THE RESPONSE OF PERIPHYTON CHLOROPHYLL *A* AND INVERTEBRATE DRIFT TO THE
END OF NUTRIENT ENRICHMENT

by

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Abstract

This thesis contains two chapters concerned with the ecology of periphyton and invertebrates in streams of southwestern, coastal British Columbia. Chapter 1 deals with periphyton and addresses the hypothesis that the hyporheic zone contributes to community resistance in the face of declining nutrient levels. Two stream systems which had been enriched (target concentrations SRP 5 $\mu g \cdot L^{-1}$, $NO_3 \cong 45$ $\mu g \cdot L^{-1}$) for several months previous, were then subjected to the termination of nutrient additions. One of the systems was a natural stream, the other was a replicated, artificial, plastic lined channel apparatus with insufficient substrate for a hyporheic zone. Treatments losing enrichment were compared to controls which had never been enriched or had enrichment maintained for the duration of the experiment. Alkaline phosphatase activity (APA) and periphyton chlorophyll a were measured at regular intervals for up to two months after nutrient enrichment ended. In the natural stream, APA levels in the reach losing enrichment were similar to levels in a reach that continued to received enrichment. Chlorophyll a levels also showed no effect of the loss of enrichment. In the artificial channel experiment, one week after enrichment was terminated, APA levels increased and chlorophyll a levels decreased compared to channels which continued to be enriched. These results are interpreted to support the hypothesis. Weaknesses of the design are acknowledged and discussed.

Chapter two tests the hypothesis that stream invertebrates trade - off potential food rewards and predation risk when making the decision to leave the substrate and enter the drift. Some data from a natural stream are presented, but the test of the hypothesis comes from the artificial channel experiment where fish (cutthroat trout presence/absence) and periphyton levels (continued enrichment and losing enrichment) were manipulated in a 2x2 factorial design. Artificial channels losing enrichment experienced a loss of periphyton chlorophyll a. Drift was measured during the day and night, and benthic samples were taken from the channels and used to calculate per capita drift rates. Baetid mayflies (*Baetis* sp.) were the

only taxa to show a significant treatment effect. Large and small baetids (separated at 3.0 mm) were analysed independently. Benthic densities of baetid mayflies dropped significantly over the course of the manipulation in channels that had lost enrichment. Daytime drift rates for both large and small baetids were significantly lower in the presence of fish. Enrichment had a significant affect on the night time drift rates of larger mayflies, with increased drift rates in channels that were losing periphyton chlorophyll a due to a loss of enrichment. Smaller baetids demonstrated a significant interaction between fish and enrichment during the day. These results indicate that fish presence is more important than food during the day for larger invertebrates, causing increased drifting due to decreasing food levels to take place at night. For smaller invertebrates, who are less susceptible to predation while drifting, predation risk and food reward appear to be evaluated more equally during the day, causing a significant interaction term.

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Introduction

Pristine stream communities experience small but significant variations in dissolved ions, usually following a seasonal pattern (Feller and Kimmins 1979). Natural (Grimm and Fisher 1989) and anthropogenic (Likens *et al.* 1970, Feller and Kimmins 1984) disturbances can cause larger fluctuations in stream water nutrient levels. This environmental variation is mediated by processes of nutrient storage, release and transfer between various functional compartments within the stream ecosystem. These processes have the potential to affect ecosystem resistance (ability to maintain community state in the face of perturbation) and resilience (ability to return to original state after deflection due to disturbance) to changes in nutrient levels. Nutrient dynamics in streams have received significant attention over the past twenty years (Elwood *et al.* 1981b, Newbold *et al.* 1982, 1983, Grimm and Fisher 1984, Bothwell 1985, Mulholland *et al.* 1985, Perrin *et al.* 1987, Stockner and Shortreed 1987, Triska *et al.* 1989, Mundie *et al.* 1991, Peterson *et al.* 1993, Rosemond *et al.* 1993, Valett *et al.* 1994). The majority of this process-based research has focused on warm, eutrophic, low gradient streams, leaving gaps in our understanding of temperate, oligotrophic, mountainous streams, like those of coastal British Columbia.

One of the major compartments mediating nutrient dynamics in streams is the hyporheic zone, defined as that portion of the channel substrate that exchanges interstitial water with the free flowing water column (Stream Solute Workshop 1990). The contribution of this zone to stream ecosystem resistance and resilience has received some attention (Grimm and Fisher 1984, 1989, Triska *et al.* 1989, Duff and Triska 1990, Valett *et al.* 1994). Organic matter and associated nutrients taken into the hyporheic zone may be stored for months to years (Metzler and Smock 1990) and are highly resistant to downstream export. Studies in desert streams have shown that the release of stored nutrients from the hyporheic zone affects primary productivity in the channel when stream water nutrient levels are low (Valett *et al.* 1994).

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However, the importance of the hyporheic zone and its potential to contribute to community resistance to changing nutrient inputs in temperate, coastal, BC streams is largely unknown.

As nutrient inputs fluctuate, it is of interest whether a corresponding change in the stream community will result. If no change in the stream community takes place, resistance can be considered high and the mechanism that provided the resistance becomes of interest. Chapter 1 of this thesis addresses the role of the hyporheic zone in the resistance of stream communities to a lost nutrient input source. I am defining resistance of an ecosystem as its ability to maintain its state characteristics (trophic state, biomass, population densities, species composition, etc.) in the face of events that have the potential to change these characteristics. The perturbation I examine is the ending of inorganic nutrient inputs after several months of enrichment, and the ecosystem state characteristic is periphyton biomass. This manipulation was performed on a natural stream system and in artificial channels that lack a hyporheic zone. By working in systems with and without a hyporheic zone, I hoped to infer some of the potential importance of the hyporheic zone in stream community resistance. Effects of ending enrichment were contrasted with equivalent systems that continued to be enriched. I acknowledge that the differences between natural and artificial channels are numerous and confounding. Though the natural and artificial channels are not replicate streams, I feel that cautious interpretation of results from these different systems can offer some insight into the importance of hyporheic processes.

Chapter 2 deals with invertebrate responses to decreasing periphyton biomass resulting from the manipulations described in Chapter 1. The downstream movement of benthic invertebrates in the water column is known as drift. Causes and patterns of drift have been extensively examined in flowing waters around the world (for reviews see: Waters 1972, Muller 1974, Brittain and Eikeland 1988). Drift can be characterised as a dispersal behaviour for stream invertebrates. Drift rates from patches with experimentally added food tend to decrease (Hildebrand 1974, Otto 1976) while drift rates from patches with declining food levels tend to increase (Keller 1975, Bohle 1978). Kohler (1985) demonstrated that

Baetis is more prone to drift from patches with low food levels than those with high food levels, and that habitat quality is judged relative to patches sampled in the recent past.

The presence of fish also has a strong impact on invertebrate drift. Strong daily and ontogenetic patterns in drift have been shown to reduce predation risk to the drifting invertebrate (Allan 1978, 1984, Newman and Waters 1984, Skinner 1985, Andersson *et al.* 1986, Malmqvist 1988). Short term manipulations of fish presence have shown plastic, adaptive responses in the timing of drift by mayflies (Douglas *et al.* 1994, Forrester 1994, Tikkanen *et al.* 1994). Dill (1987) has noted the decision to drift is likely a trade-off between the factors of food reward and predation risk. Chapter two describes a short term experiment that manipulates food level and fish presence to test the hypothesis that the reward of food and the risk of predation are traded-off by drifting invertebrates.

The manipulations in this thesis took place in two different systems. The first manipulation took place in tributaries to the Salmon River on Vancouver Island, BC. These tributaries were enriched during the summer months by the BC Ministry of Environment, Lands and Parks (now BC Ministry of Fisheries) to increase salmonid production. Data were collected from three sites: one site that was losing nutrient inputs after several months of receiving them, one site upstream that had never received nutrient inputs, and one site downstream that continued to receive nutrient inputs throughout the study (see Figure 2 in Chapter 1, page 11). Periphyton chlorophyll *a* and alkaline phosphatase activity (APA, an indicator of phosphorus limitation) and invertebrate drift were measured at regular intervals from two weeks before to eight weeks after enrichment ended in the middle site.

The second manipulation took place in an artificial stream channel apparatus in the UBC Malcolm Knapp Research Forest. Ending nutrient inputs was used to decrease food available to invertebrates while predation risk was manipulated with the presence or absence of cutthroat trout (*Oncorhynchus clarki*). The loss or maintenance of enrichment and the presence or absence of fish were used to construct a 2x2

factorial experimental design. Again, periphyton chlorophyll *a* and APA, and invertebrate drift were measured regularly. Benthic densities of invertebrates in the channels were also measured.

Results of the two manipulations are presented in two chapters organized by trophic level, not manipulation. Chapter 1 deals with the nutrient and periphyton issues of the two experiments and examines the hypothesis that the hyporheic zone contributes to stream resistance to decreasing nutrient levels. Chapter 2 covers the drift responses of the invertebrates and tests the hypothesis that the risk of predation is traded off for the reward of food by invertebrates that make the decision to drift.

This thesis adds to our knowledge of nutrient storage in streams and the response of periphyton and invertebrate communities to nutrient depletion. As nutrient additions are currently being used as a rehabilitation strategy for fish stocks (Slaney and Ward 1992), improving our knowledge of the nutrient-periphyton dynamics may improve our rehabilitation efforts and help achieve desired results more efficiently. By better understanding how changes in periphyton levels impact invertebrate drift patterns, it may be possible to increase the effectiveness of this rehabilitation practice.

Chapter 1 - Resistance of stream periphyton chlorophyll *a* levels to the loss of anthropogenic nutrient inputs.

Introduction

The initial impact of varying nutrient levels in any ecological system depends on its resistance to perturbations of this nature. Resistance of an ecosystem is defined as its ability to maintain its primary characteristics (trophic state, biomass, population densities, species composition, etc.) in the face of events that could potentially change these variables. Conversely, resilience is the ability to return to a pre-disturbance state after deflection from this state by a disturbance. While these definitions are not universally agreed upon in the literature (Connell and Sousa 1983), understanding how communities change in response to a disturbance and return to original conditions after a disturbance, remains a fundamental challenge for ecologists.

The hyporheic zone is defined as that portion of channel substrate which exchanges interstitial water with the free-flowing stream water column. The role of the hyporheic zone in a stream channel's nutrient storage and cycling (or spiralling: Newbold *et al.* 1983) has received a great deal of attention (Grimm and Fisher 1984, Triska *et al.* 1989, Duff and Triska 1990, Valett *et al.* 1994), and its role in both the resistance and resilience of stream ecosystems has been noted (Grimm and Fisher 1989, Grimm *et al.*, 1991). Organic matter and associated nutrients taken into the hyporheic zone may be stored for months to years (Metzler and Smock 1990) and can be highly resistant to downstream export. Nutrients can be subsequently released from the hyporheic zone in sufficient concentrations to affect benthic primary productivity (Valett *et al.* 1994).

To evaluate the contribution of hyporheic processes to stream characteristics it would be desirable to perform a manipulation on a stream system where the hyporheic zone is missing in a structural or functional way. However, with the exception of stream flow over bedrock it is likely that all natural

streams include a hyporheic zone. Methods of structurally removing the hyporheic zone from the stream would be highly invasive. Artificial stream channels constructed with insufficient substrate to harbour a hyporheic zone may provide a useful tool, but results must be cautiously interpreted with regards to natural streams (Manual and Minshall 1980).

The study of nutrients in streams has advanced over the past twenty years primarily using two approaches. One measures the consequences of experimental enrichment of whole communities (Elwood *et al.* 1981b, Bothwell 1985, Perrin *et al.* 1987, Stockner and Shortreed 1987, Mundie *et al.* 1991, Peterson *et al.* 1993, Rosemond *et al.* 1993) while the other measures and analyses fluxes of nutrients among various ecosystem compartments (Newbold *et al.* 1982, 1983, Grimm and Fisher 1984, Mulholland *et al.* 1985, Triska *et al.* 1989, Valett *et al.* 1994). Experimental nutrient depletion is a relatively novel approach. It is logistically difficult and only one such manipulation has been performed in streams. Water recirculation rate was varied by Mulholland *et al.* (1991) to decrease ambient nutrient levels in small, artificial, recirculating channels. The results of this manipulation were highly informative and would have been impossible to attain with an enrichment manipulation. Furthermore, as nutrient concentrations in streams vary naturally over a time scale of weeks (Feller and Kimmins 1979), understanding the ecosystem's differing response to increasing and decreasing nutrient levels is fundamental to our knowledge of basic stream ecosystem dynamics.

