

AN ABSTRACT OF THE THESIS OF

Torrey J. Tyler for the degree of Master of Science in Fisheries Science presented on May 15, 1996. Title: Interactions between Stocked Trout and Larval Salamanders (*Ambystoma macrodactylum*) in High-Elevation Lakes.

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Abstract approved: _____
William J. Liss

The long-toed salamander (*Ambystoma macrodactylum*) is the top vertebrate predator in fishless high-elevation lakes in North Cascades National Park Service Complex (NOCA), Washington. The purpose of this research was to determine the effects of physico-chemical factors and introduced trout on abundance and behavior of *A. macrodactylum* larvae. Although high-elevation lakes in NOCA were naturally fishless, trout were stocked in many lakes during this century to provide recreational angling opportunity.

Twenty fishless lakes and 25 lakes with fish were sampled from 1990 to 1994. Larval salamander density and behavior were assessed by snorkeling lake perimeters and searching through nearshore substrate material and aquatic vegetation. In fishless lakes, larval salamander densities were positively related to total Kjeldahl-N concentration (TKN) and negatively related to lake elevation. Based on analysis of salamander stomach

contents, crustacean zooplankton, especially cladocerans, were important food resources for larval A. macrodactylum. Total crustacean zooplankton, as well as cladoceran densities, were positively related to TKN concentration, suggesting that increased zooplankton food resources contributed to increased densities of A. macrodactylum.

The effects of fish introductions on larval salamander densities depended on TKN concentration and whether or not trout had established reproducing populations. Mean larval salamander densities for fishless lakes with $TKN < 0.05$ mg/l, generated from a linear regression equation with TKN and lake elevation as independent variables, were not significantly different from mean larval densities in lakes with either reproducing trout or in lakes with non-reproducing trout. However, in fishless lakes with $TKN \geq 0.05$ mg/l, mean larval densities were significantly higher than in lakes with reproducing fish where trout reached high densities. In fishless lakes with $TKN \geq 0.095$ mg/l, mean larval densities were significantly higher than in lakes with non-reproducing fish where trout fry were periodically stocked at low densities. Reduced larval salamander densities in lakes with trout likely was a consequence of trout predation. Although most larvae were associated with boulder, cobble, and woody debris substrates in nearshore areas of NOCA lakes, differences in the

proportion of larvae hidden in benthic substrates between lakes with fish and without fish were not statistically significant.

Interactions between Stocked Trout and
Larval Salamanders (Ambystoma macrodactylum) in
High-Elevation Lakes

by
Torrey J. Tyler

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DEDICATION

I dedicate my work on this thesis in loving memory
of my grandmother, Frances L. Harman.

Interactions between Stocked Trout and Larval Salamanders
(Ambystoma macrodactylum) in High-Elevation Lakes

INTRODUCTION

There is world-wide concern about declines of some amphibian species (Barinaga, 1990; Blaustein and Wake, 1990; Phillips, 1990; Wake, 1991; Crump et al., 1992; Blaustein et al., 1994a). Several authors have suggested that amphibian declines may be a consequence of human-related impacts including chemical pollution, acid precipitation, ozone depletion, habitat destruction and introductions of exotic species (Hammerson, 1982; Corn and Fogelman, 1984; Hayes and Jennings, 1986; Blaustein and Wake, 1990; Wake, 1991; Wissinger and Whiteman, 1992; Blaustein et al., 1994a). There is particular concern over amphibian declines in areas that have been relatively undisturbed by human activity, such as high-elevation locations in the west (Blaustein and Wake, 1990) and national parks (Bradford, 1989; Bradford et al., 1993).

Fish introductions have been suggested as a factor altering amphibian communities in high-elevation lakes (Cory, 1963; Hammerson, 1982). Fish are not indigenous to many high-elevation lakes in the west. Bahls (1992) reported that 95% of mountain lakes in the western U.S. may have been naturally fishless. Presently, nearly 60% of all high-elevation lakes and about 95% of the larger, deeper lakes now support fish (Bahls, 1992).

Predation by fish may account for the lack of co-occurrence of Rana muscosa tadpoles and introduced fish in high-elevation (>2500 m) lakes in Sequoia and Kings Canyon National Parks, CA (Bradford, 1989). Bradford et al. (1993) provided evidence that continued declines of R. muscosa in fishless waters may be a consequence of isolation of extant populations due to the presence, in connecting waters, of fish that inhibit recolonization of habitats where natural extinctions of R. muscosa have occurred. Blaustein et al. (1994b) suggested that a pathogenic fungus, Saprolegnia ferax, indirectly introduced with fish to montane lakes may be responsible for some amphibian declines in the western U.S. Other studies indicate that the presence of fish may affect behavior and population dynamics of amphibians (Voris and Bacon, 1966; Grubb, 1972; Whitaker, 1971; Moyle, 1973; Heyer et al., 1975; Hammerson, 1982; Cochran, 1983; Kruse and Stone, 1984).

Ambystomatid salamanders are important native aquatic predators in high-elevation lakes in the western U.S. (Dodson, 1970, 1974; Dodson and Dodson, 1971; Sprules, 1972; Taylor, 1983). Reduced abundance and absence of ambystomatid larvae from habitats with introduced fish have been reported. Burger (1950) and Blair (1951) noted the disappearance of neotenic Ambystoma tigrinum from a lake in the Rocky mountains of

Colorado following fish introductions. Both Sprules (1974a) and Taylor (1983) observed lower densities of larval Ambystoma gracile in mountain lakes with fish in British Columbia, Canada, and Oregon, respectively. Petranka (1983) reported that eggs and larvae of Ambystoma barbouri were largely confined to reaches of midwestern streams that lacked fish. He demonstrated that this distribution was a consequence of fish predation on larvae. Semlitsch (1988) found that, as a consequence of fish predation on salamander eggs, Ambystoma talpoideum occurred primarily in ponds that lacked fish in the upper coastal plain and sandhill regions of South Carolina. Sih et al. (1992) observed decreases in densities of larval A. barbouri following experimental fish introductions into pools in a Kentucky stream.

Fish have been shown to inhibit growth (Semlitsch, 1987; Figiel and Semlitsch, 1990) and reduce survival (Semlitsch, 1987; Sih et al., 1988) of larval ambystomatids in artificial ponds. Fish also can alter behavior of aquatic salamanders including shifts toward nocturnal activity by larvae (Sprules, 1974a; Taylor, 1984; Sih et al., 1992), restricted larval activity (Semlitsch, 1987; Stangel and Semlitsch, 1987; Figiel and Semlitsch, 1990), and increased refuge use by larvae (Sih et al., 1988; 1992).

Salamander distribution and abundance is influenced by abiotic factors and biotic factors other than fish. Abiotic factors influencing salamanders include elevation (Snyder, 1956; Howard and Wallace, 1985; Stebbins, 1985; Leonard et al., 1993), lake area and depth (Kezer and Farner, 1955; Sprules, 1974a; 1974b), water temperature (Snyder, 1956; Anderson, 1968), and conditions in the terrestrial habitat (Sprules, 1974a; 1974b). Suitable food resources are necessary to ensure adequate growth and survival. Salamander larvae prey upon benthic macroinvertebrates and zooplankton, especially cladocerans and copepods (Anderson, 1968; Dodson, 1970; Dodson and Dodson, 1971; Henderson, 1973; Licht, 1975; Brophy, 1980; Branch and Altig, 1981; Freda, 1983). Distribution and abundance of both zooplankton and benthic macroinvertebrates are influenced by abiotic factors such as lake elevation (Carl, 1940; Reed and Olive, 1958; Patalas, 1964; Anderson, 1971; 1974; Hoffman et al., in press), water temperature (Carl, 1940; Allen and Goulden, 1980; Byron et al., 1984; Walters et al., 1987; Hoffman et al., in press), lake area and depth (Carl, 1940; Anderson, 1971; Stoddard, 1987), and water chemistry (Sprules, 1975; Byron et al., 1984; Stoddard, 1987; Hoffman et al., in press).

The objective of this research is to understand the influence of biotic and abiotic factors on distribution

and abundance of long-toed salamander (Ambystoma macrodactylum) larvae in high-elevation lakes of North Cascades National Park Service Complex, Washington, U.S.A. Although A. macrodactylum is widespread in the Pacific Northwest (Nussbaum et al., 1983; Stebbins, 1985; Leonard et al., 1993), very little is known about its distribution within high-elevation areas, variation in larval abundance among lakes, and natural and human factors influencing distribution and abundance. Specifically, the research focused on: 1) the effects of introduced trout on larval salamander density and behavior; 2) the effects of lake physical characteristics and water chemistry on larval salamander abundance and on food resources of larval salamanders.

METHODS

Study Area

North Cascades National Park Service Complex (NOCA) is located in the Cascade Range of northern Washington, USA. There are 156 lakes of interest to fisheries managers in NOCA. All of these lakes are low in chemical ion concentrations and considered oligotrophic. All but one of these lakes were thought to be historically devoid of fish (Jarvis, 1987). Many NOCA lakes were stocked with trout, primarily Oncorhynchus clarkii and O. mykiss, during this century to provide recreational angling opportunity. Lakes were sampled from late June to mid-September each year, the period of time in which lakes are typically ice-free.

