AN ABSTRACT OF THE THESIS OF

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Title: Ecological Implications of Trout Introductions to Lakes of the Selway Bitterroot Wilderness, Idaho

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The widespread introduction of trout to naturally fishless mountain lakes in the western United States has been accompanied by little research. The ecological role of trout populations occurring in 91 lakes of the central Selway Bitterroot Wilderness, Idaho, was examined with respect to 1) the sampling variability of biological and chemical lake characteristics measured, 2) possible effects of trout on biotic communities of crustacean zooplankton, macro-invertebrates, amphibians and reptiles, and 3) the relation of fish population characteristics (condition and maximum body length) to stocking rate, angling pressure, natural recruitment and lake habitat characteristics.

Based on 22 lakes surveyed two or three times over a three year period, sampling variability was relatively low for individual species, biotic communities and length and weight of the largest fish in the population. Water conductivity measured at the lake surface from shore was the most reliable index of water quality, exhibiting low seasonal and duplicate sampling variability and a high correlation with alkalinity samples.

Based on Detrended Correspondence Analysis (DCA), an ordination method used to organize the 91 lakes by the presence or absence of taxa, the composition of indigenous biotic communities was strongly related to the presence or absence of fish. The Multi-Response Permutation Procedure indicated that the difference in communities was statistically significant. Fewer taxa were sampled in lakes with fish and the taxa expected to be most vulnerable to predation due to their large size and frequent occurrence in open water were rarely found in lakes containing fish. DCA ordinations indicated that characteristics of the fish population (fish species, condition and maximum body length) were also related to the composition of the biotic community. This was probably due to the bottom up:top down trophic level interactions of predator and prey; fish affecting the structure of biotic communities by predation and prey affecting growth and condition of fish by their abundance and availability as determined by both physical habitat characteristics and impacts of predation by fish.

Average condition and maximum body length of fish populations were related to stocking rate, natural recruitment, angling pressure and lake habitat variables by stepwise multiple regression. Average condition and maximum body length increased with decreasing level of natural recruitment for all fish population classes, except brook trout (all with high natural recruitment) and populations with no natural recruitment. Average fish condition increased with increasing angling pressure (measured by campsite impact and access distance ratings). Maximum body length of fish increased in relation to habitat variables, particularly presence of the large (2-3 mm) calanoid copepod, Diaptomus sp. Stocking rate was not related to average condition or maximum body length for any fish population class tested except one, where it may represent a spurious correlation.

The findings of this study suggest the need to re-assess high lake research and management policies that have promoted 1) widespread stocking of un-surveyed lakes on a regular basis and 2) considered stocking rate adjustments as an effective means of manipulating fish populations. Management direction can now be based on a recognition of the potential usefulness of one-time sampling of biological and chemical lake characteristics, the potential for significant impacts of fish on indigenous biotic communities, and the importance of natural recruitment, angling pressure and habitat variables in determining characteristics of the fish population. Recommendations include the identification and maintenance without further stocking of fishless lakes and lakes containing self-sustaining trout populations (wild trout lakes).

Ecological Implications of Trout Introductions
to Lakes of the Selway Bitterroot Wilderness, Idaho

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ECOLOGICAL IMPLICATIONS OF TROUT INTRODUCTIONS TO LAKES OF THE SELWAY BITTERROOT WILDERNESS, IDAHO

CHAPTER I. INTRODUCTION AND GENERAL METHODS

> We did not know what we had done because
> we did not know what we had un-done.
> - Wendell Berry

Introduction

More than 1,000 lakes occur in the mountains of Idaho. Based on stocking records kept by the Idaho Department of Fish and Game, most of the deeper lakes (>3 m maximum depth) considered suitable trout habitat have been stocked with trout every two to three years over the past three decades. Very few of these lakes are considered to have contained fish prior to stocking (Bahls, In prep.). With the exception of occasional reports from anglers and State Game Officers, most lakes have not been surveyed and little is known about appropriate stocking rates and the ecological implications of trout introductions. The High Lake Fisheries Project was initiated by the Idaho Department of Fish and Game and the Nez Perce National Forest to obtain baseline data needed to develop cooperative fishery and wilderness management plans for 191 lakes on the Nez Perce National Forest of Idaho. This study is based on data collected on lakes in a central core of the Selway Bitterroot Wilderness contained within the Moose Creek Ranger District of the Nez Perce National Forest. In the summers of 1986 and 1987, 91 lakes in the district were surveyed for biological, physical and chemical characteristics. In 1988, 22 of the lakes were re-surveyed once or twice to evaluate sample variability due to seasonal changes and methods.

The goal of this study was to assess the ecological role of trout populations occurring in lakes of the Moose Creek Ranger District in order to contribute to the management of fishery and wilderness resources of the Selway Bitterroot Wilderness. Specific research objectives included:

1) An evaluation of the sampling variability of chemical and biological characteristics measured (Chapter II).

2) An evaluation of the relationship of fish populations to zooplankton, macro-invertebrates, amphibians and reptiles (Chapter III).

3) An evaluation of the relationships of fish condition and maximum body length to stocking rate, fish species, natural recruitment, angling pressure and habitat variables (Chapter IV).

General methods

1. Study area

The Moose Creek Ranger District of the Nez Perce National Forest comprises a 226,596 ha central core of the 542,557 ha Selway Bitterroot Wilderness located in the remote Selway Bitterroot mountains of north-central Idaho. The Selway Bitterroot Wilderness is the third largest Wilderness Area in the contiguous United States and includes portions of four National Forests in Idaho and Montana. The Moose Creek Ranger District is contained within the Idaho Batholith, a fairly homogenous granitic bedrock composed mainly of granodiorite and quartz monzonite (Bennett, 1975). Most lakes in the district are in glacial cirques located at between 1520 and 2128 m in elevation. Lake basins at these elevations typically receive more than 50 percent of their precipitation as snow (Finklin, 1983). Lakes are generally free of ice-cover by late June.

The lakes sampled in this study include 91 of 115 lakes in the Moose Creek Ranger District. Lakes not sampled represent 24 of 46 small ponds (< 1 ha) occurring in the district. The 22 lakes re-sampled in 1988 were informally selected to be representative of the spatial distribution, geological and ecological diversity of lakes in the district (Figure 1).

Only three of 55 lakes with fish may have contained indigenous populations of trout prior to stocking (Bahls, 1987). Rainbow trout (*Oncorhynchus gairdneri*), cutthroat trout (*Oncorhynchus clarki*) and brook trout (*Salvelinus fontinalis*) occur in the lakes. Natural recruitment is estimated to be high in all 20 lakes containing brook trout (char) and only 5 lakes containing rainbow and/or cutthroat trout. About one-half of the lakes containing *Oncorhynchus* (trout) are estimated to maintain low to moderate levels of natural recruitment (Bahls, 1987).

2. Data collection

Methods used to gather biotic and environmental data are detailed in this section. Methods for data analysis used to complete each objective are included in the following chapters.

Baseline survey data were collected during the 1986, 1987 and 1988 summer field seasons on physical, chemical and biological characteristics of 91 lakes in that portion of the Selway Bitterroot Wilderness contained within the Moose Creek Ranger District of the Nez Perce National Forest of Idaho (Table 1). Approximately 45 lakes were surveyed each season between mid-June and mid-September in 1986 and 1987. The 1988 field season involved re-sampling 13 lakes twice and 9 lakes once (Figure 1). Backpacking was used to travel

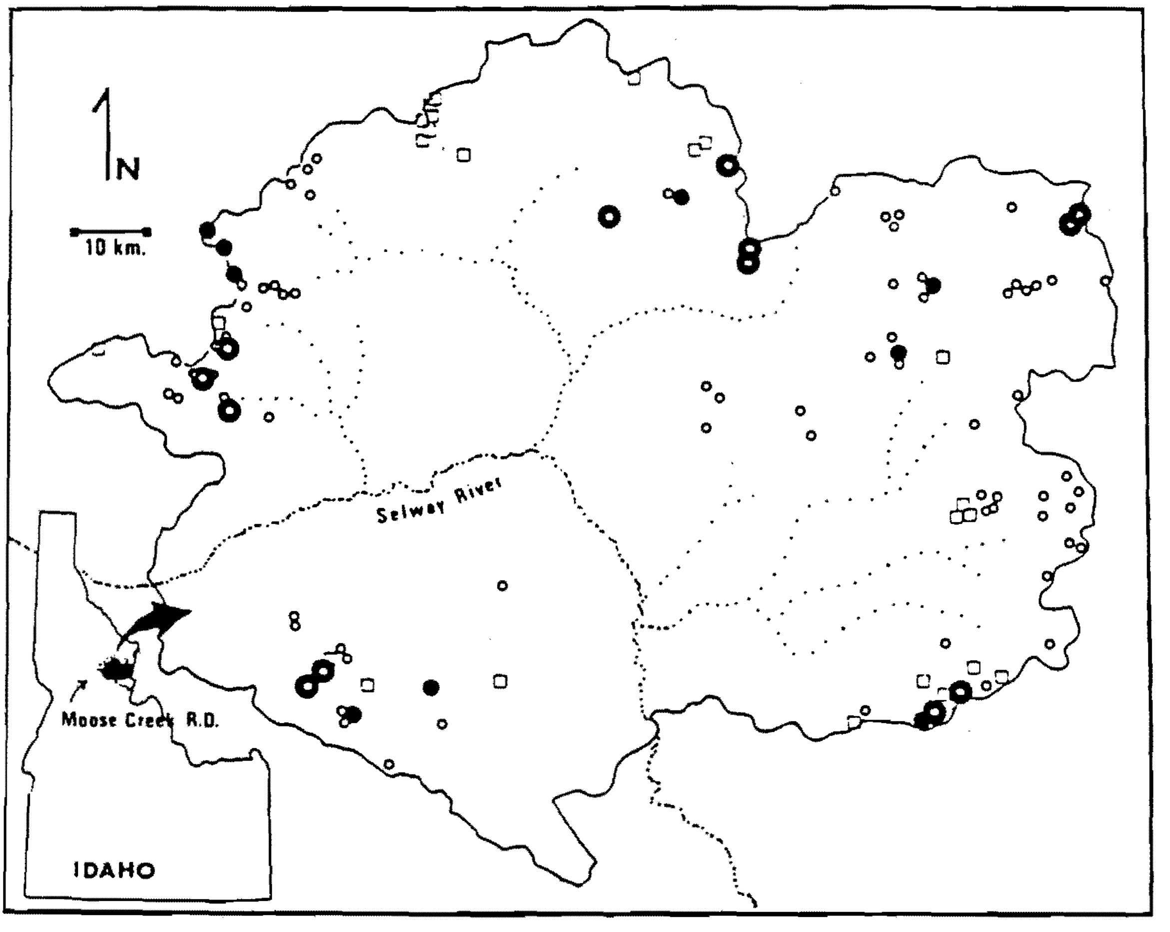

Figure 1. Locations of lakes in the Moose Creek Ranger District of the Selway Bitterroot Wilderness including 91 lakes sampled in 1986 and 1987 (∘), 9 lakes re-sampled once (●) and 13 lakes re-sampled twice (◎) in 1988, and 24 unsurveyed lakes(□).

Table 1. Physical, chemical and biological variables assessed at the study lakes.

Physical and chemical lake characteristics
Basin area
Headwall distance
Basin aspect
Elevation
Lake surface area
Lake maximum depth
% Shallow littoral area
% Deep littoral area
% Forest perimeter
% Lake substrate types (size classes)
Weighted average of substrate types
Conductivity
Alkalinity
pH

Biotic Community Variables
Presence of dominant taxonomic groups of
Crustacean zooplankton
Aquatic macro-invertebrates (Insecta, Amphipoda)
Amphibians
Reptiles
Fish population characteristics
Relative abundance
Average condition
Individual of maximum length
Individual of maximum weight

from lake to lake. The field season schedule consisted of 8 to 14 day journeys during which 5 to 9 lakes were sampled. An average of one and one-half days were needed to complete each lake survey, with one-half day between survey days for travel to the next lake. Fish were collected by angling (1986 and 1987) and angling and gill netting (1988). A small inflatable raft was used for bathymetric measurements, zooplankton collection and fishing.

A. Physical and chemical variables

Lake elevation was obtained directly from U.S.G.S. 7.5 minute topographic maps. A polar planimeter was used to obtain measurements of lake surface and flat map watershed areas. Basin aspect was measured with a compass on a 7.5 minute topographic map, with the compass oriented along a line running from the center of the lake to the direction of least blockage by mountain slopes (usually directly opposite of the glacial headwall).

The glacial headwall represents the slope that was most heavily eroded by the "pluck and scour action" of cirque glaciation (Rabe, 1985). On a topographic map, the headwall appears as the steepest slope in the lake basin and directly opposite the apparent path of glacial erosion. Headwall distance was obtained by measuring the distance between the near edge of the lake and the mountain peak closest to the headwall and most nearly aligned with the path of glacial scour.

For lake bathymetry measurements, a map of the lake perimeter was enlarged from a 7.5 minute topographic map with an overhead projector and traced onto 8.5 by 11 inch paper. Lake depths were recorded along a minimum of six transects across each lake and three meter contour intervals mapped. A polar planimeter was later used on the bathymetric map to determine the percent of the lake surface area in shallow (0 - 3 m) and deep (>3 - 6 m) littoral zones.

Lake bottom substrates in the shallow littoral zone were classified as either silt/organic, sand, gravel, rubble, boulder and bedrock or a combination of types. Substrate types occurring in areas of larger than five square meters were visually estimated and mapped on the lake perimeter map at stops made about every twenty meters around the shore. The completed map of substrate types was used to estimate the total percentage of each substrate type in the littoral zone of each lake.

The percent forest cover (all vegetation over two meters in height) in a twenty meter wide strip around the lake perimeter was estimated based on four vantage points along each lake shore.

Water chemistry data was collected only for lakes surveyed in 1988. Lakes were sampled near shore and at 1.5 meters below surface and 1.5 meters above bottom (lakes over 6 meters in maximum depth only) while located over the deepest portion of the lake. Samples were collected from an inflatable boat using a weighted bottle and cork system (Bahls, 1989) rinsed three times with lake water. Measurements of pH and conductivity were immediately conducted on duplicate samples at each station using a Beckman pH10 meter with a refillable combination electrode (1 M KCL saturated with AgCl) calibrated with standard buffers and a Cole-Palmer digital conductivity meter with a gold-cell (low conductivity range) dip cell. Alkalinity determinations were performed on duplicate 100 ml samples titrated with 0.01 N HCL dispensed from a 2-ml micrometer buret and then evaluated using Gran methods (Stumm and Morgan, 1981).

Frequency distributions of environmental variables were then examined and transformations performed if deemed necessary to normalize the distribution and reduce potential outliers. Percentages were transformed by arc-sin square root. Other variables were transformed by the natural log.

B. Biota

Crustacean plankton samples were collected from the inflatable raft by taking two vertical tows from the deepest portion of each lake and two horizontal tows of four to six meters in length in the shallow littoral zone with a conical tow net (153 um mesh, 20 cm diameter). Samples were transferred to a 30 ml bottle and preserved in 70% ethanol.

Species compositions were determined by examining entire samples under low magnification (40X) and removing individuals of various groups for examination at higher magnification (400X). Cladocerans were identified to either species or genus, Copepods were separated into three distinct groups; large bodied (>2 mm) calanoids, medium to small bodied calanoids and cycloploids.

Aquatic insects, amphipods, amphibians and reptiles were sampled by walking the entire perimeter of each lake, stopping every 10 meters to visually scan the littoral zone for organisms. To conduct a systematic survey of various habitats occurring in the nearshore zone, sampling was conducted along the lakeshore at regular intervals of 20 meters. At least two of every type of aquatic insect observed were collected with the aid of a long-handled sampling net and preserved in 70% ethanol. Every 20 meters, the near shore bottom substrate and submerged vegetation were dredged several times with the sampling net and searched for organisms. Rubble substrate was examined by manually turning over and examining rocks. Amphibians were occasionally collected or photographs taken to verify field identification.

Aquatic insects and amphipods were identified by R. C. Biggam at University of Idaho. Most individuals were identified to either genus or species. Amphibian samples and photographs were identified by Dr. H.J. Wallace at University of Idaho. The list of taxa used in most of the subsequent analysis includes only those individuals identified to either the species, genus or family level that were sampled in more than four of the 91 lake surveys included in ordination analyses. Individuals occurring less than four times were grouped if possible or deleted (see species list, Appendix A).

C. Fish populations

Fish samples were obtained by angling (1986, 1987) and angling and/or gill netting (1988). The monofilament gill net had six panels of variable mesh 150 m long by 6 m deep and a sinking bottom line. Panels ranged in mesh size from 12.7 mm to 50.1 mm bar. The net was set by attaching the small mesh end to shore and laying it perpendicular to the shore using the raft. The net was always set in the evening and retrieved after 12 hours. Angling was conducted by the author using a diversity of methods for a minimum of six hours or until twenty trout were caught. Each fish caught was identified to species, weighed to the nearest gram using a Pescola spring scale (1-1000 g) and measured (total length) to the nearest millimeter.