The logistics of decreasing nutrient levels in stream water are considerable. Removing select ions from stream water is obviously far more difficult than adding them. In small, eutrophic, man-made lakes and lake microcosms, aluminium sulphate (Babin *et al.* 1992), and ferric sulphate (Holz and Hoaglan 1996) have been used to remove phosphorus from the water column. Studies examining recovery of streams from long term anthropogenic nutrient rich pollution are usually complicated by recovery from associated organics and heavy metals (e.g. Jaques *et al.* 1986). The elaborate artificial channel apparatus used by Mulholland *et al.* (1991) is expensive and limits manipulations to relatively small microcosms. In

my study, nutrient inputs were ended in channels that received enrichment for a period of several months. It is assumed that this time is sufficient for the ecosystem to have responded to the enrichment. Periphyton mat growth in response to nutrient enrichment reaches near maximal values after ~ 30 days (Bothwell 1989). Time required for stream invertebrates to respond fully to enrichment can be fairly short (weeks) for artificial channels which are colonised by rapidly inflowing biota (Stockner and Shortreed 1987, Mundie *et al.* 1991, Mackay 1992), or can be on the order of several years in the case of whole stream manipulations which require a numerical growth response on the population scale (Peterson *et al.* 1993).

The purpose of this study is to examine the hypothesis that the hyporheic zone increases stream ecosystem resistance to a loss of nutrient inputs. I selected periphyton chlorophyll *a* concentration as the indicator of disturbance for two primary reasons. First, chlorophyll *a* levels are known to be influenced positively by nutrient levels (Bothwell 1985, Perrin *et al.* 1987, Stockner and Shortreed 1987, Mundie *et al.* 1991). Secondly, the chlorophyll *a* concentration of periphyton can affect higher trophic levels in the community (Lamberti *et al.* 1989, Hart and Robinson 1990), indicating that changes to this variable are relevant to higher trophic levels in the stream ecosystem.

The hypothesis was tested by measuring the response of periphyton chlorophyll *a* to the loss of nutrient additions in an enriched natural stream and an enriched artificial channel apparatus. If the presence of a hyporheic zone contributes to an increased resistance to a loss of nutrient inputs we might expect a smaller change in chlorophyll *a* in the natural stream, a longer time lag before any change is measured in the natural stream, or a combination of the two. Alternatively, if the two systems respond in a similar manner, it implies that the hyporheic zone does not affect stream resistance to a loss of nutrient inputs. There are limitations of my design. The absence of a hyporheic zone is only one of many differences between a natural stream system and artificial channels. That said, the results of my work provide some useful information with which to discuss the hypothesis. The potential confounding issues will be pursued in the Discussion.

Materials and Methods

Salmon River Sites

Data collection took place in two separate watersheds during consecutive years. Three sites within the Salmon River watershed (mouth of river at 125° 56' 42" W, 50° 22' 42" N) on the east coast of Vancouver Island (British Columbia, Canada) were studied from early August to late September, 1993. The sites were located in Grilse Creek and its tributary, Norris Creek, located roughly 30 km west of the town of Campbell River. The watershed has experienced extensive timber harvest to the stream bank historically, though recent cut blocks have not included the immediate riparian zone. Grilse Creek is oligotrophic with soluable reactive phosphorus (SRP) $< 1\mu g\cdot L^{-1}$ and $NO_3 \cong 20\mu g\cdot L^{-1}$ (Perrin 1991a, 1991b) indicating phosphorus limitation. Over the 57 day study, the average temperature was 14°C (range of 12.5 -16°C) and the mean water velocity was 27cm/sec (range of 10 - 65cm/s) at the sites sampled.

Water Survey Canada maintains a gauging station (station # 08HD006) near the mouth of the Salmon River. The hydrograph at this station is shown in Figure 1. While the hydrographs for smaller tributaries such as Grilse and Norris Creeks are certainly somewhat different, the overall pattern is likely similar. These data show that average and especially maximum daily discharges are much higher during the period from October to February than during the rest of the year. The enrichment tanks have been in place every summer for the same period since 1989, though there appears to be no direct enrichment holdover from the previous year's nutrient additions. Anecdotal information from field technicians indicates that periphyton levels are reduced to pre-enrichment levels by April the following year. With enrichment ending at the beginning of August, the flow pattern in this system would have ample opportunity to flush any added nutrients out of the stream reach before enrichment begins again the following May.

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Daily Discharge (m3 / s)

1800
1600
1400
1200
1000
800
600
400
200
0

Avg
Max
Min

80.6 77.9 64.3 66.2 76.1 58.4 29.7 16 21.9 74.3 98.3 97.8

Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec

Month
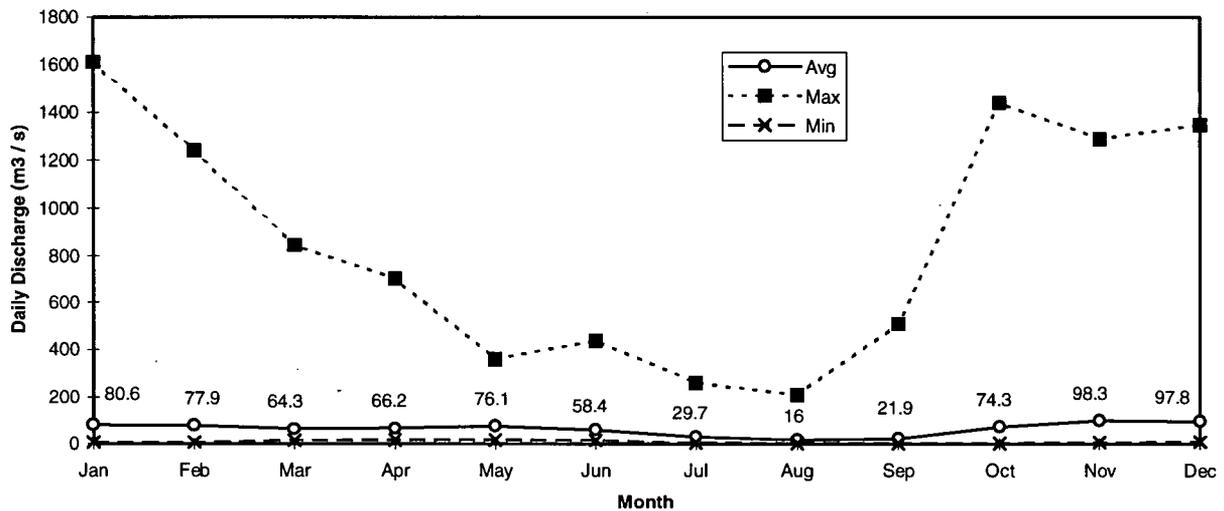
Figure 1. Average, maximum and minimum daily discharge at Water Survey Canada gauging station #08HD006, located near mouth of Salmon River (50°18'24"N, 125°53'50"W). Data collected from 1956-1997. Data labels show average daily discharge.

An active sport fishery for coho salmon (*Oncorhynchus kisutch*) and large steelhead trout (*O. mykiss*) is located on the lower half of the Salmon River. The BC Ministry of the Environment, Lands and Parks (MELP, now Ministry of Fisheries) was enriching the stream with inorganic agricultural phosphate and nitrate fertilisers (target additions SRP = 5 $\mu g \cdot L^{-1}$ and nitrate = 45 $\mu g \cdot L^{-1}$ respectively) from early May to early August during 1993. This prescription had been followed since 1989 to help re-establish fish stocks in Grilse Creek and the upper Salmon River. Enrichment was accomplished by tanks fitted with slow drip valves monitored and adjusted to stream discharge twice a week at four input stations along a 20 km stretch of stream. Water chemistry sampling upstream of the nutrient input tanks shows that natural variation in SRP ranges from <1.0 - 15 $\mu g \cdot L^{-1}$ nitrate from < 5.0 - 220 $\mu g \cdot L^{-1}$ (Perrin 1991a). Measurements were taken from early June to late July and nutrient levels tended to increase over time. The target levels for nutrient additions fall well within these values.

Whole river fertilisation is occasionally being used as a habitat rehabilitation strategy for salmonids by MELP. Reasons for enrichment have included mitigation for loss of habitat due to hydroelectric development, to aid the productivity of overfished stocks, and to help re-establish extinct populations in watersheds that have experienced extensive timber harvest (P. Slaney, Ministry of Fisheries, pers. com.). Preliminary work has demonstrated an 1.4 - 2.0 fold increase in the weight of juvenile coho salmon and steelhead trout in fertilised reaches by the end of the summer growing period (Johnston *et al.* 1990).

In order to study the effects of ending the enrichment on periphyton, I selected three sites (see Figure 2) to monitor from early August to late September. This period covered two weeks before and almost two months after nutrient additions from tank #1 were ended. The first (*never enriched* or NE) and second (*losing enrichment* or LE) sites were in Norris Creek, roughly one kilometre upstream and 500 m downstream, respectively, of the first nutrient input tank (tank #1). This tank was shut off and removed ten days into the study (Aug.11, 1993). The third site (*continued enrichment* or CE) was in Grilse Creek, roughly 100m downstream of the second fertilisation station which was in operation for the full length of the study. The second nutrient input tank was roughly 5.0 km downstream of the first. All three sampling sites were in low gradient riffles directly below less turbulent runs. The site which continued to be fertilised had somewhat less canopy closure than the other two sites.
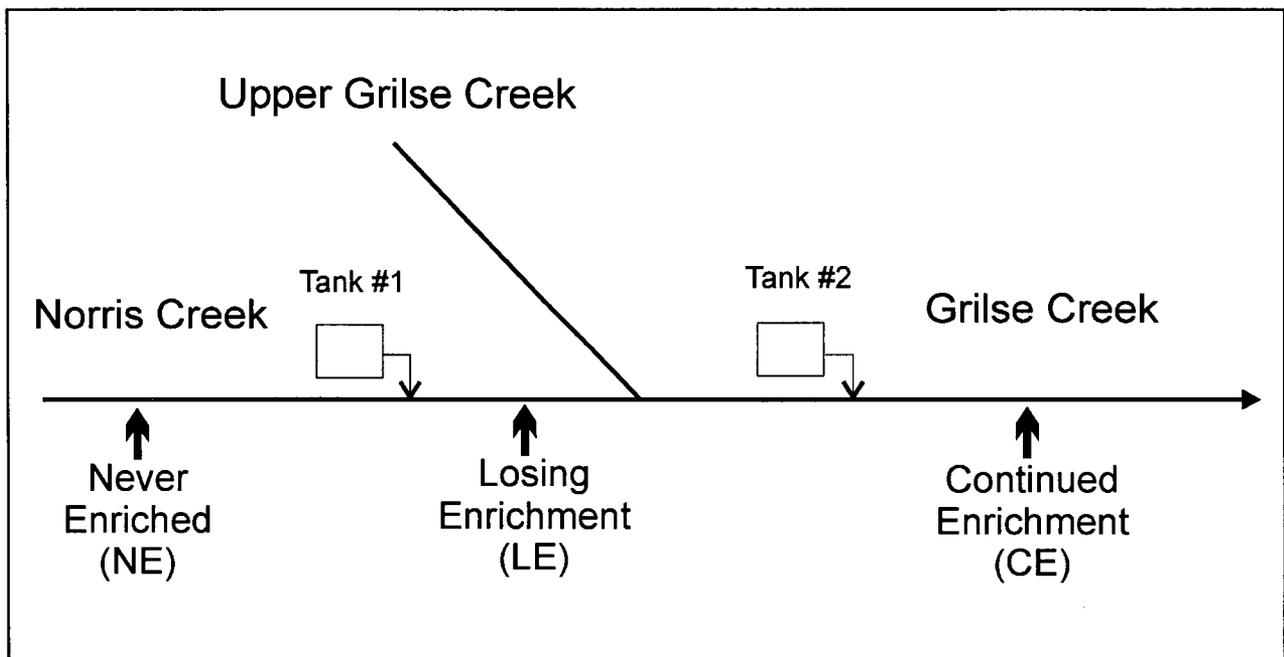
Figure 2. Schematic of the locations of nutrient input sites and sample sites in the Grilse Creek watershed. Tank #1 was removed after the first two weeks of the study period. Tank #2 was in place and functioning for the duration of the study.

