THE FISHERIES POTENTIAL OF A NEW PRAIRIE RESERVOIR: A MANAGEMENT PERSPECTIVE.

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Dedication

To my wife, Lisa Anne Campen, thank you for your love and support, without which this project would not have been possible.

Abstract

Reservoirs are the predominant standing water in the prairie regions of North America and provide major sport fishing opportunities. Reservoirs are young aquatic ecosystems. This study investigates trophic dynamics of reservoirs from three different perspectives: littoral productivity by morphometry and hydrological regimes in reservoirs; zooplankton development and production in a new reservoir; and the impact on growth and recruitment of a top predatory fish lacking appropriate food resources. Water level fluctuations significantly reduce littoral productivity and shift trophic energy flows towards pelagic resources. Pelagic production is positively influenced by appropriate nutrients and increased water residence time. A lack of intermediate zooplanktivorous fish species weakens the link between pelagic primary production and higher trophic levels. The resulting simplified food webs reduce growth and recruitment of top predatory fish. Thus, management must consider introducing species capable of linking the various resources within a reservoir to optimize the fishery potential.

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List of Abbreviations, and Nomenclature

Abbreviations	Definition
AESRD	Alberta Environment and Sustainable Resource Development
ASRD	Alberta Sustainable Resource Development
CPUE	Catch per Unit Effort
DD	Draw Down
FSL	Full Surface Level
FWIN	Fall Walleye Index Netting
FWMIS	Fish and Wildlife Information System
ILL	Index of Littoral Loss
K_d	Light Extinction Coefficient
VBGF	Von Bertalanffy Growth Function
WLF	Water Level Fluctuation
WRT	Water Residence Time
Z_{eu}	Euphotic Depth
Z_{sd}	Secchi Depth

Chapter One: **Introduction.**

Reservoirs are artificial lakes which have been created by man for over five millennia (Roberts 1977), originally to collect, store and distribute water for irrigation and drinking purposes. Large modern reservoirs are now developed to include flood control and hydroelectric power production as well (Baxter 1977a). The rate of construction of large reservoirs in developed regions peaked during the seventies, and has since diminished (Benson 1982, Rosenberg et al. 2000), primarily as a result of most prime sites having been exploited, and opposition from environmental groups (Benson 1982). However, developing countries continue to build dams at a rapid pace (Miranda 2001), and globally, the number of new reservoirs continues to increase (Downing et al. 2006, Chao et al. 2008).

Reservoirs have changed the distribution of standing water globally, especially in semi-arid regions, where natural lakes and ponds are rare (Wetzel 2001). In water-scarce regions, reservoirs facilitate settlement and the development of agriculture (Topham 1982) and therefore form a growing proportion of standing water in those regions (Fernando and Holčík 1991).

The primary functions of modern reservoirs are storage and distribution of water for drinking and irrigational purposes, flood control and hydropower production. At the same time, these water bodies are productive aquatic ecosystems systems that can contribute significantly to both commercial and recreational fisheries (Oglesby 1985) when managed appropriately. Reservoirs make a significant contribution to commercial and recreational fisheries globally (Miranda 1999).

Commercial fisheries are especially important in Asia, Africa and South America where they provide a source of high-quality, low-cost animal protein (Miranda 2001). In developed regions, such as Europe and North America and recently Australia, recreational fisheries have become a socially and economically valuable recreational activity of these water bodies (Jackson and Marmulla 2001).

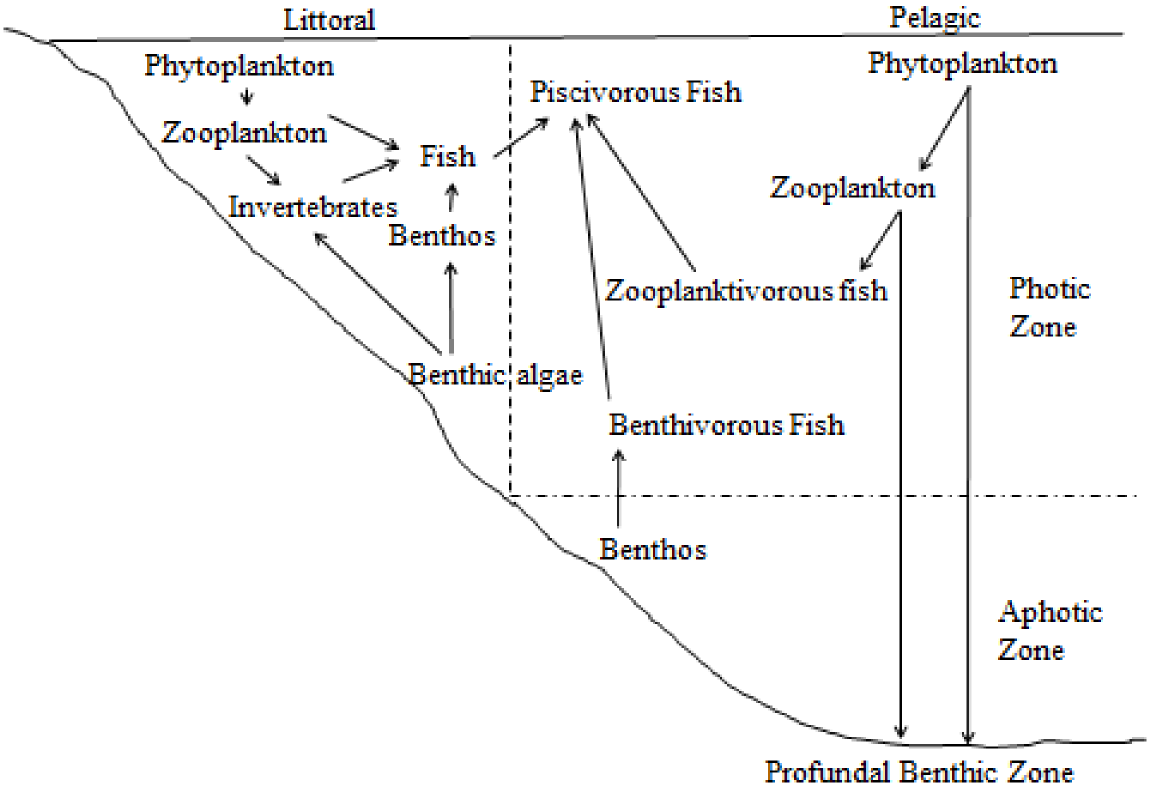

Figure 1.1. A view of a simplified natural lake food web showing the three primary trophic pathways, the littoral, pelagic and profundal, linked by highly mobile fish consumers.

The capacity of natural lakes to support productive fisheries stems primarily from food webs represented by three primary trophic pathways, the littoral, the pelagic and the profundal (Figure 1.1). The littoral pathway is supported by benthic primary production, originating from rooted plants, their epiphytes, and benthic algal communities; the pelagic pathway is supported by the production of the plankton communities, and the profundal is based primarily on sedimentation (Vander Zanden and Vadeboncoeur 2002). These trophic pathways typically have their own primary consumers, but, are usually linked by mobile higher-level consumers such as fish (Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002) (Figure 1.1).

Before 1990, reservoirs were thought of as identical to natural lakes and limnological understanding of reservoirs was based on earlier classical lake studies (Thornton et al. 1990). This perspective has changed since, and reservoirs are presently recognized as complex aquatic ecosystems in their own right, which are distinct from lakes (Wetzel 1990, Kalff 2002) with key fundamental differences reflected by morphometric and hydrological differences (Cyr 1998, Wetzel 2001, Kalff 2002). As an essentially dammed river, the resultant reservoir is often long and narrow with steep sides, and productivity is determined by water residence time and water level fluctuation (Furey et al. 2004a, 2006, Obertegger et al. 2007).

Large hydro-producing reservoirs have high water level fluctuations whereas storage reservoirs usually have low water level fluctuations (Miranda 2001, Miranda and Bettoli 2010). Reservoirs located low in the watershed have shorter water residence times than those within the headwaters of the watershed (Miranda 2001). Furthermore, the morphometry of reservoirs is characterized by narrow, steeply sloped reaches, resulting in the desired high ratio of reservoir volume to the size of the dam (Miranda 2001).

Water level fluctuation can severely limit development of littoral productivity within reservoirs (Furey et al. 2006, Cott et al. 2008), and the magnitude, duration, and timing of water level fluctuations are critical management variables that affect the productivity and development of littoral communities (Bernacsek 1984, Miranda 2001, Cott et al. 2008). The limitations imposed by water level fluctuations result due to decreased presence and stability of littoral habitat, resulting in decreased production of macrophytes, algae, and their affiliated benthic invertebrates (Sutela et al. 2013). Lowering of water levels can expose the littoral zone to the elements of wind and ice which can erode sediments and make shoreline sediments incapable of supporting aquatic plants and invertebrates. This decrease in productivity of the littoral zone makes the pelagic and profundal trophic pathways the primary resources supporting the productive capacity of reservoirs (Rooney and Kalff 2000).

Reservoirs differ from most lakes in regards to their hydrology, in that they are usually constructed in deep valleys along the main stem of higher order rivers, in contrast to lakes which are generally situated in headwater reaches (Kalff 2002). Thus water residence times tend to be much shorter in reservoirs than in lakes of the corresponding size, and short water residence time can limit the production of plankton, especially zooplankton (Baxter 1977a, Obertegger et al. 2007, Obertegger et al. 2010). Short water residence time can dilute and flush out nutrients, which negatively affect both pelagic and profundal production.

Reservoirs differ from natural lakes in their morphology, represented mainly by higher water depth and narrow, steep-sided basins with the greatest depth at the outlet (Wetzel 1990, 2001, Kalff 2002). Steeper slopes allow for higher rates of erosion of the reservoir shores and slumping of the slopes within the reservoir (Håkanson 1977). Increased erosion and slumping results in higher turbidity which in turn can adversely affect phytoplankton and littoral production due to reduced light penetration. Furthermore, basin slope has been shown to have an effect on primary littoral production as aquatic macrophyte biomass decreases with increasing slope (Duarte and Kalf 1986, Rowan et al. 1992, Evtimova and Donohue 2016).

Morphometry and hydrology can limit the productivity of all three trophic pathways resulting in major limitations on the fishery productive capacity of reservoirs. Thus management of reservoir fisheries can be very challenging. Furthermore, these challenges can be made more challenging by the scarcity or absence of lentic fish species in many river systems, and habitat fragmentation imposed by dams which inhibit access to colonizing fishes. Thus, the challenge of managing fisheries has many dimensions, and, the inability of some reservoirs to develop appropriate food webs, due to the lack of suitable species capable of linking energy resources, can further complicate the development of desired and self-sustaining higher trophic level species (Schindler and Scheuerell 2002, Vander Zanden and Vadeboncoeur 2002).

Reservoirs are colonized by the fish communities found in the parent stream or river capable of adapting to the reservoir environment (Fernando and Holčík 1991, Miranda 1999, Irz et al. 2006). Following fisheries management objectives focused primarily on maintaining sustainable, highly productive stocks, for commercial or recreational fisheries (Bernacsek 1984, Bernacsek 2001), managers frequently stock these reservoirs with exotic or indigenous high trophic level species. However, when stocked with high-trophic level species, inadequate fish assemblages might lack the appropriate species diversity to link the energy resources within the reservoir to higher trophic levels (Miranda et al. 2008). A solution to mitigate adverse impacts of sub-optimal fish assemblages is the stocking of appropriate forage fish that can provide the necessary linkages, and compensate for many of the inherent constraints on productive capacity. Stocking of forage fish has been used successfully in the United States as means of supplying food resources and linking energy resources to enhance growth and recruitment of piscivorous target species in reservoirs (Devries and Stein 1990).

Few natural lakes are present in southern Alberta, due to the semi-arid climate. Therefore, reservoirs are the predominant type of standing water body, and as such constitute the principal lentic fish habitat in the region (Mitchell and Prepas 1990). Many of the reservoirs were used as commercial fisheries in the early twentieth century and as such, they were stocked with lake whitefish, *Coregonus clupeaformis,* and walleye, *Sander vitreum* amongst other species, to augment commercial fisheries at the time (Nelson and Paetz 1992). However, commercial fisheries have declined since the peak yields of the 1950’s and 1960’s, and the demand for recreational sports fishery has greatly increased (Nelson and Paetz 1992). Commercial fisheries were discontinued in Alberta in 2014 due to unsustainability (AESRD 2014a). With a ratio of approximately 336 000 anglers to about 1100 lakes, Alberta has more anglers per lake than any other prairie province (Zwickel 2012). Saskatchewan and Manitoba have around 143 000 and 130 000 anglers respectively (Barrow 2012), and both provinces have around 100 000 lakes, reservoirs, and ponds each. The high ratio of anglers to lakes places a high demand for recreational fisheries in Alberta. Sports fishing is a socially and economically valuable recreational activity for Alberta, contributing over $488 million to the provincial economy in 2010 (Barrow 2012, Zwickel 2012). Because of this, the focus of fisheries management has shifted towards the management for recreational fisheries. One way this is achieved is by augmenting angling opportunities with extensive stocking programs (AESRD 2014b).

The stocking programs in Alberta have been focused on desired recreational target species such as various trout species and restocking species such as walleye and arctic grayling *Thymallus arcticus* to redevelop self-sustainable populations (AESRD 2014b). Development of fisheries in new water bodies is meant to increase fishing opportunities. Stocking of new water bodies with target species such as walleye is intended to produce self-sustaining populations requiring no further stocking (AESRD 2014b). Alberta, however, has no stocking programs that include forage fish species, exotic or indigenous, to enhance the fishery potential of target fisheries.

In the prairie region of southern Alberta, rivers are usually 5-6th order streams, populated by primarily benthivorous intermediate consumer species (Romanuk et al. 2006). Southern Alberta’s native lotic fish communities, however, consist of cool-water species (Mitchell and Prepas 1990, Nelson and Paetz 1992). These cool-water fish communities consist of apex predators, burbot *Lota lota* and northern pike *Esox lucius* and intermediate consumers such as white sucker *Catostomus commersonii*, longnose sucker *Catostomus catostomus*, lake chub *Couesius plumbeus*, emerald and spottail shiner *Notropis atherinoides* and *N. hudsonius*. Other cool-water species such as lake whitefish and walleye will only be present if there are upstream sources or they are stocked. Only species capable of adapting from lotic to lentic environments can successfully colonize reservoirs (Barbour and Brown 1974, Fernando and Holčík 1991). Fish adapting to lentic environments favor shallow littoral regions (Fernando and Holčík 1991). However, riverine fish communities of lower order streams generally lack zooplanktivorous species which could inhabit the pelagic zones of reservoirs (Miranda et al. 2008). This lack of mainly intermediate pelagic fish species could impair the crucial link between pelagic primary production and apex predators, resulting in impoverished food webs and energetic bottlenecks (Post et al. 2000, Brinkmann and Rasmussen 2010). There is a need for pelagic forage fish species to link energy transfer across habitats.

To support a healthy fishery of piscivorous target species such as walleye within a reservoir, managers must ensure that appropriate forage fish, which fulfills the ontogenetic requirements of the piscivorous target species, are capable of colonizing the reservoir. If no upstream sources are available to colonize the reservoirs, then these fish must be stocked to support the target fishery.

1.1 Outlook

This thesis consists of three chapters presenting research that highlights three essential elements of biological reservoir function which help in understanding the dynamics of energy transfer in the aquatic ecosystem of reservoirs in southern Alberta.

(1) The effects of hydrological regime and morphometry on the loss and availability of littoral habitat.

(2) the availability of pelagic energy resources.

(3) the growth rate and recruitment of top predatory walleye in a simplified food web ecosystem.

The first study (Chapter 2) compared metrics of basin slope, water level fluctuations, water residence time and Secchi depth to investigate differences between lakes and on- and off-stream reservoirs. A new metric, the index of littoral loss (ILL) as a function of drawdown and euphotic depth, was developed. The ILL was compared to the littoral loss as a function of littoral surface area lost and littoral surface area at full storage level measured from bathymetric maps. Furthermore, ILL was compared to a semi-quantitative assessment of macrophyte presence and abundance in lakes and reservoirs. These comparisons were to determine if ILL would be a valuable first approximation of littoral loss due to drawdown in reservoirs. Chapter 2 also characterized the relationship between the hydrological regime and zooplankton, as reflected by water residence and the abundance of zooplankton.

The second study (Chapter 3) examines the development of a pelagic zooplankton community in a newly formed prairie reservoir, Pine Coulee Reservoir. Pine Coulee's zooplankton community and biomass are compared to other reservoirs in the same geographical region to determine if the biomass of primary consumers is capable of supporting a zooplanktivorous fish community linking the pelagic resource to higher trophic levels.

Finally, the third study (Chapter 4) examines the fish community structure of Pine Coulee Reservoir, as well as the recruitment success and growth rates of walleye in the reservoir. Comparison of the fish community structure in Pine Coulee to the other reservoirs will determine if the reservoir has a suitable prey resource to support the walleye population. Comparison of the walleye community structure and growth rates in Pine Coulee to the other reservoirs will determine if recruitment and growth rates are compromised as suspected.

Together, these three aspects of the study will provide insight into possible bottlenecks in the development of reservoir ecosystems, and highlight areas which must be managed to improve ecosystem health, and the fishery potential of reservoirs.

Chapter Two: **Littoral Habitat Loss Due to Drawdown in Prairie Reservoirs.**

2.1 Introduction

Reservoirs form a considerable proportion of standing water in many areas worldwide (Fernando and Holčík 1991, Wetzel 2001, Kalff 2002, Krolová et al. 2012). Southern Alberta is a temperate semi-arid prairie region, with severe climatic limitations on agriculture. Therefore, an integral component of settlement and development of agriculture has been the development of irrigation infrastructure (Topham 1982). South western Alberta is well supplied by rivers that drain the eastern slopes of the Rocky Mountains wherein surface water acts as supply for the region's water needs. To facilitate irrigation, networks of reservoirs and canals have been built to distribute water. Storage reservoirs collect and contain water to provide supply in times of need, and in southern Alberta consist of on-stream and off-stream impoundments. On-stream reservoirs are generally constructed on large 5-6th order rivers; these reservoirs serve to regulate flows by storing the peak flow waters in spring and releasing these waters during the low flow periods of summer. Off-stream reservoirs are generally built in natural low-lying areas such as wetlands or coulees. Water is diverted from the main stems of rivers via the canal system to the off-stream reservoir systems. These systems can consist of multiple reservoirs connected by canals and are mainly used for irrigation purposes. Off-stream reservoir systems are mostly flow through systems with excess water being returned to the reservoir or river via return flow canals (AGRIC 2000).

Due to the semi-arid climate of southern Alberta the region has very few natural lakes; as a result, reservoirs are the predominant standing water habitat in the region

(Mitchell and Prepas 1990). Reservoirs have attributes similar to lakes. However, they can be very different with regards to their physical and trophic structures (Wetzel 1990, 2001, Kalff 2002). Reservoirs differ from natural lakes, reservoirs are younger and generally have steeper basins. Reservoirs have their deepest areas at the outlet end, whereas, lakes usually have their deepest point towards the center of the lake (Wetzel 2001, Kalff 2002). Natural lakes are usually situated in the upper headwater regions have fairly shallow gently sloping basins. This characteristic accentuates the development of a littoral zone within natural lakes. Natural lakes found within the prairies are predominantly kettle lakes which are supplied by ground water. In natural lakes, water level fluctuations follow natural wet and dry cycles throughout the year, with exceptions during floods or droughts at which time these fluctuations can be exacerbated (Baxter 1977b, Turner et al. 2005). Reservoirs, on the other hand, are usually situated further downstream in steep river main stems or in similarly shaped basins such as off-stream coulees, to achieve the desired high ratio of water volume to dam size (Miranda 2001). These steep-sided basins can limit the development of littoral zone within these water bodies. Furthermore, reservoirs often have rapid hydraulic through-put and thermal stratification is usually less stable compared to natural lakes (Wetzel 2001, Kalff 2002).

Natural lakes have three primary trophic pathways: the pelagic, based on plankton; the littoral, based on the rooted plant and benthic algae community; and the profundal, based on hypolimnetic production and sedimentation (Vander Zanden and Vadeboncoeur 2002). These trophic pathways are linked by mobile higher-level consumers, such as fish (Schindler and Scheuerell 2002, Vadeboncoeur et al. 2005). Except in large deep lakes, the littoral and profundal energy resources in lakes exceed those of the pelagic (Eggers et al. 1978). In reservoirs situated within steep-sided river mainstems and coulees formed by glacial outwash or wind, the littoral zone development is often severely limited (Cyr 1998). Moreover, the littoral zone is further restricted by water level fluctuations, which are usually greater in reservoirs than in natural lakes (Wetzel 2001). Wave action and associated turbidity along the shores also contribute to the reduction in littoral development in reservoirs due to erosion and sedimentation (Rowan et al. 1992, Cyr 1998). Profundal activity is affected by either the rapid throughput washing particulate matter, biological and abiological, in the water column downstream or the particulate matter decomposing in the deep basins before settling. Therefore in contrast to the situation in most natural lakes, the pelagic zone in reservoirs is often the dominant habitat, with littoral and profundal habitats much less prominent. reservoir pelagic zones often dominate the littoral and profundal zones. This can have significant consequences for higher trophic levels as these reservoirs are usually colonized by riverine species that can adapt from lotic to lentic conditions (Barbour and Brown 1974, Fernando and Holčík 1991). Riverine fish communities generally lack pelagic zooplanktivore species (Miranda et al. 2008) or species that may link inshore and offshore habitats. The piscivorous species found in these communities adapt to littoral habitat (Vadeboncoeur et al. 2005) and would thus be impacted by the lack of the littoral energy resources.

The littoral zone is the zone most impacted by the drawdown in a body of water (Furey et al. 2004b, Cott et al. 2008). Research has taken place on the effect of drawdown on aquatic macrophytes (Paller 1997), invertebrates (Furey et al. 2006) and fish (Fischer and Öhl 2005), but little research has been done on the littoral community as a whole (Gasith and Gafny 1990). With drawdown impacting the littoral area of these reservoirs, a stronger reliance on the benthic and pelagic parts of the food web is produced (Rooney and Kalff 2000).