Relative fish abundance was estimated from number of fish caught by angling per hour for lakes sampled in 1986 and 1987. The lack of adequate angling data for lakes sampled by gill netting in 1988 necessitated conversion of gill net catch rates (G) to angling catch rates (A) for comparative purposes. Based on a simple linear regression of angling and gill-net catch data obtained during seven surveys of six lakes (Figure 2), the equation $A = .32G - .64$ ($r^2 = 0.82$, $p = 0.004$) was used for the conversion. The outlier represents samples of the only brook trout population used in this analysis and is considered to accurately represent the high density of fish present in 18 of 20 lakes containing brook trout on the district.

Average fish condition was based on the ratio of actual weight (AW) to predicted weight (PW) at a given length. The predicted weight was based on a regression of total length (L) against weight for 1048 trout, which represented all trout sampled in 1986-1988 between 100 and 600 mm in length (an exclusion of 7 trout outside of this range) (Figure 3). The regression equation $PW = 3.00L - 5.05$ ($r^2 = 0.98$, $p = 0.0000$) was used to obtain a condition rating (C) for each fish where $C = PW/AW$.

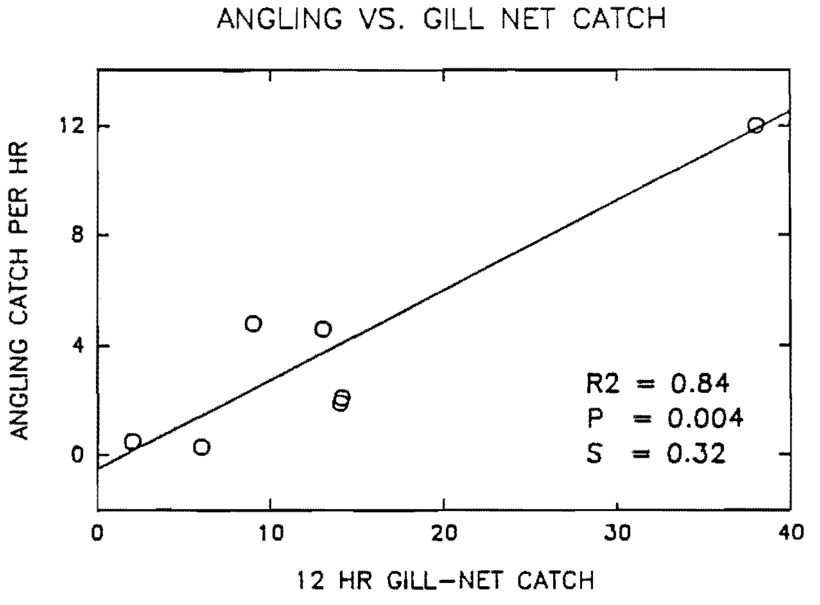

Figure 2. Comparison of fish relative abundance estimates obtained by gill net and angling methods for seven lakes.

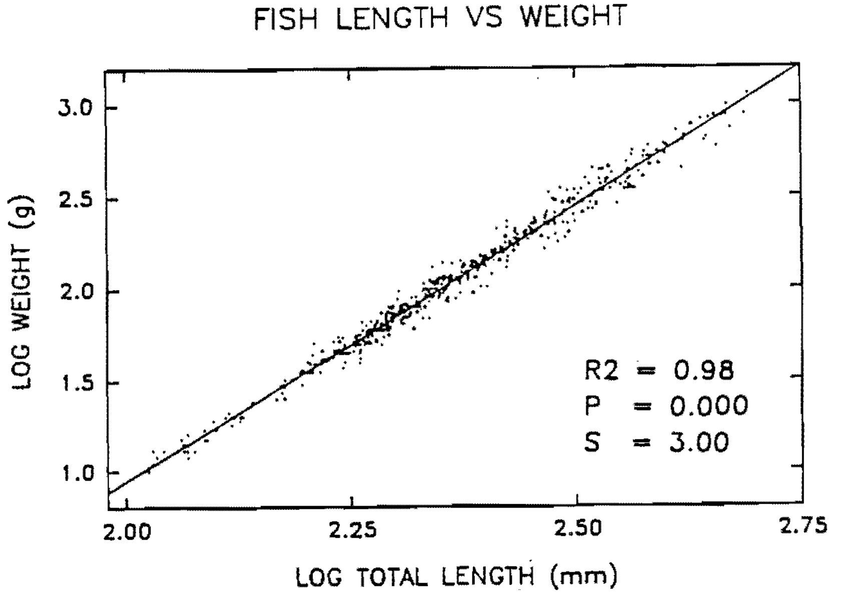

Figure 3. Simple regression of fish length and weight for 1048 fish sampled in 1986, 1987 and 1988.

CHAPTER II. EVALUATION OF SAMPLING VARIABILITY

Introduction

Little is known about the seasonal variation of aquatic invertebrate and amphibian species richness and abundance in high lakes of the western United States. Most of the survey work conducted has focused on fish (Nelson, 1985; Larson, 1984; Marcuson, 1976). The relatively small amount of survey work on aquatic biota other than fish has included aquatic insects (Johnston, 1973; Rabe, 1968; Espinosa, 1977) and zooplankton (Stoddard, 1987). Variation in species data due solely to sampling methods is poorly documented, particularly since standard methods have not been adopted by high lake researchers. The analysis conducted in later chapters examines patterns and trends apparent for the 91 lakes as a whole; thus, the reliability of the survey method for an individual lake is not essential. However, in addition to benefitting the analysis presented in later chapters, such an assessment is expected to be of general value in refining survey methods and obtaining a better understanding of seasonal dynamics of high lakes. The purpose of this chapter was to evaluate the variability of the data collected on: 1) presence or absence of individual species; 2) biotic communities comprised of zooplankton, aquatic insects, amphipods, amphibians and reptiles; 3) zooplankton communities sampled by various methods; 4) fish population characteristics; and 4) water chemistry.

Methods

1. Variability of individual taxa

In 1988, 22 lakes were re-sampled once or twice with about one month between sampling times to assess the occurrence (presence or absence) of the 47 taxa used in the ordination analysis. In total, thirteen lakes were sampled three times and nine lakes were sampled twice between 1986 and 1988. Two methods were used to assess the occurrence of individual taxa at each lake. The Percent Re-occurrence method determines the percentage of times a taxon was found in the same lake averaged over the 22 lakes. The Percentage Agreement method uses both presence and absence data to calculate the number of joint absences or presences of each taxon in multiple surveys of each lake divided by the total number of possible agreements (Table 2).

2. Variability of biotic communities

To evaluate the similarity of repeat samples of biotic communities and each sub-group of the community (zooplankton, aquatic invertebrates, amphibians and reptiles), the mean similarity of pairs of samples from the same lake (taken during different lake surveys) was compared to the mean similarity of pairs of samples from randomly selected lakes. In addition, community samples collected between June 18 and 26, 1988, when lakes were partially covered with ice (ice-cover period) were analyzed separately from samples collected during the "open water period". The (number of species common to both samples*2)/(number of species in both samples) was used to assess the percent similarity between two communities (Gauch, 1982). Three pairs of comparisons were included for each of thirteen lakes surveyed three times (samples 1-2,1-3,2-3) and one pair for nine lakes surveyed twice (samples 1-2). A total of 46 pairs of samples were analyzed; 10 pairs comparing samples collected during the ice-cover and open water seasons were analyzed separately from pairs including only communities sampled during the open water season. Randomly selected pairs of samples used for comparison included the same number of pairs within ice-cover, open water and all

Table 2. Example of Percent Re-occurrence (mean PR) and Percent Agreement (PA) indices calculated for Species 1 in seven lakes sampled two or three times (time1 - time3). Percent Re-occurrence is the mean PR for the total number of lakes from which Species 1 was sampled (TL). PA is the sum of the number of actual agreements (A) for each lake divided by the total number of possible agreements (TA).

LAKE	t1	t2	t3	PR	A
A	X	X	X	100%	2
B	X	X	0	66%	1
C	X	0	0	33%	1
D	0	0	0	NA	2
E	X	X		100%	1
F	X	0		50%	0
G	0	0		NA	1
				349	8

SPECIES 1 PR = PR/TL = 349/5 = 69.8%

PA = A/TA = 8/11 = 72.7%

lake categories, but did not distinguish between lake based on fish population status or habitat characteristics.

3. Variability of zooplankton sampling

Zooplankton samples collected in 1988 were evaluated to assess the variability between samples taken during the same lake survey (duplicate samples), samples taken approximately one month apart (seasonal) and samples taken by horizontal littoral hauls (shallow) and vertical maximum depth hauls (deep). Percent similarity of zooplankton community samples was determined for pairs of samples. Pairs including one sample collected during the period of ice-cover were evaluated separately from pairs collected during the ice-free season. Randomly selected pairs of samples collected by the standard method (sd = two shallow and two deep tows as described in Chapter I) were used as a base for comparison to duplicate and seasonal samples collected by the standard method.

4. Variability of fish populations

Six lakes were sampled twice in 1988, with approximately one month between samplings, to evaluate the variability of fish population characteristics due to sampling methods and seasonal changes. Regression plots (and corresponding r^2, p values and regression line slopes) were used evaluate the variation in measurements of relative abundance, condition, maximum body length and weight. Estimates of relative abundance were based on gill net catch data converted to angling catch per hour (as described in General Methods, Chapter I), with the exception of one lake sampled by angling only.

A comparison of fish population variables obtained by angling and gill netting was conducted because the analysis presented in later chapters uses fish sampling data collected by both methods. Three analyses were undertaken. First, as described in Chapter I, a regression analysis was used to evaluate the relationship between angling catch (number of fish) per hour and gill net (12 hour) sampling estimates of the relative abundance of the fish population in each lake. Second, t-tests were used to compare the length, weight and condition of fish obtained by angling and gill net samples of approximately 15 fish caught by each method during each of four surveys conducted at three lakes. Third, a T-test was used to compare the average condition of fish based on samples obtained by angling and gill netting during six surveys (including two surveys not included in the previous analysis due to insufficient sample sizes).

5. Variability of water chemistry

Water chemistry data is of minimal use in the analyses presented in later chapters because pH, alkalinity and conductivity data were determined only in 1988. However, the potential importance of water quality as a general measure of productivity and acid precipitation warranted its inclusion in this chapter. Alkalinity, a measure of the acid neutralizing capacity of the water, is used as the primary indicator of lakes at risk of acid precipitation (EPA, 1987) and has been recognized as an indicator of the productivity of fisheries (Johnston, 1977; Rabe, 1985; Moyle, 1956; Carlander, 1955). Field pH readings give a direct measure of lake acidity, but are generally less useful because they tend to exhibit large sampling variation due to shifting carbon dioxide levels in the sample water related to photosynthesis and atmospheric exchange (Wetzel, 1983). Specific conductance, a measure of the resistance of a solution to electric flow (which declines with increasing ion content) is closely proportional to total dissolved solids, a measure of the sum of the ionic composition of major cations and anions (Wetzel, 1983). A number of studies have shown total dissolved solids to be directly related to fish yield (Northcote and Larkin, 1956; Ryder, 1965; Donald and Anderson, 1982).

Although potentially useful, the relevance of these chemical measurements to high lake research and management depends greatly on the range of variability over the summer sampling season. In a study of an alpine lake in the Sierra Nevada, Stoddard (1987) found that both alkalinity and pH decreased dramatically during the spring snow-melt due to dilution (rather than acidification), but stabilized during the ice-free season. Thermal stratification and mixing dynamics could also influence the variability of water chemistry measurements. For high lakes of the north-central Rocky mountain region, no information exists on the variability of water chemistry due to seasonal changes and sampling error. The purpose of the analysis presented in this section was to assess the variability of alkalinity, pH and conductivity data by using regression analysis (and corresponding r^2, p value and regression line slope) to evaluate the correlation between: 1) duplicate samples, 2) samples obtained approximately one month apart, 3) samples obtained from different zones of the lake (surface, shallow and deep, see Chapter 1, General Methods), and 4) among different water quality measures (pH, alkalinity and conductivity) obtained in the same lake zone.

Results and discussion

1. Variability of individual taxa

The average Percent Re-occurrence of individual taxa sampled two or three times in 22 lakes between 1986 and 1988 (60.4, std = 18.23) was slightly lower than the average Percentage Agreement (84.3, std = 9.84), reflecting the addition of joint absence data with the use of percent agreement values

(Table 3). Taxa with high ratings for both re-occurrence and percent agreement (indicated on Table 1) may be particularly important as potential indicator species. Compared to typical plot sampling of terrestrial plants, an average of 84 percent agreement between samples indicates a relatively high degree of correspondence between surveys and a high level of reliability in repeat sampling (Bruce McCune, Department of General Science, Oregon State University, personal communication).

2. Variability of biotic communities

Pairs of samples of biotic communities and of each sub-group of the community (crustacean zooplankton, aquatic invertebrates, amphibians and reptiles) collected from the same lake were more similar than pairs of samples from randomly selected lakes (Table 4). For aquatic invertebrates and amphibians and reptiles, samples collected during the ice-cover season compared to samples collected during the open water period were more similar than pairs of samples from the open water period only. A more complete sampling of taxa during the ice-cover period, when more species would tend be in aquatic life stages in the lake may explain the higher similarity of pair comparisons that included samples collected during the ice-cover season. Similarity between zooplankton communities was very low when ice-cover samples were included, due to the small number of species present during this period. Although, zooplankton exhibited the highest degree of similarity of any group sampled during the open water period, much less variation was found by Stoddard (1987) who, using similar methods in a survey of 75 lakes in the Sierra Nevada mountains of California, found that species compositions did not change in lakes sampled several times over the course of the summer. Relative abundances varied greatly, however. Similarly, in a study of 146 alpine and subalpine lakes in western Canada, Anderson

Table 3. Sampling variability indices of Percent Re-occurrence (PR) and Percent Agreement (PA) for 47 taxa sampled from 13 lakes sampled three times and 9 lakes sampled twice. Taxa considered to have particularly high sampling reliability (PR > 60 and PA > 90) are marked (*).

Taxon	PR	PA	
Ephemeroptera Order	33.3	91.2	
Callibaetis sp.	81.5	79.4	
Siphlonurus sp.	45.0	88.2	
Anisoptera Order	41.7	94.1	
Libellulidae Family	33.3	97.1	
Enallagma sp.	64.6	85.3	
Aeshna sp.	77.5	73.5	
Somatochlora sp.	52.4	82.4	
Leucorrhinia sp.	51.5	70.6	
Notonectidae Family	50.0	85.3	
Corixidae Family	44.4	82.4	
Arctocorixa sutilis	33.3	97.1	
Callicorixa audeni	57.1	67.6	
Sigara sp.	53.3	88.2	
Notonecta kirbyi	58.3	88.2	
Gerridae Family	45.8	79.4	
Gerris incognitus	59.1	73.5	
Gerris remigis	55.6	94.1	
Limnoporus notabilis	50.0	88.2	
Tricoptera Order	58.3	58.9	
Limnephilidae Family	33.3	88.2	
Hesperophylax sp.	52.1	76.5	
Psychoglypha sp.	36.1	82.4	
Coleoptera Order	52.4	61.8	
Gyrinis sp.	79.2	94.1	*
Agabus sp.	69.4	91.2	*
Acilius sp.	61.1	94.1	*

Table 3. (continued)

Taxon	PR	PA	
Deronectes sp.	72.9	85.3	
Oreodytes sp.	50.0	97.1	
Sialus sp.	78.9	76.5	
Chironomidae Family	85.0	85.3	
Chaoborus sp.	70.8	93.9	*
Chrysops sp.	50.0	76.5	
Long Toed Salamander	81.0	91.2	*
W. Spotted Frog	82.5	79.4	
W. Terrestrial Garter Snake	38.9	91.2	
Common Garter Snake	45.2	79.4	
Bosmina sp.	100.0	100.0	*
Chydorus sp.	50.0	63.6	
Daphnia rosea	80.8	81.8	
Holopedium gibberum	87.3	84.8	
Polyphemus pediculus	66.7	84.8	
Scapholeberis kingi	41.7	87.9	
Calanoida Sub-order	90.0	81.8	
Large *Diaptomus* sp.	83.3	93.9	*
Cyclopoida Sub-order	56.1	72.7	
Hyalella azteca	100.0	100.0	*

Table 4. Mean percent similarity and 95% confidence intervals of paired biotic community and sub-group samples of aquatic macro-invertebrates (AMI), zooplankton and amphibians and reptiles (AR) from the same lake and random pairings. Pairs include all sample pairs, ice cover vs. open water pairs and pairs from the open water season only.

Biotic group	All Pairs	Ice cover vs. Open water	Open water vs. Open water
	n = 46	n = 10	n = 36
All biota	61 ± 3.6	54 ± 7.9	63 ± 3.9
random	47 ± 3.2	48 ± 10.0	47 ± 3.3
AMI	56 ± 4.2	59 ± 8.9	55 ± 4.9
random	43 ± 4.5	52 ± 11.7	40 ± 4.6
Zooplankton	68 ± 8.6	31 ± 24.3	78 ± 5.5
random	51 ± 6.3	24 ± 9.3	59 ± 5.5
AR	63 ± 11.9	71 ± 20.5	61 ± 14.3
random	56 ± 11.1	67 ± 20.5	52 ± 13.2

(1971) found that zooplankton species composition of lake communities varied little from year to year.

