

# Ecological Impact of Introduced Trout on Native Aquatic Communities in Mountain Lakes

## Phase III Final Report

by William J. Liss, Gary L. Larson, and Robert L. Hoffman, editors

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# CHAPTER 1

**Abundance and Behavior of Larval Long-toed Salamanders  
(*Ambystoma macrodactylum*) in Naturally Fishless Lakes and Lakes with Non-  
Reproducing Populations of Introduced Trout in the Northern Cascade Mountains,  
Washington, USA.**

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## ABSTRACT

Fish introduction into mountain lakes to provide recreational opportunities could potentially impact native biota, including amphibians, of these relatively pristine ecosystems. We investigated the impact of non-reproducing populations of trout (*Oncorhynchus* sp.) that were stocked at regular intervals and moderate densities on the abundance and behavior of native long-toed salamander (*Ambystoma macrodactylum*) larvae in lakes of the North Cascades National Park Service Complex, Washington, USA. Fish densities were determined from stocking records and salamander densities were estimated using snorkel methods. Eleven physical and chemical variables were also measured for each lake sampled. Stepwise multiple regression indicated that salamander density in fishless lakes was strongly positively related with total Kjeldahl-N (TKN) concentration and weakly negatively related with pH. Salamander densities in lakes with fish were not related to any of 11 physical and chemical variables investigated. Larval salamander density was statistically lower in only one lake with a non-reproducing trout population as compared to their densities in fishless lakes. The probability of encountering salamander larvae closely associated with lake substrates that potentially provided refuge was greater in lakes with fish than in fishless lakes, and greater for larger sized larvae in both lakes with and without fish. The severity of trout impact on *A. macrodactylum* larvae in mountain lakes would appear dependent upon the reproductive status of trout in a lake and lake productivity, as indicated by TKN. Theory suggests that large populations of salamanders may be less vulnerable to extinction from chance events than small populations and they may serve as important sources of colonists. Since large populations are predicted to occur in lakes with high TKN concentrations, a prudent and

precautionary management strategy would be to maximize protection of all NOCA lakes with relatively high TKN.

## INTRODUCTION

Montane lakes in the western USA are popular locations for recreational angling for stocked trout. Bahls (1992) conducted a survey of fisheries biologists and managers in western states and found that about 65% of all montane and 95% of larger, deeper lakes currently support fish. According to Bahls (1992), about 95% of these lakes could have been naturally fishless.

Concern about the potential impacts of stocked trout on native biota has been increasing. Introduced trout appear capable of altering food webs in montane by reducing abundance or eliminating larger, more visible vertebrate and invertebrate prey including some species of frogs (e.g., Bradford, 1989; Bradford et al., 1993; Fellers and Drost, 1993; Blaustein et al., 1994; Knapp and Matthews, 2000), ambystomatid salamanders (Taylor, 1983a; 1983b; Tyler et al., 1998a), and crustacean zooplankton (e.g., Starkweather, 1981; Stoddard, 1987; Donald et al., 1994; Liss et al., 1998), and by altering nutrient dynamics in lakes (e.g., Leavitt et al., 1994).

In the Pacific Northwest, ambystomatid salamanders often are among the top vertebrate predators in fishless montane lakes (Taylor, 1983a; Tyler et al., 1998a). Fish can limit the distribution of ambystomatid salamanders (Thompson et al., 1980), and can reduce survival and local population abundance (Petranka, 1983; Taylor, 1983a; 1983b; Semlitsch, 1987; 1988; Sih et al., 1988; 1992; Tyler et al., 1998a; 1998b). Several studies have demonstrated that fish can increase time that larvae spend in refuge (Sih et al., 1988; 1992; Jackson and Semlitsch, 1993), and restrict the range of substrates utilized by salamanders (Semlitsch, 1987; Stangel and Semlitsch, 1987; Figiel and Semlitsch, 1990;

Tyler et al., 1998b), thereby limiting larval feeding opportunities and reducing growth (Semlitsch, 1987; Figiel and Semlitsch, 1990; Tyler et al., 1998b).

In North Cascades National Park Service Complex (NOCA) in northern Washington, USA, lakes with trout can be grouped by the reproductive status of the trout population (Tyler et al., 1998a; Liss et al., 1998). In lakes where fish can reproduce, trout often reach high densities (average 524 fish/ha for fish larger than 177 mm total length as determined by mark-recapture; range 25-724 fish/ha; Gresswell et al., 1997) and have a complex age and size structure. In lakes where trout are incapable of reproducing, fish are periodically stocked as fry or fingerlings at low to moderate densities with intervals between successive stockings averaging about five years (average stocking density in 37 NOCA lakes = 179 fry/ha; range = 60-375 fry/ha; 1976 to 1993; unpublished; North Cascades National Park Service Complex).

Lakes in which trout do not reproduce and are periodically stocked are important in fisheries management for several reasons. In NOCA, many anglers prefer to fish in lakes with non-reproducing trout because trout densities are low and the fish can reach a large size. Furthermore, these lakes may provide the best options for lake restoration if deleterious effects on native biota are demonstrated because trout can be eliminated in a few years without the use of chemical treatment simply through cessation of stocking. In contrast, if fish impacts on native biota are not evident in lakes with non-reproducing trout, managers could consider allowing continued stocking of these lakes.

Tyler et al (1998a) examined the impact of reproducing and non-reproducing trout on larval *Ambystoma macrodactylum* in NOCA montane lakes. In fishless lakes they found that larval density was positively related to total Kjeldahl nitrogen (TKN)

concentration, an indicator of lake productivity (Lambou et al., 1983). Tyler et al. (1998) found that in lakes with TKN  $> \sim 0.045$  mg/L, larval densities in lakes with reproducing fish were significantly lower than densities in fishless lakes. In contrast, larval densities in lakes with non-reproducing fish were significantly lower than in fishless lakes only for lakes with TKN  $> \sim 0.09$  mg/L. For lakes with TKN concentrations below  $\sim 0.045$  mg/L, no differences in predicted larval densities between fishless lakes and lakes with either reproducing or non-reproducing trout were found. However, in Tyler et al.'s (1998a) study, the sample size of lakes with non-reproducing fish was small ( $n = 7$ ) and the lakes were not randomly selected.

The current study was designed specifically to evaluate the impacts of non-reproducing trout on larval *A. macrodactylum* using a larger sample size of randomly selected lakes than Tyler et al. (1998a). We tested the following hypotheses: 1) the relative density of larval *A. macrodactylum* did not differ between fishless lakes and lakes where trout cannot reproduce and are periodically stocked, and 2) the probability of salamanders being hidden in lake substrate materials (e.g., talus, woody material, etc) did not differ between fishless lakes and lakes with non-reproducing fish.

## **STUDY AREA**

The North Cascades National Park Service Complex (NOCA) is located in the Cascade Range of northern Washington, USA. There are approximately 150 lakes of interest to fisheries managers in NOCA. The principle aquatic vertebrate predators in NOCA montane lakes are stocked trout and larval ambystomatid salamanders. Although most lakes within NOCA were naturally fishless during the last century, many NOCA lakes were stocked with trout, primarily *Oncorhynchus clarki* and *O. mykiss*, to provide

recreational angling opportunities. There are only two species of ambystomatid salamanders (*Ambystoma macrodactylum* and *Ambystoma gracile*) present in NOCA lakes, and they rarely co-occur (Liss et al., 1995; Tyler et al., 1998a).

## **METHODS**

Sixteen fishless lakes were randomly selected from a pool of 69 fishless lakes, and 15 lakes with non-reproducing fish were randomly selected from a pool of 21 lakes. The selection pools of 69 fishless lakes and 21 lakes with non-reproducing fish represent lakes available for study after eliminating lakes with poor water clarity (i.e., glacial till), lakes classified as alpine (an area dominated by exposed rock and ice; dominant vegetation is clumped low in stature; generally high in elevation; Lomnický, 1996), and lakes with *A. gracile* present. Average stocking density in the 15 NOCA lakes with non-reproducing fish was 167 fry/ha (range = 63-312 fry/ha; 1976-1997; Table 1) and the average interval between stockings was 5.2 years (range = 3-8 years; Table 1).

In 1998, 17 lakes (eight fishless and nine with non-reproducing fish) were sampled. In 1999, 14 additional lakes (eight fishless and six with non-reproducing fish) were sampled. Eight fishless lakes and seven lakes with non-reproducing fish were sampled twice between mid-June and mid-September 1998. The rest of the 1998 lakes were sampled once. In 1999, lakes became accessible in late July due to an unusually heavy snow pack and consequently they were only sampled once. Fish presence or absence in lakes was confirmed during each sampling visit by visual observations during snorkeling and by setting gillnets for several hours.

Larval salamanders were censused by snorkel surveys (Tyler et al., 1998a). Snorkel methods tend to under-represent small, cryptic, and benthic individuals in density

estimates (Helfman, 1983). Therefore, larval salamander density estimates from snorkel surveys are conservative. Tyler et al. (1998a) found no difference in larval *A. macrodactylum* density estimates between surveys conducted at night and during the day. Therefore, all snorkel surveys were performed during mid-afternoon.

Four 25 m segments of shoreline were randomly chosen along the perimeter of each lake. The same shoreline segments were snorkeled on each sampling visit. During salamander surveys of the shoreline segments, a snorkeler carefully searched through substrate materials (talus, woody debris, fine organic matter, aquatic vegetation) within 2 m of the shoreline and recorded the number of larvae observed (Tyler et al., 1998a).

During the surveys for larval salamanders, the snorkeler visually estimated the total length (TL, mm) of individual salamanders with the aid of a hand-held ruler, and recorded whether individual larvae were “hidden” or “not hidden.” A salamander was classified as “hidden” if greater than half of its body was obstructed from the snorkeler’s view (i.e., the salamander was behind or beneath substrates) prior to disturbance of substrate materials (Tyler et al., 1998a).

Salamander species identification was made in the field based on larval characteristics outlined in Corkran and Thoms (1996). When species identification could not be ascertained in the field, representative larvae were captured and transported from the field. Captured larvae were reared to metamorphosis in a laboratory to confirm species identification.

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 7.5 min USGS topographical maps, and lake surface areas were determined by digitization of

lake shorelines outlined on these maps. During each sampling visit, water temperature was recorded and water samples were collected from 1 m below the lake surface over the lake's deepest point. Water samples and temperature recordings were gathered over each lake's deepest point to standardize sampling between lakes. Temperature measurements were taken during mid-afternoon with an Omega 871 thermo-couple. One L water samples were collected with a 1.5 L van Dorn-style sampling bottle. Water samples were frozen upon return from the field to facilitate transport. Frozen filtered (GF/C 1.2  $\mu$ m glass fiber filter) and unfiltered water samples were transported to the Cooperative Chemical Analytical Laboratory at Oregon State University, Corvallis, Oregon, for analyses. Analyses of filtered water included total phosphorus, total Kjeldahl-N, ammonium-N, and nitrate-/nitrite-N concentrations, whereas unfiltered water was analyzed for alkalinity, pH, and conductivity.

All statistical comparisons and regression models were judged to be significant at  $p \leq 0.05$ . Stepwise multiple regressions were used to determine relationships between abiotic factors and larval salamander densities for lakes in each fish category (fishless and non-reproducing fish). The dependent variable for each regression was the natural logarithm of average larval density in each lake. Independent variables were the average values for each of the 11 abiotic variables. A Pearson's correlation matrix was developed to investigate relationships between chemical and physical variables used in the regression analysis. A sequential Bonferroni adjustment was performed on the Pearson's correlation matrix to eliminate Type I error and maintain table-wide significance at  $\alpha = 0.05$  (Miller, 1981; Rice, 1989).

To test for differences in larval *A. macrodactylum* densities between fishless lakes and lakes with non-reproducing fish, larval density predicted from the regression model and the corresponding 95% confidence interval (CI) was determined for each fishless lake. Average salamander density and corresponding 95 % CI was determined for lakes with non-reproducing fish. Differences in larval densities between individual fishless lakes and lakes with non-reproducing fish were judged to be significantly different if the 95% CIs did not overlap (Tyler et al., 1998a).

Logistic regression analysis was performed to determine relationships between numbers of hidden larvae, length of larvae, and fish category. Two size classes of larvae were recorded and these were assumed to represent young-of-the-year *A. macrodactylum* larvae (TL < 60 mm) and over wintering, pre-metamorphic larvae (TL ≥ 60 mm; Nussbaum et al., 1983; Leonard et al., 1993). The logistic regression formula was used to determine the probability of observing a salamander classified as “hidden”.

## RESULTS

Stepwise linear regression analysis of fishless lakes identified a significant model relating salamander density to mg/L total Kjeldahl nitrogen (TKN) and pH ( $p= 0.0001$ ,  $R^2=77.2$ ). Larval salamander density was positively related to total Kjeldahl nitrogen concentration and negatively related to pH (Figure 1a and Figure 1b):

$$\log(\text{density}) = 8.049 + 153.535 (\text{TKN}) - 2.23 (\text{pH})$$

$(\pm 7.045) (\pm 24.058) \quad (\pm 0.998)$

Simple regressions revealed that salamander density was more strongly related to TKN ( $R^2 = 0.69$ ) than to pH ( $R^2 = 0.06$ ). In the full multiple regression model, TKN explained more of the total variation in larval density (partial  $R^2 = 0.76$ ) than did pH (partial  $R^2 =$

0.28). For fishless lakes, total Kjeldahl-N was correlated with total phosphorus ( $p=0.0002$ ) and pH was correlated with conductivity ( $p=0.0007$ ) and alkalinity ( $p=0.001$ ). Stepwise linear regression analysis of lakes with non-reproducing trout did not identify a significant model relating *A. macrodactylum* density to any of the 11 abiotic variables.

Since multiple regression analysis revealed no significant relationship between larval density and the abiotic variables in lakes with non-reproducing fish, larval densities in these lakes were averaged and the 95% CI for the group average was determined (Table 2). To assess fish effects on larval salamander density, the 95% CI for salamander density for lakes with non-reproducing fish was compared to the 95% CIs of individual fishless lakes predicted from the regression model.

Observed salamander densities were generally higher in fishless lakes with  $TKN > \sim 0.06$  mg/l than in lakes with non-reproducing fish, although only two lakes with trout had TKN concentrations within this range (Figure 1a). Typically, salamander larvae were absent or present at low density in lakes with  $TKN < 0.04$  mg/l, regardless of whether fish were present or absent.

In only one fishless lake was predicted larval salamander density significantly higher than in lakes with non-reproducing fish (MR2; Table 2). MR2 had the highest TKN concentration of the fishless lakes surveyed (0.09 mg/l) and the highest observed salamander densities of any surveyed lake. There was little overlap in CI's for lakes with TKN concentrations  $> 0.055$  mg/L (Table 2). In lakes with TKN concentrations  $\leq 0.05$  mg/L there was substantial overlap in CI's, except for FP9 and DD8 where average salamander densities in lakes with non-reproducing fish was higher than the predicted densities (Table 2).

Visually estimated total length (TL) of individual salamander larvae and fish category were both significant factors in determining if larvae were “hidden” or “not hidden” (logistic regression model;  $p < 0.0001$ ). The logistic regression model indicated that the probability of encountering a “hidden” larva was greater for large larvae (TL > 60mm) than small larvae (TL ≤ 60mm) in both fish categories (Table 3). The model also indicated that the probability of encountering a “hidden” larva was greater in lakes with non-reproducing fish than in fishless lakes for both large and small larvae.

## **DISCUSSION**

The abundance of larval *A. macrodactylum* varies considerably among fishless lakes in NOCA, suggesting that abiotic factors played an important role in determining larval distribution and density. Of the 11 abiotic variables we measured, only TKN concentration and to a lesser extent pH, were significantly related to larval density in fishless lakes. The positive relationship between larval densities and TKN could have been indicative of a lake productivity gradient. Total Kjeldahl-N is a measure of ammonia plus all organically derived nitrogen (Lambou et al., 1983). Algae and bacteria do not readily utilize organic nitrogen, thus TKN does not have an active role in lake energetics (Goldman and Horne, 1983). However, TKN, when correlated with phosphorus as it is in NOCA lakes, has been identified as a good predictor of lake productivity as measured by chlorophyll concentration (Lambou et al., 1983) or by total plankton biomass (Paloheimo and Fulthorpe, 1987). The link between TKN and larval salamander densities appears to be through food web associations. Through examination of salamander stomach contents, Tyler et al. (1998a) found that larval *A. macrodactylum*

utilized cladoceran zooplankton as a major food resource in NOCA lakes. Cladoceran density was positively correlated with TKN concentrations (Tyler et al., 1998a).

A simple explanation of the negative relationship between larval density and pH is not evident. The range of pH values in sampled lakes was narrow and centered around neutral (6.25 – 7.825). Only three fishless lakes had pH > 7.5 (Table 2). In two of these lakes, no salamanders were observed, possibly influencing the significance of pH in the final model. Both TKN and pH have been shown to be indicators of the trophic state in lakes (Lambou et al., 1983; Paleheimo and Fulthorpe, 1987), however, TKN and pH relate to larval *A. macrodactylum* densities in opposing manners in our study. In any event, as indicated by comparison of partial  $R^2$ 's, TKN explained a much greater proportion of the variation in larval density than pH.

Based on the present study and Tyler et al. (1998a), two factors appear to play a major role in mediating trout predation on larval *A. macrodactylum* in NOCA lakes: TKN concentration and the reproductive status of the trout population. The reproductive status of fish in NOCA lakes likely serves as an indicator of the density, and size and age structure of trout. In NOCA, fish densities tend to be higher and age and size structures more diverse in lakes with reproducing trout than in lakes with non-reproducing trout (Gresswell et al, 1997).

