

# Vegetation Benefits to Fish: A Literature Review

April 2000



*Photo courtesy of Wendy Beauchamp*

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*Prepared for:* BC Hydro Strategic Environmental Initiatives Program  
Evaluation of the Ancillary Benefits of Upper Arrow Reservoir Drawdown Zone Revegetation Project

**B.C. HYDRO  
RESERVOIR SHORELINE REVEGETATION STRATEGY**

**VEGETATION  
BENEFITS TO FISH:  
A LITERATURE REVIEW**

**Prepared for: B.C. Hydro**

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## **TABLE OF CONTENTS**

<b>EXECUTIVE SUMMARY.....</b>	<b>I</b>
<b>1.0 INTRODUCTION.....</b>	<b>1</b>
1.1 HISTORY OF FISHERIES/VEGETATION RELATED RESEARCH.....	2
1.2 RESERVOIR SPECIFIC STUDIES .....	3
1.3 WETLAND CHARACTERISTICS .....	5
<b>2.0 HABITAT FUNCTION.....</b>	<b>8</b>
2.1 PRIMARY PRODUCTION .....	8
2.1.1 <i>Methods of Assessing Plant Biomass</i> .....	9
2.1.2 <i>Above-ground Standing Crop (Biomass)</i> .....	9
2.1.3 <i>Below-ground Components</i> .....	10
2.1.4 <i>Annual Cycles</i> .....	10
2.1.5 <i>Nutrient pathways in Wetland Vegetation</i> .....	11
2.2 ORGANIC EXPORT.....	14
2.2.1 <i>Methods Employed to Assess Decomposition</i> .....	14
2.2.2 <i>DECOMPOSITION OF VEGETATION</i> .....	15
2.3 NUTRIENT CYCLING/MICROBIAL PATHS.....	20
2.3.1 <i>The early view, the 'classic' food chain.</i> .....	20
2.3.2 <i>The importance of bacteria in aquatic ecosystems.</i> .....	22
2.3.3 <i>A second discovery, autotrophic picoplankton.</i> .....	22
2.3.4 <i>The new paradigm, the 'microbial loop' and microbial food webs</i> .....	23
2.3.5 <i>Grazing</i> .....	25
2.3.6 <i>Nutrient recycling</i> .....	25
2.3.7 <i>Control of microbial food webs within a trophic gradient.</i> .....	26
2.3.8 <i>Summary</i> .....	26
2.4 SECONDARY PRODUCTION .....	28
2.4.1 <i>INVERTEBRATE / VEGETATION INTERACTIONS</i> .....	28
2.4.2 <i>FISH / INVERTEBRATE INTERACTIONS</i> .....	29
<b>3.0 HABITAT STRUCTURE.....</b>	<b>31</b>
3.1 THE STRUCTURING ROLE OF VEGETATION FOR FISH .....	31
3.2 FISH USE OF VEGETATION .....	33
3.2.1 <i>SPAWNING</i> .....	33
3.2.2 <i>REARING</i> .....	34
3.2.3 <i>COVER:</i> .....	34
3.2.4 <i>FEEDING:</i> .....	35
<b>4.0 INFORMATION NEEDS.....</b>	<b>37</b>
4.1 FISH-INVERTEBRATES-VEGETATION .....	37
4.2 RESERVOIRS.....	38
<b>5.0 LITERATURE CITED.....</b>	<b>40</b>

## EXECUTIVE SUMMARY

### Introduction and Approach

B. C. Hydro has interests in documenting the ancillary benefits of shoreline revegetation, including those to aquatic productivity. This program objective was to assess the benefits of reservoir shoreline revegetation programs to fish by conducting a literature review to document any previous studies or programs that would:

- \* quantify the role of vegetation in aquatic ecosystem productivity, in particular fish.
- \* identify the relationship between aquatic vegetative growth and decomposition to fish productivity, and the other contributions to the food web.
- \* focus on reservoirs, but include relevant information from lake and other aquatic environments.

During the course of conducting this literature review, it became apparent that much of the existing literature was not directly related to the climatic conditions, native plant species or fish populations occurring in B.C. Very little relevant research has been conducted in Canadian reservoirs or wetlands. The use of vegetated wetlands by fish is much better understood and documented for the warmwater and coolwater fishes of eastern and central Canada (e.g. sunfishes, perch, catfish, etc.) than for the coldwater salmonids (e.g. salmon, trout, char and whitefish) of western Canada. In the United States, the Army Corps of Engineers has conducted a substantial amount of research, most of it addressing reservoirs in warm southern climates. Relevant reservoir, fish, vegetation studies were reviewed from a broad north temperate perspective, with specific reference to the British Columbia situation whenever possible. General principles, as they related to the "potential" benefits of vegetation to fish were included from studies not directly applicable to B.C.

Despite their widespread distribution and economic importance, reservoirs have received limited ecological and limnological attention compared to that given to natural lakes and streams. Most reservoir research efforts in North America have focused on fisheries management, siltation, or water quality problems and relatively little comparative or holistic investigation has been attempted. Consequently, scientific understanding of reservoirs as ecological systems and, thus, of the mechanisms underlying reservoir fish production is poor. Reservoirs in North America have been built in greatest profusion in areas where natural lakes are sparse, and there is a considerable knowledge base concerning coolwater and warmwater fishes and their associated plant assemblages in these relatively shallow reservoirs and warmer climates. The fish species composition in reservoirs does not seem to differ significantly from that occurring in natural lakes located in similar latitudes.

Reservoirs generally have a scarcity of littoral vegetation as compared with natural lakes, due largely to annual water level fluctuations and a lack of protective cover from aquatic vegetation may increase predation effects on young fish using such cover. There is direct positive relationship between plant growth and invertebrate populations, so an impoverished nearshore vegetation cover would produce less food resources for higher trophic levels such as fish. The low littoral productivity of reservoirs has been attributed to drawdown effects that are predicted to lead to a decrease in growth rates of fish which feed on littoral organisms. One unique phenomenon of new reservoirs is a high initial level of fish production in response to newly flooded terrestrial vegetation that provides habitat and food for aquatic invertebrates. The establishment or enhancement of aquatic vegetation in reservoir drawdown zones has been recommended as a method to reduce or reverse this drop in fish production which eventually follows reservoir flooding.

### Primary Production

Growth rates of emergent aquatic plants generally exceed those of most terrestrial or submergent vegetation. From an aquatic perspective, the primary producers of the marsh support two food webs; the herbivores that feed directly on the live vegetation, and the detritivores that feed on senescent or decaying plant material. In aquatic systems the line between these two food webs becomes blurred as live or senescent plants can leach nutrients into

the adjacent water column and may support a microflora which may be more productive than the vascular plants themselves.

The foodweb value depends on both the quantity and quality of organic matter exported from the wetland. The quantity of organic matter can be determined by basic biomass assessments and a determination of the area occupied by the various vegetation types. The quality of organic matter is determined by the chemical composition of the plant material (which varies according to species) and environmental conditions that affect the nutrient composition, decomposition rate and colonization by microflora. The productivity of wetland plants varies according to: species, season, temperature, latitude and altitude, nutrient availability, annual cycles, and stresses to which the plants are subjected.

Plant productivity is closely related to geography, environmental conditions and species. Wetland production undergoes a seasonal pattern with active growth in the spring and summer; senescence and translocation of some elements to underground storage organs in the fall; decomposition of remaining aboveground material over the fall and winter; and mobilization of belowground storage to initiate growth in the spring. Sedges appear to thrive in many locations due to their ability to photosynthesize even during freezing conditions in winter, but the most active period of shoot growth has been noted as April, May and June. In addition to annual cycles, substantial year-to-year variability has been noted for sites that have been repeatedly sampled over time. Biomass data for British Columbia wetlands is available for only a few locations, mostly from a mild maritime climate. Sedges in temperate climates produce a maximum standing crop ranging between 400 to 1700 g·m<sup>-2</sup> yr<sup>-1</sup> (dry aboveground material). Most temperate zone sedge production values are reported in the range of 500-900 g·m<sup>-2</sup> yr<sup>-1</sup>, the equivalent of 5 to 9 t/ha (tons per hectare) of aboveground dry matter production per annum. Root/shoot ratios have been reported in the literature from as low as 0.1 to as high as 7, with the most commonly occurring value being around 0.2. Due to differences in species and environment, the biomass and productivity data from the literature cannot be applied to most reservoir environments in B.C. However, the information can be useful in determining trends and orders of magnitude of biological processes.

Wetlands can act as sources, sinks and transformers of nutrients. The role a wetland plays in the mass balance of a particular nutrient depends on: vegetation type, hydrology and hydroperiod; yearly and seasonal variations in nutrient inputs and outputs; interaction with adjacent ecosystems; wetland productivity, the degree of nutrient cycling; and anthropogenic influences. Sedge wetlands have received little attention despite indications that they have the potential to store or cycle large quantities of nutrients. Nutrient concentrations within shoots decline as shoots age. As standing live vegetation is inundated in a reservoir, there is a great potential for the leaching of nutrients from leaves flooded prior to translocation. Very few studies have explored these losses.

Compared to nutrient losses from the leaves, emergent and rooted floating-leaved angiosperms absorb almost no nutrients from the water column. Instead their roots obtain most of the required phosphorus from the sediments and function as nutrient pump to the leaves. Sedges are reported to be highly efficient at nutrient uptake compared to agricultural plants and nutrient uptake efficiencies appear to be greatest in nutrient-poor conditions. Emergent plants generally have lower N contents (due to the need for structural support) than either submersed plants or floating leaved plants, but P levels appeared to be relatively consistent between groups (submergent, floating leaved or emergents). The open characteristic of freshwater riverine marshes results in a continual subsidy and withdrawal of nutrients, with the specific patterns in a given wetland being dependent on seasonal hydrological fluctuations and biological activity.

### **Organic Export**

Very little information is available for organic export from reservoir shoreline vegetation. The information presented in this review draws on freshwater wetland and submergent macrophyte research as they apply to the general environmental conditions found in reservoirs. Wetlands and aquatic vegetation habitats vary widely and there is as yet no consistent pattern established in the literature from which to extrapolate generalizations to reservoirs. Reservoir hydrologic cycles may differ from natural lake or river flooding cycles resulting in shoreline vegetation that functions in a manner similar to a submergent macrophytes. With the immersion of the shoreline plants, portions of the organic constituents are leached into the water column, some are translocated to roots and rhizomes while others will eventually be exported. Associated with the leaching of nutrients, a microbial foodweb may evolve on and adjacent to these plants and will develop its own cycle of enrichment and export. Over an

extended inundation period, portions or all of the exposed plant begin to senesce and will be subject to mechanical and biological fragmentation. Eventually, the plant fragments will either be carried off by currents or incorporated into the substrate where they contribute to the carbon and nutrient stores.

The decomposition of litter and release of nutrients involves at least two processes. The initial loss of soluble materials is usually attributed to abiotic leaching followed by physical and biological breakdown. Leaching rates may vary with the type of plant, species, age, structure and phenology. Decomposition processes include mass losses to micro- and macro-organisms and physical and chemical changes in the remaining material. Rates of decomposition vary in wetlands. The fate of material released or adsorbed during decomposition depends on the physical and chemical composition of material as well as environmental conditions at the site of decomposition. All of these processes may occur in different magnitudes at different times of the hydrologic and growing cycle. Decomposition rates may be affected by temperature, moisture, acidity, nutrient and oxygen levels. Fluctuating water levels are generally thought to facilitate decomposition; consistently high water levels may result in anoxic conditions that may inhibit microbial activity. No satisfactory study has yet been conducted to assess the turnover rates of perennial wetland belowground components. Litterbag studies are the most common approach to studying decomposition, but they are limited by the need for processing of the plant material, resulting in decomposition rates that may not reflect natural processes. Litter turnover rates in freshwater wetlands are reported to be extremely high; patterns of nutrient release from decomposing vegetation differ between species and environments. In general, high temperatures, aerobic conditions; reduced particle size; low fiber content and young tissues accelerate decomposition.

Most wetland primary production is internally recycled. The biological processes of decomposer organisms (invertebrates and microbes) may result in nutrient losses or increases in the nutritive value of the litter. The ability of wetlands to store nutrients varies widely and depends on ambient nutrient levels and local hydrology. Wetlands may range from being oligotrophic to highly eutrophic therefore generalizations regarding nutrient capture are difficult to make. Various studies have indicated the capacity for wetlands to be a seasonal sink for inorganic nitrogen and phosphorus. Emergent vegetation may function as a nutrient pump by absorbing phosphorus from sediments and releasing it by leaching into the water as the shoots are flooded or to the sediment surface when the aboveground growth dies. There is general agreement in the literature that release of sediment derived P from live shoots of macrophytes is not as important as the nutrient release during plant decay. The downstream importance of soluble carbon and detrital material exported from wetlands is not well documented. Most organic carbon exists as detrital carbon and functions as a major source for degraders such as microbes, protozoa, rotifers and microcrustaceans.

### **Nutrient Cycling/Microbial Paths**

The early 'classic' depiction of food webs was composed of interconnected linear chains and was the accepted schematic of the functional trophic pathways for carbon flow in both aquatic and terrestrial ecosystems. Because we knew so little about the role of aquatic bacteria, fungi or protozoa, and even less about their abundance or diversity in ecosystems, their role in food webs was considered largely as 'decomposers'. The functional role of this diverse group of organisms was the reduction of refractory organic remains and feces of organisms, e.g. detritus, that settled onto sediment or soil surfaces. The 1970's research results from the pelagic of oceans and lakes using new techniques showed that bacteria were extremely abundant, and that their abundance were one to two orders of magnitude higher ( $10^5$ - $10^6$  mL<sup>-1</sup>) than previous estimates. Their annual carbon production was also considerably higher, ranging from 30 to 40% of primary production, not 10% as previously thought. These new discoveries of the ubiquity and high metabolic activity of pelagic bacteria were gradually incorporated into ecological studies of other aquatic ecosystems, including periphyton communities within the littoral zone of lakes, inter-tidal zone of estuaries, and on substrates and sediments of streams and wetlands. With the discovery of the ubiquity of picoplankton (suspended bacteria and cyanobacteria fell within the pico-size range, 0.2 - 2.0  $\mu$ m ) came recognition of their role as 'producers' within microbial food webs. They have been found in great abundance within the biofilm matrix on substrate in streams and in wetlands, but little is known of their contributions to carbon flows or production, or whether these minute and metabolically active picoplankton were 'links' or 'sinks' for energy flows within aquatic food webs.

Two new findings have emerged over the past 15 years of research:

\* that re-mineralization of N, P, and DOM is mediated largely by excretion from the grazing activity (predation) of protists, e.g. flagellates, ciliates, and small micro-grazers (rotifers) on picoplankton within complex microbial food webs; and

\* that, bacteria and cyanobacteria are tightly coupled, with cyanobacteria enhanced by nutrients and bacteria by DOM, and both populations are effective competitors of larger phytoplankton and attached algae for bioavailable nutrients N and P.

The microbial loop consists of a complex food web of bacteria + cyanobacteria -flagellates-ciliates and other microzooplankton. A large fraction of picoplankton production is grazed by a great variety of protozoa and micro- and macro-invertebrates in many diverse habitats. The micro-flagellates are currently thought to be the most important 'intermediary link' organism in the transfer of carbon from picoplankton to higher trophic levels in microbial food webs of lakes, streams, littoral sediments and wetlands). Some major predators of micro-flagellates are ciliates, rotifers, and other crustacean zooplankton in lakes, mayflies and stoneflies in streams, and chironomids in littoral assemblages and on sediment. Grazing activities are tightly linked to nutrient and DOC recycling, and are therefore vital to the maintenance of efficient flows of energy and carbon in aquatic food webs. The relative significance of the microbial food web to total nutrient recycling is highest in oligotrophic ecosystems because autotrophic and heterotrophic picoplankton are better adapted to low nutrient conditions than larger eukaryotic cells. These microbial food webs in oligotrophic habitats are largely controlled by "bottom-up" processes, i.e. nutrients, and due to their complexity and number of trophic transfers, they have high respiration rates (CO<sub>2</sub>) and provide minimal carbon flows to higher trophic levels. With increasing nutrient richness microbial food webs become progressively more controlled by "top-down" forces, i.e. grazer populations, whose activities account for much of the nutrient recycling. Even in super-rich habitats microbial food webs can often be predominant in carbon flows, recycling nutrients and channeling heterotrophic bacterial and fungal carbon via protozoan grazers (flagellates, ciliates, sarcodines), small insect larvae (e.g. chironomids) and snails to higher levels - fish. It is becoming abundantly clear from studies of lakes, streams, littoral and wetland habitats, that moderate primary and bacterial production (mesotrophic condition) is a prerequisite for maintenance of viable 'keystone' grazer populations. This is because the presence of active grazer populations means high excretion and equates to efficient carbon flows through both 'classic' and microbial food webs to the benefit of secondary consumers - fish.