Fish Density

Lakes were grouped into three categories: fishless lakes, lakes with non-reproducing trout, and lakes with reproducing trout. In NOCA, fish densities in lakes with reproducing trout are generally much higher than in lakes in which trout do not reproduce (Liss et al., 1995). Average fish density, estimated by mark-recapture in nine lakes with reproducing trout, was 524 fish/ha for fish >177mm total length (range 250-724 fish/ha except one lake at 98 fish/ha, Liss et al., 1995).

Lakes in which fish do not reproduce are periodically stocked with fry at low densities. Lack of reproduction in lakes with fish was determined from NOCA stocking records (Jarvis, 1987) and field observations (e.g., failure to observe fry or smaller fish, little variation in age and size structure of captured fish, and lack of suitable spawning habitat). In NOCA, the average density of trout fry stocked from 1976 to 1993 in 37 high-elevation lakes (≥ 1100 m) was 179 fish/ha (range 60-375 fish/ha) and the average interval between stocking was >5 years (Liss et al., 1995). Presence or absence of trout in study lakes was verified by gill netting, angling, snorkeling, and observations from shore.

Salamander Density

From 1990 through 1994, salamander larval densities were sampled in 45 NOCA lakes. Due to relatively short ice-free periods, periods of inclement weather, and wildfires, sampling frequency of lakes varied within and among years (Table 1). Larval salamanders were censused by snorkel surveys.

From 1990 to 1993, surveys were conducted only during daylight. During these surveys, termed "search surveys", a snorkeler carefully searched through substrate materials (i.e., talus, woody debris, fine organic material, and aquatic vegetation) within 2 m of the shoreline and recorded the number of larvae observed.

Table 1. The number of times each year, in parentheses, that salamander larvae were sampled in 45 NOCA lakes [20 fishless lakes (NF), 7 lakes with non-reproducing fish (NRF), and 18 lakes with reproducing fish (RF)].

NF		NRF		RF	
Lake Name	Year	Lake Name	Year	Lake Name	Year
EGG	1994 (1)	COON	1993 (1)	BATT	1991 (2)
GRNV	1993 (1)	DDU	1993 (2)	DAGG	1993 (1)
JUAN	1993 (2)	HIYU	1994 (1)		1994 (1)
KETU	1993 (2)	MM11	1993 (1)	DDL	1993 (2)
MC10	1994 (1)	MR9	1993 (2)	DOUB	1991 (1)
MR2	1990 (1)	MR11	1991 (1)		1993 (1)
	1993 (2)		1992 (1)	KETT	1993 (2)
MR3	1990 (1)		1993 (2)	LS2	1990 (2)
	1993 (1)	MR13-2	1991 (1)		1991 (1)
MR11	1990 (1)		1993 (1)		1992 (1)
MR12	1993 (2)				1993 (2)
MR13-1	1992 (1)				1994 (1)
	1993 (1)			LS7	1994 (1)
MSH4	1994 (1)			M7	1994 (1)
PM5-3	1994 (2)			M21	1994 (1)
PYRA	1990 (1)			MCAL	1990 (1)
	1991 (3)				1991 (1)
	1993 (3)				1992 (1)
	1994 (3)				1993 (1)
WADD	1991 (2)			MONO	1994 (1)
	1993 (2)			MR16	1993 (2)
WADM	1993 (1)			RAIN	1991 (2)
WILD	1994 (1)				1992 (1)
REVU	1994 (1)				1993 (1)
SILL	1993 (1)			SKYMO	1994 (2)
SILU	1993 (1)			STTP	1994 (1)
TTAR	1994 (1)			THRL	1994 (1)
				TRPL	1990 (1)
					1991 (1)
				TRPU	1990 (1)
					1991 (1)

The length of shoreline surveyed was determined following completion of each search survey.

During 1994, four 25 m segments of shoreline were randomly chosen along the perimeter of each lake. The same segments were surveyed on all sampling visits. Each segment was snorkeled along two transects parallel to shore (e.g., Taylor, 1983). One transect was approximately 2 m from shore, and the other transect was over deeper water approximately 5 m from shore. During the 2-m surveys, the snorkeler counted larvae within an area extending from the shoreline to approximately 2 m offshore. During 5-m surveys, the snorkeler counted larvae approximately 1.5 m to each side of his or her longitudinal axis. The snorkeler did not disturb substrate material during these surveys. Search surveys also were performed along the same segments of shoreline. To determine if the number of larvae observed was different between day and night, each transect was surveyed during mid-afternoon and approximately 30 min after sunset with the aid of hand-held divelights. When multiple surveys were performed at a lake, salamander density estimates were averaged for each survey technique. Salamander densities were expressed as number of individual larvae observed per 100 m of shoreline.

Stomach Contents

Stomachs were collected from 13 salamander larvae from three fishless lakes (MR2, MR3, and Waddell) in 1990 and 1991. In the field, stomachs and their contents were preserved in 95% ethanol. Organisms found in the stomachs were identified to the lowest possible taxonomic level in the laboratory using a stereomicroscope for benthic macroinvertebrate taxa and an inverted scope at 100x magnification for crustacean zooplankton taxa.

Salamander Behavior

During 1993 and 1994 search surveys, the total lengths (mm) of individual salamander larvae observed during snorkel surveys were visually estimated. The number of larvae in each of three size categories (10-30 mm, 31-60 mm, and >60 mm) was determined. Larvae also were categorized according to whether they were hidden or were not hidden in substrate materials (e.g., talus, woody debris), in rock crevices, or among dense vegetation. A larva was classified as "not hidden" if a major portion of its body was visible to the snorkeler prior to the search through substrate materials.

Benthic Habitat

During search surveys, snorkelers visually determined the composition of principle substrate materials in nearshore habitats where individual

salamander larvae were found. Habitat utilization by larvae was assessed in nine fishless lakes, five lakes with non-reproducing fish, and three lakes with reproducing fish. The number of lakes with fish in which larval habitat utilization was assessed was limited due to absence of larvae in most of these lakes. Substrate materials included sand-silt, gravel, boulder, cobble, bedrock, organic detritus, aquatic vegetation, moss, algae, and woody debris (Hoffman et al., in press).

Salamander Species Identification

There are only two species of ambystomatid salamanders (A. macrodactylum and A. gracile) in NOCA and they rarely co-occur in the same lake (Liss et al., 1995). In NOCA, A. gracile is restricted to low elevation lakes on the westslope of the Cascade Range (Liss et al., 1995).

Salamander larvae were captured using hand-nets during snorkel surveys. Captured larvae were taken to a laboratory and reared to metamorphosis to confirm species identification. When it was not possible to transport larvae from the field, larvae were determined to be A. macrodactylum based on larval characteristics (Nussbaum et al., 1983; Leonard et al., 1993; Corkran and Thoms, in press), absence of large larvae (>60mm total length) or neotenes and egg masses characteristic of A. gracile, and

the presence of pre-metamorphic individuals with adult coloration.

Lake Physical and Chemical Characteristics

Eleven abiotic variables were measured for each lake. A hand-held sonar gun was used to determine maximum depth of each lake. Lake elevations were derived from 7 1/2 min USGS topographical maps, and lake surface areas were determined by digitization of lake shorelines outlined on these maps. Each time a lake was sampled, water temperature and water chemistry samples were collected at 1 m below the lake surface over the lake's deepest point. Water samples were collected with a 1.5 l van Dorn sampling bottle. Temperature measurements were determined during mid-afternoon using an Omega 871 thermo-couple. Frozen filtered and unfiltered water samples were transported to the Cooperative Chemistry Analytical Laboratory at Oregon State University, Corvallis, for analyses of total phosphorus, total Kjeldahl-N, ammonium-N, and nitrate/nitrite-N concentrations, and alkalinity, pH, and conductivity.

Zooplankton and Nearshore Benthic Macroinvertebrates

Each time a lake was sampled, crustacean zooplankton were collected using a 20-cm-diameter number 25 (64 μ m mesh) zooplankton net. From 1990-1993, three replicate vertical tows were collected in each lake on each

sampling occasion. Only one vertical tow was performed on each visit to three lakes sampled in 1989. For each vertical tow, the net was lowered to within 1 m of the lake bottom near the deepest point in each lake and retrieved upward at a constant rate. In the field, samples were preserved in 5% neutral sugar formalin solution (Haney and Hall, 1973). In the laboratory, samples were split using a Folsom plankton splitter. Split portions were allowed to settle for 24 hrs and adult zooplankton in these samples were identified to species and counted using an inverted microscope at 100x magnification (Liss et al., 1995). Zooplankton densities were expressed as number/l.

Benthic macroinvertebrates were sampled using a 17-cm-diameter metal sampling tube (Hoffman et al., in press). All major substrate types in the lake nearshore were sampled. The tube was placed in position over each 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 μ m 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 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. Macroinvertebrate densities were expressed as number/m².

Statistical Analyses

Statgraphics versions 6.0 and 7.0 were used for all statistical analyses. Each statistical test, except the multiple Wilcoxon-Rank tests, was performed at $\alpha=0.05$. For fishless lakes, ten paired Wilcoxon-Rank tests were performed to test for differences in average larval densities between survey techniques used in 1994 (i.e., search, day 2-m, day 5-m, night 2-m, night 5-m). To maintain the Type I error rate at 0.05 for the ten pairwise comparisons, a Bonferroni adjustment (Miller, 1981) was performed and each comparison was judged to be significantly different if $p \leq 0.005$.