Populations of *A. macrodactylum* that inhabit lakes with relatively high TKN concentrations appear to be the most vulnerable to stocked trout in NOCA. Tyler et al. (1998a) found significant differences in larval abundance between fishless lakes and lakes with reproducing trout for TKN concentrations > ~ 0.045 mg/L. In contrast, both the present study and Tyler et al. (1998a) detected significant differences in predicted

larval *A. macrodactylum* densities between fishless lakes and lakes with non-reproducing fish only when fishless lakes had  $\text{TKN} \geq 0.09$  mg/l. Although there were no significant differences in predicted salamander densities between lakes with non-reproducing fish and fishless lakes with  $0.055 \text{ mg/l} > \text{TKN} \leq 0.09 \text{ mg/l}$ , there was little overlap in the 95% CI's for lakes within this TKN range. However, only two populations with non-reproducing fish were sampled within this range.

A notable feature of high elevation salamander populations in NOCA is that larval densities vary considerably among fishless lakes (0-65 individuals/100 m of shoreline in the present study) and that the variation appears to be best explained by TKN. In the fishless condition, lakes with high TKN likely would support relatively high densities of larval salamanders. Large, relatively stable populations may be less vulnerable to extinction from stochastic events than small, highly variable populations (e.g., Shaffer, 1987; Goodman, 1987a). Large populations could serve as important sources of colonists (sensu Pulliam, 1988; Harrison, 1994) that could reestablish extinct local populations or “rescue” (Stacey et al., 1996) smaller populations that are declining toward extinction. Funk et al. (1999) present evidence suggesting that *A. macrodactylum* was able to colonize lakes within 20 years following extinction of trout populations in the lakes. In addition, the degree of isolation (or distance) of sources of dispersers from vacant habitats could also be of great importance in influencing recolonization of these habitats (Sjogren-Gulve and Ray, 1997; Funk et al., 1999). A prudent and precautionary management strategy would be to maximize protection of all NOCA lakes with relatively high TKN concentrations ( $> \sim 0.05$  mg/l), regardless of the reproductive status of the fish population.

In the present study and in Tyler et al. (1998), larval densities were not found to be significantly different between lakes with fish and fishless lakes for relatively low concentrations of TKN (< ~0.05 mg/l). Larval densities in these lakes were low, presumably because of low TKN, regardless of whether fish were present. Although trout do not appear to significantly affect larval densities in these lakes, smaller populations may have importance to conservation of the species. Small populations could increase the size and persistence of a metapopulation (Goodman, 1987b; Howe et al., 1991) and enhance the genetic diversity of regional groups of populations (Lande and Barrowclough, 1987; Scudder, 1989; Tallmon et al, 2000), and thus they merit some level of protection.

The presence of fish appeared to alter the behavior of larval salamanders. The probability of encountering “hidden” larvae was greater in lakes with non-reproducing fish than in fishless lakes. “Hiding” behavior in larval *A. macrodactylum* may be a means to avoid predation risks from predatory fish. Fish presence in ponds reduced activity of ambystomatid larvae in the water column (Semlitsch, 1987, Stangel and Semlitsch, 1987; Figiel and Semlitsch, 1990), increased refuge use or time spent in refuge (Sih et al., 1992; Jackson and Semlitsch, 1993), increased nocturnal activity (Sprules, 1974; Taylor, 1983a; Stangel and Semlitsch, 1987; Sih et al., 1992), or restricted larvae to a narrower range of available habitat (Taylor, 1983b; Tyler et al., 1998b).

Time spent in refuge to avoid encounters with predatory fish can reduce forage opportunities of larval salamanders and limit larval growth and survival (Semlitsch, 1987, 1988; Sih et al., 1988; Figiel and Semlitsch, 1990; Resitarits, 1995; Tyler et al., 1998b). Slower growth rates in larval salamanders may impair survival either by increasing length

of the larval period, thus increasing susceptibility to mortality factors in the aquatic environment, or decreasing larval body size at metamorphosis, and so possibly increasing susceptibility to terrestrial threats.

The probability of encountering a “hidden” larva in NOCA lakes was higher for large larvae (TL  $\geq$  60 mm) than for small larvae (TL < 60 mm; Table 2). Amphibians may be more susceptible to predation during metamorphosis (Wassersug and Sperry, 1977; Arnold and Wassersug, 1978), and may become more secretive. Larger A. macrodactylum larvae likely were closer to metamorphosis than were small larvae in NOCA lakes, thus possibly explaining size dependent differences in behavior.

Higher probability of encountering large *A. macrodactylum* larvae classified as “hidden” than small larvae also may be related to experience with predators. Larger *A. gracile* larvae displayed a more developed flight response than smaller *A. gracile* larvae that may have resulted from larger individuals having more experience with predators (Taylor, 1983a). Sih et al. (1988) noted that emergence rates from refuge should decrease as prey increase experience with predators. Larger (and older) larval *A. macrodactylum* may have been more conditioned to the presence of predators than small larvae as a consequence of longer exposure to predators. These observations suggest that small *A. macrodactylum* have less of a propensity to seek refuge in substrates during daylight than larger larvae and, as a result, small larvae may be more vulnerable to fish predation than large larvae. Intense predation on small larvae could be a major cause for differences in densities between fishless lakes and lakes with fish.

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Figure 1. Relationships between larval *Ambystoma macrodactylum* density and total Kjeldahl-N concentration (a) and pH (b) for 16 fishless lakes and 15 lakes with non-reproducing fish.



Figure 1a.

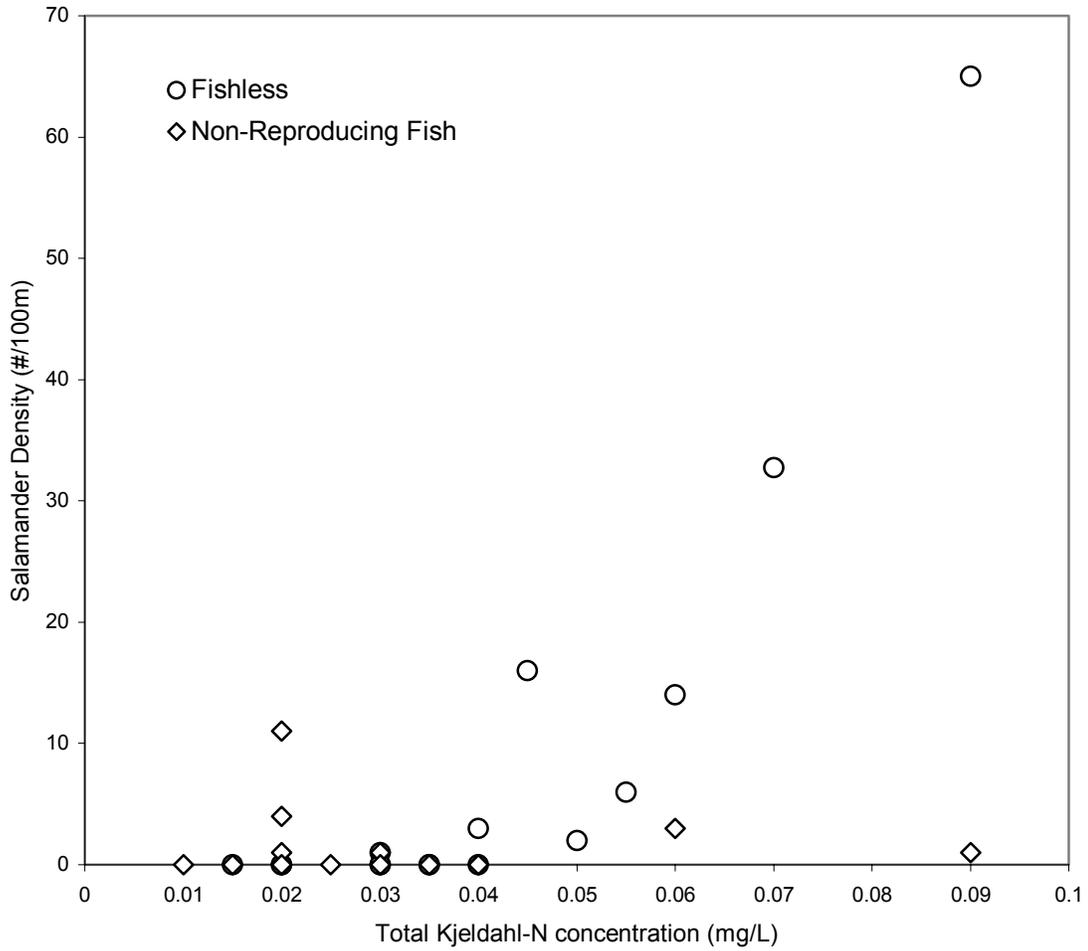


Figure 1 (continued). Relationships between larval *Ambystoma macrodactylum* density and total Kjeldahl-N concentration (a) and pH (b) for 16 fishless lakes and 15 lakes with non-reproducing fish.



Figure 1b.

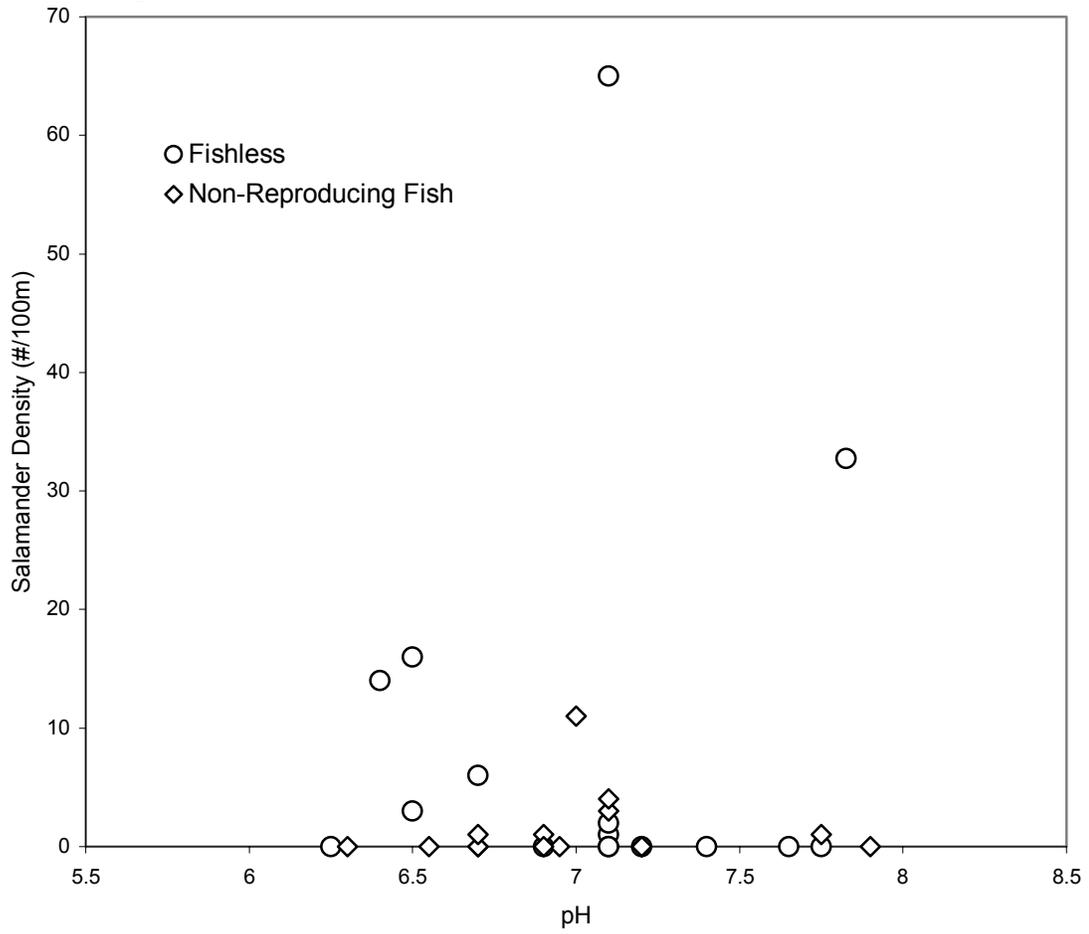


Table 1. Fish data was obtained from stocking records provided by NOCA personnel. Maximum depth (Max. Z) and elevation (Elev.) are given in meters. Average stocking density is fry or fingerling/ha with range shown in parentheses (). The average interval between fish stockings is given in years.

<u>Lake</u>	<u>Last Sampled</u>	<u>Elev.</u>	<u>Max. Z</u>	<u>Species<sup>1</sup></u>	<u>Average Stocking Density</u>	<u>Average Interval between Stockings</u>	<u>Number of Stockings</u>	<u>Last Stocked</u>
RD3*	1999	802	8.8	NA				
MR13-1*	1998	1800	2.0	NA				
MC1	1998	1762	3.0	NA				
MC2	1998	1800	11.0	NA				
MSH4	1998	1635	8.9	NA				
ML1	1998	1476	1.2	NA				
ML4	1998	1583	6.4	NA				
MC27	1998	1488	8.8	NA				

<sup>1</sup>NA= fishless lake, Rb1= Mt. Whitney rainbow trout, Rb2=Packer rainbow trout, Ct=Twin Lakes cutthroat trout, Gt= Golden trout.

\*Previously stocked fishless lake.

? – denotes unknown figure.

Table 1 (continued). Fish data was obtained from stocking records provided by NOCA personnel. Maximum depth (Max. Z) and elevation (Elev.) are given in meters. Average stocking density is fry or fingerling/ha with range shown in parentheses (). The average interval between fish stockings is given in years.

<u>Lake</u>	<u>Last Sampled</u>	<u>Elev.</u>	<u>Max. Z</u>	<u>Species<sup>1</sup></u>	<u>Average Stocking Density</u>	<u>Average Interval between Stockings</u>	<u>Number of Stockings</u>	<u>Last Stocked</u>
MR2	1999	1873	1.5	NA				
MR3	1999	1873	2.5	NA				
MR8	1999	1970	3.5	NA				
MM7	1999	1642	1.9	NA				
MM6	1999	1504	11.9	NA				
DD8	1999	1600	1.9	NA				
EP3	1999	1299	3.7	NA				
FP9	1999	1662	3.4	NA				

<sup>1</sup>NA= fishless lake, Rb1= Mt. Whitney rainbow trout, Rb2=Packer rainbow trout, Ct=Twin Lakes cutthroat trout, Gt= Golden trout.

\*Previously stocked fishless lake.

? – denotes unknown figure.

Table 1 (continued). Fish data was obtained from stocking records provided by NOCA personnel. Maximum depth (Max. Z) and elevation (Elev.) are given in meters. Average stocking density is fry or fingerling/ha with range shown in parentheses (). The average interval between fish stockings is given in years.

<u>Lake</u>	<u>Last Sampled</u>	<u>Elev.</u>	<u>Max. Z</u>	<u>Species<sup>1</sup></u>	<u>Average Stocking Density</u>	<u>Average Interval between Stockings</u>	<u>Number of Stockings</u>	<u>Last Stocked</u>
ML2	1998	1687	27.4	Rb1	117.1 ( 88.2-147.1)	4.0	3	1997
ML3	1998	1967	15.2	Rb1	85.6 ( 76.9-103.1)	5.0	3	1995
MR12	1998	1981	4.0	Rb1	311.7 (166.7-500.0)	6.0	3	1995
MR13-2	1998	1789	5.0	Rb1	190.3 ( 58.3-362.5)	4.7	4	1998
MR15-1	1998	1922	27.0	Rb2	125.0	0.0	1	1983
MM11	1998	1974	7.6	Rb1	310.7	0.0	1	1988
M19	1998	1427	24.0	Gt	120.6 (108.0-140.0)	5.3	4	1997
DD1	1998	1496	2.4	Gt	260.0 (260.0-260.0)	8.0	2	1986

<sup>1</sup>NA= fishless lake, Rb1= Mt. Whitney rainbow trout, Rb2=Packer rainbow trout, Ct=Twin Lakes cutthroat trout, Gt= Golden trout.

\*Previously stocked fishless lake.

? – denotes unknown figure.

Table 1 (continued). Fish data was obtained from stocking records provided by NOCA personnel. Maximum depth (Max. Z) and elevation (Elev.) are given in meters. Average stocking density is fry or fingerling/ha with range shown in parentheses (). The average interval between fish stockings is given in years.

<u>Lake</u>	<u>Last Sampled</u>	<u>Elev.</u>	<u>Max. Z</u>	<u>Species<sup>1</sup></u>	<u>Average Stocking Density</u>	<u>Average Interval between Stockings</u>	<u>Number of Stockings</u>	<u>Last Stocked</u>
MR9	1999	1813	4.9	Rb1	100.0 ( 88.2-111.8)	5.0	2	1993
MC7	1999	1556	27.0	Rb1	196.3 (119.4-247.7)	4.7	4	1997
M1	1999	1159	4.3	Rb1	155.6 ( 93.8-248.1)	6.3	4	1997
LS3-FS	1999	1369	6.7	Rb1	?	?	?	?
LS3	1999	1365	5.2	Ct/Rb1	173.3 (166.7-291.7)	6.7	5	1997
DD5	1999	1531	5.2	Gt	62.5 ( 57.5-76.9)	5.0	4	1995
EP5-1	1999	1543	6.0	Rb1	130.4 (111.1-147.0)	5.3	4	1997

<sup>1</sup>NA= fishless lake, Rb1= Mt. Whitney rainbow trout, Rb2=Packer rainbow trout, Ct=Twin Lakes cutthroat trout, Gt= Golden trout.

\*Previously stocked fishless lake.

? – denotes unknown figure.

Table 2. Comparison of 95% confidence intervals (shown in parentheses) between larval *Ambystoma macrodactylum* densities of individual fishless lakes (NF) and of lakes with non-reproducing fish (NRF) was used to indicate differences between fishless lakes and lakes with fish. Larval densities for 16 fishless lakes were derived from a multiple regression formula with total Kjeldahl-N (TKN) concentration and pH as independent variables. Larval densities in 15 lakes with non-reproducing fish were averaged.

