Effects of Light and Nutrients on Grazer–Periphyton Interactions

Micheline A. Kim[1]
Department of Forest Sciences, University of British Columbia,
Vancouver, BC, V6T 1Z4, Canada

John S. Richardson
Wildlife Branch, British Columbia Environment, and
Department of Forest Sciences, University of British Columbia,
Vancouver, BC, V6T 1Z4, Canada

ABSTRACT

Forest disturbance can alter light and nutrient regimes in small streams, which in turn may influence grazer–periphyton interactions within the stream community. To investigate the influence of forest disturbance on grazer–periphyton interactions, we tested the effects of light, nutrients, and grazing by tadpoles of the tailed frog (*Ascaphus truei*) on periphyton standing crop and tadpole growth rates in 2 coastal streams. Periphyton biomass was found to be under simultaneous control by light and tadpole grazing. Light exerted a strong, positive effect on periphyton standing crop and tadpole relative growth rate, indicating a tight trophic coupling between grazers and their algal food resource. Tadpole growth rate decreased significantly with increasing tadpole density, showing that tadpoles are subject to intraspecific density-dependent interactions. The 2 streams differed in both abiotic limitation of periphyton biomass and tadpole growth. This study demonstrates that several factors may act together to control periphyton biomass and grazer growth rate, and that the relative importance of these factors may vary between nearby streams.

Key words: *Ascaphus truei,* density dependence, grazer, light, nutrients, periphyton, stream, tadpole.

Food webs are a central idea in ecology and represent graphically how nutrients and energy are cycled through species interactions within ecosystems (Wilbur 1997). Plants form the basis of most food webs and exert significant control over higher trophic level interactions (Power 1992). In stream ecosystems, primary production by periphyton plays a key role in determining the structure and function of the stream community. Stream periphyton communities are subject to both bottom-up forces, such as light, nutrients, substrate, flow, season, and disturbance, and top-down control by herbivory. The quantity and quality of the algal food resource influences the type and strength of interactions at higher trophic levels. At high densities, grazers can become food-limited and competition for a limited algal resource may result in intra- or interspecific density-dependent interactions (Hart 1987, Lamberti et al. 1987). Studies involving benthic invertebrates demonstrate that algal production can limit grazers in temperate streams through competition for food, reduced growth rate, and shifts in community composition of grazers (e.g., Lamberti and Resh 1983).

Small streams provide an opportunity to test the influence of abiotic factors from forest disturbance on in-stream community processes. Primary production by algae in small, forested streams is generally limited by a closed riparian canopy which may limit light reaching the streambed to <5% of full sunlight (Hill et al. 1995). Primary production may be further limited in oligotrophic streams by inherently low concentrations of both nitrogen and phosphorus. Removal of the riparian canopy due to forest harvest or windthrow can shift production from primarily allochthonous inputs to autochthonous production. How this shift in energy resources from forest disturbance impacts grazer–periphyton interactions in these systems is a complex, poorly understood issue.

Interactions of several factors may yield complex outcomes and therefore we designed a complete block, factorial experiment to assess the effect that changes in light and nutrients from riparian forest disturbance may have on grazer–periphyton interactions in small fishless streams. An amphibian grazer, the tailed frog tadpole (*Ascaphus truei*), was selected to study the link between lotic herbivory and primary production for 2 reasons. First, ecologically, they often occur at high densities in the predominantly fishless streams that they inhabit, are morphologically specialized for feeding on epilithic periphyton, and may be dominant herbivores in some streams (Lamberti et al. 1992). Second, from a conservation perspective, the tailed frog is currently Blue-listed in British Columbia and considered vulnerable to forest disturbance (Corn and Bury 1989). Changes in abiotic factors from forest disturbance may influence the occur-

---

[1] Present address: AXYS Environmental Consulting Ltd.,
P.O. Box 2219 - 1045 Mills Rd. West, Sidney, BC, V8L 3S8, Canada
akim@axys.net

L. M. Darling, editor. 2000. Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk, Kamloops, B.C., 15 - 19 Feb.,1999. Volume Two.
B.C. Ministry of Environment, Lands and Parks, Victoria, B.C. and University College of the Cariboo, Kamloops, B.C. 520pp.

rence, density, and biomass of tailed frog tadpoles by influencing the availability of the algal food supply. This study assesses the effects of forest disturbance on abiotic factors, periphyton biomass, and larval growth response, which may be a correlate of fitness for individual tadpoles. The major objectives of this study were to:

1. examine the influence of changes in abiotic factors (light and nutrients) on primary production by stream periphyton;
2. assess whether tadpole growth is food limited under different light and/or nutrient conditions; and
3. determine whether tadpole growth is influenced by density-dependent interactions.

