

FEEDING ECOLOGY AND MOVEMENT OF
INTRODUCED YELLOW PERCH (*Perca flavescens*) IN BC LAKES

by

CARMEN TATTERSFIELD

B.N.R.S. Thompson Rivers University 2006

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

(Environmental Science)

THOMPSON RIVERS UNIVERSITY

November 2013

Acknowledgements

I would like to acknowledge my supervisor, Brian Heise, for his enthusiasm and support to help me achieve my goals over the past two years. A thanks to Karl Larsen, Don Noakes and Andrew Klassen, my committee members, for their input and feedback throughout the stages of my project.

I would especially like to thank Jimmy Arner, who provided great field and lab assistance, endless encouragement, and always showed up on time, smiling, rain or shine!

Thanks to Dave Sedgeman for his veterinary expertise, and to Sam Coggins and Nicole Glover for volunteering their time to help with a GIS dilemma. Many other people volunteered their time and resources to help with various stages of field-work including Lynda Ritchie, Jacque Sorensen, Bruce Whitehead, Sherri Schmidt, Carla Grimson, Tom Nevin and Riley Kelly. Without these people and their contributions, this research would not have been possible. Financial support was provided through an Industrial Postgraduate Scholarship from the Natural Sciences and Engineering Research Council of Canada. The Pacific Salmon Foundation provided industrial sponsorship, while Fisheries and Oceans Canada, the Fraser Salmon and Watersheds Program and CN Rail provided research funding.

Abstract

Yellow perch (*Perca flavescens*) are a non-native species in most areas of British Columbia (BC) and could impact those ecosystems where they are introduced. To address this, I investigated seasonal diet composition and basic movement of introduced yellow perch in lakes within the Okanagan Region of British Columbia. In addition, a trial of the use of artificial spawning substrates as a potential method of removing eggs was completed. Diet composition was determined during five seasonal sampling periods, by counting and identifying items within perch stomachs. I compared diet composition among lakes, and among seasons and size classes within each lake using a multivariate analysis. Diet composition of yellow perch varied by lake. Most notably, yellow perch diets did not include juvenile fishes in several lakes, but the fish consumed large proportions of zooplankton. It is possible that diet composition of introduced yellow perch could be predicted based on presence or absence of predators and refugia for prey species. Prey selectivity and diet overlap with rainbow trout was also determined. Prey selectivity of perch varied among study lakes and seasons. Significant diet overlap between yellow perch and rainbow trout occurred in one of two lakes tested, likely lake-specific due to variable strains of rainbow trout stocked. Radio telemetry showed that in summer, yellow perch were found relatively close to shore, with no significant difference found among time periods within a 24-hour tracking session. In spring, yellow perch were significantly farther from shore when ice was covering the lake, and moved closer to shore as the ice receded. This coincided with the beginning of the spawning season at temperatures of 3.8 °C, the lowest end of the known spawning temperature range. Trials using artificial spawning substrates were successful. Perch spawned multiple times on all artificial spawning substrates and eggs were removed from the lake in an attempt to reduce spawning success. Overall, yellow perch displayed the expected characteristics of a generalist species across all study lakes, as would be expected in their native range; however, some specialization within specific lakes was observed.

Keywords

Perca flavescens, Yellow perch, Introduced species, British Columbia, Diet composition, Spawning timing, Movement, Prey selection

Table of Contents

1. INTRODUCTION.....	1
Ecological changes in novel habitats	2
Yellow perch in British Columbia.....	2
Thesis objectives and format.....	4
References.....	5
2. FEEDING ECOLOGY OF INTRODUCED YELLOW PERCH IN BC LAKES...10	
Introduction.....	10
Methods.....	12
Study sites.....	12
Sampling and laboratory analysis.....	18
Prey selectivity.....	24
Dietary overlap between yellow perch and rainbow trout.....	24
Condition factor.....	25
Results.....	25
Yellow perch diet.....	25
Rainbow trout diet.....	35
Prey abundance.....	37
Yellow perch prey selectivity.....	38
Rainbow trout prey selectivity.....	39
Diet overlap.....	40
Relative condition.....	40
Discussion.....	42
Yellow perch feeding ecology.....	42
Rainbow trout feeding ecology.....	47
Diet overlap.....	48
Condition.....	49
Management implications.....	50
References.....	53

3. MOVEMENT AND HABITAT USE OF INTRODUCED YELLOW PERCH IN TWO BC LAKES	58
Introduction.....	58
Study Lakes.....	59
Methods.....	60
Fish collection and implants	60
Tracking	61
Dissolved oxygen and temperature	62
Data analysis	62
Results	63
Summer tracking.....	63
Spring tracking.....	66
Dissolved oxygen and temperature.....	68
Discussion	70
Summer 24 hour tracking.....	70
Spring tracking.....	71
References.....	72
4. CONCLUSION.....	75
Summary.....	75
Study limitations	76
Applications and future direction	77
References.....	79

APPENDICES.....	82
APPENDIX A – COMBINING INVERTEBRATE SAMPLING METHODS FOR A BETTER DETERMINATION OF OVERALL FOOD AVAILABILITY IN LAKES WHEN CALCULATING PREY SELECTION BY FISHES.....	82
APPENDIX B – DIET COMPOSITION CHARTS	96
APPENDIX C - CALIBRATION OF TELEMETRY SIGNAL LOCATION.....	106
APPENDIX D - SPAWNING TIMING AND USE OF ARTIFICIAL SPAWNING SUBSTRATES FOR INTRODUCED YELLOW PERCH IN PINAUS LAKE AND LITTLE PINAUS LAKE	107

List of Figures

Figure 1-1. Yellow perch distribution in British Columbia (from Bradford et al. 2008) ...	3
Figure 2-1. Location of study lakes within British Columbia.	13
Figure 2-2. (From Amundsen et al. 1996) Diagram for interpretation of prey importance, feeding strategy, and niche variation. Prey points in upper left of plot indicate prey that are consumed by few individuals that are displaying specialization; points in lower right represent prey items consumed occasionally, but by most individuals..	23
Figure 2-3. Summary of yellow perch diet composition among all study lakes. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials).	26
Figure 2-4. Prey importance, feeding strategy and niche width contribution for Pinaus Lake yellow perch. See Figure 2-3 text for prey category abbreviations and interpretation of graph.....	27
Figure 2-5. Prey importance, feeding strategy and niche width contribution for Bear Lake yellow perch. See Figure 2-3 text for prey category abbreviations and interpretation of graph.	29
Figure 2-6. Prey importance, feeding strategy and niche width contribution for Little Pinaus Lake yellow perch. See Figure 2-3 text for prey category abbreviations and interpretation of graph.....	30

Figure 2-7. Prey importance, feeding strategy and niche width contribution for Swan Lake yellow perch. See Figure 2-3 text for prey category abbreviations and interpretation of graph. Points in the upper right are cladocerans (CL) for spring, summer and late summer. 31

Figure 2-8. Prey importance, feeding strategy and niche width contribution for Kalamalka Lake yellow perch. See Figure 2-3 text for prey category abbreviations and interpretation of graph..... 32

Figure 2-9. Prey importance, feeding strategy and niche width contribution for Wood Lake yellow perch. See Figure 2-3 text for prey category abbreviations and interpretation of graph..... 33

Figure 2-10. Prey importance, feeding strategy and niche width contribution for Ellison Lake yellow perch. See Figure 2-3 text for prey category abbreviations and interpretation of graph..... 34

Figure 2-11. Overall rainbow trout diet composition in Pinaus and Little Pinaus Lakes, shown in proportions by prey category. Prey categories with highest total proportions are towards the top of the y-axis. See Figure 2-3 prey category abbreviations. 35

Figure 2-12. Prey importance, feeding strategy and niche width contribution for Pinaus Lake rainbow trout. See Figure 2-3 text for prey category abbreviations and interpretation of graph..... 36

Figure 2-13. Prey importance, feeding strategy and niche width contribution for Little Pinaus Lake rainbow trout. See Figure 2-3 text for prey category abbreviations and interpretation of graph..... 37

Figure 2-14. Mean Fulton condition factor for yellow perch in study lakes during each sampling period. Values less than 1 indicate fish are smaller than average (Blackwell et al. 2000)..... 41

Figure 2-15. Mean Fulton condition factor for rainbow trout in Pinaus and Little Pinaus Lakes during each sampling period. Values near 1 indicate fish are of average condition (Blackwell et al. 2000)..... 42

Figure 2-16. Predicted feeding strategy of introduced yellow perch based on diet analysis and observations of lake characteristics including presence of predators and refugia. 52

Figure 3-1. Mean distance from shore (+/- 95% CI) for yellow perch in Pinaus Lake during summer tracking for each of the three tracking periods within the 24 tracking sessions. 50% of the data points lie within the boxed area. Error bars above and below represent the higher and lower quartiles of data, which are shown as individual points..... 64

Figure 3-2. Pinaus Lake recorded depths (m) during summer tracking for each of the three tracking periods within the 24 tracking sessions. 64

Figure 3-3. Mean distance from shore (+/- 95% CI) for yellow perch in Bear Lake during summer tracking for each of the three tracking periods within the 24 tracking sessions. 65

Figure 3-4. Bear Lake recorded depths (m) during summer tracking for each of the three tracking periods within the 24 tracking sessions. 65

Figure 3-5. Mean distance from shore (m) (+/- 95% CI) for yellow perch in Pinaus Lake spring 2012 tracking sessions. First egg masses were seen on April 25, 2012..... 67

Figure 3-6. Mean daily littoral water temperatures in Pinaus Lake at approximately 0.5 m depth from March 24, 2012 – May 28, 2012. Perch were observed moving closer to shore on April 20, 2012 and first egg masses were seen April 25, 2012..... 67

Figure 3-7. Dissolved oxygen profiles for Pinaus and Bear Lakes during summer tracking sessions. 69

Figure 3-8. Dissolved oxygen profiles for Pinaus Lake during spring tracking sessions. On March 24, 2012, ice cover was present on the lake. April 27, 2012 and later were ice free..... 70

Figure A- 1. Selection indices for the three combined measures of food availability \pm S.E. Values equal to 1, indicated by the line, are neutral selection; the food resource is being used randomly. A higher or lower selection index indicates positive or negative selection. There was no significant overall selection for resources. 89

Figure A- 2. Selection indices for food availability using d-frame net measurement \pm S.E. Values equal to 1, indicated by the line, are neutral selection; the food resource is being used randomly. A higher or lower selection index indicates positive or negative selection. There was no significant overall selection for resources. 90

Figure A- 3. Selection indices for food availability using Ekman grab measurement \pm S.E. Values equal to 1, indicated by the line, are neutral selection; the food resource is being used randomly. A higher or lower selection index indicates positive or negative selection. There was no significant overall selection for resources. 90

Figure A- 4. Selection indices for food availability using plankton net measurement \pm S.E. Values equal to 1, indicated by the line, are neutral selection; the food resource is being used randomly. A higher or lower selection index indicates

positive or negative selection. Overall, significant selection for resources was indicated. 91

Figure B- 1. Pinaus Lake yellow perch diet composition. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials). 97

Figure B- 2. Bear Lake yellow perch diet composition. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials). 98

Figure B- 3. Little Pinaus Lake yellow perch diet composition. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials). 99

Figure B- 4. Swan Lake yellow perch diet composition. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran

larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans),
 HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates),
 TR(trichopterans), OA(other aquatics), and OT(other terrestrials). 100

Figure B- 5. Kalamalka Lake yellow perch diet composition. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials). 101

Figure B- 6. Wood Lake yellow perch diet composition. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials). 102

Figure B- 7. Ellison Lake yellow perch diet composition. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials). 103

Figure B- 8. Pinaus Lake, rainbow trout diet composition. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were

abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials). 104

Figure B- 9. Little Pinaus Lake, rainbow trout diet composition. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials). 105

Figure D- 1. Artificial spawning substrate constructed from a wire cage filled with willow branches, put into Pinaus Lake. 111

List of Tables

Table 2-1. Location and physical characteristics of sample lakes. Elevation, surface area and maximum depth from BCMoE (2013). Mean Secchi depths from sampling dates in Table 2-2.	13
Table 2-2. Seasonal stomach content sampling dates at study lakes.	14
Table 2-3. Lake and fish community characteristics based on field observations during fish sample collections.	17
Table 2-4. Fish community in study lakes based on field observations and BC provincial database (BCMoE, 2013).	17
Table 2-5. Summary of yellow perch samples dissected for diet analysis. The number of fish analyzed (N), mean fork length (L_F) \pm S.D. and weight (w) \pm S.D. are shown for each lake and season sampled.	19
Table 2-6. Summary of rainbow trout samples dissected for diet analysis. The number of fish analyzed (N), mean fork length (L_F) \pm S.D. and weight (w) \pm S.D. are shown for each lake and season sampled.	20
Table 2-7. Yellow perch prey selection by season for each study lake. Significant overall prey selection by season is indicated by *. Top three preferred prey categories are listed in order of highest (left) to lowest (right), based on selection indices by season, regardless of significance. See Figure 2-3 caption for prey category abbreviations.	39
Table 2-8. Rainbow trout prey selection by season for each study lake. Significant overall prey selection by season is indicated by *. Top three preferred prey categories are listed in order of highest (left) to lowest (right), based on selection indices by	

season, regardless of significance. See Figure 2-3 caption for prey category abbreviations. 40

Table 2-9. Summary of Morisita’s Overlap Indices *(>0.6 is sig.) values for yellow perch and rainbow trout in Pinaus and Little Pinaus Lakes..... 40

Table 3-1. Location and physical characteristics of sample lakes (BCMoe 2013). 59

Table 3-2. Implant and tracking dates for yellow perch in Pinaus and Bear Lakes. 60

Table 3-3. Summary of number of telemetry locations obtained for Pinaus Lake during summer and spring tracking, and Bear Lake during summer tracking. 63

Table A-1. Mean proportions of food availability by sampling method. Blanks indicate that the taxa were not found using the particular sampling method. *Zero counts were replaced by small value 0.0001 to enable selection calculation..... 87

Table A-2. Positive selection results for Manly’s selectivity indices. Check marks indicate a positive selection index for a food resource. Shaded cells indicate overlapping positive selection between combined and pooled methods. 89

1. Introduction

Invasive species have been labeled as one of the leading causes of biodiversity loss worldwide (Vitousek et al. 1996, Simberloff et al. 2005). The rate of non-native fish introductions is rapidly increasing and has become a major environmental issue of public concern (Cambray 2003, Gozlan et al. 2010). Introduced species can be a significant challenge for resource managers and can negatively impact ecosystem function through increased predation, competition and habitat degradation (Lodge 1993, Marchetti 1999, Cambray 2003, Gozlan et al. 2010).

Predation is one of the most quantifiable effects of predatory invasive species and has been documented as playing a significant role in the decline of native species (Sanderson et al. 2009). Predatory and omnivorous fish have been shown to cause some of the greatest impacts in aquatic ecosystems (Sih et al. 1985, Moyle and Light 1996). These impacts can be related to diet and behaviour, where a generalist species with a broad niche width may have a greater impact than a diet specialist (Bøhn and Amundsen 2001, Kolar and Lodge 2002). Predation has been shown to be a more important interaction between species than competition and can lead to serious impacts or extirpations of native species (Sax and Gaines 2008). However, predation in combination with competition, which may occur with a generalist piscivorous fish such as yellow perch (*Perca flavescens*), could be particularly serious. It has been shown that a higher rate of native fish extirpations can occur where piscivorous invasive species are present compared to non-piscivorous species (Mitchell and Knouft 2009). These types of predation and competition effects, which can influence species abundance, distribution and community composition, can be magnified when a predator is introduced outside its native range (Zaret and Paine 1973, Lodge 1993). In addition to a broad niche width, species that exhibit behavioural flexibility or a diversity of behaviours in new habitats can be of particular concern due to their adaptability (Wright et al., 2010).

Ecological changes in novel habitats

Introduced species are known to rapidly adapt to new environments and can exhibit changes in behaviour and life history traits in novel habitats (Mooney and Cleland 2001). Variation in foraging strategies or movement patterns in introduced species can often be attributed to the “Adaptive Flexibility Hypothesis,” where behavioural diversity could be exhibited through differences in foraging strategy and diet, triggered due to metabolic needs, predator avoidance or to utilize resources in a novel habitat (Wright et al. 2010). Behavioural variants are often greatest soon after introduction, followed by a decline in behavioural variance due to success of a particular behaviour that is perpetuated (Wright et al. 2010). Studies on invasive mosquitofish (*Gambusia*) showed that they exhibited higher feeding rates than their native counterparts (Rehage et al. 2005). In Europe, introduced pumpkinseeds (*Lepomis gibbosus*) were shown to have similar diets to native North American populations, but showed less molluscivory than in native North American populations (Garcia-Berthou and Marino-Amich 2000).

In BC lakes, yellow perch do not have natural predators, and it is unknown how this is impacting their behaviour. It is not known to what extent rainbow trout and other native fish species in BC lakes are predated upon or compete with yellow perch for invertebrate food resources. Invasive fish species, including yellow perch, have been documented to strongly impact native community structure by altering the abundance and diversity of macroinvertebrates (Zaret and Paine 1973, Post and Cucin 1984, Krakowiak and Pennuto 2008). A lack of competition or reduced risk of predation may be allowing yellow perch to utilize different food resources and broaden their habitat selection, resulting in a niche shift due to behavioural plasticity (MacArthur and Pianka 1966; Diamond 1970). Any potential changes in diet or movement patterns would be a direct indicator of behavioural flexibility (Persson and Hansson 1999, Wright et al. 2010).

Yellow perch in British Columbia

Yellow perch are native to Canada, east of the Rocky Mountains; however, their range has expanded into British Columbia (BC), likely due to illegal introductions by sport

fishers (Roberge and Slaney 2001, Brown et al. 2009). Yellow perch were confirmed present in 78 lakes, ponds and streams in 2009 in BC (Figure 1-1) (Runciman and Leaf 2009), and have since been eradicated from several smaller lakes using the piscicide rotenone (Christensen and Trites 2011). In 2011, a risk assessment on Yellow perch in BC was completed by Fisheries and Oceans Canada's Centre of Expertise for Aquatic Risk Assessment (CEARA), to determine the potential magnitude of ecological impacts (Bradford et al. 2008). Results indicated that yellow perch could cause a high level of impact in smaller lakes and moderate impacts in larger lakes including reduction of food resources within foraging areas, and significant reductions in zooplankton (Bradford et al. 2008).

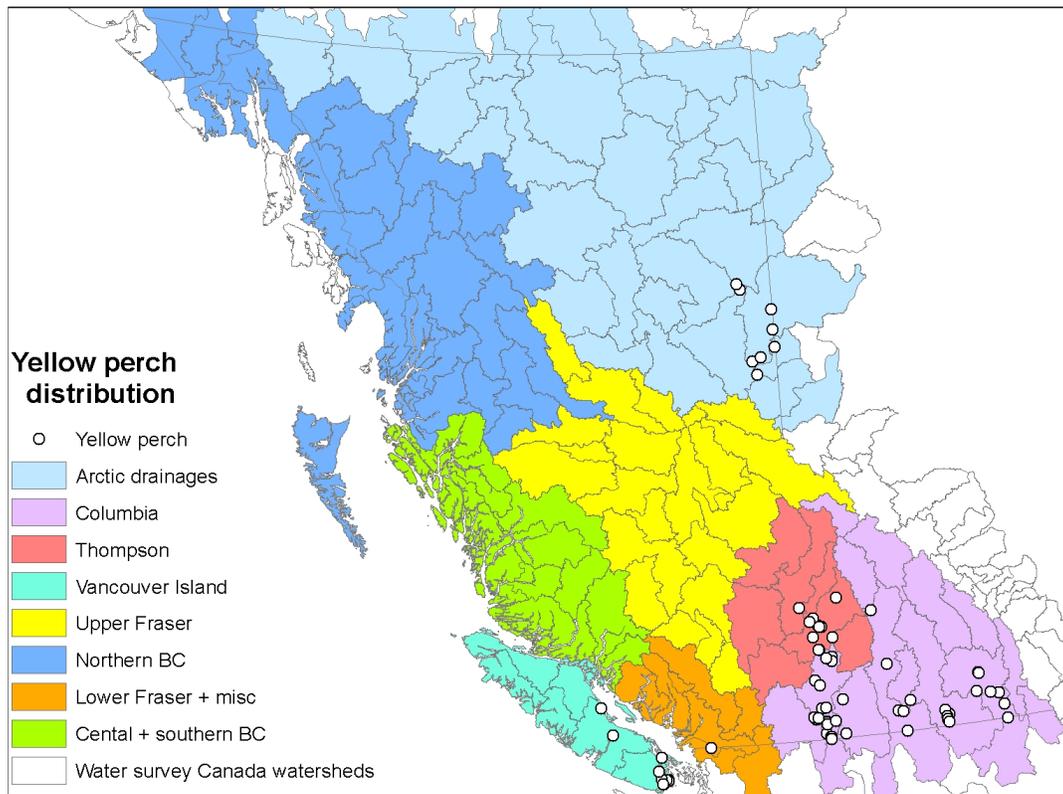


Figure 1-1. Yellow perch distribution in British Columbia (from Bradford et al. 2008)

Yellow perch possess the characteristics of a successful invader, including a wide environmental tolerance, rapid growth, high reproductive capacity and broad diet (Ricciardi and Rasmussen 1998). Yellow perch are able to adapt and live in a wide range of habitat conditions, and may negatively impact trout and native fish populations by both competing with them for food and by directly eating juveniles (Bonar et al. 2005). Introduced populations of yellow perch are expected to reduce food resources within foraging areas and cause significant reductions in zooplankton (Bradford et al. 2008). Specifically, there is concern about the impact of yellow perch on salmonid populations if they were to establish in large lake systems that provide key salmon rearing habitat (Pauley et al. 1989).

Yellow perch are commonly studied in their native habitat (Knight et al. 1984, Truemper et al. 2006, Brown et al. 2009, Weber et al. 2010). In addition, there are numerous studies on European perch (*Perca fluviatilis*), a species said to be biologically equivalent (Thorpe 1977); however, there is no specific information available on the ecology of yellow perch in British Columbia. Detailed information on components of their ecology, such as diet and movement, allow for better evaluation of their potential impacts by determining whether a broad niche width has been maintained in novel habitats, or if an adaptive response to new environment has occurred causing some deviation from the behaviour expected in native habitats.

Thesis objectives and format

The primary objective of this research was to document the diet composition and feeding strategy of yellow perch in lakes where they have been introduced.

The results of this research are presented in two independent manuscript-style chapters within this thesis. Chapter 2 describes an observational field study that was conducted to assess the feeding ecology of introduced yellow perch, by determining what they ate in seven study lakes in BC's Okanagan region through a seasonal stomach contents analysis. Diet composition was compared among lakes and seasons, and to available food

resources within the study lakes to determine if perch selected for specific food items. Yellow perch diet was also compared to rainbow trout (*Oncorhynchus mykiss*) diets in two lakes to determine if dietary overlap occurred. Null hypotheses were that introduced yellow perch would maintain a generalist feeding strategy and utilize the most plentiful food available, rather than selecting for specific resources, and that diet overlap would occur between yellow perch and trout diets in the lakes studied.

Chapter 3 describes a small radio telemetry study where locations of yellow perch were recorded to determine if they utilized near-shore or offshore habitat in two study lakes (Pinaus and Bear Lakes) during the summer. It was predicted that yellow perch would remain in relatively near-shore shallow habitat around the lakeshore, similar to what would be expected in their native habitat. Additional telemetry information was collected in Pinaus Lake in early spring to determine if similar near-shore locations were maintained during the spawning season.

Additional observations on spawning timing and temperatures were made in Pinaus Lake, during the spring telemetry study. In addition, a trial of the use of artificial spawning substrates as a potential method to remove egg masses from the lake was completed. Spawning timing and substrate trial observations are included in Appendix D.

Chapter 4 concludes this thesis, providing a summary of research, limitations of the work and application of the research including management implications for British Columbia.

References

- Bøhn, T. and Amundsen, P.A. 2001. The competitive edge of an invading specialist. *Ecology*. 82: 2150-2163.
- Bonar, S.A., Bolding, B.D., Divens, M. and Meyer, W. 2005. Effects of introduced fishes on wild juvenile coho salmon in three shallow Pacific Northwest Lakes. *Transactions of the American Fisheries Society*, 134: 641-652.

- Bradford MJ, Tovey CP, Herborg LM. 2008. Biological risk Assessment for yellow perch (*Perca flavescens*) in British Columbia. Canadian Science Advisory Secretariat Research Document 073.
- Brown, T.G., Runciman, B., Bradford, M.J. and Pollard, S. 2009. A biological synopsis of yellow perch (*Perca flavescens*). Canadian Manuscript Report of Fisheries and Aquatic. Sci. 2883, 28 p.
- Cambray, J. A. 2003. Impact on indigenous species biodiversity caused by the globalization of alien recreational freshwater fisheries. *Hydrobiologia*, 500: 217-230.
- Christensen, V. and Trites, A.W. 2011. Predation on Fraser River sockeye salmon. Cohen Commission. Technical Report. 8:129p. Vancouver, B.C.
- Department of Fisheries and Oceans (DFO), 2011. Science advice from a risk assessment of yellow perch (*Perca flavescens*) in British Columbia. DFO Canadian Science Advisory Secretariat Report, 2012/081.
- Diamond, J. M. 1970. Ecological consequences of island colonization by Southwest Pacific birds, I. types of niche shifts. *Proceedings of the National Academy of Sciences*, 67: 529-536.
- Garcia-Berthou, E. and Moreno-Amich, R. 2000. Food of introduced pumpkinseed sunfish: ontogenetic diet shift and seasonal variation. *Journal of Fish Biology*, 57: 29-40.
- Gozlan, R.E., Britton, J.R., Cowx, I. and Copp, G.H. 2010. Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology*. 76: 751-786.
- Krakowiak, P.J. and Pennuto, C.M. 2008. Fish and macroinvertebrate communities in tributary streams of eastern Lake Erie with and without round gobies (*Neogobius melanostomus*, Pallas 1814). *Journal of Great Lakes Research*, 34: 675-689.
- Knight, R.L., Margoff, F.J., and Carline, R.F. 1984. Piscivory by walleye and yellow perch in western Lake Erie. *Transactions of the American Fisheries Society*, 113: 677-693.
- Kolar, C.S. and Lodge, D. M. 2002. Ecological predictions and risk assessment for alien fishes in North America. *Science*, 298: 1233-1236.

- Lodge, D.M. 1993. Biological invasions: lessons for ecology. *Trends in Ecology and Evolution*, 8: 133-136.
- MacArthur, R.H., and Pianka, E.R. 1966. On optimal use of a patchy environment. *The American Naturalist*, 100: 603-609.
- Marchetti, M.P. 1999. An experimental study of competition between the native Sacramento perch (*Archoplites interruptus*) and introduced bluegill (*Lepomis macrochirus*). *Biological Invasions*, 1: 55-65.
- Mitchell, A.L. and Knouft, J.H. 2009. Non-native fishes and native species diversity in freshwater fish assemblages across the United States. *Biological Invasions*, 11: 1441-1450.
- Mooney, H.A. and Cleland, E.E. 2001. The evolutionary impact of invasive species. *Proceedings of the National Academy of Science*, 98: 5446-5451.
- Moyle, P.B., and Light, T. 1996. Biological invasions of freshwater: empirical rules and assembly theory. *Biological Conservation*, 78: 149-161.
- Pauley, G.B., Risher, R., and Thomas, G.L. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest): sockeye salmon. US Fish and Wildlife Service Biological Report, 82: 22 p.
- Persson, A. and Hansson, L.A. 1999. Diet shift in fish following competitive release. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 70-78.
- Post, J.R. and Cucin, D. 1984. Changes in the benthic community of a small Precambrian lake following the introduction of yellow perch, *Perca flavescens*. *Canadian Journal of Fisheries and Aquatic Sciences*, 44: 1496-1501.
- Rehage, J.S., Barnett, B.K. and Sih, A. 2005. Behavioral responses to a novel predator and competitor of invasive mosquitofish and their non-invasive relatives (*Gambusia sp.*). *Behavioural Ecology and Sociobiology*, 57: 256-266.
- Ricciardi, A. and Rasmussen, J.B., 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 1759-1765.

- Roberge, M. and Slaney, T. 2001. Life history characteristics of freshwater fishes occurring in British Columbia, with major emphasis on lake habitat characteristics. Canadian Manuscript Report of Fisheries and Aquatic Sciences, 2574: 189 p.
- Runciman, J.B. and Leaf, B.R. 2009. A review of yellow perch (*Perca flavescens*), smallmouth bass (*Micropterus dolomieu*), largemouth bass (*Micropterus salmoides*), pumpkinseed (*Lepomis gibbosus*), walleye (*Sander vitreus*) and northern pike (*Esox lucius*) distributions in British Columbia. Canadian Manuscript Report of Fisheries and Aquatic Sciences, 2882: xvi + 123 p.
- Sanderson, B.L., Barnas, K.A. and Rub, A.M.W., 2009. Nonindigenous Species of the Pacific Northwest: An Overlooked Risk to Endangered Salmon? *BioScience*, 59: 245–256.
- Sax, D.F. and Gaines, S.D. 2008. Species invasions and extinction: The future of native biodiversity on islands. *Proceedings of the National Academy of Sciences*, 105: 11490–11497.
- Sih, A., Crowley, P., McPeck, M., Petranka, J. and Strohmeier, K. 1985. Predation, competition, and prey communities: a review of field experiments. *Ecology*, 16: 269–311.
- Simberloff, D., Parker, I.M. and Windle, P.N. 2005. Introduced species policy, management, and future research needs. *Frontiers in Ecology and the Environment*, 3:12–20.
- Thorpe, J.E. 1977. Morphology, physiology, behaviour and ecology of *Perca fluviatilis* L. and *P. flavescens* Mitchill. *Journal of the Fisheries Research Board of Canada*, 34: 1504 -1514.
- Truemper, H.A., Lauer, T.E., McComish, T.S., and Edgell, R.A. 2006. Response of yellow perch diet to a changing forage base in southern Lake Michigan, 1984-2002. *Journal of Great Lakes Research*, 32: 806–816.
- Vitousek, P.M., D'Antonio, C.M., Lope, L.L. and Westbrooks, R. 1996. Biological invasions as global environmental change. *American Scientist*, 84: 468–478.
- Weber, M., Dettmers, J., Wahl, D., and Czesny, S. 2010. Effects of predator-prey interactions and benthic habitat complexity on selectivity of a foraging generalist. *Transactions of the American Fisheries Society*, 139: 1004–1013.

