Ecological Effects of Stocked Trout in Naturally Fishless High Mountain Lakes, North Cascades National Park Service Complex, WA, USA

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INTRODUCTION

This research project was initiated in response to a directive from the Director of the National Park Service (NPS), dated June 12, 1986, which related to the stocking of fish into lakes of North Cascade National Park Service Complex (NOCA). The directive was an official response to a January 1986 request from the NPS Pacific Northwest Regional Office (PNRO) for a clear statement regarding fish-stocking policies of the NPS. Stocking of non-native animals, including fish, is not allowed in units of the National Park System (NPS, 1991). Although high-mountain lakes in NOCA were originally devoid of fish, the park and the State of Washington co-signed in 1979 a variance to the NPS policy of no fish stocking so that selected lakes could continue to be stocked with non-native trout at regular intervals. Although the policy variance did not have a termination date, NOCA drafted a new memorandum of understanding (MOU) in 1985 in which the policy variance was dropped. This proposal resulted in considerable debate by the public and Congress. A supplemental agreement to the 1985 MOU was prepared in 1988 and specified the stocking levels of selected lakes to the year 2000. The stipulation also was present that the practice of stocking could be discontinued by mutual consent.

The 1986 memorandum from the Director of the National Park Service contained several key points and conclusions. The key points were: (1) fishing is an acceptable recreational activity in NOCA, (2) stocking of selected naturally fish-free waters is a practice that existed prior to the creation in 1968 of the park, and (3) the act of stocking naturally fish-free lakes or streams is to be avoided in areas managed as natural zones. Based on these points, the Director concluded that NOCA waters are to be aggregated

into three categories: natural fish-free waters, waters containing self-sustaining fish populations, and waters in which fish stocking is to be continued. The Director further concluded that all NOCA waters that are presently without fish will not be stocked, NOCA waters that are potential candidates for continued fish stocking are to be reviewed, and those NOCA waters selected to be managed as enhanced recreational fisheries are the only ones that may be stocked now and in the future. The Director also suggested that it would be desirable for the PNRO to develop and implement research to establish current fish and aquatic habitat baseline conditions, monitor the impacts of the fish stocking on fish and wildlife, and determine changes over time referenced against current baseline conditions or against undisturbed natural conditions.

Several meetings were convened in 1987 between staff of NOCA, the Washington Department of Game, and the Oregon State University Cooperative Park Studies Unit to discuss the Director's memorandum and appropriate plans to carry-out his directives. Based on these meetings, park management and the PNRO determined that the existing lake and fish data from the park would be reviewed and summarized, a literature review and synthesis would be prepared on the effect of stocked fish on native biota in temperate lakes, and a lake classification system would be developed. The focus of the first two tasks was to determine what was already known about park resources and the role of fish in lakes at other locations. The latter task was needed so that study lakes could be selected and compared relative to physiographic conditions (climate, geology, topography and vegetation) and lake morphometry.

Work on the literature review and synthesis, and the development of the lake classification system were funded in 1988 by the PNRO. Initial sampling of a few lakes

and ground-truthing of park physiography for the lake classification system were conducted in the summer of 1988. The literature review and synthesis (Goetze et al., 1989) and a preliminary lake classification system (Lomnicky et al., 1989) were completed in 1989.

Review of information available from the park revealed that much was known about fish stocks and certain aspects of lakes, but the available information was not sufficient to assess the effect of stocked fish on native biota. The literature review and synthesis of information about the role of fish in temperate lakes clearly demonstrated that little was known about the effects of stocked fish on communities of native species in naturally fishless high-mountain lakes. Most research had focused on growth, reproduction, and harvest of introduced fish, although elimination of prey species of fish in high-mountain lakes had been documented in a few studies (Nilsson, 1972; Reimers, 1958; Dawidowicz and Gliwicz, 1983; Walters and Vincent, 1973). In particular, fish were shown to alter the size structure, species composition, and species abundance of zooplankton by selectively preying on the largest species, and thereby causing the zooplankton community to be dominated by smaller species (e.g., Brooks and Dodson, 1965; Zaret, 1980). Such changes in the zooplankton community also could alter the species composition, abundance, and size-structure of phytoplankton assemblages. Fish also were shown to affect benthic macro-invertebrate communities by shifting the relative proportions of taxa (Post and Cucin, 1984; Blois-Heulin et al., 1990). In some cases benthic macro-invertebrate species (Reimers, 1958; Nilsson, 1972; Blois-Heulin et al., 1990) and amphibian species (Taylor, 1983; Bradford, 1989) were eliminated from lakes. Besides these examples of the impacts of fish on native prey species, some general patterns emerged from the literature:

1. The kinds and abundances of native species (community structure) that were in a lake before stocking fish and the types and intensities of complex interactions among species (community organization) were not the same after stocking. Changes in community composition involved phytoplankton, zooplankton, benthic macro-invertebrates and amphibians. Extinctions of some native prey species can occur in lakes.
2. The kinds of effects depended on species composition and species interactions in the communities into which fish were introduced. In particular, the level of invertebrate predation can be important in influencing fish impacts on lake communities.
3. Habitat conditions can strongly influence community organization. Prey refuges can mediate effects of predation. Fluctuations in chemical and physical conditions may reduce, enhance or even override effects of fish predation.
4. Effects on native prey communities may be influenced by the age, size structure, and densities of stocked fish. Fish of different ages and sizes may use different habitats and consume different species and sizes of prey.
5. The effects of introduced fish on the biota in naturally fishless high-mountain lakes could not be predicted with much certainty from data available for NOCA. Some of this uncertainty results from the variability among lakes in physical, chemical, and biological characteristics, as well as the complexity of interactions within lake communities. The lake classification system was developed to account for some of this natural variation by grouping lakes into classes based on watershed and lake characteristics.

RESEARCH DESIGN

The purpose of this section is to define the general hypotheses which were used to guide the research, the general objectives, and the research design. Specific objectives for research on particular taxa and detailed methods are reported in other sections.

The project has been reviewed annually, prior to each field season, by a panel of nationally distinguished scientists. The panel has played an important role in structuring the research by evaluating progress annually and recommending directions of future research.

Research in NOCA is complicated by the rugged terrain of the park, which creates logistical problems, the relatively short period of time available for field work, and relatively unpredictable weather. Field work is restricted to the period of time between ice-out (mid-June to early July) and the onset of inclement weather in fall (approximately mid-September). There is no road access to the lakes; they can be reached only by hiking or helicopter.

A three-year program of field research, funded through the NPS Natural Resource Preservation Program, was initiated in FY 1989 to investigate ecological impacts of stocked trout on naturally fishless lake communities in NOCA. Little was known about native biota and physical and chemical conditions in NOCA lakes prior to initiation of this research. The objective of the 1989 field season was to conduct an extensive survey of NOCA lakes to begin to define biotic and abiotic conditions in major lake ecosystem classes. Lake ecosystem classes were defined based on vegetation zone (alpine, subalpine, and forest) and location east or west of the crest of the

northern Cascade Mountains (see Lake Classification section). Sixty-one lakes were sampled in 1989 (Table 1). Most of the lakes were sampled only once. Sampling focused on lake morphometry, chemistry, phytoplankton, zooplankton, and benthic macro-invertebrates. The presence of fish and amphibians was noted, but densities were not estimated.

Based on the 1989 park-wide survey, we designed more systematic research for 1990 and 1991. We hypothesized that fish effects on native lake biota (salamanders, zooplankton, and benthic macro-invertebrates) increased along a gradient of increasing fish predation intensity. Results of the 1989 survey suggested that the effects of fish predation included reductions in densities and elimination of some species (e.g., salamanders, large bodied zooplankton) from lakes. Furthermore, the 1989 survey indicated that abiotic conditions and species composition of the native biota varied among vegetation zones.

For policy reasons, stocking of fish into fishless lakes was not an experimental option at NOCA. Thus, we had to infer effects of fish by comparison of community structure in lakes with fish to that in fishless lakes. Although we lacked specific information on densities of fish, fish appeared to reach much higher densities in lakes where natural reproduction occurred than in lakes where fish did not reproduce. In lakes without natural reproduction, fry are stocked periodically at relatively low densities. Thus, to approximate a gradient of increasing fish predation intensity, we stratified lakes into fishless lakes, lakes with non-reproducing fish, and lakes with reproducing fish (Table 1). We also stratified sampling by vegetation zone. We sampled subalpine lakes in 1990 and forest lakes in 1991 (Table 1). Few lakes in the

Table 1. Sampling fequency of NOCA lakes from 1989 to 1993. Vegetation zone indicated as A = alpine, S = Subalpine, F = Forest, W = West, E = East. Asterisks denote manipulated lakes.

LAKE	VEG. ZONE	1989	1990	1991	1992	1993
NO FISH PRESENT						
Egg	SW	1				
Eiley	AW	1				
Greenview	SE	1				1
Juanita	SE	1				2
Kettling, Upper	HFE	1				2
Klawatti	AW	1				
Moraine	AW	1				
MP-8	AW	1				
MR-12	SE					2
MR-13-1	SE		2	1	2	1
MR-2	SE	1	2			3
MR-3	SE	1	1			2
Nert	HFW	1	1			
Ouzel	A	1				
*Panther, Upper	LFW		2	3	2	3
PM5-3	HFW	1				
Price	SW	1				
Pyramid	LFW	2	1	3		3
Reveille, Lower	SW	1				
Reveille, Upper	SW	1				
Silent, Lower	SE					1
Silent, Upper	AE					1
Silver		1				
Skymo, Upper	SW	1		1		
Talus Tarn	SW	1				
Tapto, Middle	SW	1	2			
Tapto, Upper	SW	1	2			
Tapto, West	SW	1	2			
Vulcan	SW	1				
Waddell	HFE	2		2		3
Waddell, Middle	SE			1		2
Wiley	AW	1				
Wild	SW	1				
NON-REPRODUCING FISH						
Coon	FE	1				1
Copper	SW	1				
Dee Dee, Upper	SE					2
*LS-1	HFW	1	2	3	2	2
LS-3	SW	1		1		
MM-11	SE	1				1
*MR-11	SE		2	2	1	2
*MR-13-2	SE	1	2	2	2	1
MR-16	SE					2
MR-9	SE	1				2
*Panther, Lower	LFW	2	2	3	2	3
Redoubt	SW	1				
Ridley	LFW	1				
Sweet Pea	HFW	1				
Thornton, Lower	SW	1				
Thornton, Middle	SW	1				
Thunder	LFW	1	1	3		
Willow	LFW	1		1		
REPRODUCING FISH						
Battalion	HFE	1		3		
Bear	SW	1				
Bouck	SW			1		
Dagger	HFE				1	2
Dee Dee, Lower	SE					2
Doubtful	SE	1	2			1
EP-6	SW	1	1			
Hozomeen	LFW	1		1		
Jeanita	SW	1				
Kettling, Lower	HFE					2
LS-2	HFW	1	2	3	2	2
McAlester	HFE	1	1	2	2	1
Monogram	SW	1				
NoName	SW	1				
Rainbow	HFE	2		3	2	1
Skymo		1		1		
Trapper	SE	1	1			
Triplet, Lower	SE	1	2	1		
Triplet, Upper	SE	1	2	1		

alpine vegetation zone support fish. Our intention was to sample lakes 2-3 times during the field season depending on the length of the ice-free period. Sometimes weather conditions limited the number of times a lake was sampled. The objectives of the research were to:

1. Determine physical (lake morphometry, temperature, benthic habitat) and chemical abiotic conditions in lakes.

2. Determine the structure of pelagic (crustacean, zooplankton, rotifers, and phytoplankton) and benthic (benthic macro-invertebrates) systems. Structure included taxa composition (species or higher level taxa if identification to species was not possible), average body size (or biovolume) of major taxa, absolute and relative densities of taxa, and habitat utilized by benthic macro-invertebrates.

3. Determine species composition, age and size structure, diet, and densities of reproducing and non-reproducing trout.

4. Determine species composition, abundance of aquatic life stages (egg masses, larvae, and neotenes), and habitat utilization by salamanders.

5. Compare the composition, size structure, and densities of taxa between fishless lakes, lakes with non-reproducing fish, and lakes with reproducing fish. Develop inferences of community organization that involve the effects of fish and abiotic conditions on native species.

6. In cooperation with NPS personnel, develop a program for continual monitoring of lakes in NOCA relative to the question of fish impacts on naturally fishless lakes.

In 1990 we began manipulations of a few small lakes (LS1, MR11, MR13-2, Lower Panther, Upper Panther; Table 1). The purpose of the manipulations was to

evaluate impacts on native biota of changes through time in body size and density of a cohort of stocked fish. During the summer of 1990 the lakes were sampled and in early fall fish were removed and fry were stocked in all lakes except Upper Panther (see Fish section). Upper Panther provided a reference for Lower Panther, which was only a few meters away.

A small amount of funds remained after the first three years of scheduled work and a limited field season was added to the program in 1992. The field effort in 1992 focused on sampling the manipulated lakes and obtaining better estimates of fish densities in selected lakes.

Results of research through 1992 provided evidence of fish impacts on crustacean zooplankton and salamanders and served to further focus our hypotheses. More research, including more extensive sampling of both eastslope and westslope lakes, was needed. A proposal for a second phase of the project was submitted to the NPS Natural Resource Preservation Program in 1991 and funded in 1993. Some of the results of the second phase of the NOCA project (1993 field season) are presented in this report because the results are relevant to the evaluations of the first phase of the project.

LAKE CLASSIFICATION AND CHEMICAL AND PHYSICAL PROPERTIES OF LAKES

Numerous lake classifications have been developed during the past century with diverse origins and purposes for their use. Busch and Sly (1992) identify many approaches in their review of lake habitat classifications. Uses for classification include basic research, application in resource management and satisfying legal mandate. Lake classifications have been developed based on physical (Canfield et al., 1984; George and Maitland, 1984; Lewis, 1983; Larkin and Northcote, 1958; Pennak, 1958; Hutchinson, 1957; Rawson, 1955), chemical (Vollenwieder, 1968; Stockner and Benson, 1967), and biological characteristics (Tonn and Magnusson, 1982; Jensen and Van Der Maarel, 1980; Brundin, 1958; Round, 1958; Nygaard, 1949; Thieneman, 1909) and combinations of these characteristics (Carlson, 1977; Schindler, 1971; Ryder, 1974).

Water quality and the biological structure of high mountain lakes are influenced by elevation, lake morphology, and watershed characteristics. Mosello et al. (1990) reported that water chemistry in alpine lakes of NW Italy was determined by lithology, vegetation, and amount of atmospheric deposition. Pechlaner (1971) determined that primary production and phytoplankton biomass in high mountain oligotrophic lakes were affected by lake hydrology, temperature, winter snow cover and water chemistry. Lomnicky et al. (1989) provide a conceptual framework arguing that lakes interact with climate and watershed features, and that lake morphometry is important to the physical, chemical and biological characteristics of lakes at the spatial scales found in NOCA. Recently, Larson et al. (1994, in press) reported that limnological characteristics of high mountain lakes result from complex interactions of climatic conditions, watershed

characteristics including geographical location, aspect, surface area, elevation, geology, hydrology, soil and vegetation, and lake morphometry.

NOCA lakes are diverse in many physical attributes, although on a global scale they are quite similar (Goldman and Horne, 1983). Primarily glacially formed high mountain lakes, most would be classified oligotrophic (Likens, 1975). Lakes within NOCA differ in geologic and climatic setting, age, origin, elevation, aspect, extent of glacial influence, vegetational setting, morphometry including size and depth, and many other characteristics.

The goal of the work reported in this section was to better understand the similarities and dissimilarities among mountain lake systems in NOCA relative to physiographic characteristics (climate, topography, geology, vegetation) of the terrestrial environments.

The objectives were:

1. Develop a hierarchical classification incorporating physiographic (geological, vegetative and climatological) attributes of the terrestrial environment.

2. Determine physical and chemical properties of lakes and relate these to physiographic characteristics of the terrestrial environment through classification.

3. Use classification to identify the diversity of lake types (classes) parkwide.

Previous classification schemes reflect linkages between lake and watershed characteristics and processes, but have tended to deal either with geographical regions having a greater physical and chemical diversity among lakes or a more uniform environment than is present at NOCA. A different approach was necessary for the specialized conditions found at NOCA. A conceptual view of lake development and its relationship to the expression of lake and watershed characteristics was developed to provide context for this classification approach.

CONCEPTUAL FRAMEWORK

Lakes, like streams, are products of their surrounding watersheds. Likens and Borman (1974) recognized a linkage between land and water though they did not classify lakes. Others have taken a stronger view that water resources are embedded in land ecosystems (Swanson et al., 1988; Frissell et al., 1986; Lotspeich and Platts, 1982; Warren, 1979). Land ecosystems or watersheds are the environment of lakes (Aber and Mellilo, 1991; Warren, 1979). The influence of watershed characteristics (slope, geology, aspect, vegetation) determine rates of nutrient loading to streams and lakes (Mosello, 1990; Hem, 1989; Teti, 1984; Schindler, 1971; Vollenweider, 1968; Ohle, 1965; Gorham, 1961).

A conceptualized view of the complex interrelationships of watershed and lake components (Figure 1) highlights the importance of geology and climate in determining many performances of watersheds and lakes. The expression of physical, chemical and biological attributes, anything measurable, may be described as a performance of the lake or surrounding watershed. Examples include watershed area, vegetation, lake temperature, surface area, depth, and densities and types of organisms present. Geologic and climatic processes exert powerful influences on substrate and physical and chemical performances of lakes both directly, and indirectly through their impact on watershed structure (relief, aspect, soil maturation and vegetation development) and lake morphometry (area, depth).

Lakes can be thought of as dynamic systems that are continually changing or developing relative to changes in their watershed environments. For example, a lake recently exposed by glacial recession would likely have quite different chemical and physical characteristics than an otherwise similar lake formed by the same processes

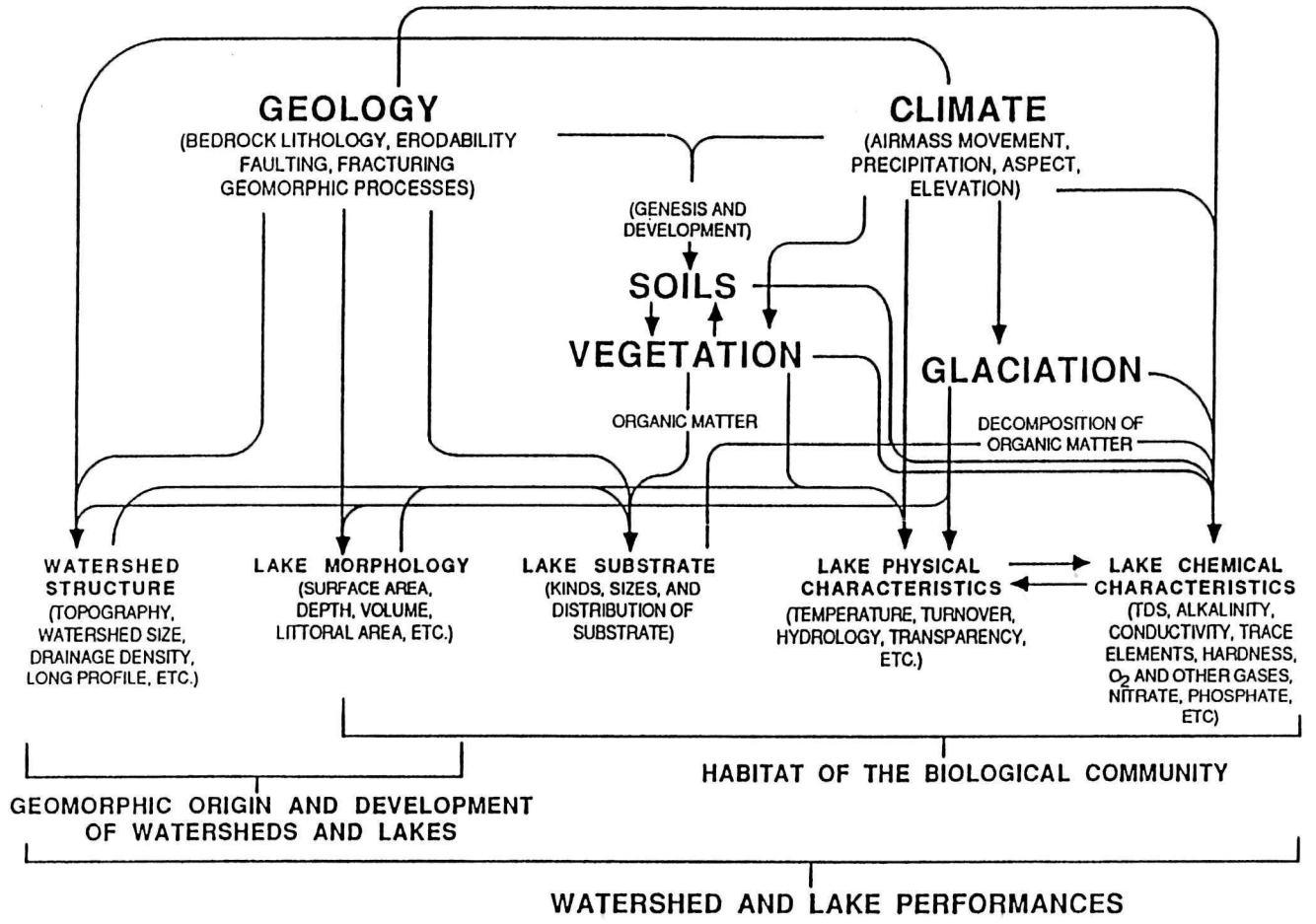


Figure 1. Interrelationships among components of watersheds and lakes.

and exposed thousands of years ago. Lake performances, then, are influenced by both the stage of development of the lake and the stage of development of its watershed environment.

Identifying and understanding the developmental processes of this glacially influenced mountainous terrain aids in recognizing those processes which ultimately constrain and define classes of lakes. Temporal and spatial scales appropriate to NOCA for developmental processes and evolutionary events are given in Table 1.

Lake and Watershed Development in NOCA

Climate and geomorphic processes such as tectonics and glaciation mold a geologic template that determines lake evolution and development. Geologic and climatic processes influence physical and chemical performances of lakes through impact on watershed structure (Aber and Melillo, 1991), lake morphometry (Rawson, 1955), rate of soil maturation (Buol, 1973), and vegetation (Mosello, 1990). Developmental processes that are constrained or enhanced by climate include drainage network development, organic material accumulation, and sedimentation (Table 1). These processes affect the rate and path of water movement through watersheds which affects nutrient concentrations in lakes.

Watersheds, lakes, and the biological communities in lakes can be thought of as codeveloping systems. Development can be considered over geologic, annual, and seasonal time frames. Watershed development over geologic time in the North Cascades has involved the working and reworking of the terrain by glaciers, downcutting by stream channels, development of soils from bedrock and till, and establishment and development of vegetation communities. This region is still in the

Table 1. Processes or events controlling systems on different spatiotemporal scales in North Cascades National Park Service Complex.

System level	Area spacial scale (km^2)[a]	Evolutionary events[b]	Developmental processes[c]	Time scale of continuous potential persistence (years)[d]
Regional (Park)	10^3	Tectonic uplift (orogeny); subsidence; volcanism; Igneous plutonic metamorphism	Planation (chemical and mechanical weathering) Drainage network development	10^5-10^6
Major Drainage Units (Skagit, Stehekin, Chiliwack/Nooksack)		Cordilleran ice sheet advance; severe glacial erosion in different lithologies of major watersheds; stream capture		10^4-10^5
Drainage Subunits (major tributaries of major drainage units)	10^1-10^2	Pleistocene (Fraser) glaciation Glacial landforms: Erosion trough valley, col, cirque hanging valley Deposition moraines (lateral,terminal) alluvial infilling Faulting (Ross Lake, Straight Creek)	Drainage network development; denudation; glacial drift agradation (till, stratified drift, outwash)	10^4
Lake Watershed	10^{-1}-10^1	Neoglaciation (alpine glaciation) Glacial erosion and deposition Lake formation trough, kettle, cirque, scour slump, moraine, fault Landslides, slumping Local faulting	Glacial transport of sediments raveling; frost riving; Mass wasting-talus skree; organic material accumulation soil formation	10^3-10^4
Lake	10^{-1}-10^1	Lake evaporates, freezes up, fills up, deices Landslides, slumping Macrophyte establishment	Allochthonous inputs organic and mineral Sedimentation, Increasing nutrient concentrations and biological complexity	10^1-10^4

[a]Spacial scales follow Lotspeich & Platts (1982).
[b]Evolutionary events change potential capacity. (i.e. extrinsic forces that create and destroy systems at that scale).
[c]Developmental processes are intrinsic, progressive changes following a systems genesis in an event.
[d]Appropriate to geologic/climatic time frame of NOCA.

process of change. Climatic change occurring only recently has led to the recession of glaciers and the formation of new lakes. Whether watershed changes are viewed over the short-term or long-term, lakes and streams will, to some extent, reflect these changes. We can conceptualize the development of lakes through time and the characteristics they exhibit at any particular time as being determined at least in part by the development and characteristics of their watershed environments.

NOCA lakes are predominantly of glacial origin, and their development has been generally initialized with glacial ablation. NOCA lake and watershed development can be understood as progressing through a scenario similar to our present day alpine, subalpine and forest states given enough time and favorable climatic (temperature, aspect) factors. Under present regional climatic conditions, alpine watersheds and lakes exist at the highest elevations while forest systems are at the lowest elevations. Subalpine systems occur between the two.

The alpine landscape is severe, a cold, rocky, barren, dessicated region filled with ice and snow for much of the year. Watershed relief tends to be steep except for lakes perched on ridgetops. There is minimal water retention in the basins except in frozen form since soil formation processes are just beginning, and steep relief hastens water exodus from the watershed. Ice-out in this environment comes late in the summer season if at all, minimizing vegetation development. A lake's local environment is not moderated by soils or surrounding vegetation. These systems are presently restricted to the higher elevations in the headwaters of drainages and consequently tend to have smaller watersheds.

Under favorable climatic conditions, development progresses from the alpine to the subalpine stage. Increasing soil maturity leads to enhanced hydrologic retention.

This increases the potential for mineral weathering and nutrient liberation to lakes from bedrock. In a subalpine climatic regime, lake iceout is generally earlier in the year than in alpine systems but later than in forest lakes. The lakes are usually warmer than alpine lakes due to an increased period for direct insolation and generally warmer ambient air temperatures at lower elevations. Though glacial inputs are decreasing, other infilling processes (colluvial transport, avalanche chutes, stream transportation) add inorganic and organic materials to the lakes which decreases lake depth. The decreased time period of winter cover provides increased opportunity for vegetative growth. Successionally, this eventually leads to a Parkland mosaic (Franklin and Dyrness, 1973), a mixture of meadows and stringers of trees which provides added organic input to lakes in the form of leaf litter and woody debris. Subalpine lakes are found near the treeline usually tucked near valley headwalls or on west-facing ridges.

Under more temperate climatic conditions with a long enough snow-free period for tree establishment, the potential exists for watersheds to develop to a forest state. Warmer temperatures lead to a reduced period of winter snowpack, increased amount of vegetation, greater soil nutrient concentrations and accumulations, and an organic horizon in the soils. Increased soil/water interactions create elevated nutrient concentrations delivered to lakes via inlets and groundwater. Infilling processes carrying suspended sediments and organic inputs reduce the mean depths of lakes. Fed by the more abundant groundwater, a greater number of permanent inlet and outlet streams exist. Weathering processes such as frost riving and colluvial raveling tend to decrease watershed slope relief, further increasing the potential for soil and water interactions. Forest lakes are found in the lower elevations of the park. They are

usually in valley bottoms away from ridge slopes since colluvial infilling processes tend to push lake shorelines towards the middle of valleys.

Factors Affecting Development

The rate of watershed and lake development can be affected by climatic regime and disturbance factors. Development may be arrested or reversed at any stage or state due to prevailing or changing climatic conditions. Elevation, latitude, basin aspect and the proximity to glaciers influence localized climate (Table 1). These varying conditions may affect the rate or potential for further development. For example, two lakes at the same elevation on a mountain may have differing aspects resulting in very different localized climates. West-facing lake basins, with warmer afternoon sun and increased precipitation relative to east-facing basins, may have progressed to a forest stage while the east-facing basin still has alpine characteristics. As a result, elevation is just one factor determining local climate in a mountainous environment.

Disturbance regimes such as fires and annual snow events can maintain a particular developmental state by resetting successional trajectories following fire or other disturbance. In the subalpine zone, snow period minimizes tree seedling survival prohibiting forest states from developing. Additionally, plant community succession may be reset following fire or other disturbance.

Classification Rationale

Based on this view of development for glacially influenced high mountain lakes and their watersheds, a classification system was devised. We approached classification as a means of ordering systems having common properties and

developmental processes. Variables used for classification should be highly determining of system performances (Warren, 1979). The variables used to define and classify systems at each hierarchical level (Table 1) must be appropriately scaled to the space-time frame of the systems composing that level (Frissell et al., 1986).

PHYSIOGRAPHY OF NOCA

NOCA is located in north central Washington on the Canadian border (Figure 2) and contains 162 alpine, subalpine and forest lakes identified by Park Service biologists as important to fisheries management. The rugged topography of the park spans the crest of the North Cascade mountains separating the park into two geographical regions, westslope and eastslope. This is a tectonically active region (Press and Siever, 1982), and many of the landforms are still being altered by processes such as faulting, uplift and subsidence (McKee, 1972). Accretion of an island microcontinent (Alt, 1984), metamorphism and intrusions of magma, have created a complex park lithology. Hard crystalline bedrock, predominately gneiss and granite with some sedimentary and volcanic lithology (Misch, 1977), underlies the region. Local soil surveys have not been completed, but regional soils are primarily young cryandempts that form during cool summers (Jackson and Kimerling, 1993).

Over the last 50,000 years, climatic processes such as glaciation have reworked the geologic template. During the Fraser period of glaciation, 25,000 to 10,000 years ago (Crandell, 1965), the major river valleys (Chilliwack, Skagit, Stehekin) were broadened and deepened. Some larger lake basins were created. Neoglaciation reworked most of the present day landforms and existing lake basins at the higher elevations about 2500 years ago (Crandell, 1965). Flowing from the headwalls,

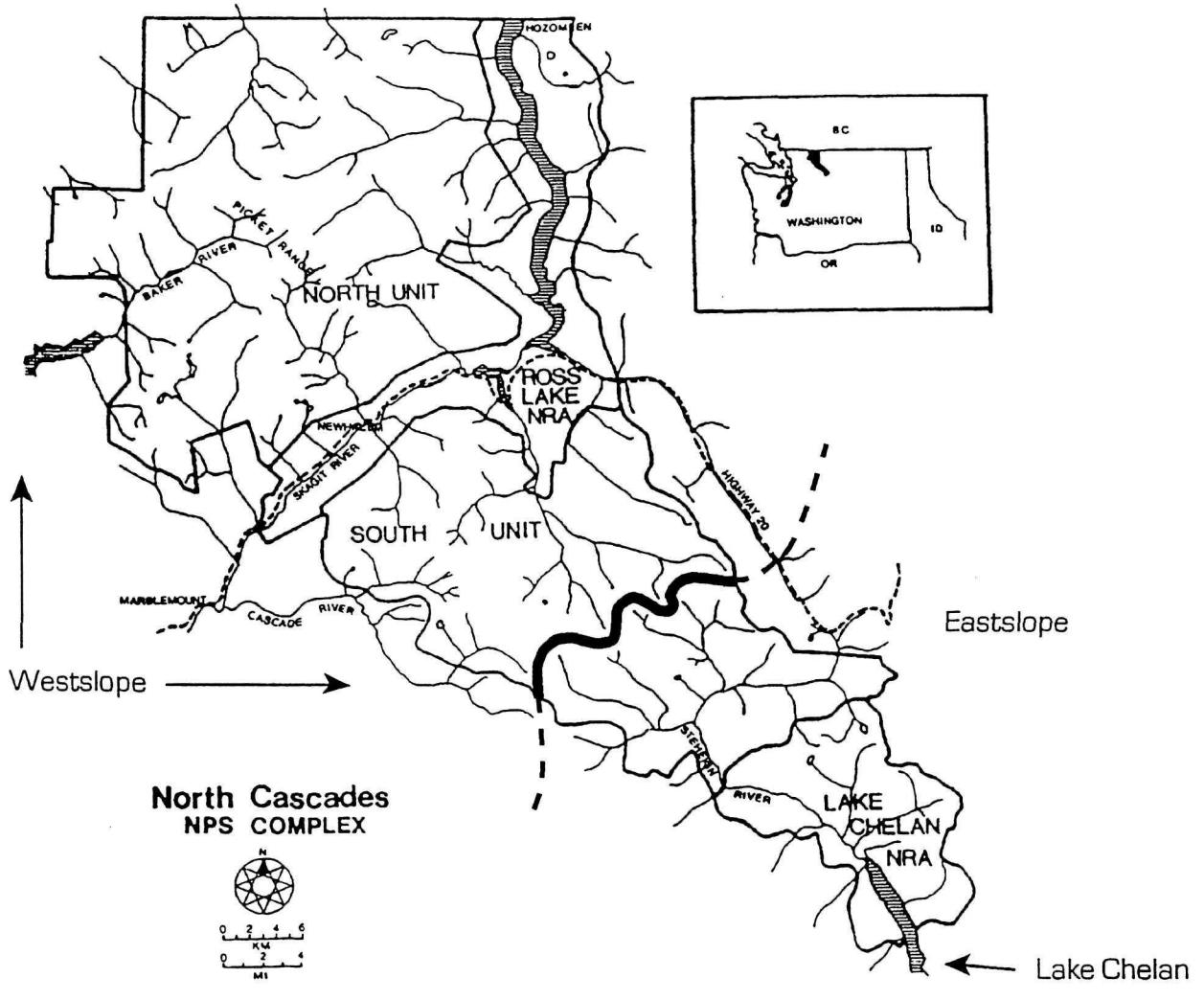


Figure 2. Location of the North Cascades National Park Service Complex in Washington. Westslope/Eastslope: relative to the hydrologic crest (Agee and Pickford, 1985).

glaciers carved depressions and created moraines and other depositional landforms of alluvium and outwash, some which have become morphogenetic features of lake basins. Today, remnant glaciers are reminders of a much more severe past climatic regime. These glaciers still influence processes within some lakes by providing turbid meltwater inputs to lakes.

Differential precipitation across the hydrologic divide separates the park into two major climatic units (Jackson and Kimerling, 1993). Westslope climate is maritime with warm, moist air coming off the Pacific Ocean and Puget Sound, creating wet relatively warm winters and cool summers. East of the crest, a more semi-arid continental climate exists with colder winters and hot dry summers. Precipitation, comprising the major weathering component of the present climatic regime, ranges from 125 cm to 305 cm per year on the eastslope and 152 cm to over 350 cm per year on the westslope (Lomnicky et al., 1989). Ice and snow blanket most lakes approximately nine months each year. A majority of the lakes are open by mid July (Lomnicky et al., 1989) and freeze over by late October to early November on the eastslope and two weeks later on the westslope (Tony Reece, pers. comm.).

Westslope vegetation is typified by lowland and montane forests. Lowland forests are generally below the permanent winter snowpack while montane forests exist in areas where snow remains the entire winter. The subalpine zone is composed of lush herbs and woody shrubs. The alpine zone is recognized by krummholtz, a growth form, rather than any particular species. Rock and ice dominate the alpine zone. Less understory exists in eastslope forests which are drier than westslope counterparts.

METHODS

Physical

U.S. Geological Survey topographic maps (7.5') were used to to determine lake watershed area, surface area, elevation, and permanent inlet streams. A BASIC program, GAP4 (GTCO 1982), was used to manually digitize the flat map watershed area and surface area of each lake. Lake elevation was recorded from the park service database.

Bathymetric maps of each surveyed lake were developed from depth measurements taken along transects using a hand-held sonar depth finder. Depth isopleths were developed and volumes, $V= h/3(A_1 + A_2 + \sqrt{(A_1A_2)})$, determined using a digitizer. With this data, mean depth was determined for each lake ($MZ= V/A_o$ where A_o = surface area).

Temperature was measured over the deepest spot in the lakes at one meter intervals from the surface to the bottom. An Omega HH70 series handheld thermometer with a single input Type K chromel-alumel thermocouple was used.

Date of ice-out, which was defined as lake surface virtually ice free was determined for most lakes from weekly aerial surveys over the park. For a few lakes, we relied on information from backcountry rangers. Precipitation values for lake watersheds were determined from a map developed by Agee and Pickford (1985) from state climatological data with revisions using local survey information.

Lake origin was determined by visual interpretation of air photographs of all park lakes using a stereoscope adapting descriptions from Hutchinson (1957). A total of 152 lakes were identified by basin origin. The origin of 10 lakes was unknown.

Chemical

A total of 142 water samples were collected (1989-1992) from 58 lakes. Water samples were collected 1 meter below the surface over the deepest spot in each lake from inflatable boats using a 1.5 liter Van Dorn style bottle. Filtered (0.7µm prewashed Watman GF/C filters) nutrient and trace element samples were placed in 1 liter acid washed polyethylene bottles. Unfiltered samples (250 ml acid washed polypropylene bottles) were collected for determination of conductivity, alkalinity and total phosphorus. Water samples were transported out of the field, frozen and then shipped to the laboratory. Chemical analyses (Table 2) for total Kjeldahl-nitrogen (TKN), nitrate-nitrogen (NO3), total phosphorus (TP) orthophosphorus (OP), alkalinity (ALK), pH, conductivity (COND), sodium (NA), potassium (K), calcium (CA), and magnesium (MG) were performed at the Cooperative Chemical Analytical Laboratory, Oregon State University.

Nutrient and water quality values for each lake were determined by averaging all samples collected for each lake from 1989 to 1992. Average pH was calculated from hydrogen ion activity.

Vegetation

Lake watershed class was identified by the predominate watershed vegetation, emphasizing nearlake vegetation. In the absence of sufficient data on climate, soil maturity, and hydrologic regimen, vegetation was used as a proxy for these factors at the watershed level. Vegetation was considered a good integrator of these components due to the long time frames for development and persistence of the vegetative communities (Aber and Melillo, 1991; Franklin et al., 1988).

Table 2. Analytical procedures used by the Cooperative Chemistry Analytical Laboratory, Oregon State University. (Cameron Jones, personal communication)

Variable (Acronym)	Method	Detection limits (Units)
Conductivity (COND)	Wheatstone Bridge, Yellow Springs model 33, corrected to 25°C	0.4 (mS/cm)
Nitrate-N (NO3)	Technicon Autoanalyzer,automated cadmium reduction	0.001 (mg/l)
Kjeldahl-N (TKN)	Nessler's Reagent finish	0.01 (mg/l)
Ammonia-N (NH3)	Technicon Autoanalyzer, colormetric automated phenate	0.005 (mg/l)
Total Phosphorus (TP)	Persulfate digestion, ascorbic acid finish	0.001 (mg/l)
Orthophosphate-P (OP)	Reactive phosphate,ascorbic acid finish	0.001 (mg/l)
pH (PH)	Portable Beckman meter 21. Orion Sureflow Standarized with pH 4 and pH 7 buffers. Measurements made following a protocol modified from Metcalf (1989) and anonymous (1987). Final reading recorded after 5 consecutive readings of the same value (usually 30-45 minutes)	0-14
Alkalinity (ALK)	Electrometric titration to pH 4.5	0.2 (mg/l)
Sodium (NA)	Flame atomic absorption	0.01 (mg/l)
Magnesium (MG)	Flame atomic absorption	0.001 (mg/l)
Calcium (CA)	Flame atomic absorption	0.06 (mg/l)
Potassium (K)	Flame atomic absorption	0.03 (mg/l)

A vegetation map, developed from LANDSAT multispectral scanner images and other data (slope, elevation, aspect) on a Geographic Information System (Agee and Pickford, 1985), was used to identify NOCA lake watershed cover types. Watersheds were identified as predominately alpine, subalpine, or forest. The forest zone was further subdivided into high and low elevation based on location above (maintains winter snow cover till spring) or below (intermittent snow free ground during the winter) permanent winter snowpack.

Predominant plant community types and associations were usually assessed in the field to verify that each lake had been placed into the correct vegetation zone. Vegetation cover of unsurveyed lakes was crosschecked with aerial photographs. Elevation ranges for each vegetation zone were determined from Agee and Pickford (1985) by grouping vegetation community types for a particular zone and recording the maximum and minimum mean ranges for the communities in each zone. The lakes were identified as west (westslope) or east (eastslope) of the hydrologic crest. Westslope lakes drain into Puget Sound and the Frazier River while eastslope lakes drain into the Columbia River.

Statistics

Kruskal Wallace/Mann Whitney-U tests (SYSTAT ver. 5.01) was used to test for statistically significant differences between various lake classes. Statistical significance was set at $\alpha = 0.05$. Level of significance for multiple comparisons with the same data was determined by dividing the chosen significance level ($\alpha=0.05$) by the number of comparisons to arrive at a conservative P value. Regression and covariance analyses

(SYSTAT ver. 5.01) were used to determine the relationships of epilimnion temperature and ice-out date to vegetation class and elevation.

The diversity of lakes by origin within a vegetation zone were determined using the AID1 program (Overton et al., 1987). Analysis of lake chemistry data was performed using ClusB4 (Overton et al., 1987), a non hierarchical clustering algorithm. Discriminate and correlation analyses (SPSS statistical package) were used on these cluster groups for graphical display and axis interpretations. Fishers Exact Test (α = 0.05) was used to compare lakes differing in maximum depth and near-surface and near-bottom temperatures.

RESULTS

Lake Classification

Three hierarchical levels were developed to classify NOCA lakes. These levels, listed in descending order within the classification hierarchy, were: (1) position relative to the hydrologic crest of the North Cascade Mountain Range, (2) vegetation zone, and (3) basin origin.

Hydrologic Crest Position

All lakes were classified either as westslope or eastslope (Figure 2) based on locations relative to the hydrologic crest of the North Cascade Mountains. Major patterns of air masses, which seasonally influenced air temperature, amount and form of precipitation, aspect of major watersheds, and geology, differed with crest position. Watersheds on the westslope of the crest were associated with the Skagit, Chilliwack, and Nooksack rivers. Eastslope watersheds were associated with the Stehekin river.

Annual temperature extremes were greater on the eastslope than on the westslope because skies on the eastslope tended to be clearer than skies on the westslope. This resulted in hotter summers and colder winters eastslope compared to westslope (Jackson and Kimerling, 1993). The southern aspect of the Stehekin watershed (Figure 2) resulted in high solar insolation in the headwater areas where most eastslope lakes were located. The Nooksack and Chilliwack watersheds on the westslope were generally oriented in a north-facing position, whereas the large and complex Skagit watershed encompassed a variety of aspects. Westslope watersheds were geologically more complex than eastslope watersheds. Gneiss was the predominate bedrock of eastslope watersheds, with only a few lakes found on a granitic pluton. Westslope lithology was dominated by gneiss, granite, sedimentary deposits, and volcanic deposits.

Vegetation Zone

The second level of the classification was based on vegetation. The alpine zone was dominated by exposed rock and ice (Table 3). Dominant vegetation was clumped, low in stature, and included sedges (*Carex* sp.), stonecrop (*Sedum* sp.), and partridgefoot (*Leutkia* sp.). The alpine zone occurred primarily in westslope watersheds where the climate was conducive to the persistence of glaciers and alpine conditions. The semi-arid climate of eastslope watersheds generally was too dry and warm for glacial and alpine conditions to persist.

The subalpine zone was intermediate to the alpine and forest zones (Table 3). Dominant vegetation included herbs, woody shrubs, and some trees aggregated in open forests. Herbs included partridgefoot (*Leutkia sp.*), a variety of ferns and mosses,

Table 3. Vegetation zones for lake basins with corresponding cover types (Agee & Pickford 1985) and cover type mean elevations for open and closed forest, lake elevations(min & max), habitat notes and NOCA lakes. Sampled lakes in bold type. Lake acronyms given in Appendix I.

Vegetation Zones	Major Cover Types found in lake basins	Mean Elevation Vegetation (m) (Lakes)	Habitat Notes	Lakes by origin[ab]
EASTSLOPE				
Forest Low	Ponderosa pine, Douglas fir	→ 880 (662)	Very dry, low elevation. Douglas fir to mid elevation. Disturbance oriented (fire, avalanche) communities.	**B-COON**
High	Subalpine fir, mt. hemlock, subalpine herb, heather	1127 → 1789 (1504 → 1717)	Subalpine fir found in more xeric areas than Mt. Hemlock. Forests communities tend to be more xeric tolerant than westside counterparts.	**C-BATT MCAL T-DAGG, KETT, KETU, RAIN, WADD**
Subalpine	Subalpine fir, Whitebark pine/larch, Subalpine herb, Rock, Snow	1558 → 2231 (1270 → 2072)	Mesic aspects east. Larch found at higher colder areas than pine. Summer warmth has allowed subalpine veg types to extend to the ridgetops in most basins.	**C-DOUB,** MA3, MLy1, MM7, MR1, **MR9, MR11, MR13-1,** MR15-1, MR15-2, TRIL **T-GNVW, TRAP I-JUAN,** ML6, **MM11, MR2, MR3,** MR8, MR12 D-MM1, **MR13-2, TRIU** B-MR16
Alpine	rock, snow	(1860 → 2127)	High elevation xeric environment. Limited summer season, and permanent winter snowpack.	I-MA2, MM3 D-MM8
WESTSLOPE				
Forest Low	Hardwood forests, High shrub, Western hemlock, Douglas fir	488 → 880 (412 → 1031)	Warm low elevation, dry to moist areas generally below permanent winter snowpack. Marked by disturbance oriented communities and Western hemlock. High shrub extends up avalanche slopes. Disturbance oriented species (Douglas fir) may be seral to Silver fir.	**C-PYRA T-HOZO***, MP5, **PANL, PANU, RIDL*, THUN, WILL*** *Sedimentary geology
High	Pacific silver fir, Douglas fir	728 → 1316 (1171 → 1687)	>100 inches/yr rainfall. Winter snowpack does not melt off periodically during winter	**C-BOUC, JEAN, LS1, LS2,** MC8, **NONA, THRL I-NERT*** D-**SWEE**[b] S-EP3 K-**PM5(1-6)**

Vegetation Zones	Major Cover Types found in lake basins	Mean Elevation Vegetation (m) (Lakes)	Habitat Notes	Lakes by origin[ab]
Subalpine	Rock, snow, subalpine herb, subalpine fir, Mt. hemlock, silver fir, heather	1220 → 1789 (1110 → 1967)	Basins tend to be meadow filled with clumps of trees if any. Often snow persists in basin throughout the summer.	C-**BEAR, COPP**, DD5, **EGG**, EP2, EP5-1, **EP6,** EP9-2, EP12, FP9, FP10, LS3, LS6, LS7[b], M11[b], M14, M17, MC3, MC7, MC16-2, MC29[b], MC34, **MONO**, MP2, MS3, MSH4, **TAP1, THRM** T-**HIDD**, M4[b], M8, MC14-1, MC14-2, **PRIC**[c], **REVL, SKYM, WILD** I-EP9-1, EP13, FP6, M24-1, M24-2, MC1 MC2, MC15, ML3, MP1(1-3), PM2, **TAP2,** TAP3, **TAP4** D-DD8, M21, MC28[c], ML1, PM12, **REDO**[b], **REVU, VULC**[b] B-M1, MC10, **TTAR**[c] F-M7 U-M15, MSH2
Alpine	Rock, snow, subalpine herb, subalpine fir	(1113 → 2083)	Severe, lots of snow, rock and ice. Vegetation, if any, is of krummholtz form.	C-EP4, EP10, LS5, M10, M13, M18, M22, MC13, MC16-1, MC23, **MP8,** MP9, MS2, MSH1[c], **OUZL**[c] T-EP11-1,**KLAW**[c], **MORA**[c], **SILV, SKYU** I-**EILE**, EP14, FP5, LS4, MC22, **WILE** D-FP1, M9, M16, MA1[b], ML5 U-EP11-2, FP8, M25, MC30, RD4

[a]Origin: C=cirque, T=trough, I= ice scour, D= moraine dam, B= bench, F= fault, S= slump, K= Kettle, U= not defined
[b]Some glacial influence
[c]Turbid glacial inflow

sedges (*Carex* sp.), and hellebores (*Veratrum* sp.). Common woody shrubs were heather (*Phyllodoce* sp.) and huckleberry (*Vaccinium* sp.). Westslope trees included Mountain hemlock (*Tsuga mertensiana*), Pacific silver fir (*Abies amablis*), and Subalpine fir (*Abies lasiocarpa*). Eastslope trees included Mountain hemlock, an occasional Alaska yellow cedar (*Chamaecyparis nootkatensis*), Subalpine fir and, at the higher elevations in the zone, Whitebark pine (*Pinus albicaulis)* and Subalpine larch (*Larix lyalli*) (Table 3).

The forest zone on both the east and westslope was subdivided according to elevation. High-forest zones experienced permanent winter snowpack, whereas low-forest zones did not. High-forest zones were dominated by Silver fir on the westslope and by Mountain hemlock and Subalpine fir on the eastslope. The low-elevation forests included Ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) on the eastslope, and Douglas fir and Western hemlock (*Tsuga heterophylla*) on the westslope. Understory vegetation was sparser on the eastslope than on the westslope.

Climatic differences between the eastslope and westslope influenced the occurrence of the vegetation zones relative to elevation. All three vegetation zones on the eastslope occurred at higher average elevations than their counterparts on the westslope (Table 3). The alpine zone was restricted on the eastslope, but occurred in a significant portion of westslope watersheds. Subalpine and high-forest zones were predominant on both the eastslope and westslope. Low-forest zones in NOCA were most common westslope and rare eastslope (Table 3).

Precipitation varied among vegetation zones. Average annual precipitation decreased from the alpine to the low-forest zone both east and west of the hydrologic crest (Table 4). Differences in precipitation were not evident between alpine and subalpine zones on the westslope. Average amounts of precipitation for each vegetation zone were lower for eastslope zones than for westslope zones (Table 4). The amount of precipitation in high-forest westslope watersheds was approximately equal to precipitation in alpine and subalpine watersheds on the eastslope.

Origin

Eight morphogenetic lake classes were identified based on basin origin -- cirque, trough, ice scour, moraine, bench, fault, slump, and kettle lakes (Hutchinson, 1957). Cirques are amphitheatre-shaped basins generally occuring at the heads of glaciated valleys, and thought to be formed by frost riving at the firn line (permanent snow line). Troughs lakes were formed in glacially scoured U-shaped valleys, and tended to be long, narrow and wedge-shaped with the deepest spots in the lakes near their outlets. Ice scour lakes, found in irregular depressions, were formed by glacial scour along fault or joint fracture lines. The lakes occur on ridgetops. Moraine lakes formed behind the unconsolidated till of terminal or lateral moraines which were deposited by glaciers. This damming feature may act alone to form the lake or increase the depth of an existing cirque or trough lake. Bench lakes were the result of glacial scouring working at two different time periods to create a step or bench along the hillslope parallel to the valley floor. Oblong in shape, they have no sheltering basin. Fault lakes were formed by bedrock dams created by differential displacement of bedrock along tectonic faults.

Table 4. Elevations (EL), precipitation (PREC), and date of ice-out for NOCA lakes by position east or west of the Cascade crest and vegetation zone.

Vegzone	Statistics	EL (m)	PREC (cm)	ICEOUT[a] (julian days)
a. Eastslope				
Alpine	mean	1961	237	NA
	N	3	3	NA
	stan. dev.	145	29	NA
Subalpine	mean	1847	211	188
	N	24	24	11
	stan. dev.	177	52	20
Forest High	mean	1648	196	176
	N	7	7	5
	stan. dev.	1	32	20
	mean	662	152	95
Forest Low	N	1	1	1
	stan. dev.	-	-	-
b. Westslope				
Alpine	mean	1601	287	216
	N	36	36	8
	stan. dev.	250	56	16
Subalpine	mean	1566	290	205
	N	67	67	18
	stan. dev.	187	53	16
Forest High	mean	1360	232	182
	N	16	16	8
	stan. dev.	125	58	16
Forest Low	mean	810	187	138
	N	8	8	7
	stan. dev.	230	38	20
c. Parkwide	mean	1564	262	187
	N	162	162	55
	stan. dev.	300	64	31

[a]Surveyed lakes, 1989

Slump lakes occur in the depression left by the rotational slip of deep seated soil. Kettle lakes were the result of irregularly deposited outwash (ground/terminal moraine) or remnant pieces of ice left in the outwash of retreating glaciers, and tended to have irregular shapes. When the ice melted, a lake was left in the resulting depression.

Applications of the Lake Classification

The lake classification was used to assess the following characteristics of NOCA lakes: distribution of the lake classes by basin origin, time of lake ice-out, epilimnetic water temperature, and water chemistry. Also considered were influences of lake depth on water temperature and influences of geology, glacial outwash, lake depth, and a measure of the integrated influence of watershed characteristics on water chemistry.

Basin Origin

Each morphogenetic class exhibited differences in landscape position, relative persistence, relative depth, presence of a permanent inlet stream, relief of the watershed basin, and several other morphogenic features (Table 5). Lakes situated in erosional landforms such as cirques and troughs tended to be deeper and more persistent than lakes situated in depositional landforms, such as moraines and slumps. Though there is a wide range of depths associated with troughs and cirques, their maximum depths were greater than other lake types. Slump lakes and kettle lakes, which were small, shallow depressions, may be shorter lived than the other lake classes. The presence of permanent inlet streams was related to lake position within a watershed. Low-elevation lakes in valleys, such as trough lakes, had the greatest occurrence of permanent inlet streams. High-elevation cirques and ice-scour lakes

Table 5. Morphogenetic lake classes listed with general descriptors associated with each class. Temporal frame of reference and depth for North Cascades lakes (Maximum age to approx. 7000 yrs.)

Lake class	Location	Relative Persistence	Relative depth[a] (m)	Permanent inlet stream	Basin relief	Morphogenetic feature
Cirque	headwall	long	shallow to deep (2-46.3)	generally no if headwall. yes if lower end of paternoster lakes	high	scoured depression at headwall with rock lip or moraine damming feature
Trough	valley	long	shallow to deep (3-137)	generally yes	low	glacially deepend valley depression with bedrock dam with occasional moraine influence
Ice Scour	ridgetop	long	shallow (1.2-8.2)	no	low	irregular depression created by glacial scour along fault or joint fracture
Moraine	valley,cirque	short to med	shallow to medium (4.3-27.4)	yes	variable	valley or cirque lake formed principally by terminal or lateral moraine dam
Bench	along valley side wall, a false ridge parallel to valley floor	medium to long	shallow to medium (3.6-5.8)	site specific	med to high	differencial valley glacier erosion along valley slope producing bench. Interaction with ancillary glacier
Fault	variable	variable	shallow to deep (11)	site specific	variable	tectonic displacement creating a bedrock dam with associated basin
Slump	on slope with deep soils, valley sidewall	short	shallow (no data)	no	medium	soil mass movement, rotational slip of deep seated soil
Kettle	ground moraine outwash	short	shallow (1-4)	no	low	stranded ice of retreating glacier leaves depression in ground moraine after melting

[a] Maximum depth relative to other classes of lakes by origin. Depths are for sampled lakes.

tended to lack inlet streams. Slump and kettle lakes also tended to lack permanent inlet streams.

Morphogenetic classes were unequally distributed across and within vegetation zones (Table 6). Trough, cirque, and ice-scour lakes occurred in all zones. The forest zone (high and low zones combined) contained the greatest diversity (HE) of morphogenetic classes (HE=1.53), although this zone contained only 20% of all lakes. The alpine zone had the lowest diversity of morphogenetic classes (HE=1.30) and contained lakes situated primarily in erosional landforms. Subalpine systems contained an intermediate diversity of morphogenetic classes (HE=1.41). The majority (58%) of the lakes in NOCA occur in this vegetation zone (Table 6). The occurrence of particular morphogenetic classes differed among vegetation zones (Table 6). The proportion of trough lakes increased from alpine to forest zones (15% in alpine, 13% in subalpine, and 33% in forest). Ice-scour and dammed lakes were less prevalent in forest than in subalpine and alpine forest zones. Cirque lakes were a major component of all zones, and as previously mentioned, slump and kettle lakes were present only in the forest zones.

Time of Ice-Out

Time of lake ice-out, measured in Julian days, increased from low-forest lakes to alpine lakes based on an analysis of pooled data for eastslope and westslope lakes (Table 4). Eastslope lakes typically iced-out somewhat earlier than westslope lakes in a given vegetation zone. Date of ice-out also was influenced by basin aspect. For example, west-facing eastslope subalpine lakes tended to ice-out earlier than lakes with an easterly aspect (Figure 3). The pattern was not as clear in westslope subalpine

Table 6. Distribution of morphogenetic classes of NOCA lakes by vegetation zone. Number in parentheses.

ORIGIN	ALPINE	SUBALPINE	FOREST
ICE SCOUR	24% (8)	25% (22)	3% (1)
CIRQUE	42% (14)	44% (39)	32% (10)
TROUGH	15% (5)	13% (11)	33% (11)
DAMMED	18% (6)	13% (11)	3% (1)
BENCH	-	4% (4)	3% (1)
FAULT	-	1% (1)	-
SLUMP	-	-	3% (1)
KETTLE	-	-	19% (6)
Totals %(N)	22% (33)	58% (88)	20% (31)

lakes (Figure 3). EP6 and Bear are deep lakes. SKYMO (SKYM) receives little precipitation, and like Talus Tarn (TTAR), is found in a rocky open basin which may have caused them to ice-out earlier than lakes in more sheltered locations.

Epilimnetic Water Temperature

Epilimnetic water temperature was warmest in low-forest lakes and coolest in alpine lakes based on measurements during the ice-free season in 1989 (Figure 4). The water temperature of subalpine and high-forest lakes was very similar, and intermediate to the temperature of alpine and low-forest lakes. Furthermore, water temperature of low-forest lakes was warmest in July, whereas the water temperature of high-forest, subalpine, and alpine lakes was warmest in September. Similar patterns were observed in 1990, even though a hot, dry August elevated water temperatures of subalpine, high-forest and low-forest lakes by approximately 4°C relative to August 1989 (data not shown). A comparison of regressions of water temperature against elevation for forest (high and low combined) and alpine zones revealed significant differences between these vegetation classes (Figure 5, ANCOVA P=0.002). This comparison suggests that local climate differed between these two zones. Water temperature varied inversely with elevation within forest and alpine vegetation zones based on an analysis of 1989 data (forest, r^2=0.45, p=0.002; alpine r^2=0.51, p=0.046; Figure 5).

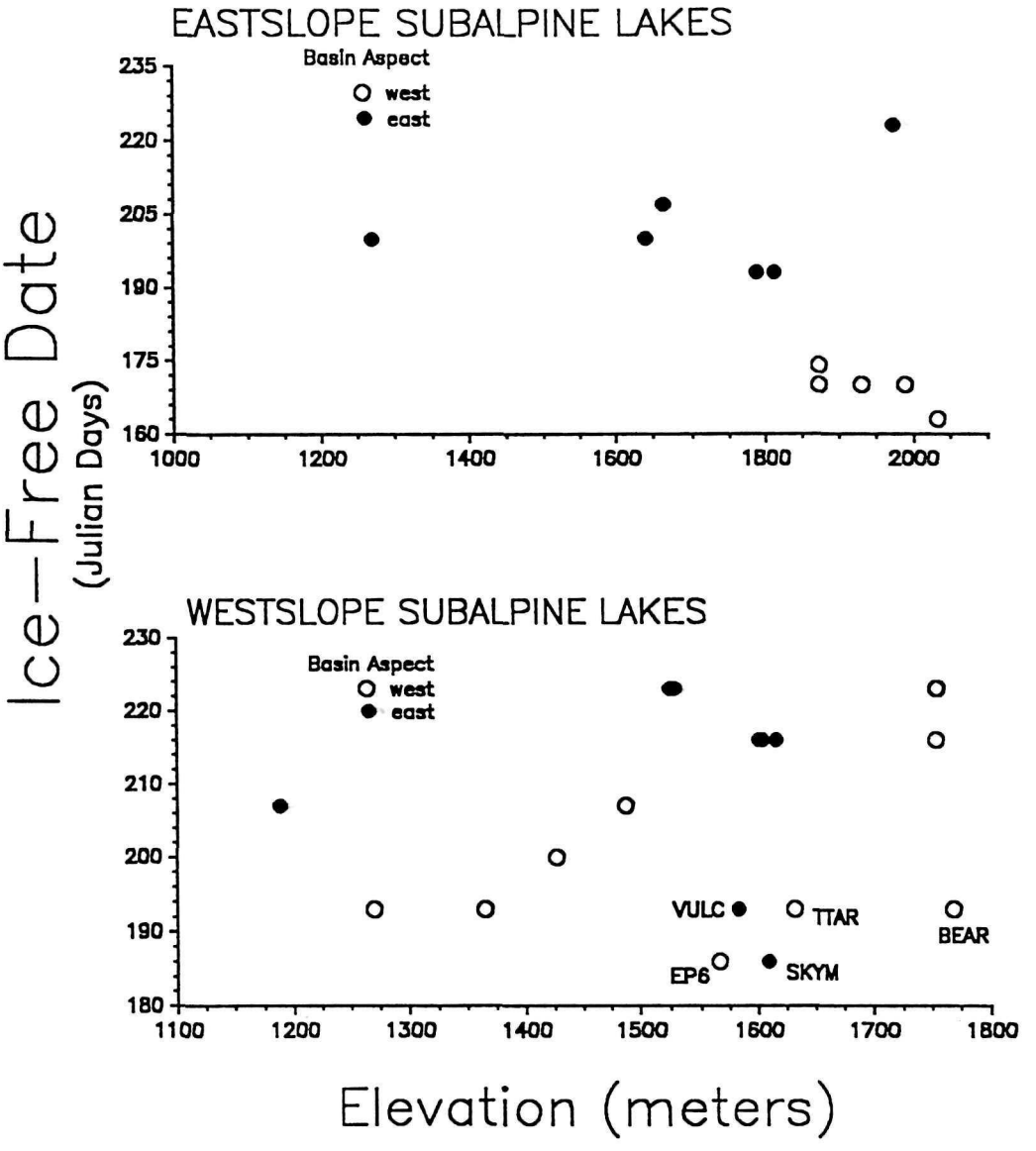


Figure 3. Relationship between estimate date of ice-out (Julian days), elevation (m), and basin aspect for eastslope and westslope subalpine lakes in 1989.

