The Limnology of Williston Reservoir: British Columbia’s Largest Lacustrine Ecosystem

John Stockner, Arne Langston, Dale Sebastian and Greg Wilson

1University of British Columbia, Fisheries Centre, 2204 Main Mall, Vancouver, British Columbia V6T 1Z4 and Eco-Logic Ltd., 2614 Mathers Avenue, West Vancouver, British Columbia V7V 2J4
2Peace Williston Fish and Wildlife Compensation Program, Ministry of Water, Land and Air Protection, 1011 Fourth Avenue, Prince George, British Columbia V2L 3H9
3Biodiversity Branch, Ministry of Water, Land and Air Protection, P.O. Box 9359 STN PROV GOVT, Victoria, British Columbia V8W 9M2
4Biodiversity Branch, Ministry of Water, Land and Air Protection, University of British Columbia, 2204 Main Mall, Vancouver, British Columbia V6T 1Z4

In surface area, Williston Reservoir is British Columbia’s largest lacustrine ecosystem. The reservoir shows remarkably little spatiotemporal variance among its three major reaches (Finlay, Parsnip and Peace), despite the immensity and biogeoclimatic diversity of its drainage basins. Williston is ultra-oligotrophic with average concentrations of total dissolved phosphorus (TDP) ranging from 3 to 5 µg/L and nitrate-nitrogen (NO₃-N) from 60 to 65 µg/L. The pelagic plankton community of Williston Reservoir is dominated by bacteria, pico-cyanobacteria, nano-flagellates and small diatoms, and the zooplankton community is comprised largely of copepods in spring and small cladocerans in summer and fall. Primary production rates are very low and most carbon is produced by the pico- and nano-sized plankters that appear to be primarily light limited due to high turbidity and frequent wind-mixing episodes, i.e., shallow light compensation depth and deep epilimnetic depth. Microbial food webs are predominant in Williston through much of the growing season, with free-living bacteria and pico-cyanobacteria as the primary carbon template, and nano-flagellates, ciliates and micro-zooplankton as the principal grazers. Loading models indicate that after impoundment in 1968, Williston was initially a moderately productive ecosystem, but the system has progressively lost nutrients, namely P, through sedimentation and outflow, but also by the scarcity of littoral carbon production due to severe water level fluctuations (drawdown) and winter ice-scouring. Hence, within the past 2 to 3 decades the ecosystem has gradually lost biogenic productive capacity and now lies within the ultra-oligotrophic trophic status and supports a low level of fish production. Daily rates of carbon production are presently at levels more typical of British Columbia fast-flushing, ultra-oligotrophic coastal ecosystems than large, interior-type oligo- and mesotrophic British Columbia lakes. Based on average values of most limnological variables we demonstrate that the Finlay Reach is currently the most productive region of Williston, and estimates of pelagic fish from hydroacoustic/trawl and gillnet surveys support this contention.

Key words: limnology, reservoir, phosphorus loads, phytoplankton, picoplankton, carbon production, zooplankton, food webs, fisheries

Introduction

British Columbia’s mountainous landscape and glacial history has fashioned a vast array of lakes of immense variability in size and depth. Most of the province’s largest lakes are a fiord type, carved by glacial recession in numerous mountain valleys during the last major glaciations, some 10,000 to 12,000 B.P., e.g., Kootenay, Arrow and Okanagan. However Williston Reservoir is man-made, created in 1968 by the impoundment of the Peace River in the Peace Canyon near Hudson’s Hope, British Columbia, for the purpose of hydroelectric generation. The W.A.C. Bennett Dam inundated three major river valleys creating the present three reaches of the reservoir: the upper Peace River basin to the west (Peace Reach), the Finlay River basin to the north (Finlay Reach) and the Parsnip River basin to the south (Parsnip Reach), and in the process created in surface area the largest water body in British Columbia. Over the past four decades there has been a paucity of studies related to water quality and fisheries potentials of the reservoir (BC Research 1976; Barrett and Halsey 1985), but none of these have been of a comprehensive limnological nature. Because of the immensity of the system, inconsistencies in station locations, sampling methods and analytical protocols of previous investigators have created considerable variance in reported results and made comparisons to earlier conditions difficult.
Here we present major findings from a 2-year (1999–2000) comprehensive limnological study of Williston and from two fisheries surveys conducted in 2000. We use these results to estimate total phosphorus (TP) loads, to assess the current trophic state of the ecosystem, and to provide first estimates of the productive capacity of each of the three major basins of the ecosystem. Finally, where possible, we compare Williston results with similar findings from other British Columbia and western Canadian large lakes/reservoirs.

**Description of Study Area**

**The Drainage Basin**

Williston Reservoir (56°N latitude, 124°W longitude) is located approximately 140 km north of Prince George in northeast British Columbia, Canada (Fig. 1). The Peace River flows east to Lake Athabasca which lies within the Mackenzie River drainage system, which flows north to discharge 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 ‘junction’ with 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 to the south, the Parsnip Reach (previous Parsnip River basin) extends in a southeast direction for approximately 110 km (Fig. 1). Monthly water releases (outflow) from the Bennett Dam during the ice-free period of this 2-year study ranged from 550 to 1500 m³/s (Fig. 2). The Williston drainage basin encompasses six biogeoclimatic sub-zones: sub-boreal spruce, sub-alpine Engleman spruce, sub-alpine fir, boreal white and black spruce, and spruce-willow-birch and alpine tundra (Farley 1979). The Finlay and Parsnip reaches lie within a wide, flat-bottomed ‘Rocky Mountain Trench’ with Omineca Mountains to the west and Rocky Mountains to the east. Glacial deposition, moraines and lacustrine deposits are common, but glacial till is the most abundant surficial deposit found within the drainage basin. The Peace Reach has a V-shaped basin and is much narrower and deeper than either the Finlay or Parsnip reaches. Steep-sloped sedimentary rock is predominant in the entrenched western half of the Peace Reach where the Peace River originally (prior to impoundment) cascaded eastward breaking through the Rocky Mountains. The eastern half of the Peace Reach extends into the Rocky Mountain Foothills, similar in topography and geologic features to those of Finlay and Parsnip reaches. Williston's drainage basin is subject to a continental climate with long, cold winters where lows of -30°C can occur any time after October. Frost may occur at any time of the year and ice formation on the reservoir begins as early as November, though complete ice cover usually does not occur until January. Ice cover normally extends to the first week of May, and the Finlay is often the last reach to be ice-free. Summer average air temperatures range from 16 to 18°C, with maximum temperatures often reaching 30°C for brief periods in July and August. Annual precipitation ranges between 40 to 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, and snowfall accounts for 35 to 45% of the total annual precipitation. Williston receives and stores most of its hydrologic input from snowmelt, and a large spring runoff that begins in mid-May and peaks in June.

**Reservoir Morphometrics**

Williston’s shoreline is dendritic in shape and estimated to be about 1770 km in length (BC Research 1976). Its mean depth (z) is 41.7 m, maximum depth is 166 m, and at maximum operating level (672.1 m elevation) has a surface area (SA) of 1779 km², making Williston Lake the largest lentic freshwater system in British Columbia. Its maximum volume is 74,257 × 10⁶ m³ and by volume it is ranked the ninth largest reservoir in the world (Maclean 1998). Williston’s catchment area (CA) is 69,930 km², an area equal to the province of New Brunswick, and its CA/SA (surface area) ratio is 39:1, Williston’s average water residence time of the reservoir is 19 months (1.26 years) and it cycles between maximum and minimum levels once per year, typically reaching a maximum level in August or September (Hirst 1991). Power generation is highest in winter months resulting in high winter discharges and deep winter draw downs, averaging 11 m/year. The minimum reservoir levels are typically reached by the end of April or early May. The water intakes (penstocks) in the dam-face are located at 41 and 72 m and through much of the summer/fall when the lake is stratified water withdrawal occurs primarily from the hypolimnion, but in some low-water years warmer, meta- and epilimnetic water is occasionally discharged in autumn.

**Methods**

**Stations and Sampling**

Five permanent stations were established with selection criterion being: (1) proximity to previous sampling sites, (2) positioning over original inundated river channels for maximum depth, and (3) well removed from major turbidity input sources (river mouths, eroding alluvial shorelines, etc.) (see map, Fig. 1). Three of the stations were located within the deepest sector of each major reservoir basin—Finlay, Parsnip and Peace
Fig. 1. Williston Reservoir and its drainage basin.
reaches, and 2 stations were located in zones of special interest—the “Junction” and the “Forebay” stations. The Junction station was situated near the original confluence of the Finlay and Parsnip rivers where their waters mix and commence flow eastward. The Forebay station is located approximately 2 km west of the W.A.C. Bennett Dam in one of the deepest sections of the reservoir. Peace Reach is the only reach with two stations—one at Clearwater, 50 km east of Junction, and at Forebay. A station for nutrient sampling only was located on the north bank of the Peace River 500 m downstream of the dam discharge. The five stations were assigned site identifier numbers and incorporated into the Ministry of Water, Land and Air Protection’s Environmental Monitoring System (EMS). The station location coordinates recorded using the Universal Transverse Mercator (UTM) projection grid and NAD27 datum were:

- Parsnip Reach: EMS 234185, UTM coordinates 10.458200.6175500
- Finlay Reach: EMS 234184, UTM coordinates 10.410111.6252000
- Junction station: EMS 234187, UTM coordinates 10.452000.6211550
- Peace Reach: EMS 234186, UTM coordinates 10.486000.6204000
- Forebay station: EMS 234188, UTM coordinates 10.550204.6210540

In both years, sampling was conducted at the start of each month beginning in May and continuing into November. A single winter sampling was done in March 1999 through the ice at Forebay station. The Finlay Reach station was not accessible in May 1999 due to ice cover. The Finlay and Parsnip reaches were also not accessible in November 1999 due to high winds and unsafe conditions. All stations and depths were sampled in 2000.

