

FACTORS INFLUENCING ZOOPLANKTON POPULATIONS IN ALASKAN  
SOCKEYE SALMON (*ONCORHYNCHUS NERKA*) NURSERY LAKES: INSIGHTS  
FROM LIMNOLOGICAL AND PALEOLIMNOLOGICAL ANALYSES

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FACTORS INFLUENCING ZOOPLANKTON POPULATIONS IN ALASKAN  
SOCKEYE SALMON (*ONCORHYNCHUS NERKA*) NURSERY LAKES: INSIGHTS  
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THESIS

Presented to the Faculty  
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for the Degree of

MASTER OF SCIENCE

By  
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Fairbanks, Alaska

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**Abstract:**

The relative importance of sockeye salmon, invertebrate predators, and other environmental factors in structuring the size and abundance of zooplankton populations was examined in a series of 23 lakes from southern Alaska. Zooplankton abundance was strongly related to sockeye density, along with nutrient availability and alkalinity. The mean size of *Bosmina longirostris*, the dominant herbivorous cladoceran, was positively correlated with the abundance of the predatory copepod, *Cyclops columbianus*. Changes in the size and abundance of *Bosmina* remains over the past 300-500 years were then determined for sediments from two lakes on Kodiak Island, Alaska. The zooplankton communities showed varying responses to past changes in salmon populations, resulting from relative changes in the magnitude of adult salmon-derived nutrient loading and in predation pressure from juvenile sockeye and cyclopoid copepods. Knowledge of how various factors impact zooplankton can have important implications for the effective management of sockeye within these lake systems.

## Table of Contents

Abstract .....	3
List of Figures .....	7
List of Tables .....	8
Acknowledgments .....	9
Preface .....	11
<b>Chapter 1: General Introduction</b>	
Background .....	12
Thesis Objectives .....	14
Thesis Outline .....	14
<b>Chapter 2: Zooplankton Assemblages in Alaskan Sockeye Salmon</b>	
<i>(Oncorhynchus nerka)</i> Nursery Lakes: Influence of Salmon, Invertebrate Predators and Environmental Factors	
Abstract .....	15
Introduction .....	16
Study Area .....	21
Methods .....	26
Data Compilation .....	26
Data Screening .....	27
Statistical Analyses .....	29

**Table of Contents (Continued)**

Results .....	31
Environmental gradients .....	31
Environmental variables influencing zooplankton abundance .....	32
Environmental factors influencing zooplankton size .....	37
Discussion .....	43
Acknowledgments .....	50
 <b>Chapter 3: Assessing the long-term impacts of sockeye salmon (<i>Oncorhynchus nerka</i>) abundance on <i>Bosmina longirostris</i> populations in two lakes from Kodiak Island, Alaska</b>	
Introduction .....	51
Study Sites .....	55
Methods .....	59
Results .....	62
Karluk Lake .....	62
Frazer Lake .....	64
Discussion .....	66
Karluk Lake .....	66
Frazer Lake .....	68
Conclusions .....	70

**Table of Contents (Continued)****Chapter 4: Summary and Conclusions**

Conclusions .....	71
Future Research .....	74
<b>Literature Cited .....</b>	<b>78</b>

<b>List of Figures</b>	<b>Page</b>
<b>Figure 2-1</b> Diagram of food web, illustrating major interactions among selected organisms in our study lakes .....	19
<b>Figure 2-2</b> Locations of the 23 sockeye salmon nursery lakes examined in the study. Lake numbers are listed in Table 2-1 .....	25
<b>Figure 2-3</b> Principal Components Analysis ordination showing the relationship between measured environmental variables (A) and the 23 sockeye salmon nursery lakes included in the study (B) .....	33
<b>Figure 2-4</b> Results of redundancy analysis of the zooplankton taxa from the study lakes .....	36
<b>Figure 2-5</b> Abundance of zooplankton taxa in the 23 Alaskan sockeye salmon lakes used in ordinations .....	40
<b>Figure 2-6</b> Mean length of dominant zooplankton in the 23 Alaskan sockeye salmon lakes compared to abundance of <i>Cyclops columbianus</i> , total phosphorus, and sockeye salmon ( <i>Oncorhynchus nerka</i> ) abundance .....	42
<b>Figure 3-1</b> Location of Frazer and Karluk Lakes (Kodiak Island, Alaska) .....	57
<b>Figure 3-2</b> Morphology of <i>Bosmina</i> , showing location of length measurements ...	61
<b>Figure 3-3</b> Historical and paleolimnological record of variation in sockeye salmon and <i>Bosmina</i> populations in Karluk Lake over the past 500 years ...	63
<b>Figure 3-4</b> Historical and paleolimnological record of variation in sockeye salmon and <i>Bosmina</i> populations in Frazer Lake over the past 300 years...	65

<b>List of Tables</b>	<b>Page</b>
<b>Table 2-1</b> Geographical, morphological and limnological data of the twenty-three lakes included in this study. Water chemistry data shown are seasonal (May-October) mean values from epilimnetic (1 m) samples; total zooplankton density is based on seasonal means of vertical net tows .....	22
<b>Table 2-2</b> Matrix of Pearson product-moment correlations between environmental variables (* indicates significant correlations at $\alpha = 0.05$ , based on Bonferroni adjusted probabilities) .....	35
<b>Table 2-3</b> Canonical coefficients, approximate t-test values, and inter-set correlations of the three forward-selected environmental variables for the first two axes of the RDA analyses .....	38
<b>Table 2-4</b> Relationships between zooplankton body size, potential predators, resource availability, and lake size .....	41
<b>Table 3-1</b> Selected physical and limnological characteristics of Karluk and Frazer Lakes (Kodiak Island, Alaska). Water chemistry data shown are based on mean seasonal (May – October) values from epilimnetic (1 m) samples; total zooplankton density is based on seasonal means of vertical net tows. (Source: Alaska Department of Fish and Game) .....	56

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## Preface

Limnological and fisheries data used in the cross-lake comparisons in Chapter 2 were made available by the Alaska Department of Fish and Game, and are archived in various locations in the department, primarily in the Limnology Laboratory in Soldotna, Alaska, and in the Westward Regional Office in Kodiak Island. Sedimentary zooplankton fossil data, including raw counts, abundance, and size data generated from this thesis will be submitted for archiving in the World Data Center for Paleoclimatology in Boulder, CO (<http://www.ngdc.noaa.gov/paleo/paleo.htm>). The paleolimnological data are also archived with Dr. B. Finney at the University of Alaska Fairbanks, and can be obtained directly from myself. Stable isotope data used for comparison with the zooplankton data were made available by Dr. Finney, and are accessible directly from him.

In both Chapter 2 and Chapter 3, B. Finney is included as coauthor. These sections of this thesis will be submitted as separate manuscripts for external publication in peer-reviewed journals. Chapter 2 represents original research I performed examining the influence of limnological and environmental factors on the structure of zooplankton communities in Alaskan sockeye nursery lakes, which was done under the supervision of Dr. Finney. Chapter 3 also contains original work I carried out as part of my thesis using paleolimnological records of fossil zooplankton in sockeye lakes. For Chapter 3, Dr. Finney provided stable isotope data that are used for comparisons to the fossil zooplankton data, and made available sediment samples from Karluk Lake for analyses.

## Chapter 1 – Introduction

### Background

Sockeye salmon, *Oncorhynchus nerka* (Walbaum), are unique among Pacific salmon species, in that they make extensive use of freshwater lakes as rearing habitat during their juvenile stages. Juvenile sockeye typically spend from one to three years in the limnetic zone of a lake prior to migrating to the ocean (Burgner 1991). They are typically the predominant planktivorous fish species in the lakes, and feed primarily on pelagic zooplankton during this period (Burgner 1991; Higgs et al 1995; Kyle et al 1996; Koenings and Kyle 1997). The importance of planktivorous fish in structuring zooplankton communities has been recognized for several decades (Hrbáček et al 1961; Brooks and Dodson 1965; O'Brien 1979; Zaret 1980; Northcote 1988; Kerfoot and Sih 1987; Carpenter and Kitchell 1993). Planktivorous fish can affect zooplankton directly, through predation, or indirectly, for example, through the reduction or removal of competitor species or invertebrate predators and through nutrient recycling (Dodson 1974; Slusarczyk 1997; Vanni 1997).

A growing number of studies have identified the importance of salmon in transporting significant amounts of marine-derived nutrients into the freshwater environment, through the decomposition of their carcasses following spawning (Krohkin 1967; Mathisen et al 1988; Kline et al 1997). Over 99% of the biomass of adult sockeye is accumulated in the marine environment (Finney et al 2000), and as a result, carcass-derived nutrients can be a significant source of nutrient loading in these oligotrophic lake ecosystems (Kline et al 1997). Food web effects, however, may affect the flow of energy

and carbon in these systems, and as a result, an understanding of trophic interactions and the factors influencing organisms in sockeye nursery lakes is important (Crowder et al 1988; Carpenter and Kitchell 1993).

Following emergence, juvenile sockeye salmon move rapidly into the limnetic region of their nursery lakes, where they feed on pelagic zooplankton (Burgner, 1991). In general, cladocerans and cyclopoid copepods dominate the diet of juvenile sockeye. For example, in the Wood River Lakes in Bristol Bay, Alaska, *Bosmina*, *Daphnia*, and *Cyclops* were the most frequent taxa in the summer diet of juvenile sockeye, followed by calanoid copepods (Rogers 1968). In Iliamna Lake, Hoag (1972) reported that *Bosmina* and *Cyclops* were the main genera in the diet of sockeye, as well as in the water column, and calanoid copepods (*Diaptomus* and *Eurytemora*) and the cladocerans *Daphnia* and *Holopedium* were of less importance. In Karluk Lake, one of the lakes included in this study, *Bosmina* was the preferred zooplankton in sockeye stomachs, followed by *Cyclops* and *Daphnia*, while in the lake *Cyclops* was the most abundant zooplankton taxa, followed by *Bosmina* (personal communication, J. Edmundson, ADF&G, Soldotna, AK) suggesting that sockeye preferentially selected *Bosmina*. Selective feeding behavior in sockeye has been observed in several lakes, and sockeye tend to exploit cladocerans at a greater rate than more motile and evasive copepods (Ricker 1937; Hoag 1972; Burgner 1991).

### **Thesis Objectives**

Given that pelagic zooplankton are the main forage items in juvenile sockeye diets, and that changes in the abundance and size of zooplankton can potentially affect

the importance of carcass-derived nutrients on new salmon production, understanding factors that influence zooplankton communities is essential for effective management of these lakes. My objectives in this thesis are twofold. First, I will examine the environmental factors important in controlling zooplankton abundance and size structure in sockeye salmon lakes, and second, I will examine long-term variation in zooplankton and sockeye salmon populations using the paleolimnological record, in order to better understand sockeye salmon – zooplankton interactions.

### **Thesis Outline**

In Chapter 2, I examine the importance of sockeye salmon, invertebrate predators and other limnological and environmental factors such as water chemistry and lake depth in regulating the abundance and size structure of zooplankton in 23 sockeye salmon nursery lakes across southern Alaska. Salmon-derived nutrients, juvenile sockeye predation, and predation from predatory copepods appear to interact to determine zooplankton abundance and body size. These trophic interactions may be critical in determining overall juvenile salmon production in the lakes. In Chapter 3, I examine shifts in zooplankton size and abundance over a much longer time scale, by reconstructing shifts in the herbivorous zooplankton, *Bosmina longirostris*, in two lakes from Kodiak Island over the past 300-500 years, based on microfossil remains in lake sediments. The final Chapter serves as a general summary of the preceding chapters, and makes some suggestions for future research.

## **Chapter 2 - Zooplankton Assemblages in Alaskan Sockeye Salmon (*Oncorhynchus nerka*) Nursery Lakes: Influence of Salmon, Invertebrate Predators and Environmental Factors<sup>1</sup>**

### **Abstract**

We evaluated the importance of sockeye salmon, invertebrate predators and other limnological and environmental factors in determining the abundance and size structure of zooplankton in 23 sockeye nursery lakes across southern Alaska. Redundancy analysis showed that sockeye, lake-water total Kjeldahl nitrogen concentrations, and alkalinity were the minimal set of significant variables that could explain the greatest variation in zooplankton abundance. The main herbivorous zooplankton species (*Bosmina longirostris*, *Diaptomus pribilofensis* and *Daphnia longiremis*) were positively correlated with sockeye abundance. *Cyclops columbianus*, the dominant predatory copepod in the lakes, also was positively correlated with salmon abundance, but *Cyclops* densities increased in a nonlinear fashion, with extremely high *Cyclops* densities occurring at the highest levels of sockeye spawners. The mean size of *Bosmina* was related to *Cyclops* abundance in the lakes, with larger *Bosmina* (that are more conspicuous to juvenile sockeye predators) occurring in lakes with high *Cyclops*. Our findings suggest that salmon-derived nutrients and predation by juvenile sockeye and invertebrate predators may interact to regulate zooplankton abundance, and that a threshold in freshwater sockeye production may occur related to *Cyclops* abundance.

---

<sup>1</sup> Sweetman, J. and Finney, B. Zooplankton Assemblages in Alaskan Sockeye Salmon (*Oncorhynchus nerka*) Nursery Lakes: Influence of Salmon, Invertebrate Predators and Environmental Factors. This Chapter will be submitted for publication to: the Canadian Journal of Fisheries and Aquatic Sciences

## Introduction

Many lakes in Alaska and throughout the North Pacific region support large populations of sockeye salmon (*Oncorhynchus nerka*) by providing essential spawning and rearing habitats (Burgner 1991; Kyle et al. 1997). Sockeye, like other Pacific salmon species, are anadromous, meaning they spend the majority of their adult lives in the marine environment, prior to entering freshwater to spawn. Sockeye are unique among Pacific salmon species, however, in that they have an extended residence time in freshwater lakes, typically spending from 1-3 years in the limnetic region of the lake prior to migrating to the ocean (Burgner 1991).

During their residence in the freshwater environment, juvenile sockeye salmon are often the predominant planktivorous fish within a lake ecosystem (Burgner 1991; Higgs et al 1995; Kyle 1996; Koenings and Kyle 1997). Juvenile sockeye are visual planktivores and preferentially feed on pelagic zooplankton species during this period (Burgner 1991; Higgs et al. 1995; Koenings and Kyle 1997). The importance of planktivorous fish in structuring zooplankton communities has been recognized for several decades (Hrbáček et al. 1961; Brooks and Dodson 1965; O'Brien 1979; Zaret 1980; Northcote 1988; Kerfoot and Sih 1987; Carpenter and Kitchell 1993). When visually feeding planktivorous fish, such as salmon, are in high abundance, large zooplankton species, or larger individuals within a species, tend to be selectively eliminated (Brooks and Dodson 1965; Hall et al 1976). When fish predation is low, however, larger zooplankton species are favoured, as they are more efficient grazers and suffer less predation from invertebrates because of their larger size (Dodson 1974). As a

result, changes in the relative abundance of sockeye salmon in a lake could have large impacts on zooplankton community structure, through changes in the degree of predation pressure from juvenile salmon.

