Effects of Water Storage Reservoirs on Downstream Water Quality and Aquatic Vegetation.

A Literature Review

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INTRODUCTION

Constructing a water reservoir on a river has a number of effects on the quantity and the physical and chemical quality of the downstream water. These effects may be significant for the aquatic plants growing below the impoundment. The peak runoff events which are normal in most rivers are usually eliminated as the water is stored. This prevents the scouring of sediments, a process that typically places limits on the extent of plant growth. It also reduces the fragmentation, uprooting and flushing out of previously established aquatic plants. Sediment accumulation may occur and vegetation does not have to recolonize again each year. Reservoir management may alter the time of year when water is released and the amount. Water levels may be affected, as well as the time at which high and low water events occur. Discharge regimes are likely to vary from those to which the vegetation is adapted. The new regime may prove to be incompatible with the life cycle of the plant, or may be sufficiently beneficial to cause the vegetation to become weedy.

Water which is released may come from the surface via overflow or from very much deeper than before. This affects the temperature, turbidity, chemical composition and dissolved gas concentrations of the water. These factors influence the species and numbers of organisms which will be found in the water. All of these factors affect the growth of aquatic vegetation downstream. The effects may be beneficial or detrimental to the plants and the increase or decrease of the plants may be an asset or a liability depending upon the downstream water uses in the river.

ALGAE

Introduction

Algae found in freshwater are commonly assigned to two groups: phytoplankton which grow within the water column and periphyton which are attached to a substrate. The periphyton can be further differentiated into several types. Epilithic algae which grow on rock surfaces and epiphytic algae which grow on aquatic macrophyte surfaces are the ones most commonly referred to in discussions of lotic or running water environments. The significance of algae in the lotic environment below water impoundments is usually related to their utilization by other biotic groups, as food, habitat or cover for invertebrates and fish, to their nuisance potential as taste and odor problems and to their physical blockage of intake structures. The major effects of reservoir discharge on algae, relative to pre-impoundment conditions, concern changes in flow regime and water quality which affect turbidity (light intensity and abrasion), nutrient levels, substrate type and size, temperature and grazing. Nordin has additional information on factors influencing algal growth in streams (Nordin-1985).

Discharge

Stream velocity is generally considered a very important factor for algal growth, with respect to both standing crop and annual production (Traaen and Lindstrom-1983, Hickman *et al.*-1982). Seasonal flow constancy and the resulting stabilization of stream-bed conditions are commonly associated with reservoir releases and can enhance the production of attached algae (Hynes-1970, Spence and Hynes-1971; Ward-1974; Crisp-1977). Only a general relationship was found between flow and epilithon development; seasonal changes in epilithon dry weight showed a good correlation with flow constancy (Ward-1974). The stream substrate must be suitable before high levels of stream periphyton will accumulate. Mud, sand and fine gravel are not suitable; gravel, cobbles, boulders and bedrock are the preferred substrates. The size of the substrate is determined by current flow and availability of parent material. Impoundments trap fine materials, but they also eliminate the spring freshet which scours out such fine sediments as do settle. Freshets scour out sediments which would otherwise accumulate from year to year; impoundments trap much of this sediment however sediments which do settle may accumulate.

In artificial stream channels with steady velocities and smooth flow, velocities up to 75 cm/s did not cause scouring or loss of biomass (Horner *et al.*-1983). In six natural streams in Washington State increasing velocities up to 50 cm/s, increased diatom accumulation rates at high phosphorus concentrations of 35 µg/L. Incremental velocity increases above 50 cm/s eroded increasingly larger proportions of the existing periphyton growth

(Horner and Welch-1981). Excessive periphytic algal growth in the Thompson River occurred at velocities between 11 and 45 cm/s (Kussat and Olan-1975, Langer and Nassichuck-1975).

Whitton examined the dependence of algal development and community structure on river flow rate. ***Cladophera glomerata*** for example, was found to form thick coralloid or plumose growths in slow flowing waters, whereas in faster currents, the angle between the branches and the main filament was less and the plant formed long, tough ropes. In currents greater than 5 m/s only those species firmly attached and able to withstand abrasive damage survived. The flora on rocks at his study sites was usually dominated by encrusting forms and filaments with no, or only moderate, branching; ***Chamaesiphon fuscus, Ulothrix zonata***, and ***Lemanea fluviatitis,*** respectively, were examples given of these three forms. It is generally thought that such species are dependent on water movement to provide a constant supply of fresh materials for metabolic processes. This prevents a layer of depleted water building up around the organism. At slower current velocities species such as ***Oedogonium tribonema,*** which form long swaying filaments on the substrate, are typically dominant (Whitton-1975)

Researchers examined the effects of flow reduction from 810 m^3/s to 150 m^3/s and subsequent flow restoration on plankton and periphyton communities of the Snake River in Idaho (Anon-1974). Plankton counts showed only small variations between flows, and the dominance of certain organisms showed that the majority were originating from the reservoir behind Hell's Canyon Dam. An increase in the number of ***Diatoma vulgare*** while the flow was increased from 150 m^3/s to 810 m^3/s, was probably due to their becoming detached during low flows. The algal community was stratified on the river's substrate in a pattern influenced in part by temporal changes and flow conditions. Riffles were typically the most productive areas of the river.