Only lakes with at least two zooplankton samples in a given year were used for zooplankton analysis. Mean densities for each taxon for each year were calculated. If lakes were sampled over several years, densities were averaged for all samples. Average densities of benthic macroinvertebrate taxa were calculated in the same manner. Pearson correlation matrices were developed to identify significant relationships between selected abiotic variables, zooplankton densities, and benthic macroinvertebrate densities.

Multiple regression was used to assess the effects of abiotic factors on larval density for each fish

category (fishless, non-reproducing fish, and reproducing fish). The dependent variable for regression was the natural logarithm of average larval density in each lake, calculated from search surveys. Values for each chemical variable were averaged over all years in which snorkel surveys were performed. Water temperature averages were calculated from temperature measurements recorded on the day of snorkel surveys. A Pearson correlation matrix was developed to examine relationships among abiotic variables used for multiple linear regression analysis.

To determine the effect of fish on larval salamander densities, mean larval density and the 95% confidence interval (CI) were determined for each fishless lake from the linear regression model with TKN concentration and lake elevation as independent variables. Mean larval densities and 95% CIs for lakes with reproducing fish and for lakes with non-reproducing fish were also determined. Differences in larval densities between individual fishless lakes and lakes in other fish categories were judged to be significant if 95% CIs did not overlap.

Differences in the proportion of hidden salamanders among larval size classes and among fish categories were investigated using analysis of variance (ANOVA). Proportion of hidden larvae was arcsin-square-root transformed for all ANOVA tests to reduce within-group variability. To test for differences in proportion of

hidden salamanders among larval size classes, fishless lakes were investigated separately from lakes with non-reproducing fish and from lakes with reproducing fish. To test for differences in proportion of hidden larvae among fish categories, larvae from all size classes were combined in each fish category and the combined densities were compared between fish categories.

RESULTS

In fishless lakes in 1994, there were no significant differences in A. macrodactylum larval densities between survey types (Table 2; Wilcoxon-Rank tests, $p > 0.061$).

Table 2. Ambystoma macrodactylum larval density estimates (larvae/100 m of shoreline) for surveys of fishless lakes (NF) and lakes with reproducing fish (RF) in 1994. Night surveys were not performed (NP) in some lakes.

Lake Name	Fish Category	DAY			NIGHT	
		Search	2-m	5-m	2-m	5-m
PYRA	NF	67	59.7	125.7	113.5	76.5
PM5-3	NF	33	36	13	44.5	44.4
MC10	NF	59	149	163	61	383
TTAR	NF	1	74	29	NP	NP
WILD	NF	0	0	0	0	0
REVU	NF	0	0	0	NP	NP
EGG	NF	0	0	0	0	0
MSH4	NF	0	0	0	0	0
MONO	RF	0	0	0	4	0
LS2	RF	0	0	0	0	0
THRL	RF	0	0	0	0	0
M7	RF	0	0	0	0	0
LS7	RF	0	0	0	0	0
STTP	RF	0	0	0	0	0
SKYM	RF	0	0	0	0	0
DAGG	RF	0	0	0	0	0
M21	RF	0	0	0	NP	NP

Differences in larval densities between survey types in lakes with reproducing fish were not tested statistically since virtually no larvae were observed either during the day or at night. In addition, no larvae were observed in 4 of 8 fishless lakes. Although there were no statistically significant differences between survey

types, search surveys appeared to provide the most conservative estimates of larval densities.

Stepwise linear regression for fishless lakes identified statistically significant relationships between larval density and total Kjeldahl-N (TKN) and elevation (Figure 1; $R^2=0.6802$; $p=0.0001$):

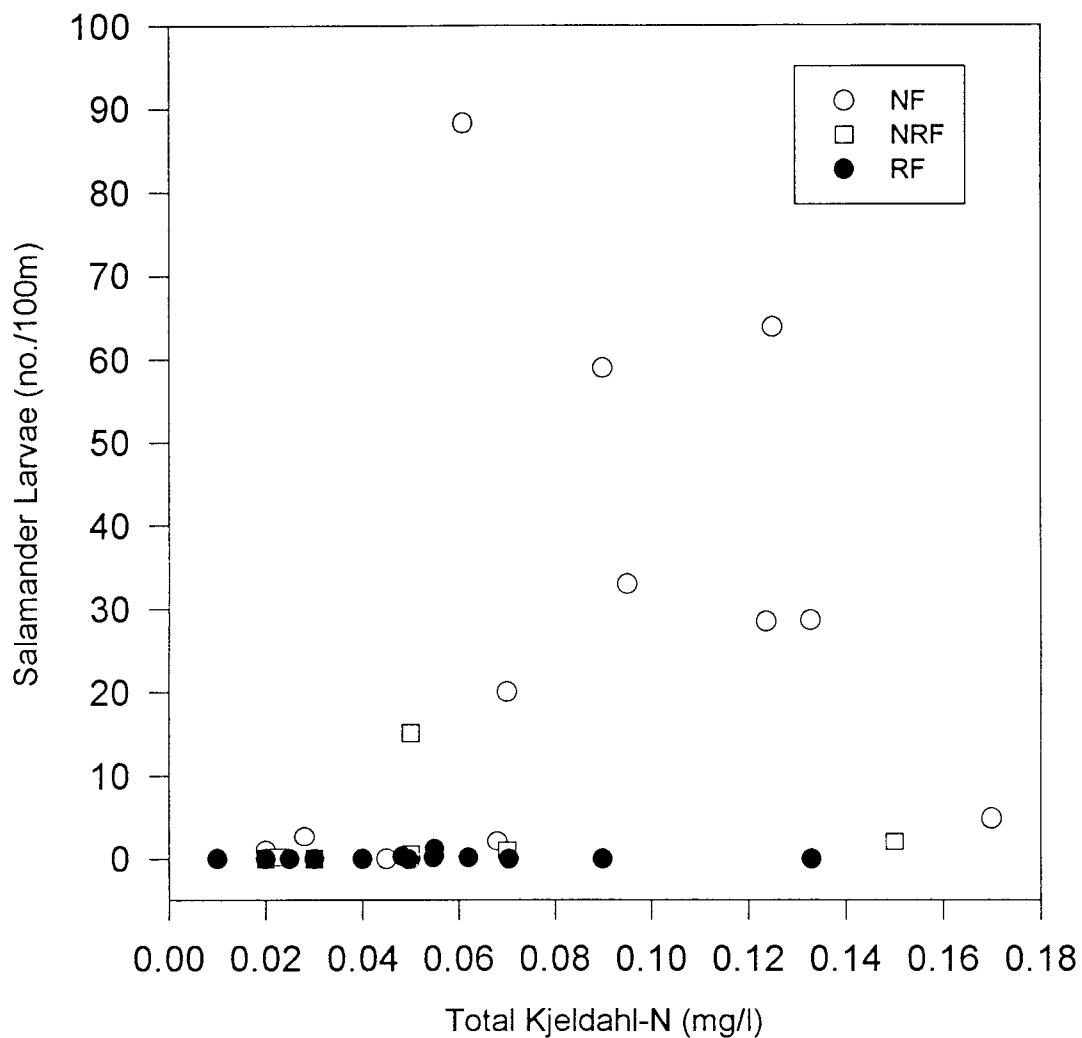
$$\ln(\text{Larval Density}) = 4.113 + 58.651 (\text{TKN}) - 0.005 (\text{Elevation})$$

The relationship with larval density was positive for TKN and negative for elevation. Pyramid, a low elevation (802m) fishless lake with high larval density, was withheld from a second regression analysis to determine the influence of this lake's elevation in the model.

Stepwise regression when Pyramid was omitted identified a statistically significant positive relationship between larval density and both TKN and conductivity ($R^2=0.6938$; $p=0.0001$). Thus, when Pyramid was omitted, lake elevation no longer had a detectable influence on larval density.

Total Kjeldahl-N had significant positive correlations with total phosphorus, water temperature, conductivity, and ammonium-N (Pearson correlation coefficients; $r=0.7393$, $p\leq 0.0001$; $r=0.5068$, $p=0.0004$; $r=0.3945$, $p=0.0073$; $r=0.4555$, $p=0.0017$, respectively), while the correlation between TKN and nitrate/nitrite-N was negative ($r=-0.3149$, $p=0.0351$). Alkalinity and

Figure 1. Relationships between Ambystoma macrodactylum larval densities and total Kjeldahl-N concentrations for fishless lakes (NF; n=20), lakes with non-reproducing fish (NRF; n=7), and lakes with reproducing fish (RF; n=18).



ammonium-N were negatively correlated with elevation ($r = -0.3688$, $p = 0.0127$; $r = -0.3389$, $p = 0.0288$, respectively). Thus, NOCA lakes with higher TKN concentrations tended to have relatively higher water temperatures, higher total phosphorus and ammonium-N concentrations, higher conductivity, and lower concentrations of nitrate/nitrite-N. Higher-elevation NOCA lakes tended to have lower alkalinities and lower ammonium-N concentrations than did lower-elevation lakes.

Salamander Stomach Contents

Benthic macroinvertebrates were identified in 75% of larval salamander stomachs (Table 3). The benthic taxon, Diptera, composed primarily of chironomid larvae, was found in the highest proportion of salamander stomachs. Beetle larvae (Coleoptera) and caddisfly larvae (Trichoptera) were also a significant proportion of larval diets. Crustacean zooplankton also were an important component of salamander diets. Cladocerans were the most common zooplankton taxon found in stomachs.