Wright, T.F., Eberhard, J.R., Hobson, E.A., Avery, M.L., and Russello, M.A. 2010. Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. *Ethology Ecology and Evolution*, 22: 393–404.

Zaret, T.M. and Paine, R.T. 1973. Species introduction in a tropical lake: a newly introduced piscivore can produce population changes in a wide range of trophic levels. *Science*, 182: 449-455.

2. Feeding Ecology of Introduced Yellow perch in BC Lakes

Introduction

Yellow perch (*Perca flavescens*) are a non-native in most areas of British Columbia (BC) (Roberge and Slaney 2001). Although native to Canada east of the Rocky Mountains, the range of yellow perch is expanding largely through illegal introductions by sport fishers (Roberge et al. 2001, Brown et al. 2009). Predatory and omnivorous fish, such as yellow perch, have been shown to cause some of the greatest impacts, particularly in aquatic ecosystems (Sih et al. 1985, Moyle and Light 1996). These impacts can be related to diet and behaviour, where a generalist species with a broad niche width may have a greater impact than a diet specialist (Bøhn and Amundsen 2001, Kolar and Lodge 2001). Potential impacts are often predicted based on how an invasive species behaves in its native habitat; however, behavioural flexibility or behavioural variants often occur as a response to new environments (Dill 1983, Wright et al. 2010).

The general ecology of yellow perch is well documented in other parts of Canada and the United States (Vander Zanden et al. 1997) as it has been considered an important commercial fish in Canada's Great Lakes (Clapp and Dettmers 2004); however, we know little about the diet of yellow perch in BC's interior. Typically, in native habitats larval yellow perch feed primarily on zooplankton, switching to larger aquatic invertebrates as the fish grows (Siefert 1972, Whiteside et al. 1985, Graeb et al. 2006, Brown et al. 2009). As adults, their diet covers a wide range of prey items including aquatic invertebrates and juvenile fish (Peterson and Martin-Robichaud 1982, Krieger et al. 1983). Although diet has been well studied in native habitats, a need for studies on yellow perch life history variation and inter-population differences was identified (Purchase et al. 2005). Numerous studies have also been completed on European perch (*Perca fluviatilis*), which is a very similar species, and considered by some to be biologically equivalent (Thorpe 1977). The diet of European perch is affected by the abundance of predators and competitors (Persson and Hansson 1999). In BC lakes, yellow perch do not have natural

predators, and it is unknown how this is impacting their behaviour. Persson and Hansson (1999) showed that in European perch, a shift in diet could occur after competitive release. If variation in diet occurs in native habitats, it is likely that behavioural flexibility causing variation in diet could also be occurring in new habitats. A lack of competition or reduced risk of predation may be causing yellow perch to utilize different prey resources and broaden its habitat selection, resulting in a niche shift due to behavioural plasticity (MacArthur and Pianka 1966, Diamond 1970). In addition, it is unknown to what extent rainbow trout (*Oncorhynchus mykiss*) and other native fish species are predated upon or compete with yellow perch for invertebrate prey resources.

Feeding ecology is often used in part to determine a species' niche or role in the ecosystem. Variation from typical feeding patterns in native habitats could indicate behavioural flexibility as a response to new environments. The aim of this study was to describe diet and prey selectivity of introduced yellow perch as a first step in evaluating potential interactions with native fish assemblages in BC lakes. My research objectives were to:

- determine the diversity, abundance and seasonal variation of prey items in the diet of yellow perch (and rainbow trout where applicable),
- determine if yellow perch in BC lakes eat similar prey to what would be expected in their native habitat,
- evaluate prey importance, feeding strategy and niche width of yellow perch (and rainbow trout where applicable),
- determine if yellow perch are actively selecting for prey items, or randomly taking prey in proportion to their availability, and
- determine if there is dietary overlap between yellow perch and rainbow trout (in applicable lakes).

Feeding ecology of yellow perch was assessed through a seasonal stomach content analysis. The composition of yellow perch diet was compared to available prey resources in the lakes to determine if they selected for specific prey items. Yellow perch diet was also compared to rainbow trout diet in two lakes to determine if dietary overlap occurred or if any unusual feeding patterns were evident in rainbow trout. Due to the generalist

nature of yellow perch diets, they have been shown to be a good indicator of changes in benthic community and have been suggested as an alternative to direct sampling of invertebrate communities (Tyson and Knight 2001). Therefore, it is expected that the proportions of prey resources in stomach contents should reflect those in each lake. Therefore, it was predicted that among study lakes, introduced yellow perch would maintain a generalist strategy and broad niche width, utilizing the most plentiful prey available rather than selecting for specific resources. It was also predicted that there would be some variation in diet among size classes, reflecting the typical ontogenetic shift seen in yellow perch, and that diet overlap would occur between yellow perch and trout in the lakes studied. In addition to diet, condition factor was calculated as a relative measure of nutritional state in comparison to average as defined in their native habitat. Condition factor can be linked to prey abundance where low relative condition is assumed to reflect prey scarcity and high relative condition reflects excess prey (Kohler and Kelly 1991).

Methods

Study Sites

The feeding ecology of introduced yellow perch was studied at seven lakes within the Okanagan Lake drainage in British Columbia (Figure 2-1 and Table 2-1). Diet overlap between yellow perch and rainbow trout was determined in two of those sample lakes (Pinaus and Little Pinaus Lakes). Sample sites within the study lakes were chosen at accessible locations with suitable perch habitat and varied depending on lake morphology, the location of perch habitat and safety of other lake users. Sample sites were consistent through all seasonal sampling periods.

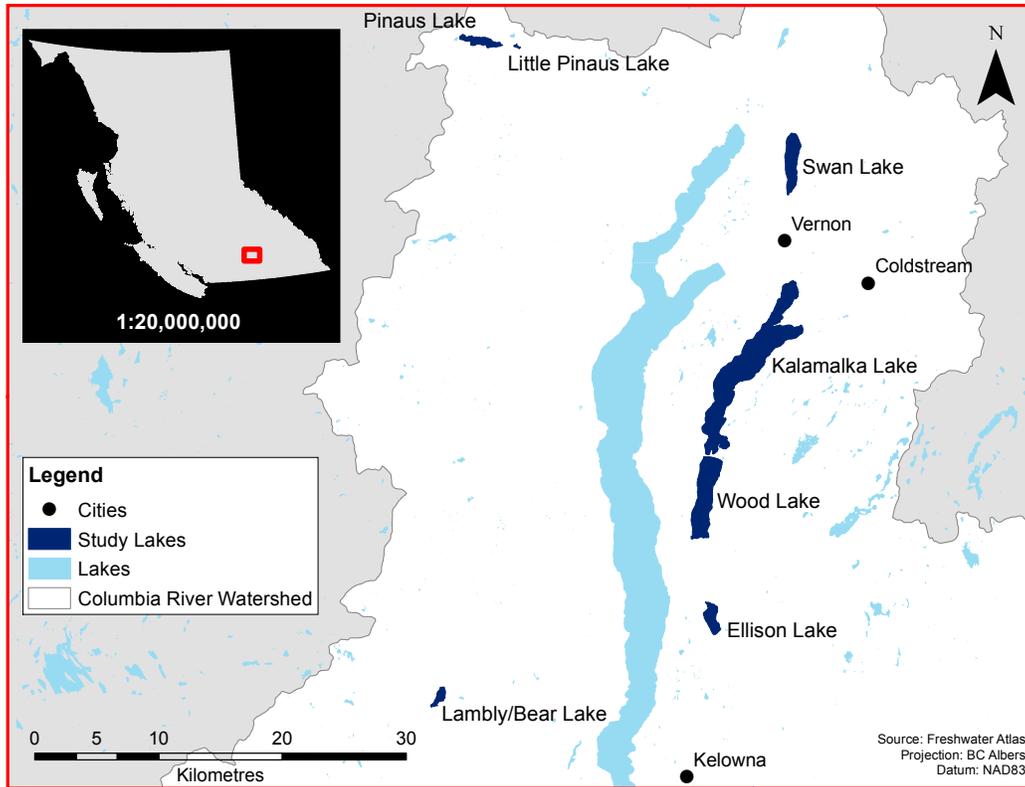


Figure 2-1. Location of study lakes within British Columbia.

Table 2-1. Location and physical characteristics of sample lakes. Elevation, surface area and maximum depth from BCMoE (2013). Mean Secchi depths from sampling dates in Table 2-2.

Lake name	UTM	Elevation (m)	Surface area (ha)	Max. depth (m)	Mean Secchi depth (m)
Pinaus Lake	11U 317357 5588663	982	168	53.6	1.9
Bear (Lambly) Lake	11U 305204 5546292	1150	81	9	2.6
Little Pinaus Lake	11U 318777 5588296	898	8.4	5.0	2.9
Swan Lake	11U 338734 5573722	391	438	9	3.5
Kalamalka Lake	11U 338228 5566843	392	2589	142	4.9
Wood Lake	11U 329649 5553597	394	916	34	3.7
Ellison Lake	11U 327969 5542037	426	207	4.3	0.9

Of the seven study lakes, Pinaus and Bear Lakes were studied intensively and sampled during 5 seasonal sampling periods (spring, summer, late summer, fall and winter). In both of those lakes, the only species present were introduced yellow perch and stocked rainbow trout. In addition, these two lakes provided a comparison between a relatively large, deep lake (Pinaus), and a smaller, shallow lake (Bear). The five other sample lakes were used for supplementary diet analysis information and to provide further information on prey selectivity and comparison among lakes with variable prey resource availability. The number of sampling periods per lake was limited by time and resources. Seasonal sampling dates for fish stomach contents at each lake are outlined in Table 2-2.

Table 2-2. Seasonal stomach content sampling dates at study lakes.

Lake name	Spring	Summer	Late Summer	Fall	Winter
Pinaus Lake	22 May 2012	26 July 2011	23 August 2011	15 October 2011	4 & 11 February 2012
Bear Lake (Lambly)	24 May 2012	4 August 2011	1 September 2011	22 October 2011	18 & 22 February 2012
Little Pinaus Lake	17 May 2012	27 July 2011	26 August 2011	NA	NA
Swan Lake	1 May 2012	28 July 2011	25 August 2011	NA	NA
Kalamalka Lake	NA	3 August 2011	31 August 2011	NA	NA
Wood Lake	NA	2 August 2011	30 August 2011	NA	NA
Ellison Lake	NA	29 July 2011	29 August 2011	NA	NA

Physical characteristics, which included elevation, surface area, maximum depth and mean Secchi depth (water clarity), varied among study lakes (Table 2-1). Fish communities also varied by lake (Table 2-4).

Further details on the study lakes are given, as they are integral in the interpretation of the diet analysis. These details are based on visual field observations taken at the time of sampling (Table 2-3).

Pinaus Lake has variable shoreline habitat, with a shallow vegetated bench along most of the shore and abundant woody debris throughout. Visibility remained relatively low throughout the ice-free season (Table 2-1). Pinaus Lake contained only introduced yellow perch and rainbow trout stocked for sport fishing. Yellow perch were found along all of the shallow vegetated bench areas. Three main strains of rainbow trout may be present in Pinaus Lake, including Pennask, Fraser Valley and Blackwater strains (BCMoE 2013). In addition, some level of natural recruitment occurs, likely among Pennask and Blackwater strains. Each strain of rainbow trout has a typical diet. Pennask strain rainbow trout are insectivorous, feeding primarily on chironomids and cladocerans, whereas Fraser Valley and Blackwater strains are more aggressive, eat larger macroinvertebrates and can be piscivorous (FFSBC 2004). Due to the mixture of strains, it was not possible to positively identify the strain of each trout with any level of confidence in order to determine if the trout were maintaining their typical diet.

Little Pinaus Lake is located directly downstream from Pinaus Lake. It is a very small lake with ample aquatic vegetation and woody debris. At times the entire depth of the lake was within the photic zone. Fish species present included introduced yellow perch and rainbow trout. Yellow perch were found all around the shoreline and in shallow vegetated bay areas. There may be natural recruitment of rainbow trout within Little Pinaus Lake and the specific strain is unknown, although it may be speculated that they could be descendants of the Beaver Lake wild strain (BCMoE 2013) or possibly Pennask trout that may have moved downstream from Pinaus Lake, as trout morphology in this lake was consistent with the Pennask strain.

Bear Lake is relatively shallow and also contains ample aquatic vegetation and woody debris. Bear Lake contained only introduced yellow perch and stocked Pennask rainbow trout.

Swan Lake is relatively shallow and its shores were lined with bulrushes and other aquatic vegetation. This lakes contained several other fish species, but these were rarely captured during gill net sampling. Yellow perch were found in all areas of Swan Lake.

Kalamalka Lake is a large lake with numerous fish species. Sampling occurred in an isolated bay of the lake. Vegetation was present in some areas, although many shorelines have only mud or sand beaches. Water clarity in this lake was extremely high and it was possible to see many juvenile fish swimming in amongst the sparse vegetation. Yellow perch were captured in these sparsely vegetated areas.

Wood Lake is very similar to Kalamalka Lake and was connected by a short canal. It was only possible to capture yellow perch in the shallow bay areas that supported minimal vegetation, in contrast to the more dominant pebble beaches.

Ellison Lake supported some vegetation along the immediate shoreline and in a shallow bay area, although the water clarity only allowed observation to 1 m depth. It can be assumed that due to this low water clarity, the vegetated littoral zone was relatively small. Yellow perch were only captured along the immediate vegetated shoreline and in the shallow bay.

Table 2-3. Lake and fish community characteristics based on field observations during fish sample collections.

	Lake and fish community characteristics (Based on field observations during fish sample collections)		
Lake	Shoreline Refugia (ample aquatic vegetation)	Predators of yellow perch observed (piscivorous rainbow trout or northern pike minnow)	Juvenile prey species (other than yellow perch) observed
Pinaus Lake	✓	✓	
Bear (Lambly Lake)	✓		
Little Pinaus Lake	✓		
Swan Lake	✓		✓
Kalamalka Lake		✓	✓
Wood Lake		✓	✓
Ellison Lake		✓	✓

Table 2-4. Fish community in study lakes based on field observations and BC provincial database (BCMoe, 2013).

	Fish Species Present									
Lake	yellow perch (<i>Percu flavescens</i>)	rainbow trout (<i>Oncorhynchus mykiss</i>)	northern pikeminnow (<i>Pychocheilus oregonensis</i>)	peamouth (<i>Mylocheilus caurinus</i>)	pumpkinseed (<i>Lepomis gibbosus</i>)	redside shiner (<i>Richardsonius balteatus</i>)	sucker (<i>Catostomus sp.</i>)	common carp (<i>Cyprinus carpio</i>)	kokanee (<i>Oncorhynchus nerka</i>)	burbot (<i>Lota lota</i>)
Pinaus Lake	✓	✓								
Bear (Lambly Lake)	✓	✓								
Little Pinaus Lake	✓	✓								
Swan Lake	✓	✓			✓	✓	✓	✓		✓
Kalamalka Lake	✓	✓	✓	✓	✓	✓	✓	✓	✓	
Wood Lake	✓		✓	✓	✓	✓	✓	✓	✓	
Ellison Lake	✓		✓	✓		✓	✓	✓		

Sampling and Laboratory Analysis

Fish sampling

To determine what yellow perch and rainbow trout were eating, fish were collected using a standard 6-paneled gill net, each panel 15.2 m x 2.4 m, ranging in mesh size from 1.27 cm to 6.35 cm to capture a wide range of fish sizes. Gill net sampling was completed during mid-morning, allowing time for yellow perch to feed before capture. The length of each set and number of sets varied depending on lake and season in order to capture the desired sample of approximately 30 yellow perch (and rainbow trout where applicable) per lake, per seasonal sample period; however, obtaining this number of perch and trout proved difficult in some study lakes, and a sample of less than 30 fish was accepted. Fish were euthanized immediately after capture. Fork length (L_F), weight and species was recorded at the time of sampling. For analysis, yellow perch were divided into 10 mm size classes and rainbow trout were divided into 50 mm size classes, due to their much larger variation in size.

Gut contents were preserved by injecting alcohol into the stomach through the mouth, using a small pipette, as soon as possible after capture. Fish samples were individually labeled, bagged and frozen until lab analysis. The sample size for each lake and season, mean fork length and mean weight are shown in Tables 2.5 and 2.6.

Table 2-5. Summary of yellow perch samples dissected for diet analysis. The number of fish analyzed (N), mean fork length (L_F) \pm S.D. and weight (w) \pm S.D. are shown for each lake and season sampled.

Lake	Season	N	Mean $L_F \pm$ S.D. (mm)	Mean w \pm S.D. (g)
Pinaus Lake	Spring	42	229.6 \pm 28.4	190.7 \pm 72.5
	Summer	32	193.3 \pm 53.4	150.6 \pm 102.6
	Late summer	16	204.6 \pm 40.4	152.8 \pm 96.1
	Fall	20	231.2 \pm 19.0	202.4 \pm 50.92
	Winter	35	216.3 \pm 15.8	166.4 \pm 44.5
Bear Lake	Spring	42	159.1 \pm 20.8	39.9 \pm 24.0
	Summer	34	163.3 \pm 24.0	49.9 \pm 25
	Late summer	34	154.7 \pm 26.2	34.0 \pm 27.4
	Fall	21	180.1 \pm 17.5	67.1 \pm 25.4
	Winter	28	149.4 \pm 18.1	38.4 \pm 19.3
Little Pinaus Lake	Spring	24	209.0 \pm 35.9	138.1 \pm 77.3
	Summer	15	231.4 \pm 14.3	196.7 \pm 40.1
	Late summer	10	212.0 \pm 40.8	163.5 \pm 62.0
	Swan Lake	Spring	31	182.5 \pm 24.9
Swan Lake	Summer	41	163.7 \pm 13.8	50.0 \pm 18.7
	Late summer	36	160.6 \pm 16.5	45.6 \pm 16.5
	Kalamalka Lake	Summer	13	107.8 \pm 19.8
Kalamalka Lake	Late summer	11	120.4 \pm 18.2	10.7 \pm 14.7
Wood Lake	Summer	14	128.1 \pm 31.3	26.4 \pm 25.6
	Late summer	36	140.8 \pm 28.7	25.7 \pm 33.2
Ellison Lake	Summer	9	168.2 \pm 61.7	91.7 \pm 139.2
	Late summer	21	170.3 \pm 29.5	62.9 \pm 34.3

Table 2-6. Summary of rainbow trout samples dissected for diet analysis. The number of fish analyzed (N), mean fork length (L_F) \pm S.D. and weight (w) \pm S.D. are shown for each lake and season sampled.

Lake	Season	N	Mean $L_F \pm$ S.D. (mm)	Mean w \pm S.D. (g)
Pinaus Lake	Spring	28	195.2 \pm 75.4	138.7 \pm 136.3
	Summer	32	270.0 \pm 75.2	251.5 \pm 153.7
	Late summer	23	253.0 \pm 54.6	215 \pm 129.1
	Fall	21	272.0 \pm 73.04	230.6 \pm 145.2
	Winter	8	289.8 \pm 48.93	271.4 \pm 144.2
Little Pinaus Lake	Spring	20	261.6 \pm 44.85	205.9 \pm 82.57
	Summer	16	269.6 \pm 37.01	234.3 \pm 87.9
	Late summer	14	256.1 \pm 39.61	189.0 \pm 80.73

Lake (available prey) resources

Prey abundance was determined for yellow perch, by measuring zooplankton, littoral benthic macroinvertebrates and profundal benthic macroinvertebrates. These three invertebrate categories covered the spectrum of prey items found in the stomachs of yellow perch in the lakes, as determined by stomach content analysis. Previous studies have not combined different measures of invertebrate abundance estimates due to differences in units of measurements (Chippis and Garvey 2007). To provide a more comprehensive measurement of food availability by incorporating invertebrates found in different lake habitats, three gear types were used, and a new method was devised to combine measurements and quantify overall food availability. Three replicates of each sample type were taken near the same location and time that fish were collected for diet analysis to provide as close to simultaneous estimates of prey available and prey consumed as possible. This sampling was not designed to rigorously quantify prey availability, but to provide an estimate of prey abundance.

A Wisconsin plankton net (250 μm mesh) was used to sample zooplankton. The number of individuals in each vertical haul were estimated by calculating organisms per volume of water sampled by determining the area of the opening at the top of the net (0.013 m^2) and multiplying by the depth sampled (m). Oxygen was measured first in each instance to ensure the entire depth of the zooplankton haul was within the oxygenated depth of water. Littoral macroinvertebrates were sampled using a D-Frame sweep net (100 μm mesh) samples in a 1 m^2 quadrat. Organisms per volume of water were calculated by multiplying the net height (0.25 m) by the quadrat frame size. Profundal macroinvertebrates were sampled using an Ekman grab sampler, sieved through 150 μm mesh. The volume of the Ekman grab was calculated based on the size of the grab sampler (0.0035 m^3). Full samples (soft lake substrate) were calculated using this entire volume, whereas half full samples (hard lake substrate) were calculated using half the volume. All samples were put into Whirl-Packs® and preserved in 70% ethanol solution until lab analysis. Invertebrates in each sample were identified to order and enumerated using a dissecting microscope to provide proportional counts on the types of invertebrates available as prey in each lake. Sub-sampling was used for large samples. Zooplankton hauls were sub-sampled to 200 individuals using a Folsom plankton splitter. Littoral sweeps were sub-sampled to 200 individuals using a Caton-type grid sub-sampler (Caton 1991). No sub-sampling was needed for the Ekman grab samples.

For each sample, counts of invertebrates from lake samples were converted to organisms per 1 m^3 . For example, the number of amphipods in the D-frame net sample was determined by multiplying counts in each replicate by the volumetric multiplier of 4 to provide a count per 1 m^3 . The multiplier $1 / (1 \text{ m}^2 \times 0.25 \text{ m}) = 4$, was determined using a quadrat size of 1 m^2 and a net height of 0.25 m. For example, in D-frame replicate 1, a total of 1611 amphipods were counted, then multiplied by 4 giving a total of 6444 amphipods per 1 m^3 . The proportion of total prey items was then calculated for each replicate. Then, the mean proportion of the three replicates was determined. The results were then converted into proportions of prey abundance per sample, and the mean proportion of three replicates was taken for each gear type. Availability values of zero

were replaced with a small value of 0.0001 for taxa found in perch diets, but not in availability samples. This was done because although the taxa weren't detected in the lake availability sampling, they were found in the fishes' diet, indicating that they were present at some level in the lake. Further details on calculations, advantages and disadvantages of this new method are described in Appendix A.

Diet analysis

Diet composition, relative prey importance, and feeding strategy were used to describe yellow perch in combination with measures of prey selectivity and diet overlap with rainbow trout. Limitations to the methods used are discussed in Hyslop (1980), Johnson (1980), Wallace and Ramsey (1981), Amundsen et al. (1996), and Chipps and Garvey (2007).

Diet composition, prey importance and feeding strategy

To analyze diet, entire stomachs were removed from each fish and examined under a dissecting microscope. Prey items were identified to order and enumerated exclusively from the stomach as digestion times of prey items can vary in the intestines and bias results towards hard-bodied invertebrates. The condition of stomach contents varied from well preserved to moderately digested; therefore, organisms were only counted if a head or whole unit was identified to prevent duplicate counts. Empty stomachs were not included in the analysis. Proportions, frequency of occurrence, and prey specific abundance were used to describe the diet. Multi-variate statistical analyses were completed using the 'Mvabund' package in R, which performs analysis of deviance for multivariate generalized linear model fits for abundance data (Warton et al. 2012, Wang et al. 2012) and was designed specifically for multivariate abundance data in ecology (Warton et al. 2011). A negative binomial distribution was used to calculate the likelihood ratio statistic (LR) to compare diet composition (%N) among lakes and among seasons and size classes within each lake. The P-value was calculated using 999 sampling iterations without replacement.

A graphical method was used to show prey importance and feeding strategy by plotting Frequency of Occurrence (FO) against Prey specific abundance (Pi) (Amundsen et al. 1996). Pi is a mean value of "the percentage that a prey taxon comprises of all prey items, in only those predators in which the prey item occurs," and FO is the frequency of occurrence for each prey. Feeding strategy, prey importance and niche width can be interpreted based on the distribution of points along the axes of the plot and the diagonals between them (Figure 2-2). This method also allows one to distinguish between individual and population specialization. This method has been used as an alternative to compound indices for use with count data rather than prey biomass, and is easier to interpret than tabular methods (Wilhelm et al. 1999, Kido et al. 1999, Caiola et al. 2001) (see Amundsen et al. 1996 for detailed description of method).

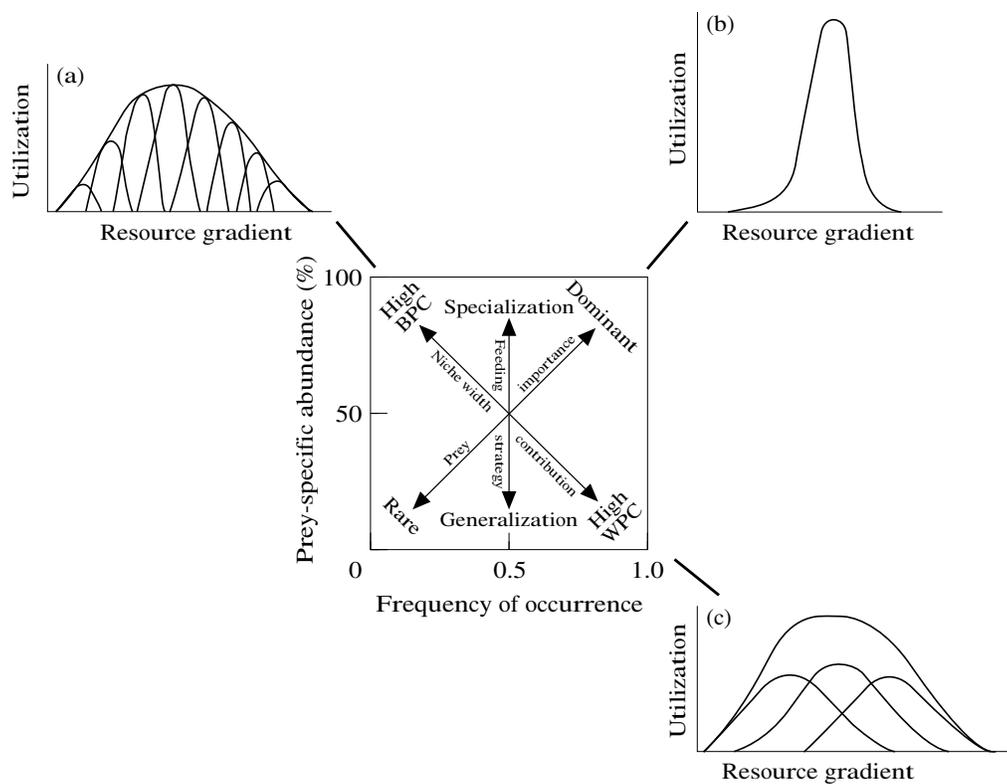


Figure 2-2. (From Amundsen et al. 1996) Diagram for interpretation of prey importance, feeding strategy, and niche variation. Prey points in upper left of plot indicate prey that are consumed by few individuals that are displaying specialization; points in lower right represent prey items consumed occasionally, but by most individuals.

Prey selectivity

Prey selectivity was calculated in the study lakes based on the methods of Manly et al. (2002) and Calenge (2006). Prey selection was tested for each fish sampled. Selection indices were then pooled and a global test of random resource use was completed (Log-likelihood statistic) to determine if overall significant selection occurred, or if fish ate prey in proportion to availability. If prey resources were consumed in the same proportions as available, the selection index would be equal to 1. A higher or lower selection index indicated positive or negative selection. For example, a selection index of 2 indicated a prey resource was being used twice as much as would be expected if it were being used randomly. Significance referred to a comparison of selection indices at an alpha level = 0.05. The computation of selection indices was completed in R Statistical Software (R Core Team 2012), using the package AdeHabitat HS (Calenge 2006).

Dietary overlap between yellow perch and rainbow trout:

Dietary overlap was determined for rainbow trout and yellow perch in Pinaus and Little Pinaus Lakes. Percent diet compositions were compared using Morisita's Overlap Index (Smith and Zaret 1982, Chipps and Garvey 2007). This provided a standardized value where overlap >0.6 is considered significant (Wallace et al. 1981, Brodeur and Pearcy 1990). Mean overlap values, standard deviations and 95% confidence intervals were calculated using 999 bootstrap iterations. The computation of overlap indices was completed in R Statistical Software (R Core Team 2012) using the package SPAA (Jinlong et al. 2010).

Condition Factor

Mean condition factor was calculated for yellow perch and rainbow trout for each season within study lakes using Fulton's length-ratio,

$$K_{FL} = (W/L^b)$$

where K_{FL} is condition of the fish based on fork length, W is weight (g), and L is length (mm). The value of b is 3.0 with the assumption of isometric growth (i.e., the relative proportions of body length to height do not change as fish increase in weight). To adjust for the specific growth form of yellow perch, a value of 3.23 was used based on the standard weight equations for yellow perch across their native range in Canada and USA (Blackwell et al. 2000). This value allows a comparison of yellow perch in the study lakes to an average yellow perch in native habitat.

A value of 3.0 was maintained for rainbow trout. K_{FL} values of 1 indicate an "average fish" (Blackwell et al. 2000). Due to differences in sample size, 24 fish were randomly selected from each season in each lake, for comparison of relative condition among lakes using one-way ANOVA.

Results

Yellow perch diet

A total of 565 yellow perch stomachs were analyzed from the seven study lakes. Stomachs contained a variety of prey resources that were categorized into 15 prey categories as follows: amphipods (AM), cladocerans (CL), copepods (CO), dipteran larvae (DL), dipteran pupae (DP), ephemeropterans (EP), fish (FI), hirudineans (HI), hydrachnidians (HY), molluscs (MO), mysids (MY), odonates (OD), trichopterans (TR), other aquatics (OA), and other terrestrials (OT). Insects with rare occurrence (<1% total proportion of diet) were lumped together into 'other aquatic' or 'other terrestrial' categories. Among all yellow perch sampled, the most highly consumed prey categories (by proportion) included cladocerans, dipteran larvae and dipteran pupae (Figure 2-3);

however, yellow perch diets varied significantly among lakes (Dev = 282.90, P = 0.001) with the highest proportion of variance explained by differences in consumption of fish (Dev = 109.85, P = 0.001) and cladocerans (Dev = 88.89, P = 0.001).

