THE INFLUENCE OF LIGHT AND NUTRIENTS ON INTERACTIONS BETWEEN A TADPOLE GRAZER AND PERIPHYTON IN TWO COASTAL STREAMS

by

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ABSTRACT

In small streams, shading from the riparian canopy can limit production by stream algae. Removal of the riparian canopy due to 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, I conducted an experiment to test for the effects of light, nutrients, and grazing by tadpoles of the tailed frog (Ascaphus truei) on periphyton standing crop. Light, nutrients, and tadpole density were manipulated in replicated, in situ, flow-through enclosures in two streams using a complete block, fully-factorial design to test for effects on periphyton biomass measured as ash-free dry weight (AFDW), chlorophyll a, and individual tadpole relative growth rates. The experiment was conducted over a six-week period from August to September 1997.

Light exerted a strong, positive effect on periphyton production resulting in a two to seven-fold increase in chlorophyll a abundance and a 30-40% increase in AFDW over the shaded treatment. The response of periphyton to light differed strikingly between the two study streams, with Dipper Creek responding more strongly than Klondike Creek. Nutrients had no significant effect on chlorophyll a, and a positive effect on periphyton biomass on cobbles but not on tiles. Tadpole grazing significantly decreased periphyton biomass across all densities at both streams.

Tadpoles showed an absolute rate of increase of 13-17% in body weight over the six-week period. Thirty percent of the variation in growth rates was attributable to differences between the two streams. Mean growth rate of tadpoles was 45% higher at Klondike Creek than at Dipper Creek. Light exerted a significant positive effect on tadpole growth resulting in a 14% increase over the shaded treatment. Tadpole density exerted a significantly negative effect on
tadpole growth rate and accounted for a greater percentage (38%) of the overall variation than did light. Nutrient addition did not significantly influence tadpole growth rate.

Periphyton production was found to be under simultaneous control by light and tadpole grazing. The strong, positive effect of light on periphyton production and tadpole relative growth rate indicates a tight trophic coupling between grazers and their algal food resource, and a potential positive direct effect of light on grazers. The decrease in individual tadpole growth rates with increasing tadpole density indicates that tadpoles are subject to intraspecific density-dependent interactions, probably resulting from food-limitation. This study demonstrates that several factors may act in unison to control periphyton production and grazer growth rate, and that the relative importance of these factors may vary significantly between nearby streams.
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INTRODUCTION

Food webs are a central idea in ecology and provide a graphical representation of how nutrients and energy are cycled through species interactions within ecosystems (Wilbur 1997). Interactions between different species have been explored theoretically through the development of models aimed at predicting which factors control the distribution and abundance of organisms. The "bottom-up" view of food webs states that primary production is the fundamental control of higher trophic level interactions (Hunter and Price 1992; Power 1992). The "top-down" view predicts that plants accumulate when herbivores are kept in check by predators (e.g. for odd-numbered food chains), and that even-numbered food chains result in grazer limitation of plants (Hairston et al. 1960; Fretwell 1977, 1987).

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 (Minshall 1978). Stream periphyton communities are subject to both bottom-up forces, such as light, nutrients, substrate, flow, season, and disturbance (Lamberti and Feminella 1996; Pringle and Triska 1996), and top-down control by herbivory (Sumner and McIntire 1982; Hart 1985; Hill and Knight 1988; Feminella and Resh 1990; Lamberti et al. 1995). Periphyton production has been shown to be limited by light (Steinman and McIntire 1987; Hill and Knight 1988; Steinman et al. 1989; Steinman 1992; Wellnitz et al. 1996a,b) and nutrients (Stockner and Shortreed 1978; Elwood et al. 1981; Triska et al. 1983; Perrin et al. 1987; Hershey et al. 1988; Hill and Knight 1988; Lohman et al. 1991). The importance of grazers in controlling stream periphyton production has also been demonstrated (Hart 1987; Hill and Knight 1987; Steinman et al. 1987; Power et al. 1988; Feminella et al. 1989; Lamberti and Resh 1983; Lamberti et al. 1995).
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 inter-specific density dependent interactions (Hart 1981, 1985, 1987; Hill and Knight 1987; Lamberti et al. 1987; Hershey et al. 1988). 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 (Lamberti and Resh 1983; McAuliffe; 1984a,b; Behmer and Hawkins 1986; Fuller et al. 1986; Vaughn 1986; Hawkins and Furnish 1987; Hill and Knight 1987; Richards and Minshall 1988; Feminella and Resh 1990; Hart and Robinson 1990; Dudgeon and Chan 1992).

Theoretical models of food webs are generally static and do not incorporate spatial and environmental variability (Hunter and Price 1992; Wilbur 1997). Therefore controlled experiments are required to test for the validity of their assumptions. For example, recent experiments have demonstrated simultaneous limitation of stream periphyton by both top-down and bottom-up forces (Hunter and Price 1992; Steinman 1992; Rosemond 1993; Rosemond et al. 1993; Hill et al. 1992, 1995; Wellnitz and Ward 1998). Contrary to previous studies that implicated either abiotic (bottom-up) or grazer (top-down) control of periphyton production, these studies provide evidence for dual control of periphyton by both top-down and bottom-up forces. In addition, the relative importance of top-down and bottom-up forces in food webs may be highly variable and fluctuate through both space and time (Hunter and Price 1992), for example in response to natural or anthropogenic disturbance events (Feminella et al. 1989) or seasonal or ontogenetic shifts in species morphology or behavior (Wilbur 1997).
Small streams provide an opportunity to test for the influence of abiotic factors resulting from forest disturbance on instream community processes. A growing appreciation for the complexity of interactions that occur between ecosystems has generated a number of studies which address the impacts of disturbance in adjacent terrestrial habitats to stream ecosystem processes (e.g., Hansmann and Phinney 1973; Gregory 1980; Murphy and Hall 1981; Hawkins et al. 1983, 1988; Gregory et al. 1987; Corn and Bury 1989; Bilby and Bisson 1992; Feminella et al. 1989; Lamberti et al. 1991). Primary production by algae in small, forested streams is generally limited by the presence of a closed riparian canopy which may limit light reaching the streambed to less than 5% of full sunlight (Stockner and Shortreed 1976; Hill et al. 1995). Primary production may be further limited in oligotrophic streams by inherently low concentrations of both nitrogen and phosphorus (Perrin et al. 1987). Removal of the riparian canopy due to forest harvest or windthrow can result in a shift in production from primarily allochthonous inputs to autochthonous production. How this shift in energy resources resulting from forest disturbance impacts lotic grazer-periphyton interactions in these systems is a complex issue that is not well understood.

Interactions of several factors may yield complex outcomes, therefore I designed a complete block, factorial experiment to assess how changes in light and nutrients resulting from riparian forest disturbance may influence grazer-periphyton interactions in small fishless streams. I selected an amphibian grazer, the tailed frog tadpole (*Ascaphus truei*), to study the link between lotic herbivory and primary production for two reasons. First, from an ecological perspective, they often occur at high densities in the predominantly fishless streams that they inhabit (Bury 1988), are morphologically specialized for feeding on epilithic periphyton (Altig and Brodie 1972), and may function as dominant herbivores in some streams (Lamberti et al. 1992; Rosenfeld 1997). Although few studies have considered the role of amphibian grazing in stream food webs
(but see Lamberti et al. 1992; Kupferberg 1997a,b), there is evidence that they play an important role in stream energetics (Burton and Likens 1975; Pough 1980; Murphy and Hall 1981; Hairston 1987; Bury and Corn 1988). Secondly, from a conservation perspective, the tailed frog is considered vulnerable to forest disturbance (Corn and Bury 1989). Several studies suggest that changes in abiotic factors resulting from forest disturbance may influence the occurrence, density, and biomass of tailed frog tadpoles by influencing the availability of the algal food supply (Gray 1992; Kelsey 1995; Richardson and Neill 1998). Brown (1990) suggested that food resources might be an important factor limiting *Ascaphus* larval growth rates and pointed to the need to study the interaction between tadpole grazing and the algal community in mountain stream habitats. The present study addresses this issue by assessing the effects of forest disturbance on periphyton biomass and tadpole growth response, which may be a correlate of fitness for individual tadpoles.

The major objectives of this study were to determine:

1. The relative importance of light, nutrients, and grazing on stream periphyton.
2. Whether tadpole growth is food-limited under different light and/or nutrient conditions.
3. Whether tadpole growth is influenced by density dependent interactions.
STUDY ORGANISM

Distribution and Status

The tailed frog (*Ascaphus truei* Stejneger, Ascaphidae) is endemic to the Pacific Northwest region of the United States and adjacent areas within British Columbia. It is found along the Pacific Coast from the B.C.-Alaska divide to northwestern California. An isolated set of populations occurs on the west slope of the Rocky Mountains in southeastern Washington, northern Idaho, northwestern Montana and the extreme southeast corner of B.C. (Leonard et al. 1993). Tailed frogs are found from sea level to over 1,360 m in elevation (Richardson and Neill 1995) and require clear, cold (≤18°C), permanent, headwater streams with coarse substrate for larval development (de Vlaming and Bury 1970; Claussen 1973; Green and Campbell 1984).

The tailed frog is a riparian-dependent amphibian currently classified as a sensitive species and blue-listed by the British Columbia Ministry of Environment, Lands and Parks (B.C. MELP 1996b). This designation is reserved for indigenous taxa considered vulnerable in British Columbia because of characteristics that make them particularly sensitive to human activities or natural events. The tailed frog is listed as a species of special concern in the states of California and Oregon (Jennings and Hayes 1994).

Phylogeny and Life History

The tailed frog is considered among the most unique and primitive frog species in the world (Duellman and Trueb 1994). Until several years ago the genus *Ascaphus* and the genus *Leiopelma* of New Zealand were considered to belong to the same family representing the most
primitive group of living anurans (Green and Cannatella 1993). This classification was based on symplesiomorphy and on historical biogeography which suggests that the leiopelmatids were widely distributed prior to the breakup of Pangaea during the early Jurassic Period (160-180 mya), and that living genera with primitive traits represent relicts of this ancient group of anurans (Duellman and Trueb 1994). However, there is insufficient evidence for this classification and the two groups are presently considered to belong to distinct families (Green and Cannatella 1993; Hay et al. 1995; Cogger and Zweifel 1998).

