Journal of Herpetology, Vol. 38, No. 4, pp. 578–585, 2004

Responses of *Ambystoma gracile* to the Removal of Introduced Nonnative Fish from a Mountain Lake

ROBERT L. HOFFMAN,[1,2] GARY L. LARSON,[1] AND BARBARA SAMORA[3]

[1]*United States Geological Survey, Forest and Rangeland Ecosystem Science Center, 777 Northwest 9th Street, Suite 400, Corvallis, Oregon 97330, USA; E-mail: robert_hoffman@usgs.gov*
[3]*Mount Rainier National Park, Tahoma Woods, Star Route, Ashford, Washington 98304, USA*

ABSTRACT.—**Introduced, nonnative brook trout (*Salvelinus fontinalis*) were removed from a mountain lake in Mount Rainier National Park, Washington, to examine the capacity of native *Ambystoma gracile* (Northwestern Salamander) in the lake to respond to the intentional removal of fish. Temporal trends ($\bar{\Delta}$N) were calculated for *A. gracile* larvae/neotene and egg mass relative abundances in the Fish Removal and an adjacent Fishless Lake. The diel and spatial patterns of *A. gracile* in the lakes were also enumerated during time-intervals of fish presence in and after fish removal from the Fish Removal Lake. Sixty-six fish were removed from the Fish Removal Lake. The $\bar{\Delta}$Ns for relative abundances in the Fish Removal Lake were positive for the study period and indicated that the number of larvae/neotenes and egg masses observed in the lake increased concurrent with the removal and extirpation of fish from the lake. Numbers of larvae/neotenes and egg masses observed in the Fishless Lake varied annually, but no overall positive or negative trends were evident during the study. *Ambystoma gracile* in the Fish Removal Lake, during fish presence, were predominantly nocturnal and located in the shallow, structurally complex nearshore area of the lake. After fish were removed, the number of *A. gracile* observed in the lake increased, especially during the day and in the deeper, less structurally complex offshore area of the lake. Fishless Lake *A. gracile* were readily observed day and night in all areas of the lake throughout the study. The *A. gracile* in the Fish Removal Lake behaviorally adapted to the presence of introduced fish and were able to recover from the affects of the fish following fish removal. This study underscores the important relationship between species life history and the variability of responses of montane aquatic-breeding amphibians to fish introductions in mountain lakes.**

The decline of amphibians worldwide has generated much interest in the potential for revitalizing or restoring perturbed species and populations (Semlitsch, 2002). Restoration efforts, however, can be complicated by the considerable variation in life-history requirements expressed by amphibian species and populations. This variability is, in part, caused by the diversity of habitats occupied by amphibians and the types of naturally occurring and anthropogenically created stressors affecting them. In the western United States, the widespread introduction of fish into naturally fishless mountain lakes has been a major source of perturbation of aquatic-breeding amphibian populations and other native fauna (Knapp et al., 2001a,b; Pilliod and Peterson, 2001). The primary focus of studies investigating interactions between introduced fish and native fauna in western mountain lakes has been on the negative impacts of fish, for example, the fragmentation, isolation, and extirpation of anuran populations in lakes of the Sierra Nevada of California (Bradford, 1989; Bradford et al., 1993; Knapp and Matthews, 2000; Matthews et al., 2001); decreased observed abundances of salamander populations in western mountain lakes (Tyler et al., 1998; Pilliod and Peterson, 2001; Larson and Hoffman, 2002); and reduction of large-bodied crustacean zooplankton densities in lakes of the northern Cascade Mountains of Washington (Liss et al., 1998) and the Sierra Nevada (Knapp et al., 2001b). Conversely, few if any studies have examined the capacity of western montane aquatic-breeding amphibian species and other native fauna to respond to and recover from the impacts of introduced fish after the intentional removal of fish from mountain lakes (see, for example, Vredenburg, 2004).

Although several aquatic-breeding amphibian species (e.g., *Ambystoma macrodactylum*, *Pseudacris regilla*, *Rana cascadae*, and *Rana muscosa*) have been excluded or eliminated from western mountain lakes by introduced fish (Bradford et al., 1993; Fellers and Drost, 1993; Funk and Dunlap, 1999; Knapp and Matthews, 2000; Matthews et al., 2001), other species (e.g., *Bufo boreas* and *Ambystoma gracile*) persist with introduced fish (Kiesecker et al., 1996; Petranka, 1998; Larson and Hoffman, 2002). Persistence in this context means the ability to maintain at least a minimal level of reproductive viability and recruitment in the presence of an introduced

[2] Corresponding Author.

predator. Species unable to persist in the presence of fish have life-history requirements and behavioral attributes that increase the risks associated with predation and compromise their ability to maintain viable populations (Sih, 1987; Kats et al., 1988; Pilliod and Peterson, 2001). Amphibian species that are able to coexist with fish express antipredator traits such as unpalatability and temporal-spatial behavioral shifts that can reduce predation pressure and risk (Sih, 1987; Kats et al., 1988).