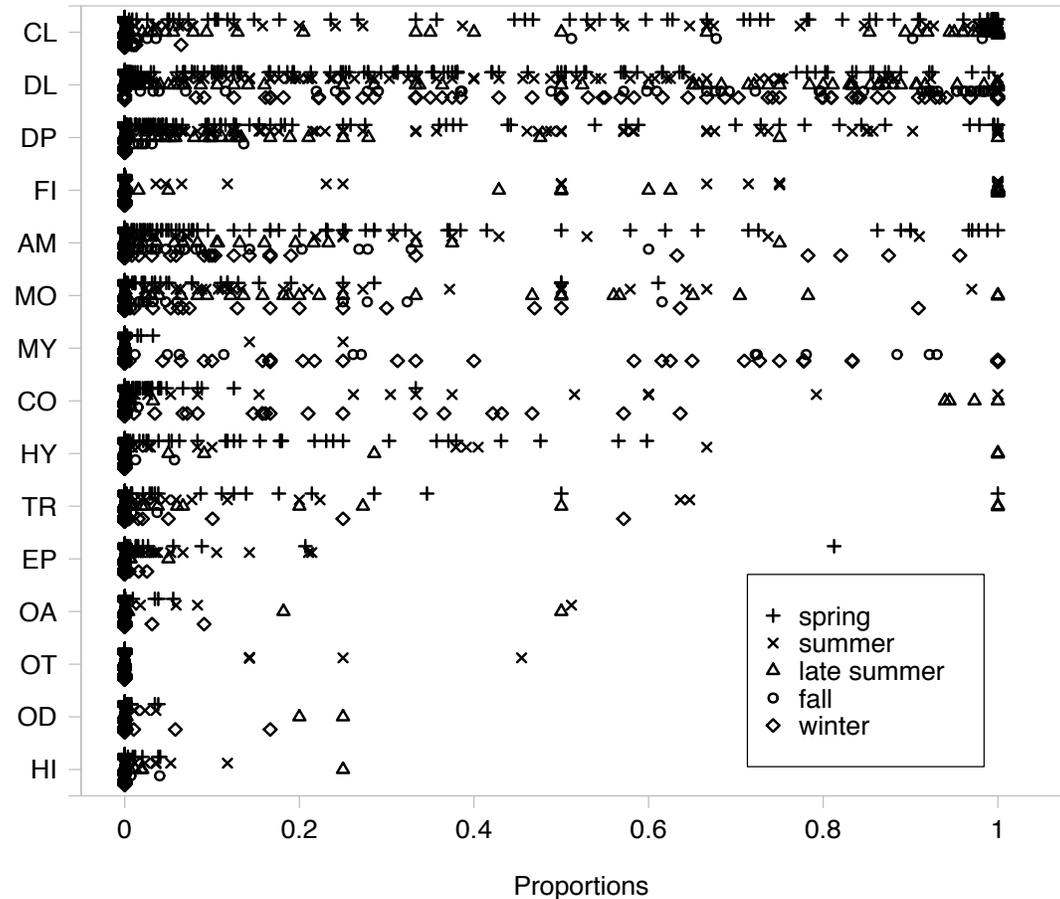


Figure 2-3. Summary of yellow perch diet composition among all study lakes. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials).

Within each study lake, overall diet composition was determined and multivariate analysis was completed to identify variation in diet composition among seasons and size classes. Diet composition charts for each lake showing proportions of food categories consumed are provided in Appendix B.

In Pinaus Lake, a significant difference in yellow perch diet composition (proportions of prey items) was found among seasons ($P = 0.001$), with the most variation explained by differences in proportions of dipteran pupae ($P = 0.001$). The variation in proportions of dipteran pupae is likely due to hatch and sample timing. Overall, no significant difference was found in diet composition among size classes in Pinaus Lake. Graphical analysis (Figure 2-4), revealed a mixed feeding strategy with varying degrees of specialization and generalization for different prey types and seasons.

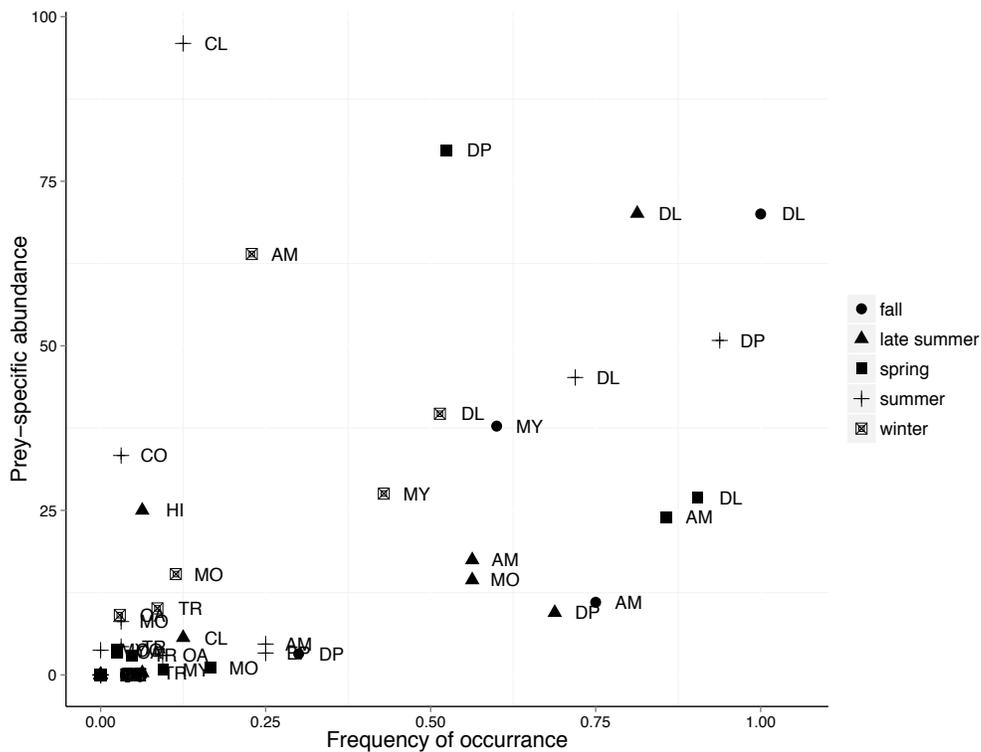


Figure 2-4. Prey importance, feeding strategy and niche width contribution for Pinaus Lake yellow perch. See Figure 2-3 text for prey category abbreviations and text on pg 27 for interpretation.

Prey points in the upper left of the plot indicate prey that are consumed in large quantities but only by a few individuals displaying specialization for that prey; points in the lower right represent prey items consumed occasionally, but by most individuals. Prey points in the upper right indicate the most important prey items for the population, whereas, points in the lower left are unimportant prey items, consumed in low

proportions by few individuals. In spring, the population showed specialization for dipteran pupae, with dipteran larvae and amphipods making up the majority of the remaining diet. In summer, some individuals had a specialized diet composed of cladocerans with the remaining population showing a relatively narrow niche width consuming mostly dipteran larvae and pupae. In late summer and fall, the population again showed a more generalist strategy with many prey points located in the lower right, although the population still showed some specialization for dipteran larvae as the most important prey resource. In winter, a generalist strategy was shown.

In Bear Lake, a significant difference in yellow perch diet was found among seasons (Dev = 30.75, P = 0.001) with the most variation explained by differences in consumption of cladocerans (Dev = 24.58, P = 0.001). In spring, perch showed a generalist feeding strategy with cladocerans and dipteran larvae as the most important prey items (Figure 2-5). All other seasons showed a level of population specialization. Summer and late summer diets showed specialization towards cladocerans. In fall and winter, there was some specialization towards dipteran larvae, with cladocerans becoming less important. A significant difference was found among size classes (Dev = 8.38, P = 0.002) with the significant source of variation found in consumed proportions of cladocerans (Dev = 5.72, P = 0.007). The smaller size classes ate more cladocerans, making up 78% (111 - 130 mm), 33% (131 – 150 mm), 54% (151 – 170 mm), 0% (171 – 190 mm) and 13% (191 – 210 mm) of diet composition within each of the five size classes in Bear Lake.

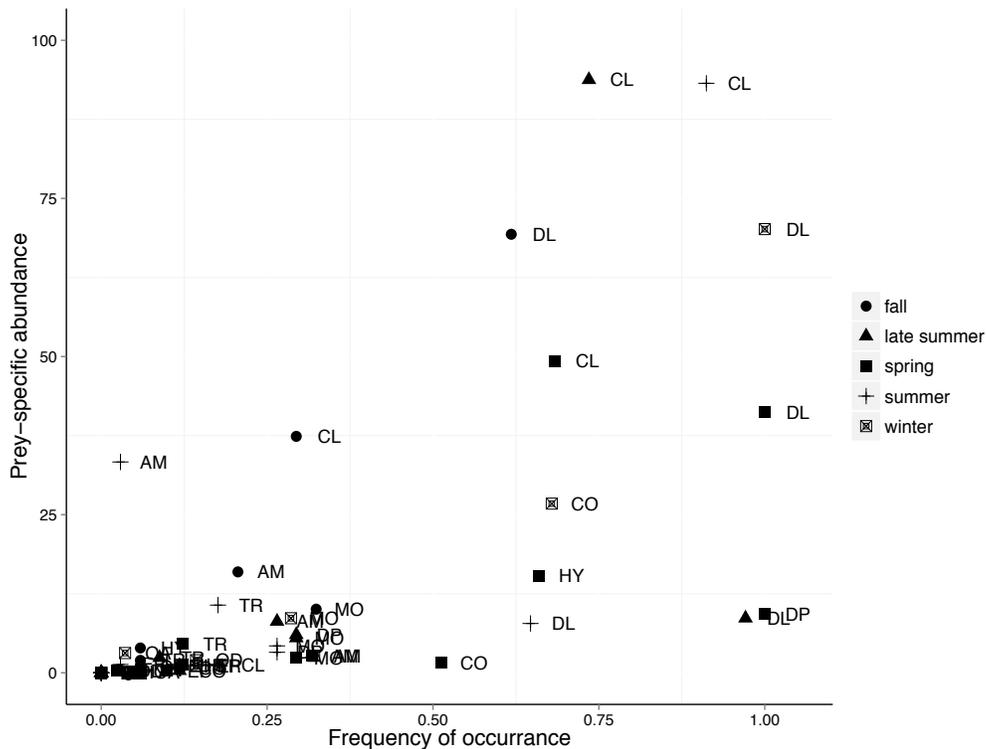


Figure 2-5. Prey importance, feeding strategy and niche width contribution for Bear Lake yellow perch. See Figure 2-3 text for prey category abbreviations and text on pg 27 for interpretation.

In Little Pinaus Lake, there was no significant difference in diet composition among seasons or size classes; however, the feeding strategy among seasons was somewhat variable. A generalist feeding strategy was shown in summer with the dominant prey items being dipteran pupae and amphipods. In spring and late summer, some specialization was shown towards cladocerans, which made up about half the diet in about 50% of the fish (Figure 2-6).

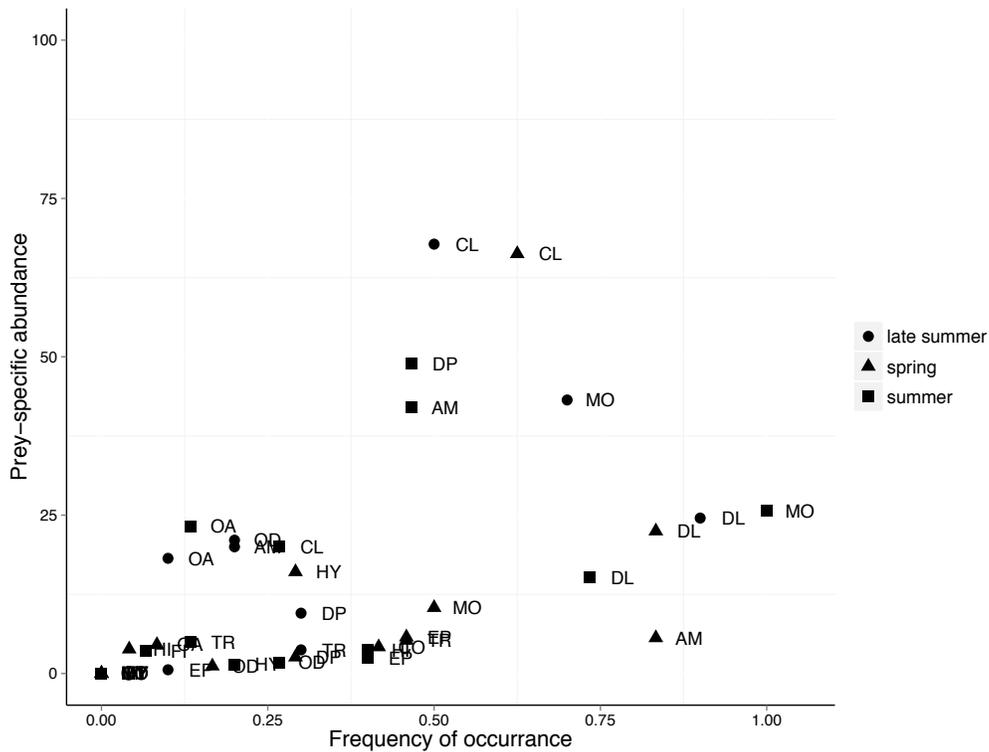


Figure 2-6. Prey importance, feeding strategy and niche width contribution for Little Pinaus Lake yellow perch. See Figure 2-3 text for prey category abbreviations and text on pg 27 for interpretation.

In Swan Lake, yellow perch diets were almost completely composed of cladocerans; however, there was a significant difference in proportions of cladocerans among seasons (Dev = 19.52, P = 0.001). The yellow perch population in Swan Lake displayed a narrow niche width, and relied on cladocerans as the main prey source. Dipteran larvae were also consumed by upwards of 75% of all fish sampled, but in very low proportions (Figure 2-7). No significant difference in diet was found among size classes.

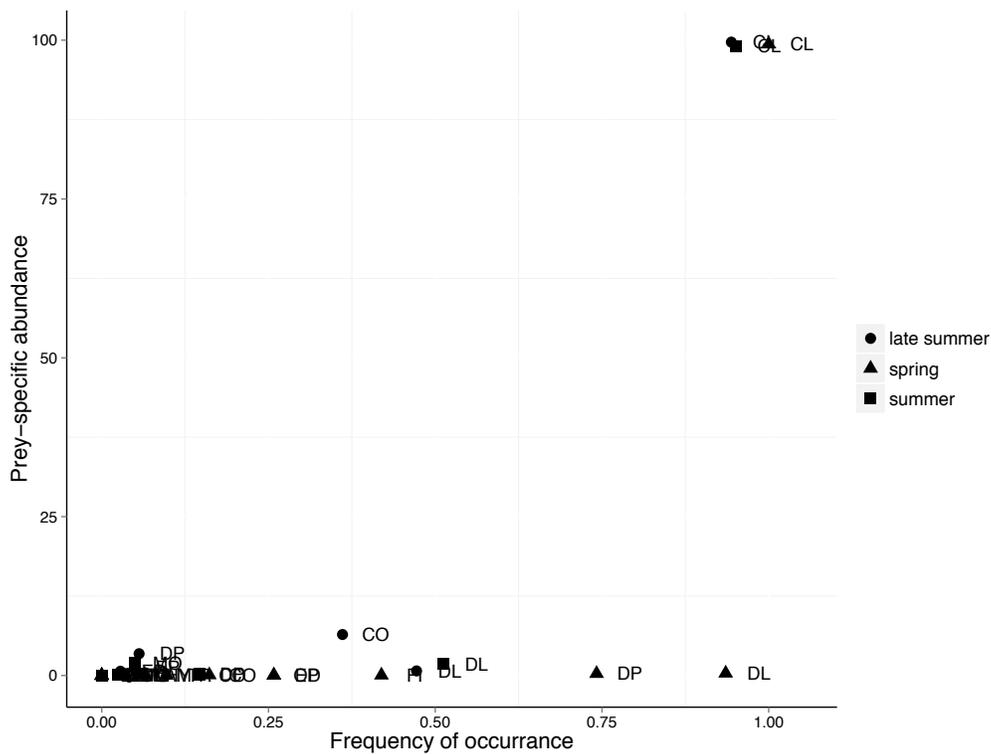


Figure 2-7. Prey importance, feeding strategy and niche width contribution for Swan Lake yellow perch. See Figure 2-3 text for prey category abbreviations and text on pg 27 for interpretation. Points in the upper right are cladocerans (CL) for spring, summer and late summer.

In Kalamalka Lake, no significant difference in diet composition was found among seasons or size classes. An overall generalist feeding strategy was evident, with fish as a main prey resource, although some individual specialization was shown in summer, where less than 25% of individuals consumed only copepods (Figure 2-8). Similarly, in late summer, about 25% of the fish showed individual specialization and consumed high proportions of copepods and trichopterans.

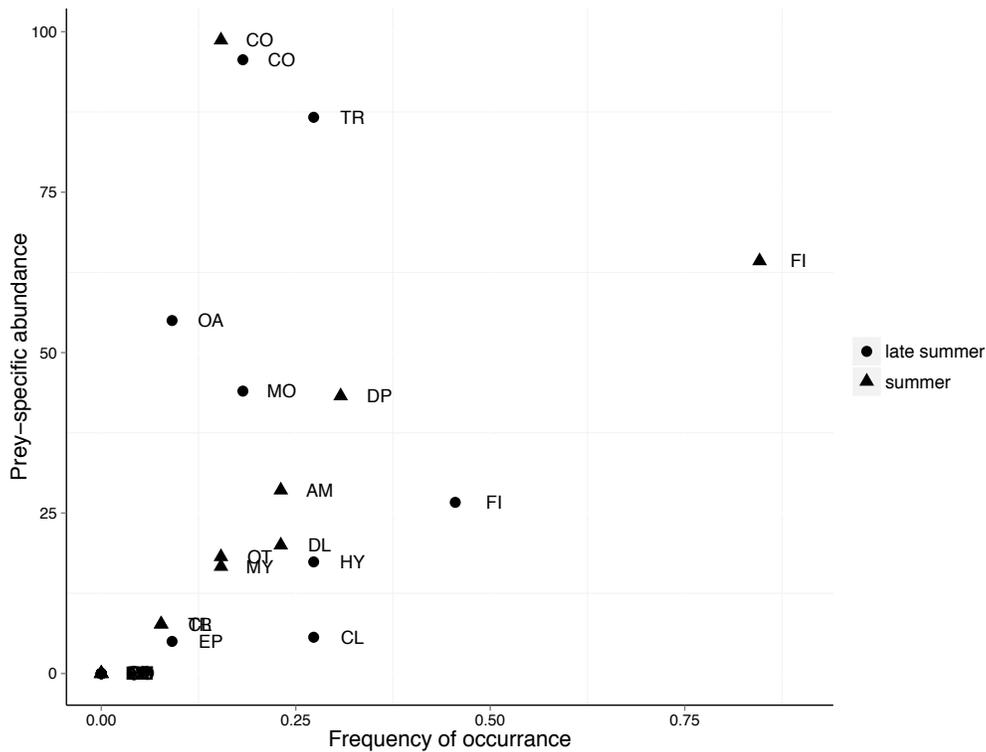


Figure 2-8. Prey importance, feeding strategy and niche width contribution for Kalamalka Lake yellow perch. See Figure 2-3 text for prey category abbreviations and text on pg 27 for interpretation.

In Wood Lake, significant variation in diet composition was found among seasons (Dev = 11.92, P = 0.002) with the most variation explained by differences in consumption of cladocerans (Dev= 10.54, P = 0.002). In summer, yellow perch showed a generalist feeding strategy and a broad niche width. In late summer, the pattern changed and the population showed a narrow niche width and a strong preference for cladocerans (Figure 2-9). No significant variation in diet among size classes was found.

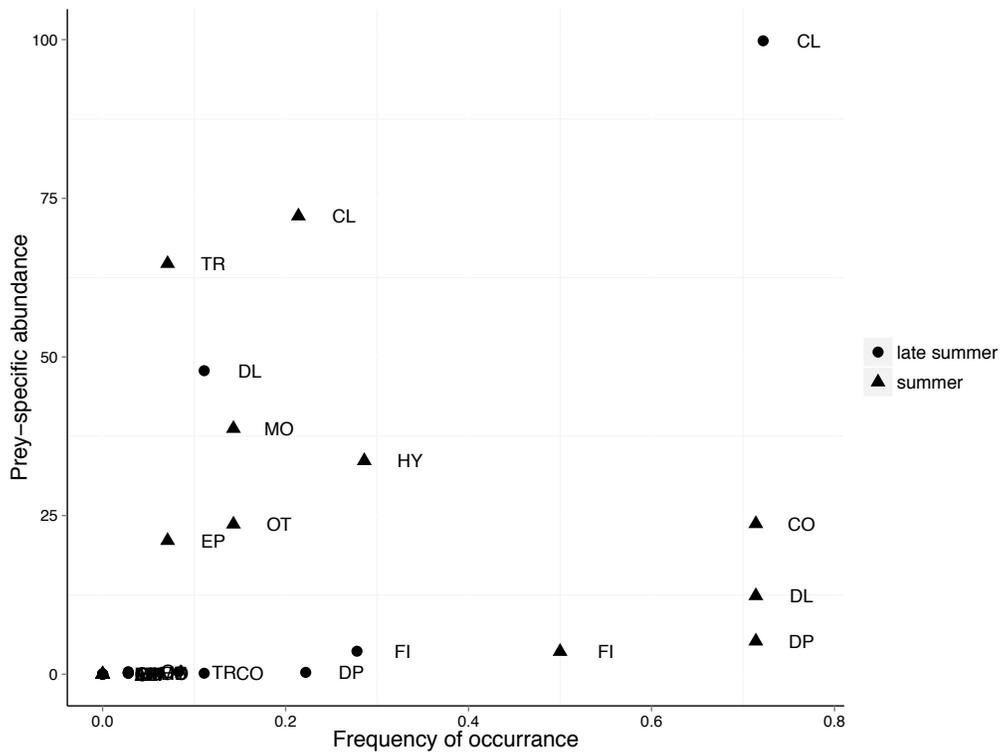


Figure 2-9. Prey importance, feeding strategy and niche width contribution for Wood Lake yellow perch. See Figure 2-3 text for prey category abbreviations and text on pg 27 for interpretation.

In Ellison Lake, no significant difference in diet composition was found among seasons or size classes. A specialist feeding strategy and narrow niche width was shown by the population, with fish and dipteran larvae being the most important prey items (Figure 2-10). The prey fish species was often unknown due to digestion, yet many juvenile yellow perch were identified.

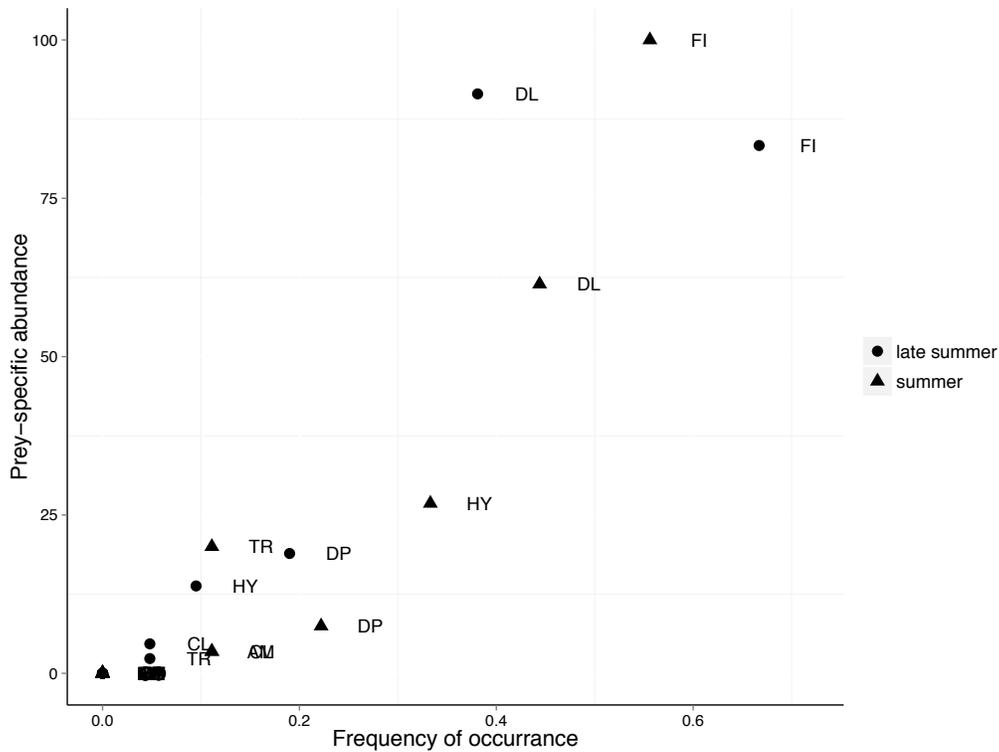


Figure 2-10. Prey importance, feeding strategy and niche width contribution for Ellison Lake yellow perch. See Figure 2-3 text for prey category abbreviations and text on pg 27 for interpretation.

Rainbow trout diet

A total of 163 rainbow trout stomachs were analyzed from Pinaus and Little Pinaus Lakes. Stomachs contents were categorized into the same 15 prey categories as the yellow perch samples for comparison purposes. Among all rainbow trout sampled, prey categories consumed in the highest proportions included dipteran pupae, dipteran larvae, cladocerans, and molluscs (Figure 2-11). Diet composition varied significantly between lakes (dev = 32.25, $p = 0.001$), with the most variation explained by differences in consumption of cladocerans (dev = 21.16, $p = 0.001$). Within both study lakes, overall diet was determined and multivariate analysis was completed to find variation in diet composition among seasons and size classes. Diet composition charts for each lake, showing proportions of food categories consumed are in Appendix B.

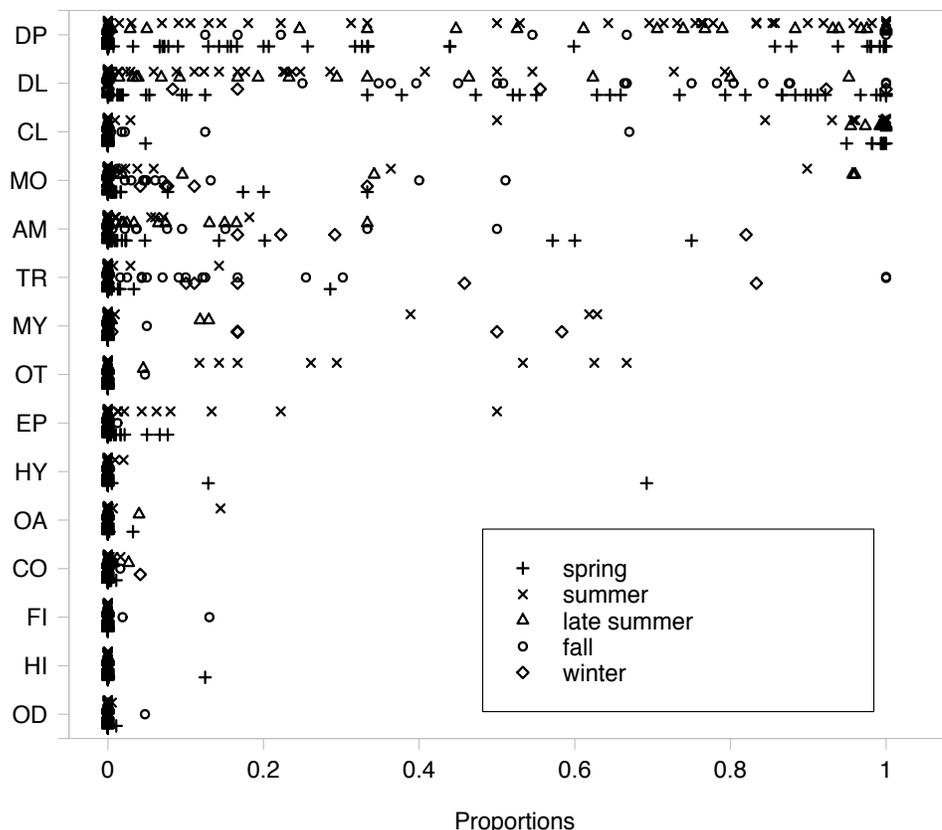


Figure 2-11. Overall rainbow trout diet composition in Pinaus and Little Pinaus Lakes, shown in proportions by prey category. Prey categories with highest total proportions are towards the top of the y-axis. See Figure 2-3 text for prey category abbreviations.

In Pinaus Lake, there was no significant difference in rainbow trout diet composition among seasons. Variable diet composition among size classes (Dev = 13.59, P = 0.002) was found, with significant variation in consumption of dipteran pupae (dev = 7.92, P = 0.026). Rainbow trout in Pinaus Lake showed mixed feeding strategies among seasons and prey items (Figure 2-12). In spring, dipteran pupae were the main prey consumed by the population. In summer and late summer, individual specialization was shown for cladocerans, while dipteran pupae continued to be the main food resource for the remaining population. In fall, the majority of fish consumed mostly dipteran larvae. A more generalist strategy was shown in winter, with amphipods and dipteran larvae as a main food resource.

