

Carbon Sources Supporting Fish Growth in Lake Diefenbaker

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Abstract

There are two main carbon sources for consumers in aquatic ecosystems: allochthonous sources, those generated through primary production outside of the waterbody, and autochthonous sources, those generated through both benthic and pelagic primary production within the waterbody. Lake Diefenbaker, a large prairie reservoir located on the South Saskatchewan River in central Saskatchewan, contains an additional carbon source for consumers via waste products from an aquaculture facility located within the reservoir. This study set out to identify the importance of each potential carbon source to four common fish species throughout the length of Lake Diefenbaker. Lake Whitefish (*Coregonus clupeaformis*), Northern Pike (*Esox lucius*), Walleye (*Sander vitreus*) and White Sucker (*Catostomus commersoni*) were sampled in 2012 and 2013 and the importance of each potential carbon source was examined using stable isotope analysis and the Bayesian mixing model SIAR. Lake Whitefish in the area surrounding the aquaculture facility were using the waste feed from the fish farm as a diet subsidy; however, the effect was extremely localized and only fish in the immediate vicinity of the cages showed any contribution from aquaculture waste. Whitefish feeding on the pelleted fish feed were larger in size and in better condition than those that were not using the diet subsidy. Benthic autochthonous primary production was the most important source to Northern Pike, Walleye and White Sucker, while pelagic autochthonous production was the primary source supporting Lake Whitefish throughout the reservoir. Allochthonous carbon was of little importance to any of the fish species studied throughout the downstream reaches of Lake Diefenbaker, but was of slightly higher importance at the most upstream site in the riverine zone of the reservoir.

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Dedication

This work is dedicated to my parents. Thank you for your ever-present love and support.

Table of Contents

Permission to Use.....	i
Abstract.....	ii
Acknowledgments.....	iii
Dedication.....	iv
Table of Contents.....	v
List of Tables.....	x
List of Figures.....	xii
List of Abbreviations.....	xvi
Chapter 1. General Introduction.....	1
1.1 Review of Carbon Sourcing Literature.....	1
1.1.1 Introduction.....	1
1.1.2 Aquaculture Subsidies in Wild Fish Populations.....	2
1.1.2.1 Marine Aquaculture.....	3
1.1.2.2 Freshwater Aquaculture.....	5
1.1.3 Allochthonous and Autochthonous Carbon Sources.....	8
1.1.3.1 Lakes.....	9
1.1.3.2 Rivers.....	11
1.1.3.3 Reservoirs.....	12
1.1.4 Stable Isotope Analysis.....	14
1.1.4.1 Carbon.....	16
1.1.4.2 Nitrogen.....	17
1.2 Research Introduction.....	18

1.2.1 Lake Diefenbaker.....	18
1.2.2 Rationale for Study.....	20
1.2.3 Objectives.....	21
1.2.3.1 Study Design.....	21
Chapter 2. Assimilation of aquaculture waste by Lake Whitefish, <i>Coregonus clupeaformis</i>, in Lake Diefenbaker.....	24
2.1 Introduction.....	24
2.1.1 Importance of Aquaculture.....	24
2.1.2 A Brief History of Aquaculture in Lake Diefenbaker.....	24
2.1.3 Trends in Other Aquaculture Studies.....	25
2.1.4 Expected Results.....	26
2.2 Methods.....	27
2.2.1 Field Sampling.....	27
2.2.1.1 Lake Whitefish, Domestic Rainbow Trout and Pelleted Fish Feed.....	27
2.2.1.2 Aquatic Baseline Samples.....	28
2.2.2 Stable Isotope Analysis.....	29
2.2.2.1 Discrimination Factors.....	31
2.2.3 Mixing Models.....	31
2.2.4 Fish Condition.....	32
2.2.5 Statistical Analysis.....	33
2.3 Results.....	34
2.3.1 Fish Size and Condition.....	34
2.3.2 Stable Isotope Analysis.....	34

2.3.3	Mixing Models.....	42
2.3.4	Fish Condition by Carbon Source.....	44
2.4	Discussion.....	48
2.4.1	Assimilation of Aquaculture Waste.....	48
2.4.2	Distance from the Aquaculture Cages.....	51
2.4.3	Fish Condition.....	52
2.4.4	Spatial and Temporal Comparisons.....	54
2.4.5	Comparison with Other Systems.....	55
2.5	Conclusion.....	57
Chapter 3. The importance of allochthonous and autochthonous carbon sources to the diets of fish throughout Lake Diefenbaker.....		59
3.1	Introduction.....	59
3.1.1	Allochthonous and Autochthonous Support of Food Webs.....	59
3.1.2	Lentic Systems.....	59
3.1.3	Lotic Systems.....	60
3.1.4	Reservoirs.....	61
3.1.5	Expected Results.....	62
3.2	Methods.....	63
3.2.1	Field Sampling.....	63
3.2.1.1	Fish.....	63
3.2.1.2	Aquatic Baseline Samples.....	64
3.2.2	Stable Isotope Analysis.....	64
3.2.3	Discrimination Factors.....	65

3.2.4	Mixing Models.....	66
3.2.5	Fish Condition.....	66
3.2.6	Statistical Analysis.....	67
3.3	Results.....	67
3.3.1	Fish Size and Condition.....	67
3.3.1.1	Lake Whitefish.....	67
3.3.1.2	Northern Pike.....	68
3.3.1.3	Walleye.....	69
3.3.1.4	White Sucker.....	70
3.3.2	Stable Isotope Analysis.....	76
3.3.3	Mixing Models.....	84
3.3.3.1	Lake Whitefish.....	84
3.3.3.2	Northern Pike.....	85
3.3.3.3	Walleye.....	91
3.3.3.4	White Sucker.....	91
3.3.4	Fish Condition by Carbon Source.....	92
3.4	Discussion.....	103
3.4.1	Carbon Sources: Allochthony versus Autochthony.....	103
3.4.2	$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Along the Length of Lake Diefenbaker.....	105
3.4.3	Where Does the Change in Resource Use Occur?.....	110
3.4.4	Fish Condition Throughout Lake Diefenbaker.....	111
3.4.5	Spatial and Temporal Comparisons.....	115
3.4.6	Comparison with Other Systems.....	117

3.5 Conclusions.....	118
Chapter 4. General Conclusions.....	121
4.1 Study Accomplishments.....	121
4.2 Support of Lake Whitefish Diets through Aquaculture Waste.....	121
4.3 The Importance of Allochthonous and Autochthonous Support of Food Webs.....	122
4.4 Limitations of the Current Study and Potential Room for Improvement.....	123
4.5 Future Directions.....	125
Literature Cited.....	127

List of Tables

Chapter 2

Table 2.1. Characteristics of Lake Whitefish (*Coregonus clupeaformis*) captured at sites 1 – 8 in spring 2012. Values are listed as the mean \pm standard deviation (SD) and the range is included in brackets.....35

Table 2.2. Characteristics of Lake Whitefish (*Coregonus clupeaformis*) captured at sites 1 – 8 in fall 2012 and at site FF, directly adjacent to the fish farm cages, in fall 2013. Values are listed as the mean \pm SD and the range is included in brackets.....36

Table 2.3. Characteristics of Lake Whitefish (*Coregonus clupeaformis*) captured at sites 1 – 8 in spring 2013. Values are listed as the mean \pm SD and the range is included in brackets.....37

Table 2.4. Seasonal contribution of pelagic primary production, benthic primary production, and aquaculture waste to Lake Whitefish diets as determined through the stable isotope mixing model SIARsolo. Lake Whitefish were caught at sites 1 – 8 in spring 2012 (S12), fall 2012 (F12), and spring 2013 (S13), while those at site FF were caught in fall 2013 (F13). Domestic Rainbow Trout were included as they were known to have a diet of entirely pelleted fish feed, but still show a proportion of their diet from benthic and pelagic sources due to the inclusion of all sources in the mixing model. Proportions are reported as the seasonal mean \pm SD for each site, while the range of values is reported in brackets.....38

Table 2.5. Size and fecundity of Lake Whitefish caught in Lake Diefenbaker in the fall of 2012 and 2013. Lake Whitefish were separated by sex and those with a greater than 50 % contribution of aquaculture waste to their diets (AW Specialist) were separated from fish with between 15 – 50 % diet contribution from aquaculture waste (AW Generalists) and from fish with < 15 % diet contribution from aquaculture waste (No AW). No sexually mature AW Generalists were caught in this study, so they are not included in the table.....47

Chapter 3

Table 3.1. Characteristics (mean \pm SD) of Lake Whitefish (LKWH), Northern Pike (NRPK), Walleye (WALL) and White Sucker (WHSC) caught at sites 1 – 12 in spring 2012 (S12), fall 2012 (F12), spring 2013 (S13) and the overall mean for each species. Data for sample size (n), total length (TL), weight (Wt.), relative weight (W_r), $\delta^{13}C$ and $\delta^{15}N$ are included.....69

Table 3.2. Characteristics (mean \pm SD) of Lake Whitefish (*Coregonus clupeaformis*) caught in spring (S12) and fall 2012 (F12) and spring 2013 (S13). Data for sample size (n), total length (TL), weight (Wt.), relative weight (W_r), $\delta^{13}C$ and $\delta^{15}N$ are included, or listed as NA when no fish were caught.....71

Table 3.3. Characteristics (mean \pm SD) of Northern Pike (*Esox lucius*) caught in spring (S12) and fall 2012 (F12) and spring 2013 (S13). Data for sample size (n), total length (TL), weight (Wt.), relative weight (W_r), $\delta^{13}C$ and $\delta^{15}N$ are included, or listed as NA when no fish were caught.....72

Table 3.4. Characteristics (mean \pm SD) of Walleye (*Sander vitreus*) caught in spring (S12) and fall 2012 (F12) and spring 2013 (S13). Data for sample size (n), total length (TL), weight (Wt.), relative weight (W_r), $\delta^{13}C$ and $\delta^{15}N$ are included, or listed as NA when no fish were caught.....73

Table 3.5. Characteristics (mean \pm SD) of White Sucker (*Catostomus commersoni*) caught in spring (S12) and fall 2012 (F12) and spring 2013 (S13). Data for sample size (n), total length (TL), weight (Wt.), relative weight (W_r), $\delta^{13}C$ and $\delta^{15}N$ are included, or listed as NA when no fish were caught.....74

Table 3.6. Characteristics and fecundity data (mean \pm SD) for all sexually mature Lake Whitefish (LKWH), Northern Pike (NRPK), Walleye (WALL) and White Sucker (WHSC) caught at sites 1 – 12 in spring 2012 (S12), fall 2012 (F12), spring 2013 (S13).....75

Table 3.7. The relationship between condition factors and the proportion of diet contribution of each carbon source for four species of fish in Lake Diefenbaker Saskatchewan. Significant relationships ($P < 0.05$) are shown in bold text (model I linear regression). Sex is indicated as either (M) for male or (F) for female for gonad weight and GSI.....101

List of Figures

Chapter 1

Figure 1.1. Location of all sampling sites throughout Lake Diefenbaker and the South Saskatchewan River used in this study. The location of the Wild West Steelhead aquaculture facility and site FF used in Chapter 2 are indicated with a white arrow. Sites used in Chapters 2 and 3 are labeled with the separate site numbers used in each chapter in the format: Chapter 2 site #/Chapter 3 site #.....23

Chapter 2

Figure 2.1. Stable isotope biplot of all Lake Whitefish (*Coregonus clupeaformis*) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values collected in spring 2012 (S12), fall 2012 (F12), spring 2013 (S13) and fall 2013 (F13) (open symbols) and the mean (\pm SD) of potential dietary sources corrected for trophic enrichment (closed symbols). POM was corrected for two trophic levels by doubling the trophic enrichment factors applied to it due to it being a basal resource whereas other sources were primary consumers. Potential dietary sources include bulk zooplankton (ZP), particulate organic matter (POM), lymnaeid snails (LS), *Gammarus lacustris* (GA), and pelleted fish feed (PFF)...39

Figure 2.2. Individual site stable isotope biplots of Lake Whitefish (*Coregonus clupeaformis*) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from spring 2012 (S12), fall 2012 (F12), spring 2013 (S13) and fall 2013 (F13). Domestic Rainbow Trout collected at the fish farm facility (DRT) were included for site FF. The mean (\pm SD) of potential dietary sources including POM, zooplankton (ZP), *G. lacustris* (GA), lymnaeid snails (LS), and pelleted fish feed (PFF) were corrected for trophic enrichment and plotted alongside consumers (POM was corrected for two trophic levels as it was a basal resource whereas other sources were primary consumers).....40

Figure 2.3. The relationship between Lake Whitefish total length (mm) and $\delta^{13}\text{C}$ (model I linear regression). Plot “A” shows data for all Lake Whitefish, while plot “B” has the Lake Whitefish which were subsidizing their diets with pelleted fish feed (AW specialists) removed from the plots. Note the difference in scale on both the X and Y axes between the plots.....41

Figure 2.4. The relationship between Lake Whitefish total length (mm) and $\delta^{15}\text{N}$ (model I linear regression). Plot “A” shows data for all Lake Whitefish, while plot “B” has the Lake Whitefish which were subsidizing their diets with pelleted fish feed (AW specialists) removed from the plots. Note the difference in scale on both the X and Y axes between the plots.....41

Figure 2.5. The relationship between Lake Whitefish total length (mm) and W_r (model I linear regression). Plot “A” shows data for all Lake Whitefish, while plot “B” has the Lake Whitefish which were subsidizing their diets with pelleted fish feed (AW specialists) removed from the plots.....42

Figure 2.6. Boxplots showing the proportional contribution of each potential carbon source to the diets of all Lake Whitefish (*Coregonus clupeaformis*) at each sample site (site numbers are listed in the top right corner of each plot). The potential dietary sources include pelagic primary production represented by zooplankton (ZP), benthic primary production represented by two

aquatic macroinvertebrates, lymnaeid snails (LS) and *G. lacustris* (GA), and aquaculture waste, represented by pelleted fish feed (PFF) from the aquaculture facility. The inner, central and outer portions of the boxplots represent the 50 %, 75 % and 95 % credible intervals of the data.....43

Figure 2.7. Mean relative weight (W_r) for all Lake Whitefish (*Coregonus clupeaformis*) captured at each site throughout 2012 and 2013. Plot “A” includes all Lake Whitefish caught in this study, while plot “B” has those fish which were specialists on aquaculture waste excluded. Error bars represent 95 % confidence intervals for the means. Means with a common letter are not significantly different from one another.....46

Figure 2.8. Mean relative weight (W_r) for all Lake Whitefish (*Coregonus clupeaformis*) captured during spring 2012 (S12), fall 2012 (F12), spring 2013 (S13) and fall 2013 (F13). Plot “A” includes all Lake Whitefish caught in this study, while plot “B” has those fish which were specialists on aquaculture waste excluded. Error bars represent 95 % confidence intervals for the means and means with a common letter are not significantly different from one another.....48

Chapter 3

Figure 3.1. Stable isotope biplot for Lake Whitefish caught at sites 1 – 12 in spring 2012 (yellow), fall 2012 (blue) and spring 2013 (green). Potential dietary sources were adjusted for trophic level of each species and are indicated by black symbols with error bars representing the standard deviation. These include pelagic autochthonous sources (zooplankton (ZP) and particulate organic matter (POM)), benthic autochthonous sources (lymnaeid snails (LS) and *Gammarus lacustris* (GA)), unionid mussels from the tributary inflow (UM) and an allochthonous source (leaf litter (LL)).....77

Figure 3.2. Stable isotope biplot for Northern Pike caught at sites 1 – 12 in spring 2012 (yellow), fall 2012 (blue) and spring 2013 (green). Potential dietary sources were adjusted for trophic level of each species and are indicated by black symbols with error bars representing the standard deviation. These include pelagic autochthonous sources (zooplankton (ZP) and particulate organic matter (POM)), benthic autochthonous sources (lymnaeid snails (LS) and *Gammarus lacustris* (GA)), unionid mussels from the tributary inflow (UM) and an allochthonous source (leaf litter (LL)).....78

Figure 3.3. Stable isotope biplot for Walleye caught at sites 1 – 12 in spring 2012 (yellow), fall 2012 (blue) and spring 2013 (green). Potential dietary sources were adjusted for trophic level of each species and are indicated by black symbols with error bars representing the standard deviation. These include pelagic autochthonous sources (zooplankton (ZP) and particulate organic matter (POM)), benthic autochthonous sources (lymnaeid snails (LS) and *Gammarus lacustris* (GA)), unionid mussels from the tributary inflow (UM) and an allochthonous source (leaf litter (LL)).....79

Figure 3.4. Stable isotope biplot for White Sucker caught at sites 1 – 12 in spring 2012 (yellow), fall 2012 (blue) and spring 2013 (green). Potential dietary sources were adjusted for trophic level of each species and are indicated by black symbols with error bars representing the standard deviation. These include pelagic autochthonous sources (zooplankton (ZP) and particulate organic matter (POM)), benthic autochthonous sources (lymnaeid snails (LS) and *Gammarus*

lacustris (GA)), unionid mussels from the tributary inflow (UM) and an allochthonous source (leaf litter (LL)).....80

Figure 3.5. Stable isotope biplots for Lake Whitefish (black), Northern Pike (yellow), Walleye (blue) and White Sucker (green) caught in spring 2012 (triangle), fall 2012 (circle) and spring 2013 (square) at each of the twelve sampling sites located throughout Lake Diefenbaker. The number in the top right corner of each plot corresponds to the site number.....81

Figure 3.6. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of particulate organic matter (POM) and zooplankton with increasing distance downstream of the Highway 4 Bridge, located near the upstream end of Lake Diefenbaker. Each point in each panel represents a single sample. A LOESS smoothed line is fitted to each variable and shown on each graph, while the shaded area represents the 95 % confidence interval. POM samples were collected in May, June, July, August, September, October, and November at sites throughout the reservoir, while zooplankton samples were collected at sites 1 – 12 in spring, summer and fall.....86

Figure 3.7. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of both benthic macroinvertebrates, *Gammarus lacustris* and lymnaeid snails, with increasing distance downstream of the Highway 4 Bridge, located near the upstream end of Lake Diefenbaker. Each point in each panel represents a single sample. A LOESS smoothed line is fitted to each variable and shown on each graph, while the shaded area represents the 95 % confidence interval. Aquatic invertebrate samples were collected in summer and fall of each open water season at sites 1 – 12. No aquatic macroinvertebrates were collected during attempted sampling in spring.....87

Figure 3.8. The relationship between total length (mm) and $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and relative weight (W_r) for Lake Whitefish, Northern Pike, Walleye and White Sucker at all 12 sites over both sampling years (model I linear regression). Note the difference in scales on the X axis for each species...88

Figure 3.9. Boxplots of the proportional contribution of each potential carbon source to the diets of Lake Whitefish (*Coregonus clupeaformis*) at sites 1 – 12 in Lake Diefenbaker. The potential dietary sources include pelagic primary production represented by zooplankton, benthic primary production represented by two aquatic macroinvertebrates, lymnaeid snails and *G. lacustris*, and allochthonous primary production, represented by leaf litter. The inner, central and outer portions of the boxplots represent the 50 %, 75 % and 95 % credible intervals of the data. For site locations within Lake Diefenbaker, please refer to Fig. 1.1.....89

Figure 3.10. Boxplots of the proportional contribution of each potential carbon source to the diets of Northern Pike (*Esox lucius*) at sites 1 – 12 in Lake Diefenbaker. The potential dietary sources include pelagic primary production represented by zooplankton, benthic primary production represented by two aquatic macroinvertebrates, lymnaeid snails and *G. lacustris*, and allochthonous primary production, represented by leaf litter. The inner, central and outer portions of the boxplots represent the 50 %, 75 % and 95 % credible intervals of the data. For site locations within Lake Diefenbaker, please refer to Fig. 1.1.....90

Figure 3.11. Boxplots of the proportional contribution of each potential carbon source to the diets of Walleye (*Sander vitreus*) at sites 1 – 12 in Lake Diefenbaker. The potential dietary

sources include pelagic primary production represented by zooplankton, benthic primary production represented by two aquatic macroinvertebrates, lymnaeid snails and *G. lacustris*, and allochthonous primary production, represented by leaf litter. The inner, central and outer portions of the boxplots represent the 50 %, 75 % and 95 % credible intervals of the data. For site locations within Lake Diefenbaker, please refer to Fig. 1.1.....93

Figure 3.12. Boxplots of the proportional contribution of each potential carbon source to the diets of White Sucker (*Catostomus commersoni*) at sites 1 – 12 in Lake Diefenbaker. The potential dietary sources include pelagic primary production represented by zooplankton, benthic primary production represented by two aquatic macroinvertebrates, lymnaeid snails and *G. lacustris*, and allochthonous primary production, represented by leaf litter. The inner, central and outer portions of the boxplots represent the 50 %, 75 % and 95 % credible intervals of the data. For site locations within Lake Diefenbaker, please refer to Fig. 1.1.....94

Figure 3.13. Mean $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, total length, and relative weight (W_r) for all Lake Whitefish, Northern Pike, Walleye and White Sucker captured at sites 1 – 12 throughout 2012 and 2013. Error bars represent 95 % confidence intervals for the means. Means with a common letter are not significantly different from one another. Both main channel sites (closed circles) and sites located within embayments (open circles) are included. For site locations within Lake Diefenbaker, please refer to Fig. 1.1.....102

Figure 3.14. Seasonal mean $\delta^{13}\text{C}$ (‰), $\delta^{15}\text{N}$ (‰), total length (mm), and relative weight (W_r) for all Lake Whitefish, Northern Pike, Walleye and White Sucker captured at sites 1 – 12 during spring 2012 (S12), fall 2012 (F12), and spring 2013 (S13). Error bars represent 95 % confidence intervals for the means. Means with a common letter are not significantly different from one another.....103

List of Abbreviations

^{13}C – Carbon-13

^{12}C – Carbon-12

^{15}N – Nitrogen-15

^{14}N – Nitrogen-14

^2H – Hydrogen-2

^{18}O – Oxygen-18

^{34}S – Sulfur-34

ANOVA – Analysis of variance

AW Specialist – Aquaculture waste specialist (Lake Whitefish with > 50 % contribution of aquaculture waste to their diet).

AW Generalists – Aquaculture waste generalist (Lake Whitefish with between 15 % to 50 % contribution of aquaculture waste to their diet).

DRT – Domestic Rainbow Trout

F12 – Fall 2012

F13 – Fall 2013

FF – Fish farm

GA – *Gammarus lacustris*

GFF – Glass fiber filter

GSI – Gonadosomatic Index

HSD – Honest significant difference

IGFA – International Game Fish Association

LKWH – Lake Whitefish

LL – Leaf litter

LOESS – Local regression

LS – Lymnaeid snails

MT – Metric Ton (1000 kg)

No AW – No aquaculture waste (< 15 % of diet made up of aquaculture waste)

NRPK – Northern Pike

PFF – Pelleted fish feed

POC – Particulate organic carbon

POM – Particulate organic matter

PN – Particulate organic nitrogen

TEF – Trophic enrichment factor

S12 – Spring 2012

S13 – Spring 2013

SD – Standard deviation

SIAR – Stable Isotope Analysis in R

SIARsolo – Stable Isotope Analysis in R for individual organisms

TL – Total length

UM – Unionid mussels

W – Weight

WALL – Walleye

WHSC – White Sucker

W_r – Relative weight

W_s – Standard weight

ZP – Zooplankton

CHAPTER 1. General Introduction

1.1 Review of Carbon Sourcing Literature

1.1.1 Introduction

Saskatchewan is home to 58 species of native fish, as well as eleven additional species which have either invaded or have been intentionally introduced (Atton and Merkowsky 1983; Liaw 1991). These fish are found in over 50,000 fish bearing lakes, rivers, streams and reservoirs throughout the province (Ashcroft et al. 2006), where they play an important role in Saskatchewan's economy via recreational and commercial fisheries (Duffy 2006; GOS 2011). This is especially true within the northern regions of the province where the majority of Saskatchewan's fishing outfitters are located and where commercial fishing is one of the major forms of employment for communities such as Kinoosao, located on the north eastern shores of Reindeer Lake. Recreational fishing also plays an important role throughout the rest of Saskatchewan. In 2010, sport fishing was responsible for generating \$496 million in direct and indirect revenue (GOS 2011). Much of the angling pressure in Saskatchewan is directed at lakes and reservoirs in the southern and central portion of the province due to their proximity to urban centres. Tobin Lake, Last Mountain Lake, Lake Diefenbaker and the Qu'Appelle Lakes are consistently the top angling destinations in Saskatchewan (Duffy 2006) due to their proximity to major cities combined with their excellent fisheries.

Fisheries management relies on productivity estimates for particular waterbodies in order to ensure recreational and commercial harvest levels are sustainable. Productivity estimates for aquatic systems are often estimated based on relatively few physical and chemical variables (e.g. nutrient concentrations, bathymetry, and surface area). Knowing where the energy supporting a lake food web comes from, along with the relative importance of each potential carbon pathway

to the upper trophic levels in that food web can allow for more precise estimates of the productivity of aquatic ecosystems. In turn, this allows for more accurate estimates of the productivity of fish populations which can be used to manage harvest rates more effectively to ensure the sustainability of the fishery.

1.1.2 Aquaculture Subsidies in Wild Fish Populations

In the world of agricultural practises, aquaculture is still in its infancy compared to other forms of food production. The recent increase in the demand for high protein diets in developing nations of the world has sparked increased interest in the consumption of fish. However, with most of the commercially viable fisheries across the world already harvested at or above their productive capacity and with most wild fisheries in decline (Pauly et al. 2002; Worm et al. 2009; Pitcher and Cheung 2013; Lam 2016) there is no room to increase commercial production on wild caught fisheries. With the supply of wild caught fish in decline, the world is turning to aquaculture to increase production of fish for consumption (Brander 2007; FAO 2014).

Aquaculture production has increased steadily since the 1960s and in 2012 it accounted for 66.6 million tonnes or 42 % of the world's production of seafood (FAO 2014). Currently, aquaculture is the world's fastest growing agricultural industry. Production from aquaculture is expected to meet 60 % of the world's commercial fish supply by 2020 (FAO 2014). Much of the aquaculture industry relies on cage culture facilities where fish are kept within floating cages. These cages allow for the exchange of water and aquaculture waste products with the surrounding environment. The ecological impacts of these facilities on the surrounding environment are a major concern, especially with the ongoing expansion of aquaculture (Black 2001).

Extensive research has been carried out on the potential ecological impacts of aquaculture (Black 2001). Much of the early research concentrated on marine systems while more recent studies have also expanded into freshwater ecosystems (Black 2001; DFO 2006). Most research has focused on abiotic factors such as nutrient deposition and oxygen depletion in waters immediately surrounding cage culture facilities (Black 2001; Guo and Li 2003; Clerk et al. 2004; Yan 2005). The results indicate the impacts of aquaculture on the abiotic environment are localized, only impacting the waters underneath and immediately adjacent to the cage culture facilities (Black 2001; Mente et al. 2006; Silva 2012). Less research has been conducted on the impacts of aquaculture facilities on wild fish populations. A large portion of the research concerning wild fish has focused on the negative impacts associated with parasite and pathogen transfer between farmed and wild fish (Beveridge et al. 1994; Sanchez-Jerez et al. 2008; Diana 2009; Arechavala-Lopez et al. 2013) and the increase in wild fish densities associated with aquaculture facilities (Carrs 1990; Dempster et al. 2002; Dempster et al. 2004; Dempster et al. 2009; Dempster et al. 2010; Boyra et al. 2004). More recently studies have begun to examine the impacts of aquaculture on the diets of wild fish populations in both marine and freshwater habitats and the effects these changes in diet may have on the wild fish populations (Gabrielsen 1999; Skog et al. 2003; Vita et al. 2004; Fernandez-Jover et al. 2007; Fernandez-Jover et al. 2008; Kullman et al. 2009; Otterå et al. 2009; Johnston et al. 2010; Strictar-Pereira et al. 2010; Dempster et al. 2011; Fernandez-Jover et al. 2011; Bagdonas et al. 2012).

1.1.2.1 Marine Aquaculture

Marine aquaculture accounts for 40 % of the world's total aquaculture production, a large proportion of which is produced in cage culture facilities (Bostock et al. 2010). Wild fish are often found in much higher abundance immediately around the cage culture facilities than in

surrounding waters (Carss 1990; Boyra et al. 2004; Dempster et al. 2004; 2009; Sudirman et al. 2009; Bagdonas et al. 2012). The higher abundance around cage culture facilities is thought to be linked to both the additional structural habitat provided by the facilities themselves (Powers et al. 2007), as well as the waste feed from the fish farm entering the food chain (Cromeey et al. 2002; Gabrielsen 1999; Sudirman et al. 2009; Fernandez-Jover et al. 2011; Bagdonas et al. 2012). Otterå et al. (2009) found that up to five percent of the total pelleted feed went uneaten by the caged salmon and entered the local food web. The wasted feed is only available in close proximity to the cages because uneaten pellets sink, preventing them from drifting long distances (Black 2001; Cromeey et al. 2002). Small fish around the cage culture facilities are often attracted to the area to feed on the wasted feed (Felsing et al. 2005; Sudirman et al. 2009; Dempster et al. 2010; Bagdonas et al. 2012) while larger predatory species are attracted by the greater abundance of smaller prey species (Bagdonas et al. 2012; Serra-Llinares et al. 2013), or by the escaped farmed species (Ugelm et al. 2014). In some cases, juvenile fish were attracted to the cage culture facilities to feed on zooplankton which were found in higher abundance around the cages than in control areas (Fernandez-Jover et al. 2009).

A common observation in many studies of marine cage culture is the increased abundance of wild fish in the areas adjacent to the aquaculture facilities in both temperate and tropical regions of the world. Often, the impact of aquaculture waste on the benthos below and adjacent to the cages is diminished as a result of wild fish consuming aquaculture waste (Sanz-Lázaro et al. 2011; Ugelm et al. 2014). Some of these wild fish species were found to stay within close proximity to the cages throughout their life cycles (Dempster et al. 2010), while other species traveled away from the cages and between sites more frequently (Ugelm et al. 2009;

Sudirman et al. 2009; Otterå and Skilbrei 2014). When fish move away from cage culture sites, they disperse nutrients (e.g., NH₃) taken up at the aquaculture sites over a greater area.

Species presence around the cages often varied throughout the year and was suspected to be linked to water temperature as well as the spawning periods for some fish species (Valle et al. 2007). Although the increased densities of fish around marine cage culture facilities may increase the spread of parasites and pathogens between fish (Beveridge et al. 1994; Sanchez-Jerez et al. 2008; Diana 2009; Arechavala-Lopez et al. 2013), the wild fish in close proximity to the aquaculture sites were often in better condition (i.e., increased condition factors) than those from control sites (Fernandez-Jover et al. 2011; Dempster et al. 2011). Increases in fish condition were thought to be the result of the increased food supply via trophic subsidies in areas surrounding the cages from aquaculture waste (Fernandez-Jover et al. 2011; Dempster et al. 2011). Increases in body condition, especially increases in lipid concentrations, may allow for higher production of gametes due to increased energy stores (Marshall et al. 1999; Izquierdo et al. 2001). However, this hypothesis has not yet been tested.

1.1.2.2 Freshwater Aquaculture

Although freshwater makes up only 3 % of the earth's water, 60 % of the world's aquaculture production occurs in freshwater systems (Bostock et al. 2010). Carp and other cyprinid species account for over 65 % of the freshwater aquaculture production. The majority of the production of cyprinid species takes place in small pond culture facilities where few or no other fish species are present, resulting in little or no impact on wild fish populations (Bostock et al. 2010). However, many fish species are reared in cage culture facilities throughout the world's lakes, rivers and reservoirs. Cage culture is an important part of freshwater aquaculture production in the developed world and is becoming more important in the developing world as

an affordable source of high protein food (Bostock et al. 2010). In 2004 cage culture facilities accounted for almost half of the freshwater aquaculture production in Canada (Bostock et al. 2010). Freshwater cage culture facilities resemble their marine counterparts in structure, but the impacts on local ecosystems can often be magnified due to the smaller size of the receiving waters where the facilities are located (Kullman et al. 2009; Bostock et al. 2010).

Similar to marine aquaculture research, most of the studies on the impacts of freshwater aquaculture facilities have focused on eutrophication and oxygen depletion in the surrounding waters as a result of nutrient loading from aquaculture waste. In freshwater systems eutrophication is often a larger concern than in marine environments simply due to the smaller volume of the receiving waters. Many of the impacts of cage culture facilities on freshwater fish species are the same as those seen in marine environments. Numerous studies have found increased abundance of wild fishes around the cage culture facilities compared to reference sites (Johnston et al. 2010; Demétrio et al. 2012; Gondwe et al. 2012; Brandão et al. 2013; Ramos et al. 2013; Brandão et al. 2014) or prior to the cage culture operations (Johnston et al. 2010; Demétrio et al. 2012; Gondwe et al. 2012; Brandão et al. 2013; Ramos et al. 2013; Brandão et al. 2014).

Wild fish around cage culture facilities often show signs of diet subsidies from the assimilation of aquaculture waste. Gut content analysis is commonly used to confirm if fish have recently been feeding directly on particulate aquaculture waste (Phillips et al. 1985; Gabrielsen 1999; Strictar-Pereira et al. 2010; Demétrio et al. 2012; Brandão et al. 2013; Ramos et al. 2013; Brandão et al. 2014). Stable isotope analysis is also used to determine if fish, as well as invertebrates, are assimilating aquaculture waste over longer periods of time either directly by feeding on the particulate waste products (Grey et al. 2004; Kullman et al. 2009; Gondwe et al.

2012), or indirectly when dissolved waste products enter the food web via nutrient uptake by primary producers (Kullman et al. 2009; Benedito et al. 2013). Both gut content analysis and stable isotope analysis have proved useful in determining when the diet of wild fish is subsidized directly or indirectly with aquaculture waste. Bašić et al. (2015) found that pelleted fish feed used as bait by anglers to attract and catch European barbel (*Barbus barbus*) contributed up to 50 % of the assimilated diet of the population in three of four rivers studied using stable isotope analysis. Some of these fish were specialists with diets consisting of up to 79 % pelleted feed. In areas surrounding cage culture facilities, where higher volumes of pelleted feed are introduced as waste, the diets of wild fish in the area can consist of even higher proportions of the pelleted fish feed due to some species selective preference for this highly nutritious food source (Bašić et al. 2015).

Fish often had increased condition factors when subsidizing their diets with aquaculture waste (Gabrielsen 1999; Ramos et al. 2008; Brandão et al. 2013; Ramos et al. 2013). Brandão et al. (2014) found changes in fecundity, via an increased number of smaller eggs, in those fish utilizing aquaculture subsidies. In certain instances fish occurred in greater abundance around cages because they fed on invertebrates or other fish and not directly on the particulate aquaculture waste; such fish often had a decrease in condition (Strictar-Pereira et al. 2010), or no change at all (Ramos et al. 2013). Fish that feed on aquaculture waste have been observed to travel away from the cage culture sites (Gabrielsen 1999; Gondwe et al. 2012; Ramos et al. 2013; Brandão et al. 2014). This causes the dispersion of the waste products over a larger area, resulting in a decreased impact on the sediments and benthic organisms below the cages (Gondwe et al. 2012; Ramos et al. 2013). This, in turn, leads to lower rates of oxygen depletion in the waters immediately below the cages, providing a net positive effect for both the fish and

the environment around the cages. With the rapidly expanding aquaculture industry it is vital to have an understanding of the potential impacts of waste feed on the ecosystems around cage culture facilities.

1.1.3 Allochthonous and Autochthonous Carbon Sources

Two major carbon sources exist for aquatic consumers including fish: autochthonous sources, those generated through benthic and pelagic primary production within a waterbody, and allochthonous sources, those generated through primary production outside of the waterbody. Lake Diefenbaker contains a third possible source of nutrients to consumers via allochthonous inputs of waste products from the aquaculture facility located within Cactus Bay. The relative importance of allochthonous and autochthonous organic matter sources to consumers depends on many factors, including the size, shape and trophic status of the waterbody (Dolson et al. 2009; Solomon et al. 2011), as well as the availability of each organic matter source throughout the year (DeLong and Thorp 2006; Bašić et al. 2015). On top of these physical parameters, variations in the feeding habits between fish species, as well as within a single species, play a role in the organic matter sources on which fish rely (Weidel et al. 2008). Although many factors are at play in the importance of each potential carbon source, some of the variation in the importance of allochthonous and autochthonous carbon can be attributed to the type of water body being studied. Knowing the relative importance of each potential carbon source to the diets of fish throughout Lake Diefenbaker may allow for a better estimation of the potential yields of fish within the reservoir and an understanding of how this may change with year to year variations in the water residence time. This in turn is important for the potential management implications of the valuable sport fishery within Lake Diefenbaker, now and in the future.

1.1.3.1 Lakes

Benthic and pelagic sources of autochthonous primary production are of high importance to consumers within lentic ecosystems (Hecky and Hesslein 1995). However, the relative importance of allochthonous carbon to consumers within lakes has been debated and is the topic of recent research. Del Giorgio and Peters (1993) found algal production and planktonic respiration to be closely correlated to chlorophyll concentrations in lakes across a wide range of trophic gradients. However, in oligotrophic lakes respiration often exceeded photosynthetic production (Del Giorgio and Peters 1993), meaning an additional source of carbon from outside the waterbody was being utilized. These allochthonous subsidies could be occurring in three different forms including dissolved organic carbon, non-living particulate carbon (i.e., leaf litter), or terrestrial organisms such as insects (Cole et al. 2006). Allochthonous carbon sources were important for consumers in oligotrophic and dystrophic lakes (Jones et al. 1998; Carpenter et al. 2005), but as the gross primary production of lakes increased, the importance of terrestrially derived carbon decreased (Cole et al. 2000).

In boreal lakes, littoral fish species can be dependent on terrestrially derived carbon for part of their energy, linking the lake ecosystems with the adjacent forest (France 1997). Benthic macroinvertebrates often rely on allochthonous inputs of leaf litter from the surrounding forest (Solomon et al. 2011; Glaz et al. 2012), and fish species such as brook trout can derive up to 90 % of their carbon from terrestrial sources by feeding mainly on these macroinvertebrates (Glaz et al. 2012). The importance of allochthonous carbon is highest in dystrophic lakes where light penetration is low due to high levels of terrestrial dissolved organic carbon (Carpenter et al. 2005; Solomon et al. 2011; Karlsson et al. 2015). Interestingly, removal of the forest buffer along boreal lakes by clear cutting resulted in an increase in the importance of autochthonous

carbon to the diets of brook trout as they fed more heavily on zooplankton following the clear cutting and subsequent decrease in terrestrial subsidies (Glaz et al. 2014).

The contribution of terrestrial carbon to consumers increases with the concentration of terrestrially derived dissolved organic carbon (Karlsson et al. 2015). However, even at exceedingly high concentrations of allochthonous carbon, consumers still rely on autochthonous primary production for some of their diet (Karlsson et al. 2012) indicating that allochthonous sources alone may have an upper limit to their contribution to the biomass of upper trophic level consumers. This may be due to the low quality of most allochthonous carbon sources when compared to autochthonous sources such as phytoplankton (Brett et al. 2012). Certain consumers, such as zooplankton preferentially rely on autochthonous carbon sources (Cole et al. 2002; Pulido-Villena et al. 2005) with the majority of their diets reflective of these autochthonous sources (Mohamed and Taylor 2009). Other consumers such as many Ephemeroptera species preferentially rely on terrestrially derived carbon regardless of abundance (Weidel et al. 2008; Glaz et al. 2012). This specialization on different carbon sources seen in primary consumers is reflected in higher trophic level consumers, such as fish. As a result, zooplanktivorous fish have a larger amount of their carbon derived from autochthonous sources (Cole et al. 2002; Christensen and Moore 2009) while fish feeding mainly on benthic macroinvertebrates often have an increased contribution from allochthonous carbon compared to pelagic species (Christensen and Moore 2009; Glaz et al. 2012; Glaz et al. 2015). Allochthonous carbon can be an important contributor to food webs present in lentic systems, especially in oligotrophic and dystrophic lakes (Jones et al. 1998; Carpenter et al. 2005; Pulido-Villena et al. 2005). However, autochthonous carbon sources are still important to consumers at all trophic

levels even when autochthonous sources are in much lower abundance than allochthonous sources (Brett et al. 2012; Karlsson et al. 2012).

1.1.3.2 Rivers

The primary carbon sources supporting lotic food webs have long been a topic of both study and debate (Humphries et al. 2014). The River Continuum Concept (Vannote et al. 1980) was one of the earliest models that described the processing of organic matter throughout a river system. It emphasized the importance of terrestrial inputs of organic matter in headwater streams that are transported longitudinally to the lower reaches of large rivers as the primary source of organic matter in river ecosystems. The Flood Pulse Concept (Junk et al. 1989) stressed the importance of the floodplain of the watershed as the primary source of organic matter for a river. The organic matter from the river's floodplain is delivered laterally in pulses during periods of high water when connectivity between a river and its floodplain is at its greatest. Thorp and Delong (1994) introduced The Riverine Productivity Model which proposed that some large river systems derive most of their organic matter from autochthonous sources such as phytoplankton, benthic algae and aquatic macrophytes within the river. This model did not contradict either the Flood Pulse Concept or the River Continuum Concept, but rather suggested they may both be relevant depending on the type of river and the river section.