Ambystoma gracile (Northwestern Salamander) is a common ambystomatid salamander species distributed throughout the Pacific Northwest (United States and Canada) that inhabits lakes with and without fish. Researchers have observed that, in lakes with fish, *A. gracile* abundances can be reduced (Larson and Hoffman, 2002) and that the *A. gracile* are almost exclusively nocturnal and active in shallow, structurally complex habitats (Efford and Mathias, 1969; Neish, 1971; Sprules, 1974; Taylor, 1983). In fishless lakes, *A. gracile* are active day and night, and habitat use is not restricted (Sprules, 1974; Taylor, 1983). *Ambystoma gracile* is a good example of a salamander species that can, through shifts in behavior, coexist with fish.

However, the response of salamanders (e.g., *A. gracile*) that inhabit lakes with introduced fish to the systematic removal of fish from the lakes has not, to our knowledge, been examined. In one study that did not involve the direct removal of fish, *A. macrodactylum* successfully recolonized mountain lakes after the introduced fish populations in the lakes had become extinct (Funk and Dunlap, 1999). To examine the capacity of salamanders to respond to the intentional removal of introduced fish from a mountain lake, we systematically removed brook trout (*Salvelinus fontinalis*) from a lake inhabited by *A. gracile* in Mount Rainier National Park, Washington. We also recorded the relative abundances of *A. gracile* larvae/neotenes and egg masses in this Fish Removal Lake and an adjacent Fishless Lake. The objectives of this study were to (1) calculate temporal trends in the abundances of larvae/neotenes and egg masses in the two lakes; (2) identify diel and spatial patterns of *A. gracile* in each lake; and (3) document responses of *A. gracile* in the Fish Removal Lake to the presence and absence of fish.

MATERIALS AND METHODS

Study Area.—The study lakes were located in the northeast quadrant of Mount Rainier National Park (Pierce County, Washington) approximately 4 km from Sunrise Visitor Center. The lakes were situated approximately 100 m apart along the Palisades Lakes Trail. The Fish Removal Lake (LW11) and the Fishless Lake (LW12) were similar in size (0.5 and 0.4 ha, respectively), maximum depth (4.0 and 2.5 m, respectively), and elevation (1732 and 1726 m, respectively). The nearshore area of each lake was dominated by sand-silt, organic detritus, and fine and coarse woody debris (primarily submerged logs). The offshore area of each lake was composed primarily of sand-silt covered by flocculent-organic material and occasional pieces of coarse woody debris.

Ambystoma gracile Life History.—*Ambystoma gracile* occurs from sea level to approximately 3000 m elevation on the west side of the hydrologic crest of the Cascade Range of the Pacific Northwest (Nussbaum et al., 1983; Leonard et al., 1993; Corkran and Thoms, 1996). The species is facultatively paedomorphic throughout its range. The frequency of neotenes (i.e., reproductively mature aquatic gilled adults) increases with elevation, and in Pacific Northwest mountain lakes, it is uncommon for individuals to transform to the terrestrial life stage (Snyder, 1956; Efford and Mathias, 1969; Eagleson 1976; Taylor, 1983). Larvae that do eventually transform can take up to three or more years to do so and range in size from 56–72 mm snout–vent length (SVL; Eagleson, 1976). The size range of neotenes in mountain lakes is approximately 80 to $\geq$ 94 mm SVL (Snyder, 1956; Hoffman et al., 2003). Montane *A. gracile* typically inhabit relatively large ($\geq$ 0.3 ha), deep ($\geq$ 2.0 m) lakes (Larson and Hoffman, 2002; Hoffman et al., 2003) and reproduce in late-June through July (Snyder, 1956; Efford and Mathias, 1969; Eagleson, 1976; Taylor, 1983; RLH, pers. obs.). Female neotenes attach firm, globular, gelatinous egg masses, 80–150 mm in diameter (Nussbaum et al., 1983), to branches of submerged coarse wood, and the egg masses are relatively easy to identify and observe (RLH, pers. obs.). Although transformed adult *A. gracile* can be noxious to predators, nontransformed individuals, especially larvae < 50 mm SVL, are relatively palatable to predators because of the limited development of glandular patches (Brodie and Gibson, 1969; Licht and Sever, 1993).