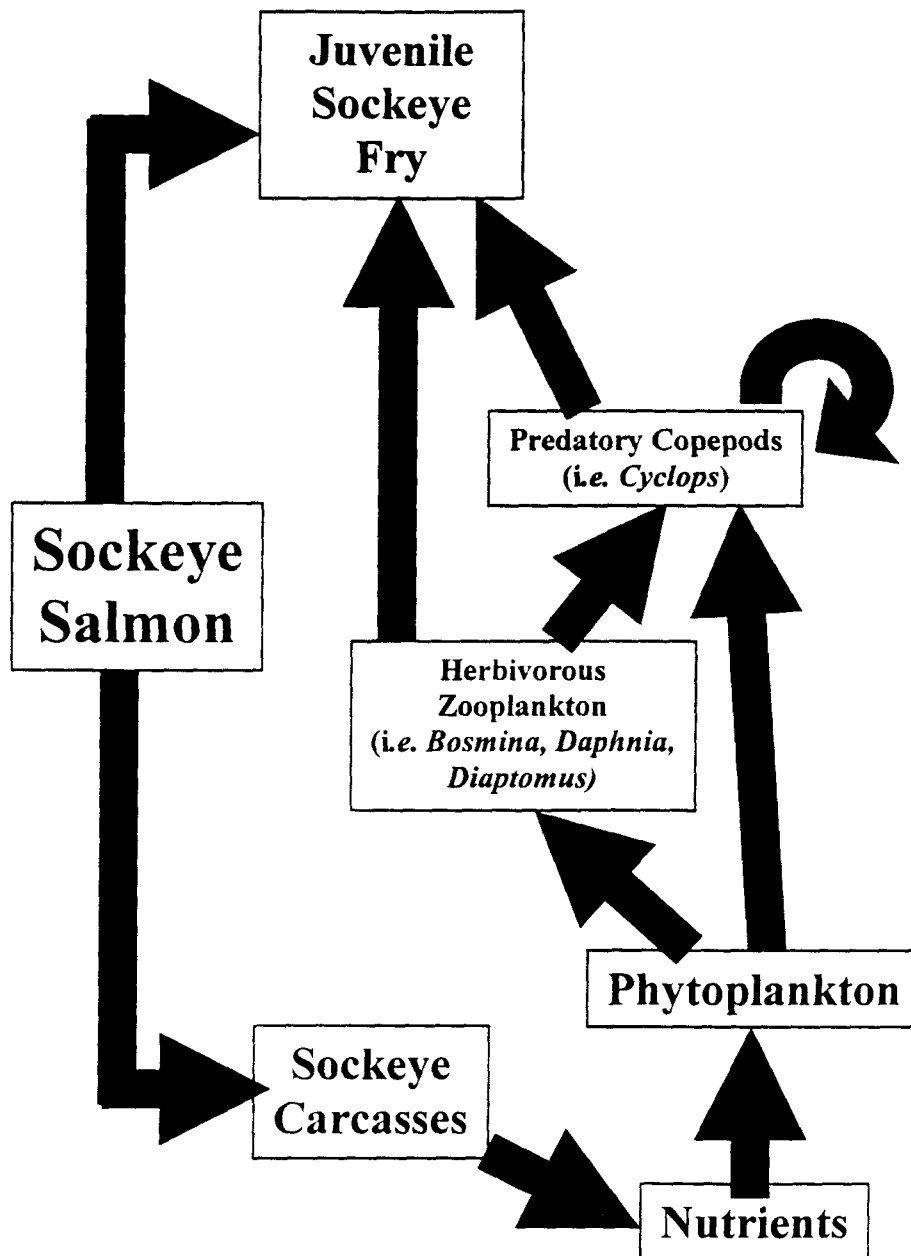
In addition to shifts in juvenile salmon predation, adult sockeye salmon returning to lakes may import large amounts of nutrients through the decay of their carcasses (Krokhin 1967; Mathisen et al 1988; Kline et al 1993; Kline et al 1997). Sockeye typically spend 2-3 years feeding in the North Pacific Ocean, following which they migrate to their natal lake system to spawn and die (Burgner 1991). Over 99% of the biomass of adult sockeye salmon is accumulated in the marine environment (Finney et al 2000), and as a result, carcass-derived nutrients can be a significant source of nutrient loading in these oligotrophic lake ecosystems (Kline et al. 1997). Lake productivity generally increases with the number of salmon returning to the lake, which may provide a “positive feedback” system in salmon lakes, with nutrients from salmon carcasses resulting in enhanced sockeye production (Kline et al 1997; Cederholm et al 1999).

Nutrients released during the decomposition of spawned-out sockeye salmon carcasses could have a strong impact on food web processes and zooplankton dynamics in sockeye nursery lakes. An increase in nutrient availability in salmon nursery lakes, which are, in general, highly oligotrophic, results in increased primary productivity, which in turn, leads to increased production of zooplankton (Kyle et al 1997; Kline et al 1997; Finney et al. 2000). Increased zooplankton populations within the lake could also increase internal recycling of nutrients, and further enhanced productivity (Vanni 1997). Urabe (1991) found that carapace size, brood size, and survivorship of *Bosmina*

*longirostris* (the predominant cladoceran species in Alaskan sockeye lakes) increased with increases in food concentration. In sockeye lakes that were fertilized to increase salmon productivity, either in Coastal British Columbia (Hyatt and Stockner 1985) or Alaska (Kyle et al 1997), additions of nutrients resulted in increases in both the biomass and size of zooplankton in the lakes.

Sockeye salmon can affect zooplankton in lakes both from changes in nutrients and changes in the abundance of juvenile salmon. Fluctuations in sockeye salmon could also indirectly cause a shift in the abundance of invertebrate predators. Predation by invertebrates could also have an impact on the zooplankton community structure (Kerfoot 1977; Lane 1979; Neill and Peacock 1980; Peacock 1982; Williamson 1987; Neill 1988). Many invertebrate predators, including cyclopoid copepods, prefer smaller prey items that are easier to handle and ingest, and therefore when invertebrate predation is strong, larger zooplankton species are more successful (Dodson 1974; Kerfoot 1977, 1978; Williamson 1987; Neill 1988). Cyclopoid copepods are omnivorous, with the naupli being herbivores, while adults preferentially prey on other zooplankton (Kerfoot 1977; 1978; Neill and Peacock 1980). Complex trophic interactions could result from changes in the abundance of sockeye salmon, predatory copepods and zooplanktivorous prey (Crowder et al 1988: Figure 2-1).

Factors other than those related to salmon variability also have the potential to influence zooplankton communities (Swadling et al. 2000; Shuter and Ing 1997; Patalas



**Figure 2-1:** Diagram of food web, illustrating major interactions among selected organisms in our study lakes.

1990; Tessier and Horwitz 1990; Pinel-Aloul et al 1990). For example, Swadling et al. (2000), found that chloride, silica and temperature were significantly related to zooplankton community composition in a set of lakes from the Yukon and Northwest Territories.

The relative importance of sockeye salmon in structuring zooplankton communities has not been studied in detail. When salmon have been introduced into lakes that previously did not have an anadromous fish population, zooplankton abundances declined dramatically, demonstrating a strong top-down influence from salmon predation (Reischauer 1996; Kyle 1996; Koenings and Kyle 1997). However, the response of zooplankton to fish is difficult to assess on short-time scales, such as those from fish introductions, as the full response to changes in predation regime is generally much longer than the limited observational time of such manipulation-type studies (Ramcharan et al 1995; Kratz et al 1987).

Knowledge of which factors may be important in influencing zooplankton assemblages has important implications for the effective management of salmon lakes. Shifts in lake food webs could significantly alter the processes in which changes in nutrient loading (from fertilization or fluctuations in salmon escapement) affect freshwater ecosystems (Stockner 1987; Crowder et al. 1988). Since pelagic zooplankton are the primary forage base for juvenile salmon, changes in food web structure could have important impacts on sockeye salmon production.

The objective of this study was to assess the importance of sockeye salmon abundance, invertebrate predators, and other limnological and environmental factors in

regulating the abundance and size of zooplankton in sockeye nursery lakes. To do this, we examined zooplankton communities in a set of 23 sockeye salmon nursery lakes from southern Alaska, representing a broad range of salmon densities and limnological conditions (Figure 2-2; Table 2-1). We compared the abundance and size structure of zooplankton species within these lakes to salmon abundance and morphological and limnological data from the lakes.

### **Study area**

Twenty-three sockeye salmon lakes from southern Alaska, for which there was available information on sockeye salmon escapement (number of returning spawners), zooplankton abundance, and water chemistry (Figure 2-2, Table 2-1), were selected. The lakes spanned a large gradient in sockeye salmon abundance from <1 to 40,000 salmon km<sup>-2</sup> (Table 2-1). The lakes are classified as oligotrophic to slightly mesotrophic, with mean seasonal (May-October) total phosphorus values ranging from 3-16 µg L<sup>-1</sup>, and mean seasonal chlorophyll *a* values ranging from 1-4 µg L<sup>-1</sup>.

The lakes span several ecoregions from the Subarctic Coastal Plains in the west, through the Alaska Peninsula Mountains, to coastal western Hemlock –Sitka Spruce forested regions in the east. In the coastal plains and peninsula mountains, graminoid herbaceous communities dominate, with dwarf scrub communities occurring. Lakes in the eastern half of the gradient have watersheds dominated by spruce and hemlock forests (Gallant 1995).

Sockeye salmon (*Oncorhynchus nerka*) usually were the dominant fish in the pelagic zone of the lakes, but high numbers of threespine stickleback (*Gasterosteus*

**Table 2-1** Geographical, morphological and limnological data of the twenty-three lakes included in this study. Water chemistry data shown are seasonal (May – October) mean values from epilimnetic (1 m) samples; total zooplankton density is based on seasonal means of vertical net tows.

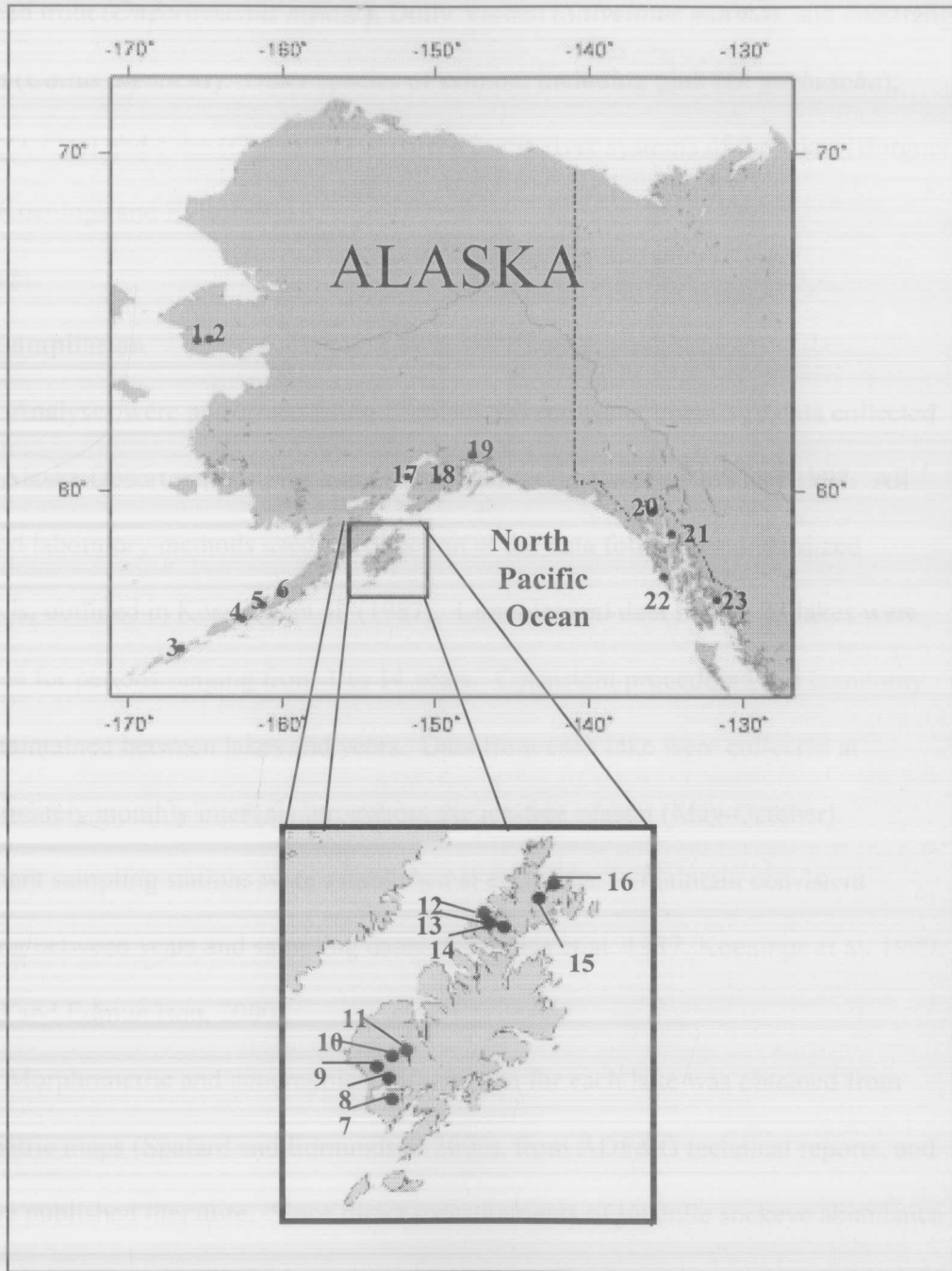
Lake Name	Lake Number	Latitude (N°)	Longitude (W°)	Area (x10 <sup>6</sup> m <sup>-2</sup> )	Volume (x10 <sup>6</sup> m <sup>-3</sup> )	Depth (m)
Glacial	1	64°52'	165°42'	4.0	23.0	22
Salmon	2	64°54'	165°00'	7.5	95.0	40
Unalaska	3	53°52'	166°32'	0.4	2.1	9
Charlie Hansen	4	54°58'	163°06'	7.0	29.1	14.6
Sapsuk	5	55°41'	161°01'	11.0	443.1	87
Bear	6	56°00'	160°15'	25.6	826.5	104
Upper Station	7	57°04'	154°10'	7.9	208.0	80
Akalura	8	57°08'	154°15'	6.7	67.0	22
Red	9	57°15'	154°20'	8.4	208.0	48
Frazer	10	57°16'	154°08'	16.6	554.0	59
Karluk	11	57°25'	154°05'	39.4	1920.0	126
Lower Malina	12	58°10'	153°05'	0.7	4.6	15
Upper Malina	13	58°10'	153°05'	1.2	18.4	34
Afognak	14	58°07'	152°55'	5.5	43.0	23
Portage	15	58°16'	151°37'	1.6	15.0	23
Laura	16	58°23'	152°18'	4.2	50.5	33
Packers	17	60°28'	154°55'	2.0	25.0	32
Upper Russian	18	57°04'	154°10'	4.7	127.0	81
Coghill	19	61°04'	147°29'	11.9	563.0	78
Chilkat	20	59°15'	135°53'	9.8	319.0	57
Auke	21	58°22'	134°38'	0.9	17.0	34
Redoubt	22	56°53'	135°15'	11.2	819.0	90
McDonald	23	55°55'	131°47'	3.5	158.0	112

**Table 2-1.** Continued

Lake Name	Conductivity ( $\mu\text{S cm}^{-1}$ )	pH (Units)	Alkalinity ( $\text{mg l}^{-1}$ )	Color (Pt. units)	Turbidity (NTU)	Calcium ( $\text{mg l}^{-1}$ )
Glacial	68.17	7.02	11.75	4.00	0.83	7.40
Salmon	130.25	7.46	47.94	5.13	0.59	17.31
Unalaska	75.75	6.88	17.50	2.75	1.13	6.83
Charlie Hansen	98.88	6.88	14.66	2.63	1.24	7.85
Sapsuk	67.81	6.85	16.29	3.38	0.59	5.96
Bear	78.30	6.71	11.98	4.13	1.26	7.40
Upper Station	48.25	6.85	9.25	3.22	1.06	5.06
Akalura	58.90	6.99	14.95	6.22	1.72	4.88
Red	60.50	7.00	15.72	4.94	1.19	5.40
Frazer	52.65	6.90	13.51	6.09	0.79	4.63
Karluk	64.70	7.18	22.62	5.52	0.84	7.32
Lower Malina	78.32	7.04	20.98	9.78	0.79	7.38
Upper Malina	76.12	7.02	19.74	8.30	0.97	6.70
Afognak	55.00	6.66	10.32	10.24	1.36	3.42
Portage	51.75	6.64	10.90	20.59	1.45	3.97
Laura	67.09	6.60	10.13	15.97	1.12	3.83
Packers	48.13	6.66	9.13	23.38	0.86	3.70
Upper Russian	63.50	7.14	22.90	5.77	0.55	10.37
Coghill	70.40	6.98	18.30	5.20	4.88	7.04
Chilkat	160.59	7.85	59.63	8.68	1.01	25.79
Auke	30.20	6.51	8.44	41.00	1.01	4.22
Redoubt	167.85	6.51	5.96	9.68	0.81	3.06
McDonald	7.66	5.86	2.39	20.08	0.80	0.90

Table 2-1. Continued

Lake Name	Total Phosphorus ( $\mu\text{g l}^{-1}$ )	Total Kjeldahl Nitrogen ( $\mu\text{g l}^{-1}$ )	Chloro-phyll <i>a</i> ( $\mu\text{g l}^{-1}$ )	Particulate Organic Carbon ( $\mu\text{g l}^{-1}$ )	Sockeye Salmon Density (1000's fish $\text{km}^{-2}$ )	Total Zooplankton Density (1000's $\text{m}^{-2}$ )
Glacial	4.02	70.28	1.12	108.67	3371	71.40
Salmon	3.50	60.49	0.95	80.13	289	208.54
Unalaska	4.35	60.40	0.75	119.50	<1	1.34
Charlie Hansen	7.28	51.54	0.58	162.88	104	28.95
Sapsuk	3.44	55.19	1.14	111.75	24205	384.61
Bear	4.00	55.63	1.42	99.25	18164	500.65
Upper Station	10.54	146.89	2.34	341.03	28149	590.81
Akalura	13.00	184.89	4.16	404.55	7837	127.46
Red	15.87	158.23	2.66	256.23	39535	540.62
Frazer	5.51	96.59	1.34	156.04	13947	206.75
Karluk	6.98	103.66	1.72	226.27	15362	538.98
Lower Malina	6.21	139.47	1.89	180.19	12760	15.65
Upper Malina	7.60	158.35	3.45	298.28	7443	135.20
Afognak	8.40	174.05	2.66	256.92	13896	195.46
Portage	10.66	190.56	3.11	245.51	3751	94.12
Laura	10.75	186.19	3.60	272.85	2979	108.77
Packers	10.78	230.39	1.92	115.13	15072	99.41
Upper Russian	3.98	97.75	1.20	134.81	28792	583.59
Coghill	10.34	97.56	2.27	259.82	693	25.18
Chilkat	6.06	109.48	1.17	201.76	15662	543.40
Auke	8.00	140.20	1.36	168.67	7820	173.65
Redoubt	5.73	84.08	1.36	137.45	2411	87.48
McDonald	7.35	135.87	2.07	254.02	22846	97.12



**Figure 2-2** Locations of the 23 sockeye salmon nursery lakes examined in the study. Lake numbers are listed in Table 2-1.