Subsequent studies have linked stream order to the importance of allochthonous and autochthonous carbon sources to the diets of consumers (Finlay 2001). As stream order increases, the stream channel widens, decreasing the amount of riparian stream cover shading the streambed, which results in higher levels of instream primary production (Stockner and Shortreed 1976; Webster and Meyer 1997). Removal of the forest canopy along streams through logging or fire decreases allochthonous inputs to the system and increases light penetration and

autochthonous production, resulting in higher levels of autochthonous organic matter use by macroinvertebrates and fish (Hansmann and Phinney 1973; Spencer et al. 2003). Consumers in higher order streams often show a greater contribution from autochthonous carbon than those in headwater streams (Finlay 2001). The importance of autochthonous carbon to consumers has been linked to watershed size, with the transition from predominantly allochthonous to autochthonous carbon occurring when watersheds reach $\sim 10 \text{ km}^2$ (Finlay 2001) and increasing in year round importance as catchment size increases further (McCutchan 1999). In higher order rivers, allochthonous carbon is still important during periods of high flow (Kendall et al. 2001) and for certain species which specialize on allochthonous carbon (Herwig et al. 2007; Hladyz et al. 2012; Jardine et al. 2012). Overall, lotic systems often have food webs driven by allochthonous organic matter in the headwater reaches, but with autochthonous primary production becoming more important as stream order and catchment size increase (Finlay 2001; Kendall et al. 2001; Humphries et al. 2014). There are obvious exceptions to this and all systems must be considered on a river by river or even a reach by reach basis and certain consumers will always differ due to species specific specializations in feeding habits.

1.1.3.3 Reservoirs

There are currently 16 to 17 million reservoirs greater than 0.01 hectares worldwide (Lehner et al. 2011) which have a storage capacity of approximately 10 % of the world's freshwater lakes. The number of reservoirs across the world is expected to continue to grow as the demand for fresh water increases due to humanity's increased reliance on water from impoundments for commercial, agricultural, municipal and recreational use (Uhlmann et al. 2011). The carbon sources supporting reservoir food webs have been studied in less detail compared to the food webs of lakes and rivers. However, there has been a recent surge in the

number of studies being conducted on reservoir carbon sources around the world. Similar to lakes and rivers, reservoirs display variation in the primary source of carbon supporting food webs. Much of the variation seen in the allochthonous and autochthonous support of reservoir food webs is a result of highly variable water residence times (Perga et al. 2005; Chen and Jia 2009; Hou et al. 2013; Lee et al. 2013). Increased turbidity during periods of high inflow into a reservoir corresponds to decreases in chlorophyll *a* concentrations and autochthonous primary production (Yip et al. 2015), while the same high flows increase the availability of allochthonous carbon (Sanchez-Vidal et al. 2013). Reservoir age (De Merona et al. 2003; Perga et al. 2005; Lucas et al. 2015) and land use practises prior to impoundment (Perga et al. 2005) also play a role in which carbon sources support reservoir food webs.

Reservoirs are generally thought to act as a trap for particulates because the particulates settle out of suspension with decreases in water velocity (Kaymak et al. 2015). This in turn causes an increase in water clarity in the downstream lacustrine zone of reservoirs allowing for greater light penetration and increased phytoplankton abundance (Kimmel and Groeger 1984; Chen et al. 2005; Yip et al. 2015). This increase in autochthonous primary production in the lacustrine zone of reservoirs produces particulate organic matter (POM) with strong algal signatures when compared to POM in tributaries (Kendall et al. 2001). For this reason, reservoir food webs are thought to be supported largely by autochthonous carbon in their lower reaches, especially during low flow periods (Chen et al. 2005; Hoeinghaus et al. 2007; Kaymak et al. 2015). This is often shown to be the case in stable isotope studies showing greater variation in particulate organic matter and consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values within reservoirs than in the tributary reaches upstream which rely mainly on allochthonous carbon (Chen et al. 2005; Mercado-Silva et al. 2008; Kaymak et al. 2015). River reaches immediately downstream of

reservoirs often have food webs which rely almost entirely on autochthonous carbon of planktonic origin produced in the upstream reservoir (Kendall et al. 2001). As a result, reservoirs which lie in close proximity downstream of another reservoir have lower inputs of allochthonous carbon (Kendall et al. 2001).

Allochthonous support of reservoir food webs is common in newly formed reservoirs (Perga et al. 2005; Chen and Jia 2009; Hou et al. 2013; Lee et al. 2013; Lucas et al. 2015), especially if the impounded area was forested prior to flooding (Perga et al. 2005). Allochthonous carbon loads from flooded landscapes decline as reservoirs age and autochthonous primary production becomes more important (De Merona et al. 2003; Lucas et al. 2015). Allochthonous carbon can be important throughout the riverine, transitional and lacustrine zones of a reservoir during periods of high flow or flooding (Perga et al. 2005; Chen et al. 2009; Hou et al. 2013; Lee et al. 2013; Min-Seob et al. 2014). High flow events prevent terrestrial carbon from sedimenting out in the upper reaches of the reservoir and allow for its incorporation into the food web further downstream compared to periods of low flow (Perga et al. 2005; Chen et al. 2009; Hou et al. 2013; Lee et al. 2013; Min-Seob et al. 2014). Reservoirs with regular periods of high inflow act as optimal study sites to test the importance of allochthonous carbon to consumers throughout the reservoir.

1.1.4 Stable Isotope Analysis

Isotopes are different forms of the same element which differ in the number of neutrons in their nuclei, resulting in differences in their atomic weights. Stable isotopes are those isotopes that do not undergo radioactive decay. Different isotopes of the same element are functionally equivalent, but the differences in atomic weight cause them to behave differently in many chemical reactions (Peterson and Fry 1987; Fry 2006). This results in isotopic discrimination

during chemical reactions resulting in different ratios of the heavy to light stable isotopes before and after a reaction (Peterson and Fry 1987). The degree of isotopic discrimination differs for each element and for different chemical reactions. Metabolic reactions involving the stable isotopes of hydrogen, carbon, nitrogen, oxygen and sulfur have been well studied (Fry 2006). These are the most commonly used isotopes for stable isotope analysis in ecological studies because they are present throughout the biosphere and cycle predictably with organic matter (Fry 2006).

The isotopic value of a sample is given in delta (δ) notation, measured as the distance from an international standard in permil (‰), also known as parts per thousand, according to the following formula:

$$\text{Equation 1.1: } \delta X = [(R_{\text{sample}}/R_{\text{standard}})-1] * 10^3$$

where X is the heavy isotope of either ^{13}C or ^{15}N and R is the ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ in the sample (R_{Sample}) and in the international standard (R_{Standard}).

The international standards against which the isotopic values of samples are measured are PeeDee Belemnite limestone for $\delta^{13}\text{C}$ (Craig 1957), atmospheric nitrogen for $\delta^{15}\text{N}$ (Mariotti 1983), primordial sulfur from the Canyon Diablo meteorite for $\delta^{34}\text{S}$ (Rees et al. 1978) and Vienna Standard Mean Ocean Water for both $\delta^2\text{H}$ and $\delta^{18}\text{O}$ (Coplen 1994). These international standards are by definition set at a value of 0 ‰ for each respective element. The δX value for a sample can be either positive or negative relative to the standards, indicating more or less of the heavy isotope of the measured element in the sample, respectively. The current study uses both carbon and nitrogen stable isotopes to track different organic matter sources (i.e., allochthonous and autochthonous carbon and aquaculture waste) through the food web of Lake Diefenbaker.

1.1.4.1 Carbon

The isotopes of carbon used in stable isotope analysis are ^{13}C and ^{12}C . The $\delta^{13}\text{C}$ value of atmospheric CO_2 is currently at -8‰ (Fry 2006) when compared to the international standard. When plants take in CO_2 during photosynthesis, isotopic discrimination occurs in a predictable manner, resulting in $\delta^{13}\text{C}$ values around -28‰ for most terrestrial C_3 plants (Peterson and Fry 1987; Fry 2006). Less discrimination occurs between carbon isotopes during photosynthesis in C_4 plants resulting in $\delta^{13}\text{C}$ values around -13‰ (Peterson and Fry 1987). In marine environments, phytoplankton are the primary producers and their $\delta^{13}\text{C}$ values can range from -19‰ to -24‰ (Fry 2006). Due to the planktonic origin of particulate organic matter (POM) in the oceans, its $\delta^{13}\text{C}$ values generally mirror that of marine phytoplankton (Fry 2006). The $\delta^{13}\text{C}$ value of freshwater primary producers varies more widely due to the use of carbon from multiple sources including atmospheric CO_2 , the respiratory products of organic matter, and carbonate rock (Fry 2006). However, the $\delta^{13}\text{C}$ value of freshwater POM is commonly within the range of -28 to -35‰ (Fry 2006; Marty and Planas 2008).

As carbon moves through food webs, the $\delta^{13}\text{C}$ changes very little (between 0 to 1 ‰) with each trophic level (Rounick and Winterbourn 1986; Peterson and Fry 1987; France and Peters 1997; Post 2002) due to its mean trophic enrichment factor of 0.4 ‰ per trophic level (Post 2002). Because of the predictable isotopic discrimination of carbon stable isotopes with increasing trophic levels, the $\delta^{13}\text{C}$ of freshwater primary producers can be approximated by measuring the $\delta^{13}\text{C}$ values of primary consumers feeding directly on them (DeNiro and Epstein 1978; Peterson and Fry 1987; Vander Zanden and Rasmussen 1999; Post 2002; Marty and Planas 2008). Therefore, the $\delta^{13}\text{C}$ values of primary consumers can be used to track different carbon sources to the diets of higher level consumers (Peterson and Fry 1987; Post 2002; Fry 2006).

This makes stable isotopes of carbon valuable tracers for food web and nutrient sourcing studies as well as for differentiating between diet sources and tracking animal migrations (Hobson 1999; Cunjak et al. 2005). The $\delta^{13}\text{C}$ value of freshwater aquatic primary producers can even be used to differentiate between habitat types as periphyton and phytoplankton growing in the same river can have different $\delta^{13}\text{C}$ values due to the differences in water velocity, with faster flowing stretches characterized by depleted ^{13}C values compared to nearby slower flowing stretches (Finlay et al. 1990).

1.1.4.2 Nitrogen

The majority of the nitrogen in the biosphere is atmospheric N_2 which is used as the international standard for nitrogen stable isotope analysis due to the well mixed nature of the atmosphere and its almost constant composition of ^{15}N and ^{14}N (Mariotti 1983). Most of the pools of nitrogen within the biosphere contain $\delta^{15}\text{N}$ values between 10 and -10 ‰. The relatively low range of $\delta^{15}\text{N}$ values seen in nature occurs because nitrogen is often a limiting nutrient, causing all available nitrogen to be used with little or no isotopic discrimination (Fry 2006). However, in freshwater lakes nitrogen is often not limiting, resulting in the possibility for larger discrimination factors (Fry 2006). As a result, the $\delta^{15}\text{N}$ values of primary producers in freshwater ecosystems can often be useful for differentiating between allochthonous and autochthonous sources (Fry 2006).

Nitrogen behaves in a predictable manner when transferred from one trophic level to the next with consumer $\delta^{15}\text{N}$ values increasing by 3 to 4 ‰ (mean = 3.4 ‰) relative to their food source (DeNiro and Epstein 1981; Peterson and Fry 1987; Post 2002). This predictable discrimination of nitrogen isotopes occurs because of the assimilation of ^{15}N into tissues and through the preferential excretion of the ^{14}N as metabolic waste in urine (Ponsard and Averbuch

1999). This results in $\delta^{15}\text{N}$ values being a useful indicator of trophic position when the $\delta^{15}\text{N}$ values of the baseline primary producers are known (Peterson and Fry 1987; Post 2002). The predictable nature of nitrogen stable isotopes makes them useful for tracking nutrient sources used by consumers as well as measuring consumer trophic level. Anthropogenic alterations to watersheds are often evident throughout aquatic food webs in the $\delta^{15}\text{N}$ values of organisms and particulate organic matter making nitrogen isotopes useful for identifying anthropogenic influences on aquatic systems (Finlay and Kendall 2007).

1.2. Research Introduction

1.2.1 Lake Diefenbaker

Located in southern Saskatchewan, Lake Diefenbaker was formed in 1969 from the creation of two large earth filled dams, the main Gardiner Dam and the Qu'Appelle Dam. Lake Diefenbaker is the largest reservoir on the South Saskatchewan River at 394 km² and 182 km long (Sadeghian et al. 2015; SWA 2012). Throughout the majority of its length, Lake Diefenbaker acts as a dimictic reservoir, but in the upper most riverine sections it does not thermally stratify most years (Hudson and Vandergucht 2015). The ice free period lasts from early to mid-May until December or January depending on the year (Hudson and Vandergucht 2015). Peak runoff generally occurs in mid to late June with the onset of mountain runoff (Hudson and Vandergucht 2015). Mean annual flow into the reservoir generally falls between 200 and 300 m³s⁻¹ with mean peak flows of 1252 m³s⁻¹ from 1967 to 2010. The reservoir is classed as mesotrophic based on its total nitrogen, total phosphorus and chlorophyll *a* levels (Abirhire et al., 2015). The reservoir was constructed for water storage, irrigation, hydroelectric power generation, recreation and flood control (Royer 1972). In recent times the reservoir has become renowned for its sport fishery (Duffy 2006).

In the original fisheries assessment on the reservoir, twenty-five species of fish were found to exist within Lake Diefenbaker (Royer 1972). Today at least 18 species of large bodied fish exist within the reservoir, with Goldeye, Northern Pike, Yellow Perch, Rainbow Trout, Sauger, Walleye and Lake Whitefish being the most sought after fish by sport fishermen (Wallace et al. 2010). From 1991 until 2013 a spawn camp was operated near Gardiner Dam at Coteau Bay. The camp captured spawning Walleye and collected their eggs and milt for stocking Walleye throughout the province (Wallace and Jensen 2004; Wallace et al. 2010). Starting in 2004, $\geq 5\%$ of the total Walleye fry collected from Coteau Bay were released back into Lake Diefenbaker in an effort to reduce any impacts of the spawn camp on Walleye populations. Fish stocking efforts first took place in 1969 with the introduction of Lake Whitefish and Walleye to supplement the natural populations of these species. Since then, over 100 million fry and fingerlings of seven species of fish have been stocked in attempts to establish new sport fishing opportunities or supplement existing fisheries within Lake Diefenbaker. In addition to these intentional stocking efforts, hundreds of thousands of domestic Rainbow Trout have escaped into Lake Diefenbaker from the aquaculture facility located at Cactus Bay. A commercial fishery for Lake Whitefish was in operation on Lake Diefenbaker from 1978 until 1986 when it was closed due to a drop in both the size and numbers of fish captured. No commercial fishery has operated on the reservoir since the closure of the Lake Whitefish fishery.

A recent study published by Donald et al. (2015) was conducted on the upstream reaches of Lake Diefenbaker near Highway 4, linking mercury bioaccumulation in fish to their $\delta^{15}\text{N}$ values. Donald et al. (2015) also tested for relationships between mercury bioaccumulation and the levels of benthic and pelagic resource use in some species. Doing so, they measured the values of each potential resource and found pelagic primary consumers to be depleted in ^{13}C by

5.9 ‰ and enriched in ^{15}N by 3.3 ‰ relative to benthic primary consumers, showing there is a detectable difference in benthic and pelagic primary production within Lake Diefenbaker.

1.2.2 Rationale for Study

Lake Diefenbaker is often referred to as Saskatchewan's prairie jewel (North et al. 2015). It is located in the semi-arid region of southern Saskatchewan and serves many purposes including as a popular recreational getaway (North et al. 2015). The world class fishery has produced the International Game Fish Association (IGFA) all tackle world records for Rainbow Trout (*Oncorhynchus mykiss*) and Burbot (*Lota lota*) (IGFA: www.igfa.org) in 2009 and 2010, respectively. Due to its large size and convenient location near Saskatchewan's major population centres, Lake Diefenbaker is a popular angling destination in Saskatchewan (Duffy 2006). The aquaculture facility located within Cactus Bay is one of the largest freshwater cage culture facilities of its kind in Canada and has recently expanded to a second site within nearby Kadla Coulee after the completion of this study. Lake Whitefish have been observed feeding on waste feed around the cage culture facility at certain times of the year (Jeff Sereda, personal communication April 25th, 2012).

Inflow to the reservoir varies from year to year and recent years of high flow have resulted in large plumes of turbidity throughout the reservoir (Yip et al. 2015; Hudson and Vandergucht 2015) which may increase the availability of allochthonous carbon sources downstream in the reservoir while at the same time decreasing the availability of autochthonous sources by limiting primary production (Chen et al. 2005; Min-Seob et al. 2014; Yip et al. 2015). In years of drought and low flow, the opposite may be true and allochthonous carbon may only be available to the diets of fish in the upper most reaches of the reservoir while autochthonous primary production may be consumed throughout the remainder of the reservoir (Chen et al.

2005; Yip et al. 2015; Lucas et al. 2015). The recent variation in both the volume and timing of major inflows into Lake Diefenbaker likely results in seasonal and annual variation in the availability of allochthonous and autochthonous carbon throughout the reservoir. The relative importance of varying seasonal flows and aquaculture subsidies on the food web throughout Lake Diefenbaker, and in particular wild fish, is unknown.

1.2.3 Objectives

The three major objectives of this study are as follows:

1. To determine the degree to which Lake Whitefish in the vicinity of the aquaculture facility are subsidizing their diets with waste feed from the cage culture facility and to determine the spatial extent of these diet subsidies.
2. To assess the importance of allochthonous and autochthonous carbon pathways to the diets of the native and naturalized fish assemblages of Lake Diefenbaker.
3. To determine if fish relying on different carbon sources (i.e., allochthonous sources, autochthonous sources, or aquaculture waste products) differ in their overall condition or fecundity.

1.2.4 Study Design

To address the above objectives, the study was divided into two sections. The first section of the study was designed to examine the diets of Lake Whitefish in the area adjacent to the aquaculture facility at Cactus Bay. Eight sampling sites were used in this portion of the study: two located within Cactus Bay, two located within Kadla Coulee and four sites on the main channel of the reservoir, two upstream and two downstream of Cactus Bay (Fig 1.1). In addition to these eight sampling sites, Lake Whitefish were sampled directly adjacent to the fish farm cages in the fall of 2013 to increase sample size of fish using aquaculture waste as a diet subsidy.

Main channel sites were used to determine if the subsidy extended to Lake Whitefish found in the main channel of the reservoir, while the sites within Kadla Coulee were used as reference sites for the sites within Cactus Bay.

The second portion of this study evaluates the importance of allochthonous and autochthonous carbon sources to the diets of four common fish species throughout Lake Diefenbaker. I hypothesize that the importance of each carbon source changes with distance downstream of the river input, with allochthonous sources being of greatest importance in the riverine zone of the reservoir and decreasing with distance downstream. Eight study sites along the main channel of Lake Diefenbaker as well as the four sample sites within Cactus Bay and Kadla Coulee were used for this portion of the study (Fig 1.1). Baseline isotopic samples as well as the four study species of fish, Lake Whitefish (*Coregonus clupeaformis*), White Sucker (*Catostomus commersoni*), Northern Pike (*Esox lucius*), and Walleye (*Sander vitreus*) were collected at each site. In addition to these sites, baseline samples were also collected at the South Saskatchewan River before entering the reservoir and supplementary POM data from 10 additional sites along the length of the reservoir (Fig 1.1) were used to determine the change in importance of allochthonous and autochthonous carbon sources down the length of the reservoir.

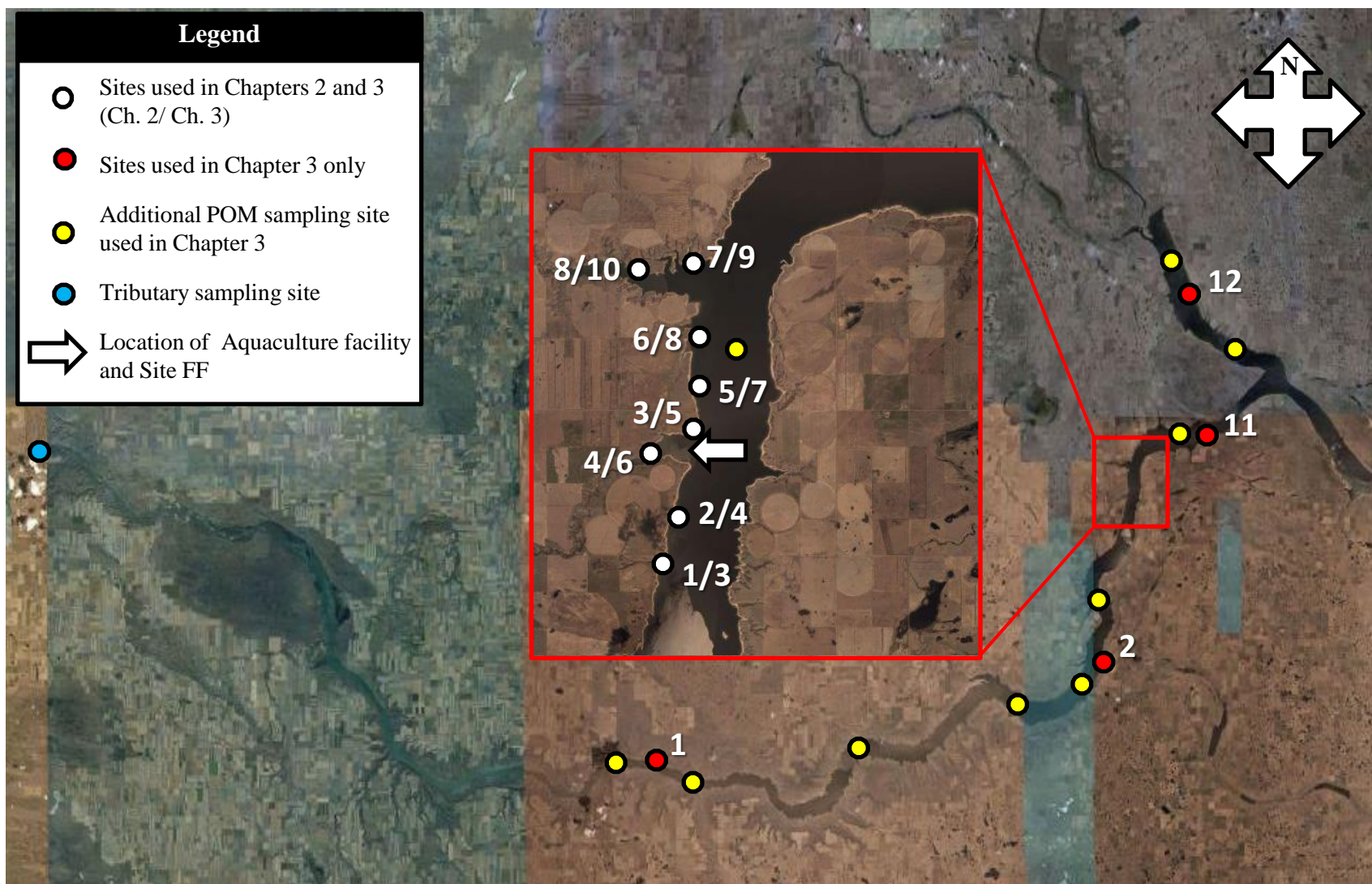


Figure 1.1. Location of all sampling sites throughout Lake Diefenbaker and the South Saskatchewan River used in this study. The location of the Wild West Steelhead aquaculture facility and site FF used in Chapter 2 are indicated with a white arrow. Sites used in Chapters 2 and 3 are labeled with the separate site numbers used in each chapter in the format: Chapter 2 site #/Chapter 3 site #.

CHAPTER 2. Assimilation of aquaculture waste by Lake Whitefish, *Coregonus clupeaformis*, in Lake Diefenbaker.

2.1 Introduction

2.1.1 Importance of Aquaculture

Aquaculture is one of the world's fastest growing agricultural practises. By the year 2020 freshwater and marine aquaculture is predicted to account for 60 % of the world's production of seafood (FAO 2014). The recent increase in aquaculture production is a result of the increased demand for high protein food across many developing nations combined with the over allocation and collapse of many wild caught fisheries across the globe (Pauly et al. 2002; Worm et al. 2009; Pitcher and Cheung 2013; Lam 2016). The impacts of this rapidly expanding industry include eutrophication and oxygen depletion in surrounding waters as a result of nutrient deposition from the aquaculture waste (Black 2001; Guo and Li 2003; Clerk et al. 2004; Yan 2005). These environmental impacts are often localized, affecting the environment only in close proximity to the aquaculture operations (Black 2001; Mente et al. 2006; Silva 2012). However, in freshwater environments the environmental impacts can be much greater due to the lower volume of the receiving waters.

2.1.2 A Brief History of Aquaculture in Lake Diefenbaker

The first commercial aquaculture operation on Lake Diefenbaker began in 1992 with one site located at Kadla Coulee operated by AgPro Fish Farms (Sweeney International 2010). In 1994, the facility was moved to Cactus Bay where it is located today (Sweeney International 2010). In 1998, ownership of the aquaculture facility was transferred to the Saskatchewan Wheat Pool and the name was changed to CanGro Processors (Sweeney International 2010). In 2004, the facility was sold to Nil-Ray Farms Ltd. and changed names to Wild West Steelhead (Sweeney International 2010). The operation is still under the same name and ownership today.

The production capacity of the facility has continuously increased from 225 metric tons a year (MT y⁻¹) in 1993 to 1450 MT y⁻¹ throughout the duration of this study (Sweeney International 2010). Recently, the establishment of a second site at Kadla Coulee has increased the production capacity to 1750 MT y⁻¹. However, the Cactus Bay site remains at 1450 MT y⁻¹ and the additional site at Kadla Coulee was not in operation until fall 2014, after the completion of the field sampling portion of this study. Rainbow Trout have been the only species produced since 1998 when the production of Atlantic Salmon was phased out.

The aquaculture facility operates under a “zero waste” feed policy (Sweeney International 2010), but inevitably some waste feed, fish faeces and fines enter the surrounding water (Kullman et al. 2009). Fines are the portion of the pelleted fish feed which are too small to be ingested directly by the domestic fish and can comprise up to 3.7 % of the total mass of the feed (Clark et al. 1985). During periods of feeding, Lake Whitefish are often seen around the cages and are believed to be supplementing their diets on the aquaculture waste (Jeff Sereda, personal communication, April 25th, 2012).

2.1.3 Trends of Other Aquaculture Studies

Much of the past research on aquaculture has focused on the ecological impacts to the surrounding environment via increased nutrient deposition and oxygen depletion (Black 2001; Guo and Li 2003; Clerk et al. 2004; Yan 2005). Recently, more emphasis has been placed on the biotic community surrounding the cages including the examination of the impacts on local fish and invertebrate communities. Studies in both marine and freshwater environments generally indicate an increase in fish abundance near the cages (Carrs 1990; Boyra et al. 2004; Dempster et al. 2010), although the number of wild fish surrounding the cages can vary seasonally (Dempster et al. 2002). Wild fish are attracted to the physical structure of the cages (Powers et al. 2007), as

well as the increased productivity in the area resulting from both increased nutrient concentrations and the direct addition of aquaculture waste (Fernandez-Jover et al. 2011; Dempster et al. 2011). Wild fish surrounding the cages often subsidize their diets with aquaculture waste (Phillips et al. 1985; Gabrielsen 1999; Strictar-Pereira et al. 2010; Brandão et al. 2014) and can have increased condition factors when compared to fish that were not utilizing the aquaculture waste (Gabrielsen 1999; Fernandez-Jover et al. 2011; Dempster et al. 2011). This increase in body condition is believed to result in increased fecundity in some fish species. Brandão et al. (2014) identified an increased number of smaller eggs in fish using aquaculture waste as a diet subsidy in a Brazilian reservoir when compared to reference groups of fish.

2.1.4 Expected Results

Impacts of the aquaculture facility on the diets of the Lake Whitefish community in Lake Diefenbaker are believed to be localized to the area surrounding the fish farm. It is anticipated that as distance increases away from the cage culture facility the importance of aquaculture waste to the diets of Lake Whitefish will decrease. The significance of this diet subsidy is examined directly adjacent to the fish farm cages, immediately upstream and downstream from the cages, and within the coulee where the aquaculture facility is located. All sample sites were located within a 10 km radius of the aquaculture cages. It is predicted that the waste feed will be of little importance to fish outside of Cactus Bay where the fish farm is located, but fish in the vicinity of the aquaculture facility will be using the diet subsidy as found in other studies (Phillips et al. 1985; Gabrielsen 1999; Strictar-Pereira et al. 2010; Brandão et al. 2014). Fish subsidizing their diets with aquaculture waste are expected to have higher relative weights and fecundity than fish not using this diet subsidy.

2.2 Methods

2.2.1 Field Sampling

Eight sites in the area surrounding the aquaculture facility were sampled in spring (May – June), summer (July – September) and fall (October – November) of 2012 and 2013. Four sites (1, 2, 5 and 6) were located on the main channel of Lake Diefenbaker while two sites were located within Cactus Bay (sites 3 and 4) and two sites were located within Kadla Coulee (sites 7 and 8) to act as a reference to the sites within Cactus Bay (Fig. 1.1). One site in both Cactus Bay and Kadla Coulee was located near the mouth of the embayment (sites 3 and 5) and one site was located 1.5 km within the embayment (sites 4 and 8). Due to the sheer size of Lake Diefenbaker only locations within close proximity of the aquaculture facility were included in this study in order to increase the likelihood of capturing fish that were consuming aquaculture waste. In addition to these eight sites, Lake Whitefish were also sampled directly adjacent to the cage culture facility at site FF in the fall of 2013. This sampling was done to increase the sample size of fish that may be subsidizing their diets with aquaculture waste in an area where fish were observed to be feeding directly on the pelleted feed.

2.2.1.1 Lake Whitefish, Domestic Rainbow Trout and Pelleted Fish Feed

Lake Whitefish were sampled in the spring of 2012 and 2013 and in the fall of 2012 using two gill nets at each of the eight sampling sites. The nets consisted of seven 4.27 metre panels of nylon monofilament mesh measuring 25, 38, 51, 63, 76, 89 and 102 mm, for a total length of 30 metres and a height of 2.13 metres. Gill nets were set perpendicular to shore starting in water ≥ 2 metres deep and extending out for the 30 metre length of the net with the smallest mesh set inshore. The nets were set to run along the bottom. In the fall of 2013 Lake Whitefish were collected directly adjacent to the cages at the aquaculture facility at site FF using a large dip

net. Domestic Rainbow Trout were collected from within the cages at the aquaculture facility using a dip net in August of 2012 and 2013 and November 2013 and were used to calculate a trophic enrichment factor from pelleted fish feed to consumer. All Lake Whitefish and trout were measured for total length, fork length, weight, sex, state of maturity, and stomach contents. In mature fish fecundity was measured by weighing the ovaries and testes in the field to the nearest gram. Ovaries were then brought back to the lab where a subsample of eggs (0.500 to 1.000 g) was taken and preserved in phosphate buffered formalin. The number of eggs and egg diameter were determined at a later date. A subsample of boneless and skinless dorsal muscle was collected from the central part of each fish above the lateral line for C and N stable isotope analysis. Pelleted fish feed (PFF) was sampled directly from the feed storage area at the aquaculture facility in February and August of 2012 and again in August and November of 2013.

2.2.1.2 Aquatic Baseline Samples

Aquatic baseline samples were collected at each site three times throughout the open water season. Particulate organic carbon (POC) and particulate nitrogen (PN) (collectively known as particulate organic matter (POM)), zooplankton and aquatic macroinvertebrates (lymnaeid snails and *Gammarus lacustris*) were sampled three times throughout each open water season. Water was collected from a depth of 2.0 metres using a 6.4 L van Dorn sampler. Zooplankton were collected with vertical tows using a 1.5 metre long plankton net with a hoop diameter of 30 cm and a mesh size of 153 μm from a depth of 10 metres to the surface. When inadequate numbers of zooplankton were collected in one net tow, tows were repeated until an adequate number had been collected. Aquatic macroinvertebrates were collected in the littoral area immediately adjacent to sampling sites using a D frame net and a kick and sweep method. Kick sweeps were performed along 100 metres of shoreline at a depth of 0.3 to 1.0 m and

repeated until enough macroinvertebrates were collected, or 10 passes had been completed. When possible, duplicate POC, PN, zooplankton and aquatic macroinvertebrate samples were collected to assess variability between samples.

All water, zooplankton and macroinvertebrate samples were transported back to the University of Saskatchewan in 4 litre carboys in coolers. Zooplankton and aquatic macroinvertebrates were filtered through a 153 μm filter and then left overnight in deionized water to void any stomach contents (Marty and Planas 2008). Zooplankton samples were individually hand sorted to remove filamentous algae, large predatory zooplankton species (i.e., *Espichura* spp., *Leptidora* spp., *Mesocyclops* spp.), and particulate contaminants or debris (Post 2002; Marty and Planas 2008) before being placed in glass vials. Aquatic macroinvertebrates were sorted to remove any debris and placed into aggregates of 5 to 25 individuals. Only the soft tissues of lymnaeid snails were kept for analysis as the shells do not represent carbon from the snail's diet, but rather inorganic carbon from their environment (Post 2002). Water samples were filtered onto pre-combusted 25 mm GFF (nominal pore size of 0.7 μm) filters in 2012 and 25 mm quartz filters (Advantec QR-100) in 2013, using vacuum filtration. POM filters, zooplankton, and macroinvertebrate samples were dried at 60°C for 48 hours.

2.2.2 Stable Isotope Analysis

Lipid extraction was performed on all pelleted fish feed, zooplankton, aquatic macroinvertebrate and fish tissue samples using a 2:1 chloroform:methanol solution. Samples were soaked in the solution for 24 hours before the solution containing lipids was decanted and the method was repeated until the chloroform:methanol solution was clear after soaking for 24 hours. Following lipid extraction, samples were allowed to air dry for 24 hours and then ground into a homogeneous powder using a mortar and pestle. Subsamples were weighed out to 1.0 mg

and weight recorded to the nearest 0.001 mg before being placed into 4 x 6 mm ultrapure tin capsules. POM filters were subdivided into two groups: those for particulate $\delta^{15}\text{N}$ (PN) were set aside while those for particulate organic $\delta^{13}\text{C}$ (POC) were acidified to remove carbonates. Acidification was performed by fumigating the POC filters for 4 hours using concentrated (37 %) hydrochloric acid following the same methodology as Dubourg et al. (2015). Following acidification, POC filters were treated the same as PN filters. All filters were sealed inside 8 x 11 mm ultrapure tin capsules.

All stable isotope analyses were performed in the Department of Soil Sciences Stable Isotope Lab at the University of Saskatchewan. Samples were processed using a Thermo Scientific Delta V mass spectrometer manufactured in Bremen, Germany, coupled to an ECS4010 elemental analyzer manufactured by Costech Analytical Technologies Inc. of Valencia, California, USA. Pee Dee Belemnite and atmospheric nitrogen were used as the C and N international references, respectively. When analyzing the POC and PN samples, an internal laboratory standard made of pea grain flour was included after every 5 samples to determine the precision associated with the mass spectrometer. Repeat analysis of this laboratory standard (n = 132) resulted in a precision of < 0.2 ‰ and < 0.1 ‰ for nitrogen and carbon, respectively. All macroinvertebrate, zooplankton, pelleted fish feed and fish tissue samples were analyzed with an internal laboratory standard of egg albumen (n = 164) after every 11 samples. This laboratory standard provided a precision of < 0.06 ‰ for nitrogen and < 0.04 ‰ for carbon. Every 15th sample of fish tissue, macroinvertebrate tissue, zooplankton and pelleted fish feed was run in duplicate to determine within sample variability, which was found to be 0.07 ‰ and 0.04 ‰ for nitrogen and carbon, respectively. An internal standard made from Walleye dorsal muscle was included in each 96 well plate of fish and invertebrate samples (n = 8) and had a measurement

precision of < 0.4 ‰ for nitrogen and < 0.1 ‰ for carbon. All stable isotope values are reported in ratios of the heavy isotope to the light isotope ($^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$) and expressed in parts per thousand (‰) relative to the international standards in delta notation following equation 1.1.

2.2.2.1 Discrimination Factors

Discrimination factors, also known as trophic enrichment factors (TEFs), were applied to each source to account for isotopic discrimination which occurs with increases in trophic level from source to consumer. The TEFs used in this study were 0.39 ± 1.3 ‰ for $\delta^{13}\text{C}$ and 3.4 ± 0.98 ‰ for $\delta^{15}\text{N}$ (Post 2002) for all sources except aquaculture waste which had TEFs of 2.65 ± 0.63 ‰ and 2.33 ± 1.06 ‰ for carbon and nitrogen respectively. The TEFs used for aquaculture waste were calculated from the difference in isotopic values between the pelleted fish feed at Wild West Steelhead and the dorsal muscle tissue from the domestic Rainbow Trout (DRT) which are known to have a diet of 100 % pelleted feed. This allowed for a more accurate estimation of trophic enrichment over literature values. Pelleted fish feed samples ($n = 14$) were collected four times throughout the two year study period while domestic Rainbow Trout ($n = 16$) were collected three times during the study period.

2.2.3 Mixing Models

To determine the proportion of each carbon source to the diet of fish, the Bayesian mixing model SIAR was used for each site (Parnell et al. 2010; R Core Development Team 2013). The relative importance of each food source to the diet of each individual Lake Whitefish was determined with SIARsolo mixing model in R. SIAR and SIARsolo use a Bayesian approach to estimate the probability distributions of source contributions to the tissue of consumers (Parnell et al. 2010). Both models account for uncertainties associated with the input data such as the isotopic values of the different diet sources and the TEFs (Parnell et al. 2010).

Mixing models were run using both ^{13}C and ^{15}N . Four sources were used in both the SIAR and SIARsolo mixing models which included pelagic (zooplankton) and benthic (lymnaeid snails and *G. lacustris*) primary production pathways and aquaculture waste (pelleted fish feed).

Zooplankton samples were used as the proxy for pelagic primary production, while lymnaeid snails and *G. lacustris* samples were used as proxies of benthic primary production. Results from these two benthic primary consumers were pooled a posteriori following Phillips et al. (2005), due to significant difference between both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for these consumers (T-test: $\delta^{13}\text{C}$: $T = -6.06$, $P < 0.001$; $\delta^{15}\text{N}$: $T = 2.85$, $P < 0.01$). The combined contribution of lymnaeid snails and *G. lacustris* to the diets of Lake Whitefish represented the benthic primary production pathway. Pelleted fish feed was used as the source representing aquaculture waste. Primary consumer samples from all eight sampling locations were averaged over the two year study period prior to input into the mixing models to account for spatial and temporal variations throughout the sampling region (Jardine et al. 2014).

2.2.4 Fish Condition

Relative weight (W_r) was used to determine the condition of each Lake Whitefish caught in the study using the formula:

$$\text{Equation 2.1: } W_r = (W/W_s) * 100$$

where W is the actual weight of the fish and W_s is the standard weight of a fish of the same species of the same total length.

Standard weight (W_s) equations were developed using populations throughout the entire range of a fish species (Blackwell et al. 2000). A W_r value below 100 indicates a fish is in poor body condition while values above 100 indicate the fish is considered to be in good condition (Blackwell et al. 2000; Bonar et al. 2009). The equation for Lake Whitefish W_s was taken from

Rennie and Verdon (2008) which was developed for Lake Whitefish of both sexes using the following formula:

$$\text{Equation 2.2: } \log_{10}(W_s) = -5.559919 + (3.218445 * \log_{10} TL)$$

where W_s is the standard weight and TL is the Lake Whitefish's total length in mm.

Fecundity was calculated as the total number and size of eggs by capturing images with a flatbed scanner and using the software ImageJ following methods outlined in Klibansky and Juanes (2008) to determine both egg number and size for each sample. Egg numbers were standardized based on fish body weight. The gonadosomatic index (GSI) was calculated to make comparisons between different size ranges of fish (DeVlaming et al. 1982).

2.2.5 Statistical Analysis

Relationships between fish total length and $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and W_r were examined to identify any ontogenetic trends in the data (model I linear regression). Differences in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and W_r between sites and between seasons were tested to determine any spatial or temporal differences throughout the study (one way ANOVAs with Tukey's HSD post hoc tests for pairwise comparisons). Whitefish were separated into three groups based on SIARsolo output: those with < 15 % of their diet made up of aquaculture waste (No AW: n = 131), those with 15 – 50 % of their diet made up of aquaculture waste (AW Generalists: n = 3) and those with > 50 % of their diet made up of aquaculture waste (AW Specialists: n = 10). Differences in W_r and fecundity between the three groups were tested to determine if differences in condition factors were present between groups (one way ANOVAs and post hoc Tukey Tests). All statistical analyses were performed in the statistical software R (R version 3.0.2, R Project for Statistical Computing) with a level of significance of $P < 0.05$.