**Physicochemical**

A YSI model 58 oxygen/temperature meter was used to collect dissolved oxygen (ppm or mg/L) and temperature (°C) at depth (m). A 20-cm standard Secchi disc vertically cast from the shaded side of the boat measured Secchi depth (i.e., water transparency). Water depth was measured with a digital Hummingbird depth sounder. Cloud cover was recorded to the nearest 10%. In 2000 light attenuation (extinction, k) and compensation depths (1% of surface intensity) were estimated from vertical light profiles obtained using a Li-Cor submersible quantum sensor (400–700 µm, Model Li 192s). Total daily solar radiation was measured at Finlay Landing in close proximity to the Junction Station using a Model 190S Li-Cor quantum sensor. Reservoir elevation data was provided to the nearest 0.1 m by BC Hydro, W.A.C. Bennett Dam operational staff.

Water samples were collected with a van Dorn sampler. Samples were shipped in ice-filled containers and analyzed within 72 hours of collection. Analyses of total phosphorus (TP), total dissolved phosphorus (TDP), nitrate (NO3-N), TDS and total chlorophyll were conducted at Environment Canada’s Pacific Environmental Science Centre (PESC), North Vancouver, British Columbia. Laboratory methods employed at PESC follow guidelines established by McQuaker (1994). Water samples for alkalinity for 14C assays were analyzed at the University of British Columbia, Environmental Engineering Laboratory, Vancouver, British Columbia. A digital handheld pH meter provided field pH measurements. Water samples collected for chlorophyll a content were field-filtered through a 0.45-µm cellulose acetate filter at
a maximum vacuum pressure of 1.05 kg/cm². The filters were frozen, stored and submitted for analysis at the end of each sampling trip.

**Phytoplankton**

A 250-mL sample of water from 1-, 3- and 5-m depths was obtained monthly from May to November from each station. Each phytoplankton sample was preserved in acid Lugol’s iodine preservative and stored in a cool location until analysis. Prior to quantitative enumeration by the Utermohl (1958) method samples were gently shaken for 60 s, carefully poured into 25-mL settling chambers and allowed to settle for a minimum of 8 h. Counts were done using a Carl Zeiss inverted phase-contrast plankton microscope. Counting followed a 2-step process: first random fields (5–10) were examined at 250x magnification (16x objective) and large microphytoplankton (20–200 µ), e.g., diatoms, dinoflagellates, filamentous blue-greens, were enumerated, and secondly all cells within a random transect (ranging from 10 to 15 mm) were counted at 1560x magnification (100x objective). This high magnification permitted quantitative enumeration of minute (<2 µ) autotrophic picoplankton cells (0.2–2.0 µ) (class Cyanophyceae), and also of small auto-, mixo- and heterotrophic nanoflagellates (2.0–20.0 µ) (classes Chrysophyceae and Cryptophyceae). In total, between 250 to 300 cells were enumerated in each sample to assure statistical accuracy (Lund et al. 1958). The compendium of Canter-Lund and Lund (1995) was used as the taxonomic reference.

**Bacteria and Pico-cyanobacteria (APP)**

Water samples from 1-, 3- and 5-m depths were mixed and two 15-mL subsamples were obtained monthly from May to November 2000 from each station for analysis of bacteria and pico-cyanobacteria. Bacteria samples (15 mL) were preserved with gluteraldehyde and placed in a sterile capped test tube, and 15 mL was filtered onto pre-stained Irgalen black 0.2 µ polycarbonate Nuclepore filters, placed in an envelope and stored in a cool, dark location until microscopic analysis. Bacteria and pico-cyanobacteria densities were determined at the University of British Columbia, using both the acridine orange and DAPI stained direct-count epifluorescence method (Maclsaac et al. 1981). Random fields were counted at 1250x magnification oil immersion after filtration of 10- to 15-mL samples onto 0.2 µ Irgalen black stained filters using a Zeiss epifluorescence microscope and blue-band excitation filter at wavelengths of 450 to 490 nm. APP were enumerated using the epifluorescence method described by Maclsaac and Stockner (1985). Up to 30 random fields were counted using a wide-band filter excitation (397–560 nm). Results are reported as cells/mL.

**Zooplankton**

Sampling occurred monthly at each station between May and November each year. At each station, duplicate macro-zooplankton samples were collected with a vertically (0–30 m) towed Wisconsin (80 µ mesh) net, 50 cm in diameter, and 74 µ mesh window in the collection cup. The net was raised at a speed of approximately 0.5 m/sec, and samples were preserved in 70% ethanol. The total volume of the sample was split with a Folsom splitter to a volume that contained >100 post nauplii of the most abundant taxa. A random subsample was then enumerated for species, size, sex, stage of maturity and reproductive condition. Enumeration was conducted using GSZ Zeiss Stereo microscope under suitable magnification (10–100x). Adult calanoid copepods were identified using Wilson (1959) and adult cyclopoids after Yeatman (1959). Cladoceran identifications followed Brooks (1959) and Devey and Devey (1971). Biomass estimates were made by measuring body length of 10 to 15 individuals from each group present in the sample. Lengths of zooplankters were converted to body mass (µg DW) using length-weight relationships developed by McCauley (1984).

**Primary Productivity**

Primary production experiments to estimate phytoplankton photosynthetic rates (carbon production) were done in July and September in 1999, and monthly from May to November in 2000. Primary production was estimated using the H¹⁴CO₃⁻ (carbon labelled bicarbonate) method (Strickland 1960). Water samples were collected from 1-, 3-, 5- and 7.5-m depths and transferred to three 300-mL BOD (biochemical oxygen demand) bottles. The two clear bottles allowed light to penetrate and photosynthesis to occur, while the third dark bottle excluded light and measured dark uptake or respiration. Each of the sample bottles was inoculated with 1 mL of 3.7 µCIE/mL H¹⁴CO₃⁻. After inoculation sample bottles were lowered to their respective collection depths and incubated for 2 to 3 h. Incubation was initiated as close to 1000 h as possible, but no later than 1300 h. The water samples were retrieved after incubation and stored in a light-tight metal box to prevent further exposure to light. Within 3 to 4 h the samples were filtered through a 0.45-µm, 47-mm diameter cellulose nitrate membrane filter. The filters were transferred to scintillation vials and 4 drops of 6 N HCL were added. The vials were shipped to the Radiation Laboratory, University of British Columbia Medical School, for analysis on a Beckman Beta scintillation counter. In August and September 2000 production runs were size-fractionated into three plankton size categories: pico- (0.2–2.0 µ), nano- (2.0–20.0 µ) and micro- (20.0–200.0 µ) to estimate contribution to total C production by size.
Fish Surveys

Hydroacoustics

Night collections of hydroacoustic data in pelagic habitats were gathered during August 2000 during the new-moon period with concurrent trawl and gillnet sampling. The survey consisted of 29 standard transects, 19 in the main basin (Parsnip and Finlay reaches) and 10 in the Peace reach. Transect locations were similar to locations used in a 1988 survey. Acoustic survey data were collected using Simrad models EY200P 70 KHz single-beam and EY500 120 KHz split-beam systems. Transducers on planers were towed alongside the boat at a depth of 1.5 m and data collected continuously along survey lines at 1 to 2 pings/s while cruising at 2 m/s. Data from both systems were compiled and stored on computers that provided preliminary data analysis and target verification between systems. Data from the two echo-sounders was backed up on Sony Digital Audio Tape (DAT) and writable CDs. Population estimates were extrapolated only to pelagic habitat area since all sampling was done in deep water.

Trawl Sampling

The survey design consisted of six stations with three replicate trawls per station (18 trawls), but due to sampling conditions only one replicate was completed at station 6, and two at station 3 for a total of 15 trawls. Three trawl stations were situated on the Peace Reach and only one station on Junction, Finlay and Parsnip reaches. Stepped-oblique trawls were used to sample representative volumes of water at all depths. The net was fished for 15 minutes over six consecutive depth layers that sampled from 30 m to the surface. The trawl net was a 15-m beam-trawl with a 5 × 5 m opening towed at 0.8 m/s. The net consisted of graduated mesh panels from 10 cm at head bar to 0.6 cm at cod-end. Net depths were estimated from the cable angle and the length of cable deployed. A global positioning system (GPS) was used to determine distances travelled and resulting trawl sample volumes.

