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Abundances of Northwestern Salamander Larvae in Montane Lakes With and Without Fish, Mount Rainier National Park, Washington

Abstract

In Mount Rainier National Park, the northwestern salamander usually inhabits relatively large and deep lakes and ponds (average size = 0.3 ha; average depth > 2 m) that contain flocculent, organic bottom sediments and abundant coarse wood. Prior to 1970, salmonids were introduced into many of the park's lakes and ponds that were typical habitat of the northwestern salamander. The objective of this study was to compare, in lakes and ponds with suitable habitat characteristics for northwestern salamanders, the observed abundances of larvae in lakes and ponds with and without these introduced salmonids. Day surveys of 61 lakes were conducted between 1993 and 1999. Fish were limited to lakes and ponds deeper than 2 m. For the 48 lakes and ponds deeper than 2 m (i.e., 25 fishless lakes and 23 fish lakes), the mean and median observed abundances of northwestern salamander larvae in fishless lakes and ponds was significantly greater than the mean and median observed abundances of larvae in lakes and ponds with fish. Northwestern salamander larvae were not observed in 11 fish lakes. These lakes were similar in median elevation, surface area, and maximum depth to the fishless lakes. The 12 fish lakes with observed larvae were significantly lower in median elevation, larger in median surface area, and deeper in median maximum depth than the fishless lakes. Low to null observed abundances of northwestern salamander larvae in lakes and ponds with fish were attributed to a combination of fish predation of larvae and changes in larval behavior.

Introduction

Salamander larvae are the top native aquatic vertebrate predators in many lakes and ponds in the Cascade Range of the Pacific Northwest (Taylor 1983; Tyler et al. 1998a). The two dominant taxa in the Cascades of Washington State are the long-toed salamander (*Ambystoma macrodactylum* Baird) and the northwestern salamander (*Ambystoma gracile* [Baird]) (Nussbaum et al. 1983). At North Cascades National Park Service Complex (NOCA) in northern Washington, only the long-toed salamander is present east of the hydrological divide of the Cascade Range. Long-toed salamander larvae occupy a wide variety of habitats ranging from shallow ephemeral ponds to deep lakes (Tyler et al. 1998a). Although both species are present on the west side of the divide, distribution of the northwestern salamander in NOCA is more restricted than the long-toed salamander (Nussbaum et al. 1983) and limited to the deeper lakes and ponds. On the west slope,

the long-toed salamander appears to be absent from lakes and ponds inhabited by the northwestern salamander (Liss et al. 1995). Compared to fishless systems, observed abundances of long-toed salamander and northwestern salamander larvae are reduced in lakes and ponds inhabited by introduced fish in NOCA (Liss et al. 1995; Tyler 1998a).

About 150 km south of NOCA, long-toed salamanders and northwestern salamanders are widely distributed in Mount Rainier National Park (MORA). The species are seldom sympatric (Brokes 2000). The long-toed salamander inhabits small, shallow ponds (mean size = 0.08 ha; mean depth = 0.6 m) with muddy or consolidated bottom sediments (Brokes 2000). The northwestern salamander typically inhabits larger, deeper systems (mean size = 0.3 ha; mean depth > 2 m) than does the long-toed salamander, and these systems have flocculent, organic bottom sediments and abundant coarse wood (Brokes 2000).

Reproducing populations of introduced salmonids, which were stocked prior to 1970, inhabit 27 of the deeper lentic systems at MORA (Barbara Samora, Mount Rainier National Park, personal communication). Thus, in MORA