2.3 Results

2.3.1 Fish Size and Condition

A total of 135 Lake Whitefish were collected from sites 1 – 8 and an additional 9 were collected directly adjacent to the fish farm cages (site FF) for a total sample size of 144 (Tables 2.1 – 2.3). Total length ranged from 274 – 681 mm (mean 414 ± 66 mm) and weight ranged from 174 – 3650 g, with a mean of 675 ± 563 g (Tables 2.1 – 2.3). Relative weight values ranged widely from 53 – 126 with a mean value of 82 ± 11 (Tables 2.1 – 2.3). In total, 27 Lake Whitefish caught in fall 2012 and fall 2013 were sexually mature (female: $n = 14$, male: $n = 13$). Male testes weight ranged from 2 – 100 g (mean 18 ± 27 g) with a GSI range of 0.3 – 3.4 (mean = 1.3 ± 0.8). Female ovaries weighed between 50 – 435 g (mean 137 ± 128 g) with a GSI range of 8.8 – 15.1 (mean = 11.8 ± 2.0). Egg counts ranged from 10,270 – 91,740 (mean $28,170 \pm 24,220$). Once standardized per gram of body weight, egg counts ranged from 15.9 – 32.2 eggs per gram of body weight (mean 24.1 ± 5.3 eggs/g). Egg diameter ranged from 2.01 – 2.50 mm and had a mean of 2.23 ± 0.14 mm. A total of 16 domestic Rainbow Trout (DRT) were collected from the aquaculture facility. Total length ranged from 287 – 552 mm (mean 440 ± 76 mm) and weight ranged from 270 – 2450 g (mean 1225 ± 609 g).

2.3.2 Stable Isotope Analysis

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of all Lake Whitefish along with their potential dietary sources can be seen in Table 2.4 and Fig. 2.1. Lake Whitefish from individual sites along with potential sources can be seen in Fig. 2.2. The $\delta^{13}\text{C}$ values for Lake Whitefish ranged from -31.3 to -18.4 ‰ with a mean of -27.5 ± 2.5 ‰ and the $\delta^{15}\text{N}$ values ranged from 11.0 to 19.2 ‰ with a mean of 16.9 ± 1.5 ‰. Particulate organic matter samples had $\delta^{13}\text{C}$ values which ranged from -40.1 to -27.6 ‰ with a mean of -31.8 ± 2.5 ‰, while the $\delta^{15}\text{N}$ values ranged from 4.3 to

14.9 ‰ with a mean of 9.8 ± 2.6 ‰. Zooplankton samples had a narrower range and were slightly enriched in both $\delta^{13}\text{C}$ (range -35.7 to -28.1 ‰, mean -31.4 ± 1.6 ‰) and $\delta^{15}\text{N}$ (range 10.3 to 21.3 ‰, mean 14.5 ± 2.6 ‰) compared to POM samples. Macroinvertebrate samples had a narrower range in both their $\delta^{13}\text{C}$ (*G. lacustris*: -25.6 to -23.1 ‰, lymnaeid snails: -28.9 to -24.5 ‰) and $\delta^{15}\text{N}$ values (*G. lacustris*: 8.1 to 10.8 ‰, lymnaeid snails: 8.6 to 11.7 ‰) than both zooplankton and POM. Mean $\delta^{13}\text{C}$ values for macroinvertebrates (*G. lacustris*: -24.1 ± 0.7 ‰, lymnaeid snails: -26.2 ± 1.3 ‰) were enriched in ^{13}C compared to those of zooplankton while the $\delta^{15}\text{N}$ values were ^{15}N depleted (*G. lacustris*: 9.5 ± 0.7 ‰, lymnaeid snails: 10.4 ± 1.1 ‰). Pelleted fish feed was enriched in $\delta^{13}\text{C}$ (range -22.3 to -20.3 ‰, mean -21.1 ± 0.6 ‰) and depleted in $\delta^{15}\text{N}$ (range 7.7 to 10.7 ‰, mean 9.0 ± 0.9 ‰) compared to zooplankton and macroinvertebrates.

Table 2.1. Characteristics of Lake Whitefish (*Coregonus clupeaformis*) captured at sites 1 – 8 in spring 2012. Values are listed as the mean \pm standard deviation (SD) and the range is included in brackets.

Site	n	Total Length (mm)	Weight (g)	Relative Weight (W_r)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1	6	366 ± 19 (340 - 385)	442 ± 26 (400 - 470)	92 ± 15 (78 - 111)	-28.7 ± 0.3 (-29.1 - -28.4)	17.4 ± 0.3 (16.6 - 18.0)
2	6	400 ± 17 (378 - 422)	538 ± 122 (425 - 760)	82 ± 8 (76 - 98)	-28.1 ± 0.3 (-28.7 - -27.9)	17.4 ± 0.3 (16.8 - 17.8)
3	12	405 ± 25 (370 - 458)	542 ± 89 (400 - 725)	80 ± 8 (67 - 92)	-27.9 ± 0.9 (-29.1 - -25.7)	17.3 ± 0.9 (16.4 - 18.4)
4	6	357 ± 42 (310 - 412)	395 ± 151 (210 - 660)	85 ± 14 (66 - 106)	-28.7 ± 0.3 (-29.3 - -28.5)	17.8 ± 0.3 (17.5 - 18.2)
5	6	393 ± 24 (348 - 414)	498 ± 75 (370 - 565)	81 ± 5 (75 - 89)	-28.1 ± 0.2 (-28.6 - -27.9)	17.1 ± 0.2 (16.6 - 18.0)
6	6	380 ± 48 (296 - 430)	435 ± 167 (200 - 600)	75 ± 10 (56 - 83)	-28.0 ± 0.7 (-28.9 - -27.0)	17.6 ± 0.7 (17.1 - 18.0)
7	6	388 ± 44 (320 - 430)	575 ± 175 (400 - 750)	96 ± 16 (81 - 126)	-27.6 ± 0.8 (-29.0 - -26.8)	17.4 ± 0.8 (16.8 - 18.1)
8	6	407 ± 17 (390 - 430)	573 ± 110 (400 - 730)	83 ± 12 (65 - 101)	-27.8 ± 0.8 (-29.1 - -26.6)	17.3 ± 0.8 (16.5 - 18.3)

Domestic Rainbow Trout collected from the aquaculture facility had enriched $\delta^{13}\text{C}$ (mean -18.4 ± 0.2 ‰, range -19.1 to -18.1 ‰) and $\delta^{15}\text{N}$ values (mean 11.3 ± 0.3 ‰, range 10.2 to 12.2 ‰) compared to the pelleted fish feed, their sole dietary source (Fig. 2.2, Table 2.4). The isotopic differences between the pelleted fish feed and the domestic Rainbow Trout dorsal muscle tissue resulted in trophic enrichment factors (TEFs) of 2.65 ± 0.63 ‰ and 2.33 ± 1.06 ‰ for carbon and nitrogen, respectively.

Table 2.2. Characteristics of Lake Whitefish (*Coregonus clupeaformis*) captured at sites 1 – 8 in fall 2012 and at site FF, directly adjacent to the fish farm cages, in fall 2013. Values are listed as the mean \pm SD and the range is included in brackets.

Site	n	Total Length (mm)	Weight (g)	Relative Weight (W_r)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1	3	407 \pm 17 (391 - 425)	537 \pm 32 (500 - 560)	78 \pm 8 (69 - 82)	-28.9 \pm 0.4 (-29.3 - -28.6)	17.8 \pm 0.4 (17.4 - 18.4)
2	6	378 \pm 70 (274 - 450)	518 \pm 273 (174 - 900)	87 \pm 5 (82 - 94)	-28.8 \pm 1.4 (-31.3 - -27.0)	17 \pm 1.4 (16.6 - 17.3)
3	8	426 \pm 96 (290 - 636)	832 \pm 847 (220 - 2900)	85 \pm 9 (72 - 100)	-27.7 \pm 3.9 (-30.8 - -18.7)	16.8 \pm 3.9 (11.9 - 18.3)
4	6	408 \pm 27 (375 - 455)	648 \pm 167 (450 - 950)	92 \pm 10 (78 - 108)	-28.6 \pm 1.0 (-30.0 - -27.0)	17.4 \pm 1.0 (16.9 - 18.4)
5	5	384 \pm 17 (366 - 404)	432 \pm 60 (350 - 510)	75 \pm 4 (71 - 80)	-28.8 \pm 0.4 (-29.1 - -27.9)	17 \pm 0.4 (16.6 - 17.4)
6	6	402 \pm 22 (365 - 430)	517 \pm 117 (350 - 700)	77 \pm 7 (68 - 85)	-28.5 \pm 0.3 (-28.9 - -27.9)	17.2 \pm 0.3 (16.3 - 17.7)
7	3	462 \pm 50 (430 - 520)	850 \pm 312 (600 - 1200)	79 \pm 7 (73 - 86)	-27.9 \pm 1.0 (-28.8 - -26.8)	16.3 \pm 1.0 (16.0 - 16.8)
8	5	413 \pm 26 (395 - 460)	560 \pm 138 (450 - 800)	76 \pm 5 (68 - 80)	-28.1 \pm 1.0 (-29.0 - -26.5)	17 \pm 1.0 (14.6 - 19.2)
FF*	9	615 \pm 46 (565 - 681)	2564 \pm 592 (1875 - 3650)	97 \pm 6 (88 - 107)	-19.2 \pm 0.7 (-20.5 - -18.4)	12 \pm 0.7 (11.0 - 13.3)

*Site FF was located directly adjacent to the fish farm cages and was the only site sampled in fall 2013.

The relationships between Lake Whitefish total length and $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and W_r can be seen in Fig. 2.3, 2.4 and 2.5, respectively. Both $\delta^{13}\text{C}$ and W_r showed significant positive correlations with total length for all Lake Whitefish ($\delta^{13}\text{C}$: $F = 487$, d.f. = 1, 142, $R^2 = 0.77$, $P <$

0.001; W_r : $F = 5.8$, d.f. = 1, 142, $R^2 = 0.04$, $P < 0.05$), but when the Lake Whitefish which were feeding on pelleted fish feed were removed the relationship between total length and W_r showed a significant decrease in relative weight as total length increased ($F = 10.8$, d.f. = 1, 132, $R^2 = 0.08$, $P < 0.01$). The relationship between total length and $\delta^{13}\text{C}$ remained positively correlated and significant when the Lake Whitefish feeding on pelleted fish feed were removed ($F = 44.7$, d.f. = 1, 132, $R^2 = 0.25$, $P < 0.001$). Lake Whitefish $\delta^{15}\text{N}$ showed a significant negative correlation to total length when all Lake Whitefish were included ($F = 232$, d.f. = 1, 142, $R^2 = 0.62$, $P < 0.001$), but when fish feeding on pelleted fish feed were excluded the relationship was no longer significant ($F = 1.8$, d.f. = 1, 132, $R^2 = 0.01$, $P = 0.18$).

Table 2.3. Characteristics of Lake Whitefish (*Coregonus clupeaformis*) captured at sites 1 – 8 in spring 2013. Values are listed as the mean \pm SD and the range is included in brackets.

Site	n	Total Length (mm)	Weight (g)	Relative Weight (W_r)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1	2	404 \pm 0 (404 - 404)	600 \pm 35 (575 - 625)	89 \pm 5 (85 - 93)	-27.5 \pm 1.1 (-28.3 - -26.7)	16.4 \pm 1.1 (16.3 - 16.5)
2	4	410 \pm 27 (381 - 445)	544 \pm 147 (400 - 750)	76 \pm 5 (72 - 89)	-27.8 \pm 0.5 (-28.2 - -27.1)	17.6 \pm 0.5 (17.0 - 17.8)
3	6	408 \pm 18 (392 - 440)	552 \pm 85 (440 - 650)	79 \pm 7 (72 - 89)	-27.4 \pm 1.0 (-28.5 - -25.6)	16.9 \pm 1.0 (16.3 - 17.7)
4	6	408 \pm 27 (376 - 444)	532 \pm 123 (410 - 700)	76 \pm 6 (68 - 84)	-27.8 \pm 1.2 (-29.0 - -25.7)	16.9 \pm 1.2 (16.4 - 17.6)
5	5	403 \pm 26 (371 - 434)	535 \pm 84 (425 - 625)	79 \pm 4 (74 - 84)	-27.7 \pm 0.6 (-28.3 - -26.8)	16.8 \pm 0.6 (16.3 - 17.5)
6	6	400 \pm 25 (369 - 424)	500 \pm 86 (380 - 580)	76 \pm 5 (71 - 85)	-28.1 \pm 0.6 (-29.0 - -27.3)	17.3 \pm 0.6 (16.1 - 18.0)
7	6	425 \pm 14 (410 - 450)	562 \pm 124 (375 - 725)	70 \pm 10 (53 - 81)	-28.1 \pm 1.0 (-29.1 - -26.4)	17.4 \pm 1.0 (16.6 - 18.6)
8	4	392 \pm 20 (365 - 408)	514 \pm 92 (400 - 600)	83 \pm 3 (80 - 86)	-27.9 \pm 0.4 (-28.4 - -27.4)	16.9 \pm 0.4 (16.5 - 17.2)

Table 2.4. Seasonal contribution of pelagic primary production, benthic primary production, and aquaculture waste to Lake Whitefish diets as determined through the stable isotope mixing model SIARsolo. Lake Whitefish were caught at sites 1 – 8 in spring 2012 (S12), fall 2012 (F12), and spring 2013 (S13), while those at site FF were caught in fall 2013 (F13). Domestic Rainbow Trout were included as they were known to have a diet of entirely pelleted fish feed, but still show a proportion of their diet from benthic and pelagic sources due to the inclusion of all sources in the mixing model. Proportions are reported as the seasonal mean \pm SD for each site, while the range of values is reported in brackets

Site	Season	n	Source					
			Pelagic (%)		Benthic ¹ (%)		Aquaculture Waste (%)	
1	S12	6	55.4 \pm 3.7	(50.3 - 60.0)	32.7 \pm 4.0	(28.0 - 37.9)	6.3 \pm 3.5	(6.0 - 6.9)
	F12	3	58.1 \pm 4.9	(54.6 - 64.7)	29.8 \pm 4.6	(24.6 - 33.0)	6.2 \pm 4.1	(5.8 - 6.5)
	S13	2	44.8 \pm 4.1	(42.0 - 47.7)	42.0 \pm 1.8	(40.7 - 43.3)	9.2 \pm 3.1	(7.0 - 11.4)
2	S12	6	52.2 \pm 1.9	(48.8 - 53.7)	35.0 \pm 2.3	(33.0 - 39.1)	7.3 \pm 0.5	(6.2 - 7.7)
	F12	6	54.9 \pm 8.2	(45.5 - 69.7)	29.7 \pm 7.9	(20.6 - 35.3)	5.6 \pm 1.2	(4.3 - 6.5)
	S13	4	51.9 \pm 1.9	(50.3 - 53.9)	34.4 \pm 2.1	(23.9 - 37.5)	8.0 \pm 1.3	(7.1 - 9.9)
3	S12	12	51.0 \pm 6.0	(40.5 - 59.6)	35.2 \pm 4.7	(27.8 - 43.6)	8.4 \pm 2.9	(5.9 - 16.5)
	F12	8	51.0 \pm 21.6	(2.7 - 70.4)	27.6 \pm 9.6	(12.5 - 40.0)	16.1 \pm 26.4	(4.6 - 81.2)
	S13	6	46.7 \pm 5.3	(40.3 - 55.6)	39.1 \pm 4.3	(31.8 - 43.5)	9.7 \pm 3.8	(6.7 - 17.3)
4	S12	6	57.7 \pm 2.2	(54.5 - 61.1)	29.9 \pm 2.0	(27.2 - 33.0)	6.4 \pm 3.9	(5.7 - 6.7)
	F12	6	55.2 \pm 4.6	(50.0 - 61.3)	32.1 \pm 3.7	(27.4 - 36.6)	6.9 \pm 1.7	(5.1 - 10.0)
	S13	6	49.1 \pm 6.4	(38.9 - 54.4)	37.3 \pm 4.3	(32.8 - 43.7)	8.8 \pm 4.1	(5.9 - 16.8)
5	S12	6	50.1 \pm 2.6	(47.2 - 55.0)	36.4 \pm 3.3	(30.1 - 40.8)	7.3 \pm 4.4	(6.5 - 7.7)
	F12	5	53.6 \pm 2.7	(50.8 - 57.6)	34.6 \pm 2.6	(30.6 - 37.6)	6.3 \pm 5.3	(5.9 - 7.2)
	S13	5	47.5 \pm 2.4	(43.8 - 50.0)	39.3 \pm 2.3	(35.6 - 41.1)	8.4 \pm 1.5	(6.9 - 10.8)
6	S12	6	53.5 \pm 3.6	(47.9 - 57.4)	33.0 \pm 2.9	(29.9 - 37.0)	7.6 \pm 1.4	(6.1 - 9.9)
	F12	6	53.0 \pm 2.9	(49.4 - 56.3)	34.8 \pm 3.1	(31.2 - 39.5)	6.7 \pm 0.6	(6.0 - 7.8)
	S13	6	52.0 \pm 2.6	(47.8 - 54.9)	35.1 \pm 2.6	(31.4 - 37.9)	7.4 \pm 1.2	(5.9 - 9.1)
7	S12	6	50.1 \pm 5.6	(43.4 - 60.5)	36.0 \pm 4.9	(27.3 - 41.9)	8.7 \pm 1.8	(6.1 - 10.9)
	F12	3	46.1 \pm 6.5	(39.6 - 52.7)	41.5 \pm 5.3	(35.8 - 46.4)	8.4 \pm 2.7	(6.2 - 11.5)
	S13	6	52.7 \pm 6.1	(44.7 - 59.6)	34.0 \pm 5.3	(27.6 - 40.1)	7.9 \pm 5.3	(5.8 - 12.6)
8	S12	6	50.1 \pm 6.8	(40.9 - 58.9)	36.3 \pm 6.1	(29.1 - 43.5)	8.5 \pm 2.2	(6.0 - 12.3)
	F12	5	51.2 \pm 10.3	(33.7 - 60.2)	35.9 \pm 10.2	(24.7 - 51.9)	8.1 \pm 3.2	(5.9 - 13.5)
	S13	4	48.7 \pm 3.4	(44.2 - 52.7)	38.7 \pm 3.4	(34.8 - 43.0)	7.7 \pm 9.5	(6.8 - 9.0)
FF	F13	9	3.2 \pm 0.9	(2.5 - 5.2)	16.3 \pm 6.6	(10.9 - 30.3)	76.4 \pm 8.3	(58.7 - 83.3)
	DRT ²	16	2.4 \pm 0.1	(2.2 - 2.6)	10.4 \pm 0.9	(9.2 - 12.2)	84.1 \pm 1.2	(81.8 - 85.8)

¹Results for lymnaeid snails and *G. lacustris* were combined a posteriori following Phillips et al. (2005) to account for all benthic production.

²Domestic Rainbow Trout (DRT) were sampled from the aquaculture facility in August of 2012 and again in August and November of 2013 and results were combined.

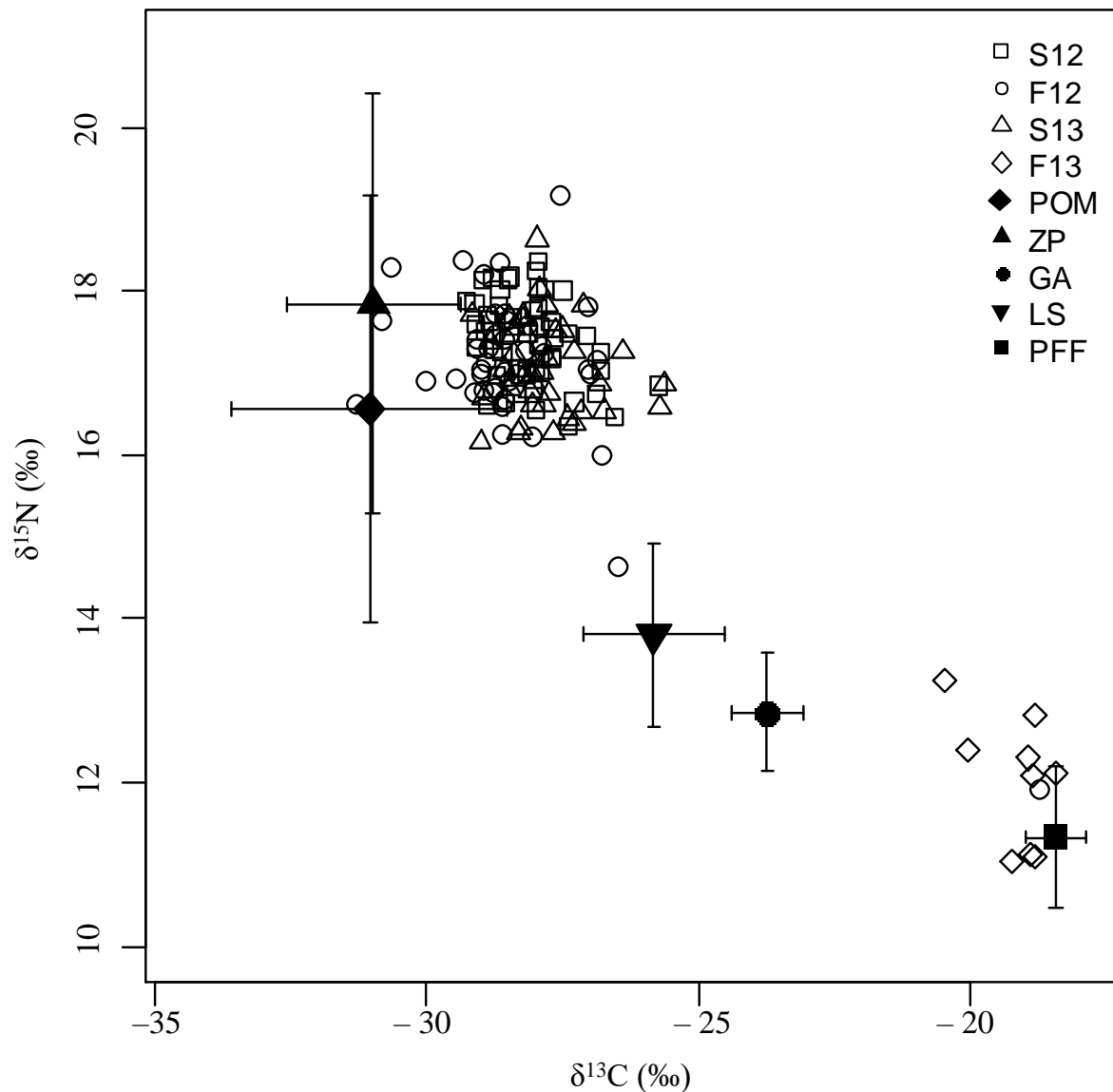


Figure 2.1. Stable isotope biplot of all Lake Whitefish (*Coregonus clupeaformis*) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values collected in spring 2012 (S12), fall 2012 (F12), spring 2013 (S13) and fall 2013 (F13) (open symbols) and the mean (\pm SD) of potential dietary sources corrected for trophic enrichment (closed symbols). POM was corrected for two trophic levels by doubling the trophic enrichment factors applied to it due to it being a basal resource whereas other sources were primary consumers. Potential dietary sources include bulk zooplankton (ZP), particulate organic matter (POM), lymnaeid snails (LS), *Gammarus lacustris* (GA), and pelleted fish feed (PFF).

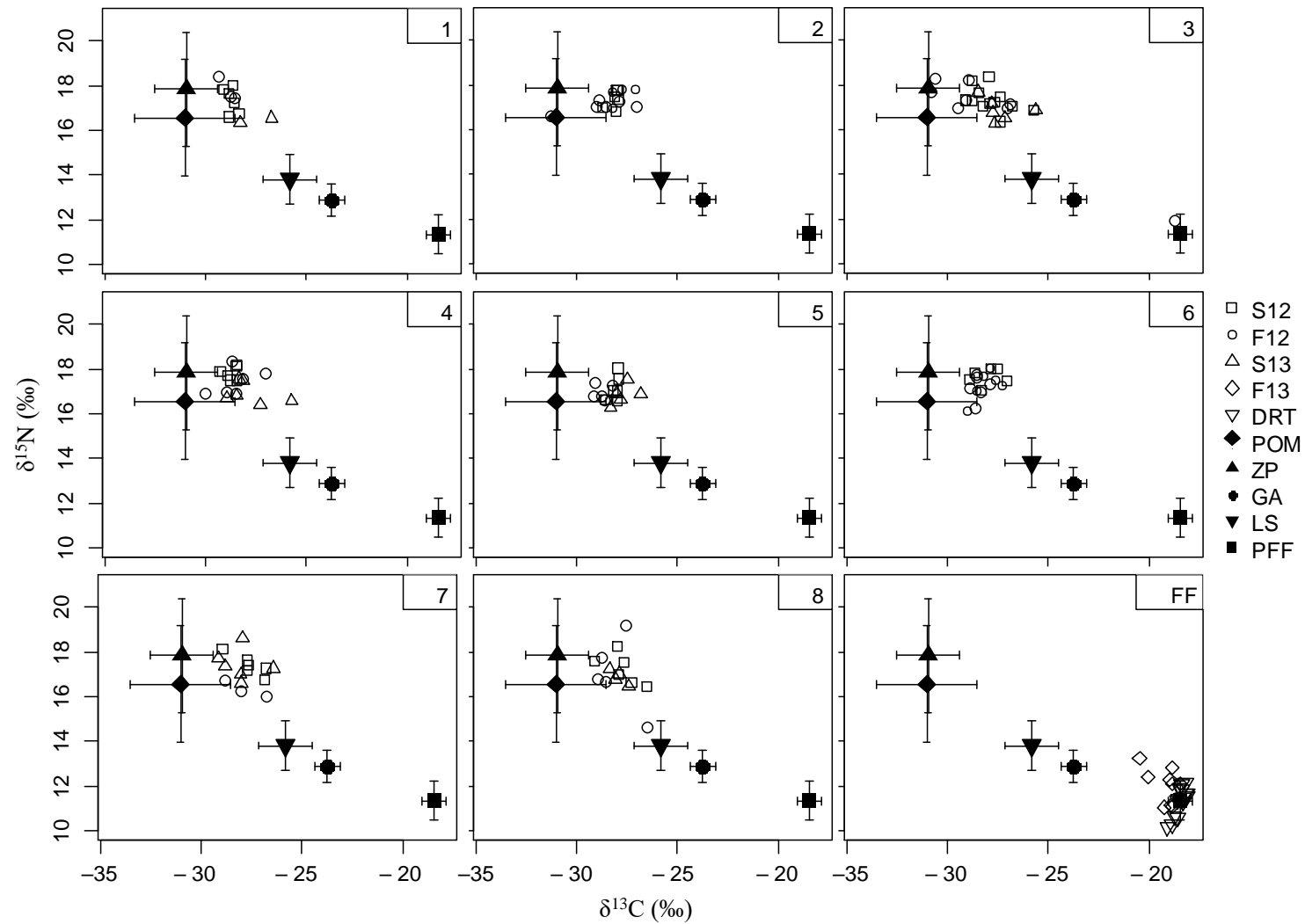


Figure 2.2. Individual site stable isotope biplots of Lake Whitefish (*Coregonus clupeaformis*) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from spring 2012 (S12), fall 2012 (F12), spring 2013 (S13) and fall 2013 (F13). Domestic Rainbow Trout collected at the fish farm facility (DRT) were included for site FF. The mean (\pm SD) of potential dietary sources including POM, zooplankton (ZP), *G. lacustris* (GA), lymnaeid snails (LS), and pelleted fish feed (PFF) were corrected for trophic enrichment and plotted alongside consumers (POM was corrected for two trophic levels as it was a basal resource whereas other sources were primary consumers).

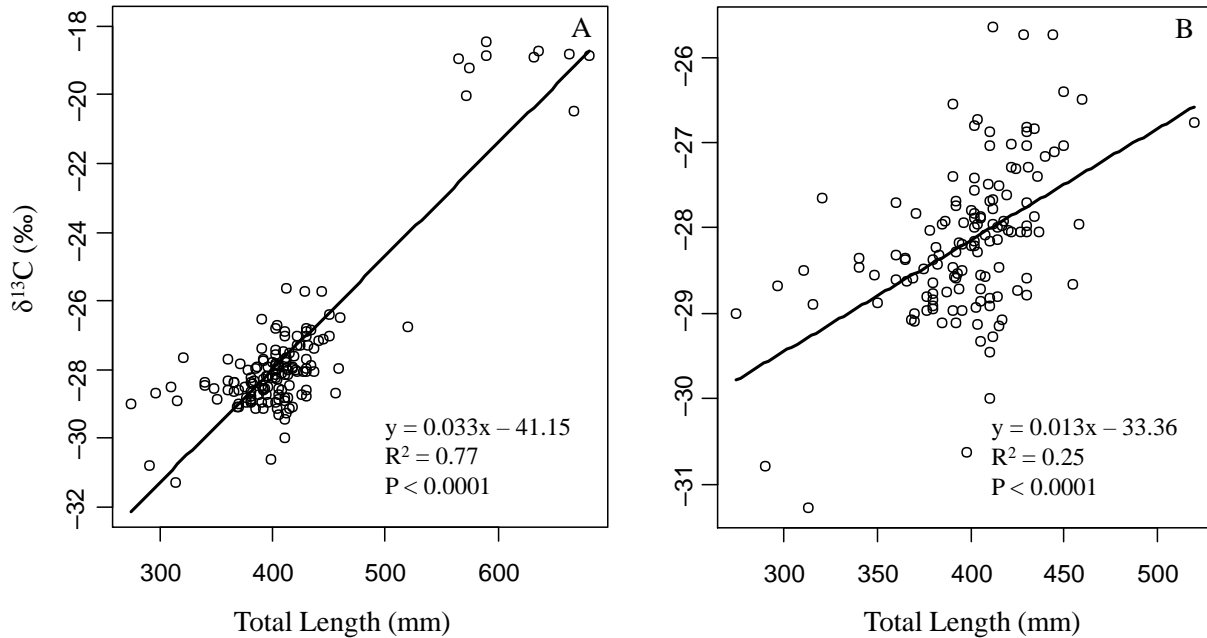


Figure 2.3. The relationship between Lake Whitefish total length (mm) and $\delta^{13}\text{C}$ (model I linear regression). Plot “A” shows data for all Lake Whitefish, while plot “B” has the Lake Whitefish which were subsidizing their diets with pelleted fish feed (AW specialists) removed from the plots. Note the difference in scale on both the X and Y axes between the plots.

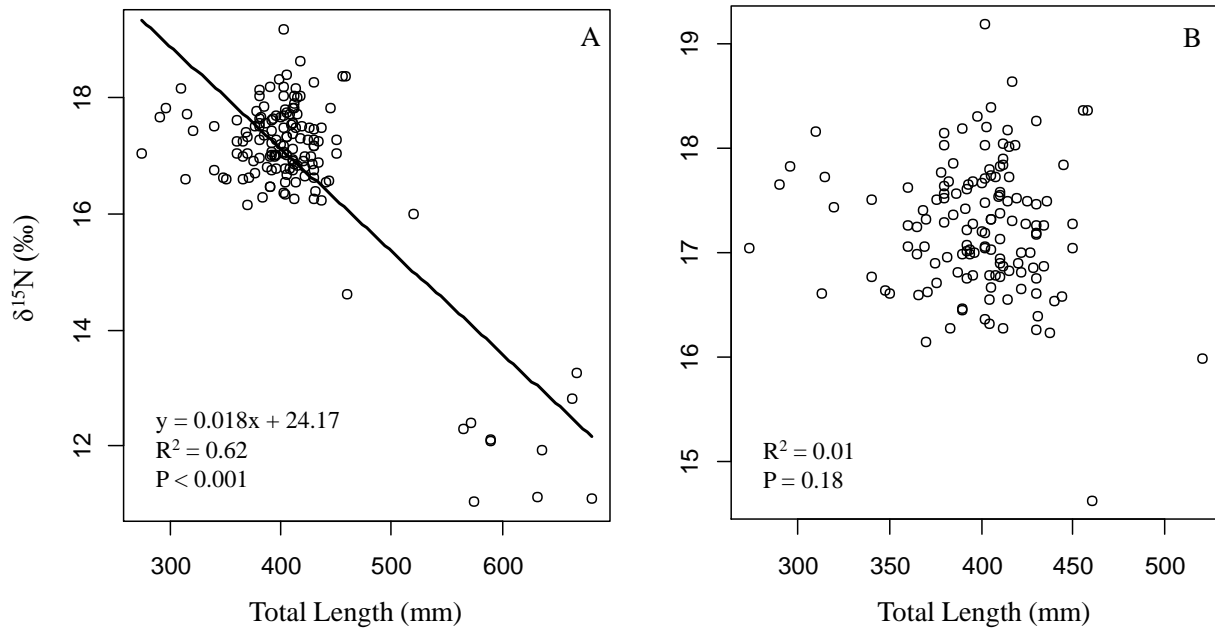


Figure 2.4. The relationship between Lake Whitefish total length (mm) and $\delta^{15}\text{N}$ (model I linear regression). Plot “A” shows data for all Lake Whitefish, while plot “B” has the Lake Whitefish which were subsidizing their diets with pelleted fish feed (AW specialists) removed from the plots. Note the difference in scale on both the X and Y axes between the plots.

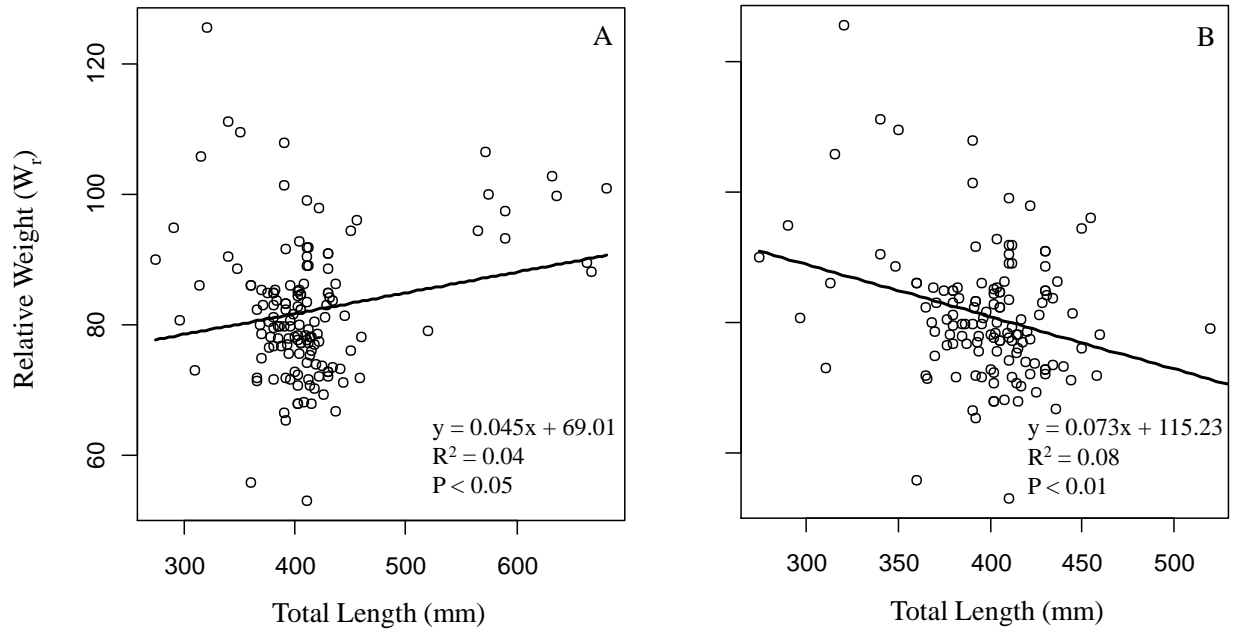


Figure 2.5. The relationship between Lake Whitefish total length (mm) and W_r (model I linear regression). Plot “A” shows data for all Lake Whitefish, while plot “B” has the Lake Whitefish which were subsidizing their diets with pelleted fish feed (AW specialists) removed from the plots.

2.3.3 Mixing Models

Pelagic primary production, represented by bulk zooplankton samples, was the most important carbon source to the diets of Lake Whitefish throughout the study area with a mean contribution of 48.7 ± 13.8 % (range 2.5 – 70.4 %). The second most important source was benthic primary production, represented by combined benthic macroinvertebrates lymnaeid snails and *G. lacustris* with a mean contribution of 33.1 ± 7.1 %, (range 10.9 – 51.9) (Fig. 2.6, Table 2.4). Aquaculture waste, represented by pelleted fish feed, was the least important source to the diets of most Lake Whitefish throughout the study area (mean 12.5 ± 17.9 %, range 4.3 – 83.3 %). However, the high standard deviation seen in the mean contribution of PFF to the diets of Lake Whitefish and the large range of contributions at site 3 in the fall of 2012 (Table 2.4) shows one Lake Whitefish captured at site 3 was a specialist, with 81.2 % of its diet made up of aquaculture waste. This is also evident in the fish captured directly adjacent to the aquaculture

cages (site FF) which have very similar proportional contribution of all three potential sources as the domestic Rainbow Trout collected from within the cage culture facility (Table 2.4). These aquaculture waste specialists with high diet contribution from pelleted fish feed are the reason for the high standard deviation associated with the mean contribution of aquaculture waste.

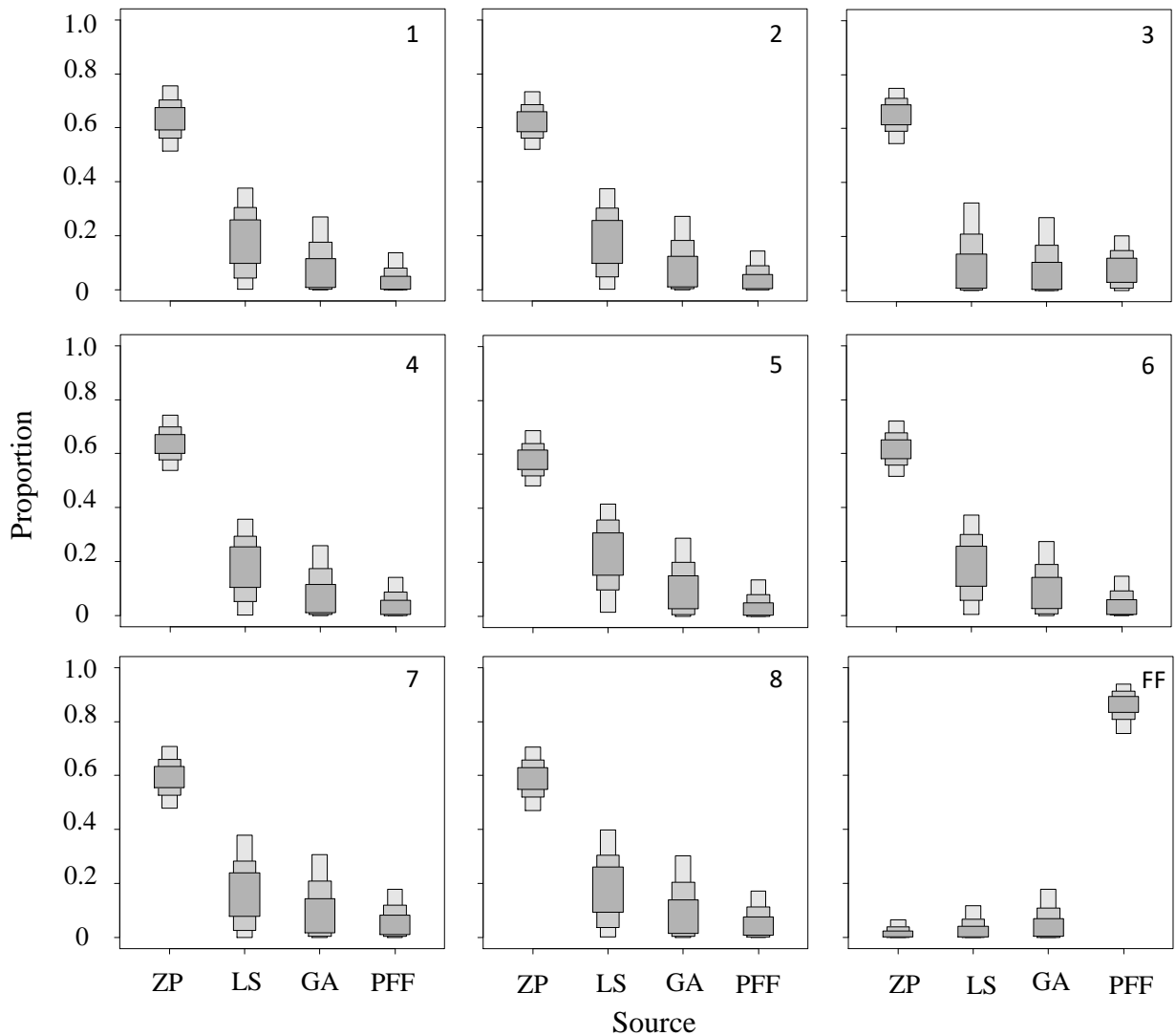


Figure 2.6. Boxplots showing the proportional contribution of each potential carbon source to the diets of all Lake Whitefish (*Coregonus clupeaformis*) at each sample site (site numbers are listed in the top right corner of each plot). The potential dietary sources include pelagic primary production represented by zooplankton (ZP), benthic primary production represented by two aquatic macroinvertebrates, lymnaeid snails (LS) and *G. lacustris* (GA), and aquaculture waste, represented by pelleted fish feed (PFF) from the aquaculture facility. The inner, central and outer portions of the boxplots represent the 50 %, 75 % and 95 % credible intervals of the data.

