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The effects of nutrients and hydrology on periphyton and phytoplankton in Fraser River tributaries, British Columbia

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Abstract

Physical and chemical variables were measured in riffle zones of 20 Fraser River tributaries, British Columbia, to examine which factors explain variation in algal biomass and taxonomic composition. July epilithic periphyton chlorophyll *a* was weakly correlated with TN, while October periphyton was significantly related to DP and conductivity. The phytoplankton biomass in July was best predicted by TP (r^2=0.70, $p \leq 0.001$, n=19), while October phytoplankton was best predicted by a multiple regression with conductivity, current velocity and TN. In terms of taxonomic composition in October, Bacillariophyta was most abundant, followed by Chlorophyta, Cyanobacteria and Phaeophyta. DP and current velocity explained 25% of the taxonomic variation among the rivers in a CCA. While changes in the relative abundance of specific diatom taxa were observed, shifts in division dominance were not. River algal biomass could be predicted from environmental variables, however the empirical models differed between July and October.

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Abstract

In order to determine the physical and chemical variables that best explain the variation in algal biomass and composition among rivers in British Columbia, riffle zones of 20 salmonid rivers in the Fraser River watershed were sampled during July and October, 2001. Velocity and turbidity were measured, along with a number of chemical characteristics (dissolved nutrients, total nutrients, conductivity, pH). Epilithic periphyton biomass, estimated as chlorophyll *a* and ash-free dry mass, was significantly higher in October than July. July periphyton chlorophyll *a* was weakly correlated with water residence time ($r^2=0.33$, $p<0.05$) and total nitrogen concentration ($r^2=0.23$, $p<0.05$), while October periphyton was related to dissolved phosphorus concentrations ($r^2=0.46$, $p=0.001$) and conductivity ($r^2=0.35$, $p=0.008$). The phytoplankton biomass in July was best predicted with a simple regression with total phosphorus ($r^2=0.70$, $p=0.000$, $n=19$), while the October phytoplankton was best predicted by a multiple regression with conductivity, current velocity and total nitrogen ($r^2=0.57$, $p=0.004$, $n=19$). The taxonomic composition of October periphyton samples was further analyzed. Bacillariophyta (diatom division) was the most common taxonomic group, followed by Chlorophyta, Cyanobacteria and Phaeophyta. The biomass of the three main divisions was positively related with conductivity. At the genus level, the diatoms *Epithemia* and *Amphora* clustered together in a canonical correlation analysis of community composition, but were also strongly positively correlated with total phosphorus, which supports previous reports of their eutrophic nature. The small diatom *Acnanthidium minutissium*, which was found at all sites, was negatively related to total phosphorus. A forward selection CCA analysis found that with all the environmental variables included, dissolved phosphorus and current velocity were the most important variables and explained 25% of the taxonomic variation among the rivers. Overall, no significant shifts in division dominance were observed among the Fraser tributaries, only changes in the relative abundance of specific diatom taxa. While river algal biomass could be predicted from environmental variables, the empirical models differed between the period of declining discharge (July) and the more stable flows of fall (October).

Résumé

Pour déterminer les variables physiques et chimiques qui expliquent le plus de variation dans la biomasse et la composition des algues dans les rivières de la Colombie Britannique, les radiers de 20 rivières à saumon du bassin de la Rivière Fraser ont été échantillonnés en juillet et octobre, 2001. La vélocité du courant et la turbidité ont été mesurées, ainsi que les caractéristiques chimiques de l'eau (nutriments, conductivité, pH). La biomasse du périphyton épilithique, estimée par la chlorophylle *a* et la masse sèche du biofilm, était significativement plus élevée en octobre qu'en juillet. La concentration en chlorophylle *a* du périphyton de juillet était corrélée avec le temps de transit de l'eau (r^2=0.33 $p<0.05$) et la concentration d'azote total (r^2=0.23, $p<0.05$), alors que pour le périphyton d'octobre, la concentration en chlorophylle *a* était corrélée avec le phosphore dissout (r^2=0.46, p=0.001) et la conductivité (r^2=0.35, p=0.008). La biomasse du phytoplancton de juillet pouvait être prédite selon une régression simple avec le phosphore total (r^2=0.70, p=0.000, n=19), alors que la biomasse d'octobre était mieux prédite avec une régression multiple incluant la conductivité, la vélocité et l'azote total (r^2=0.57, p=0.004, n=19). La composition taxonomique du périphyton d'octobre a été examinée. Les bacillariophytes (embranchement des diatomées) était le groupe taxonomique le plus important, suivi par les chlorophytes, les cyanobactéries et les phaeophytes. La biomasse des trois embranchement principaux était reliée avec la conductivité. Dans une analyse de corrélation canoniale (CCA) sur la composition des communautés, les diatomées *Epithemia* et l'*Amphore* étaient groupées ensemble. Ce qui soutient des études précédentes sur leur nature eutrophique. La petite diatomée A*cnanthidium minutissium*, qui a été trouvée à tous les sites, était négativement reliée au phosphore total. Une analyse canonique de sélection a montré qu'avec toutes les variables environnementales incluses, le phosphore dissous et la vélocité du courant étaient les variables les plus importantes et expliquaient 25% de la variation taxonomique entre les rivières. En général, aucun changement significatif dans la dominance au niveau de l'embranchement a été observé et seulement des changements dans l'abondance relatif des espèces de diatomées ont eu lieu. Alors que la biomasse des algues pouvait être prédite par les variables environnementales, les modèles empiriques différaient entre la période de débit déclinante (juillet) et la période plus stable (octobre).

General Introduction

Flowing waters, or lotic ecosystems, are vitally important ecologically and economically, yet they are being threatened around the globe by contaminants, dams, eutrophication and changing weather patterns (Dodds and Welch 2000). For this reason, it is critical to understand the basic ecological functions of lotic systems and develop models to manage these resources.

A major step in the development of models for flowing waters was the River Continuum Concept (RCC) of Vannote et al. (1980). The RCC is a descriptive model that outlines the structure and function of lotic ecosystems from the headwaters of a river to the mouth (Vannote et al. 1980). The RCC links stream size, organic matter (energy) inputs and processing with the structure of biological communities within a river system. The model emphasizes the idea that communities and ecosystems are in equilibrium with their environment and assumes that lotic systems are structured in a predictable manner along a continuum of physical or resource gradients.

The RCC applies mainly to forested streams in the North Temperate Zone and, therefore, other concepts have been proposed for other systems, such as the flood pulse concept (Junk et al. 1989). This concept is based primarily on observations from tropical rivers and proposes that long, predictable pulses in discharge, expanding the river onto the floodplain, can sometimes be the dominant hydrological event (Junk et al. 1989). However, the applicability of the flood pulse concept to temperate rivers remains uncertain.

The RCC focuses mainly on macro-invertebrate communities and their changes along the river gradient; however, algal communities are also discussed. As the macro-invertebrate communities shift from a co-dominant community of shredders and collectors in the headwaters to an increasing dominance of collectors in the larger river, the algal community also shifts (Vannote et al 1980). The principal community in the headwaters is periphyton, which gradually decreases in dominance, while the phytoplankton increases in importance as the river order increases and the river becomes more lentic (Kalff 2002).

Phytoplankton

Phytoplankton in most streams consists of benthic algal species dislodged from periphyton microhabitats (Korte and Blinn 1983; Stevenson 1984; McCormick and Stevenson 1998; Barnese and Lowe 1992) and phytoplankton washed in from lakes. However, a true riverine phytoplankton community (potamoplankton) that reproduces *in situ* usually develops in medium to large rivers (Reynolds 1988; Yang et al. 1997).

Various studies have sought to identify the factors that might control the biomass of phytoplankton in rivers. Within in large rivers, chlorophyll *a* concentrations have been found to vary inversely with discharge (Jones 1984; Schmidt 1994). As the discharge increases, the time available for phytoplankton reproduction decreases because of the continuous removal of organisms by downstream flow (Baker and Baker 1979; Soballe and Kimmel 1987; Reynolds and Descy 1996). Several studies on large European rivers have found that nutrient limitation is uncommon, which has been attributed to the high levels of nutrient enrichment in the European systems (Reynolds 1988; Reynolds and Descy 1996; Wehr and Descy 1998). Consequently discharge may be the principal factor regulating river phytoplankton (Schmidt 1994; Reynolds and Descy 1996).

In contrast, studies on North American rivers have found significant positive relationships between river phytoplankton abundance and total phosphorus concentration (Soballe and Kimmel 1987; Basu and Pick 1996; Van Niewenhuyse and Jones 1996; Heiskary and Markus 2001). Basu and Pick (1996) found that in rivers of Eastern Ontario and Quebec, with a water residence time greater than 3 days, the total phosphorus concentration and not water residence time (which is related to discharge) was the better predictor of algal biomass.

Periphyton

Periphyton, the algal component of the benthos, is essential for ecosystem functioning, often forming the basis of the food chain in streams (Stevenson 1996). However, under certain circumstances periphyton can proliferate, causing a number of undesirable effects, such as oxygen depletion and degradation of benthic invertebrate habitat (Welch et al. 1988). Along with these effects, other water resource management problems, such as degradation of aesthetic, recreational and biodiversity values, can arise.

Because of the complexity of lotic ecosystems, empirical models for periphyton biomass and composition in natural streams and rivers are rare (Welch et al. 1988; Biggs and Close 1989; Lohman et al. 1992). Furthermore, the relative importance of physical versus chemical factors in affecting biomass varies between models. In lowland rivers of Eastern Canada, Chételat et al. (1999) found that total phosphorus was the best predictor of both benthic chlorophyll *a* and the biomass of nuisance, filamentous taxa. However, in New Zealand gravel-bed rivers, Biggs and Close (1989) found that the hydrological regime was as important as nutrients when considering periphyton development.

Flooding disturbance may be the reason why strong nutrient-biomass relationships have not been found in some stream studies (Lohman et al. 1992). Biggs (2000a) found that this factor explained more variation in both mean monthly and maximum chlorophyll *a* than nutrient concentrations. Biggs and Gerbeaux (1993) found no significant correlations between chlorophyll *a* and ambient water nutrient concentrations, but instead found that variations in periphyton occurred as a direct function of macro-scale catchment conditions (land-use, geology).

In many rivers, the time available for growth (i.e., time between flood events) and nutrient concentrations interact to determine biomass levels (e.g. Biggs 2000). The interaction of nutrients and hydrologic conditions can change seasonally within a river. For example, during extended periods of low flow, nutrients are the main predictor of algal biomass accrual (Biggs and Smith 2002). However, during periods of frequent flooding or high discharge rates, the hydrological regime becomes the primary factor in determining periphyton communities (Biggs 1996).

Current velocity can also play a role in shaping periphyton communities. Higher velocities enhance transfer of nutrients and metabolites to and from the periphyton resulting in higher metabolism and growth rates (e.g. Biggs 2000b). However, with an increase in velocity a greater amount of drag is exerted on the communities. This means that tightly attached species will be favoured over filamentous or pedunculate species in the community and therefore a change in community structure occurs (Biggs 1996; Stevenson 1996).

Many of these periphyton models are based on mesotrophic to eutrophic rivers, whereas models for oligotrophic rivers have not been developed. This means that the existing models may not apply universally, and creates the need for development and testing of regional models for use in water management. In particular, the Pacific coastal regions of North America have generally low periphyton biomass due to the low ambient nutrient concentration (Welch et al. 1988).

In British Columbia, the periphyton community is of particular importance because of the compromised state of salmon stocks (FRAP 1995; PSC 2001). Benthic algae can form the major diet of heterotrophs such as insects, crustaceans and snails (Kalff 2002). Some insects such as midges burrow into the periphyton and make tube dwellings within the mat (Biggs 2000b). These invertebrate communities, which can be limited by periphyton abundance, support fish populations, such as salmon (Hill et al.1992). For example, benthic algae are major items in the diet of larval mayflies (ephemeropterans) which are an important food for juvenile pink salmon (*Oncorhynchus gorbuscha*) in British Columbia rivers (Heard 1991).

Increases in benthic invertebrate abundance have been observed experimentally with the addition of nutrients (Hart and Robinson 1990; Johnston et al 1990) and have been attributed to an increase in periphyton productivity (Hershey et al. 1988; Perrin and Richardson 1997). An increase in the availability of invertebrates can produce an increase in the biomass and yield of fish (Johnston et al. 1990; Deegan and Peterson 1992). The fertilization of oligotrophic lakes in British Columbia, for salmonid enhancement, has illustrated this effect, where a positive response was observed at all trophic levels. Stockner and MacIsaac (1996) found that sockeye fry foraged on an increased abundance of small cladocerans and copepods and grew larger with the addition of nutrients. The same response was found in rivers, where the short-term fertilization of the Nechako River, BC increased periphyton chlorophyll *a*, which was coupled with an increase in emergence rates of adult aquatic insects (Perrin and

Richardson 1997). The benthic invertebrates that increased most in abundance corresponded to the predominant prey in chinook salmon (*Oncorhynchus tshawytscha*) fry diets. Slaney and Ward (1992) also report a positive response of periphyton, insects and salmonids to nutrient addition in BC streams.

Thesis Objectives

River systems need to be better understood and described, particularly in terms of the importance of hydrology and water chemistry on the algal communities, which are often affected by anthropogenic activities. The objective of this thesis was to quantify the relative importance of these drivers on the periphyton and phytoplankton communities in tributaries of the Fraser River, British Columbia. The reasons for choosing the Fraser River network include the fact that the system covers a wide range of discharge and nutrient concentrations and currently there are no river models for this large region.

Many different ways to assess phytoplankton and periphyton communities exist (Table 1). There are strengths and weaknesses in taxonomic and non-taxonomic approaches, with each illustrating a different aspect of the community. While biomass estimates, such as chlorophyll *a* and ash-free dry mass, are relatively easy to obtain, they provide limited information about community structure. Taxonomic descriptors (taxa composition or species richness) can provide information on the quality of the community, such as identifying nuisance taxa. Therefore both of these methods, biomass estimates and taxonomic enumeration, were used in the current study to assess and describe the periphyton and phytoplankton communities.

In this thesis, in Chapter 1, I focus on the relative importance of hydrological variables (discharge, current velocity) and water chemistry (e.g. total phosphorus and total nitrogen concentration, conductivity) on the biomass of phytoplankton and epilithic periphyton (chlorophyll *a*, ash-free dry mass) during the periods of declining discharge (July) and stable flow (October). In Chapter 2, the October periphyton taxonomic composition was examined in relation to the hydrological and chemical variables.

Table 1: Algal attributes and associated indicators commonly employed in biological studies and monitoring programs.

Attribute	Indicator/Method	Example citations (from periphyton literature)
Community structure		
Biomass	Ash-free-dry mass	Biggs 1989
	Cell biomass	Stevenson and Lowe 1986 Williams 1972
	Chlorophyll *a*	Amblard et al. 1990 Biggs 1989 Delong and Brusven 1992
Diversity	Taxa composition	Hill et al. 2000 Amblard et al. 1990
	Species richness	Winter and Duthie 2000 Raschke 1993
	Similarity indices	Marshall and Mellinger 1980 Raschke 1993 Stevenson 1984
Community Metabolism		
Productivity	Relative specific growth rate	Biggs 1990
	Oxygen evolution	Crossey and LaPoint 1988 Uehlinger and Brock 1991
	Radioisotopic tracer (C^{14})	Lewis 1992 Munawar et al 1986
Bioaccumulation	nutrients	Grimshaw et al 1993 Lyngby 1990
	metals	Ramelow et al. 1992

Modified from McCormick and Cairns (1994)

Study Site

The Fraser River watershed drains approximately 25% of British Columbia and is one of Canada's most valued ecosystems, both ecologically and economically. The river drains 230 000 km^2 and flows 1400 km from the Rocky Mountains to its outlet in the Strait of Georgia (Northcote and Larkin 1989). The complex geology, extensive glacial history and diversity of climatic conditions in BC have led to the characterization of 12 distinct limnological regions (Northcote and Larkin 1966) (Figure 1). The Fraser passes through four of them, the Rocky Mountains and Foothills, the North Interior Plateau and Mountains, the Southern Interior Plateau and the Insular and Coastal Mountains.

The Fraser River is the largest producer of sockeye salmon in the world. The river provides migration habitat for five Pacific salmon species: chinook, chum, coho, pink and sockeye. The salmon runs are among the largest in the world and provide major commercial catches of all five salmon species, important native food fisheries and a significant sport fishery (Swain et al. 1998).

Despite the importance of the Fraser River watershed, there is a lack of research on the system as a whole. There have been river fertilization projects, with the intent of revitalizing dwindling fish stocks, without basic knowledge of the algal community drivers. It is for this reason that the Fraser River system was chosen for study.

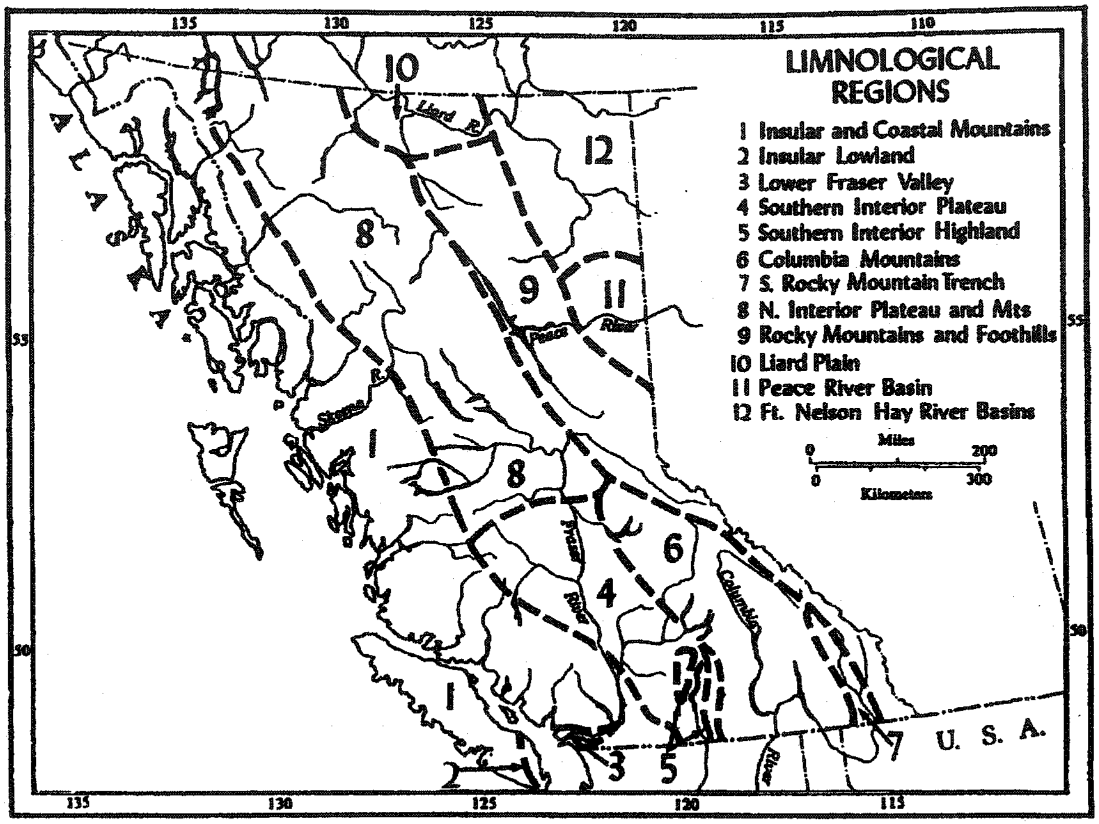

Figure 1: Limnological regions of British Columbia (modified from Northcote and Larkin 1966)

CHAPTER 1:

The relative importance of nutrients and hydrology on periphyton and phytoplankton biomass in Fraser River tributaries, British Columbia

Introduction

Algal communities play important roles in lotic systems, often as the dominant primary producers (Vannote et al. 1980). Many factors can affect primary producers in rivers, including nutrient availability, hydrodynamics, conductivity, pH, turbidity, light and herbivory (Stevenson 1996). Consequently, it is useful to understand the relative importance of environmental factors that affect these communities (Dodds and Welch 2000).

