CONTROLS ON BENTHIC ALGAL GROWTH ON ARTIFICIAL SUBSTRATES IN LIMNOCORRALS RECEIVING PULSES OF SEDIMENT AND NUTRIENTS IN A MACKENZIE DELTA LAKE

by

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Controls On Benthic Algal Growth On Artificial Substrates In Limnocorrals Receiving Pulses Of Sediment And Nutrients In A Mackenzie Delta Lake

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ABSTRACT

Title of Thesis: **Controls on Benthic Algal Growth on Artificial Substrates in Limnocorrals Receiving Pulses of Sediments and Nutrients in a Mackenzie Delta Lake**

The Mackenzie Delta is a lake-rich environment where the distribution and abundance of phytoplankton, macrophytes, and benthic algae among the lakes may be controlled by an interaction between nutrient supply and sediment in the water column, and episodic reductions in light availability associated with river flooding. To simulate the effects of episodic river inflow on benthic algae, limnocorrals (Z = 3m) received high or low weekly additions of nutrients (N and P) and sediments, delivered as a pulse (1 x per week), or distributed incrementally through each week (3 x per week), in a balanced triplicated design (15 limnocorrals). Artificial substrates, enriched to mimic the supply of nutrients at the sediment/water interface, were suspended in the limnocorrals at 2 m depth for 6 weeks in July and August, 1995. Maximum average levels of phytoplankton biomass (indicated by chlorophyll *a*) occurred in the treatment where light extinction was highest (High-Distributed treatment) and lowest levels occurred where light extinction was lowest (Control). Multiple regression of concurrent concentrations of total suspended sediments (TSS) and phytoplankton chlorophyll *a* against light extinction in the corrals indicate that light availability was controlled primarily by TSS but that planktonic chlorophyll contributed significantly to light extinction. By contrast,

maximum average accrual of benthic algal biomass on the artificial substrates occurred in the Control while lowest accrual occurred in the High-Distributed treatment. Under equivalent *in situ* light conditions, areal net photosynthesis of the benthic algae (O_2-change during light and dark incubations) was highest in the Control and lowest in the High-Pulsed treatment. Net photosynthetic rate per unit chlorophyll of benthic algae was highest in the Low-Distributed treatment and lowest in the High-Pulsed treatment. Lastly, biomass accrual rates among the treatments show a strong inverse relation with average light extinction among the corrals over the duration of the experiment. Given that the benthic algae should not have been nutrient limited and that grazing appeared to be negligible, these results indicate that light availability was primarily responsible for maximum biomass accrual in the Control and was the dominant control on accrual rates among treatments. Overall, this study suggests that the abundance of benthic algae, among Mackenzie Delta lakes, may progressively increase as light availability becomes greater, while phytoplankton abundance may peak in lakes with intermediate transparencies by responding to nutrient additions despite interruption of the light environment by suspended sediments.

DEDICATION

This thesis is dedicated to my daughter, Melinda Tennessee.

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Many others contributed to this project. John Richardson provided sound advise on my research proposal, reviewed an earlier verson of this thesis, and has offerred scientific and professional guidance throughout my undergraduate and graduate career. Louis Druehl listened patiently to my research proposal, and suggested useful additions to the final version of this thesis. Les Kutney and Allen Fehr of the Inuvik Research Centre in the Northwest Territories provided assistance in the laboratory, and invaluable logistical support as did Brian Turner, and members of the Inuvik Volunteer Fire Department- who filled SCUBA tanks at our convenience, not theirs. However, my deepest thanks go to my mate Will, and offspring- Carolina, Rose, Virginia and Melinda, who have fully supported my pursuit of a scientific career, and to my parents Bill and Talie Squires and grandfather Wayne Plastridge who have nurtured, encouraged and supported my interest in science. Will also voluntarily served as my field assistant for this project.

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In conjunction with the logistical support provided by the Polar Continental Shelf Project I have to mention my high regard for the pilots and engineers employed by Canadian Helicopters who are consistently competent. In particular, Will and I wish to posthumously thank David Nasagalawak. David gained our respect and personal regard, and we were both saddened at his untimely death in the course of duty.

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INTRODUCTION

The physical process resulting in formation of floodplain lakes has been described by Hutchinson (1957). When a major distributary reaches the ocean, its sediment is deposited suddenly as current velocity falls. When a river building the delta varies in volume, as is nearly always the case, the banks deposited will be built up above mean sea level as levees, resulting in numerous lakes in the central portion of a delta. Lakes of this type typify all major deltas of the world.

Floodplain lakes may be highly productive and support diverse food webs including substantial fisheries in the tropic, temperate and arctic regions of the world (Welcomme, 1979). Overall our understanding of limnological processes among floodplain lakes remains poor compared to the well-studied lake districts of North America and Europe for which it has been established that lakes derive most of their water and nutrients from surrounding drainage basins. By contrast, annual inundation with nutrient-rich river water may replenish nutrients and drive phytoplankton production in floodplain lakes (e.g. Lesack & Melack, 1995; Doyle, 1991; Forsberg *et al*, 1988), although local drainage and atmospheric inputs may also be important (e.g. Lesack & Melack, 1991; Forsberg *et al*, 1988). However, overall, benthic production by periphyton and macrophytes may comprise

fifty percent or more of the carbon production in shallow delta lakes since light may penetrate to the lake bottom (Ramlal *et al*, 1994; Hecky *et al*, 1991; Doyle, 1991). Moreover, since benthic producers are rooted or adnate to fertile deltaic sediments they are not likely to be nutrient-limited but instead be may be light-limited. Besides representing a potentially important source of new nutrients to lakes, river water typically contains high concentrations of suspended sediments which may influence lake productivity by reducing light availability and/or by acting as a source of [clay-bound] nutrients (e.g. Carignan & Planas, 1994; Setaro & Melack, 1984; Engle & Melack, 1993; Guilford & Hecky, 1987;). The relative importance of nutrients and sediments in regulating primary productivity in floodplain lakes may vary seasonally (e.g. Engle & Melack, 1993), with distance from the source of riverine sediment and nutrients (e.g. Marsh & Hey, 1991), or with the frequency and duration of episodic river inflow events (e.g. Lesack *et al*, 1991). Also, complex interactions between nutrients and sediments may ultimately set limits on lake productivity (e.g. Litchman, 1996; Healey, 1985; Titman, 1976). Overall, our understanding of controls on primary productivity in floodplain lakes world-wide is improving (cf. Lesack *et al*, in press; Engle and Melack, 1993; Doyle, 1991; Hamilton & Lewis, 1990).

Progress has also been made in our appreciation of the effects of suspended sediment on lake productivity in general. Impoundment, agricultural enterprise, suburban development and forest harvest may all increase erosion and the suspended sediment load carried by streams and rivers which ultimately flow into lakes. *In situ* field research has shown

that the effect of increased turbidity on the biological components of lake systems may be minimal (e.g. Threlkeld and Soballe, 1988; Guilford *et al*, 1987). For example, phytoplankton primary productivity did not change appreciably after impoundment of Southern Indian Lake, Manitoba. By contrast, Cuker (1993 and Cuker *et al*, 1987 & 1990) demonstrated that the effect of increased turbidity on the biological productivity and community organization of lake systems may be substantial, including alteration of trophic interactions among plankton, change in zooplankton assemblages, and shifts in net community productivity.

Twenty-five thousand lakes and a convolution of interconnected channels are dominant features of the expansive Delta of the Mackenzie River near its mouth at the Beaufort Sea. Influx of river water is a primary determinant of the chemical, physical and biological character of the shallow Delta lakes (Lesack *et al*, 1991; Ramlal *et al*, 1991; Anema *et al*, 1990a & 1990b; Fee *et al*, 1988). Considerable variation in the temporal dynamics of river inflow among the Delta lakes results in a gradient of physical and chemical conditions depending on the degree of influence of turbid river water with consequences for the aquatic plant community.

Broad-scale patterns of river inflow have a significant effect on the availability of light for primary producers and lake productivity. For example, total net photosynthesis in lakes selected to represent a strong light gradient among Delta lakes ranged from 2-3 mmoles C m^{-2} day^{-1} in turbid lakes, to greater than 60 mmoles C m^{-2} day^{-1} in clear lakes (Figure 1.1) (Hecky *et al*, 1991). Conversely, there is evidence that distinct classes of primary producers respond differentially to the light gradient

across the Delta (Figure 1.1). For example, phytoplankton areal photosynthetic rates varied less than two-fold among Delta lakes (Guilford *et al*, 1991). Phytoplankton productivity is low due to light limitation in very turbid lakes, and only slightly higher in clear lakes due to nutrient limitation (Guilford *et al*, 1991). These results suggest a nearly constant rate of phytoplankton areal photosynthetic rates despite the strong light gradient among the Delta lakes. Only moderate changes in phytoplankton productivity despite substantial changes in turbidity-related environmental conditions has been observed in other systems (e.g. Hecky & Guilford, 1984). The biological mechanisms considered responsible for the compensatory response of phytoplankton to a range of light and nutrient conditions have been described by Healey (1985). In contrast to phytoplankton, areal macrophyte net photosynthesis in Delta lakes varied over a factor of twenty between turbid lakes and the clearest lakes (Cordes & McLennan, 1991; Hecky *et al*, 1991). Rooted macrophytes grow in a nutrient-rich environment due primarily to diagenetic processes occurring near the sediment-water interface. Consequently light is the principle factor regulating macrophyte growth. Overall, macrophytes dominate in clear Delta lakes where they account for more than 95% of community photosynthesis, and phytoplankton account for most net photosynthesis in turbid lakes, since macrophytes are completely absent. Not accounted for is the potential contribution of periphyton (attached algae growing on illuminated subsurfaces) to lake productivity. For example, production of benthic algae (algae growing on lake bottom sediments) is potentially considerable since extensive littoral regions in

Delta lakes provide abundant subsurface for agal growth. Moreover, stable isotope analysis of the Delta lake food web has demonstrated that carbon derived from benthic algae is a dominant source of fixed energy up to and including the highest trophic levels (Hecky & Hesslein, 1995).

The relative contribution of carbon fixed by phytoplankton, benthic algae and macrophytes to the Delta lake food web has been possible by analysis of stable isotopes of carbon since benthic communities live on relatively undisturbed fixed substrates. Rate of supply of CO_2 to benthic algae is frequently diffusion-limited due to development of a significant boundary layer. As a consequence there is less discriminatory uptake of carbon isotope species by benthic algae resulting in less negative isotope ratios relative to phytoplankton and macrophytes. A unique carbon isotopic signal is passed on to consumers in a predictable manner (France, 1995; Peterson & Fry, 1987; Kitting *et al*, 1984). Benthic algal carbon has emerged as a significant source of fixed energy to consumers up to and including highest trophic levels in lakes across latitudes including the Mackenzie Delta lakes (Hecky & Hesslein, 1995). Although epiphytic algal carbon (attached algae using macrophytes as a substrate for growth) is potentially important to consumers, its contribution to higher trophic levels is unclear since terrestrial plants have a carbon isotopic signal comparable to the epiphyton of the Delta lakes.

Rate of photosynthesis by epipelon (algae growing on soft deltaic sediments) has been estimated for South Lake, Mackenzie Delta. Results suggest that epipelic algal biomass is similar to phytoplanktonic biomass. Specifically, areal epipelic algal biomass sampled along a depth gradient

from 1.0 to 1.75 m was as low as 0.7 and as high as 14.8 mg m^{-2} (Ramlal *et al*, 1991). In comparison, areal biomass of phytoplankton, based on mean depth of South Lake, ranged from 4.5 to 11.9 mg m^{-2}, and from 1.1 to 17.7 mg m^{-2} in 1985 & 86 respectively (Fee, *et al*, 1988). Net photosynthetic rates of phytoplankton and epipelon were also measured. Biomass specific net photosynthesis (mg C hr^{-1} mg chlorophyll a^{-1}) at saturating irradiance ($P^{B}m$) for phytoplankton in South Lake ranged from 0.9 to 3.47 and from 0.9 to 1.82 in 1985 & 86, respectively (Fee *et al*, 1988). In contrast $P^{B}m$ for epipelon in South Lake ranged from only 0.23 to 0.95 in 1986 (Ramlal *et al*, 1991). Since epipelic biomass may be similar to phytoplankton biomass but rates of photosynthesis per mg chlorophyll may be considerably lower, there may be a substantial mismatch between the apparent productivity of epipelon and contribution of epipelic carbon to the Delta lake food webs based on stable isotope analysis relative to phytoplankton. There are several possible explanations. Epipelon is difficult to separate from soft deltaic sediments and previous studies of epipelon have relied on separation techniques with variable efficiency (Moss and Eaton, 1966). Consequently, estimates of biomass may be low for methodological reasons. Another possible explanation for the apparent mismatch between production of epipelon and its assimilation by consumers is that benthic algae may represent a more concentrated and nutrient-rich food source than phytoplankton since epipelic algal communities develop on fertile sediments. Therefore benthic algal carbon may be more efficiently grazed and incorporated into consumer biomass than planktonic organic matter, meaning that the importance of epipelon

relative to phytoplankton may not be accurately reflected in relative photosynthetic rates. Future work that compares the efficiency of incorporation of phytoplanktonic and epipelic carbon into consumer biomass may be necessary to clarify functional aspects of the delta lake food webs.

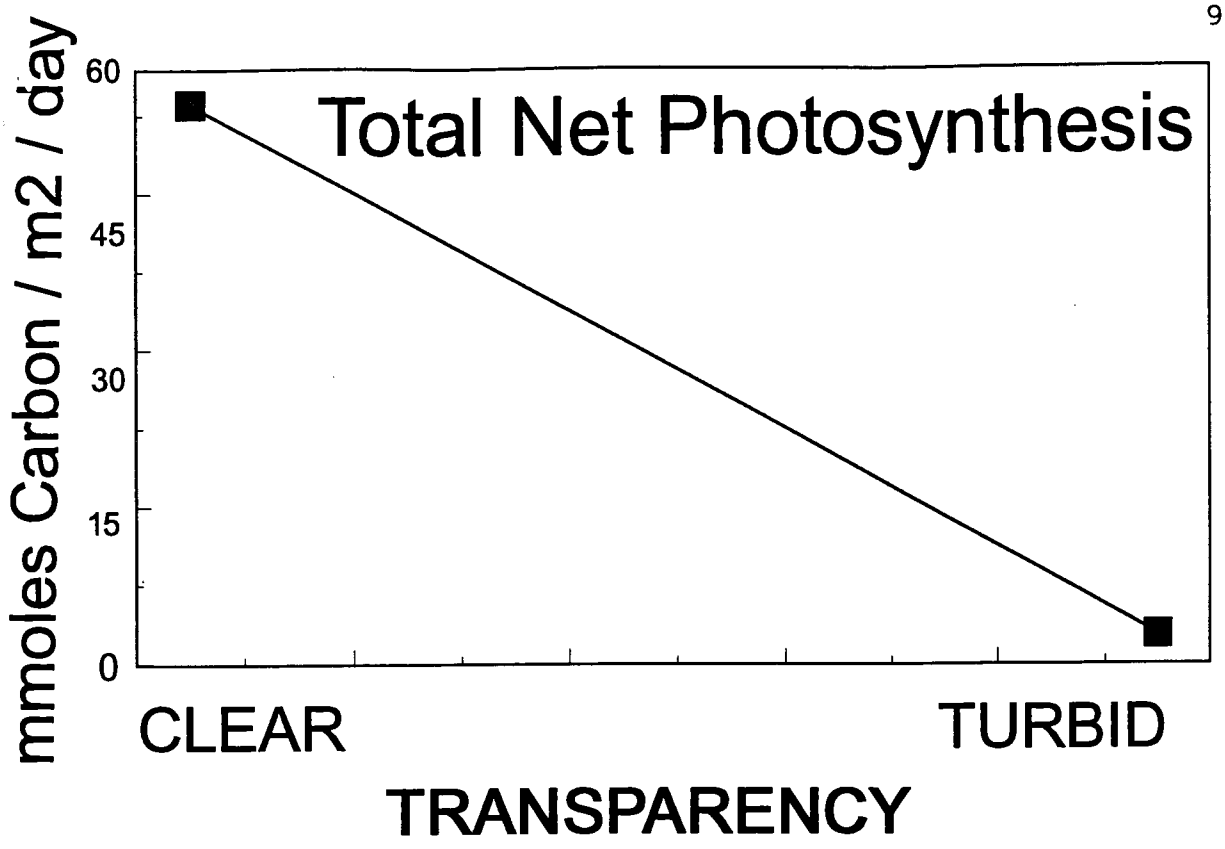
The objective of this research was to examine the relation between benthic algal growth and episodic river inflow in order to identify the light-nutrient environment which optimizes benthic algal growth. I expected that total suspended sediment concentration was a primary control on transparency and that benthic algal productivity would increase with increasing light transparency consistent with the increasing importance of benthic algae to consumers with improved light transparency as revealed by carbon isotope ratios. Furthermore, light availability should be indirectly related to the frequency and duration of river inflow events. I predicted that benthic algal growth would be greatest where river inflow was infrequent and of low duration since phytoplankton growth might be more depressed by low levels of inorganic turbidity than benthic algal growth, meaning low organic turbidity. I reasoned that benthic algae might be better adapted to low light conditions than phytoplankton since low light conditions may persist at depth, whereas surface light may be only episodically interrupted, meaning that phytoplankton photosynthesis may be comparatively less efficient than benthic algal photosynthesis under conditions of reduced light (e.g. Sand-Jensen, 1989). Also benthic algae might benefit from settling of phosphorus-rich clay particles. I predicted that light attenuation would be greatest and benthic algal growth lowest

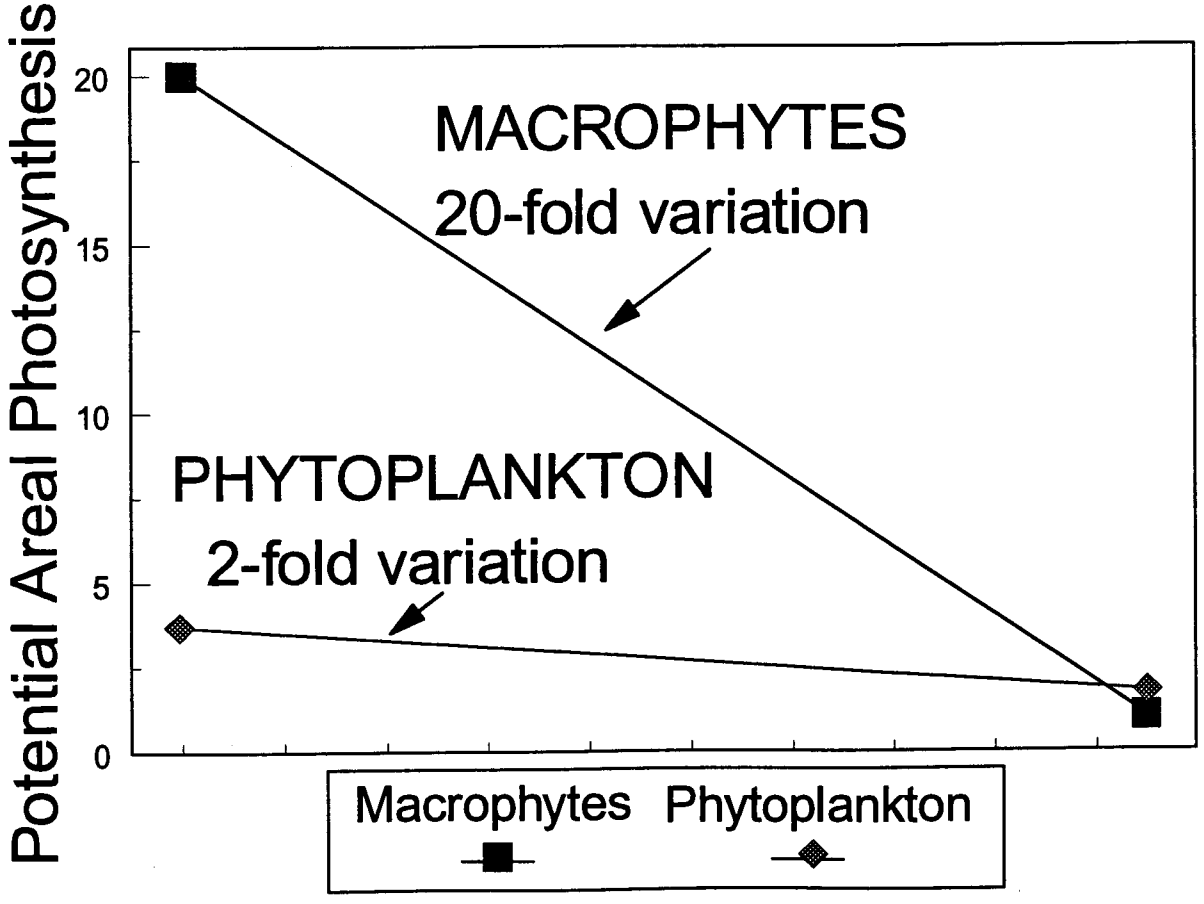
where river inflow was most frequent and of high duration due to high levels of inorganic turbidity and light attenuation. I suspected that some phytoplankton growth could be supported by nutrient flux from sediments to the water column in lakes receiving no river inflow, meaning that phytoplankton chlorophyll or organic turbidity might be high enough to reduce the light available for benthic algal growth relative to lakes receiving infrequent and low duration river inflow events.

I used limnocorrals and enriched clay substrates to clarify how the frequency and duration of river inflow events influenced benthic algal growth. I suspended artificial substrates at a 2-metre depth in limnocorrals that were dosed with sediment-nutrient additions at delivery regimes both chosen to mimic episodic river inflow to the Delta lakes during the summer period. Benthic algal response was measured as biomass accrual and community metabolism.

Figure 1.1. Conceptual diagram of the range of total net photosynthesis among the Delta lakes with varying degrees of closure corresponding to light conditions ranging from clear to turbid. The diagram is based on the extremes of primary productivity measured in selected lakes during the growing season of June through August in 1987, which were reported in an abstract for otherwise unpublished material, by Hecky *et al* (1991) (**top**).

The range of potential response, as areal net photosynthesis of macrophytes and phytoplankton, between a turbid, channel-connected lake and the clearest lakes (**bottom**).


Total Net Photosynthesis
mmoles Carbon / m2 / day
60
45
30
15
0
CLEAR
TURBID
TRANSPARENCY


Potential Areal Photosynthesis
20
15
10
5
0
MACROPHYTES
20-fold variation
PHYTOPLANKTON
2-fold variation
Macrophytes
Phytoplankton

Chapter 2 Methods and Materials

STUDY AREA

Mackenzie River

The Mackenzie River is globally distinct as one of the longest, unregulated northward flowing rivers, and is representative of a climatic extreme on the continuum of large rivers being ice-covered for a considerable portion of the year. Approximately 4200 km long the Mackenzie is the tenth longest river in the world. The Mackenzie River is the eleventh largest in mean annual discharge and the twelfth largest in basin area.

From Great Slave Lake and headwaters of major tributaries in northern British Columbia, Alberta and Saskatchewan, the Mackenzie River drains 1.79 million km^2 including some of the driest portions of Canada (Figure 2.1). Within the Mackenzie Basin annual precipitation ranges from 450 mm in southern portions to 127 mm in northern areas (Inland Waters Directorate, 1973). The river's large flow is primarily attributable to large surface area. Major tributaries include the Athabasca, rising in western Alberta, the Peace, rising in northeastern British Columbia and the Liard rising in southeastern Yukon (Figure 2.2). Of these, only the Liard lacks major lake basins, explaining the significant increase in sediment load downstream of the confluence with the Liard.

The Mackenzie River spans a large latitudinal and climatic gradient, from sub-arctic to tundra, before ultimately discharging into the Beaufort Sea. The Delta of the Mackenzie River is located (Figure 3.2) wholly within the zone of continuous permafrost.

Mackenzie Delta

The modern Mackenzie Delta is the largest Delta in Canada and one of the major northern deltas in the world covering an area approximately 20,000 km^2. North-south length is approximately 200 km and width is approximately 65 km (Figure 2.4).

Since retreat of the Wisconsonian Ice Sheet, deposition of sediment discharged from the Mackenzie Basin, and from the Peel and Rat River basins, has brought about substantial aggradation in the region of the Delta. Aggrading northwards from Point Separation, the Delta is a lake-rich environment (Figure 2.5) fed by a complex system of interconnected channels (Figure 2.5). Permafrost, which limits subsurface drainage and influences erosion within the Delta plain, in concert with climatic and hydrologic conditions have contributed to creation of the large number of freshwater lakes, ca. 25,000, which cover up to 50% of the Delta. Channels are maintained by a tendency to develop levees, when sediment-rich water spills over banks during high water.

Among the network of channels and interconnecting lakes of the Mackenzie Delta four channel types can be distinguished Mackay, 1963). Distributary channels (1) diminish as they send off distributaries, for example Big Lake Channel. River channels (2) receive tributaries, and network channels (3) link distributary and tributary systems. Two network

channels may unite to form one larger channel or one may subdivide into two. Many lakes "open" onto the channels, or the channels may "flow" through lakes. Lake channels (4) interconnect lakes with other lakes or with other types of channels. Lake channels are usually the smallest of all channels.

Threat of Environmental Disturbance

The size of the Mackenzie Basin and the lake-rich Mackenzie Delta contribute to the large and varied wildlife population associated with the Mackenzie River system (Inland Waters Directorate, 1973). The fisheries resource base includes a substantial domestic fishery in the Delta area. The Mackenzie Delta also serves as nesting habitat and staging area for water fowl, including endangered species such as trumpeter swan, and is primary habitat for muskrat, the mainstay of the local trapping industry. Barrenground caribou migrate across the Mackenzie Delta to their summer breeding grounds on the tundra.

Existing studies of the Mackenzie Delta environment have demonstrated interactions between lake hydrologic regime and biological productivity. For example, ice-induced flooding of Delta lakes is tightly coupled to lake water balance (Bigras, 1987), extent of littoral zones (Marsh & Ferguson, 1988), annual input of inorganic nutrients (Lesack *et al*, 1991) and availability of light, with substantial implications for primary production (Fee *et al*, 1988; Hecky & Guilford, 1984) and consumers. Also, seasonal input of freshwater may be critical to fish migration (Bond & Erikson, 1985). Flooding regime potentially limits primary and secondary productivity in the Delta ecosystem. It follows that alteration of flood

regime due to hydroelectric development may negatively affect the productivity of the Delta. For example, since construction of the Peace River Dam there has been a decline in the flooding of the Peace/Athabasca Delta has led to drying of lakes and wetlands and loss of highly productive ecosystems (Prowse, 1994). Further, since evaporation is greater than summer precipitation and run-off is negligible in the Mackenzie Delta (Marsh & Bigras, 1988) these lakes may be even more susceptible to reduction in frequency of lake flooding related to flow regulation.

Study of sediment regimes associated with the Mackenzie River have demonstrated that the Delta is a sink for sediments largely derived from the Liard River Basin (Church *et al*, 1987). Dams on the Liard may reduce peak flows and therefore the input of water and fertile sediments to lakes, with a potentially negative effect on biological productivity. Also, offshore oil extraction at Norman Wells, continued gas and oil exploration and production within the Mackenzie Basin, and ultimate construction of the Mackenzie Valley Pipeline increase the likelihood that sediments discharging into the Mackenzie River will carry hydrocarbon contaminants and the risk of introduction of toxins to Delta food webs.

The present study is part of a larger combined research effort by, among others, the National Hydrology Research Institute, Department of Fisheries and Oceans and Simon Fraser University. Research has been aimed at quantification of the linkages between hydrologic regime and biological consequences. The ultimate goal is to increase our ability to predict changes in the biological productivity of the Mackenzie Delta related to development within the Mackenzie Basin, and possibly to

climatic warming. Given the northern location and the lengthy north-flowing drainage of the Mackenzie River, the Delta may be particularly susceptible to the effects of global climate change, from either upstream changes in precipitation or from downstream changes in sea level (Lesack *et al*, in press). Also, warming could lead to changes in the depth and /or duration of river ice, potentially reducing the extent of seasonal flooding of the Delta lakes which is linked to the formation of ice jams in the Delta area. Accurately predicting the consequences of regional scale perturbation will require a knowledge of the fundamental biogeochemical and ecosystem processes which result in the considerable chemical and ecological variation among the delta lakes.

Delta Lakes

Typical of northern rivers where significant precipitation occurs as snow, peak flows in the Mackenzie River are during spring melt. Ice disappears from Mackenzie Delta lakes in early June, when the Mackenzie River reaches its maximum flood stage during spring break-up in response to snow melt in southern portions of the basin, and frequently to ice-jamming in northern portions, leading to extensive flooding of the Delta and intrusion of sediment-laden, nutrient-rich river water to most lakes (Bigras, 1990). Post-break-up water levels fall rapidly in main and distributary channels with a coincident drop in lake levels. From June until freeze-up in late September or early October, the surface elevation of the Mackenzie River drops by as much as 4 metres (Marsh & Bigras, 1988) and summer flow regime is a long period of gradually declining discharge. Superimposed on this falling-water hydrograph are small discharge peaks

related to sporadic rain events in the northeastern portion of the basin, i.e. the Liard River watershed. Peaks correspond to channelized inflow of turbid river water into Delta lakes, and these lakes experience reversing inflow-outflow discharge patterns dependent on fluctuations in water levels in distributary channels. This pattern of flow reversals persists until after freeze-up in late September or early October.

Biological productivity of the Delta ecosystem is largely driven by regular flooding of Delta lakes which corresponds to replenishment of nutrients for primary producers and sediment flux into lakes which reduces light availability. Lakes occur over a range of elevations relative to major distributary channels experiencing different flooding regimes which make them very different physically and biologically. Understanding critical links between hydrologic regimes and lake productivity requires knowledge of frequency, timing and duration of flooding events. Accordingly, Delta lakes have been classified by sill elevation and water levels in distributary channels. Sill elevation has been operationally defined as the highest elevation along the thalweg of the channel connecting the lake and the river channel, and have been determined for several hundred lakes by an aerial survey technique (Marsh and Hey, 1989). Sill elevations and long-term water level records for selected channels have been used to establish the flooding regime of lakes.

These results have provided operational quantification of a simple lake classification scheme proposed by Mackay (1963). No-closure lakes exchange water with main channels throughout the open water period and are defined as lakes with sill elevations lower than the one year return

period for summer low-water river levels. High-closure lakes do not flood annually and are not connected to main channels over the summer, and are defined as lakes with sill elevation greater than the one year return period for spring peak water levels. Low-closure lakes are intermediate between these two extremes, flooding each spring but disconnected from main channels for some portion of the summer, and are defined by sill elevations higher than no-closure but less than the one-year return period for spring peak water levels in the river.

Factors controlling Delta lake water chemistry have also been evaluated, on both an annual and interannual basis. Preliminary study has documented the importance of sill elevation, and corresponding pattern of frequency and duration of annual river inflow events, in controlling lake water chemistry across the Delta (Anema *et al*, 1985 & 1986.) Evaluation of heterogeneity in water chemistry as a function of both annual, and interannual flood frequency, also a function of sill elevation, substantiated the significant role of seasonal river inflow events. This work also revealed the potential importance of within lake biogeochemical processes for controlling lake chemistry, particularly for high sill lakes which do not flood on an annual basis (Lesack *et al*, 1991).

Closure status has direct consequences for primary producers. For example, in no-closure lakes which receive river inflow continuously throughout the open water period, sediment loading is high, lakes remain turbid, and phytoplankton dominates since severe light limitation restricts littoral production (Fee *et al*, 1988; Hecky *et al*, 1991). As high-closure lakes become disconnected from main channels, sediment loading is

substantially lowered. These lakes achieve much higher transparencies and are dominated by benthic producers since light penetrates to the bottom of lakes permitting extensive littoral production, and since phytoplankton become nutrient limited (Fee *et al*, 1988; Hecky *et al*, 1991). Low-closure lakes receive river inflow for short periods of time and are more variable in transparency and in the relative importance of benthic and planktonic primary producers.

Water levels, which control flooding regime of lakes, have been measured at numerous channels and lakes, but long-term records are available only for East Channel of the Mackenzie River, a major distributary near Inuvik. East Channel water levels have been applied to upper Delta lakes near Inuvik (Figure 2.6) to document the relationship between flooding regime and sill elevation. With this information, a smaller group of lakes covering a wide range of closure was selected for more intensive study, in particular South Lake, Skidoo Lake and NRC Lake (Figure 2.7).

NRC Lake has the highest closure among these three lakes, and may flood when discharge peaks in the Mackenzie River, but is isolated from Big Lake Channel, which branches off of East Channel, for the remainder of the open water period. Skidoo Lake has lower closure, receiving water from Big Lake Channel as well as several minor channels throughout most of the summer. Skidoo Lake experiences infrequent flow reversals. The majority of Delta lakes have multi-channel systems and complex flow patterns. South Lake is a no-closure lake, remaining connected to Big Lake Channel the entire open water period and experiencing upwards of twenty flow reversals. Since South Lake is characterized by a single

connecting channel much of the lake becomes transparent enough for development of macrophytes in the littoral zone and periphyton in the littoral and littoriprofundal zone (Hecky & Hesslein, 1995). Estimates of annual macrophyte production in South Lake show it to be five to ten times higher than phytoplankton production (Guilford *et al*, unpub.)

South Lake

Permanent connection and easy access from Inuvik by motor boat via Big Lake Channel and suitable depth for enclosure work made South Lake an ideal study site (Figure 2.8) for field work conducted during the open-water period of 1995.

General description

South Lake is approximately 5 km southwest of Inuvik . The lake is relatively small (0.38 $km^{2)}$ with a typical maximum depth of 4 m in mid-summer (Figure 2.9), although mean depth may reach 5 m during spring break-up and fall to less than 1 m. South Lake Channel, connecting the lake to Big Lake Distributary Channel, is short, narrow and steep-banked (Figure 2.10).

A prominent Delta is situated where South Lake Channel enters the lake (Figure 2.11). Average annual sediment accumulation over South Lake is on the order of 1 cm. Like many Delta lakes, the largest portion of the annual load, approximately 60%, is delivered during spring break-up when discharge in the Mackenzie River peaks (Ferguson, 1990), the balance delivered throughout the remainder of the open water season. Sediment distribution is disproportionate, with approximately 53%

deposited over a small area of the lake near the mouth of South Lake Channel (Ferguson, 1990). Annual sedimentation rates range from 5 mm, to less than 0.02 mm in isolated bays (Marsh & Ferguson, 1988).

Site conditions in 1995

Spring break-up was early in 1995, but still within the two week window of time considered average for break-up at this latitude. On May 26 some candle ice remained but was restricted to deeper portions of the lake. On June 11 the lake was ice-free and water level had fallen at least 2 metres. In mid-June secchi depth was 0.55 m, total suspended sediment concentration (TSS) concentration was 18 mg L^{-1}, and water temperature was 5° C. A few days later, on June 15, lake levels had dropped almost another m and transparency had substantially improved. Secchi depth was 1.15 m and TSS concentration was 5 mg L^{-1}. Water temperature had increased considerably, to 16° C, except for bottom water which was only 7. Throughout the remainder of the summer maximum lake depth fluctuated between 2.5 and 3.5 m in response to fluctuations in water levels of main channels.

A consequence of low water levels, the northeastern end of the lake (heretofore referred to as Front Bay) in closest proximity to Big Lake distributary, was nearly isolated from the central portion of the lake through July and August. A narrow Inner Channel (Figure 2.12), approximately 2 m wide and less than a m deep provided the only access to central South Lake where experimental enclosures were located . The northwestern side of Front Bay was the site of an extensive growth of *Equisetum.* The southeastern side was nearly bare sediments (Figure

2.13), suggesting that in most years this area is covered with water. Inner Channel as well as the portion of the lake immediately southwest were sites of extensive growth of the aquatic macrophytes *Potamageton, Carex* and Ranunculaceae. Further southwest of Inner Channel, the lake deepens and macrophytes become more sparse except at the lake perimeter. The littoriprofundal zone is colonized by epipelic algae. The Inner Channel allowed easy detection of flow reversals because macrophytes were always bent in the direction of the current. Surface currents were sometimes misleading reflecting only direction of the prevailing wind rather than direction of net movement of water. South Lake Channel was always turbid during inflow events, and clear when water levels temporarily stabilized or during outflow from the lake.

METHODS AND MATERIALS

Limnocorrals

Construction and installation

In order to experimentally manipulate river inflow under near-natural environmental conditions, a series of replicated *in situ* limnocorrals constructed of polyethylene film (cf. Goldman, 1962) were used to enclose a portion of the water column and lake bottom. The basic design of limnocorrals is that of a long tube, approximately 3 m in diameter and 4 m in length with buoyant material inserted in a sleeve at the top of the tube to provide flotation and a barrier against waves. Tubes were constructed of three 5 m x 3.3 m sheets of 6 ml UV-resistant translucent polyethylene and taped together lengthwise. Two seams were taped inside and out with 5.5 cm wide water resistant Poly Patch® tape supplied by *Sharp &*

Sons in Langley, BC. The third seam was overlapped 2.75 cm and secured with two-sided water resistant RS2000® tape, supplied by *Rainbow Industrial Products* in North Vancouver. The third seam was left open near the top so that approximately 15 cm could be folded down to form a sleeve by taping the upper edge to the enclosure wall, with two-sided RS2000 tape. A 3.2 m x 16.5 cm x 3.5 cm strip of closed cell foam, supplied by *Allfoam* of Richmond, BC, was inserted into the sleeve. A hoop formed of three lengths of PVC pipe (OD = 1.4 cm, length = 3.65 m) coupled with copper tubing (length = 10 cm) crimped in place, was attached to the inside of the corral approximately 1.2 m below the foam collar, to retain the shape of the cylinder top. The hoop was held in place by six 10 cm x 6 cm poly belt loops attached to the tube wall with two-sided RS2000® tape. Finally, a length of 0.5 cm galvanized cable was woven through the poly one metre from the tube bottom of the tube. The cable functioned to give the bottom of the enclosure some shape, and lead weights were hung over the cable and pushed into sediments to anchor limnocorrals to the lake bottom.

