

Experimental Enrichment of a Coastal Stream in British Columbia: Effects of Organic and Inorganic Additions on Autotrophic Periphyton Production

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Periphyton accumulation rates and alkaline phosphatase activity were examined in reaches of the Keogh River, British Columbia, following additions of grain and inorganic fertilizer as separate treatments during spring–summer 1981. Two different levels of N and P addition were used: one to attain ambient N and P concentrations of 200 and 15 $\mu\text{g}\cdot\text{L}^{-1}$, respectively, and the other to attain 400 and 20 $\mu\text{g}\cdot\text{L}^{-1}$, respectively. Grain (rolled barley) was added monthly at 280 $\text{g}\cdot\text{m}^{-2}$. N and P additions increased chlorophyll a accrual rates by more than an order of magnitude. Diatoms dominated the periphyton community until midsummer. In July and most of August, the relative importance of chlorophytes increased and biomass levels declined markedly in spite of continued nutrient additions. Grain additions resulted in no detectable change in periphyton accrual, but alkaline phosphatase activity increased by 35% over control levels. These results suggest that additions of labile organic matter to nutrient-deficient coastal streams can increase autotrophic P deficiency. Based on responses of juvenile salmonids, additions of inorganic nutrients to increase autotrophic production can maximize trophic enhancement in nutrient-deficient streams.

Les auteurs ont étudié les taux d'accumulation et l'activité de la phosphatase alcaline chez le périphyton peuplant des sections de la rivière Keogh (Colombie-Britannique) après l'apport séparé de fertilisants organiques et inorganiques au printemps et à l'été de 1981. Deux teneurs différentes en N et P ont été utilisées : la première visait une concentration ambiante respective de N et de P de 200 et de 15 $\mu\text{g}\cdot\text{L}^{-1}$ et la seconde, de 400 et de 20 $\mu\text{g}\cdot\text{L}^{-1}$ respectivement. L'apport mensuel de céréales (flocons d'orge) s'est effectué à un taux de 280 $\text{g}\cdot\text{m}^{-2}$. L'apport de N et de P a entraîné une augmentation des taux d'accumulation de chlorophylle a de plus d'un ordre de grandeur. Les diatomés dominaient la communauté périphytonique jusqu'à la mi-été. En juillet et pendant la plus grande partie d'août, l'importance relative des chlorophycophytes a augmenté tandis que les niveaux de la biomasse ont fortement baissé malgré l'apport continu de bioéléments. L'addition de céréales n'a pas entraîné de variation discernable du taux d'accumulation du périphyton, mais l'activité de la phosphatase alcaline a augmenté de 35 % par rapport au niveau témoin. Les résultats portent à croire que l'apport de matières organiques labiles dans des cours d'eau côtiers pauvres en bioéléments peut accroître le déficit en P autotrophe. D'après les réactions des salmonidés juvéniles l'apport de bioéléments inorganiques en vue d'accroître la production autotrophe peut maximiser la stimulation des niveaux trophiques dans les cours d'eau pauvres en bioéléments.

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Techniques for enhancing wild stocks of anadromous salmonids on Canada's Pacific coast include efforts to increase food supply for juveniles that rear in freshwater. Potential enhancement is based on evidence presented by Ricker (1962) and later by Peterman (1982) and Bilton et al. (1982) showing that on average, larger smolts have greater marine survival and produce less variability in adult returns than smaller smolts. Hence, increased food supply must lead to enhanced growth of juveniles and increased size of smolts to be potentially useful.

Two general approaches to increase food supply to juvenile salmonids have been considered in British Columbia. One is exemplified by the Lake Enrichment Program (LEP) (Hyatt and Stockner 1985; LeBrasseur et al. 1978), a group of projects that include both experimental and operational fertilizer additions to coastal lakes for the enhancement of sockeye salmon (*Oncorhynchus nerka*). In the LEP, inorganic N and P are added to stimulate trophic productivity. The other approach considered for enhancement of stream-rearing salmonids has been enrichment using particulate organic matter (POM)

(Mundie et al. 1983). Unlike the LEP, stream enrichment using POM has not been developed to include streams other than that used for initial experiments.

A study was conducted in the upper Keogh River, British Columbia, in 1981 to compare the effects of organic and inorganic enrichment on food supply and growth of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). This paper compares changes in P deficiency and productivity of benthic algae in adjacent stream reaches enriched with POM and inorganic fertilizer in spring and summer.

Study Site

The Keogh River flows for 32 km from a 129-km² watershed located at 127.4°W and 50.6°N. Headwaters originate in the Vancouver Island mountain range and the river discharges into Queen Charlotte Strait on the northeast side of Vancouver Island (Fig. 1). Discharge is highly variable since recording began in 1975; the minimum flow has been 0.1 m³·s⁻¹ (1978) and the maximum was 225 m³·s⁻¹ (1975). Mean summer discharge is 1.6 m³·s⁻¹ (1976–80). Flow patterns are “flashy” and correspond directly to precipitation. Mean annual total precipitation is 173 cm (Environment Canada Weather Office, Port Hardy), with most occurring as rain in autumn and winter. Snowpack occurs only at higher elevations of the Keogh watershed. During midsummer there is a dry period of about 4 wk when the river has a stable low flow.

Our study was conducted in Reach Z (Fig. 1), a 5-km section at the upstream end of the Keogh River. Reach Z has an average width in summer of about 6 m, a gradient of 0.84%, and a mixed gravel and cobble bottom. Habitat proportions by area are 40% riffle, 26% pool, and 34% run (Ward and Slaney 1979). Chemical records (Ward and Slaney 1979) show that average annual concentrations of both anions and cations are low, giving a filterable residue of <40 mg·L⁻¹ and a specific conductance of 2.0–3.0 mS·m⁻¹. Total alkalinity and pH during spring and summer average 7.0 mg CaCO₃·L⁻¹ and 6.9, respectively. Soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP) concentrations are about 1 and 5 µg·L⁻¹, respectively (Perrin and Johnston 1985). Ammonia is rarely detectable and NO₃⁻ + NO₂⁻-N rarely exceeds 15 µg·L⁻¹. Riparian growth is dominated by red alder (*Alnus rubra*), salal (*Gaultheria shallon*), willow (*Salix* spp.), and several sedges and grasses. Tree species include Western hemlock (*Tsuga heterophylla*), red cedar (*Thuja plicata*), and sitka spruce (*Picea sitchensis*). These species occurred mainly as early seral regeneration (up to about age 20) because of forest harvesting over the past 30 yr. The forest canopy was not closed in Reach Z.