There are several features that make the tailed frog unique among the more than 3,800 species of anurans worldwide. *Ascaphus truei* is the only anuran species known to possess an intromittent organ, or posterior extension of the cloaca, in males. This “tail” permits copulation which distinguishes this species from all other anurans and is thought to be an adaptation to ensure fertilization in fast-flowing water and to allow the female to store sperm over winter (Duellman and Trueb 1994). Several skeletal features distinguish the tailed frog from other anurans: *Ascaphus truei* is the only anuran species with postpubic bones that lie within the tail, and free ribs. Like other stream-dwelling anurans, the tailed frog is voiceless and lacks tympana which limits auditory function (Duellman and Trueb 1994). The tongue of the tailed frog is attached to the back of the mouth rather than the front, therefore it cannot be flipped out to catch flying insects as in most frog and toad species (Green and Campbell 1984). The ability of the tailed frog to orient itself with respect to shoreline is thought to be an ancient mechanism that dates back to very early stages in amphibian evolution (Stebbins and Cohen 1995).

A reproductive strategy is defined as the combination of physiological, morphological, and behavioral attributes that act in concert to produce the optimal number of offspring under certain environmental conditions (Duellman and Trueb 1994). Among vertebrates, anurans exhibit the greatest diversity of reproductive strategies which reflect over 200 million years of evolution in
diverse habitats on six different continents. The reproductive strategy of *A. truei* reflects an adaptation to temperate climatic conditions with cold weather and short growing seasons. Adaptations to these environmental conditions include a relatively small clutch size with large eggs, low frequency of oviposition, long developmental period of larvae, late age at first reproduction, internal fertilization, lack of parental care, and long reproductive life span.

The reproductive mode of *Ascaphus* is summarized as follows: Adults mate in the stream (generally in slower moving water) or adjacent bank in the late summer to early fall and are the only anuran known to engage in copulation (Stebbins and Cohen 1995). Females store the sperm over the winter and fertilize the eggs internally (Metter 1964b; Brown 1989). Females may lay eggs every year (as observed in coastal areas) or every other year in inland areas (Metter 1964a). A small number (37-85) of large eggs (ca. 4 mm) are deposited in strings under rocks in fast-flowing streams in June to July (Noble and Putnam 1931; Nussbaum et al. 1983). *Ascaphus* eggs are the largest eggs of any North American frog species and exhibit the slowest embryonic development (Brown 1975, 1989). *Ascaphus* eggs also have the narrowest range of thermal tolerance (5-18°C) and lowest upper limiting temperature (18.5°C) of any frog species (Brown 1989). Hatching of eggs requires approximately 20-30 days (Noble and Putnam 1931). Hatchlings (ca. 13-15 mm) remain in the 'egg nest' below large boulders where they slowly utilize the stored yolk to grow into moderately large tadpoles before emerging. This may represent an evolutionary adaptation that helps them to avoid predation and survive in a high flow environment (Brown 1989). Larvae require 1-4 years to develop in the stream prior to metamorphosis (Dupuis and Friele 1996; Wahbe 1996). Age at first reproduction may be as late as 7-8 years (Daugherty and Sheldon 1982). Adult male frogs reach total lengths of 30 to 40 mm and possess a fleshy "tail" (Green and Campbell 1984). Females may reach 50 mm in length (Green and Campbell 1984). Maximum longevity is at least 14 years (Daugherty and Sheldon 1982).
Ecology and Behavior

Tailed frog tadpoles are primary consumers that feed by grazing periphyton (Bury and Corn 1988). They possess a large, suctorial mouth, which allows them to cling to rocks in turbulent flow conditions and remove periphyton by scraping along the rock surface (Corkran and Thoms 1996). The primary source of food for tadpoles is diatoms (Metter 1964a). Tadpoles feed exclusively by grazing and have been observed under laboratory conditions to be unable to filter particles from the water (Altig and Brodie 1972). Contrary to previous studies indicating that tadpoles feed nocturnally and hide below rocks during the day, i.e., negatively phototactic (Altig and Brodie 1972; Leonard et al. 1993), I observed tadpoles grazing on the surface during the day at both sites and failed to observe any tadpoles grazing at night (personal observation).

Although no data are available on seasonal growth of tadpoles, several studies suggest that tailed frog tadpoles grow primarily during the warmer months (May to October) when periphyton productivity is high, and occupy winter hibernacula where they slow or cease growth during the cold winter months (Brown 1975; Gray 1992).

Potential predators of tailed frogs include the Pacific Giant Salamander (*Dicamptodon tenebrosus*), sculpins (*Cottus* spp.), cutthroat trout (*Oncorhynchus clarki*), brook trout (*Salvelinus fontinalis*), dippers (*Cinclus mexicanus*), red-legged frog (*Rana aurora*), garter snakes (*Thamnophis* spp.), and raccoons (*Procyon lotor*) (Metter 1964a; Feminella and Hawkins 1994). Predation of *Ascaphus* has not been studied, however Feminella and Hawkins (1994) found that tadpoles altered their feeding behavior in the presence of non-visual cues from predators including giant salamanders, cutthroat trout, and brook trout, but were apparently unable to detect cues from sculpins.
Tadpole Densities

The distribution of tailed frog tadpoles is highly variable at the reach scale, stream scale, and landscape scale (Richardson and Neill 1995). For example, Dupuis and Friele (1996) found tadpole densities in clear-cuts in southwestern British Columbia ranging from 0.9 – 65.5 per square meter and Bury (1988) found 109 frog tadpoles in a single 10-m stream reach in Washington. Three previous studies have experimentally manipulated *Ascaphus* tadpoles to study community interactions. Lamberti et al. (1992) conducted experimental manipulations of tadpoles at densities ranging from 0 – 96 m$^2$ at streams near Mt. St. Helens where Hawkins et al. (1988) estimated densities to range from 0.6 – 4.4 m$^2$. Feminella and Hawkins (1994) reported maximum mean density of tadpoles in their study area to be approximately 15 m$^2$, but used densities of 45 m$^2$ in experimental enclosures to study the effects of various predators. Rosenfeld (1997) used a density of 21 m$^2$ in experimental troughs, which he reported to be within the upper range of observed densities.
STUDY SITES

The study was conducted in two high-gradient, permanently flowing, first-order creeks in the Chilliwack River drainage, approximately 115 km east of Vancouver in southwestern British Columbia, Canada. The creeks were chosen based on the presence of *Ascaphus* larvae, accessibility, and physical characteristics such as stand age, aspect, elevation, and stream width (see Table 1). The two creeks selected are approximately six kilometers apart (straight-line distance) and were found to be similar in terms of many physical attributes. No other creeks in the vicinity were deemed suitable for comparison.

Both Klondike Creek and Dipper Creek are classified as S5 streams according to the B.C. Forest Practices Code. S5 streams are defined as non-fish bearing streams with an average channel width of >3m that do not occur within a community watershed (B.C. MoF/MELP 1995). Dominant tree species at both sites include Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), with red alder (*Alnus rubra*) occurring within the riparian zone. Dominant understorey species include thimbleberry (*Rubus parviflorus*), salmonberry (*Rubus spectabilis*), devil’s club (*Oplopanax horridus*), sword fern (*Polystichum munitum*), and lady fern (*Athyrium filix-femina*). Major land use practices in the area include timber harvesting (primarily clear-cut logging), with demolition training activities for the Canadian Forces Base (Chilliwack) occurring within the vicinity of Dipper Creek.

Both Klondike and Dipper Creeks are located south of the Chilliwack River in southwestern British Columbia. Klondike Creek runs through 30-40 year old second growth forest and discharges directly into the Chilliwack River. Klondike Creek occurs within the Coastal Western Hemlock biogeoclimatic zone montane very wet maritime subzone (CWHvm2) (Green and Klinka 1994). Mean annual precipitation ranges from 2760-2850 mm. Stream
substrate consists of boulders, cobble, and gravel with some areas of exposed bedrock. Dipper Creek originates from a small alpine lake, runs through 30-year old second growth forest on Department of National Defense Land, and discharges into Slesse Creek. Dipper Creek occurs within the Coastal Western Hemlock dry maritime zone (CWHdm) (Green and Klinka 1994). Mean annual precipitation ranges from 1367-2412 mm. The dominant stream substrate at Dipper Creek consists of cobble and gravel with some large boulders.
Table 1. Summary of physical and environmental characteristics for Klondike and Dipper Creeks. Ranges are provided for variables that changed during the duration of the experiment (August – September 1997).