The area which was repeatedly exposed as a result of discharge fluctuations appeared as an ash-grey zone from the remains of periphyton on the rocks. Below this zone was a productive algal community dominated by ***Cladophora*** , a filamentous green algae. Diatoms in this zone were attached to these filaments. The investigators felt that the periphyton community could re-establish itself under any given flow regime in a continually wetted zone. However, the greater the magnitude of seasonal and daily fluctuation in flow, the greater the area of reduced productivity. Other investigators have attributed downstream biotic gradients to other parameters such as turbidity, nutrients and temperature.

Turbidity

Algae are very responsive to the degree of turbidity in the water column. Turbidity has several effects; it reduces light intensity thus reducing photosynthesis and it is also an abrasive. Turbidity associated with spring freshets may reduce periphyton standing crops significantly, through abrasion and substrate movement (Northcote *et al.*-1975). Impoundments allow sediments to settle out thus reducing the amount of abrasive material and increasing the light intensity. Dams also eliminate the spring freshet. The result is increased algal growth in a season and accumulation of periphyton from season to season.

Fredeen investigated changes that occurred in the South Saskatchewan River as a result of impoundment of Lake Diefenbaker. Since its completion in 1968, the reservoir has stabilized flows and served as a trap for suspended solids. The clear, shallow water below the impoundment has allowed greatly increased photosynthesis where virtually none occurred before. Along with the establishment of some aquatic macrophyte growth, there has been a dramatic increase in the production of filamentous algae and presumably phytoplankton (Fredeen-1977). Soltero documented a 60-fold decrease in mean turbidity of outflow water from Bighorn Lake in Montana, a deep discharging impoundment. Although downstream eutrophication was not studied, it was noted that taste and odor problems in domestic water supplies, due to increased algal growths, coincided with impoundment of the Bighorn River (Soltero-1973).

Nutrients

The factor most often implicated in studies of primary production rates is nutrient availability, with nitrogen, phosphorus or carbon found to be growth limiting under most circumstances. Planktonic production in particular is regulated by nutrient availability. In 1978, Martin and Arneson studied the effects of a nutrient-rich hypolimnial discharge from Hebgen Lake in Montana. The average standing crop of phytoplankton in Quake Lake, which is downstream, was found to be three and one-half times greater than in Hebgen Reservoir. This was attributed to the four-fold increase in nitrate in the upper layer of Quake Lake. It was postulated that the higher nitrate concentrations provided a competitive advantage for flagellates and diatoms downstream, although temperature and other factors probably had an influence as well.

Researchers have realized that periphyton and its resident diatom populations provides an excellent opportunity to study the effects of nutrient enrichment by a reservoir discharge on downstream community function and structure. Periphyton remains in a fixed location, integrating the environmental parameters which impact on it, and it has a relataively short response time. Some algae can form large populations in a body of water within a week (Bachman-1978).

Marcus studied periphytic communities, using glass-slide substrates, at sites 10 m, 1.9 km, 4.0 km and 7.3 km downstream of Hyalite Reservoir in Montana, which has a hypolimnial outlet. Comparison of the most upstream site with the three lower sites determined that the reservoir release stimulated periphytic productivity. Dense growth of the chlorophytes ***Prasiola*** sp. and ***Hydrurus*** sp. carpeted the stream bed immediately below the dam. Marcus also found an increase in the periphytic proportion of chlorophyll a in the organic accumulations and increased diatom species diversity and evenness. Only ammonia-nitrogen and total-nitrogen concentrations correlated with periphytic growth variations at all sites (Marcus-1980).

Marcus suggests that nitrogen fixed by algae in Hyalite Reservoir eventually becomes available for downstream release in the form of ammonia, which is the preferred form of nitrogen by algae in a nitrogen limited system such as Hyalite Creek. The nitrogen-to-phosphorus ratio was less than one. He summarized that the nutrient-enriching discharge was the major influence on periphytic growth. Net productivity at the upstream site averaged four times greater than that for the three sites further downstream; it appeared that nitrogen was rapidly depleted by benthic algae soon after discharge.

Cocconeis placentula dominated 70-80 percent of the diatom communities at the three lower sites, but was virtually absent at the upper site. A study of diatom succession, following colonization of the microscope slides, suggested that this species was dominant further downstream because it possessed a more efficient method of incorporating limited nitrogen resources. Other species dominated the diatom communites in which nitrogen concentrations were enriched, apparently because of the higher potential growth rates that could be realized under the elevated nutrient conditions. Marcus makes particular mention that other parameters such as flow, substrate, and water temperature were similar and their effects on algal growth secondary, at all study sites in Hyalite Creek.

Temperature

Water temperature is a factor in algal growth but is likely less important than other factors like nutrients and current velocity. The higher temperatures of surface flow from a reservoir would increase algal growth; a ten degree rise would likely double the growth rate. However, low temperature water from a deep discharge is not a limitation (Bothwell-1985) and if other conditions, such as light and nutrients, are favorable, nuisance algal growths could still occur.

