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# Complex interactions of light, nutrients and consumer density in a stream periphyton–grazer (tailed frog tadpoles) system

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## Summary

1. Consumer–resource interactions may be modified by complex environmental interactions. We experimentally manipulated light, nutrients, consumer density (tailed frog tadpoles – *Ascaphus truei*), and enclosure sizes in two small and steep streams of coastal British Columbia, Canada. We used flow-through, screened enclosures *in situ* as experimental units and measured the responses of algae (as chlorophyll *a*), periphyton (ash-free dry mass) and growth rates of tailed frog tadpoles using a factorial model design.

2. Light exerted a strong, positive effect on algae and periphyton production with 30–40% higher biomass over shaded treatments, and a 14% higher relative growth rate of tadpoles. Nutrient additions had little to no effect on any measure, alone or in interaction with other factors. Tadpole growth, algae and periphyton standing crop were significantly reduced along a gradient of increasing consumer density. Enclosure size had a large effect on all three measures.

3. Algae and periphyton production were under simultaneous top-down (tadpole grazing) and bottom-up control (light); however, the relative importance of these effects was stream-dependent. At Klondike Creek algae and periphyton production was influenced primarily by grazing, and by light levels at Dipper Creek.

4. Mean growth rate of tadpoles was on average 45% higher at Klondike Creek than at Dipper Creek. Most of the effects of the abiotic treatments and consumer density interacted statistically with stream identity, despite these streams being very similar and < 6 km apart. The strong effect of stream on the outcomes may be a consequence of large temperature differences.

5. This study demonstrated that light, consumer density, stream, enclosure size and nutrients alone and in combination affected algae and periphyton production, and grazer growth rate. While the interactions between consumer and resources were tightly coupled, the relative importance of the driving factors varied significantly between nearby streams.

**Key-words:** *Ascaphus truei*, density-dependent interactions, grazer–periphyton interactions, light, nutrients.

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## Introduction

Consumer–resource dynamics may be influenced by complex interactions with environmental factors. Demon-

stration of causal mechanisms determining complex interactions requires multifactor experiments (Holland 1986; Eberhardt & Thomas 1991; Wilbur 1997). For instance, light and nutrients may have strong interacting effects on primary producers through limitation of production, but nutrient limitation may only be evident when light is not limiting (e.g. Sterner *et al.* 1997). The form of limitation on basal resources affects both rates of production and the quality of resources in terms of C : N ratios (Sterner *et al.* 1997). Consumption further

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complicates the identification of system drivers. The relative strength of top-down and bottom-up forces in food webs has generated considerable interest, and local abiotic conditions may mediate the outcome of species interactions.

In streams, primary production by algae (as chlorophyll *a*; a component of periphyton) and periphyton (as the ash-free dry mass on stone surfaces) provides a key basal resource to food webs (Minshall 1978) and can be limited simultaneously by both top-down and bottom-up forces (Hill, Boston & Steinman 1992; Hunter & Price 1992; Steinman 1992; Rosemond 1993; Hill, Ryon & Schilling 1995; Wellnitz & Ward 1998; Rosemond, Mulholland & Brawley 2000). The relative importance of specific drivers in food webs may vary through both space and time (Feminella, Power & Resh 1989; Hunter & Price 1992; Wilbur 1997; Hill, Mulholland & Marzolf 2001).

Primary production by algae in small, forested streams is generally light-limited by the presence of a closed riparian canopy, but may also be nutrient-limited in oligotrophic streams (Naiman, Bilby & Bisson 2000; Hill *et al.* 2001). In turn, the quantity and quality of the algal food resource influences the type and strength of interactions at higher trophic levels (Stelzer & Lamberti 2002). Grazers in shaded, oligotrophic streams can become food-limited and experience competition (Hart 1987; Hill & Knight 1987; Lamberti, Feminella & Resh 1987). Disturbance of riparian forests, such as occurs with forest harvesting (Kiffney, Richardson & Bull 2003), can shift the intensity of limitation of algae by removal of shading by vegetation.

We designed a multifactorial experiment to test whether changes in light, nutrients, enclosure size and consumer density influence grazer–periphyton interactions in two small, fishless streams. We selected the tadpole of the tailed frog (*Ascaphus truei* Stejneger) to study the link between lotic herbivory and primary production for two reasons. First, these tadpoles are specialized periphyton grazers (Altig & Brodie 1972) and may function as dominant herbivores in the streams that they inhabit (Lamberti *et al.* 1992; Kiffney, Richardson & Bull 2004). Brown (1990) suggested that *A. truei* larval growth rates may be food-limited. Secondly, from a conservation perspective, the tailed frog is considered vulnerable to forest disturbance (Corn & Bury 1989), which may influence the availability of the algal food supply (Richardson & Neill 1998; Kiffney & Richardson 2001). The species is listed officially as a species of concern in parts of its range, including British Columbia. This study addresses both issues by assessing the effects of simulated forest disturbance on algae and periphyton biomass, and tadpole growth, the latter of which may be a proxy for individual fitness.