Artificial channels

During the summer of 1994, research was carried out at the Mayfly Creek artificial streamside channel apparatus in the Malcolm Knapp Research Forest of the University of British Columbia, (previously described by Richardson 1991). The channels differ from the previous description in that there are twelve replicates and the substrate is entirely 3-5cm diameter rounded gravel, 5-10cm deep. The gravel was arranged to create four, 1.5m long pools equally spaced along the 14m long flow-through channels. The remainder of the channel habitat was riffle. Mayfly, Grilse and Norris Creeks are similarly oligotrophic and the artificial channels are roughly the same gradient as the sites in Grilse and Norris Creeks. The channels were allowed to colonise with invertebrates and organic matter from Mayfly Creek for two months while being fertilised with KH_2PO_4 (target conc. SRP = 5 µg $\cdot$ L^{-1}) and KNO_3 (target conc. $NO_3^- = 40$ µg$\cdot L^{-1}$) solution dripped from Mariotte bottles monitored daily. Relatively stable levels

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of periphyton were maintained for several weeks before nutrients were shut off in six of the twelve channels creating two treatments: channels that continued to be enriched (CE) and channels that lost enrichment (LE).

Parameter measurement

Periphyton chlorophyll a concentration and alkaline phosphatase activity (APA) were measured at regular intervals throughout the study. APA is used as a measure of phosphorus limitation (Pettersson 1980). In periphyton, an increase in periphyton APA indicates an increased reliance on internal biofilm phosphorus cycling (Mulholland et $al.$ 1991). Chlorophyll a was used as an indicator of algal biomass. A change in periphyton chlorophyll a could be taken to indicate a deflection in state and therefore, a failing resistance.

Periphyton samples for alkaline phosphatase activity (APA) were taken in all sites for both studies before and several weeks after fertilization was terminated, near the end of the study periods. Three arbitrarily selected rocks were placed on ice upon removal from the stream and frozen at -10°C within a few hours. Rocks were thawed within 6 months of storage and periphyton removed with a stiff brush and suspended in 100µM tris buffer, pH 9.5 with 500µM added calcium. Fluorometric methods for APA analysis follow Bothwell (1988) and Pettersson (1980). Three 4.5ml subsamples were taken per rock and incubated in 100µM 4-methylubelliferyl phosphate (MUP) at 35 C for 20-40 minutes. Fluorometric measurements of 4-methylubelliferyl (MU) evolution were taken regularly during this time and the final rate change was standardised per unit of chlorophyll a as a measurement of APA. Two 0.5 ml subsamples were taken from the original suspension and added to 4.5ml 100% acetone for chlorophyll a determination.

In Grilse and Norris Creeks periphyton chlorophyll a was measured weekly at the NE and CE sites and twice a week at the LE site. Five rocks were arbitrarily selected from the stream bottom and

periphyton was removed with a stiff brush and suspended in stream water. Subsamples of the resultant

slurry were filtered onto Whatman GF/F filters which were frozen at -10 °C in the dark for several weeks

until extracted in 90% acetone for 8 hours at 0°C. Chlorophyll *a* concentration of the extractant was

measured fluorometrically. The lengths of the three axes of each rock were measured in the field. Lengths

ranged from 1.0-13.0 cm in Grilse Creek and from 1.0 to 8.0 in the artificial channels. A predictive model

($p=0.001$, $r^2=0.91$, $n=60$) between the surface area of stream rocks (as measured with aluminium foil) and

the log of the three axis lengths was used to estimate rock surface area. Periphyton chlorophyll *a* was

measured in the artificial steam channels twice a week. Whole rocks were removed from the channel,

frozen, returned to the lab, thawed, and extracted directly in 90% acetone. Otherwise, the methodology

was similar to that used in Grilse and Norris Creeks.

Data analysis

Repeated measures ANOVA (SAS procedure GLM, SAS Institute 1985) was used to test for the

effects of site (Grilse and Norris Creeks) or treatment (artificial channels) on APA and chlorophyll *a*.

Repeated measures ANOVAs are used to detect treatment effects that vary over time, making them well

suited to the anticipated changes in APA and chlorophyll *a* over the duration of my experiment. Both

univariate analysis of variance with repeated measures (ANOVAR) and multivariate analysis of variance

with repeated measures (MANOVAR) are performed by SAS and both detect the same thing: differences

that change over time due to treatment. The difference between the two methods is in the mathematical

means used to calculate significance tests. The reason for the two different types of tests is that ANOVAR

provides more statistical power than MANOVAR, but ANOVAR has assumptions of compound symmetry

of the variance-covariance matrix (sphericity) which MANOVAR does not (Potvin *et al.* 1990).

Mauchley's criterion test for sphericity with corrected significance levels was generated as part of the

analysis and usually the data satisfied the assumption. However, for the sake of consistency, I will present only the results of the multivariate tests based on Wilks' Lambda. Results of the other multivariate tests (Pillai's Trace, Hotelling-Lawley Trace, and Roy's Greatest Root) provided similar results, and the univariate test (ANOVAR) had no meaningful differences. While many of my predictions are directional, and an argument for one tailed tests is defensible, I will present probability values for two tailed tests.

When there was a significant response in the repeated measures analysis, simple ANOVAs were performed for each individual date to determine at which dates the treatments caused significant effects. For these tests the significance criterion was corrected to keep $p = 0.05$ over the entire experiment. For Grilse and Norris Creek data, replicate samples within a site were used as treatment replicates. As such, the statistical differences between these treatments can only be strictly interpreted as site differences. I am cautiously interpreting and discussing these results as they might apply to treatments effects. In the artificial channel experiment, the channel was the experimental unit with each treatment having 6 replicates.

Results

Salmon River sites
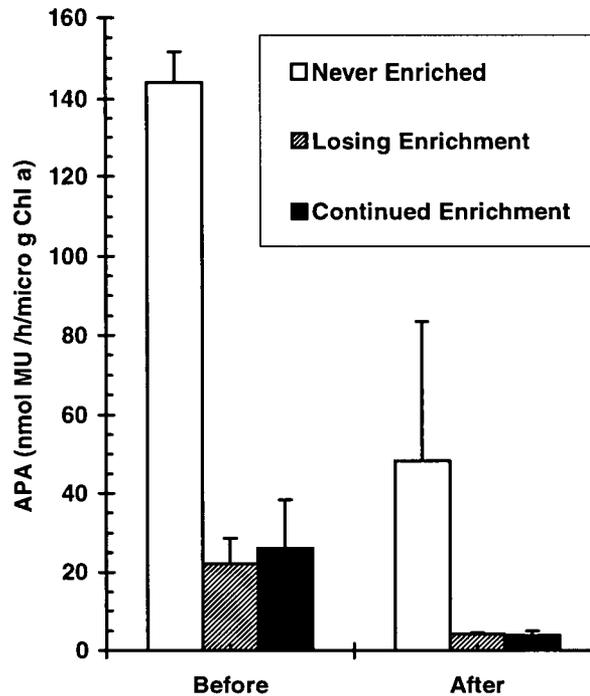
Figure 3. Alkaline phosphatase activity (APA) of periphyton at three sites in the Salmon River. APA is measured as nanomols of 4-methylubelliferyl (MU) produced per hour per microgram of chlorophyll a. Samples were taken immediately before and several weeks after inputs ended in the losing enrichment site. Error bars show 95 % confidence limits (n=3).

APA values in all sites were lower several weeks after enrichment ended in the LE site (Figure 3).

This created a significant between treatment effect ($F_{2,6}$=65.82, p < 0.0001). Between treatment effects

are calculated independent of time, pooled over the length of the experiment. APA decreased by 67% in the

NE site and >80% in the LE and CE sites. This discrepancy between treatments in the amount of decline

over time created a significant within treatment effect ($F_{2,6}$ = 15.80, p = 0.0041). Within-subject effects

are time x treatment interactions. The impact of these effects change over the duration of the experiment.

For both dates, APA levels were 5 to 12 times higher in the NE site than in the LE and CE sites.

ANOVA's performed on each date separately showed this difference between sites was significant on both dates ($F_{2,6}$ =223.95, p<0.0001 and $F_{2,6}$ =6.00, p<0.0037 for the first and second samples respectively). No significant difference between the LE and CE sites was detected.
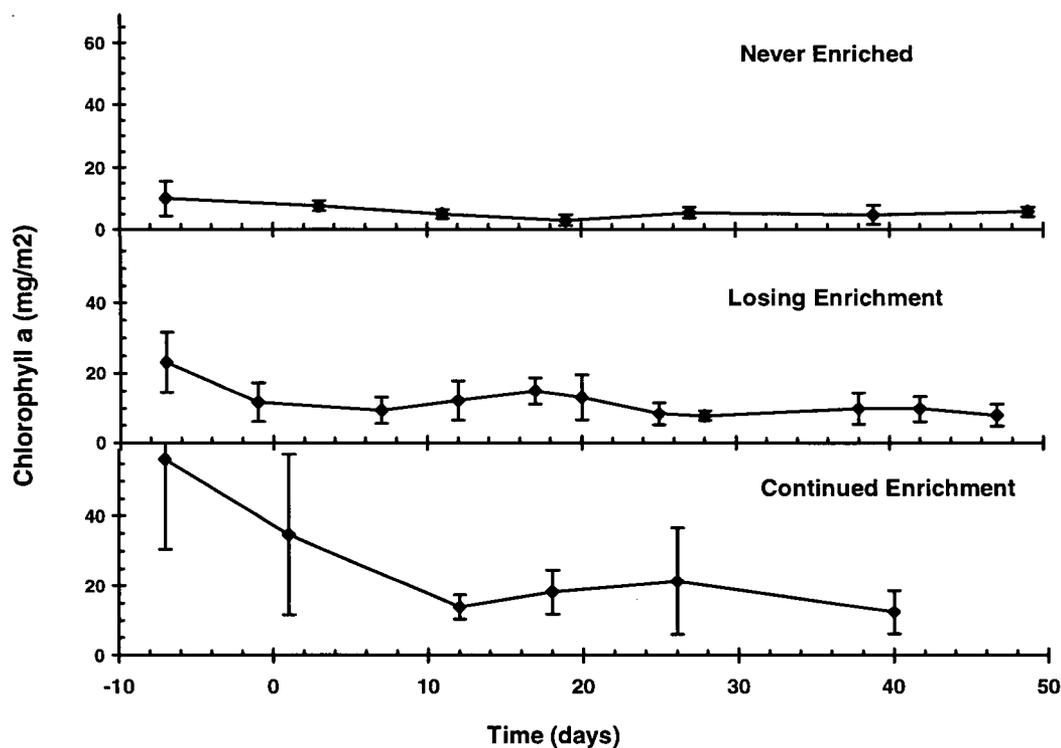
Figure 4. Periphyton chlorophyll a measured at the three sites in the Salmon River. Chlorophyll a is expressed per substrate surface area. Nutrient additions in the losing enrichment site ended at day 0. Error bars show 95 % confidence limits.

Over the length of the study the NE site had an average of 5.8 mg chlorophyll $a \cdot m^{-2}$, the LE site 11.6 mg·m^{-2}, and the CE site 26.1 mg·m^{-2} (Figure 4). MANOVAR detected a significant ($F_{10,16}$ = 4.927, p=0.002) within treatment effect. Within treatment effects are interaction terms with time, showing treatment effects that change over the duration of the experiment. In this case, a decline in chlorophyll a levels at the beginning of the experiment in the CE site created the significant effect. This reflects a refining of the sampling technique used at this site and not a change in community state. The other sites did not vary significantly over time. There was no significant drop in chlorophyll a levels in the LE site.