Ward studied regulated sections of the South Platte River in Colorado, to determine the effects of a deep release dam on receiving waters. Most algal species appeared to thrive in the cool water, provided that flow remained relatively constant. Stable substrates, increased nutrient supply, and higher winter water temperatures were also cited as beneficial for growth. Increased algal production was correlated with flow stabilization, while standing crop and temperature appeared to be negatively correlated, or unrelated, except in winter. During that season, relatively warm release water and lack of surface ice probably contributed to the high macroalgae development observed. Water temperature was considered to have an important influence on species composition; ***Cladophora*** and ***Ulothrix*** were the dominant genera except during the diatom peak in July and August, and the spring development of ***Hydrurus*** (Ward-1974).

Bachman, in his discussion of reservoir effects on algae, mentions that the relationship between temperature and algal growth has not been well defined. One researcher cited by this reviewer contends that temperature is important for algal growth rate, but rarely is it directly involved in algae acclimatization (Bachman-1978). Gore investigated the clear, cold, hypolimnial discharge below the Tongue River Reservoir Dam in Montana and found increased periphyton growth in the form of dense mats of ***Cladophora***. Further downstream, as the original temperature scheme was re-established, ***Cladophora*** cover was reduced. Gore mentions that this species of green algae is commonly enhanced below impoundments, but does not mention the causal factor(s). Nutrient levels and turbidity were probably an influence in this case (Gore-1977).

MACROPHYTES

Introduction

Algae and submersed macrophytes form the base of the food chain in aquatic environments. However, the importance of macrophytes to the riverine community lies more in the role of modifying and diversifying habitats than in the supply of organic matter (Westlake-1975). Changes to a natural watercourse originating from impoundment, such as increased bed stability and reduced turbidity, often result in enhanced primary productivity. This provides additional food and niche diversification for aquatic life. Examples of increased plant production below water impoundments are well documented in the literature (Hynes-1970, Hagan and Roberts-1972, Ward-1974, Ridley and Steel-1975, Fredeen-1977, Holmes and Whitton-1977, Pokorny *et al* -1984).

Macrophytes are abundant in many rivers and can form enormous stands. Excessive growth of aquatic plants can adversely affect utilization of waterways by:

—creating habitats favorable for the production of bloodsucking insects that attack man and domestic animals
—interfering with navigation and boating
—fouling industrial and potable water supply systems
—affecting stream flow patterns and increasing the potential for flooding
—affecting the distribution of benthic invertebrates and their predators
—blocking the migration of salmon and resident fish
—affecting water chemistry
—clogging irrigation and drainage canals
—depreciating the monetary and aesthetic value of waterfront properties
—interfering with sport fishing, swimming, and other recreational pursuits.

Large beds of decaying or respiring macrophytes can cause fish-kills by reducing dissolved oxygen levels markedly (Stanley *et al*.-1974, Chambers *et al*.-1991, Gregg and Rose-1982, Madsen and Warncke-1983, Spicer and Catling-1988, Buscemi-1958, Chittenden *et al*.-1976, Mayes *et al*.-1977, Rawlence and Whitton-1977, Rorslett *et al*.-1985).

The literature contains examples of both enhanced and reduced levels of primary productivity below reservoirs, depending on the nature of alteration to the principal factors that control growth. Westlake explains that riverine situations are particularly complicated due to the inter-relation of possible factors influencing growth. The most obvious or easily measured variable may be only remotely or non-linearly related to the real cause of a particular effect (Westlake-1975). Some of the work directed at defining the effects of modified flow and water quality on downstream aquatic vegetation is summarized here.

Current speed

Current speed may be the most important factor in lotic systems which determines submerged plant distribution, species composition and performance (Butcher-1933, Beaumont-1975, Vannote *et al.*-1980, Madsen and Warncke-1983, Chambers *et al.* -1991, Westlake-1975, Holmes and Whitton-1977, Haslam-1978). Plants which are usually successful in strong currents have numerous, strong roots or rhizomes, have stems which are flexible and resistent to pulling strains and have streamlined narrow leaves. Peltier and Welch explain that the morphology of ***Potamogeton pectinatus***, a narrow-leaved plant with low drag coefficient, was largely responsible for its dominance where the current was highest, directly downstream of Fort Patrick Henry Dam on the Holston River in Tennessee (Peltier and Welch-1969).

Table 1 shows how current speed determines the particle size of the river bed sediments; 0.2 to 0.3 m/s results in a sand bottom, 0.1 to 0.2 m/s results in a silt bottom and velocities below 0.1 m/s result in a mud bottom Minnikin-1920). Large particles, from sand size and up, are poor in nutrients; slow rivers with silt and mud sediments are rich in nutrients and have abundant submerged plant growth (Minnikin-1920, Nichols and Shaw-1986, Chambers *et al.* 1991)

Current speed may also prevent the establishment of aquatic plants and cause uprooting and breakage of existing submerged plants; if velocities are too high, plants will neither become established nor be able to maintain their presence at a site. The physical stress of high currents also causes reduced photosynthesis rates. (Nichols and Shaw-1986, Butcher-1933, Chambers *et al.*-1991, Madsen and Sondergaard-1983). ***Elodea canadensis*** is reported to grow best at current velocities below about 0.1 m/s (French and Chambers-1992, 1993). Aquatic plant species diversity in the Savaran, a Swedish stream, was greatest between 0.3 and 0.5 m/s (Nilsson-1987), species richness declined at slower and faster velocities.