*aculeatus*) could also be present. Other fish species in the lakes included rainbow and steelhead trout (*Oncorhynchus mykiss*), Dolly Varden (*Salvelinus malma*), and coastrange sculpin (*Cottus aleuticus*). Other species of salmon, including pink (*O. gorbuscha*), chum (*O. keta*) and coho (*O. kisutch*) occurred in the river systems of the lakes (Burgner 1991; Koenings and Kyle 1991).

## **Methods**

### **Data Compilation**

Analyses were performed using zooplankton and water chemistry data collected by the Alaska Department of Fish and Game (ADF&G) between 1980 and 1997. All field and laboratory methods used in collection of the data followed standardized protocols, outlined in Koenings et al. (1987). Limnological data for the 23 lakes were available for periods ranging from 1 to 14 years. Consistent procedures and taxonomy were maintained between lakes and years. Data from each lake were collected at approximately monthly intervals throughout the ice-free season (May-October). Permanent sampling stations were established at each lake, to maintain consistent sampling between years and sampling dates (Koenings et al. 1987, Koenings et al. 1990, Spafard and Edmundson, 2000).

Morphometric and geographical information for each lake was obtained from bathymetric maps (Spafard and Edmundson 2000), from ADF&G technical reports, and from the published literature. Since direct measurements of juvenile sockeye abundance were available for only a limited number of lakes, we used the number of returning spawners (escapement) from the year prior to the limnological data as an index of

juvenile sockeye salmon rearing in the lake (Kyle et al 1988). Salmon escapement data were obtained from various ADF&G technical reports, and directly from the Alaska Department of Fish and Game (Patty Nelson; Steve Schrof, ADF&G, Kodiak, AK; Ben Van Alen, ADF&G, Douglas, AK, personal communications). For comparative purposes, we expressed sockeye abundance as fish per km<sup>2</sup>.

For each lake, we summarized zooplankton and corresponding water chemistry data as mean seasonal values (Table 2-1; Figure 2-2). Within each lake, several stations, typically at the deepest point of each major basin, were used for collection of limnological samples. Water chemistry was measured at 1 m below the surface of the lake. Zooplankton were collected from paired 50 m or bottom to surface vertical tows using either a 0.2 or 0.5 m diameter, 153  $\mu$ m mesh conical zooplankton net (Koenings et al. 1987, Koenings et al. 1990). An estimate of mean zooplankton size for each species was obtained from three 1 ml subsamples, with approximately ten individuals of each species encountered per subsample measured. Total body length (distance from the top of the head to the end of the carapace) for each individual was measured to the nearest 0.01 mm (Koenings et al 1987). For the present study, we averaged all sampling stations and years from each lake to obtain estimates of mean annual values for zooplankton and environmental data. Only lakes that were sampled a minimum of four times per year during the May-October period were used in the analyses.

### **Data Screening**

A total of 8 zooplankton taxa were used in the multivariate analyses: three cladocerans (*Bosmina longirostris*, *Daphnia longiremis* and *Holopedium gibberum*) and

five copepod taxa (*Cyclops columbianus*, *Diaptomus pribilofensis*, *Epischura nevadensis*, *Ergasilus* spp. and *Eurytemora* spp.). Rotifer taxa reported in the initial data were not analyzed, as the mesh size of the net used did not allow for an accurate estimates of rotifer abundance. Copepod nauplii were also reported in the zooplankton data, but were excluded from analyses, as the net mesh size may have underestimated nauplii abundance, and as multiple species of copepods occurred within each lake and nauplii could not be separated to species. An unidentified harpacticoid copepod was also reported as present in a few of the lakes used in the study, but occurred very infrequently in the lakes and was not included in any analyses. Multivariate ordinations are sensitive to rare species, and the high abundance of a rare species at a particular site can disproportionately influence the outcome of ordinations (Jongman et al. 1995).

A total of 16 physical, chemical, geographical, and biological variables were available for the lakes: latitude, longitude, surface area, depth, volume, conductivity, pH, alkalinity, water color, turbidity, calcium, total phosphorus, total Kjeldahl nitrogen, chlorophyll *a*, particulate organic carbon and sockeye salmon density (Table 2-1). The distributions of 10 variables were either square root transformed (sockeye salmon, pH, alkalinity, Ca, Longitude, Maximum depth) or log ( $x + 1$ ) transformed (conductivity, color, surface area, volume) to improve assumptions of normality and heteroscedascity (Sokal and Rohlf 1981). For nitrogen data, only total Kjeldahl nitrogen was used in analyses, as  $\text{NH}_3$  and  $\text{NO}_2^- + \text{NO}_3^-$  measurements were both below the detection limits in several lakes, and several anomalous values occurred in the chemistry database.

To minimize the effects of high turbidity that could override the effects of other potentially important variables (Lloyd et al. 1987), lakes that were glacially fed, with high turbidity measurements ( $\geq 5$  nephelometric turbidity units), were excluded from the present study. Koenings et al. (1990) reported that cladoceran zooplankton species were not present in highly turbid Alaskan glacial lakes, and that the macro-zooplankton community in these lakes was composed of only a single copepod species, *Cyclops columbianus*.

Influential site outliers were detected in the data set by i) examining site scores which fell outside  $\pm 2$  SD of the mean of the first two axes of a detrended correspondence analysis (DCA) of the species data and a principal components analysis (PCA) of the environmental data (Hall and Smol 1992; Gregory-Eaves et al. 2000) and ii) by examining leverage diagnostics calculated through redundancy analysis (RDA) (ter Braak and Šmilauer 1998). McDonald Lake, which has the lowest pH, alkalinity, and conductivity of all the lakes, was found to be an outlier using the first technique, and the lake was excluded from further analyses. Coghill Lake had environmental variables with extreme influence ( $> \times 55$ ) or 'leverage' in preliminary RDA, and so was also removed from subsequent analyses. Coghill Lake is a meromictic system, and has relatively high turbidity levels due to silt-laden runoff from surrounding glaciers (Edmundson et al. 1997).

### **Statistical Analyses**

All ordinations were performed using the computer program CANOCO (ter Braak and Šmilauer 1998) version 4.0. Detrended Correspondence Analysis (DCA) of the

zooplankton species was used to determine if unimodal or linear based methods would be more appropriate for the analyses (ter Braak, and Šmilauer 1998). If the gradient length is less than 1.5 SD, most species are responding monotonically along the axis, and a linear-based method of analysis, such as Redundancy Analysis (RDA) would be more appropriate (ter Braak and Prentice 1988). At longer gradient lengths, species tend to be distributed in a unimodal (i.e. Gaussian-like) fashion, and an ordination method which assumes a unimodal response such as Canonical correspondence analysis (CCA) would be more appropriate (ter Braak and Prentice 1988).

Redundancy Analysis (RDA, also known as reduced-rank regression) was then used to identify relationships between the zooplankton species densities and environmental variables (ter Braak and Prentice 1988). RDA is essentially an extension of PCA, except that it is a direct gradient analysis method, where ordination axes are constrained to be linear combinations of environmental factors (ter Braak and Prentice 1988; Jongman et al. 1995; ter Braak and Šmilauer 1998). To avoid artificially increasing the explained variation, environmental variables were screened using forward selection with Monte Carlo permutation testing (199 permutations) to remove superfluous variables. Prior to forward selection procedures, a Pearson correlation matrix was calculated between environmental variables, and the significance (with Bonferroni adjusted probabilities) of correlated environmental variables was identified (Table 2-2). To avoid inclusion of highly multicollinear variables describing the same environmental gradient, we ran a preliminary RDA with forward selection, to determine which environmental variables in each group of significantly correlated variables could account

for the most variance in the zooplankton data. This variable was used in subsequent analyses as a representative of that particular set of correlated variables (Hall and Smol 1992). Partial redundancy analysis (ter Braak 1988) was used to evaluate whether zooplankton assemblages were related to sockeye salmon abundance after the removal of the effects of other significant forward-selected environmental variables (Monte Carlo permutation test for the significance of the sum of all eigenvalues, 999 permutations) (ter Braak 1988).

Variability in size of zooplankton species was analyzed by simple correlations. Mean size estimates of *Bosmina* and *Daphnia* were compared to environmental variables to test the relationship between individual body size and environmental factors (including salmon abundance). *Cyclops* densities were also included as a possible explanatory variable, as predatory copepods have been shown to be an important factor in controlling cladoceran zooplankton size (Kerfoot 1977a; Wong 1981; Gliwicz and Umana 1994; Post et al. 1995). The sample size (23 lakes) was not large enough to allow examination of size structure of the other zooplankton species, as they were relatively rare or absent in several of the lakes.

## **Results**

### **Environmental gradients**

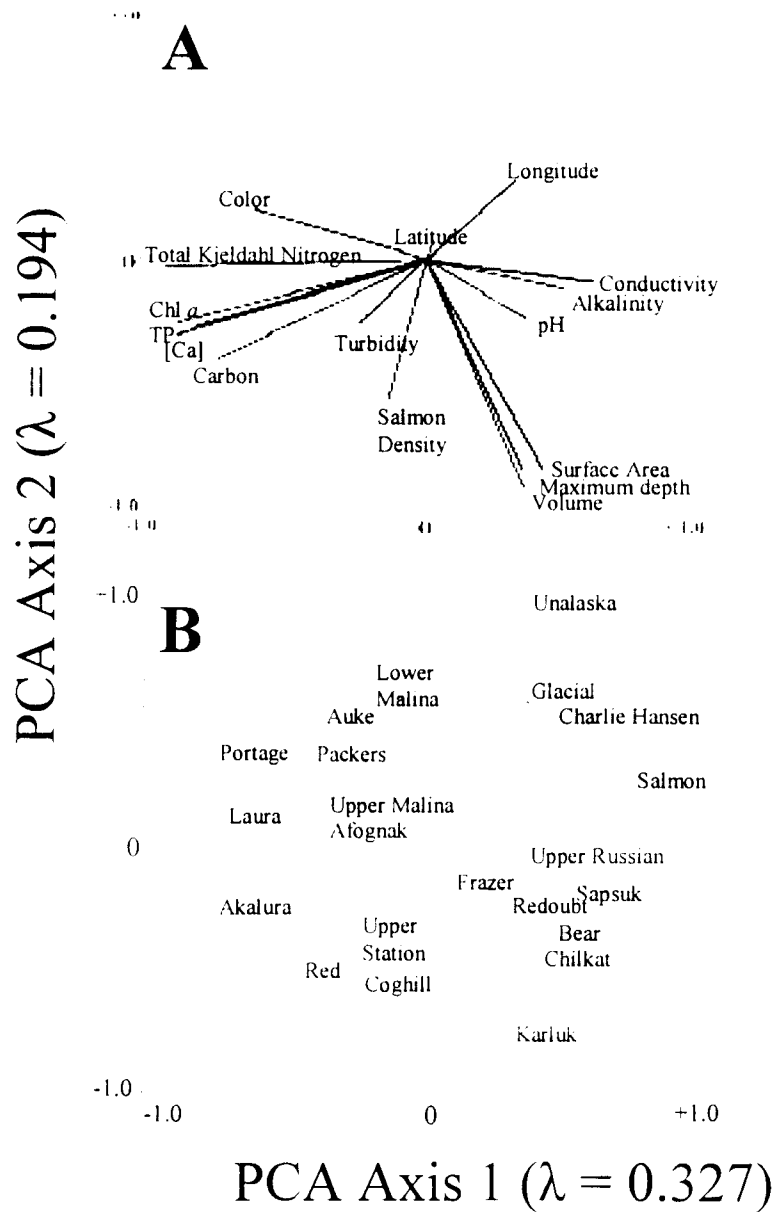
The first two axes of the principal components analysis (PCA) captured 52.1% of the variance (Figure 2-3) among the environmental variables in the lake set. The first axis, which accounted for 32.7% of the variance, and describes the strongest direction of variation in the environmental data, can be described as a gradient in lake productivity

and water chemistry. Total Kjeldahl nitrogen, calcium, chlorophyll a, total phosphorus, particulate organic carbon, color, along with conductivity, alkalinity, and pH are all correlated with this axis (Figure 2-3A). Along this gradient, lakes towards the left half of the ordination diagram (Figure 2-3B) are more productive, while increasing water hardness and lower productivity values occur towards the right half of the diagram.

The second axis is correlated with lake size (surface area, depth, volume), as well as with salmon density. Lakes from the same regions generally clustered together, with lakes in a particular area showing similar limnological characteristics. For example, lakes from Afognak Island (Afognak, Upper and Lower Malina, Portage and Laura Lakes) are clustered on the top left half of the ordination diagram. These lakes tend to be more productive, and have higher color values, with inputs of allochthonous DOC from the surrounding watershed, which is heavily forested. Kodiak Island Lakes (Akalura, Red, Upper Station, Frazer, and Karluk Lakes) tend to be distributed in the bottom half of the diagram, representing relatively deeper lakes, with higher salmon abundances. Lakes from the Seward Peninsula (Glacial and Salmon Lakes) and the Alaska Peninsula (Unalaska, Charlie Hansen, Sapsuk, Bear) are characterized by relatively lower productivity, and higher alkalinity, conductivity and pH values, but tend to vary with lake size and salmon densities.