Fish Removal.—Fish removal efforts were conducted between approximately late June to mid–September 1993–1998. The Fish Removal Lake had been periodically stocked since the 1940s (unpublished park stocking records) and supported a minimally reproducing low-density population of introduced nonnative brook trout (*Salvelinus fontinalis*). The Fishless Lake was never stocked (unpublished park stocking records). Fish stocking in the park was discontinued in 1972.

Brook trout were removed from the Fish Removal Lake using monofilament gill nets that were 42 m long with 12.5, 18.5, 25, and 33 mm mesh panels 2 m deep. Brook trout were removed 1993–1995 by placing 1-3 gill nets in the lake for one to almost five hours during the day, once to several times during a field season. From 1996–1998, and in 1999 and 2002, 2–4 gill nets were placed in the lake from one to three days, once to several times during a field season. Nets remained in the lake overnight during multiple day fishing efforts. The Fishless Lake was gill netted once in 1993 to verify the absence of fish. No fish were caught, and no signs of fish activity were observed in the lake from 1993–2003.

Snorkel Surveys.—Snorkel surveys were conducted in the study lakes, 1993–2003 (Table 1), to quantify the observed relative abundances of *A. gracile* larvae/neotenes and egg masses. The *A. gracile* observed during surveys ranged in size from recent hatchlings (14–15 mm total length; Nussbaum et al., 1983) to neotenes and were labeled as larvae/neotenes since neotenes are gilled adults rather than larvae. The first survey of each field season was conducted as soon as the study lakes could be accessed following the melting of lake snow and ice cover (i.e., as early as 28 June and as late as 17 August). If a second survey was completed during a field season, it was performed 20–44 days after the first survey (Table 1). Day surveys were performed in the afternoon and night surveys, begun in 1996, were performed after sunset. Eighteen larvae/neotene day surveys were completed for the Fish Removal Lake, and 17 were completed for the Fishless Lake. Five larvae/neotene night surveys and 10 egg mass surveys were completed for both study lakes.

In all surveys, snorkelers counted the number of larvae/neotenes and/or egg masses observed in the open or hidden among lake substrates (e.g., rock, coarse wood, organic detritus). From 1993–1995, only day surveys were conducted in the nearshore area of each lake. These surveys were of varying length (ranges: Fish Removal Lake, 50–266 m; Fishless Lake, 40–100 m) and were accomplished by swimming a transect parallel to the shoreline of each lake. In 1996, surveys were standardized by randomly selecting in each study lake four nearshore transects parallel to the lake shoreline and two offshore transects perpendicular to the shoreline. Transects were 25 m long. Nearshore transect widths extended from the shoreline to approximately 2 m from shore. Offshore transects began 2 m from the shoreline and extended away from the shoreline to the center of the lake. The number of larvae/neotenes or egg masses observed in the four nearshore and two offshore transects constituted a complete survey (i.e., number/150 m).

The frequency of interaction between *A. gracile* in the study lakes was considered to be limited based on the reported high frequency of neotenic individuals inhabiting mountain lakes of the Pacific Northwest (Snyder, 1956; Efford and Mathias, 1969; Eagleson, 1976; Taylor, 1983) and the low occurrence of transformed adults observed in snorkel surveys completed in both lakes during the study (i.e., 7 per 2618 individuals observed or 0.3%). However, the presence of even this low number of transformed adults indicated that some larvae did metamorphose and were capable of moving between lakes.

TABLE 1. Temporal distribution of snorkel surveys, 1993–2003.

	Survey		
Year	Day	Night	Egg mass
1993	13 July, 24 Aug	none	13 July
1994	21 July, 22 Aug	none	21 July
1995	20 Sep	none	none
1996	9 July, 22 Aug	22 Aug	13 July
1997	22 July	13 Aug	22 July
1998	7 July, 27 July	2 Sep	7 July
1999	17 Aug, 14 Sep	none	17 Aug
2000	25 July, 29 Aug	30 Aug	25 July
2001	7 Aug	7 Aug	28 June
2002	23 July	none	23 July
2003	23 July, 26 Aug	none	23 July

Data Analysis.—Temporal trends for the relative abundances of *A. gracile* larvae/neotenes and egg masses observed in study lakes during surveys completed from 1996–2003 were calculated using the ΔN method developed by Houlahan et al. (2000). This method was originally used to quantitatively estimate temporal trends across multiple amphibian populations and has been shown to be a useful tool for estimating potential increases or declines in amphibian populations. The formulae used were

$$\Delta N = \log(N+1)_{t+1} - \log(N+1)_t, \quad (1)$$

for successive years, and

$$\bar{\Delta}N = \sum_{to}^{t} \Delta N/n, \quad (2)$$

to measure temporal trend.