## Materials and methods

Two headwater streams in south-western British Columbia, Canada (49°5′ N, 121°3′ W) were used for this experi-

ment. These streams flow through Coastal Western Hemlock forest in the Cascade Mountain Range and receive over 2400 mm of precipitation annually. The creeks were chosen based on the presence of *A. truei* larvae, accessibility and physical characteristics. The two creeks, approximately 6 km apart, were physically similar and both had open second-growth canopies resulting from logging about 30 years previous to the study. Stream substrates were cobble, boulders and gravel. Watershed areas of both streams were about 1.1 km<sup>2</sup> with bankfull widths approximately 6 m. Both Klondike Creek (785 m a.s.l.) and Dipper Creek (385 m a.s.l.) drain northwards. Water temperatures during the experiment were measured at 15-min intervals using dataloggers. Water samples were placed directly onto ice and frozen for nutrient analysis. Measures of summer water chemistry of these two circumneutral streams were conductivity of 93–152 µS s<sup>-1</sup>, soluble reactive phosphorus (PO<sub>4</sub>-P) from 1 to 2.85 µg l<sup>-1</sup> and nitrate (NO<sub>2</sub>-NO<sub>3</sub>-N) from below detection to 4.3 µg l<sup>-1</sup>.

Light, nutrient levels, tadpole density and enclosure size were altered experimentally to test their effects on periphyton standing crops in enclosures in the two streams for 42 days (August–September). We use periphyton as the general term to include both algae and total periphytic biomass, but refer to algae (as chlorophyll *a*) or periphyton (as AFDM) in most of the paper. Light levels (shaded, unshaded), nutrient levels (ambient, elevated), enclosure size (small, medium, large) and tadpole density (0, 10, 14, 29, 57, 86 tadpoles m<sup>-2</sup>) were manipulated in two streams in a complete block, factorial design with density as a continuous variable. Enclosures were built from PVC pipe cut in half lengthwise and the ends and top covered with 1-mm mesh to keep tadpoles in and allow exchange of water and the flux of light. The three enclosure sizes were intended to achieve a broader range of densities of tadpoles for our experiment. Small enclosures were 0.035 m<sup>2</sup> in area (design modified from Lamberti & Feminella 1996), and were assigned randomly no, one, two or three tadpoles to produce densities of 0, 29, 57 or 86 tadpoles m<sup>-2</sup>. Medium enclosures measured two times the area of small enclosures (0.07 m<sup>2</sup>) and large enclosures were three times the area (0.105 m<sup>2</sup>). Medium and large enclosures allowed for lower densities with one tadpole in each, resulting in 14 or 10 tadpoles m<sup>-2</sup>, respectively. A set of medium enclosures with two tadpoles per trough and large enclosures with three tadpoles per trough provided 29 tadpoles m<sup>-2</sup>, to be directly comparable for density with the small enclosures with one tadpole. There were four replicates for small enclosures and two replicates each for the medium and large enclosures for each treatment combination, in each stream. A total of 64 small enclosures, 16 medium enclosures and 16 large enclosures were used at each stream for an experiment-wise total of 192 enclosures and 304 tadpoles.

Enclosures were placed in streams approximately 5–15 cm below the surface of the water. Stream cobbles and unglazed ceramic tiles (5 × 10 cm) were placed into

each enclosure and conditioned for 5 weeks prior to introduction of tadpoles. At each stream a total of 152, second-year (to avoid age-specific differences in growth rates) *A. truei* tadpoles were collected. Each tadpole was individually weighed and assigned randomly to enclosures. Light levels were manipulated using 90% industrial shade cloth (American Horticultural Supplies, Oxnard, CA, USA) to simulate closed canopy conditions. Surface irradiance was measured at several locations in both the open and shaded sections on 10 August using a PAR-quantum light sensor (Licor, Lincoln, NE, USA) to compare the effective light reduction provided by the shade cloth. Nutrient levels were manipulated using slow-release osmocoated nutrient pellets (IMC Vigoro Inc., Winter Haven, FL, USA) deposited 10 m upstream of half of the enclosures (at the midpoint of the study reach) as increased nutrients cannot be applied randomly to enclosures in streams. The remaining enclosures served as upstream ambient nutrient controls.

After 42 days substrates were collected for analysis of algae chlorophyll *a* concentration and periphytic AFDM. Tiles and cobbles were scraped thoroughly and brushed for periphyton and the resulting slurry collected in a small volume of water. Half of each periphyton sample was filtered through a Whatman GF/F filter, dried at 55 °C for 24 h, weighed, combusted at 550 °C for 1 h, and reweighed to estimate AFDM. The other half of the periphyton sample was filtered and processed for chlorophyll *a* analysis following standard methods (Strickland & Parsons 1972). We present results only for cobbles, as the results from tiles were similar. Ninety-five per cent of tadpoles were recovered at the end of the experiment, weighed and measured and released.

