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A Limnological Assessment of Four Williston Reservoir Embayments, 2004.

S. L. Harris, A. R. Langston, J. G. Stockner and L. Vidmanic
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ABSTRACT

Williston Reservoir, created by the impoundment of three river systems over 30 years ago, is a complex reservoir system with many large embayments. Basic limnological information of these embayments and the effects of the embayments on the ecology of the pelagic region of Williston Reservoir are currently lacking. This study examined key physical, chemical and biological parameters and examined production capacity of the embayments. This report summarizes results of the limnological data for the embayments and provides comparison with the 2-yr monitoring program conducted in 1999 and 2000 on the pelagic region of Williston Reservoir. This is the first limnological study of the embayments of Williston Reservoir.

Studies were conducted in June, July and October 2004 while size-fractionated chlorophyll and primary productivity were examined in July 2004 only. Studies were completed at one station in each of Nation, Manson, Omineca and Clearwater embayments. This overall objective of this study was to identify an embayment most suited for a detailed multi-year research project.

All of the major chemical and biological variables monitored indicate that Williston Reservoir embayments are ultra-oligotrophic, typical of old reservoir systems. Average chlorophyll concentration in the embayments was very low, ranging from 1.1-1.6 $\mu g \cdot L^{-1}$. Rates of primary production were less than 50 mg C m^{-2} d^{-1}, which are much lower than production rates of other similar large interior BC lakes and reservoirs. Nutrient stress was identified in all four embayments. Dissolved inorganic nutrient concentrations indicate that all embayments were phosphorus limited while Nation and Omineca embayments were co-limited by phosphorus and nitrogen. Primary production in Manson embayment was also limited by light availability caused by a combination of high turbidity and by a deep mixed layer.

Nation and Omineca embayment share many similar characteristics. Nutrient concentrations are low ($NO_3 < 1.5\ \mu g \cdot L^{-1}$), N:P ratios are <1, phytoplankton biomass and rates of productivity are high (>10 mg Chl m^{-2} and > 30 mg C m^{-2} d^{-1}) relative to Manson and Clearwater and zooplankton densities were low (<10 $\mu g \cdot L^{-1}$). Despite the similarities of two embayments, Omineca is dominated by picoplankton production while in Nation embayment is dominated by nanoplankton production. Picoplankton sized phytoplankton are typical of microbial food webs and are not efficiently consumed by large herbivorous zooplankton which leads to reduced fish production.

Average TDS concentration was lower in the embayments than the pelagic regions of the Reservoir where TDS was found to be 73 and 106.5 $mg \cdot L^{-1}$ respectively. Phytoplankton biomass levels in Manson and Clearwater embayments were similar to the Reservoir, while biomass in Nation and Omineca was on average 60% and 40% higher than in the Reservoir. The productivity of Nation and Clearwater was similar to rates measured in the Reservoir while in Omineca productivity was ~29% higher and in Manson productivity was 44% lower than productivity in the Reservoir.

Based on a ranking of key parameters, this study shows that Omineca embayment has the highest potential to influence Williston Reservoir. In consideration of the high production potential and the presence of large numbers of kokanee spawners (*Oncorhynchus nerka*) and other important species such as Arctic grayling (*Thymallus arcticus*), it is recommended that future work examining the role of embayments on the ecology of Williston Reservoir be completed on Omineca embayment.

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INTRODUCTION

Background & Scope

The impoundment of the Peace River in 1968 for hydroelectric generation created Williston Reservoir, BC's largest lake/reservoir system. Extensive fisheries research has provided an assessment of distribution, age, fecundity and length-at-age of the dominate species (Barrett and Halsey 1985, Johnson and Yesaki 1989, Blackman 1992, Sebastian et al. 2003). Game species found in Williston include rainbow trout (*Oncorhynchus mykiss*), bull trout (*Salvelinus confluentus*), lake whitefish (*Coregonus clupeaformis*), mountain whitefish (*Prosopium williamsoni*), lake trout (*Salvelinus namycush*), Arctic grayling (*Thymallus arcticus*), burbot (*Lota lota*), and kokanee salmon (*Oncorhynchus nerka*). Non game species include but are not limited to, Peamouth chub (*Mylocheilus caurinus*), pygmy whitefish (*Prosopium coulteri*), Northern pikeminnow (*Ptychocheilus oregonensis*), two species of sculpins *Cottus asper, C. cognatus*, and 3 species of suckers *Catostomus catostomus*, *C. macrocheilus*, and *C. commersoni*.

The limnology of Williston Reservoir is less studied but previous research has determined the current physical, biological and chemical status of the Reservoir (BC Research 1976, Stockner et al. 2001). The limnology studies identify changes that have occurred and are ongoing, and have revealed complex ecological relationships and processes.

Detailed limnological studies were conducted on the pelagic zone of Williston Reservoir in 1999 and 2000 (Stockner et al. 2001). This study has shown that primary production rates in the reservoir are very low and appear to be light limited primarily by turbidity and frequent deep mixing episodes. Daily carbon production values are much lower than most interior BC lakes and are at levels more typical of ultra-oligotrophic coastal BC lakes. Stockner et al. (2001) suggest that the system has slowly lost productive capacity over the past 2-3 decades and now lies within the ultra-oligotrophic range.

Stockner et al. (2005) calculated the rearing capacity of Williston Reservoir for fish production using a photosynthetic rate (PR) based model and found that the potential rearing capacity (estimated by annual photosynthetic carbon production) of Williston Reservoir is similar to the rearing capacity of Shuswap Lake that is 80% smaller than Williston Reservoir. The modelling results were confirmed with the hydroacoustic, trawl and gill net surveys (Sebastian et al. 2003) and are synthesized in Stockner et al. (2005).

Williston Reservoir has many large embayments and to date, detailed limnological, habitat or fish inventory studies have not been completed. A few project specific studies have been completed (G3 Consulting Ltd. "*Williston Reservoir environmental effects monitoring"*, and Carmichael's "*Environmental impact assessment of Chichouyenily Arm…"*) however these data is useful only as background information and does not address specifically the role of embayments. We suspect the embayments play an important role in the overall Williston Reservoir ecology, but linkages between the Reservoir and the embayments have not been studied. Embayment areas may represent critically important habitat for many of Williston watersheds species including kokanee, rainbow trout, bull trout and Arctic grayling. Understanding the linkages between the Reservoir and the embayments is the ultimate objective of this direction of research.

Due to the large number of embayments and the logistical difficulties of research on such a large reservoir system, the cost in terms of staff time and dollars of a science based project to determine the role of the embayments is high. We determined it was prudent to commit effort and funds "up front" to identify the embayment that is the most suited for a detailed multi-year research project. All Williston Reservoir embayments were considered and the available habitat information, fish species presence information and the logistical implications of studying a particular embayment were reviewed. We considered many criterion when selecting candidate embayments including size, suspected or known fish species presence, current habitat state (pristine or impacted), road access, use by industry (log booming area), turbidity, and other factors. We selected four embayments, the Nation, Manson, Omineca and Clearwater for further investigation.

Study objectives

This project represents the first step towards determining the role of embayments in the ecology of Williston Reservoir. The data collected in this one year study will be integral to the planning and development of future projects and will form part of the data set for those projects. Future use may include identification of habitat improvement opportunities. The overall objective of is this one year study is to identify an embayment suitable for a multi-year, detailed research project entitled "*Ecological role of embayments*".

DESCRIPTION OF STUDY AREA

Williston Reservoir (56° N latitude, 124° W longitude) is located approximately 140 km north of Prince George in northeast British Columbia, Canada (inset Fig. 1). The reservoir was created in 1968 by impounding the Peace River by the W.A.C. Bennett Dam in the canyon near Hudson's Hope, B.C. The Peace River flows east to Lake Athabasca within the Mackenzie River drainage system, which flows north and ultimately discharges into the Arctic Ocean.

The W.A.C. Bennett Dam inundated the upper Peace River canyon creating the Peace Reach that extends westward approximately 120 km to a junction of the confluence of the Parsnip and Finlay Reaches. From the junction, the Finlay Reach (previous Finlay River basin) extends in a northwest direction about 120 km, and the Parsnip Reach (previous Parsnip River basin) extends in a southeast direction for approximately 110 km (Fig. 1) passing the town of Mackenzie. The reservoir has a mean depth of 44 m and a maximum depth of 166 m (BC Research 1977). The shoreline of Williston Reservoir is dendritic in shape and estimated to be about 1,770 km in length (BC Research 1977). With a surface area of 1,779 km^2 at a maximum normal operating level of 672.1 m (BC Hydro 1988), Williston Reservoir is the largest lentic freshwater system in British Columbia. The catchment area of the Williston drainage basin is 69,930 km^2, equal in size to the province of New Brunswick (BC Hydro 1996), and accordingly the catchment area to surface area ratio (CA/SA) for Williston Reservoir is also very large - 39:1. The reported average water residence time of the reservoir varies from 19 months (Hirst 1991) to 2.2 years (Fleming et al. 1991, unpublished data). With a storage capacity of $74,257 \times 10^6$ m^3 of water, Williston Reservoir by volume is ranked the ninth largest reservoir in the world (Maclean 1998). Most of the hydrologic input is from snowmelt and the spring run-off peaks in late May and early June.

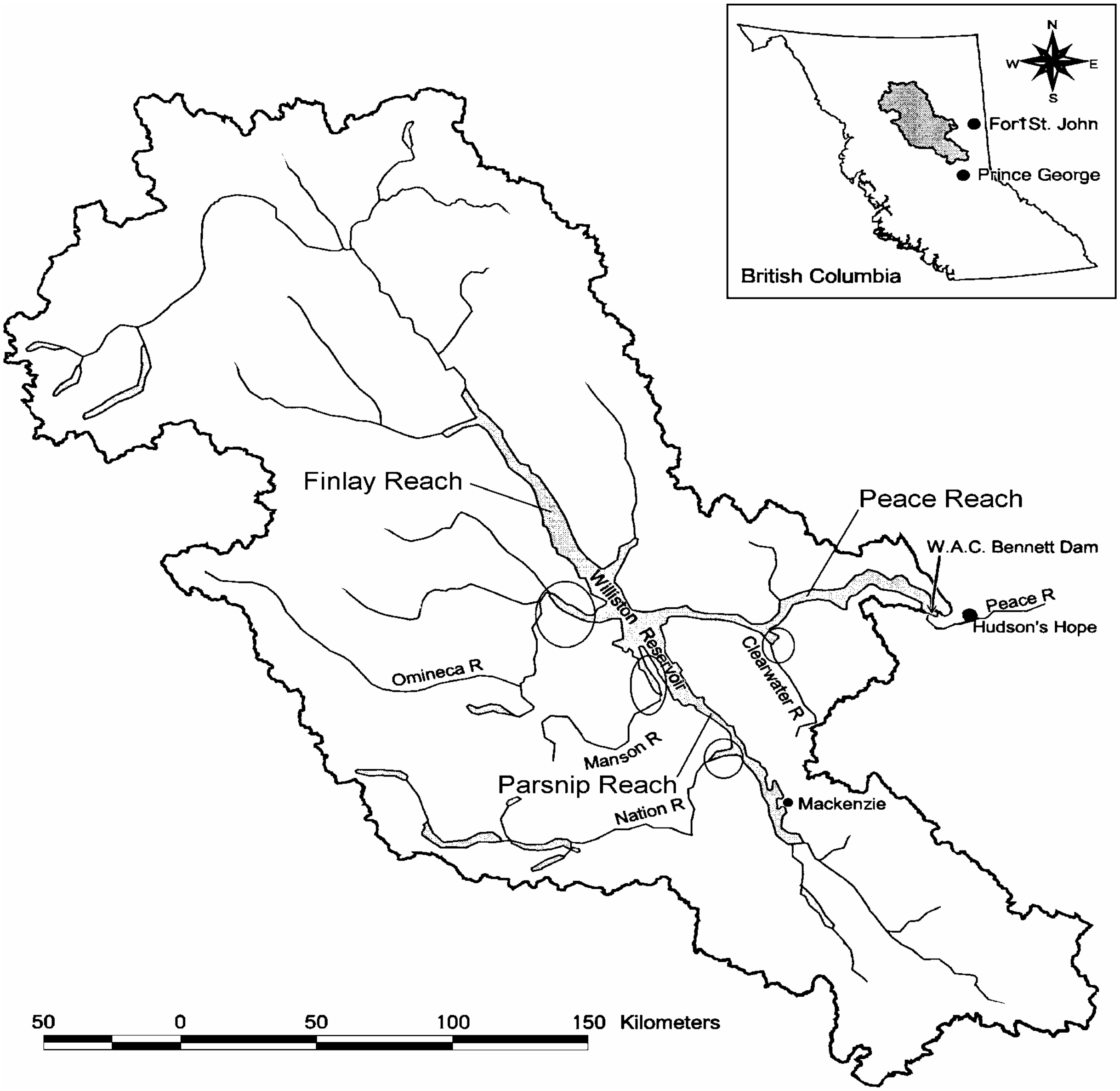

Figure 1. Williston Reservoir showing Nation, Manson, Omineca, and Clearwater embayments.

The Williston watershed is subject to a continental climate with long, cold winters. Temperatures as low as -30°C can occur after October, with sub-zero temperatures often extending well into April. Frost may occur at any time of the year (Maclean 1998), and ice formation on the reservoir can begin as early as November, though complete coverage usually does not occur until January. Ice cover normally extends to approximately the first week of May. The summer average air temperatures range from 16°C-18°C, with maximum temperatures reaching 30°C (G3 Consulting Rep. 1994). Annual precipitation ranges between 40–50 cm in most of the catchment basin, with the exception of greater amounts (75–100 cm) in the Rocky Mountains east of the Finlay Reach (BC Hydro 1988). Snowfall accounts for 35-45% of the total annual precipitation.

The pelagic zone of Williston Reservoir exhibit dimictic circulation patterns, characterized by 2 distinct periods of deep-mixing, one in spring and another in late autumn. The onset of thermal stratification, with a discernable epilimnion, metalimnion and hypolimnion occurs usually by late May or early June, and usually lasts well into October or early November and the beginning of major winter storms. Stratification is weakest and shortest in duration in the shallow Finlay and Parsnip Reaches and strongest and longest in the much deeper Peace Reach. In winter from late February and lasting until ice-out in early May, the reservoir shows a typical 'inverse' stratification, with colder and less dense 1-2^{o} C water on top of dense 4^{o} C water extending to the bottom. No information is available on the circulation patterns or thermal stratification of the embayments.

The reservoir cycles between maximum and minimum levels once a year. Typically the water level in the reservoir reaches a maximum level in August and September peaking near the 672.1 m Maximum Normal Level (MNL) above sea level. Increased discharge and low winter inflow result in deep winter draw down, averaging 11 $m \cdot yr^{-1}$ attained in April or early May (Hirst 1991). The resulting drawdown is most pronounced in shallow embayments with gradually sloped shorelines where a 1m water surface decline can equate to several 100 m of shoreline retreat, and ice scour induced erosion.

The Nation, Manson (Parsnip Reach) and Omineca (Finlay Reach) embayments (Figs. 1-4) are situated in low gradient topography where glacial deposition, moraines and lacustrine deposits are common. Glacial till is the most abundant surficial deposit. The Clearwater embayment (Figs. 1 and 5) is situated in the Peace Reach where steep-sloped sedimentary rock is predominant in the entrenched western half of the Peace Reach (as exhibited by the Clearwater embayment) where the Peace River originally (prior to impoundment) cascaded eastward through the Rocky Mountains. General physical attributes of each embayment are from reservoir elevations at or near the maximum annual level. The surface area and lengths given for Manson and Nation embayment are much smaller in April when the reservoir is drawn down by 11+ meters. Selection of the reservoir/embayment confluence point (embayment end point) was subjective and estimated from existing land topography.

Nation Embayment

The Nation embayment (55°28’ N 123°30’ W) receives water exclusively from the Nation River (6th order, 153 km length) and is oriented west to east (Figs. 1 and 2). The embayment waters enter the Parsnip Reach from the west approximately half way up the Parsnip Reach. Surface area is approximately 700 ha with a length of 6 km.

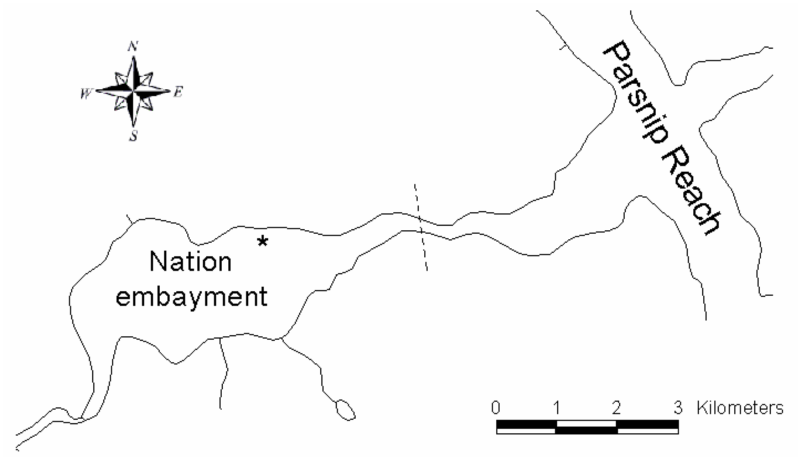

Figure 2. Nation embayment (∗ denotes station location).

Manson Embayment

The Manson embayment (55°45’ N 123°50’ W) is headed by the Manson River (5th order, 106 km length) and is oriented parallel to the Reservoir in a roughly south to north direction. It flows into the Parsnip Reach near the junction point of all three reaches (Figs. 1 and 3). Manson River is the primary source of water to Manson embayment with Eklund Creek (4th order, 31 km length) contributing a smaller volume of water mid-length along the embayment from the west. Surface area is approximately 2,500 ha with a length of 23 km.

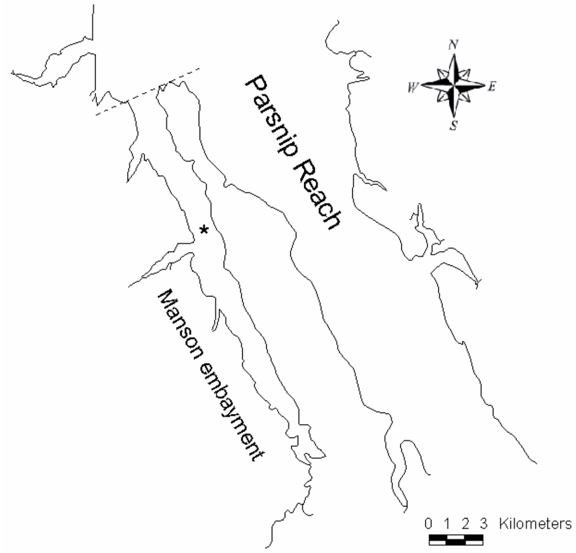

Figure 3. Manson embayment (∗ denotes station location).

Omineca Embayment

The Omineca embayment (56°05’ N 124°20’ W) receives water from the Omineca River (6th order, 261.7 km length) and the Mesilinka River (6th order, 170.7 km length). The embayment is oriented on a northwest-southeast axis and flows into the Finlay Reach of Williston Reservoir, north of the Junction area (Figs. 1 and 4). Surface area is approximately 3,500 ha with a length of 22 km. Omineca embayment is the largest embayment examined during this study.

