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Fluctuation in a Rocky Mountain Population of Salamanders: Anthropogenic Acidification or Natural Variation?

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ABSTRACT.— **We monitored the demographics of the salamander *Ambystoma tigrinum nebulosum* as part of a community-wide study on the effects of acidification in sub-alpine (elevation 3600 m) ponds in central Colorado. A decline in *A. t. nebulosum* at this site from 1982 to 1988 has been hypothesized to result from embryonic mortality during a pulse of acidity that accompanies snowmelt in spring. Since 1988 we have monitored salamander population size, reproduction, and recruitment, and compared survival and individual growth rates among ponds which differ five-fold in acid-neutralizing capacity (ANC).**

Larval recruitment fluctuated dramatically from year to year, but we found no evidence that survival of either embryos or larvae was affected by pH. In each year, the pulse of snowmelt acidification was either benign, or occurred earlier than egg deposition. During 1990 and 1991 we followed individual egg masses and found that embryonic survival was high in all ponds and did not differ between high and low ANC ponds. In permanent ponds, survival of first-year larvae was high and independent of pH. Within cohorts, second-year larvae were actually larger in ponds with low ANC than in high ANC ponds. The largest source of mortality in the population between 1988 and 1991 was related to pond drying; about half of all hatchlings that survived to July perished in autumn when many of the ponds dried. Our results suggest that fluctuation in hydroperiod is as viable a working hypothesis as snowmelt acidification for the recent decline in this population. Our water chemistry data show that many ponds at Mexican Cut remain poorly buffered and that this acid-sensitive watershed should continue to be closely monitored.

The apparent decline of numerous amphibian populations has recently attracted considerable attention in the scientific and popular literature (Barinaga, 1991; Blaustein and Wake, 1990; Cowen, 1990; Phillips, 1990; Wyman, 1990; Wake, 1991; Pechmann et al., 1991). Although there are few data on the relative importance of purported causes, habitat acidification is often cited as a likely culprit. This is especially true in northeastern North America where chronic acidification of surface waters is well documented (Schindler, 1988; Schindler et al., 1989; Tan, 1989; Baker et al., 1991), and where the negative effects of acidification on amphibian habitat choice, breeding success, egg mortality, and larval growth have been studied most extensively (see reviews by Pierce, 1985; Freda, 1986; Freda et al., 1991).

Acidic deposition is less severe in western North America than in northeastern areas and chronic acidification of aquatic habitats does not appear to be widespread (Turk and Campbell, 1987; Schindler, 1988; Vertucci, 1988; Eilers et al., 1989; Turk and Spahr, 1991). However, many montane habitats in western North America are vulnerable to acidification because of thin soils and crystalline bedrock (Dodson, 1982; Melack et al., 1982; Kling and Grant, 1984; Tonnessen, 1984; Harte et al., 1985; Landers et al., 1987). There is evidence that natural waters in some areas are episodically acidified during peak snowmelt or other runoff events (Lewis and Grant, 1979, 1980; Grant and Lewis, 1982; Blanchard et al., 1987; Harte and Hoffman, 1989). Declines in amphibian populations have been documented in western North America, but

acidification does not appear to be the causal factor in most cases (Corn and Fogleman, 1984; Hayes and Jennings, 1986; Bradford, 1989; Corn et al., 1989; Corn and Vertucci, 1992). The best evidence linking amphibian decline to acidification in western North America is presented by Harte and Hoffman (1989) for a high-altitude population of the salamander *Ambystoma tigrinum nebulosum* in central Colorado. They hypothesized that low recruitment and a decreasing total population size at their study site during the 1980s was due to embryonic mortality caused by an acidic pulse that accompanied snowmelt in some but not all years.

Since August, 1988, we have been monitoring the same salamander population that Harte and Hoffman (1989) studied. In this paper we report on the status of this *Ambystoma* population and assess the impact of acidification on salamander demography during the past four years. Our results, combined with those of Harte and Hoffman (1989), provide 10 years of census data which we use to assess whether trends in population size are the result of acidification or are related to long-term fluctuations in survival and recruitment due to natural or other anthropogenic causes (Pechmann et al., 1991; Freda et al., 1991). The data reported here are part of a long-term and community-wide study to assess the effects of acidification on this remote watershed.