Crustacean Zooplankton and Benthic Macroinvertebrates

Total crustacean zooplankton density and cladoceran density were positively correlated with TKN (Pearson correlation coefficients; $r = 0.5728$, $p = 0.0053$, Figure 2; $r = 0.6946$, $p = 0.0003$, Figure 3; respectively). Furthermore, there was a significant positive

Table 3. Percent of stomachs from 13 Ambystoma macrodactylum larvae containing benthic macroinvertebrate and crustacean zooplankton taxa.

<u>Taxon</u>	<u>Percent</u>
Benthic Macroinvertebrates	75.0
Diptera	66.7
Chironomidae	41.7
Coleoptera	58.3
Trichoptera	50.0
Ephemeroptera	25.0
Amphipoda	16.7
Plecoptera	8.3
Pelecypoda	8.3
Crustacean Zooplankton	41.7
Cladocerans	41.7
Unidentified	41.7
Imm. Daphnids	25.0
<u>Daphnia rosea</u>	25.0
<u>Ceriodaphnia quadrangula</u>	16.7
<u>Chydorus sphaericus</u>	8.3
Copepods	16.7
Cylopoids	16.7
Calanoids	8.3
Harpatacoids	8.3

relationship between percent of cladocera composing the crustacean zooplankton community and TKN ($r=0.5882$, $p=0.0040$, Figure 4). At low TKN concentrations ($0.0\text{--}\approx 0.05$ mg/l), zooplankton density was very low and the zooplankton community was composed almost exclusively of copepods. Both total zooplankton density and the percent of cladocerans composing the zooplankton community increased with increases in TKN. There was no statistically significant relationship between TKN and total benthic macroinvertebrate density (Pearson

Figure 2. Relationship between total Kjeldahl-N concentration and crustacean zooplankton density for sampled lakes.

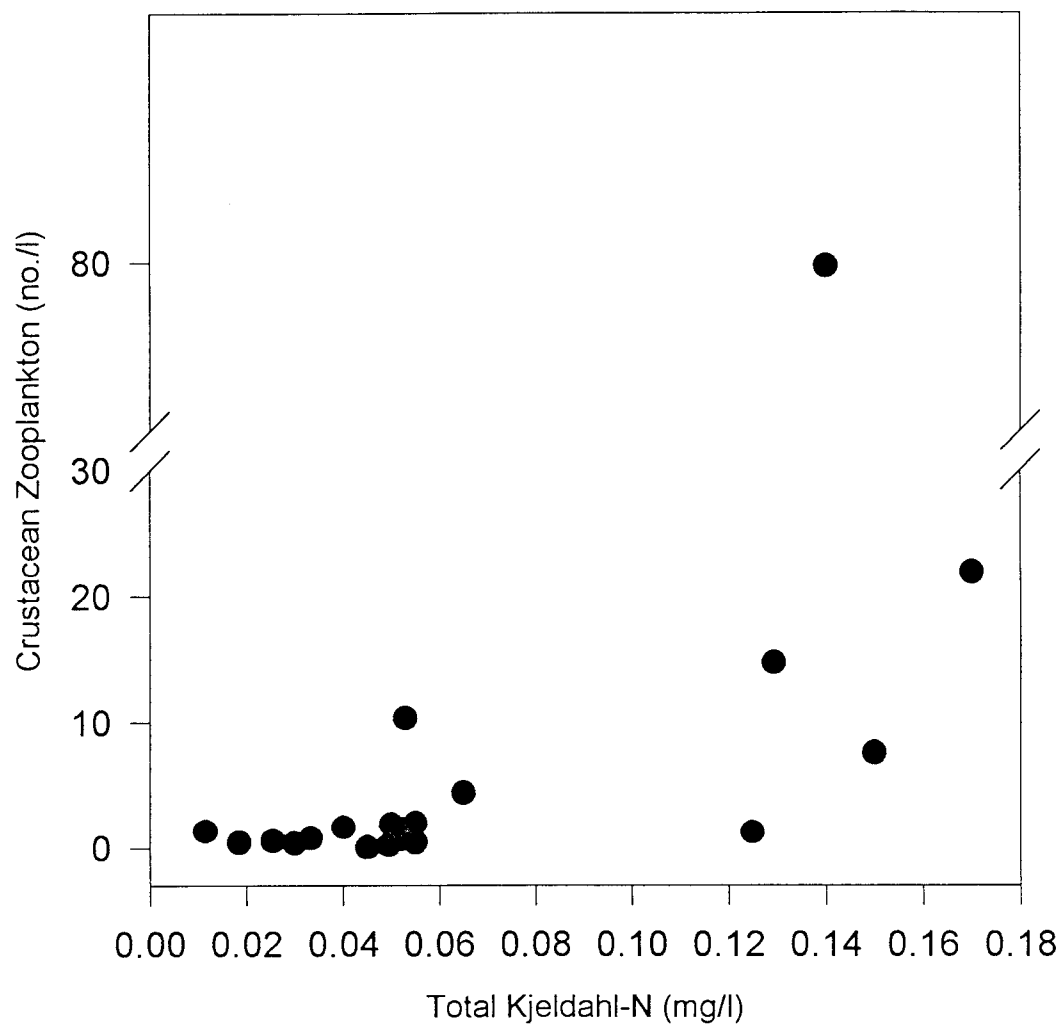


Figure 3. Relationship between total Kjeldahl-N concentration and cladoceran zooplankton density. Holopedium gibberum density was not included in the calculation of cladoceran density.

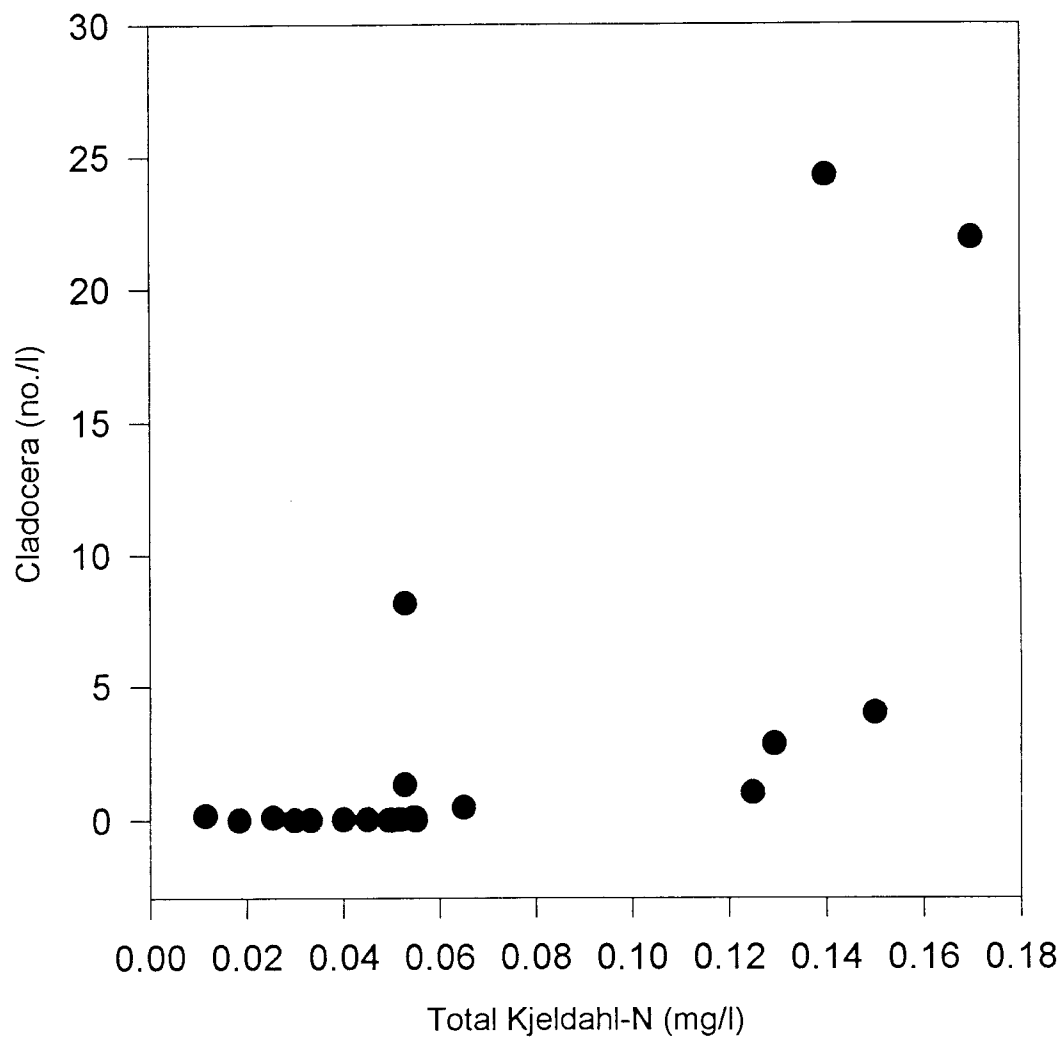
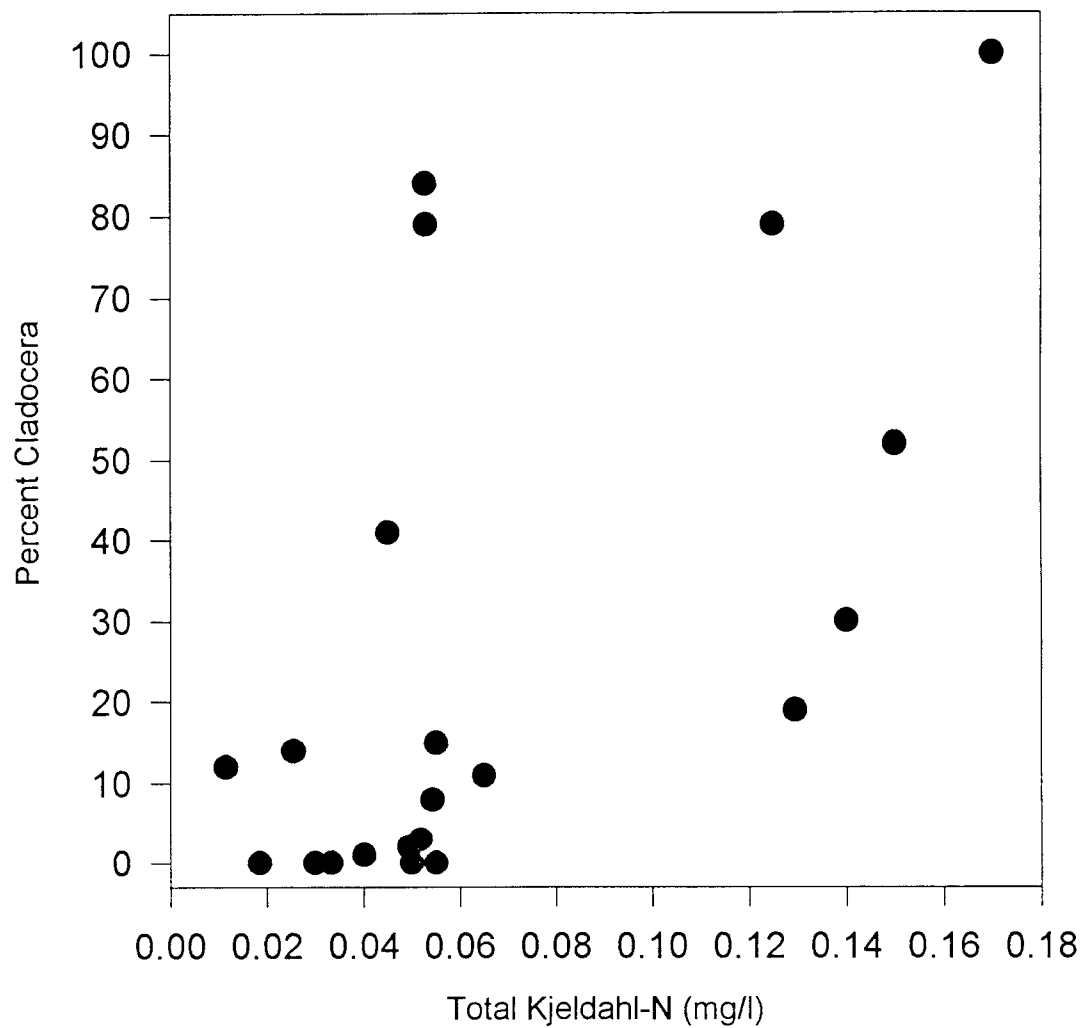