Limnocorrals were constructed completely on land, collapsed to a circular bundle, tied with ropes, then stacked eight high in a tarp large enough to securely wrap them. Two pallets were placed in the center of each load to provide weight before bundles were air-lifted by helicopter to a clearing on a small island in South Lake (Figure 2.14). Limnocorrals were installed over a ten day period in early June by moving four at a time downslope on a tarp and out into the water, and then towing to an appropriate depth off-shore, i.e. 3 m contour (Figure 2.14). One at a time

corrals were positioned, three strips of lead approximately 10 cm x 30 cm folded over the cable, ropes untied and the tube allowed to settle to the lake bottom. During periods of high wind (>20 km) we had only limited control over positioning. After four corrals were installed in this manner , a SCUBA diver submerged, shoved the ends of lead weights into sediments, and piled sediments and additional weights onto the lip or the tube bottom to ensure a good seal with the bottom and adequate anchoring. Because of the flexibility of the cable, dimensions at the bottom of the tube tended to be smaller than the top.

During the course of the experiment water levels in South Lake repeatedly fell and rose on the order of 1 m. When lake levels fell, corral walls had a tendency to billow inwards. To compensate the tops of enclosures were rolled down and this process was reversed when water levels rose.

Experimental design and manipulation

The experiment consisted of five triplicated treatments assigned randomly. The experiment controlled for load, i.e. load to the Control was 0, and addressed the frequency question, i.e. high of low sediment and nutrient loads were delivered once a week or three times a week. A planned contrast between low-infrequent dosing and high-infrequent dosing addressed the loading question. Target weekly sediment and nutrient additions, in units of mg L^{-1}, were chosen to typify high and low sediment and nutrient concentrations typical of South Lake, and lakes in the Inuvik area, during the low flow open-water period as reported by Anema *et al* (1990a & 1990b) . Sediment-nutrient additions to individual

corrals were calculated based on their depths at the start of the experiment by multiplying individual corral volume in litres times the target additions. Among corrals depth varied as much as 0.75 m. To simulate the natural variability of episodic river inflow, low and high target additions were delivered as either a single pulse or distributed incrementally over three days. Total weekly addition was the same among low, and among high treatments. Also, dose per day was the same for Low-Pulsed and High-Distributed treatments, but load per week was different. Target additions and delivery regimes are detailed in Figure 2.15. Manipulations began on July 8 and continued until August 21. Based on a 7-day week, corrals were dosed on Day 4 (Pulsed) , or on Days 1, 4 and 6 (Distributed), and were sampled weekly on Day 3 (day before dosing), with the exception of the last sampling day (August 9) which occurred on Day 5 (day after dosing). After August 9 we began pulling corrals out of the lake, but continued sediment-nutrient additions to those remaining.

Sediment-nutrient additions were composed of wet sediments collected from the banks of South Lake Channel, stock solutions of KNO_3, KH_2PO_4 and prepared in the field (Figure 18) with water withdrawn from individual enclosures, and were added as a well-stirred slurry mixed with a paddle. Nitrate represents the most prevalent form of nitrogen in Mackenzie River water. In order to measure wet sediments in the field, 50 ml samples of wet sediment were oven-dried at 60° C to constant weight to establish a conversion factor between volume of wet sediments and dry weight. Each dosing day a 50 ml sub-sample of sediment was oven-dried to constant weight and weighed (Appendix 1). Over the course of the

experiment average error in converting volume to dry weight of sediment was 6%, where error = {[(actual weight/volume rated weight) - 1] x 100}.

Grain-size was determined for two composite bank sediment samples by hydrometric methods (Klute, 1986).

Sampling and analyses

Since it was expected that sediment additions would have a direct effect on the light environment of corrals, I used several methods to measure transparency on a weekly basis. Secchi disk depth is the easiest transparency measurement to make. A secchi disk (diameter = 30 cm, with quadrants painted alternately black and white) was lowered into the water column until it disappeared, then raised until it reappeared, and the average of the two depths used as an estimate of secchi. The usefulness of this technique was limited by the shallow depth of South Lake, since the disk often encountered the bottom before disappearing. TSS concentration was determined weekly for 1-L water samples withdrawn from the center of the corrals by suspending a weighted plastic bottle to a 1-m depth. Samples were filtered onto a pre-weighed Gelman® Type A/E 47 mm glass fiber filter, dried to constant weight at 60° C, and TSS concentration estimated from dry mass divided by sample volume. TSS concentration may be of limited usefulness at low to moderate transparency (Fee *et al*, 1988). Vertical extinction of photosynthetically active radiation (PAR) was measured periodically with a PAR meter (Licor® photometer equipped with an underwater quantum sensor), suspended from a sampling pole into the center of corrals. To avoid shading the sensor, readings were taken on the sunny side of the sampling raft, and followed the protocol of Fee *et al*

(1988). First, a measurement in air was made. The sensor was then lowered to lake bottom and measurements made here and at increments of 0.5 m, the final underwater measurement taken at subsurface. Another measurement was made in air, and if this differed from the mean of initial and final air measurements by more than 10% (because of variations in cloudiness), results were discarded and the procedure repeated. Finally, vertical light extinction was characterized as the extinction coefficient , η, where

$$\eta = (\ln I_0 - \ln I_z)/ z \quad , \qquad (1)$$

and I_0 is subsurface PAR and z is depth, and alternatively as the negative slope of the regression of $\log_e$ light as a function of depth. Both methods produced nearly identical results. Extinction profiles are the preferred method of measuring transparency since results have similar precision for both very turbid and very clear water.

To determine the instantaneous effect of sediment-nutrient additions on the light and nutrient environment , on a single occasion one corral per treatment level was sampled for TSS concentration, nutrients, secchi depth and light extinction before and after additions.

Since phytoplankton chlorophyll, as well as inorganic particles, e.g. suspended sediments, can contribute to light extinction, ambient chlorophyll *a* concentrations were measured weekly. A 1-L water sample was collected and filtered in the same manner as for TSS concentration. Filters and filtrate were then placed in a glass tissue grinder and chlorophyll *a* extracted in buffered 90% acetone according to methods in Wetzel and Likens (1991). After extraction, chlorophyll *a* and its

degradation products were measured colorimetrically with a spectrophotometer, according to monochromatic methods of Lorenzen (1967).

Since nutrient additions were expected to stimulate phytoplankton growth relative to controls, nutrient concentrations were followed over the course of the experiment. Water samples were collected as above in 500 ml HDPE bottles rinsed with sample, and filtered as above into new HDPE bottles. Within 24 hours phosphate was determined colorimetrically after Murphy and Riley (1962) by molybdenum blue-ascorbic acid method. the limit of detection for phosphorus determination by this method is 0.01 *u*M according to Wetzel & Likens (1991). Ammonium was determined by the phenol-hypochlorite method (Solarzano, 1969). The limit of detection for ammonia determination by this method is 0.2 *u*M according to Strickland & Parsons (1972). Nitrate was reduced to nitrite by cadmium-copper reduction (Wood *et al*, 1967) and measured colorimetrically by the diazotization technique according to Strickland and Parsons (1972). The limit of detection for this method of nitrate determination is 0.1 *u*M according to Wetzel & Likens (1991).

To determine if corrals generally reflected physical properties of South Lake, temperature profiles were measured periodically in South Lake and selected limnocorrals, with a YSI® Model 58 Oxygen meter.

Data analysis

Significance tests have been applied to the data in order to test the hypothesis put forth about the expected effect of sediment-nutrient additions on benthic algal growth. Put another way, tests have been

conducted to remove any ambiguity that might exist in the interpretation of the effect of treatments. Before giving the details of the tests, the type and the magnitude of error that I considered acceptable are discussed.

It was desirable to keep the Type II (β) error rate low, that is to reduce the probability of not finding a treatment effect when there actually is an effect. An important consequence of keeping β small is the increase in the power of the test, 1- β, or the probability of detecting a real treatment effect. By contrast, when β error is high, power is low and negative results (non-rejection of the null hypothesis) are ambiguous. A second less desirable result of keeping β small is the increase in the risk of making a Type I (α) error, or the probability of finding an effect when in fact there is none.

Overall, power is a function of α, the ratio of squared effect size (magnitude of difference between means) to variance, and sample size, *n*. There are two important implications of the use of limnocorrals for power of the test. First, sample size, *n*, is low since manpower and costs were limited, and second, variance may be high relative to effect size as a result of the stochastic behaviour of the limnocorrals which mimic the inherent complexity of natural systems. Left then may be a single option for keeping the β error rate low, specifically, that of permitting α to be high. In some cases a Type I error to be less serious then a Type II error and I expect that this tradeoff may result in useful insight into the behaviour of the complex system being manipulated and generate hypotheses around which future studies can be organized. A probability of 0.05 or less has been considered evidence of a treatment effect. A probability as low as

0.1 has been interpreted as suggesting a pattern or trend but not a causal relation.

Among the variables measured weekly in the limnocorrals, specifically TSS and phytoplankton chlorophyll, observations from triplicate treatments could depart substantially from normality, and homoscedasticity (equality of variance) among treatments was not consistently observed. These conditions indicated that nonparametric methods, as opposed to parametric, might be the most suitable since their power is less affected by failure of the assumptions associated with parametric tests. The Kruskal-Wallis test (nonparametric) was conducted to test the effect of treatment on TSS, phytoplankton chlorophyll, and to test for differences among means for all possible pairs of treatments and the Control (single grouping factor; single degree of freedom tests). In the non-parametric case, all possible multiple comparisons can be made without risk of bias due to the non-independence of results which is generally guarded against by lowering the α of parametric tests, since nonparametric tests are inherently conservative (Sokal & Rohlf, 1981). For comparative purposes, in addition to non-parametric tests, a factorial analysis of variance with repeated measures (Week) was conducted to test for main effects of delivery regime, and sediment-nutrient additions on TSS and phytoplankton chlorophyll (test degrees of freedom = 2).

Light reduction in the limnocorrals receiving sediment-nutrient additions was indicated by the differences in average light extinction between the treated limnocorrals and the Control, and among the various treatment regimes. The Kruskal Wallis test was used to test for effect of treatment

on average light extinction (weeks were treated as replicates), and associated multiple comparisons were conducted to test for differences in light extinction between all possible pairs of the treatments and the Control (single grouping factor; single degree of freedom tests). In addition to testing the differences in average light extinction among the treatments and the Control, an equally important question was whether differences could be considered biologically significant, or in other words, whether the difference in the size of the effect on light extinction among treatments and the Control was large enough to have significantly affected benthic algal growth in the limnocorrals. A review of studies where sediments were added to limnocorrals (cf. Guilford *et al*, 1987; Hecky, 1984; Hecky & Guilford, 1984) indicated that differences in light extinction of 0.3 m^{-1} may have a biologically significant effect on production of phytoplankton. Here, a difference in light extinction of at least 0.3 m^{-1} was considered to be biologically significant to benthic algal growth.

Artificial substrates

Preparation and nutrient loading

Epipelic algae- periphyton which grows on and in soft substrates, is difficult to separate from its substrate for the purposes of quantifying growth characteristics (Eaton & Moss, 1966). To circumvent this problem, improve reproducibility, and provide a replicable unit for quantifying algal growth and photosynthesis, I used porous clay saucers as a substrate for algal growth. Periphyton that colonizes clay tiles has been shown to be representative of communities that colonize natural substrates (Tuchman & Stevenson, 1980; Lamberti and Resh, 1985). Clay saucers have the

added advantage of being an inert surface, in contrast to natural substrata where processes unrelated to the metabolism of the periphyton community may contribute to respiratory demand. Finally, they can be enriched to provide nutrients for algal growth, replacing natural substrata as source of nutrient supply.

Fairchild *et al* (1985) have demonstrated that porous, clay containers, filled with nutrients, sealed and placed *in situ*, slowly release nutrients over many weeks and promote establishment of periphyton communities on their outer surfaces. In this experiment, clay saucers (bottom diameter = 11 cm., height = 2 cm.) with a surface area of 0.025 m^2 were initially heated with a propane torch to burn off a silicone sealant (into which saucers had been dipped by the supplier to reduce surface porosity), soaked in deionized water for two days to remove any ions associated with the clay, then air dried. In order to attach the lid of a disposable petri dish, a groove was ground into the saucer rim. A 0.5 cm hole was ground into each saucer bottom for filling, and later plugged with a stopper. Plastic lids were attached to saucers with silicone, forming a 350 ml chamber that was filled with a warm solution of 1.5% agar, 0.5 M phosphate and 0.5 M nitrate. Fairchild *et al* (1985) have demonstrated that laboratory nutrient release rates (RR) (uM day^{-1}) from chambers fertilized with 0.5 M nitrate are described by

$$\ln(RR) = 9.31 - 0.07(Days), \quad (2)$$

($r^2 = 0.59$), and for 0.5 M phosphorus are described by

$$\ln(RR) = 5.83 - 0.04(Days) \quad (3)$$

($r^2 = 0.87$). In the lab, one enriched saucer was immersed in deionized water which was replaced regularly and analyzed for nutrients over a three week period to ensure that nutrients were diffusing freely.

Placement

It was necessary to incubate substrates at a depth where light was sufficient for net photosynthesis. The depth of 1% surface light or compensation point in corrals with the lowest transparency, i.e. High-Distributed, placed a theoretical constraint on substrate depth, since net photosynthesis is assumed to be "0" below this light level. However, due to high settling rates and shallow depth, sufficient light penetrated to the bottom of all corrals, and the maximum depth at which substrates could be incubated was the depth of the shallowest corral, approximately 2.2 m. To prevent disturbance of bottom sediments and to reduce grazer accessability, substrates were incubated at 2 m. For easy retrieval, six or seven clay saucers were attached with light gauge wire to 1 m x 1 m chicken wire trays reinforced with strips of wood, spaced approximately 10 cm from each other (Figure 2.16). Lightweight cord was attached to tray corners, then gathered together and tied to a single ring approximately 1 metre above the tray. A length of cord attached to the ring and a float suspended the tray at a 2 m depth. A second longer rope tied to the ring and a smaller float allowed retrieval of trays with a sampling pole extended from a small raft pulled along side limnocorrals. An anchor attached to each tray prevented trays from drifting off-center. Prior to suspension in limnocorrals, trays were suspended in the lake for one day to wash off any nutrients that may have collected on the outside of saucers. Trays

and saucers were positioned in the center of limnocorrals on July 8, 1995. Over the course of the experiment, winds greater than 15 km hr^{-1} tended to push the tops of enclosures in the direction of the prevailing wind, giving the appearance that saucers were not centered. However, enclosures returned to a vertical position soon after winds died down.

Nutrient flux from sediments

In order to verify that the rate of nutrient release from enriched clay saucers realistically reflected the potential of sediments to supply nutrients for growth of benthic algae, and to evaluate the extent to which enriched substrates may have represented a source of nutrients to the overlying water column, pore-water samplers were deployed at three sites to measure the concentration gradient of nutrients across the sediment-water interface and ultimately determine nutrient flux rates from sediments. Interstitial sediment waters are frequently measured to characterize fluxes at the sediment-water interface because they are considered sensitive indicators of incipient diagenetic change, and their chemical analyses are generally less ambiguous than chemical analysis of sediments (Berner, 1980). Plexiglas® "peepers" (Hesslein, 1976) with 10 ml cups were filled with distilled deionized water and sealed with Spectra/Por® Molecularporous dialysis membrane (regenerated cellulose). This high molecular weight cut-off membrane eliminates the need for filtering since particulate matter is excluded. Peepers (approximately 40 cm in length) were inserted remotely, approximately 30 cm into sediments such that several cells were left exposed to the overlying water column, and allowed to equilibrate for two weeks. Fifteen days is considered adequate

equilibration time for dissolved chemical species in warm sediments (Carignan, 1984). Peepers were transported to the lab and samples were withdrawn with a syringe under aerobic conditions, diluted and analyzed colorimetrically within 12 hours as previously outlined.

Concentration gradients across the sediment-water interface represent only a snap-shot in time, but if certain assumptions are met, can be used as an indirect measure of diffusive flux rates of nutrients from sediments to the overlying water column with Fick's first law of diffusion (Crank, 1975):

$$\partial N/\partial t = - \varnothing D_s (\partial C/\partial z) \quad (4)$$

where

$\partial N/\partial t$ = diffusion flux in sediments per area per unit time

$\partial C/\partial z$ = derivative of linear portion of nutrient profile

D_s = coefficient of molecular diffusion for sediments (Li & Gregory, 1974), and

$\varnothing$ = sediment porosity for South Lake surface sediments.

Sediment porosity was calculated as follows (Engelhardt, 1977),

$$\varnothing = M_W / (M_W + M_S)\ \varphi \quad (5)$$

where

M_W = mass of water

M_S = mass of sediment, and

φ = average density of dry solids (a constant equal to 2.2 g cm^{-3}).

The primary assumption which must be met in order to calculate nutrient flux from sediments as a function of diffusion, is that a boundary layer has formed at the sediment-water interface, as a result of decreased

turbulence near lake bottom. Consequently, ions must pass through this layer by diffusion. A second assumption is that bioturbation and groundwater flux into or out of lake sediments are negligible, such that molecular diffusion becomes the rate-limiting diffusive process at the sediment-water interface. I did not measure boundary layer thickness, which generally varies between 500 and 1000 *u*m in lakes. The pore-water samplers used here, with a resolution of 1 cm, are considered adequate for measuring concentration gradients across a boundary layer of this magnitude.

Periphyton sampling and analysis

Starting on 25 July, five saucers were retrieved at once, one per treatment level, by pulling a tray slowly to the surface after threading the rope attached to the small float through a hook at the end of the sampling pole. While submerged, the tray was pulled close enough to the boat to allow the wires holding a saucer to be carefully clipped. The removed saucer was placed immediately in a Tupperware® container filled with enclosure water and stored in a cooler.

In order to measure community metabolism of periphyton associated with artificial substrates by changes in dissolved oxygen (DO), a single clay substrate was placed in a cylindrical Plexiglas® chamber, approximately 4.4 L, (walls = 0.95 cm thick, diameter = 20 cm, height = 20 cm) (Rodgers *et al*, 1978) (Figure 2.17). Water tight Plexiglas® chamber lids housed a small submersible pump in order to mix chamber water by recirculation, prior to withdrawing water samples. During actual incubations water was not circulated in order to simulate static water

conditions, considered characteristic of lake substrata (Stevenson & Glover, 1993). Pumps were powered by a 12-volt battery and speed was controlled with a "pulse width proportional DC motor speed control" connected to an ammeter which allowed average current to a motor to be held constant. This system resulted in achievement of approximately equivalent flows from motors with random variation in resistance. By operating at approximately 85% efficiency, the speed control device eliminated frequent recharging of the battery. To allow simultaneous injection and extraction of water samples with 60 ml syringes a pair of sample ports equipped with three-way stop-cocks were installed in the chamber lids.

For deployment, chambers were held in a weighted basket made of light cord and suspended from a clear 1-L float (Figure 2.18). Because it was necessary for all incubations to be at one fixed light level, all chambers were suspended in South Lake. This light level was theoretically constrained to the light level experienced in control corrals at a 2 m depth. Since light levels in South Lake were nearly identical to those in the control, chambers were incubated at a 2 m depth.

Dissolved oxygen (DO) changes provide a sensitive and reproducible method for direct evaluation of community metabolism. In order to quantify benthic algal productivity DO concentration was measured at the beginning and at the end of each light and dark incubation period. A reduced volume technique, for the modified version of Winkler methods developed by Carpenter (1985), was developed to minimize the amount of water extracted and replaced from chambers while maintaining

measurement accuracy of plus or minus 1%, and an acceptable titrant resolution with a 2-ml Gelmont® titrant dispenser. Under ideal conditions of sampling, fixation, and titration, DO can be as precise as 0.02 mg/L, however these conditions are rarely met in experimental situations, and precision deteriorates as a result (Wetzel & Likens, 1991).

In the field, chambers were submersed 20-L pails while lids were applied (Figure 2.19). While submersed, two 60 ml syringes filled with water and voided of air bubbles were attached to stop-cocks mounted on chamber lids. One syringe was emptied by flushing water out the stop-cock side port. Just as the syringe emptied, the side port was closed and the port leading inside the chamber was opened. Approximately 10 ml were flushed from the second syringe before closing the side port and opening the chamber port. Water was re-circulated for 5 to 7 minutes and then a 51-52 ml sample was extracted from the chamber coincident with injection of 51-52 ml. The now empty syringe was left in place. Before removing the full syringe from the stop-cock the inner port was closed. Once removed, the sample syringe was immediately inverted, reduced to exactly 50 ml and a three-way stop-cock attached for the purpose of adding reagents. Reagent-filled 10 ml syringes were sequentially attached to the stop-cock, air bubbles removed coincident with flushing the headspace, and 0.7 ml drawn into the sample syringe using the sample plunger and calibrations on the 10 ml syringe, as per the Winkler protocol. The stop-cock was rinsed thoroughly with water between reagents. After all reagents had been added the stop-cock was removed, the open end of the syringe sealed with Parafilm ®, and the inverted syringe placed in a

test-tube holder, and stored in a darkened box for the trip to the lab (Figure 2.20). Before deploying the chamber *in situ*, a second water-filled syringe voided of air bubbles was attached to a chamber lid stop-cock. Photosynthesis and respiration were measured sequentially, rather than simultaneously, for a single substrate. Therefore a single water sample represented DO at the end of a light incubation and the beginning of a dark incubation. Respiration was measured by covering chambers with three black garbage bags and resuspending. At the end of a sequential photosynthesis/respiration run, chambers were pulled slowly to the surface and submersed immediately in a 20-L pail. After mixing, a final water sample was withdrawn and DO fixed immediately. Titrations to determine DO were completed at the lab within 24 hours.
At the end of each productivity sequence, saucers were removed from chambers to Tupperware® containers and stored in the dark for the trip back to the lab, where algae was removed for chlorophyll analysis.

In order to measure biomass accrual on clay substrates, the bottom and sides of saucers were carefully brushed with a hard-bristled scrubber to remove periphyton, and rinsed copiously with deionized water. The volume of the resultant slurry was recorded, including any water in the Tupperware® container and algae or organisms dislodged from the saucer, then mixed vigorously, and a 50 ml subsample withdrawn for chlorophyll analysis. Chlorophyll samples were filtered onto a Gelman® Type A/E 47 mm glass fiber filters at low vacuum pressure to avoid damaging chloroplasts. Filter papers were folded in half, placed in small petri dish and wrapped in tin foil. When chlorophyll could not be extracted

immediately filters were frozen, however frequently chlorophyll analysis was run the same day. Chlorophyll pigments were extracted in 90% buffered acetone as per Wetzel & Likens (1991). Chlorophylls *a*, *b*, and c_1 and c_2 were measured spectrophotometrically according to trichromatic methods of Jeffery & Humphrey (1975) and carotenoids as per modifications for algae harvested from sediments (as opposed to phytoplankton harvested from the water column) according to methods of Strickland and Parsons (1972). Chlorophyll degradation products, i.e. a variety of phaeopigments, were measured spectrophotometrically for chlorophyll *a* according to methods of Lorenzen (1967). Analysis for degradation products of other chlorophylls was not done, since this requires chromatographic methods which are considered too tedious for routine analysis of large numbers of samples (Strickland & Parsons, 1972). Further, Strickland & Parsons (1972) consider a measure of non-active chlorophyll *a* as sufficient in terms of the quantity of phaeopigments present. Algal biomass is reported as the sum of all chlorophylls measured, corrected for degraded chlorophyll a. Acetone extraction methods are not as sensitive as fluorometric determination but are fully satisfactory for periphyton samples which are nearly always much more concentrated relative to phytoplankton samples. A more detailed description of the detection limits for a variety of chlorophyll pigments is given by Strickland & Parsons (1972)

Net photosynthesis, and respiration were computed as O_2-change m^{-2} hr^{-1} during light and dark incubations, respectively. Gross productivity was computed by adding dark respiration to net

photosynthesis. It was assumed that dark respiration was equivalent to light respiration, and this simplifying assumption is usually reasonable for periphyton communities (Doyle, 1991). Assumptions and errors associated with measurements of primary productivity by the O_2-change method are more fully discussed by Wetzel & Likens (1991). Biomass specific rates of net and gross photosynthesis were computed by dividing rates of O_2-change by total algal chlorophyll, for corresponding clay substrates. Radiation data recorded at the Inuvik airport was used to normalize photosynthesis rates for incident light, after correcting for light attenuation at depth.

For comparative purposes, O_2 units were also converted to carbon units with photosynthetic and respiratory quotients (PQ and RQ). Studies of algal production often assume that these quotients are both equal to 1.0 (Carpenter, 1985), although deviations from theoretical values, e.g., PQ > 1, and RQ < 1, are not uncommon (e.g. Doyle, 1991). I have followed the protocol described by Wetzel and Likens (1991), i.e. PQ = 1.2 and RQ = 1.0.

In conjunction with a project to reconstruct paleoflooding of the Mackenzie Delta Murray Hay, a student of J. Smol's at Queens University, has identified the diatom species associated with clay saucers from each of the limnocorrals, for an enriched and unenriched clay saucer suspended in South Lake, and for an unenriched clay saucer anchored on the lake bottom at South Lake.

Data analysis

Periphyton biomass data for a series of substrate exposures of increasing duration for each treatment level was plotted and instantaneous rate of periphyton growth calculated as the derivative of slope for colonization, Day 0 to Day 23, and exponential growth stanzas, Day 23 to Day 34.

Factorial analysis of variance with repeated measures (Day) was conducted to test the effect of treatment (single grouping factor; test degrees of freedom = 4) and the main effects of delivery regime (pulsed vs distributed) and sediment-nutrient additions (high vs low) on benthic algal biomass over the course of the experiment and on a per day basis (test degrees of freedom = 2). A planned contrast to test the loading question was conducted between the Low-Pulsed and the High-Distributed where daily dose was equivalent but load per week was different (single degree of freedom test). The Fisher's l*east significant difference* test was conducted to test differences among means on Day 34 for all possible pairs of the treatments and the Control (single grouping factor; single degree of freedom tests). Finally, to test simultaneouly for the effect of sediment-nutrient additions, delivery regime and the interaction between these two factors on benthic algal biomass over the course of the experiment and on a per day basis,a factorial analysis of variance with repeated measures (Day) was conducted with the Control eliminated from the analysis (single degree of freedom tests)

The Kruskal-Wallis test was conducted to test the effect of treatment on areal net photosynthetic rates normalized for incident light (days were

treated as replicates) and to test the differences among means for all possible pairs of the treatments and the Control (single grouping factor; single degree of freedom tests).

Figure 2.1. Map of the Mackenzie Basin, approximately 2 million km^2, spanning a large latitudinal gradient and including portions of British Columbia, Alberta and Saskatchewan (Mackenzie Basin River Committee, 1981).

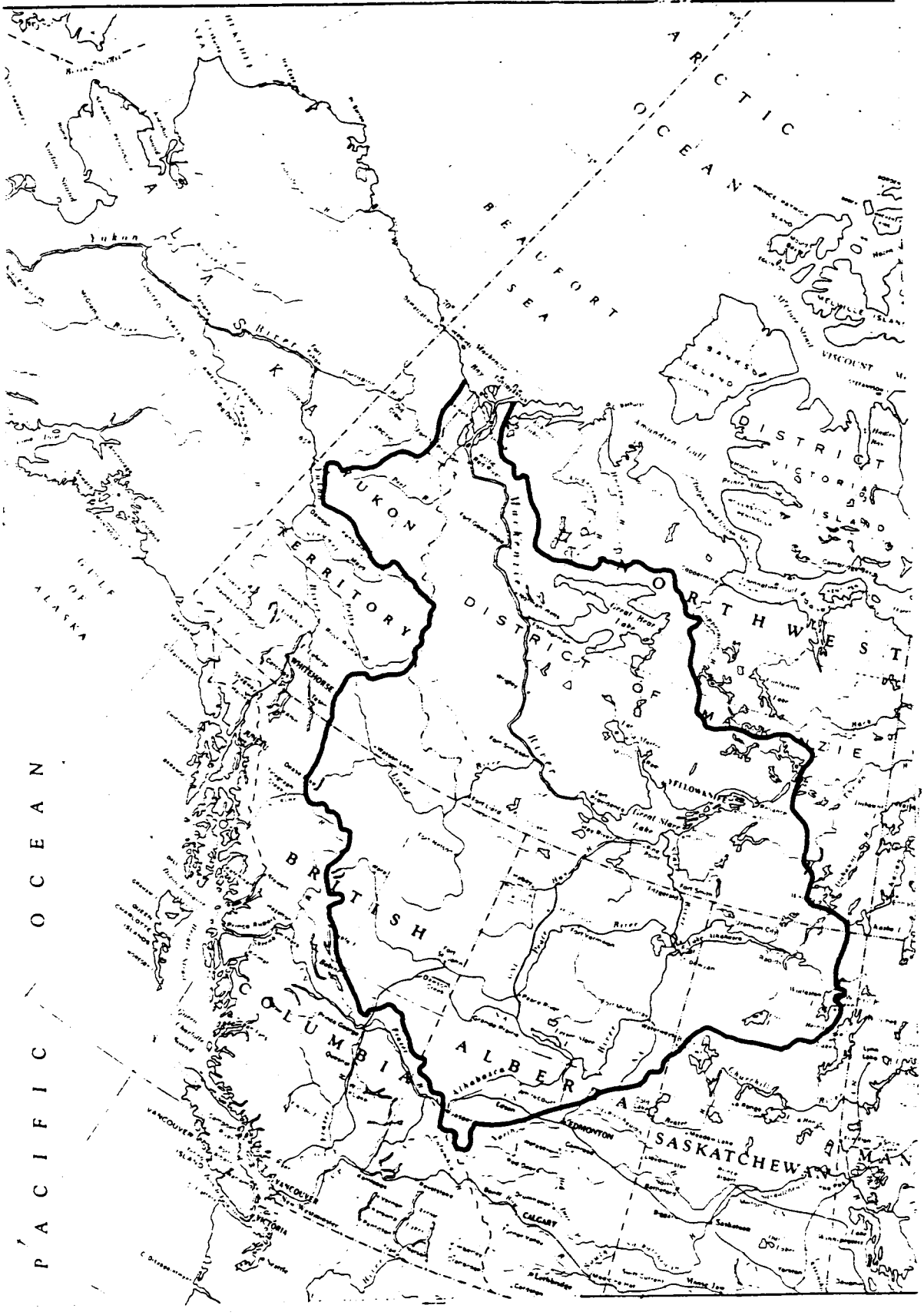

ARCTIC OCEAN
BEAUFORT SEA
ALASKA
Yukon
YUKON TERRITORY
DISTRICT OF MACKENZIE
NORTHWEST TERRITORIES
DISTRICT OF VICTORIA
BRITISH COLUMBIA
ALBERTA
SASKATCHEWAN
PACIFIC OCEAN
GULF OF ALASKA
WHITEHORSE
YELLOWKNIFE
EDMONTON
CALGARY
VANCOUVER
VICTORIA

Figure 2.2 Map of the Mackenzie River system, the largest in drainage area in Canada and the longest in Canada. Major tributaries are the Peace, Athabasca and Liard Rivers (from left to right) (Information Canada, 1973).

Figure 2.3. Map of the Mackenzie Delta, located at the mouth of the river near the Beaufort Sea and located within the zone of continuous permafrost (Information Canda, 1973).

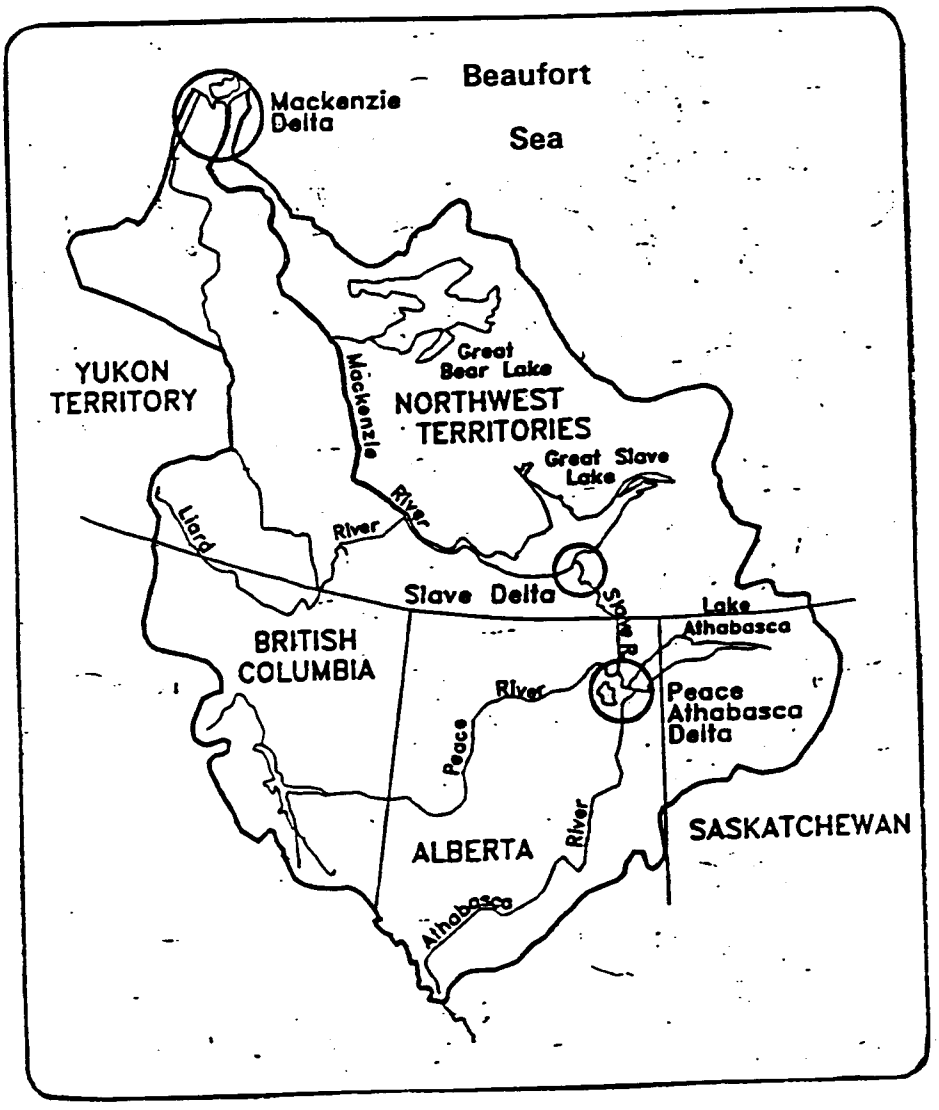

Beaufort
Sea
Mackenzie
Delta
YUKON
TERRITORY
Great
Bear Lake
NORTHWEST
TERRITORIES
Mackenzie
River
Great Slave
Lake
Liard
River
Slave Delta
Slave R.
Lake
Athabasca
BRITISH
COLUMBIA
River
Peace
Athabasca
Delta
Peace
River
ALBERTA
SASKATCHEWAN
Athabasca

Figure 2.4. Map of the main channels of the Mackenzie Delta and features adjacent to the Delta (Fee *et al,* 1988).

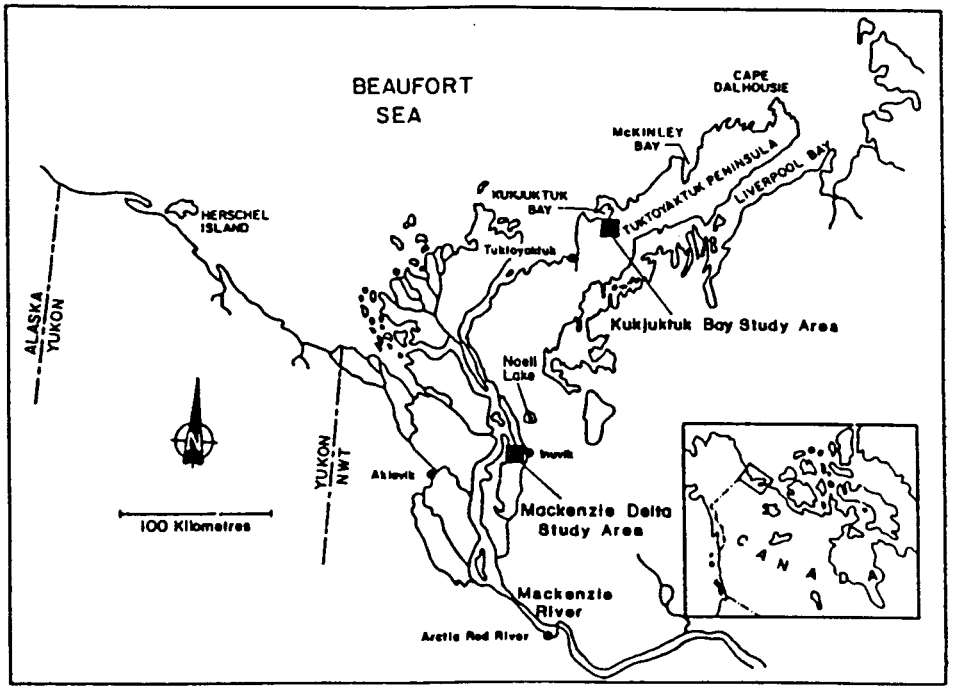

BEAUFORT
SEA
CAPE
DALHOUSIE
McKINLEY
BAY
KUKJUKTUK
BAY
TUKTOYAKTUK PENINSULA
LIVERPOOL BAY
HERSCHEL
ISLAND
ALASKA
YUKON
Tuktoyaktuk
Kukjukhuk Bay Study Area
Noell
Lake
YUKON
N.W.T.
Inuvik
Aklavik
100 Kilometres
Mackenzie Delta
Study Area
Mackenzie
River
Arctic Red River
CANADA

Figure 2.5. Aerial view of the lake-rich Mackenzie Delta environment (**top**), a complex system of ca. 25,000 lakes and a convolution of interconnected channels (**bottom**) (photos by W. Kolenchuk).

Figure 2.6. Map of selected lakes of the upper Mackenzie Delta near Inuvik (Fee *et al*, 1988).