Methods

Study Site.—The Mexican Cut Nature Preserve contains a series of 25 subalpine (3600 m) ponds located in the Elk Mountains of south-central Colorado. This pristine watershed is owned by The Nature Conservancy and is managed by the Rocky Mountain Biological Laboratory. The "lower shelf" of the preserve contains 19 ponds (L1–L19) which lie in close proximity but differ in hydroperiod, acid-neutralizing capacity, (ANC), and community composition (Fig. 1). We categorized the ponds into three hydroperiod patterns: (1) vernal ponds are small, shallow depressions in the rocks that dry each year in July–August; (2) semi-permanent ponds are larger and may or may not dry during late autumn in a given year; and (3) permanent ponds are those that have remained aquatic for at least the past 50 years (R. Willey, pers. comm.). During snowmelt many of the ponds are interconnected to form three drainages that differ in water chemistry. The drainage that flows through ponds L1-L5-L18 receives runoff that flows over local outcrops of metamorphosed limestone, and these ponds therefore have higher ANC (August 1991 $\bar{x}$ = 243.2 ± 33.9 SD) than the ponds in the other two drainages which are underlain by quartzite (L12–L9 $\bar{x}$ = 40.4 ± 13.5 SD, and L8–L6 42.5 ± 14.1 SD).

Water Chemistry.—We measured pH during 1989, 1990, and 1991 in all ponds and streams in the Mexican Cut watershed using an Orion 25A portable pH meter with temperature compensation. Initially we sampled all ponds at six different locations including different depths and distances from shore. We found negligible variability and subsequently reduced our sampling to three recordings at one location in each pond (usually the outflow). During 1991, biweekly or monthly replicate water samples were taken from each pond from ice-out in spring to ice-cover in fall (or until they dried) for chemical analysis at the USDA-Forest Service Biogeochemistry Laboratory in Fort Collins, Colorado (EPA approved adherence to QA/QC protocols). The pH values reported for these water samples corresponded well to those measured on the same date with the portable meter. Water chemistry data for the lower shelf ponds at Mexican Cut in 1991 are summarized in Appendix 1.

Salamander Natural History.—The ponds on the lower shelf at Mexican Cut contain a rich biota including a diverse benthic invertebrate community (Wissinger, unpubl. data) and a well-studied zooplankton assemblage (Dodson, 1970, 1974; Sprules, 1972). Adult and larval tiger salamanders, *Ambystoma tigrinum nebulosum*, are the only aquatic vertebrates in the ponds. Previous studies have shown that the presence and abundance of *A. t. nebulosum* larvae and paedomorphs as top predators play an important role in maintaining interpond differences in zooplankton community composition (Dodson and Dodson, 1971; Sprules, 1972; Dodson, 1974). There is also evidence that the salamanders play an important role in maintaining interpond differences in benthic community structure (Wissinger, unpubl. obs). This study site is near the maximum upper elevational limit known for *A. t. nebulosum* (Behler and King, 1979).

The population is uniquely stage-structured (sensu Wilbur, 1984) with both metamorphic (transformed) and paedomorphic (reproductively mature larvae) adults, and three to four year-classes of immature larvae. In contrast to lower elevations where larval development is completed in one season, larvae at Mexican Cut require a minimum of 14 months to metamorphose, and many larvae do not transform until the third or fourth summer (Whiteman and Wissinger, unpubl. data). Because of this elongated life cycle, we have the opportunity to study the possible effects of acidification on a variety of life stages (eggs, hatchlings, 2nd–4th year larvae, metamorphic adults, and paedomorphic adults) of the same species.