3. Variability of zooplankton sampling

The highest similarity was found between pairs of duplicate samples collected by the standard method (sd-sd dupl), where each sample included two shallow littoral tow samples (s) and two vertical tow samples in the deepest portion of the lake (d) (see General Methods, Chapter 1). Standard samples collected during the open water period were approximately double the similarity of randomly paired standard samples (Table 5). The somewhat lower similarity of standard samples collected about one month apart (sd-sd seas) suggests a slight seasonal change in zooplankton community composition. Seasonal variation of vertical tows samples only (d-d seas) was somewhat less than for standard samples (sd-sd seas) and much less than for shallow samples only (s-s seas). The low similarity between shallow and deep samples collected from the same lake at the same time (s-d dupl) was probably attributable to fewer species sampled from the shallow littoral zone. Sampling variability was highest for shallow samples collected at different times (s-s seas). Thus, most of the slight variability of duplicate and seasonal standard samples can probably be attributed to the relatively high variability of shallow littoral samples; most likely caused by seasonal shifts of species abundance and rare species infrequently sampled in this zone.

Table 5. Mean percent similarity and 95% confidence intervals for pairs of zooplankton samples collected by different methods in 1988 including all sample pairs, ice cover vs. open water pairs and pairs from the open water season only.

Sample Pair Type*	All Pairs	Ice-cover vs. Open water	Open water vs. Open water	No.pairs
sd-sd dupl	88 ± 5.6	80 ± 70.2	89 ± .044	26,3,23
sd-sd rand	40 ± 12.5	18 ± 18.4	52 ± 13.5	22,8,14
sd-sd seas	62 ± 14.6	32 ± 28.9	79 ± 7.9	22,8,14
s-d dupl	58 +100.0	39 ± 42.4	63 ± 8.7	32,6,26
d-d seas	70 ± 21.8	37 ± 58.8	87 ± 13.4	12,4,8
s-s seas	46 ± 21.5	17 ± 45.9	60 ± 21.7	12,4,8

*Sample Pair Types s = Combination of two 5 m horizontal hauls in the littoral near shore, d = Combination of two vertical hauls within 2 m of bottom in the deepest portion of the lake, dupl = samples during the same lake survey (duplicate) seas = samples taken about one month apart in the same lake, rand = random pairing of samples.

4. Variability of fish populations

Estimates of fish abundance and condition for 6 lakes sampled twice indicated a relatively high repeat sampling error (Figure 4). The low correspondence between samples may be a result of a decrease in the fish population in certain lakes due to gill netting and sports angling mortality. However, it is also likely that gill net and angling catch estimates were effected by seasonal changes in fish activity and behavior. Fish condition, a ratio of weight to length, will vary seasonally due to changes in the reproductive condition of the fish and feeding habits. Also, an estimate of the average condition of fish in a lake does not account for potential differences in condition between separate fish species or stocks occurring in the same lake and probably sampled in disproportionate numbers during each survey. Maximum lengths and weights were much less variable between samples, suggesting that the largest and heaviest fish in the lakes were reliably sampled by these methods (Figure 4).

Fish population characteristics obtained by angling and gill netting were evaluated with three methods. First, relative abundance was found to be moderately correlated between methods (see Chapter I). Second, the results of t-tests comparing fish population characteristics obtained by angling and gill netting in four lakes were somewhat inconclusive; average length, weight and condition of fish were significantly different ($p < .05$) in two of the four comparisons. A comparison of the frequency of fish lengths obtained by angling versus gill netting for these four lakes supports Nelson's (1988) finding that a major difference between sampling methods is that gill net samples include a smaller size range of fish (80-200 mm) (Figure 5). Third, there was no significant difference ($p > .05$) in average condition of fish caught by angling or gill netting, suggesting that the variation in average condition due to

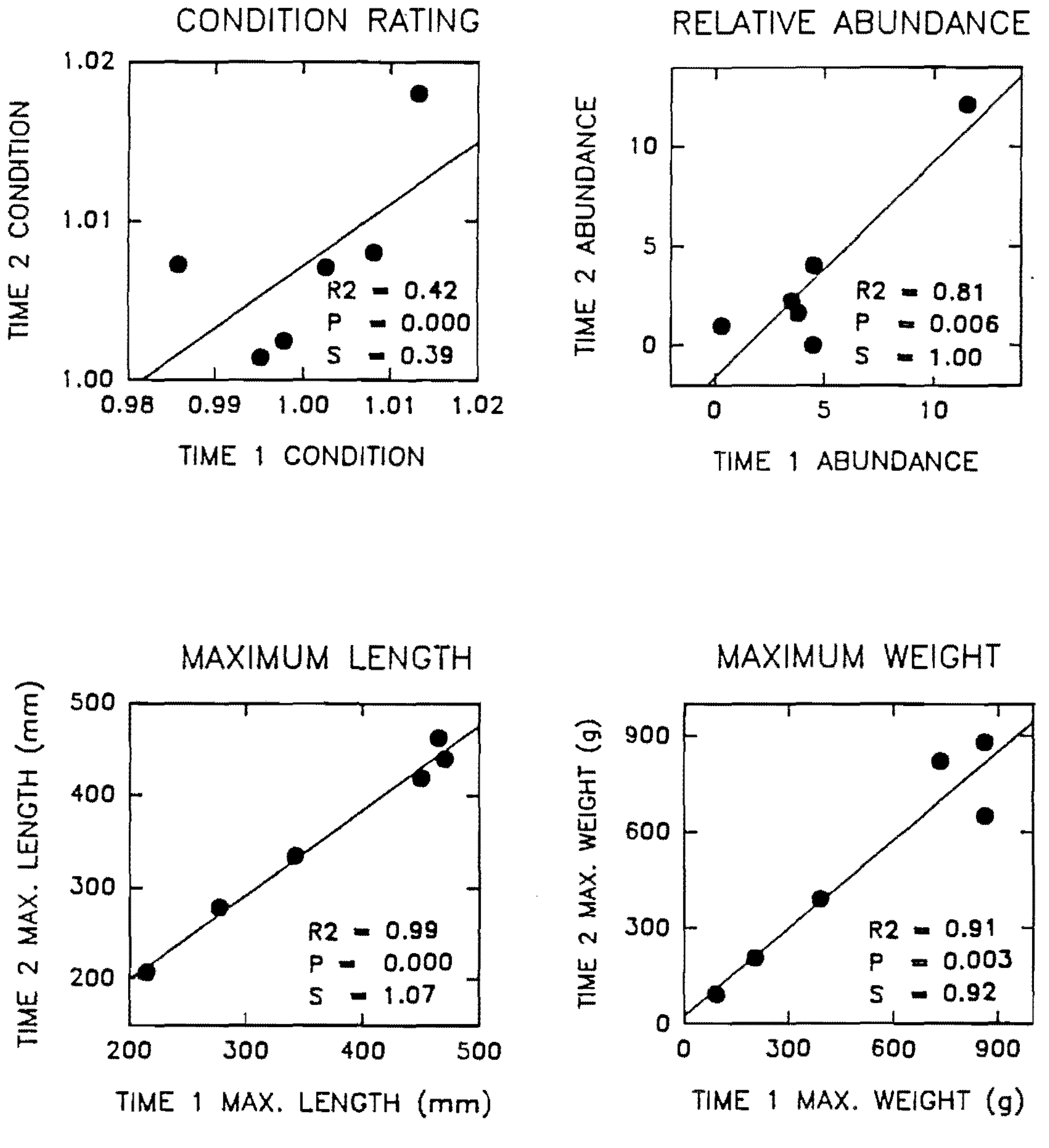

Figure 4. Simple regression plots of fish population characteristics in six lakes sampled twice with about one month between samplings.

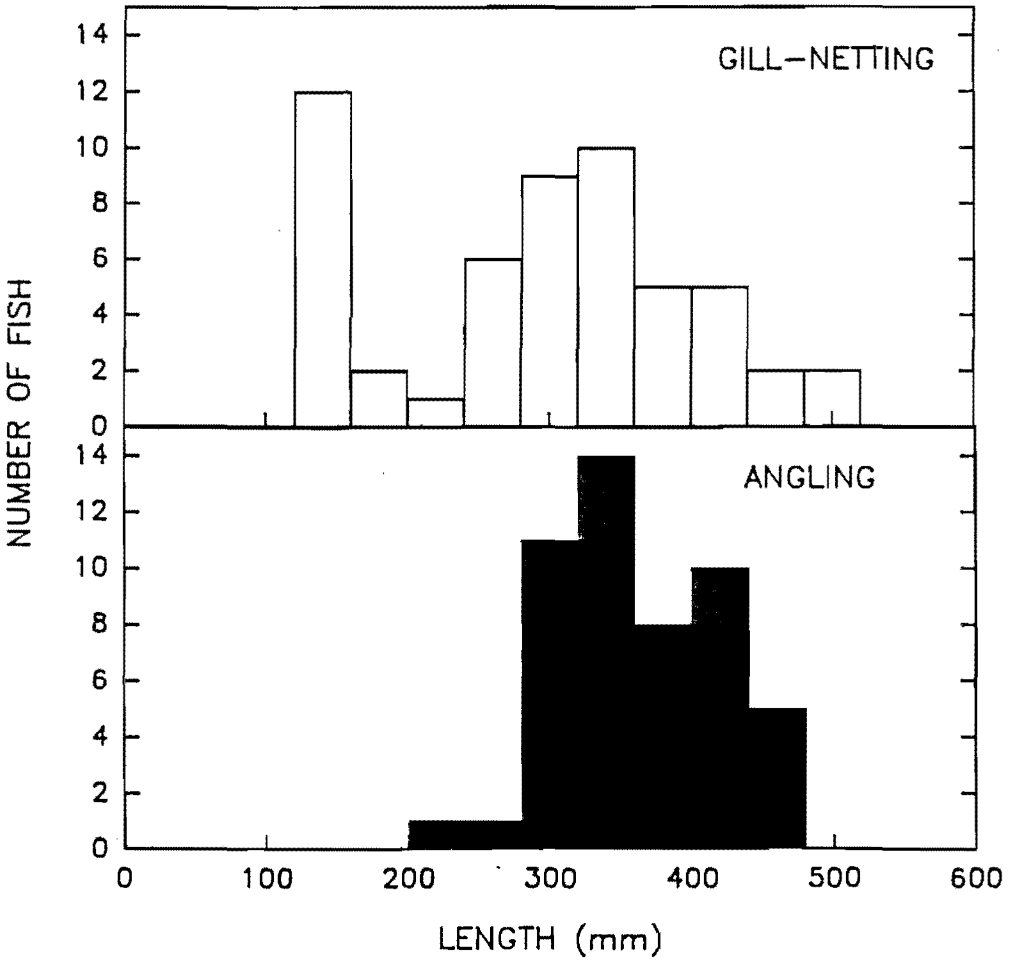

Figure 5. Total frequency distribution of fish lengths obtained by angling and gill netting in four lakes.

the choice of sampling methods is less than the variability in condition between surveys.

5. Variability of water chemistry

Results of the regression analysis of water chemistry samples for duplicate, seasonal and lake zone sampling are summarized in Table 6. Repeat sampling error of water chemistry samples was generally low; error was lower for deep water (1.5 m above bottom) pH samples than for shallow water (1.5 m below surface) pH, and lowest for conductivity and alkalinity samples (Table 6). Removal of sample pairs that included one sample collected during the ice-cover season (open water period only) improved the seasonal (time1 versus time2) conductivity correlations significantly. Surface conductivity measured during the open water period showed the smallest seasonal variability followed by shallow, deep and outlet samples. An analysis of seasonal variability was not possible for alkalinity and pH samples due to the small number of samples (<4). No significant relationship was found between shallow and deep samples for alkalinity, pH or conductivity, but shallow water conductivity samples were strongly correlated with surface water samples.

Results of regression analysis used to evaluate the

Table 6. Results of the regression analysis used to evaluate the variability of water chemistry measurements. The variability of surface (Su), shallow (Sh), deep (Dp) and outlet stream samples of pH, alkalinity and conductivity collected from the same lake is evaluated for duplicate samples, samples collected about one month apart (seasonal) and between different sampling areas of the lake (Su, Sh and Dp). Seasonal samples include all samples (all), and only samples collected during the open water season (open).

Table 6.

		Seasonal		Lake Zones		
Sample Type	Duplicate	All	Open	Su-Dp	Sh-Dp	Su-Sh
<u>pH</u>						
shallow						
# lakes	25				16	
slope	.88				.60	
p	.00				.12	
r^2	.82				.16	
deep						
# lakes	14					
slope	1.01					
p	.00					
r^2	.95					
<u>Conductivity</u>						
surface						
# lakes	31	9	7	17	23	30
slope	1.00	1.12	1.03	.73	1.02	.96
p	.00	.00	.00	.00	.00	.00
r^2	1.00	.74	.95	.81	.66	.98
shallow						
# lakes	32	13	8			
slope	1.02	.73	.96			
p	.00	.08	.00			
r^2	.99	.25	.86			
deep # lakes	19	7	5			
slope	1.00	.62	.51			
p	.00	.08	.02			
r^2	1.00	.49	.88			
inlet stream						
# lakes	26	6				
slope	1.00	.66				
p	.00	.18				
r^2	.99	.40				
outlet stream						
# lakes	31	9	6			
slope	.99	1.31	1.44			
p	.00	.00	.01			
r^2	1.00	.70	.83			
<u>Alkalinity</u>						
shallow						
# lakes	23			16		
slope	.96			1.10		
p	.00			.00		
r^2	.97			.66		
deep						
# lakes	13					
slope	.98					
p	.00					
r^2	.98					

variability between alkalinity, conductivity and pH measurements indicated a high correlation between alkalinity and conductivity measurements (Table 7). A high correlation between alkalinity and conductivity would be expected in low ionic strength water and with calcium bicarbonate being the major ion measured by both methods. Nelson (1988) found that for 73 high lakes in Colorado, both surface alkalinity and total solids were highly correlated with conductivity. In the present study, surface samples of conductivity were more closely related to shallow samples of alkalinity than shallow conductivity samples, probably because of the greater sampling precision of surface conductivity measurements.

In general, the results suggest that after the spring snow melt period, water quality of lakes of this region remains fairly stable. Water quality dynamics may be similar to what Stoddard (1987) found for a high elevation, unacidified lake in the Sierra Nevada, which underwent an annual cycle of low alkalinity during the ice-free season.

Table 7. Results of simple regression analysis used to evaluate the variability between shallow (Sh) and deep (Dp) alkalinity, conductivity and pH measurements in the same lake.

Independent variable	Dependent variable	#	Slope	P	R^2
Alk-Sh	pH-Sh	25	14.33	.39	.03
Alk-Sh	Co-Sh	26	818.95	.00	.95
Alk-Sh	Co-Su	20	884.75	.00	.97
Alk-Dp	pH-Dp	16	-9.00	.63	.02
Alk-Dp	Co-Dp	16	814.03	.00	.91
Co-Sh	pH-Sh	26	2.10	.31	.05
Co-Su	pH-Sh	20	.02	.48	.02

Surface water conductivity appears to be the most stable parameter for general use since it exhibited the lowest repeat sampling error, highest seasonal stability and highest correlation with shallow water conductivity and shallow water alkalinity. This finding may be particularly useful to future survey efforts, since the need to measure only surface water conductivity from the shoreline could save several hours of unnecessary water chemistry sampling at each lake.

Summary

An analysis of the variability of biotic and chemical samples collected from 22 lakes sampled two and three times indicated that: 1) individual taxa displayed relatively low sampling variability (84 percent average agreement); 2) biotic community samples from the same lake were less variable than randomly selected and paired community samples, 3) zooplankton community samples were most variable for comparisons of shallow water samples and seasonal samples that included a sample collected during the ice-cover season; 4) measurements of characteristics of fish populations in six lakes sampled twice in 1988 indicated that average condition and relative abundance were somewhat variable, but maximum body length and weight exhibited low variability. A comparison of angling and gill netting methods indicated a weak relationship between methods for estimates of average fish condition, moderate relationship for relative abundance and a larger number of small fish caught by gill-netting methods; 5) variability of water chemistry measurements generally ranged from highest for pH to lowest for conductivity, with surface conductivity having the lowest overall variability between duplicate, seasonal and shallow and deep conductivity and with shallow water alkalinity samples.

CHAPTER III. RELATIONSHIP OF FISH TO BIOTIC COMMUNITIES

Introduction

According to recent reviews of the literature (Goetze et. al., 1989; Northcote, 1988), little is known about the effects of fish introductions on indigenous species and biotic communities occurring in high mountain lakes naturally barren of fish. The purpose of this chapter is to evaluate the possible effects of fish on crustacean zooplankton, macro-invertebrates, amphibians and reptiles. While most work on this subject has focused on intensive study of one or several lakes, this analysis takes a broader perspective by: 1) including a greater number of groups within the biotic community than has been done in other studies, and 2) comparing communities occurring in 55 lakes containing trout populations to 36 fishless lakes. Such an approach involved collecting a small amount of data on a large number of lakes. This approach increased the risk of obscuring pertinent relationships in noisy data, but also allowed development of patterns and conclusions based on the broad range of lake habitats and biotic communities of the region.

Specific objectives of the analysis are to evaluate the variation in biotic communities in terms of: 1) fish presence or absence, 2) potential prey vulnerability, and 3) fish population characteristics (relative abundance, condition, maximum weight and maximum length).