If velocities are too slow photosynthesis and respiration are reduced due to depletion of carbon and oxygen in stagnant boundary layers of water. Photosynthesis in macrophtes and algae is often limited by the slow rate of CO_2 diffusion, the rate in water is 10^6 times less than that in air (Elzenga and Prins-1988, DeGroote and Kennedy-1977). Removing, or decreasing the thickness of, this stagnant boundary layer facilitates CO_2 diffusion rates from the water to the leaves (Smith and Walker-1980).

Up to a limit, both respiration and photosynthesis increase as current speeds increase. Photosynthesis and respiration of ***Ranunculus peltatus*** and ***Potamogeton pectinatus*** increased as the current speed increased from 0 to 0.005 m/s. At 0.005 m/s the rate of photosynthesis for ***R. peltatus*** was 6 times the rate at 0 m/s. Above 0.005 m/s the rate of photosynthesis began to decrease again (Westlake-1967). The rate of photosynthesis in ***Callitriche stagnalis*** increased with increasing current speed up about 0.008 to 0.012 m/s; at faster currents the rate of photosynthesis dropped rapidly (Madsen and Sondergaard-1983).

The higher flows in June, 1986 appear to have contributed, along with reduced nutrients, to the observed decrease in submerged plants in the Bow River downstream of Calgary (Chambers *et al.*-1991). Dense growth of aquatic plants has also been recorded in the South Saskatchewan River downstream of Saskatoon. Surveys taken in May to September of 1984, 1985, 1988 and 1992 found dry biomass values for submerged plants in the range of 0.5 to 1398 g/m^2 in the 100 km reach downstream from the Saskatoon sewage treatment plant outfall.The dominant species were ***Potamogeton pectinatus, P. filiformis*** and ***P. vaginatus***. Surveys showed that coverage was 100% during low-flow years but less than 50 % during higher-flow years (Chambers-1993).

Despite elevated open-water phosphorus concentrations of 255 µg/L, as compared to upstream values of 20 µg/L, rooted plants are essentially absent from the North Saskatchewan River downstream from Edmonton, Alberta. High discharges appear to have prevented aquatic plant growth (Anderson *et al.*-1986). Similarly, rooted aquatic plants are uncommon in the Red Deer and Oldman Rivers, despite high nutrient loading from the communities of Red Deer and Lethbridge, respectively (Blachford and Ongley-1984, Charlton *et al.*-1986).

It is often difficult to determine if the effects of current are direct, as in physical control of establishment, physical damage, or physical effects on metabolic rates, or indirect, through the effects of water movement on the substrate. Westlake notes that the distribution of plant species is primarily correlated with the nature of the substratum; however, the real causal factor is often water movement affecting both plants and sediments. In many instances, flows experienced during extreme fluctuations during snow melt and reservoir discharge, are more important than the average flows. Changes in flow regime are often within the tolerance range of established aquatic vegetation (Westlake-1975). Haslam estimates that a frequent (less than two year interval) change between turbulent eroding flow and a slow silting one is the worst possible flow regime for plants. As soon as, or even before, a community is established, it is destroyed by the change in flow regime (Haslam-1978).

In the natural state, high water levels of spring freshets break up and flush out rooted plant colonies so there is a constant cycle of colonization and breakdown (Ham *et al.* -1981). In regulated rivers the spring discharge may not be adequate to flush out previous years sediment and vegetation. Hynes reports that the reason for extensive populations of aquatic vegetation below many dams in North America is due to an unnaturally imposed stable discharge regime. The Shand Dam releases cool water in the summer to the Grand River in Ontario and has produced a long stretch of weedy and algal covered substratum resulting from the stabilization of flows (Hynes-1970).

Ridley and Steel, citing work done by Fraser in 1972, also report on large downstream increases in macrophyte growth associated with a marked reduction in maximum scouring flows. Stabilized low flows in the lower Tuolumne River of California contributed towards favorable conditions for luxuriant growths of ***Eichhornia*** sp. (Ridley and Steel-1975). Some data on the relationship between the percent cover of ***Elodea canadensis*** and the current speed in a stream in New York, show that the vegetated area decreases rapidly with increasing velocity. Coverage was 70 percent at about 0.04 m/s and dropped to about 15 percent at 0.1 m/s. There were virtually no plants when velocities exceeded 0.3 m/s. For ***Potamogeton crispus*** however the maximum, 50 percent, cover occurred at a current speed of 0.2 m/s and dropped to 5 percent cover at 0.1 m/s and 0.35 m/s. (Bilby-1977).

An obvious change in the aquatic vegetation in the Tees River in England has occurred since 1971 as a result of the closure of Cow Green Reservoir (Holmes and Whitton-1977). Prior to water impoundment, floods typically scoured the rocky substratum of the river. The most recent occurred in 1968, prior to impoundment, and removed much of the ***Ranunculus fluitans*** population along one section of the Tees River. The large scale disappearance of ***Potamogeton perfoliatus, P. pusillus,*** and ***Elodea canadensis,*** which occurred between 1965 and 1970, was also likely a result of floods. Only ***E. canadensis*** has since been found in the river. Since it was present in tributaries it has probably recolonized through fragmentation. Holmes and Whitton postulate that ***P. crispus, Zannichellia palustris, Myriophyllum spicatum*** and ***R. penicillatus*** were able to colonize the middle reaches of the Tees River after construction of the reservoir eliminated the scouring flows (Holmes and Whitton-1977).