<table>
<thead>
<tr>
<th></th>
<th>Klondike Creek</th>
<th>Dipper Creek</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude (N)</td>
<td>49° 5' 05”</td>
<td>49° 3' 91”</td>
</tr>
<tr>
<td>Longitude (W)</td>
<td>121° 3' 31”</td>
<td>121° 67' 08”</td>
</tr>
<tr>
<td>Elevation (m a.s.l.)</td>
<td>785</td>
<td>385</td>
</tr>
<tr>
<td>Aspect</td>
<td>NE</td>
<td>NE</td>
</tr>
<tr>
<td>Order</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Stream Class</td>
<td>S5</td>
<td>S5</td>
</tr>
<tr>
<td>Drainage basin area (km²)</td>
<td>~1.1</td>
<td>~1.3</td>
</tr>
<tr>
<td>Channel slope (%)</td>
<td>45</td>
<td>32</td>
</tr>
<tr>
<td>Mean wetted width (m)</td>
<td>0.9 - 1.2</td>
<td>1.4 - 1.7</td>
</tr>
<tr>
<td>Mean bankful width (m)</td>
<td>6.9</td>
<td>5.6</td>
</tr>
<tr>
<td>Mean depth (m)</td>
<td>0.25</td>
<td>0.4</td>
</tr>
<tr>
<td>Velocity (m·s⁻¹)</td>
<td>0.05 - 0.65</td>
<td>0.15 - 0.7</td>
</tr>
<tr>
<td>Discharge (m³·s⁻¹)</td>
<td>0.15</td>
<td>0.45</td>
</tr>
<tr>
<td>Temperature (°C)</td>
<td>8.1 - 14.9</td>
<td>7.8 - 11.2</td>
</tr>
<tr>
<td>pH</td>
<td>6.9</td>
<td>7.1</td>
</tr>
<tr>
<td>Conductivity (μS·s⁻¹)</td>
<td>93</td>
<td>152</td>
</tr>
<tr>
<td>Dissolved oxygen (mg·l⁻¹)</td>
<td>11.5 - 11.75</td>
<td>11.6 - 11.85</td>
</tr>
<tr>
<td>NO₃ + NO₂ - N (μg·l⁻¹)</td>
<td>not detected</td>
<td>1.24 - 4.34</td>
</tr>
<tr>
<td>P0₄ - P (μg·l⁻¹)</td>
<td>1.0 - 1.9</td>
<td>1.2 - 2.85</td>
</tr>
</tbody>
</table>

¹Stream class determined according to the Forest Practices Code of British Columbia Riparian Management Area Guidebook (BC MELP/MoF 1995).
MATERIALS AND METHODS

Experimental Design

From August to September 1997, I examined the influence of light, nutrient levels, tadpole density, and selected interactive effects on periphyton levels in experimental stream enclosures in two creeks. Two light levels (shaded and unshaded), two nutrient levels (ambient and high), and four tadpole densities (0, 29, 57, 86 tadpoles m\(^{-2}\)) were manipulated in experimental stream enclosures in each stream in a two x two x two x four complete block, fully factorial design (Figure 1). These densities were determined by the random assignment of zero, one, two, or three tadpoles to experimental enclosures within each array. Each array consisted of eight experimental enclosures, each measuring 0.035 m\(^2\). There were four replicates of each treatment combination in each stream. Enclosures were constructed using PVC and 1-mm mesh screen to prevent emigration/immigration of tadpoles and other stream grazers (enclosure design was modified from Lamberti and Feminella 1996). Additional arrays with enclosures measuring two times (0.07 m\(^2\) = medium) and three times (0.105 m\(^2\) = large) the size of small enclosures were used to test for the effect of enclosure size, and to allow for two additional density treatments (10 and 14 tadpoles \(\text{m}^{-2}\) respectively) which more closely reflect the expected range of tadpole densities (see Table 7). These densities were determined by random assignment of one or two tadpoles to medium enclosures, and one or three tadpoles to large enclosures. A total of eight arrays of small enclosures, four arrays of medium enclosures, and four arrays of large enclosures were used at each stream (Figure 1). In order to isolate the effect of enclosure size, the number of cobbles and tiles per grazer was kept constant: small enclosures had one cobble and one tile; medium enclosures had two cobbles and two tiles; and large enclosures had three cobbles and three tiles.
**Figure 1.** Schematic of complete block, fully factorial design to test for effects of light, nutrient levels, and tadpole density on periphyton production. Experimental stream enclosures were used to manipulate tadpole density. Enclosures were placed in each stream section (2 shaded; 2 unshaded) and nutrients were added to the lower two sections. The experiment was conducted simultaneously in two streams in southwestern British Columbia in August-September 1997.
Field Sampling Methods

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 × 10 cm) and stream cobbles were placed in each enclosure and conditioned for five weeks prior to introduction of tadpoles. A total of 152 *A. truei* tadpoles per stream were collected from within a 200 m reach at each stream using the hand collection method (Bury and Corn 1991). During tadpole collection, an effort was made to collect tadpoles representing a single cohort at each stream to avoid potential differences in growth rates between cohorts. Initial observations in July and August indicated that there were two cohorts present at each stream. Tadpoles representing what were assumed to be 1+ year olds were selected for use in this study for two reasons: (1) they were the most abundant, and (2) they were not expected to begin metamorphosis during the experiment. Larger tadpoles, which I assumed to be 2+ year olds, were much less frequently encountered during collection and had developing hind limbs, often jointed. During September, several of these tadpoles were observed upstream of the study area at Dipper Creek undergoing metamorphosis and had developed front limbs and were reabsorbing their tails. During August, very small tadpoles (ca. 10-12 mm) were observed. I suspect that these were much less abundant because they were only beginning to emerge during the collection period, and because they were utilizing habitat within the stream not easily accessible by hand-collection methods (i.e., near nests below large boulders).

Tadpoles were individually identified based on color and tail spot pattern, which allowed for clear distinction between individual tadpoles. In a previous study, *Ascaphus* larval color and presence of the tail spot did not change when larvae were kept in a lab for several months, indicating that these characters do not change with age (Metter 1967). Information on larval
color and tail spot for all larvae used in this study is provided in Appendix 1. Distinguishing individuals in this way avoided the use of marking techniques that may either alter the weight of the tadpole (e.g., tail clipping), or exert stress on the animal that could result in a change in its physiology or behavior (e.g., injection of colored elastomer). Individual tadpole total lengths and weights were recorded and tadpoles randomly assigned to enclosures. Wet weight was measured to the nearest 0.001g by gently blotting tadpoles to remove excess water and using an OHaus digital balance. Total length was measured to the nearest millimetre by placing tadpoles on a clear metric ruler.

Light levels were manipulated using 90% industrial shade cloth (American Horticultural Supplies) to simulate closed canopy conditions. Surface irradiance was measured on August 10, 1997 using a PAR-quantum light sensor (LI-COR, Nebraska). Irradiance was measured just below the surface of the stream at several locations in both the open and shaded sections. Measurements were repeated several times and values converted to quantum units (\(\mu\text{E}\cdot\text{m}^2\cdot\text{s}^{-1}\)).

Nutrient levels were manipulated using slow-release osmo-coated nutrient pellets \((\text{MgNH}_4\text{P}_2\text{O}_7\cdot\text{H}_2\text{O})\) deposited 10 m upstream of half of the enclosures. The remaining half of the enclosures in the upstream portion served as ambient nutrient controls. Previous research in southwestern British Columbia streams has shown that phosphorus \((\text{PO}_4\text{-P})\) concentrations of 0.3-0.6 \(\mu\text{g}/\text{L}\) saturate specific growth rates of unicellular periphytic diatoms, and that concentrations greater than 10 \(\mu\text{g}/\text{L}\) may cause unacceptable accumulations of periphytic biomass (Bothwell 1988, 1989). For this study, I used the target concentration of 3 \(\mu\text{g}/\text{L}\) of phosphorus recommended by Mouldey Ewing and Ashley (1998). The amount of fertilizer added in the form of nutrient pellets was determined based on methods developed by Mouldey Ewing and Ashley (1998) (see Appendix II for calculations).
During the six-week experiment, the outside of each enclosure was cleaned of debris every second day to prevent mesh from becoming blocked and impeding flow, and enclosures were checked to ensure tadpoles had not escaped. Tiles and cobbles were gently lifted and replaced in alternate positions every second day to avoid position effects. Grazing invertebrates (primarily *Baetis* sp.) were occasionally observed colonizing tiles and were removed by gently rinsing or with forceps. At the end of the experiment, tiles and cobbles were removed and individually placed in ziploc bags, stored on ice and transported back to the laboratory for analysis of periphyton biomass (AFDW) and chlorophyll *a* abundance. Triplicate water samples were taken from each stream prior to the experiment and after completion of the experiment both above and below the point where nutrients were added. Stream temperature was monitored throughout the duration of the experiment using an Optic StowAway™ temperature sensor. Ninety-five percent of tadpoles were recovered at the end of the 42-day experiment, weighed and measured, and released into the stream. The five percent that were not recovered either died during the experiment or escaped through small holes in the mesh.

**Periphyton Analysis**

Periphyton was removed from cobbles and tiles by scrubbing the entire surface with a toothbrush and rinsing with distilled water. The slurry was shaken thoroughly and divided into two subsamples of 50 mL each. To determine periphyton biomass, 50 mL 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 ash-free dry weight by loss on ignition. For chlorophyll *a* analysis, 50 mL was filtered through a Whatman GF/F filter. The pigments were extracted in 90% acetone for 24
hours. Chlorophyll $a$ was measured by absorbance on a Turner fluorometer (model 10-005 R) using methods outlined in Strickland and Parsons (1972). Surface area for each cobble was determined by carefully wrapping each cobble with aluminum foil and cutting the excess foil away. The foil was then removed from the cobble and weighed to within 0.0001 g using a Sartorius digital scale. Surface area was calculated using the relationship of 0.0064 g foil/cm$^2$. All tiles measured 50 cm$^2$.

**Nutrient Analysis**

Water samples were placed directly on ice and frozen for nutrient analysis. Nutrient concentrations were measured using a Technicon AutoAnalyzer II. Nitrogen ($\text{NO}_3 + \text{NO}_2 - \text{N}$) concentrations were determined to the closest 0.001 mg/L following methods outlined in Wood et al. (1967). Phosphorous ($\text{P}_4 - \text{P}$) concentrations were determined to the closest 0.001 mg/L following methods outlined in Hager et al. (1968).