Gillnetting

Gillnet data were collected in August 2000 concurrent with trawl and acoustic surveys. Floating monofilament gillnets were used and each net was 2.4 m deep and 94 m long and comprised of six panels 2.4 m deep and 15.3 m long. Stretch mesh sizes of the six panels were 25, 76, 51, 89, 38 and 64 mm. The nets were set in areas closely associated with the trawl and hydroacoustic survey transects. At each sampling location, three gillnets were set overnight, parallel to the shoreline. The nets were set “end-to-end” with a 50-m gap between each of the three nets. All fish captured were subsampled (maximum of 30) for length (mm) and weight (g). Stomach contents were not recorded due to deterioration of contents normally associated with netting of pelagic fishes.

Results

Physicochemical

Temperature. Williston Reservoir is a dimictic system, with two periods of deep mixing (May and November) and 2 periods of stratification—June to October and February to April. Open-water stratification commences in June at all stations and lasts to late October or early November. The epilimnion depth is variable, depending on duration and strength of wind episodes, but on average ranges from 15 to 25 m in Parsnip Reach, >35 to 40 m in Peace Reach, and at Junction and in Finlay Reach between 20 to 30 m. Maximum temperatures are attained in July/August and range from a low of 13°C in the Peace Reach (Clearwater station) to a high of 19°C at Forebay station. Hypolimnetic temperatures were uniform throughout the reservoir and ranged from 4 to 6°C.

Oxygen. Dissolved oxygen profiles were orthograde with O₂ concentrations showing a uniform depth distribution with little variation both among stations and between years. Oxygen concentrations at most depths were near saturation with respect to temperature and pressure, and there were no discernible zones of reduction (O₂ deficits) or super-saturation. The only exception to the above occurred at the Forebay station where values a few metres above the sediment surface abruptly declined.

Water transparency (Secchi depth, extinction coefficient). Water transparency at all Williston stations in 1999 was generally low with mean Secchi depths of between 3 to 4 m. At most stations lowest Secchi values were in June and July during the peak ‘freshet’ period then increased gradually through August and into fall. The highest Secchi depth recorded in 1999 was 7.0 m in October in Finlay Reach, while the lowest occurred at Forebay in September. The highest Secchi depth recorded in 2000 was 7.0 m in October in Finlay Reach, while the lowest occurred at Forebay in October and in Finlay Reach in July.

Seasonally, the Peace Reach station at Clearwater was the least turbid and Forebay the most turbid. In 2000 there was less variance in Secchi depths, and mean values for the 5 stations ranged between 3.5 to 5.0 m. Clearwater station in both years was the least turbid station with average Secchi depth of 5 m, but Junction station, not Forebay, was the most turbid sector of the reservoir in 2000 (Table 1). Highest average extinction coefficients (greatest light extinction and shallowest compensation depth) occurred in Finlay Reach (0.98), and lowest (least extinction and deepest compensation depth) occurred at Forebay (0.57).
Total dissolved solids (TDS). The highest average TDS values occurred in the Finlay Reach (118 mg/L), and the next highest were at Forebay station (111 mg/L) and Peace Reach at Clearwater (109 mg/L), and the lowest occurred in the Parsnip Reach (85 mg/L). The distribution pattern of TDS noted in 1999 was nearly the same as noted in 2000, the only exception being slightly higher TDS values in 2000 noted in Finlay Reach (Table 1).

Nitrogen (NO$_3$). Ammonia levels were undetectable and hence were not measured in this study. Nitrate concentrations in Williston averaged 57 µg/L in 1999 and 62 µg/L in 2000, and values were always well above detection limits at all stations except in Finlay Reach, where epilimnetic values fell to 13 µg/L in June and to below detection levels in August in both years. Highest epilimnetic nitrate concentrations occurred in the Parsnip Reach, exceeding 130 µg/L in June 1999 and 142 µg/L in May 2000. Nitrate values at Junction and the two Peace Reach stations averaged between 55 to 65 µg/L in both years, and showed no mid-summer declines.

Phosphorus. Concentrations of total phosphorus (TP) averaged 6.2 for the whole reservoir and seasonally ranged between highs of 11 µg/L to lows of 2 to 3 µg/L in 1999. In 2000 TP was slightly higher at all stations, averaging 7.4 and ranging between 6.2 to 9.2 µg/L. The only discernible spatiotemporal pattern was a period of higher concentrations in July/August during the freshet period. Total dissolved phosphorus (TDP) values were about 30 to 40% lower than TP and averaged 3.6 µg/L in 1999 and 4.7 µg/L in 2000. Concentrations were highest in both years in the Parsnip Reach (>5 µg/L) and lowest in Finlay Reach (3 µg/L) and at Forebay (3 µg/L) in both years.

NO$_3$-N:TDP ratio. The NO$_3$-N:TDP ratio was used to assess possible N or P limitation of phytoplankton populations in Williston. Values averaged 15.7 in 1999 and 13.5 in 2000 for the whole system, and were lowest in the Finlay Reach (4.7 in 1999 and 2.9 in 2000), and highest (20 in 1999) in the Peace Reach, and in 2000 in the Parsnip Reach (18.7) and Forebay station (17.1). Seasonally, the highest ratios occurred in May/June and lowest in August/September (Table 1).

TABLE 1. Mean annual values for selected physicochemical and biological variables from Williston Reservoir from May to November 2000

<table>
<thead>
<tr>
<th>Variables</th>
<th>Parsnip reach</th>
<th>Finlay reach</th>
<th>Junction station</th>
<th>Peace</th>
<th>Peace (Forebay)</th>
<th>Williston mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Epilimnion average depth (m)</td>
<td>20</td>
<td>25</td>
<td>22</td>
<td>30</td>
<td>37</td>
<td>26</td>
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<tr>
<td>maximum epi-temp (°C)</td>
<td>16.0</td>
<td>13.2</td>
<td>14.5</td>
<td>14.8</td>
<td>16.2</td>
<td>14.9</td>
</tr>
<tr>
<td>Secchi depth (m)</td>
<td>4.1</td>
<td>4.0</td>
<td>3.5</td>
<td>5.0</td>
<td>4.1</td>
<td>4.1</td>
</tr>
<tr>
<td>Extinction coefficient</td>
<td>0.74</td>
<td>0.98</td>
<td>0.69</td>
<td>0.70</td>
<td>0.57</td>
<td>0.74</td>
</tr>
<tr>
<td>TDS (mg/L)</td>
<td>94</td>
<td>122</td>
<td>103</td>
<td>105</td>
<td>109</td>
<td>107</td>
</tr>
<tr>
<td>TP (µg/L)</td>
<td>7.9</td>
<td>9.2</td>
<td>7.4</td>
<td>6.2</td>
<td>6.4</td>
<td>7.4</td>
</tr>
<tr>
<td>NO$_3$ (µg/L)</td>
<td>105</td>
<td>16</td>
<td>58</td>
<td>65</td>
<td>67</td>
<td>62</td>
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<tr>
<td>TDP (µg/L)</td>
<td>5.6</td>
<td>5.4</td>
<td>4.5</td>
<td>4.1</td>
<td>3.9</td>
<td>4.7</td>
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<tr>
<td>NO$_3$:TDP</td>
<td>18.7</td>
<td>2.9</td>
<td>12.9</td>
<td>15.8</td>
<td>17.1</td>
<td>13.5</td>
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<tr>
<td>Pico-cyanobacteria (No./mL)</td>
<td>20,340</td>
<td>22,461</td>
<td>16,788</td>
<td>14,660</td>
<td>23,830</td>
<td>19,615</td>
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<tr>
<td>Bacteria (No. x 10$^9$/mL)</td>
<td>1230</td>
<td>1450</td>
<td>1196</td>
<td>1144</td>
<td>1154</td>
<td>1234</td>
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<tr>
<td>Chlorophyll a (µg/L)</td>
<td>1.5</td>
<td>1.6</td>
<td>1.5</td>
<td>1.3</td>
<td>1.1</td>
<td>1.4</td>
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<td>Phyto density (cells/mL)</td>
<td>4471</td>
<td>5858</td>
<td>3854</td>
<td>3311</td>
<td>5358</td>
<td>4571</td>
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<td>Phyto bioV. (mm$^3$/L)</td>
<td>0.334</td>
<td>0.418</td>
<td>0.179</td>
<td>0.207</td>
<td>0.228</td>
<td>0.273</td>
</tr>
<tr>
<td>Primary production</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(mg C/m$^2$/h)</td>
<td>9.8</td>
<td>12.4</td>
<td>9.3</td>
<td>9.6</td>
<td>7.1</td>
<td>9.6</td>
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<tr>
<td>(mg C/m$^2$/day)</td>
<td>33.9</td>
<td>44.5</td>
<td>32.9</td>
<td>34.7</td>
<td>23.3</td>
<td>34.3</td>
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<tr>
<td>Prod/biomass (P/B ratio)</td>
<td>22.6</td>
<td>27.8</td>
<td>21.9</td>
<td>26.7</td>
<td>23.0</td>
<td>24.3</td>
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<td>Zooplankton (No./L)</td>
<td>10.3</td>
<td>2.3</td>
<td>5.9</td>
<td>3.4</td>
<td>8.7</td>
<td>5.7</td>
</tr>
<tr>
<td>Biomass (µg/L)</td>
<td>53</td>
<td>9</td>
<td>17</td>
<td>10</td>
<td>29</td>
<td>24</td>
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</tbody>
</table>

Biological

**Bacteria.** The average abundance of free-living bacteria in the epilimnion (0–5 m) of Williston Reservoir was $1.2 \times 10^9$/mL and ranged from $3 \times 10^8$/mL in Parsnip Reach in May to $600 \times 10^9$/mL in Parsnip Reach in November. Apart from the exceptionally large peak in May in Parsnip Reach, bacterial densities in Williston...
tended to be lower in spring and early summer (May, June, July) and higher in late autumn (September, October, November) (Fig. 3). The highest fall values were measured at Finlay Reach and the Peace Reach stations, with the notable occurrence of a very large population increase $>2 \times 10^6$/mL in November at the dam Forebay station. Highest average density was in Parsnip Reach and lowest at Forebay Station with a trend toward declining bacterial density moving from west to east in the reservoir (Fig. 4).