Data were tested for normality using the Shapiro–Wilk statistic and satisfied that assumption. Tadpole relative growth rate (RGR) was calculated as:  $RGR = [(mass_{initial} - mass_{final})/mass_{initial}]/no. \text{ of days of the experiment}$ . We assumed that the non-random applications of nutrient amendments were unbiased and enclosures independent as nutrient addition could not have been conducted otherwise in an open system and it was applied in both streams; this assumption allowed us to examine the factorial model. The primary statistical design was an incompletely crossed (not all densities were in each enclosure size) factorial ANCOVA model, with tadpole density as the covariate (PROC MIXED—SAS version 8.02). We examined the main and interactive effects of light, nutrients, grazer density, enclosure size and stream on chlorophyll *a*, periphyton AFDM and tadpole growth. Least-squared means and standard errors generated from one-way ANOVAs were plotted to depict responses to density treatments.

## Results

### STREAM PHYSICAL DATA AND WATER CHEMISTRY

Addition of nutrients resulted in a sixfold increase in nitrate ( $NO_3 + NO_2-N$ ) concentration and a twofold

increase in soluble reactive phosphorus ( $PO_4-P$ ) concentration in Dipper Creek. Phosphorus concentration at Dipper Creek following fertilization was just above the target concentration of  $3 \mu g L^{-1}$ . Nitrogen concentration at Klondike Creek was below detection limits (i.e.  $< 1 \mu g L^{-1}$ ) prior to addition of nutrient pellets but increased to  $4 \mu g L^{-1}$  after fertilization. Phosphorus concentration at Klondike Creek remained below the target of  $3 \mu g L^{-1}$  following fertilization.

Shade cloth reduced light levels by 85–90%, which is comparable to shading by a mature or second-growth forest. Mean PAR for Dipper Creek was  $217 \mu E m^{-2} s^{-1}$  in the open sections (range =  $195–240 \mu E m^{-2} s^{-1}$ ,  $n = 3$ ) and  $31 \mu E m^{-2} s^{-1}$  in the shaded sections (range =  $25–36 \mu E m^{-2} s^{-1}$ ,  $n = 3$ ). Mean light level for Klondike Creek was  $313 \mu E m^{-2} s^{-1}$  in the open sections (range =  $280–360 \mu E m^{-2} s^{-1}$ ,  $n = 3$ ) and  $36 \mu E m^{-2} s^{-1}$  in the shaded sections (range =  $31–43 \mu E m^{-2} s^{-1}$ ,  $n = 3$ ). Water temperature for Klondike Creek during the experiment ranged from 8.1 to 14.9 °C (mean = 12.3 °C), and that of Dipper Creek ranged from 7.8 to 11.2 °C (mean = 9.5 °C).

### LIGHT, NUTRIENT AND STREAM EFFECTS ON PERIPHYTON

Light resulted in both higher chlorophyll *a* and higher periphyton biomass (Table 1) and accounted for 24% of the observed variation in chlorophyll *a*. Chlorophyll *a* abundance was from 23% to 66% higher under light conditions than in shade and the light effect was significantly greater at Dipper Creek than at Klondike Creek (light  $\times$  stream interaction, 18% of explained variance, Table 1, Fig. 1a). However, periphyton biomass exhibited a smaller response to light treatments than chlorophyll *a* (~2% of observed explained variance, Table 1, Fig. 1b). At Dipper Creek, periphyton biomass was 30–40% higher in the presence of light; periphyton biomass at Klondike Creek exhibited little response to light treatments. Nutrients alone, or in combination with other factors, had no significant effect on chlorophyll *a* or biomass (Table 1) and accounted for around 1% of the explained variance in both measures.

The differences in periphyton measures between streams were very large (Table 1, Fig. 1a,b). Chlorophyll *a* was 50% higher (range: 2% lower to 90% higher) and AFDM was 80% higher (range 56–120% higher) in Dipper Creek, depending on treatment. By itself, the stream accounted for 18% of the variance in chlorophyll *a*, and nearly 30% of the variance in AFDM. Stream also figured prominently in several of the interaction terms (Table 1).

### GRAZER EFFECTS ON PERIPHYTON

One of the largest effects on periphyton was the inverse relation with grazer density, explaining 14.4% and 29.8% of the explained variance in chlorophyll *a* and AFDM, respectively (Table 1, Fig. 2). The effect of tadpole density also interacted significantly with stream for AFDM

**Table 1.** Main and interaction effects for full five-way factorial ANCOVA design using all enclosures and interactions (density as covariate). Response measures were tadpole relative growth rate, periphytic chlorophyll *a* and ash-free dry mass from the cobble surfaces. Abbreviations: STR, stream; LT, light; NP, nutrients; ENC, enclosure size; DENS, tadpole density. None of the four-way or the five-way interactions were significant (all with  $P > 0.1$ ) and are not shown for brevity