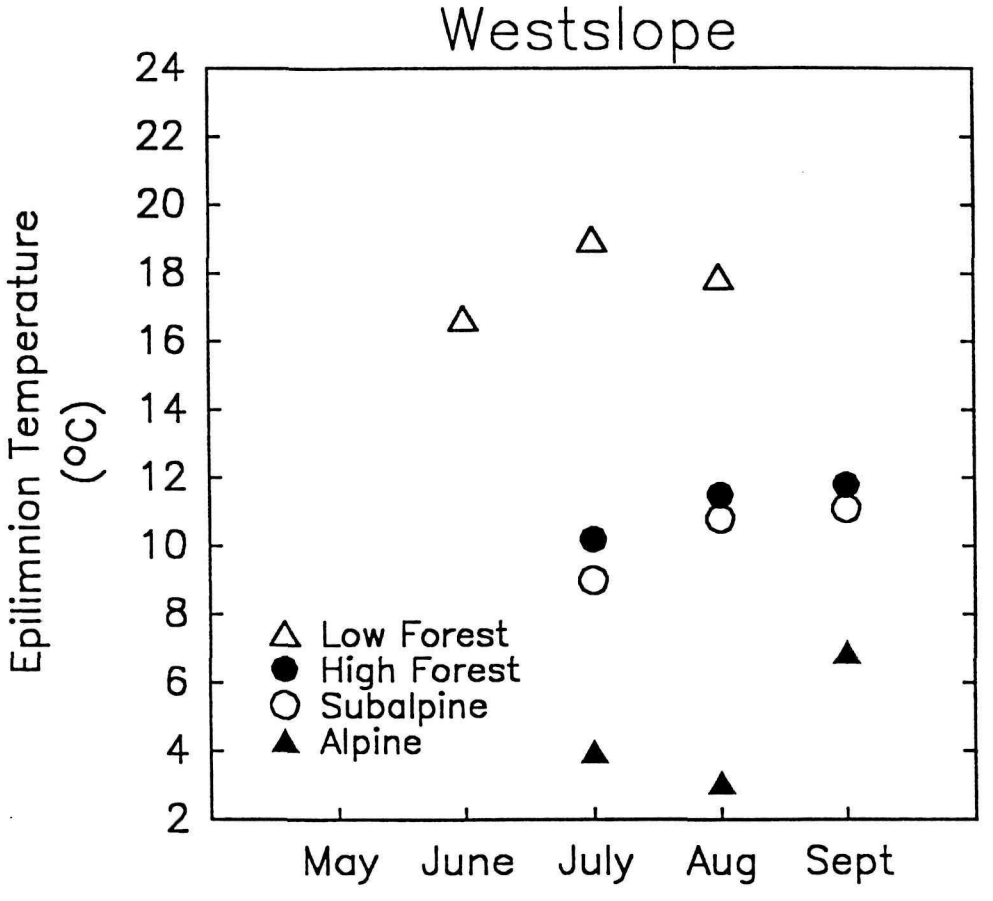


Figure 4. Relationship between epilimnion temperature (°C) and month for westslope vegetation zones. Each symbol represents the average temperature of all lakes sampled in a particular vegetation zone each month.

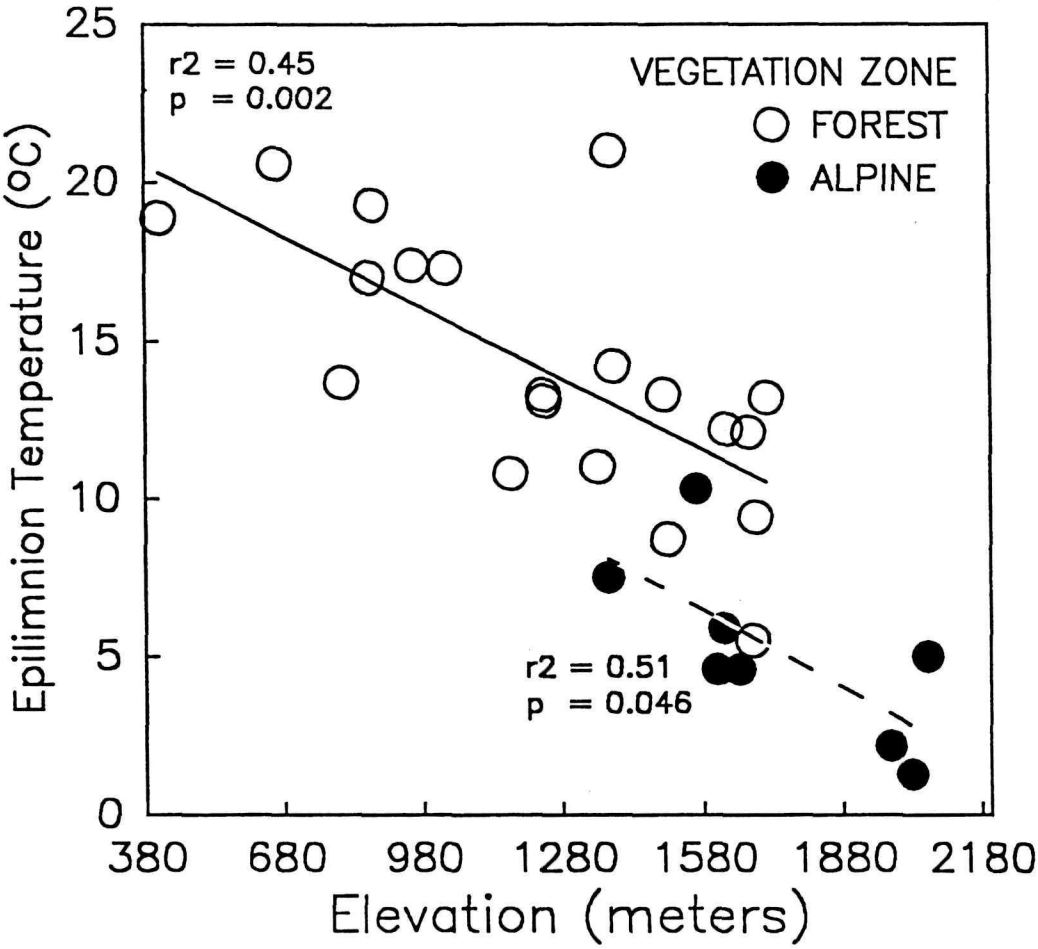


Figure 5. Relationship between epilimnion temperature (°C) and elevation (m) for forest and alpine zones.

Water Chemistry

Classification of lakes using crest position and vegetation zones did not clearly order the lakes relative to chemical characteristics. With the exception of westlope low-forest lakes, there were few significant differences in concentrations of nutrients (total Kjeldahl-nitrogen, total phosphorus, orthophosphorus, nitrate-nitrogen, and ammonia-nitrogen), pH, alkalinity, conductivity, and concentration of cations (sodium, potassium, calcium, and magnesium) between eastslope and westslope lakes and lakes in different between vegetation zones (Table 7). Westslope low-forest lakes differed significantly (Kruskall-Wallis, $P<0.008$) from all other westslope vegetation zones in pH, alkalinity, conductivity, cations (Na, K, Mg, Ca) and total Kjeldahl-nitrogen (except high forest). Although there were few significant differences among westlsope vegetation zones, pH, alkalinity, conductivity, concentrations of total Kjeldahl-nitrogen, potassium, calcium, and magnesium tended to decrease from low-forest to alpine westslope lakes, and concentration of nitrate-nitrogen tended to increase (ALP > WLF; Kruskall-Wallis, $P<0.008$). Total phosphorus was significantly higher in concentration in alpine than low forest lakes (Kruskall-Wallis, $P<0.008$). Westslope low-forest lakes also differed significantly (Kruskall-Wallis, $P<0.008$) from eastslope subalpine lakes in pH, conductivity, alkalinity, and cations (except Mg). Other significant differences between eastslope and westslope lakes were few (TP, ESA > WSA; Na, EHF > WALP, WLF > EHF).

The lakes exhibited little seasonal and annual variation in their chemical characteristics based on a cluster analysis of all samples collected from 1989 to 1992. A five-cluster structure was selected. Cluster 5 was dominated by alpine and subalpine lakes receiving glacial outwash (Table 8). Subalpine lakes dominated cluster 1, and

Table 7. Means and standard deviations (in parenthesis) for water chemistry variables 1989-1992. LF= Low Forest; HF= High Forest; SA= Subalpine; ALP= Alpine

	Eastslope			Westslope			
VAR	LF	HF	SA[1]	LF	HF	SA	ALP
N	1	5	12	7	9	16	8
TKN (mg/l)	0.147 (0.000)	0.064 (0.061)	0.055 (0.037)	0.112 (0.052)	0.045 (0.026)	0.024 (0.018)	0.018 (0.016)
TP (mg/l)	0.011 (0.000)	0.007 (0.003)	0.009 (0.006)	0.010 (0.003)	0.005 (0.003)	0.005 (0.005)	0.010 (0.009)
OP (mg/l)	0.002 (0.000)	0.001 (0.000)	0.001 (0.000)	0.001 (0.000)	0.001 (0.001)	0.001 (0.001)	0.002 (0.002)
NO3 (mg/l)	0.000 (0.000)	0.003 (0.002)	0.007 (0.009)	0.001 (0.000)	0.005 (0.006)	0.008 (0.008)	0.013 (0.011)
NH3 (mg/l)	0.004 (0.000)	0.005 (0.001)	0.005 (0.002)	0.008 (0.004)	0.006 (0.004)	0.006 (0.005)	0.003 (0.003)
PH	7.2	7.3	7.0	7.9	7.2	6.7	6.7
ALK (mg/l)	2.262 (0.000)	2.699 (1.680)	1.840 (1.164)	9.678 (5.597)	2.451 (1.753)	1.007 (0.878)	0.915 (0.479)
COND (µS/cm)	21.040 (0.000)	22.060 (14.295)	16.366 (12.371)	82.815 (41.854)	22.046 (16.671)	14.903 (18.773)	7.546 (4.393)
NA (mg/l)	0.620 (0.000)	0.488 (0.181)	0.425 (0.227)	1.160 (0.267)	0.368 (0.211)	0.274 (0.103)	0.189 (0.083)
K (mg/l)	0.270 (0.000)	0.194 (0.115)	0.155 (0.091)	0.434 (0.223)	0.155 (0.129)	0.114 (0.092)	0.159 (0.120)
CA (mg/l)	3.530 (0.000)	3.266 (2.494)	2.239 (1.879)	12.643 (7.661)	3.214 (2.766)	1.502 (1.505)	0.864 (0.724)
MG (mg/l)	0.521 (0.000)	0.282 (0.174)	0.236 (0.194)	1.330 (0.791)	0.350 (0.346)	0.142 (0.185)	0.107 (0.097)

[1]The three alpine lakes were not sampled.

Table 8. Summary of lake groups developed using cluster analysis, based on water chemistry variables, 1989-1992. Each lake sample was considered an individual point. Two lakes with multiple samples had a single sample in a second group. Lakes occurring in more than one group were placed in the group containing the majority of samples for that lake. Lake acronyms given in Appendix I.

			Vegetation Zone (percent)			
Group	N[a]	Lakes	A	S	FH	FL
5						
Westslope	3		67	33	0	0
ALP		KLAW,OUZE				
SA		PRIC[b]				
1						
Westslope	32		16	63	21	0
HF		BOUC,LS1,NONA,PM53,THR				
SA		L				
		BEAR,COPP,EGG,EP6,LS3,				
		MONO,REVL,SKYM,TAP1,				
ALP		TAP2,TAP4,THRM,WILD				
		EILE,MP8,SILV,SKYU,WILE				
Eastslope						
HF						
SA		RAIN,WADD				
		DOUB,GNVW,MM11,MR3				
		MR11,M131,M132				
4						
Westslope	18		6	44	39	11
LF		PANU				
HF		JEAN,LS2,NERT,SWEE				
SA		SKYM,TTAR,VULC				
ALP		MORA				
Eastslope						
LF		COON				
HF		BATT,DAGG,MCAL				
SA		JUAN,MR2,TRAP,TRIL,TRIU				
2						
Westslope	3		0	0	0	100
LF		PANL,PYRA,THUN				
3						
Westslope	3		0	0	0	100
LF		HOZO,RIDL,WILL				

[a]N represents the number of different lakes in each group
[b]Essentially alpine- from heavy glacial influence

subalpine and high-forest lakes dominated cluster 4. Clusters 2 and 3 contained only low-forest westslope lakes. A discriminate analysis was performed on the clusters to graphically determine their relative similarity in ordination space (Figure 6). Axis one was correlated with alkalinity (r^2=0.903), pH (r^2=0.760), conductivity (r^2=0.894), total Kjeldahl nitrogen (r^2=0.437), Ca (r^2=0.948), Na (r^2=0.903), K (r^2=0.790), and Mg (r^2=0.363). Axis two was correlated weakly with potassium (r^2=0.482). Axis three was negatively correlated with total phosphorus (r^2=-0.632) and ortho-phosphorus (r^2=-0.882). Thus, westslope low-forest groups (2 and 3) were distinguished from other groups (1,4, and 5) along axis one by tending to have higher alkalinity, pH, conductivity, TKN, and cations. Group 5, alpine and subalpine glacially influenced lakes, was distinguished by having higher levels of phosphorus than other groups (Table 9). Groups 1 and 4 contained the majority of the lakes, although the lakes in group 4 tended to be lower in elevation than the lakes in group 1.

Groups 2 and 3, both containing westslope low-forest lakes, were differentiated by geology. Group 2 contained lakes found in gneiss, a metamorphosed crystalline bedrock. Lakes in group 3 (HOZO, RIDL, and WILL) had the highest alkalinity, conductivity and pH, and highest concentrations of TKN, Mg, and Ca. These lakes occurred in a metamorphosed interbedded sedimentary and volcanic bedrock termed greenstone.

Lakes of various depths occurred within each vegetation zone, and lake depth influenced water chemistry. For example, concentrations of total Kjeldahl-nitrogen and total phosphorus tended to decrease with increasing lake depth (Figure 7). A wide variety of watershed characteristics such as glacial influence (note KLAW, PRIC and OUZL) also probably influenced ambient chemical concentrations in the lakes, further

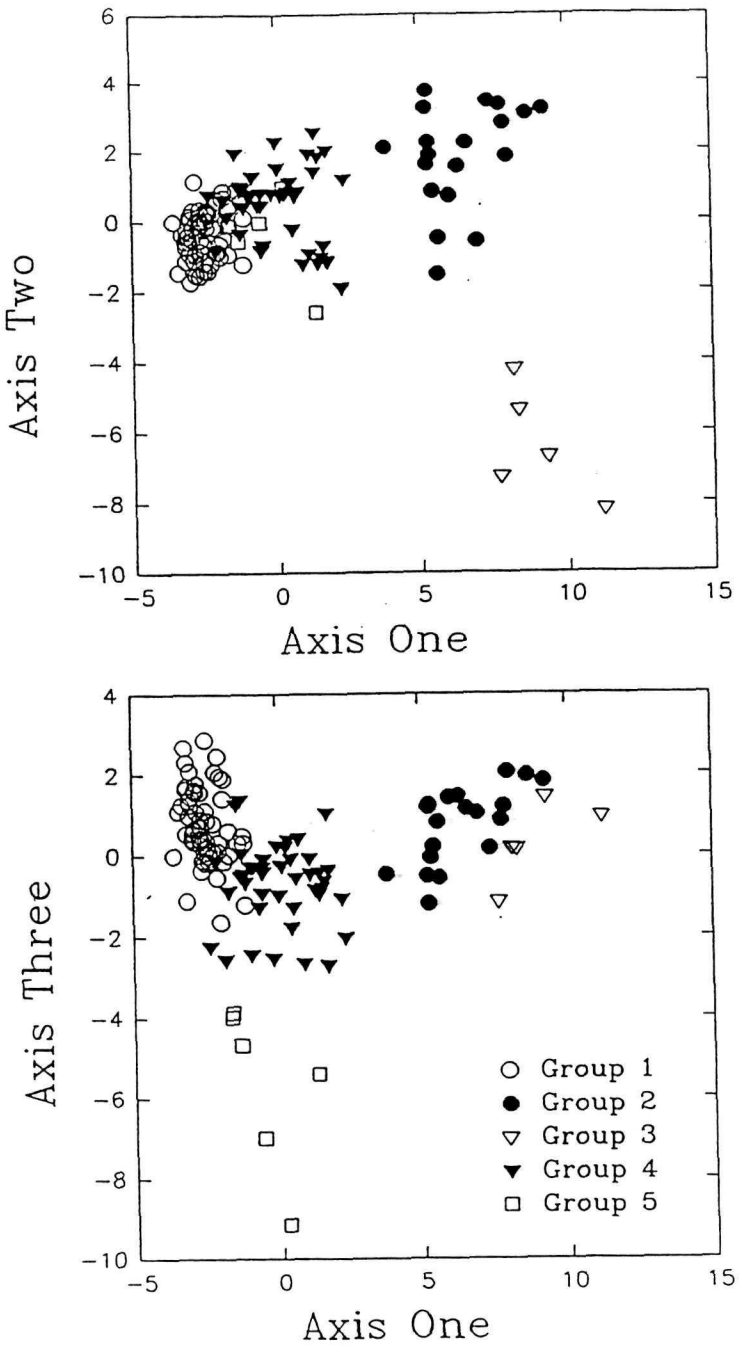


Figure 6. Ordination of water chemistry variables for lakes sampled from 1989-1992. Groups defined by cluster analysis (Table 9) are shown. Discriminant analysis was used to graphically represent the clusters in ordination space. A total of 142 samples represent 58 lakes.

Table 9. Cluster group means of selected water chemistry variables, 1989-1992.

Group	N	EL (m)	TKN (mg/l)	TP (mg/l)	OP (mg/l)	NH3 (mg/l)	PH	ALK (mg/l)	COND (µS/cm)	NA (mg/l)	K (mg/l)	CA (mg/l)	MG (mg/l)
5	6	1490	0.036	0.016	0.005	0.006	7.0	2.01	17.4	0.270	0.188	2.097	0.154
1	69	1621	0.033	0.005	0.001	0.005	6.7	1.15	10.6	0.272	0.097	1.243	0.124
4	43	1540	0.078	0.009	0.001	0.005	7.5	3.41	30.4	0.613	0.246	4.481	0.439
2	19	748	0.075	0.008	0.001	0.008	7.8	7.17	65.0	1.450	0.643	9.271	1.498
3	5	896	0.119	0.011	0.001	0.007	8.1	13.25	112.5	0.990	0.272	18.42	1.686

TKN:Total Kjeldahl Nitrogen, TP:Total Phosphorus, OP:Ortho Phosphorus, NO3-N:Nitrates, NH3-N:Ammonia
ALK:Alkalinity, COND:Conductivity, NA:Sodium, K:Potassium, CA:Calcium, MG:Magnesium

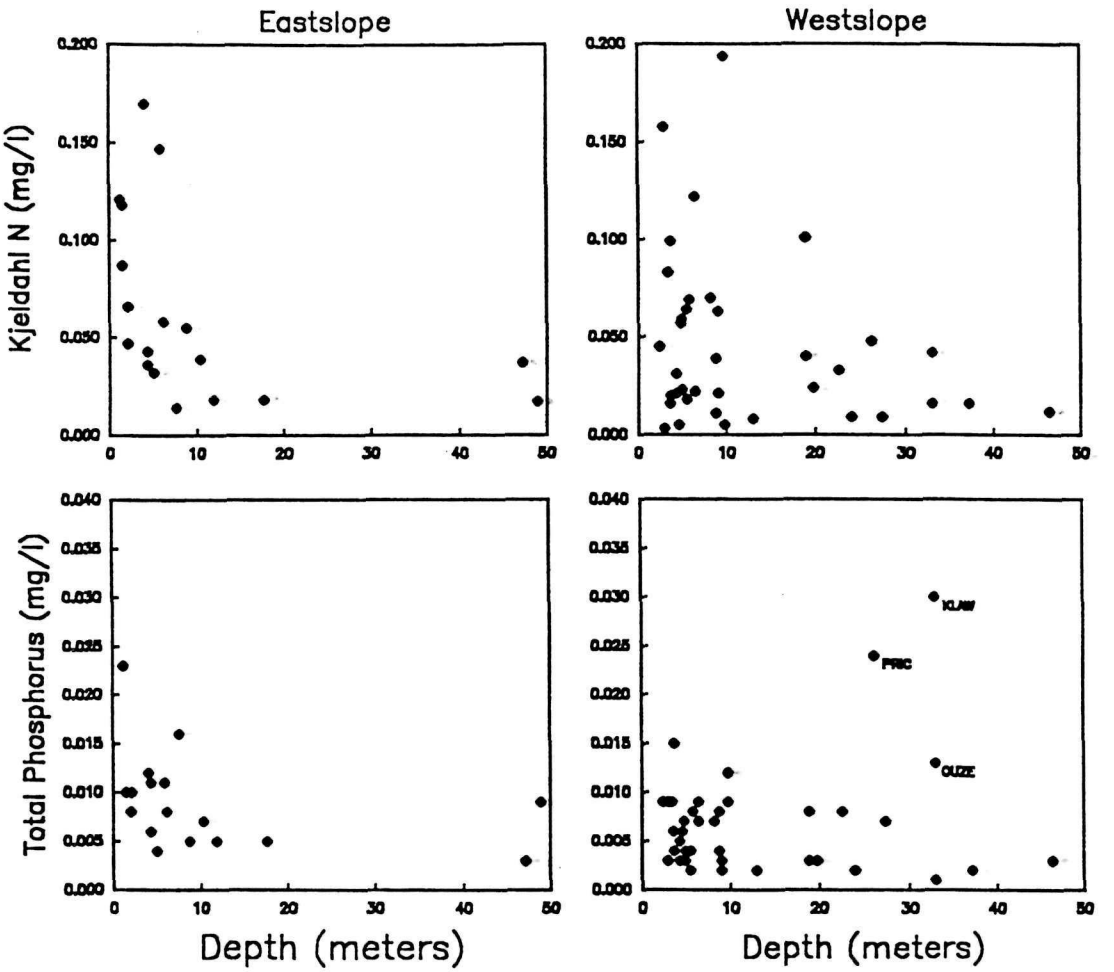


Figure 7. Relationship between total Kjeldahl nitrogen (mg/l), total phosphorus (mg/l) and maximum lake depth for eastslope and westslope lakes.

adding to the variability observed within each vegetation zone. Schlinder's ratio (A_o+ A_d)/V, where A_o= watershed area, A_d= lake surface area, V= lake volume) indicates the potential flushing ratio for each lake (Schlinder 1971). Total concentration of Kjeldahl-nitrogen appeared to increase and then decrease with an increase in Schlinder's ratio for each vegetation class (Figure 8). Hand-drawn curves suggested that for a given ratio, total Kjeldahl-nitrogen decreased from low forest to alpine zones.

DISCUSSION

NOCA lakes exhibited a relatively narrow range of water qualities and nutrient concentrations. The most productive lakes were marginally mesotrophic, whereas the majority of lakes were either ultraoligotrophic or oligotrophic based on concentrations of nitrogen and phosphorus (Likens, 1975). Hydrologic crest position, vegetation, and lake morphometry influenced the physical and chemical characteristics of NOCA lakes. Individual vegetation zones were located at higher elevations east of the hydrologic crest than west owing to the sharp climate gradient. In fact, the climatic differences essentially excluded the alpine zone on the eastside of the hydrologic crest. Vegetation state (alpine to low forest) was associated with increased epilimnetic water temperature and earlier dates of ice-out. For a given vegetation zone, lakes east of the hydrologic crest iced-out earlier than lakes west of the crest. Furthermore, lakes in west-facing watersheds iced-out earlier than lakes in east-facing watersheds in some vegetation zones. Lakes with late ice-out dates (i.e. alpine lakes) were generally colder throughout the ice-free season than lakes that iced-out earlier in the season.

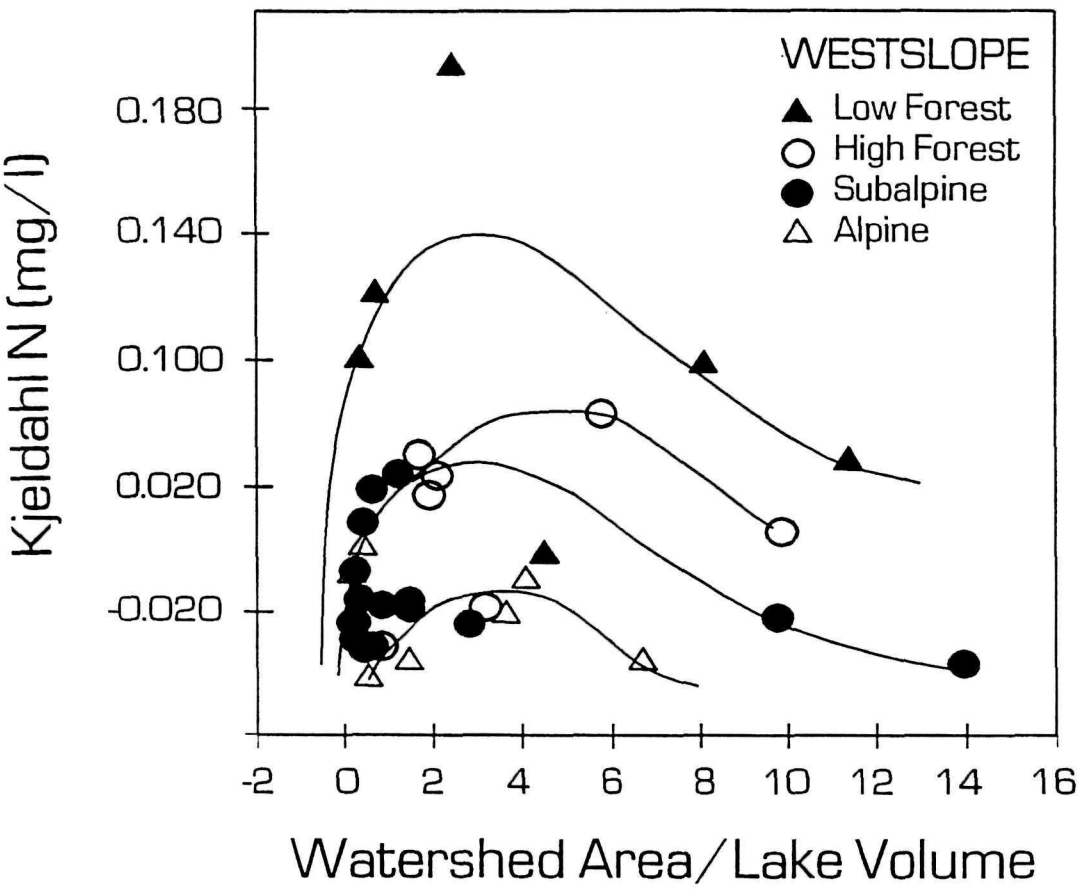


Figure 8. Relationship between total Kjeldahl nitrogen (mg/l) and an index of flushing ratio (watershed area/lake volume) for westslope vegetation zones.

Vegetation zones did not clearly order many water chemistry parameters, although there was a tendency for pH, alkalinity, and concentrations of TKN and certain cations to decrease from the low forest to the alpine zone on the westslope. The low forest zone had the latest vegetation successional state, greatest potential for water and soil interactions, and had been deglaciated for the longest period of time. However, concentrations of total phosphorus were high in alpine lakes receiving glacial outwash, comparable to those of low-forest lakes. Phosphorus concentrations in subalpine lakes were low relative to those in alpine lakes because glacial influences were much reduced. Sedimentary rock elevated the water quality (pH, alkalinity, conductivity) of several low-forest lakes relative to those lakes lacking this rock type in their watersheds.

Lake origin was useful in identifying potential differences in longterm persistence, basin location, and the diversity of lakes parkwide. Some morphogenetic lake types were found in all vegetation zones (e.g., ice scour, cirque, trough, and dammed lakes) whereas other were restricted to specific vegetation zones. Lake basins formed by erosional processes may be more persistent than lakes created by depositional landforms (Table 5). Amount of infilling is a function of both morphogenetic origin and lake age. Older low-forest trough lakes no longer cover entire valley floors as young alpine trough lakes often do, and they tend to be shallower than alpine trough lakes. Relatively shorter-lived slump lakes originate from a rotational slip in deep seated soils, and only occur in the forest zone in NOCA, the zone which has the greatest soil maturity and soil depth. Kettle lakes occur in one park drainage though they are generally restricted to ground moraines deposited across the continental plains.

Limnologists have developed several types of lake classification systems during the last 60 years. Much of the research has addressed physical attributes, morphometrics, nutrients or combinations of these variables on very diverse groups of lakes. Larkin and Northcote (1958) sampled a group of British Columbia lakes with a wide range of mean depths and determined that conductivity decreased with increasing mean depth. The range of mean depths among NOCA lakes was narrow in relation to the lakes studied by Larkin and Northcote, and the relationship between mean depth and conductivity was weak and not significant (r^2= -0.123). George and Maitland (1984) used lake basin morphometric characteristics as the basis of classifying lochs in Scotland which, unlike NOCA, differ little in climatic extremes. Hutchinson (1957) described 76 types of lakes by origin. Relatively few of these types occur in NOCA. Mean depth was found to be a good indicator of fish production in Canadian lakes much larger than those existing at NOCA (Rawson 1955). Pennak (1958) used elevation to classify lakes in the Colorado Rockies that were similar with respect to basin geology, origin, and aspect. Lewis (1983) used temperature and mixing to classify lakes in different climates worldwide. Based on this classification, NOCA lakes would be grouped into a single class (dimictic), although some of the lakes may be amictic in some years.

Some lake classification systems have focused primarily on rates of nutrient loading. Vollenwieder (1968) determined that total phosphorus loading rate was an indicator of the trophic status of lakes. Almost without exception, NOCA lakes are oligotrophic or ultraoligotrophic. The range of total phosphorus concentrations in NOCA lakes was small in comparison to the range used by Vollenweider. Schindler (1971) determined that concentrations of nitrogen and phosphorus in lakes in the

Experimental Lakes Area (ELA) were associated with the ratio of [lake and watershed area /lake volume] . Unlike NOCA, the ELA area is of relatively uniform topography, vegetation, and geology. Schindler found linear relationships between concentration of nutrients and a relatively limited range of watershed-to-volume ratios (0 to 7). At NOCA the range of ratios was much larger than for the ELA lakes and the relationships appeared to be curvilinear. These results suggest that after watershed-to-volume ratios exceed about seven, concentrations of Kjeldahl N decrease, perhaps due to increased flushing rate.

Biological approaches to lake classification have existed for most of the century. Thieneman (1909) grouped a diverse range of lakes by the presence or absence of specific chironomid taxa. NOCA lakes include a very narrow range of these lake types. Tonn and Magnusson (1982) classified lakes based on the number of fish taxa present. Fish are not indigenous to NOCA high mountain lakes. Round (1958) and Nygaard (1949) used phytoplankton quotients to classify lakes. However, the taxa used are not important in NOCA phytoplankton communities.

A number of lake classifications have combined chemical and physical approaches. The Morphoedaphic Index (MEI) developed by Ryder (1974) combines mean depth and total dissolved solids (TDS) to classify lakes for potential fish production. The index was originally intended for lakes greater than 260 ha in surface area and less than 600 m in elevation with low flushing rates and inorganic turbidity and within an area with relatively homogenous environmental conditions. Climatic and limnological characteristics of NOCA lakes violate these restrictions. The Trophic State Index (TSI) developed by Carlson (1977) was developed using a set of lakes with a very wide range of Secchi disk transparencies and concentrations of chlorophyll and

total phosphorus. Chlorophyll was used as an index of algal biomass. The TSI is not appropriate for glacial systems or lakes of extreme clarity. Algal biomass is very low in NOCA lakes (see Phytoplankton section) and the water is extremely clear (Secchi disk visibility extends to the bottom in many lakes). Thus the TSI is of little value for classifying NOCA lakes.

FISH

Trout are not indigenous to most high mountain lakes in the west (Bahls, 1992). Trout were stocked in NOCA lakes during this century to provide recreational angling opportunities (Jarvis, 1987). The principle species that have been stocked in NOCA are cutthroat (Oncorhynchus clarki) and rainbow trout (O. mykiss). In some lakes, trout have established reproducing populations which can reach high densities. In other lakes, trout do not reproduce and fry are periodically stocked at relatively low densities.

A central hypothesis of this research is that effects of fish on native biota vary along a gradient of increasing fish predation intensity. Predation intensity is related to density and size structure of fish populations. Thus, it was necessary to obtain at least a relative estimate fish density in study lakes.

METHODS

Population Estimates

Population estimates were conducted on 13 lakes between 1990 and 1993. Eight of these lakes support reproducing populations of trout. Fish in the other five lakes do not successfully reproduce (Table 1) and must be periodically stocked. Lack of reproduction was indicated by absence of suitable spawning habitat, failure to observe fry or smaller fish, and little variation in age and size structure. Abundance was estimated using two basic methods; fishing success and mark-and-recapture.

Table 1. Mean length, weight, and condition factor (K) for fish captured in gill nets set in lakes of North Cascades National Park Service Complex, 1990-1993.

			Non-reproducing Populations		
			Mean		
Lake	Species*	Date	Length	Weight	Condition Factor (K)
LS1	CTT	9/10/90	208	107	1.05
LS1	CTT	8/18/92	203	72	0.85
MR9	CTT/RBT	8/31/93	314	290	0.91
MR13-2	RBT	9/4/90	208	115	1.06
Lower Panther	CTT	8/10/90	278	210	0.96
Lower Panther	CTT	8/14/92	263	173	0.93
Upper Panther	CTT	8/9/90	242	125	0.88
Mean			231	138	0.98

			Reproducing Populations		
			Mean		
Lake	Species*	Date	Length	Weight	Condition Factor (K)
Dagger	CTT	9/15/93	224	94	0.77
Kettling	RBT	8/3/93	183	64	0.95
LS2	CTT	9/17/91	218	186	0.78
LS2	CTT	9/14/92	209	80	0.82
McAlester	CTT	9/17/91	204	71	0.78
McAlester	CTT	9/21/92	194	65	0.85
MR16	CTT	7/27/93	226	114	0.95
Rainbow	RBT	8/14/91	200	74	0.84
Rainbow	RBT	9/17/92	197	74	0.89
Lower Triplet	CTT	8/7/91	187	57	0.85
Upper Triplet	CTT	8/8/91	235	114	0.83
Mean			203	79	0.86

*CTT = cutthroat trout; RBT = rainbow trout

Fishing success method

In 1990, as part of the lake manipulations, an attempt was made to remove all fish from LS1, MR13-2, Lower Panther, and Upper Panther lakes using gill nets. These are all relatively small lakes with low fish density, and none supported reproducing populations of fish. From one to three gill nets were set in each lake for varying periods of time. When nets were retrieved, all fish were removed, and the gill nets were reset immediately. The period of time that each net was fished was recorded. This procedure continued until fish were no longer captured in the nets. Following removal, fry were stocked in Lower Panther, LS1, MR13-2, and MR11 (a lake with a history of stocking that was fishless in 1990 and probably for several prior years). Fry were not restocked in Upper Panther.

Catch per unit effort estimates were combined for all nets fished during a given time period. Regression of catch per unit effort on cumulative catch from gill nets was used to estimate total populations for these lakes according to the Leslie method (Ricker, 1975). Ninety-five percent confidence limits were calculated for each estimate (Ricker, 1975).

Mark-recapture estimates

Population density was estimated in a total of 11 lakes by mark-and-recapture. Fish density was estimated in two lakes (LS1, Lower Panther) by fishing success in 1990 and by mark-recapture in 1992. Lakes where mark-recapture was attempted were small (≤6.3 ha), and angling was the best available method for capturing fish. Fish in the mark sample were collected by angling, fin-clipped, and released. We were able to mark and release fish by angling from the shore along the entire perimeter of

most lakes. Fish also were captured and marked from an inflatable boat. Injured fish (e.g., bleeding from gills or tongue) were either released unmarked or sacrificed. Two groups, each with 12 fish, were held overnight after capture and marking to estimate post-release mortality due to handling and marking.

Fish were recaptured with monofilament gill nets. The nets were usually set the day after marking was completed. To minimize reduction in capture efficiency, nets were checked frequently to insure that fish did not accumulate. Overnight sets were checked the following morning. In the course of recapturing, net locations were changed often.

In 1991, mark-recapture was conducted twice at McAlester, Rainbow, Lower Triplet and Upper Triplet lakes, and three times at LS2. Three mark-recapture estimation procedures were compared at LS2. Initially, marked (M), total fish captured by gillnetting (C), and marked fish recaptured by gillnetting (R) from each of the three sample periods at LS2 were combined, and population abundance was estimated with a single-census Petersen estimator ($N = (M+1)(C+1)/(R+1)$; Ricker, 1975). A repeated census procedure used the mean of three single-census estimates (one for each sample period) to provide a second assessment of the population in LS2. The Schnabel multiple-census procedure was similar to the single census using all fish, except the product of marked and sampled fish was calculated separately for each sample period ($N = \Sigma(C_t M_t)/\Sigma R$; Ricker, 1975). Single-census estimates were used for all other lakes sampled in 1991. In 1992 and 1993, mark-recapture was conducted only one time at each lake, and density was estimated by a single-census Petersen procedure.

Assumptions associated with the single-census Petersen estimate include equal natural mortality and vulnerability to capture for marked and unmarked fish (Ricker, 1975). Marks must be retained and remain recognizable throughout the period. Distribution of marked and unmarked fish is assumed to be random, or if not random, subsequent sampling is proportional to the number of fish in different areas. Finally, recruitment should be negligible during the sample period (Ricker, 1975). Requirements for the Schnabel estimator are similar, except no mortality or recruitment can occur (Ricker, 1975).

Differences in gear selectivity may bias the outcome of mark-recapture estimates (Ricker, 1975). Size selectivity may be exacerbated in this study because angling may be selective for a different size range of fish than gill nets. Detection of unequal vulnerability can be accomplished by comparing capture and recapture rate for fish of different sizes, and the effects of selectivity can be minimized by dividing estimates among two or more size groups or excluding fish near the limits of a given fishing gear.

Fish caught by angling and marked were not measured prior to release; however, fish in the recapture sample provided an estimate of the size distribution of fish caught by angling. To evaluate the magnitude of possible differences in size selectivity of angling and gillnetting, mean size of marked fish in the recapture sample (an estimate of size of fish captured by angling) was compared to the mean size of all fish captured by gillnetting (ANOVA). Additionally, a direct comparison (ANOVA) of length-samples of angler-captured trout (measured to the nearest 25 mm) and those captured in gill nets was conducted on samples from Lower Triplet and Upper Triplet lakes in 1991. Because abundance estimates of larger fish may be more precise (Ricker 1975), abundances of fish > 170 mm and > 200 mm (TL) also were estimated.

Population estimates were converted to densities by dividing estimated abundance by lake surface area (ha). For each lake, mean individual weight for fish was estimated from a weight-length equation using the mean length of fish captured as the predictor variable. Density for each lake was multiplied by the mean individual weight of the sample to approximate biomass per ha ($kg \cdot ha^{-1}$). Abundance of fish in lakes with reproducing populations of fish (a single mean value was used for lakes with more than one abundance estimate) was compared to fish abundance in lakes where reproduction did not occur (all estimates included) using one-way ANOVA.

In 1992 and 1993, we used gill nets with somewhat smaller mesh size than the nets used in 1991. To test for possible differences in net efficiencies, samples collected in 1991 and 1992 from LS2, McAlester, and Rainbow lakes were compared (ANOVA).

Age, Length, Weight

Fish captured in gill nets were measured to the nearest 1 mm (total length TL and fork length) and weighed to the nearest 10 g. Otoliths were removed from a subsample of fish from each lake for age determination. Mean length (TL), weight, and Fulton's condition factor (K; Ricker, 1975) were calculated for fish captured at each lake. A weight-length relationship was estimated for each population using a GM functional regression (Ricker, 1973; 1975). Age was estimated for individual fish by counting annuli occurring on otoliths (Secor et al., 1991).

Only a small number of fish from each lake have been aged so far, but age distribution of the these fish was expanded to the entire number of fish captured in each lake using an age-length key (Kimura, 1977; Westerheim and Ricker, 1978). Initially, age composition was determined for 10-mm length intervals in the subsample of fish

that were aged at each lake. Subsequently, the proportion of fish of a particular age in each 10-mm size group (aged-fish only) was multiplied by the total number of fish captured in the respective size interval. Mean age for each sample was estimated from the expanded distribution at each lake. Because age information was limited to age-at-capture, growth comparisons were based on variables obtained by the Brody-Bertalanffy procedure (Ricker, 1975). Mean length was estimated for each age group in the subsample of fish that were aged. The Brody Growth Coefficient (K) and the theoretical asymptotic length (L_∞) were estimated by fitting mean length for each age group to a specialized form of the von Bertalanffy growth formula (surface factor (D) = 1; Pauly, 1984). Age groups with less than two fish were not included in the growth analysis. Age and growth information for a limited number of lakes is presented here. Analysis of age and growth for all lakes is continuing.

Trout Diet

In general, taxa from stomach contents were identified to the family level. Identified taxa were placed into food categories according to their probable location in the lake (benthic, water column, lake surface) when ingested.

RESULTS

Age, Length, and Growth

Mean length, weight, and condition factor of fish captured in gill nets from North Cascades lakes (Table 1) differed significantly among lakes ($P < 0.01$). Largest mean lengths were recorded in MR9 in 1993 (314 mm) and Lower Panther Lake in 1990 and 1992 (278 and 263 mm, respectively), and the smallest fish were captured in Kettling

Lake in 1993 (183 mm) and Lower Triplet Lake in 1991 (187 mm). Mean length, weight, and condition factors for fish from lakes with reproducing populations (Table 1) were significantly smaller ($P < 0.01$) than estimates from lakes without reproduction.

Mean age of fish in lakes with reproducing populations (Table 2) ranged from 3.3 years in LS2 (1991) to 4.9 years in Upper Triplet Lake (1991). Although observed longevity was greatest in Upper Triplet Lake, distribution of fish among age groups suggests substantial variation in reproductive success in this lake.

Fish sampled in LS1 and Lower Panther Lake in 1992 were from the cohort of fry ($1091 \cdot kg^{-1}$) stocked in 1990; thus all fish from these lakes were 2 years old (Table 2). Significant differences in the mean length of fish from the two lakes suggests that growth rate of fish is much greater in Lower Panther than in LS1; however, it is apparent that fish in both of these lakes are growing at a much faster rate than those in lakes with natural reproduction (Table 3).

Brody growth coefficients were quite similar for LS2, McAlester, and Lower Triplet lakes (Table 3). Results from this technique suggest that fish in Upper Triplet Lake are growing at a much faster rate than fish in the other three lakes. Sample size is small, however, and among lake comparisons are tentative. Analysis of age and growth is continuing.

Population Estimates

Fishing success method

Fish did not reproduce in LS1, MR 13-2, Upper Panther, and Lower Panther lakes. In 1990, population estimates were very low for these lakes (Table 4), but snorkeling observations and total fish removals suggest that these estimates were

Table 2. Age distribution (%) estimated from an age-length key for fish captured in gill nets from lakes in North Cascades National Park Complex, 1991-1992.

Lakes with Natural Reproduction

		Age								Expanded Age Sample	
Lake Name	Year	1	2	3	4	5	6	7	Mean Age	Mean Length	n
LS2	1991	3	6	58	25	4	3		3.3	218	120
McAlester Lake	1992	3		8	75	13			4.0	198	68
Lower Triplet Lake	1991		16	31	53				3.4	187	50
Upper Triplet Lake	1991	9	4	22	40		22	1	3.9	235	88

Lakes without Natural Reproduction

		Age								Expanded Age Sample	
Lake Name	Year	1	2	3	4	5	6	7	Mean Age	Mean Length	n
LS1	1992		100						2.0	203	24
Lower Panther Lake	1992		100						2.0	263	20

Table 3. Mean length and number of otolith samples (n) of each age group of fish captured in gill nets from lakes in North Cascades National park Service Complex, 1991-1992.

		Lakes with Natural Reproduction								
		Age								
Lake Name	Year	1	2	3	4	5	6	7	K *	Length (∞)**
LS2	1991	125 (2)	153 (4)	196 (15)	247 (7)	281 (1)	317 (1)		0.07	885
McAlester Lake	1992	123 (2)		179 (6)	194 (33)	216 (7)			0.09	429
Lower Triplet Lake	1991		139 (1)	188 (3)	202 (5)				0.10	333
Upper Triplet Lake	1991	122 (2)	187 (1)	216 (3)	243 (2)		276 (2)	285 (1)	0.35	308

		Lakes without Natural Reproduction								
		Age								
Lake Name	Year	1	2	3	4	5	6	7	K *	Length (∞)
LS1	1992		203 (24)						--	--
Lower Panther Lake	1992		263 (20)						--	--

* Brody Growth Coefficient (Ricker, 1975)

** Asymptotic length

Table 4. Trout population estimates (N) and upper and lower confidence limits (LCL and UCL; p = 0.05) for lakes in North Cascades National Park Service Complex, 1990-1993.

		Leslie Estimator		
Lake	Date	N	LCL	UCL
LS1	8/14/90	11	--	--
MR13-2	9/04/90	48	36	81
Lower Panther	8/09/90	8	6	11
Upper Panther*	8/10/90	6	na	na

* Not estimated.

					Chapman Estimator **		
		Marked	Captured	Recaptured	(M+1)(C+1)/(R+1)		
Lake	Date	(M)	(C)	(R)	N	LCL	UCL
LS2	9/17/91	273	136	51	722	552	943
McAlester	9/17/91	299	115	11	2900	1681	5438
Rainbow	8/14/91	251	79	5	3360	1587	7754
Lower Triplet	8/07/91	200	31	9	643	357	1286
Upper Triplet	8/08/91	150	77	23	491	333	755
LS1	8/18/92	34	24	8	97	52	199
LS2	9/14/92	101	70	9	724	402	1448
McAlester	9/21/92	210	134	10	2590	1468	4997
Lower Panther	8/14/92	28	30	13	64	39	114
Rainbow	9/17/92	145	208	5	5086	2403	11736
Dagger	9/15/93	181	198	14	2415	1478	4163
Kettling	8/03/93	310	316	73	1332	1063	1669
MR9	8/31/93	9	9	3	25	10	63
MR16	7/27/93	50	47	24	98	67	149

** Based on combined-samples single-census estimate.

realistic. Six fish were removed from Upper Panther Lake by both gillnetting and angling; this was believed to represent the total number present in the lake. Upper Panther Lake is small (0.1 ha) and shallow (2.0 m maximum depth), and fish can be easily observed.

After fish were removed from the lakes, fry were stocked in September 1990 (except in Upper Panther) at the normal stocking rate for each lake. Although stocking rate was highly variable, with the exception of Lower Panther, stocking density was ≤ 313 fish/ha (Table 5). Lower Panther, a relatively low elevation lake, is apparently stocked more heavily than other lakes, perhaps because fishing pressure is relatively high.

Mark-recapture estimates

Post-release mortality in the two overnight experiments was low. Only one of 24 fish died, and that fish was bleeding from the gills when placed in the holding area. According to normal procedures, injured fish would not have been included in the marked sample.

Population estimates based on single-census Petersen estimators ranged from 5086 (Rainbow Lake, 1992) to 25 (MR9, 1993; Table 4). Single-census, repeated single-census, and multiple-census estimates at LS2 were 722, 469, and 472 fish, respectively. Although the latter two estimates are substantially lower than the single-census calculation, confidence limits for the three estimates overlapped. Furthermore, the single-census figure in 1991 is most similar to the estimate obtained in 1992 (Table 4).

Table 5. Trout density in lakes that do not support reproducing populations, North Cascades National Park Service Complex, 1990-1992.

				Density (no./ha)	
Lake	Date	Area (ha)	Number Fry Stocked	All Fish	Fry
LS1	1990	0.4	125	28*	313
MR13-2	1990	1.2	180	40*	150
Lower Panther	1990	0.2	150	40*	750
Upper Panther	1990	0.1	0	60*	0
MR11	1990	1.3	160	0	123
LS1	1992	0.4		243**	
Lower Panther	1992	0.2		320**	

* Estimates of fish removed prior to fry stocking in September 1990.

**Represent fish surviving from fry stocked in 1990, estimated by mark-recapture (Table 6).

Substantial differences were apparent in the length-frequency distributions of all fish captured by gillnetting and recaptured-fish in the gill net catch (Figure 1a, b). Mean lengths were 209 and 235 mm for all fish captured and recaptured-fish, respectively, and the differences were statistically significant ($P < 0.01$). These results suggest that angling was selecting for larger fish than gillnetting; however, neither method sampled smaller fish in proportion to their relative abundance in the lake.

Differences between fish captured in gill nets and by angling in Upper Triplet Lake (187 and 213 mm, respectively) and Lower Triplet Lake (235 and 260 mm, respectively) in 1991 were not statistically significant ($P > 0.60$ and $P > 0.13$, respectively). The observed differences at both lakes (approximately 30 mm) were similar to those noted between unmarked and recaptured fish in gill-net samples. These results also suggest that angling selects for larger fish in the population. Lack of statistical significance may reflect high sample variance or difference in measurement techniques. Fish captured by angling were measured to the nearest 25 mm, but measurements of gill-net captured fish were to the nearest 1 mm.

In LS2, Rainbow, and McAlester lakes, comparison of mean length of fish captured in nets used in 1991 and nets with a smaller mesh used in 1992 suggests that differences in the size of fish were greater than would be expected by chance alone (210 and 198 mm, respectively; $P < 0.01$). It is difficult to assess the effects of these differences on population estimates because abundance estimates obtained in the two sample years for each of these lakes are within respective confidence intervals (Table 4).

Figure 1. Frequency (a) and number (b) of all fish caught in gill nets and recaptured fish (an indicator of the length of fish marked by angling) during the mark-recapture procedures in 13 lakes in North Cascades National Park Service Complex.

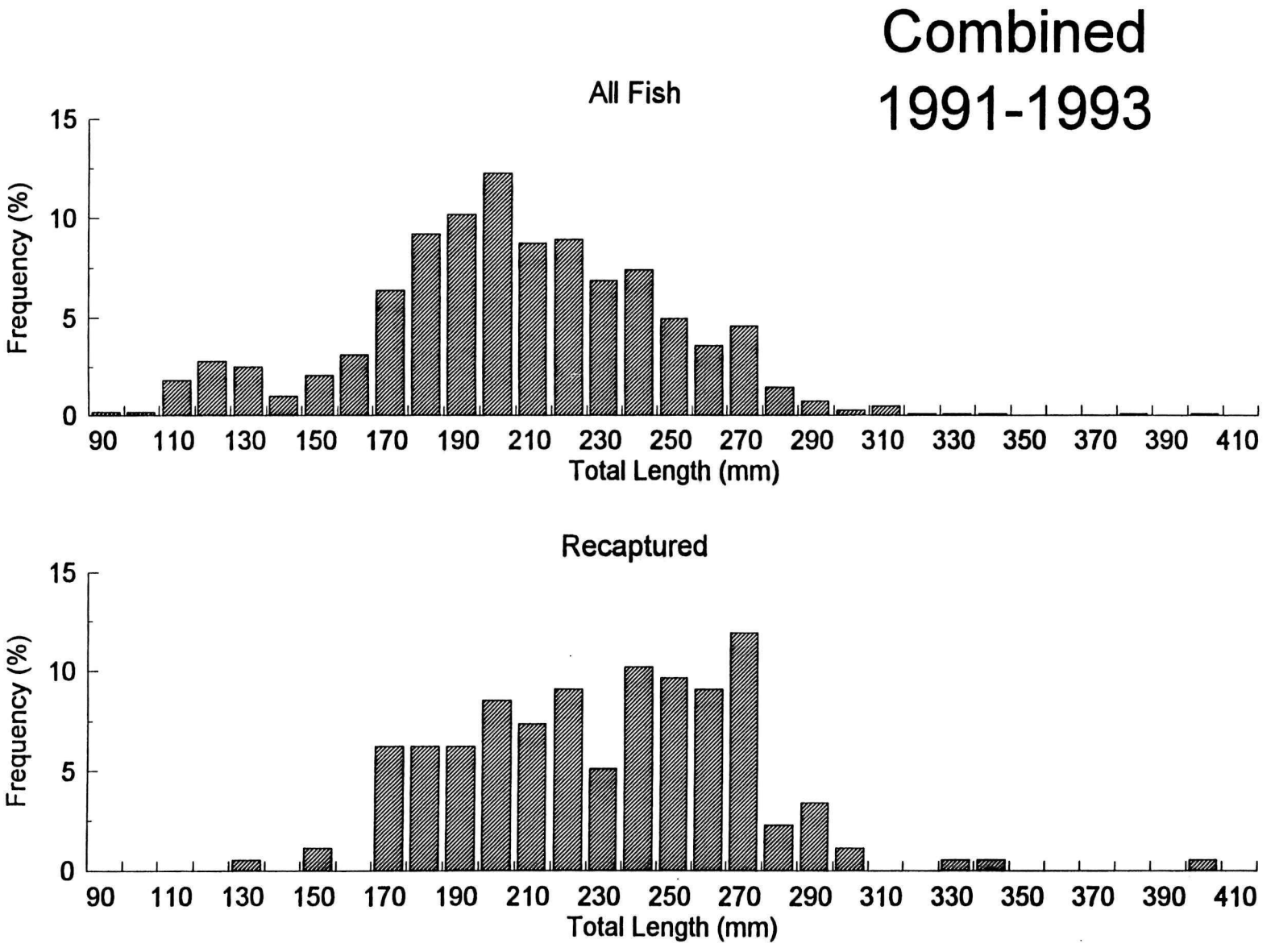

Combined
1991-1993
All Fish
Frequency (%)
15
10
5
0
90 110 130 150 170 190 210 230 250 270 290 310 330 350 370 390 410
Total Length (mm)
Recaptured
Frequency (%)
15
10
5
0
90 110 130 150 170 190 210 230 250 270 290 310 330 350 370 390 410
Total Length (mm)

Figure 1a.

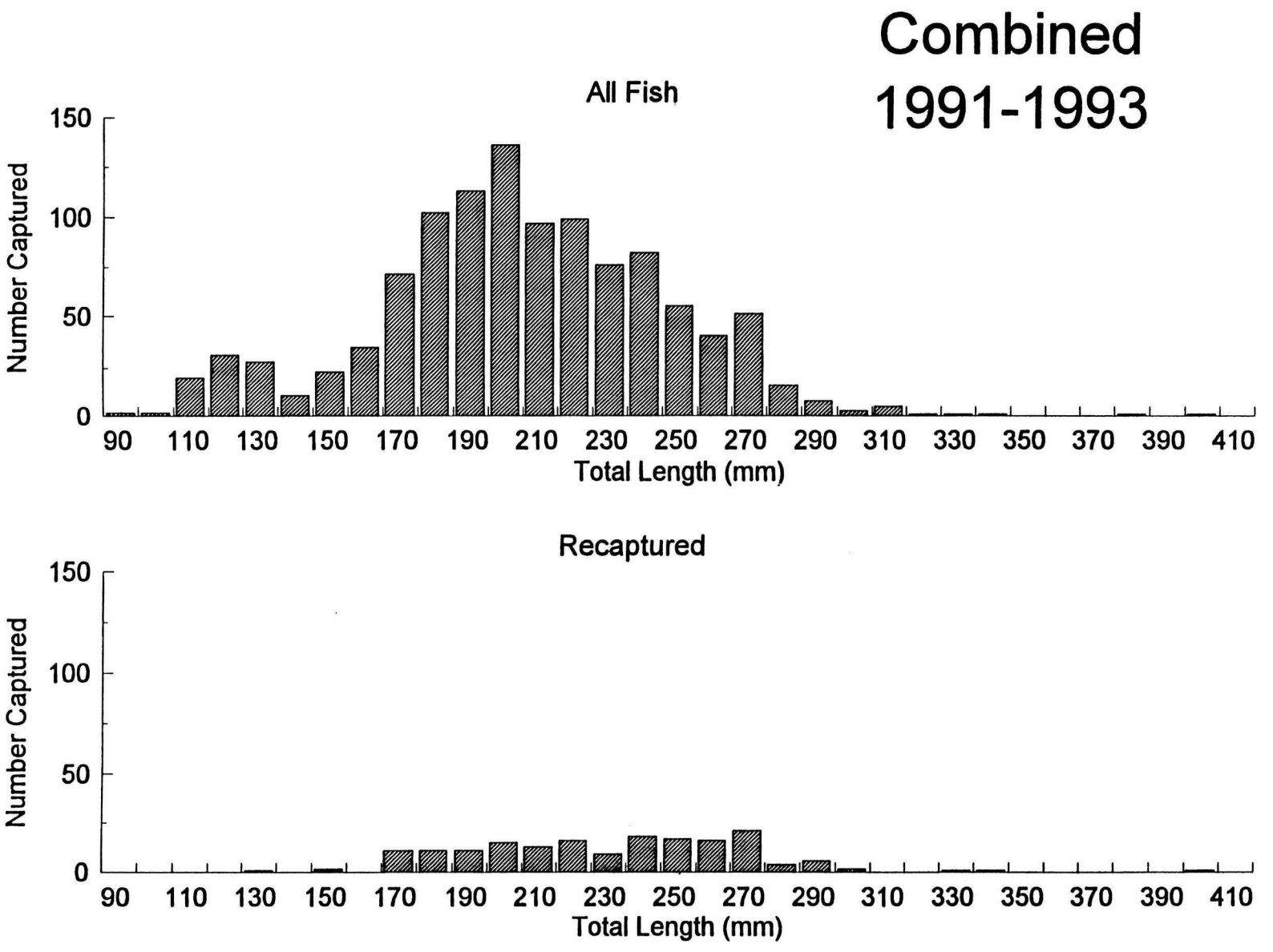

Combined
1991-1993
All Fish
Number Captured
150
100
50
0
90 110 130 150 170 190 210 230 250 270 290 310 330 350 370 390 410
Total Length (mm)
Recaptured
Number Captured
150
100
50
0
90 110 130 150 170 190 210 230 250 270 290 310 330 350 370 390 410
Total Length (mm)

Figure 1b.

Comparison of Lakes with Reproducing and Nonreproducing Fish

The difference in mean population densities (all fish; Table 6) for lakes with reproducing fish populations (524 fish·ha^{-1}; n = 8) and lakes that did not support reproducing fish (106 fish·ha^{-1}; n = 7) was statistically significant ($P < 0.01$). The difference in mean biomasses of fish in lakes with and without reproducing fish (39 and 15 kg·ha^{-1}, respectively) was also statistically significant ($P < 0.01$). However, confidence intervals of the estimates are rather wide. The confidence intervals of the 1992 estimates for LS1 and Lower Panther, both with non-reproducing fish, overlap the confidence intervals of most reproducing populations. The fish in LS1 and Lower Panther are the remaining members of the cohorts of fry stocked in 1990.

Given the possible bias in population estimates due to size selection for larger fish, comparison among lakes may be most meaningful when limited to larger fish in the population. Within-lake similarity between estimates for all fish in the population and those limited to fish > 170 mm (Table 6) suggest that fish smaller than 170 mm may not be represented in the all-fish estimates in proportion to their abundance in the lake. Estimates of biomass within a given lake also were similar when all-fish and fish > 170 mm estimates were compared. Unfortunately, problems arise when comparisons were restricted by size because in some lakes the low number of recaptures caused statistical bias (Robson and Regier, 1964) in estimates (e.g., MR9). Limiting comparisons to fish > 200 mm substantially reduced abundance, density, and biomass estimates when compared to estimates for all fish and for fish > 170 mm, and furthermore, statistical bias was more common in estimates of fish > 200 mm (Table 6).