This study compares the morphometry of storage reservoirs, both on-stream and off-stream, situated within the irrigation system of southern Alberta to that of comparably sized Alberta lakes (Mitchell and Prepas 1990). The primary focus of these comparisons is on metrics that reflect the capacity of littoral development and stability. These metrics include reservoir basin slope (Duarte and Kalff 1986, Rowan et al. 1992), seasonal water level fluctuations (Cooke 1980, Coops and Hosper 2002, Van Geest et al. 2005), water residence time (Obertegger et al. 2007) and Secchi depth (Canfield et al. 1985, Chambers and Kaiff 1985, Chambers and Prepas 1988). These metrics are compared to an index of littoral loss ratio based on drawdown and the euphotic depth in the reservoirs. The index of littoral loss could be a valuable first approximation for managers to determine the limitation imposed on the ability of littoral development in a reservoir by water level fluctuations. Knowing the limitation imposed on littoral development within reservoirs by water level fluctuations is crucial for the development of sustainable fisheries.

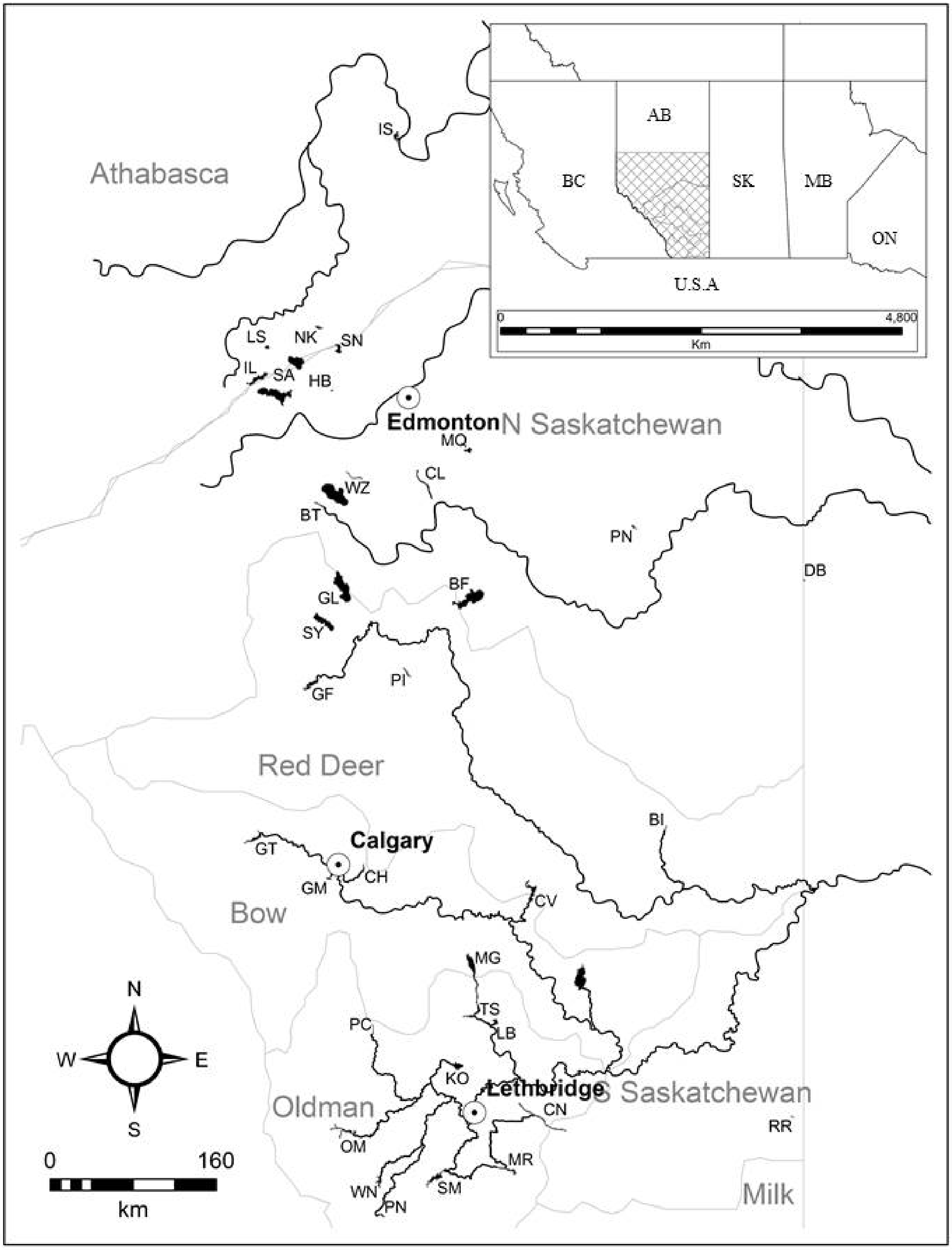

Figure 2.1. Reservoir and Lake locations within southern Alberta. Lake and reservoir abbreviations listed in Table 2.1.

2.2 Methods and Study Area

2.2.1 Study Area

South central Alberta is temperate semi-arid prairie region which forms the northwestern extreme of the North American Great Plains area. This ecosystem stretches east across three Canadian provinces, Alberta, Saskatchewan and Manitoba and south through numerous states in the United States to the Rio Grande river. The area falls within the rain shadow of the Rocky Mountains, on the western border of the province. The twenty reservoirs and the eighteen lakes of this study lie within the southern half of the province between the 49th and 54th parallel. Twenty reservoirs in south central Alberta were selected (Mitchell and Prepas 1990) to represent typical reservoirs found within the Canadian prairie eco zone. Eighteen comparable lakes, located within the same region, were selected from literature for comparison to these reservoirs (Figure 2.1).

2.2.2 Methods

Morphometric data were collected for all waterbodies from Alberta Sustainable Resource Development (ASRD), data collected during 2012 sampling season, and literature (Mitchell and Prepas 1990). The data was used to compare the differences between lakes and reservoir sub-types (on-stream and off-stream) to determine differences with respect to metrics that reflect the capacity of littoral development and stability.

Bathymetric maps and depth-area hypsographic graphs were used to calculate the percent basin slope, littoral area (km^2) available at full storage level (FSL) and littoral area loss due to water level fluctuation. Water level fluctuation (WLF), water residence time (WRT) and Secchi depths (Z_{sd}) measures were obtained from literature and the ASRD. The reservoirs surface area ranged from 0.51 to 63.07 km^2, and the lakes had surface area's ranging from 0.40 to 96.70 km^2. Maximum depth varied from 5.5 to 68.6 m for reservoirs and 3.1 to 30.0 m for lakes (Table 2-1).

Bathymetric maps and hypsographic curves were used to determine the average slope of the reservoir and lake basins. The average slopes were used to compare and determine the relationship if any with regards to the semi-quantitative index of littoral development and stability. The average basin slopes for each reservoir was calculated by utilizing Adobe Acrobat Pro 10 to determine the surface area for each isobath interval from bathymetric maps. The area was then treated as the area of a circle. The formula was then converted to determine the radius. The radii from each isobath area were then subtracted from each subsequent isobath area individually to determine the difference between radii, using rise over run, and the isobath interval is divided by the difference in radius and multiplied by 100 to get percent slope for each contour interval. These slopes were averaged to determine the average slope for each reservoir basin. Basin slope was compared between on-stream and off-stream reservoirs and drainage and seepage lakes as well as being compared to the macrophyte presence for lakes and reservoirs.

The littoral area available within a reservoir at (FSL) was calculated from bathymetric maps using the euphotic zone depth (m) (Z_{eu}). The surface area of each isobath was calculated and used to determine the surface area available to littoral development assuming stable water levels. This was done for the low level after the drawdown. The difference was then calculated as a percentage of the original littoral zone lost after the drawdown of the reservoir surface.

Water level fluctuation data, an average of the annual rise and fall of the water level, for these reservoirs and lakes was compared to the categories of on-stream, off-stream, and drainage, seepage and macrophyte presence. The WLF data was obtained from the ASRD website for 2012 summer season, for the lakes not covered by ASRD the data was obtained from literature (Mitchell and Prepas 1990) (Figure 2.2).

Water residence times, the time taken for the water volume in a water body to be completely replaced (Wetzel 2001, Kalff 2002), was obtained from ASRD and literature (Mitchell and Prepas 1990). For the reservoirs not covered by these sources, WRT was determined by the average outflow volume (m^3/sec) and the volume of the reservoir (Wetzel 2001, Kalff 2002). Seepage and evaporation were not taken into account.

Secchi depth was used to calculate the Z_{eu} within the reservoirs and lakes. The calculation for the euphotic zone was done by calculating the vertical light extinction coefficient (K_d) and using the conversion factor, 1.7, developed by H. H. Poole and W. R. G. Atkins (1929) (Kalff 2002) (Equation 1).

$$K_d = \frac{1.7}{Z_{sd}}$$

Equation 1

The vertical light extinction was then used to calculate Z_{eu} (Equation 2) for each water body.

$$Z_{eu} = \frac{\ln 100}{K_d}$$

Equation 2

The lakes and reservoirs were ordered into three categories based on macrophytes presence, 1; dense, covering large areas with dense growth within the reservoir, causing complaints by users, 2; sparse, covering small areas with sparse growth within the reservoir, no general complaints from users and 3; none, no discernible macrophyte beds present within the reservoir. Macrophyte presence was determined from descriptive reports in the literature (Mitchell and Prepas 1990) and observations from the summer seasons of 2011 and 2012 for five reservoirs not found in the literature. Chin, Keho, Oldman, Pine Coulee and Waterton reservoirs were five of eight reservoirs sample fished during the 2011 and 2012 sampling season. The perimeters were navigated during angling between gill net set times. Reservoirs were visited monthly for the summer season resulting in a total of eight visits to each reservoir.

Furthermore, the reservoirs were ordered into two sub-types based on location, on-stream and off-stream reservoirs.

The approximate index of littoral loss (ILL) was determined by dividing drawdown (DD) by the euphotic depth (Z_{eu}).

$$ILL = \frac{DD}{Z_{eu}}$$

Equation 3

The littoral area lost was measured from bathymetric maps so that it could be compared to the ILL, to determine the strength of the metric. This index could provide a valuable first approximation of littoral loss due to drawdown for managers (figure 2.2).

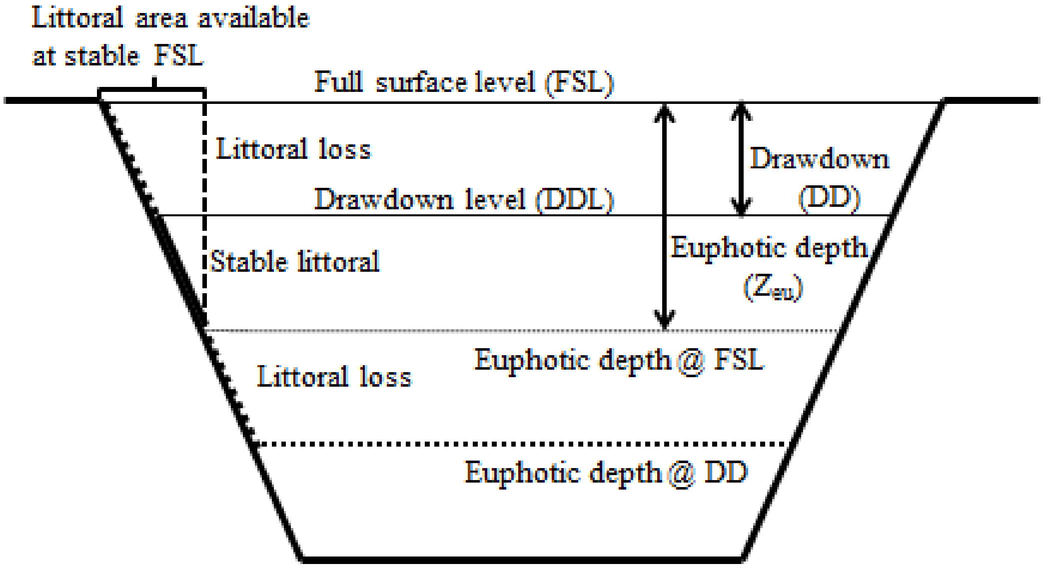

Figure 2.2. Diagram showing Littoral area and effects of drawdown. FSL, full storage level. DDL, drawdown level. DD, drawdown. Zeu, euphotic depth.

All statistical analyses were performed using the JMP 10.0.2 software package from SAS Institute Inc. 2012. Basin slope, water level fluctuation, Secchi depth and water residence time were compared between, lakes and reservoirs, and lake and reservoir sub-types (on-stream and off-stream) using one-way analysis of variance (ANOVA). Furthermore, the metrics were compared to macrophyte presence using one-way ANOVA. Post hoc Tukey-Kramer HSD was used to test for significant differences between the means of the factors. Regression analysis was used to investigate the relationship between the littoral loss ratio measured from bathymetric maps and the ILL. Rejection probability for all analyses set at $\alpha = 0.5$ level and all means are reported with ± SE unless otherwise stated.

Table 2.1. Location and physical parameters of the water bodies in the study, Reservoirs (top) and Lakes (bottom). Max depth represented by Z, mean depth - Z_{mean}, secchi depth - Z_{eu}, water level fluctuation – WLF and water residence time – WRT. Symbols represent, ‡- on-stream, §- hydro producer, ¶- saline water and N/A, not available.

Reservoir	N: Latitude	W: Longitude	Volume x10^6 (m^3)	Surface Area @ FSL (km^2)	Z (m)	Z_{mean} (m)	Z_{sd} (m)	WLF (m)	WRT (yr)	Weed Presence
Blood Indian Creek Reservoir † ‡	50º15′4.48″	111º12′34.05″	6.4	1.0	13.3	4.6	2.1	1.00	24.50	Dense
Chestermere Lake †	51º2′9.47″	113º48′54.08″	9.2	2.7	7.0	3.5	2.8	1.45	0.03	Dense
Chin Reservoir † §	49º36′7.51″	112º11′2.48″	200.9	15.7	22.6	12.8	1.8	4.50	0.31	Sparse
Coal Lake † ‡	53º4′13.34″	113º15′43.50″	38.8	10.9	5.5	3.5	1.8	1.00	0.85	Dense
Crawling Valley Reservoir †	50°54'36.97"	112°21'11.31"	130.0	23.2	16.8	5.7	2.6	0.60	1.40	Dense
Ghost Lake † ‡ §	51°11'40.91"	114°46'4.73"	159.1	10.1	34.0	14.5	6.4	5.30	0.03	Sparse
Gleniffer Lake † ‡	52°1'40.97"	114°16'9.64"	205.0	17.6	33.0	11.6	3.1	7.75	0.20	None
Glenmore Reservoir † ‡ §	50°59'10.14"	114°6'45.55"	23.4	3.8	21.1	6.1	7.5	3.45	0.07	N/A
Keho Lake †	49°57'2.82"	113°0'42.65"	98.2	22.1	6.9	4.6	2.2	0.63	0.47	Dense
Lake Newel †	50°23'56.35"	111°57'0.27"	321.0	63.1	12.2	3.9	2.5	0.88	1.50	Dense
Little Bow Lake †	50°11'40.00"	112°40'25.99"	23.6	5.4	16.8	6.4	3.4	0.35	0.06	Dense
McGregor Lake †	50°31'51.92"	112°54'1.97"	333.0	49.0	12.0	6.8	3.2	0.65	0.90	Dense
Milk River Ridge Reservoir †	49°22'4.95"	112°33'52.07"	128.3	13.7	19.2	7.8	1.2	2.28	0.38	Sparse
Oldman River Dam † ‡ §	49°34'59.50"	113°56'13.74"	128.3	24.3	68.6	20.2	1.2	7.18	0.17	None
Payne Lake †	49°6'39.00"	113°39'13.00"	9.2	2.2	7.3	3.8	2.5	0.78	0.40	Dense
Pine Coulee Reservoir † ‡	50°8'5.97"	113°44'7.60"	50.6	5.1	50.0	10.0	2.8	1.45	1.61	Sparse
Reesor Reservoir †	49°39'51.60"	110°6'20.40"	1.9	0.5	6.5	3.8	2.9	0.38	6.00	Dense
StMary's Reservoir † ‡ §	49°19'17.19"	113°11'5.67"	396.0	32.6	56.4	15.9	2.2	4.50	0.38	Sparse
Travers Lake † ‡	50°11'42.21"	112°46'14.88"	413.0	22.5	38.7	14.3	4.0	2.15	0.82	Dense
Waterton Reservoir † ‡ §	49°18'15.22"	113°40'52.13"	114.3	10.9	43.0	10.5	3.5	8.50	0.19	None
Battle Lake ‡	52º58′2.20″	114º10′53.99″	31.6	4.6	13.1	6.9	3.8	0.5	6	Dense
Buffalo Lake ‡ ¶	52º29′21.98″	112º52′49.34″	248.0	93.5	6.5	2.8	2.9	0.2	100	Dense
Dillberry Lake	52º34′36.17″	110º0′14.96″	2.2	0.8	10.7	2.8	4.6	0.2	100	Dense
Gull Lake	52º32′54.25″	113º59′45.62″	437.0	80.6	8.0	5.4	3.1	0.3	100	Dense
Hubbles Lake	53º33′50.67″	114º5′30.09″	4.0	0.4	30.0	10.1	3.9	0.2	100	Dense
Island Lake	54º50′57.73″	113º33′15.34″	29.2	7.8	18.0	3.7	4.3	0.2	16	Dense
Isle Lake ‡	53º38′3.91″	114º42′26.20″	94.8	23.0	7.5	4.1	1.8	0.5	9.5	Dense
Lac Ste Anne ‡	53º41′49.96″	114º23′34.56″	263.0	54.5	9.0	4.8	2.2	0.3	12	Dense
Lessard Lake	53º47′13.89″	114º39′21.37″	12.5	3.2	6.0	3.9	1.9	0.3	100	Dense
Miquelon Lake ¶	53º15′21.89″	112º54′8.62″	23.8	8.7	6.0	2.7	3.4	0.2	100	Dense
Nakamun Lake ‡	53º53′7.81″	114º12′36.24″	15.8	3.5	8.0	4.5	0.8	0.3	21	Dense
Peninsula Lake ¶	52º51′34.52″	111º29′9.71″	2.9	1.4	3.1	2.1	1.1	0.5	100	Sparse
Pigeon Lake	53º2′19.08″	114º5′43.19″	0.6	96.7	9.1	6.2	2.0	0.3	100	Dense
Pine Lake ‡	52º5′21.65″	113º26′26.88″	20.6	3.9	12.2	5.3	1.8	0.3	9	Dense
Sandy Lake ‡	53º46′35.84″	114º1′57.28″	29.4	11.4	4.4	2.6	1.5	0.3	100	Dense
Sylvan Lake ‡	52º21′17.25″	114º8′22.90″	412.0	42.8	18.3	9.6	4.7	0.3	100	Dense
Wabamun Lake ‡	53º32′47.47″	114º33′19.64″	513.0	81.8	11.0	6.3	2.3	0.3	100	Dense
Wizard Lake ‡	53º6′34.47″	113º50′6.91″	14.8	2.5	11.0	6.2	2.9	0.3	13.5	Dense

2.3 Results

The mean basin slopes for lakes and reservoirs ranged from 0.1 to 4.3 % with a mean of 0.5 ±0.2 % and 0.4 to 4.8 % with a mean of 1.8 ±0.3 % respectively. Basin slope for off-stream reservoirs ranged from 0.5 to 4.8 % with a mean of 1.7 ± 0.4 % and on-stream reservoirs basin slope ranged from 0.4 to 4.4 % with a mean of 1.9± 0.4 (Table 2.2). Mean basin slope was significantly steeper for the reservoirs than for the lakes in the area. Basin slope between on and off-stream reservoirs were not significantly different. However, there was a significant difference between lakes and both on-stream and off-stream reservoirs (Figure 2.4 a).

Mean water level fluctuation for the lakes ranged from 0.2 to 0.5 m with a mean of 0.3 ± <0.1 m. Reservoirs ranged from 0.4 to 8.5 m with a mean of 2.7 ±0.6 m (Table 2.2). WLF was significantly higher for reservoirs than lakes. Water level fluctuations for Off-stream reservoirs ranged from 0.4 to 4.5 m with a mean of 1.2 ± 0.4 m and on-stream reservoirs had WLF, which ranged from 1.0 to 8.5 m with a mean of 4.6 ± 0.9 m. Analysis indicated that the difference between lakes and on-stream and off-stream reservoirs were significant. On-stream reservoirs had the greatest WLF, followed by off-stream reservoirs and lakes with the lowest WLF (Figure 2.3 and 2.4 c).

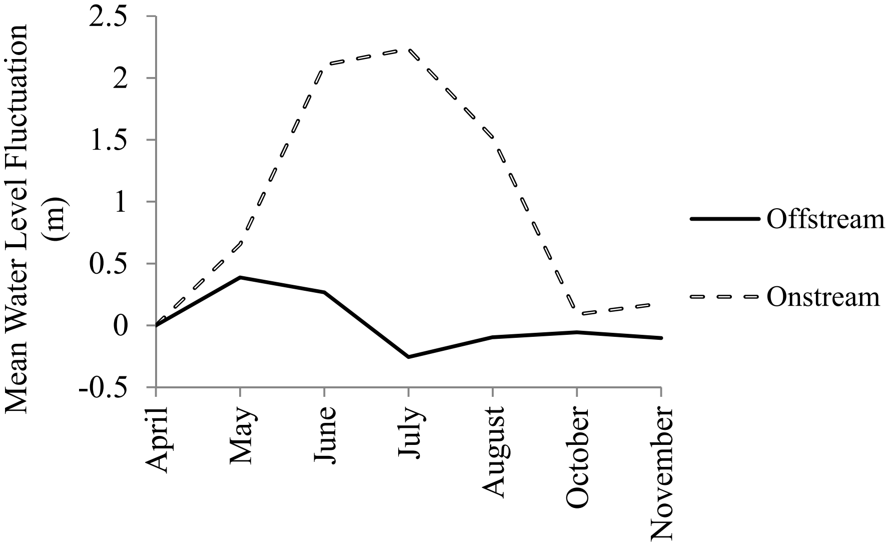

Figure 2.3. Mean water level fluctuation regimes during the open-water period for on-stream and off-stream reservoirs in south central Alberta.