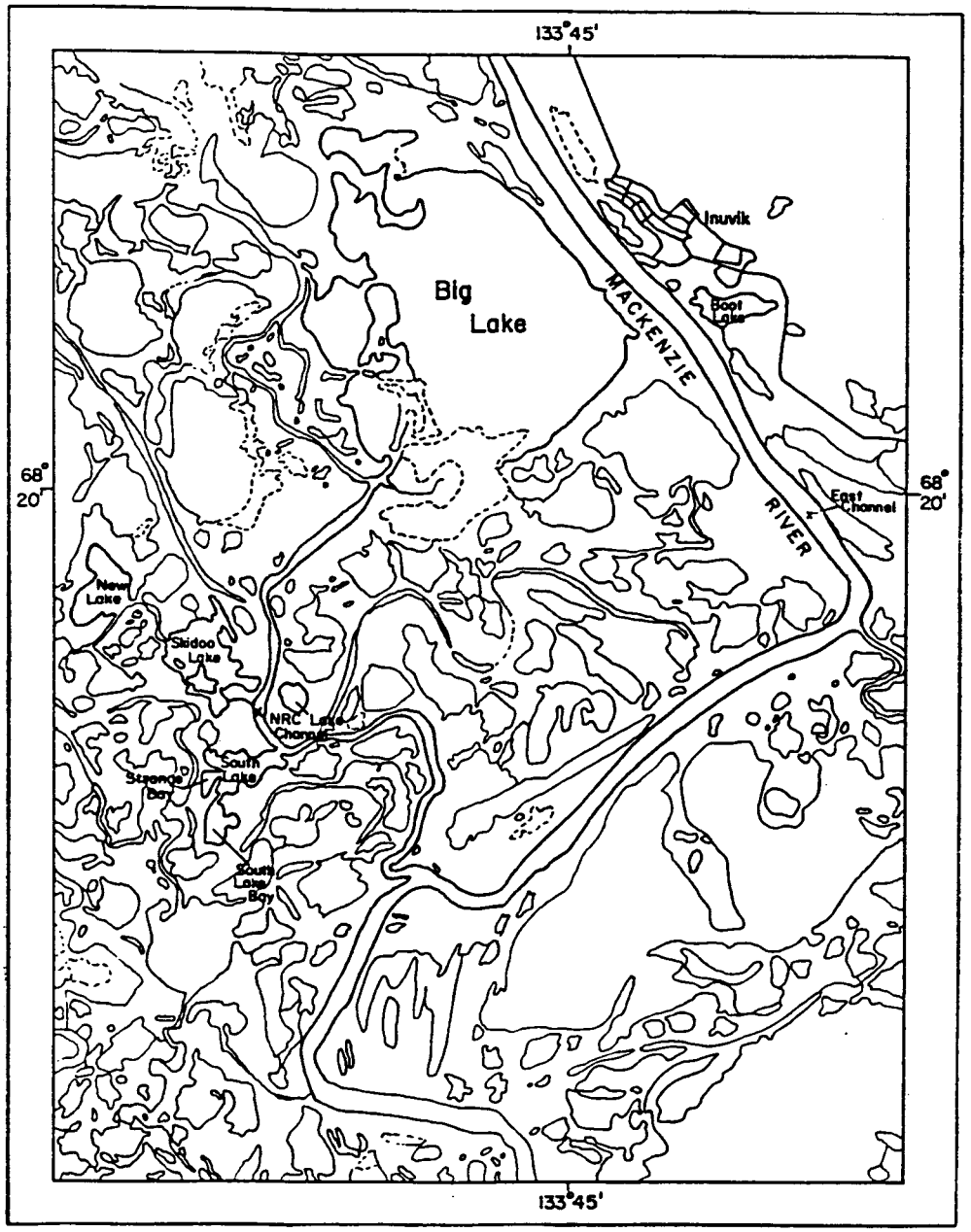

133°45'
Inuvik
Big
Lake
MACKENZIE
RIVER
Boot
Lake
68°
20'
East
Channel
New
Lake
Skidoo
Lake
NRC Lake
Channel
South
Lake
Strange
Bay
South
Lake
Bay
133°45'

Figure 2.7. Map of selected Mackenzie Delta lakes in the Inuvik area and representing a range of closure (Fee *et al*, 1988).

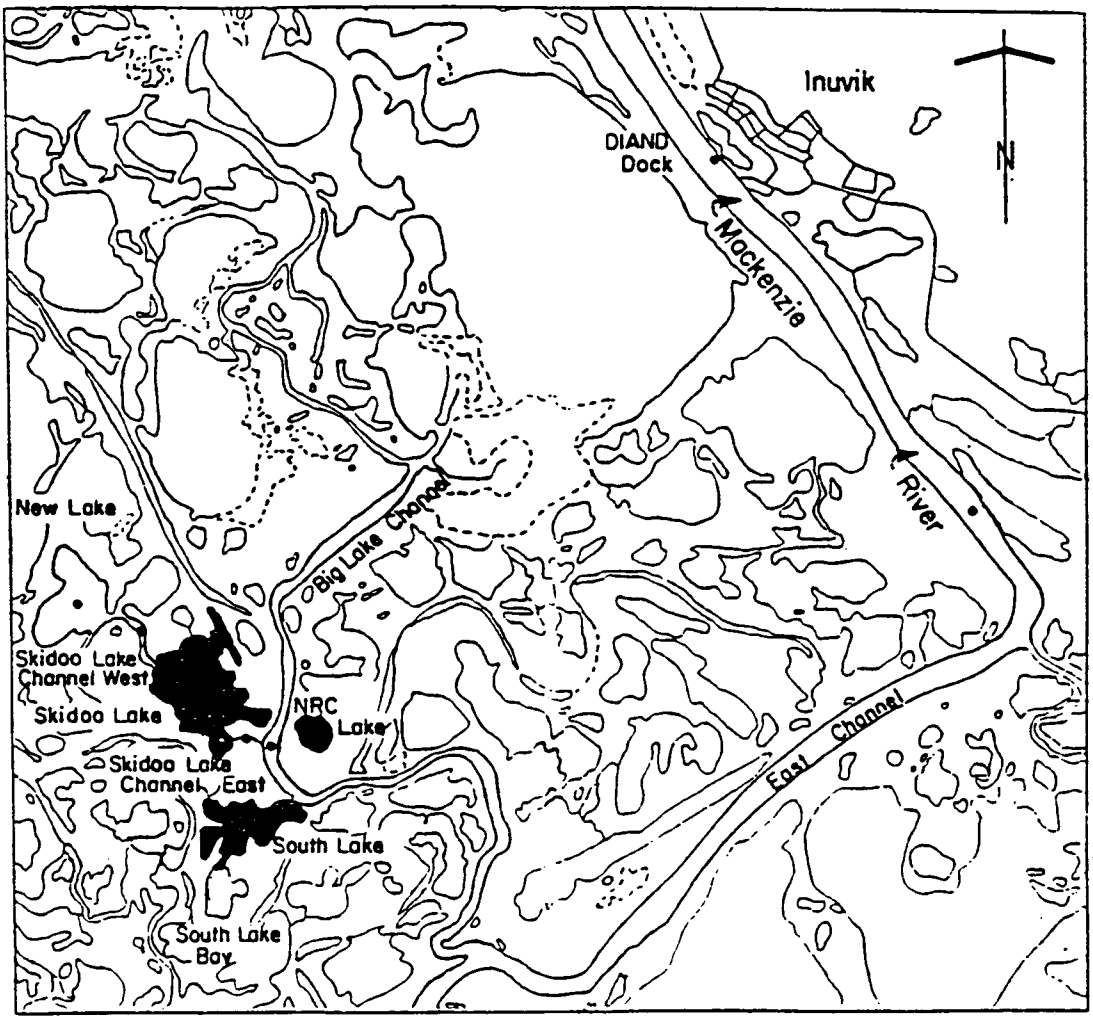

Inuvik
DIAND
Dock
N
Mackenzie
River
New Lake
Big Lake Channel
Skidoo Lake
Channel West
Skidoo Lake
NRC
Lake
Skidoo Lake
Channel East
East Channel
South Lake
South Lake
Bay

Figure 2.8. Aerial view of the study area: 1) Inuvik, 2) Big Lake Channel, 3) South Lake Channel, and 4) limnocorrals in South Lake, Mackenzie Delta (photo by W. Kolenchuk).

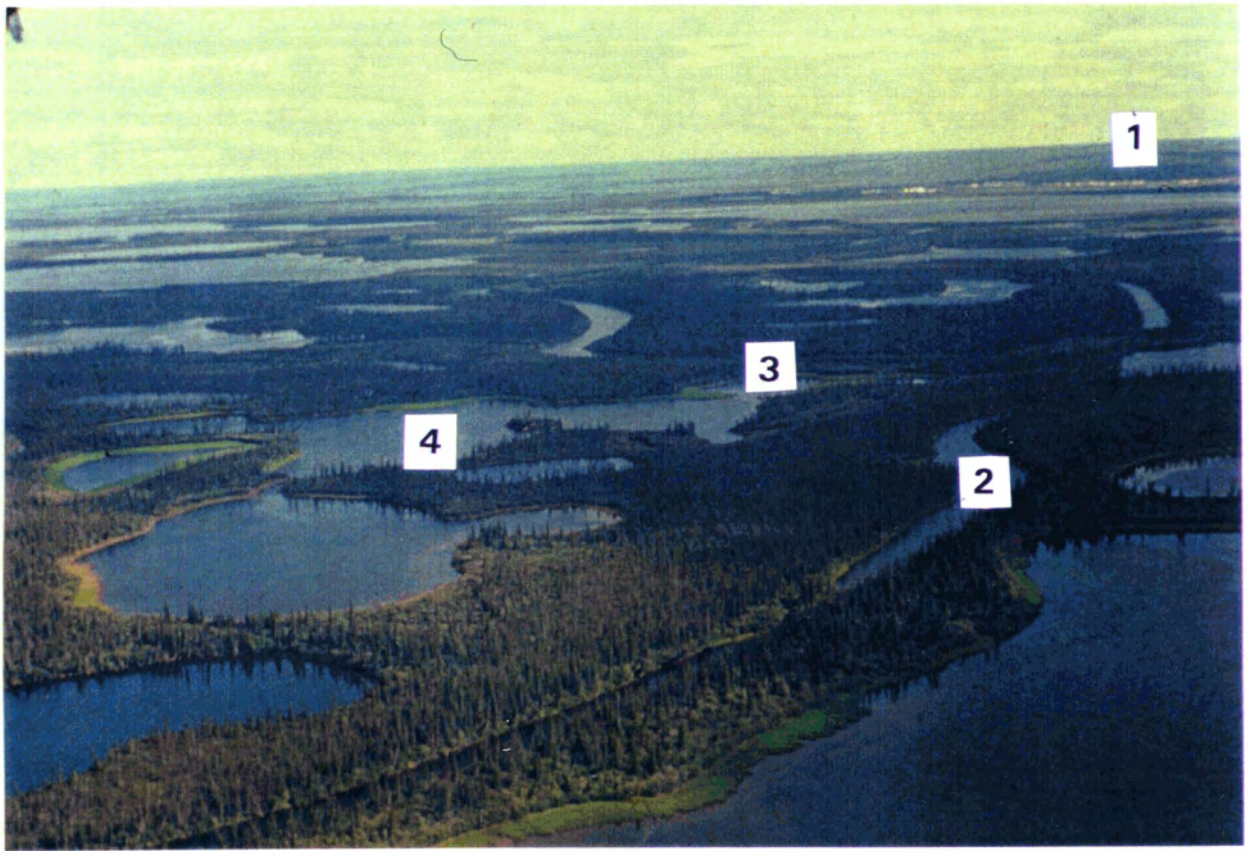

1
2
3
4

Figure 2.9. Map of the bathymetry map of South Lake, Mackenzie Delta (Ramlal *et al*, 1991).

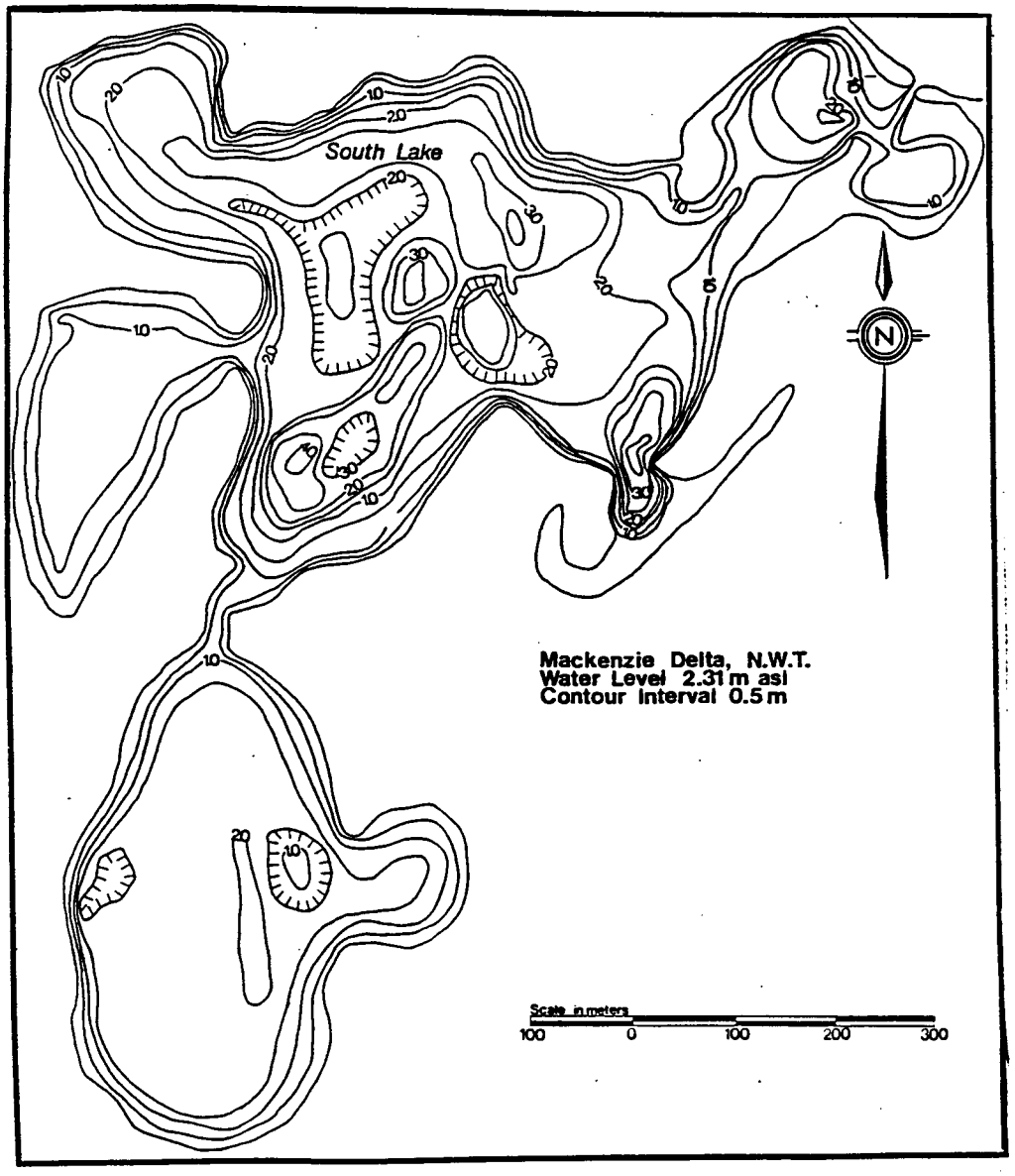

South Lake
Mackenzie Delta, N.W.T.
Water Level 2.31 m asl
Contour Interval 0.5 m
N
Scale in meters
100 0 100 200 300

Figure 2.10. South Lake Channel which connects South Lake to Big Lake Distributary Channel, Mackenzie Delta (photo by W. Kolenchuk).

Figure 2.11. South Lake Delta situated at the interface between Big Lake Distributary Channel and South Lake proper, Mackenzie Delta (photo by W. Kolenchuk).

Figure 2.12. Inner Channel connecting Front Bay of South Lake and South Lake proper, Mackenzie Delta (photo by W. Kolenchuk).

Figure 2.13. Bare sediments (near shore) contrasted with macrophyte beds (far shore) at South Lake, Mackenzie Delta (photo by W. Kolenchuk).

Figure 2.14. Portion of the island located in South Lake proper which was cleared for air-drop of limnocorrals by helicopter (**top**) (photo by W. Kolenchuk).

Approximate location (**X**) of the mid-summer 3-metre contour where limnocorrals were installed in South Lake Mackenzie Delta (**bottom**) (photo by W. Kolenchuk).

Figure 2.15. Diagram of low and high weekly additions of sediment and nutrients to limnocorrals, and pulsed and distributed delivery regimes. Doses were determined by multiplying concentrations of N, P, and sediment by the volume of water in each limnocorral. Pulsed deliveries were added as a slug once per week. Distributed treatments were delivered incrementally three times per week.

Weekly Nutrient & Sediment Additions

LOW	HIGH
0.9 *u*M P	2.7 *u*M P
3 *u*M N	9 *u*M N
6 mg/ L sediment	18 mg/ L sediment

Delivery Regime

Pulsed	Pulsed
Distributed	Distributed

Figure 2.14. Portion of the island located in South Lake proper which was cleared for air-drop of limnocorrals by helicopter (**top**).
Approximate location (**X**) of the mid-summer 3-metre contour where limnocorrals were installed in South Lake Mackenzie Delta (**bottom**) (photos by W. Kolenchuk).

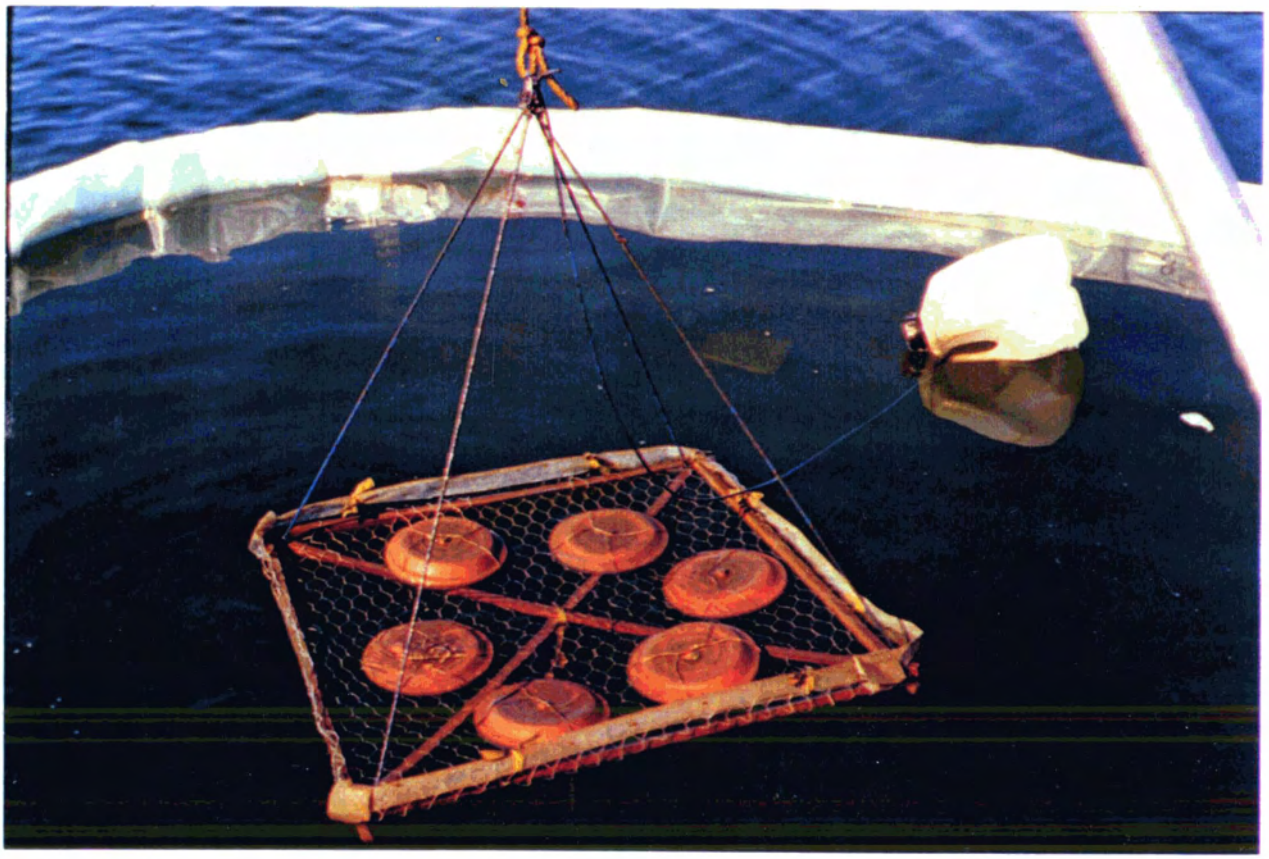


Figure 2.17. Plexiglas® chambers with clay substrates used to measure photosynthetic rates of benthic algae by O_2-change (photo by W. Kolenchuk).

Figure 2.18. Plexiglas® chambers are suspended from the clear plastic jugs, in South Lake, Mackenzie Delta (photo by W. Kolenchuk).

Figure 2.19. Plexiglas® chamber submersed in 20-L pail during the mixing process prior to extraction of water sample for determination of dissolved oxygen (photo by W. Kolenchuk).

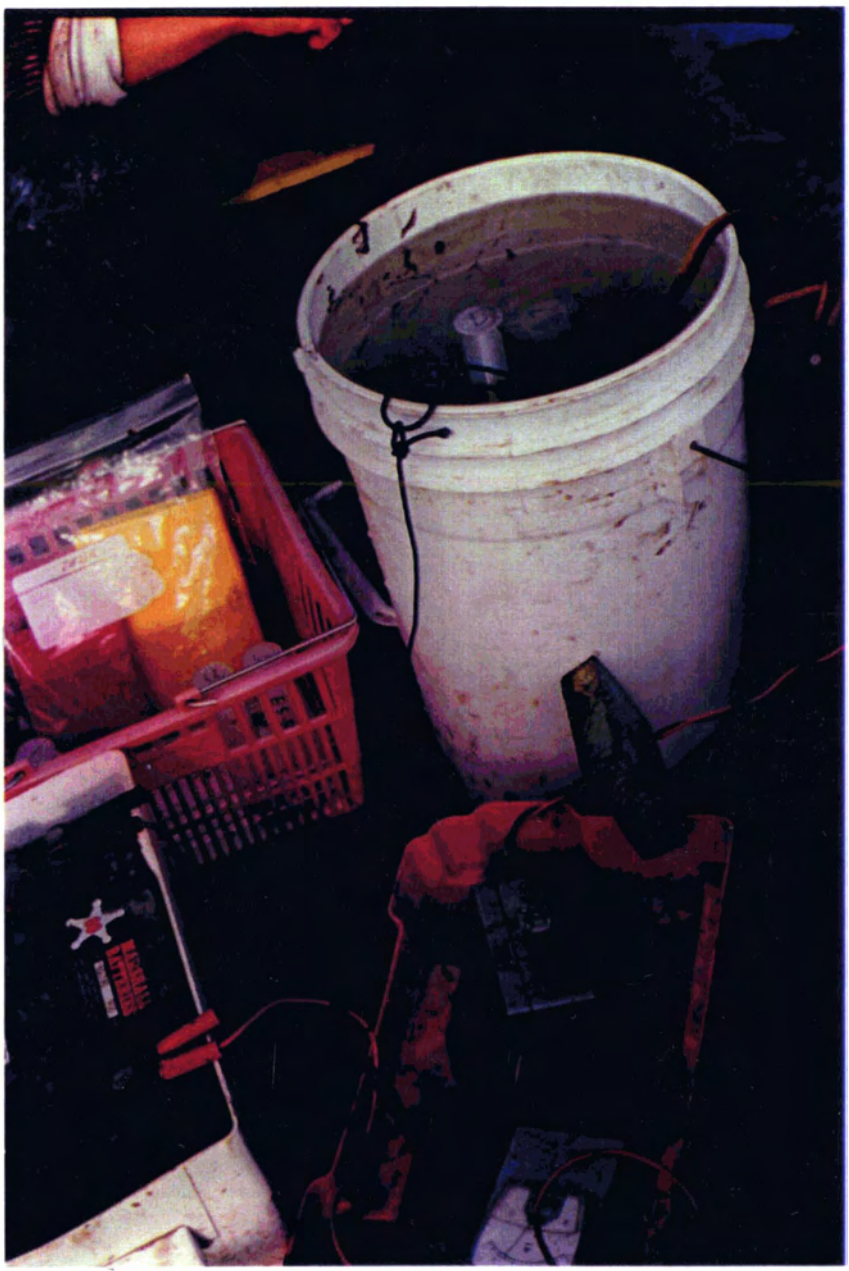
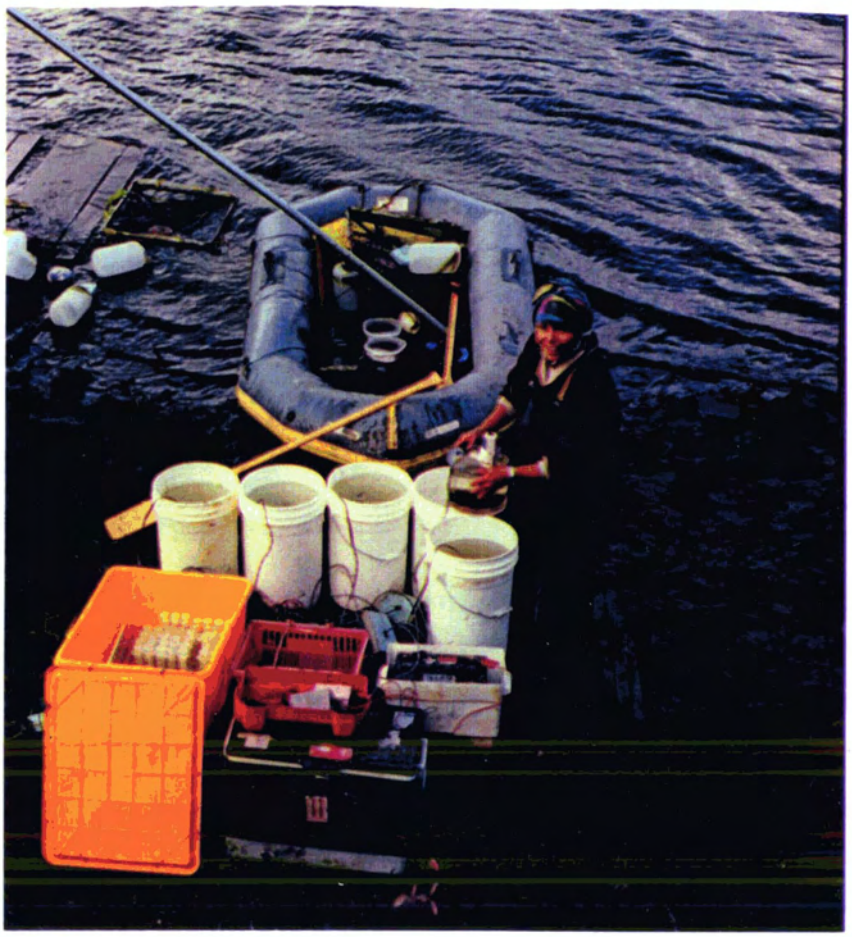


Figure 2.20. Water samples for dissolved oxygen determination were extracted with 60 ml syringes and fixed immediately (**top**) .
"Fixed" water samples were transported to the lab in Inuvik for titration (**bottom**) (photos by W. Kolenchuk).



Chapter 3 Results and Discussion

PHYSICAL AND CHEMICAL DYNAMICS OF LIMNOCORRALS

In situ field research utilizing limnocorrals effectively addressed the question of the effects of episodic river inflow on benthic algal growth in the Mackenzie Delta lake system. The general suitability of the limnocorral approach for investigating the effects of turbidity on lake systems is more throughly discussed in the final chapter of this paper.

Relation between light, TSS concentration and phytoplankton chlorophyll *a*

Because light was a major factor being manipulated in the limnocorrals, it was desirable to quantify the average light environment for each regime of sediment-nutrient additions. Simultaneous measurements of vertical light extinction, TSS concentration and phytoplankton chlorophyll *a* were made eight times over the course of the experiment. A scatterplot of this data appears in Figure 3.1. Since TSS concentration varied logarithmically with extinction these values were log-transformed. With these two variables and multiple regression techniques I established an empirical relation between vertical light extinction, and TSS and phytoplankton chlorophyll *a* concentration.

The equation describing vertical light extinction coefficients (η) as a function of Ln(TSS concentration) and phytoplankton chlorophyll *a* is :

$$\eta = 0.316 + 0.568 \text{ Ln(TSS concentration)} + 0.151 \text{ chlorophyll.} \quad (6)$$

Standard errors, *p* values and coefficient of determination are presented in Table 3.1. Observed versus predicted extinction coefficients are plotted in Figure 3.2. Based on the regression results, TSS concentration exerts strong control over light extinction, and while the influence of phytoplankton chlorophyll *a* is weaker, there is a significant effect of planktonic chlorophyll *a* on light attenuation.

With this empirical relation and weekly means per treatment ($n = 3$) of TSS and phytoplankton chlorophyll *a* concentration, I derived weekly extinction coefficients for each treatment and the Control. Finally, I averaged the weekly light extinctions (weeks = 5) to arrive at an extinction coefficient which characterized the average light conditions over the course of the experiment per treatments and the Control (Figure 3.3).

Average light extinction was different among the treatments ($p < 0.05$) (Table 3.2). Average light extinction for High-Distributed, 2.3 m^{-1}, was higher than for all other treatments, followed by High-Pulsed, 1.7 m^{-1}, Low-Distributed and Low-Pulsed, 1.1 m-1, and last the Control, 0.9 m-1. Multiple comparisons (Table 3.2) show that light extinction is higher in the High-Distributed than in the Control ($p < 0.05$; effect size = 1.4 m^{-1}), higher in the High-Pulsed than in the Control ($p = 0.07$; effect size = 0.8 m^{-1}), higher in the High-Distributed than in the Low-Pulsed ($p < 0.05$; effect size = 1.2 m^{-1}), higher in the High-Pulsed than in the Low-Pulsed ($p = 0.05$; effect size = 0.6 m^{-1}), higher in the High-Distributed than in the Low-Distributed ($p < 0.05$; effect size = 1.2 m^{-1}),

and higher in the High-Pulsed than in the Low-Distributed ($p < 0.05$; effect size = 0.6 m^{-1}). Overall, light extinction increases and available light decreases in a more or less linear fashion from the Control to the High-Distributed. Differences in average light extinction correspond to biologically significant differences, i.e. the difference is greater than 0.3 m^{-1}. There were no biologically or statisticallysignificant differences in average light extinction between the Control and the low treatments, nor between the pulsed and distributed regimes for either low or high additions.

In order to better understand how TSS and phytoplankton chlorophyll *a* independently contributed to light extinction I examined the means per treatment for these two variables. Treatment means for phytoplankton chlorophyll *a* and TSS concentrations appear in Figures 3.4 & 3.5, respectively. Parametric tests show an effect of sediment-nutrient additions on TSS ($p < 0.05$) and on phytoplankton chlorophyll *a* ($p < 0.05$) (Table 3.3). Non-parametric tests show a positive effect of treatment (combined sediment-nutrient additions and delivery regime) ($p = 0.05$) for only TSS (Table 3.3). Multiple comparisons (non-parametric) show that TSS is higher in the High-Distributed than in the Control ($p < 0.05$), higher in the High-Pulsed than in the Control ($p < 0.05$), higher in the High-Pulsed than in the Low-Pulsed ($p < 0.05$), and higher in High-Pulsed than in Low-Distributed ($p < 0.05$). Extinction tends to be higher in the High-Distributed than in the Low-Distributed ($p = 0.1$) and higher in the High-Distributed than in High-Pulsed ($p = 0.1$). Overall, sediment-nutrient additions had a substantial positive effect on TSS in the treated relative to the Control limnocorrals, and on the high relative to the low treatments.

Multiple comparisons (non-parametric) show that phytoplankton chlorophyll *a* is higher in the High-Pulsed than in the Control ($p = 0.05$), and higher in the High-Pulsed than in the Low-Distributed ($p = 0.06$). Phytoplankton chlorophyll *a* tends to be higher in the High-Distributed than in the Control ($p = 0.1$). Overall, the average planktonic chlorophyll *a* concentrations among treatments and the Control is low, ranging between approximately 2 and 10 *u*g L^{-1}, but occasionally reached unexpectedly high levels for high treatments considering the simultaneous reduction in light availability with nutrient additions. The highest phytoplankton chlorophyll observed among all the sampling days was for the High-Distributed limnocorrals.

An evaluation of the potential contribution of the observed range of average phytoplankton chlorophyll *a* concentrations to light extinction per treatment and the Control required an analog system where planktonic chlorophyll *a* was the primary control on light extinction, over and above extinction due to dissolved color and the properties of water. Lakes on the Kukjuktuk Peninsula, an abandoned delta of the Mackenzie River, no longer receive river inflow and consequently contain very low concentrations of suspended matter (Hecky *et al*, 1991). Phytoplankton chlorophyll *a* concentrations vs light extinction for Lake 10 on the Kukjuktuk Peninsula are plotted in Figure 3.6 (Fee *et al*, 1988). Planktonic chlorophyll *a* concentrations between 0 and approximately 10 *u*g L^{-1} correspond to light extinction coefficients between 0.5 and 1.0 m^{-1}. The data for Lake 10 suggest that the range of average phytoplankton chlorophyll *a* concentrations among limnocorrals, i.e. 2 to 10 *u*g L^{-1}, may have contributed approximately 0.5 to 1.0 m^{-1} to light extinction in the

limnocorrals. Further, plotting extinction coefficients against chlorophyll concentrations (Figure 3.6) the slope of the line, 0.07, is the exctinction per mg of chlorophyll. Slopes of 0.01 to 0.03 have been reported for other systems (c.f. Oliver & Ganf, 1988). The Y-intercept, 0.67, represents background attentuation. The accuracy of these parameters rests on the assumption that background attenuation remains unchanged when there is change in phytoplankton biomass. These data suggest that approximately 30% of the light extinction may be attributable to phytoplankton chlorophyll. Other studies which have distinguished the light extinction attributable to TSS, phytoplankton chlorophyll, and dissolved organic carbon indicate that 15 to 20% of light extinction may generally be due to phytoplankton chlorophyll in systems where TSS is low (e.g. Linda Ayoub, 1996; Sanderson & Katz, 1996).

Based on the information available, TSS was apparently primarily responsible for the higher average extinction in the limnocorrals receiving high sediment loads, consistent with earlier studies of the Mackenzie Delta lakes that have shown that total suspended solids is the major factor determining light penetration in the Delta lakes (Fee *et al*, 1988). Earlier studies did not consider the separate contribution of phytoplankton chlorophyll to light extinction. My results suggest a previously underappreciated potential for phytoplankton chlorophyll *a* to contribute to light extinction, particularly for the intermediate closure lakes. Intermediate lakes lie between the extremes represented by very turbid, low closure lakes and very clear, high closure lakes, experiencing numerous flow-reversals during the summer low-flow period. Apparently in intermediate closure

lakes phytoplankton may respond to new nutrients associated with river inflow despite the reduction in light due to suspended sediments. A reasonable estimate of the contribution of phytoplankton chlorophyll *a* to light extinction in the limnocorrals seems to be 20 to 30%.

Representativeness of light extinction in limnocorrals

Among the limnocorrals, extinction coefficients range from 2.3 m^{-1} (High-Distributed) to 0.9 m^{-1} (Control). Although both higher and lower extinction coefficients have been reported for Mackenzie Delta lakes in the Inuvik area during July (Fee *et al*, 1988; Ramlal *et al*, 1991), extremes for limnocorrals are lower but roughly bracket light extinction for selected lakes representing a range of sill elevations and flooding regimes. Light extinction in the Controls fell over the course of the experiment in roughly the same manner as light extinction fell in South Lake (Figure 3.7). This is not surprising since South Lake receives little additional input of sediment after the spring flood. Overall, the range of light conditions in the limnocorrals seem to have approximated those of the Delta.

Among lakes of the Inuvik area, phytoplankton chlorophyll *a* concentrations ranged between 1.5 and 8 *u*g L^{-1} during the 1985 open water season (Anema *et al*, 1985). Excluding a single week, weekly means of phytoplankton chlorophyll *a* per treatment in the limnocorrals ranged from 1.5 to 8 *u*g L^{-1}, exactly bracketing the values observed for Delta lakes.

Among Delta lakes for which light extinction is reported, a TSS concentration of approximately 18 mg L^{-1} corresponds to light extinction coefficients approaching 3 m^{-1}. Although weekly target TSS addition to the

high treatments was 18 mg L^{-1}, average light extinction coefficients for the High-Distributed and the High-Pulsed treatments were lower than 3 m^{-1}, i.e. approximately 2.3 and 1.7 m^{-1}, respectively. Part of the difficulty in achieving and sustaining high TSS concentrations and light extinction in corrals is that sediment suspension time is less protracted compared to natural conditions, since limnocorrals evidently act as a barrier to advection currents and reduce turbulence, and resuspension of bottom sediments (cf. Bloesch *et al*, 1988).

In order to quantify the clearance of added sediment from the water column of the limnocorrals, I measured TSS concentration before dosing and 24 hours after dosing over a single 24 hour period for one limnocorral per treatment level. These results are shown in Figure 3.8. Loss of sediment from the water column is substantial during the 24 hour period following additions. Losses are related to total sediment additions, that is the higher the sediment dose, the greater the loss of sediment over a 24-hour period. Since pulsed treatments tended to settle more quickly out of the water column, distributed additions, although lower in sediment concentration than pulsed treatments, probably had a greater negative effect on light attenuation, meaning that pulsed treatments effected the light environment intermittently, and distributed treatments effected the light environment more or less continuously.

Results of grain-size analysis for a composite bank sample from South Lake Channel is shown in Figure 3.10. Silt and sand comprise 90% and clay the remaining 10% of the bank sediment. The representativeness of

South Lake Channel sediments compared to lake suspended sediments is discussed in the final chapter of this paper.