<u>Fish Category</u>	<u>Lake</u>	<u>TKN</u>	<u>pH</u>	<u>Observed density</u>	<u>Predicted density</u>
NF	MC27	0.015	6.25	0	0.018 (-0.007, 0.277)
	FP9	0.02	7.2	0	0.000 (-0.008, 0.024) <sup>a</sup>
	DD8	0.02	7.1	0	0.000 (-0.008, 0.031) <sup>a</sup>
	ML1	0.03	7.65	0	0.002 (-0.008, 0.063)
	MM7	0.03	7.1	1	0.032 (0.003, 0.125)
	EP3	0.03	7.1	0	0.032 (0.003, 0.125)
	ML4	0.035	7.75	0	0.011 (-0.007, 0.129)

<sup>a</sup>Predicted fishless lake density less than 0. NRF density significantly greater than density in fishless lake.

<sup>b</sup>MR2 density significantly higher than NRF density.

Table 2 (continued). Comparison of 95% confidence intervals (shown in parentheses) between larval *Ambystoma macrodactylum* densities of individual fishless lakes (NF) and of lakes with non-reproducing fish (NRF) was used to indicate differences between fishless lakes and lakes with fish. Larval densities for 16 fishless lakes were derived from a multiple regression formula with total Kjeldahl-N (TKN) concentration and pH as independent variables. Larval densities in 15 lakes with non-reproducing fish were averaged.

<u>Fish Category</u>	<u>Lake</u>	<u>TKN</u>	<u>pH</u>	<u>Observed density</u>	<u>Predicted density</u>
NF (continued)	MSH4	0.035	7.4	0	0.036 (0.002, 0.163)
	MR8	0.04	6.9	0	0.292 (0.097, 0.844)
	MC1	0.04	6.5	3	0.727 (0.151, 3.371)
	MC2	0.045	6.5	16	1.579 (0.329, 7.431)
	MM6	0.05	7.1	2	0.888 (0.291, 2.667)
	MR13-1	0.055	6.7	6	4.711 (1.110, 19.878)
	MR3	0.06	6.4	14	19.852 (2.703, 145.392)

<sup>a</sup>Predicted fishless lake density less than 0. NRF density significantly greater than density in fishless lake.

<sup>b</sup>MR2 density significantly higher than NRF density.

Table 2 (continued). Comparison of 95% confidence intervals (shown in parentheses) between larval *Ambystoma macrodactylum* densities of individual fishless lakes (NF) and of lakes with non-reproducing fish (NRF) was used to indicate differences between fishless lakes and lakes with fish. Larval densities for 16 fishless lakes were derived from a multiple regression formula with total Kjeldahl-N (TKN) concentration and pH as independent variables. Larval densities in 15 lakes with non-reproducing fish were averaged.

<u>Fish Category</u>	<u>Lake</u>	<u>TKN</u>	<u>pH</u>	<u>Observed density</u>	<u>Predicted density</u>
NF (continued)	RD3	0.07	7.825	32.75	3.834 (0.340, 42.172)
	MR2 <sup>b</sup>	0.09	7.1	65	417.3 (27.98, 6222.3)
NRF	average				1.594 (0.033, 3.154)

<sup>a</sup>Predicted fishless lake density less than 0. NRF density significantly greater than density in fishless lake.

<sup>b</sup>MR2 density significantly higher than NRF density.

Table 3. The probability of encountering “hidden” larval *Ambystoma macrodactylum* during snorkel surveys was affected by larval total length and whether observations were made in a fishless lake (NF) or in a lake with non-reproducing fish (NRF). Probabilities were derived from logistic regression analysis.

<u>Fish Category</u>	<u>Total Length</u>	<u>Probability of Larva “Hidden”</u>
NRF	≥ 60 mm	0.9326
NRF	< 60 mm	0.5592
NF	≥ 60 mm	0.6339
NF	< 60 mm	0.1369

## CHAPTER 2

### **Changes in the Behavior of *Ambystoma gracile* Larvae After the Removal of Fish from a Mountain Lake**

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## ABSTRACT

*Ambystoma gracile* (Baird) larvae were surveyed in two adjacent lakes in North Cascades National Park Service Complex, Washington, USA, between 1994 and 1999. One lake (Upper Panther) was fishless. The other lake (Lower Panther) was inhabited by introduced trout (*Oncorhynchus clarki*). The objective of this research was to identify any changes in larval salamander behavior after fish removal from Lower Panther was completed in June 1997. We investigated the diel habits and spatial use of larvae in each lake before and after fish removal. *Ambystoma gracile* in Upper Panther were readily observed during day surveys in immediate shoreline, 2 m, and 5 m transects, and were active day and night during the entire period. Prior to fish removal, larvae in Lower Panther were primarily observed during night surveys and restricted to the immediate shoreline habitat. After fish removal, the percent of larvae observed during day surveys increased significantly as did the percent of larvae observed in 2 m and 5 m transects. Changes in Lower Panther indicate that larval behavior becomes less restricted and secretive after fish are removed. This response is indicative of the ecological release of *A. gracile* larvae from the threat of predation by introduced trout.

## INTRODUCTION

Prey attributes that decrease predation risk include unpalatability, reduction or restriction of activity level, and occupation of habitats that may be ephemeral, stressful for predators, or have complex structure that provides refuge from predation (Sih, 1987). Many amphibian species have noxious and/or toxic skin secretions that reduce their palatability to predators (Duellman and Trueb, 1986). These secretions are less developed in larval amphibians (Formanowicz and Brodie, 1982; Duellman and Trueb, 1986), and, thus, larvae rely on behavioral adaptations to escape threats of predation (Sih, 1987; Kats et al., 1988). In the presence of predators, larvae may alter their use of microhabitats (Kiesecker and Blaustein, 1998) and increase their use of structural components of habitat (e.g., coarse woody debris, rock-talus, and aquatic vegetation) as refugia (Kats et al., 1988; Sih et al., 1988; Tyler et al., 1998b). Larvae have also been shown to become more secretive, shift their diel patterns of behavior (Taylor, 1983; Resetarits, 1995), and increase the tendency to display flight behavior (Taylor 1983).

Laboratory studies have shown that larval ambystomatids increase their use of refuge in the presence of fish. In artificial ponds with fish, larval ambystomatids increase their time spent in refuge (Sih et al., 1992; Jackson and Semlitsch, 1993), and restrict their activity to a narrower range of available substrates (Semlitsch, 1987; Stangel and Semlitsch, 1987; Figiel and Semlitsch, 1990; Tyler et al., 1998b). However, little is known about larval salamander refuge use in response to the presence of fish in natural systems. Taylor (1983) observed lower densities and less activity of larvae in lakes with fish in comparison to lakes without fish. While investigating startle responses of two larval *Ambystoma gracile* (Baird) populations, he observed that higher numbers of larvae

were present in the shallow, nearshore areas of a lake with fish than in a fishless lake. Taylor (1983) speculated that the shallow areas of the fish lake may have offered greater refuge from fish predation.

Another behavioral adaptation of ambystomatid larvae is increased nocturnal activity in the presence of fish. Stangel and Semlitsch (1987) noted decreased diurnal activity in larval *Ambystoma talpoideum* (Holbrook) in artificial ponds with fish. The addition of predatory fish to stream pools decreased the diurnal activity of larval *Ambystoma barbouri* Kraus and Petranka (Sih et al., 1992). Several field studies have indicated that *A. gracile* larvae shift toward increased nocturnal activity when fish are present in lakes (Efford and Mathias, 1969; Neish, 1971; Efford and Tsumura, 1973; Sprules, 1974; Taylor, 1983). In view of these results, the objective of this research was to document the diel distributions of *A. gracile* larvae in a lake before and after fish removal.

## **METHODS**

Upper Panther (the control lake) and Lower Panther (the treatment lake) are separated by about 4 m and are located at an elevation of 1031 m within the boundaries of the North Cascades National Park Service Complex (NOCA), Washington, USA. Upper Panther is smaller (surface area = 0.1 ha; maximum depth = 3 m) than Lower Panther (surface area = 0.3 ha; maximum depth = 5.8 m). Flocculent organic material is the predominant substrate present in the deeper, offshore area of each lake. Both lakes have shorelines consisting of bedrock, talus, and woody debris, although Lower Panther contains more woody debris than Upper Panther. Lower Panther has additional shoreline areas of overhanging vegetation and undercut banks.

Both lakes have a history of cutthroat trout (*Oncorhynchus clarki*) introductions. Beginning in 1990, removal of fish from the lakes by angling and gillnetting was initiated. Gillnets were set extending from the lake shoreline to the center of the lake. Each gillnet was 42 m long and 2 m deep with four sections of monofilament panels of 12.5 mm, 18.5 mm, 25 mm, and 33 mm mesh. The last trout were removed from Upper Panther in July 1992. In Lower Panther, trout were stocked twice following fish removal efforts. In September 1990, trout were stocked at a density of 750 fry/ha in an attempt to introduce a known number of fish into the lake. In 1994, an unauthorized stocking of trout occurred at an unknown density. Using mark-recapture methods we estimated that there were 320 trout/ha in Lower Panther in 1992 (Gresswell et al., 1997), and 250 trout/ha in 1996 (Torrey Tyler, unpublished data). Fish have not been collected or observed in Lower Panther since seven fish were removed in June 1997.

From 1994 through 1999, densities of *A. gracile* larvae in both lakes were estimated from snorkel surveys (Tyler et al., 1998a). In Lower Panther, surveys were conducted along four 25 m segments randomly selected along the lake's perimeter. In Upper Panther, the entire lake perimeter (100m) was snorkeled. All surveys were conducted parallel to the shoreline. The same shoreline segments were sampled on all subsequent sampling visits.

Three types of surveys were performed during each sampling visit (Tyler et al., 1998a). Search surveys were conducted near to (i.e., within approximately 1 m) and along the immediate shoreline of each lake. Substrate materials (e.g., talus, woody debris, organic detritus, and aquatic vegetation) present in this nearshore area of each lake created a relatively complex structured habitat potentially useful to larvae as refuge.

Larvae were often obscured from the snorkeler's view by these materials. Therefore, during search surveys, snorkelers searched through these substrate materials for larvae and recorded the number of larvae observed. Search surveys were only conducted during mid-afternoon. Two-meter surveys were conducted approximately 2 m from shore where water depth was typically  $\geq 1$  m. During two-meter surveys, snorkelers counted the number of larvae they could observe without disturbing nearshore substrates within an area extending from their 2 m offshore position toward the shore. Five-meter surveys were conducted approximately 5 m from shore where water depth was typically  $\geq 2$  m. During five-meter surveys, snorkelers counted salamanders without disturbing substrates within an area extending approximately 1.5 m to each side of the snorkeler's longitudinal axis. Two-meter and 5 m surveys were performed once during mid-afternoon, and again 30 min after sunset with the aid of a handheld dive-light. Since 2 m and 5 m surveys were conducted without disturbing substrate materials, these surveys only censused larvae observed in the open and not obscured from the snorkeler's view by substrate materials. The sequence of surveys proceeded from 5 m to 2 m to search. Sampling was conducted systematically so as to avoid recounting larvae potentially flushed from shoreline refugia and moving out to deeper areas of the lake.

Salamander surveys were typically conducted twice a year during the period from mid-June to late August. Both lakes were sampled only once in 1994 due to a forest fire. Equipment failure prevented night surveys during the August 1996 sampling. Nine day surveys and eight night surveys were completed for each lake.

Two-meter and 5 m surveys were combined to investigate differences between day and night larval relative densities in each lake when fish were present in Lower

Panther (i.e., 6/94 - 6/97) and after fish were no longer collected or observed in Lower Panther (i.e., 7/97 - 8/99). The combined survey counts were expressed as the percent of all larvae that were observed during the day versus at night. Paired T-tests were performed to test for significant (i.e.,  $p \neq 0.05$ ) within and between lake differences in the percent of larvae observed during day surveys before and after fish were removed from Lower Panther. In each lake there were four dates before fish removal when both day and night surveys were completed (i.e.,  $n = 4$ ) and four day and night survey dates after fish removal (i.e.,  $n = 4$ ).

To investigate differences in the number of larvae observed in the immediate shoreline area of each lake before and after fish removal, survey counts were expressed as the percentage of total larvae (i.e., search + 2 m + 5 m surveys) observed per day search surveys. The rationale for comparing search surveys with combined 2 m and 5 m surveys was as follows: search surveys expressed the number of larvae associated with refuge in each lake, while 2 m and 5 m surveys represented the number of larvae in the open and typically not near refuge. Mann-Whitney tests were used to test for significant within lake differences (i.e.,  $p \neq 0.05$ ) in the percent of larvae observed during day search surveys before (i.e., 6/94 - 6/97) and after (i.e., 7/97 - 8/99) the removal of fish from Lower Panther. Paired T-tests were used to examine between lake differences. There were five day survey dates prior to fish removal (i.e.,  $n = 5$ ) and four day survey dates after fish removal (i.e.,  $n = 4$ ) for each lake.

NCSS 2000 (Hintze, 1998) was used to calculate Paired T-test and Mann-Whitney test results.

## RESULTS

The percent of larvae observed during day versus night surveys in Lower Panther was quite low (i.e., 1% - 6%, average = 4%; Figure 1) when fish were present in the lake (i.e., 6/94 - 6/97; survey<sub>dates</sub> = 4); whereas the percent of larvae observed during day surveys after fish were removed (i.e., 7/97 - 8/99; survey<sub>dates</sub> = 4) increased significantly to 29% - 48% (average = 41%)(Paired T-test,  $p = 0.002$ ). In Upper Panther, typically 30% - 50% (average = 40%) of the total number of larvae counted during day and night surveys were observed during the day (Figure 1). Furthermore, no significant difference in the relative percentage of larvae observed in Upper Panther during the day occurred before (survey<sub>dates</sub> = 4) versus after (survey<sub>dates</sub> = 4) fish were removed from Lower Panther (Paired T-test,  $p = 0.46$ ). Comparisons between lakes showed that the relative percentage of larvae observed during the day in Lower Panther (survey<sub>dates</sub> = 4) was significantly lower than in Upper Panther (survey<sub>dates</sub> = 4) prior to fish removal from Lower Panther (Paired T-test,  $p = 0.002$ ); whereas after fish removal the two lakes did not significantly differ (Paired T-test,  $p = 0.71$ ; survey<sub>dates</sub> = 4 in both lakes)(Figure 1).

Day search surveys revealed within and between lake differences in the proportion of *A. gracile* larvae observed in the immediate shoreline areas of each lake. There was a significant decrease in the proportion of larvae observed during the day in the immediate shoreline area of Lower Panther after all fish had been removed from the lake (i.e., by June 1997)(Mann-Whitney test,  $p = 0.01$ ). Prior to fish removal (i.e., 6/94 - 6/97; survey<sub>dates</sub> = 5) the percent of larvae observed was above 80% (range = 80% - 99%; average = 87%) and then dropped below 50% (range = 14% - 49%; average = 30%) after fish were removed (i.e., 7/97 - 8/99; survey<sub>dates</sub> = 4)(Figure 2). In fishless Upper Panther,

the percent of larvae observed in day search surveys ranged from 16% - 52% (average = 33%), and was typically < 40% of all larvae observed (i.e., search + 2 m + 5 m surveys)(Figure 2). The percent of larvae observed in Upper Panther search surveys conducted prior to when fish were removed from Lower Panther (range = 16% - 44%, average = 28%; survey<sub>dates</sub> = 5) did not differ significantly from the percentage observed after fish were removed from Lower Panther (range = 26% - 52%, average = 39%; survey<sub>dates</sub> = 4; Mann-Whitney test, p = 0.11). Between lake comparisons showed that the percentage of larvae observed in the immediate shoreline area of each lake differed before but not after fish removal from Lower Panther. Prior to fish removal a significantly greater mean percentage of larvae were observed in Lower Panther search surveys than in Upper Panther search surveys (Paired T-test, p = 0.002; survey<sub>dates</sub> = 5 for each lake)(Figure 2). After fish removal the average percentage of larvae observed in search surveys did not significantly differ between lakes (Paired T-test, p = 0.12; survey<sub>dates</sub> = 4 for each lake)(Figure 2).

## **DISCUSSION**

This study provides experimental evidence based on whole-lake manipulations that indicates that *A. gracile* larval behavior differs between lakes with and without fish. This study also documents the response of *A. gracile* larvae to the removal of fish from a lake. Prior to the removal of all trout from Lower Panther, *A. gracile* larvae tended to be primarily active at night. Larvae were mostly restricted to the shallow, shoreline area of the lake that contained substrates that created complex habitat structure. This structure provided refuge for larvae from predation by trout. During this same period, salamander larvae in fishless Upper Panther were active day and night and were observed throughout

the lake. In this context, the secretive and restricted behavior of *A. gracile* larvae in Lower Panther can be seen as indicative of an anti-predator response to the presence of fish in the lake.

Previous studies have observed that *A. gracile* larvae in response to the threat of predation by trout may decrease their diurnal activity and restrict the number and types of habitats they occupy in a lake. Efford and Mathias (1969) attributed the secretive and wary behavior of *A. gracile* larvae in Marion Lake, British Columbia, Canada, to predation by trout. In ponds and lakes containing fish in British Columbia and Oregon, *A. gracile* larvae are almost exclusively nocturnal (Efford and Mathias 1969; Sprules 1974; Taylor, 1983). Liss et al. (1995) found that although *A. gracile* larvae could be detected during day surveys in some NOCA lakes with fish, most of these larvae were observed in refuges (e.g., woody debris, rock-talus, undercut banks). At one NOCA lake containing fish, counts of larvae at night were ten times greater than day counts. Taylor (1983) reported that in three lakes with fish in the Oregon Cascade Mountains, *A. gracile* larvae were detected only in nearshore refugia where the water was #1.3 m deep. Tyler et al. (1998b) determined that *A. gracile* larvae in experimental ponds with fish utilized a narrower range of available habitats (e.g., rock and wood) than did larvae in fishless controls. In contrast to the nocturnal and secretive behavior of larvae in lakes with fish, *A. gracile* larvae in fishless lakes tend to be readily detected during the day, more active throughout a lake, and do not appear overly wary or secretive in behavior (Sprules 1974; Taylor 1983).