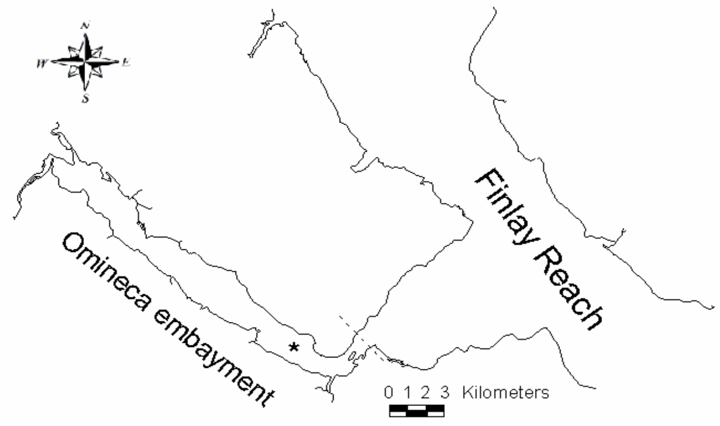

Figure 4. Omineca embayment (* denotes station location).

Clearwater Embayment

The Clearwater embayment (56°00’ N 22°45’ W) headed by Clearwater Creek (5th order, 47 km length) is oriented on a north-south axis flowing northward into the Peace Reach of Williston Reservoir (Figs. 1 and 5). A smaller contribution of water is received from Ducette Creek (5th order, 28 km length) entering Clearwater embayment mid length from the east. Owing to its deep narrow “fjord” like setting of steep sloped sedimentary rock shoreline, the surface area does not decline as dramatically as the other embayments in response to the annual Reservoir draw down. Surface area is approximately 350 ha with a main length of 9 km and a secondary embayment (Ducette) adding a further 2.5 km in length running east to west. Clearwater embayment is the smallest embayment examined in this study.

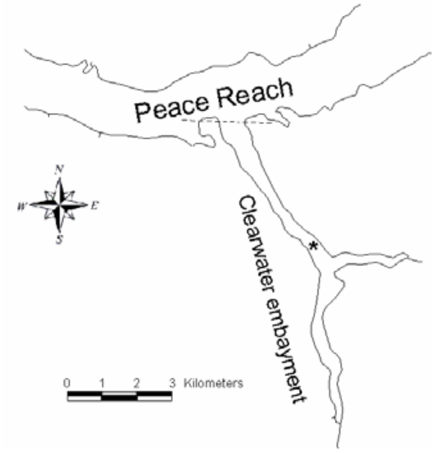

Figure 5. Clearwater embayment (* denotes station location).

METHODS

Stations and Sampling

Station selection criterion included positioning over the original inundated river channels to achieve maximum depth, distancing the location from any major turbidity input sources such as river mouths, eroding alluvial shorelines and ensuring site was in the transitional/lacustrine zone of the embayment to avoid complete de-watering by annual drawdown process. The coordinates (NAD 83 datum), collected with Hewlett Packard iPAQ Navigation System (GPS) for the sampling sites are:

Nation embayment,	UTM co-ordinates 10.470805.6151756
Manson embayment,	UTM co-ordinates 10.442970.6189170
Omineca embayment,	UTM co-ordinates 10.422350.6208370
Clearwater embayment,	UTM co-ordinates 10.489610.6199830

Each station was occupied once during a sampling trip. Three sampling trips were completed in 2004 to coincide with presumed seasonal variation in physical and chemical properties and phytoplankton seasonal growth. The first sampling trip on June 22-24, 2004 provided data on chemical, physical, and biological conditions shortly after the spring turnover. The mid season sampling trip, July 23–26 was conducted with the intent of collecting samples from the presumed primary production peak (based on limnology data collected in 1999 and 2000 in the reservoir). Primary productivity experiments were only conducted during the mid-season sampling trip. The final sampling period, conducted October 6–10, was intended to capture data near the end of the phytoplankton growing season. Bathymetry data was collected for all embayments, except Manson, during the October sampling trip when reservoir water level (668 m) was at near maximum levels for the year.

Bathymetry

Bathymetric data was collected for Nation, Omineca and Clearwater embayments using Nova Marinetek Ltd *PC* Sounder. The hardware included a dual transducer arrangement, with time stamp signature and GPS position capturing ability. Transect locations were selected based on topographic features and areas of interest selected from satellite imagery collected when reservoir was at a low elevation (659 m, May 2003). No bathymetric data was collected for Manson embayment due to time constraints.

Physical & Chemical Sampling

Water depth was measured with a Raymarine FishFinder L470 depth sounder and recorded to the nearest meter. Vertical profiles of dissolved oxygen, pH and temperature were collected with an YSI model 650 multi parameter sonde meter. A standard 20 cm Secchi disc was used without a viewing chamber to measure the water clarity from the shaded side of the boat. The euphotic zone and extinction coefficients were determined by light penetration with a Licor LI-192s quantum sensor and meter at 1 m intervals from the surface down to at least 1% of surface light values. Reservoir elevation data was collected to the nearest 0.1 m by an electronic gauge at the W.A.C. Bennett Dam.

Discrete water samples were collected with a Van Dorn sampling bottle from 1, 3, 5 and 6.5 or 7.5 m depths. After dispensing water for primary productivity measurements (July only), water was immediately taken for total and dissolved nutrients, chlorophyll *a*, total dissolved solids and alkalinity analysis. Care was taken to limit light exposure of Chl *a* and primary productivity samples during sampling and handling. All samples were stored in the dark and on ice and shipped within a few days to the analytical laboratories.

Total phosphorus (TP), total dissolved phosphorous (TDP) and total dissolved solids (TDS) were analyzed by the Pacific Environmental Science Centre (PESC), Environment Canada, North Vancouver, B.C. following laboratory methods established by McQuaker (1994). Water samples collected for TDP determination were field filtered through a 0.75 µm combusted GF/F filter at low vacuum pressure and the filtrate submitted for analysis. Water samples for nitrate + nitrite (NO_3^- + NO_2^-) and silicic acid ($Si(OH)_4$) were filtered (0.75 µm combusted GF/F filter) into acid-cleaned Nalgene® bottles and stored at -20°C until analysis at the University of British Columbia (UBC). Nitrate plus nitrite and silicic acid were processed using an Autoanalyzer® III using the procedures of Wood et al. (1967) and Armstrong et al. (1967), respectively. Combined NO_3^- + NO_2^- concentrations are reported as NO_3^-. Replicate water samples were collected for dissolved nutrient and Chl *a* analysis.

Water for alkalinity determination was collected from 1 and 7.5 m in 1 L polycarbonate bottles. A Beckman 44 pH meter and electrode was used to determine total alkalinity according to the standard potentiometric method of APHA (1995). Each sample was titrated with 0.02 N H_2SO_4 to pH 4.5. All samples had an initial pH of less than 8.3. Titrations were performed in duplicate or triplicate to check the analytical precision of the results.

Chlorophyll *a* values provide an estimate of the standing stock of autotrophic phytoplankton biomass in the reservoir. Chlorophyll *a* is a photosynthetic pigment that is specific to photoautotrophs and can be measured with ease and sensitivity (Holm-Hanson et al. 1965). Chl *a* corrected for phaeopigments was determined by *in vitro* fluorometry (Yentsch and Menzel 1963). Water samples (0.25-1 L) were field filtered using parallel filtration onto 47-mm diameter 0.2, 2.0 and 20.0 µm polycarbonate Nuclepore™ filters using a vacuum pressure differential of <100 mm of Hg. Samples were stored at –20°C prior to analysis at the UBC. All Chl *a* samples were analyzed within two weeks of collection. Chl *a* was extracted in 8-10 ml of 90% acetone and stored in the dark for 20-24 h at 4°C. The fluorescence of the acetone extract was measured before and after the addition of three drops of 10% HCl in a Turner Designs™ Model 10-AU fluorometer calibrated with a solution of commercially available Chl *a*. Calculations for Chl *a* were made using the equations of Parsons et al. (1984) and were vertically integrated according to procedures of Ichimura et al. (1980).

Primary Productivity

Primary production experiments were conducted only during the July sampling trip. Water samples were collected from 1, 3, 5 and 7.5 m at all embayments except at Manson embayment where the 7.5 m sample was substituted with a 6.5 m sample. Samples were transferred directly from the Van Dorn bottle into two light and one dark 300 ml acid-cleaned BOD bottles using a silicon filling tube. Each BOD bottle was rinsed 3 times with lake water before filling. Care was taken to eliminate contact with latex since latex is toxic to phytoplankton (Price et al. 1986). The samples were maintained under low light conditions during all manipulations until the start of the incubation usually within 1 h of sampling. The ^{14}C incorporation into the dark bottle determined non-photosynthetic ^{14}C incorporation.

Samples were inoculated with 0.185 MBq (5 μCi) of $NaH^{14}CO_3$ New England Nuclear (NEC-086H) and primary productivity was determined from the amount of ^{14}C incorporated into the particulate organic carbon retained on a filter (Steemann Nielsen, 1952). The BOD bottles were attached to an acrylic plate and were suspended at the same depths they were taken from for 4-6 h, generally incubation were initiated as close to 11:00 hrs as possible, but no later than 13:00 hrs.

Following retrieval of the incubation array, the BOD incubation bottles were stored in a dark box. The incubations were terminated within 1-1.5 hrs by parallel filtration of 100 ml of sample through each of a 0.2, 2.0 and 20.0 μm 47-mm polycarbonate filter using <100 mm Hg vacuum differential (Joint and Pomroy, 1983). Each folded wet filter was placed in a 7-ml scintillation vial and stored in the dark until processing at the UBC.

In the fumehood, 100 μL of 0.5 N HCl was added to each vial to eliminate the unincorporated inorganic $NaH^{14}CO_3$. The scintillation vials were left uncapped in the fumehood until the filters were dry (approx. 48 h) and 5 ml of Ecolite® scintillation fluor was added to each vial. The vials were stored in the dark for >24 hours before the samples were counted using a Beckman® Model #LS 6500 liquid scintillation counter. Each vial was counted for up to 10 minutes operated in an external standard mode to correct for quenching. The specific activity of the C^{14} stock solution was determined by adding 100 μL ^{14}C-bicarbonate solution to scintillation vials containing 100 μL of ethanolamine and 5 ml Ecolite® scintillation cocktail.

Rates were calculated according to Parsons et al. (1984) to obtain hourly primary productivity and were vertically integrated according to procedures of Ichimura et al. (1980).

Given that primary productivity incubations are conducted during only a portion of the total sunlight hours (between 11 am – 6 pm), it is necessary to calculate a factor that represents the ratio of the total solar radiation during the incubation to the total daily solar radiation. Solar radiation for the incubation period and for the incubation day was calculated by integrating the data for the incubation time period and for the entire day, respectively. Monthly solar radiation data is also necessary to determine if the sampling day was typical for the month and to calculate the primary productivity for an average day in the month.

Solar radiation data for Prince George, BC were requested from Environment Canada, but at the time of report writing the data were not available. Consequently, solar radiation data for a typical cloudy or sunny day off the northern tip of west coast Vancouver Island was used to estimate the conversion factor and to calculate daily primary productivity rates. Although Vancouver Island is located approximately 5° south of Williston Reservoir and the solar radiation received by the Earth is a function of latitude, at this time of the year the daily solar radiation received at Vancouver Island and Williston Reservoir is similar. The difference between the two locations is the length of the day: the more northerly location, Williston Reservoir, will have a slightly longer day than the southerly location. Consequently the conversion factor may be overestimated by up to 6%, leading to a small underestimate of primary productivity. This error is not an issue in this study, as the primary productivity of the 4 embayments are compared relative to each other and to the primary productivity of the pelagic regions which were also subject to this error.

Phytoplankton

A sample was collected from each of 1, 3, and 5 m water depth at each of the 4 stations during each sampling trip. Water was collected in a dark glass bottle and preserved in acid Lugol's iodine preservative and stored in the dark until analysis. The samples were gently shaken for 60 seconds and poured into 25 mL settling chambers and allowed to settle for a minimum of 24 hr (Utermohl 1958). Counts were done using a Carl Zeiss© inverted phase-contrast plankton microscope. Counting followed a 2-step process. Initially, several random fields (5-10) were examined at low power (250X magnification) for large microplankton (20-200 μm), e.g. colonial diatoms, dinoflagellates, filamentous blue-greens. A second step involved examining all cells within a random transect ranging from 10 to 15 mm were counted at high power (1,560X magnification). This high magnification permitted quantitative enumeration of minute (<2 μm) autotrophic picoplankton cells [Class Cyanophyceae], and also of small auto-, mixo- and heterotrophic nanoflagellates (2.0-20.0 μm) [Classes Chrysophyceae and Cryptophyceae]. In total between 250-300 cells were consistently enumerated in each sample to assure statistical accuracy (Lund et al. 1958). The compendium of Canter-Lund & Lund (1995) was used as the taxonomic reference.

Zooplankton

Duplicate macrozooplankton samples were collected at each station during each of the sampling trips. Samples were collected with a vertically towed, 80 μm mesh Wisconsin plankton net, with a 50 cm throat diameter, and a 74 μm mesh window for straining water from the collection cup. Zooplankton sampling at the Omineca and Clearwater embayments consisted of a vertical haul from 30 m depth to the surface. Manson and Nation embayment zooplankton were collected with vertical to surface hauls from 20 m and 16 m depths, respectively. The net was raised at a speed of approx. 0.5 $m \cdot sec^{-1}$. Samples were placed in 4% $NaHCO_3$ to prevent egg loss from addition of the preservative and then after approximately 60 seconds, the samples were preserved with 70% ethanol.

Zooplankton samples were analyzed for species density, biomass (estimated from empirical length-weight regressions, McCauley 1984), and fecundity. Samples were re-suspended in tap water filtered through a 74 μm mesh and sub-sampled using a four-chambered Folsom-type plankton splitter. Splits were placed in gridded plastic petri dishes and stained with Rose Bengal to facilitate viewing with a Wild M3B dissecting microscope (at up to 400X magnification). For each replicate, organisms were identified to species level and counted until up to 200 organisms of the predominant species were recorded. If 150 organisms were counted by the end of a split, a new split was not started. The lengths of 30 organisms of each species were measured for use in biomass calculations, using a mouse cursor on a live television image of each organism. Lengths were converted to biomass (μg dry-weight) using empirical length-weight regression from McCauley (1984). The number of eggs carried by gravid females and the lengths of these individuals were recorded for use in fecundity estimations. Zooplankton species were identified with reference to taxonomic keys (Sandercock and Scudder 1996, Pennak 1989, Wilson 1959, Brooks 1959).

RESULTS

Bathymetry

Bathymetric data collected for Clearwater, Omineca and Nation embayments was processed and plotted after the sampling trip. The distance between transect lines (often greater than 1 km) was too great to confidently interpolate contour lines using Marinetek Ltd. *Contour Utility* software. All bathymetric data files will be retained and additional transects added in the future to obtain satisfactory bathymetry.

The maximum depths observed at each embayment were, 99 m (Clearwater), 57 m (Omineca), and 30 m (Nation). Clearwater embayment is steep sided, fjord-like, with little exposed littoral zone in response to annual Reservoir drawdown. Conversely, Omineca embayment is shallow near its genesis (Omineca and Mesilinka River mouths) and this shallow area will temporarily be exposed in spring. This shallow area of approximately 600 ha including the entire Mesilinka embayment sub-basin is dewatered annually. Another 100+ ha near the mouth of the embayment at Black Canyon similarly will be exposed under normal draw down regimes. The Nation embayment also has extensive shallow areas along the south shoreline that are dewatered annually.

Physical & Chemical Limnology

Temperature The embayments of Williston Reservoir are dimictic, with mixing in the fall and the early spring. Surface warming and thermal stratification of the water column had begun prior to the first sampling trips in late June with surface water temperatures between 17-21^{o}C. Shallow and poorly defined epilimnions were generally noted at all four embayments (Appendix A). Surface water temperatures peak in July and range from a low of 17.5^{o}C in the Clearwater embayment to a high of

22°C at the Nation embayment. The clearest epilimnion was observed in July in Omineca and Clearwater embayments where the epilimnion usually extended down to a depth of 6-7 m. Deep water temperatures were colder in July than in June in both Nation and Omineca embayments. Epilimnetic temperatures decrease to 8-10°C by October and the epilimnion and thermocline increase in depth indicating that fall turnover of the water column would soon occur. The thermal regime in Clearwater embayment is different compared to the other embayments as the water temperature of the surface was generally 2-4°C degrees cooler.

Oxygen Dissolved oxygen profiles generally show concentration increasing with depth during June and July, with concentrations > 8 $mg \cdot L^{-1}$ (Appendix A1). These orthograde profiles are typical of low productivity lakes, with concentrations at depth showing a uniform distribution and little variation at most stations (Appendix A1). Oxygen values at most depths were near saturation with respect to temperature and pressure. By October, oxygen concentrations decrease below the epilimnion at all embayments. These are clinograde profiles, which are more typical of higher productivity (Wetzel 2001) and suggest microbial consumption of oxygen due to decomposition of organic matter at depth.

Water transparency Secchi depths greater than 10 m depict good water clarity (high transparency) while readings less than 5 m suggest a moderate degree of turbidity imparted by either particulate or dissolved organic matter (low water transparency). Average water transparency at the four embayments is low with seasonal means of Secchi depths ranging from a low of 1.7 m to a high of only 4.0 m (Table 1). In contrast, greater water transparency is observed at Williston Reservoir pelagic stations in 2000 where the mean, not the highest Secchi depth was approximately 4 m. At most stations transparency tended to increase seasonally from low transparency in June and July during the peak of freshet, to a greater transparency in October. The highest Secchi depth measured was in October at Omineca embayment with a depth of 5.7 m, while the lowest occurred at Manson embayment in June with a depth of 0.8 m. Manson embayment was the most turbid embayment studied with Secchi depths averaging 1.7 m and never exceeding 2.1 m. Clearwater embayment was the least turbid with the exception of the low transparency recorded in June. Light extinction coefficients, calculated from Secchi depths and vertical profiles of photosynthetic active radiation (400-700 nm) are given in Table 2.

Table 1. Secchi depths for the embayments of Williston Reservoir, 2004.

	Nation	**Manson**	**Omineca**	**Clearwater**
June	2.5	0.8	1.7	2.3
July	4.0	2.1	4.5	4.5
Oct.	2.8	2.1	5.7	5.3
Average	**3.1**	**1.7**	**4.0**	**4.0**

Table 2. Light extinction coefficients for the embayments of Williston Reservoir, 2004.

	Nation	Manson	Omineca	Clearwater
June	0.68	2.16	1.7	0.74
July	0.87	0.83	0.59	0.65
Oct.	0.61	0.81	0.30	0.32
Average	**0.72**	**1.27**	**0.86**	**0.57**

Total Dissolved Solids (TDS) Total dissolved solids reflect the degree and characteristics of hydro-geological weathering and anthropogenic disturbance within the drainage basin. Given the embayments geographic spatial separation and differing surficial geology, the TDS values at the embayment stations displayed surprising homogeneity ranging from 63–91 mg·L^{-1}. The highest average TDS values occurred in Manson embayment with values of 91 mg·L^{-1} (Table 3) which coincides with the lowest Secchi disk depth discussed above. The highest average TDS values in Williston Reservoir pelagic stations occurred in the Finlay Reach (119 mg·L^{-1} in 1999, 122 in 2000), and the next highest were in the Forebay station (111 mg·L^{-1} in 1999, 109 in 2000). The lowest average embayment station TDS value observed in 2004 was 63 mg·L^{-1} in Omineca embayment. The lowest pelagic station TDS values occurred in the Parsnip Reach (88 mg·L^{-1} in 1999, 94 in 2000). These data show that the TDS is lower in the embayments than in the pelagic area of the Reservoir. At all embayment stations a trend in seasonal TDS consisted of a rise from lowest values in June to a “peak” in the July, followed by a retreating value in October values.