**Data Analysis**

To examine the main and interactive effects of light, nutrients, grazer density, enclosure size, and stream on periphyton biomass, chlorophyll $a$, and tadpole growth, multi-way analyses of variance (ANOVA) were used. Prior to statistical analysis, growth data were tested for normality using the Shapiro-Wilk statistic, which is considered a highly conservative test (Zar 1984). This analysis was conducted using the PROC UNIVARIATE function in SAS (SAS Institute 1996). ANOVA was used to determine whether the two streams differed in terms of periphyton
production and tadpole condition (weight/length ratio). ANOVA was also used to determine whether use of different sizes of artificial stream enclosures significantly influenced periphyton biomass, chlorophyll \( a \) abundance, and/or tadpole relative growth rate and to compare periphyton biomass and chlorophyll \( a \) abundance on artificial substrates (tiles) compared with natural substrates (cobbles). Tadpole relative growth rate (RGR) was calculated as:

\[
RGR \ (g/g/d) = \frac{[(weight_{\text{initial}} - weight_{\text{final}})/weight_{\text{initial}}]}{\# \text{ days of the experiment}}.
\]

A two-way analysis of variance (ANOVA) was used to test for the main and interactive effects of tadpole grazing and stream on periphytic dry weight and ash weight. Analysis of covariance (ANCOVA), using density as the covariate, was used to test for differences between cobbles and tiles. ANCOVA, using chlorophyll \( a \) as a covariate, was used to test for the effect of enclosure size on tadpole relative growth rate in order to determine whether differences in growth were attributable to changes in food resources. ANOVAs and ANCOVAs were conducted using the PROC GLM function in SAS (Statistical Analysis System Release 6.1.2, SAS Institute 1996). Type III sums of squares were used in all analyses. Least Squared Means and standard errors generated from one-way ANOVA’s were plotted to depict tadpole growth response to density treatments.

**RESULTS**

**Stream Physical Data and Water Chemistry**

Addition of nutrient pellets resulted in a six-fold increase in nitrogen \((N_0_3 + N_0_4 - N)\) concentration and a two-fold increase in phosphorus \((P_0_4 - P)\) concentration in Dipper Creek.
(Figure 2). Phosphorus concentration (PO₄ – P) at Dipper Creek following fertilization was just above the target concentration of 3 μg/L. Nitrogen (NO₃ + NO₄ – N) concentration at Klondike Creek was below detection limits (i.e., <0.001mg/L) prior to addition of nutrient pellets but increased to 4 μg/L after fertilization. Phosphorus (PO₄ – P) concentration at Klondike Creek remained below the target of 3 μg/L following fertilization (Figure 2). This may have been due to the fact that the pellets had not completely dissolved by the end of the experiment.

Shade cloth reduced light levels by 85-90%. Mean photosynthetically active radiation (PAR) for Dipper Creek was 217 μE·m⁻²·s⁻¹ in the open sections (range=195-240 μE·m⁻²·s⁻¹, n=3) and 31 μE·m⁻²·s⁻¹ in the shaded sections (range=25-36 μE·m⁻²·s⁻¹, n=3). Mean light level for Klondike Creek was 313 μE·m⁻²·s⁻¹ in the open sections (range=280-360 μE·m⁻²·s⁻¹, n=3) and 36 μE·m⁻²·s⁻¹ in the shaded sections (range=31-43 μE·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). Water temperatures at Dipper Creek during the experiment ranged from 7.8 to 11.2°C (mean = 9.5°C). Temperature profiles for both creeks for the duration of the six-week experiment are shown in Figure 3.
Figure 2. Nutrient concentrations at Klondike and Dipper Creeks before and after (+NP) fertilizer addition.

Figure 3. Streamwater temperature profiles for Klondike (——) and Dipper (…) Creeks during the experimental period (August – September 1997).
Tadpole Data

Size-frequency distributions for tadpoles at each creek indicate that tadpoles used in this experiment likely represent a single cohort of one-year olds (see Appendix III). Tadpoles at Klondike and Dipper Creeks were very similar in terms of mean total length (Table 2). The mean lengths of tadpoles collected at both creeks are within the range found for one-year olds by Kelsey (1995) in western Washington and by Metter (1964) in northern Idaho and eastern Washington. Kelsey (1995) documented tadpole total lengths at the end of the first year of development ranging from 29 – 57 mm (mean = 38.4 mm). Metter (1964) documented tadpole total lengths at the end of the first year ranging from 24 – 41 mm (mean = 32 mm). Mean total lengths from this study are intermediate between total length for one- and two-year old tadpoles from northwestern Washington determined by Brown (1990).

Descriptive statistics for tadpoles are provided in Table 2. Analysis of covariance (ANCOVA) showed that stream \( (p<0.0001, F_{1,300}=160.2) \), tadpole length \( (p<0.0001, F_{1,300}=803.99) \), and the interaction between stream and tadpole length \( (p<0.0001, F_{1,300}=30.77) \), all contributed significantly to tadpole weight. Allometric relationships between length and weight for tadpoles at both creeks provide a quantitative assessment of natural tadpole condition in the creeks prior to conducting the experiment (Figure 4). Slopes of the allometric regressions differed by a factor of 1.5 between the two creeks (Dipper = 0.028; Klondike = 0.019), indicating that tadpole condition (e.g., weight/length ratio) differed significantly between the two creeks with tadpoles at Dipper Creek weighing on average 50% more for a given length than tadpoles at Klondike Creek.
Table 2. Descriptive statistics for tadpoles at Klondike and Dipper Creeks (1997).

<table>
<thead>
<tr>
<th></th>
<th>Klondike Creek</th>
<th>Dipper Creek</th>
</tr>
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<tbody>
<tr>
<td>length (mm)</td>
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<td>33.64</td>
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<tr>
<td>weight (g)</td>
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<td>0.35</td>
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<td>0.18 - 0.62</td>
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<td>Number (n)</td>
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</table>

Figure 4. Length-weight relations for tailed frog tadpoles from (A) Klondike Creek (n=152) and (B) Dipper Creek (n=152).
Light and Nutrient Effects on Periphyton

Analysis of variance (ANOVA) showed that light exerted a significantly positive effect on chlorophyll \(a\) on both cobbles \(p<0.0001\) and tiles \(p<0.0001\) and on periphyton biomass on both cobbles \(p<0.0302\) and tiles \(p<0.0004\) (Table 3). Light accounted for 44% of the observed variation in chlorophyll \(a\) abundance on cobbles and 37% of the variation in chlorophyll \(a\) abundance on tiles. However, light accounted for only 1% of the observed variation in periphyton biomass on cobbles and 5% of the observed variation in periphyton biomass on tiles. Chlorophyll \(a\) abundance was between two to seven 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*stream interaction, \(p<0.0001\), Table 3, Figure 5). Periphyton biomass exhibited a smaller response to light treatments than did chlorophyll \(a\) (Table 3, Figure 6). At Dipper Creek, periphyton biomass increased 30-40% in the presence of light; periphyton biomass at Klondike Creek exhibited little response to light treatments.

Nutrients had no significant effect on chlorophyll \(a\) on cobbles \(p=0.802\) and on periphyton biomass on tiles \(p=0.433\). However, nutrients had a small negative effect on chlorophyll \(a\) on tiles \(p=0.025\) and a significant positive effect on periphyton biomass on cobbles \(p<0.0001\). Overall, nutrients accounted for less than 1% of the variation in chlorophyll \(a\) abundance on cobbles and 3% of the variation in chlorophyll \(a\) abundance on tiles. Nutrient addition resulted in an unexpected decline in chlorophyll \(a\) abundance on tiles. In contrast, nutrients had a strong positive influence on periphyton biomass on cobbles, accounting for 28% of the explained variation and resulting in a 25-50% increase in AFDW. Nutrients accounted for 28% of the variation in periphyton biomass on cobbles but less than 1% of periphyton biomass on tiles.
Light and nutrients interacted significantly to influence both chlorophyll $a$ abundance and periphyton biomass on cobbles. There was no significant interaction between light and nutrients for chlorophyll $a$ abundance or periphyton biomass on tiles. The difference between the two streams and light interacted significantly to influence both chlorophyll $a$ abundance and periphyton biomass on tiles, and chlorophyll $a$ abundance on cobbles. However, there was no significant interaction between stream and light for periphyton biomass on cobbles. Stream and nutrients interacted significantly to influence chlorophyll $a$ abundance on tiles but not on cobbles. The interaction between stream and nutrients did not significantly influence periphyton biomass on cobbles or tiles.
Table 3. Main and interaction effects table: F-values for ANOVAs showing main effects: stream, light, nutrients, tadpole density, enclosure size; and interaction effects on periphytic chlorophyll a and ash-free dry weight (AFDW). Degrees of freedom (df) for each term are shown in brackets. Error degrees of freedom (df) and total number of observations (n) are provided.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>r-square</th>
<th>Light</th>
<th>Nutrients</th>
<th>Density</th>
<th>Stream</th>
<th>Enclosure</th>
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<td>113.48 (1)***</td>
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<td>14.03 (5)***</td>
<td>26.09 (1)***</td>
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<td>4.32 (5)**</td>
<td>44.97 (1)***</td>
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<td>cobble AFDW (mg/cm²)</td>
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<td>151.75 (1)***</td>
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<td>2.16 (1)</td>
<td>17.48 (2)***</td>
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<td>13.13 (1)**</td>
<td>0.62 (1)</td>
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<td>99.23 (1)***</td>
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</table>

*P<0.05; **P<0.01 ***P<0.0001

<table>
<thead>
<tr>
<th>Parameter</th>
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<th>Stream × Nutrients</th>
<th>Light × Nutrients</th>
<th>Error df</th>
<th>Total n</th>
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<tbody>
<tr>
<td>cobble chl a (μg/cm²)</td>
<td>32.23 (1)***</td>
<td>2.22 (1)</td>
<td>10.3 (1)**</td>
<td>176</td>
<td>189</td>
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<td>tile chl a (μg/cm²)</td>
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<td>9.76 (1)**</td>
<td>0.26 (1)</td>
<td>178</td>
<td>191</td>
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<tr>
<td>cobble AFDW (mg/cm²)</td>
<td>2.16 (1)</td>
<td>2.16 (1)</td>
<td>10.03 (1)**</td>
<td>178</td>
<td>191</td>
</tr>
<tr>
<td>tile AFDW (mg/cm²)</td>
<td>10.67 (1)**</td>
<td>0.02 (1)</td>
<td>0.36 (1)</td>
<td>177</td>
<td>190</td>
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</table>

*P<0.05; **P<0.01 ***P<0.0001
Figure 5. Effect of light and nutrients on chlorophyll a on cobbles and tiles. Ambient treatment represents upstream control section; +NP represents downstream fertilized section. Bars represent means ± 1 S.E. for all cobbles (n=64/stream) and tiles (n=64/stream) from small enclosures.
Figure 6. Effect of light and nutrients on periphytic ash-free dry weight (AFDW) on cobbles and tiles. Ambient treatment represents upstream control section; +NP represents downstream fertilized section. Bars represent means ± 1 S.E. for all cobbles (n=64/stream) and tiles (n=64/stream) from small enclosures.
Grazer Effects on Periphyton

A two-way analysis of variance using data from small enclosures was used to test for the effects of tadpole density on chlorophyll $a$ and periphyton biomass (AFDW) and to test for potential differences between the two streams. Small enclosures only were used because they were found to be significantly different from medium and large enclosures in both periphyton and grazer growth (see Figures 10 and 11), and because they had twice as many replicates and density treatments per enclosure than medium or large enclosures (see Figure 1). Results of the ANOVA show that density had a significant negative effect on chlorophyll $a$ on both cobbles ($p<0.0001$, $F_{1,121} = 11.14$) and tiles ($p=0.0241$, $F_{1,121} = 3.25$) and on periphyton biomass on both cobbles ($p<0.0001$, $F_{1,121} = 25.31$) and tiles ($p<0.0001$, $F_{1,121} = 42.6$). 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 (Figure 7). This shows that the introduction of a single tadpole resulted in a 50% decline in chlorophyll $a$ abundance relative to the no tadpole control for cobbles.