1. Fish presence and absence

Although generalizations concerning the effect of fish on biota over the whole range of diverse temperate lake systems is to be done with caution, Goetze et. al (1989) summarize four patterns that emerge concerning the effects of stocked fish on previously fishless high mountain lakes:

1) Introduced fish alter the structure of lake communities, in that the abundances and kinds of species present before stocking are not the same as after (from Brooks and Dodson, 1965).

2) Introduced fish also alter the organization of lake communities, in that the types and intensities of interactions among the various members of the lake community. In fact, changes in the organizational pattern may prevent species that became extinct from recolonizing lakes as long as the fish are present (Gliwicz and Rowan, 1984).

3) Lake systems whose biological communities evolved without the influence of a vertebrate predator have different species compositions than lake systems in which fish are present. Many species that have evolved in naturally fishless communities are extremely vulnerable to fish predation. Fish are known to have caused extinction of prey species in particular lakes (Nilsson and Pejler, 1973; Reimers, 1958).

4) As long as there are enough lake systems without fish within a region, those species that evolved in fishless lakes can persist. However, if a great majority of these lake systems are stocked, the persistence of some of these species within a region may become endangered.

Most research has focused on the effects of fish predation on particular species, the structure of zooplankton or benthic macro-invertebrate communities (Geotze et. al., 1989; Nilsson, 1972; Nilsson and Pejler, 1973; Stoddard, 1987; Reimers, 1958). Effects of trout introductions on distributions of amphibians and reptiles has not been studied, although several studies have documented behavioral differences (lower activity) in the presence of fish for salamanders related to the central race of the Long Toed Salamander (Ambystoma macrodactylum) found in the study area; namely A. gracile (Taylor, 1983), A. talpoideum and A. maculatum (Semlitsch, 1987). No research has evaluated the effects of fish on the structure of a larger biotic community composed of zooplankton, macro-invertebrates, amphibians and reptiles. For the northern Rocky Mountains of Idaho and Montana, virtually nothing is known about the possible ecological effects of trout introductions, although fish stocking has occurred on a regular basis in most of the larger lakes for more than 30 years (Bahls, in prep.).

2. Prey vulnerability

Many studies have implicated fish predation on vulnerable prey species as a primary cause of changes in the biotic community. However, Goetze et. al. (1989) state that the predator-prey relationship is only one of a multitude of complex interactions, varying in space and time, between biotic and physical components of the system that ultimately affect the structure of the biotic community. For example, the effect of predation can depend on the type of refuge areas available for prey (Crowder and Cooper, 1982; Macan, 1977, 1975; Weir, 1972) and fish introductions have been shown to cause changes in biotic structure through changes in mutualistic relationships or indirect facilitation (see Goetze et. al, 1989). Also, fish may have an indirect effect on biotic communities by altering nutrient cycles, such as sequestering phosphorus and nitrogen in their biomass, making these nutrients unavailable to lower trophic levels (Andersson et. al, 1988).

Although the role of predation in structuring communities is not well understood, numerous studies have documented some general characteristics of prey species that make them more vulnerable to predation than co-occurring species. These characteristics are large visible size, color, low escape ability and sharing the same habitat with the predator (Goetze et al., 1989). The purpose of the present analysis is to use the relative prey vulnerability of taxa to obtain an indirect measure of the role of predation in explaining the variability between lakes with and without fish.

3. Fish population characteristics

Many studies have documented a strong relationship between characteristics of a fish population, such as stocking density and condition, and the abundance and types of prey species present (Rabe, 1967, 1967, 1968; Johnston, 1973; Reimers, 1958,1979). However, in their review of the literature, Goetze et al. (1989) concluded that making the assumption that local extinctions and other changes in community structure and organization are a simple function of stocking density is, in light of the complexity of interactions, certainly erroneous. The purpose of this analysis is to evaluate the relationship between selected fish population characteristics, namely relative abundance, condition, maximum body length and weight, and the biotic communities occurring in high mountain lakes of the Moose Creek Ranger District.

Methods

1. Fish presence and absence

A. Ordination

Ordination by Detrended Correspondence Analysis (DCA) (Gauch, 1982) was used to organize the 91 lakes by biotic communities of zooplankton, aquatic macro-invertebrates, amphibians and reptiles. Ordination analysis, which allows the variability of multi-dimensional community data to be summarized along several axes, is a potentially useful method of separating the variability in lake communities related to the fish from that of the physical and chemical habitat. Fish population characteristics and physical and chemical habitat variables associated with each lake (see

General Methods, Chapter I) were used to interpret the variation in community structure by: 1) examination of the correlation coefficients (r^2 values) between each environmental variable and the ordination axes, and 2) overlays of environmental variables on the ordination plot of lakes in species space. The 1988 survey data was used for lakes surveyed more than once. Data from lakes surveyed during the 1988 spring snow-melt period were not used since the zooplankton and water chemistry analysis presented in Chapter 2 suggests that this period is not representative of summer conditions.

B. Multi-response Permutation Procedure

Multi-response Permutation Procedure (MRPP) was used to test whether the observed difference between biotic communities of fish and fishless lakes was statistically significant. MRPP is a non-parametric procedure for testing the hypothesis of no difference between two or more groups of entities. The MRPP test is based on the within-group average of pairwise distance measures between euclidean data space as compared to the null distribution of the test statistic based on the collection of all possible permutations of the objects into groups having specified sizes (Zimmerman, 1985). Discriminant analysis is a parametric procedure that can be used on the same general class of questions. However, MRPP has the advantage of not requiring assumptions (such as multivariate normality and homogeneity of variances) that are seldom met with community data (McCune, 1987).

The MRPP test, unlike ordination analysis, allows no intrinsic method of evaluating the difference in biotic communities related to fish from that of other factors, such as physical habitat characteristics. Differences in biota between fish and fishless lakes may be related to systematic differences in habitat between the two types of lakes. Only three lakes on the Moose Creek Ranger District are considered to have contained indigenous trout prior to stocking (Bahls, 1987). At present, trout inhabit all of the larger and deeper lakes (Figure 6). Fish occur in all 31 lakes with a surface area greater than 3.07 ha and all 16 lakes with a maximum depth greater than 14.5 m. Fish occur in only two of 15 lakes with a surface area less than 0.80 hectares and were absent in the seven shallowest lakes (<1.1 m). Seven lakes, ranging widely in maximum depth and surface acres, were stocked at least once in the past, but no longer contained fish.

Ordination analysis did not indicate a relationship between the community structure and either lake depth or surface area (see Results and Discussion). However, the non-random distribution of fish populations in relation to these variables, as discussed above, indicated the need to consider their potential influence in the MRPP test. The smallest (<0.72 ha) and most shallow (<0.6 ha) lakes, most of which were fishless, and the largest (>3.68 ha) and deepest (>14.9 ha) lakes, most of which contained fish, were not included in the analysis. The MRPP test included 24 lakes with fish and 24 lakes without fish within the middle range of maximum depth (0.6 - 14.9 m) and surface area (.72 - 3.68 m) (Figure 6).

C. Paired lake comparison

The purpose of this analysis was to compare the biota of a unique pair of physically similar lakes, one containing fish and one without. Although statistical limitations prevented making larger generalizations based on only two lakes, the analysis represented a third and complementary approach to evaluate the relationship between fish and the biotic community.

North and South Bellpoint lakes were located about 150 m apart, but were not connected by surface water. Physical

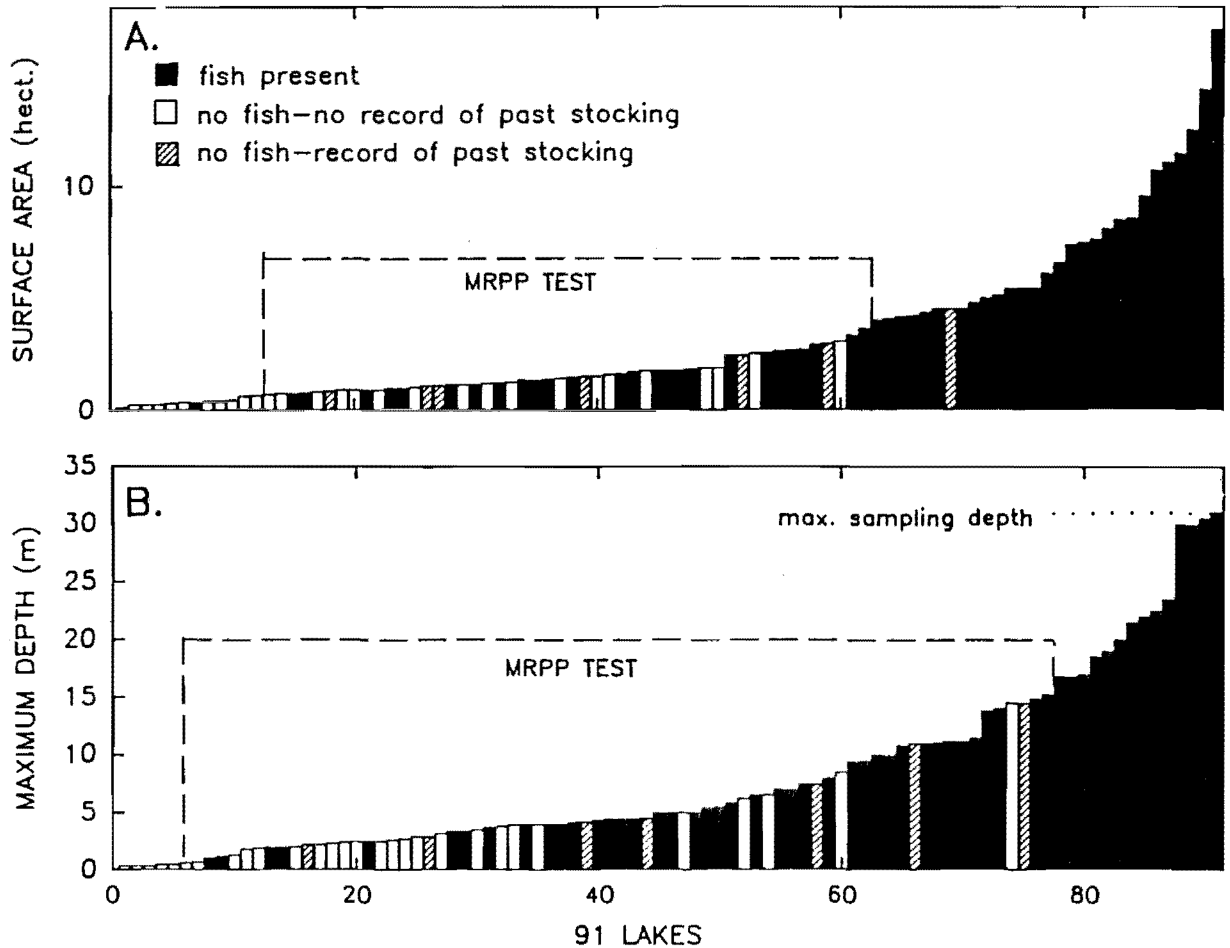

Figure 6. Status of fish populations in 91 lakes arranged by increasing surface area (A) and maximum depth (B).

and chemical characteristics of the two lakes were remarkably similar (Table 8). Very few people appeared to visit these remote lakes located two miles from the nearest trail and eight miles from the nearest road. No sign of human use was observed during three surveys in 1987 and 1988. Angling and gill net sampling indicated that South Bellpoint lake did not contain fish and no record of prior stocking was found. North Bellpoint lake contained a relatively abundant population of slow-growing rainbow trout and cutthroat trout which exhibited no natural recruitment. Ages of trout obtained by otolith analysis using the break and burn technique (Chilton and Beamish, 1982) were correlated with stocking dates and indicated that the rainbow and cutthroat trout were stocked in 1980 and 1982,

Table 8. Selected physical and chemical characteristics of North Bellpoint lake and South Bellpoint lake.

Parameter	Bellpoint, N	Bellpoint, S
elevation (m)	1933	1933
max. depth (m)	2.5	2.5
shallow (<3 m) littoral%	100	100
surface area (ha)	.36	.32
watershed area (ha)	7.74	16.63
pH (8/2/88)	7.01 ± .075*	6.88 ± .005*
conductivity (umhos/cm) (7/3/88)	7.75 ± .002*	8.15 ± .005*
conductivity (umhos/cm) (8/2/88)	8.70 ± .002*	8.15 ± .002*
alkalinity (ueq/L) (8/2/88)	67.46 ± .424*	60.75 ± .432*

*standard deviation

Table 9. Selected characteristics of the fish population sampled three times in South Bellpoint lake.

Fish population	Survey Dates		
	6/24/87	7/3/88	8/2/88
relative abundance (angling catch/hour)	6.7	4.5	4.6
mean condition	1.02+.016*	1.00+.0285*	1.00+.014*
max. length (mm)	243	277	278
max. weight (g)	135	202	203
number caught rainbow:cutthroat	8:3	5:4	4:3

*standard deviation

respectively. Fish sampling conducted once in 1987 and twice in 1988 showed that fish population characteristics remained fairly stable during this time period (Table 9).

Biotic communities were surveyed June 24, 1987, July 3, 1988 and August 2, 1988. In addition, during both surveys in 1988, more intensive benthic plot sampling was conducted in each lake. Insects were sampled in six benthic plots 25 m apart in each lake by placing an aluminum cylinder (1.5 m diameter, 1 meter height) 25 cm from shore and 10 cm deep in bottom sediments. A long handled net was used to scoop sediment from within the cylinder and to a sediment depth of about 10 cm. The dredged sediment was examined visually for aquatic insects. Insects were collected for later identification. Sampling of sediment by repeated dredging and searching was continued for a five minute period at each plot.

Statistical analysis involved comparing the two lakes for: 1) total number of taxa (t-test); 2) Jack-knife estimate of the total number of taxa in existence (Heltshe and Forrester, 1983); and 3) number of insect taxa in all benthic plot samples (t-test).

2. Prey vulnerability

Three approaches were used to examine the distribution of taxa among fish and fishless lakes relative to potential vulnerability to fish predation. First, taxa that had a greater than 20% difference in distribution between fish and fishless lakes were identified. Second, to allow a more systematic interpretation, taxa were lumped into six classes relative to vulnerability to predation and evaluated in terms of occurrence in fish and fishless lakes. Classification was based on two general characteristics of potential prey that probably determined their relative vulnerability to fish predation: body size and the type of habitat used (Goetze et al., 1989). The expected vulnerability of each class was then compared to actual differences in distribution between fish and fishless lakes to determine if there was a general correspondence. Prey classes are listed below in decreasing order of expected vulnerability.

1) Big/Water column - taxa greater than 3 mm in length and often found in open water. This group included the Western Long-toed Salamander (including larvae) , Chaoborus sp., Coleoptera, Notonectidae and Corixidae.

2) Surface - taxa found only on the water surface (Gerridae family).

3) Clinger - taxa usually found clinging on aquatic vegetation or on bottom substrates, but not restricted to living on or within bottom sediments. This group included Aeshnidae climbing dragonflies, Coenagrionidae, Tricoptera and some Ephemeroptera.

4) Crawler - taxa usually found in close association with lake bottom sediments. This group included some Odonata taxa, Chironomidae, Hyallela azteca (shrimp), Siphlonurus sp.(mayfly) and Sialus sp.

5) Semi-terrestrial - taxa of amphibians and reptiles usually found in the near shore zone of a lake. This group

included the Western Spotted Frog and Western Terrestrial and Common Garter Snakes.

6) Small/Water column - organisms less than 3 mm in length and often found in open water. This group consisted of crustacean zooplankton, including the large Diaptomus sp. (2-3 mm in length).

The third approach was an ordination of taxa by the lakes in which they occurred to determine if the distribution of taxa among lakes was related to vulnerability classes.

3. Fish population characteristics

Ordination analysis was used to determine the relation of fish population characteristics (relative abundance, condition, maximum body length and weight) to the structure of biotic communities. Circles representing the relative size of a characteristic and scaled in size from 0 to 100 percent of the range of the variable were overlain on the ordination of 91 lakes by taxa. To reduce the dimensionality of the data set, fish population characteristics were overlain on an additional ordination including only 55 lakes containing fish.

The analysis of the relationship between characteristics of the fish populations and the structure of biotic communities was potentially weakened by the high sampling error of characteristics measured (see Sampling Variability, Chapter 2). Thus, a second approach was utilized which did not rely on measurements of fish population characteristics per se, but on comparing distinct fish species that are generally regarded as having quite different population characteristics, namely brook trout (char) and rainbow and/or cutthroat trout. The ability of brook trout to spawn successfully and maintain dense populations of stunted fish in high mountain lakes is well known (Reimers, 1958). Brook trout were last stocked in the

1940's on the Moose Creek District and are estimated to naturally maintain high densities of stunted fish in 18 of 20 lakes containing this species (Bahls, 1987). Trout are generally less prolific spawners in mountain lakes, usually requiring large inlet or outlet streams for successful reproduction (Marcuson, 1976). To determine if there were broad differences between the biotic communities of lakes containing trout and brook trout, the two population types were identified on the ordination plot of 91 lakes ordinated by taxa and a second ordination including only 55 lakes containing fish. A random distribution of brook trout and salmonid populations among the diversity of lake habitats is probable, because brook trout populations occurred in 38% of the lakes containing fish and species were not stocked according to a systematic habitat evaluation.