Water residence time (WRT) was significantly different between lakes and reservoirs with lakes ranging from 6.0 to <100 yrs., mean of 66 ± 10 yrs., significantly higher than that of reservoirs which ranged from <0.1 to 25 yrs., mean of 2.0 ± 1.2 yrs. (Figure 2.4 b).

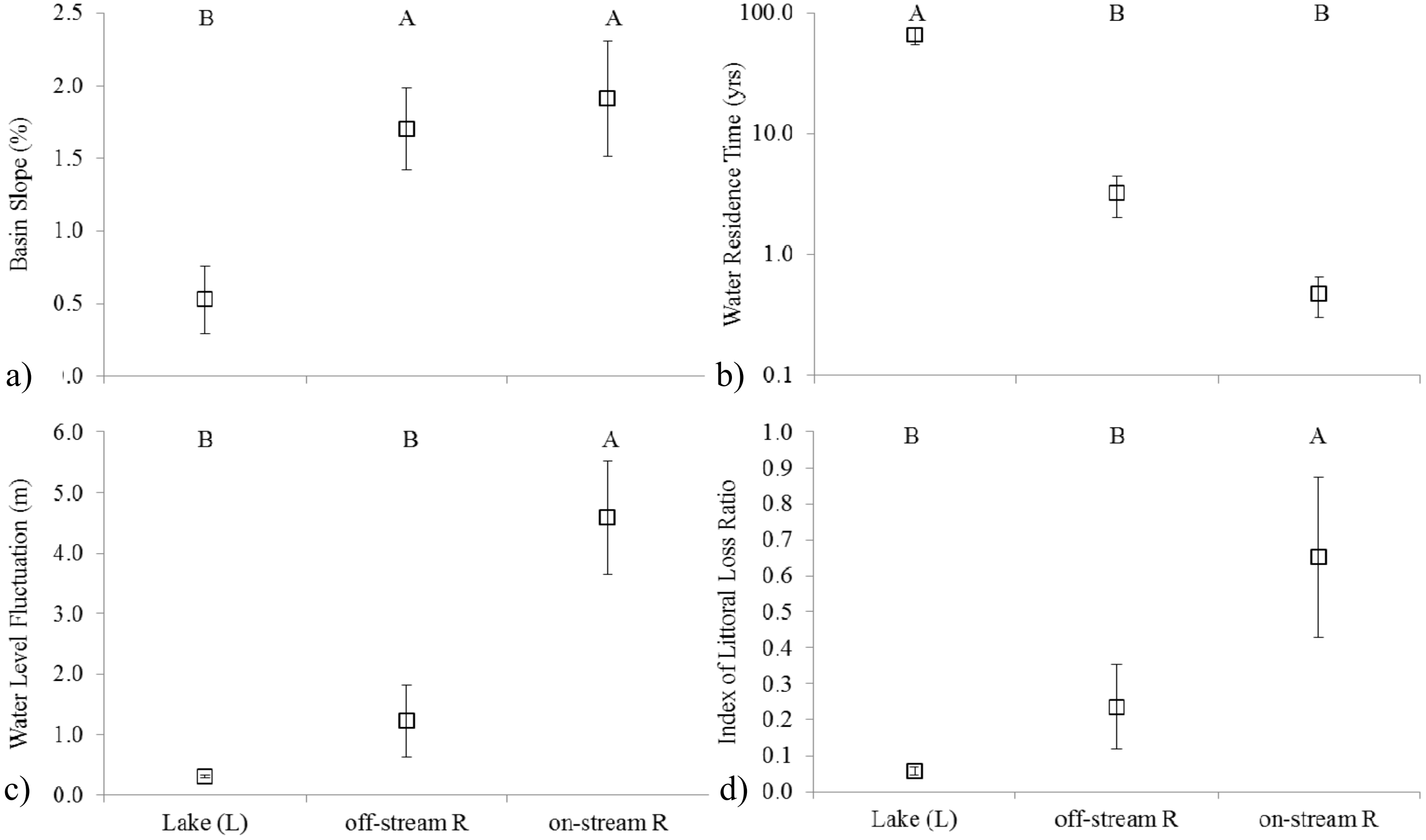

Figure 2.4. The comparison of the metrics which affect the capacity of littoral development and stability between natural lakes and on-stream, off-stream reservoir sub-groups. Waterbodies not connected by the same capital letter are significantly different. a) Basin Slope, ANOVA, $F_{2,35} = 5.809$, $p = 0.006$, b) Water Residence Time, ANOVA, $F_{2,35} = 20.258$, $p < 0.001$, c) Water Level Fluctuation, ANOVA, $F_{2,35} = 25.291$, $p < 0.001$, and, d) the Index of Littoral Loss, ANOVA, $F_{2,35} = 8.390$, $p = 0.001$. Lakes, n = 18; on-stream reservoir, n = 9 and off-stream reservoirs, n = 11, bars represent standard error.

Off-stream reservoirs had WRT's ranging from <0.1 to 25 yrs., with a mean of 3.3 ± 2.2 which were significantly longer than the on-stream reservoirs with WRT's ranging from <0.1 to 1.6 yrs., with a mean of 0.5 ± 0.2 yrs. (Table 2.2).

Secchi depth (Z_{sd}) was not significantly different between the reservoirs and the lakes or between lakes and reservoir sub-types, Lake Z_{sd} ranged from 0.8 to 4.7 m with a mean of 2.7 ±0.3 m, SE= and reservoirs ranged from 1.2 to 7.5 m with a mean of 3.0 ±0.4 m. Off-stream reservoir Z_{sd} ranged from 1.2 to 3.4 m with a mean of 2.5 ± 0.2 m and on-stream reservoirs ranged from 1.2 to 7.5 m with a mean of 3.6 ± 0.7 m (Table 2.2).

Linear regression of the index of littoral loss and the measured littoral loss of lakes and reservoirs revealed that ILL is a significant predictor of measured littoral loss, measured littoral loss = 0.973 ILL + 0.012, (Figure 2.5).

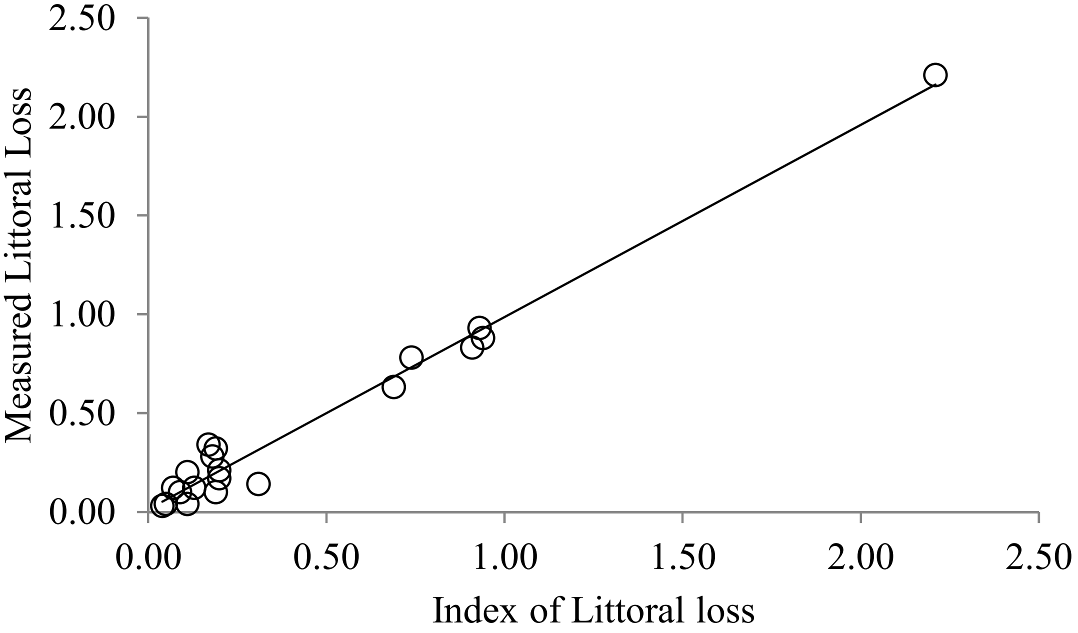

Figure 2.5. Linear regression model for the approximate index of littoral loss and measured littoral loss for reservoirs and lakes, $r^2 = 0.973$, $P = < 0.001$. Lakes encompassed in the area represented by the square.

The index of littoral zone loss based on drawdown was strongly related to the semi-quantitative biotic index based on macrophyte abundance (dense, sparse and none) (Table 2.2).

Table 2.2. The comparison of the index of littoral loss to the description of macrophyte presence in lakes and reservoir from literature. One-way ANOVA $F_{(2,16)} = 19.219$; $p < 0.001$, The macrophyte density categories not connected by the same letter are significantly different.

Index of littoral loss	Macrophyte presence	Waterbody type	Number (n)	Post Hoc
≤ 20%	Dense	Lake/Reservoir	18/11	A
> 20%	Sparse	Reservoir	5	B
> 70 %	None	Reservoir	3	C

Table 2.3. Metrics used to compare reservoirs (top) to Lakes (bottom). Symbol meanings; ‡ on-stream; § Hydro power producing; ¶ Saline. Headings; Z_{sd}, Secchi depth; WLF, water level fluctuations; WRT, water residence time; K_d, light extinction coefficient and Zeu, euphotic depth.

Reservoir	Z_{sd} (m)	WLF (m)	WRT (yr)	K_d	Z_{eu} (m)	Basin Slope (%)	Index of Littoral Loss	Measured Littoral Loss
Blood Indian Creek Reservoir ‡	2.1	1.0	24.5	0.8	5.7	1.3	0.2	0.3
Chestermere Lake	2.8	1.5	0.0	0.6	7.6	0.9	0.2	0.3
Chin Reservoir §	1.8	4.5	0.3	1.0	4.8	3.6	0.9	0.9
Coal Lake ‡	1.8	1.0	0.9	0.9	4.9	0.6	0.2	0.2
Crawling Valley Reservoir	2.6	0.6	1.4	0.7	7.0	0.6	0.1	0.1
Ghost Lake ‡ §	6.4	5.3	0.0	0.3	17.3	2.1	0.3	0.1
Gleniffer Lake ‡	3.1	7.8	0.2	0.6	8.3	1.5	0.9	0.9
Glenmore Reservoir ‡ §	7.5	3.5	0.1	0.2	20.3	0.4	0.2	0.3
Keho Lake	2.2	0.6	0.5	0.8	5.9	1.1	0.1	<0.1
Lake Newel	2.5	0.9	1.5	0.7	6.8	0.7	0.1	0.1
Little Bow Lake	3.4	0.4	0.1	0.5	9.2	1.9	<0.1	<0.1
McGregor Lake	3.2	0.7	0.9	0.5	8.7	0.5	0.1	0.1
Milk River Ridge Reservoir	1.2	2.3	0.4	1.4	3.3	2.2	0.7	0.6
Oldman River Dam ‡ §	1.2	7.2	0.2	1.4	3.3	2.0	2.2	2.2
Payne Lake	2.5	0.8	0.4	0.7	6.8	1.1	0.1	0.2
Pine Coulee Reservoir ‡	2.8	1.5	1.6	0.6	7.6	4.4	0.2	0.1
Reesor Reservoir	2.9	0.4	6.0	0.6	7.9	4.8	<0.1	<0.1
St. Mary's Reservoir ‡ §	2.2	4.5	0.4	0.8	6.1	2.4	0.7	0.8
Travers Lake ‡	4.0	2.2	0.8	0.4	10.8	1.3	0.2	0.2
Waterton Reservoir ‡ §	3.5	8.5	0.2	0.5	9.4	2.4	0.9	0.8
Battle Lake	3.8	0.5	6.0	0.4	10.3	0.6	<0.1	0.1
Buffalo Lake ¶	2.9	0.2	>100	0.6	7.9	0.1	<0.1	0.1
Dillberry Lake	4.6	0.2	>100	0.4	12.5	1.2	<0.1	<0.1
Gull Lake	3.1	0.3	>100	0.5	8.4	0.1	<0.1	<0.1
Hubbles Lake	3.9	0.2	>100	0.4	10.6	4.3	<0.1	<0.1
Island Lake	4.3	0.2	16.0	0.4	11.6	0.4	<0.1	<0.1
Isle Lake	1.8	0.5	9.5	0.9	4.9	0.1	0.1	0.1
Lac Ste Anne	2.2	0.3	12.0	0.8	6.0	0.1	0.1	<0.1
Lessard Lake	1.9	0.3	>100	0.9	5.1	0.3	0.1	0.1
Miquelon Lake ¶	3.4	0.2	>100	0.5	9.2	0.2	<0.1	0.2
Nakamun Lake	0.8	0.3	21.0	2.2	2.1	0.2	0.1	0.1
Peninsula Lake ¶	1.1	0.5	>100	1.5	3.0	0.3	0.2	0.1
Pigeon Lake	2.0	0.3	>100	0.9	5.4	0.1	0.1	0.1
Pine Lake	1.8	0.3	9.0	0.9	4.9	0.4	0.1	0.2
Sandy Lake	1.5	0.3	>100	1.1	4.1	0.1	0.1	<0.1
Sylvan Lake	4.7	0.3	>100	0.4	12.7	0.2	<0.1	0.1
Wabamun Lake	2.3	0.3	>100	0.7	6.2	0.1	<0.1	<0.1
Wizard Lake	2.9	0.3	13.5	0.6	7.9	0.6	<0.1	0.1

2.4 Discussion

The results of this study highlight the differences between the natural lakes as well as differences between on-stream and off-stream reservoirs particularly in regards to the degree of development of littoral habitat. Of the metrics that reflect the capacity of littoral development and stability namely, basin slope, water level fluctuations, water residence time and Secchi depth, all except Secchi depth were shown to have an influence on littoral development and stability within the reservoirs. Furthermore, the strength of these metrics with respect to the ratio of littoral loss based on drawdown and the euphotic zone is also demonstrated.

Basin slope was found to be significantly steeper in the reservoirs than in the natural lakes. This difference can be attributed to the construction of reservoirs predominantly in steep-sided coulees and river main stem channels. There was, however, no difference in basin slopes between on-stream and off-stream reservoirs or lakes. Basin slope is known to be a factor in the littoral development as it affects sediment distribution and stability (Håkanson 1977, Duarte and Kalf 1986). Fine grain sediments accumulate predominantly on slopes of less than 3% and rarely on slopes steeper than 10% (Rasmussen 1988a, Rasmussen 1988b). Steeper slopes also limit macrophyte development as steeper slopes are more prone to erosion by wave action to a deeper depth than shallow slopes (Rowan et al. 1992, Cyr 1998). The littoral slope has also been determined to be a predictor of the biomass of submerged macrophytes (Duarte and Kalff 1986). Shallow-slope water bodies offer greater sediment exposure than do those with steeper slopes and the sediment exposed increases with greater water level fluctuation.

Water level fluctuations are significantly greater in the reservoirs than in the lakes within the area. Water level fluctuations in the lakes are not regulated by weirs or any form of control structure and are small reflecting the natural wet and dry cycles throughout the year. Water level drawdown in these lakes can be enhanced by drought when they occur (Baxter 1977b, Turner et al. 2005). The large water level fluctuations in reservoirs, on the other hand, are mainly a reflection of the management function of the reservoir and can differ greatly in both timing and magnitude.

Overall, WLF's are known to be greater in reservoirs than in natural lakes (Lindström 1973); and differ among reservoirs based on their function, either water storage, flood control or hydro production (Baxter 1977b, Rørslett 1989). WLF for the on-stream reservoirs is significantly higher than that of their off-stream counterparts, this results in decreased littoral productivity, as littoral fish habitat, based on macrophyte development, tends to be greater in off-stream than on-stream reservoirs. Water level fluctuations are known to negatively affect aquatic macrophytes (Wilcox and Meeker 1991, Paller 1997, Furey et al. 2004a), invertebrates (Aroviita and Hämäläinen 2008, McEwen and Butler 2010) and fish (Paller 1997, Fischer and Öhl 2005, Benejam et al. 2008). Additional to the magnitude of WLF, timing can also have adversely impact on the littoral zone, low levels through winter in the area leaves the shores open to wind erosion and ice scouring. The timing of WLF may also affect fish production due to inundation or desiccation of spawning grounds. The largest rise and fall of water levels in these local reservoirs occurs April through October. The water levels are relatively stable through the winter months November to March, which are usually the lowest water levels (Figure 2.3). This pattern leaves the reservoir shores exposed during the winter months which in this area leave them vulnerable to ice scour and wind erosion that degrades their ability to develop littoral habitat.

Water residence time is much shorter in reservoirs than in natural lakes, WRT can be as short as a few weeks in some reservoirs, and may have important consequences for plankton productivity (see Chapter 3). Furthermore, WRT is significantly lower in the off-stream than the on-stream reservoirs. Short residence time in reservoirs is known to produce a longitudinal gradient in biological, chemical and physical factors that is based on flow. This contrasts the vertical gradient, based on thermal stratification, found in most lakes with a long residence time (Kennedy and Walker 1990). Water residence time can affect zooplankton and nutrient loading within water bodies. Short residence time can have a washout effect of nutrients released into the water column and limit deposition of fine sediments. Reduction in deposits can have negative impacts on the littoral zone with respect to macrophyte colonization. However, residence time cannot be considered to be a major limiting factor in the development of littoral zone within these water bodies as some of the reservoirs with short residence time have dense macrophyte beds.

Water transparency in this study did not differ between lakes and reservoirs, nor between on-stream and off-stream reservoirs. Light penetration is known to be a major factor in determining the maximum depth of macrophyte coverage (Canfield et al. 1985). However, the data indicates that the euphotic zone or depth of littoral zone is not different between the lakes and reservoirs of the region. This would indicate that the water quality with respect to transparency is similar between lakes and reservoirs, and thus the light regime should permit the development of littoral habitat to similar depths. Lakes in Alberta are known to be different than other north temperate lakes with the water being less colored due to less dissolved organic material (Chambers and Prepas 1988). This lack of colour is attributed to the small drainage areas of the lakes due to low relief. This cannot be concluded for reservoirs as Secchi depth is not only influenced by color but the turbidity produced by dissolved suspended solids and phytoplankton. Since reservoirs generally have much larger drainage areas than lakes they should have greater color and higher turbidity than lakes, these effects were not large enough to result in differences regarding Secchi disk transparency between reservoirs and lakes

The approximate index of littoral loss (ILL) based on drawdown and the euphotic zone is not significantly different from that derived from the detailed measurements on bathymetric maps of the reservoirs. The relationship between ILL and aquatic macrophyte development within the reservoirs reveals the existence of an important biotic threshold when drawdown starts to exceed 20% of the euphotic zone depth, no reservoir with drawdown more than 20% exhibits dense macrophyte growth, even though there is sufficient light to allow this. Reservoirs with drawdowns more than 20% of the euphotic depth exhibited spars macrophyte development and those with drawdown more than 70% support neither submerged nor emergent macrophytes (Table 2.2).

Reservoirs with no macrophytes generally experience drawdown exceeding euphotic zone leading to the inability of plants to establish and grow, likely due to the light regime traversing too rapidly along the basin slope. Reservoirs with dense macrophyte presence are similar to lakes, in that drawdowns are only 2 – 15% of the euphotic zone depth.

The comparison of lakes to reservoirs indicated that there are major differences between natural and constructed waterbodies with respect to morphometry and hydrology. Indeed, there were large differences in basin slope, water residence time and water level fluctuation, between natural lakes and reservoirs, as well as between on stream and off stream sub-types of these water bodies. These differences have important ramifications for littoral habitat stability capable of limiting the productive capacity of these reservoirs to support fisheries. The most important factor limiting the littoral habitat in these reservoirs, and likely in reservoirs, in general, is WLF. Water level fluctuations limit littoral development by exposure of the sediments within the euphotic zone to degrading factors such as desiccation and ice scouring and loss due to exposure during the growing season. The ability of reservoirs to develop substantial and stable littoral habitat to support the fish communities that colonize these reservoirs can be severely restricted by management regimes. The approximate index of littoral loss can provide a valuable first approximation of the impacts of drawdown on littoral habitat development within reservoirs. The ILL can be used to determine the need for alternate energy pathways to sustain reservoir fisheries. Reservoirs with limited littoral energy resources due to loss and instability of littoral habitat will benefit from linking to alternate energy resources such as that of the pelagic zooplankton to the fisheries. In large deep water bodies, the pelagic environment forms substantial habitat for zooplankton development. The zooplankton in littorally limited reservoirs can be a substantial energy resource provided that fish species capable of utilizing this resource effectively are present.

Chapter Three: **Changes in the Zooplankton Community of a Newly Formed Prairie Reservoir, Lacking an Efficient Zooplanktivore, and its Current Status after Twelve Years.**

3.1 Introduction

Changes in zooplankton community in newly formed reservoirs have been studied in a few locations (Robarts et al. 1992, Campbell et al. 1998), but there is little knowledge of zooplankton changes in newly formed reservoirs within the prairie environments. Zooplankton is an integral part of aquatic food webs in that they link the primary producers, phytoplankton, to fish and invertebrate predators (Paterson 2000). In reservoirs where littoral habitat is often limited due to water level fluctuations and morphometry (Chapter 2), the pelagic zooplankton becomes a critical food resource. Zooplankters have very short generation times, 5-7 days for rotifers and 3-4 weeks for cladocerans at 10°C (Allan 1976) and copepods have a slightly longer generation time around 4-6 weeks based on *Diaptomus* (Wetzel 2001). This short generation time allows zooplankton to inhabit a reservoir and build a community within the reservoir environment rapidly. However, zooplankton communities are known to fluctuate during the first few years after filling of a reservoir (Ostrofsky 1978, Ostrofsky and Duthie 1980, Grimard and Jones 1982), and as such considerable time may be required for the composition and abundance to stabilize. Reservoirs tend to go through trophic upsurge following impoundment and then trophic depression, caused by changes in nutrient levels, although these effects can be important , there is little definitive information on the time required for composition and abundance to stabilize (Ostrofsky 1978, Ostrofsky and Duthie 1980).