Source	d.f.	Tadpole relative growth rate (109 error d.f.)	Cobble – chlorophyll <i>a</i> (142 error d.f.)	Cobble – AFDM (143 error d.f.)
STR	1	< 0.0001	0.0001	< 0.0001
LT	1	0.055	< 0.0001	0.029
NP	1	0.055	0.293	0.237
ENC	2	0.293	0.525	< 0.0001
DNS	1	< 0.0001	0.0006	< 0.0001
STR × LT	1	0.942	0.0001	0.150
STR × NP	1	0.604	0.545	0.500
STR × ENC	2	0.112	0.083	0.013
LT × NP	1	0.461	0.538	0.113
LT × ENC	2	0.103	0.822	0.376
NP × ENC	2	0.254	0.167	0.689
STR × LT × NP	1	0.280	0.481	0.831
STR × LT × ENC	2	0.725	0.274	0.079
STR × NP × ENC	2	0.611	0.354	0.720
LT × NP × ENC	2	0.218	0.820	0.229
DNS × STR	1	0.597	0.130	< 0.0001
DNS × LT	1	0.929	0.645	0.399
DNS × STR × LT	1	0.592	0.135	0.671
DNS × NP	1	0.023	0.637	0.254
DNS × STR × NP	1	0.911	0.335	0.326
DNS × LT × NP	1	0.989	0.965	0.356
DNS × ENC	2	0.0002	0.464	< 0.0001
DNS × STR × ENC	2	0.369	0.302	0.007
DNS × LT × ENC	2	0.587	0.936	0.468
DNS × NP × ENC	2	0.065	0.600	0.453

(8.2% of variance), indicating differences in slopes of the relations between streams, but this effect was not significant for chlorophyll *a* (Table 1, Fig. 2). Density interacted significantly with enclosure size (see below, Table 1, and 8% of explained variance) with small enclosures having higher AFDM for a given density.

The effects of grazing are demonstrated most clearly by contrasting the control (no tadpoles) with the lowest density treatment (10 tadpoles m<sup>2</sup>, one tadpole per enclosure) at Klondike Creek (Fig. 2) where a single tadpole resulted in a 50% decline in chlorophyll *a* abundance relative to the no-tadpole control. The highest density treatments showed declines in periphyton AFDM of up to 66% compared to the no-tadpole control (Fig. 2). At Dipper Creek a significant decline in periphyton was detected at densities of 29 tadpoles m<sup>2</sup> or greater.

#### GRAZER GROWTH RESPONSE

The ANCOVA explained 70% of the variance in tadpole growth rates (Table 1). Tadpole density, stream, light and enclosure size, alone or in combination, accounted for 93% of the explained variation in growth rates. However, differences between the two streams accounted for a further 15.6% of the explained variation from the ANCOVA. Light and nutrients alone were both nearly significant with small positive impacts on growth rates (Fig. 1c). Enclosure size alone was not significant, but

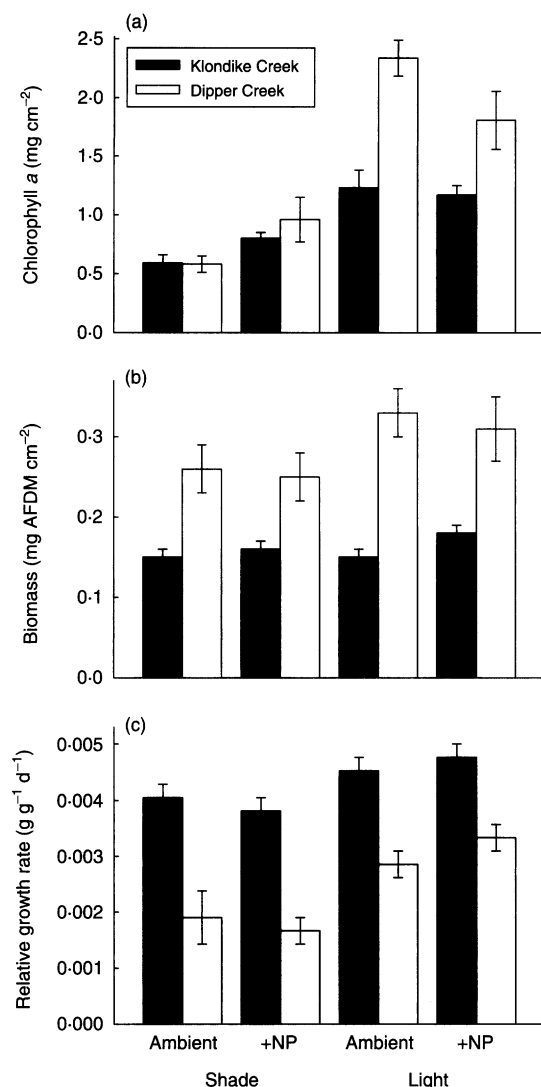
in interactions with density and stream accounted for an additional 10.4% of the explained variation (Table 1).

Tadpole growth rates were significantly density-dependent (Fig. 3 and 47.4% of explained variance). There was a significant decline in tadpole relative growth rate relative to the lowest density at densities of 14 tadpoles m<sup>2</sup> in Dipper and 29 tadpoles m<sup>2</sup> in Klondike (Fig. 3). Tadpole relative growth rate was approximately 35% higher at Klondike Creek than at Dipper Creek across all densities.