All relative abundances for larvae/neotenes observed during day and night surveys and for egg masses were expressed as number/150 m/year. Larvae/neotene day survey relative abundances were averaged for years when more than one survey was completed (Table 1). A positive $\bar{\Delta}N$ indicated population increase and a population decline was indicated by a negative $\bar{\Delta}N$.

The relationship between fish presence-absence and the location (i.e., nearshore and offshore) of larvae/neotenes in the Fish Removal Lake during day and night surveys was examined using a 2 × 2 contingency table. The test statistic was chi-square with Yates' Correction for Continuity (see Fowler et al., 1998). Larvae/neotene relative abundances for two time inter-

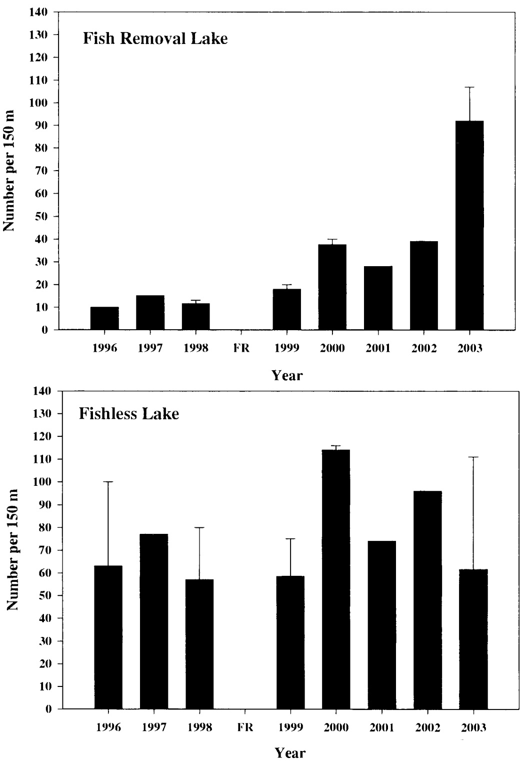

FIG. 1. Mean number of larvae/neotenes observed per year during day surveys in study lakes, 1996–2003. FR = Fish Removed and separates time intervals of fish presence in (1996–1998) and after all fish were removed from (1999–2003) the Fish Removal Lake. Error bars indicate standard error in years when two surveys were completed.

vals (i.e., fish present in and fish absent from the Fish Removal Lake) were expressed as mean/year/time-interval/area. The distribution of larvae/neotenes in the Fishless Lake were also examined by grouping surveys according to the two time intervals. Relative abundances were only used to compare within areas and not between them. The level of significance for this analysis was Bonferroni adjusted to $P = 0.0125$.

Larvae/neotene day and egg mass surveys completed during 1993–1995 were not used in either analysis because survey lengths during this time-interval were not standardized and only the nearshore area of the lakes was surveyed.

RESULTS

Fish Removal.—Sixty-six brook trout were removed from the Fish Removal Lake between 1993–1998. Fifty-four fish (82%) were removed in the first two years of gill netting (mean total length (TL) = 260 mm; range = 200–305 mm TL). Twelve additional fish (mean TL = 207 mm; range = 67–335 mm TL) were removed from the lake from 1995–1998. The last fish was removed on 2 September 1998 (241 mm TL, 245 g) and had an *A. gracile* larva (40 mm SVL) in its stomach. Gill nets also were placed in the lake during the day on 18 August 1999 and 5 September 2002. No fish were captured. No fish or indications of fish activity were observed during lake visits 2000–2003.

Snorkel Surveys, 1993–1995.—Few *A. gracile* larvae/neotenes or egg masses were observed in the Fish Removal Lake during daytime nearshore surveys completed from 1993–1994. Five larvae/neotenes were observed in one of four surveys (survey length range = 50–266 m) and 11 egg masses were observed in two surveys (survey lengths = 50 and 266 m). These surveys began when fish density in the Fish Removal Lake was at its highest and ended 22 August 1994 after 20 fish had been removed from the lake. In the Fishless Lake (1993–1994), 267 larvae/neotenes were observed during four surveys (survey length range = 40–100 m) and 102 egg masses were counted in two surveys (survey lengths = 40 and 100 m).

The number of larvae/neotenes observed on 20 September 1995 in the Fish Removal Lake during the daytime nearshore survey was substantially higher (i.e., 67/133 m) than the number observed during the previous surveys. This survey was completed one year after most of the fish had been removed from the lake. Individuals observed during this survey were predominantly > 60 mm SVL.