Instantaneous effect of sediment-nutrient additions

On a single occasion, TSS, phosphorus, and nitrogen concentrations were measured before and immediately after sediment-nutrient additions for a single limnocorral per treatment level. Results were compared to respective target TSS, phosphorus, and nitrogen weekly loads, Figures 3.11A, B and C, respectively. For all the treatments, the sediment-nutrient additions had a positive effect on TSS and nutrient concentrations, actually exceeding targets. Higher than target concentrations are not surprising since our ability to mix additions was limited to stirring the top 0.5 m with a paddle. Light extinction was measured for two High-Distributed corrals before and after sediment-nutrient additions (Figure 3.12). Light extinction increased by approximately one third immediately following sediment-nutrient additions.

Temporal dynamics of TSS

Since the sediment-nutrient addition regimes were constant throughout the experiment, and the sampling regime was consistent with the exception of the final week, I did not expect any systematic change in TSS among treatments over the course of the experiment. In order to evaluate this assumption I plotted a time series of weekly means of TSS concentration for all the treatments (Figure 3.13). Overall, TSS concentrations fell slightly in all the treatments from initial conditions to final conditions, except for High-Pulsed which was noticeably higher on the last sampling day than on any other sampling day. This comparatively higher TSS on the final sampling

day probably reflects the change in sampling regime and as expected the change was most noticeable for the limnocorrals, i.e. High-Pulsed, which received the highest daily dose of sediment. Overall, the small but consistent decrease in TSS among limnocorrals probably reflects the settling of fine silts and clays present in the lake water initially over the course of the experiment. TSS concentrations for individual corrals, weekly means and treatment means are presented in Appendix 2.

Temporal dynamics of phytoplankton chlorophyll *a*

Effect of nutrient spiking

Weekly additions and delivery regimes of nutrients to the treated limnocorrals are shown in Figure 2.15, e.g. the low treatments were based on weekly loads of 0.9 *u*M phosphorus and 3 *u*M nitrogen and the high treatments were based on 2.7 *u*M phosphorus and 9 *u*M nitrogen. Mean phosphate, nitrate and ammonium concentrations for each treatment and South Lake are compared in Figure 3.14. It seems clear from this comparison that, on average, nutrient availability for phytoplankton was non-limiting among the treated corrals, but that phosphorus may have been occasionally limiting in the Control and in South Lake. Overall, nutrient availability tended to be greatest for the high treatments. Nutrient availability in low treatments tended to be greater than in the Controls and in South Lake.

Mean phosphate and nitrate concentration per treatment are compared to weekly target phosphate and nitrate additions in Figures 3.15 & 3.16, respectively. This comparison suggests substantial draw-down of phosphorus and nitrogen for the High-Pulsed and the High-Distributed

treatments, and moderate draw-down of available nutrients for all other treatments. Nutrient draw-down was in all liklihood due to uptake by phytoplankton.

Temporal dynamics

A time series of weekly means for phytoplankton chlorophyll *a* per treatment is shown in Figure 3.17. Phytoplankton chlorophyll *a* shows the potential for dynamic response to nutrient additions. In particular this is evident for the High-Distributed treatment where phytoplankton appeared to bloom and crash over the course of the experiment. These observations seem consistent with observations by Hecky *et al* (1991) that phytoplankton productivity is variable over the course of the open-water season within individial intermediate closure lakes.

In addition to between treatment variability, phytoplankton chlorophyll *a* could be highly variable within treatments. This suggests that phytoplankton may respond to a variety of variables (other than sediment-nutrient additions) which were not controlled for, for example grazing pressure and plankton assemblages, which probably varied randomly among corrals. Planktonic chlorophyll *a* concentrations for individual corrals, weekly means and treatment means are in presented in Appendix 2.

Nutrient availability

Mean phosphate, nitrate and ammonium

Generally, mean phosphate and nitrate concentrations in the treated limnocorrals tended to be lower than the target weekly loads (Figures 3.15 & 3.16, respectively). Phosphate was nearly always detectable, and nitrate

was always detectable with the exception of week one. Nitrate levels in South Lake were slightly lower but comparable to Controls except on May 25, just after ice-out, when nitrate in South Lake was approximately 3 *u*M.

Ammonium was not directly manipulated. Generally, mean ammonium concentration was low, less than 0.5 *u*M, and did not vary much among the limnocorrals. South Lake ammonium levels were approximately 1 *u*M early in the open water season, but fell to levels near or below concentrations in the limnocorrals over the course of the experiment.

Temporal dynamics

Phosphorus may frequently limit aquatic primary production and it was therefore of interest of examine phosphorus dynamics among the treatments over the course of the experiment. A time series of phosphate concentrations for each treatment is shown in Figure 3.18. A general pattern of very low phosphate concentration for all treatments characterizes the early part of the experiment. Phosphate concentrations increase, particularly for the High-Distributed and the Low Distributed, during the latter weeks of the experiment. The relatively higher phosphate for all treatments on the final sampling day in all liklihood reflects the change in sampling regime from the day before dosing to the day after dosing in week 5. The general increase in phosphate concentrations among corrals near the end of the experiment may also reflect the seasonal reduction in solar irradiance which could have resulted in a reduction of phytoplankton growth and lower demand for nutrients. Phosphate concentrations for individual limnocorrals, weekly means and treatment means are presented in Appendix 3.

Since nitrogen was potentially an important limiting nutrient in South Lake and in the treated and Control limnocorrals it was of interest to examine nitrogen dynamics over the course of the experiment. A time series of nitrate concentrations per treatment is shown in Figure 3.19. Generally nitrate concentrations fell slightly in all limnocorrals after the initial treatment. Consistently higher nitrate for treated limnocorrals on the final sampling day probably reflects the change in sampling regime from the day before dosing to the day after dosing in week five. South Lake nitrate concentration increased in small increments over the course of the experiment, from near zero concentrations at week one. Weekly nitrate concentrations for individual limnocorrals, weekly means, and treatment means are presented in Appendix 3.

Since nitrate is the principal form of nitrogen available to phytoplankton in the Delta system, ammonium was not directly manipulated in this experiment. I did not expect any substantial differences in ammonium concentrations among treatments. Overall ammonium was low for all of the limnocorrals over the course of the experiment, usually less than 0.25 *u*M, but tended to be slightly higher in the High-Distributed corrals. Since ammonium is the preferred form of nitrogen used by microbes and phytoplankton, ammonia levels are expected to be low. Weekly ammonium concentrations for limnocorrals, weekly means and treatment means are presented in Appendix 3.

Phosphorus and nitrogen were at detectable levels in the Control. It is possible that nitrogen-fixing cyanobacteria represented a source of nitrogen

to the Control, and/or that nutrient flux from sediments resulted in measurable levels in the Control.

Nutrient flux from sediments

Artificial clay substrates were enriched to ensure unlimited supply of nutrients for periphyton growth over the course of the experiment. I assumed that nutrient availability was non-limiting to benthic producers in the shallow Delta lakes since diagenetic processing , e.g. bacterial decomposition and mineralization, should be substantial near the sediment-water interface resulting in sharp concentration gradients, and significant diffusion of nutrients out of sediments. The assumption that sediments represent a major source of nutrients for benthic production is supported by the prolific growth of rooted macrophytes in many of the Delta lakes (c.f. Chambers, 1987; Barko & Smart, 1986; Barko, 1981). Pore-water samplers offered an opportunity to evaluate this assumption.

Application of a diffusion-based model to calculate fluxes from sediments requires accurate determination of sediment porosity (Ø), and molecular diffusion coefficients for sediments (**Ds**) and vertical concentration gradients ($\partial C/\partial z$) for the chemical species of interest.

The parameter Ø (Engelhardt, 1977) is the easiest to determine. Theoretically, Ø = the ratio of volume of interconnected water to volume of total sediment. Two simplifying assumptions make Ø easy to determine. First, in practice Ø is taken to be the ratio of total void space to volume of total sediment, or total porosity (which strictly speaking is not the same as porosity) since isolated fluid-filled pores through which water cannot flow are rare in shallowly buried sediments, and total porosity is considered a

good estimate of $\varnothing$. Second, since porosity is primarily a function of grain size, and grain size is usually constant with depth, $\varnothing$ is assumed constant with depth. The porosity of material from the bank of South Lake Channel was 0.73 cm^{-3}. Lake bottom sediments probably have a higher proportion of clay than bank sediments, and porosities approaching 0.9 cm^{-3} may more accurately characterize lake substrata.

Empirically-derived molecular diffusion coefficients for water (Li & Gregory, 1974) must be corrected for diffusion in the local sediments. Molecular diffusion in sediments is always less than in water primarily due to the effect of tortuosity. Tortuosity results from the presence of solid particles, since ions must follow a tortuous path around sediment. Li & Gregory (1974) have described the relation between diffusion in water and diffusion in sediments as follows:

$$D_S = D_W \alpha/\theta^2 \qquad (6)$$

where

D_S = diffusion coefficient in sediment,

D_W = diffusion coefficient in water,

α = ratio of viscosity of bulk solution to that of interstitial water, and

θ = is the ratio of actual path length, L, straight distance of the path interval, x.

Since $L > x$, $\theta > 1$. Tortuosity is normally determined indirectly, by measuring the diffusion coefficient in bulk solution, and also in sediments where pore-water is equal in ionic composition to bulk water. Here, I relied on estimates of tortuosity that have been made for sea sediments. For example, Li and Gregory (1974) have reported θ for deep sea red clay

sediments to be 1.35. Adjusting to fresh-water requires a knowledge of α, which is a function of both sediment porosity and ionic concentration of interstitial fluid. For deep sea sediments α is considered to be a constant near one (Li & Gregory 1974). I did not find any values in the literature for α in freshwater, although Li & Gregory (1974) report that α is usually less than one in dilute waters. Nevertheless $\alpha = 1$ seems to have become the convention for both marine and freshwater sediments (cf. Berner, 1980). Alternatively, Manheim & Waterman (1974) have defined tortuosity (θ) as follows:

$$\theta^2 = \varnothing F \qquad (7)$$

where F = a formation factor equal to the ratio of electrical resistivity of sediments to the resistivity of interstitial fluid alone. For deep sea clay-rich nanno ooze at 7 metres, $\varnothing = 0.72\ cm^{-3}$, $F = 2.5$, and $\theta = 1.34$, which is very close to the value reported by Li & Gregory (1974) for deep sea red-clay sediments, 1.35. For deep sea clayey, diatom ooze at < 1 metre, $\varnothing = 0.87\ cm^{-3}$, $F = 1.6$ and $\theta = 1.18$.

Since I did not find any published estimates of tortuosity for lake sediments I here used the value of 1.2, reported by Manheim & Waterman (1974) for deep sea clayey diatom ooze. This sediment description seemed to best fit the general character of South Lake bottom sediments. Dividing $\alpha = 1$ by $\theta = 1.35$ results in a correction factor of 0.69 for conversion of diffusion coefficients for water to diffusion coefficients for South Lake sediments. The appropriateness of this value for South Lake sediments is somewhat uncertain. The resultant diffusion coefficients (D_S) for

phosphate, nitrate and ammonium, at 18° C (temperature corrections per Li & Gregory, 1974), are reported in Table 3.4.

Determination of $\partial C/\partial z$ is critical to estimates of nutrient flux at the sediment-water interface. I estimated $\partial C/\partial z$ from pore-water concentrations in the top cm of sediment at the sediment-water interface and from nutrient concentrations of 1 cm of water just above the sediment-water interface. The complete nutrient profiles derived from the samplers are in Appendix 4. I used regression to determine the slope of the best-fit line describing $\partial C/\partial z$ for each nutrient. Derivatives for phosphate, nitrate and ammonium for three sites- South Lake, a Control corral and a High-Distributed corral, are summarized in Table 3.5. Among sites, derivatives are variable, particularly for phosphate. Since measurement of phosphate in pore-water may be subject to a variety of analytical errors (Carignan, 1984), a particularly low value for phosphate , i.e. -0.12, has been ignored. Average derivatives (2 sites for phosphate , and for 3 sites for nitrate and ammonium) were used for estimation of diffusive fluxes from sediments.

The average nutrient flux of phosphate, nitrate and ammonium from South Lake sediments are in Table 3.6. Phosphate flux is on the order of 5 uM m^{-2} day^{-1}, nitrate flux is on the order of 10 uM , m^{-2} day^{-1}, and ammonium flux is on the order of 1.5 uM m^{-2} day^{-1}. Flux rates from South Lake sediments are lower, by as much as 2 orders of magnitude, compared to typical values for shallow aerobic lakes (cf. Kipphut *et al*, 1996; Kamp-Nielson, 1974). Therefore the nutrient fluxes reported here are considered conservative estimates for South Lake sediments. One possible explanation for underestimation could be that algal growth at the peeper site reduced

the apparent nutrient flux from sediments. Also no attempt was made to test the assumptions on which calculation of nutrient fluxes from concentration gradients are based, specifically that bioturbation and groundwater flux are negligible.

Nutrient fluxes are necessary but not sufficient to demonstrate that sediment-derived nutrients support unlimited growth of benthic algal. Flux rates must meet algal demands. Nutrient uptake rates for epipelic algae are not available. In conjunction with a study to determine the relative importance of epipelon to total primary productivity of south Lake, Ramlal *et al* (1988) measured phosphorus deficiency for epipelon from South Lake and its Bays. Moderate phosphorus deficiency was observed on 4 out of 30, and severe deficiency on 2 out of 30 sampling days in 1986. These results suggest that phosphorus probably does not limit epipelic algal growth in South Lake. In conclusion, it seems likely that benthic algal demands may be met by nutrient fluxes from sediment.

Comparison of South Lake sediment fluxes with fluxes from enriched clay substrates show them to be substantially less than the theoretical nutrient flux reported by Fairchild *et al* (1985) from enriched clay pots after 50 days which were on the order of 2 mM phosphate m^{-2} day^{-1}, and 10 mM nitrate m^{-2} day^{-1}. Actual rate of nutrient flux from *in situ* colonized clay substrates has not been determined but is probably less than laboratory release-rates determined by Fairchild (1985) which are based on diffusion from clean uncolonized substrates and continual replacement of overlying water. Periphyton colonizing the enriched clay substrates used in this study undoubtedly grew in an environment where nutrients were available in

nonlimiting supply. Finally, the information available suggests that nutrient fluxes from sediments could support unlimited algal growth but this has yet to be demonstrated.

PERIPHYTON RESPONSE

Growth rates

Periphyton response to sediment-nutrient treatments was measured as biomass accrual over time on the clay substrates. Periphyton was harvested from replicate substrates on days 23, 34 and 44. This data is plotted in Figure 3.20. Growth between Day 0 and Day 23 represents a colonization phase. Growth between Day 23 and Day 34 represents a phase of exponential growth. After Day 34 growth levels off in all of the treated limnocorrals, and appears to begin leveling off in the Control. On Day 34 the Control had reached a much higher level of biomass accrual compared to all of the treatments. Lowest biomass accrual occurred in the High-Distributed limnocorrals. Between these two extremes, in order of decreasing biomass, were the Low-Distributed, the Low-Pulsed and the High-Pulsed.

Colonization and exponential growth rates among treatments are compared in Figure 3.21. Colonization growth rates ranged between 0.29 and 0.44 mg m^{-2} day^{-1}. The Control colonization growth rate is highest and the High-Pulsed is lowest, but overall colonization growth rates are similar among treatments and the Control. By contrast, exponential growth rates vary 3-fold among the treated corrals and the Control. The Control growth rate is highest, 3 times the lowest growth rate observed for the High-Distributed, followed by the Low-Pulsed where growth rate is twice the

rate of the High-Distributed. Exponential growth rate for the High-Pulsed and the Low Distributed are similar, roughly 60% of the Control growth rate.

These results suggest two potentially important functional attributes of the periphyton communities colonizing substrates. First, the general pattern of standing crop over time among the treatments and the Control is similar, conforming to the classic sigmoid growth curve. Second, although colonization rates are similar among the limnocorrals, exponential growth rates and ultimately biomass accrual differed substantially between the Control and all the treated corrals. Specifically, growth is greatest where light is uninterrupted (Control) and lowest where light is more or less continuously reduced (High-Distributed). Exponential growth rates are what we might expect considering the more or less linear increase in light extinction among the limnocorrals from the Control to the High-Distributed.

ANOVA results (Table 3.7) show that the effect of sediment-nutrient additions and delivery regime was to depress benthic algal biomass accrual over the course of the experiment ($p < 0.02$). Treatment effects are non-significant on Day 23 but highly significant on Day 34 and Day 44 ($p < 0.01$). The planned contrast between the Low-Pulsed and the High-Distributed treatments which received equivalent doses per day (e.g. 6 mg L^{-1} sediment) but contrasting loads per week (i.e. pulsed load = 6 mg L^{-1}, distributed load = 18 mg L^{-1}) is not highly significant ($p = 0.1$). Paired comparisons for Day 34 show that algal biomass is higher in the Control than in the Low-Pulsed ($p < 0.05$), higher in the Control than in High-Pulsed ($p < 0.01$), and higher in the Control than High-Disributed

($p < 0.01$). Also biomass tends to be higher in the Control than in the Low-Distributed ($p = 0.1$). Overall these results indicate a significant negative effect of sediment-nutrient treatments on biomass accrual over time and the effect increases with increasing light extinction.

Net Photosynthetic rates

Persistent cloudy conditions in the Inuvik area significantly reduced opportunities to measure photosynthesis. Four sets of photosynthesis data (out of eleven) were considered coherent for data analysis. A set consists of one measurement per treatment and the Control on a single day. During photosynthesis measurements, all of the Plexiglas® chambers were suspended in South Lake so that light conditions were identical among the treatments and the Control. In order to compare photosynthetic rates that were measured on different days, photosynthetic rates were normalized for irradiance on a particular incubation day. Light corrections were made with hourly radiation data collected at the Inuvik Airport by Environment Canada, reported as MJoules m^{-2} day^{-1}, after adjustment for reflection and light extinction at incubation depth in South Lake on incubation days. Photosynthetic rates before and after correction for light for four incubation days per treatment and the Control are presented in Appendix 6.

I expected that the pattern of areal net photosynthetic rates among treatments would correspond to the pattern of growth rates derived from direct measurement of change in algal biomass over time on clay substrates since both represent a measure of net growth over time. Average areal net photosynthesis per MJoule light for all the treatments and the Control is shown in Figure 3.22. Average areal net photosynthetic rate is highest for

the Control, but the Control rate is only marginally higher than the average rate for the Low-Distributed, and approximately 25% higher than the average rate observed for the Low-Pulsed. By contrast, biomass accrual measured by harvesting in the Control was 50 % higher than in the Low-Pulsed and 75% higher than in the Low-Distributed. As expected, photosynthesis rates for the Control, the Low-Pulsed and the Low-Distributed are all considerably higher than for the High-Pulsed and the High-Distributed. Interestingly, areal net photosynthetic rates are higher for the distributed delivery regimes for both the low and high sediment-nutrient additions, compared to their pulsed counterparts.

Significance tests show an effect of treatment on areal net photosynthesis per MJoule ($p < 0.05$) (Table 3.8). Paired comparisons (Table 3.8) show that areal net photosynthesis is higher in the Control than in the High-Pulsed ($p < 0.05$), higher in the Low-Pulsed than in the High-Pulsed ($p < 0.05$), and higher in the Low-Distributed than in the High-Pulsed. Biomass tends to be higher in the Control than in the High-Distributed and higher in the Low-Distributed than in the High-Distributed ($p = 0.08$). Generally, these results reflect the net heterotrophy which was frequently observed for both of the high treatments, compared to net autotrophy was observed in the Control and in the low treatments.

Overall photosynthetic results are roughly what we might expect considering biomass accrual on the clay saucers, but there are some obvious discrepancies between algal biomass accrual and areal productivity, particularly for the Control. Biomass accrual in the Control was considerably higher than for all the treatments, but light normalized areal

net photosynthesis was only slightly higher for the Control than for the low treatments, although considerably higher than for the high treatments. There are several possible explanations for the discrepancy between the Control biomass accrual over the course of the experiment and areal net productivity. First- variation in nutrient availability among treatments, second- variable grazing pressure among treatments, third- variation in efficiency of the photosynthesis process among treatments, and fourth- variation in light availability among treatments.

Presumably all of the nutrient-diffusing substrates were working properly and there was no significant variation in nutrient availability for benthic algal growth among the treatments and the Control. Alternatively, grazers can crop substantial algal biomass, and grazing pressure may vary spatially such that differences based on treatment may not be apparent from a series of snap-shots in growth-curve time. Also, it is expected that grazers actually consume a substantial portion of the annual benthic algal production in the Delta lakes since benthic algae has been shown to be a dominant source of carbon to the Delta lake food web. However, in this experiment it was assumed that grazing was negligible since substrates were suspended off of the bottom which should have substantially reduced grazer-accessibility to the clay substrates. This assumption was supported by observations made while the handling the clay saucers, specifically, a single grazer was encountered on each of two saucers over the entire course of the experiment.

Another possible explanation for the discrepancy between the Control biomass accrual and areal photosynthetic rates is that the efficiency of the

photosynthetic process per mg of algal chlorophyll may have been higher among the treatments than for the Control, such that higher biomass would not be as strongly expressed in areal photosynthetic rates for the Control compared to the treatments. Photosynthetic efficiency may vary for a variety of reasons, for example, with history of illumination, or rates may vary among algal species. To compare photosynthetic efficiencies, light-normalized areal net photosynthetic rates were corrected for biomass per substrate (Appendix 6). Average biomass-specific photosynthetic rates per treatment are shown in Figure 3.23. Overall, there is much less variation among average photosynthetic rates per mg algal chlorophyll per treatment than for average areal net photosynthetic rates. Average biomass-specific photosynthetic rate is highest for the Low-Distributed treatment. Average biomass-specific rates for the Control, the Low-Pulsed and the High-Distributed are similar, approximately one-half the average Low-Distributed rate. The average High-Pulsed rate is considerably lower than for all other treatments and the Control. The average High-Distributed rate is higher than the average High-Pulsed rate. Overall, however, biomass-specific rates of photosynthesis are about average and do not explain the discrepancy between biomass accrual and areal photosynthetic rates for the Control.

Daily photosynthetic measurements for all the treatments and the Control were conducted under identical light conditions. But, light availability in the *home* corrals was variable among the treatments and the Control. Specifically, light was undisturbed by sediment-nutrient additions in the Control, and light was intermittently or continuously disturbed in the pulsed and distributed treatments, respectively. If benthic algae is not

nutrient limited and grazing is negligible, then biomass accrual should be proportional to available light, which it apparently is. The average light environment for each treatment, characterized as extinction coefficients is shown in Figure 3.3. Basically, there is a linear increase in light extinction from the Control, the Low-Pulsed, the Low-Distributed, the High-Pulsed and the High-Distributed. Comparison of average extinction coefficients with natural log of the growth rates suggests an inverse relation between light availability and log of growth rate (mg m^{-2} day^{-1}) (Figure 3.24). In conclusion, the relatively higher biomass accrual in the Control was apparently the result of overall better average light conditions.

Respiration and gross photosynthesis

Since net heterotrophy was frequently observed for both the High-Pulsed and the High-Distributed treatments it was of interest to examine respiration rates for any systematic effects of the treatments, or any correspondence with photosynthetic rates that might indicate light penetration during the dark incubations. Since most productivity studies assume that respiration rates are independent of irradiance, I compared biomass-specific respiration rates without normalizing for light. Biomass-specific respiration is compared to biomass-specific net photosynthesis in Figure 3.25. On a per incubation-day basis, with two exceptions (High-Pulsed on August 9 and High-Distributed on August 11), the respiration rates vary approximately two-fold among the treatments and the Control. With two exceptions (High-Pulsed on August 9 and High-Distributed on August 11), the biomass-specific respiration rates for all treatments on all days ranged between approximately 0.2 and 0.9 mg O_2 hr^{-1} mg algal chlorophyll^{-1}, or four-fold. The highest

respiration rate was recorded for High-Distributed on August 11, i.e. 1.2, and the lowest for High-Pulsed on August 09, i.e. 0.04 mg O^{-2} hr mg algal chlorophyll^{-1}. There is no evidence for systematic variation in the respiration rates among the treatments and the Control.

Gross photosynthesis refers to the gross true photosynthesis of organic matter resulting from exposure to light, in contrast to net photosynthesis which refers to the net formation of organic matter after losses due to respiration, death and other metabolic activities. To determine if there were any systematic differences in the losses among the treatments and the Control, gross photosynthetic rates were examined before and after biomass correction, and are shown in Figures 3.26 and 3.27, respectively. Excluding net heterotrophy, areal gross productivity among the treatments and Control varied three-fold on each of August 9, 13, and 11, and two-fold on August 21. Among all the treatments on all the incubation days, areal gross productivity ranged between approximately 0 and 60 mg O_2 m^{-2} hr^{-1}, and biomass-specific gross productivity ranged between approximately 0 and 3 mg O_2 mg algal chlorophyll^{-1}. Basically, gross photosynthesis appears to be related to light exposure, as expected.

Community metabolism was net heterotrophic for high treatments on several occasions. Specifically, with the exception of August 21, respiration rates nearly equaled or exceeded photosynthetic rates in both high treatments. There are several factors which may be contributing to net heterotrophy in the high treatments. First, low biomass, low incident light and sediments on the clay saucers may have interacted to result in net heterotrophy. Sediments accumulated on saucers may have scattered and

adsorbed light, further reducing already low light levels due to cloudy conditions. For instance, on August 21 when net autotrophy was observed for the high treatment, irradiance was approximately 30% higher than on two other incubation days, and 50% higher than one other incubation day. This suggests that light may not have been adequate to pass the threshold for net carbon fixation for high treatments on cloudy days. Second, decomposition of any organic matter associated with sediment settled onto clay saucers may have elevated O_2-demands in the high treatments relative to the low treatments and the Control. Also, if flocculation of phytoplankton and clay suspeniods and subsequent sedimentation of organic flocs occurred in the limnocorrals (e.g. Avnimelech *et al*, 1982) and was proportional to sediment-nutrient additions, then accumulation of flocculated organics may have been greater in high treatments and may have increased decomposition and O_2-losses relative to the low treatments and the Control.

SUMMARY OF RESPONSES TO TREATMENT

The effect of sediment-nutrient treatments on average light extinction, TSS, phytoplankton chlorophyll , nutrients, benthic algal biomass and photosynthetic rates are summarized in Table 3.9. The table is useful in evaluating interactions among the variables and the effect of sediment-nutrient additions on periphyton growth. Variables are ranked on a scale of 0 to 4, where 0 is low and 4 is high, for the Control and the treatments which correspond to a transparency gradient from clear to turbid.

Overall average light extinction tended to increase more or less steadily between the Control and the High-Distributed, but was indistinguishable

between Low-Pulsed and Low-Distributed. The relation between average TSS, and to a lessor degree phytoplankton chlorophyll *a,* and treatment is similar to the relation between light extinction and treatment. Average phosphorus tended to increase from the Control to the High-Distributed, but was higher in the High-Pulsed than in High-Distributed treatment. Average nitrate tended to increase from the Control to the High-Distributed but was higher in the Low-Pulsed than for the Low-Distributed. Average biomass accrual was substantially higher in the Control than for all the other treatments. Average biomass accrual was similar for the low treatments, followed by the High-Pulsed, and was lowest for the High-Distributed. Areal net photosynthesis was highest for the Control, but not much higher than the Low-Distributed and the Low-Pulsed, although substantially higher than the high treatments. Areal net photosynthesis was higher in the High-Distributed than in the High-Pulsed. Biomass-specific net photosynthesis was highest for the Low-Distributed, followed but not closely by the High-Distributed and the Low-Pulsed, then the Control and the High-Pulsed.

Overall, light extinction was apparently affected by both weekly load of sediment-nutrients, i.e. high or low, and frequency of dosing, i.e. pulsed or distributed, since light extinction tended to increase with both weekly load and frequency of delivery. This conclusion is supported by the significant contrast in light extinction between Low-Pulsed and High-Distributed where weekly load and delivery regime explain differences in light extinction. Also, significant differences between High-Distributed and Low-Distributed are explained by weekly load. Contrasts, however, between the Control and

the low treatments and between pulsed and distributed delivery regimes for both low and high treatments were non-significant.

It is surprising that the substantial difference in biomass accrual between the Control and all of the treatments does not correspond to a more substantial difference in light extinction between the Control and all of the treatments. The weak correspondence between relative biomass accrual and relative light extinction for the Control, and the absence of substantial differences in light extinction between pulsed and distributed delivery regimes at high and low additions are very likely a result of having quantified light extinction as a function of TSS and phytoplankton chlorophyll, since these measurements were made once a week on the day before dosing. Comparison of weekly measurements of TSS with target additions suggest that weekly measurements of TSS on the day before dosing did not adequately represent the reduction in light due to treatments especially immediately after dosing, particularly for the pulsed delivery regime.

Finally, although light extinction is apparently primarily a function of TSS, phytoplankton chlorophyll *a* may also contribute to light extinction particularly when weekly nutrient loads are high and delivered in small doses throughout the week rather than as a single pulse.

Overall, algal biomass accrual and areal photosynthetic rates are more or less proportional to light availability. Caution should be taken not to over-interpret the results of the photosynthetic rate measurements since ideally conclusions should be based on a greater number of photosynthesis measurements.

REPRESENTATIVENESS OF THE RESULTS

Carbon production

Preliminary estimates of epipelic algal productivity have been reported by Ramlal *et al* (1991). Comparison of these published values with the photosynthetic rates observed in this study provides a useful check on the accuracy of the latter measurements. Previous estimates of primary production in the Delta lakes have been based on ^{14}C methodology and have required harvesting of epipelon from surface sediments by tissue trapping techniques (Eaton & Moss ,1966). After harvesting, algal samples were incubated in the laboratory at four different light intensities ranging from 33 to 3900 *u*Einsteins m^{-2} sec^{-1}. Fixation of ^{14}C is not exactly equal to photosynthesis measured by the O_2-change method but is generally considered to approximate net productivity. Rates of areal carbon production reported for epipelon by Ramlal *et al* (1991) range from approximately 0 to 20 mg C m^{-2} hr^{-1} for a range of light intensities, and rates of biomass-specific photosynthesis range between approximately 0 and 2 mg C hr^{-1}mg algal chlorophyll^{-1}. For comparative purposes, net photosynthesis in mg O_2 has been converted to mg Carbon. The highest areal net carbon production, without normalizing for light, for benthic algae growing on clay saucers was 24 mg m^{-2} hr^{-1}, which is approximately equal to the highest carbon production for epipelon reported by Ramlal *et al* (1991). The highest biomass-specific net carbon production per mg algal chlorophyll on artificial substrates was roughly one-half the highest biomass-specific photosynthetic rates reported by Ramlal *et al* (1991). Possible

explanations for the discrepancy between biomass-specific rates of photosynthesis are discussed below.

Periphyton biomass

The highest levels of periphyton biomass reported in this study (Control limnocorrals) are approximately triple the benthic algal biomass reported by Ramlal *et al* (1991) who sampled South Lake epipelon in 1985 and 1986. There are several possible explanations for this discrepancy. First, previous algal biomass may have been underestimated, second, South Lake may not represent an appropriate analog to the experimental Control, third, grazing in South Lake may negatively effect biomass accrual, fourth, algal production is likely to vary interannually, and last, the higher biomass associated with enriched substrates may be an experimental artifact.

There are several methodological reasons why previous studies may have underestimated epipelic biomass. First, previous studies used the tissue trapping methods of Eaton and Moss (1966). Moss & Eaton report that their method may underestimate algal biomass by approximately 15%. Previous studies have relied on fluorometric measurement of algal chlorophyll *a* . Although fluorometry is a more sensitive technique than spectrophotometric measurements of chlorophyll *a*, pigments other than chlorophyll *a* , for example chlorophylls *a, b,* c_1, c_2 and carotenoids which were measured spectrophotometrically in this study; are not routinely measured by fluorometry. Since chlorophyll *a* comprised from 60 to 80% of the total chlorophyll associated with clay substrates, 40 to 20% of the biomass measured came from chlorophylls other than chlorophyll

a . Together, my measurement of pigments other than chlorophyll *a* and underestimation by tissue-trapping techniques could account in part for higher biomass values observed in the Control limnocorrals compared to previous studies.

Average light extinction (over seven weeks) in South Lake was 1.14 m^{-1}, which is comparable to the low treatments where average light extinction was 1.1 m^{-1}. Contrasting previous estimates of epipelic algal biomass in South Lake with the low treatments, where algal biomass accrual was 30% lower than in the Control, may actually be more a more appropriate comparison. The areal biomass of South Lake epipelon was one-half that of the low treatments. If as discussed above previous methods underestimated benthic algal biomass by 15 to 20%, and measurement of chlorophylls other than chlorophyll *a* in this study inflated biomass estimates by 20 to 40%, then the experimental biomass in the low treatments approximates previous biomass estimates for South Lake epipelon.

Since benthic algal carbon is an important source of fixed carbon to higher trophic levels grazing is expected to be considerable and may keep natural rates of biomass accrual at lower levels than might be attained under controlled conditions in the absence of grazing. Also, algal productivity may vary substantially between years. For example, benthic algal productivity may have been below average in 1985 and 1986 or above average in 1996.

Finally, it is possible that the higher biomass values were an experimental artifact. Nutrient availability may have been higher on the clay substrates than at the sediment-water interface, although it seems probable

that nutrient fluxes from South Lake sediments meet the nutrient demands of benthic algae. Also, clay saucers represent a solid, stable substrate compared to soft deltaic sediments and it is possible that clay saucers favored slightly different algal assemblages than are naturally associated with soft delta lake sediments, with implications for relative rates of benthic algal accrual.

A complete set of clay saucers, i.e. one per limnocorral, plus an enriched and unenriched clay saucer that were suspended in South Lake over the course of the experiment and an unenriched saucer that was anchored on the bottom of South Lake were sent to J. Smol's lab at Queens University. M. Hay (a student of Smol's) characterized the diatom assemblages per saucer and these results appear in Appendix 7. Although a thorough analysis of this data has not yet been completed, generally the diatom assemblages for the Control saucers are very similar to the diatom assemblages which colonize the sediment of the Mackenzie Delta lakes and diatom assemblages in all of the treated corrals were slightly less diverse than the Control communities (M. Hay, pers. comm.). Overall, these results suggest that the algal species colonizing the clay saucers were typical of the benthic algal species colonizing soft deltaic sediments.

Thermal dynamics

Temperature profiles in selected limnocorrals are compared to temperature profiles in South Lake in Appendix 8. Generally, the limnocorrals reflected the temperature regimes of South Lake, where the epilimnion extended to the lake bottom throughout the experiment.

Deviations of the Control from South Lake represent "enclosure effects". Based on the physical and chemical dynamics observed for South Lake and the Controls, it is apparent that divergence from background conditions was minimal over the course of the experiment.

Within treatment variability

Substantial within treatment variability among limnocorrals has been well documented (cf. Bloesch *et al*, 1988). Generally, variability is attributed to natural variability in aquatic environments, such as the spatial distribution of zooplankton populations. It is unlikely that zooplankton and phytoplankton assemblages were identical for all enclosures, and we infrequently we observed a 4 to 5 cm long *Esox lucius* in one or more of the limnocorrals. Overall, stochastic variability probably accounted for a large portion of the within treatment variability.

For example, limnocorral 6 (High-Distributed), had a visibly significant zooplankton population, lower than treatment average phytoplankton chlorophyll *a*, the highest ammonium levels observed among the corrals, and was clearer than other similarly treated limnocorrals. Zooplankton have been observed to have an impact on turbidity, for example by grazing and enhanced particle sedimentation (cf. Bloesch *et a*l, 1988).

It is possible that corral 6 had a slightly different initial plankton assemblage than the other corrals and therefore may have responded differently to sediment-nutrient additions and ultimately achieved higher zooplankton densities, with implications for water clarity. A second example of the inherent variability among limnocorrals is suggested by the low-level treatments where light extinction was nearly indistinguishable between

Low-Pulsed and Low-Distributed treatments. A possible explanation is that the treatment effects were diluted as a result of variation in initial light conditions.

Pore-water profiles

Replicate pore-water profiles were obtained for three sites in the vicinity of the limnocorrals in South Lake. Between site variation in concentration gradients, position of redox boundaries, and maximum concentrations of nutrients , particularly ammonium, was considerable. Variability may be due to temporal and/or spatial variability, or related to analytical error. Since peepers were inserted within metres of one another, it was expected that local horizontal variation in sedimentation, burial rates of organic matter, or diagenetic and diffusive processes was not likely to be significant, although irregular distribution of macroinvertebrates could have resulted in inconsistency in mechanisms of transport with implications for pore-water profiles near the sediment-water interface. Alternatively, seasonal temperature changes could have resulted in variability in profiles since peepers were pulled from the lake progressively later meaning that sediments would have warmed substantially causing increased microbial activity, a concomitant upwards shift in the oxic/anoxic boundary layer profiles, and increases in rate of molecular diffusion, and ultimately increases in flux rates from sediments over the course of the experiment. Analytical error may have been a factor in variability among phosphorus profiles since delay in withdrawing samples may have substantially reduced concentrations of phosphate and ammonium from anoxic sediments, and to a lesser degree in samples from oxic sediments (Carignan, 1984).

Overall, vertical profiles for ammonium are all unique in that concentrations less than 2.5 *u*M characterize the top 5 to 15 cm of pore-water profiles, then increase rapidly with depth. Explanation requires consideration of the oxygen environment near the sediment-water interface. Here, oxygen availability is a function of 1) balance between production of O_2 by photosynthesis and depletion of O_2 by decomposition of organic matter, and 2) diffusion of O_2 from the water column into sediments. Generally in shallow lakes which do not stratify , sediments remain aerobic, however oxygen availability decreases with depth and at some point beneath the sediment-water interface the environment becomes reducing instead of oxidizing. Within oxic sediments nitrification, or oxidation of ammonium to nitrite by bacteria, is prevalent. An abrupt increase in NH_4 at depth signifies a transition from oxic to anoxic conditions, or a redox boundary, where NH_4 is no longer oxidized but accumulates as a by-product of decomposition. The oxic/anoxic boundary varies between the South Lake site and corrals, but these changes are consistent with expectations based on warming of sediments. Specifically, the oxic/anoxic boundary is shifted upwards in later profiles.