Differences between the two study streams significantly influenced chlorophyll $a$ on tiles ($p<0.0001$, $F_{1,121} = 24.22$) and periphyton biomass on cobbles ($p<0.0001$, $F_{1,121} = 42.6$), but had no significant effect on tile periphyton biomass ($p=0.201$, $F_{1,121} = 1.65$) or cobble chlorophyll $a$ ($p=0.0796$, $F_{1,121} = 3.13$). There were no significant interaction effects between stream and density for chlorophyll $a$ or periphyton biomass on either rocks or tiles. Figure 7 shows the relation between tadpole density and periphytic chlorophyll $a$ and periphyton biomass on cobbles and tiles for all densities at Klondike and Dipper Creeks. At both creeks tadpole density was inversely related to both chlorophyll $a$ and periphyton biomass. At Dipper Creek, a significant decline in both chlorophyll $a$ abundance and periphyton biomass was detected at tadpole densities
greater than 29 tadpoles·m$^{-2}$. At Klondike Creek, a significant decline in chlorophyll $a$ abundance was noted even for the lowest density treatments (10 and 14 tadpoles·m$^{-2}$).

The ANCOVA to determine whether tadpole grazing resulted in significant changes in the dry weight (inorganic + organic) and/or the ashed fraction (inorganic) of the periphyton found significant differences between cobbles and tiles. Grazing had no significant effect on either dried (p=0.098, $F_{1,284}=2.75$) or ashed (p=0.314, $F_{1,284}=1.02$) fractions of the periphyton on tiles. However, grazing did exert a significant effect on the dried (p=0.0357, $F_{1,283}=4.45$) and the ashed (p=0.0143, $F_{1,283}=6.07$) fractions of the periphyton on cobbles. Periphyton dry weight (8.10 ± S.E. 0.09) and ashed weight (7.85 ± S.E. 0.08) for cobbles was 50-60% greater than periphyton dry weight (5.25 ± S.E. 0.03) and ashed weight (5.12 ± S.E. 0.02) on tiles. No significant interaction effect between stream and tadpole density was detected (p>0.05).
Figure 7. Relation between tadpole density (#tadpoles·m⁻²) and chlorophyll a on (A) cobbles and (B) tiles and ash-free dry weight (AFDW) on (C) cobbles and (D) tiles at Klondike (●) and Dipper (○) Creeks. Dots represent means ± 1 S.E. for all cobbles and tiles.
Top-down vs. Bottom-up Effects

To test for the relative effects of abiotic limitation (bottom-up) and grazer control (top-down) on stream algae, I compared the effects of light elimination (using artificial shade cloth) vs. the lowest tadpole density (29 tadpoles/m²: 1 tadpole only) on mean periphyton biomass (AFDW) and chlorophyll a values. Light was used to test for bottom-up limitation as it was found to be more important than nutrients in limiting algal productivity in these two streams (Figure 5). Only small enclosures were used in order to eliminate enclosure effects, since enclosure size was found to have a significant effect on both chlorophyll a (Figure 10) and tadpole growth rate (Figure 11).

At Klondike Creek, shade resulted in a 14% decrease in chlorophyll a on cobbles, whereas addition of 1 tadpole resulted in a 25% decrease in chlorophyll a on cobbles. On tiles, shading resulted in a 36% decrease in chlorophyll a, whereas addition of 1 tadpole resulted in a 43% decrease. Shade resulted in a 5% decrease in cobble AFDW, whereas addition of 1 tadpole resulted in a 29% decrease. Shade resulted in a 4% decrease in tile AFDW compared with a 27% decrease with addition of 1 tadpole.

At Dipper Creek, shading resulted in a 73% decrease in chlorophyll a on cobbles, whereas addition of 1 tadpole resulted in a 49% decrease. On tiles, shading resulted in an 85% decrease in chlorophyll a, whereas addition of 1 tadpole resulted in a 12% decrease. Both shade and addition of 1 tadpole each resulted in a 45% decrease in cobble AFDW. Shade resulted in an 18% decrease in tile AFDW compared with a 27% decrease with addition of 1 tadpole.

These results show a distinct difference between creeks in the relative importance of top-down vs. bottom-up control of periphyton. At Klondike Creek, all measures of periphyton were influenced more strongly by top-down control by grazing. At Dipper Creek, all measures (except for cobble AFDW) were influenced more strongly by bottom-up limitation by light. These results
also indicate differences in grazing effects on natural vs. artificial substrates between creeks. The effects of grazing on cobbles and tiles were similar at Klondike Creek, however grazing exerted a stronger influence on cobbles than on tiles at Dipper Creek.

Grazer Growth Response

In order to reject the null hypothesis of normality, I examined the probability associated with the test statistic (Pr<W). Since Pr<W for growth data (n=291; Pr<W = 0.1299) was found to be greater than the level chosen (0.05), I failed to reject the null hypothesis and concluded that the growth data were normally distributed (SAS Institute 1996). Table 4 provides the results of the ANOVA used to analyze the effect of stream, light, nutrients, enclosure size, and tadpole density on tadpole relative growth rate. The main effects and selected interactions explained 70% of the observed variation in tadpole relative growth rate (Table 4). Tadpole density, differences between the two streams, light, and enclosure size accounted for 93% of the explained variation in tadpole relative growth rate. Tadpole relative growth rate was found to significantly decrease with increasing tadpole density (p<0.0001) which accounted for 38% of the variation in tadpole relative growth rate. Differences between the two study streams accounted for 30% of the explained variation in tadpole relative growth rate (p<0.0001). Light positively influenced tadpole relative growth rate (p<0.0001) and accounted for 14% of the explained variation. Enclosure size accounted for an additional 11% of the explained variation (p<0.0001). Nutrients accounted for only 1% of the explained variation in relative growth rate (p>0.05). None of the interactions tested were statistically significant (Table 4).
Tadpole relative growth rate declined with increasing tadpole density at both Klondike Creek ($p<0.0001$, $r^2 = 0.98$) and Dipper Creek ($p<0.0001$, $r^2 = 0.97$) (Figure 8). Tadpole relative growth rate was approximately 35% higher at Klondike Creek than at Dipper Creek across all density treatments.

Figure 9 shows the effects of light and nutrients on tadpole relative growth rate for Klondike and Dipper Creeks. Relative growth rate was significantly higher in the unshaded treatments than in the shaded treatments at both Klondike ($1.2 \times$) and Dipper ($1.5 \times$) creeks. Addition of nutrients resulted in a small but non-significant decline in relative growth rates in the shaded treatments and a small, non-significant increase in relative growth rates in the unshaded treatments at both creeks.
Table 4. F-values for ANOVA showing main and selected interaction effects on tailed frog tadpole relative growth rate (RGR) expressed as g/g/d. Degrees of freedom (df) for each term are shown in brackets.

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<thead>
<tr>
<th>Parameter</th>
<th>r-square</th>
<th>Light</th>
<th>Nutrients</th>
<th>Density</th>
<th>Stream</th>
<th>Enclosure Size</th>
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*p>0.10; **p<0.05; ***p<0.0001

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*p<0.05; **p<0.01 ***p<0.0001
Figure 8. Effect of tadpole density on tadpole relative growth rate (RGR). Dots represent means ± 1 S.E (n=152 tadpoles per stream).

Figure 9. Effect of light and nutrients on tadpole relative growth rate. Bars represent means ± 1 S.E. across all enclosure and density classes (n=152 tadpoles per stream).
Effectiveness of Experimental Treatments

Effect of Enclosure Size

An ANOVA was performed to determine the effect of enclosure size on tadpole relative growth rate (RGR), periphyton biomass (AFDW), and chlorophyll $a$ abundance. Given that experimental stream enclosures do not perfectly mimic the natural stream environment, this analysis allowed me to assess whether the different enclosure sizes used in the experiment were sufficiently different "habitats" from each other as to significantly alter biological responses during the experimental period. Density effects were eliminated by using only those enclosures containing tadpoles at densities of 29 tadpoles-m$^{-2}$.

At Klondike Creek, chlorophyll $a$ in small enclosures was significantly higher than chlorophyll $a$ in medium and large enclosures on cobbles ($p=0.012, F_{2,29} = 5.13$). However, chlorophyll $a$ on tiles at Klondike Creek did not differ among the different enclosure sizes ($p=0.92, F_{2,29} = 0.08$) (Figure 10A). Periphyton biomass at Klondike Creek was significantly higher in small enclosures than medium or large enclosures for both cobbles ($p<0.0001, F_{2,29} = 18.0$) and tiles ($p=0.0056, F_{2,29} = 6.23$). Periphyton biomass did not differ significantly between medium and large enclosures (Figure 10B).