Temporal Trends, 1996–2003.—Temporal trends for *A. gracile* larvae/neotene (L/N) and egg mass (EM) relative abundances (i.e., number/150 m) in the Fish Removal Lake were each positive ($\bar{\Delta}N_{L/Nday} = 0.132 \pm 0.19$; $\bar{\Delta}N_{L/Nnight} = 0.091 \pm 0.48$; $\bar{\Delta}N_{EM} = 0.162 \pm 0.39$). The changes in day survey larvae/neotene and egg mass relative abundances between successive years were predominantly positive ($\Delta N_{L/Nday}$ = 5 of 7 years; ΔN_{EM} = 6 of 7 years; Figs. 1, 2), whereas positive and negative changes between successive years for night survey larvae/neotene relative abundances were evenly split (2 of 4 years, respectively; Fig. 3). The positive night survey $\bar{\Delta}N$ was primarily caused by the high number of larvae/neotenes observed during the 2001 survey, which was completed three years after all fish had been removed from the lake.

Temporal trends for larvae/neotene and egg mass relative abundances in the Fishless Lake were either slightly negative ($\bar{\Delta}N_{L/Nday} = -0.001 \pm 0.18$; $\bar{\Delta}N_{EM} = -0.005 \pm 0.23$) or positive ($\bar{\Delta}N_{L/Nnight} = 0.017 \pm 0.48$). The changes in relative abundances between successive years were either just positive ($\Delta N_{L/Nday}$ = 4 of 7 years; Fig. 1), just negative (ΔN_{EM} = 4 of 7 years; Fig. 2), or evenly split ($\Delta N_{L/Nnight}$ = 2 of 2 years; Fig. 3).

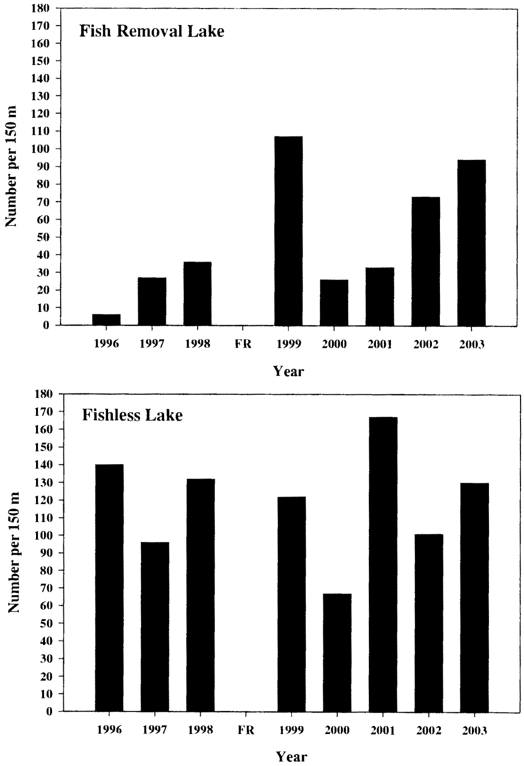

FIG. 2. Total number of egg masses observed during day surveys in study lakes, 1996–2003. FR = Fish Removed and separates time intervals of fish presence in (1996–1998) and after all fish were removed from (1999–2003) the Fish Removal Lake.

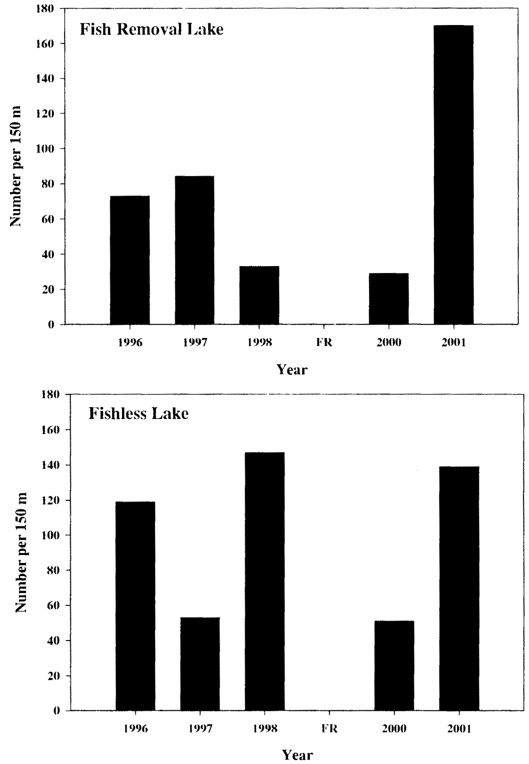

FIG. 3. Total number of larvae/neotenes observed during night surveys in study lakes, 1996–2001. FR = Fish Removed and separates time intervals of fish presence in (1996–1998) and after all fish were removed from (2000–2001) the Fish Removal Lake.