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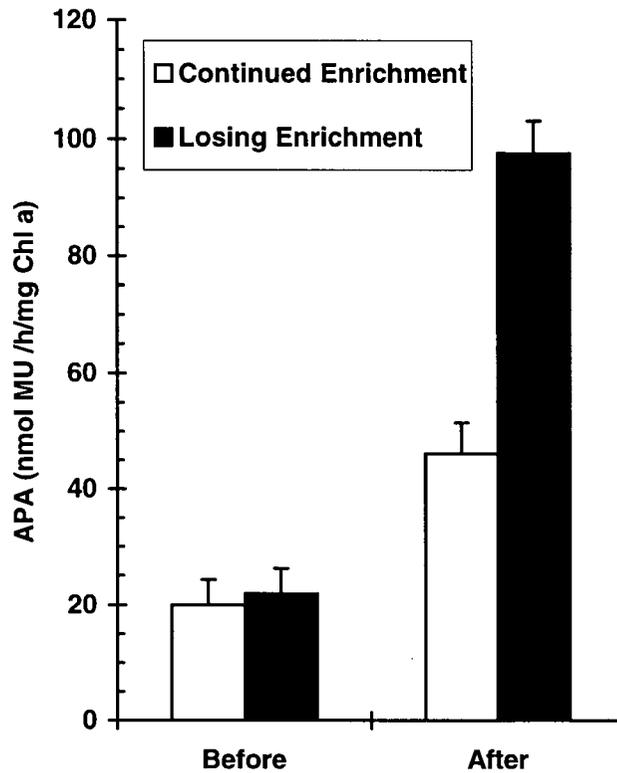
Figure 5. Alkaline phosphatase activity (APA) of periphyton in the artificial channels. APA is measured as nanomols of 4-methylubelliferyl (MU) produced per hour per micro gram of chlorophyll *a*. Samples were taken immediately before and several weeks after enrichment ended in the channels losing enrichment. Error bars show 95 % confidence limits.

In the artificial channels, APA levels were higher in both treatment groups on the second sampling date than the first (Figure 5). The data prior to nutrient cut-off demonstrate no significant differences between the LE and CE channels but the data measurement taken three weeks later shows a relatively strong difference between the two treatment groups. This change caused the MANOVAR to show significant within treatment ($F_{1,10}$= 112.2, p<0.0001) and between treatment ($F_{1,10}$= 19.3, p<0.0013) effects. Periphyton in the LE channels had APA levels 2.1 times the CE channels during the second sampling date.
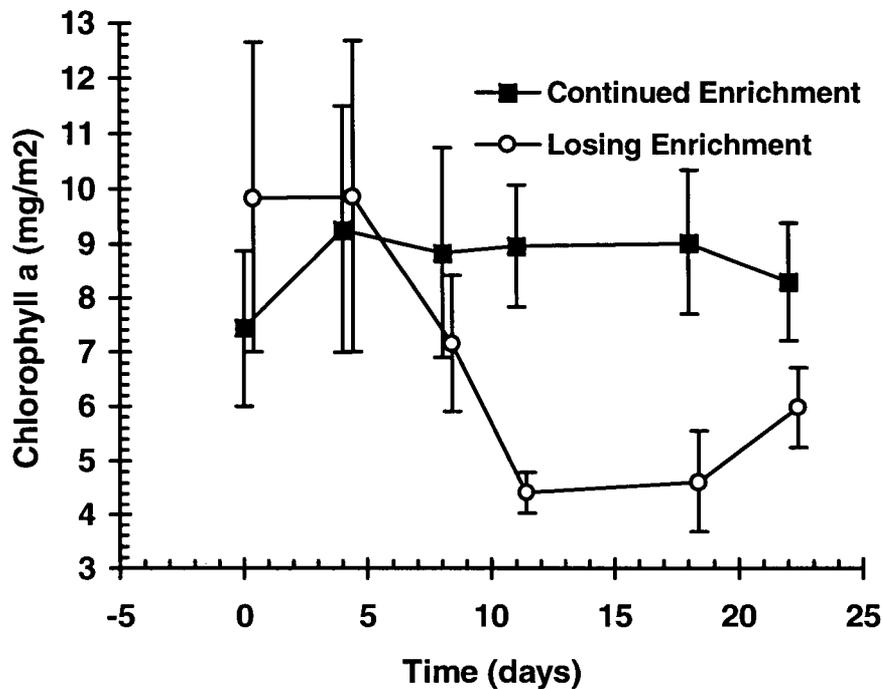
Figure 6. Periphyton chlorophyll *a* measured in the artificial channels. Chlorophyll *a* is expressed per substrate surface area. Nutrient inputs to the LE treatment ended at day 0. Error bars show 95 % confidence limits.

Periphyton chlorophyll *a* in the CE and LE channels maintained similar concentrations of chlorophyll a at the beginning of the manipulation (roughly 9 mg·m^2) but after 11 days, levels in the LE treatment group had dropped significantly to roughly 4 mg·m^2 chlorophyll *a* (Figure 6). MANOVAR shows a significant within treatment effect ($F_{5,6}$ = 6.03, p<0.0003). Simple ANOVAs performed on each date show that the treatment groups differ at day 11, 18 and 22 ($F_{1,10}$ =56.02, p<0.0001; $F_{1,10}$=28.37, p=0.0003; $F_{1,10}$= 11.92, p=0.0062, respectively). There was no effect of treatment on other days.

Discussion

APA is a useful measure of phosphorus limitation (Healey and Hendzel 1979) and has also been inversely associated with relative growth rates of phosphorus-limited periphyton communities in the interior of British Columbia (Bothwell 1989). At very low phosphorus concentrations (<3.0 $\mu g \cdot L^{-1}$), where the precision of direct phosphorus measurement is difficult to attain, APA provides a much more sensitive and reliable means of determining the impact of phosphorus concentration on periphyton growth (Bothwell 1988). Decreased APA and increased levels of chlorophyll a in fertilised reaches of coastal British Columbia streams have been measured previously (Perrin *et al.* 1987), but such data has not been collected during the period after enrichment was terminated. The extended period of apparent enrichment after nutrient inputs have ceased raises many questions about phosphorus dynamics and storage within coastal BC streams, and lends some support to the hypothesis that hyporheic storage of phosphorus could influence stream community resistance to a loss of nutrient inputs.

The maintenance of relatively low APA levels and relatively high amounts of periphyton chlorophyll a in the LE site suggests that enriched levels of phosphorus were still present at this site even two months after the end of enrichment. My ability to measure a decline in chlorophyll a and an increase in APA in the artificial channels indicates that the methodology was sufficiently sensitive to resolve a similar pattern within the natural system had it occurred. While my ability to detect very small changes in chlorophyll a may have been limited by sample size (Morin and Cattaneo 1992), the expected changes were relatively large. Furthermore, although APA is very sensitive to changes in ambient phosphorus concentration (Bothwell 1988), losing enrichment had no effect on APA. This strongly suggests that the effects of enrichment were maintained after anthropogenic nutrient inputs ended. The mechanisms by which this would be accomplished can be divided into two groups: internal cycling within the periphyton

mat (Mulholland *et al.* 1991), or some compartment external to the periphyton which releases nutrient into the water column where it becomes available to the periphyton (spiralling, Newbold *et al.* 1983).

Diffusion within the biofilm matrix of the periphyton is much slower than that of the surrounding water (Riber and Wetzel 1987) allowing for an increased potential for retention and recycling of organic phosphates released into the biofilm. Two factors suggest that internal recycling of phosphorus is not responsible for maintaining the enriched state of the LE site after nutrient inputs ended. First, a shift towards a greater reliance on internal recycling after a decrease in ambient nutrient concentration is associated with an increase in APA (Mulholland *et al.* 1991). My results showed no such increase in APA in sites losing enrichment. Second, nutrient cycling mechanisms within the periphyton mat require a biofilm thick enough for the formation of a boundary layer that inhibits the transport of remineralised nutrients away from the biofilm (Riber and Wetzel 1987). Mulholland *et al.* (1991) found internal cycling of phosphorus to be significant in periphyton biofilms with chlorophyll *a* levels of 45 mg • m^{-2} but not in biofilms with 20 mg • m^{-2}. Periphyton chlorophyll *a* concentrations measured in my study were usually within 5-20 mg • m^{-2}.

If concentrations of periphyton chlorophyll *a* were not maintained by increased internal phosphorus cycling, the phosphorus that maintained enriched conditions in the LE site may have been released from some other source into the water column and taken up by periphyton. Research on phosphorus retention and spiralling in the stream channel has demonstrated that the majority of phosphate in the water column is taken up by microbial processes associated with coarse (CPOM) and fine (FPOM) particulate organic matter (Newbold *et al.* 1983, Mulholland *et al.* 1985, Elwood *et al.* 1988), though Mulholland *et al.* (1985) found that the mass specific absorption of phosphate by periphyton biofilms was higher than by POM. Standing crops of POM are usually an order of magnitude higher than periphyton biomass in small forested streams and CPOM levels in coastal BC streams are extremely high relative to periphyton levels (Richardson 1992). It is possible that in the LE site in Norris Creek, phosphorus was released from this

source in sufficient amounts to maintain periphyton chlorophyll *a* after nutrient inputs ended. Though this mechanism should also have functioned in the artificial channel LE treatment, these channels lost periphyton chlorophyll *a* quickly after nutrient inputs ended (Figure 6). I cannot reject the hypothesis that phosphorus was released from POM after nutrient inputs to the LE treatment in Norris Creek ended, however the data from the artificial channels show that any phosphorus released from POM did not maintain periphyton chlorophyll *a* after nutrient inputs ended in these systems.

Several different nutrient storage or cycling mechanisms could have been functioning in Norris Creek but not in the artificial channels. Internal periphyton recycling and channel POM are the obvious candidates and have been discussed. However there are other, more poorly understood factors such as abiotic adsorption (Elwood *et al.* 1981) which affect the movement of nutrients in streams. Having acknowledged this, I will limit my discussion to the most likely and well understood mechanisms. After internal recycling and channel POM, hyporheic storage is another strong candidate as a compartment for nutrient storage. Hyporheic hydraulic exchange is especially worthy of consideration as it remains one of the most fundamental differences between a natural stream and artificial channels enclosed in polyethylene plastic.

Significant attention has been given to the hyporheic zone's role in nitrogen dynamics and retention (Grimm and Fisher 1984, Triska *et al.* 1989, 1993, Valett *et al.* 1994). Much of the research has taken place in nitrogen limited systems and little information is available for phosphorus limited systems. The mechanism of nutrient storage in the hyporheic zone is not understood, but is assumed to be one or a combination of the following: hydraulic storage of nutrient rich water (Grimm *et al.* 1991, Triska *et al.* 1989); biotic uptake by organic matter (dissolved or particulate) (Grimm et al. 1991); or abiotic absorption to the hyporheic substrates (Elwood *et al.* 1981, Valett *et al.* 1994). In contrast, areas in the hyporheic zone with sufficient reducing potential can be permanent sinks of nitrogen through denitrification (Duff and Triska 1990).

Valett *et al.*'s (1994) examination of nitrate and soluble reactive phosphorus release from hyporheic zones shows elevated levels of nitrate in upwelling zones relative to downwelling zones over a 90 day post flood successional period. Soluable reactive phosphorus, a non-limiting nutrient in Sycamore Creek, was not found in higher concentrations in upwelling zones. The authors credit hyporheic storage of nitrogen resulting from the flood and/or nitrification for the increased nitrate in upwelling zones. A similar mechanism for phosphorus in the Salmon R. could have supplied phosphate to the LE site in my study. Furthermore, hyporheic storage operates on the temporal scale of months (Metzler and Smock 1990). This is a similar time scale to that observed in the Grilse and Norris Creeks. I feel my results offer some preliminary support of the hypothesis that the hyporheic zone is the nutrient storage mechanism that is contributing to the stream's resistance in the face of this perturbation. Further work, more specifically directed at tracing phosphorus storage and transport, is needed to support this claim.

Much has been written about the role of mesocosms in the study of stream ecosystems (Manuel and Minshall 1980, Beyers and Odum 1993, Lamberti *et al.* 1993). The benefits of working with mesocosms of any kind include experimental control, an increased control of environmental factors, ease of manipulation, and many replicates around which to design experiments. The primary disadvantage is the degree to which the artificial apparatus provides a realistic representation of the natural ecosystem. I feel this work provides some useful insight into how the intrinsic differences between artificial and natural systems can be exploited to make inferences about ecosystem function based on how the two systems react differently to similar manipulations. Assuming that artificial streams mimic processes taking place in the water and on the surface of the channel substrate, it is then permissible to consider exterior (including hyporheic) processes when explaining different responses by these systems.

The long term storage of nutrients in the Salmon River has implications for fisheries rehabilitation programs. When conducting nutrient additions for the purpose of rehabilitating fish stocks, it is desirable to create the maximum positive effect with the least effort. Any potential negative effects on the target area

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or areas downstream would be lessened by smaller inputs. My data show that effects of nutrient inputs last long after they have been eliminated from a stream. Therefor, a period of enrichment can be attained with a nutrient input program significantly shorter than the full duration of the target period.

Chapter 2 - Drift patterns of benthic invertebrates under food stress and predation risk by a drift - feeding predator.