**Chlorophyll a.** Chlorophyll a concentrations in both years were remarkably uniform, varying from spring lows of <0.4 µg/L to highs of 3.7 µg/L at 5 m in Finlay Reach in June. The average concentration for the reservoir in 2000 was 1.4 µg/L. In 1999 the highest average concentrations occurred in the Parsnip Reach (1.6 µg/L), and lowest was observed at Forebay station (1.3 µg/L). In 2000 the highest average station value was in Finlay Reach (1.6 µg/L) and the lowest at Forebay.

**Phytoplankton abundance and biomass.** In 1999 average phytoplankton population densities ranged from a high of about 5700 cells/mL at the Junction to a low of just over 3700 cells/mL at Peace Reach Clearwater station, and the average for the whole reservoir was 4729 cells/mL. In 2000 densities were similar to those of 1999, but with higher densities in Finlay Reach and Forebay. Average cell density in 2000 for the reservoir was 4571 cells/mL, which was considerably lower than in 1999. Phytoplankton biovolume in 1999 ranged from a high at Finlay Reach of 0.50 mm³/L to a low of 0.18 mm³/L at Forebay. The average phytoplankton biovolume for the whole system was 0.33 mm³/L in 1999 and slightly lower in 2000 at 0.27 mm³/L.

Seasonally, among stations, the Finlay Reach had the highest density and greatest biomass of diatoms and lowest of picoplankton, while Parsnip Reach had the highest density and biomass of nano-flagellates and second lowest abundance of nano-flagellates in 1999. This trend was reversed in 2000 with Finlay having higher overall densities of most groups than Parsnip. Phytoplankton abundance and biomass in the Peace Reach Clearwater station were the lowest in the reservoir in both years. There was only a single, somewhat protracted, mid-summer diatom, nano-flagellate and dinoflagellate increase with low populations in both spring and fall periods. In both years there was a trend toward diminishing phytoplankton biomass from western reaches to the eastern Peace Reach, with Finlay and Parsnip reaches showing considerably higher biomass than either Peace Reach Clearwater or Forebay stations with Junction station values lying between these extremes (Fig. 5).

In both 1999 and 2000 small pico-cyanobacteria (Cyanophytes) were numerically dominant at all stations, with the nano-flagellates (Chrysophytes and Cryptophytes) the next most abundant group, followed by diatoms (Bacillariophytes), dinoflagellates (Dinophytes), and...
Stockner et al.

and green algae (Chlorophytes). There were no notable peaks or blooms, and surprisingly little seasonal variation in either abundance or biomass in both years. Highest average densities occurred at Parsnip Reach and Junction in 1999, and at Finlay Reach and Forebay in 2000. Lowest phytoplankton population densities occurred in May and peaks in abundance and biomass occurred at most all stations in July/August.

![Graphs showing phytoplankton abundance and biomass by major group in 1999 and 2000 for different stations.](image)

**Fig. 5.** Williston Reservoir phytoplankton abundance, biomass by major group in 1999 and 2000.
Species. Phytoplankton species assemblages were very similar among the five stations and were numerically dominated by the small cyanobacteria *Synechococcus* sp. and a very small, rod-shaped *Oscillatoria* sp. The most common diatoms found at all stations in the reservoir in both years were *Cyclotella stelligera*, *Cyclotella comta*, *Asterionella formosa*, *Fragilaria crotonensis*, *Fragilaria* spp., *Aulacoseira distans* and *Stephanodiscus* sp. There was also a great diversity of nano-flagellates ranging in size from 2 to 20 µ, and the most common genera were *Chromulina*, *Chroomonas*, *Chrysochromulina*, *Cryptomonas*, *Rhodomonas* and *Dinobryon*. The dinoflagellates *Peridinium* and *Gymnodinium* were not common and seldom attained large populations in the reservoir, but owing to their size made a significant contribution to biomass in August and September in Parsnip Reach in 1999 and in Finlay Reach in 2000.

Vertical distribution. Throughout much of the growing season there was little variation in either abundance or biomass among depths sampled (1, 3, 5 m). In 1999 there were two exceptions, the first in Parsnip Reach where populations at 1 m in June and July were 2 to 3 times higher than those at 5 m, and the second at Junction where a pico-cyanobacteria population peak occurred at 5 m in early July. In 2000 the only major difference in depth distribution among major groups was a 3- to 5-m peak of pico-cyanobacteria at Finlay Reach station in July. Otherwise, populations showed a very consistent and uniform distribution within the upper epilimnion throughout the year at all stations.

Pico-cyanobacteria (APP). In Williston in 2000 pico-cyanobacteria populations ranged from peaks of >80,000 cells/mL in May in Parsnip and July at Forebay to lows of <10,000 cells/mL at all stations in autumn (Fig. 6). Their average density in the reservoir was 19,615 cells/mL (N = 35). The largest populations of pico-cyanobacteria occurred in spring months (May, June and July) at all stations and populations rapidly declined in August and remained low throughout the rest of season. As noted with bacteria, there was a trend toward diminishing pico-cyanobacteria seasonal average abundance moving west to east in the reservoir with the exception of Dam Forebay station where average densities tended to be higher (Fig. 7).

Primary Production

Spatial, Seasonal and Vertical Trends—2000

Average hourly values of primary production or photosynthetic rate (PR) for Williston in 2000 were 9.6 mg C/m²/h and 34.3 mg C/m²/d, and as noted in 1999 highest values were in Finlay Reach and the lowest were at Forebay station (Fig. 8). Junction, Parsnip and Peace stations had similar averages of about 10 mg C/m²/h and >30 mg C/m²/day. Highest monthly production values were in August at all stations and the lowest were in spring, May to June. Production declined abruptly in September at all stations but increased again to moderately high levels in October and November, the reservoir’s autumn transition (deep mixing) period. May, June and July 2000 are best characterized as low production months with similar daily and hourly values that range from 5 to 20 mg C/m²/d. In August PR increased about four- to fivefold over spring values, with largest increases in the Parsnip Reach (9x) and at Forebay (8x) stations (Fig. 8).

The striking August production peaks were coincident with peaks of phytoplankton biomass and density at all stations. In October and November production values increased again to moderately high levels with Finlay Reach values the highest among stations during both months (Fig. 9). The depth distribution of production rates mirrored the vertical distribution of phytoplankton, showing little spatiotemporal variation, and highest rates of carbon production at 1 and 3 m and diminishing values with increasing depth. There was no strong indication of any major light inhibition of growth in surface waters, and maximum values most often...
occurred at either 1- or 3-m depths, depending on month and ambient light conditions.

Size-Fractionated Production—2000 (Fig. 10)
Primary production measurements in August and September were fractionated into three phytoplankton size categories (pico- at 0.2–2 µ, nano- at 2–20 µ, micro- at >20 µ) to determine contribution by size to total C production. Pico- and nanoplankton contributed greater than 80% of the C production at all stations in both months, the only exception being Finlay Reach in September where the presence of large diatoms increased the contribution of microplankton to about 30% of total. The most productive fraction was clearly picoplankton (i.e., the pico-cyanobacteria *Synechococcus* sp. and *Synechocystis* sp.), contributing about 35 to 45% to total production. Nanoplankton which included most of the Chryso- and Crypto-flagellates and some small green algae, were the next most productive fraction contributing around 25 to 35% to total C, and the least productive was microplankton contributing <10% and consisting mostly of diatoms and dinoflagellates. These values are remarkably similar to findings from size-fractionation studies in Chilko Lake, a large pre-alpine, slightly turbid sockeye salmon nursery lake (Stockner and Shortreed 1994).

Zooplankton

Abundance and biomass

The pelagic zooplankton populations in Williston show a diverse assemblage, with similar population abundance and biomass between years (6.5/L and 22 µg/L in 1999 and 5.7/L and 23.5 µg/L in 2000, respectively). Junction, Parsnip and Clearwater stations had the lowest population densities, and Forebay and Finlay Reach stations the largest. Populations increased in the Finlay Reach from 6/L in 1999 to 10/L in 2000, the highest average density recorded at any site in 2000 (Table 2, 3). Seasonally, zooplankton density peaked concurrent with phytoplankton peaks in July/August at values of 4 to 10/L at most stations, with the exceptions of the Dam Forebay site where density peaked at 25/L in 1999 and 16/L in 2000, and at the Finlay Reach site where density peaked earlier in June, at 17/L in 2000. The average reservoir population composition was similar between years, with 90% copepods and 10% cladocerans (by density), but there was a wide range between sites. The Finlay Reach contained the largest percent of cladocerans at 23%, and Peace Reach the lowest at 2%. Fifteen species of macrozooplankton were identified in the samples, with *Leptodiaptomus ashlandi*, *Diacyclops bicuspidatus thomasi* and *Daphnia galeata mendotae*
being the most common. There were three species of Daphnia and four species of Leptodiaptomus identified, along with the rarely seen Heterocope septentrionalis. Several rotifer species were observed (e.g., Keratella quadrata, K. cochlearis, Polyarthra sp., Asplanchna sp., Kellicottia sp.), but not discussed owing to obvious losses due to the large mesh net (80 µ).