Nitrogen (N) Of the utilizable forms of N by phytoplankton, ammonium and nitrate are the inorganic forms that are most readily assimilated. Ammonium is generated by bacterial decomposition of organic matter and by excretion of waste products of aquatic animals. Ammonium concentrations are generally undetectable by chemical analysis as ammonium is quickly converted to nitrite by bacteria in oxygenated water hence nitrate (NO_3+NO_2-N) becomes the most important form of dissolved N supporting algal growth (Wetzel 2001). Ammonium concentrations were not measured in 2004. Nitrate concentrations in the embayments were generally very low and the concentrations ranged from 1.3-28.5 µg·L^{-1} (Table 3). Average nitrate concentrations were highest in Clearwater embayment during each sampling trip while the lowest were generally found in the Omineca embayment. The low nitrate concentration in the epilimnion in June suggest that the nitrate concentrations were drawn down prior to the first sampling trip as the concentrations measured in each embayment was less than concentrations observed in October. Nitrate concentration in the epilimnion was generally <20 µg·L^{-1} in Nation and Omineca embayments. Nitrate concentrations that are <20 µg·L^{-1} are generally considered limiting to phytoplankton growth (Wetzel 2001). Nitrate limitation was observed at all sampling depths in Nation and Omineca in July while the concentration found in Manson and Clearwater was only slightly above concentrations considered limiting. These results are in contrast to those found in 1999 and 2000 for the pelagic region where concentrations were on average 57 µg·L^{-1} in 1999 and 62 µg·L^{-1} in 2000, and values were always well above detection limits at all stations except in the Finlay Reach, where epilimnetic concentrations were limiting to phytoplankton growth. The highest epilimnetic concentration found for the embayments was 38.1 $\mu g \cdot L^{-1}$ in Clearwater in October while the highest epilimnetic nitrate concentrations in the Reservoir occurred in the Parsnip Reach, exceeding 177 $\mu g \cdot L^{-1}$ in June 1999 and 195 $\mu g \cdot L^{-1}$ in June 2000. This suggests either; a) interannual variations were responsible for lower nutrient loading in 2004 relative to 2000, b) the nutrient loading to the embayments or deep water mixing is lower than the pelagic zone c) phytoplankton drawdown of dissolved inorganic nitrogen (phytoplankton growth) is greater in the embayment than in the pelagic regions. At this point it is not possible to assess the likelihood of interannual variations in nutrient loading to the Reservoir but the similar production rates in the embayments and the Reservoir do not suggest that phytoplankton growth is higher in the embayments and therefore phytoplankton growth may not account for the differences observed between the embayments and the Reservoir.

Phosphorus Concentrations of total phosphorus (TP) ranged from 6-10 $\mu g \cdot L^{-1}$ the embayment stations with the highest levels of 25 $\mu g \cdot L^{-1}$ in June (Table 3). Values of TP are highest in Manson embayment (10 $\mu g \cdot L^{-1}$), while Nation and Omineca embayments were the lowest (6 $\mu g \cdot L^{-1}$) with samples containing less than the minimum detectable level (2 $\mu g \cdot L^{-1}$). Concentrations of TP averaged 6.2 $\mu g \cdot L^{-1}$ for the reservoir pelagic stations and seasonally ranged between highs of 11 $\mu g \cdot L^{-1}$ to lows of 2-3 $\mu g \cdot L^{-1}$ in 1999. In year 2000 TP was slightly higher at all pelagic stations, averaging 7.4 $\mu g \cdot L^{-1}$ and ranging between 6.2-9.2 $\mu g \cdot L^{-1}$.

TDP values were at least 35% lower than TP and were almost always below or just at the detection limit (2 $\mu g \cdot L^{-1}$). TDP values were below detection levels during each sampling trip and at all depths at the Omineca and Clearwater embayments. Only 3 TDP samples collected at Manson embayment (3 $\mu g \cdot L^{-1}$ June 23, 1m: 2 $\mu g \cdot L^{-1}$ June 23, 3m: and 2 $\mu g \cdot L^{-1}$ July 24, 5m) had concentrations above the detection limits. TDP values in the pelagic area of the Reservoir were also about 30-40% lower than TP, and average TDP concentrations were higher at 3.6 µg·L-1 in 1999 and 4.7 in 2000. Concentrations were highest in both years in the Parsnip Reach >5 $\mu g \cdot L^{-1}$ and were lowest in Finlay Reach - 3 $\mu g \cdot L^{-1}$in 1999, and Peace Reach – Clearwater and Forebay in 2000 – 3.9 $\mu g \cdot L^{-1}$. Considering TDP was at or near detection limits for the embayments it is likely that phytoplankton growth was limited by phosphorus availability.

N:P ratio The N:P ratio is used as a measure of nutrient limitation in a lake. Ratios greater than 15 (by weight) indicate phosphorus limitation, ratios less than 10 indicate nitrogen limitation and ratios between 10 and 15 indicate neither or both are limiting algal growth (Downing and McCauley 1992). Due to the large contribution of refractory organics and inorganic particulates in Williston Reservoir that are included in both TN and TP measurements, a TN:TP ratio has little relevance when looking for potentially limiting nutrients to phytoplankton growth. A more meaningful assessment of potential nutrient limitation can be obtained by looking at a ratio based on dissolved nutrients that are easily assimilated by phytoplankton, namely nitrate + ammonium:dissolved phosphorus. Since ammonium concentrations were not analyzed the NO_3-N:TDP ratio was used as the best ratio to assess possible N or P limitation of phytoplankton growth in the reservoir. A ratio of inorganic nitrogen and dissolved phosphorus of 7 or greater is suggested for a "healthy" population of all phytoplankton species to co-exist (Stockner, pers. comm.).

Table 3. Mean values for selected physical, chemical and biological variables from the embayments June – October 2004, and Williston Reservoir pelagic stations mean, 1999 and May – Nov., 2000. (Units are $\mu g \cdot L^{-1}$ unless otherwise noted)

Variables	Nation embayment	Manson embayment	Omineca embayment	Clearwater embayment	Williston (1999) Reservoir Mean	Williston (2000) Reservoir Mean
Epilimnion Ave. depth (m)	10.3	9.7	7.3	12.6	28	26
Max. Epi-Temp (C^{o})	21.9	21.0	20.5	17.5	16	15
Secchi depth (m)	3.1	1.7	4.0	4.0	3.5	4.1
Extinction coefficient	0.72	1.3	0.86	0.57	-	0.77
TDS (mg·L^{-1})	70	91	63	67	106	107
TP	6.0	10.0	6.0	7.0	6.2	7.4
NO_3	1.2	21.8	1.3	28.5	57	62
TDP	2.0	<2.0	<2.0	<2.0	3.6	4.7
NO_3:TDP	0.6	11	0.7	14.3	15.7	13.5
Chl *a*	1.6	1.2	1.4	1.1	1.4	1.4
Integrated Chl *a* (mg m^{-2})	12.5	8.9	10.6	9.2	7.8	7.3
Phyto density (cells·mL^{-1})	3,274	2,520	3697	3092	4,729	4,571
Phyto BioV. (mm^{3}/L)	0.35	0.22	0.31	0.30	0.33	0.27
PP (mgCm-^{2}hr^{-1})	4.1	2.1	4.2	4.2	-	9.6
(mgCm-^{2}day^{-1})	30.7	19.2	44.1	36.3	-	34.3
PP/Biomass (P/B ratio)	2.7	1.7	3.9	3.3	-	3.4
Zooplankton (#·L^{-1})	2.0	11.9	2.0	12.1	6.5	5.8
Biomass ($\mu g \cdot L^{-1}$)	9.9	25.9	8.9	30.9	21.9	23.5

The N:P ratio was <1 for Nation and Omineca embayment which suggests severe nitrogen limitation of phytoplankton growth (Table 3). These ratios obtained for Nation and Omineca were lower than the N:P ratio in Finlay Reach (N:P=4.7), the lowest N:P value obtained in the pelagic system in 1999 and 2000. These ratios are in contrast to N:P values averaging 12 for Manson and Clearwater embayments which are similar to N:P values obtained for the pelagic system (15.7 in 1999 and 13.5 in 2000 for the whole pelagic system).

Phytoplankton

Total Chlorophyll a Chlorophyll *a* concentrations in the embayments were remarkably low during all sampling dates, ranging from 6.2 $mg \cdot m^{-2}$ in Clearwater in June to highs of 16.8 $mg \cdot m^{-2}$ in Nation Embayment in June (Fig. 6). Clear peaks in biomass were observed in Nation and Omineca embayment in June while the phytoplankton biomass among the embayments was remarkably similar in July and October. Biomass in Nation and Omineca embayments was 2-3 fold higher than in Manson or Clearwater embayments. Despite low biomass levels throughout the growing season, some seasonal variability in phytoplankton was observed for Nation, Manson and Clearwater embayments (Fig. 6). The phytoplankton biomass decreased 30% in Nation in July relative to June, while in contrast the biomass in Manson and Clearwater increased 56% and 75% respectively during the same time period.

Despite the seasonal variation observed in Nation, Manson and Clearwater embayments, phytoplankton biomass lacked any clear signs of a bloom (i.e.>10-20 fold increase). A spring bloom was not evident in the embayments but it is possible that the spring bloom had occurred prior to the June sampling trip. If we can assume that the nutrient concentration observed in October are similar to Spring nutrient concentration, then the June nutrient data indicates nitrogen drawdown occurred prior to the sampling trip which suggests an earlier spring phytoplankton growth.

Phytoplankton biomass was on average highest in Nation embayment followed by Omineca, Clearwater and Manson embayments (Fig. 7) but the differences between the highest and the lowest embayment was only ~30%. Phytoplankton biomass in the embayments was consistently higher in the embayment than the average biomass in the Reservoir (Fig. 7). Phytoplankton biomass in Manson and Clearwater were similar to the levels found in the Reservoir. In contrast, biomass was higher in Nation or Omineca biomass where on average biomass was 60% and 40% higher than in the Reservoir. The biomass levels in the embayments, while higher than the levels observed in the Reservoir are still indicative of oligotrophic conditions (Wetzel, 2001).

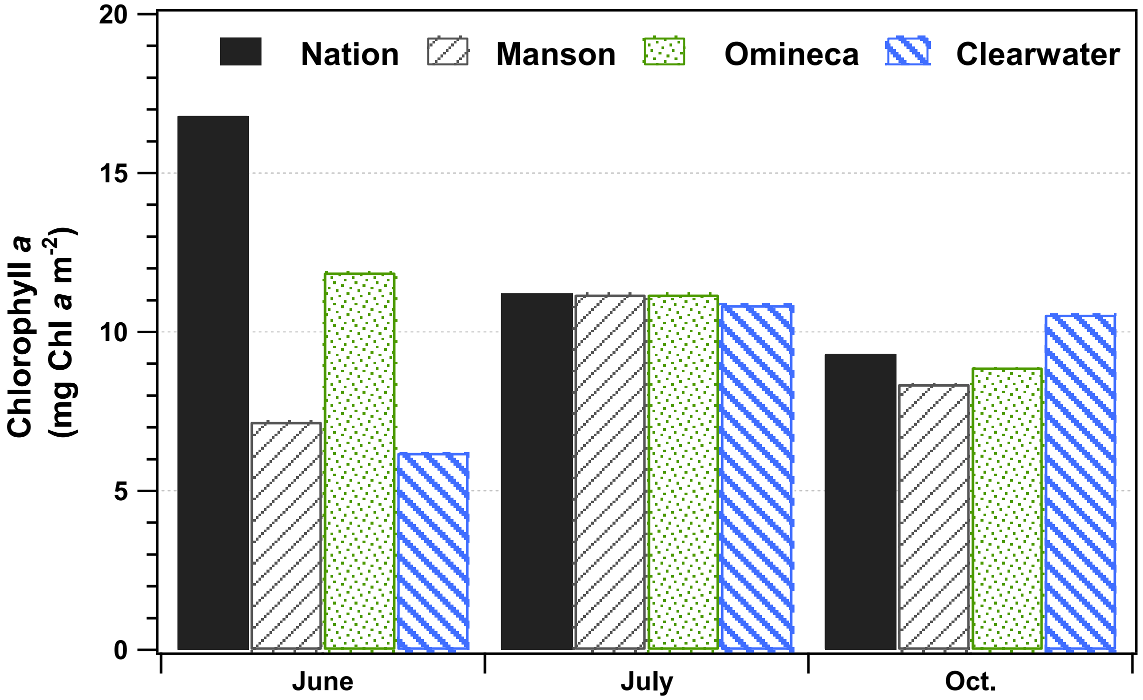

Figure 6. Vertically integrated chlorophyll a (mg Chl *a* m^{-2}) in June, July and October 2004 in the embayments of Williston Reservoir.

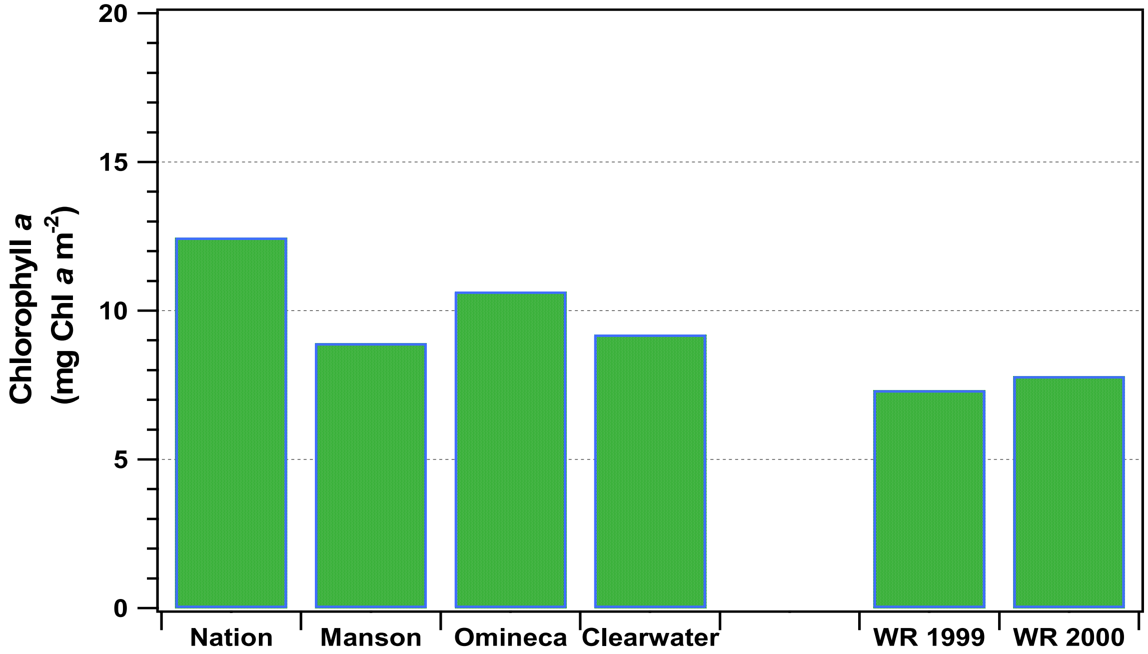

Figure 7. Mean integrated chlorophyll a in the embayments of Williston Reservoir, 2004 and in the pelagic region of Williston Reservoir in 1999 and 2000. (values are integrated 0-5 m)

Size-fractionated Chlorophyll Picoplankton and nanoplankton contributed greatly to the phytoplankton biomass in the embayments (Fig. 8). In Nation and Omineca embayments, the picoplankton biomass generally varied from 40-49%, nanoplankton biomass varied from 41-42% and microplankton biomass varied from 9-18% of the total biomass. One notable difference was observed in Omineca embayment in July where the contribution of nanoplankton decreased by half and the contribution of microplankton doubled (Fig. 8). As was observed for total biomass, the size composition data indicates that Manson and Clearwater embayments were similar to each other and different than Nation and Omineca embayment. In Manson and Clearwater, nanoplankton sized cells dominated the biomass followed by picoplankton and microplankton. One exception was observed in Clearwater in July where the contribution by microplankton increased by 5-fold and was similar to the contribution by picoplankton. In Manson and Clearwater embayments, the contribution by nanoplankton varied between 39-70%, picoplankton varied between 23-26% and microplankton varied between 7-32% (Fig. 8). In terms of food availability for zooplankton, the high contribution by nanoplankton in all embayments is encouraging.

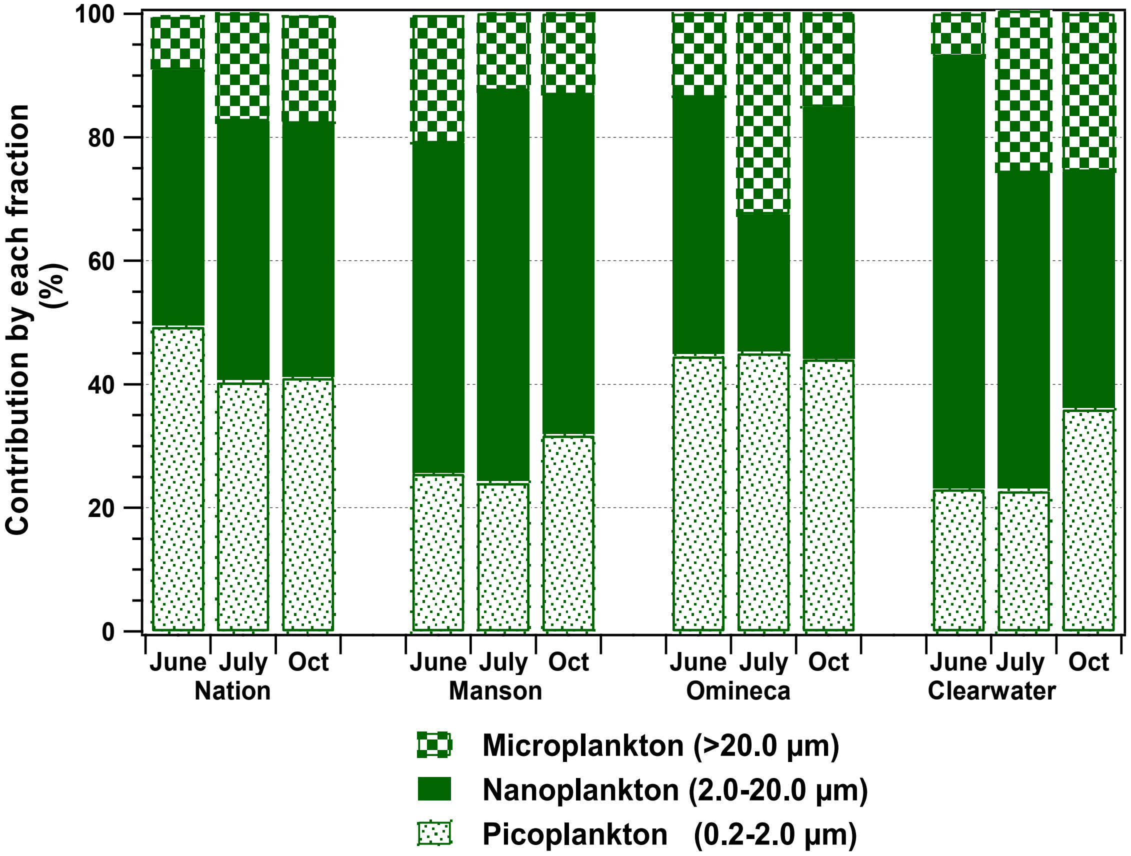

Figure 8. Seasonal distribution of picoplankton, nanoplankton and microplankton in the embayments in June, July and October, 2004.