After all of the fish were removed from Lower Panther by June 1997, the behavior of *A. gracile* larvae changed and became strikingly similar to the larval behavior

in fishless Upper Panther (Figs. 1 and 2). In essence, upon the removal of fish from Lower Panther the proportion of larvae observed in the lake during day surveys increased as did the proportion of larvae observed in the transects (i.e., 2 m and 5 m) further from the shoreline of the lake. To our knowledge, the present study is the first to indicate that *A. gracile* larval behavior can shift following the removal of fish from a lake. The change in the level of diurnal activity and location of larvae in Lower Panther might be explained as a form of ecological release, and more specifically as a release from predation. In general, ecological release is expressed when prey exhibit density compensation and/or habitat expansion upon reduction of the level of interspecific competition or predation within an ecosystem (MacArthur et al., 1972; Cox and Ricklefs, 1977; Ricklefs, 1979). The suppressed species can become more abundant, more active, and less restricted in the habitats it is able to occupy or exploit. For instance, sea urchin sizes and densities were higher on Kenyan reefs where the exploitation of predatory fish was high as compared to reefs where exploitation was low (McClanahan and Muthiga 1988). Furthermore, species richness and total abundance of young-of-the-year non-piscivorous fishes were greater on predator removal coral reefs than on control reefs (Caley 1993). In a study examining ecological release in amphibians, the relative abundance of green frogs (*Rana clamitans* Latreille) in Point Pelee National Park, Ontario, Canada, increased four-fold after the extirpation of the green frogs' potential competitor and predator, the bullfrog (*Rana catesbeiana* Shaw; Hecnar and M'Closkey 1997).

The shift in *A. gracile* larval behavior in Lower Panther occurred relatively soon after the last fish were removed from the lake. *Ambystoma gracile* larvae can co-exist with introduced trout in mountain lakes albeit at lower densities than in lakes without

trout (Liss et al., 1995; Robert Hoffman and Torrey Tyler, personal observations). They survive in lakes with trout by becoming secretive and wary, and by restricting their diurnal activity to lake habitats that provide refuge from predation. Being able to coexist with introduced trout enhances this species' ability to reestablish potentially threatened populations upon the removal or extinction of fish from a lake. This outcome is certainly encouraging as resource managers attempt to deal with issues related to declining amphibian populations in the western United States. Future research should include additional amphibian species, especially those that may be less able to coexist with introduced fish (e.g., *Ambystoma macrodactylum* Baird; see Tyler et al., 1998a), so that we may better understand the full potential of amphibian population recovery associated with the removal of introduced fish from mountain lakes.

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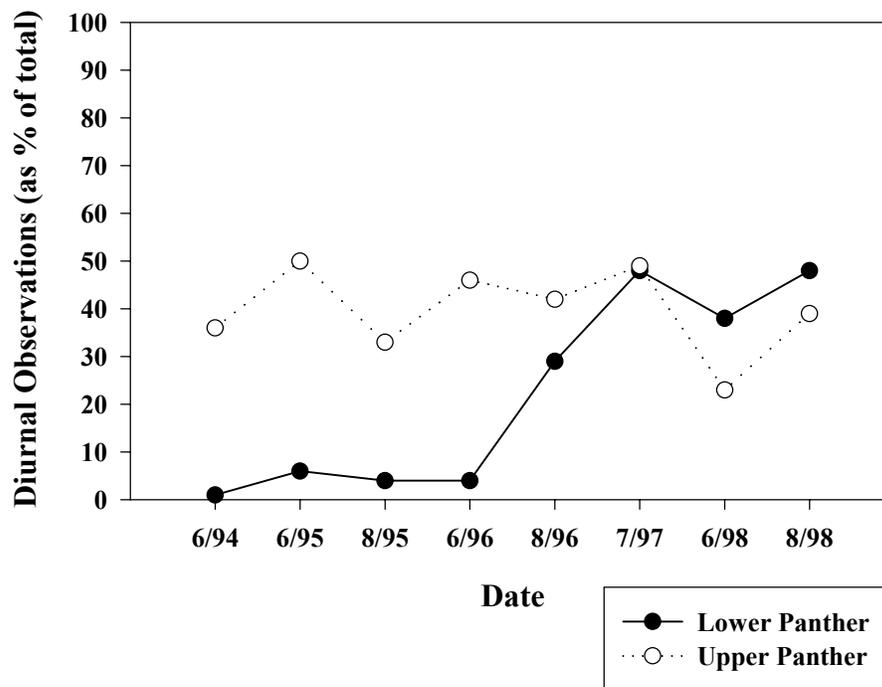
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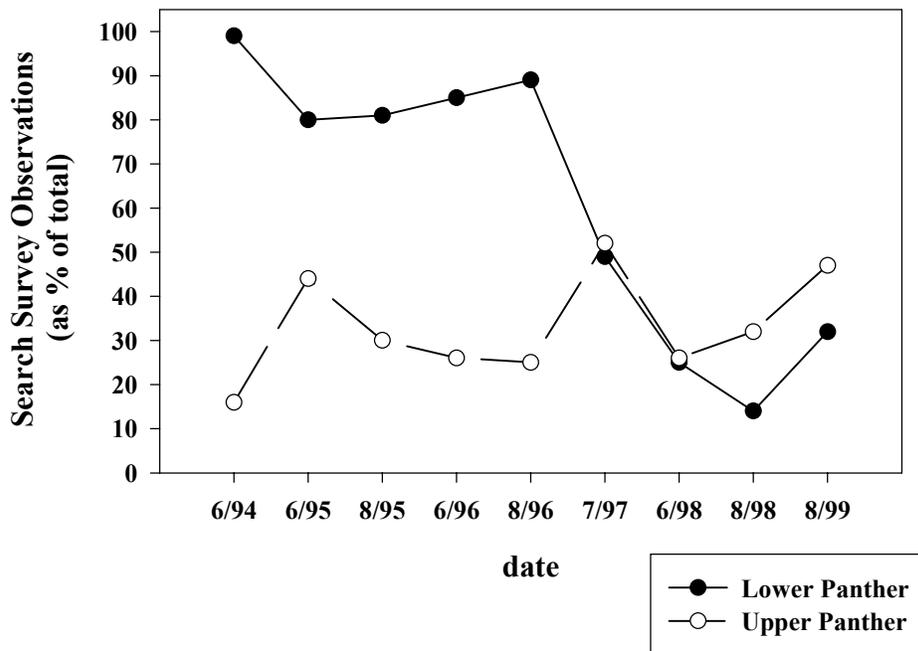
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**Figure 1.** Percent of *Ambystoma gracile* observed during day (versus night) 2 m and 5 m surveys in Lower Panther and Upper Panther Lakes. No fish were observed in Lower Panther Lake after June 1997. FR indicates when Lower Panther Lake was considered fishless.



**Figure 2.** Percent of *Ambystoma gracile* larvae observed in the immediate shoreline areas of Lower Panther and Upper Panther Lakes during day search versus day 2 m + 5 m surveys. No fish were observed in Lower Panther Lake after June 1997. FR indicates when Lower Panther Lake was considered fishless.

## CHAPTER 3

### **Distributions and Abundances of Larval Salamanders (*Ambystoma macrodactylum*) and Large Copepods (*Diaptomus* sp.) in Relation to Introduced Trout and Abiotic Factors in Mountain Lakes of North Cascades National Park Service Complex**

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## ABSTRACT

From 1989 through 1999 we conducted research to determine the impacts of stocked trout on native biota in mountain lakes in North Cascades National Park Service Complex (NOCA), located in the Northern Cascades Province of northern Washington, USA. We performed a meta-analysis of data for larval salamanders for all lakes sampled from 1990-1994 and 1998-1999 ( $n = 63$  lakes) and data for crustacean zooplankton for all lakes sampled from 1989-1994 ( $n = 70$  lakes). The purpose of the analysis was to determine the influence of a suite of abiotic factors on the distributions and abundances of larval *Ambystoma macrodactylum* and diaptomid copepods, and to test whether observed larval abundances of *A. macrodactylum* and densities of large diaptomid copepods differed among fishless lakes, lakes with non-reproducing trout populations that are periodically stocked with fry at low densities, and lakes with reproducing trout populations that tend to reach high fish densities. For fishless lakes ( $n = 28$ ), observed larval salamander abundance was positively related to total Kjeldahl-N (TKN) concentration and water temperature. Larval abundances were low and no differences in abundances were detected among fishless lakes ( $n = 17$ ) and lakes with non-reproducing ( $n = 10$ ) or reproducing ( $n = 9$ ) trout populations when lake TKN concentration was  $< 0.045$  mg/L. For lakes with  $\text{TKN} \geq 0.045$  mg/L, lakes with reproducing trout populations ( $n = 8$ ) had significantly lower abundances of larvae than fishless lakes ( $n = 11$ ) and lakes with non-reproducing trout populations ( $n = 7$ ). Observed larval abundances in fishless lakes and lakes with non-reproducing trout populations did not differ significantly in lakes with  $\text{TKN} \geq 0.045$  mg/L. However, larval abundances in fishless lakes with  $\text{TKN} \geq 0.055$  mg/L ( $n = 8$ ) were significantly greater than abundances

in lakes with non-reproducing trout populations over the same TKN range ( $n = 4$ ), although sample size of lakes with non-reproducing trout populations was small. Analysis using a general linear model with reproductive status of the fish population as a categorical variable revealed that large copepod density was influenced by maximum lake depth, total phosphorus concentration, and water temperature. Of these three abiotic variables only temperature was a significant factor when the presence/absence and reproductive status of the fish population in lakes were considered. Large copepod densities were significantly different between fishless lakes and lakes with reproducing trout populations for temperatures  $> 12^{\circ}\text{C}$ . There were no significant differences in large diaptomid densities between fishless lakes and lakes with non-reproducing trout populations. These results suggest that larval salamanders and large crustacean zooplankton may be at greatest risk from introduced trout in lakes with reproducing fish populations that have TKN concentrations  $\geq 0.045\text{mg/L}$  and water temperatures  $> 12^{\circ}\text{C}$ . Larval salamanders also appear to be at risk in lakes with non-reproducing trout populations that have TKN concentrations  $\geq 0.055\text{mg/L}$ . Native biota appear to be at minimum risk in lakes with TKN concentrations  $< 0.045\text{ mg/L}$  regardless of fish presence/absence or reproductive status.

## INTRODUCTION

Most mountain lakes in the western USA were originally fishless and considered “barren”. These lakes were stocked with fish during the early to mid-20<sup>th</sup> century primarily to provide recreational angling opportunities (Bahls 1992). Although mountain lakes in the western USA are popular locations for recreational angling, the possible environmental impacts of introduced non-native fish on native biota are a concern. A reduction in abundance or elimination of some species of frogs (e.g., Bradford, 1989; Bradford et al., 1993; Fellers and Drost, 1993; Blaustein et al., 1994; Knapp and Matthews, 2000), ambystomatid salamanders (Taylor, 1983a; 1983b; Tyler et al., 1998a), and crustacean zooplankton (e.g., Starkweather, 1990; Stoddard, 1987; Donald et al., 1994; Liss et al., 1998) have been attributed to the introduction of trout into mountain lakes. Food web alterations in mountain lakes associated with the introduction of trout also have contributed to changes in the nutrient dynamics of these lakes (e.g., Leavitt et al., 1994).

Ambystomatid salamanders often are among the top vertebrate predators in fishless mountain lakes in the Pacific Northwest (Taylor, 1983a; Tyler et al., 1998a). Introduced non-native fish can limit the distribution of salamanders (Thompson et al., 1980), restrict the range of habitats they utilize (Semlitsch, 1987; Stangel and Semlitsch, 1987; Figiel and Semlitsch, 1990; Tyler et al., 1998b), reduce growth by limiting larval feeding opportunities (Semlitsch, 1987; Figiel and Semlitsch, 1990; Tyler et al., 1998b), and reduce survival and local population abundance (Petranka, 1983; Taylor, 1983a, 1983b; Semlitsch, 1987, 1988; Sih et al., 1988, 1992; Tyler et al., 1998a, 1998b).

Diaptomid copepods are among the largest, most visible zooplankters in mountain lakes (e.g., Dodson, 1970; Anderson, 1971; Stoddard, 1987; Donald et al., 1994; Liss et al., 1998). Planktivorous predators such as some fish species and salamanders can prey selectively on larger, more visible zooplankton and can reduce their abundance or eliminate them from lakes (Dodson, 1970; Sprules, 1972; Zaret, 1980; Morin, 1987; Stein et al., 1987; Gliwicz and Pijanowska, 1989). Impacts of planktivorous vertebrate predators are thought to be greatest in lakes where predation intensity is high (e.g., Gliwicz and Prejs, 1977; Dodson, 1979; Zaret, 1980; McQueen et al., 1986; Post and McQueen, 1987; Liss et al., 1998). Predation intensity on zooplankters can increase if a community shifts in composition toward predator species that are more planktivorous (e.g., Bays and Crisman, 1983; Hessen et al., 1995), if the size distribution shifts toward smaller individuals that may be more prone to planktivory than larger individuals, or if a planktivore population increases in abundance (e.g., Zaret, 1980; Carpenter et al., 1985).

Abiotic factors such as lake depth can mediate interactions between vertebrate planktivores and their zooplankton prey. In deep lakes, zooplankton may undergo vertical migrations and escape predation from visually oriented predators (e.g., Zaret, 1980; Stich and Lambert, 1981; Gliwicz and Pijanowska, 1988; Donald et al., 1994). Thus, impacts of vertebrate predation on zooplankton are most likely to be observed in shallow lakes where deep-water refugia may not be available (Gliwicz and Prejs, 1977; Donald et al., 1994; Liss et al., 1998).

From 1989 through 1999, we conducted research to determine the impacts of stocked trout on native biota in lakes in North Cascades National Park Service Complex (NOCA), located in the North Cascades Province of northern Washington, USA.

Analyzing data collected from 1990-1994, Tyler et al. (1998a) found that the abundance of larval long-toed salamanders (*Ambystoma macrodactylum*) in NOCA lakes was positively related to lake productivity as indicated by total Kjeldahl-N concentration (TKN). The effects of stocked trout on larval salamanders appeared to be related to a lake's TKN concentration and the reproductive status of the introduced trout population. The abundances of salamander larvae in fishless lakes were significantly higher than abundances in lakes with non-reproducing trout populations only in lakes with TKN > 0.09 mg/L (Tyler et al., 1998a). These populations were composed of fish that did not reproduce in a lake but instead were periodically stocked as fry at low densities. However, larval abundances in fishless lakes were significantly greater than in lakes with reproducing trout populations in lakes with TKN  $\geq$  0.045 mg/L (Tyler et al., 1998a). At TKN < 0.045 mg/L there were no significant differences in larval abundances among fishless lakes, lakes with non-reproducing trout populations, and lakes with reproducing trout populations. One difficulty with the Tyler et al. (1998a) study was that the sample size of lakes with non-reproducing trout populations was small (i.e., n = 7). Chapter 1 of this report presented the results of research conducted from 1998-1999 that was specifically directed at assessing the impacts of non-reproducing trout populations on larval salamander abundance and behavior. The results and conclusions of the work conducted in 1998-1999 were consistent with the results of Tyler et al. (1998a).

Liss et al. (1998) reported results of research on the potential effects of stocked trout on crustacean zooplankton in NOCA lakes, sampled at least twice per year, from 1989-1994 (n = 28). They found that the density of large diaptomid copepods in lakes with high densities of reproducing trout and maximum depths  $\leq$  10 m was significantly

lower than in deeper lakes (maximum depth > 10 m) with reproducing or non-reproducing trout populations. In lakes where conditions were suitable for the small herbivorous diaptomid, *D. tyrrelli*, the small copepod was often abundant in lakes where trout densities were high and large predaceous diaptomids were absent or in low abundance.

This chapter presents a meta-analysis of the combined sets of data for larval salamanders collected from 1990-1994 and 1998-1999 (n = 63 lakes), and data for crustacean zooplankton for all lakes that were sampled from 1989-1994 (n = 70 lakes). The purpose of this analysis is: 1) to determine the influence of a suite of abiotic factors on the distributions and abundances of larval *Ambystoma macrodactylum* and diaptomid copepods; 2) to test whether observed *A. macrodactylum* larval abundances and densities of large diaptomid copepods differed among fishless lakes, lakes with non-reproducing trout populations, and lakes with reproducing trout populations; 3) to compare the results of the meta-analysis embodied in objectives 1 and 2 with the earlier work by Tyler et al. (1998a), the results from Chapter 1 of this report (1998-1999), and the work by Liss et al. (1998); and 4) to develop inferences concerning the influence of biotic and abiotic factors on the relative risk of larval salamanders and large diaptomids from stocked trout in NOCA lakes.

## **METHODS**

There are approximately 154 lakes in NOCA of interest to National Park Service (NPS) and Washington Department of Fish and Wildlife (WDFW) managers. The lakes range in elevation from 412 m to over 2000 m. We restricted our analysis to lakes higher than 800 m, the elevation range where most of the lakes in NOCA occur. Although lakes

within NOCA are thought to be historically fishless, during the last century, many NOCA lakes were stocked with trout, primarily *Oncorhynchus clarki* and *O. mykiss*, to provide recreational angling opportunities. There are two species of ambystomatid salamanders (*Ambystoma macrodactylum* and *A. gracile*) present in NOCA lakes. These species rarely co-occur (Liss et al., 1995).