At Dipper Creek, chlorophyll $a$ did not differ significantly between small, medium, and large enclosures on cobbles ($p=0.606, F_{2,29} = 0.51$) or tiles ($p=0.105, F_{2,29} = 2.44$) (Figure 10C). Periphyton biomass at Dipper Creek was slightly, but not significantly, higher in small enclosures than in medium or large enclosures on both cobbles ($p=0.052, F_{2,29} = 3.29$) and tiles ($p=0.061, F_{2,29} = 3.09$). Periphyton biomass did not differ significantly between medium and large enclosures (Figure 10D).
Figure 10. Effect of enclosure size on chlorophyll $a$ and AFDW on cobbles and tiles at Klondike (A and B) and Dipper (C and D) Creeks. Bars represent mean ± 1. S.E. for all cobbles and tiles. Total number of cobbles and tiles used at each stream: small (n=16); medium (n=8); large (n=8). For enclosures containing >1 tile and cobble, mean values were used for each substrate type.
Overall, enclosure size accounted for 2% of the variation in chlorophyll $a$ abundance on cobbles, 5% of the variation in chlorophyll $a$ abundance on tiles, 7% of the variation in periphyton abundance on cobbles, and 3% of the variation in periphyton abundance on tiles. Enclosure size had a significant effect on tadpole relative growth rate at both Klondike and Dipper Creeks (Figure 11). Tadpoles in small enclosures had significantly higher relative growth rates in small enclosures than in medium or large enclosures at both Klondike ($p=0.0003, F_{2,29} = 10.86$) and Dipper Creeks ($p=0.0228, F_{2,29} = 4.32$). Relative growth rates in medium and large enclosures did not differ significantly from one another. Overall, enclosure size accounted for 11% of the observed variation in tadpole relative growth rate.

**Natural versus Artificial Substrates**

An ANOVA was performed to determine whether periphyton biomass and/or chlorophyll $a$ differed significantly between natural substrates (cobbles) and artificial substrates (ceramic tiles). Results of the ANOVA show that substrate type alone did not account for a significant difference in chlorophyll $a$ ($p=0.632, F_{1,183} = 0.23$). However, the difference in chlorophyll $a$ on cobbles versus tiles did vary significantly between the two study streams ($p<0.0001, F_{1,183} = 25.99$). There was also a significant interaction effect between stream and substrate type ($p=0.0004, F_{1,183} = 12.66$). Periphyton biomass differed significantly between cobbles and tiles ($p<0.0001, F_{1,183} = 78.29$). Both stream and the interaction between stream and substrate type exerted significant effects on periphyton biomass ($p<0.0001, F_{1,183} = 30.53$ and $p<0.0001, F_{1,183} = 40.49$ respectively).

Descriptive statistics for periphyton biomass and chlorophyll $a$ on cobbles and tiles are provided in Table 5. Figure 12 shows regressions for periphyton biomass versus chlorophyll $a$ for cobbles and tiles at both Klondike and Dipper Creeks. Visual observation over the duration of the experiment confirmed that the algal assemblage colonizing tiles consisted primarily of diatoms.
This assemblage was assumed to be essentially the same as that of natural cobbles (Lamberti and Resh 1985).
Figure 11. Effect of enclosure size on tadpole relative growth rate at Klondike and Dipper Creeks. Only channels containing 29 tadpoles·m⁻² were used to isolate enclosure effect. Bars represent means ± 1 S.E.
Table 5. Descriptive statistics for periphytic chlorophyll *a* and AFDW for cobbles and tiles at Klondike and Dipper Creeks. Values are for all experimental treatments.

<table>
<thead>
<tr>
<th></th>
<th>Klondike Creek</th>
<th></th>
<th>Dipper Creek</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>chlorophyll a (µg·cm⁻²)</td>
<td>AFDW (mg·cm⁻²)</td>
<td>chlorophyll a (µg·cm⁻²)</td>
<td>AFDW (mg·cm⁻²)</td>
</tr>
<tr>
<td></td>
<td>cobble</td>
<td>tile</td>
<td>cobble</td>
<td>tile</td>
</tr>
<tr>
<td>Mean</td>
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<td>Number (n)</td>
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</table>
Figure 12a. Chlorophyll $a$ – periphyton biomass (AFDW) regressions for cobbles and tiles at Klondike Creek. Data for all tiles and cobbles are shown ($n=144$ tiles + 144 cobbles).
**Figure 12b.** Chlorophyll a – periphyton biomass (AFDW) regressions for cobbles and tiles at Dipper Creek. Data for all tiles and cobbles are shown (n=144 tiles + 144 cobbles).
Light and Nutrient Effects on Periphyton

Periphyton, the major food resource of tailed frog larvae, was found to be limited by light. Shade cloth reduced ambient light levels by approximately 85-90%, which is comparable to shading by a mature or second growth forest (Gregory et al. 1987). Shading had a significant negative effect on periphyton standing crop compared with the open treatment. Light was the most important factor in determining chlorophyll $a$ abundance, accounting for 44% of the observed variation in chlorophyll $a$ on cobbles and 37% of the observed variation on tiles. This finding is in agreement with studies showing increased insolation following clear-cutting resulting in increased primary production (Hansmann and Phinney 1973; Gregory 1980; Steinman and Lamberti 1988).

A significant interaction between light and stream resulted in a greater response of algae to light treatments at Dipper Creek than at Klondike Creek. Chlorophyll $a$ abundance at Dipper Creek decreased 2-4× on cobbles and 3-5× on tiles in response to shade. At Klondike Creek, chlorophyll $a$ abundance decreased by 2× on cobbles and 2-5× on tiles. At Dipper Creek, periphyton biomass decreased 30-40% in the presence of shade, however periphyton biomass at Klondike Creek exhibited little response to shading. Overall levels of periphyton (chl $a$ and AFDW) at Dipper Creek were higher than at Klondike Creek throughout the duration of the experiment. This is probably attributable to the higher ambient nutrient levels at Dipper Creek compared to Klondike Creek (see Figure 2). An alternative explanation for this could be that small, shallow streams at high elevations are subject to higher ultraviolet radiation (UVR) which may cause photoinhibition of periphyton growth (Bothwell et al. 1993; Wellnitz et al. 1996a).
Klondike Creek was shallower, at a higher elevation, and received higher levels of photosynthetically active radiation (PAR) than Dipper Creek. Because only two light treatments were used in this experiment, it is not known whether light could have had a greater impact on periphyton at an intermediate light level.

Nutrient manipulations did not result in discernable effects on grazer-periphyton interactions, indicating that the small (zero to two-fold) increases in phosphorus concentrations resulting from fertilization did not increase periphyton standing crop enough to be reflected in tadpole growth rates. Nutrient addition either did not significantly affect periphyton (cobble chl $a$, tile AFDW), resulted in a small decrease in periphyton (tile chl $a$), or significantly increased periphyton in the presence of light (cobble AFDW). Overall, the effects of nutrients had a lower magnitude of impact than the effects of the other four factors (light, stream, tadpole density, and enclosure size), in determining periphyton standing crop. These results make the overall effect of nutrients on periphyton in these streams difficult to interpret. Bothwell (1988) showed that phosphorus concentrations of 0.3-0.6 $\mu$g/L saturate specific growth rates of unicellular periphytic diatoms in other streams in southwestern British Columbia, and that concentrations greater than 10 $\mu$g/L may cause unacceptable accumulations of periphytic biomass (Bothwell 1989). Based on these estimates, nutrient addition may have failed to have a strong effect in Klondike and Dipper Creeks because nutrients were not limiting. The fact that positive effects of nutrients were sometimes observed in the presence of light indicates that periphyton is primarily light-limited in these systems.

Light and nutrients interacted significantly to positively influence periphyton (both chl $a$ and AFDW) on cobbles, but not on tiles. The difference between natural and artificial substrates will be discussed in a later section. In addition to the observed effects of light and nutrients on periphyton biomass, there may have been changes in the species composition of the algal
community that were not detected during this study, but that may have important consequences for stream grazers in terms of their edibility and/or food value (Anderson and Cummins 1979; Vaughn 1986).

**Grazer Effects on Periphyton**

Tadpole grazing resulted in a significant decrease in periphyton (chl \( \alpha \) and AFDW) on cobbles and tiles. The existing literature on stream herbivory suggests that herbivores (1) have a greater effect on their food resources in aquatic than in terrestrial ecosystems, and (2) more frequently affect the trophic level below them than do carnivores (Feminella and Hawkins 1995). The relative strength of top-down vs. bottom-up interactions in food webs depends partly on the efficiency with which consumers can exploit their prey (Power 1992). For example, tadpoles of different species exhibit varying efficiency in their ability to scrape periphyton from substrate (Dickman 1968; Kupferberg 1997b). Although the effects of anuran grazing on algae are not well-understood (Cattaneo and Mousseau 1995; Holomuzki 1998), there are several studies indicating that anuran tadpoles are capable of significantly decreasing the algal food resource (Dickman 1968; Morin et al. 1988; Bronmark et al. 1991; Liebold and Wilbur 1992; Kupferberg 1997b). A previous study by Lamberti et al. (1992) found that tailed frog tadpoles are capable of significantly reducing algal biomass in streams near Mount St. Helens in Washington.

Grazing by tailed frog tadpoles in this study significantly reduced chlorophyll \( \alpha \) and AFDW levels on cobbles and tiles at both creeks. The most dramatic effect was at Klondike Creek where introduction of a single tadpole resulted in a 50% decline in chlorophyll \( \alpha \) compared with the no tadpole control. Tadpole grazing also resulted in significant changes in the dry weight (inorganic + organic) and the ashed fraction (inorganic) of the periphyton on cobbles but not on
tiles. This finding demonstrates that tadpole grazing can significantly alter the inorganic fraction of the periphyton in addition to the organic fraction on cobbles.