Results and discussion

1. Fish presence and absence

A. Ordination

The ordination of the 91 lakes by taxa shows a distinct separation of fish and fishless lakes (Figure 7). Variation in communities along the first axis appears to be most strongly related to fish presence or absence. The distinct separation between biotic communities of fish and fishless lakes continues through all habitat types, suggesting the strong relationship of fish to the composition of the biotic community, regardless of physical lake habitat characteristics. Seven fishless lakes which were stocked more than ten years prior to the time of survey show no obvious differences from "pristine" fishless lakes. Assuming that prior to stocking these seven lakes contained biotic communities similar to those sampled in "pristine"

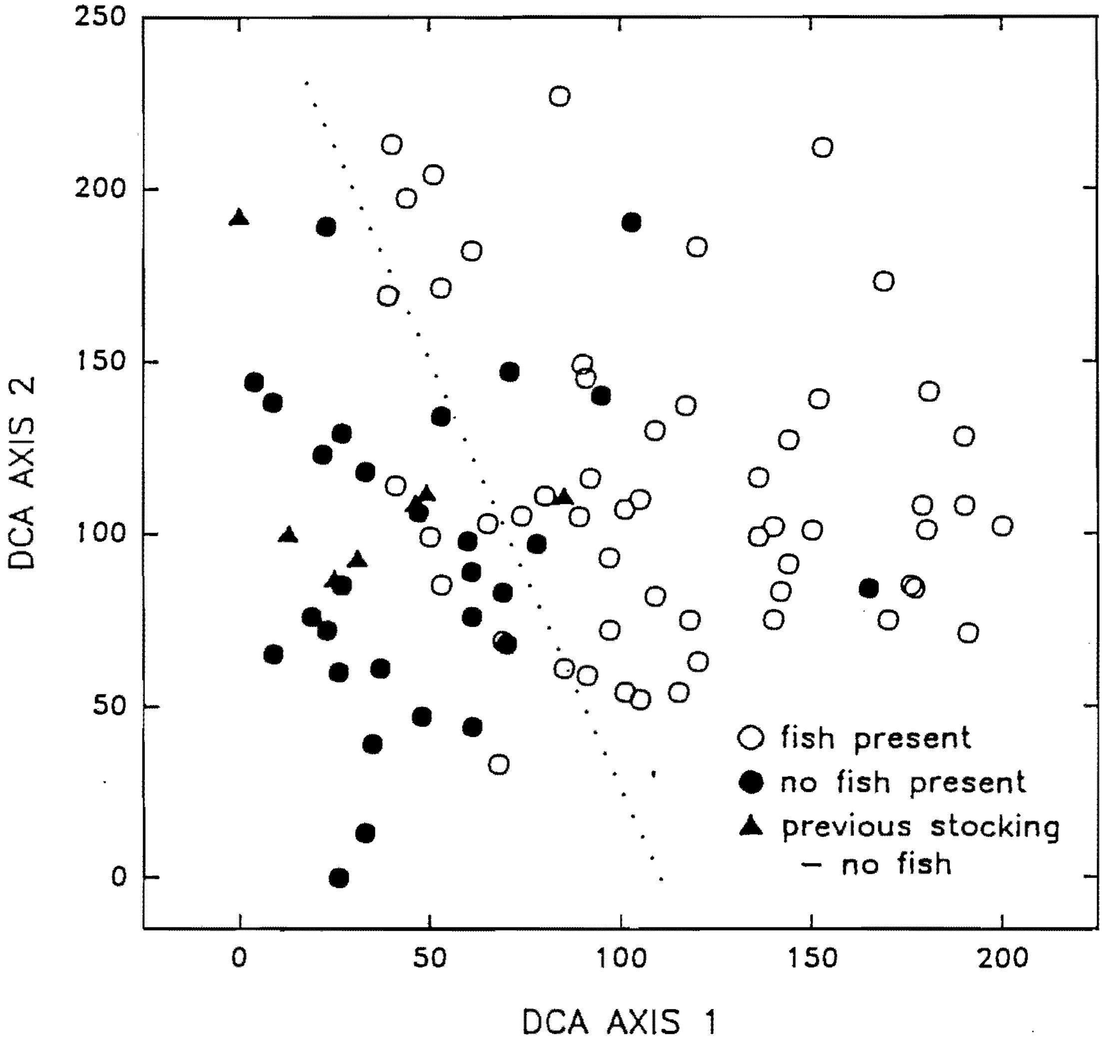

Figure 7. DCA ordination of 91 lakes by occurrence of taxa.

lakes, this observation suggests that in the absence of a fish population maintained by natural recruitment or periodic stocking, lakes can recover biotic communities similar to that which occurred before stocking was initiated.

Variation of communities along the second ordination axis is most closely related to various measures of bottom substrates (Figure 8). The percentage of substrate types in the littoral zone (arc-sin square root transformation of the weighted average of types, from silt = 1, bedrock = 5) and the percentage of sand and gravel littoral substrates (arc sin square root transformation) showed the strongest relationships (Figure 8). Although water chemistry data was obtained only for lakes sampled in 1988, conductivity appeared to be weakly related to the ordination of lakes along the second axis, with high conductivity restricted to lakes with finer substrates (Figure 8). No relationships were found among any of the first three ordination axes and other physical habitat characteristics considered, such as maximum depth, surface area or percent forest cover (see General Methods, Chapter I).

The distribution of individual taxa among lakes as shown by overlays of each taxon on the ordination of 91 lakes (Figure 8 and see Figure 7 for original ordination)

Figure 8. Overlays of environmental variables (circle size scaled from 0-100% of the total range of the variable) and presence (circle) or absence (dot) of individual species on the DCA ordination plot of 91 lakes by taxa. Environmental variables include the arc-sin transformation of the weighted average of percent bottom substrate types from 100% silt (1) to 100% bedrock (5), the arc-sin transformation of percent sand and gravel substrate and normal log of conductivity (dots indicate no conductivity data).

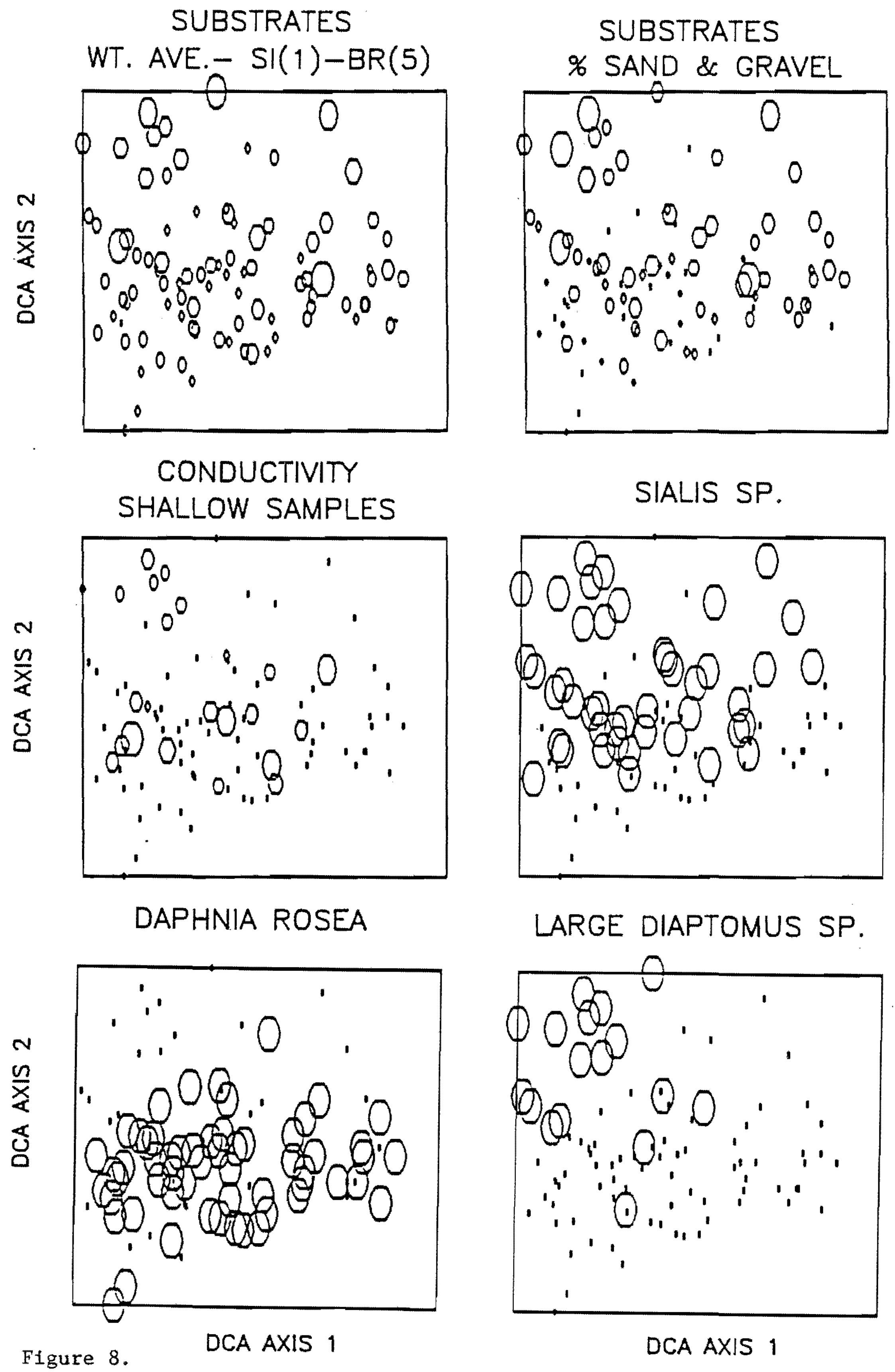
SUBSTRATES
WT. AVE.— SI(1)—BR(5)
SUBSTRATES
% SAND & GRAVEL
CONDUCTIVITY
SHALLOW SAMPLES
SIALIS SP.
DAPHNIA ROSEA
LARGE DIAPTOMUS SP.
DCA AXIS 2
DCA AXIS 2
DCA AXIS 2
DCA AXIS 1
DCA AXIS 1

Figure 8.

indicates that some species distributions are strongly related to physical habitat, regardless of fish presence or absence (Sialus sp., Figure 8). Crustacean zooplankton, Daphnia rosea and large Diaptomus sp., exhibit a negative association, with large Diaptomus sp. occupying the lakes dominated by mineral substrates in the shallow littoral zone, such as bedrock and boulders (large substrates) and sand and gravel (Figure 8). Daphnia rosea has been identified primarily as a montane species in previous studies in Canada (Anderson, 1971, 1974; Patalas, 1964) where it was found only rarely in alpine and subalpine lakes. The large, red Diaptomus sp. is probably D. shoshone, a large, highly pigmented species confined to high elevation areas (e.g. Sprules, 1987). D. shoshone is also reported as exhibiting a negative association with Chaoborus sp. (e.g. Sprules, 1987); also the case for the large Diaptomus sp. sampled in this study (Figure 8). A high percentage of exposed mineral substrates in the littoral zone may merely be an indicator of other habitat characteristics, such as low primary productivity and unique phytoplankton assemblages, to which large Diaptomus sp. is adapted or to which D. rosea cannot effectively compete with the calanoid. However, a causal relationship between large Diaptomus sp. and mineral substrates may also exist, since the author has frequently observed large Diaptomus sp. feeding on a fine organic layer (probably diatoms) attached to boulders near shore.

B. MRPP statistical test

Results of MRPP analysis indicate that fish and fishless lakes do not have similar communities ($p=0.0000$) for the 48 lakes tested that are within the middle range of maximum depths and surface areas. This finding gives statistical validity to the pattern observed in the ordination and strengthens the hypothesis that the observed difference between fish and fishless lakes is related primarily to fish rather than habitat characteristics.

C. Paired lake comparison

A significantly larger number of taxa were found during the biotic surveys in South Bellpoint lake (fishless) than in North Bellpoint lake (p=0.007) (Table 10). The Jackknife Estimate indicates that total taxa richness was significantly greater in South Bellpoint than North Bellpoint (confidence interval of 95%). The number of taxa in benthic plot samples was significantly greater in South Bellpoint than North Bellpoint for the first sampling period, July 3, 1988 (p=0.004) , but not for the second period, August 2, 1988 (p=0.19). When sampling periods were combined for a total of 12 plots from each lake, a significantly greater number of insect taxa were found in benthic plot samples from South Bellpoint (p=0.04). The weaker difference in species richness between lakes as obtained by the benthic sampling method relative to the general survey method is probably due to: 1) the small sample size, 2) sampling of aquatic insects only and 3) under-representation of the most vulnerable insect prey species, which swim in the water column and escaped entrapment by the benthic sampling cylinder as it was placed in the water. This difference between methods illustrated the potential for bias of using benthic data exclusively.

2. Prey vulnerability

A. General Distribution of Taxa

The relative vulnerability to predation of each taxon provides a likely explanation for the distinct differences

Table 10. Presence (1) or absence (0) of taxa sampled in three surveys (t1 - t3) of North Bellpoint lake (fish present) and South Bellpoint lake (no fish present).

	S. Bellpoint			N. Bellpoint		
Taxa	t1	t2	t3	t1	t2	t3
Callibaetis sp.	1	1	1	1	1	1
Aeshna sp.	1	1	1	0	0	0
Leucorrhinia sp.	0	0	1	0	0	0
Somatochlora sp.	1	1	0	0	1	0
Callicorixa audeni	0	0	1	0	0	0
Notonectid kirbyi	0	1	1	0	0	0
Gerris incognitus	1	1	1	1	1	0
Limnoporus notabilis	0	0	0	0	1	1
Ecclisisomyic sp.	0	0	0	1	0	0
Lenarchus sp.	0	1	0	0	0	0
Acilius sp.	1	1	1	0	0	0
Agabus sp.	0	0	1	0	0	0
Bidessus sp.	0	0	0	0	1	0
Haliplus sp.	1	1	1	0	0	0
Ceratopogonidae	1	0	0	0	0	0
Chaoborus sp.	1	1	1	0	0	0
Chironomidae	0	1	0	1	1	1
Chrysops sp.	0	1	1	0	0	0
Calanoida	1	1	1	1	1	1
Chydorus sp.	1	0	0	1	0	0
Cyclopoida	0	1	0	0	0	0
Daphnia rosea	0	1	1	0	1	1
Holopedium gibberum	1	1	1	1	1	0
Long-toed salamander	1	1	1	0	0	0
W. Spotted frog	1	1	1	1	1	1
Common garter snake	0	0	0	0	0	1
Number of taxa sampled	13	18	16	8	10	9
Total taxa present (Jackknife estimate, 95% C.I.)	25.6 - 29.1			18.3 - 19.7		

in biotic communities between fish and fishless lakes apparent in the ordination of 91 lakes by taxa (Figure 7). Many taxa occurred in a higher percentage of lakes without fish than lakes with fish, although several taxa occurred in a higher percentage of lakes containing fish (Table 11). The Long Toed Salamander (Central race), Chaoborus sp., some members of Coleoptera, Notonectidae, Corixidae and some members of Gerridae were in a much higher percentage of lakes without fish than lakes with fish. These taxa share several characteristics that might be expected of highly vulnerable prey species, namely large body size (> 3 mm) and occurrence in the water column or on the surface. The average number of taxa per lake comprising the biotic community and each sub-group of the community (except the crustacean zooplankton sub-group) was significantly higher (t-test, $p=0.000$) for lakes without fish than lakes with fish (Table 12).

Conclusions of this study regarding changes in taxa diversity and possible elimination of vulnerable taxa need to be carefully qualified. Identification of taxa to species was not possible for most specimens. Also, taxa found in less than five of the 91 lakes were clumped or deleted for ordination analysis (Appendix A). Thus, some taxa, such as Chironomidae (midges), may actually have increased in diversity of species with the effects of fish. The results of this study allow no conclusions regarding the effect of fish on the total number of species in communities. Also, vulnerable taxa may not have been completely eliminated from lakes with fish as the results imply, but may have gone undetected in sampling due to a vulnerable taxon's reduced population level or change in behavior to avoid predation. However, five of 11 taxa (45%) that had a much higher occurrence in fishless lakes than lakes containing fish (> 20% difference in percent occurrence) were also considered to have particularly high sampling reliability (Percent Re-occurrence > 60 and Percent Agreement > 90, Table 3). The same characteristics that seem to make taxa vulnerable to predation, i.e. large size, frequent occurrence in the water column and continuous aquatic existence during the summer season, also make for reliable sampling of these taxa. This suggests that some species of vulnerable taxa may actually have been eliminated from lakes containing fish.

Overlays showing the occurrence of individual taxa on the ordination of 91 lakes (see Figure 7 for original ordination) were useful for interpreting the distribution of selected taxa in relation to fish population characteristics and habitat variables (Figure 9). Some taxa were sampled in only a small percentage of fishless lakes, such as the large water beetle <u>Acilius</u> sp.. Other taxa were found in most of the fishless lakes with finer substrates, such as <u>Chaoborus</u> sp., collected from the water column as a 1-2 cm long larvae. <u>Limnoporus</u> <u>notabilis</u>, the largest water strider known from Idaho (Biggam, 1989), was mostly found in fishless lakes. The climbing dragonfly nymph, <u>Aeshna</u> sp., was collected from most lakes, excepting some brook trout lakes with high densities of fish. <u>Hyallela</u> <u>azteca</u>, a small benthic shrimp occurring in 10 lakes was found in a higher percentage of lakes containing fish than lakes without fish, including 5 lakes containing high densities of either brook trout or cutthroat trout. Finally, some species, such as the crustacean zooplankter <u>Holopedium</u> <u>gibberum</u>, were found to occur in most lakes with no apparent relationship to fish or physical habitat characteristics. However, distributions of individual taxa cannot be easily interpreted to provide information on the major variables influencing the structure of communities, particularly with the large number of uncommon taxa included in the analysis. Ordination analysis

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Figure 9. Overlays of presence (circle) or absence (dot) of individual species on the DCA ordination of 91 lakes by taxa (from Figure 7).