Figure 4. Relationship between total Kjeldahl-N concentration and cladoceran density as a percent of total zooplankton density. Holopedium gibberum was not included in the calculation of percent cladocera.



correlation coefficient, $r=-0.3216$, $p>0.05$; Figure 5) or chironomid density ($r=-0.0899$, $p>0.05$; Figure 5).

Benthic Habitat

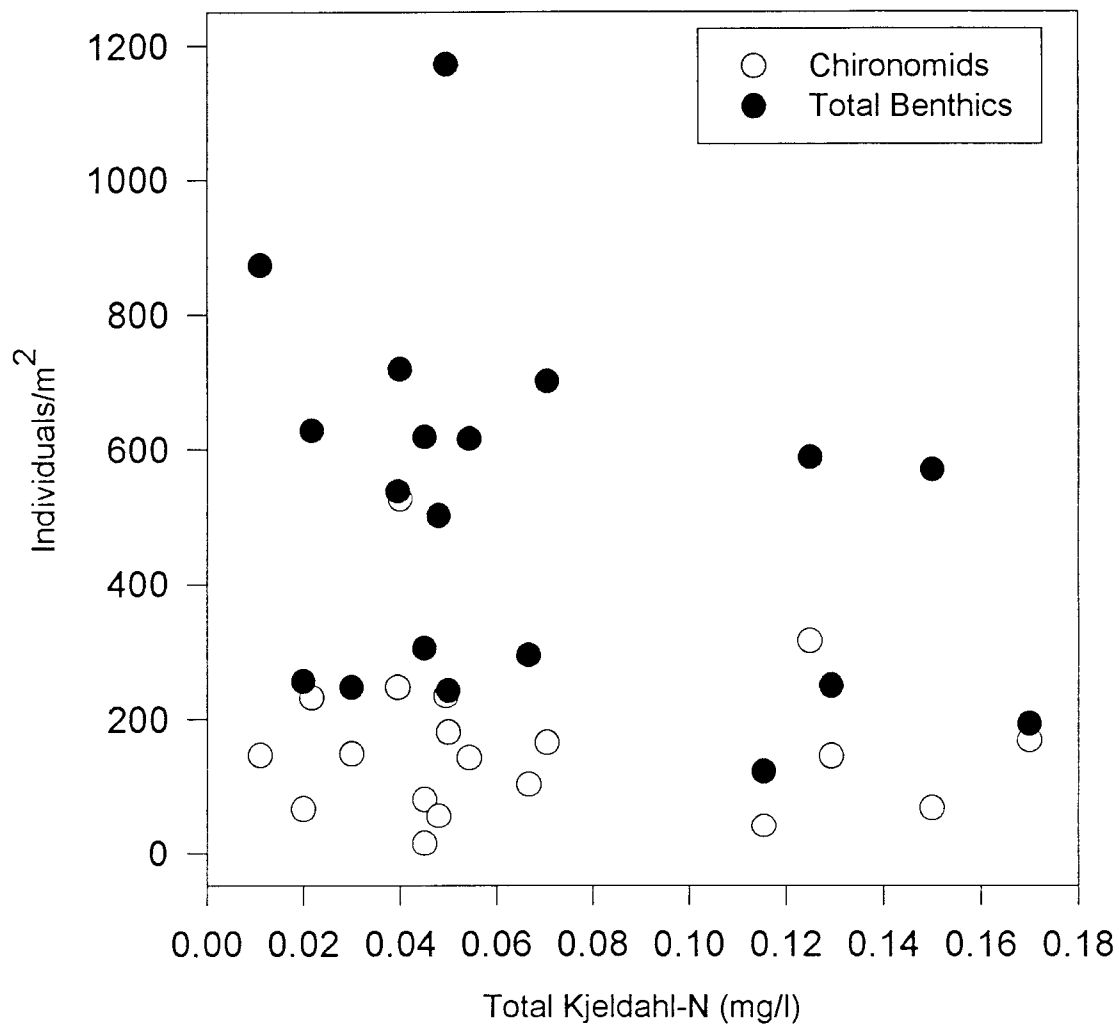
Most larvae were found in complex habitats comprised of substrate materials which provided interstitial spaces. Nearly half of the larvae were associated with habitats consisting primarily of boulder, cobble, and woody debris (Table 4). Almost 70% of the larvae were found in habitats with woody debris as a major substrate component.

Table 4. Percent of larvae observed in nearshore habitats in 17 lakes, 1990-1994. Habitats were identified by principle substrate materials.

<u>Substrate Materials</u>	<u>Percent of Larvae</u>
Boulder-Cobble, Woody Debris	44.3
Woody Debris, Silt/Sand	10.3
Woody Debris	6.7
Woody Debris, Organic Detritis	5.8
Boulder-Cobble	5.5
Emergent Vegetation	4.7
Boulder-Cobble, Organic Detritis	3.4
Woody Debris, Bedrock	2.7
Organic Detritis	2.7
Others	13.9*

* Fifteen habitats which individually accounted for fewer than 2.5% of observed larvae.

Figure 5. Relationship between total Kjeldahl-N concentration and the densities of chironomids and total benthic macroinvertebrates.



Fish Effects

No significant linear relationships between larval density and any abiotic factor were identified by stepwise linear regression for lakes with reproducing fish or for lakes with non-reproducing fish. When larval densities in lakes with reproducing fish were fit to a regression model with TKN and elevation as independent variables, neither TKN slope nor elevation slope were significantly different from zero (Figure 1; $p=0.6807$, $p=0.3897$, respectively). A similar regression analysis of larval densities in lakes with non-reproducing fish also found that TKN slope ($p=0.3504$) and elevation slope ($p=0.5611$) were not significantly different from zero (Figure 1).

Larval densities in reproducing fish lakes were low, making detection of significant relationships with abiotic variables difficult. Larval densities in lakes with non-reproducing fish also were low and detection of significant relationships between larval density and abiotic variables for these lakes was further limited by a small sample size ($n=7$).

Since multiple regression revealed no significant relationships between larval density and abiotic factors for either lakes with reproducing fish or for lakes with non-reproducing fish, larval densities from all lakes in each group were averaged and the 95% CI for each group

average was determined. To assess fish effects on larval density, the 95% CIs for lakes with reproducing fish and for lakes with non-reproducing fish were compared to 95% CIs for individual fishless lakes determined from the multiple regression model with TKN and elevation as independent variables.