Larvae/Neotene within Lake Distributions, 1996–2003.—Mean numbers of larvae/neotenes per year observed in the nearshore and offshore areas of the Fish Removal Lake were significantly different between the time-intervals of fish presence in and absence from the lake (day surveys: $\chi^2 = 8.75$, df = 1, $P < 0.01$; night surveys: $\chi^2 = 8.99$, df= 1, $P < 0.01$). Mean relative abundances increased in the nearshore area during the day, and offshore, day and night, after all fish had been removed from the lake (Fig. 4). In the Fishless Lake, larvae/neotenes were relatively abundant in both areas of the lake (Fig. 4). Fishless Lake night survey mean relative abundances differed significantly between time intervals ($\chi^2 = 8.40$, df = 1, $P < 0.01$), decreasing in the nearshore area and increasing offshore, 2000–2001. However, the most salient aspect of *A. gracile* distribution in the Fishless Lake during the study was the relatively high presence of larvae/neotenes offshore, especially during the day (Fig. 4).

DISCUSSION

The temporal trends of *A. gracile* larvae/neotene and egg mass relative abundances were different in the study lakes. Relative abundances in the Fishless Lake varied annually (Figs. 1–3), but these fluctuations did not represent any overall positive or negative changes during the study. In contrast, the temporal trends for relative abundances in the Fish Removal Lake were each positive and represented overall increases in the number of larvae/neotenes and egg masses observed in the lake during the study (Figs. 1–3). These increases occurred concurrent with the removal and extirpation of the low-density brook trout population from the lake.

The diel and spatial patterns of *A. gracile* in the Fish Removal Lake also varied relative to the presence and absence of fish. In the presence of fish, *A. gracile* were primarily active at night almost exclusively in the nearshore area of the lake (Fig. 4). The few larvae/neotenes observed during day surveys (Fig. 1) were also located in the shallow, nearshore area (Fig. 4). These patterns have also been observed for *A. gracile* in

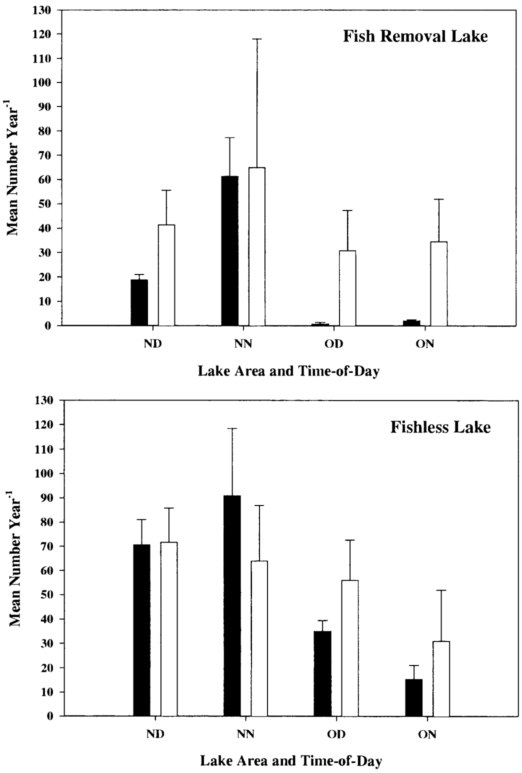

FIG. 4. Distribution of larvae/neotenes in study lakes during the time intervals of fish presence in (1996–1998) and after fish removal from (1999–2003, day; 2000–2001, night) the Fish Removal Lake. ND = nearshore day; NN = nearshore night; OD = offshore day; ON = offshore night. ■ = fish present; □ = after fish removed. Error bars indicate standard error.

other Pacific Northwest lakes inhabited by introduced fish (Efford and Mathias, 1969; Neish, 1971; Sprules, 1974; Taylor, 1983). After all fish had been removed from the Fish Removal Lake, the number of *A. gracile* observed during day surveys and offshore, day and night, increased (Figs. 1, 4). These changes indicated increased larvae/neotene diurnal activity and presence in a greater proportion of the lake. In the Fishless Lake, during the study, *A. gracile* were readily observed day and night throughout the lake (Figs. 1, 2, 4). The propensity for *A. gracile* to be active during the day and widely distributed in a lake has also been documented for larvae/neotenes in several other naturally fishless lakes in the Pacific Northwest (Sprules, 1974; Taylor, 1983).