Several studies have examined the relationship between nutrient concentration and algal biomass in rivers. Suspended algal biomass has been positively related with total phosphorus (TP) (Basu and Pick 1996, Van Nieuwenhuyse and Jones 1996, Basu and Pick 1997, Heiskary and Markus 2001) and total nitrogen (TN) (Yang et al. 1997, Heiskary and Markus 2001). Benthic or attached algal biomass in streams has also been directly linked to conductivity, nitrogen and phosphorus concentrations (e.g., Lohman et al. 1992, Dodds et al. 1997, Bourassa and Cattaneo 1998, Chételat et al. 1999). Conductivity is often a better predictor of periphyton biomass than nitrogen or phosphorus (Chételat et al. 1999). Biggs (1990) suggested that conductivity is an indicator of nutrient enrichment and therefore captures many chemical characteristics in one measurement.

However, other studies have found that hydrodynamics are at least equally important as nutrients in affecting algal biomass (Horner and Welch 1981, Biggs and Close 1989, Horner et al. 1990, Biggs and Gerbeaux 1993, Biggs et al. 1998). Phytoplankton chlorophyll *a* concentrations vary inversely with discharge in large rivers (Jones 1984; Schmidt 1994) and some studies have found that discharge has been the principal factor in regulating river phytoplankton (Schmidt 1994; Reynolds and Descy 1996). Biggs (2000a) found that a combination of hydrodynamic disturbance and inorganic nutrients was best at predicting periphyton biomass in New Zealand streams. It appears that current velocity complicates the relationship between nutrients and periphyton (Stevenson 1996).

Another hydrological measure that has been found to affect phytoplankton is water residence time (WRT) (Soballe and Kimmel 1987). In rivers, WRT is an estimate of the how long the water at a sampling point has been in the drainage basin, or can be considered the "age" of the water at the sampling site. It is determined as a function of discharge and upstream drainage area (Soballe and Kimmel 1987). While some studies have concluded that WRT influences phytoplankton standing stock (Soballe and Kimmel 1987; Yang et al. 1997), others have found no relationship (Basu and Pick 1997).

The relationship between current velocity and periphyton accrual and loss is not a simple one. The response of chlorophyll *a* to increased velocity or discharge, such as a flood, largely depends on the nutrient conditions of the stream (Horner and Welch 1981, Lohman et al. 1992). At low nutrient conditions, velocity tends to increase biomass because of enhanced nutrient uptake and efflux of waste products (Lock and John 1979, Dodds 1989). As current velocity increases, the increase in biomass due to the nutrient transfer effect is counter-acted by the removal by sloughing due to shear stress (Horner and Welch 1981, Clausen and Biggs 1997). It therefore appears that a hyperbolic relationship exists between benthic algal biomass and current velocity (Biggs and Gerbeaux 1993, Stevenson 1996, Biggs et al. 1998).

Primary producers can be an important determinant of fish production in aquatic systems (e.g., Stockner and MacIsaac 1996, Perrin and Richardson 1997). Many rivers in

British Columbia are naturally low in nutrients and the algal biomass may not be sufficient to support commercial fisheries (Slaney and Ward 1992, Stockner and MacIsaac 1996, Perrin and Richardson 1997). Experimental fertilization of rivers has been conducted in an attempt to enhance fish production on the Pacific Northwest (Slaney and Ward 1992). However, the relative importance of physical versus chemical factors in controlling algal biomass has not been established in this region and few studies have examined the basic river ecology.

The purpose of this study was to investigate phytoplankton and epilithic periphyton biomass in Fraser River tributaries. Specifically, I examined the relative importance of hydrodynamics and nutrient concentrations on algal biomass, using regression models, during two different times of the year that corresponded to declining hydrographs (July) and stable base flows (October). I predicted that during the period of stable flow, nutrients would be more important than hydrological factors (current velocity and discharge) in predicting both periphyton and phytoplankton biomass. In July, when water flow of the study rivers was high and declining, the discharge was expected to be more important than nutrients in determining periphyton and phytoplankton biomass.

Materials and Methods

Study sites

The Fraser is one of the largest undammed rivers of the world, draining 238 000 km^2, which accounts for one quarter of British Columbia (Cameron 1996). It is one of the most valued rivers in Canada, both ecologically and economically and is the world's largest source of salmon (Northcote and Larkin 1989). The Fraser drainage basin crosses four geological belts (Cameron 1996), two of which were represented in the study sites. Five rivers (Nechako, Chilako, Salmon, Bowron and Willow) are found in the Omineca Belt, an uplifted region of metamorphosed sedimentary rocks and granites. The rest of the sites were located in the central part of the Fraser Basin, the Intermontane Belt, which is comprised of volcanic rocks and associated sedimentary rocks cut by granites (Cameron 1996).

A total of 20 salmonid Fraser River tributaries were sampled in central British Columbia (Fig. 1.1). The sample tributaries had a range in mean monthly discharge of <1 m^3s^{-1} to 1630 m^3s^{-1}(Table 1.1). The rivers encompass a range of drainage basin areas from 596 km^2 (Tranquille River) to 54 600 km^2 (Thompson River) (Water Survey of Canada 2001). Historically all the rivers were gauged, but stations on seven of the rivers have been dropped. Data for the Quesnel River were incomplete and were therefore not reported or used in statistical analyses. Gauging stations are operated by the Water Survey of Canada and measure discharge on a daily basis continuously throughout the year. The riparian vegetation also varied among the rivers, from relatively undisturbed forest to pastures.

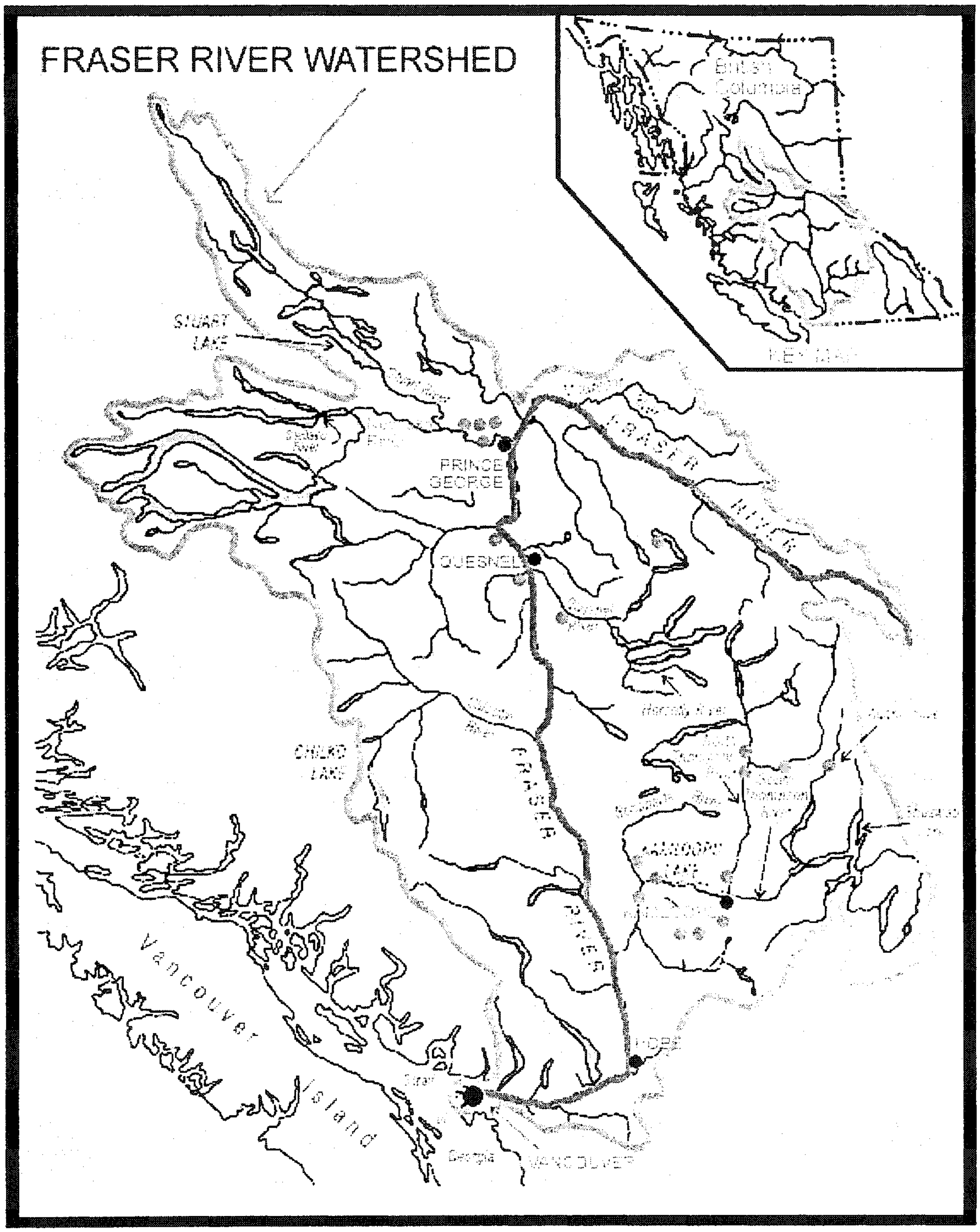

Figure 1.1: Fraser River drainage basin and location of sampling sites (indicated by ●) (for GIS co-ordinates see Appendix 1).

Field procedures

Samples from each river were collected on two sampling dates, during July and October 2001 (Appendix 2, 3). One riffle zone, closest to a gauging station in each tributary was selected. The light attenuation coefficient was first determined by making a minimum of four light readings at the surface, 10 cm, 20 cm and 30 cm using a LiCor 4-185B photometer. From this the coefficient was calculated according to Wetzel and Likens (1991). Two sites were then sampled within each riffle zone, approximately 10 m apart. Sites were chosen randomly by walking across the riffle zone to a depth of 15-30 cm. At the first site, a 2 L sample of river water for phytoplankton analysis was taken. At both sites within the riffle zone, the temperature and conductivity were measured with an S-C-T meter, YSI model 33. The water chemistry sample was taken with a separate 1L Nalgene bottle. The velocity readings were taken twice using a Gurley No. 625 Pygmy Current Meter, 3-5 cm above the rocks to be collected, in order to obtain an average micro-current velocity. Four small rocks (on average 5cm diameter) were then collected from each site, placed in a Ziplock bag and stored in a cooler until processed.

Within 12 hours of collection, 500 – 1000 ml of river water was filtered through Whatman Glass microfibre 934-AH 42.5 mm filters, which were immediately frozen and later analyzed for planktonic chlorophyll *a*. The rocks were then scrubbed with a nylon bristled nailbrush and rinsed with 500 - 800 ml of filtered river water. Between 20–50 ml of the periphyton wash was filtered through Whatman Glass microfibre 934-AH 42.5 mm filters and was immediately frozen for subsequent chlorophyll *a* analysis. To estimate ash-free dry mass (AFDM, $g \cdot m^{-2}$), 30 – 120 ml of periphyton wash was filtered through pre-ashed filters (heated at 500°C for 15 min (Chételat et al. 2000) and also frozen. A 20 ml sample of the river water and periphyton wash from both sites was preserved in 0.5 ml of Lugol's solution.

The surface area of the rocks was determined by wrapping the rock in aluminum foil and multiplying the mass of the foil by an area/mass conversion factor. Both periphyton chlorophyll *a* ($mg \cdot m^{-2}$) and AFDM ($g \cdot m^{-2}$) are reported per unit of rock surface area.

Laboratory procedures

Pigments were extracted from the thawed samples with 5 ml of dimethylsulfoxide (DMSO). Then 10 ml of 90% acetone was added and the absorbancies were measured with a spectrophotometer. Chlorophyll *a* concentration was calculated with a trichromatic equation according to Wetzel and Likens (1991). AFDM, a measure of the total organic matter of a benthic biofilm, was calculated as the mass of carbon based material, such as algae and invertebrates, lost upon combustion (Chételat et al. 2000). The dry mass was estimated by weighing dried filters (that were left overnight at 65°C in a drying oven) after which they were ashed at 500°C for 4 hours and then re-weighed.

The Pacific Environmental Sciences Center (PESC), using the methods of Environment Canada (1979), analyzed the water chemistry samples. Turbidity (minimum detection limit (MDL): 0.05 NTU), ammonium (NH_3, MDL: 0.005 mg/l), total nitrogen (TN, MDL: 0.02 mg/l), nitrate-nitrite ($NO_2 + NO_3$, MDL: 0.002 mg/l), total phosphorus (TP, MDL: 0.002 mg/l), dissolved phosphorus (DP, MDL: 0.001 mg/l) and reactive silica (SiO_2, MDL: 0.1 mg/l).

Daily discharge values for the rivers were obtained from Water Survey of Canada gauging sites. The three-day and seven-day mean discharges were calculated as the average of the daily discharges prior to and including the sampling date in a manner similar to that of Basu and Pick (1997). Drainagae area influences discharge and nutrient loading to rivers and was obtained for each river from the Water Survey of Canada. The drainage area for each site represents the upstream watershed area at each gauging site. WRT was estimated as a function of river discharge and drainage area (Soballe and Kimmel 1987), using Leopold's equation (Leopold et al. 1964):

$$R_d=0.08A_d^{0.6}/Q_d^{0.1}$$

Where R_d is water residence time at the sampling site (d), A_d is watershed area (km^2) and Q_d is the seven-day mean discharge ($m^3\ s^{-1}$) of the river (Soballe and Kimmel 1987).

Data Analyses

The biological variables were separately correlated (Pearson correlation coefficients and Bonferroni-corrected probabilities were used) with each of the chemical and physical variables, in order to conduct a preliminary investigation of interrelationships.

Linear regression equations were derived to predict the biological (dependent) variables from the independent variables, such as TP, TN and WRT. All of the variables, except the October current velocity, were log transformed to satisfy the assumptions of a linear regression. The data were log transformed after they were graphically examined for normal distributions and checked for homogeneity of variance, using the Kruskal-Wallis Test Statistic. Once log transformed, a series of multiple regressions were conducted in order to determine the best predictor variables. The best regression equations were defined as having the highest r^2 and limited multicollinearity ($r < 0.6$ between any pair of independent variables) (Zar 1998).

Results

Physical and chemical parameters

Mean river discharge increased in relation to drainage basin size of the tributaries. Mean monthly discharge rates ranged in July from 2.2 m^3 s^{-1} in Deadman river to 1630 m^3s^{-1} in the Thompson River (Table 1.1). In October the lowest monthly discharge was also in Deadman River at 0.8 m^3 s^{-1}, while the largest discharge was 368 m^3 s^{-1}, again in the Thompson River. The discharge in July was significantly higher than in October, which was evident both visually (Figure 1.2) and statistically with a comparison of the monthly means (mean monthly discharge for all rivers (± SD): July 198.5 ± 325.9 m^3 s^{-1}; October 70.2 ± 112.0 m^3 s^{-1}; 2 tailed $t = 6.94$, $p<0.001$, $n=13$).

The mean current velocity (± SD, $n=19$) in the riffle zones was 29.3 ± 12.3 cm s^{-1} in July and was slightly higher in October with a mean velocity of 33.5 ± 20.3 cm s^{-1}. The highest velocity in July was measured in Spius Creek at 50.8 cm s^{-1}, while the lowest was 11.4 cm s^{-1} in the North Thompson River. In October, the highest velocity was 80.4 cm s^{-1} in Barrier River and the lowest was 1.9 cm s^{-1} in the Nechako River.

In July, the log-transformed mean daily was negatively related to velocity ($r= -0.75$, $p=0.001$). The same negative relationship was observed in October, although it was not as strong (log-transformed mean monthly discharge $r=-0.49$, $p>0.05$, log-transformed daily discharge $r= -0.53$, $p=0.06$). Current velocity was also negatively correlated with drainage area (July $r= -0.54$, $p=0.02$; October $r= -0.40$, $p>0.05$).

For all the rivers, flood events, defined as greater than three times median flow (Clausen and Biggs 1997), only occurred during the snowmelt months of April and May. The yearly maximum flow occurred during April and May for all the rivers. The lowest flow period occurred during February and March, although by October the hydrograph of all the rivers had reached a stable low flow, which only decreased further during winter conditions. Even after the most severe flooding event periphyton biomass has been found to take a maximum of 70 to 100 days to recover (Biggs and Stokseth 1996). Therefore, because of the lack of flooding events less than 70 days before both sampling periods, flooding events were not used in any subsequent analysis.

The water chemistry of the rivers covered a wide range of values for most of the variables, total phosphorus (TP) and total nitrogen (TN) ranged in July from 2 to 222 μg L^{-1} and 30 to 575 $\mu g\ L^{-1}$ respectively (Table 1.2a). In October, the TP concentrations of five rivers were below detection level (2 $\mu g/l$) and were assigned a value of 1$\mu g/l$.

Some of the physical and chemical variables were highly correlated with each other (Table 1.3). The water chemistry variables were not significantly correlated with any of the hydrological variables except for conductivity (log conductivity with log monthly mean discharge $r= -0.724$, $p<0.001$, $n=13$, Appendix 4). The TN/TP ratio also varied greatly, from 2.4 to 43.8 in July and 4.1 to160.0 in October (Table 1.2a). A TN/TP ratio of less than 15 suggests that nitrogen may be the limiting nutrient for algal growth (Stelzer and Lamberti 2001). In July, seven of the 19 rivers sampled were potentially nitrogen limited, whereas in October only three of the rivers may have been nitrogen limited (Table 1.2a).

Phytoplankton

The phytoplankton chlorophyll *a* was significantly higher in July compared to October ($t= 6.3$, $p<0.05$) and had a much larger range (Table 1.2b, 1.4). The phytoplankton biomass in July was best predicted with a simple regression with total phosphorus (log chl *a* = 0.51 log TP - 0.30; r^2=0.70, p<0.001, n=19, Fig. 1.3). The October phytoplankton was best described by a multiple regression with conductivity, current velocity and total nitrogen (log chl *a* = 1.72 log conductivity + 0.78 log velocity + 0.86 log TN - 7.71; r^2=0.57, p=0.004, n=19). When TN was removed the regression explained 48% of the variation (p=0.005). The July phytoplankton was not significantly related to discharge (daily, three-day and seven-day discharge means). In October there was a stronger, but not significant, negative correlation between daily discharge and chlorophyll *a* (r= -0.43, p=0.08). Only a small positive correlation was found between the chlorophyll *a* concentration and WRT in July (r=0.278, p=0.04), while in October there was no correlation (r= -0.14, p= 0.64).