Growth rates of tadpoles were predicted to be a direct effect of algal biomass and density dependence mediated through this resource. We used a reduced ANCOVA using chlorophyll *a* (covariate) and stream to determine the effects on growth rates. The model accounted for 43% of the variance in growth rates, with significant effects of chlorophyll *a* abundance ( $P < 0.0001$ ) and stream ( $P = 0.0002$ ). The interaction term was marginally insignificant ( $P = 0.057$ ).

#### EFFECT OF ENCLOSURE SIZE

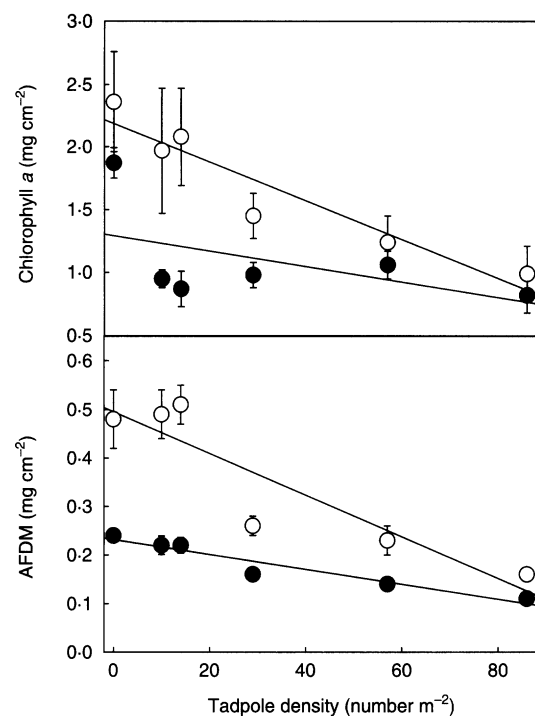
Experimental enclosures do not perfectly mimic the natural stream environment and specific results may be a consequence of enclosure size and allometry. Enclosure size affected tadpole growth rates, chlorophyll *a* abundance and periphyton biomass (Table 1), either directly or through interactions with other factors



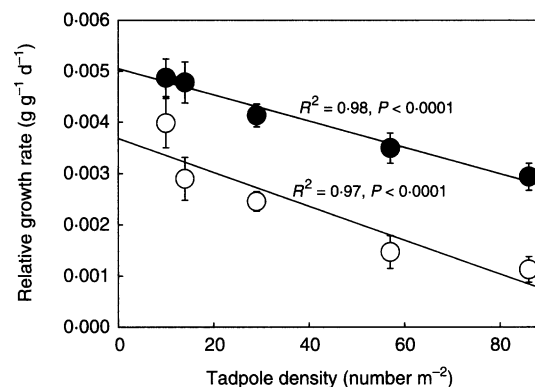
**Fig. 1.** Effects of light and nutrients in the absence of tadpoles on chlorophyll *a* (a) and ash-free dry mass (b). Ambient treatment represents upstream control; + NP represents downstream fertilized section. Bars represent means  $\pm$  1 SE for all cobbles ( $n = 64$  per stream) from small enclosures. (c) Effect of light and nutrients on tadpole relative growth rate. Bars represent means  $\pm$  1 SE across all enclosure and density classes ( $n = 160$ ).

(density and stream) in the full model. We used a reduced model including only enclosures with densities of 29 tadpoles m<sup>2</sup>. At Klondike Creek, chlorophyll *a* (ANOVA,  $P = 0.012$ , Fig. 4a) and periphyton biomass ( $P < 0.0001$ , Fig. 4b) in small enclosures was significantly higher than in medium and large enclosures. At Dipper Creek, chlorophyll *a* (Fig. 4a) and periphyton biomass (Fig. 4b) did not differ significantly between small, medium and large enclosures. Tadpoles in small enclosures had significantly higher relative growth rates in small enclosures than in medium or large enclosures (Fig. 4c) at both Klondike ( $P = 0.0003$ ) and Dipper Creeks ( $P = 0.023$ ).

We performed another analysis using only data from small enclosures (four-way ANCOVA; Table 2). The results were similar to the five-way analysis, in that density, stream and stream  $\times$  density had the largest effects on