Several other studies documented the ability of western montane lake amphibians to recover from the affects of introduced fish (Funk and Dunlap, 1999; Knapp et al., 2001b; Vredenburg, 2004). In two studies, *A. macrodactylum* and *R. muscosa* eliminated from lakes by introduced fish recolonized the lakes after the fish had gone extinct (Funk and Dunlap, 1999; Knapp et al., 2001b). However, the revitalization of these species in the lakes took up to 20 years or more. This lengthy interval of response and recovery from the affects of introduced fish has also been documented for diatom and zooplankton assemblages in mountain lakes (Drake and Naiman, 2000; Donald et al., 2001). In contrast, a recent study has shown that *R. muscosa* were capable of recovering relatively quickly (i.e., within three years) in mountain lakes after the intentional removal of introduced fish from the lakes (Vredenburg, 2004). This timely recovery was attributed to the closeness of large source populations of potential *R. muscosa* colonists to the impacted lakes.

The relative abundances of *A. gracile* larvae/neotenes and egg masses in the Fish Removal Lake increased during the 8+ years of the study, associated, in part, with the removal of brook trout from the lake. However, these increases may also have been the result of natural fluctuation or because of the relatively small sample size of the study. Additional lake-specific and population-level attributes that can help better define the intraspecific dynamics of montane *A. gracile* will need to be more fully understood before these results can be extrapolated to the landscape-level. These attributes include knowing (1) the rate of larval recruitment in mountain lakes with and without fish; (2) the frequency of metamorphosis in the lakes; and (3) the landscape-level movement patterns and frequency of terrestrial adult immigration into lakes with fish. The present study has clearly shown that resource managers and researchers interested in assessing and monitoring the status and trends of *A. gracile* in mountain lakes need to be aware of the capacity of this species to behaviorally adapt to the presence of fish. Night surveys, especially, should be included as an important assessment tool in fish-bearing lakes. Fundamentally, the severity of the impact of introduced fish on montane amphibians varies according to species. Therefore, survey designs and sampling protocols for amphibian monitoring and recovery programs should be based on the life-history characteristics and landscape-level population dynamics of the species of concern and be of sufficient duration to allow for the observation and quantification of site-specific and population-level recovery (Pilliod and Peterson, 2001; Semlitsch, 2002; Kats and Ferrer, 2003).

Acknowledgments.—We thank B. Warncke, B. Hasabe, M. Clancy, and the staff of the Aquatics section of the Natural and Cultural Resources Division, Mount Rainier National Park, for their quality assistance during this project and C.

Pearl for his helpful comments and suggestions. Thanks also to M. Boone and one anonymous reviewer for comments and suggestions that helped improve this manuscript. This research was funded by the USGS Forest and Rangeland Ecosystem Science Center in Corvallis, Oregon, and the National Park Service.

Literature Cited

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

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

Brodie Jr., E. D., and L. S. Gibson. 1969. Defensive behavior and skin glands of the Northwestern Salamander, *Ambystoma gracile*. Herpetologica 25: 187–194.

Corkran, C. C., and C. Thoms. 1996. Amphibians of Oregon, Washington, and British Columbia: A Field Identification Guide. Lone Pine Publishing, Renton, WA.

Donald, D. B., R. D. Vinebrooke, R. S. Anderson, J. Syrgiannis, and M. D. Graham. 2001. Recovery of zooplankton assemblages in mountain lakes from the effects of introduced sport fish. Canadian Journal of Fisheries and Aquatic Sciences 58:1822–1830.

Drake, D. C., and R. J. Naiman. 2000. An evaluation of restoration efforts in fishless lakes stocked with exotic trout. Conservation Biology 14:1807–1820.

Eagleson, G. W. 1976. A comparison of the life histories and growth patterns of populations of the salamander *Ambystoma gracile* (Baird) from permanent low-altitude and montane lakes. Canadian Journal of Zoology 54:2098–2111.

Efford, I. E. and J. A. Mathias. 1969. A comparison of two salamander populations in Marion Lake, British Columbia. Copeia 1969:723–735.

Fellers, G. M., and C. A. Drost. 1993. Disappearance of the Cascade Frog, *Rana cascadae*, at the southern end of its range, California, USA. Biological Conservation 65:177–181.

Fowler, J., L. Cohen, and P. Jarvis. 1998. Practical Statistics for Field Biology. 2nd ed. John Wiley and Sons, Chichester, U.K.