Two Lake Whitefish collected at site 3 show minor contributions of 16.5 and 17.3 % pelleted fish feed captured in spring 2012 and spring 2013, respectively. Only one other Lake Whitefish that was captured at sites 1 – 8 showed a contribution of aquaculture waste greater than 15 %. This fish was captured at site 4 in spring 2013 and had a diet contribution of 16.8 % from aquaculture waste. All nine Lake Whitefish collected adjacent to the aquaculture cages (site FF) in fall 2013 were calculated to almost entirely rely on aquaculture waste with proportional contributions between 58.7 and 83.3 %, similar to that of the domestic Rainbow Trout (81.8 – 85.8 %).

Figure 2.6 shows the proportional contribution of each source to the diets of Lake Whitefish at each site. Boxplots for sites 1 – 8 look almost identical with pelagic primary production (zooplankton) contributing the majority of the biomass to Lake Whitefish followed in importance by benthic primary production in the form of lymnaeid snails and *G. lacustris*.

2.3.4 Fish Condition by Carbon Source

Of the 144 Lake Whitefish collected in this study, 10 had greater than 50 % contribution of their diet from aquaculture waste, 3 showed diet contribution between 15 and 20 % and the remaining 131 showed little or no contribution from aquaculture waste (Table 2.4). For statistical analysis between the different groups, the above groupings were defined as aquaculture waste specialists (AW specialists), aquaculture waste generalists (AW generalists), and fish with no reliance on aquaculture waste (No AW), respectively. These groupings were used to test for differences between fish with similar diet preferences even if captured at different sites. Total length and weight differed between groups (total length: $F = 183.4$, d.f. = 2, 141, $P < 0.001$; weight: $F = 502$, d.f. = 2, 141, $P < 0.001$), with AW specialists having significantly higher total lengths and weights compared to both the AW generalists and No AW groups (Tukey's tests, $P <$

0.001). Neither total length nor weight differed between the AW generalists or No AW groups (Tukey's test, total length: $P = 0.29$; weight: $P = 0.51$). Relative weight also differed significantly between the groups ($F = 12.7$, d.f. = 2, 141, $P < 0.001$) with the AW specialists having a significantly higher W_r than either the AW generalists (Tukey's test, $P < 0.05$) or the No AW groups (Tukey's test, $P < 0.001$). The W_r of the AW generalists and No AW groups did not differ significantly (Tukey's test, $P = 0.99$).

A total of 14 sexually mature female Lake Whitefish were caught in the study (AW specialist: $n = 4$, AW generalist: $n = 0$, No AW: $n = 10$) (Table 2.5). Both gamete weight and egg number showed significant differences between groups (gonad weight: $F = 50.9$, d.f. = 1, 12, $P < 0.001$; egg number: $F = 33.0$, d.f. = 1, 12, $P < 0.001$), but when standardized for body weight, there was no significant difference between groups (egg number per gram body weight: $F = 1.2$, d.f. = 1, 12, $P < 0.30$). Egg diameter and GSI did not differ significantly between groups (egg diameter: $F = 3.3$, d.f. = 1, 12, $P = 0.09$; GSI: $F = 0.04$, d.f. = 1, 12, $P = 0.85$). A total of 13 sexually mature male Lake Whitefish were caught in the study (AW specialists: $n = 4$, AW generalists: $n = 0$, No AW: $n = 9$). Gonad weight of males differed significantly between groups ($F = 11.9$, d.f. = 1, 11, $P < 0.01$), but when standardized for body weight, the resulting GSI did not differ significantly between groups ($F = 4.1$, d.f. = 1, 11, $P = 0.06$).

The two year means for W_r for each site differed significantly from each other ($F = 4.4$, d.f. = 8, 135, $P < 0.001$), with site mean W_r for site FF significantly different from all sites (Tukey's test, $P < 0.01$) except site 1 (Tukey's test, $P = 0.40$) (Fig. 2.7A). However, after the AW specialists were removed, there were no significant differences between sites ($F = 1.8$, d.f. = 7, 126, $P = 0.09$) (Fig. 2.7B). The seasonal mean relative weight for all Lake Whitefish was found to be significantly different between sampling seasons ($F = 10.7$, d.f. = 3, 140, $P < 0.001$), with

spring 2012 differing significantly from spring 2013 (Tukey’s test $P < 0.05$) and fall 2013 differing from all other seasons (Tukey’s test $P < 0.001$) (Fig. 2.8A). When the fish subsidizing their diets with aquaculture waste feed (AW specialists) were removed, relative weight still differed between seasons ($F = 4.6$, d.f. = 2, 131, $P < 0.05$) with spring 2012 and 2013 differing significantly from one another (Tukey’s test: $P < 0.01$), but neither differed significantly from fall 2012 (Tukey’s test: $P > 0.05$), (Fig. 2.8B). No Lake Whitefish other than AW specialists were captured in the fall of 2013.

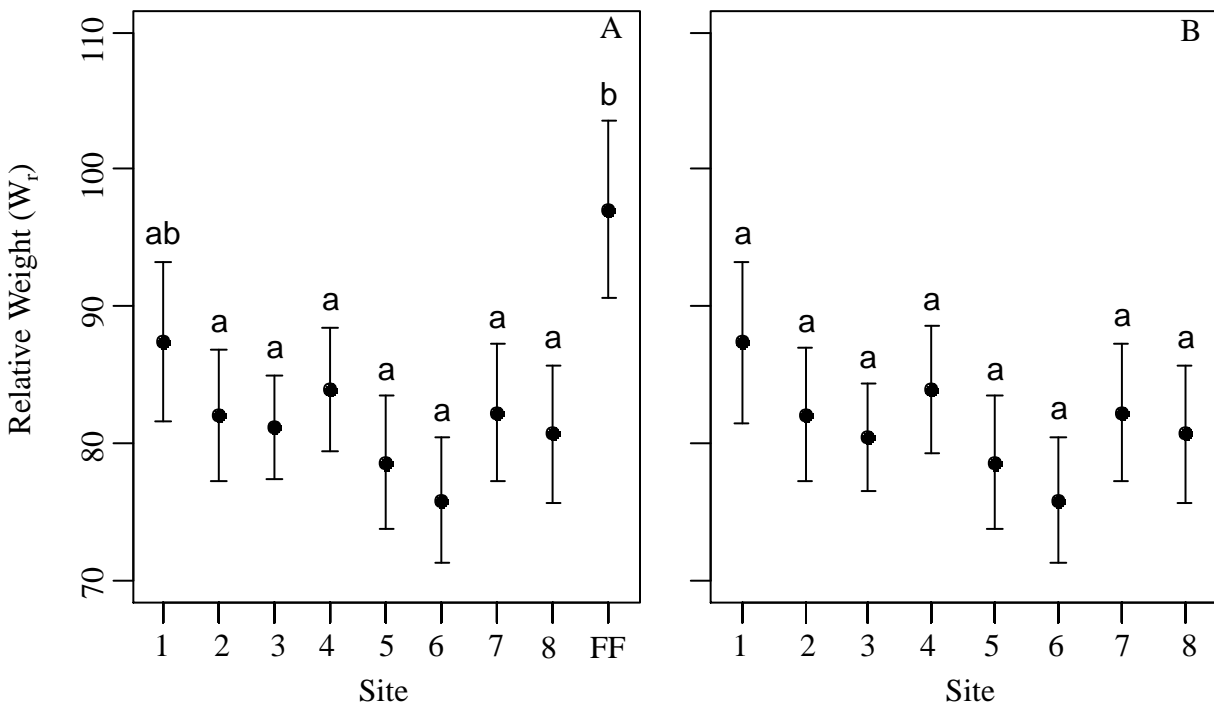


Figure 2.7. Mean relative weight (W_r) for all Lake Whitefish (*Coregonus clupeaformis*) captured at each site throughout 2012 and 2013. Plot “A” includes all Lake Whitefish caught in this study, while plot “B” has those fish which were specialists on aquaculture waste excluded. Error bars represent 95 % confidence intervals for the means. Means with a common letter are not significantly different from one another.

Table 2.5. Size and fecundity of Lake Whitefish caught in Lake Diefenbaker in the fall of 2012 and 2013. Lake Whitefish were separated by sex and those with a greater than 50 % contribution of aquaculture waste to their diets (AW Specialist) were separated from fish with between 15 – 50 % diet contribution from aquaculture waste (AW Generalists) and from fish with < 15 % diet contribution from aquaculture waste (No AW). No sexually mature AW Generalists were caught in this study, so they are not included in the table.

Category	Sex	n	TL (mm)	Fish Wt. (g)	Gonad Wt. (g)	GSI	Egg Diameter (mm)	Egg # (1000s)	Egg #/gram Body Weight
All	F	14	475 ± 97 391 - 681	1228 ± 1045 450 - 3650	147 ± 134 50 - 435	11.8 ± 2.0 8.8 - 15.1	2.23 ± 0.14 2.01 - 2.50	28.1 ± 24.2 10.3 - 91.7	24.1 ± 5.3 15.9 - 32.2
No AW	F	9	419 ± 23 391 - 460	632 ± 143 450 - 900	74 ± 18 50 - 95	11.8 ± 2.0 8.8 - 15.1	2.19 ± 0.11 2.01 - 2.35	15.4 ± 3.2 10.3 - 20.0	25.7 ± 4.7 15.9 - 32.2
47 AW Specialist	F	4	615 ± 52 572 - 681	2719 ± 722 2100 - 3650	331 ± 118 210 - 435	12.0 ± 2.1 10.0 - 14.9	2.33 ± 0.15 2.19 - 2.50	59.8 ± 25.5 36.7 - 91.7	21.7 ± 6.6 16.7 - 31.4
All	M	13	475 ± 91 395 - 636	1131 ± 847 500 - 2900	18 ± 27 2 - 100	1.3 ± 0.8 0.3 - 3.4			
No AW	M	9	421 ± 38 395 - 520	619 ± 222 500 - 1200	6 ± 3 2 - 10	1.0 ± 0.5 0.0 - 1.8			
AW Specialist	M	4	595 ± 30 565 - 636	2281 ± 438 1875 - 2900	46 ± 37 15 - 100	1.9 ± 1.1 0.8 - 3.4			

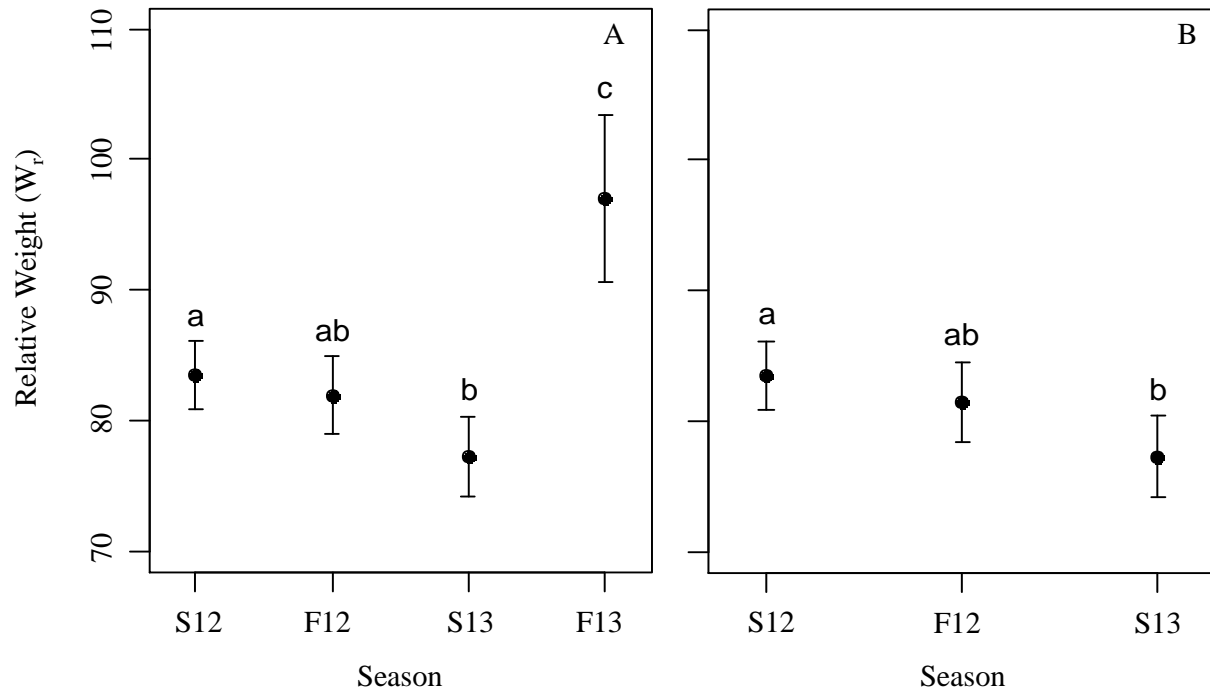


Figure 2.8. Mean relative weight (W_r) for all Lake Whitefish (*Coregonus clupeaformis*) captured during spring 2012 (S12), fall 2012 (F12), spring 2013 (S13) and fall 2013 (F13). Plot “A” includes all Lake Whitefish caught in this study, while plot “B” has those fish which were specialists on aquaculture waste excluded. Error bars represent 95 % confidence intervals for the means and means with a common letter are not significantly different from one another.

2.4 Discussion

2.4.1 Assimilation of Aquaculture Waste

Only Lake Whitefish in the immediate vicinity of the aquaculture facility had isotopic values indicating the use of aquaculture waste as a diet subsidy. All nine Lake Whitefish caught directly adjacent to the fish farm cages had $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values indicating they were specialists on aquaculture waste (AW specialists). Only one other fish, caught at site 3, showed isotope values indicative of a specialist on aquaculture waste. Two fish caught at site 3, one each in spring of 2012 and 2013, showed isotopic values which indicated a small contribution of aquaculture waste (AW generalists). One other fish caught at site 4 within Cactus Bay also had isotopic values indicating it was an AW generalist. In an oligotrophic lake in Norway, Gabrielsen (1999) found Arctic Charr containing pelleted fish feed in their stomach contents up to 1.5 km

from the aquaculture cages, indicating short term movements to and from the cage culture facilities to feed. Most of the Arctic Charr containing pelleted fish feed were believed to be aquaculture specialists, as they were larger and had higher condition factors than other Arctic Charr in the lake (Gabrielsen 1999). A single Lake Whitefish collected at site 3, located 400 metres from the aquaculture cages, had a calculated diet contribution of 81.2 % aquaculture waste, indicating it fed almost exclusively at the aquaculture cages because this value was similar to that of domestic Rainbow Trout. It was the largest fish collected at any site, other than directly adjacent to the cage culture facility and had a relative weight of 100, considerably higher than either the mean value of 85 at site 3 during the fall of 2012 or the study wide mean of 82.

All AW specialists were caught during fall either at site 3 or directly adjacent to the fish farm cages. The turnover time for fish muscle tissue varies with the speed of growth, but represents a long term average of dietary intake (Hesslein et al. 1993; Grey 2006) indicating that these fish had been relying on aquaculture waste for a large portion of their diet for a prolonged period of time (contribution of 58.7 – 83.3 % aquaculture waste). The upper range of the diet contribution for these fish was similar to that of domestic Rainbow Trout, known to be feeding exclusively on pelleted fish feed. Due to the nature of the mixing models in SIAR, all sources included in the model are fit with some diet contribution. In the case of fish with a diet of almost exclusively aquaculture waste such as the domestic Rainbow Trout or AW specialists, the other potential sources still appear to contribute 15 – 20 % to the diet of each fish, likely an over estimation resulting from the inclusion of these sources in the mixing models. In the case of the AW specialists, the lower proportion of their diet from aquaculture waste (i.e., 50 – 75 %), may be the result of the slow turnover time for fish dorsal muscle tissue (Hesslein et al. 1993), or it could mean these fish stray from the aquaculture facility and feed on other sources at certain

times throughout the year. However, these fish likely feed almost exclusively on aquaculture waste, indicated by their large size (total length range of 565 – 681 mm) and high relative weights (88 – 107). In addition to the aquaculture specialists, three fish showed a contribution of aquaculture waste of > 15 % to their diets, as indicated by the SIARsolo mixing models. Two of these fish were from site 3, one from spring 2012 and another in spring 2013, while the other was from site 4 in spring 2013.

There are three potential explanations for these fish referred to as aquaculture waste generalists (AW generalists). They could be fish which opportunistically feed on aquaculture waste while in the area of the fish farm, they could have only recently begun to feed as specialists on aquaculture waste and the slow turnover time of their tissue reflects this recent change in diet, or they could be fish with a stronger reliance on benthic primary production than most other fish. Due to the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the benthic primary production sources falling between the aquaculture waste and pelagic primary production sources, the mixing models cannot differentiate between a high reliance on benthic sources versus a lower reliance on aquaculture waste (Phillips et al. 2014). As a result, this may have caused the model output to have a mid-range contribution from aquaculture waste for these individuals rather than a higher benthic contribution. This is one of the inherent problems associated with the output of mixing models such as SIARsolo when the sources all fall in a relatively linear distribution (Fig. 2.1). All three of these AW generalist fish were captured within Cactus Bay at sites 3 and 4, so it is likely that they had fed on aquaculture waste previously, but either did not specialize on it, or only recently begun to feed specifically on it. If these were fish with higher contributions of benthic resources, fish with similar contributions from aquaculture waste would have likely been detected at sites 7 and 8 at the mouth and inside of Kadla Coulee. These sites are similar to sites

3 and 4 within Cactus Bay, with the exception of the cage culture facility, so they act as reference sites. An interesting test would be to return to sites 7 and 8 and collect Lake Whitefish in those areas now that a cage culture facility is operational in Kadla Coulee to see if there have been any changes to the isotopic values for Lake Whitefish following the establishment of the aquaculture facility there.

2.4.2 Distance from the Aquaculture Cages

Other than the nine Lake Whitefish caught immediately outside of the fish farm cages, only one other AW specialist was caught. This fish was caught at site 3, located 400 metres from the cage culture facility. A total of 26 Lake Whitefish were caught at site 3 throughout the two field seasons. Other than the one AW specialist, only two fish were estimated to have a higher than normal contribution from aquaculture waste. This could mean AW specialists rarely stray far from the cage culture facility throughout the spring and fall when sampling was conducted. Interestingly the one AW specialist caught at site 3 in fall 2012 was a mature male. Brandão et al. (2014) found a species of catfish in a Brazilian reservoir that would feed on aquaculture waste around the cage culture facilities throughout the year, but when this fish reached sexual maturity it would migrate to spawning habitat. A similar situation may be occurring for the Lake Whitefish around the cage culture facility in Lake Diefenbaker during the fall spawning season. Lake Whitefish are known to spawn around water temperatures of 7 – 8 °C (Scott and Crossman, 1973), which occur in November in Lake Diefenbaker when spawning has been observed along shorelines. All three AW generalists were also caught within Cactus Bay as well, two at site 3 and one at site 4, indicating that these fish do not stray far from the aquaculture cages either. However, the consumption of waste feed by wild fish at cage culture facilities distributes the waste over a greater area, which in turn leads to a reduced impact on the benthic sediments

directly below the cage culture facilities (Gondwe et al. 2012; Ramos et al. 2013; Brandão et al. 2014). The Lake Whitefish consuming aquaculture waste in Lake Diefenbaker likely play a role in spreading the nutrients associated with waste feed from the aquaculture facility over a greater area reducing the impacts on the bottom sediments immediately below the cage culture facility.

2.4.3 Fish Condition

The study wide average for relative weight (W_r) for Lake Whitefish was 82 ± 11 , lower than the value of 100 which is defined as the average across the range of the species (Blackwell et al. 2000). Aquaculture waste specialists (site FF mean $W_r = 97 \pm 6$) had higher relative weights than any other group of fish. This indicates a diet consisting of aquaculture waste has a positive impact on body condition in Lake Whitefish, similar to what is seen in other fish species subsidizing their diets with aquaculture waste (Gabrielsen 1999; Fernandez-Jover et al. 2011; Dempster et al. 2011; Brandão et al. 2014).

When comparing the W_r values for individual Lake Whitefish to their total lengths (Fig. 2.5A) there is an apparent increase in W_r as total length increases, but this is mainly driven by the high W_r values at the highest end of the total length spectrum. Once the AW specialists are removed from the relationship, W_r decreases with increasing total length (Fig. 2.5B), although this trend is only slightly significant ($R^2 = 0.08$, $P < 0.01$). This trend is associated with the pattern of decreasing $\delta^{15}\text{N}$ and increasing $\delta^{13}\text{C}$ as total length increases when aquaculture waste specialists are removed from the relationships (Fig. 2.3B and 2.4B). All three relationships appear to be the result of Lake Whitefish switching from pelagic to benthic resource use as they increase in total length. This switch in resource utilization is apparent in the stable isotope values which reflect those of macroinvertebrates at higher total lengths (i.e., enriched $\delta^{13}\text{C}$ and depleted $\delta^{15}\text{N}$) and zooplankton at shorter total lengths (Fig. 2.3 and 2.4). Similar ontogenetic diet shifts

are seen in Lake Whitefish populations in the great lakes where smaller fish feed heavily on zooplankton and switch to benthic macroinvertebrates and mussels at larger sizes (Pothoven and Nalepa 2006). Lake Whitefish feeding on zooplankton have been found to have slower growth than those feeding on larger benthic macroinvertebrates (Ihssen et al. 1981). This may explain why smaller Lake Whitefish have more pelagic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, as they have not yet transitioned onto benthic resources. Benthic resource use is often attributed to increased condition in Lake Whitefish when compared to pelagic resource use (Ihssen et al. 1981; Fagan et al. 2008), the opposite of what is seen in this study (Fig. 2.5B). This could be due to the limited littoral area present in Lake Diefenbaker and the vast amount of pelagic habitat (Sadeghian et al. 2015) that may effectively limit the supply of benthic resources. Lake Diefenbaker experiences annual water level fluctuations of up to seven metres (Sadeghian et al. 2015). Such fluctuations in water level are known to cause a reduction in both macrophyte and benthic macroinvertebrate biomass within the area of the littoral zone influenced by drawdown (McEwen and Butler 2010; Mjelde et al. 2013), further limiting benthic production within Lake Diefenbaker.

Significant differences in gonad weight were detected between the AW specialists and other Lake Whitefish for both males and female fish. Female Lake Whitefish also showed a significant difference between the number of eggs in AW specialists compared to the other fish caught. However, the size of the eggs did not differ between groups and when egg number was standardized per gram of body weight, a significant difference was no longer present. Once standardized for body weight, the GSI was not significantly different between groups. In some species of fish gametogenesis is linked to condition, with increases in fecundity present when condition increases (Kamler 2005). Muir et al. (2014) found that Lake Whitefish with low body condition in the great lakes maintained egg quality by decreasing the total number and size of

eggs. However, in my study, Lake Whitefish in poorer condition did not have significantly smaller eggs. They did have smaller gonads and lower egg counts than the fish with higher W_r that specialized on aquaculture waste, but once standardized per gram of body weight, this relationship did not hold between groups ($P > 0.05$). This may mean that Lake Whitefish in the study area with low W_r are sacrificing body condition to achieve maximum fecundity for their size, while those specializing on aquaculture waste do not have to sacrifice their own condition for high fecundity.

2.4.4 Spatial and Temporal Comparisons

Lake Whitefish specializing in aquaculture waste were only caught during the fall of 2012 and 2013. However, site FF immediately adjacent to the fish farm cages was only sampled in fall 2013 and only one Lake Whitefish caught in fall 2012 at site 3 was an AW specialist. With such a low sample size, it is not possible to say that AW specialists were not present at site 3 at other times of the year, however if they were widespread it is likely that more than one would have been caught at sites 1 – 8. Gabrielsen (1999) found Arctic Charr in a Norwegian lake with stomach contents containing pelleted feed from an aquaculture facility up to 1.5 km from the nearest cages. Studies on Lake Malawi in Africa have found that large schools of wild fish will migrate to cage culture facilities at feeding times on a daily basis, but disperse once the feeding period is over (Gondwe 2009; Gondwe et al. 2011). These habits may also be present in the Lake Whitefish in Lake Diefenbaker and may explain the sole aquaculture specialist fish that was caught 400 metres from the cages, i.e., fish may be migrating to and from the cage culture facility at feeding times.

The only significant differences in W_r between seasons occurred between the spring of 2012 and spring 2013 (Fig. 2.5), with the exception of fall 2013 when only site FF was sampled.

Relative weight is known to change seasonally with most fish having the highest relative weight of the year immediately before spawning (Blackwell et al. 2000). For Lake Whitefish, this means the highest W_r values would be present in the fall, immediately before spawning with lower values present in spring. However, this was not the case in this study, as W_r was higher in spring 2012 than in either fall 2012 or spring 2013. This difference may be related to the later date of ice-off in 2013 compared to 2012. In 2012, ice was off Lake Diefenbaker by late April, but in 2013 ice-off did not occur until May 12th for the majority of the reservoir (personal observation). The longer winter in 2013 may have been responsible for depleting fat reserves due to lower abundance of prey items during late ice as is seen in other species (Woodward and Wilson 1989), resulting in lower condition for Lake Whitefish in Lake Diefenbaker in 2013 when sampling was conducted immediately after ice off.

Mean relative weight at each site had a general decreasing trend from site 1 to 8, with the main channel sites (sites 1, 2, 5 and 6) showing a decrease with distance downstream. However, there were no significant differences between sites 1 to 8. This decreasing trend in relative weight with distance downstream may be the result of differences in habitat type between sites, but is likely just variation in the low sample sizes of Lake Whitefish caught at these sites (Tables 2.1 to 2.3) because no significant differences were present between sites.

2.4.5 Comparison with Other Systems

Aquaculture operations are known to subsidize fish diets in marine and freshwater environments, with an estimated 5 – 30 % of total feed entering the local food web (Beveridge 1984; Otterå et al. 2009). This substantial amount of feed attracts both fish which feed directly on the waste feed, as well as larger predatory fish. In marine systems, changes in abundance and species composition often occur seasonally due to differences in water temperature (Valle et al.

2007). However, some species do remain around the cages year round when conditions are adequate (Dempster et al. 2010). This is also the case in freshwater systems where fish travel away from the cage culture facilities either on a regular or seasonal basis (Gabrielsen 1999; Gondwe et al. 2012; Ramos et al. 2013; Brandão et al. 2014). The movement of fish may be species dependent. For example, Lake Whitefish in Lake Diefenbaker appear to be present at the aquaculture facility all year, albeit in varying abundance (Jeff Sereda, personal communication April 25th, 2012). During the summer when surface temperatures warm, Lake Whitefish are suspected of remaining in the vicinity of the cage culture facility, but moving to the deeper cooler water below the cages. This appears to be the case for Lake Whitefish specializing on aquaculture waste, as their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, as well as, the contribution of aquaculture waste to their diets are almost identical to those of the domestic Rainbow Trout. This indicates the majority of their diet is made up of aquaculture waste year round, even when they are not visible in the surface waters around the cage culture facility. The rate of feeding at the aquaculture facility varies throughout the year and is highest when water temperatures are optimal for growth of domestic trout during spring and fall (Sweeney International 2010). Consequently, the highest volume of aquaculture waste and the corresponding highest density of Lake Whitefish likely occur around the cage culture facility during these periods of peak feeding.

In both marine and freshwater systems, diet subsidies from aquaculture waste are often associated with increased fish condition (Gabrielsen 1999; Ramos et al. 2008; Fernandez-Jover et al. 2011; Dempster et al. 2011; Ramos et al. 2013; Brandão et al. 2014), as seen in the Lake Whitefish that utilize aquaculture waste in Lake Diefenbaker. Increases in fecundity are not as well studied, but some studies (Marshall et al. 1999; Izquierdo et al. 2001) have found that increases in condition and total lipid content can lead to increases in fecundity. Brandão et al.

(2014) found an increased number of eggs, but a corresponding decrease in egg size in fish utilizing aquaculture waste as a diet subsidy in a reservoir in Brazil, similar to the increase egg numbers seen in the Lake Whitefish specializing on aquaculture waste in Lake Diefenbaker. Brandão et al. (2014) did not standardize their egg numbers by the body weight of the fish so it is not known if the egg number per gram body weight differed between net cage and reference sites. In Lake Diefenbaker, when standardized for body weight, the egg number per gram of body weight did not differ between aquaculture waste specialists and those fish not consuming aquaculture waste products.

2.5 Conclusions

Stable isotopes of carbon and nitrogen can be used to identify which Lake Whitefish in Lake Diefenbaker are subsidizing their diets with aquaculture waste from the Wild West Steelhead aquaculture facility. The impact of the aquaculture facility on the diets of Lake Whitefish appears to be restricted to the area immediately surrounding the aquaculture cages and possibly within Cactus Bay to some extent. However, even within Cactus Bay, the diet subsidy is very limited with the majority of the Lake Whitefish caught at site 3, located 400 metres from the cages, estimated as having a negligible influence from the aquaculture waste diet subsidy. Lake Whitefish outside of Cactus Bay were estimated as having no contribution from aquaculture waste. Only Lake Whitefish in the immediate vicinity of the aquaculture cages are utilizing aquaculture waste for the majority of their diets. These aquaculture waste specialists have significantly longer total lengths, greater body weights, and higher relative weights than other Lake Whitefish found elsewhere in the reservoir. Once sexually mature, both male and female aquaculture waste specialists have larger gonads and females have an increased number of eggs compared to Lake Whitefish caught elsewhere in Lake Diefenbaker. However, once standardized

for body weight, the gonadosomatic index and number of eggs per gram of body weight were not significantly different between groups. The main benefit of feeding on aquaculture waste appears to be increased size and relative weight with a corresponding increase in gonad size and egg number in females, but without an increase in the number of eggs per gram of body weight or the gonadosomatic index.

CHAPTER 3. The importance of allochthonous and autochthonous carbon sources to the diets of fish throughout Lake Diefenbaker

3.1 Introduction

3.1.1 Allochthonous and Autochthonous Support of Food Webs

Aquatic food webs are supported through both primary production generated within a waterbody, known as autochthonous production, and also through inputs to the system from primary production outside of the waterbody, known as allochthonous production. The relative importance of allochthonous and autochthonous carbon sources to the diets of aquatic consumers varies widely throughout different aquatic systems based on many factors including the morphometry of the waterbody (Dolson et al. 2009; Solomon et al. 2011), the spatial and temporal availability of each carbon source (DeLong and Thorp 2006; Bašić et al. 2015), and the feeding habits of different consumers (Wallace and Webster 1996; Weidel et al. 2008; Christensen and Moore 2009). Even with all these factors considered, the importance of allochthonous and autochthonous carbon sources to the diets of fish can often be related to the category of waterbody being studied.

3.1.2 Lentic systems

The importance of benthic and pelagic autochthonous primary production to consumers in lake ecosystems has been a topic of considerable discussion with both sources known to be of high importance to lake food webs (Hecky and Hesslein 1995; Vander Zanden and Vadeboncoeur 2002). In more recent years, the importance of allochthonous primary production to higher trophic levels has been a topic of increased study. Allochthonous carbon sources have been found to be more important to consumers in oligotrophic and dystrophic lakes (Del Giorgio and Peters 1993; Carpenter et al. 2005; Soloman et al. 2011), and decrease in importance as lakes increase in trophic status (Del Giorgio and Peters 1993; Cole et al. 2000; Carpenter et al. 2005)

and decrease in dissolved organic carbon concentrations (Solomon et al. 2011; Karlsson et al. 2015). Allochthonous carbon sources are generally of lower nutritional value when compared to autochthonous sources such as phytoplankton (Brett et al. 2012). As a result, consumers such as zooplankton often preferentially use autochthonous resources even when allochthonous carbon is abundant (Cole et al. 2002; Weidel et al. 2008). Other consumers, such as some benthic insects, feed almost entirely on terrestrially derived carbon. These consumers are often important dietary sources for higher trophic levels, such as fish; hence allochthonous terrestrial carbon can be important by indirect means to upper trophic levels (Glaz et al. 2012). Habitat and diet preferences are largely responsible for the importance of autochthonous and allochthonous carbon contributions to the diets of fish, as different fish preferentially feed on benthic, pelagic or terrestrially derived carbon (Weidel et al. 2008; Christensen and Moore 2009).

3.1.3 Lotic systems

The roles and importance of allochthonous and autochthonous carbon sources in river systems has been a topic of debate for decades. It is generally accepted that stream order plays a large role in the importance of organic matter sources for consumers within lotic systems (Finlay 2001). Increasing stream order is often positively correlated to the importance of instream autochthonous primary production (Webster and Meyer 1997). This shift in resource use with increasing stream order is thought to be linked to decreases in stream cover as stream channel size increases (Hansmann and Phinney 1973; Finlay 2001). In stream primary production and autochthonous resource use both increase with stream channel width (Finlay 2001; Delong and Thorp 2006), but allochthonous carbon is still of importance to some specialist consumers even in higher order rivers (Herwig et al. 2007; Jardine et al. 2012). During periods of high flow and flooding, allochthonous resource availability increases (Kendall et al. 2001; Oliveira et al. 2005)

and the use of this resource by consumers often increases until flows subside (Oliveira et al. 2005; Sanchez-Vidal et al. 2013).

3.1.4 Reservoirs

Reservoirs act as an intermediate between lentic and lotic systems with regards to carbon cycling. The relative importance of allochthonous and autochthonous resource use by consumers is largely driven by short water residence time and seasonal differences in flow; similar to what is seen in rivers (Kendall et al. 2001; Perga et al. 2005; Lee et al. 2013). Reservoirs can be divided into three zones with a riverine zone in the upstream reaches, a lacustrine zone in the downstream reaches and a transitional zone in between (Kimmel and Groeger 1984). The availability of allochthonous carbon is highest in the riverine zone and decreases with distance downstream from the tributary inflow as particulates sediment out of the water column (Chen et al. 2009; Kaymak et al. 2015; Lucas et al. 2015). The opposite is true for autochthonous carbon as the increased water clarity in the lacustrine zone results in greater light penetration and increased phytoplankton and macrophyte growth (Kendall et al. 2001; Yip et al. 2015). During periods of high flow, allochthonous carbon is transported further downstream, increasing its availability to consumers in the transitional and lacustrine zones (Perga et al. 2005; Min-Seob et al. 2014) while at the same time the associated increase in turbidity decreases phytoplankton growth and autochthonous carbon availability (Yip et al. 2015). As a result, allochthonous carbon is generally of highest importance to aquatic consumers in the upstream reaches of reservoirs and during periods of high flow, while autochthonous carbon is most important in the lacustrine zone and during periods of low flow in reservoirs (Chen et al. 2005; Kaymak et al. 2015).

3.1.5 Expected Results

Average flows into Lake Diefenbaker are $200 - 300 \text{ m}^3\text{s}^{-1}$ with peak flows generally occurring in June and July when mountain runoff occurs (Hudson and Vandergucht 2015). Water levels fluctuate seasonally up to 7 metres as a result of drawdown throughout the winter months for hydroelectric power generation at Gardiner Dam (Sadeghian et al. 2015). The average water residence time is between 1.5 and 2.5 years with a range of 0.7 to 3.4 years (Costa 2011; Hudson and Vandergucht 2015). As a result of the short water residence time and the high inflow in June and July, it is expected that allochthonous inputs from the watershed will be of importance to the reservoir food web in the upstream reaches of the reservoir (Site 1), but their importance will decrease with distance downstream of the Highway 4 Bridge. Allochthonous support of the food web is expected to be highest during periods of high inflow (summer months) and to be of little importance during periods of lower flow in the spring and fall. Fish act as long term integrators of carbon sources due to the slow turnover time of their muscle tissue (Hesslein et al. 1992). As a result, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fish tissue will reflect the long term averages of items assimilated in their diet. The importance of allochthonous and autochthonous carbon sources to the diets of fish are expected to vary in importance both spatially and between species. Autochthonous sources are expected to be most important to the diets of all fish species, especially in the downstream reaches of the reservoir. Pelagic production is expected to be of greater importance than benthic production to all four fish species due to the physical characteristics of Lake Diefenbaker. The steep shoreline, mean average depth of 22.9 metres, and water level fluctuations of up to 7 metres per year all contribute to a potential higher importance of pelagic primary production to the food web of Lake Diefenbaker.

Fish of the same species found throughout different areas of Lake Diefenbaker may use different carbon sources for their diet. These fish are expected to differ in condition factors, including relative weight and different measures of fecundity due to the difference in the quality of each potential carbon source to lower trophic levels (Brett et al. 2012).

3.2 Methods

3.2.1 Field Sampling

Twelve sites throughout Lake Diefenbaker and one site upstream on the tributary, the South Saskatchewan River, were sampled in spring (May – June), summer (July – September) and fall (October – November) of 2012 and 2013. Eight sites (1, 2, 3, 4, 7, 8, 11 and 12) were located on the main channel of Lake Diefenbaker while four sites were located within embayments (sites 5 and 6 in Cactus Bay and sites 9 and 10 within Kadla Coulee) (Fig. 1.1). Sites were not located equidistantly throughout the reservoir, with the highest density of sites located in the mid reaches of the reservoir near the aquaculture facility due to a parallel study (as described in Chapter 2). Both main channel and embayment sites were used in order to increase sample size and representation of the reservoir. There were no major differences between the embayment and main channel sites as all locations were sampled in similar depths (2 to 15 m) along shoreline areas. This was evident in the homogeneity of data from embayment and main channel sites for all fish species seen in Fig. 3.13.

3.2.1.1 Fish

Four common fish species found in Lake Diefenbaker were used in this study. Lake Whitefish (*Coregonus clupeaformis*), Northern Pike (*Esox lucius*), Walleye (*Sander vitreus*) and White Sucker (*Catostomus commersoni*) were sampled in the spring and fall of 2012 and again in spring 2013. Fish were sampled using monofilament gill nets following the methodology

described for sampling Lake Whitefish in Chapter 2 (Section 2.2.1.1). All fish were measured for total length, fork length, weight, sex, state of maturity, and stomach contents. Sexually mature fish had their fecundity calculated following the methods outlined for Lake Whitefish in Chapter 2 (Section 2.2.1.1) and in Klibansky and Juanes (2008). Boneless, skinless dorsal muscle tissue was collected from the central part of each fish above the lateral line for C and N stable isotope analysis.

3.2.1.2 Aquatic Baseline Samples

The tributary inflow site at Lemsford Ferry along the South Saskatchewan River was sampled in the spring, summer and fall of 2012 and 2013 for particulate organic matter (POM) at a depth of 0.1 metre. As well, unionid mussels were collected in the summer and fall of each year, but were unavailable in spring due to high flows. Particulate organic carbon (POC), particulate nitrogen (PN), zooplankton and aquatic macroinvertebrates (lymnaeid snails and *Gammarus lacustris*) were sampled three times throughout each open water season at each site within Lake Diefenbaker. Methods used for sampling were the same as previously described in Chapter 2 (Section 2.2.1.2). All samples were transported back to the limnology laboratory at the University of Saskatchewan for further processing.

Leaf litter data from the South Saskatchewan River watershed was obtained from Painter et al. (2015). These samples were collected throughout the headwaters of the South Saskatchewan River basin in the Kananaskis region of Alberta Canada. Approximately 98 % of the inflow to Lake Diefenbaker originates in Alberta (SWAS 2012); hence the majority of allochthonous inputs to the system will be from Alberta which makes the leaf litter data from Painter et al. (2015) a good approximation of allochthonous inputs to the reservoir.

3.2.2 Stable Isotope Analysis

Lipid extraction was performed on all zooplankton, macroinvertebrate, and fish tissue samples using a 2:1 chloroform:methanol solution following the protocol outlined in Chapter 2 (Section 2.2.2). All fish tissue, zooplankton, macroinvertebrate, and POM samples were analyzed using the same methodology as outlined in Chapter 2 (Section 2.2.2). Leaf litter samples were weighed to 3.0 mg and packed into tin capsules (Painter et al. 2015).

All stable isotope analyses, with the exception of leaf litter, were performed at the Department of Soil Sciences Stable Isotope Laboratory within the College of Agriculture at the University of Saskatchewan. The methods, equipment and precision of the equipment used are described in Chapter 2 (Section 2.2.2). Leaf litter samples were analyzed at the UC Davis Stable Isotope Facility in the Department of Plant Sciences at the University of California using a PDZ Europa ANCA-GSL elemental analyzer coupled to a PDZ Europa 20-20 CFIR mass spectrometer (Sercon Ltd., Cheshire, UK). Repeat analysis of laboratory standards that were similar in composition to samples had a precision of 0.3 ‰ and 0.2 ‰ for nitrogen and carbon, respectively.