In 6 of 8 lakes with reproducing populations, estimates of density of fish > 170 mm were between 450 and 650 fish·ha^{-1} (Table 6). MR16 was the only lake with

Table 6. Trout density and biomass (mean weight per fish estimated from weight-length equation) estimates for lakes in North Cascades National Park Service Complex, 1990-1993.

		Reproduction		Density (fish/ha)									Biomass (kg/ha)		
Lake	Date	Yes/No	Area (ha)	All Fish	LCL	UCL	>170mm	LCL	UCL	>200mm	LCL	UCL	All Fish	>170mm	>200mm
LS1	8/14/90	N	0.4	28	--	--	--	--	--	--	--	--	2.6	--	--
MR13-2	9/04/90	N	1.2	40	30	68	--	--	--	--	--	--	4.7	--	--
Lower Panther	8/09/90	N	0.2	40	30	55	--	--	--	--	--	--	8.2	--	--
Upper Panther	8/10/90	N	0.1	60	--	--	--	--	--	--	--	--	--	--	--
LS2*	9/17/91	Y	1.0	722	552	943	617	471	806	450	336	617	57.1	56.2	45.9
McAlester*	9/17/91	Y	5.0	580	336	1088	562	326	1054	678**	248	1694	38.5	38.7	54.4
Rainbow*	8/14/91	Y	6.3	533	252	1231	500	236	1154	214**	65	390	33.2	33.8	19.6
Lower Triplet	8/07/91	Y	1.0	643	357	1286	477	256	976	301	142	695	35.3	31.9	22.2
Upper Triplet	8/08/91	Y	1.0	491	333	755	459	311	707	428	290	658	52.2	53.1	51.7
LS1	8/18/92	N (Stocked 9/90)	0.4	243	130	498	243	130	498	152**	68	383	17.3	17.4	11.9
LS2	9/14/92	Y	1.0	724	402	1448	640	332	1347	456	215	1052	54.0	53.4	43.4
McAlester	9/21/92	Y	5.0	518	294	999	483	274	933	155	77	339	30.5	32.7	12.7
Lower Panther	8/14/92	N (Stocked 9/90)	0.2	320	195	570	320	195	570	320	195	570	54.1	54.1	54.1
Rainbow	9/17/92	Y	6.3	807	381	1863	649	307	960	409	182	1021	54.3	53.9	40.9
Dagger	9/15/93	Y	3.6	671	411	1156	640	392	1104	590	361	1017	58.0	62.5	66.4
Kettling	8/03/93	Y	4.0	333	266	417	254	201	320	101	79	129	18.9	25.9	12.8
MR9	8/31/93	N	1.7	15**	6	37	15**	6	37	15**	6	37	4.1	4.1	4.2
MR16	7/27/93	Y	1.0	98	67	149	92	63	140	74	49	116	10.6	10.4	9.6

* All samples combined for single estimate, multiple marked fish removed adjusted.

** Statistically biased (Robson and Regier, 1964)

natural reproduction where fish density and biomass was low. In contrast, all estimates of the density of fish > 170 mm in lakes without natural reproduction (n = 3, LS1 and Lower Panther in 1992, MR9 in 1993) were ≤ 320 fish·ha^{-1}. In 1990, estimates of fish density by the Leslie method were all < 60 fish·ha^{-1} (n = 4). If the mark-recapture estimates are compared statistically, differences are greater than would be expected by random variation ($P < 0.01$). Average density of fry stocked in NOCA from 1976 to 1993 was 179 fish/ha (range 59.8 - 375 fish/ha; N = 37) except for Thunder, Upper Panther, and Lower Panther Lakes which are relatively heavily stocked. The average interval between stocking was > 5 years (Reed Glesne, North Cascades National Park Service Complex, 2105 Highway 20, Sedro Wooley, WA, 98284).

Trout Diet

Taxa found in trout stomach are given in Table 7. Diets reported in Table 8 are simply quantities of food types consumed, and do not reflect food preference or electivity. Food preference would entail evaluation of the amount of food consumed of a given type relative to the availability of that food type in the lake (Ivlev, 1961).

In forested and subalpine lakes trout fed on benthic, water column, and surface organisms (Table 8A). In both vegetation zones, benthic prey comprised the largest proportion of the diet. They tended to be the most common food type early in the season in the subalpine. Benthic organism were more common in the diet of fish in forested lakes than in subalpine lakes.

Benthic larvae and pupae consumed by fish were primarily chironomids (Table 8B and C). In forested lakes, odonates (dragonflies and damselflies) and leeches, which are large prey items, were found occasionally in trout stomachs.

Table 7. Stomach contents of fish in 1990.

1. Benthic (Larva)
    - Coleoptera
        - Dytiscidae
        - Hydroporidae
        - Gyrinidae
            - Gyrinus
    - Diptera
        - Chironomidae
        - Ceratopogonidae
        - Simuliidae
        - Tipulidae
            - Ormosia
    - Ephemeroptera
        - Baetidae
            - Callibaetis
        - SiphloNeuridae
            - Ameletus
    - Odonata
        - Anisoptera
            - Aeshnidae
                - Aeshna
            - Corduliidae
                - Somatochlora
        - Zygoptera
            - Coenagrionidae
    - Pelecypoda
    - Plecoptera
        - Chloroperlidae
        - Perlidae
    - Tricoptera
        - Limnephilidae
            - Apatania
            - Asynarchus
            - Desmono mono
            - Halesochila taylori
            - Hydropsychidae

2. Benthic (pupa)
    - Diptera
        - Chironomidae
    - Tricoptera
        - Limnephilidae

3. Water Column
    - Acari
        - Acarina
    - Diptera
        - Chaoboridae
            - Chaoborus
    - Hemiptera
        - Notoniectidae
            - Notonecta (adult)
    - Cladocera
    - Copepoda

4. Surface (Aquatic Adults)
    - Diptera
        - Ceratopogonidae
        - Empididae
    - Ephemeroptera
        - Baetidae
            - Callibaetis
    - Neuroptera
        - Sisyridae
            - Sisyra
    - Plecoptera
        - Chloroperlidae
        - Perlodidae

5. Surface (Terrestrial, primarily adults)
    - Arachnidae
    - Chilopoda
    - Coleoptera
        - Curculionidae
        - Elateridae
    - Homoptera
        - Aphidae
        - Cercopidae
        - Cicadellidae
    - Hymenoptera
        - Formicidae
    - Hemiptera
    - Thysanoptera

6. Surface (Unknown)
    - Brachycera (adult)
    - Tipulidae (adult)

7. Benthic and water column
    - Amphipoda
        - Gammaridae
            - Gammarus
    - Coleoptera
        - Dytiscidae
            - Agabus
            - Potomonectes griseostriatus
    - Hirudinea
    - Nematoda
    - Turbellaria

8. Other
    - Salamander
        - Ambystoma sp.

Table 8a. Percentage of major food groups in trout diet determined from numbers of organisms found in stomachs.

Lake	Date	Benthic	Water Column	Surface	Other
Subalpine					
TRIU	7/10	75.4	0.2	24.4	0
TRIL	7/10	33.6	4.9	61.5	0
M132	7/25	23.7	76.2	0.1	0
DOUB	7/30	64.0	0	8.5	27.5
TRAP	8/01	68.9	21.7	9.4	0
EP6	8/20	69.6	8.7	21.7	0
TRAP	8/21	38.3	55.5	5.2	0
DOUB	8/25	3.5	96.5	0	0
TRIU	8/27	9.3	12.1	78.6	0
M132	9/04	1.4	0	98.7	0
AVERAGE		38.75	25.23	33.44	2.5
Forested					
LS2	7/17	36.7	0.3	61.1	0
PANU	8/10	6.1	86.8	7.1	0
PANL	8/10	14.3	0	84.3	0.2
THUN	8/13	73.0	1.8	25.2	0
LS1	8/15	59.5	40.2	0.2	0
LS2	9/11	100.0	0	0	0
AVERAGE		48.18	21.52	29.98	0.03

Table 8b. Macroinvertebrate and vertebrate organisms recovered from trout-stomach samples (NOCA lakes, Summer 1990). Average number of prey organisms per fish for each food grouping arrange by vegetation zone.

			BENTHIC		FREE SWIMMING			SURFACE					
Lake	Date	# ind	Bl	Bp	WC	ZP	BC	Sa	St	Su	Sp	Sal	Tot
Subalpine													
TRIU	7/10	4	9.3	133.3	0	0*	0.8	8.3	38.0	0	0	0	189.5
TRIL	7/10	4	15.5	2.3	0	0*	2.5	15.3	17.3	0	0	0	53.3
M132	7/25	4	47.3	11.8	0	190.0**	0	0	1.0	0	0	0	250.0
DOUB	7/30	4	1.5	45.8	0	0**	0	4.5	1.8	0	20.3	0	73.8
TRAP	8/01	6	16.3	55.2	0	0**	22.5	0.7	8.5	0.5	0	0	103.7
EP6	8/20	5	1.2	2.0	0	0	0.4	0.2	0.8	0	0	0	4.6
TRAP	8/21	5	13.6	6.0	0	26.0	2.4	0.4	3.0	0	0	0	51.4
DOUB	8/25	6	15.3	26.0	0	1170.0	0.5	0.3	0.2	0	0	0	1212.3
TRIU	8/27	8	3.4	0.3	0.3	0***	4.5	2.6	28.5	0	0	0	39.5
TRIL	8/27		11.5	0.3	0.5	0***	0	2.8	15.	0	0	0	30.1
M132	9/04	7	2.3	0.3	0	0	0	0.9	187.9	0	0	0	191.3
No./fish/lake			12.5	25.8	0.1	126.0	3.0	3.3	27.5	0	1.8	0	199.9
Forested													
LS2	7/17		24.6	2.6	0.2	0*	0	7.8	39.0	0	0	0	74.2
PANU	8/10		2.0	0	28.3	0	0	0	2.3	0	0	0	32.6
PANL	8/10		2.0	0	0	0	0	11.2	0.6	0	0	0.2	14.0
THUN	8/13		40.5	0	0	0***	1.0	14.0	0	0	0	0	55.5
LS1	8/15		128.4	26.2	90.0	90.0	14.6	0.6	0	0	0	0	259.8
LS2	9/11		0.3	0	0	0**	0	0	0	0	0	0	0.3
No./fish/lake			33.0	4.8	19.8	15	2.6	5.6	7.0	0	0	0	72.7

Abbreviations:
Bl = benthic larvae
Bp = benthic pupae
WC = water column
Sa = surface/aquatic
St = surface/terrestrial
Su = surface/unknown
Sal = salamander
Sp = trout eggs
BC = benthic and water column
CT = cutthroat
RB = rainbow
ZP = zooplankton

* very low zooplankton density
** low density (,0.2/l) of D. kenai/D. arcticus adults
*** no D. kenai/D. arcticus found in lake

Table 8c. Percent of prey organisms per fish for each food group arranged by vegetation zone.

		BENTHIC		FREE SWIMMING			SURFACE				
Lake	Date	Bl	Bp	WC	ZP	BC	Sa	St	Su	Sp	Sal
Subalpine											
TRIU	7/10	4.9	70.3	0	0*	0	4.4	20.0	0	0	0
TRIL	7/10	29.1	4.3	0	0*	4.7	28.7	32.5	0	0	0
M132	7/25	18.9	4.7	0	76.0	0	0	0	0	0	0
TRAP	8/01	15.7	53.2	0	0	21.7	0.7	8.2	0.5	0	0
DOUB	7/30	2.0	62.0	0	0*	0	6.1	2.4	0	27.5	0
EP6	8/20	26.0	43.5	0	0	8.7	4.3	17.4	0	0	0
TRAP	8/21	26.5	11.7	0	50.6	4.7	0	5.1	0	0	0
DOUB	8/25	1.3	2.1	0	96.5	0	0	0	0	0	0
TRIU	8/27	8.6	0.8	0.8	0	11.4	6.6	72.2	0	0	0
TRIL		38.2	0.1	1.7	0	0	9.3	49.8	0	0	0
M132	9/04	1.2	0.2	0	0	0	0.5	98.2	0	0	0
Avg %/Fish/Lake		15.7	23.0	0.2	23.0	4.7	5.5	27.8	0	2.5	0
Forested											
LS2	7/17	33.2	3.5	0.3	0	0	10.5	52.6	0	0	0
PANU	8/10	6.1	0	86.8	0	0	0	7.1	0	0	0
PANL	8/10	14.3	0	0	0	0	80.0	4.3	0	0	0.2
THUN	8/13	73.0	0	0	0	1.8	25.2	0	0	0	0
LS1	8/15	49.4	10.1	0	34.6	5.6	0.2	0	0	0	0
LS2	9/11	100.0	0	0	0	0	0	0	0	0	0
Avg %/Fish/Lake		46.0	2.3	20.3	5.8	1.2	19.3	10.7	0	0	0

Abbreviations: Bl = benthic larvae
Bp= benthic pupae
WC = water column
Sa = surface/aquatic
St = surface/terrestrial
Su = surface/unknown
Sal = salamander
Sp = trout eggs
BC = benthic and water column
CT = cutthroat
RB = rainbow
ZP= zooplankton

Zooplankton occurring in fish stomachs were principally copepods, although Daphnia were found in one fish stomach in Trapper Lake. In the subalpine, prey from the water column were mostly zooplankton, but in forested lakes water column organisms other than zooplankton (Table 7) were most numerous in the diet. While benthic and surface organisms were found in the stomachs of fish from nearly all lakes, zooplankton were completely absent from fish stomachs in many lakes. In many of these lakes, particularly in the subalpine, the density of the largest common zooplankter, either D. kenai or D. arcticus, was very low (Table 8B and C). In some lakes this large zooplankter was not present (Upper and Lower Triplet and Thunder). Zooplankton, primarily Daphnia, also occurred in salamander diets, but contents of salamander stomachs have not yet been processed.

The majority of prey taken from the lake surface were terrestrial in origin (Table 8B and C). Terrestrial prey were largely coleopterans and formicids. Adults of aquatic insects did not occur very often in the diet. Fish from a few forested lakes had consumed empidids and callibaetids. A salamander was found in one stomach from Lower Panther Lake. A few other fish stomachs from this lake, as yet unprocessed, also contained salamander larvae.

Overall it appeared that fish were opportunistic feeders. Many fish appeared to be selective feeders. For example, in Upper Triplet on the first sample date, two fish concentrated on ants, another on terrestrial beetles and hemipterans, and another on chironomid pupae. At LS 1, one fish consumed chironomid pupae and Chaoborus, another selected chironomid larvae, a third concentrated on a Limnophilid, Asynarchus, and a fourth had consumed about 450 copepods.

CONCLUSIONS

1. The data analyzed to date suggest that reproducing fish populations have higher densities, lower individual growth rates, and are in poorer condition than fish from lakes where reproduction does not occur. In lakes with non-reproducing fish, fry are periodically stocked at relatively low densities and cohort density declines after stocking.
2. The mark-recapture procedure does not provide a reliable estimate of all fish in the population. Smaller fish were undersampled by both angling and gillnetting. Thus the estimates are, at best, indices of population density.
3. Angling and gillnetting tend to sample somewhat different segments of the population. Angling tends to select for a larger fish than gillnets. Thus, abundance estimates may be more meaningful when limited to larger fish (e.g., > 170 mm).
4. The mark-recapture technique seems to work best in relatively small lakes (< 5-6 ha). Success also depends on the species and race of trout. Cutthroat and rainbow trout initially stocked several decades ago (Jarvis, 1987) were more vulnerable to both angling and gillnetting than Mt. Whitney rainbow, which have been recently stocked in NOCA lakes. In 1992 we were unable to obtain estimates of density in two manipulated lakes (MR13-2 and MR11) which had been stocked with the Mt. Whitney strain in 1990, because we were unable to capture by angling and mark a sufficient number of fish.
5. Trout in NOCA are opportunistic feeders. They preyed on benthic, water column, and surface organisms. Diets were highly variable between lakes.

AMPHIBIANS

Concern has been acute over world-wide declines in amphibians (Blaustein and Wake, 1990; Wake, 1991). These declines include reductions in abundance and extinction of populations, increased isolation of extant populations (e.g., Bradford et al., 1993), and restrictions in geographic ranges of many species. There is particular concern over amphibian declines in areas that have been relatively undisturbed by human activities, such as high elevation locations in the west (Blaustein and Wake, 1990) and national parks (Bradford, 1989; Bradford et al., 1993).

Of the many possible causes for amphibian declines (e.g., habitat destruction, pollution, global climate change, increased UV radiation), the impact of exotic species on native amphibians has received considerable attention (Blaustein and Wake, 1990; Wake, 1991). Bullfrogs (Rana catesbeiana) have been implicated in declines of native ranids in the west (Moyle, 1973). Hayes and Jennings (1986) suggested that predation by introduced fish was a likely cause of decline in western ranids, but they concluded that evidence was inadequate to distinguish between fish, bullfrogs, and other possible causes of decline. Bradford (1989) found that Rana muscosa did not co-occur with introduced trout in Sequoia and Kings Canyon National Parks, CA. Bradford et al. (1993) suggested that continued declines in R. muscosa in fishless waters may be a consequence of isolation of extant populations due to the presence of fish in connecting waters.

Salamanders are important aquatic predators in many fishless high mountain lakes in the western US (e.g., Dodson 1970, 1974; Dodson and Dodson, 1971; Sprules, 1972; Giguere, 1979; Taylor, 1983). Several studies have reported reduced

abundance or absence of ambystomid larvae from habitats with fish. Sprules (1974a) found 16 times more paedogenic Ambystoma gracile in fishless ponds than in ponds with fish. He also reported observing paedogenic Ambystoma tigrinum only in small fishless ponds in the Rockies in central Colorado. Similarly, Taylor (1983) found much greater abundances of A. gracile in fishless lakes than in lakes with fish in the Oregon Cascades. In the east, Semlitsch (1988) found that Ambystoma talpoideum in the upper coastal plain and sandhill regions of South Carolina occurred primarily in ponds that lacked fish. He demonstrated that this was likely a consequence of fish predation on eggs. In Kentucky streams, Petranka (1983) reported that eggs and larvae of Ambystoma barbouri were largely confined to sections of streams that lacked fish. He showed that this disjunct distribution of salamanders and fish was likely a result of fish predation on larvae.

Fish have been shown to inhibit growth (Semlitsch, 1987; Figiel and Semlitsch, 1990) and reduce survival of larval ambystomids (Semlitsch, 1987; Sih et al., 1988) in artificial ponds. In the presence of fish, larvae may exhibit reduced activity and remain confined to refuges for longer periods of time than when fish are absent (Taylor, 1983; Stangel and Semlitsch, 1987; Semlitsch, 1987; Sih et al., 1988, Figiel and Semlitsch, 1990). However, factors other than the presence of fish especially physical conditions such as temperature and lake drying (Snyder, 1956; Anderson, 1967, 1968; Sprules, 1974a,b; Sexton & Bizer, 1978; Figiel & Semlitsch, 1990), availability of food (Anderson, 1967; Dodson & Dodson, 1971), and winter kill from freezing in shallow lakes can influence salamander life histories, distribution, and abundance.

The amphibian section of this report is divided into three parts. In the first part, we report the influence of trout and other biological and physical variables on the

abundance and distribution of long-toed salamander (Ambystoma macrodactylum) larvae in high mountain lakes. Nearly all of the lakes included in this study are eastslope lakes. Although A. macrodactylum is widespread throughout the northwest (Ferguson, 1961; Nussbaum et al., 1983; Leonard et al., 1993), demographic data on high elevation populations is sparse and, although distributions of A. macrodactylum and introduced trout overlap geographically, effects of trout on this salamander are unknown. In the second part, we examine patterns of distribution and abundance of fish and salamanders (A. macrodactylum and A. gracile) in westslope lakes. To date, only a limited number of westslope lakes have been sampled for salamanders. Consequently, we consider the observed patterns only as suggestive, but they serve as a basis for hypotheses that will direct field work on the westslope in 1994 and 1995. In the last section, we report observations on anuran taxa in the Complex.

PART I. ABUNDANCE OF LARVAL A. MACRODACTYLUM IN FISH AND FISHLESS LAKES IN THE NORTHERN WASHINGTON CASCADES

METHODS

We sampled 13 lakes (six fishless lakes and seven lakes with fish) from 1990-1992. Twelve of the lakes were east of the Cascade crest (within the Stehekin River drainage). Eastslope fishless lakes and lakes with fish were geographically interspersed. Fishless lakes ranged in elevation from 1504-1873 m and lakes with fish ranged from 1629-1988 m. Ambystoma macrodactylum was the only salamander found in eastslope lakes. Pyramid Lake, a lower elevation lake (802 m), is the only westslope lake we sampled with allopatric A. macrodactylum.

Some of the study lakes that are presently fishless lakes have a history of fish stocking. MR 11, an eastslope lake, was fishless in 1990 and probably for several previous years. It was stocked with a low density of fingerling rainbow trout in late fall of 1990. The fish had reached a total length of 250-350 mm by 1992. In our analysis, MR 11 was treated as a fishless lake in 1990 and a fish lake in 1991 and 1992. Two lakes that are presently fishless had been stocked with fish at least once in the past. Pyramid Lake was last stocked in 1968 and MR 13-1 in 1984 (Jarvis, 1987).

Each lake was sampled one-three times in summer and early fall, depending on the length of the ice-free period. Larval densities were estimated by snorkeling the lake perimeter during daylight. Initially we attempted to estimate larval salamander densities with funnel traps (Carpenter, 1953), searches from the shoreline, and snorkeling. Snorkeling proved to be the most effective technique for detecting larvae. We captured very few larvae with funnel traps. Although we were able to detect larvae with searches from shoreline, when snorkeling we could more effectively search a wider area of the lake perimeter, more easily locate larvae hidden in bottom substrates, and see larvae more clearly underwater.

During sampling the snorkeler carefully searched through talus, woody debris, fine organic material, and emergent vegetation to determine number and location of larvae. The area from the lake edge to 2-3 m offshore (up to a depth of about 1 m) was searched. Behavior, particularly whether salamanders were concealed in the bottom substrates or moving freely in the open, was noted. Quantitative data on actual number of larvae hidden or in the open was not recorded. Lake area and lineal meters of lake perimeter were estimated with a digitizer from 7 1/2 min USGS topographic maps. Relative density was expressed as number of larvae observed/100 m of shoreline.

Normally the entire lake perimeter was snorkeled. If a lake was large or the water very cold it was sometimes not possible to snorkel the entire shoreline. For partial surveys the number of meters of shoreline sampled was estimated by multiplying the total length of the lake perimeter by the estimated proportion of shoreline sampled. When partial surveys were conducted at least 50% of the lake perimeter was snorkeled. Sampling was usually conducted by a single snorkeler, although in very large lakes it was sometimes necessary to employ two snorkelers.

Crustacean zooplankton, an important food resource for larval salamanders (Anderson, 1968; Dodson and Dodson, 1971), were sampled with a #25 (64 micron mesh) net with collecting basket. Counts from three vertical tows taken over the deepest point in the lake were averaged to provide an estimate of density on each sample date. Presence of fish was initially determined from park records (Jarvis, 1987) and verified by angling, gill-netting, snorkeling, and visual observation from shore and from an inflatable boat. Water temperature was measured at the lake surface and at 1 m intervals to the lake bottom with an Omega 871 thermo-couple. Lake elevation was determined from 7 1/2 min USGS topographic maps. Maximum depth was determined with a hand-held sonar gun.

The Mann-Whitney U test (Snedecor and Cochran, 1989) was used to determine if fishless lakes differed statistically (α=0.05) from lakes with fish in average summer densities of salamander larvae, average summer densities of crustacean zooplankton, average maximum water temperature 1 m below the lake surface, and lake depth, surface area, and elevation. When a lake was sampled for two or more years, densities of larvae and zooplankton and maximum temperature were averaged over all years.

To investigate relationships between larval salamander density and other variables, log transformed larval density was regressed on each variable separately for fishless lakes (N=6) and for lakes with fish (N=7). Initially both a linear and quadratic term were used in each regression. If the regression coefficient of the quadratic term was not significantly different from zero (α=0.05), the quadratic term was omitted and the linear term was tested for significance (α=0.05).

RESULTS

Larval salamander densities in lakes with fish were significantly lower than in fishless lakes (Table 1; Mann-Whitney U test, P=0.0059). When larval densities in eastslope fishless lakes (Pyramid omitted) were compared with lakes with fish, differences were still significant (Table 1; P=0.0104). Salamander larvae were present in several lakes with fish and were moderately abundant in MR 11 in 1991 and 1992. However, we never observed larval densities in lakes with fish that approached the highest densities (>70/100 m) found in fishless lakes. Fishless lakes did not differ significantly from lakes with fish in zooplankton density, water temperature, or lake depth, surface area and elevation, either when Pyramid Lake was included in the analysis or when it was omitted (Table 2).

Larval densities were highly variable among fishless lakes and ranged from near 170/100 m in Pyramid to 2.2/100 m in MR 11 (1990) and Waddell. However, in fishless lakes and lakes with fish, regression analysis revealed no statistically significant relationship between larval density and zooplankton density (fishless lakes, P=0.35; fish lakes, P=0.53), water temperature (fishless lakes, P=0.12; fish lakes, P>0.99), elevation (fishless lakes, P=0.50; fish lakes, P=0.660), surface area (fishless lakes, P=0.07; fish

Table 1. Average and range interval (in parenthesis) of larval densities of A. macrodactylum, years each lake was sampled and total number of snorkel surveys in each year (in parenthesis) in North Cascades National Park Service Complex, WA, USA.

Fishless Lakes			Lakes with Fish		
Lake	Year	Larval Density (no./100 m)	Lake	Year	Larval Density (no./100 m)
Pyramid	1990 (1) 1991 (3)	125.2 (80.7-169.7)	Rainbow	1991 (2) 1992 (1)	0.3 (0-0.05)
MR 2	1990 (2)	73.0	McAlester[a]	1990 (1) 1991 (1) 1992 (1)	0.0
MR 3	1990 (1)	18.3	Battalion[b]	1991 (2)	0.0
MR 13-1	1992 (1)	19.8	MR 11	1991 (2) 1992 (1)	8.4 (7.4-9.5)
Waddell	1991 (2)	2.2	MR 13-2	1991 (1)	0.4
MR 11	1990 (1)	2.2	L. Triplet	1990 (1) 1991 (1)	0.0
			U. Triplet[c]	1990 (1) 1991 (1)	0.0

a: One adult found in fish stomach
b: Five eggs identified
c: Two larvae observed while sampling benthos

Table 2. Average and 95% confidence interval (in parenthesis) of physical and biological variables in fish and fishless lakes in North Cascades National Park Service Complex, WA, USA. P-values are for comparisons of fish and fishless lakes using the Mann-Whitney U test ($\alpha = 0.05$). P-values for comparisons among all lakes and for eastslope lakes (Pyramid Lake omitted) are given.

Variable	Fishless Lakes	Lakes with Fish	P-Value (All Lakes)	P-Value (Eastslope Lakes)
Area (ha)	1.08 (0.0-2.69)	2.61 (0.6-4.62)	0.072	0.142
Depth (m)	5.67 (1.14-10.20)	5.79 (3.35-8.23)	0.830	0.514
Elevation (m)	1453 (932-1973)	1799 (1675-1923)	0.720	0.871
Temperature (°C)	16.32 (11.85-20.79)	13.99 (11.9-16.08)	0.153	0.223
Zooplankton (#/l)	11.88 (0.0-25.86)	8.14 (0.0-16.4)	0.775	0.9353

lakes, P=0.50), or depth (fishless lakes, P=0.30; fish lakes, P=0.66). However, when Pyramid Lake was omitted (eastslope lakes only), there was a significant negative relationship between maximum lake depth and larval density (r^2=0.82; N=5; P=0.03) in fishless lakes. On the eastslope, the highest densities of salamander larvae occurred in smaller, shallower lakes (MR 2, MR 3, MR13-1; maximum depth ≤3m and surface area ≤0.3 ha). Pyramid, a westslope lake with the highest density of larvae observed in this study, was small (0.3 ha) but relatively deep (8.8 m).

In fishless lakes larvae were observed moving freely in the open across the substratum, swimming in the water column, and concealed on the lake bottom in woody debris, conifer needles, organic detritus, cobble, and talus boulders. In contrast, most larvae found in lakes with fish were well hidden in bottom materials, although a few were observed in open areas.

DISCUSSION

Trout are not indigenous to many high elevation lakes of the west. Bahls (1992) reported that nearly 60% of all high mountain lakes and 95% of larger, deeper lakes in the western US support fish. About 95% of lakes now supporting fish were estimated to have been originally fishless.

Taylor (1983) considered A. gracile to be the top carnivore in many fishless Cascade mountain lakes. In North Cascades National Park Service Complex, A. macrodactylum is a major vertebrate predator, particularly in eastslope lakes. The species is widespread in the Pacific Northwest and occurs from sea level to high elevations (Ferguson, 1961; Nussbaum et al., 1983; Leonard et al., 1993).

Salamander distribution and abundance in high mountain lakes is determined by a complex of biological and physical factors. Population variation and periodic population extinction in amphibians may be related to natural fluctuations in local environments (Corn and Fogelman, 1984; Pechmann et al., 1991; Wissinger and Whiteman, 1992), often making it difficult to distinguish anthropogenic from natural causes of local declines (Pechmann et al., 1991; Wake, 1991). In North Cascades National Park Service Complex, we found significantly higher abundances of A. macrodactylum larvae in fishless lakes than in lakes with fish. Furthermore, we found no significant differences between fishless lakes and lakes with fish in zooplankton density, temperature, and lake elevation, surface area, and depth. Our results are consistent with several other studies that have shown that fish can reduce survival and abundance of larval salamanders (Sprules, 1974a; Taylor, 1983; Petranka, 1983; Semlitsch, 1987, 1988; Sih et al., 1988, 1992).

Variability in larval abundance among fishless lakes in our study indicates that factors other than introduced trout may also affect larval abundance. In particular, on the eastslope, A. macrodactylum tended to reach greatest abundance in smaller, shallower lakes. Some of these lakes, although permanent, may be too shallow to support trout and, thus, they may provide productive refuges for A. macrodactylum. Furthermore, we have observed A. macrodactylum larvae in shallow pools in lake inlet and outlet streams that may not be accessible to trout, and in small temporary ponds and seeps near lakes with fish. Apparently A. macrodactylum is able to persist in the same geographic area as introduced trout by utilizing habitats that may be relatively unfavorable or inaccessible to fish.

Ambystoma macrodactylum also occur in larger, deeper lakes (Kezer and Farner, 1955; Anderson, 1967). Of all lakes sampled in the Complex through 1992, the highest densities of A. macrodactylum larvae occurred in Pyramid Lake, a relatively small (0.3 ha), deep (8.8 m), low elevation (802 m) lake. However, larval densities were relatively low in two larger, deeper lakes, Waddell (surface area = 4.1 ha, maximum depth = 11.9 m) and MR11 (surface area 1.3 ha, maximum depth 8.8 m). Many deeper, permanent lakes can support fish and in these lakes A. macrodactylum larvae may be vulnerable to fish predation.

In both field and laboratory studies, fish have been shown to alter salamander behavior (Stangel and Semlitsch, 1987; Semlitsch, 1987; Figiel and Semlitsch, 1990). Ambystoma gracile appear to be more reclusive in lakes with fish, staying hidden at least during daylight hours and possibly foraging for food mainly at night (Efford and Mathias, 1969; Sprules, 1974a; Taylor, 1983). This is generally consistent with our observations of A. macrodactylum behavior in lakes with fish, although larvae in fishless lakes were often hidden in talus, woody debris, and fine organic detritus accumulated on the lake bottom. Avoidance behavior by larvae in fishless lakes may have been related, in part, to intraspecific predation because larger A. macrodactylum larvae may consume smaller larvae (Leonard et al., 1993; personal observation).

Sih et al. (1988) discuss the importance of the dynamics of refuge use in determining prey survival. They emphasize that, even though few prey may be observed outside of refuges, prey populations may be rapidly reduced by predators if emergence rates of prey from refuge are high and the prey are quickly killed after emerging. Moreover, shifts in behavior and habitat use to avoid predation, while increasing probability of larval survival (Figiel and Semlitsch, 1990), may reduce food

consumption and growth by decreasing foraging efficiency (Semlitsch, 1987; Figiel and Semlitsch, 1990). Eventually larvae may need to leave refuge to forage and so become vulnerable to predation. Thus refuge use within a lake may not necessarily ensure long-term survival.

Little is also known of the ability of A. macrodactylum to recolonize high mountain lakes where they have been eliminated. Howard and Wallace (1981) suggested that dispersal may be overland as well as along waterways. Salamanders are abundant in two lakes (Pyramid, MR 13-1) that had been stocked with fish in the past, but are presently fishless. We do not know if stocked trout fry survived long enough in either lake to have had an effect on larval abundance. If the life expectancy of adult A. macrodactylum is long, as documented for other ambystomatids (Bowler, 1977), the adult population may be buffered against short-term catastrophic losses of larvae. Many years may be required for adult populations to be locally extirpated. Furthermore, the ability of A. macrodactylum to utilize habitats near trout lakes that may be unsuitable for fish may favor recolonization and salamander population recovery if fish were removed from the lake.

In 1991 and 1992, larval salamander densities in MR 11 were relatively high compared to other lakes with fish. The reasons for these comparatively high densities are unknown. The lake apparently has had a rather sporadic history of fish stocking. Trout fry were stocked at low density in fall 1990. The fish were relatively small during summer 1991, but had grown considerably (250-350 mm total length) by summer 1992, probably from feeding on abundant amphipods, and were certainly large enough to consume salamanders. Fish density in 1992 is not known (we were unable to estimate density by mark-recapture due to difficulty in capturing fish by angling or gill-netting).

Perhaps, by 1992, fish density had declined so much that there was little impact on salamander larvae or, possibly, more adequate refugia were present in MR 11 than in other lakes with fish.

Diving techniques have been used previously to census ambystomids in lakes (Neish, 1971; Taylor, 1983). Of the census techniques we tried (including funnel traps and searches from shoreline), snorkeling was the most effective in detecting larvae. In both fish and fishless lakes, by careful searching we were routinely able to detect larvae hidden in leaf litter and other organic debris and in talus along the shoreline. However, larvae hidden deeply in heavy cover such as dense submerged log jams are very difficult to detect. It is possible that larvae may be more deeply hidden in lakes with fish and thus, with snorkeling and other techniques that rely on visual detection, larval densities may be underestimated more in lakes with fish than in fishless lakes. In lakes with reproducing trout we found no significant differences in larval densities betweten surveys conducted during the day and at night (unpublished data).

Failure to detect any larvae in lakes with fish by snorkeling may not necessarily imply that salamanders were extirpated from these lakes. In some lakes where no larvae were observed, even after several years of sampling, there was occasionally evidence of salamander use (an egg mass was observed, an adult was found in a fish stomach; Table 1). However, it is unlikely that failure to observe larvae due behavioral differences was sufficient to account for the orders-of-magnitude differences in densities between lakes with fish and fishless lakes with the highest larval densities.

PART II. DISTRIBUTION AND ABUNDANCE OF FISH AND SALAMANDERS IN WESTSLOPE LAKES, NORTH CASCADES NATIONAL PARK SERVICE COMPLEX

METHODS

Salamanders in westslope lakes were sampled following the procedure described in the previous section. In lakes with A. gracile, both embryo masses and larvae were counted while snorkeling. No attempt was made to distinguish mature from immature forms of neotenic A. gracile. Both mature and immature forms are grouped as larvae in this report. In LS-1 in 1993, larvae were counted during the day by snorkeling and at night from the shoreline using a flashlight. In a few lakes, species identifications were made, but larval density was not assessed quantitatively.

Some westslope lakes (LS-1, LS-2, Upper Panther, Lower Panther) were sampled annually from 1990 through 1993 (Table 3). Quantitative sampling was conducted in Pyramid Lake in 1990, 1991, and 1993, but not in 1992. All fish were removed from Upper Panther, Lower Panther, and LS-1 in late summer in 1990. Lower Panther and LS-1 were restocked with fry (Table 4). Upper Panther was not restocked with fish.

Distinguishing species of small larval salamanders in the field was difficult. When possible, larvae were taken from the field and reared to metamorphosis under controlled conditions to distinguish A. macrodactylum from A. gracile.

Larval size and characteristics of embryos were also used to distinguish species. Ambystoma macrodactylum are not known to be paedomorphic and have been reported to metamorphose when their snout-vent length (SVL) reaches 30 - 46 mm (Nussbaum et al., 1983). Ambystoma gracile are paedomorphic at high elevations

Table 3. Physical characteristics of westslope lakes and number of times each lake was sampled annually, North Cascades National Park Service Complex, WA, U.S.A.

Lake	Vegetation Zone	Elevation (m)	Max. Depth (m)	Number of Times Each Lake was Sampled				
				1989	1990	1991	1992	1993
PM5-3	Forest	1382	9.1	1				
Talus Tarn	Subalpine	1632	3.6	1				
Pyramid	Forest	802	8.8		1	3	1	3
LS1	Forest	1241	3.4		3	3	2	2
LS2	Forest	1243	4.9		3	3	2	2
Hozomeen	Forest	861	19.0			1		1
Lower Panther	Forest	1031	5.8		2	3	2	3
Upper Panther	Forest	1031	3.0		2	3	2	3
Nert	Forest	1388	8.2		1			
Thunder	Forest	412	6.4		1	2		

Table 4. Density estimates (see Fish section) and average total length (TL) of trout in four westslope lakes, North Cascades National Park Service Complex, WA, U.S.A.

	1990		1991		1992		1993	
Lake	Density (No./ha.)	Average TL (mm)	Density (No./ha.)	Average TL (mm)	Density (No./ha.)	Average TL (mm)	Density (No./ha.)	Average TL (mm)
L. Panther	40[a]	281						
	750[b]	fry		229	320[c]	263	present*	
U. Panther	60[a]	246	0		0		0	
LS1	28[a]	208						
	312.5[b]	fry			243[c]	203		247
LS2			617[c]	216	640[c]	209		

a: estimate using fish removal technique (Ricker, 1975)
b: stocking density of fry
c: estimate using mark-recapture, fish > 170 mm
*: three fish observed during September snorkel for salamanders

(Snyder, 1956; Sprules, 1974a; Leonard et al., 1993). Neotenes have been reported to reach sexual maturity between 50 and 60 mm SVL (Efford and Mathias, 1969; Neish, 1971; Sprules, 1974a). We commonly found A. gracile larvae 50-80 mm SVL. Thus, the presence of A. gracile was indicated by occurrence of large larvae (≥ 50 mm SVL) having the external morphological characteristics of this species (Nussbaum et al., 1983).

Embryos of A. gracile have a thick outer jelly coat and are often deposited in grapefruit-sized clusters. A symbiotic algae frequently imparts a green hue to the clusters (Nussbaum et al., 1983). Ambystoma gracile embryo masses are often attached to woody debris or vegetation and are highly visible when snorkeling. Ambystoma macrodactylum eggs are laid singly or in smaller, loose clusters (Stebbins, 1985). The embryos are attached to various substrates and do not have a green hue (Slater, 1936; Nussbaum et al., 1983; Leonard et al. 1993). We had difficulty detecting A. macrodactylum embryos.

RESULTS

While A. macrodactylum occurred in both east- and westslope lakes, A. gracile and Taricha granulosa were found only in westslope lakes (Table 5). Taricha granulosa larvae were found in 1991 in Pyramid Lake (802 m). These distributions are consistent with other reports of distributions of these species (Dunn, 1944; Nussbaum et al., 1983; Stebbins, 1985; Leonard et al., 1993).

Ambystoma gracile was found more commonly in westslope lakes with fish than A. macrodactylum. Three of the five westslope lakes with A. macrodactylum were fishless (Table 5). Ambystoma macrodactylum was present in very low densities in LS2

Table 5. Occurrence of Ambystoma and Taricha in westslope lakes, North Cascades National Park Service Complex, WA, U.S.A.

		Life Stage				
Lake	Salamander Species	Eggs	Larvae	Fish	Reared Out	Survey
PM5-3	A. macrodactylum		x	N	N	V
Talus Tarn	A. macrodactylum		x	N	N	V
Pyramid	A. macrodactylum	x	x	N	Y	S
	T. granulosa		x		N	
LS2	A. macrodactylum		x[a]	Y	N	S
LS1	A. macrodactylum	x	x	Y	Y	S
	A. gracile		x		Y	
Hozomeen	A. gracile	x		Y	N	S
Nert	A. gracile	x	x	Y	N	V
L. Panther	A. gracile	x	x	Y	Y	S
U. Panther	A. gracile	x	x	N[b]	Y	S
Thunder	A. gracile	x	x	Y	Y	S

S= indicates snorkel survey; V= indicates visual observation from shore

a: very low density (0.79 individuals/100 m shoreline)
b: last stocked in 1988, fish removed in fall 1990

(Table 6), a lake with high fish density (Table 4). All six lakes with A. gracile support trout or have a recent history of stocking.

In westslope lakes sampled between 1990 and 1993, A. gracile and A. macrodactylum co-occurred only in LS-1 (Table 5). In LS-1, the two species appear to be spatially segregated. Ambystoma gracile larvae were found only in the main body of the lake. A. macrodactylum larvae also occurred in the lake (confirmed by rearing larvae), but their relative densities were unknown since it is difficult to distinguish small A. gracile and A. macrodactylum larvae while snorkeling. However, densities of A. macrodactylum larvae in the main body of the lake may be low. In1993, a few small larvae, which could be A. macrodactylum, were observed during daylight snorkeling, while during the 1993 night survey we observed only large larvae which were likely A. gracile. However, in 1993 in LS-1, A. macrodactylum larvae were abundant (180 larvae/100 m) in shallow pools of slow-moving water in the lake outlet. No A. gracile or fish were observed in these pools during the day or at night.

Ambystoma gracile may be able to maintain higher larval densities in lakes with fish than A. macrodactylum. Larval A. macrodactylum densities in eastslope lakes with fish were very low, averaging between 0.0 and 0.4 larvae/100 m shoreline with the exception of MR 11, where the average larval density was 8.4 larvae/100 m shoreline (see subsection I of Amphibian section). The density of larval A. macrodactylum could not be determined for LS-1 but, in LS-2, a westslope lake with high fish density, larval density was low (Table 6). In contrast, in fishless lakes, A. macrodactylum larvae can reach high densities. Pyramid Lake, a westslope fishless lake, had the highest densities of A. macrodactylum larvae of any surveyed lake (average of 113.6

Table 6. Annual average densities of salamander life stages determined by snorkel surveys in five westslope lakes, North Cascades National Park Service Complex, WA, U.S.A.

		Density of Salamander Life Stages (Number/100 m Shoreline)									
		1990		1991		1992		1993		Average	
Lake	Species	Embryo Masses	Larvae	Embryo Masses	Larvae	Embryo Masses	Larvae	Embryo Masses	Larvae	Embryo Masses	Larvae
Pyramid	A. macrodactylum		169.70		80.77		present	3.71	90.29	1.24	113.60
Pyramid	T. granulosa				22.86						22.86
L. Panther	A. gracile	115.73	7.31	89.89	35.40	78.65	8.71	23.04	20.41	76.83	17.96
U. Panther	A. gracile	79.00	23.00	105.00	27.50		35.00	145.00	126.33	109.70	52.96
LS1	both Ambystomids	5.43	1.55	7.36	0.39	0.39	6.20	15.89	1.93	7.27	2.52
LS1-night	A. gracile								20.93		20.93
LS2	A. macrodactylum		0.00		0.00		0.00		0.79		0.20

a: larvae observed while sampling benthos

larvae/100 m shoreline). On the eastslope, average larval densities in fishless lakes ranged from 2.2 to 73 larvae/100 m shoreline (see subsection I of Amphibian section).

Quantitative samples of larval A. gracile density are available for only three lakes, all of which supported fish (Table 6). Ambystoma gracile density in Upper Panther in 1990, prior to fish removal, was 23 larvae/100 m shoreline. In Lower Panther, densities averaged nearly 18 larvae/100 m shoreline over the four years in which the lake was studied. In LS-1, a night survey revealed nearly 21 larvae/100 m shoreline. These densities are much higher than the highest densities of A. macrodactylum larvae in lakes with fish. Moreover, numerous embryo masses (average 38.6 embryos/mass, range 17-56 embryos/mass, N=38) were observed in Lower Panther and in Upper Panther prior to fish removal, suggesting substantial reproductive potential.

Although A. gracile may be able to maintain higher larval densities in the presence of fish than A. macrodactylum, A. gracile larvae may still be affected by trout. In Upper Panther, the density of embryo masses and larvae increased considerably following removal of fish in 1990 (Table 6). In 1993, we observed nearly twice as many embryo masses and over five times as many larvae in Upper Panther than in 1990 and many larvae were in the open during daylight. Although we do not know what proportion of the increase in observed larvae from 1990 to 1993 resulted from actual density increases rather than behavior changes, the increase in density of embryo masses suggests an increase in number of reproductive individuals. In LS-2, which has a relatively high density of reproducing trout, no A. gracile larvae or egg masses were observed in four years of sampling even though this species is present in LS-1, which is

about 100 m away. The outlet streams of the two lakes discharge into a common tributary.

There was considerable interannual variation in densities of embryo masses and larvae in Lower Panther (Table 6). This variation may be related to changes in fish size and density of the cohort of trout stocked in fall 1990. In 1990, prior to fish removal, large fish were present at low density in Lower Panther (Table 3). Larval A. gracile density also was relatively low. Following removal of large trout and stocking of fry in fall 1990, larval density appeared to increase in 1991. Larval density declined from 1991 to 1992. This decline may be related to increased size of fish (Table 3) and, thus, intensity of fish predation. By 1992 fish from the 1990 cohort had reached a relatively large size (263 mm) and fish density was high (320 fish/ha). Larger fish may more effectively prey on a greater size range of larvae than smaller fish. Larval A. gracile density increased from 1992 to 1993. In 1993 we observed only three fish in Lower Panther. Density was undoubtedly much lower in 1993 than in 1992, due both to removal of nearly half the estimated number of fish by the mark-recapture procedure in September 1992 and to natural and angling mortality. In LS-1, a similar relationship between changes in larval density and fish density and size was not evident.

DISCUSSION

The number of westslope lakes that were sampled for salamanders was limited. Thus, we emphasize that conclusions concerning interactions of trout and salamanders are tentative and are intended to serve as the basis for generating hypotheses that will direct more intensive and detailed research on interactions of fish and salamanders in westslope lakes in 1994 and 1995.

Density and behavior of larval A. gracile may be affected by fish. Other studies have reported reduced densities of A. gracile in the presence of fish (Sprules, 1974a; Taylor, 1983). However, A. gracile may be less vulnerable to fish predation than A. macrodactylum. In westslope lakes, A. gracile were found more frequently and reached higher densities in lakes with fish than A. macrodactylum. We know of no studies that have addressed the relative vulnerability of these two species to fish predation. Differences in vulnerability to fish predation of A. gracile and A. macrodactylum may relate to differences in patterns of refuge use, body size, and defense mechanisms.

Sih (1987) categorized anti-predator mechanisms as responses to avoid encounters with predators and responses to ensure survival after encounters. Refuge use is a response to avoid encounters with predators. Sih et al. (1988) argue that patterns of refuge use and survival of prey can be understood mechanistically in terms of attack and capture rates by predators, rates of emergence of prey from refuge, and rates of re-entry of prey into refuge (a function of attack and capture rates). For example, increased short-term survival could be a consequence of reduced emergence rates (i.e., more time spent in refuge) and higher re-entry rates (i.e., less time spent outside refuge) and result in reduction in proportion of prey observed outside the refuge. However, emergence and re-entry rates may be influenced not only by predation risk but also by feeding and reproductive requirements. If food resources are scarce inside the refuge, larvae may eventually have to leave the refuge to feed or to deposit eggs and so become susceptible to predation (Sih et al., 1988).

Ambystoma gracile and A. macrodactylum may differ in dynamics of refuge use. Perhaps A. gracile are more reclusive in the presence of fish than A. macrodactylum.

Patterns of refuge use by A. gracile may differ temporally. Taylor (1983) showed that neotenic A. gracile were more active at night than during the day in lakes with fish. Both Efford and Mathias (1969) and Sprules (1974a) also suggest that A. gracile tend to be more nocturnal in the presence of fish. In NOCA lakes with fish, larval A. gracile were found almost exclusively in refuges (e.g., woody debris, talus, and undercut banks) during daylight. However, in lakes where fish density was very low (e.g.,Nert Lake) or absent (e.g.,Upper Panther in 1993), many larvae were observed in the open during daylight. The night survey at LS-1 suggests that A. gracile tend to be more active at night (or at least more visible to the human observer) in lakes with fish. The night survey estimate of A. gracile density was more than ten times greater than the estimate derived from daylight snorkeling. In contrast, in MR-11, an eastslope lake with fish, a daylight snorkeling survey revealed over 2 1/2 times more larval A. macrodactylum than a night survey, perhaps indicating that diel patterns of refuge use are not as prevalent in A. macrodactylum as in A. gracile. Increased noctural activity may reduce attack and capture rates, allowing emergence rates to increase and re-entry rates to decrease (sensu Sih et al., 1988), thus increasing time spent foraging for food.

Vulnerability to predation may be influenced by larval body size. Semlitsch (1987) found that bluegill (Lepomis macrochirus) predation was directed at the smallest individuals in an experimental salamander population. He also suggested that predation by a "gape-limited" predator was probably rare after larvae attained a large body size. Larval A. gracile, particularly paedomorphs, may reach larger sizes than A. macrodactylum larvae (Efford and Mathias, 1969; Neish, 1971; Stebbins, 1985) and so may be less susceptible to fish predation (i.e., attack, capture, and re-entry rates may

be reduced and emergence rates increased). However, predation on larvae may also depend upon fish size. Efford and Mathias (1969) suggested that rainbow trout (Oncorhynchus mykiss) reached about 250 mm fork length before they were able to effectively prey upon neotenic A. gracile in Marion Lake, British Columbia. Thus, there may be a positive relationship between maximum size of larvae consumed by fish and fish body size. Populations of fish with larger individuals may be able to prey effectively on a greater size range of larvae. Consequently, attack and capture rates may vary with body size of both fish and larvae.

Mechanisms that help prey survive encounters with predators can be considered anti-predator responses (Sih et al., 1987). Development of noxious skin secretions has been postulated as an anti-predator mechanism (Voris and Bacon, 1966; Brodie and Gibson, 1969; Heyer et al., 1975; Formanowicz and Brodie, 1982; Sih, 1987). Brodie and Gibson (1969) suggested that A. gracile may have the most highly developed noxious secretions among Ambystomids and that the glands responsible for the secretions are present in larvae. Leonard et al. (1993) suggest that both the larvae and adults of A. gracile are toxic and distasteful and this may allow A. gracile to persist in lakes with fish. Noxious secretions as a defense against fish predation have not been reported for A. macrodactylum. As with increased body size, noxious secretions may reduce attack, capture, and re-entry rates, and increase emergence rates.

Ambystoma gracile and A. macrodactylum may have different strategies for persisting in the same geographic area as introduced trout. Ambystoma macrodactylum may be highly vulnerable to fish predation in deeper, permanent lakes with fish. However, it appears to be able to utilize habitats that are either unsuitable or inaccessible to fish and can reach high densities in some of these habitats (see

subsection I of Amphibian section). Ambystoma macrodactylum are known to inhabit temporary ponds as well as deeper, permanent lakes (Kezer and Farner, 1955). We have observed larval A. macrodactylum in permanent ponds and lakes, in temporary ponds, in pools and shallow areas in inlet and outlet streams, and in small seeps adjacent to lakes with fish. The use of temporary ponds by amphibians has been suggested as a response to avoid predation (Heyer et al., 1975; Heyer, 1976).

Ambystoma gracile, on the other hand, apparently requires deeper, permanent lakes to complete its long larval period (Sprules, 1974a). These are the same kinds of lakes that typically support trout. Ambystoma gracile is probably able to persist in the same lakes with fish through behavioral and morphological adaptations (e.g., refuge use, large body size, noxious skin secretions) that enable it to reduce impacts of predation.

A. macrodactylum and A. gracile rarely appeared to co-occur in westslope lakes. The caveat is that the number of lakes sampled was relatively small and, additionally, it is difficult to distinguish smaller larvae of the two species. LS-1 is the only lake in which both species were definitively identified. Both A. gracile and A. macrodactylum occurred in the main body of the lake but, in 1993, A. macrodactylum larvae were found primarily in small, shallow pools in the outlet.

Apparent lack of co-occurrence in most westslope lakes and habitat partitioning in LS-1 may result from predation and/or competition. Cortwright and Nelson (1990) found significant predation on Ambystoma jeffersonium larvae by Ambystoma opacum larvae, but no significant competition between the two Ambystomids. They suggest that salamander predation largely determines the composition of amphibian communities.

Competition between fish and larval salamanders and between species of salamanders has been postulated as a mechanism affecting co-occurrence. Morin (1981) suggested that larger larvae in an experimental salamander community competed with Lepomis macrochirus for available food resources. Efford and Tsumura (1973) found an overlap in diets for O. mykiss and A. gracile in Marion Lake, British Columbia. They suggest that the species may compete for food. Anderson and Graham (1967) postulated that competition may occur between two larval Ambystomids for food and habitat resources. Taylor (1984) suggested competition for food resources between larval A. gracile and T. granulosa in lakes in the Oregon Cascades.

Distribution and abundance of A. gracile and A. macrodactylum in westslope lakes is undoubtedly influenced by abiotic factors that may include elevation (Snyder, 1956; Stebbins, 1985; Leonard et al., 1993), lake area and depth (Kezer and Farner, 1955; Sprules, 1974a,b), lake temperature (Snyder,1956; Anderson, 1968), and conditions in the terrestrial habitat (Sprules, 1974a,b). We did not attempt analysis of the influence of abiotic factors since the number of lakes with quantitative information on larval densities was small.

PART III. ANURAN TAXA IN NOCA

Five anuran taxa were found in NOCA (Table 7). The Western or Boreal Toad, Bufo boreas, was present in or near five lakes (Battalion, Lower Thornton, PM 5-3, Trapper, Willow). The lakes varied in size (<2.5 ha. to 59.0 ha.), depth (<3.7m to 49.0m), and elevation (870m to 1629m). Adults were typically seen in talus slopes and near ponds associated with the larger lakes. Tadpoles were observed at Trapper Lake. Adult Pacific Treefrogs, Hyla regilla, were found in a variety of habitats near three low

Table 7. Anuran taxa found in NOCA Lakes (A=adult, L=larva, T=tadpole).

Taxa	Lake or Stream	Park Location	Elev. (m)	Lake Surface Area	Lake Maximum Depth (m)	Life Stage
Bufonidae						
Bufo boreas	Battalion L.	Battalion Ck. (Stehekin R.)	1629	2.5	4.3	A
	PM 5-3	Skymo Ck. (Ross Lake)	1382	0.1		A
	Thornton L. (Lower)	Thornton Ck. (Skagit R.)	1367	23.5	26.0	A
	Trapper L.	Pelton Basin (Stehekin R.)	1270	59.0	49.0	T,A
	Willow L.	Lightning Ck. (Ross Lake)	870	8.2	3.7	A
Hylidae						
Hyla regilla	(pond above)	Pyramid Lake				T,A
	Ridley L.	Hozomeen Ck. (Ross Lake)	958	4.3	9.8	A
	Willow	Lightning Ck. (Ross Lake)	870	8.2	3.7	A
Leiopelmatidae						
Ascaphus truei	Bridge Ck.					T
	Nert L.	Bacon Ck.	1388	1.0	8.2	T,A
	Pyramid Creek	East Fork				T
	Waddell L.	Waddell Ck. (Bridge Ck.)	1504	4.1	11.9	A
Ranidae						
Rana pretiosa	Coon L.	Cook Ck. (Stehekin R.)	662	8.2		A
	McAlester lake	McAlester Ck. (Bridge Ck.)	1679	5.0	6.1	T,A
	McAlester Pass		1846			A
	McAlester Creek (East Fork)	near Dagger Lake	1674			A

elevation (807m to 958m) lakes (Pyramid, Willow, Ridley). Tadpoles were captured from a pond above Pyramid Lake. The Spotted Frog, Rana pretiosa, was identified at one low elevation (Coon, 662m) and three high elevation sites (McAlester Creek, 1674m; McAlester Lake, 1679m; McAlester Pass, 1846m) east of the hydrologic crest. At two locations (Coon and McAlester Lakes) adults and tadpoles were found primarily in wet-meadow habitat through which the outlet stream flowed, and around the lake perimeter. They were also found in a ephemeral stream channels associated with a meadow spring seep (McAlester Pass) and a marshy area created by the outflow from a nearby lake (East Fork of McAlester Creek from Dagger Lake). Tadpoles of the Tailed Frog, Ascaphus truei, were found at two stream sites; one within the Complex (East Fork of Pyramid Creek), and another one mile from the Complex boundary (Bridge Creek). A. truei adults and tadpoles were also observed near or in the outlet streams of Nert and Waddell Lakes.

PHYTOPLANKTON

The taxonomic structure of phytoplankton assemblages in lakes located in mountainous regions and lakes at high latitudes have been shown to correspond to a variety of environmental, physical, and chemical variables such as climate, lake depth, lake area, water clarity, water quality, nutrients, and lake productivity (Pechlaner, 1971; Ilmavirta et al., 1984; Arvola, 1986; Earle et al., 1986; Earle et al., 1987; Knoechel and Cambell, 1988; Pinel-Alloul et al., 1990). Lakes in NOCA vary in water quality among the four main vegetation zones (alpine, subalpine, high forest and low forest). For example, alpine lakes have low water temperature and high concentrations of nitrate-nitrogen relative to low-forest lakes. Decreasing elevation and associated changes in vegetation zone tend to correspond with increases in water temperature, pH, alkalinity, conductivity, concentration of total nitrogen, and concentration of ammonia-nitrogen. Given this array of lake characteristics, a reasonable hypothesis was that characteristics of phytoplankton assemblages in NOCA lakes would correspond with the variation in physical and chemical conditions that exists among lakes in different vegetation zones. The objectives of this study were to:

(1) document the characteristics of phytoplankton assemblages of NOCA lakes;

(2) examine relationships between phytoplankton assemblages and the physical and chemical features of the lakes.

An additional objective was to assemble a phytoplankton data base to assess correspondence between the characteristics of phytoplankton and zooplankton

communities. The third objective was addressed in the crustacean zooplankton section of this report.

METHODS

From June 1988 through September 1993, 182 phytoplankton samples were collected from 64 lakes in NOCA (Table 1). Phytoplankton samples were collected throughout the park from lakes in vegetation zones ranging from low-elevation forest to alpine. Most of the samples were collected between July and September (Table 1).

All samples were collected using a Van-Dorn-style water sampler from a depth of 1 m near the deepest portion of each lake. Each 1-liter phytoplankton sample was preserved in Lugol's solution. The phytoplankton in each sample were enumerated using an inverted microscope (McIntire et al., 1993). In nearly all cases, 500 cells were counted per sample. Counts of only 100 cells were made in five of the samples because of the presence of large amounts of debris from glacial out-wash. A multiplier was estimated for each taxon based on cell diameter and was used to tranform count data into estimates of cell biovolume.

Analysis of the phytoplankton data was conducted in two parts. The first was an analysis at the division level, or in the case of Chrysophyta, the class level of classification using data collected from 1988 through 1993. Acronyms for the division and class levels of classification were as follows: Chlorophyta (CHL), Chrysophyta (CHR), Bacillariophyta (BAC), Cyanophyta (CYN), Pyrrhophyta (PYR), Cryptophyta (CRY), Euglenophyta (EUG), and unknown (UNK). The second was an analysis of the phytoplankton at the lowest possible taxonomic level (usually at the species level) and included only the data collected in 1989. Ordinations of the data at the division

Table 1. Number of NOCA phytoplankton samples collected by month and year and the number of lakes sampled each year from 1988 to 1993.

Year	Month	Number of Samples	Number of Lakes
1988	July	11	27
	August	6	
	September	10	
		27	
1989	June	5	57
	July	19	
	August	15	
	September	22	
		61	
1990	June	1	18
	July	9	
	August	13	
	September	8	
		31	
1991	May	2	19
	June	4	
	July	14	
	August	10	
	September	9	
		39	
1992	August	9	10
	September	9	
		18	
1993	July	1	3
	August	3	
	September	2	
		6	
	Total	182	

and species levels were performed using detrended correspondence analysis and the program DECORANA (Hill and Gauch, 1980). Proportional abundances and biovolumes were calculated using the program AIDN (Overton et al., 1987). A cluster analysis (McIntire, 1973) was used to group the samples in ordination space. The SYSTAT (Wilkinson, 1987) program, MGLH, was used for multiple regression tests. Correlation analyses were run on the SYSTAT program, CORR.