Introduction

Invertebrate drift is generally defined as any downstream movement of the organism facilitated by flowing water. The downstream drift of benthic invertebrates occurs in all streams and rivers and has been studied extensively (for reviews see: Waters 1972, Muller 1974, Brittain and Eikeland 1988). Many mechanisms for the initiation of drift have been identified and they can be broadly categorised as "passive", involving accidental departure or dislodgement from the substrate, or "active", involving a choice or at least a physical attempt to enter the water column. "Passive" drift is often referred to as "constant" or "background" drift while "active" drift is often referred to as "behavioural" drift. These terms do not have consistent definitions in the literature and I will restrict my terminology to "active" or "passive", referring to the drift entry mechanism. Environmental stress such as rapid acidification of stream water (Bernard *et al.* 1990, Kratz *et al.* 1994), or the addition of pesticides (Dudgeon 1990) cause large amounts of drift referred to as catastrophic drift. Biotic factors such as food limitation (Keller 1975, Bohle 1978), the threat of invertebrate predation (Peckarsky 1980, Walton, O.E. 1980), or defeat in a competitive behavioural interaction (Hildrew and Townsend 1980, Matczak and Mackay 1990) have been found to result in active drift.

Because some fish feed exclusively on drifting invertebrates (Hughes and Dill 1990) it follows that drifting should incur a cost of increased predation risk to invertebrates in streams with drift feeding fish. A pattern of higher drift rates during the night in fish bearing streams has been documented in streams world wide. This has been hypothesised to be a method of avoiding drift feeding fish (Kroger 1974) whose ability to feed on drifting invertebrates decreases exponentially with decreasing light levels (Wilzbach and Cummins 1986). Natural variation in fish populations across an altitude gradient in Andean (Flecker

1992) and Himalayan (Brewin and Ormerod 1994) streams have shown no daily drift pattern where fish are absent and a strong day-night pattern where drift feeding fish are numerous. Streams that were historically fishless demonstrate daily patterns in the presence of introduced fish populations (established 50 years previously) while neighbouring streams with no introduced fish show no day-night differences in drift (Malmqvist 1988). Allan (1984) further demonstrated that smaller insects, which are less visible to drift feeding fish, have much less pronounced daily drift patterns. Numerous other studies also noted this pattern (Newman and Waters 1984, Skinner 1985, Andersson *et al.* 1986, Malmqvist 1988).

Several studies seeking to demonstrate changes in drift patterns in response to short term manipulations of drift feeding fish have failed to do so (Allan 1982, Williams 1990, Flecker 1992). This suggests that daily patterns of invertebrate drift in fish-bearing streams may be due to a genetically fixed behavioural response caused by long term selective forces against drifting during the day. However, recent work in this area suggests that some mayfly taxa are capable of altering their drift behaviour in an adaptive manner in the presence of drift feeding fish. Forrester (1994) measured increased per capita night-time drift of two mayfly taxa (*Baetis* and *Paraleptophlebia*) with increasing brook trout density in a New Hampshire stream. Short term fish additions into fishless streams resulted in decreased daytime drift rates (Douglas *et al.* 1994). Tikkanen *et al.* (1994) used recirculating aquaria and found that larger mayflies increased drift periodicity slightly in when fish odour was added to the water and strongly in the presence of a foraging fish. These plastic responses to predation risk have allowed us to predict adaptive patterns of drifting during short-term manipulations.

As a means of explaining why upstream reaches do not become completely depopulated of invertebrates, Waters (1961) hypothesised that drift represents benthic production in excess of carrying capacity. The density dependence predicted by Waters has been supported by some studies under certain flow regimes (Walton 1980) or with certain substrate types (Walton *et al.* 1977), but has by no means received universal support (Hildebrand 1974, Corkum 1978, Ciborowski 1983). Another method of testing

the excess production hypotheses is to vary the environment's carrying capacity. Small scale

manipulations have been performed by introducing ungrazed substrate with high periphyton biomass into

mesocosms stocked with grazers. Hildebrand (1974) and Otto (1976) measured a decrease in drift upon

addition of a food source. Keller (1975) and Bohle (1978) both measured an increase in drift as an

introduced food source was depleted. Based on experiments manipulating food level and distribution,

Kohler (1985) demonstrated that *Baetis* had higher drift rates from areas with low food levels than areas

with high food levels. Well-fed *Baetis* appeared to judge habitat quality differently than starved nymphs

indicating that the *Baetis* judged the quality of a patch relative to recent, past experience.

Because *Baetis* can apparently evaluate both the relative food abundance in its local area and the

predation risk associated with drifting, it follows that the initiation of drifting involves an evaluation of both

these factors. The decision involves a trade-off of the risk of predation and the reward of food in such a

way as to maximise fitness (Dill 1987). Experiments involving trade-offs of this nature are common in the

testing of optimal foraging theory and patch use models (Charnov 1976). The trade-off faced by a

potential drifting mayfly however, is not easily compared to other patch use models. These models

consider the choice amongst patches of varying levels of food and predation risk (Lima and Dill 1990,

Scrimgeour and Culp 1994). However, no current patch use model I have found includes both a predation

risk specific to dispersal in between patches, and unconfirmed amounts of food in the destination patch.

In order to test the hypothesis that invertebrates trade-off predation risk and food reward when

making the decision to drift, I performed two manipulations involving declining levels of food for drifting

invertebrates, measured as spatial concentration of chlorophyll *a* in periphyton. The first manipulation

takes place in a natural stream system in which nutrient enrichment was terminated in one reach, continued

in a second reach, while a third reach remained in an un-enriched state. This manipulation was meant to

provide information on the drift patterns of invertebrates under declining food levels. The second

manipulation was performed in artificial streams and included treatments where fish were present or

absent, and where nutrient enrichment was terminated or continued. These treatments were replicated and arranged in a factorial design.

As the risk of fish predation while drifting depends on light levels, the response to the manipulations should depend on the time of day. At night, when the risk of predation while drifting is greatly reduced, I predict no effect of fish presence on drift levels, but a strong effect of food, i.e., higher drift levels from the treatments losing enrichment. During the day, when both fish and food should have an effect, I would predict that treatments with constant food levels and fish present would create the lowest levels of drift, treatments with decreasing food levels and no fish, the highest. If the two factors are being traded-off, the two remaining treatments (decreasing food-fish present, constant food-fish absent) should lead to intermediate levels of daytime drift. If invertebrates do not trade-off predation and food when deciding to drift, I expect no effect of one of the two factors, indicating that one receives overriding priority compared to the other.

Materials and Methods

Data collection took place in the Salmon River watershed on the east coast of Vancouver Island

(British Columbia, Canada) in August and September 1993, and in the Mayfly Creek artificial streamside

channel apparatus in the Malcolm Knapp Research Forest of the University of British Columbia during the

same months of 1994. The Salmon River sites and the channel apparatus have been previously described

in Chapter 1, and by Richardson (1991). Detailed descriptions of the experimental designs are also

contained in Chapter 1 but shall be summarised here.

Salmon River

To measure the effects of nutrient enrichment on invertebrate drift, three sites were monitored in

the Salmon River watershed. The BC Ministry of the Environment, Lands and Parks (MELP, now the

Ministry of Fisheries) has enriched streams within this watershed with small amounts of inorganic

agricultural phosphate and nitrate fertilisers (target additions SRP = $5\mu g \cdot L^{-1}$ and $NO_3 = 40\mu g \cdot L^{-1}$) from

early May to early August since 1989 to enhance salmonid populations (Slaney and Ward 1992).

Enrichment is accomplished by tanks fitted with slow drip valves adjusted to stream discharge twice a

week. The most upstream site in this study (never enriched or NE) was roughly one kilometre upstream of

one of the addition tanks in Norris Cr. The second site (losing enrichment or LE) was approximately 500

m downstream of this tank which had been adding nutrients for the preceding three months before being

removed 10 days into the study (Aug.11, 1993). The third site (continued enrichment or CE) was

approximately 11 km downstream of the first tank and roughly 100 m downstream of a second tank which

was in operation for the duration of the study (see Figure 2, page 11). Unfortunately, the desired

manipulation was not achieved as ending enrichment seemed to have had no effect on periphyton levels in

the Norris Creek (see Chapter 1).

Drifting invertebrates were sampled in the Salmon River watershed with drift nets placed in the stream for the first two hours of darkness. Allan and Russek (1985) found that much of the variation in drift between sites during the entire day can be explained by the variation in drift during this period alone. Two drift nets were attached to aluminium boxes with a 2.5 cm by 20 cm opening to decrease invertebrate escape and net blockage due to twigs and leaves. However, the large number of deciduous leaves in the stream water during the early fall made it necessary to clean the intake of nets every half hour. Water velocity and wetted net opening were measured during sampling to calculate volume of water passing through the net. Drift was measured in all sites before nutrients were shut off in the LE treatment on August 11, 1993 and weekly thereafter until the end of September. The nets were washed down and the contents preserved in 80% ethanol in the field and brought back to the lab for further processing and analysis.

Artificial channels

In the second year of study I used 12 plastic lined, flow-through channels, 20 cm wide and 14 m long. Gravel was provided as a substrate and was piled up to create pools and riffles. Water from Mayfly Creek (for description see Richardson 1991) was diverted to fill the channels. The intake from Mayfly Creek is located 35 m downstream of an impassable fish barrier. The reach between the barrier and the intake was electrofished extensively (>20 passes), and all fish captured were moved downstream. This was done to prevent heavy fish odour in the channels which were to represent fishless treatments. While total fish absence in this reach is impossible to prove, at the very least fish densities were severely impacted. During the two and a half month colonisation period, nitrate and phosphate fertilisers were added to the channel water using Mariotte bottles (target concentrations 5 μg SRP$\cdot$L^{-1} and 40 μg NO$_3^-$ $\cdot$L^{-1}). Stable levels of algal biomass were maintained for several weeks prior to beginning the experiment. Cutthroat trout (*Oncorhynchus clarki*) were captured by electrofishing from a nearby creek. Four fish (average

weight of 12.3 g each) were added to pools in half of the channels to create fish (F) and no-fish (NF) treatments before sampling started. The fishes' mouths were sutured closed prior to their release into the channels to minimise their impact on drifting invertebrate numbers by predation. This treatment appeared to affect their activity levels; they were often, but not always, observed resting on the bottom of the channel instead of maintaining an active feeding position in the pool. The fish seemed otherwise unaffected and returned to normal activity levels when the suture was removed, and the fish replaced at the end of the week. Also, six to ten trout were placed in nitex net cages at the head of the fish treatment channels to further increase fish odour in the channel. At day 0 of the experiment, nutrient additions were ended in half the channels to create a losing-enrichment (LE) and a continuing-enrichment (CE) treatment. The treatments were arranged to create a two by two factorial design with 3 replicates for each of the four treatment groups. The channels losing enrichment experienced a decrease in periphyton chlorophyll a from about 10 mg/m^2 at the start of the experiment down to about 4 mg/m^2 ten days later. This lower level was maintained for the rest of the experiment (see Chapter 1).

Drift and benthos in each channel were sampled twice immediately before enrichment ended, and again eight and seventeen days after enrichment ended. The downstream ends of all of the streams were fitted with nets to capture emigrating invertebrates. The nets were fixed to the channels for the day light period (roughly 7:30am to 8:45pm), then emptied and replaced at dusk for the night sample (roughly 8:45pm to 7:30am). The duration of night and day samples varied by less than 20 minutes over the course of the study. The benthos was quantitatively sampled using a miniature Surber sampler (20cm*20cm area) for two replicate samples from each channel the day after drift was measured. All invertebrate samples were preserved in 80% ethanol for later laboratory analysis.

Drift and benthic samples from both years were examined under magnifying lamps and the invertebrates removed. Invertebrate identification followed Merritt and Cummins (1984). Numbers of

each taxonomic group were counted and body lengths measured with a dissecting scope, drawing tube and a calibrated digitising tablet.

Data analysis

For the Salmon R. manipulation, drifting invertebrate data are expressed per water volume. The data from this manipulation are of limited use for two reasons. Firstly, the data do not constitute a proper experimental design to test the effects of enrichment. Secondly, the desired manipulation, i.e., a decline in periphyton chlorophyll a, did not occur in the site that lost enrichment (see Chapter 1). Consequently, I did not perform a statistical analysis of these data.