## **SECONDARY PRODUCTION**

### ***Invertebrate / Vegetation Interactions***

Aquatic invertebrates provide the critical ecosystem linkages in energy, nutrient and carbon flows between primary producers (algae and vascular plants), microbial assemblages, and higher consumers such as fish, waterfowl and other wildlife. Invertebrates may use live aquatic vegetation for food and a substrate for attachment. Decaying plants provide a source of nutrients for bottom-dwelling invertebrates and for microfloral and microfaunal assemblages which form the base of the aquatic food web. Aquatic plants have been shown to positively alter conditions of water velocity, substrate, detritus (food) availability, etc. for invertebrates. Aquatic invertebrate populations are significantly higher in vegetated sites compared to non-vegetated sites.

Aquatic macroinvertebrates are classified into functional groups based on common or similar feeding characteristics; shredders break down coarse particulate organic matter (CPOM) such as leaves and needles, while scrapers feed on periphyton (algae and their associated microbial assemblages) attached to plant and bottom substrates. Collectors utilize fine particulate organic matter (FPOM), often conditioned or processed by microbiota. Predators feed upon other animals, either by complete or partial ingestion (swallowers) or by draining bodily fluids (suckers). Significantly higher abundances of shredder, scraper and predator guilds were associated with vegetated substrates in contrast with unvegetated substrates. Aquatic macrophytes often support heavy growths of attached algae (epiphyton or periphyton) which is, in turn, an important energy source for both detrital and grazing food chains. Numerous studies indicate that invertebrate grazers play an important role in controlling periphyton populations in lakes.

### ***Fish/Invertebrate Interactions***

Studies on the food habits of temperate coldwater fish species, such as salmonids, have largely been directed towards anadromous species (salmon) in lotic environments (streams and rivers). Most salmonids have adopted a somewhat generalist food habit in concert with an opportunistic feeding strategy and littoral, benthic and pelagic invertebrates, and other fish, constitute their major food items.

The main groupings of aquatic macroinvertebrates of interest to fish include crustaceans (freshwater shrimp), leeches and aquatic insects. Aquatic insects are often the dominant group of invertebrates in aquatic systems. They are generally represented by a broad range of Orders including Ephemeroptera (Mayflies), Odonata (Damselflies and Dragonflies), Trichoptera (Caddisflies), Coleoptera (Water Beetles) and Diptera (True Flies, e.g. Chironomids). Aquatic insects undergo three or four life stages in developing from egg to adult. In general, the adult stage is the shortest and also is the only terrestrial component of the complete life history. The intermediate stages (larvae and pupae) are most important as food resources to fish. Fish are generally opportunistic predators, which focus their feeding activities on points of vulnerability in their prey item's life cycle and habitat utilization characteristics. Typical points of vulnerability for an aquatic insect would include swimming (food gathering), drifting, pre-adult emergence migrations, hatching, etc. Thus the more mobile guilds such as the scrapers, shredders and predators constitute important prey for fish while the more sessile collector guild is likely of lesser importance overall. The mobile guilds, which represent important food resources to many species of fish, appear to be most closely associated with aquatic macrophytes and their epiflora.

Studies of whole systems with a full complement of trophic levels, from plants to fish, are lacking. The macrophyte-periphyton-invertebrate (grazer)-fish (predator) system is complex, and generally poorly understood in temperate systems. Of particular importance in the periphyton-grazer-fish interaction is the functioning of herbivorous invertebrates as an alternative food source for fish thereby reducing the pressure on zooplankton. Without such invertebrates, all fish would compete for the same food resource. While there is general agreement that fish have a major structuring role with respect to lake zooplankton communities, there is less agreement as to how the cascading effect to lower levels of the food chain varies with lake nutrient status.

## **HABITAT STRUCTURE**

### ***The Structuring Role of Vegetation for Fish***

The utilization of littoral vegetation by fish in reservoirs is an area of study that has received little attention. Wetlands are well known for their capacity to buffer water flow and to retain sediments. This is of particular concern around reservoir shorelines where large expanses of unvegetated substrates may be mobilized during heavy rainstorms.

The value of vegetation to fish is in part dependent on the structural complexity that the plants provide. Generally, wetlands with a greater diversity of plant species support a more diverse fish community. Structural complexity of aquatic vegetation provides as a refuge for juvenile fishes, and adults of forage fish species, from predators. The stems and leaves of aquatic plants provide hiding places for small fish and also restrict the movements of predators. Vegetation can also limit the effectiveness of visual predators in detecting their prey. The potential for aquatic vegetation to provide structural refuge for fish is dependent on macrophyte growth form. Related to growth form are biomass and density of aquatic macrophytes; an intermediate stem density is optimal for fish use, whereas excessively dense vegetation can impair feeding by restricting movement and visibility of fish. Generally, more plant biomass is considered desirable (to some optimal level), as greater surface areas provide more substrate for attachment of macroinvertebrates, a rich food source for fish.

Most studies of vegetation as fish habitat have focused on the common littoral zone fish species, such as cyprinids (minnows and carps), the centrarchids (bass and sunfish), perch, northern pike and muskellunge. Commonly, salmonids and other species are not included in the tabulation of sport fish catches of wetland-associated fish in eastern Canada. This is not necessarily evidence that these species do not occur in vegetation, but possibly that they are migratory in their use of vegetation, and may only frequent that habitat type during only one life history stage, or on daily cycles of inshore-offshore use. Young trout are very susceptible to predation in the littoral zones of lakes and reservoirs, where they are preyed on by not only conspecifics and other fish species, but also by avian predators. In lakes, young-of-the-year of these species are often found in association with shoreline

cover. Adult salmonid use of vegetation has not been examined carefully in the literature. Many species of salmonids have been documented to exhibit piscivory (on other species as well as in the form of cannibalism), including rainbow trout, Dolly Varden, and cutthroat trout. Since many fish forage species, as well as other typical prey organisms, such as terrestrial insects and aquatic insect larvae, inhabit vegetated habitats, it seems plausible that these salmonid predators would utilize these habitats as a food source.

### ***Fish Use of Vegetation***

Fish utilization of vegetation can be classified according to use; four types can be distinguished: spawning, nursery/rearing, feeding and cover. It is important to note, however, that the actual use of vegetation by fish is ultimately dependent on the species of fish under consideration. What is eventually needed in the development of a strategy for individual reservoirs is an assessment of which species of fishes will be utilizing the littoral vegetation, and at what times of year.

Warmwater fish use flooded vegetation for spawning whereas coldwater species are not known to do so. Seasonally flooded meadow marshes with grasses and sedges are important because they maintain their structure and allow water circulation to oxygenate the eggs. Reproduction of most wetland fishes is closely related to the timing, extent and duration of flooding

Littoral zone macrophytes have long been associated with increased productivity of juvenile fishes. Stems and leaves of aquatic plants provide hiding places for young fish and restrict movements of predators. Many fish species may opportunistically use wetlands as nursery areas. The littoral area of lakes may be used as rearing habitat for some salmonids, for example, Quesnel Lake for rearing by sockeye salmon.

Cover as defined for fisheries purposes includes shelter or refuge from waves and currents, predators, unfavourable temperatures (low or high) and sunlight. Predation has been identified as the principal biotic factor involved in structuring fish communities. In general, attack and capture rates of predators are reduced with increasing structural complexity and, thus, increased structural complexity from aquatic vegetation generally increases the survival of small fish in the presence of piscivores. In a study of the importance of cover to predation rates on juvenile rainbow trout in reservoirs, nearshore cover increased juvenile survival. Another study suggested that littoral habitat may provide a refuge that may be crucial in preventing the total elimination of year-class strength by piscivory. In general, wetlands have smaller waves compared to those areas lacking vegetation, lending support to the theory that vegetated habitats are more protective in nature. Cover can play a particularly important role during water level fluctuations. In normal riverine flood conditions, the strength of any year class of fish depends on the area flooded during the wet phase because restriction of fish to the "main channel" during the dry phase, leads to higher population densities and increased predation. Increased survival of juveniles during high water, through the introduction of cover in the form of macrophytes, will result in an increase in recruitment to the population in the long term.

Feeding includes direct feeding on plant material and attached algae, detritus from decaying plants, and on invertebrates and vertebrates living in the wetland plant community and associated substrate. Areas with submerged plants have been attributed with more amphipods, insects and other invertebrates than open water and exposed lake bottom. Patchiness within vegetation may provide prey fishes with a habitat where cover from predators is in close proximity to open spaces that harbor zooplankton. The effect of macrophyte habitat may be greater on fish communities of waterbodies with relatively larger littoral zones, such as shallow lakes or reservoirs.

Macrophyte habitat, as used for feeding purposes, is strongly related to risk of predation. Studies of juvenile salmonids in lentic systems show that individuals tend to restrict their movements to nearshore areas, and are consistently found in close proximity to cover (inundated vegetation, logs or boulders). Such selection of nearshore habitat by juvenile rainbow trout has been shown to reduce predation rates. Fish respond to both relative predation risk and habitat profitability in choosing habitats in which to feed.

## **INFORMATION NEEDS**

Despite several decades of scientific investigations into the structural and functional roles of vegetation for fish, there is a general consensus that even those freshwater ecosystems that have received the most attention (i.e. shallow eutrophic lakes) are poorly understood. The lack of scientific knowledge and understanding is even more pronounced for reservoirs particularly in western North America.

Aquatic and emergent vascular plants are recognized as important producers of large volumes of organic material and may function as exporters, transformers or repositories of nutrients in the aquatic ecosystem. These functions vary tremendously according to local environmental and biological factors. Site and species specific information is essential for an understanding of the contribution of the primary producers to the aquatic foodweb.

The epifloral and epifaunal assemblages associated with macrophytes are key elements in nutrient and energy transfer within aquatic ecosystems. The importance of this microbial loop to trophic cycling has only just begun to be appreciated. Macroinvertebrates form the critical linkage between periphyton grazers and fish. Aquatic vegetation provides structural habitat complexity for invertebrates and juvenile fish as well as rich feeding grounds for both. To date some understanding has been gained about individual trophic levels and to a limited extent, some of the linkages and interactions between adjacent trophic levels. What is missing, however, is a deeper understanding at the ecosystem level of the intricate responses, interactions and interdependencies of freshwater biota.

Reservoirs are characterized by periodic water level fluctuations as water is alternately released and retained for various purposes. The potential effects of these fluctuations are greatest in the nearshore littoral zone, a zone which is generally considered to be the most productive area in natural lakes. The biotic responses of the macrophyte-periphyton-invertebrate-fish system to periodic inundation and exposure of littoral habitats are largely unknown. Similarly the potential for cascading effects from the littoral system to the pelagic system is not understood. An understanding of the complexities of biotic processes in reservoirs will lead to more effective management of multipurpose reservoir ecosystems.

## 1.0 INTRODUCTION

During the past decade, B. C. Hydro has undertaken shoreline revegetation in drawdown zones on the Arrow Reservoir, Williston Reservoir, and more recently the Stave Reservoir. These programs have been undertaken to fulfil a number of objectives, primarily dust control on Arrow and Williston reservoirs and as compensation at Stave Reservoir for the Stave Falls Powerplant Replacement Project. Vegetation in the drawdown zone is usually planted in early spring and is inundated at some time during the summer when the reservoir fills. Permanent wetland communities are also inundated on a similar cycle. Although the value of the nutrients and other organics released to the aquatic ecosystem during inundation is implicitly assumed, an assessment of the value of these nutrients and their manifestation as benefits to fish has not been documented.

B. C. Hydro has interests in documenting the ancillary benefits of shoreline revegetation, including those to aquatic productivity.

### **Program Objective**

*To assess the benefits of reservoir shoreline revegetation programs on fish.*

In order to address the program objective, B. C. Hydro assembled a multidisciplinary team to assume various tasks related to determining the value of shoreline vegetation to fish. The first of these tasks was to conduct a literature review to document any previous studies or programs that would:

- quantify the role of vegetation in aquatic ecosystem productivity, in particular fish.
- identify the relationship between aquatic vegetative growth and decomposition to fish productivity, and the other contributions to the food web.
- focus on reservoirs, but
- include relevant information from lake and other aquatic environments.

This information gathered during the literature review is to serve as a resource for the other tasks.

### **Approach**

A preliminary list of references (approximately 3000) considered for the literature review was assembled from a variety of library, Internet and government publication sources. This list was refined to those most applicable to the project objective. All reviewed citations, their abstracts and keywords were entered into a searchable database and pertinent information derived from the literature is summarized in this report.

B.C. Hydro operates 31 reservoirs (B.C. Hydro website) in a variety of biogeoclimatic zones throughout B.C. All of the reservoirs have different hydrologic regimes. During the course of

conducting this literature review, it became apparent that much of the existing literature was not directly related to the climatic conditions, native plant species or fish populations occurring in B.C. Very little relevant research has been conducted in Canadian reservoirs or wetlands. Canadian research focusing on fish and wetland interactions has been centered on the Great Lakes area; however, western aquatic systems are very different from eastern aquatic systems. In the United States, the Army Corps of Engineers has conducted a substantial amount of research, most of it addressing reservoirs in warm southern climates. Information from the Northwest states (Washington, Oregon, Idaho, Montana) is probably of greatest relevance to B.C., but even so, climatic and species differences abound. Based on a preliminary review of the types of information available, we chose not to dismiss those studies which were not directly applicable to B.C., but to evaluate general principles addressed in these studies and to address the "potential" benefits of vegetation to fish, as identified in the literature. Relevant reservoir, fish, vegetation studies are reviewed from a broad north temperate perspective, with specific reference to the British Columbia situation whenever possible. The resulting synthesis is not comprehensive in detail for reasons evident in the section on information needs. However, every effort was taken to make the synthesis comprehensive in scope by covering all aspects of the project objectives identified above.

### ***1.1 HISTORY OF FISHERIES/VEGETATION RELATED RESEARCH***

On a worldwide basis, most studies of fish and vegetation interactions have largely addressed warmwater and coolwater fishes and thus much of the available literature deals with research results from the southern and eastern United States and northern Europe. In a recent international symposium on the structuring role of submerged macrophytes in lakes (Jeppesen 1998), the overwhelming majority of contributors (and studies) were from northern Europe and the eastern and southern United States. The main interactions between vegetation and warmwater fish are identified by Persson and Crowder (1998) as follows:

- Vegetation offers a physical structure that affects both competitive and predatory interactions between fish.
- Vegetation is associated with high densities of invertebrate prey, which have been shown to affect food consumption and growth of the fish.
- Macrophytes and associated epiphytic algae support fish food webs.

In a recent, comprehensive assessment of the international literature on fish-plant interactions, Dibble et al. (1996) reviewed some 203 published studies. They included most of the primary literature on associations between aquatic plants and fish assemblages published over the past 40 years. It is interesting to note that only 1%, or 2 out of 203 publications, referred to members of the family Salmonidae.

In Canada, the use of vegetated wetlands by fish is much better understood and documented for the warmwater and coolwater fishes of eastern and central Canada (e.g. sunfishes, perch, catfish, etc.) than for the coldwater salmonids (e.g. salmon, trout, char and whitefish) of western Canada, notably British Columbia. Hall-Armstrong et al. (1996), in a recent literature review of fish use of wetlands, report that forty of the ninety species of fish in northwestern Ontario make use of

wetland habitat at some stage in their life cycle. Similarly, Jude and Pappas (1992) found that of the total of 113 fish species in the Great Lakes, 47 species were closely associated with coastal wetlands, while another 35 species made use of wetlands to a lesser extent. With respect to fish production in vegetated littoral areas of the Great Lakes, Randall et al. (1996) determined that an index of fish production was significantly higher in littoral habitats with abundant submergent macrophytes than in adjacent areas with low macrophyte abundance.

In discussing the use of wetlands by fish in Canada, Whillans (1987) notes that pelagic, profundal and stream salmonidae - salmon, trout, char, and whitefish in particular - have received more scientific attention than coolwater and warmwater littoral fish. It is also true, however, that coolwater and warmwater littoral fish have received far more attention than littoral salmonidae. Whillans states "Many, in fact most other Canadian fish species, make at least short seasonal or life stage specific appearances in wetlands. It is generally accepted that families such as pike (Esocidae) and sunfish (Centrarchidae) use wetlands for many purposes: spawning, nursery, foraging, and cover. Other families, perch (Percidae) and catfish (Ictaluridae), for example, depend on wetlands for nursery and foraging. Yet others such as salmon, trout and whitefish (Salmonidae) benefit more from wetland-dependant food organisms than wetlands directly."