Phosphorus profiles are variable between sites, but all show a gentle gradient across the sediment-water interface, beneath which phosphorous concentration is relatively constant before increasing again with depth. Phosphorus concentrations are also influenced by O_2 environment, however phosphate differs from ammonium in that it is adsorbed under oxic conditions onto ferric oxides and precipitates to form authigenic minerals, and does not undergo oxidation. Phosphorus profiles are consistent with

precipitation within the oxic zone. Concentrations may be constant if a steady state has been reached due to rapid attainment of equilibration, or if reactions are substrate-limited. Under reducing conditions phosphorus is liberated to solution. Decomposition also contributes to phosphorus increase at depth. Phosphorus profiles are generally consistent with this scenario, although redox boundaries appear to vary between sites, but these variations are consistent with expected shifts in redox boundaries related to warming of sediments and seasonal increases in microbial activity oxygen demand.

Nitrate profiles show a steep gradient across the sediment-water interface, beneath which nitrate is fairly constant with depth or decreases slightly , then increases, approaching a maximum at depth. Nitrification in the oxic layer at the top of the sediment profile results in the formation of nitrate and may explain the sharp gradient in the top few cm of sediment. Beneath, in the anoxic zone, denitrification, or bacterial reduction of nitrate to N_2 and N_2O occurs, and may explain stable or decreasing concentrations of nitrate, but does not explain increase in nitrate at depth. There is little evidence for significant denitrification in South Lake sediments. Low rates of denitrification may be the result of restriction of warming of sediments to the upper few centimeters. If lake sediments do not warm appreciably at depth preventing significant denitrification, the Delta lakes may represent systems where release of nitrate to the overlying water column is of greater importance than in temperate or tropical systems as a source of nutrients for benthic producers.

Figure 3.1. Relation between light extinction vs phytoplankton chlorophyll *a* concentrations (**top**) and total suspended sediment concentrations (**bottom**).

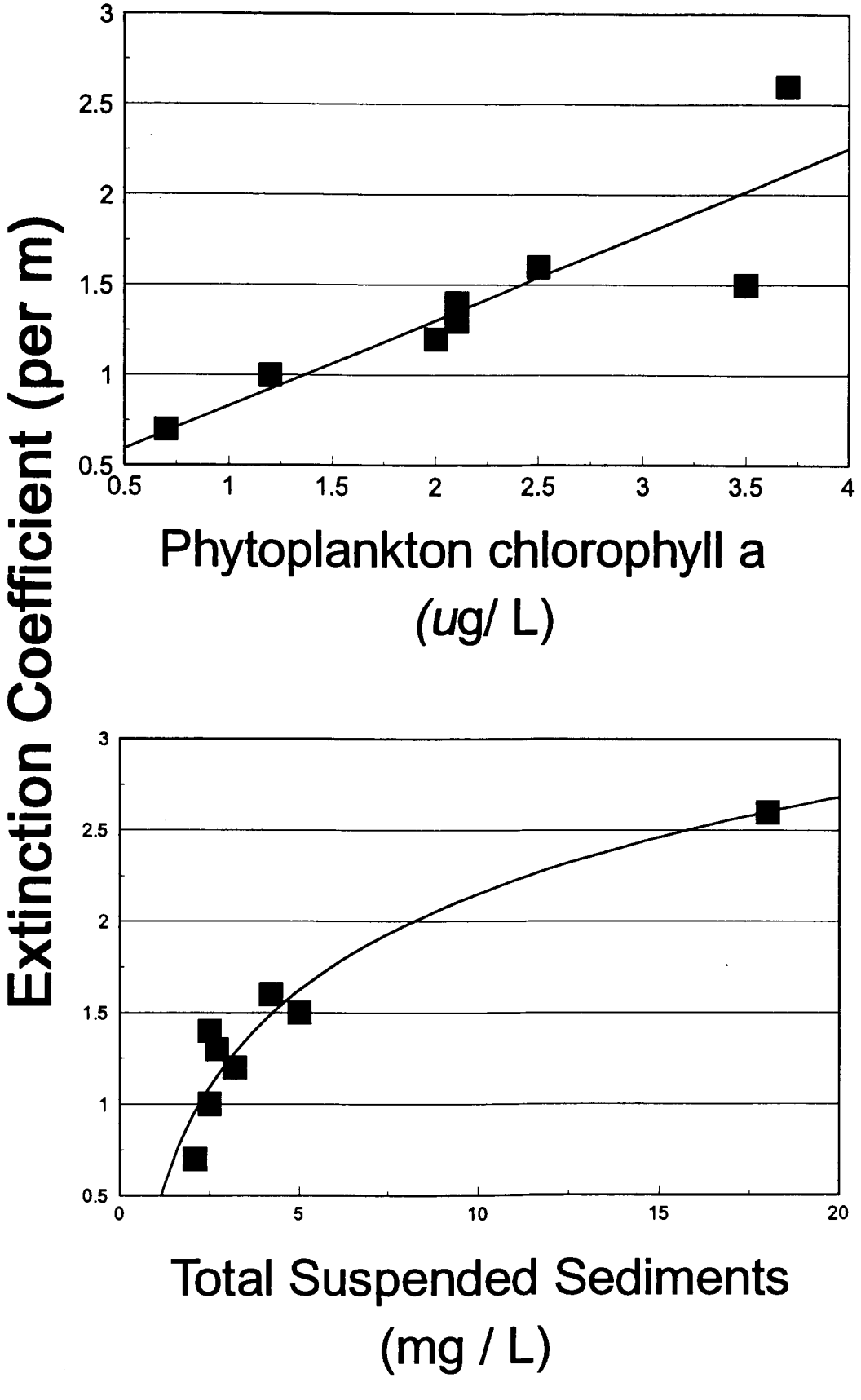

Extinction Coefficient (per m)
3
2.5
2
1.5
1
0.5
0.5
1
1.5
2
2.5
3
3.5
4
Phytoplankton chlorophyll a
(ug/ L)
3
2.5
2
1.5
1
0.5
0
5
10
15
20
Total Suspended Sediments
(mg / L)

Figure 3.2. Observed light extinction coefficients vs extinction coefficients predicted from the empirical relation between TSS and phytoplankton chlorophyll.

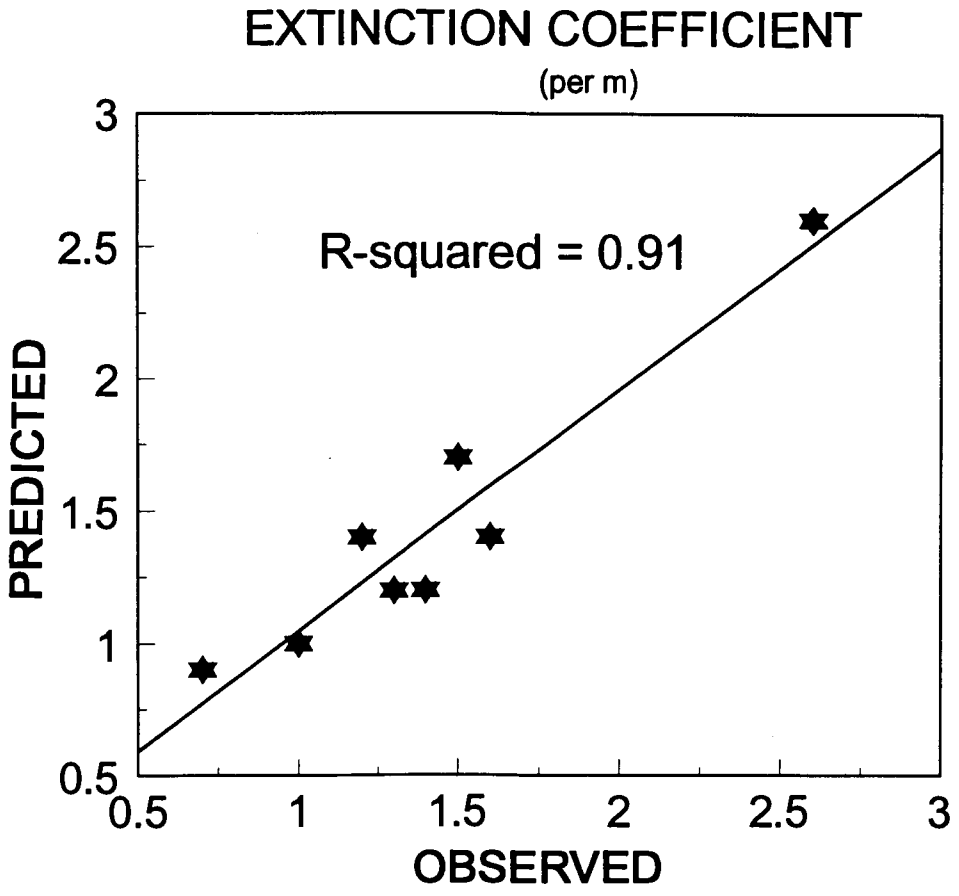

EXTINCTION COEFFICIENT
(per m)
R-squared = 0.91
PREDICTED
OBSERVED
3
2.5
2
1.5
1
0.5
0.5
1
1.5
2
2.5
3

Figure 3.3. Average extinction coefficients (± 1 SE) for the Control, treatments and South Lake (b is different from c & d).

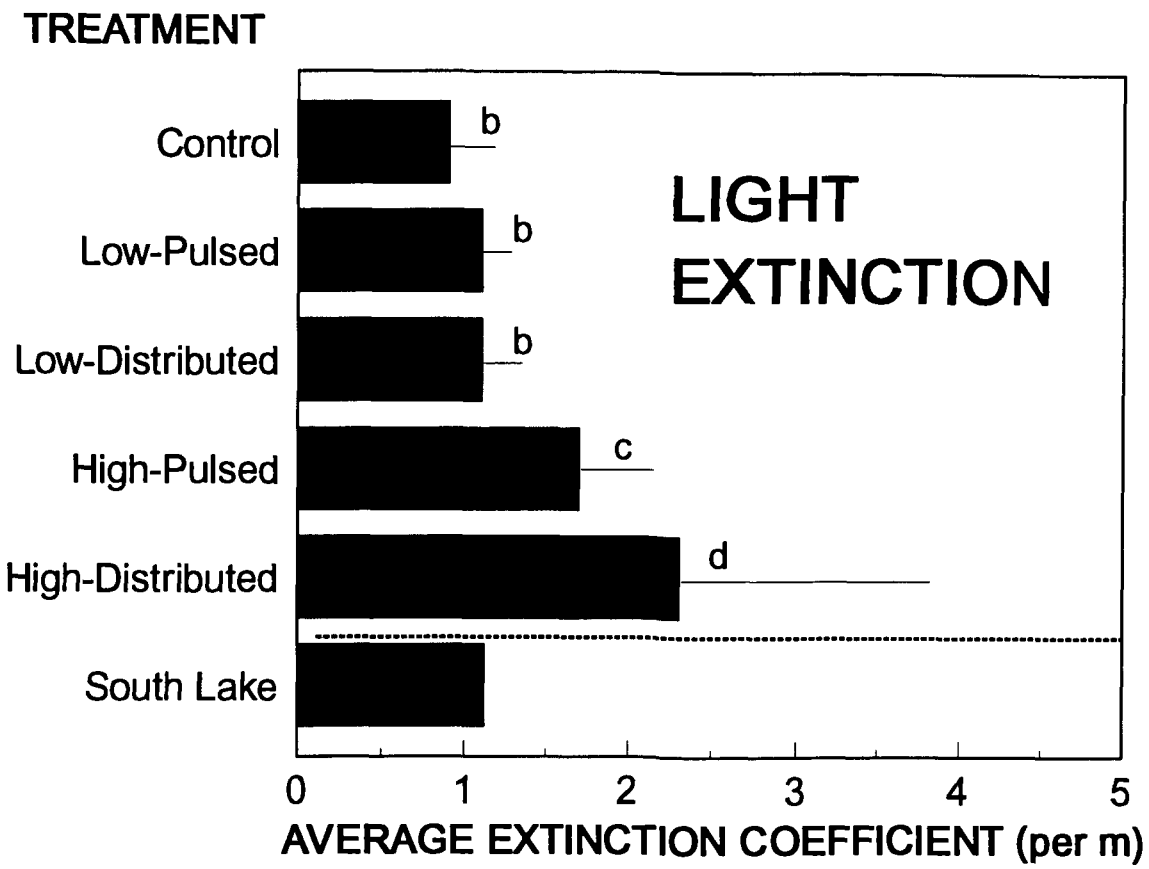

TREATMENT
Control
Low-Pulsed
Low-Distributed
High-Pulsed
High-Distributed
South Lake
b
b
b
c
d
LIGHT
EXTINCTION
0
1
2
3
4
5
AVERAGE EXTINCTION COEFFICIENT (per m)

Figure 3.4. Average total suspended sediments (± 1 SE) for the Control, treatments and South Lake (a is different from c & d; b is different from c; c is different from d).

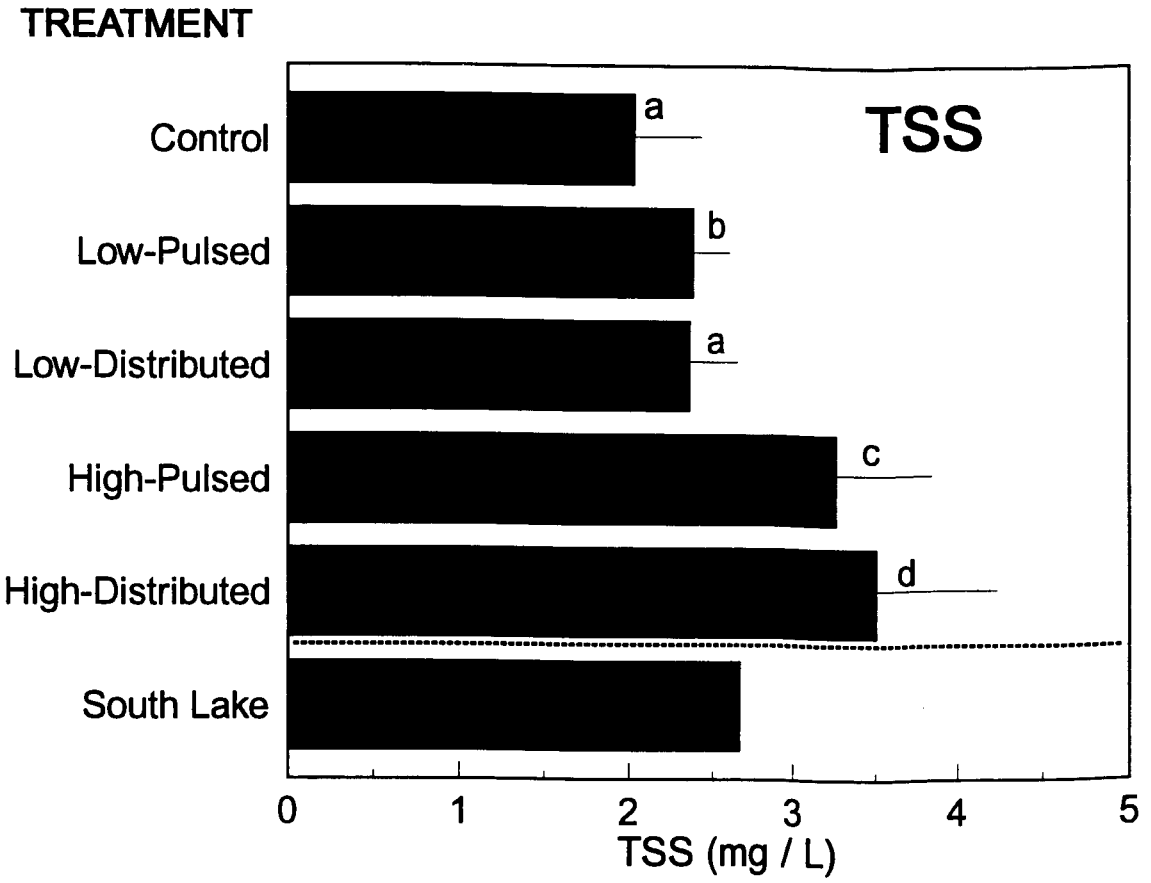

TREATMENT
Control
Low-Pulsed
Low-Distributed
High-Pulsed
High-Distributed
South Lake
a
b
a
c
d
TSS
0
1
2
3
4
5
TSS (mg / L)

Figure 3.5. Average phytoplankton chlorophyll *a* concentrations for South Lake, the Control and treatments (error bars omitted due to high variance) (a is different from d & e; c is different from d).

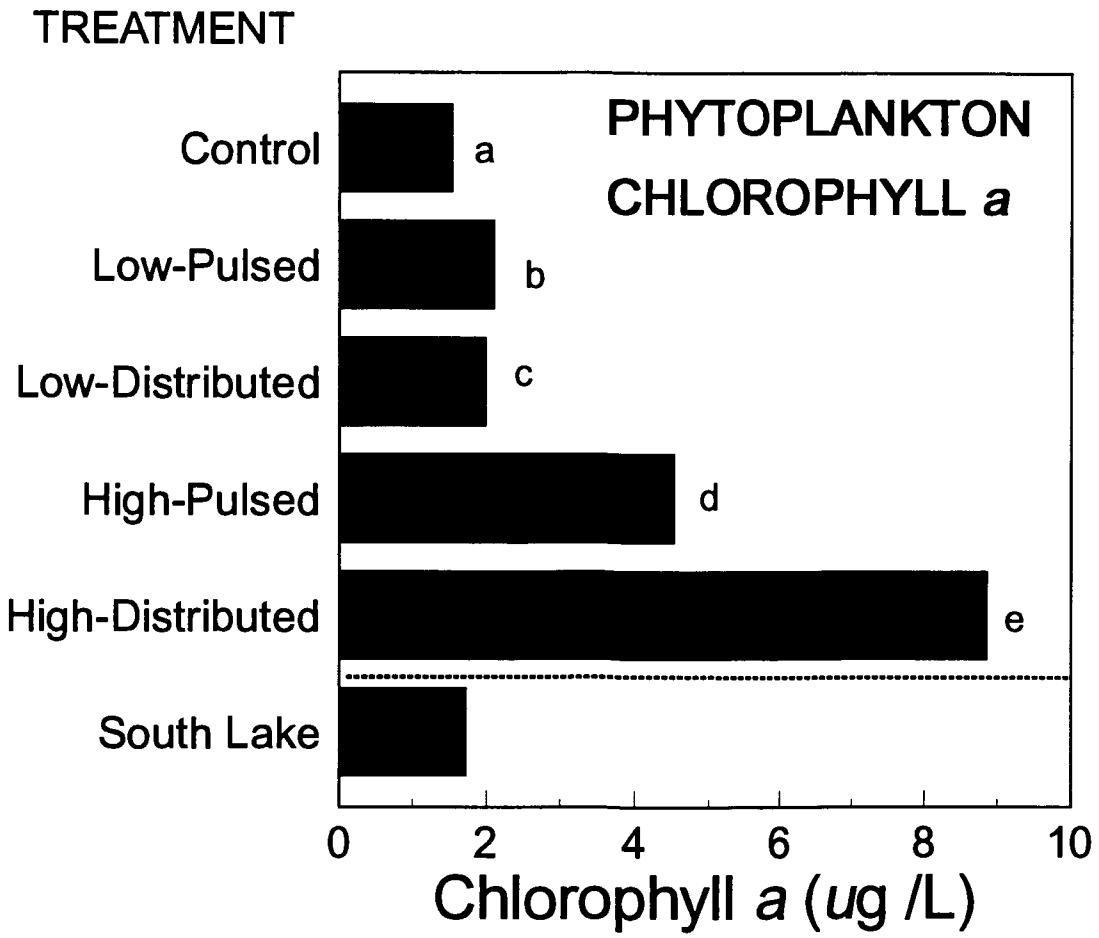
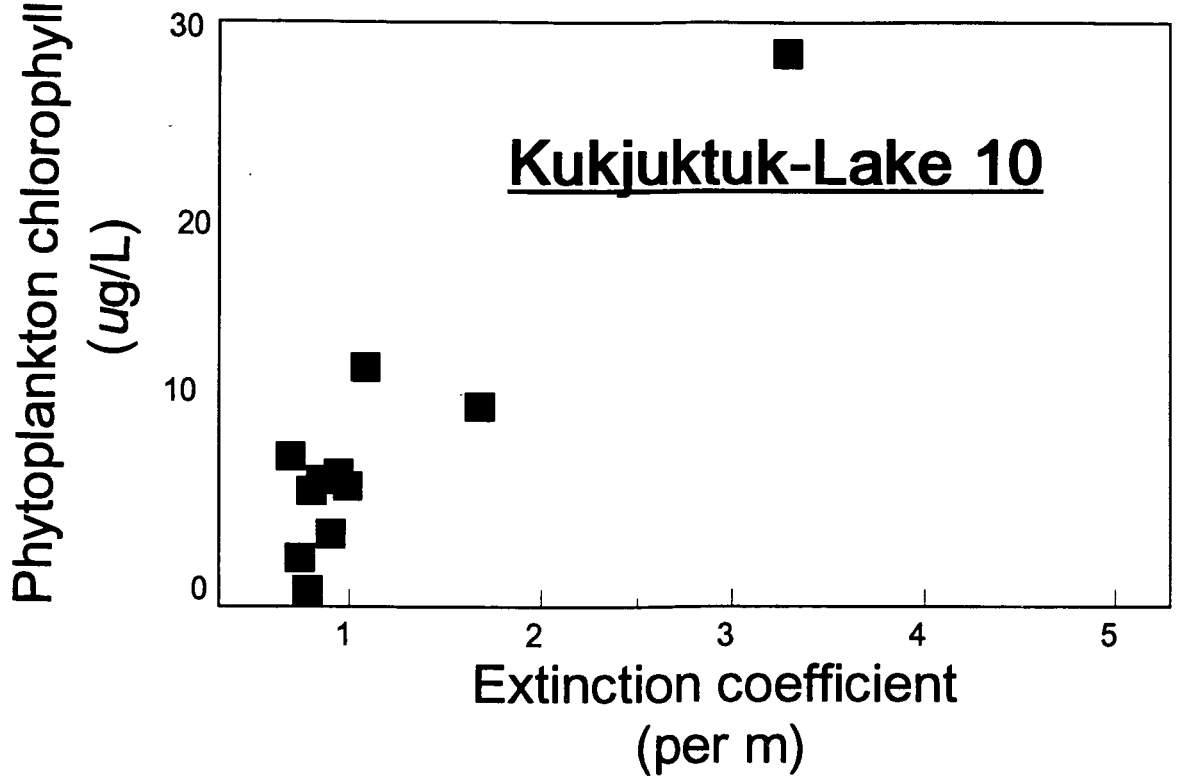

TREATMENT
Control
Low-Pulsed
Low-Distributed
High-Pulsed
High-Distributed
South Lake
a
b
c
d
e
PHYTOPLANKTON
CHLOROPHYLL a
0
2
4
6
8
10
Chlorophyll a (ug /L)

Figure 3.6. Phytoplankton chlorophyll *a* concentrations vs light extinction for Lake 10 on the Kukjuktuk Peninsula (Fee *et al*, 1988) **(top)** and light extinction vs phytoplankton chlorophyll *a* concentration for Lake 10 **(bottom)**.


Kukjuktuk-Lake 10
Phytoplankton chlorophyll (ug/L)
30
20
10
0
1
2
3
4
5
Extinction coefficient (per m)

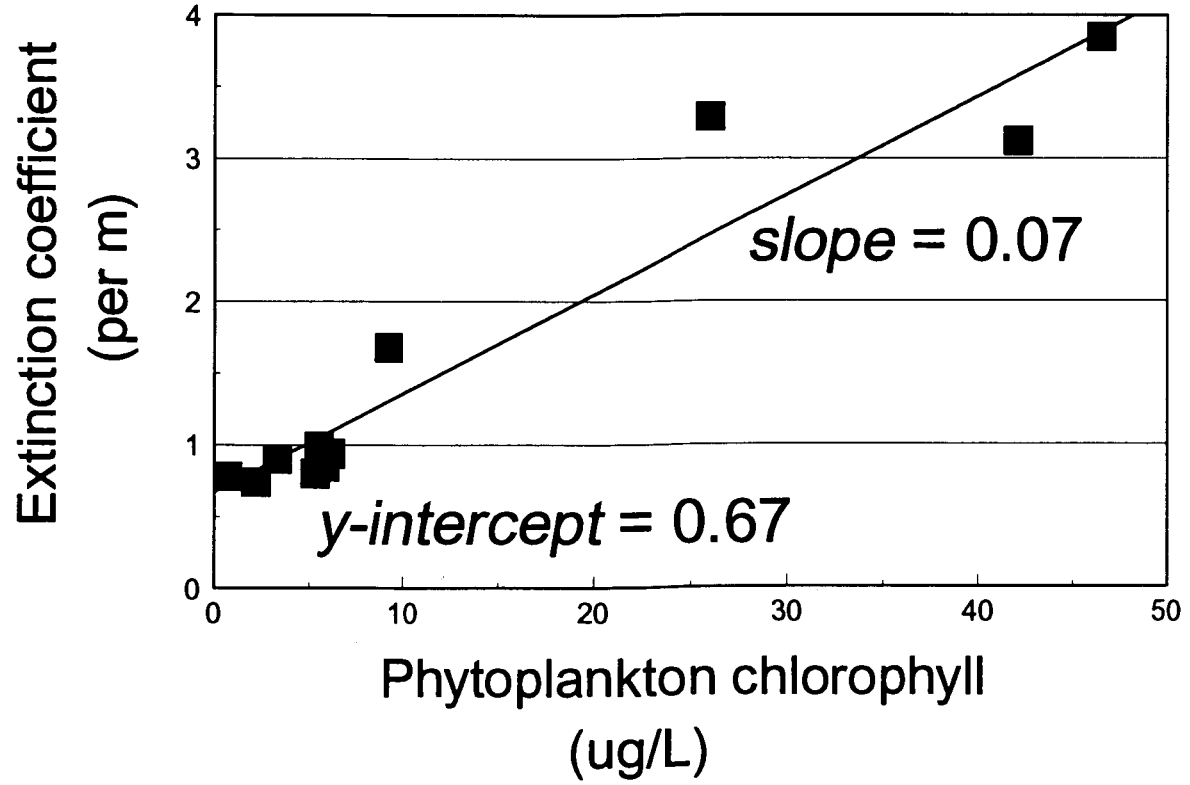

Extinction coefficient (per m)
4
3
2
1
0
slope = 0.07
y-intercept = 0.67
0
10
20
30
40
50
Phytoplankton chlorophyll (ug/L)

Figure 3.7. Extinction coefficients for South Lake and the Control. Negative numbers refer to pre-experimental observations in South Lake.

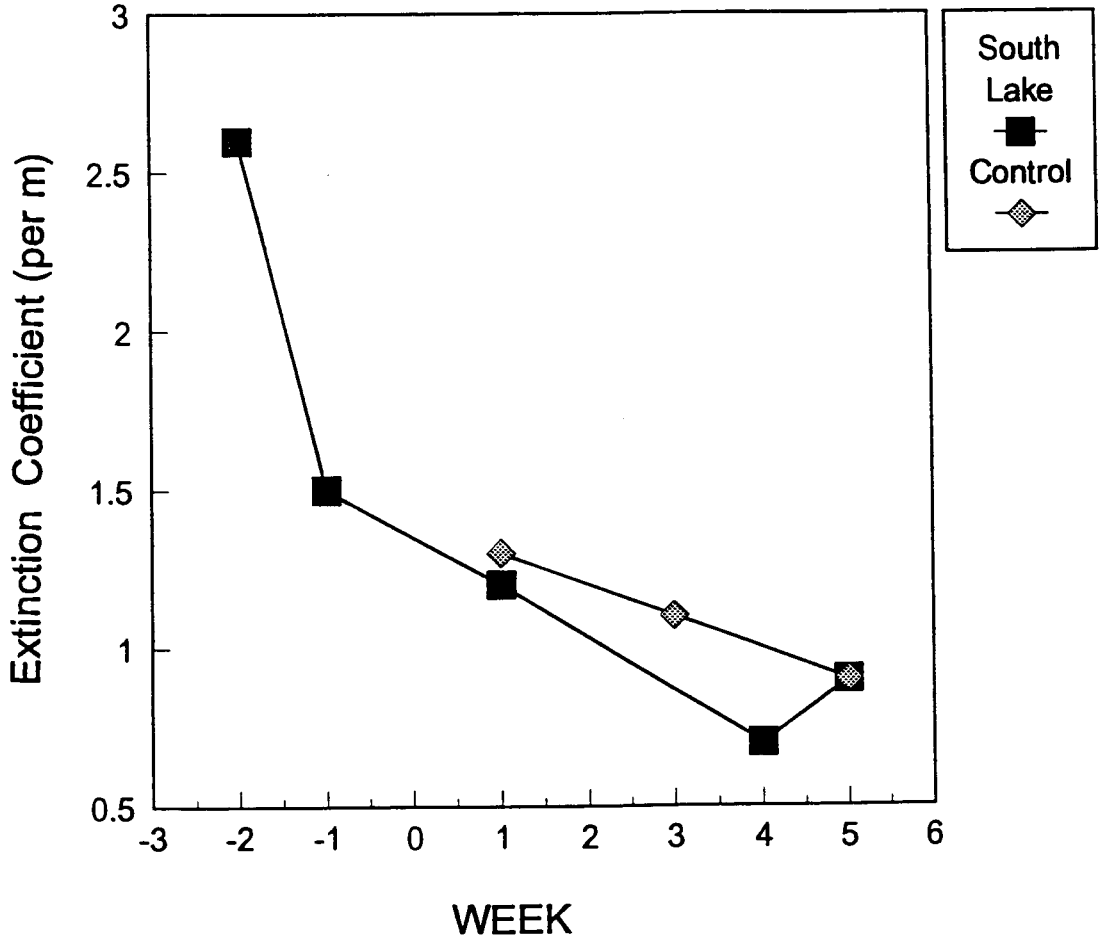

Extinction Coefficient (per m)
3
2.5
2
1.5
1
0.5
-3
-2
-1
0
1
2
3
4
5
6
WEEK
South Lake
Control

Figure 3.8. Sediment settling rates derived over a 24-hour period following dosing for the Control and treatments.

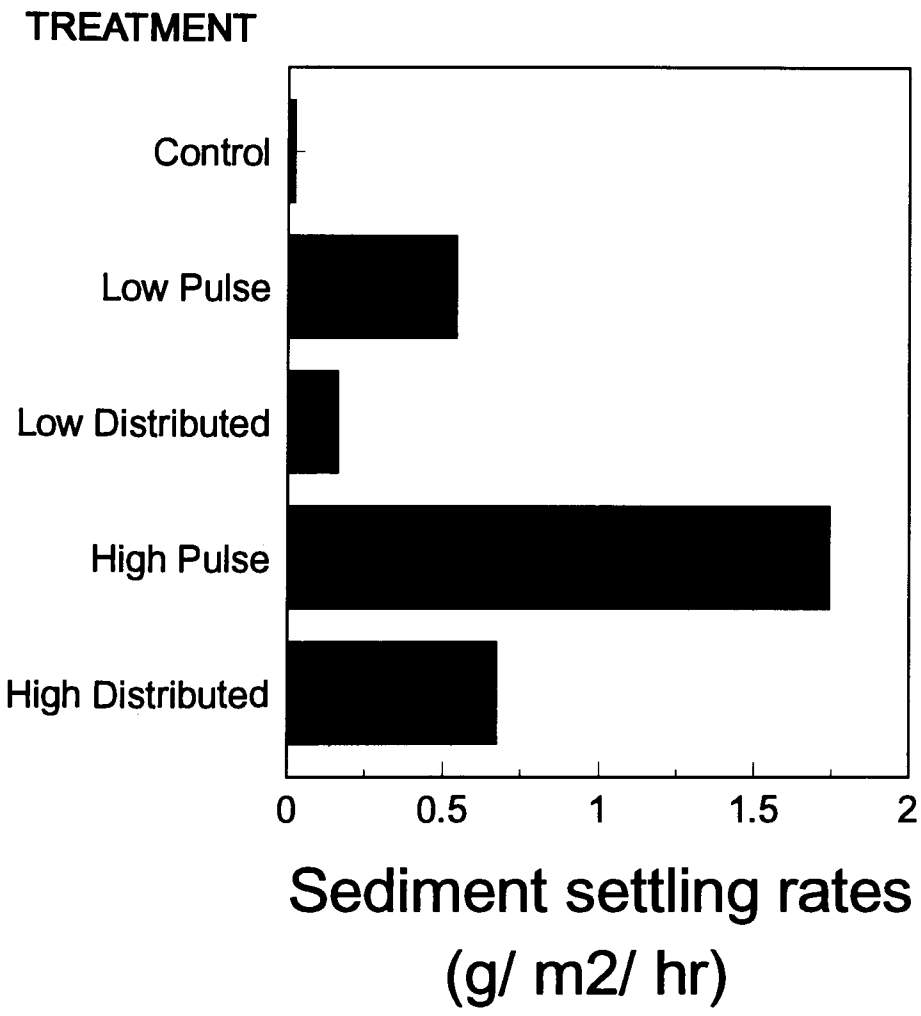

TREATMENT
Control
Low Pulse
Low Distributed
High Pulse
High Distributed
0
0.5
1
1.5
2
Sediment settling rates
(g/ m2/ hr)

Figure 3.9. Total suspended sediment treatment means vs weekly target additions.

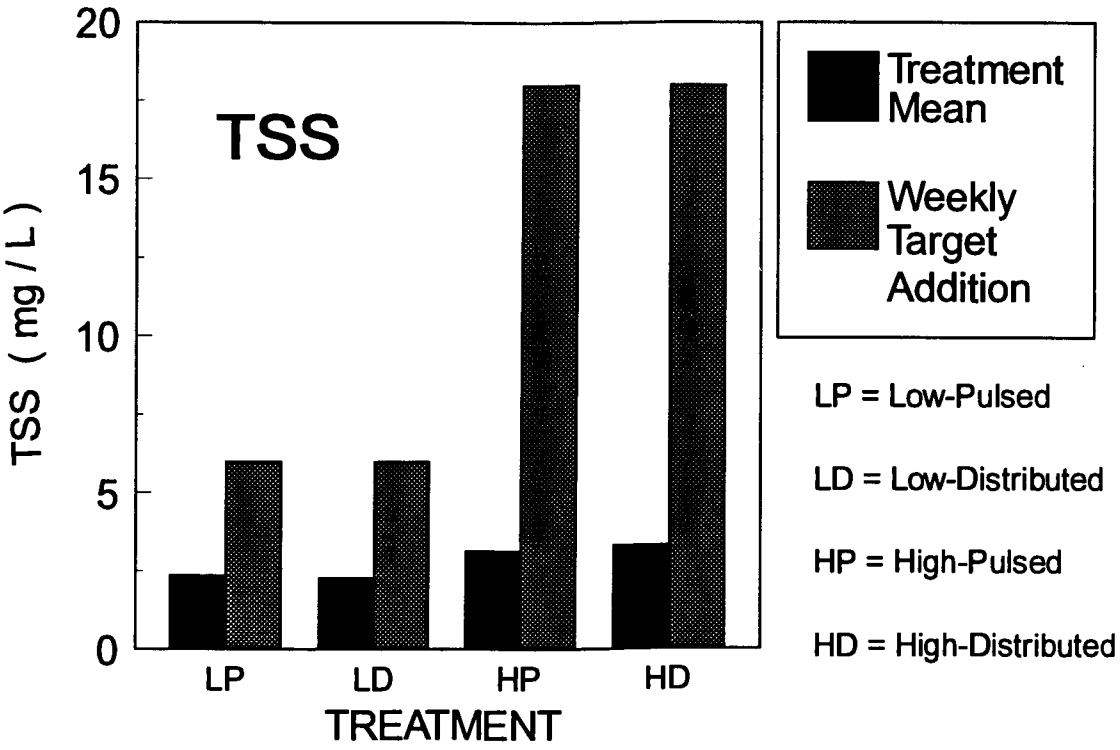

TSS
20
15
10
5
0
TSS (mg / L)
LP
LD
HP
HD
TREATMENT
Treatment Mean
Weekly Target Addition
LP = Low-Pulsed
LD = Low-Distributed
HP = High-Pulsed
HD = High-Distributed

Figure 3.10. Results of grain-size analysis for sediments from South Lake Channel.

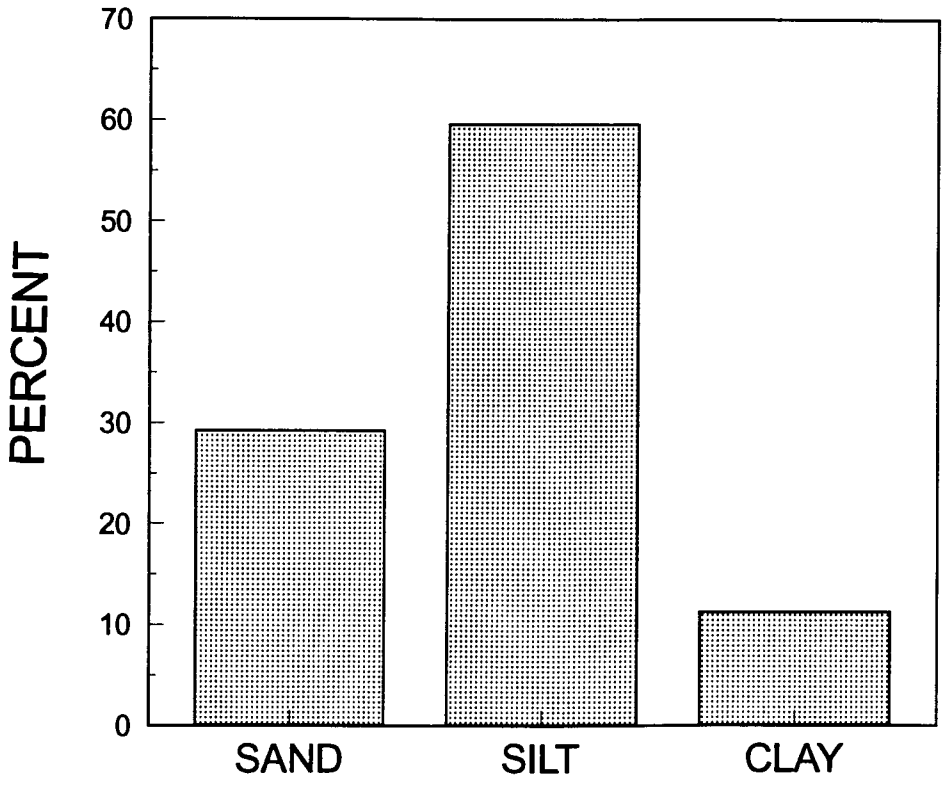

70
60
50
40
30
20
10
0
PERCENT
SAND
SILT
CLAY

Figure 3.11. Total suspended sediments before and after dosing compared to weekly target additions (**A**), phosphate before and after dosing compared to weekly target additions (**B**), and nitrate before and after dosing compared to weekly target additions (**C**).