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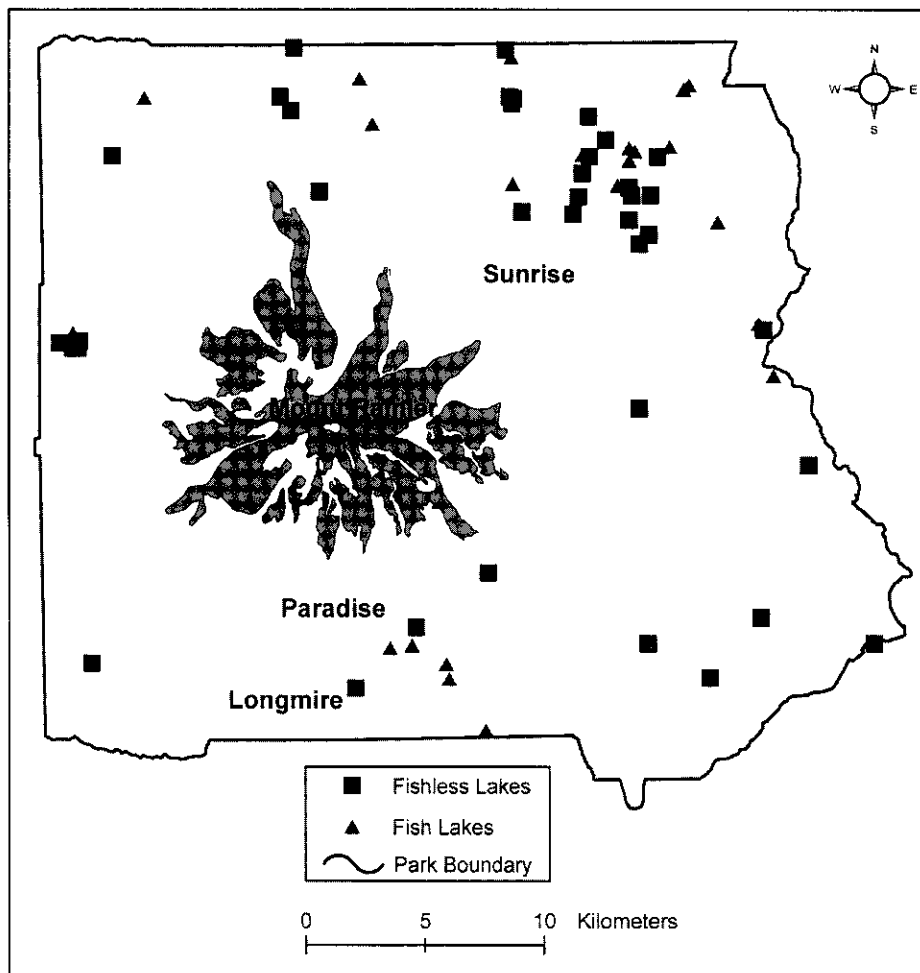


Figure 1. Location of 61 survey lakes in Mount Rainier National Park, Washington.

northwestern salamander larvae likely interact more with introduced fish than do long-toed salamander larvae. The objectives of this study were: 1) compare the observed abundances of northwestern salamander larvae in lentic systems with and without reproducing populations of introduced salmonids; and 2) determine if introduced salmonids have affected larval populations of the northwestern salamander.

Study Area

Mount Rainier National Park is located on the western slopes of the Cascade Range in south-central Washington State (Figure 1). Mount Rainier (4393 m) dominates the 969 km² park. The rugged, mountainous, volcanic terrain has a diver-

sity of climatic and geologic conditions, soils, and vegetation. Annual precipitation is ~ 150 cm at the lower elevations and > 250 cm at higher elevations. More than 75% of the precipitation falls as snow between October and March (Richardson 1972). Park lakes are covered with deep snow and granular ice in winter (Larson et al. 1994). The open-water season for lakes and ponds generally begins in late June to early July and lasts until October-November.

From 1993 through 1999, we surveyed 61 montane lakes and ponds across the landscape of MORA (Table 1; Figure 1) to document the observed abundances of northwestern salamander larvae in lentic systems with and without fish (Table 1). The presence of fish in a lake or pond was

TABLE 1. Physical attributes and larval salamander counts (number per 100 m) in 61 lakes, Mount Rainier National Park (MORA).

Parameter	Fishless Lakes	Fish Lakes
Number of lakes:	38	23
sampled in one year	32	17
sampled multiple years	6	6
Elevation (m):		
range	670–1772	974–1784
mean	1561	1493
median	1591	1492
Surface area (ha):		
range	0.05–5.32	0.11–7.33
mean	0.94	2.99
median	0.69	2.60
Maximum depth (m):		
range	0.4–20.0	2.6–29.0
mean	4.2	10.0
median	2.5	8.5
Larval counts:		
range	1.6–395.0	0–27.6
mean	76.8	6.4
median	58.1	0.3

determined either by direct observation of fish or, when the presence of fish was not obvious, through the use of gillnets set for several hours during a survey visit.