In the artificial channel experiment, the numbers of organisms drifting from a channel during the sampling period were divided by benthic densities in that channel. The resulting per capita drift rate is more meaningful than the traditional units of drift, i.e., invertebrate numbers per water volume or invertebrate numbers per unit time. Flow rate was kept nearly constant between the channels by adjusting individual valves twice daily. Flow rates were measured daily and never differed by more than 10-20%. Analysis using both flow and time corrected and uncorrected units of drift measurement produced similar results. I will present non-corrected data. Day and night drift rates were analysed separately. The median size of all drifting baetid mayflies in the artificial channel experiment was roughly 3.0 mm and I analysed animals larger and smaller than this separately since the effect of fish presence on drift has been found to depend on body size (Allan 1984).

All data was $\log_{10}$ transformed before statistical analysis to homogenise variances and normalise distributions. Because there were few replicates per treatment normality was tested on the distribution of the pooled residuals. Repeated measures ANOVA (SAS procedure GLM, Repeated statement, SAS Institute 1985), was used to test for the effects of fish, enrichment, and fish x enrichment effects. Use of this analysis was similar to Chapter 1.

Twenty seven different invertebrate taxonomic groups were tested individually. To avoid biases due to multiple tests, a sequential Bonferonni adjustment (Holm 1979) was performed. When there was a significant response in the repeated measures analysis, simple ANOVAs were performed for each individual date to determine at which dates the treatments caused significant effects. For these tests the significance criterion was corrected to keep $\alpha = 0.05$ over the entire experiment.

Results

Salmon River

Baetid (*Baetis* sp.) and ameletid (*Ameletus* sp.) mayflies, blackflies (Simuliidae), and chironomids (95% Orthocladiinae) made up 99% of the organisms found in the drift during the Salmon River study. Figure 7 shows the drift of these taxonomic groups in the three sites over the duration of the study. I did not pursue a statistical analysis of the data for reasons outlined in the Materials and Methods section. Nevertheless, the differences between enriched and unenriched reaches are noteworthy, and strong enough not to require significance testing.

There were consistently more organisms in the drift at the two enriched sites (LE and CE) than at the unenriched site (NE). Pooled over the duration of the experiment, *Baetis* sp., *Ameletus* sp., blackfly and chironomid drift rates were 4.6, 15.5, 7.8 and 7.4 times higher, respectively, in the sites that received enrichment. Drift of baetid mayflies generally appear to have increased over time in all the treatments while drift of the other taxa tended to appear to have decrease over the duration of the study (Figure 7).
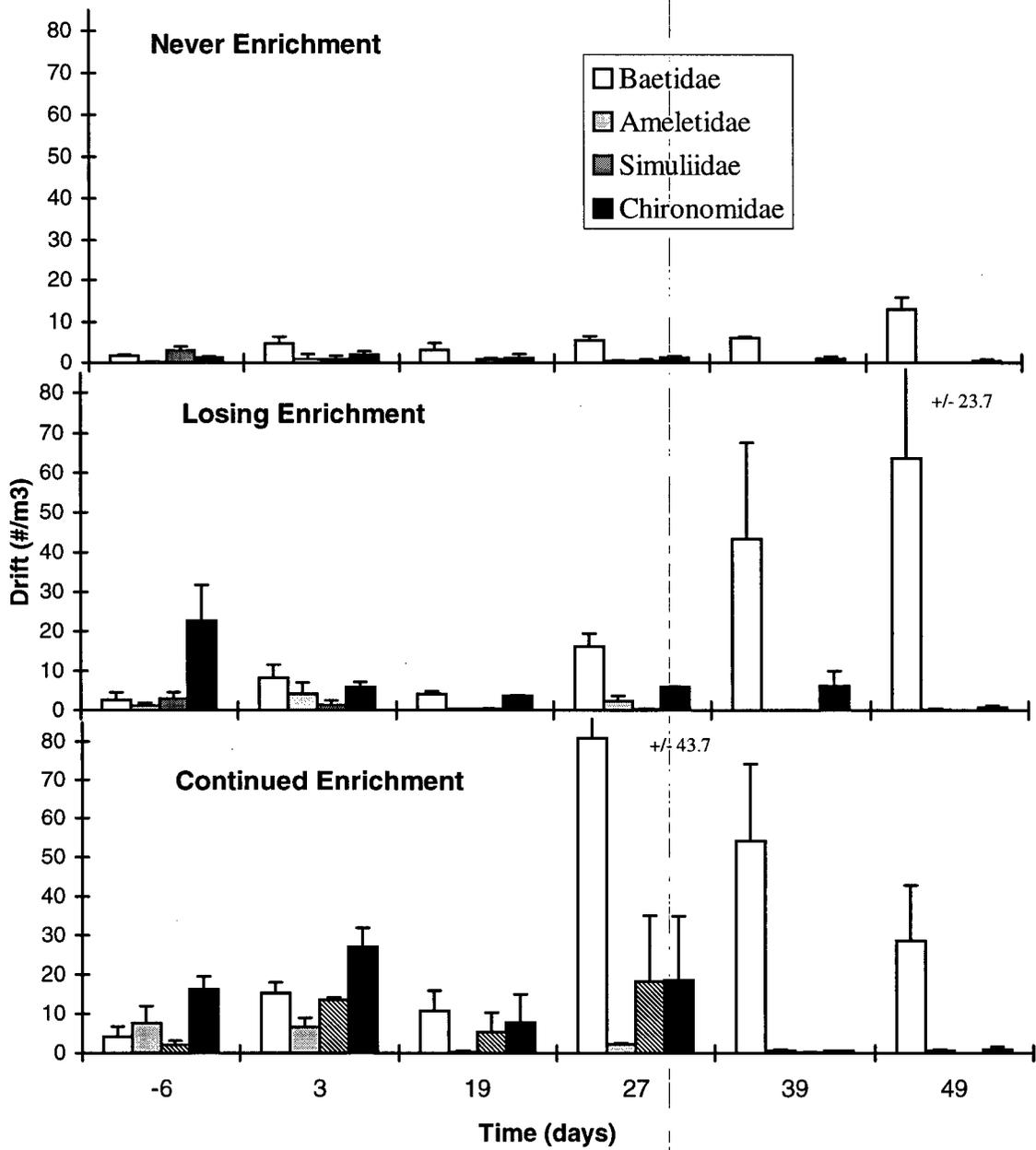
Figure 7. Mean drift rates of some common invertebrate taxa measured in Salmon River during the study. Enrichment to the site losing fertilization ended at day = 0. Error bars show standard deviation within the site (n=2).

Artificial Channel Experiment

Twenty seven different taxonomic groups were identified during the sample sorting. Mayflies,

stoneflies, caddisflies and beetles were grouped by family or genus where possible, dipterans were grouped

by family except for chironomids, which were lumped by subfamily. Over all treatments, orthoclad

chironomids numerically dominated the day-drift while *Baetis* sp. was the most numerous taxon found in

the night-drift samples (Table 1). With all sample data pooled, the strongest daily drift pattern was

demonstrated by stoneflies of the family Nemouridae and *Baetis*, which were 26.7 and 13.0 times more

numerous, respectively, in the night drift than in the day drift. The weakest daily drift pattern was

demonstrated by orthoclad chironomids which were only 1.6 times more likely to appear in the night drift

(Table 1).

Table 1. Absolute number and percent total numbers of counted invertebrates that drifted
out of all treatment channels during the entire experiment. Only taxa that comprised
greater than 2.0% of either day or night drift are included. The night : day ratio is based
on total numbers, not percentages, and is not corrected for time.

		Total	Baetidae	Nemouridae	Limnephilidae	Orthocladiinae	Tanypodinae
Day	Total #	11,390	1,574	244	172	8,528	217
	Percent of total		13.8%	2.1%	1.5%	74.9%	1.9%
Night	Total #	43,316	20,513	6,505	469	13,601	873
	Percent of total		47.4%	15.0%	1.1%	31.4%	2.0%
Night:Day		3.80	13.03	26.66	2.73	1.59	4.02

Repeated measures ANOVAs were performed on day and night per capita drift data of all

taxonomic groups individually to identify significant treatment effects. Size classes were not considered in

this first analysis. *Baetis* was the only taxon with significant treatment effects. Even without Bonferonni

adjustments, data from the other taxa failed to demonstrate any significant treatment effects. Iterative

computer programs are required to determine the power of repeated measures ANOVA with multiple

factors (Vaughan and Corballis 1969, Vonesh and Schork 1986). This was not included as part of my analysis.

Table 2. Multivariate repeated measures analysis of variance (MANOVAR) results for *Baetis* per capita drift rates and benthic densities in the artificial channel experiment.

Day-time drift, *Baetis* < 3.0 mm

Within-subject effects					Between-subject effects				
Source	Wilks' Lambda	df	F	P	Source	MS	df	F	P
Time x Fish	0.98047	2,7	0.07	0.9333	Fish	0.08118	1	0.52	0.491
Time x Enrichment	0.74308	2,7	1.21	0.3537	Enrichment	0.26401	1	1.69	0.229
Time x Fish x Enrichment	0.25710	2,7	10.11	**0.0086**	Fish x Enrichment	0.01241	1	0.08	0.785
Time	0.08041	2,7	40.03	0.0001	Error	0.15592	8		

Day-time drift, *Baetis* > 3.0 mm

Within-subject effects					Between-subject effects				
Source	Wilks' Lambda	df	F	P	Source	MS	df	F	P
Time x Fish	0.78391	2,7	0.97	0.4265	Fish	0.45626	1	12.3	**0.008**
Time x Enrichment	0.75902	2,7	1.11	0.3810	Enrichment	0.06194	1	4.75	0.061
Time x Fish x Enrichment	0.61496	2,7	2.19	0.1842	Fish x Enrichment	0.09600	1	0.65	0.445
Time	0.64241	2,7	1.95	0.2125	Error	1.18060	8		

Night-time drift, *Baetis* < 3.0 mm

Within-subject effects					Between-subject effects				
Source	Wilks' Lambda	df	F	P	Source	MS	df	F	P
Time x Fish	0.83520	2,7	0.69	0.5324	Fish	0.18789	1	0.52	0.484
Time x Enrichment	0.68060	2,7	1.64	0.2601	Enrichment	1.58898	1	1.69	0.066
Time x Fish x Enrichment	0.57375	2,7	2.60	0.1431	Fish x Enrichment	0.01191	1	0.08	0.858
Time	0.04557	2,7	73.31	0.0001	Error	2.79622	8		

Night-time drift, *Baetis* > 3.0 mm

Within-subject effects					Between-subject effects				
Source	Wilks' Lambda	df	F	P	Source	MS	df	F	P
Time x Fish	0.93461	2,7	0.72	0.5199	Fish	10^{-8}	1	1.62	0.239
Time x Enrichment	0.63684	2,7	5.13	**0.0425**	Enrichment	0.00220	1	5.74	**0.044**
Time x Fish x Enrichment	0.44703	2,7	1.16	0.3661	Fish x Enrichment	0.54407	1	0.29	0.608
Time	0.02201	2,7	16.90	0.0021	Error	0.07923	8		

Benthic Densities, *Baetis* < 3.0 mm

Within-subject effects					Between-subject effects				
Source	Wilks' Lambda	df	F	P	Source	MS	df	F	P
Time x Fish	0.93460	2,7	0.24	0.7892	Fish	10^{-8}	1	0	0.998
Time x Enrichment	0.63684	2,7	2.00	0.2061	Enrichment	0.00220	1	0.03	0.872
Time x Fish x Enrichment	0.44703	2,7	4.32	0.5096	Fish x Enrichment	0.43959	1	0.544	6.870
Time	0.02200	2,7	155.55	0.0001	Error	0.47811	8		

Benthic Densities, *Baetis* > 3.0 mm

Within-subject effects					Between-subject effects				
Source	Wilks' Lambda	df	F	P	Source	MS	df	F	P
Time x Fish	0.60466	2,7	2.29	0.1719	Fish	0.00101	1	0.01	0.922
Time x Enrichment	0.36961	2,7	5.96	**0.0307**	Enrichment	0.80049	1	7.94	**0.023**
Time x Fish x Enrichment	0.54479	2,7	2.92	0.1193	Fish x Enrichment	0.00805	1	0.08	0.785
Time	0.18227	2,7	15.70	0.0026	Error	0.10076	8		

The numbers of *Baetis* in the benthos was estimated from the two Surber samples taken from each channel. Repeated measures ANOVA was used to detect significant treatment effects. As further analysis of *Baetis* drift was partitioned by size classes, the benthic data was also considered in this way. The results of all repeated measured analyses performed on *Baetis* data are shown in Table 2. MANOVAR found a significant within-subject ($F_{2,7} = 5.96$, p = 0.031) and between-subject ($F_{1,8} = 7.94$ p=0.023) effect for baetids greater than 3.0 mm. The simple ANOVAs used on each sample date show that these results are due to many fewer of the larger baetids in the benthos of the LE channels during the final sampling date ($F_{1,8} = 18.01$, p = 0.003). This pattern is shown in Figure 8.