Materials and Methods

Stream flow, light, and temperature were continuously measured at the W103 bridge location (Fig. 1). Water level was measured using a Leupold and Stevens (Beaverton, Oregon) model F water level recorder. A calibration curve for calculating stream flow was determined by rating periodic flow measurements to gauge height. Flow was measured by multiplying wetted cross-sectional area by average current velocity measured with a Marsh McBirney (Rockville, Maryland) electromagnetic velocity sensor. Light intensity was monitored using a LI-COR (Lincoln, Nebraska) printing integrator

LI-550B equipped with a quantum sensor. The sensor was located at a site 1 km downstream of the W103 bridge that was typical of the experimental reach in that an overhead forest canopy was absent, but there was lateral shading in early morning and late afternoon. A Ryan (Kirkland, Washington) model J-90 submersible thermograph was used for continuous recordings of stream temperature, and the instrument was calibrated weekly.

Within 2 km of Reach Z, four 300-m experimental sections were designated, each having similar aspect, cover, gradient, and substrata characteristics (Fig. 1). The upstream-to-downstream layout was as follows:

(1) Control.

(2) Treatment 1 (T1): addition of 280 g rolled barley·m⁻² applied once per month for the period May 16 through September 15, 1981.

(3) Treatment 2 (T2): inorganic fertilizer (34-0-0 plus 11-55-0) addition to achieve ambient concentrations of 15 µg P·L⁻¹ and 200 µg N·L⁻¹ from May 14 through September 15, 1981.

(4) Treatment 3 (T3): inorganic fertilizer (34-0-0 plus 11-55-0) addition to achieve ambient concentrations of 20 µg P·L⁻¹ and 400 µg N·L⁻¹ from May 14 through September 15, 1981.

Adjacent treatments were separated by a 300-m buffer zone where no treatment was applied. Two fertilizer treatments were used in the present study to determine if periphyton accumulation rates continued to increase at higher levels of enrichment.

Fertilizer was dispensed using two equally spaced DF1-A Sweeney feeders (Boerne, Texas) in each of the fertilized sections (Fig. 1). Feeders were equipped with electronic timers set to dispense approximately 700 g of fertilizer once per hour. Input rates were adjusted to varying flow conditions.

In T1, rolled barley (total C = 39.24%, H = 6.59%, total N = 1.88%, total P = 0.40% based on air dry weights) was applied evenly by hand over the stream substratum after soaking the grain for about 30 min in plastic containers. Soaking prevented the grain from floating downstream after application. Flow conditions distributed the grain evenly in runs but deposited clumps in pools. In riffles, grains lodged into interstitial spaces within gravel and cobble.

Within each of the control and treatment sections, two 15-m-long riffles were selected for sampling of dissolved nutrients, periphyton accumulation rates, species composition, and alkaline phosphatase activity. In fertilized sections, these riffle sites were 100 m downstream of each fertilizer dispenser. These equal distances were intended to result in similar dissolved inorganic nutrient concentrations at each sampling riffle. By defining the spatial confines of our sampling units as specific riffle sites that received similar levels of enrichment of each treatment, riffle sites within treatments can be considered replicates.

Sampling at each riffle site was initiated April 10, 1981. Water samples to be used for dissolved nutrient measurements were collected weekly and passed through 0.45-µm Millipore filters. All samples were packed in coolers and shipped to Vancouver for analysis within 48 h of sample collection. NO₃⁻ + NO₂⁻-N was determined using the cadmium reduction method of Strickland and Parsons (1972). Ammonia was measured colorimetrically, as described by Traversy (1971), and SRP was determined by the ascorbic acid reduction method of Murphy and Riley (1962).