**Grazer Growth Response**

The results of this study indicate that changes in light and nutrient regimes in small, headwater streams can result in significant changes in 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 with respect to tadpole growth was that differences between the two study streams was the most important factor determining tadpole growth, accounting for 33% of the explained variation in relative growth rate. Tadpole relative growth rate was between 1.2 and 2.5 times higher at Klondike than at Dipper Creek, despite the lower levels of periphyton at Klondike Creek. The most probable explanation for this difference is the warmer streamwater temperature at Klondike Creek. Although stream temperatures at both Klondike and Dipper Creeks during the experiment were within the range of tolerance for tailed frog embryonic development (Brown 1975), de Vlaming and Bury (1970) report temperature preferences for tadpoles in their second year of between 12-16°C. According to this estimate, Klondike Creek remained within the optimal temperature range for tadpole growth (mean temperature during experimental period: 12.3°C), whereas Dipper Creek was several degrees below the optimal range (mean temperature during the experimental period: 9.5°C).

In this study, light was found to have a significant positive effect on tadpole relative growth rate at both streams. The positive effect on growth is presumably mediated by an increase in primary production, and indicates a tight trophic coupling between tadpole grazing and the
algal food resource. This may be true only for streams lacking secondary consumers, such as the two streams studied here, and not for streams where the presence of predators may result in a change in larval foraging behavior or larval survival rate. Hill et al. (1995) found similar results at White Oak Creek where growth of algae was found to be simultaneously affected by both bottom-up factors (light and nutrients) and top-down control by grazers for a community with two functional trophic levels. In addition to this direct, top-down effect, light may also affect tadpoles by influencing their behavior. Altig and Brodie (1972) suggested that Ascaphus tadpoles are negatively phototactic and forage primarily at night. However, I frequently observed tadpoles foraging during the day and failed to observe tadpoles on the surface during two night searches. One possible explanation may be that in the presence of predators, tadpoles may prefer to forage at night and hide below rocks during the day. Feminella and Hawkins (1994) showed that tailed frog tadpoles alter their feeding behavior in the presence of cutthroat trout and Pacific giant salamanders. In the streams where I conducted my experiments, there were few predators, which may reduce the risk to tadpoles foraging during the day.

Nutrients had no significant effect on tadpole growth rate under shaded conditions, and a slight but non-significant positive effect on tadpole growth rate under unshaded conditions. This finding 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. In addition, there is no evidence for nutrients influencing grazers directly.
Intraspecific Density-dependent Interactions

Wilbur (1980) stated that “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”. By applying a complete block, fully-factorial design, this study demonstrates that Ascaphus tadpole relative growth rate 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, indicates that temperature differences between streams may have had a strong effect on growth rates (see Figure 3). 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 the fact that the decrease in tadpole growth rate with increasing tadpole density makes sense in terms of the decline in periphyton standing crop with increasing density (compare Figures 7 and 8). At Klondike Creek, where growth rates were higher, algae was depressed even at the lowest densities (e.g. 10 tadpoles/m²), whereas at Dipper Creek there was a more gradual decline in algae with increasing tadpole density (see Figure 7). It is important to note that the effects of density dependence were observed at even the lowest density treatments in this study, and that these densities are within the range naturally encountered in previous surveys conducted in British Columbia (Dupuis and Friele 1996, Rosenfeld 1997).

An alternative explanation for the observed decline in growth rates would be interference competition among tadpoles. When density was controlled for, tadpole growth in small enclosures (where only one tadpole was present) was higher than in medium and large enclosures (where 2 and 3 tadpoles were present respectively), which suggests that interference among
tadpoles may account for lower growth rates. Another possibility is that some of the periphyton may be inaccessible to grazers because it is either in small crevices or too close to the substrate.

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 (Wilbur and Collins 1973; Wilbur 1980; Fauth et al. 1990), longer-term studies are required 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 the tailed frog.

Effectiveness of Experimental Treatments

Enclosure size

Several periphyton parameters were found to vary significantly with enclosure size, indicating a microhabitat effect. At Klondike Creek, chlorophyll \(a\) and biomass on cobbles and tiles were all greater in small enclosures than medium or large enclosures. At Dipper Creek, periphyton biomass was slightly, but not significantly, higher in small enclosures than in medium or large enclosures for both cobbles and tiles. Medium and large enclosures did not differ significantly for any parameters measured. Tadpole growth rates followed the same trend, with the highest growth rates occurring in small enclosures. Given that density per enclosure size and the number of substrates (cobbles and tiles) per tadpole were both controlled for in the experiment, this finding indicates that interference competition may have influenced growth in medium and large enclosures where more than one tadpole was present. As a main effect, enclosure size accounted for a much smaller percentage of the explained variation for both
periphyton (only 2-7%) and tadpole relative growth (only 11%) than tadpole density, stream, and light.

The effect of enclosure size may be attributable to a difference in physical factors (e.g., flow, refugia) influencing periphyton standing crop, and consequently tadpole growth. For example, substrates in small enclosures, constructed of smaller diameter PVC, had more contact with the sides of the enclosure, which may have altered flow patterns and provided more refugia for both periphyton production and tadpole forage. Pearman (1993) found that growth rates of *Bufo* tadpoles maintained at identical densities in differently sized artificial ponds were inversely related to habitat size. Robson and Barmuta (1998) found that microhabitat architectural complexity in streams acts to increase grazer density and decrease algal biomass, indicating that refuges from flow may be as important to grazing macroinvertebrates as their food source. In this experiment, the fact that both algae and tadpole growth decreased with increasing enclosure size suggests that environmental factors, rather than changes in tadpole foraging behavior, were responsible for enclosure size effects on algae and tadpole growth rate.

*Natural vs. artificial substrates*

In this study tiles were conditioned for five weeks prior to initiation of the experiment. At the end of the six-week experiment, chlorophyll $a$ did not differ significantly between tiles and cobbles, however periphyton biomass (AFDW) was significantly higher on tiles than on cobbles. Differences between streams, and the interaction between stream and substrate type significantly influenced both chlorophyll $a$ and AFDW on natural versus artificial substrates. In a previous study Lamberti and Resh (1985) found that unglazed clay tiles conditioned for four weeks accurately represented chlorophyll $a$ abundance of the natural stream rocks, but that nine weeks were required to accurately represent ash-free dry weight. Robson and Barmuta (1998) found that
four weeks were sufficient to condition ceramic tiles so that chlorophyll $a$ and algal densities had reached levels equivalent to those on adjacent natural cobble surfaces. These results indicate that the appropriate conditioning time for artificial substrates may vary on a regional basis and also from stream to stream and is probably best determined by conducting trials prior to initiating the experiment.

There are two plausible explanations for the observed differences in periphyton standing crop between artificial and natural substrates in this study. First, algal communities on tiles may have still been in the initial colonization phase, and thus differed in species composition and/or production compared to the natural substrates. Second, surface characteristics of tiles may differ significantly in terms of algal colonization or susceptibility to physical forces within the stream. It has been shown in previous studies that the nature of the stream substrate is of critical importance in determining the periphyton community (Miller et al. 1987; Gale et al. 1979; Tuchman and Stevenson 1980). For example, the flat surface of tiles may make them more susceptible to scour and shear stress than natural substrates, which may in turn influence the colonization rate and species composition of the algal community. Susceptibility to scour may, over time, favor prostrate or adpressed diatom species rather than stalked or erect species. For example, Dudley and D’Antonio (1991) found that substrate heterogeneity provides refuges from herbivory and disturbance for establishing macroalgae in streams.

The effects of grazing on cobbles and tiles were similar at Klondike Creek, however grazing exerted a stronger influence on cobbles than on tiles at Dipper Creek. This finding suggests that tadpoles at Klondike Creek, where periphyton standing crop was lower and periphyton was primarily under grazer control, foraged on any available substrate. At Dipper Creek, where periphyton standing crop was greater and primarily limited by light, tadpoles fed preferentially on cobbles. This finding indicates that tadpoles may exhibit discrimination in
foraging behavior which may change with food availability. Tadpole grazing significantly altered the dried and ashed fractions of periphyton on cobbles, but not on tiles. Cobbles had 50-60% more inorganic material than tiles, which is probably attributable to a higher degree of surface heterogeneity for trapping fine particles such as sand and silt.

CONCLUSIONS

Complex interactions require complex experiments in order to address causal mechanisms (Wilbur 1997). In this study, simultaneous manipulation of several factors to assess their relative importance on stream periphyton and grazer growth response resulted in complex outcomes. Light, tadpole density, nutrients, and several interactions between these factors exerted significant effects on stream periphyton (Table 5). Tadpole relative growth rate was significantly influenced by light and tadpole density (Table 6). This study demonstrates that abiotic factors (bottom-up effects) can be as important as grazing by herbivores (top-down effects) in controlling stream periphyton. In addition to these observed effects, a significant difference between the two study streams was observed in terms of tadpole growth rates, and the relative importance of top-down and bottom-up effects on stream periphyton. 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. Controlled experiments, if properly designed and replicated, have a distinct advantage over observational studies or descriptive sampling techniques because they provide causal inference rather than possible causation, correlation, or observed effects (Holland 1986; Eberhardt and Thomas 1991).
MANAGEMENT IMPLICATIONS

The tailed frog is a species with a complex life cycle (sensu Wilbur 1980) whose habitat requirements are not understood. The importance of gaining an understanding of the habitat requirements of the tailed frog and the effects of current forest practices on their populations is underlined by the current lack of adequate protection for their habitat - headwater streams - in the Pacific Northwest (Kelsey and West 1998). Headwater streams in British Columbia are classified as S4, S5 and S6 streams and are currently afforded no riparian reserve zone unless they are known to contain resident game or anadromous fish species or to occur within a community watershed (B.C. MoF/MELP 1995). In order to determine the habitat requirements of a species, one must be able to predict how habitat changes will affect populations, and to ensure that habitat changes remain within the bounds that will not adversely affect populations.