The difference between within-subject effects and between-subject effects is important and required some explanation. Repeated measures ANOVA includes a test for both between and within subject - effects. Between-subject effects are equivalent to comparisons among treatments pooled over the entire duration of the experiment. The effects are therefore independent of time. In contrast, within-subject effects are the time x treatment interactions. The impact of these effects change over the duration of the experiment. Detection of within-subject effects is the primary use of repeated measures analysis of variance.
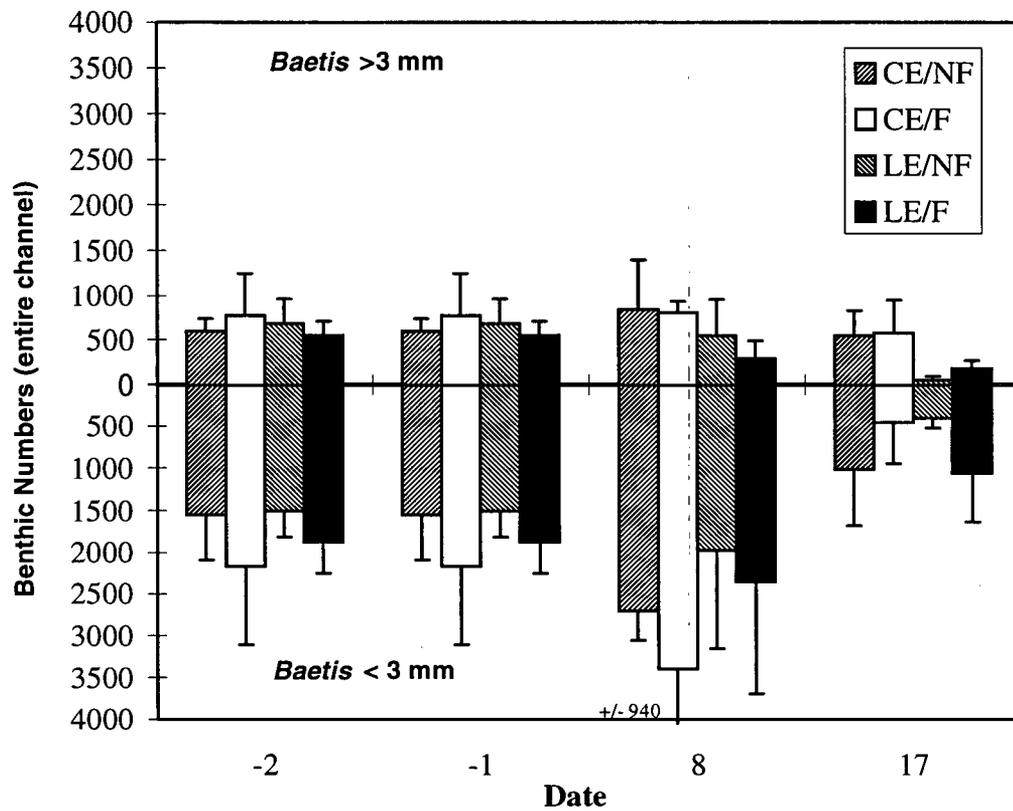
Figure 8. Benthic density of *Baetis* sp. in the artificial channel treatments. Enrichment was ended in losing enrichment treatment at day 0. CE = continued enrichment, LE = losing enrichment, F = fish present, NF = fish absent. Error bars show the standard deviation from the mean.

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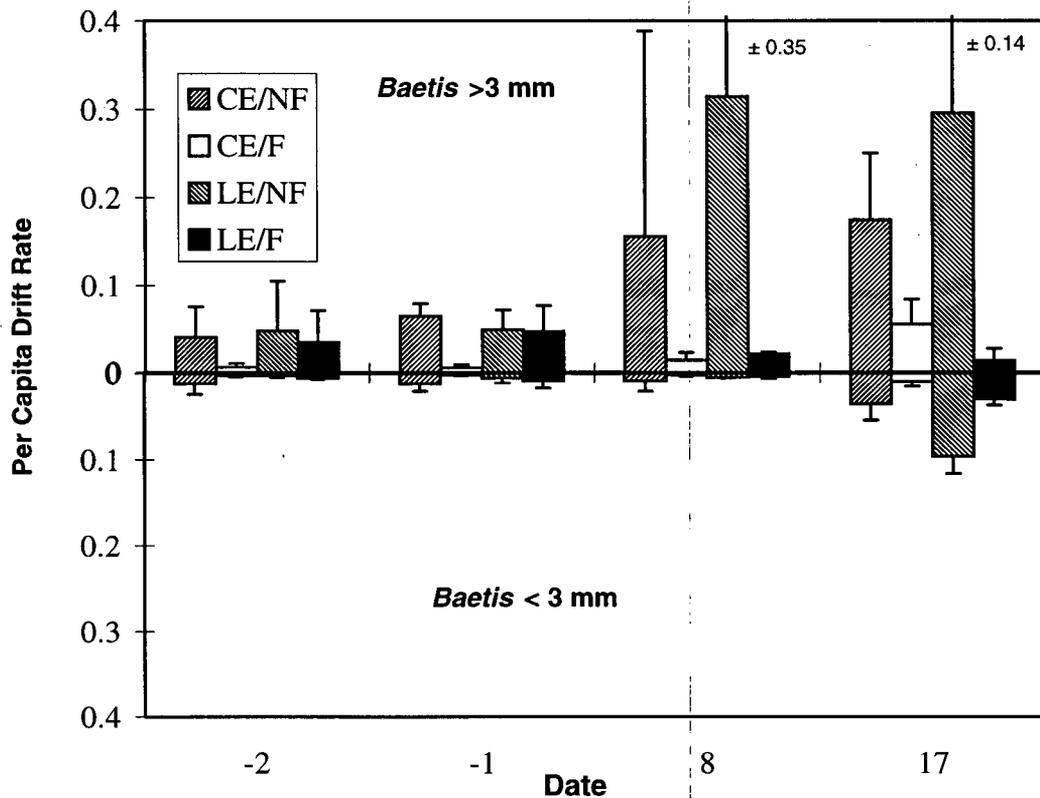
Figure 9. Daytime per capita drift rates of *Baetis* sp., by size class, in artificial channel treatments. Enrichment was ended in losing enrichment treatment at day 0. CE = continued enrichment, LE = losing enrichment, F = fish present, NF = fish absent. Error bars show standard deviations from the mean.

Baetis per capita drift appeared to be affected by both changes in enrichment and the presence of fish. During the day, per capita drift rates were almost always lower in the presence of fish (Figure 9). The effect was strong enough to be a significant ($F_{1,8}$= 12.3, p = 0.008) between-subject effect (i.e., independent of time) on the larger mayflies. The date by date ANOVA tests for day-time drift of larger *Baetis* showed a significant effect of fish on day-drift during the dates before enrichment ended and the last sampling date. The difference between F and NF treatments was not significant during the sampling 8 days

after enrichment ended (Figure 9). Day-drift from the NF channels during this date was highly variable with two channels having extremely high levels of drift and the remaining four lower levels.

Again for day-drift, there was a significant ($F_{2,7} = 10.11$, p = 0.0086) within-subject effect (i.e., effect that changes over time) for the time x fish x enrichment interaction term for smaller *Baetis*. Date by date ANOVA analysis found no significant interaction effect on an individual date.
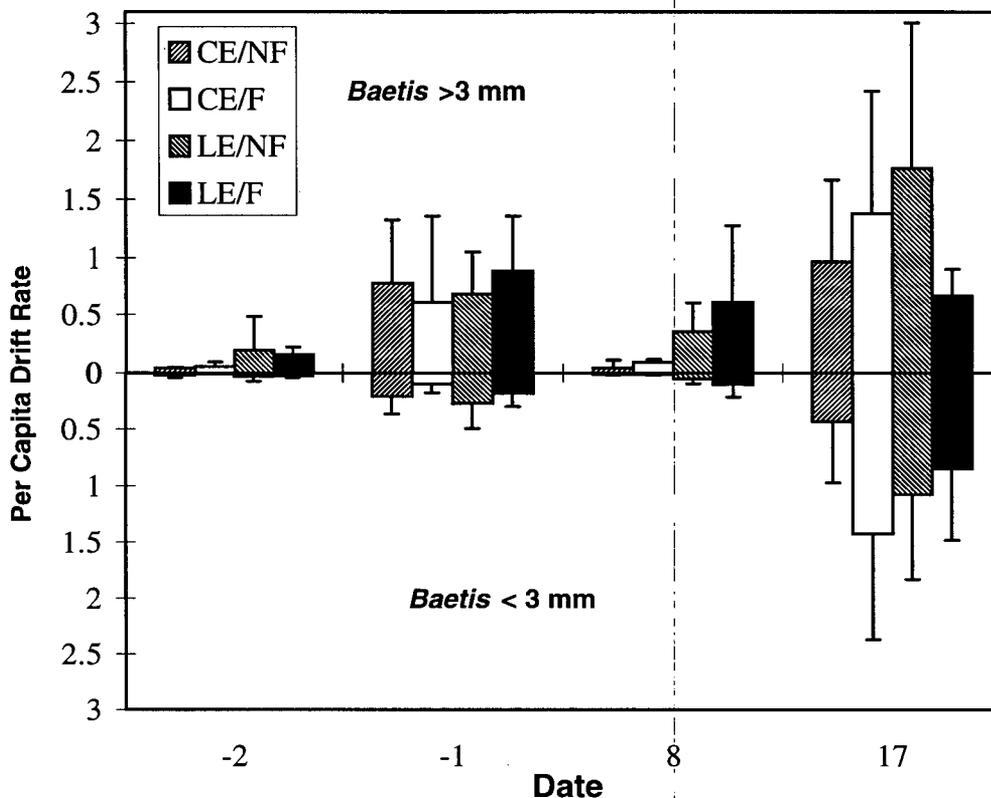
Figure 10. Night-time Per capita drift rate of Baetis sp., by size class, in artificial channel treatments. Enrichment was ended in losing enrichment treatment at day 0.
CE = continued enrichment, LE = losing enrichment, F = fish present, NF = fish absent.
Error bars show standard deviations from the means.

Enrichment had a significant within subject effect ($F_{2,7}$ = 5.13, p = 0.0425), and between subject effect ($F_{1,8}$=5.74, p = 0.044) on the night-time drift rates of baetid mayflies greater than 3.0 mm (Figure 10). Date by date ANOVA showed that per capita drift rates were higher in the LE treatments on the eighth day after enrichment ended ($F_{1,8}$ =8.38, p = 0.02). This date corresponds with the time at which standing crops of chlorophyll a were rapidly decreasing in these treatments (Chapter 1). Date by date ANOVA also showed a significant enrichment effect ($F_{1,8}$=11.29, p = 0.01) for this date on night-drift of smaller mayflies, though this did not translate into a significant repeated measures effect (Table 2). Night-time Baetis drift rates were not found to be affected by fish presence.

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I used linear regressions to attempt to find a relationship between *Baetis* per capita day and night drift rates and several periphyton chlorophyll *a* related variables (absolute levels, changes in chlorophyll *a* levels, untransformed and various transformations). Data from different dates were tested together and independently. Day and night data were tested independently. I found no significant relationship with any of these tests.

Discussion

The CE and LE treatment reaches of the Salmon River maintained higher levels of periphyton chlorophyll *a* than the reach that was never fertilised (see Chapter 1). My sampling found 4.6-15.5 times more drifting invertebrates in the enriched reaches. These results contrast with those of Hinterleitner-Anderson *et al.* (1992) who found higher amounts of drifting *Baetis* in water from unenriched reaches of the Kuparuk River when compared with enriched reaches. This was interpreted as showing that the unenriched reach was less suitable habitat than the fertilised reach. Differences between my drift results and the results from the Kuparuk River can potentially be attributed to different benthic responses to the enrichment. Sampling in the Kuparuk River found no effect of enrichment on benthic invertebrate densities (Hinterleitner-Anderson *et al.* 1992). In contrast, sampling by MELP in Grilse and Norris Creeks has shown a four fold increase in benthic numbers in enriched sites (Quamme 1995). Per capita drift rates may indeed be lower in the enriched reaches of Grilse and Norris Creeks, but the drift per volume data would not show this pattern because they are not corrected for the larger numbers of benthic organisms in enriched reaches.