As previously noted, published studies regarding salmonid utilization of vegetated littoral areas are scarce. Levings (1986) states "The role of littoral vegetation as a habitat feature for salmonids and other fish in Pacific Northwest lakes, rivers and ponds has been poorly investigated." Similarly, the value of flooded terrestrial vegetation "in northern latitude reservoirs and fish communities is not well known but still may be considerable" (Northcote and Atagi 1997). In a recent study on the functioning of marshes of the Lower Fraser River as fish habitat, Levings and Nishimura (1997) report that invertebrate abundance was significantly higher at vegetated sites than unvegetated sites. The authors go on to recommend that unvegetated shorelines be planted to increase fish food invertebrate production. Juvenile salmon can also avoid predation by hiding in vegetation (Burns 1970, Gregory and Levings 1996).

## ***1.2 RESERVOIR SPECIFIC STUDIES***

A thorough analysis of the similarities and differences between lakes and reservoirs appears in Wetzel (1990). Although reservoirs often have much in common with natural lakes, Wetzel summarized the major differences as follows:

Extreme and irregular water level fluctuations commonly occur in reservoirs as a result of flood inflow characteristics, land-use practices not conducive to water retention, channelization of primary influents, flood control, and large, irregular water withdrawals for hydropower generation operations. Multiplicative effects on loadings result. Large areas of sediments are alternately inundated and exposed; these manipulations usually prevent the establishment of productive, stabilizing wetland and littoral flora. Erosion and resuspension of floodplain sediments augment high loadings from drainage basin sources. Sediments are alternately shifted between aerobic and anaerobic conditions, which enhances nutrient release. The reduction or elimination of wetland and littoral communities around many reservoirs minimizes their extensive nutrient and physical sieving capacities that function effectively in most natural lake ecosystems.

In a trophodynamic approach to fish production in reservoirs, Adams et al. (1983) note:

*"Reservoirs occupy an intermediate position between rivers and natural lakes in regard to their organic matter sources as well as their morphologic and hydrodynamic characteristics (Ryder et al. 1974; Ryder 1978; Goldman and Kimmel 1978). Despite their widespread distribution and economic importance, reservoirs have received limited ecological and limnological attention compared to that given to natural lakes and streams. Most reservoir research efforts in North America have focused on fisheries management, siltation, or water quality problems and relatively little comparative or holistic investigation has been attempted. Consequently, scientific understanding of reservoirs as ecological systems and, thus, of the mechanisms underlying reservoir fish production is poor (Gerking 1977; Goldman and Kimmel 1978)."*

The authors conclude that trophic dynamics analyses are particularly sensitive to assumptions of trophic conversion efficiency and that only in reservoirs where phytoplankton production was limited by turbidity, did allochthonous organic matter make a substantial contribution to the reservoir food web. However they recommend more ecosystem-oriented questions and research on reservoirs. With respect to nutrient dynamics in reservoirs, Kennedy and Walker (1990) identify that a transfer of nutrients from the littoral to the pelagic zone occurred with decreasing lake levels (due to hydropower drawdown). In a study of a lake subject to large annual water level fluctuations (WLF) due to domestic water withdrawal, Gasith and Gafney (1990) note:

*"Littoral habitats may play a disproportionate role in large lacustrine ecosystems. Disturbances caused by WLFs may contribute to the temporal and spatial heterogeneity of this region. Further studies are needed to elucidate the littoral-pelagic relationship in large lakes and the possible dependency of higher trophic levels on littoral resources."*

Reservoirs in North America have been built in greatest profusion in areas where natural lakes are sparse, that is to say in non-glaciated areas such as the southern, eastern and midwestern United States (O'Brien 1990). Consequently most studies on the biota of reservoirs have been conducted in these areas and there is a considerable knowledge base concerning coolwater and warmwater fishes and their associated plant assemblages in these relatively shallow reservoirs and warmer climates. This combination of warmer climate and shallower reservoirs "virtually assures a fish composition excluding most cold water fish such as the salmonids, trout and white fishes" (O'Brien 1990). The author also observes that fish species composition in reservoirs does not seem to differ significantly from that occurring in natural lakes located in similar latitudes. While the species composition of reservoirs and natural lakes may be similar, there are often differences in the relative density distribution of particular species. The author postulates that several factors may be responsible. Reservoirs generally have a scarcity of littoral vegetation as compared with natural lakes; due largely to annual water level fluctuations (Meals and Miranda 1991), and this likely influences the spawning success of those species which utilize flooded vegetation for spawning. Similarly a lack of protective cover, such as aquatic vegetation, in the littoral zones of reservoirs would increase predation effects on young fish using such cover (Aggus and Elliot 1975). The direct positive relationship between plant growth and invertebrate populations is well appreciated, so again, an impoverished nearshore vegetation cover would produce less food resources for higher trophic levels such as fish. Geen (1974) attributes the low littoral productivity of reservoirs to drawdown and predicts a decrease in growth rates of fish such as rainbow trout, which feed on littoral organisms. Within the Blue River Reservoir in

Oregon the low standing crop biomass of benthic invertebrates was attributed to annual dewatering of the reservoir (Taxon 1993).

One unique phenomenon of new reservoirs is a high initial level of fish production in response to newly flooded terrestrial vegetation that provides habitat and food for aquatic invertebrates, termed "trophic upsurge" or "reservoir aging" by Straskraba et al. (1993). Terrestrial detritus derived from inundated soils and vegetation enhances fish production in reservoirs for 5-10 years after filling (Ploskey 1981 and 1985). With the decline in terrestrial vegetation comes a drop in biomass and production of fish within the reservoir. Smart et al. (1996) recommend aquatic plants as desirable in reservoirs for fish habitat benefits, and Durocher et al. (1984) recommend a program to increase submerged vegetation in reservoirs, either through introductions or water-level manipulations, to increase standing crop and recruitment of fish. The establishment of aquatic vegetation in reservoir drawdown zones is another way to reduce or reverse this drop in fish production that eventually follows reservoir flooding.

In reviewing ecological interactions in the flooded littoral zone of the Nechako hydroelectric reservoir in British Columbia, Northcote and Atagi (1997) conclude that... *"fish abundance and harvests are higher in littoral areas of reservoirs with, than without, flooded terrestrial vegetation. Very few studies have been made on north temperate reservoirs with salmonid species."* They go on to state... *"Better attention to fisheries requirements will demand much more experimental research on north temperate conditions and fish communities in order to effect appropriate littoral zone treatment."*

### **1.3 WETLAND CHARACTERISTICS**

Very little information was available in the literature concerning the function of shoreline vegetation in reservoir systems, therefore vegetation values for fish were mainly extrapolated from natural wetland systems. Vegetated reservoir shorelines are different in many ways from natural wetlands (lacustrine or riverine) although they may function in the same way as natural wetlands. At times reservoirs may function as lakes, as rivers or as river/floodplain combinations. The defining characteristics of a wetland include:

- the presence of water for at least part of the year
- soils which have been modified by inundation
- vegetation which is adapted to wet conditions

Numerous wetland definitions are common in the literature; the following two have received general acceptance:

*Wetland is defined as land having the water table at, near, or above the land surface or which is saturated for a long enough period to promote wetland or aquatic processes as indicated by hydric soils, hydrophytic vegetation, and various kinds of biological activity which are adapted to the wet environment.*

(Tarnocai 1979) - Canadian Wetland Registry definition

*Wetlands are lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water....Wetlands must have one or more of the following three attributes: (1) at least periodically, the land supports predominantly hydrophytes, (2) the substrate is predominantly undrained hydric soil, and (3) the substrate is nonsoil and is saturated with water or covered by shallow water at some time during the growing season of each year.*

(Cowardin et al., 1979) - U.S. Fish and Wildlife definition

The major differences between reservoirs and natural wetlands systems include:

**Hydroperiod** - the cycle of flooding and drawdown is usually modified dramatically from the natural hydrologic cycles.

**Extended drought and inundation** - reservoir wetlands are subject to much greater extremes of dry and wet periods than are natural wetlands. This means that there are limited numbers of species (primarily plants because other organisms can be transient) which are able to tolerate such extremes. However, those species that can tolerate the extremes often do so very successfully and can become extremely productive. Gill (1977) lists vegetation species or genera identified as occurring in reservoirs in Europe and North America. These genera match those that have been utilized for reservoir revegetation in northwestern North America and for B.C. Hydro projects (Moody 1998).

**Function in the system** - A wetland that is flooded by several meters of water does not function as a typical wetland. At times it functions more as a submergent macrophyte bed which provides refuge and food sources to fish which are freely able to swim in it and through it unlike a natural wetland which is rarely submerged. At times it functions more as a floodplain or terrestrial community which is exposed for extended periods following flooding. Any of the organisms occupying this type of habitat have to be adaptable enough to tolerate the extreme conditions or mobile enough to avoid the extremes. The "benefits" of the shoreline vegetation to fish depend on the hydrological cycle of the reservoir and on how the hydrology coincides with the life cycles of resident fish populations.

**Pulsing of the system** - Natural wetlands undergo annual cycles of inundation and drawdown. They are almost never completely flushed and cleared of all surface organics. Water level extremes are rare in wetlands normally associated with standing water and these normally do not occur during the growing season but when they do, then there is a movement of particulate organic matter into the adjacent water body (Wetzel 1989). The flushing of organic material from the wetland surface is key to understanding its role in functioning as a nutrient sink or pump.

Aquatic ecosystem function has been addressed by a number of authors who have sought to explain the processes involved in complex and productive aquatic communities. The River Continuum Concept (RCC) (Cummins, 1974, Vannote et al., 1980, Minshall et al., 1985, 1983) postulates that most organic matter is derived from terrestrial sources in the headwaters of the streams. The organic material is reduced in size as it travels downstream resulting in an extended nutrient spiral.

The Flood Pulse Concept (FPC) (Junk et al. (1989) is probably more appropriate for a dammed river/reservoir/lake as it refers to floodplain/large river systems. The pulsing of the river discharge is presumed to be a major force controlling biota in the floodplains as a result of the exchange between the river channel, the floodplain and nutrient cycling within the floodplain. Flood pulses are thought to contribute to high productivity by providing (Brinson et al. 1981b):

- abundant water
- a supply of nutrients
- an oxygenated root zone
- removal of waste products

## 2.0 HABITAT FUNCTION

### 2.1 PRIMARY PRODUCTION

Physiological and morphological adaptations in emergent aquatic plants result in growth rates which exceed those of most terrestrial or submergent vegetation (Wetzel 1983, Wetzel and Grace 1983, 1988, Odum 1971, Keefe 1972). Wetland production studies conducted in Alberta, and Minnesota have shown emergent aquatic vegetation to have approximately 30% higher standing crops than adjacent terrestrial meadows (van der Valk & Bliss, 1971; Bernard 1974). Such luxuriant growth, not only provides structural cover and refugia for a variety of organisms, but is also the critical foundation of many life support functions, both aquatic and terrestrial.

From an aquatic perspective, the primary producers of the marsh support two food webs; the herbivores that feed directly on the live vegetation, and the detritivores that feed on senescent or decaying plant material. In aquatic systems the line between these two food webs becomes blurred as live or senescent plants leach nutrients into the adjacent water column and may support a microflora which may be more productive than the vascular plants themselves (see section 2.3).

The food web value depends on both the quantity and quality of organic matter exported from the wetland (Hill 1985). The quantity of organic matter can be determined by basic biomass assessments (addressed in this section) and a determination of the area occupied by the various vegetation types. The quality of organic matter is determined by the chemical composition of the plant material (which varies according to species) and environmental conditions which affect the nutrient composition, decomposition rate and colonization by microflora (refer to subsequent sections). Particulate aquatic plant detritus is considered a high quality food source both for wetland and adjacent lake ecosystem consumers (Brinson 1977, Brinson et al. 1981). To estimate the potential of wetlands for export or capture of nutrients, it is necessary to understand hydrology, concentration of constituents, mass flow, seasonality, and other factors (Whillans 1987).

The productivity of wetland plants varies according to:

- species (Bernard et al. 1988 )
- season (Bernard, 1974; Bernard and MacDonald 1974),
- temperature (Gorham and Somers 1973, Gorham 1974, Keefe 1972),
- latitude and altitude (Bernard, 1973, Pearsall & Newbould 1957, Dennis et al. 1978, Reynolds et al. 1978, Solander 1983 a,b,c),
- nutrient availability (Pearsall and Gorham 1956, Gorham 1974, Gorham & Bernard 1975, Auclair et al. 1976)
- annual cycles, (Kvet 1983, Bernard et al. 1988 Solander 1983 a,b,c ), and
- stresses to which the plants are subjected (Grime and Campbell 1991).

Sedges and grasses often dominate in highly productive northern temperate wetlands and have been noted among those species known to colonize reservoir shorelines (Gill 1977). Research has indicated that increasing severity of climate results in decreased aboveground production, with monthly mean temperature the most important environmental factor controlling biomass production (Bernard 1973; Gorham 1974). Although shoot numbers were increased by fertilization of sedge sites in northern Sweden, the growth of individual shoots was still regulated by summer temperature (Solander 1983a,b).

### **2.1.1 Methods of assessing plant biomass**

Biomass refers to the amount of standing plant material (usually designated as aboveground or belowground, depending on the component measured) at the time of measurement. Production is defined as the change in biomass of the entire plant over time. Net primary production (NPP) is usually derived from a series of standing crop harvests and calculated from the incremental growth over time. This is usually considered to be an underestimate of actual production since it does not account for losses to grazers and shoot turnover. Shoot mortality has been reported to be as high as 80-90% during the growing season (Bernard 1975; Bernard and Gorham 1978) and high turnover rates have been noted in temperate wetlands (Wetzel and Howe (1999).

Respiration measurements have been attempted for wetland vegetation but without great success.

Most wetland production research has reported primarily aboveground values due to the difficulty in sampling belowground components. Where root harvests have been attempted, there has been difficulty in isolating root components from mineral substrates; avoiding losses of organic material; and determining live versus dead components.

### **2.1.2 Above-ground standing crop (biomass)**

Plant productivity is closely related to geography, environmental conditions and species. In order to make this discussion regionally relevant, we focussed on plant species, geographic areas and climatic zones similar to those found in B. C. A number of biomass studies have been conducted in sedge (*Carex*) dominated wetlands with a few species having been studied extensively (*C. lacustris*, *C. gracilis*, *C. rostrata*, *C. lasiocarpa*, and *C. vesicaria*). Of these, only the last 3 species occur in B.C. and only *C. rostrata* has been utilized in shoreline revegetation programs (Moody 1998). A limited amount of research has been conducted in Alberta, however this relates primarily to peat dominated wetlands (van der Valk and Bliss 1971, Gorham and Somers 1973, Szumigalski and Bayley 1996, Thormann and Bayley 1997).

Biomass data for British Columbia wetlands is available for only a few locations (Appendix 1), mostly from a mild maritime climate. Wetland biomass has been measured primarily in the Fraser River estuary (Yamanaka 1975, Moody 1978, Kistritz et al. 1983), the Squamish estuary (Levings and Moody 1976) and in the Pitt River marshes (Ogwang 1979, Barnard 1975) (Appendix 1). Interior or northern B.C. marshes have been researched almost exclusively from the perspective of agricultural development (McLean et al. 1963, Pringle and van Ryswyk 1965, 1968, van Ryswyk et al. 1973, 1974, Cariboo Poorly Drained Soils Development Extension Committee, 1992).

Most temperate zone sedge production has been reported to range between 500-900 g m<sup>-2</sup>, the equivalent of 5 to 9 t/ha (tons per hectare) of aboveground dry matter production per annum (Appendix 2). The aboveground production have been reported to range from 300 to more than 1000 g m<sup>-2</sup> (3-10 t/ha); belowground production is reportedly approximately half of the aboveground values 180 to > 500 g m<sup>-2</sup> (1.8-5 t/ha) (Bernard et al. 1988). Agronomic studies of "native forage vegetation" in central British Columbia (presumably a mixture of sedges and grasses) have shown that unfertilized meadows produce approximately 1.5 t/ha, which increases to 3 t/ha when fertilized (Cariboo Poorly Drained Soils Development Extension Committee 1992).

### 2.1.3 Below-ground components

The information available for belowground biomass of wetland species is, in general, inadequate to address the topics of annual productivity or of nutrient cycling. Root/shoot ratios have been reported in the literature from as low as 0.1 to as high as 7 with the most commonly occurring value being around 0.2 (Appendix 2). In cases where extremely high root-shoot ratios are reported, the below-ground standing crop may represent the accumulation of several years of growth (e.g. Ogwang 1979). In coastal Alaska, high root/shoot ratios were attributed to low soil temperatures, low nutrient levels and high soil moisture content which reduced the effectiveness of nutrient and water uptake (Shaver and Billings 1975). That study also noted that up to 98% of the vascular plant biomass at peak season was composed of roots and rhizomes. Root longevity was determined to be approximately 7 years with an estimated turnover rate of 100 g m<sup>-2</sup> yr<sup>-1</sup>.