3.2.2.1 Discrimination Factors

Discrimination factors, or trophic enrichment factors (TEFs), were applied to each source to account for isotopic discrimination with increases in trophic level from source to consumer. Due to the difference in feeding ecology for each of the four fish species, the trophic level for each species was determined using FishBase.org (Froese and Pauly 2017). The mean trophic level for each species was calculated based on the average of North American studies for that species as 3.08, 4.22, 4.40 and 2.99 for Lake Whitefish, Northern Pike, Walleye and White Sucker, respectively (Depew et al. 2013). The TEFs used in this study were 0.39 ± 1.3 ‰ for $\delta^{13}\text{C}$ and 3.4 ± 0.98 ‰ for $\delta^{15}\text{N}$ per trophic level for all sources (Post 2002). These TEFs were

multiplied by the difference in trophic level between potential dietary sources and each fish species for input into the mixing models. Due to the use of primary consumers for autochthonous sources (i.e., trophic level 2), the TEF for leaf litter data was increased by an additional trophic level to account for the lower trophic level (i.e., trophic level 1) of this basal resource.

3.2.3 Mixing Models

To determine the proportion of each carbon source to the diet of fish throughout the study area, the Bayesian mixing models SIAR and SIARsolo were used for the population at each site and for each individual fish, respectively (Parnell et al. 2010; R Core Development Team 2013). The methodology used for these mixing models is outlined in Chapter 2 (Section 2.2.3). Similarly, as in Chapter 2, the results from the two benthic primary consumers (Lymnaeid snails and *G. lacustris*) were pooled a posteriori following Phillips et al. (2005), due to a significant difference in the $\delta^{13}\text{C}$ values between these benthic consumers, even though the $\delta^{15}\text{N}$ values did not differ significantly ($\delta^{13}\text{C}$: $T = -4.45$, $p < 0.001$; $\delta^{15}\text{N}$: $T = 1.44$, $p = 0.159$). Leaf litter data from the headwaters of the South Saskatchewan River Basin were used as the source representing allochthonous inputs to the system. Primary consumer samples from each sampling location were averaged over the two year study period prior to input into the mixing models to account for spatial and temporal variations throughout the study (Jardine et al. 2014).

3.2.4 Fish Condition

Relative weight (W_r) was used to determine the condition of each individual fish using the same methods as in Chapter 2 (Equation 2.2; Section 2.2.4). The standard weight (W_s) equation for Lake Whitefish was taken from Rennie and Verdon (2008) and is outlined in Equation 2.3 while Northern Pike, Walleye and White Sucker were taken from Blackwell et al. (2000). The formulas for each of these species are listed below:

Equation 3.1: Northern Pike: $\log_{10}(W_s) = -5.437 + (3.096 \cdot \log_{10} TL)$

Equation 3.2: Walleye: $\log_{10}(W_s) = -5.453 + (3.18 \cdot \log_{10} TL)$

Equation 3.3: White Sucker: $\log_{10}(W_s) = -4.755 + (2.94 \cdot \log_{10} TL)$

For all equations W_s is the standard weight and TL is the fish's total length in mm.

Fecundity was assessed as the total number and size of eggs and standardized for body weight using the same methods as outlined for Lake Whitefish in Chapter 2 (Section 2.2.4).

Fecundity was only calculated during spawning seasons for sexually mature fish which had not yet spawned.

3.2.5 Statistical Analysis

Relationships between each fish species' total length and $\delta^{13}C$, $\delta^{15}N$, and W_r were tested to identify ontogenetic changes in any of the variables (model I linear regression). The relationships between the percent contribution of each carbon source with W_r and each measure of fecundity were tested in order to identify any links between carbon sources and condition factors in each species (model I linear regression). Differences in $\delta^{13}C$, $\delta^{15}N$, total length, W_r and fecundity between sites and seasons were tested to determine any spatial or temporal differences in each of the variables (ANOVAs with Tukey's HSD post hoc tests for pairwise comparisons). Measures of fecundity were tested for differences between spawning seasons for Northern Pike, Walleye and White Sucker (T-tests). All statistical analyses were performed in the statistical software R (R version 3.0.2, R Project for Statistical Computing) with a level of significance of $P < 0.05$.

3.3 Results

3.3.1 Fish Size and Condition

3.3.1.1 Lake Whitefish

A total of 176 Lake Whitefish were caught at sites 1 – 12 (Tables 3.1 and 3.2) in spring 2012 (n = 66), fall 2012 (n = 56) and spring 2013 (n = 54). Total length ranged from 172 – 520 mm (mean = 398 ± 39 mm), while weight ranged from 30 – 1200 g with a mean of 532 ± 147 g. Relative weight ranged from 53 – 126 with a mean of 81 ± 10 . A total of 23 sexually mature Lake Whitefish were caught (Table 3.6), with males (n = 10) having a mean gonad weight of 6 ± 2 g (range 2 – 10 g) and females (n = 13) having a mean gonad weight of 72 ± 18 g (range 50 – 95 g). The mean GSI value for male Lake Whitefish was 0.9 ± 0.4 (range 0.3 – 1.6) and was 11.8 ± 2.4 (range 8.8 – 16.1) for females. The average number of eggs per Lake Whitefish was 15,130 $\pm 4,080$ (range 6,750 – 21,620) but once standardized for body weight, the average number of eggs was 24.8 ± 6.4 eggs/g (range 12.2 – 36.0 eggs/g). Egg size ranged from 1.8 – 2.6 mm and had a mean size of 2.2 ± 0.2 mm. One Lake Whitefish captured in fall 2012 at site 5 was excluded from all analysis as it was deemed to be feeding almost exclusively on aquaculture waste (see chapter 2) and was much larger (TL = 636 mm, weight = 2900 g) and had a higher $\delta^{13}\text{C}$ value (-18.7 ‰) and a lower $\delta^{15}\text{N}$ value (11.9 ‰) than any other Lake Whitefish collected at sites 1 – 12.

3.3.1.2 Northern Pike

A total of 139 Northern Pike were caught at sites 1 – 12 (Tables 3.1 and 3.3) in spring 2012 (n = 59), fall 2012 (n = 28) and spring 2013 (n = 52). Total length ranged from 175 – 1060 mm (mean = 626 ± 176 mm), while weight ranged from 120 – 9160 g with a mean of 2061 ± 2035 g. Relative weight ranged from 43 – 143 with a mean of 91 ± 15 . A total of 60 sexually mature Northern Pike were caught (Table 3.6), with males (n = 38) having a mean gonad weight of 33 ± 33 g (range 5 – 130 g) and females (n = 22) having a mean gonad weight of 651 ± 525 g (range 45 – 1675 g). The mean GSI value for male Northern Pike was 1.7 ± 0.8 (range 0.5 – 3.8)

and was 14.1 ± 5.3 (range 4.1 – 24.1) for female Northern Pike. The average number of eggs per female Northern Pike was $105,915 \pm 91,540$ (range 6,800 – 310,600), but once standardized for body weight, the average number of eggs was 22.6 ± 9.5 eggs/g (range 6.2 – 44.6 eggs/g). Egg size ranged from 2.2 – 3.0 mm and had a mean size of 2.7 ± 0.2 mm.

Table 3.1. Characteristics (mean \pm SD) of Lake Whitefish (LKWH), Northern Pike (NRPK), Walleye (WALL) and White Sucker (WHSC) caught at sites 1 – 12 in spring 2012 (S12), fall 2012 (F12), spring 2013 (S13) and the overall mean for each species. Data for sample size (n), total length (TL), weight (Wt.), relative weight (W_r), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are included.

Species	Date	n	TL (mm)	Wt. (g)	W_r	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
LKWH	S12	66	389 ± 33	499 ± 126	83 ± 12	-28.0 ± 0.7	17.3 ± 0.6
	F12	56	397 ± 51	542 ± 186	81 ± 9	-28.6 ± 0.9	17.1 ± 0.8
	S13	54	412 ± 25	561 ± 114	78 ± 8	-28.0 ± 0.9	17.0 ± 0.6
	Mean	176	398 ± 39	532 ± 147	81 ± 10	-28.2 ± 0.9	17.1 ± 0.7
NRPK	S12	59	644 ± 202	2433 ± 2341	93 ± 15	-27.5 ± 0.7	18.3 ± 1.4
	F12	28	607 ± 162	1764 ± 1923	89 ± 15	-27.8 ± 1.2	18.4 ± 1.3
	S13	52	615 ± 151	1798 ± 1653	92 ± 17	-27.6 ± 0.8	18.7 ± 0.6
	Mean	139	626 ± 176	2061 ± 2035	91 ± 15	-27.6 ± 0.9	18.5 ± 1.2
WALL	S12	70	418 ± 111	783 ± 609	84 ± 18	-27.7 ± 0.8	19.1 ± 1.2
	F12	55	433 ± 116	915 ± 636	87 ± 11	-27.7 ± 0.8	18.9 ± 1.1
	S13	53	447 ± 109	930 ± 772	81 ± 7	-27.5 ± 0.6	18.8 ± 1.3
	Mean	178	432 ± 112	871 ± 671	83 ± 9	-27.7 ± 0.7	19.0 ± 1.2
WHSC	S12	71	435 ± 38	1015 ± 246	99 ± 9	-26.7 ± 0.9	15.8 ± 0.9
	F12	55	443 ± 32	1045 ± 207	97 ± 7	-26.5 ± 1.0	15.8 ± 0.7
	S13	63	441 ± 36	1014 ± 288	95 ± 7	-26.9 ± 1.0	15.9 ± 0.9
	Mean	189	439 ± 35	1023 ± 250	97 ± 8	-26.7 ± 1.0	15.8 ± 0.9

3.3.1.3 Walleye

In total, 178 Walleye were caught at sites 1 – 12 (Tables 3.1 and 3.4) throughout spring 2012 (n = 70), fall 2012 (n = 55) and spring 2013 (n = 53). Total length for all Walleye ranged from 126 – 770 mm (mean = 432 ± 112 mm), while weight ranged from 15 – 4475 g with a mean

of 871 ± 671 g. Relative weight ranged from 42 – 106 with a mean of 83 ± 9 . A total of 42 sexually mature Walleye were caught (Table 3.6), with males ($n = 35$) having a mean gonad weight of 21 ± 11 g (range 5 – 55 g) and females ($n = 7$) having a mean gonad weight of 253 ± 68 g (range 125 – 350 g). The mean GSI value was 2.7 ± 1.0 (range 0.7 – 5.6) for male Walleye and was 18.3 ± 2.7 (range 14.4 – 22.0) for females. The average number of eggs per female was $101,475 \pm 30,955$ (range 44,490 – 144,100) but once standardized for body weight, the average number of eggs was 73.0 ± 13.1 eggs/g (range 51.1 – 87.9 eggs/g). Egg size ranged from 1.7 – 2.3 mm and had a mean size of 1.9 ± 0.2 mm.

3.3.1.4 White Sucker

White Sucker were the most abundant species caught in the study, with a total of 189 captured at sites 1 – 12 (Tables 3.1 and 3.5) throughout spring 2012 ($n = 71$), fall 2012 ($n = 55$) and spring 2013 ($n = 63$). Total length for all White Suckers ranged from 280 – 580 mm (mean = 439 ± 35 mm), while weight ranged from 240 – 2500 g with a mean of 1023 ± 250 g. Relative weight ranged from 72 – 124 with a mean of 97 ± 8 . A total of 101 sexually mature White Sucker were caught (Table 3.6), with males ($n = 53$) having a mean gonad weight of 46 ± 13 g (range 10 – 76 g) and females ($n = 48$) having a mean gonad weight of 174 ± 56 g (range 95 – 420 g). The mean GSI value for male White Suckers was 5.2 ± 1.1 (range 1.2 – 7.1) and was 14.6 ± 2.3 (range 9.0 – 20.7) for females. The average number of eggs per female White Sucker was $42,800 \pm 14,170$ (range 19,552 – 100,620) but once standardized for body weight, the average number of eggs was 36.0 ± 7.0 eggs/g (range 21.8 – 49.7 eggs/g). Egg sized ranged from 2.1 – 2.8 mm and had a mean size of 2.4 ± 0.1 mm.

Table 3.2. Characteristics (mean \pm SD) of Lake Whitefish (*Coregonus clupeaformis*) caught in spring (S12) and fall 2012 (F12) and spring 2013 (S13). Data for sample size (n), total length (TL), weight (Wt.), relative weight (W_r), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are included, or listed as NA when no fish were caught.

Site	Date	n	TL (mm)	Wt. (g)	W_r	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1	S12	0	NA	NA	NA	NA	NA
	F12	6	405 \pm 55	555 \pm 170	80 \pm 8	-28.8 \pm 0.4	17.2 \pm 0.9
	S13	6	421 \pm 25	667 \pm 146	85 \pm 7	-29.4 \pm 0.5	16.4 \pm 0.9
2	S12	0	NA	NA	NA	NA	NA
	F12	1	172	30	70	-27.9	16.0
	S13	0	NA	NA	NA	NA	NA
3	S12	6	366 \pm 19	443 \pm 26	92 \pm 15	-28.7 \pm 0.3	17.4 \pm 0.6
	F12	3	407 \pm 17	537 \pm 32	78 \pm 8	-28.9 \pm 0.4	17.8 \pm 0.5
	S13	2	404 \pm 0	600 \pm 35	89 \pm 5	-27.5 \pm 1.1	16.4 \pm 0.2
4	S12	6	400 \pm 17	538 \pm 121	82 \pm 8	-28.1 \pm 0.3	17.4 \pm 0.4
	F12	6	378 \pm 70	518 \pm 273	87 \pm 5	-28.8 \pm 1.4	17.0 \pm 0.2
	S13	4	410 \pm 27	544 \pm 147	76 \pm 5	-27.8 \pm 0.5	17.6 \pm 0.4
5	S12	12	405 \pm 25	542 \pm 89	80 \pm 8	-27.9 \pm 0.9	17.3 \pm 0.5
	F12	7	396 \pm 44	537 \pm 142	83 \pm 7	-29.0 \pm 1.4	17.5 \pm 0.5
	S13	6	409 \pm 18	553 \pm 85	79 \pm 7	-27.4 \pm 1.0	16.9 \pm 0.5
6	S12	6	357 \pm 42	395 \pm 151	85 \pm 14	-28.7 \pm 0.3	17.8 \pm 0.3
	F12	6	408 \pm 27	648 \pm 167	92 \pm 10	-28.6 \pm 1.0	17.4 \pm 0.6
	S13	6	408 \pm 27	533 \pm 123	76 \pm 6	-27.8 \pm 1.2	16.9 \pm 0.5
7	S12	6	393 \pm 24	498 \pm 75	81 \pm 5	-28.1 \pm 0.2	17.1 \pm 0.6
	F12	5	384 \pm 17	432 \pm 60	75 \pm 4	-28.8 \pm 0.4	17.0 \pm 0.3
	S13	5	403 \pm 26	535 \pm 84	79 \pm 4	-27.7 \pm 0.6	16.8 \pm 0.5
8	S12	6	381 \pm 48	435 \pm 167	75 \pm 10	-28.0 \pm 0.7	17.6 \pm 0.4
	F12	6	402 \pm 22	517 \pm 117	77 \pm 7	-28.5 \pm 0.3	17.2 \pm 0.5
	S13	6	400 \pm 25	500 \pm 86	76 \pm 5	-28.1 \pm 0.6	17.3 \pm 0.7
9	S12	6	388 \pm 44	575 \pm 175	96 \pm 16	-27.6 \pm 0.8	17.4 \pm 0.5
	F12	3	462 \pm 50	850 \pm 312	79 \pm 7	-27.9 \pm 1.0	16.3 \pm 0.4
	S13	6	425 \pm 14	563 \pm 124	70 \pm 10	-28.1 \pm 0.9	17.4 \pm 0.7
10	S12	6	407 \pm 17	573 \pm 110	83 \pm 12	-27.8 \pm 0.8	17.3 \pm 0.7
	F12	5	413 \pm 26	560 \pm 138	76 \pm 5	-28.1 \pm 1.0	17.0 \pm 1.7
	S13	4	392 \pm 20	514 \pm 92	83 \pm 3	-27.9 \pm 0.4	16.9 \pm 0.3
11	S12	6	369 \pm 25	435 \pm 91	85 \pm 8	-27.9 \pm 0.6	17.2 \pm 0.3
	F12	1	410	600	85	-28.4	16.9
	S13	6	428 \pm 39	626 \pm 136	77 \pm 10	-27.4 \pm 0.8	16.9 \pm 0.7
12	S12	6	405 \pm 33	513 \pm 140	75 \pm 17	-27.6 \pm 0.7	16.3 \pm 0.5
	F12	7	391 \pm 26	485 \pm 87	80 \pm 10	-28.6 \pm 0.9	17.1 \pm 0.8
	S13	3	417 \pm 15	517 \pm 52	70 \pm 12	-28.7 \pm 0.7	16.6 \pm 0.5

Table 3.3. Characteristics (mean \pm SD) of Northern Pike (*Esox lucius*) caught in spring (S12) and fall 2012 (F12) and spring 2013 (S13). Data for sample size (n), total length (TL), weight (Wt.), relative weight (W_r), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are included, or listed as NA when no fish were caught.

Site	Date	n	TL (mm)	Wt. (g)	W_r	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1	S12	6	475 \pm 88	643 \pm 317	82 \pm 8	-26.9 \pm 0.9	14.8 \pm 1.8
	F12	3	489 \pm 103	800 \pm 397	101 \pm 37	-27.1 \pm 0.7	15.2 \pm 0.5
	S13	2	707 \pm 323	3160 \pm 3578	93 \pm 8	-28.0 \pm 0.2	18.4 \pm 1.7
2	S12	3	625 \pm 230	2150 \pm 2556	92 \pm 17	-27.7 \pm 0.5	18.2 \pm 0.7
	F12	1	923	5370	97	-27.7 \pm 0.5	20.2
	S13	6	641 \pm 122	1829 \pm 1073	93 \pm 12	-27.5	18.8 \pm 0.6
3	S12	6	682 \pm 222	2700 \pm 2292	92 \pm 16	-27.4 \pm 0.5	18.7 \pm 0.4
	F12	2	495 \pm 92	688 \pm 336	82 \pm 6	-27.1 \pm 0.7	18.2 \pm 0.1
	S13	5	589 \pm 211	1758 \pm 2423	86 \pm 7	-27.5 \pm 0.7	18.6 \pm 0.5
4	S12	6	604 \pm 191	2086 \pm 2512	95 \pm 16	-26.9 \pm 0.7	18.4 \pm 0.6
	F12	1	707	2350	97	-29.0	18.1
	S13	6	501 \pm 51	830 \pm 328	95 \pm 11	-26.4 \pm 0.9	18.5 \pm 0.6
5	S12	3	592 \pm 328	2252 \pm 3289	88 \pm 16	-27.6 \pm 0.2	18.8 \pm 0.8
	F12		NA	NA	NA	NA	NA
	S13	4	693 \pm 226	2894 \pm 3666	87 \pm 14	-27.2 \pm 1.1	17.9 \pm 0.6
6	S12	3	623 \pm 169	1897 \pm 1533	101 \pm 4	-26.9 \pm 2.2	18.5 \pm 1.6
	F12	5	575 \pm 65	1180 \pm 647	86 \pm 14	-26.5 \pm 1.8	18.0 \pm 0.9
	S13	3	622 \pm 83	1475 \pm 781	85 \pm 8	-28.1 \pm 0.5	18.6 \pm 0.6
7	S12	3	564 \pm 241	1628 \pm 2107	87 \pm 10	-27.6 \pm 0.2	18.4 \pm 0.3
	F12	2	905 \pm 131	5325 \pm 2581	98 \pm 5	-28.1 \pm 0.9	18.6 \pm 0.5
	S13	3	512 \pm 71	693 \pm 362	71 \pm 16	-27.5 \pm 0.7	19.1 \pm 0.1
8	S12	7	821 \pm 222	5026 \pm 3330	104 \pm 20	-27.6 \pm 0.4	19.1 \pm 0.7
	F12	2	620 \pm 101	1513 \pm 937	87 \pm 14	-28.1 \pm 1.0	19.3 \pm 0.7
	S13	5	685 \pm 198	2100 \pm 1495	82 \pm 9	-27.4 \pm 0.6	18.9 \pm 0.4
9	S12	7	532 \pm 160	1305 \pm 1691	93 \pm 11	-27.9 \pm 0.3	18.4 \pm 0.9
	F12	1	520	910	97	-27.7	19.3
	S13	2	727 \pm 207	2950 \pm 2263	100 \pm 4	-28.2 \pm 0.1	19.1 \pm 0.1
10	S12	6	730 \pm 211	3423 \pm 2310	95 \pm 26	-28.0 \pm 0.4	19.0 \pm 0.2
	F12	3	762 \pm 249	3730 \pm 3475	96 \pm 6	-28.0 \pm 0.6	18.8 \pm 0.3
	S13	5	635 \pm 144	2005 \pm 1428	97 \pm 17	-27.7 \pm 0.5	18.9 \pm 0.6
11	S12	3	715 \pm 35	2560 \pm 546	101 \pm 10	-27.7 \pm 0.2	18.5 \pm 0.3
	F12	2	480 \pm 31	580 \pm 106	79 \pm 1	-28.0 \pm 0.2	18.8 \pm 0.4
	S13	5	599 \pm 124	1555 \pm 1322	92 \pm 11	-28.0 \pm 0.6	18.8 \pm 0.4
12	S12	6	705 \pm 149	2447 \pm 1721	87 \pm 11	-28.2 \pm 0.2	19.0 \pm 0.4
	F12	6	538 \pm 40	842 \pm 186	80 \pm 12	-28.8 \pm 0.2	19.1 \pm 0.2
	S13	6	592 \pm 102	1688 \pm 894	114 \pm 32	-28.5 \pm 0.5	18.8 \pm 0.4

Table 3.4. Characteristics (mean \pm SD) of Walleye (*Sander vitreus*) caught in spring (S12) and fall 2012 (F12) and spring 2013 (S13). Data for sample size (n), total length (TL), weight (Wt.), relative weight (W_r), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are included, or listed as NA when no fish were caught.

Site	Date	n	TL (mm)	Wt. (g)	W_r	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1	S12	6	355 \pm 142	501 \pm 407	78 \pm 8	-28.0 \pm 1.2	17.4 \pm 1.6
	F12	5	447 \pm 39	827 \pm 176	87 \pm 6	-27.5 \pm 0.8	17.2 \pm 1.8
	S13	6	497 \pm 245	1829 \pm 1867	83 \pm 7	-27.4 \pm 0.7	17.3 \pm 1.9
2	S12	6	419 \pm 99	694 \pm 587	73 \pm 9	-27.7 \pm 0.4	19.4 \pm 0.5
	F12		NA	NA	NA	NA	NA
	S13	1	432	650	77	-27.3	18.1
3	S12	6	399 \pm 104	644 \pm 369	82 \pm 8	-27.9 \pm 0.5	19.1 \pm 0.8
	F12	6	343 \pm 186	580 \pm 698	78 \pm 18	-27.8 \pm 1.9	19.2 \pm 0.4
	S13	5	381 \pm 106	547 \pm 320	81 \pm 5	-27.8 \pm 0.6	19.0 \pm 0.4
4	S12	6	378 \pm 127	570 \pm 509	77 \pm 3	-27.4 \pm 0.6	19.0 \pm 0.4
	F12	6	380 \pm 158	766 \pm 685	91 \pm 9	-27.9 \pm 1.0	19.3 \pm 1.0
	S13	6	450 \pm 92	889 \pm 531	79 \pm 10	-28.0 \pm 0.3	19.4 \pm 0.7
5	S12	6	482 \pm 46	1050 \pm 289	85 \pm 4	-27.1 \pm 1.3	19.1 \pm 1.2
	F12	6	520 \pm 33	1446 \pm 295	94 \pm 6	-27.5 \pm 0.2	18.9 \pm 1.1
	S13	6	519 \pm 87	1204 \pm 635	75 \pm 4	-27.1 \pm 0.9	19.7 \pm 0.8
6	S12	6	495 \pm 140	1407 \pm 1360	90 \pm 11	-28.0 \pm 0.2	19.8 \pm 0.8
	F12	6	410 \pm 155	860 \pm 730	88 \pm 9	-27.5 \pm 0.5	18.9 \pm 0.6
	S13	2	359 \pm 237	835 \pm 1117	87 \pm 22	-27.0 \pm 1.2	16.7 \pm 3.9
7	S12	4	448 \pm 18	808 \pm 103	85 \pm 5	-28.0 \pm 0.1	19.4 \pm 0.1
	F12	6	469 \pm 136	1233 \pm 1279	85 \pm 12	-27.6 \pm 0.9	19.3 \pm 1.0
	S13	6	422 \pm 48	654 \pm 222	81 \pm 4	-27.8 \pm 0.3	19.2 \pm 0.7
8	S12	6	416 \pm 124	837 \pm 573	88 \pm 8	-28.0 \pm 0.6	19.2 \pm 0.8
	F12	4	478 \pm 29	931 \pm 221	79 \pm 11	-27.7 \pm 0.3	18.7 \pm 1.1
	S13	6	415 \pm 56	667 \pm 301	85 \pm 6	-27.5 \pm 0.3	19.2 \pm 0.7
9	S12	6	334 \pm 100	390 \pm 337	81 \pm 7	-28.1 \pm 0.6	19.8 \pm 0.6
	F12	4	501 \pm 33	1138 \pm 284	83 \pm 4	-28.0 \pm 0.2	19.5 \pm 0.7
	S13	6	451 \pm 39	808 \pm 217	82 \pm 6	-27.4 \pm 0.8	19.4 \pm 0.5
10	S12	6	463 \pm 98	1025 \pm 449	105 \pm 56	-27.5 \pm 0.5	19.1 \pm 1.5
	F12	6	384 \pm 65	564 \pm 333	87 \pm 9	-27.7 \pm 0.4	18.9 \pm 0.8
	S13	6	452 \pm 23	867 \pm 145	88 \pm 5	-27.5 \pm 0.3	18.2 \pm 0.9
11	S12	4	508 \pm 88	1173 \pm 565	80 \pm 8	-27.5 \pm 0.1	19.5 \pm 0.6
	F12		NA	NA	NA	NA	NA
	S13	2	493 \pm 74	1013 \pm 477	76 \pm 1	-27.6 \pm 0.2	18.4 \pm 1.3
12	S12	6	373 \pm 99	519 \pm 438	81 \pm 3	-28.4 \pm 0.5	19.8 \pm 0.3
	F12	6	436 \pm 48	867 \pm 340	95 \pm 6	-28.2 \pm 0.2	19.1 \pm 0.6
	S13	1	432	675	80	-27.7	19.5

Table 3.5. Characteristics (mean \pm SD) of White Sucker (*Catostomus commersoni*) caught in spring (S12) and fall 2012 (F12) and spring 2013 (S13). Data for sample size (n), total length (TL), weight (Wt.), relative weight (W_r), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are included, or listed as NA when no fish were caught.

Site	Date	n	TL (mm)	Wt. (g)	W_r	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1	S12	6	433 \pm 77	990 \pm 372	93 \pm 8	-27.3 \pm 1.1	15.0 \pm 1.3
	F12	1	335	425	91	-28.1	13.5
	S13	6	433 \pm 44	954 \pm 265	94 \pm 5	-28.2 \pm 0.9	14.7 \pm 1.4
2	S12	6	444 \pm 33	1042 \pm 282	96 \pm 15	-26.8 \pm 0.9	16.1 \pm 1.0
	F12		NA	NA	NA	NA	NA
	S13	6	425 \pm 22	888 \pm 152	94 \pm 5	-27.2 \pm 0.8	16.6 \pm 1.5
3	S12	6	431 \pm 35	983 \pm 272	98 \pm 6	-26.7 \pm 1.0	16.4 \pm 1.3
	F12	6	453 \pm 33	1121 \pm 158	99 \pm 10	-26.6 \pm 0.4	15.9 \pm 0.7
	S13	6	472 \pm 59	1317 \pm 612	98 \pm 10	-25.9 \pm 1.1	16.1 \pm 0.6
4	S12	6	435 \pm 28	1039 \pm 196	103 \pm 8	-26.5 \pm 1.0	15.9 \pm 0.8
	F12	6	440 \pm 13	1050 \pm 71	101 \pm 5	-25.4 \pm 1.0	15.6 \pm 0.5
	S13	6	429 \pm 20	875 \pm 128	90 \pm 7	-26.3 \pm 1.1	16.1 \pm 0.7
5	S12	5	438 \pm 15	1001 \pm 72	98 \pm 7	-26.9 \pm 0.7	15.9 \pm 1.0
	F12	6	438 \pm 35	1025 \pm 206	99 \pm 8	-26.5 \pm 1.3	15.9 \pm 1.1
	S13	6	466 \pm 46	1183 \pm 327	94 \pm 9	-26.1 \pm 0.5	15.5 \pm 0.5
6	S12	6	417 \pm 21	983 \pm 146	111 \pm 8	-26.7 \pm 0.6	15.9 \pm 0.6
	F12	6	451 \pm 42	1104 \pm 294	97 \pm 6	-26.2 \pm 0.9	15.6 \pm 0.6
	S13	6	456 \pm 19	1106 \pm 132	95 \pm 3	-26.9 \pm 0.6	15.5 \pm 0.6
7	S12	6	419 \pm 25	893 \pm 184	98 \pm 5	-26.5 \pm 0.8	15.5 \pm 0.5
	F12	5	437 \pm 8	955 \pm 54	93 \pm 4	-26.0 \pm 0.7	16.0 \pm 0.4
	S13	6	427 \pm 15	942 \pm 131	98 \pm 6	-27.9 \pm 0.5	16.7 \pm 0.7
8	S12	6	438 \pm 61	1057 \pm 434	97 \pm 6	-26.0 \pm 1.0	15.5 \pm 1.0
	F12	6	460 \pm 29	1100 \pm 216	92 \pm 6	-25.6 \pm 0.9	15.6 \pm 0.7
	S13	6	436 \pm 30	932 \pm 231	91 \pm 5	-26.3 \pm 0.3	15.7 \pm 0.6
9	S12	6	436 \pm 40	970 \pm 300	94 \pm 9	-26.8 \pm 1.4	16.4 \pm 0.8
	F12	4	475 \pm 26	1221 \pm 190	94 \pm 6	-26.2 \pm 0.6	16.0 \pm 0.7
	S13	2	400 \pm 1	738 \pm 18	94 \pm 2	-26.2 \pm 1.5	15.5 \pm 0.2
10	S12	6	420 \pm 22	890 \pm 160	97 \pm 9	-27.0 \pm 1.0	15.9 \pm 0.3
	F12	4	431 \pm 11	944 \pm 66	96 \pm 3	-26.9 \pm 0.5	16.1 \pm 0.5
	S13	1	430	875	90	-28.0	16.9
11	S12	6	456 \pm 24	1220 \pm 141	106 \pm 11	-26.3 \pm 0.8	15.1 \pm 0.5
	F12	7	425 \pm 31	911 \pm 180	96 \pm 6	-27.5 \pm 0.5	16.4 \pm 0.5
	S13	6	428 \pm 29	994 \pm 205	103 \pm 4	-26.9 \pm 0.7	15.9 \pm 0.4
12	S12	6	454 \pm 34	1107 \pm 171	97 \pm 8	-26.5 \pm 0.7	16.0 \pm 0.3
	F12	4	455 \pm 13	1213 \pm 118	105 \pm 4	-27.5 \pm 0.6	15.3 \pm 0.6
	S13	6	452 \pm 33	1063 \pm 232	94 \pm 5	-27.3 \pm 0.6	15.8 \pm 0.5

Table 3.6. Characteristics and fecundity data (mean \pm SD) for all sexually mature Lake Whitefish (LKWH), Northern Pike (NRPK), Walleye (WALL) and White Sucker (WHSC) caught at sites 1 – 12 in spring 2012 (S12), fall 2012 (F12), spring 2013 (S13).

Species	Date	Sex	n	TL (mm)	Fish Wt. (g)	Gonad Wt.(g)	GSI	Egg Diameter (mm)	Egg # (1000s)	Egg #/gram Body wt.
LKWH	F12	F	13	414 \pm 22	618 \pm 127	72 \pm 18	11.8 \pm 2.4	2.2 \pm 0.2	15 \pm 4	24.8 \pm 6.4
	F12	M	10	421 \pm 31	615 \pm 182	6 \pm 2	0.9 \pm 0.4			
NRPK	S12	F	10	925 \pm 73	6371 \pm 1595	1125 \pm 305	17.9 \pm 3.8	2.7 \pm 0.2	186 \pm 66	29.2 \pm 8.3
	S13	F	12	638 \pm 112	1958 \pm 1404	256 \pm 275	11.0 \pm 4.2	2.7 \pm 0.1	39 \pm 41	17.0 \pm 6.4
	Mean	F	22	769 \pm 174	3964 \pm 2680	651 \pm 525	14.1 \pm 5.3	2.7 \pm 0.2	106 \pm 92	22.6 \pm 9.5
	S12	M	12	697 \pm 106	2429 \pm 1074	46 \pm 35	1.8 \pm 0.9			
	S13	M	26	594 \pm 151	1516 \pm 1274	26 \pm 32	1.6 \pm 0.8			
	Mean	M	38	626 \pm 145	1804 \pm 1274	33 \pm 33	1.7 \pm 0.8			
75 WALL	S12	F	5	506 \pm 32	1214 \pm 341	250 \pm 83	18.2 \pm 2.3	2.0 \pm 0.2	98 \pm 37	70.5 \pm 13.9
	S13	F	2	528 \pm 3	1425 \pm 283	260 \pm 14	18.7 \pm 4.7	1.8 \pm 0.1	111 \pm 5	79.2 \pm 12.2
	Mean	F	7	511 \pm 30	1261 \pm 326	253 \pm 68	18.3 \pm 2.7	1.9 \pm 0.2	101 \pm 31	73.0 \pm 13.1
	S12	M	9	469 \pm 66	942 \pm 406	21 \pm 8	2.6 \pm 0.9			
	S13	M	26	439 \pm 51	744 \pm 246	21 \pm 12	2.7 \pm 1.0			
	Mean	M	35	441 \pm 48	764 \pm 235	21 \pm 11	2.7 \pm 1.0			
WHSC	S12	F	23	445 \pm 29	1140 \pm 221	161 \pm 47	13.9 \pm 2.1	2.4 \pm 0.1	39 \pm 12	33.6 \pm 6.4
	S13	F	25	467 \pm 36	1220 \pm 320	186 \pm 62	15.2 \pm 2.3	2.4 \pm 0.1	47 \pm 15	38.2 \pm 6.9
	Mean	F	48	421 \pm 22	881 \pm 148	174 \pm 56	14.6 \pm 2.3	2.4 \pm 0.1	43 \pm 14	36.0 \pm 7.0
	S12	M	22	421 \pm 28	921 \pm 179	48 \pm 12	5.2 \pm 0.9			
	S13	M	31	421 \pm 18	853 \pm 116	45 \pm 14	5.2 \pm 1.3			
	Mean	M	53	421 \pm 22	881 \pm 148	46 \pm 13	5.2 \pm 1.1			

3.3.2 Stable Isotope Analysis

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each fish species and their potential dietary sources can be seen in Table 3.1 and in Fig. 3.1, 3.2, 3.3 and 3.4 for Lake Whitefish, Northern Pike, Walleye and White Sucker, respectively. Fig. 3.5 shows $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each species of fish at each site while the site and seasonal mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for Lake Whitefish, Northern Pike, Walleye and White Sucker can be seen in Tables 3.2, 3.3, 3.4, and 3.5. The $\delta^{13}\text{C}$ values for Lake Whitefish were the lowest of all four fish species and ranged from -31.3 to -25.6 ‰ with a mean of -28.2 ± 0.9 ‰. Lake Whitefish $\delta^{15}\text{N}$ values were lower than both Northern Pike and Walleye, but higher than White Sucker, ranging from 14.6 to 19.2 ‰ with a mean of 17.1 ± 0.7 ‰. Northern Pike had $\delta^{13}\text{C}$ values slightly higher compared to those of Lake Whitefish ranging from -29.1 to -23.9 ‰ (mean -27.6 ± 0.9 ‰) and $\delta^{15}\text{N}$ values ranging from 11.3 to 20.2 ‰ (mean 18.5 ± 1.2 ‰), considerably higher than those of Lake Whitefish and White Sucker, but slightly lower than those of Walleye. Walleye $\delta^{13}\text{C}$ values were similar to Northern Pike and slightly higher compared to those of Lake Whitefish and ranged from -30.1 to -24.4 ‰ (mean -27.7 ± 0.7 ‰). Walleye had the highest $\delta^{15}\text{N}$ values of any fish species, even higher than Northern Pike, ranging from 13.9 to 20.9 ‰ (mean 19.0 ± 1.1 ‰), reflecting both the high trophic level they occupy as well as their increased lifespan when compared to Northern Pike. White Sucker had the highest $\delta^{13}\text{C}$ values ranging from -29.0 to -24.1 ‰ with a mean of -26.7 ± 1.0 ‰. White Sucker $\delta^{15}\text{N}$ values ranged from 12.4 to 19.6 ‰ with a mean of 15.8 ± 0.9 ‰, which were the lowest of any fish species, considerably lower than those of Northern Pike, Walleye and even Lake Whitefish.

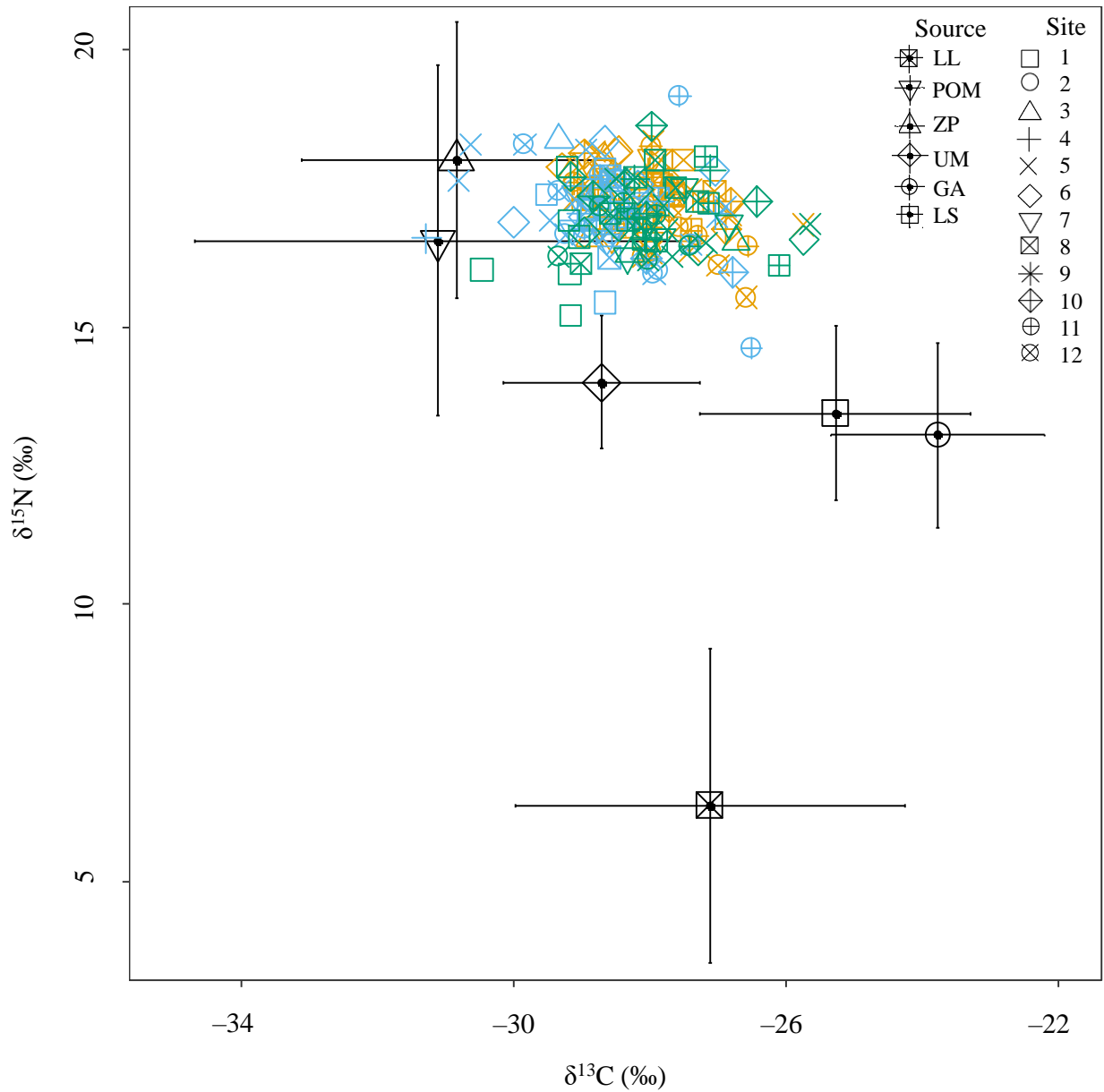


Figure 3.1. Stable isotope biplot for Lake Whitefish caught at sites 1 – 12 in spring 2012 (yellow), fall 2012 (blue) and spring 2013 (green). Potential dietary sources were adjusted for trophic level of each species and are indicated by black symbols with error bars representing the standard deviation. These include pelagic autochthonous sources (zooplankton (ZP) and particulate organic matter (POM)), benthic autochthonous sources (lymnaeid snails (LS) and *Gammarus lacustris* (GA)), unionid mussels from the tributary inflow (UM) and an allochthonous source (leaf litter (LL)).