For fishless lakes with $TKN < 0.05$ mg/l, mean larval densities generated by the linear regression equation were not significantly different from mean larval densities in either lakes with reproducing fish or lakes with non-reproducing fish (Table 5). However, for all ten fishless lakes with $TKN \geq 0.05$ mg/l, mean larval densities were significantly greater than in lakes with reproducing fish ($p < 0.05$). Of the reproducing fish lakes with $TKN \geq 0.05$ mg/l, none had larval densities that exceeded 1.22 larvae/100m of shoreline. Only four of the ten fishless lakes with $TKN \geq 0.05$ mg/l had significantly higher mean larval densities than lakes with non-reproducing fish ($p < 0.05$). These fishless lakes all had relatively high concentrations of TKN (≥ 0.095 mg/l).

Behavior

In fishless lakes, there were no significant differences among the three larval size classes in proportion of larvae hidden in substrate material (Table 6; ANOVA, $p = 0.160$). Lakes with non-reproducing fish and lakes with reproducing fish were not tested for

Table 5. Comparison of 95% confidence intervals (CIs) for larval A. macrodactylum densities between individual fishless lakes (NF), lakes with non-reproducing fish (NRF), and lakes with reproducing fish (RF). Mean larval densities and 95% CIs were determined from a multiple linear regression model using total Kjeldahl-N concentration (TKN) and lake elevation as independent variables.

<u>Fish Category</u>	<u>Lake Name</u>	<u>TKN (mg/l)</u>	<u>Elevation (m)</u>	<u>Mean Larval Density</u>	<u>Lower Limit 95% CI</u>	<u>Upper Limit 95% CI</u>	<u>Difference*</u>
NF	WILD	0.01	1488	0.1182	0.0287	0.4874	
	REVU	0.02	1528	0.1769	0.0503	0.6225	
	TTAR	0.02	1632	0.1097	0.0316	0.3208	
	WADD	0.028	1504	0.3158	0.0967	1.0314	
	SILL	0.03	2044	0.0297	0.0051	0.1729	
	MSH4	0.03	1635	0.1945	0.0642	0.5890	
	GRNV	0.03	1664	0.1703	0.0557	0.5201	
	SILU	0.04	2127	0.0365	0.0057	0.2344	
	KETU	0.04	1693	0.2679	0.0974	0.7373	
	EGG	0.05	1604	0.7249	0.2850	1.8433	A
	PYRA	0.0609	802	54.6626	2.8671	1042.1592	A
	MR11	0.068	1863	0.6340	0.2262	1.7771	A
	M131	0.07	1800	0.9522	0.3718	2.4385	A
	MC10	0.09	1556	9.0317	2.9124	30.5844	A
	PM53	0.095	1382	28.1399	5.7158	138.5401	B
	MR3	0.1237	1873	15.8833	3.5612	70.8419	B
	MR12	0.125	1981	10.4382	2.1128	51.5679	A
	MR2	0.1328	1873	27.0855	5.2653	139.3321	B
	JUAN	0.17	2033	115.1137	11.1828	1184.9549	B
NRF	Average	0.056	1597.4	0.5118	0.0756	3.4666	
RF	Average	0.046	1602.8	0.0821	0.0514	0.1310	

- * A. indicates a significant difference in larval density between a fishless lake and lakes with reproducing fish.
 B. indicates a significant difference in larval density between a fishless lake and both lakes with reproducing fish and lakes with non-reproducing fish.

Table 6. Total number of larval Ambystoma macrodactylum observed and the number and percent hidden in substrate materials during search surveys of fishless lakes (NF; n=10), lakes with non-reproducing fish (NRF; n=5), and lakes with reproducing fish (RF; n=5) in 1993 and 1994. Larval size is estimated total length (mm).

Fish Category	Larval Size	N ^a	Number Observed	Number Hidden	Percent Hidden
NF	10-30	8	342	131	38.3
	31-60	7	262	68	26.0
	>60	8	309	152	49.2
NRF	10-30	4	15	6	40.0
	31-60	3	52	36	69.2
	>60	3	31	28	90.3
RF	10-30	4	14	4	28.6
	31-60	2	4	4	100.0
	>60	0			

^a Number of lakes where individuals of that larval size were observed.

differences in proportion of hidden larvae between size classes because few lakes in these categories contained all three larval size classes. There were no significant differences in the proportion of hidden larvae among fish categories (Table 6; ANOVA, $p=0.495$). Although statistical analysis did not identify any significant differences in proportion of hidden larvae among larval size classes and among fish categories, there was a tendency for the percent of hidden larvae to increase as larval size increased in each fish category. Furthermore, there was a tendency for a greater

percentage of larger larvae (>30mm) to be hidden in lakes with both non-reproducing and reproducing fish than in fishless lakes.

DISCUSSION

The abundance of larval A. macrodactylum in NOCA lakes was influenced both by lake productivity as indicated by TKN and by trout. According to McQueen et al. (1986), the potential productivity at all trophic levels in freshwater lakes is set by nutrient supply. High-elevation NOCA lakes are oligotrophic, or poorly productive (Lomnicky, 1995). Nevertheless, larval density in fishless lakes was positively related to the concentration of TKN. In turn, cell density of phytoplankton, which are fed upon by herbivorous zooplankters, was positively correlated with TKN in NOCA lakes (Liss et al., in review). Total Kjeldahl-N also was positively correlated with total phosphorus concentration and conductivity, both indicators of lake trophic state (Wetzel, 1983).

Total Kjeldahl-N is a measure of ammonia plus all organically derived nitrogen (Lambou et al., 1983). Organic nitrogen is not readily utilized by algae and bacteria, thus TKN does not play an active role in the energetics of lakes (Goldman and Horne, 1983). However, TKN when correlated with phosphorus concentration and water temperature has been identified as a good predictor of lake productivity as measured by chlorophyll density (Lambou et al., 1983) or by total plankton biomass (Paloheimo and Fulthorpe, 1987). Thus, TKN in NOCA

lakes, which was correlated with total phosphorus concentration and water temperature, provided a reasonable predictor of lake productivity.

The link between TKN and larval density appears to be through the pelagic food web. The density of crustacean zooplankton, an important food resource for larval A. macrodactylum, increased with increased TKN. Moreover, at high TKN, herbivorous cladocerans, which were identified in more larval stomachs than any other zooplankton, composed a greater proportion of crustacean zooplankton than did copepods. Other researchers also have demonstrated an association between the composition of crustacean zooplankton and nitrogen concentration in high-elevation lakes (Byron et al., 1984; Stoddard, 1987; Liss et al., 1995; in review).

Several researchers have reported that larval ambystomatid salamanders from western North America prey upon crustacean zooplankton, especially early in larval development. Anderson (1968) found that small larvae of both A. macrodactylum croceum and A. m. sigillatum fed mainly on cladocerans and copepods. Dodson (1970) and Dodson and Dodson (1971) reported that zooplankton were a major food item for larval A. tigrinum early in larval development. Licht (1975) reported that larval A. gracile fed on crustaceans, including cladocera, throughout larval development in Marion Lake, British

Columbia. Other studies of salamanders from eastern North America support the contention that zooplankton are important in larval salamander diets (Brophy, 1980; Branch and Altig, 1981; Freda, 1983; Taylor et al., 1988).

Ambystomatid larvae have been shown to utilize benthic macroinvertebrates as food resources (Henderson, 1973; Licht, 1975; Brophy, 1980), particularly when larvae become larger (Anderson, 1968; Dodson, 1970; Dodson and Dodson, 1971; Freda, 1983; Taylor et al., 1988; McWilliams and Bachmann, 1989). Benthic macroinvertebrates, especially chironomid larvae, also were a large component of larval salamander diets in NOCA lakes. However, no significant relationship between TKN and either total benthic macroinvertebrate density or chironomid density was detected in NOCA lakes. This was not unexpected since aquatic insects are capable of tolerating wide ranges of many chemical variables (Ward, 1992). Furthermore, the distribution and abundance of benthic macroinvertebrates in lakes can be influenced by an array of physical and chemical factors including the composition of benthic substrates [e.g., amount of woody debris, large and small inorganic material, rooted vegetation (Hoffman et al.; in press)], lake depth and phytoplankton biomass (Johnson and Wiedenholm, 1989), water temperature (Hoffman et al., in press), and other

water chemistry factors including salinity, dissolved oxygen, water hardness, and acidity (Ward, 1992).

The effects of trout on larval salamander density depended upon TKN concentration and whether or not trout had established reproducing populations. Larval salamander densities were low (≤ 2.76 larvae/100m) in lakes with $TKN < 0.05$ mg/l regardless of whether trout were present or absent. No statistically significant differences in mean larval densities between fishless lakes and lakes with fish were detected within this range of TKN concentrations. In contrast, all fishless NOCA lakes with $TKN \geq 0.05$ mg/l had significantly higher mean larval densities than did lakes with reproducing trout. Trout usually reach high densities and have diverse age and size structures in NOCA lakes where fish reproduction occurs (Liss et al., 1995). These results suggest that fish predation is likely responsible for reducing larval A. macrodactylum abundance in lakes with reproducing trout. Such a conclusion is supported by several laboratory and field studies that have demonstrated that fish can reduce the abundance of ambystomatid salamanders or eliminate them from aquatic systems when fish were permitted to invade bodies of water where salamanders were present (Burger, 1950; Blair, 1951; Sprules, 1974a; Thompson et al., 1980; Petranka, 1983; Taylor, 1984;

Semlitsch, 1987, 1988; Sih et al., 1988, 1992; Dobler, 1994).