Zooplankton species range in size from a few tens of microns to 20 mm (Allan 1976, Paterson 2000). Zooplankton can be divided into two size groups; microzooplankton which range between 20-200 µm and mesozooplankton which range between 0.2-20 mm (Sieburth et al. 1978). The microzooplankton fraction consists of the major taxonomic groups; Rotifera, and the nauplii of Copepoda, and the mesozooplankton consists of the major taxonomic groups; Cladocera, and the copepod sub-orders Calanoida, and Cyclopida.

The mesozooplankton is the portion of the zooplankton community which would form the prey base for fry of walleye *Saunder vitreus* (Johnston and Mathias 1994) and zooplanktivorous fish species such as lake whitefish *Coregonus clupeaformis* (Pothoven and Nalepa 2006). Lake whitefish are an important forage species to juvenile and adult northern pike *Esox lucius* and walleye in prairie reservoirs. Therefore, zooplankton fulfills a major functional role in lake and reservoir food webs, and the zooplankton biomass constitutes the major energy resource to pelagic fishes (McCauley and Kalff 1981, Obertegger et al. 2007). The energy resource provided by zooplankton to the fish community is of particular importance in reservoirs with limited littoral habitat; however, fish assemblages present often lack pelagic zooplanktivorous species that can link the zooplankton to top piscivores.

Pine Coulee (PC) is an example of a reservoir which lacks a pelagic zooplanktivore as a result of having been colonized by species found in the parent stream before impoundment, resulting in a littoral community. The most important zooplanktivores found in this community are minnows (Cyprinidae) such as spottail shiner *Notropis hudsonius* and stickleback *Culea inconstans*, neither of which will adapt to the role of pelagic zooplanktivore. In an attempt to build a recreational fishery walley have been stocked, however, the lack of an efficient zooplanktivore fish community capable of linking pelagic zooplankton production to the top piscivores such as walleye and pike. Thus, the energy flow appears to be bottlenecked, limiting the success of the fishery.

Lake whitefish are an essential part of lake food webs in western Canada (Scott and Crossman 1973) and influence growth and recruitment rates of many piscivorous sports fish (Baldwin and Polacek 2011). Common whitefish *Coregonus lavaretus* and lake whitefish of all sizes will avail themselves of zooplankton, especially in summer (Tolonen 1998, Eckmann et al. 2002, Kahilainen et al. 2003). The presence of lake whitefish or a functionally comparable zooplanktivorous forage fish would link the large pelagic zooplankton resource to piscivorous fish (Post et al. 2000) and likely enhance the productivity and sustainability of the walleye fishery in PC.

Zooplankton data for PC, from 1999 to 2002 provided by Alberta Environment (Anderson 2000, 2002, 2003, 2004), unpublished data, as well as zooplankton samples collected in 2012 from PC and seven other reservoirs within the same geographic region were analyzed. The data were used to describe the current zooplankton community and provide insight into the progression of the zooplankton community and development of the biomass over the four-year period after the filling of the reservoir. The data allowed the comparison of the current zooplankton to that of 2002 within PC to determine further changes within the zooplankton community structure and biomass as well as to determine whether abundance and composition of the zooplankton community had stabilized. The zooplankton community of PC was compared to that of seven other nearby reservoirs. Due to the lack of a pelagic zooplankltivore in PC, it is hypothesized that the zooplankton biomass will be substantially greater on average than that of the other reservoirs. Lake whitefish are present and abundant in six of the seven reservoirs, and, if the hypothesis holds true, it is expected that the zooplankton biomass in the reservoirs containing lake whitefish will be lower than that of PC. This would indicate that the zooplankton biomass in PC is likely sufficient to support a zooplanktivorous forage fish, such as lake whitefish, which would likely enhance the stability and productivity of the walleye fishery in PC.

Therefore, the objectives of this study are:

1) Describe changes of the zooplankton community over time to determine whether and when the zooplankton community had stabilized.
2) Compare the zooplankton community structure and biomass of PC to that of seven other local reservoirs with regards to composition and abundance to determine if PC has sufficient zooplankton biomass to support a zooplanktivorous forage fish such as lake whitefish.

3) To investigate the possible relationship between zooplankton abundance in the reservoirs studied to water residence time and nutrients, total phosphorus and total nitrogen.

3.2 Methods and Study Area

3.2.1 Study Area

Pine Coulee Reservoir (PC) is a reservoir located 115 km south of Calgary and 7.1 km west of Stavely, Alberta, Canada, 12 U 304734 E, 5560544 N, (figure 3.1). The reservoir was completed and filled in 1999 (Rood et al. 2005), the reservoir is 13 km long, with a maximum depth of 50 m and a mean depth of 10 m. The capacity of the reservoir at full surface level is 50,600 cubic decametres (dam^3) with a surface area of 508 ha. PC is considered an off-stream reservoir, but has two water inlets; Pine Creek that flows into the reservoir at its north end, and Willow Creek at the southwest end, which enters PC via a head pond and a diversion canal, and constitutes the main water source to the reservoir. The outflow situated at the south end discharges into Pine Creek, which enters Willow Creek. At present, water reserves in PC reservoir are not fully utilized, and as such, the drawdown is only 1.5 m over the summer months and has a long water residence time of approximately 586 days. Primary land use around the reservoir is cattle ranching and crop farming. The other seven reservoirs sampled for comparison to PC were Chin, Keho, McGregor (McGR), Milk River Ridge (MRRR) St.Mary's (StMR), Oldman River Dam (OMRD) and Waterton Reservoir (WTTN). All the reservoirs are located east of the Rocky Mountains in southern Alberta. The sample sites for these reservoirs ran from inlet to outlet and temporally were sampled a month apart over a period of four months.

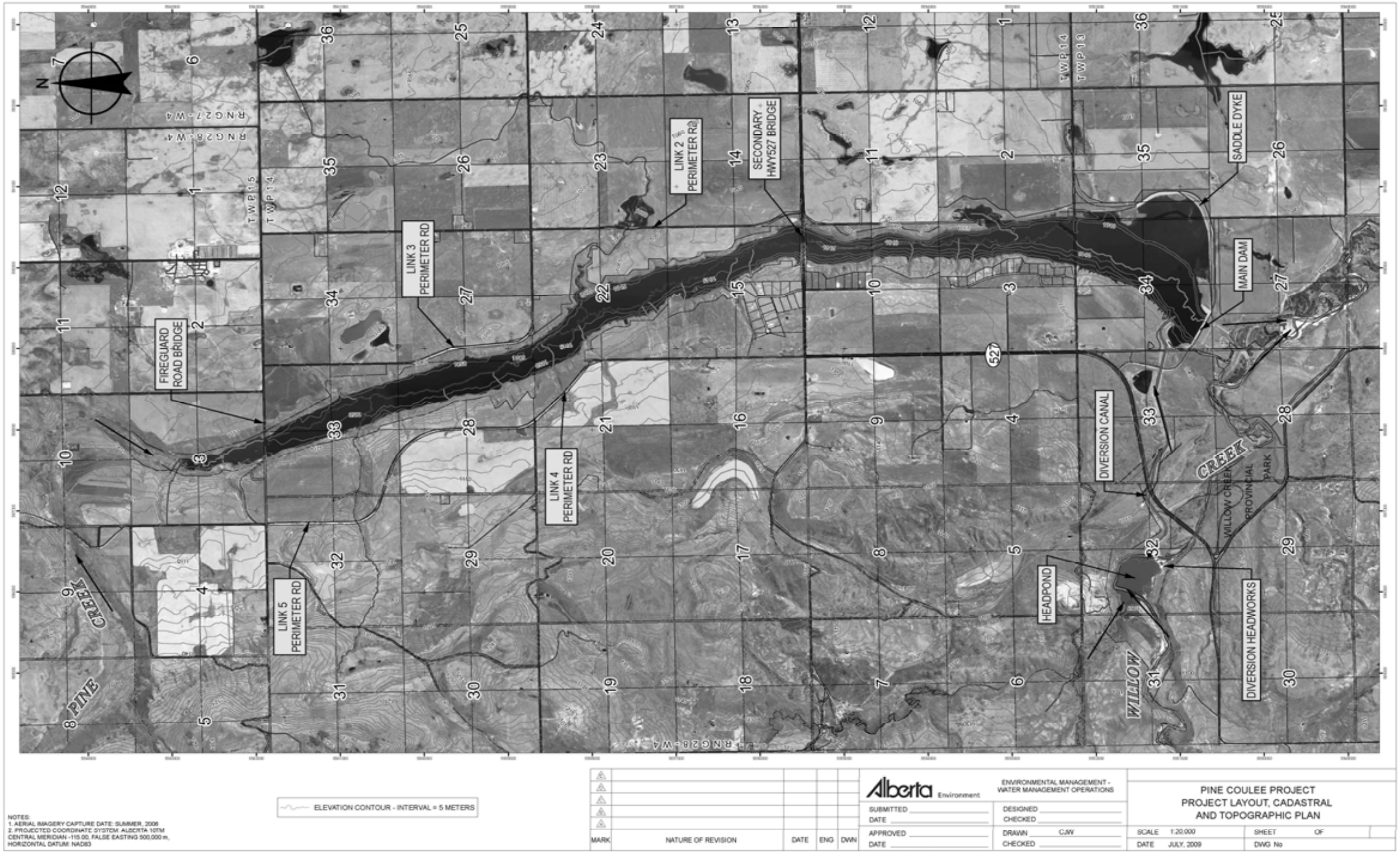

Figure 3.1. Pine Coulee Reservoir, displaying the Pine Creek inflow to the north and the canal inflow in the southwest with the Pine Creek outflow in the south.

3.2.2 Survey Methods

All reservoirs were sampled at four different locations along the length, from the inlet to outlet. All sites were sampled once per month during the summer. Samples were collected from all sites in June, July, August and September 2012. Each site was sampled with a conical plankton net with 63 µm mesh size and an opening of 0.196 m^2 and a dolphin bucket collector. The nets were drawn through the full water column from 0.3 m above the reservoir bed to prevent the inclusion of benthic organisms. A mechanical flow meter (manufactured by General Oceanic) with a low-flow impeller was used to determine the amount of water sampled. The samples collected were rinsed into the dolphin bucket and transferred to a cooler with ice for transport to the laboratory. Samples of water were collected from the inlet and the outlet of each reservoir in September and outsourced for total nitrogen and total phosphorous. Secchi depth and temperature were recorded at each site.

3.2.3 Laboratory methods

Zooplankton samples were filtered and rinsed through a 63 µm sieve then placed in 240 ml containers with a solution consisting of 4:1 water: 5% buffered formalin solution with sucrose added to prevent distortion of the specimens (Haney and Hall 1973, Prepas 1978). Samples were stored in a refrigerator at 8º Celsius until they could be processed at a later date.

Due to the large size of samples obtained, the samples were split into manageable fractions using a Folsom plankton splitter. The fraction not utilized were placed in sealable centrifuge tubes and stored in the fridge at 6 degrees Celsius for future reference.

The split fraction kept for analysis was then sieved through Nitex mesh screens to partition the sample into size fractions of ≥1000 µm, 999-500 (500 µm), 499-243 (243 µm), 242-118 (118 µm) and 117-63 (63 µm). The fractions were then transferred to 58 cm^2 Petri dishes scribed with 1x1 centimeter square grid system for identification and enumeration under a dissecting microscope. Each dish was treated with 2-3 drops of diluted Sunlight dish detergent to reduce the surface tension of the water and settle out as many of the floating specimens as possible (Grace 1994, Goswami 2004). The remaining floating specimens were counted first, followed by the specimens on the grid. Exoskeletons were counted if there was enough to form a definitive identification; eggs found in the samples were not counted.

All of the 1000 and 500 µm sample fractions were completely enumerated. The smaller size fractions were split to reduce processing time due to the large numbers of individuals. The samples were split with the Fulsome Plankton Splitter and then enumerated. Counting was only done on the PC samples to allow for comparison to the earlier data; the other reservoir samples were not enumerated due to time constraints. The numbers were multiplied by the split factor to determine full sample values. The fractions that had been split for enumeration were recombined and then re-run through the Nitex screens, and the size fractions were then moved to pre-weighed aluminum dishes and dried (60° C for 72 hours). Once dry the fractions were re-weighed to determine the dry mass. The dry weight and numerical data from the PC samples were used to determine a mean weight per individual by taxa to convert the density data from 1999 to 2002 to biomass for comparison.

All statistical analyses were performed using the JMP 10.0.2 software package from SAS Institute. Zooplankton biomass was compared by prevalent taxa and mean biomass per cubic meter using one-way analysis of variance (ANOVA) for years and post hoc Tukey-Kramer HSD (α=0.05). Zooplankton biomass was compared by size fraction and average total mass per cubic meter using one-way analysis of variance (ANOVA) for reservoir and post hoc Tukey-Kramer HSD (α=0.05). All reported values are mean ± SE unless specified. Linear regression performed to determine the relationship of zooplankton biomass to reservoir water residence time, total phosphorous and total nitrogen. Rejection probability for all analyses set at α = 0.5 level.

3.3 Results

3.3.1 Zooplankton 1999-2002 and 2012 in Pine Coulee Reservoir

The composition of the zooplankton community increased from 9 taxa in 1999 to 10 taxa in 2000, which represented the appearance of Bosminidae; the following two years showed an increase to 12 taxa. However that increase was made up by taxa which together formed < 2 % of the zooplankton community; Macrothricidae and Sididae, found in both 2001 and 2002. Harpactacoidae in 2001 was present, represented by one specimen out of all the samples collected that season (Anderson 2003), and Leptodoridae was present in 2002.

Major taxa were taxa that formed a biomass greater than 5 % of the mean biomass of the zooplankton community excluding the rotifer portion within any of the years sampled; these were taxa that form more than 98 % of the zooplankton community. The major taxonomic groups were the cladoceran families, Chydoridae, Daphnidae, and the copepods families, Cyclopidae, Diaptomidae, and nauplii and Rotifera.

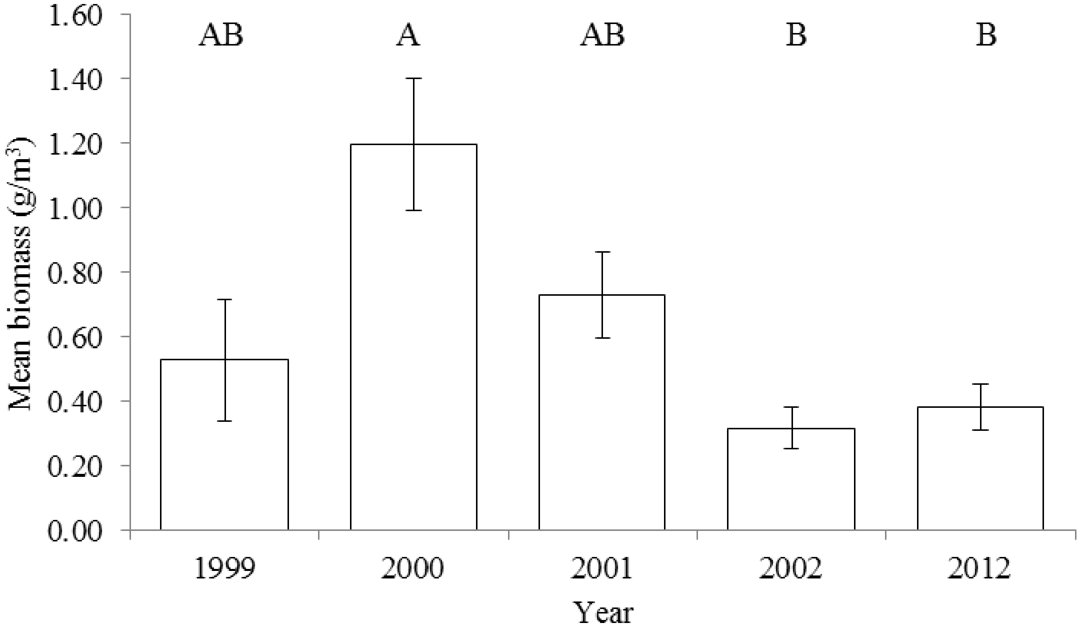

Figure 3.2. Mean biomass (g/m^3) for each of the years sampled in Pine Coulee Reservoir, one-way ANOVA $F_{(4,39)} = 5.790$; $p < 0.001$, those years not connected with the same letter are significantly different. Bars represent SE.

The total mean summer zooplankton biomass of the major taxa from 1999 to 2002 fluctuated, overall zooplankton mean biomass was 0.53 g/m^3 in 1999, peaking in 2000 with more than double the previous year's biomass with 1.20 g/m^3. 2001 saw a decrease by almost 40% with 0.73 g/m^3, and 2002 saw a greater than 55 % decrease from 2001 to 0.32 g/m^3.The mean summer zooplankton biomass in 2012, ranged from 0.51 to 1.30 g/m^3 with a mean biomass of 0.38 g/m^3 for the season.The zooplankton mean biomass for 2002 was significantly lower than that of 2000. However, there was no significant difference between 2002 and 2012 (Figure 3.2). The crustacean as well as the rotifer portion of the zooplankton biomass both increased from 1999 to 2000 from 0.30 to 0.71 g/m^3 for crustaceans and from 0.23 to 0.49 g/m^3 for rotifers. 2001 and 2002 saw crustaceans decrease to 0.51 and 0.23 g/m^3 respectively, and rotifer decreased to 0.22 and 0.08 g/m^3 respectively (Figure 3.3a). The composition of the zooplankton community crustacean biomass saw it increase over time, 56.4 %, 59.3 %, 70.1 %, 73.6 % through the period 1999 to 2002. Crustaceans increased over the period 1999 to 2002 and made up >85% of the community biomass in 2012 (Figure 3.3b).

The mean biomass of the major taxa in 2012 was: Chydoridae ranged from 0.6 to 232.1 and had a mean of 53.6 mg/m^3 and formed 14.0 % of the mean summer density. Cyclopidae ranged from 13.3 to 254.0 with a mean of 79.1 mg/m^3 at 20.7 %. Daphnidae ranged from 18.0 to 209.2 with a mean of 79.3 mg/m^3 and forming 20.8 %. Diaptomidae with a mean of 55.9 mg/m^3 ranged from 10.5 to 166.5 mg/m^3 formed 14.6 %. nauplii at 60.6 mg/m^3 at 15.9% and ranging from 3.5 to 290.2 mg/m^3 and Rotifers at 52.1 mg/m^3 at 13.6 % and ranging from 4.6 to 198.5 mg/m^3.

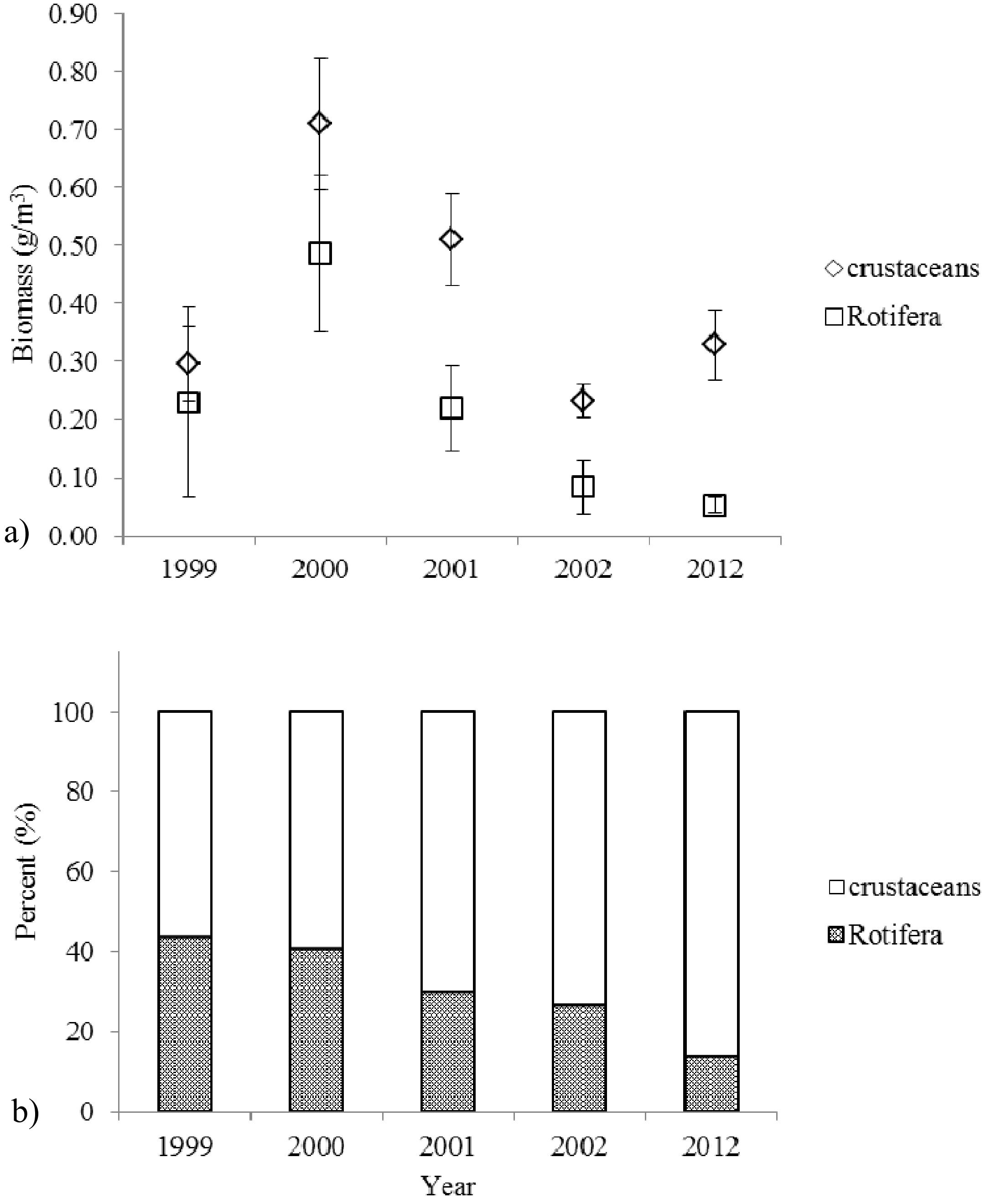

Figure 3.3. a) Mean biomass for crustacean and rotifer portion of the zooplankton in Pine Coulee Reservoir for each year sampled, bars represent SE. b) The proportion of the mean zooplankton community made up of the crustacean and rotifer portion for each year sampled.