### **Environmental variables influencing zooplankton abundance**

Eigenvalues ( $\lambda_1 = 0.27$ ,  $\lambda_2 = 0.10$ ) of the first two DCA axes captured 54.5% of the cumulative variation in the zooplankton data. The primary direction of variation of the zooplankton density data had a gradient length of 1.54 SD, with the second DCA axis



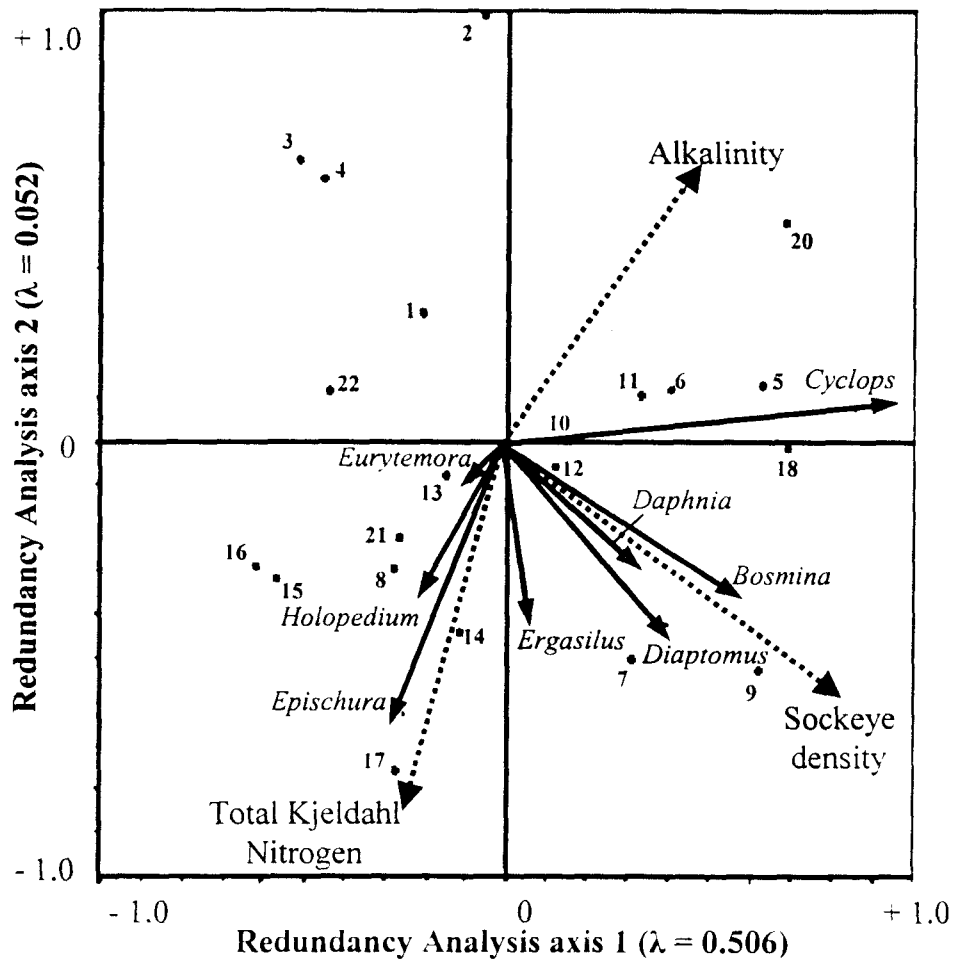
**Figure 2-3** Principal Components Analysis ordination showing the relationship between measured environmental variables (A) and the 23 sockeye salmon nursery lakes included in the study (B).

having a gradient of 1.56 SD, suggesting that linear based methods were appropriate for the analyses (ter Braak and Prentice 1988).

Prior to RDA the sixteen environmental variables in the analysis were: salmon density, conductivity, alkalinity, pH, total Kjeldahl nitrogen, total phosphorus, chlorophyll *a*, carbon, [Ca], color, turbidity, latitude, longitude, surface area, maximum depth, and volume. Sockeye density, conductivity, turbidity, color, latitude, and longitude were not significantly correlated with any other environmental variables at the  $\alpha = 0.05$  level, with Bonferroni adjusted probabilities (Table 2-2). The remaining variables were significantly correlated with one or more variables, and thus represent groups of significantly inter-correlated variables. Alkalinity, for example was included in the analysis, but was significantly correlated with pH. Total phosphorus was significantly correlated with particulate organic carbon. Total Kjeldahl nitrogen also represented chlorophyll *a* and [Ca], and volume was highly correlated with two other measures of lake size, maximum depth and surface area (Hall and Smol 1992). Following the removal of highly correlated variables, 10 variables remained: sockeye density, conductivity, turbidity, color, latitude, longitude, alkalinity, total phosphorus, total Kjeldahl nitrogen, and volume.

Forward selection procedures in RDA with Monte Carlo permutation tests (199 permutations,  $p < 0.05$ ) revealed that sockeye salmon density, alkalinity, and total Kjeldahl nitrogen were the minimal set of significant variables that could explain the greatest variation in the data set (Figure 2-4). Most of the variance in the zooplankton





**Figure 2-4** Results of redundancy analysis on the zooplankton taxa from the study lakes. Circles represent lakes, with numbers corresponding to Table 2-1. Arrows with solid lines indicate the response of zooplankton species. Arrows with broken lines indicate environmental variables that exert significant and independent influences on the distribution of zooplankton taxa, as detected by forward selection in RDA. Sockeye salmon densities and alkalinity were square-root transformed.

taxa was explained by the first axis (41.2%) while axis two only accounted for 4.8% of the variance. Axis one is most strongly influenced by sockeye salmon (Inter-set correlation = 0.70; Table 2-3), while total Kjeldahl nitrogen had the strongest influence on Axis two (Inter-set correlation = -0.64; Table 2-3). This relationship is also observed in the ordination diagram (Figure 2-4). Most of the variance in the zooplankton data was due to variation in the density of *Cyclops columbianus* and *Bosmina longirostris*. *Cyclops* density was related to variations in sockeye salmon. Alkalinity (which was correlated with pH) also was related to the density of *Cyclops*. The dominant herbivorous grazers, *Bosmina longirostris*, *Diaptomus pribilofensis* and *Daphnia longiremis*, were correlated with sockeye salmon densities in the lakes. The remainder of the taxa were more strongly influenced by overall nutrient concentrations in the lakes.

The pattern of zooplankton distribution in the study lakes is also illustrated in Figure 2-5, arranged in order of increasing sockeye salmon density within the lakes. In lakes with high densities of sockeye, *Cyclops columbianus* is extremely abundant. The increase in *Cyclops*, however, is not linearly related with salmon abundance. There is a dramatic increase in *Cyclops* densities at high levels of sockeye salmon. In general, there are increases in *Bosmina* and *Diaptomus* along the gradient of increasing sockeye salmon. *Ergasilus*, *Eurytemora*, *Epischura*, and *Holopedium* all tend to have their highest densities in lakes with moderate salmon densities.

### **Environmental factors influencing zooplankton size**

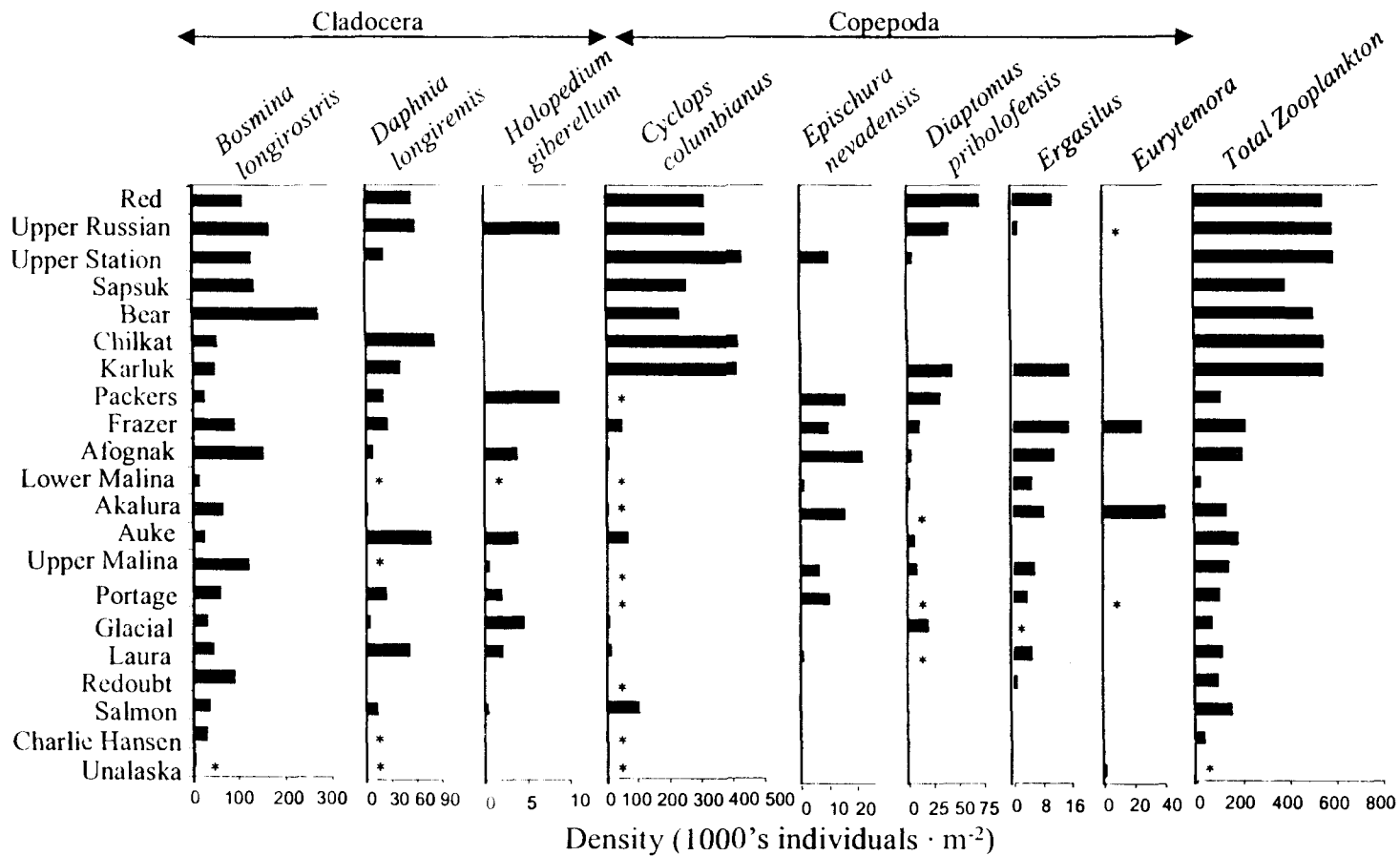
Table 2-4 shows the relationships between mean individual zooplankton Lengths and sockeye salmon abundance, *Cyclops columbianus* abundance, lake

**Table 2-3** Canonical coefficients, approximate t-test values, and inter-set correlations of the three forward selected variables for the first two axes of the RDA analyses.

<b>Canonical coefficients</b>	Axis 1	Axis 2
Salmon density	0.9142	-0.4224
Alkalinity	0.3516	0.4232
Total Kjeldahl Nitrogen	-0.3793	-0.6007
<b>Approximate t-test values</b>	Axis 1	Axis 2
Salmon density	6.2121**	-2.0616
Alkalinity	2.3562**	2.0373
Total Kjeldahl Nitrogen	-2.4624**	-2.8013**
** Significant at $\alpha = 0.05$		
<b>Inter-set Correlations</b>	Axis 1	Axis 2
Salmon density	0.7027	-0.4478
Alkalinity	0.3883	0.4701
Total Kjeldahl Nitrogen	-0.2205	-0.6435

productivity and lake size determined by correlation analyses. Salmon density was significantly correlated with the mean length of *Bosmina*, *Daphnia*, and *Cyclops*, where significantly larger individuals were found in lakes with high salmon levels. The density of *Cyclops* was highly correlated with the mean lengths of the herbivorous cladocerans, *Bosmina* and *Daphnia*. Indexes of lake productivity, however, were not significantly correlated with mean zooplankton size for any of the species. Of these three zooplankton taxa, *Bosmina* was the only species showing consistent, but weak, positive correlations with the nutrient and chlorophyll data. *Bosmina* mean length was also significantly positively correlated to all three measures of lake morphometry. The mean length of *Cyclops* was also correlated with maximum depth and volume, but not surface area. *Daphnia* length was not significantly related to lake morphometry at the  $\alpha = 0.05$  level, but mean *Daphnia* length was significantly positively correlated with lake depth at the  $\alpha = 0.10$  level.

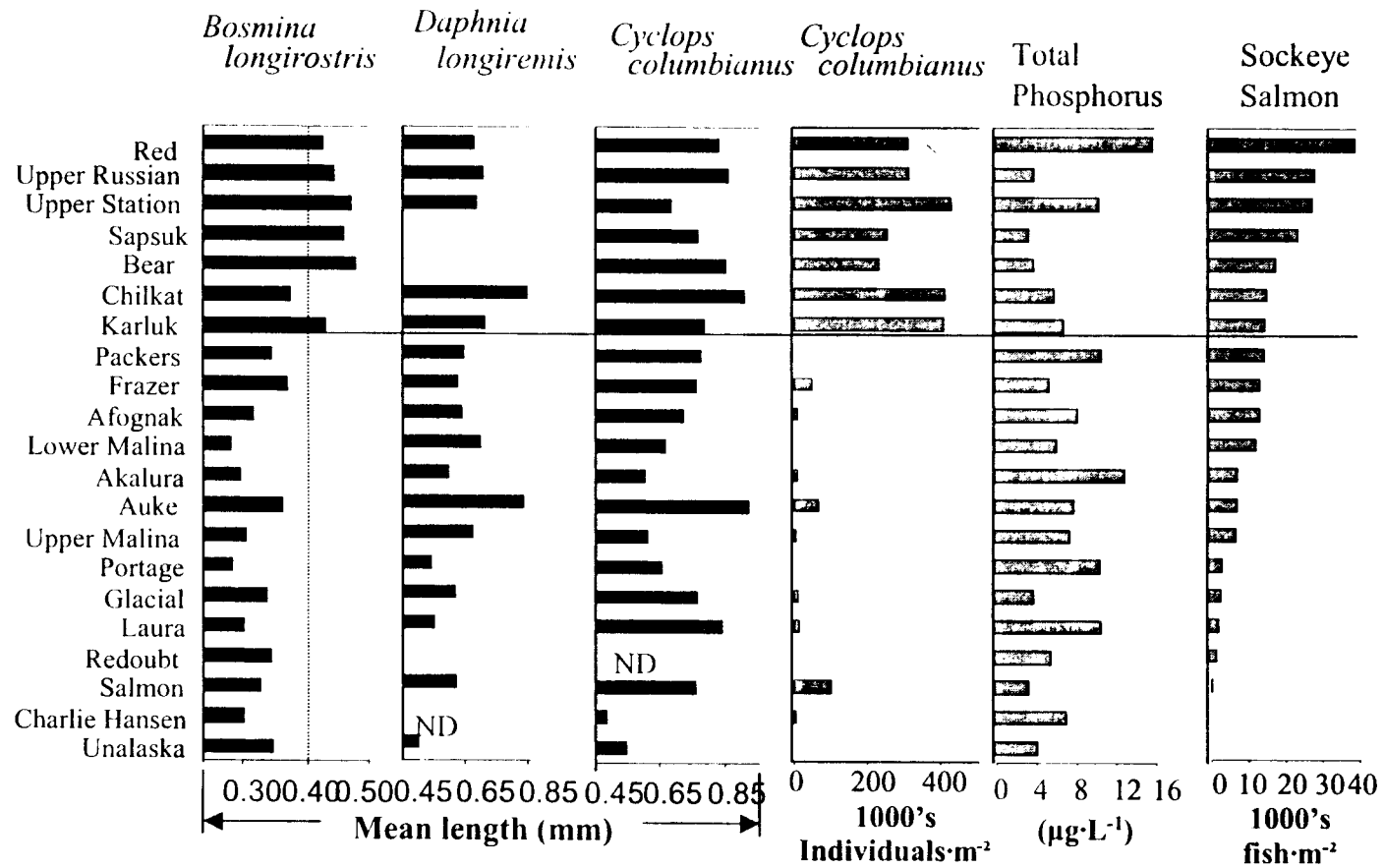
The general patterns in the mean length (mm) of the dominant zooplankton taxa in the study lakes are illustrated in Figure 2-5. The mean length of *Bosmina longirostris* is highly correlated to the density of *Cyclops* in the lakes. Lakes in which the mean length of *Bosmina* populations is greater than 0.40 mm all occur where there is a high density of *Cyclops*.