In an excellent study of primary production and nutrient cycling in a Fraser River estuary sedge marsh Kistritz et al. (1983) report on annual variability in the various plant components and nutrient levels. They concluded that the aboveground standing crop represented 25% of the total belowground biomass but made no attempt to segregate live from dead components and did not attempt to determine annual production.

Due to differences in species and environment, the data from the above studies cannot be applied to inland wetlands in B.C. However, the information can be useful in determining trends and orders of magnitude of biological processes.

### 2.1.4 Annual cycles

Wetland production undergoes a seasonal pattern with active growth in the spring and summer; senescence and translocation of some elements to underground storage organs in the fall; decomposition of remaining aboveground material over the fall and winter; and mobilization of belowground storage to initiate growth in the spring. It is this cyclic pattern and the determination of aboveground vs. belowground components which makes an accurate estimate of production so difficult. The aboveground growth is in essence deciduous, whereas belowground growth is perennial and offers nutrient support for the aboveground cycles. However, the life histories of plants which are able to tolerate extended inundation and drawdown are similar in that all have shoots that develop late in the summer and overwinter as small shoots just above or below the soil surface. These shoots grow rapidly in the spring, in part by translocating nutrient reserves, estimated at 15-25% of spring growth (Roseff and Bernard 1979) from rhizomes. *Carex* shoots grow rapidly in spring and early summer but cease

growth by mid-summer when new rhizome growth begins (Kistritz et al. 1983, Bernard and Bernard 1989, Hill 1985). By late summer, a portion of the plant's production is translocated to the belowground storage organs. Kistritz et al. (1983) determined this translocation to be approximately 38% of the standing crop.

In addition to annual cycles, substantial year-to-year variability has been noted for sites that have been repeatedly sampled over time (Bernard et al. 1988). Over a 10 year period, Kvet (1983) noted a range of standing crops in response to climatic variability, from 126-507 g m<sup>-2</sup> per annum. More than 20% annual variability in production was reported for *C. rostrata* marshes in N. Sweden (Solander 1983).

Sedges appear to thrive in many locations due to their ability to photosynthesize even during freezing conditions in winter. An increase in standing crop was noted for *C. rostrata* during winter conditions (Gorham & Somers 1973) and growth was noted very early in the growing season, before the ground was thawed (Bernard 1974). Sedge stands were considered to be multi-aged late in the year as some shoots were initiated the previous fall (Bernard and MacDonald 1974). Annual variability in winter shoot development has been noted in response to climatic variations (Moody pers. obs.) with more robust overwintering shoot growth apparent during extended warm fall conditions or mild winters. This pattern of increased winter biomass with increasingly milder winters is also evident in the data from the following geographic ranges. Winter standing crops of 5-11 g m<sup>-2</sup> have been noted in northern Sweden (Solander 1983), in the Squamish estuary 33 g m<sup>-2</sup> (Levings and Moody 1976) and 114 g m<sup>-2</sup> to 200 g m<sup>-2</sup> in New York (Bernard and Bernard 1977). The most active period of shoot growth has been noted as April, May and June.

### **2.1.5 Nutrient pathways in wetland vegetation**

Wetlands can act as sources, sinks and transformers of nutrients. The role a wetland plays in the mass balance of a particular nutrient depends on: vegetation type, hydrology and hydroperiod; yearly and seasonal variations in nutrient inputs and outputs; interaction with adjacent ecosystems; wetland productivity, the degree of nutrient cycling; and anthropogenic influences. Closed wetland systems such as bogs have little opportunity for export, most nutrients entering a bog are quickly absorbed by plants and incorporated into plant tissue. At senescence the nutrients are either incorporated into the substrates, or are leached out and taken up by other live plants. In general, the output of nutrients from bogs is very low. In contrast, riparian wetlands are open biogeochemical systems characterized by a great opportunity for nutrient exchange during flood periods. Nutrients are received in inorganic form (e.g., ammonium and nitrate ions, inorganic phosphorus) and released as organic matter (senescent aboveground plant components) or are leached directly from the live vegetation when it is flooded.

Sedge wetlands have received little attention despite indications that they have the potential to store or cycle large quantities of nutrients (Auclair, 1977, 1982, Bernard & Solsky 1977, Bernard & Hankinson 1979, Chamie and Richardson, 1978). Most *Carex* species display similar shoot nutrient concentrations (Appendix 4); 0.6-2.1%N, (average 1.5) and 0.13% for P (Bernard et al. 1988). Large quantities of nutrients may be absorbed during the growing season and translocated to belowground organs for storage in various wetland species (Bjork 1967, Davis and van der Valk 1983, Boyd 1978, Prentki et al. 1978). Contrary to several other studies,

Bernard and Solsky (1977) and Bernard and Hankinson (1979) did not find large amounts of nutrients transferred in either spring or fall. Dykyjova and Pribil (1975) noted that the variation in energy content of higher aquatic plants was less than the variation in other chemical constituents either by species or by time. Probably the greatest variation occurs in chemical composition between plant structures (leaves, roots, rhizomes) for submergent aquatics (Musil & Breen 1977 in Boyd 1978), as well as emergents (Gaudet 1975 in Boyd 1978, Moody & Moody 1985, Moody 1990).

Emergent plants generally have lower N contents (due to the need for structural support) than either submersed plants or floating leaved plants, but P levels appeared to be relatively consistent between groups (submergent, floating leaved or emergents). Species, which produce high standing crops usually, have lower percentages of N than species that produce low standing crops (Boyd 1978, Chapin et al. 1986).

Nutrient concentrations within shoots decline as the shoots age. This may be attributed to nutrient losses by leaching from live shoots, translocation to belowground parts, and eventually senescence and decomposition losses. The concentrations of macronutrients (N, P and K) in many temperate sedges reach peak concentrations soon after spring shoot growth begins but decrease as the shoots age (Chapin et al., 1975, Bernard and Solsky, 1977; Bernard and Hankinson, 1979; Auclair, 1982, Dykyjova, 1983; Solander, 1983b,c; Verhoeven et al., 1983). In the Fraser estuary, the peak concentration of N occurred in May (2.75% Moody 1978; 2.26% Kitritz et al. 1983) then declined steadily to less than 1% by July. The peak nutrient standing crop in other areas was found to coincide with maximum shoot biomass (Bernard and Solsky, 1977; Bernard and Hankinson, 1979; Dykyjova, 1983), or to precede the peak biomass by 2-4 weeks (Auclair, 1982; Kistritz et al., 1983; Solander, 1983b). Nutrient concentrations in belowground components tend to be lower than in aboveground ones (Bernard and Solsky, 1977; Bernard and Hankinson, 1979, Kistritz et al., 1983; Solander, 1983b) but reflect a seasonal pattern similar to the shoots. After the peak above-ground biomass, there is often a rapid decrease in the above-ground nutrients and a rise in the below-ground nutrients due to translocation from dying leaves (Bernard and Hankinson, 1979). A seasonal pattern of low belowground standing stocks of nutrients in late June-early July has been noted, presumably when maximum translocation has occurred (Bernard & Solsky, 1977, Bernard & Hankinson 1979). Kistritz et al. (1983) reported that aboveground nutrient stocks reached a peak in late June that coincided with the minimum levels of underground nutrients. The subsequent gain in underground nutrient stocks matched the aboveground decline, confirming the translocation process.

As standing live vegetation is inundated in a reservoir, there is a great potential for the leaching of nutrients from leaves flooded prior to translocation. Very few studies have explored these losses. Kistritz et al. (1983) calculated a leaching rate of 23.9 mg N and 7.8 mg P m<sup>-2</sup> per day for estuarine sedge marshes which were flooded daily. Prentki et al., (1978) reported the total P loss from living shoots of *C. aquatilis* in a tundra pond to be 0.4 mg P m<sup>-2</sup> (0.5% ) of the above-ground standing stock. Kairesalo and Uusi-Rauva, (1983) reported low P release by *Equisetum fluviatile* L. which was at once taken up by the epiphytic algae. Dissolved organic carbon leaching rates calculated for a *Spartina* marsh in Georgia were calculated using a loss of 125µg C per g of leaf dry weight per hour (Gallagher et al. 1976). A comparable rate of 119µg C per g of leaf dry weight per hour was calculated to be approximately 14% of ANPP based on a 8 hour

tidal exposure (Kistritz et al. 1983). Phosphorus export, extrapolated from calculations of P content of marsh vegetation ranged from 200 kg P ha<sup>-1</sup> for reed-canary grass (*Phalaris arundinacea*) to 300 kg P ha<sup>-1</sup> for bluejoint/rush (*Calamagrostis/Scirpus*) at Pitt Meadows, B.C. (Bernard 1975).

Compared to nutrient losses from the leaves, emergent and rooted floating-leaved angiosperms absorb almost no nutrients from the water column. Instead their roots obtain most of the required phosphorus from the sediments and function as nutrient pump to the leaves (Wetzel 1988). In contrast, algae and submergent macrophytes absorb nutrients directly from the water column by foliar absorption and prolific epiphytic algal growth is related to high concentrations of nutrients in the water (Wetzel 1988). It is to be expected that the ability of inundated vegetation to host an epiphytic flora is in part related to the ambient nutrient levels (either substrate or water, depending on the type of vegetation) and in part to the "leakiness" of the host plant in leaching P into the water column.

Sedge species are reported to be highly efficient at nutrient uptake compared to agricultural plants (Atwell et al., 1980) and nutrient uptake efficiencies appear to be greatest in nutrient-poor conditions (Chapin and Oechel, 1983; Shaver and Melillo 1984; Veerkamp and Kuiper, 1982)). At low P and N availability, *Carex* species demonstrated higher Root:Shoot ratios than in higher fertility sites (Veerkamp et al., 1980; Noble and Marshall, 1983; Shaver and Melillo, 1984). Many sedge habitats are considered to be impoverished in nutrients. This has been confirmed in the plants' responses to fertilizer treatment by increased shoot density and biomass (Pringle and van Ryswyck 1968; Shaver and Chapin, 1980; Solander, 1983b; Verhoeven, 1983; Vermeer, 1986). Fertilization of "native forage vegetation" in central British Columbia (presumably a mixture of sedges and grasses) produced a doubling of yield, from 1.5 t/ha, to 3 t/ha (Cariboo Poorly Drained Soils Development Extension Committee 1992). Native vegetation responded more strongly to nitrogen than to phosphorus or sulphur enrichment (Cariboo Poorly Drained Soils Development Extension Committee 1992). Fertilization experiments in other wetlands have shown that N, and P can increase shoot biomass production (Noble and Marshall, 1983; Solander, 1983a; Verhoeven et al., 1983; Vermeer, 1986). Sedges were reported as having yield responses to a combination of N and P or P only, but not to N alone (McLean et al. 1963). A continued carryover response to P and K was noted for the next 5 years. The increases in N, P and K levels in the substrate were noted in sedge shoot responses by Chapin et al. (1975). However, Shaver and Melillo (1984) observed a limit to luxury uptake of one element when another was strongly limited. All species in their experiments had about the same 'optimum' N:P ratio.

The open characteristic of freshwater riverine marshes results in a continual subsidy and withdrawal of nutrients, with the specific patterns in a given wetland being dependent on seasonal hydrological fluctuations and biological activity. Marshes differ from terrestrial systems by virtue of their inundation patterns and the prevalence of anaerobic soils that show seasonal nutrient variations. Concentrations of N, P, K, Ca, and Mg have been observed to follow predictable trends over the growing season (Klopatek 1978).

## **2.2 ORGANIC EXPORT**

Nutrient export from wetlands may occur in minor amounts on a regular basis or may be large and episodic, depending on a number of factors, including hydrology (Richardson 1978). Prior to flooding, export from wetlands is mainly a result of limited herbivory by terrestrial vertebrates and invertebrates. A much greater proportion of plant production is exported to the aquatic system during submersion. Even within the aquatic system, most of the aboveground production of wetlands is not consumed by herbivores but decomposes on the wetland surface (Gallagher, 1978; Polunin, 1982) and is exported in pulses associated with the hydrologic cycle.

In a reservoir, the hydrologic cycle may be dramatically different from "normal" lacustrine or riverine flooding cycles. This often results in emergent vegetation being submersed completely, and functioning for variable periods of time (depending on hydrology) in a manner similar to a submergent macrophyte community. With the immersion of these plants, portions of the organic constituents will be leached in to water column, some will be translocated to roots and rhizomes while others will eventually be exported. Associated with the leaching of nutrients, a microbial foodweb may develop on and adjacent to these plants (Section 2.3) and will evolve its own cycle of enrichment and export. Over an extended inundation period, portions or all of the exposed plant begin to senesce and will be subject to mechanical and biological fragmentation. Eventually, the plant fragments will either be carried off by currents or incorporated into the substrate where they contribute to the carbon and nutrient stores.

This section will first summarize methods which have been used to address the problem of measuring decomposition, followed by a synthesis of the research into decomposition of emergent and submergent macrophytes. Very little information is available pertaining to decomposition and organic export in reservoir systems. The information presented here draws on research from freshwater wetland and submergent macrophyte domains as it applies to the general environmental conditions found in reservoirs. Wetlands and aquatic vegetation habitats vary widely and there is as yet no consistent pattern established in the literature from which to extrapolate generalizations for reservoir shoreline vegetation.

### **2.2.1 Methods employed to assess decomposition**

Most studies have explored weight loss and composition changes of senescent or dead material in litterbags; some mounted on poles, others on ground, some buried. Such studies are reproducible and provide an approximation of decomposition rates, but their main limitation is the need for processing of the plant material (harvested, cleaned, dried and weighed) prior to its placement in the litterbags. This results in changes in the physical and chemical characteristics of the plant material and may result in decomposition rates which do not reflect natural processes. In their natural habitats, aboveground components may remain standing for a long time after senescence, prior to contact with the sediment surface. Belowground components remain alive for several years. However, the difficulty in dealing with a complex topic such as decomposition, necessitates the use of techniques that do not always reflect natural conditions.

The following summarizes the most frequently used methods addressed in the literature.

- Litterbags (Ogwang 1979 [Fraser Estuary], Taxon 1993 [Oregon], Thormann and Bayley 1997 [Alberta]; Grout et al. 1997 [Fraser Estuary], Puriveth 1980 [Wisconsin])
- Soil Respiration (Bridgham & Richardson 1992)
- Peat Microstructure Changes (Johnson et al. 1990)
- Degree Of Humification (Malmer 1986)
- C:N Quotient Of Peat (Malmer and Holm 1984)
- Measurement of ATP (adenosine triphosphate - as an index of biomass) (Godshalk and Wetzel 1978)
- Decomposition Measurements Using Cellulose (Filter Paper Or Cotton Strips) to Compare Decay Rates Between Sites (French 1988, Verhoeven et al. 1990, Santelmann 1991, Thormann and Bayley 1997)
- Standard Plant Species (Ohlson 1987, Johnson & Damman 1991, Szumigalsi & Bayley 1996)

### 2.2.2 Decomposition of vegetation

The decomposition of litter and release of nutrients involves at least two processes. The initial loss of soluble materials is usually attributed to abiotic leaching (Boyd, 1970; Gosselink and Kirby, 1974; Godshalk and Wetzel, 1978a, 1978b, Melillo et al., 1984) followed by physical and biological breakdown (Puriveth 1979, Brinson et al. 1981).

#### Leaching

Leaching losses are initiated at inundation with or without micro-organism activity (Willoughby 1974). Differences in leaching rates may occur with the type of plant, species, age and phenology. Live plant material has been observed to decompose more than twice as fast as senesced material (Nelson 1990). Wrubleski et al. (1997) suggested that their finding of higher than normally reported leaching rates for the reed *Phragmites communis* (up to 19% d<sup>-1</sup>) might be due to their use of live plant material as opposed to the conventionally used senescent material. Laboratory investigations of sedges have revealed leaching losses ranging from 5-8 % of *Carex aquatilis* mass during the first 7 days in vitro (Thorman and Bayley 1997) compared to 14% for *C. rostrata* (Ohlson 1987). Calculations based on field studies of living shoots produced leaching rates of 23.9 mg N and 7.8 mg P m<sup>-2</sup> per day for estuarine sedge marshes (Kistritz et al. 1983) and 0.4 mg P m<sup>-2</sup> (0.5% ) of the above-ground standing stock of *C. aquatilis* in a tundra pond (Prentki et al. 1978). The structure and physical composition of the plant may also influence leaching rates. Water soluble organic substances were lost from deciduous leaves in 1 week, whereas from pine and spruce needles they substances remained up to 3 weeks (Nykqvist cited in Willoughby 1974). In general, due to the number of variables involved in quantifying leaching losses, the studies which have been conducted to date are not able to provide a complete picture of nutrient release from inundated emergent vegetation.