An indirect influence of water movement on aquatic plants is through alteration of the substrate. Sections of river beds which receive the highest current and most direct scouring, directly below a reservoir release, may be reduced to bare rock. Bryophytes (mosses) are generally most abundant here. Where silts begin to deposit and exposed rock is less common, higher plants such as ***Ranunculus*** sp., ***Myriophyllum*** sp. and ***Potamogeton*** sp., become established (Holmes and Whitton-1977). During freshet or similar intermittant levels of high discharge below an impoundment, a large quantity of fine sediments are carried and deposited downstream where flows are reduced.

Peltier and Welch measured sediment deposition among maturing aquatic plants at their first sampling station below Fort Patrick Henry Dam. ***Potamogeton pectinatus*** was dominant here, and usually found in gravel with sediment filled interstices. They also note that other workers have referred to ***P. pectinatus*** as a member of the silted community. ***P. crispus*** , a broad-leaved plant, was found near the reduced current but was more abundant at the second sampling station further downstream where ***P. pectinatus*** was scarce (Peltier and Welch-1969).

Since extensive bands of plants reduce water velocity and act as a silt sieve, they promote the deposition of nutrient-rich, fine particles that would otherwise be flushed further downstream, and may cause the formation of sediment hummocks (Haslam-1978, Swain-1985). Thus, the growth of river plants can positively reinforce the preparation of their own habitat. In addition the growth of one species, which can tolerate higher flow rates, may slow the current and provide a flexible barrier (Sellin-1968, Madsen and Warnke-1983) behind which another less current-tolerant species can become established.

In the Nechako River ***Myriophyllum sibiricum,*** which tolerates higher velocities (Butcher-1933, Westlake-1973) grows first in the spring. The stand of milfoil causes a reduction in water velocity creating conditions suitable for ***Elodea canadensis*** (French *et al.*-1992, 1993) to grow. Once clean gravels are colonized by rooted plants, the eventual infilling of the gravel interstices with silt will cause a decline in sub-surface flows. Such reductions can be fatal to fish eggs and to some invertebrates (Hynes-1970).

Westlake states that a permanent loss of current and depth can often increase the proportion of wetted width habitatable by aquatic vegetation (Westlake-1975). Certain plants are usually found in rivers of a particular character and individual species may either be excluded or become dominant according to local habitat variations. Westlake describes a stylized river as one that would be lined by emergent macrophytes extending onto the banks, with floating-leaved macrophytes in slightly deeper water and submerged macrophytes in still deeper water.

Water Level

Any induced alteration to flow, such as a substantial reduction in discharge downstream of an impoundment, will obviously change the water level accordingly. Short-term fluctuations in depth late in the growing season can greatly increase the quantity and potential nuisance of aquatic vegetation at the surface. Doherty and Roi conducted a two year field study which included the effects of water level fluctuation on the aquatic and semi-aquatic plant communities in selected water bodies of the North Peace-Athabasca Delta in Alberta. The Peace River's influence on the complex delta system, regulated by the W. A. C. Bennett Dam in British Columbia, is dominant in the north section of the Delta. The investigations found that if autumn water levels were sufficiently low in some of the study areas, ice formation could extend through the water column into the sediments such that freeze-killed species, ***Myriophyllum exalbescens*** and ***Potamogeton praelongus,*** were effectively limited to deeper water the following summer. The effects of ice-scour are also reported as having the capability to gouge and displace entire plant communities and their accumulated organic substrates (Doherty and Roi-1972).

Holcomb and Wegener investigated the response of emergent aquatic vegetation to the drawdown of Lake Tahopekaliga in Florida. The effects of water level changes in lentic and lotic situations should be analagous. The distribution of littoral vegetation was found to be determined mainly by prevailing water levels during the growing season and not by water stage duration. Extreme lows of water fluctuation during the growing season largely determined the maximum limit of emergent vegetation (Holcomb and Wegener-1971). One would expect a similar relationship to hold true for submergent plants as well. Exposing emersed aquatic macrophytes by lowering the water level can reduce or eliminate the perennating structures, seeds, fruits, fragments, rhizomes and turions. Thus, water level control can be an effective tool for controlling excessive growth of submersed aquatic vegetation; however, a permanent flow reduction in a riverine environment would merely result in a lateral adjustment of site boundaries of submersed species (Stanley et al.-1974).

Plant species can be grouped according to their response to flow and water level changes. It is then possible to predict, by the species present in a system, which groups would be favored by a perturbation of flow. Table 2, based on observations by Haslam in 1978, predicts the degree of tolerance of different groups of riverine plants to a decline in water level.

The reverse condition, where rooted aquatic plants affect flowing water, also occurs. The reduction in water velocity and resulting promotion of silt deposition has been discussed. Water level can also be raised as a result of the resistance to flow as velocities within the plant bed decrease, and increase in plant-free regions. The water is forced to rise until the weed-free, cross-sectional area is sufficient to allow the discharge of the river to pass (Westlake-1971).