Blaustein et al. (1994b) suggested that Saprolegnia ferax caused declines of Rana cascadae in the Oregon Cascades and that the fungus, S. ferax, could be spread by introduced fish. Although we observed no A. macrodactylum eggs or larvae that appeared to be infected with S. ferax, the fungus cannot be eliminated as a possible factor contributing to reductions in larval salamanders in NOCA lakes.

Although all ten fishless lakes with $TKN \geq 0.05$ mg/l had significantly higher mean larval densities than did lakes with reproducing trout, only four of these ten fishless lakes had significantly higher larval densities than lakes with non-reproducing trout. Lakes with non-reproducing trout were periodically stocked with low densities of fry (Liss et al., 1995). Thus, fish densities in lakes with non-reproducing trout are likely lower and age and size structure less complex than in lakes with reproducing trout. Moreover, significant differences in mean larval densities between fishless lakes and lakes with non-reproducing trout were detected only in lakes with high TKN concentrations ($TKN \geq 0.095$ mg/l), where the highest mean larval densities in fishless lakes were predicted. Comparison of larval densities between fishless lakes and lakes with non-

reproducing trout was hampered by small sample size (n=7) of lakes with non-reproducing trout. Further research on the effects of non-reproducing trout on larval salamanders in high-elevation NOCA lakes is needed.

The proportion of larvae hidden in benthic substrates tended to increase as a function of both larval total length and fish presence, although the increases were not statistically significant. In both fishless lakes and lakes with fish, a greater proportion of larger salamander larvae were hidden than were smaller larvae. Anderson (1967) reported that metamorphosing larval A. macrodactylum became more secretive and congregated in nearshore areas of mountain lakes in California. The increase in proportion of larvae hidden as larval total length increased may be related to metamorphosis as amphibians may be particularly susceptible to predation at this critical stage of development (Wassersug and Sperry, 1977; Arnold and Wassersug, 1978).

Although not a statistically significant trend, it appeared that a greater proportion of larvae were hidden in lakes with fish than in fishless lakes. In both field and laboratory studies, fish have been shown to alter salamander behavior (Stangle 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 restricting foraging to night (Efford and Mathias, 1969; Sprules, 1974a; Taylor, 1983). Shifts in behavior and habitat use to avoid intra- and interspecific 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). Sih et al. (1988) emphasize the importance of the dynamics of refuge use in determining larval survival. 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.

Most larvae observed in NOCA lakes were associated with nearshore habitats containing boulder, cobble, and woody debris. Larval occurrence in these nearshore habitats may be related to refuge use or forage opportunity. Anderson (1967) suggested that A. m. sigillatum in Sierra Nevada mountain lakes use different habitats, including woody debris, to minimize intraspecific competition and possibly cannibalism. Holomuzki (1986) reported that fitness rates of larval A. tigrinum from Colorado were higher in complex microhabitats than in simple microhabitats. Complex habitats in streams provided larval A. texanum with more

refuge and higher densities of food organisms than other, more simple, habitats (Holomuzki, 1989).

Metapopulation processes may be important in regional persistence of amphibian populations (Sjogren, 1991; Bradford et al., 1993). Metapopulations are spatially structured systems of local populations connected by dispersal (Hanski and Gilpin, 1991). Gill (1978) suggested that red-spotted newt (Notophthalmus viridescens) populations in the northeastern U.S. resembled a core-satellite metapopulation. In metapopulations with core-satellite structures, there is considerable variation in population abundance among local populations (Harrison, 1991; 1994). Core populations are large populations that occupy high quality habitat and have relatively low probabilities of extinction. Satellite populations are smaller populations that are more susceptible to extinction than are core populations (Harrison, 1991; 1994). Core populations can provide stable sources of dispersing individuals that recolonize satellite habitats where local extinction has occurred (Sjogren, 1991; Harrison, 1994). Identification and protection of vital core populations is critical in regional conservation strategies (Rieman and McIntyre, 1993; Schlosser and Angermeier, 1995).

Very little is known about metapopulation processes in high-elevation A. macrodactylum including long-term stability and persistence of populations and dispersal of individuals among habitats. However, if local populations of A. macrodactylum in NOCA function as a metapopulation, then its structure may be similar to a core-satellite structure. The relatively large local populations that occur toward the upper end of the TKN gradient may function as core-type populations, while the small populations that occur toward the lower end of the gradient may function as satellite populations. From a metapopulation perspective, introduced trout could indirectly influence regional population distribution by inhibiting recolonization of habitats where extinction has occurred either through elimination of critical core populations, which could serve as relatively stable sources of population dispersers, or by impeding dispersal between habitats. Bradford et al. (1993) presented evidence that the continued decline in mountain yellow-legged frogs (Rana muscosa) in Sequoia and Kings Canyon National Parks could have resulted from the inability of dispersing individuals to recolonize ponds where local extinction had occurred. Bodies of water that could have provided avenues for movement among ponds were often populated with introduced fish.

Our results imply that assessment of fish impacts on amphibians requires an understanding of natural abiotic and biotic factors and processes influencing amphibian distribution and abundance (e.g., Pechmann et al., 1991). In NOCA, larval A. macrodactylum abundance was dependent upon TKN in lakes which indicated the availability of zooplankton, an important food resource for larvae. Fish had little detectable influence on larval A. macrodactylum densities in lakes with low TKN concentrations, as salamander densities were very low in these lakes regardless of fish presence. Fish effects on A. macrodactylum were only detectable in lakes with high TKN where predicted larval density was high.

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APPENDIX

Appendix 1. Averages and ranges (shown in parentheses) of biotic and abiotic variables for lakes with Ambystoma macrodactylum. Fishless lakes (NF), lakes with non-reproducing fish (NRF), and lakes with reproducing fish (RF) were sampled from 1990-1994. Larval density is number of larvae/100m of shoreline.

Fish Category	Lake Name	Elevation (m)	Surface Area(ha)	Maximum Depth(m)	Larval Density	Temp. (°C)	TKN (mg/l)	TP (mg/l)	NO ₃ -N (mg/l)	NH ₃ -N (mg/l)	Alka (mg/L)	pH	Cond (µmhos/cm)
NF	EGG	1604	0.8	5.0	0.0	14.5	0.05	0.007	0.001	0.006	0.74	6.5	7.2
	GRNV	1664	16.1	47.3	0.0	15.2	0.03	0.005	0.0	0.007	1.03	7.0	6.5
	JUAN	2033	0.2	1.2	5.0 (0.4, 9.6)	12.4	0.17 (0.15, 0.19)	0.016	0.001	0.0085 (0.007, 0.01)	1.25	6.9	101.0
	KETU	1693	0.6	2.1	0.0	12.85 (12.5, 13.2)	0.04	0.008	0.003 (0.002, 0.004)	0.004 (0.003, 0.005)	3.22 (3.12, 3.32)	7.5 (7.4, 7.7)	32.8 (31.3, 33.8)
	MC10	1556	0.4	4.9	59.0	15.3	0.09	0.007	0.001	0.006	1.33	6.8	9.4
	MR2	1873	0.3	1.5	28.61 (16.82, 39.88)	13.8 (9.6, 19.8)	0.1328 (0.047, 0.22)	0.0132 (0.006, 0.02)	0.0016 (0.0, 0.003)	0.0056 (0.003, 0.007)	2.34 (2.16, 2.49)	7.36 (6.9, 7.9)	17.69 (15.1, 19.8)
	MR3	1873	0.2	1.0	28.5 (18.33, 38.67)	13.766 (8.8, 17.4)	0.1237 (0.091, 0.18)	0.009 (0.007, 0.011)	0.002	0.0087 (0.007, 0.011)	0.66 (0.61, 0.73)	6.4 (6.3, 6.5)	15.297 (3.79, 38.3)
	MR11	1863	1.3	8.0	2.15	14.75 (14.7, 14.8)	0.068 (0.021, 0.115)	0.0055 (0.005, 0.006)	0.0015 (0.0, 0.003)	0.004 (0.002, 0.006)	2.709 (2.48, 2.938)	7.35 (7.2, 7.5)	21.82 (18.95, 24.69)
	MR12	1981	0.6	4.0	63.85 (17.7, 110.0)	12.1	0.125 (0.08, 0.17)	0.009 (0.008, 0.01)	0.0	0.0025 (0.002, 0.003)	1.995 (1.87, 2.12)	7.25 (7.1, 7.4)	14.95 (13.8, 16.1)
	MR13-1	1800	0.3	2.0	20.05 (19.78, 20.33)	13.63 (8.0, 20.8)	0.07 (0.06, 0.09)	0.0117 (0.009, 0.016)	0.0003 (0.0, 0.001)	0.004 (0.003, 0.005)	0.9867 (0.94, 1.07)	6.77 (6.7, 6.8)	7.56 (6.7, 8.9)
	MSH4	1635	1.4	4.6	0.0	8.9	0.03	0.004	0.038	0.004	1.85	7.1	16.2

Appendix 1. Continued.