RESULTS

Community Characteristics: 1988 - 1993

The phytoplankton samples processed during the six-year study contained a total of 153 taxa, which included 52 chlorophytes (Chlorophyta), 43 chrysophytes (Chrysophyceae), 28 diatoms (Bacillariophytceae), 18 cyanobacteria (Cyanophyta), 4 dinoflagellates (Pyrrhophyta), 4 cryptomonads (Cryptophyta), 1 euglenoid (Euglenophyta), and 3 unknown taxa (Table 2). Collectively for all samples with 500 cell counts, *Chlorella* sp. and *Aphanocapsa delicatissima* had the highest average proportional abundances at 0.171 and 0.156, respectively (Table 3). Twenty other taxa had average proportional abundances of between 0.01 and 0.06. The remaining 131 taxa (data not shown) had average proportional abundances of less than 0.01. The average proportional abundances of the taxa increased when the averages were calculated using data only from the lakes in which each taxon was found (Table 3).

Collectively for all samples with 500 cell counts, cyanobacteria, chrysophytes, and chlorophytes were the dominant organisms (Table 4). Cyanophyta had the highest proportional cell densities, whereas the proportional cell biovolumes

Table 2. NOCA phytoplankton data: 1988-1993. List of taxa with division and codes.

Taxa I.D.	Division	Name[1]
100	CHR	UNKNOWN
101	CHL	CHLORELLA sp.
102	CYN	DIOGENES(?) bean shape
103	CHL	OOCYSTIS SOLITARIA Wittrock
104	CHR	CHROMULINA sp.
105	BAC	STEPHANODISCUS sp.
106	CYN	APHANOCAPSA DELICATISSIMA West & West
107	CHR	STATOSPORE
108	CHR	CHROMULINA PARVULA Conr.
109	CHR	CHRYSOMONADALES (long flagella)
110	CHR	STATOSPORE
111	CHR	STATOSPORE (DINOBRYON?)
112	CRY	RHODOMONAS sp.
113	CHR	OCHROMONAS OVALIS Dolf.
114	CHR	UNKNOWN
115	CHR	OPHIOCYTIUM PARVULUM (Perty) A. Br.
116	BAC	NAVICULA SUBATOMOIDES Hust.
117	CYN	APHANOTHECE CLATHRATA West et West
118	CHR	CHRYSOIKOS SKUJAE Naunerck
119	CYN	GLOEOCAPSA GELATINOSA Kutz.
120	PYR	PERIDINIUM INCONSPICUUM Lemm.
121	CHR	PSEUDOKEPHYRION sp.
122	CHR	CHROMULINA sp.
123	CHR	CHROMULINA sp.(?)
124	CHL	COSMARIUM sp.
125	CHR	DICERAS CHODATII(?)
126	CHL	VOLVOCALEAN
127	CRY	CHROOMONAS ACUTA
128	CHR	DINOBRYON BORGEI Lemm.
129	CHR	KEPHRION OVALE (Lackey) H-P
130	CHL	UNKNOWN (no flagella)
131	BAC	GOMPHONEMA sp.
132	BAC	MELOSIRA sp.
133	UNK	UNKNOWN
134	BAC	SYNEDRA ULNA (Nitzsch) Ehr.
135	CHL	OOCYSTIS SUBMARINA Lagerheim
136	CHR	OCHROMONAS sp.
137	CHL	CHLAMYDOMONAS GLOBOSA Snow
138	CHR	CHLOROCLOSTER-LIKE
139	CHR	MALLOMONAS
140	CYN	SYNECHOCYSTIS sp.
141	UNK	UNKNOWN
142	CHL	FRANCEIA DROESCHERI (Lemm) G.M. Smith
143	CHR	DINOBRYON/EPIPYXIS sp.
144	CHR	DINOBRYON BAVARICUM
145	BAC	NITZSCHIA GRACILIS Hantz.
146	CYN	ANABEANA sp.

Table 2. (continued)

Taxa I.D.	Division	Name
147	BAC	ACHNANTHES sp.
148	CHR	OCHROMONAS SPHAGNALIS Conrad
149	CRY	CRYPTOMONAS OVATA Ehren.
150	BAC	CYCLOTELLA COMTA
151	PYR	AMPHIDINIUM LUTEUM
152	CHR	CHROMULINA sp.
153	CHL	UNKNOWN
154	BAC	CYCLOTELLA STELLIGERA(?)
155	CHL	ELAKATOTHRIX GELATINOSA Wille.
156	CHL	CRUCIGENIA TETRAPEDIA
157	CHL	OOCYSTIS PARVA West et West
158	CHR	CHROMULINA STATOSPORE
159	PYR	GYMNODINIUM-LIKE
160	CHL	TETRAEDRON MINIMUM (A. Braun) Hansgirg
161	BAC	UNKNOWN
162	BAC	NAVICULA sp.
163	CHR	OPHIOCYTIUM COCHLEARE A. Br.
164	PYR	GYMNODINIUM sp.
165	CHR	DINOBRYON DIVERGENS Imhof
166	BAC	NAVICULA sp.
167	CHL	UNKNOWN
168	CHR	OCHROMONAS PINGUIS Conr.
169	BAC	MELOSIRA GRANULATA (Ehr.) Ralfs
170	BAC	SYNEDRA TENERA W. Smith
171	CHR	TRIBONEMA-LIKE
172	BAC	CYMBELLA sp.
173	BAC	SURIRELLA sp.
174	CHL	SCENEDESMUS DENTICULATUS var linearis Lagerheim
175	CHR	TRIBONEMA-LIKE
176	CHR	CHROMULINA-LIKE
177	CYN	DACTYLOCOCCOPSIS ACUCULARIS Lemm.
178	CYN	CHROOCOCUS MINIMUS (Keissl.) Lemm.
179	CHL	HAEMATOCOCCUS LACUSTRIS (Girod.) Rostafinski
180	CHL	TETRAEDRON sp.
181	BAC	DIATOMA sp.
182	BAC	HANNAEA ARCUS (Ehr) Patr.
183	CHR	CHRYSIDIASTRUM CATENATUM Lauterborn
184	CHL	SPONDYLOSIUM sp.
185	CHL	SCHROEDERIA SETIGERA (Schroed.) Lemm.
186	CHL	STAURASTRUM sp.
187	CHL	SCENEDESMUS ABUNDANS (Kirch.) Chodat
188	CHL	GLOEOCYSTIS PLANCTONICA (West & West) Lemm.
189	CHL	ANKISTRODESMUS FALCATUS var MIRABILIS (West&West)
190	CYN	MERISMOPEDIA TENUISSIMA Lemm.
191	CHL	DINOBRYON SERTULARIA Ehr.
192	CRY	RHODOMONAS MINUTA var. NANOPLANTICA Skuja
193	BAC	NAVICULA sp.
194	CHR	UNKNOWN STATOSPORE
195	CYN	RHABDODERMA LINEARE Schmidle & Lauterborn
196	CHL	OOCYSTIS APICULATA W. West

Table 2. (continued)

Taxa I.D.	Division	Name
197	CHL	TETRADESMUS SMITHII Prescott
198	CHL	CHLAMYDOMONAS PSEUDOPERTYI Pascher
199	CYN	RHABDODERMA SIGMOIDEA fa. MINOR Moore & Carter
200	CHL	CHRYSIDIASTRUM sp.
201	BAC	NAVICULA sp.
202	CHL	PEDIASTRUM BORYANUM (Turp.) Meneghini
203	CYN	RHABDODERMA like
204	CHR	OPHIOCYTIUM CAPITATUM Wolle
205	CYN	DIMORPHOCOCCUS LUNATOS A. Braun
206	CYN	OSCILLATORIA ANGUSTA Koppe
207	BAC	FRAGILARIA CROTONENSIS Kitton
208	CHL	MOUGEOTIA sp.
209	BAC	PENNATE
210	CHL	OOCYSTIS ELLIPTICA W. West
211	CHR	UNKNOWN STATOSPORE (6-7 microns)
212	CHL	CRUCIGENIA sp.
213	EUG	EUGLENA sp.
214	BAC	TABELLARIA FLOCCULOSA (Roth.) Kutz.
215	CHL	HYDRODICTYON RETICULATUM (L.) Lagerheim
216	CHL	COLEOCHAETE sp.
217	CHL	TREUBARIA SETIGERUM (Archer) G.M. Smith
218	BAC	FRAGILARIA sp.
219	CHL	UNKNOWN
220	CHL	UNKNOWN
221	CHR	CHRYSAMOEBA RADIAN Klebs
222	BAC	NITZSCHIA sp.
223	CYN	RAPHIDIOPSIS CURVATA Fritsch et Rich
224	CHL	UNKNOWN
225	CHL	CLOSTERIDIUM sp.
226	CYN	DACTYLOCOCCOPSIS SMITHII Chodat et Chodat
227	CHR	UNKNOWN STATOSPORE
228	CYN	LYNGBYA sp.
229	CHR	STATOSPORE
230	CHR	TRIBONEMA-LIKE
231	CHL	SPERMATOZOOPIS sp.
232	BAC	CYMBELLA sp. 2
233	CHL	CARTERIA KLEBSII (Dang.) Dill
234	CHL	COSMARIUM GRANATUM Breb.
235	CHL	KIRCHNERIELLA LUNARIS (Kirch.) Moebius
236	BAC	NITZSCHIA OREGANA Sov.
237	CYN	APHANOCAPSA ELACHISTA West & West
238	UNK	UNKNOWN
239	CHR	STATOSPORE
240	CHR	STATOSPORE
241	CHL	FRANCEIA OVALIS (France) Lemm.
242	CHL	CHLOROCOCCUM HUMICOLA (Naeg.) Rabenorst
243	CHL	ANKISTRODESMUS FALCATUS (Corda) Ralfs
244	CHL	STAURASTRUM sp.
245	CHL	MOUGEOTIA sp.
246	CHR	UNKNOWN

Table 2. (continued)

Taxa I.D.	Division	Name
247	BAC	FRUSTULIA sp.
248	CHL	SCENEDESMUS OBLIQUIS (Turp.) Kuetzing
249	CHL	STAURASTRUM sp.
250	CHR	CHRYSIOKOS BICORNIS Willen
251	CHR	CHRYSAMOEBA sp.
252	CHL	SELENASTRUM WESTII G.M. Smith

[1]CHR = Chrysophyta
CHL = Chlorophyta
BAC = Bacillariophyta
CRY = Cryptophyta
CYN = Cyanophyta
EUG = Euglenophyta
PYR = Pyrrhophyta
UNK = Unknown

Table 3. Average proportional abundances (≥ 5%) for phytoplankton taxa in the 178 samples collected during the period from 1988 to 1993, number of samples in which each taxon was present, and average proportional abundance in all samples in which each taxon was present.

Taxa	Number of Samples Taxa Present	Average Proportional Abundance	
		All Samples	Samples Present
Chlorella sp.	87	.171	.348
Aphanocapsa delicatissima	72	.156	.385
Chromulina parvula	62	.060	.170
Synechocystis sp.	65	.043	.116
Chromulina sp.	63	.041	.119
Ochromonas pinguis	42	.039	.163
Unidentified chrysophyte[1]	64	.033	.091
Aphanothece clathrata	19	.031	.289
Diogenes sp.	27	.031	.199
Ochromonas sp.	58	.031	.094
Chrysophyte statospore[2]	49	.023	.064
Unknown chrysophyte[3]	65	.021	.058
Chroococus minimu	17	.018	.189
Oocystis solitaria	42	.016	.068
Ochromonas ovalis	18	.016	.155
Unidentified[4]	23	.015	.114
Gleocystis planctonica	16	.014	.150
Rhodomonas sp.	51	.013	.040
Gymodinium-like	37	.013	.063
Unknown chlorophyte[5]	18	.011	.109
Chrysophyte statospore[6]	33	.010	.053
Pseudokephyrion sp.	36	.010	.051

[1]Taxon I.D. No. 114
[2]Taxon I.D. No. 107
[3]Taxon I.D. No. 100
[4]Taxon I.D. No. 141
[5]Taxon I.D. No. 126
[6]Taxon I.D. No. 110

were dominated by the Chrysophyta. Although low in number in the counts and proportional cell densities, dinoflagellates had the second highest proportional cell biovolume at 0.157.

The sample data were separated into alpine, subalpine, high-forest and low-forest vegetation zones based on the lake classification (Lomnicky et al., 1989; Liss et al., 1991). Subalpine and high-forest lakes had the largest number of taxa per sample, and alpine lakes had the smallest number (Table 5). However, taxa from each taxonomic division and class were found in each vegetation zone (Table 5). Alpine lakes contained a fairly even number of diatom, chlorophyte and chrysophyte taxa. Subalpine lakes and high-forest lakes were dominated by chrysophyte and chlorophyte taxa, where as chrysophyte taxa dominated low-forest lakes. The number of diatom taxa per sample was greatest in subalpine lakes, and the number of chlorophyte taxa was greatest in subalpine and high-forest lakes. The number of chrysophyte taxa per lake was highest in subalpine, high-forest and low-forest lakes. The numbers of Cryptophyta, Cyanophyta, Euglenophyta, and Pyrrhophyta taxa per lake were low, but evenly distributed among the four vegetation zones.

Representatives of the chlorophytes and chrysophytes were the dominant taxa in alpine lakes based on 500 cell counts (Table 6). Chlorophytes, chrysophytes, and cyanobacteria were the dominant taxa in subalpine lakes and high-forest lakes. Cyanobacteria were the dominant taxa in low-forest lakes. Similar results were found for proportional cell densities, except that cyanobacteria taxa dominated both high-forest and low-forest lakes (Table 6). Chrysophyte taxa dominated the proportional biovolumes of all lake types (Table 6). Dinoflagellate biovolumes were lowest in low-

Table 4. Proportional abundances in samples with 500 cell counts, proportional cell densities and cell biovolumes for each taxonomic division and class during the period between 1988 and 1993.

Division	Proportional Sample Count	Proportional Cell Density	Proportional Cell Biovolume
BAC	0.020	0.007	0.052
CHL	0.270	0.117	0.087
CHR	0.299	0.104	0.597
CRY	0.027	0.015	0.049
CYN	0.346	0.750	0.057
EUG	<0.001	<0.001	<0.001
PYR	0.017	0.005	0.157
UNK	0.021	0.002	0.002

Table 5. Average number of phytoplankton taxa by taxonomic division and class in alpine, subalpine, high-forest and low-forest lakes during the period from 1988 to 1993.

Forest Type	BAC	CHL	CHR	CRY	CYN	EUG	PYR	UNK	Total
Alpine	15	17	18	4	10	1	3	1	69
Subalpine	27	36	34	4	17	1	4	2	125
High Forest	21	37	38	4	14	1	4	3	122
Low Forest	10	28	37	4	13	1	4	3	100

Table 6. Proportional abundances in samples with 500 cell counts and proportional cell densities and biovolumes by taxonomic division and class in alpine, subalpine, high-forest and low-forest lakes during the period between 1988 and 1993.

Alpine Lakes

Division	Prop. Count	Prop. Density	Prop. Biovolume
BAC	0.0436	0.0674	0.1597
CHL	0.2344	0.2794	0.1644
CHR	0.3894	0.3097	0.3675
CRY	0.1136	0.1643	0.0895
CYN	0.1424	0.1186	0.0024
EUG	0.0014	0.0005	0.0000
PYR	0.0426	0.0253	0.2089
UNK	0.0326	0.0348	0.0075

Subalpine Lakes

Division	Prop. Count	Prop. Density	Prop. Biovolume
BAC	0.0188	0.0153	0.0526
CHL	0.3252	0.3364	0.1091
CHR	0.3361	0.2448	0.4775
CRY	0.0140	0.0111	0.0195
CYN	0.2552	0.3665	0.0180
EUG	0.0001	0.0001	0.0000
PYR	0.0228	0.0168	0.3186
UNK	0.0278	0.0091	0.0047

High-Forest Lakes

Division	Prop. Count	Prop. Density	Prop. Biovolume
BAC	0.0101	0.0053	0.0221
CHL	0.2773	0.1622	0.1005
CHR	0.2944	0.1949	0.5260
CRY	0.0235	0.0269	0.0788
CYN	0.3646	0.5919	0.0263
EUG	0.0000	0.0000	0.0000
PYR	0.0129	0.0153	0.2447
UNK	0.0171	0.0034	0.0017

Low-Forest Lakes

Division	Prop. Count	Prop. Density	Prop. Biovolume
BAC	0.0274	0.0059	0.0629
CHL	0.1646	0.0744	0.0612
CHR	0.2236	0.0647	0.7049
CRY	0.0334	0.0116	0.0397
CYN	0.5365	0.8415	0.0920
EUG	0.0006	0.0000	0.0000
PYR	0.0055	0.0014	0.0388
UNK	0.0084	0.0004	0.0005

forest lakes, whereas diatom, chlorophyte and cryptophyte biovolumes were highest in alpine lakes. Taxa in the other divisions did not contribute substantially to the phytoplankton biovolumes of any lake type.

Vegetation zones were distributed in ordination space relative to the distribution of the organisms by taxonomic division or class to relate the scores of the first two axes to environmental and water quality variables (Fig. 1). The distribution of the phytoplankton divisions and classes corresponded to the distribution of the vegetation zones relative to the maximum proportional abundances of each division or class (Table 6). Although low in abundance, Cryptophyta (CRY) and Bacillariophyta (BAC) were at maximal proportional abundances in alpine lakes, whereas Cyanophyta (CYN) were abundant in low-forest lakes. The other divisions or classes (Euglenophyta and unknowns were deleted because they were rare) had maximal abundances in subalpine and alpine lakes. None of the divisions or classes had maximum proportional abundances in high-forest lakes. Increasing scores on axis one corresponded to increasing elevation and concentration of nitrate-nitrogen and decreasing water temperature, pH, alkalinity, conductivity, concentration of Kjeldahl-nitrogen, and concentration of ammonia-nitrogen (Figs. 2-4). Increasing scores on axis two corresponded to increasing concentrations of total phosphorus (Fig. 4).

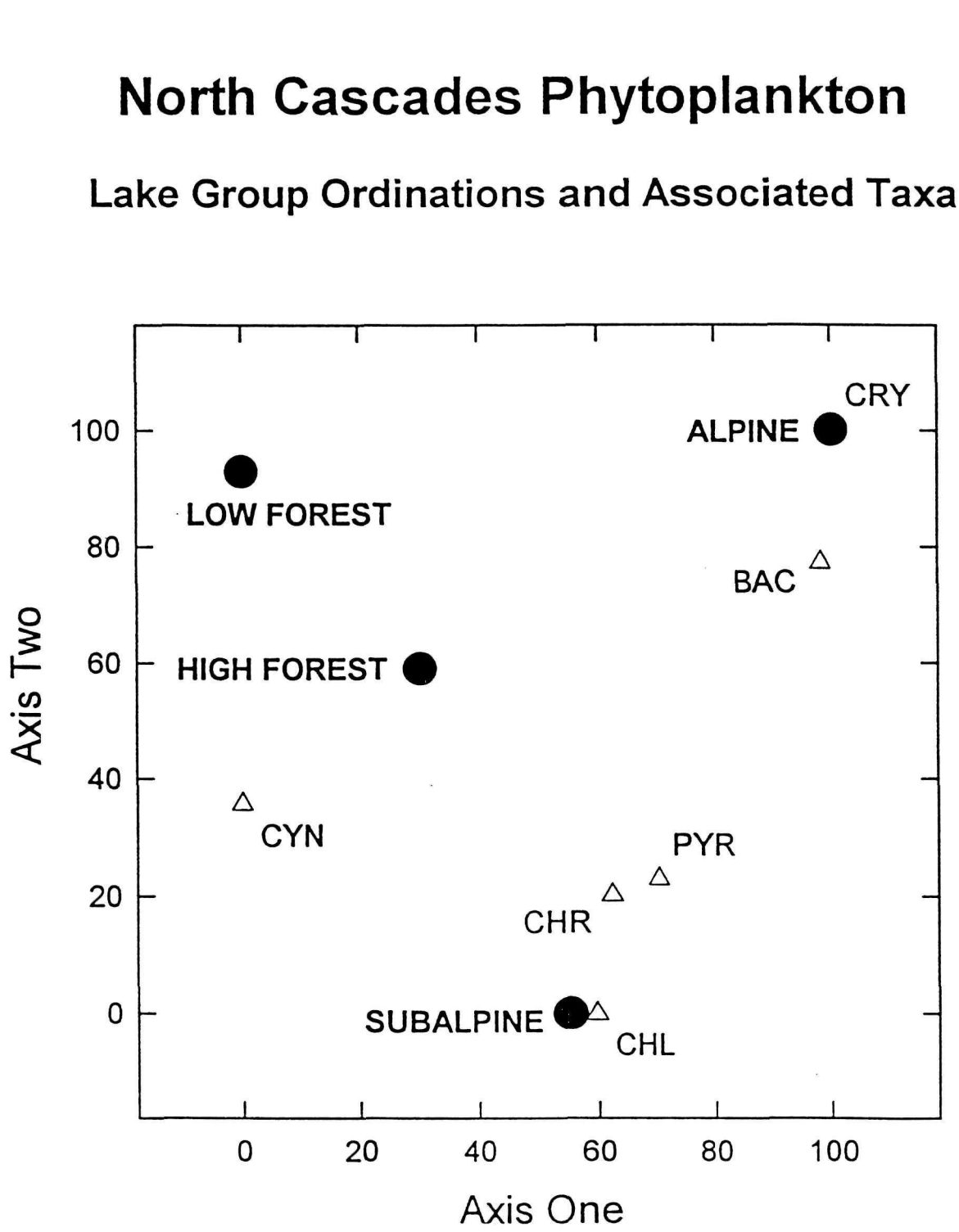


Figure 1. Ordinations of the phytoplankton divisions and the four lake types (alpine, subalpine, high forest and low forest) relative to the taxonomic composition of the phytoplankton at the division level during the period from 1988 to 1993.

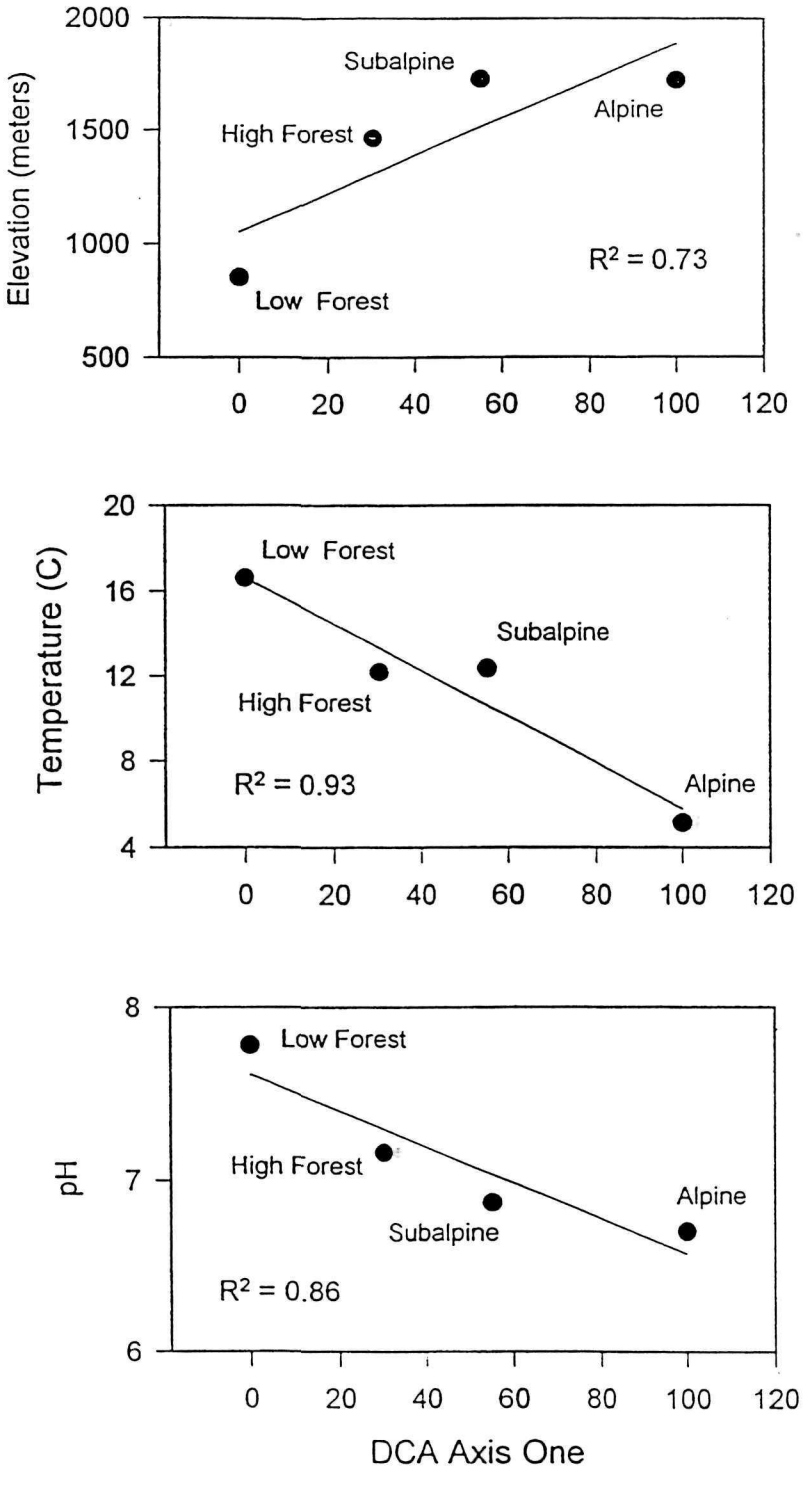


Figure 2. Relationships among elevation, temperature and pH, and the scores of the X axis of the ordination of the four lake types (Fig. 1).

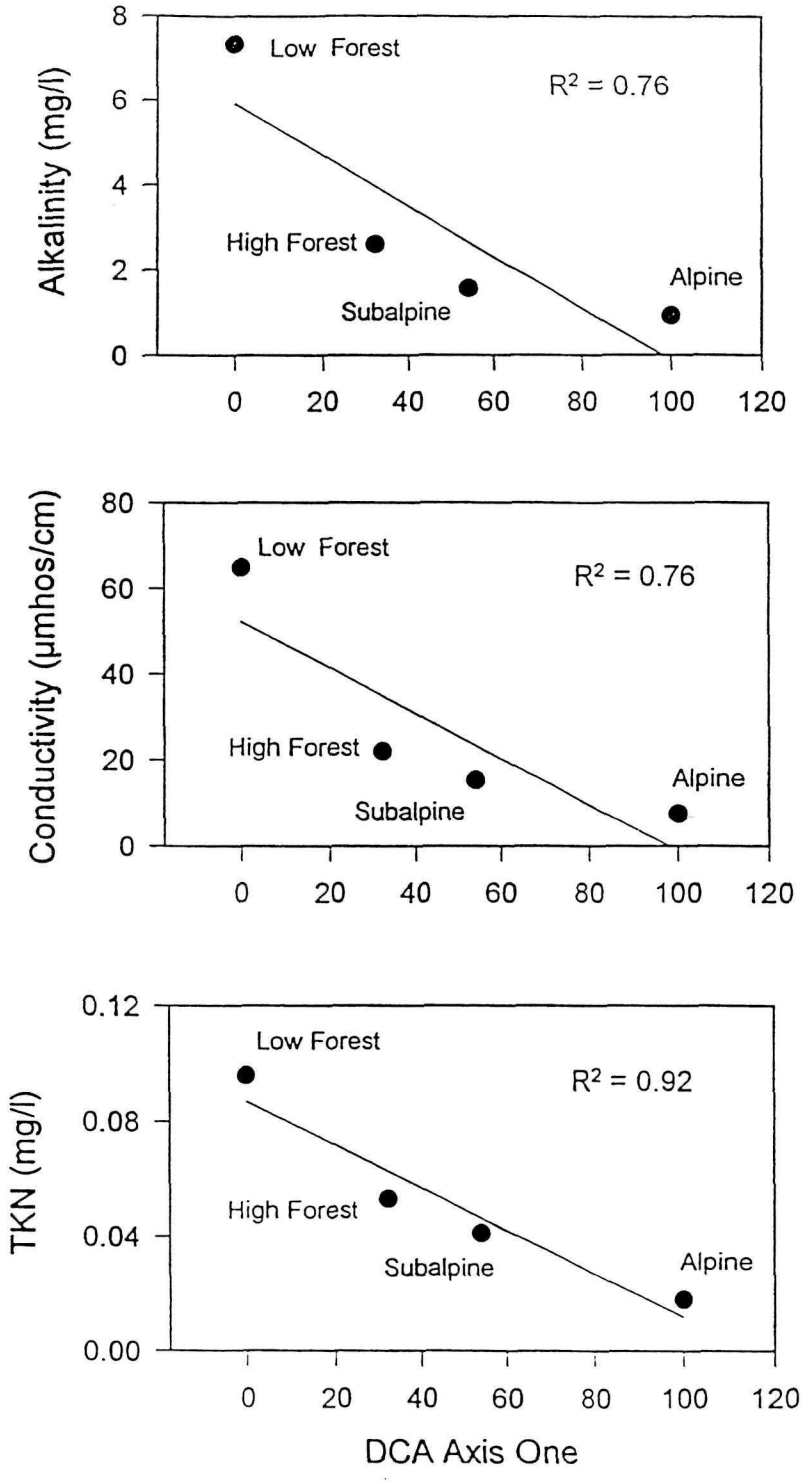


Figure 3. Relationships among alkalinity, conductivity and Kjeldahl-nitrogen, and the scores of the X axis of the ordination of the four lake types (Fig. 1).

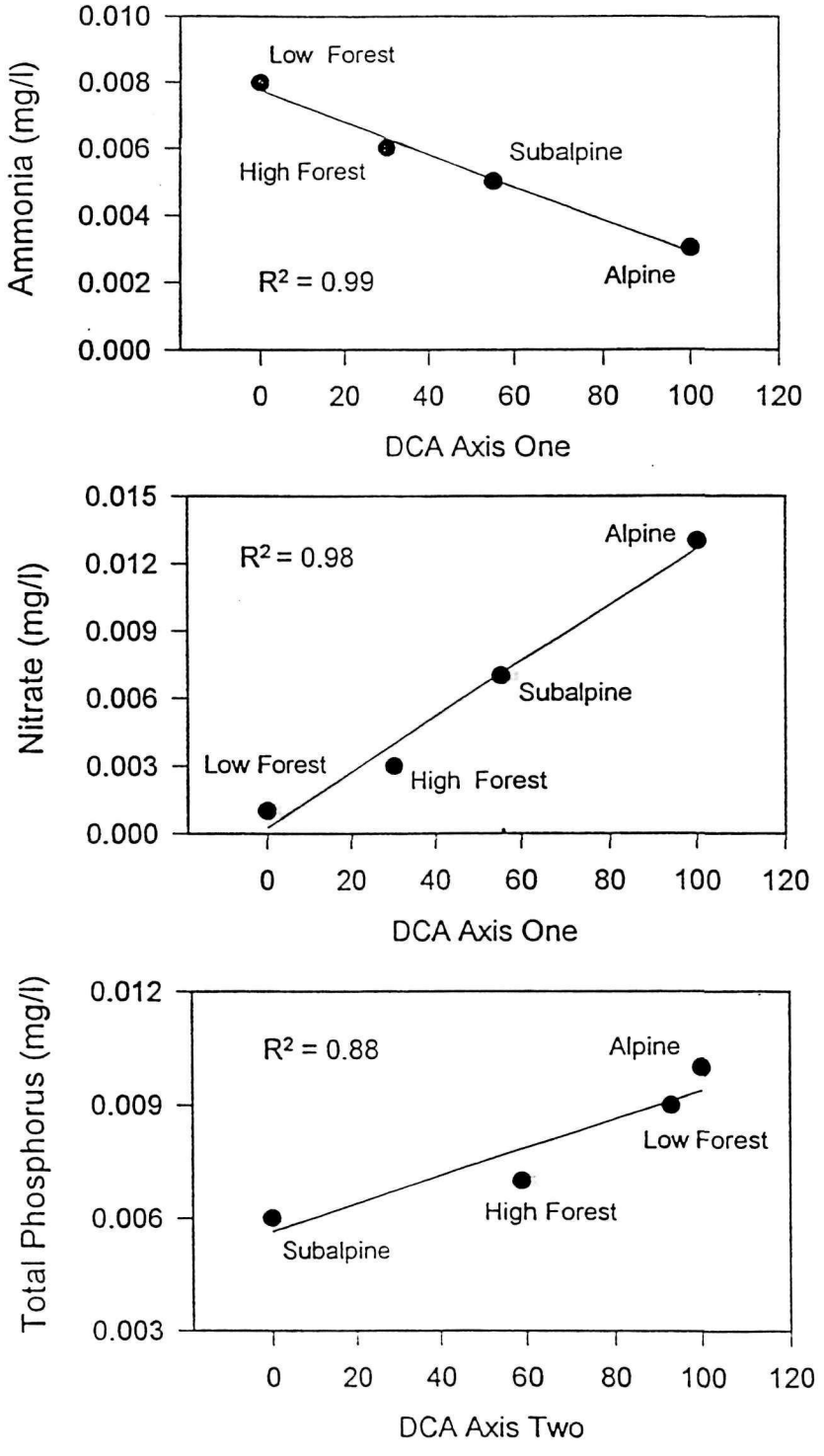


Figure 4. Relationships among ammonia-nitrogen and nitrate-nitrogen and the scores of the X axis, and the relationship between total phosphorus and scores of the Y axis of the ordination of the four lake types (Fig. 1).

Community Characteristics: 1989

Lake ordinations corresponding to species ordinations (data not shown) were used to relate the axis scores to environmental and water quality variables for samples collected in 1989 (Fig. 5). Increasing scores along axis one corresponded to increasing concentrations of Kjeldahl-nitrogen and a transition in vegetation zones from alpine to low-forest (multiple regression analysis, $r^2 = 0.606$, $p<0.01$). Increasing scores on axis two corresponded to decreasing concentrations of orthophosphate-phosphorus and increasing water temperature (multiple regression analysis, $r^2 = 0.254$, $p<0.01$). Seven regions of the lake ordination were identified by cluster analysis (Fig. 5, Table 7). With the exception of cluster 5, which included only east-side subalpine lakes, the clusters contained mixtures of lakes from several vegetation zones (Table 8). Nonetheless, cluster 3, which was located on the left-side of the graph, included six glacially influenced west-side alpine and subalpine lakes, and cluster 4, which was located on the right-side of the graph, contained two high-forest lakes and four low-forest west-side lakes. Environmental, physical, and chemical characteristics among lakes in the seven clusters are shown in Appendix 1.

Lakes in each cluster differed in terms of the dominant taxa and composition of particular taxonomic groups (Table 9). Lakes in cluster 3 were dominated by *Chromulina parvula,* and cyanobacteria were low in proportional abundance (<5%). Lakes in cluster 7 were dominated by two unidentified chlorophyte taxa. Lakes in cluster 1 were dominated by *Chlorella* sp. and *Aphanocapsa delicatissima,* and lakes in cluster 2 were dominated by *A. delicatissima.* Lakes in cluster 5 were dominated by *Ochromonas sphagnalis* and *Diogenes* sp. (a cyanobacterium). Lakes in cluster 6

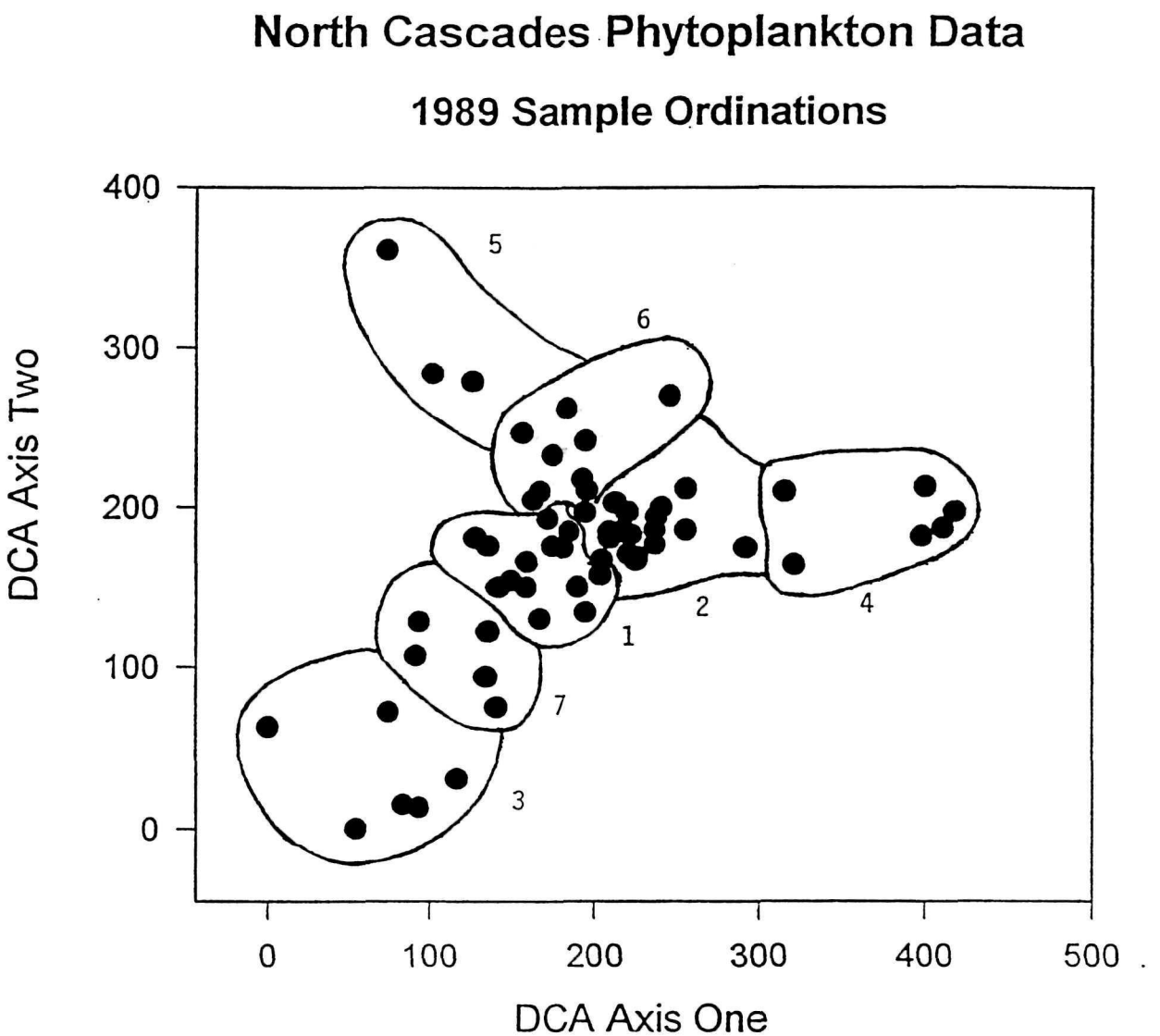


Figure 5. Ordination of the phytoplankton community assemblages by lake and the position of each cluster of lakes for samples collected in 1989.

Table 7. Samples in each cluster of the lake ordination relative to the taxonomic composition of phytoplankton in samples collected in 1989.

Cluster	Lake
1	BATT, MORA, TRAP, MM11, MR132, SKYU, KETU, VULC, SWEE, REDO, THRM, MCAL, TAPW, LS1
2	RAIN[1], WADD[1], PANL[1], PYRA[1], GRVW, EGG, COON, SKYM, NONA, PM53, MR2, MR3, EP6, MONO
3	OUZE, KLAW, REVL, WILE, EILE, REVU
4	THUN, WILL, NERT, HOZO, RIDL, LS2
5	JUAN, TRIL, MR9
6	DOUB, TAPM, TAPU, SILV, WILD, BEAR, LS3, THRL, COPP
7	TRIU, PRICE, MP8, JEAN, TTAR

[1]Two samples each

Table 8. Number of alpine, subalpine, high-forest and low-forest lakes relative to the eastside (E) and westside (W) of the park in each cluster of the lake ordination in 1989.

Cluster		Forest Type A	SA	FH	FL	Sum
1	Total	2	7	5	0	14
	W	2	4	2	0	8
	E	0	3	3	0	6
2	Total	0	7	4	3	14[1]
	W	0	4	2	2	8
	E	0	3	2	1	6
3	Total	4	2	0	0	6
	W	4	2	0	0	6
	E	0	0	0	0	0
4	Total	0	0	2	4	6
	W	0	0	2	4	6
	E	0	0	0	0	0
5	Total	0	3	0	0	3
	W	0	0	0	0	0
	E	0	3	0	0	3
6	Total	1	7	1	0	9
	W	1	6	1	0	8
	E	0	1	0	0	1
7	Total	1	3	1	0	5
	W	1	2	1	0	4
	E	0	1	0	0	1

[1]Duplicate samples from four lakes deleted.

Table 9. Dominant phytoplankton taxa in each cluster of the lake ordination for samples collected in 1989.

Cluster 1	*Chlorella* sp. (19.1),[1] *Aphanocapsa delicatissima* (12.5), unknown chlorophyte (8.6), *Diogenes* (7.6), *Ochromonas* sp. (6.5), *Synechocystis* sp. (5.4), chlorophyte (5.0)
Cluster 2	*Aphanocapsa delicatissima* (25.3), *Chlorella* sp. (11.2), *Chromulina* sp (7.8), *Synechocystis* sp. (6.4)
Cluster 3	*Chromulina parvula* (28.8), *Chroomonas acuta* (18.9), *Ochromonas* sp. (10.1), unknown (6.6), *Chrysophyte* (5.5), *Pseudokephyrion* sp. (5.3)
Cluster 4	*Aphanotheca clarthrata* (51.4), *Gleocopsa* sp. (6.9)
Cluster 5	*Ochromonas sphagnalis* (33.9), *Diogenes* sp. (33.4), *Chromulina* sp. (6.7), chlorophyte (5.0)
Cluster 6	*Diogenes* sp. (23.1), *Aphanocapsa delicatissima* (12.6), *Chlorella* sp. (8.9), *Chromulina* sp. (7.1), *Synechocystis* sp. (6.5), unknown *chrysophyte* (5.7), *Cyclotella stelligera* (5.6)
Cluster 7	Unknown chlorophyte (25.2), unknown chlorophyte (20.0), *Chromulina parvula* (9.0), *Ochromonas pinguis* (8.3), *Chlorella* sp. (8.2)

[1]Proportional abundance (%)

Table 10. Average number of taxa and phytoplankton cell densities per sample in each cluster of the lake ordination, east-side (E) lakes, west-side (W) lakes, and all lakes collectively for samples collected in 1989.

			Cell Density			
Cluster or location	n	No. of taxa	Average (NO/cm^3)	Min	Max	SD
1	14	18.8	1584	183	3559	1061
2	18	22.1	2869	125	6744	2258
3	6	10.8	1290	63	4377	1793
4	6	18.5	11422	391	38926	11422
5	3	20.0	4677	636	10527	5188
6	9	17.3	1334	55	3139	810
7	5	16.6	1244	99	2296	893
E	20	20.6	2816	125	10537	2469
W	41	17.7	3074	55	38926	6453
All	61	18.6	2989	55	38926	5450

were dominated by *Diogenes*, and lakes in cluster 4 were dominated by *Aphanotheca clarthrata*. Lakes in cluster 5 and cluster 1 had the lowest and highest species diversity, respectively. Variation in cell densities among the lakes in each cluster was high (Table 10). The average cell densities were highest in lakes in cluster 4 and second highest in lakes in cluster 5. Overall, the average number of taxa per lake was 18.6, with an average of 20.6 taxa in east-side lakes and 17.7 taxa in west-side lakes. Cluster 3 had the lowest average number of taxa at 10.8 per sample.

DISCUSSION

Several aspects of the results supported our hypothesis that the taxonomic compositions of phytoplankton assemblages in NOCA lakes would correspond with the different physical and chemical conditions that exist among lakes in the four vegetation zones. Based on the analysis of samples collected between 1988 and 1993, decreasing elevation and corresponding shifts in vegetation zone from alpine to low-forest were associated with increased water temperature, pH, alkalinity, conductivity, and concentrations of total nitrogen in NOCA lakes. Alpine lakes were high in total phosphorus and nitrate-nitrogen and low in other water quality variables. These lakes were dominated in density by chrysophyte and chlorophyte taxa, but the highest proportional abundances of Cryptophyta and Bacillariophyta also occurred in these lakes. Cyanobacteria were the dominant taxa in low-forest lakes, which were high in temperature, pH, alkalinity, conductivity, Kjeldahl-nitrogen, ammonia-nitrogen and total phosphorus. Chlorophytes, chrysophytes and cyanobacteria were the dominant taxa in subalpine and high-forest lakes. These lakes were intermediate in temperature, water quality, and concentrations of nutrients relative to alpine and low-forest lakes.

The distributions of phytoplankton taxa in the clusters of the ordination of the 1989 samples were not as consistent with the analysis of the data collected from 1988 through 1993 relative to vegetation zone. Most of the clusters contained lakes from different vegetation zones, especially contiguous zones. In no instance, however, were alpine lakes and low-forest lakes located in the same cluster. Nonetheless, there appears to be two extreme types of phytoplankton assemblages in NOCA lakes. Chrysophyte taxa (*Chromulina* and *Ochromonas*) were the dominant taxa, and Cryptophyta were subdominant taxa in the glacially influenced alpine and subalpine lakes in cluster 3. The four low-forest lakes and 2 high-forest lakes in cluster 4 were dominated by *Aphanotheca*. Lakes in the other clusters exhibited considerable variation relative to the taxonomic composition of the phytoplankton assemblages. However, the effects of seasonal and annual changes of the climate on the phytoplankton assemblages in NOCA lakes remain unresolved because most of the lakes were sampled only once in 1989. Temporal patterns of the phytoplankton assemblages in the NOCA lakes will be addressed in the final report for Phase II of the project.

Phytoplankton assemblages in NOCA lakes were similar in total number of taxa, average number of taxa per sample, and ranges of cell densities relative to phytoplankton studies in lakes in Quebec (Pinel-Alloul et al., 1990), Finland (Arvola, 1986), Olympic National Park (Larson et al., 1991) and Mount Rainier National Park (Larson et al., In Press) (Table 11). Collectively, duration of the ice-free period, geographic location within a study area, lake size, flushing rate, transparency, water temperature, hardness, and nutrients were some of the variables shown to be important factors influencing the taxonomic structures of the phytoplankton assemblages in these

Table 11. Total number of phytoplankton taxa, average number of taxa per sample, and the ranges of cell densities in lakes in Quebec, Finland, Olympic National Park, Mount Rainier National Park, and NOCA (1989).

Location	Total number of taxa	Average number of taxa/sample	Range of density per ml	Author
Quebec (54 lakes)	129	24	690-9163	Pinel-Alloul et al 1990
Finland (54 lakes)	103	18	192-27726	Arvola 1986
Olympic N.P. (7 lakes)	172	--	311-5216	Larson et al 1991
Mt. Rainier N.P. (27 lakes)	203	20	1047-5505	Larson et al, In press
NOCA	153	19	1290-11422	Present work

Table 12. Dominant phytoplankton assemblages (proportional abundances) at the division level in lakes at high latitude or elevations.

Location	Dominant taxa	Author
Finland	CHR and CHL	Arvola 1986
Finland		
Clear oligotrophic	CHR > CHL > CRY	Ilmavirta et al 1984
Mesotrophic	CYN and CHL	Ilmavirta et al 1984
Quebec		
Deep and clear	CHR	Pinel-Alloul et al 1990
California (Castle Lake)		
Spring	BAC and CHR	Elser 1992
Summer	PYR, CYN, and small flagellates	Elser 1992
Olympic National Park	CHR or CYN	Larson et al 1991
Mt. Rainier National Park	CHR, CHL, or CYN	Larson et al, In press
Antarctic	CRY or CHR	Park et al 1982

other studies. In NOCA lakes, however, vegetation zone and associated water quality and concentrations of nutrients were the apparent factors influencing the taxonomic structures of the phytoplankton assemblages.

Pechlaner (1971) noted that phytoplankton assemblages in alpine and subalpine lakes were dominated by chrysophytes or dinoflagellates. Results from more recent studies have supported this generalization in some cases, but in other studies, the phytoplankton assemblages were dominated by chlorophytes, cyanobacteria, or cryptomonads (Table 12). Results from the NOCA studies supported the conclusion that phytoplankton assemblages in mountain lakes are more complex than originally determined by Pechlaner (1971).

ROTIFERS

Most rotifer taxa are believed to have powerful passive dispersal strategies (Dumont 1983; Pennak 1978) though knowledge of the extent of biogeographic distribution for particular species is modified as understanding of a confusing taxonomy (created by the great degree of parthenogenesis and extensive morphological plasticity in some species) changes (Dumont 1983; Sudzuki 1964; Ruttner-Kolisko 1993). Most pelagic species appear to have fairly wide physiological tolerances (Gannon and Stemberger 1978). In spite of these wide tolerances and powerful dispersal strategies, planktonic rotifer communities in lakes are often strongly dominated by a single species (Green 1993).

Relative density and dominance by particular rotifer taxa is related in part to lake trophic state (Gannon and Stemberger 1978) and trophic state indicators like total phosphorous (Siegfried et al. 1989; Berzins and Bertilsson 1989) and conductivity (Berzins and Bertilsson 1989). Though boundaries between trophic states are not sharply defined, lake trophy is a holistic indicator of physical and chemical conditions (Wetzel 1975), of the productivity, composition (Hutchinson 1967; Wetzel 1975), and size structure (Gliwicz 1969) of the phytoplankton, and of bacterial production (Geller and Muller 1981; Wetzel 1975). The structure of the microorganismic community (planktonic algae, bacteria, and protists) is linked to lake trophic state (Pejler 1983; Stockner and Shortreed 1989; Stockner 1987; Hutchinson 1967), and individual rotifer species have different microorganismic food preferences and food size requirements (Pourriot 1977; Arndt 1993) because of the connections between feeding (mechanisms, requirements, and efficiency) and the microorganismic community (available food size

and type). For example, Brachionid rotifers such as Keratella and Kellicottia species are relatively unselective microfiltrators which feed on picoplankton (0.2 - 2 um) and small nannoplankton (2 - 20 um; Pourriot 1977; Arndt 1993; Moore 1978). Small-bodied rotifers like the above mentioned taxa also have lower food concentration thresholds than larger rotifers (Stemberger and Gilbert 1987a), thereby allowing population growth when food sources are relatively less dense. Because microbial systems in ultraoligo- and oligotrophic lakes tend to be dominated by pico- and nanno-plankton (Stockner and Shortreed 1989; Stockner 1987; Pejler 1983), Brachionids may dominate rotifer communities in these unproductive lakes (Pejler 1983). Conversely, dominant rotifer taxa in lakes of greater productivity are more likely to include grasping feeders or predators, such as Polyarthra or Synchaeta species, which feed on larger microorganisms (Pourriot 1977). This is likely since lakes of greater productivity also are more likely to contain larger microorganisms (Stockner 1987; Pejler 1983). Therefore, physico-chemical conditions (and lake trophic state) operate through microorganismic food resources to structure the rotifer communities.

Besides characteristics of the physico-chemical environment and food resources, rotifer communities are structured by the presence and density of crustacean zooplankton which may act as predators, competitors, or both. Daphnids, as obligate filter feeders, utilize food size fractions which are within the same range as that utilized by microfiltrating rotifers: that is, in the 0.2 - 20 um range, depending on species (Gilbert 1985; Geller and Muller 1981). Daphnids may also utilize much larger foods (Gilbert 1985), and appear to be competitively superior to most rotifers under all but very productive conditions (Gilbert 1985).

Diaptomid copepods may either filter feed or exhibit predatory behavior (Zaret 1980; Williamson 1987). While filter feeding allows them to exploit algae (Zaret 1980; Moore 1978), they have been reported to feed on relatively larger microbes and microzooplankton including rotifers. While Diaptomids generally reject loricated rotifers (hard-bodied taxa like Brachionids) as food (Williamson 1987), they prey on soft-bodied rotifer taxa including Polyarthra and Synchaeta species (Williamson 1987, Anderson 1980).

Density of particular rotifer taxa may also be affected by vertebrate predators. Large or colonial rotifers like Asplanchna or Conochilus may be directly preyed upon by fish (Stenson 1982). Changes in density of some rotifers may also occur indirectly because of their interactions with crustacean zooplankton (Stenson 1982), the larger of which may be preyed upon by fish (Anderson 1972).

The objectives of this study were to determine the distribution and relative density of rotifers in mountain lakes in North Cascades National Park Service Complex, and to relate their distribution and density to physico-chemical conditions, the presence of crustacean zooplankton, and the presence of vertebrate predators. Few studies of rotifers conducted in North America have focused on western mountain systems (Larson et al. 1994; Neill 1984; Anderson 1980).

METHODS

Lake depth was determined with a handheld sonar gun along transects parallel and perpendicular to the long axis of a lake. Surface area was estimated by digitizing 7.5 min USGS topographical maps. Elevation was determined from these maps. Each time a lake was sampled, water temperature was measured at 1 m intervals from the

lake surface to the bottom over the deepest point in the lake using an Omega 871A digital thermo-couple. Water temperature at 1 m below the surface was recorded at each sampling occasion. Water samples were taken from a depth of 1 m over the deepest point in a lake using a 1.5 L Van Dorn bottle. Frozen filtered and unfiltered water samples were transported to the Forest Sciences Laboratory at Oregon State University for chemical analysis (total Kjeldahl nitrogen (TKN); total phosphorous; ortho-phosphorous; nitrate; ammonia; pH; alkalinity; conductivity).

Vertical tows for zooplankton (crustaceans and rotifers) were taken from 66 lakes between 1989 and 1993 (Table 1). Sampling occurred only between the period after ice-out and before the return of inclement fall weather (approximately mid-June through mid-September). Samples were taken with a 20 cm diameter number 25 (64 um mesh) zooplankton net. The net was lowered either to within one meter of the bottom of the lake, or to at least 10 meters in deep lakes, and towed upward at a rate of 0.5 meters per second. Three replicate vertical tows were taken near the deepest spot in the lake, except for lakes sampled in 1989 when only one vertical tow was taken. In the field, samples were preserved in 5% neutral sugar formalin (Haney and Hall 1973). In the lab, samples were split using a Folsom plankton splitter. The split portion was poured into a settling chamber and left to settle for 24 hours. Organisms were counted using an inverted microscope at 100X magnification.

Mean densities of each taxon at each sampling occasion (referred to as `sample means') were calculated from the three replicate vertical tows (except for 1989 data). These data were used to calculate the proportional abundance of each taxon among all lakes. A single mean for each taxon in each lake was calculated by averaging data within each year (if the lake had been sampled more than once in a particular year),

Table 1. Number of times each lake was sampled in each year. Lakes with an asterisk were used in cluster analysis and to examine effects of crustacean zooplankton on rotifers.

	LAKENAME	1989	1990	1991	1992	1993
*	Battalion	1		3		
	Bear	1				
	Bouk			1		
*	Coon	1				1
	Copper	1				
*	Dagger				1	2
	Dee Dee, Lower					2
	Dee Dee, Upper					2
*	Doubtful	1	2			1
	Egg	1				
	EP-6	1	1			
	Greenview	1				1
*	Hozomeen	1		1		
*	Jeanita	1				
*	Juanita	1				2
*	Kettling, Lower					2
*	Kettling, Upper	1				2
	Klawatti	1				
*	LS-1	1	2	3	2	2
*	LS-2	1	2	3	2	2
*	LS-3	1		1		
	MR-13-1		2	1	2	1
	MR-13-2		2	2	2	1
*	McAlester	1	1	2	2	1
	MM-11	1				1
*	Monogram	1				
	Moraine	1				
	MP-8	1				
*	MR-11		2	2	1	2
	MR-12					2
	MR-16					2
*	MR-2	1	2			3
*	MR-3	1	1			2
*	MR-9	1				2
*	Nert	1	1			
	NoName	1				
	Ouzel	1				
*	Panther, Lower	2	2	3	2	3
*	Panther, Upper		2	3	2	3
	Pyramid	2		3		3
*	Redoubt	1				

Table 1. Continued

	LAKENAME	1989	1990	1991	1992	1993
	Reveille, Upper	1				
*	Ridley	1				
	Skymo	1		1		
	Skymo, Upper	1		1		
	Silent, Lower					1
	Silent, Upper					1
	Sweet Pea	1				
	Tapto, Middle	1	2			
	Tapto, Upper	1	2			
	Tapto, West	1	2			
	Thornton, Lower	1				
*	Thornton, Middle	1				
*	Thunder	1	1	3		
	Trapper	1	1			
*	Triplet, Lower	1	2	1		
*	Triplet, Upper	1	2	1		
	Talus Tarn	1				
	Vulcan	1				
*	Waddell	2		2		3
	Waddell, Middle					2
	Wild	1				
*	Willow	1		1		

then averaging again over all years (if the lake had been sampled more than one year). These data are referred to as `overall means.'

Hierarchical agglomerative cluster analysis was used to group lakes according to overall means of proportional density of rotifer taxa. Cluster analysis was performed only on lakes where overall mean rotifer density was > 1.0 per liter (30 lakes). The resemblance measure selected was relative Euclidean distance, and the fusion strategy was group average. Means of physical and chemical parameters for each cluster of lakes and means of absolute density of groups of crustacean zooplankton were calculated. These groups were: all adult Cladocerans (primarily Daphnia rosea and Holopedium gibberum, but also others; see Liss et al. 1995); adult Daphnids (primarily Daphnia rosea, but also D. longiremis, D. middendorffiana, and D. schodleri); adult large-bodied Diaptomids (primarily Diaptomus kenai, but also D. arcticus and D. leptopus); and adult small-bodied Diaptomids (primarily Diaptomus tyrrelli, but also D. lintoni). Detrended correspondence analysis was also run on species proportional abundance data from these 30 lakes, and the resulting axis scores for each lake were correlated, through use of Pearson product-moment correlations, with chemical and physical data, and with proportional density of the major crustacean zooplankton.

Scatter plots and chi-square contingency table analyses were used to examine relationships between density of rotifers and crustacean zooplankton groups. Data used for these analyses were sample means from the 30 lakes described above. A cumulative frequency histogram was plotted for the density (number per liter) of loricated rotifers (all taxa combined, excluding Keratella armadura). The curve of this histogram first climbed steeply for each whole number increase. Fourty-four percent of all samples had less than one loricated rotifer per liter. An additional twelve percent of

the samples had between one and two rotifers per liter. The curve of the histogram then tapered off. Samples which had densities above 5.0 rotifers per liter (31% of the samples) were more evenly distributed. Each whole number increment above 5.0 per liter accounted for 2% or less of the total samples. The distribution of densities of adult Cladocerans and adult small Diaptomids showed similar trends. Therefore, for chi-square analyses, density categories were formed depending on whether the sample mean of that species (or group) was greater than or less than 5 individuals per liter. For large Diaptomids however, density categories were greater than zero and equal to zero individuals per liter. These categorizations resulted in 2 x 2 tables. Resulting chi-squares were then corrected for continuity since the distribution of chi-square in a 2 x 2 table is discreet (Snedecor and Cochran 1967).

In order to examine potential effects of vertebrate predation on rotifer groups, 27 east slope lakes were grouped according to types of vertebrate predators present (Table 2). These 27 lakes were all those (except for 2 west-slope lakes) for which adequate information existed on presence and density of vertebrate predators. Trout (cutthroat, Onchorhynchus clarkii, and rainbow, O. mykiss) were categorized as non-reproducing or reproducing in each lake. Lakes with reproducing fish generally had a more complex age and size structure, and much higher densities of fish than did lakes with non-reproducing fish (Liss et al. 1995). Other east-slope lakes had salamanders (Ambystoma macrodactylum) as their only vertebrate predators (Liss et al. 1995), and a few lakes had no vertebrate predators.

An overall mean was calculated for each lake for the following rotifer groups or species: illoricated rotifers (soft-bodied and generally larger taxa including Polyarthra, Synchaeta, Asplanchna, and Asplanchnopus species); loricated rotifers (hard-bodied

Table 2. Twenty-seven east-slope lakes grouped according to vertebrate predation category. Kruskal-Wallis tests were used to test for differences between categories in rotifer taxa.

Reproducing Trout Lakes (N = 10)	Non-Reproducing Trout Lakes (N = 6)	Salamanders Only (N=6)	No Vertebrate Predators (N = 5)
Battalion	Coon	Juanita	Greenview
Dagger	Dee Dee, Upper	MR-12	Kettling, Upper
Dee Dee, Lower	MM-11	MR-13-1	Silent, Lower
Doubtful	MR-13-2	MR-2	Silent, Upper
Kettling, Lower	MR-16	MR-3	Waddell, Middle
McAlester	MR-9	Waddell	
Rainbow			
Trapper			
Triplet, Lower			
Triplet, Upper			

taxa including all Brachionids except Keratella cochlearis, as well as Colurella, Lecane, Lepadella, Monostyla, and Trichotria species); Conochilus unicornis; and Keratella cochlearis. The latter taxon is a form distinct from Keratella cochlearis faluta, but it has no form name (R. Stemberger, personal communication). Kruskal-Wallis one-way analyses were run on each of these rotifer groups or species where the classification factor or rank was vertebrate predation category.