Periphyton was sampled from four replicate 30 × 30 ×

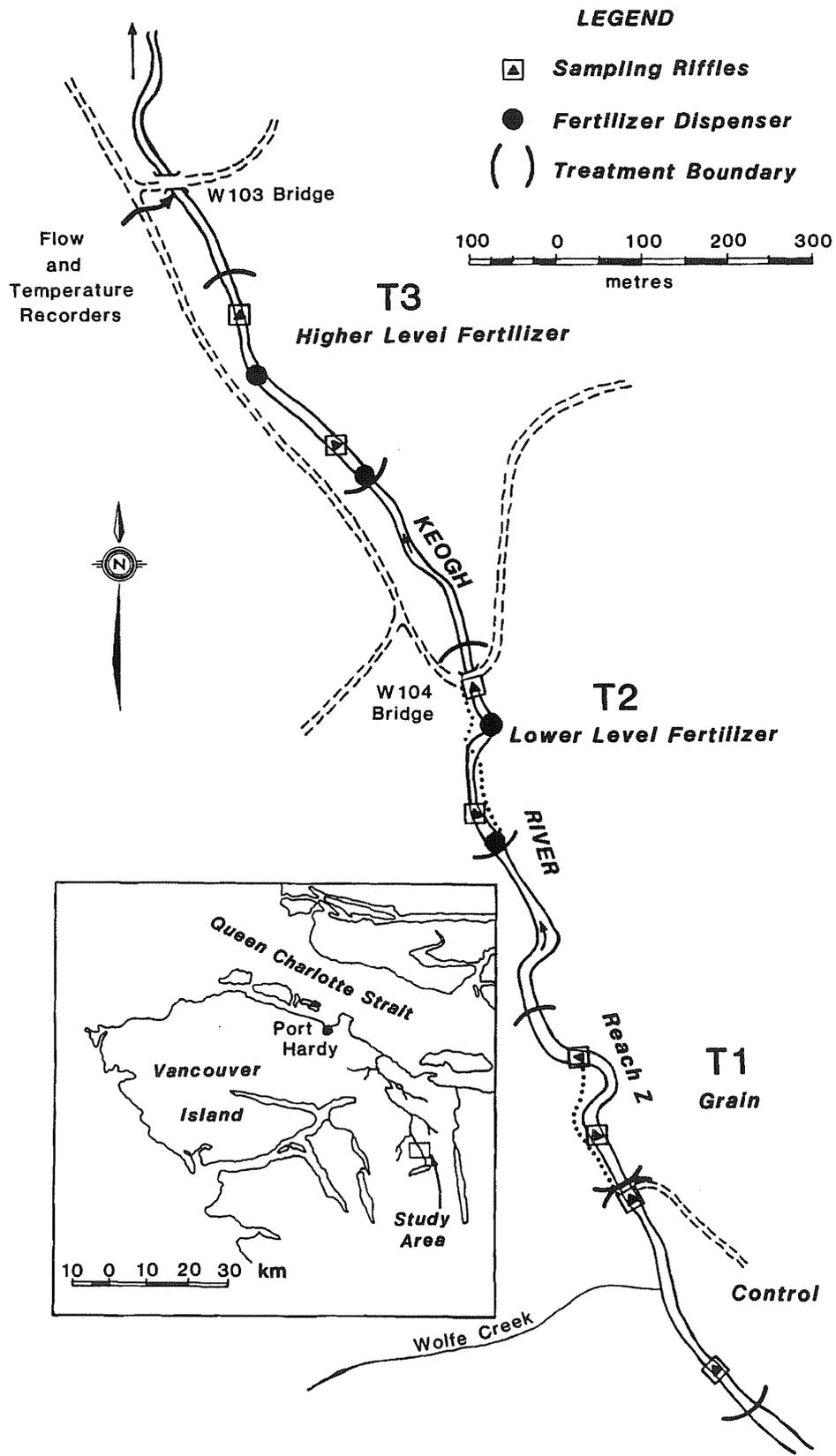


FIG. 1. Site detail of study reaches in Keogh River Reach Z.

TABLE 1. Photosynthetically active radiation (PAR) during each periphyton accumulation series.

Periphyton accumulation series	Dates	PAR (Einst·m ⁻² ·d ⁻¹)		
		Mean	Max	Min
1	Apr. 10–May 15	—	—	—
2	May 16–May 28	—	—	—
3	June 24–July 9	57.0	70.3	37.14
4	July 12–Aug. 13	49.29	69.06	26.84
5	Aug. 15–Sept. 22	46.82	59.13	38.50

0.64 cm sheets of styrofoam-DB (Snowfoam Products, El Monte, California) substrata located in each riffle. The styrofoam was attached to a 0.7-cm-thick acrylic surface which was bolted to a 5.1 × 30.5 × 30.5 cm concrete block embedded in the stream bottom. All plate assemblies were located where the current velocity was approximately 40 cm·s⁻¹ and water depth above the styrofoam surface was 10 cm. When flows and water depth changed, sampling substrata were moved to maintain the intended physical conditions.

The styrofoam was sampled for chlorophyll *a* every 4–7 d. On each date, one sample was collected from each replicate plate by removing a core with the open end of a 12-dram (8.55-cm² core area) plastic vial. Acidification was prevented by adding a few drops of MgCO₃. Samples were stored in the dark at -20°C for up to 1 wk before extraction of the cores in 90% acetone and analysis using the spectrophotometric technique of Strickland and Parsons (1972).

Five time-course sequences of chlorophyll *a* accumulation in each section were made from April through September. The first series was run before treatments began, and the four others were run during treatment (dates shown in Table 1). As an aid in detecting differences between treatments, an analysis of covariance was used to test for differences between slopes of the linear part of the increase in chlorophyll *a* concentrations. All slopes were determined by least squares analysis. It should be noted that although these slopes represent the net rate of periphyton accumulation, they are not the same as specific growth rate measurements. Care was taken to install the artificial substrata at similar depths and current velocities, but site-to-site variation in passive settlement and insect grazing were uncontrolled.

At the end of each accumulation period, two additional cores were collected from each plate: one for a determination of alkaline phosphatase activity (APA) and the other for taxonomic examination. Since APA is inversely related to the supply of external P (Perry 1972), APA was considered useful for evaluating P deficiency. Cores for APA analysis were frozen at -20°C in the dark until analysis using 100 μm of 3-*O*-methylfluorescein phosphate (MFP) as the reactive substrate (Healey and Hendzel 1979). These values were normalized to chlorophyll *a* determined from subsamples of the same homogenized core material used for the APA analysis. Taxonomy samples were preserved in Lugol's acetate solution and stored at room temperature for up to 3 mo before examination. The relative abundance of each algal class or phyla and genera was determined from periphytic material which was scraped from the styrofoam with a stiff-bristle toothbrush. Samples were allowed to settle in Utermohl chambers for at least 8 h. Several transects were then examined at 500× magnification to determine the percent composition, as

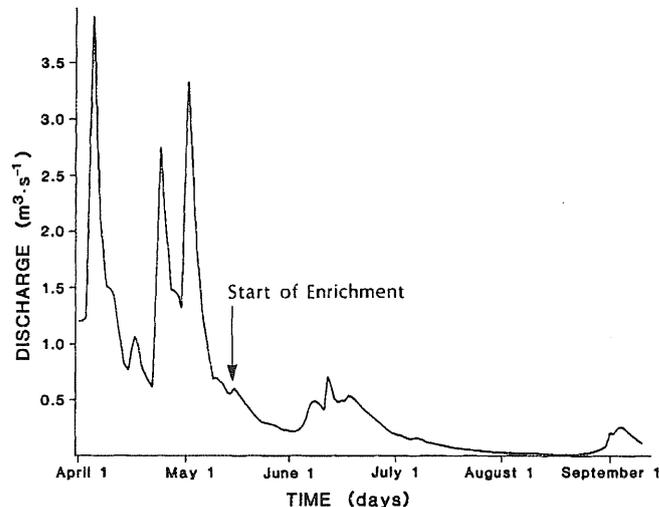


FIG. 2. Keogh River flow rates at the W103 location of Reach Z during spring and summer 1981. Stream enrichment began on May 16.