#### Physical and biological decomposition

Subsequent to the leaching of soluble organic matter, decomposition proceeds with mass losses to micro-organisms and with physical and chemical changes in the remaining material (Brinson et al. 1981). Initial weight losses in spruce needles (approximately 30% of initial mass) were attributed to leaching and microbial conditioning with subsequent losses attributed to macroinvertebrate, primarily chironomid, feeding (Crawford and Rosenberg 1984). The microbial conditioning was marked by fungal colonization that began as early as 3 days after submergence. The authors demonstrated that spruce needles were not palatable to

macroinvertebrates until sufficient conditioning had occurred (after 41 days); prior to that it was likely that any colonizing macroinvertebrates fed on the periphyton (Crawford and Rosenberg 1984). Analyses of decomposition processes in emergent vegetation by litterbag analyses revealed initial leaching of nutrients, followed by colonization by microorganisms (Puriveth 1979). An increase in litter nitrogen levels was attributed to an increase in the microbial biomass. Suppression of the microbial community by sterilization and by antibiotics resulted in inhibition of the decomposition and in no net weight loss beyond the initial leaching period. The later stages of decomposition included a breakdown of plant litter by arthropods, annelids and epiphytes and were strongly influenced by the nature of the plant material; high fiber tissues degraded slowly (Puriveth 1979).

### **Decomposition rates**

Rates of decomposition vary in wetlands (Holding et al., 1974; Odum and Heywood, 1978; Davis and van der Valk, 1978 1983; Chamie and Richardson, 1978; Neely and Davis, 1985). The fate of material released or adsorbed during decomposition depends on the physical and chemical composition of material (Gosselink and Kirby, 1974; Davis and van der Valk, 1978; Day, 1982; DeBusk and Dierberg, 1984), as well as environmental conditions at the site of decomposition (Gallagher, 1978; Day, 1982). All of these processes may occur in different magnitudes at different times of the hydrologic and growing cycle. Decomposition rates may be affected by temperature, moisture, acidity, nutrient and oxygen levels (Brinson et al. 1981, Bartsch and Moore 1985, Gorham 1991). Fluctuating water levels are generally thought to facilitate decomposition (Thorman and Bayley 1997). Litter decay may be enhanced in sites flooded for part of year; but, consistently high water levels may result in anoxic conditions that may inhibit microbial activity (Brinson et al. 1981). This did not appear to be the case in a freshwater marsh, in which the biomass of metaphyton was found to increase significantly when the marsh was flooded to higher levels than normal (Hosseini and van der Valk 1989). Significant differences were noted in epiphytes between plant species in a freshwater marsh; differences in growth between species were attributed to the possibility of self-shading in vertically oriented species or to differences in tissue nutrient concentrations (Cronk and Mitsch 1994). The authors determined the net epiphyte productivity to be between 2 and 85 g carbon m<sup>-2</sup> per year and the calculated uptake of phosphorus was calculated to be approximately 1 to 3 mg P m<sup>-2</sup> of wetland area. Wrubleski et al. (1997) investigated decomposition of roots and rhizomes and found little difference in losses of root mass between unflooded and flooded soils. The depth of flooding was found to have little effect on decomposition rate, which they attributed to burial of the bags in saturated soils. The root litter lost up to 90 % of its nitrogen and phosphorous contents within the first 112 days, beyond which the decomposition rates remained stable. Decay rates were found to be similar for aboveground shoots. However a major limitation of this study was the method which only dealt with "dead" roots. It did not represent the normal process of a gradual turnover of roots and rhizomes over several years. No satisfactory study has yet been conducted to assess the turnover rates of perennial wetland belowground components.

Decomposition processes in freshwater wetlands are poorly understood but litter turnover rates are reported to be extremely high (Odum et al., 1984); and the patterns of nutrient release from decomposing vegetation differ between species and environments (Odum and Heywood, 1978; Simpson et al., 1983a; Odum et al., 1984). It is generally recognized in the literature that:

1. Higher temperatures accelerate decomposition (Gallagher 1978, Godshalk & Wetzel 1978b, Brinson et al. 1981)
2. Aerobic conditions accelerate decomposition (Godshalk & Wetzel 1978b)
3. Reducing particle size increases decomposition rates; fragmentation of whole plant parts greatly increases surface area (Davis & van der Valk 1978, Chamie & Richardson 1978)
4. Decay rates are negatively correlated with total fiber content of plant (Godshalk & Wetzel 1978b, Brinson et al. 1981, Davis & van der Valk 1978)
5. Younger tissues decompose more rapidly than older (Ogwang 1979, Nelson et al. 1990)
6. Decomposition rates vary according to species (Chamie & Richardson 1978)
7. The status of knowledge regarding belowground production and decomposition is poor (Brinson et al. 1981; Wrubleski et al. 1997)

Decomposition rates have been found to be highest during the first 30 days of exposure (Wigham et al. 1989, Ogwang 1979). This may partially be due to the higher temperatures generally present during the late summer to early fall period when decomposition is initiated. Godshalk and Wetzel (1978) found a gradient of decomposition from slow in cold, anaerobic environments, to fast in warm aerobic conditions. The most temperature dependent process was the conversion of particulate organic matter to dissolved organic matter. Conversion of dissolved organic matter to CO<sub>2</sub> was severely restricted by anaerobic and cold conditions (Godshalk and Wetzel 1978).

In B.C. Lower Mainland marshes Ogwang (1979) also found a strong temperature response as decomposition occurred much more rapidly in early fall and late spring than in winter. The greatest differences observed in his study were in the in-vitro decomposition rates of young shoots versus mature plant material. Decomposition rates of young shoots were 4-6 times that of the mature shoots (42% vs. 10% *Carex sitchensis*; 60% vs. 9% *Phalaris arundinacea*) in the first three weeks of the experiment. Losses over the subsequent three-week period were relatively minor. The increasing age of a plant is usually correlated with increasing fiber content. The structure of plants influence decomposition loss over time with the most rapid decay occurring as expected in submersed aquatics which lack a rigid supportive tissue. However, Godshalk and Wetzel (1978) examined two species of *Scirpus*, one that functions as a submergent (*S. subterminalis*) and the other as an emergent (*S. acutus*). Both species displayed similar decay rates indicating a similarity of structural and decompositional characteristics within the genus.

Habitats do not appear to be a major factor in decomposition processes. Contrary to expectations, flooding and drawdown had little effect on decomposition as indicated by percent organic matter; pore water NH<sub>4</sub>-N and soluble reactive P increased during flooding and decreased during drawdown (Kadlec 1989). The effects of alternating inundation and exposure are not clear; Day (1982), found no significant differences in litter alternately exposed and inundated, whereas McKee and Seneca (1982) determined that continuous flooding inhibited decomposition and Godshalk and Wetzel (1978b) reported the most favourable decomposition rates for litter in aerobic alternating wet and dry environments. Although moisture is identified as important in decomposition processes (Brinson 1977, Odum and Heywood 1978, Day 1982), no significant

difference was found in litter which was exposed for 25 days and then flooded for 154 days over that which was flooded for a continuous 154 days (Hill 1985). This study did find that species differences were significant, and most weight loss patterns were related to initial nitrogen concentrations.

### **Nutrient levels - wetlands as transformers, filters or sinks.**

Most wetland primary production is internally recycled thereby resulting in "tight cycles of mineral nutrients" (Pratt et al. 1989). The biological processes of decomposer organisms (invertebrates and microbes) may result in nutrient losses or increases in the nutritive value of the litter (Davis and van der Valk, 1978; Puriveth, 1980). The net effect is that some materials are released and may be recycled into plant growth near the point of origin, while other nutrients are immobilized or stored. The ability of wetlands to store nutrients varies widely and depends on ambient nutrient levels and local hydrology (Mitsch and Gosselink 1993). The proportion of nutrients retained in freshwater wetlands is relatively small and is reported to decrease as nutrient inputs increase. Only 20 % of nutrients flowing into a Wisconsin marsh were retained in the system (Sloey et al. 1978). Patterns of nutrient uptake and release in litter determine the efficiency of the marsh as a nutrient sink (Davis and Van der Valk, 1983). The intertidal sedge, *Carex lyngbyei*, lost 38, 37 and 25% of the maximum above-ground standing crop respectively to translocation below-ground, tidal export and sediment burial, (Kistritz et al., 1983). Other research has indicated that 18 to 23% of the initial litter weight in perennial species was resistant to decay and was accumulated in the sediments (Morris and Lajtha, 1986).

Wetlands may range from being oligotrophic to highly eutrophic therefore generalizations regarding nutrient capture are difficult to make (Mitsch and Gosselink 1993). Various studies have indicated the capacity for wetlands to be a seasonal sink for inorganic nitrogen and phosphorus (Klopatek 1978, Simpson et al. 1978). Wetlands have been utilized to absorb nutrients from wastewater with retention of nitrogen in constructed wastewater treatment systems being in the order of 50% where inflow is up to  $100\text{g N m}^{-2}\cdot\text{yr}^{-1}$ . Phosphorus absorption is less predictable (Mitsch and Gosselink 1993). The processes whereby nitrogen is incorporated into the wetland vary according to differences in inputs, climatic factors, geological differences among others (Richardson 1989). Sedge litter is reported to accumulate nitrogen from its surroundings as a result of microbial colonization (Chamie and Richardson, 1978; Davis and van der Valk, 1978; Kistritz et al., 1983). Litter levels of other nutrients may also increase over time (Prentki et al. 1978; Davis and van der Valk 1983). Immobilization of nutrients through microbial processes, however, can only continue to the point where an optimal carbon to nutrient ratio is reached. Morris and Lajtha (1986) found in experiments with litter bags an accumulation of N and P in the litter during the first 5 months of decomposition. This nutrient accumulation was followed by nutrient release, once the litter became available to the plant roots. Most species lost 80% or more of the original weight within 1 year and almost all species eventually lost N and P, suggesting that litter is only a short-term sink for those nutrients (Wigham et al. 1989).

Phosphorus is generally reported to be bound to sediments within littoral zone (Dierberg 1993) but may be released from sediments during anoxic conditions. Emergent vegetation may function as a nutrient pump by absorbing phosphorus from sediments and then releasing it by leaching into the water as the shoots are flooded or to the sediment surface when the aboveground growth dies (Mitsch and Gosselink 1993). There is general agreement in the literature that release of

sediment derived P from live shoots of macrophytes is not as important as the nutrient release during plant decay (Dierberg 1993 cites Graneli and Solander 1988). Phosphorus loss rates of between 2.5 and 25% day<sup>-1</sup> of the tissue total P initially present have been reported in the literature (Howard-Williams and Davies 1979, Carpenter 1980). Puriveth (1979) noted rapid early leaching of P (up to 50% lost in the first month) and subsequent accumulation which was attributed to the microbial biomass. Hodkinson (1975) also reported a rapid decrease in % P during first 20 weeks (up to 75% of the original P content) with dramatic differences noted between species. The greatest losses occurred in the rush (*Juncus*) as opposed to minor losses in willow leaves (*Salix*), grass (*Deschamsia*), and conifer needles. By contrast willow leaves showed the greatest increase in nitrogen enrichment (Hodkinson 1975).

The downstream importance of soluble carbon and detrital material exported from wetlands is not well documented (Richardson 1989). However, macrophytes have been identified "*as an active component in the DOC (dissolved organic carbon) dynamics and metabolic activity of shallow lakes and their impact on the pelagic microbial food web*" (Søndergaard et al. 1998). Most organic carbon exists as detrital carbon and functions as a major source for degraders such as microbes, protozoa, rotifers and microcrustaceans (Henreby and Cairns cited in Pratt et al. 1989). Protozoa are thought to consume much of the bacterial production associated with DOM (dissolved organic matter) and to function as a link between the microbial and the grazing food chain (Azam et al. 1990).

## **2.3 NUTRIENT CYCLING/MICROBIAL PATHS**

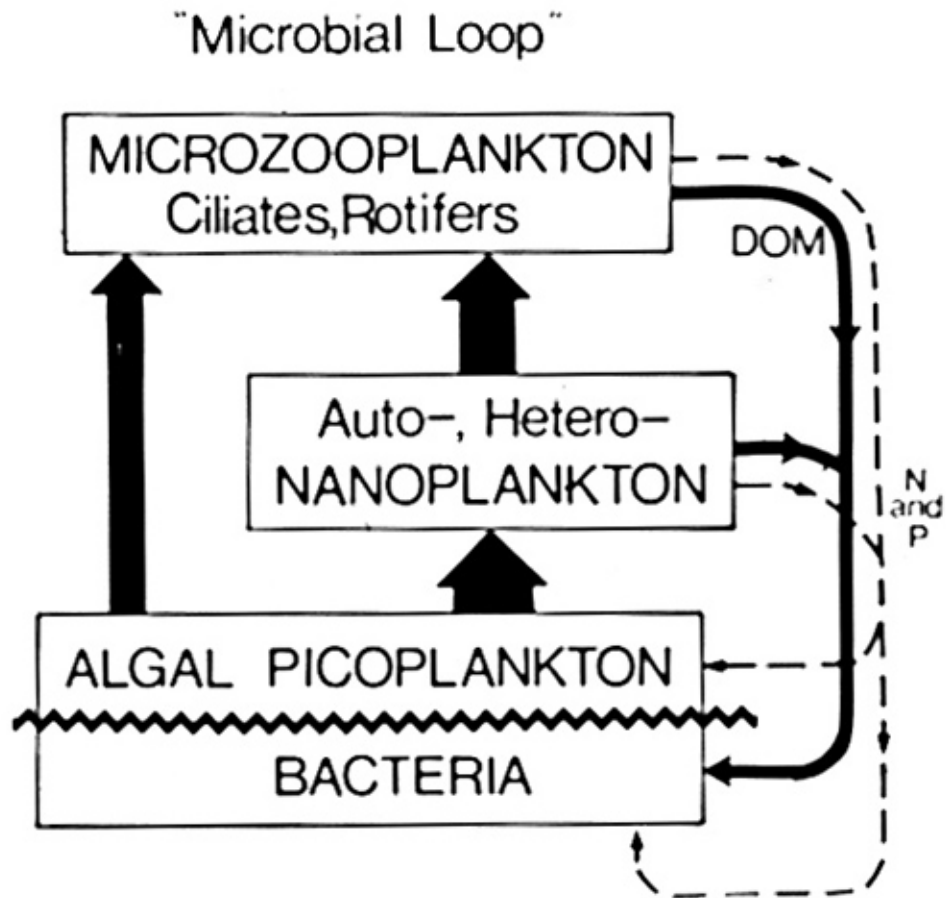
The role of microorganisms in nutrient and carbon fluxes in aquatic ecosystems: a new paradigm.

### **2.3.1 The early view, the 'classic' food chain.**

Until the 1970's our conception of food chains was simple, linear and based on the concept of functional feeding (trophic) categories, e.g. decomposers, primary producers, herbivores, primary (herbivores) and secondary (carnivores) consumers (Fig. 1). This early 'classic' depiction of food webs was composed of interconnected linear chains based on the pioneering work of Lindeman (1942), and for nearly 3 decades was the accepted schematic of the functional trophic pathways for carbon flow in both aquatic and terrestrial ecosystems. Because we knew so little about the role of aquatic bacteria, fungi or protozoa, and even less about their abundance or diversity in ecosystems, their role in food webs was considered largely as 'decomposers'. The functional role of this diverse group of organisms was the reduction of refractory organic remains and feces of organisms, e.g. detritus, that settled onto sediment or soil surfaces. Thus the 'decomposers' were in reality a rather poorly understood group relegated to a - 'black box', from which emerged reduced dissolved and particulate organic matter (DOM, POM), soluble nutrients phosphorus (P) and nitrogen (N), and CO<sub>2</sub>, CH<sub>3</sub> and H<sub>2</sub>S (Fig. 1). The conceptual changes in our understanding of the significance of pelagic microorganisms that were about to unfold in the decade of the 70s were so profound that Pomeroy (1974), in a seminal article in *Bioscience* spoke of a changing "new paradigm" for the ocean's food web.

Over the next decade these new discoveries of the ubiquity and high metabolic activity of pelagic bacteria were gradually incorporated into ecological studies of other aquatic ecosystems, including periphyton communities within the littoral zone of lakes, inter-tidal zone of estuaries, and on substrates and sediments of streams and wetlands. A similar picture of discovery is emerging, one emphasizing the major contributions by attached epiphytic, epilithic and epibenthic bacteria to ecosystem carbon flows and system productivity (Simon 1987, Cole et al. 1988, Tornblom & Sondergaard 1998).