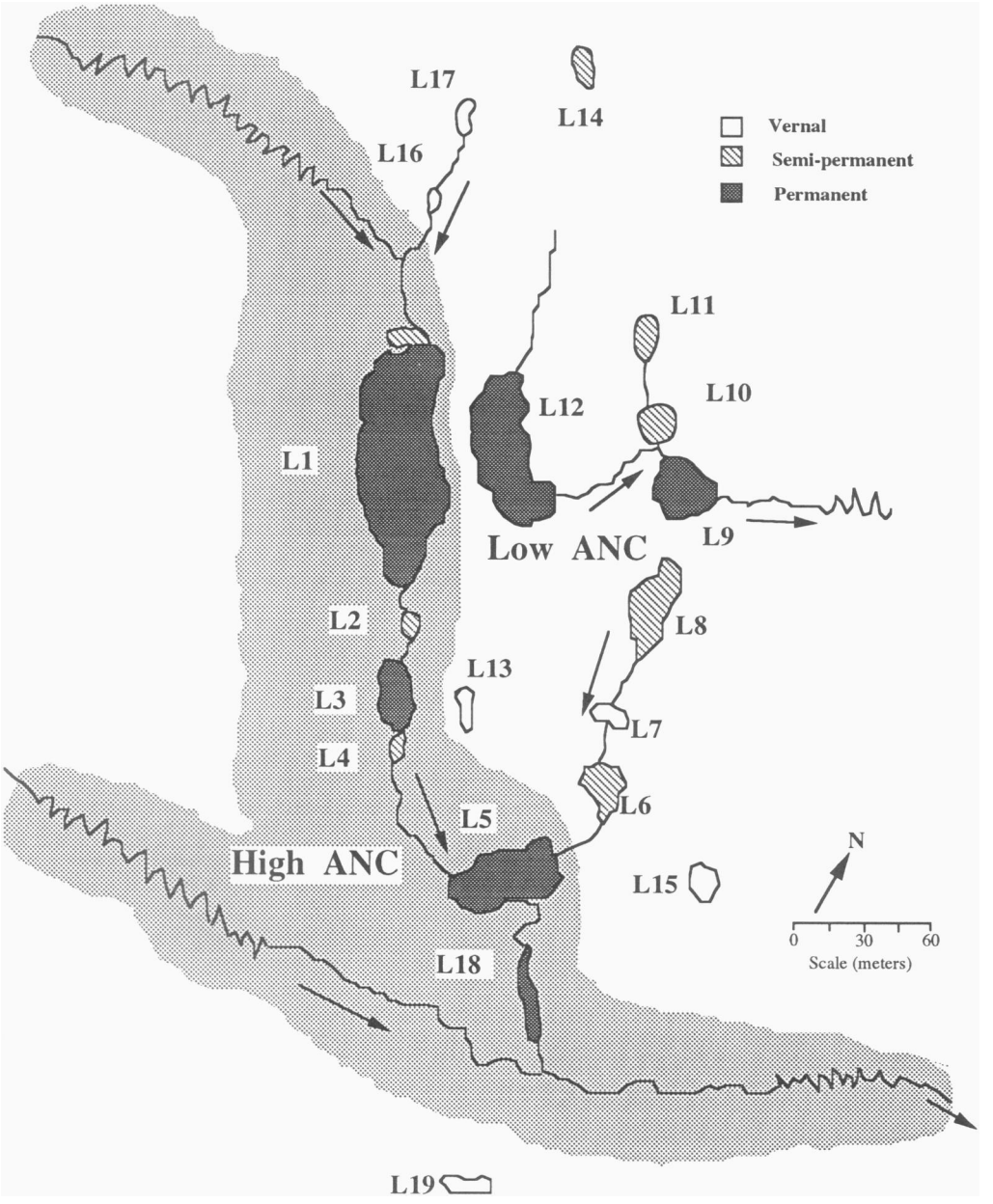

FIG. 1. Schematic map of the lower shelf drainages at the Mexican Cut Nature Reserve. Vernal ponds dry each year during summer, semi-permanent ponds may or may not dry in a given year during late autumn, and permanent ponds have remained aquatic for at least the past 50 years. The shaded area indicates ponds with high (200 to 300 μeq/L) ANC as compared to that of the other ponds on the lower shelf (<10 to 70 μeq/L) (see also Appendix 1).

Salamander Censuses.—We censused the Mexican Cut salamander population in several ways. Since 1989 we have been marking individual metamorphs, paedomorphs, and 2–4 year old larvae with unique toe clips. Individual salamanders were caught by hand or with long-handled nets from shore or from an inflatable raft. We measured snout-vent length (SVL; tip of snout to posterior margin of cloaca), mass, and gape width, and recorded sex, morph or

larval age class, and physical condition. Continuous mark-and-recapture allowed us to monitor the location, movements, and growth of individuals as well as population estimates of density and survival. Population sizes of both adult morphs were determined by total population counts of marked animals, and numbers of 2nd–4th year larvae were estimated by mark-recapture using a Lincoln-Peterson index (Southwood, 1978).

Because of their small size, hatchlings were not individually marked. During 1988 and 1989, we estimated minimum hatchling recruitment in July (when larvae are less damaged by handling) by removing a large fraction of the hatchlings from each pond, and then conducting a visual census of remaining larvae. This technique undoubtedly underestimated recruitment in the large ponds, but was effective in the small shallow ponds where most or all larvae were easily captured and/or sighted. Because two of the large ponds are in the high ANC drainage (L1 and L5) and two are in the low ANC drainages (L12 and L9), our findings in relation to water chemistry should be equally biased by this census technique. In 1990 and 1991 we improved our technique for estimating the number of hatchlings by conducting Lincoln-Peterson mark-recapture censuses on hatchlings marked with a small clip in the dorsal fin of the tail.