Copepods were numerically the dominant macrozooplankton group in Williston Reservoir, averaging 90% of total zooplankton density and 60% of biomass. The largest copepod populations in each year were found at the Forebay site, averaging 13.5/L and 8.1/L in 1999 and 2000, respectively, with densities ranging from 2 to 8/L at the other sites. Copepod densities peaked in August at most stations, except at Junction and Finlay Reach sites where densities peaked in June. Diaptomus, with an average density of 3 to 4/L was the most numerous genus of zooplankton captured, especially at the Dam Forebay and Finlay Reach. Four species of Leptodiaptomus were found with L. pribilofensis and L. ashlandi the most numerous. Diacyclops with an average density of 1.8/L in both years was the next most abundant copepod.

Of the two Diacyclops species captured, D. scutifer was the more numerous with populations peaking at 0.1 to 3/L usually in late July, and D. bicuspidatus peaked later in the summer at densities around 0.25/L. A few Heterocope septentrionalis were captured in mid to late summer at each station but at low densities (<0.003/L).

Cladocerans were occasionally captured in May (when sampling began) and June, but significant populations did not develop until July or August. Peak densities were generally 1 to 4/L (20–40% of total density), with the highest seasonal densities at the Finlay Reach site, including the highest single cladoceran density of 6.5/L recorded in September 2000. Cladoceran densities of <0.25/L at the Peace Reach site were very low compared to the others stations.

Despite their low overall abundance compared to copepods, cladoceran biomass generally peaked at 15 to 20 µg/L, or approximately 65% of total biomass, with an overall average of 41% of the June to October biomass. Five genera of cladocerans were identified with Daphnia clearly the dominant cladoceran genera, accounting for approximately 90% of cladoceran density and 70% of biomass. The largest Eubosmina populations were found in Finlay Reach peaking at 1/L, or 20% of total cladoceran density. Three species of Daphnia were found, with D. galeata mendotae the dominant, numerically accounting for 88% of the Daphnia and 82% of cladoceran density, with D. pulex and D. longiremis occurring at very low density (0.35/L).

**Fish Surveys**

**Hydroacoustic**

The total area of pelagic or deep-water habitat (>20 m depth) was estimated to be 141,800 ha or 57% of reservoir surface area at the time of survey. Pelagic habitat area ranged from 22 to 46% of surface area in the Parsnip and Finlay reaches compared with 62 to 90% in the deeper Junction and Peace reaches. Both Parsnip and Finlay reaches therefore had significant areas of near-shore (<20 m) habitat that was not sampled during this survey. Fish densities at individual transects ranged from 28 to 219 fish/ha. Average densities by reach for Finlay, Parsnip, Peace and Junction were 139, 101, 70 and 44 fish/ha, respectively. Finlay Reach had highest densities with a range of 59 to 219 fish/ha. Lowest average densities were found in the

<table>
<thead>
<tr>
<th></th>
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<th></th>
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<td></td>
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<tr>
<td>Daphnia spp.</td>
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<td>1.09</td>
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<td>0.01</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>0.01</td>
<td>0.02</td>
</tr>
<tr>
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<tr>
<td>Diacyclops spp.</td>
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<td>1.24</td>
<td>3.54</td>
<td>1.62</td>
<td>1.91</td>
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<td>0.86</td>
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<td>4.3</td>
<td>2.0</td>
<td>1.7</td>
</tr>
<tr>
<td>Total zooplankton</td>
<td>2.6</td>
<td>2.3</td>
<td>6.1</td>
<td>10.3</td>
<td>4.1</td>
<td>3.9</td>
</tr>
</tbody>
</table>

![Fig. 10. Average contribution (%) to total phytoplankton production by phytoplankton size class in Williston Reservoir, August and September 2000.](image-url)
Junction Reach (28–67 fish/ha) and in the lower half of the Peace Reach (17–28 fish/ha) (Fig. 11).

Vertical fish distribution ranged from 2.5 to 35 m (0–2.5 m could not be sampled acoustically). Fish in both Parsnip and Finlay reaches showed increasing abundance with decreasing depth with highest concentrations near the surface. Fish were found to be deeper and spread over a wider depth range in deeper Junction and Peace reaches with fewer fish in shallower, surface layers. Estimates of fish density and abundance are considered to be conservative for the Finlay and Parsnip reaches, as they do not include fish above 2.5 m of depth.

Extrapolating the proportions by depth to the surface would suggest that an additional 50 to 60% or an additional 2 million fish should be added to the 0 to 2.5 m depth-stratum in Finlay Reach, but not in Parsnip, Peace or Junction reaches. This “Finlay adjustment” increases the total reservoir population estimate to about 8 million fish.

Trawl catch rates were extremely low in Williston Reservoir and a total of only 37 fish was captured in 15 trawls. Excluding the Forebay station where no fish were caught, the trawl catch per unit effort (CPUE) ranged from 6 to 15 fish/ha and demonstrated that lake whitefish and kokanee were the main fish species in pelagic habitat.

Gillnetting

A total of 679 fish distributed among five species were caught at seven pelagic netting sites. The species captured listed in order of relative abundance were: lake whitefish (Coregonus clupeaformis) 45%, peamouth chub (Mylocheilus caurinus) 25%, rainbow trout (Oncorhynchus mykiss) 20%, kokanee (Oncorhynchus nerka) 8% and bull trout (Salvelinus confluentus) 2%. Since sampling occurred when adult kokanee were entering spawning streams, a large component of the adult kokanee population was absent from the pelagic zone in all reaches. There were significant differences (HSD Tukey, Alpha = 0.05) among sampling locations for lengths and weights of rainbow trout, peamouth chub and lake whitefish.

Discussion

Overview

By the nature of its inception 30 years ago by impoundment of three major river systems, Williston Reservoir became a complex and very large lacustrine ecosystem with two major western basins (Finlay and Parsnip Reach) and in the lower half of the Peace Reach (17–28 fish/ha) (Fig. 11).

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reaches) in a north–south alignment, and a single long, deep third basin (Peace Reach) in an east–west alignment. The Junction was conjectured to be the major zone of ‘mixing’ for north-flowing Parsnip and south-flowing Finlay basin waters, while the narrower, deeper, east-flowing Peace was the reservoir’s zone of ‘integration’ where chemical and biological components of the larger western basins are mixed by frequent, strong wind episodes within the old Peace River Canyon. Owing to Williston’s size, the discussion will first summarize conditions in each major basin, and then present a picture of the current trophic status and productivity of biotic communities. Previous studies from the 1970s and early 1980s provided a glimpse at Williston’s communities during the more productive ‘boom’ phase of its ontogeny (BC Research 1976), and we present a second look at our current understanding of system function at a less productive phase of its maturation, approximately 30 years after impoundment.

Basin Summaries

Parsnip Reach. The Parsnip Reach, the most southerly of Williston’s basins, has the shallowest average epilimnetic depth (20 m), highest maximum temperatures (16°C) and lowest TDS (94 mg/L). The addition to the basin of high N and C from effluents discharged from municipal sewage and pulp mill treatment plants, contributes to high average values of dissolved NO$_3$ (105 µg/L) and free-living bacteria (1.23 $\times$ 10$^6$/mL). This Reach receives water input mainly from the Parsnip and Pack river drainages from the south and west, and these rivers input the lowest alkalinity (TDS), but highest nitrogen and phosphorus loadings of all major Williston basins. Owing to the high average NO$_3$:TDP ratio (16–18) and detectable concentrations of nitrate and TDP throughout the summer, phytoplankton in Parsnip Reach were considered limited by light (average Secchi 4.1 m, $k = 0.74$) rather than nutrients. In terms of average primary production, Parsnip was the third most productive basin and in phytoplankton biomass the second highest in 2000, but it had the lowest zooplankton biomass and abundance in both years. Fish populations were also among the lowest recorded in 2000, contrary to reports from earlier work in the 1980s that noted high fish production in Parsnip (Barrett and Halsey 1985).

Finlay Reach. The Finlay Reach, Williston’s most northern basin, is the largest and receives the greatest volume of inflow water (>2-fold higher than Parsnip). This Reach receives water input mainly from the Parsnip and Pack river drainages from the south and west, and these rivers input the lowest alkalinity (TDS), but highest nitrogen and phosphorus loadings of all major Williston basins. Owing to the high average NO$_3$:TDP ratio (16–18) and detectable concentrations of nitrate and TDP throughout the summer, phytoplankton in Parsnip Reach were considered limited by light (average Secchi 4.1 m, $k = 0.74$) rather than nutrients. In terms of average primary production, Parsnip was the third most productive basin and in phytoplankton biomass the second highest in 2000, but it had the lowest zooplankton biomass and abundance in both years. Fish populations were also among the lowest recorded in 2000, contrary to reports from earlier work in the 1980s that noted high fish production in Parsnip (Barrett and Halsey 1985).