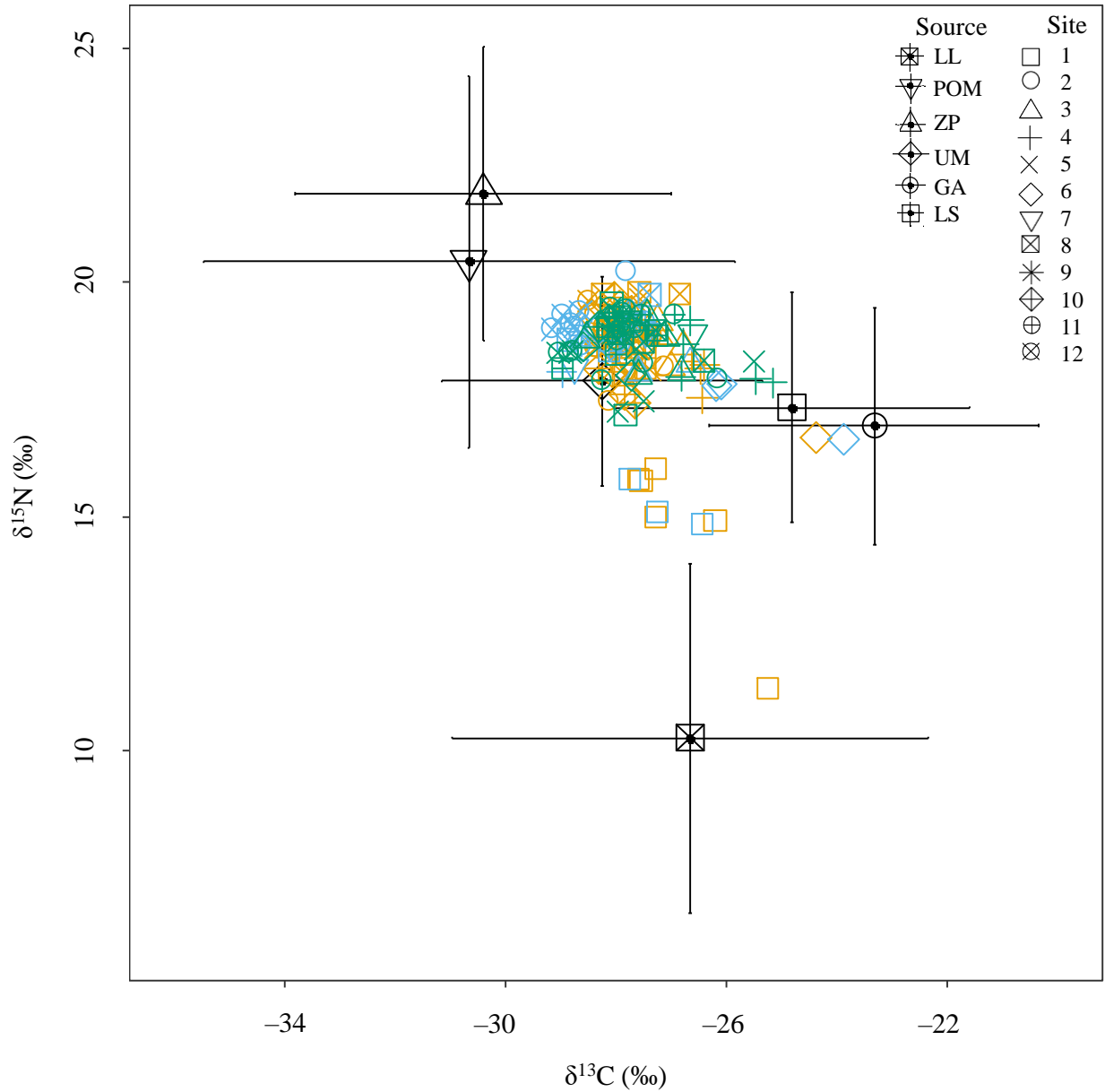


Figure 3.2. Stable isotope biplot for Northern Pike caught at sites 1 – 12 in spring 2012 (yellow), fall 2012 (blue) and spring 2013 (green). Potential dietary sources were adjusted for trophic level of each species and are indicated by black symbols with error bars representing the standard deviation. These include pelagic autochthonous sources (zooplankton (ZP) and particulate organic matter (POM)), benthic autochthonous sources (lymnaeid snails (LS) and *Gammarus lacustris* (GA)), unionid mussels from the tributary inflow (UM) and an allochthonous source (leaf litter (LL)).

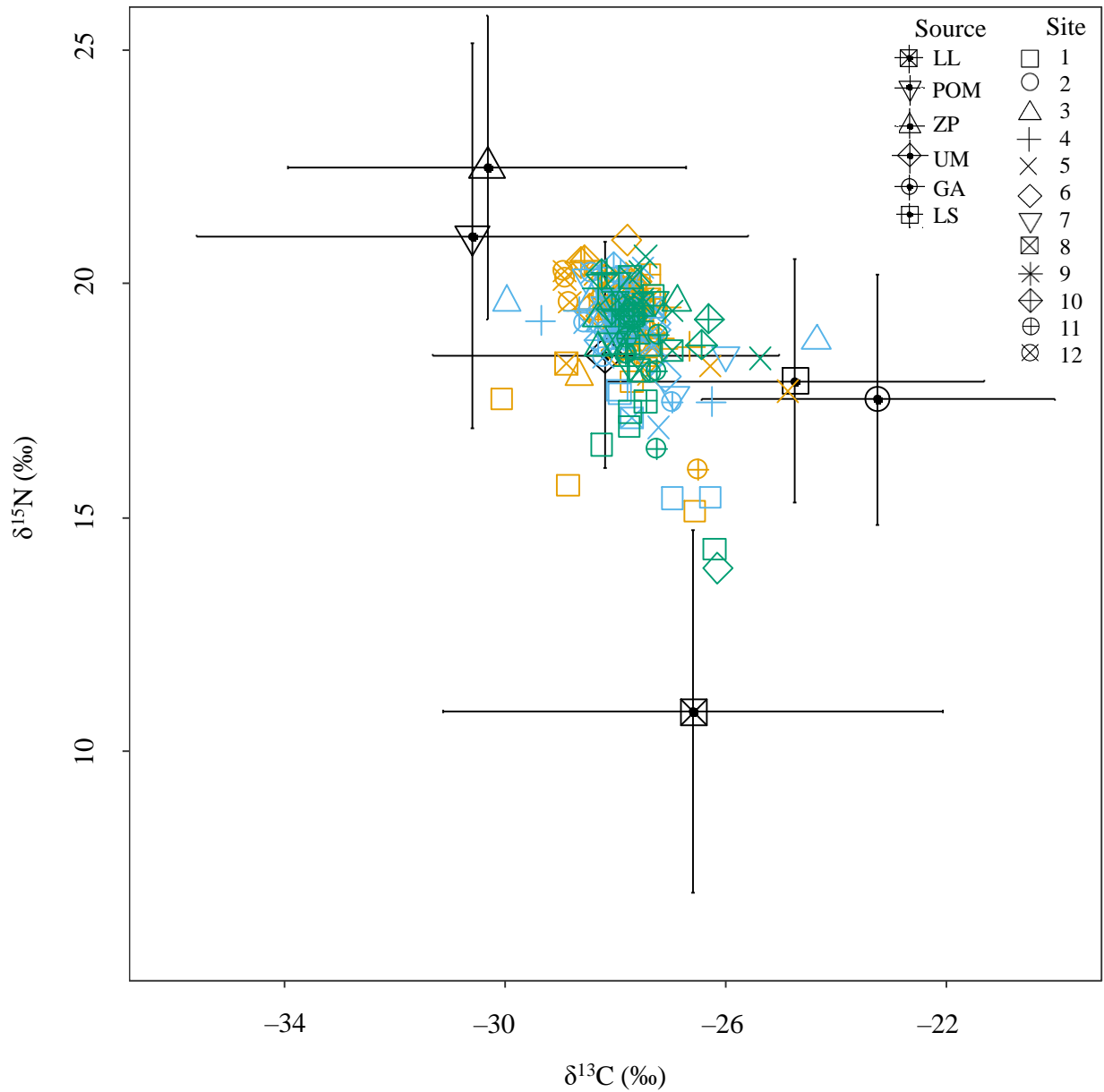


Figure 3.3. Stable isotope biplot for Walleye caught at sites 1 – 12 in spring 2012 (yellow), fall 2012 (blue) and spring 2013 (green). Potential dietary sources were adjusted for trophic level of each species and are indicated by black symbols with error bars representing the standard deviation. These include pelagic autochthonous sources (zooplankton (ZP) and particulate organic matter (POM)), benthic autochthonous sources (lymnaeid snails (LS) and *Gammarus lacustris* (GA)), unionid mussels from the tributary inflow (UM) and an allochthonous source (leaf litter (LL)).

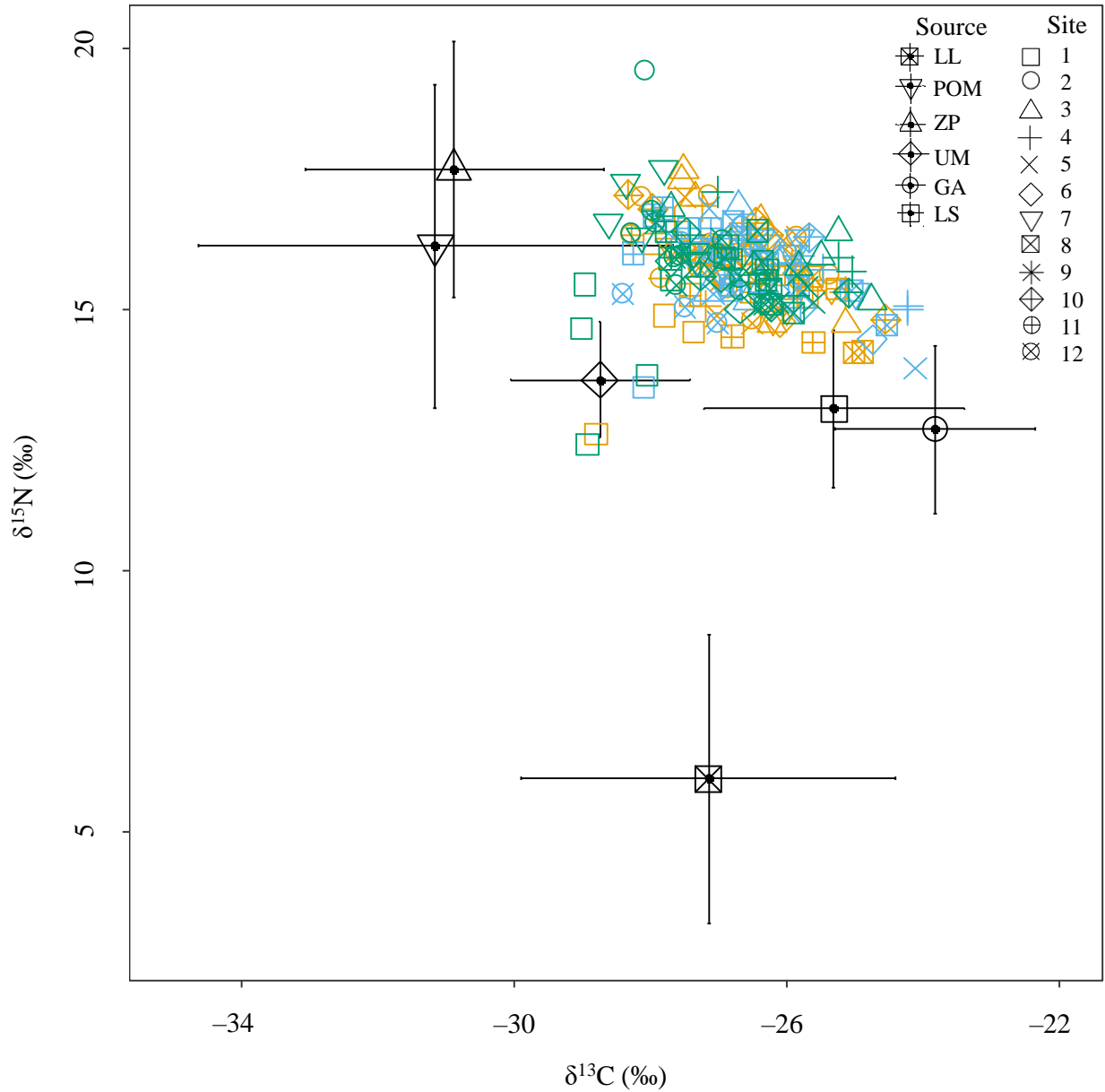


Figure 3.4. Stable isotope biplot for White Sucker caught at sites 1 – 12 in spring 2012 (yellow), fall 2012 (blue) and spring 2013 (green). Potential dietary sources were adjusted for trophic level of each species and are indicated by black symbols with error bars representing the standard deviation. These include pelagic autochthonous sources (zooplankton (ZP) and particulate organic matter (POM)), benthic autochthonous sources (lymnaeid snails (LS) and *Gammarus lacustris* (GA)), unionid mussels from the tributary inflow (UM) and an allochthonous source (leaf litter (LL)).

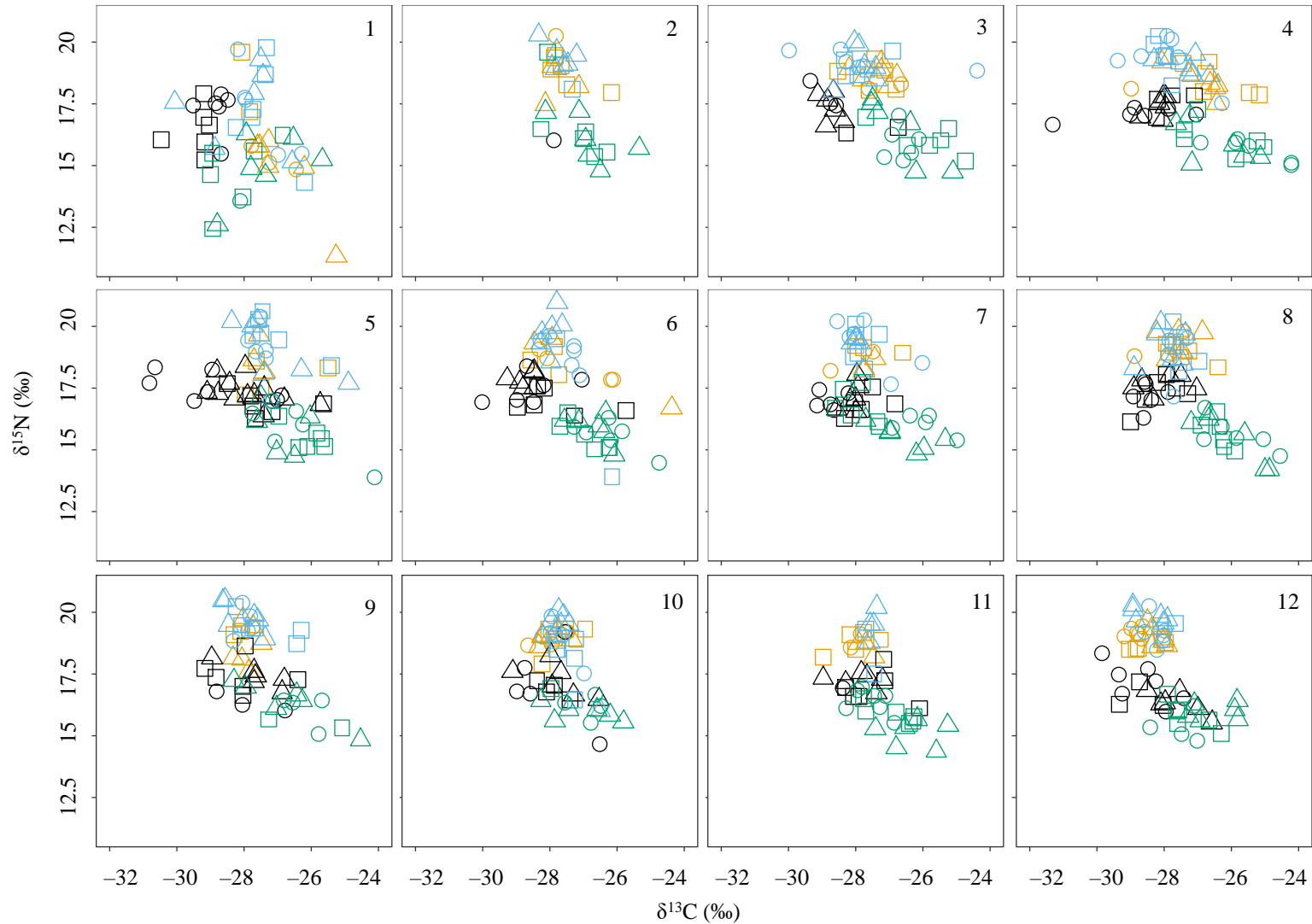


Figure 3.5. Stable isotope biplots for Lake Whitefish (black), Northern Pike (yellow), Walleye (blue) and White Sucker (green) caught in spring 2012 (triangle), fall 2012 (circle) and spring 2013 (square) at each of the twelve sampling sites located throughout Lake Diefenbaker. The number in the top right corner of each plot corresponds to the site number.

Particulate organic matter (POM) samples had the widest range of $\delta^{13}\text{C}$ values from -40.1 to -20.8 ‰ with a mean of -31.0 ± 2.3 ‰. The $\delta^{15}\text{N}$ values of POM ranged from 1.3 to 14.9 ‰ with a mean of 9.2 ± 2.3 ‰. Zooplankton samples had a narrower range and were slightly depleted in ^{13}C ($\delta^{13}\text{C}$ range -35.7 to -28.1 ‰, mean -31.3 ± 1.8 ‰) and enriched in ^{15}N ($\delta^{15}\text{N}$ range 10.3 to 21.3 ‰, mean 14.3 ± 2.2 ‰) when compared to POM samples. Zooplankton had the lowest $\delta^{13}\text{C}$ and highest $\delta^{15}\text{N}$ values of any of the potential dietary sources. Both aquatic macroinvertebrates had a narrower range in their $\delta^{13}\text{C}$ values (*G. lacustris*: -25.6 to -22.4 ‰, lymnaeid snails: -28.9 to -22.7 ‰) and their $\delta^{15}\text{N}$ values (*G. lacustris*: 5.5 to 12.4 ‰, lymnaeid snails: 7.6 to 11.7 ‰) than either zooplankton or POM. The mean $\delta^{13}\text{C}$ values for macroinvertebrates (*G. lacustris*: -24.2 ± 0.7 ‰, lymnaeid snails: -25.7 ± 1.4 ‰) were higher compared to those of zooplankton and POM, while the $\delta^{15}\text{N}$ values were lower in comparison (*G. lacustris*: 9.4 ± 1.3 ‰, lymnaeid snails: 9.8 ± 1.2 ‰). Leaf litter samples had $\delta^{13}\text{C}$ values (range -30.0 to -26.1 ‰, mean -27.9 ± 0.9 ‰) intermediate to zooplankton and benthic macroinvertebrates but were depleted in ^{15}N ($\delta^{15}\text{N}$ range -4.5 to 3.4 ‰, mean -0.7 ± 2.0 ‰) compared to the other sources. Even though the mean $\delta^{13}\text{C}$ value of leaf litter was intermediate to that of zooplankton and the macroinvertebrates, the $\delta^{15}\text{N}$ value of leaf litter was isotopically distinct from all other potential dietary sources even after taking into account its lower trophic position.

The relationship between distance downstream of the Highway 4 Bridge and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for POM and zooplankton can be seen in Fig. 3.6, while those for *G. lacustris* and lymnaeid snails can be seen in Fig. 3.7. As distance downstream increases, the $\delta^{13}\text{C}$ values of POM and zooplankton show a general decreasing trend as evident in the LOESS fitted line on each plot. The $\delta^{13}\text{C}$ values for *G. lacustris* show no major change with distance downstream

while lymnaeid snails show a slight increase as distance downstream increases. The $\delta^{15}\text{N}$ values for POM and zooplankton increase with distance downstream, opposite of the trend seen in $\delta^{13}\text{C}$. However, at around 130 km downstream of the Highway 4 Bridge, the $\delta^{15}\text{N}$ value of POM plateaus and begins to decrease slightly for the remaining 20 km of the reservoir. The $\delta^{15}\text{N}$ values of *G. lacustris* show a decrease from site 1 to site 2, but then remain relatively constant for the remainder of the reservoir. The opposite is seen for lymnaeid snails, which show a slight increase in $\delta^{15}\text{N}$ values from site 1 to site 2, but then also remain relatively constant throughout the rest of the reservoir downstream.

The relationships between fish total length and $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and W_r for each of the four fish species are seen in Fig. 3.8. There was a positive and significant relationship between $\delta^{13}\text{C}$ and total length for Lake Whitefish ($F = 26.0$, d.f. = 1, 174, $R^2 = 0.125$, $P < 0.00001$), Walleye ($F = 16.1$, d.f. = 1, 174, $R^2 = 0.079$, $P < 0.0001$) and White Sucker ($F = 26.9$, d.f. = 1, 187, $R^2 = 0.121$, $P < 0.0001$) and a significant negative relationship for Northern Pike ($F = 4.0$, d.f. = 1, 137, $R^2 = 0.021$, $P = 0.047$). There was no relationship between $\delta^{15}\text{N}$ and total length for either Lake Whitefish ($F = 0.8$, d.f. = 1, 174, $R^2 = 0.001$, $P = 0.37$) or White Sucker ($F = 0.2$, d.f. = 1, 187, $R^2 = 0.004$, $P = 0.65$). $\delta^{15}\text{N}$ was positively related to total length for Northern Pike and Walleye and the relationship was significant for Northern Pike ($F = 18.6$, d.f. = 1, 137, $R^2 = 0.113$, $P < 0.0001$), but not for Walleye ($F = 1.7$, d.f. = 1, 174, $R^2 = 0.004$, $P = 0.19$). Relative weight in Lake Whitefish decreased significantly as total length increased ($F = 10.4$, d.f. = 1, 174, $R^2 = 0.051$, $P < 0.01$), but the opposite was true for Northern Pike and Walleye which showed an increase in relative weight with total length. This relationship was significant for Northern Pike ($F = 27.6$, d.f. = 1, 137, $R^2 = 0.161$, $P < 0.00001$) but not for Walleye ($F = 3.089$,

d.f. = 1, 173, $R^2 = 0.012$, $P = 0.08$). Relative weight in White Sucker was not related to total length ($F = 0.142$, d.f. = 1, 187, $R^2 = 0.005$, $P = 0.71$).

Mean $\delta^{13}\text{C}$ values for main channel sites were not significantly different from embayment sites for POM ($F = 0.002$, d.f. = 1, 76, $P = 0.96$), zooplankton ($F = 0.11$, d.f. = 1, 70, $P = 0.74$), lymnaeid snails ($F = 0.51$, d.f. = 1, 28, $P = 0.48$), or *G. lacustris* ($F = 0.101$, d.f. = 1, 26, $P = 0.75$). The same was true for $\delta^{15}\text{N}$ values, with no significant differences present between main channel and embayment sites for POM ($F = 0.007$, d.f. = 1, 76, $P = 0.457$), zooplankton ($F = 0.018$, d.f. = 1, 70, $P = 0.89$), lymnaeid snails ($F = 0.02$, d.f. = 1, 28, $P = 0.90$), or *G. lacustris* ($F = 0.0001$, d.f. = 1, 26, $P = 0.98$).

3.3.3 Mixing Models

3.3.3.1 Lake Whitefish

The main carbon source contributing to the diets of Lake Whitefish in Lake Diefenbaker was pelagic primary production (Fig. 3.9), represented by zooplankton, which made up 50.7 ± 6.1 % of the diets of all Lake Whitefish (range 31.1 – 68.5 %). The next most important source was benthic primary production, represented by the combined *G. lacustris* and lymnaeid snails, which contributed 36.6 ± 6.8 % to the diets of all Lake Whitefish (range 19.1 – 54.9 %). Allochthonous primary production, represented by leaf litter, was the least important carbon source to the diets of Lake Whitefish in Lake Diefenbaker, with only 6.9 ± 1.4 % of all Lake Whitefish diets being contributed by this source (range 4.6 – 13.9 %). Interestingly, with the exception of site 2, pelagic primary production was most important at the most upstream sites, with the lowest importance occurring at the more downstream sites. The opposite was true for benthic primary production which generally increased in importance with distance downstream, again with the exception of site 2. Allochthonous primary production was generally of low

importance, but was of highest importance in the most upstream sites, although the difference between upstream and downstream sites was mostly negligible. Site 2 was the exception to the trends seen for the importance of both benthic and pelagic primary production. However, only a single juvenile Lake Whitefish was caught at site 2, so this does not likely represent the true average for the site.

3.3.3.2 Northern Pike

Benthic primary production was the most important carbon pathway to the diets of Northern Pike in Lake Diefenbaker, with an average contribution of 48.1 ± 2.7 % and a range of 39.8 – 57.4 % (Fig. 3.10). The next most important source of carbon to the diets of pike was pelagic primary production which had a mean contribution of 32.6 ± 4.4 % (range 9.0 – 38.8 %). Allochthonous carbon had the lowest importance to the diets of Northern Pike with a range in the contribution of 11.6 – 45.1 % and a mean contribution of 17.9 ± 4.3 %. The contribution of benthic carbon was highest throughout the mid ranges of the reservoir at sites 2 – 8 and lowest at site 12, the most downstream site. Site 1, the most upstream site had the second lowest contribution from benthic primary production, but it was similar to the values for sites 9 – 11. Pelagic primary production was least important at the most upstream site and highest at the most downstream site, but relatively constant from sites 2 – 11, although there was a slight increasing trend visible as distance increased downstream. Allochthonous primary production was the least important source to the diets of Northern Pike at sites 2 – 12 where it had a relatively constant contribution to the diets of pike. However, at site 1, allochthonous sources contributed 28.5 ± 7.4 % (range 13.7 – 45.1 %) to the diet of Northern Pike, higher than the 23.6 ± 6.9 % (range 9.0 – 37.0 %) contributed from pelagic primary production.

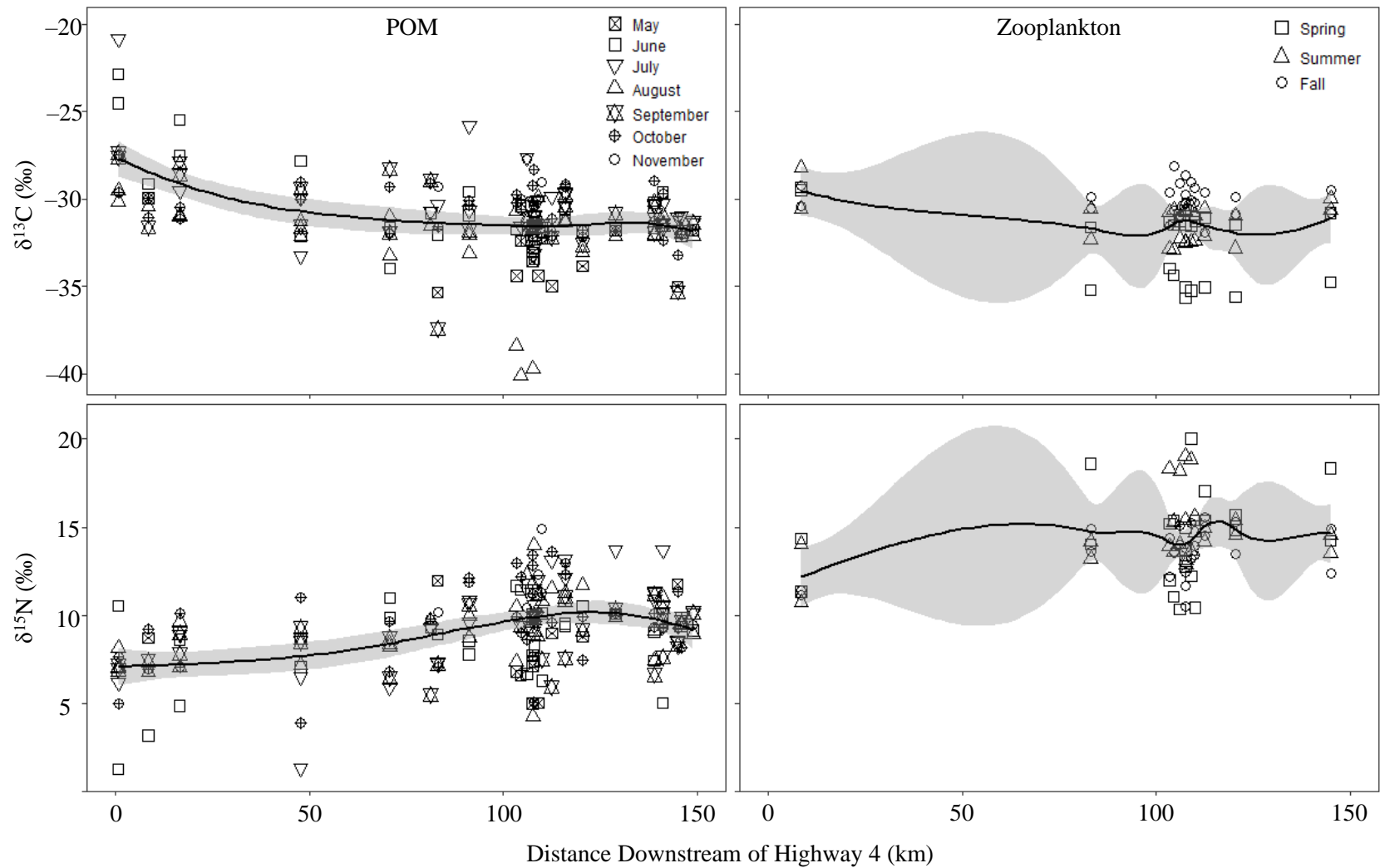


Figure 3.6. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of particulate organic matter (POM) and zooplankton with increasing distance downstream of the Highway 4 Bridge, located near the upstream end of Lake Diefenbaker. Each point in each panel represents a single sample. A LOESS smoothed line is fitted to each variable and shown on each graph, while the shaded area represents the 95 % confidence interval. POM samples were collected in May, June, July, August, September, October, and November at sites throughout the reservoir, while zooplankton samples were collected at sites 1 – 12 in spring, summer and fall.

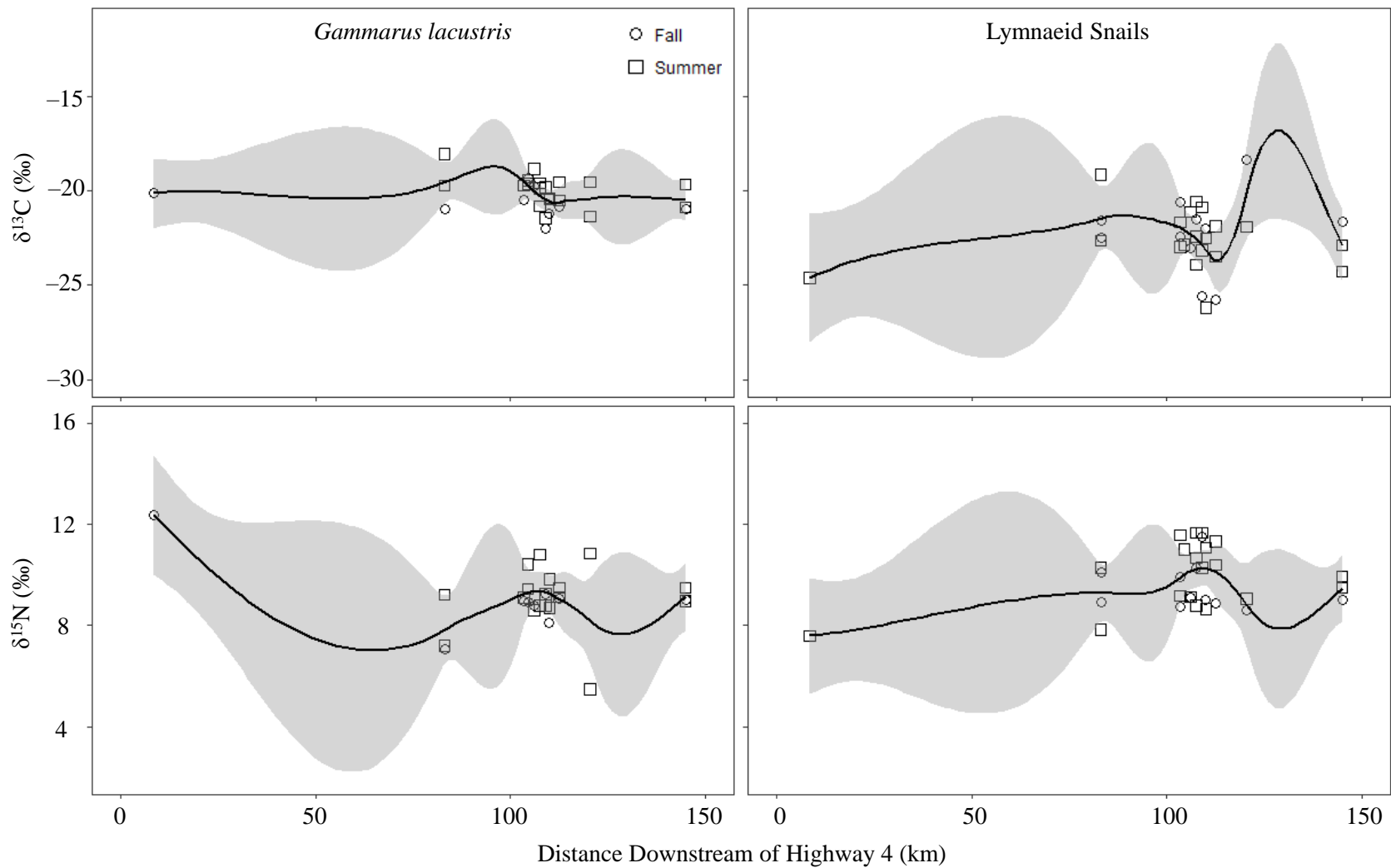


Figure 3.7. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of both benthic macroinvertebrates, *Gammarus lacustris* and lymnaeid snails, with increasing distance downstream of the Highway 4 Bridge, located near the upstream end of Lake Diefenbaker. Each point in each panel represents a single sample. A LOESS smoothed line is fitted to each variable and shown on each graph, while the shaded area represents the 95 % confidence interval. Aquatic invertebrate samples were collected in summer and fall of each open water season at sites 1 – 12. No aquatic macroinvertebrates were collected during attempted sampling in spring.

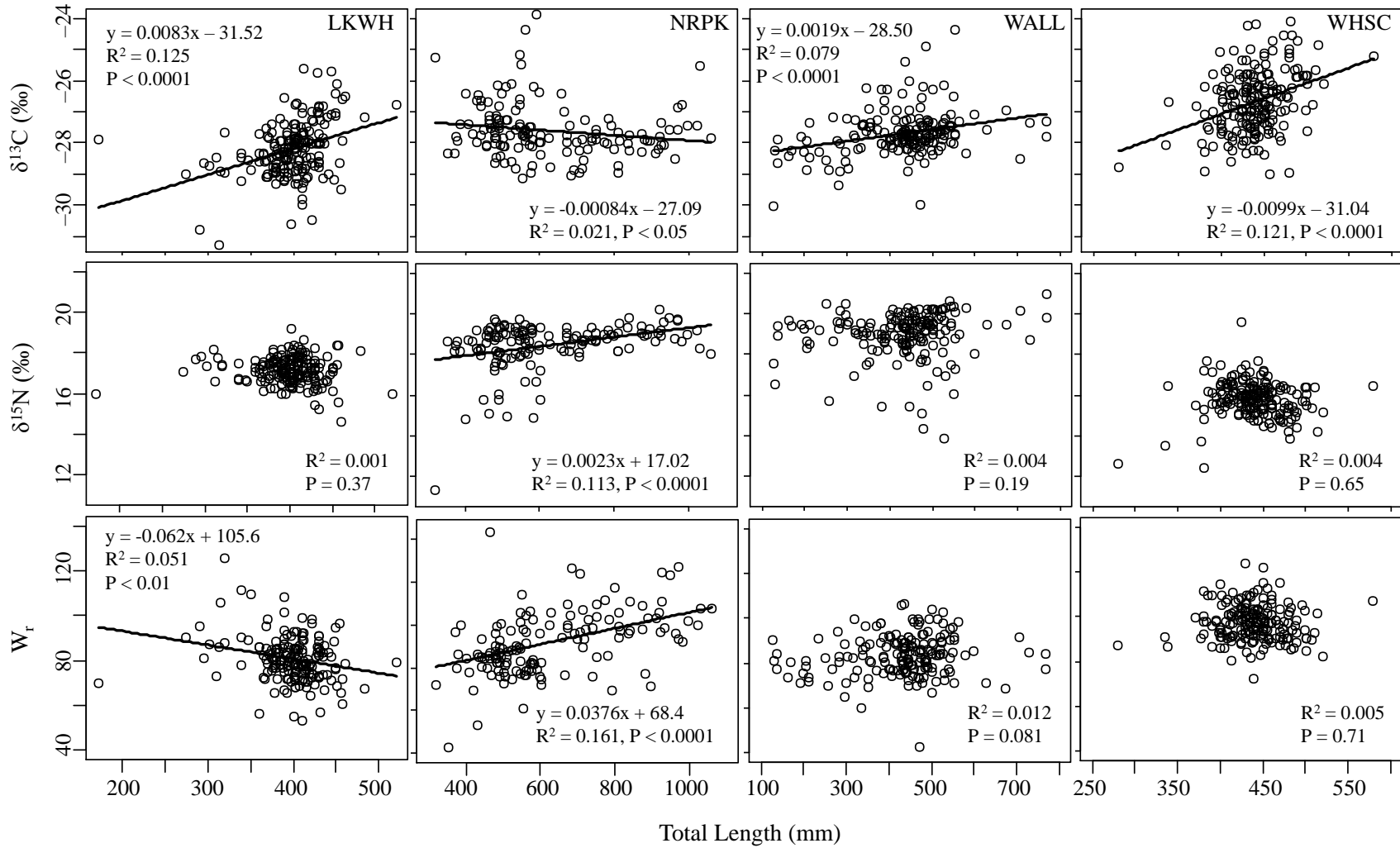


Figure 3.8. The relationship between total length (mm) and $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and relative weight (W_r) for Lake Whitefish, Northern Pike, Walleye and White Sucker at all 12 sites over both sampling years (model I linear regression). Note the difference in scales on the X axis for each species.

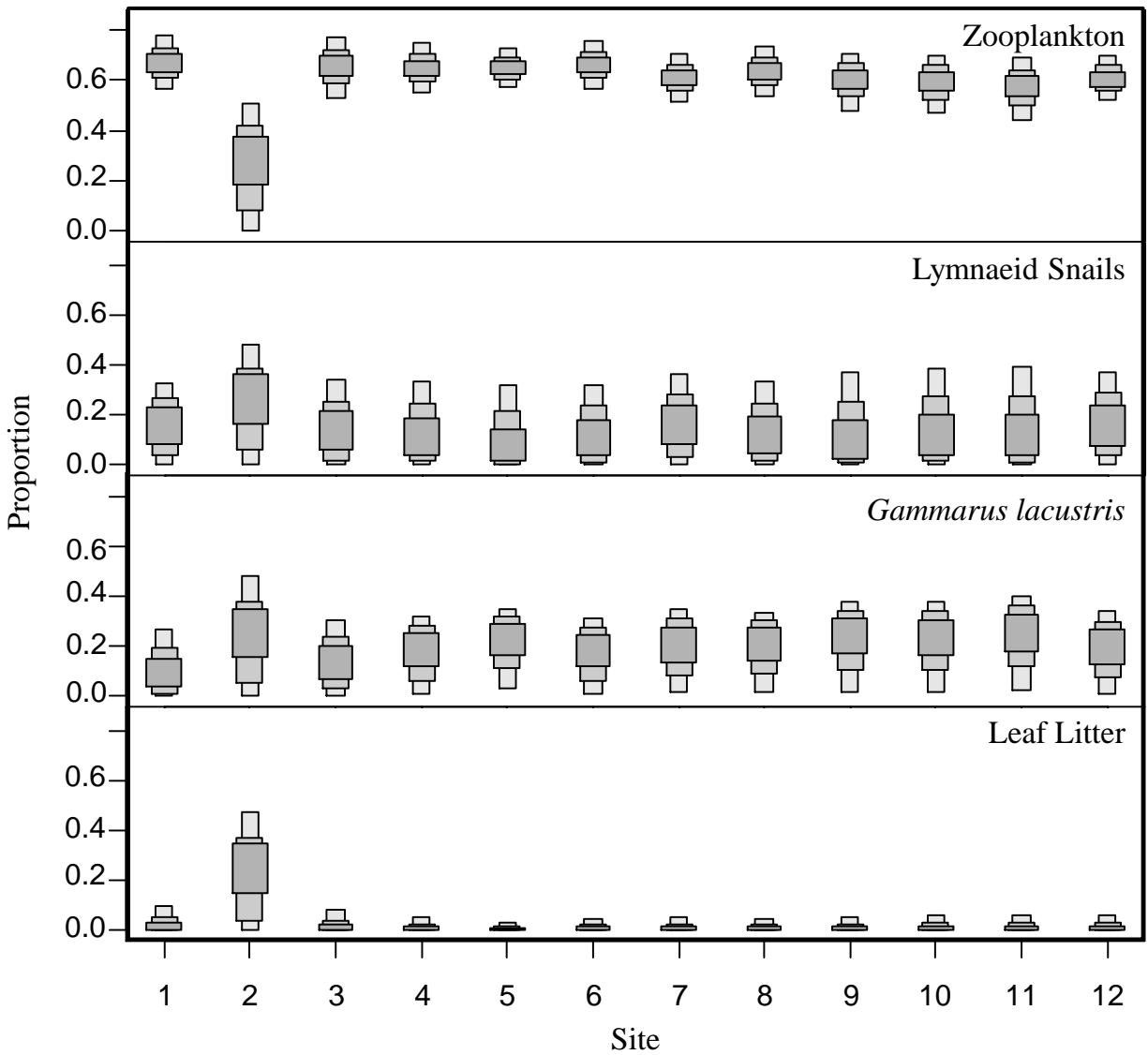


Figure 3.9. Boxplots of the proportional contribution of each potential carbon source to the diets of Lake Whitefish (*Coregonus clupeaformis*) at sites 1 – 12 in Lake Diefenbaker. The potential dietary sources include pelagic primary production represented by zooplankton, benthic primary production represented by two aquatic macroinvertebrates, lymnaeid snails and *G. lacustris*, and allochthonous primary production, represented by leaf litter. The inner, central and outer portions of the boxplots represent the 50 %, 75 % and 95 % credible intervals of the data. For site locations within Lake Diefenbaker, please refer to Fig. 1.1.