At NOCA, lakes with trout can be grouped by the reproductive status of the trout population (Tyler et al., 1998a; Liss et al., 1998). In lakes where fish successfully reproduce, trout often reach high densities and have a complex age and size structure (Gresswell et al., 1997). In mark-recapture studies of fish density in nine lakes with reproducing trout, average fish density was 524 fish/ha for fish larger than 177mm total length (range 250-724 fish/ha, except one lake at 98 fish/ha; Gresswell et al., 1997). In lakes where trout do not successfully reproduce, fish were periodically stocked as fry or fingerlings at low to moderate densities with intervals between successive stockings averaging about five years (average stocking density in 37 NOCA lakes = 179 fry/ha; range = 60-375 fry/ha; 1976 to 1993; Liss et al., 1998). The reproductive status of trout populations in NOCA lakes was determined from NOCA records (Jarvis, 1987) and verified with field observations. Lack of successful reproduction in a lake was inferred from failure to observe fry or smaller fish, little variation in size and age structure of fish captured by gill net and angling, and a lack of suitable spawning habitat. Gillnets were fished for several hours in each fishless lake to confirm that fish were absent.

From 1990 through 1999, 28 fishless lakes, 17 lakes with non-reproducing trout, and 18 lakes with reproducing trout were sampled to determine the effects of trout on larval salamanders. These lakes represent 41% of the 154 NOCA lakes of interest to fish

NPS and WDFW managers. In addition, from 1989-1994, zooplankton were sampled in 32 fishless lakes, 17 lakes with non-reproducing trout populations, and 21 lakes with reproducing trout populations, collectively representing 45% of the lakes of interest. The number of lakes sampled in each fish category and the number of times that lakes in each category were sampled varied over the course of the study (Tables 1 and 2). Lakes were sampled between ice-out in late June or early July and the onset of inclement weather in late September.

Larval salamanders were censused by snorkel surveys (Tyler et al., 1998a). Snorkel methods tend to under-represent small, cryptic, and benthic individuals in density estimates (Helfman, 1983). Therefore, larval salamander abundance estimates from snorkel surveys are conservative. Tyler et al. (1998a) found no difference in larval *A. macrodactylum* abundance estimates between surveys conducted at night and during the day. Therefore, the data used in the analysis were from snorkel surveys performed during mid-afternoon.

In lake shoreline surveys conducted from 1990 to 1993, a snorkeler carefully searched through substrate materials (talus, woody debris, fine organic matter, aquatic vegetation) within 2 m of the shoreline and recorded the number of larvae observed and the length of the shoreline sampled (Tyler et al., 1998a). From 1994 to 1999, snorkel surveys were conducted over four 25 m segments of shoreline that were randomly chosen along the perimeter of each lake. The same shoreline segments were snorkeled on each successive sampling visit.

Salamander species identification was made in the field based on larval characteristics outlined in Corkran and Thoms (1996). When species identification could

not be ascertained in the field, representative larvae were captured and reared to metamorphosis in a laboratory to confirm species identification.

To sample crustacean zooplankton in each lake, three replicate vertical tows were taken near the deepest part of the lake with a 20 cm diameter number 25 (64  $\mu\text{m}$  mesh) zooplankton net, except in 1989 when only one vertical tow was taken. The net was lowered to within one meter of the lake bottom and towed upward at a rate of about 0.5 m/sec. 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. A 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. The average body length of adult female crustacean zooplankters of each taxon was determined. Mean density of adult crustacean zooplankton was calculated for each lake.

Eleven abiotic variables were measured for each lake during each sampling visit. A hand-held sonar gun was used to determine maximum depth of each lake. Lake elevations were derived from 7.5 min USGS topographical maps, and lake surface areas were determined by digitization of lake shorelines outlined on these maps. During each sampling visit, water temperature was recorded and water samples were collected from one meter below the lake surface over the lake's deepest point. Water samples and temperature recordings were gathered over the deepest point in each lake to standardize sampling among lakes. Temperature measurements were taken during mid-afternoon with an Omega 871 thermo-couple. Water samples were collected with a 1.5 L van Dorn-style sampling bottle. One liter of collected water was filtered in the field using a 0.7  $\mu\text{m}$  Whatman GF/C mesh glass fiber filter. Water samples were frozen upon return from the

field to facilitate transport. Frozen filtered and unfiltered water samples were transported to the Cooperative Chemical Analytical Laboratory at Oregon State University, Corvallis, Oregon, for analyses of total phosphorus, total Kjeldahl-N, ammonium-N, and nitrate-/nitrite-N concentrations, and for alkalinity, pH, and conductivity.

Statistical analyses were conducted using Statgraphics Plus Version 4 and SAS. Log-transformed larval salamander abundances, log-transformed diaptomid copepod densities, and abiotic variables were compared among fishless lakes, lakes with non-reproducing trout populations, and lakes with reproducing trout populations using the Kruskal-Wallis test ( $\alpha = 0.05$ ). If a statistically significant difference was found, the Mann-Whitney test was used to conduct pair-wise comparisons of the fish categories to determine which categories were significantly different. The level of significance was set at  $\alpha = 0.017$  to adjust for Type I error for the three pair-wise comparisons ( $\alpha = 0.05/3$ ). Some variables were natural logarithm-transformed to satisfy the assumption of equality of variance among fish categories.

Stepwise multiple regression was used for each fish category (fishless,  $n = 28$ ; non-reproducing trout,  $n = 17$ ; reproducing trout,  $n = 17$ ) to determine relationships between abiotic factors and observed larval salamander abundance. MR 16, a lake with a reproducing trout population, was eliminated from the data set because it had an unusually low fish density (as determined by mark-recapture) relative to other lakes with reproducing fish populations. The response variable for each regression was the natural logarithm of average larval abundance in each lake. Similar data collected on multiple occasions from the same lake were averaged to obtain a single value for each variable for each lake. Explanatory variables were the average values for each of the 11 abiotic

variables for each lake. Stepwise selection of variables was terminated when variables added to models were no longer significant at  $\alpha \leq 0.05$ .

A general linear model was used to determine relationships between abiotic factors and large copepod density. The response variable for the regression was the natural logarithm of average copepod density. Fish category (fishless, non-reproducing trout, reproducing trout) was used as a categorical variable. Explanatory variables were the average values for each of the 11 abiotic variables for each lake. Terms consisting of the interaction of fish category with each of the abiotic variables were also introduced. All of the terms were placed in the full model and then removed in a stepwise fashion. We removed non-significant interaction terms first. We then evaluated the significance of the main effect of the abiotic variable in each non-significant interaction term and removed it from the model if it was not significant. If an abiotic variable interacted significantly with fish category we did not remove it from the model. The main effect of fish category also was kept in the model. We used a contrast statement in SAS to generate confidence intervals for differences in predicted values of the response variable between fishless lakes and lakes with reproducing trout, and between fishless lakes and lakes with non-reproducing trout for selected values of the explanatory variables. The differences were deemed insignificant if the confidence intervals included zero.

To determine if large diaptomid copepods affected the abundance of the small herbivorous copepod, *Diaptomus tyrrelli*, we used a stepwise regression procedure similar to the one used for large copepods. The natural logarithm of *D. tyrrelli* was the response variable, fish category (fishless, non-reproducing trout, reproducing trout) was a

categorical variable, and the explanatory variables were the average values for each of the 11 abiotic variables for each lake.

Pearson's correlation matrices were developed to investigate significant relationships between chemical and physical variables used in the regression analyses. A sequential Bonferroni adjustment was performed on the Pearson's correlation matrices to eliminate Type I error and maintain table-wide significance at  $\alpha = 0.05$  (Miller, 1981; Rice, 1989).

Stepwise multiple regression was used to determine relationships between observed larval salamander abundance and the density of large diaptomid copepods. The response variable was natural log-transformed large copepod density, and the explanatory variables were abiotic variables and observed larval salamander abundance. Analysis was conducted only for fishless lakes because larval *A. macrodactylum* were absent or present in low abundance in lakes with fish (Tyler et al., 1998a). Larval salamander abundance was estimated in 17 of the 32 fishless lakes in the zooplankton data set. Densities of larval salamanders in fishless lakes ranged from zero to 73 larvae/100 m of shoreline.

## **RESULTS**

### ***Larval Salamanders***

Observed abundances of larval salamanders varied considerably among all lakes, and larvae were absent from many lakes in each fish category (i.e., fishless lakes, lakes with non-reproducing trout populations, and lakes with reproducing trout populations) (Figure 1). Larvae were present in 50% ( $n = 14$ ) of fishless lakes sampled ( $n = 28$ ), in 65% ( $n = 11$ ) of lakes sampled with non-reproducing trout populations ( $n = 17$ ), and in

24% (n = 4) of lakes sampled with reproducing trout populations (n = 17). Larval abundances > 20 larvae/100 m of shoreline surveyed were found only in fishless lakes.

There were significant differences in larval salamander abundances among fishless lakes, lakes with non-reproducing trout, and lakes with reproducing trout (Kruskal-Wallis; p = 0.016; Table 3). Lakes with reproducing trout had significantly lower larval abundances than did fishless lakes (Mann-Whitney; p = 0.017) and lakes with non-reproducing trout (Mann-Whitney; p = 0.004). Observed larval abundances did not differ significantly between fishless lakes and lakes with non-reproducing trout populations. Of the 11 abiotic variables, lake surface area (Kruskal-Wallis; p = 0.0008), total phosphorus (Kruskal-Wallis; p = 0.036), and maximum depth (Kruskal-Wallis; p = 0.048) differed significantly among the fish categories (Table 3). The surface area of fishless lakes was significantly smaller than the surface areas of lakes supporting non-reproducing trout populations (Mann-Whitney; p = 0.0008) and lakes with reproducing trout populations (Mann-Whitney; p = 0.004). Lakes with non-reproducing trout were significantly deeper than fishless lakes (Mann-Whitney; p = 0.017), but not significantly deeper than lakes with reproducing trout. Fishless lakes had significantly higher total phosphorus concentrations than did lakes with non-reproducing trout (Mann-Whitney; p = 0.005).

The observed larval salamander abundances in fishless lakes were positively related to total Kjeldahl-N (TKN) concentration and water temperature (p < 0.0001, R<sup>2</sup> = 0.59; Figure 2a and 2b):

$$\ln(\text{Density}) = \beta_0 + \beta_1(\text{TKN}) + \beta_2(\text{TEMP})$$

[where,  $\beta_0 = -9.72 \pm 1.87$ ;  $\beta_1 = 47.18 \pm 12.62$ ; and  $\beta_2 = 0.48 \pm 0.15$ ].

Of the abiotic variables, TKN concentration was the most strongly related to larval abundance ( $R^2 = 0.43$ ). Temperature was less strongly related to larval abundance ( $R^2 = 0.36$ ). In the regression model, a slightly greater proportion of the total variation in larval abundance was explained by TKN concentration (partial  $R^2 = 0.36$ ) than by temperature (partial  $R^2 = 0.29$ ). In fishless lakes, TKN concentration was positively correlated with total phosphorus ( $p < 0.0001$ ) and water temperature was negatively correlated with nitrate-/nitrite-N ( $p = 0.0040$ ). Regression analysis did not calculate a significant equation relating larval *A. macrodactylum* abundances to any of the 11 abiotic variables for lakes with non-reproducing or reproducing trout populations.

In fishless lakes, larvae were absent from 13 of the 17 lakes with  $TKN < \sim 0.045$  mg/L (Table 4). Observed larval abundances in the remaining fishless lakes with  $TKN < \sim 0.045$  mg/L were less than four larvae/100m of shoreline surveyed (Table 4 and Figure 2a). In contrast, larvae were present in ten of the 11 fishless lakes with  $TKN \geq 0.045$  mg/L, and were abundant (i.e.,  $> 10$  individuals/100 m of shoreline surveyed) in eight of these lakes (Table 4 and Figure 2a).

Given this relationship between abundance and TKN concentration, the larval abundances of lakes with  $TKN \geq 0.045$  mg/L were compared among fish categories using the Kruskal-Wallis test. For lakes within this TKN range, there were significant differences in observed larval salamander abundances among fishless lakes, lakes with non-reproducing trout, and lakes with reproducing trout (Kruskal-Wallis;  $p = 0.001$ ). Lakes with reproducing trout had significantly lower abundances (average = 0.14 larvae/100 m shoreline; median density = 0.12 larvae/100 m shoreline;  $n = 8$ ; Table 4) than fishless lakes (average = 28.5 larvae/100 m shoreline; median density = 19.5

larvae/100 m shoreline;  $n = 11$ ; Mann-Whitney;  $p = 0.003$ ) and lakes with non-reproducing trout populations (average = 4.71 larvae/100 m shoreline; median density = 2.5 larvae/100 m shoreline;  $n = 7$ ; Mann-Whitney;  $p = 0.003$ ). Larval abundances in fishless lakes and lakes with non-reproducing trout populations did not differ significantly in lakes with  $\text{TKN} \geq 0.045$  mg/L (Mann-Whitney;  $p = 0.046$ ). However, observed larval abundances for fishless lakes with  $\text{TKN} \geq 0.055$  mg/L (average = 37.1 larvae/100 m shoreline; median density = 31.6 larvae/100 m shoreline;  $n = 8$ ) were significantly greater than abundances in lakes with non-reproducing trout populations over the same TKN range (average = 1.89 larvae/100 m shoreline, median = 1.9; Mann-Whitney test,  $p = 0.009$ ), although sample size of lakes with non-reproducing trout was small ( $n = 4$ ).

The surface areas of lakes with  $\text{TKN} \geq 0.045$  mg/L differed among fish categories (Kruskal-Wallis;  $p = 0.0005$ ). Fishless lakes were found to be significantly smaller (average = 0.5 ha; median = 0.3 ha;  $n = 11$ ) than lakes with non-reproducing trout populations (average = 2.1 ha; median = 1.2 ha;  $n = 7$ ; Mann-Whitney test;  $p = 0.006$ ) and lakes with reproducing trout (average = 6.1 ha; median = 4.2 ha;  $n = 8$ ; Mann-Whitney test;  $p = 0.0005$ ). Surface area did not differ significantly among the fish categories for lakes with  $\text{TKN} < 0.045$  mg/L (Kruskal-Wallis;  $p = 0.217$ ).

Concentrations of  $\text{TKN} \geq 0.045$  mg/L tend to be found in shallower NOCA lakes ( $\sim < 10.0$  m; Figure 3), which is generally consistent with the distribution of abundant salamander populations (Figure 4). Shallow lakes where salamanders were not abundant usually had low TKN (Table 4). Trout generally are not found in NOCA lakes with maximum depths  $< 2.0$  m.

### ***Diaptomid Copepods***

The largest crustacean zooplankters in NOCA are *Diaptomus kenai* (mean length = 1.88 mm) and *Diaptomus arcticus* (mean length = 2.04 mm). *Diaptomus kenai* is the most ubiquitous, occurring in 65% of all the lakes that were sampled. *Diaptomus arcticus* is present in 9% of the sampled lakes.

Large diaptomid copepod densities, like observed larval salamander abundances, varied considerably among all sampled lakes (Figure 5). Large copepods were present in 61% (n = 19) of the fishless lakes sampled (n = 32), in 88% (n = 15) of sampled lakes with non-reproducing trout populations (n = 17), and in 59 % (n = 12) of sampled lakes with reproducing trout populations (n = 21).

There were significant differences in large copepod densities among fishless lakes, lakes with non-reproducing trout populations, and lakes with reproducing trout populations (Kruskall-Wallis,  $p = 0.021$ ; Table 5). The median density of large copepods in lakes with non-reproducing trout populations was significantly higher than the median density of large copepods in lakes with reproducing trout (Mann-Whitney;  $p = 0.003$ ). The median density of large copepods in fishless lakes was not significantly different from median densities in lakes with non-reproducing or reproducing trout populations. Lake surface area was the only abiotic variable that varied significantly among fish categories. Lakes with reproducing trout populations were significantly larger than fishless lakes (Mann-Whitney;  $p = 0.012$ ).

Maximum depth, total phosphorus, and temperature were significant in the general linear model created when the presence or absence of reproducing trout (RF) or non-reproducing trout populations (NRF) in the study lakes were used as categorical

variables. The regression equation was:

$$\text{Ln Density} = \beta_0 + \beta_1 \text{NRF} + \beta_2 \text{RF} + \beta_3 \text{MAXZ} + \beta_4 \text{TEMP} + \beta_5 \text{TP} + \beta_6 (\text{TEMP} * \text{RF}) + \beta_7 (\text{TEMP} * \text{NRF})$$

[where,  $\beta_0 = -6.070 \pm 1.038$ ,  $\beta_1 = -1.644 \pm 2.086$ ,  $\beta_2 = 3.495 \pm 1.933$ ,  $\beta_3 = 0.054 \pm 0.016$ ,  $\beta_4 = 0.329 \pm 0.075$ ,  $\beta_5 = -98.967 \pm 37.569$ ,  $\beta_6 = 0.192 \pm 0.169$ , and  $\beta_7 = -0.401 \pm 0.158$ ].

In the regression model, RF and NRF were assigned a value of one when an observation was from a lake with either reproducing trout (RF) or non-reproducing trout (NRF) populations and a value of zero otherwise. There were no significant interactions between maximum depth or total phosphorus and fish category, whereas the slope of the relationship between diaptomid copepod density and temperature differed among fish categories ( $p = 0.0132$ ). In lakes with water temperatures  $> 12^\circ\text{C}$ , large diaptomid copepod densities were significantly different between fishless lakes and lakes with reproducing trout populations (Table 6). There were, however, no significant differences in large diaptomid copepod densities between fishless lakes and lakes with non-reproducing trout populations (Table 6) with water temperature  $> 12^\circ\text{C}$ . The range of temperatures was comparable for lakes in each fish category.