**Figure 2-5** Abundance of zooplankton taxa in the 23 Alaskan sockeye salmon lakes used in ordinations. Lakes are arranged in order of increasing sockeye spawner density (1000's fish · m<sup>-2</sup>), with lakes near the bottom of the diagram having the fewest fish, and lakes near the top of the diagram having the highest sockeye densities. Low densities of zooplankton occurring in a lake are indicated by the symbol (\*).

**Table 2-4** Relationships between zooplankton body sizes, potential predators, resource availability, and lake size.

<b>Dependent Variable</b>	<b>Independent Variable</b>	<b>n</b>	<b>r</b>	<b>p</b>
<b>Potential Predators</b>				
<i>Bosmina</i> length	Sockeye Density	21	0.68	<0.001
<i>Daphnia</i> length	Sockeye Density	17	0.53	0.03
<i>Cyclops</i> length	Sockeye Density	20	0.52	0.02
<i>Bosmina</i> length	Cyclops Density	21	0.83	<0.0001
<i>Daphnia</i> length	Cyclops Density	17	0.57	0.02
<b>Food Resources</b>				
<i>Bosmina</i> length	Chlorophyll <i>a</i>	21	0.33	ns
<i>Daphnia</i> length	Chlorophyll <i>a</i>	17	0.29	ns
<i>Cyclops</i> length	Chlorophyll <i>a</i>	20	0.12	ns
<i>Bosmina</i> length	Total Phosphorus	21	0.18	ns
<i>Daphnia</i> length	Total Phosphorus	17	0.088	ns
<i>Cyclops</i> length	Total Phosphorus	20	0.066	ns
<i>Bosmina</i> length	Total Kjeldahl Nitrogen	21	0.35	ns
<i>Daphnia</i> length	Total Kjeldahl Nitrogen	17	0.064	ns
<i>Cyclops</i> length	Total Kjeldahl Nitrogen	20	0.053	ns
<b>Lake size</b>				
<i>Bosmina</i> length	Volume	21	0.67	<0.001
<i>Daphnia</i> length	Volume	17	0.36	ns
<i>Cyclops</i> length	Volume	20	0.48	0.03
<i>Bosmina</i> length	Maximum Depth	21	0.80	<0.0001
<i>Daphnia</i> length	Maximum Depth	17	0.47	(0.056)
<i>Cyclops</i> length	Maximum Depth	20	0.56	0.01
<i>Bosmina</i> length	Surface Area	21	0.57	<0.01
<i>Daphnia</i> length	Surface Area	17	0.19	ns
<i>Cyclops</i> length	Surface Area	20	0.31	ns



**Figure 2 -6** Mean length of dominant zooplankton taxa in the 23 Alaskan sockeye salmon lakes compared to the abundance of *Cyclops columbianus*, total phosphorus, and sockeye salmon (*Oncorhynchus nerka*) abundance.

## Discussion

Sockeye salmon appeared to play an important role in determining the abundance and size structure of zooplankton populations in our study lakes. Sockeye spawner abundance was highly correlated with the abundance of the dominant herbivorous zooplankton species in the lakes (Figure 2-4; Table 2-3). In addition, *Cyclops columbianus* populations were extremely abundant in lakes with high sockeye spawner densities, and at much lower abundances at low and intermediate salmon levels (Figure 2-5). The size of the main herbivorous cladoceran, *Bosmina longirostris* also appeared to be controlled by the density of *Cyclops* (Figure 2-6). Sockeye salmon can potentially impact zooplankton populations both through changes in the degree of predation pressure from juvenile sockeye and through fluctuations in the supply of nutrients to the lake due to decomposition of adult carcasses following spawning (Kyle 1996; Koenings and Kyle 1997; Kline et al. 1997).

The role of sockeye in influencing zooplankton has been recognized for several decades. Juday et al. (1932) noted that "The rich crop of plankton produced by these lakes is due, in part at least, to fertilizing substances contributed to their waters by the decomposing carcasses of the salmon". Goodlad (1974) speculated that:

The highly selective feeding of sockeye should be reflected in the composition of the zooplankton. Most utilized species should be less abundant relative to less exploited ones, and differences in zooplankton size and species composition should be evident between lakes, as well as between years of high and low sockeye densities within one lake.

In the present study, the relative importance of salmon predation and nutrient loading in regulating zooplankton populations is difficult to assess based on the available data. Predation from sockeye did not appear to be a strong controlling factor. If predation was an important factor in controlling zooplankton, it might be expected that smaller sized zooplankton should occur in lakes with high salmon levels due to selective grazing on larger organisms, and preferred prey items should be reduced in abundance. In several studies, comparisons of gut contents of juvenile sockeye to zooplankton in Alaskan lakes have indicated that sockeye preferentially select individual *Bosmina* larger than 0.40 mm. In the lake set, however, zooplankton increased in abundance with increased salmon densities, and the largest individuals of *Bosmina* (greater than 0.40 mm) actually occurred in lakes with the highest levels of juvenile sockeye.

The lack of evidence for strong top-down influences on zooplankton might suggest that salmon-derived nutrients are much more important than salmon predation in regulating zooplankton communities in the study lakes. However, we observed little direct evidence of the impact of nutrient availability on the dominant zooplankton taxa. Within the data set that we analyzed, values for nutrients and chlorophyll were not unusually high in lakes with high levels of sockeye salmon, and variation in lake water nutrient concentrations did not appear to be strongly related to salmon abundance. Despite this, variation in nutrients was associated with the greatest amount of variance among the measured environmental variables across the lake set, based on Principal Components Analysis of the data (Figure 2-3). In the analyses of the zooplankton abundance and size structure, however, nutrients were not significantly related to

zooplankton density, even though salmon variability was shown to be an important factor (Figure 2-4; Table 2-3). Changes in food-based resources had no significant impacts on mean zooplankton sizes, as nutrients and chlorophyll *a* were only weakly correlated with the mean zooplankton size of the dominant taxa present in the lakes (Table 2-4).

In several of the study lakes, sockeye salmon have been shown to contribute substantially to overall nutrient loading within the lakes (Kyle 1996; Kyle et al 1997; Schmidt et al 1999). For example, in Karluk Lake, nutrients from salmon carcasses during some years were estimated to contribute to over half of the annual nutrient loading in the lake (Schmidt et al 1999). There is a considerable amount of information from lake fertilization and nutrient addition experiments that suggest that zooplankton in sockeye nursery lakes respond rapidly to nutrient enrichment. In Leisure Lake and Frazer Lake, Alaska, for example, zooplankton density and size increased following nutrient additions (Koenings and Kyle 1997). Similar responses have been observed in many lakes in Alaska, including several lakes used in the present study (Kyle 1996; Koenings et al. 1997; Schrof et al 2000). An increase in overall zooplankton abundance has been observed following fertilization in British Columbian sockeye salmon lakes as well (Rankin 1980; Stockner and MacIsaac 1996).

One possible explanation for this apparent discrepancy is that the measured nutrient and chlorophyll data did not reflect nutrient availability or primary productivity in the lakes. The water chemistry values used in the analyses were from epilimnetic values, taken at 1 m depth. In general, the increase in salmon densities in the study lakes was also associated with an increase in lake depth, with larger, deeper lakes generally

having more salmon. Many of the lakes thermally stratify, and thus the 1 m depth becomes depleted in nutrients, and does not represent the zone of maximum productivity. Because the zooplankton data were collected from either integrated tows of the entire water column or the upper 50 m, differences in vertical distribution of nutrients and algal production may have resulted in an underestimation of available nutrients in the deeper lakes. Preliminary analyses of the hypolimnetic nutrient data from the Kodiak Island lakes, however showed that in most lakes, there were not noticeable differences in nutrient and chlorophyll data between surface and mean hypolimnetic values. Analyses of the nutrient data from the entire water column may provide a better relationship between water column nutrients and salmon abundance, and better reflect the food resources available to zooplankton populations in the lakes. Alternatively, measures of nutrient concentration and phytoplankton standing stock (chlorophyll *a*) may not accurately reflect the rates of primary productivity in these systems. Low nutrient levels could be due to inherently low nutrient supply, or to high utilization.

Although the data used in this study did not include information on the vertical distribution of zooplankton in the lakes, previous studies on diel vertical migrations in Alaskan sockeye lakes have shown that zooplankton are generally not distributed near the surface, but are concentrated at depths lower in the water column. Yanusz (1991), however, reported that for Frazer Lake zooplankton were mostly distributed at depths > 10 m.

Across the gradient of increasing sockeye salmon abundance in the lakes, a dramatic increase in the density of *Cyclops* populations was observed. This substantial

shift seems at odds with the traditional view of invertebrate predators, which are typically eliminated at high fish levels (Brooks and Dodson 1965). There are several possible explanations that, together or independently, could account for the large increase in *Cyclops* abundance in lakes with high levels of sockeye salmon abundance. First, nutrient loading from salmon carcasses most likely caused the increase in *Cyclops* abundance. The nauplii of *Cyclops* are herbivorous. Assuming there was an increase in overall lake productivity with increases in sockeye abundance, *Cyclops* nauplii may have increased production due to increases in available food. Because invertebrates can respond much faster to nutrient enrichment than juvenile salmon, nutrient loading may have favored the development of high *Cyclops* populations, with *Cyclops* abundance able to increase at a greater rate than juvenile sockeye, so the effective grazing pressure is lower in lakes with high *Cyclops* (Neill and Peacock, 1982). In addition to increased growth in juvenile cyclopoid copepods, adult *Cyclops* are omnivorous, and tend to prey upon zooplankton (Kerfoot 1977a; 1977b; Post et al. 1995). Increases in herbivorous zooplankton abundance (i.e. *Bosmina*) due to increased productivity would result in increased food availability for adult *Cyclops*.

A second possible reason that may have contributed to high *Cyclops* abundance in lakes with high sockeye levels is Cyclopoid copepods are highly motile and evasive, and can avoid being captured by juvenile salmon (Kyle et al. 1988). In analyses of stomach contents and net-tows from the surrounding water column from several of the lakes in this study, *Cyclops* was relatively more abundant in the water column than in sockeye

stomachs (Kyle et al. 1988; personal communication, J. Edmundson, ADF&G, Soldotna, Alaska).

Another possible explanation for an increase in *Cyclops* is that in general, lakes with higher salmon levels were also deeper. *Cyclops* may be able to avoid predation due to increased availability of refugia. Deep lakes offer more opportunities for vertical exclusion (Kitchell and Kitchell 1980). This explanation was ruled out, however, as several relatively deep lakes did not have high *Cyclops* populations. Frazer Lake on Kodiak Island for example, has a maximum depth of 59 m, and mean depth of 33 m, yet *Cyclops* populations have been at low concentrations since introduction of sockeye salmon to the lake (Kyle, 1988; Chapter 3).

Finally, changes in water chemistry or other factors may have been responsible for the success of *Cyclops* in the high sockeye lakes. In the RDA of zooplankton abundance, alkalinity was also shown to be significant in influencing *Cyclops* densities (Figure 2-4). Although alkalinity (and pH, which was highly correlated with alkalinity) did not change very much over the gradient in the study lakes, alkalinity or pH did appear to impact *Cyclops* densities to some degree. Tessier and Horwitz (1990) observed a shift from large-bodied zooplankton species to small rotifers, with decreasing water hardness, relating this to calcium shortages. In our lakes, Ca concentrations were highly correlated to lake productivity, which was negatively correlated with changes in water hardness in analyses on the limnological gradients (PCA, Figure 2-3). Hessen et al. (1995) also found a similar relationship with Ca, water hardness, and zooplankton communities in a set of Norwegian lakes. Heavily calcified *Cyclops* may be less successful in lakes with

high Ca limitation. Changes in water chemistry, however, do not adequately explain the dramatic shift in *Cyclops* abundance.

The increase in *Cyclops* abundance did influence other zooplankton species, and thus indirectly affected sockeye production in the lakes. Because *Cyclops* predation was higher in high sockeye lakes, mean sizes of *Bosmina* increased to avoid predation by *Cyclops* (Figure 2-6). The increased size of *Bosmina* may make *Bosmina* more susceptible to predation by juvenile sockeye. Analyses of stomach contents did indicate that sockeye preferentially selected larger *Bosmina* as well as cyclopoid copepods (Kyle et al. 1988). The increase in sockeye spawners to a lake, then, may lead to increased nutrient availability, and large increases in *Cyclops*, which in turn alters *Bosmina* populations, and increases sockeye production in the lake. Invertebrate predators, therefore, may have an important role in moderating the “positive feedback loop” between carcass-subsidized nutrients and increased salmon production.

In conclusion, variations in adult sockeye salmon abundance appear to have a strong influence on the abundance and body size of zooplankton populations in the nursery lakes. I examined the importance of sockeye and other limnological and environmental factors in structuring zooplankton abundance and sizes in a set of 23 sockeye nursery lakes across Alaska. Salmon abundance, in addition to alkalinity and nutrients, could explain the main directions in zooplankton variation, with salmon abundance accounting for the primary gradient in zooplankton density. One of the most interesting and unexpected results from this research was the occurrence of a dramatic shift in *Cyclops columbianus* abundance in sockeye salmon lakes, with much higher

numbers of *Cyclops* being present in lakes with higher levels of sockeye production. The high density of *Cyclops* in these lakes also resulted in larger-sized populations of *Bosmina* being present in the same lakes, as *Bosmina* increased their body size to avoid being captured by predatory *Cyclops*. The increased abundance and size of zooplankton in these lakes probably contributes to enhanced salmon production, and the threshold between lakes with high *Cyclops* and low *Cyclops* densities may represent a delimitation between density-dependent and density-independent systems. If nutrient loading from adult sockeye salmon carcasses is the major factor in driving this increase in *Cyclops* production, *Cyclops* abundance and their interaction with other organisms may regulate whether a positive feedback occurs between carcass-derived nutrients and increased salmon production.

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**Chapter 3: Assessing the long-term impacts of sockeye salmon (*Oncorhynchus nerka*) abundance on *Bosmina longirostris* populations in two lakes from Kodiak Island, Alaska<sup>1</sup>**

**Introduction:**

Predation has long been known to be a major factor in controlling zooplankton communities (Brooks and Dodson 1965; Kerfoot and Sih 1987; Northcote, 1988). Increased predation from size selective planktivores, such as fish, generally results in the reduction of large zooplankton species. Subsequently, smaller, less detectable species become more abundant. In addition to the removal of larger species, the mean size of individual zooplankton species remaining in a lake has been shown to decrease at high levels of fish predation (Mills and Forney 1988; Northcote 1988; Gliwicz and Pijanowska 1989).

Invertebrate predators can also be important in controlling zooplankton communities (Kerfoot, 1977; Neill and Peacock 1980; Soranno et al. 1993). Invertebrate predators are generally size-selective tactile predators, and remove smaller individuals from the zooplankton community. When invertebrate predators are dominant, there is a shift in zooplankton size-structure to favour larger zooplankton (Dodson, 1974; Gliwicz and Pijanowska 1989). When both vertebrate and invertebrate predators are present, many zooplankton species develop large defensive spines or other morphological structures, to protect against invertebrate predators, but still retain a small body size to

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<sup>1</sup> Sweetman, J. and Finney, B.

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remain inconspicuous to large visually orientated predators (Dodson 1974; Kerfoot 1977; Gliwicz and Pijanowska 1989).

The availability of food resources is also an important factor in structuring zooplankton communities (Neill and Peacock 1980; Vanni 1987; Gliwicz 1990; Urabe 1991). Generally, increased nutrient loading leads to increased primary production, which in turn leads to increased production of zooplankton (Hyatt and Stockner 1985; Kyle et al. 1997). Changes in food availability and quality can lead to a shift in the competitive advantage of zooplankton, and a shift in species dominance, size and abundance (DeMott 1989; Carpenter and Kitchell 1993).

