.72x$, $P < 0.05$). This could indicate that other factors such as competition for limited food resources affect this system in the absence of critical temperature influences. Site 2 had the smallest mean snail size and lowest number of juveniles/female, also indicating competition for food resources may have been occurring to a greater extent than at other sites. However, during most of the time at these sites, temperature appears to override such relationships.

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