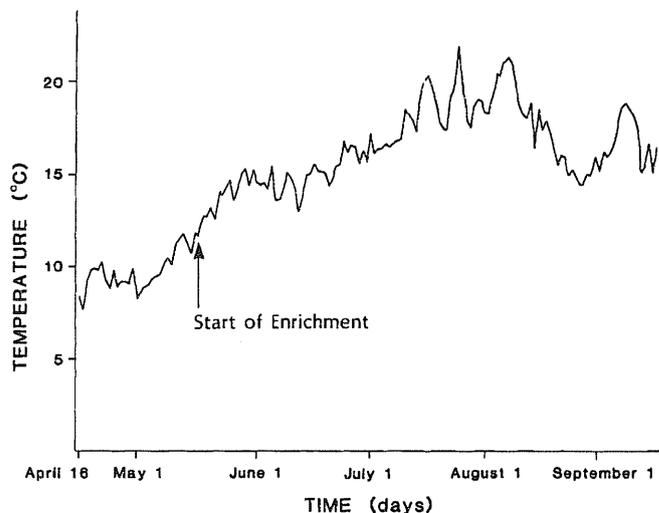


FIG. 3. Keogh River water temperature at the W103 location of Reach Z during spring and summer 1981.

described by Northcote et al. (1975). Extracellular products (e.g. gelatinous stalks) were included in the estimate. Reference works used for identification were Hustedt (1930), Cleve-Euler (1951–55), Prescott (1962), and Patrick and Reimer (1975).

Results

Physico-chemistry

Physical data collected in Reach Z were typical of dry summer conditions without freshets. Average stream flow from April to September was 0.54 m³·s⁻¹, and a low summer flow of approximately 0.2 m³·s⁻¹ was reached by late July (Fig. 2). Photosynthetically active radiation (PAR) (Table 1) ranged from an average high value of 57 Einst·m⁻²·d⁻¹ when recording began in late June to a lower level of approximately 47 Einst·m⁻²·d⁻¹ by the end of July. Water temperatures (Fig. 3) were <10°C in late April, peaked at 22°C during early

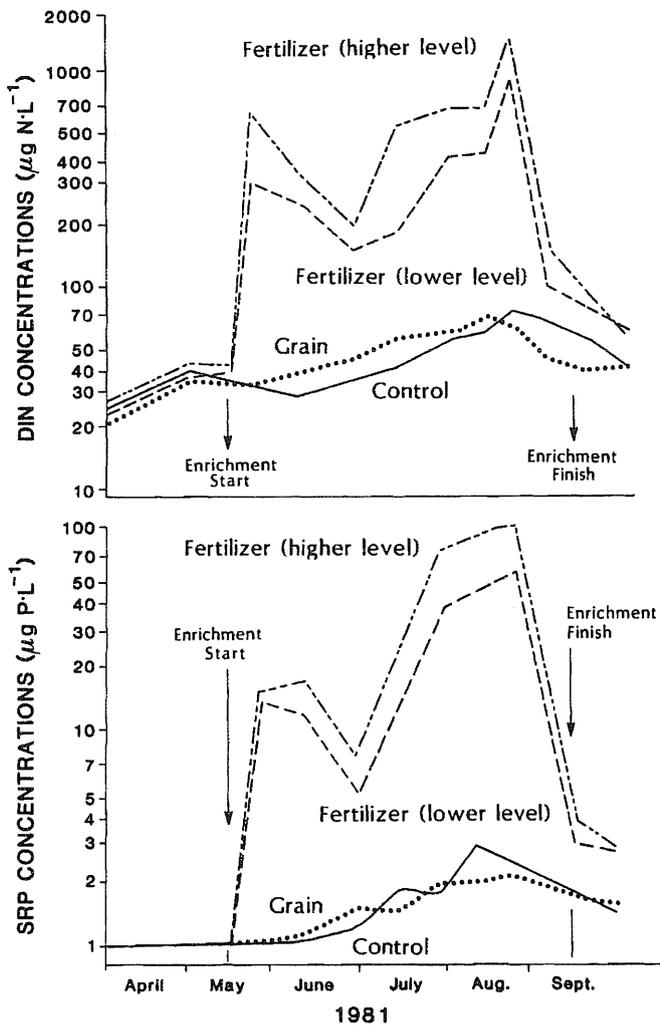


FIG. 4. Macronutrient concentrations before and during enrichment in Keogh River Reach Z for each treatment and control section. Ordinate scales are logarithmic. Nitrogen concentrations are as $\text{NO}_3^- + \text{NO}_2^- + \text{NH}_3 + \text{NH}_4^+\text{-N}$ (DIN).

August, and were 17°C at the termination of the study in September.

Initial background dissolved nutrient levels in the river were very low (Fig. 4): SRP was $\leq 1 \mu\text{g}\cdot\text{L}^{-1}$, the average $\text{NO}_3^- + \text{NO}_2^- \text{-N}$ level was $10 \mu\text{g}\cdot\text{L}^{-1}$ and $\text{NH}_3 + \text{NH}_4^+\text{-N}$ was undetectable ($< 5 \mu\text{g}\cdot\text{L}^{-1}$). These low concentrations were unchanged by the grain treatment. However, some small changes in background nutrient levels were noted during the study (Fig. 4). SRP, $\text{NO}_3^- + \text{NO}_2^- \text{-N}$ and $\text{NH}_3 + \text{NH}_4^+\text{-N}$ increased to 3, 60, and $10 \mu\text{g}\cdot\text{L}^{-1}$, respectively, by August. Thereafter, concentrations declined to reach pretreatment levels by mid-September. In fertilized sections, nutrient concentrations rarely declined below the intended treatment level, but there was considerable temporal fluctuation due both to periodic feeder malfunction and changes in stream flow (Fig. 4). Average SRP and dissolved nitrogen (DIN) concentrations were 15 and $250 \mu\text{g}\cdot\text{L}^{-1}$, respectively, in T2 and 25 and $480 \mu\text{g}\cdot\text{L}^{-1}$, respectively, in T3.

Although there was no movement of grain into sections downstream of T1, analysis of water samples collected upstream of T3 immediately after fertilization started showed

that elevated N and P levels from T2 continued into T3. Consequently, fertilizer applications in T3 were constantly adjusted to prevent nutrient concentrations from exceeding the intended level. Similar adjustments were made to feeders within treatments to ensure that replicate riffles received a similar level of enrichment. Macronutrient concentrations up to threefold greater than those measured in the control were also detected in periodic samples collected 2 km downstream of the study site.

Periphyton Accrual

Accumulation rates of periphyton prior to treatment (Fig. 5a) were similar in all sections ($0.10 \text{ mg Chl } a \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, $p < 0.05$). Chlorophyll *a* standing crops never exceeded $10 \text{ mg}\cdot\text{m}^{-2}$, and the mean was only $4.72 \text{ mg}\cdot\text{m}^{-2}$ ($\text{SE} = 0.31$). This level is typical of periphyton abundance which has been reported for other nutrient deficient streams at 10°C (Stockner and Shortreed 1978; Peterson et al. 1983). In late May, accumulation rates in the control and T1 more than tripled to approximately $0.35 \text{ mg Chl } a \cdot \text{m}^{-2} \cdot \text{d}^{-1}$.