STUDY AREA

The study was conducted in 2 high-gradient, permanently flowing, first-order creeks in the Chilliwack River drainage, approximately 115 km east of Vancouver, in southwestern British Columbia, Canada. The 2 creeks selected are approximately 6 km apart (straight-line distance). Both Klondike Creek and Dipper Creek were classified as S5 streams according to the *Riparian Area Management Guidebook* (B.C. Ministry of Forests and B.C. Ministry of Environment, Lands and Parks 1995). Both streams flow through second-growth forest dominated by Douglas-fir (*Pseudotsuga menziesii)* and western hemlock (*Tsuga heterophylla*), with red alder (*Alnus rubra*) occurring within the riparian zone.

METHODS

From August to September 1997, light, nutrient levels, and tadpole density were experimentally altered to test for their effects on periphyton levels in experimental stream enclosures in 2 creeks. Two light levels (shaded and unshaded), 2 nutrient levels (ambient and high), and 4 tadpole densities (0, 29, 57, and 86 tadpoles/m^2) were manipulated in experimental stream enclosures in each stream in a 2 x 2 x 2 x 2 complete block, fully factorial design. Each treatment combination was replicated 4 times in each stream. Densities were determined by the random assignment of 0, 1, 2, or 3 tadpoles to enclosures within each array. Each array consisted of 8 enclosures, each measuring 0.035 m^2. Enclosure design was modified from Lamberti and Feminella (1996). Additional arrays with enclosures measuring 2 times (0.07 m^2 = medium) and 3 times (0.105 m^2 = large) the size of small enclosures were used to allow for 2 additional density treatments (10 and 14 tadpoles/m^2, respectively). Eight arrays of small enclosures, 4 arrays of medium enclosures, and 4 arrays of large enclosures were used at each stream.

Experimental enclosures were placed in uniform areas within runs approximately 5–15 cm below the surface of the water to simulate conditions where tadpoles were most likely encountered within the stream channel (personal observation). Unglazed ceramic tiles (5 x 10 cm) and stream cobbles were placed in each enclosure and conditioned for 5 weeks before introduction of tadpoles. A total of 152 *Ascaphus truei* tadpoles per stream were collected from within a 200 m reach at each stream. Individual tadpole total lengths and weights were recorded and tadpoles randomly assigned to enclosures. Light levels were manipulated using 90% industrial shade cloth (American Horticultural Supplies) to simulate closed canopy conditions. Surface irradiance was measured at several locations in both the open and shaded sections on 10 August 1997 using a PAR-quantum light sensor (LI-COR, Nebraska). Nutrient levels were manipulated using slow-release osmo-coated nutrient pellets deposited 10 m upstream of half of the enclosures. The remaining half of the enclosures in the upstream portion served as ambient nutrient controls.

During the 6-week experiment, the outside of each enclosure was cleaned of debris every 2 days and enclosures were checked to ensure tadpoles had not escaped. At the end of the experiment, tiles and cobbles were collected for analysis of periphyton biomass (ash-free dry weight, AFDW) and chlorophyll *a* concentration. Water chemistry and stream temperature were measured during the experiment. At the end of the 42-day experiment, 95% of tadpoles were recovered, weighed, measured, and released. Periphyton was removed from cobbles and tiles by scrubbing the entire surface with a toothbrush and rinsing with distilled water. To determine periphyton biomass, half the sample was filtered through a Whatman GF/F filter (Whatman Inc., Kent, U.K.), dried at 55°C for 24 hours, weighed, combusted at 550°C for 1 hour, and reweighed to estimate AFDW by loss on ignition. Chlorophyll *a* analysis followed methods outlined in Strickland and Parsons (1972). Water samples were placed directly on ice and frozen for nutrient analysis. Nutrient concentrations were measured using a Technicon Auto Analyzer II (Technicon Corporation).

Prior to statistical analysis, data were tested for normality. Tadpole relative growth rate (RGR) was calculated as: RGR (g) = $[(\text{weight}_{\text{initial}} - \text{weight}_{\text{final}})/\text{weight}_{\text{initial}}]$/no. of days of the experiment. Effects were evaluated with analysis of variance (ANOVA) and analysis of covariance (ANCOVA) using the PROC GLM function in SAS (SAS Institute 1996). Least squared means and standard errors generated from 1-way ANOVAs were plotted to depict tadpole growth response to density treatments.