In many freshwater lakes in Alaska and throughout the North Pacific, large populations of anadromous sockeye salmon (*Oncorhynchus nerka*) occur (Burgner 1991). Variability in the annual number of sockeye salmon returning to lakes to spawn can subsequently influence the number of planktivorous juvenile sockeye, and greatly contribute to nutrient loading, both of which can have significant impacts on zooplankton populations inhabiting the lake (Koenings and Kyle 1997; Kline et al 1997: Chapter 2). Upon hatching, juvenile sockeye salmon typically remain in a lake system from one to three years, during which time they are typically the predominant planktivorous fish in the limnetic region (Eggers 1977; Burgner 1991; Kyle 1996). Juvenile sockeye preferentially prey on cladoceran zooplankton while in the lake ecosystem (Kyle et al. 1988; Burgner 1991; Kyle et al. 1996). In addition to altering predation regimes due to changes in juvenile sockeye abundance, spawning salmon also transport significant amounts of marine-derived nutrients into the freshwater environment through the

decomposition of their carcasses (Mathiesen 1988; Kline et al. 1997). Most lakes that support sockeye populations are oligotrophic, and salmon-derived nutrients may contribute substantially to nutrient loading (Burgner 1991; Kline et al. 1997; Kyle et al. 1997). Thus, variability in sockeye salmon populations can have significant impacts on zooplankton populations through both top-down and bottom-up processes (Chapter 2).

As pelagic zooplankton populations are the primary food source of juvenile sockeye, understanding how zooplankton respond to salmon is highly relevant to the proper management of sockeye salmon nursery lakes. The annual abundance of sockeye salmon is highly variable, and populations have fluctuated considerably in these lakes in the past (Finney et al. 2000). Several researchers have examined the response of zooplankton in lakes where sockeye have been stocked or introduced (Kyle 1996; Koenings and Kyle 1990; Reischauer 1997), but few studies have examined responses of zooplankton to natural fluctuations in salmon abundance. Chapter 2 compared zooplankton communities among lakes with different levels of salmon abundance. Here, I take another approach, and examine long term records of zooplankton abundance and morphology in response to fluctuations in salmon within two of these lakes.

Historical records of zooplankton communities in sockeye lakes are relatively short, and long-term responses of lakes to changes in salmon abundance may not be detected in the historical record (Kratz et al. 1987; Leavitt et al. 1993; Ramcharan 1995). Paleolimnological studies have the potential to extend limited available historical records (Frey 1960; Smol 1992). Lake sediments accumulate over time, and analyses of biological and geochemical fossils preserved in the sediments can provide information on

changes about past food-web dynamics and nutrient loading (Leavitt et al. 1993; Bos 2000). The remains of cladoceran zooplankton have shown to be well preserved in lake sediments (Frey 1960). Because cladoceran zooplankton occupy an intermediate food-web position, cladoceran-based paleolimnological studies have proven useful both in reconstructing past changes in fish and invertebrate predators and in examining shifts in lake trophic status. (Kerfoot 1981; Leavitt et al. 1989; Jeppesen et al. 2001).

We examined the response of populations of *Bosmina longirostris* to fluctuations in sockeye salmon abundance in two lakes on Kodiak Island, Alaska. The lakes were extremely similar in morphological, physical and chemical characteristics, but differed in that one lake (Karluk Lake) had a large natural run of sockeye salmon, while the other lake (Frazer Lake) had no natural sockeye salmon run, due to a waterfall downstream from the lake that prevented migration of sockeye into the lake. Frazer Lake was stocked with sockeye salmon in the 1950s, and in the 1960s and 1970s, two fishpasses were installed, allowing a population of sockeye salmon to become established in the lake. Significant natural fluctuations have occurred in Karluk Lake sockeye populations (Finney et al. 2000).

The response of zooplankton to salmon variability was assessed by examining changes in *Bosmina* morphology and abundance. Changes in *Bosmina* morphology can be used to infer past changes in predation by vertebrate (*i.e.* salmon) and invertebrate predators. Longer morphological features (antennules, mucrones) reduce predation by invertebrate predators (Kerfoot 1974; 1977; 1981; Post et al. 1995). Predation from planktivorous fish has been shown to reduce the average body-size of *Bosmina* (Kerfoot

1981; Salo et al. 1989; Leavitt et al. 1994; Ślusarczyk 1997). Historical information on sockeye salmon escapement, based on weir-counts, and records of sedimentary  $\delta^{15}\text{N}$  were used as records of salmon escapement.  $\delta^{15}\text{N}$  has been shown to be an excellent indicator of past inputs of salmon-derived nutrients, and has been used as a proxy for past salmon abundance (Finney 1998; Finney et al. 2000).

### Study Sites

The two study lakes were selected because of their similarities in geographical, morphological, physical and chemical characteristics (Table 3-1). Karluk Lake ( $57^{\circ}24'\text{N}$ ,  $154^{\circ}05'\text{W}$ ) and Frazer Lake ( $57^{\circ}15'\text{N}$ ,  $154^{\circ}10'\text{W}$ ) are large, oligotrophic lakes located side by side on the southwestern end of Kodiak Island Alaska, approximately 10 km apart (Figure 3-1). The lakes are primarily located within the Kodiak National Wildlife Refuge. Karluk Lake, which is slightly larger than Frazer Lake, has a surface area of  $39.5 \text{ km}^2$ , a mean depth of 48.6 m, and a volume of  $1920 \times 10^6 \text{ m}^3$  (Juday et al. 1932; Koenings and Burkett 1987). Frazer Lake has a surface area of  $16.6 \text{ km}^2$ , a mean depth of 33.2 m and a volume of  $551.1 \times 10^6 \text{ m}^3$  (Kyle et al. 1988).

The region is strongly influenced by the prevailing marine climate. Karluk Lake has a mean annual precipitation of 172 cm, with a watershed area of  $282 \text{ km}^2$ , resulting in an estimated water residence time of 4.8 years (Koenings and Burkett 1987). Frazer Lake has a mean annual precipitation of 185 cm, with a watershed area of  $181 \text{ km}^2$ , resulting in an estimated water residence time of approximately 2.1 years (Kyle et al. 1988). Vegetation in the area consists of dwarf scrub communities at higher elevations and on windswept areas, and low scrub communities in more protected areas (Gallant et al. 1995).

**Table 3-1** Selected physical and limnological characteristics of Karluk and Frazer Lakes (Kodiak Island, Alaska). Water chemistry data shown are based on mean seasonal (May-October) values from epilimnetic (1 m) samples; zooplankton densities are based on seasonal means of vertical net tows. (Source: Alaska Department of Fish and Game)

	<b>Karluk Lake</b>	<b>Frazer Lake</b>
<b>Latitude (°N)</b>	57°24'	57°15'
<b>Longitude (°W)</b>	154°05'	154°10'
<b>Elevation (m)</b>	106	108
<b>Surface Area (km<sup>2</sup>)</b>	39.5	16.6
<b>Mean Depth (m)</b>	48.6	33.2
<b>Maximum Depth (m)</b>	126	59
<b>Volume (x10<sup>6</sup> m<sup>3</sup>)</b>	1920	551.1
<b>Watershed Area (km<sup>2</sup>)</b>	282	181
<b>Annual Precipitation (cm)</b>	172	185
<b>Water Residence Time (yrs)</b>	4.8	2.1
<b>Euphotic Zone Depth (m)</b>	23	16.9
<b>Total Phosphorus (µg·l<sup>-3</sup>) (May-October mean)</b>	7.8	5.8
<b>Total Nitrogen (µg·l<sup>-3</sup>) (May-October mean)</b>	121.3	135.5
<b>Chlorophyll a (µg·l<sup>-3</sup>) (May-October mean)</b>	2.5	0.86
<b>Mean <i>Bosmina</i> density (individuals·m<sup>-2</sup>)</b>	53.023	115.724
<b>Mean <i>Cyclops</i> density (individuals·m<sup>-2</sup>)</b>	478.751	79.936
<b>Mean Total Zooplankton density (individuals·m<sup>-2</sup>)</b>	627.047	207.225
<b>Mean sockeye salmon escapement</b>	220,098	646,330
<b>Mean Total Length of <i>Bosmina</i> (mm)</b>	0.43	0.37

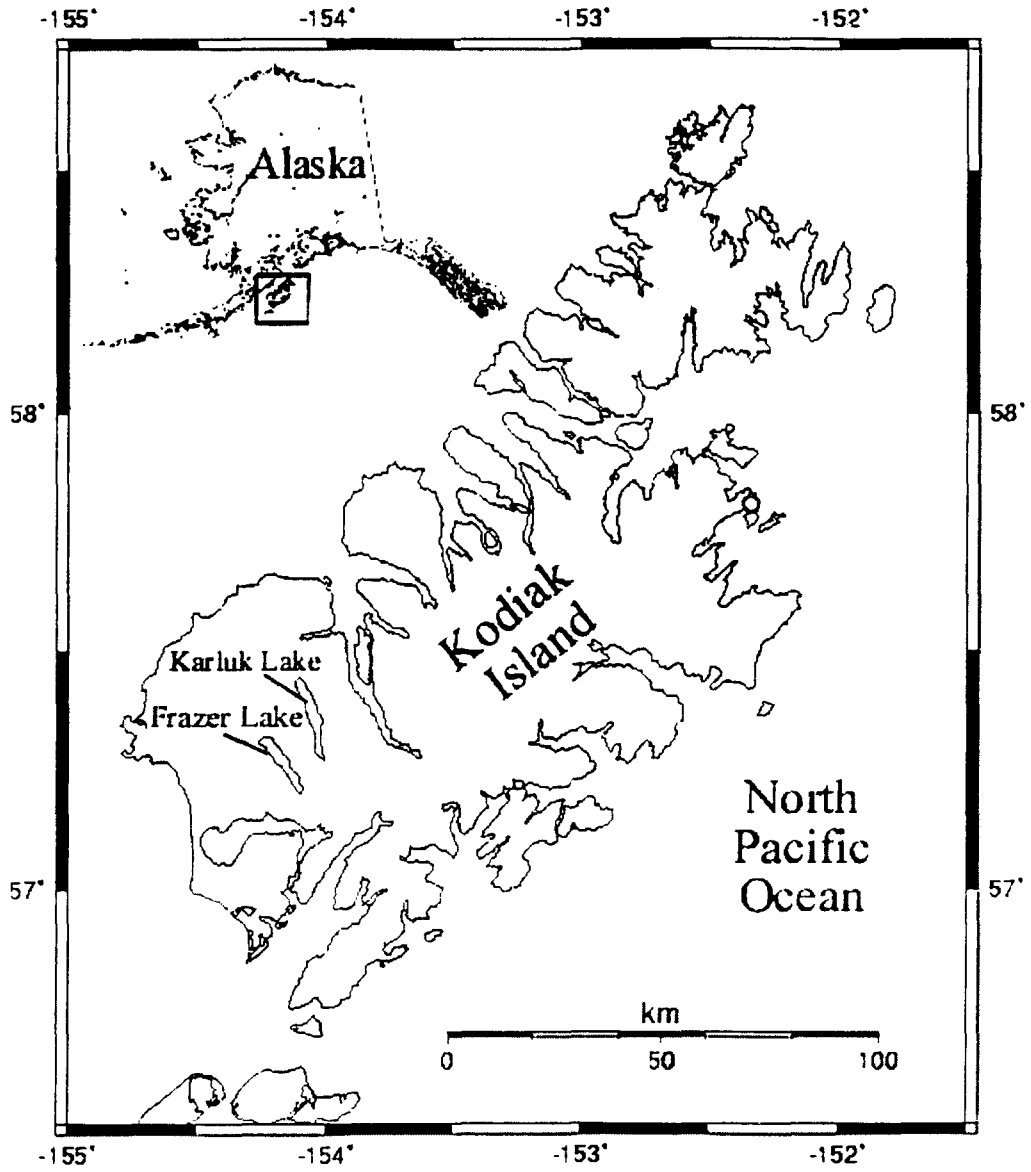


Figure 3-1 Location of Frazer and Karluk Lakes (Kodiak Island, Alaska)

Karluk Lake has a long history of fisheries and limnological research (Bean 1891; Juday et al. 1932; Barnaby 1944; Gard and Bottorff in press). Historically, Karluk Lake was one of the most productive sockeye salmon lakes in the North Pacific (Koenings and Burkett 1987; Burgner 1991; Schmidt et al. 1998). Records indicate the number of returning sockeye was in excess of a million fish at the turn of the century, and dramatically decreased in the 20<sup>th</sup> century. The number of salmon returning to the lake has increased in recent times, but is still below historically high levels.

Historically, Frazer Lake had no salmon inhabiting the lake because of a 10 m high waterfall approximately 0.8 km downstream from the lake outlet (Burger et al. 2000). Sockeye salmon fry were introduced into the lake in 1951, and stocking continued until 1971. In 1962 and 1979, two fishpasses were installed, allowing the returning adult sockeye salmon access to Frazer Lake (Blackett 1979; Kyle et al. 1988; Burger et al. 2000). Since then, the sockeye salmon run has developed into a fairly significant run, with sockeye escapements peaking in 1985 at 486,000 fish, and with an annual average escapement in the 1990s around 200,000 fish (Schrof et al. 2000; Burger et al. 2000).

The modern zooplankton communities of the two lakes are generally similar, with two dominant cladoceran species occurring, *Bosmina longirostris* and *Daphnia longiremis*, and the primary copepod species being *Cyclops columbianus* and *Diaptomus pribilofensis* (Kyle et al. 1988; Koenings and Burkett 1987; Schmidt et al. 1998; Schrof et al. 2000). Sockeye salmon (*Oncorhynchus nerka*) are usually the dominant fish in the pelagic zone of the lakes, but high numbers of threespine sticklebacks (*Gasterosteus aculeatus*) can also be present. Other fish species in the lakes include rainbow or

steelhead trout (*Oncorhynchus mykiss*), Dolly Varden (*Salvelinus malma*), and coastrange sculpin (*Cottus aleuticus*). Other species of salmon, including pink (*Oncorhynchus gorbuschka*), chum (*Oncorhynchus keta*), and coho (*Oncorhynchus kisutch*) were present in the river systems below the lakes (Burger et al. 2000; Burgner 1991; Koenings and Kyle 1997).

#### **Methods:**

Sediment cores were collected in August of 1995 (Karluk Lake) and July of 1998 (Frazer Lake) from the lakes using a hand operated gravity-type corer with a messenger-activated valve. A 43 cm long sediment core was recovered from the main basin of Karluk Lake from the deepest part of the basin. A 22.5 cm core was recovered from Frazer Lake from the deepest part of the northern basin in the lake. The Karluk Lake core was sampled continuously at 0.5-cm intervals, while the Frazer Lake core was sampled at continuous 0.25-cm intervals. Further details of sediment coring procedures are given in Finney (1998) and Finney et al (2000).

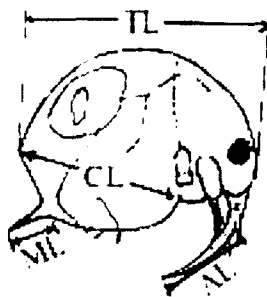
Sediments were analyzed for  $^{210}\text{Pb}$  and  $^{137}\text{Cs}$  content, and sediment age and mass accumulation rates ( $\text{g cm}^{-2} \text{ yr}^{-1}$ ) were calculated, based on assumptions of a constant sediment accumulation rate on a dry mass basis with minor adjustments based on tephra stratigraphy (Finney et al. 2000). Volcanic ash layers were identified by the presence of peaks in magnetic susceptibility and were verified by microscopic observation.

Correlations between lake cores were based on the stratigraphic position of ash layers, supplemented by microprobe analysis of glass shards. Two ash layers were found in the cores. The upper ash is the 1912 Katmai event, and the older ash is from a previously

unidentified event. The age of this older ash, extrapolated from the radioisotope data, is  $1710 \pm 10$  in both lakes (Finney et al. 2000). We made slight adjustments in accumulation rates in individual cores, where needed, by setting the age of this event to 1710. Errors of the extrapolated ages can be assessed in Karluk Lake, where a new longer core contains the 1912 and 1710 ashes, and has an AMS radiocarbon date on terrestrial macrofossils (1029 AD, calibrated) further downcore. Age estimates of the early 1800s  $\delta^{15}\text{N}$  minimum, based on the age model used here, and an age model based on interpolation between the 1912 Katmai ash and the calibrated radiocarbon date, are within 10 years. The character of the sediments in these cores is uniform throughout (except for the tephra layers), suggesting no major changes in depositional processes. The  $\delta^{15}\text{N}$  profiles from two replicated cores collected at the same sampling station in Karluk Lake show the excellent reproducibility in coring, isotope, and dating techniques (Finney et al. 2000). Additional information on the chronology of these cores is provided in Finney et al (2000).