RESULTS

Many rotifer taxa were relatively widely distributed. Twenty of the 41 taxa (49%) occurred in more than 10% of the sampled lakes (Table 3), and 12 of these taxa (29%) occurred in more than 25% of sampled lakes. Kellicottia longispina was the most ubiquitous rotifer, occurring in over 90% of sampled lakes. Conochilus unicornis, the second most common species, was found in over 70% of lakes.

Hierarchical agglomerative cluster analysis grouped lakes according to their dominant taxa (Figure 1). Dominance by single taxa was generally high.

Cluster One

Cluster one represented the most common type of rotifer community among lakes in the complex which had overall mean rotifer densities greater than 1.0 per liter (Table 4). The dominant taxon in these lakes was Conochilus unicornis, which had a mean proportional density of 83%. Other taxa occurred at lower proportions. Lakes in this cluster were generally lower elevation lakes and had the highest mean alkalinity and conductivity, pH, and temperature of all clusters (Table 5). These lakes had

Table 3. Percent of 66 lakes in which taxa and proportional abundance of taxa among all lakes in which vertical tows were taken.

Taxon	Percent of Lakes in which Taxon Occurs	Proportional Abundance Among All Lakes
Kellicottia longispina	90.9	0.104
Conochilus unicornis	72.7	0.083
Keratella hiemalis	59.1	0.068
Polyarthra spp.	57.6	0.066
Keratella cochlearis faluta	39.4	0.045
Keratella armadura	37.9	0.043
Monostyla lunaris	33.3	0.038
Ascomorpha ecaudis	33.3	0.038
Lepadella spp.	31.8	0.036
Bdelloidea	30.3	0.035
Collotheca mutabilis	28.8	0.033
Monostyla spp.	25.8	0.029
Synchaeta spp.	22.7	0.026
Lecane flexilis	19.7	0.023
Gastropus spp.	16.7	0.019
Notholca michiganensis	16.7	0.019
Lecane mira	16.7	0.019
Notholca squamula	13.6	0.016
Keratella cochlearis cochlearis	12.1	0.014
Notholca laurentiae	12.1	0.014
Euchlanis spp.	7.6	0.009
Microcodon spp.	7.6	0.009
Colurella obtusa	7.6	0.009
Keratella serrulata curvicornis	6.1	0.007
Trichotria pocillum	4.5	0.005
Cephalodella spp.	4.5	0.005
Asplanchnopus spp.	4.5	0.005
Lecane tudicola	4.5	0.005
Trichocerca longiseta	3.0	0.004
Testudinella parva	3.0	0.004
Lecane luna	3.0	0.004
Keratella ticinensis	3.0	0.004
Keratella taurocephala	3.0	0.004
Filinia spp.	3.0	0.004
Collotheca pelagica	3.0	0.004
Asplanchna spp.	3.0	0.004
Notholca labis	1.5	0.002
Lepadella acuminata	1.5	0.002
Lecane crepida	1.5	0.002
Stephanoceros spp.	1.5	0.002
Lecane tenuiseta	1.5	0.002

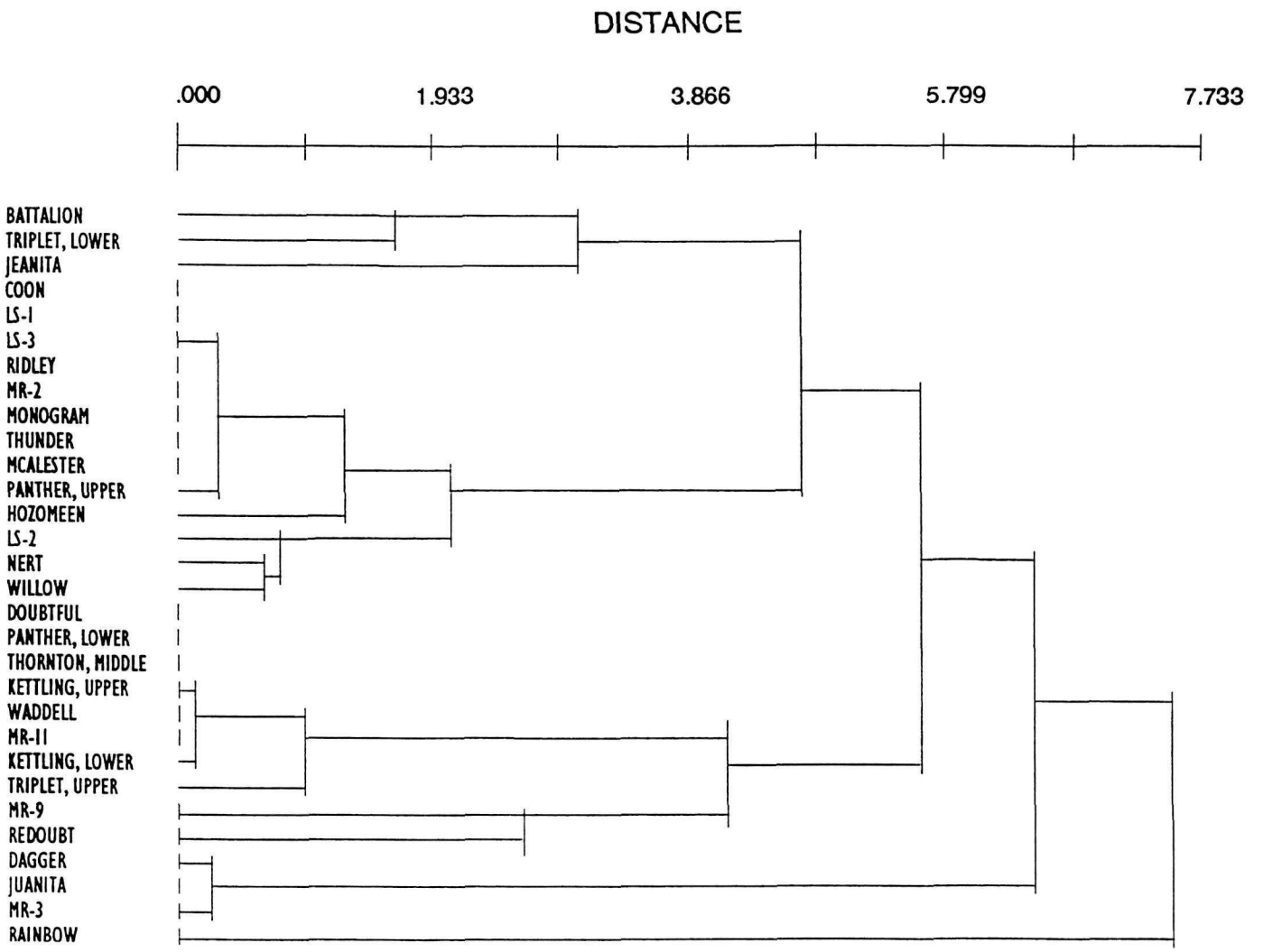


Figure 1. Dandrogram from a hierarchical agglomerative cluster analysis of lakes which had mean rotifer densities > 1.0 per liter (30 lakes).

Table 4. Characteristics of lake clusters: Dominant taxa in each cluster with means of their proportional abundance among lakes in that cluster; other taxa in each cluster which had means of proportional abundance greater than 0.01 per liter. Lakes in each cluster are listed.

Cluster No.	N	Dominant Taxon	Proportional Abundance of Dominant	Other Taxa	Proportional Abundance of Other Taxa	Lakes
1	13	Conochilus unicornis	0.83	Keratella cochlearis faluta	0.06	Coon, Hozomeeen, LS-1, LS-2,
				Polyarthra spp.	0.04	LS-3, McAlester, Monogram,
				Keratella armadura	0.02	MR-2, Nert, Panther (Upper),
				Keratella hiemalis	0.02	Ridley, Thunder, Willow
				Kellicottia longispina	0.01	
				Synchaeta spp.	0.01	
2	8	Kellicottia longispina	0.77	Collotheca mutabilis	0.13	Doubtful, Kettling (Lower and
				Conochilus unicornis	0.09	Upper), MR-11, Panther (Lower),
						Thornton (Middle), Triplet
						(Upper), Waddell
3	3	Keratella cochlearis faluta	0.64	Collotheca mutabilis	0.02	Battalion, Jeanita,
		Polyarthra spp.	0.30	Ascomorpha ecaudis	0.01	Triplet (Lower)
				Kellicottia longispina	0.01	
				Keratella hiemalis	0.01	
4	3	Keratella armadura	0.93	Conochilus unicornis	0.04	Dagger, Juanita, MR-3
				Polyarthra spp.	0.02	
5	2	Keratella hiemalis	0.90	Kellicottia longispina	0.04	MR-9, Redoubt
				Keratella cochlearis faluta	0.03	
				Conochilus unicornis	0.02	
				Polyarthra spp.	0.01	
6	1	Collotheca mutabilis	0.87	Ascomorpha ecaudis	0.12	Rainbow
				Kellicottia longispina	0.01	

Table 5. Means of chemical and physical variables from lakes within each cluster. Asterisks indicate those variables that had statistically significant correlations with ordination axes scores from a detrended correspondence analysis.

Cluster No.	N	Elev.* (m)	Mean Depth (m)	Max. Depth (m)	Surf. Area (ha)	TKN* (mg/l)	Total-P* (mg/l)	Ortho-P* (mg/l)	NO_3 (mg/l)	NH_4 (mg/l)	pH	Alk. HCO_3-C (mg/l)	Cond. (umho/cm)	Temp. * (C)
1	13	1143	3.6	8.7	5.5	0.100	0.009	0.001	0.001	0.008	7.510	5.715	53.850	16.1
2	7	1585	4.6	11.4	3.9	0.040	0.007	0.001	0.008	0.005	7.185	2.820	25.003	12.5
3	2	1780	1.6	3.2	1.8	0.054	0.007	0.002	0.005	0.005	7.309	3.146	26.745	11.9
4	3	1862	1.2	2.2	1.3	0.137	0.014	0.002	0.001	0.007	7.031	2.358	36.109	14.9
5	1	1813	2.9	4.9	1.7	0.032	0.004	0.001	0.002	0.005	6.950	1.375	10.750	11.9
6	1	1717	4.9	10.4	6.3	0.055	0.008	0.001	0.002	0.004	7.033	1.422	11.242	13.8

relatively high mean densities of adult Cladocerans, and large-bodied and small-bodied Diaptomids (Table 6).

Cluster Two

Lakes falling within cluster two were characterized by high proportions of Kellicottia longispina (Table 4), though Collotheca mutabilis and Conochilus unicornis were also relatively abundant, composing on average 13% and 9% of the rotifer communities in these lakes. Lakes in cluster two were deep and had relatively low concentrations of total nitrogen (TKN) and total phosphorus (Total P; Table 5). Although Kellicottia longispina was dominant only in lakes in this cluster, it was present in all other clusters except cluster four (Table 4). Crustacean zooplankton communities in lakes in this cluster were characterized by low densities of adult Daphnids (and Cladocerans in general), relatively high densities of large Diaptomids, and moderately high densities of small Diaptomids (Table 6).

Cluster Three

Lakes in cluster three were dominated by Keratella cochlearis faluta and Polyarthra species (Table 4). Other taxa occurred at very low proportions. Relative to other clusters, lakes in this group tended to lie at higher elevations, and had cooler temperatures though they were also relatively small and shallow. They had intermediate levels of total nitrogen, alkalinity, and conductivity (Table 5). These lakes were characterized by low densities of adult Cladocerans and small and large Diaptomids (Table 6).

Table 6. Means (and ranges) of crustacean zooplankton density from lakes within each cluster. Asterisks indicate those taxa whose proportional abundance had staistically significant correlations with ordination axes scores from a detrended correspondence analysis.

Cluster No.	N	+All Adult Cladocerans		++Adult Daphnids*		Holopedium gibberum*		@Large-bodies Diaptomids*		@@Small-bodied Diaptomids	
1	13	3.94	(0.26 - 10.56)	1.80	(0.05 - 5.23)	0.38	(0.0 - 2.17)	0.38	(0.0 - 2.11)	1.00	(0.0 - 6.97)
2	8	0.42	(0.09 - 1.37)	0.19	(0.0 - 1.08)	0.17	(0.0 - 0.63)	0.36	(0.0 - 0.94)	1.19	(0.0 - 9.29)
3	3	0.12	(0.07 - 0.21)	0.09	(0.0 - 0.21)	0.00	(-)	0.02	(0.0 - 0.04)	0.14	(0.0 - 0.41)
4	3	14.61	(13.21 - 17.31)	9.96	(0.05 - 17.25)	0.10	(0.0 - 0.30)	0.00	(0.0 - 0.0)	27.15	(4.57 - 56.74)
5	2	0.00	(0.0 - 0.003)	0.00	(0.0 - 0.0)	0.00	(-)	0.16	(0.0 - 0.31)	0.36	(0.0 - 0.73)
6	1	2.13	(-)	0.01	(-)	2.10	(-)	0.001	(-)	0.00	(-)

+ Includes primarily Daphnia rosea and Holopedium gibberum, but also others (see Liss et al. 1994).
++ Includes primarily Daphnia rosea, but also D. longiremis, D. middendorffiana, and D. schodleri.
@ Includes primarily Diaptomus kenai, but also D. arcticus, and D. leptopus.
@@ Includes primarily Diaptomus tyrrelli, but also D. lintoni.

Cluster Four

Lakes in cluster four were characterized by very high dominance of Keratella cochlearis (Table 4), with low densities of other taxa. Lakes in this cluster had the highest mean total nitrogen and total phosphorous concentration of all clusters, though alkalinity and conductivity were intermediate (Table 5). These lakes were relatively small and shallow and had relatively high temperatures. Crustacean communities in these lakes were characterized by very high densities of both adult Cladocerans, primarily Daphnids, and adult small Diaptomids, primarily D. tyrrelli, but had no large Diaptomids (Table 6).

Cluster Five

The two lakes in this cluster were characterized by high dominance of Keratella hiemalis (Table 4), with low proportions of other taxa. These lakes had relatively low concentrations of total nitrogen and total phosphorous, low pH, alkalinity, conductivity, and relatively low temperature (Table 5). These lakes also had very low densities of adult Cladocerans, moderate densities of large Diaptomids, and low densities of small Diaptomids (Table 6).

Cluster Six

The one lake in cluster six was characterized by high dominance of Collotheca mutabilis although Ascomorpha ecaudis composed 12% of the total rotifer community (Table 4). This was a relatively large deep lake with low alkalinity and conductivity (Table 5). Diaptomids occurred in the lake at extremely low densities (Table 6). Adult Cladocerans reached moderate densities, but almost all were Holopedium gibberum.

These results were roughly consistent with those obtained with detrended correspondence analysis (DCA) run on species proportional abundance data. Lakes grouped on the first two DCA axes according to their dominant taxa (Figure 2). Statistically significant positive correlations (Pearson product-moment correlation coefficients) were found between the first ordination axis scores and total nitrogen ($r = 0.657$, $p < 0.01$), total phosphorous ($r = 0.529$, $p < 0.01$), and temperature ($r = 0.402$, $p = 0.03$), indicating a tendency of lakes with high axis one scores to have relatively high values of these variables. The second ordination axis correlated positively with elevation ($r = .387$, $p = 0.04$), and orthophosphate (Ortho-P; $r = 0.397$, $p = 0.03$), and correlated negatively with temperature ($r = -0.404$, $p = 0.03$).

Proportional abundance of all Cladocerans was not significantly correlated with first axis scores. This may be partially explained by the fact that the two dominant Cladoceran taxa which are commonly found in these lakes, Daphnids (primarily Daphnia rosea) and Holopedium gibberum, tended to reach high densities in lakes with different physical and chemical characteristics (Liss et al. 1995). While proportional abundance of Daphnids was positively correlated with axis one ($r = 0.373$, $p = 0.05$), proportional abundance of Holopedium gibberum was negatively correlated ($r = -0.477$, $p < 0.01$). Though proportional abundance of all Cladocerans was not significantly correlated with first axis scores, absolute density of all Cladocerans was significantly correlated ($r = 0.711$, $p < 0.01$), probably because Daphnids reached much higher absolute density (maximum overall mean = 17.3 per liter) than Holopedium gibberum (maximum overall mean = 2.2 per liter). Negative correlations were found between first axis scores and proportional abundance of large Diaptomids ($r = -0.436$, $p = 0.02$). Proportional abundance of small Diaptomids was not significantly correlated with axis

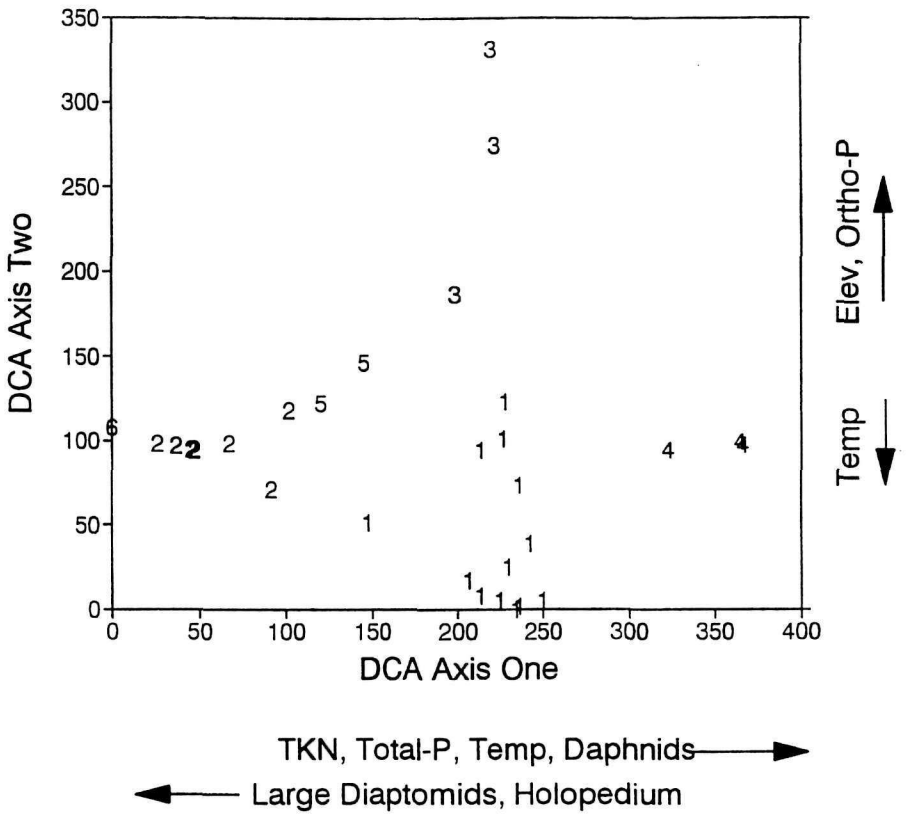


Figure 2. Graph of axis scores for each lake from detrended correspondence analysis. Axis one scores correlated positively with total Kjeldahl nitrogen (TKN), total phosphorous (Total P), temperature, and proportional abundance of adult Daphnids using Pearson product-moment correlation coefficients. Axis one scores correlated negatively with proportional abundance of large Diaptomids and Holopedium gibberum. Axis two scores correlated positively with elevation and ortho-phosphorous (Ortho P), but correlated negatively with temperature. Lakes are numbered according to cluster.

one ($p > 0.10$), though absolute abundance was significantly correlated ($r = 0.438$, $p = 0.016$).

Physical and chemical variables and crustacean zooplankton densities that were significantly correlated with ordination axes showed the same general tendencies with groups of lakes in DCA as in cluster analysis. That is, lakes where Keratella cochlearis dominated (cluster 4) had high axis one scores, high total nitrogen and total phosphorous, tended to have high temperatures, high proportional densities of Daphnids, but no large Diaptomids. Lakes in which Kellicottia longispina dominated (cluster 2) had low first axis scores, low total nitrogen and phosphorous, low proportional densities of Daphnids (but relatively high proportional densities of Holopedium gibberum), and high proportional densities of large Diaptomids. On axis two, lakes in which Keratella cochlearis faluta and Polyarthra dominated (cluster 3) occurred at relatively high elevation and had low temperature. Lakes in which Conochilus unicornis dominated (cluster 1) occurred at relatively low elevation and had high temperatures.

Densities of some rotifers or rotifer groups were related to densities of crustacean zooplankton groups. The density of Kellicottia longispina was related to the density of all adult Cladocerans (chi-square, $p = 0.025$; Figure 3a). When Kellicottia density was low (less than 5 per liter), the number of samples where Cladoceran density was high (greater than 5 per liter) was greater than expected under a random distribution. With high density of Kellicottia, the number of samples with high Cladoceran density was less than expected. A negative relationship is thus suggested (Figure 3a). This corresponds with the relationship between all loricated rotifers

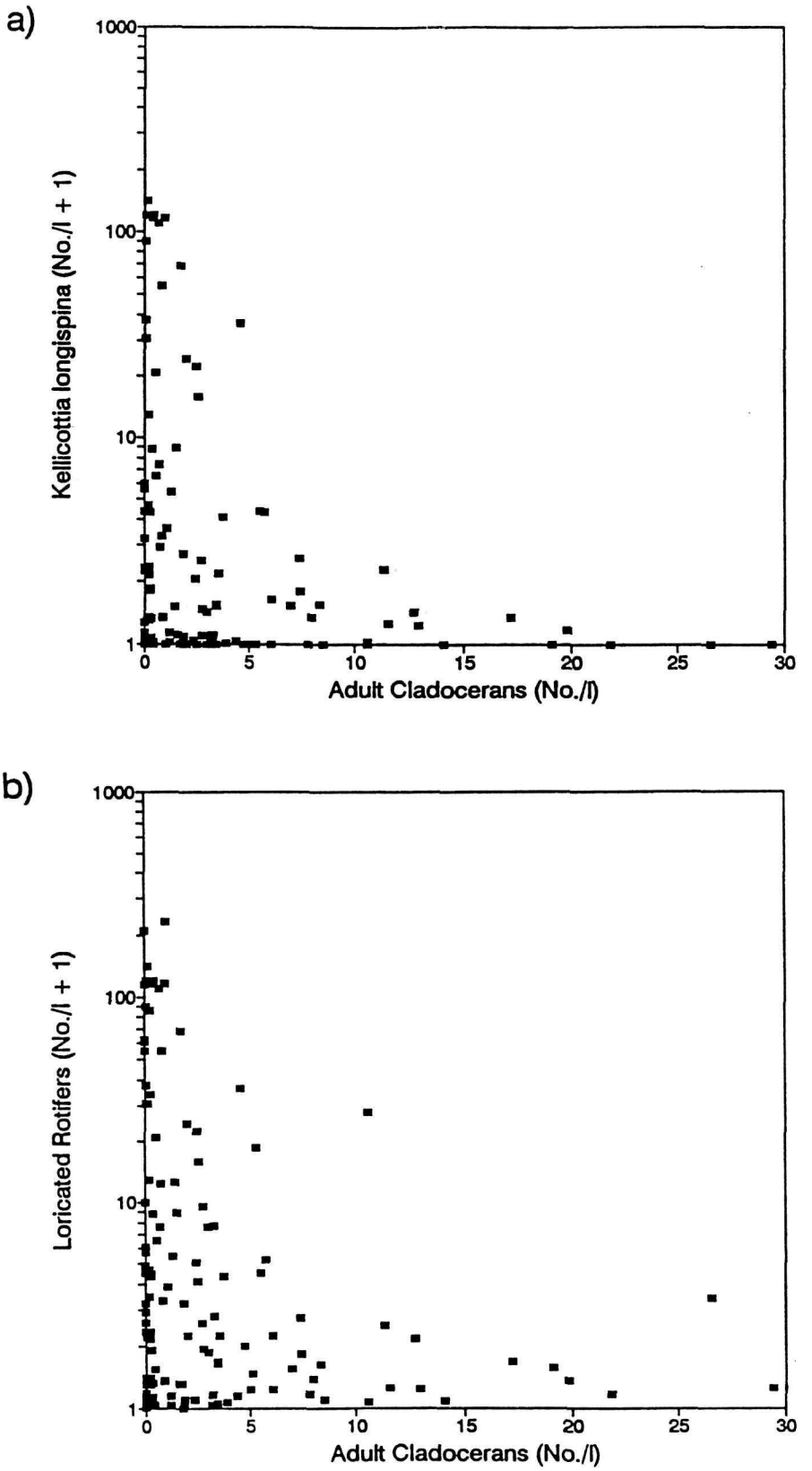


Figure 3. Plot densities (number per liter) of adult Cladocerans against densities of: a) Kellicottia longispina; b) and all loricated rotifers combined. Data used are sample means.

(excluding Keratella cochlearis) and adult Cladocerans (chi-square, p = 0.01; Figure 3b).

The density category of Keratella cochlearis was also related to the density of Cladocerans (chi-square, p = 0.01). However, with high densities of Keratella cochlearis, the number of samples with high densities of Cladocerans was greater than expected. This suggests a positive relationship. In fact, Keratella cochlearis occurred at very high densities (447.0 per liter in Dagger Lake) in lakes where the density of adult Cladocerans was quite high (21.9 per liter). This was the only loricated rotifer which appeared to have a positive relationship to Cladoceran density. Density of adult Diaptomids (either all Diaptomids combined, or large and small Diaptomids tested separately) had no statistically significant effect on loricated rotifers.

Presence of Polyarthra spp. was related to the absence of large Diaptomids (D. kenai and D. arcticus; chi-square, p = 0.05). The two taxa rarely co-occurred. However, density of Polyarthra was not related to density of either small Diaptomids (p > 0.10) or adult Cladocerans (p > 0.10) based on the chi-square statistic.

There was no evidence that density of Conochilus unicornis was related to density of either Diaptomids (p > 0.10; all taxa combined, or large and small Diaptomids tested separately) or Cladocerans (p > .10) based on the chi-square statistic. Conochilus reached very high densities (>100 per liter) with high densities of either Diaptomids or Cladocerans.

Kruskal-Wallis analyses were used to examine potential effects of vertebrate predation on rotifer groups or species. There were statistically significant differences in rotifer densities between vertebrate predation categories only for Conochilus unicornis (p = 0.03; Table 7). When lakes with no vertebrate predators were omitted from this

Table 7. Means (and ranges) of densities (no/l) of rotifer taxa within each vertebrate predation category for twenty-seven east-slope lakes. P-values of Kruskal-Wallis tests are listed.

Rotifer Taxon	Reproducing Trout Lakes	Non-Reproducing Trout Lakes	Lakes with Salamanders Only	Lakes with No Vertebrate Predators	Kruskal-Wallis P Value
Loricated+ Rotifers	13.41 (0.15-69.25)	20.18 (0.05-19.13)	3.16 (0.23-15.25)	0.68 (0.10-2.17)	P = .35
Illoricated Rotifers	3.75 (0.00-23.26)	0.16 (0.00-0.88)	0.16 (0.00-0.73)	0.00 (0.00-0.01)	P = .12
Conochilus unicornis	3.81 (0.00-20.58)	69.15 (0.00-414.34)	49.99 (0.00-299.60)	0.00 (0.00-0.00)	P = .03
Keratella cochlearis	47.24 (0.00-471.50)	0.63 (0.00-3.61)	10.78 (0.00-33.70)	0.03 (0.00-0.15)	P = .06

+The "Loricated Rotifers" category does not include Keratella cochlearis.

analysis, there were no significant differences between the remaining three vertebrate predator categories ($p > 10$). Though there are large differences between the means of vertebrate predation categories for several of the rotifer groups, variability within groups is high (Table 7).

DISCUSSION

Many of the rotifer taxa found in North Cascade lakes are relatively widely distributed (Table 3). This finding is consistent with the view that, world-wide, rotifers are generally widely distributed (Dumont 1983), and that they generally have powerful passive dispersal strategies (Pennak 1978). It also indicates that the rotifer species pool for each lake is large.

In spite of these factors, dominance by single rotifer taxa is generally high in lakes where overall mean rotifer densities are > 1.0 per liter (Table 4). This is consistent with findings by Green (1993) that lakes generally have high single-species dominance.

Dominance of rotifers related to physico-chemical conditions and crustacean zooplankton

Dominance by a particular taxon may be a function of the interaction between physico-chemical conditions and crustacean zooplankton densities. The dominant taxon in 13 lakes (cluster 1) was Conochilus unicornis (Table 4). Dominance by this taxon may be related, in part, to its food preference for bacteria and detritus (Pourriot 1977), both of which may be more abundant in relatively more productive systems (Geller and Muller 1981; Wetzel 1975). Lakes in cluster one had the highest mean

alkalinity and conductivity (Table 5), the latter being one indicator of greater productivity (Berzins and Bertilsson 1989). Lakes in cluster one also had moderately high mean densities of both adult Cladocerans and Diaptomids (Table 6). Perhaps Conochilus unicornis can occur at high densities in lakes where densities of Diaptomids are high because the mucus sheath and the coloniality of Conochilus unicornis protect it from predation by crustacean zooplankton (Stemberger and Gilbert 1987b).

The dominant taxon in 16 of the 30 lakes (clusters 2, 3, 4, and 5) was a small-sized Brachionid rotifer (Kellicottia longispina or a Keratella species; Table 4). In general, Brachionidae are relatively unselective microfiltrators which feed on bacteria, detritus, smaller flagellates and ciliates in the 0.2 to 20 um size range (Pourriot 1977; Arndt 1993; Moore 1978). The microbial systems in ultraoligotrophic and oligotrophic lakes tend to be dominated by plankton in this size range (pico- and nanno-plankton; Pejler 1983; Stockner and Shortreed 1989; Stockner 1987), perhaps because of the ability of these small plankton to efficiently uptake nutrients and grow rapidly at low nutrient concentrations (Stockner 1987).

Although there is variation between clusters of lakes in nutrient levels, alkalinity, and conductivity (Table 5), on a worldwide scale, lakes in the North Cascades National Park Service Complex generally have low nutrients, alkalinity, and conductivity. In fact, the most productive lakes examined would only be classified as oligo-mesotrophic (Liss et al. 1991). Small, microfiltrating rotifers may dominate rotifer communities in many of these lakes because they can feed efficiently on the small microorganisms (Pourriot 1977; Arndt 1993; Moore 1978) which generally occur in ultraoligo- and oligotrophic systems (Pejler 1983; Stockner and Shortreed 1989; Stockner 1987). These microfiltrating rotifer taxa are also relatively small-bodied (100-200 um excluding

posterior spines; Stemberger 1979), and tend to have low threshold food levels (Stemberger and Gilbert 1987a), a factor that would work to their advantage in relatively unproductive lakes. In fact, the rotifer communities in ultraoligo- and oligotrophic mountain and subarctic lakes in western North America are generally dominated by taxa such as Kellicottia longispina and Keratella cochlearis, at least for part of the year (Neill 1984; Anderson 1980; Moore 1978).

Many of the lake clusters dominated by loricated rotifers had relatively high mean densities of Diaptomids (clusters 1,2,4; Table 6). Because they are generally rejected by Diaptomids as food (Williamson 1987), loricated rotifers may occur at high densities in lakes with high Diaptomid densities. The negative relationship suggested between most loricated rotifer taxa and Cladocerans (Figure 3a,b) is consistent with the view that Daphnids specifically, and perhaps medium- to large-bodied Cladocerans in general, are competitively superior to microfiltrating rotifers (Gilbert 1985). In fact, in the clusters dominated by Kellicottia longispina, Keratella cochlearis faluta, or Keratella hiemalis (clusters 2,3,5), densities of Daphnids and total Cladocerans were relatively low (Table 6).

The loricate Keratella cochlearis occurred at high densities in east-slope lakes where densities of both Cladocerans and small Diaptomids were high (cluster 4; Table 6). There is no clear explanation for this co-occurrence with Cladocerans, though one possibility is that Keratella cochlearis may utilize different food sources, or a different portion of the food size spectrum, than either Daphnids or the other dominant loricated rotifers. The potential for greater productivity of these lakes (reflected by higher total nitrogen, total phosphorous, and conductivity) may allow much higher densities of bacterial food resources (Geller and Muller 1981). The positive relationship between

Keratella cochlearis and small Diaptomids is likely related to the fact that small Diaptomids, specifically Diaptomus tyrrelli, reach high densities only in lakes with higher levels of total Kjeldahl nitrogen and phosphorous (Liss et al. 1995).

Rotifers which are grasping feeders or predators (Polyarthra and Synchaeta species) were a significant component of only a few lakes (cluster 3). This may be related, in part, to the generally low productivity of the study lakes. Large microorganisms (the food sources of grasping and predacious rotifer taxa) are not likely to be abundant in ultraoligo- and oligotrophic lakes (Pejler 1983; Stockner 1987). These predacious rotifer taxa are also soft-bodied, and another reason for their general lack of dominance may be the apparent strongly negative effects of predacious large Diaptomids on Polyarthra and other illoricates (Anderson 1980; Williamson 1987) coupled with the general ubiquity of large Diaptomids in these lakes (Liss et al. 1995). Only one cluster of lakes had Polyarthra as a subdominant (cluster 3; Table 4), and these lakes had low mean densities of large Diaptomids (Table 6). Only clusters 4 and 6 had lower densities of large Diaptomids. The one lake in cluster six was relatively unproductive (deep, with low conductivity, and intermediate levels of total nitrogen and total phosphorous; Table 5) perhaps preventing the presence of grasping feeders. Lakes in cluster four all had very high densities of Cladocerans (>20 per liter) as well as high densities of small Diaptomids (>5 per liter). In spite of the lack of statistical significance of the relationship between Polyarthra and either Cladocerans or small Diaptomids, the latter two may have some negative effect on Polyarthra through competition when either crustacean occurs at very high density.

Dominance of rotifers related to categories of vertebrate predation

Lack of any statistically significance relationship between rotifer taxa and vertebrate predators may be related to the small sample sizes and very high standard error of the means. This high standard error could be caused, in part, by sampling lakes too rarely to be assured of determining high points of population density of dominant taxa. However, high standard errors may also result because a classification based only on category of vertebrate predation does not adequately capture the complexity of factors which structure presence and dominance of specific rotifer taxa. Dominance by specific taxa is not only related to density of crustacean zooplankton groups which may be differentially affected by vertebrate predators, but is also likely related to a complex interaction of physical and chemical parameters (nutrient levels, alkalinity, conductivity, temperature regime, lake size and depth) and of the microorganismic community.

CRUSTACEAN ZOOPLANKTON

Crustacean zooplankton are important components of the pelagic community in high mountain lakes. The distribution and abundance of crustacean zooplankton in high elevation lakes is influenced by abiotic factors including temperature (Anderson, 1971; Moore, 1978), lake morphometry (Stoddard, 1987), and lake chemistry (Anderson, 1974; Stoddard, 1987) and biotic factors particularly invertebrate (Sprules, 1972; Dodson, 1974; Giguere, 1979; Neill, 1989) and vertebrate (Sprules, 1972, Dodson, 1974: Giguere, 1979, Anderson, 1980; Stoddard, 1987) predation

We hypothesized that effects of vertebrate predation on crustacean zooplankton would vary along a gradient of increasing predator density with the greatest effects occurring at high vertebrate predator densities. Vertebrate predators may prey selectively on larger species causing the zooplankton to be dominated by smaller-bodied froms (Brooks and Dodson, 1965; Zaret, 1980). The purpose of this section is to examine the relative importance of abiotic conditions and biotic factors including predation by invertebrates, salmanders, and fish in determining the distribution and abundance of crustacean zooplankton in NOCA lakes.

METHODS

Crustacean zooplankton were sampled in 53 lakes from 1989-1993 (Table 1). In each lake, three replicate vertical tows and a horizontal tow were taken with a 20 cm diameter number 25 (64 µm mesh) zooplankton net, except in 1989 when only one vertical tow was taken. The vertical tows were taken near the deepest part of the lake.

Table 1. Aspect (east or west of Cascade crest), vegetation zone (F = forest, S = subalpine, A = alpine), and sampling frequency of lakes used in analysis of crustacean zooplankton.

LAKE	ASPECT	VEG	1989	1990	1991	1992	1993
BATT	E	F	1		2		
BEAR	W	S	1				
BOUK	W	F			1		
COON	E	F	1				1
COPP	W	S	1				
DAGG	E	F				1	2
DEEU	E	S					2
DOUB	E	S	1	2			1
EGG	W	S	1				
EP6	W	S	1	1			
GRVW	E	S	1				1
HOZO	W	F	1		1		
JUAN	E	S	1				2
KETL	E	F					2
LS1	W	F	1	2	3	2	2
LS2	W	F	1	2	3	2	2
LS3	W	F	1		1		
M131	E	S		2	1	2	1
M132	E	2		2	2	2	1
MCAL	E	F	1	1	2	2	1
MM11	E	S	1				1
MONO	W	S	1				
MR11	E	S		2	2	1	2
MR12	E	S					2
MR16	E	S					2
MR2	E	S	1	2			3
MR3	E	S	1	1			2
MR9	E	S	1				2
NERT	W	S	1	1			
PANL	W	F	2	2	3	2	3
PANU	W	F		2	3	2	3
PM53	W	F	1				
PYRA	W	F	2	1	3		3

	ASPECT	VEG	1989	1990	1991	1992	1993
RAIN	E	F	2		3	2	1
REVL	W	S	1				
RIDL	W	F	1				
SKYM	W	F	1		1		
SLTL	E	S					1
SLTU	E	S					1
TAPM	W	S	1	2			
TAPU	W	S	1	2			
TAPW	W	S	1	2			
THRL	W	S	1				
THRM	W	S	1				
THUN	W	F	1	1	3		
TRAP	E	S	1	2			
TRIL	E	S	1	2	1		
TRIU	E	S	1	2	1		
VULC	W	S	1				
WADD	E	F	2		2		3
WADM	E	F			1		2
WILD	W	S	1				
WILL	W	F	1		1		

The net was lowered to within one meter of the lake bottom and towed upward at a rate of about 0.5 m/sec. The horizontal tow was taken by towing the net nearshore with an inflatable boat. In the field, samples were preserved in 5% neutral sugar formalin (Haney and Hall, 1973). In the laboratory, samples were split using a Folsom plankton splitter. The split portion was poured into a settling chamber and left to settle for 24 hours. Organisms were counted using an inverted microscope at 100X magnification. Average body length of adult female zooplantkers of each taxon was measured.

Mean density of adult crustacean zooplankton at each sampling occasion was calculated from the replicate vertical tows. If a lake was sampled more than once per year, mean density for each taxon for each year was calculated. If a lake was sampled over several years, densities were averaged over all sample years. Thus, in each lake, each taxon was represented by a single mean density. Data from the horizontal tows are difficult to accurately quantify and were used only to assess presence of species in a lake.

Methods for sampling abiotic variables [elevation (elev), maximum depth, surface area, water temperature at a depth of one meter, alkalinity, conductivity, pH, total Kjeldahl nitrogen (TKN), nitrate (NO_3), ammonia (NH_3), total phosphorus (TP), and ortho-phosphorus (OP)] were described in previous sections of this report (see Lake Classification and Rotifer section). For each lake, values for each of these variables were averaged first for each year and then over all years that the lake was sampled. Sampling procedures for salamanders were described in the Amphibian section of this report.

Lakes with fish were grouped into two categories: lakes with non-reproducing fish and lakes with reproducing fish. In general, naturally reproducing fish populations

have a more complex size and age structure and higher densities than do non-reproducing fish (see Fish section). Densities of fish > 170 mm length in eight lakes with reproducing fish were estimated by mark-recapture and ranged from 450-600 fish/ha with the exception of MR 16 (92 fish/ha). In lakes without fish reproduction, average density of stocked trout fry from 1976 to 1993 was 179 fish/ha (range 59.8-375 fish/ha; N=37), except for Thunder, Lower Panther, and Upper Panther lakes which are relatively heavily stocked (data provided by Reed Glesne, North Cascades National Park Service Complex, 2105 Highway 20, Sedro Wooley, WA, 98284).

Data Analysis

The relative occurrence of crustacean zooplankton taxa among lakes in NOCA was assessed by determining the proportion of lakes in which each taxon occurred and by calculating niche breadth, B, :

$$B = \exp[-\Sigma(P_{ij}/R_i) \log_e (P_{ij}/R_{ij})$$

where P_{ij} is the proportion of individuals of the i-th species found in the sample from the j-th lake, and R_{ij} is the summation of the proportions of the i-th species over all lakes. The variable B can range from 1, when a species is present in only one lake, to 53 when a species is equally common in all lakes.

Major kinds of crustacean zooplankton communities were identified with hierarchical agglomerative cluster analysis (Ludwig and Reynolds, 1988) based upon the average proportion of each taxon in each lake. The fusion strategy was the unweighted pair-grouping method (group average) and the resemblance measure was the Euclidean distance. Species diversity for each lake cluster was expressed by

Shannon's information measure (Shannon and Weaver, 1949):

$$H = -\Sigma(n_i/N)\log_e(n_i/N)$$

where n_i is the number of organisms belonging to the i-th taxon in a sample of N individuals. Similarity in taxonomic composition among clusters was expressed as Percentage Similarity (Ludwig and Reynolds, 1988):

$$\% \text{ SIM} = \frac{\Sigma\min(p_{ij}, p_{ik})}{\Sigma(p_{ij}+p_{ik})} \times 200$$

where p_{ij} and p_{ik} are the mean proportions of species i in samples belonging to clusters j and k, respectively.

An ordination of the proportional species abundance data was performed using detrended correspondence analysis (DCA, Hill and Gauch, 1980). Principal Components Analysis (Ludwig and Reynolds, 1988) was performed on abiotic variables. To relate variation between lakes along the DCA axes to abiotic variables, DCA axis scores were regressed against the first four principal components (only the first four components has eigenvalues >1.0). A t-test was used to determine if each of the standardized partial regression coefficients was significantly different from zero (α=0.05).

The Wilcoxon rank sum test (Snedecor and Cochran, 1989) was used to determine if lakes with reproducing fish differed statistically from lakes with non-reproducing fish in average densities (no/l) of the copepods Diaptomus kenai and Diaptomus tyrrelli and in average values of each abiotic variable. Relationships among D. kenai and D. tyrrelli and abiotic variables were investigated by determining Pearson Correlation Coefficients and testing the coefficients for significance using a t-test. To investigate patterns of co-occurrence of D. kenai and D. tyrrelli we compared the

proportion of lakes in which the two species co-occurred with the proportion in which they did not co-occur (t-test, Steel and Torrie, 1980, pg. 482).

RESULTS

Crustacean Zooplankton Communities

Crustacean zooplankton communities were agggregated into eight clusters (Figure 1, Table 2). A single species was dominant (> 50% proportional abundance) in each cluster. In some clusters single-species dominance was high (> 80% proportional abundance, clusters I and V). Several subdominant species (> 5% proportional abundance) were usually present in each cluster. Percentage similarity of clusters was low (Table 3), indicating a high degree of uniqueness in taxa composition and proportional abundances among clusters.

Clusters are identified on the ordination in Figure 2. The first four PCA components accounted for 77.5% of the variation among abiotic factors. The first component was an expression of physical variables related to climate and certain chemical variables (Table 4). Temperature, pH, alkalinity, conductivity, and TKN had high positive loadings and elevation had high negative loading with the first component. For the regression of DCA axis 1 scores against PCA components, the standardized partial regression coeefficient (b) of the first component was highly significant (b=0.615, t-test, $P<0.0001$) suggesting that abiotic factors that loaded heavily in this component could explain some of the variation among lake clusters along DCA axis 1 (Figure 2). The second PCA component was an expression of lake size (area, depth) and NO_3 and had a weak but significant negative relationship with DCA axis 1 (b=-0.219, t-test, $P=0.038$). The third component had high positive loadings of NH_3 and OP while the

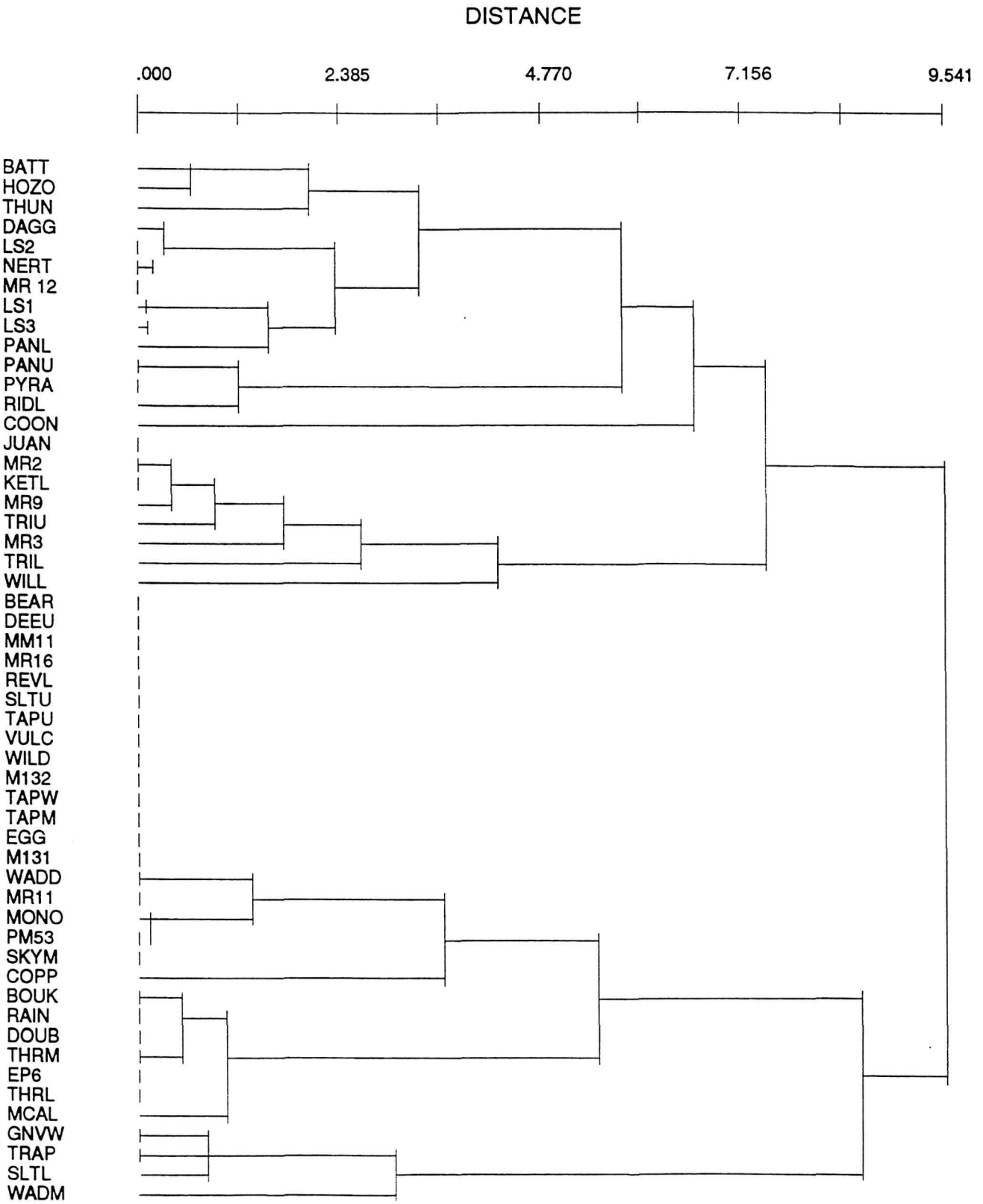


Figure 1. Cluster analysis of 53 lakes based on proportional abundance of crustacean zooplankton species, North Cascades National Park Service Complex.

Table 2. Lake clusters based on proportional abundance of crustacean zooplankton species in North Cascades National Park Service Complex. Dominants are species with ≥ 50% proportional abundance. Subdominants are species with ≥ 5% proportional abundances. Average number of species in each cluster is in parenthesis.

Cluster Type	Number of Lakes	Dominant Species	Average Proportion of Dominant	Subdominant species	Average Proportion of Subdominants	Species Diversity (H)	Lakes	
I	20	Diaptomus kenai	0.89	Holopedium gibberum Daphnia	0.05 0.05	0.52 (2.3)	BEAR MR15-1 MM 11 MR 16 REVL MA2 TAP1 VULC WILD MR 13-2	TAP4 TAP2 EGG MR 13-1 WADD MR11 MONO PM5-3 SKYM COPP
II	10	Daphnia rosea	0.60	Diaptomus kenai Bosmina longirostris Diaphanosoma brachyurum	0.12 0.06 0.05	1.49 (6.7)	BATT HOZO THUN DAGG LS2	NERT MR12 LS1 LS3 PANL
III	7	Holopedium gibberum	0.75	Diaptomus kenai	0.19	0.78 (4.1)	BOUC RAIN DOUB THRM	EP6 THRL MCAL
IV	7	Diaptomus tyrrelli	0.68	Daphnia rosea Cyclopoid copepods Ceriodaphnia quadrangula	0.08 0.06 0.06	1.33 (5.1)	JUAN MR 2 KETT MR 9	TRIU MR 3 TRIL
V	4	Diaptomus arcticus	0.80	Chydorus sphaericus Diaptomus kenai	0.11 0.09	0.66 (2.0)	GNVW TRAP	MA3 WADM
VI	3	Diaphanosoma brachyurum	0.62	Diaptomus kenai Bosmina longirostris Daphnia rosea	0.13 0.11 0.10	1.25 (10.7)	PANU RIDL	PYRA
VII	1	Diaptomus lintoni	0.56	Ceriodaphnia reticulata Daphnia rosea	0.24 0.20	1.03 (4.0)	COON	
VIII	1	Daphnia middendorffiana	0.52	Diaptomus tyrrelli Diaptomus leptopus	0.35 0.13	0.99 (4.0)	WILL	

Table 3. Percentage similarity of lake clusters based on proportional abundance of crustacean zooplankton species in North Cascades National Park Service Complex.

Clusters	I	II	III	IV	V	VI	VII	VIII
I	100.0							
II	17.7	100.0						
III	24.6	21.6	100.0					
IV	4.4	23.2	8.2	100.0				
V	9.4	9.1	8.9	5.7	100.0			
VI	12.9	36.3	15.2	18.3	8.9	100.0		
VII	0.3	19.6	0.5	8.3	0.0	9.9	100.0	
VIII	1.5	4.1	4.1	34.9	0.0	2.4	0.0	100.0

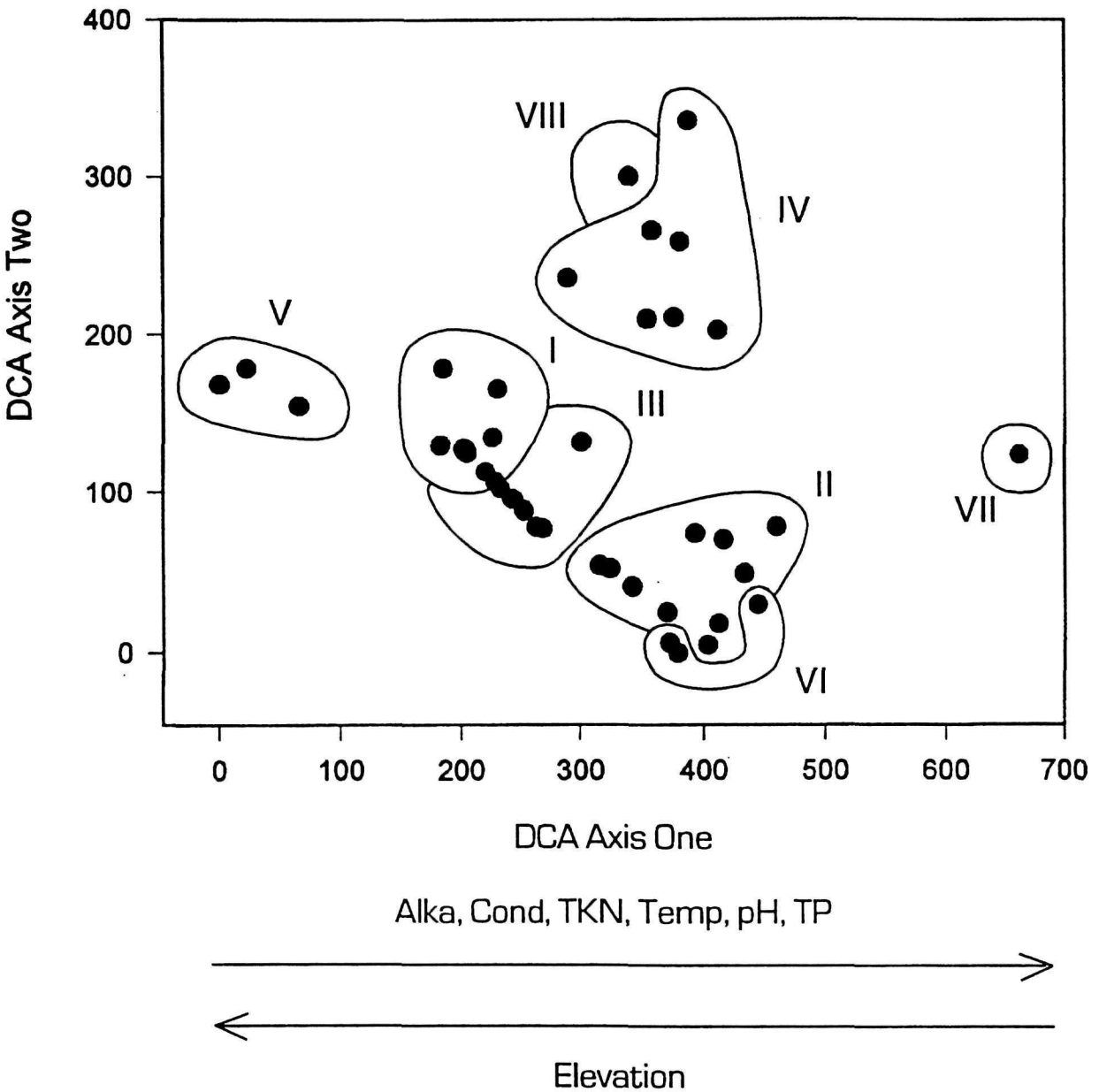


Figure 2. Ordination of lakes based on proportional abundance of crustacean zooplankton species in each lake. Lake clusters (Table 2) are shown. Arrows indicate direction of increase of abiotic variables along axis one.

Table 4. PCA component loadings for each abiotic variable. Heavily-loaded variables in each component are indicated in bold type.

	PCA Components			
Abiotic Variables	1	2	3	4
ELEV	**-0.601**	-0.411	0.269	0.352
AREA	0.048	**0.850**	-0.001	0.168
DEPTH	-0.324	**0.839**	0.026	-0.105
TEMP	**0.798**	-0.020	0.127	-0.218
pH	**0.780**	0.180	0.271	0.243
ALKA	**0.855**	0.250	0.106	0.026
COND	**0.859**	0.232	0.175	0.026
TKN	**0.836**	-0.203	-0.054	0.017
NO_3	-0.384	**0.697**	-0.017	0.334
NH_3	0.400	0.124	**-0.737**	-0.350
TP	**0.715**	-0.199	0.086	0.353
OP	0.172	-0.132	**-0.644**	**0.651**
% of Variance	39.4	19.5	9.8	8.8

fourth component also heavily loaded OP. Neither the third nor the fourth component had a statistically significant relationship with DCA axis 1 (b=-0.142, P=0.174 and b=-0.043, P=0.678, respectively).

None of the first four PCA components was significantly correlated with DCA axis 2. This means that variation along axis 2 cannot be related to the measured abiotic variables.

Cluster I

Cluster I (Table 2) represents the most common type of zooplankton community in the park. Thirty-eight percent of the surveyed lakes occurred in this cluster. This type of community is dominated by Diaptomus kenai, one of the largest diaptomid copepods (Table 5) and the most ubiquitous zooplankter in NOCA (Table 6). Proportional abundance of D. kenai is high (0.89) in these lakes and species diversity is low (H=0.52). Forty-five percent of the lakes in this cluster contained only D. kenai. The next most common species was Holopedium gibberum, followed by two species of Daphnia, D. pulex and D. middendorffiana. These species are the largest daphnids in the park but they are relatively uncommon (Table 6).

Most lakes in this cluster are relatively high elevation lakes. Ninety percent of the lakes occur in the alpine or subalpine vegetation zone on both the east and westslope of the Cascade range. Communities in these lakes are most similar to those in cluster III (Table 3), which is dominated by H. gibberum with D. kenai as the major subdominant species.

Table 5. Average length of crustacean zooplankton species and the number of individuals measured (N) in North Cascades National Park Service Complex.

Species	Average Length	N
Diaptomus arcticus	2.042	48
Diaptomus kenai	1.882	978
Diaptomus leptopus	1.808	13
Daphnia middendorffiana	1.800	17
Daphnia schodleri	1.554	24
Daphnia pulex	1.500	20
Diaptomus lintoni	1.470	20
Daphnia rosea	1.349	472
Diaptomus tyrrelli	1.176	236
Paracyclops fimbriatus	1.175	4
Holopedium gibberum	0.992	87
Cyclops vernalis	0.927	11
Orthocyclops modestus	0.871	7
Macrocyclops fuscus	0.770	10
Diaphanosoma brachyurum	0.769	146
Polyphemus pediculus	0.765	66
Ceriodaphnia quadrangula	0.761	62
Ceriodaphnia reticulata	0.761	18
Schapholeberis kingi	0.634	35
Alona affinis	0.600	10
Bosmina longirostris	0.355	138
Alona guttata	0.320	10
Alonella nana	0.300	9
Chydorus sphaericus	0.280	35

Table 6. Relative occurrence of crustacean zooplankton taxa in 53 lakes in North Cascades National Park Service Complex.

Taxon	Proportion of Lakes	Ubiquity Index
Diaptomus kenai	0.79	28.9
Daphnia rosea	0.45	14.3
Holopedium gibberum	0.34	11.5
Chydorus sphaericus	0.32	2.7
Diaptomus tyrrelli	0.30	10.4
Diaphanosoma brachyurum	0.25	5.3
Polyphemus pediculus	0.21	4.3
Bosmina longirostris	0.17	4.8
Macrocyclops fuscus	0.15	2.6
Alona guttata	0.13	4.8
Macrocyclops sp.	0.13	1.7
Diaptomus arcticus	0.11	4.7
Alona affinis	0.11	3.3
Ceriodaphnia quadrangula	0.11	2.4
Chydorus sp.	0.09	1.5
Eucyclops agilis	0.09	1.2
Daphnia middendorffiana	0.08	2.5
Cyclops sp.	0.08	2.1
Scapholeberis kingi	0.08	1.3
Ceriodaphnia sp.	0.06	1.8
Alonella nana	0.06	1.6
Diaptomus leptopus	0.06	1.3
Eucyclops sp.	0.04	1.8
Streblocerus serricaudatus	0.04	1.5
Cyclops vernalis	0.04	1.4
Daphnia pulex	0.04	1.2
Ceriodaphnia reticulata	0.04	1.0
Alona exisa	0.02	1.0
Alona/Alonella sp.	0.02	1.0
Ceriodaphnia affinis	0.02	1.0
Daphnia longiremis	0.02	1.0
Daphnia schodleri	0.02	1.0
Diaptomus lintoni	0.02	1.0
Orthocyclops modestus	0.02	1.0
Paracyclops fimbriatus	0.02	1.0

Lakes in this cluster are relatively deep and are characterized by low temperature, alkalinity, conductivity, TKN, and TP (Table 7). They appear to be relatively low productivity lakes.

Cluster II

Cluster II represents another common type of community (Table 2). Lakes in this cluster are dominated by Daphnia rosea, the most common daphnid and second most-common zooplankter in NOCA (Table 6). Diaptomus kenai is the major subdominant, but two species of cladocerans are also relatively common subdominants. Species diversity is the highest of all clusters (H=1.49).

Lakes in this cluster are mid-elevation lakes, although the lowest elevation lake in the park, Thunder Lake, occurs in the cluster. Ninety percent of the lakes occur in the forest zone. Temperature, alkalinity, conductivity, TKN, and TP are moderate relative to other clusters and nitrate concentration is low (Table 7). Lakes in cluster II are most similar to those in cluster VI. Both clusters have relatively high proportions of D. kenai and D. rosea.

Cluster III

This cluster is composed of large, deep, relatively high elevation lakes dominated by H. gibberum (Table 2). Holopedium gibberum is the third most-common crustacean zooplankton species among the surveyed lakes (Table 6). The subdominant species, D. kenai, maintains high relative abundance in these lakes. Lakes in this cluster are subalpine or high elevation forest lakes. Like cluster I, species diversity is low (H=0.78).

Table 7. Chemical and physical properties of lake clusters.