*Diaptomus tyrrelli* density was positively related to TKN concentration, total phosphorus, and water temperature, and negatively related to large copepod density ( $p < 0.00001$ ;  $R^2 = 0.57$ ;  $n = 68$ ). The regression equation was:

$$\text{Ln Density} = \beta_0 + \beta_1 \text{TKN} + \beta_2 \text{TP} + \beta_3 \text{TEMP} + \beta_4 \ln(\text{large diaptomid density})$$

[where,  $\beta_0 = -8.48 \pm 0.86$ ,  $\beta_1 = 20.44 \pm 5.72$ ,  $\beta_2 = 73.46 \pm 35.06$ ,  $\beta_3 = 0.20 \pm 0.067$ , and  $\beta_4 = -0.30 \pm 0.09$ .]

There were no significant interactions between any of the abiotic variables and fish category. After accounting for all other statistically significant explanatory variables,

TKN concentration, large copepod density, and water temperature each explained about the same amount of variation (partial  $R^2$ 's ranged from 0.13-0.17), and total phosphorus explained 6% of the variation in *D. tyrrelli* density. Regression analysis did not calculate a significant equation relating large copepod density to any of the abiotic variables or to observed larval salamander abundance for the 17 lakes where larval abundances had been determined.

## **DISCUSSION**

### ***Potential Interactions of Native Biota and Introduced Trout in NOCA Lakes***

The distribution of larval *Ambystoma macrodactylum* among NOCA lakes > 800 m in elevation was patchy, even in lakes without fish. No larvae were observed in over 50% of the fishless lakes sampled. This patchiness suggests that environmental parameters and their variation between lakes may influence salamander distribution.

Total Kjeldahl-nitrogen (TKN) concentration was the abiotic variable most strongly related to the observed abundances of salamander larvae in fishless NOCA lakes. Tyler et al. (1998a), and Chapter 1 of this report, also found the positive relationship between TKN concentration and larval salamander abundance in fishless NOCA lakes to be significant. TKN concentration is a measure of ammonia plus all organically derived nitrogen (Lambou et al., 1983). Although, organic nitrogen is not readily utilized by autotrophs (Goldman and Horne, 1983), TKN concentration 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), especially when it is correlated with phosphorus and temperature, as it is in NOCA lakes. A further indication of the usefulness of TKN concentration as a predictor of lake

productivity is the positive correlation between cladoceran zooplankton density and TKN concentration in NOCA lakes (Tyler et al., 1998a). Through examination of salamander stomach contents, Tyler et al. (1998a) found that larval *A. macrodactylum* in NOCA lakes primarily consumed benthic macroinvertebrates and cladoceran zooplankton, particularly *Daphnia rosea*. These positive relationships between TKN concentration and various productivity attributes suggest that there is a positive link between lake primary and secondary productivity and larval salamander abundance.

Observed larval salamander abundances between fishless lakes and lakes with fish also differed relative to the reproductive status of the fish population in lakes with fish. For lakes with TKN  $\geq 0.045$  mg/L, fishless lakes and lakes with non-reproducing trout populations had significantly higher larval abundances than did lakes with reproducing trout populations. Fishless lakes with TKN  $\geq 0.055$  mg/L also had significantly higher larval abundances than abundances in non-reproducing trout lakes with TKN  $\geq 0.055$  mg/L, although the sample size of lakes with non-reproducing trout was small ( $n = 4$ ). In a previous study (i.e., Tyler et al., 1998a), the difference in *A. macrodactylum* larval abundance between fishless NOCA lakes and NOCA lakes with non-reproducing trout was only significant for one non-reproducing trout lake with TKN  $\geq 0.09$  mg/L. Thus, results of the present analysis identified a lower TKN concentration at or above which larval abundances in fishless lakes were significantly higher than abundances in lakes with non-reproducing trout populations. In none of the analyses were larval salamander abundances significantly different among fish categories for lakes with TKN  $< \sim 0.045$  mg/L.

Large copepod densities among NOCA lakes were quite variable. Maximum lake

depth, total phosphorus, and water temperature were correlated with this variation in large copepod density, although densities were significantly different only in the interaction between water temperature and fish category. In lakes with average water temperatures  $\leq \sim 10^\circ \text{C}$ , large copepods were virtually absent from lakes regardless of fish category. In these lakes, cold temperatures may slow development and delay maturation, making large copepod persistence difficult in lakes at elevations where the ice-free season is relatively short (Allan and Goulden, 1980). However, large copepod densities in lakes with average water temperatures  $> 12^\circ \text{C}$  and that supported reproducing trout populations were significantly lower than in fishless lakes with average water temperatures  $> 12^\circ \text{C}$ . These results suggest that at NOCA, large copepods occur more often in lakes with higher water temperatures and that reproducing trout populations can reduce the abundance of or possibly eliminate large copepods from these types of lakes.

Analysis of the interaction between maximum lake depth, total phosphorus, and fish category indicated that the relationship between large copepod density and each of these two abiotic variables did not vary significantly relative to the reproductive status of the trout population in study lakes. However, Liss et al. (1998), analyzing a smaller NOCA lake data set, did determine that large copepod densities in reproducing trout lakes  $> 10 \text{ m}$  maximum depth were significantly higher than densities in reproducing trout lakes  $< \sim 10 \text{ m}$  maximum depth. Donald et al. (1994), in lakes of the Canadian Rockies, found differences in large zooplankton abundances between shallow fishless lakes and shallow lakes with fish, but not in deep lakes. Perhaps large zooplankton (e.g., diaptomid copepods) persist in deeper lakes with fish because in these systems they are able to diurnally migrate to refuge in deeper water to escape vertebrate predation (e.g., Zaret and

Suffern, 1976; Stich and Lambert, 1981; Gliwicz and Pijanowska, 1988; Donald et al., 1994). Large copepod density was negatively related to total phosphorus in fishless lakes (Table 6). It is unclear why this relationship would be negative since NOCA lakes with higher concentrations of total phosphorus support a greater total number of zooplankton species, including more species of cladocerans and the small herbivorous diaptomid, *D. tyrrelli*, than do lakes with lower total phosphorus concentrations (W. J. Liss, unpublished NOCA data).

*Diaptomus tyrrelli* density in NOCA lakes was positively related to water temperature, TKN concentration, and total phosphorus, and negatively related to large copepod density (also, see Liss et al., 1998). It is unclear whether the inverse relationship between small and large copepod density is a consequence of lake environmental conditions “favoring” species of one size-group over another or due to predation of small copepods by large copepods. It is well known that invertebrate predation can influence the structure of zooplankton communities. For example, predacious large copepods (e.g., *D. arcticus*) can prey on smaller copepods (e.g., *D. tyrrelli*) and reduce their abundance or eliminate them from lakes (e.g., Anderson, 1970; Dodson, 1970, 1974; Sprules, 1972; Paul et al., 1995). However, a reduction in large copepod abundance by introduced fish can be followed by a corresponding increase in small copepod abundance (Anderson, 1970). This relationship in NOCA lakes has been implied by observations that densities of *D. tyrrelli* were typically high in relatively shallow (i.e.,  $< \sim 10$  m maximum depth) lakes, with relatively high TKN concentration (i.e.,  $> \sim 0.05$  mg/L) and reproducing trout populations, where large copepods were absent and assumed eliminated by the introduced fish (Liss et al., 1998). These kinds of cascading effects in food webs may be most

evident in montane oligotrophic systems (Gliweicz and Prejs, 1977; Dodson, 1979; McQueen et al., 1986; Neill, 1987; Carney, 1990); and in NOCA, potential representative lakes include Dagger, Kettling, and Upper Triplet (Liss et al., 1998).

There was no significant relationship between larval salamander abundance and large copepod density in fishless lakes. Thus, in contrast to the apparent negative impact of reproducing trout populations on large copepod density, larval *A. macrodactylum* appear to have little impact on the abundance of large copepods. Although larval salamanders prey on crustacean zooplankton in NOCA lakes (Tyler et al., 1998a), analysis of stomach contents of larval *A. macrodactylum* from NOCA lakes found that diaptomid copepods were present in only 16% of the stomachs examined and were not a major food item.

#### ***Relative Risk to Native Biota From Introduced Trout in NOCA Lakes***

TKN concentration and water temperature were measured, either through this research or earlier lake surveys, in 83 of 154 NOCA lakes of interest to NPS and WDFW managers. Salamanders or zooplankton were not sampled in many of the 83 lakes, and these lakes do not include lakes where TKN concentration and water temperature were measured but were known to contain *Ambystoma gracile* (Northwestern Salamander) larvae. The 83 NOCA lakes were not randomly selected for sampling and thus may not be representative of all NOCA lakes. These lakes, however, represent 54% of all NOCA lakes of interest to managers and have biotic and abiotic characteristics that are broadly representative of lakes in the northern Cascade Mountains.

The relative risk to native biota from introduced trout in NOCA lakes appears to be associated primarily with lake TKN concentration, water temperature, and the

reproductive status of the trout population. Native biota appear to be at greatest risk in NOCA lakes with the following attributes: 1) TKN concentration  $\geq 0.045$  mg/L; 2) water temperature  $>12^{\circ}\text{C}$ ; and 3) a reproducing trout population (indicating a relatively high density of fish). Six of the 83 NOCA lakes identified above had these attributes (Appendix I, Table A). The range of larval *A. macrodactylum* abundances in these lakes was quite low (i.e., 0 – 1.2 per 100 m survey), as were large copepod densities (i.e., 0 – 0.12 /L; Liss et al., 1998). These low abundances and densities appear to be indicative of the capacity of reproducing trout to significantly reduce or eliminate larval *A. macrodactylum* and large copepods from these lakes. In lakes with non-reproducing trout populations, larval salamander abundances were not significantly lower than abundances in fishless lakes until lake TKN concentration was  $\geq 0.055$  mg/L. Three lakes with non-reproducing trout populations had TKN  $\geq 0.055$  mg/L and water temperatures  $>12^{\circ}\text{C}$  (Appendix I, Table B).

Differences in larval salamander abundances among fishless lakes and lakes with non-reproducing or reproducing trout were not statistically significant in lakes with TKN concentration  $< 0.045$  mg/L. Larval salamander abundances in lakes within this range of TKN concentrations typically were quite low or larvae were not observed (Table 4). Large diaptomid copepods, however, could be at risk in some of the lakes with reproducing trout and water temperatures  $> 12^{\circ}\text{C}$  ( $n = 6$ ; Appendix I, Table B), but apparently not in the lakes with non-reproducing trout. Thus, the native biotic community could be at minimal risk in lakes with non-reproducing trout and TKN  $< 0.045$  mg/L.

Twenty-three of the 83 lakes with known TKN concentration and water temperature had average temperatures  $< 10^{\circ}\text{C}$  (Appendix I, Table C). Larval

salamanders were absent from most of these lakes regardless of whether fish were present or absent (Table 4) and statistically significant differences in large copepods density among fish categories were not detected.

Lakes with relatively high TKN concentrations (i.e.,  $\geq 0.045 - 0.055$  mg/L) and water temperatures (i.e.,  $>12^{\circ}\text{C}$ ) likely are more productive habitat for native biota, especially larval salamanders, than lakes with TKN concentrations and water temperatures below these levels. Of the 83 lakes with known TKN concentrations, 23 (28%) had TKN concentrations  $\geq 0.045$ mg/L and temperatures  $> 12^{\circ}$  C, and of these 23 lakes only ten lakes were fishless (Appendix I, Table A). These “more productive” lakes in NOCA, that are fishless, typically have relatively high larval salamander abundances and these “large” populations may play an important ecological role in montane areas. Large populations may be less vulnerable to extinction from stochastic events than “small” populations (e.g., Shaffer, 1981; Goodman, 1987) and so could serve as important sources of dispersing individuals (*sensu* Pulliam, 1988; Harrison, 1994) that could colonize vacant habitats. *Ambystoma macrodactylum* apparently was able to colonize lakes in the Rocky Mountains within 20 years following extinction of trout populations in these lakes (Funk and Dunlap, 1999). Recolonization of habitats where local population extinctions have occurred also depends on the degree of isolation (or distance) between sources of dispersers and vacant habitats available for colonization (Sjogren-Gulve and Ray, 1996; Funk and Dunlap, 1999). Many NOCA lakes occur in relatively isolated watersheds. This isolation could make it difficult (in terms of time and distance), if not impossible, for dispersers to emigrate to and colonize vacant habitat. Yet, given that NOCA lakes with TKN  $\geq 0.045$  mg/L are apparently productive habitats for

native biota, and the likelihood that lakes with productive habitat for native biota represent a relatively small fraction of all NOCA lakes, a prudent and precautionary management strategy would be to maximize protection of all NOCA lakes with TKN  $\geq \sim 0.045$ .

### ***Summary***

The results of this analysis generally are consistent with the view that the impacts of vertebrate predators on their prey vary along a gradient of increasing vertebrate predation pressure (Stenson, 1972; Langeland, 1978; Dodson, 1979; Zaret, 1980; McQueen et al., 1986; Post and McQueen, 1987; Liss et al., 1998), with effects on the prey likely to be greatest in lakes with high vertebrate predation intensity (Gliwicz and Prejs, 1977; Donald et al., 1994). The reproductive status of a trout population may serve as a surrogate for predation intensity in NOCA lakes. Reproducing trout populations in NOCA lakes tend to reach higher densities and have a more diverse age and size structure than non-reproducing trout in lakes that are periodically and usually stocked with trout fry or fingerlings at relatively low densities (Gresswell et al., 1997; Tyler et al., 1998a; Liss et al., 1998).

Environmental conditions, however, can mediate effects of vertebrate predators on prey in NOCA lakes. The highly patchy distributions of larval salamanders and large copepods at NOCA can be partly explained by variation in environmental conditions among lakes. Both TKN concentration and water temperature were potentially important in mediating predator effects in NOCA lakes. Larval salamanders and large copepods may be at greatest risk from introduced trout in lakes with reproducing trout populations that have TKN concentrations  $\geq 0.045\text{mg/L}$  and water temperatures  $> 12^\circ\text{C}$ . Lakes with

these conditions are likely to be relatively shallow (maximum depth  $< \sim 10\text{m}$ ). Larval salamanders also appear at risk in lakes with non-reproducing trout populations and TKN concentrations  $\geq 0.055 \text{ mg/L}$ . Native biota appear to be at minimum risk in lakes with  $\text{TKN} < 0.045 \text{ mg/L}$  supporting non-reproducing trout.

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Figure 1. Observed larval *Ambystoma macrodactylum* abundances in NOCA lakes

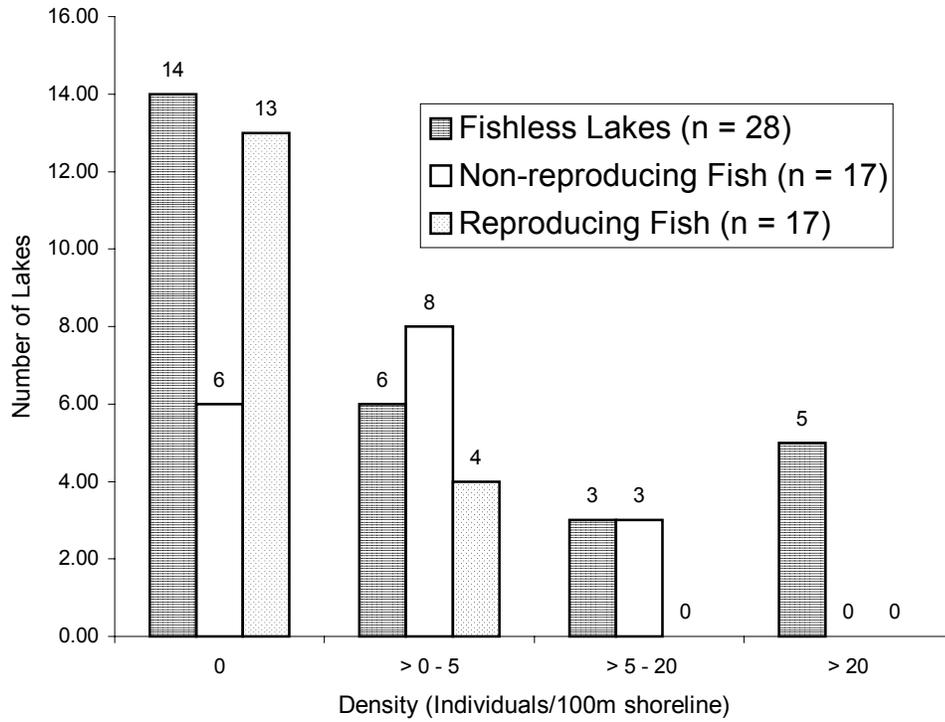


Figure 2a. Relationships between larval *Ambystoma macrodactylum* abundances and total Kjeldahl-N concentration for 28 fishless lakes, 17 lakes with non-reproducing trout populations, and 17 lakes with reproducing trout populations in North Cascades National Park Service Complex, Washington, USA.