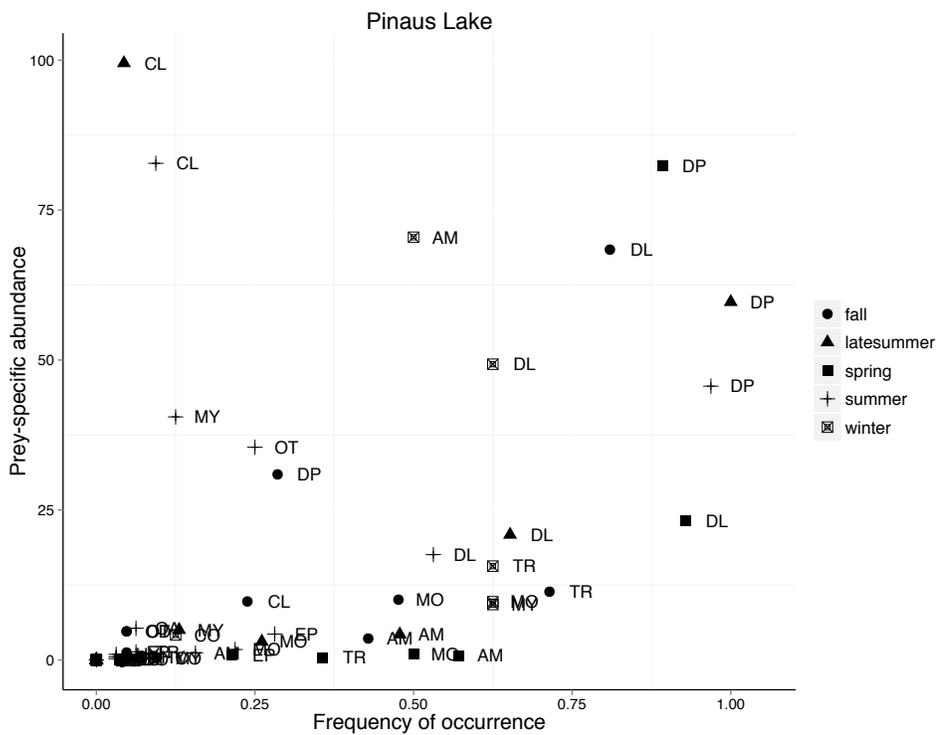


Figure 2-12. Prey importance, feeding strategy and niche width contribution for Pinaus Lake rainbow trout. See Figure 2-3 text for prey category abbreviations and text on pg 27 for interpretation.

In Little Pinaus Lake, rainbow trout showed no significant variation in diet composition among seasons or size classes. Trout in this lake demonstrated mixed feeding strategies. In spring, summer and late summer the population specialized in consumption of cladocerans; however some individuals showed specialization towards molluscs in summer and late summer. Dipteran larvae were consumed by most individuals in low quantities (Figure 2-13).

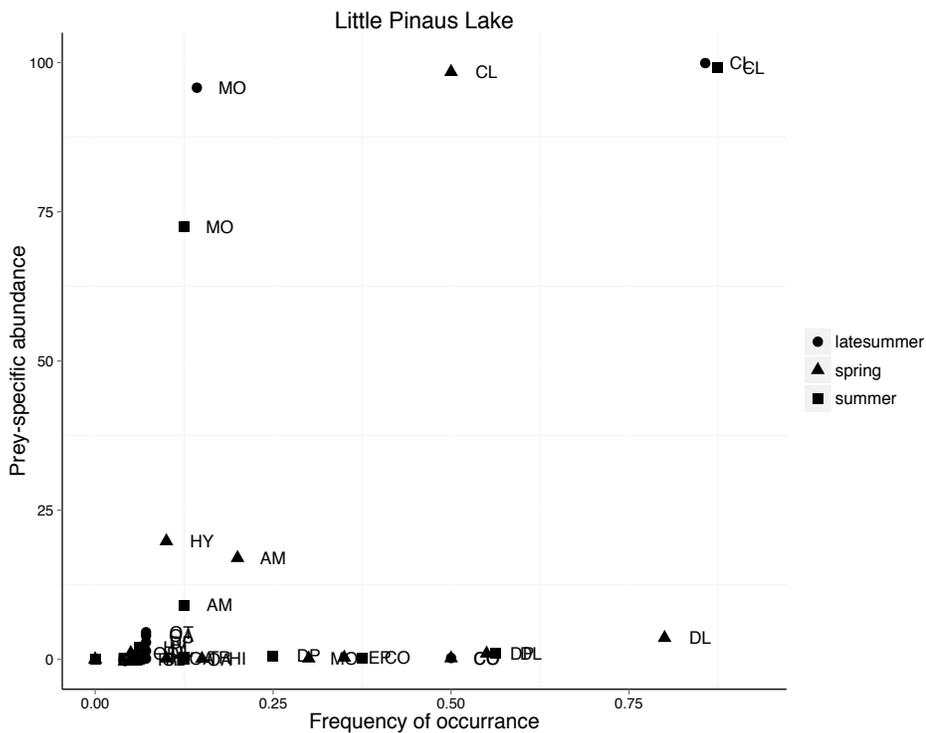


Figure 2-13. Prey importance, feeding strategy and niche width contribution for Little Pinaus Lake rainbow trout. See Figure 2-3 text for prey category abbreviations and text on pg 27 for interpretation.

Prey abundance

Identified prey resources were split into the same prey resource categories as prey consumed in all sample lakes for comparison purposes. Overall proportions of invertebrate resource categories available varied by lake (dev = 25.05, p = 0.006);

however, the only significant difference in prey abundance among lakes was the proportion of copepods (dev = 22.14, $p = 0.001$).

Within each lake, proportions of available prey resources were compared among seasons. Significant variation among seasons was only found in Bear Lake (dev = 21.42, $p = 0.004$), with the variation being explained by differences in proportions of dipteran larvae (dev = 13.169, $p = 0.010$). All other study lakes showed no significant difference in prey abundance among seasons. Although minimal seasonal variation was shown in terms of proportions of prey items sampled, it is important to note that the sampling methods did not capture differences in the proportions of dipteran pupae throughout the seasons due to the nature of sporadic hatch timing.

Yellow Perch Prey Selectivity

The top three preferred prey categories for yellow perch in each lake and season are shown in Table 2-7; however, the significance of selectivity was variable among seasons. Dipteran pupae were consistently selected for in all lakes when available, with the exception of Kalamalka Lake, where dipteran pupae were not found in stomachs or lake samples, likely due to sample timing.

Table 2-7. Yellow perch prey selection by season for each study lake. Significant overall prey selection by season is indicated by *. Top three preferred prey categories are listed in order of highest (left) to lowest (right), based on selection indices by season, regardless of significance. See Figure 2-3 caption for prey category abbreviations.

Lake	Season	Top three selected prey categories		
Pinaus Lake	Spring *	MY	DP	AM
	Summer *	DP	OA	CL
	late summer	DP	HI	MO
	Fall	AM	MY	DL
	Winter *	MY	AM	TR
Bear Lake	Spring	HY	DP	HI
	Summer *	DP	MO	TR
	Late summer	DP	MO	CL
	Fall	MO	HI	CL
	Winter	MO	OD	DL
Little Pinaus Lake	Spring	TR	DP	HI
	Summer	DP	TR	OA
	Late summer	DP	TR	OD
Swan Lake	Spring	CL	DP	DL
	Summer *	DP	CL	MO
	Late summer *	CL	DP	CO
Kalamalka Lake	Summer *	MY	OT	AM
	Late summer *	CO	TR	OA
Wood Lake	Summer	OT	DP	CO
	Late summer *	DP	CL	MO
Ellison Lake	Summer	HY	TR	DP
	Late summer	DP	HY	DL

Rainbow Trout Prey Selectivity

The top three preferred prey categories for rainbow trout in each lake and season are shown in Table 2-8; however, the significance of selectivity was variable among seasons. In Pinaus Lake, rainbow trout consistently selected for dipteran pupae in spring, summer and late summer. Trichopterans, mysids, molluscs and amphipods were also selected for particularly in fall and winter. In Little Pinaus Lake, a similar pattern was evident in that dipteran pupae were selected for in spring, summer and late summer. In late summer, other terrestrial prey items were the most highly selected for. Cladocerans were also consistently selected for in Little Pinaus Lake in all three seasons.

Table 2-8. Rainbow trout prey selection by season for each study lake. Significant overall prey selection by season is indicated by *. Top three preferred prey categories are listed in order of highest (left) to lowest (right), based on selection indices by season, regardless of significance. See Figure 2-3 caption for prey category abbreviations.

Lake	Season	Top three selected prey categories		
Pinaus	Spring	DP	TR	DL
	Summer *	DP	OT	MY
	Late summer *	DP	MY	DL
	Fall	TR	MO	AM
	Winter *	MY	TR	AM
Little Pinaus	Spring	DP	HI	CL
	Summer	DP	TR	CL
	Late summer *	OT	DP	CL

Diet Overlap

Significant diet overlap occurred between yellow perch and rainbow trout in Pinaus Lake in all seasons except late summer (Table 2-9). Overlap was less prominent in Little Pinaus Lake, occurring only in spring.

Table 2-9. Summary of Morisita's Overlap Indices (>0.6 is sig.) values for yellow perch and rainbow trout in Pinaus and Little Pinaus Lakes.

Lake	Spring	Summer	Late summer	Fall	Winter
Pinaus Lake	0.78 *	0.91 *	0.43	0.83 *	0.86*
Little Pinaus Lake	0.88 *	0.26	0.52	N/A	N/A

Relative Condition

Mean condition factor for yellow perch varied significantly among study lakes (ANOVA: $F = 42.37$, $P = <2^{e-16}$) for overlapping sampling periods. Relative condition of yellow perch was highest in Pinaus and Little Pinaus Lakes. This is consistent with visual observations and the general size of fish in those two lakes being greater than the other sample lakes. Kalamalka Lake had the overall lowest relative condition of all study lakes. Seasonal variation in mean condition was evident and a decrease in condition occurred between summer and late summer in all study lakes (Figure 2-14). Condition of yellow

perch in all lakes was less than 1, indicating that condition may be lower than average (Blackwell et al. 2000).

The mean relative condition of rainbow trout in Pinaus and Little Pinaus Lake were not significantly different (Figure 2-15). Values were close to 1, indicating average condition (Blackwell et al. 2000), with the exception of higher values in Pinaus Lake in summer.

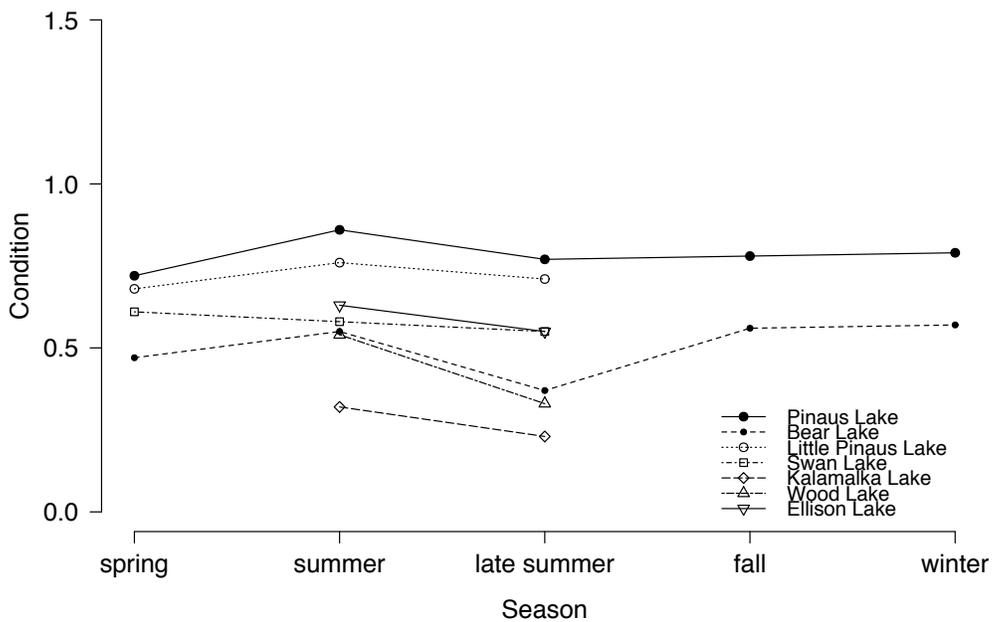


Figure 2-14. Mean Fulton condition factor for yellow perch in study lakes during each sampling period. Values less than 1 indicate fish are smaller than average (Blackwell et al. 2000).

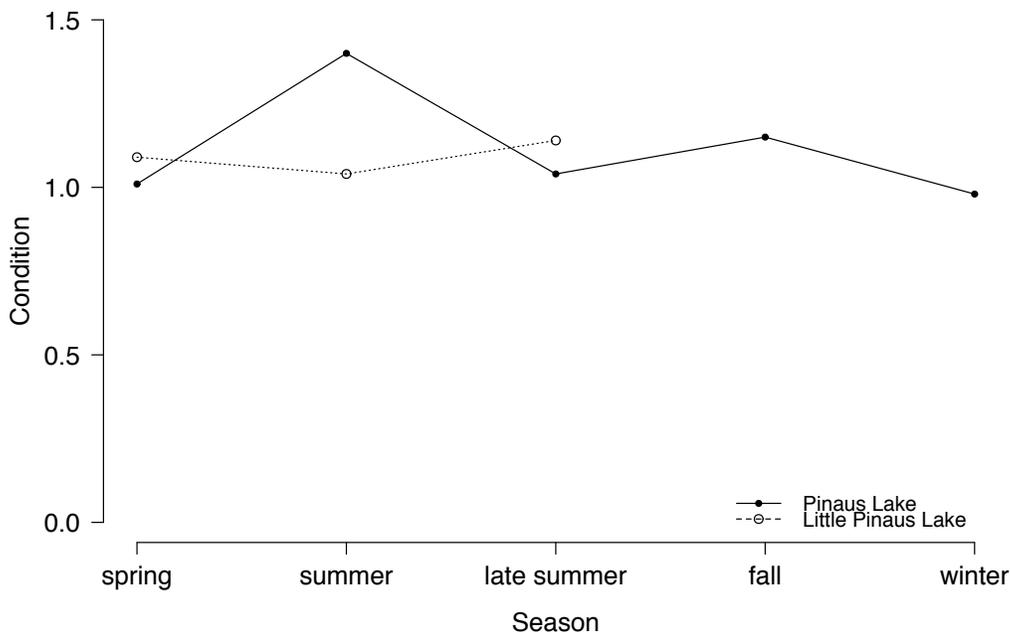


Figure 2-15. Mean Fulton condition factor for rainbow trout in Pinaus and Little Pinaus Lakes during each sampling period. Values near 1 indicate fish are of average condition (Blackwell et al. 2000).

Discussion

Feeding ecology of introduced yellow perch was analyzed in seven British Columbia lakes to determine if there were trends in feeding habits among lakes, and if any feeding habits may be occurring that could be unusual in terms of documented habits in their native range. Rainbow trout diets were also documented in two of seven study lakes to determine the level of dietary overlap occurring with yellow perch.

Yellow Perch Feeding Ecology

Diet composition and feeding strategy

It was predicted that among study lakes, introduced yellow perch would maintain a generalist strategy and broad niche width, utilizing the most plentiful prey available rather than selecting for specific resources. In addition, it was expected that larger yellow perch would show a highly piscivorous diet. The wide range and varying abundances of prey items found in the yellow perch diets studied did reflect an overall generalist feeding

strategy in five of seven study lakes, as was expected based on documented habits of yellow perch in their native range (Peterson and Martin-Robichaud 1982, Krieger et al. 1983), with the exception that piscivory was not present in all study lakes, despite the presence of prey fishes.

Some individual specialization did occur in Pinaus Lake where a small number of individuals ate mainly cladocerans in summer, and in Kalamalka Lake where a small number of fish ate mainly copepods and trichopterans in summer and late summer. Individuals within these lakes are not all alike, although this between-individual variation contributed to the overall broad niche width of the population within the study lakes, as a population's broad niche width can be made up from individuals with narrow, but different niche widths, or by a number of broad niches (Amundsen et al. 1996).

Fish in Swan and Ellison Lakes were an exception to the generalist feeding strategy, in that the entire population of yellow perch displayed a narrow niche width. In Swan Lake, yellow perch showed a specialist strategy, the diet being almost entirely composed of cladocerans, and in Ellison Lake the population consumed almost entirely fish and dipteran larvae.

Some unique patterns and differences were found in feeding strategies among the seven study lakes. One of the most noticeable differences among lakes was the planktivorous specialization and narrow niche width of the yellow perch population in Swan Lake. Overall, diet composition varied significantly among lakes mainly due to differences in the importance of cladocerans and fish as main food resources. Based on estimated prey availabilities, there was no significant difference in the abundance of cladocerans among lakes, so this variation was likely due to factors other than availability. Typically, it would be expected that as the perch grew, they would begin to consume more variety and larger macroinvertebrates (Siefert 1972; Whiteside et al. 1985; Brown et al. 2009). Based on prey abundance estimates in Swan Lake, other food resources were available, but were not utilized. Determining the underlying cause of

variation in feeding strategy is beyond the scope of this study; however, studies on European perch (*Perca fluviatilis*), a species very closely related to yellow perch (Thorpe 1977), have shown that when perch have no predators and most competition is removed, they eat mostly zooplankton and expand their habitat out of typical shoreline areas. This holds true in Swan Lake, where there were few or no predators. Very few northern pikeminnows or trout were captured in Swan Lake during gill net sampling. This could be an example of a predator-induced habitat shift (Diehl and Eklöv 1995), where a lack of predators has promoted use of the entire lake, as observed in Swan Lake, and has resulted in more consumption of pelagic prey such as cladocerans. The observed lack of predators in Swan Lake could also be exacerbating the documented “growth bottle neck” that is often attributed to a macroinvertebrate prey shortage (Persson 1986, Heath and Roff 1996). Persson and Eklöv (1995) found that perch in treatments with no predators depleted prey resources to a greater extent than in treatments containing predators, possibly limiting perch to a diet of cladocerans and leading to an overall stunted population. A study in Lake Erie, within their native range, describes yellow perch switching to a diet of small dipteran larvae and zooplankton when large bodied macroinvertebrates were depleted in the lake (Tyson and Knight 2001). Although prey abundance estimates in Swan Lake showed no significant difference to the other sample lakes, macroinvertebrate food resources could still be a limiting factor for the population. Although no stock assessment has been completed, large numbers of small stunted perch were captured easily in relatively short timeframes during gillnet sampling. This is reflected in the below average condition of yellow perch sampled in Swan Lake (Figure 2-14). In addition to a lack of predators, this feeding strategy could also be influenced by the trophic state of the lake. A study on European perch in Lake Constance showed that perch diets became almost entirely composed of zooplankton after the eutrophication of the lake (Eckmann et al. 2006). This trend was reversed when the lake moved to a more oligotrophic state later on, and perch transitioned back to a more omnivorous broad diet, as would be more typically expected (Schleuter and Eckmann 2008). The trophic status of Swan Lake was not assessed as part of this study, but potential eutrophic conditions could be a contributing factor. Although Secchi depths were on average 3.5 m, relatively

high visibility, Swan Lake visually appears to support productive conditions in terms of aquatic vegetation and plankton.

The environment in Bear Lake was similar to that of Swan Lake in that a large population of stunted, relatively low condition (Figure 2-14) yellow perch were present. No predators of another species exist, as the only other species present is stocked planktivorous Pennask strain rainbow trout (BCMoE 2013). Yellow perch also occupied offshore areas of the lake, as they did in Swan Lake. Feeding patterns are somewhat different in that perch have not solely become zooplankton specialists. Perch exhibited an overall generalist feeding strategy, consuming large proportions of macroinvertebrates; however, in summer and late summer a specialist strategy emerged where cladocerans were the most important food resource, making up almost 100% of the diet composition of about 75% of perch sampled. Anecdotal information, from the owner of a fishing camp on Bear Lake, suggests that yellow perch have been declining in size in recent years, and it could be anticipated that as the population grows and depletes other food resources, condition may decline and a trend toward a diet solely composed of zooplankton may occur.

The other major difference in diet composition among lakes was in the consumption of fish. The abundance of fish as a prey resource was not determined, but it was recognized that juvenile fish populations vary among lakes. In addition to yellow perch, Pinaus, Little Pinaus and Bear Lakes contain only rainbow trout, which are stocked at sizes too large to be consumed by yellow perch. Therefore, the only fish available as prey within those lakes are juvenile yellow perch. The other study lakes including Swan Lake, Kalamalka Lake, Wood Lake and Ellison Lake all naturally recruit other fish species, which could be preyed upon (Table 2-4). During sample collection schools of juvenile fish were visible in Kalamalka and Wood Lakes, confirming the presence of juvenile fish as a prey resource. The variation in fish prey communities could explain the difference in proportions of juvenile fish consumed by yellow perch. This variation does not explain why yellow perch in Pinaus, Little Pinaus and Bear Lake did not consume any juveniles

of their own species. Studies on European perch show that when predators were present, perch diets shifted to include larger macroinvertebrates and fish as perch grew (Persson 1986, Persson and Eklöv 1995). This holds true in Pinaus Lake where rainbow trout are predated upon yellow perch, and perch diets were dominated by macroinvertebrates. In Ellison, Kalamalka and Wood Lakes, a similar situation occurs as yellow perch face predation from northern pikeminnows, as was determined through field stomach samples and visual evidence of northern pikeminnows eating yellow perch directly off of sampling gill nets. Another study by Diehl and Eklöv (1995) showed that in the presence of vegetation and predators, 0+ perch switched from use of open water to vegetated littoral areas. Persson and Eklöv (1995) also concluded that European perch contained prey fish in their diets when minimal or no refugia was present. This may be relevant in Kalamalka, Wood and Ellison lakes, where large proportions of fish were consumed and the relative amount of refugia (aquatic vegetation and woody debris) was limited as compared to Pinaus Lake, Little Pinaus Lake and Swan Lake. The water was also very clear in Kalamalka and Wood Lakes (Table 2-1), possibly increasing encounter rates between perch and juvenile prey fishes. Yellow perch is known to be a visual predator with greater abilities to capture mobile prey in lakes with higher visibility (Janssen 1997, Persson and Hansson 1999).

Seasonal variation and selectivity

Diet composition of yellow perch varied significantly among seasons in four of seven study lakes. This variation was not reflected in the prey availability estimates, and therefore, is likely due to some level of diet selectivity. Little information is available in the literature for comparison of seasonal variation and selectivity in yellow perch diets, likely due to their typical generalist feeding strategy. In Pinaus Lake, seasonal change may be due to hatch timing or variation in abundance of dipterans. Seasonal variation in proportions of cladocerans consumed also occurred in Bear, Swan and Wood Lakes, although no seasonal change in prey abundance of cladocerans was detected. Yellow perch in those lakes consumed greater proportions of cladocerans in summer and late summer than in other sample seasons. This increased consumption of cladocerans,

despite the lack of their increase in availability, was reflected in Swan Lake and Wood Lake where yellow perch showed significant selectivity towards cladocerans in summer (Swan Lake) and late summer (Swan and Wood Lakes).

In addition to Swan and Wood Lakes, significant prey selectivity for prey categories consumed in large proportions occurred in Pinaus Lake for dipteran pupae in spring and summer, in Bear Lake for molluscs in summer, and in Kalamalka Lake for copepods and trichopterans in late summer. It is important to note that these prey resources, which formed the largest proportions of the diet, were consumed in larger proportions than their estimated availability. This type of consumption could have potentially, or may have already, changed the macroinvertebrate community (Cobb and Watzin 1998). Other significant prey selectivity occurred for less important prey, consumed in lower proportions.

Rainbow Trout Feeding Ecology

Diet composition, feeding strategy

Rainbow trout in Pinaus and Little Pinaus Lakes had significantly different diet compositions, feeding strategies and niche widths. The broad niche width and generalist feeding strategy in Pinaus Lake contrasted with the narrow niche width and specialized population of trout in Little Pinaus Lake. This difference in feeding strategy was likely due to differences in the strains of rainbow trout present in each lake.

In Pinaus Lake, a number of different rainbow trout strains were present including the planktivorous Pennask strain, along with the more aggressive and piscivorous Fraser Valley and Blackwater strains (BCMoE 2013). In addition, it is thought there are some naturally recruiting rainbow trout in Pinaus Lake, which could be descendants from Pennask or Blackwater strains. Due to this mixture of stocks, it was not possible to positively identify each trout with confidence. The presence of some planktivorous Pennask trout could explain why some individual specialists were identified eating solely zooplankton.

It is unknown what rainbow trout strain is present in Little Pinaus Lake, and natural recruitment may be occurring; however, this lake is directly downstream and connected to Pinaus Lake, and may contain Pennask trout or descendants of that strain. This theory was corroborated by visual identification of trout captured in Little Pinaus Lake; they all had the appearance of Pennask strain trout. The typical planktivorous diet of that strain was reflected in the results of this study.

Overall, trout diet compositions found in Pinaus and Little Pinaus Lakes were similar to documented diet descriptions, which would typically include benthic organisms and cladocerans for Pennask strain, and larger macroinvertebrates and fishes for the Fraser Valley strain (FFSBC 2004).

Diet Overlap

It was hypothesized that diet overlap would occur between yellow perch and rainbow trout in the lakes studied. Diet overlap did occur in Pinaus Lake at significant levels in all seasons but late summer. Due to this level of overlap, competitive interactions between yellow perch and rainbow trout in Pinaus Lake was suggested, but not proven. Rainbow trout and yellow perch were captured in the same areas within the lake indicating that spatial overlap also occurs between the two species.

Diet overlap can also indicate high resource abundances such as seasonal peaks in prey availability (Chipps and Garvey 2007). This is likely the case in Pinaus Lake, where the main food resources (dipteran larvae, dipteran pupae and cladocerans) were also available in larger proportions. The level of overlap that occurred within Pinaus Lake could potentially be higher than in lakes where yellow perch utilize juvenile fish as an important food resource. In recent years more aggressive strains of rainbow trout have been stocked in Pinaus Lake (Fraser Valley and Blackwater) (BCMoe 2013), which are better able to compete with the voracious yellow perch; however, the introduction of

these strains may have promoted more diet overlap than would have been present with the planktivorous Pennask strain, which was historically stocked. Although diet overlap occurred, rainbow trout in Pinaus Lake successfully predated upon the introduced yellow perch; juvenile yellow perch were found in trout stomachs in late summer. Rainbow trout piscivory was not reflected in yellow perch diets, possibly due to the high density of aquatic macrophytes acting as refugia for juvenile prey fishes. This factor could be eliminating piscivory, as was seen in European perch, when ample refugia and predators were present and perch diets shifted to include larger macroinvertebrates and fish were less piscivorous (Persson 1986, Persson and Eklöv 1995).

In Little Pinaus Lake diet overlap was less prominent, and only significant in spring, when yellow perch consumed large proportions of cladocerans. The rainbow trout population seemed to occupy a narrower niche width than yellow perch in this lake, as most of the trout diets were composed of zooplankton, compared to the broad niche width and generalist feeding strategy the yellow perch population maintained.

In Pinaus and Little Pinaus Lakes, rainbow trout appeared to have a typical diet based on the stocked strains present within each lake (FFSBC 2004); however, this may not be the case in all lakes where both species are present and results would be very specific to the lakes studied.

Stocking more aggressive strains of rainbow trout, such as piscivorous Blackwater or Fraser Valley trout may have caused increased diet overlap with perch in some circumstances; however, they may be better able to compete and predate upon yellow perch.

Condition

Mean condition factor of yellow perch in study lakes varied seasonally, but consistently indicated that yellow perch were below average size (Blackwell et al. 2000). This was particularly visible in Wood, Swan, Bear and Kalamalka Lakes where yellow perch were skinny and were generally stunted in size.

Despite significant differences in relative condition among lakes, seasonal variation in condition was constant among lakes and the highest condition occurred in all lakes in summer, declining to late summer and increasing in the fall. The fall increase could be due to greater body mass from development of gonads, as documented in European perch (Craig 1977), and the following winter decrease could be due to decreased photoperiod over the previous winter months. Yellow perch are visual predators and only feed during daylight hours. Photoperiod has been found to have significant effects on growth of yellow perch (Huh and Stuibler 1976).

Variation in relative condition among lakes could be related to variation in diet patterns. Condition factor was relatively highest in Pinaus and Little Pinaus Lakes where a generalist diet strategy occurred and most important prey items were large macroinvertebrates including dipteran larvae and pupae. Lowest relative condition occurred in Wood and Kalamalka Lakes where diets were mainly composed of fish. The lower relative condition in lakes where perch were primarily piscivorous could be due to the overall higher energy expenditure needed to capture highly mobile prey, as shown in Graeb et al. (2006), where the switch to piscivory occurred when the energetic gains and foraging costs of consuming fish outweighed that of consuming invertebrates. Typically, the smallest size at which yellow perch become piscivorous is around 130 mm (Fullhart et al. 2002). The minimum documented size at which this energy balance shifts is 80 mm (Graeb et al. 2006). Piscivorous yellow perch were found in Kalamalka Lake at 95 mm, and were on average smaller sizes than in the other study lakes. Due to the small size at which yellow perch in Kalamalka Lake become piscivorous, it is possible they may not be getting the same energetic gain from that prey source as larger fish in Ellison Lake, and therefore have a relatively lower condition than perch in the other study lakes.

Management Implications

Yellow perch are undoubtedly affecting fish and invertebrate communities to some extent within the lakes where they have been introduced due to predation and competition effects, and the inherent changes to ecosystem integrity that occur when species are

introduced (Sih et al. 1985, Moyle and Light 1996). European perch were shown to have a significant impact on the macroinvertebrate community and it was predicted that they control macroinvertebrate density (Persson 1986). This may be especially true in the lakes where the most dominant invertebrate prey items are being selected for, such as in Swan Lake, where cladocerans are being consumed in greater proportions to estimated abundance. Therefore, in lakes where yellow perch have been introduced it is likely that macroinvertebrate communities have changed or will change as perch densities fluctuate.

In Swan Lake, it is clear that yellow perch are occupying a specialist niche, and are specifically selecting for cladocerans as their main prey source, particularly in late summer. Continued consumption of this prey resource in proportions greater than the estimated prey abundance could lead to changes in the zooplankton community, as caused by yellow perch in native habitats (Cobb and Watzin 1998). Such changes in prey community could cause significant impacts to native species and stocked rainbow trout, particularly where planktivorous species are present, including potential reductions in numbers and biomass as observed by Keonings and Kyle (1997) in juvenile sockeye salmon after intense predation and changes in the zooplankton community.

Stocking piscivorous strains of rainbow trout in lakes containing yellow perch would be beneficial, as they could provide a level of interspecific competition and predate upon juvenile yellow perch. This would be particularly important in those lakes containing no other piscivorous species or a limited number of predators, such as in Swan Lake.