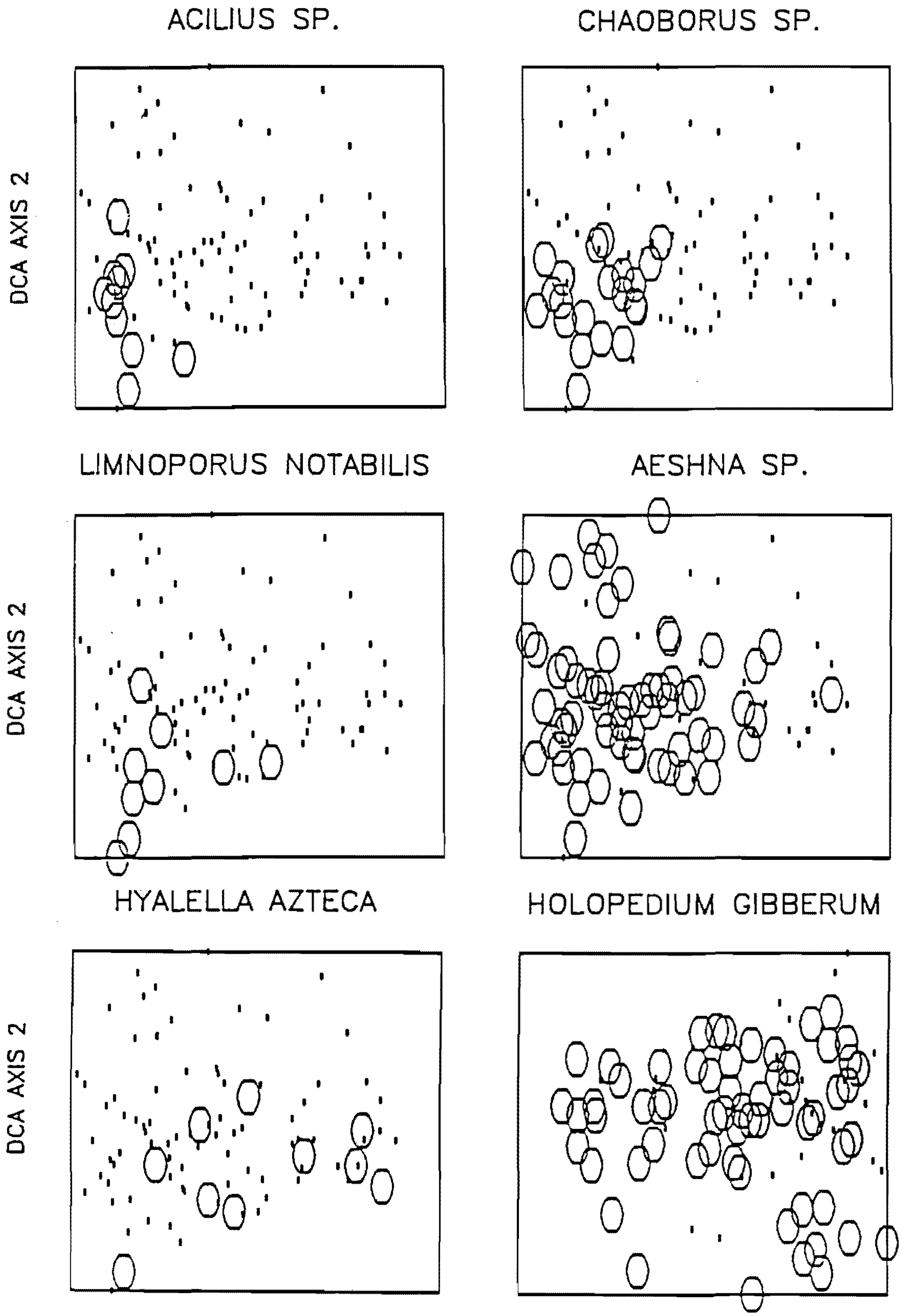
ACILIUS SP.
CHAOBORUS SP.
LIMNOPORUS NOTABILIS
AESHNA SP.
HYALELLA AZTECA
HOLOPEDIUM GIBBERUM
DCA AXIS 2
DCA AXIS 2
DCA AXIS 2
DCA AXIS 1
DCA AXIS 1

Figure 9.

Table 11. Number and percent of 36 lakes without fish and 55 lakes with fish in which each taxon was found. The full name of each taxon and list of 47 taxa used in the ordination analysis is given in Appendix 1. * > 20% difference for a taxon in % occurrence between lakes with and without fish.

Taxon Code	Without Fish No.lakes	Without Fish %lakes	With Fish No.lakes	With Fish %lakes
Ephemeroptera				
EPHEME	1	3	2	4
BAETID	1	3	0	0
CALLIB *	26	72	24	44
CENTRO	0	0	1	2
HEPTAG	1	3	2	4
AMELET	1	3	2	4
SIPHLO	3	8	7	13
Odonata				
ANISOP	1	3	8	15
LIBELL	1	3	4	7
ENALLA *	7	19	24	44
LESTES	1	3	0	0
AESHNA *	29	81	34	62
SOMATO	2	6	8	15
LEUCOR	11	31	15	27
Hemiptera				
CORIXI	3	8	7	13
ARCSUT	5	14	1	2
CALAUD *	20	56	9	16
HESLAE	1	3	0	0
SIGARA	3	8	4	7
NOTUSP	4	11	1	2
NOTKIR *	15	42	1	2
NOTUND	0	0	1	2
GERRID	4	11	8	15
GERINC *	17	47	9	16
LIMNOT	5	14	4	7
GERREM	2	6	7	13
BELOST	1	3	0	0
Tricoptera				
TRICSE	7	19	4	7
LIMNEP	8	22	5	9
ASYNAR	0	0	2	4
ECCLIS	0	0	1	2
HESPER	2	6	3	5
HOMOPH	1	3	0	0
LENARC	0	0	0	0
LIMNSP	2	6	2	4

Table 11. (continued)

Taxon	Without Fish		With Fish	
Code	No.lakes	%lakes	No.lakes	%lakes
Tricoptera (continued)				
NEOTHR	0	0	1	2
PSYCHO	7	19	3	5
LEPIDO	0	0	2	4
MYSTAC	1	3	0	0
PHRYGA	1	3	1	2
POLYCE	2	6	1	2
RHYACO	1	3	0	0
Coleoptera				
COLESE	6	17	5	9
AMPHIZ	0	0	0	0
GYRINI *	22	61	5	9
BEROSU	0	0	0	0
LACCOB	1	3	0	0
CRENIT	1	3	0	0
ENOCHR	0	0	1	2
HYDROB	1	3	0	0
HALIPL	0	0	1	2
HALGRA	1	3	1	2
HALLEE	0	0	0	0
ACILIU *	9	25	1	2
AGABUS *	14	39	8	15
BIDESS	1	3	1	2
COLYMB	0	0	0	0
DERONE	6	17	9	16
DEROVA	2	6	1	2
DYTISC	2	6	0	0
GRAPHO	1	3	0	0
HYDROV	1	3	0	0
HYDROP	1	3	2	4
ILYBIU	0	0	1	2
OREODY	2	6	3	5
RHANTE	3	8	0	0
Megaloptera				
SIALUS	17	47	27	49
Diptera				
CERATA	2	6	2	4
CHAOBO *	19	53	2	4
CULICI	2	6	1	2
CHIRON	23	64	43	78
CHRYSO	10	28	9	16
Amphipoda				
HYAAZT	1	3	9	16

Table 11. (Continued)

Taxon Code	Without Fish No.lakes	Without Fish %lakes	With Fish No.lakes	With Fish %lakes
Amphibia				
CLTSAL *	22	61	0	0
PGSALA	1	3	0	0
TAIFRO	1	3	0	0
WSFROG	30	83	44	80
Retilia				
WTGSNA	3	8	6	11
CGSNAK	6	17	4	7
Cladocera				
BOSMIN	1	3	9	16
CHYDOR	12	33	22	40
DAPROS	24	67	34	62
DIABRA	0	0	2	4
HOLGIB	22	61	40	73
POLPED *	5	14	23	42
SIDCRY	2	6	2	4
SCAKIN	6	17	10	18
MACROR	1	3	1	2
ALOQUA	1	3	0	0
Copepoda				
CALANO	31	86	50	91
LDIAPT	6	17	11	20
CYCLOP *	9	25	24	44
HARPAC	0	0	1	2

Table 12. Average number of taxa per lake and standard deviations for all taxa and sub-groups of benthic macro-invertebrates (BMI), amphibians and reptiles (A-R) and crustacean zooplankton from sampling of 55 lakes containing fish and 36 lakes without fish.

Biotic group	Average no.taxa/lake: No fish	Average no.taxa/lake: Fish
BMI	9.58 ± 2.60	6.18 ± 3.00
A-R	1.75 ± .95	.98 ± .67
Zooplankton	3.33 ± 1.08	4.16 ± 1.29
Total	14.69 ± 3.20	11.35 ± 3.67

provides an additional layer of information, indicating that variability in the distribution of taxa among communities is primarily related to the presence or absence of fish.

In an attempt to explain these patterns of species distribution among fish and fishless lakes, taxa were grouped into six classes of potential vulnerability to predation based on their aquatic body size and habitat usage (see Methods). The expected vulnerability of each class was found to closely correspond to the relative percentage of fish and fishless lakes in which the class occurred. (Table 13). Climber, surface and big/water column classes, in increasing order of expected vulnerability, occurred in an increasingly larger percentage of lakes without fish than lakes with fish.

A more detailed analysis of the distribution of taxa among lakes was possible by overlaying prey vulnerability classes on an ordination of the 47 taxa according to the lakes in which they occurred (Figure 10). Variability in the distribution of a taxon among lakes appeared to be related to a gradient of increasing vulnerability to predation along the first axis of the ordination. Taxa within the classes

Table 13. Number and percent of fish (F) and fishless (NF) lakes in which at least one taxon in each prey vulnerability class was found.

Prey vulnerability	No.	No Fish		Fish		NF-F
class	Taxa	#	%lakes	#	%lakes	%diff.
big/water column	14	36	100.0	30	54.5	45.5
surface	4	24	66.7	27	49.1	17.6
climber	9	36	100.0	50	90.9	9.1
semi-terrestrial	3	30	83.3	44	80.0	3.3
benthic	8	34	94.4	53	96.4	-1.9
small/water column	9	35	97.2	55	100.0	-2.8

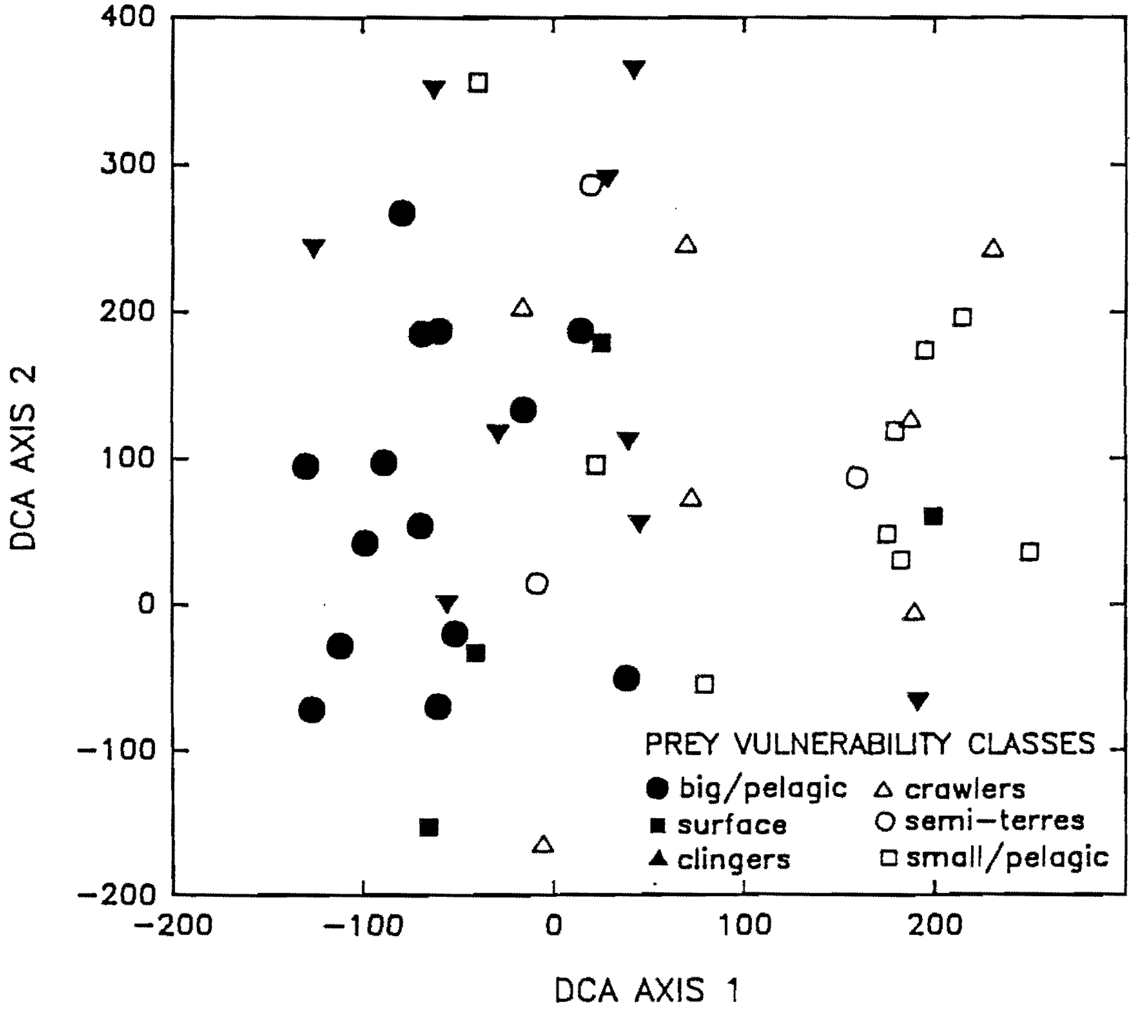

Figure 10. DCA ordination of 47 taxa by 91 lakes in which they occurred.

expected to be most vulnerable to fish predation were clustered together on the left side of the axis, occurring in many of the same fishless lakes. Thus, the ability to explain much of the variability in the distribution of taxa among lakes based on a general classification of their relative vulnerability to predation provides a strong biological basis for suggesting the importance of predation in structuring biotic communities.

B. Paired lake comparison

A comparison of taxa sampled during each survey at Bellpoint, North and Bellpoint, South lakes (Table 10) indicated that aquatic Coleoptera, Western Long-toed Salamander and Aeshnidae climbing dragonfly were consistently sampled in the fishless lake, but were not found in the lake with fish. These findings are consistent with the prior analysis which suggested that the larger (>3 mm) species frequently using the water column are the most vulnerable to predation and eliminated from lakes with fish.

3. Fish population characteristics

Overlays of fish population characteristics on the community ordination of 91 lakes by taxa discussed previously (see Figures 7 and 8) show that fish populations with the longest fish occurred in lakes with biotic communities most similar to fishless lakes and in lakes dominated by rock substrates (Figure 11.A) Overlays of fish condition exhibited a similar, but weaker pattern, with higher condition fish populations occurring in lakes with biota most similar to fishless lakes (not shown). Relative abundance showed no apparent relationship to community structure, probably due to the high sampling variability associated with this parameter. The pattern of increasingly strong relationships between biotic community composition and the fish population characteristics of relative abundance, condition and maximum body length and weight, respectively, probably reflected in part the general decrease in sampling error for these parameters (see Chapter II). Overlays on the community ordination including only the 55 lakes containing fish showed a similar pattern in the relationship between fish and biotic communities (Figure 11.C).

The occurrence of larger fish in lakes with communities most similar to fishless lakes probably reflected the effect of density dependent predation by fish on biotic communities. However, density of populations could only be assessed indirectly by assuming an inverse relationship of density to fish condition and maximum body length. A high intensity of fish predation, such as in lakes containing a dense population of stunted brook trout, would be expected to reduce the diversity and presumably the abundance of potential prey species. Under such conditions, growth rate and condition of fish would be low due to both the larger number of individuals competing for food and the impacted prey base. In contrast, a smaller population of fish would be expected to cause a lesser reduction in the diversity and abundance of biota and lakes would remain more similar to fishless lakes. Individual fish would be larger due to the higher growth rate and condition possible with fewer individuals competing for food and a better condition prey base.

Figure 11. Overlays of fish maximum body length (circle size scaled to fish length) on the DCA ordination of 91 lakes by taxa and a DCA ordination including only 55 lakes with fish. Large <u>Diaptomus</u> sp. distribution (E) and substrate type (F) are overlain on the DCA ordination of lakes with fish.