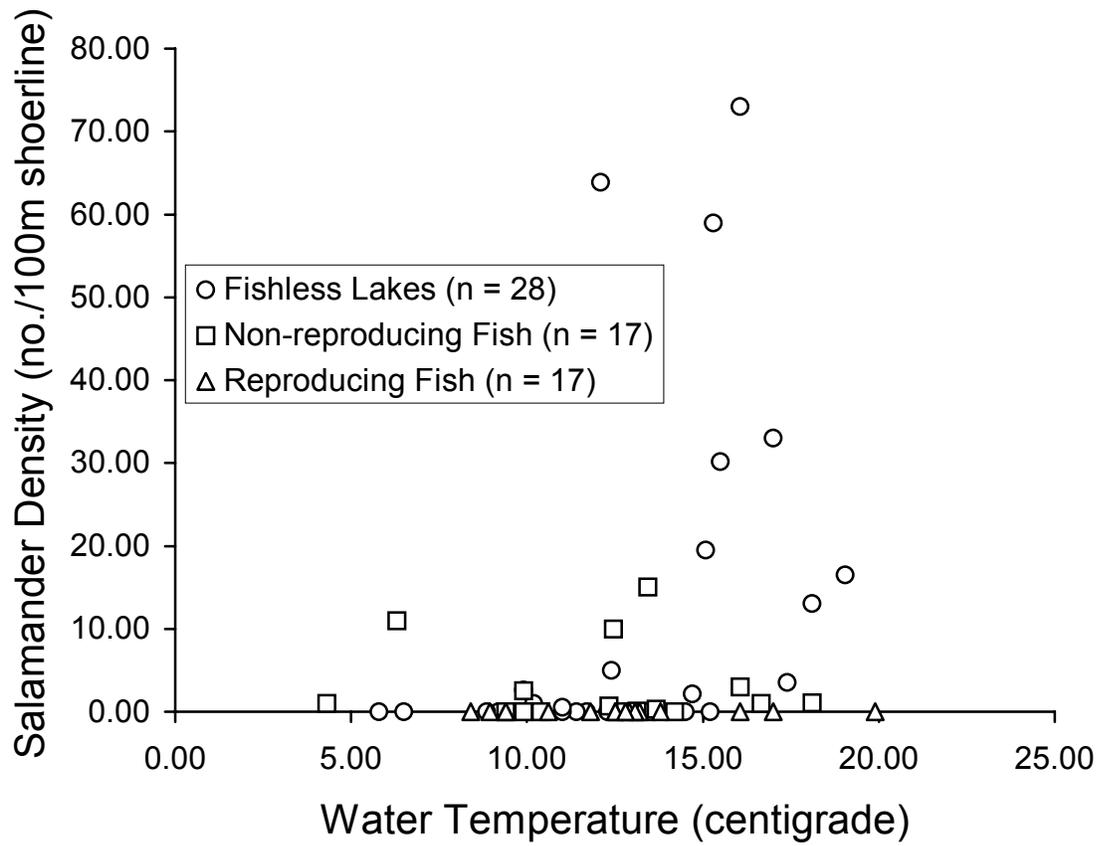


Figure 3. Relationships between total Kjeldahl-N concentration and maximum depth for 83 NOCA lakes. Larval salamander abundances were not estimated in all 83 lakes.



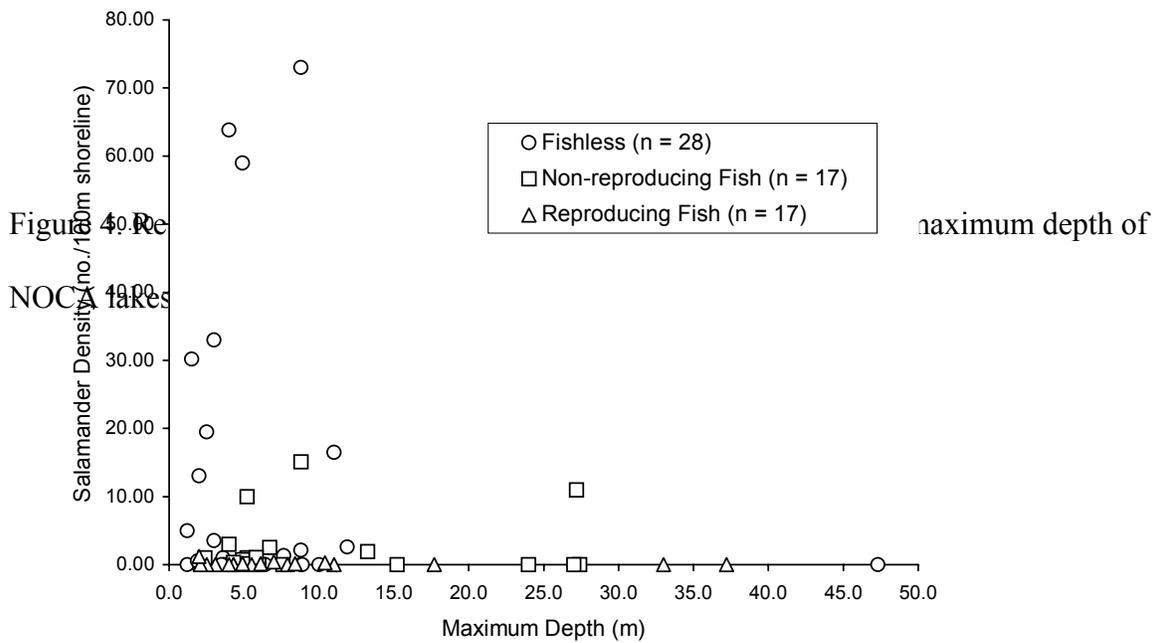
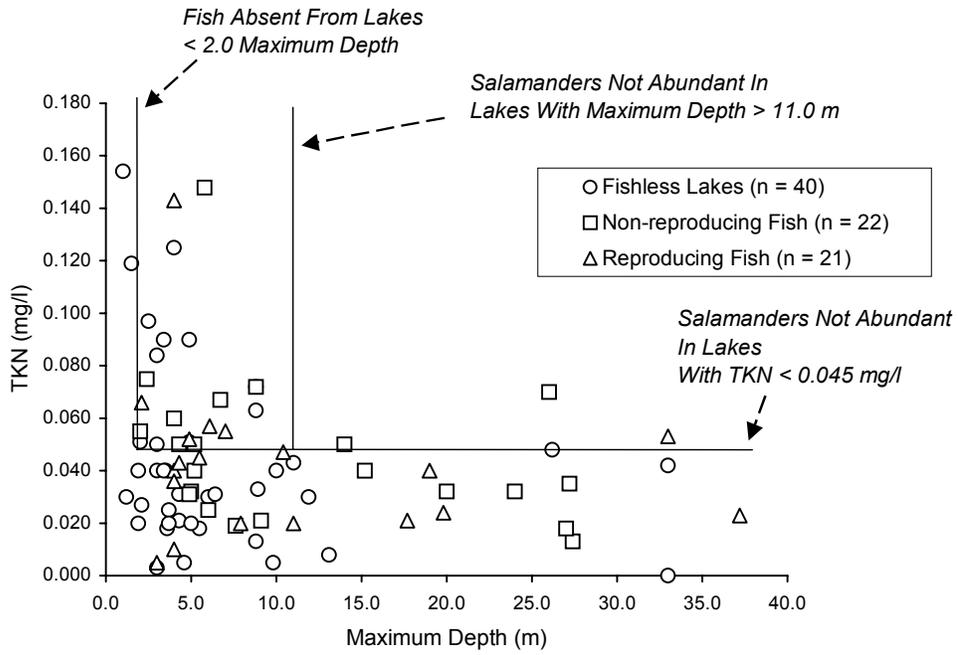




Figure 5. Large copepod densities in NOCA lakes.



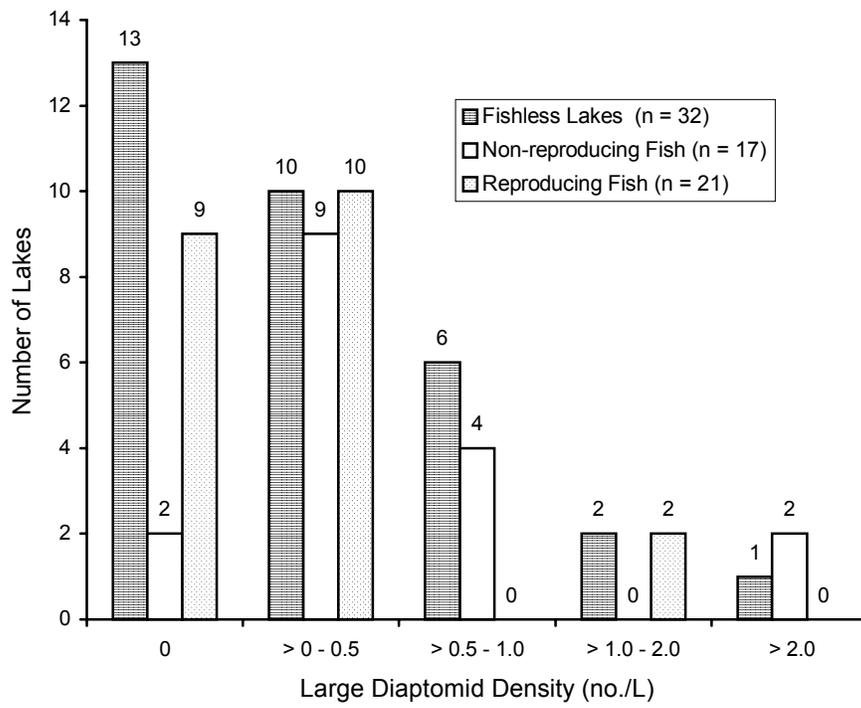


Table 1. The number of lakes in each fish category that were sampled for larval salamanders and crustacean zooplankton in each year of the study. Some lakes were sampled in more than one year.

Year	Fishless Lakes		Non-reproducing Trout		Reproducing Trout	
	Salamanders	Zooplankton	Salamanders	Zooplankton	Salamanders	Zooplankton
1989	0	25	0	14	0	12
1990	4	8	0	4	4	7
1991	2	8	2	3	6	7
1992	1	2	1	3	3	4
1993	10	13	6	15	8	8
1994	8	7	1	3	9	4
1995	1		0		0	
1996	1		0		0	
1997	3		4		0	
1998	8		8		0	
1999	8		7		0	

Table 2. The number of lakes in each fish category sampled from 1 to  $\geq 5$  times for larval salamanders and crustacean zooplankton from 1990 through 1999.

Samples	Fishless Lakes		Non-reproducing Trout		Reproducing Trout	
	Salamanders	Zooplankton	Salamanders	Zooplankton	Salamanders	Zooplankton
$\geq 5$	3	6	1	4	1	3
4	2	2	2	0	2	5
3	3	7	3	1	0	2
2	8	9	6	5	8	4
1	12	8	5	6	7	5

Table 3. Averages and medians of larval salamander abundances and abiotic variables for lakes in each fish category. Statistical comparisons were made using Kruskal-Wallis tests,  $\alpha = 0.05$ . Pair-wise comparisons among fish categories were made using the Mann-Whitney test,  $\alpha = 0.017$ .

Variable	Fishless Lakes		Non-reproducing Trout		Reproducing Trout		P value
	Average	Median	Average	Median	Average	Median	
Density (No./100m shoreline)	11.5	0.25	2.69	0.71	0.06	0.0	0.016
Elevation (m)	1674	1652	1595	1556	1585	1629	0.472
Maximum Depth (m)	6.5	3.9	11	6.0	9.6	5.5	0.048
Surface Area (ha)	1.6	0.7	2.8	1.6	4.3	2.8	0.0008
TKN (mg/L)	0.052	0.04	0.044	0.03	0.040	0.03	0.489
TP (mg/L)	0.006	0.005	0.004	0.004	0.005	0.006	0.036
Nitrate-N (mg/L)	0.006	0.002	0.005	0.004	0.01	0.004	0.321
Ammonia-N (mg/L)	0.006	0.006	0.008	0.004	0.005	0.005	0.360
PH	7.07	7.1	7.04	6.6	7.24	7.3	0.141
Alkalinity (mg/L)	1.84	1.34	1.67	1.48	2.38	2.19	0.073
Conductivity ( $\mu$ S/cm)	18.82	13.38	14.57	11.33	20.59	17.8	0.147
Water Temperature ( $^{\circ}$ C)	12.83	12.56	12.13	12.56	12.67	12.8	0.942

Table 4. Averages of larval salamander abundances and abiotic variables for lakes with TKN  $\leq$  0.045 mg/L and lakes with TKN  $>$  0.045 mg/L from 1990-1999.

LAKE	ABUND	ELEV	MAX DEPTH	SURFACE AREA	TKN	TP	NO3	NH3	pH	ALK	COND	TEMP
<i>Fishless Lakes</i>												
MC27	0.00	1488	8.8	4.6	0.001	0.001	0.004	0.003	6.33	0.573	6.733	13.1
DD8	0.00	1600	1.9	0.9	0.020	0.005	0.032	0.013	7.10	1.180	18.000	6.5
FP9	0.00	1662	3.4	0.5	0.020	0.004	0.003	0.003	7.20	1.990	1.990	9.2
M6	1.00	1632	3.6	0.6	0.020	0.002	0.028	0.001	7.70	2.780	22.700	10.2
MC21-1	0.00	1528	5.0	1.2	0.020	0.007	0.000	0.002	6.60	0.820	21.800	5.8
MR11	2.15	1863	8.8	1.3	0.021	0.005	0.003	0.006	7.20	2.480	18.950	14.7
MM6	2.60	1504	11.9	4.1	0.028	0.005	0.005	0.004	7.14	1.918	15.320	9.9
EP3	0.00	1299	3.7	0.4	0.030	0.004	0.007	0.009	7.10	1.230	9.300	11.7
GM2	0.00	1664	47.3	16.1	0.030	0.005	0.000	0.007	7.00	1.030	6.500	15.2
MA3	0.00	2044	6.0	1.3	0.030	0.006	0.000	0.007	7.10	1.570	11.800	12.3
ML1	0.00	1476	1.2	0.2	0.030	0.005	0.024	0.009	7.65	3.155	33.250	8.9
MSH4	0.00	1635	8.9	1.4	0.033	0.005	0.019	0.007	7.30	2.097	18.500	10.4
ML4	0.00	1583	6.4	3.3	0.035	0.003	0.002	0.006	7.75	2.695	20.900	12.8
MA2	0.00	2127	10.0	1.0	0.040	0.009	0.000	0.007	7.10	1.350	9.800	11.4
MC1	3.50	1762	3.0	1.2	0.040	0.002	0.007	0.009	6.50	0.650	4.500	17.4
MR6	0.00	1693	2.1	0.6	0.040	0.008	0.003	0.004	7.55	3.220	32.550	12.9
MR8	0.00	1970	3.5	0.3	0.040	0.005	0.010	0.001	6.90	1.230	8.200	11.0
<b>Average</b>	<b>0.54</b>	<b>1678.2</b>	<b>8.0</b>	<b>2.3</b>	<b>0.028</b>	<b>0.005</b>	<b>0.009</b>	<b>0.006</b>	<b>7.13</b>	<b>1.763</b>	<b>15.341</b>	<b>11.37</b>
MC2	16.50	1800	11.0	1.2	0.045	0.003	0.001	0.004	6.50	0.675	7.600	19.1
MC4	0.00	1604	4.9	0.8	0.050	0.007	0.001	0.006	6.50	0.740	7.200	14.5
MM7	0.50	1642	1.9	0.8	0.055	0.005	0.003	0.005	7.20	2.110	16.550	11.0
MR13-1	13.03	1800	2.0	0.3	0.058	0.008	0.001	0.006	7.50	0.973	7.300	18.1
RD3	73.00	802	8.8	0.3	0.064	0.008	0.001	0.006	7.79	8.520	74.066	16.1
MR3	19.50	1873	2.5	0.2	0.080	0.009	0.002	0.010	6.30	0.598	3.523	15.1
MC10	59.00	1556	4.9	0.4	0.090	0.007	0.001	0.006	6.80	1.330	9.400	15.3
PM5-3	33.00	1382	3.0	0.1	0.095	0.007	0.001	0.006	6.60	0.985	6.700	17.0
MR12	63.85	1981	4.0	0.6	0.125	0.009	0.000	0.003	7.25	1.995	14.950	12.1
MR2	30.17	1873	1.5	0.3	0.137	0.015	0.000	0.006	7.36	2.316	17.830	15.5
SM1	5.00	2033	1.2	0.2	0.170	0.016	0.001	0.009	6.90	1.250	101.000	12.4
<b>AVERAGE</b>	<b>28.50</b>	<b>1667.8</b>	<b>4.15</b>	<b>0.5</b>	<b>0.088</b>	<b>0.008</b>	<b>0.001</b>	<b>0.006</b>	<b>6.97</b>	<b>1.954</b>	<b>24.193</b>	<b>15.10</b>