The diet of yellow perch in these seven study lakes seems to be an indicator of habitat use, as found in Persson and Hanson's (1999) study on European perch. It also seems that based on lake conditions including the presence or absence of predators and refugia for juvenile prey species, it may be possible to predict the feeding strategy of introduced yellow perch, if they were to be released into other lakes (Figure 2-16). These behaviours that deviate from the typical generalist behaviour of yellow perch in native habitats may be examples of behavioural innovation triggered by metabolic needs or as an adaptive response to new environments (Wright et al. 2010).

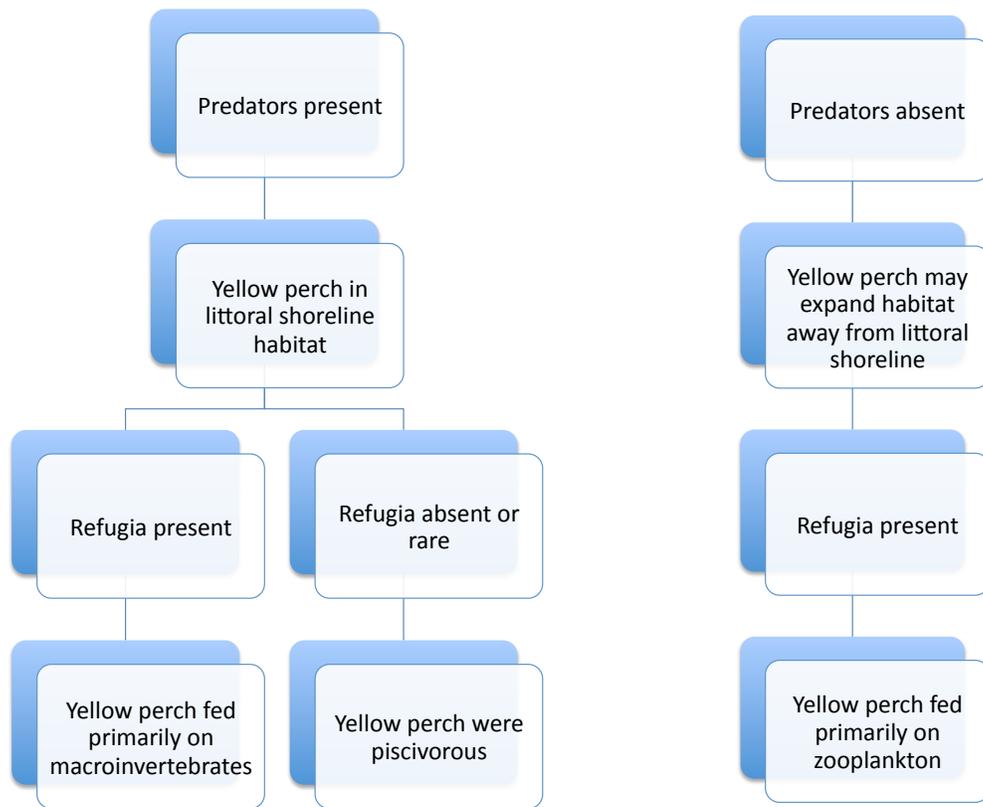


Figure 2-16. Predicted feeding strategy of introduced yellow perch based on diet analysis and observations of lake characteristics including presence of predators and refugia.

Based on the findings here, if predators are present, yellow perch will maintain typical use of littoral shoreline habitat. Within those lakes, if refugia are present yellow perch will tend to utilize macroinvertebrates as a main resource, rather than piscivory (Persson and Eklöv 1995). If there is minimal or no refugia compounded with high water clarity, there will be a higher consumption of juvenile fish as a main prey resource (Janssen 1997, Persson and Hansson 1999). This is mainly expected in larger oligotrophic lakes, where there is typically less refuge for juvenile fishes.

If no predators are present within the lake, then yellow perch may expand their habitat, eat mostly zooplankton, and likely will not complete the ontogenetic shift to a

state of piscivory (Diehl and Eklöv 1995). This may also be compounded by trophic status, where a change in fish community may occur from predominantly planktivorous fish to predominantly piscivorous fish with decreasing lake productivity (Eckmann et al. 2006, Schleuter and Eckmann 2008).

The behavioural plasticity exhibited by yellow perch in the study lakes implies that assumptions about an invasive species' behavioural characteristics, particularly diet, are not always reasonable or correct if based on descriptions of behaviour from native habitats. In lakes where yellow perch have been introduced, specific knowledge of their diet and therefore habitat use, would lead to more informed management decisions. This is particularly important in lakes where the sustainability or management of other fish species is a concern.

References

- Amundsen, P.A., Gabler, H.M. and Staldvik, F.J. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data-modification of the Costello (1990) method. *Journal of Fish Biology*, 48: 607–614.
- Blackwell, B.G., Brown, M.L. and Willis, D.W. 2000. Relative weight (W_r) status and current use in fisheries assessment and management. *Reviews in Fisheries Science*, 8: 1–44.
- Bøhn, T. and Amundsen, P-A. 2001. The competitive edge of an invading specialist. *Ecology*, 82: 2150–2163.
- Bradford MJ, Tovey CP, Herborg LM. 2008. Biological risk Assessment for yellow perch (*Perca flavescens*) in British Columbia. Canadian Science Advisory Secretariat Research Document 073.
- British Columbia Ministry of Environment (BCMoE). 2013. Fisheries inventory data queries. [Internet]. [cited April 2, 2013]. Available: <http://a100.gov.bc.ca/pub/fidq/stockedSpeciesSelect.do>
- Brodeur, R.D. and Pearcy, W.G. 1990. Trophic relations of juvenile Pacific salmon off the Oregon and Washington coast. *Fishery Bulletin*, 88(4), p.617–636.

- Brown, T.G., Runciman, B., Bradford, M.J., and Pollard, S. 2009. A Biological Synopsis of Yellow Perch (*Perca flavescens*). Canadian Manuscript Report of Fisheries and Aquatic Sciences 2883: 1-19.
- Caiola, N., Vargas, M.J. and de Sostoa, A. 2001. Feeding ecology of the endangered Valencia toothcarp, *Valencia hispanica* (Actinopterygii: Valenciidae). Hydrobiologia, 448: 97–105.
- Calenge, C. 2006. The package Adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling, 197: 516-519.
- Caton, L.W. 1991. Improved subsampling methods for the EPA “Rapid Bioassessment” benthic protocols. Bulletin of the North American Benthological Society, 8(3), p. 317-319.
- Chipps, R.S., and Garvey, J.E. 2007. Assessment of diets and feeding patterns. p.473-514 in Guy, C.S., and Brown, M.L. editors. 2007. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.
- Clapp, D.F. and Dettmers, J.M., 2004. Yellow perch research and management in Lake Michigan: Evaluating Progress in a Cooperative Effort 1997 – 2001. Fisheries, 29: 11–19.
- Cobb, S.E. and Watzin, M.C., 1998. Trophic interactions between yellow perch (*Perca flavescens*) and their benthic prey in a littoral zone community. Canadian Journal of Fisheries and Aquatic Sciences, 55: 28–36.
- Craig, J.F., 1977. The body composition of adult perch, *Perca fluviatilis* in Windermere, with reference to seasonal changes and reproduction. Journal of Animal Ecology, 46: 617–623.
- Diamond, J.M., 1970. Ecological consequences of island colonization by southwest pacific birds, I. Types of niche shifts. Proceedings of the National Academy of Sciences of the United States of America, 67: 529–36.
- Diehl, S. and Eklöv, P. 1995. Effects of piscivore-mediated habitat use on resources, diet, and growth of perch. Ecology, 76: 1712-1726.
- Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. Canadian Journal of Fisheries and Aquatic Sciences, 40: 398 – 408.
- Eckmann, R., Gerster, S., and Kraemer, A. 2006. Yields of European perch from upper Lake Constance from 1910 to present. Fisheries Management and Ecology, 13: 381–390.

- Freshwater Fisheries Society of BC (FFSBC). 2004. Rainbow trout strains currently stocked in BC waters. p.1-22
- Fullhart, H.G., Parsons, B.G., Willis, D.W., and Reed, J.R. 2002. Yellow perch piscivory and its possible role in structuring littoral zone fish communities in small Minnesota Lakes. *Journal of Freshwater Ecology*, 17: 37–43.
- Graeb, B.D., Mangan, M.T., Jolley, J.C., Wahl, D.H., and Dettmers, J.M. 2006. Ontogenetic changes in prey preference and foraging ability of yellow perch: insights based on relative energetic return of prey. *Transactions of the American Fisheries Society*, 135: 1493–1498.
- Heath, D.D. and Roff, D.A., 1996. The role of trophic bottlenecks in stunting: a field test of an allocation model of growth and reproduction in yellow perch, *Perca flavescens*. *Environmental Biology of Fishes*, 45: 53–63.
- Huh, H.T. and Stuber, D.A. 1976. Effects of temperature and light on growth of yellow perch and walleye using formulated feed. *Transactions of the American Fisheries Society*, 105: 53-63.
- Hyslop, E.J., 1980. Stomach contents analysis-a review of methods and their application. *Journal of Fish Biology*, 17: 411–429.
- Janssen, J., 1997. Comparison of response distance to prey via the lateral line in the ruffe and yellow perch. *Journal of Fish Biology*, 51: 921–930.
- Jinlong Z., Qiong D. and Jihong H. 2010. SPAA: species association analysis. R package version 0.2.0.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61: 65-71.
- Kido, M.H., Heacock, D.E. and Asquith, A. 1999. Alien rainbow trout (*Oncorhynchus mykiss*) (Salmoniformes: Salmonidae) diet in Hawaiian streams. *Pacific Science*, 53: 242–251.
- Koenings, J.P. and Kyle, G.B., 1997. Consequences to juvenile Sockeye Salmon and the zooplankton community resulting from intense predation. *Alaska Fisheries Research bulletin*, 4: 120–135.
- Kohler, C. C. and A. M. Kelly. 1991. Assessing predator-prey balance in impoundments. In: *Warmwater Fisheries Symposium I*. (Cooper, J. L. and R. H. Hamre, Eds.). pp. 257-260. Fort Collins, CO: U.S. Forest Service, General Technical Report RM-207 (1991).

- Kolar, C.S. and Lodge, D.M., 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution*, 16: 199–204.
- Krieger, D.A., Terrell, J.W. and Nelson, P.C., 1983. Habitat suitability information: yellow perch. US Fish and Wildlife Service. p. 1-47.
- MacArthur, R.H. and Pianka, E.R. 1966. On optimal use of a patchy environment. *The American Naturalist*, 100: 603–609.
- Manly, B.F.J., McDonald, L.L. Thomas, D.L., McDonald, T.L., Erickson, W.P. 2002. Resource selection by animals: statistical design and analysis for field studies, Second Edition. p.1-221.
- Moyle, P.B. and Light, T. 1996. Biological invasions of fresh water: empirical rules and assembly theory. *Biological Conservation*, 78: 149–161.
- Peterson R. H. and Martin-Robichaud D.J. 1982. Food habits of fishes in 10 New Brunswick Lakes. Canadian Technical Report of Fisheries and Aquatic Sciences 1094.
- Persson, L. 1986. Effects of reduced interspecific competition on resource utilization in perch (*Perca fluviatilis*). *Ecology*, 67: 355-364.
- Persson, L. and Eklöv, P. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology*, 76: 70–81.
- Persson, A. and Hansson, L-A. 1999. Diet shift in fish following competitive release. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 70–78.
- Purchase, C.F. Collins, N.C., Morgan, G.E., and Shuter, B.J. 2005. Predicting life history traits of yellow perch from environmental characteristics of lakes. *Transactions of the American Fisheries Society*, 134: 1369–1381.
- R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: <http://www.R-project.org/>
- Roberge, M., Slaney, T. and Minns, C.K. 2001. Life history characteristics of freshwater fishes occurring in British Columbia , with major emphasis on lake habitat requirements. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2574: 1-189.
- Schleuter, D. and Eckmann, R. 2008. Generalist versus specialist: the performances of perch and ruffe in a lake of low productivity. *Ecology of Freshwater Fish*, 17: 86–99.

- Siefert, R.E. 1972. First food of larval yellow perch, white sucker, bluegill, emerald shiner, and rainbow smelt. *Transactions of the American Fisheries Society*, 101: 219–225.
- Sih, A., Crowley, P., Mcpeek, M. Petranka, J., Strohmeier, K. 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics*, 16: 269–311.
- Smith, E.P. and Zaret, T.M., 1982. Bias in estimating niche overlap. *Ecology*, 63: 1248–1253.
- Thorpe, J.E. 1977. Morphology, physiology, behaviour and ecology of *Perca fluviatilis* L. and *P. flavescens* Mitchill. *Journal of the Fisheries Research Board of Canada*, 34: 1504 -1514.
- Tyson, J.T. and R.L. Knight. 2001. Response of yellow perch to changes in the benthic invertebrate community of western Lake Erie. *Transactions of the American Fisheries Society*, 130: 766-782.
- Vander Zanden, M., G. Cabana, and J. Rasmussen. 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios (15-N) and literature dietary data. *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 1142-1158.
- Wallace, R.K. and Ramsey, J.S. 1981. Reliability in measuring diet overlap. *Canadian Journal of Fisheries and Aquatic Sciences*, 40: 347–351.
- Warton, D.I., Wright, S.T. and Wang, Y. 2012. Distance-based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution*, 3: 89–101.
- Wang, Yi., Naumann, U., Wright, S. and Warton, D. 2012. mvabund: an R package for model-based analysis of multivariate data. R package version 3.6.11. *Methods in Ecology and Evolution*, 3: 471-474.
- Whiteside, M.C., Swindoll, C.M. and Doolittle, W.L. 1985. Factors affecting the early life history of yellow perch, *Perca flavescens*. *Environmental Biology of Fishes*, 12: 47–56.
- Wilhelm, F.M., Parker, B.R., Schindler, D.W., and Donald, D.B. 1999. Seasonal prey habits of bull trout from a small alpine lake in the Canadian Rocky Mountains. *Transactions of the American Fisheries Society*, 128: 1176–1192.
- Wright, T.F., Eberhard, J.R., Hobson, E.A., Avery, M.L., and Russello, M.A. 2010. Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. *Ethology Ecology and Evolution*, 22: 393–404.

3. Movement and Habitat use of Introduced Yellow Perch in Two BC Lakes

Introduction

Yellow perch (*Perca flavescens*) have been introduced into many lakes in the interior of British Columbia (BC), Canada. In order to assess their potential impacts, local knowledge of their ecology, including movement patterns and habitat use, is needed to make more precise management decisions.

Yellow perch are known to spend most of their time in shallow littoral habitats where food resources are plentiful (Whiteside et al. 1985; MacPhail 2007). As noted in Bachelor et al. (2011), numerous studies on yellow perch have been completed yet consistent relationships between yellow perch and habitat variables are not common. Specifically, some uncertainty exists around the movement patterns of yellow perch in their native habitats, as their behaviour and daily movements can vary by lake basin (McCarty 1990, Bauer et al. 2009). In addition, habitat used by invasive species has the potential to be different than what would be expected in their native habitat (MacArthur and Pianka 1966, Diamond 1970). In British Columbia, yellow perch are an introduced species and do not have natural predators. It is unknown how this may affect their behaviour. Numerous studies have also been completed on European perch (*Perca fluviatilis*), which is a very similar species, considered by some to be biologically equivalent (Thorpe 1977). European perch increased their use of vegetation in the presence of piscivores (Diehl and Eklöv 1995); therefore, yellow perch could potentially decrease their use of vegetated areas if no piscivores were present. Persson and Hansson (1999) showed that in European perch, a shift in diet could occur after competitive release, and diet is known to directly influence movement patterns (Persson and Hansson 1999). These types of behavioural variation could be attributed to the Adaptive Flexibility Hypothesis, where an adaptive response occurs due to changes in environmental conditions (Wright et al. 2010). Specific data on movement patterns of introduced yellow perch in BC are not available and would

contribute to a better understanding of yellow perch movement and habitat use within novel habitat in BC lakes, leading to improved descriptions of population characteristics, and more precise sampling for assessing the populations of introduced yellow perch. Movement data was collected for yellow perch within two lakes in BC’s interior, Pinaus Lake and Bear Lake.

General movements of yellow perch were determined using radio telemetry during summer and in the spring spawning season. The two study objectives were: (1) to determine if in summer, yellow perch in Pinaus and Bear Lakes used relatively shallow near-shore habitat, or moved off shore into deeper water; and (2) to determine if use of shallow near-shore habitat was maintained during spring spawning in Pinaus Lake. It was predicted that, (1) in summer yellow perch would remain in relatively shallow habitat around the lakeshore, similar to the typical habitat selection shown in their native range and (2) that perch would use similar, relatively shallow, shoreline habitat during the spawning season.

Study Lakes

Pinaus and Bear Lakes are located within the Okanagan Lake watershed in BC’s interior (Table 3-1). Both of these lakes contained only introduced yellow perch and stocked rainbow trout (BCMoE 2013), and provided a comparison between a relatively large, deep lake (Pinaus Lake), and a smaller, shallow lake (Bear Lake). Pinaus Lake had a variable shoreline with a shallow vegetated bench in many areas. Bear Lake supported aquatic vegetation around the entire lake shore and in shallower offshore areas.

Table 3-1. Location and physical characteristics of sample lakes (BCMoE 2013).

Lake name	UTM	Elevation (m)	Surface area (ha)	Max. depth (m)
Pinaus Lake	11U 317357 5588663	982	168	53.6
Bear (Lambly) Lake	11U 305204 5546292	1150	81	9

Methods

Summer and spring movements of yellow perch in Pinaus and Bear Lakes were determined using radio telemetry. Transmitters were implanted into five fish in each lake during the summer season to determine diel movement. Telemetry data were collected over two 24-hour periods in each lake (Table 3-2). In addition, a second set of five fish were implanted with transmitters in March 2012 in Pinaus Lake to record daily locations during the pre-spawning and spawning season (Table 3-2). The first three of 11 tracking sessions were completed while the lake was still ice covered (March 24, April 6, April 9). The later sessions were completed during the spawning period. The transmitters used were Lotek™ MST-820-T, 8 mm x 22 mm, weight 2.2 grams (Pinaus Lake) and Lotek™ MST 820, 8 mm x 20 mm, weight 2.1 grams (Bear Lake).

Table 3-2. Implant and tracking dates for yellow perch in Pinaus and Bear Lakes.

Lake	Implant date	Tracking dates
Pinaus Lake: 24 hr diel movements	13 July, 2011	9-10 August, 2011 24-25 August, 2011
Bear Lake: 24 hr diel movements	25 July, 2011	3-4 August, 2011 17-18 August, 2011
Pinaus Lake: Daily locations during pre-spawning and spawning season	10 March, 2012	24 March, 2012 (ice) 6 April, 2012 (ice) 9 April, 2012 (ice) 20 April, 2012 27 April, 2012 2 May, 2012 4 May, 2012 7 May, 2012 11 May, 2012 16 May, 2012 28 May, 2012

Fish Collection and Implants

Angling was used to capture fish and barbless hooks were used in all instances to minimize trauma. Collected fish were measured and weighed, then anaesthetized using MS-222 solution until they lost equilibrium. A minimum fish weight of 215 g was required for implant so transmitter weight remained less than 2% of body weight (Rogers

and White 2007). The surgery was completed with the fish upside down in a V-shaped trough. The anesthetic was dissolved in water and manually pumped to aerate the gills and anesthetize the fish. A small incision was made in the belly of the fish, posterior to the pectoral fins, about 1.5 times the length of the transmitter, the transmitter implanted, and the incision sutured, taking approximately 5 minutes per fish. Fish were then put into a safe holding tank to recover. Fish were released once they had regained full equilibrium and were swimming forcefully. All methods followed the Canadian Council on Animal Care (CCAC) protocols on anesthesia.

Tracking

Tracking followed a 21-day recovery period after surgery, in which it was expected that yellow perch would resume their normal movement patterns (Rogers and White 2001). In August 2011, tracking was completed in four-hour blocks over two, 24-hour periods in both lakes. The four-hour blocks included the diurnal period (two hours before and after solar noon), the dusk period (two hours before and after sunset) and the dawn period (two hours before and after sunrise). These times were adjusted according to seasonal variation in daylight. The fully dark periods after sunset and before sunrise provided a sense of what occurred during night hours.

Fish locations were determined using a Lotek™ SRX_400 receiver and antenna attached to the front of the boat. The boat was driven until a strong signal was received, then oars were used to close the distance. Each fish location was recorded using Global Position System (GPS) UTM's (Garmin 76S), along with water depth (m) (Lowrance Mark 5X-DSI) and time. Fish were found repeatedly for the time frame allocated. Water depth (m) was recorded as a surrogate for fish depth, to provide a maximum depth at which the fish could have been located. This approach has been used in other studies, as yellow perch are known to be demersal species (Radabaugh et al. 2010). Calibration exercises were completed to provide a baseline level of acceptable signal strength in each lake, as signals can vary depending on conductivity (Appendix C).

In spring 2012, tracking began when the lake was still frozen. Fish were located while walking on the ice until a maximum signal strength was achieved. Depth measurements were not possible. Once the ice melted, fish were located in the same manner as the previous summer using a boat.

Dissolved Oxygen and Temperature

Dissolved oxygen was measured in both lakes (YSI Model 85), on each tracking day, to determine if oxygen was a limiting factor in depth of yellow perch. During early spring tracking sessions with ice cover, the meter was lowered through a hole in the ice.

Littoral water temperatures in Pinaus Lake were recorded on an hourly basis throughout the early spring and spawning season using a TidbiT v2 Water Temperature Data Logger, which was installed in approximately 0.5 m of water near the shoreline in a sheltered bay similar to other areas where yellow perch spawned.

Data Analysis

Fish locations and lake perimeters (UTM's) were input to Fishtel 1.4, a telemetry analysis program designed to calculate mean distance from shore (Rogers and White 2001). Distance from shore was calculated for the summer telemetry sessions in Pinaus and Bear Lakes, and then for the spring telemetry sessions in Pinaus Lake. These calculated distances were compared using one-way ANOVA among time periods and among individuals within each lake, and among spring telemetry sessions in Pinaus Lake. Tukey pair-wise comparisons were used to determine where significance difference occurred. Depths, which were recorded during tracking sessions, were compared similarly using one-way ANOVA. Linear regression was used to determine if the relationship between distance from shore and lake temperature was significant.

Results

Summer tracking

During the summer tracking sessions, each tagged fish was successfully located a minimum of 4 times within each 4 hour tracking segment (dawn, diurnal, dusk) within each 24-hour session. A total of 129 and 95 locations were successfully obtained in Pinaus and Bear Lakes respectively. During the spring tracking sessions in Pinaus Lake a total of 79 locations were obtained (Table 3-3).

Table 3-3. Summary of number of telemetry locations obtained for Pinaus Lake during summer and spring tracking, and Bear Lake during summer tracking.

Lake	Number of locations			
	Dawn	Diurnal	Dusk	Total
Pinaus Lake Summer	55	32	42	129
Bear Lake Summer	29	30	36	95
Pinaus Lake Spring	NA	79	NA	79
Total	84	141	80	305

During the summer tracking sessions yellow perch were, on average, located farthest from shore during the diurnal period in Pinaus Lake (Figure 3-1) and during the dawn period in Bear Lake (Figure 3-3). No significant difference in distance from shore was found among individuals in either lake.

Measured depths ranged from 0.5 m - 9.6 m in Pinaus Lake, and 0.3 m – 8.5 m in Bear Lake during the summer tracking sessions (Figure 3-2 and Figure 3-4). No significant differences were found in depths among time periods within lakes.

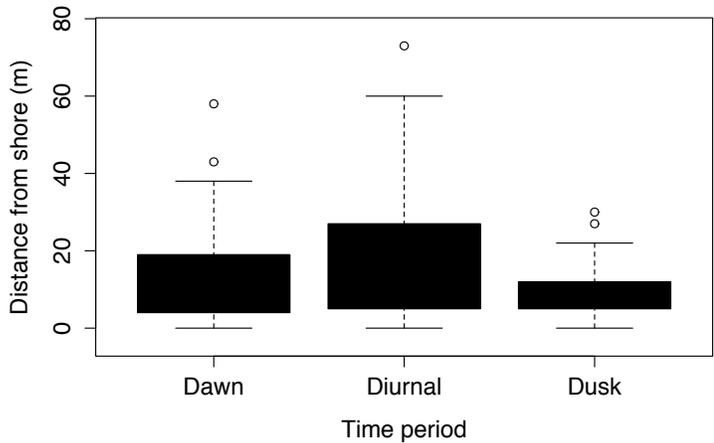


Figure 3-1. Mean distance from shore (+/- 95% CI) for yellow perch in Pinaus Lake during summer tracking for each of the three tracking periods within the 24 tracking sessions. 50% of the data points lie within the boxed area. Error bars above and below represent the higher and lower quartiles of data, which are shown as individual points.

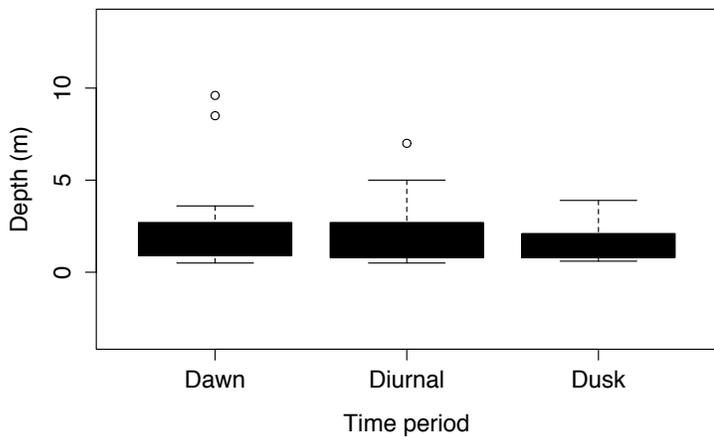


Figure 3-2. Pinaus Lake recorded depths (m) during summer tracking for each of the three tracking periods within the 24 tracking sessions.

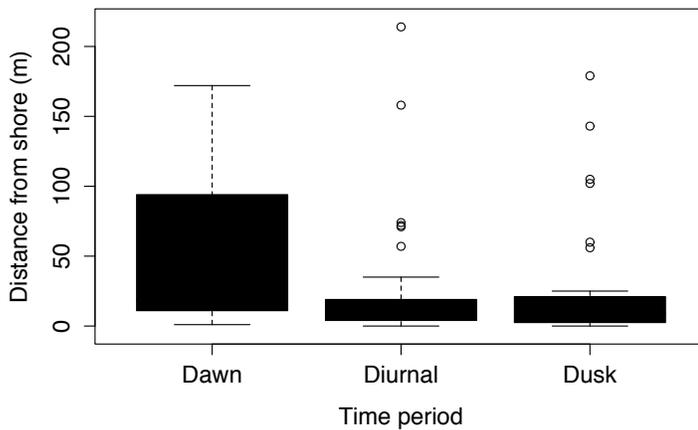


Figure 3-3. Mean distance from shore (+/- 95% CI) for yellow perch in Bear Lake during summer tracking for each of the three tracking periods within the 24 tracking sessions.

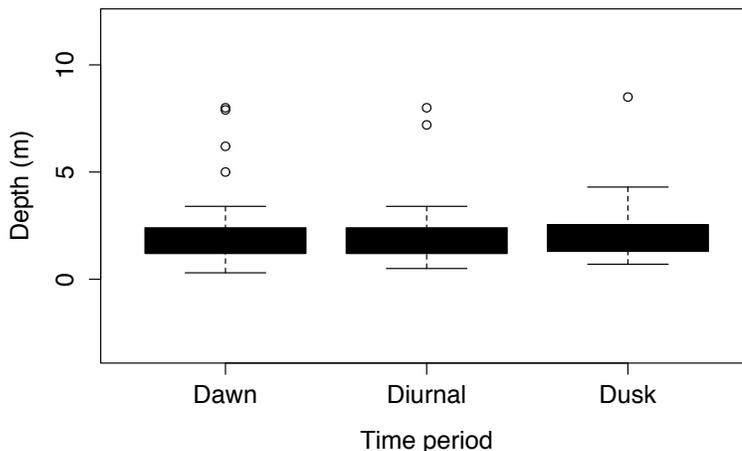


Figure 3-4. Bear Lake recorded depths (m) during summer tracking for each of the three tracking periods within the 24 tracking sessions.

Specific movement rates or distance travelled per day was not within the scope of this study, although basic observations of movement patterns were possible. Fish moved parallel to the shoreline predominantly during the dawn and dusk periods. During the dark periods at the end of the dusk tracking session and beginning of the dawn tracking session yellow perch did not move at all, remaining in the same location.

During a 24 hour tracking period, there was one instance where a tagged perch was near the release location at 10 am, moved along the lake shore during the midday period,

and was then found on the opposite side of the lake around 8 pm, an approximate shoreline distance of 4 km, assuming the perch remained close to shore while travelling. Other tagged fish tended to remain in more local locations during a 24-hour period, moving in short segments back and forth along the shoreline within a few hundred metres.

Spring tracking

During the spring tracking sessions in Pinaus Lake, yellow perch were located farther from shore during the first three tracking sessions when the lake was ice covered (Figure 3-5). One-way ANOVA showed that distance from shore varied significantly across all tracking dates ($F = 6.46$; $df = 10, 67$; $p = 6.86^{-7}$); however, no significant difference was found among individuals. Tukey post-hoc comparisons of the 11 tracking sessions indicate that perch locations from the first three tracking sessions (March 24, April 6, and April 9) were significantly farther from shore than locations from the later tracking sessions. During the April 20th tracking session, yellow perch were found closer to shore. This movement coincides with the first visual observations of egg masses on April 25, 2012 and temperatures increasing to approximately 3.8 °C (Figure 3-6).

Depths were not available for the first three tracking sessions due to ice cover; however, depths for the later 8 tracking sessions ranged from 0.7 m – 15 m.