Fish Category	Lake Name	Elevation (m)	Surface Area(ha)	Maximum Depth(m)	Larval Density	Temp. (°C)	TKN (mg/l)	TP (mg/l)	NO ₃ -N (mg/l)	NH ₃ -N (mg/l)	Alka (mg/l)	pH	Cond (µmhos/cm)
NF	PM5-3	1382	0.1	3.0	33.0 (1.0, 65.0)	17.0 (16.9, 17.1)	0.095 (0.06, 0.13)	0.007	0.0005 (0.0, 0.001)	0.0055 (0.003, 0.008)	0.985 (0.98, 0.99)	6.6	6.7 (6.5, 6.9)
	PYRA	802	0.3	8.8	88.33 (10.29, 169.71)	15.63 (9.9, 20.6)	0.0609 (0.0, 0.12)	0.0102 (0.006, 0.021)	0.0011 (0.0, 0.001)	0.0062 (0.004, 0.015)	8.676 (5.79, 11.22)	7.8 (7.6, 8.0)	76.6 (45.79, 98.0)
	WADD	1504	4.1	11.9	2.76 (0.0, 4.26)	10.68 (4.9, 14.8)	0.028 (0.0, 0.05)	0.0054 (0.003, 0.007)	0.005 (0.0, 0.023)	0.0046 (0.002, 0.007)	2.05 (1.6, 2.49)	7.18 (7.0, 7.4)	16.54 (12.6, 20.5)
	WADM	1642	1.0	1.0	0.0	10.75 (8.4, 13.1)	0.045 (0.01, 0.08)	0.0055 (0.005, 0.006)	0.0035 (0.0, 0.007)	0.003 (0.002, 0.004)	2.25 (2.1, 2.4)	7.2 (7.1, 7.3)	18.0 (16.8, 19.2)
	WILD	1488	4.6	8.8	0.0	10.5	0.01	0.001	0.001	0.001	0.71	6.5	8.1
	REVV	1528	1.2	5.0	0.0	5.8	0.02	0.007	0.0	0.002	0.82	6.6	21.8
	SILL	2044	1.0	10.0	0.0	12.3	0.03	0.006	0.0	0.007	1.57	7.1	11.8
	SILU	2127	1.3	6.0	0.0	11.4	0.04	0.009	0.0	0.007	1.35	7.1	9.8
	TTAR	1632	0.6	3.6	1.0	10.2	0.02	0.002	0.028	0.001	2.78	7.7	22.7
NRF	COON	662	8.2	5.8	2.14	17.0	0.15	0.016	0.001	0.04	3.43	7.4	28.9
	DDU	1922	4.8	27.0	0.0	13.45 (11.8, 15.1)	0.03 (0.02, 0.04)	0.0055 (0.004, 0.007)	0.0345 (0.019, 0.05)	0.0075 (0.003, 0.012)	2.155 (1.89, 2.42)	7.3 (7.2, 7.3)	20.85 (17.2, 24.5)
	HIYU	1159	1.6	4.3	1.0	11.1	0.07	0.005	0.002	0.003	1.13	6.7	8.5
	MM11	1974	1.4	7.6	0.0	11.9	0.02	0.003	0.0	0.001	0.78	6.6	0.0
	MR9	1813	1.7	4.9	0.57 (0.16, 0.97)	13.25 (13.1, 13.4)	0.05	0.0065 (0.006, 0.007)	0.001	0.004	1.375 (1.27, 1.48)	6.95 (6.9, 7.0)	10.75 (9.8, 11.7)

Appendix 1. Continued.

Fish Category	Lake Name	Elevation (m)	Surface Area(ha)	Maximum Depth(m)	Larval Density	Temp. (°C)	TKN (mg/l)	TP (mg/l)	NO ₃ -N (mg/l)	NH ₃ -N (mg/l)	Alka (mg/l)	pH	Cond (µmhos/cm)
NRF	MR11	1863	1.3	8.0	15.08 (6.33, 38.67)	13.24 (7.9, 17.5)	0.05 (0.03, 0.06)	0.005 (0.004, 0.007)	0.0024 (0.0, 0.01)	0.004 (0.001, 0.007)	2.67 (2.43, 2.81)	7.32 (7.0, 7.5)	21.66 (19.7, 23.5)
	MR13-2	1789	1.2	5.0	0.2 (0.0, 0.4)	10.35 (5.6, 12.6)	0.0225 (0.02, 0.03)	0.0045 (0.004, 0.005)	0.004 (0.0, 0.012)	0.0035 (0.001, 0.011)	1.22 (1.12, 1.31)	6.95 (6.8, 7.0)	9.63 (8.6, 10.5)
RF	BATT	1629	2.5	4.3	0.0	10.6 (7.8, 13.0)	0.03 (0.02, 0.04)	0.0063 (0.005, 0.008)	0.0063 (0.001, 0.015)	0.005 (0.004, 0.006)	2.75 (2.49, 2.97)	7.23 (7.2, 7.3)	22.77 (21.0, 24.2)
	DAGG	1679	3.6	4.0	0.0	17.47 (12.6, 23.0)	0.133 (0.1, 0.17)	0.0103 (0.01, 0.011)	0.001	0.0087 (0.006, 0.013)	4.55 (4.0, 5.05)	7.9 (7.7, 8.0)	37.4 (31.4, 42.6)
	DDL	1909	0.3	3.0	0.0	8.85 (8.6, 9.3)	0.01	0.006	0.041	0.008	2.21	7.3	21.5
	DOUB	1642	12.0	17.7	0.0	13.1	0.03	0.003	0.001	0.005	0.93	6.7	11.8
	KETT	1639	4.0	7.0	0.4 (0.0, 0.8)	16.05 (15.7, 16.4)	0.055 (0.04, 0.07)	0.0085 (0.008, 0.009)	0.001	0.005 (0.004, 0.006)	2.74 (2.65, 2.83)	7.45 (7.4, 7.5)	24.3 (23.3, 25.5)
	LS2	1243	1.0	4.8	0.134 (0.0, 0.94)	13.23 (7.0, 20.4)	0.0547 (0.024, 0.07)	0.0083 (0.004, 0.016)	0.0015 (0.0, 0.004)	0.005 (0.0, 0.01)	5.971 (2.02, 7.94)	7.71 (6.9, 8.5)	53.81 (16.16, 71.0)
	LS7	1510	2.8	7.9	0.0	12.5	0.02	0.002	0.005	0.005	1.78	7.3	17.8
	M7	1363	3.2	11.0	0.0	12.5	0.02	0.003	0.001	0.001	1.34	7.1	10.9
	M21	1205	1.6	3.1	0.0	8.4	0.01	0.0	0.059	0.0	2.19	7.2	17.5
	MCAL	1679	5.0	6.1	0.12 (0.0, 0.48)	13.08 (6.9, 18.3)	0.062 (0.04, 0.12)	0.0092 (0.004, 0.016)	0.0014 (0.0, 0.004)	0.0054 (0.0, 0.013)	2.116 (1.48, 2.63)	7.28 (7.0, 7.5)	16.66 (11.3, 21.4)
	MONO	1270	13.5	37.2	0.0	17.0	0.03	0.002	0.001	0.004	1.66	7.3	13.2

Appendix 1. Continued.

Fish Category	Lake Name	Elevation (m)	Surface Area(ha)	Maximum Depth(m)	Larval Density	Temp. (°C)	TKN (mg/L)	TP (mg/L)	NO ₃ -N (mg/L)	NH ₃ -N (mg/L)	Alka (mg/L)	pH	Cond (µmhos/cm)
RF	MR16	1900	0.6	2.0	1.22 (0.81, 1.64)	15.45 (14.0, 16.9)	0.055 (0.04, 0.07)	0.0085 (0.008, 0.009)	0.001 (0.0, 0.002)	0.0065 (0.005, 0.008)	1.325 (0.98, 1.67)	6.9 (6.8, 7.0)	9.4 (5.8, 13.0)
	RAIN	1717	6.3	10.4	0.298 (0.0, 0.52)	12.02 (3.8, 19.0)	0.0483 (0.02, 0.1)	0.0057 (0.004, 0.007)	0.0028 (0.0, 0.015)	0.0042 (0.0, 0.008)	1.377 (1.06, 1.6)	6.98 (6.6, 7.2)	10.73 (7.8, 12.5)
	SKYMO	1609	4.3	5.5	0.0	9.4 (5.3, 13.5)	0.025 (0.02, 0.03)	0.0035 (0.003, 0.004)	0.005 (0.001, 0.009)	0.0155 (0.002, 0.009)	2.28 (2.25, 2.31)	7.25 (7.2, 7.3)	19.15 (18.7, 19.6)
	STTP	1580	0.6	2.5	0.0	13.2	0.04	0.001	0.0	0.002	1.73	7.1	13.1
	THRL	1357	10.0	33.0	0.0	12.8	0.09	0.003	0.018	0.006	0.85	6.6	6.1
	TRPL	1931	1.0	2.1	0.0	12.7 (11.6, 13.8)	0.0705 (0.051, 0.09)	0.0115 (0.006, 0.017)	0.0045 (0.001, 0.008)	0.0045 (0.004, 0.005)	3.675 (3.26, 4.01)	7.4 (7.3, 7.5)	32.1 (28.75, 35.45)
	TRPU	1988	1.0	4.3	0.0	11.45 (10.6, 12.3)	0.0495 (0.03, 0.069)	0.0125 (0.009, 0.016)	0.016 (0.005, 0.027)	0.005 (0.003, 0.007)	3.724 (3.34, 4.108)	7.85 (7.6, 8.1)	33.09 (29.55, 36.63)