Periphyton

The July periphyton chlorophyll *a* was uniformly low, as was the ash-free dry mass (AFDM); these ranged from 0.9-7.6 $g{\cdot}m^{-2}$ and 0.6-5.1 $g{\cdot}m^{-2}$ respectively (Table 1.2b, 1.4). In October, the periphyton chlorophyll *a* and AFDM were significantly higher (t=-5.07, p<0.000 and t=-4.71, p<0.000 respectively) than in July (Table 1.2b,1.4).

In July, periphyton chlorophyll *a* was correlated with TP, TN, conductivity, WRT and turbidity. The only significant regressions were with WRT (r^2=0.33, p=0.04, n=13) and TN (r^2=0.23, p=0.04, n=19) (Fig. 1.4, Table 1.5). However, these two variables did not explain much of the variation in periphyton chlorophyll *a*. With respect to AFDM, no significant relationship with TN was found. The regressions explained slightly more of the variation found in the AFDM (Table 1.5).

In October, only three variables were correlated with the periphyton chlorophyll *a*, TP, DP and conductivity (Table 1.5). Conductivity alone explained 35% of the variation ($p=0.008$), while DP alone accounted for 46% ($p=0.001$). In a simple regression TP was significantly related with biomass ($r^2 = 0.34$, $p < 0.05$) (Fig. 1.4). However, in a backward step-wise multiple regression, TP was removed to leave DP and conductivity with a fairly strong relationship, explaining 54% of the variation ($p=0.002$, $n=19$) (Table 1.5). The October AFDM was only significantly related to DP ($r^2=0.47$, $p=0.001$, $n=19$). Current velocity was not significantly related to either July or October biomass and there was no evidence of non-linear relationships.

Comparison with published algal biomass models

The models developed above for the Fraser tributaries were compared to published models from other regions. Basu and Pick (1996) examined 31 rivers in southern Ontario and western Quebec, using similar methodology and found a strong relationship between planktonic chlorophyll *a* and water column TP ($r^2=0.76$). The ranges of TP and phytoplankton chlorophyll *a* in the Basu and Pick (1996) data were 7.3 to 212.3 $\mu g \cdot l^{-1}$ and 1.8 to 27.6 $\mu g \cdot l^{-1}$ respectively, compared with the B.C. data, which covered a TP range of 2.0 to 222 $\mu g \cdot l^{-1}$ and chlorophyll *a* range of 0.9 to 18.9 $\mu g \cdot l^{-1}$ in July. For comparison with the July data (the October phytoplankton data were not used in the analysis because there was no significant relationship between TP and chlorophyll *a*), the entire data set was log-transformed and TP was regressed with chlorophyll *a*:

Present study regression ($r^2=0.70$, $p<0.001$, RMS = 0.03, $n=19$)

$$\log \text{chlorophyll } a = 0.51 \log TP - 0.32$$

Basu and Pick (1996) ($r^2=0.76$, $p<0.001$, RMS = 0.03, $n=31$)

$$\log \text{chlorophyll } a = 0.72 \log TP - 0.25$$

The slopes of these two lines were significantly different ($F_{1,51}=64.0$, $p<0.05$) based on analysis of covariance.

A similar comparison of regression slopes was carried out with the findings of Chételat et al. (1999) which reported a significant relationship between chlorophyll *a* of periphyton and TP ($r^2=0.56$, $p<0.001$) for 13 rivers in Eastern Ontario and Western Quebec. The range of Chételat et al. (1999) TP was 6.0 to 130.0 $\mu g \cdot l^{-1}$ and the periphyton chlorophyll *a* was 9.0 to 470 $mg \cdot m^{-2}$, compared with the B.C. data, which covered a TP range of 1.0 to 73 $\mu g \cdot l^{-1}$ and mean chlorophyll *a* range of 1.7 to 55.7 $mg \cdot m^{-2}$ in October. The Chételat data were then compared with the October periphyton data (the July periphyton data were not used because there was no significant relationship between chlorophyll *a* and TP). When the slopes of the following equations were compared, they were significantly different ($F_{1,53}= 85.5$, $p<0.05$).

Present study regression ($r^2 = 0.34$, RMS = 0.16, $p<0.005$, $n =19$)

$$\log \text{chlorophyll } a = 0.46 \log \text{TP} + 0.69$$

Chételat et al. (1999) ($r^2 = 0.56$, RMS = 0.071, $p<0.001$, $n=33$),

$$\log \text{chlorophyll } a = 0.91 \log \text{TP} + 0.49$$

Table 1.1: Summary of hydrological characteristics[1] of the Fraser River tributaries, sampled in July and October 2001. Standard deviation in parenthesis.

River	Drainage Area (km^2)	Mean Monthly Discharge (m^3 s^{-1})		Yearly Discharge Range (m^3 s^{-1})[3]	Mean Current Velocity (cm s^{-1})	
		July	October		July	October
Deadman	862	2.2 (1.7)	0.8 (0.02)	0.59 - 13.7	47.6 (1.1)	63.4 (29.3)
Spius	780	2.7 (1.2)	1.2 (0.8)	0.5 – 67.2	50.8 (1.3)	9.4 (4.3)
Bonaparte	5020	6.8 (2.1)	3.4 (0.1)	1.6 – 20.5	43.5 (12.4)	54.3 (13.5)
Nicola	4350	7.1 (2.5)	3.6 (0.5)	2.9 – 57.1	33.4 (0.5)	32.6 (15.5)
Baker	1570	7.6 (4.2)	1.7 (0.2)	0.75 – 22.1	19.3 (7.6)	52.1 (11.2)
Barriere	1140	22.7 (7.7)	3.5 (0.4)	2.25 – 92.7	42.9 (9.5)	80.4 (8.5)
Willow	3110	63.7 (35.8)	27.4 (4.8)	7.3 - 163	21.0 (0.8)	32.1 (3.8)
Bowron	3420	139.3 (75.7)	50.4 (5.1)	12.2 - 352	26.5 (4.7)	43.4 (6.1)
Adams	3080	156 (16.2)	44.8 (5.6)	12.5 - 197	34.3 (33.8)	37.8 (8.4)
Nechako	42 500	455.4 (43.7)	168.4 (10.6)	103 - 528	11.5 (7.0)	1.9 (0.3)
North Thompson	4450	371 (78.4)	68.2 (13.3)	19.6 - 682	11.4 (4.5)	17.0 (1.2)
Clearwater	10 200	527 (60.0)	106 (18.0)	33.1-797.0	23.6 (8.4)	32.4 (3.3)
Thompson	54 600	1630 (130.1)	368 (60.2)	182 - 2250	13.1 (0.3)	12.8 (1.4)
Cariboo	2870	----[2]	----	----	31.3 (2.8)	10.0 (9.2)
Chilako	3390	----	----	----	25.3 (12.4)	20.5 (4.0)
Coldwater	914	----	----	----	22.3 (2.9)	33.3 (4.6)
Cottonwood	1910	----	----	----	22.5 (8.2)	30.8 (1.9)
Salmon	4300	----	----	----	45.4 (1.7)	51.1 (1.8)
Tranquille	596	----	----	----	31.6 (13.4)	21.6 (16.1)

[1] discharge and drainage area obtained from the Water Survey of Canada (2001)

[2] dashed line indicates discharge data not available

[3] minimum and maximum discharge values are from the sampling year, 2001

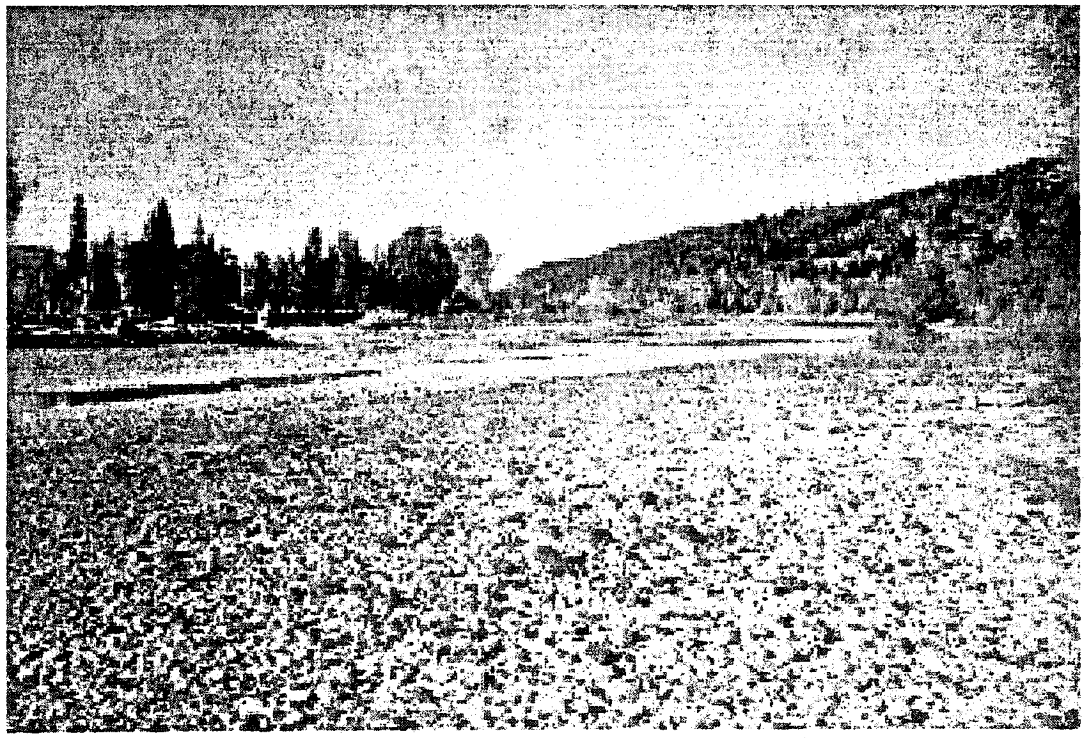

Figure 1.2: Cariboo River at high flow in July, 2001 (above) and the Clearwater River at low flow in October, 2001.

Table 1.2a: Summary of water chemistry characteristics, of the study rivers for July and October 2001 (TP, total phosphorus; TN, total nitrogen). SD in parentheses.

River	Conductivity (µS/cm)		Turbidity (NTU)		TP (µg/l)		TN (µg/l)		TN/TP	
	Jul	Oct	Jul	Oct	Jul	Oct	Jul	Oct	Jul	Oct
Adams			3.4	0.6	11	1	160	160		
	20	70	(0.2)	(0.0)	(5.6)	(0.0)	(0.0)	(56.6)	14.5	160
North Thompson			8.1	1.4	11	1	105	150		
	35	55	(0.3)	(0.0)	(0.0)	(0.0)	(7.1)	(14.1)	9.5	150
Spius			0.3	0.1	3	1	50	115		
	40	109	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(63.6)	16.7	115
Clearwater			0.5	0.3	4	2	175	190		
	60	85	(0.0)	(0.4)	(0.0)	(1.4)	(7.1)	(28.3)	43.8	95
Cottonwood			1.8	1.2	7.5	6.5	135	150		
	60	55	(0.1)	(0.1)	(0.7)	(1.4)	(7.1)	(28.3)	18.0	23.1
Willow			11.9	5.7	28.5	16.5	200	315		
	62	58	(1.4)	(4.0)	(9.2)	(0.7)	(0.0)	(205)	7.0	19.1
Thompson			1.3	0.4	7	7	145	215		
	65	85	(0.2)	(0.0)	(0.0)	(0.0)	(7.1)	(91.9)	20.7	30.7
Barriere			0.4	0.2	3	1	90	145		
	70	110	(0.1)	(0.0)	(0.0)	(0.0)	(0.0)	(63.6)	30.0	145
Nechako			3.6	2.0	15	8.5	250	170		
	82	71	(0.0)	(0.4)	(0.0)	(2.1)	(0.0)	(0.0)	16.7	20
Coldwater			0.3	0.2	2	1	35	30		
	94	142	(0.0)	(0.0)	(0.0)	(0.0)	(7.1)	(34.6)	17.5	30
Bowron			2.5	1.3	10	4	100	65		
	105	95	(0.1)	(0.1)	(1.4)	(0.0)	(0.0)	(7.1)	10.0	16.3
Salmon			2.2	1.9	13	10	345	230		
	112	90	(0.0)	(0.1)	(0.0)	(0.0)	(7.1)	(0.0)	26.5	23
Baker			5.1	2.9	79	73	475	300		
	120	125	(0.4)	(0.3)	(0.0)	(1.4)	(7.1)	(0.0)	6.0	4.1
Cariboo			2.0	0.9	6	4	105	140		
	130	75	(1.7)	(0.2)	(2.8)	(0.0)	(63.6)	(14.1)	17.5	35
Chilako			9.0	3.1	59	37.5	420	280		
	170	185	(0.4)	(0.4)	(2.8)	(0.7)	(7.1)	(14.1)	7.1	7.5
Deadman			0.6	0.4	11.5	6	200	180		
	190	195	(0.2)	(0.0)	(0.7)	(0.0)	(14.1)	(42.4)	17.4	30
Nicola			2.4	1.2	17.5	8.5	275	575		
	200	205	(0.6)	(0.2	(0.7)	(0.7)	(7.1)	(106)	15.7	67.6
Bonaparte			2.8	1.0	25	12.5	345	210		
	285	225	(0.1)	(0.2)	(1.4)	(0.7)	(7.1)	(0.0)	13.8	16.8
Tranquille			33.8	0.2	222	35	525	205		
	412	147	(0.2)	(0.0)	(1.4)	(1.4)	(7.1)	(77.8)	2.4	5.9
Median	94	95	2.4	1.0	11	6.5	175	180	16.7	30
Mean	121.7	114.8	4.8	1.3	28.2	12.4	217.6	201.3	16.4	52.3
SD	96.7	53.9	7.7	1.4	51.0	18.1	144.0	115.6	9.5	52.9

Table 1.2b: Summary of biological characteristics, of the study rivers for July and October 2001. SD in parenthesis.

River	Phytoplankton Chl *a* (µg/l)		Periphyton Chl *a* (mg/m^2)		Periphyton AFDM (mg/m^2)	
	Jul	Oct	Jul	Oct	Jul	Oct
Barriere	0.58	0.83	0.95	7.67	0.65	1.65
	(0.38)	(0.93)	(0.27)	(1.17)	(0.28)	(0.08)
Coldwater	0.84	0.04	1.99	6.22	1.05	1.53
	(0.06)	(0.01)	(0.42)	(3.15)	(0.19)	(0.43)
Cariboo	0.91	0.03	4.15	13.92	1.35	7.66
	(0.01)	(0.01)	(2.85)	(7.02)	(0.37)	(0.89)
Cottonwood	0.95	0.03	1.27	2.46	0.99	2.08
	(0.02)	(0.01)	(0.37)	(0.15)	(0.70)	(0.24)
Spius	0.98	0.03	2.60	2.48	1.32	3.94
	(0.03)	(0.00)	(0.03)	(0.85)	(0.13)	(2.02)
N. Thompson	1.09	0.02	5.40	10.06	2.06	4.96
	(0.04)	---	(1.10)	(3.58)	(0.47)	(4.67)
Bowron	1.16	0.02	3.01	10.93	1.59	3.52
	(0.04)	(0.00)	(0.68)	(10.34)	(0.12)	(2.45)
Willow	1.24	0.06	3.05	1.74	1.63	15.05
	(0.31)	(0.02)	(1.20)	(0.32)	(0.47)	(1.21)
Thompson	1.26	0.07	4.92	11.25	1.80	1.16
	(0.07)	(0.01)	(1.48)	(0.79)	(0.19)	(0.32)
Clearwater	1.28	0.94	4.11	2.42	1.29	0.74
	(0.32)	(1.27)	(1.03)	(0.42)	(0.24)	(0.29)
Adams	1.39	0.03	2.07	2.58	1.30	1.85
	(0.04)	(0.01)	(0.01)	(1.23)	(0.20)	(0.51)
Salmon	2.15	0.03	5.25	14.68	2.60	10.93
	(0.13)	(0.00)	(0.00)	(2.32)	(0.08)	(11.84)
Baker	2.37	2.04	2.15	55.69	0.94	9.71
	(0.18)	(2.78)	(0.40)	(6.94)	(0.16)	(8.60)
Deadman	2.75	2.02	6.20	24.43	1.72	5.57
	(0.14)	(0.20)	(1.12)	(2.21)	(0.35)	(2.28)
Bonaparte	2.77	1.66	4.77	25.56	1.50	7.68
	(0.14)	(0.83)	(6.15)	(13.27)	(1.92)	(8.72)
Nechako	2.97	0.98	6.54	21.58	5.12	9.18
	(0.45)	(1.31)	(1.44)	(16.07)	(1.05)	(7.86)
Chilako	3.22	0.06	5.53	20.72	2.68	12.96
	(0.38)	(0.02)	(1.22)	(9.51)	(0.12)	(4.60)
Nicola	3.79	1.48	2.84	23.49	1.15	4.37
	(0.01)	(1.97)	(0.51)	(13.08)	(0.22)	(1.56)
Tranquille	16.68	0.01	7.65	71.11	3.09	1.71
	(3.12)	(0.01)	(6.50)	(17.06)	(0.51)	(0.13)
Median	1.26	0.4	3.05	10.93	1.35	3.94
Mean	2.55	0.54	3.92	17.31	1.78	5.59
SD	3.55	0.75	1.90	18.32	1.03	4.32

Table 1.3: Pearson correlation matrix of the physical and chemical variables**

July

	Turbidity	TN	TP	$NO_{2,3}$	DP	Light	Conduct	pH	Temp
Turbidity	1.00								
TN	0.64	1.00							
TP	0.85*	0.84*	1.00						
$NO_{2,3}$	0.00	-0.21	-0.30	1.00					
DP	0.63	0.50	0.74*	-0.19	1.00				
Light	0.55	0.13	0.45	-0.06	0.21	1.00			
Conduct	0.27	0.57	0.61	-0.54	0.54	0.28	1.00		
pH	-0.38	-0.04	-0.24	-0.33	-0.25	-0.27	0.36	1.00	
Temp	-0.30	0.17	-0.01	-0.56	-0.34	-0.02	0.41	0.44	1.00

October

	Turbidity	TN	TP	$NO_{2,3}$	DP	Light	Conduct	pH	Temp
Turbidity	1.00								
TN	0.45	1.00							
TP	0.48	0.57	1.00						
$NO_{2,3}$	-0.30	0.13	-0.61	1.00					
DP	0.11	0.29	0.74*	-0.47	1.00				
Light	0.52	0.22	0.47	-0.38	0.14	1.00			
Conduct	-0.27	0.13	0.35	-0.11	0.51	-0.02	1.00		
pH	0.07	-0.06	0.01	0.04	-0.06	-0.15	0.22	1.00	
Temp	-0.13	0.27	-0.03	0.24	-0.36	0.15	-0.02	-0.23	1.00

* Bonferroni-corrected probability $p<0.05$

** for correlation matrix and hydrological variables see Appendix 4

Note: all variables were log transformed

Table 1.4: Summary of biological measures (mean ± SD) of the study rivers for July and October 2001. Range in parentheses.