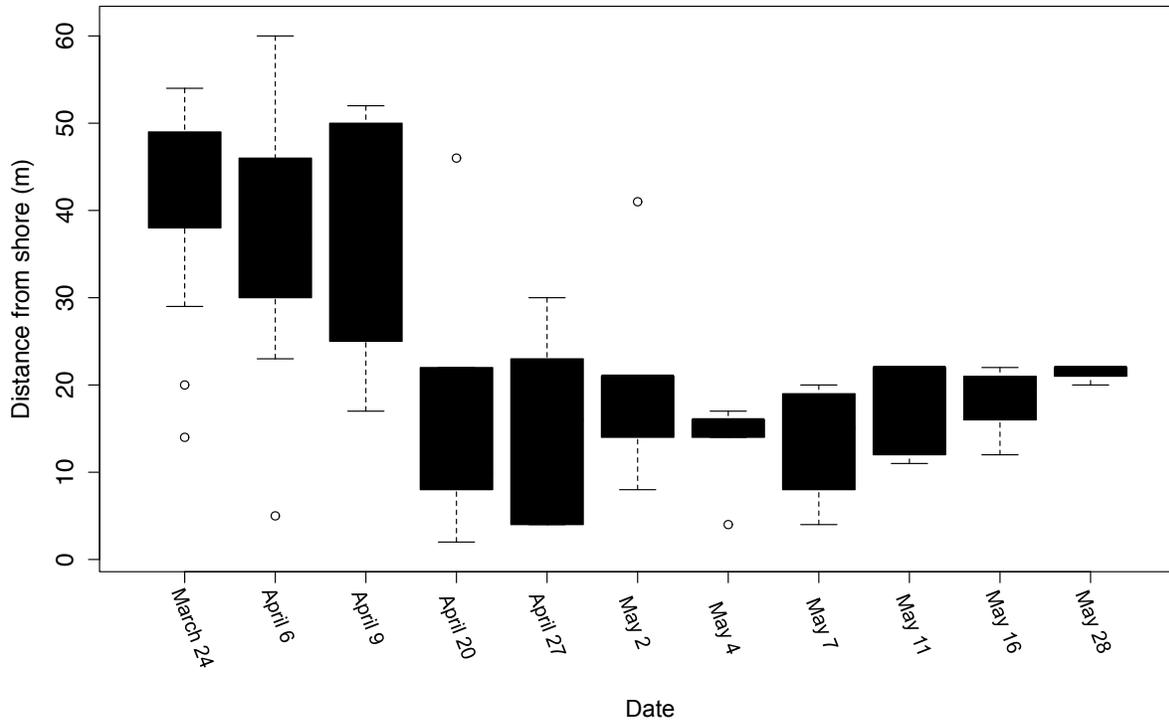


Figure 3-5. Mean distance from shore (m) (+/- 95% CI) for yellow perch in Pinaus Lake spring 2012 tracking sessions. First egg masses were seen on April 25, 2012.

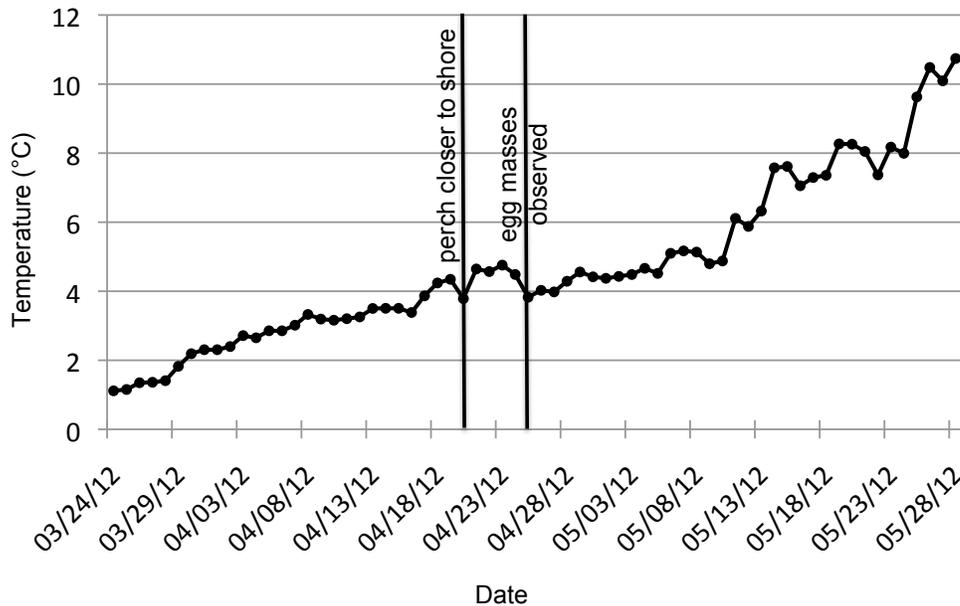


Figure 3-6. Mean daily littoral water temperatures in Pinaus Lake at approximately 0.5 m depth from March 24, 2012 – May 28, 2012. Perch were observed moving closer to shore on April 20, 2012 and first egg masses were seen April 25, 2012.

Fish had remained very close to their release location while ice was covering the lake, as observed on March 24, April 6 and April 9 tracking sessions. By April 20th, the perch were closer to shore and all had moved away from the release location, either to the far east or west end of the lake, which was approximately 1300 m – 1700 m distance. The tagged perch continued to move between tracking sessions from April 27 to May 7. One fish moved between far ends of the lake, twice between April 9th and 27th, a distance of approximately 3200 m each time. After May 7, tagged perch were found in local areas on successive tracking dates.

Dissolved Oxygen and Temperature

During the summer tracking sessions, dissolved oxygen remained on average 5.03 mg/l in Pinaus Lake up to a depth of 20 m during the tracking periods. In Bear Lake, dissolved oxygen was slightly lower, becoming extremely low near the bottom of the lake below depths of 6 m (Figure 3-7).

During the spring tracking sessions, dissolved oxygen in Pinaus Lake was on average 7.59 mg/l. Higher than average values were present in the top 2 m on March 24, 2012, that could be due to oxygenation of the water due to mixing from the ice auger (Figure 3-8).

Littoral water temperatures ranged from 1 °C – 10.7 °C during the spring tracking sessions. Temperatures of 3.8 °C on April 20, 2012 were associated with perch moving closer to shore, followed by the first observed egg strands on April 25, 2012. Temperatures reached 4.8 °C between the observed shift towards shore and the onset of spawning (Figure 3-6). Linear regression indicated that a significant relationship between distance from shore and mean daily temperature was present ($R^2 = 0.2288$, $p < 0.001$).

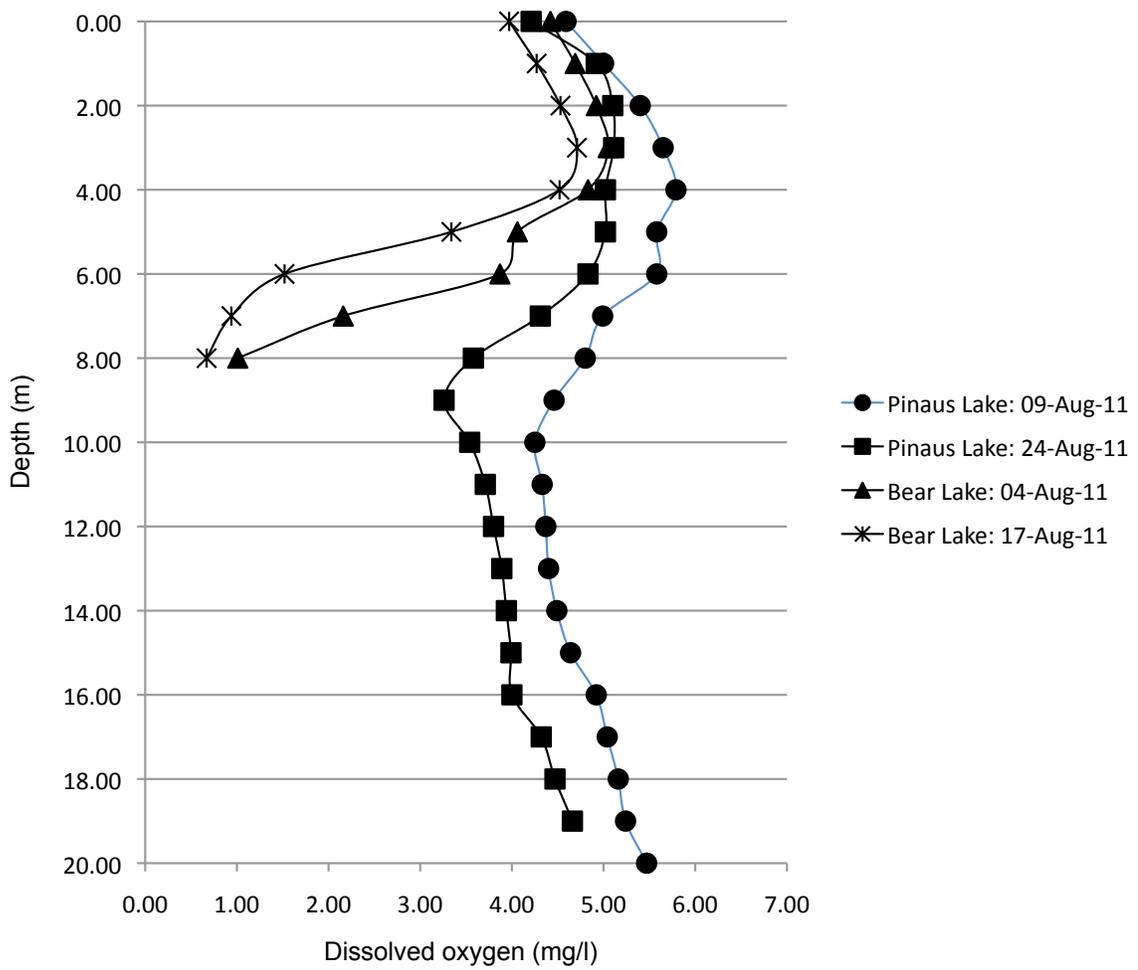


Figure 3-7. Dissolved oxygen profiles for Pinaus and Bear Lakes during summer tracking sessions.

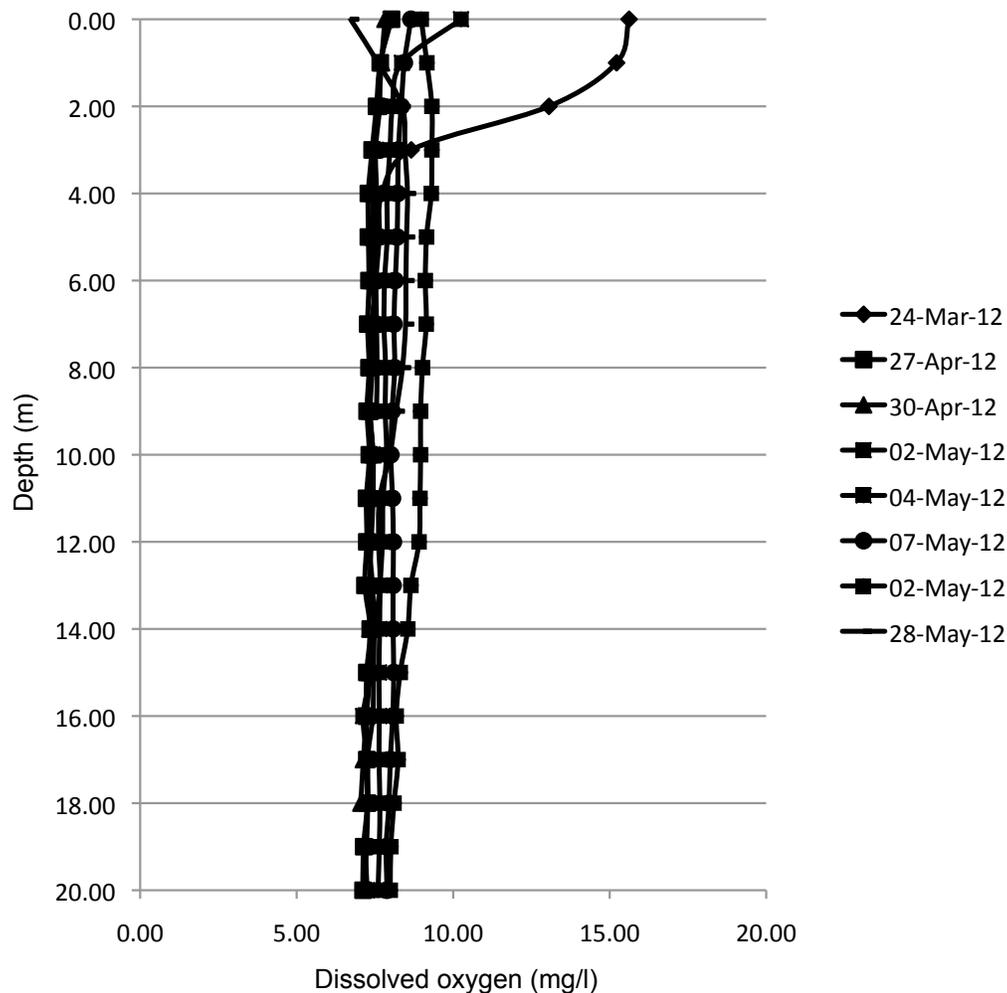


Figure 3-8. Dissolved oxygen profiles for Pinaus Lake during spring tracking sessions. On March 24, 2012, ice cover was present on the lake. April 27, 2012 and later were ice free.

Discussion

Summer 24 Hour Tracking

Similar patterns were seen in both Pinaus and Bear Lakes during the summer tracking sessions where distance from shore and associated depth did not vary significantly over the 24 hour tracking period. Though not statistically significant, distance from shore in Pinaus Lake was slightly greater during the diel period than either dawn or dusk periods, as was found by Jansen and Mackay (1992), when yellow perch moved closer to shore

during dawn and dusk feeding periods. These results are reflected in similar studies on yellow and European perch movement and habitat use, where there was also no significant difference found in daily distance from shore or depth during summer periods (Imbrock et al. 1996, Bauer et al. 2009, Radabaugh et al. 2010). Additional observations indicating that all movement occurred during the daylight periods, and ceased during darkness, is also established within the literature (McCarty 1990, Jansen and Mackay 1992).

Yellow perch were found, on average, slightly farther from shore in Bear Lake (32.5 m) compared to Pinaus Lake (12.8 m). Associated depths were similar in both lakes averaging 2.19 m in Bear Lake and 1.85 m in Pinaus Lake. The higher average distance from shore in Bear Lake likely reflected the overall shallow bathymetry of the lake. Yellow perch utilized a much larger area within the lake, while remaining in water of comparable depth. In Pinaus Lake, only a narrow strip of shallow habitat was located around the lakeshore, although depths up to 20 m had sufficient oxygen concentrations. On tracking days dissolved oxygen averaged 5.39 mg/l up to 20 m depth, well above the lower lethal limit of 1.5 mg /l, and near the optimal dissolved oxygen level of 5 mg/l (Krieger et al. 1983, Suthers and Gee 1986). It appears that yellow perch remained close to shore, as was expected, to maintain a relatively shallow depth near vegetation, which provides cover and access to macroinvertebrate food resources (Krieger et al. 1983, Cobb and Watzin 1998, Brown et al. 2009).

Spring Tracking

While ice was covering Pinaus Lake yellow perch were found further from shore, likely inhabiting slightly greater depths. This pattern was observed by Imbrock et al. (1996), with fish moving closer to shore after ice melt. Yellow perch and the similar European perch have been known to spawn at variable depths from 0.5 m -12.3 m (Thorpe 1977, Gillet and Dubois 1995, Čech et al. 2012), most commonly spawning at depths of 0.5 m - 3.0 m (Thorpe 1977). This is well within the observed range of 0.7 m –

15 m depths where yellow perch were found in Pinaus Lake during the spawning season. The in-shore movement was consistent with an increase in water temperature to around 3.8 °C and the first visual observations of egg masses on April 25, 2012 just after ice off. Dissolved oxygen was not a limiting factor for depth during this season either, and remained above the optimal dissolved oxygen level or 5 mg/l (Krieger et al. 1983) up to 20 m depths.

Introduced yellow perch in Pinaus and Bear Lakes are occupying habitat within the expected depth range that has been recorded in natural habitat (Krieger et al. 1983, Cobb and Watzin 1998, Brown et al. 2009). Behavioural plasticity is not being demonstrated with respect to movement patterns in these two lakes. Distance from shore may be directly related to depth, as yellow perch were located farther from shore in Bear Lake, where the maximum lake depth is only 9 m. Further studies and sampling protocols for yellow perch should take this into account. In shallow lakes, yellow perch may occupy offshore habitat, provided the depth is not too great.

References

- Bacheler, N.M., Paoli, T.J. and Schacht, G.M. 2011. Controls on abundance and distribution of Yellow Perch: predator, water quality, and density-dependent effects. *Transactions of the American Fisheries Society*, 140: 989–1000.
- Bauer, W.F., Radabaugh, N.B. and Brown, M.L. 2009. Diel movement patterns of yellow perch in a simple and a complex lake basin. *North American Journal of Fisheries Management*, 29: 64–71.
- British Columbia Ministry of Environment (BCMoE). 2013. Fisheries inventory data queries. [Internet]. [cited April 2, 2013]. Available: On-Accessed: <http://a100.gov.bc.ca/pub/fidq/stockedSpeciesSelect.do>
- Brown, T.G., Runciman, B., Bradford, M.J., and Pollard, S. 2009. A Biological Synopsis of Yellow Perch (*Perca flavescens*). Canadian Manuscript Report of Fisheries and Aquatic Sciences 2883: 1-19.

- Čech, M., Vejřík, L., Peterka, J., Říha, M., Muška, M., Jůza, T., Draštík, V., Kratochvíl, M., and Kubečka, J. 2012. The use of artificial spawning substrates in order to understand the factors influencing the spawning site selection, depth of egg strands deposition and hatching time of perch (*Perca fluviatilis* L.). *Journal of Limnology*, 71: 170–179.
- Cobb, S.E. and Watzin, M.C., 1998. Trophic interactions between yellow perch (*Perca flavescens*) and their benthic prey in a littoral zone community. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 28–36.
- Diamond, J.M., 1970. Ecological consequences of island colonization by southwest pacific birds, I. Types of niche shifts. *Proceedings of the National Academy of Sciences of the United States of America*, 67: 529–36.
- Diehl, S. and Eklöv, P. 1995. Effects of piscivore-mediated habitat use on resources, diet, and growth of perch. *Ecology*, 76: 1712–1726.
- Gillet, C. and Dubois, J.P. 1995. A survey of the spawning of perch (*Perca fluviatilis*), pike (*Esox lucius*), and roach (*Rutilus rutilus*), using artificial spawning substrates in lakes. *Hydrobiologia*, 300/301: 409–415.
- Imbrock, F., Appenzeller, A. and Eckmann, R. 1996. Diel and seasonal distribution of perch in Lake Constance: a hydroacoustic study and in situ observations. *Journal of Fish Biology*, 49: 1–13.
- Jansen, W.A. and Mackay, W.C. 1992. Foraging in yellow perch, *Perca flavescens*: biological and physical factors affecting diel periodicity in feeding, consumption, and movement. *Environmental Biology of Fishes*, 34: 287–303.
- Krieger, D.A., Terrell, J.W. and Nelson, P.C., 1983. Habitat suitability information: yellow perch. US Fish and Wildlife Service. p.1-47.
- MacArthur, R.H. and Pianka, E.R. 1966. On optimal use of a patchy environment. *The American Naturalist*, 100: 603–609.
- MacPhail, J.D. 2007. *The freshwater fishes of British Columbia*. The University of Alberta Press.
- McCarty, J. P. 1990. Diel periodicity of movement and feeding of yellow perch (*Perca flavescens*) in Lake Mendota, Wisconsin. *Transactions of the Wisconsin Academy of Sciences, Arts and Letters*, 78:65-76.

Persson, A. and Hansson, L-A. 1999. Diet shift in fish following competitive release. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 70–78.

Radabaugh, N.B., Bauer, W.F. and Brown, M.L., 2010. A comparison of seasonal movement patterns of yellow perch in simple and complex lake basins. *North American Journal of Fisheries Management*, 30: 179–190.

Rogers, K.B. and White, G.C. 2007. Chapter 14 Analysis of movement and habitat use from telemetry data, p.625–676 in Guy, C.S., and Brown, M.L. editors. *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda, Maryland.

Suthers, I.M. and Gee, J.H. 1986. Role of hypoxia in limiting diel spring and summer distribution of juvenile yellow perch (*Perca flavescens*) in a prairie marsh. *Canadian Journal of Fisheries and Aquatic Sciences*, 43: 1562 – 1570.

Thorpe, J. E. 1977. Morphology, physiology, behavior, and ecology of *Perca fluviatilis* L. and *P. flavescens* Mitchill. *Journal of the Fisheries Research Board of Canada*. 34: 1504–1514.

Whiteside, M.C., Swindoll, C.M. and Doolittle, W.L. 1985. Factors affecting the early life history of yellow perch, *Perca flavescens*. *Environmental Biology of Fishes*, 12: 47–56.

Wright, T.F., Eberhard, J.R., Hobson, E.A., Avery, M.L., and Russello, M.A. 2010. Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. *Ethology Ecology and Evolution*, 22: 393–404.

4. Conclusion

Summary

In the majority of the study lakes, yellow perch had a generalist feeding strategy, as was expected based on studies of yellow perch in its native habitat (Peterson and Martin-Robichaud 1982, Krieger et al. 1983); however, the specialist strategy shown in Swan Lake was unanticipated. The lack of cannibalism was also unexpected in Pinaus and Bear Lakes. Variations in the generalist diet breadth could be attributed to behavioural innovations, or learned behaviours, as described by the Adaptive Flexibility Hypothesis (Wright et al. 2010), where diet composition and foraging behaviour are likely different among lakes, as a response to variable conditions.

Diet composition varied significantly among seasons in four of seven study lakes. Much of this difference is likely due to seasonal variations in hatch timing and abundances of invertebrates. Selectivity for dipterans and cladocerans was fairly consistent among lakes, indicating they are a preferred food item regardless of lake. Significant diet overlap with trout only occurred in one of two study lakes. This may be due to difference in the strain of rainbow trout within each lake, and why it would be difficult to extrapolate on perch-trout interactions in any other lakes in BC.

Juvenile fish were a main food resource in only three of seven study lakes. There may be other factors besides availability contributing to this variation, possibly including the presence or absence of predators, refuge availability for juveniles, and trophic status of the lake. Based on these factors, it is likely that if predators were present, yellow perch would maintain typical use of littoral shoreline habitat. Within those lakes, if refugia were present, yellow perch would tend to utilize macroinvertebrates as a main resource, rather than piscivory (Persson and Eklöv 1995). If there were minimal or no refugia compounded with high water clarity, there would be a higher consumption of juvenile fish as a main prey resource (Janssen 1997, Persson and Hansson 1999). If no predators were present within the lake, then yellow perch could expand their habitat, eat mostly zooplankton and likely would not complete the ontogenetic shift to a state of piscivory

(Diehl and Eklöv 1995). This may also be compounded by the trophic status of the lake, where more piscivory is likely present in oligotrophic lakes (Eckmann et al. 2006, Schleuter and Eckmann 2008).

Telemetry locations from Pinaus and Bear Lakes indicated that yellow perch utilized habitat locations in relatively shallow water, as was expected based on studies on yellow perch movement (Whiteside et al. 1985; MacPhail 2007). Locations were likely related to depth rather than distance from shore. Yellow perch remained close to shore to maintain a relatively shallow depth near vegetation, which provides cover and access to macroinvertebrate food resources (Krieger et al. 1983, Cobb and Watzin 1998, Brown et al. 2009). During the early spring and spawning season, yellow perch were also located near shore, but significantly closer to shore after the ice melted and spawning had began. Based on the temperature measurements and visual observations of spawning timing, it is evident that yellow perch began to spawn immediately after the ice melted at temperatures as low as 3.8 °C, slightly below the typical range of 4 – 19 °C recorded for yellow perch in native habitats (Hokanson 1977).

Study limitations

Time and resource limitations were major factors during data collection, and the reason why fall and winter diet analysis was limited to two study lakes. Further multi-season analyses could be completed in the future in the other study lakes, to determine if the feeding strategy seen in summer seasons continued, such as the exclusive consumption of zooplankton in Swan Lake.

One of the most difficult aspects to this research was attempting to quantify food availability for fishes to determine prey selectivity. No standard methods have been developed for quantifying the overall availability of invertebrates in lakes, where multiple habitat types needed to be included. This prompted the development of a new method of combining different measures of invertebrate abundances into one overall estimate. A supplementary paper on this method and quantifying food availability in lakes was completed in addition to this thesis (Appendix A).

Applications and future direction

This research was originally initiated based on concern for native salmonid populations, in lakes that do not yet contain yellow perch, to facilitate further management options for this introduced species. This study follows the 2011 risk assessment on Yellow perch in BC, completed by Fisheries and Oceans Canada's Centre of Expertise for Aquatic Risk Assessment (CEARA) (DFO 2011), which stated that yellow perch could cause a high level of impact in smaller lakes and moderate impacts in larger lakes including reduction of food resources within foraging areas and significant reductions in zooplankton (Bradford et al. 2008). My findings correspond with those of the DFO risk assessment, with the exception that my observations also suggest that there is potential for native species, such as certain strains of rainbow trout and northern pikeminnows, to become effective predators of yellow perch.

In order to develop alternate management strategies and control measures for this species, more information on the feeding ecology and movement of introduced yellow perch was needed. This research contributed to that goal, and specifically, predicts at some level that if yellow perch were introduced into BC's large salmon nursery lakes, such as Adams Lake or Shuswap Lake, they have the potential to consume juvenile salmonids and other native fish juveniles as a main food resource. This is mainly anticipated in the larger oligotrophic lakes, where there is less refuge for juvenile fishes. In smaller lakes, where no potential predators are present, and there is ample refuge for juvenile fishes, yellow perch may develop a more specialist feeding strategy, consuming large proportions of zooplankton. These results are consistent with the findings in a risk assessment (Bradford et al. 2008) where it was predicted that yellow perch in small eutrophic lakes would consume mostly zooplankton and benthic invertebrates, and yellow perch in larger oligotrophic lakes would be more piscivorous. However, deviation from the typical generalist feeding pattern, as seen in this study through individual and population specialization was not predicted in that risk assessment. In smaller lakes where yellow perch select for specific invertebrate food items or for zooplankton, there is potential that they could have significant impact on the macroinvertebrate community and even control

macroinvertebrate density, as was shown in lakes containing both yellow perch (Cobb and Watzin 1998) and European perch (Persson 1986). In this way, specific strains of rainbow trout may be negatively impacted, such as Pennask strain rainbow trout, which typically consume small invertebrates and zooplankton. In addition, reductions or changes in zooplankton communities could have negative impacts on rearing sockeye salmon, which are pelagic and prey upon zooplankton (Pauley et al. 1989).

Based on the results of the movement study in Pinaus and Bear Lakes, it appears that yellow perch inhabit a similar range of depths and associated distances from shore as could be expected in their native habitat during summer and during the spawning season.

It is anticipated that these results will be used toward further control and management of yellow perch in British Columbia Lakes. Determining the diet of introduced yellow perch, and therefore potential habitat use, allows further studies to be designed with more confidence. This includes the need for further investigation into research on new methods to control populations without the use of rotenone. Trials using artificial spawning substrates were successful, and yellow perch spawned multiple times on each substrate. Eggs from each substrate were successfully removed from the lake. This method would likely be too labour intensive to use as a method of controlling populations by removal of egg masses, but could easily and successfully be used as a method of detecting yellow perch presence in lakes. Based on the successful preliminary trials of artificial spawning substrates in Pinaus Lake, further studies should be undertaken keeping in mind that spawning might occur earlier and at lower temperatures than anticipated, as soon as ice recedes.

The demonstrated adaptive flexibility of yellow perch in the study lakes indicates that this invasive species has the ability to vary its foraging behaviour more than anticipated based on diet descriptions in native habitats. Although information on feeding ecology (resource use) and location is not adequate to assess ecological impact, it does provide further direction for managers with respect to which invertebrate populations or prey fish species could be monitored in lakes where yellow perch have been introduced. This may be crucial, as changes in invertebrate communities could have an effect on native fish

populations (Gozlan et al. 2010), and is particularly relevant in lakes where the sustainability or management of native fish species such as sockeye salmon is a concern. In addition, my feeding and movement data for introduced yellow perch helps to confirm their ecology in novel habitats with respect to potential ecological consequences by predation and competition and contributes to further development of appropriate management options as their range continues to expand.

References

- Bradford, M.J., Tovey C.P., and Herborg, L.M. 2008. Biological risk assessment for yellow perch (*Perca flavescens*) in British Columbia. Canadian Science Advisory Secretariat Research Document 073.
- Brown, T.G., Runciman, B., Bradford, M.J., and Pollard, S. 2009. A Biological Synopsis of Yellow Perch (*Perca flavescens*). Canadian Manuscript Report of Fisheries and Aquatic Sciences, 2883: 1-19.
- Cobb, S.E. and Watzin, M.C. 1998. Trophic interactions between yellow perch (*Perca flavescens*) and their benthic prey in a littoral zone community. Canadian Journal of Fisheries and Aquatic Sciences, 55: 28–36.
- Department of Fisheries and Oceans (DFO), 2011. Science advice from a risk assessment of yellow perch (*Perca flavescens*) in British Columbia. DFO Canadian Science Advisory Secretariat Report, 2012/081.
- Diehl, S. and Eklöv, P. 1995. Effects of piscivore-mediated habitat use on resources, diet, and growth of perch. Ecology, 76: 1712-1726.
- Eckmann, R., Gerster, S., and Kraemer, A. 2006. Yields of European perch from upper Lake Constance from 1910 to present. Fisheries Management and Ecology, 13: 381–390.
- Gozlan, R.E., Britton, J.R., Cowx, I. and Copp, G.H. 2010. Current knowledge on non-native freshwater fish introductions. Journal of Fish Biology, 76: 751-786.
- Hokanson, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. Canadian Journal of Fisheries and Aquatic Sciences. 34: 1524–1550.
- Janssen, J. 1997. Comparison of response distance to prey via the lateral line in the ruffe and yellow perch. Journal of Fish Biology, 51: 921–930.