The major taxa made up more than 98 % of the mean summer biomass for the PC zooplankton community in 2012, and, the zooplankton community of 2012 was not significantly different from that of 2002 (Figure 3.3). The biomass comparison of individual taxa revealed no significant differences between years 1999 – 2002 and 2012 for two of the major taxa, Daphnidae, and Bosminidae. However, significant differences were observed for the other taxa. Across the first four years, there were significant differences observed for Diaptomidae, which dropped significantly from 22.2 mg/m^3 in 1999 to 3.6 mg/m^3 in 2000. In 2001, Diaptomidae biomass increased again to 14.7 mg/m^3. The Diaptomidae biomass in 2012 at 55.9 mg/m^3 was significantly higher than that of 2002 with 11.0 mg/m^3. Chydoridae followed the same trend with a decrease from 0.8 mg/m^3 in 1999 to 0.3 mg/m^3 in 2000 then increased to 1.6 and 3.1 mg/m^3 through 2001 and 2002 respectively; however, there was no significant difference in the biomass between years. Chydoridae biomass was significantly higher in 2012 with 53.6 mg/m^3 than any prior year sampled. Cyclopidae biomass increased from 65.0 mg/m^3 in 1999 to 157.3 mg/m^3 in 2000, a significant increase, 2001 saw no change at 157.4 mg/m^3 and 2002 saw a decrease to 59.6 mg/m^3. The Cyclopidae biomass in 2012 was 79.1 mg/m^3, not significantly different from 2002. Nauplii and rotifer biomass both followed the same trend spiking in 2000 and then decreasing through the following years. Nauplii and rotifer biomass did not change significantly during the period 1999 – 2002. However, nauplii in 2012 with 60.6 mg/m^3 were significantly lower than that of 2000 and 2001 where nauplii biomass was 440.4 and 259.9 mg/m^3 respectively. Rotifer biomass was significantly lower in 2012 with 52.1 mg/m^3 than in 2000 which had a biomass of 486.2 mg/m^3 present (Figure 3.4).

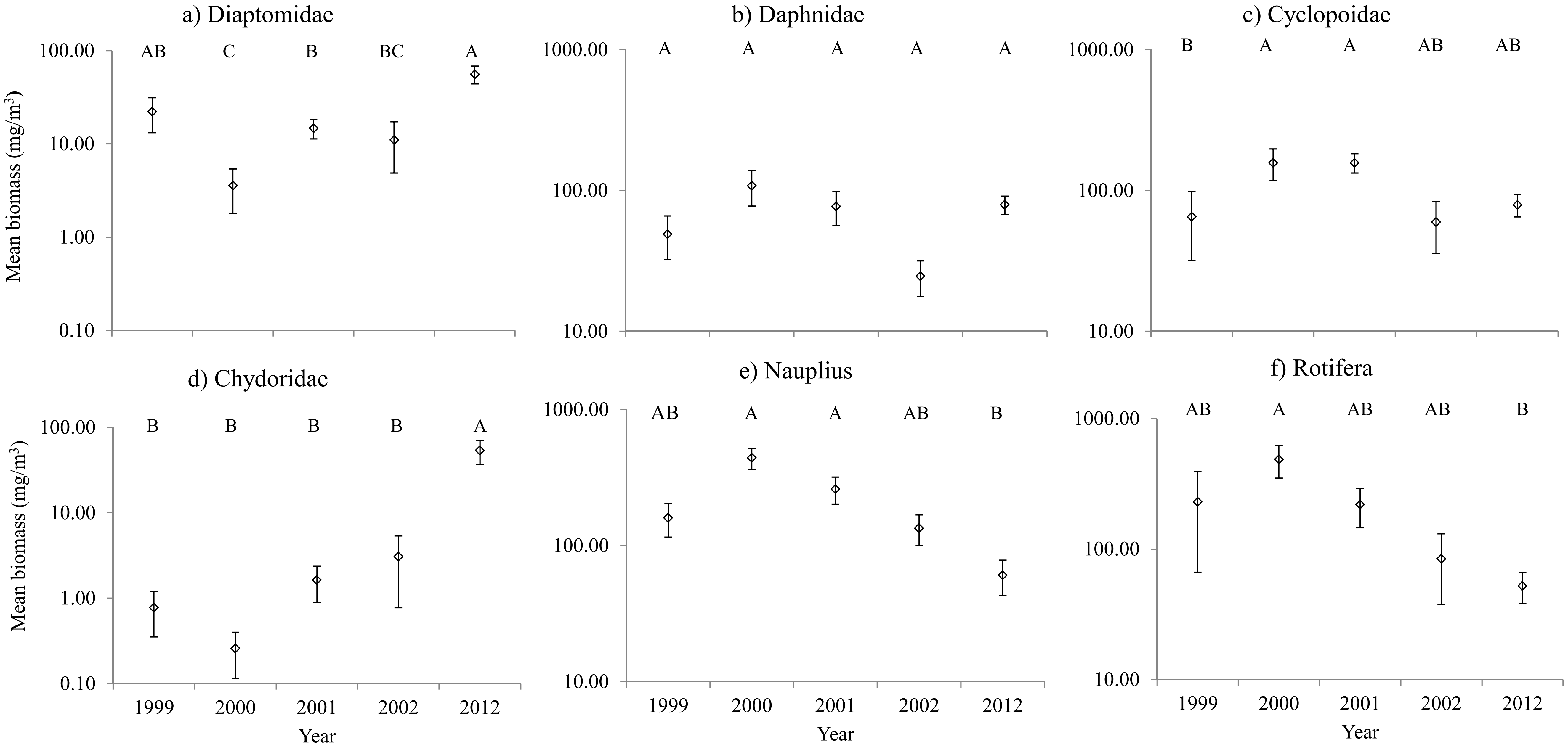

Figure 3.4. The changes in zooplankton taxa mean biomass (dry weight mg/m^3) during the first four years and differences noted in 2012. One-way ANOVA's; a) Diaptomidae, $F_{(4,39)} = 8.98$; $p < 0.001$; b) Daphnidae, $F_{(4,39)} = 2.54$; $p < 0.055$; c) Cyclopidae, $F_{(4,39)} = 4.08$; $p = 0.007$; d) Chydoridae, $F_{(4,39)} = 10.40$; $p < 0.001$; e) Nauplius, $F_{(4,39)} = 9.47$; $p < 0.001$; f) Rotifera, $F_{(4,39)} = 4.22$; $p = 0.006$. Those years not connected by the same letter are significantly different (post hoc Tukey-Kramer HSD (α=0.05)). Bars represent SE

3.3.2 Zooplankton Taxa for all Reservoirs Sampled

Thirteen taxa were collected during the open water season amongst all the reservoirs sampled in 2012. Chin had the highest number of taxa of all reservoirs with 12; Keho, MRRR, StMR and WTTN all had 10 taxa and McGR, OMRD had 9 and PC had 8. Of the taxa collected, Chydoridae, Cyclopidae, Daphnidae, Diaptomidae, Nauplii, and Rotifers were present in all the reservoirs. Sididae was present in all reservoirs except PC and Bosminidae were found to be present in all reservoirs but MRRR. Chaoboridae present in PC and WTTN, Moinidae were only present in Chin. Centropagidae was present in all reservoirs except PC. Leptodoridae was present in Chin, MRRR, and PC. Chaoboridae, Hydrachnidae, Leptodoridae, and Ostracoda were the primary miscellaneous taxa collected each representing ≤ 0.1 % of the total zooplankton collected for the 2012 season in PC. The major taxa formed the bulk of the zooplankton communities in all the reservoirs.

3.3.3 Zooplankton Biomass

The mean summer zooplankton biomass of PC at 0.44 dw g/m^3, (Figure 3.5 a), was significantly higher than that of any of the other reservoirs which ranged from MRRR with 0.26 and OMRD with 0.03 g/m^3. Fractionation of the zooplankton samples into mesozooplankton was done by combining the 243 μm and the larger fractions.

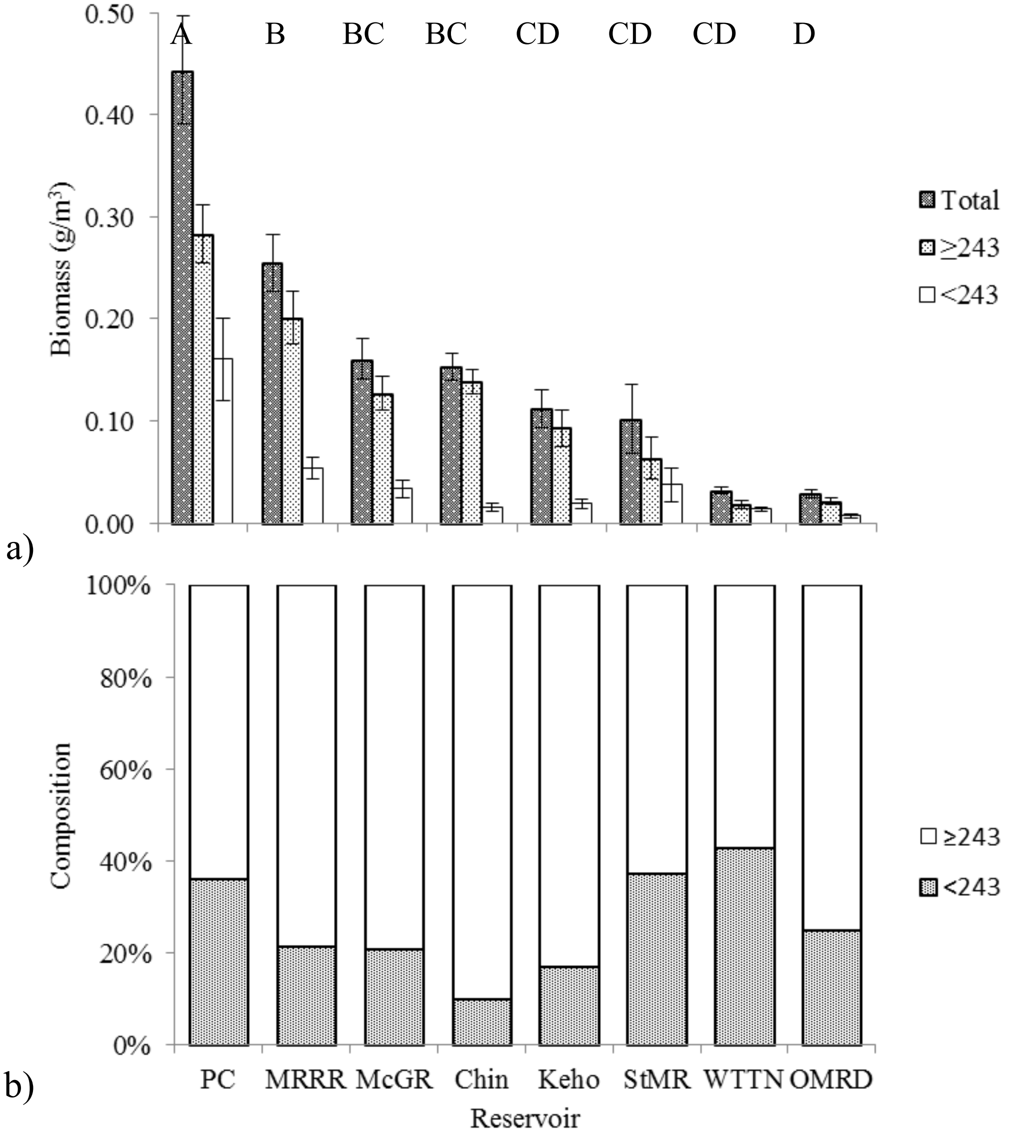

Figure 3.5. a) The difference between reservoirs for the mean total biomass, one-way ANOVA $F_{(7,109)} = 23.73$; $p < 0.001$; mesozooplankton (≥243) one-way ANOVA $F_{(7,109)} = 23.04$; $p < 0.001$; and microzooplankton (<243) one-way ANOVA $F_{(7,109)} = 8.53$; $p < 0.001$, post hoc Tukey-Kramer HSD results for total mean biomass only, those not connected by the same letter are significantly different. Bars represent SE. b) The percent composition of the zooplankton community made up of the micro and mesozooplankton. Reservoirs are; PC, Pine Coulee Reservoir; MRRR, Milk River Ridge Reservoir; McGR, McGregor Lake; Chin Lake; Keho Lake; StMR, St Mary Reservoir; WTTN, Waterton Reservoir and OMRD, Oldman River Dam.

The mesozooplankton was significantly higher in PC than in all other reservoirs. The microzooplankton consisting of everything less than 243 µm was significantly higher in PC as well (Figure 3.5 a).

Table 3.1. Physical and chemical parameters of the eight reservoirs sampled in 2012

Reservoir	SA (ha)	Vol (dam^3)	Z (m)	Z_{mean} (m)	WRT (days)	TN (µg/L)	TP (µg/L)	Mean mass (g/m^3)
Chin	1569	201000	20.0	12.8	113	330	20	0.15
Keho	2212	98200	6.0	4.4	172	400	19	0.11
McGregor	4903	333000	9.7	6.8	94	714	16	0.16
Milk River	1370	107000	16.5	7.8	139	459	20	0.26
StMary's	3257	519000	56.4	15.9	139	121	9	0.10
Pine Coulee	508	50600	50.0	10.0	586	773	45	0.45
Oldman	2429	493000	68.5	20.3	63	526	14	0.03
Waterton	1094	114000	43.0	10.5	24	161	6	0.03

Linear regression performed on the $\log_{10}$ transformed data of mean zooplankton biomass and total phosphorous (TP), total nitrogen (TN) and water residence time (WRT). Regression analysis of Mean zooplankton biomass ranging from OMRD with 0.03 g/m^3 to PC with 0.45 g/m3 to TP which ranged from WTTN with 6 µg/l to PC with 45 µg/l indicated a significant positive relationship ($y = 1.239x + 0.520$, $R^2 = 0.655$, $p = 0.015$). The mean zooplankton biomass with respect to TN, which ranged from StMR with the lowest level of 121 µg/l to PC with the highest at 773 µg/l showing there was no significant relationship. There was a significant positive relationship between zooplankton biomass and WRT which ranged from 24 days in WTTN to 586 days in PC ($y = 0.892x + 0.219$, $R^2 = 0.725$, $p = 0.007$) (Figure 3.6, Table 3.1). A significant positive relationship was also noted on TP response to WRT ($y = 0.577x + 0.009$, $R^2 = 0.764$, p =

0.005) (figure 3.6). Multiple linear regression was performed to predict zooplankton biomass from TP and WRT. Data for the model was supplemented by litterature data from Duthie and Ostrofsky (1975), Campbell et al. (1998) and Marty et al. (2005) to increase sample size, $n = 34$. Log transformed zooplankton biomass was significantly predicted by these variables ($R^2 = 0.66$; $T_{log10TP} = 6.6$; $p < 0.001$; $T_{log10WRT} = 5.5$; $p < 0.001$). The resulting model equation is:

$$\text{Log}_{10}\ \text{zooplankton biomass} = -\ 0.590 + 0.793\ \log_{10}\ \text{TP} + 0.666\ \log_{10}\ \text{WRT}$$

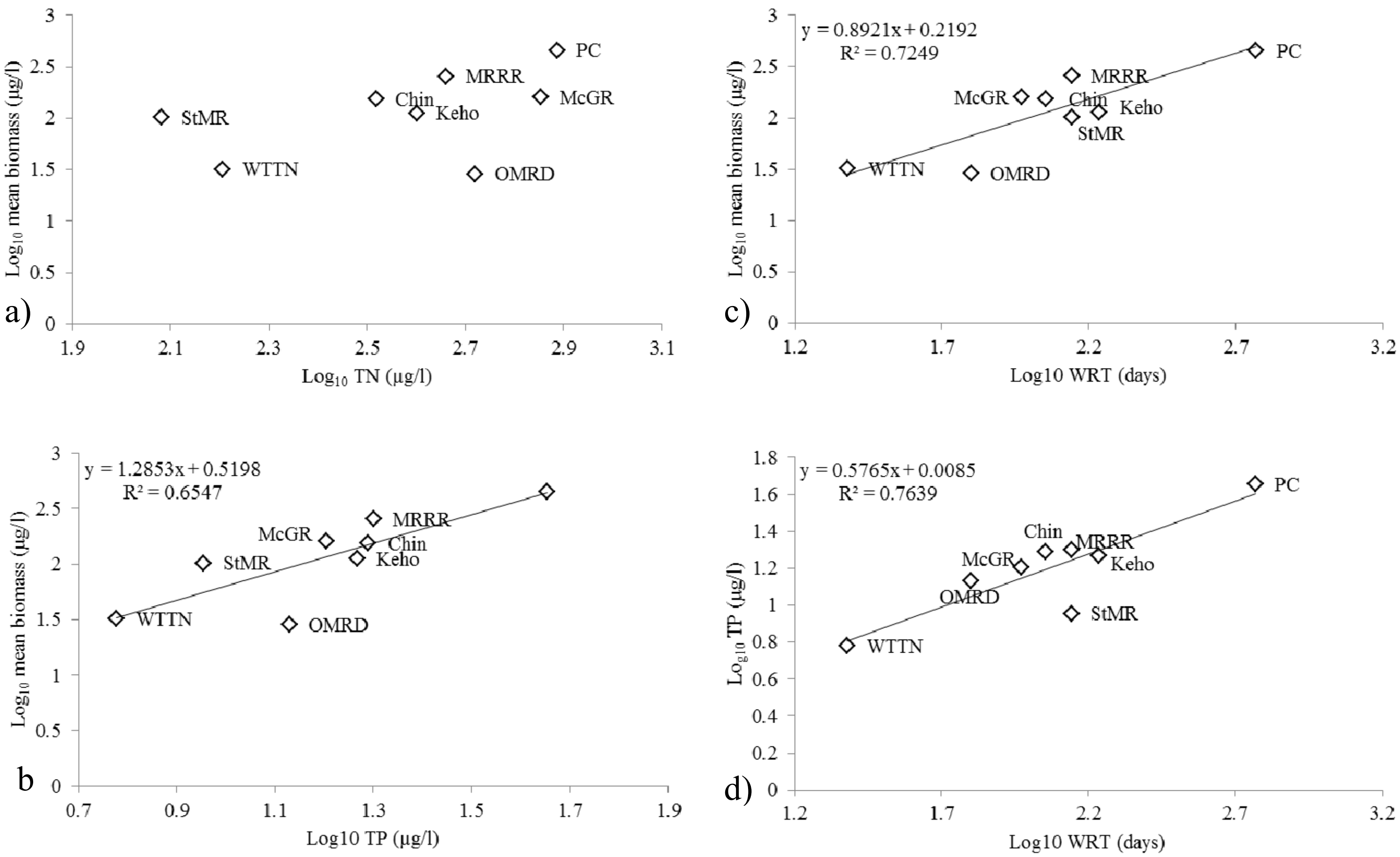

Figure 3.6. Linear regression of the $\log_{10}$ transformed data for; a) mean biomass (µg/l) and total nitrogen (µg/l), $r^2 = 0.221$, $p = 0.240$; b) Biomass and total phosphorous (µg/l), $r^2 = 0.655$, $p = 0.015$ and, c and d) biomass and total phosphorous to water residence time (days), $r^2 = 0.725$, $p = 0.007$ and $r^2 = 0.764$, $p = 0.005$ respectively.

3.4 Discussion

Zooplankton biomass in PC fluctuated significantly over the first four years following impoundment (1999 & 2002), with a significant increase in the first two years (1999 & 2000) followed by a rapid leveling off (2001 & 2002) to a level similar to that recorded in 2012. The zooplankton community composition also changed significantly during the early phase of operation. Rotifers, the smallest size fraction, which produce the most rapidly (Allan 1976) made up > 40% of the biomass in the first year and declined gradually over time as larger taxa became increasingly dominant. No major changes in either abundance or composition of the zooplankton community were observed after the fourth year (2002). However, there were statistically significant increases in Diaptomidae and Chydoridae in 2012 compared to 2002. These increases indicate that changes were still taking place in the zooplankton community after four years of operation.

Cat Arm Reservoir, (Newfoundland, Canada) is a reservoir which is much larger than PC, with a shorter WRT but similar phosphorous levels and taxonomic richness. The zooplankton biomass in Cat Arm showed a similar trend as observed in PC, biomass increased rapidly in the first two years following impoundment and then declined over the following six years. Water residence time in Cat Arm was extremely short (4 days) during the early stages of filling, resulting in low zooplankton biomass consisting of predominantly rotifers. Zooplankton biomass increased rapidly in response to increasing WRT as the reservoir is filled, and copepods and cladocerans increased to dominate the community. The rise and fall of the zooplankton community in Cat Arm tracked the phosphorous levels and phytoplankton biomass. Rotifer dominated zooplankton communities during early years of operation, followed by gradual increase in crustacean abundance during later years were also noted in northern Quebec reservoirs by Pinel-Alloul (1989). Although phosphorus levels were not measured in the early years at PC, the pattern of rapid rise and gradual decline of total zooplankton biomass in PC corresponds to the patterns of rise and decline observed in Cat arm (Campbell et al. 1998) and other studies of zooplankton succession in young reservoirs (Duthie and Ostrofsky 1975, Ostrofsky 1978, Grimard and Jones 1982, Pinel-Alloul et al. 1989) where the pattern tracks the rise and fall of phosphorous levels. The time required for zooplankton communities to stabilize in these studies ranged from 5 – 10 years, the changes in abundance and composition depended on a combination of increasing WRT and trophic upsurge and depression caused by post flooding pulse and depression of nutrients resulting from flooding of soils and vegetation within the reservoir basin. The pattern exhibited by zooplankton biomass with TP and WRT shown in Albertan reservoirs (Figure 3-5) are consistent with the zooplankton development in these early reservoir studies as well as with studies of zooplankton biomass in natural lakes (McCauley and Kalff 1981, Campbell and Knoechel 1988, Knoechel and Campbell 1988, Geraldes and Boavida 2007, Obertegger et al. 2007). While both WRT and TP are important determinants of zooplankton biomass, it is difficult to partition their effects using multiple regression since TP concentration tends to increase with WRT due to increased nutrient retention (Vollenweider 1975).