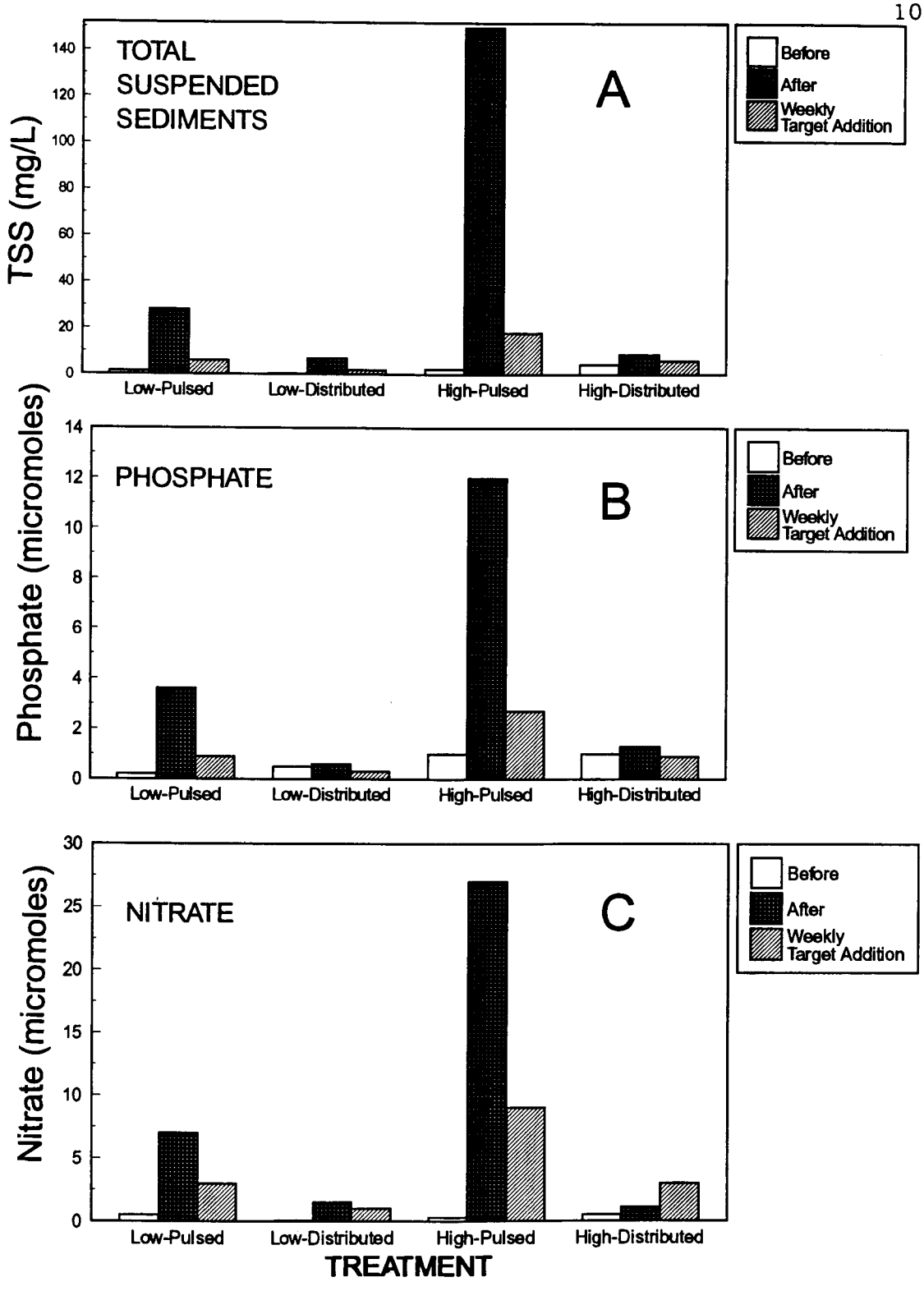
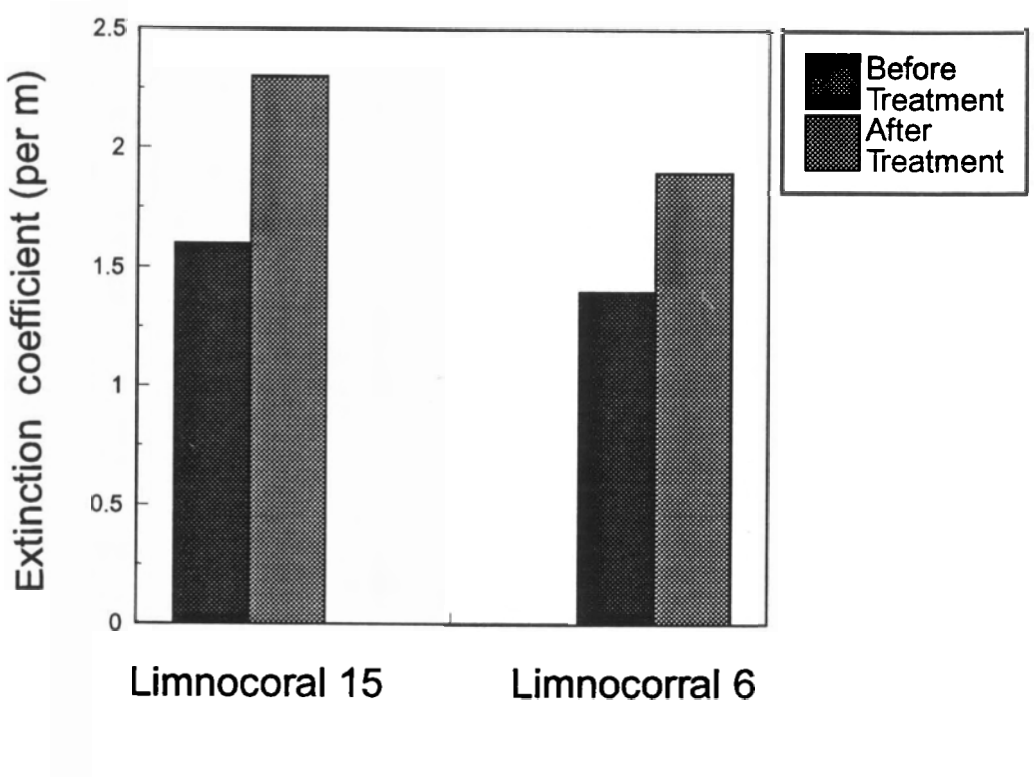

TOTAL
SUSPENDED
SEDIMENTS
A
TSS (mg/L)
140
120
100
80
60
40
20
0
Low-Pulsed
Low-Distributed
High-Pulsed
High-Distributed
Before
After
Weekly
Target Addition
PHOSPHATE
B
Phosphate (micromoles)
14
12
10
8
6
4
2
0
Low-Pulsed
Low-Distributed
High-Pulsed
High-Distributed
Before
After
Weekly
Target Addition
NITRATE
C
Nitrate (micromoles)
30
25
20
15
10
5
0
Low-Pulsed
Low-Distributed
High-Pulsed
High-Distributed
TREATMENT
Before
After
Weekly
Target Addition

Figure 3.12. Light extinction before and after dosing with sediment-nutrient additions to High-Distributed limnocorrals.



HIGH-DISTRIBUTED TREATMENT

Figure 3.13. Total suspended concentrations over the course of the experiment for South Lake, the Control and treatments.

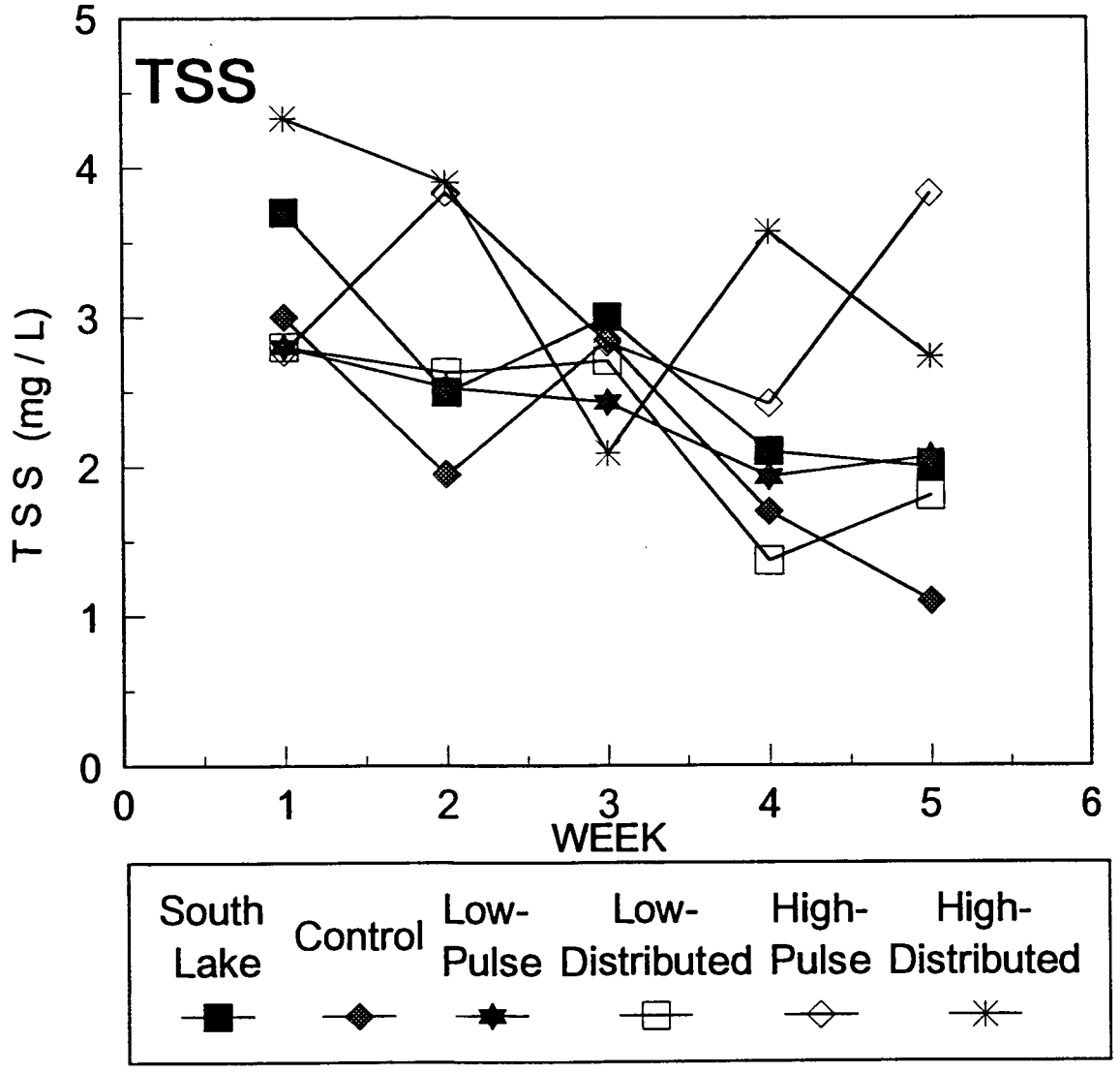

TSS
TSS (mg / L)
WEEK
0
1
2
3
4
5
6
South Lake
Control
Low-Pulse
Low-Distributed
High-Pulse
High-Distributed

Figure 3.14. Phosphate, nitrate and ammonium means for South Lake, the Control and treatments.

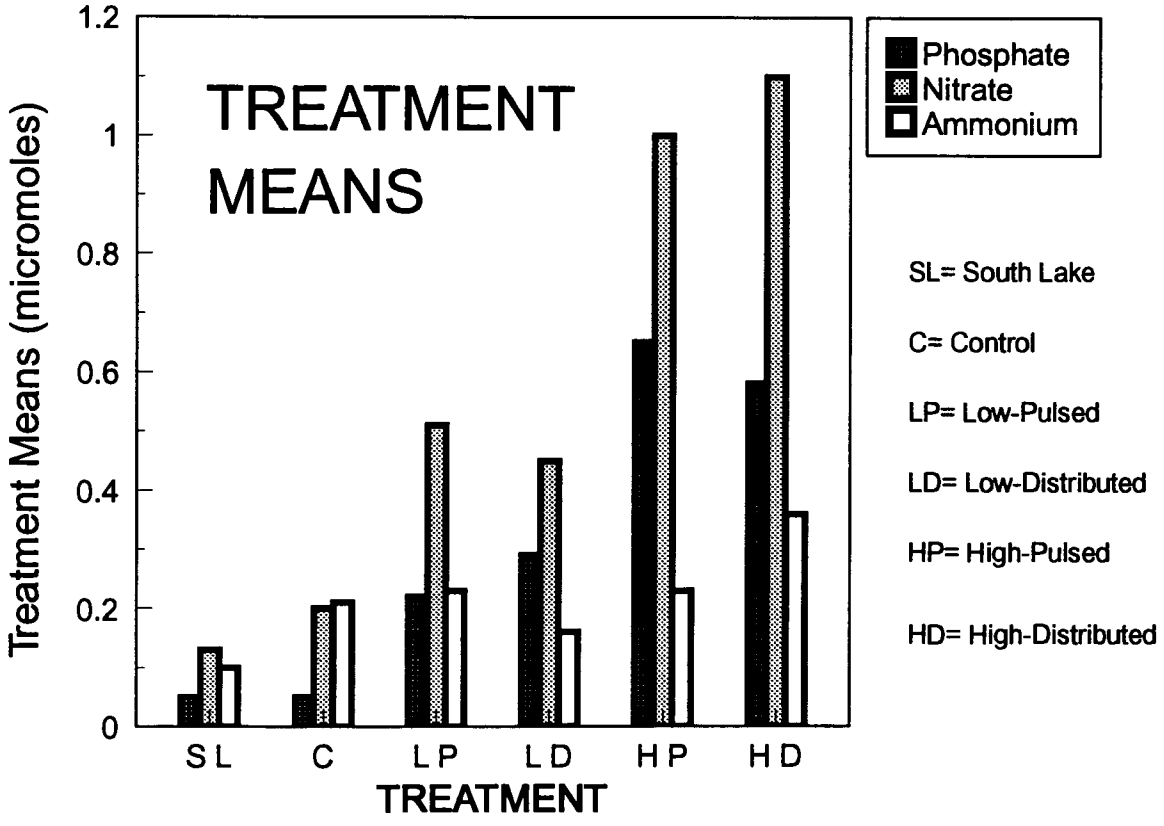

TREATMENT MEANS
Treatment Means (micromoles)
1.2
1
0.8
0.6
0.4
0.2
0
SL
C
LP
LD
HP
HD
TREATMENT
Phosphate
Nitrate
Ammonium
SL= South Lake
C= Control
LP= Low-Pulsed
LD= Low-Distributed
HP= High-Pulsed
HD= High-Distributed

Figure 3.15. Phosphate treatment means vs weekly target additions.

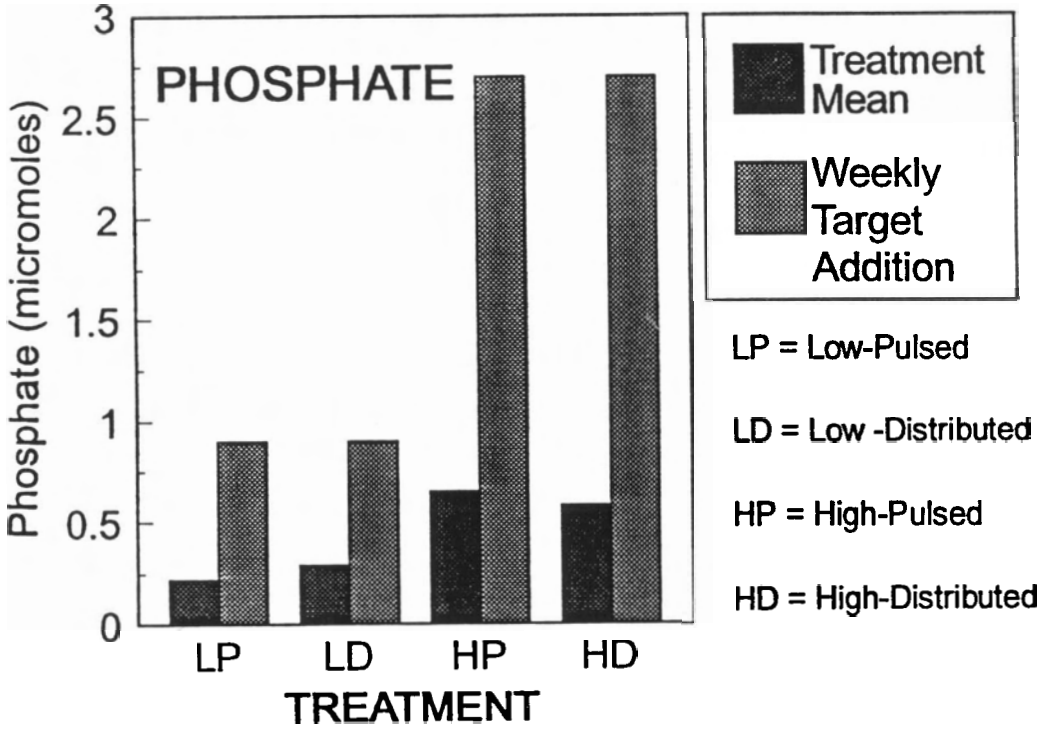

PHOSPHATE
Phosphate (micromoles)
3
2.5
2
1.5
1
0.5
0
LP
LD
HP
HD
TREATMENT
Treatment Mean
Weekly Target Addition
LP = Low-Pulsed
LD = Low -Distributed
HP = High-Pulsed
HD = High-Distributed

Figure 3.16. Nitrate treatment means vs weekly target additions.

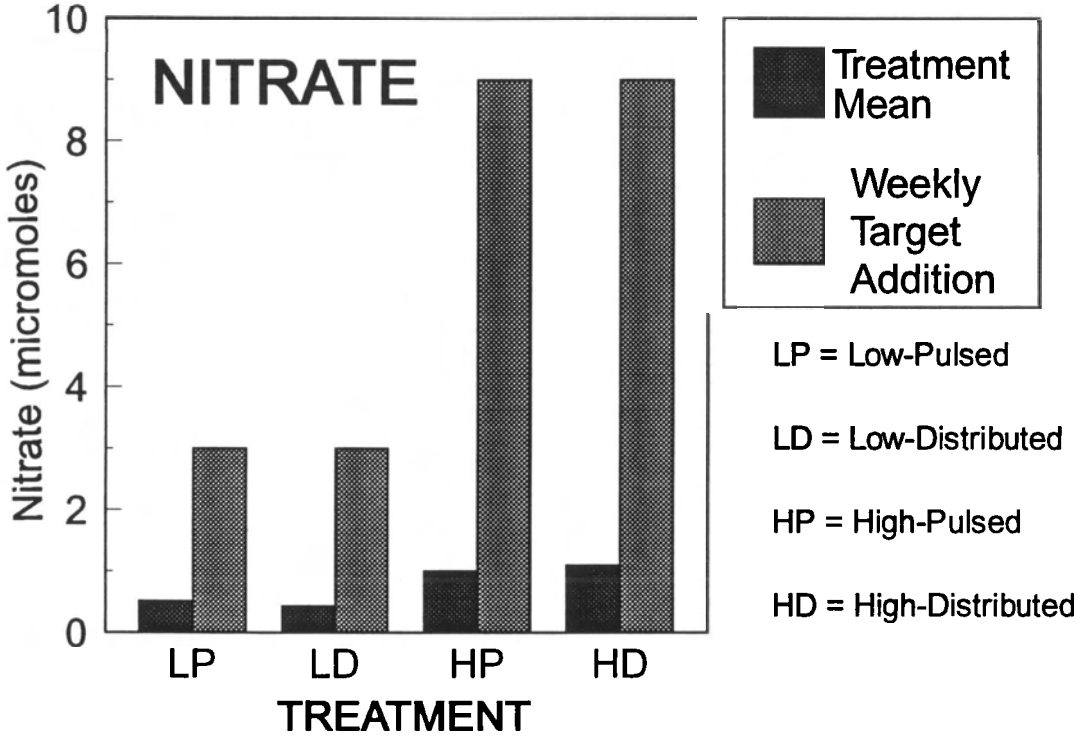

NITRATE
Nitrate (micromoles)
10
8
6
4
2
0
LP
LD
HP
HD
TREATMENT
Treatment Mean
Weekly Target Addition
LP = Low-Pulsed
LD = Low-Distributed
HP = High-Pulsed
HD = High-Distributed

Figure 3.17. Phytoplankton chlorophyll *a* concentrations over the course of the experiment for South Lake, the Control and treatments.

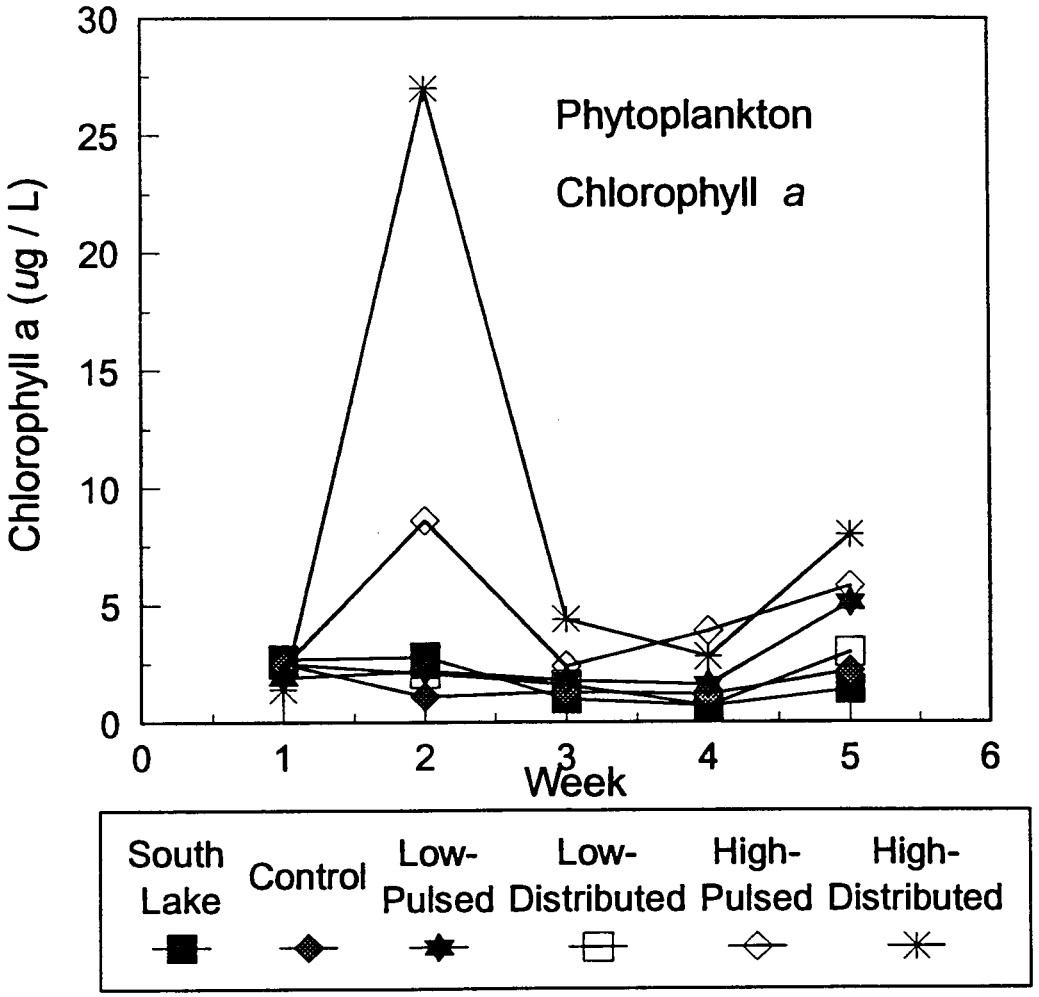

Phytoplankton
Chlorophyll a
Chlorophyll a (ug / L)
30
25
20
15
10
5
0
0
1
2
3
4
5
6
Week
South Lake
Control
Low-Pulsed
Low-Distributed
High-Pulsed
High-Distributed

Figure 3.18. Phosphate concentrations over the course of the experiment for South Lake, the Control and treatments. Note that the sampling regime changed in week 5 from the day before dosing to the day after dosing.

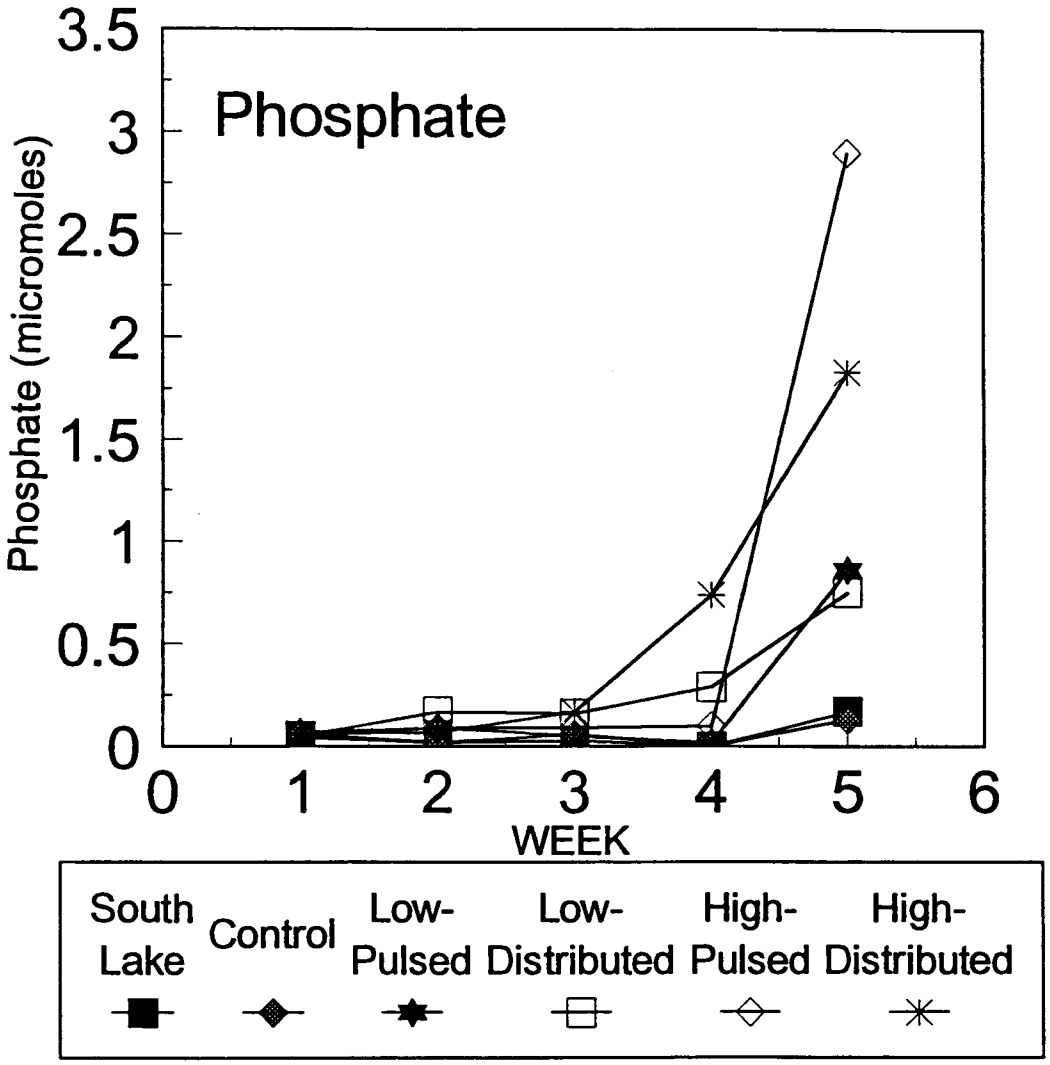

Phosphate
Phosphate (micromoles)
3.5
3
2.5
2
1.5
1
0.5
0
0
1
2
3
4
5
6
WEEK
South Lake
Control
Low-Pulsed
Low-Distributed
High-Pulsed
High-Distributed

Figure 3.19. Nitrate concentrations over the course of the experiment for South Lake, the Control and treatments. Note that the sampling regime changed in week 5 from the day before dosing to the day after dosing.

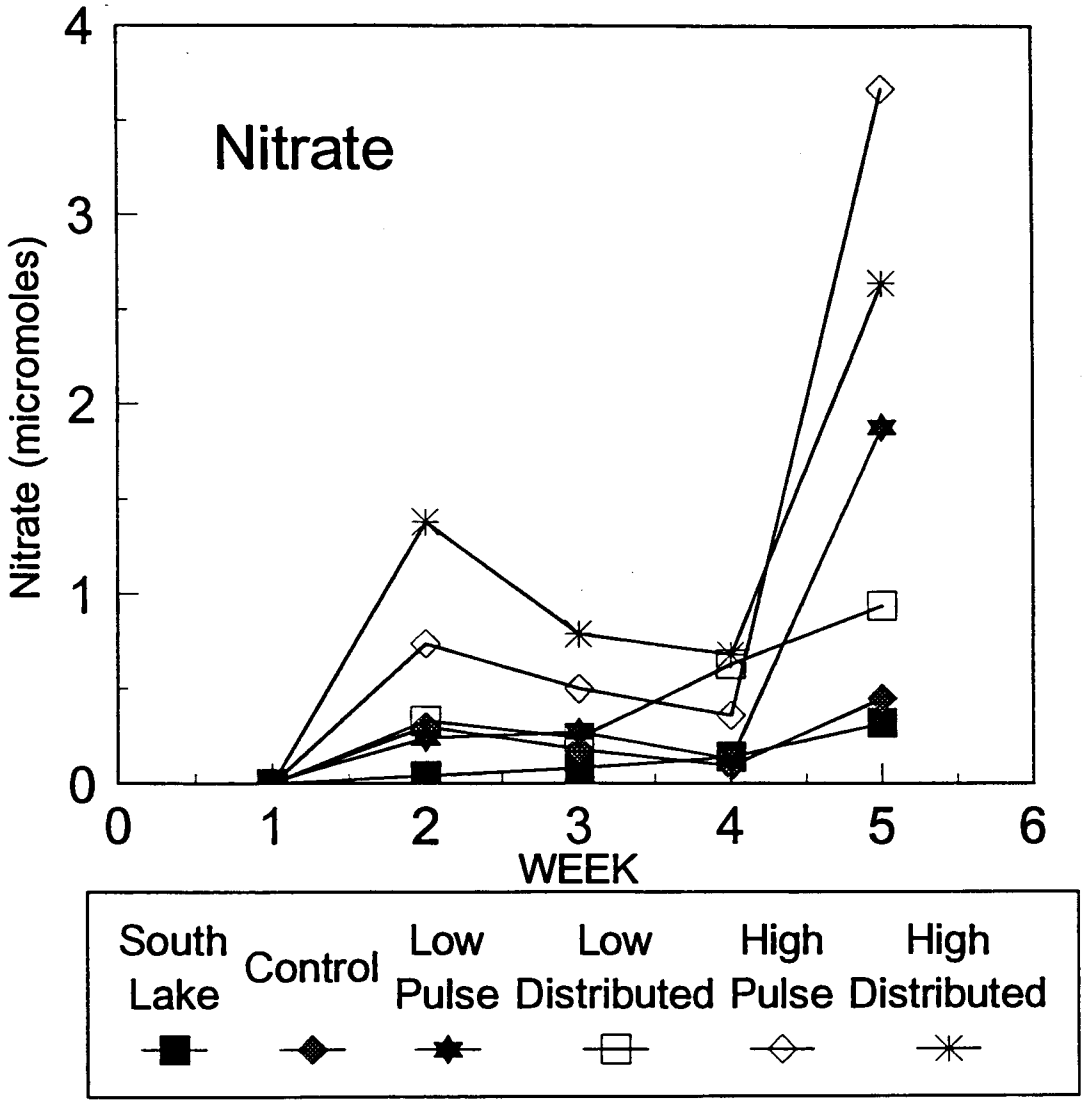

Nitrate
Nitrate (micromoles)
0
1
2
3
4
0
1
2
3
4
5
6
WEEK
South Lake
Control
Low Pulse
Low Distributed
High Pulse
High Distributed

Figure 3.20. Benthic algal biomass accrual over the course of the experiment for the Control and treatments.

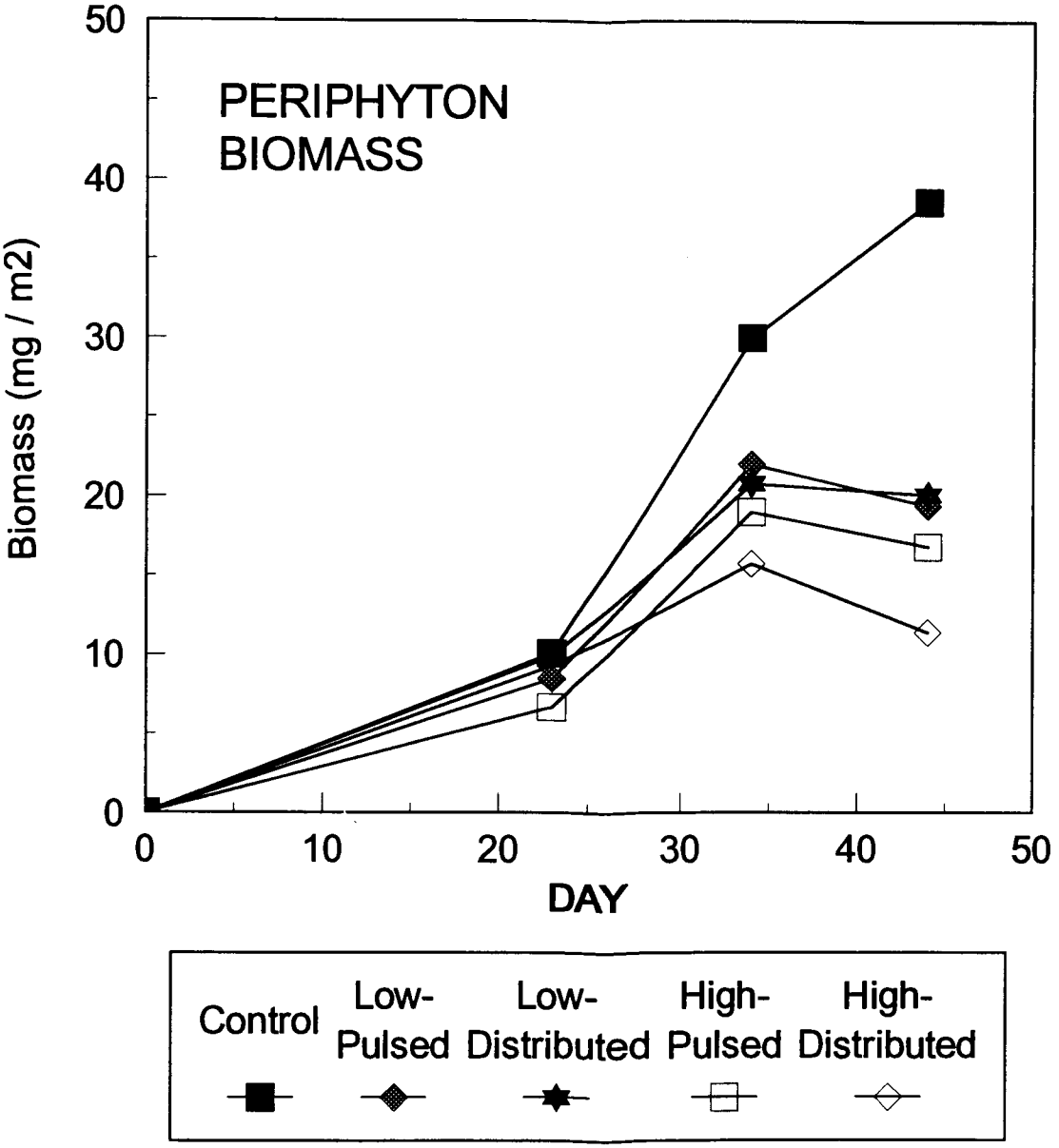

PERIPHYTON
BIOMASS
Biomass (mg / m2)
50
40
30
20
10
0
0
10
20
30
40
50
DAY
Control
Low-Pulsed
Low-Distributed
High-Pulsed
High-Distributed

Figure 3.21. Benthic algal growth rates on the artificial substrates for the colonization and exponential growth stanzas.