- Krieger, D.A., Terrell, J.W. and Nelson, P.C. 1983. Habitat suitability information: yellow perch. US Fish and Wildlife Service, p.1-47.
- MacPhail, J.D. 2007. The freshwater fishes of British Columbia. The University of Alberta Press. 620 p.
- Pauley, G.B., Risher, R., and Thomas, G.L. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest): sockeye salmon. US Fish and Wildlife Service Biological Report, 82: 22 p.
- Persson, L. 1986. Effects of reduced interspecific competition on resource utilization in perch (*Perca fluviatilis*). Ecology, 67: 355-364.
- Persson, L. and Eklöv, P. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. Ecology, 76: 70–81.
- Persson, A. and Hansson, L.A. 1999. Diet shift in fish following competitive release. Canadian Journal of Fisheries and Aquatic Sciences, 56:70–78.
- Peterson R. H. and Martin-Robichaud D.J. 1982. Food Habits of Fishes in 10 New Brunswick Lakes. Canadian Technical Report of Fisheries and Aquatic Sciences, 1094 p.
- Schleuter, D. and Eckmann, R. 2008. Generalist versus specialist: the performances of perch and ruffe in a lake of low productivity. Ecology of Freshwater Fish, 17: 86–99.
- Whiteside, M.C., Swindoll, C.M. and Doolittle, W.L. 1985. Factors affecting the early life history of yellow perch, *Perca flavescens*. Environmental Biology of Fishes, 12: 47–56.
- Wright, T.F. et al., 2010. Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. Ethology Ecology and Evolution, 22: 393–404.

Permissions

The fish collection work was conducted under permit number PE12-77026 granted by the British Columbia Ministry of Forests Lands and Natural Resource Operations. This research was approved by the Thompson Rivers University Animal Care Committee, protocol no. 2011-08.

Appendices

Appendix A – Combining invertebrate sampling methods for a better determination of overall food availability in lakes when calculating prey selection by fishes

Abstract

Studies on feeding ecology, specifically the relationship between prey species and predator, can lead to an understanding of a species' niche or role in the ecosystem. The relationship between a predator and its prey can be described quantitatively by calculating a selectivity index such as Manly's alpha, by comparing proportions of prey available and prey consumed. Available prey is defined by the investigator and can be somewhat arbitrary, particularly if only one food type (e.g., benthos versus zooplankton) is examined or measured. Determining prey availability for fish in lakes can be challenging due to the variety of gear types used to sample invertebrates in different habitats. As part of a larger study in British Columbia on the food habits of introduced yellow perch (*Perca flavescens*), a generalist feeder, a new method was developed to quantify invertebrate food availability in lakes for prey selectivity calculations. Invertebrate samples using three gear types were combined to quantify invertebrates available in a lake in multiple invertebrate habitats, to provide a more complete and comparable estimate of prey selectivity. Selectivity values calculated using the combined measure were compared with selectivity values calculated independently for each sampling gear, showing variable results with respect to the number and type of food items selected for in addition to the level of selection. Selection for food categories missing from the availability sample was biased upwards due to the proportional nature of compositional data. This method is recommended for generalist fish species that consume food resources in a variety of lake habitats, which cannot be sampled using one gear type. By including multiple sample methods, a more complete measure of food availability was possible for yellow perch, leading to more realistic estimates of food selection for a generalist fish species.

Introduction

Feeding ecology is often used in part to determine a species' niche or role in the ecosystem. The relationship between prey species and predator is key to understanding such roles, based on two central concepts in feeding ecology (Järv et al. 2011); Lindeman's Trophodynamic Views (Lindeman 1942) and Optimal Foraging Theory (MacArthur and Pianka 1966). This relationship can be described by analyzing both prey availability and prey consumed, and then determining prey selectivity or the likelihood that the resource will be selected if offered on an equal basis with others (Manly et al. 2002). Calculating preference or selection can be complementary to fish feeding ecology studies, which typically look at gut contents for diet analyses. This can provide additional information not always evident by looking only at proportions of food categories consumed. For example, at one location a highly favoured (selected) resource may be hard to find and relatively unimportant in the fishes' diet at that location or specific time, whereas, at another location that same resource may still be highly favoured, and readily available, so forms a relatively important component of the diet (Manly et al. 2002).

Selectivity can be calculated using an index like Manly's alpha, which takes into account varying resources availabilities (Manly 1974, Chesson 1983), to determine if the predator feeds randomly and prey is consumed in proportion to its abundance in the environment, or if prey are selected or avoided. One of the key assumptions when determining prey selectivity is that food availability is accurately determined (Manly et al. 2002). Quantifying prey consumed is easily done through gut content analysis; however, determining prey availability can be challenging. Likely, this is why many fish feeding ecology studies focus only on prey consumed to determine common prey items, but not prey selectivity. Although important on a local scale, common prey items in the stomach are not as meaningful or comparable to other locations or seasons as prey selectivity, because prey availability may vary by site or season.

Availability is typically measured as a proportion or percentage of each taxa within the predator's habitat; however, difficulties can arise when quantifying prey availability, which may vary depending on the species and habitat of interest. When determining what food is available to a predator, the investigator uses knowledge of species biology to determine what, where, when, and how to sample. These sampling procedures may not truly reflect what is available to the predator in natural conditions, but rather, what is deemed available to the predator by the investigator (Johnson 1980, Chipps and Garvey 2007).

Quantifying food availability in a lake is particularly difficult, where food resources are wide ranging, occupy different habitat types within the lake, and often require variable sampling gears. Generally, only one invertebrate habitat would be selected and sampled as most representative of food availability. This is acceptable for feeding specialists that may only eat one type of food resource and so, are easily sampled with one sampling gear; however, this prevents a complete estimate of food availability for feeding generalists. In some circumstances, where the fish is known to have a more specified diet (i.e., only fish, or zooplankton), one gear type may provide an accurate estimate of overall food availability (Sampson et al. 2009), but this is not the case with generalist fish that consumes multiple types of invertebrate food resources.

To overcome this challenge, many studies on diet selection or preference are limited to only one food type, life stage, or sampling method, or are conducted in a laboratory setting where measurement of food availability is more straightforward (Rehage et al. 2005, Fulford et al. 2006, Oscoz et al. 2009, Järv et al. 2011, Kalogirou et al. 2012). Multiple gear types have been used in other instances to quantify food availability, but selection indices for prey species were calculated separately for each sampling gear type (Olson et al. 2003). This prevents meaningful comparison between predators, as food preference is determined for each food group independently of total food availability and may mislead results on overall food preference (Pledger et al. 2007).

Typically, sampling methodologies that provide benthic invertebrate counts per square meter and volumetric estimates of zooplankton are not combined when quantifying

invertebrates in a lake. Rather, an overall measure of availability would provide a more meaningful result (Pledger et al. 2007). Here I propose combining invertebrate counts from different sampling methods and habitats to provide an overall estimate of food availability for a more complete estimate of prey selectivity. This methodology was developed as part of a seasonal feeding study involving introduced yellow perch (*Perca flavescens*) in seven lakes in British Columbia's southern interior. The larger study was initiated to determine if a change in feeding niche might be expected in this novel yellow perch habitat. Determining prey selectivity will allow a comparison of food selectivity among lakes, despite different prey availabilities. Here, selectivity indices were calculated using combined counts from three sampling gear types in one of those lakes, and then compared with selectivity indices calculated separately for each gear type.

Methodology

Data for this methodology report, involving the determination of food availability was collected during the summer (July 26, 2011) in Pinaus Lake, located in the Okanagan region of southern interior British Columbia. The fish community in the lake is composed only of rainbow trout, regularly stocked for sport fishing, and an established population of introduced yellow perch.

To determine what yellow perch were eating, fish were collected using a standard 30 m multi-panelled gill net with mesh sizes ranging from 1.27 cm to 6.35 cm to capture a wide range of fish sizes. Gill net sampling was completed during mid-morning, allowing time for yellow perch to feed before capture. A total of 32 fish were captured and the stomachs analyzed to determine food utilized. Sample fish ranged in size from 101 mm – 274 mm fork length with an average length of 193.25 mm. Food items were identified to Order and enumerated exclusively from the stomach because digestion times of food items can vary in the intestines and bias results towards hard bodied invertebrates. The condition of stomach contents varied from well preserved to moderately digested, therefore, organisms were only counted if a head or whole unit was identified to prevent duplicate counts.

Food availability was determined for yellow perch, a feeding generalist, by measuring zooplankton, littoral benthic macroinvertebrates and profundal benthic macroinvertebrates. These three invertebrate categories covered the spectrum of prey items found in the stomachs of yellow perch in the lake, determined by stomach content analysis. No piscivory occurred in this lake and therefore, juvenile fish were not included in the determination of food availability. To quantify these three invertebrate categories, which are found in different lake habitats, three gear types were used. Three replicates of each sample type were taken near the same location and time that fish were collected for diet analysis to provide as close to simultaneous estimates of prey available and prey consumed as possible.

A Wisconsin plankton net (250 μm mesh) was used to sample zooplankton. The number of individuals in each vertical haul were estimated by calculating organisms per volume of water sampled by determining the area of the opening at the top of the net (0.013 m^2) and multiplying by the depth sampled (m). Littoral macroinvertebrates were sampled using D-Frame sweep net (100 μm) samples in a 1 m^2 quadrat. Organisms per volume of water were calculated by multiplying the net height (0.25 m) by the quadrat frame size. Profundal macroinvertebrates were sampled using an Ekman grab sampler, sieved through 150 mm mesh. The volume of the Ekman grab was calculated based on the size of the grab sampler (0.0035 m^3). Full samples (soft lake substrate) were calculated using this entire volume, whereas half full samples (hard lake substrate) were calculated using half the volume. Invertebrates in each sample were identified to Order and enumerated using a dissecting microscope.

For each sample, counts were converted to organisms per 1 m^3 . For example, the number of amphipods in the D-frame net sample was determined by multiplying counts in each replicate by the volumetric multiplier of 4 to provide a count per 1 m^3 . The multiplier $1/(1\text{m}^2 \times 0.25 \text{ m}) = 4$, was determined using a quadrat size of 1 m^2 and a net height of 0.25 m. In D-frame replicate 1, a total of 1611 amphipods were counted, then multiplied by 4 giving a total of 6444 amphipods per 1 m^3 . Proportion of total food items was then calculated for each replicate. Then, the mean proportion of the three replicates was determined. The results were then converted into proportions of food availability per

sample, and the mean proportion of three replicates was taken for each gear type (Table A-1).

Table A-1. Mean proportions of food availability by sampling method. Blanks indicate that the taxa were not found using the particular sampling method. *Zero counts were replaced by small value 0.0001 to enable selection calculation.

Food category	Combined sampling methods	Ekman grab	D-frame net	Wisconsin plankton net
Amphipoda	0.052	*	0.157	*
Copepods	0.312	*	*	0.936
Cladocerans	0.021	*	*	0.064
Dipteran larvae	0.532	0.945	0.650	*
Ephemeroptera	0.014	*	0.043	*
Gastropoda	0.046	*	0.137	*
Hirudinea	*	*	*	*
Hydrachnidia	0.003	*	0.008	*
Pelecypoda	*	*	*	*
Mysidacea	0.019	0.055	0.001	*
Trichoptera	*	*	0.001	*
Other insects	0.001	*	0.004	*
Total	1	1	1	1

For comparison purposes, Manly's selection indices were calculated using mean proportions from the combined sampling methods, and then with mean proportions of food availability from each separate gear type. Availability values of zero were replaced with a small value 0.0001 for taxa found in perch diets, but not in availability samples. This was done because although the taxa were not detected in the lake availability sampling, they were found in the fishes' diet, indicating that they were present at some level.

Based on the methods of Calenge (2006) and Manly et al. (2002), prey selection was tested for each fish sampled. Selection indices were then pooled and a global test of random resource use was completed (Log-likelihood statistic) to determine if overall significant selection occurred, or if fish ate food in proportion to availability. If food resources were consumed in the same proportions as available, the selection index would be equal to 1. A higher or lower selection index indicated positive or negative selection. For example, a selection index of 2 indicated a food resource was being used twice as much as would be

expected if it were being used randomly. Significance referred to a comparison of selection indices at an alpha level = 0.05. The computation of selection indices was completed in R Statistical Software (R Core Team 2012), using the package AdeHabitat HS (Calenge 2006).

Results

A total of 12 food categories were identified based on prey consumed. Insects with rare occurrence (<1% total proportion of diet) were lumped together into the 'other insects' category. Selection indices calculated from total food availability, using the three combined invertebrate sampling methods, indicated that perch positively selected for five food categories including cladocerans, dipteran larvae, Ephemeroptera, Trichoptera and other insects, but no significant overall selection ($p=0.365$) for food resources (Table A-2, Figure A-1). Of the food groups positively selected for, large standard error bars indicate a wide variation in individual fishes' selection for that resource, where some fish consumed the resource in large quantities, and others in small quantities.

Positive selection for copepods and cladocerans was indicated when using the D-frame net samples as the measure of food availability, with no overall significance shown ($p=0.140$) (Figure A-2). Selection calculated using the Ekman grab as the measure of food availability indicated positive selection for amphipods, copepods, cladocerans and other insects, but no overall significant selection ($p=0.138$) (Figure A-3). Wisconsin plankton net samples as the measure of food availability showed positive selection for amphipods, dipteran larvae and Ephemeroptera and significant overall selection was shown based on resource availabilities ($p < 0.000$) (Figure A-4). When the results from each individual method were pooled, results indicated positive selection for six food categories (Table A-2). This included amphipods and copepods, not positively selected for with the combined methods.

Overlapping positive selection occurred for four food categories including cladocerans, dipteran larvae, Ephemeroptera and other insects, between the combined and pooled method

results. Only the combined sampling method showed positive selection for Trichoptera, whereas the separate sample methods, when pooled, showed positive selection for amphipods and copepods.

Table A-2. Positive selection results for Manly’s selectivity indices. Check marks indicate a positive selection index for a food resource. Shaded cells indicate overlapping positive selection between combined and pooled methods.

Availability measurement	Amphipoda	Copepods	Cladocerans	Dipteran larvae	Ephemeroptera	Gastropoda	Hirudinea	Hydrachnidia	Pelecypoda	Mysidacea	Trichoptera	Other insects	Overall Significant Selection
Combined samples (3 methods)											√		No
Separate sample methods													
D-frame net		√	√										No
Ekman grab	√	√	√		√							√	No
Plankton net	√			√	√								Yes
Pooled result	√	√											NA

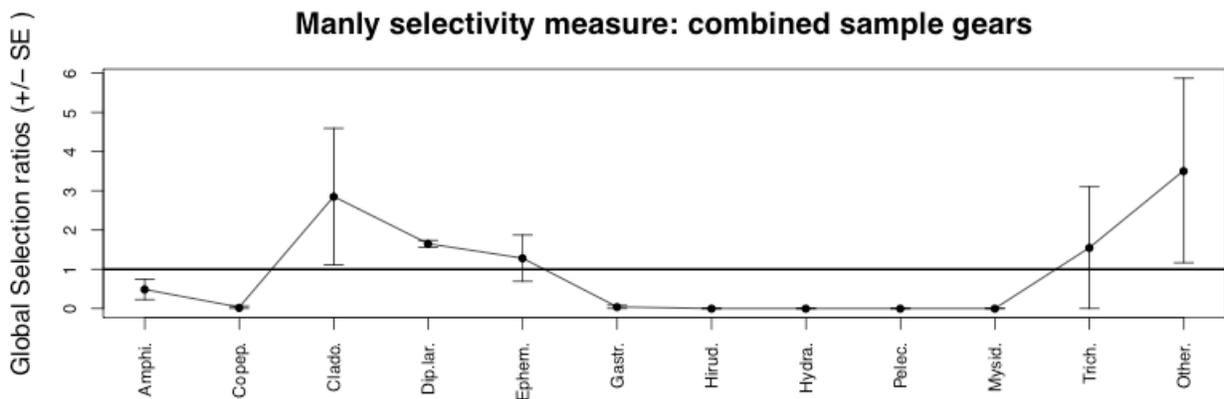


Figure A- 1. Selection indices for the three combined measures of food availability ±S.E. Values equal to 1, indicated by the line, are neutral selection; the food resource is being used randomly. A higher or lower selection index indicates positive or negative selection. There was no significant overall selection for resources.

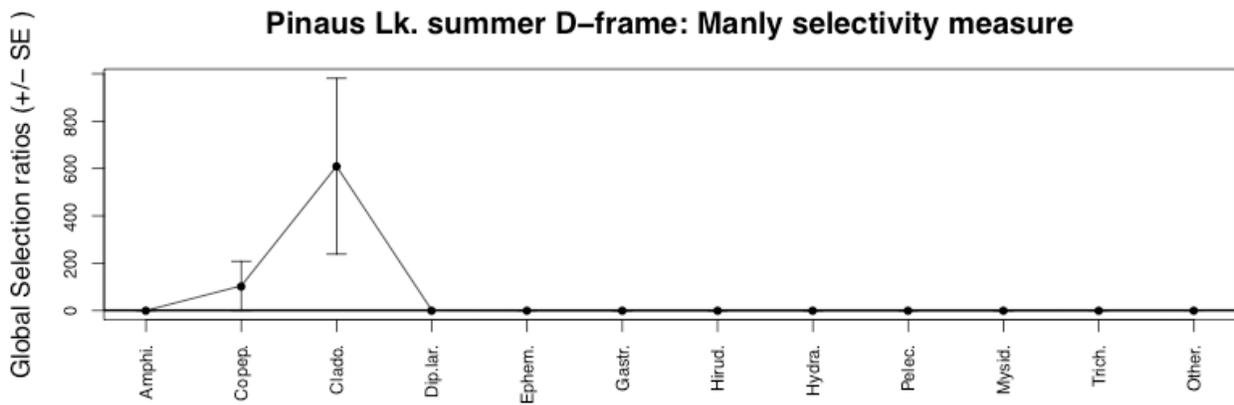


Figure A- 2. Selection indices for food availability using D-frame net measurement \pm S.E. Values equal to 1, indicated by the line, are neutral selection; the food resource is being used randomly. A higher or lower selection index indicates positive or negative selection. There was no significant overall selection for resources.

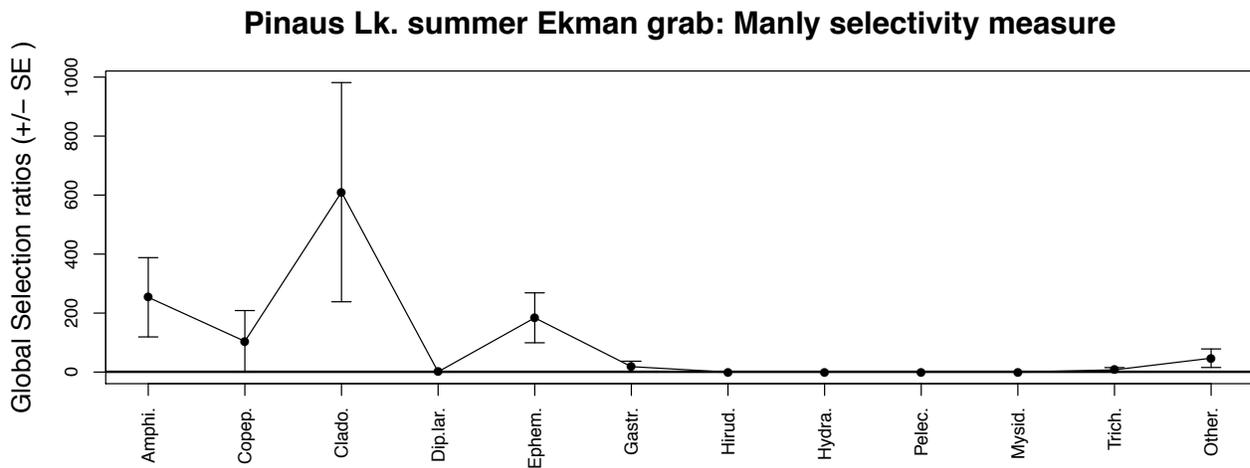


Figure A- 3. Selection indices for food availability using Ekman grab measurement \pm S.E. Values equal to 1, indicated by the line, are neutral selection; the food resource is being used randomly. A higher or lower selection index indicates positive or negative selection. There was no significant overall selection for resources.

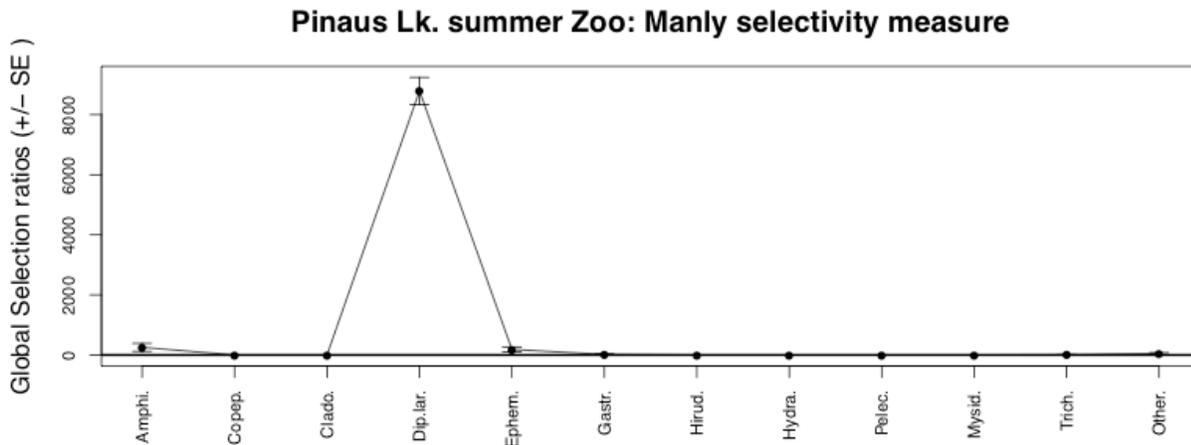


Figure A- 4. Selection indices for food availability using plankton net measurement \pm S.E. Values equal to 1, indicated by the line, are neutral selection; the food resource is being used randomly. A higher or lower selection index indicates positive or negative selection. Overall, significant selection for resources was indicated.

Discussion

The Ekman grab, D-frame net, and Wisconsin plankton net were chosen for this study because they each sample distinctly different invertebrate habitats that could provide food resources for yellow perch. Combining these gear types provided a better representation of all possible food resources for a generalist feeder, like yellow perch. The selectivity indices calculated using the combined gear types provided a more tempered result, and no overall significant selection for food resources; however by excluding any of the sampling methods, the selectivity results were biased towards invertebrates that were not sampled or were poorly represented in the sample of availability. The separate gear type calculations, with pooled results, showed positive selection for a larger number of food categories as well as significant selection for dipteran larvae in the calculation using data from the plankton net sample. These results are problematic, because they exaggerate the level of selection due to the limited number of taxa included in each separate availability measurement. Indices calculated using the Wisconsin plankton net samples resulted in the least number of taxa in the availability estimate, and consequently showed extremely high selection indices for dipteran larvae (Figure A-4), which were shown as not available based on the sampling method (Table A-1), resulting in an overall significant selection result.

Selectivity estimates are based on compositional data that sum to one; therefore, when selectivity for one resource increases, the others inherently decrease. This is a challenge if consumed resources have been left out of the sample of availability. By calculating selectivity indices for each sample gear separately, it biases results by showing strong positive selection for invertebrate resources that did not show up in that particular sampling method. Therefore, limitations of the sampling methods must be considered when making statements about selection or preference.

Studies on food habits of fishes commonly include calculations of prey selectivity using Manly's alpha or another comparable index; however, many of these studies limit sampling of food availability to one gear type, or two gear types with selectivity calculated separately for each (Oscoz et al. 2005, Teixeira and Cortes 2006, Polacik and Reichard 2010). These studies were conducted in rivers where available habitats types are more limited and can be sampled representatively using only one or two sampling gears. Alternatively, selection is only calculated for a limited number of food resources consumed; calculating selectivity based on a "sub-grouping" of stomach contents or only one taxa of interest, such as zooplankton or prey fish in studies by Kalogirou et al. (2012) and Sampson et al. (2009) who determined selectivity for a piscivorous fish and planktivorous fish respectively, and therefore, sampled only for that specific food resource. I am not aware of any directly comparable studies on a generalist lacustrine fish species or studies using the method described in this report, although it is often difficult to compare studies in the literature due to a lack of detailed methods.

The premise around the methods presented here could be applied to any diet study looking at selectivity of a generalist fish species, which feeds on numerous invertebrate groups occupying different habitats that are not possible to sample with one gear type. If the fish species were to feed on juvenile fish or vegetation in addition to invertebrates, another layer of complexity would be added to the determination of availability, and other methods of sampling would need to be employed. Typically, adult perch eat juvenile fishes; however, in this particular lake, fish do not make up a component of the diet, likely because

juvenile yellow perch are the only small fish present, and the trout are stocked at a larger size. Thus, it is crucial to know what the study fish are eating before determining which sampling methods will sufficiently describe available food resources. For example, if one is specifically studying the early juvenile life stage of a fish, when it only consumes zooplankton, it is not necessary to sample all invertebrates that would be considered available food resources for the adult of that species.

It is also clear that caution must be taken when interpreting results based on the possible bias towards positive selection results for food resources that are weakly represented in the samples of availability. Even with the combined sampling methods, no trichopterans were detected in the availability samples, although they were found in perch stomachs. This could be due to a truly low occurrence of trichopterans in the lake habitat, or possibly that the sampling methods were not adequate to detect trichopterans present. Therefore, when interpreting the positive selection result for Trichoptera, the investigator must be aware that the positive result could be exaggerated due to inadequate sampling of availability.

To alleviate this problem, one unified sampling method would be preferable for quantifying all invertebrates in all lake habitats, as recommended in Pledger et al. (2007); however, this may not be possible, depending on the types of food resources the study fish may consume. Converting counts from multiple gear types into comparable measures is a simple way to estimate a more inclusive measure of food availability by incorporating more habitat types and taxa in the food availability estimate. Investigators already struggle to deal with the subjectivity of assigning what is available to a fish species naturally; therefore, it would be best to include as many potential food options as possible in the assessment, when studying generalist feeders, providing a more realistic estimate of feeding preference. There is inherently some level of error introduced into the calculation by pooling sampling methods; however, it may provide a better understanding of overall food preference, which would not otherwise be available, not just preference within one food category. This is particularly important for a generalist species such as yellow perch, which consume such a wide variety of invertebrate organisms utilizing multiple lake habitats.

References

- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197: 516-519.
- Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. *Ecology*, 64: 1297-1304.
- Chipps, R.S., and Garvey, J.E. 2007. Assessment of diets and feeding patterns. pp.473-514 in Guy, C.S., and Brown, M.L. editors. *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda, Maryland.
- Fulford, R.S., Rice, J.A., Miller, T.J., Binkowski, F.P., Dettmers, J.M. and Belonger, B. 2006. Foraging selectivity by larval yellow perch (*Perca flavescens*): implications for understanding recruitment in small and large lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 28–42.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61: 65-71.
- Järv, L., Kotta, J., Kotta, I., Raid, T. 2011. Linking the structure of benthic invertebrate communities and the diet of native and invasive fish species in a brackish water ecosystem. *Annales Zoologici Fennici*, 48: 129–141.
- Kalogirou, S., Mittermayer, F., Pihl, L., Wennhage, H. 2012. Feeding ecology of indigenous and non-indigenous fish species within the family Sphyraenidae. *Journal of Fish Biology*, 80: 2528–2548.
- Lindeman, R.L. 1942. The trophic-dynamic aspect of ecology. *Ecology*, 23: 399–417.
- MacArthur, R.H. and Pianka, E.R. 1966. On optimal use of a patchy environment. *The American Naturalist*, 100: 603–609.
- Manly, B.F.J. 1974. A model for certain types of selection experiments. *Biometrics*, 30: 281–294.
- Manly, B.F.J., McDonald, L.L. Thomas, D.L., McDonald, T.L., Erickson, W.P. 2002. *Resource selection by animals: statistical design and analysis for field studies*, Second Edition: 1-221.
- Olson, N.W, Paukert, C.P., and Willis, D.W. 2003. Prey selection and diets of bluegill *Lepomis macrochirus* with differing population characteristics in two Nebraska natural lakes. *Fisheries Management and Ecology*, 10: 31–40.
- Oscoz, J., Leunda, P.M., Campos, F., Escala, M.C., Garcia-Fresca, C., and Miranda, R. 2005. Spring diet composition of Rainbow Trout, *Oncorhynchus mykiss* (Walbaum,

- 1792) in the Urederra River (Spain). *Annales de Limnologie - International Journal of Limnology*, 41: 27–34.
- Pledger, S., Geange, S., Hoare, J. and Alejandro, P. 2007. Resource Selection: Tests and estimation using null models. Victoria University of Wellington, 1-22.
- Polacik, M. and Reichard, M. 2010. Diet overlap among three sympatric African annual killifish species *Nothobranchius* spp. from Mozambique. *Journal of Fish Biology*, 77: 754–768.
- R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: <http://www.R-project.org/>
- Rehage, J.S., Barnett, B.K. and Sih, A. 2005. Foraging behaviour and invasiveness: do invasive *Gambusia* exhibit higher feeding rates and broader diets than their noninvasive relatives? *Ecology of Freshwater Fish*, 14: 352–360.
- Sampson, S.J., Chick, J.H. and Pegg, M. A. 2009. Diet overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi rivers. *Biological Invasions*, 11: 483–496.
- Teixeira, A. and Cortes, Rui. M.V. 2006. Diet of stocked and wild trout, *Salmo trutta*: Is there competition for resources? *Folia Zoologica*, 55: 61–73.

Appendix B – Diet Composition Charts

This appendix provides data showing diet composition for yellow perch and rainbow trout in individual study lakes (Figures B-1 through B-9), which supplements data in Chapter 2. Each point represents the proportion of a particular prey category for one fish. Proportions are also distinguished by season. Prey categories consumed in the greatest proportions overall are shown toward the top of the y-axis. Diet composition was divided up into the following 15 prey categories including: AM (amphipoda), CL (cladocerans), CO (copepods), DL (dipteran larvae), DP (dipteran pupae), EP (ephemeropterans), FI (fish), HI (hirudineans), HY (hydrachnidians), MO (molluscs), MY (mysids), OD (odonates), TR (trichopterans), OA (other aquatics), and OT (other terrestrials). Invertebrates with rare occurrence (<1% total proportion of diet) were lumped together into ‘other aquatic’ or ‘other terrestrial’ categories.