Dawson determined that biomass of ***Ranunculus calcareus*** caused considerable drag and a disproportionately high increase in the depth of water for any given discharge, in a small chalk stream in England. The relationship between the Manning hydraulic coefficient "n" (based on bed slope/energy and discharge) and biomass was almost linear. Plant biomass increased from 1 to 350 gm/m^2 dry weight while Manning's "n" went from 0.05 to 0.3-0.4. Consequently, harvesting of ***R. calcareus*** was necessary to minimize the risk of flooding (Dawson-1978).

Similarly, excessive growth of ***Myriophyllum spicatum*** in a 2 km section of the Okanagan River channel below Vaseux Lake in British Columbia, has contributed to a reduction in the river's capacity to carry peak flows. An increase in Manning's "n" values of 0.032 to 0.040 on June 16, 1981, to 0.042 to 0.052 on July 22, 1981, was attributed to an increase in plant biomass (Brown-1981). Harvesting trials in the channel in 1982 effectively reduced the head 0.37 m at S.O.L.I.D. Dam 2 km downstream of Vaseux Lake and relieved upstream flood conditions around the lake (McNeil-1982).

Kern-Hansen and Holme used a stage-discharge model to calculate the "flood-safe" level of aquatic plant biomass of some Danish waterways. They report that the "flood-safe" biomass varied between streams according to stream slope and adjacent land use, but that 100 to 200 g/m^2 dry weight in streams with a 1 to 2 percent slope was typical (Kern-Hansen and Holme-1982).

Water Clarity

Reservoirs act as settling basins for suspended solids, and the turbidity of discharge water is usually lowered markedly. Fredeen found that impoundment of Lake Diefenbaker on the South Saskatchewan River, resulted in clear, downstream release water. Photosynthesis became possible on a much larger scale than was previously possible under pre-impoundment conditions, and the first aquatic plants in the area became established (Fredeen-1977). Similarly, Hagan and Roberts report that a clear water release in the Missouri River system allowed light to penetrate to greater depths. This resulted in dense growth of aquatic vegetation that has created difficult passage for boaters (Hagan and Roberts-1972).

In some situations, the suspended solids load in regulated waters can be enhanced. Peltier and Welch conducted studies on factors affecting growth of aquatic vegetation in the Holston River below Fort Patrick Henry Dam in Tennessee. Turbidity, along with water velocity and depth, were found to have the most influence on plant distribution and production. The relation of plant growth to available light was demonstrated at one sampling station where the reduction in net change in biomass coincided with a 24 percent reduction in mean daily available light. This was due to increased water depth and high turbidity during a period of variable flow regulation (Peltier and Welch-1969).

Doherty and Roi found that the quantity and quality of sediment contained in flood water had an adverse affect on certain plant species in the Peace-Athabasca Delta, a system regulated by the W. A. C. Bennett Dam. In the Revillon Coupe, a reversing outflow channel of Lake Athabasca, a large and fluctuating suspended sediment load greatly reduced light penetration such that submerged macrophytes were absent. Even the riparian cover in the Coupe was adversely affected in terms of species richness and abundance (Doherty and Roi-1972).

Nutrients

Reservoir effects on downstream temperature, dissolved gasses, and nutrients are not as likely to influence the growth of aquatic vegetation as other physical factors (Peltier and Welch-1969; Westlake-1975). Furthermore, Westlake states that the effects of mineral nutrient concentrations on aquatic plant growth are difficult to demonstrate. He generalizes that lowland waters likely contain nutrients in excess of the concentrations required for growth but that phosphorus, sometimes nitrogen, and possibly potassium may be insufficient for optimum growth in oligotrophic waters in mountainous areas. Nutrient levels may also be an important consideration where hypolimnial water is discharged.

The basic physiology of aquatic plants is similar to terrestrial plants, although aquatics often have special problems arising from the reduction of light intensity underwater and have access to nutrients through their leaves as well as from their roots. It is generally understood that plants will take up nutrients along the path of least resistance, the relative importance of root or shoot nutrient uptake will be influenced by the relative abundance of nutrients in the sediment or water. For example, nutrient rich reservoir release water could enhance downstream growth if the substrates were nutrient-poor rock or sand, for example.

In the Bow River downstream from Calgary, abundant rooted aquatic plant growth has been observed for several decades. Studies by Alberta Environment between 1980 and 1983 documented dry biomass from 500 to 1000 g/m^2 in the 50 km reach downstream from the Calgary sewage treatment plant outfalls. The dominant plants were ***Potamogeton vaginatus*, *P. pectinatus*, *P. crispus*** and ***Zannichellia palustris***.. Recent surveys since the 1983 implementation of advanced phosphorus removal at the sewage treatment plants showed decreased plant biomas (Sosiak-1990).