The separation of zooplankton biomass into size fractions allows for the partitioning of the larger size fraction (mesozooplankton) which is the fraction targeted by zooplanktivorous fish. Lake whitefish fry feed mainly on zooplankton in their first years of life (Hoyle et al. 2011), although the importance of zooplankton decreases as the fish grow, fish larger than 350 mm TL will still consume some zooplankton (Pothoven and Nalepa 2006). Lake whitefish feed on Cladoceran species such as Bosminidae, Chydoridae and Daphnidae and copepod species Cyclopidae and Diaptomidae (Hoyle et al. 2011).

The zooplankton biomass of PC is significantly higher than all the sampled reservoirs, and this holds true for both the microzooplankton and the mesozooplankton. The high biomass of the zooplankton found in PC may support a zooplanktivorous forage fish such as lake whitefish. The lack of a pelagic zooplanktivore within PC cannot solely account for the high zooplankton biomass as other factors are known to affect the community structure and biomass.

This study revealed that the all the major zooplankton taxa were present from the start-up of the reservoir, however, the zooplankton community requires time to reach a stable state. The fluctuations seen in the zooplankton community in PC follows the pattern witnessed in other newly formed reservoirs, where 5–10 years is required for communities to stabilize with respect to abundance and composition. Zooplankton biomass in PC may be deemed capable of supporting zooplanktivorous fish such as lake whitefish by its high abundance compared to other reservoirs. Lake whitefish may contribute to the productivity and sustainability of the walleye fishery in PC by linking the pelagic energy resources to these fish.

Chapter Four: **Growth and Recruitment of Walleye *Sander Vitreus* in a Prairie Reservoir.**

4.1 Introduction

Reservoirs in southern Alberta are constructed primarily for the purpose of water storage and in some cases hydro production as a secondary consideration. These reservoirs fulfill an additional function as recreational water bodies for boating and angling. Managing reservoirs for recreational fishing often involves manipulating the fish community through stocking of popular sportfish, and in Alberta, the walleye *Sander vitreus*, a top piscivore, has been stocked in many reservoirs and lakes for this purpose. Establishing recreational fisheries in Southern Alberta irrigation reservoirs serves to offset the enormous recreational fishing pressure on natural lakes (Chapter 1), and to mitigate fisheries impacts from dams on the Oldman River and its tributaries and irrigation infrastructure on other rivers systems (Alberta Environment and Parks 2015) The particular focus on walleye was directed by its ranking as a highly desirable recreational fish species to the public, combined with the highly significant decline in walleye fisheries in Alberta over the last two decades (Post et al. 2002; ASRD 2015). In lakes, walleye generally occupy depth zones of 5-15 m and tend to be found near the bottom in littoral to sublittoral habitat, though they will feed offshore throughout the water column if pelagic forage fish are present (Scott and Crossman 1973; Paetz and Nelson 1992).

Due to bathymetry and drawdown during the irrigation season, the littoral habitat, and therefore the little forage fish available to the fish community can be limited, forcing a stronger reliance on pelagic and benthic resources. Zooplankton and phytoplankton are the dominant energy sources within the pelagia in deep steep-sided reservoirs similar to large lakes (Eggers et al. 1978).

Development of the forage fish community in these reservoirs relies on natural colonization of fish from within a stream or river situated upstream of the reservoir. Pelagic forage fish, particularly lake whitefish *Coregonus clupeaformis*, which are crucial for linking pelagic zooplankton to piscivorous fish in aquatic food webs, can only colonize reservoirs situated downstream of headwater lakes unless introduced through stocking.

This method of colonization can lead to a different community structure than that of the parent stream because only those species in the parent community that are capable of adapting from a lotic to a lentic environment will be able to colonize the reservoir (Barbour and Brown 1974, Fernando and Holčík 1991). Fish community structure is an important aspect of lake ecosystems (Carpenter et al. 1985) since random assemblages rarely result in an energetically efficient food web structure. Food web structure is an essential aspect of research into productivity as it maps the energy flow through the system from primary producers to top consumers (Johnson et al. 2002, Karlsson and Bystrom 2005).

In natural lakes, energy reaches piscivorous fish through three different pathways, the pelagic, the profundal and the littoral pathway as outlined in Chapter 1. Fish are critical integrators of energy reserves between food chains such as benthic, pelagic and littoral (Vander Zanden and Vadeboncoeur 2002). In lake systems even the most isolated food chains are often linked to each other by highly mobile consumers such as fish (Hairston and Hairston 1993, Polis and Strong 1996). However, the littoral zone communities in reservoirs can be severely limited by morphometry and hydrological regime within reservoirs (Chapter 2). This limiting of the productive capacity of the littoral zone highlights the need for a species that is capable of linking the pelagic energy resources to the piscivorous species within a reservoir. Communities that lack this link will be impoverished from the fisheries perspective, because of an energetic ‘bottleneck or sink’ since key species that comprise the ‘fishery’ will be unable to access energy flow from an abundant trophic resource (Chapter 3). The Riverine fish communities in lower order streams lack zooplanktivous species (Miranda et al. 2008) which would inhabit the pelagic zone of these reservoirs feeding on the abundant plankton present there, and attracting piscivorous fish to forage on them offshore. It is only with the presence of upstream sources or with anthropogenic stocking that a zooplanktivorous species such as lake whitefish would be able to colonize reservoirs.

To support an optimal fishery for piscivorous target species such as walleye, a popular game fish stocked in Alberta (Berry 1995); the reservoir must provide habitat and forage to support the growth and recruitment of these fish. The growth rates of apex consumers are dependent on energy efficient flow through the food web (Pazzia et al. 2002). Walleye are specialist piscivores which actively select fish prey items (Graeb et al. 2005), walleye undergo diet shifts during their ontogeny from zooplankton to invertebrates from small fish to larger fish as they grow. The diet shifts to larger prey are typically followed by increased growth rates (Werner and Gilliam 1984). Suitable forage fish are required for optimal growth and recruitment of walleye, fish that can fulfill the size requirements needed by the walleye. In systems lacking suitable forage fish, the piscivorous fish may be unable to shift to larger prey items (Sherwood et al. 2002) and be forced to rely on invertebrates or small prey items throughout their ontogeny (Pazzia et al. 2002). The inability to switch to larger prey through their ontogeny can result in lower growth rates of piscivores (Henderson et al. 2004, Graeb et al. 2005, Brinkmann and Rasmussen 2010) and therefore lower recruitment (Olson 1996).

This study investigates the prey community effect on recruitment and growth of the walleye within Pine Coulee Reservoir to other reservoirs within the same region.

The objectives of this study are:

1) Compare the fish community structure of Pine Coulee Reservoir to other local reservoirs that contain pelagic zooplanktivorous forage fish, to ascertain the availability of appropriate forage fish for walleye.
2) Compare the recruitment of walleye in the Pine Coulee population to other local reservoirs that contain pelagic zooplanktivorous forage fish to measure differences in walleye recruitment between PC and these other reservoirs. This objective will be met by comparing the distribution of age classes from FWIN netting and catch data for each reservoir
3) Compare the growth rate of the Pine Coulee walleye to walleye in other local reservoirs to ascertain if the walleye in PC are stunted. This objective will be met by fitting the Von Bertalanffy growth models to length at age measurements from multiple years of catch data for each reservoir.

4.2 Methods and Study Area

4.2.1 Study Area

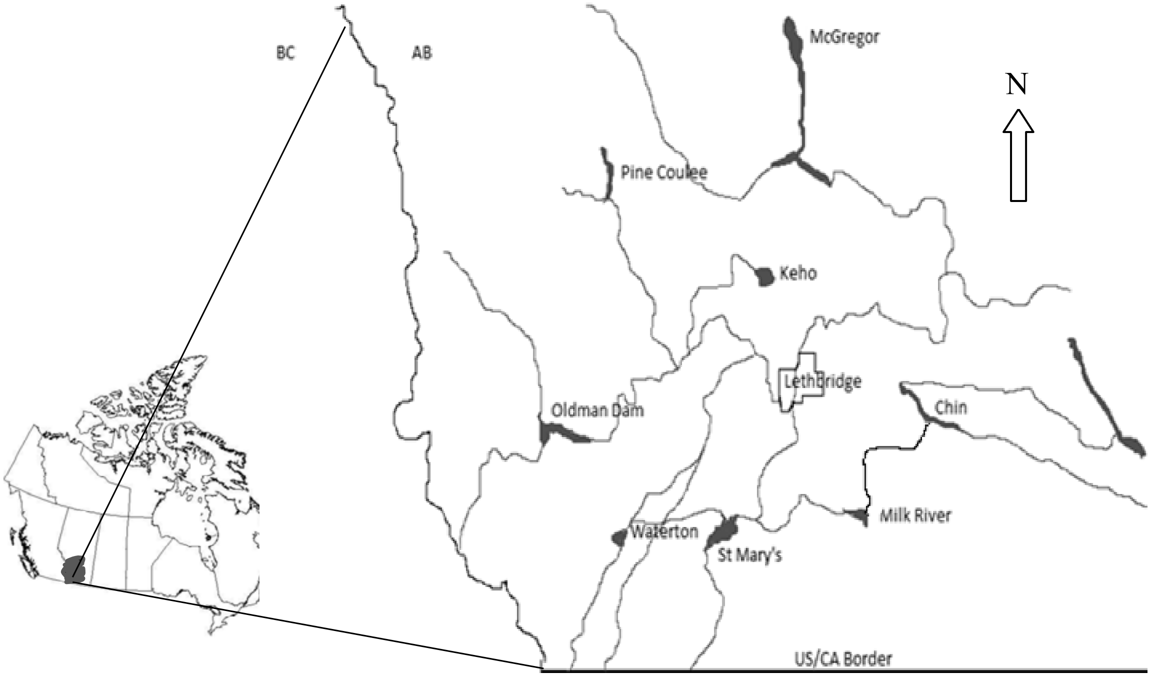

Figure 4.1. The location of Pine Coulee Reservoir and the comparison reservoirs in south western Alberta, also displayed are the connections between the reservoirs by rivers and canal systems.

Pine Coulee Reservoir is situated 115 km south of Calgary and 7.1 km west of Stavely, Alberta, Canada. N Latitude 50°08'5.97'', W Longitude 113°44'7.60'' (figure 4.1). The reservoir was completed and filled in 1999. Pine Coulee is a reservoir with a length of 13 km, a maximum depth of 50 m and a mean depth of 10 m. The capacity of the reservoir is 50600 dam^3 (cubic decameters), and the surface area is 508 hectares.

Pine Coulee is an on-stream reservoir built on Pine Creek with two inlets. Pine Creek flows into the reservoir at its north end, and the south end a diversion canal feeds in water from the head pond on Willow Creek. The outflow, situated at the south end, feeds into Pine Creek just before its confluence with Willow Creek. The reservoir is presently not being fully utilized and as such the drawdown is very slight compared to many other storage reservoirs (Chapter 2), currently on the order of 1.5 m over the summer months. The reservoir supplies drinking water to the town of Claresholm and discharges into Pine Creek to maintain creek flow. The area surrounding the reservoir is primarily used as grazing farmland with a campground at the southeastern end.

The reservoir was stocked in 2000 with 2.2 million walleye fry and again in 2003 with 1.9 million walleye fry (Daryl Wigg and Mike Bryski, personal communication) to establish a viable, self-sustaining walleye population to support a recreational fishery. Pine Coulee is considered a small reservoir and is built in a steep sided coulee. Thus, Pine Coulee is a predominantly pelagic reservoir with limited littoral habitat which is limited further by the drawdown due to the hydrological regime imposed on it. The limitations imposed on littoral production drives a need for other energy reserves, being primarily pelagic, the plankton energy reserves are dominant in this reservoir. The littoral habitat in PC will likely be even more severely limited if irrigation demand in the area increases and the reservoir will be used to capacity since drawdown will likely increase by several meters.

4.2.2 Survey Methods

Fish community structure was determined by taking multiple years of data from Fish and Wildlife Management Information System (FWMIS) as well as direct fisheries studies. Species' composition in this reservoir was determined from this data. Fish fin clips from fish netted in 2009 were supplied by Alberta Environment and were used to age the fish and to determine the population composition of the different age cohorts.

Fish samples were collected in 2011 using both angling and gill nets, set for a maximum of 90 minutes; two nets were used. The first net consisted of seven panels at 2 m high by 7 m long each, mesh size stretched, 25, 35, 45, 60, 75, 100 and 120 mm and a total area of 98 m^2. The second net consisted of eight panels 2m high by 7m long with mesh size stretched, 25, 35, 45, 60, 75, 100, 120 and 150 mm and a total area of 112 m^2.

Catch per unit effort (CPUE) was calculated and standardized to #walleye/100m^2/24h from FWMIS and direct catch data. The CPUE data was used to determine an estimate of the relative abundance of walleye per age cohort and fork length groups. The fish caught in 2011 were collected and moved to the laboratory for analysis. The length and weight data were recorded, and then the fish were dissected; stomach content was collected and used to describe the diet.

The various aging structures: scales, otoliths, opercular bones and fin clips were obtained. These structures were cleaned, and the age of individual fish was determined by correlating growth rings to years of growth (Mackay 1990). Age structures for walleye caught in 2009 were supplied by the Alberta Sustainable Resource and Development; further age cohorts were determined from all netting data available, where age could be determined from the date of release and date of capture.

Growth analysis of the walleye was done using von Bertalanffy growth functions and comparing among the different reservoirs using the likelihood ratio test as developed by Kimura (1980).

4.3 Results

4.3.1 Fish Community Composition

FWMIS beach seine data for all six reservoirs combined led to a total of 17 species identified as capable of inhabiting these reservoirs within southern Alberta. The reservoir fish communities ranged from 9 species in Milk River Ridge to 15 species in McGregor, of the six reservoirs Pine Coulee (PC) is ranked 2nd with 12 species present (Table 4.2).

The beach seine catch for all netting in 2000 in PC resulted in a catch of nine species all from inshore habitats. A total of 180 fish were caught, consisting of brook stickleback *Culaea inconstans* (n = 6, 3.3%), this species is noted to be present only in PC and not in any of the other reservoirs; emerald shiner *Notropis atherinoides* (n = 2, 1.1%), is present in all reservoirs with the exception of St. Mary's reservoir; fathead minnow *Pimephales promelas* (n = 73, 40.6%), is only present in McGregor, St. Mary's and PC; lake chub *Couesius plumbeus* (n = 18, 10.0%) is present in Chin, McGregor, and PC; longnose dace *Rhinichthys cataractae* (n = 2, 1.1%) is present in all the reservoirs with the exception of Chin and Milk River; longnose sucker *Catostomus catostomus* (n = 1, 0.6%); walleye *Sander vitreus* (n = 70, 38.9%) and white sucker *Catostomus commersoni* (n = 7, 3.9%) are present in all reservoirs; trout-perch *Percopsis omiscomaycus* (n = 1, 0.6%) are shown present in all reservoirs except Keho. Other species known to be present in PC but not included in the 2000 seine netting data are burbot *Lota lota*, northern pike *Esox Lucius* and spottail shiner *Notropis hudsonius*. Three species found in the other reservoirs but not PC were rainbow trout *Oncorhynchus mykiss*, present only in St.Mary's and McGregor reservoirs; mountain whitefish *Prosopium williamsoni* were present in Keho and

McGregor and lake whitefish *Coregonus clupeaformis* were present in all reservoirs except PC (Table 4.1).

The test gill nets set in May and October of both 2003 and 2004 and November of 2007 (number of sets and duration not recorded in the FWMIS database) yielded four species. Netting during May and October 2003, yielded only walleye; n = 13 and 51 respectively, and May 2004 netting again yielded only walleye, n=16, and in October 2004 the catch was walleye, n = 51, 98.6% and white sucker, n = 1, 1.4%.

In November 2007 three nets yielded 62 fish including burbot (n = 2, 3.2%), northern pike (n = 3, 4.8%), walleye (n = 51, 82.3%) and white suckers (n = 6, 9.7%). The 2009 netting yielded walleye (n = 129, 84.87%) , white suckers (n = 20, 13.16%), northern pike (n = 2, 1.32%) and longnose suckers (n = 1, 0.66%) (Table 4.1). The 2011 netting yielded walleye (n = 12, 100%) mean catch rate of 2.4 fish per net. Since its completion, the Pine Coulee Reservoir has relied on the natural colonization of species found in the Pine Creek system and the stocking of walleye in 2000 and 2003, and no pelagic zooplanktivores such as lake whitefish, ciscoes, and yellow perch have colonized the reservoir.

Table 4.1. The fish community determined from multiple gill net sets, set during the same year.

	Gill Net Catches											
	Chin 1998		Keho 2006		McGregor 2008		Milk River Ridge 2005		StMary's 1996		Pine Coulee 2007	
Species	n	%	n	%	n	%	n	%	n	%	n	%
Walleye	32	27	236	17	260	55	283	22	38	17	53	83
Northern Pike	6	5	214	15	69	15	67	5	11	5	3	5
Lake Whitefish	64	55	957	67	123	26	892	70	59	26		
Longnose Sucker	1	1	4	<1	1	0	12	1	14	6		
White Sucker	5	4	3	<1	12	3	17	1	68	30	6	9
Spottail Shiner	5	4	6	<1	1	0	4	<1	34	15		
Emerald Shiner			1	<1								
Trout Perch	2	2							1	<1		
Yellow Perch					8	2						
Burbot	2	2	1	<1							2	3
Total # Fish	117		1422		474		1275		225		64	
Number of Species	8		8		7		6		7		4	

Table 4.2. Fish community structure determined from all available data supplied by ASRD. Community composition is determined from multiple seine trawls performed within the same year. Fish which are known to be present in the reservoirs but not represented in the trawl data denoted by *

	Seine Trawl's											
	Chin 1997		Keho 2003		McGregor 2003		Milk River Ridge2003		StMary's 1996		Pine Coulee 2000	
Species	n	%	n	%	n	%	n	%	n	%	n	%
Walleye	*		26	31.3	12	28.6	4	16.7	*		70	38.9
Lake Whitefish	6	13.0	4	4.8	3	7.1	2	8.3	5	10.4		0.0
Burbot	*		*		*		*		4	8.3	*	
Emerald shiner	10	21.7	16	19.3	*		*				2	1.1
Brook Stickleback											6	3.3
Fathead Minnow					*				1	2.1	73	40.6
Lake Chub	2	4.3			1	2.4					18	10.0
Longnose Dace			*		1	2.4			2	4.2	2	1.1
Mountain Whitefish			*		*							0.0
Northern Pike	11	23.9	*		2	4.8	1	4.2	3	6.3	*	
Spottail Shiner	4	8.7	21	25.3	14	33.3	10	41.7	12	25.0	*	
Spoonhead Sculpin	4	8.7										0.0
Trout Perch	1	2.2			*		1	4.2	8	16.7	1	0.6
Yellow Perch					3	7.1						0.0
Longnose Sucker	2	4.3	2	2.4	*		*		7	14.6	1	0.6
White Sucker	6	13.0	14	16.9	6	14.3	6	25.0	6	12.5	7	3.9
Rainbow Trout					*				*			
Total # Fish	46		53		42.0		24.0		48.0		180.0	
Number of Species	11		10		15		9		11		12	

4.3.2 Age, Size and Growth of Walleye

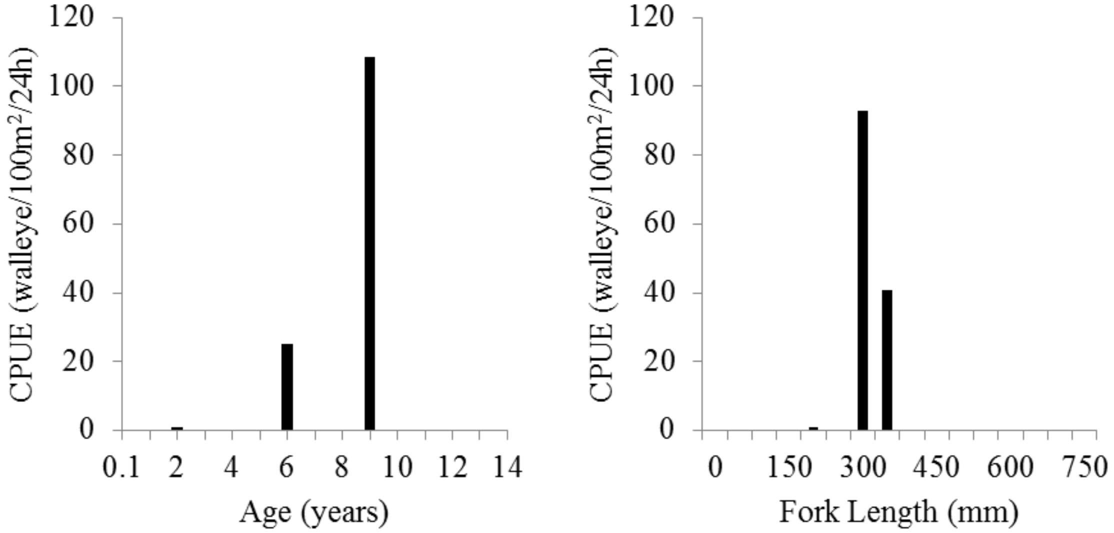

Figure 4.2. Pine Coulee catch per unit effort for age groups (years) and fork length (mm) for 2009 sampling: n = 129 and CPUE = 134.66 walleye / 100 m^2 / 24 h.