Figure 1: The Classic Food Chain



### **2.3.2 The importance of bacteria in aquatic ecosystems.**

The 1970's heralded the discovery of new, novel techniques for looking at the abundance, biomass and production of bacteria (e.g. flouochrome stains, epifluorescence microscopy, <sup>3</sup>H-Thymidine and <sup>14</sup>C Lucine incorporation). Research results from the pelagic of oceans and lakes using these new techniques showed that bacteria were extremely abundant, and that they were not particle associated, but suspended as free-living, single cells that were metabolically active (Azam et al. 1983, 1990). New estimates of their abundance were one to two orders of magnitude higher ( $10^5$ - $10^6$  mL<sup>-1</sup>) than previous estimates based on plate counts, serial dilution and phase-contrast microscopy techniques (Williams 1981). Their annual carbon production was also considerably higher, ranging from 30 to 40% of primary production, not 10% as previously thought (Cole et al. 1988; Azam et al. 1990; Nagata 1990).

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### **2.3.3 A second discovery, autotrophic picoplankton.**

A few years after the discovery of suspended, free-living bacteria came new observations from epifluorescence microscopy of a minute (<2µm) photosynthetic 'free living' phytoplankter (cyanobacteria) that was ubiquitous and very abundant in lakes and oceans, but heretofore had not been seen by microscopists (Fogg 1986, Platt and Li 1986, Stockner & Antia 1986). The sizes of both the suspended bacteria and cyanobacteria fell within the pico-size range, 0.2 - 2.0 µm, and hence today they are called - 'picoplankton'. The photosynthetic pico-cyanobacteria (blue-green algae) are related to and closely resemble bacteria, their heterotrophic cousins. They are the most abundant primary producers in most aquatic ecosystems, e.g. in lakes  $10^4$ - $10^5$  mL<sup>-1</sup>, and studies have shown that up to 90% of the total phytoplankton net production and biomass (chlorophyll a) in oligotrophic oceans and lakes is contributed by pico-cyanobacteria (Stockner & Antia 1986, Stockner 1988, 1991). In more nutrient-rich habitats their contribution to total phytoplankton biomass and production is generally less, but may still exceed 50% (Stockner & Shortreed 1989, 1991; Pick & Agbeti 1991, Weisse & Schweizer 1991). They have been found in great abundance within the biofilm matrix on substrate in streams and in wetlands, but little is known of their contributions to carbon flows or production (Lock et al. 1984).

### **2.3.4 The new paradigm, the 'microbial loop' and microbial food webs.**

With the discovery of the ubiquity of picoplankton came recognition of their role as 'producers' within microbial food webs. Over the past 15 years, there has been considerable debate within the scientific community as to whether these minute and metabolically active picoplankton were 'links' or 'sinks' for energy flows within aquatic food webs (Ducklow 1991). The debate has catalyzed much research effort, results of which have greatly improved our understanding of their ecological role within food webs, and our views of how microbial food webs function. Two new findings have emerged:

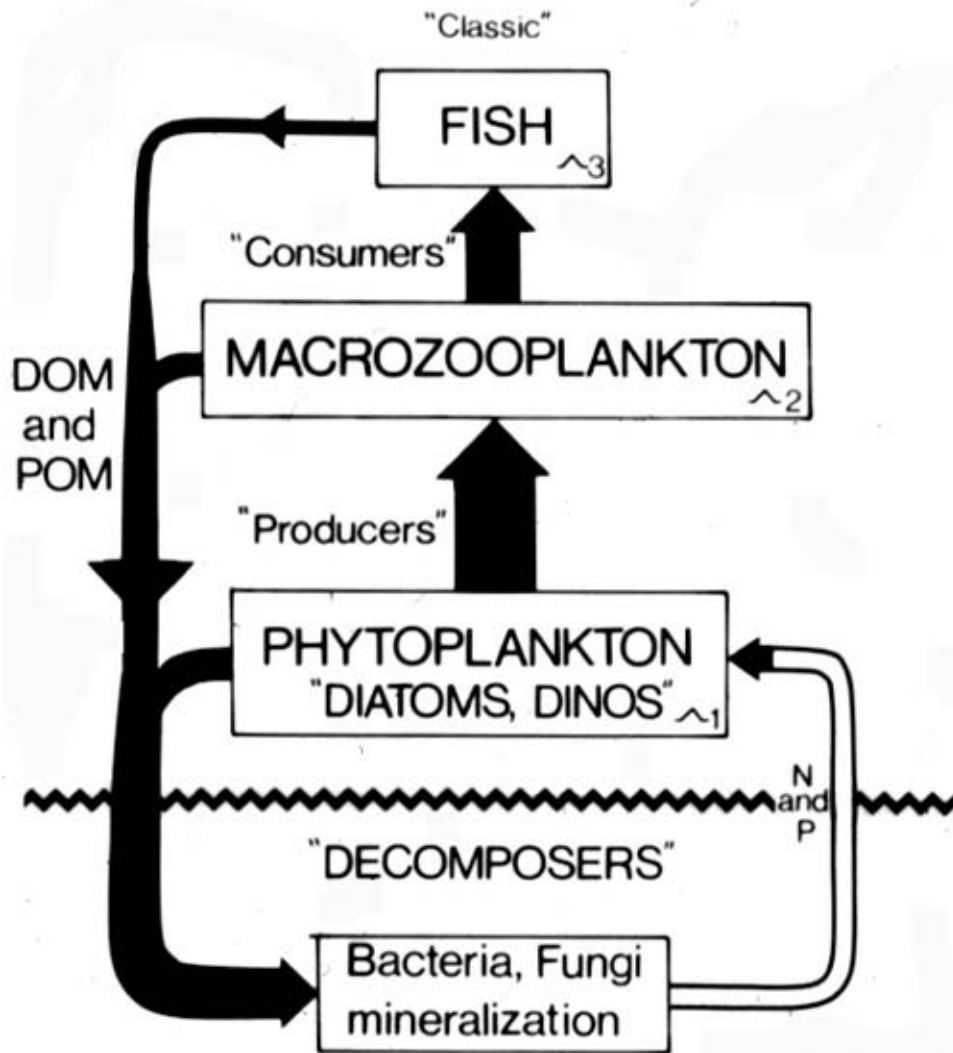
The 'classic' food chain depiction of the decomposer compartment (i.e. the black box) is now transparent. We have learned that re-mineralization of N, P, and DOM is mediated largely by excretion from the grazing activity (predation) of protists, e.g. flagellates, ciliates, and small micro-grazers (rotifers) on picoplankton within complex microbial food webs (Azam et al. 1983, Berman 1990, Caron 1991).

In contrast to earlier conjecture, bacteria and cyanobacteria are tightly coupled (commensalism), with cyanobacteria enhanced by nutrients and bacteria by DOM, and both populations are effective competitors of larger phytoplankton and attached algae for bioavailable nutrients N and P.

In an important paper, Azam et al. (1983) coined the term 'microbial loop' for the total activities of all microorganisms (picoplankton to microzooplankton) within pelagic microbial food webs (Fig. 2). Conceptually, these microorganisms form a 'loop' within the pelagic carbon flow because:

1. a significant portion of the photosynthetically produced carbon and organically bound nutrients are transferred to pelagic bacteria and are thus withdrawn from the 'classic' grazing food chain, i.e. phytoplankton-zooplankton-fish (Fig. 1) (Fenchel 1988); and
2. a significant portion of the bacterial C production and nutrients are returned (recycled) to the planktonic food web via protozoan and metazoan grazing and excretion within the microbial consortia. The microbial loop consists of a food web of bacteria + cyanobacteria -flagellates-ciliates and other microzooplankton. But the loop is very complex due to the great abundance and variety of protozoa and microzooplankton involved. The existence of such complex microbial food webs has been demonstrated both in the ocean (Rassoulzadegan & Sheldon 1986; Weisse & Scheffel-Moser 1991), in lakes (Nagata 1988; Weisse 1990), on substrata in streams, wetlands, and within humus, organic soil (Lock et al. 1984, Golladay & Sinsabaugh 1991, Neckles et al. 1994).

Figure 2: The Microbial Loop



### 2.3.5 Grazing.

Since picoplankton populations in most aquatic habitats show very little temporal variation compared to phytoplankton, macrophytes or emergent aquatic vegetation, it was early inferred that loss processes (mortality) must balance production rates (McManus & Fuhrman 1988, Pace 1988, Tornblom & Sondergaard 1998). We now know that the major source of bacterial mortality is grazing or predation by a great variety of protozoa and micro- and macro-invertebrates (Gifford 1991, Wylie & Currie 1991, Mulholland et al. 1991). Recent studies have also implicated virus induced cell-lysis as another mortality factor to both bacteria and cyanobacteria, albeit of less significance than grazing (Proctor & Furhman 1990). Numerous grazing studies which document cyano- and bacterivory by nanoplankton-sized (2.0-20 µm) flagellates and ciliates have shown that a large fraction of picoplankton production is cropped by these protozoan grazers in many diverse habitats (Sherr & Sherr 1987, Berninger et al. 1991, Sanders 1991). Current theory places micro-flagellates as the most important 'intermediary link' organism in the transfer of carbon from picoplankton to higher trophic levels in microbial food webs of lakes, streams, littoral sediments and wetlands (Mazzella & Russo 1989, Lodge 1991, Hondeveld et al. 1992, Neckles et al. 1994). Some major predators of micro-flagellates are ciliates, rotifers, and other crustacean zooplankton in lakes (Stockner 1991; Weisse 1993, Pernthaler et al. 1996), mayflies and stoneflies in streams (Lamberti et al. 1987), and chironomids in littoral assemblages and on sediment surfaces (Wipfli et al. 1998).

### 2.3.6 Nutrient recycling

Grazing activities within microbial and classic food webs are tightly linked to nutrient and DOC recycling, and are therefore vital to the maintenance of efficient flows of energy and carbon in aquatic food webs. Without grazing, biomass accumulates, bottlenecks are created and the productivity of the ecosystem slows (Robinson et al. 1997). To illustrate, consider what happens when you lose a 'keystone' grazer in plankton communities. In moderately productive, meso-eutrophic lakes microbial food webs can be 'switched off' during periods of high abundance of the large cladoceran *Daphnia* because they can effectively graze all sizes (1-100µm) of organisms comprising the microbial loop. Thus in the presence of effective grazer populations the predominant pathway of carbon flow reverts to larger organisms within 'classic' food chains, and most nutrient and DOM recycling results from grazer 'sloppy feeding' (damaged cells, lysis) and excretion (Pace et al. 1990). But when *Daphnia* are absent or rare during spring and autumn transition periods, the microbial loop consortia again play the important nutrient recycle function.

In oligotrophic ecosystems, low food supplies often prevent larger 'keystone' grazers from forming viable populations, and it is here that microbial food webs serve as the primary source of nutrient regeneration and material flux (Stockner & Antia 1986, Weisse 1993, Stockner & MacIsaac 1996). But even in hyper-eutrophic systems, excessive nutrients, anoxic conditions and persistent, inedible or toxic algal blooms often exclude key grazers (Lampert 1981, Paerl 1988, Hawkins & Lampert 1989, Robinson et al. 1997). Thus, even in super-rich habitats microbial food webs can often be predominant in carbon flows, recycling nutrients and channeling heterotrophic bacterial and fungal carbon via protozoan grazers (flagellates, ciliates, sarcodines), small insect larvae (e.g. chironomids) and snails to higher levels - fish (Wallace et al. 1982, Riemann & Christoffersen 1993, Wipfli et al. 1998).

### **2.3.7 Control of microbial food webs within a trophic gradient.**

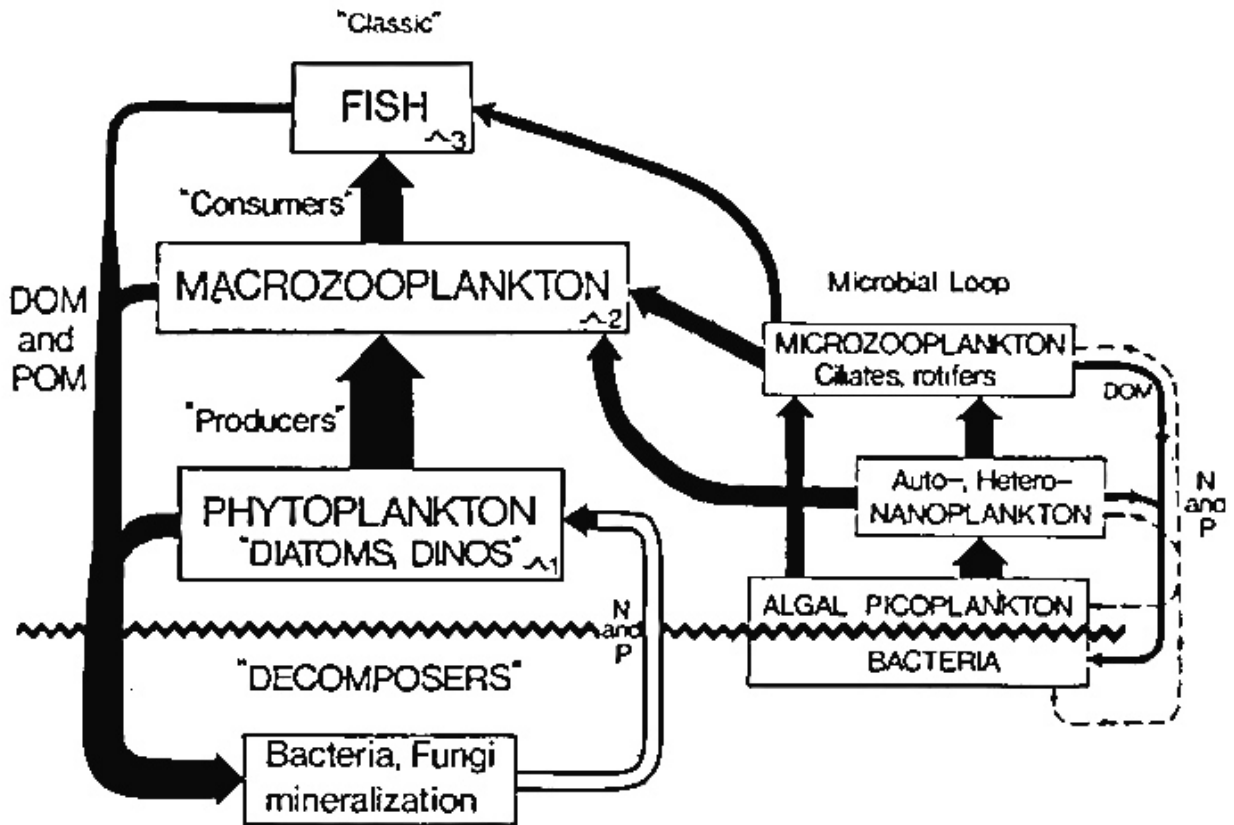
The relative significance of the microbial food web to total nutrient recycling is highest in oligotrophic ecosystems because autotrophic and heterotrophic picoplankton are better adapted to low nutrient conditions than larger eukaryotic cells (Weisse 1993). These microbial food webs in oligotrophic habitats are largely controlled by "bottom-up" processes, i.e. nutrients, and due to their complexity and number of trophic transfers, they have high respiration rates (CO<sub>2</sub>) and provide minimal carbon flows to higher trophic levels. However, the microbial consortia or loop does impart an efficient nutrient recycling system with minimal loss by sedimentation or 'export' production (Eppley & Peterson 1979). As previously note, with increasing nutrient richness microbial food webs become progressively more controlled by "top-down" forces, i.e. grazer populations, whose activities account for much of the nutrient recycling (Jeppesen et al. 1997; Riemann & Christoffersen 1993).

### **2.3.8 Summary.**

It must be emphasized that life in the pristine, ultra-oligotrophic ecosystem is basically microbial. From an evolutionary point of view, the microbial food web might be considered the original, primordial plankton community (Stockner & Porter 1988). Larger eukaryotic algae and a large array of their metazoan grazers likely evolved later when environmental conditions became less extreme and more favorable. Under extreme oligotrophy, where optimal survival advantage rests with small-sized picoplankton, moving carbon from bacteria and APP requires several trophic transfers, reduces macro-invertebrate grazers, lengthens and attenuates food chains, slows production and dissipates carbon (CO<sub>2</sub>) through inefficient microbial food webs (Stockner 1987, Stockner & Shortreed 1989) (Fig. 3). It is becoming abundantly clear from studies of lakes, streams, littoral and wetland habitats, that moderate primary and bacterial production (mesotrophic condition) is a prerequisite for maintenance of viable 'keystone' grazer populations. This is because the presence of active grazer populations means high excretion and equates to efficient carbon flows through both 'classic' and microbial food webs to the benefit of secondary consumers - fish (Stockner & Porter 1988). Under balanced, mesotrophic conditions carbon is flowing, nutrients are recycling, and primary production close to 'optimal', and microbial food web efficiency is also maximal (Ducklow 1991, Wylie & Currie 1991, Gaedke & Straile 1994).