Previous studies examining effects of forest disturbance on tailed frog larval populations have been correlative in nature. The results of these studies suggest that factors associated with channel instability (sediment, %undercut bank, gradient) are negatively associated with tadpole density, whereas factors associated with channel stability (substrate size, large woody debris, presence of undisturbed forest upstream) are positively associated with tadpole density (Table 6). Potential positive effects of forest disturbance on tailed frog larval populations come from comparative studies of old growth, clear-cut, and second growth sites. Richardson and Neill (1998) conducted extensive surveys of tailed frogs tadpoles in the Chilliwack River area and found no significant differences in the frequency of occurrence between clear-cut, second growth and old growth stands. However, tadpole densities were highest in clear-cuts and lowest in second growth stands (see Table 7). Wahbe (1996) found that tailed frog tadpole mean weight was highest in clear-cut creeks, followed by old growth, and then by second growth, and that
tadpoles were larger in both length and weight in clear-cut sites compared with old growth and buffered sites. The results of these studies suggest that, unless there was surveyor bias or differences in detection of tadpoles among sites, there may be either a) higher rates of oviposition within clear-cut sites, b) higher survival rates and/or growth of larvae within clear-cut sites, or c) immigration of tadpoles into clear-cut sites. The fact that the lowest densities were found in second growth sites, which are often heavily shaded, suggests that light-limitation may play a role in determining larval success in streams under different forest management regimes.

While correlative studies can provide valuable information on habitat preference, they do not address causal mechanisms. In addition, tailed frog populations are patchily distributed at all habitat scales (reach, stream, basin, landscape), therefore absence or low densities may reflect problems with dispersal of terrestrial adults and/or tadpoles rather than unsuitability of instream habitat. Table 7 provides a summary of available data on tailed frog tadpole densities under different management regimes. It is very difficult to draw conclusions from these data, however, as they do not conform to a standardized method for collection, cover a broad geographic range, and differ in terms of both sample size and definitions of “logged” or “unlogged” sites. Specific habitat information is more useful than stand age in predicting the effects of habitat alteration on populations, and methods should be standardized for collection of both larval data and site-specific habitat information so that comparisons between different studies can be made. Experimental studies can build on correlative studies by selecting environmental factors likely to influence populations and to test for their relative effects.

Results of my research demonstrate that both biotic and abiotic factors are important in determining periphyton biomass during the summer in small streams, and that tadpole growth is mediated by the availability of the periphyton food resource. In this experiment, light, tadpole density, the difference between streams, and several interactions were found to simultaneously
exert significant effects on periphyton standing crop and tadpole growth, which is a correlate of fitness for larval amphibians. These results demonstrate that increased light resulting from forest disturbance may enhance food availability, thereby stimulating growth, which may in turn increase larval survival rates.

Best management practices should consider the potential cumulative effects of all these factors on populations, and how they may vary temporally (i.e. both on a seasonal basis, and in the long-term as the forest regenerates) and at different spatial scales (i.e. reach, stream, basin, landscape). My study shows that open canopy conditions during the summer and fall positively influence algae and tadpole growth. However, as the forest regenerates and shading intensifies, algal food resources may become increasingly limited, resulting in density-dependent growth. In addition, previous research shows that factors associated with channel instability may negatively influence the success of larval populations. Therefore short-term positive effects on tadpole growth resulting from canopy removal may be masked by longer-term detrimental effects of increased sedimentation and/or stream temperature and the eventual decline in periphyton growth as the canopy regenerates. The relative effects of these factors may vary with elevation, latitude, aspect, or forest type. All of these factors should be considered when managing for populations.
Table 6. Summary of environmental factors correlated with *Ascaphus* tadpole densities in small streams in the coastal temperate rainforest.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Effect</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stream temperature</td>
<td>• negatively correlated with tadpole density</td>
<td>Wahbe (1996)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>deVlaming and Bury (1970)</td>
</tr>
<tr>
<td>Channel gradient</td>
<td>• no significant relationship</td>
<td>Corn and Bury (1989)</td>
</tr>
<tr>
<td></td>
<td>• negatively correlated with tadpole density</td>
<td>Richardson and Neill (1995)</td>
</tr>
<tr>
<td>Substrate size</td>
<td>• positively correlated to tadpole occurrence</td>
<td>Corn and Bury (1989)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Richardson and Neill (1995)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Altig and Brodie (1972)</td>
</tr>
<tr>
<td>Pool area</td>
<td>• negatively correlated with tadpole density</td>
<td>Richardson and Neill (1995)</td>
</tr>
<tr>
<td>% Undercut bank</td>
<td>• negatively correlated with tadpole density</td>
<td>Richardson and Neill (1995)</td>
</tr>
<tr>
<td>Volume of Large Woody Debris (LWD)</td>
<td>• positively correlated to tadpole density</td>
<td>Kelsey (1995); Richardson and Neill (1995)</td>
</tr>
<tr>
<td>Presence of undisturbed forest upstream</td>
<td>• higher frequency of tadpole occurrence</td>
<td>Corn and Bury (1989)</td>
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<tr>
<td>Fine suspended sediment</td>
<td>• negatively correlated to tadpole density</td>
<td>Welsh and Ollivier 1998</td>
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<tr>
<td></td>
<td></td>
<td>Kelsey (1995)</td>
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<td></td>
<td></td>
<td>Dupuis and Friele (1996)</td>
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Table 7. Summary of available information on *Ascaphus* larval densities from British Columbia, Washington, and Oregon

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<th>LOCATION</th>
<th>DENSITY</th>
<th>SOURCE</th>
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<td>0.63 (n=8) (clear-cut within 0-25 years)</td>
<td>Richardson and Neill (1995)</td>
</tr>
<tr>
<td></td>
<td>0.10 (n=5) (second growth: 25+ years old)</td>
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<tr>
<td></td>
<td>0.35 (n=7) (old growth: never cut)</td>
<td></td>
</tr>
<tr>
<td>British Columbia</td>
<td>6.94 (n=7; range: 0.9-65.5) (logged)</td>
<td>Dupuis and Friele (1996)</td>
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<tr>
<td></td>
<td>11.1 (n=12; range: 0.1-17.9) (old growth)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>9.11 (n=14; range: 1.2-36.2) (logged with buffer)</td>
<td></td>
</tr>
<tr>
<td>Washington</td>
<td>0.58 (n=6) (<em>no forest</em>)</td>
<td>Hawkins et al. (1988)</td>
</tr>
<tr>
<td></td>
<td>4.4 (n=3) (<em>forested headwater</em>)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2.72 (n=4) (<em>forested</em>)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.5 (n=23) (managed stands)</td>
<td></td>
</tr>
<tr>
<td>Oregon</td>
<td>0.37 (n=20) (clear-cut within 14-40 years)</td>
<td>Corn and Bury (1989)</td>
</tr>
<tr>
<td></td>
<td>0.76 (n=23) (uncut: 60-400+ years old)</td>
<td></td>
</tr>
<tr>
<td>Oregon</td>
<td>0.41 (n=40)</td>
<td>Welsh (1987)</td>
</tr>
</tbody>
</table>

1 includes only streams where tailed frogs were found  
2 corrected for frequency of occurrence, i.e., removal of sites where tadpoles were not found  
3 including samples of zero, and assuming an average stream width of 2m, 15 m section searched  
4 forest blown down by Mount St. Helens blast  
550-70% of forest blown down but headwater forest intact  
6 forest intact, age of forest not given
LITERATURE CITED


APPENDICES
APPENDIX I. Color and pattern of larval *Ascaphus* for Klondike and Dipper Creeks (1997). Individual tadpoles were distinguished on the basis of three traits: color (mottled or slate gray), presence/absence of a tail spot, presence/absence of a tail notch.

<table>
<thead>
<tr>
<th>Stream</th>
<th>Slate/Spot</th>
<th>Slate/No Spot</th>
<th>Slate/Spot/Notch</th>
<th>Mottled/Spot</th>
<th>Mottled/No Spot</th>
<th>Mottled/Spot/Notch</th>
<th>Sample Size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Klondike</td>
<td>73</td>
<td>24</td>
<td>4</td>
<td>47</td>
<td>3</td>
<td>1</td>
<td>152</td>
</tr>
<tr>
<td>Dipper</td>
<td>63</td>
<td>31</td>
<td>1</td>
<td>55</td>
<td>1</td>
<td>1</td>
<td>152</td>
</tr>
<tr>
<td>Total:</td>
<td>136</td>
<td>55</td>
<td>5</td>
<td>102</td>
<td>4</td>
<td>2</td>
<td>304</td>
</tr>
</tbody>
</table>
APPENDIX II. Calculations for addition of nutrient fertilizer.

Nutrients were added in the form of osmocoated nutrient pellets, a new product developed in 1994/95 by IMC Vigoro Inc. (Winter Haven, Florida) and the British Columbia Fisheries Research Section (B.C. Ministry of Fisheries). The fertilizer has the formulation of 7-40-0 (N-P₂O₅-K₂O; percent by weight) and is composed of magnesium ammonium phosphate, formula: MgNH₄PO₄ H₂O. The amount of fertilizer added to each stream was determined to meet the target phosphorus concentration of 3 μg·L⁻¹ using the following formula (from Mouldey Ewing and Ashley 1998):

\[
\text{Tot. P (kg)} = \text{flow (m}^3\cdot\text{s}^{-1}) \times 1,000 \times 86,400 \times 3 \times [1\text{E}^{-9} (\text{kg} \cdot \mu\text{g}^{-1})]
\]

**Klondike Creek:**

\[
\text{Tot. P (kg)} = 0.15 \times 1,000 \times 86,400 \times 42 \times [1\text{E}^{-9} (\text{kg} \cdot \mu\text{g}^{-1})]
\]

\[= 1.63 \text{ kg}\]

Each pellet weighs 7g. Therefore 233 pellets were added 10 meters above enclosures targeted for nutrient enrichment.

**Dipper Creek:**

\[
\text{Tot. P (kg)} = 0.45 \times 1,000 \times 86,400 \times 42 \times [1\text{E}^{-9} (\text{kg} \cdot \mu\text{g}^{-1})]
\]

\[= 4.9 \text{ kg}\]

Each pellet weighs 7g. Therefore 700 pellets were added 10 meters above enclosures targeted for nutrient enrichment.
APPENDIX III. Length and weight distributions for tadpoles at Klondike and Dipper Creeks. Length values represent total length of individual tadpoles. Weight values represent wet weight of live animals. N=152 tadpoles for each creek. Data are for all tadpoles used during the experiment (1997).