In the channel experiment, the lack of drift response of other invertebrates besides *Baetis* is somewhat surprising. With all the statistical tests performed, other significant test results would have been expected simply by chance. Baetid mayflies' unique position among the invertebrate drift has been noted (Rader 1997). In my study, numbers of baetid mayflies were second only to numbers of orthoclad chironomids in the drift. Baetids also showed one of the strongest day/night drift patterns.

I assumed that the carrying capacity for grazing invertebrates was limited by food in the artificial channels, and thus, a decrease in standing crops of periphyton, measured as chlorophyll *a*, would mean a decrease in the carrying capacity of a channel. Feeding sites, refugia from predators, or amount of suitable physical habitat could also be limiting population sizes. Baetid mayflies may not even rely heavily on

periphyton as a food source. Examinations of the stomach contents of baetid mayflies have found that detritus makes up the bulk of the diet, with algae not even present in the gut (Brown 1961, Moore 1977). However, past work has demonstrated baetids responding to changes in periphyton levels (Kohler 1984, 1985, Palmer 1995) and chlorophyll *a* has been extracted from the guts of baetids (Cowan and Peckarsky 1990). My algal and benthic invertebrate data suggest that carrying capacity for *Baetis* was altered in my study. Channels in the treatment losing enrichment experienced a 50% drop in chlorophyll *a* while the treatment that continued to receive enrichment retained constant levels (Chapter 1). The drop in food levels in the LE treatment channels was matched by 75% fewer baetid mayflies greater than 3.0 mm in the benthos of the LE treatment channels during the last sampling date (Figure 8). This supports the conclusion that a decrease in periphyton levels did lower the carrying capacity for the larger baetid mayflies.

Daily drift patterns and differences in the size classes of baetids mayflies were observed in the artificial channel experiment. Although not statistically tested, Figure 9 and Figure 10 clearly show that drift rates were much higher for the larger individuals. Also, drift rates during the night tended to be higher than during the day, especially for the larger invertebrates in channels with fish. Higher night time drift rates of larger invertebrates was first described by Allan (1978) as a means of countering a higher visibility to drift feeding predators. My choice of 3.0 mm body length to divide large from small baetids for analysis was based on the median size of these organisms in the drift during my study. This dividing point may have no functional relevance to predation by drift feeding fish and may have caused me to over or underestimate the response to the presence of fish. Based on the length to weight regressions of Smock (1980) a 3.0 mm baetid mayfly weighs roughly 0.1 mg. Examination of Allan's (1984) data for diel activity of *Baetis bicaudatus* finds a switch to more nocturnal drift activity in animals greater than 0.1 mg. This offers some support that 3.0 mm was an appropriate dividing line.

The larger baetids emigrated at night from the channels losing enrichment. The increase in nocturnal drift was measured only when periphyton levels were dropping during the first week after enrichment ended. Once the periphyton had stabilised at a lower level, per capita emigration was not significantly different than from the channels that continued to be enriched. These results indicate that the larger *Baetis* responded quickly to changes in dropping chlorophyll *a* levels. Although it has long been known that invertebrate drift patterns are affected by food levels (Hildebran 1974, Keller 1975, Otto 1976, Bohle 1978, Kohler 1985, Richardson 1991) it is significant that this drift response to decreasing periphyton levels was measured outside the laboratory in a naturally colonised, multi-species community. Furthermore, as this manipulation was accomplished with modest changes in nutrient levels, it is possible that a similar phenomenon occurs in streams due to naturally fluctuating nutrient levels (Feller and Kimmins 1979, Perrin 1991a).

The presence of fish decreased the drift rates of larger baetid mayflies during the day. This is similar to the results of Douglas *et al.* (1994) who measured a decrease in the day drift of baetid mayflies downstream of rainbow trout (*Oncorhynchus mykiss*) enclosures in fishless streams. In contrast, Forrester (1994) measured an increase in night-time drift with fish presence in a fish bearing stream. He hypothesised that this was a means for the mayflies to disperse to areas of lower fish density. Significance during the day or night aside, the consistent trend is a shift from day-time drift to night-time drift in the presence of fish for larger *Baetis*.

For smaller baetid mayflies, the only significant repeated measures effect was a within-subject fish x enrichment effect found for day drift. Though the date by date analysis shows no significant effect, this significant interaction term between fish and enrichment seems to have been caused by the results of the final sampling date. The repeated measures-within subject pattern is significant and noteworthy. Data from the final sampling date indicate that the highest drift rates came from the LE/NF channels and the

lowest levels of drift come from the CE/F channels with the other two treatments intermediate (Figure 9). This is the pattern I stated would support the hypothesis for a trade-off between food and predation.

A baetid in a low food area of a fish bearing stream during the day can do one of three things. First, it could drift at that time, attempting to find an area with more food. Second, it could move to another area by locomotion within the substrate. Third, it could wait for night and drift then. The second alternative is more energetically costly than drifting and would increase the risk of predation by benthic predators (Peckarsky 1980). As well, drift has been found to be the primary mechanism of dispersal for baetid mayflies when compared to locomotion in the substrate (Bird and Hynes 1981, Bergey and Ward 1989). The question of trading-off the food reward and predation risk lies in the first and third choices.

If the baetid that would drift during the day in the absence of fish remains in the substrate until night in the presence of fish, the energetic cost is the loss of food that would have been consumed that day in a higher food patch. This hypothesis would predict an increase in nightly drift to match the decrease in day-drift of baetids in the fish-present treatments. I did not find such an increase. However, as the amount of day drift is so small when compared to night drift, a change in nightly drift rates of similar magnitude to that which occurred during the day may not be detectable given the statistical power of this experiment.

My data suggest that the risks and rewards associated with drifting are evaluated differently by different size classes. For larger invertebrates, where the risk of fish predation is greater, the two factors are not traded-off. Fish presence is the most influential factor during the day, and food level is the most influential factor at night. For smaller invertebrates, for whom the risk of predation by fish is reduced, both food and predation risk appear to be considered. Day-time drift rates are highest where both factors favour drifting, lowest where both factors favour remaining in the substrate, and intermediate when the two factors are conflicting.

The effects of fish presence on invertebrate drift patterns appears to depend on previous exposure to fish and may include genetically fixed behaviours. The removal of fish from fish-bearing streams has

been attempted in order to show a change in daily drift patterns (Allan 1982, and Flecker 1992), with no success. However, the strength of a fish manipulation depends on the experimenter's ability to completely remove or apply the stimulus of fish presence. In fish bearing streams, complete removal of fish is difficult to attain using reasonable methods, and this can limit the manipulative strength in these systems. After Allan's (1982) attempts to remove fish from 1.2 km length of stream, 25% of the fish biomass was still present. Flecker's (1992) fish exclusion experiment used cages only 10 m long. While these manipulations certainly had some effect on fish numbers or fish in the immediate area, it is unlikely that this was sufficient to translate into a clear signal of fish absent to the invertebrates. Some studies suggest that chemical cues are used by invertebrates to evaluate fish presence (Douglas *et al.* 1994, Tikkanen *et al.* 1994, Cowan and Peckarsky 1994, McIntosh and Peckarsky 1996). The range of these chemical cues is not known, but it is reasonable to assume tens of meters. This problem is complicated by the results of one recirculating channel study that shows adding fish odour affects fish-naive baetids while removal of fish odour to fish adapted baetids has no effect (Cowan and Peckarsky 1994). In more natural stream systems, studies involving additions of fish or fish odour to fishless system appears to offer the strongest potential for a clean fish presence/absence signal and a measurable response (Douglas *et. al.* 1994, Cowan and Peckarsky 1994).

I am uncertain how I would classify my invertebrate community with regards to past experience with fish. From a genetic standpoint, members of mayfly populations from streams with and without fish would be able to lay eggs in Mayfly Creek. From a phenotypic standpoint, Mayfly Creek is fish bearing for only 35 m upstream of the channels and non-fish bearing further upstream. Many electrofishing passes removed the bulk of fish from the short, fish bearing reach; but it is unlikely that all were removed. Small fish were captured from this reach sporadically (one fish roughly once every 4th pass) after the 10th pass with the electrofisher. So while it is likely that the invertebrates in my channels have been at least briefly exposed to fish or fish odour, they still appear to be responsive to changes in fish presence and absence.

Forrester (1994) manipulated fish density in a fish bearing stream. While he didn't measure a decline in day drift rates from patches with increased fish densities, he did measure an increase in night drift rates from these patches. This was interpreted as being an adaptive method for transport to areas with lower fish densities, in systems with a patchily distributed fish population. Continued research into how drift patterns are affected by an organism's previous experience with fish has the potential to demonstrate a new layer of complexity in this issue and further our understanding considerably.

In conclusion, it appears that for larger baetid mayflies, the threat of predation over rides the reward of immediately moving to a more food rich patch during the day. A larger baetid mayfly will drift from a low food patch at night, when the predation risk is essentially eliminated. For smaller baetids, which are less visible to drift feeding fish, food and predation risk appear to be equally important in predicting drift patterns during the day. These results are significant in that they provide insight into the interaction between these two fundamental biotic factors as affect invertebrate drift in streams.

Conclusion

Periphyton APA and chlorophyll *a* levels in sampled reaches of the Salmon River that lost nutrient inputs did not demonstrate either an increase in phosphorus limitation, or a decrease in periphyton standing crops during the two months following the end of enrichment. The mechanism for this high degree of resistance to the loss of nutrient additions must play a major role in nutrient dynamics within the stream. By comparing this response with that of artificial channels that lost nutrient inputs in a similar fashion, I provide some reasons to infer that this nutrient storage mechanism is the hyporheic zone.

There is a strong need for detailed, process level, investigations into the nutrient dynamics of our coastal streams to further our understanding of these systems. My data offers no real proof supporting one nutrient storage mechanism over another. Nevertheless, the differences I show between the behaviour of natural and artificial systems experiencing the end of enrichment provides a basis from which further research can continue. Tracing phosphorus transport, uptake, storage, and release by the different components of coastal stream ecosystem is the obvious next step in furthering the understanding of nutrient processes that contribute to stream ecosystem resistance.

Study of the effects of food and predation risk on the initiation of drift has been ongoing for decades. However, the two factors have never been tested simultaneously. My data indicate that these two opposing factors are equally important for smaller baetid mayflies during the day. Larger baetids appear to give priority to the possibility of fish predation during the day, and drift only at night in response to decreasing food levels.

The interplay between predation and food is definitely influenced by the size of the invertebrate. This is certainly partially due to the decreased predation risk for smaller, drifting invertebrates. However, the role of size in enduring food deprivation should not be ignored. The price of not drifting during the day but waiting until night to move to a higher food area may be more costly for a smaller baetid than a larger

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one. The physiology of this question has never been fully investigated for aquatic invertebrates. Based on past research, previous experience with fish also plays a role in how invertebrates will respond to manipulation involving fish. We still do not have a full understanding of when drift patterns are behaviourally fixed and when they are phenotypically flexible.

This thesis was motivated by the desire to provide information that would help improve stream fertilization as a rehabilitation tool for fish stocks. By determining the resistance of an enriched stream to the end of nutrient additions I hoped to provide information that would help improve the timing and duration of prescribed enrichment regimes. As well, by tracking drift rates through a decline in system primary productivity, I hoped to find increased drift rates during the day. This would allow for a much more efficient trophic transfer from the benthic invertebrates to the drift feeding fish.

This thesis contributes to our knowledge of how stream fertilization affects primary and secondary productivity, however, many aspects of this rehabilitation technique remain only partially understood. The loss of enrichment condition in a stream to which inorganic nutrient inputs have ended has not been observed. Further work should be undertaken with the goal of predicting enrichment decay rates of fertilised systems, the length downstream that would be affected by nutrient inputs, and other such parameters. This information could be used to apply more precise nutrient prescriptions that achieve the greatest results with the least effort.

It is reasonable to assume that larger baetids drifting at night are unavailable to fish. If we also assume that it is possible to create declining food levels in natural streams by ending nutrient inputs, my results indicate that if nutrient inputs are ended for the purpose of increasing drift levels for drift feeding fish, the response would be from smaller baetids. The relative importance of such an increase to the total annual food intake of a drift feeding salmonid would require further investigation to evaluate its importance.

The end.

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