Freeze-dried sediment subsamples equivalent to approximately  $1 \text{ cm}^3$  were analyzed for *Bosmina* microfossils at 1.0 cm intervals in both lakes. Preparations followed Frey (1986). The samples were deflocculated in 10% KOH at  $80^\circ\text{C}$  for 1 hour, rinsed with distilled water, and finally sieved through a  $37 \mu\text{m}$  mesh screen. Following sieving, sediment retained on the screen were transferred to a vial with distilled water.  $50 \mu\text{l}$  subsamples were mounted on glass slides in a 50% glycerin/water mixture (Kerfoot et al. 1999).

Cladoceran counts were made using a Zeiss Axioskop compound microscope, at magnifications of 100x and 400x. As the headshields and carapaces of cladocerans often disarticulate in the sediments, they were tabulated separately, and the total number of *Bosmina* was estimated following the formula of Frey (1986), using the most abundant exoskeletal component as an estimate of population size for each sample (Hann and Warner 1987). Microscope slides were systematically scanned until a minimum of 100 *Bosmina* remains had been enumerated. *Bosmina* abundances were converted into flux of individuals to the sediment ( $\text{numbers}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$ ) based on dry bulk sediment density data and calculated sedimentation rates, since concentration measures can be diluted from enhanced inorganic sedimentation, such as volcanic ash layers (Hann and Warner 1987; Kerfoot et al. 1999). *Bosmina* were identified to species based on De Melo and Hebert (1994) and Goulden and Frey (1963). The only species of *Bosmina* preserved throughout the sediment cores was *B. longirostris*. The length of *Bosmina* carapaces, tail spines, and antennules were measured using an eyepiece micrometer (Figure 3-2).



**Figure 3-2** Morphology of *Bosmina*, showing location of length measurements (TL, total length; CL, carapace length; ML, micro length; AL, antennule length). After Kerfoot (1975; 1995).

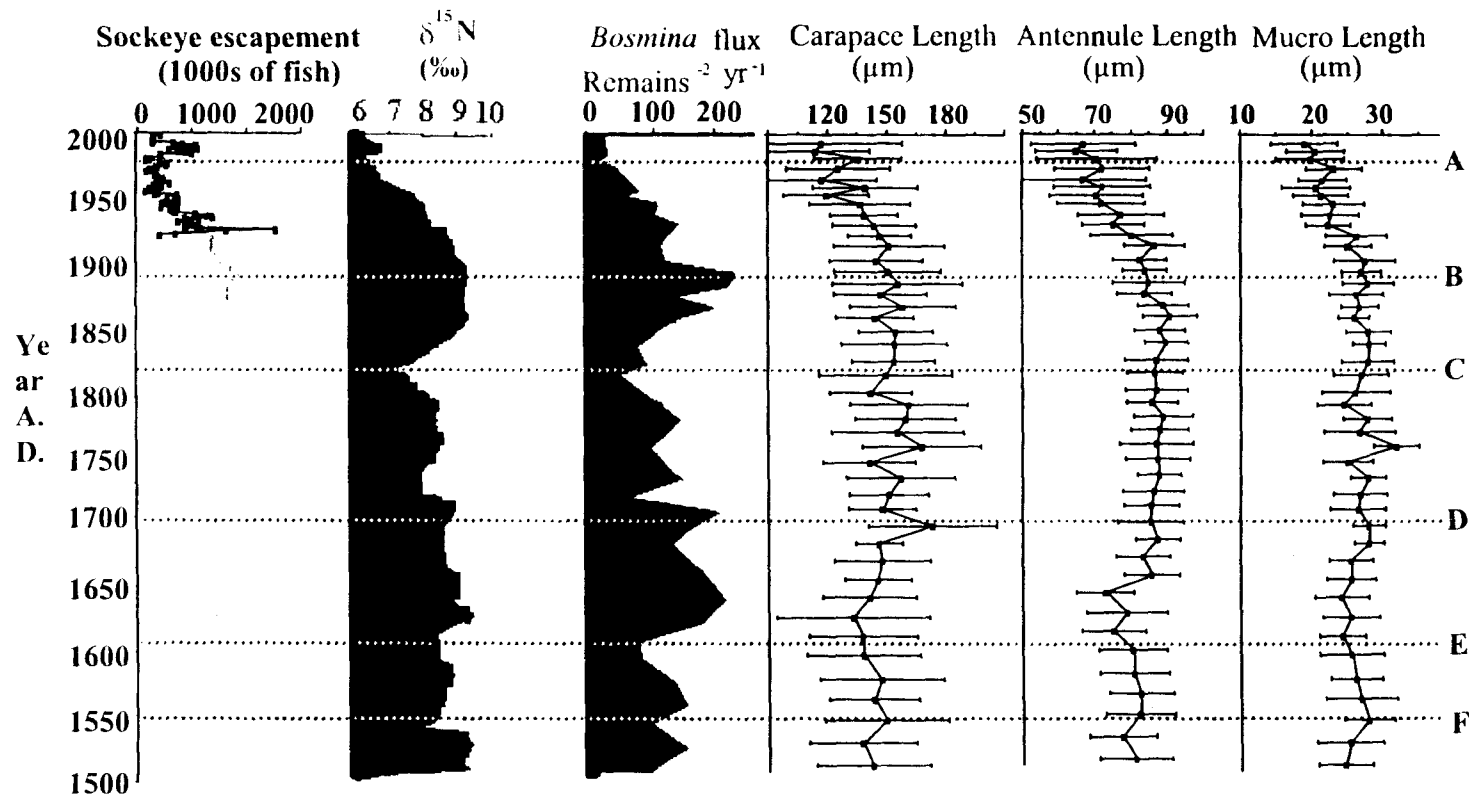
Nitrogen isotopes were measured on dried, homogenized, bulk samples using a Finnigan Delta Plus or Europa Scientific 20/20 mass spectrometer. Isotopic analyses are reported in standard  $\delta$  notation relative to atmospheric  $N_2$ . Analytical precision is better than  $\pm 0.2\%$ . Further details are described in Finney (1998).

## **Results:**

### **Karluk Lake**

The sedimentary  $\delta^{15}N$  record from Karluk Lake is highly correlated with adult sockeye salmon abundance ( $r^2 = 0.86$ ; Schmidt et al. 1998). Over the 20<sup>th</sup> century (the period for which historical sockeye salmon records are available), a decline in sockeye abundance in Karluk Lake, and then an increase since ~1975 are captured extremely well by the  $\delta^{15}N$  record, indicating that sedimentary  $\delta^{15}N$  is a good proxy for tracking past salmon abundance (Finney 1998; Finney et al. 2000). Sockeye abundance, and associated shifts in the amount of salmon derived nutrients, as indicated by the record of sedimentary  $\delta^{15}N$  (Figure 3-3), varied throughout the sediment core record..

The flux of *Bosmina* remains to the lake sediments closely tracks changes in sedimentary  $\delta^{15}N$ . ( $r = 0.75$ ,  $p < 0.0001$ ). *Bosmina* abundance was the highest during periods of high sockeye salmon abundance, as recorded by high sedimentary  $\delta^{15}N$  values, and decreased with decreasing sockeye salmon returns (Figure 3-3). In general, despite a large amount of variability in size at each depth in the sediment core, the mean lengths of *Bosmina* carapaces, antennules, and mucrones were all larger during periods of high salmon abundance, and decreased with decreasing salmon abundance (Figure 3-3).



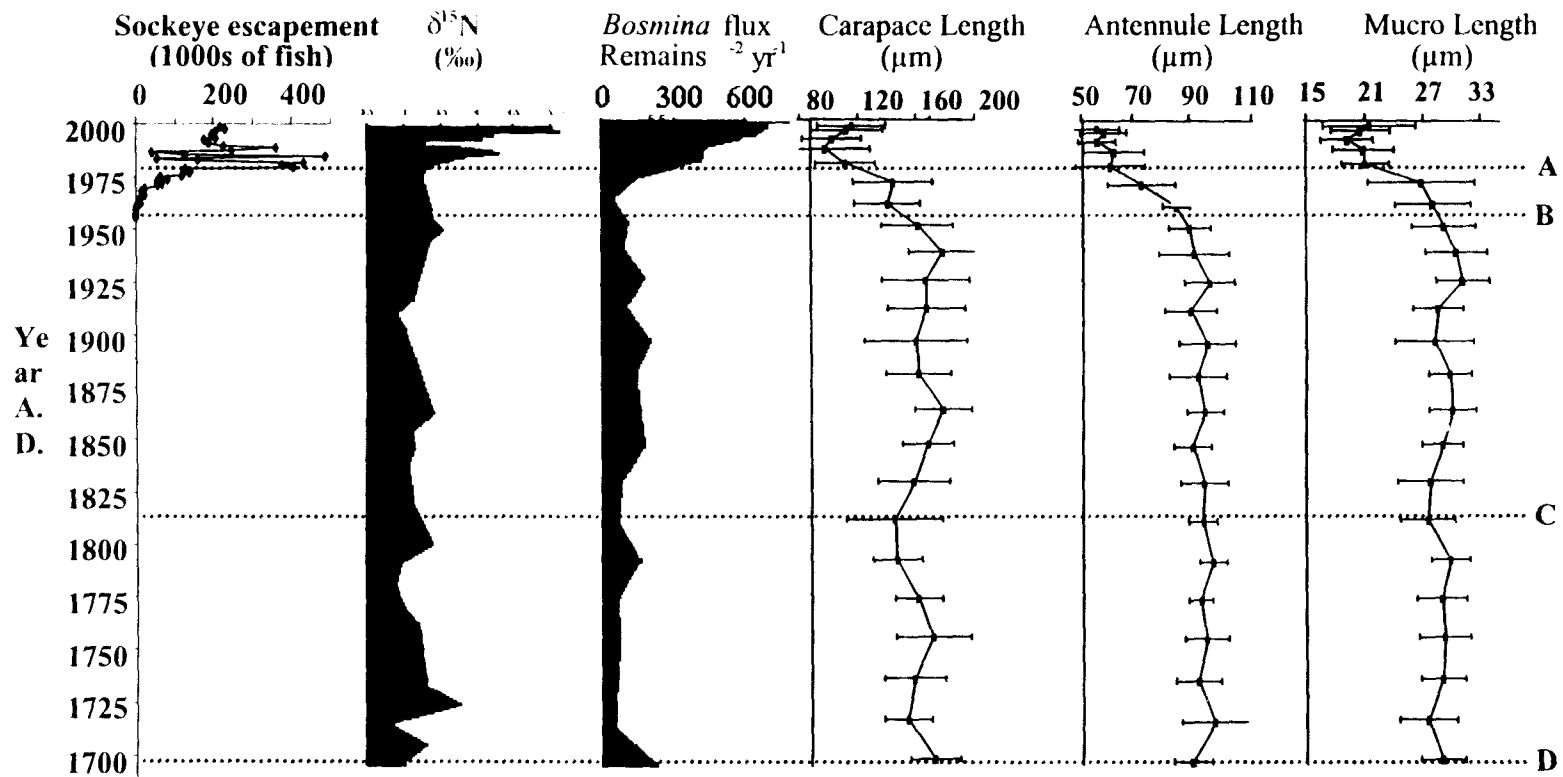
**Figure 3-3** Historical and paleolimnological record of variation in sockeye salmon and *Bosmina* populations in Karluk Lake over the past 500 years. The historical data for Karluk Lake sockeye salmon consist of escapement counts from a weir on the Karluk River beginning in 1921. For reference, inferred sockeye escapement based on the relationship between sedimentary  $\delta^{15}\text{N}$  and a 10-year running mean escapement is shown as a dotted line prior to the historical record. Sedimentary  $\delta^{15}\text{N}$  are also shown. Changes in the abundance of *Bosmina* over the period are indicated by flux of microfossil remains to the sediments. Changes in the morphology of *Bosmina* (carapaces, antennules, mucrones) are plotted with plus or minus 1 SD about the means.

## Frazer Lake

Sedimentary  $\delta^{15}\text{N}$  values for Frazer Lake increased following salmon introductions into the lake (Figure 3-4). Adult sockeye first returned to Frazer Lake in 1956, with escapements increasing through the 1960s and 1970s (Blackett, 1979). Following the installation of the second fishpass in 1979, escapements averaged over 250,000 potential spawners, peaking at 486,000 adults in 1985 (Kyle, 1988). The mean  $\delta^{15}\text{N}$  values following 1980 were 4.13‰, with a maximum value around 1996 of 5.17‰. During the period prior to sockeye introduction into Frazer Lake,  $\delta^{15}\text{N}$  values had a mean value of 3.28‰ (1690-1950), much lower than Karluk Lake (~ 8‰).

The abundance of *Bosmina longirostris* in Frazer Lake, as indicated by the flux of *Bosmina* remains to the lake sediments, also showed a dramatic increase following installation of the 1979 fishpass (Figure 3-4). Prior to sockeye introductions, the mean flux of *Bosmina* remains to the sediments averaged 146 individuals  $\text{cm}^{-2} \text{yr}^{-1}$  (1690-1950). Following salmon introduction (1950-present), *Bosmina* flux averaged 406 individuals  $\text{cm}^{-2} \text{yr}^{-1}$ . Following the installation of the 1979 fish pass (1979-present), the flux of *Bosmina* averaged 579 individuals  $\text{cm}^{-2} \text{yr}^{-1}$  (Figure 3-4).

Concurrent with the increase in *Bosmina* populations, the mean carapace, antennule, and mucro lengths all showed major decreases in size following the introduction of sockeye salmon into Frazer Lake (Figure 3-4). Mean carapace length averaged  $163.3 \pm 23 \mu\text{m}$  during the pre-sockeye salmon period, decreasing to  $123.2 \pm 24 \mu\text{m}$  following sockeye introduction, with a mean carapace length averaging  $108.0 \pm 24$



**Figure 3-4** Historical and paleolimnological record of variation in sockeye salmon and *Bosmina* populations in Frazer Lake over the past 300 years. The historical data for Frazer Lake sockeye salmon consist of escapement counts from a weir near the Frazer Lake Fish Pass. Sockeye were first introduced in the 1950s (B) and fish passes were installed in 1963 and 1979 (A). Sedimentary  $\delta^{15}\text{N}$  values are also shown. Changes in the abundance of *Bosmina* over the period are indicated by flux of microfossil remains to the sediments ( $\text{Remains cm}^{-2} \text{ yr}^{-1}$ ). Changes in the morphology of *Bosmina* (Carapaces, antennules, mucrones) are plotted with plus or minus 1 SD about the means.

$\mu\text{m}$  following installation of the two fishpasses. Similarly, mean antennule length averaged  $94.4 \pm 7.9 \mu\text{m}$  (presockeye),  $68.8 \pm \mu\text{m}$  following salmon introductions, and  $60.3 \pm 9.1 \mu\text{m}$  following fishpass installation; and mean micro length averaged  $29.1 \pm 2.7 \mu\text{m}$  (presockeye),  $23.4 \pm 3.6 \mu\text{m}$  after sockeye introduction, and  $20.7 \pm 3.2 \mu\text{m}$  following installation of the second fishpass (Figure 3-4).

## Discussion

### Karluk Lake

In Karluk Lake, *Bosmina* populations were most abundant during periods of high sockeye salmon abundance. This suggests that increased nutrient loading from sockeye salmon carcasses resulted in increased food resources available to *Bosmina*, allowing them to increase in abundance with increasing salmon spawners returning to the lake. Urabe (1991) found that growth rates of *Bosmina* increased with increasing food concentrations. Vanni (1987) suggested that population densities of zooplankton are affected much more by food availability than fish predation. The results from Karluk Lake are consistent with this viewpoint, suggesting bottom-up influences of salmon-derived nutrients were important in controlling *Bosmina* abundance.