Following the start of enrichment, stimulatory effects of inorganic fertilizer additions were clearly visible. Chlorophyll *a* accumulation rate in T2 increased by more than an order of magnitude to $4.1 \text{ mg}\cdot\text{m}^{-2} \cdot \text{d}^{-1}$, and that in T3 ($8.6 \text{ mg}\cdot\text{m}^{-2} \cdot \text{d}^{-1}$) was more than double T2. Within 15 d the average chlorophyll *a* standing crop increased from < 10 to approximately $90 \text{ mg}\cdot\text{m}^{-2}$ in T2 and $150 \text{ mg}\cdot\text{m}^{-2}$ in T3. However, no differences in periphyton biomass were detectable between grain (T1) and control sections ($p < 0.05$).

In series 3 (Fig. 5b), the spread of rates and standing crop between T2 and T3 narrowed. Chlorophyll *a* accumulation rate in T3 increased by approximately 20% to $11.0 \text{ mg}\cdot\text{m}^{-2} \cdot \text{d}^{-1}$, but T2 rates doubled to $8.8 \text{ mg}\cdot\text{m}^{-2} \cdot \text{d}^{-1}$ from the earlier measurements, resulting in a marked increase in maximum chlorophyll *a* levels in T2 after 15 d compared with the same duration in series 2.

In series 4, temperature reached a maximum, flow reached a minimum, and treatment effects changed markedly (Fig. 5c). Chlorophyll *a* accumulation rates in the control and T1 were again similar to previous levels, but those in both T2 and T3 declined by up to 90%. In addition, previous differences between T2 and T3 were no longer detectable ($p < 0.05$). Although significant differences in both accumulation and chlorophyll *a* standing crop remained between fertilized sections and control, the order of magnitude difference seen in series 3 had declined to only a threefold difference. By mid-July, sloughing of large mats of accumulated biomass was visibly obvious despite continuous additions of N and P. In series 5, there was a renewed response to elevated nutrients that corresponded with declining temperature and light levels. Although the large responses observed in series 3 did not reoccur, accumulation rates of chlorophyll *a* in T2 ($2.8 \text{ mg}\cdot\text{m}^{-2} \cdot \text{d}^{-1}$) and T3 ($5.4 \text{ mg}\cdot\text{m}^{-2} \cdot \text{d}^{-1}$) increased up to an order of magnitude greater than control levels (series 5, Fig. 5d). However, over the latter 15-d period in series 5, maximum biomass in T3 was only 60% of that during a similar length of time in series 3, and biomass in T2 only reached approximately $50 \text{ mg Chl } a \cdot \text{m}^{-2}$, about half of the response in series 3.

Periphyton Taxonomy

Diatoms comprised most of the biomass of the attached algal

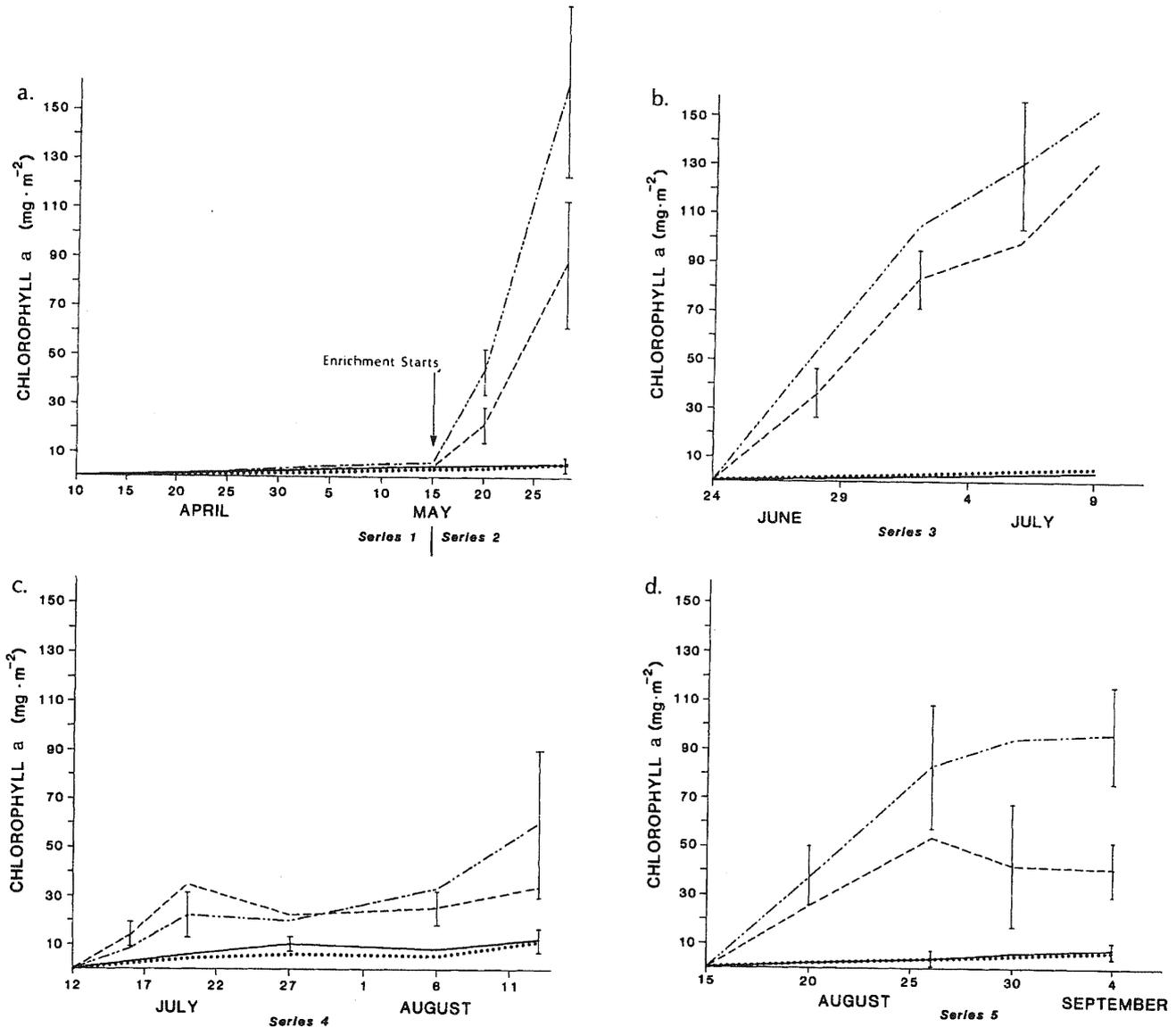


FIG. 5. Chlorophyll *a* accumulation on in situ styrofoam substrata in control (—), grain (···), lower level fertilizer (---), and higher level fertilizer (— · —) treatments during each of five accumulation series. Note that abscissa scales are different between series. (a) pretreatment (series 1) and during treatment (series 2); (b) series 3; (c) series 4; (d) series 5. Error bars represent 95% confidence intervals.