### Table 4. Fish abundance estimates by reach and depth stratum for pelagic habitat of Williston Reservoir, August 2000

<table>
<thead>
<tr>
<th>Stratum Depth (m)</th>
<th>Parsnip</th>
<th>%</th>
<th>Junction</th>
<th>%</th>
<th>Finlay</th>
<th>%</th>
<th>Peace</th>
<th>%</th>
<th>Total</th>
<th>%</th>
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<tbody>
<tr>
<td>2.5–5</td>
<td>80,800</td>
<td>34</td>
<td>0</td>
<td>0</td>
<td>1,674,500</td>
<td>45</td>
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<td>0</td>
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<td>5–10</td>
<td>88,200</td>
<td>37</td>
<td>27,500</td>
<td>5</td>
<td>644,300</td>
<td>17</td>
<td>215,300</td>
<td>15</td>
<td>975,300</td>
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<tr>
<td>10–15</td>
<td>45,800</td>
<td>19</td>
<td>167,900</td>
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<td>466,100</td>
<td>12</td>
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<td>906,000</td>
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<td>109,700</td>
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<td>280,000</td>
<td>7</td>
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<td>15</td>
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<td>25–30</td>
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<td>200,000</td>
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<td>223,700</td>
<td>3</td>
</tr>
<tr>
<td>Total</td>
<td>238,600</td>
<td>100</td>
<td>532,400</td>
<td>100</td>
<td>3,739,100</td>
<td>100</td>
<td>1,410,900</td>
<td>100</td>
<td>5,921,000</td>
<td>100</td>
</tr>
<tr>
<td>% Total</td>
<td>4%</td>
<td>9%</td>
<td>63%</td>
<td>23%</td>
<td>100%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Table 5. Summary of mean lengths and weights of fish from pelagic netting Williston Reservoir, August 2000 (sample size is less than catch totals due to subsampling)

<table>
<thead>
<tr>
<th>Species</th>
<th>No. Fish sampled</th>
<th>Mean length (mm)</th>
<th>Range (mm)</th>
<th>SD</th>
<th>Mean weight (g)</th>
<th>Range (g)</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lake Whitefish</td>
<td>139</td>
<td>252.0</td>
<td>148–297</td>
<td>30.4</td>
<td>184.9</td>
<td>34.4–311</td>
<td>57.3</td>
</tr>
<tr>
<td>Kokanee</td>
<td>47</td>
<td>230.2</td>
<td>128–292</td>
<td>44.1</td>
<td>169.2</td>
<td>21.8–333.6</td>
<td>83.4</td>
</tr>
<tr>
<td>Rainbow trout</td>
<td>91</td>
<td>282.2</td>
<td>117–404</td>
<td>53.0</td>
<td>272.2</td>
<td>40.1–639.2</td>
<td>125.4</td>
</tr>
<tr>
<td>Peamouth Chub</td>
<td>84</td>
<td>188.7</td>
<td>122–217</td>
<td>21.3</td>
<td>80.5</td>
<td>22.7–117.8</td>
<td>20.7</td>
</tr>
<tr>
<td>Bull trout</td>
<td>6</td>
<td>419.7</td>
<td>155–669</td>
<td>172.5</td>
<td>1109.3</td>
<td>35.8–3461.7</td>
<td>1364.2</td>
</tr>
</tbody>
</table>
with the lowest NO₃:TDP ratio (3–5) among stations, Finlay phytoplankton growth in August/September was likely N-limited, but also light-limited due to turbid conditions throughout much of the growing season (Secchi 4 m, \( k = 0.98 \)). It supported the highest bacterial density (1.45 \( \times 10⁶/mL \)), the second highest APP abundance, the highest phyto- and zooplankton abundance and biomass, the highest rates of primary production and highest pelagic fish densities in September 2000. Finlay Reach at this stage of Williston’s ontogeny, is clearly the most productive sector of the reservoir.

**Junction.** Waters at the ‘Junction’ are a mixture of Parsnip and Finlay reach waters, and summer winds blowing either south/north or east/west from Peace Canyon create a well-mixed epilimnion that averages 22 m with a maximum temperature of 14.5°C. Values for a number of variables were more similar to those of Finlay than Parsnip. Junction had a moderately low phytoplankton abundance/biomass and higher zooplankton biomass than Parsnip but lower than Finlay. Primary production at Junction station was second lowest in 2000. With strong mixing of Finlay water with nitrate-rich Parsnip water there were no recorded periods of nitrate depletion, but nitrate values and the NO₃:TDP ratio were the second lowest in the reservoir. Junction had the lowest average Secchi reading (3.5 m, \( k = 0.69 \)) in Williston so it is likely that light was the most significant factor limiting photosynthesis at this sector of the reservoir.

**Peace Reach (Clearwater station).** The Peace Reach is much deeper, narrower and more wind-mixed than either Parsnip or Finlay reaches, with an average epilimnetic depth of >30 m and maximum epilimnion temperature that ranges around 14.8°C. Clearwater station sampled mid-Peace Reach and was one of the least productive regions of the reservoir, with lowest bacteria (1.14 \( \times 10⁶/mL \)), APP (14,660 cells/mL) and phytoplankton densities and the second lowest zooplankton abundance and biomass, but the second highest average daily primary productivity. With a NO₃:TDP ratio ranging from 16 to 21 there does not appear to be any nutrient limitation of phytoplankton at Clearwater, but owing to persistent high winds, a deep well-mixed epilimnion, and moderate turbidity (Secchi 5 m), phytoplankton here were more likely limited by light.

**Peace Reach (Forebay station).** Forebay station sampled waters adjacent to the Bennett Dam in the most eastern and deepest (>190 m) sector of the Peace Canyon basin. There was a striking similarity between Forebay and Clearwater stations in most all measured variables, the only notable departures being a greater epilimnetic depth (>40 m), a higher maximum temperature (16°C), and a greater turbidity at Forebay (Secchi 4.1 m). In 2000 the highest pico-cyanobacteria populations were at Forebay (23,830 cells/mL), but the second lowest bacterial abundance. Zooplankton was abundant at Forebay ranking either first or second in abundance and biomass in both years, but primary production was lowest among all stations in both years. With the high average NO₃:TDP ratio (17) it is unlikely that nutrient availability limits production here, but like Clearwater, turbid conditions, shallow compensation depth, and a very deep epilimnion create light-limiting conditions throughout much of the growing season. Advection of biogenic materials eastward by water discharge from the dam during the growing season with potential withdrawals from the epilimnion in September, create high loss rates of biogenic material and may be one of the key factors for such low production at this station.

**Annual Phosphorus Load and Productive Capacity**

**Phosphorus load.** Average TP and TN values from early surveys in 1975 and again in 1988 show that over this 13-year period both TP and TN declined to current levels (2000), and this suggests that there have been no further reductions in ambient nutrients from the lows recorded in 1988, nearly 20 years after impoundment. Using the average TDP (not TP due to the high component of sediment, i.e., unavailabe P) values for 2000 we calculated the present areal P load \( (L_p) \) to Williston (322 mg P/m²/year) (Vollenweider1968) and \( L_p \) corrected for residence time (Fig. 12) (Vollenweider 1976). Its position on the plot is indicative of the current low production status of the reservoir. Stave Reservoir, a very fast-flushing coastal system is even more unproductive, while Arrow, a larger Columbia River mainstem reservoir undergoing nutrient supplementation shows considerably higher values of \( L_p \) (Pieters et al. 2000). Based on the areal P load it was possible to calculate the annual load to Williston (569 tonnes P/year) for 2000. In a similar manner using the average monthly values of Williston’s daily C production for 2000 we estimated the annual carbon production to range from 10 to 12 g C/m²/year. Converting this annual C rate to total Williston production provides an estimate of whole-system production that ranges from 17,800 to 21,350 tonnes C/year. A second estimate (22,760 tonnes C/year) using the Redfield ratio (40C:7N:1P) for aquatic biomass (Valentyne 1974) is similar to, but higher than, that based on integrated average monthly \(^{14}\)C values.

**Phosphorus, chlorophyll and trophic state.** Using Williston’s average values of TP (6.2 µg/L) and chlorophyll (1.4 µg/L) values for 2000 provides a comparison with a variety of lakes of various trophic conditions and an assessment of current trophic state (Fig. 13). We include average values of TP and chlorophyll from 1975 and 1988 to give some sense of how Williston has
changed since impoundment some 30 years ago. The pattern emerging is that Williston, for the first decade after impoundment, was doubtless a more productive ecosystem, using abundant nutrients from land/soil inundation and decomposition of flooded vegetation (boom cycle). Though exhibiting, like any northern ecosystem, high interannual variability, it seems clear that after three decades the system has gradually lost nutrients (P) through outflow and sedimentation and has become progressively less productive. It now lies well within the oligotrophic condition, with low chlorophyll, phytoplankton and zooplankton biomass, primary production and a moderately low abundance of bacteria and pico-cyanobacteria (APP). Because of its climatic setting

**Fig. 12.** Annual P load \((L_p)\) as a function of average chlorophyll \(a\) in Williston (2000), Stave (2003) and Arrow (2002) reservoirs.