This short review of the recent paradigm shift has attempted to outline in general terms across a gradient of habitats and trophic conditions, some of the more important relationships that influence the way we think about nutrient release and recycle within aquatic foodwebs. It is important to keep in mind that it was within the pelagic plankton community dynamic that many of the new discoveries emerged and have been best studied and processes understood. The paradigm shift occurred largely because research results improved our understanding of relation among three basic ecological processes - commensalism, predation and competition within heretofore undiscovered microbial consortia. And that it was these processes, tightly coupled within microbial food webs, that were responsible for most of the nutrient recycling within ecosystems. It has only been within the past 10-15 years that this microbial-nutrient paradigm has been extended to studies of streams, littoral and wetland habitats, with similar findings but differing castes of characters! Thus we know far less about the microbial communities in these habitats, but do know that the processes and principles apply across habitats.

Figure 3: Integrated Food Web



## **2.4 SECONDARY PRODUCTION**

### **2.4.1 Invertebrate / vegetation interactions**

Aquatic invertebrates make use of aquatic vegetation in many ways. "Invertebrates use live aquatic vegetation for food and as a substrate for attachment." (Hall-Armstrong et al. 1996). The same authors note that decaying plants provide a substrate and a source of nutrients for bottom-dwelling invertebrates and for the phytoplankton, bacteria and the microfloral and microfaunal assemblages which form the base of the aquatic food web. Indeed, aquatic invertebrates provide the critical ecosystem linkages in energy, nutrient and carbon flows between the primary producers (algae and vascular plants), the microbial assemblages described in the preceding section, and higher consumers (such as fish, waterfowl and other wildlife) of social and economic interest to the human population.

Aquatic plants have been shown to positively alter conditions of water velocity, substrate, detritus (food) availability, etc. for invertebrates (Gregg and Rose 1982). Numerous studies have been conducted on the invertebrate fauna associated with macrophytes (see Gregg and Rose 1985). In general, aquatic invertebrate populations are significantly higher in vegetated sites compared to non-vegetated sites (Diehl and Kornijow 1998; Levings 1997). Hargeby (1990) attributes the higher abundance of macroinvertebrates in vegetated areas to the increased colonizable substrate area offered by the plants, more abundant food in terms of periphytic algae and detritus, and lower vertebrate predation rate in the more complex habitats.

Invertebrate animal populations in aquatic ecosystems typically exhibit non-random (aggregated) spatial distributions in response to environmental heterogeneity (Downing 1991). Cyr and Downing (1998) found a correlation between the average biomass of plants and the abundance of invertebrates in eastern Canadian lakes. Littoral invertebrate abundance was also positively related to macrophyte architecture and sediment water and organic matter composition. Several studies have also documented significantly higher species richness (diversity) and community abundances of invertebrates associated with aquatic macrophytes (Gregg and Rose 1985, Hargeby 1990, Schramm and Jirka 1989).

The classification of aquatic macroinvertebrates into functional groups, based on common or similar feeding characteristics, is one method of relating organisms directly to ecosystem energy and material flows (i.e. ecosystem function). Four consumer functional groups, based on morphobehavioral adaptations to food gathering, are recognized in aquatic animals (Merritt and Cummins 1996). Shredders break down coarse particulate organic matter (CPOM) such as leaves and needles, while scrapers feed on periphyton (algae and their associated microbial assemblages) attached to plant and bottom substrates. Collectors utilize fine particulate organic matter (FPOM), often conditioned or processed by microbiota. Predators feed upon other animals, either by complete or partial ingestion (swallowers) or by draining bodily fluids (suckers). These four functional feeding groups are analogous to guilds, or groups of organisms utilizing similar resource classes.

In looking at the influences of aquatic macrophytes on invertebrate guild structure, significantly higher abundances of shredder, scraper and predator guilds were associated with vegetated

substrates in contrast with unvegetated substrates (Gregg and Rose 1985). The authors conclude that macrophytes "... *increase physical heterogeneity and their large surface areas benefit invertebrate community abundances by creating additional living spaces in the water column where none exist above unvegetated substrate.*" With respect to the influences of aquatic invertebrates on macrophytes, Lodge (1991) notes that "*our general understanding of the impact of grazing on macrophyte populations, communities, and material flow is currently dismal.*" He also observes that... "*Any lack of grazing on macrophytes is not the result of low nutrient concentrations in macrophyte tissue. The nitrogen content of macrophytes is similar to that of algae and much terrestrial forage.*"

Aquatic macrophytes often support heavy growths of attached algae (epiphyton or periphyton) which is, in turn, an important energy source for both detrital and grazing food chains. Numerous studies indicate that invertebrate grazers, in turn, play an important role in controlling periphyton populations in lakes. Jones et al. (in Jeppesen 1997) review a number of detailed investigations into periphyton-grazer systems and observe... "*Most studies on grazer-periphyton relationships have been in streams with less information from still waterbodies, where emphasis has been on snail grazing.*"

#### **2.4.2 Fish / invertebrate interactions**

As previously noted, our review of the pertinent literature established that most studies of fish and vegetation interactions have dealt with European and eastern North American aquatic systems and, hence, coolwater and warmwater fish species. It is hardly surprising, therefore, that most of the existing information interactions at higher trophic levels (fish and their prey) covers these same fish faunas. Studies on the food habits of temperate coldwater fish species, such as salmonids, have largely been directed towards anadromous species (salmon) in lotic environments (streams and rivers). Most salmonids have adopted a somewhat generalist food habit in concert with an opportunistic feeding strategy and littoral, benthic and pelagic invertebrates, and other fish, constitute their major food items.

The main groupings of aquatic macroinvertebrates of interest to fish include crustaceans (freshwater shrimp), leeches and aquatic insects. Aquatic insects are often the dominant group of invertebrates in aquatic systems. They are generally represented by a broad range of Orders including Ephemeroptera (Mayflies), Odonata (Damselflies and Dragonflies), Trichoptera (Caddisflies), Coleoptera (Water Beetles) and Diptera (True Flies, e.g. Chironomids). To give but two examples of the species diversity of aquatic insects it is estimated that there are over 2000 species of chironomids and 700 species of mayflies in North America. Aquatic insects undergo three (incomplete metamorphosis) or four (complete metamorphosis) life stages in developing from egg to adult. In general, the adult stage is the shortest and also is the only terrestrial component of the complete life history. The intermediate stages (larvae and pupae) are most important as food resources to fish. Fish are generally opportunistic predators, which focus their feeding activities on points of vulnerability in their prey item's life cycle and habitat utilization characteristics. Typical points of vulnerability for an aquatic insect would include swimming (food gathering), drifting, pre-adult emergence migrations, hatching, etc. Thus the more mobile guilds such as the scrapers, shredders and predators constitute important prey for fish while the more sessile collector guild is likely of lesser importance overall. The mobile

guilds, which represent important food resources to many species of fish, appear to be most closely associated with aquatic macrophytes and their epiflora.

Studies of whole systems with a full complement of trophic levels, from plants to fish, are lacking. The macrophyte-periphyton-invertebrate (grazer)-fish (predator) system is complex, potentially rife with complicated interactions, and generally poorly understood in temperate systems.

In a study of the effects of submerged macrophytes on fish-zooplankton-phytoplankton interactions in large enclosures in a shallow eutrophic lake, Schriver et al.(1995) found that fish predation had less impact on the zooplankton community in the more structured environment of macrophyte beds. They also noted that even small improvements in macrophyte abundance may have a substantial positive impact on zooplankton. Unfortunately the authors did not investigate the role of epiphytic algae in the system.

In reviewing the effects of predators on grazers in the periphyton-grazer system, Jones et al. (in Jeppesen 1998) conclude that...

*"Studies on the importance of cascading trophic interactions (top-down) effects in freshwater benthic food chains to the periphyton trophic level have focussed on fish and not on invertebrate predators ...".*

The authors cite several studies where fish predation on grazing invertebrates resulted in higher biomass and productivity values for periphyton, and to a lesser extent, macrophytes. They go on to state that ...

*"The most important aspect of the periphyton-grazer-fish interaction in lakes is that these herbivorous invertebrates provide an alternative food source for fish and hence reduce the pressure on zooplankton. Without such invertebrates, the ontogenetic shifts seen in the feeding of adult fish would not occur and all fish would compete for the same food resource, a situation seen in plantless eutrophic lakes."*

While there is general agreement that fish have a major structuring role with respect to lake zooplankton communities, there is less agreement as to how the cascading effect to lower levels of the food chain varies with lake nutrient status.

*"How the importance of top-down control of zooplankton by fish varies along a trophic gradient is debated extensively. McQueen et al.(1986) suggested that the cascading effect of zooplanktonivorous fish is stronger in oligotrophic lakes than in eutrophic lakes, but a growing body of literature argues that the cascading effect of fish is greater in eutrophic and hypertrophic lakes with respect to the food web in the classic sense and the microbial web."* Jeppesen et al.(1991).

### **3.0 HABITAT STRUCTURE**

#### ***3.1 THE STRUCTURING ROLE OF VEGETATION FOR FISH***

The utilization of littoral vegetation by fish in reservoirs is an area of study that has received little attention. Wetland research tends to focus on vegetation, climate, and soil; the zoological component (except for waterfowl) is conspicuously underrepresented (Whillans 1987) and the fisheries component particularly so. Many Canadian fish species make at least short seasonal or life stage-specific appearances in wetlands (Whillans 1987). At least 19 families of freshwater fishes have been documented to occupy vegetated habitats during at least one of their life stages (Dibble et al. 1996).

Wetlands are well known for their capacity to buffer water flow and to retain sediments. B.C. Hydro's shoreline revegetation programs have utilized the ability of vegetation to bind sediments and reduce airborne transport of fine particulate matter (dust) (Carr et al. 1993). Riparian and littoral wetlands are able to function as sponges, retaining water, nutrients and sediments which would otherwise directly enter lakes or streams during large runoff events (Wetzel 1989) thereby minimizing negative impacts on littoral communities and fish populations. This is particularly relevant around reservoir shorelines where large expanses of unvegetated substrates may be mobilized during heavy rainstorms.

The value of vegetation to fish is in part dependent on the structural complexity that the plants provide. Generally, wetlands with a greater diversity of plant species support a more diverse fish community (Jude and Pappas 1992). Weaver et al. (1997) found evidence of this trend in Lake Mendota, Wisconsin. They observed greater abundance and species diversity of fishes in areas densely vegetated with submergent macrophytes as compared with barren (unvegetated) areas. Several other authors corroborate these observations, especially with regard to age 0+ fishes (Dewey and Jennings 1992; Werner et al. 1977; Heck and Crowder 1991, Dibble et al. 1996).

Structural complexity of aquatic vegetation provides a refuge for juvenile fishes, and adults of forage fish species, from predators. The stems and leaves of aquatic plants provide hiding places for small fish and also restrict the movements of predators. Vegetation can also limit the effectiveness of visual predators in detecting their prey. The potential for vegetation structure to alter the outcome of predator-prey interactions is well-documented (Crowder and Cooper 1979). In general, attack and capture rates of predators are reduced with increasing structural complexity (Crowder and Cooper 1979), thus increasing survival rates for small fish in the presence of predators (Savino and Stein 1982).

The potential for aquatic vegetation to provide structural refuge for fish is dependent on macrophyte growth form. A review by Heck and Crowder (1991) found contradictory opinions throughout the literature. Early investigators reported that plants with finely divided leaves provided the most protection for prey (Krecker 1939; Andrews and Hasler 1943 in Heck and Crowder 1991). Heck and Orth (1980) expected better protection from predation in stands of plants with complex leaves (i.e. greater surface area per unit biomass) than in those with morphologically simple leaves. Other studies found results that both substantiated and disproved this hypothesis. Differences in results between studies seemed to arise not only as a result of the

system under study (marine and freshwater natural systems vs. closed experimental ponds), but also varied with the individual characteristics of the predator and prey under study. For example, the degree of matching between prey species and the colour and shading of the aquatic vegetation, the foraging strategy of the predator, the avoidance behaviour of the prey, and the relative sizes of predator and prey (Heck and Crowder 1991 and citations therein) all produced extremely variable outcomes in different vegetated habitat types. Generally, tall robust types of vegetation provide better protection from waves and currents, and for fish that spawn in vegetated habitats, grasses and sedges are important as they maintain their structure and allow water circulation to oxygenate the eggs (Hall-Armstrong et al. 1996). Although there is little substantive proof, it is presumable that these taller types of plants, whose stems extend throughout the water column, would also provide better cover from predators than a mat or rosette-forming type of aquatic macrophyte. This topic is not covered in current literature, and is deserving of further consideration.

Related to growth form are biomass and density of aquatic macrophytes. The importance of these factors are demonstrated throughout the literature. By example, Brazner and Beals (1997) found that the extent and density of macrophyte coverage in Lake Michigan were critical components of nursery habitats for immature fishes. It is the general consensus in the literature that an intermediate stem density is optimal for fish use. Engel (1995) notes that excessively dense vegetation can impair feeding by restricting movement and visibility of fish. Extremely dense submergent vegetation is sometimes avoided by fish, particularly in late summer and fall, when decomposing foliage reduces oxygen availability (Engel 1995). Generally, more plant biomass is considered desirable (to some optimal level), as greater surface areas provide more substrate for attachment of macroinvertebrates, a rich food source for fish (Dibble et al. 1996).

Most studies of vegetation as fish habitat focus on the common littoral zone fish species. The most recognized sets of species are the cyprinids (minnows and carps), the centrarchids (bass and sunfish) and the percids (perch). In areas where other predaceous fishes occur, such as northern pike and muskellunge, they are also included. These groups are well known for their use of wetland and littoral zone vegetation for spawning, rearing, and feeding purposes; as a result, the majority of literature focused on vegetation use by fish tends to favour the study of these species.

Commonly, salmonids and other species are not included in the tabulation of sport fish catches of wetland-associated fish (Whillans 1987, Hall-Armstrong et al, 1996). This is not necessarily evidence that these species do not occur in vegetation, but possibly that they are migratory in their use of vegetation, and may only frequent that habitat type during only one life history stage, or on daily cycles of inshore-offshore use (Jude and Pappas 1992). Salmonid species vary greatly in their life histories. Generally, salmonids do not use vegetation for spawning purposes, but rather migrate to inlet or outlet streams, build nests (redds) by digging in gravel substrate, deposit eggs in the depression, and cover them with loose gravel. Emergent fry will spend some time resident in streams, this is extremely variable not only by species but also with geographic location and other environmental factors. For example, the young of lake-resident, spring spawning rainbow trout move up (or down) their natal streams to the lake almost immediately or by autumn, or may spend as long as 1 to 3 years in the streams (Scott and Crossman 1973). Young trout are very susceptible to predation in the littoral zones of lakes and reservoirs, where they are preyed on by not only conspecifics and other fish species, but also by avian predators. In lakes, young-of-the-year of these species are often found in association with shoreline cover

(Biro and Ridgway 1995; Post et al. 1998). Pond experiments conducted by Tabor and Wurtsbaugh (1991) found that structurally complex habitats can be used by juvenile rainbow trout to reduce predation. At a larger scale, these authors discovered that juvenile rainbow trout selected day habitats in reservoirs that provided escape cover from predators. This facultative behaviour by juvenile rainbow trout was also observed by Post et al. (1998).

Adult salmonid use of vegetation has not been examined carefully in the literature. Many species of salmonids have been documented to exhibit piscivory (on other species as well as in the form of cannibalism), including rainbow trout, Dolly Varden, and cutthroat trout. Since many fish forage species, as well as other typical prey organisms, such as terrestrial insects and aquatic insect larvae, inhabit vegetated habitats, it seems plausible that these salmonid predators would utilize these habitats as a food source. Some species, such as lake-resident sockeye salmon, or kokanee, are known to be pelagic (open-water) dwellers for the most part, but in summer exhibit extensive daily vertical and onshore-offshore movements, which have been attributed to temperature and food preferences (Scott and Crossman 1973). Adults of this species are not known to be piscivorous, and feed mainly on plankton in open waters. The young of this species are known to be consumed by a wide variety of predaceous fishes, including rainbow trout, cutthroat trout, Dolly Varden, coho salmon and squawfish, as well as diving birds (Scott and Crossman 1973). Lake-resident sockeye salmon (kokanee) generally spawn in the fall, and may spawn in streams or along gravel sections of lake shores (Scott and Crossman 1973). Morton and Williams (1990) observed extensive use of the littoral area of Quesnel Lake for rearing by sockeye salmon. Scott and Crossman (1973) comment on the value of cover to young kokanee in avoiding predation by Dolly Varden as they emerge from their natal streams.

### ***3.2 FISH USE OF VEGETATION***

Fish utilization of vegetation can be classified according to use; four types can be distinguished: spawning, nursery/rearing, feeding and cover (Hall-Armstrong et al. 1996 and others). It is important to note, however, that the actual use of vegetation by fish is ultimately dependent on the species of fish under consideration. What is eventually needed in the development of a strategy for individual reservoirs, then, is an assessment of which species of fishes will be utilizing the littoral vegetation, and at what times of year.