Cluster	Elev (m)	Depth (m)	Area (ha)	Temp (°C)	pH	Alka (mg/l)	Cond. (µmho/cm)	TKN (mg/l)	NO_3 (mg/l)	TP (mg/l)
I	1699	12.1	2.6	11.98	6.75	1.18	10.50	0.029	0.005	0.005
II	1283	6.4	5.2	14.92	7.48	4.76	48.55	0.091	0.001	0.007
III	1509	18.6	8.6	10.87	6.67	1.02	8.61	0.031	0.009	0.004
IV	1879	3.2	1.2	14.49	7.14	2.20	25.61	0.082	0.005	0.011
V	1655	26.6	19.4	12.28	7.19	2.10	20.41	0.032	0.009	0.007
VI	930	7.2	1.6	16.10	7.84	10.38	83.04	0.130	0.001	0.010
VII	662	5.4	8.2	18.80	7.30	3.03	24.97	0.149	0.001	0.014
VIII	870	3.7	8.2	18.90	8.05	11.43	105.45	0.099	0.001	0.015

Lakes with H. gibberum and D. kenai as major co-occuring species are somewhat more common than indicated by cluster analysis. Cluster III is most similar to cluster I (Table 3), where D. kenai is the dominant species. Lakes with both species were placed in cluster I or III depending on the proportion of each of the two species. For nine of the 53 lakes (17%), the sum of the proportions of the two species was ≥ 0.90. Two of these lakes (PM 5-3 and M. Skymo) were placed in cluster I rather than III because the relative abundance of D. kenai was greater than H. gibberum.

The lakes in this cluster are characterized by high nitrate, but low temperature, alkalinity, conductivity, TKN, and TP and, like lakes in cluster I, they may be relatively less productive than lakes in other clusters.

Cluster IV

Lakes in this cluster (Table 2) are small, shallow, high elevation eastslope lakes (Table 7) dominated by the small-bodied diaptomid copepod Diaptomus tyrrelli (Table 5). Diaptomus tyrrelli maintains high densities in many of these lakes. Lakes in this cluster are either subalpine (6 lakes) or high elevation forest lakes. This is the only community type where cyclopoid copepods are relatively common. Chydorus sphaericus and the cladoceran predator Polyphemus pediculus are present in low abundance in a relatively large number of lakes. Dagger Lake maintains a high density of D. tyrrelli but was placed in cluster II rather than IV because the relative proportion of D. rosea (0.71) is greater than the proportion of D. tyrrelli. Species diversity in cluster IV is relatively high (H=1.33). Lakes in this cluster are characterized by moderate temperature, alkalinity, conductivity, TKN and high TP relative to other clusters (Table 7).

Cluster V

This cluster (Table 2), composed of only four lakes, is dominated by the copepod Diaptomus arcticus, the largest zooplankter in the park (Table 5). Proportional abundance of D. arcticus in these lakes is high (0.80). All lakes in this cluster are eastslope subalpine lakes. In NOCA, D. arcticus is relatively uncommon (Table 6) and was found in only 11% of surveyed lakes. Chydorus sphaericus and D. kenai are subdominant species. Like lakes in clusters I and III, species diversity is low (H=0.66).

Lakes in cluster V are large, deep (except M. Waddell) high elevation lakes (Table 7). The lakes are characterized by moderate temperature, alkalinity, conductivity, and TP, low TKN, and high concentrations of NO_3.

Cluster VI

This cluster is composed of three low elevation westslope forest lakes (Table 2 and 7). The lakes are dominated by the cladoceran Diaphanosoma brachyurum. Subdominant species, D. kenai, D. rosea, and Bosmina longirostris, are present in relatively high proportions. Cluster VI is most similar to cluster II (Figure 2, Table 3). The two clusters have the same species in common but the species differ in relative proportions between the clusters (Table 2). Cluster VI is characterized by relatively high temperature, conductivity, alkalinity, TKN, and TP (Table 7).

Clusters VII and VIII

These two clusters are each composed of a single low elevation forest lake (Tables 2 and 7). Cluster VII is an eastslope lake dominated by the large copepod Diaptomus lintoni. This copepod is extremely rare in NOCA high lakes (Table 2). It was

found only in Coon Lake. Cluster VIII is a westslope lake dominated by the large daphnid, Daphnia middendorfianna (Table 5). Lakes in these two clusters may be some of the most productive lakes in NOCA. The two clusters have the highest average water temperature and TP of all lake clusters in NOCA (Table 7). TKN is also relatively high in both clusters. Cluster VIII has the highest alkalinity and conductivity of all clusters.

Patterns of Co-Occurrence of Vertebrate Predators and Crustacean Zooplankton

Distribution of Diaptomid Copepods

Five species of diaptomid copepods were found in NOCA. Three of these species, D. kenai, D. arcticus, and D. tyrrelli, are relatively common (Table 6). The other species, D. lintoni and D. leptopus, were found only in low elevation lakes. Diaptomus kenai and D. arcticus are the largest zooplankters in NOCA (Table 5) and are likely to be predacious (Zaret, 1980; Anderson, 1967, 1970, 1972). Diaptomus tyrrelli is a relatively small herbivorous copepod.

Diaptomus kenai is found in lakes at all elevations on both the east and westslope of NOCA (Table 8). In high elevation eastslope lakes, (>1600 m), D. kenai co-occurred with D.arcticus in four of the five lakes in which D. arcticus was found (Table 8). However, in eastslope lakes, neither large copepod commonly co-occurred with the small diaptomid, D. tyrrelli. In contrast, in low elevation westslope lakes, D. kenai and D. tyrrelli commonly co-occurred (Table 8).

Abiotic Factors and Invertebrate Predation

Abiotic factors may affect distribution and co-occurrence of large and small diaptomids. The density (no/l) of D. kenai was not significantly correlated with any of the

Table 8. Distribution of adult diaptomid copepods in North Cascades National Park Service Complex, 1989-1993. Based on vertical and horizontal net tows.

Lake	Elev(M)	Veg Zone	D. kenai	D. arcticus	D. tyrrelli	Other
Silver	2063	A	X			
L. Silent	2044	SA	X			
MR 12	1981	SE	X			
MM 11	1974	SE	X			
Dee Dee	1922	SE	X			
MR 16	1908	SE	X			
MR 11	1863	SE	X			
MR 13-2	1789	SE	X			
Bear	1769	SW	X			
U. Tapto	1755	SW	X			
M. Tapto	1754	SW	X			
W. Tapto	1754	SW	X			
Rainbow	1717	HFE	X			
Sweet Pea	1687	HFW	X			
Doubtful	1642	SE	X			
U. Skymo	1610	A	X			
M. Skymo	1609	SW	X			
Egg	1604	SW	X			
Copper	1601	SW	X			
Vulcan	1583	SW	X			
MP 8	1566	A	X			
EP 6	1566	SW	X			
L. Reveille	1528	SW	X			
Waddell	1504	HFE	X			
Wild	1488	SW	X			
M. Thorton	1427	SW	X			
Nert	1388	HFW	X			
PM 5-3	1382	HFW	X			
Moraine	1378	A	X			
LS 3	1365	SW	X			
L. Thornton	1357	HFW	X			
Monogram	1270	SW	X			
LS 2	1243	HFW	X			
Bouck	1174	HFW	X			
U. Silent	2127	A	X	X		
MR 13-1	1800	SE	X	X		
Greenview	1664	SE		X		
M. Waddell	1642	SE	X	X		
Trapper	1270	SE	X	X		
Juanita	2033	SE			X	
Triplet Pond	2013	SE			X	
U. Triplet	1988	SE			X	
L. Triplet	1931	SE	X		X	
MR 2	1873	SE			X	
MR 3	1873	SE			X	
MR 9	1813	SE	X	X	X	
McAlester	1680	HFE	X		X	
Dagger	1679	HFE			X	
Kettling	1639	HFE			X	
LS 1	1241	HFW	X		X	
U. Panther	1031	LFW	X		X	
L. Panther	1031	LFW	X		X	
Ridley	958	LFW	X			X
Willow	870	LFW			X	X
Hozomeen	861	LFW	X		X	
Pyramid	802	LFW	X		X	
Coon	662	LFE				X
Thunder	412	LFW	X		X	X

measured abiotic variables (Table 9). The lack of correlation of D. kenai density with abiotic factors reflects the ability of this species to tolerate a relatively wide range of abiotic conditions in NOCA, which in part accounts for its status as the most ubiquitous crustacean zooplankter in high mountain lakes in the Complex (Table 6).

While density of D. kenai was not significantly correlated with any abiotic variable, density of D. tyrrelli had significant positive correlations with both TKN and TP (Table 9). Furthermore, many of the other abiotic variables were significantly correlated with TKN and TP (Table 10). In particular, TKN and TP were negatively related to lake depth.

Patterns of co-occurrence of D. kenai and D. tyrrelli are related to TKN, TP, and lake depth. Lakes where D. tyrrelli was allopatric or sympatric with D. kenai were relatively shallow lakes with moderate to high TKN (>≈ 0.03 mg/l) and TP (>≈0.004 mg/l) (Figures 3 and 4). Diaptomus kenai occurred, either allopatrically or sympatrically with D. tyrrelli, over the entire range of lake depths and concentrations of TKN (Figure 3), but was absent from lakes with very high TP (TP>≈0.11, Figure 4).

Although the densities of D.kenai and D. tyrrelli were not significantly correlated with water temperature (possibly due to reduced densities of both species at the extremes of their temperature ranges), the two species may differ in temperature tolerance. Diaptomus kenai rarely occurred in lakes with an average water temperature over 15-16°C (Table 11). It occurred at very low densities in Thunder Lake (21°C) in late spring before the water warmed. It was not found in this lake over the summer. Diaptomus kenai density was low in Hozomeen Lake (0.03/l, 17.5°C), however, this lake also supports reproducing trout. Diaptomus kenai was found only in horizontal tows in Ridley Lake (17.9°C), indicating that its density in this lake is very low

Table 9. Pearson correlation coefficients and associated P-values (in parenthesis) between densities of D. kenai, D. tyrrelli, D. rosea and H. gibberum and selected environmental variables for all lake samples.

Variable	D. kenai	D. tyrrelli	D. rosea	H. gibberum
Elevation	0.74	0.225	0.035	-0.038
	(0.595)	(0.106)	(0.804)	(0.785)
Area	-0.218	-0.100	-0.088	<0.001
	(0.116)	(0.478)	(0.529)	(1.000)
Depth	-0.117	-0.181	-0.209	-0.012
	(0.405)	(0.195)	(0.133)	(0.933)
Temp	0.016	0.196	0.233	-0.002
	(0.909)	(0.159)	(0.993)	(0.991)
pH	-0.056	-0.050	0.143	-0.097
	(0.693)	(0.723)	(0.309)	(0.488)
Alkalinity	-0.134	-0.068	0.059	-0.150
	(0.339)	(0.629)	(0.675)	(0.285)
Conductivity	-0.149	0.113	0.217	-0.085
	(0.287)	(0.419)	(0.119)	(0.547)
TKN-N	-0.128	0.352*	0.524*	-0.017
	(0.360)	(0.010)	(<0.001)	(0.905)
NO_3-N	-0.211	-0.121	-0.180	-0.052
	(0.130)	(0.390)	(0.200)	(0.712)
NH_3-N	-0.126	0.002	0.032	-0.108
	(0.370)	(0.988)	(0.819)	(0.444)
TP	-0.005	0.529*	0.557*	-0.021
	(0.972)	(<0.001)	(<0.001)	(0.880)

*Statistically significant correlations

Table 10. Pearson correlation coefficients and associated p-values (in parentheses) between TKN and TP and selected environmental variables for all lake samples.

Variables	TKN	TP
Elevation	-0.355 (0.009)	-0.131 (0.351)
Depth	-0.388 (0.004)	-0.375 (0.006)
Temp	0.607 (<0.001)	0.529 (<0.001)
pH	0.546 (<0.001)	0.532 (<0.001)
Alk	0.579 (<0.001)	0.435 (<0.001)
Cond	0.587 (<0.001)	0.484 (<0.001)
TKN	—	0.736 (<0.001)
NO^3	-0.370 (0.006)	-0.218 (0.117)
NH^3	0.396 (0.003)	0.191 (0.170)
TP	0.736 (<0.001)	---
OP-P	0.221 (0.112)	0.333 (0.015)

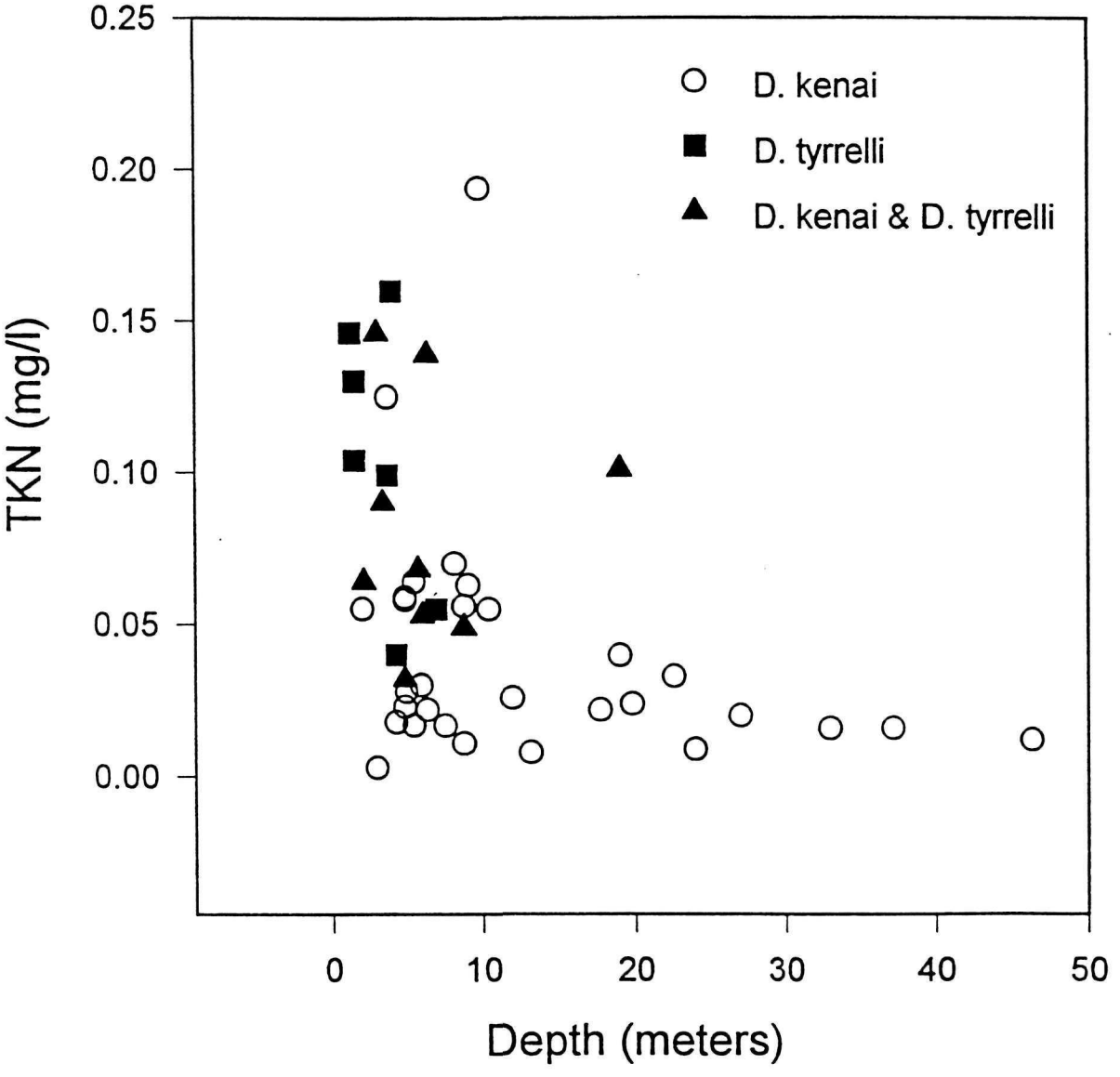


Figure 3. Relationship between the concentration of Kjeldahl nitrogen and lake depth relative to the occurrence of *D. kenai, D. tyrrelli,* and lakes inhabited by both species.

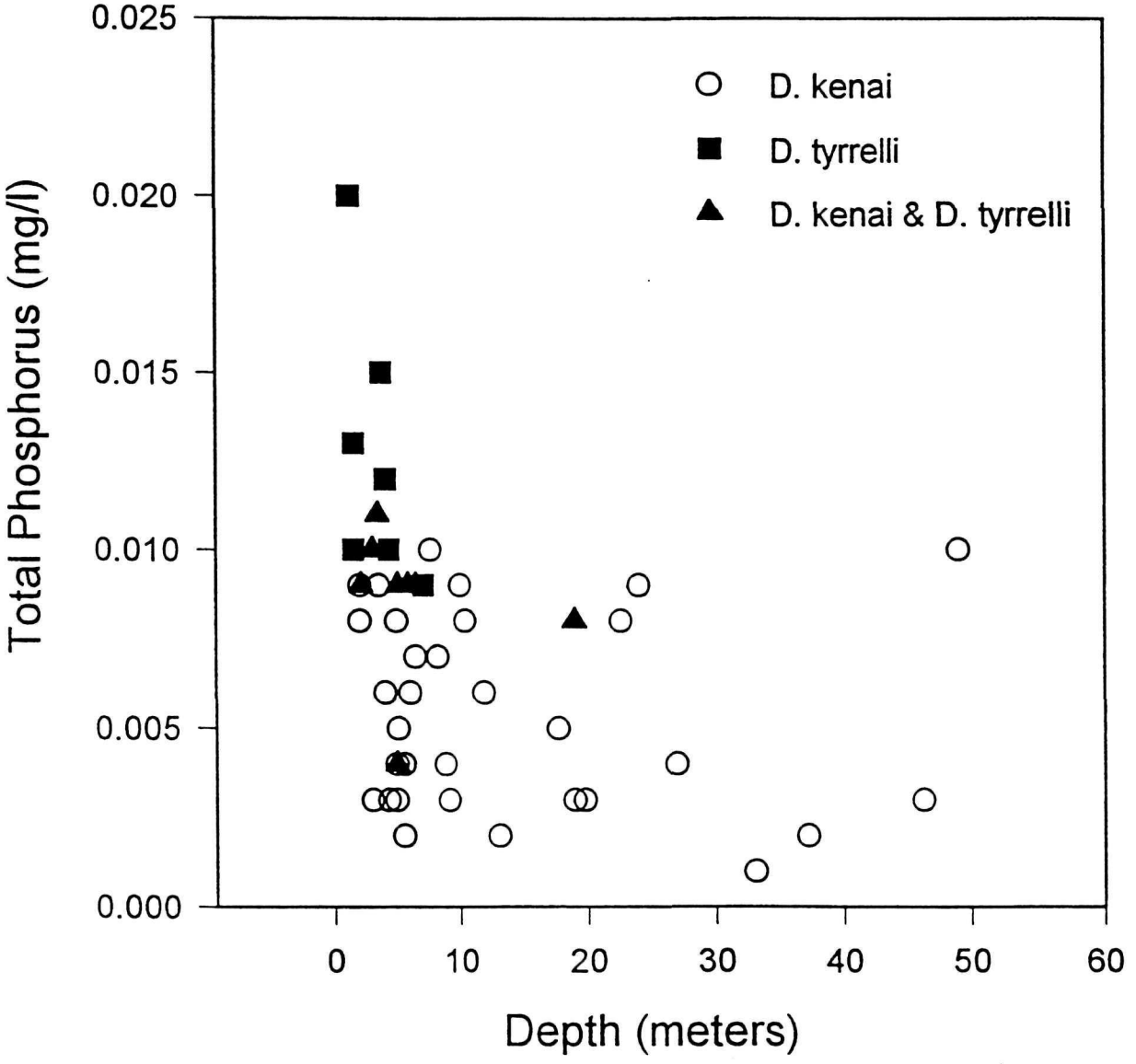


Figure 4. Relationship between the concentration of total phosphorus and lake depth relative to the occurrences of *D. kenai*, *D. tyrrelli*, and lakes inhabited by both species.

Table 11. Average temperatures of D. tyrrelli lakes, and lakes inhabited by D. tyrrelli and D. kenai, and the temperature range of D. kenai lakes.

Lake	Temperature °C
D. tyrrelli Lakes	
Dagger	11.9
Juanita	19.7
Lower Kettling	16.1
MR2	16.9
MR3	16.9
Upper Triplet	11.4
Willow	19.5
D. kenai and *D. tyrrelli* Lakes	
Hozomeen	17.5
LS1	14.8
McAlester	12.5
MR9	13.3
Lower Panther	15.5
Upper Panther	15.8
Pyramid	14.9
Thunder	21.0
Lower Triplet	12.0
D. kenai Lakes	
31 Lakes (w/o Ridley)*	6.3-15.9

*Ridley Lakes = 17.9°C

(<0.001/l). In Figure 4, the two lakes with the highest TP concentrations are both very warm (Juanita, 19.7°C; Willow, 19.5°C). Perhaps D. kenai does not occur in these lakes because of their high temperature.

In contrast to D. kenai, Diaptomus tyrrelli is able to maintain high densities in lakes with relatively high water temperatures (e.g., Juanita, Lower Kettling, MR 2, MR 3) (Table 11). Thus, D. tyrrelli may be capable of tolerating somewhat warmer water than D. kenai, while D. kenai (and D. arcticus) may be able to withstand colder water than D. tyrrelli. However, there is considerable overlap in the temperature ranges of all these species (Table 11).

Abiotic factors alone are insufficient to completely explain the distribution and abundance of D. tyrrelli. Of the 27 lakes with abiotic conditions within the range that D. tyrrelli occurs, the small copepod is absent from 11 lakes (40%; absent from 38% if the lower limit of TP=0.007; Table 12). Seven of the 11 lakes are high elevation eastslope lakes.

Perhaps predation on the small copepod by large copepods, particularly the ubiquitous D. kenai, may be responsible, in part, for absence of D. tyrrelli from some of the lakes with abiotic conditions apparently favorable for this species. Diaptomus tyrrelli maintains higher densities when it is allopatric than when it co-occurs with large copepods (Table 12). Most of the lakes where the small copepod is allopatric are high elevation eastslope lakes. In these lakes, the density of large copepods was lower in lakes where they co-occurred with D. tyrrelli than in lakes where they were allopatric (Table 12), possibly suggesting that the smaller copepod is able to colonize and increase in density when the density of larger copepods is reduced.

Table 12. Density of D. tyrrelli and large copepods in lakes where TKN ≥ 0.04, TP ≥ 0.004, and temp ≥ 11.4°C.

		D. tyrrelli Absent	D. tyrrelli Allopatric	D. tyrrelli Sympatric
Large copepod density				
	Eastslope	1.15 (0.00-2.42)	0.00	0.18 (0.01-0.32)
	Westslope	0.36 (0.09-0.81)	0.00	1.06 (0.03-2.11)
	All Lakes	0.88 (0.00-2.42)	0.00	0.75 (0.01-2.11)
D. tyrrelli density				
	Eastlope	0.00	7.95 (0.13-20.14)	0.73 (0.41-0.95)
	Westlope	0.00	2.04	0.17 (0.11-0.36)
	All Lakes	0.00	2.64 (0.13-20.14)	0.27 (0.001-0.95)
N	Eastlope	7	6	3
	Westslope	4	1	6
	All Lakes	11	7	9

Although co-occurrence of the two species was common in low elevation westslope lakes, in lakes where the two species were sympatric, D. kenai maintained higher densities than did D. tyrrelli (Table 12). In the only low elevation lake where it was allopatric (Willow Lake), D. tyrrelli density was considerably higher than in low elevation lakes where it was sympatric with D. kenai. Thus, although the two species are capable of co-occurring in low elevation westslope lakes, D. kenai may still depress the density of D. tyrrelli density.

Vertebrate Predators

At present, analysis of the potential effects of vertebrate predators has been conducted only for eastslope lakes. Vertebrate predators are common in eastslope lakes. Of 26 lakes surveyed for vertebrate predators (see Fish and Amphibian sections), 21 supported either fish or salamander (A. macrodactylum) larvae (Table 13). In lakes with fish, larval salamander densities were very low. In some fishless lakes, salamander larvae were very abundant.

A few lakes had no vertebrate predators. The reason salamanders are absent in these lakes is not yet clear. Most of the lakes lacking salamanders are relatively cold. Two lakes, Upper and Lower Silent, are the highest elevation lakes on the eastslope in NOCA, occurring at over 2000 m. Their watersheds, and that of Greenview, the coldest lake without vertebrate predators (9.1°C), are almost entirely rock and snow and may be unfavorable habitat for metamorphosed A. macrodactylum.

Both D. kenai, a large copepod, and D. middendorfianna, the largest daphnid in NOCA occur in lakes with low densities of salamander larvae (Table 14). In contrast the small copepod, D. tyrrelli, and small cladocerans occur in lakes where larval

Table 13. Vertebrate predators in eastslope lakes, North Cascades National Park Service Complex, 1989-1993.

Lake	Trout*	A. macrodactylum**	No Vertebrate Predators
Battalion	RB	0.0	
Coon	CT	2.1	
Dagger	CT	0.0	
Dee Dee	RB	0.0	
Doubtful	CT	0.0	
Kettling	RB	0.4	
MR 13-2	RB	0.2	
McAlester	CT	0.1	
MM 11	RB	0.0	
MR 16	CT	1.2	
MR 9	CT/RB	0.6	
Rainbow	RB	0.3	
L. Triplet	CT	0.0	
U. Triplet	CT	0.0	
MR 11	RB	13.1	
Juanita		5.0	
MR 13-1		36.6	
MR 2		65.9	
MR 3		28.5	
MR 12		63.9	
Waddell		2.8	
Greenview			X
U. Kettling			X
L. Silent			X
U. Silent			X
M. Waddell			X

* CT = cutthroat trout, RB = rainbow trout

** number of larvae/100 m shoreline determined by snorkel survey (see Amphibian section for sampling technique).

Table 14. Body length of crustacean zooplankton taxa and density of larval salamanders (A. macrodactylum) in fishless eastslope lakes, North Cascades National Park Service Complex

Lake	Larval Density (No/100 m)	Diaptomid Copepod Present	Copepod Body Length (mm)	Dominant Cladoceran Present	Cladoceran Body Length (mm)
MR 2	73.0	D. tyrrelli	1.11	D. rosea	1.19
MR 3	18.3	D. tyrrelli	1.00	C. quadrangula	0.78
MR 13-1	19.8	D. arcticus	1.53	D. brachyurum	0.77
				C. sphaericus	0.34
Waddell	2.2	D. kenai	1.96	D. middendorffiana	1.80
				H. Gibberum	0.99
MR 11*	2.2	D. kenai	2.56	D. middendorffiana	2.25

*1990, prior to stocking fish

salamander density is high. However, there are important exceptions to the putative association of small-bodied crustaceans with high densities of larval salamanders. D. tyrrelli occurs in Juanita Lake (Table 8) but larval salamander density in this lake in 1993 was relatively low (Table 13). Although Juanita occurs at high elevation (2033 m), it is a shallow lake perched on a ridgeline and water temperature can be rather high (19.7°C), perhaps excluding D. kenai and allowing D. tyrrelli to successfully colonize. In MR 12, salamander density is very high (Table 12), but D. kenai is present, although at relatively low density (0.27/l). Further analysis of the relationship of crustacean zooplankton and salamander larvae is necessary.

Examination of the effects of fish predation on large copepods in eastslope lakes is hindered by the scarcity of lakes with no vertebrate predators (Table 13). Adult copepods were found in three of the five eastslope lakes without vertebrate predators.

The copepods in these lake were all large-bodied species but their densities were low. At this point in our analysis it is not clear why densities of large copepods are low in these lakes, however, low water temperature may be a factor.

The density of large copepods in lakes with reproducing fish was significantly lower than in lakes with non-reproducing fish (Table 15, Wilcoxon test, P=0.01). When MR 16, a lake with a low density of reproducing fish, was omitted from the reproducing trout category and added to the non-reproducing trout group (essentially resulting incomparison of copepod densities between lakes with high and low fish densities), the difference in large copepod densities between lakes with reproducing fish (excluding MR 16) and the group of lakes including non-reproducing fish and MR 16 was highly significant (P<0.001).

Table 15. Densities (no/l) of adult copepods Diaptomus kenai and Diaptomus tyrrelli in eastslope lakes with reproducing trout, non-reproducing trout, and no vertebrate predators.

Reproducing Trout			Non-reproducing Trout			No Vertebrate Predation		
Lake	D. kenai	D. tyrrelli	Lake	D. kenai	D. tyrrelli	Lake	D. kenai	D. tyrrelli
Battalion	0.000	0.000	Dee Dee	0.435	0.000	Greenview	0.162	0.000
Dagger	0.000	4.567	MR 13-2	0.771	0.000	L. Silent	0.004	0.000
Doubtful	0.423	0.000	MM 11	0.440	0.000	M. Waddell	0.022	0.000
Kettling	0.000	9.29	MR 11	0.843	0.000			
McAlester	0.006	0.945	MR 9	0.313	0.728			
MR 16[a]	2.06	0.000						
Rainbow	0.001	0.000						
Trapper	0.355	0.000						
L. Triplet	0.015	0.407						
U. Triplet	0.000	0.128						
Average	0.29	1.53		0.56	0.146		0.063	0.000

[a]Low fish density

There was no significant difference in the density of D. tyrrelli between lakes with reproducing and non-reproducing fish (Wilcoxon test, P>0.2). However, D. tyrrelli was present in five of the ten lakes with reproducing fish. In 2 of the 5 lakes (Doubtful, Trapper) with reproducing fish where the small copepod is absent, abiotic conditions were not within the range of conditions that D. tyrrelli occurs. Diaptomus kenai density is high in MR 16, perhaps preventing D. tyrrelli from colonizing. It is unclear why the small copepod is absent from Battalion and Rainbow Lakes. Rainbow is relatively large (6.3 ha and deep (10.4 m). All crustacean zooplankton are scarce in Battalion Lake. In four of the five lakes with non-reproducing fish, abiotic conditions were not within the range of conditions that that the small copepod occurs.

The elevation of lakes with non-reproducing trout was significantly higher than the elevation of lakes with reproducing trout (Table 16, Wilcoxon test, P=0.05). There were no statistically significant differences in other abiotic factors between lakes with reproducing and non-reproducing fish (Table 14). It is unlikely that the difference in elevation between lakes with reproducing and non-reproducing fish can account for the difference in densities of large copepods. Diaptomus kenai density was not significantly correlated with elevation (Table 9). Furthermore the elevation ranges of both lakes with reproducing fish and lakes with non-reproducing fish was well within the elevation zone where both species of large copepods occur. Average water temperature was not significantly different between lakes with reproducing and non-reproducing fish. Thus, relative to lakes with low densities of fish, high densities of reproducing trout can reduce or eliminate large copepods from lakes . However, we cannot conclude that non-reproducing fish have no effect on large copepods in eastslope lakes since we do not

Table 16 . Averages, ranges (in parenthesis) and P-values for statistical comparison (Wilcoxon rank sum test) of lakes with reproducing and non-reproducing fish.

	Elev (m)	Depth (m)	Area (ha)	Temp (°C)	TKN (mg/l)	TP (mg/l)	NO_3(mg/l)	NH_3(mg/l)	pH
Non-reproducing Fish	1872 (1789-1974)	10.7 (4.9-27.0)	2.08 (1.2-4.8)	12.6 (10.8-14.2)	0.031 (0.017-0.056)	0.006 (0.004-0.01)	0.006 (0.001-0.019)	0.004 (0.002-0.005)	7.0 (6.6-7.3)
Reproducing Fish	1707 (1270-1931)	10.69 (2.0-17.7)	9.5 (0.6-59)	13.47 (11.7-15.5)	0.057 (0.019-0.16)	0.009 (0.005-0.012)	0.008 (0.001-0.03)	0.005 (0.003-0.007)	7.3 (6.6-7.7)
P-value	0.05*	>0.2	>0.2	>0.2	0.1<0.2	0.05<p<0.1	>0.2	>0.2	0.1

*Statistically significant difference between lakes with reproducing and non-reproducing fish.

know at what densities large copepods would occur if lakes with non-reproducing fish were fishless.

DISCUSSION

Several different types of crustacean zooplankton communities were identified in NOCA. Variation in physical and chemical conditions in lakes due principally to variation in elevation, aspect, extent of development of soils and vegetation, lake morphometry, and, to a some extent, lithology create different environments suitable for different suites of species. High elevation westslope lakes belonged predominantly to clusters I and III (Figure 5). The dominant species in these clusters were D. kenai and H. gibberum. These lakes were characterized by low average water temperature and low alkalinity and nutrients (TKN, TP). The lakes may be poorly productive relative to other NOCA lakes. D. kenai and H. gibberum are apparently well-suited to these conditions.

High elevation zooplankton communities are more diverse on the eastslope than on the westslope (Figure 5). Communities belonging to clusters I and III also were present on the eastslope. Cluster V, dominated by D. arcticus, was found only on the eastslope. Lakes in cluster V are deep lakes and, like clusters I and III, they may be lower productivity lakes characterized by low water temperature, pH, alkalinity, and nutrients. Cluster IV also occurred only on the eastslope. Lakes in this cluster, dominated by the small copepod D. tyrrelli, were smaller, shallower lakes

Low elevation lakes tend to have higher water temperatures, alkalinity, conductivity, and concentration of nutrients than high elevation lakes, with the exception of lakes in cluster IV. Zooplankton communities belonging to clusters II and VI were the

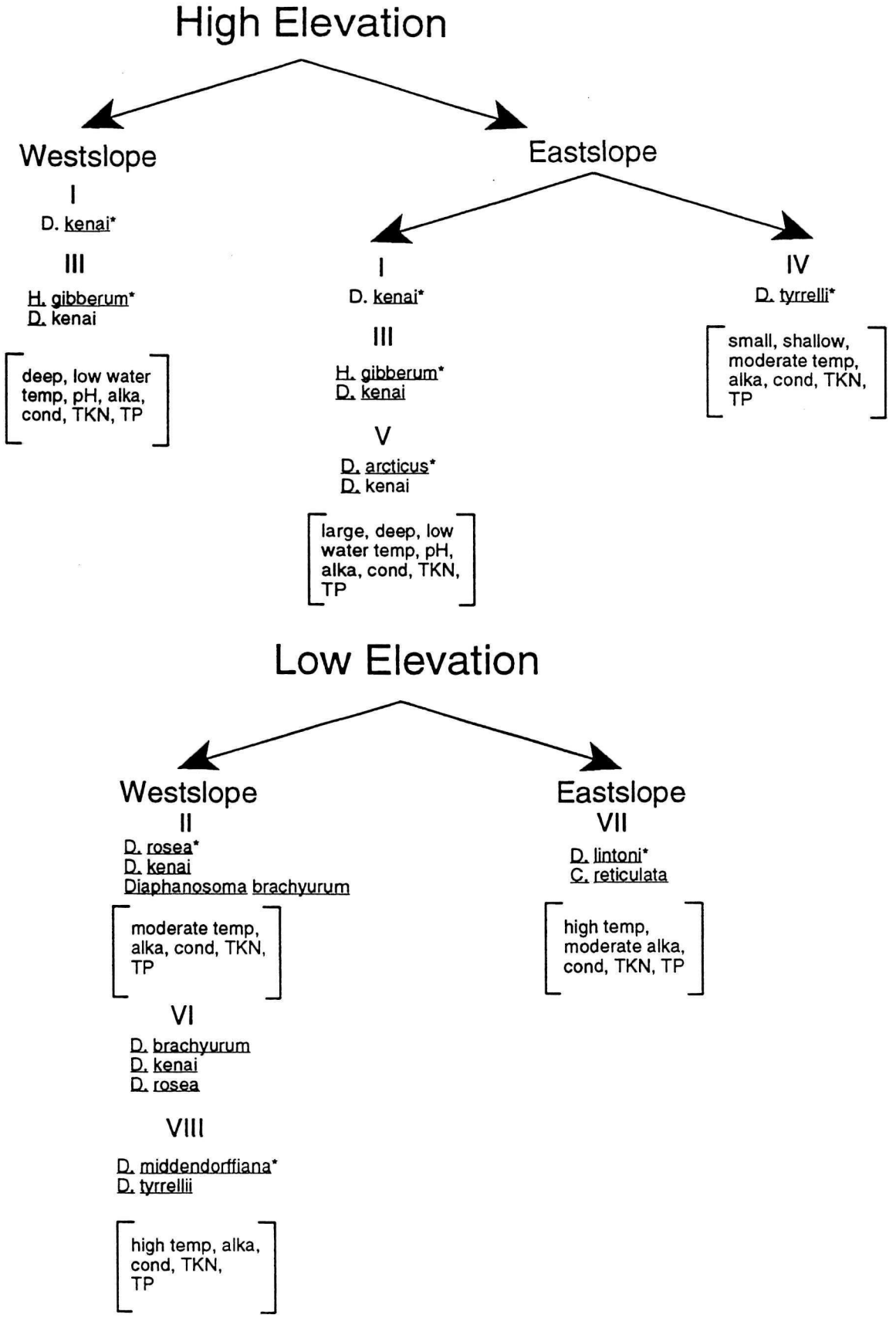


Figure 5 Crustacean zooplankton communities at high and low elevation on the east and westslope of the crest of the Cascades, North Cascades National Park Service Complex. Dominant species indicated by an *.

major kinds of communities in low elevation westslope lakes (Figure 5). These clusters share similar species and are characterized by similar abiotic conditions.

Distribution and patterns of co-occurrence of large and small copepods in NOCA is related to abiotic conditions including lake morphometry, water chemistry, and possibly water temperature, and to biotic factors especially vertebrate and invertebrate predation (Figure 6). The large copepod Diaptomus kenai is widespread in NOCA and is apparently able to tolerate a wide range of abiotic conditions. However, its abundance and distribution may be limited by water temperature (range of occurrence approximately 9-10°C to 16-17°C). In eastslope lakes the large copepod D. arcticus occurs over a more limited temperature range (9.1-13.8°C) than D. kenai, suggesting that it may be less capable than D. kenai of tolerating relatively high temperatures.

In NOCA D. tyrrelli is apparently not able to tolerate as wide a range of abiotic conditions as D. kenai. Diaptomus tyrrelli appears to prefer lakes with higher water TKN (>≈0.03 mg/l) and TP (>≈0.008 mg/l). In NOCA, lakes with these characteristics are usually relatively shallow (<≈ 5-6 m maximum depth). Undoubtedly D. tyrrelli is absent from many lakes due to unfavorable abiotic conditions (low temperature and concentrations of TKN and TP) and high water temperature may limit the distribution of large copepods. However, the abiotic factors we measured alone are not sufficient to completely explain patterns of distribution and abundance of D. tyrrelli or large copepods. Diaptomus kenai and D. tyrrelli are absent from many lakes with abiotic conditions that are apparently suitable for these species. Diaptomus kenai distribution and abundance appears to be influenced by the level of vertebrate predation, particularly fish predation (Figure 6). Reproducing populations of trout that reach high densities can reduce D. kenai density and apparently eliminate the species from some

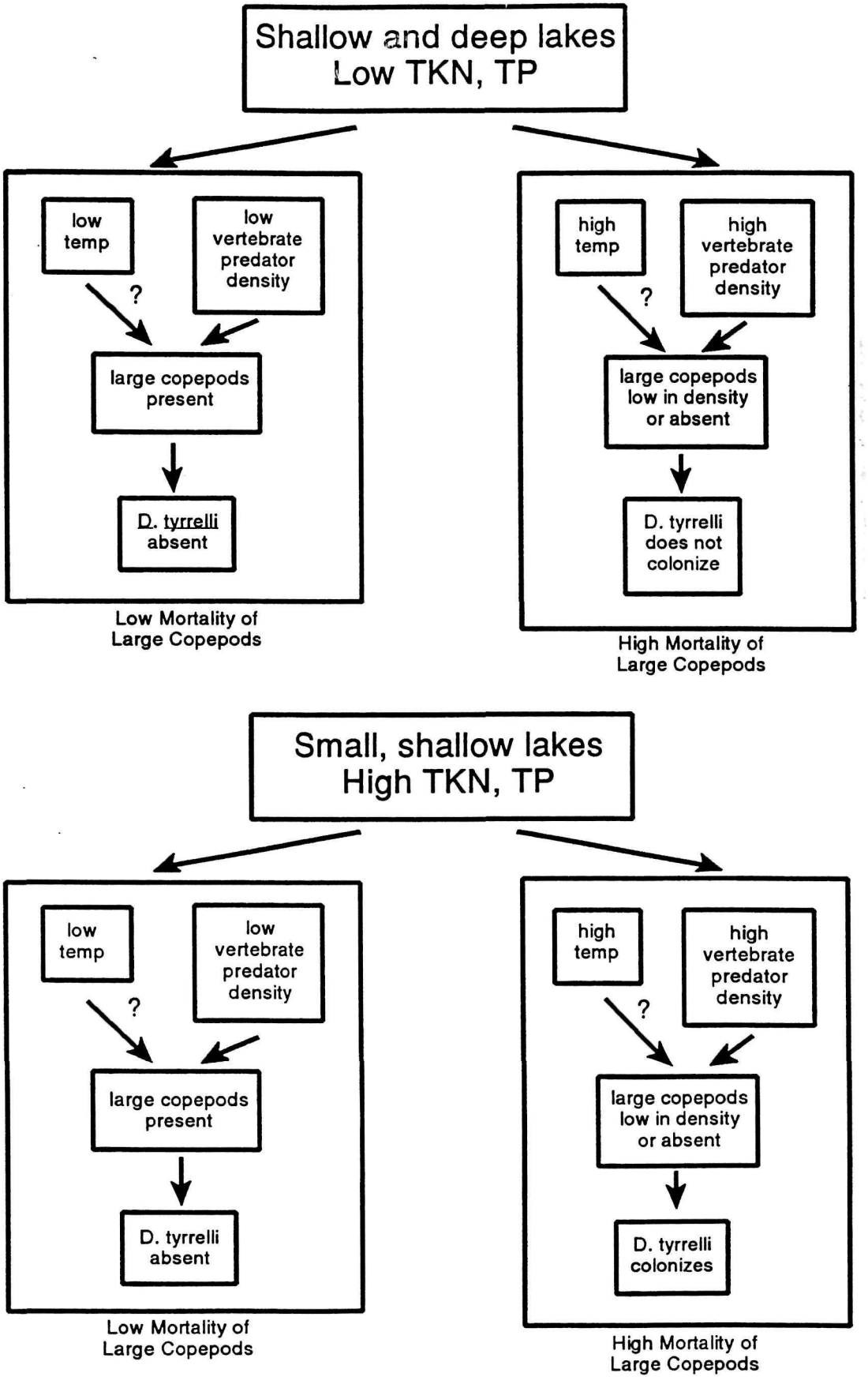


Figure 6. Conceptual model of the possible interactions of lake morphometry, water, temperature, water chemistry, and invertebrate and vertebrate predation in determining distribution and abundance of diaptomid copepods in NOCA.

eastslope lakes. Anderson (1967) noted the disappearance of large crustacean zooplankton, including D. arcticus and Daphnia middendorffiana, from lakes in the Canadian Rockies following introduction of trout. Stoddard (1987) documented the absence of large-bodied crustacean zooplankton including large diaptomids, from mountain lakes in the Sierra Nevada.

In eastslope Lakes in NOCA, D. tyrrelli rarely co-occurs with large copepods and when large and small diaptomids do co-occur, the density of large copepods is usually low. Although co-occurrence of large and small diaptomids in low elevation westslope lakes is common, the density of D. tyrrelli in lake with D. kenai is depressed relative to its density in lakes without the large copepod. Possibly, predation by large copepods can reduce D. tyrrelli density or eliminate the small copepod from some lakes. Anderson (1967) documented the appearance and subsequent increase in abundance of D. tyrrelli in lakes in the Canadian Rockies after large diaptomids had been elimnated by fish introductions. Interestingly, he also noted an increase in densities of cyclopoid copepods, presumably from feeding on abundant juvenile stages of D. tyrrelli. Cyclopoids were most abundant in lakes with high D. tyrrelli densities in NOCA.

In NOCA, if large copepod density is reduced or large copepods are eliminated by either high temperature or high fish (and perhaps larval salamander) density, D. tyrrelli may colonize and become abundant. Whether the small copepod successfully colonizes may depend on water temperature and nutrient conditions (Figure 6).

Cluster analysis showed that lakes with D. tyrrelli as the dominant species (cluster IV) composed an important type of crustacean zooplankton community in NOCA. Moreover, in cluster VIII (Willow Lake) D. tyrrelli was an important subdominant species. The second axis of the ordination of lakes separated clusters IV and VIII

(Willow Lake) from the other cluster and was not significantly correlated with any of the measured abiotic variables. Variation among lakes along the second axis on the ordination may be related in part to high vertebrate predation and possibly high temperature (Willow Lake).

MACROINVERTEBRATES

Macroinvertebrates are important members of aquatic ecosystems. They contribute significantly to the processing and cycling of nutrients (Merritt, Cummins, and Burton 1984) and comprise a major portion of the secondary productivity of streams and lakes (Benke 1984). In high elevation mountainous areas, macroinvertebrates have adapted to unique and often extreme environmental conditions (Mani 1968). In general, high elevation areas are typically cooler than lowland locations, and the length of time free of ice and snow is limited. Periods of macroinvertebrate development are often restricted and the availability of food resources can be reduced and irregular. In addition, dispersal and distribution of high mountain macroinvertebrates are complicated by topographic and physiographic barriers, and availability of appropriate habitats (Mani 1968).

Although nearshore macroinvertebrates play a potentially important role in lentic systems, knowledge of ecological factors influencing their distributions in high mountain lakes is limited. The distributions of nearshore macroinvertebrates in the high mountain lakes of North Cascades National Park Service Complex (NOCA), Washington, USA, were investigated to further understanding of baseline environmental conditions and factors influencing distribution. Prior to initiation of this research very little was known about taxonomic composition and distribution of nearshore macroinvertebrates in NOCA lakes. Research objectives included: 1) identification of potential abiotic factors affecting macroinvertebrate distribution; 2) elucidation of the relationship between macroinvertebrate distributions and the types of benthic substrates in nearshore microhabitats; 3) determination of the potential impact of vertebrate predators on

macroinvertebrate distributions; and 4) assessment of the correspondence of benthic substrate and taxa distribution with a lake classification system (Lomnicky, unpublished manuscript; Liss et al. 1991) that grouped lakes based on regional physiographic characteristics of the terrestrial environment.

Macroinvertebrate species colonizing a lake originate from a species pool (Browne 1981, Wevers and Warren 1986). Successful colonization depends, in part, on the ability to overcome barriers to dispersal and arrive in a place conducive to continued survival (Barnes 1983; Sheldon 1984; Voshell and Simmons 1984; Bass 1992; MacKay 1992). Once organisms arrive at a site their ability to survive is determined, in part, by prevailing habitat conditions (Crowder and Cooper 1982; Gilinsky 1984; Frissell et al. 1986; and Wevers and Warren 1986). Southwood (1977) described habitat as a fundamental template for community organization. Browne (1981) and Friday (1987) identified lake age, isolation and surface area, and factors associated with overall habitat such as habitat diversity and biotic interactions as important in influencing successful colonization and species composition of lakes.

Temperature and water chemistry are important factors affecting the distribution, diversity, and abundance of aquatic organisms. Temperature has been implicated as a mechanism influencing spatial and temporal isolation (Ward 1992), and as one of several primary factors influencing life history patterns of aquatic insects (Sweeney 1984). Various aspects of water chemistry, e.g., acidity, dissolved oxygen, water hardness, etc. (Bell 1971; Pennak 1978; Fryer 1980; Faith and Norris 1989; Schell and Kerekes 1989; Foster 1991) also influence the distribution of freshwater taxa, although ascertaining the effects of selected chemical factors can be difficult (Ward 1992).

Vertebrate predators may also affect macroinvertebrate distribution. Most lakes

of the northern Cascade Mountains were historically fishless. Salamanders (Ambystoma gracile and A. macrodactylum) are typically the primary vertebrate predators in fishless high mountain lakes in NOCA (Liss et al. 1991). Taylor (1983) considers Ambystoma gracile (Baird) to be one of the top carnivores in fishless lakes of the Oregon Cascades. Trout have been introduced in Cascade Range lakes since the turn of the century (Jarvis 1987; Bahls 1992). Trout can reduce or eliminate A. gracile (Sprules 1972; Taylor 1983) and A. macrodactylum (Liss et al., in review) from lakes. However, in NOCA, A. gracile appears to be less vulnerable to fish predation than A. macrodactylum and thus capable of co-occurring with trout (see Amphibian section in this report).

Numerous potential effects of vertebrate predators on aquatic macroinvertebrates have been described. Salamander predation on macroinvertebrates has been documented (Efford and Tsumura 1973; Licht 1975; Taylor et al. 1988). Conflicting results concerning effects of salamanders on macroinvertebrate community composition and species abundance have been reported (Dodson 1970; Sprules 1972; Taylor et al. 1988; Petranka 1989). Fish have been shown to alter the size-structure (Post and Cucin 1984; Blois-Heulin et al. 1990; Chilton and Margraf 1990; Diehl 1992), species composition (Macan 1966, 1977; Johnsen 1978; Thorp and Bergey 1981; Gilinsky 1984; Healey 1984), and species abundance (Macan 1977; Healey 1984) of benthic macroinvertebrate communities. The attenuation and elimination of specific taxa (e.g., Chaoborus) has also been reported (Pope, Carter, and Power 1973; Stenson 1978). Macroinvertebrate abundance in ponds and small lakes may change relative to changes in fish abundance (Healey 1984).

Conflicting views concerning predator impact on freshwater communities have been summarized by Murdoch and Bence (1987) and Thorp (1986). Murdoch and Bence (1987) concluded that predators were sources of instability in freshwater environments, while Thorp (1986) proposed that predators contributed directly and indirectly to community regulation and population stability.

STUDY SITE

NOCA, located in northern Washington, is 204,000 ha in area and encompasses parts of three major watersheds (Chilliwack-Nooksack, Skagit, Stehekin) containing hundreds of tributary drainages and >160 lake basins of importance to fisheries management. All lakes within the complex are considered oligotrophic. Glacial activity during the Pleistocene, and alpine glaciation approximately 2500 years ago formed a diversity of lake basin types (e.g., bench, cirque, ice scour, tarn, morainal deposition, landslide).

Lomnicky (unpublished manuscript; Liss et al. 1991) classified NOCA lakes according to vegetation zone, elevation, and location west or east of the crest of the Cascade Range (Table 1). West slope lakes are present in the Chilliwack-Nooksack and Skagit River watersheds and east slope lakes are located in the Stehekin River watershed. Vegetation zone can be viewed as an indicator of local climate and soil development (Lomnicky et al. 1989). Three vegetation zones were identified: forest (F), subalpine (S), and alpine (A). NOCA forest lakes occur in basins with open and closed canopy forests of mixed conifer with variable levels of understory development (Agee and Pickford 1985). Trees (e.g., western and mountain hemlock, Pacific silver fir, subalpine fir, Douglas fir, etc.) are predominant with an understory consisting typically

Table 1. Lake classification categories developed by Lomnicky (unpublished manuscript; Liss et al. 1991) and the number of lakes sampled in each category.

Vegetation Zone	Elevation (m)		Crest Position	Category Abbrev.	Number of Lakes
Forest					14
	low	(412-1031)	west	FLW	4
	high	(1171-1496)	west	FHW	6
	high	(1504-1717)	east	FHE	4
Subalpine					22
		(1270-1769)	west	SW	13
		(1270-1998)	east	SE	9
Alpine		(1566-1982)	west	ALP	5

of tall shrubs (e.g., Sitka alder, willows, and vine maple) and lowland grasses and herbs. Elevation was used to more finely differentiate the forest zone (Table 1). Vegetation in the subalpine zone is a mosaic of meadow and forest flora (Franklin and Dyrness 1973). The dominance of trees decreases relative to the forest zone. Trees occur more often in patches or clumps, and the presence of open areas inhabited by various communities of subalpine shrubs, herbs and other meadow plants increases. In alpine basins vegetation is limited and talus, snow, and glacial ice predominate. Low growing herbs and stunted, isolated clumps of conifers grow where conditions are amenable.

Environmental conditions also differ relative to the location of the Cascade crest. The west slope of NOCA tends to be wetter and cooler than the east slope (Lomnicky et al. 1989). The upper elevation boundary of all vegetation zones is higher on the east slope than on the west slope (Franklin and Dyrness 1973) and, consequently, east slope alpine lakes are rare.

METHODS

A total of 41 lakes were studied from 1989 through 1991 (Table A.1, Appendix). Each lake had previously been assigned to one of six lake classification categories (Table 1). Lakes are located in remote and rugged terrain, and were accessed only by hiking or helicopter. Field seasons were restricted to the period after ice-out and before the return of inclement fall weather (approximately mid-June through mid-September). Thirty-eight of 41 lakes were sampled in 1989, 21 of 41 lakes in 1990, and 16 of 41 lakes in 1991. Of the 41 study lakes, 15 were sampled once, 18 were sampled two to four times, and eight lakes were sampled five to seven times throughout the duration of

the study. Each lake sampled once or twice was visited during the middle to late portion of the field season.

Physical and Chemical Variables

Lake depth was determined with a handheld sonar gun along transects parallel and perpendicular to the long axis of a lake. Surface area was estimated by digitizing 7.5 min USGS topographical maps. Each time a lake was sampled water temperature was measured at 1 m intervals from the lake surface to the bottom over the deepest point in the lake using an Omega 871A digital thermo-couple. Maximum temperature at 1 m below the surface was defined as the highest temperature recorded at that depth during all visits (1989-1991). Water samples were collected at a depth of 1 m over the deepest point in a lake using a 1.5 L Van Dorn bottle. Frozen filtered and unfiltered water samples were transported to the Forest Sciences Laboratory (CCAL), Oregon State University for chemical analysis.

The nearshore area was subdivided into three habitats: water surface, water column, and benthic stratum. The benthic habitat was composed of inorganic and organic substrates. Inorganic substrates included silt (ST), sand (SD), gravel (GR), cobble (CB), boulder (BL), and bedrock (BD). Categories were defined by particle size ranges presented in Ward (1992) based on modification of the Wentworth (1922) Scale by Cummins (1962). Organic substrates included emergent/submergent vegetation (ESV, e.g., grasses, sedges, vascular hydrophytes), coarse wood (CW, e.g., logs, snags, branches), fine wood (FW, e.g., twigs, wood pieces, needles), organic detritus (OD), and moss (MS).

Nearshore benthic substrates usually occurred in combinations (e.g., GR-SD-CB, OD-CW-ESV, etc.) which were termed microhabitats. The nearshore benthic habitat of a lake was assessed by reconnaissance of the entire shoreline perimeter (Smith et al. 1981), at which time microhabitats and the substrates composing them were identified and mapped. All major lake perimeter structures (e.g., inlet and outlet streams, rock outcrops and cliffs, talus slopes, etc.) also were identified and mapped.

Macroinvertebrates

Macroinvertebrates were collected from the nearshore microhabitats in each lake. Qualitative samples were taken utilizing a sweepnet or by removing individuals from the water column and substrates with a hand net and forceps. Triplicate core samples were taken from benthic microhabitats using a 17 cm diameter metal sampling tube. The tube was placed in position over the chosen sampling site and depressed into the substrate. Material was extracted from the tube to an approximate depth of 5 cm and placed into a 250 µm sieve (U.S.A. Standard Tyler No. 60). Material in the sieve was rinsed with water removed from the tube with a plastic-baster. The material was then placed into a plastic container and handpicked for organisms. All organisms were preserved in 70% ethanol.

In the laboratory, organisms were identified to the lowest taxonomic level possible using a stereomicroscope. Fifty-two percent of all taxa were identified to genus. These were groups where larvae could be identified to the generic level with relative certainty (e.g., Ephemeroptera, Trichoptera, Coleopotera). An additional 43% were identified to family. Three groups of taxa (i.e., Hirudinea, Oligochaeta, and Turbellaria) were identified to Class, and nematodes were identified by Phylum.

Macroinvertebrates were categorized according to their habitat relationship (Figure 1): pleuston (water surface), plankton and nekton (water column), or benthos (bottom substrate)(Ward 1992). Benthic organisms were subdivided into substrate preference groups modified from Ward's (1992) general faunal categories. Organisms were placed in substrate preference groups based on life history information for each taxon. The determination of functional feeding group associations was based on information in Merritt and Cummins (1984).

Vertebrates

A preliminary analysis was conducted to determine if effects of vertebrate predators on nearshore macroinvertebrates were evident. A more comprehensive analysis of vertebrate predator impacts on macroinvertebrate distribution and abundance, utilizing data from 1989 through 1993, will be undertaken this year. Four vertebrate predation categories were identified for the preliminary analysis: a) no vertebrate predators (NVP, n=7); b) salamanders and no fish (S, n=6); c) non-reproducing trout with a moderate abundance of salamanders, usually A. gracile (FNR, n=5); and d) reproducing trout with salamanders absent or very low in abundance (FR, n=6). Only lakes for which the composition of the vertebrate predator complex was known were used in this analysis. Two species of salamander, Ambystoma gracile (Baird) and Ambystoma macrodactylum Baird, are the primary native vertebrate predators in NOCA lakes (Liss et al. 1991; see Amphibian section in this report). Salamander abundance was determined by snorkeling the lake perimeter and carefully searching through bottom material. The number of observed salamander larvae was recorded (Liss et al. 1991, in review). Cutthroat trout, Oncorhynchus clarki

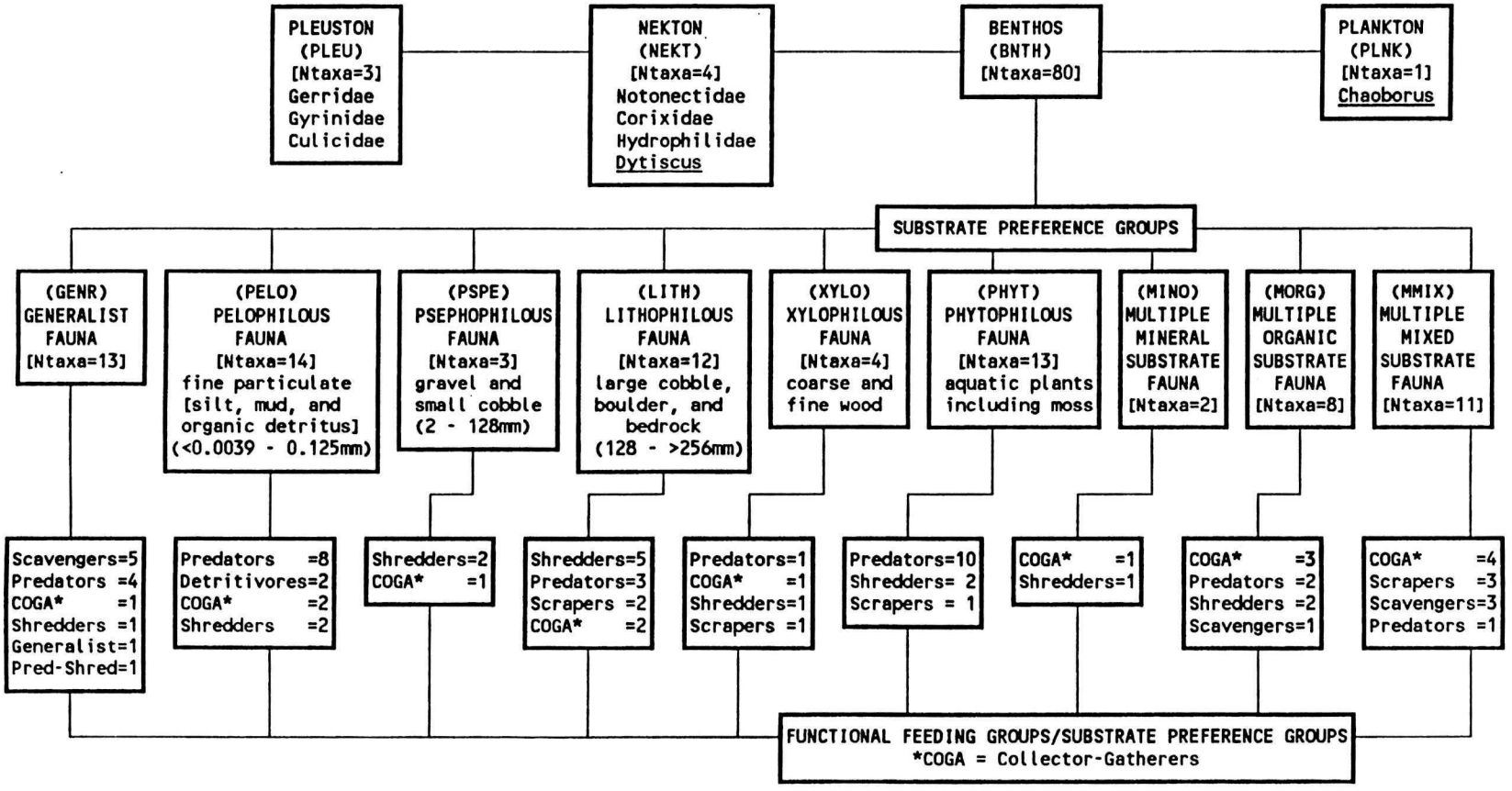


Figure 1. Generalized model of the organization of nearshore macroinvertebrate communities in the lakes of the North Cascades National Park Service Complex, with Substrate Preference Groups (after Faunal Categories, Ward 1992) and Functional Feeding Groups (after Merritt and Cummins 1984).