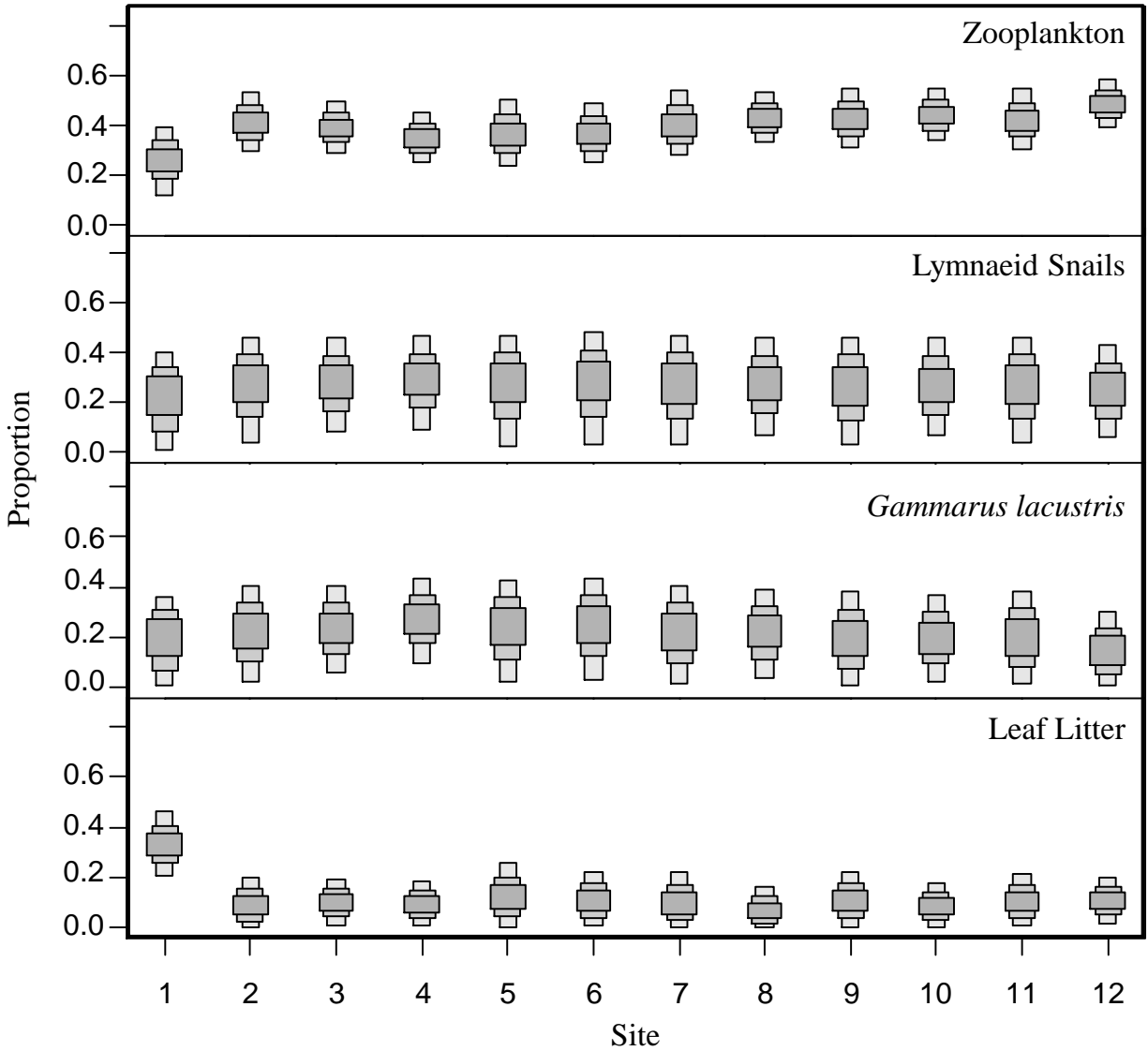


Figure 3.10. Boxplots of the proportional contribution of each potential carbon source to the diets of Northern Pike (*Esox lucius*) at sites 1 – 12 in Lake Diefenbaker. The potential dietary sources include pelagic primary production represented by zooplankton, benthic primary production represented by two aquatic macroinvertebrates, lymnaeid snails and *G. lacustris*, and allochthonous primary production, represented by leaf litter. The inner, central and outer portions of the boxplots represent the 50 %, 75 % and 95 % credible intervals of the data. For site locations within Lake Diefenbaker, please refer to Fig. 1.1.

3.3.3.3 Walleye

Similar to Northern Pike, the carbon pathway most important to the diets of Walleye in Lake Diefenbaker was benthic primary production, with an average contribution of 48.0 ± 2.2 % and a range of 39.5 – 56.5 % (Fig. 3.11). This was followed in importance by pelagic primary production which had a mean contribution of 32.2 ± 3.8 % and a range of 15.4 – 38.8 %. Allochthonous carbon contributed between 11.9 – 35.5 %, with a mean contribution of 18.5 ± 3.9 % to the diets of Walleye, making it the least important carbon pathway. For the most part, the contribution of benthic and pelagic carbon did not differ much between sites, with the exceptions of sites 1 and 12. Site 1 had the highest contribution from allochthonous carbon with a mean value of 24.6 ± 5.7 % (range 15.5 – 33.8 %) and the lowest contribution from pelagically derived carbon with a mean value of 27.5 ± 5.3 % (range 16.5 – 35.0 %), similar to what was seen in Northern Pike. Site 12 had the highest contribution from pelagic primary production to the diets of Walleye at 34.7 ± 2.2 % (range 31.5 – 38.4 %), while also having the lowest contribution from benthic primary production with a mean contribution of 46.3 ± 1.7 % (range 43.5 – 48.5 %). Site 12 also had one of the lowest contributions from allochthonous derived carbon at 16.9 ± 2.0 % (range 14.3 – 20.9 %), second only to site 9 located at the mouth of Kadla Coulee, where allochthonous carbon had a mean contribution of 16.4 ± 1.9 % (range 13.5 – 19.6 %). Interestingly, site 9 also had the second highest contribution from pelagically derived carbon to the diets of Walleye with a mean value of 34.1 ± 2.7 % (range 29.1 – 38.5 %), only slightly below that of site 12.

3.3.3.4 White Sucker

As seen in Northern Pike and Walleye, the carbon pathway most important to the diets of White Sucker in Lake Diefenbaker was benthic primary production, with an average contribution

of 50.0 ± 7.8 % (range of 21.6 – 70.9 %) to their diets (Fig. 3.12). This was followed in importance by pelagic primary production with a mean contribution of 39.2 ± 7.1 % and a range of 15.4 – 68.6 %. Allochthonous carbon contributed very little to the diets of White Sucker, with a mean contribution of 7.6 ± 2.9 % (range 4.4 – 28.2 %). The highest contribution from benthic carbon to the diets of White Suckers was at sites 4 and 8 with mean contributions of 53.5 ± 8.3 % (range 41.0 – 67.9 %) and 54.7 ± 6.3 % (range 46.1 – 66.5 %), respectively. The lowest contribution from benthic carbon occurred at the upstream most sites 1 and 2 with mean contributions of 44.7 ± 6.5 % and 45.9 ± 10.5 % and ranges of 36.4 – 58.1 % and 21.1 – 58.3 %, respectively. The highest contribution from pelagic carbon occurred at site 2 (mean 43.4 ± 10.1 %, range 33.3 – 68.6 %), while the lowest contribution occurred at site 8 (mean 35.2 ± 6.9 %, range 22.6 – 44.2 %). The contribution of allochthonous carbon to the diets of White Sucker was relatively stable at all sites, with the exception of site 1 where it contributed close to double the amount of most other sites (mean 13.9 ± 7.5 %; range 6.4 – 28.2 %).

3.3.4 Fish Condition by Carbon Source

The only spawning season for Lake Whitefish when sampling was conducted was fall 2012. During this sampling season, 13 sexually mature female Lake Whitefish and 10 sexually mature males were caught at sites 1 – 12 (Table 3.6). When examined by site, there were no significant differences between sites for male gonad weight ($F = 0.5$, d.f. = 7, 3, $P = 0.80$) or GSI ($F = 0.3$, d.f. = 6, 3, $P = 0.89$). Female Lake Whitefish also had no significant difference between sites for gonad weight ($F = 0.6$, d.f. = 9, 7, $P = 0.74$), GSI ($F = 0.4$, d.f. = 9, 7, $P = 0.88$), egg diameter ($F = 3.0$, d.f. = 7, 5, $P = 0.12$), egg number ($F = 2.8$, d.f. = 7, 5, $P = 0.14$), or number of eggs standardized per gram of body weight ($F = 1.6$, d.f. = 7, 5, $P = 0.32$).

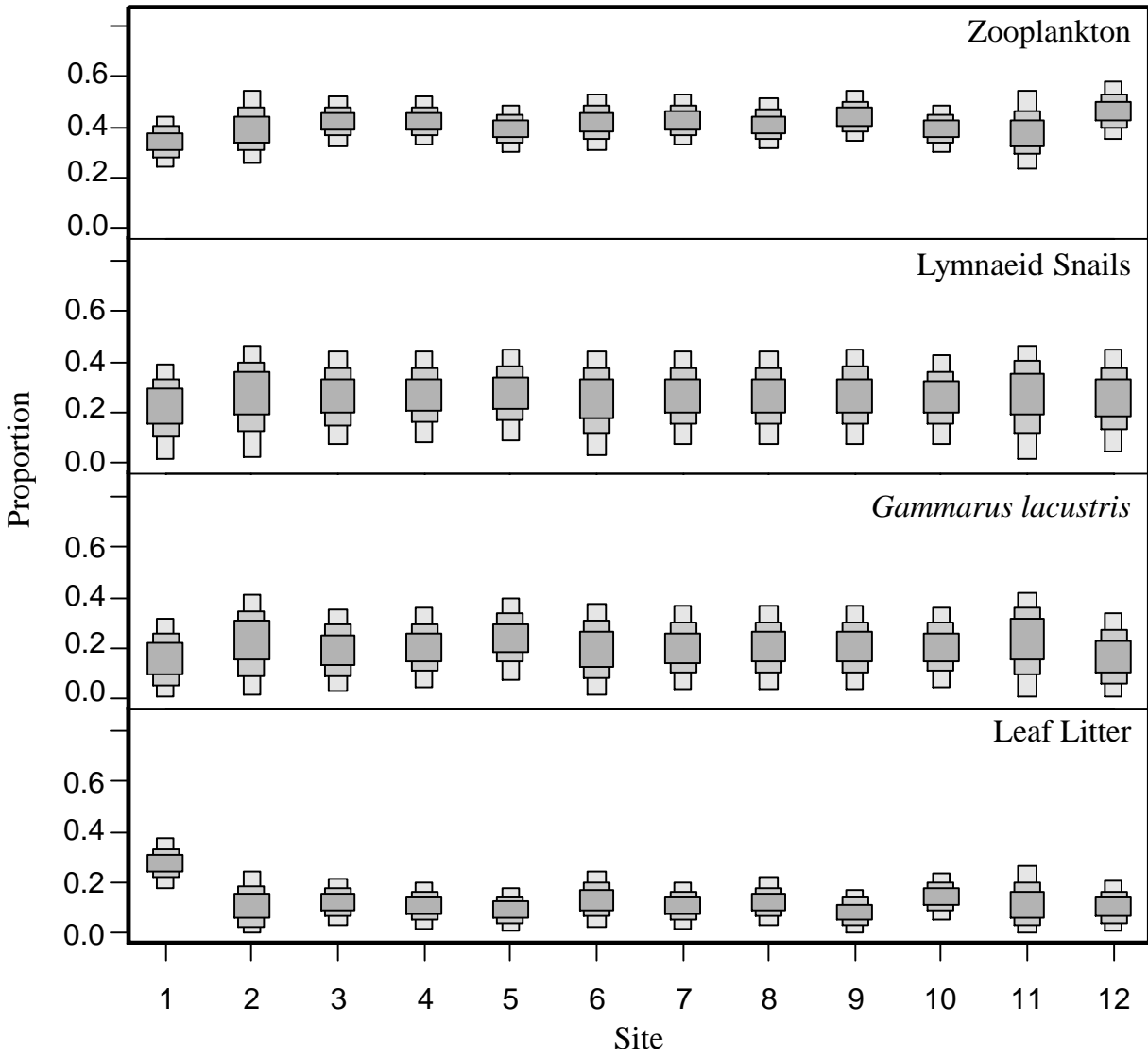


Figure 3.11. Boxplots of the proportional contribution of each potential carbon source to the diets of Walleye (*Sander vitreus*) at sites 1 – 12 in Lake Diefenbaker. The potential dietary sources include pelagic primary production represented by zooplankton, benthic primary production represented by two aquatic macroinvertebrates, lymnaeid snails and *G. lacustris*, and allochthonous primary production, represented by leaf litter. The inner, central and outer portions of the boxplots represent the 50 %, 75 % and 95 % credible intervals of the data. For site locations within Lake Diefenbaker, please refer to Fig. 1.1.

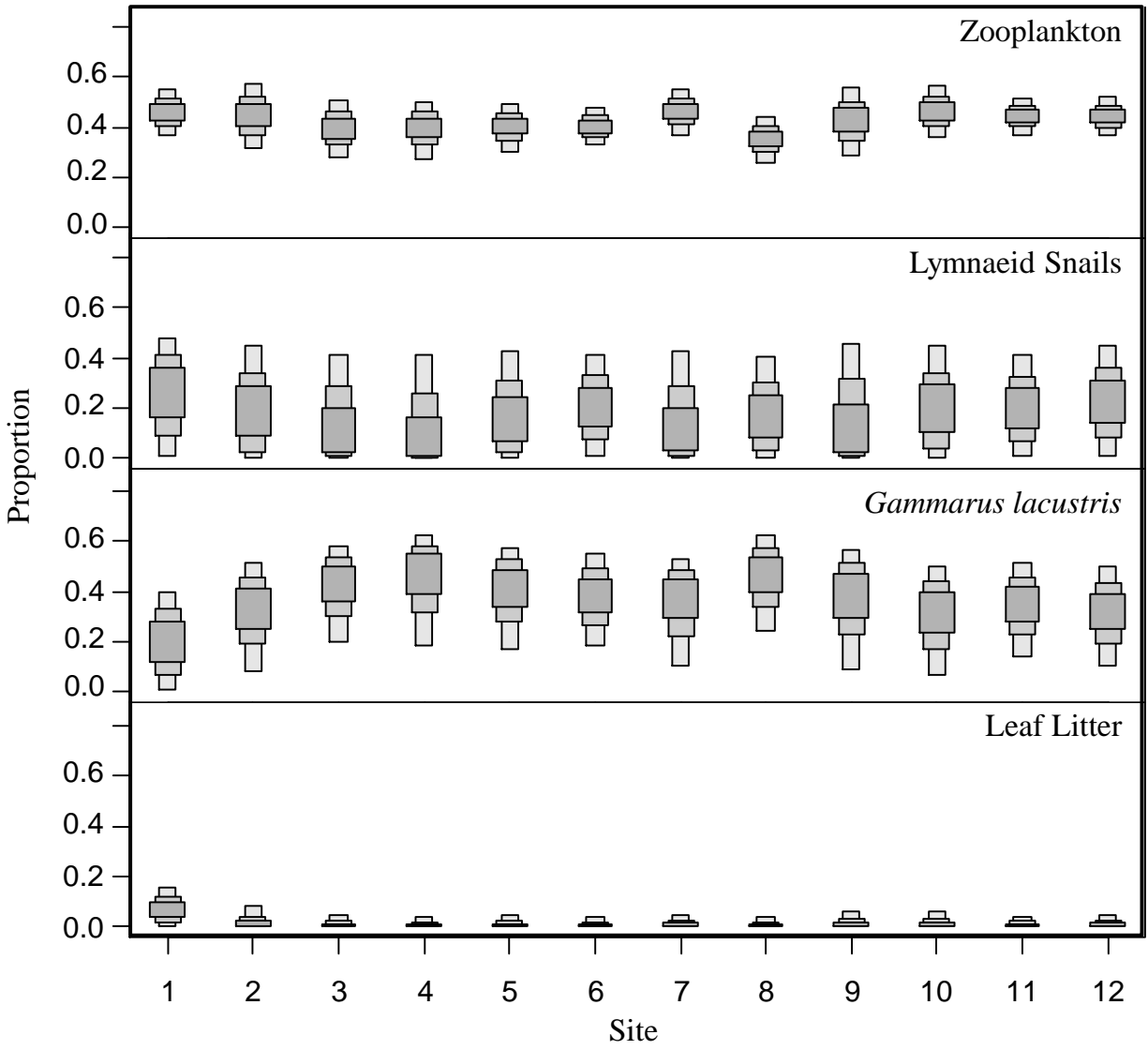


Figure 3.12. Boxplots of the proportional contribution of each potential carbon source to the diets of White Sucker (*Catostomus commersoni*) at sites 1 – 12 in Lake Diefenbaker. The potential dietary sources include pelagic primary production represented by zooplankton, benthic primary production represented by two aquatic macroinvertebrates, lymnaeid snails and *G. lacustris*, and allochthonous primary production, represented by leaf litter. The inner, central and outer portions of the boxplots represent the 50 %, 75 % and 95 % credible intervals of the data. For site locations within Lake Diefenbaker, please refer to Fig. 1.1.

In total, 22 mature female and 38 mature male Northern Pike were caught between the two spring sampling seasons (Table 3.6). There were no significant differences between sites for male gonad weight ($F = 0.8$, d.f. = 10, 27, $P = 0.61$) or GSI ($F = 0.8$, d.f. = 10, 27, $P = 0.60$) or between sampling seasons (gonad weight: $F = 3.1$, d.f. = 1, 36, $P = 0.09$; GSI: $F = 0.2$, d.f. = 1, 36, $P = 0.62$). For female Northern Pike, there were also no significant differences between sites for gonad weight ($F = 0.8$, d.f. = 9, 12, $P = 0.61$), GSI ($F = 0.9$, d.f. = 9, 12, $P = 0.55$), egg diameter ($F = 1.9$, d.f. = 9, 12, $P = 0.14$), egg number ($F = 0.7$, d.f. = 9, 12, $P = 0.74$), or egg number standardized per gram body weight ($F = 0.7$, d.f. = 9, 12, $P = 0.71$). However significant differences were present between sampling years for gonad weight ($F = 49.3$, d.f. = 1, 20, $P < 0.001$), GSI ($F = 16.0$, d.f. = 1, 20, $P < 0.001$), egg number ($F = 40.7$, d.f. = 1, 20, $P < 0.001$), and egg number standardized per gram body weight ($F = 15.2$, d.f. = 1, 20, $P < 0.001$). Egg diameter of Northern Pike eggs was not significantly different between spring 2012 and spring 2013 ($F = 0.002$, d.f. = 1, 20, $P = 0.96$).

Between the two spawning seasons when sampling was conducted, a total of 42 sexually mature Walleye were caught in Lake Diefenbaker. However, only seven of the 42 were females. The males showed no significant difference in gonad weight between the sites ($F = 1.2$, d.f. = 10, 24, $P = 0.36$), but the GSI for male Walleye was significantly different between sites ($F = 4.1$, d.f. = 10, 24, $P < 0.01$), with site 4 having the highest GSI value and being significantly different from sites 2, 3, 5, 7, 9, and 12 (Tukey's test, $P < 0.05$). Neither male gonad weight ($F = 0.03$, d.f. = 1, 33, $P = 0.87$) nor GSI ($F = 0.1$, d.f. = 1, 33, $P = 0.72$) were significantly different between 2012 and 2013. Female Walleye did not show any significant difference between sites for gonad weight ($F = 0.1$, d.f. = 3, 3, $P = 0.98$), GSI ($F = 0.7$, d.f. = 3, 3, $P = 0.62$), egg diameter ($F = 2.2$, d.f. = 3, 3, $P = 0.27$), egg number ($F = 0.1$, d.f. = 3, 3, $P = 0.94$), or egg number per gram of body

weight ($F = 1.1$, d.f. = 3, 3, $P = 0.47$). There were no differences between 2012 and 2013 for female Walleye gonad weight ($F = 0.03$, d.f. = 1, 5, $P = 0.87$), GSI ($F = 0.05$, d.f. = 1, 5, $P = 0.83$), egg diameter ($F = 1.2$, d.f. = 1, 5, $P = 0.33$), egg number ($F = 0.24$, d.f. = 1, 5, $P = 0.64$), or egg number standardized per gram of body weight ($F = 0.6$, d.f. = 1, 5, $P = 0.48$).

More sexually mature White Suckers were caught than any other species of fish, with 48 mature females and 53 mature males caught over the two years of study (Table 3.6). Male White Suckers showed no difference between sites for either gonad weight ($F = 1.2$, d.f. = 10, 42, $P = 0.33$), or GSI ($F = 0.7$, d.f. = 10, 42, $P = 0.76$), nor were there any significant differences between the sampling seasons (gonad weight: $F = 0.9$, d.f. = 1, 51, $P = 0.36$; GSI: $F = 0.01$, d.f. = 1, 51, $P = 0.93$). Female White Suckers also showed no significant differences between sites for gonad weight ($F = 1.0$, d.f. = 10, 37, $P = 0.49$), GSI ($F = 0.4$, d.f. = 10, 37, $P = 0.93$), egg diameter ($F = 0.4$, d.f. = 10, 37, $P = 0.93$), egg number ($F = 1.0$, d.f. = 10, 37, $P = 0.50$), or egg number standardized per gram of body weight ($F = 0.2$, d.f. = 10, 37, $P = 0.997$). Between the 2012 and 2013 spawning seasons there were no significant differences between gonad weight ($F = 2.5$, d.f. = 1, 46, $P = 0.122$), GSI ($F = 3.8$, d.f. = 1, 46, $P = 0.06$), or egg diameter ($F = 0.3$, d.f. = 1, 46, $P = 0.58$). However, there were significant differences between sampling seasons for both egg number ($F = 4.2$, d.f. = 1, 46, $P < 0.05$) and egg number standardized for body weight ($F = 5.9$, d.f. = 1, 46, $P < 0.05$).

Relationships between each of the dietary sources of carbon for individual fish and the relative weight and fecundity of each fish species were examined using linear regression. There were no significant relationships between the percent contributions of each carbon source with relative weight for each species (Table 3.7). However, when the different measures of fecundity were examined, some were found to be significantly related to the percent contribution of

different carbon sources (Table 3.7). In Lake Whitefish, the contribution from benthic carbon was negatively related to egg number standardized per gram body weight ($F = 5.10$, d.f. = 11, $R^2 = 0.25$, $P < 0.05$). In Northern Pike, female gonad weight ($F = 7.14$, d.f. = 20, $R^2 = 0.23$, $P < 0.05$), GSI ($F = 10.13$, d.f. = 20, $R^2 = 0.30$, $P < 0.01$), egg number ($F = 4.42$, d.f. = 20, $R^2 = 0.14$, $P < 0.05$), and egg number standardized per gram body weight ($F = 4.90$, d.f. = 20, $R^2 = 0.16$, $P < 0.05$) were all significantly positively related to the contribution from pelagic carbon to the diets of individual fish. As well, female gonad weight ($F = 9.77$, d.f. = 20, $R^2 = 0.29$, $P < 0.01$), GSI ($F = 4.36$, d.f. = 20, $R^2 = 0.14$, $P < 0.05$), and egg number ($F = 5.77$, d.f. = 20, $R^2 = 0.19$, $P < 0.05$) were all significantly negatively related to the contribution from allochthonous carbon. Walleye showed no significant relationships between condition factors and the percent contribution from each carbon source. The percent contribution of benthic carbon to the diets of individual White Suckers was positively related to both gonad weight ($F = 12.52$, d.f. = 46, $R^2 = 0.20$, $P < 0.001$) and egg number ($F = 10.84$, d.f. = 46, $R^2 = 0.17$, $P < 0.01$), with both relationships being significant. White Sucker also showed significant negative relationships between the percent contributions of carbon from pelagic sources with both female gonad weight ($F = 10.13$, d.f. = 46, $R^2 = 0.16$, $P < 0.01$) and egg number ($F = 9.08$, d.f. = 46, $R^2 = 0.15$, $P < 0.01$).

The two year mean $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, total length and W_r values for each species at each site can be seen in Fig. 3.13. Lake Whitefish $\delta^{13}\text{C}$ values differed significantly between sites ($F = 2.2$, d.f. = 11, 164, $P < 0.05$) and had an increasing trend in the mean $\delta^{13}\text{C}$ values as distance increased downstream from site 1, with sites 5, 9, 10 and 11 having significantly higher $\delta^{13}\text{C}$ values than site 1 (Tukey's test, $P < 0.05$). There were no significant differences between sites for $\delta^{15}\text{N}$ values ($F = 2.0$, d.f. = 11, 164, $P = 0.06$). Total length did differ significantly between

sites ($F = 4.9$, d.f. = 11, 164, $P < 0.0001$), with site 2 significantly different from all other sites (Tukey's test, $P < 0.05$). Lake Whitefish W_r values showed no significant differences between sites ($F = 1.5$, d.f. = 11, 164, $P = 0.12$), although there was a slight decrease in relative weight visible with increasing distance downstream.

Northern Pike $\delta^{13}\text{C}$ values were also significantly different between sites ($F = 5.2$, d.f. = 11, 127, $P < 0.0001$) but showed the opposite trend from Lake Whitefish with $\delta^{13}\text{C}$ values showing a significant decrease from site 1 to sites 9 – 12 (Tukey's test, $P < 0.05$). Northern Pike $\delta^{15}\text{N}$ values at site 1 differed significantly from all other sites ($F = 15.5$, d.f. = 2, 127, $P < 0.0001$; Tukey's test, $P < 0.001$). A large range in both total length and W_r was evident at each site for Northern Pike, as shown in the size of the error bars representing 95 % confidence intervals in Fig. 3.13, but no sites were significantly different from one another (Total length: ($F = 1.6$, d.f. = 11, 127, $P = 0.11$; W_r : $F = 0.5$, d.f. = 11, 127, $P = 0.87$). Walleye had a similar trend to Northern Pike in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with site 12 having the lowest mean $\delta^{13}\text{C}$ values and site 1 having the lowest $\delta^{15}\text{N}$ value. However, the $\delta^{13}\text{C}$ values were only significantly different between site 5 and site 12 for Walleye ($F = 1.2$, d.f. = 11, 164, $P < 0.05$; Tukey's test, $P < 0.01$). The $\delta^{15}\text{N}$ value for Walleye at site 1 was significantly lower than all other sites ($F = 5.9$, d.f. = 11, 164, $P < 0.0001$; Tukey's test, $P < 0.01$). Mean total length values were very similar between sites, but site 3 was significantly lower than site 5 ($F = 1.6$, d.f. = 11, 164, $P < 0.05$; Tukey's test, $P < 0.05$); no other sites showed any significant difference. The mean W_r values for each site showed a general increase with site as distance increased downstream, but the only significant difference was between site 2 and site 6 ($F = 2.1$, d.f. = 11, 163, $P < 0.05$; Tukey's test, $P < 0.05$), which had the lowest and highest W_r values, respectively.

White Sucker site mean $\delta^{13}\text{C}$ values show an interesting trend, increasing with distance downstream of Highway 4, until site 4 and then decreasing again until a peak at site 8 followed by another decrease until site 12. Sites 3, 4, 5, 6, 8 and 9 had significantly higher $\delta^{13}\text{C}$ values than site 1 ($F = 4.4$, d.f. = 11, 177, $P < 0.0001$; Tukey's test, $P < 0.05$). The mean $\delta^{15}\text{N}$ value at site 1 was significantly lower than all sites ($F = 3.4$, d.f. = 11, 177, $P < 0.001$; Tukey's test, $P < 0.05$), with the exception of sites 6 and 8. The total length and W_r values for all sites were similar, with no significant differences between sites for White Sucker (total length: $F = 1.2$, d.f. = 11, 177, $P = 0.31$; W_r : $F = 2.01$, d.f. = 11, 177, $P = 0.05$).

The seasonal means for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, total length and W_r values for each species can be seen in Fig. 3.14. Mean $\delta^{13}\text{C}$ values for Lake Whitefish differed significantly between seasons ($F = 8.6$, d.f. = 2, 173, $P < 0.001$), with the $\delta^{13}\text{C}$ value in fall of 2012 significantly lower than either spring 2012 or 2013 (Tukey's test, $P < 0.01$). The seasonal mean $\delta^{15}\text{N}$ value for Lake Whitefish differed significantly through time ($F = 3.8$, d.f. = 2, 173, $P < 0.05$) with the highest value in spring 2012 and the lowest value in spring 2013, with these two being significantly different from one another (Tukey's test, $P < 0.05$), but neither different from fall 2012 (Tukey's test, $P > 0.05$). Total length also differed significantly by sampling season ($F = 5.5$, d.f. = 2, 173, $P < 0.01$) with spring 2012 differing from spring 2013 (Tukey's test, $P < 0.01$), but fall 2012 again not differing from either (Tukey's test, $P > 0.05$). Relative weight also differed significantly between seasons ($F = 4.0$, d.f. = 2, 173, $P < 0.05$) and showed the same trend as seen in $\delta^{15}\text{N}$ with the highest value in spring 2012 differing significantly from the lowest value in spring 2013 (Tukey's test, $P < 0.05$), but neither differing from fall 2012 (Tukey's test, $P > 0.05$). Northern Pike showed no significant differences between seasons for $\delta^{13}\text{C}$ ($F = 0.8$, d.f. = 2, 136, $P = 0.46$), $\delta^{15}\text{N}$ ($F = 1.7$, d.f. = 2, 136, $P = 0.19$), total length ($F = 0.6$, d.f. = 2, 136, $P = 0.57$), or

relative weight values ($F = 0.7$, d.f. = 2, 136, $P = 0.48$). Walleye also had no significant differences between the seasons for $\delta^{13}\text{C}$ ($F = 1.8$, d.f. = 2, 173, $P = 0.17$), $\delta^{15}\text{N}$ ($F = 1.9$, d.f. = 2, 173, $P = 0.15$), or total length values ($F = 0.9$, d.f. = 2, 173, $P = 0.39$), but the relative weight did differ significantly between the seasons ($F = 6.8$, d.f. = 2, 172, $P < 0.01$) with fall 2012 differing from both spring 2012 (Tukey's test, $P < 0.01$) and spring 2013 (Tukey's test, $P < 0.01$), but no difference between either spring season (Tukey's test, $P > 0.05$). White Sucker were similar to Walleye in that there were no significant differences between seasons for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and total length but again, relative weight did show a significant difference between seasons ($F = 4.4$, d.f. = 2, 186, $P < 0.05$). White Sucker had the highest relative weight in spring 2012, which differed significantly from spring 2013 (Tukey's test, $P < 0.01$), while fall 2012 did not differ from either of the spring sampling seasons (Tukey's test, $P > 0.05$).

Table 3.7. The relationship between condition factors and the proportion of diet contribution of each carbon source for four species of fish in Lake Diefenbaker Saskatchewan. Significant relationships ($P < 0.05$) are shown in bold text (model I linear regression). Sex is indicated as either (M) for male or (F) for female for gonad weight and GSI.

Condition Factor	Source	Lake Whitefish				Northern Pike				Walleye				White Sucker			
		F	d.f	R ²	P	F	d.f	R ²	P	F	d.f	R ²	P	F	d.f	R ²	P
W _r	ZP	0.01	174	-0.01	0.944	0.77	137	-0.02	0.382	2.50	173	0.01	0.116	1.68	187	0.00	0.196
	MI	0.09	174	-0.01	0.770	0.01	137	-0.01	0.927	0.33	173	0.00	0.569	1.39	187	0.00	0.241
	LL	0.53	174	0.00	0.467	1.10	137	0.00	0.296	1.84	173	0.00	0.177	0.01	187	0.00	0.754
Gonad Wt. (M)	ZP	0.07	9	-0.10	0.794	2.98	36	0.05	0.093	0.50	33	-0.01	0.483	2.00	51	0.02	0.163
	MI	0.08	9	-0.10	0.783	4.07	36	0.08	0.051	0.00	33	-0.03	0.953	1.76	51	0.01	0.190
	LL	0.00	9	-0.11	0.980	1.13	36	0.00	0.294	1.26	33	0.01	0.269	0.44	51	-0.01	0.508
GSI (M)	ZP	0.04	8	-0.12	0.841	2.25	36	0.03	0.143	0.12	33	-0.03	0.729	0.38	51	-0.01	0.539
	MI	0.04	8	-0.12	0.843	2.57	36	0.04	0.118	0.11	33	-0.03	0.747	0.26	51	-0.01	0.610
	LL	0.04	8	-0.12	0.843	1.03	36	0.00	0.318	0.02	33	-0.03	0.892	0.03	51	-0.02	0.875
Gonad Wt. (F)	ZP	1.06	15	0.00	0.319	7.14	20	0.23	0.015	0.97	5	-0.01	0.370	10.13	46	0.16	0.003
	MI	0.68	15	-0.02	0.422	0.46	20	-0.03	0.508	0.89	5	-0.02	0.388	12.52	46	0.20	0.001
	LL	1.25	15	0.02	0.282	9.77	20	0.29	0.006	1.01	5	0.00	0.360	0.30	46	-0.02	0.588
GSI (F)	ZP	1.65	15	0.04	0.219	10.13	20	0.30	0.005	0.19	5	-0.16	0.678	1.99	46	0.02	0.165
	MI	2.34	15	0.08	0.147	3.91	20	0.12	0.062	1.75	5	0.11	0.243	2.12	46	0.02	0.152
	LL	0.13	15	-0.06	0.720	4.36	20	0.14	0.050	0.20	5	-0.15	0.677	1.67	46	0.01	0.203
Egg diameter	ZP	0.51	11	-0.04	0.489	0.11	20	-0.04	0.743	0.02	5	-0.20	0.898	0.00	46	-0.02	0.990
	MI	0.94	11	0.00	0.353	0.00	20	-0.05	0.968	0.08	5	-0.18	0.787	0.02	46	-0.02	0.897
	LL	0.52	11	-0.04	0.485	0.16	20	-0.04	0.693	0.01	5	-0.20	0.918	1.16	46	0.00	0.288
Egg #	ZP	0.00	11	-0.09	0.963	4.42	20	0.14	0.048	2.65	5	0.22	0.164	9.08	46	0.15	0.004
	MI	0.04	11	-0.09	0.842	0.31	20	-0.03	0.586	1.05	5	0.01	0.352	10.84	46	0.17	0.002
	LL	1.09	11	0.01	0.320	5.77	20	0.19	0.026	2.56	5	0.21	0.171	0.64	46	-0.01	0.426
Egg #/g	ZP	3.54	11	0.17	0.087	4.90	20	0.16	0.039	0.25	5	-0.14	0.638	1.19	46	0.00	0.282
	MI	5.10	11	0.25	0.045	2.37	20	0.06	0.139	2.39	5	0.19	0.183	1.16	46	0.00	0.288
	LL	0.03	11	-0.09	0.862	2.07	20	0.05	0.166	0.20	5	-0.15	0.677	2.20	46	0.02	0.145

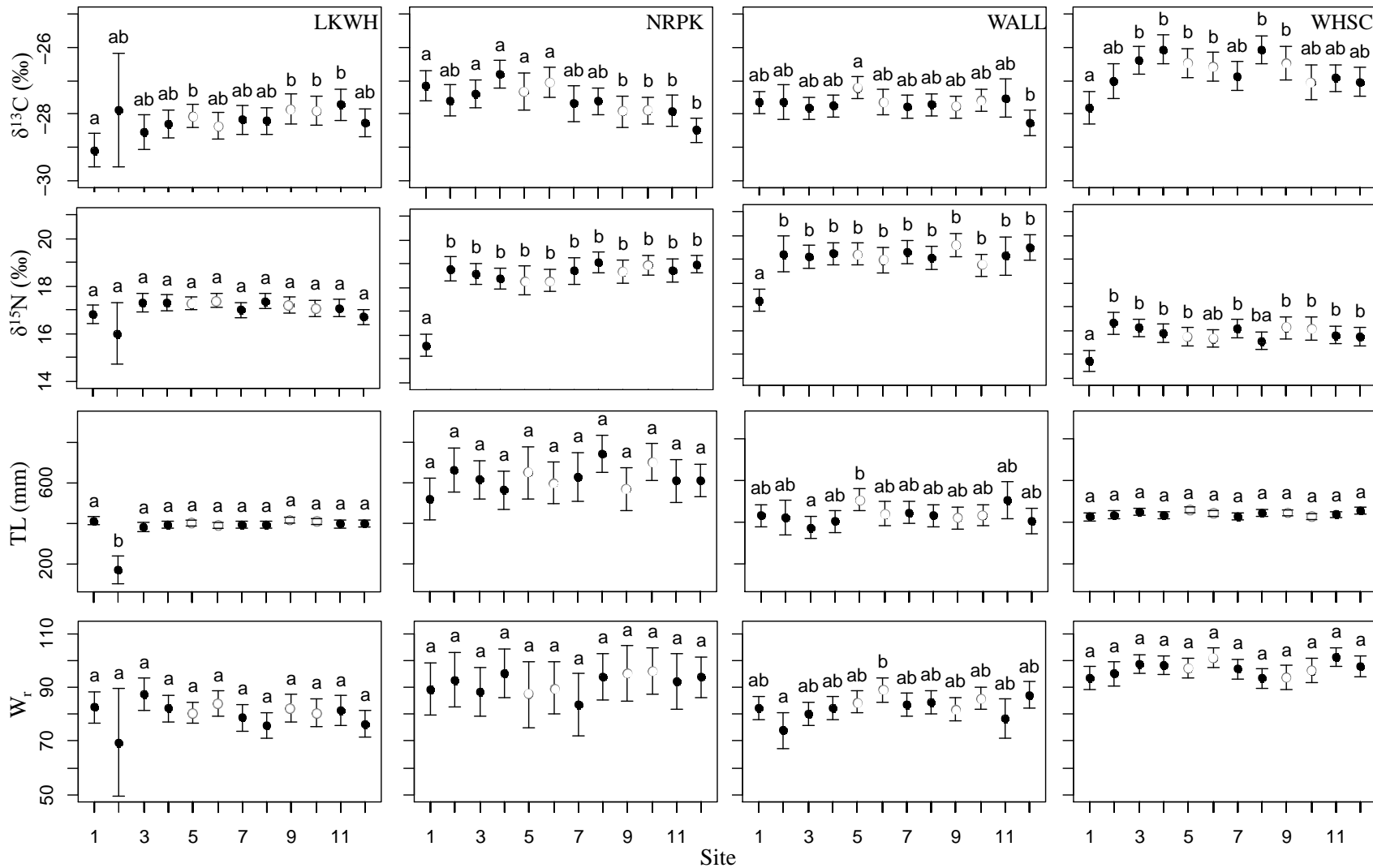


Figure 3.13. Mean $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, total length, and relative weight (W_r) for all Lake Whitefish, Northern Pike, Walleye and White Sucker captured at sites 1 – 12 throughout 2012 and 2013. Error bars represent 95 % confidence intervals for the means. Means with a common letter are not significantly different from one another. Both main channel sites (closed circles) and sites located within embayments (open circles) are included. For site locations within Lake Diefenbaker, please refer to Fig. 1.1.