On average, picoplankton sized cells contributed significantly to the phytoplankton biomass (44%) in the Nation and the Omineca embayment, while in Manson and Clearwater the contribution of picoplankton was considerably lower (~28%) (Fig. 9). Picoplankton communities are typical of oligotrophic lakes (Stockner 1981) because the small cells have high surface area to volume ratios that allow them to efficiently scavenge nutrients when nutrient concentrations are low. When nutrient concentrations are low the small cells will have a competitive advantage over larger cells and will occur in greater abundance. In fact an examination of the nutrient data reveals that the average NO_3^- concentrations in Nation and Omineca embayments was 1.2 $\mu g \cdot L^{-1}$ which was much lower than 25.2 $\mu g \cdot L^{-1}$ of NO_3^- found in Manson and Clearwater embayments. Nitrate concentrations in Nation and Omineca are considering limiting to phytoplankton growth and therefore small cells will dominate.

A healthy contribution by nanoplankton was observed in all four embayments ranging from 35-57% of the total biomass (Fig. 9). The highest contribution by nanoplankton was seen in Manson embayment and the lowest was observed in Omineca embayment (Fig. 9). Microplankton on average contributed the least in all four embayment during each sampling trip. Approximately 18% of the biomass was accounted for by the large microplankton sized cells for all four embayments. Based on nutrient data, total biomass concentrations and the size distribution of the biomass, it appears that Nation and Omineca share many similar characteristics while Manson and Clearwater can be similarly grouped.

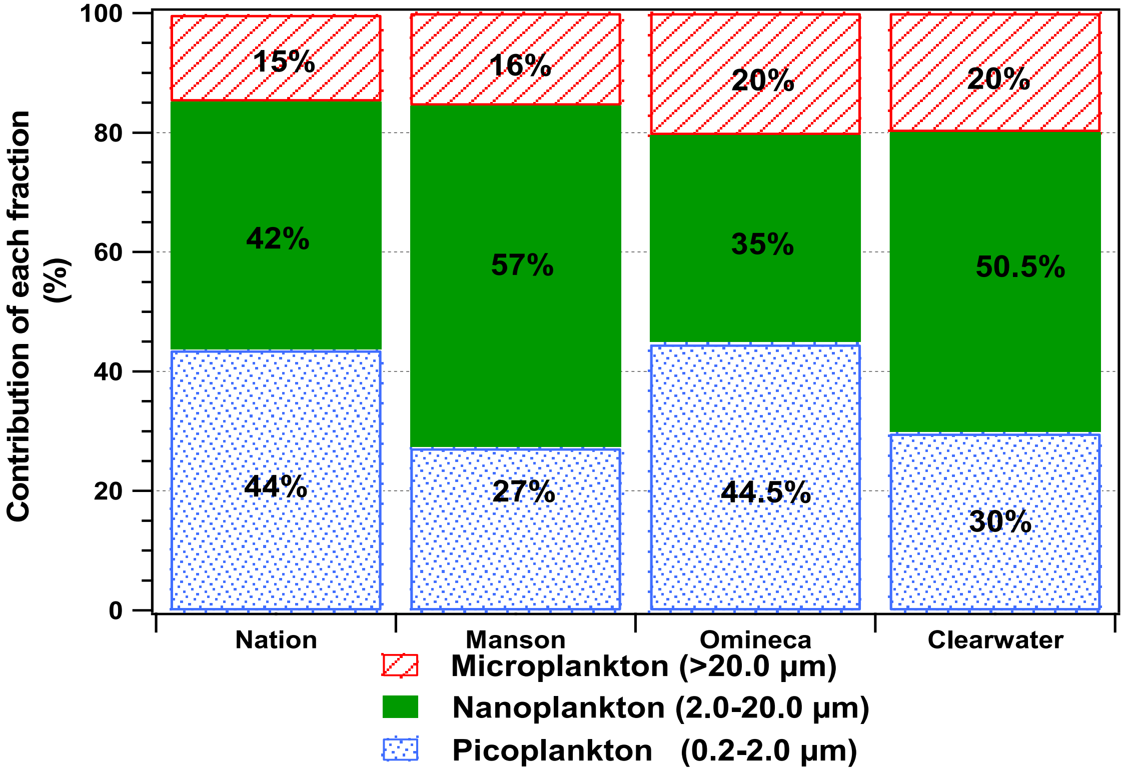

Figure 9. Relative contribution of picoplankton, nanoplankton and microplankton to chlorophyll in 2004. (mean of June, July and October values).

Taxonomy-Abundance and biovolume The most striking feature of phytoplankton abundance is the consistently low densities in all embayments, where cell densities never exceed 3,500 cells·ml^{-1} (Fig. 10). The densities that occurred in 2004 in the embayments were nearly 64% lower than the average phytoplankton densities (1999-2003) observed in oligotrophic Okanagan Lake, 5,469 cells·ml^{-1} (Stockner *in* Andrusak et al. 2004). Average phytoplankton population densities ranged from a high of 3,341 cells·ml^{-1} in Omineca embayment to a low of 2,520 cells·ml^{-1} in Manson embayment (Fig. 10). In fact phytoplankton density was 30% lower in Manson compared to Omineca embayment. Phytoplankton biovolume was also consistently low in all of the embayments, where biovolume was <0.35 mm^3·L^{-1} which was <50% of the biovolume observed in oligotrophic Okanagan Lake (Stockner *in* Andrusak et al. 2004). Phytoplankton biovolume was the highest in Nation embayment (0.35 mm^3·L^{-1}) largely due to the occurrence of dinoflagellates of the genus *Peridinium* spp and *Gymnodinium* spp in June.

The densities observed in the embayments were considerably lower (54%) than the calculated mean for the pelagic region of Williston Reservoir in 1999 and 2000 (Fig. 10). Despite lower densities in the embayments, the average phytoplankton biovolume in 2004 was equivalent to the average biovolume in the 1999 and 2000 pelagic region. This discrepancy between abundance and biovolume was caused by the prevalence of larger nanoflagellates in the 2004 embayment samples as opposed to the smaller picoplankton prevalent in the pelagic samples in 1999 and 2000.

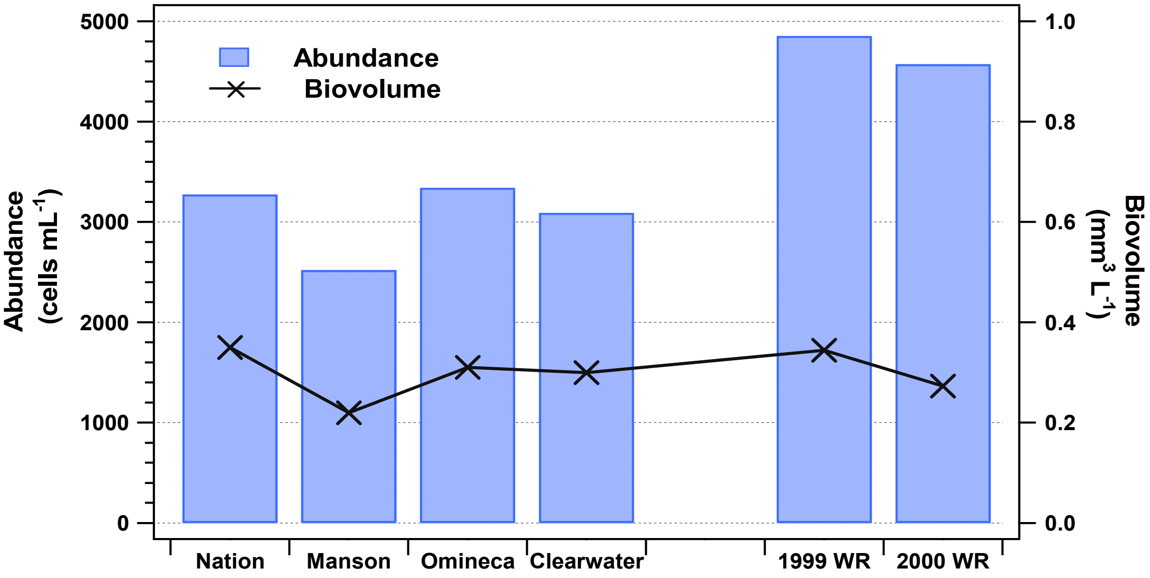

Figure 10. Mean epilimnetic phytoplankton abundance and biovolume in the embayments and pelagic of Williston Reservoir. (mean of June-October values)

There were no major peaks or blooms, and surprisingly little seasonal variation in either phytoplankton abundance or biomass in the embayments in 2004. There were also no consistent seasonal trends in the phytoplankton abundances in all of the embayments. Phytoplankton densities in Nation and Clearwater decreased as the growing season progressed (Fig. 11). Densities peaked early in the summer in June, decreased by approximately 36% in mid-summer and decreased again in the fall in October. This is in contrast to the seasonal pattern observed for Manson and Omineca embayments. In these embayments, cell numbers increased approximately 10% to a mid summer maximum in July and decreased 43% and 33% in Manson and Omineca in the fall. While it is possible that the June sampling trip occurred after the spring bloom it appears that either a fall bloom did not occur or it too was missed because of the low frequency of sampling. The characteristic bi-modal diatom peak that occurs in large, dimictic lakes after spring and fall mixing periods was not seen in the embayments in 2004 or in the pelagic zone of Williston Reservoir in 1999 and 2000, rather only mid-summer diatom, nanoflagellate and dinoflagellate increases were noted (Fig 12.).

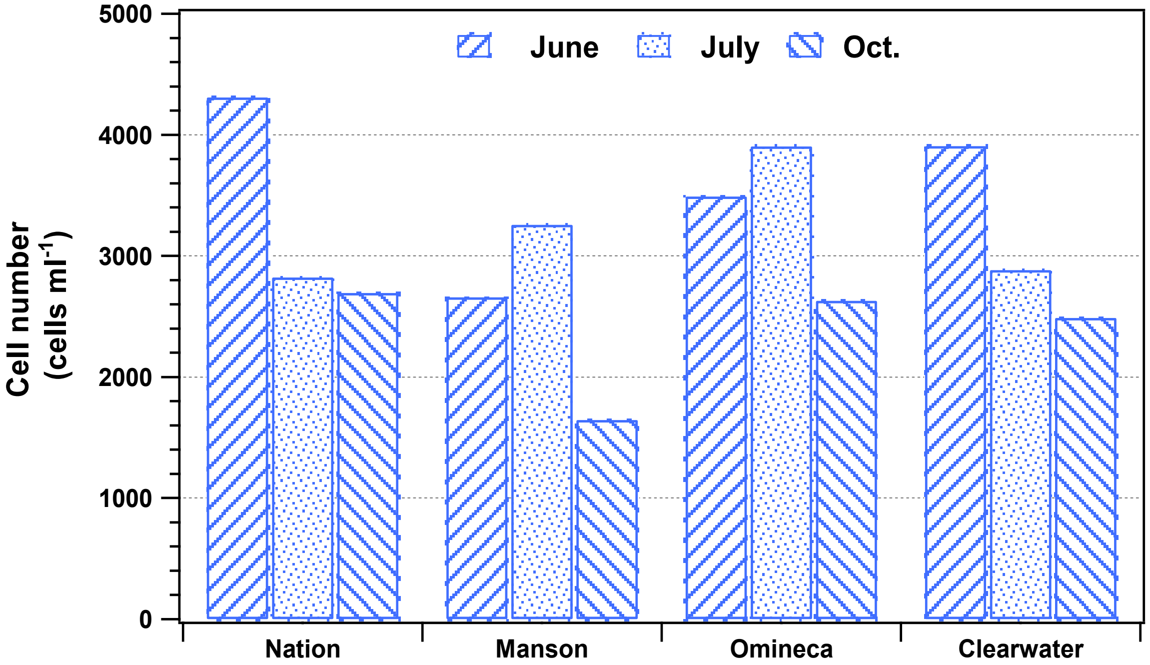

Figure 11. Seasonal abundance of epilimnetic phytoplankton community of the embayments of Williston Reservoir in June, July and October 2004.

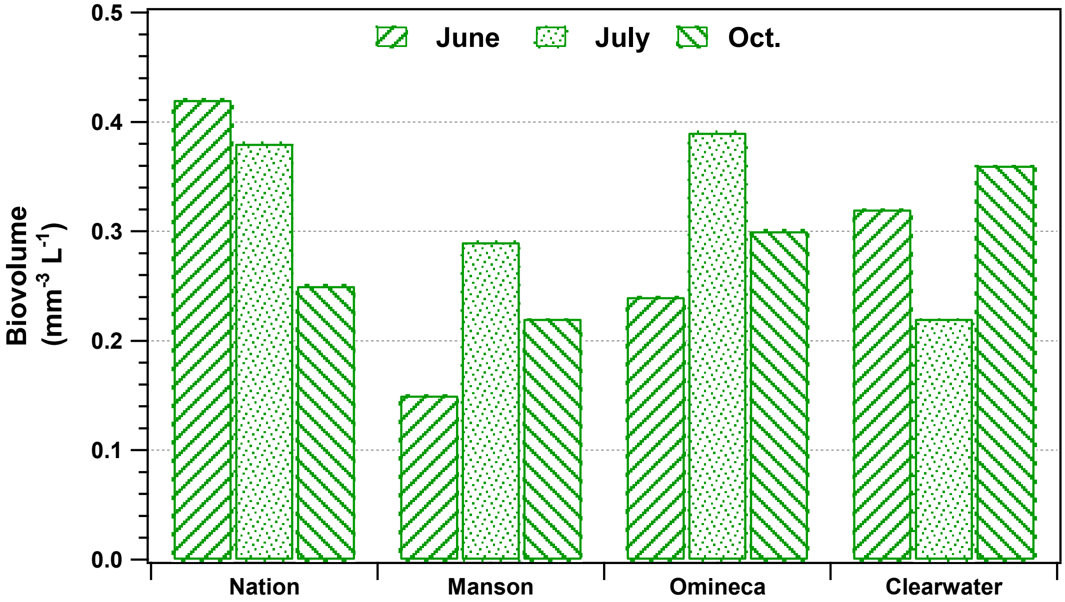

Figure 12. Seasonal biovolume of epilimnetic phytoplankton community of the embayments of Williston Reservoir in June, July and October 2004.

Generally the two seasonal patterns discussed above for cell abundances were apparent in the biovolume data with the exception of the October data in Clearwater, where a 68% increase in biovolume was observed in October relative to July (Fig. 12). Diatoms account for more than 46% of the biovolume and were entirely responsible for the increase in biovolume in the fall. The diatom community consisted of the *Asterionella formosa* var1, *Aulicoseira italica*, *Tabellaria fenestrate* and *Fragilaria crotonensis*.

Trends in Major groups Phytoplankton species assemblages were very similar among the four embayments (Fig. 13). Chrysophytes and Cryptophytes (nanoflagellates) were the dominant class at all stations followed closely by small pico-cyanobacteria (Cyanophytes), then diatoms (Bacillariophytes), dinoflagellates (Dinophytes) and finally green algae (Chlorophytes).

Cryptoflagellates and Chrysoflagellates account for 39% of the abundance and biovolume. There was also a great diversity of nanoflagellates ranging in size from 2-20 µm, and the most common genera were *Chromulina* spp., *Chrysochromulina* spp., *Chroomonas* spp., *Cryptomonas* spp., *Rhodomonas* spp., and *Dinobryon* spp.. This is in contrast to the dominate role of the Cyanophytes in the pelagic regions of the Reservoir in 1999 and 2000.

The second most common group in terms of abundance was the blue-green algae (Cyanophytes). In 2004, 35.6% of the abundance was accounted for by blue-green algae. The following genera were commonly observed in the embayments;

Synechococcus spp., *Oscillatoria* spp. *Lyngbya* spp. and *Anabaena cirinalis*. Minute *Synechococcus* spp. accounted >72% of the Cyanphyte abundances and due to their small size they make only a small contribution (5%) to total biovolume.

The third most common group in terms of abundance was the diatoms (Bacillariophyceae). In 2004, 18% of the total abundance and 27% of the biovolume were accounted for by the diatoms. The most common genera included *Asterionella formosa*, *Fragilaria crotonensis* var1*, Rhizosolenia* spp., *Aulicoseira italica*, *Tabellaria fenestrate*, and *Cyclotella* spp.

The fourth most common group in terms of abundance and biovolume were the dinoflagellates (Dinophyceae). In 2004, <4% of the total abundance and 27% of the biovolume were accounted for by the dinoflagellates The most common genera, *Peridinium* and *Gymnodinium* were present in all embayments, but were not common and they never attained large populations, but because of their large size they did make a significant contribution to biomass.

The least abundant and accounting for the least biovolume were the green algae (Chlorophytes). The most common genera observed were *Ankistodesmus* sp. *Chlorella* spp. and *Monoraphidium* spp. Though genera from this class were present in all four embayments they were never common. The list of phytoplankton species encountered in the 1999 and 2000 reservoir limnology study and this 2004 embayment study are provided in Appendix C.

Phytoplankton Vertical distribution Throughout the growing season in 2004 there was no clear trend in the vertical structure of phytoplankton population density or biomass among depths sampled - 1, 3, and 5 m. Generally the highest overall densities occurred at a depth of either 1 or 3 m with the exception at Manson and Omineca embayments in July and Omineca and Clearwater embayments in October where the highest abundance occurred at a depth of 5 m (Fig. 14). The highest overall abundance of phytoplankton (5,332 cells·ml^{-1}) occurred at Nation embayment at a depth of 3 m in June (Fig. 14). Clearwater embayment had the next highest overall abundance (5,261 cells·ml^{-1}) at a depth 3 m in June.

The most obvious examples of vertical structure in the embayments appears in Omineca in July where biomass is 2.6-fold higher at 5 m relative to the abundances at 1 m (Fig. 15). Vertical structure is also apparent in Clearwater embayment in June when biomass is almost 2-fold higher at 3 m than at 5 and in Nation embayment in June the abundances are 1.6-fold higher at a depth of 3 m relative to the abundances at 5 m.

In general there was no clear trend in the species composition throughout the water column in terms of abundance and biovolume.