In many rivers, the throughput of nutrients in the water alone are ample to produce the biomasses found. Peltier and Welch found no correlation between growth of ***Potamogeton pectinatus*** and ***Najas*** sp., and nitrogen and phosphorus at sites in the Holston River where the water contained 0.2 to 3 mg/L NO_3-N and 0.03 to 0.08 mg/L PO_4-P. As discussed earlier, other physical factors, current and turbidity, probably accounted for the variability in growth observed. Their laboratory study on the stem growth rate of ***P. pectinatus*** in sediment with tapwater, 0.44 mg/L NO_3-N and 0.03 mg/L PO_4-P, determined that growth could not be increased significantly by increasing the nutrient concentrations. Growth rates in sediment were 15.0 percent greater than in sand under nutrient concentrations of 0.89 mg/L NO_3-N and 0.11 mg/L PO_4-P and 15.5 percent greater under nutrient concentrations of 1.71 mg/L NO_3-N and 0.26 mg/L PO_4-P. Nutrient levels in the Holston River were considered to be in excess of optimum levels because the growth increment in the tapwater medium was only 5.4 percent less than the growth in the medium containing 3.7 times the NO_3-N and 8.7 times the PO_4-P concentrations. The tapwater nutrient concentrations, 0.44 mg/L NO_3-N and 0.03 mg/L PO_4-P, were below the values found in the river; therefore, the limiting nutrient concentrations for growth were probably below these levels (Peltier and Welch-1969).

When nutrients are absorbed by submerged aquatic plants, the area immediately surrounding the site of uptake is depleted of nutrients. Water flow then replenishes the nutrient supply. Some researchers maintain that flow is more important for the carbon supply (both carbon dioxide and bicarbonate) to submersed plants than for the mineral supply, because carbon is more likely to be limiting for aquatic plant growth (Westlake-1971; Haslam-1978). Westlake explains that carbon may be an important limiting nutrient in some situations, particularly where the water is clear, the flow is slow, the pH is either very high or very low and nitrogen, phosphorus and potassium are readily available.

Although considerable quantities of bicarbonate are normally available in natural waters, the diffusion coefficient for carbon dioxide, or bicarbonate, in water is very low; about 104 times slower in water than in air. Bicarbonate will convert to carbon dioxide readily, given sufficient mass transfer through flow and turbulence, but there is nearly always a stagnant layer covering the surface of aquatic plant leaves. Since this layer is approximately 1 mm in thickness and the path lengths for internal diffusion are 1 to 10 μ, this boundary layer offers a significant resistance to photosynthesis. Increases in flow have been shown to increase photosynthesis over the range of velocities expected within weed beds in rivers of 1 to 5 mm/sec. Data published by Westlake demonstrate a positive photosynthetic response to flow related to the improved supply of metabolites to ***Ranunculus calcareus*** in running water. Oxygen output increased three to six times between static conditions and a velocity of 5 mm/sec (Westlake-1975).

It is not possible to say that any particular nutrient is generally limiting, as each site and plant combination must be considered independently; in many cases some other factor such as excessive flow or turbidity will be more important (Westlake-1975).

Temperature and Dissolved Gases

In the immediate downstream vicinity of the discharge from a water storage reservoir the dissolved gases and temperature can be markedly affected. Surface water discharges will be higher in dissolved gases and warmer than deep water discharges. Turbulent tailrace waters are often supersaturated with gases to the extent that they are harmful to fish (Fowler-1978). The relationship of temperature and dissolved oxygen affects the relative competitive advantage of different groups of macrophytes and of algae and macrophytes in a fairly complex way. Alterations in the timing and method of discharge can affect the plant community immediately downstream.

Plants fix carbon by photosynthesis in two major different ways, the difference can have considerable ecological significance. C_3 plants use the Calvin cycle and C_4 plants the beta carboxylation or hatch-slack pathway (Fitter and Hay-1987). C_3 plants use ribulose biphosphate carboxylase (RuBP carboxylase) for the initial carbon fixation; RuBP carboxylase is both a carboxylase and an oxygenase. C_4 plants however use the enzyme phosphoenolpyruvuic acid carboxylase (PEPA carboxylase) for the initial carbon fixation; PEPA carboxylase is only a carboxylase (Weirer *et al.*-1982).

In water with high dissolved oxygen levels, O_2 can compete with carbon for RuBP carboxylase in C_3 plants (photorespiration) and thus photosynthesis decreases with increasing dissolved oxygen for C_3 plants like ***Elodea canadensis***. This is important when considering the relationships between C_3 macrophytes and epiphytic algae. It is suggested that growth of the epiphytic algae, ***Cladophora glomerata*** and ***Spirogyra*** sp. decrease the rate of photosynthesis in ***Elodea canadensis*** by increasing oxygen concentrations and decreasing carbon dioxide concentrations next to the leaves (Simpson and Eaton-1986). Thus, epiphytes may decrease the photosynthetic efficiency of C_3 macrophytes by inducing photorespiration.

Since RuBP carboxylase has a lower activation energy than PEPA carboxylase, C_3 plants like ***Elodea canadensis*** have an advantage over C_4 plants at cold temperatures (Fitter and Hay-1987). C_4 plants tend to be more prevalent in warm tropical areas. ***Elodea canadensis*** prefers cool temperatures with an optimum of 10 to 25 degrees (Cook and Urmi-Konig-1985).

NECHAKO RIVER STUDIES

The following information is taken primarily from DRAFT documents authored by Mr. Tod French, a graduate student at the University of Alberta, and Dr. Patricia Chambers of the National Hydrology Research Institute in Saskatoon. The data is subject to correction and refinement as further work occurs on this thesis research project of Mr. French. The documents are NHRI Contribution No. CS-93003 and CS-92013 and were prepared for the BC Ministry of Environment Lands and Parks who are partial sponsors and supporters of this research.