**Fig. 13.** Log-log plot of seasonal average TP versus chlorophyll from a variety of British Columbia, Alberta and Yukon Territory lakes and reservoirs.
(short summer, long winter) and very short residence
time, coupled with extreme water level fluctuations
drawdown) that suppress littoral periphyton produc-
tion, it will more than likely retain in perpetuity these
dominant characteristics and low productive capacity.
But this prognosis does not account for possible changes
in productivity that could accompany global warming,
logging or catastrophic events such as forest fires or
earthquakes, that could alone or collectively increase/
dermine the oligotrophic characteristics and low productive capacity.

But this prognosis does not account for possible changes
in productivity that could accompany global warming,
logging or catastrophic events such as forest fires or
earthquakes, that could alone or collectively increase/
derminate the oligotrophic characteristics and low productive capacity.

Not surprisingly, by sharing similar geographic
and biogeochemical settings, Williston’s average
TP/Chl values fit close to the centre of a cluster of 16
Yukon lakes, and are also contiguous with the large
Arrow and Kootenay lakes, but distant from more pro-
ductive Alberta prairie lakes and from the low produc-
tive lakes of the interior (Fig. 13). Owing to the absence of large populations of zoo-
planktivorous fishes, e.g., kokanee, whitefish, Yukon
lakes support a very high abundance of large macro-
zooplankton, and therefore the pelagic chlorophyll val-
ues are more in line with Williston due largely to graz-
ing or ‘top-down’ control rather than to nutrient or
light limitation as is the case in Williston, i.e., bottom-up control
as is the case in Williston (Shortreed and Stockner
1986). Irregardless, it must be noted that the chloro-
phyll values for Williston are exceptionally low for an
ecosystem of this size and geographic setting, where
similar, contiguous large lakes, e.g., Babine, Takla, Stuart
and Tremblear, all show much higher average seasonal chlorophyll than Williston (Stockner 1987; Stock-
ner and Shortreed 1983).

The Limitation of Primary Production

When compared to seasonal average photosynthetic
rates (PR) from several British Columbia coastal and
large interior lakes, Williston’s PR rates are very low,
and more similar to ultra-oligotrophic coastal lakes (Fig.
14, Table 6) (Stockner and Shortreed 1985). Though
some N-limitation may occur in late summer in Finlay
Reach, it is unlikely that Williston is currently limited by
ambient nutrient concentrations. The prevalence of
strong winds and the continual erosion of clay and silt
from unstable shorelines coupled with large spring
freshet inputs of high-turbidity Parsnip and Findlay river
discharges in June/July, assures the persistence of high
turbidity throughout the whole reservoir during the
active growing season (June to October). Light penetra-
tion (compensation-depth) is limited to the upper 5 to
7 m of the reservoir, and mixing depths in the epil-
imnion range from 20 to 30 m in mid-summer and even
deeper (>35 m) by September/October. Thus, phyto-
plankters are exposed to a much lower average light in
such a strongly mixed, deep epilimnion that is further
exacerbated by the ubiquitous high turbidity. As has
been shown by Stockner and Shortreed (1975) in the
large, narrow Babine Lake, there can be positive effects
for the dominance of phytoplankton populations from wind-driven deep-
mixing episodes, i.e., nutrient entrainment and re-supply
from recycled N and P, but these are usually overridden
by the negative effects of protracted periods in subopti-
mal light (light limitation), especially so in the heavily
wind-mixed turbid surface waters of Williston which are
strikingly similar to those of a large northern Manitoba
Churchill River reservoir where comparable findings
have been reported (Hecky and Guildford 1982; Guild-
ford et al. 1987).

We opine that Williston’s wind-mixed deep epil-
imnion and persistent turbidity does not permit sufficient
daily average light to support optimal phytoplank-
ton growth. It is not surprising that pico-cyanobacteria
(APP) are the predominant phytoplankters in terms of
both abundance and their contribution to total daily
pelagic C production in Williston (>50 contribution)since they are known to grow optimally at lower light conditions (Stockner and Antia 1986; Shortreed and
Stockner 1991). The fast-flushing, short residence time
of Williston further reduces productivity by export of both nutrient and phytoplankton and zoo-
plankton biomass from the system at crucial times, e.g.,
fall/winter/spring periods.

The Major Carbon Producers

The predominance of picoplankton (bacteria +
cyanobacteria) and nano-plankters (flagellates)
0.2–20 µ) portends the major importance of a diverse,
microbially based community within the pelagic habitat
of Williston Reservoir (Stockner 1991). Seasonally, over
85% of Williston’s photosynthetic carbon production is
by organisms within the pico- and nano- size range, con-
trasted to <15% by micro-plankters (20–200 µ), e.g.,
diatoms and dinoflagellates (Table 6). There is a clear
trend in both lakes and oceans that documents the shift

![Fig. 14. Average photosynthetic rate (PR) versus chlorophyll for a variety of British Columbia lakes (Williston Reservoir–large circle) (K. Shortreed and E. Maclsaac, Department of Fisheries and Oceans, unpublished data).](image-url)
of carbon production from pico- and nano-plankton to micro-plankton as ambient nutrient concentrations increase. This shift can be seen in eutrophic Fraser Lake and mesotrophic Shuswap and Okanagan lakes where a large contribution to total carbon production is by micro-plankton (Table 6). This table also shows how extremely low the average daily rate of carbon production is in Williston when compared with other large, interior British Columbia lakes (Table 6). The average abundance of pico-cyanobacteria in Williston was about $20 \times 10^3$ cells/mL, below the average of $32 \times 10^3$ cells/mL in British Columbia coastal lakes (untreated) and less than half the average for Yukon basin lakes ($55 \times 10^3$ cells/mL) (Stockner 1991). But the average seasonal abundance of heterotrophic free-living bacteria in Williston ($1.2 \times 10^6$) is higher than estimates from coastal British Columbia untreated lakes ($0.7 \times 10^6$), but lower than the average densities measured in fertilized British Columbia lakes of $1.4 \times 10^6$ (Stockner and MacIsaac 1996). This discrepancy between low APP and high bacterial abundance is likely related to a depression of phytoplankton populations (especially some flagellates) due to Williston’s high turbidity and suboptimal light climate, while bacteria have more favourable conditions, i.e., independent of light they have sufficient organic C (notably in Parsnip reach), N and P, and reduced flagellate ciliate grazing for them to sustain populations at modest levels. In highly turbid Kitlope Lake and in other glacially turbid lakes with high turbidity and particle density, bacteria often sustain larger populations than APP (MacleIsaac et al. 1981; Stockner and Shortreed 1991; Stockner et al. 1993). The moderate abundance of both bacteria and APP in Williston serve as key food items (prey) for both autotrophic and heterotrophic nano-flagellate (predators) populations that seasonally were not overly abundant ($1-3 \times 10^3$ cells/mL).

The extraordinarily large bacteria populations ($>3 \times 10^6$/mL) in Parsnip Reach in May 2000 are likely associated with both pulp and paper and municipal STP effluent discharges that ‘enrich’ the Parsnip Reach waters with high dissolved organic and inorganic C, N and P, especially in winter under ice-cover during low-water and low-flow conditions. We conjecture that it is possible that the very large bacterial populations found at Forebay in autumn are residuals of this large spring bacterial biomass emanating from the lower Parsnip reaches and advected by density current interflows to the Peace sector by September and October. The answers must come from further research on currents and hydraulic residence times in Parsnip and Peace reaches.

### The Forage Base—Zooplankton

Hanson and Peters (1984) found a significant relationship between zooplankton biomass and average TP concentration in temperate lakes across North America. Williston Reservoir’s average biomass value for 1999 to 2000 fits well with their regression, but lies well below a similar regression for 17 Yukon River basin lakes (Fig. 15). Yukon lakes have a much greater zooplankton biomass than Williston despite similar ambient TP levels, owing largely to the absence of both vertebrate (kokanee) and invertebrate (Mysis) predators. In comparison to other large, interior British Columbia lakes/reservoirs, Williston has a low average zooplankton density (6/L), similar to the Arrow Reservoir (7/L) (Pieters et al. 2000), but considerably lower than in Kootenay Lake that has fluctuated between 17 to 23/L from 1992 to 1997 (Ashley et al. 1997), and Okanagan Lake (18/L) from 1997 to 2000 (Andrusak et al. 2002). In contrast, total zooplankton density in Stave Reservoir, a coastal ultra-oligotrophic reservoir, was <1/L (J. Stockner, unpublished data). Cladocerans accounted for approximately 10% of the total zooplankton density in Williston Reservoir, a value that is above their percentages in more productive Kootenay and Okanagan lakes but where large populations of *Mysis relicta* occur and effectively graze on zooplankton prey, most notably on larger cladocerans (Table 7) (Grossnickle 1979; Bowers 1988).