Methods

Forty-nine of the lakes and ponds in this study were sampled once from late July to early September between 1993 and 1999 (Table 1). Counts of salamander larvae for these lakes or ponds were extrapolated to the number of larvae observed per 100 m. Observed larval abundances for the 12 lakes and ponds sampled in multiple years (Table 1) are averages of the extrapolated counts for all survey years (Table 2). Larval counts in a lake can vary considerably from year to year. Therefore, counts based on averaging multiple year surveys may not adequately represent this variability (Table 2). Only lakes and ponds with habitat characteristics determined to be typical of MORA systems inhabited by northwestern salamander larvae, especially lakes and ponds with flocculent, organic bottom sediments, were included in this study.

We determined species distributions and the observed abundances of salamander larvae by visual encounter and snorkeling surveys (Thoms et al. 1997; Tyler et al. 1998a; Brokes 2000). Al-

TABLE 2. Variation of larval salamander counts (number per 100 m) in lakes surveyed in multiple years. Larvae were observed in all six fishless lakes and in only two of six fish lakes sampled in multiple years.

Lake	Fish Status	Years Sampled	Number	Annual Mean
LM23	Fishless	1996	94.3	
		1999	45.3	69.8
LM26	Fishless	1996	4.4	
		1999	79.3	41.8
LM30	Fishless	1996	42.5	
		1999	130.0	86.2
LM32	Fishless	1996	101.3	
		1999	11.3	56.3
LO26	Fishless	1997	69.1	
		1998	14.6	41.8
LZ31	Fishless	1996	13.3	
		1999	136.8	75.1
LC01	Fish	1997	5.1	
		1999	6.1	5.6
LM17	Fish	1996	0	
		1999	1.3	0.6

though care was taken to use each method as efficiently and effectively as possible, each survey method may have underestimated the actual abundances of larvae in the survey lakes or ponds. Therefore, larval counts were considered to represent the observed rather than actual relative abundance of salamander larvae in each system. Visual encounter surveys were used in two ponds that were too shallow to snorkel (<0.7 m) (Brokes 2000). These surveys were performed according to protocol described by Thoms et al. (1997), and involved searching for salamander larvae while slowly walking/wading the shoreline and nearshore area of each pond. Snorkel surveys were accomplished by swimming transects parallel to the lake or pond shoreline, recording larvae observed within a band extending from the shoreline to 2 m offshore.

Number Cruncher Statistical System 2000 (NCSS 2000) was used for all statistical analyses (Hintze 1998). Lakes were grouped according to the presence or absence of fish and maximum depth (i.e., < 2 m or ≥ 2 m). All lakes occupied by fish were ≥ 2 m in maximum depth since fish were typically introduced into deeper mountain lakes where they could survive winter lake conditions at high-elevation (Bahls 1992). Fishless lakes were grouped into lakes < 2 m and lakes ≥ 2 m maximum

depth. The grouping of fishless lakes into two depth categories was done so that the observed abundances of salamander larvae in fish lakes could be compared to the observed abundances in fishless lakes that were deep enough (i.e., ≥ 2 m) for fish survival if fish were to be introduced into these systems. One-way ANOVA (Hintze 1998) was used to compare the mean number of larvae observed per 100 m in fishless lakes ≥ 2 m maximum depth ($n = 25$) and fish lakes ($n = 23$). Kruskal-Wallis One-way ANOVA on Ranks (Hintze 1998) was used to compare the median number of larvae observed per 100 m in the fishless lakes ≥ 2 m maximum depth and the fish lakes. These tests were also used to compare the observed abundances of larvae in fishless lakes < 2 m ($n = 13$) with fishless lakes ≥ 2 m maximum depth. The level of significance for each analysis was $P = 0.05$. Kruskal-Wallis One-way ANOVA on Ranks (Hintze 1998) was also used to compare the median physical attributes of elevation, surface area, and maximum depth of the fishless lakes ≥ 2 m maximum depth with fish lakes with observed salamander larvae ($n = 12$) and fish lakes without observed salamander larvae ($n = 11$). The level of significance for these comparisons was Bonferroni adjusted to $P = 0.025$.