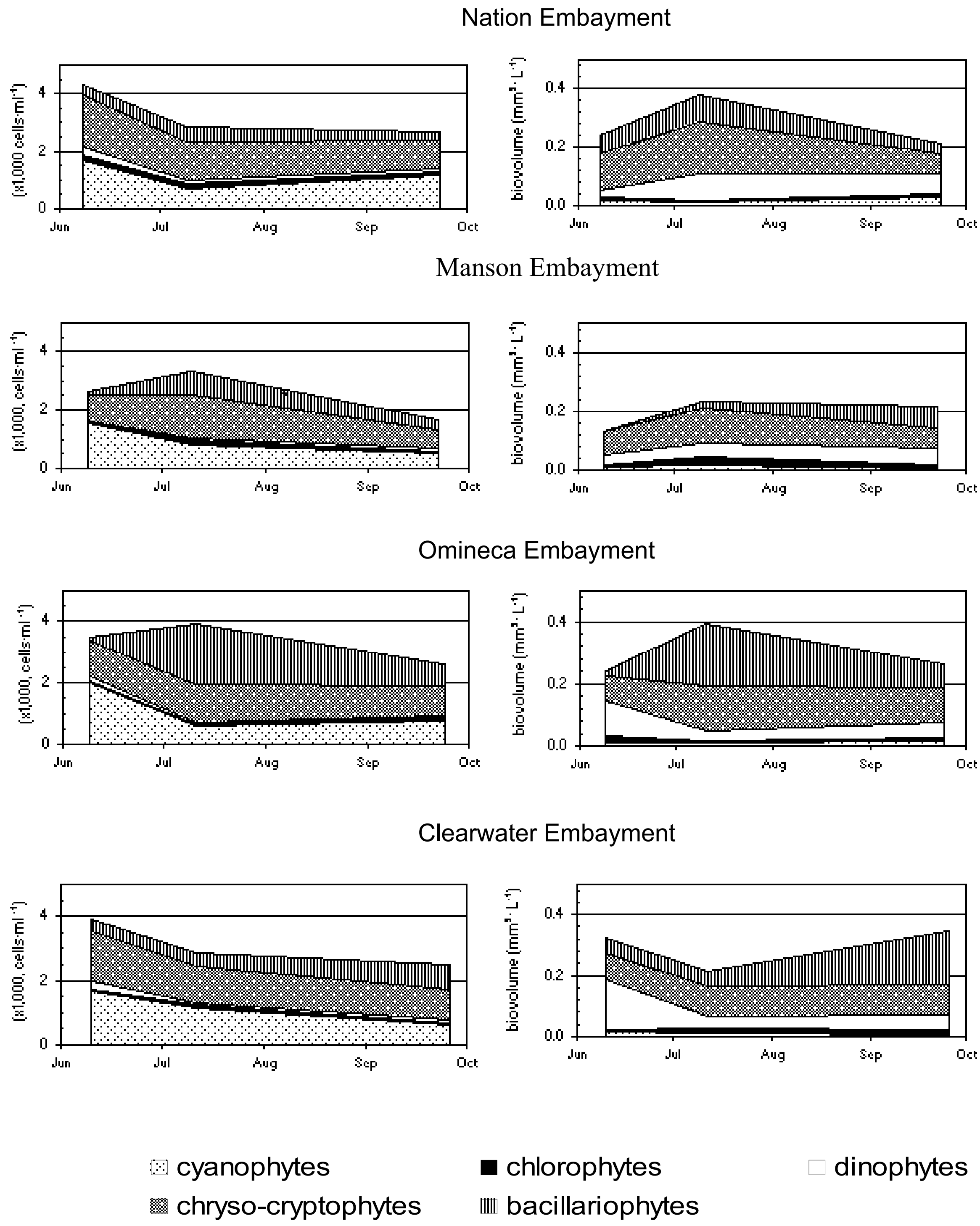

Figure 13. Seasonal abundance and biomass of the major phytoplankton classes in the embayments of Williston Reservoir, June-October 2004.

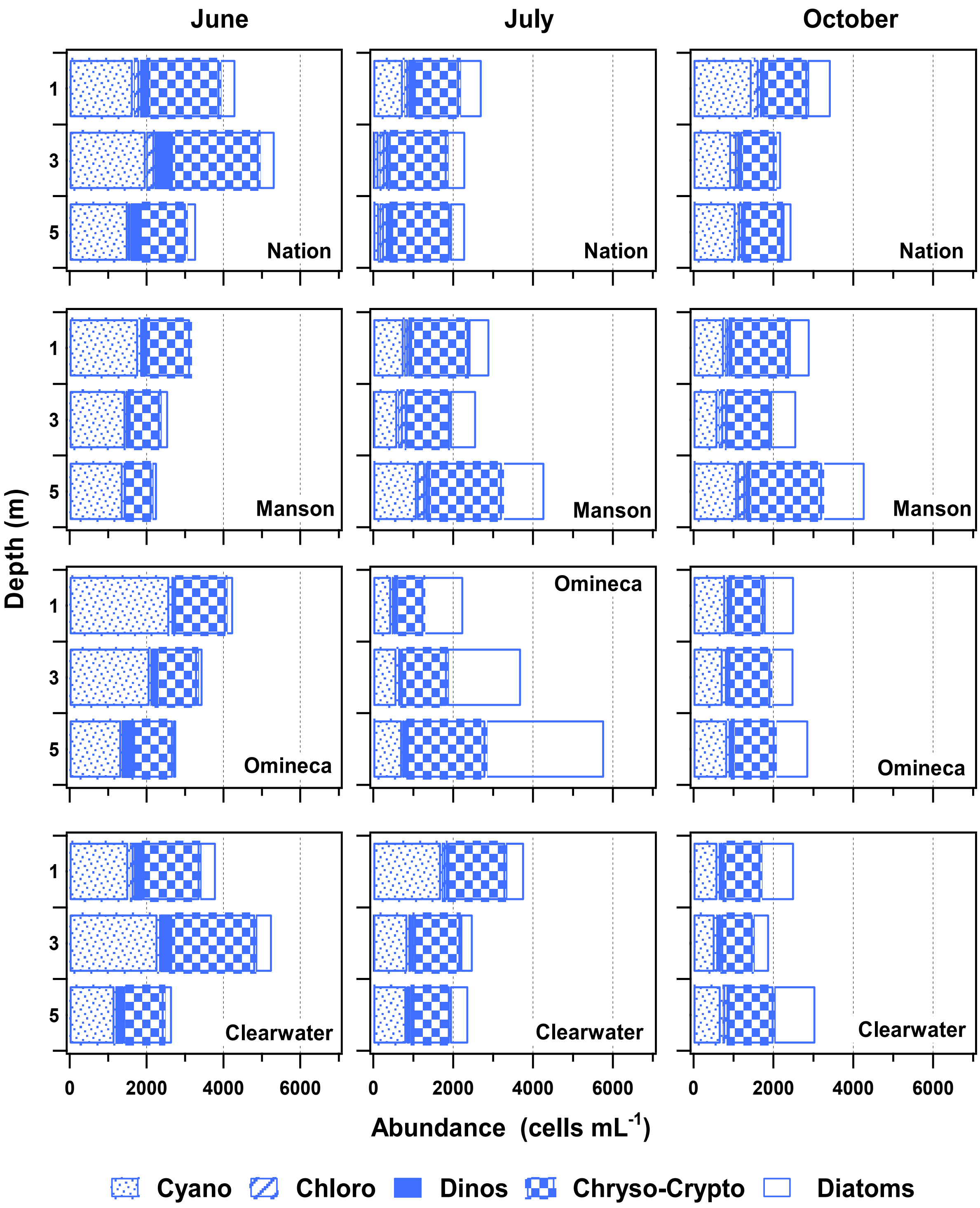

Figure 14. Vertical profiles of the density of the major phytoplankton classes in the embayments of Williston Reservoir in June, July and October 2004.

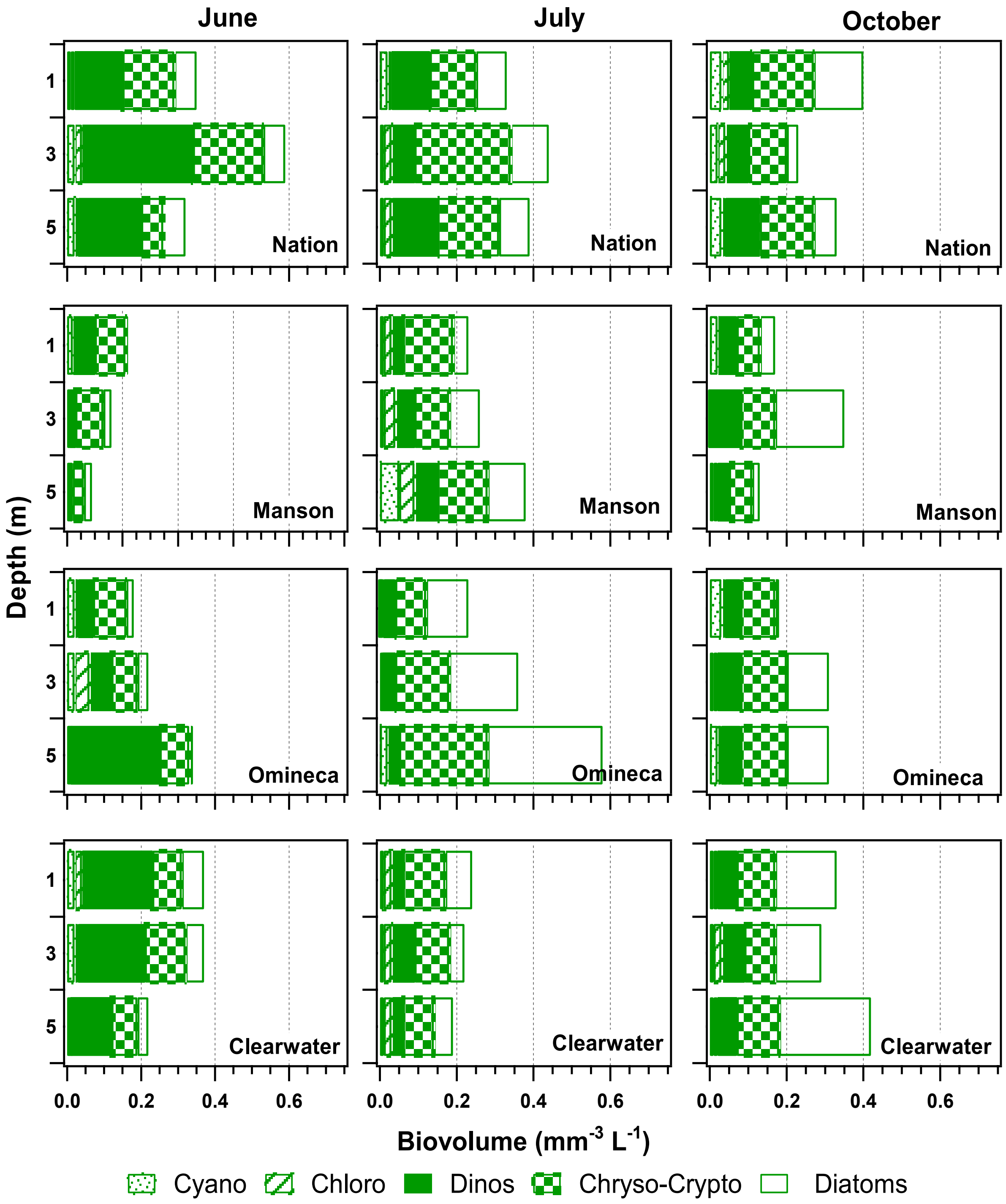

Figure 15. Vertical profiles of the biovolume of the phytoplankton classes in the embayments of Williston Reservoir in June, July and October 2004.

Primary Production

Primary productivity was consistently low in all four embayments (Fig. 16) and rates never exceeded 50 mg C m^{-2} d^{-1}. These rates fall at the lower end of the classification for ultra-oligotrophic lakes (Wetzel, 2001). This classification is further supported by the low TP concentrations, orthograde oxygen profiles and by low total biomass. The highest photosynthetic rates found in Omineca embayment (44.1 mg C m^{-2} d^{-1}) were 2.3-fold higher than the lowest rates that were observed in Manson embayment (19.2 mg C m^{-2} d^{-1}). The low rates of primary productivity in Manson embayment are likely due to a combination of light and phosphorus limitation. The Secchi depths were 0.8 m in June which was the shallowest measured of the four embayments. In terms of limiting nutrients, dissolved phosphorus in Manson was at or near the detection limits and the nitrate concentration was only slightly above concentrations considered limiting to phytoplankton growth.

Productivity was 18% higher and biomass was 13% higher in Omineca than in Clearwater. Examination of the nutrient data suggest that both embayments were limited by phosphorus but only Omineca was limited by NO_3^- availability. It is likely that the phytoplankton growth at least partly explains the low NO_3^- concentrations. Lower NO_3^- concentration in Omineca embayment was coincident with the occurrence of moderate populations of *Oscillatoria* spp. and *Anabaena* spp., nitrogen-fixing colonial blue-green algae.

On average the productivity of the embayments were similar to rates measured in the Reservoir in 2000. Productivity in Omineca embayment was approximately 28% higher than productivity in the Reservoir while the Reservoir production was 68% higher than Manson embayment (Fig. 16).

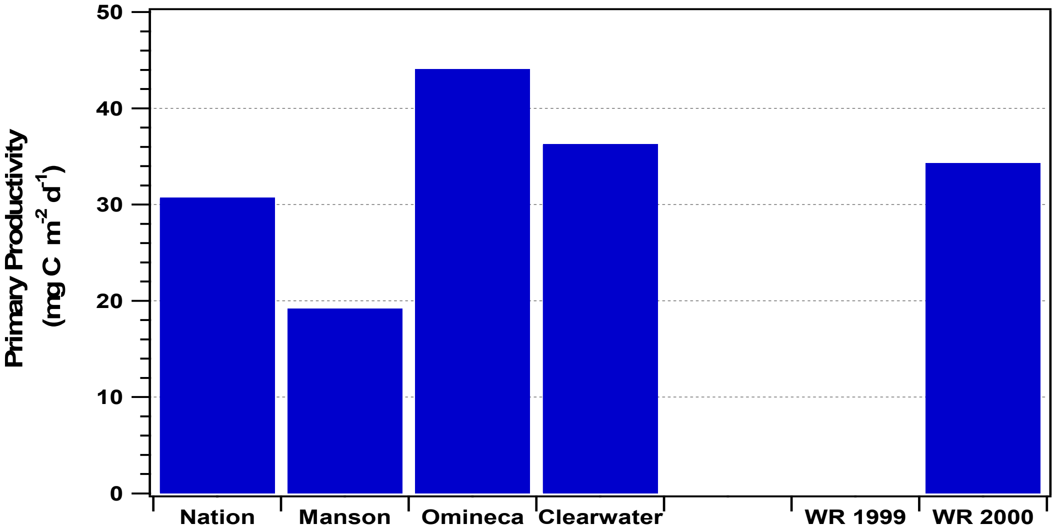

Figure 16. Depth integrated primary productivity (mg C m^{-2} d^{-1}) in July 2004 in the embayments of Williston Reservoir. Data was not collected in 1999.

Size fractionated Primary Productivity

In Nation and Manson embayments, nanoplankton production is clearly the greatest of the three fractions, followed by picoplankton and microplankton contributing approximately 24 and 19%, respectively (Fig. 17). These results show that the nanoplankton size fraction is indeed growing faster than the smaller (pico) and larger (micro) size fractions, albeit it is important to stress that all three fractions are growing at a very low rate. The picoplankton fraction was dominated by *Synechococcus* spp while the nanoplankton fraction was composed largely of small green algae and Chryso and Crypto-flagellates. The microplankton were the least productive fraction contributing less than 20% to the primary production

These results indicate that the size distribution of primary production of the embayments and the reservoir are clearly different. While the nanoplankton dominated the production of the embayments, in the Reservoir the picoplankton fraction was the most productive fraction (i.e. *Synechococcus* sp.), contributing about 45-55% to total production.

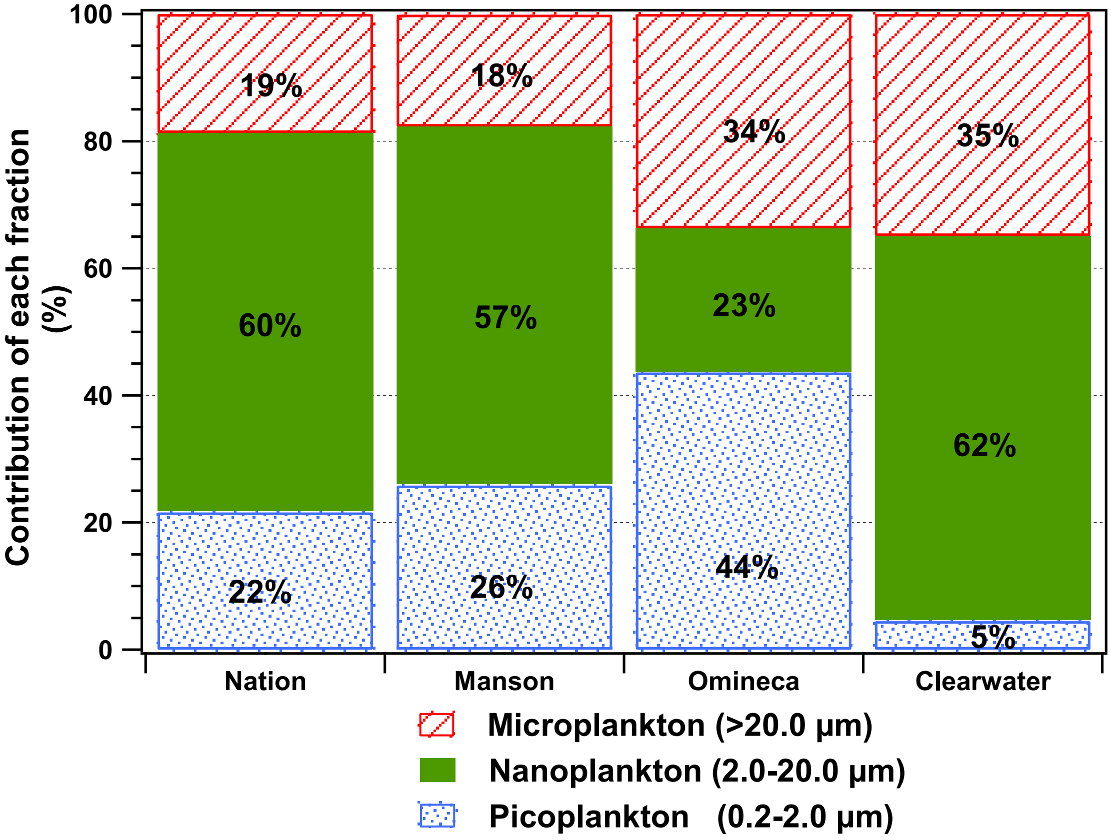

Figure 17. Relative contribution of picoplankton, nanoplankton and micro-phytoplankton to primary productivity in 2004.

The size distribution of primary productivity in the Omineca embayment was clearly different from the other embayments (Fig. 17) and it more closely followed the size distribution of the chlorophyll concentration where production was dominated by picoplankton > microplankton > nanoplankton. In Omineca embayment, nanoplankton accounted for only 23% of the total production which was more than 2-fold lower than in the other embayments. Picoplankton production in Omineca accounted for nearly 44% of the total productivity, which was nearly 2-fold higher than in Nation or Manson embayments and was followed closely by microplankton production (34%). This high contribution by microplankton was coincident with large populations of the large chain forming diatom *Asterionella* spp., which accounted for more than 50% of the phytoplankton cell abundance and biovolume. The high production by microplankton in Omineca embayment is in contrast to the results obtained for the Reservoir where the least productive fraction was microplankton contributing <10% to the total productivity.