In Karluk Lake, evidence of strong fish predation at high levels of sockeye abundance seem to be absent. Mean *Bosmina* carapace lengths were the largest at high sockeye levels, and the smallest at low sockeye densities. This observation is opposite to the accepted view that larger zooplankton are excluded when planktivorous fish are present (Brooks and Dodson 1965; Dodson 1974; Northcote 1988). In Chapter 2, sockeye salmon lakes with the highest salmon densities all were shown to have large

*Bosmina* present in the lakes, with mean lengths generally greater than 0.40 mm, which is the size at which planktivorous sockeye juveniles selectively prey on *Bosmina* (Kyle et al. 1988). This evidence would also suggest that nutrient loading was a much more important factor than salmon predation in Karluk Lake. Eggers (1977) calculated that "in moderately productive systems with high zooplankton abundance, strongly zooplanktivorous juvenile sockeye salmon (*Oncorhynchus nerka*) may crop less than 2% of the annual zooplankton production". This may be the case in Karluk Lake, where predation pressure was not an important factor in structuring zooplankton populations, and nutrient loading was a much greater factor.

The role of nutrients in controlling *Bosmina* populations is complicated by the additional affect of *Cyclops* predation in Karluk Lake, however. Evidence from antennule and mucro lengths of fossil *Bosmina* suggests that *Cyclops* abundance in the lake was highest at periods when sockeye were also abundant. Increases in carapace length may also be a response to cyclopoid predation. If sockeye predation pressure was not particularly important in Karluk Lake, larger sized *Bosmina* would not only be more efficient grazers (Brooks and Dodson 1965; Urabe 1981), but would be less susceptible to *Cyclops* predation. In Chapter 2, *Cyclops* abundance was shown to be high in lakes with the highest sockeye salmon densities (including Karluk Lake). There may be a threshold in *Cyclops* production that is triggered by increased nutrient loading from salmon (Neill and Peacock 1980). *Cyclops* are herbivorous in their early life stages, and become predatory during there adult phases (Kerfoot 1977; 1978). Increases in nutrient loading

may cause increased *Cyclops* abundance in Karluk Lake, but the paleoevidence suggests that *Cyclops* has always been high and above the threshold level identified in Chapter 2.

### **Frazer Lake**

Changes in the population of *Bosmina* in Frazer Lake following the introduction and establishment of sockeye salmon in the lake suggested that sockeye predation on *Bosmina* was an important factor in controlling *Bosmina* dynamics within Frazer Lake. Sockeye salmon introductions into the lake began in 1951, with eggplants and stocking of juvenile fry and continued through to 1971 (Blackett 1979). The abundance of sockeye salmon, however, was minimal until construction of fishpasses in 1962 and 1979. By the 1980s, mean annual sockeye returns had increase to over 256,000 adults, and peaked at nearly 486 000 fish in 1985 (Kyle et al. 1988; Burger 2000). The fossil record of *Bosmina* reflects the impact of increasing juvenile sockeye fry in the lake, showing a dramatic increase in *Bosmina* abundance with the increase in sockeye populations. Several researchers have observed increases in *Bosmina* density following an increase in planktivorous fish species (Brooks and Dodson 1965; Zaret and Kerfoot 1975; Stenson 1976; Ślusarczyk 1997). Typically, larger zooplankton species, such as *Daphnia*, are reduced or eliminated, and *Bosmina*, which is able to reduce its size, can avoid being captured by visually feeding fish.

Evidence for a reduction in size in *Bosmina* in Frazer Lake was observed in the sediment data, with decreases in the mean carapace length of the organisms, which also supports the idea that predation from sockeye salmon was high in Frazer Lake following salmon introductions (Stenson 1976; Kerfoot 1981; Salo et al. 1989). Ślusarczyk (1997)

reported a decrease in the mean size of *Bosmina* following exposure to high levels of fish predation. Kyle et al. (1988) examined stomach contents of sockeye salmon from Frazer Lake, and found that sockeye juveniles actively selected *Bosmina* larger than 0.40 mm in length. They noted that in 1985 and 1986, *Bosmina* mean lengths in the lake were less than 0.40 mm in the lake, and predicted that the mean length of *Bosmina* should have decreased over the years of increasing sockeye escapements. The paleolimnological data confirms this prediction.

During the period of increasing sockeye salmon in Frazer Lake, the primary invertebrate predator (*Cyclops columbianus*) decreased dramatically (Kyle et al. 1988). The decline in *Cyclops* density in Frazer Lake is also recorded in the fossil record of *Bosmina* morphology. Over the period following salmon introduction into the lake, both mean antennule and micro lengths decreased dramatically. The length of these features has been clearly linked to copepod predation (Kerfoot 1974; 1977; 1981; 1995; Wong 1981; Leavitt et al. 1994; Post et al. 1995). Kyle et al. (1988) reported that very few *Cyclops* were found in sampled sockeye stomachs, and suggested that sockeye predation was not the main reason for the decline in *Cyclops* densities in the lake. However, Kyle et al. sampled stomach contents only in 1985 and 1986, after *Cyclops* populations had already declined considerably. Also, Cyclopoid copepods remains may not have preserved as well as cladoceran body parts in the sockeye stomachs, leading to an underestimate of predation on *Cyclops* by juvenile sockeye.

## Conclusions

The response of *Bosmina* populations to changes in sockeye salmon abundance illustrates complex adaptations to changing predation regimes and resource availability. In Frazer Lake, paleolimnological records of *Bosmina* faithfully reconstructed known changes in juvenile sockeye salmon abundance, *Cyclops* abundance, and salmon-derived nutrient loading (Kyle et al. 1988). In Karluk Lake, *Bosmina* remains also reconstructed the interactions between *Cyclops*, juvenile sockeye and salmon-derived nutrients. Examining the importance of invertebrate predators relative to sockeye predation in salmon nursery lakes is important for successful management of these lakes. The trophic interactions between organisms in these lakes may have important affects on salmon productivity. Paleolimnological studies are useful, in that they can provide a long-term perspective on past trophic level changes, and help to evaluate the importance of sockeye salmon in controlling zooplankton in lakes.

## **Chapter 4 – Summary and Conclusions**

Sockeye salmon are the most valuable salmonid species in the North Pacific (Stockner and MacIsaac 1996). In addition to being important economically, sockeye are culturally and socially vital to many communities throughout the Pacific coastal region. Fluctuations in the abundance of sockeye salmon can have significant impacts on the people of the North Pacific. As juvenile sockeye salmon make extensive use of freshwater lakes as rearing environments, understanding how changes in sockeye salmon abundance can impact lake ecosystems is crucial for the effective management of these systems.

Understanding what factors influence pelagic zooplankton communities in sockeye salmon nursery lakes is of key importance for the effective management of these ecosystems. Zooplankton are the primary forage item of juvenile sockeye during their lake residence, and changes in the availability and size of zooplankton could dramatically alter sockeye production (Burgner 1991; Kyle et al. 1997). Because zooplankton hold an intermediate position in the trophic web, they can be influenced by both “top-down” processes, such as predation, and from “bottom-up” processes, such as shifts in nutrient availability (Carpenter and Kitchell 1993).

Shifts in sockeye salmon abundance have the potential to alter the abundance of juvenile sockeye in lakes, shifts in salmon also alter nutrient loading to these generally oligotrophic lakes through changes in the amount of post-spawning carcasses transported to the lake (Kline et al 1997). Changes in the level of nutrient loading can

indirectly affect other factors in the lakes, such as the number of invertebrate predators, which may also affect zooplankton communities.

Sockeye salmon populations are inherently variable. The annual abundance of sockeye fluctuates considerably from system to system, and over the past century, commercial harvesting, habitat alteration, hatcheries, and other anthropogenic factors in addition to natural factors such as climate change, have caused shifts in salmon abundance (Finney et al. 2000). Historical limnological and fisheries records are relatively short, and assessing the importance of salmon variability and its impacts on freshwater ecosystems is difficult without long-term records capturing this past variability. Paleolimnological records offer a potentially useful archive of past trophic interactions in these lakes.

For this thesis, I attempted to combine the use of contemporary limnological research with paleoecological analyses in order to examine the trophic relationships between populations of sockeye salmon and their zooplanktivorous prey. In Chapter 2, I examine the importance of sockeye and other limnological and environmental factors in structuring zooplankton abundance and sizes in a set of 23 sockeye nursery lakes across Alaska. One of the most interesting and unexpected results from this portion of the research was the occurrence of a dramatic shift in *Cyclops columbianus* abundance in sockeye salmon lakes, with much higher numbers of *Cyclops* being present in lakes with higher levels of sockeye production. The high density of *Cyclops* in these lakes also resulted in larger-sized populations of *Bosmina* being present, as *Bosmina* increased their body size to avoid being captured by predatory *Cyclops*. The increased abundance and

size of zooplankton in these lakes probably contributes to enhanced salmon production, and the threshold between lakes with high and low *Cyclops* densities may represent a deliniation between density-dependent and density-independent systems. If nutrient loading from adult sockeye salmon carcasses is the major factor in driving this increase in *Cyclops* production, as I suggest in Chapter 2, *Cyclops* abundance and their interactions with other organisms may regulate whether a positive feedback occurs between carcass-derived nutrients and increased salmon production.

In Chapter 3, I examine zooplankton-salmon trophic interaction on a longer time-scale, by examining changes in fossil *Bosmina* populations in relation to shifts in salmon abundance. I examine the response of *Bosmina* to shifts in salmon abundance in two lakes on Kodiak Island. One lake, Frazer Lake, had no sockeye salmon run prior to the 1950s, when sockeye eggs and fry were introduced into the lake. Fishpasses constructed in 1963 and 1979 enabled adult sockeye to return to Frazer Lake. The other lake, Karluk Lake had a large run of sockeye historically, but salmon abundance has fluctuated considerably over the last few centuries (Finney et al. 2000). In both lakes, *Bosmina* were most abundant when sockeye were at their highest levels of abundance in the lakes, suggesting carcasses derived nutrients contributed substantially to increasing *Bosmina* production. However, opposite trends in the size of *Bosmina* were observed in the two lakes. In Karluk Lake, *Bosmina* mean carapace lengths were largest at high sockeye levels, and mean mucro and antennule lengths were also large, suggesting strong predation by cyclopoid copepods, and less intense predation pressure from sockeye. These findings are consistent with the interlake comparisons of modern data in Chapter 2.

In Frazer Lake, however, *Bosmina* morphologies were small at the highest levels of sockeye salmon in the lake. Historical limnological records suggest that *Cyclops* populations in Frazer Lake were drastically reduced following sockeye introduction (Kyle et al 1988), and the small size of *Bosmina* probably represents a much stronger top-down effect from sockeye salmon predation.

### **Future Research**

Alaskan sockeye salmon lakes are primarily managed using spawner-escapement goals and stock-recruitment analysis. Recently, there has been an increasing attempt to incorporate limnological data into management strategies to allow more realistic escapement goals (Schmidt et al. 1998). Understanding trophic dynamics and how interactions between herbivorous zooplankton, invertebrate predators and juvenile sockeye effect the transfer of energy from carcass-derived nutrients is essential in understanding the role of salmon nutrients in sockeye nursery lake ecosystems. Multiple pathways in the foodweb of sockeye lakes may divert production from juvenile sockeye. A better understanding of the role of invertebrate predators, such as *Cyclops*, and potential competitor species (*i.e.* sticklebacks) in the lake foodweb could provide interesting insights into the importance of salmon-derived nutrients in lake ecosystems.

The large differences in the abundance of *Cyclops* between lakes with high levels of salmon abundance and lakes with low salmon abundance identified in Chapter 2 of my thesis is particularly interesting. If *Cyclops* can increase their abundance rapidly in response to increasing nutrient loading from salmon carcasses, and *Cyclops* populations increase more rapidly than juvenile sockeye can respond, a “bottleneck”

effect may occur (Neill and Peacock 1980). Further research into what factors control *Cyclops* production in Alaskan sockeye nursery lakes is needed. In lakes with high sockeye production, *Cyclops* was not only much more abundant, but the predation of *Cyclops* on *Bosmina* appears to have forced *Bosmina* to respond by increasing their mean body size to reduce predation pressure from *Cyclops* (Zaret and Kerfoot 1975; Stenson 1976; Gliwicz and Umana 1994).

The impact of increased *Cyclops* predation levels in lakes with high salmon levels could potentially have some important impacts on other trophic levels, both directly by increased predation levels from *Cyclops* and indirectly, through changes in life history characteristics and behavioral modifications of herbivorous cladoceran prey, such as *Bosmina* (Stenson 1976; Lane, 1979; O'Brien 1980; Kerfoot and Sih 1987; Carpenter and Kitchell 1993). Sockeye salmon are visual feeders, and require light in order to see their prey (Eggers 1977; Burgner 1991). *Cyclops*, on the other hand, are tactile predators, and can forage independent of visual light, and therefore feed at deeper levels than sockeye salmon (Kerfoot 1977a; 1977b; Gliwicz and Umana 1994; Post et al. 1995). At high *Cyclops* levels, *Bosmina*, the preferred prey item of sockeye in many Alaskan lakes (Kyle et al. 1988; Burner 1991) shift to larger body sizes. Typically when high fish predation occurs, zooplankton vertically migrate lower in the water column, to reduce their visibility to fish and reduce predation rates (Zaret and Kerfoot 1975; Lampert 1989). In lakes where tactile feeding predatory *Cyclops* and juvenile sockeye salmon populations are both extremely abundant, *Cyclops* probably migrate lower in the water column to reduce their chance of being eaten by juvenile sockeye. This would not only

allow *Cyclops* to maintain high numbers, but *Cyclops* may force *Bosmina* and other prey higher in the water column. The combination of increased size and vertical migration responses in response to predation pressure from abundant *Cyclops* populations may make *Bosmina* more available as a food source for juvenile sockeye salmon. There may be an internal feedback loop in sockeye salmon lake food webs, where increased nutrient loading from salmon carcasses leads to increased *Cyclops* abundance, increased *Bosmina* body sizes and increased visibility of *Bosmina* in the water column. The increased availability and quality of zooplankton may in turn result in increased salmon abundance, and in turn result in further nutrient loading and increased secondary production. Changes in the abundance of sockeye due to external factors such as changes in oceanic or climatic conditions may disrupt this feedback loop. I would suggest further studies examining vertical migration of *Cyclops*, *Bosmina*, and sockeye salmon, and feeding of *Cyclops* and *Bosmina*, either experimentally in enclosures or via observations of natural populations.

In this study, I examined the trophic interactions of “macro” zooplankton. In these oligotrophic lakes, rotifers make up a substantial component of the zooplankton community (Kyle 1996; Kyle et al 1997). Unfortunately, rotifers were not adequately sampled in the ADF&G database I examined, and their soft-tissued bodies typically don't leave any biological microfossils preserved in lake sediments. Rotifers, however, probably make up an important part of the diet of predatory copepods such as *Cyclops* (Kerfoot 1977b; Kerfoot and Sih 1987) and trophic interactions between rotifer populations and *Cyclops* may also be an important part of the picture.

The analyses of fossil *Bosmina* populations along with stable isotopic analyses provided additional insights into zooplankton-sockeye interactions and showed the veracity of the paleolimnological record as a means of reconstructing past ecological relationships. Other paleolimnological indicators from additional trophic levels such as diatoms or algal pigments could provide additional information on the importance of carcass derived nutrients in these systems (Finney et al. 2000). Currently, research on diatoms from Karluk and Frazer Lakes is being carried out (Irene Gregory Eaves, Queen's University, Kingston, Ontario, Personal Communication), and together with the zooplankton record, will hopefully provide an integrated picture on foodweb dynamics in sockeye salmon lakes.

Finally, in Chapter 2 I identified a distinct dichotomy in sockeye lakes: those with high salmon, high *Cyclops*, and large *Bosmina*, and those with low salmon, low *Cyclops*, and small *Bosmina*. Frazer Lake was somewhat anomalous, because sockeye were only recently introduced, and the zooplankton community appears to have not fully recovered from the strong top-down effects of sockeye following introduction and overescapement. Paleolimnological records from lakes above and below the "*Cyclops* threshold" should be examined to see if the relationship seen in Karluk Lake is repeated elsewhere, and if lakes on either side of this "threshold" could change to the other state.

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