(Richardson), were present in seven of the fish lakes and rainbow trout, Oncorhynchus mykiss (Richardson), in four fish lakes. Presence of trout was assessed by gill netting, angling and snorkeling. Lakes with non-reproducing trout are periodically stocked and, in general, trout density is lower than in lakes with reproducing trout (Liss et al. 1991; see Fish section in this report).

The effects of vertebrate predators on the distribution of 15 nearshore macroinvertebrate taxa (Table 2) was examined. These taxa were either the most widely distributed among all forest and subalpine lakes, or taxa of particular interest (e.g., Chloroperlidae, Gerridae, Notonectidae, Potamonectes, Taenionema), and generally occurred in all vegetation zones both west or east of the Cascade crest. Since many taxa in NOCA are restricted in distribution to a few lakes, using more widely distributed taxa minimizes the possibility that absence of a taxon from a lake was due to factors not related to vertebrate predation.

Statistical Analysis

The k-means clustering algorithm (NCSS version 5.03, Hintze 1992) was used to cluster lakes according to number of taxa, maximum temperature, and lake elevation.

Discriminant analysis (NCSS vers. 5.03, Hintze 1992) was used to examine how a set of predictor variables representing characteristics of the aquatic environment would influence the placement of lakes into the six classification categories (i.e., FLW, FHW, FHE, SW, SE, ALP) of the terrestrially-based lake classification (Lomnicky, unpublished manuscript; Liss et al. 1991). According to Tabachnick and Fidell (1989) discriminant analysis is an effective tool designed to elucidate the relationship between predictor variables and groups, and to examine the capacity of these combined

Table 2. The distributions of 15 taxa examined for predator impacts.

	NUMBER OF LAKES									
	Vegetation Zone		Crest Position		Classification Category					Percent of all F and S Lakes
Taxon	F	S	W	E	FLW	FHW	FHE	SW	SE	(n=35)
Hirudinea	10	5	9	6	4	4	2	1	4	43
Sphaeriidae	15	10	14	11	4	6	5	4	6	71
Callibaetis	14	8	12	10	4	5	5	3	5	63
Ameletus	4	15	11	8	0	1	3	10	5	54
Chloroperlidae	4	4	2	6	0	1	3	1	3	23
Taenionema	0	7	6	1	0	0	0	6	1	20
Desmona	4	17	10	11	0	2	2	8	9	60
Halesochila	8	8	8	8	2	3	3	3	5	46
Limnephilus	13	6	9	10	4	4	5	1	5	54
Psychoglypha	6	13	11	8	0	3	3	8	5	54
Agabus	10	16	14	12	1	5	4	8	8	74
Hydroporus	7	10	5	12	0	3	4	2	8	49
Potamonectes	1	8	4	5	0	1	0	3	5	26
Gerridae	6	0	5	1	4	1	1	0	0	17
Notonectidae	6	2	5	3	3	1	2	1	1	23

F = Forest Zone
S = Subalpine Zone
W = West
E = East
FLW = Forest Low West
FHW = Forest High West
FHE = Forest High East

variables to predict group membership. In this analysis the predictor variables (i.e., independent variables) consisted of: a) the proportion of microhabitats per lake in which each of 10 substrates were present and, b) the proportion of taxa per lake in each of 10 substrate preference groups (including pleuston and nekton). The dependent variable was made up of the terrestrially-based classification category designations for study lakes. The discriminant analysis program calculated multiple canonical variate scores for each lake, and ordination of these scores helped to show how individual lakes and lake categories were associated. The relationships between predictor variables and canonical variates were determined by calculating Pearson product-moment correlations (NCSS vers. 5.03, Hintze 1992). Finally, the usefulness of the aquatic-based predictor variables in predicting the membership of lakes in the terrestrially-based classification categories was elucidated, using discriminant analysis, by: 1) the construction of a classification matrix according to the assignment of lakes to the classification categories; 2) determination of classification accuracy by calculation of the percent reduction in classification error due to the predictor variables; 3) determination of the number of misclassified lakes; and 4) calculation of the number of lakes expected to be correctly placed into classification categories by chance alone (Tabachnick and Fidell 1989).

Multiple regression analysis (NCSS vers. 5.03, Hintze 1992) was used to determine the relationship of number of taxa per lake (dependent variable) and maximum temperature, elevation, surface area, and maximum depth (NCSS vers. 5.03, Hintze 1992). Confidence limits were set at 95%.

Two nonparametric methods (NCSS vers. 5.03, Hintze 1992) were used to test for statistical significance ($p<0.05$). The Mann-Whitney Two Sample Test was used to

compare sample means among vegetation zones for number of taxa per lake, maximum temperature per lake, proportion of microhabitats containing inorganic and organic substrates, and the proportion of taxa per lake in two general substrate preference categories (i.e., generalists and inorganic substrates; organic substrates). Sample means for pH, alkalinity, and $[Ca^{2+}]$ of lakes with and without gastropods and Potamonectes were also compared. Significant differences in the presence of macroinvertebrate taxa in lakes with different types and abundances of vertebrate predators were determined using Fisher's Exact Test.

RESULTS

Sixteen taxonomic groups of nearshore macroinvertebrates were present in NOCA lakes with a total of 88 taxa (Table 3). Trichoptera, Coleoptera, and Diptera had the greatest number of taxa per group. Several taxonomic groups were represented by only a single taxon.

Many taxa were restricted in distribution. Twenty-five percent of all taxa were collected from individual sites while 47% were restricted to <20% of all study lakes. Eighty-nine percent of all taxa, representing all 16 taxonomic groups, were collected from lakes in the forest zone (Table 3). Fifty-six percent of all taxa (12 groups) were collected from subalpine zone lakes and 20% (9 groups) from alpine lakes. Four groups (i.e., Gastropoda, Lepidoptera, Megaloptera, Odonata) were collected only from forest lakes, and the number of taxa in four groups (i.e., Coleoptera, Diptera, Ephemeroptera, Hemiptera) decreased from the forest to alpine zones. The number of amphipod, plecopteran, sphaeriid, and trichopteran taxa was nearly equivalent in forest

Table 3. Taxonomic groups in NOCA lakes

Groups	Total No. Taxa per Group	Level of Identification	Total No. of Taxa/Group in Each Zone F	S	A
Turbellaria	1	Class	1	1	1
Oligochaeta	1	Class	1	1	1
Nematoda	1	Phylum	1	1	1
Hirudinea	1	Class	1	1	1
Sphaeriidae	1	Family	1	1	0
Amphipoda	2	Genus	2	2	0
Gastropoda	4	Family	4	0	0
Odonata	6	Family	6	0	0
Ephemeropter	8	Genus	7	4	1
a	7	Family	6	6	2
Plecotpera	20	Genus	16	15	6
Trichoptera	1	Genus	1	0	0
Megaloptera	6	Family	6	2	0
Hemiptera	14	Genus	13	7	1
Coleoptera	14	Family	11	8	4
Diptera	1	Genus	1	0	0
Lepidoptera					
Total Taxa	88		78	49	18
Percent			89	56	20

and subalpine lakes. Hirudinea, nematodes, oligochaetes and turbellarians were present in all zones.

Physical Variables and Macroinvertebrate Distribution

Number of taxa per lake was positively related to maximum temperature and negatively related to elevation (Table 4, Figure 2). Temperature was negatively related to elevation (r=-0.3927). Surface area and maximum depth did not directly affect number of taxa per lake.

The k-means clustering algorithm placed lakes in four groups (Table 5). Mean number of taxa per lake and maximum temperature increased from cluster I to cluster IV. Elevation varied little between clusters I, II, and III, but cluster IV, with the highest mean number of taxa and maximum temperature, had the lowest mean lake elevation.

Lake clusters were also related to vegetation zone. Lakes with the lowest number of taxa and lowest maximum temperature (cluster I) were predominantly alpine. Clusters II and III were composed principally of subalpine lakes and cluster IV was made up exclusively of forest lakes.

The relationship between number of taxa and maximum temperature was also demonstrated for lakes grouped according to classification categories (Table 6). At the vegetation zone-level, the number of taxa per lake decreased significantly from the forest to alpine zone (F>S, S>A, Mann-Whitney test, $p<0.05$). The mean maximum temperature per lake also decreased from the forest to alpine zone, with the difference in maximum temperature between forest and subalpine lakes significant at the $\alpha<0.10$ level (p=0.08, Mann-Whitney Test), while the difference between forest and alpine lakes was significant at $\alpha<0.05$ (p=0.002, Mann-Whitney Test). In general, lake

Table 4. Results of multiple regression analyses of the relationship of number of taxa per lake and maximum temperature, elevation, surface area and maximum depth. (Level of Significance $p < 0.05$)

Independent Variable	Correlation Coefficient	p-Value
Maximum Temperature	0.7087	<0.00001
Elevation	-0.4800	0.0015
Surface Area	0.0561	0.7274
Maximum Depth	0.0341	0.8322

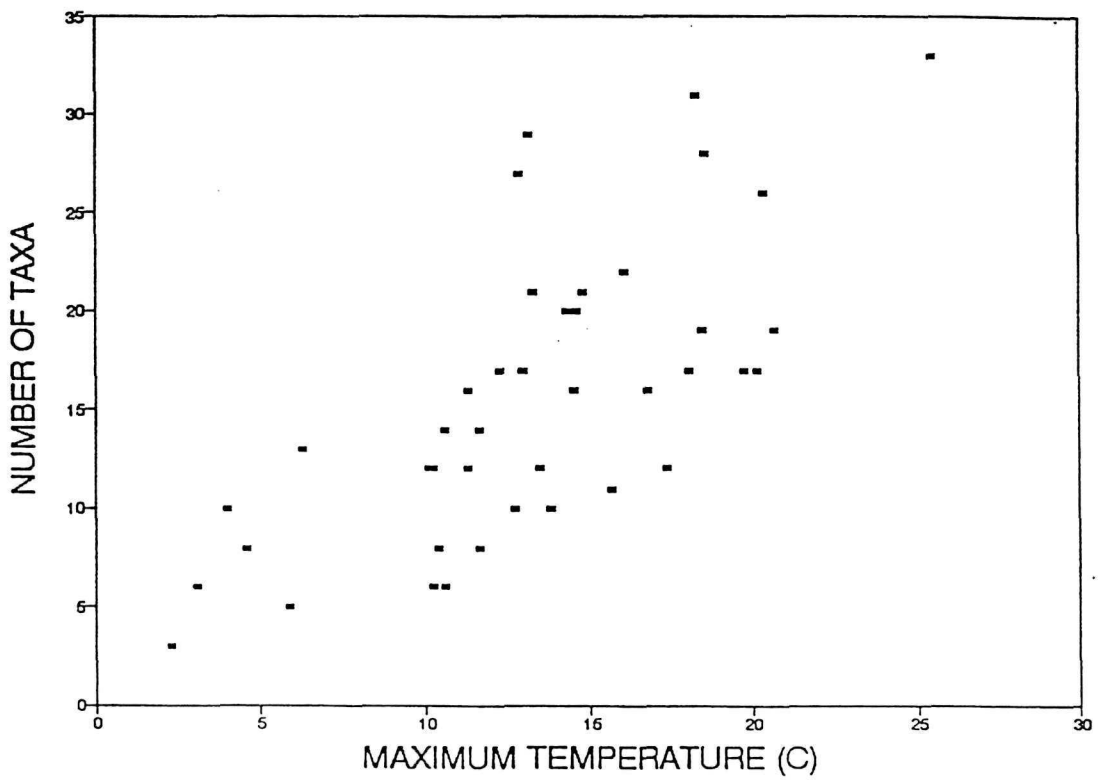


Figure 2. Relationship of the number of taxa per lake and maximum water temperature.

Table 5. Non-hierarchical clustering of lakes (NCSS, k-means algorithm) by number of taxa per lake, maximum temperature and lake elevation.

	CLUSTER			
	I	II	III	IV
Number of Lakes	5	14	16	6
Mean Number Taxa/Lake	6.4	10.9	18.9	25.7
Mean Maximum Temp. (C)	3.9	11.0	15.3	20.6
Elevation (m)	1680.6	1541.8	1693.7	960.8
Percent of Lakes per Vegetation Zone in Each Cluster:				
Forest	0.0	21.4	31.3	100.0
Subalpine	20.0	71.4	68.7	0.0
Alpine	80.0	7.1	0.0	0.0

Table 6. The mean number of taxa per lake, maximum temperature, and elevation for lakes in each classification category.

	FOREST				SUBALPINE			ALPINE
	Low West	High West	High East	Entire Zone	West	East	Entire Zone	Entire Zone
Number of Lakes	4	6	4	14	13	9	22	5
Number of Taxa/Lake	27.7	15.7	23.7	21.4	12.1	16.6	13.9	6.8
Maximum Temp./Lake (C)	20.8	14.4	13.8	16.1	11.9	15.1	13.2	5.4
Elevation/Lake (m)	820.2	1285.5	1632.2	1251.6	1603.8	1782.1	1676.7	1688.2

categories with higher mean maximum temperatures tended to have higher mean numbers of taxa. For instance, FLW lakes had the highest number of taxa, highest maximum temperature, and lowest elevation. Conversely, lakes in the SW and ALP categories had the lowest number of taxa and lowest maximum temperatures.

Microinvertebrate-Habitat Substrate Relationships

Substrate composition of lake microhabitats varied between vegetation zones (Table 7). In general, the percent of microhabitats in each vegetation zone with at least one inorganic substrate was high. Yet, of the six inorganic substrates, ST, SD, GR, and CB were present in a greater percentage of microhabitats in subalpine and alpine zone lakes than in forest zone lake microhabitats. Conversely, the percent of microhabitats in forest zone lakes containing at least one organic substrate was significantly higher (Mann-Whitney Test, $p<0.05$) than in subalpine and alpine zone microhabitats. Organic substrates of all types occurred less frequently in the subalpine zone than in the forest zone. Organic substrates were virtually absent from alpine zone microhabitats.

Substrate preference group associations generally parallelled the vegetation zone trends shown for substrates (Table 7). The percent of taxa representing GENR and inorganic substrate preference groups (i.e., PSPE, LITH, and MINO) was significantly higher (Mann-Whitney, $p<0.05$) in alpine (71%) and subalpine (63%) lakes than in forest lakes (41%). Conversely, the percent of taxa representing organic substrate preference groups (i.e., PELO, XYLO, PHYT, and MORG) and preference groups associated with the water column and surface (i.e, PLEU and NEKT) was significantly higher (Mann-Whitney, $p<0.05$) in the forest zone (45%) than in the subalpine (24%) and alpine (23%) zones. The remainder of taxa in all three zones

Table 7. Percent of inorganic and organic substrates and combined substrate preference groups in NOCA lakes.

	Forest	Subalpine	Alpine
Percent of microhabitats with at least one inorganic substrate	80	93	100
Percent of microhabitats with at least one organic substrate	93	60	8
Percent of microhabitats in which each substrate is present:			
Inorganic			
Silt (ST)	39	55	54
Sand (SD)	17	28	46
Gravel (GR)	24	43	46
Cobble (CB)	32	57	77
Boulder (BL)	36	24	54
Bedrock (BD)	5	16	0
Organic			
E/S Vegetation (ESV)	25	1	0
Coarse Wood (CW)	58	38	8
Fine Wood (FW)	68	29	8
Organic Detritus (OD)	69	24	0
Moss (MS)	7	4	0
Mean percent of taxa per lake in combined substrate preference groups:			
Generalists and Inorganic Substrates	41	63	71
Organic Substrates plus Pleuston and Nekton	45	24	23
Mixed Inorganic and Organic Substrates	14	13	6

E/S = Emergent/Submergent

represented organisms associated with combined inorganic and organic substrate preferences (MMIX).

Microhabitat substrates and substrate preference group associations were also used, per discriminant analysis, to examine the relationship of lakes relative to the six classification categories. Five canonical variate scores for each study lake were calculated during the analysis and the first two variates retained 74% (i.e., variate one = 56%, variate two = 18%) of the among-group variability. Pearson correlations of the predictor variables with variates one and two (Table 8) revealed that canonical variate one was positively correlated with organic substrates, organic-based substrate preference groups, and water surface (pleuston) and water column (nekton) taxa, and negatively correlated with inorganic substrates (except BL), generalist taxa, and inorganic-based substrate preference groups. Patterns of correlation of substrates and substrate preference groups with canonical variate two were less clear. Predictor variables most strongly correlated with canonical variate two were MINO taxa and the substrate FW.

Ordination of lake scores for canonical variates one and two (Figure 3) revealed three major groups of lakes (i.e., A=FLW, D=SW, and B-C-E-F=FHW-FHE-SE-ALP). Relative to the other lake groups, FLW lakes had the highest mean proportional presence of organic substrates in microhabitats and the highest mean number of taxa in organic-based substrate preference groups (including pleuston and nekton). SW lakes had the highest mean proportion of taxa in inorganic-based substrate preference groups (i.e., PSPE, MINO, and LITH). ALP lakes (i.e., F) were more similar to SW lakes than to the other lake groups and had the highest mean proportions of inorganic substrates and generalist taxa relative to all other groups. The mean proportions of

Table 8. Pearson product-moment correlations between predictor variables and the first two canonical variates calculated during discriminant analysis.

Variables	CV1	CV1
Inorganic Substrates:		
Silt (ST)	-0.383	-0.213
Sand (SD)	-0.350	-0.117
Gravel (GR)	-0.408	-0.332
Cobble (CB)	-0.453	0.073
Boulder (BL)	0.236	-0.111
Bedrock (BD)	-0.124	0.243
Organic Substrates:		
E/S Vegetation (ESV)	0.809	0.221
Coarse Wood (CW)	0.481	-0.101
Fine Wood (FW)	0.553	-0.448
Organic Detritus (OD)	0.508	-0.116
Inorganic-based Substrate Preference Groups:		
Generalists (GENR)	-0.399	0.006
Psephophilous (PSPE)	-0.097	-0.129
Lithophilous (LITH)	-0.504	0.186
Mixed Inorganic (MINO)	-0.642	0.499
Organic-based Substrate Preference Groups:		
Pelophilous (PELO)	0.347	-0.345
Xylophilous (XYLO)	0.094	0.398
Phytophilous (PHYT)	0.734	0.017
Mixed Organic (MORG)	0.243	-0.345
Water Surface and Water Column Taxa:		
Pleuston (PLEU)	0.878	0.278
Nekton (NEKT)	0.527	-0.222

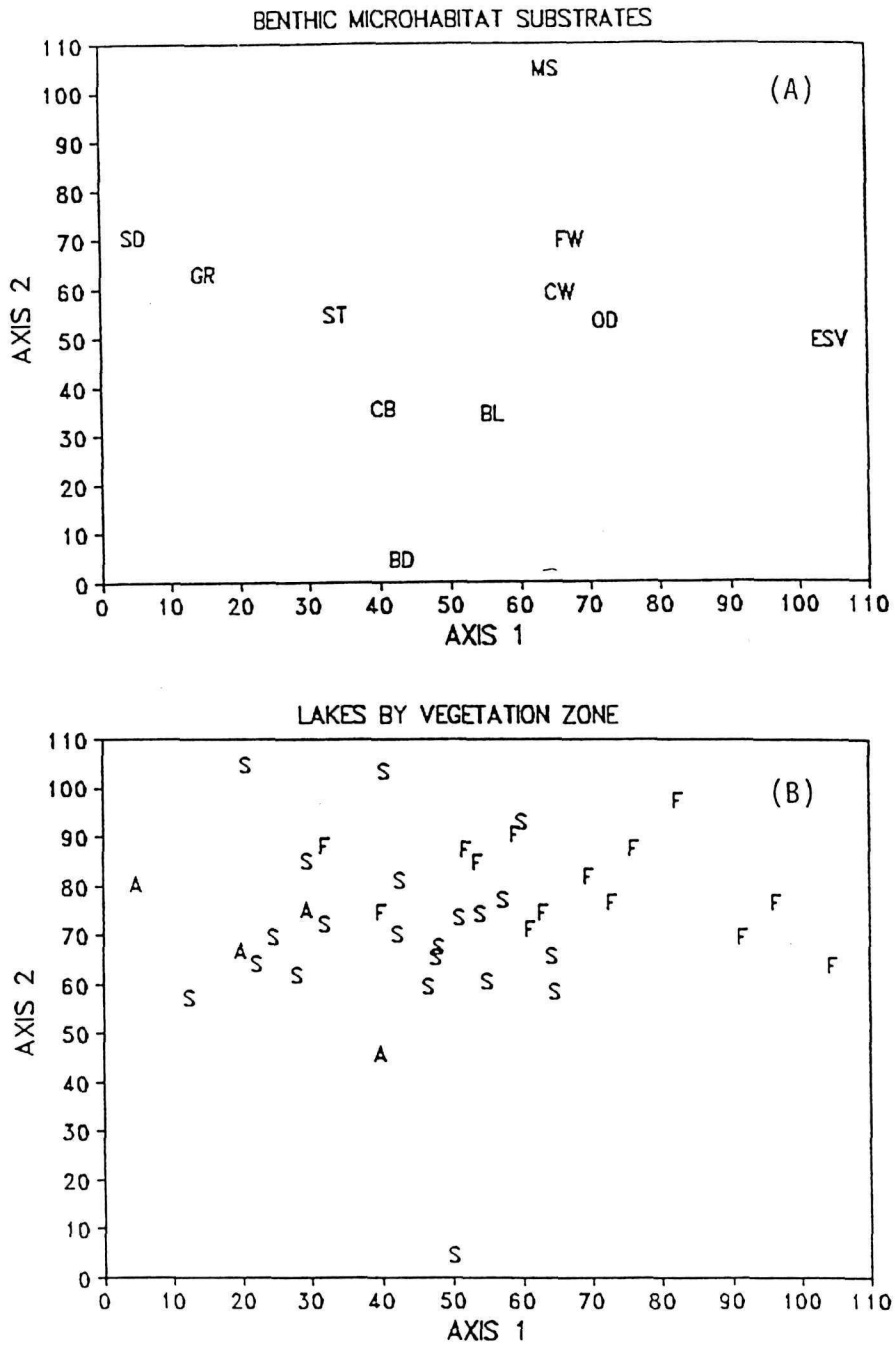


Figure 3. Ordination of benthic substrates (A) and lakes by vegetation zone (B) based on axes derived from DECORANA analysis of substrates matrix.

inorganic and organic substrates and substrate preference groups calculated for FHW (i.e., B), FHE (i.e., C), and SE (i.e., E) lakes, in general, fell between those calculated for FLW, and SW and ALP lakes, and tended to be more similar to each other than to the other three groups. These results indicate that differences between groups can be associated with differences in the proportional presence of inorganic and organic substrates and substrate preference groups.

Discriminant analysis also helped to demonstrate the usefulness of aquatic-based predictor variables in the prediction of the membership of lakes in classification categories based on characteristics of the terrestrial environment. A classification equation based on the predictor variables was calculated for each classification category (i.e., FLW through ALP), and a classification matrix was constructed during the assignment of lakes to the categories. During this process, each lake was predicted to be a member of the classification category to which it had been previously assigned according to the terrestrially-based classification. Therefore, no lakes were misclassified and the accuracy in classification, based on the percent reduction in classification error, was 100%. Further, calculation of the number of lakes (i.e., 8.5) expected to be correctly placed into classification categories by chance alone appeared to be sufficiently low enough to support the conclusion that the classification equations developed by this analysis were useful in assigning lakes to categories (Tabachnick and Fidell 1989). These results demonstrate the utility of using variables associated with lake substrates and their associated taxa in the prediction of the membership of lakes in the terrestrially-based classification categories.

Distribution of Function Feeding Groups

All functional feeding groups were present in each vegetation zone (Table 9). Predators were predominant in forest categories. Subalpine (especially SW) and alpine lakes tended to have a more equitable distribution of taxa among functional groups than forest lakes. Scrapers, with mouth parts adapted for removing periphyton from rock surfaces (Lamberti and Moore 1984), increased in SW lakes possibly due to the relatively greater importance of larger inorganic substrates (i.e., CB and BL) in the microhabitats of these lakes. Although the mean percent of detritivore taxa (i.e., oligochaetes and sphaeriids) varied among categories, they were widely distributed among all lakes. Oligochaetes occurred in 98% and sphaeriids in 61% of all lakes.

Habitat Conditions and Distribution of Individual Taxa

Snails representing four Gastropoda families were collected only from three FLW lakes. This limited distribution was directly associated with pH, alkalinity, and $[Ca^{2+}]$. Mean pH (based on calculation of mean free $[H^+]$), alkalinity, and $[Ca^{2+}]$ were significantly higher in the three FLW lakes with snails than in 31 lakes without snails (Mann- Whitney Test, $p<0.05$). The beetle, Potamonectes griseostriatus (DeGeer) was present in eight subalpine lakes and only one forest lake. The difference in mean pH per lake between the lakes with Potamonectes (pH=6.40) and the forest lakes without this taxon (pH=7.45) was significant (Mann-Whitney Test, $p=0.002$), indicating that this species might be restricted from forest lakes, in part, because of higher pH levels. The difference in mean pH between subalpine lakes with and without Potamonectes was not significant, suggesting that factors other than pH (e.g., microhabitat substrates) might be responsible for restricting the distribution of this beetle in the subalpine zone.

Table 9. Functional Feeding Groups in NOCA lake classification categories

Classification Category	Functional Feeding Groups* (mean percent taxa/lake)					
	PRED	SCAV	COGA	SHRD	SCRP	DETR
FLW	47	20	15	10	1	7
FHE	40	10	23	13	5	9
FHW	38	9	23	15	3	12
SE	37	11	17	19	5	11
SW	27	10	23	16	12	12
ALP	17	24	31	7	3	17

* PRED: Predator
SCAV: Scavenger
COGA: Collector-Gatherer
SHRD: Shredder
SCRP: Scraper
DETR: Detritivore

Odonates were collected only from forest lakes. This may have been related, in part, to the increased availability of microhabitats with organic substrates (e.g., ESV, OD, and FW) which are preferred by odonates (Pennak 1978; Corbet 1980; Merritt and Cummins 1984). Callibaetis (Baetidae) was the dominant mayfly in the forest zone, occurring in 93% of lakes compared to 40% of subalpine zone lakes. Callibaetis was not present in alpine lakes. This pattern appears associated with the need for this genus to be near aquatic vegetation and its tolerance for higher water temperatures and fluctuations in pH (Edmunds, Jensen, and Berner 1976; Hafele and Hughes 1981). Ameletus (Siphlonuridae), associated with clean inorganic substrates (Edmunds et al. 1976) such as GR and CB , was most prevalent in the subalpine (75% of lakes) and alpine (83% of lakes) zones, and present in only 33% of forest lakes. The trichopterans Limnephilus and Halesochila (Limnephilidae), and Polycentropus (Polycentropodidae) were present in a greater percent of forest lakes (87%, 53%, 53%, respectively for each taxon) than subalpine and alpine lakes combined (27%, 31%, 8%, respectively for each taxon). Polycentropus tends to be more tolerant of warmer water temperatures and Halesochila requires habitats with detritus and bottom sediments soft enough for burrowing (Wiggins 1977). Desmona mono (Denning), Psychoglypha, and Ecclisomyia (Limnephilidae) were present in a greater percent of subalpine and alpine lakes (73%, 58%, 35%, respectively for each taxon) than forest lakes (27%, 40%, 20%, respectively for eachtaxon). D. mono is a LITH organism, and Psychoglypha and Ecclisomyia are reported to be cold-adapted species (Anderson 1976; Wiggins 1977).

Vertebrate Predators

The distribution of three of 15 nearshore macroinvertebrates appeared to be affected by vertebrate predators (Table 10). Three taxa (i.e., Taenionema, Ameletus,and Desmona) were found in significantly fewer lakes with predators (Fisher's Exact Test, $p<0.05$). The stonefly, Taenionema, was not collected from lakes with salamanders or trout but was found in 5 of 7 lakes with no vertebrate predators. The mayfly, Ameletus, was present in a significantly greater number of lakes without vertebrate predators (Fisher's Exact Test, $p=0.002$). Its restricted distribution in these lakes may be due more to salamanders than trout, since no significant difference between lakes with and without fish was found and some FNR lakes can have well established populations of the salamander A. gracile. The caddisfly, Desmona, may be limited in distribution by trout. Desmona was found in a significantly higher number of lakes without fish (Fisher's Exact Test, $p=0.006$). Differences among vertebrate predation categories for the other 12 taxa were not significant.

DISCUSSION

The distribution of nearshore macroinvertebrates in high mountain lakes is affected by interrelated factors (Figure 4) associated with life history, habitat, and trophic relationships (Wevers and Warren 1986). The life history of freshwater macroinvertebrates is determined by those innate and acquired capacities which promote reproductive success and survival including: 1) the ability to disperse and colonize other locations; 2) the ability to acquire necessary resources for growth and maintenance; 3) adult fecundity; and 4) intra- and interspecific behavior (Oliver 1979; Butler 1984; Sweeney 1984; Wevers and Warren 1986). Inorganic and organic

Table 10. Vertebrate predation category comparisons for three macroinvertebrate taxa in NOCA lakes (Fisher's Exact Test, $p < 0.05$).

	NUMBER OF LAKES IN EACH PREDATION CATEGORY						
	NVP	S	FNR	FR	VP	F	NF
TAXON (n =	7	6	5	6	17	11	13)
Taenionema	5	0	0	0	0	0	5
Ameletus	7	1	1	3	5	4	8
Desmona	7	5	2	2	9	4	12

P-VALUES FOR PAIRWISE COMPARISONS AMONG CATEGORIES		
TAXON	Comparison	p - Value
Taenionema	NVP > VP	0.0005
Ameletus	NVP > VP	0.002
Desmona	NF > F	0.006

1. NVP : No vertebrate pradation
2. VP : Vertebrate preadtion (lakes with salamanders and fish)
3. S : Salamanders and no fish
4. FNR : Non-reproducing fish with salamanders
5. FR : Reproducing fish with minimal or no salamanders
6. NF : No fish (NVP + S)
7. F : Fish (non-reproducing and reproducing)

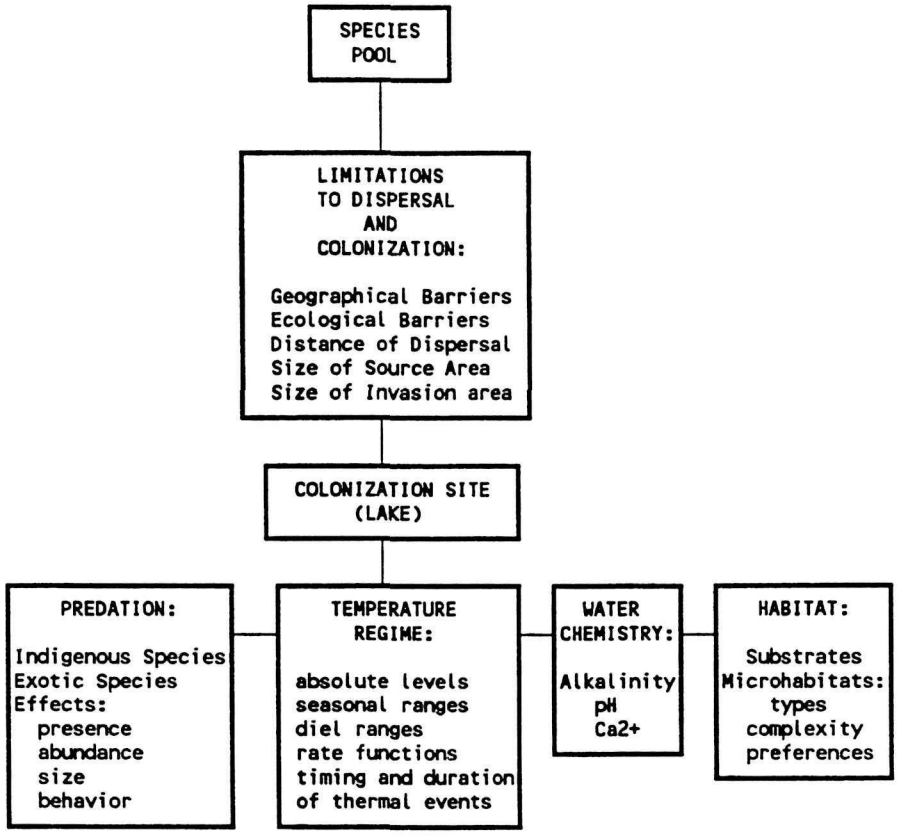


Figure 4: Factors affecting the presence of macroinvertebrates in high mountain lakes.

substrates, as well as water chemistry and temperature regime impart organization and structure to habitats. Trophic organization is related to the energy and material relations that interconnect the parts of a community (Liss and Warren 1980). Competition and predation are two types of interactions that can affect acquisition and utilization of resources and, therefore, successful colonization and persistence (Friday 1987; Bass 1992; Mackay 1992).

Lakes in the northern Cascade Mountains are isolated in rugged terrain in a region which is tectonically active (Press and Siever 1982) and geologically young (McKee 1972). Lakes often lack physical connection via inlet and outlet tributaries, and basin characteristics (e.g., geology, climate, elevation, aspect, vegetation, etc.) typically vary between sites (Lomnicky et al. 1989). These conditions may limit dispersal and contribute to the limited distribution of many macroinvertebrates in NOCA study lakes.

The distribution of taxa within an area reflects the concordance of habitat conditions and habitat requirements of organisms. Habitat diversity contributes to the persistence of organisms in lentic systems and enhances species diversity (Liss and Warren 1980; Crowder and Cooper 1982; Gilinsky 1984). In the present study, three fundamental aspects of habitat affected the distribution of nearshore macroinvertebrates: 1) maximum water temperature; 2) water chemistry variables, especially pH, alkalinity, and [Ca^{2+}]; and 3) the types of substrates present in the nearshore areas of lakes.

The mean number of nearshore macroinvertebrate taxa inhabiting a lake was directly related to maximum temperature. Forest zone lakes tended to have warmer average maximum temperatures and higher mean numbers of taxa than subalpine and alpine zone lakes. Departures from this general trend appeared related, in part, to

differences in elevation and availability of benthic microhabitat substrates.

Temperature influences aquatic insect life history, especially larval growth, adult size and fecundity (Sweeney 1984), and potentially controls many aspects of insect development (Vannote and Sweeney 1980). According to Ward and Stanford (1982), cool headwaters of streams may have been the ancestral habitat for many aquatic insect groups, and evolutionary adaptation to different thermal conditions made colonization of lower river reaches and lentic systems possible. An increasing number of taxa became associated with wider daily and annual temperature variations, creating a greater range of temperature requirements for cool- and warm-adapted species.

Although many water chemistry variables have wide natural ranges (Ward 1992) to which numerous macroinvertebrates are tolerant, certain variables (e.g., pH, alkalinity, and water hardness) may have a particularly important influence on distribution of taxa in aquatic systems. The level of successful emergence in aquatic insects (Bell 1971), species diversity in Crustacea (Fryer 1980), and species richness of macroinvertebrates in lakes (Schell and Kerekes 1989) have all been shown to be positively correlated with pH. Foster (1991) identified three species of Coleoptera in Britain, including P. griseostriatus, that were restricted to acidic conditions in standing water. Some macroinvertebrates also are limited by water hardness. For example, mollusks and some crustaceans have high physiological demands for calcium and therefore specific hardness levels (Ward 1992). In NOCA, the distribution of gastropods and P. griseostriatus appeared to have been limited by habitat requirements related to aspects of water chemistry, (e.g., pH, alkalinity, and $[Ca^{2+}]$).

The influence of benthic habitat substrates on the distribution and diversity of macroinvertebrates in aquatic systems has been associated with substrate particle size

in stream habitats (Wevers and Warren 1986), spatial heterogeneity of habitat in the littoral zone of a pond (Gilinsky 1984), and the substrate preference of organisms in aquatic systems in general (Ward 1992). Substratum and substrate particle size influence the abundance and distribution of aquatic insects (Minshall 1984). Crowder and Cooper (1982), Gilinsky (1984), and Diehl (1992) found that habitats with submerged vegetation support higher abundances of benthic macroinvertebrates and greater species richness.

In the forest zone in NOCA, organic substrates were present in a high percentage of microhabitats. Of the three forest categories, FLW lakes had the highest proportion of microhabitats with organic substrates and the highest proportion of taxa comprising organic-based substrate preference groups. As elevation increased in the forest zone (i.e., from FLW to FHW and FHE), and as vegetation zone changed to subalpine and alpine, the proportion of microhabitats containing organic substrates decreased.

As the presence of inorganic substrates increased in nearshore microhabitats so to did the proportion of taxa representing inorganic-based substrate preference groups. This change, which occurred in higher elevation forest lakes (i.e., FHW and FHE), as well as in subalpine and alpine zone lakes was due, in part, to increases in the number of LITH and MINO taxa.

Aquatic systems should be viewed in a broad, integrative framework which expresses the physical environment (Frissell et al. 1986; Lomnicky et al. 1989). Lomnicky (unpublished manuscript; Liss et al. 1991) classified lakes in NOCA according to physiographic characteristics of the terrestrial environment. These characteristics are vegetation zone, crest position (regional topography), and elevation

within the forest zone. They indirectly reflect climatic regime and geology. Climate is expressed, in part, by cycles of precipitation and temperature which influence vegetation complexes. Regional topography influences the development of microclimatic conditions within individual lake basins. Variations in the physical and chemical weathering of different lithologies contribute to the formation of different complexes of weathering products (e.g., types of rock fragments, solutions, and secondarily produced new materials; Ollier 1984), as well as to the differential genesis and development of soils and vegetation.

In our research, predictor variables based upon characteristics of the aquatic environment were found to be useful in assigning lakes to terrestrially-based classification categories. This outcome is representative of patterns in the data that are consistent with the hypothesis that abiotic and biotic conditions within lakes are dynamically interconnected with characteristics and processes in the terrestrial environment. Physiographic factors in the terrestrial environment determine characteristics of lake habitat including quantity and type of inorganic and organic substrates, temperature regime, and water chemistry which, in turn, influence distribution and abundance of lake biota.

Macroinvertebrate communities in forest, subalpine, and alpine lakes reflected the relationship between changing habitat conditions and the habitat requirements of organisms. These changes occurred along a continuum associated with vegetation zone, crest position, and elevation (Table 11). Forest zone lakes, in general, had high numbers of taxa and elevated water temperatures. A typical forest lake community was dominated by predators, and included organisms (e.g., Callibaetis, Gastropoda, Halesochila, leeches, Limnephilus, Odonata, Megaloptera, Polycentropus, Sphaeriidae,

Table 11. Parameters of habitat and taxa in NOCA lake classification categories.

Category	Primary Substrates (1) Inorganic	Primary Substrates (1) Organic	Dominant Preference Groups (2)	Important Taxonomic Groups (3)	No. Taxa Groups (n=16)
FLW	BL	OD,CW, FW, ESV	PEO, GENR, PHYT, MMIX	COLE DIPT-TRIC ODON GAST-EPHE	16
FHW	ST,GR,CB	OD,CW,FW	PELO,GENR, MMIX	DIPT TRIC COLE EPHE-PLEC-HEMI	15
FHE	CB,ST,BL,SD	FW,OD,CW	GENR,PELO, MMIX,LITH	TRIC EPHE PLEC-HEMI-COLE-DIPT	14
SW	CB,ST,GR	CW,FW	GENR,LITH, PELO,MINO, MMIX	TRIC COLE PLEC	10
SE	ST,CB,GR	FW,CW	GENR,PELO, LITH,MMIX	TRIC DIPT PLEC COLE	12
ALP	CB,GR,ST,SD		GENR,PELO, LITH,MINO	TRIC DIPT PLEC	9

(1) Substrates in > 35% of microhabitats and listed in decreasing order of proportional presence
(2) Listed by decreasing proportion of taxa/group
(3) Groups representing 67-76% of taxa/category: COLE = Coleoptera; DIPT = Diptera; EPHE = Ephemeroptera; GAST = Gastropoda; HEMI = Hemiptera; ODON = Odonata; PLEC = Plecoptera; TRIC = Trichoptera

etc.) tolerant of warmer water temperatures and requiring complex habitats composed, in part, of fine particulate substrates and aquatic vegetation. Taxa associated with these habitat parameters were dominant in FLW lakes and present to a lesser extent in FHW and FHE communities. Relative to FLW lakes, FHW and FHE lakes had a higher percentage of microhabitats containing inorganic substrates, decreased water temperatures, and taxa tolerant of these conditions. In subalpine zone lakes, the number of taxa and water temperature were reduced relative to forest lakes. The percentage of microhabitats with inorganic substrates was higher than in forest zone lakes and microhabitats containing organic substrates were greatly reduced. Taxa (e.g., Ameletus, Desmona, Psychoglypha, Ecclisomyia, small-bodied dytiscid beetles, etc.) associated with inorganic substrates and colder water temperatures increased in subalpine communities, and taxa tolerant of warmer water and varying habitat conditions diminished. Predators became less dominant and the proportion of taxa per functional group became increasingly more equitable possibly due, in part, to a general decrease in the number of taxa per lake. SW communities, more so than communities in SE lakes, tended to exhibit a strong relationship between low taxa diversity and reduced water temperature. Alpine lake communities further illustrated the attenuation of macroinvertebrate diversity and distribution related to reduced water temperature and diminished habitat complexity, especially the lack of organic substrates. ALP lakes were inhabited almost exclusively by organisms adapted to colder temperatures and microhabitats composed of inorganic substrates, and the percent of taxa per functional group in this zone was more "even" than in the forest and subalpine zones.

Salamanders and trout have been implicated as affecting macroinvertebrate populations. Ambystoma gracile and Ambystoma macrodactylum larvae prey upon

nearshore macroinvertebrates (Anderson 1968; Efford and Tsumura 1973) which are also important prey of trout (Efford and Tsumura 1973; Johnsen 1978; Stenson 1981). Ambystoma have been shown to affect the size-structure and species composition of zooplankton communities in Colorado alpine ponds (Dodson 1970; Sprules 1972). The elimination of prey species or groups of species by fish in high mountain lakes has also been documented (Nilsson 1972; Walters and Vincent 1973; Dawidowicz and Gliwicz 1983; Bahls 1991). Reimers (1958) reported that brook trout (Salvelinus fontinalis (Mitchell)) were able to deplete mayfly and caddisfly populations in a small, high-altitude lake in the eastern Sierra Nevada, California, USA. Johnsen (1978) has demonstrated that trout predation upon various groups of macroinvertebrates (e.g., surface organisms, macrobenthos, plankton) changed with weather conditions, season, and prey availability. Trout also induce changes in behavioral responses of nearshore macroinvertebrates (Pierce 1988; Feltmate and Williams 1989; Feltmate, Williams, and Montgomerie 1992). Feltmate and Williams (1989) and Feltmate et al. (1992) found that stoneflies selected darker substrates and changed diurnal activity patterns in the presence of trout. Odonates and stoneflies increased predator avoidance behavior (Pierce 1988; Feltmate and Williams 1989), and odonates decreased use of exposed microhabitats in the presence of fish (Pierce 1988).

Results from the present study indicate that the distributions of three taxa may be affected by vertebrate predators. Several factors may mitigate the impact of vertebrate predators on nearshore macroinvertebrates in NOCA lakes. Prey species and predators that have coexisted over long periods of time have developed relationships which are tightly integrated and relatively stable (Thorp 1986). Members of the salamander family Ambystomatidae are indigenous to North America (Nussbaum

et al. 1983), and have probably been present in Cascade Range lakes for some time. Taylor et al. (1988) suggested that although larval Ambystoma talpoideum (Holbrook), Eurycea quadridigitata (Holbrook), and Notophthalmus viridescens (Rafinesque) of different size selectively preyed upon planktonic and benthic macroinvertebrates in a temporary pond in South Carolina, USA, they did not adversely affect macroinvertebrate community composition or abundance. Petranka (1989) determined that Ambystoma opacum (Gravenhorst) larvae did not reduce zooplankton biomass in 11 natural ephemeral ponds in North Carolina, USA. Trout, having more recently been introduced into NOCA lakes, may have a greater potential of adversely impacting macroinvertebrate distributions. Luecke (1990) found that cutthroat trout introduced into Lake Lenore, Washington, USA, decreased densities of dominant macroinvertebrates in profundal and pelagic regions, but not in the littoral zone. This outcome was attributed to increased refugia in the littoral zone, as well as to the relationship between salmonid mouth structure, prey-search pattern and the ability to access partially concealed prey. Bahls (1991) found that large water-column organisms (e.g., Chaoborus and Coleopteran and Hemipteran taxa) in lakes of the Selway Bitterroot Wilderness, Idaho, USA, were present in fewer lakes with trout. Large water-column taxa were restricted in distribution in NOCA. Nine of 10 of these taxa were found in <20% of study lakes with five taxa collected only from individual locations. The potential for detecting impacts of trout predation on these taxa through the comparison of their distributions in fish and fishless lakes in NOCA was limited by their attenuated distributions.

SUMMARY

A high percentage of nearshore macroinvertebrates were restricted in distribution in northern Cascade Range lakes. Distributions were influenced by ecological factors such as water temperature, benthic habitat substrates and taxa substrate preferences, water chemistry parameters, and, to a limited extent, the type and presence of vertebrate predators in lakes. Discriminant analysis was used to examine how variables representing characteristics of the aquatic environment (i.e., nearshore microhabitat substrates and their associated taxa) influenced the predicted placement of lakes into six lake classification categories based on physiographic characteristics of the terrestrial environment. This analysis helped to demonstrate the interconnection between processes in the terrestrial environment and the physical, chemical, and biological conditions in lakes. Future research interests should include a more specific examination of those aspects of temperature regime which are important in influencing macroinvertebrate distributions. Investigation of the impact of vertebrate predators on macroinvertebrate distribution, abundance and behavior should also be continued. Perhaps the best way to assess effects of fish on lentic macroinvertebrates is through some form of experimental manipulation of lakes. The distributions of offshore organisms needs to be elucidated. This information would complement what is already known concerning nearshore macroinvertebrate distributions. Finally, research designed to examine the contribution of macroinvertebrates to the secondary productivity of high mountain lakes, as well as to elucidate the specific roles of macroinvertebrates in the processing and cycling of nutrients would contribute significantly to a more complete understanding of high mountain lake macroinvertebrate ecology.

CONCLUSIONS REGARDING EFFECTS OF STOCKED TROUT ON NATIVE BIOTA IN NOCA

1. Salamander larvae are the top vertebrate predators in many fishless lakes in NOCA. Larvae of Ambystoma macrodactylum appear to be relatively sensitive to predation from introduced trout. There were statistically significant differences in larval densities between lakes with fish and fishless lakes. We found few or no larvae in lakes with trout with the exception of MR 11, a lake with sporadic history of trout stocking. However, larval density in fishless lakes was variable indicating that abiotic factors possibly related to lake size were influencing larval abundance. Limited sampling of lakes with A. gracile suggests that this species may be less vulnerable to trout predation than A. macrodactylum. In lakes with trout, A. gracile maintained higher densities of embryo masses and larvae than A. macrodactylum. Ambystoma macrodactylum may persist in the same geographic area as stocked trout by utilizing habitats that are unsuitable or inaccessible to trout such as smaller, shallower lakes and ponds. These habitats can support relatively high densities of larvae. Ambystoma gracile may persist in the same geographic region as trout by possessing behavioral and morphological adaptations such as noxious skin sectretion, more reclusive or nocturnal behavior, or large size that enable it to live in lakes with fish.
2. Effects of introduced trout on the limnetic food web appear to be influenced by trout density and size structure and lake nutrient levels. In general, reproducing trout maintain higher densities and a more complex age and size structure than lakes in trout which do not reproduce are periodically stocked as fry. The large

copepod Diaptomus kenai is the most ubiquitous crustacean zooplanktoer in NOCA. It is apparently able to persist across a wide range of abiotic factors in NOCA lakes, but may be limited by higher temperatures in some lakes. The small copepod, D. tyrrelli, was found only in lakes with higher nutrient levels. These lakes tended to be smaller, shallower lakes. Large copepods appear to negatively affect D. tyrrelli, probably through predation. In eastslope lakes, densities of D. kenai were significantly lower in lakes with reproducing fish than in lakes with non-reproducing trout. We were unable to determine if if there were differences in D. kenai densities between lakes with non-reproducing trout and lakes with no vertberate predators since most eastside lakes maintained either trout or salmander larvae. We hypothesize that reproducing trout at high densities can reduce or eliminate large copepods. In smaller, shallower lakes with nutrient levels suitable for D. tyrrelli, the small copepod may increase in abundance following reduction or elimination of large copepods by trout predation.

3. Three of 15 taxa of nearshore macroinvertebrates were found in significantly fewer lakes with vertebrate predators (trout and salamanders) than in lakes with no vertebrate predators. The distribution of only one of these taxa, Desmona, may be limited solely by trout. Distribution and abundance of rotifer taxa appear largely unrelated to vertebrate predators.

LITERATURE CITED

Aber, J.D., and J.M. Melillo. 1991. *Terrestrial ecosystems.* Philadelphia Saunders College Publishing, 429 pp.

Agee, J.K., and S.G. Pickford. 1985. Vegetation and fuel mapping of North Cascades National Park Service Complex. Final Report CX-9000-3-E029. 111 pp.

Alt, D. 1984. *Roadside geology of Washington.* Mountain Press Pub. Co. Missoula, Montana. 282 pp.

Anderson, J.D. 1967. A comparison of the life histories of coastal and mountain populations of Ambystoma macrodactylum in California. Am. Midl. Nat. 77: 323-354.

Anderson, J.D., and R.E. Graham. 1967. Vertical migration and stratification of larval Ambystoma. Copeia 1967: 371-374.

Anderson, J.D. 1968. A comparison of the food habits of Ambystoma macrodactylum sigillatum , Ambystoma macrodactylum croceum, and Ambystoma tigrinum Californiense. Herpetologica 24: 273-284.

Anderson, N.H. 1976. The distribution and biology of the Oregon Trichoptera. *Technical Bulletin 134, Agricultural Experiment Station*, Oregon State University, Corvallis, OR. 152 pp.

Anderson, R.S. 1970b. Preadtor-prey relationships and predation rates for crustacean zooplankters from some lakes in western Canada. Can. J. Zool. 48:1229-1240.

Anderson, R.S. 1971. Crustacean plankton of 146 alpine and subalpine lakes and ponds in western Canada. J. Fish. Res. Bd. Canada 28:311-321.

Anderson, R.S. 1972. Zooplankton composition and change in an alpine lake. Verh. Internat. Verein. Limnol. 17:264-268.

Anderson, R.S. 1974. Crustacean plankton communities of 340 lakes and ponds in and near the National Parks of the Canadian Rocky Mountains. J. Fish. Res. Board Can. 31:855-869.

Anderson, R.S. 1980. Relationships between trout and invertebrate species as predators and the structure of the crustacean and rotiferan plankton in mountain lakes. In: Evolution and Ecology of Zooplankton Communities: special symposium volume 3, American Society of Limnology and Oceanography. W.C. Kerfoot (ed.). Univ. Press of New England, Hanover, N.H. 793 pp.

Arndt, H. 1993. Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates) - a review. Hydrobiology 255/256: 231-246.

Arvola, L. 1986. Spring phytoplankton of 54 small finish lakes in southern Finland. Hydrobiol. 137: 125 - 134.

Bahls, P.F. 1991. Ecological implications of trout introductions to lakes of the Selway Bitterroot Wilderness, Idaho. *M.S. Thesis*, Oregon State University, Corvallis, OR. 85 pp.

Bahls, P. 1992. The status of fish populations and management of high mountain lakes in the western United States. Northwest Science 66: 183-193.

Barnes, E.B. 1983. The colonization of ball-clay ponds by macroinvertebrates and macrophytes. *Freshwater Bio.* 13, 561-578.

Bass, D. 1992. Colonization and succession of benthic macroinvertebrates in Arcadia Lake, a South-Central USA reservoir. *Hydrobiol.* 242, 123-131.

Bell, H.L. 1971. Effect of low pH on the survival and emergence of aquatic insects. *Water Research* 5, 313-319.

Benke, A.C. 1984. Secondary production of aquatic insects. (in V.H. Resh and D.M. Rosenberg, eds., *The Ecology of Aquatic Insects.*) 289-322.

Berzins, B., and J. Bertilsson. 1989. On limnic micro-crustaceans and trophic degree. Hydrobiology 185: 95-100.

Blaustein, A.R. and D.B. Wake. 1990. Declining amphibian populations: A global phenomenon? Trends Ecol. Evol. 5: 203-204.

Blois-Heulin, C., P.H. Crowley, M. Arrington, and D.M. Johnson. 1990. Direct and indirect effects of predators on the dominant invertebrates of two freshwater Littoral communities. Oecologia. 84:295-306.

Bowler, J.K. 1977. Longevity of reptiles and amphibians in North American collections. Herpetol. Circ. 6:1-32.

Bradford, D.F. 1989. Allopatric distribution of native frogs and introduced fishes in high Sierra Nevada lakes of California: implication of the negative effect of fish introductions. Copeia 1989: 775-778.

Bradford, D.F., F. Tabatabai, and D.M. Graber. 1993. Isolation of remaining populations of the native frog, Rana muscosa, by introduced fishes in Sequoia and Kings Canyon National Parks, California. Cons. Biol. 7: 882-888.

Brodie, E.D., and L.S. Gibson. 1969. Defensive behavior and skin glands of the northwestern salamander, Ambystoma gracile. Herpetologica 25: 187-194.

Brooks, J.L. and S.I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150: 28-35.

Browne, R.A. 1981. Lakes as islands: biogeographic distribution, turnover rates, and species composition in the lakes of central New York. *J. Biogeogr.* 8, 75-83.

Brundin, L. 1958. The bottom faunistical lake type system and its application to the southern hemisphere. Moreover a theory of glacial erosion as a factor of productivity in lakes and oceans. Verh. Internat. Ver. Limnol. 13:288-297.

Buol, S.W., F.D. Hole, and R.J. McCracken. 1973. *Soil genesis and classification.* The Iowa State Univ. Press, Ames Iowa. 360 pp.

Busch, W.D.N., and P.G. Sly. 1992. *The development of an aquatic habitat classification system for lakes.* CRC Press. Boca Raton, Florida. 225 pp.

Butler, M.G. 1984. Life histories of aquatic insects. (in V.H. Resh and D.M. Rosenberg, eds., *The Ecology of Aquatic Insects.*) 24-55.

Canfield, D.E., Jr., S.B. Linda, and L.M. Hodgson. 1984. Relations between color and some limnological characteristics of Florida lakes. Wat. Res. Bull. 20(3):323-

Carlson, R.E. 1977. A trophic state index for lakes. Limnol. Oceanogr. 22:361-369.

Carpenter, C.C. 1953. Trapping technique for aquatic salamanders. Herpetologica 8: 183.

Chilton II, E.W. and F.J. Margraf. 1990. Effects of fish predation on invertebrates associated with a macrophyte in Lake Onalaska, Wisconsin. *J. Freshwater Ecol.* 5(3): 289-296.

Corbet, P.S. 1980. Biology of Odonata. *Ann. Rev. Entomol.* 25: 189-217.

Corn, P.S. and J.C. Fogelman. 1984. Extinction of montane populations of the northern leopard frog (Rana pipiens) in Colorado. J. Herpetol. 18: 147-152.

Cortwright, S.A., and C.E. Nelson. 1990. An examination of multiple factors affecting community structure in an aquatic amphibian community. Oecologica 83: 123-131.

Crandell, D.R. 1965. The glacial history of western Washington and Oregon. In [Wright, H.E., Jr., and Frey, D.G., eds.] p. 341-353. *The Quaternary of the United States*: Princeton, J.J., Princeton Univ. Press.

Crowder, L.B. and W.E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63(6), 1802-1813.

Cummins, K.W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *Am. Midl. Nat.* 67, 477-504.

Dawidowicz, P. and E.N. Gliwicz. 1983. Food of brook char in extreme oligotrophic conditions of an alpine lake. Env. Biol. Fish. 8:55-60.

Diehl, S. 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. *Ecology* 73, 1646-1661.

Dodson, S.I. 1970. Complementary feeding niches sustained by size-selective predation. Limnol. Oceanogr. 15: 131-137.

Dodson, S.I. and V.E. Dodson. 1971. The diet of Ambystoma tigrinum larvae from western Colorado. Copeia 1971: 614-624.

Dodson, S.I. 1974. Zooplankton competition and predation: an experimental test of the size-efficiency hypotheses. Ecology 55: 605-613.

Dumont, H.J. 1983. Biogeography of rotifers. Hydrobiology 104: 19-30.

Dunn, E.R. 1944. Notes on the salamanders of the Ambystoma gracile Group. Copeia 1944: 129-130.

Earle, J.C., H.C. Duthie and D.A. Scruton. 1986. Analysis of the phytoplankton composition of 95 Labrador lakes with special reference to natural and anthropogenic acidification. Can. J. Fish. Aquat. Sci. 43: 1804 - 1811.

Earle, J.C., H.C. Duthie and D.A. Scruton. 1987. Factors influencing the distribution of phytoplankton in 97 headwater lakes in insular Newfoundland. Can. J. Fish. Aquat. Sci. 44: 639 - 649.

Edmunds, G.F., S.L. Jensen and L. Berner. 1976. *The Mayflies of North and Central America.* University of Minnesota Press, Minneapolis. 330 pp.

Efford, I.E. and J.A. Mathias. 1969. A comparison of two salamander populations in Marion Lake, British Columbia. *Copeia* 1969: 723-736.

Efford, I.E., and K. Tsumura. 1973. A comparison of the food Salamanders and fish in Marion Lake, British Columbia. Trans. Am. Fish. Soc. 1973: 33-47.

Elser, J.J. 1992. Phytoplankton dynamics and the role of grazers in Castle Lake, California. Ecology. 73: 887 - 902.

Faith, D.P. and R.H. Norris 1989. Correlation of environmental variables with patterns of distribution and abundance of common and rare freshwater macroinvertebrates. *Bio. Conserv.* 50, 77-98.

Feltmate, B.W. and D.D. Williams. 1989. Influence of rainbow trout (Oncorhynchus mykiss) on density and feeding behaviour of a perlid stonefly. *Can. J. Fish. Aquat. Sci.* 46, 1575-1580.

Feltmate, B.W., D.D. Williams and A. Montgomerie. 1992. Relationship between diurnal activity patterns, cryptic coloration, and subsequent avoidance of predaceous fish by perlid stoneflies. *Can. J. Fish. Aquat. Sci.* 49, 2630-2634.

Ferguson, D.E. 1961. The geographic variation of Ambystoma macrodactylum Baird, with the description of two new subspecies. Amer. Midl. Nat. 65(2): 311-338.

Figiel, C.R. and R.D. Semlitsch. 1990. Population variation in survival and metamorphosis of larval salamanders (Ambystoma maculatum) in the presence and absence of fish predation. Copeia 1990: 818-826.

Formanowicz, D.R., and E.D. Brodie. 1982. Relative palatabilities of members of a larval amphibian community. Copeia 1982: 91-97.

Foster, G.N. 1991. Aquatic beetle population changes associated with recreating a trout fishery by limiting a lake catchment. *Arch. Hydrobiol.* 122(3), 313-322.

Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service General Technical Report PNW-8. 417 pp.

Franklin, J.F., W.H. Moir, M.A. Hemstrom, S.E. Greene, and B.G. Smith. 1988. The forest communities of Mount Rainier National Park. National Park Service, Scientific Monograph Series No. 19, 194 pp.

Friday, L.E. 1987. The diversity of macroinvertebrate and macrophyte communities in ponds. *Freshwater Bio.* 18, 87-104.

Frissell, C.A., Liss, W.J., Warren, C.E., and M.D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environ. Mgt. 10(2):199-214.

Fryer, G. 1980. Acidity and species diversity in freshwater crustacean faunas. *Freshwater Bio.* 10, 41-45.

Ganio, L. - Statistician at MANTECH, Corvallis, Oregon.

Gannon, J.E., and R.S. Stemberger. 1978. Zooplankton (especially crustaceans and rotifers) as indicators of water quality. Trans. Amer. Micros. Soc. 97(1): 16-35.

Geller, W.J., and J. Muller. 1981. The filtration apparatus of Cladocera: filter mesh-sizes and their implications on food selectivity. Oecologia 49: 316-321.

Giguere, L. 1979. An experimental test of Dodson's hypothesis that Ambystoma (a salamander) and Chaoborus (a phantom midge) have complementary feeding niches. Can. J. Zool. 57: 1091-1097.

Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology* 65(2), 455-468.

George, D.G., and P.S. Maitland. 1984. The fresh waters of Shetland: physical and morphometric characteristics of lochs. Fresh. Biol. 14:95-107.

Gilbert, J.J. 1985. Competition between rotifers and Daphnia. Ecology 66(6): 1943-1950.