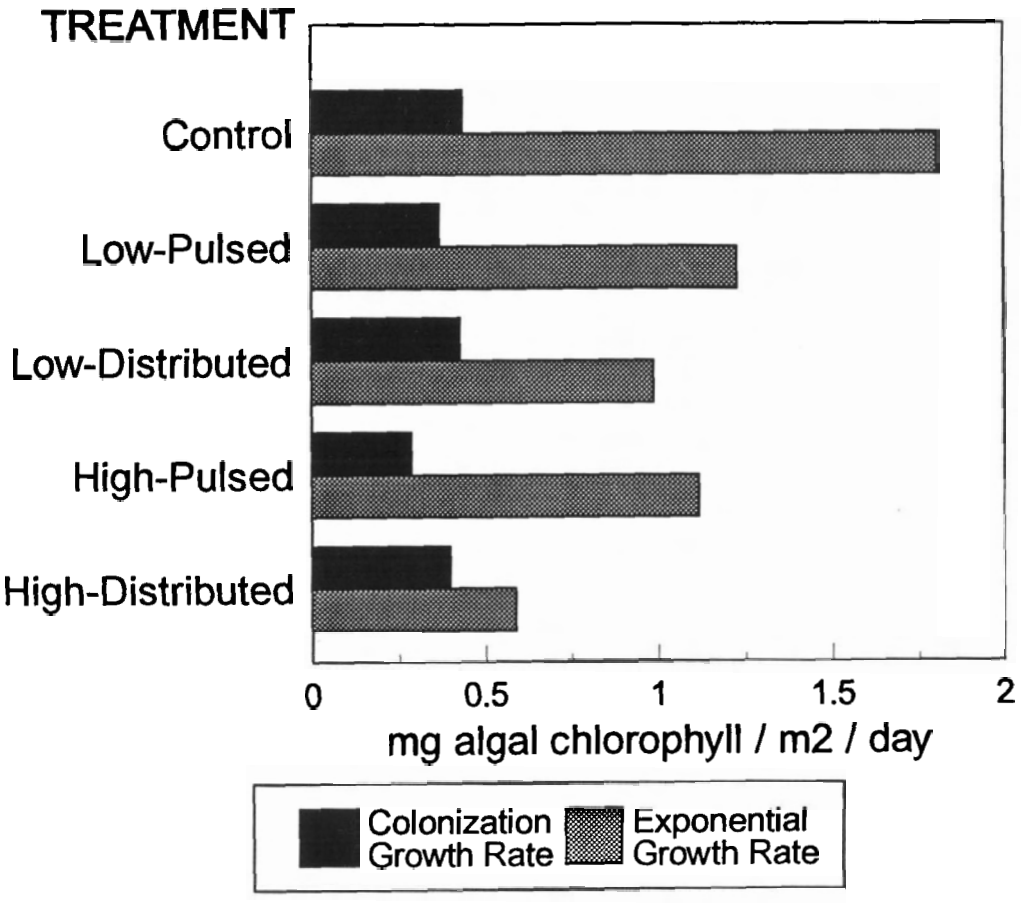

TREATMENT
Control
Low-Pulsed
Low-Distributed
High-Pulsed
High-Distributed
0
0.5
1
1.5
2
mg algal chlorophyll / m2 / day
Colonization Growth Rate
Exponential Growth Rate

Figure 3.22. Benthic algal average areal net photosynthesis (± 1 SE) , corrected for irradiance, for the Control and treatments. (a is different from c & d; b is different from c).

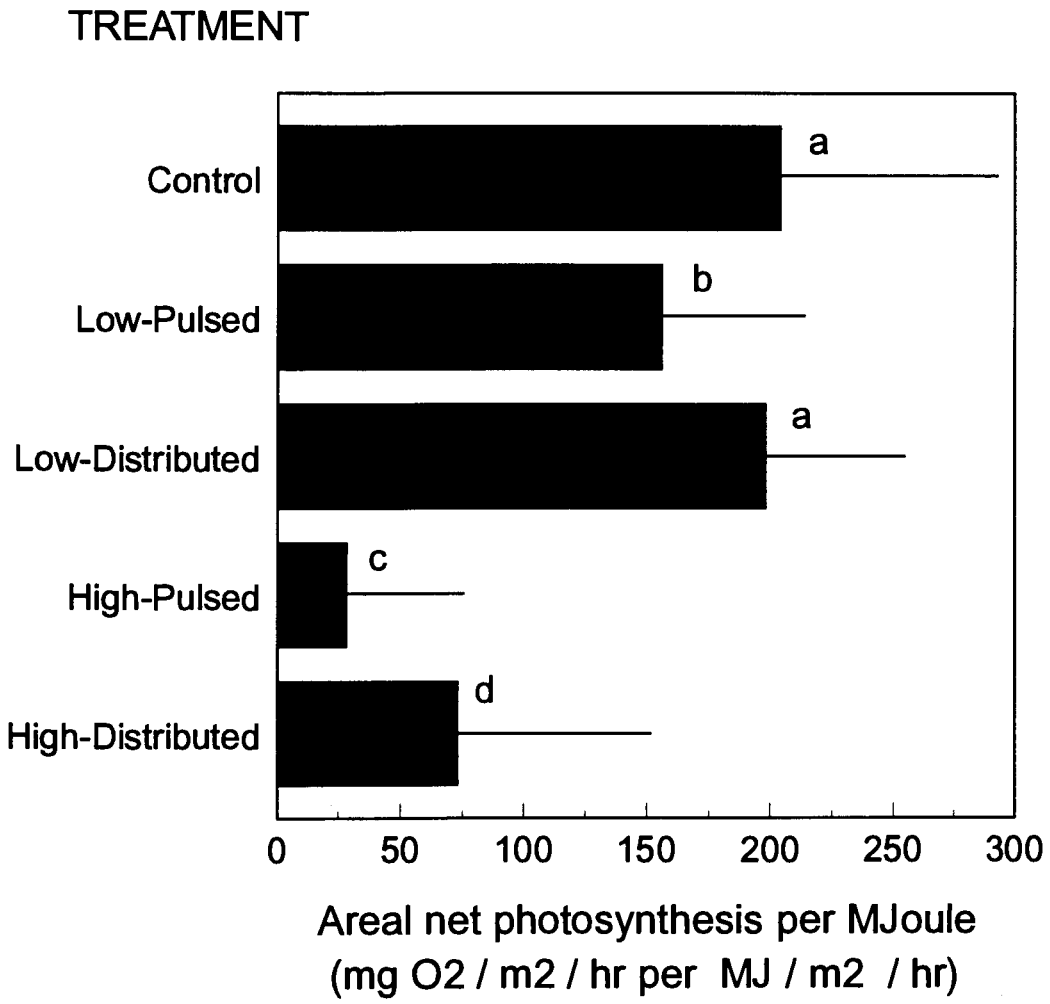

TREATMENT
Control
Low-Pulsed
Low-Distributed
High-Pulsed
High-Distributed
a
b
a
c
d
0
50
100
150
200
250
300
Areal net photosynthesis per MJoule
(mg O2 / m2 / hr per MJ / m2 / hr)

Figure 3.23. Benthic algal average biomass specific net photosynthesis (± 1 SE) , corrected for irradiance, for the Control and treatments.

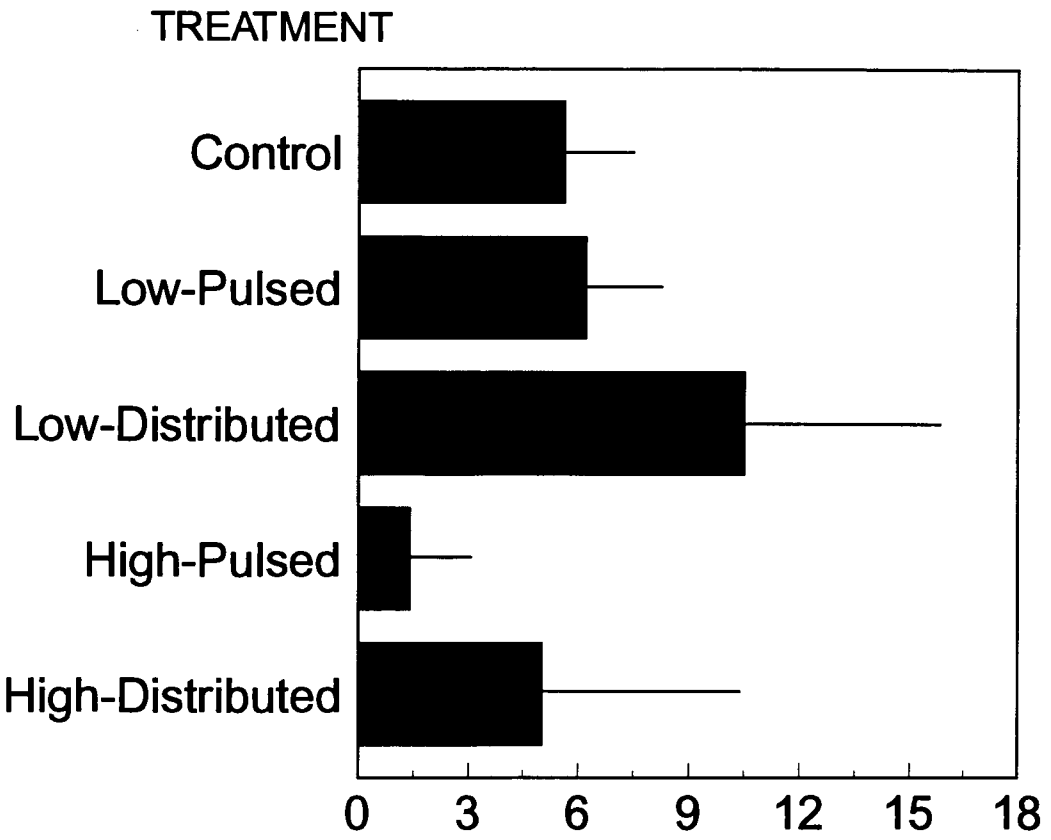
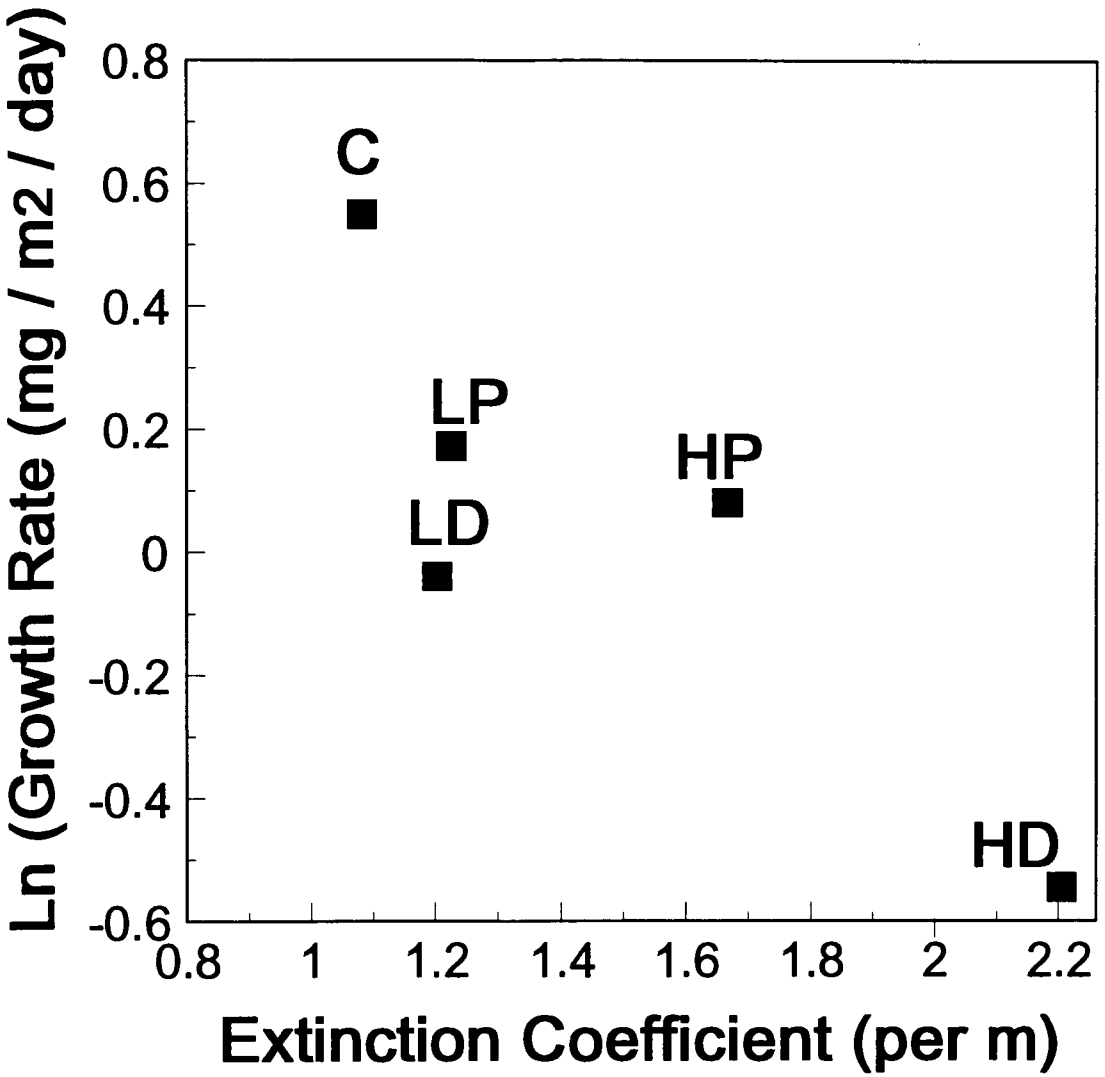

TREATMENT
Control
Low-Pulsed
Low-Distributed
High-Pulsed
High-Distributed
0
3
6
9
12
15
18
Biomass specific net photosynthesis per MJoule
(mg O2 / mg chlorophyl l/ MJ)

Figure 3.24. Relation between natural log of growth rate and light extinction among the Control and treatments.

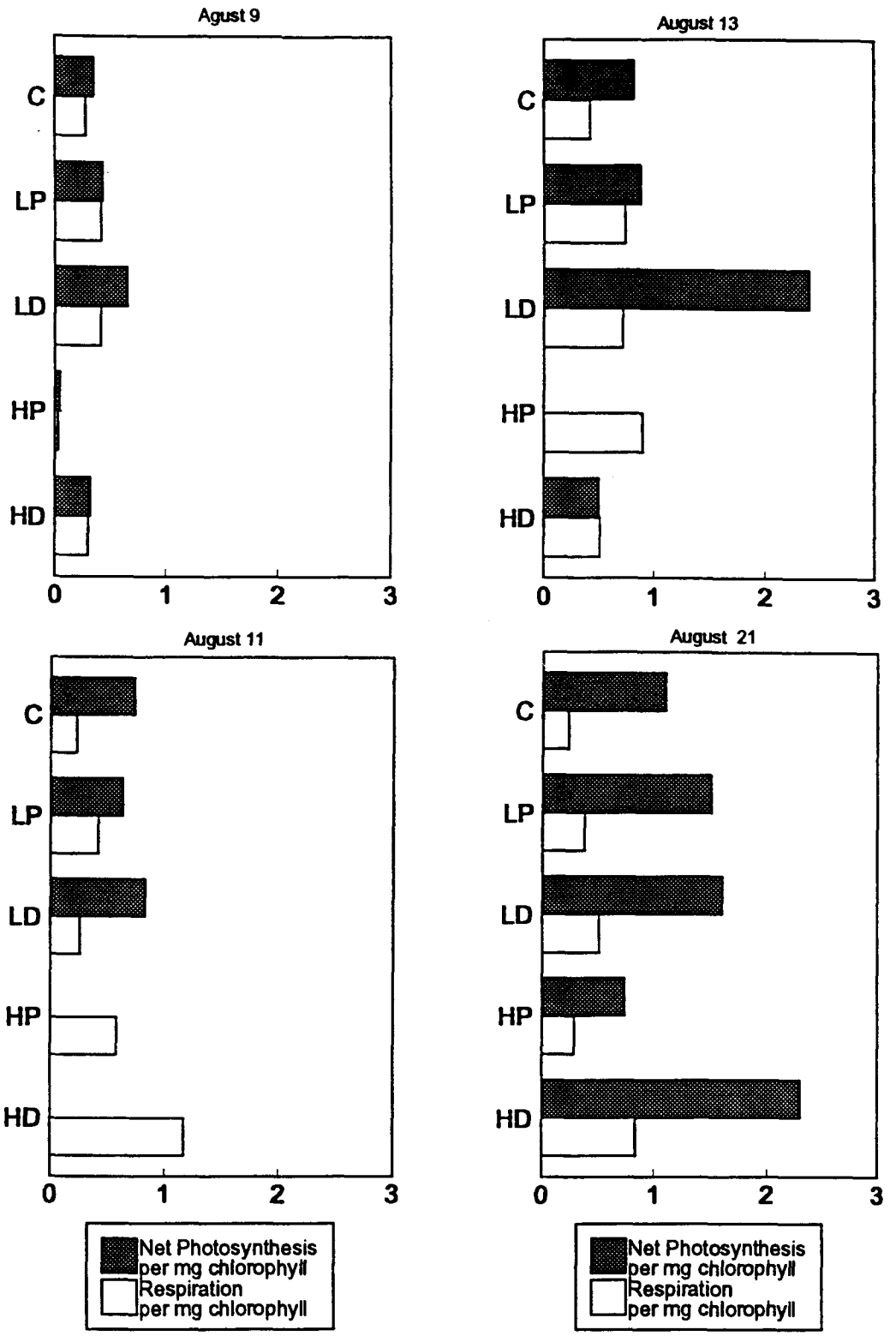


C = Control HP = High--Pulsed

LP = Low-Pulsed HD = High-Distributed

LD = Low- Distributesd

Figure 3.25. Benthic algal biomass specific respiration compared to biomass specific net photosynthesis for the Control and treatments per incubation day.



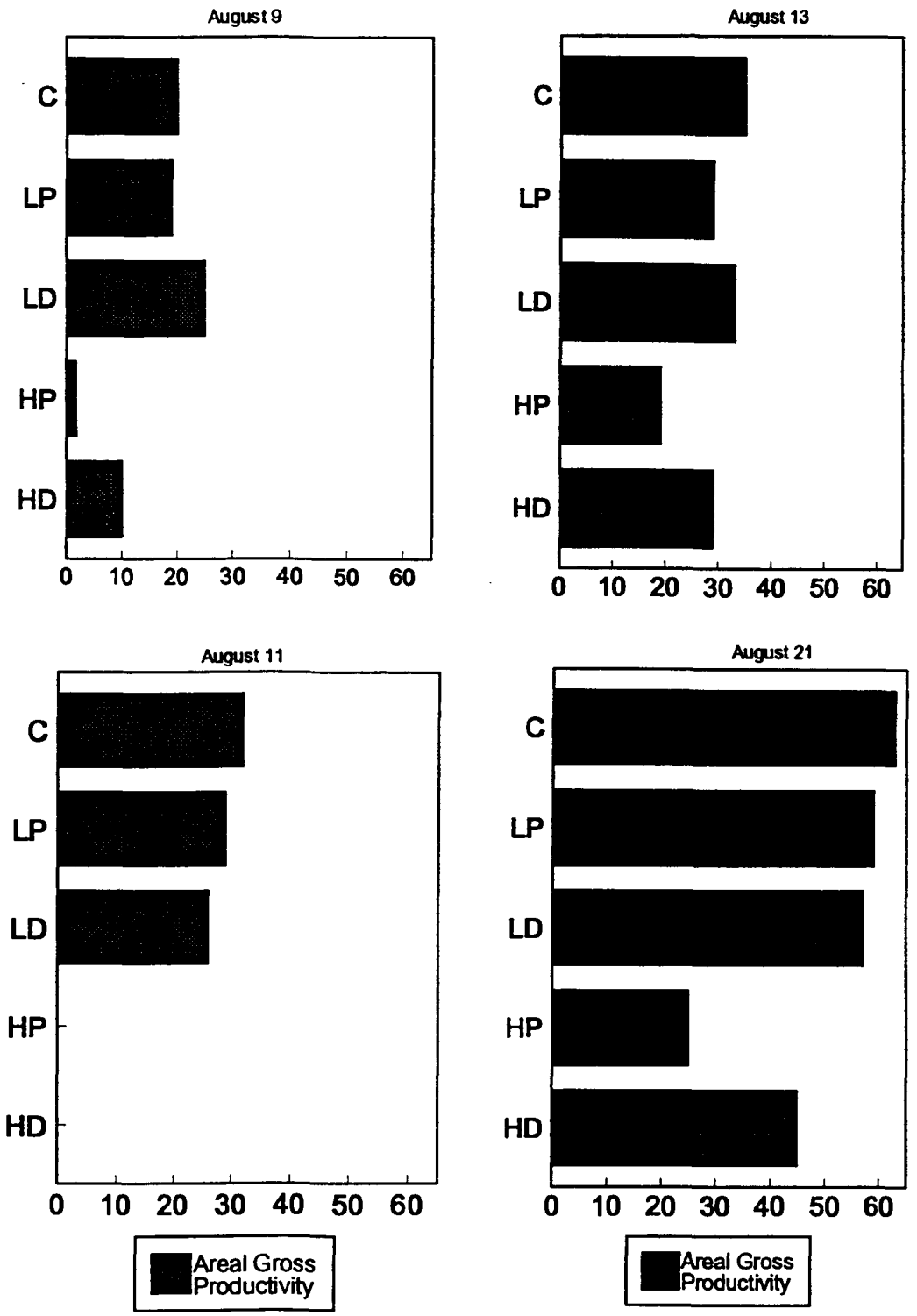
mg O2 / hr / mg chlorophyll

C = Control HP = High-Pulsed

LP = Low-Pulsed HD = High-Distributed

LD = Low-Distributed

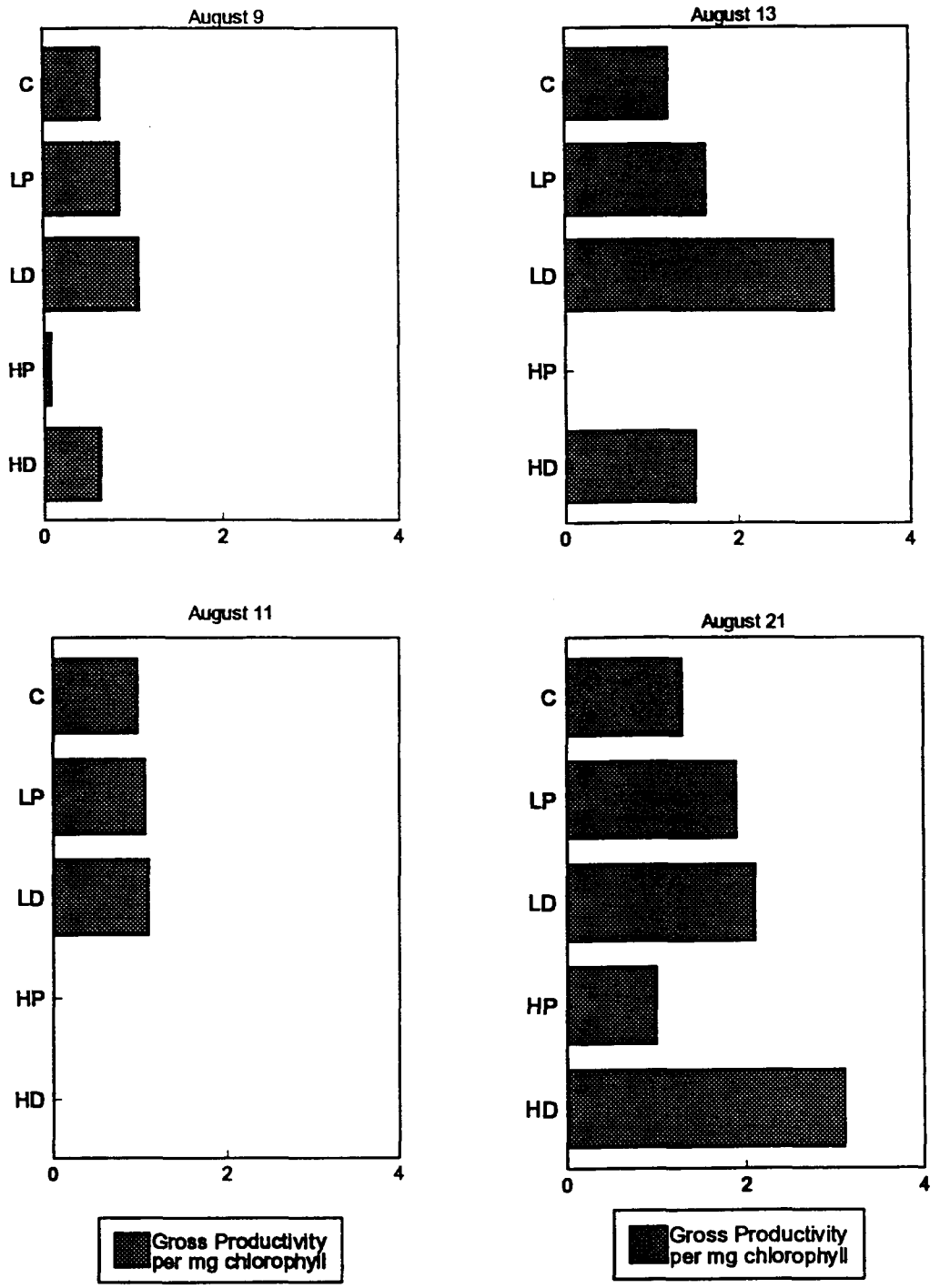
Figure 3.26. Benthic algal areal gross productivity for the Control and treatments per incubation day.



mg O2 / m2 / hr

C = Control HP = High-Pulsed
LP = Low -Pulsed HD = High-Distributed
LD = Low -Distributed

Figure 3.27. Benthic algal gross productivity per mg algal chlorophyll for the Control and treatments per incubation day.



mg O2 / hr / mg chlorophyll

C = Control
HP = High-Pulsed
LP= Low-Pulsed
HD = High-Distributed
LD = Low- Distributed

TABLE 3.1.

Regression R-squared, standard errors and p values for the empirical relation established between light extinction and the variables ln(TSS) and phytoplankton chlorophyll.

variable	std. error	P-value	R-squared
Extinction	0.198	0.002	0.91
constant	0.178	0.14	
ln(TSS)	0.195	0.03	
chlorophyll	0.133	0.3	

TABLE 3.2.

Summary of Kruskal-Wallis test (K-W) and multiple comparisons (Test Stats & p values) for LIGHT EXTINCTION. (df = degrees of freedom) Stastistic designated by * p=0.1; ** p<=0.05.

	Test Stat	p value
Treatment (single grouping factor) (df = 4)	11.99	0.017 **
multiple comparisons		
Control vs Low-Pulsed (df = 1)	10.5	0.67
Control vs Low-Distributed (df = 1)	13.5	0.83
Control vs High-Pulsed (df = 1)	4	0.07 *
Control vs High-Distributed (df = 1)	2.5	0.03 **
Low-Pulsed vs Low-Distributed (df = 1)	15	0.59
Low-Pulsed vs High-Pulsed (df = 1)	3.5	0.05 **
Low-Pulsed vs High-Distributed (df = 1)	1.5	0.02 **
Low-Distributed vs High-Pulsed (df = 1)	2	0.02 **
Low-Distributed vs High-Distributed (df = 1)	1	0.02 **
High-Pulsed vs High-Distributed (df = 1)	9.5	0.52

TABLE 3.3.

Summary of ANOVA, Kruskal-Wallis test (K-W) and multiple comparisons (Test Stats & p values) for TSS and PHYTOPLANKTON CHLOROPHYLL. (df = degrees of freedom) Statistics designated by *p = 0.1; ** p <= 0.05.

ANOVA : TSS	F - value	p value	
Source of variation between subjects			
Effect of sediment-nutrient additions (df = 2	7.542	0.008	**
Effect of delivery regime (df = 2)	0.626	0.56	
Error (df = 12)			
ANOVA : CHLOROPHYLL			
Source of variation between subjects			
Effect of sediment-nutrient additions (df = 2	7.271	0.009	**
Effect of delivery regime (df = 2)	1.596	0.24	
Error (df = 12)			
K-W: TSS	Test Stat	p value	
Treatment (single grouping factor) (df = 4)	9.364	0.05	**
multiple comparisons			
Control vs Low-Pulsed (df = 1)	88	0.31	
Control vs Low-Distributed (df = 1)	100	0.60	
Control vs High-Pulsed (df = 1)	62	0.03	**
Control vs High-Distributed (df = 1)	63.5	0.04	**
Low-Pulsed vs Low-Distributed (df = 1)	123.5	0.65	
Low-Pulsed vs High-Pulsed (df = 1)	62.5	0.04	**
Low-Pulsed vs High-Distributed (df = 1)	81	0.19	
Low-Distributed vs High-Pulsed (df = 1)	60	0.03	**
Low-Distributed vs High-Distributed (df = 1)	72.5	0.10	*
High-Pulsed vs High-Distributed (df = 1)	104	0.11	*
K-W: CHLOROPHYLL			
Treatment (single grouping factor) (df = 4)	6.023	0.2	
multiple comparisons			
Control vs Low-Pulsed (df = 1)	84	0.24	
Control vs Low-Distributed (df = 1)	109.5	0.90	
Control vs High-Pulsed (df = 1)	65.5	0.05	**
Control vs High-Distributed (df = 1)	75.5	0.11	*
Low-Pulsed vs Low-Distributed (df = 1)	127	0.55	
Low-Pulsed vs High-Pulsed (df = 1)	91	0.37	
Low-Pulsed vs High-Distributed (df = 1)	87.5	0.30	
Low-Distributed vs High-Pulsed (df = 1)	67.5	0.06	*
Low-Distributed vs High-Distributed (df = 1)	80.5	0.18	
High-Pulsed vs High-Distributed (df = 1)	105	0.75	

TABLE 3.4.

Diffision coefficients for nutrients in sediment
(**D s**) at 18 degrees Celsius.

Nutrient	**D s** (10-6 cm2 sec-1)
(H2)PO4	4.93
NH4	11.59
NO3	11.11

TABLE 3.5.

Derivatives (dC/dz) of nutrient concentration gradients at the sediment/water interface.

	date	PO4	NO3	NH4
			(umol cm-1)	
South Lake	05-Jun-95	-0.96	-1.15	-0.15
Control	20-Jul-95		-1.58	-0.10
High Frequent	23-Jul-95	-1.75	-0.46	-0.31
	average slope	-1.35	-1.06	-0.18

TABLE 3.6.

Diffusive flux of nutrients from South Lake sediments.

	porosity		
	0.7	0.8	0.9
	Diffusive fluxes (uM / m2/ day)		
PO4	4.0	4.6	5.2
NO3	7.9	8.5	9.5
NH4	1.3	1.4	1.5

TABLE 3.7.

Summary of ANOVAs and multiple comparisons (Test Stats & p values) for BENTHIC ALGAL ACCRUAL. (df = degrees of freedom)
Statistics designated as * p = 0.1; ** p <= 0.05

			Day 23		Day 34		Day 44	
ANOVA (with Control)	F - value	p value	F- value	p value	F- value	p value	F- value	p value
Source of variation betwteen subjects								
Sediment-nutrient additions (df = 2)	7.592	0.007 **	0.25	0.78	10.789	0.002 **	8.438	0.005 **
Delivery regime (df = 2)	6.015	0.016 **	0.471	0.63	8.372	0.005 **	7.32	0.009 **
Error (df = 12)								
ANOVA (with Control)								
Source of variation between subjects								
Treatment (single grouping factor) (df = 4)	3.249	0.059	0.264	0.90	5.088	0.02 **	3.844	0.04 **
Error (df = 10)								
FISHER'S LSD for Day 34								
Multiple comparisons								
Control vs Low-Pulsed (df = 1)		0.04 **						
Control vs Low-Distributed (df = 1)		0.14						
Control vs High-Pulsed (df = 1)		0.006 **						
Control vs High-Distributed (df = 1)		0.002 **						
Low-Pulsed vs Low-Distributed (df = 1)		0.53						
Low-Pulsed vs High-Pulsed (df = 1)		0.28						
Low-Pulsed vs High-Distributed (df = 1)		0.1 *						
Low-Distributed vs High-Pulsed (df = 1)		0.62						
Low-Distributed vs High-Distributed (df = 1)		0.28						
High-Pulsed vs High-Distributed (df = 1)		0.53						
ANOVA (without Control)								
Source of variation between subjects								
Sediment-nutrient additions (df = 1)	1.843	0.21	0.241	0.64	2.956	0.11 *	1.372	0.2
Delivery regime (df = 1)	0.107	0.75	0.706	0.43	0.937	0.36	0.239	0.64
Delivery X Sediment-nutrient / additions (df =1)	0.091	0.77	0.078	0.79	0	1	0.402	0.54
Error (df = 8)								

TABLE 3.8.

Summary of Kruskal-Wallis test (K-W) and multiple comparisons (Test Stats and p values) for AREAL NET PHOTOSYNTHESIS. (df= degress of freedom) Statistics designated as * p = 0.1; ** p <= 0.05

	Test Stat	p value	
Treatment (single grouping factor) (df = 4)	14.191	0.04	
multiple comparisons			
Control vs Low-Pulsed (df = 1)	10.5	0.47	
Control vs Low-Distributed (df = 1)	8	1	
Control vs High-Pulsed (df = 1)	15	0.04	**
Control vs High-Distributed (df = 1)	14	0.08	**
Low-Pulsed vs Low-Distributed (df = 1)	4	0.25	
Low-Pulsed vs High-Pulsed (df = 1)	15	0.04	**
Low-Pulsed vs High-Distributed (df = 1)	13	0.15	
Low-Distributed vs High-Pulsed (df = 1)	16	0.02	**
Low-Distributed vs High-Distributed (df = 1)	14	0.08	*
High-Pulsed vs High-Distributed (df = 1)	4	0.25	

TABLE 3.9.

Summary of variables, ranked from 0 (low) to 4 (high), along the transparency gradient from clear to turbid and corresponding treatment levels.

transparency:	CLEAR----------->TURBID				
treatment:	Control	Low-Pulsed	Low-Distributed	High-Pulsed	High-Distributed
variable					
Light extinction	0	1	1	3	4
TSS	1	1	1	3	4
Phytoplankton chlorophyll a	0	1	1	3	4
Phosphorus	0	1	2	4	3
Nitrate	0	2	1	3	4
Biomass accrual	4	2	2	1	0
Areal net photosynthesis*	4	2	3	0	1
Net photosynthesis per mg chlorophyll*	1	2	4	0	2

*photosynthesis rates are corrected for light

Chapter 4 General Discussion

IMPLICATIONS OF RESULTS

This study has further substantiated the established link between the hydrology and the biological productivity of the Mackenzie Delta ecosystem. Specifically, the frequency and duration of river inflow to the Delta lakes has considerable consequences for the productivity of the aquatic plant community including epipelic algae. The major mechanism linking hydrology and productivity in the Delta lake system has been considered to be the light attenuation due to the high suspended sediment loads delivered to the lakes by distributaries of the Mackenzie River, and the related reduction in light availability for primary producers. The results of this study have emphasized the importance of suspended sediments in controlling the light environment of the Delta lakes. Also, this study suggests that nutrients supplied by river water may stimulate phytoplankton growth at intermediate transparencies relative to the clearest and the most turbid lakes. Further, phytoplankton chlorophyll *a* may contribute to light extinction with implications for benthic algal growth in these lakes.

I expected that epipelic algal productivity would be highest where sediment-nutrient additions were low and infrequent. This prediction was based on three assumptions. First, phosphorus rich clay particles which

settle out of the water column might promote algal growth compared to lakes which receive no additional inputs of turbid riverine water after spring break-up. Second, turbidity, due to phytoplankton chlorophyll, might be greater in clear lakes- a result of better average light conditions, than in lakes receiving infrequent sediment inputs. Third, benthic algae with a lower compensation point than phytoplankton should be able to photosynthesize more efficiently than phytoplankton where light is only marginally reduced. Therefore optimal light-nutrient conditions for benthic algal growth might occur when river inflow is infrequent and of low duration. Instead, my study suggests that the relation between transparency and benthic algal productivity is direct. For example, benthic algal biomass accrual and areal net photosynthesis should be greatest in clear lakes and lowest in turbid lakes. In this study benthic algal growth was 3 to 4 fold higher in the Control vs the High-Distributed treatment. I expect that the benthic algal growth corresponding to the full gradient of light transparency experienced among the Mackenzie Delta lakes may potentially range 5 to 10 fold. The relation between benthic algal growth and light is not completely surprising since epipelic algae grows in close proximity to sediments and is in all likelihood supported by nutrient flux from sediments such that nutrients are not likely to limit growth. Therefore production should be proportional to available light. Finally, the relation between sediment-nutrient additions and phytoplankton chlorophyll is opposite to what was predicted. Specifically, phytoplankton growth was not necessarily damped by sediments, but was stimulated by nutrients at intermediate tranparencies.

The relation between phytoplankton productivity and transparency suggested by previous studies of the Delta lakes indicates that phytoplankton response to a wide range of sediment-nutrient conditions may be a small change in productivity. My results suggest that the relation between phytoplankton productivity and transparency may be more complex than previous studies suggest. Specifically, phytoplankton growth may be greatest at intermediate transparencies, between the extreme conditions represented by the clearest and most turbid lakes. Here, average phytoplankton chlorophyll *a* tended to be higher for the high treatments than for the low treatments. Apparently, high sediment-nutrient additions may stimulate phytoplankton growth compared to low or no sediment-nutrient additions. Also, the tendency for phytoplankton chlorophyll *a* to be higher in the High-Distributed relative to the High-Pulsed treatment suggests that the frequency of nutrient additions can have a positive effect on phytoplankton growth (e.g. Bill Neill, pers. comm.). Alternatively, phytoplankton may be equipped to respond to episodic light availability. It is also possible that phytoplankton growth is controlled by interaction between opposing fluctuations in light and nutrient availability. For example, an episode of river inflow may represent conditions of high nutrient but low light availability. A flow reversal, that is water flow out of lakes in response to a fall in water levels in main channels, may represent conditions of low nutrient but high light availability. Finally, the potential contribution of phytoplankton chlorophyll to light extinction, estimated to be 20 to 30 % , may be underappreciated in the Delta lakes.

RECOMMENDATIONS

Two questions stand out as being critical to a complete understanding of the fundamental links between the hydrology and biological productivity of the Mackenzie Delta ecosystem. First, in consideration of the demonstrated importance of benthic algae to higher trophic levels, precise estimates of epipelic algal production among the Delta lakes needs to be coupled with knowledge of the efficiency with which epipelic algal carbon is assimilated into consumer biomass. Second, the relative importance of epiphytes using macrophytes as a substrate for growth to the Delta lake food web requires clarification.

At present it is not clear whether epipelic algal production in the Delta lakes has been underestimated, relative to phytoplankton, or whether epipelic organic matter is of higher quality than phytoplanktonic carbon and therefore more efficiently assimilated into consumer biomass. Brunskill & Rosenberg (1973) observed a substantial increase in zoobenthos density in Delta lakes at TSS less than 10 to 15 mg L^{-1}. Based on my study, if zoobenthos are grazing on epipelic algae, which seems likely, then I expect that benthic feeders increase in density in response to increased algal productivity as lakes improve in water clarity. A clear understanding of the mechanisms responsible for the substantial transfer of benthic algal carbon to higher trophic levels requires that estimates of algal productivity be coupled with information about the efficiency of assimilation of algal organic matter by grazers.