	July	October
Phytoplankton chlorophyll *a*	2.6±3.55	0.5±0.8
$(\mu g \cdot l^{-1})$*	(0.9-18.9)	(0.2-4.0)
Periphyton chlorophyll *a*	3.9±1.9	17.3±18.3
$(mg \cdot m^{-2})$ *	(0.9-7.6)	(1.7-71.1)
AFDM $(g \cdot m^{-2})$ *	1.8±1.0	5.6±4.3
	(0.6-5.1)	(0.7-13.0)

*significant difference between July and October means (two tailed *t*-test, $p<0.05$)

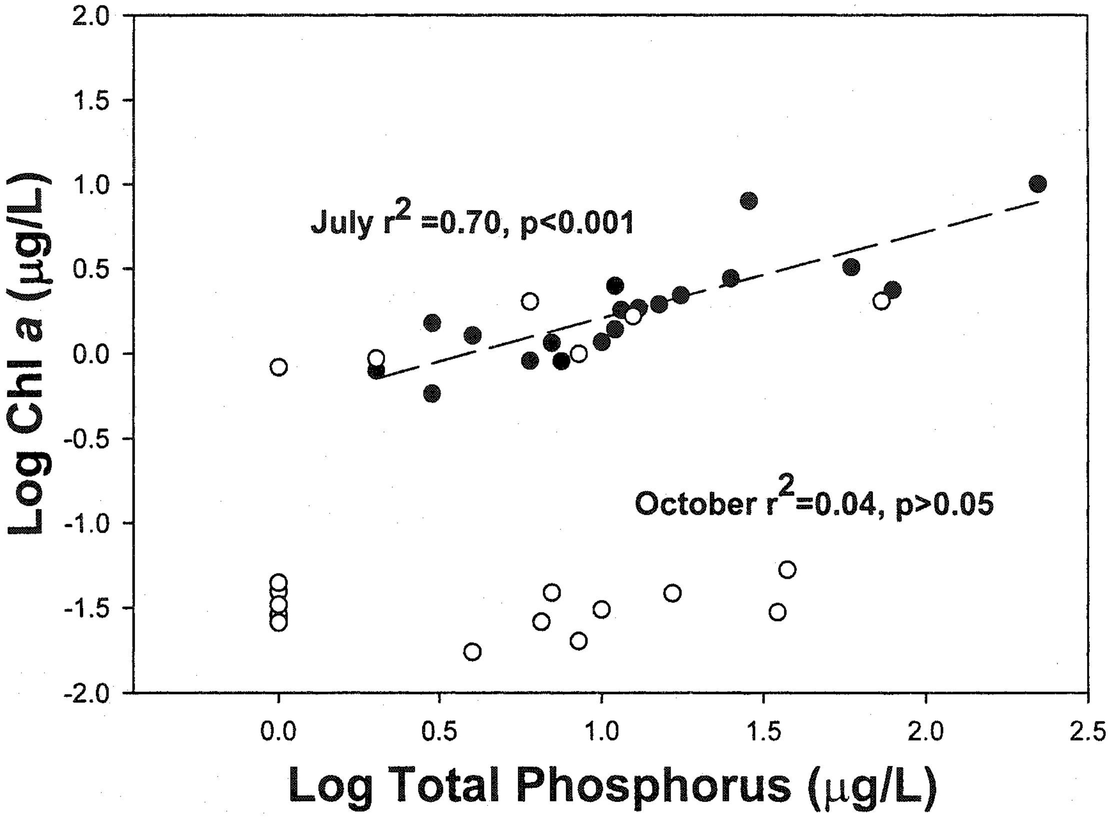

Figure 1.3: Linear regression between phytoplankton chlorophyll *a* and TP for 19 Fraser River tributaries in July (•) and October (◦), 2001. Regression line through July data (log chlorophyll *a* = 0.51 logTP - 0.32).

Table 1.5: Summary of significant regression models relating July and October periphyton chlorophyll *a* ($mg \cdot m^{-2}$) and AFDM ($mg\ m^{-2}$) and environmental variables (n=19 for all variables except WRT where n=13).

Equation	r^2	F	P
July			
log chl *a* = 0.499 log WRT + 0.066	0.33	5.43	0.04
log chl *a* = 0.368 log TN - 0.290	0.23	5.0	0.04
log AFDM = 0.206 log turbidity + 0.129	0.28	6.50	0.02
log AFDM = 0.489 log WRT – 0.271	0.41	7.53	0.02
October			
log chl *a* = 0.43 log DP + 0.79 log cond - 0.7	0.54	9.4	0.002
log chl *a* = 0.57 log DP + 0.85	0.46	14.3	0.001
log chl *a* = 1.43 log cond - 1.86	0.35	9.1	0.008
log AFDM = 0.46 log DP + 0.42	0.47	14.9	0.001

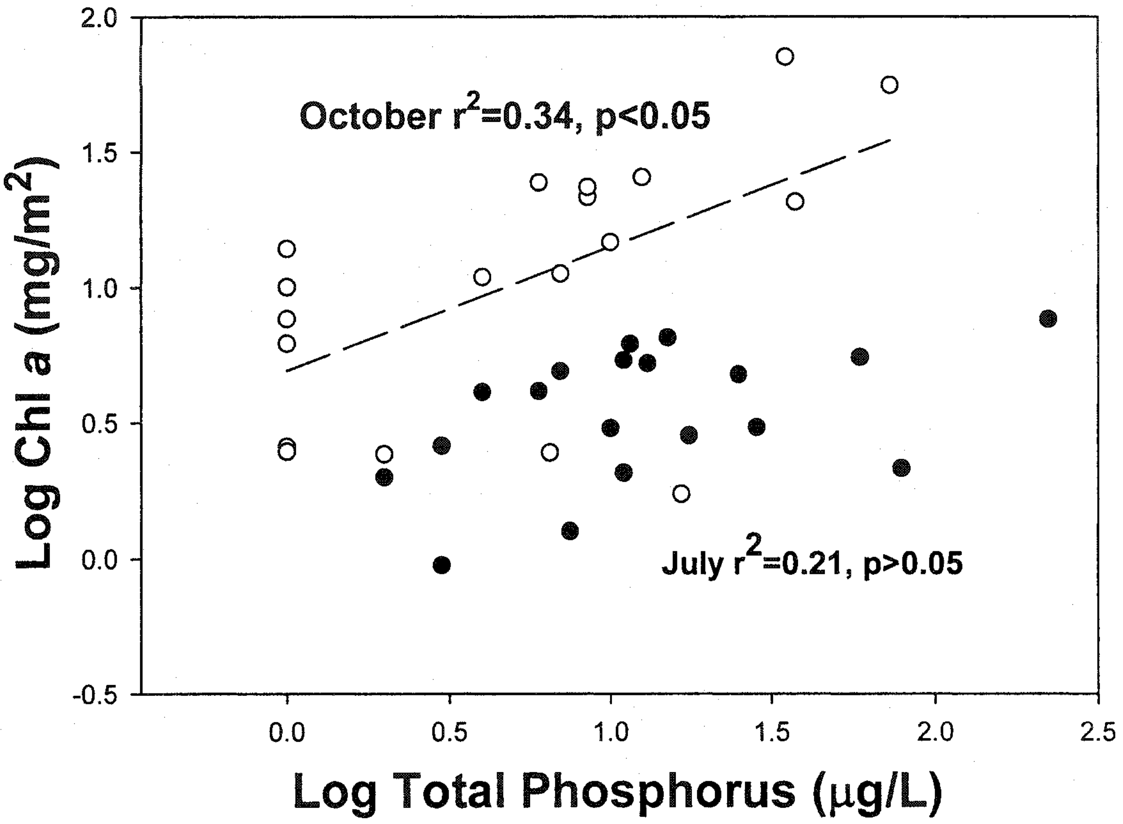

Figure 1.4: Linear regression between periphyton chlorophyll *a* and TP for 19 Fraser River tributaries sampled in July (•) and October (◦), 2001. Regression line through October data (log chlorophyll *a* = 0.46 logTP + 0.69).

Discussion

In unenriched streams with hard metamorphic rocks and low conductivity, such as the Fraser River tributaries, it is typical to have low algal biomass levels (Biggs 1996). The designations for oligotrophic and eutrophic streams can be based on nutrient concentrations or chlorophyll *a*. According to Biggs (1996) an oligotrophic stream has a mean periphyton chlorophyll *a* of 1.7 $mg \cdot m^{-2}$, while a mesotrophic stream begins at 21 $mg \cdot m^{-2}$ and a eutrophic stream has higher than 84 $mg \cdot m^{-2}$ of chlorophyll *a*. By this definition, all the streams were oligotrophic in July, while some of them reached mesotrophic levels in October. However, several other sites in October had total phosphorus concentrations at the detection limit, suggesting ultra-oligotrophy.

Phytoplankton chlorophyll *a* showed almost the reverse seasonal trend from the periphyton. In July, nutrients were highly correlated with chlorophyll *a*, with TP explaining 70% of the variation, while in October current velocity and conductivity accounted for 48% (Fig. 1.4). It should be noted that in October there were six rivers with higher phytoplankton biomass values than the other rivers. No similarity was found between these six rivers and the difference is likely due to unmeasured factors, such as grazing.

Van Nieuwenhuyse and Jones (1996) compiled data from 24 published and unpublished sources of rivers in North America and Europe and found a very strong, significant relationship between phytoplankton and TP ($r^2 = 0.67$). Basu and Pick (1996) examined 31 rivers in southern Ontario and western Quebec, over a similar TP range, and found a strong relationship of riverine phytoplankton with TP ($r^2=0.76$).

The slope of TP versus chl *a* model of the BC model was compared to the Basu and Pick (1996) with an analysis of covariance findings, and the Basu and Pick (1996) slopes was significantly higher and steeper than this thesis' model. A similar analysis with the Van Nieuwemhuyse and Jones (1996) model that covered a broader range of TP lead to a similar result. Less planktonic chl *a* was produced in Fraser River tributaries per unit of TP in comparison to the Ontario/Quebec rivers. The dissimilarity of these regressions points to the need for regional models when assessing stream phytoplankton-nutrient dynamics.

The periphyton also showed a relationship with total phosphorus, but in October, which is opposite to what was observed with phytoplankton biomass (Fig. 1.3, 1.4). While a significant relationship was found with TP and periphyton chlorophyll *a*, it should be noted that there were five rivers with considerably lower biomass levels in October. These rivers do not correspond to the rivers with high phytoplankton biomass mentioned previously. The only similarity among the five rivers is that they are the rivers with the five lowest conductivity levels (Table 1.2). This result is not surprising because a multiple regression including both TP and conductivity explained a larger amount of the variation than TP alone. Previous studies have also found conductivity to be a significant predictor of periphyton communities (e.g., Biggs 1990).

Although a significant relationship was found with TP and chlorophyll *a*, the October periphyton biomass was best predicted by a multiple correlation with ambient concentrations of phosphorus and conductivity. The studies of Aizaki and Sakamoto (1988), Dodds et al. (1997) and Chételat et al. (1999) reported relationships between periphyton and both TN and TP. Biggs and Close (1989) found dissolved phosphorus (DP) best explained biomass variation in conjunction with velocity. These studies were conducted during the low flow period of summer months, which corresponds to the low flow period in October in BC rivers. Horner and Welch (1981) found that phosphorus concentrations affected the response of periphyton to different current velocities, in streams near Seattle, Washington. Chételat et al. (2000) also found a positive relationship with total phosphorus and chlorophyll *a* in riffle zones of three large rivers in Ontario. Low flow periods are often extended periods of stable hydrological conditions, during which point nutrients will be most important in influencing biomass accrual in streams (Biggs 2000b).

While the best predictive model was a multiple regression with conductivity and DP, conductivity alone explained 35% of the variation of chlorophyll *a* in October. Chételat et al. (1999) also found that conductivity was a better predictor of periphyton biomass than TP in Eastern Ontario rivers ($r^2 = 0.71$ and $r^2 = 0.56$ respectively).
The difference in the responses of periphyton biomass levels in July compared to October may be in part related to changes in nutrient limitation. In July the rivers tended to be either moderately phosphorus limited or nitrogen limited, indicated by a low TN:TP ratio (Table 1.2). Perrin and Richardson (1997) found that nitrogen was likely the limiting factor in the development of periphyton in the Nechako River (one of this thesis' study rivers), BC. They found that additions of N +P in the spring (the period of high flow) increased periphyton growth more than additions of phosphorus alone.

Water residence time (WRT) was related to periphyton biomass in July but the regression only explained a small amount of the variation. WRT is a function of discharge and drainage area, however since only the former changes seasonally, discharge would also be expected to be related to periphyton biomass. This was not the case as found in the correlations of chl *a* (or AFDM) with velocity, discharge or catchment size. This implies that the significant regression of WRT and periphyton may not be biologically significant and does not provide insight into the functioning of the system.

A comparison of regression slopes was carried out with the findings of Chételat et al. (1999) who reported a significant relationship between chlorophyll *a* of periphyton and TP in riffle zones of Eastern Ontario and Western Quebec rivers. Their slope was significantly different from the B.C. slope. This implies that, as in the case of the phytoplankton, the periphyton biomass yield per unit TP differs between the two regions.

Few studies have examined both the periphyton and phytoplankton communities simultaneously in rivers. In the Fraser River system, the large and opposite changes in phytoplankton and periphyton biomass from July to October imply a seasonal shift in dominance in the riffle zones of these tributaries. Because the rivers tended to be shallower in October, the low phytoplankton biomass is even lower when calculated on an areal basis (m^2) compared to July when water levels (and chlorophyll *a*) were higher. In October, the periphyton biomass exceeds the areal phytoplankton biomass and the converse is true for July.

It is possible that the switch in dominance is mainly related to changes in hydrology. In spring the rivers have very high discharge and frequent flooding events, consequently the periphyton get scoured from the rocks. The biomass then increases until stable flow is reached and remains high until winter, when there is a large decrease in biomass, likely due to freezing and light limitation (Biggs and Gerbeaux 1993).

However, the role of invertebrates (benthic or planktonic) in regulating algal biomass levels may also be a factor in the changes of biomass and was not investigated in this study. Benthic filter feeders have the potential to remove large quantities of phytoplankton in rivers (eg. Basu and Pick 1987), particularly in shallow depths. The invertebrate communities may have also changed between the two sampling dates and this should be further investigated.

CHAPTER 2:

Community composition in tributaries of the Fraser River, BC and the relationship with physical and environmental variables

Introduction

The structure of algal communities has a strong influence on energy transfer and food web interactions in aquatic systems (e.g., McCormick and Cairns 1994, Mullen-Navarra et al. 2000). Algal taxa vary greatly in their edibility and shifts in species composition can affect feeding relationships, population growth and biomass of higher trophic levels (Porter 1976; Lamberti and Moore 1986; DeMott and Moxter 1991; Biggs 2000b). For example, high nutrient loading in rivers can cause a shift from a diatom-dominated community to large filamentous algae (Chételat et al. 1999). Diatoms appear to be the best periphyton diet for most invertebrates because they are generally high in fats and lipids and are also easily grazed as they usually form moderate to thin films on stones (Biggs 2000b). In contrast, the diameter of large filamentous algae may be too large for grazers to process. Filamentous green algae or cyanobacteria may have little food value, or they may have anti-herbivory chemicals that render them unpalatable (Biggs 2000b).

The factors that affect algal community structure are clearly important to examine. In rivers, hydrology and nutrient availability appear to be the main factors affecting the periphyton community. Current velocity is the hydrological variable that appears to most directly influence periphyton communities. Biggs et al. (1998) summarized the effects of changes in current velocity as a function of the dominant periphyton growth form (Fig 2.1). For filamentous green algal communities (e.g., *Oedogonium*, *Spirogyra*, *Zygnema*), the highest biomass is often found at low velocities and any increase in velocity tends to result in major reductions in biomass because of the drag on the filaments. For communities dominated by loosely woven stalked diatoms and short filamentous taxa (e.g., *Didymosphenia, Gomphonema*), maximum biomass occurs at moderate velocities (~ 0.5 m/s). Increases in the transfer of nutrients enhance biomass accrual at the low end of the velocity gradient, whereas above 0.5 m/s, loss processes become progressively important. A third type of response is found in communities that form mucilaginous films (e.g., the diatom *Gomphoneis*). In these communities, biomass continues to increase with increases in velocity within the normal 0–1.0 m/s range found in most streams. The community is resistant to high current velocities and seems to require such conditions to form thick films (Biggs and Hickey 1994).

Another important hydrological variable that affects periphyton communities is the flood regime. Clausen and Biggs (1997) found that periphyton diversity was strongly reduced in streams with significant and frequent floods. However, the effect of the flood regime appears to be dependent on the nutrient status of the river (Biggs and Smith 2002). While Biggs and Smith (2002) found that flow perturbations generally reduced richness, the highest species richness occurred in streams with low to intermediate flood disturbance and intermediate to high concentrations of periphyton phosphorus.

Even with the complicating factor of hydrological disturbances, several studies have been able to develop models based solely on nutrients. Pan et al. (1996) developed diatom inference models for pH and total phosphorus concentration in streams in the Appalachian Mountains. Winter and Duthie (2000) found that eight environmental variables: temperature, total suspended solids, TP, conductivity, biological oxygen demand, pH, TN and alkalinity, each explained significant and independent directions of variance in diatom species in south-western Ontario rivers. Taxonomic changes at the division level have also been observed with respect to nutrient concentrations in some regional surveys of rivers (Biggs and Price 1987; Biggs 1990, Chételat et al. 1999).

This study examined the effects of hydrological and nutrient factors, during base flow conditions, on periphyton communities in tributaries of the Fraser River, British Columbia. I predicted that there would be a community change in relation to velocity, as described by Biggs (200b)(Fig. 2.1). I also predicted that taxa indicative of eutrophication would increase with higher nutrient concentrations.

The approach taken was to sample different tributaries, covering a broad range of discharge and nutrient concentrations. Two sites were sampled within a riffle zone because previous studies have successfully characterized periphyton and their habitats with as little as a single site per river (Biggs and Price 1987; Biggs 1988, 1990). Biggs and Gerbeaux (1993) concluded that results from one site could be used to characterize the river's environment and community because between-river differences are usually still greater than within-river differences.

In this study, the periphyton community structure was assessed to the genus level. This level of taxonomic resolution was used because of the success of previous genus based models. For example, Prygiel and Coste (1993) found that pollution indices based on algal genera had sufficient resolution to detect differences in most cases. Coste et al. (1991) also found that because of a strong correlation between a species versus genus level diatom index for water quality in French wetlands, it was possible to accurately assess water quality from a genus-level index. However, they found a marked decrease in the correlation as water quality deteriorated. Because of the considerable resources, expertise and expense needed to assess diatoms to species level (McCormick and Cairns 1994), a genus-based model would be a useful tool for management of rivers. To date, there are few ecological models for rivers in British Columbia in contrast to the extensive research on rivers of eastern North America.