The research concerns environmental factors, primarily current speed, water depth and nutrients, as they affect the growth of plants in the Nechako River. The intent of this research is to generate a mathematical model which will predict aquatic plant distribution and abundance in the Nechako River as a function of current speed, water depth and biologically available phosphorus levels in the bottom sediments.

Spring discharge is typically reduced in regulated rivers, but mid-summer discharge in the Nechako is usually increased to allow passage of spawning salmon. The migrating sockeye, ***Oncorhynchus nerka***, require low water temperatures. This high discharge occurs at a time when ***Elodea canadensis*** is near maximum height and susceptible to breakage by the current. This results in fragments, and their associated reproductive meristems, being carried downstream where they may settle and establish new colonies. High summer discharges may help to spread and increase the ***Elodea canadensis*** weed problem in the Nechako River.

Submerged aquatic plants are presently abundant in the Nechako River between Vanderhoof and the Stuart River. ***Elodea canadensis*** comprises about 70 percent of the plant biomass in this reach of the river and up to 40 percent of the channel may be covered by plants. ***Elodea canadensis*** biomass reaches 768 g/m^2 dry weight and total plant biomass reaches 1700 g/m^2. Correlation of biomass with other parameters gave a positive correlation with phosphorus in the sediments and negative correlations with current speed and water depth. This suggests that the reduced spring and summer velocity in the Nechako River due to the Kenney Dam has already led to increased plant growth. Further reductions in the summer velocity arising from the Kemano Completion project, and subsequent increases in phosphorus levels, should lead to further increases in the phosphorus pool, sedimentation and plant biomass.

The flow in the Nechako River has already dropped to about 40-70 percent of what it was before the Kenney Dam. The amount of biologically available phosphorus and nitrogen increases logarithmically as velocity decreases from 0.7 to 0.05 m/s; faster currents presumably do not allow deposition of the nutrient-rich fine sediments, but keep them in suspension. Additionally, controlling the discharge of the river has eliminated the normal annual peak-runoff events which scoured and carried away the fine sediments deposited during low-flow periods of the year. Thus, these fine sediments continue to accumulate.

The Nechako River already has nutrient-rich sediments in the Vanderhoof to Stuart reach with sufficient biologically available phosphorus and nitrogen to support rooted plant growth. During the low flow period from August to May, phosphorus and nitrogen levels should increase even more as increased sedimentation of fine materials occurs in the absence of scouring to remove previous depositions. The consequent large plant biomass may result in large diurnal swings in pH, dissolved oxygen and the form of dissolved carbon. Siltation of spawning beds and changes in the benthos can also be expected. Current velocity will be reduced and recreation activities such as boating, fishing and swimming, will be affected.

Based on the New York work (Bilby-1977) it would appear that current velocities in the Nechako River would have to be maintained above about 0.1 m/s in order to prevent excessive growth of ***Elodea canadensis*** and above about 0.3 m/s to virtually eliminate this species. The work on the Bow River (Chambers *et al.*-1991) indicates that current velocities above 1 m/s may be needed to completely eliminate aquatic plant growth. An extended annual high-flow and high-velocity flush just prior to the growing season, to scour out any accumulated sediments, would also help to prevent nuisance levels of ***Elodea canadensis*** from getting established.

TABLES

Table 1

The Composition of the River Bed as Modified by Current Speed*

Current Speed in m/s	Nature of River Bed
>1.2	Rocks
0.9 to 1.2	Heavy Shingle
0.6 to 0.9	Light Shingle
0.3 to 0.6	Light Gravel
0.2 to 0.3	Sand
0.1 to 0.2	Silt
<0.1	Mud, alluvial deposits

After Minikin-1920.

Table 2

Critical Water Depths for Different Groups of River Plants.

Type of Plant and Depth Preference	Normal Summer Depths in cm. at Stream Center		
	damaging	critical	safe
Fringing herbs	0	10	20
Tall emerged monocotyledons*	10	20	30
Water-supported plants			
—shallow-preference	10	20	30
—medium-preference	30	40	50
—deep-preference	40	50	60

*excluding ***Phalaris arundinacea***

'damaging' means some loss in species presence, usually between two and five out of ten occurrences.
'critical' means satisfactory for one summer, but leading to damage if continued for long periods.
'safe' means recommended for the preservation of the species.

The water-supported plants comprise submerged species and floating ones rooted in the sediment.

'shallow-preference' species include: ***Callitriche*** sp., ***Elodea canadensis*** (to some extent), ***Ranunculus aquatilis*** (short-leaved), ***Ranunculus peltatus*** (short-leaved).

'medium-preference' species include: ***Ceratophyllum demersum, Elodea canadensis, Hottonia palustris, Myriophyllum spicatum, Myriophyllum verticillatum, Ranuneulus calcareus, Ranunculus penicillatus*** and other medium-leaved species. ***Schoenoplectus lacustris, Sparganium emersum,*** and ***Zannichellia palustris*** are also medium-preference species except in chalk streams where shallower water is tolerated).

'deep-preference' species include: ***Nuphar lutea, Ranunculus fluitans*** and ***Sagittaria sagittifolia.***

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