community in all sections up to mid-July (Fig. 6). *Tabellaria* and *Synedra* were most common. *Achnanthes* spp. numerically comprised up to 50% of some samples. Other genera including *Fragilaria* and *Diatoma* were of relatively minor importance. Planktonic forms of chlorophytes were also present. Blue-greens were a very small component of the attached community.

By early July (series 3), stream flows were steadily declining and there was an increase in the diversity of genera that are typically found in slow-water environments. In fertilized sections the filamentous chlorophyte *Ulothrix* was abundant, turning those areas a vivid green colour. In series 4, the relative abundance of diatoms declined markedly and the proportion of both tychoplanktonic and euplanktonic chlorophytes increased in all sections (Fig. 6). *Ulothrix* virtually disappeared and the diversity and proportionate importance of desmids and other pool-dwelling genera was particularly striking. *Spirogyra*

replaced *Ulothrix* in the fertilized reaches. At this time, the proportionally smaller diatom community was also made up of different genera including *Cymbella* and *Cyclotella*. The blue-green *Oscillatoria* remained insignificant in control and grain treatments but did increase by 2–5% in fertilized areas. During series 5 the diatom flora regained its relative dominance in T3 (Fig. 6), but even as late as September 22, a wide diversity of desmids and other planktonic genera remained common.

APA

Before addition of nutrients on May 16, APA values in all sections ranged from approximately 70–145 nmol MFP· μg Chl *a*⁻¹·h⁻¹ (Fig. 7). Eleven days following the commencement of treatments, APA in both T2 and T3 declined to levels indicative of no P deficiency (Healey and Hendzel 1979). Simultaneously, APA in the control and grain-enriched sections increased significantly to levels suggesting extreme P