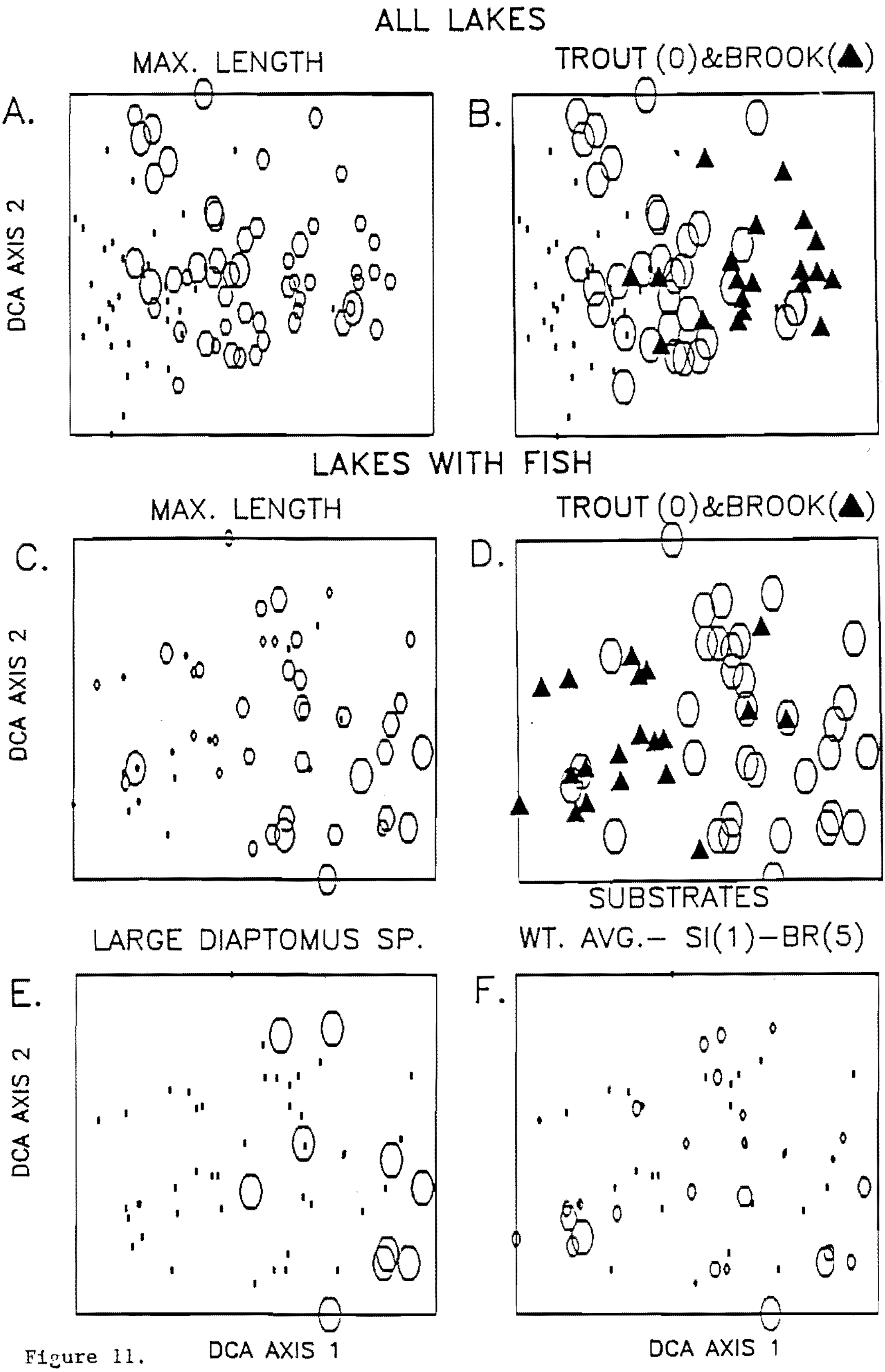
ALL LAKES
MAX. LENGTH
TROUT (0)&BROOK(▲)
A.
B.
DCA AXIS 2
LAKES WITH FISH
MAX. LENGTH
TROUT (0)&BROOK(▲)
C.
D.
DCA AXIS 2
SUBSTRATES
LARGE DIAPTOMUS SP.
WT. AVG.– SI(1)–BR(5)
E.
F.
DCA AXIS 2
DCA AXIS 1
DCA AXIS 1

Figure 11.

Physical and chemical variations in lake habitats were also expected to influence fish population characteristics. The finding of the larger fish in lakes containing high percentages of rocky substrates, exhibiting low conductivity and occurring at high elevations seems to contradict established theories that relate habitat features to prey productivity (see Chapter IV). However, these lakes support a large (2-3 mm), red pigmented Diaptomus calanoid that some fish feed on selectively. The small size and abundance of this prey item may make it a stable food source relatively invulnerable to low-intensity predation. Figures 11.C and 11.E illustrate the correspondence between lakes supporting large fish and lakes supporting the large Diaptomus sp. However, large Diaptomus sp. was not found in lakes containing brook trout (typically high density populations, although some of these lakes appeared to have suitable habitat as indicated by a high percentage of mineral substrates (Figures 11.D, E and F). (See Figure 8 for the relationship of large Diaptomus sp. to substrate type). Thus, the relationship between fish size and the biotic community probably reflects a complex interaction between the effect of particular prey species associated with certain lake habitats on fish and the effect of variable fish predation pressure on biotic communities.

An overlay of trout and brook trout populations on the ordination of 91 lakes by taxa shows that variation in communities is strongly related to the type of fish population, with a progression along the first axis from biotic communities of fishless lakes to trout lakes to brook trout lakes (11.B). The first axis may represent an underlying gradient of increasing fish predation pressure, since communities generally decreased in diversity along the axis and brook trout populations were generally more dense than trout populations (see Chapter IV). An overlay of trout and brook trout populations on the ordination of 55 lakes with fish again shows a distinct separation between brook trout and trout lakes along the first axis (11.D). Variation of biotic communities is weakly related to other environmental variables along the second axis, most notably to substrate types (11.F). Because brook trout and trout populations were assumed to be fairly randomly distributed among lake habitat types (see Methods) and communities were not related to habitat variables along the first axis in either ordination, the broad differences in biotic communities between lakes with brook trout and lakes with trout (Figures 11.B and 11.D) provides stronger circumstantial evidence that the relation between fish populations and biotic communities is primarily due to the effect of fish on biota, rather than the effect of variation among lakes in physical habitat and associated prey types on fish.

Considering the higher density and degree of stunting typical of brook trout populations (see Methods), differences between brook trout and trout populations in the type and intensity of predation are probably largely responsible for the observed differences in biotic communities. The sampling of significantly fewer taxa in each brook trout lake than each salmonid lake supports this theory.

Summary

1) Biotic community composition, in terms of presence or absence of taxa of zooplankton, macro-invertebrates, amphibians and reptiles, is strongly related to the presence or absence of fish.

2) Predation by fish on vulnerable prey appears to be a major cause for differences in biotic communities between lakes with fish and lakes without fish.

3) Characteristics of the fish population (fish species, condition and maximum body length) are related to the composition of the biotic community, probably through

both the effect of fish in depleting the prey base and the effect of variation in lake habitat and prey type on fish.

Although numerous studies have documented the effect of predation by fish in eliminating particular prey species (see Introduction), this study provides the first documentation of the effect of trout on a larger biotic community composed of crustacean zooplankton, aquatic invertebrates, amphibians and reptiles. Similarly, most studies have focused on species interactions occurring in one or several lakes and conclusions are necessarily limited. This study documents the dominant role of fish in relation to the structure of biotic communities for the range of fish populations, habitat conditions and biotic communities occurring within a large geographic region.

This study represents the first evaluation of the effect of fish on biotic communities of high lakes in the Rocky Mountains of North America. Subsequent sampling in 1989 of an additional 99 lakes of the Nez Perce National Forest and located in the portions of the Frank Church - River of No Return Wilderness, Gospel Hump Wilderness and Hells Canyon Wilderness yielded similar results; large differences between the biotic communities of fish and fishless lakes (Bahls, 1990). However, preliminary findings of a similar on-going study in the North Cascades of Washington State did not show the pronounced relationship of fish presence or absence to the structure of biotic communities found in this study (William Liss, Department of Fisheries and Wildlife, Oregon State University, personal communication). In the North Cascades study, the effect of fish on biotic communities is probably obscured by a number of sampling problems. First, the North Cascades area may have a greater diversity of biotic communities due to a greater diversity of lake habitats (more diverse bedrock geology, geomorphology, climatic conditions and terrestrial vegetation types). Second, the North Cascades study includes a smaller number of lakes containing brook trout (one versus

20). In the present study, brook trout appeared to have a greater impact on biotic communities than salmonid populations. With few lakes containing brook trout included in the North Cascades study, differences between communities of fish and fishless lakes might not be as clear. Third, the North Cascades study includes a smaller number of lakes and smaller number of fishless lakes, especially at lower elevations, than were included in the present study. In summary, large differences between biotic communities of fish and fishless may be obscured in the North Cascades study by a smaller sample size of lakes with possible under-representation of fishless lakes, lesser impacts of fish due to fewer lakes with brook trout and higher variability between communities due to more diverse lake habitats.

In relation to theories of community structure and organization, this study adds support to the bottom up:top down model of community interactions (McQueen et al., 1989). Although analysis of the effect of predation on each sub-group of the biotic community (crustacean zooplankton, aquatic invertebrates, amphibians and reptiles) was beyond the scope of this research, the general analysis indicated that impacts of fish were most severe on the more vulnerable prey taxa, which occurred in the higher trophic levels. Conversely, the occurrence of large, red Diaptomus sp. in lakes with certain physical habitat characteristics and the apparent positive effect of this zooplankter on fish growth, average fish condition and attainable body length, suggests the bottom up influence of lower trophic levels on higher levels. Additional research on the relation of fish population characteristics (such as density and condition) to each sub-group of the community may reveal additional effects on trophic levels that were obscured in the broader analyses.

Based on the results of this study, stocking of a fishless lake in this region would probably result in a significant change in the biotic community inhabiting the lake. Larger, more vulnerable species would be reduced in number, or possibly extirpated from the lake. Such an action would not be in accordance with the 1964 Wilderness Act governing the management of this region, which states that each Wilderness Area is to be "protected and managed so as to preserve its natural conditions" (Public Law 88-577). With relatively few lakes remaining in a naturally fishless condition, particularly deep, large lakes, stocking a fishless lake risks losing unique types of communities or species from an entire region (Goetze et al., 1989). Also, stocking a fishless lake risks additional colonization of downstream systems by exotic species, an impact which may already be widespread in the region (Bahls, 1990). Under the Wilderness Act, federal policy and guidelines concerning fish stocking state that "aerial stocking of fish shall be permitted for those waters in Wilderness where this was an established practice before Wilderness designation" [and], "barren lakes and streams may be considered for stocking, if there is mutual agreement that no appreciable loss of scientific values or adverse effects on wilderness resources will occur" (USDA, 1986). The significant impact of fish on biotic communities suggested by this study would seem to indicate that stocking of a fishless lake would violate federal management policy by constituting both an appreciable loss of scientific values and adverse effects on wilderness resources.

The existing abundance of lakes containing a diversity of fishery recreation opportunities and rarity of lakes remaining in a naturally fishless condition increases the importance of maintaining lakes without fish. Naturally fishless lakes are valuable as representative, pristine lakes for wilderness and natural heritage purposes and as baseline areas for scientific research and environmental monitoring (i.e. the effect of acid precipitation on Long Toed Salamanders). Furthermore, an adequate number and distribution of fishless lakes may be necessary to maintain the biological diversity and ecological integrity of aquatic systems within a region; serving such functions as genetic reservoirs for periodic recolonization of prey species in lakes with fish and allowing restoration of natural communities in lakes that have been mistakenly stocked. In consideration of the potential for trout introduction to alter biotic communities of naturally fishless lakes and the rarity, unique values and the legal management guidelines associated with these lakes, fishless lakes (including seven lakes recorded as having been previously stocked) are recommended for maintenance without fish stocking.

A second management recommendation is prompted by the apparent density dependent relationship found in this study between characteristics of the fish population and the organization of biotic communities. Biotic communities containing fish and most dissimilar to communities of naturally fishless lakes were often those containing fish populations with a relatively lower average condition rating and smaller maximum body size (stunted or dense populations). In an attempt to lessen possible impacts of fish on biotic communities, as well as increase the fishery quality (fish body size and condition) of particular lakes, no further stocking is recommended for potential self-sustaining trout populations (potential wild trout lakes). For fish populations where future sustainability without stocking is in question, a ten year suspension of stocking followed by a fish population survey is recommended to determine the fishery status. An fishery analysis of 190 lakes in the Nez Perce National Forest found that about 50 percent of the 137 lakes containing fish were potential wild trout lakes and that 50 percent of these wild trout lakes had been stocked about every three years (Bahls, 1990). Thus, the approach of maintaining potential wild trout lakes and fishless lakes without further stocking appears to hold potential for greatly improving the condition of fisheries and aquatic ecosystems.

CHAPTER IV. RELATIONSHIP OF FISH CONDITION AND MAXIMUM LENGTH TO FISH POPULATION AND HABITAT VARIABLES

Introduction

Much of the limited research on mountain lakes has documented an inverse relationship between stocking density and the condition and growth rate of trout (Rabe, 1967, 1968; Donald and Anderson, 1982; Mottley, 1941; Larkin et al.,1957; Rawson, 1956). Most high lake fisheries survey and management efforts have focused on developing stocking rates (i.e. number of fish stocked and frequency of stocking) for individual lakes based on estimates of lake productivity and expected angling pressure (Johnston, 1973; Nelson, 1988). However, no long-term evaluation or testing of stocking rate models has been conducted and little is known about the relative importance and interactions of stocking rate and other environmental variables to fish population characteristics in high mountain lakes. For example, two important characteristics, fish condition and growth, are probably not simple functions of stocking rate and lake productivity, but expressions of the complex interactions among habitat, angling pressure, stocking rate, fish survival, the level of natural recruitment and species. The objective of this chapter was to determine which descriptive variables, including stocking rate, best predicted the average condition and maximum body length of the fish population in a given lake.

Methods

Maximum body length and average condition were chosen as fish population characteristics to be used as dependent variables in the analysis for four reasons: 1) low seasonal sampling variability (Chapter II); 2) relevance to fishery management in terms of fish health and recreational opportunity; 3) direct relationship to condition of the prey base, and 4) best available general measures of fish growth rate.

Based on a conceptual model (Figure 12), selected environmental and fish population variables were evaluated to assess their relation to fish maximum body length and average condition. Methods used to obtain measurements of the ten independent variables used in the analysis are described below.

SPECIES (categorical, 1 or 2) - lakes dominated (>10:1 sampling ratio) by 1) brook trout or 2) rainbow and/or cutthroat trout.

NATURAL RECRUITMENT (categorical 1, 2, 3 or 4) - qualitative estimate of the level of natural recruitment occurring in a fish population based on the size (length) classes of fish sampled, correlation with stocking records, observation of fry or fingerlings in stream inlets, outlets and littoral zone, and potential stream spawning habitat; 1 = no evidence for natural recruitment, 2 = possible natural recruitment, 3 = low to moderate natural recruitment, 4 = high natural recruitment.

CAMPSITE IMPACT - Surveyors classified sites based on a qualitative estimate of the percentage duff layer and perennial vegetation remaining on the site (Bahls, 1989). Campsite impact represented the sum of each low (1), moderate (2) and high (4) impact site.