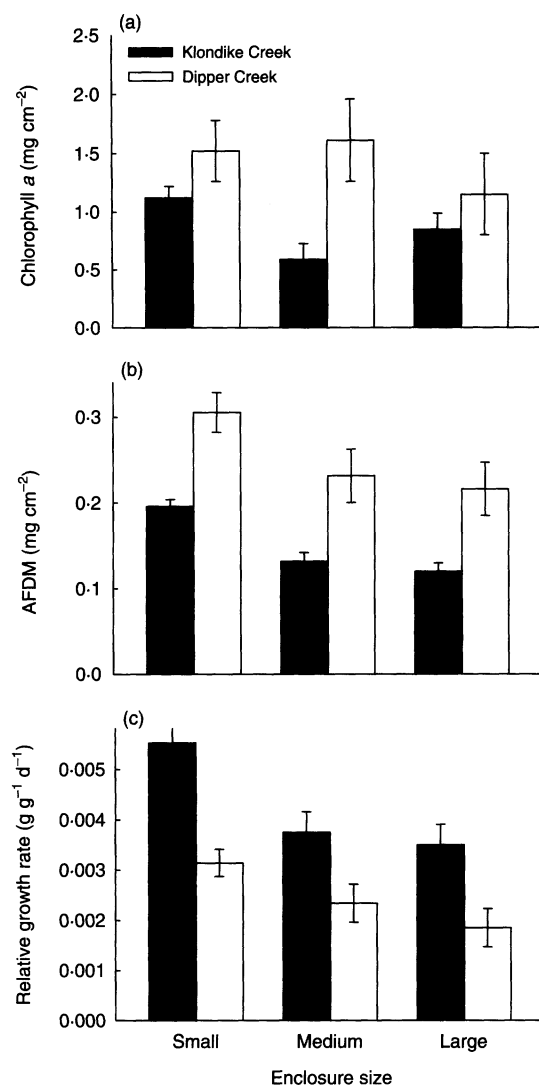


**Fig. 2.** Relation between tadpole density (number of tadpoles m<sup>2</sup>) and periphytic chlorophyll *a* (a) and ash-free dry mass (b) at Klondike and Dipper Creeks. Dots represent means  $\pm$  1 SE for all cobbles.



**Fig. 3.** Effect of tadpole density on tadpole relative growth rate (RGR). Dots represent means  $\pm$  1 SE ( $n = 160$ ).

all response measures. These three terms combined accounted for 92.6%, 42% and 72.6% of the explained variance for tadpole growth, chlorophyll *a* and biomass, respectively. As in the five-way analysis, light and light  $\times$  stream together accounted for much of the explained variation in chlorophyll *a* abundance (43.1%; Table 2), but only 14.7% of that for AFDM. Unlike the five-way analysis, nutrients had a significant effect on AFDM through the stream  $\times$  nutrients and stream  $\times$  nutrients  $\times$  density interactions, accounting for about 5.6% of the variance. The results of the five-way and four-way analyses (i.e. without medium and large enclosures) were very similar in the significance and magnitude of the effects of the various factors.



**Fig. 4.** Effect of enclosure size on periphytic chlorophyll *a* (a), AFDM (b) and tadpole relative growth rates (c) at Klondike and Dipper Creeks. Only enclosures containing 29 tadpoles  $\text{m}^2$  were used to isolate enclosure effects. Bars represent mean  $\pm 1$  SE for all cobbles. Total number of cobbles used at each stream: small ( $n = 16$ ); medium ( $n = 8$ ); large ( $n = 8$ ). Mean values were used for enclosures containing  $> 1$  cobble.

## TOP-DOWN VS. BOTTOM-UP EFFECTS

We tested the relative effects of abiotic limitation (bottom-up) and grazer control (top-down) on stream algae. We compared the effects of light (full light vs. shaded) vs. the grazer (present or absent: including the lowest density enclosures with 10 or 14 tadpoles  $\text{m}^2$ ) on mean periphyton biomass (AFDM) and chlorophyll *a* values. We did not account for grazing invertebrates in the no tadpole enclosures, so the differences may be conservative if there were more invertebrates when tadpoles were absent. We found that the relative importance of top-down vs. bottom-up forces was stream-dependent (Fig. 5). At Klondike Creek, grazing resulted in a 49% decrease in chlorophyll *a*, whereas shade resulted in a 14% decrease. At Dipper Creek, shade accounted for a 73% decrease in chlorophyll *a*, whereas grazing resulted in a 20% decrease.

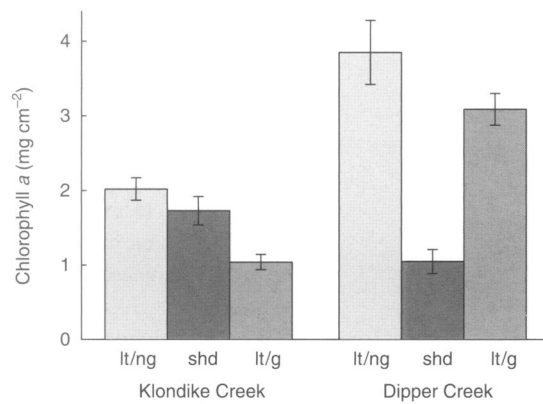
## Discussion

### LIGHT AND NUTRIENT EFFECTS ON PERIPHYTON

Periphyton, the food resource of tailed frog larvae, was light-limited in these two streams. This effect has been noted following leaf flush in streams draining deciduous forests (Rosemond *et al.* 2000; Hill *et al.* 2001) and due to increased light from clear-cutting of riparian forest (e.g. Hansmann & Phinney 1973). Overall levels of periphyton at Dipper Creek were higher than at Klondike Creek throughout the experiment. This could be attributable to the slightly higher ambient nutrient levels at Dipper Creek compared to Klondike Creek producing more periphyton in the absence of light limitation. An alternative explanation could be that warmer water temperatures at Klondike Creek may have inhibited diatom growth, resulted in higher grazing rates, promoted faster turnover of algae biomass (i.e. higher productivity), or some combination.