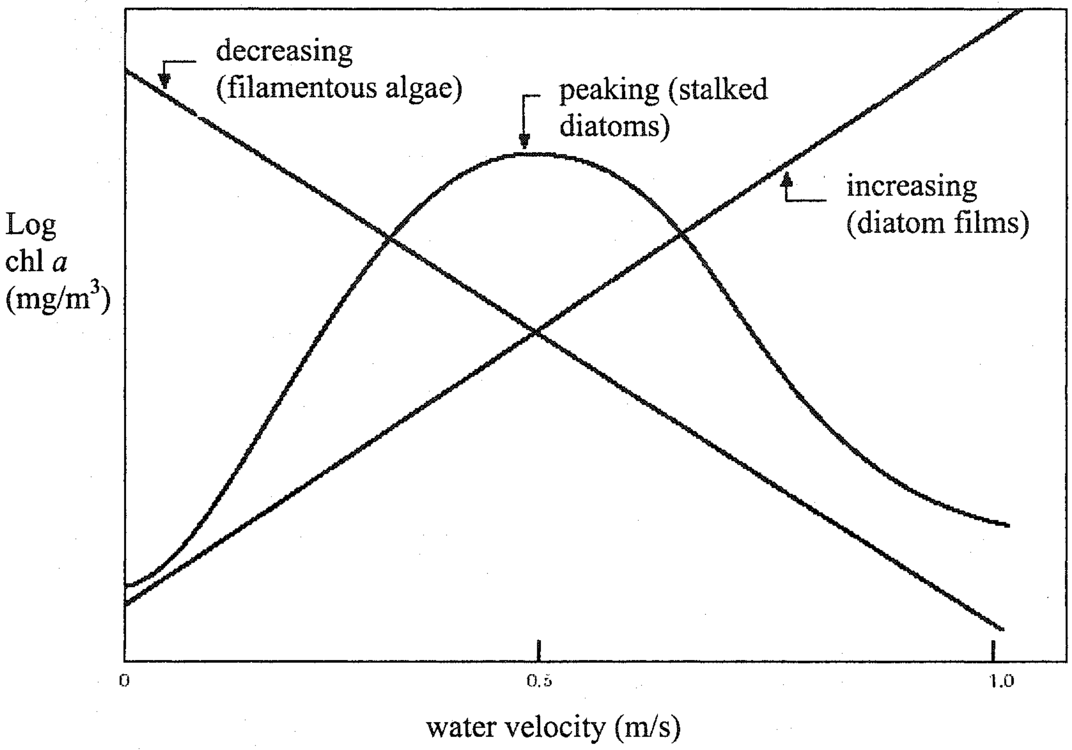

Fig 2.1: Three types of periphyton community responses to increasing water velocity (reproduced from Biggs 2000b)

Materials and Methods

A description of the Fraser River tributaries and field procedures can be found in the Materials and Methods section of Chapter 1 (pp 15-18).

Laboratory procedures

Four rocks were collected from two sites on each river, as described in Chapter 1. They were scrubbed with a nylon bristled nailbrush and rinsed with 500 - 800 ml of filtered river water. A 20 ml sample of the periphyton wash from both sites was preserved in 0.5 ml of Lugol's iodine solution. The surface area of the rocks was determined by wrapping the rock in aluminum foil and multiplying the mass of the foil by an area/mass conversion factor. A sub-sample of each preserved sample (0.4 – 1.5 ml) was then settled overnight (16 hours) in 25mm diameter sedimentation chambers. The settled sample was then enumerated by light microscopy on a Carl-Zeiss light microscope. For each sample, 300 to 1000 cells were counted along randomly selected transects (the diameter of transect equal to the diameter of the chamber) to ensure 85% to 90% counting accuracy (Lund et al. 1958). Cells were counted either at 100X or 400x magnification depending on their size dimensions. Cell counts and dimensions were recorded on an computer program to calculate cell biomass (Gosselain and Hamilton 2000). Non-diatom taxa were identified using Prescott (1973), and diatom identifications were based on Round et al. (1990) and Cox (1996).

Estimations of biovolume were based on measurements of four to twenty cells per taxon and the geometric shapes of cells as described by Hillebrand et al. (1999). Cell biomass was calculated based on biovolume ($mg\cdot m^{-3}$) converted to biomass ($mg\cdot m^{-2}$) assuming a density of one and normalized per unit surface area of rock. Total biomass was also separated into seven main divisions: Cyanobacteria, Chlorophyta, Bacillariophyta, Chrysophyta, Cryptophyta, Pyrrhophyta and Euglenophyta, of which only the first four were recorded in the samples. The raw data are provided in Appendix 5, along with the codes for the genera.

Data Analysis

The taxonomic data were analysed using two statistical approaches. First, Pearson correlations of the total periphyton biomass, division biomass and relative division biomass (percent contribution of a division to the total sample biomass) were conducted with the physical and chemical variables. Then a Pearson correlation matrix with common (found in >50% of the samples) and abundant (more than 5% of the total density of cells or total biomass) genera was also completed with the physical and chemical variables.

Secondly, community associations were first analysed using a correspondence analysis (CA) with Canoco software (Ter Braak 1998). A CA is an unconstrained ordination technique which can detect similarities in communities composition. A canonical correspondence analysis (CCA) was then done also using Canoco software (Ter Braak 1998). A CCA combines ordination with multiple regression analyses to detect patterns in species related to environmental variables. CCA is a direct gradient ordination method, which is appropriate to biological data having unimodal responses to environmental gradients and remains robust with absences. Axes (eigenvectors) are linear combinations of environmental variables against which species distributions are regressed. The assumption of unimodality of the genus biomass data was tested using a detrended correspondence analysis (DCA). If the gradient lengths were greater than two units of standard deviation, then a CCA is appropriate (Lowe and Pan 1996).

The gradients were long enough (3.3 SD for the first axis) to apply canonical correspondence analysis (Ter Braak 1998). Environmental variables required log-transformation due to their skewed distributions. Outliers were considered points with more than three standard deviations from the mean and none were detected (McIntire et al. 1996). Relative abundances of the diatom taxa were square-root transformed. Taxa that accounted for less than 5% of the total biomass in all the sites in which they occurred were removed from the analysis.

Results

The chemical and physical data are described in Chapter 1. Total phosphorus, total nitrogen and conductivity values for the 14 rivers with discharge data are provided again in Table 2.2.

Periphyton community

Total periphyton biomass ranged from 3.5 to 470.3 $mg \cdot m^{-2}$. On average, Bacillariophyta (diatoms) accounted for the largest percent of total biomass (mean ± SD: 76% ± 25.2), followed by Chlorophyta (21% ± 28.7), Cyanophyta (3.2% ± 5.9) and then Chrysophyta (0.03% ± 0.12) (Table 2.1). Genera richness was highest among diatoms (with a total of 31 genera), followed by Chlorophyta (14), Cyanobacteria (9) and Chrysophyta (Phaeophyceae) (1). The number of periphyton genera collected from the rivers ranged from seven to 22 (Appendix 5).

The rivers differed in terms of the dominance of specific taxa (Table 2.2). Genera were considered dominant if they were among the top ranking taxa that cumulatively accounted for 70% of total biomass (Chételat et al. 1999). Four rivers were characterised by one or two dominant genera, while the rest of the rivers had a more even distribution of taxa (Table 2.2). The North Thompson was dominated by one species, *Didymosphenia geminata*, which accounted for 77.1% of the mean biomass from both sites. Only two other rivers contained *D. geminata*, the Nicola and South Thompson, both with low levels of this species (<10% of the total biomass). *Epithemia sorex* and *Amphora ovalis* dominated the Baker River.

Strong dominance was also observed in the Cariboo River, with *Spirogyra* (filamentous Chlorophyta), accounting for most of the biomass. However, unlike other rivers, the two sites sampled differed in total biomass. One site contained additional biomass due to the presence of an unusual freshwater brown alga (*Heribaudiella fluviatilis*, Fig. 2.2). The two sites of the Barriere River also differed from each other. One site was dominated by *Synedra* (a diatom), while the second site was dominated by *Ulothrix* (a chlorophyte). The sites of both the Cariboo and Barriere rivers differed in turbidity and current velocity, which may have accounted for the observed differences in taxonomic composition.

There were three taxa found in all the rivers. The small diatom *Achnanthidium minutissima* was ubiquitous, ranging from 1 to 20 % of the total biomass. *Gomphonema* (mainly *G. olivaceum* and *G. parvuulum*) was also present at all sites, contributing from 1 to 28% of the total biomass. *Navicula* was the only other genus found at all the sites, ranging from 1 to 39% of the total periphyton biomass. Another commonly observed diatom was *Synedra*, which was dominant in eight of the rivers (Table 2.2).

Correlation Analyses

The total periphyton enumeration biomass (estimated from the count data) was highly correlated with the periphyton chlorophyll *a* ($r=0.81$, $p<0.001$), which is another estimate of algal biomass as discussed in Chapter 1. The enumeration biomass reflected the same trends with the environmental variables as chlorophyll *a* and was correlated with conductivity ($r= 0.57$, $p= 0.003$), total phosphorus (TP) ($r = 0.44$, $p= 0.02$) and dissolved phosphate (DP) ($r = 0.53$, $p= 0.005$). When included in a multiple backward stepwise regression, conductivity and DP remained and described 42% of the variation ($\log \text{biomass} = 1.4 \log \text{cond} + 0.86 \log \text{DP} - 1.14$; $p= 0.002$).

The only independent variable that was related to the total biomass of any phyla was conductivity, although sometimes weakly. In a regression with diatom biomass, conductivity explained 35% of the variation (log diatom-biomass=2.0 logcond -2.2; p=0.03) (Fig. 2.3). Chlorophyta biomass was not significantly related to conductivity ($r^2 = 0.1$, $p = 0.3$) or any other variables (Fig. 2.4). Cyanophyta biomass was only weakly related to conductivity, although not significantly ($r^2 = 0.30$, $p = 0.06$) (Fig. 2.5). The relative biomass of all three phyla, when considered separately, was not significantly related to any variable. The total and relative biomass of Chrysophyta was not used in any analysis because it was present only in one sample and therefore could not be statistically evaluated.

Along with phyla responses, four of the individual genera biomass estimates were also significantly related to conductivity, TP or DP (Table 2.3). These genera were ones that consisted of 1 or 2 species, with the exception of *Navicula*. With respect to relative biomass, only two genera, *Achnanthidium* and *Epithemia*, were correlated with TP (Table 2.3). The visible difference in taxonomic composition between rivers with high versus low phosphorus concentrations was visible, particularly because of the presence of *Epithemia* in the more enriched sites (Fig. 2.6 and 2.7). The lack of other pair-wise correlations between genera and environmental gradients is due to the unimodal responses, determined by a DCA, of all the other genera. Because of this, it was deemed that a CCA would be appropriate.

Ordination analyses

Preliminary correspondence analysis (CA) results, with no data transformations, detected significant differences between each river's periphyton community (Appendix 6). Baker, Cariboo and North Thompson rivers were significantly different from the other rivers in terms of their assemblages. This was likely due to the unique species that dominated each one (Table 2.2). It was found that the sites within a river clustered together.

The data were then transformed and genera that accounted for less than 5% of the biomass were removed from the analysis. A forward selection CCA, with the abundant genera (a total of 30 genera were used in the analysis) and the environmental variables, was conducted on the square-root transformed genus relative biomass data (Fig. 2.8). Current velocity and DP were the 2 significant vectors that explained 25% of the variation found in the genera data (Table 2.5).

Table 2.1: Relative biomass and total biomass of the three main periphyton algal phyla, determined through taxonomic enumerations, in Fraser River tributaries sampled October, 2001 (n=14).

	Bacilliariophyta	Chlorophyta	Cyanophyta	Chrysophyta
Mean relative contribution to biomass (%)				
Mean	76.2	20.6	3.2	0.03
Standard Dev	25.2	28.7	5.9	0.12
Minimum	12.1	0.0	0.0	0.0
Maximum	99.3	84.8	21.7	0.44
Total mean biomass (mg/m^2)				
Mean	111.0	39.1	6.1	0.3
Standard Dev	122.4	81.9	14.0	1.12
Minimum	2.6	0.0	0.0	0.0
Maximum	460.3	304.3	52.9	4.35

Table 2.2: Dominant genera of river periphyton communities in October with corresponding water chemistry variables and total biomass enumeration estimates (mean of both sites).

River	Biomass (mg/m^2)	Conductivity (µS/cm)	TN (µg/l)	TP (µg/l)	Dominant Genera (% contribution to total biomass)
Adams	3.5	70	160	1	*Navicula* (21), *Cymbella* (17), *Achnatidium* (16), *Stigoclonium* (13), *Gomphonema* (9)
Willow	8.3	58	315	16.5	*Synedra* (31), *Closterium* (28), *Navicula* (21)
Spius	17.3	109	115	1	*Synedra* (52), *Gomphonema* (11), *Epithemia* (10)
Clearwater	23.6	85	190	2	*Synedra* (55), *unknown desmid* (24)
Nechako	37.3	71	170	8.5	*Amphora* (18), *Diatoma* (16), *Cymbella* (15), *Navicula* (10), *Lyngbya* (8)
Bowron	106.9	95	65	4	*Synedra* (39), *Tabellaria* (20), *Navicula* (9)
Barrier	128.7	110	145	1	*Synedra* (45), *Ulothrix* (26)
N. Thompson	137.2	55	150	1	*Didymosphenia* (77)
Thompson	169.7	85	215	7	*Synedra* (32), *Stigoclonium* (18), *Didymosphenia* (9), *Fragillaria* (8)
Deadman	169.9	195	180	6	*Diatoma* (31), *Navicula* (25), *Gomphonema* (11), *Synedra* (9)
Bonaparte	235.3	225	210	12.5	*Synedra* (29), *Gomphonema* (19), *Navicula* (12), *Diatoma* (11)
Nicola	244.1	205	575	8.5	*Synedra* (25), *Navicula* (22), *Lyngbya* (15), *Cosmarium* (7)
Cariboo	358.7	75	140	4	*Spirogyra* (74)
Baker	470.3	125	300	73	*Epithemia* (76), *Amphora* (11)

Figure 2.2: The unusual freshwater brown alga *Heribaudiella fluviatilis* in the Cariboo River, magnification 400x.

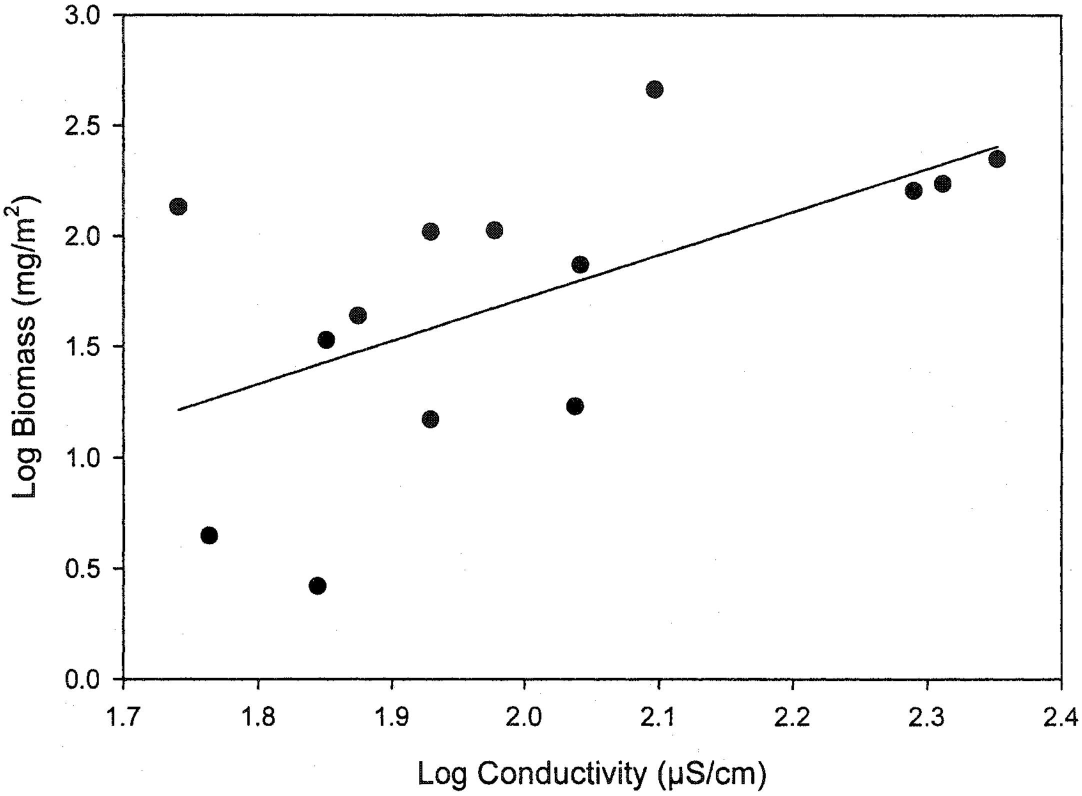

Figure 2.3: Linear regression of total diatom biomass in relation to conductivity (log biomass = 1.95 log conductivity – 2.18; $r^2 = 0.35$, $p = 0.03$, $n = 14$) from rivers in the Fraser River watershed, British Columbia, collected October 2001.

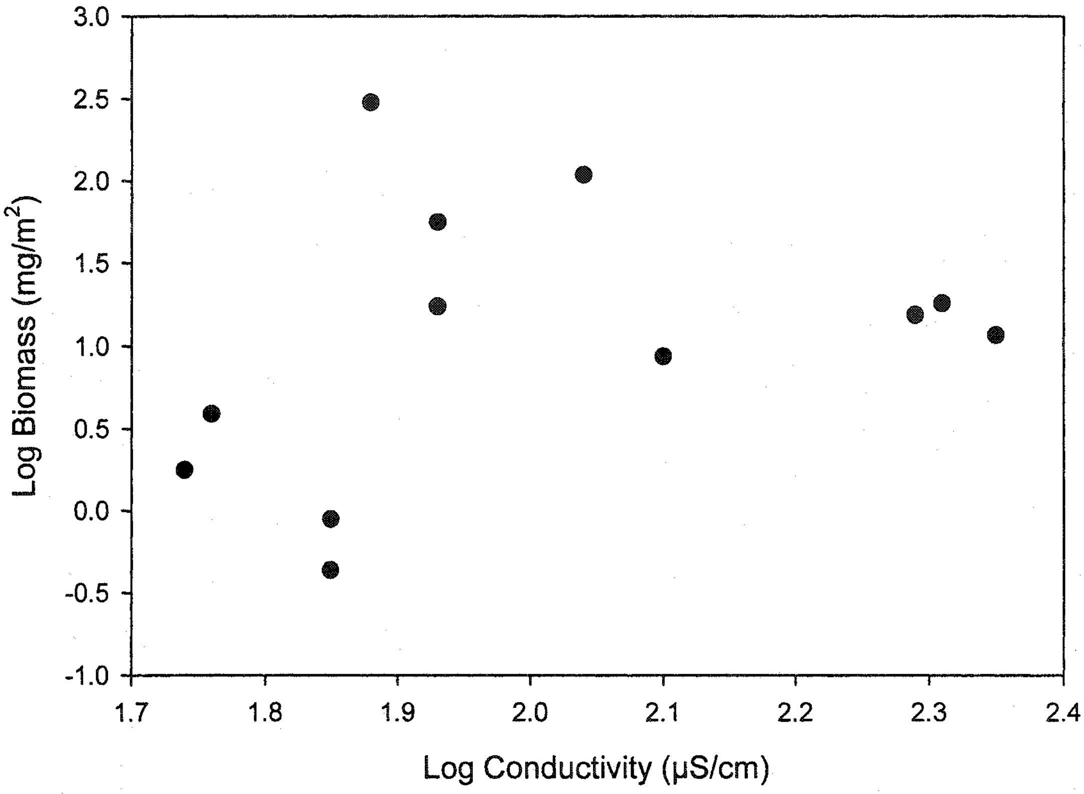

Figure 2.4: Linear regression of total Chlorophyta total biomass in relation to conductivity ($r^2 = 0.1$, $p = 0.3$, $n = 12$) from rivers in the Fraser River watershed, British Columbia, collected October 2001.