Although macrophyte production (based on harvest techniques that included separation of epiphytes from macrophytes) dominates total net

photosynthesis in clear lakes and may be substantial in the littoral zones of lakes with intermediate transparencies, stable isotope analysis has demonstrated that macrophytic carbon is of little importance to the Delta lake food web. Macrophytes may be important to lake productivity in other ways. For example, it is possible that the epiphytic algae colonizing macrophytes contribute substantially to the Delta food web. Also, extensive macrophyte growth will shade bottom sediments and thereby reduce illumination and productivity of benthic algae with potential implications for the importance of epiphytic algae relative to benthic algae to consumers.

Alternatives to analysis of the Delta lake food web by stable isotopes are required to establish the importance of epiphytic algal carbon to higher trophic levels since it is indistinguishable from terrestrial detritus. In the event that its importance is demonstrated, future work should examine controls on epiphytic productivity among the Delta lakes and the grazer community associated with epiphytes.

Based on the results of this study I can make four recommendations for future research aimed at improving our general understanding of the role of periphyton, including epiphytes, to the Delta lake food web. First, while the substrata on which macrophytes and epipelic algae grow represents an environment where nutrients are not likely to limit growth, it should not be presumed that the only consequence of riverine inflow for benthic production is the effect of suspended sediments on light extinction. For example, in this study the light available to benthic producers was apparently controlled by both TSS and the interaction between nutrient

additions and phytoplankton chlorophyll. Second, epiphyte growth on the illuminated stems and leaves of macrophytes may be directly and/or indirectly influenced by river inflow. For example, reduction in available light is a direct consequence of inflow of turbid river water. But epiphytes, unlike benthic counterparts, may be dependent on new nutrients for growth and potentially compete with phytoplankton for nutrients and therefore phytoplankton may lower light availability, and compete with epiphytic algae for available nutrients. Third, since the flow environment in the Delta lakes may be important to epiphytic production as a mechanism for nutrient replenishment, limnocorrals, where flow and natural turbulence are greatly reduced, may not represent the most suitable method for working with epiphytic algae.

Last, the mechanisms of nutrient supply to the aquatic plant community of the Delta lakes require clarification, specifically the ability of nutrients derived from lake sediments to support the growth of epipelic algae (discussed previously), and the ability of Mackenzie River water to act as a source of new nutrients to the Delta lakes during the open-water period. At present our understanding of nutrient uptake by these algal communities is limited to nutrient-status indicators for epipelon and phytoplankton measured for selected lakes during the post-flood open water period in 1985 and 1986 (Ramlal *et al*, 1991). For example, phytoplankton in South Lake was never nitrogen-deficient and infrequently phosphorus-deficient(2 out 8 sampling days). In NRC phytoplankton was never nitrogen-deficient but frequently phosphorus-deficient (3 out of 8 sampling days). In Skidoo Lake phytoplankton was rarely nitrogen-

deficient (1 out of 8 sampling days) but frequently phosphorus-deficient (4 out or 8 days). Further investigation is required to fully assess whether nutrients supplied by sediments and river inflow are sufficient to support unlimited algal growth in the Delta lakes.

Overall, the limnocorrals seem to have roughly approximated the nutrient conditions typical of Mackenzie Delta lakes, except perhaps, the Control. The Controls were considered representative of high-closure lakes where in the absence of river inflow phosphorus limits phytoplankton and is frequently below detection limits. Somewhat unexpectedly phosphorus was usually detectable in the Control. This observation suggests that phosphorus may have been efficiently recycled within the water column, that some other nutrient may have been limiting, or that nutrient flux from sediments may be sufficient to meet algal demands. Final, any future limnocorral work will benefit from the clarification of the nutrient chemistry status of the Mackenzie River water.

SUITABILITY OF THE LIMNOCORRAL APPROACH

Limnocorrals have been used frequently for studies designed to examine the effects of added nutrients and sediments, and biomanipulation on specific components of the food web as well as on whole ecosystems (cf. Carignan & Planas, 1994; Cuker, 1993; Bloesch *et al*, 1988; Cuker, 1987; Guilford, 1985), with mixed reviews from investigators. For example, Guilford (1985) concluded that limnocorral experiments made valid predictions about the effects on water quality and primary productivity and should therefore be considered an effective approach to predicting the effect of different flooded material on algal

productivity and nutrient status. Bloesch *et al*, (1988) concluded that although biomanipulation experiments performed in limnocorrals should be viewed with regard to the fact that whole lake ecosystems may behave differently, the technique was successful in the study of the influence of crustacean zooplankton on the epilimnetic fluxes of carbon and phosphorus. By contrast, after using limnocorrals to study the effects of mineral turbidity on food web structure and function, Cuker (pers. comm.) concluded that limnocorrals show significant differences compared to real lake conditions that prevent extrapolation of results from limnocorral experiments. Finally, Carignan & Planas (1994) compared the outcome of multiple methods including limnocorrals for addressing nutrient and light limitation in the shallow, turbid mixed layers of lakes in the Paraná floodplain. They concluded that the use of enclosures was limited in this type of environment since total suspended sediment concentration decreased in the limnocorrals and light penetration increased resulting in an increased demand for nutrients by phytoplankton which confounded results.

Adding sediment to limnocorrals in a manner which reflects natural conditions is hampered by the absence of horizontal advection and decreasing vertical eddy diffusion in limnocorrals relative to lake systems (Bloesch *et al*, 1988). This problem can be at least partially overcome by using very fine grained material with > 85% clay fraction (Guilford *et al*, 1987; Ben Cuker, pers. comm.), and by re-suspension and dispersion of sediment with power tools (cf. Guilford *et al*, 1987; Ben Cuker, pers. comm.). In this experiment, it is possible that sediment suspension time

in limnocorrals may have been less protracted relative to South Lake, due to the character of the sediments from the banks of South Lake Channel (10% clay, 60% silt and 30 % sand). Silt and sand settle out of the water column faster than clay and heavier particles are probably deposited near the mouth of lake channels. Consequently, river inflow that travels some distance from distributary channels may contain primarily clay suspenoids with more protracted suspension time relative to sand and silt. It follows that the bank sediments used for dosing limnocorrals could have had a lesser proportion of clay and shorter suspension time than is actually characteristic of the average conditions in the Delta lakes, particularly at some distance from lake channels. None-the-less this limnocorral experiment which examined the effect of episodic river inflow on benthic algae was successful in that it provided information about the relation between transparency and benthic algal productivity among the Mackenzie Delta lakes. The success of future limnocorral experiments d designed to study the effects of inorganic turbidity on primary production may be improved by efforts to locate a local source of sediment with a substantially higher clay content than used here, and use of power tools to re-suspend and disperse sediments.

CONCLUSIONS

In conclusion, the present study has experimentally demonstrated the inverse relation between benthic algal productivity and episodic river inflow events in the Mackenzie Delta lake system. These results suggest that light limits benthic algal production in the Delta lakes. In addition, this study has contributed new information about the relation between

phytoplankton and river inflow regimes to the Delta lakes. Specifically, phytoplankton biomass may be greatest at intermediate transparencies representing a trade-off between light and nutrient availability. This result was surprising considering the simultaneous reduction in light that is coincident with nutrient additions. Furthermore, phytoplankton chlorophyll may have the potential to reduce the light available for growth of epipelic algae.

Finally, the Mackenzie Delta lakes and generally floodplains of the world may offer significant opportunities to improve our understanding of how fluctuating light and nutrient availability may set limits on primary production, and/or affect population dynamics and community structure of the phytoplankton. For example, Carignan & Planas (1994) argue that phytoplankton may not physiological adapt to low light conditions in turbid freshwaters but instead may be equipped to respond to episodic exposures to high light conditions. Further, Litchman (1996) has demonstrated that fluctuating light can change the magnitude and direction of phytoplankton responses predicted by the steady state growth-irradiance curves. Last, Neill (pers. comm.) argues that the frequency of nutrient additions can have a positive effect on phytoplankton growth. Finally, fluctuating light and/or nutrient availability may help explain why phytoplankton species appear remarkably diversified, in view of the fact that the majority are competing for the same materials in a relatively uniform environment under which conditions we would expect an approach to a unispecific equilibrium- the "paradox of the plankton" (Hutchinson, 1961).

APPENDIX 1.

Error in conversion of sediment volume to dry weight per dosing day.

preliminary rating: 50 mls = 61 g

Dose #	vol (mls)	dry wt (g)	mean dry wt.	error* %	ave.% error
1	50	66	63.6	8	6
2	50	61		0	
3	50	60	std.dev.	2	
4	50	66	3.9	8	
5	50	67		10	
6	-	-		-	
7	50	61		0	
8	50	65		7	
9	50	58		5	
10	50	69		13	
11	50	64		5	
12,13	50	59		3	
14	50	61		0	
15	50	70		15	
16	50	59		3	

*error = [(actual weight/volume-rated weight)-1]

APPENDIX 2.

Weekly Secchi Depth ,& weekly and mean Total Suspended Sediments (TSS) and chlorophyll a (chl a) for Limnocorrals and South Lake.

			Treatment = Control			Treatment = Low- Pulsed			Treatment = Low- Distributed			Treatment= High- Pulsed			Treatment=High- Distributed		
	South Lake	Corral #	3	11	13	2	8	9	7	10	14	1	4	12	5	6	15
date			Secchi Depth (m)			Secchi Depth (m)			Secchi Depth (m)			Secchi Depth (m)			Secchi Depth (m)		
25-May-95	0.55																
-1 15-Jun-95	1.15																
1 02-Jul-95	1.35		1.65	1.05	1.35	1.80	1.70	1.55	1.60	1.75	1.75	1.55	1.70	1.50	1.60	1.15	1.10
2 15-Jul-95	2.15		-	2.20	2.40	2.25	1.95	1.70	1.70	2.05	-	1.60	1.75	1.35	1.20	1.40	1.20
3 22-Jul-95	1.70		2.35	1.50	1.80	1.85	1.90	1.70	1.90	1.60	-	1.85	1.90	2.00	1.50	-	1.85
4 31-Jul-95	2.45		-	2.20	2.05	-	-	1.60	-	-	-	1.60	2.05	2.10	1.40	-	-
5 09-Aug-95	2.60		-	-	-	-	-	1.60	-	2.50	-	1.20	2.50	2.40	1.30	-	-
7 wk mean=	1.71																
std.dev.	0.74																
5 wk mean =	2.05																
std.dev.	0.52																
date			TSS (mg / L))					week mean std.dev.	TSS (mg /L)					week mean std.dev.	TSS (mg / L)					week mean std.dev.	TSS (mg / L)					week mean std.dev.	TSS (mg / L)					week mean std.dev.
25-May-95	18.00																														
15-Jun-95	5.00																														
1 02-Jul-95	3.70		2.70	4.20	3.30	3.40	0.78	2.60	3.10	2.50	2.80	0.30	3.30	2.20	2.90	2.80	0.56	2.20	2.80	3.30	2.77	0.55	2.80	5.30	4.90	4.33	1.34
2 15-Jul-95	2.50		1.70	4.30	2.20	2.73	1.38	2.60	2.60	2.20	2.53	0.31	2.70	2.50	2.70	2.63	0.12	3.20	3.90	4.40	3.83	0.60	4.60	4.10	3.00	3.90	0.82
3 22-Jul-95	3.00		2.80	3.70	2.90	3.13	0.49	3.20	2.10	2.00	2.43	0.67	2.03	3.00	3.10	2.71	0.59	3.80	2.90	2.00	2.83	0.60	2.90	1.37	2.00	2.09	0.77
4 31-Jul-95	2.10		2.10	1.20	1.30	1.53	0.49	1.70	2.00	2.10	1.93	0.21	1.70	1.70	0.71	1.37	0.57	3.90	2.60	0.77	2.42	1.58	3.60	6.00	1.10	3.57	2.45
5 09-Aug-95	2.00		1.00	1.70	1.20	1.30	0.36	2.20	2.00	2.00	2.07	0.12	2.10	2.10	1.24	1.81	0.50	6.50	2.50	2.50	3.83	2.31	5.10	1.93	1.20	2.74	2.07
7 wk mean=	7.61		5 wk treatment mean =			2.42			5 wk treatment mean =			2.35			5 wk treatment mean =			2.27			5 wk treatment mean =			3.14			5 wk treatment mean =			3.33	
std.dev.	9.66					std.dev.	1.10					std.dev.	0.45					std.dev.	0.73					std.dev.	1.29					std.dev.	1.62	
5 wk mean=	2.66																														
std.dev.	0.70																														
date			Ambient Chl a (ug / L)					week mean std.dev.	Ambient Chl a (ug / L)					week mean std.dev.	Ambient Chl a (ug / L)					week mean std.dev.	Ambient Chl a (ug / L)					week mean std.dev.	Ambient Chl a (ug / L)					week mean std.dev.
25-May-95	2.70																														
15-Jun-95	3.50																														
1 02-Jul-95	2.70		2.10	2.50	2.90	2.50	0.40	1.70	1.70	2.40	1.93	0.40	1.40	3.10	2.90	2.47	0.93	2.40	1.70	3.00	2.37	0.65	0.02	2.10	2.10	1.41	1.20
2 15-Jul-95	2.80		0.40	1.20	1.60	1.07	0.61	1.70	2.10	2.80	2.20	0.56	4.20	1.00	1.20	2.13	1.79	1.70	10.80	13.20	8.57	6.07	29.90	25.40	27.90	27.73	2.26
3 22-Jul-95	1.00		1.00	1.40	1.40	1.27	0.23	0.70	1.70	3.10	1.83	1.21	2.80	0.70	1.40	1.63	1.07	4.50	1.70	1.00	2.40	1.85	8.80	0.40	4.20	4.40	4.10
4 31-Jul-95	0.70		1.40	0.70	1.40	1.17	0.40	1.00	0.40	3.50	1.63	1.64	1.00	0.40	0.70	0.70	0.30	8.70	1.70	0.00	3.87	4.61	7.30	0.70	0.40	2.80	3.90
5 09-Aug-95	1.40		2.40	2.40	1.70	2.17	0.40	2.10	2.10	11.20	5.13	5.25	3.50	4.50	1.04	3.01	1.78	11.47	4.52	1.39	5.79	5.16	19.30	3.13	1.39	7.94	9.88
7 wk mean=	2.11		5 wk treatment mean =			1.83			5 wk treatment mean =			2.65			5 wk treatment mean =			1.99			5 wk treatment mean =			4.52			5 wk treatment mean =			8.86	
std.dev.	1.07					std.dev.	0.71					std.dev.	2.54					std.dev.	1.37					std.dev.	4.32					std.dev.	10.9	
5 wk mean=	1.72																														
	0.97																														

underlined values - corral seam open

"-" refers to secchi depths which indeterminate because the disk was on the bottom before disappearing

APPENDIX 3.

Weekly and mean concentrations of Phosphate, Nitrate, and Ammonium for Limnocorrals and South Lake

			Treatment = Control					Treatment = Low- Pulsed					Treatment = Low- Distributed					Treatment = High- Pulsed					Treatment = High- Distributed				
		South Lake	3	11	13			2	8	9			7	10	14			1	4	12			5	6	15		
	date		PHOSPHATE (uM)					PHOSPHATE (uM)					PHOSPHATE (uM)					PHOSPHATE (um)					PHOSPHATE (uM)				
	25-May-95	0.31																									
=	15-Jun-95	0.04				week mean	std.dev.				week mean	std.dev.				week mean	std.dev.				week mean	std.dev.				week mean	std.dev.
1	02-Jul-95	0.04	0.07	0.08	0.05	0.06	0.01	0.06	0.07	0.07	0.07	0.01	0.05	0.05	0.05	0.05	0.00	0.08	0.08	0.07	0.08	0.01	0.05	0.05	0.07	0.06	0.01
2	15-Jul-95	0.02	0.06	0.00	0.00	0.02	0.04	0.03	0.09	0.16	0.09	0.07	0.08	0.14	0.30	0.17	0.11	0.20	0.06	0.00	0.09	0.10	0.07	0.06	0.07	0.07	0.01
3	22-Jul-95	0.03	0.12	0.03	0.03	0.06	0.05	0.09	0.03	0.04	0.05	0.03	0.13	0.04	0.31	0.16	0.14	0.12	0.12	0.04	0.09	0.05	0.07	0.31	0.14	0.17	0.12
4	31-Jul-95	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.06	0.02	0.03	0.16	0.20	0.52	0.29	0.20	0.15	0.05	0.09	0.10	0.05	0.32	0.32	1.58	0.74	0.73
5	09-Aug-95	0.17	0.20	0.08	0.10	0.13	0.06	1.11	0.50	0.97	0.86	0.32	0.88	0.87	0.69	0.75	0.11	3.63	1.85	3.23	2.90	0.93	1.33	1.24	2.96	1.83	0.97
	7 wk mean =	0.09	5 wk treatment mean =			0.05		5 wk treatment mean =			0.22		5 wk treatment mean =			0.29		5 wk treatment mean =			0.85		5 wk treatment mean =			0.58	
	std.dev.	0.11				std.dev.	0.06				std.dev.	0.36				std.dev.	0.27				std.dev.	1.22				std.dev.	0.84
	5 wk mean =	0.06																									
	std.dev.	0.07																									
	date		NITRATE (uM)					NITRATE (uM)					NITRATE (uM)					NITRATE (um)					NITRATE (uM)				
	25-May-95	2.89																									
	15-Jun-95	0.13				week mean	std.dev.				week mean	std.dev.				week mean	std.dev.				week mean	std.dev.				week mean	std.dev.
1	02-Jul-95	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	15-Jul-95	0.04	0.35	0.25	0.30	0.30	0.50	0.44	0.00	0.29	0.24	0.22	0.27	0.21	0.52	0.33	0.16	0.42	0.24	1.56	0.74	0.72	1.37	1.35	1.42	1.36	0.04
3	22-Jul-95	0.08	0.25	0.06	0.23	0.18	0.11	0.59	0.13	0.06	0.27	0.26	0.21	0.34	0.17	0.24	0.09	0.23	0.36	0.92	0.50	0.37	0.40	0.93	1.05	0.79	0.35
4	31-Jul-95	0.14	0.07	0.09	0.12	0.09	0.03	0.12	0.14	0.14	0.13	0.01	0.47	0.66	0.75	0.63	0.15	0.14	0.23	0.07	0.36	0.30	0.05	1.10	0.69	0.66	0.56
5	09-Aug-95	0.32	0.76	0.18	0.40	0.45	0.29	2.13	2.11	1.41	1.88	0.41	1.00	1.05	0.76	0.94	0.15	4.90	2.80	3.30	3.67	1.10	0.13	4.20	3.58	2.64	2.19
	7 wk mean =	0.30	5 wk treatment mean =			0.20		5 wk treatment mean =			0.51		5 wk treatment mean =			0.43		5 wk treatment mean =			1.00		5 wk treatment mean =			1.10	
	std.dev.	0.35				std.dev.	0.20				std.dev.	0.75				std.dev.	0.35				std.dev.	1.48				std.dev.	1.26
	5 wk mean =	0.13																									
	std.dev.	0.13																									
	date		AMMONIUM (uM)					AMMONIUM (uM)					AMMONIUM (uM)					AMMONIUM (um)					AMMONIUM (um)				
	25-May-95	0.96																									
	15-Jun-95	0.54				week mean	std.dev.				week mean	std.dev.				week mean	std.dev.				week mean	std.dev.				week mean	std.dev.
1	02-Jul-95	0.19	0.22	0.14	0.14	0.17	0.05	0.19	0.14	0.08	0.13	0.07	0.17	0.22	0.11	0.16	0.06	0.08	0.25	0.11	0.14	0.10	0.25	0.14	0.22	0.20	0.06
2	15-Jul-95	0.08	0.13	0.15	0.15	0.14	0.01	0.16	0.27	0.10	0.18	0.09	0.10	0.10	0.33	0.18	0.13	0.28	0.31	0.23	0.27	0.04	0.31	0.10	0.33	0.25	0.13
3	22-Jul-95	0.16	0.11	0.13	0.11	0.14	0.01	0.37	0.08	0.00	0.15	0.20	0.03	0.13	0.00	0.05	0.07	0.21	0.48	0.21	0.30	0.16	0.48	1.06	0.00	0.51	0.53
4	31-Jul-95	0.03	0.00	0.00	0.53	0.18	0.31	0.14	0.25	1.01	0.47	0.47	0.08	0.45	0.08	0.20	0.22	0.00	0.45	0.00	0.15	0.26	0.45	0.79	0.39	0.54	0.22
5	09-Aug-95	0.05	0.85	0.43	0.05	0.44	0.40	0.23	0.28	0.20	0.24	0.04	0.15	0.35	0.18	0.23	0.11	0.30	0.30	0.23	0.28	0.04	0.30	0.00	0.56	0.29	0.28
	7 wk mean =	0.50	5 wk treatment mean =			0.21		5 wk treatment mean =			0.23		5 wk treatment mean =			0.16		5 wk treatment mean =			0.23		5 wk treatment mean =			0.36	
	std.dev.	1.05				0.23					std.dev.	0.24				std.dev.	0.13				std.dev.	0.14				std.dev.	0.29
	5 wk mean =	0.10																									
	std.dev.	0.07																									

underlined values- enclosure seam open

APPENDIX 4.

Pore-water profiles for South Lake , Control and High Distributed limnocorrals.

South Lake			June 1	Control		June 15		High- Distributed			June 22
depth* (cm)	PO4 (uM)	NO3 (uM)	NH4 (uM)	depth* (cm)	PO4 (uM)	NO3 (uM)	NH4 (uM)	depth* (cm)	PO4 (uM)	NO3 (uM)	NH4 (uM)
9	0.29	1.27	0.70	13	0.63	0.52	4.59	3	1.63	4.37	12.08
8	0.19	0.76	0.59	12	0.00	0.42	2.16	2	1.38	3.10	6.60
7	0.00	0.59	0.32	11	0.00	0.70	2.30	1	0.40	1.57	2.11
6	0.29	0.43	0.16	10	0.94	0.05	1.35	***0***	***0.25***	***3.91***	***2.25***
5	0.19	0.43	0.11	9	0.83	0.70	2.16	-1	0.63	5.89	1.41
4	0.19	0.25	0.27	8	0.05	1.08	1.76	-2	0.88	2.39	0.84
3	0.19	0.25	0.27	7	0.00	0.70	1.35	-3	1.13	5.42	0.14
2	0.48	0.59	0.27	6	0.00	0.70	1.49	-4	1.13	1.92	0.00
1	0.19	0.76	0.27	5	0.17	1.08	2.03	-5	1.63	5.31	0.00
0	***0.40***	***1.93***	***0.75***	4	0.00	0.14	1.62	-6	0.63	4.84	0.00
-1	2.03	4.45	0.48	3	0.00	0.00	2.43	-7	1.00	2.39	2.81
-2	1.45	4.11	0.59	2	0.17	0.33	1.49	-8	1.26	1.81	3.09
-3	3.87	5.76	0.48	1	0.00	0.14	0.81	-9	2.26	1.81	12.50
-4	1.84	5.12	0.59	***0***	***0.05***	***0.14***	***0.81***	-10	2.89	3.21	13.63
-5	3.48	5.62	0.64	-1	0.05	1.83	1.00	-11	1.13	3.56	17.14
-6	2.23	5.96	0.70	-2	0.05	1.92	0.68	-12	3.14	3.44	24.00
-7	3.60	4.45	0.64	-3	0.28	2.84	1.08	-13	0.75	4.50	26.69
-8	2.61	5.96	1.12	-4	0.50	3.24	0.68	-14	3.52	1.22	27.39
-9	3.58	4.28	0.59	-5	0.50	3.14	1.00	-15	3.52	4.37	12.08
-10	3.48	5.62	1.55	-6	1.38	4.36	0.68	-16	6.78	5.66	10.52
-11	3.87	3.61	0.86	-7	0.72	3.42	1.00	-17	5.65	8.80	19.38
-12	3.00	4.78	0.78	-8	1.49	2.77	5.94	-18	6.91	6.71	47.57
-13	3.58	3.61	0.91	-9	1.60	2.39	8.00	-19	6.40	6.25	45.73
-14	1.74	3.55	6.74	-10	2.70	2.67	13.50	-20	6.03	5.00	47.19
-15	4.16	6.12	2.68	-11	2.37	2.77	17.01	-21	6.53	9.15	26.12
-16	1.16	2.27	10.27	-12	2.79	2.96	22.14	-22	6.78	6.94	40.17
-17	1.06	6.12	23.97	-13	3.36	2.67	31.05	-23	5.53	5.77	44.24
-18	1.45	3.10	17.33	-14	3.03	2.25	40.23	-24	13.06	8.45	37.78
-19	3.48	5.45	16.91	-15	2.79	2.11	35.00	-25	16.58	7.40	48.74
-20	4.06	5.45	3.48	-16	3.47	1.74	45.00	-26	13.81	7.07	50.98
-21	5.51	5.96	37.77	-17	5.24	3.80	51.30	-27	10.67	7.40	63.90
-22	1.45	3.94	7.80	-18	5.13	2.02	53.50	-28	9.42	8.45	65.73
-23	5.51	5.62	40.98	-19	5.13	3.24	58.59	-29	11.81	8.10	57.30
-24	1.55	5.27	6.63	-20	5.24	3.71	64.13	-30	14.69	10.32	64.33
-25	7.25	10.65	27.55	-21	3.80	3.80	61.02	-31	11.68	11.02	82.23
-26	5.42	10.90	2.68	-22	5.02	3.42	70.20				

*- depth= distance below sediment/water interface
+depth= distance above sediment/water interface
0 = sediment/water interface

APPENDIX 5.

Periphyton biomass on Day 23, 34,and 44, means and standard deviations per treatment, recorded over the course of the experiment.

Treatment	Corral #	Day	chl* (mg m-2)
Control	11	23	5.5
	13	23	7.4
	3	23	17.4
		mean	10.1
	std.	dev.	6.4
	3	34	24.3
	3	34	32.5
	13	34	33.2
		mean	30.0
	std.	dev.	4.8
	3	44	28.0
	13	44	36.9
	3	44	50.8
		mean	38.6
	std.	dev.	11.4
Low-Pulsed	9	23	5.5
	8	23	7.9
	8	23	12.1
		mean	8.5
	std.	dev.	3.4
	2	34	15.8
	8	34	22.6
	9	34	27.5
		mean	22.0
	std.	dev.	5.8
	9	44	17.4
	9	44	8.5
	8	44	32.2
		mean	19.4
	std.	dev.	11.9
Low- Distributed	7	23	7.6
	14	23	11.3
	7	23	10.6
		mean	9.9
	std.	dev.	1.9
	7	34	15.8
	14	34	20.2
	7	34	23.2
	14	34	23.8
		mean	20.8
	std.	dev.	1.9
	10	44	10.8
	14	44	22.5
	7	44	27.1
		mean	20.1
	std.	dev.	8.5

Treat	Corral#	Day	chl* (mg m-2)
High-Pulsed	4	23	2.4
	1	23	8.1
	4	23	9.5
		mean	6.7
	std.	dev.	3.7
	1	34	16.2
	12	34	15.8
	1	34	24.2
	12	34	19.8
		mean	19.0
	std.	dev.	4.1
	4	44	10.4
	12	44	15.8
	1	44	24.1
		mean	16.8
	std.	dev.	6.9
High-Distributed	15	23	3.7
	5	23	16.0
	5	23	8.3
		mean	9.3
	std.	dev.	6.2
	5	34	14.5
	5	34	17.9
	15	34	14.9
		mean	15.8
	std.	dev.	1.5
	5	44	12.9
	15	44	6.6
	5	44	14.5
		mean	11.4
	std.	dev.	4.2

*chlorophyll is sum of chl's a, b, c1, c2 & carotenoids

APPENDIX 6.

Areal net photosynthetic rates, areal net photosynthetic rates per MJoule of light, and biomass specific net phototsynthesis per MJ light for treatments and the Control.

	AREAL NET PHOTOSYNTHESIS (MG O2 / M2 / HR)				AREAL NET PHOTOSYNTHESIS PER MJ LIGHT						BIOMASS SPECIFIC NET PHOTOSYNTHESIS PER MJ LIGHT					
	August 09	August 11	August 13	August 21	August 09	August 11	August 13	August 21			August 09	August 11	August 13	August 21		
MJoules at depth (MJ / hr / m2)	**0.12**	**0.1**	**0.13**	**0.17**	**0.12**	**0.1**	**0.13**	**0.17**			**0.12**	**0.1**	**0.13**	**0.17**		
Control	11.4	24.2	22.9	51.5	95	242	176	303	ave.	**204**	3	7.3	6.3	5.9	ave.	**5.6**
									std.dev.	89					std.dev.	1.9
Low-Pulsed	9.7	17.6	15.4	42.7	81	176	119	251	ave.	**156**	3.5	6.3	7	7.8	ave.	**6.2**
									std.dev.	74					sdt.dev.	1.9
Low-Distributed	15	19.8	25.1	47.1	25	198	193	277	ave.	**198**	5.4	8.3	18	10.3	ave.	**10.5**
									std.dev.	62.2					std.dev.	5.4
High-Pulsed	0.9	0	0	17.8	7.5	0	7.6	105	ave.	**28**	0.3	0	0.8	4.4	ave.	**1.4**
									std.dev.	51					std.dev.	2
High-Distributed	5.3	0.3	6.6	33	44	3	50	194	ave.	**73**	2.8	0.15	3.9	13	ave.	**5**
									std.dev.	83					std.dev.	5.6

APPENDIX 7.

Diatom assemblages for enriched clay substrates suspended in limnocorrals, enriched and unenriched substrates suspended in South Lake, and an unenriched substrate anchored to the bottom of South Lake.

TREATMENT:	CONTROL			LOW-PULSED			LOW-DISTRIBUTED			HIGH-PULSED			HIGH-DISTRIBUTED			Bottom	Suspend	Suspend
LIMNOCORRAL#:	3	11	13	2	8	9	7	10	14	1	4	12	5	6	15	UN	UN	EN
DIATOM SPECIES:	NUMBER PER ALIQUOT:																	
Ach daui					2													
Ach petersenii																		7
Ach pusilla		2														11	1	
Ach subatomoides			1			2											1	3
Achnanthes minutissima	2	16	17	10	10	8	2	9	1	10	10	4	7			22	50	60
Amph inariensis		4														12	2	
Amph pediculus		1																2
Amphipleura pellicula	2	2																
Asterionella formosa	43	22	28	27	42	18	22	49	21	13	6	20	19	16	16		5	1
Aulacoseira islandica				4				3										
Brachysira vitrea		1	8	2	5												5	
Cal cf silicula		2																
Cal silicula																2		
Caloneis bacillum		2		2	3			2		1						18	2	
Cocc placentula v. euglypta				2														3
Cocc placentula v. lineata		2														4		
Cocc placentula v. placentula			1															
Cocconeis placentula				1		2												1
Crat molestiformis																	2	
Cyclo occelata			1															
Cyclo pseudostelligera		3	1								2							1
Cyclo sp 1																	2	
Cyclo stelligera																		
Cyclotella michiganiana	1																	
Cymb cistula																	1	
Cymb mesiana																	1	
Cymb silesiaca			2															
Cymbella microcephala		5		2	2					2			2			8	12	1
Dent kuetzingi					2	4												
Diat moniliformis																6		
Diatoma tenuis		4	9	6	7	5	2	12	4		3	17	11	9	1		2	
Diplo occulata																5	2	2
Diplo pseudovalis large																5	4	
Diploneis pseudovalis (small)		2	1	2											2	9	5	
Epith turgida											2					8	4	6
Frag capucina	26	32	124	28					26	46	20			163			4	6
Frag crotonensis		8																
Frag delicatissima						2												2
Frag famelica					7	4		4			1							
Frag gracilis										2				2			1	
Frag tenera	4	2	28	18	31	7	30	14	10	12	2	10	2	1	4		3	
Frag ulna v. acus		1	8		2			3	1			2	2				2	
Frag ulna v. ulna							2				1	1		2			1	
Fragilaria nanana		27	10	21	38	45	16	13	8	82	15	61	5	8	8			1
Gomp clavatum																2		
Gomp parvulum			4															
Gomp sp 1																		1
Gyro acuminatum			1													2		1
Nav accomoda										2								
Nav agrestis		2														5		68
Nav capitata v. hungarica		1															2	
Nav cf absoluta																3		
Nav cf bahuensis																2		
Nav cf bryophila		2																
Nav cf cryptofallax																2	4	
Nav cf hoffmanniae		2			2											4		
Nav cf hoffmanniae fo 2			2															
Nav cf hoffmanniae fo 3			2															
Nav cf phyllepta																2		
Nav cf rhyncocephala																	2	
Nav cf seminulum																	1	
Nav cryptocephala		8														8		
Nav cryptofallax																		
Nav cryptotenella A											2					3		
Nav cryptotenella B		2	4															
Nav cryptotenella C																1	19	
Nav elgensis			1															
Nav gregaria																	4	
Nav lenzii			2													2		
Nav libonensis																4	1	
Nav medioconvexa				2			2									3		
Nav menisculus v. menisculus			2													6	3	
Nav minima	3	6	2	2	8	16	2									3		16
Nav miniscula								1		1						1	2	1
Nav phyllepta											2							
Nav pupula v. pupula																3		
Nav radiosa				1														
Nav rhyncocephala		1	4								2					4		2
Nav sp 1																4		
Nav sp B																4	2	
Nav sp D		4	2	1									2			6		

Diatom assemblages for enriched clay substrates suspended in limnocorrals, enriched and unenriched substrates suspended in South Lake, and an unenriched substrate anchored to the bottom of South Lake.

TREATMENT:	CONTROL			LOW-PULSED			LOW-DISTRIBUTED			HIGH-PULSED			HIGH-DISTRIBUTED			Bottom	Suspend	Suspend
LIMNOCORRAL#:	3	11	13	2	8	9	7	10	14	1	4	12	5	6	15	UN	UN	EN
DIATOM SPECIES:	NUMBER PER ALIQUOT:																	
Nav vitabunda		2			2													
Navicula accomoda										2								
Nitz acicularis			2	1			6		2				12		4			
Nitz acidoclinata		1																
Nitz amphibia		10	2					2	2							8	1	12
Nitz angustata			2													12	2	
Nitz bacillum				2													3	
Nitz capitellata	6						2		12	2	11	9	6	10	10			
Nitz cf acicuioides			2							2					7			
Nitz cf acuta																	4	
Nitz cf aequorea				2													2	
Nitz cf agnita										2						2		
Nitz cf alpina				2														
Nitz cf capitellata				6			2											
Nitz cf egiei				2														
Nitz cf flexoides										2						2	13	18
Nitz cf gracilformis				6	3							26		17				
Nitz cf gracilis		2		6			3									2	6	
Nitz cf liebetruthii fo 1			10		6				2						4	4	17	1
Nitz cf palea fo 2					2													
Nitz cf perminuta		2						2							2			
Nitz cf pseudofonticola		2																
Nitz cf pura	4						2		10		1							
Nitz cf pusilla		2																
Nitz cf sociabilis											2							
Nitz cf subacicularis		2											2					
Nitz cf vermicularis																	8	
Nitz diss v. diss		2			8									2				4
Nitz diss v. media				2				2									7	
Nitz dravellensis	14	8	8		25	68	60	17	4	27		29	78	40	20	2		
Nitz fonticola fo 1			2															5
Nitz frustulum									6									
Nitz gracilformis	22	14	7			24	31	9	5	4	6		16		19	8	4	
Nitz heufleriana		2																
Nitz incognita	42	35	31	28	34	6	10	58	53	4	10		2	16	22	2	6	37
Nitz intermedia										1								
Nitz liebetruthii fo 2		4																
Nitz lineata		8			2		2	13									2	
Nitz ovalis		2	4															
Nitz palaecea fo 1	42		1	20	24	21	24	19	15	28	14	6	70	12	21	2	10	5
Nitz palaecea fo 2	80	21	24	84	49	110	165	79	120	63	180	163	166	86	154	4	6	
Nitz palea fo 1	16	2	2	8	2	4			25	3	6	4	2	7	15	6		31
Nitz palea fo 2	7	6		17	2		2	1	9	17	16	4	2	10	5	14	2	
Nitz palea fo 3	2									4								
Nitz palea fo 4		2																
Nitz pura	9				2				3		2		1	1	5		2	
Nitz recta																	2	
Nitz rostellata								2										
Nitz sinuata v. tabellaria																	2	
Nitz sp 6																4		
Nitz sp 7		1																
Nitz sp 8		1																
Nitz sp 9															2			
Nitz sp A											2				4			2
Nitz sp C				10										5			2	
Nitz valdecostata								2										
Nitzschia cf acicularis																7		
Rhopalodia gibba v. gibba			10		7			2								4	5	4
Simon delongei long		4														4		
Simon delongei short			2						2							4		2
Steph alpinus							1											
Steph minutulus		2	2														1	
Steph parvus		5	1		3	4		2				1					2	
Steph sp 1								1										
Surirella brebisonnii v. kuetzingii		2				1												
Thalassiora																	1	
Total per aliquot:	325	310	377	327	334	353	388	323	341	332	318	357	407	407	325	277	262	307

UN= unenriched; EN= enriched; * = seam open

APPENDIX 8.

Temperature profiles in South Lake and selected corrals at the beginning and end of the experiment.

Initial Conditions : July 2

Depth (m)	Temperature (Celsius)		
	South Lake	corral 3	corral 11
0.1	**16.7**	19.4	17.1
0.5	**18.8**	18.9	18.6
1.0	**18.9**	18.2	18.3
1.5	**18.9**	17.7	18.0
2.0	**18.1**	17.0	17.7
2.5	**15.2**	14.8	16.4
3.0	**13.0**	13.5	13.7

Final Conditions : August 17

	South Lake	corral 3	corral 13
0.1	**15.9**	15.7	15.7
0.5	**15.9**	15.7	15.8
1.0	**16.0**	15.7	15.8
1.5	**15.9**	15.7	15.8
2.0	**15.9**	15.7	15.8
2.5	**16.0**	15.7	15.8

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