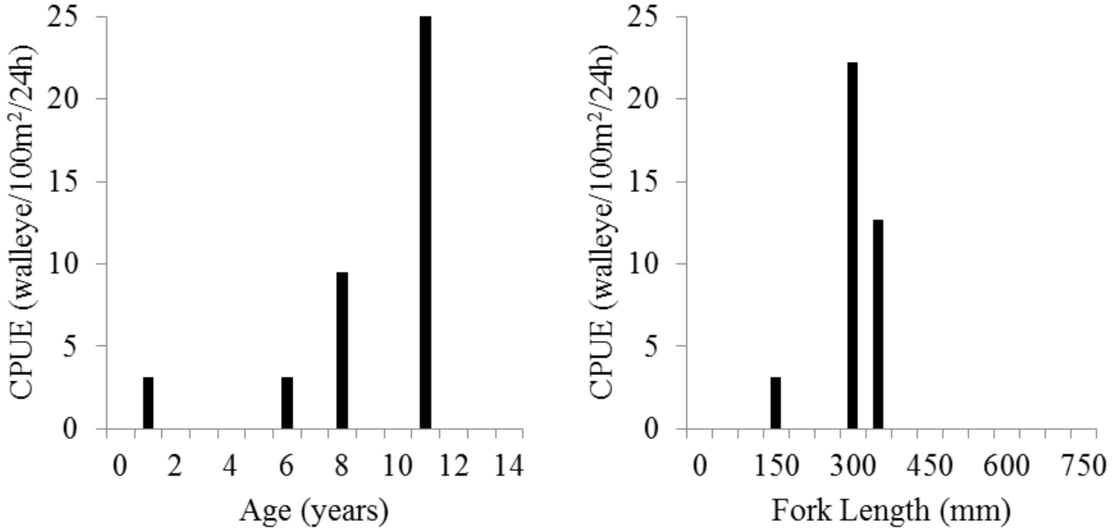

Figure 4.3. Pine Coulee catch per unit effort for age groups (years) and fork length (mm) for 2011 sampling: n = 12, CPUE 38.07 walleye / 100 m^2 / 24 h

Walleye minimum and maximum fork length in 2009 ranged from 250 – 390 mm dominated by walleye within the 300 – 349 mm range (Figure 4.2). The 2011 walleye minimum and maximum fork length ranged from 170 – 380 mm, dominated by walleye within the 300 – 349 mm range (Figure 4.3). The distribution of the average lengths of these fish have not changed significantly in two years, and the 300 – 349 mm class is still the predominant group. The catch of 2009 yielded three age classes, 2-year-old fish, n = 1; 6-year-old fish, n = 24 and 9-year-old fish, n = 104 (Figure 4.2). The 2011 catch yielded four age classes; 1-year-old fish, n = 1; 6-year-old fish, n = 1; 8-year-old fish, n = 5 and 11-year-old fish, n = 8 (Figure 4.3). Also, the walleye stocked in 2003 make up only 18% of the catch in 2009. Almost as many fish were stocked in 2003 as in 2000 (1.9 million in 2003 vs. 2.2 million in 2000), survival of the second stocked cohort (2003) is lower than the group originally stocked in 2000

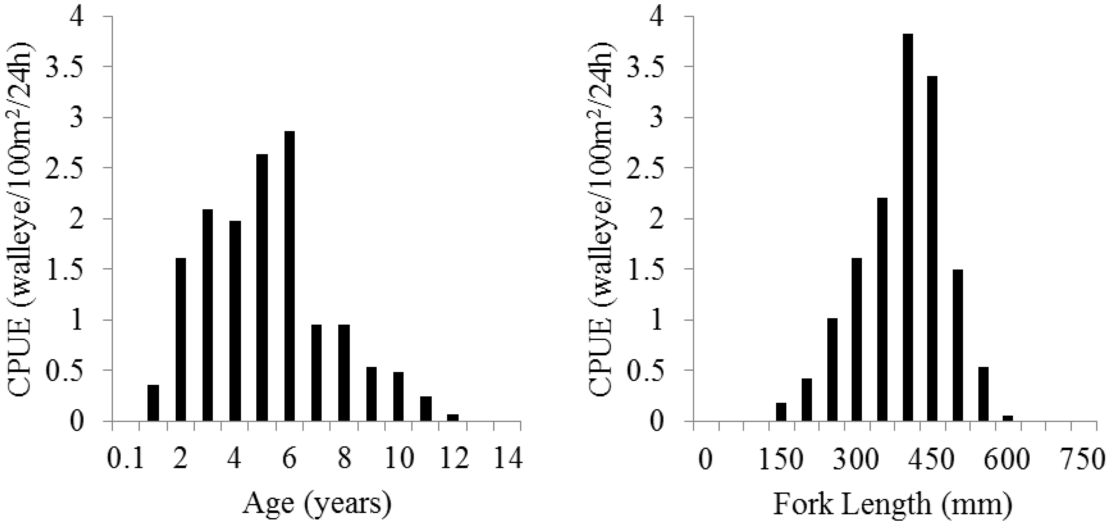

Figure 4.4. CPUE for age groups (years) and fork length (mm) using FWIN data from McGregor in 2008, n=247, total CPUE = 14.77 walleye / 100 m^2 / 24 h

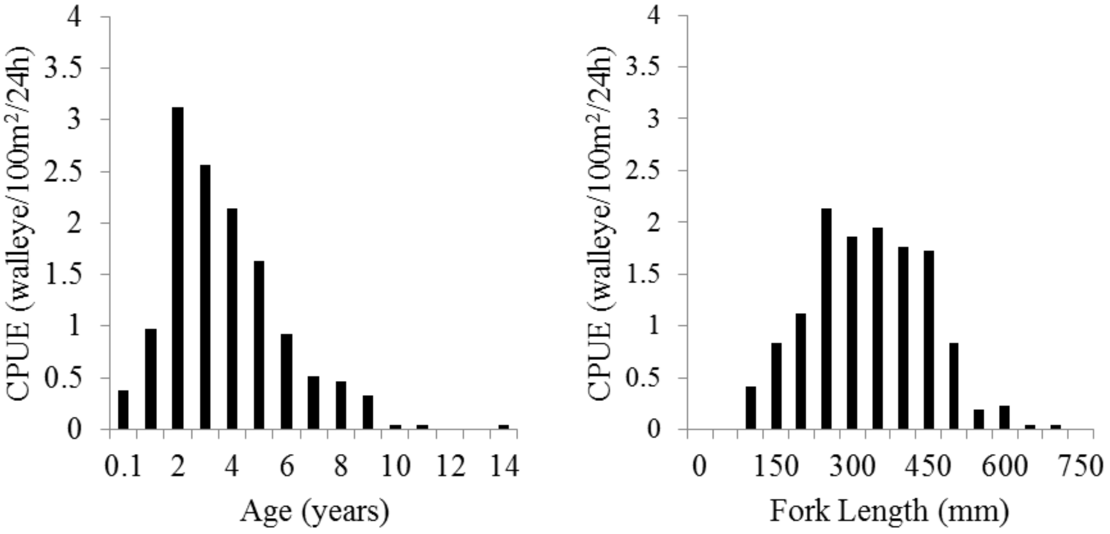

Figure 4.5. CPUE for age groups (years) and fork length (mm) using FWIN data from Milk River Ridge in 2005, n = 283, total CPUE = 13.16 walleye / 100 m^2 / 24 h.

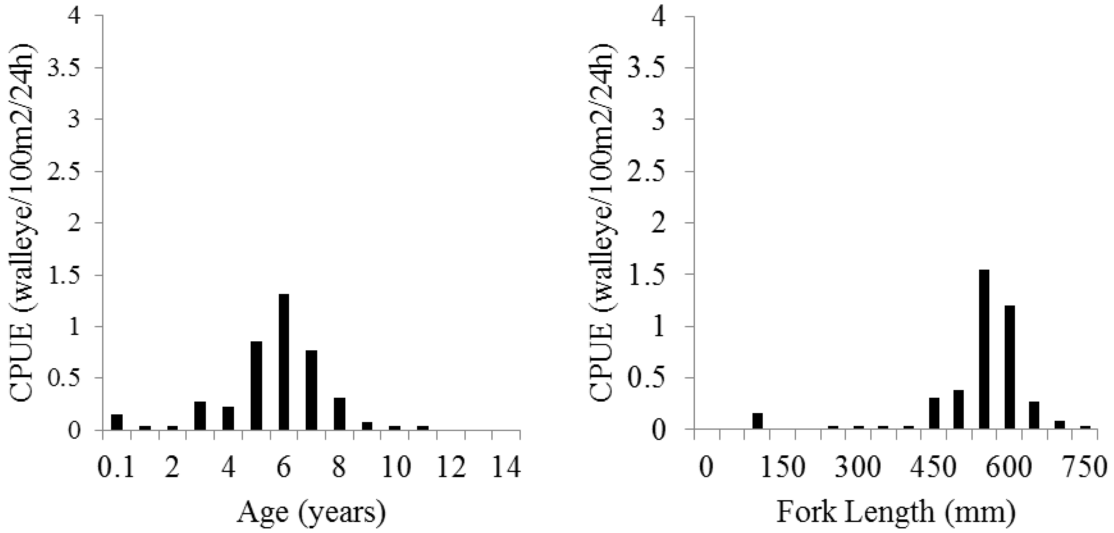

Figure 4.6. CPUE for age groups (years) and fork length (mm) using FWIN data for Keho in 2009, n = 107 and total CPUE is 4.14 walleye / 100 m^2 / 24 h.

The walleye catch from PC yielded far fewer age classes than the reservoirs used for comparison, McGregor (Figure 4.4), Milk River Ridge (Figure 4.5) and Keho (Figure 4.6). The fork lengths of the walleye are substantially longer in the three reservoirs than they are in Pine Coulee. There is also a larger distribution of size classes in these reservoirs compared to Pine Coulee. In neither sample from 2009 or 2011 did the oldest walleye (9 and 11 years old respectively) reach 400 mm (Figure 4.2 and 4.3). In the other reservoirs, walleye reached the 400 mm fork length between 5 and 6 years of age and the 500 mm length between 8 and 10 years. Keho is an exception where the data indicates a very fast growing population with a 500 mm fork length being attained by age 5. When comparing the growth rates between Chin, Keho, McGregor, Milk River Ridge, St. Mary's and Pine Coulee (Figure 4.7) the differences are apparent. The VBGF parameters for PC are significantly different. Asymptotic length ($L\infty$) is significantly lower, and the curvature parameter (k) of PC is significantly higher than those of the other reservoirs. There was no significant difference evident in the estimated length at birth parameter (t0) between the reservoirs (Table 4.3).

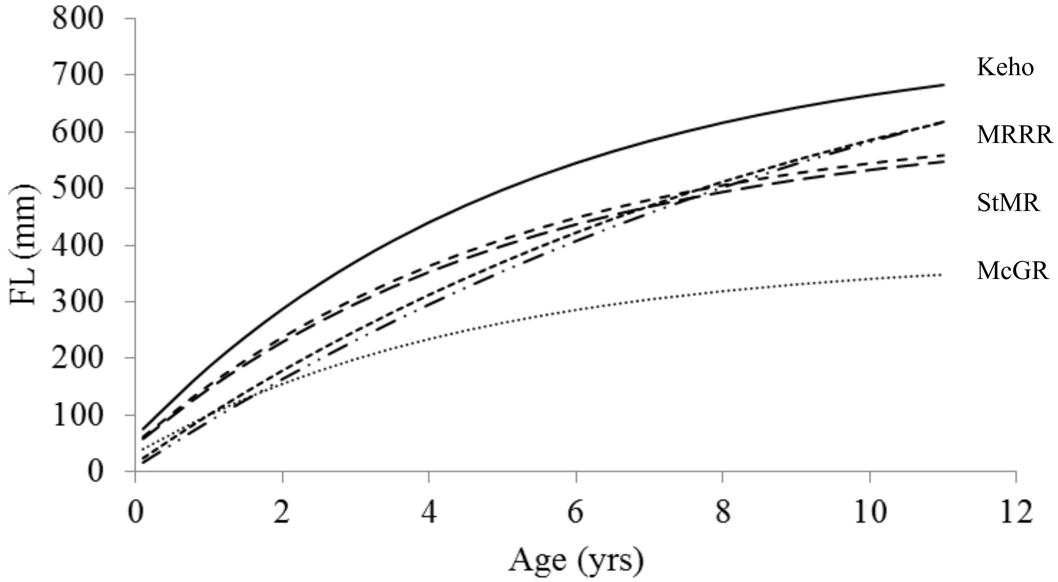

Figure 4.7.Von Bertalanffy Growth Function (VBGF) Growth curves based on all available data obtained from FWMIS and catch data. Chin (n=79), Keho (n=811), McGregor (n=502), Milk River Ridge (n=840), Pine Coulee (n=530) and St. Mary's (n=38).

Table 4.3. Von Bertalanffy growth functions (VBGF) summary for walleye. Models were constructed from all available length at age data available from FWMIS and catch results.

Reservoir	**L∞**	**K**	**t_0**
Pine Coulee	351	0.415	-0.468
Chin	708	0.125	-0.717
McGregor	518	0.309	-0.382
Keho	723	0.209	-0.142
Milk River Ridge	680	0.162	-0.990
St. Mary's	1550	0.038	-2.136

Table 4.4. Comparison of the growth rate of the walleye in Pine Coulee to the other reservoirs, likelihood results.

Comparison	Test	Statistic				Model	Figure
Growth rates of walleye among reservoirs	Likelyhood ratio test (Kimura 1980)	Ho	df	x^2	P		4.7
		PC = All				PC	
		L∞ = L∞	1	227.9	0.000	$Lt = 351 * (1-e^{-0.416(t+0.467)})$	
		k = k	1	55.19	0.000		
		t0 = t0	1	0.58	0.446	All	
		L∞ = L∞, k = k, t0 = t0	3	1689.97	0.000	$Lt = 640 * (1-e^{-0.210(t+0.548)})$	

Walleye length-weight relationship for the Pine Coulee Reservoir in 2009 and the combined data show that the increase in weight to length of these fish increases proportionately in a typical ratio for the species. This is also confirmed when comparing to the combined data length-weight relationship for the Milk River Ridge, Keho, McGregor, and Pine Coulee reservoirs (Figure 4.8).

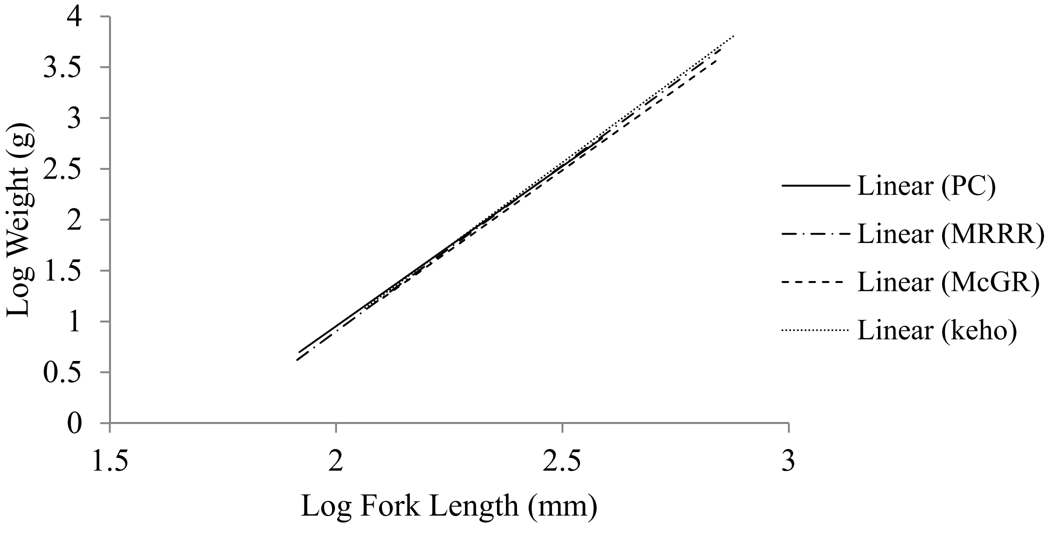

Figure 4.8. Log weight to log length ratio of the walleye from all reservoirs.

4.3.3 Walleye Stomach Contents

Current food web data is based on stomach content for the walleye in Pine Coulee Reservoir and Keho, McGregor, and Milk River Ridge reservoirs, determined from catches recorded in the FWMIS with stomach content. Out of all walleye captured in the reservoir in 2009 and 2011, approximately 85% and 87% respectively, stomach contents consisted entirely of invertebrates; 14% and 13% respectively had empty stomachs. The reservoirs, other than PC, exhibit higher incidence of fish in the stomach content; Keho 62%, McGregor 23% and Milk River Ridge with 68% and lower incidence of Invertebrates and amphipods; Keho 0%, McGregor 8% and Milk River Ridge with 4% (Table 4.5).

Table 4.5. Stomach content of walleye from three local reservoirs and Pine Coulee.

	Stomach Content				
Reservoir	**Fish**	**Invertebrates / Amphipods**	**Empty**	**Unidentified**	**Total n**
Keho 2003, # / %	24 / 62	0 / 0	15 / 38	0 / 0	39
McGregor 2003, # / %	9 / 23	3 / 8	28 / 70	0 / 0	40
Milk River Ridge 2003, # / %	19 / 68	1 / 4	7 / 25	1 / 4	28
Pine Coulee 2009, # / %	0 / 0	110 / 85	18 / 14	1 / 1	128
Pine Coulee 2011, # / %	0 / 0	13 / 87	2 / 13	0 / 0	15

4.4 Discussion

Comparison of fish community, walleye size and growth curves and walleye stomach contents between PC and other reservoirs, showed that (a) PC lacked lake whitefish, although nearshore forage fish were present (b) walleye from PC were smaller for their age compared to those from other reservoirs where lake whitefish were present, and (c) walleye stomachs from PC contained exclusively invertebrates compared to other reservoirs where stomachs contained predominantly fish and very few invertebrates, or were empty. Empty stomachs are an indicator of a piscivorous fish population (Chapman and Mackay 1990). Although there are some records of non-piscivorous walleye populations (Barton 2011), this is not typical for this species, as prey size has been shown to be a critical factor in growth efficiency of predatory fish (Kerr 1971). Instability in walleye recruitment and growth has been shown to be linked to the abundance of suitable forage fish (Forney 1977). The stomach contents recorded from fish samples in the different reservoirs show a high incidence of piscivory except in the Pine Coulee Reservoir.

These differences between PC and other reservoirs are consisted with the perception that the walleye introduction to PC has failed to yield the viable fishery intended. Although the survivorship of the initially introduced cohort in the year 2000 was reasonable, and spawning has been observed (M. Bryski. ASRD. pers. comm.) recruitment has been negligible, and the subsequent cohort introduced in 2001 was less successful and makes up a lower proportion of the catch as reflected by the size and age structure (Figure 4.2 and 4.3). Of the 129 fish caught in 2009, only one 2-year-old fish was present and in 2011, only two fish were not assigned to the initially released cohorts. The age distribution indicates that the existing population consists predominantly of the groups stocked in 2000 and 2003. Thus the poor growth rates exhibited by the two introduced cohorts is reflected in much poorer recruitment than similar age classes from the other reservoirs, which indicates that the walleye population in PC could be sustained only by further introductions to offset mortality. The new recruits, therefore, are dying before they can acquire sufficient size to winter successfully in their first year (Forney 1976). Although no walleye were identified in the walleye stomach contents, walleye are known to be cannibalistic, and this is the probable explanation of the poorer success of the second introduced cohort. Other piscivorous species such as northern pike and burbot may also contribute to predation pressure on walleye fry. Thus further introductions would likely suffer similar consequences. Regardless of the exact source of the mortality, it is evident from the weak growth and age class structure that this walleye population is unstable and its prospects for long-term survival, under the present circumstances, are considered nonviable.

The fish community of PC consists of 12 species of fish. As far as species richness, this is comparable to the other sampled reservoirs; Keho at 10 different species, McGregor at 15 different species, Milk River Ridge at 9 different species and St. Mary’s at 11 different species. Thus the impoverished trophic structure of PC is not reflected directed by species richness, but rather, by the absence of a key functional group found in all other walleye containing reservoirs studied here. The apparent link that makes pelagic plankton production, the main energy source in such a reservoir, available to top trophic levels is entirely lacking in PC but is well represented in all of the other reservoirs by lake whitefish. The lake whitefish inhabit the pelagic zone of the comparison reservoirs, and feed on the abundant plankton present there for several years in their life-history (Pothoven and Nalepa 2006, Johnson et al. 2009), and attracting piscivorous fish to forage on them offshore, will connect the rich zooplankton resource to walleye. The walleye, a top piscivore, which occupy depth zones of 5-15 m, and tend to be found near the bottom in littoral to sublittoral habitat, though they will feed offshore throughout the water column if pelagic forage fish are present (Paetz and Nelson 1992). Had lake whitefish been present in PC, impoverished walleye growth and recruitment described here would likely not have occurred. Lake whitefish are also known to enhance recruitment and growth rates of many other sports fish in addition to walleye (Baldwin and Polacek 2011).

Considering the morphometry, Pine Coulee is predominantly pelagic reservoir offering limited littoral resources. The littoral habitat in PC will likely be even more severely limited if irrigation demand in the area increases and the reservoir will be used to capacity since drawdown will likely increase by several meters (Chapter 2). The simplified food web found in PC is similar to that found in Twin Valley Reservoir where poor growth rates were observed for northern pike (Brinkmann and Rasmussen 2010). Based on the slow growth rates of walleye in PC and northern pike in Twin Valley, any piscivory occurring at this date is not sufficient to support the high growth rates required for a productive sports fishery. Pike in Twin Valley feed mainly on invertebrates and some littoral minnow such as spottail shiner; however, Twin Valley Reservoir, like PC remains underutilized due to current irrigation demand, and consequently drawdown is low and littoral habitat, including macrophytes required and invertebrate production remains reasonably intact. Were drawdown to increase by several meters as is the case in heavily utilized reservoirs, littoral habitat would be severely reduced, which further reduce the growth of pike and reduce its spawning habitat and therefore recruitment.