Results

Day surveys of 61 lakes at MORA indicated that the observed abundances of northwestern salamander larvae differed significantly between fishless lakes and lakes with fish (Table 1; Figure 2). The mean number of larvae observed in all fishless lakes ($n = 38$) was 12 times greater than in all fish lakes ($n = 23$), and the median number

of larvae observed in fishless lakes was quite large compared to the median number observed in lakes with fish (Table 1). Salamander larvae were observed in all fishless lakes surveyed, whereas of the 23 fish lakes surveyed, larvae were observed in 12 (52%) of the lakes.

The mean and median numbers of northwestern salamander larvae observed in the 25 fishless lakes ≥ 2 m maximum depth were significantly greater than the mean and median numbers of larvae observed in the fish lakes (mean: F-ratio = 25.52, $P < 0.001$; median: $\chi^2 = 28.4$, $P < 0.001$; Table 3). Abundances of ≥ 50 larvae per 100 m were observed in 16 (64%) of the fishless lakes ≥ 2 m maximum depth, and there were over 100 larvae per 100 m observed in six of these lakes. The highest number of larvae observed in the fish lakes was 27.6 per 100 m and this observed abundance was 11.5 times lower than the maximum observed abundance for the fishless lakes ≥ 2 m maximum depth. There were no significant differences in the mean and median numbers of larvae observed between the two categories of fishless lakes (Table 3).

TABLE 3. Larval salamander counts (number per 100 m) in fishless and fish survey lakes. Maximum depth is labeled Zmax, and asterisk signifies significant difference with fishless lakes, ≥ 2 m maximum depth.

	Lake Status		Fish All Lakes
	Fishless < 2 m Zmax	Fishless ≥ 2 m Zmax	
Number of lakes	13	25	23
Mean	78.9	75.7	6.4*
Median	41.8	69.8	0.3*
Range	1.6-395.0	5.8-314.4	0-27.6

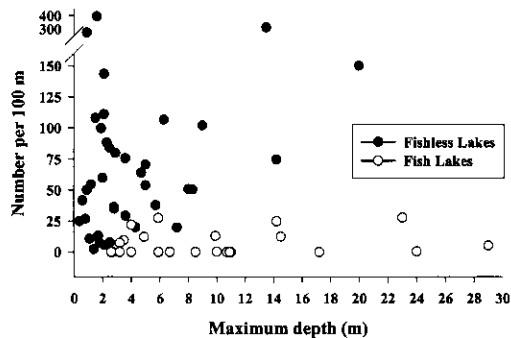


Figure 2. Observed abundances of northwestern salamander larvae in survey lakes of different depths and fish status, Mount Rainier National Park.

The physical attributes of survey lakes differed when compared by lake group. On average, the fishless lakes were higher in elevation, smaller in surface area, and shallower in maximum depth than the fish lakes (Table 1). These differences were significant between fishless lakes ≥ 2 m maximum depth ($n = 25$) and fish lakes in which salamander larvae were observed ($n = 12$). The fish lakes with observed salamander larvae were lower in median elevation ($\chi^2 = 5.84$, $P = 0.02$), larger in median surface area ($\chi^2 = 7.16$, $P = 0.007$), and deeper in median maximum depth ($\chi^2 = 6.66$, $P = 0.01$) than the fishless lakes ≥ 2 m maximum depth (Table 4). These attributes did not differ

significantly between the 11 fish lakes with no observed larvae and fishless lakes ≥ 2 m maximum depth (Table 4).

TABLE 4. Median physical attributes of survey lakes. Maximum depth is labeled Zmax, and asterisk signifies significant difference with fishless lakes ≥ 2 m maximum depth.

Attribute	Lake Status		
	Fishless ≥ 2 m Zmax	with larvae	Fish without larvae
Number of lakes	25	12	11
Elevation (m)	1654	1478*	1617
Surface Area (ha)	0.92	2.99*	2.12
Maximum depth (m)	4.3	9.9*	6.7

Discussion

Northwestern salamander larvae were not readily observed in lakes containing fish and we conclude that the observed abundances of larvae were significantly lower in fish lakes compared to fishless lakes (Table 3; Figure 2). Similar conclusions were reached in other studies of the observed abundances of northwestern salamander larvae in lakes with and without fish (Sprules 1974; Taylor 1983). In fact, no larvae were observed in 11 (48%) of the MORA lakes with fish, which suggests that fish either eliminated larvae from the lakes or larvae were extremely difficult to detect. These lakes were similar in elevation, size, and depth to fishless lakes ≥ 2 m maximum depth where salamander larvae were typically observed. Conversely, salamander larvae were observed in 12 fish lakes which were significantly lower in elevation, larger in surface area, and deeper in maximum depth than fishless lakes ≥ 2 m maximum depth. This result indicates that northwestern salamander larvae are able to co-exist with introduced fish in these larger and deeper systems.