**Table 2.** Probabilities of main and interaction effects from ANCOVA (PROC MIXED: density as covariate) using only small enclosures. See Table 1 for abbreviations of main effects. The four-way effect was not significant for any measure and was omitted for brevity

Source	d.f.	Tadpole relative growth rate (77 error d.f.)	Cobble – chlorophyll <i>a</i> (110 error d.f.)	Cobble – AFDM (111 error d.f.)
STR	1	< 0.0001	0.022	< 0.0001
LT	1	0.693	< 0.0001	0.0001
NP	1	0.816	0.493	0.060
DNS	1	< 0.0001	< 0.0001	< 0.0001
STR $\times$ LT	1	0.722	< 0.0001	< 0.0001
STR $\times$ NP	1	0.636	0.189	0.034
LT $\times$ NP	1	0.463	0.125	0.830
DNS $\times$ STR	1	0.353	0.274	0.0002
DNS $\times$ LT	1	0.025	0.029	0.015
DNS $\times$ NP	1	0.501	0.690	0.153
STR $\times$ LT $\times$ NP	1	0.805	0.587	0.585
DNS $\times$ STR $\times$ LT	1	0.777	0.001	0.015
DNS $\times$ STR $\times$ NP	1	0.291	0.792	0.034
DNS $\times$ LT $\times$ NP	1	0.528	0.535	0.419



**Fig. 5.** Top-down vs. bottom-up effects regulating periphyton at Klondike and Dipper Creeks (lt = light; shd = shade; g = grazing; ng = no grazing).

Nutrient manipulations had very minor effects on periphyton measures. Nutrient additions slightly increased growth rates of tadpoles (detectable when only small enclosures were analysed), perhaps through an increase in food quality (Stelzer & Lamberti 2002). Bothwell (1989) showed that phosphorus concentrations of  $< 1 \mu\text{g L}^{-1}$  can saturate specific growth rates of unicellular periphytic diatoms in other streams in south-western British Columbia. However, we did not observe evidence of any significant interaction between light and nutrients on periphyton or tadpole growth, as would be predicted from the balance of these two key resources for algal productivity or food quality (Sterner *et al.* 1997; Hill *et al.* 2001). Nutrient additions had minor effects in our streams despite the low ambient concentrations of P and N. However, addition of nutrients in experimental stream channels 100 km away from our study sites, in full light and receiving water with even lower ambient nutrient concentrations than the two streams here, resulted in a fourfold increase in tailed frog tadpole growth rates (Kiffney & Richardson 2001). These contrasting results further indicate the dependence of complex outcomes on the particular environmental context.

Grazing by tailed frog tadpoles significantly reduced periphyton standing stock in our streams. This is similar to the magnitude of periphyton reduction observed in other stream herbivore studies using tadpoles (Lamberti *et al.* 1992; Kupferberg 1997; Ranvestal *et al.* 2004). Natural mean densities of tailed frog tadpoles in streams can be as high as  $65 \text{ m}^{-2}$  (Hawkins, Gottschalk & Brown 1988; Rosenfeld 1997; Dupuis & Steventon 1999). Tadpoles of tailed frogs can often occur in localized, transient groups at high density. In some tropical streams average densities of grazing tadpoles can be  $\sim 60 \text{ m}^{-2}$  (Ranvestal *et al.* 2004). The densities of tadpoles in our streams were at the low end of our density gradient, consistent with the evidence of strong limitation of growth by density effects. The interactions of biotic and abiotic factors in food webs depend partly on the efficiency with which consumers exploit their prey (Power & Dietrich 2002) and tailed frog tadpoles appear

to be functionally important in determining periphyton biomass where they occur. The effects noted here for tailed frog tadpoles may only accrue when predators are rare and do not strongly affect their foraging. The strong density-dependent relation of growth rates demonstrates that food limitation of tailed frog tadpoles may provide one of the feedbacks that determine their recruitment rates.

Regulation of periphyton production differed between the two study streams. At Klondike Creek, grazing by *A. truei* tadpoles was a more important control of periphyton standing crop than light level, whereas the magnitude of these two effects was reversed at Dipper Creek. This difference between two nearby creeks illustrates that the relative importance of top-down vs. bottom-up forces regulating lotic periphyton may be context-dependent.

Enclosure size had a significant impact on periphyton measures and tadpole growth rates. The effect of enclosure size may be caused by a difference in physical factors, perhaps the greater contact of cobbles with the enclosure sides or differences in flow patterns (Robson & Barmuta 1998). Pearman (1993) found that growth rates of *Bufo* tadpoles maintained at identical densities in differently sized artificial ponds were inversely related to habitat size. The effects of enclosure size suggest that environmental factors, rather than changes in tadpole foraging behaviour, were responsible for enclosure size effects. The specific results of studies may be related to the particular architecture of enclosures, something rarely considered.