RESULTS

Addition of nutrient pellets resulted in a 6-fold increase in nitrate concentration and a 2-fold increase in phosphate concentration in Dipper Creek. Shade cloth reduced light levels by 85–90%. Water temperature for Klondike Creek during the experiment ranged from 8.1 to 14.9°C (mean =

12.3°C). Water temperatures at Dipper Creek during the experiment ranged from 7.8 to 11.2°C (mean = 9.5°C). Size–frequency distributions for tadpoles at each creek indicate that tadpoles used in this experiment likely represent a single cohort of 1 -year olds. Slopes of allometric regressions differed by a factor of 1.5 between the 2 creeks (Dipper = 0.028; Klondike = 0.019), indicating that tadpole condition (e.g., weight/length ratio) before the experiment differs significantly between the 2 creeks with tadpoles at Dipper Creek weighing on average 50% more for a given length than tadpoles at Klondike Creek ($P < 0.0001$, $F_{1,300} = 160.2$).

LIGHT AND NUTRIENT EFFECTS ON PERIPHYTON

ANOVA showed that light exerted a significant positive effect on chlorophyll *a* ($P < 0.0001$) and periphyton biomass ($P < 0.0302$). Light accounted for 44% of the observed variation in chlorophyll *a* abundance. However, light accounted for only 1% of the observed variation in periphyton biomass. Chlorophyll *a* abundance was 2–7 times higher under light conditions than in shade and showed a significantly greater response to light treatments at Dipper Creek than at Klondike Creek (light x stream interaction, $P < 0.0001$, Fig. 1). Periphyton biomass exhibited a smaller response to light treatments than did chlorophyll *a*. At Dipper Creek, periphyton biomass increased 30–40% in light but exhibited little response at Klondike Creek. Nutrients had no significant effect on chlorophyll *a* ($P = 0.802$) but had a significant positive effect on periphyton biomass ($P < 0.0001$). Overall, nutrients accounted for <1% of the variation in chlorophyll *a* abundance, and 28% of the variation in AFDW, resulting in a 25–50% increase in AFDW. Light and nutrients interacted significantly to influence both chlorophyll *a* abundance and periphyton biomass. Stream and light interacted significantly to influence chlorophyll *a* abundance; however, there was no significant interaction between stream and light for periphyton biomass.

GRAZER EFFECTS ON PERIPHYTON

Results of the ANCOVA show that tadpole density had a significant negative effect on chlorophyll *a* ($P < 0.0001$, $F_{1,121} = 11.14$) and on periphyton biomass ($P < 0.0001$, $F_{1,121} = 25.31$). The effects of grazing are most clearly demonstrated by contrasting the control (0 tadpoles) with the lowest density treatment (10 tadpoles/m^2, 1 tadpole) at Klondike Creek (Fig. 2). This result shows that the introduction of a single tadpole resulted in a 50% decline in chlorophyll *a* abundance relative to the no tadpole control. Differences between the 2 study streams significantly influenced periphyton biomass ($P < 0.0001$, $F_{1,121} = 42.6$), but had no significant effect on chlorophyll *a* ($P = 0.0796$, $F_{1,121} = 3.13$). There were no significant interactions between stream and density for chlorophyll *a* or periphyton biomass.

GRAZER GROWTH RESPONSE

Tadpole relative growth rate decreased significantly with increasing tadpole density ($P < 0.0001$), which accounted for 39% of the variation in tadpole relative growth rate (Fig. 3). Differences between the 2 study streams accounted for 33% of the explained variation in tadpole relative growth rate ($P < 0.0001$). Tadpole relative growth rate was approximately 35% higher at Klondike Creek than at Dipper Creek across all density treatments. Light positively influenced tadpole relative growth rate ($P < 0.0001$) and accounted for 14% of the explained variation. Relative growth rate was signifi-

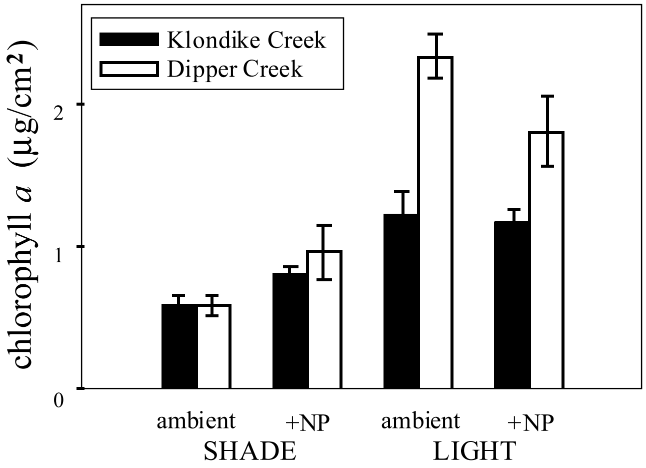

Figure 1. Effect of light and nutrients on chlorophyll *a*. Ambient treatment represents upstream control section; +NP represents downstream fertilized section. Bars represent means (±1 SE for all cobbles (n = 64/stream) from small enclosures.