We do not know, however, how representative these observed abundance estimates were of the actual size of the populations that were studied. In lakes and ponds with fish, estimates of northwestern salamander numbers can be low because larvae generally become less active and are capable of altering their diel pattern of behavior and habitat utilization in an effort to reduce exposure to predation (Efford and Mathias 1969; Sih 1987). Reducing exposure to fish predation may take the form of increased use of refugia such as coarse woody debris, rock talus, and aquatic vegetation

(Taylor 1983; Tyler et al. 1998b), which would reduce the visibility of salamander larvae to snorkelers. Northwestern salamander larvae also tend to be nocturnal in lakes and ponds that contain fish (Efford and Mathias 1969; Sprules 1974; Taylor 1983; Tyler et al. 1998a). In fact, the numbers of northwestern salamander larvae were 10 times higher at night than were counts obtained during day surveys in a NOCA lake with fish (Liss et al. 1995). Therefore, we conclude that the lower observed abundances of northwestern salamander larvae that we detected in MORA lakes with fish were due, in part, to a combination of direct fish predation on larvae and changes in larval behavior to avoid fish predation.

Northwestern salamander larvae were not typically associated with shallow ponds (i.e., < 2 m maximum depth) at MORA when the ponds were either ephemeral or when the composition of the bottom substrate was firm and inorganic (Brokes 2000). The shallow ponds inhabited by the larvae in this study had soft, organic bottom substrates. Introduced salmonids do not typically survive in ponds < 2 m depth. Thus, these shallow systems provided an additional refuge for northwestern salamander larvae from fish predation. Nonetheless, across the landscape of MORA, northwestern salamander larvae were able to persist in over 50% of the lakes with introduced salmonids.

The relationships between introduced fish and salamander larvae were different between MORA and NOCA, which raises some interesting management issues. At MORA, only northwestern salamander larvae were impacted by fish, although the present distribution of long-toed salamanders in MORA lentic systems could reflect past fish stocking patterns in park lakes. Larvae of both northwestern and long-toed salamanders were impacted by introduced salmonids at NOCA (Liss et al. 1995; Tyler et al. 1998a). Yet, in both parks the interaction between fish and salamander larvae was mostly related to the distributions of the two salamander species in the Pacific Northwest (Nussbaum et al. 1983) and their interspecific interactions (Hoffman and Larson 1999). Northwestern salamanders and long-toed salamanders have overlapping distributions at the landscape level at MORA, which is on the west side of the hydrological divide of the Cascade Range. In MORA, northwestern salamander larvae inhabit large, deep, permanent lakes in which fish can

survive, whereas long-toed salamander larvae are restricted to small, shallow, semi-permanent to permanent systems uninhabitable by fish (Brokes 2000). In NOCA, the northwestern salamander occurs only on the west side of the hydrological divide where its distribution is limited, whereas the long-toed salamander is widely distributed on both sides of the divide. For this reason, long-toed salamander larvae were able to inhabit larger and deeper lakes on the east side of NOCA that would have been occupied by northwestern salamander larvae at MORA. This pattern of salamander species distribution was a factor in the impact of both species by introduced fish at the landscape level at NOCA. These results suggest

that natural resource managers should be careful about transposing research information from one location to another.

Acknowledgements

We thank Barbara Samora, Mount Rainier National Park resource management specialist, for her ongoing support of this project. We also thank Brendan Brokes and his field crews for collecting the data. Financial support was provided by Mount Rainier National Park (Tahoma Woods, Star Route, Ashford, WA 98304) and the USGS Forest and Rangeland Ecosystem Science Center (3200 SW Jefferson Way, Corvallis, OR 97331).

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Received 14 May 2001

Accepted for publication 3 September 2001