Clear differences were also noted for the size distribution of productivity in Clearwater embayment (Fig. 17). The dominance of nanoplankton productivity in Clearwater embayment was similar to that observed in Nation and Manson embayments but the near 2-fold increase in microplankton productivity and the near 5-fold decrease in picoplankton productivity were striking.

***Production to biomass ratio (P/B*).** The P/B ratio, sometimes called the 'assimilation efficiency' provides a snapshot of the rate of C production per unit of phytoplankton biomass (chlorophyll), i.e. how many mg C are produced by a mg of chlorophyll per unit time (hrs, days). Also a major source of variation in primary productivity rates is related to the amount of biomass hence normalization of production rates by biomass should reduce the variance. The most efficient production in the embayments of Williston Reservoir was at Omineca where P/B=3.9 and the next highest was found at Clearwater where P/B=3.3 (Table 3). Considering the light and nutrient limitation found it is not surprising that the least efficient assimilation rate was observed in Manson embayment. These rates found for the embayments were similar to those found in the Reservoir where on average P/B= 3.4

Zooplankton

Species Seven calanoid copepod species have been identified in the embayments of Williston Reservoir. *Leptodiaptomus ashlandi* (Marsh) and *Leptodiaptomus pribilofensis* (Juday & Muttkowski) had high densities during the whole sampling season. *Epishura nevadensis* (Lillj.) was present in samples from June to October but in considerably lower number, while *Heterocope septentrionalis* (Juday & Muttkowski) was present only in June and July. *Leptodiaptomus sicilis* (Forbes), *Acanthodiaptomus denticornis* (Wierzejski) and *Aglaodiaptomus leptopus* (Forbes) were seen only occasionally. Six cyclopoid copepod species were observed in 2004. *Diacyclops bicuspidatus thomasi* (Forbes), *Diacyclops scutifer* (Sars) and *Cyclops vernalis* (Fischer) were common in samples during the sampling season, while *Eucyclops speratus* (Lilj.), *Macrocyclops albidus* (Jurine) and *Mesocyclops sp* were also observed, although rarely. For a complete list of all species found see Appendix C.

Fourteen species of Cladocera were present in the embayments during the studied period. *Daphnia galeata mendotae* (Birge), *D. pulex* (Leydig), *D. longiremis* (Sars), *D. rosea* (Sars), *D. schoedleri* (Sars), *Diaphanosoma leuchtenbergianum* (Fischer), *Eubosmina longispina* (Leydig), *Holopedium gibberum* (Zaddach) and *Leptodora kindtii* (Focke) were common during the sampling season, while *Leydigia leydigi* (Schoedler), *Sida crystallina* (O.F.M.), *Acroperus harpae* (Bird), *Biapertura affinis* (Leydig) and *Chydorus sphaericus* (O.F.M) were observed sporadically.

Leptodiaptomus spp, *Diacyclops* spp. and *Daphnia* spp. were not identified to species for density counts. Eleven Rotatoria species were identified in samples: *Asplanchna sp., Chromogaster sp., Euchlanis sp., Keratella cochlearis, K. quadrata, Kellicottia sp., Pleosoma sp., Polyarthra sp., Synchaeta sp., Trichocerca sp. and Trichotria sp.* The large mesh size (80 µm) only captured a portion of the Rotatoria community in Williston Reservoir, and will not be discussed in this report.

Zooplankton - Density and Biomass

Zooplankton populations in the embayments were numerically dominated by copepods, which averaged 94% of the 2004 combined embayment population (Fig. 18). Copepods were comprised of calanoids and cyclopoids. Calanoids were the dominate copepod in all embayments with exception in the Nation embayment where cyclopoids comprised over 80% of the individuals counted. *Daphnia* comprised 5%, while cladocerans other than *Daphnia* comprised just 0.6%. Copepods were the most abundant zooplankter in all embayments in 2004. Copepods dominated during the whole sampling season, with populations peaking in July. On a biomass ($\mu g \cdot L^{-1}$) basis, *Daphnia* comprised a notably larger component of the overall populations in Nation and Omineca embayments, and were relatively equal with copepod biomass in Clearwater embayment. Corresponding with a numeric near-absence of individuals, *Daphnia* comprised only 4% of total biomass in Manson embayment.

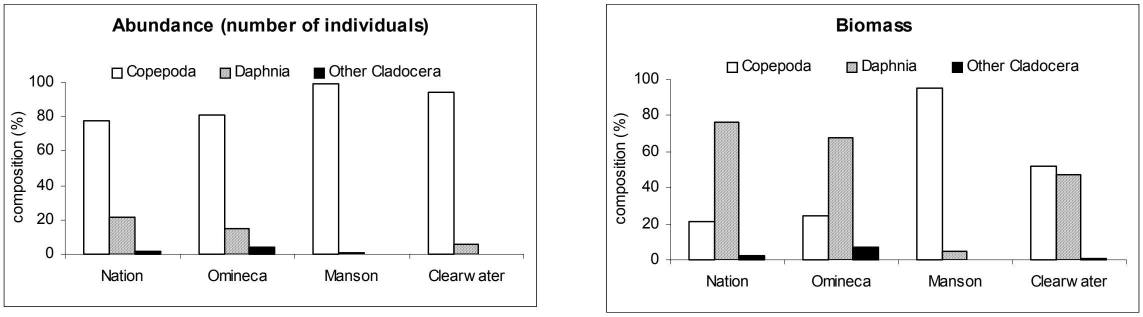

Figure 18. Seasonal average density and biomass composition of zooplankton in the embayments of Williston Reservoir, 2004.

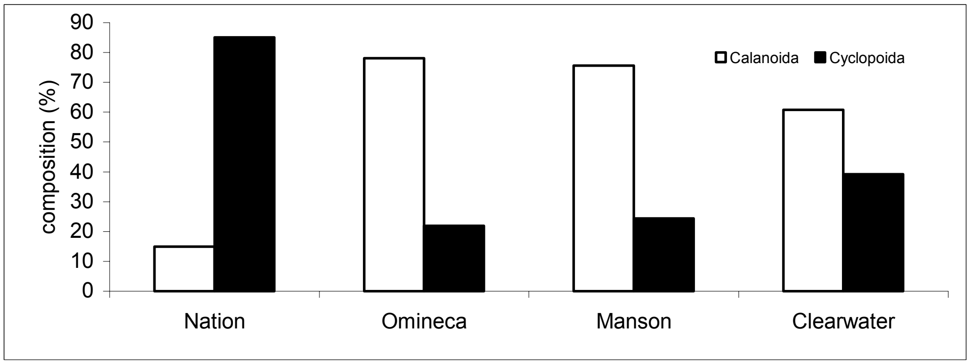

Figure 19. Copepod composition analysis (calanoid and cyclopoida components).

The seasonal average zooplankton abundance (density) in the embayments (June to October 2004) was 7.0 individuals·L^{-1} compared to 6.5 and 5.8 individuals·L^{-1} in 1999 and 2000 at the pelagic stations. The slight increase in density in the embayments was the result of an increase in Copepods, while *Daphnia* spp. and other Cladocera abundance decreased significantly compared to the pelagic stations. Zooplankton density was highest in the Clearwater and Manson embayments averaging 12 individuals·L^{-1} while zooplankton densities were lowest in Nation and Omineca embayments at 2 individuals·L^{-1}. The higher densities in Clearwater and Manson embayments are almost exclusively due to an order of magnitude increase in copepod populations (Table 5).

Table 4. Annual average zooplankton density (# individuals L^{-1}**) in Williston Reservoir, 1999-2004.**

	Nation	Manson	Omineca	Clearwater	Embayment stations 2004	Pelagic stations 1999	Pelagic stations 2000
Total	2.03	11.93	1.96	12.10	7.01	6.50	5.78
Copepoda	1.57	11.82	1.59	11.37	6.59	5.82	5.10
Daphnia	0.43	0.08	0.30	0.70	0.38	0.61	0.64
other Cladocera	0.03	0.03	0.07	0.03	0.04	0.07	0.04

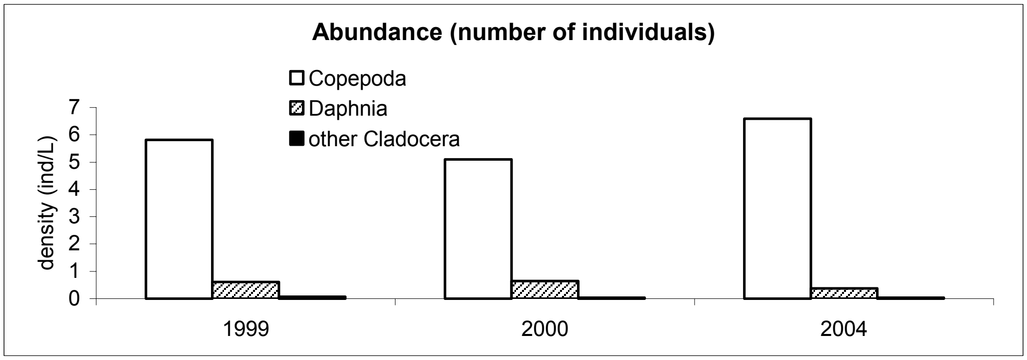

Figure 20. Average annual zooplankton density in the embayments of Williston Reservoir, 1999-2004.

Zooplankton biomass in all categories in the embayment stations in 2004 was less than the biomass found in the Reservoir pelagic stations in 1999 and 2000. Zooplankton biomass was 18.9 μg·L^{-1} compared to pelagic stations of 21.9 μg·L^{-1} and 23.5 μg·L^{-1} in 1999 and 2000 respectively. The decrease of total zooplankton biomass was due to a large decrease in the biomass of *Daphnia* spp. *Daphnia* spp. made up 45%, 45% and 39% of the total zooplankton biomass in 1999, 2000 and 2004 respectively. Zooplankton biomass was highest in the Clearwater embayment (30.9 μg·L^{-1}), followed by Manson embayment (25.9 μg·L^{-1}). Nation (9.9 μg·L^{-1}) and Omineca (8.9 μg·L^{-1}) embayments had the lowest biovolumes.

Table 5. Annual average zooplankton biomass (μg·L^{-1}) in Williston Reservoir, 1999-2004.

	Nation	Manson	Omineca	Clearwater	Embayment stations 2004	Pelagic stations 1999	Pelagic stations 2000
Total	9.93	25.85	8.90	30.91	18.90	21.9	23.5
Copepoda	2.12	24.63	2.20	16.08	11.26	11.7	12.5
Daphnia	7.58	1.13	6.05	14.51	7.32	10.0	10.8
other Cladocera	0.23	0.09	0.65	0.32	0.32	0.2	0.2

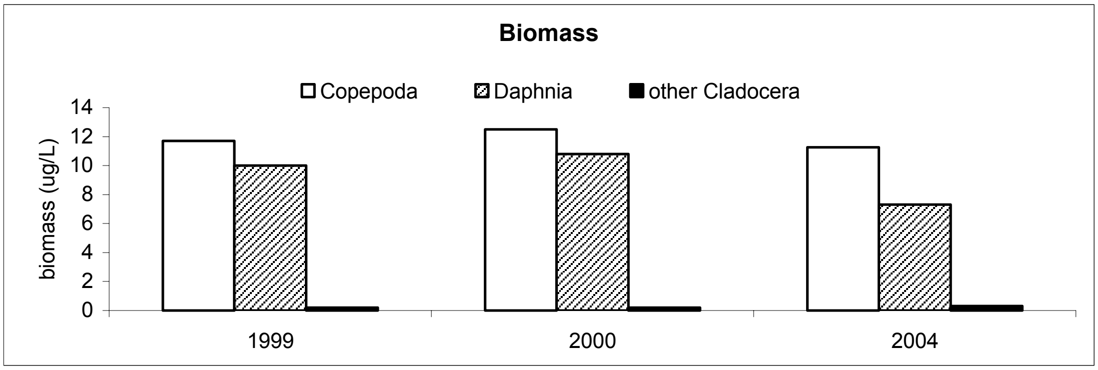

Figure 21. Average annual zooplankton biomass in Williston Reservoir, 1999-2004.

The largest zooplankton population was seen in June at the Manson embayment site (15.88 individuals·L^{-1}), while in July and August the most numerous populations were at the Clearwater embayment site (15.56 and 9.34 individuals·L^{-1}). *Daphnia* spp. were present during each sampling trip with the highest density occurring in July at the Clearwater embayment with 1.43 individuals·L^{-1} and biomass of 26.12 μg·L^{-1}, which accounted for 56% of the total biomass. It is interesting that *Daphnia* was present in all samples collected at Clearwater embayment, and that in July *Daphnia* has the highest density and biomass, while in previous years *Daphnia* spp. was rarely seen at the pelagic Clearwater station located only 5 km north in the Peace Reach of the Reservoir.

Data comparisons with 1999 and 2000 seasons should be used with extreme caution. The 2004 seasonal average values of zooplankton abundance (density) and biomass are calculated for samples collected in June, July and October at four relatively shallow embayment stations Nation, Manson, Omineca and Clearwater. In 1999 and 2000 the sampling season started in May, extending on a monthly basis through to November at five deep open water Reservoir stations (Finlay Reach, Parsnip Reach, Peace Reach-2 stations, and Junction-mid reservoir).

Fecundity

Fecundity data was collected from the two common copepods and for a cladoceran. The proportion of gravid (egg bearing) females was the highest in *Leptodiaptomus spp.* population which averaged 0.30 over the sampling season (Table 7). *Diacyclops* spp. and *Daphnia* spp. populations had a lower proportion of gravid females, which averaged 0.24 and 0.17. The seasonal average number of eggs per gravid female for these three populations were 6.10, 24.81 and 3.02 respectively. Across the sampling season the number of eggs per litre of water averaged 0.11, 2.10 and 0.15 eggs·L^{-1}. The number of eggs per capita averaged 0.09, 1.75 and 0.53 eggs·individual^{-1} over the same period. In the October samples of all four embayments a large number of *Daphnia* ephippium were observed.

Table 6. Fecundity data for copepod *Leptodiaptomus* spp. and *Diacyclops* spp. and for the cladoceran *Daphnia* spp. of Williston Reservoir embayments, 2004.

	Leptodiaptomus spp.	*Diacyclops* spp.	*Daphnia* spp.
Proportion of gravid females	0.30	0.24	0.17
# Eggs per gravid Female	6.10	24.81	3.02
# Eggs per Litre	0.11	2.10	0.15
# Eggs per Capita	0.09	1.75	0.53

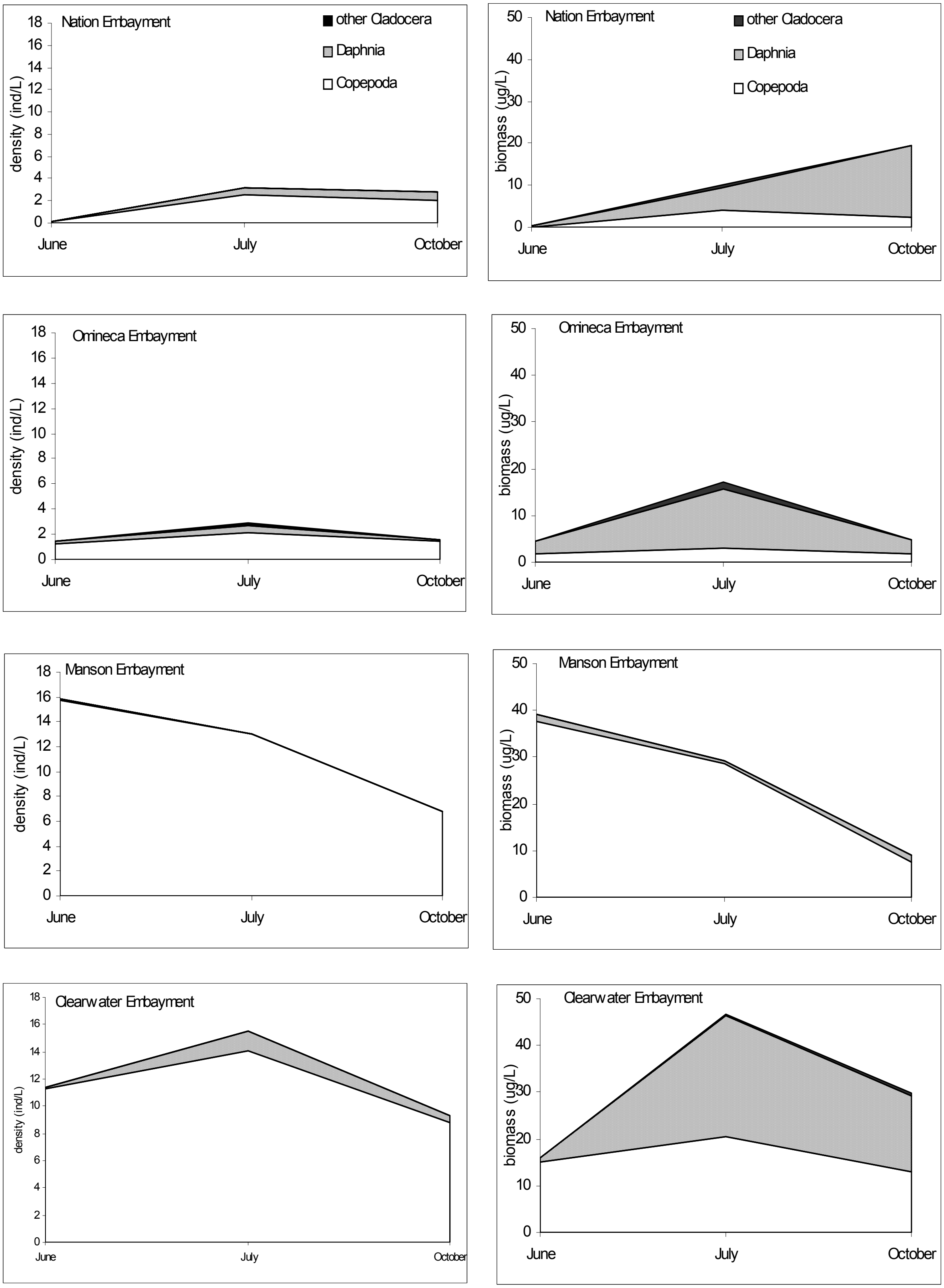

Figure 22. Density and biomass of cladoceran and copepod zooplankton in Williston Reservoir embayments, June-October 2004.

DISCUSSION

General

Williston Reservoir, by nature of its impoundment of three river systems over 30 years ago created a complex reservoir system with many large embayments. The significance of the embayments to the ecology of the pelagic zone in the Reservoir is not presently known. Selection of four embayments for detailed limnological studies was based on the available fish habitat information and fish species presence information. In addition owing to Williston's large size, logistical implications were considered when selecting the 4 embayments. The discussion to follow will focus first on each embayment separately presenting the key limnological features and suggested causes for differences.