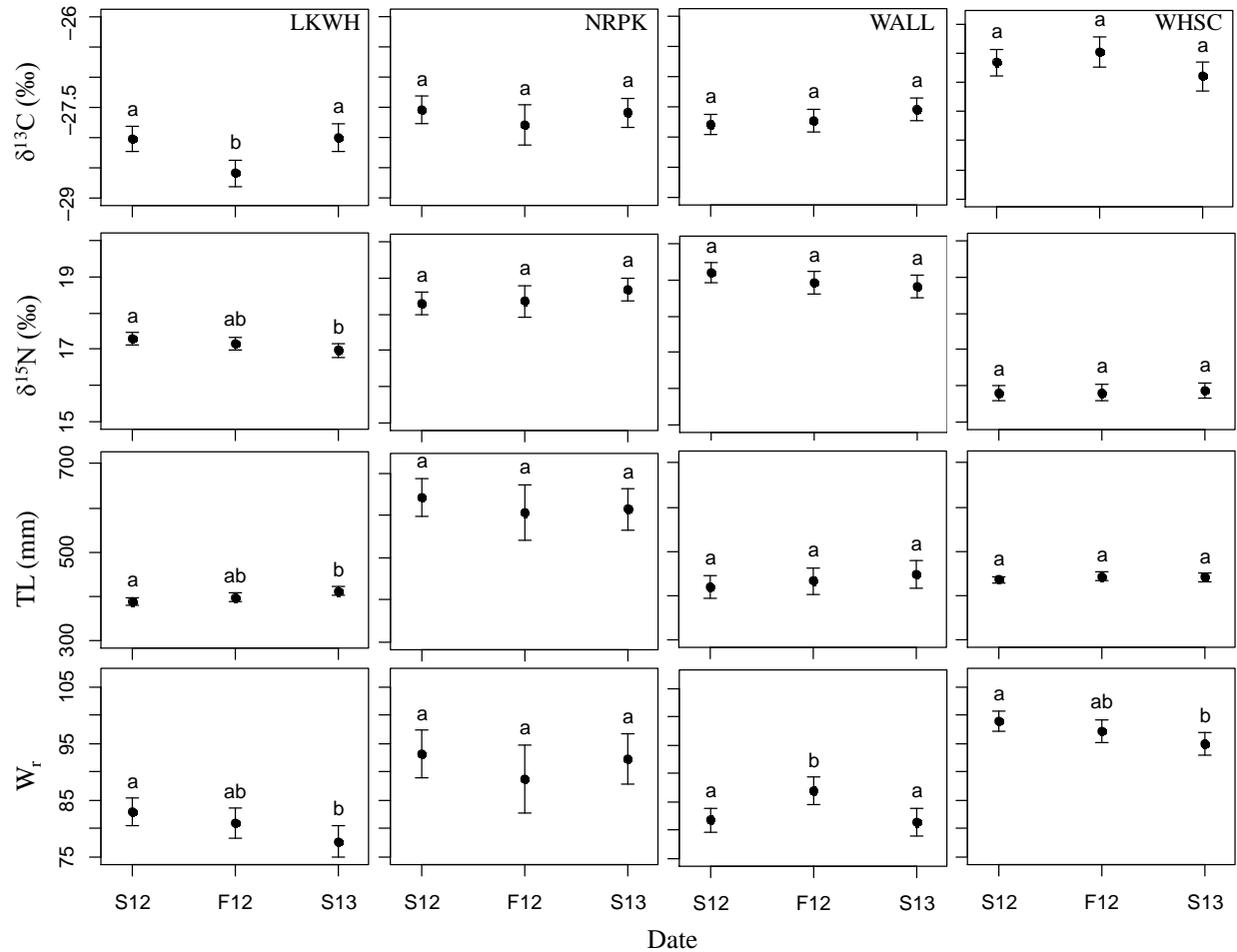


Figure 3.14. Seasonal mean $\delta^{13}\text{C}$ (‰), $\delta^{15}\text{N}$ (‰), total length (mm), and relative weight (W_r) for all Lake Whitefish, Northern Pike, Walleye and White Sucker captured at sites 1 – 12 during spring 2012 (S12), fall 2012 (F12), and spring 2013 (S13). Error bars represent 95 % confidence intervals for the means. Means with a common letter are not significantly different from one another.

3.4 Discussion

3.4.1 Carbon Sources: Allochthony versus Autochthony

The majority of carbon supporting the growth of Lake Whitefish, Northern Pike, Walleye and White Sucker in Lake Diefenbaker is of autochthonous origin. Lake Whitefish and White Sucker show the least assimilation of allochthonous carbon of the four study species, with negligible contributions at all sites other than in the most upstream reaches of the reservoir at site 1. Site 2 also had a relatively high contribution for Lake Whitefish, but only a single juvenile

Lake Whitefish was caught at this site, so this may be an artifact of the very limited sample size. Northern Pike and Walleye both had higher contributions of allochthonous carbon to their diets than either Lake Whitefish or White Sucker. Again, the highest contributions from this source were at site 1 in the upstream reaches of Lake Diefenbaker. This higher average contribution of allochthonous carbon to the diets of Northern Pike and Walleye compared to Lake Whitefish and White Sucker could be a result of the predatory nature of these species which may be consuming prey species that have a higher reliance on allochthonous carbon. Another reason the contribution to the predatory species may be higher could be the result of their increased trophic levels on the SIAR and SIARsolo model output. The increased trophic levels of these predatory species result in increased trophic enrichment factors as well as increased standard deviations of these enrichment factors. Increased variability associated with the trophic enrichment factors can cause model performance to decrease (Parnell et al 2010), resulting in the potential overestimation of the importance of certain carbon sources.

Although autochthonous carbon far outweighed the importance of allochthonous carbon to the diets of all four fish species, the importance of each autochthonous source varied between species. Benthic autochthonous production was more important than pelagic production to the diets of Northern Pike, Walleye and White Sucker. Pelagic primary production was on average, the most important carbon source to the diets of Lake Whitefish throughout the entire reservoir. However, the importance of this source decreased slightly with distance downstream, marked by a corresponding increase in Lake Whitefish dependence on benthic carbon in the lower reaches of the reservoir. Northern Pike showed a similar but opposite trend, with pelagic carbon becoming more important and benthic carbon less important with increasing distance downstream. There is little variability in the contribution of benthic carbon to the diets of

Walleye throughout the reservoir, but the lowest contribution from benthic carbon and the highest contribution from pelagic carbon both occur at site 12, the most downstream site. White Sucker had the lowest contribution from benthic carbon at sites 1 and 2 in the upstream reaches and the importance of benthic carbon remained relatively constant among the other downstream sites.

The quality and the availability of each carbon source to the diets of consumers throughout Lake Diefenbaker are likely the main drivers in the importance of each source to the diets of each fish species. Allochthonous carbon is generally thought to be of lower nutritional quality (Brett et al. 2012), resulting in the preferential use of autochthonous carbon by some consumers. This is the case even when autochthonous carbon is in lower abundance (Karlsson et al. 2012), such as in dystrophic lakes (Carpenter et al. 2005). The ratio of littoral to pelagic habitat is lowest in the downstream reaches of Lake Diefenbaker (Sadeghian et al. 2015). This is likely why the predatory species have a higher diet contribution from pelagic carbon sources in the downstream reaches of Lake Diefenbaker where habitat overlap with pelagic prey species such as Cisco are more likely to occur due to the limited littoral habitat available. Interestingly, Lake Whitefish have the lowest contribution from pelagic sources in the same downstream regions of the reservoir, although it is still the most important carbon source contributing to their diets.

3.4.2 $\delta^{13}C$ and $\delta^{15}N$ Along the Length of Lake Diefenbaker

The $\delta^{13}C$ and $\delta^{15}N$ values of POM and primary consumers (Fig. 3.6 and 3.7) change with distance downstream of the tributary inflow for each autochthonous carbon source. Both pelagic sources, POM and zooplankton, show a decrease in their $\delta^{13}C$ values and an increase in their $\delta^{15}N$ values as distance increases downstream, which both level off between site 1 and 2 in the

transitional zone of the reservoir (Fig. 3.6). This transition likely is the result of autochthonous production becoming more lacustrine compared to the more riverine values reflected in the POM isotopic values at site 1 and further upstream. However, both benthic macroinvertebrates have isotopic values that remain relatively unchanged throughout much of the reservoir downstream of site 1. Macroinvertebrates were never found in abundance at the most upstream site (site 1), so the difference between this site and others further downstream may be a result of the low sample size which did not capture the temporal changes in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. When compared to values found by Donald et al. (2015) for the area of Lake Diefenbaker around site 1, the $\delta^{13}\text{C}$ values for bulk zooplankton were identical at -31.3‰ while the Sphaeriid mussels used to represent littoral benthic macroinvertebrates had a value of -25.4‰ , very similar to the values of -24.2 and -25.7‰ found for *G. lacustris* and lymnaeid snails, respectively. However, the mean $\delta^{15}\text{N}$ value for bulk zooplankton found by Donald et al. (2015) was 10.1‰ , much lower than the mean value found in this study of 14.3‰ . The mean $\delta^{15}\text{N}$ value for Sphaeriid mussels was not given in Donald et al. (2015). The difference seen in $\delta^{15}\text{N}$ values in Donald et al. (2015) is likely the result of all samples being collected near the upstream end of Lake Diefenbaker near site 1 of this study, which had lower $\delta^{15}\text{N}$ values from the rest of the reservoir (Fig. 3.6 and 3.7), although still higher than those found by Donald et al. (2015).

The $\delta^{13}\text{C}$ values for Lake Whitefish, Northern Pike, Walleye and White Sucker from Donald et al. (2015) were similar to the values found in this study for all four study species. However, the $\delta^{15}\text{N}$ values from Donald et al. (2015) were all lower than those seen in this study, but were similar to the values for site 1, located in the same area where sampling by Donald et al. (2015) took place. The lower $\delta^{15}\text{N}$ values seen for all four fish species in Donald et al. (2015) are likely the result of the limited sampling area in that study, which focused on the upstream

reaches of Lake Diefenbaker in the riverine zone. The $\delta^{15}\text{N}$ values for Northern Pike, Walleye and White Sucker in this study were considerably lower at site 1 than for the rest of the reservoir and similar to the mean $\delta^{15}\text{N}$ values seen in Donald et al. (2015). The $\delta^{15}\text{N}$ values for Lake Whitefish at site 1 were lower than the mean value for Lake Diefenbaker, but did not differ as greatly from the other sites as the $\delta^{15}\text{N}$ values of the other species.

The decrease seen in $\delta^{13}\text{C}$ values of POM and zooplankton with increasing distance downstream (Fig. 3.6) is also seen in Northern Pike (Fig. 3.13). This may be the result of the increased importance of pelagically derived carbon to the diets of Northern Pike in the downstream reaches of Lake Diefenbaker. Pelagic carbon had a more negative $\delta^{13}\text{C}$ value than benthic carbon and became increasingly more negative with distance downstream (Fig. 3.6 and 3.7). The decrease in $\delta^{13}\text{C}$ values of pelagic carbon with distance downstream is likely the result of increased levels of primary production in the downstream reaches of the reservoir (Wiesenberger et al. 2012). Yip et al. (2015) found Secchi disk depth to be highest in the lower reaches of the reservoir and turbidity to be highest in the upstream reaches, as the result of suspended sediment and allochthonous inputs. Furthermore, Dubourg et al. (2015) found that light limitation was common throughout Lake Diefenbaker and the highest gross primary production in the system occurred in the downstream reaches in June. This trend may have been magnified by the timing of this study, as both 2012 and 2013 were high water years with large inflows to the system (Hudson and Vandergucht 2015).

During years of low water, the $\delta^{13}\text{C}$ values of both POM and zooplankton would likely be more negative in the upstream reaches due to increased light penetration and potentially increased primary production (Wiesenberger et al. 2012). This would occur alongside a decrease in the input of allochthonous carbon (Sanchez-Vidal et al. 2013; Yip et al. 2015) with higher

$\delta^{13}\text{C}$ values than pelagic autochthonous production (Fig. 3.1). Future flows are predicted to be lower in the South Saskatchewan River (Tanzeeba and Gan 2012; Vogt et al. 2015), but the potential for flooding from extreme rainfall events is also increasing (Dankers et al. 2013). This may result in $\delta^{13}\text{C}$ values of POM and zooplankton being more negative in the upstream reaches of Lake Diefenbaker, similar to those currently seen further downstream in this study. In turn, this would lead to increased homogeneity of $\delta^{13}\text{C}$ values of POM and zooplankton between upstream and downstream sites. However, this would also result in a stronger differentiation between pelagic and benthic carbon pathways in the upstream reaches of the reservoir, due to the higher $\delta^{13}\text{C}$ values associated with benthic primary production. The opposite would be true during high water years, with a decrease in the $\delta^{13}\text{C}$ values of POM and zooplankton with increasing distance downstream. During low water years, the importance of allochthonous carbon to the diets of all four fish species studied is expected to be even lower than in high water years such as 2012 and 2013 when this study was conducted.

The increase in POM and zooplankton $\delta^{15}\text{N}$ values with distance downstream (Fig. 3.6) is also seen in the $\delta^{15}\text{N}$ values for Northern Pike and Walleye, although it is not as evident (Fig. 3.13). Site 1 had the lowest $\delta^{15}\text{N}$ values for all species of fish, except Lake Whitefish, which have relatively constant $\delta^{15}\text{N}$ values throughout all sites. The increase seen in $\delta^{15}\text{N}$ values in the POM and zooplankton likely reflects an increase in the $\delta^{15}\text{N}$ value of inorganic nitrogen in the system. This increase may be due to the addition of nitrogen to the system with a higher $\delta^{15}\text{N}$ value, such as manure from livestock, causing the $\delta^{15}\text{N}$ values of the POM and zooplankton to increase with increasing nitrogen loads from such sources (Kendall et al. 2007). Nitrogen fixation by cyanobacteria results in the addition of nitrogen to the system with $\delta^{15}\text{N}$ values near 0 ‰ (Kendall et al. 2007), which in turn lowers the $\delta^{15}\text{N}$ values for the POM and zooplankton,

the opposite of what is occurring with increased distance downstream in Lake Diefenbaker. Hodell and Schelske (1998) found that the sedimentation of phytoplankton in Lake Ontario from the epilimnion caused increasing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values due to the preferential sedimentation of ^{12}C and ^{14}N . In turn, this led to isotopically heavier phytoplankton and POM. A similar process may be happening in Lake Diefenbaker, leading to the increase in $\delta^{15}\text{N}$ values with increasing distance downstream, even with Lake Diefenbaker's much smaller size and shallower waters. Lucas et al (2015) analyzed the upper 1 cm of bottom sediments and found the $\delta^{13}\text{C}$ value to be relatively stable downstream of the riverine zone after an initial drop, but the $\delta^{15}\text{N}$ value of the sediment increased with distance downstream, similarly to what is seen for POM in this study (Fig. 3.6) and reflected in the Northern Pike and Walleye (Fig. 3.13).

The $\delta^{15}\text{N}$ values of primary producers and POM within undisturbed rivers are often in the range of -1 to $+7$ ‰ (Finlay and Kendall 2007). Rivers with high inputs of either waste water or animal manure often have $\delta^{15}\text{N}$ values in the range of 10 to 25 ‰ (Kendall and Caldwell 1998), similar to the $\delta^{15}\text{N}$ values seen in the downstream reaches of Lake Diefenbaker. Anderson and Cabana (2005) found $\delta^{15}\text{N}$ values of primary consumers, predatory macroinvertebrates, and certain fish species were all positively correlated with the percent agricultural land in the watershed. However, this relationship was weakest in fish, which was attributed to the ability of fish to move around rapidly within a watershed resulting in a weaker relationship than seen in more sedentary taxa. The increase in $\delta^{15}\text{N}$ with increasing percentage of agricultural land in the catchment was attributed to the addition of manure and fertilizer with high $\delta^{15}\text{N}$ values as well as further increases in $\delta^{15}\text{N}$ values through biogeochemical processes (Battaglin et al. 2001; Anderson and Cabana 2005). High $\delta^{15}\text{N}$ values in POM are often associated with inputs of either animal waste, sewage, or the influx of groundwater that has been significantly affected by

denitrification (Mariotti 1986). Wiesenberger et al. (2012) reported increased levels of autochthonous primary production in a number of Quebec reservoirs lead to an increase in $\delta^{15}\text{N}$ values. Interestingly, the increased $\delta^{15}\text{N}$ values were most often associated with decreased $\delta^{13}\text{C}$ values, both of which were attributed to increased levels of primary production (Wiesenberger et al. 2012). A similar pattern was seen for both isotopes in Lake Diefenbaker as distance increased downstream of the tributary inflow. The high $\delta^{15}\text{N}$ values seen in the downstream reaches of Lake Diefenbaker are likely due to a combination of the high percentage of agricultural land within the watershed, inputs from both manure and water treatment plants upstream of the reservoir and the increased levels of primary production with increasing distance downstream.

3.4.3 Where Does the Change in Resource Use Occur?

The major change in the importance of allochthonous sources for all species occurs in the riverine zone of the reservoir between site 1 and 2, as predicted by the longitudinal zonation concept (Kimmel and Groeger 1984). This is a large area of the reservoir where fish sampling was not conducted, so the exact location is not possible to pin point, but likely a gradual change in the importance of allochthonous carbon occurs throughout the riverine zone. All four study species showed the greatest contribution from allochthonous carbon in the upstream reaches of the reservoir where it was most readily available. Further downstream, the contribution of allochthonous carbon to the diets of all four fish species remained relatively unchanged throughout sites 2 through 12, located in the transitional and lacustrine zones of the reservoir (Hudson and Vandergucht 2015). Lake Whitefish differed slightly from the other species in that they only had a minor difference in the contribution from allochthonous carbon between site 1 and the rest of the sites. Lake Whitefish abundance has been found to be low in the upstream reaches of the reservoir during periods of warm water temperature in late spring and summer

(Wallace et al. 2010). This was evident in June of 2012 when Lake Whitefish were not caught at site 1. The lower contribution of allochthonous carbon to the diets of Lake Whitefish at site 1 compared to the other study species may be a result of Lake Whitefish leaving the area when water temperatures become too high in late spring, corresponding to the timing of peak inflow and the highest inputs of allochthonous carbon to the system (Yip et al. 2015). Lake Whitefish may be moving downstream to areas with their preferred lower water temperature (Scott and Crossman 1973) during summer months and moving back into the upstream reaches after the water decreases in temperature in the fall. This seasonal movement of Lake Whitefish may result in the lower contribution from allochthonous carbon to their diets at site 1 relative to the other study species. However, due to the slow turnover time of fish tissue (Hesslein et al. 1992), this could not be tested directly.

Autochthonous carbon was the most important carbon source for all four fish species at all 12 sites, indicating that even in the riverine zone with high allochthonous inputs, autochthonous production was still more important. The two study years were during periods of high flow in the South Saskatchewan River which likely resulted in higher than average inputs of allochthonous carbon to Lake Diefenbaker. As a result, the importance of allochthonous carbon would be expected to be even lower in periods of low flow or drought in the watershed (Lee et al. 2013; Min-Seob et al. 2014).

3.4.4 Fish Condition Throughout Lake Diefenbaker

Relative weight for Lake Whitefish, Northern Pike and White Sucker did not differ between sites, but Walleye did show a significant difference between site 2 and site 6 (Fig. 3.13). Even though significant differences were not present between sites for Lake Whitefish, there was a general decrease in W_r from upstream to downstream. A similar, but opposite trend is seen in

Walleye with increasing W_r values as distance increases downstream of Highway 4.

Interestingly, the decrease in Lake Whitefish W_r corresponds with a decrease in the importance of pelagically derived carbon with distance downstream. However, the relationships between relative weight and potential carbon sources were not significant for any species of fish (Table 3.7).

Total length was positively related to $\delta^{13}\text{C}$ for Lake Whitefish, Walleye and White Sucker, indicating a shift from pelagic to benthic resource use with increasing fish size. A significant negative relationship was present between total length and W_r in Lake Whitefish. This drop in W_r with increasing total length indicates the increase in benthic carbon to Lake Whitefish diets with increasing total length comes at the cost of body condition. As well, a significant negative relationship between the percent contribution of benthic carbon to the diets of individual Lake Whitefish and the number of eggs standardized per gram body weight was identified. The ontogenetic shift in Lake Whitefish diet with increasing size observed in this study has also been observed in other Lake Whitefish populations in North America (Tohtz 1993; Pothaven et al. 2001) and Common Whitefish (*C. lavaretus*) populations in Europe (Kahilainen et al. 2003). Ihssen et al. (1981) found that Lake Whitefish feeding on benthic prey sources grow faster than those feeding on zooplankton. However, Lake Whitefish populations can feed heavily on zooplankton during summer months when they are abundant or in periods when benthic food sources are in short supply (Tohtz 1993). In a comparison between Lake Ontario and Lake Erie, Lake Whitefish were found to be in lower condition and have lower GSI values in Lake Ontario which had lower abundance and a less diverse benthic community (Lumb et al. 2007). In Lake Diefenbaker, the switch to increased consumption of benthic resources with increased total length may be driven by necessity if zooplankton are not readily available

throughout much of the year. Lake Whitefish stocks in Lake Huron showed decreased growth rates and condition following the invasion of zebra mussels (*Dreissena polymorpha*) which caused a decrease in the diversity and abundance of many benthic prey sources (McNickle et al. 2006). The decrease seen in W_r and number of eggs standardized for body weight seen with increased total length in Lake Diefenbaker is likely the result of low abundance of benthic food sources throughout the reservoir, which are increasingly important to Lake Whitefish diets with increased size (Pothoven and Nalepa 2006).

Northern Pike were the only fish species that showed a significant negative relationship between total length and $\delta^{13}\text{C}$. Combined with the positive relationship between $\delta^{15}\text{N}$ and total length in Northern Pike (Fig. 3.8), this indicates a switch to a more pelagic based diet with increasing size. Increased consumption of Cisco (*Coregonus artedi*) or small Lake Whitefish at larger sizes could drive this change as both are largely zooplanktivorous (Scott and Crossman 1973; Gamble et al. 2011; this study) and rely heavily on carbon of pelagic origin. Northern Pike of all sizes are often associated with shallow macrophyte beds in the littoral zone of lakes (Chapman and Mackay 1984), but larger individuals are also known to inhabit open water areas and have higher rates of movement than smaller fish (Vehanen et al. 2006). Northern Pike undergo ontogenetic diet shifts, with adults being largely piscivorous (Scott and Crossman 1973). Large Northern Pike in Lake Diefenbaker appear to be either utilizing the pelagic habitat available within the reservoir and preying on Cisco and Lake Whitefish populations, or the pelagic prey species are acting as vectors between the pelagic and benthic habitats. Both Cisco and Lake Whitefish spawn in fall in shallow water and often remain there until the water warms again in spring (Scott and Crossman 1973). This increases their availability as a prey source for Northern Pike due to habitat overlap during this cool water period. The drop in $\delta^{13}\text{C}$ and rise in

$\delta^{15}\text{N}$ with increased total length was associated with a significant increase in W_r as well as female gonad weight, GSI, egg number, and egg number standardized per gram body weight, indicating a link between body condition and fecundity with increasing diet contributions from pelagic sources (Table 3.7). This may be the result of pelagic carbon sources being of higher nutritional value than either benthic carbon or allochthonous carbon sources for Northern Pike. Kaufman et al (2006) found that predation on Cisco resulted in increased growth potential in Walleye due to the high energy value of Cisco and increased foraging efficiency when feeding on this species. A similar situation may be occurring in Northern Pike in Lake Diefenbaker, resulting in higher W_r at increased sizes. Fish with higher W_r values generally have more energy to allocate to reproductive fitness and growth (Blackwell et al. 2000), which further helps to explain why the largest Northern Pike had the highest W_r as well as different measures of fecundity. However, when examining fish condition based on the carbon sources utilized by individual fish, there were no significant relationships between percent contribution of each potential carbon source and W_r for Northern Pike (Table 3.7).

Walleye total length was positively related to $\delta^{13}\text{C}$ values indicating an increased contribution from benthic carbon with increased size. The relationship between total length and W_r was also slightly positive, but not significant (Fig. 3.8). The percent contribution of each carbon source to Walleye diet was not related to any measure of fecundity or W_r (Table 3.7). This could be due to the population being below the carrying capacity of the reservoir, as Walleye are known to have increased body condition and growth rates when the population is heavily exploited or below carrying capacity (Sprangler and Payne 1977, Blackwell et al. 2000). Water level fluctuations in reservoirs can result in large year to year variations in Walleye recruitment, often causing reservoir Walleye populations to be at or below carrying capacity

(Kerr et al. 1997). This may be the case in Lake Diefenbaker, resulting in similar condition factors and fecundity for Walleye regardless of which carbon source they are utilizing. The study wide mean W_r value of 83 ± 9 for Walleye is below the optimal value of 100, but within the range of northern populations of Walleye (Blackwell et al. 2000). Some measures of fecundity of female Walleye may have been overlooked due to the limited sample size of sexually mature female Walleye in this study.

White Sucker W_r was not related to total length, despite their diet becoming increasingly more benthic with increased size (Fig. 3.8). However, both gonad weight and egg number in female White Suckers were positively related to the percent contribution of benthic carbon and negatively related to the percent contribution of pelagic carbon. However, there was no noticeable change in W_r with the increased contribution of either benthic or pelagic carbon. Gonad weight and egg number are expected to be higher in large females, so the correlation between increased contribution from benthic carbon and increased total length may be the driver behind the increases seen in White Sucker fecundity. Munikittrick and Dixon (1988) hypothesized that a shortage of food sources in some contaminated lakes resulted in lower fecundity and growth in female White Suckers after sexual maturity was reached. There is no indication of a shortage of prey items for White Sucker in Lake Diefenbaker, as female gonad weight and egg number continuously increased, and there was no noticeable drop in W_r with increasing size.

3.4.5 Spatial and Temporal Comparisons

No seasonal differences in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, or total length were present for Northern Pike, Walleye or White Sucker, but Lake Whitefish showed significant differences for all three variables (Fig. 3.14). Lake Whitefish had a significantly lower $\delta^{13}\text{C}$ value in fall 2012 than in

either spring 2012 or spring 2013, likely the result of increased pelagic resource use during summer months. Lake Whitefish of all size classes are known to feed heavily on zooplankton during the summer when this prey source is most abundant (Tohtz 1993). The decrease in $\delta^{13}\text{C}$ values in fall could also be the result of increased surface water temperatures during summer, which are not ideal for Lake Whitefish in shallow water areas (Scott and Crossman 1973). This would force them into deeper water where benthic prey sources may be less abundant. A combination of these two factors were likely responsible for the increased pelagic resource use seen in Lake Whitefish in the fall of 2012.

The $\delta^{15}\text{N}$ values of Lake Whitefish did not differ between fall 2012 and spring of 2012 and 2013, but $\delta^{15}\text{N}$ values were significantly lower in spring 2013 than in spring 2012. This could be the result of Lake Whitefish feeding at a lower trophic level in the spring of 2013, or having higher reliance on benthic carbon with a lower $\delta^{15}\text{N}$ value (Fig. 3.1). Interestingly, the opposite trend was seen in total length, with Lake Whitefish in spring 2013 significantly longer than those caught in spring 2012. The difference in total length between spring 2012 and spring 2013 may be the cause of the difference in $\delta^{15}\text{N}$ values as Lake Whitefish undergo ontogenetic diet shifts from pelagic to benthic prey sources with increased size (Tohtz 1993; Pothaven et al. 2001).

The relative weight of Lake Whitefish dropped throughout the sampling period from a high in spring 2012 to a significantly lower value in spring 2013. A similar and significant decrease in W_r values from spring 2012 to spring 2013 was also seen in White Sucker. However, there was no corresponding drop in White Sucker $\delta^{15}\text{N}$ values or an increase in total length between the seasons as seen in Lake Whitefish. This may mean the later date of ice off, longer winter and the earlier dates of fish sampling resulted in a shorter growing season in 2013 before

fish were sampled compared to spring 2012. This may be responsible for the decrease in Lake Whitefish and White Sucker W_r in 2013.

The different measures of fecundity did not differ between sites for any fish species except Walleye. Male Walleye at site 4 had a significantly higher GSI than at sites 2, 3, 5, 7 and 9. However, the sample size of sexually mature fish for all species was relatively low at each site, so the difference seen in GSI in male Walleye may be the result of low sample size.

Female Northern Pike and White Sucker had significant differences between spring 2012 and spring 2013 in some measures of fecundity, with Northern Pike having significantly higher values for each variable in spring 2012 and White Suckers in spring 2013. Both are likely the result of the larger average size of female Northern Pike caught in spring 2012 compared to spring 2013 and the larger average size of sexually mature White Suckers caught in spring 2013 when compared to 2012 (Table 3.6). However, relative weight was not significantly different between seasons for Northern Pike.

3.4.6 Comparison with Other Systems

All four fish species obtained the majority of their carbon through autochthonous sources indicating that in situ primary production was the most important carbon source within Lake Diefenbaker. Small rivers often have food webs supported largely by allochthonous carbon while the food webs of large rivers are supported mainly by autochthonous carbon (Finlay 2001). Allochthonous carbon is of greater importance during periods of high flow in most river systems (Kendall et al. 2001). Of three major carbon cycling models for rivers, the Riverine Productivity Model (Thorp and DeLong 1994) most accurately describes the dominant carbon pathways within Lake Diefenbaker compared to the River Continuum Concept (Vannote et al 1980) or the Flood Pulse Concept (Junk et al. 1989). Reservoir food webs often have a higher contribution from

autochthonous carbon sources than the riverine food webs in their tributaries (Hoeinghaus et al. 2007). Even when allochthonous carbon sources are plentiful in reservoirs, certain consumers such as *Daphnia* spp. often rely almost entirely on autochthonous organic matter for their diets (Min-Seob et al. 2014). This is common in lakes, where zooplankton are known to rely heavily on autochthonous organic matter when allochthonous carbon is abundant (Cole et al. 2002; Mohamed and Taylor 2009). In turn, this leads to the higher importance of autochthonous carbon to all higher trophic levels throughout the planktonic food web.

Allochthonous carbon is most important to reservoir food webs during or immediately after periods of high flow in the tributaries (Chen and Jia 2009; Sanchez-Vidal et al. 2013). Increased turbidity during periods of high inflow into Lake Diefenbaker is also associated with low concentrations of chlorophyll (Yip et al. 2015). In 2012 and 2013 Lake Diefenbaker was characterized by high flow events from the South Saskatchewan River (Hudson and Vandergucht 2015). The associated large loads of allochthonous organic carbon to Lake Diefenbaker during these events should have resulted in greater contributions of allochthonous carbon to consumer diets (Perga et al. 2005). However, the importance of allochthonous carbon to the diets of all fish species was still low when compared to the importance of autochthonous carbon during these years. This could be due in part to the slow turnover times of fish tissue (Hesslein et al. 1992), but is more likely an indicator that even during periods of high flow, allochthonous carbon is of little importance to the prey of these fish species throughout Lake Diefenbaker.

3.5 Conclusions

The diets of four common fish species within Lake Diefenbaker (i.e., Lake Whitefish, Northern Pike, Walleye and White Sucker) predominantly consist of carbon of autochthonous origin. Allochthonous carbon is of little importance to the diets of any of these fish species

throughout the reservoir. The only site with a noticeably higher contribution of allochthonous carbon to the diets of fish was site 1, located in the most upstream reaches of the reservoir in the riverine zone. Autochthonous carbon produced through benthic primary production was the most important source to the diets of Northern Pike, Walleye and White Sucker. Pelagically derived autochthonous carbon was the most important source for Lake Whitefish. The contribution of pelagic carbon to the diets of Lake Whitefish decreased with increasing distance downstream, but increased for Northern Pike and White Sucker. Walleye did not show a major increase or decrease in the contribution of pelagic carbon to their diets with the exception of site 1, which had the lowest contribution from this carbon source. Secondly, it was predicted that pelagic carbon would be of higher importance than benthic carbon to all four fish species due to the physical properties (i.e., mean depth of 22.9 metres, high levels of shoreline erosion and fluctuating water levels) of Lake Diefenbaker. However, benthic carbon contributed more to the diets of Northern Pike, Walleye and White Sucker than pelagic carbon, but pelagic carbon contributed more to the diets of Lake Whitefish, just as predicted.

Fish condition often corresponded to the proportion of the diet made up by each carbon source for most species. Lake Whitefish had lower W_r as well as some measures of fecundity in those fish with a higher contribution of benthic carbon and a corresponding decrease in the contribution of pelagic carbon to their diets. This was most commonly seen in fish from the downstream reaches of the reservoir. Northern Pike showed an increase in W_r and measures of fecundity with increasing contributions from pelagic carbon to their diets. This corresponded to a decrease in some measures of fecundity with increasing contributions from allochthonous carbon. Interestingly White Suckers showed a decrease in some measures of fecundity with increasing contributions from pelagically derived carbon, the opposite of what was seen in Lake

Whitefish and Northern Pike. Walleye W_r and some measures of fecundity were not related to the percent contribution of each carbon source to their diets. The importance of each carbon source as well as the quality of that carbon source to the diets of fish within Lake Diefenbaker varies between species, but it is clear that autochthonous carbon is of greater importance to the diets of all four fish species at all sites within the reservoir when compared to allochthonous carbon.

CHAPTER 4. General Conclusions

4.1 Study Accomplishments

This study set out to determine the importance of different carbon sources to the diets of Lake Whitefish, Northern Pike, Walleye and White Sucker within Lake Diefenbaker using stable isotope analysis. Carbon and nitrogen stable isotope values of aquaculture waste were different from both benthic and pelagic autochthonous primary production as well as allochthonous primary production. This allowed for the identification of fish that were subsidizing their diets with aquaculture waste and differentiating from those which were not. Differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between the potential carbon sources allowed for the use of the stable isotope mixing models SIAR and SIARsolo to estimate the contribution of each carbon source to the diets of fish within Lake Diefenbaker. Resource use varied by species both spatially and temporally in some cases. Differences in resource use were often linked to differences in condition factors including relative weight and fecundity.

4.2 Support of Lake Whitefish Diets through Aquaculture Waste

Only Lake Whitefish that were caught in close proximity to the cages showed any contribution from aquaculture waste to their diets. Lake Whitefish caught immediately adjacent to the fish farm cages in fall 2013 and one other Lake Whitefish caught approximately 400 metres from the cages were calculated to rely almost entirely on aquaculture waste. Three Lake Whitefish caught within Cactus Bay where the aquaculture facility is located showed some contribution from aquaculture waste, but were not yet specializing on it or had only recently begun to do so.

Those Lake Whitefish specializing on aquaculture waste were larger and had higher relative weights than either the aquaculture waste generalists or Lake Whitefish not utilizing this

diet subsidy. When examining the different measures of fecundity, both male and female aquaculture waste specialists had larger gonads and females had higher egg counts than those Lake Whitefish not utilizing aquaculture waste. However, once standardized for body weight, there were no differences between the groups for egg number per gram of body weight or GSI for either males or females. Any benefits to the Lake Whitefish population in Lake Diefenbaker from the addition of aquaculture waste appeared to be limited to the area immediately surrounding the cage culture facility. Lake Whitefish may act as vectors of dispersion, helping to distribute nutrients from the aquaculture facility to the surrounding area, but this dispersion also appears to be limited to the area immediately surrounding the fish farm.

4.3 The Importance of Allochthonous and Autochthonous Support of Food Webs

Allochthonous carbon sources were of little importance to the diets of Lake Whitefish, Northern Pike, Walleye and White Sucker throughout most of Lake Diefenbaker. The only site that had higher contributions of allochthonous carbon to the diets of the study species was the most upstream site located in the riverine zone of the reservoir near the Highway 4 Bridge. Lake Whitefish showed almost no contribution from allochthonous carbon at any sites including those in the riverine zone. Pelagic primary production was expected to be of highest importance to the diets of all four fish species studied due to the morphometry of the reservoir (i.e., the system was steep sided with little littoral habitat and a mean depth of 22.9 metres). However, pelagic primary production was the most important carbon source only for Lake Whitefish. Northern Pike, Walleye and White Sucker showed higher contributions from benthic carbon to their diets than from pelagic primary production. The importance of each carbon source to the diets of each fish species often differed between sites, with Lake Whitefish becoming increasingly more benthic and Northern Pike becoming increasingly more pelagic with distance downstream. No clear

trends were apparent for Walleye and White Sucker which both showed relatively stable contributions from benthic and pelagic carbon throughout sites located in the lacustrine zone of Lake Diefenbaker.

Differences in resource use between members of the same species often corresponded to differences in fecundity or relative weight. Lake Whitefish had lower relative weight and some measures of fecundity with increasing contributions of benthic carbon to their diet. Northern Pike showed increases in fecundity and relative weight with increased contributions of pelagic carbon and decreased contributions from allochthonous carbon. On the other hand, White Sucker had decreases in some measures of fecundity with increased contributions from pelagic carbon and decreased contributions from benthic carbon. Walleye did not show any major differences in fecundity or relative weight with different contributions from each potential carbon source.

4.4 Limitations of the Current Study and Potential Room for Improvement

The complexity of most large reservoirs makes them interesting, but difficult to study. One of the limitations to both studies was the spatial extent to which sampling was carried out. In hindsight, more sites should have been located in close proximity to the fish farm cages (i.e., within 1000 metres) as Lake Whitefish specializing in aquaculture waste were not found further than 400 metres from the cages. If more sampling was conducted in this area of the reservoir, a greater number of fish feeding on aquaculture waste may have been encountered. However, the impact of the fish farm on the diets of Lake Whitefish in Lake Diefenbaker would likely still only have been noticeable in the area immediately surrounding the cages and would have remained a very minor contribution on the overall wild stock of the reservoir. As well, more sites should have been located within the riverine zone of the reservoir to test for allochthonous resource use in the area of the reservoir where allochthonous carbon was highest in abundance.

This would have allowed for a greater spatial representation of both of these resource subsidies to the food webs in Lake Diefenbaker.

One of the biggest limitations of the current study was time. Time from when sampling was conducted until when stable isotope analysis results were received made for an exceptionally long study. Sampling fewer locations within the lacustrine zone of Lake Diefenbaker and focusing more on the riverine zone of the reservoir and in the area immediately around the fish farm cages would have allowed for a more efficient use of the time allocated to this study. A more rapid turnaround time of samples would have permitted adjustments to the study design following the first field season and allowed for a redistribution of sites in the riverine zone of the reservoir for better spatial coverage.

Both 2012 and 2013 were flood years with higher than average inflow into Lake Diefenbaker (Hudson and Vandergucht 2015). It would have been beneficial to test allochthonous and autochthonous resource use in years with high flow as well as low flow to account for the variability seen in reservoirs. Unfortunately, inflow into Lake Diefenbaker cannot be controlled from year to year and is one of the variables which may play a key role in the variation of the contribution of allochthonous and autochthonous resources to the diets of consumers from year to year. If the study had included a year of low water, it is likely that allochthonous carbon would have been of even lower importance compared to the results from 2012 and 2013.

The addition of other fish species to this study may have helped to further characterize the importance of each carbon source. Other benthic feeding species, such as Lake Sturgeon, Burbot, or Shorthead Redhorse may have been utilizing aquaculture waste directly below the cage culture facility. Pelagic fish species, such as Cisco would likely have shown a higher

contribution from pelagic carbon, while species such as Goldeye, known to prefer turbid waters (Scott and Crossman 1973) may have had a higher contribution from allochthonous carbon than other species. However, all things considered, the four species studied were the only species encountered at all study sites. The other species had sporadic distributions and were only present at a few locations, or in the case of Burbot were not present in any of the gill net catches. If any other species were used in this study, different sampling methodology would have been necessary as they were not commonly encountered in the gill net catches in this study.

4.5 Future Directions

The recent expansion of Wild West Steelhead to another site located at Kadla Coulee, one of the sites used in this study, allows for a follow up study in this location. The data collected in this study could be used as baseline information before the fish farm cages were located in Kadla Coulee. In addition to this, it would be beneficial to have a larger degree of sampling located in close proximity (i.e., 1000 metres) to the aquaculture cages to address the limited spatial distribution for which Lake Whitefish subsidizing their diets on aquaculture waste were found. This would allow for a better estimation of the distribution of Lake Whitefish specializing on aquaculture waste and the potential area over which nutrients from the fish farm are dispersed by these fish. Another useful addition to this study could involve tagging Lake Whitefish around the aquaculture cages with acoustic telemetry tags in order to track their movements around the cage culture facility. This would provide additional information on the range of these aquaculture waste specialists within the reservoir and provide information on the dispersal of nutrients by these fish.

The most important addition to this study would likely come from an increase in the number of sites located in the riverine zone, including sites upstream of the Highway 4 Bridge.

This would allow for a better estimation of allochthonous resource use in the area of the reservoir where allochthonous resources are plentiful. Allochthonous carbon was of little importance to all four fish species in the lacustrine regions of the reservoir, so any additional sampling should be focused on the upstream regions of Lake Diefenbaker. In addition, using a species commonly found throughout the riverine zone of the reservoir, such as Goldeye, could provide further insight into the use of allochthonous carbon by a fish species that specializes in the upstream reaches of the reservoir.

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