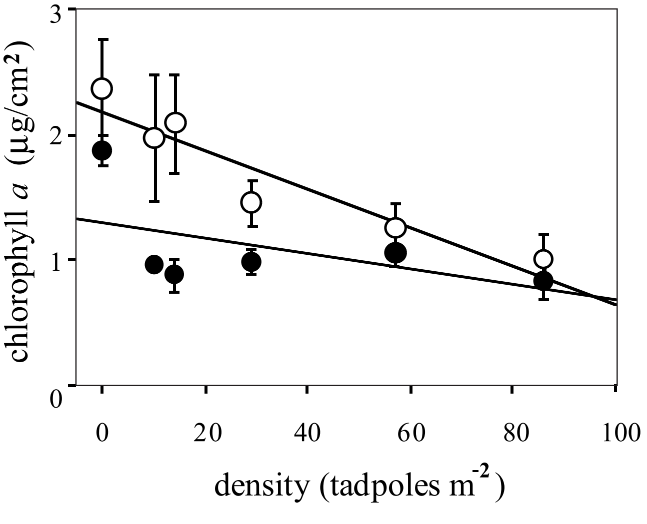

Figure 2. Relations between tadpole density and chlorophyll *a* for Klondike (●) and Dipper (○) Creeks. Dots represent means ±SE for all cobbles (n = 64/stream).

cantly higher in the unshaded treatments than in the shaded treatments at both Klondike (1.2x) and Dipper (1.5x) creeks. Nutrients had no significant effect on tadpole relative growth rate ($P = 0.491$). None of the interactions tested were statistically significant.

DISCUSSION

The results of this study indicate that changes in light and nutrient regimes in small, headwater streams can significantly change periphyton production, which in turn can influence tadpole growth rates. Enhanced growth rates of tadpoles may lead to shorter time to metamorphosis, larger size at metamorphosis, and/or enhanced survivorship of the juvenile stage (Duellman and Trueb 1994). The most striking result about tadpole growth was that differences between the 2 study streams were the most important factors determining tadpole growth, accounting for 33% of the explained variation in relative growth rate. Tadpole relative growth rate was 1.2–2.5 times higher at Klondike than at Dipper Creek. The most probable explanation for this difference is the warmer stream water temperature at Klondike Creek.

In this study, light was found to have a significant positive effect on tadpole relative growth rate at both streams. This growth is presumably mediated by an increase in primary production, and indicates a tight trophic coupling between tadpole grazing and the algal food resource. Nutrients had only a slight but nonsignificant positive effect on tadpole growth rate under unshaded conditions, which reflects the fact that nutrients had little effect on the periphyton food resource. The small, positive effect of nutrients under unshaded conditions indicates that light is the primary limiting factor, and that the positive effects of nutrients may only be expressed once periphyton production is released from light limitation.

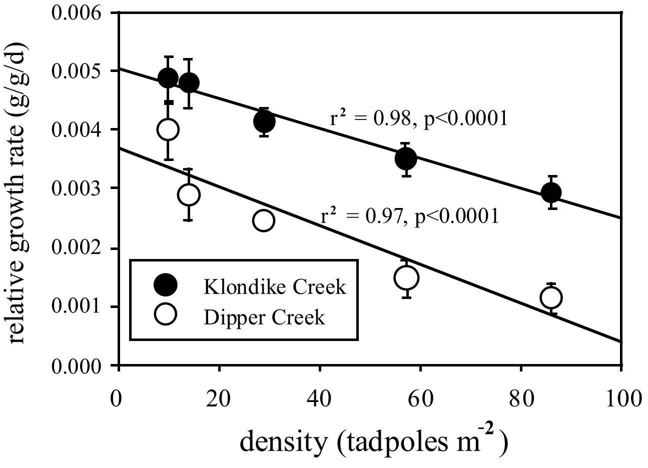

Figure 3. Effect of tadpole density on tadpole relative growth rate. Dots represent means (±1 SE for all tadpoles ($n = 152$/stream).