The mandate of the ASRD to create new walleye fisheries in southern Alberta is a result of the high recreational fishery demands on natural lakes and a significant decline in the existing walleye fishery. Furthermore, the new fisheries are also to mitigate impacts from dams within the South Saskatchewan River system. The decline in recreational fisheries, particularly walleye, places the spotlight on the unsustainable PC fishery and necessitates a critical evaluation of the approach used by ASRD to establish this fishery. The state-of-the-art approach with respect to fishery management practiced in the U.S.A (Ploskey and Jenkins 1982) and in many central European countries (Seda et al. 2000, Scharf 2008, Říha et al. 2009, Vašek et al. 2016) has for decades been based on ecological principals, rather than simply stocking desirable target species into the reservoirs. Fisheries management considerations in these countries are given high priority within the overall management framework of the reservoirs. Therefore, fisheries management is considered to be equally important to functional needs, such as water supply, flood control, and hydropower generation. The need to recognize the importance of recreational fisheries in such a context results from the fact that much of the public perception of such development projects is based to a considerable degree on recreational users of the waterbody. The recreational fishing public, especially, is the group which has most direct contact with these reservoirs and are most likely to be numerous and vocally critical. These fish communities are managed with an emphasis on balanced trophic structure by the introduction of important functional groups, e.g., pelagic zooplanktivores etc., determined by geography and native fauna of the region, to facilitate maximal energy flow to the prime target species. The theoretical underpinnings of this approach as outlined very clearly by Ploskey and Jenkins (1982) could be applied at any latitude and in any country or geographical setting, and are consistent with the findings of this study. The absence of a functional group capable of linking pelagic energy resource, the largest in the reservoir, to the top predatory fish walleye, was not accounted for during planning of the fishery (AESRD 2014b) and is the primary cause of the fisheries deficiencies. In order for viable recreational fisheries to be implemented, managers must take into consideration the species naturally present in the reservoir and the functional trophic structure required to support the desired fishery and the possible need for introductions of forage fish which help achieve this structure. Thus, the fish community must be built from the "bottom up". This type of ecological planning has been the basis for successful reservoir fisheries in the Czech Republic (Seda et al. 2000, Říha et al. 2009, Vašek et al. 2016). This type of ecological planning should be employed by fisheries managers in every province across Canada, and strongly advocated, where it is currently discouraged by the Department of Fisheries and Oceans (DFO) and many provincial agencies, purportedly to limit the need for species introductions. The Department of Fisheries and Oceans does recognize the importance to forage fish to food webs and the supporting role they play in fisheries (DFO 2009). However, their concern with potential impacts of exotic invaders appears to result in a general discouragement of forage fish introductions. Forage fish introductions have played a very prominent role in fisheries management in the U.S. (Ploskey and Jenkins 1982), a prime example of this is the importance placed on alosid planktivores namely gizzard and threadfin shad which provide the trophic support for their highly productive and successful centrarchid based fisheries.

While the trophic structure preferably should be planned prior to the stocking of the target species, it is probable that the walleye fishery in PC could be considerably enhanced by the introduction of lake whitefish. This species is a common native species found throughout Alberta; however, they will fail to colonize reservoirs if upstream lakes are not present or for some reason lack this species. Lake whitefish are present in some reservoirs through natural colonization from upstream sources, St. Mary's and Waterton reservoirs, and present in other local reservoirs by stocking. If lake whitefish are not present in a specific system, they are an important and common native fish east of the Canadian Rockies. Therefore, concerns about the introduction of exotic species, a serious concern of both provincial and federal fisheries managers in Canada are not warranted with regard to lake whitefish.

Chapter Five: **Conclusions.**

5.1 Thesis Summary

The objective of this thesis was to determine the requirements needed for the development of a sustainable top predatory fishery within newly developed prairie reservoirs. Thus, I studied the effects of morphometry and hydrological regime on the availability of littoral habitat in reservoirs compared to natural lakes (Chapter 2); the development and availability of pelagic zooplankton resources in a prairie reservoir (Chapter 3) and the fish community and recruitment success and growth rate of the top predatory walleye in the same reservoir system (Chapter 4).

5.2 Littoral Habitat Loss Due to Drawdown in a Prairie Reservoir.

In natural lakes, with the exception of large deep lakes, littoral and profundal energy resources exceed those of the pelagia (Eggers et al. 1978). Littoral habitat is important to the life history of many different fish and invertebrate species. Littoral habitat provides refuge and breeding habitat and food resources. The littoral habitat and energy resources are limited by littoral instability and loss. Littoral habitat loss, due to drawdown, was identified as a key influencing factor of reservoir secondary productivity.

The results of the study indicate the instability of reservoirs with respect to natural lakes in the region. It can be seen that water level fluctuations imposed on the reservoirs are the most detrimental to the development of littoral habitat within these water bodies. Water level fluctuations in this region leave the shores exposed to degrading factors such as desiccation and ice scouring. Furthermore with water level fluctuations occurring during spring and late summer impact the growing season and further limit macrophyte growth at these times. We can, therefore, see that reservoirs with large water level fluctuations are limited in their ability to develop substantial and stable littoral habitat.

The approximate index of littoral zone development and stability based on drawdown and euphotic zone describes littoral loss due to drawdown. The loss described by this index was not significantly different from the littoral loss calculated from bathymetric maps. A significant relationship exists with this index and the semi-quantitative descriptors of macrophyte presence and abundance (Campbell et al. 1998).

A functional littoral zone within a body of water is important habitat for both fish and invertebrate life histories. Littoral habitat provides breeding and nursery habitat and cover for various fish species. Furthermore, littoral habitat provides the same for invertebrates which provide food resources for many fish species. Limitations imposed on littoral habitat such as that found in reservoirs drives the need for alternative energy resources such as those of the pelagic plankton.

5.3 Zooplankton Biomass

Zooplankton is widely known to occupy a key position in pelagic food webs (Naselli-Flores and Barone 1997, Abrantes et al. 2006). Reservoirs are known to be unstable due to pronounced water level fluctuations over short time periods. These water level fluctuations can severely limit littoral productivity as well as influencing the zooplankton community due to rapidly changing flushing rates (water residence time) (Naselli-Flores and Barone 1997).

The zooplankton community in Pine Coulee fluctuated with respect to the number of taxa present in the community within the four years after completion. However, this fluctuation in species variability was driven by taxa that made up less than 5% of the biomass of the community, within a given year. Six taxa contributed 98% of the zooplankton community biomass and were present from the first year of operation. This fact indicates that the prevalent taxa colonize the reservoir immediately. The prevalent taxa in Pine Coulee were; Reservoirs Cladocerans; Chydoridae and Daphnidae and Copepods; Cyclopidae and Diaptomidae; Nauplii and Rotifers.

The mean zooplankton biomass during the first four years of operation of Pine Coulee followed a pattern of increase and decrease, indicative of trophic upsurge and depression which reservoirs undergo after initial impoundment (Ostrofsky 1978, Ostrofsky and Duthie 1980, Grimard and Jones 1982). This study suggests that the community as observed in 2012 can be stable and variability seen over the prior years was likely linked to changes in nutrient levels associated with flooding of the landscape together with changes in residence time associated with the filling of the reservoir and the subsequent water management regime.

The abundance and diversity of phytoplankton and zooplankton are known to differ in fresh water bodies due to trophic state (Jeppesen et al. 2000). A significant positive relationship was noted for zooplankton biomass with respect to water residence time and total phosphorous. Increase in levels of phosphorous, increase phytoplankton productivity which in turn increases zooplankton production (Grimard and Jones 1982). Longer water retention times result in higher zooplankton biomass are water residence time (Geraldes and Boavida 2007, Obertegger et al. 2007), Pine Coulee had the highest zooplankton biomass of all reservoirs sampled in 2012. Furthermore, Pine Coulee has the longest water residence time and the highest total phosphorous than all reservoirs in the comparison.

Relative to the biomass data the zooplankton community of Pine Coulee can be deemed capable of supporting a zooplanktivore forage fish species such as lake whitefish.

5.4 Growth and Recruitment of a top predator in a prairie reservoir

Fish community structure is important in determining the presence or absence of species required to link energy resources to higher trophic fish. Fish community structure maps the energy flow within the reservoir environment and highlights missing links in food web structure which can impact the growth of higher trophic species.

The fish community in Pine Coulee consists of 11 species which colonized the reservoir naturally and 1 stocked, walleye, to create a fishery. Of these species 6 are common to all the reservoirs in this study; Walleye *Sander vitreus*, burbot *Lota lota* and northern pike *Esox lucius*, apex predators and intermediate consumers, spottail shiners *Notropis hudsonius*, long nose and white suckers *Catastomus catastomus* and *Catastomis commersoni*. Fish communities between the reservoirs ranged from 9 to 15 species, Pine Coulee falls in the middle of this range. The fish community in Pine Coulee includes species not common to all the reservoirs in this study; emerald shiner *Notropis atherinoides*, brook stickleback, fathead minnow *Pimephales promelas*, longnose dace *Rhinichthys cataractae* and lake chub *Couesius plumbeus*, which are generally small species seldom exceeding 15 cm (Nelson and Paetz 1992).

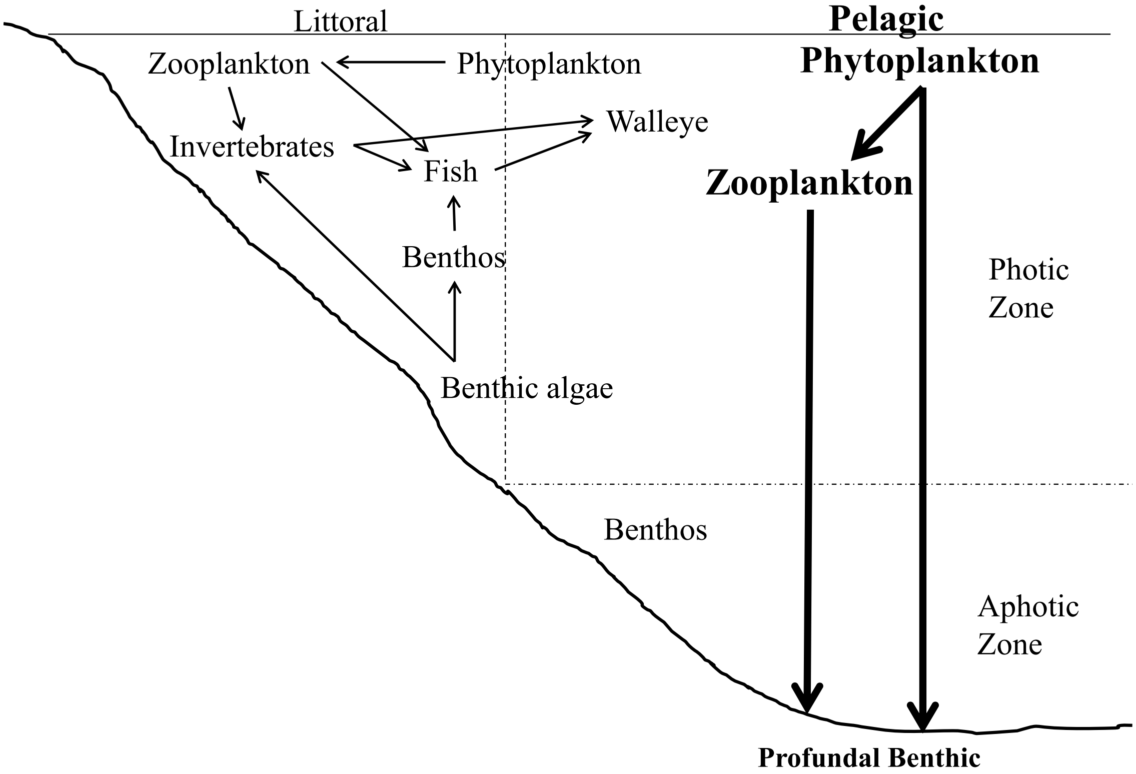

Figure 5.1. The current simplified food web of Pine Coulee Reservoir which lacks a forage fish which can link the pelagic plankton energy resources to the piscivorous species within.

Walleye recruitment in Pine Coulee is negligible. Spawning by the mature walleye has been observed, but successful maturation has not. The walleye community consists of predominantly two age groups which correspond to the two cohorts stocked in 2000 and 2003. The lack of other age classes indicates that new recruits are dying before they can acquire sufficient size to winter successfully in their first year (Forney 1976). This could be due to predation of the eggs by suckers (Roseman et al. 2006), predation by pike and burbot known piscivores (Nelson and Paetz 1992) or cannibalism by the originally released cohorts (Forney 1976).

The growth rates of the walleye in Pine Coulee are low. Stomach content analysis indicates that the walleye community relies on benthic invertebrates to a much larger extent than those of the other reservoirs. Furthermore, the incidence of empty stomachs, an indicator of piscivory (Chapman and Mackay 1990), in Pine Coulee is low, less than 1% of all fish for which stomach content data was available.

Walleye growth rates and recruitment have been linked to prey abundance (Forney 1977) and prey size (Kerr 1971). Pine Coulee lacks a forage fish which can fulfill the size requirements for prey items for walleye such as lake whitefish (Figure 5.1). The lack of optimal prey in a littorally limited reservoir with no forage fish linking the pelagic energy reserves to the walleye has led to a stunted, non-reproductive fishery in Pine Coulee.

These studies have demonstrated that the reservoirs in the southern Alberta prairie region can be unstable and unable to produce substantial and stable littoral habitat due mainly to water level fluctuations. Furthermore, under the right conditions with respect to water residence time, these reservoirs can produce substantial pelagic energy resources. These pelagic resources cannot be utilized by top trophic piscivorous species unless species capable linking the resource are available in up-stream sources which can naturally colonize the reservoir or they are introduced. The resultant walleye fishery in a reservoir with no suitable pelagic zooplanktivore and limited littoral habitat suffers poor growth rates and limited recruitment.

5.5 Management Directions for Fisheries in New Reservoirs

Reservoirs fisheries management face unique challenges for maintaining viable fisheries based on apex consumers. Reservoir systems were stocked with walleye and lake whitefish to support and enhance commercial fisheries in the early twentieth century resulting in the establishment of lake whitefish and walleye populations within the same water body and inadvertently linked the pelagic energy resource to apex predators within the reservoir (Figure 5.2).

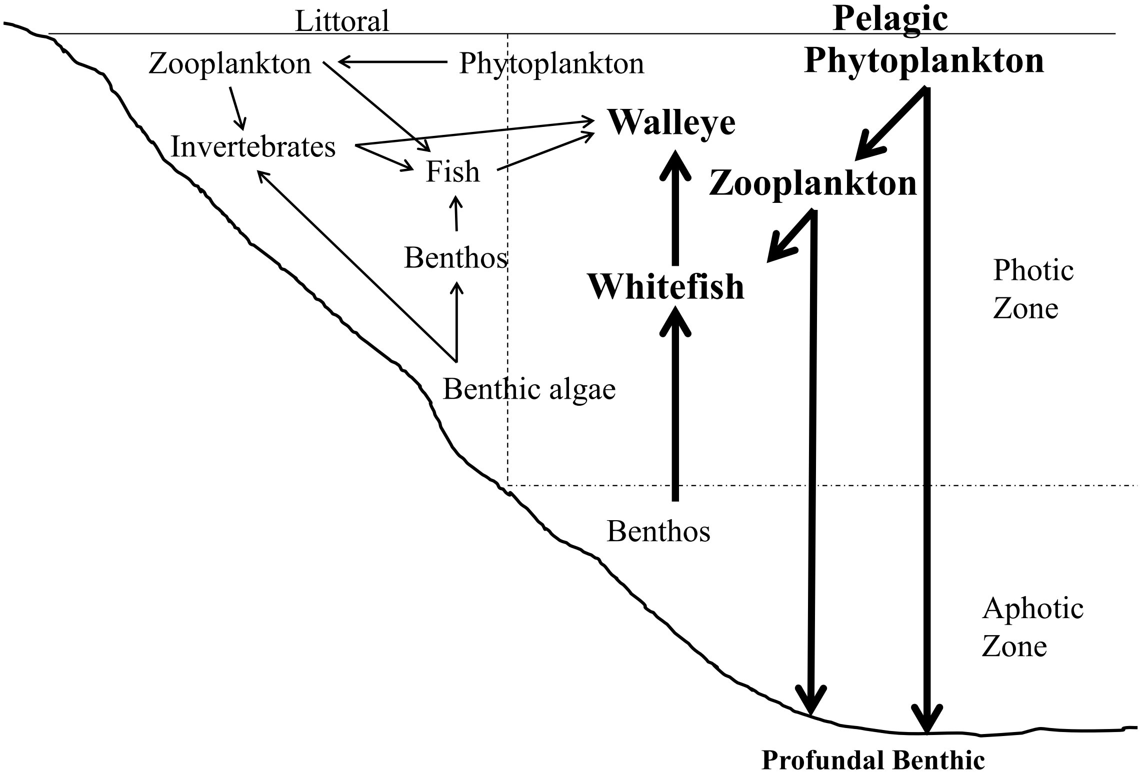

Figure 5.2. The food webs developed unintentionally in the reservoirs stocked for commercial fisheries.

However, as commercial fishing is no longer permitted by the ASRD within the region, stocking is now done with sports fish such as walleye in mind. Lake whitefish are not stocked any longer. This results in simplified food webs in newly formed reservoirs without up-stream sources of lake white fish, and as a result apex species such as walleye lack larger prey resources (Figure 5.1). Fisheries managers must consider the food web energy resources available within a reservoir and introduce the prey species required to link them when they are not present naturally. Food webs must be established from the bottom up to support the diet shift which apex predators undergo through their ontogeny. The forage species chosen must also be able to fulfill the size requirements as the apex predator grows. A successful fishery is dependent on growth rates and yields of target species. In order to obtain optimal growth and yields of target species, the food webs must be integrated, similar to those found in natural lakes, by species missing in parent river communities. This will lead to maximization of the fishery potential of reservoirs and additional fisheries to just the target species.

The introduction of forage fish to support trophic structure of food webs in American and Central and Eastern European reservoirs is an important component of their reservoir fisheries management (Ploskey and Jenkins 1982, Seda et al. 2000, Říha et al. 2009, Vašek et al. 2016). Planktivores such as gizzard and threadfin shad are commonly used to channel pelagic energy from plankton to top piscivores. These species are particularly useful in reservoirs as they are capable of feeding on both phytoplankton and zooplankton due to numerous fine gill rakers and as such can suppress blooms as well as function effectively in reservoirs with short WRT and reduced zooplankton biomass. However, such ‘omni-planktivores’are not part of Canada’s native fish fauna, however, whitefish, roach, and perch, pelagic zooplanktivores are and play a prominent role in European reservoir management. Reservoir fisheries can also benefit not only from pelagic energy flow but also profundal energy flow, especially in very deep reservoirs where this may be “bottlenecked” (Figure 5-2). The species listed in Table 5.1

includes profundal benthivores, such as carp, tench, bream, and redhorse. While most reservoirs often exhibit poor littoral development due to steep morphometry and high drawdown (Chapter 2) some with shallow basins and limited drawdown can support dense macrophyte growth which as an energy source can also become bottlenecked and therefore, herbivore and detritivore species such as the carps and carpsuckers have also played a useful role in reservoir food web management. As a result fish managers have been able to enhance energy flow to target species, usually piscivores, by linking a wide range of energy resources through forage fish from all types of functional groups.

While many species listed are not available naturally to managers of higher latitude reservoirs due to zoogeographical limitations, there are many species that are available (Table 5.1). The principal of enhancing fisheries through the management of forage fish has considerable scope for application in most parts of Canada. Although the DFO management policy recognizes and attributes considerable importance to food web structure and the supporting role of forage fish in fisheries (DFO 2009), their concern with impacts of exotic invaders appears to discourage forage fish introductions. Reservoirs are often limited in regards to species which naturally colonize them as the fauna of the impounded rivers usually do not contain many lacustrine specialists. Any species native to the regional fish fauna if lacking in reservoirs can be introduced without violating policies against the introduction of exotic species, a factor which seems not well understood by either federal or provincial regulatory agencies. For example, lake whitefish are not found in the Willow Creek watershed, they are however native to Alberta and are found in headwater lakes of other Oldman River tributaries such as Waterton and St. Mary Lakes. Therefore, they are an important component of the fish fauna of the South Saskatchewan system, and can in no way be considered exotic, even if they are not locally present in some sub-watersheds.

Table 5.1. Forage fish commonly used in reservoir management in North America and Europe and their functional role in trophic structure (Ploskey and Jenkins 1982, Seda et al. 2000, Vašek et al. 2016) and fish capable of being used as forage in Canada and their functional role in trophic structure (Scott and Crossman 1973).

Species	**Trophic function**	**Geographic region**
Gizzard Shad *Dorosoma cepedianum*	Pelagic planktivore	Mid-Western & SE U.S.A
Threadfin Shad *Dorosoma petenense*	Pelagic planktivore	SE USA
Redhorse *Moxostoma* spp	Profundal benthivore	Eastern U.SA, Southern Canada
Silversides *Atherinus* spp	Pelagice planktivore	Southern USA, South Central Canada
Bluegill Sunfish *Lepomis macrochirus*	Littoral benthivore	Eastern and Southern U.SA
Longear Sunfish *Lepomis megalotis*	Littoral benthivore	Eastern and Southern U.S.A
Green Sunfish *Lepomis* spp	Littoral benthivore/molluscivore	Eastern & Southern USA
Crappies *Pomoxis* spp	Benthivore/planktivore	Eastern & mid-western U.SA
Yellow Perch *Perca flavescens*	Pelagic zooplanktivore/ littoral benthivore	Northern & mid-western USA, Canada
European Perch *Perca fluviatilis*	Pelagic zooplanktivore	Europe
Freshwater Drum *Aplodonotes grunniens*	Profundal benthivore	Southern & Eastern USA
Kokanee Salmon *Oncorhynchus nerka*	Pelagic zooplanktivore	Western Canada & U.S.A
Common whitefish *Coregonus laveratus*	Pelagic zooplantivore /profundal benthivore	Central & Eastern Europe
Rainbow smelt *Osmerus mordax*	Pelagic zooplanktivore	North Eastern U.S.A, Eastern Canada
Carpsuckers *Carpiodes* spp	Herbivore/detritivore	Southern & Eastern USA
Bullheads &Madtom *Noturus* spp	Profundal benthivore	Southern & Eastern USA
Roach *Rutilus rutilus*	Littoral and profundal benthivore/planktivore	Europe
Bream *Abramus*	Littoral and profundal benthivore	Europe
Tench *Tinca tinca*	Littoral & profundal benthivore	Eurasia and Western Europe
Common carp *Cyprinus carpio*	Littoral and profundal benthivore/detritivore	Europe
Lake whitefish *Coregonus clupeaformis*	Pelagic zooplantivore /profundal benthivore	Canada
Lake chub Couesius plumbeus	Littoral and profundal benthivore/planktivore	Canada
Cisco *Coregonus artedii*	Pelagic zooplantivore /profundal benthivore	Canada
Quillback *Carpiodes cyprinus*	Profundal Benthivore	South Central Canada

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