Table 4 continued

LAKE	ABUND	ELEV	MAX DEPTH	SURFACE AREA	TKN	TP	NO3	NH3	PH	ALK	COND	TEMP
<i>Non-reproducing Trout</i>												
ML3	0.00	1967	15.2	1.3	0.010	0.004	0.000	0.002	7.20	1.480	12.900	13.4
ML2	0.00	1687	27.4	3.4	0.015	0.003	0.006	0.028	7.90	2.725	28.350	9.4
MR15-1	0.00	1922	27.0	4.8	0.018	0.003	0.018	0.010	7.20	1.943	18.330	12.6
DD5	1.00	1531	5.2	5.2	0.020	0.004	0.007	0.003	6.70	0.930	7.000	4.3
EP5-1	0.00	1543	6.0	2.7	0.020	0.003	0.006	0.004	6.90	1.030	7.800	9.9
MC7	11.00	1556	27.2	6.7	0.020	0.004	0.007	0.003	7.00	1.670	25.300	6.3
MM11	0.00	1974	7.6	1.4	0.020	0.003	0.005	0.002	6.67	0.810	5.033	14.2
MR9	0.71	1813	4.9	1.7	0.027	0.006	0.002	0.007	6.93	1.293	9.867	12.3
MR13-2	0.10	1789	5.0	1.2	0.030	0.004	0.004	0.004	6.93	1.203	9.200	13.1
M19	0.00	1427	24.0	5.0	0.035	0.001	0.012	0.006	6.55	0.670	4.850	10.4
<b>Average</b>	<b>1.28</b>	<b>1720.9</b>	<b>15.0</b>	<b>3.3</b>	<b>0.021</b>	<b>0.003</b>	<b>0.007</b>	<b>0.007</b>	<b>7.00</b>	<b>1.38</b>	<b>12.86</b>	<b>10.59</b>
LS3	10.00	1365	5.2	1.2	0.045	0.004	0.004	0.004	6.45	0.835	6.350	12.5
M1	0.33	1159	4.3	1.6	0.050	0.004	0.001	0.003	6.87	1.443	11.333	13.7
MR11	15.08	1863	8.8	1.3	0.050	0.005	0.003	0.004	7.33	2.688	21.875	13.4
MR12	3.00	1981	4.0	0.6	0.060	0.004	0.001	0.014	7.10	1.530	11.050	16.1
LS3-FS	2.50	1375	6.7	1.2	0.085	0.002	0.004	0.010	6.95	1.615	12.850	9.9
DD1	1.00	1496	2.4	0.5	0.090	0.004	0.001	0.009	7.75	3.320	29.600	16.7
MM10	1.07	662	5.8	8.2	0.145	0.012	0.001	0.027	7.30	3.160	25.950	18.1
<b>AVERAGE</b>	<b>4.71</b>	<b>1414.4</b>	<b>5.3</b>	<b>2.1</b>	<b>0.075</b>	<b>0.005</b>	<b>0.002</b>	<b>0.010</b>	<b>7.11</b>	<b>2.084</b>	<b>17.001</b>	<b>14.32</b>
<i>Reproducing Trout</i>												
MR15-2	0.00	1909	3.0	0.3	0.001	0.006	0.021	0.004	7.30	2.210	21.500	9.0
M21	0.00	1205	3.1	1.6	0.010	0.000	0.059	0.000	7.20	2.190	17.500	8.4
LS7	0.00	1510	7.9	2.8	0.020	0.002	0.005	0.005	7.30	1.780	17.800	12.5
M7	0.00	1363	11.0	3.2	0.020	0.003	0.001	0.001	7.10	1.340	10.900	12.5
MLY2	0.00	1629	4.3	2.5	0.025	0.007	0.009	0.005	7.20	2.640	22.050	9.4
CP1	0.00	1642	17.7	12.0	0.030	0.003	0.001	0.005	6.70	0.930	11.800	13.1
M23	0.00	1270	37.2	0.4	0.030	0.002	0.001	0.004	7.30	1.660	13.200	17.0
SM2-2	0.00	1988	4.3	1.0	0.030	0.009	0.027	0.003	7.60	3.340	29.550	10.6
EP9-1	0.00	1580	2.5	0.6	0.040	0.001	0.000	0.002	7.10	1.730	13.100	13.2
<b>Average</b>	<b>0.00</b>	<b>1570.5</b>	<b>9.7</b>	<b>2.9</b>	<b>0.023</b>	<b>0.004</b>	<b>0.013</b>	<b>0.004</b>	<b>7.21</b>	<b>2.010</b>	<b>17.655</b>	<b>11.51</b>
LS2	0.13	1243	4.9	1.0	0.045	0.007	0.002	0.006	7.64	5.837	52.941	12.9
PM3	0.00	1609	5.5	4.3	0.045	0.004	0.005	0.016	7.25	2.280	19.150	9.4
MR14	0.30	1717	10.4	6.3	0.048	0.006	0.004	0.003	6.95	1.340	10.400	11.8
MR10	0.12	1679	6.1	5.0	0.050	0.007	0.002	0.005	7.30	2.033	16.167	13.1
SM2-1	0.00	1931	2.1	1.0	0.051	0.006	0.008	0.004	7.30	3.260	28.750	13.8
MR5	0.40	1639	7.0	4.0	0.055	0.009	0.001	0.005	7.45	2.740	24.400	16.1
M20	0.00	1357	33.0	23.5	0.090	0.003	0.018	0.006	6.60	0.850	6.100	12.8
MR4	0.00	1679	4.0	3.6	0.115	0.010	0.001	0.010	7.85	4.300	34.800	19.9
<b>AVERAGE</b>	<b>0.14</b>	<b>1606.4</b>	<b>9.6</b>	<b>6.1</b>	<b>0.065</b>	<b>0.007</b>	<b>0.005</b>	<b>0.006</b>	<b>7.30</b>	<b>2.909</b>	<b>24.794</b>	<b>14.33</b>

Table 5. Averages and medians of zooplankton densities and abiotic variables for lakes in each fish category. Statistical comparisons were made using Kruskal-Wallis tests,  $\alpha = 0.05$ . Pair-wise comparisons among fish categories were made using the Mann-Whitney test,  $\alpha = 0.017$ .

Variable	Fishless Lakes		Non-reproducing Trout		Reproducing Trout		P value
	Average	Median	Average	Median	Average	Median	
Density (No. L <sup>-1</sup> )	0.343	0.039	0.487	0.364	0.113	0.0045	0.021
Elevation (m)	1630	1634	1529	1496	1576	1622	0.477
Maximum Depth (m)	9.1	5.0	11.0	7.6	15.2	9.2	0.154
Surface Area (ha)	3.5	1.0	2.0	1.4	7.6	3.8	0.026
TKN (mg/L)	0.049	0.033	0.040	0.033	0.041	0.040	0.997
TP (mg/L)	0.008	0.007	0.006	0.007	0.006	0.006	0.534
Nitrate-N (mg/L)	0.006	0.002	0.004	0.001	0.008	0.005	0.294
Ammonia-N (mg/L)	0.005	0.005	0.005	0.004	0.005	0.005	0.531
PH	6.94	7.0	7.05	6.95	7.11	7.25	0.350
Alkalinity (mg/L)	1.68	1.27	2.19	1.38	2.18	1.76	0.234
Conductivity ( $\mu$ S/cm)	16.82	12.19	22.01	17.20	19.97	15.93	0.534
Water Temperature ( $^{\circ}$ C)	11.51	11.67	12.09	12.28	12.18	12.23	0.799

Table 6. Confidence intervals for differences in predicted values of large copepod density between fishless lakes (NF) and lakes with reproducing trout (RF), and between fishless lakes and lakes with non-reproducing trout (NRF) for selected temperatures. Confidence intervals that do not contain zero indicate statistically significant differences and are denoted by an asterisk.

Comparison	Confidence Interval	
	Lower	Upper
<i>RF vs. NF</i>		
6°C	-0.969	3.149
10°C	-1.561	0.535
12°C	-2.167	-0.462*
14°C	-3.192	-1.040*
15°C	-3.810	-1.224*
<i>NRF vs. NF</i>		
6°C	-2.738	1.749
10°C	-0.881	1.425
12°C	-0.262	1.573
14°C	-0.086	2.163
15°C	-0.117	2.578

**Appendix I.** Table A. Lakes with TKN  $\geq 0.045$  mg/L and water temperature  $> 12^{\circ}\text{C}$ . NF = fishless lake; NRF = lake with non-reproducing trout; RF = lake with reproducing trout.

CODE	FISH	ELEV	MAX Z	S. AREA	TKN	TEMP	TP	NO3	NH3	PH	ALK	COND
MC1	NF	1762	3.0	1.2	0.050	17.40	0.002	0.005	0.011	6.53	0.673	5.100
MR13-1	NF	1800	2.0	0.3	0.051	14.97	0.008	0.003	0.007	7.05	0.882	6.365
MC4	NF	1604	4.9	0.8	0.051	12.40	0.005	0.002	0.012	6.23	0.560	4.733
RD3	NF	802	8.8	0.3	0.063	16.05	0.008	0.001	0.006	7.82	8.406	73.180
PM53	NF	1382	3.0	0.1	0.084	17.00	0.007	0.001	0.005	6.53	0.910	6.113
FP6	NF	1690	3.4	0.5	0.090	11.90	0.006	0.001	0.007	6.70	0.940	5.600
MC10	NF	1556	4.9	0.4	0.090	15.30	0.007	0.001	0.006	6.80	1.330	9.400
MR3	NF	1873	2.5	0.2	0.097	14.25	0.010	0.002	0.009	6.33	0.637	9.463
MR2	NF	1873	1.5	0.3	0.119	14.98	0.014	0.001	0.006	7.28	2.318	17.634
SM1	NF	2033	1.2	0.2	0.154	16.05	0.020	0.001	0.006	6.85	1.211	55.235
LS3	NRF	1365	5.1	1.4	0.050	13.23	0.004	0.002	0.004	6.53	0.873	30.397
M1	NRF	1159	4.3	1.6	0.050	13.67	0.004	0.001	0.003	6.87	1.443	11.333
MR11	NRF	1863	8.8	1.3	0.050	13.24	0.005	0.002	0.004	7.32	2.670	21.660
M20	NRF	1357	33.0	23.5	0.053	12.15	0.003	0.016	0.010	6.55	0.769	6.040
MR12	NRF	1981	4.0	0.6	0.060	16.05	0.004	0.001	0.014	7.10	1.530	11.050
DD1	NRF	1496	2.4	0.5	0.075	15.37	0.004	0.001	0.007	8.07	3.494	32.093
MM10	NRF	662	5.8	8.2	0.145	18.1	0.0115	0.001	0.0265	7.3	3.16	25.95
LS2	RF	1243	4.9	1.0	0.052	13.22	0.007	0.001	0.006	7.70	6.044	54.529
MR16	RF	1900	2.0	0.6	0.055	15.45	0.009	0.001	0.007	6.90	1.325	9.400
MR5	RF	1639	7.0	4.0	0.055	16.05	0.009	0.001	0.005	7.45	2.740	24.400
MR10	RF	1679	6.1	5.0	0.057	12.87	0.009	0.001	0.005	7.25	2.055	16.267
SM2-1	RF	1931	2.1	1.0	0.066	12.20	0.010	0.005	0.004	7.37	3.538	30.640

MR4 RF 1679 4.0 3.6 0.143 16.08 0.011 0.001 0.008 7.88 4.803 39.625

**Appendix I** (continued)

Table B. Lakes with TKN < 0.045 mg/L and water temperature > 12°C. NF = fishless lake; NRF = lake with non-reproducing trout; RF = lake with reproducing trout.

CODE	FISH	ELEV	MAX Z	S. AREA	TKN	TEMP	TP	NO3	NH3	PH	ALK	COND
MC27	NF	1488	8.8	4.6	0.013	12.35	0.001	0.006	0.002	6.33	0.557	6.528
MC17-2	NF	1754	5.5	0.3	0.018	14.57	0.002	0.001	0.005	6.27	0.465	3.843
EP3	NF	1299	3.7	0.4	0.025	12.90	0.004	0.006	0.006	7.00	1.205	9.600
MC17-1	NF	1755	13.1	4.0	0.008	14.50	0.002	0.001	0.002	6.20	0.463	3.660
MA3	NF	2044	6.0	1.3	0.030	12.30	0.006	0.000	0.007	7.10	1.570	11.800
ML4	NF	1583	6.4	3.3	0.031	12.27	0.003	0.001	0.005	7.87	2.778	22.087
MC2	NF	1800	11.0	1.2	0.043	16.37	0.003	0.002	0.004	6.53	0.683	6.700
MM11	NRF	1974	7.6	1.4	0.019	13.35	0.006	0.004	0.003	6.63	0.754	4.673
MR15-1	NRF	1922	27.0	4.8	0.023	12.58	0.003	0.024	0.014	7.20	1.943	18.333
LS7	RF	1510	7.9	2.8	0.020	12.50	0.002	0.005	0.005	7.30	1.780	17.800
GM1	RF	1270	49.0	59.0	0.017	13.80	0.009	0.029	0.005	7.40	3.219	41.383
M7	RF	1363	11.0	3.2	0.020	12.50	0.003	0.001	0.001	7.10	1.340	10.900
CP1	RF	1642	17.7	12.0	0.021	12.20	0.005	0.011	0.004	6.60	0.760	10.070
M23	RF	1270	37.2	12.7	0.023	15.25	0.002	0.002	0.005	7.25	1.646	14.065
EP9-1	RF	1580	2.5	0.6	0.040	13.20	0.001	0.000	0.002	7.10	1.730	13.100

**Appendix I** (continued)

Table C. Lakes with water temperature < 12°C. NF = fishless lake; NRF = lake with non-reproducing trout; RF = lake with reproducing trout.

CODE	FISH	ELEV	MAX Z	S. AREA	TKN	TEMP	TP	NO3	NH3	PH	ALK	COND
FP4	NF	1624	33.0	12.0	0.000	6.00	0.030	0.001	0.008	7.00	1.087	9.060
MC21-2	NF	1525	3.0	1.6	0.003	10.60	0.003	0.004	0.003	6.40	0.560	22.470
MC24	NF	1982	4.6	1.0	0.005	2.30	0.006	0.008	0.000	6.50	0.605	3.710
MS4	NF	1659	9.8	2.0	0.005	4.60	0.009	0.035	0.006	6.60	0.658	5.350
MC25	NF	2028		2.4	0.007	1.10	0.004	0.022	0.001	5.90	0.363	1.920
M6	NF	1632	3.6	0.6	0.018	10.95	0.002	0.024	0.003	7.60	2.950	24.900
DD8	NF	1600	1.9	0.9	0.020	6.50	0.005	0.032	0.013	7.10	1.180	18.000
MC21-1	NF	1528	5.0	1.2	0.020	5.80	0.007	0.000	0.002	6.60	0.820	21.800
MP8	NF	1566	3.7	0.9	0.020	10.40	0.004	0.004	0.003	6.80	0.900	8.210
MC17-4	NF	1754	4.3	0.8	0.021	11.70	0.003	0.001	0.005	6.07	0.449	6.127
MR6	NF	1693	2.1	0.6	0.027	11.63	0.008	0.002	0.003	1.73	3.220	32.550
ML1	NF	1476	1.2	0.2	0.030	8.23	0.005	0.022	0.007	7.87	3.203	34.967
MM6	NF	1504	11.9	4.1	0.030	10.70	0.005	0.003	0.005	7.18	1.998	16.094
PM4	NF	1610	4.3	3.0	0.031	3.40	0.005	0.014	0.000	7.10	1.935	16.230
MS1	NF	2063	137.0	65.1	0.033	5.00	0.005	0.018	0.004	6.60	0.705	6.310
MSH4	NF	1635	8.9	1.4	0.033	10.37	0.005	0.019	0.007	7.30	2.097	18.500
FP9	NF	1662	3.4	0.5	0.040	9.15	0.005	0.010	0.010	7.40	2.065	10.445
MA2	NF	2127	10.0	1.0	0.040	11.40	0.009	0.000	0.007	7.10	1.350	9.800
ML6	NF	1961	3.0	0.2	0.040	11.20	0.004	0.005	0.019	7.30	1.540	15.800
MM7	NF	1642	1.9	0.8	0.040	10.13	0.005	0.004	0.004	7.17	2.107	16.633
MR8	NF	1970	3.5	0.3	0.040	11.00	0.005	0.010	0.001	6.90	1.230	8.200
FP7	NF	1378	33.0	32.5	0.042	7.60	0.013	0.004	0.003	7.10	1.070	9.580

**Appendix I.** (continued)

Table C (continued). Lakes with water temperature < 12°C. NF = fishless lake; NRF = lake with non-reproducing trout; RF = lake with reproducing trout.

CODE	FISH	ELEV	MAX Z	S. AREA	TKN	TEMP	TP	NO3	NH3	PH	ALK	COND
MSH3	NF	1188	26.2	16.0	0.048	5.00	0.024	0.025	0.012	6.90	0.999	11.240
ML2	NRF	1687	27.4	3.4	0.013	8.43	0.003	0.004	0.019	7.80	2.838	30.380
PM1	NRF	1171	9.1	4.4	0.021	10.20	0.002	0.007	0.005	7.20	2.449	20.660
MR9	NRF	1813	4.9	1.7	0.024	11.88	0.006	0.002	0.007	6.93	1.293	9.867
EP5-1	NRF	1543	6.0	2.7	0.025	11.50	0.003	0.006	0.004	6.85	1.000	7.500
MC6	NRF	1601	21.3	5.2	0.032	11.05	0.002	0.013	0.010	6.65	0.788	6.660
MR13-2	NRF	1789	5.0	1.2	0.032	10.06	0.004	0.005	0.005	6.93	1.206	9.190
M19	NRF	1427	24.0	5.0	0.032	9.10	0.001	0.013	0.006	6.48	0.656	4.763
MC7	NRF	1556	27.2	6.7	0.035	9.80	0.006	0.004	0.006	7.15	1.790	29.450
DD5	NRF	1531	5.2	5.2	0.040	5.70	0.005	0.005	0.003	6.70	0.905	7.100
ML3	NRF	1967	15.2	1.3	0.040	10.25	0.004	0.001	0.006	7.30	1.570	14.500
MR1	NRF	2072	26.0	4.0	0.070	6.10	0.005	0.017	0.008	6.90	1.170	9.800
LS3-FS	NRF	1375	6.7	1.2	0.085	9.90	0.002	0.004	0.010	6.95	1.615	12.850
MR15-2	RF	1909	3.0	0.3	0.005	8.95	0.006	0.021	0.004	7.30	2.210	21.500
M21	RF	1205	3.1	1.6	0.010	8.40	0.000	0.059	0.000	7.20	2.190	17.500
MC12	RF	1769	46.3	11.4	0.012	11.30	0.003	0.016	0.004	6.60	0.726	5.660
EP6	RF	1566	19.8	3.0	0.024	10.90	0.003	0.004	0.007	6.40	0.699	4.900
MLY2	RF	1629	4.3	2.5	0.036	11.15	0.006	0.005	0.005	7.25	2.775	23.173
DD4	RF	1174	19.0	5.2	0.040	6.30	0.003	0.016	0.010	6.50	0.890	6.900
SM2-2	RF	1988	4.3	1.0	0.043	11.37	0.011	0.020	0.004	7.73	3.614	32.027
PM3	RF	1609	5.5	4.3	0.045	9.05	0.004	0.006	0.010	7.23	2.119	17.665
MR14	RF	1717	10.4	6.3	0.047	10.73	0.007	0.002	0.004	6.99	1.378	10.875
MC11-1	RF	1616	14.0	5.6	0.050	9.30	0.007	0.001	0.011	6.70	0.840	15.600