Nation Embayment

The Nation Embayment is the most southerly of the four embayments and was the third largest embayment examined in this study. It is located approximately half way up the west side of the Parsnip Reach. The epilimnion was poorly defined in June, July or October. The July sampling trip occurred during an extended period of hot ambient temperatures and surface temperatures of Nation embayment reached a high of 21°C. Secchi disk depths were on average 3 m. Phytoplankton biomass and biovolume were the highest of the embayments studied. Nation embayment had the highest phytoplankton biomass, as measured by chlorophyll *a,* and the 3rd highest rates of primary productivity. Phytoplankton biomass was 12.5 $mg \cdot m^{-2}$, productivity was 30.7 $mg\ C\ m^{-2}\ d^{-1}$ and both parameters were dominated by nanoplankton. Despite high nanoplankton production, the preferred food source of herbivorous zooplankton, zooplankton levels are the 3rd lowest. Kokanee may occur in the embayment because adult spawners have been observed upstream in the Nation River but abundance of kokanee is currently unknown therefore grazing pressure on herbivorous zooplankton by kokanee cannot be determined. However, relative kokanee escapements to Nation River have averaged <1,000 spawners since 2002. While the ranking of variables for the assessment of production capacity for the top three embayments was very close, Nation embayment ranked as the 3rd most productive system.

Manson Embayment

Manson embayment is situated north of the Nation embayment and it flows into the Parsnip Reach. Manson was poorly stratified with a weakly defined epilimnion. One of the most striking features of the Manson embayment was the high turbidity accompanied by the highest TDS concentrations of the four embayments. Manson embayment was the most turbid embayment studied and *in situ* light levels are potentially limiting to photosynthesis. The Secchi depth averaged just 1.7 m, but ranged from 0.8 m in June to 2.1 m for the remainder of the growing season. Photoautotrophic phytoplankton rely on light as the sole energy source, light is necessary for various metabolic processes including nutrient assimilation and for growth. In addition to high light attenuation, the mixed layer depth was greater than the euphotic zone throughout the growing season. The base of the euphotic zone is called the compensation depth where gross daily photosynthetic productivity balances phytoplankton respiratory losses. Above the compensation depth, net productivity is positive i.e. a cell will grow, but below this depth net productivity is negative and the respiratory losses will be greater than the photosynthetic growth and consequently the cell will die. For instance, in July the euphotic depth was at approximately 5 m water depth but the mixed layer extended down to 12 m. This has dire consequences for a phytoplankton cell as it is mixed from the surface where light is sufficient for growth to deep in the water column where light is not adequate to support growth and in fact in July, because the mixed layer depth was twice as deep as the euphotic zone a phytoplankton cell would spend an equal amount of time in the dark as it did in the light. The consequence of the light limitation is seen in the phytoplankton biomass and in the rates of production in Manson embayment as they were both the lowest of the embayments studied. Phytoplankton biomass was 8.9 mg Chl m^{-2} and productivity was 19.2 mg C m^{-2} d^{-1} and was dominated by nanoplankton. Not surprising the assimilation ratio in Manson is the lowest of the four embayments. In addition to the chronic light limitation, nutrient limitation was also observed. Dissolved phosphorus concentrations were limiting during each sampling trip and dissolved inorganic nitrogen was limiting during June and July. The phytoplankton community was dominated by flagellates and small autotrophic cyanobacteria such as *Synechococcus* sp. Overall Manson ranked 4th or last, and was the least productive embayment in Williston Reservoir. This embayment generally ranked 3rd or 4th for all parameters classified with the exception of high zooplankton abundance and biomass where the embayment ranked 2nd. While kokanee spawners have varied from zero to 6,000 between 2002 and 2005 in Manson River, it is not known if kokanee use the embayment as a rearing habitat.

Omineca Embayment

Omineca embayment is located north of Manson embayment and it flows into the southwest end of the Finlay Reach. Omineca embayment was the largest embayment studied and was the only embayment studied that flowed into Finlay Reach. The epilimnion was poorly defined in June but in July the epilimnion depth was 6 m which was less than the euphotic zone which was 8 m deep. Omineca embayment is clearly the most productive embayment examined in this study. Phytoplankton biomass, primary productivity and phytoplankton abundance in Omineca were the highest of the four embayments. Although this was the most productive embayment studied, it appears that phytoplankton production is limited by nutrient availability. Phosphorus and NO_3^- were below detection limits, with a N:P ratio less than 1, which suggests severe nitrogen limitation. The low NO_3^- concentrations were coincident with the occurrence of moderate populations of nitrogen-fixing colonial blue-greens however the phytoplankton community was still on average clearly dominated by small minute *Synechococcus* sp. cells. It should be noted that the community structure is similar to the that found in the pelagic regions of the Reservoir but is in contrast to that found for the other embayments where nanoplankton were the most productive fractions. A notable exception to the prevalence of picoplankton in Omineca was observed in July where the phytoplankton community was instead dominated by diatoms, specifically *Asterionella formosa* var1. Despite high abundances of primary producers, primary consumers were very low. Zooplankton biomass and abundances in

Omincea embayment were the lowest observed in this study. It is possible that this trophic level is controlled by top down effects as phytoplankton and zooplankton production appears to be uncoupled. Estimates of kokanee spawners for this embayment are not available but aerial counts show more than 90% of Williston Reservoir kokanee spawners use Omineca River, with more than 100,000 kokanee spawners returning to the river each year since 2003. The high production capacity and large surface area suggest that this embayment has the highest fish rearing capacity of all the embayments studied.

Clearwater Embayment

Clearwater embayment, that flows into Peace Reach, was the smallest embayment studied. The lowest epilimnion temperatures were recorded in Clearwater in June, July and October. It is unlikely that production was limited by light as the Secchi depth was nearly 4 m deep and the mixed layer depth was 7 m which was shallower than the euphotic zone depth at 7.5 m. As was seen for the other embayments, phosphorus limitation of phytoplankton growth was apparent during all three sampling trips. Phosphorus limitation is also supported by high N:P ratios (~14) in the embayment. Nitrogen concentrations were generally above concentrations considering limiting to phytoplankton growth with exception in June where nitrogen limitation was observed. The highest total zooplankton densities and biomass occurred in Clearwater embayment, as did the highest *Daphnia* densities and biomass. *Daphnia* are the preferred food source for kokanee salmon (Thompson, 1999). We suggest that high *Daphnia* populations are due to favorable “bottom up” and “top down” effects. Favorable bottom up effects are suggested because nanoplankton (2.0-20.0 μm) are considered to be the main size fraction of phytoplankton consumed by herbivorous zooplankton (Leibold, 1989), and this study has shown that nanoplankton primary production is high in Clearwater embayment, which would support high *Daphnia* production. In addition, low grazing pressure (top down control) on *Daphnia* in Clearwater embayment is also suggested because of the absence of or low populations of juvenile and kokanee spawners and other planktivores in the reservoir such as Lake Whitefish. No kokanee have been observed in Clearwater embayment during annual helicopter based escapements surveys initiated in 2001. The high *Daphnia* populations can also have a positive impact on phytoplankton. Grazing of phytoplankton by *Daphnia* spp. releases dissolved nitrogen and phosphorus into the water column leading to efficient nutrient recycling (Elser, 1990). This efficient nutrient recycling supported by high herbivorous zooplankton could partially explain why Clearwater was the 2nd most productive embayment studied and why despite high primary productivity and relatively high biomass, the nitrogen levels were not depleted. Clearwater embayment scored 2nd in the ranking of productive capacity but due to the small size of the embayment, just 350 ha, the total potential rearing capacity is much lower than Omineca embayment.

Nutrients and Trophic State

Phytoplankton growth and species composition can be controlled by the availability of nutrients. For example, it is well established that nutrient load and productivity are correlated linearly (Vollenweider 1976, Schindler 1978), such that increased loading leads to higher productivity in the lake. Of the many micro and macronutrients necessary for growth, it has traditionally been demonstrated that in lakes phosphorus was limiting to phytoplankton growth but it is now well established that phosphorus and/or nitrogen can limit phytoplankton production in freshwater systems (Hecky and Kilham 1988). Liebig's Law of the Minimum states that the element present in the lowest concentration relative to its demand is the limiting element. Therefore, as stated, only one element can be limiting at any one time but there are several studies that have shown both P and N deficiencies where co-limitation of phytoplankton communities exists (Suttle and Harrison 1988, Elser et al. 1990, Davies et al. 2004). This apparent discrepancy is resolved by noting that Liebig's limitation relates to limitation of the maximum standing stock or yield whereas the second type of limitation relates to limitation of instantaneous growth rates. This distinction is important to understanding the phytoplankton dynamics in a lake or reservoir. The identification of nutrient limitation and the identification of the factor or factors limiting productivity are important in our understanding of the ecology of Williston Reservoir.

Typically nutrient ratios (or elemental ratios) of phytoplankton or of the water that phytoplankton grows in, have been used to identify the factor limiting phytoplankton growth. Phytoplankton typically take up nutrients according to Redfield ratios of 106 Carbon:16 Nitrogen:1 Phosphorus and although nutrient ratios have been shown to deviate from classical Redfield ratios (Hecky et al. 1993, Falkowski 2000) and are affected by other variables besides nutrients, they can still be used as a tool to evaluate nutrient limitation, particularly Liebig's limitation. N:P ratios in the Nation and Omineca embayments of Williston Reservoir are <1 which suggests severe nitrogen limitation. Unfortunately, data is not available on the turnover rate of nitrogen or phosphorus which is necessary for clearly understanding the role of nutrients in the embayments. N:P ratios are higher in Manson and Clearwater embayments, between 11-14, which is more similar to the pelagic zone and the ratios indicates either nitrogen, phosphorus, or nitrogen and phosphorus limitation.

However, ratios alone can be misleading. For example, a N:P =10 could be due to a) N=100 $\mu g \cdot L^{-1}$ and P=10 $\mu g \cdot L^{-1}$ or b) N=10 $\mu g \cdot L^{-1}$ and P=1 $\mu g \cdot L^{-1}$. Obviously the growth of phytoplankton is not limited or even stressed for nutrient concentrations in scenario A but eventually as phytoplankton grow they will *eventually* become nitrogen limited in scenario A. Therefore it is important to examine the absolute concentrations of nutrients in the water, not just the ratios. Phosphorus concentrations in the embayments are generally at detection levels in all four embayments from June-October. This is in contrast to ~4 $\mu g \cdot L^{-1}$ in the pelagic zone of the Reservoir. Nitrogen concentrations in both Nation and Omineca embayments were generally less than 3 $\mu g \cdot L^{-1}$ for June, July and October, which suggests nitrogen limitation. As suggested by dissolved nutrient concentrations, it appears that the phytoplankton community is co-limited by phosphorus and nitrogen in Nation and Omineca and limited by phosphorus only in Manson and Clearwater embayments. During summer stratification biological activity can drawdown nutrient concentrations in the epilimnion to below detection levels and because the first sampling trip was completed in June it is not known if low concentrations in June are due to biological activity or due to low nutrient loading. The high cell densities and high productivity in the two embayments with the low nitrogen concentrations suggest that biological activity is responsible for the low nitrogen concentrations but further sampling is necessary to confirm this hypothesis.

Silicic acid was measured in the four embayments and although concentrations are well above levels considered limiting to phytoplankton growth, drawdown was noted in July in Omineca embayment. Silica is used primarily in the formation of the frustule of diatoms and the taxonomic data shows that in July diatoms populations in Omineca embayment increased over 19-fold to 1,942 cells·L^{-1}, where they accounted for nearly 50% of the cell densities and biovolume. It is interesting that diatoms dominated the phytoplankton community in Omineca embayment because typically diatoms thrive in nutrient replete regions as opposed to the severe nutrient limitation observed in Omineca embayment. Omineca is a large embayment with a long fetch and it is possible that a wind storm mixed the water column a few days preceding the July sampling trip, replenishing the surface nutrients, allowing diatoms to thrive. Nitrogen or phosphorus deficient cells exhibit rapid nutrient uptake kinetics and often when nutrients are limiting the maximum uptake rate is faster than is needed to support growth. It is likely that once stratification reestablished, nutrients were quickly depleted and high biomass and high rates of production were achieved.

Production

Primary productivity is the rate of formation of new organic material by phytoplankton and autotrophic bacteria over a period of time. Primary productivity measurements, unlike biomass measurements that are confounded by losses such as grazing, sinking and transport, allow for a direct assessment of the "health" of the system. Production in the embayments of Williston Reservoir is extremely low, rates never exceed 50 mg C m^{-2} d^{-1} which are some of the lowest rates recorded to date (Table 7). The embayments are classified as ultra-oligotrophic (Wetzel, 2003), as is the pelagic zone of Williston Reservoir (Stockner et al. 2005). Production in the embayments is significantly lower than the production rates of Arrow Reservoir, Kootenay Lake or even Alouette Reservoir (Table 7) and are more in line with values from ultra-oligotrophic coastal lakes (Stockner 1981, 1987). Slocan Lake, BC, an ultra-oligotrophic lake in the Kootenay region is nearly 2-fold more productive than Williston Reservoir. Nutrient or light limitation or both are likely responsible for the low rates of production. Nitrogen and phosphorus are likely limiting in Nation and Omineca embayments while phosphorus is likely limiting in Manson and Clearwater embayments. Light limitation is caused by high light attenuation and deep mixing depths that exceed the compensation depth. Light limitation was suggested to limit productivity in Manson embayment. Given that primary productivity and fish productivity are highly correlated (Nelson 1958; Shortreed et al. 1998), it appears that low productivity measured in the embayments support limited productive capacity in Williston Reservoir. The most productive embayment and the embayment capable of the largest production capacity for fish is Omineca.

Table 7. Depth integrated chlorophyll *a* and daily primary productivity for various lakes and reservoirs in BC. The shaded cells indicate fertilized systems.

	Chlorophyll *a* (mg Chl m^{-2})	Primary Productivity (mg C m^{-2} d^{-1})
Williston, embayment	10.3	32.6
Williston, pelagic	7.6	34.3
Slocan*	26.3	59.3
Okanagan, North Basin**	22.2	80.3
Okanagan, South Basin	32.2	64
Alouette***	36.8	139.6
Kootenay North Arm*	58.9	367.6
Kootenay South Arm*	44.1	238.8
Arrow Reservoir Upper*	55.4	260.6
Arrow Reservoir Lower*	42.1	263

* mean of April-September
** mean of July and September
***mean of June, July, Aug., and Sept.

By incorporating size fractionation into the study we can assess the “health” or organic carbon production of each size fraction of phytoplankton. The three most commonly studied size fractions are the picoplankton (0.2-2.0 µm), nanoplankton (2.0-20 µm) and microplankton (>20.0 µm). The size structure of the phytoplankton community is fundamentally important to the productive capacity of the embayment. Food chains are relatively inefficient, as only 10% of the carbon is “passed on” or assimilated in the biomass of the next level of the food chain. As such, lakes with short food chains are more efficient systems, as a high proportion of the base of the food chain, the phytoplankton, are incorporated into the biomass of the end consumer. Small cells are not efficiently consumed by large herbivorous zooplankton such as *Daphnia*, instead micrograzers such as ciliates or rotifers consume the small cells, then the micrograzers in turn are consumed by the larger zooplankton, requiring an extra step in the food chain.

Phytoplankton size is also important to understanding nutrient dynamics in the system. It has been show that typically smaller size fractions (<3 µm) are more limited by phosphorus while the larger fractions are typically limited by nitrogen, therefore understanding that size structure of the phytoplankton can aid in predicting and understanding how phytoplankton abundance and composition are regulated.

In all of the embayments, except Omineca, nanoplankton accounted for the greatest proportion of productivity. As discussed earlier, this is encouraging because although the rates of production are extremely low, the size class most easily grazed by herbivorous zooplankton is in fact growing. The phytoplankton communities are the photosynthetic carbon producers that determine the structure of the food web in the reservoir and ultimately, the productivity of the reservoir and the potential production of fish populations. The dominant role of nanoplankton in the embayments is in contrast to the pelagic regions where picoplankton clearly dominated the phytoplankton community. The predominance of the picoplankter *Synechococcus* spp. and a diverse group of nanoflagellates suggest a major role of the microbial food web in the pelagic regions of the Reservoir. Unfortunately, the predominance of the microbial food web in the pelagic regions results in low forage production and sub-optimal rearing conditions for both herbivorous zooplankton such as *Daphnia* and herbivorous fishes such as kokanee. The multiple pathways of trophic exchange in microbial food webs can be inefficient in transferring carbon up the food chain especially when compared to classical short food webs e.g. nanoplankton-zooplankton-fish versus picoplankton-ciliates-zooplankton-fish (Stockner and Porter, 1988). It appears that the size structure of Omineca embayment is more similar to the pelagic region.

The results of this study were ranked and a mean ranking for each embayment was calculated to determine the relative productive capacity of each embayment. We determined that Omineca embayment had the highest production potential, followed closely by Clearwater and Nation and the least productive embayment was Manson. It should be noted that the productive capacity of Omineca, Clearwater and Nation were quite similar and the outlier was Manson. To determine the potential contribution of each embayment to the Reservoir, we incorporate a consideration of the size of each embayment (primary productivity x surface area) to calculate the maximum contribution or influence on the Reservoir. This rough calculation does not attempt to consider the volume of the embayment or exchange with the Reservoir. Omineca embayment owing to its large size and high productivity may have the greatest influence on the Reservoir, followed by Manson (low productivity but large surface area), Nation (high productivity but small surface area) and finally Clearwater embayment (high productivity but very small surface area). This "back of the envelope" calculation shows that although Clearwater embayment has relatively high rates of primary productivity, its surface area is an order of magnitude smaller than Omineca or Manson embayments, consequently the influence of Clearwater on production of Williston Reservoir may be low. This estimate of the maximum contribution of each embayment to the reservoir has important implications for the understanding the ecology of the Reservoir and for future work on the Reservoir. Manson ranked 2nd in terms of potential contribution/influence, due largely to the relatively large size of the embayment, not on actual rates of primary productivity. We have shown that primary productivity in Manson is the lowest of the 4 embayment because of severe limitation by light and nutrients, consequently Manson embayment is colimited. Therefore, Manson embayment is not an ideal candidate for future work because of the high turbidity and low productivity while Omineca embayment has relatively high productivity and has the highest potential influence on the Reservoir of the 4 embayment studied.

It is interesting to examine the findings of the previous limnological study of the pelagic region of Williston Reservoir which found that the Finlay Reach was the most productive sector or sub-basin of the reservoir for pelagic fish production. Our current study has shown that Omineca embayment, the embayment that flows into Finlay Reach, was the most productive of the embayments studied. This suggests a possible linkage between the production of the embayments and the Reservoir but at this point the degree of influence the embayment has on the ecology of the Reservoir is currently unknown and warrants further examination.

Table 8. Ranking of variables for assessment of productive capacity of Williston Reservoir embayments, 2004.