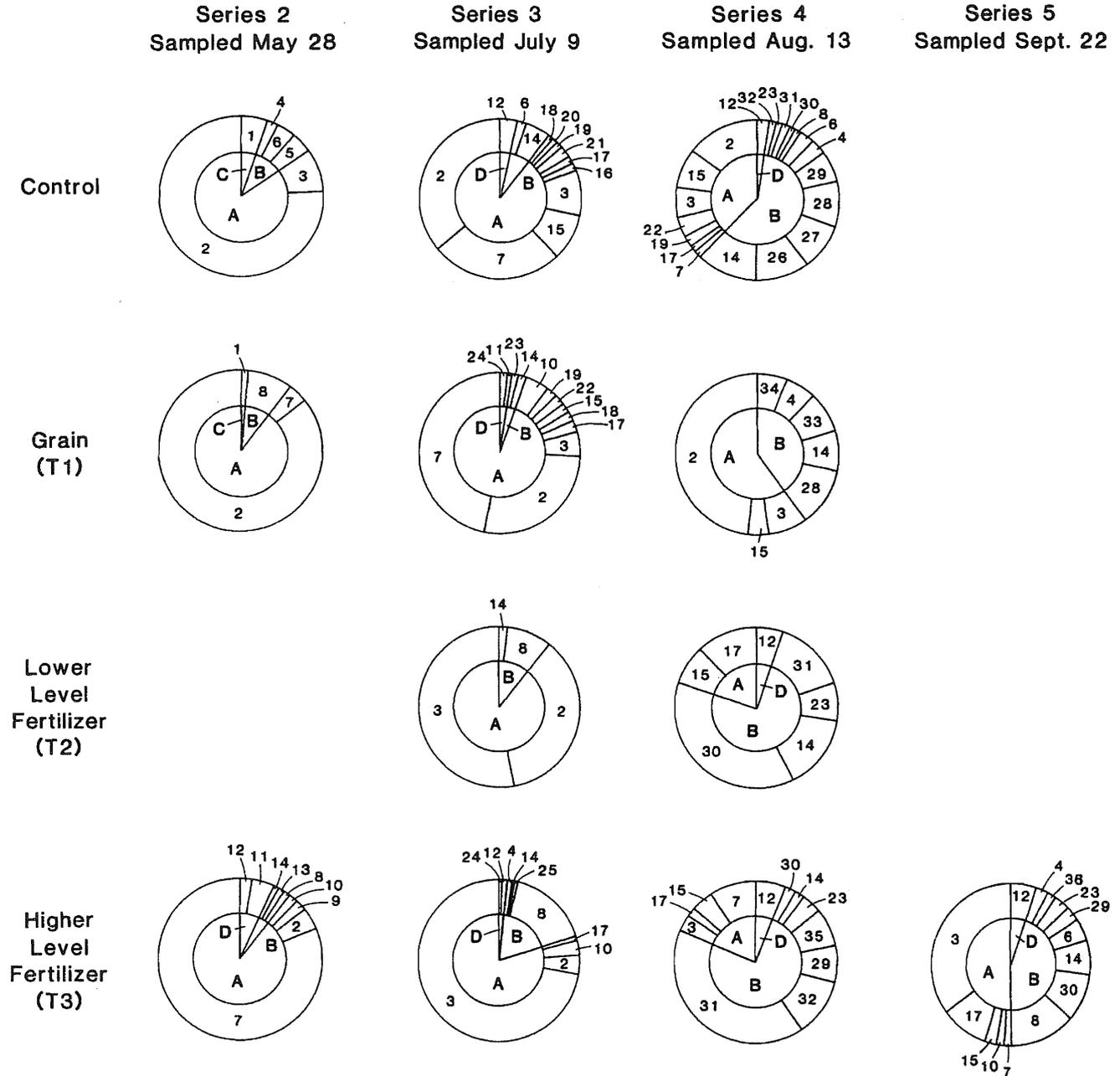


FIG. 6. Proportions of algal classes or phyla and genera on styrofoam substrata at the end of accumulation series 2-5. Data are missing for the control, T1, and T2 in series 5 and for T2 in series 2. The inner circle shows percent composition of Bacillariophyceae (A), Chlorophyta (B), Chrysophyta (C), and Cyanophyta (D). Numbers in the outer circle correspond to the genera listed below. Divisions in the outer circle represent percent composition of these genera within the class or phyla. 1, *Dinobryon*; 2, *Tabellaria*; 3, *Synedra*; 4, *Staurastrum*; 5, *Penium*; 6, *Closterium*; 7, *Achnanthes*; 8, *Ulothrix*; 9, *Diatoma*; 10, *Fragillaria*; 11, *Chamoesiphon*; 12, *Oscillatoria*; 13, *Zygnema*; 14, *Cosmarium*; 15, *Navicula*; 16, *Melosira*; 17, *Gomphonema*; 18, *Nitzschia*; 19, *Eunotia*; 20, *Denticula*; 21, *Cyclotella*; 22, *Cymbella*; 23, *Ankistrodesmus*; 24, *Anabaena*; 25, *Trachlmonas*; 26, *Teilingia*; 27, *Tetraedron*; 28, *Bulbochaete*; 29, *Chlamydomonas*; 30, *Scenedesmus*; 31, *Spirogyra*; 32, *Selenastrum*; 33, *Spondylosium*; 34, *Pediastrum*; 35, *Sirogonium*; 36, *Mougeotia*.

deficiency ($p < 0.05$). For the duration of summer, APA values in the nutrient-enriched sections remained very low. Values in T3 were no different from those in T2 ($p < 0.05$). High APA values in the control and grain treatment areas persisted throughout the summer. APA in the grain enrichment was always significantly higher than in the control by a 35% margin ($p < 0.05$).

Discussion

Periphyton Accrual

Accumulation rates of periphytic algae in the Keogh River clearly increased with additions of N and P. In T2 and T3, increases were at least in part due to elimination of P deficiency, a finding supported by other studies on nutrient defi-

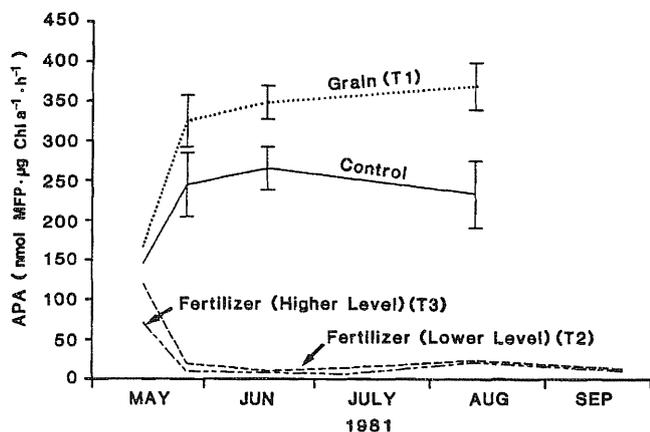


FIG. 7. Alkaline phosphatase activity (APA) in control (—), grain (···), lower level fertilizer (---), and higher level fertilizer (----) treatments section of Keogh River Reach Z during summer 1981.

ciency and growth of benthic algae. Bothwell (1985), for example, found that P concentration limits algae production in the Thompson River system, British Columbia, and that SRP concentrations of only 3–4 $\mu\text{g}\cdot\text{L}^{-1}$ are sufficient to saturate P-limited growth rates. Recent studies by M. L. Bothwell (National Hydrology Research Centre, Saskatoon, Sask., unpubl. data) suggest that growth may be saturated at even lower concentrations of P. In a study at Carnation Creek, Vancouver Island, where streamside troughs were used to examine periphyton accumulation, Stockner and Shortreed (1978) found that by increasing SRP levels from <1 to 8–10 $\mu\text{g}\cdot\text{L}^{-1}$, chlorophyll *a* levels increased by more than 10 times. By adding inorganic N, as well as P, a further doubling of biomass to >200 mg Chl *a*·m⁻² was reported. In laboratory streams, Horner et al. (1983) found that SRP levels of 15–25 $\mu\text{g}\cdot\text{L}^{-1}$ produced what were considered “nuisance” conditions of algal biomass at 100–150 mg Chl *a*·m⁻². Periphyton biomass in excess of 100 mg Chl *a*·m⁻² were common in T2 and T3, particularly in series 3, but the increase from control levels was not perceived as a negative impact, since mean weights of juvenile salmonids increased by up to 80% due to treatment (P. A. Slaney, B.C. Ministry of Environment and Parks, Fisheries Branch, University of British Columbia, Vancouver, B.C., unpubl. data).

No change in periphyton accumulation was detectable in response to the grain addition. However, APA was greater in T1 than in the control by 35% ($p < 0.05$). Hence, although differences in periphyton accumulation between T1 and the control were not detectable using the artificial substrata, the addition of POM may have reduced specific growth rates due to higher P deficiency. This difference in P deficiency between the control and T1 will be further discussed below.

In three of the four incubation series when fertilizer was added, algal accumulation rates were significantly greater in T3 than in T2. Higher accumulation rates at higher concentrations of N and P are consistent with findings of Horner and Welch (1981) showing that biomass of stream periphyton may remain P limited at concentrations exceeding 40 $\mu\text{g}\cdot\text{L}^{-1}$. Evidence that P-limited growth of periphytic diatoms saturates at only 3–4 $\mu\text{g}\cdot\text{L}^{-1}$ (Bothwell 1985) suggests that diffusion limitation of P may be important in dense algal mats. Thus, relatively high P concentrations are required to saturate rates of biomass accrual. The possibility of differences in P deficiency

in algal mats between T2 and T3 is, however, at odds with APA data that suggest that periphyton in both T2 and T3 were P replete.