#### **3.2.1 Spawning**

A number of the reviews cited earlier in this report provide detailed information concerning the use of flooded vegetation for spawning by warmwater fish, see Dibble et al. (1996) for a summary. Coldwater species are not known to utilize flooded vegetation for spawning.

According to Hall-Armstrong et al. (1996), warmwater fish spawn in a wide variety of wetland types. Some depend on protection from waves and currents provided by tall, robust vegetation. Early spring spawners often seek plant species that overwinter or emerge early in the spring. Seasonally flooded meadow marshes with grasses and sedges are important because they maintain their structure and allow water circulation to oxygenate the eggs. Reproduction of most wetland fishes is closely related to the timing, extent and duration of flooding (Killgore and Baker 1996).

### 3.2.2 Rearing

*"Littoral zone macrophytes have long been associated with increased productivity of juvenile fishes"* (Gregory and Levings 1996 cite Stein 1979; Crowder and Cooper 1982). Stems and leaves of aquatic plants provide hiding places for young fish and restrict movements of predators. Conrow et al. (1990, cited in Northcote and Atagi 1997) attribute the use of vegetated regions as nursery areas for fishes in Florida to the structural complexity that the vegetation provides. Hall-Armstrong et al. (1996) note *"Many fish species (e.g. trout and suckers) use wetlands as nursery areas if they are nearby, but may not deliberately seek out vegetated habitat."* Morton and Williams (1990) observed extensive use of the littoral area of Quesnel Lake for rearing by sockeye salmon. There is also evidence for utilization of lake littoral areas as coho juvenile rearing habitat (Levy and Slaney 1993). Brazner and Beals (1997) found that the extent and density of macrophyte coverage were critical components of nursery habitats for immature fishes in Lake Michigan. Hayse and Wissing (1996) investigated the effect of stem density on the use of artificial macrophytes by age 0 bluegills. Their results showed significant increases in bluegill densities with increasing stem density.

### 3.2.3 Cover:

Cover as defined for fisheries purposes includes shelter or refuge from waves and currents, predators, unfavourable temperatures (low or high) and sunlight (Hall-Armstrong et al. 1996).

### Predation

Predation has been identified as the principal biotic factor involved in structuring fish communities (Brazner and Beals 1997). It is well known that structural complexity of aquatic vegetation can alter the outcome of predator-prey interactions. In general, attack and capture rates of predators are reduced with increasing structural complexity (Crowder and Cooper 1979). Thus, increased structural complexity from aquatic vegetation generally increases the survival of small fish in the presence of piscivores (Gregory and Levings 1996). In Kenya, Bayley (1977) attributed improved fish survival to better protection offered to young fish in flooded terrestrial grasses. In a study of the effects of stem density on fish abundance and growth, Hayse and Wissing (1996) concluded that medium and high-density vegetation offered reduced predation risk to small fish, without compromising growth for safety.

Gregory and Levings (1996) tested the significance of cover (vegetation and turbidity) in reducing predation rate of adult salmonids on juvenile salmonids. Vegetative cover in the experiments was selected to simulate conditions likely to be encountered by salmonids in littoral areas and in ephemeral marsh habitats in lakes, rivers, and estuaries. As expected, the presence of cover resulted in a 10-75% reduction in mean predation rate. More importantly, the effect of vegetation alone was significant in reducing predation rate, while the effects of turbidity alone were not significant.

Several recent studies have looked at the effects of cover in reducing predation risk for young salmonids. Biro et al. (1997) report that young-of-the-year brook charr remain in the littoral zone of lakes during May and early June each year in close proximity to shoreline vegetation and woody debris. In a study of the importance of cover to predation rates on juvenile rainbow trout

in reservoirs, Tabor and Wurtsbaugh (1991) found that nearshore cover increased juvenile survival. Indeed, Post et al. (1999), in an investigation into the risk of piscivory of juvenile rainbow trout in British Columbia, suggest that ... *"the littoral habitat may provide a refuge that may be crucial in preventing the total elimination of year-class strength by piscivory."*

### **Other Factors**

Brazner and Beals (1997) found that wetlands had smaller waves compared to beach areas (those lacking vegetation) in Green Bay. This lends more support to the theory that wetlands are more protective in nature as a result of their vegetated habitats. They found a distinct and significant negative correlation between wave height and increasing macrophyte density. Wind and wave energy is one of the most important factors in the structure of macrophyte communities in the Great Lakes (Brazner and Beals 1997, Keddy 1982).

Cover can play a particularly important role during water level fluctuations. Welcomme (1989) points out that (in normal riverine flood conditions) the strength of any year class of fish clearly depends strongly on the area flooded during the wet phase ---- because during the "dry" season, mass migration of fish to the "main channel" leads to higher population densities, and predation by other fish, birds, and mammals are maximized. Increased survival of juveniles during high water, through the introduction of cover in the form of macrophytes, will result in an increase in recruitment to the population in the long term. Similarly, Saltveit and Styrvold (1982) note *"water level will influence available living space for fish, giving higher densities at low levels"*. Their unpublished results showed that in regulated rivers, juvenile salmon and trout stayed close to shore. Cohen and Radomski (1993) found that fluctuations in YMXR (the difference between yearly maximum and yearly minimum water levels) resulted in changes in the frequency and amplitude of fish population dynamics in the Rainy and Namakan reservoirs.

### **3.2.4 Feeding:**

Feeding includes direct feeding on plant material and attached algae, detritus from decaying plants, and on invertebrates and vertebrates living in the wetland plant community and associated substrate (Hall-Armstrong et al, 1996). Areas with submerged plants have more amphipods, insects and other invertebrates than open water and exposed lake bottom (Engel 1995). One of the first investigations into the role of macrophytes as habitat and its effect on feeding efficiency of predatory fishes was undertaken by Crowder and Cooper (1979). Their pond experiments support the hypothesis that fish will maximize their feeding efficiency and growth at some intermediate level of structural complexity. Trebitz and Nibbelink (1996) cite from (Cooper and Crowder 1979, Engel 1987, Diehl 1988 and Savino and Stein 1982) that biological interactions are often intensified in vegetation adjacent to open water and that food resources are often more accessible to fish at edges because of better visibility and greater ease in maneuvering. Weaver et al. (1997) found that patchiness within vegetation provides prey fishes with a habitat in which shelter (cover from predators) is in close proximity to open spaces that harbor zooplankton. They also suggested that the effect of macrophyte habitat may be greater on fish communities of waterbodies with relatively larger littoral zones, such as shallow lakes or reservoirs. Schriver et al. (1995) studied the impact of changes in submerged macrophyte density on fish-zooplankton-phytoplankton interactions in a shallow lake and discovered major shifts in the biovolumes of phytoplankton and zooplankton in response to changes in macrophyte cover and fish density.

Macrophyte habitat, as used for feeding purposes, is strongly related to risk of predation. Werner et al. (1983) found that bluegills of different size classes used similar habitats in which to feed, and that those patterns of habitat use maximized foraging returns. However, in the presence of largemouth bass (a predator), the smaller size classes of bluegill, those more vulnerable to predation, obtained a greater fraction of their diet in vegetated habitat, where foraging returns were suboptimal (~ one-third of those in more open habitats), but predation risk reduced. Studies of juvenile salmonids in lentic systems show that individuals tend to restrict their movements to nearshore areas, and are consistently found in close proximity to cover (inundated vegetation, logs or boulders) (Biro et al. 1997; Tabor and Wurtsbaugh 1991). Such selection of nearshore habitat by juvenile rainbow trout has been shown to reduce predation rates (Tabor and Wurtsbaugh 1991). Biro (unpubl. data) found that young-of-the-year brook charr in small lakes were entirely absent from open water areas away from shore, unless in proximity with fallen, floating logs. This demonstrates the importance of structural complexity in the foraging movements of young-of-the-year salmonids in lentic systems (Biro and Ridgway 1995). They conclude... *"that riparian habitat features, such as inundated shoreline vegetation and woody debris, are important elements of their early habitat as they relate to YOY (young-of-the-year) brook charr foraging behaviour."*

In natural lakes small fish are restricted to weedbeds; they do not adhere to model predictions regarding optimal habitat use from the standpoint of foraging rates (Werner et al. 1983 cite Hall and Werner 1977, Mittelbach 1981). It is postulated that predation risk due to piscivorous fish is responsible for the deviation from predicted behaviour (Werner et al. 1983). Fish respond to both relative predation risk and habitat profitability in choosing habitats in which to feed (Werner et al. 1983).

## 4.0 INFORMATION NEEDS

In reviewing a wide range of scientific studies into the structural and functional roles of vegetation for fish, it became apparent that this broad topic has received uneven treatment from several perspectives. Geographically far more studies have been conducted in Europe and eastern North America than in western North America. Physiographically far fewer studies have been undertaken in mountainous terrain than in flat or hilly regions. In terms of nutrient status of the waterbody under investigation, most research has focussed on eutrophic rather than oligotrophic conditions. Similarly most of the available literature consists of investigations completed on natural waterbodies (lakes and streams) as opposed to man-made impoundments (reservoirs). To describe the literature regarding western reservoirs, which are typically oligotrophic and located in steep valley bottoms, as inadequate or impoverished would not be an understatement. This is not to imply, however, that even shallow eutrophic lakes are well understood with respect to the macrophyte-periphyton-grazer-predator system.

### 4.1 FISH-INVERTEBRATES-VEGETATION

Diehl and Kornijow (1998) state... *"The understanding of large-scale, long-term effects of submerged vegetation on fish-macroinvertebrate interaction is still sketchy and will require increased efforts to identify and quantify feedback mechanisms among processes in littoral, benthic and pelagic habitats."* They also go on to note *"In the future, high priority should be given to the study of behavioral interactions between macroinvertebrates and fish. This includes the systematic study of the effects of submerged vegetation on the search behavior, prey choice, and feeding and growth performance of different species and size classes of fish, as well as the study of the behavioral responses of macroinvertebrates to their invertebrate and fish predators."* Heck and Crowder (1991) also identify a great need for further research into invertebrate-fish dynamics in vegetated habitats, specifically *"...we believe there is much behavioral ecology yet to be done to elucidate the interactions between vegetation characteristics and those of particular predator-prey combinations."* Persson and Crowder (1998) postulate that vegetated habitats, in their role as refugia, may serve to provide a stabilizing effect on fish population fluctuations and suggest... *"To analyze this potential stabilizing effect of vegetation on population and overall community dynamics is a challenging task for future modelling research."*

In a recent review of vegetation-zooplankton-fish research Jeppesen et al.(1998) call for large scale, whole-system investigations because, in their opinion, *"Most of the former studies of the interactions between fish, macrophytes, and zooplankton were undertaken with only one or two species of prey fish and typically one species of predatory fish. Because interactions between a given fish species and zooplankton may change in the presence of other species (Persson and Eklov, 1995), there is a great need for multispecies experiments. A better insight into the interactions between fish and zooplankton also requires a more thorough knowledge of the feeding behavior of the various zooplanktivorous fish. This is crucial because it is not possible from data on distribution alone to determine where and when the interactions between fish and zooplankton are particularly strong. It is necessary to undertake investigations under more natural conditions than hitherto has been the case. This means on a scale that allows horizontal migration for both zooplankton and fish (i.e., a large scale and whole lake basis). Empirical studies of seasonal and diel variations in fish and zooplankton in the pelagic and littoral zones, with contrasting nutrient*

*levels, fish communities, and macrophyte abundance and composition, may contribute to the understanding of natural interactions."*

In a similar review of periphyton-invertebrate-fish research, Jones et al. (in Jeppesen 1997) comment "*...there is a shortage of studies of whole communities, containing more than two trophic levels.*". The authors highlight "*...the urgent need for research, both in the field and laboratory, due to the paucity of information concerning lacustrine nonmolluscan groups in the following areas: ingestion and digestion rates; assimilation efficiencies; effects of grazer type (including mouthpart morphology), selectivity, size, density, multiple species action, disturbance, and nutrient enhancement on individual species and whole communities of periphyton including standing crop, production and composition; the effect of periphyton on grazer abundance, distribution, growth rates, production and community composition; interrelationships between grazing species; and the effect of predation on grazers, and hence periphyton.*"

There is also much to be learned with respect to the effects of grazing on freshwater macrophytes. Lodge (1991) summarizes his review of the topic by stating "*The potential impact of grazing on aquatic ecosystems is large (Carpenter and Lodge 1986), but our general understanding of the impact of grazing on macrophyte populations, communities and material flow is currently dismal. To remedy the situation, we need surveys and experiments identifying plant grazers and documenting their impact along environmental gradients, and among plant species.*"

#### **4.2 RESERVOIRS**

Research needs in reservoirs are greater than for natural systems because they have received far less scientific attention to date and, consequently, our level of understanding of ecological systems and processes in regulated waterbodies is less complete. In an important study of trophic-dynamics in reservoirs, Adams et al. (1983) conclude "*Better information on the autochthonous and allochthonous organic matter inputs to reservoirs, on the biological availability of these inputs, and on the actual trophic transfer efficiencies of aquatic food webs is required to distinguish the relative contributions of various organic matter sources to reservoir food production. Clearly, detailed investigations of the production and food web processes underlying reservoir productivity are required to advance our understanding of reservoirs as ecological systems and, thereby, enhance our abilities to predict, manage, and improve the fisheries potential of multiple-use impoundments.*"

Several parallels have been drawn between water level fluctuations in freshwater systems and the marine equivalent of intertidal ecosystems. Gasith and Gafny (1990) attribute the lower levels of biological diversity and productivity in the littoral regions of fluctuating freshwater systems, as compared to intertidal marine systems, to the lower predictability of fluctuations for the former situation. The higher "pulse stability" of intertidal ecosystems is a result of the high predictability (and regularity) of the tidal flooding cycle. One would anticipate that a productivity and diversity gradient would exist over the range between flashy and unpredictable systems and highly regular systems. This phenomenon has not been the focus of scientific inquiry to date.

Straskraba et al. (1993) comment on some of the effects of infrequent pulses of water and nutrients in reservoirs and call for more information about the risks of pulse generation in different reservoir sites. Again, specific information is required for individual reservoirs and for reservoirs in general. Looking at the effects of periodic, recurrent disturbances such as floods and drought on stream

biota, Li and Li (1996) observe that " *...the severity of these disturbances can be ameliorated when the habitat is complex because habitat complexity confers refugia. In summary, biological interactions may be very important community structuring agents in physically stable and complex streams, whereas the ability to disperse and colonize may be dominant factors in streams subject to harsh recurrent disturbances.*" Periodic and unpredictable water level fluctuations in reservoirs may serve the same purpose as those described above for streams. Hargeby (1990) argues that " *In newly created habitats the colonization rates of the invertebrates initially is the main factor structuring the community (Sheldon 1984). The species structure of associated invertebrates in newly established stands of submerged plants could thus be predicted to be highly dependent on the colonization ability of the animals. This could also be applicable for areas covered by annual plants, where the seasonal changes in habitat structure could be viewed as a disturbance, which is likely to reset the invertebrate community to an earlier phase in the colonization path (Pickett and White 1985).*"

To what degree biotic responses in reservoirs can be predicted, based on a limited body of information from reservoirs and a much larger knowledge base from natural lakes and streams, is a question that cannot be answered until detailed information is gathered that can be applied to reservoirs, in a general sense, but will also take into account the inherent variability within and between regulated waterbodies. In a landmark review of the similarities and differences between reservoirs and natural lakes, Wetzel (1990) concluded:

*"Predictability is based on biological unity and is a primary objective of limnological understanding. The irregular and extreme variations in physical factors in many reservoirs frustrate our search for unity and order and for generalized management techniques among these ecosystems. These irregular characteristics place additional analytical burdens upon persons with responsibilities for effective management of reservoir resources. Consequently, much information of individual reservoir properties is required to obtain reasonably sensitive predictability of biotic and water quality responses to irregular inputs and manipulations. Predictive models of biotic responses, developed mainly from a larger database from natural lakes, must be used with great caution when applied to reservoirs. The process responses are the same, but the input variables are more complex and dynamic than in many natural lakes.*

*Time is a critical factor in nearly all response functions. In order for most of the processes (e.g., stratification, sedimentation, population growth, competitive exclusion, etc.) as we conventionally know them largely from natural lake ecosystems, to come into play and be effective, adequate time is required under relatively undisturbed conditions. As natural or manipulated conditions become more irregular and variable, responses are increasingly incomplete before they are altered or destroyed. The result is an increasingly chaotic succession of responses, reductions in interdependability, and less biotic stability. Although certain physical factors (e.g., precipitation rates) are beyond the control of reservoir management, many factors (e.g., outflow discharge rates, stratification-withdrawal relationships, water renewal rates) can be effectively regulated. An appreciation of the complexities of biotic processes can only lead to much more effective management of multipurpose reservoir ecosystems."*

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