Tadpole growth rates differed significantly between the two nearby streams. Tadpole growth rate was higher at Klondike than at Dipper Creek, despite the lower levels of periphyton at Klondike Creek. Our explanation for this difference was the warmer water temperatures in Klondike Creek and higher turnover rates and depression of algal production by consumers. Although stream temperatures at both Klondike and Dipper Creeks during the experiment were within the tolerance range for tailed frog tadpole development (Brown 1975), de Vlaming & Bury 1970) reported temperature preferences for tadpoles in their second year of between 12 and 16 °C. Klondike Creek remained within the optimal temperature range for tadpole growth (mean temperature during experiment: 12.3 °C), whereas Dipper Creek was several degrees below the optimal range (mean temperature during the experiment: 9.5 °C).

The foraging activities of larger consumers can cause engineering effects, such as the clearing of fine sediments on the surface of stones (e.g. Zhang, Richardson & Negishi 2004). Tailed frog tadpoles can act as ecosystem engineers as their feeding activities had different effects on chlorophyll *a* (a more direct measure of algae) and the AFDM, the latter of which includes fine sediments accumulating on surfaces. These kinds of effects of large grazers have been noted previously, including for grazing tadpoles in streams (Flecker, Feifarek & Taylor 1999; Ranvestal *et al.* 2004).



INTRASPECIFIC DENSITY-DEPENDENT  
INTERACTIONS

Wilbur (1980) stated, 'a critical question for field ecologists studying anurans is how much the maximum growth rate set by the temperature regime is reduced by density-dependent food limitation'. This study demonstrated that *A. truei* tadpole growth rate was density dependent in both streams, and the mechanism was food limitation through resource shortage or intraspecific interference. However, given that the effects of density were evident even with one tadpole per enclosure (across the three enclosure sizes), interference is not a sufficient explanation. Higher growth rates at Klondike Creek, despite the fact that food resources were lower, suggests that temperature or some other differences between streams had a strong effect on growth rates. Note that the effects of density dependence were observed at even the lowest density treatments in this study, and that these densities were well within the range naturally encountered (Rosenfeld 1997; Dupuis & Steventon 1999).

If consumer growth rates mediated through algal productivity and consumer density are linked to survival or growth during the larval period, then these effects may carry over to the juvenile and adult stages of the life cycle, depending on other compensating processes. These fitness consequences include time to metamorphosis, size at metamorphosis, and/or survivorship. In another experimental study approximately 100 km west of our study streams, a gradient of reduced light resulted in lower growth rates and survival of tailed frog tadpoles (Kiffney *et al.* 2004). Because population size for amphibians is determined largely by the larval stage (e.g. Wilbur 1980, 1997), these consumer–resource dynamics are probably crucial in the life history of the tailed frog.

The very large differences in our results between streams were unexpected and fortuitous. This dependence on the environmental context suggests that there are further dimensions to understanding the dynamics of this particular consumer–resource system beyond the scope of this study. With only two streams we are not able to conclude anything about the actual cause of these differences. These results illustrate the difficulty of generalizing from experiments in single systems.

CONSERVATION CONCERNS AROUND FOREST  
HARVESTING

The tailed frog is considered vulnerable to changes in land use, particularly from forestry activities (Corn & Bury 1989; Welsh & Ollivier 1998). However, the associations with forest harvesting are complex, and the impacts apparently vary geographically (e.g. Richardson & Neill 1998). Our results suggest that light limitation of algal production in closed-canopy forest streams reduces the growth rates, and presumably densities of tadpoles in these streams (also see Kiffney *et al.* 2004). The tadpoles are considered to be extremely sensitive

to high temperatures (deVlaming & Bury 1970) that can result from clearing of riparian canopy. However, the temperatures recorded in our streams indicate that tadpoles spend most of the year at temperatures well below optimal growth temperatures, and temperatures never approached lethal levels. If temperature is a major reason for concern with this species, then this influence will depend on latitude and aspect (our streams flowed northward), a suggestion consistent with the observation of increased duration of tadpole stages with increasing latitude (Brown 1975; Bury & Adams 1999). Another impact of land use is the increase in fine inorganic sediments transported into streams, which can smother algae, further reducing growth rates and densities of tailed frog tadpoles (Welsh & Ollivier 1998). However, we saw no evidence of this in our streams, which perhaps was a consequence of having had over a decade to recover from the actual harvesting activities. It is important to note that as in all amphibians, the juveniles and adults are primarily terrestrial, and evidence from these life stages in the same study area indicates that forest harvesting may be detrimental to the terrestrial life stages (Matsuda & Richardson 2005). The population-level responses to forest disturbance of organisms with ontogenetic shifts cannot be discerned from a single life stage alone.

Complex interactions require multifactor experiments in order to address causal mechanisms (Holland 1986; Eberhardt & Thomas 1991; Wilbur 1997). Light, tadpole density, nutrients, enclosure size and several interactions between these factors exerted significant and complex effects on stream periphyton and consumer growth rates, many of which were strongly influenced by site. Abiotic factors (bottom-up effects) can be as important as grazing by herbivores (top-down effects) in controlling stream periphyton. *In situ* multifactorial experiments are key to understanding the underlying dynamics of complex systems.

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