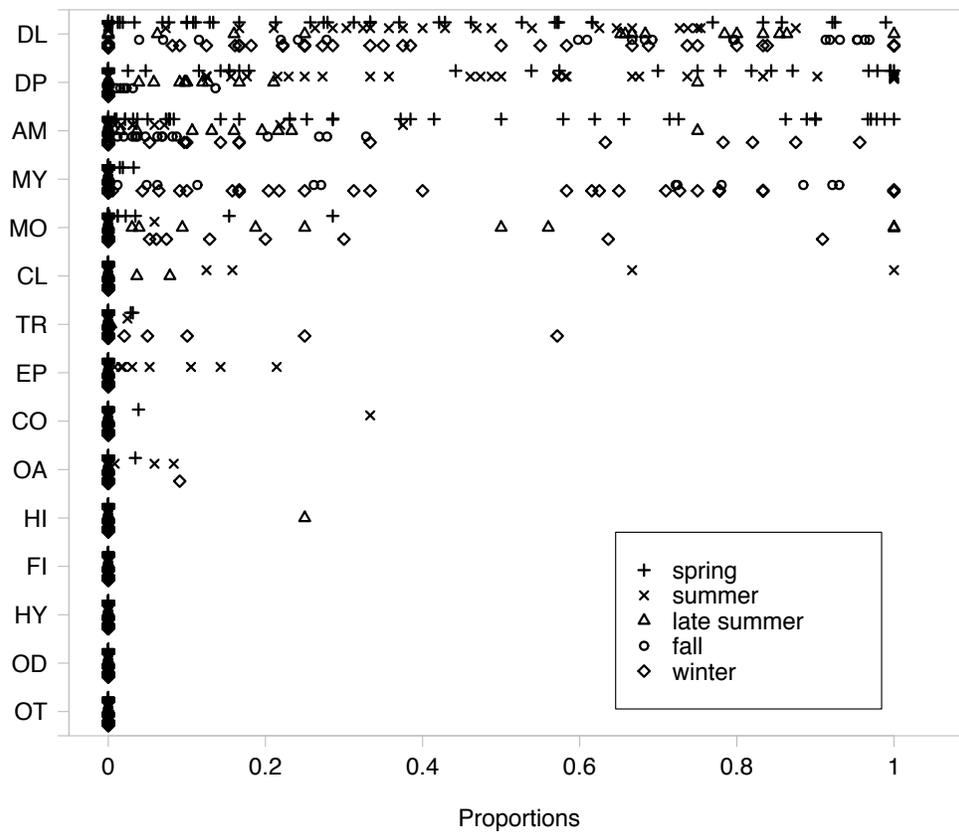


Figure B- 1. Pinaus Lake yellow perch diet composition. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials).

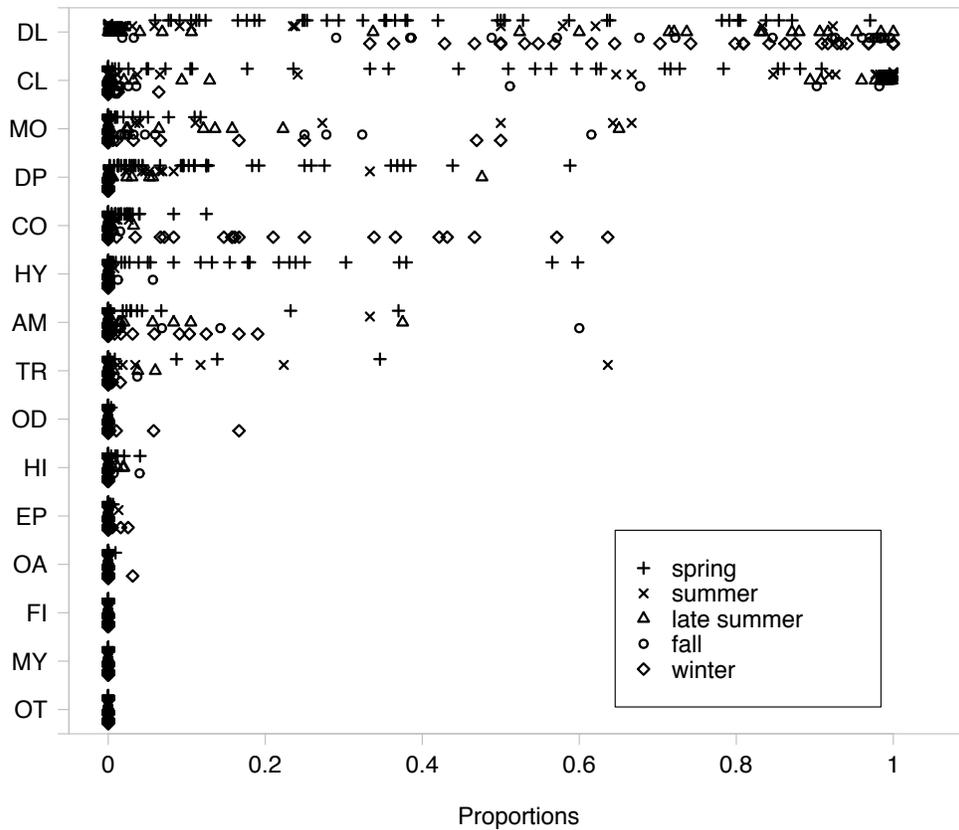


Figure B- 2. Bear Lake yellow perch diet composition. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials).

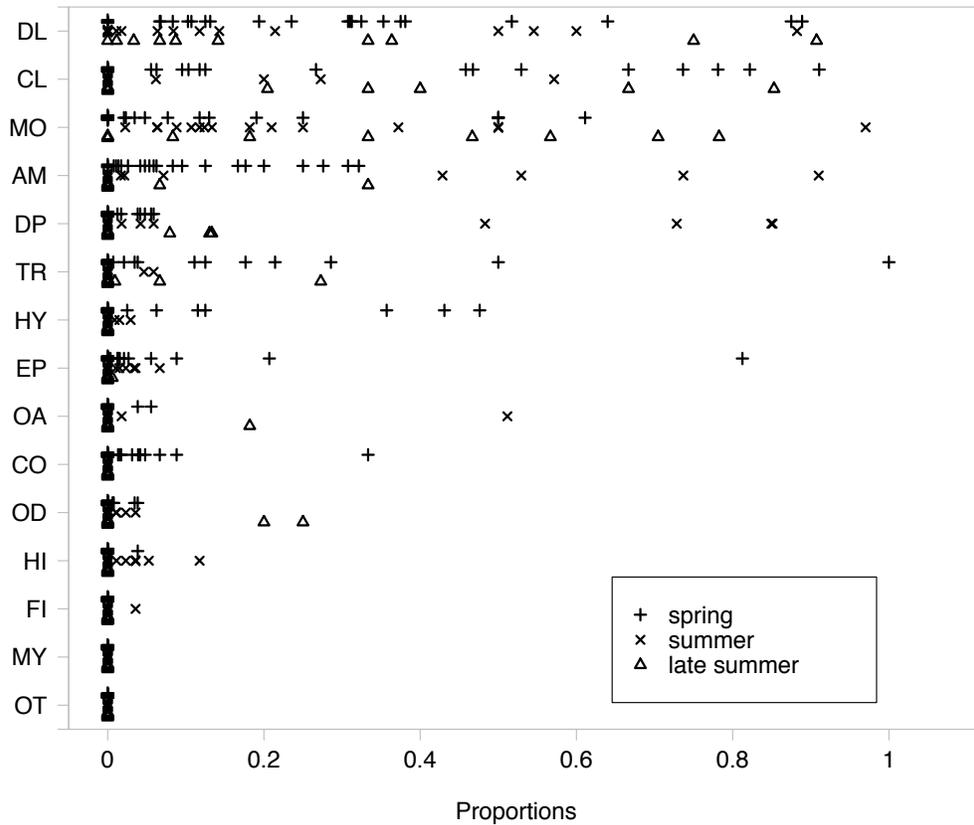


Figure B- 3. Little Pinaus Lake yellow perch diet composition. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials).

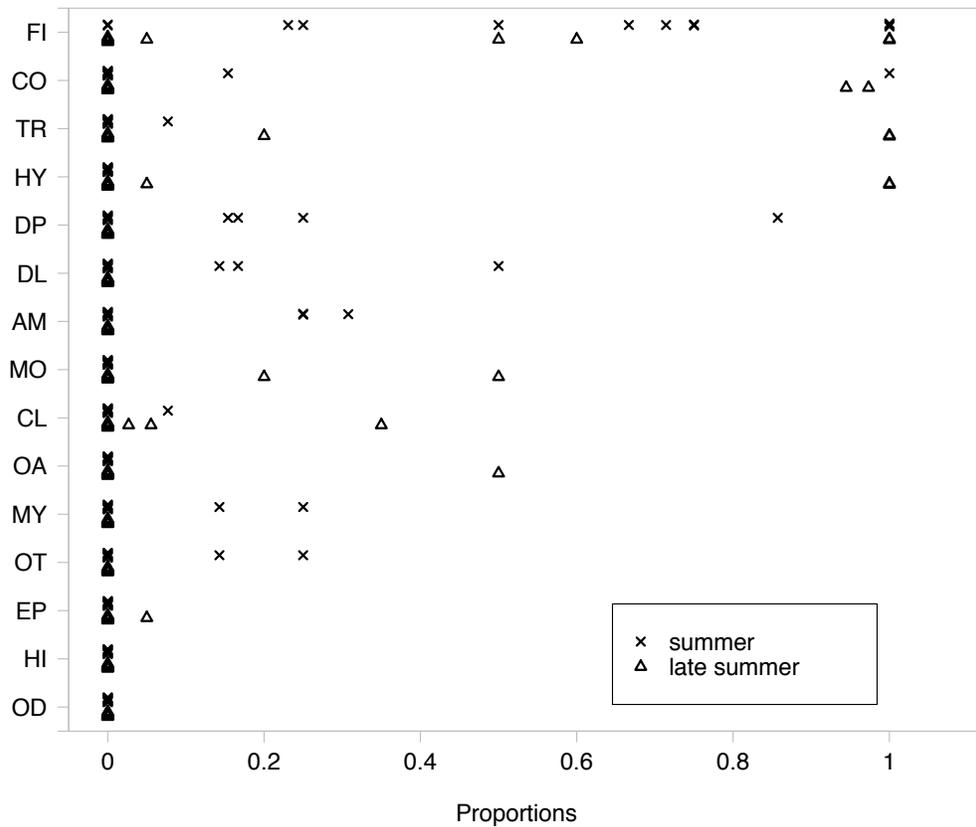


Figure B- 5. Kalamalka Lake yellow perch diet composition. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials).

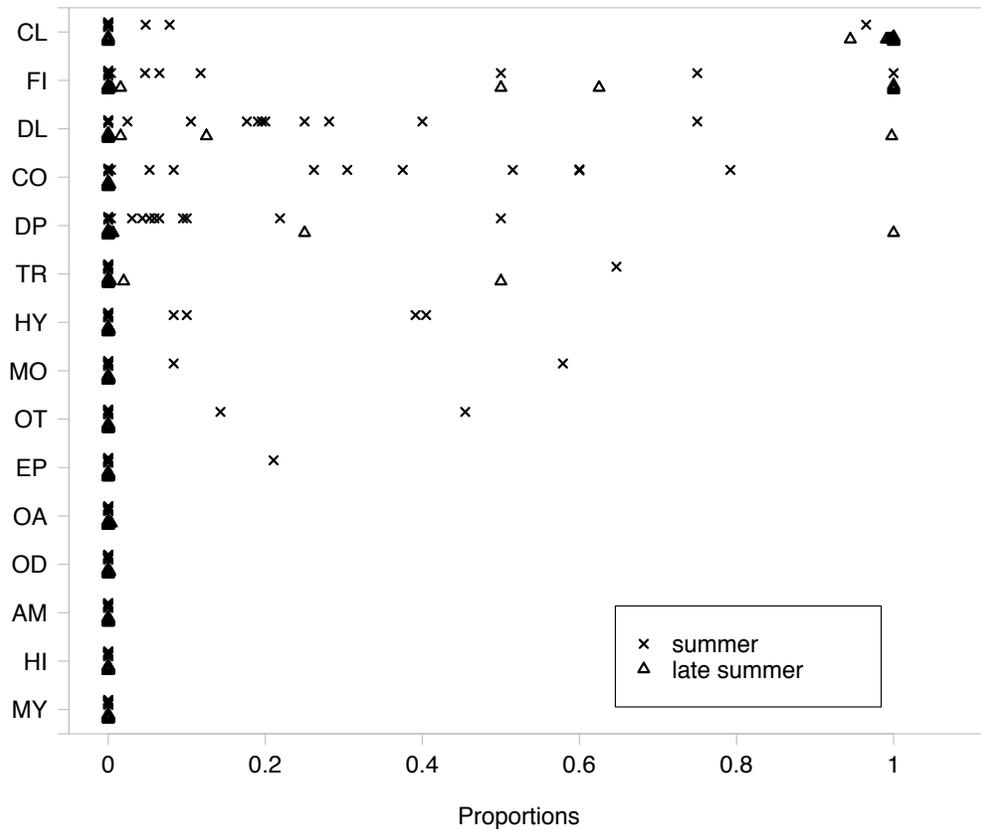


Figure B- 6. Wood Lake yellow perch diet composition. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials).

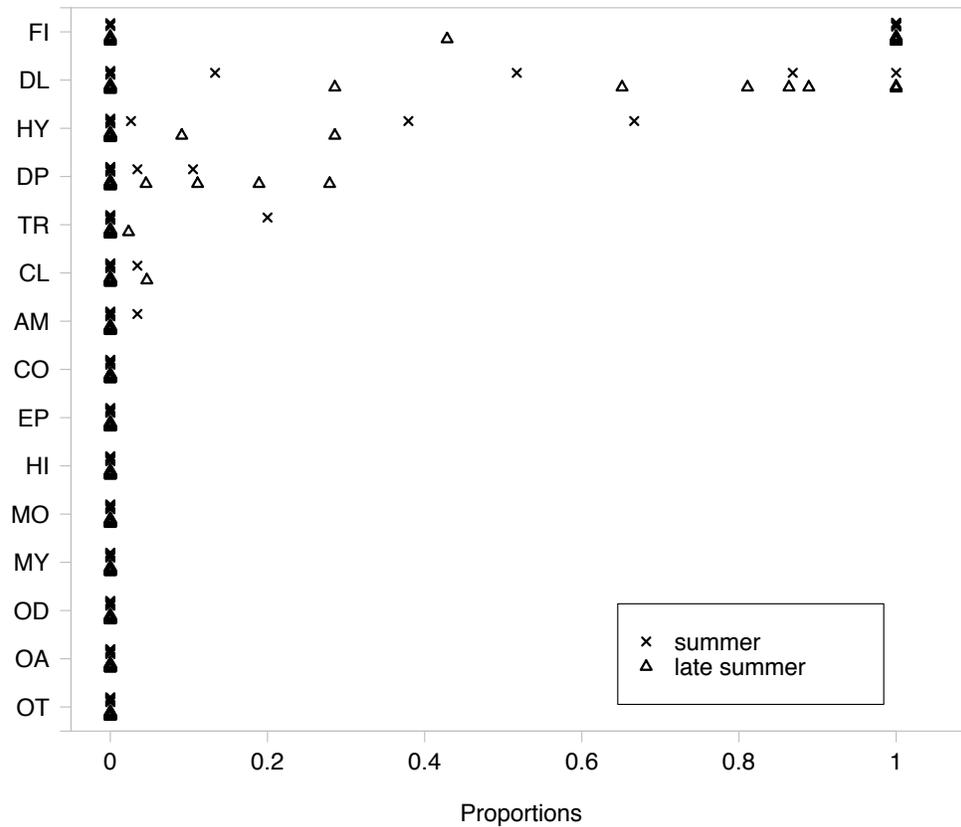


Figure B- 7. Ellison Lake yellow perch diet composition. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials).

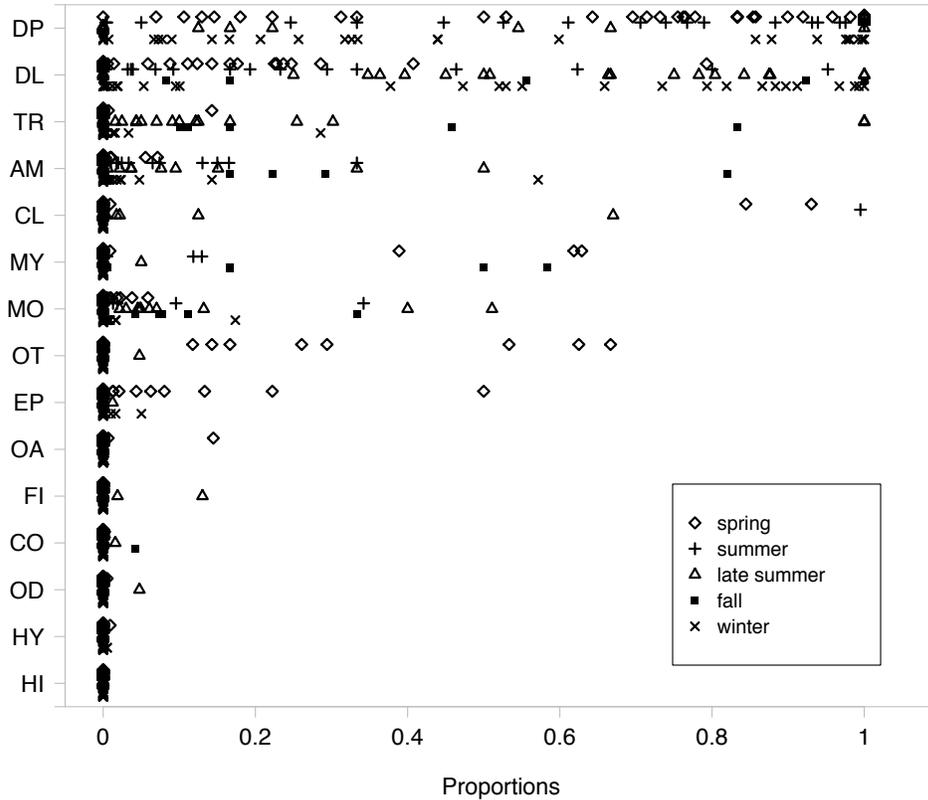


Figure B- 8. Pinaus Lake, rainbow trout diet composition. Each point represents the proportion of a given prey category for one fish. Prey categories with highest total proportions (among fish) are towards the top of the y-axis. Prey categories were abbreviated as: AM(amphipods), CL(cladocerans), CO(copepods), DL(dipteran larvae), DP(dipteran pupae), EP(ephemeropterans), FI(fish), HI(hirudineans), HY(hydrachnidians), MO(molluscs), MY(mysids), OD(odonates), TR(trichopterans), OA(other aquatics), and OT(other terrestrials).

Appendix C - Calibration of Telemetry Signal Location

Three calibration exercises were completed in Pinaus and Bear Lakes to record a baseline for the signal at depth, distance and in a weed bed and to ensure that signals were not likely to be missed based on depth, distance or interference from vegetation. For depth calibration, a transmitter was lowered into the water at 1 m intervals directly below the antenna on the boat, the power reading, at a gain of 20, was recorded until a depth was reached where the gain had to be increased to receive a signal. This calibration provided the maximum depth at which a fish could be detected at the highest possible gain and power. The distance calibration provided a range of detection in 1 m of water and was completed by lowering a transmitter into 1 m of water and moving away in the boat until the signal could not be detected. A third calibration was completed in a weed bed, where perch are often found, by lowering a transmitter down into the water directly below the boat antenna at 1 m intervals and comparing results to the calibration in open water, thereby determining if the weeds affect the signal.

Calibration Results

Pinaus Lake

A signal was received at a depth of 10 m with a gain of 20 and power reading of over 100. This allowed us to know that we had full capability of locating fish in depths of over 10 m of water. A maximum horizontal distance of 120 m at 1 m depth was attained while still receiving a signal. Signal strength was tested in both dense and sparse weeds. Signal strength remained high in aquatic vegetation.

Bear Lake

A signal was received at the maximum lake depth of 9 m with a gain of 20 and power of 70. Therefore, it would have been possible to locate fish in the deepest area of the lake. A maximum horizontal distance of 116 m at 1 m depth was attained while still receiving a signal. Similarly to Pinaus Lake, signal strength remained strong in aquatic vegetation.

Appendix D - Spawning Timing and use of Artificial Spawning Substrates for Introduced Yellow perch in Pinaus Lake and Little Pinaus Lake

Introduction

Recent introductions of yellow perch into British Columbia lakes with direct connectivity to larger nursery lakes where sockeye salmon and other important native species are present have caused concern. To remove the potential for yellow perch to move downstream into these larger lakes, a number of smaller lakes were treated using the piscicide rotenone (Christensen and Trites 2011). In lakes where the use of rotenone is not feasible, alternate control methods are needed. A study of European perch (*Perca fluviatilis*) showed that artificial substrates, such as bundles of brushwood, can be used to promote spawning and collect eggs (Pedicillo et al. 2008). There are also records of yellow perch spawning on sampling nets (Radabaugh et al. 2010). Therefore, it may be possible to promote yellow perch spawning on artificial substrates and then remove the egg masses from the lake to reduce spawning success; however, little information is available on the spawning timing and habits of introduced yellow perch in lakes in British Columbia's Okanagan Region.

Yellow perch typically spawn in spring when water temperatures begin to rise, typically from Mid-April until as late as July (Roberge and Slaney 2001). Variation in peak spawning time occurs across their geographical distribution (Hokanson 1977), and may occur at a later date and at lower temperatures in more northern locations (Thorpe 1977).

Environmental cues initiating the last stages of gonadal development are a combination of photoperiod and water temperature (Hokanson 1977, Dabrowski et al. 1996). Yellow perch may have optimal gamete viability at temperatures of 8 °C - 11 °C, but viable ova have been recorded at temperatures ranging from 3.7 °C - 18.6 °C, with reduced viability below 8 °C and above 11 °C (Hokanson 1977). Spawning usually begins when lake

temperatures reach that optimal temperature range; however, it is believed that yellow perch can adapt to different temperature regimes by utilizing different ranges of spawning temperatures, thereby keeping spawning timing relatively consistent at the expense of gamete viability (Hokanson 1977). Therefore, it is possible that in novel habitat, such as Pinaus Lake, yellow perch spawning timing may not be predictable simply based on an expected temperature threshold.

Yellow perch have been known to spawn at variable depths from 0.5 m - 12.3 m (Thorpe 1977, Alto and Newsome 1989), most commonly spawning at depths of 0.5 m - 3.0 m (Thorpe 1977). Many other spawning studies are on European perch (*Perca fluviatilis*), a closely related species that has been said to be biologically equivalent (Thorpe 1977). In European perch, it has been observed that depth does not appear to be dependent on substrate, but rather wave action, temperature and daylight hours (Čech et al. 2012). Spawning tends to occur at shallower depths in smaller lakes, and deeper in larger lakes, possibly to protect egg masses from wave action (Gillet and Dubois 1995). In addition, European perch may spawn at more shallow depths at the beginning of the spawning period, and slightly deeper as time goes on, possibly due to a warming trend within the lake (Gillet and Dubois 1995).

The gelatinous egg masses are deposited on dead and living vegetation and woody debris. Little is known about the preferred spawning substrate of yellow perch; however, research on preferred substrates and the use of artificial spawning substrates has been completed with European perch (*Perca fluviatilis*).

The objectives of this observational study were to gain general knowledge on spawning timing, relative location and depth at which introduced yellow perch were spawning in two study lakes. By determining when the yellow perch in the study lakes were spawning, it was possible to complete trials using artificial spawning substrates. The goal was to have the fish spawn on the artificial substrates and then remove the egg masses from the lake, thereby reducing the number of viable eggs within the lake in an attempt to reduce the

yellow perch population. Due to the observational nature of this study and no practical replication, there were no testable hypotheses.

Methods

A series of observations were completed in late winter and spring 2012 to determine spawning timing, relative location and depth of introduced yellow perch in Pinaus and Little Pinaus Lakes. Little Pinaus Lake is a small pond-like lake, located directly downstream from Pinaus Lake, which is much larger and deeper (Chapter 2, Figure 2-1). These observations were completed as part of a larger study looking at ecology of introduced yellow perch in British Columbia's Okanagan Region.

Summary of visual spawning surveys:

Pinaus Lake

Visual spawning surveys were completed to determine when the spawning season began. Egg development in yellow perch was monitored in late winter by ice fishing. If fish were caught full of eggs, it was assumed that spawning hadn't started. In early March, fish were still full of eggs and milt, indicating that spawning had not started under the ice. Ice fishing ended April 9, as ice was getting dangerous. Fish were caught easily up to that date. On April 9th, fish would not bite. On April 23, a thin ice covering remained on Pinaus Lake, but it was melting around the shoreline.

Visual monitoring began April 25 by snorkeling around the shoreline at a location where it was common to catch yellow perch in winter and summer. No sign of egg masses were visible in the shallow shoreline areas.

Boat monitoring started April 25 and was ongoing every 2-3 days to look for evidence of new egg masses and to record lake temperature profiles and shoreline temperatures at eggs.

Little Pinaus Lake

Visual spawning surveys began in Little Pinaus Lake as soon as access was possible (April 25, 2012) and were completed by boat every 2-3 days to look for evidence of egg masses and to record lake temperature and shoreline temperatures at eggs.

Artificial Substrates:

Pinaus Lake:

Artificial spawning substrates were bundles of small willow branches bound by a wire cage (Figure D-1). Bundles were weighted down and were attached to an identifying float on the surface of the lake. Four spawning substrates were put into the lake, through the ice in March, into 3 m of water.

On April 25th, they were moved into 1+ m of water, after the majority of egg masses had been observed at that depth. Each day monitored, new egg masses on the substrates were recorded, and evidence of spawning in the vicinity around the substrates was recorded.



Figure D- 1. Artificial spawning substrate constructed from a wire cage filled with willow branches, put into Pinaus Lake.

Observations

Spawning timing

Egg masses were first observed on April 25, 2012 in both Pinaus and Little Pinaus Lakes. This was two days after ice was off Pinaus Lake. Water temperatures at the egg masses were 3.8 °C in Pinaus Lake and 4 °C in Little Pinaus Lake. New egg masses were observed in both lakes on April 30th, and May 2nd. On May 4th, there were not a lot of new egg masses visible indicating that spawning was slowing down. Based on visual observations of new egg masses, peak spawning may have been around May 2, 2012.

Egg masses were generally located in localized clumps in shallow areas, along shoreline and in protected areas with reduced wave action. Most of the natural substrates used included the finer branches of fallen Douglas fir trees, fine woody debris clustered along the lake shore, and in Little Pinaus Lake, aquatic plants were the most prominent spawning substrate utilized.

Monitoring continued until May 28, 2012 when most eggs had hatched or disappeared, at which point water temperatures at the locations where egg masses had been located reached 13 °C and 10.3 °C in Pinaus and little Pinaus Lakes, respectively.

Artificial spawning substrates

Egg masses were observed on the artificial spawning substrates on 4 occasions including April 30, May 2, May 4, and May 7. A total of 8 egg masses were counted on the substrates. Substrates were located between 0.7 m and 1.3 m deep. No other signs of spawning occurred in the vicinity of the substrates, although other natural substrate materials were available. This suggests the perch preferred the artificial substrate (willow branches) to the natural substrates in that area, which were generally birch branches.

Summary

Spawning occurred in both lakes as the ice was coming off the lakes. Water temperature recorded at the first egg masses seen was 3.8 °C and 4.0 °C, in Pinaus and Little Pinaus Lakes, with both of the temperatures being lower temperature than expected. Based on the literature, spawning does occur at temperatures as low as 3.7 °C; however, there is generally reduced viability below temperatures of 8 °C (Hokanson 1977).

Artificial spawning substrates were successful in Pinaus Lake at depths of 0.7 m – 1.3 m. Yellow perch might have preferred the artificial substrate to natural materials available. The observational trial proved successful in that yellow perch egg masses were removed from the lake from the artificial substrates. With further development, this type of management strategy could be implemented as a method to reduce spawning success by removing egg

masses; however, it may be time and labour intensive, as constant monitoring would be required. This would include monitoring ice conditions and lake temperatures in early spring to avoid missing the narrow spawning window immediately after ice off.

References

- Aalto, S.K. and Newsome, G.E. 1989. Evidence of demic structure for a population of yellow perch (*Perca flavescens*). Canadian Journal of Fisheries and Aquatic Sciences. 46: 184–190.
- Čech, M., Vejřík, L., Peterka, J., Říha, M., Muška, M., Jůza, T., Drašík, V., Kratochvíl, M., and Kubečka, J. 2012. The use of artificial spawning substrates in order to understand the factors influencing the spawning site selection, depth of egg strands deposition and hatching time of perch (*Perca fluviatilis* L.). Journal of Limnology. 71: 170–179.
- Christensen, V. and Trites, A.W. 2011. Predation on Fraser River sockeye salmon. Cohen Commission. Tech. Rept. 8: 129p. Vancouver, B.C.
- Dabrowski, K., Ciereszko, R.E., Ciereszko, A., Toth, G.P., Christ, S.A., El-Saidy, D., and Ottobre, J.S. 1996. Reproductive physiology of yellow perch (*Perca flavescens*): environmental and endocrinological cues. Journal of Applied Ichthyology. 12: 139–148.
- Gillet, C. and Dubois, J.P. 1995. A survey of the spawning of perch (*Perca fluviatilis*), pike (*Esox lucius*), and roach (*Rutilus rutilus*), using artificial spawning substrates in lakes. Hydrobiologia. 300/301: 409–415.
- Hokanson, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. Canadian Journal of Fisheries and Aquatic Sciences. 34: 1524–1550.
- Pedicillo, G., Merulli, F., Carosi, A., Viali, P., and Lorenzoni, M. 2008. The use of artificial spawning substrates as media to support the reproduction of Eurasian perch in Lake Piediluco. Hydrobiologia. 609: 219–223.
- Radabaugh, N.B., Bauer, W.F., and Brown, M.L. 2010. A comparison of seasonal movement patterns of yellow perch in simple and complex lakes. North American Journal of Fisheries Management. 30: 179-190.
- Roberge, M. and Slaney, T. 2001. Life history characteristics of freshwater fishes occurring in British Columbia, with major emphasis on lake habitat characteristics. Canadian Manuscript Report of Fisheries and Aquatic Sciences. 2574: 189 p.

Thorpe, J. E. 1977. Morphology, physiology, behavior, and ecology of *Perca fluviatilis* L. and *P. flavescens* Mitchill. Journal of the Fisheries Research Board of Canada. 34: 1504–1514.