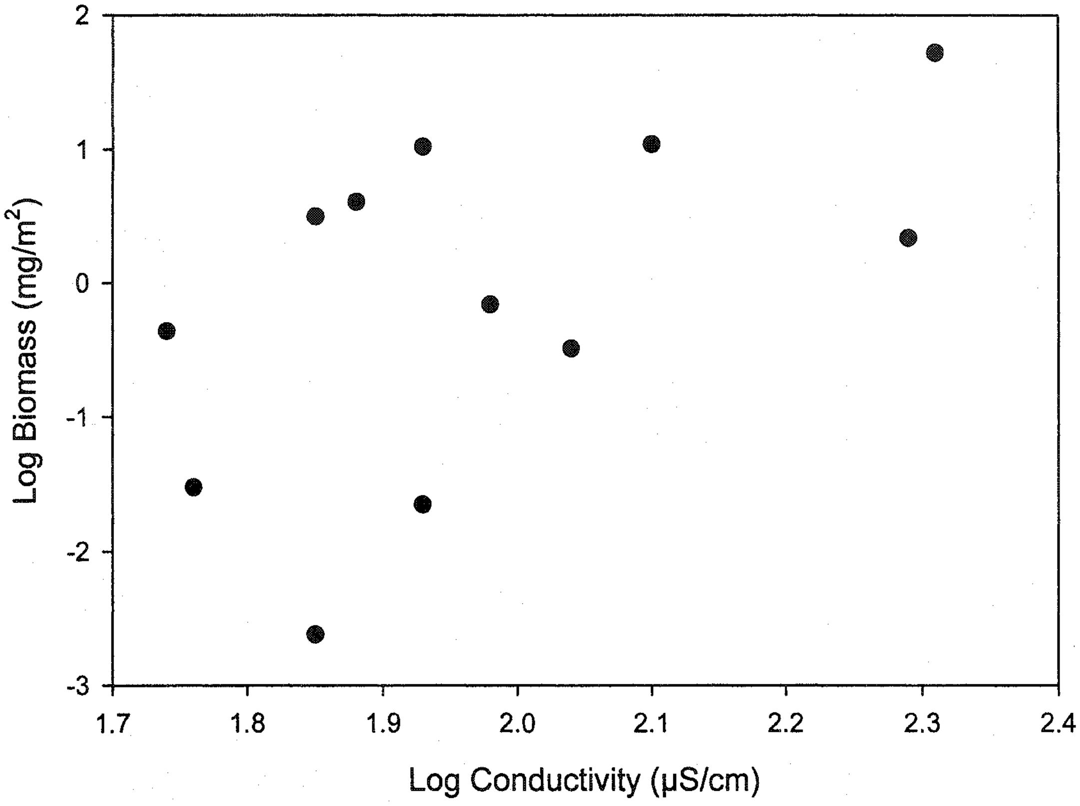

Figure 2.5: Linear regression of total Cyanophyta total biomass in relation to conductivity ($r^2 = 0.3$, $p = 0.06$, $n = 12$) from rivers in the Fraser River watershed, British Columbia, collected October 2001.

Table 2.3: Periphyton genera and species, identified in 14 British Columbian rivers and their correlation with conductivity and total phosphorus.

Genus	Species	Conductivity		TP	
		r	p	r	p
Biomass					
Amphora	*A. ovalis*	NS	---	0.69	0.004
Epithemia		NS	---	0.62	0.02
Gomphonema[1]	*G. angustum* *G. olivaceum*	0.72	0.001	NS	---
Navicula		0.67	0.008	NS	---
Relative Biomass					
Achnanthidium[1]	*A. minutissimum*	NS	---	- 0.76	0.001
Epithemia		NS	---	0.61	0.04

[1] log transformed

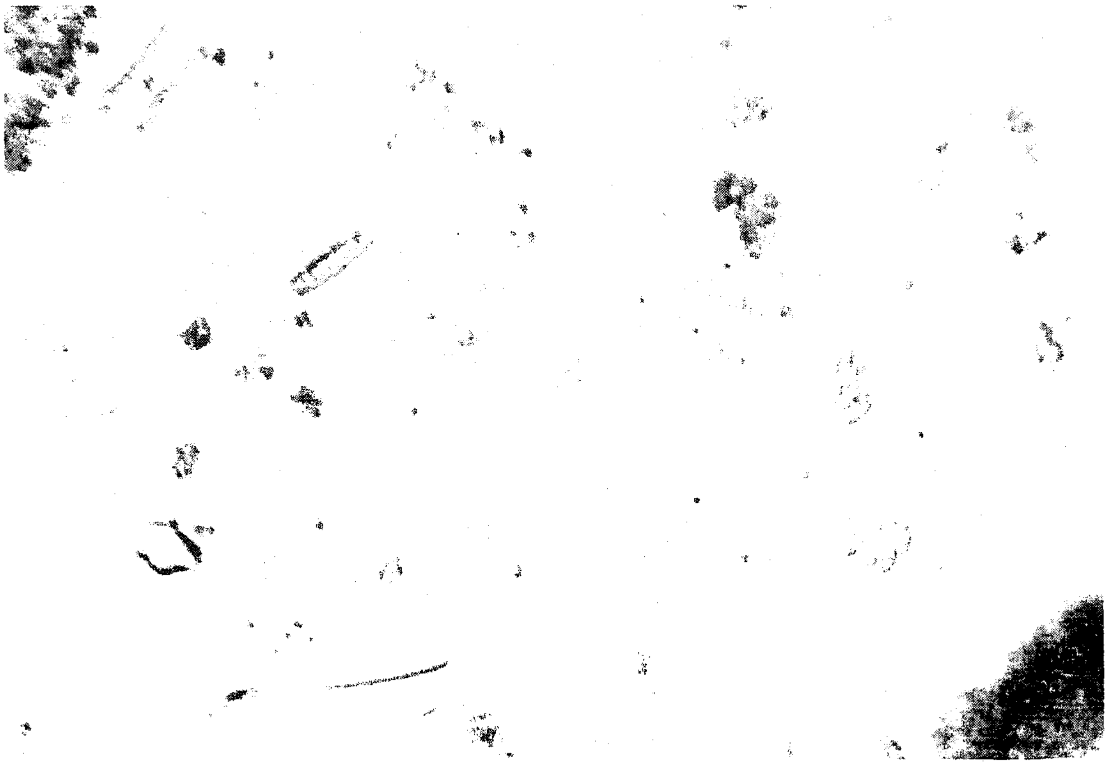

Fig. 2.6: Periphyton sample preserved in Lugol's solution, of the mesotrophic Nicola River (8 µg/l TP) at 100x, (0.5 mL settled). Various chlorophytes, such as *Scenedesmus sp.* and *Merismopedia sp.*, along with co-dominant taxa *Navicula sp.* are present.

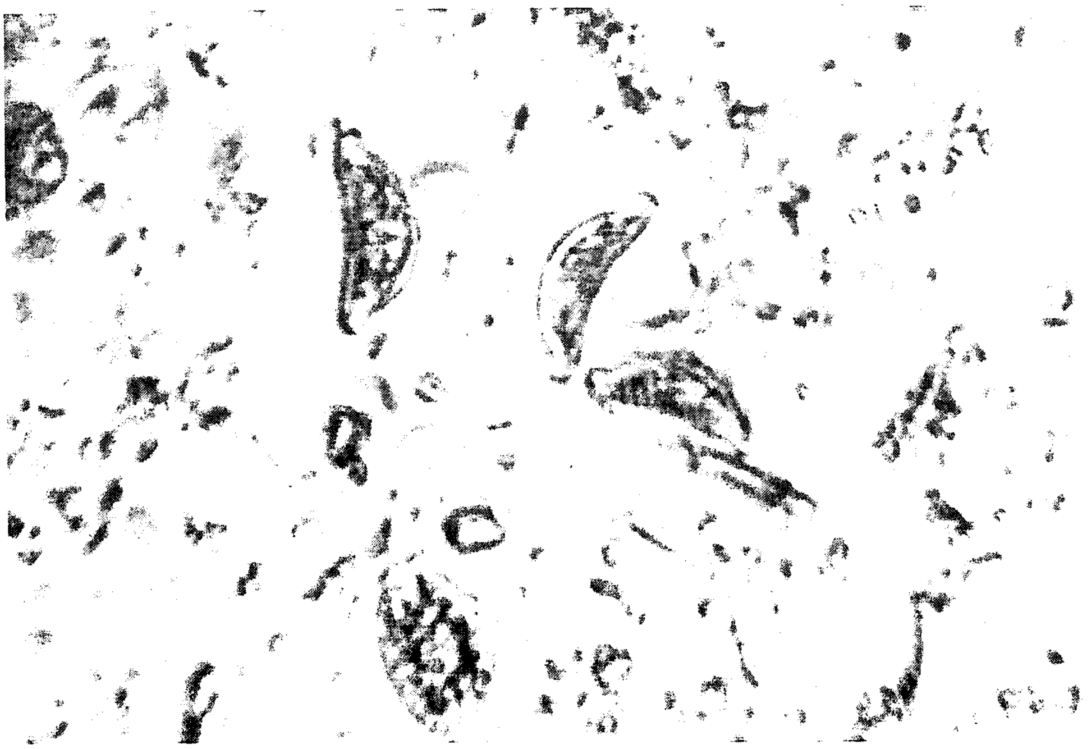

Figure 2.7: Periphyton sample preserved in Lugol's solution, of the eutrophic Baker River (72 µg/l TP) from October 400x (0.5 mL settled). Dominant taxon, *Epithemia* sp., in center.

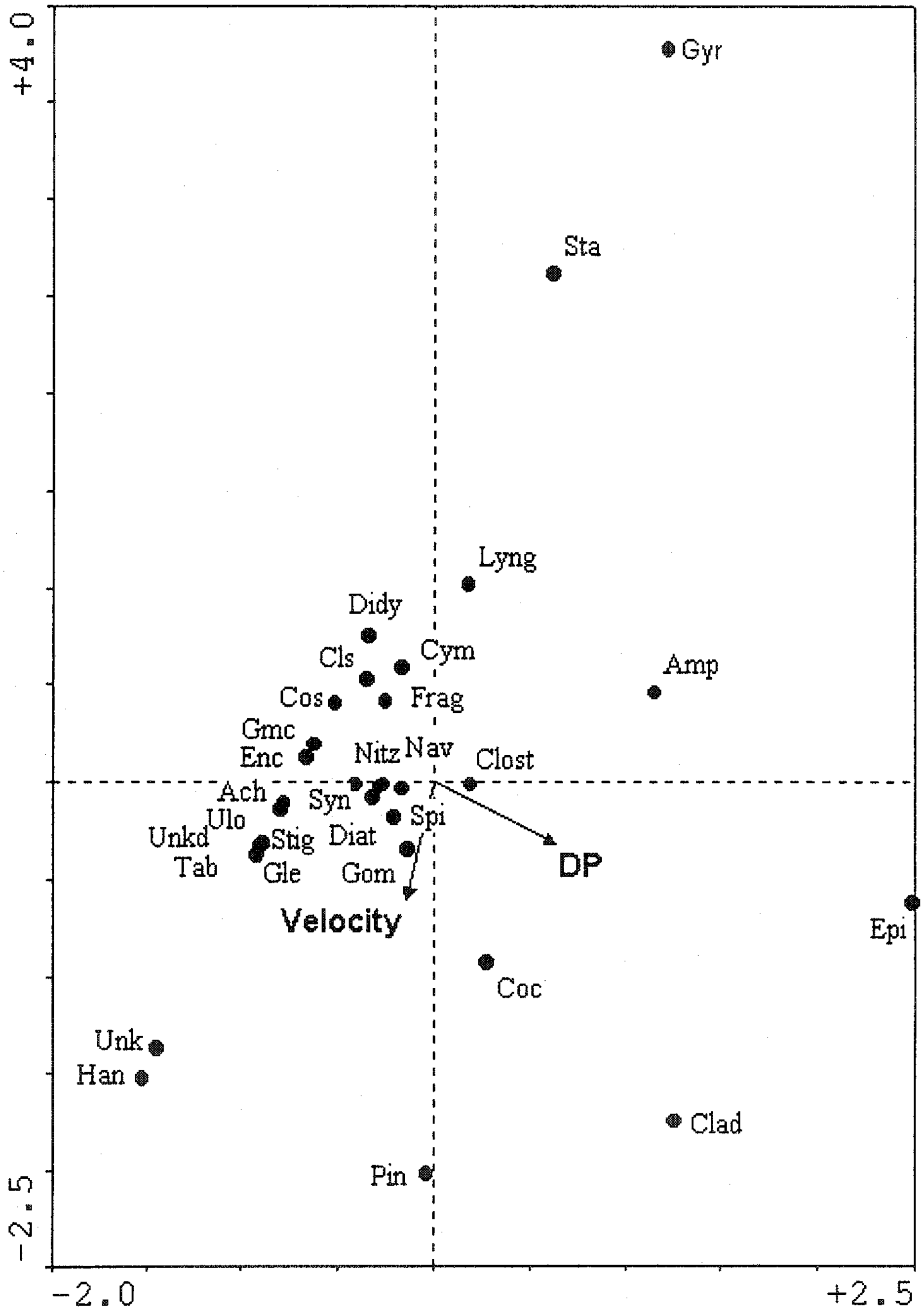

Figure 2.8: CCA of dominant periphyton genera of 14 Fraser River tributaries, with current velocity and DP vectors. Data were square-root transformed and the two vectors account for 25% of the variation in the genera distribution.

Table 2.4: Canonical coefficients, t-values of canonical coefficients and intraset correlations of environmental variables in the first two CCA axes.

Environmental	Canonical	coefficients	t-values		Intraset	correlations
variable	axis 1	axis 2	axis 1	axis 2	axis 1	axis 2
DP	0.77	-0.17	14.3*	-2.1	0.83	-0.56
Velocity	-0.44	-0.56	-8.2*	-7.2*	-0.25	-0.97

* $p \leq 0.05$

Discussion

The objective of this study was to determine the importance of chemical and physical variables to the periphyton community. First, to assess the overall reliability of microscope counts, the total epilithic algal biomass was compared to chlorophyll *a*, another estimate of biomass, from the same samples. The total periphyton biomass was highly correlated with the chlorophyll *a* measurement and reflected similar relationships with both conductivity and phosphorus.

Along with total algal biomass, phyla estimates of biomass were also related to conductivity (Fig. 2.3 to 2.5). However, Bacillariophyta was the only phylum significantly related to conductivity. Both Chlorophyta and Cyanophyta biomass were only weakly related to conductivity. Previous studies in New Zealand streams, have found significant correlations with conductivity and periphyton biomass (Biggs and Price 1987; Biggs 1988, 1990, 1995). Biggs (1990, 2000b) concluded that because conductivity is an indicator of catchment geology and dissolved nutrients, it integrates several stream characteristics and, as such, explains a greater proportion of periphyton variability (Biggs 1990). This may also be the case in the Fraser River tributaries; however, in British Columbia rivers, conductivity was only weakly correlated with dissolved nutrients (Appendix 4).

While conductivity is a useful measure of the general chemical condition of streams, and thus is appropriate for classification and planning purposes, it has some limitations. In areas with bedrock that is high in certain mineral components (e.g., some volcanic rocks high in sulphur) the conductivity–nutrient link breaks down and much higher nutrient supply may be indicated than occurs (Biggs 2000b). Secondly, conductivity cannot be used for predictions when assessing the potential effects of nutrient discharges to streams (Biggs 2000b).

While nutrients, specifically phosphorus, were not found to be correlated with total phylum biomass or relative phylum biomass, three individual diatom genera, *Achnanthidium, Amphora*, and *Epithemia* were found to be correlated with both TP and DP (Table 2.3). *Achnanthidium* was negatively correlated with TP and DP (Table 2.3). *Achnanthidium* is considered to be a generalist (Rott et al. 1998) and at higher phosphorus levels it may be outcompeted by other diatoms, such as *Epithemia*. Stelzer and Lamberti (2001) experimentally manipulated nutrient concentrations of streamside flumes and found a decrease in *Achnanthidium* with increasing TP. They hypothesized that it may be related to *Achnanthidinium*'s adnate growth form and lack of motility. These traits may make it vulnerable to light limitation as the mat biomass increases and thereby thickens.

Amphora is considered a eutrophic genus (Hill et al. 2000), so the positive relationship of *Amphora* biomass with TP was not surprising. Both the biomass and relative abundance of *Epithemia* was also positively related to TP and DP and was the single dominant genus of the most enriched site (Baker River), which also implies that it is a eutrophic taxon. In the canonical correlations analysis *Amphora* and *Epithemia* clustered together along the phosphorus vector (Fig. 2.6). The appearance of these taxa supports the hypothesis that eutrophic genera would appear with higher nutrient concentrations. One exception to this, however, was the lack of *Cladophora* in the samples with relatively high nutrients.

Cladophora typically dominates enriched streams and is considered a nuisance alga because of its potential for high biomass accumulations. Chételat et al. (1999) found

Cladophora as the dominant alga in rivers with as little as 21 μg TP l^{-1} in eastern Ontario and western Quebec. However, in the Fraser River tributaries, even the most enriched study sites were largely free of *Cladophora* (e.g. Baker River with a TP of 73 μg/l). Biggs and Price (1987) developed a model that predicts the appearance of *Cladophora*, based on conductivity. However, in their study sites conductivity was highly correlated with nutrient concentrations, which is not the case for the Fraser River tributaries.

The absence of *Cladophora* may be due to the water temperature of the tributaries during base flow. There are reported differences in temperature optima for growth between *Cladophora*, *Stigeoclonium* and *Ulothrix* and only the latter taxa were found in the tributaries. Entwisle (1989) found that *Stigeoclonium* sp. could only outcompete *Cladophora* in winter and spring when water temperatures are below 15°C. Growth of *Cladophora glomerata* is optimal in the laboratory at 13-17°C, whereas *Ulothrix zonata* has an optimum of 5°C (Graham et al. 1985). In the study rivers, the mean water temperature (± SD) in October was 7.7 ± 2.0°C (range 4 – 14°C). The only two rivers (Adams and Barrier) that contained *Ulothrix* had temperatures of 7°C, while the two rivers (Adams and Thompson) with *Stigeoclonium* had temperatures below 15°C. In addition, both *Ulothrix* and *Stigeoclonium* are the most common green algae in unenriched streams (Biggs and Price 1987). Therefore the lack of *Cladophora* during base flow conditions in BC rivers is probably due to a combination of water temperature and lower nutrient concentrations.