Variable	Nation embayment	Manson Embayment	Omineca embayment	Clearwater Embayment
TP	1	3	1	2
Chlorophyll *a*	1	4	2	3
Phyto density (cells·ml^{-1})	2	4	1	3
Phyto BioV. (mm^3·L^{-1})	1	4	2	3
Primary Production (mgCm^{-2} day^{-1})	3	4	1	1
Prod/Biomass (P/B ratio)	3	4	1	2
Zooplankton (#·L^{-1})	3	2	3	1
Zooplankton Biomass (µg·L^{-1})	3	2	4	1
Average Rank	2.1	3.4	1.9	2.0
Final Rank	**3**	**4**	**1**	**2**

Future Research

This study has examined key limnological characteristics in each of the four embayments of Williston Reservoir. This study has suggested a potential role of both light and nutrient limitation of reservoir production, specifically phosphorus and nitrogen. It has identified Omineca as the embayment with the highest production capacity based on the limnological evidence available. Our understanding of the limnology of the embayments would be further enhanced with knowledge of the abundance of planktivorous and piscivorous fish species in the embayments. Limited information on the fishery is available for Williston Reservoir but is currently lacking for the embayments. This information is necessary in order to fully understand the importance of top down effects of the food web in the embayments. Many studies have shown that the base of the food chain, the phytoplankton community structure can influence fish communities but equally, many studies have shown that the fish communities can exert dramatic top-down effects on phytoplankton communities. Future research should seek to identify fish species present in the embayments and the relative densities of those species. In addition, it would be beneficial to identify if fish use the embayments as a rearing area for the juveniles or if the juveniles migrate to the pelagic region. Without knowledge of the dynamics of higher trophic level in the embayments, it is difficult to completely understand ecology of the embayments and the role of the embayments on the ecology of Williston Reservoir.

SUMMARY

Williston Reservoir, by nature of its impoundment of three river systems over 30 years ago, created a complex reservoir system with many large embayments. The ecology of these embayments is not known nor is the significance of the embayments to the ecology of the pelagic zone in the Reservoir. Standing stock of biomass at all trophic levels in the embayments is *very* low, and rates of primary production are much lower than measured in other similar large interior BC lakes. There are two significant factors that account for the low productivity: nutrient and light availability. Nutrient limitation, either nitrogen or phosphorus or both nitrogen and phosphorus, was identified in all four embayments. Phosphorus limitation was observed in all embayments while nitrogen limitation was observed in Nation and Omineca and therefore Nation and Omineca embayment are co-limited by both nitrogen and phosphorus. Light limitation was observed in Manson embayment, therefore production capacity was co-limited by light and phosphorus. All of the major chemical and biological variables monitored indicate that the embayments of Williston Lake can be defined as ultra-oligotrophic systems.

It was determined that Omineca embayment has the highest potential to influence Williston Reservoir. The turbidity is low and the euphotic zone is shallower than the mixed layer depth, consequently productivity is relatively high in the embayment, and owing to its large size it has the greatest potential to influence the ecology of the Reservoir. Nation embayment and Omineca embayment share many similar characteristics, such as low nutrient conditions, low N:P ratios, relatively high phytoplankton biomass and rates of productivity and similar zooplankton communities. However, an important difference is the size structure of the phytoplankton production in Omineca is generally dominated by picoplankton while in Nation embayment, which is a smaller embayment, is dominated by nanoplankton. In consideration of the production potential and the presence of large numbers of kokanee spawners and other important species such as arctic grayling, it is recommended that future work examining the role of embayments on the ecology of Williston Reservoir be completed on Omineca embayment. Unfortunately this embayment is the most remote of the four embayments studied and as such provides logistical problems. Omineca embayment is clearly the most productive embayment studied and may have the greatest influence on the ecology of Williston Reservoir.

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Appendix A

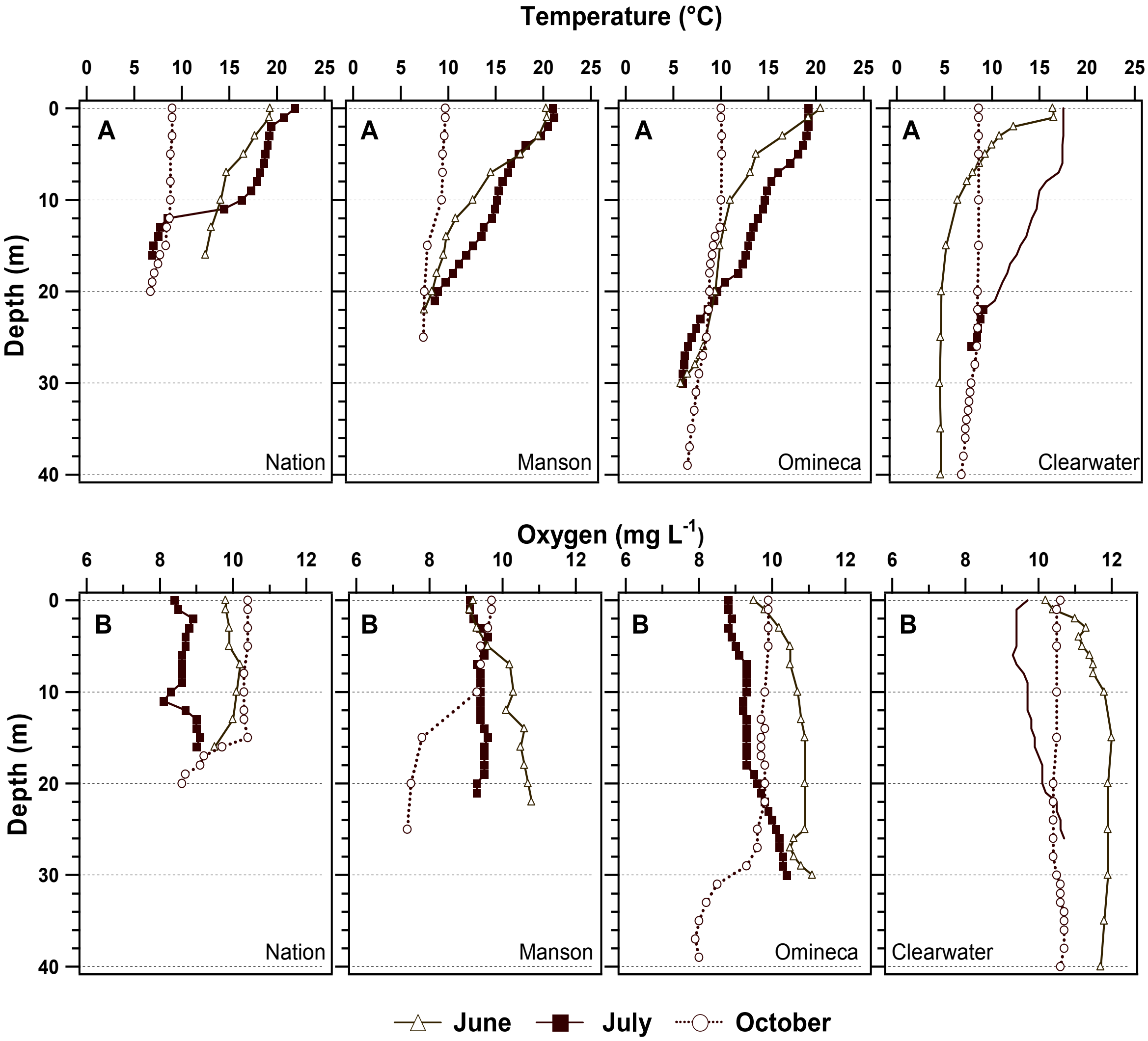

Figure A1. Depth profiles for A) temperature and B) oxygen for four Williston Reservoir embayments, June-October 2004.

APPENDIX B

Water sample analysis raw data

Key for water sample raw data table

Date	Depth	Chl-a	Pico Chl	Nano Chl	Micro Chl	NO3	TP	TDP	pH	TDS	S-D
1	2	3	4	5	6	7	8	9	10	11	12

1. Date- date samples were collected.
2. Depth- depth (meters) sample was collected from.
3. Total Chl-a- chlorophyll-a content (μg·L) on a 0.2 μm filter
4. Pico Chl- chlorophyll in the picoplankton size range (μg·L)
5. Nano Chl- chlorophyll in the nanoplankton size range (μg·L)
6. Micro Chl- chlorophyll in the microplankton size range (μg·/L)
4. NO_3- nitrite and nitrate (μg·L).
5. TP- total phosphorous (mg·L).
6. TDP- total dissolved phosphorous (mg·L).
7. pH- pH in field reading to nearest 0.1 value.
8. TDS- total dissolved solids, residue filterable (mg·L).
9. S-D- Secchi disk depth recorded to nearest 0.1 m.

Mean values at the bottom of the tables are the calculated seasonal mean and incorporate data collected from all four depths. For calculation purposes when a “less than detection limit” was obtained, one gradation lower than the lowest detection value was used for calculating the mean (i.e. if value reported was <0.002, 0.001 was used for the calculation. If the calculated mean value was less than the minimum detection level, the minimum detection level was reported in the table. The NO_3 seasonal mean, was calculated using the mean NO_3 concentration for each sampling trip. A depth value followed by an asterisk (*) indicates a depth where a replicate sample was collected. In the case of replicates the mean result for a given analysis is presented. In some cases, a hyphen (–) indicates data is not available due to loss of sample.

Nation embayment site

Date	Depth	Total Chl-a	Chl pico	Chl nano	Chl micro	NO_3	TP	TDP	pH	TDS	S-D
22-Jun	1	1.89	0.88	0.83	0.18	-	0.01	0.003	7.8	<10	2.5
22-Jun	3*	2.38	1.23	0.94	0.21	0	0.01	0.003	7.7	13	
22-Jun	5	2.41	1.26	0.99	0.16	-	0.012	0.002	7.7	25	
22-Jun	7.5	2.07	1	0.87	0.19	6.7	<0.002	0.008	7.6	20	
23-Jul	1	1.57	0.84	0.57	0.17	0	<0.002	<0.002	7.9	213	4.0
23-Jul	3	1.96	0.88	0.85	0.23	0	0.003	0.003	7.9	105	
23-Jul	5	1.3	0.59	0.46	0.25	0	<0.002	<0.002	7.9	95	
23-Jul	7.5	0.82	0.15	0.45	0.023	0	<0.002	<0.002	7.7	87	
07-Oct	1	1.30	0.54	0.55	0.21	0	0.005	<0.002	7.8	63	2.8
07-Oct	3	1.33	0.53	0.56	0.24	0	0.007	<0.002	7.7	70	
07-Oct	5	1.20	0.54	0.43	0.23	0.8	0.009	0.002	7.7	80	
07-Oct	7.5	1.07	0.42	0.48	0.17	0	0.01	<0.002	7.7	60	
Mean		1.61	0.74	0.66	0.19	1.2	0.006	0.002	7.8	70	3.1

Manson embayment site

Date	Depth	Total Chl-a	Chl pico	Chl nano	Chl micro	NO3	TP	TDP	pH	TDS	S-D
23-Jun	1	0.98	0.20	0.47	0.31	2.7	0.017	0.003	7.8	82	0.8
23-Jun	3	1.13	0.09	0.71	0.33	-	0.022	0.002	7.8	41	
23-Jun	5	0.81	0.34	0.35	0.11	15.6	0.025	<0.002	7.8	54	
23-Jun	7.5	0.85	0.27	0.51	0.07	13.3	0.014	<0.002	7.7	61	
24-Jul	1	1.34	0.49	0.70	0.16	8.3	<0.002	<0.002	8.1	106	2.1
24-Jul	3	1.98	0.62	1.18	0.18	13.0	<0.002	<0.002	8.1	154	
24-Jul	5	1.79	0.27	1.36	0.16	28.6	0.002	0.002	8.0	104	
24-Jul	6.5	1.46	0.19	0.97	0.30	29.4	<0.002	<0.002		102	
06-Oct	1	1.09	0.41	0.53	0.15	38.3	0.008	<0.002	7.8	89	2.1
06-Oct	3	1.09	0.38	0.58	0.14	34.2	0.009	<0.002	7.8	92	
06-Oct	5	1.23	0.44	0.63	0.17	34.0	0.009	<0.002	7.8	92	
06-Oct	7.5	0.98	0.19	0.67	0.12	33.7	0.009	<0.002	7.7	117	
Mean		1.23	0.32	0.72	0.18	21.8	0.010	<0.002	7.9	91	1.7

Omineca embayment site

Date	Depth	Total Chl-a	Chl pico	Chl nano	Chl micro	NO3	TP	TDP	pH	TDS	S-D
23-Jun	1	1.26	0.55	0.52	0.19	2.9	0.01	<0.002	7.8	43	1.7
23-Jun	3	1.58	0.82	0.57	0.18	0.5	0.009	<0.002	7.6	93	
23-Jun	5	2.24	1.05	0.80	0.39	0	0.009	<0.002	7.6	37	
23-Jun	7.5	0.79	0.28	0.43	0.08	0	0.008	<0.002	7.5	<10	
25-Jul	1	0.75	0.38	0.18	0.19	0	0.016	<0.002	7.9	73	4.5
25-Jul	3	2.38	1.88	0.23	0.28	0	<0.002	<0.002	7.9	79	
25-Jul	5	0.90	0.09	0.27	0.55	0	<0.002	<0.002	7.9	68	
25-Jul	7.5	1.66	0.68	0.44	0.53	0	<0.002	<0.002	7.8	80	
08-Oct	1*	0.94	0.28	0.48	0.18	3.0	0.002	<0.002	7.8	78	5.7
08-Oct	3	1.07	0.52	0.38	0.17	2.9	0.003	<0.002	7.8	72	
08-Oct	5	1.48	0.88	0.45	0.15	3.1	0.007	<0.002	7.8	56	
08-Oct	7.5	1.18	0.44	0.56	0.18	3.5	0.007	<0.002	7.8	71	
Mean		1.35	0.65	0.44	0.26	1.3	0.006	<0.002	7.8	63	4.0

Clearwater embayment site

Date	Depth	Total Chl-a	Chl pico	Chl nano	Chl micro	NO3	TP	TDP	pH	TDS	S-D
24-Jun	1	0.94	0.55	0.31	0.08	-	0.010	<0.002	8.0	46	2.3
24-Jun	3	1.08	0.34	0.67	0.06	20.4	0.009	<0.002	8.0	<10	
24-Jun	5	0.64	0.16	0.43	0.05	9.7	0.014	<0.002	7.9	<10	
24-Jun	7.5	0.53	0.06	0.43	0.04	25.1	0.020	<0.002	8.1	<10	
26-Jul	1*	-		0.49	0.35	25.8	<0.002	<0.002	8.1	97	2.6
26-Jul	3	1.49	0.49	0.61	0.39	28.4	<0.002	<0.002	8.1	96	
26-Jul	5	1.54	0.47	0.70	0.37	27.0	<0.002	<0.002	8.1	86	
26-Jul	7.5	1.13	0.15	0.60	0.39	34.5	<0.002	<0.002	8.1	104	
10-Oct	1	1.43	0.56	0.56	0.30	40.0	0.004	<0.002	8.0	98	5.3
10-Oct	3	1.39	0.54	0.47	0.37	37.5	0.003	<0.002	8.0	87	
10-Oct	5	1.41	0.49	0.59	0.33	36.6	0.007	<0.002	8.0	96	
10-Oct	7.5	1.40	0.48	0.55	0.37	38.0	0.007	<0.002	8.0	67	
Mean		1.18	0.39	0.53	0.26	28.5	0.007	<0.002	8.0	67	3.4

Appendix C

Williston Embayments and Reservoir Phytoplankton Species

Bacillariophytes *diatoms*

Achnanthes sp.
Asterionella Formosa var1
Asterionella Formosa var2*
Cocconeis sp.*
Cyclotella bodanica*
Cyclotella comta
Ceratoneis sp.
Cyclotella stelligera
Cyclotella glomerata
Cyclotella sp*
Cymbella sp. (large)*
Cymbella sp.
Diatoma sp.
Eunotia sp.*
Fragilaria construens
Fragilaria crotonensis
Fragilaria capucina
Gomphonema sp.
Aulicoseira distans
Aulicoseira italica
Aulicoseira granulate*
Aulicoseira sp.*
Navicula sp.
Nitzschia sp.
Pinnularia sp.*
Rhizosolenia sp.
Stephanodiscus hantschii*.
Stephanodiscus sp.
Fragilaria acus
Fragilaria angustissima
Fragilaria ulna
Suriella*
Fragilaria sp.*
Tabellaria fenestrate
Tabellaria flocculosa*
Diploneis sp.*

Chryso-Cryptophyte *flagellates*

Bitrichia sp.
Chilomonas sp.*
Chromulina sp1
Chroomonas acuta
Chryptomonas sp.
Chrysochromulina sp.
Dinobryon sp1*
Dinobryon sp2
Kephyrion sp.
Isthmochloron*
Mallomonas sp1*
Mallomonas sp2
Stenokalyx*
Small microflagellates
Ochromonas sp.*
Pseudokephrion sp.
Pseudopedinella sp.*
Chrysoikos sp.*
Synura
Rhodomonas sp.
Chrysidiastrum*

Chlorophytes

Staurodesmus sp.*
Quadrigula*
Ulothrix
Closteriopsis*
Monoraphidium
Nephrocytium*
Staurastrum sp.*
Planctonema sp.*
Planctosphaeria
Paulschultzia sp.*
Chlorella
Kirchneriella sp.*
Pediastrum sp.*
Pandorina sp.*
Tetraedron
Volvox*
Xanthidium*
Clamydocapsa sp.**
Golenkinia radiate**
Closterium**
Actinastrum hantschii**
Gleotila sp**

Chlorophytes

Ankistrodesmus sp.
Coccomyxa sp.
Coelastrum sp.*
Cosmarium sp.*
Crucigenia sp.
Crucigeniella apiculata*
Dichtyosphaerium*
Langerheimia*
Elakatothrix sp3
Euglena*
Gonium*
Oocystis sp.
Scenedesmus sp.*

Dinophytes *Dinoflagellates*
Gymnodinium sp1*
Gymnodinium sp2
Ceratium sp.
Peridinium sp1
Peridinium sp2*

Cyanophytes *Cyanobacteria*
Anabaena sp*
Anabaena circinalis
Aphanothecae sp.
Aphanizomenon sp.*
Merismopedia sp.
Oscillatoria sp2
Oscillatoria limnetica*
Synechococcus sp. (<2 um)
Synechocystis*
Lyngbya sp.**
Microcystis sp.**

* Found only in the pelagic stations in the 1999 & 2000 limnology study.
**Found only in the 2004 embayment study.
All others were found both in the embayments (2004) and the reservoir sampled in 1999 and 2000.

Appendix D

Williston Embayments and Reservoir Zooplankton Species

Cladocerans

*Acroperus harpae***
*Biapertura affinis***
*Chydorus sphaericus***
Daphnia galeata mendotae
Daphnia pulex
Daphnia longiremis
*Daphnia rosea***
*Daphnia schoedleri***
Diaphanosoma leuchtenbergianum
Eubosmina longispina
Holopedium gibberum
*Leydigia leydigi***
Leptodora kindtii
*Sida crystalline***

Copepods

Calanoid copepods
Acanthodiaptomus denticornis
*Aglaodiaptomus leptopus***
Epishura nevadensis
Heterocope septentrionalis
Leptodiaptomus ashlandi
Leptodiaptomus pribilofensis
Leptodiaptomus sicilis
Cyclopoid copepods
*Cyclops vernalis***
Diacyclops bicuspidatus thomasi
Diacyclops scutifer
*Eucyclops speratus***
*Macrocyclops albidus***
*Mesocyclops sp.***

* Found only in the pelagic stations in the 1999 & 2000 limnology study.
**Found only in the 2004 embayment study.
All others were found both in the embayments (2004) and the reservoir sampled in 1999 and 2000.

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