### Table 6. Comparison of Williston’s size-fractionated (August) production with seasonal values from several large interior British Columbia lakes

<table>
<thead>
<tr>
<th>System</th>
<th>Pico-0.2–2.0 µ</th>
<th>Nano-2.0–20.0 µ</th>
<th>Micro-20.0–200 µ</th>
<th>Total (mg C/m²/d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Williston Reservoir (N = 5)</td>
<td>51</td>
<td>36</td>
<td>13</td>
<td>24.9</td>
</tr>
<tr>
<td>Okanagan Lake Ave (N = 4)</td>
<td>23</td>
<td>53</td>
<td>24</td>
<td>165</td>
</tr>
<tr>
<td>Babine Lake*</td>
<td>45</td>
<td>40</td>
<td>15</td>
<td>123</td>
</tr>
<tr>
<td>Fraser Lake*</td>
<td>16</td>
<td>32</td>
<td>52</td>
<td>336</td>
</tr>
<tr>
<td>Shuswap Lake*</td>
<td>29</td>
<td>38</td>
<td>33</td>
<td>140</td>
</tr>
<tr>
<td>Quesnel Lake*</td>
<td>40</td>
<td>36</td>
<td>24</td>
<td>102</td>
</tr>
</tbody>
</table>

* K. Shortreed, Department of Fisheries and Oceans, Cultus Lake Laboratory, British Columbia, unpublished data.
Fisheries Potential

In its present state Williston is clearly a low production ecosystem as seen at most all trophic levels, including fish. The very low fish densities in Williston indicate both a low productivity (food production) and/or rearing habitat bottleneck for many fishes, and this low fish production is consistent with signals sent from most of the limnological variables reported herein. The yearly cycle of summer inundation and winter desiccation effectively leaves the littoral habitat devoid of significant biogenic production, and all but eliminates any potential for spawning/rearing of fishes, except perhaps in numerous tributary rivers and stream mouths. The presence of a dysfunctional littoral and an enormous pelagic zone implies that the pelagic is the most desirable habitat for fish and the littoral is the least desirable habitat. Not surprisingly, the average hydroacoustic estimates of pelagic fish densities from transects contiguous to major limnological stations are reasonably well correlated with estimates of daily primary production in 2000 (Fig. 16).

Johnson and Yesaki (1989) estimated the total pelagic fish abundance in Williston in September 1988 to range from 7.8 to 14.5 and average 11.2 million. Although acoustic abundance estimates were similar between 1988 and 2000 surveys, the distribution of pelagic fishes was very different. In 1988 the Junction Reach had the largest proportion of total fish and Finlay Reach had the second lowest, but in 2000 it was the opposite—Finlay Reach had the largest populations and Junction the second lowest (Table 8). Numbers of fish in Parsnip and Peace reaches were similar between surveys.

Food Webs

Microbial communities, and the numerical dominance of the picoplankter *Synechococcus* sp., currently dominate the phytoplankton assemblages of Williston, together with a diverse assemblage of micro-flagellates, ciliates and other small nano-plankters, is clear and unambiguous evidence of the current oligotrophic condition of the reservoir. The predominance of these groups of opportunistic species in the pelagic community confirms the predominant role of microbial food webs in mediating carbon metabolism and nutrient fluxes in all of Williston’s three reaches (Stockner and Porter 1988) (Fig. 17). Unfortunately, the predominance of microbial food webs in low production ‘kokanee’ reservoirs also portends low benthic/pelagic coupling, low forage production (macrozooplankton) and suboptimal rearing conditions for kokanee, whitefish and other salmonids, e.g., rainbow trout, bull trout. This is because microbial food webs are made up of multiple pathways of trophic exchange, and at each carbon transfer energy is dissipated so these food webs are viewed as inefficient, e.g., coastal, when compared to short pathways in more mesotrophic interior lakes, e.g., micro-phytoplankton to macro-zooplankton to fish.

Though Williston Reservoir is clearly an interior ecosystem in terms of TDS, TP and nitrate, its low chlorophyll *a* and rate of primary production typify the fast-flushing coastal ecosystems (Stockner 1981, 1987). The perpetuation of such a low production system is driven by several factors that are common to hydroelectric reservoirs, the more salient being: (1) short water residence times with a high net export of C, N and P, (2) low P retention (sedimentation), and (3) a very low production littoral zone (Stockner et al. 2000). Williston’s high climatic variability exacerbates the above factors.

### TABLE 7. Comparisons of total zooplankton density (No./L) and biomass (µg/L) between Williston and 3 large British Columbia interior lakes/reservoirs

<table>
<thead>
<tr>
<th>System</th>
<th>Kootenay</th>
<th>Arrow&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Okanagan&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Finlay Reach</th>
<th>Parsnip Reach</th>
<th>Peace Reach&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density</td>
<td>19</td>
<td>7</td>
<td>20</td>
<td>2.5</td>
<td>8.2</td>
<td>6.6</td>
</tr>
<tr>
<td>Biomass</td>
<td>23</td>
<td>36</td>
<td>25</td>
<td>49</td>
<td>11</td>
<td>43</td>
</tr>
</tbody>
</table>

<sup>a</sup>1998 Pre-fertilization data.

<sup>b</sup>All stations except OK8, Armstrong Arm.

<sup>c</sup>Average of Junction, Clearwater (Peace Reach) and Forebay stations.
and creates a coastal-like ecosystem in an interior biogeochemical and climatic setting.

Present State of the Reservoir

The impoundment of the Peace River Canyon in 1968 created British Columbia’s largest lake/reservoir ecosystem in what was previously three large river valleys and the Peace canyon. The inundation of approximately 1700 km² of forested land that was only minimally harvested prior to flooding catalyzed an abrupt major release of dissolved and particulate nutrients to the new reservoir, resulting in elevated carbon production in the ecosystem over its first decade of development (Hall et al. 1999; Stockner et al. 2000). But this source of nutrients from reduction of organic soil and flooded vegetation was limited, and by the middle of the second decade (1980s) and well into the third decade (1990s) the reservoir gradually lost its higher ambient nutrient concentrations, due largely to low P retention (high flushing) and to high export losses of C, N and P (discharge). The reservoir has also lost most all of its littoral biogenic production owing to wave-erosion and ice-scour during the >11-m annual drawdown and annual cycle of summer/fall inundation and winter/spring desiccation. We opine that through the past three decades, collectively these events (export, drawdown, flushing, sedimentation) have resulted in a gradual nutrient deficit where nutrient losses have outweighed inputs and led to the process of ‘oligotrophication’ of the ecosystem with ever declining biogenic C production (Stockner et al. 2000). This type of boom and bust sequence is common in newly created riverine valley reservoirs such as Williston, and this pattern of aging eventually to a stage of equilibrium with a new, more balanced nutrient input/output requires about 20 to 30 years (Ostrofsky and Duthie 1980; Grimmard and Jones 1982). Based on an analysis of nutrient data from 1975 to 1988 the trophic status of Williston Reservoir was oligotrophic. Our 2000 limnological and fisheries results now place its trophic state to ultra-oligotrophic. Further studies will be necessary to ascertain whether equilibrium with nutrient supply in each of the three major basins after 40 years of ontogeny has in fact occurred.

Conclusions

Williston Reservoir, British Columbia’s largest lacustrine ecosystem is a physically complex and highly dynamic, wind-driven system, strongly influenced by the amalgam-

![Fig. 16. Trends in average C primary production and average fish densities by reach based on limnological and acoustic surveys in 2000.](image)

| TABLE 8. Comparison of 1988 and 2000 average acoustic fish abundances in each reach of Williston Reservoir |
|-------------------------------|------------------|------------------|
| Reach                        | B.C. Fisheries August 2000 | Biosonics September 1988 |
| (No.)                        | (No./ha)          | (No.)            | (No./ha) |
| Parsnip                      | 239,000           | 73               | 366,000  | 109        |
| Junction                     | 532,000           | 26               | 2,350,000| 115        |
| Finlay                       | 3,739,000         | 133              | 1,423,000| 50         |
| Peace                        | 1,410,000         | 52               | 1,659,000| 60         |
| Total                        | 5,920,000         | 75               | 5,798,000| 72         |

*Weighted average densities derived from reach populations.
Acknowledgements

The Peace/Williston Fish and Wildlife Compensation Program funded this work. $^{14}$C primary productivity counts were counted and tabulated by Shannon Harris, Department of Earth and Ocean Sciences, University of British Columbia. Her work and the support of Ken Hall, Institute of Resources and Environment, and Paul Harrison, Department of Earth and Ocean Sciences, University of British Columbia, are most appreciated. Special thanks are extended to Behzad Imanium, Earth and Ocean Sciences, University of British Columbia, for bacterial enumeration, and to Danusia Dolecki, Fisheries Research, University of British Columbia, for zooplankton identification, enumeration and reporting. Thanks also to George Scholten, Ministry of Water, Land and Air Protection, for conducting hydroacoustic surveys, Patricia Woodruff, British Columbia Conservation Foundation, for assisting in data analyses and to Don Miller and Mike Lindsay of Kootenay Wildlife Services, Nelson, for trawl sampling. Tim Stiemer of Williston Lake Charters provided and operated the boat for hydroacoustic surveys. Finally, we wish to acknowledge the field support of R. Zemlak and R. Pillipow with sample collection, and the extra effort given by Peter Kyllo (owner/operator Finlay Bay Resort) for jet-boat service and assistance. His willingness to offer schedule flexibility was an important component for the successful completion of this logistically difficult project.

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Fig. 17. Schematic of the pelagic food webs of interior and coastal British Columbia lakes (Stockner and Porter 1988).


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