By applying a complete block, fully factorial design, this study demonstrates that the relative growth rate of *Ascaphus* tadpole decreases as tadpole density increases, indicating that tadpoles were subject to intraspecific density-dependent food limitation. Higher tadpole growth rates at Klondike Creek, despite the fact that food resources were lower, suggest that temperature differences between streams had a strong effect on growth rates. However, the fact that the growth response to increased larval density followed the same pattern at both streams is most logically explained by density-dependent food limitation. This conclusion is supported by decreases in tadpole growth rate and periphyton standing crop as tadpole density increases (Figs. 2 and 3). At Klondike Creek, where growth rates were higher, algae were depressed even at the lowest densities (e.g., 10 tadpoles/m^2), whereas Dipper Creek had a more gradual decline in algae with increasing tadpole density. If density dependent growth rates are linked to survival during the larval period, then survival rates will also show density-dependence, which can carry over to the juvenile and adult stages of the life cycle. Because population size for amphibians is largely determined by the larval stage, longer-term studies are needed to determine how changes in environmental conditions attributable to forest disturbance influence time to metamorphosis, size at metamorphosis, and survivorship of tadpoles and juveniles of *Ascaphus*.

Complex interactions require complex experiments to address causal mechanisms (Wilbur 1997). In this study, manipulation of abiotic and biotic factors to assess their relative importance on stream periphyton and grazer growth response resulted in complex outcomes. Light, nutrients, grazer density, and several interactions between these factors simultaneously influenced stream periphyton production and growth rates of tadpoles. Differences in the response of periphyton and tadpole growth to the treatments at the 2 streams demonstrate that the relative importance of these factors can be site specific. At Klondike Creek, bottom-up control by light was a more important limiting factor for periphyton standing crop than grazing. However, at Dipper Creek grazer control of periphyton was more important than light limitation.

MANAGEMENT IMPLICATIONS

This study demonstrates that several factors (light, nutrients, tadpole density) can act together to determine periphyton production and growth rates of tadpoles. Because growth rate may be a correlate of fitness for individual tadpoles, managers should consider how changes in environmental conditions within the riparian zone influence in-stream processes. Although increased insolation to the stream may enhance primary production and grazer growth, other factors may reduce production, thereby making the overall effects of forest disturbance difficult to predict (Murphy and Hall 1981). The size and duration of these effects will vary between streams; therefore, a site-specific approach should be taken when managing for conservation of in-stream habitat. Finally, the tailed frog has a complex life history which includes a multiyear aquatic larval stage and a terrestrial juvenile and adult phase. Management of riparian forests for conservation of the tailed frog should consider habitat requirements for all life history phases.

ACKNOWLEDGEMENTS

We thank Dr. B. Neill and Dr. S. Hinch for their comments and support. Thanks to R. Stott for assistance in the field and D. White for assistance in the lab. Financial support for this project was provided by Forest Renewal British Columbia and the Donald McPhee Fellowship.

LITERATURE CITED

B.C. Ministry of Forests, and B.C. Ministry Environment, Lands and Parks. 1995. Riparian management area guidebook. Victoria, BC.

Corn, P. S., and R. B. Bury. 1989. Logging in western Oregon: Responses of headwater habitats and stream amphibians. For. Ecol. Manage. 29:39–57.

Duellman, W. E., and L. Trueb. 1994. Biology of amphibians. Johns Hopkins Univ. Press, Baltimore, MD.

Hart, D. D. 1987. Experimental studies of exploitative competition in a grazing stream insect. Oecologia 73:41–47.

Hill, W.R., M.G. Ryon, and E.M. Schilling. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. Ecology 76:1297–1309.

Lamberti, G. A., and J. W. Feminella. 1996. Plant-herbivore interactions. Chap. 19 *in* F. R. Hauer, and G. A. Lamberti, eds. Methods in stream ecology. Academic Press, San Diego, CA.

_____, _____, and V. H. Resh. 1987. Herbivory and intraspecific competition in a stream caddisfly population. Oecologia 73:75–81.

_____, _____, C. P. Hawkins, R. C. Wildman, L. R. Ashkenas, and D. M. DeNicola. 1992. Plant-herbivore interactions in streams near Mount St Helens. Freshwater Biol. 27:237–247.

_____, and V. H. Resh. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology 64:1124–1135.

Murphy, M. L., and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Can. J. Fish. Aquat. Sci. 38:137–145.

Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73:733–746.

SAS Institute. 1996. SAS procedures guide. Release 6.1.2. Cary, NC.

Strickland, J. D. H., and T. R. Parsons. 1972. Pigment analysis: Spectrophotometric determination of chlorophylls and total carotenoids. Section IV.3.I *in* A practical handbook of seawater analysis. 2nd ed. Fish. Res. Board Can., Ottawa, ON. Bull. 167.

Wilbur, H. M. 1997. Experimental ecology of food webs: complex systems in temporary ponds. Ecology 78:2279–2302.