A number of studies have also found phosphorus to be related to periphyton community structure. Winter and Duthie (2000) also found that epilithic diatom composition could be related to TN and TP concentrations in southwestern Ontario streams. Biggs and Gerbeaux (1993) found that nutrients play an important role in governing growth and accumulation rates during inter-flood periods. However, site specific micro-scale hydraulic factors were important for regulating yield during extended periods of low flows. In the present study, while phosphorus appeared to be the primary determinant (first vector in the CCA) of the taxonomic composition, velocity was the second.

It should be noted that the importance of hydrological factors might have been over-emphasized during these stable low flow periods, as determined by the CCA analysis (Fig 2.8). This is because the CCA does forward selection of the next most significant variable that is not correlated with the first vector. This rules out many variables, including conductivity, which was significant when used alone in the CCA.

I predicted that periphyton community would vary with riffle zone velocity. Biggs (2000b) model describes the responses of biomass of three main types of community growth forms, filamentous algae, stalked diatoms and diatom films (Fig. 2.1). The three main phyla found in the present study did not show a significant relationship with current velocity. This may be due to several factors. One reason for the absence of an observed relationship may be that the sample size was not sufficient to detect a relationship. Another reason may be due to the use of the mean value for the rivers in the analysis. The current velocity between the two sites of a river varied more than any other variable. In fact, when the data were analyzed with the site biomass and current velocity, a significant correlation emerges for Chlorophyta and Cyanophyta ($r = 0.57$, $p = 0.01$; $r = -0.49$, $p = 0.04$ respectively). However, the positive correlation of Chlorophyta is opposite to what was predicted by Biggs (2000b). The Biggs (2000b) model also fails to describe the response of non-filamentous Cyanobacteria, which made up a significant proportion of the Cyanobacteria found the in BC rivers. It is evident from these results that more research is required to determine if the model developed for New Zealand rivers applies more generally.

One nuisance species was identified, the colonial pennate diatom *Didymosphenia geminata*. It is the only species of this genus to occur in Western North America (Kociolek and Spaulding 2003). The mass of mucilaginous stalks of this species can cover surfaces and foul water intake pipes, reaching nuisance proportions (Kociolek and Spaulding 2003). In the two rivers where it was found (North Thompson and South Thompson Rivers) the biomass of *D. geminata* did not reach particularly high levels.

In this study, differences in algal community composition generally involved changes in relative abundance of diatom taxa. Dramatic shifts among higher taxonomic orders (from diatoms to greens) were absent. Large division shifts, such as described by Biggs (1996) and Chételat et al. (1999) were likely due to eutrophication, which was not evident in the Fraser River tributaries. Unlike the Eastern Canada rivers, some of the Fraser River tributaries had low N:P ratios, which has been found to lead to dominance by Cyanobacteria in rivers (Peterson and Grim 1992; Mulholland et al. 1995), but this also was not observed.

Summary and Conclusions

In tributaries of the Fraser River, the importance of physical and chemical factors on primary producers varied with the type of algal community and the season. In terms of biomass (chlorophyll *a*), the July phytoplankton levels were significantly higher than the October levels, while the epilithic periphyton biomass was significantly higher in October than July. This implies that, on an areal basis, phytoplankton biomass likely exceeds periphyton biomass in July, indicating a possible seasonal shift in dominance in the major primary producers in these rivers, which has not been reported before. This shift is most likely due to changes in hydrological factors, rather than nutrient concentrations, because of the drastic differences in water levels between July and October (Fig. 1.2). However, the potential role of invertebrates in modulating these changes needs to be further examined.

Nutrient concentrations were found to have an important role in algal biomass levels within a season. In agreement with previous findings on rivers in other regions (e.g. Van Nieuwenhuyse and Jones 1996, Basu and Pick 1997) water column total phosphorus was strongly related to phytoplankton chlorophyll *a* in July. Periphyton biomass was also strongly related to dissolved phosphorus and conductivity, during base flow conditions, which is consistent with much of the literature (Biggs 2000a, Chételat et al. 1999).

The phytoplankton and periphyton biomass were low in October and July respectively. At these times, their relationships with the environmental variables were not as strong as when the communities were dominant.

No major changes in the periphyton composition at the division level were observed along the environmental gradients considered, perhaps because of the oligotrophic nature of most of the Fraser River tributaries. Furthermore, contrary to predictions, neither current velocity nor any of the hydrological variables, predicted community type, such as Biggs described (2000a) where filamentous green algae are present under low velocity conditions versus stalked diatoms under high velocity.

Differences in the taxonomic composition were observed among the rivers, such as changes in biomass and relative abundance of specific diatom taxa (e.g. *Achnanthidium, Epithemia, Amphora*) in relation to phosphorus and conductivity. Conductivity emerged as an important variable. It is a variable which integrates several higher level watershed processes and described more variance in the periphyton than any one of the other variables. The other observed patterns, such as with phosphorus and current velocity, can be explained as a complex function of accrual (nutrient resources) and loss (high current velocity) variables that operate over small to large spatial and temporal scales. A manipulative field experiment would be useful to determine causal relationships between epilithic periphyton, nutrients and hydrology.

Because of the novelty of this study, there are several topics stemming from this thesis which may warrant further research. The Fraser River tributaries are fairly oligotrophic and much of the periphyton literature focuses on eutrophication concerns. This may be the reason the periphyton communities in the Fraser River tributaries did not always agree with previous findings on other river systems. Therefore empirical models examining the effects of anthropogenic disturbances, such as logging and damning, on oligotrophic streams, in terms of biomass and taxonomy, would be informative. Also, an understanding of the seasonal development and interaction of periphyton and phytoplankton communities in rivers of the Pacific Northwest would be useful for management purposes, particularly in terms of fish rehabilitation efforts.

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Appendix 1: Location and hydrological characteristics of 19 Fraser River Tributaries

River	Lat[1]	Long	Drainage area (km^2)	Mean monthly discharge (m^3 s^{-1})		Daily discharge[2] (m^3 s^{-1})		WRT	
				Jul	Oct	Jul	Oct	July	October
Adams	51 10 85	120 07 93	3080	156	44.8	132	50	6.1	6.7
Baker	52 59 09	122 30 89	1570	7.62	1.72	4.43	1.78	5.5	6.1
Barriere	51 10 85	120 07 93	1140	22.7	3.49	13.5	2.96	4.2	4.9
Bonaparte	50 50 03	121 22 22	5020	6.83	3.39	4.08	3.51	11.4	11.7
Bowron	53 58 92	122 10 20	3420	139.32	50.44	74.8	49	6.7	7.2
Cariboo	52 56 74	121 10 40	2870	---[3]	---	---	---	---	---
Chilako	53 46 89	122 59 34	3390	---	---	---	---	---	---
Clearwater	51 38 97	120 04 12	10 200	527	106	430	115	11.0	12.5
Coldwater	49 58 99	120 55 74	914	---	---	---	---	---	---
Cottonwood	53 05 84	122 21 91	1910	---	---	---	---	---	---
Deadman	50 54 00	120 58 50	862	2.2	0.752	1.18	0.718	4.6	4.8
Nechako	53 58 85	123 17 85	42 500	455.35	168.42	417	186	26.2	28.3
Nicola	50 08 51	120 55 54	4350	7.12	3.55	5.68	3.09	10.1	10.1
North Thompson	51 36 13	119 54 93	4450	371	68.2	322	80	6.9	7.9
Salmon	54 06 98	122 41 68	4300	---	---	---	---	---	---
Spius Cr	50 08 14	121 01 79	780	2.71	1.23	1.85	0.64	4.0	4.6
Thompson	50 25 30	121 20 15	54 600	1630	368	1140	393	26.8	30.3
Tranquille	50 43 62	120 31 48	596	---	---	---	---	---	---
Willow	54 04 02	122 28 05	3110	63.74	27.38	33.8	26.7	6.8	7.1

[1] Lat and Long refer to the latitude and longitude of the sampling locations, which were located as close as possible to river gauging stations

[2] Daily discharge values listed for the date of sampling

[3] dashed line indicates discharge data not available

Appendix 2a: Physical characteristics of the 19 Fraser River tributaries

River	Conductivity (µS/cm)		pH		Light (% absorption over 0.5m)		Temperature (°C)	
	Jul	Oct	Jul	Oct	Jul	Oct	Jul	Oct
Adams	20	70	7.0	8.2	25.0	18.2	12	7
Baker	120	125	7.6	8.4	46.2	39.8	20	6
Barriere	70	110	7.4	8.2	30.0	20.0	16.4	7.5
Bonaparte	285	225	8.5	8.9	31.8	22.7	17.5	8.8
Bowron	105	95	8.0	8.4	92.7	25.0	16	5.5
Cariboo	130	75	8.4	8.2	30.8	12.7	11	7.5
Chilako	170	185	7.1	8.2	65.9	50.0	17	7
Clearwater	60	85	7.5	8.1	18.4	18.9	13.8	10.5
Coldwater	94	142	7.7	8.7	25.0	22.2	16	7
Cottonwood	60	55	7.9	8.2	25.0	45.8	15	6.5
Deadman	190	195	8.3	8.6	9.1	11.8	15	7.5
Nechako	82	71	7.2	8.2	33.3	17.8	17	9
Nicola	200	205	8.4	8.7	23.4	25.0	18	8.7
North Thompson	35	55	7.0	8.8	26.1	14.3	11.5	4.9
Salmon	112	90	8.0	8.4	20.5	40.0	17	7.5
Spius Cr	40	109	8.1	8.4	16.7	0.0	14.5	8.1
Thompson	65	85	7.5	8.4	18.2	33.3	16	14
Tranquille	412	147	6.8	8.6	72.7	11.8	13.7	5.5
Willow	62	58	7.5	8.4	53.6	28.6	18	8.5

Appendix 2b: Chemical characteristics of the 19 Fraser River tributaries

River	Site	Turbidity (NTU)		NH_3 (µg/l)		NO_2+NO_3 (µg/l)		TN (µg/l)	
		Jul	Oct	Jul	Oct	Jul	Oct	Jul	Oct
Adams	1	3.58	0.61	4.9	5.8	86	101	160	200
	2	3.29	0.64	4.9	4.9	86	97	160	120
Baker	1	4.8	3.05	9	7	1.9	1	480	300
	2	5.42	2.68	5	6	1.9	1	470	300
Barriere	1	0.32	0.22	4.9	7	19	29	90	190
	2	0.43	0.22	6	8	19	29	90	100
Bonaparte	1	2.72	1.17	4.9	5	2	2	350	210
	2	2.88	0.89	4.9	4.9	2	1	340	210
Bowron	1	2.47	1.28	4.9	7	13	11	100	70
	2	2.6	1.37	4.9	5	13	11	100	60
Cariboo	1	0.81	0.77	4.9	4.9	27	63	60	130
	2	3.21	1.05	4.9	4.9	118	81	150	150
Chilako	1	9.25	3.35	11	6	1.9	1	420	290
	2	8.67	2.75	4.9	6	1.9	1	420	270
Clearwater	1	0.54	0.39	4.9	4.9	112	77	180	210
	2	0.54	0.29	4.9	4.9	112	77	170	170
Coldwater	1	0.27	0.19	4.9	4.9	2	1	40	50
	2	0.33	0.24	4.9	5	1.9	1	30	1
Cottonwood	1	1.69	1.18	4.9	7	1.9	1	140	130
	2	1.83	1.28	4.9	5	1.9	2	130	170
Deadman	1	0.51	0.39	15	6	2	7	190	210
	2	0.75	0.46	6	5	4	7	210	150
Nechako	1	3.58	2.27	4.9	5	1.9	1	250	170
	2	3.64	1.71	4.9	4.9	1.9	1	250	170
Nicola	1	2.88	1.36	6	5	5	244	280	500
	2	1.99	1.04	6	5	4	243	270	650
N. Thompson	1	8.36	1.42	4.9	4.9	74	119	100	140
	2	7.87	1.47	4.9	4.9	74	121	110	160
Salmon	1	2.25	1.79	4.9	5	1.9	1	340	230
	2	2.24	1.95	4.9	5	1.9	1	350	230
Spius	1	0.33	0.14	4.9	4.9	2	2	50	70
	2	0.29	0.13	5	4.9	3	2	50	160
Thompson	1	1.16	0.42	7	10	76	61	140	150
	2	1.39	0.4	8	13	76	63	150	280
Tranquille	1	33.6	0.21	5	14	1.9	1	520	260
	2	33.9	0.22	4.9	5	1.9	1	530	150
Willow	1	12.9	2.84	4.9	5	4	1	200	170
	2	10.8	8.5	4.9	5	3	1	200	460

Appendix 2b continued

River	Site	DP (µg/l)		TP (µg/l)		SIO$_2$ (mg/l)		Velocity (cm/s)	
		Jul	Oct	Jul	Oct	Jul	Oct	Jul	Oct
Adams	1	0.9	1	15	1	4.2	6.3	63.5	90
	2	0.9	1	7	1	4.3	6.2	5.0	61
Baker	1	49	51	79	72	26.3	--	25.0	121.3
	2	49	51	79	74	26.1	--	12.3	85
Barriere	1	0.9	1	3	1	8.2	8.9	9.5	178.3
	2	0.9	1	3	1	8.2	8.9	76.2	146.5
Bonaparte	1	3	5	26	13	13.3	13.4	32.8	131.5
	2	3	5	24	12	13.3	13.4	54.3	86.7
Bowron	1	0.9	1	9	4	4.5	--	22.2	97
	2	0.9	1	11	4	4.5	--	29.0	77.3
Cariboo	1	3	1	8	1	3.6	--	29.0	4.0
	2	0.9	1	4	1	1.9	--	33.5	36
Chilako	1	19	20	61	37	14.8	--	37.7	34.5
	2	19	21	57	38	14.8	--	15	47.5
Clearwater	1	0.9	1	4	3	3.7	3.6	33.5	59.5
	2	0.9	1	4	1	3.6	3.6	16.8	70.3
Coldwater	1	0.9	1	2	1	6.9	7.8	19.8	74.3
	2	0.9	1	2	1	6.9	7.8	24.8	60
Cottonwood	1	0.9	1	8	6	6.2	--	16.2	64
	2	0.9	1	7	7	6.2	--	29.5	59
Deadman	1	4	3	11	6	17.2	16.4	47.5	177.5
	2	4	3	12	6	17	16.3	47.8	76
Nechako	1	0.9	1	15	10	5	--	5.0	4.0
	2	0.9	1	15	7	5	--	17.5	3.5
Nicola	1	0.9	1	18	8	5.2	5.4	33.3	92
	2	0.9	1	17	9	5.2	5.4	33.5	38.5
N. Thompson	1	10	1	11	1	3.2	5.7	7.5	36
	2	0.9	1	11	1	3.2	5.7	15.25	32
Salmon	1	1	1	13	10	7	--	45.75	105
	2	0.9	1	13	10	7	--	45	99.5
Spius	1	0.9	1	3	1	7.9	10.4	51.25	27
	2	0.9	1	3	1	8	10.5	50.25	13
Thompson	1	0.9	1	7	7	5.1	4.6	13	24
	2	0.9	1	7	7	5	4.6	13.25	27
Tranquille	1	19	31	221	34	17.4	21.6	43.25	15
	2	18	32	223	36	17.3	21.6	20	71
Willow	1	0.9	1	22	16	7.2	--	20.5	60.3
	2	0.9	1	35	17	7.3	--	21.5	69.5

[1] dashed line indicates data not available

Appendix 3: Periphyton and Phytoplankton estimates of biomass for July and October

River	Site	Periphyton chlorophyll *a* (mg·m^{-2})		Periphyton AFDM (g·m^{-2})		Phytoplankton chlorophyll *a* (µg·L^{-1})	
		Jul	Oct	Jul	Oct	Jul	Oct
Adams	1	2.07	1.71	1.16	2.21	1.36	0.02
	2	2.06	3.45	1.44	1.49	1.41	0.03
Baker	1	1.87	60.60	0.82	15.79	2.50	4.00
	2	2.43	50.78	1.05	3.63	2.24	0.07
Barriere	1	0.76	6.84	0.45	1.70	0.85	1.49
	2	1.14	8.50	0.84	1.59	0.31	0.17
Bonaparte	1	9.12	16.17	2.86	1.51	2.87	1.07
	2	0.42	34.94	0.14	13.84	2.67	2.24
Bowron	1	3.49	3.61	1.67	1.79	1.19	0.02
	2	2.53	18.24	1.50	5.25	1.14	0.02
Cariboo	1	6.16	18.88	1.61	7.03	0.91	0.02
	2	2.13	8.95	1.09	8.29	0.90	0.03
Chilako	1	6.39	13.99	2.76	16.21	2.95	0.07
	2	4.67	27.44	2.59	9.71	3.49	0.04
Clearwater	1	4.83	2.72	1.46	0.94	1.05	1.83
	2	3.38	2.12	1.12	0.53	1.50	0.04
Coldwater	1	2.29	8.45	1.18	1.83	0.80	0.05
	2	1.69	3.99	0.91	1.22	0.88	0.03
Cottonwood	1	1.53	2.35	1.48	1.91	0.93	0.02
	2	1.00	2.56	0.49	2.25	0.96	0.03
Deadman	1	5.41	25.99	1.47	7.18	2.65	2.16
	2	6.99	22.87	1.96	3.96	2.85	1.88
Nechako	1	5.52	10.22	4.37	3.62	3.29	0.05
	2	7.56	32.94	5.86	14.73	2.65	1.90
Nicola	1	3.20	32.74	1.30	5.47	3.80	0.09
	2	2.48	14.24	0.99	3.26	3.78	2.87
N. Thompson	1	4.62	12.59	1.73	8.26	1.06	0.02
	2	6.18	7.53	2.39	1.66	1.12	----
Salmon	1	5.25	13.04	2.65	2.56	2.24	0.03
	2	5.25	16.32	2.54	19.30	2.06	0.03
Spius	1	2.58	1.88	1.41	2.51	0.96	0.03
	2	2.62	3.08	1.22	5.36	1.00	0.03
Thompson	1	3.87	10.69	1.66	0.93	1.31	0.06
	2	5.96	11.81	1.93	1.38	1.21	0.07
Tranquille	1	12.24	83.17	3.45	1.80	18.88	0.00
	2	3.05	59.04	2.73	1.61	14.47	0.02
Willow	1	2.20	1.51	1.30	15.90	1.46	0.04
	2	3.89	1.96	1.96	14.19	1.02	0.07