Gliwicz, Z.M. 1969. The share of algae, bacteria and trypton in the food of the pelagic zooplankton of lakes with various trophic characteristics. Bull. de L'Acad. Polonaise des Sci. 17(3): 159-165.

Goetze, B., W.J. Liss and G.L. Larson. 1989. Ecological implications of fish introductions into temperate lakes: A review. National Park Service Technical Report. 61 p.

Goldman, C.R., and A.J. Horne. 1983. *Limnology.* McGraw Hill Publ. New York, N.Y. 464 pp.

Gorham, E. 1961. Factors influencing supply of major ions to inland waters, with special reference to the atmosphere. Bull. Geol. Soc. Amer. 72:795-840.

Green, J. 1993. Diversity and dominance in planktonic rotifers. Hydrobiology 255/256: 345-352.

GTCO. 1982. Graphics analysis package #1 for the IBM Personal Computer. Document No. 21A67A1. GTCO Corp., Rockville, MD.

Hafele, R. and D. Hughes. 1981. *The Complete Book of Western Hatches.* Frank Amato Publications, Portland, OR. 223 pp.

Haney, J.F., and D.J. Hall. 1973. Sugar-coated Daphnia: A preservation technique for Cladocera. Limnol. Oceanogr. 18(2): 331-333.

Hayes, M.P. and M.R. Jennings. 1986. Decline of ranid frog species in western North America: Are bullfrogs (Rana catesbeiana) responsible? J. Herpetol. 20: 490-509.

Healey, M. 1984. Fish predation on aquatic insects. (in V.H. Resh and D.M. Rosenberg, eds., *The Ecology of Aquatic Insects.*) 255-288.

Hem, J.D. 1989. Study and interpretation of the chemical characteristics of natural water. Third edition. U.S.Geological Survey Water-Supply Paper 2254, 263 pp.

Heyer, W.R., R.W. McDiarmid, and D.L. Weigmann. 1975. Tadpoles, predation and pond habitats in the tropics. Biotropica 7: 100-111.

Heyer, W.R. 1976. Studies in larval amphibian habitat partitioning. Smith. Cont. Zool. 242.

Hill, M.O. and H.G. Gauch. 1980. Detrended correspondence analysis: An improved ordination technique. Vegetatio. 42:47-58.

Hintze, J.L. 1992. *Number Cruncher Statistical System, Version 5.03.* Kaysville, Utah.

Howard, J.H. and R.L. Wallace. 1981. Microgeographical variation of electrophoretic loci in populations of Ambystoma macrodactylum columbianum (Caudata: Ambystomatidae). Copeia 1989: 466-471.

Hutchinson, G.E. 1957. *A treatise on limnology.* Vol. I. New York, John Wiley & Sons, Inc. 1015 pp.

Hutchinson, G.E. 1967. *A treatise on limnology.* Volume II: Introduction to LakeBiology and the Limnoplankton. John Wiley and Sons, New York. 1115 pp.

Ilmavirta, K., P. Huttunen and J. Merilainen. 1984. Phytoplankton in 151 eastern Finnish lakes: Species composition and its relations to the water chemistry. Verh. Internat. Verein. Limnol. 22: 822 - 828.

Jackson, P., and J. Kimerling. 1993. *Atlas of the Pacific Northwest.* Oregon State University Press, Corvallis, 136 pp.

Jarvis, J. 1987. Natural lakes management and fish stocking meeting, North Cascades National Park Service Complex, November 30, 1987.

Jensen, S., and E. Van Der Maarel. 1980. Numerical approaches to lake classification with special reference to macrophyte communities. Vegetatio 42:117-128.

Johnsen, B.O. 1978. Seasonal variations in the diet of the brown trout (Salmo trutta L.) in a Norwegian mountain lake compared with variations in the plankton and bottom fauna. *Astarte* 11(1), 37-44.

Jones, C. Chemist for Cooperative Chemical Analytical Laboratory, Oregon State University, Corvallis, Oregon.

Kezer, J. and D.S. Farner. 1955. Life history patterns of the salamander Ambystoma macrodactylum in the high Cascade Mountains of southern Oregon. Copeia 1955: 127-131.

Kimura, D.K. 1977. Statistical assessment of the age-length key. Journal of the Fisheries Research Board of Canada 34:317-324.

Knoechel, R. and C.E. Cambell. 1988. Physical, chemical, watershed and plankton characteristics of lakes on the Avalon Peninsula, Newfoundland, Canada: A multivariate analysis of interrelationships. Verh. Internat. Verein. Limnol. 23: 282-296.

Lamberti, G.A. and J.W. Moore. 1984. Aquatic insects as primary consumers. (in V.H. Resh and D.M. Rosenberg, eds., *The Ecology of Aquatic Insects.*) 164-195.

Larkin, P. and T.G. Northcote. 1958. Factors in lake typology in British Columbia, Canada. Ver. Int. Ver. Limnol. 13:252-263.

Larson, G.L., E.K. Thomas, C. Hawkins and C.D. McIntire. 1991. Limnological characteristics of isolated and connected high mountain lakes in Olympic National Park. National Park Service, Cooperative Park Studies Unit, College of Forestry, Oregon State University. Technical Report CPSU/OSU 91-4. 53p.

Larson, G.L., A., Wones, C.D. McIntire, and B. Samora. 1994. Integrating limnological characteristics of high mountain lakes into the landscape of a Natural Area. Environ. Mgt.

Leonard, W.P., H.A. Brown, L.L.C. Jones, K.R. McAllister, and R.M. Storm. 1993. Amphibians of Oregon and Washington. Seattle Audubon Society, Seattle, WA.

Lewis, W.M., Jr. 1983. A revised classification of lakes based on mixing. Can. J. Fish. Aquat. Sci. 40:1779-1787.

Licht, L.E. 1975. Growth and food of larval Ambystoma gracile from a lowland population in southwestern British Columbia. *Can. J. Zool.* 53(11): 1716-1722.

Likens, G.E., and F.H. Bormann. 1974. Linkages between terrestrial and aquatic ecosystems. Bioscience 24(8):447-456.

Likens, G.E. 1975. Primary production of inland aquatic ecosystems. In [H. Lieth and R.H. Whittaker, eds.] p. 185-202. *The primary productivity of the Biosphere.* New York, Springer-Verlag.

Liss, W.J., E.K. Deimling, R. Hoffman, G.L. Larson, G. Lomnicky, C.D. McIntire and R. Truitt. 1991. Ecological effects of stocked fish on naturally fishless high mountain lakes: North Cascades National Park Service Complex. Annual Report 1990-1991. 167 p.

Liss, W.J., E.K. Deimling, G.A. Lomnicky, R.L. Hoffman, S.D. Buhler, G.L. Larson, and L. Ganio. (In Review) Abundance of larval salamanders in fish and fishless lakes in the northern Washington Cascades, USA. *J. Herpetol.*

Liss, W.J. and C.E. Warren. 1980. Ecology of aquatic systems. (in R.T. Lackey and L.A. Nielson, eds., *Fisheries Management.*) 41-80.

Lomnicky, G.A. (*Unpublished Manuscript*) Classification of lakes in the glacially influenced mountainous landscape of the North Cascades, Washington, USA.

Lomnicky, G., W.J. Liss, and G.L. Larson. 1989. Toward a classification of the watersheds and lakes of the North Cascades National Park Service Complex. Final Report, National Park Service. 107 pp.

Lotspeich, F.B., and W.S. Platts. 1982. An integrated land-aquatic classification system. North American Journal of Fisheries Management 2:138-149.

Ludwig, J.A. and J.F. Reynolds. 1988. Statistical Ecology. John Wiley & Sons, New York. 337pp.

Luecke, C. 1990. Changes in abundance and distribution of benthic macroinvertebrates after introduction of cutthroat trout into a previously fishless lake. *Trans. Amer. Fish. Soc.* 119: 1010-1021.

Macan, T.T. 1966. The influence of predation on the fauna of a moorland fishpond. *Arch. Hydrobiol.* 61(4), 432-452.

Macan, T.T. 1977. The influence of predation on the composition of fresh-water animal communities. *Bio. Rev.* 52, 45-70.

Mackay, R.J. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. *Can. J. Fish. Aquat. Sci.* 49, 617-628.

Mani, M.S. 1968. *Ecology and Biogeography of High Altitude Insects.* Dr. W. Junk N.V. Publishers, the Hague. 527 pp.

McIntire, C.D. 1973. Diatom associations in Yaquina Estuary, Oregon: A multivariate analysis. J. of Phycology. 9:254-259.

McIntire, C.D., G.L. Larson, R. Truitt, M. Buktenica and M. Debacon. 1993. Phytoplankton. Pages 359-456 *in* [G. L. Larson, C. D. McIntire and R. W. Jacobs eds.] Crater Lake limnological studies, Final Report, National Park Service Technical Report NPS/PNROSU/NRTR-93103.

McKee, B. 1972. *Cascadia.* Stuart Press, Univ. of Washington. 394 pp.

Merritt, R.W. and K.W. Cummins. 1984. *An Introduction to the Aquatic Insects of North America, 2nd ed.* Kendall/Hunt Publishing Co., Dubuque, Iowa. 722 pp.

Merritt, R.W., K.W. Cummins and T.M. Burton. 1984. The role of aquatic insects in the processing and cycling of nutrients. (in V.H. Resh and D.M. Rosenberg, eds., *The Ecology of Aquatic Insects.*) 134-163.

Minshall, G.W. 1984. Aquatic insect-substratum relationships. (in V.H. Resh and D.M. Rosenberg, eds., *The Ecology of Aquatic Insects.*) 358-400.

Misch, P. 1977. Bedrock geology of the North Cascades. In [Brown, E.H. and Ellis, R.C., eds.] Geological Excursions in the Pacific Northwest: Geological Society of America field guide, annual meeting, Seattle, p. 1-62.

Moore, J.W. 1978. Composition and structure of zooplankton communities in eighteen arctic and subarctic lakes. Int. Rev. ges. Hydrobiol. 63(4): 545-565.

Morin, P.J. 1981. Predatory salamanders reverse the outcome of competition among three species of anuran tadpoles. Science 212: 1284-1286.

Mosello, A. Marchetto, A. Boggero and G.A. Tartari. 1990. Relationships between water chemistry, geographical and lithological features of the watershed of Alpine lakes located in NW Italy. Verh. Internat. Verein. Limnol. 24:155-157.

Moyle, P.B. 1973. Effects of introduced bullfrogs, Rana catesbeiana, on the native frogs of the San Joaquin Valley, California. Copeia 1973: 18-22.

Murdoch, W.W. and J. Bence. 1987. General predators and unstable prey populations. (in W.C. Kerfoot and A. Sih, eds., *Predation: Direct and Indirect Impacts on Aquatic Communities*, Univ. Press of New England, Hanover and London.) 17-30.

National Park Service. 1991. Natural resources management guideline, NPS-77. U.S. Department of Interior, National Park Service, Washington, D.C.

Neill, W.E. 1984. Regulation of rotifer densities by crustacean zooplankton in an oligotrophic montane lake in British Columbia. Oecologia 61: 175-181.

Neill, W.E. 1987. Complex interactions in oligotrophic lake food webs: Responses to nutrient enrichment. In Complex Interactions in Lake Communities (Stephen R. Carpenter, ed.) Pg 30-44.

Neish, I.C. 1971. Comparison of size, structure, and distributional patterns of two salamander populations in Marion Lake, British Columbia. J. Fish. Res. Bd. Canada 28: 49-58.

Nilsson, Nils-Arvid. 1972. Effects of introductions of salmonids into barren lakes. J. Fis. Res. Bd. Canada. 29: 693 - 697.

Nussbaum, R.A., E.D. Brodie, and R.M. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. University of Idaho Press, Moscow.

Nygaard, G. 1949. Hydrobiological studies on some Daanish ponds and lakes. Part II. The quotient hypothesis and some new or little known phytoplankton organisms. Kongel. Danske Vidensk. Selskab Biol. Skrift. 7(1), 293 pp.

Ohle, W. 1965. Nährstoffanreicherung der Gewässer durch Düngemittel und Meliorationen. Münchner Beiträge 12:54-83.

Oliver, D.R. 1979. Contribution of life history information to taxonomy of aquatic insects. *J. Fish.Res. Bd. Can.* 36, 318-321.

Ollier, C. 1984. *Weathering* (second edition). Longman, London and New York. 270 pp.

Overton, W.S., B.G. Smith and C.D. McIntire. 1987. AID programs: analysis of information and diversity. Department of Botany and Plant Pathology, Oregon State University. 34 pp.

Park, B.C., G.M. Simmons, Jr., K.G. Seaburg, D.D. Cathing, and F.C.T. Allnutt. 1982. Comparative ecology of plankton communities in seven Antarctic oasis lakes. J. Plankton Res. 4: 271 - 281.

Pauly, D. 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. International Center for Living Aquatic Resources Management Studies and Reviews 8, Manila.

Pechlaner, R. 1971. Factors that control the production rate and biomass of phytoplankton in high-mountain lakes. Mitt. Internat. Verein. Limnol. 19:125-145.

Pechmann, J.H.K., D.E.Scott, R.D. Semlitsch, J.P. Caldwell, L.J. Vitt, J.W. Gibbons. 1991. Declining amphibian populations: The problem of separating human impacts from natural variation. Science 253: 892-895.

Pejler, B. 1983. Zooplanktic indicators of trophy and their food. Hydrobiology 101: 111-114.

Pennak, R.W. 1958. Regional lake typology in northern Colorado, U.S.A. Verh. internat. Ver. Limnol. 13:264-283.

Pennak, R.W. 1978. Fresh-water Invertebrates of the United States (Second Edition). John Wiley and Sons, New York. 803 pp.

Petranka, J.W. 1983. Fish predation: a factor affecting the spatial distribution of a stream breeding salamander. Copeia 1983: 624-628.

Petranka, J.W. 1989. Density-dependent growth and survival of larval Ambystoma: evidence from whole-pond manipulations. *Ecology* 70(6), 1752-1767.

Pierce, C.J. 1988. Predator avoidance, microhabitat shift, and risk-sensitive foraging in larval dragonflies. *Oecologia* 77, 81-90.

Pinel-Alloul, B., G. Methot, G. Verrault and Y. Vigneault. 1990. Phytoplankton in Quebec lakes: Variation with lake morphology, and with natural and anthropogenic acidification. Can. J. Fish. Aquat. Sci. 47: 1047 - 1057.

Pope, G.F., J.C.H. Carter, and G. Power. 1973. The influence of fish on the distribution of Chaoborus spp. (Diptera) and the density of larvae in the Matamek River system, Quebec. *Trans. Am. Fish. Soc.* 102: 707-714.

Post, J.R. and D. Cucin. 1984. Changes in the benthic community of a small Precombrian lake following the introduction of yellow perch, Perca flauescens. Can. J. Fish. Aquat. Sci. 41: 1496-1501.

Pourriot, R. 1977. Food and feeding habits of Rotifera. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8: 243-260.

Press, F. and R. Siever. 1982. *Earth.* Third Edition. W.H. Freeman Press., San Francisco, CA. 613 pp.

Rawson, D.S. 1955. Morphometry as a dominant factor in the productivity of large lakes. Verh. Int. Ver. Limnol. 12:164-175.

Reece, A.- Owner of Hi-Line Helicopters, Darrington, Washington.

Reimers, N. 1958. Conditions of existence, growth, and longevity of brook trout in a small high-altitude lake of the eastern Sierra Nevada. Cal. Fish and Game. 44:319-333.

Ricker, W.E. 1973. Linear regressions in fishery research. Journal of the Fisheries Research Board of Canada 30:409-434.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Department of Environment, Fisheries and Marine Service, Fish. Res. Bd. Can. Bull. 191, Ottawa, Canada.

Robson, D.S., and H.A. Regier. 1964. Sample size in Petersen mark-recapture experiments. Transactions of the American Fisheries Society 93:215-226.

Round, F.E. 1958. Algal aspects of lake typology. Verh. Int. Ver. Limnol. 13:306-310.

Ruttner-Kolisko, A. 1993. Taxonomic problems with the species Keratella hiemalis. Hydrobiology 255/256: 441-443.

Ryder, R.A., Derr, S.R., Loftus, K.H., and H.A. Regier. 1974. The morphoedaphic index, a fish yield estimator-- a review and evaluation. J. Fish. Res. Board Can. 31:663-688.

Schell, V.A. and J.J. Kerekes. 1989. Distribution, abundance, and biomass of benthic macroinvertebrates relative to pH and nutrients in eight lakes of Nova Scotia, Canada. *Water, Air, and Soil Pollution* 46, 359-374.

Schindler, D.W. 1971. A hypothesis to explain differences and similarities among lakes in the Experimenatal Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Canada 28:295-301.

Secor, D.H., J.M. Dean, and E.H. Laban. 1991. Manual for otolith removal and preparation for microstructural examination. Electric Power Research Institute and Belle W. Baruch Institute for Marine Biology and Coastal Research, Columbia, SC.

Semlitsch, R.D. 1987. Interactions between fish and salamander larvae. Oecologia 72: 481-486.

Semlitsch, R.D. 1988. Allopatric distribution of two salamanders: effects of fish predation and competitive interactions. Copeia 1988: 290-298.

Sexton, O.J. and J.R. Bizer. 1978. Life history patterns of Ambystoma tigrinum in montane Colorado. Am. Midl. Nat. 99: 100-118.

Shannon, C.E. and W. Weaver. 1949. The Mathematical Theory of Communication. Univ. of Illinois Press, Urbana, Illinois.

Sheldon, A.L. 1984. Colonization dynamics of aquatic insects. (in V.H. Resh and D.M. Rosenberg, eds. *The Ecology of Aquatic Insects)* 196-254.

Siegfried, C.A., J.A. Bloomfield, and J.W. Sutherland. 1989. Planktonic rotifer community structure in Adirondack, New York, U.S.A. lakes in relation to acidity, trophic status and related water quality characteristics. Hydrobiology 175: 33-48.

Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. In "Predation: direct and indirect impacts on aquatic communities." W. C. Kerfoot and A. Sih, eds, Univ. Press of New England, Hanover, N. H.

Sih, A., J.W. Petranka, and L.B. Kats. 1988. The dynamics of prey refuge use: a model and tests with sunfish and salamander larvae. Am. Nat. 132: 463-483.

Sih, A., L.B. Kats, and R.D. Moore. 1992. Effects of predatory sunfish on the density, drift, and refuge use of stream salamander larvae. Ecology 73(4): 1418-1430.

Slater, J.R. 1936. Notes on Ambystoma gracile (Baird) and Ambystoma macrodactylum (Baird).Copeia 1936: 234-236.

Smith, B.D., P.S. Maitland, M.R. Young and M.J. Carr. 1981. The littoral benthos. (in P.S. Maitland, ed., *The Ecology of Scotland's Largest Lochs: Lomond, Awe, Ness, Morar and Shiel, Monographie Biologicae* 44, 155-203.

Snedecor, G.W. and W.G. Cochran. 1989. Statistical Methods. Iowa State University Press, Ames.

Snyder, R.C. 1956. Comparative features of the life histories of Ambystoma gracile (Baird) from populations at low and high elevations. Copeia 1956: 41-50.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies ? *J. Anim. Ecol.* 46, 337-365.

Sprules, W.G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology 53: 375-386.

Sprules, W.G. 1974a. The adaptive significance of paedogenesis in North American species of Ambystoma (Amphibia: Caudata): an hypothesis. Can. J. Zool. 52:393-400.

Sprules, W.G. 1974b. Environmental factors and the incidence of neoteny in Ambystoma gracile (Baird) (Amphibia: Caudata). Can. J. Zool. 52: 1545-1552.

Stangel, P.W. and R.D. Semlitsch. 1987. Experimental analysis of predation on the diel vertical migrations of a larval salamander. Can. J. Zool. 65: 1554-1558.

Stebbins, R.C. 1985. A field guide to western amphibians and reptiles. Houghton Mifflin Co., Boston.

Steel, R.G. and J.H. Torrie. 1980. Principles and procedures of statistics: a biometrical approach. 2nd edition. McGraw-Hill, N.Y.

Stemberger, R.S. 1979. A Guide to Rotifers of the Laurentian Great Lakes. U.S. Environmental Protection Agency 600/4-79- 021. 185 pp.

Stemberger, R.S., and J.J. Gilbert. 1987a. Rotifer threshold food concentrations and the size-efficiency hypothesis. Ecology 68(1): 181-187.

Stemberger, R.S., and J.J. Gilbert. 1987b. Defenses of planktonic rotifers against predators. In W.C. Kerfoot and A. Sih (eds), Predation: Direct and indirect

impacts on aquatic communities. Univ. Press of New England, Hanover and London: 227-239.

Stenson, J.A.E. 1978. Differential predation by fish on two species of Chaoborus (Diptera, Chaoboridae). *Oikos* 31: 98-101.

Stenson, J.A.E. 1981. Predator-prey relations between fish and invertebrate prey in some forest lakes. *Rep. Inst. Freshw. Res. Drottiningholm* 58: 166-183.

Stenson, J.A.E. 1982. Fish impact on rotifer community structure. Hydrobiology. 87: 57-64.

Stockner, J.G., and W.W. Benson. 1967. The succession of diatom assemblages in the recent sediments of Lake Washington. Limnol. Oceanogr. 12:513-532.

Stockner, J.G. 1987. Lake fertilization: the enrichment cycle and lake sockeye salmon (Oncorhynchus nerka) production. Can. Spec. Publ. Fish. Aquat. Sci. 96: 198-215.

Stockner J.G., and K.S. Shortreed. 1989. Algal picoplankton production and contribution to food-webs in oligotrophic British Columbia lakes. Hydrobiolog173: 151-166.

Stoddard, J.L. 1987. Microcrustacean communities of high-elevation lakes in the Sierra Nevada, California. J. Plankton Res.9: 631-650.

Sudzuki, M. 1964. New systematical approach to the Japanese planktonic rotifers. Hydrobiology 23(1,2): 1-124.

Swanson, F.J., T.K. Kratz, N. Caine, and R.G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. Bioscience 38(2):92-98.

Sweeney, B.W. 1984. Factors influencing life history patterns of aquatic insects (in V.H. Resh and D.M. Rosenberg, eds., *The Ecology of Aquatic Insects.*) 56-100.

Systat Ver. 5.01., Systat Incorporated.

Tabachnick, B.G. and L.S. Fidell. 1989. Using Multivariate Statistics, second edition. Harper Collines Publishers, Inc., New York. 746 pp.

Taylor, B.E., R.A. Estes, J.H.K. Pechmann, and R.D. Semlitsch. 1988. Trophic relations in a temporary pond: larval salamanders and their macroinvertebrate prey. *Can. J. Zool.* 66, 2191-2198.

Taylor, J. 1983. Orientation and flight behavior of a neotenic salamander (Ambystoma gracile) in Oregon. Am. Midl. Nat. 109: 40-49.

Taylor, J. 1984. Comparative evidence for competition between the salamanders Ambystoma gracile and Taricha granulosa. Copeia 1984: 672-683.

Teti, P. 1984. Time-variant differences in chemistry among four small streams. Wat. Res. Research. 20(3):347-359.

Thienemann. A. 1909. Vorlaufige Mitteilung über Probleme Ziele der biologischen Erforschung der neun westfaalischen talsperren. Ber. Versamml. Bot. Zool. Ver. Rheinl.-Westf. pp. 101-108.

Thorp, J.H. 1986. Two distinct roles of predators in freshwater assemblages. *Oikos* 47, 75-82.

Thorp, J.H. and E.A. Bergey. 1981. Field experiments on interactions between vertebrate predators and larval midges (Diptera : Chironomidae) in the littoral zone of a reservoir. *Oecologia (Berlin)* 50, 285-290.

Tonn, W.M., and J.J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology 63:1149-1166.

Vannote, R.L. and B.W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *Am. Nat.* 115(5), 667-695.

Vollenweider, R.A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nnitrogen and phosphorus as factors in eutrophication. Paris, Rep. Organization for Economic Cooperation and Development, DAS/CSI/68.27, 192 pp.;Annex, 21pp.; Bibliography, 61 pp.

Voris, H.K., and J.P. Bacon. 1966. Differential predation on tadpoles. Copeia 1966: 594-598.

Voshell, J.R. and G.M. Simmons. 1984. Colonization and succession of benthic macroinvertebrates in a new reservoir. *Hydrobiol.* 112, 27-39.

Wake, D.B. 1991. Declining amphibian populations. Science 203: 860.

Walters, C.J. and R.F. Vincent. 1973. Potential productivity of an alpine lake as indicated by removal and reintroduction of fish. Trans. Am. Fish Soc. 102: 675 - 697.

Ward, J.V. and J.A. Stanford. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Ann. Rev. Entomol.* 27, 97-117.

Ward, J.V. 1992. *Aquatic Insect Ecology: 1. Biology and Habitat.* John Wiley and Sons, New York. 438 pp.

Warren, C.E. 1979. Toward classification and rationale for watershed management and stream protection. U.S. Environ. Protect. Agency, Ecol. Res. Ser. EPA-600/3-79-059. 143 pp.

Wentworth, C.K. 1922. A scale of grade and class terms for clastic sediments. *J. Geol.* 30, 377-392.

Westerheim, S.J., and W.E. Ricker. 1978. Bias in using an age-length key to estimate age frequency distributions. Journal of the Fisheries Research Board of Canada 35:184-189.

Wetzel, R.G. 1975. Limnology. 1st ed. Holt, Rinehart and Winston. Philadelphia, PA. 743 pp.

Wevers, M.J. and C.E. Warren. 1986. A perspective on stream community organization, structure, and development. *Arch. Hydrobiol.* 108(2), 213-233.

Wiggins, G.B. 1977. *Larvae of the North American Caddisfly Genera (Trichoptera).* University of Toronto Press, Toronto. 401 pp.

Wilkinson, L. 1987. SYSTAT: The system for statistics. Evanston, IL, SYSTAT, Inc.

Williamson C.E. 1987. Predator-prey interactions between omnivorous diaptomid copepods and rotifers: The role of prey morphology and behavior. Limnol. Oceanogr. 32(1): 167-177.

Wissinger, S.A. and H.H. Whiteman. 1992. Fluctuation in a Rocky Mountain population of salamanders: Anthropogenic acidification or natural variation? J. Herpetol. 26: 377-391.

Zaret T.M. 1980. Size dependent predators. In: Predation and Freshwater communities. Yale University Press, New Haven, Connecticut. 187 pp.

APPENDIX

Table A.1. Number of times each lake was sampled, 1989-1991

LAKE		1989	1990	1991	TOTAL
Battalion	(BATT)	1		2	3
Bear	(BEAR)	1			1
Bouck	(BOUC)			1	1
Doubtful	(DOUB)	1	2		3
Eiley	(EILE)	1			1
EP-6	(EP6X)	1	1		2
Jeanita	(JEAN)	1			1
Klawatti	(KLAW)	1			1
LS-1	(LS1X)	1	2	3	6
LS-2	(LS2X)	1	2	3	6
McAlester	(MCAL)	1	1	2	4
Monogram	(MONO)	1			1
MP-8	(MP8X)	1			1
MR-2	(MR2X)	1	2		3
MR-3	(MR3X)	1	1		2
MR-11	(MR11)		2	2	4
MR-13-1	(M131)	1	1	2	4
MR-13-2	(M132)	1	2	2	5
Nert	(NERT)	1	1		2
No Name	(NONA)	1			1
Ouzel	(OUZE)	1			1
Panther (L)	(PANL)	2	2	3	7
Panther (U)	(PANU)		2	3	5
Pyramid	(PYRA)	1	1	3	5
Rainbow	(RAIN)	2		3	5
Redoubt	(REDO)	1			1
Reveille (L)	(REVL)	1			1
Reveille (U)	(REVU)	1			1
Skymo	(SKYM)	1		1	2
Skymo(U)	(SKYU)	1		1	2
Talus Tarn	(TTAR)	1			1
Tapto (M)	(TAPM)	1	2		3
Tapto (U)	(TAPU)	1	1		2
Tapto (W)	(TAPW)	1	2		3
Thunder	(THUN)	2	1	3	6
Trapper	(TRAP)	1	2		3
Triplet (L)	(TRIL)	1	2		3
Triplet (U)	(TRIU)	1	2		3
Vulcan	(VULC)	1			1
Waddell	(WADD)	2		2	4
Wild	(WILD)	1			1
West		26	11	9	
East		12	10	7	
Total		38	21	16	

Table A.2. Physical, biological, and classification information for NOCA study lakes.

LAKE	VEGETATION ZONE PLACEMENT: INITIAL	WATERSHED UNIT	CREST POSITION	ELEV(m)	SURFACE AREA (ha)	MAX. DEPTH (m)	MAX. TEMP (c)	#MHS	#TAXA	PREDATORS
Battalion	FHE	Stehekin	East	1629	2.5	4.3	13.0	7	17	FR
Bear	SW	C-N	West	1769	11.4	46.3	11.3	2	12	FR
Bouck	FHW	Skagit	West	1174	5.2	14.0	6.3	4	13	FR
Doubtful	SE	Stehekin	East	1642	12.0	18.0	13.3	3	21	FR
Eiley	ALP	Skagit	West	1982	1.0	4.6	2.3	5	3	none
EP-6	SW	Skagit	West	1566	9.3	19.8	14.5	6	16	FR
Jeanita	FHW	Skagit	West	1496	0.5	2.4	12.8	3	10	FR
Klawatti	ALP	Skagit	West	1624	12.0	10.0	5.9	4	5	none
LS-1	FHW	Skagit	West	1241	0.4	3.4	20.2	3	17	FNR
LS-2	FHW	Skagit	West	1243	1.0	4.9	20.4	4	26	FR
McAlester	FHE	Stehekin	East	1679	5.0	6.1	16.1	5	22	FR
Monogram	SW	Skagit	West	1270	12.7	37.2	13.5	4	12	FR
MP-8	ALP	Skagit	West	1566	0.9	3.7	10.4	1	8	none
MR-2	SE	Stehekin	East	1873	0.3	1.5	19.8	5	17	S
MR-3	SE	Stehekin	East	1873	0.2	1.5	17.4	4	12	S
MR-11	SE	Stehekin	East	1863	1.3	7.3	14.8	4	21	FNR
MR-13-1	SE	Stehekin	East	1800	0.3	3.0	15.7	4	11	S
MR-13-2	SE	Stehekin	East	1789	1.2	6.0	14.6	5	20	FNR
Nert	FHW	Skagit	West	1388	1.0	8.2	16.8	4	16	S
No Name	FHW	Skagit	West	1171	4.4	9.1	10.2	3	12	FR?
Ouzel	ALP	Skagit	West	1659	2.0	9.8	4.6	1	8	none
Panther (L)	FLW	Skagit	West	1031	0.2	5.8	18.6	5	28	FNR
Panther (U)	FLW	Skagit	West	1031	0.1	2.0	20.7	4	19	FNR
Pyramid	FLW	Skagit	West	807	0.3	8.8	18.3	5	31	S
Rainbow	FHE	Stehekin	East	1717	6.3	10.4	13.2	4	29	FR
Redoubt	SW	C-N	West	1616	5.6	14.0	10.2	5	6	FNR*
Reveille (L)	SW	C-N	West	1525	1.6	3.0	10.6	1	6	none
Reveille (U)	SW	C-N	West	1528	1.2	4.9	3.1	1	6	none
Skymo	SW	Skagit	West	1609	4.3	5.5	10.6	4	14	FR
Skymo (U)	ALP	Skagit	West	1610	3.0	4.3	4.0	2	10	none
Talus Tarn	SW	Skagit	West	1632	0.6	3.6	11.7	2	8	none
Tapto (M)	SW	C-N	West	1754	0.3	5.5	18.5	3	19	none
Tapto (U)	SW	C-N	West	1755	4.0	13.1	11.7	4	14	none
Tapto (W)	SW	C-N	West	1754	0.8	4.3	18.1	4	17	none
Thunder	FLW	Skagit	West	412	3.0	6.4	25.5	5	33	FNR
Trapper	SE	Stehekin	East	1270	59.0	49.0	14.3	4	20	FNR*
Triplet (L)	SE	Stehekin	East	1931	1.0	2.1	13.8	3	10	FR
Triplet (U)	SE	Stehekin	East	1998	1.0	4.3	12.3	5	17	FR

Table A.2. (continued)

LAKE	VEGETATION ZONE PLACEMENT INITIAL	VEGETATION ZONE PLACEMENT DA	WATERSHED UNIT	CREST POSITION	ELEV(m)	SURFACE AREA (ha)	MAX. DEPTH (m)	MAX. TEMP (c)	#MHS	#TAXA	PREDATORS
Vulcan	SW	SW	Skagit	West	1583	3.3	6.4	11.3	4	16	none
Waddell	FHE	FHE	Stehekin	East	1504	4.1	11.9	12.9	3	27	S
Wild	SW	SW	Skagit	West	1488	4.6	8.8	10.1	5	12	none

Abbreviations:

FLW	:	Forest Low West
FHW	:	Forest High West
FHE	:	Forest High East
SW	:	Subalpine West
SE	:	Subalpine East
ALP	:	Alpine
MHS	:	Microhabitats
C-N	:	Chilliwack-Nooksack
F	:	Fish
S	:	Salamanders
FNR	:	Non-reproducing fish with salamanders (* salamander presence not established)
FR	:	Reproducing fish with minimal or no salamanders

Table A.3. Nearshore macroinvertebrates in lakes of North Cascades National Park Service Complex: habitats, substrate preference groups, and functional feeding group affiliations, with life history references.

Class-Order	Family	Genus	Habitat	Substrate Preference Group	Functional Feeding Group	References
TURBELLARIA			BNTH	GENR	SCAV	12,15
NEMATODA			BNTH	GENR	SCAV	9,15
OLIGOCHAETA			BNTH	PELO	DETR	15
HIRUDINEA			BNTH	MMIX	SCAV	15
PELECYPODA	Sphaeriidae		BNTH	PELO	DETR	15
AMPHIPODA	Gammaridae	Gammarus	BNTH	MMIX	SCAV	10,15
	Talitridae	Hyalella azteca	BNTH	MMIX	SCAV	15
GASTROPODA	Ancylidae		BNTH	GENR	SCAV	15
	Lymnaeidae		BNTH	GENR	SCAV	15
	Physidae		BNTH	MORG	SCAV	15
	Planorbidae		BNTH	GENR	SCAV	15
ODONOTA	Aeshnidae	Aeshna	BNTH	PHYT	PRED	5,14,15
	Coenagrionidae		BNTH	PHYT	PRED	5,14,15
	Corduligastridae		BNTH	PELO	PRED	5,14,15
	Corduliidae		BNTH	PELO	PRED	5,14,15
	Lestidae		BNTH	PHYT	PRED	5,14,15
	Libellulidae		BNTH	PHYT	PRED	5,14,15
EPHEMEROPTERA	Baetidae	Baetis	BNTH	MMIX	COGA	8,14
		Callibaetis	BNTH	MMIX	COGA	8,14
	Caenidae	Caenis	BNTH	MORG	COGA	8,14,17
	Heptageniidae	Cinygma	BNTH	MMIX	SCRP	7,8,14,17
		Cinygmula	BNTH	MMIX	SCRP	7,8,14
	Leptophlebiidae	Paraleptophlebia	BNTH	GENR	COGA	8,14
	Siphlonuridae	Ameletus	BNTH	MINO	COGA	8,14
		Siphlonurus	BNTH	LITH	COGA	8,14,17
PLECOPTERA	Capniidae		BNTH	LITH	SHRD	6,14,15,17
	Chloroperlidae		BNTH	LITH	PRED	6,14,15,17
	Leuctridae		BNTH	PSPE	SHRD	6,14,15,17
	Nemouridae		BNTH	MORG	SHRD	2,6,14,15
	Perlidae		BNTH	MMIX	PRED	6,7,14,15
	Pteronarcyidae		BNTH	LITH	SHRD	14,17
	Taeniopterygidae	Taenionema	BNTH	LITH	SHRD	14
TRICHOPTERA	Brachycentridae	Brachycentrus	BNTH	PSPE	COGA	14,18
	Lepidostomatidae	Lepidostoma	BNTH	PELO	SHRD	1,14,18
	Leptoceridae	Oecetis	BNTH	PELO	PRED	14,18
	Limnephilidae	Apatania	BNTH	XYLO	SCRP	1,7,14,18
		Asynarchus	BNTH	LITH	SHRD	1,14,18
		Chyranda	BNTH	XYLO	SHRD	1,14,18
		Desmona mono	BNTH	LITH	SHRD	14,18
		Dicosmoecus	BNTH	LITH	SCRP	1,14,18
		Ecclisocosmoecus	BNTH	MMIX	SCRP	14,18
		Ecclisomyia	BNTH	LITH	COGA	1,14,18
		Halesochila	BNTH	PELO	COGA	1,14,18
		Hesperophylax	BNTH	MINO	SHRD	1,14,16a,18
		Homophylax	BNTH	PSPE	SHRD	14,18
		Imania	BNTH	LITH	SCRP	14,18
		Lenarchus	BNTH	MORG	COGA	14,18
		Limnephilus	BNTH	GENR	SHRD	14,18

Table A.3. (continued)

Class-Order	Family	Genus	Habitat	Substrate Preference Group	Functional Feeding Group	References
TRICHOPTERA	(continued)					
	Limnephilidae	Onocosmoecus	BNTH	MORG	SHRD	14,18
		Psychoglypha	BNTH	MMIX	COGA	1,14,18
	Phryganeidae	Banksiola	BNTH	PHYT	SHRD/PRED	1,14,18
	Polycentropodidae	Polycentropus	BNTH	GENR	PRED	14,18
HEMIPTERA	Corixidae		NEKT		PRED	14
	Gerridae		PLEU		PRED	14
	Macroveliidae		BNTH	PHYT	PRED	14,16c
	Nepidae		BNTH	PHYT	PRED	14,15
	Notonectidae		NEKT		PRED	14
	Saldidae		BNTH	PHYT	PRED	14
MEGALOPTERA	Sialidae	Sialis	BNTH	PELO	PRED	14,15,17
COLEOPTERA	Chrysomelidae	Donacia	BNTH	PHYT	SHRD	14
	Dytiscidae	Agabus	BNTH	GENR	PRED	14,15,16b
		Colymbetes	BNTH	XYLO	PRED	14
		Dytiscus	NEKT		PRED	14
		Eretes	BNTH	PHYT	PRED	14
		Graphoderus	BNTH	PELO	PRED	14
		Hydroporus	BNTH	GENR	PRED	14
		Oreodytes	BNTH	LITH	PRED	14
		Potamonectes	BNTH	GENR	PRED	
		Rhantus	BNTH	PHYT	PRED	14
		Sanfiloppodytes	BNTH	LITH	PRED	
	Gyrinidae	Gyrinus	PLEU		PRED	14
	Haliplidae		BNTH	PELO	PRED	14,17
	Hydrophilidae		NEKT		PRED/COGA	14
DIPTERA	Ceratopogonidae		BNTH	PELO	PRED	13b,14
	Chironomidae		BNTH	GENR	COGA/PRED	13d,14
	Chaoboridae		PLNK		PRED	14,17
	Culicidae		PLEU		COGA	14
	Dixidae		BNTH	XYLO	COGA	7,14
	Dolichopodidae		BNTH	PELO	PRED	13h,14
	Empididae		BNTH	MORG	PRED	13i,14
	Ephydridae		BNTH	PELO	COGA	3,4,11,14
	Nymphomyiidae		BNTH	PHYT	SCRP	13c,14
	Psychodidae		BNTH	MORG	COGA	7,13g,14
	Sciomyzidae		BNTH	MORG	PRED	3,14
	Simuliidae		BNTH	MMIX	COGA	13f,14
	Tabanidae		BNTH	PELO	PRED	4,11,13e,14
	Tipulidae		BNTH	GENR	PRED/SHRD	13a,14
LEPIDOPTERA	Pyralidae	Crambus	BNTH	PHYT	SHRD	14

BNTH = Benthic
NEKT = Nektonic
PLEU = Pleustonic
PLNK = Planktonic
GENR = Generalist
LITH = Lithophilous
MINO = Mixed Inorganic
MMIX = Mixed Inorganic and Organic
MORG = Mixed Organic
PELO = Pelophilous
PHYT = Phytophilous
PSPE = Psephophilous
XYLO = Xylophilous
COGA = Collector-Gatherer
DETR = Detritivore
PRED = Predator
SCAV = Scavenger
SCRP = Scraper
SHRD = Shredder

Table A.3 (continued) References

1. Anderson, N.H. (1976) The distribution and biology of the Oregon Trichoptera. *Technical Bulletin 134*, Ag. Exp. Sta., Oregon State University. 152 pp.

2. Baumann, R.W., A.R. Gaufin and R.F. Surdick (1977) The stoneflies (Plecoptera) of the Rocky Mountains. *Memoirs of the Em. Ent. Soc.*, Number 31. 208 pp.

3. Borror, D.J., D.M. Delong and C.A. Triplehorn (1976) Introduction to *the Study of Insects (4th edition)*. Holt, Rinehart, and Winston. 852 pp.

4. Cole, F.R. (1969) *The Flies of Western North America*. Univ. of Calif. Press. 693 pp.

5. Corbet, P.S. (1980) Biology of Odonata. *Ann. Rev. Entomol.* 25: 189-217.

6. Donald, D.B., and R.S. Anderson (1980) The lentic stoneflies (Plecoptera) from the Continental Divide Region of southwestern Canada. *Can. Ent.* 112(8): 753-758.

7. Dudley, T. and N.H. Anderson (1982) A survey of insects associated with wood debris in aquatic habitats. *Melandria* 39: 1-21.

8. Edmunds, G.F., S.L. Jensen and L. Berner (1976) *The Mayflies of North and Central America*. Univ. of Minn. Press. 330 pp.

9. Ferris, V.R., L.M. Ferris and J.P. Tjepkema (1976) Genera of freshwater nematodes (Nematoda) of eastern North America (2nd printing). *Water Control Research Series 18050 ELD01/72*, USEPA. 38 pp.

10. Holsinger, J.R. (1976) The freshwater amphipod crustaceans (Gammaridae) of North America. *Water Control Research Series 18050 ELD04/72*, USEPA. 89 pp.

11. Johannsen, O.A. (1935) Aquatic Diptera, part II, Orthorrhapha-Brachycera and Cyclorrhapha. *Memoir 177*, Ag. Exp. Sta., Cornell Univ. 62pp.

12. Kenk, R. (1976) Freshwater planarians (Turbellaria) of North America. *Water Control Research Series 18050 ELD02/72*, USEPA. 81 pp.

Table A.3 (continued) References

13. McAlpine, J.F., B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth and D.M. Wood, eds. (1981) Manual of Nearctic Diptera, Vol 1. *Monograph 27*, Research Branch, Agriculture Canada. 674 pp.

    a. Alexander, C.P. and G.W. Byers. Tipulidae. 153-190.
    b. Downes, J.A. and W.W. Wirth. Ceratopogonidae. 393-421.
    c. Kevan, D.K.M. and F.E.A. Cutten. Nymphomyiidae. 203-208.
    d. Oliver, D.R. Chironomidae. 423-458.
    e. Pechuman, L.L. and H.J. Teskey. Tabanidae. 463-478.
    f. Peterson, B.V. Simuliidae. 355-392.
    g. Quate, L.W. and J.R. Vockeroth. Psychodidae. 293-300.
    h. Robinson, H. and J.R. Vockeroth. Dolichopodidae. 625-639.
    i. Steyskal, G.C. and L.V. Knutson. Empididae. 607-624.

14. Merritt, R.W. and K.W. Cummins (1984) *An Introduction to the Aquatic Insects of North America (2nd edition)*. Kendall/Hunt Publishing. Co. 722 pp.

15. Pennak, R.W. (1978) *Freshwater Invertebrates of the United States (2nd edition)*. John Wiley and Sons, Inc. 803 pp.

16. Usinger, R.L., ed. (1956) *Aquatic Insects of California*. Univ. of Calif. Press. 508 pp.

    a. Denning, D.G. Trichoptera. 237-270.
    b. Leech, H.B. and H.P. Chandler. Aquatic Coleoptera. 293-371.
    c. Usinger, R.L. Aquatic Hemiptera. 182-228.

17. Ward, J.V. (1992) *Aquatic Insect Ecology, 1. Biology and Habitat*. John Wiley and Sons, Inc. 438 pp.

18. Wiggins, G.B. (1977) *Larvae of the North American Caddisfly Genera (Trichoptera)*. Univ. of Toronto Press. 401 pp.

Table A.4. Distribution of nearshore macroinvertebrates in NOCA lakes

TAXON	BAT	BEA	BOU	DOU	EIL	EP6	JEA	KLA	LS1	LS2	MCA	MON	MP8	MR2	MR3	MR1	M131	M132	NER	NON	OUZ	PAN	PAN	PYR	RAI	REDO	REVL	REVU	SKYM	SKYU	TTAR	TAPM	TAPU	TAPW	THUN	TRAP	TRIL	TRIU	VULC	WADD	WILD
Turbellaria						X				X			X							X	X				X	X			X	X		X		X	X			X		X
Nematoda	X			X	X				X	X	X	X	X	X	X			X	X	X	X		X	X	X			X			X	X	X			X	X			
Oligochaeta	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Hirudinea	X			X		X				X	X					X			X			X	X	X					X			X		X	X	X	X			
Sphaeriidae	X	X	X			X	X		X	X	X	X		X		X	X	X	X			X	X	X	X				X					X	X	X	X	X	X	
Gammarus																X		X						X											X		X		X	
Hyalella azteca						X					X											X	X	X										X					X	
Ancylidae																						X		X										X						
Lymnaeidae																								X										X						
Physidae																								X																
Planorbidae																						X		X										X						
Aeshnidae	X						X		X	X	X					X			X			X	X	X										X					X	
Coenagrionidae																						X	X	X										X						
Corduligastridae									X																															
Corduliidae									X	X	X								X			X	X	X										X		X				
Lestidae																								X										X						
Libellulidae																								X										X						
Baetis									X	X														X																
Callibaetis	X		X			X			X	X	X			X	X	X		X	X	X		X	X	X	X			X			X			X		X	X		X	
Caenis																																		X							
Cinygma																										X									X				X	
Cinygmula																																			X			X		
Paraleptophlebia																						X	X	X	X														X	
Ameletus		X	X	X		X		X		X	X		X					X		X	X				X	X	X	X	X		X	X	X	X		X		X	X	X
Siphlonurus											X																														
Capniidae				X						X																					X	X			X					
Chloroperlidae		X	X	X							X													X									X		X				X	
Leuctridae						X								X										X																
Nemouridae		X								X														X														X	X	
Perlidae				X					X									X						X														X	X	
Pteronarcyidae																						X																		
Taenionema																				X						X	X	X			X	X			X					X
Brachycentrus																								X																
Lepidostoma																						X	X	X																
Oecetis																																		X						
Apatania						X																									X						X	X	

Table A. 4. (continued)

TAXON	BAT	BEAR	BOUC	DOUB	EILE	EP6X	JEAN	KLAW	LS1X	LS2X	MCAL	MONO	MP8X	MR2X	MR3X	MR11	M131	M132	NERT	NONA	OUZE	PANL	PANU	PYRA	RAIN	REDO	REVL	REVU	SKYM	SKYU	TTAR	TAPM	TAPU	TAPW	THUN	TRAP	TRIL	TRIU	VULC	WADD	WILD
Asynarchus			X						X		X			X		X																							X	
Chyranda																								X															X	
Desmona mono				X		X								X	X	X	X	X	X					X	X	X	X	X	X	X	X	X	X		X		X	X	X	X
Dicosmoecus				X			X				X							X		X			X	X											X					
Ecclisocosmoecus		X				X																									X	X								
Ecclisomyia		X		X				X	X					X							X			X					X	X							X	X	X
Halesochila	X		X						X					X	X	X	X	X	X	X		X		X							X		X				X	X	
Hesperophylax							X					X				X	X		X						X				X		X		X			X			
Homophylax		X		X														X							X														
Imania				X																																		X		X
Lenarchus	X																																X					X		
Limnephilus	X		X	X					X	X	X			X	X	X		X	X			X	X	X	X							X	X	X				X	X	X
Onocosmoecus				X																X													X							
Psychoglypha		X	X	X		X				X	X	X	X	X						X					X				X	X	X	X	X	X			X	X		X	X
Banksiola																																			X						
Polycentropus			X						X	X		X						X				X	X	X	X									X							
Corixidae	X																																								
Gerridae	X									X												X	X	X										X							
Macroveliidae	X																																								
Nepidae																																		X							
Notonectidae											X			X		X	X					X		X										X						X	
Saldidae							X			X																												X			
Sialis										X	X											X		X										X							
Donacia																																		X							
Agabus		X	X	X		X	X		X	X	X				X	X	X	X	X						X		X	X	X		X	X	X	X	X	X	X		X	X	X	X
Colymbetes												X																														
Dytiscus																						X																			
Eretes																						X		X																	
Graphoderus																X																									
Hydroporus	X		X	X		X				X	X			X		X	X	X							X				X		X		X		X		X		X	
Oreodytes												X			X				X						X				X		X		X		X		X			
Potamonectes												X		X	X	X	X	X							X				X		X		X							
Rhantus							X															X		X																	
Sanfiloppodytes		X		X																					X						X	X						X	X	
Gyrinus																						X	X	X										X							
Haliplidae																																		X							
Hydrophilidae												X																						X							

Table A. 4. (continued)

TAXON	BATT	BEAR	BOUC	DOUB	EILE	EP6X	JEAN	KLAW	LS1X	LS2X	MCAL	MONO	MP8X	MR2X	MR3X	MR11	M131	M132	NERT	NONA	OUZE	PANL	PANU	PYRA	RAIN	REDO	REVL	REVU	SKYM	SKYU	TTAR	TAPM	TAPU	TAPW	THUN	TRAP	TRIL	TRIU	VULC	WADD	WILD
Ceratopogonidae	X						X		X	X	X		X		X	X			X			X	X	X	X									X	X		X	X			
Chrionomidae	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Chaoboridae																		X																							
Culicidae																																				X					
Dixidae																						X		X										X							
Dolichopodidae															X																				X						
Empididae	X										X					X		X			X	X			X			X							X					X	
Ephydridae														X																											
Nymphomyiidae										X																															
Psychodidae				X																																					
Sciomyzidae																																		X							
Simuliidae										X						X																									
Tabanidae																			X			X	X											X							
Tipulidae	X			X		X		X		X		X	X	X		X	X	X			X				X						X				X		X		X	X	X	X
Crambus										X																								X							

Table A.5. Substrates, particulate sizes, and faunal category relationships.

Substrate Type	Substrates	Particulate Sizes (mm)*	Faunal Categories**
Fine Particulates	silt, organic detritus, sand	<0.0039-2	Pelophilous
Small-Moderate Mineral	fine-coarse gravel	2-16	Psephophilous
Moderate-Large Mineral	small-large cobble, boulder	16->256	Lithophilous
Wood	fine and coarse		Xylophilous
Emergent/Submergent Vegetation	macrophytes and moss		Phytophilous

* after Ward (1992), Table 7.1, p. 235
** after Ward (1992), Table 7.4, p. 238

Table A.6. Lake codes, acronyms and official USGS names. Unofficial names are in parentheses.

Park Code[1]	Acronym[2]	Lake Name
CP1	DOUB	Doubtful
DD1	JEAN	Jeanita
DD4	BOUC	Bouck
DD5	DD5	Unnamed (Upper Bouck)
DD8	DD8	Intermittent
EP2	EP2	Unnamed
EP3	EP3	Unnamed-Wilcox
EP4	EP4	Unnamed
EP5-1	EP5-1	Unnamed (Lower Wilcox/Sandy)
EP6	EP6	Unnamed (Upper Wilcox/Lily)
EP9-1	EP9-1	Stout Lake Pond
EP9-2	EP9-2	Stout Lake
EP10	EP10	Unnamed
EP11-1	EP11-1	Unnamed
EP11-2	EP11-2	Unnamed
EP12	EP12	Unnamed
EP13	EP13	Unnamed
EP14	EP14	Unnamed (Hidden Lk Tarn)
FP1	FP1	Unnamed
FP4	KLAW	Klawatti
FP5	FP5	Unnamed
FP6	FP6	Unnamed
FP7	MORA	Moraine
FP8	FP8	Unnamed
FP9	FP9	Unnamed
FP10	FP10	Unnamed
GM1	TRAP	Trapper
GM2	GNVW	Green View
HM2	HOZO	Hozomeen
HM3	RIDL	Ridley

Park Code[1]	Acronym[2]	Lake Name
HM4	WILL	Willow
LS1	LS1	Unnamed (Diobsud No. 1)
LS2	LS2	Unnamed (Diobsud No. 2)
LS3	LS3	Unnamed (Diobsud No. 3)
LS4	LS4	Unnamed
LS5	LS5	Unnamed
LS6	LS6	Ipsoot
LS7	LS7	Blum (Lower/West, No. 4)
M1	M1	Unnamed (Hi-Yu)
M4	M4	Green
M5	NERT	Unnamed (Nert)
M6	TTAR	Unnamed (Talus Tarn)
M7	M7	Unnamed (Lower Berdeen)
M8	M8	Berdeen
M9	M9	Unnamed (Upper Berdeen)
M10	M10	Unnamed
M11	M11	Blum (Largest/Middle, No. 3)
M13	M13	Unnamed
M14	M14	Unnamed
M16	M16	Mt. Triumph (S)
M17	M17	Unnamed (Triumph)
M18	M18	Thornton (Upper)
M19	THRM	Thornton (Middle)
M20	THRL	Thornton (Lower)
M21	M21	Unnamed (Doug's Tarn)
M22	M22	Unnamed
M23	MONO	Monogram
M24-1	M24-1	Unnamed (Upper Quill)
M24-2	M24-2	Unnamed (Lower Quill)
M25	M25	Ice Fall
MA1	MA1	Unnamed
MA2	MA2	Silent (Upper)

Park Code[1]	Acronym[2]	Lake Name
MA3	MA3	Silent (Lower)
MC1	MC1	Blum (Small/North, No. 2)
MC2	MC2	Blum (Vista/Northwest, No. 1)
MC3	MC3	Unnamed
MC4	EGG	Egg
MC6	COPP	Copper
MC7	MC7	Unnamed (Kwahnesum)
MC8	MC8	Hanging
MC10	MC10	Unnamed (Ruta)
MC11	REDO	Redoubt
MC12	BEAR	Bear
MC13	MC13	Unnamed
MC14-1	MC14-1	East Lakes (Upper)
MC14-2	MC14-2	East Lakes (Lower)
MC15	MC15	Tiny
MC16-1	MC16-1	Middle (Upper)
MC16-2	MC16-2	Middle (Lower)
MC17-1	TAP1	Tapto (Upper)
MC17-2	TAP2	Tapto (Middle)
MC17-3	TAP3	Tapto (Lower)
MC17-4	TAP4	Tapto (West)
MC21-1	REVU	Reveille (Upper)
MC21-2	REVL	Reveille (Lower)
MC22	MC22	Unnamed
MC23	MC23	Unnamed
MC24	EILE	Eiley
MC25	WILE	Wiley
MC27	WILD	Wild
MC28	MC28	Unnamed
MC29	MC29	Luna
MC30	MC30	Unnamed
MC34	MC34	Unnamed

Park Code[1]	Acronym[2]	Lake Name
ML1	ML1	Unnamed (Sourpuss)
ML2	SWEE	Unnamed (Sweet Pea)
ML3	ML3	Unnamed (Torment)
ML4	VULC	Unnamed (Vulcan)
ML5	ML5	Unnamed
ML6	ML6	Unnamed
ML7	ML7	Unnamed
MLY1	MLY1	Unnamed (Upper Battalion)
MLY2	BATT	Battalion
MM1	MM1	Unamed
MM3	MM3	Unnamed (Last Chance)
MM6	WADD	Waddell (Lower/Sandalee)
MM7	WADM	Unnamed (Mid. Waddell)
MM8	MM8	Unnamed (Sandalee)
MM10	COON	Coon
MM11	MM11	Unnamed (Upper Rainbow, West)
MP1-1	MP1-1	Unnamed (W)
MP1-2	MP1-2	Unnamed (S)
MP1-3	MP1-3	Unnamed (N)
MP2	MP2	Unnnamed (Firn)
MP5	MP5	Unnamed (Big Beaver Pond)
MP8	MP8	Unnamed
MP9	MP9	Azure
MR1	MR1	Unnamed (Stilletto)
MR2	MR2	Unnamed (Twisp Pass Pond, N.)
MR3	MR3	Unnamed (Twisp Pass Pond, S.)
MR4	DAGG	Dagger
MR5	KETT	Kettling
MR6	KETU	Unnamed (Upper Kettling)
MR8	MR8	Unnamed
MR9	MR9	Unnamed
MR10	MCAL	McAlester

Park Code[1]	Acronym[2]	Lake Name
MR11	MR11	Unnamed
MR12	MR12	Unnamed
MR13-1	M131	Unnamed (Upper Rainbow, North)
MR13-2	M132	Unnamed (Upper Rainbow, South)
MR14	RAIN	Rainbow
MR15-1	MR15-1	Unnamed (Dee Dee/Tamarack)
MR15-2	MR15-2	Unamed (Lower Dee Dee)
MR16	MR16	Unnamed
MS1	SILV	Silver
MS2	MS2	Unnamed
MS3	MS3	Unnamed
MS4	OUZL	Ouzel
MSH1	MSH1	Sulphide
MSH2	MSH2	Unnamed
MSH3	PRIC	Price
MSH4	MSH4	Unnamed
PM1	NONA	No Name
PM2	PM2	Unnamed (Skymo Pond)
PM3	SKYM	Skymo
PM4	SKYU	Unnamed (Upper Skymo)
PM5-1	PM5-1	Unnamed
PM5-2	PM5-2	Unnamed
PM5-3	PM5-3	Unnamed
PM5-4	PM5-4	Unnamed
PM5-5	PM5-5	Unnamed
PM5-6	PM5-6	Unnamed
PM12	PM12	Sourdough
RD2	THUN	Thunder
RD3	PYRA	Pyramid
RD4	RD4	Unnamed
RD5-1	PANU	Panther Potholes (Upper)
RD5-2	PANL	Panther Potholes (Lower)

Park Code[1]	Acronym[2]	Lake Name
SB1	SB1	Hidden
SM1	JUAN	Juanita
SM2-1	TRIL	Triplet (Lower)
SM2-2	TRIU	Triplet (Upper)

[1]Code used by North Cascades National Park Service Complex
[2]Acronyms used by present study

Table A.7. Average elevation, surface area, maximum depth, ice-out date of the lakes, and average physical and chemical characteristics of the samples collected in 1989 in each cluster of the lake ordination.

	Cluster						
Variable	1	2	3	4	5	6	7
El (m)	1595 (203.8)[1]	1376.8 (379.2)	1724.3 (224.2)	955.3 (341.0)	1925.7 (1101.1)	1643.8 (224.2)	1574.0 (287.2)
Area (ha)	8.8 (16.6)	3.4 (4.1)	3.4 (4.3)	9.3 (14.5)	1.0 (.8)	14.2 (20.4)	3.8 (6.8)
Z (m)	11.5 (13.3)	12.0 (11.9	10.3 (12.8)	8.7 (5.5)	2.7 (1.9)	32.1 (41.6)	8.1 (10.4)
Temp °C	10.1 (2.9)	13.8 (4.3)	4.6 (3.4)	16.9 (2.4)	13.8 (5.1)	11.2 (2.8)	10.2 (3.1)
pH	7.04 (0.62)	7.12 (.57)	6.47 (.36)	8.02 (.39)	7.05 (.35)	6.48 (.19)	7.48 (.76)
Alk (mg/l)	1.8 (1.1)	2.7 (2.5)	0.6 (.2)	10.7 (6.1)	2.6 (1.5)	0.7 (.2)	2.5 (1.4)
Cond (μmhos/cm)	17.1 (13.4)	23.3 (22.7)	9.8 (8.1)	89.6 (44.4)	18.6 (12.9)	14.1 (24.3)	22.7 (12.4)
TKN-N (mg/l)	.026 (015)	.055 (.037)	.004 (.003)	.123 (.052)	.064 (.054)	.022 (.017)	.032 (.014)
NO_3-N (mg/l)	.007 (.009)	.002 (.003)	.014 (.014)	.001 (0)	.003 (.004)	.008 (.007)	.015 (0.12)
NH_3-N (mg/l)	.003 (.002)	.006 (.005)	.004 (.003)	.010 (.007)	.003 (.002)	.005 (.004)	.005 (.004)
TP (mg/l)	.007 (.005)	.007 (.004)	.009 (.010)	.011 (.005)	.015 (.012)	.004 (.003)	.010 (.008)
OP-P (mg/l)	.001 (0)	.001 (.001)	.003 (.002)	.001 (0)	.001 (0)	.001 (0)	.002 (.002)
Ice-out (Julian days)	199.5 (18.7)	168.8 (29.2)	221.5 (11.9)	155.2 (36.8)	166.5 (5.0)	204.4 (13.5)	191.2 (25.0)

[1]One standard deviation.





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