Funk, W. C., and W. W. Dunlap. 1999. Colonization of high-elevation lakes by Long-Toed Salamanders (*Ambystoma macrodactylum*) after the extinction o introduced trout populations. Canadian Journal of Zoology 77:1759–1767.

Hoffman, R. L., G. L. Larson, and B. J. Brokes. 2003. Habitat segregation of *Ambystoma gracile* and *Ambystoma macrodactylum* in mountain ponds and lakes, Mount Rainier National Park, Washington, USA. Journal of Herpetology 37:24–34.

Houlahan, J. E., C. S. Findlay, B. R. Schmidt, A. H. Meyer, and S. L. Kuzmin. 2000. Quantitative evidence for global amphibian population declines. Nature 404:752–755.

Kats, L. B., and R. P. Ferrer. 2003. Alien predators and amphibian declines: review of two decades of science and the transition to conservation. Diversity and Distributions 9:99–110.

Kats, L. B., J. W. Petranka, and A. Sih. 1988. Antipredator defenses and the persistence of amphibian larvae with fishes. Ecology 69:1865–1870.

Kiesecker, J. M., D. P. Chivers, and A. R. Blaustein. 1996. The use of chemical cues in predator recognition by Western Toad tadpoles. Animal Behaviour 52:1237–1245.

Knapp, R. A., and K. R. Matthews. 2000. Non-native fish introductions and the decline of the Mountain Yellow-Legged Frog from within protected areas. Conservation Biology 14:428–438.

Knapp, R. A., P. S. Corn, and D. E. Schindler. 2001a. The introduction of nonnative fish into wilderness lakes: good intentions, conflicting mandates, and unlimited consequences. Ecosystems 4:275–278.

Knapp, R. A., K. R. Matthews, and O. Sarnelle. 2001b. Resistance and resilience of alpine lake fauna to fish introductions. Ecological Monographs 71: 401–421.

Larson, G. L., and R. L. Hoffman. 2002. Abundances of Northwestern Salamander larvae in montane lakes with and without fish, Mount Rainier National Park, Washington. Northwest Science 76:35–40.

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

Licht, L. E., and D. M. Sever. 1993. Structure and development of the parotid gland in metamorphosed and neotenic *Ambystoma gracile*. Copeia 1993:116–123.

Liss, W. J., G. L. Larson, E. A. Deimling, L. M. Ganio, R. L. Hoffman, and G. A. Lomnicky. 1998. Factors influencing the distribution and abundance of diaptomid copepods in high-elevation lakes in the Pacific Northwest, USA. Hydrobiologia 379:63–75.

Matthews, K. R., K. L. Pope, H. K. Preisler, and R. A. Knapp. 2001. Effects of nonnative trout on Pacific Treefrogs (*Hyla regilla*) in the Sierra Nevada. Copeia 2001:1130–1137.

Neish, I. C. 1971. Comparison of size, structure, and distributional patterns of two salamander populations in Marion Lake, British Columbia. Journal of the Fisheries Research Board of Canada 28:48–58.

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

Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, DC.

Pilliod, D. S., and C. R. Peterson. 2001. Local and landscape effects of introduced trout on amphibians in historically fishless watersheds. Ecosystems 4:322–333.

Semlitsch, R. D. 2002. Critical elements for biologically based recovery plans of aquatic-breeding amphibians. Conservation Biology 16:619–629.

Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. *In* W. C. Kerfoot and A. Sih (eds.), Predation, Direct and Indirect Impacts on Aquatic Communities, pp. 203–224. Univ. Press of New England, Hanover, NH.

Snyder, R. C. 1956. Comparative features of the life histories of *Ambystoma gracile* (Baird) from populations at low and high altitudes. Copeia 1956:41–50.

Sprules, W. G. 1974. The adaptive significance of paedogenesis in North American species of *Ambystoma* (Amphibia: Caudata): an hypothesis. Canadian Journal of Zoology 52:393–400.

Taylor, J. 1983. Orientation and flight behavior of a neotenic salamander (*Ambystoma gracile*) in Oregon. American Midland Naturalist 109:40–49.

Tyler, T. J., W. J. Liss, L. M. Ganio, G. L. Larson, R. Hoffman, E. Deimling, and G. Lomnicky. 1998. Interaction between introduced trout and larval salamanders (*Ambystoma macrodactylum*) in high-elevation lakes. Conservation Biology 12:94–105.

Vredenburg, V. T. 2004. Reversing introduced species effects: experimental removal of introduced fish leads to rapid recovery of a declining frog. Proceedings of the National Academy of Sciences 101:7646–7650.

Accepted: 31 August 2004.