ACCESS DISTANCE (LOG) - the weighted sum of the distance from the nearest access road to a lake as measured in .5 mile increments on a 1:100,000 trail map. Each mile of trail was weighted as follows: main trail = 1, minor trail = 4,

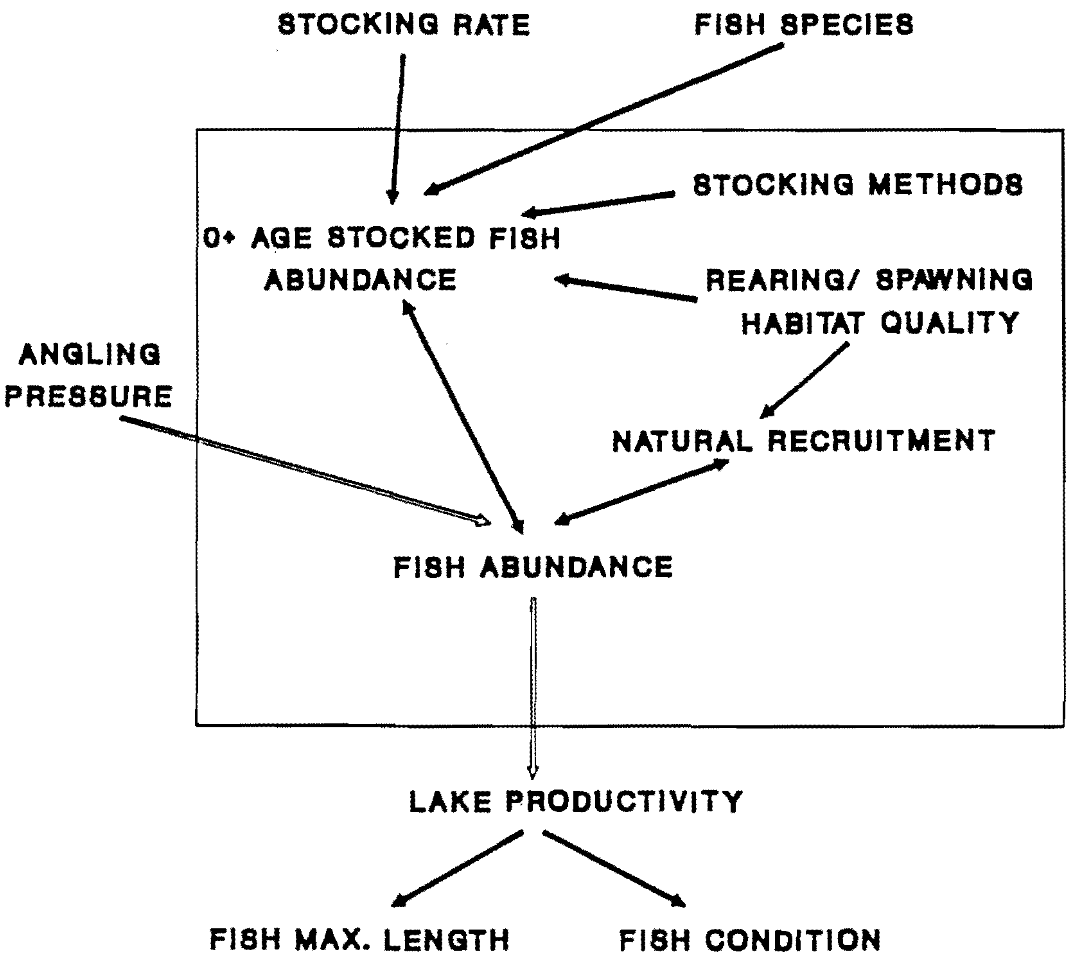

Figure 12. A conceptual model of the relation of maximum body length and average condition of a fish population to environmental and population variables. An arrow indicates the direct (solid arrow) or inverse (clear arrow) effect of one variable on another. Variables outside of the box were used in stepwise regression analysis.

and bushwack = 8.

ELEVATION - lake surface elevation obtained from USGS 7.5 minute topographic maps.

LARGE DIAPTOMUS - presence (1) or absence (0) of the large (>2 mm) red pigmented Diaptomus sp., as determined from zooplankton samples.

BOTTOM SUBSTRATES - the weighted average (transformed by arc-sine square root) of percentage bottom substrates in the shallow littoral zone from 100% silt (1) to 100% bedrock (5).

SHALLOW LITTORAL - percentage (transformed by arc-sin square root) of the lake surface area between shore and the three meter contour interval.

BASIN AREA - lake watershed area (planar) obtained from USGS 7.5 minute topographic maps.

STOCKING RATE - an estimate of stocking density that accounted for stockings during a seven year period prior to the year of survey. An annual survival percentage of 90 percent of the original stocking was assumed. This survival estimate was based on Nelson's (1988) estimate of about 50 percent annual survival in a high lake in Colorado that received annual plantings. Survival was assumed to be substantially higher in lakes of the study area due to less frequent stocking (usually every third year), much lower angling pressure and more amenable lake habitats for rearing and growth of fish (e.g. lower elevation, woody debris for rearing cover). Stocking rate was calculated as the sum of annual survival per surface acre for each stocking that occurred during the seven year period. Data on the number of fish stocked each year were obtained from records kept by the Idaho Department of Fish and Game. Trout were usually stocked as fingerlings (3-5 cm length) by fixed wing aircraft in August or September.

Fish populations were grouped by specific characteristics into five classes for analysis: 1) all 74 populations surveyed between 1986 and 1988; 2) 51 populations containing rainbow and/or cutthroat trout; 3) 23 populations containing brook trout; 4) 50 populations stocked within seven years from the time of survey; and 5) 18 populations exhibiting no natural recruitment.

Multiple regression with stepwise backward selection was used to build models of maximum body length and condition for each fish population class. Some descriptive variables could not be evaluated for particular fish population classes, since the variable was constant for all populations in the class (e.g. high level of reproduction for all brook trout populations). Descriptive variables with an F ratio of less than 4 were progressively eliminated from the model. All descriptive variables and final models had significance levels of less than $p = 0.05$. To avoid spurious correlations, the maximum number of independent variables in a single model was limited to one-third the size of the number of fish populations in the smallest class, with the exception of Class 5 which included data from only 18 fish populations. Values of r^2 were calculated to evaluate the goodness-of-fit of multiple regression models.

Results and discussion

Results of the stepwise regression analysis (Tables 14 and 15) are summarized below.

1) Most of the variability of average condition and maximum body length was not accounted for by final models.

2) Natural recruitment and fish species were used as predictors of maximum body length and condition for all fish

Table 14. Coefficients of independent variables, r^2 and p values for final models of FISH CONDITION for each fish class. Variables that were constant values for a fish class (*) were not included in the analysis.

Independent variable	Fish class				
	All (1)	Stocked (2)	Rbw/Cut (3)	Brook (4)	No recr. (5)
Stocking rate				*	
Species	-.014	*	*	*	*
Natural recruitment	-.007	-.007	-.008	*	*
Camp impacts	+.002	+.002	+.003		+.002
Access distance				-.027	-.040
Elevation					
Large <u>Diaptomus</u> sp.			+.010	*	
Substrate types					
Littoral %					
Basin area					
Model r^2	.20	.27	.32	.26	.48
Model p	.0003	.0003	.0001	.0078	.0150

Table 15. Coefficients of independent variables, r^2 and p values for final models of FISH MAXIMUM LENGTH for each fish class. Variables that were constant values (*) for a fish class were not included in the analysis.

Independent variable	Fish class				
	All (1)	Stocked (2)	Rbw/Cut (3)	Brook (4)	No recr. (5)
Stocking rate	-.066			*	
Species	+65.691	*	*	*	*
Natural recruitment	-26.351	-34.730	-39.886	*	*
Camp impacts					
Access distance				-30.206	
Elevation	+.072	+.111	+.142	+.032	
Large <u>Diaptomus</u> sp.	+63.180	+52.303		*	+114.738
Substrate types				-116.459	-470.527
Littoral %					-375.523
Basin area		+93.239	+123.178	-27.206	
Model R2	.56	.37	.35	.67	.55
Model P	.0000	.0001	.0000	.0001	.0026

classes in which this variable could be evaluated (Class 1,2 and 3).

3) Angling pressure estimates (campsite impact level and access distance) were predictors of fish condition for all fish classes.

4) Habitat characteristics, especially presence of large Diaptomus sp. and elevation were predictors of maximum body length for all fish classes.

5) Stocking rate, as measured, was not a significant predictor of fish population characteristics for any lake class except Class 1 (all populations), where it may have been a spurious correlation.

Although the low r^2 values for nearly all final models suggest that much of the variability remained undefined, the positive and inverse relationships (denoted by positive and negative coefficients, respectively) of angling pressure, natural recruitment and habitat variables to fish maximum body length and average condition were generally consistent among fish classes. Also, the relationships determined in final models were consistent with the relationships portrayed in the conceptual model (Figure 12). Stocking rate was used as an independent variable only in Class 1 (all populations), suggesting that increased stocking rate is correlated to decreased condition. The large number of unstocked lakes included in this class makes this finding dubious at best and probably a spurious correlation. It may be that the influence of stocking rate was not adequately represented by the variable used in the model, especially considering the difficulty in accurately assessing this factor. Using stepwise regression methods, Donald and Anderson (1982) found that 38 percent of the variability in weight of age two rainbows in 23 mountain lakes of west-central Alberta could be attributed to stocking density and 42 percent to total dissolved solids. The present study differs substantially from theirs by examining the influence of a diversity of stocking rates on the average condition and maximum body length of the fish population as a whole, rather than the effect of a single stocking on the growth rate of one age class of one species. Thus, within the broader context of diverse stocking rates, fish populations and lake habitats included in this study, the influence of stocking rate on average fish condition and maximum body length appeared to be relatively insignificant.

Perhaps the most important finding is that the level of natural recruitment was included as a descriptive variable for all fish classes for which it could be evaluated (an exclusion of Class 4 (brook trout with high natural recruitment) and Class 5 (no natural recruitment)). Models based on Class 1 (all populations) , Class 2 (stocked) and Class 3 (rainbow and/or cutthroat) predict that condition and maximum body length increase with a decreasing level of natural recruitment. Also, the use of fish species (brook trout or trout) as a descriptive variable in models of maximum body length and condition for Class 1 probably reflects the high correlation of fish species (brook trout or trout) to the level of natural recruitment in both models (.68 and .59, respectively). All brook trout populations were estimated to have high levels of natural recruitment relative to low to moderate levels of recruitment estimated for most trout populations. Dense populations of stunted brook trout would be expected to have relatively smaller maximum lengths than trout populations, as indicated in the model (Table 15).

Average condition of fish populations exhibited an opposite pattern, with brook trout in better condition than trout. Stunting, or the suppression of growth, provides the most likely explanation for this pattern. Fish stunted at a small size would require less food to maintain their weight, and hence condition (a length to weight ratio). Also, independent of the possible effects of stunting on condition, brook trout body shape may be slightly different than trout, yielding higher conditions relative to the overall regression line.

In addition to natural recruitment, one or both measures of angling pressure were included in models of average condition for all fish classes. Increased campsite impacts and decreased access distances were inversely related to increased fish condition, as might be expected if higher angling pressure resulted in a smaller fish population with more food available for each individual. The presence or absence of large Diaptomus sp. appears to be of minor importance in relation to fish condition; this variable was included for Class 3 populations only.

Habitat variables, not angling pressure estimates, were used in models of maximum body length for all classes with the exception of Class 4 (brook trout) where both angling pressure and habitat variables were used. Presence of large Diaptomus sp. was related to increased maximum body length for Classes 1,2 and 5, suggesting that this was an important food resource. Large Diaptomus sp. was restricted primarily to lakes containing rock substrates (see Chapter III), but was not found in association with brook trout populations (Class 3). The abundance and small size of this prey probably allows a reliable food source that can only be decimated by an extremely dense population of fish such as occurs in most lakes containing brook trout. Fish stomach contents indicated that some fish fed selectively on this prey type.

Basin area, elevation, percent shallow littoral area and substrate types were also included in various combinations as predictors of maximum body length. These variables may be related to the productivity of the habitat for sustaining fish growth and/or the level of natural recruitment occurring in the lake. For Class 4 populations (brook trout), habitat variables were probably related to the level of natural recruitment and winter survival. Maximum body length of brook trout populations was predicted to be greater in lakes with shorter access distances (higher angling pressure) as might have been expected, but also lakes occurring at higher elevations in smaller watersheds and containing a larger proportion of smaller substrates. These habitats may provide less suitable spawning and rearing habitat due to lower water temperature (higher elevation), marginal spawning substrate (silt) and insufficient surface and ground water flow (smaller watershed size) required for spawning sites (Webster and Gudny, 1976). Partial winter kill of fish populations due to oxygen depletion under the ice cover might also be more frequent in higher elevation lakes with less water flow.

The use of habitat variables, but not measures of angling pressure, in models of maximum body length may be due to a non-linear effect of high angling pressure in removing the fish before they become large, while also increasing fish growth rate and condition of the surviving fish. Low angling pressure may promote higher survival and longevity, but also a denser population of fish unable to grow to a larger size due to insufficient food resources.

Summary

Although stocking density has been implicated in numerous studies as an important factor in determining fish population characteristics that reflect growth rate, such as average condition and maximum body length of fish, this study suggests that for the wide range of lake habitats and fish population types actually occurring within a region, natural recruitment, angling pressure and lake habitat characteristics may play a more important role in determining characteristics of the fish population. Broadening research and management efforts to consider these factors may provide more effective means of manipulating existing fish populations to improve the quality of high lake fisheries (larger size and condition of fish). The recommended priority for high lake fishery researchers and managers is to take immediate action to develop and implement reliable and rapid means of identifying lakes containing self-sustaining trout populations (wild trout lakes) and discontinue stocking of these lakes. In addition, the potential for using more restrictive angling regulations (i.e. limits on the size and number of fish caught) to maintain quality wild trout fisheries needs to be evaluated.

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APPENDIX

APPENDIX A. TAXA LIST

APPENDIX A. List of taxa (and code names) identified from 125 lake surveys, 1986-1988. The list denotes the 47 taxa included in sampling variability and ordination analysis (X). Taxa occurring in less than 5 of the selected 91 lakes of the ordination analysis were either combined into a higher taxonomic group (C) or deleted (D) if combination was not possible due to isolation of the taxon.

EPHEMEROPTERA

X	EPHEME	Ephemeroptera order
C	BAETID	Baetidae family
X	CALLIB	B-Callibaetis sp.
C	CENTRO	B-Centroptilum sp.
C	HEPTAG	Heptagenidae family
C	AMELET	S-Ameletus sp.
X	SIPHLO	S-Siphlo. sp.(large and small)

ODONATA

X	ANISOP	Anisoptera sub-order
X	LIBELL	Libellulidae family
X	SOMATO	L-Somatochlora sp.
X	LEUCOR	L-Leucorrhinia sp.
X	ENALLA	C-Enallagma sp.
D	LESTES	L-Lestes sp.
X	AESHNA	A-Aeshna sp.

HEMIPTERA

X	CORIXS	Corixidae family
X	ARCSUT	C-Arctocorixa sutilis
X	CALAUD	C-Callicorixa audeni
C	HESLAE	C-Hesperocorixa laevigata
X	SIGARA	C-Sigara sp.
X	NOTUSP	Notonectidae family
X	NOTKIR	Notonecta kirbyi
C	NOTUND	Notonecta undulata
X	GERRID	Gerridae family
X	GERINC	G-Gerris incognitus
X	LIMNOT	G-Limnoporus notabilis
X	GERREM	G-Gerris remigis
D	BELOST	B-Belostoma flumineum

TRICOPTERA

X	TRICSE	Tricoptera order
X	LIMNEP	Limnephilidae family
C	ASYNAR	L-Asynarchus sp.
C	ECCLIS	L-Ecclisomyia sp.
X	HESPER	L-Hesperophylax sp.
C	HOMOPH	L-Homophylax sp.

APPENDIX A. (Continued)

TRICOPTERA (continued)
C LENARC L-Lenarchus sp.
C LIMNSP L-Limnephilus sp.
C NEOTHR L-Neothremma sp.
X PSYCHO L-Psychoglypha sp.
C LEPIDO LEPI-Lepidostoma sp.
C MYSTAC LEPT-Mystacides(?) sp.
C PHRYGA Phryganeidae family
X POLYCE POLY-Polycentropus sp.
C RHYACO RHYA-Rhyacophila sp.

COLEOPTERA
X COLESE Coleoptera order
C AMPHIZ A-Amphizoa insolens
X GYRINI G-Gyrinis sp.
C BEROSU Hyd-Berosus sp.
C LACCOB Hyd-Laccobius sp.
C CRENIT Hyd-Crenitis sp.
C ENOCHR Hyd-Enochrus sp.
C HYDROB Hyd-Hydrobius sp.
C HALIPL Hal-Haliplus sp.
C HALGRA Hal-Haliplus gracilis
C HALLEE Hal-Haliplus leechi
X ACILIU D-Acilius sp.
X AGABUS D-Agabus sp.
X BIDESS D-Bidessus sp.
C COLYMB D-Colymbetes(?) sp.
X DERONE D-Deronectes sp.
C DEROVA D-Derovatellus sp.
C DYTISC D-Dytiscus sp.
C GRAPHO D-Graphoderus sp.
C HYDROV D-Hydrovatus sp.
X HYDROP D-Hydroporus sp.
C ILYBIU D-Ilybius sp.
X OREODY D-Oreodytes sp.
C RHANTE D-Rhantus sp.

MEGALOPTERA
X SIALUS S-Sialus sp.

DIPTERA
C CERATA Ceratopogonidae family
X CHAOBO Chaoborus sp.
C CULICI Culicidae family
X CHIRON Chironomidae family
X CHRYSO Tab-Chrysops sp.

AMPHIPODA
X HYAAZT Hyalella azteca

APPENDIX A. (Continued)

AMPHIBIA

X	CLTSAL	Long toed salamander (Central race)
D	PGSALA	Pacific giant salamander
D	TAIFRO	Tailed frog
X	WSFROG	Western spotted frog

REPTILIA

X	WTGSNA	W.terrestrial garter snake
X	CGSNAK	Common garter snake

CLADOCERA

X	BOSMIN	Bosmina sp.
X	CHYDOR	Chydoridae family
X	DAPROS	Daphnia rosea
D	DIABRA	Diaphanosoma brachyurum
X	HOLGIB	Holopedium gibberum
X	POLPED	Polyphemus pediculus
D	SIDCRY	Sida crystallina
X	SCAKIN	Scapholeberis kingi
D	MACROR	Macrothricidae family
D	ALOQUA	Alona quadrangularis
D	SIMEXO	Simophalus exospinus

COPEPODA

X	CALANO	Calanoida suborder-small, med.(<1.5 mm)
X	LDIAPT	Large Diaptomus species (>1.5 mm)
X	CYCLOP	Cycloploida suborder
D	HARPAC	Harpacticoida suborder