Appendix 4: Pearson correlation matrix of hydrologcial and chemical variables

July	Drainage	1 d	3 d	7 d	WRT	Velocity	Turbidity	TN	TP	DP	Conductivity
Drainage area	1.00										
1 d discharge	0.80*	1.00									
3 d discharge	0.81*	0.99*	1.00								
7 d discharge	0.81*	0.99*	0.99*	1.00							
WRT	0.98*	0.65	0.66	0.66	1.00						
Velocity	-0.71	-0.75*	-0.76*	-0.77*	-0.62	1.00					
Turbidity	0.25	0.26	0.26	0.27	0.22	-0.59	1.000				
TN	0.24	-0.11	-0.11	-0.11	0.35	-0.19	0.78	1.00			
TP	0.03	-0.20	-0.19	-0.18	0.11	-0.27	0.49	0.83*	1.00		
DP	-0.31	-0.36	-0.36	-0.35	-0.26	-0.13	0.30	0.50	0.64*	1.00	
Conductivity	-0.04	-0.52	-0.52	-0.52	0.14	0.25	-0.03	0.58	0.42	0.31	1.00

October	Drainage	1 d	3 d	7 d	WRT	Velocity	Turbidity	TN	TP	DP	Conductivity
Drainage area	1.00										
1 d discharge	0.84*	1.00									
3 d discharge	0.84*	0.99*	1.00								
7 d discharge	0.85*	0.99*	0.99*	1.00							
WRT	0.98*	0.73	0.72	0.74	1.00						
Velocity	-0.62	-0.47	-0.46	-0.45	-0.63	1.00					
Turbidity	0.21	0.24	0.25	0.26	0.18	-0.07	1.00				
TN	0.13	-0.16	-0.15	-0.08	0.19	0.09	0.37	1.00			
TP	0.16	-0.13	-0.11	-0.09	0.24	0.05	0.67	0.55	1.00		
DP	-0.28	-0.45	-0.44	-0.45	-0.20	0.34	0.31	0.27	0.69*	1.00	
Conductivity	-0.33	-0.71	-0.71	-0.68	-0.19	0.44	-0.23	0.29	0.32	0.42	1.00

* Bonferroni-corrected probability $p<0.05$

Note: all variables were log transformed

Appendix 5a: Taxon Code sheet corresponding to periphyton biomass data sheets (Appendix 5b)

Taxon Code	Genus	Taxon Code	Genus
Ach	Achnanthidium	Han	Hannae
Amp	Amphora	Herb	Heribaudiella
Ana	Anacystis	Lut	Luticola
Ank	Ankistrodesmus	Lyn	Lyngbya
Aph	Aphanocapsa	Mas	Mastogloia
Ast	Asterionella	Mer	Merismopedia
Cal	Calothrix	Mic	Microcystis
Chl	Chlorococcum	Nav	Navicula
Chr	Chlorella	Nitz	Nitzschia
Clad	Cladophora	Nos	Nostoc
Clos	Closterium	Osc	Oscillatoria
Coc	Cocconeis	Ped	Pediastrum
Cos	Cosmarium	Pinn	Pinnularia
Cra	Craticula	Rei	Reimera
Cro	Crotonensis	Sce	Scenedesmus
Cym	Cymbella	Scy	Scytonema
Diat	Diatoma	Spi	Spirogyra
Didy	Didymosphenia	Sta	Stauronensis
Enc	Encyonema	Stig	Stigeoclonium
Spi	Epithemia	Syn	Synedra
Euc	Eucocconeis	Tab	Tabellaria
Fra	Fragillaria	Toly	Tolypothrix
Gcy	Gomphocymbella	Ulo	Ulothrix
Gle	Gloeocapsa	Unkd	unknown desmid
Gom	Gomphonema	Unk1	unknown diatom
Gyr	Gyrosigma	Unk2	unknown green

Appendix 5b: Periphyton cell biomass (mg.m^{-2}) data

River	Site	Ach	Amp	Ana	Ank	Aph	Ast
Adams	1	0.44	0.00	0.00	0.00	0.00	0.00
	2	0.65	0.14	0.00	0.00	0.00	0.00
Baker	1	0.77	55.40	0.00	0.00	0.00	0.00
	2	0.84	46.22	0.00	0.00	0.00	0.00
Barriere	1	1.69	0.00	0.00	0.00	0.00	0.00
	2	3.58	0.00	0.00	0.00	0.00	0.00
Bonaparte	1	0.79	8.84	0.00	0.00	0.00	0.00
	2	1.38	9.28	0.00	0.00	0.00	0.00
Bowron	1	3.36	0.41	0.00	0.00	0.00	0.00
	2	2.57	0.00	0.00	0.00	0.00	0.00
Cariboo	1	0.53	0.00	0.00	0.00	0.00	0.00
	2	0.88	0.14	0.00	0.00	0.19	0.00
Chilako	1	0.93	0.00	0.00	0.00	0.00	0.00
	2	0.96	0.00	0.00	0.00	0.00	0.00
Clearwater	1	1.47	8.50	0.18	0.12	0.00	0.00
	2	3.14	0.00	0.00	0.00	0.00	0.00
Coldwater	1	2.18	4.77	0.00	0.00	0.00	0.00
	2	1.34	3.77	0.00	0.00	0.00	0.00
Cottonwood	1	0.66	9.69	0.00	0.00	0.00	0.00
	2	0.50	3.91	0.00	0.00	0.00	0.41
Deadman	1	0.45	0.00	0.00	0.34	0.00	0.00
	2	2.51	1.18	0.00	0.62	0.00	0.00
Nechako	1	7.05	3.32	0.00	0.00	0.00	0.00
	2	2.46	0.00	0.00	0.00	0.00	0.00
Nicola	1	0.41	0.00	0.00	0.00	0.00	0.00
	2	0.14	2.58	0.00	0.00	0.00	0.00
N. Thompson	1	1.23	0.90	0.00	0.00	0.00	0.00
	2	3.59	1.87	0.00	0.04	0.00	0.00
Salmon	1	0.16	0.39	0.00	0.00	0.00	0.00
	2	0.07	0.00	0.00	0.00	0.00	0.00

River	Site	Cal	Chl	Chr	Clad	Clos	Clr
Adams	1	0.00	0.00	0.00	0.00	0.00	0.05
	2	0.00	0.10	0.00	0.00	0.00	0.03
Baker	1	4.87	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	6.26	2.54	0.00
Barriere	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Bonaparte	1	0.00	0.00	0.00	4.95	0.00	0.00
	2	0.00	0.00	0.00	10.95	0.00	0.00
Bowron	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Cariboo	1	3.03	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Chilako	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Clearwater	1	0.00	0.00	0.00	0.00	11.79	0.00
	2	0.00	0.00	0.00	0.00	1.48	0.00
Coldwater	1	0.00	0.00	0.00	15.51	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Cottonwood	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.02	0.00	0.00	0.00	0.00	0.00
Deadman	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	8.11	0.00
Nechako	1	0.00	0.00	0.00	0.00	2.90	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Nicola	1	0.00	0.00	0.17	0.00	0.00	0.00
	2	0.00	0.00	0.23	0.00	0.00	0.00
N. Thompson	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	1.05	0.00	0.00	0.00	0.00	0.00
Salmon	1	0.00	0.00	0.00	0.00	6.87	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00

River	Site	Cls	Coc	Cos	Cra	Cro	Cym
Adams	1	0.00	0.00	0.00	0.00	0.00	1.28
	2	0.00	0.00	0.00	0.00	0.00	0.03
Baker	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Barriere	1	0.00	0.00	0.00	0.00	0.00	1.72
	2	0.00	0.00	0.00	0.00	0.00	1.17
Bonaparte	1	0.00	24.89	0.00	0.00	0.00	2.60
	2	0.00	0.00	7.45	0.00	0.00	0.00
Bowron	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Cariboo	1	0.00	0.00	0.00	3.08	0.00	3.90
	2	0.00	0.00	0.00	0.00	0.00	16.32
Chilako	1	0.00	0.00	0.00	0.00	0.00	0.11
	2	0.00	0.00	0.00	0.00	0.00	0.25
Clearwater	1	0.00	0.00	0.00	0.00	0.00	5.30
	2	0.00	0.00	0.00	0.00	0.00	0.00
Coldwater	1	0.00	28.42	0.00	0.00	0.00	1.06
	2	0.00	2.40	0.00	0.00	0.00	4.81
Cottonwood	1	0.00	0.00	0.71	0.00	0.00	9.00
	2	0.00	0.00	0.00	0.00	0.00	2.39
Deadman	1	0.00	0.00	13.17	0.00	0.00	1.65
	2	0.00	4.90	14.77	6.34	0.00	6.00
Nechako	1	0.00	0.00	0.00	0.00	0.00	1.45
	2	0.00	0.00	4.75	0.00	0.00	2.80
Nicola	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
N. Thompson	1	1.82	2.52	1.67	0.00	0.00	2.52
	2	2.62	1.04	2.04	0.00	0.00	6.10
Salmon	1	0.00	0.00	0.55	0.00	0.00	0.06
	2	0.31	0.00	0.00	0.00	0.03	0.00

River	Site	Diat	Didy	Enc	Epi	Euc	Fra
Adams	1	0.06	0.00	0.00	0.00	0.00	0.00
	2	0.20	0.00	0.00	0.00	0.00	0.00
Baker	1	0.00	0.00	0.00	449.76	0.00	0.00
	2	0.00	0.00	0.00	271.67	0.00	0.00
Barriere	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Bonaparte	1	20.11	0.00	0.67	3.41	0.00	0.00
	2	24.01	0.00	1.33	35.26	0.00	0.00
Bowron	1	1.44	0.00	1.24	2.11	0.00	5.89
	2	1.79	0.00	0.73	2.65	0.60	11.98
Cariboo	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.57	0.00	0.00	0.00
Chilako	1	0.00	0.00	0.04	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Clearwater	1	6.18	0.00	0.57	0.00	0.00	0.00
	2	0.00	20.14	0.50	0.00	0.00	0.00
Coldwater	1	90.79	0.00	5.38	0.00	0.00	3.04
	2	24.54	0.00	1.60	0.00	0.00	0.00
Cottonwood	1	2.68	0.00	0.00	0.95	0.00	0.00
	2	8.81	0.00	0.57	2.99	0.00	0.00
Deadman	1	13.48	0.00	10.84	0.00	4.74	0.00
	2	13.19	29.84	8.01	0.00	0.00	0.00
Nechako	1	6.70	92.30	0.38	0.00	0.00	0.00
	2	0.00	119.94	0.78	0.00	0.00	0.20
Nicola	1	0.00	0.00	0.26	0.00	0.00	1.09
	2	0.00	0.00	0.00	3.15	0.00	1.88
N. Thompson	1	0.00	7.44	0.48	0.00	0.00	8.04
	2	0.00	14.86	1.77	0.00	0.00	5.02
Salmon	1	0.00	0.00	0.02	0.00	0.00	0.00
	2	0.00	0.00	0.07	0.00	0.00	0.00

River	Site	Gcy	Gle	Gom	Gyr	Han
Adams	1	0.00	0.34	0.17	0.00	0.00
	2	0.00	0.00	0.44	0.00	0.00
Baker	1	0.00	0.00	10.72	0.00	0.00
	2	0.00	0.00	3.98	0.00	0.00
Barriere	1	0.00	0.00	13.55	0.00	3.05
	2	1.51	0.00	10.54	0.00	6.78
Bonaparte	1	0.00	0.00	26.76	0.00	0.00
	2	0.00	0.00	60.74	0.00	0.00
Bowron	1	1.79	0.00	6.89	0.00	0.00
	2	1.27	0.00	3.01	0.00	0.00
Cariboo	1	0.00	0.00	9.18	0.00	0.00
	2	0.00	0.00	5.59	0.00	0.25
Chilako	1	0.00	0.00	3.63	0.00	0.00
	2	0.00	0.00	0.77	0.00	0.00
Clearwater	1	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	17.69	0.00	3.66
Coldwater	1	0.00	0.00	27.90	0.00	0.00
	2	0.00	0.00	10.15	0.00	0.00
Cottonwood	1	0.00	0.00	0.75	1.73	0.00
	2	0.00	0.00	1.23	1.70	0.00
Deadman	1	0.00	0.24	4.21	0.00	0.00
	2	0.00	0.00	0.58	0.00	0.00
Nechako	1	0.61	0.44	0.66	0.00	0.00
	2	0.00	0.00	0.88	0.00	0.00
Nicola	1	0.00	0.00	2.60	0.00	0.00
	2	0.00	0.00	1.27	0.00	0.00
N. Thompson	1	0.00	0.07	2.13	0.00	0.00
	2	17.67	0.06	6.47	0.00	0.00
Salmon	1	0.00	0.00	0.33	0.00	0.00
	2	0.00	0.00	0.51	0.00	0.00

River	Site	Herb	Lut	Lyn	Mas	Mer	Mic
Adams	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Baker	1	0.00	0.00	6.08	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Barriere	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Bonaparte	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Bowron	1	0.00	0.00	1.33	4.98	0.48	0.00
	2	0.00	0.00	0.07	4.17	0.00	0.00
Cariboo	1	0.00	0.00	0.00	0.00	0.00	0.60
	2	13.56	0.00	0.00	0.00	3.33	0.17
Chilako	1	0.00	0.00	0.02	0.00	0.00	0.00
	2	0.00	0.00	0.02	0.00	0.00	0.00
Clearwater	1	0.00	0.00	0.00	2.30	0.00	0.00
	2	0.00	0.00	0.94	0.00	0.00	0.00
Coldwater	1	0.00	0.00	2.18	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Cottonwood	1	0.00	0.00	3.51	0.00	0.00	0.00
	2	0.00	0.00	2.82	0.00	0.00	0.00
Deadman	1	0.00	0.00	2.55	0.00	0.03	0.55
	2	0.00	0.84	102.86	0.00	0.09	0.00
Nechako	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Nicola	1	0.00	0.00	0.25	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
N. Thompson	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	18.82	0.43	0.00	0.00
Salmon	1	0.00	0.00	0.03	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00

River	Site	Nav	Nitz	Nos	Osc	Ped	Pin
Adams	1	0.54	0.08	0.00	0.00	0.00	0.00
	2	0.92	0.21	0.00	0.00	0.00	0.00
Baker	1	4.04	0.49	0.00	0.00	0.00	0.00
	2	3.50	0.00	0.00	0.00	0.00	0.00
Barriere	1	0.97	0.17	0.00	0.00	0.00	0.00
	2	2.63	0.11	0.00	0.00	0.00	0.00
Bonaparte	1	8.05	0.98	0.00	0.00	0.00	0.00
	2	58.69	7.92	0.00	0.00	0.00	0.00
Bowron	1	3.40	3.61	0.00	0.00	0.00	0.00
	2	16.27	3.73	0.00	0.00	0.00	0.00
Cariboo	1	2.20	4.28	0.22	2.97	0.00	0.00
	2	7.10	4.73	0.03	0.01	0.00	0.00
Chilako	1	0.51	0.13	0.00	0.00	0.00	0.00
	2	0.65	0.00	0.00	0.00	0.00	0.00
Clearwater	1	3.34	1.08	0.00	0.00	0.00	252.61
	2	2.74	1.11	0.00	0.00	0.00	18.79
Coldwater	1	23.82	2.12	0.00	0.00	0.00	12.29
	2	44.39	3.03	0.00	0.00	0.00	0.00
Cottonwood	1	2.91	0.22	0.00	0.00	0.00	0.00
	2	4.33	0.29	0.00	0.00	0.00	0.00
Deadman	1	50.84	0.40	0.00	0.00	3.53	0.00
	2	20.09	2.62	0.00	0.00	1.06	0.00
Nechako	1	7.10	1.45	0.00	0.00	0.00	0.00
	2	5.89	1.41	0.00	0.00	0.00	0.00
Nicola	1	0.24	0.15	0.00	0.00	0.00	0.00
	2	1.76	0.17	0.00	0.00	0.00	0.00
N. Thompson	1	0.86	0.82	0.94	0.01	0.00	0.00
	2	31.28	1.03	0.00	0.00	0.00	0.00
Salmon	1	2.81	0.15	0.00	0.00	0.00	0.00
	2	0.81	0.11	0.00	0.00	0.00	0.00

River	Site	Rei	Sce	Scy	Spi	Sta	Stig
Adams	1	0.00	0.00	0.00	0.00	0.00	0.98
	2	0.00	0.00	0.00	0.00	0.00	0.04
Baker	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Barriere	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Bonaparte	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Bowron	1	0.00	0.00	0.00	0.00	2.26	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Cariboo	1	0.00	0.00	1.55	479.26	0.00	0.00
	2	0.00	0.20	0.00	96.67	0.00	0.00
Chilako	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Clearwater	1	0.00	0.00	0.00	104.08	0.00	0.00
	2	0.00	0.00	0.00	6.93	0.00	22.24
Coldwater	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
Cottonwood	1	0.00	0.13	0.00	0.00	0.00	0.00
	2	0.00	0.03	0.00	0.00	5.85	0.00
Deadman	1	0.00	0.13	0.00	6.61	0.00	0.00
	2	5.81	0.76	0.00	0.00	0.00	0.00
Nechako	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.63	0.00	0.00
Nicola	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
N. Thompson	1	0.00	0.02	0.00	0.00	0.00	0.00
	2	0.00	0.05	0.00	0.00	0.00	100.71
Salmon	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00

River	Site	Syn	Tab	Toly	Ulo	Unkd	Unk1	Unk2
Adams	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.12	0.00	0.00	0.25	0.00	0.00	0.00
Baker	1	31.17	0.00	0.00	0.00	0.00	0.00	0.00
	2	42.19	0.00	0.00	0.00	0.00	0.00	0.00
Barriere	1	25.79	0.00	0.00	0.00	0.00	0.00	0.00
	2	75.28	0.00	0.00	0.00	0.00	108.91	0.00
Bonaparte	1	27.51	0.00	0.00	0.00	0.00	0.00	0.00
	2	123.97	0.00	0.00	0.00	0.00	0.00	0.00
Bowron	1	37.27	25.94	0.00	0.00	0.00	0.00	0.00
	2	45.97	16.57	0.00	0.00	0.00	0.00	0.00
Cariboo	1	8.04	10.60	0.85	0.00	0.00	0.00	31.02
	2	6.35	0.00	0.00	0.00	0.00	0.00	0.00
Chilako	1	13.10	0.18	0.00	0.00	17.49	0.00	0.00
	2	8.14	0.20	0.00	0.00	0.00	0.00	0.00
Clearwater	1	258.94	0.00	0.00	0.00	0.00	0.00	0.00
	2	34.12	0.00	0.00	0.00	0.00	0.00	0.00
Coldwater	1	9.27	0.00	0.00	0.00	0.00	0.00	0.00
	2	15.11	0.00	0.00	0.00	0.00	0.00	0.00
Cottonwood	1	5.82	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Deadman	1	19.49	0.00	0.00	0.00	0.00	0.00	0.00
	2	124.66	0.00	0.00	0.00	0.00	0.00	0.00
Nechako	1	10.39	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nicola	1	13.11	0.00	0.00	0.00	0.00	0.00	0.00
	2	5.10	0.00	0.00	0.00	0.00	0.00	0.00
N. Thompson	1	23.61	0.05	0.00	0.00	0.00	0.00	0.00
	2	60.78	7.05	0.00	0.00	0.00	0.00	0.00
Salmon	1	1.01	0.09	0.00	0.00	0.00	0.00	0.00
	2	2.29	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 6: Unconstrained CA ordination of sample river sites based on their taxonomic assemblages