One explanation for this disparity may be the confounding effect of passive settlement on measurements of algal accumulation rates, an effect that was originally described by Bothwell and Jasper (1983). Algal settlement rates (milligrams chlorophyll *a* per square metre per day) are, in part, controlled by the concentration of suspended algae (milligrams chlorophyll *a* per cubic metre) that has sloughed from upstream substrata. Hence, the large increase in attached biomass in T2 and presumably that in the buffer reach between T2 and T3 may have increased algal drift and subsequent settlement downstream in T3. Settlement in T3 would have resulted in measurements of greater biomass accumulation rates in T3 even if biomass accrual due to growth within T3 was similar to that in T2. Another explanation for differences in periphyton accrual between fertilized reaches relates to differences in rates of insect grazing. Although Perrin and Johnston (1985) reported no significant difference in the biomass of collector or scraper invertebrates between T2 and T3, invertebrate production may have differed and impacted on accrual of periphyton biomass.

A most striking feature of the periphyton accrual data was the decline in accumulation rate in T2 and T3 beginning in early to mid-July despite continuous enrichment. There are a variety of explanations to be considered related to biological and physical factors.

First, July was a period of highest irradiance and some of the highest temperatures were also recorded at this time. Because of very low flows, water depths in many areas, particularly riffles, where <10 cm. These are conditions when ultraviolet toxicity may be suspected to limit growth (Soeder and Stengel 1974) due to photodestruction of chlorophyll (Meeks 1974) and inactivation of chloroplasts (Cock 1982). Recently, M. L. Bothwell (unpubl. data) has clearly shown that periphyton growth rates can be inhibited under natural UV exposure during summer months at the Thompson River.

A second possibility is change in insect grazing activity. Lamberti and Resh (1983) have shown that patterns of periphyton accrual follow a fluctuating pattern of biomass increase and decrease related to the competitive spacing of insects. Hart (1981) also suggested that insect larvae exploit periphyton resources, and Jacoby (1985) found that periphyton biomass was about four times less in enclosures containing high densities of snails compared with periphyton biomass in enclosures where snail densities were 10 times lower. Significant changes in cropping rates seem unlikely in our data, however, because of differences in timing between the decline in periphyton accumulation rates and temporal responses by collector and grazer insects that dominated the benthic community. Perrin and Johnston (1985) have shown that invertebrate biomass did not increase ($p < 0.05$) until late August, a time when algal accumulation rates were returning to higher levels. Results, however, may have been confounded with cropping of invertebrates by fish which were growing rapidly during the decline in algal biomass.

A third explanation is algal cell lysis caused by bacteria, fungi, and/or actinomycetes. There is a broad correlation between bacteria activity and algal production (Hobbie and Rublee 1977) in a variety of aquatic ecosystems. Hence, one would expect bacterial activity to have increased in response to a greater standing crop of algae in T2 and T3. The same would

also occur due to loading of organic matter in T1. Although the presence of any lytic bacteria was not examined in our study, Daft et al. (1975) has shown that lysis of a cyanophyte can be extremely rapid after an initial chemotactic response followed by bacteria attachment to the cell wall. Also, *Scenedesmus* spp. can become infected with a bacterium that digests cells from the inside out (Schnepf et al. 1974). It appears that all lysis can be selective to species or stages of cell division that have weak cell wall structures (Gunnison and Alexander 1975).

A fourth explanation relates to seasonal shifts in micro-nutrient supply. Silica concentrations were determined on an irregular basis but ranged between 4000 and 4500 $\mu\text{g}\cdot\text{L}^{-1}$, well above a level considered to limit growth of a typical planktonic diatom (Kilham 1975). Although most micro-nutrients were not measured, any decline in concentrations could have limited growth rates and, in particular, contributed to the shift in community taxonomy shown in Fig. 6 (cf. Patrick 1978).

Finally, the effects of flow cannot be ignored. Diatoms examined from all sections are considered typical of the fast-flowing habitats that existed prior to mid-July (Smith 1950; Prescott 1962). The increase in importance of planktonic genera occurred at the same time of minimum flow when quiescent backwater and pools were common. This shift in the physical environment may have selectively inhibited diatom growth. However, the specific process involved is difficult to resolve. Nutrient supply at the cell boundary can decline at low flow and reduce rates of nutrient uptake and respiration (Whitford and Schumacher 1964), but Lock and John (1979) suggested that this boundary effect may not be important in nutrient-replete conditions as were characteristic of T2 and T3.

APA

Regardless of these temporal trends in biomass accumulation, differences in the physiological status of periphyton remained constant between sections. Very low APA levels in T2 and T3 suggest continuous P sufficiency. Of even greater interest, however, is the relative increase in APA due to additions of grain in T1. There are three possible explanations for this increase in APA over control levels. The most obvious is that algae may have become more P limited because of increased competition from bacteria for a limited supply of ambient P. Compared with most algae, heterotrophic bacteria are known to be superior competitors for phosphate (Rhee 1972; Brown et al. 1981). When heterotrophs are not limited by organic carbon, they can outcompete algae under P-limited conditions (Brown et al. 1981; Schindler 1975). Competition for P increases P limitation in the autotrophs and is consistent with our observation of an increase in APA following POM additions. A second explanation is that if heterotrophic demand for P did increase as a result of POM additions, then any increase in bacteria biomass on the substrata in T1 would result in higher APA values when concentrations are normalized to chlorophyll *a*. The third possibility is that bacterial APA may have increased independent of any change in heterotrophic biomass. Bacteria biomass was not quantified, so we cannot distinguish between these alternative explanations.

Conclusions

The interactions between autotrophic and heterotrophic processes and the relative dominance of each in providing a food

supply to the invertebrate community are important in the context of choice of materials that can be added to nutrient-deficient streams for salmonid enhancement purposes. Grain has been advocated as a desirable supplement (Mundie et al. 1983) because it is inexpensive and provides a direct source of food for a variety of fish food organisms. This proposal was based on experiments conducted in a nutrient-replete side channel of the Big Qualicum River, British Columbia.

As part of the present study, P. A. Slaney (unpubl. data) found that grain additions significantly increased mean weights of coho fry by up to 58% over fry weights in the control reach. By comparison, juvenile coho growth increased rapidly with the onset of fertilizer additions, resulting in up to an 82% gain in mean weights in the same growing season. Mean weights of juvenile steelhead trout were not significantly different between the control and T1 but were 67% heavier in fertilized reaches compared with the control. Hence, while grain additions can increase insect standing crop in nutrient-replete streams (Mundie et al. 1983), increased autotrophic production by nutrient addition results in greater benefit for growth of salmonids in a nutrient-deficient stream.

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