We also monitored egg masses to determine if differences in pH or ANC influenced embryonic survival. During the breeding season in 1990 and 1991 (mid-June to early July), we searched each pond for the presence of eggs laid on sticks, submerged stems, or on the pond bottom. Each group of eggs was marked with an identification tag and monitored every other day for abnormal development and survival. "Normal" embryos were those that hatched from dorsally dark embryos; "deformed" eggs were opaque white with signs of abnormal or interrupted development (Whiteman, unpubl. obs.; Harte and Hoffman, 1989).

Statistical Analyses.—We used SPSS/PC for all statistical analyses (Norusis 1990). A two-way ANOVA was conducted for the effect of date and ANC (high, low) on pond pH and to compare larval survival among ponds. One-way ANOVA was used to compare larval growth rates between high and low ANC ponds. Differences between treatment means in the one-way ANOVA were inferred using Tukey's a posteriori compromise test. For all ANOVAs we found no serious deviations from normality and in all cases variances were homoscedastic (all Bartlett Box tests not significant; $P > 0.05$). Single and multiple linear regression models were used to quantify the effects of abiotic habitat characteristics (pH, pond area, ice cover, and temperature) on habitat choice by terrestrial adults during the breeding season. A chi-square test was used to compare the proportion of embryos that died in high vs. low ANC ponds.

Results

Phenology of Snowmelt and pH Pulse.—In 1989, 1990, and 1991 peak snowmelt and runoff at Mexican Cut occurred during late-May to mid-June. The ice on the surface of the ponds began to melt during the last two weeks of this period. The ponds that melted earliest each year (e.g., L8, L9, L13, L16) were usually ice-free by the third week of June, and all ponds were completely ice-free by the fourth week of June. The order of melting was similar in each year with small and/or exposed ponds melting earliest and large and/or shaded ponds latest.

During ice melt in June 1991, we monitored the pH of runoff from remnant snowpacks surrounding the largest permanent (L1) and semi-permanent (L8) ponds. The pH of snowmelt (temp. 2.0–3.5 C) entering these ponds as overland flow in June was consistently near 5.8 ($\bar{x} = 5.83 \pm 0.10$ SD; $N = 8$). The pH in low ANC ponds during this period in 1991 averaged 5.8, whereas that of the high ANC ponds averaged 6.4 (Fig. 2). In all 3 years, average pH was lower in the low ANC drainages (L6–12) during ice melt than those in the high ANC drainage (Fig. 2; Table 1). The pH increased in all ponds during summer, but the springtime difference between drainages persisted through autumn. Thus, there was no interaction between the effects of date and ANC on pH (Table 1).

Pond pH, Egg Deposition, and Embryonic Development.—Terrestrial adult salamanders first appeared at the ponds during the second week of June in each of the three years of the study. During the 3rd and 4th weeks of June of each year, adults bred and deposited eggs in all but the two smallest (L2, L4) semi-permanent ponds in the main drainages. Although ponds differed during this period in percent ice cover, temperature, and pH, regression analysis indicated that the number of breeding metamorphs was not significantly affected by any of these abiotic variables (Table 2).

During egg deposition and throughout the subsequent 3 weeks of embryonic development in 1989 and 1991, pH was always >6.5 and >6.0 in the high and low ANC ponds, respectively (Fig. 2). In 1990, pH in the low ANC ponds dropped during the first week of July to 5.5–5.7, but we found no evidence that this affected embryonic development or survival. Embryonic mortality in 1990, as measured by the number of dead eggs within egg masses, did not differ between low alkalinity (13/157 = 8%) and

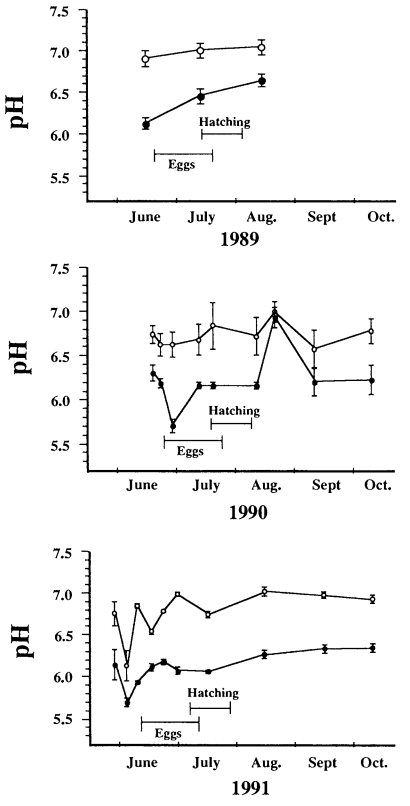

FIG. 2. pH in high (open circles) and low (closed circles) ANC ponds at the Mexican Cut Nature Reserve during 1989, 1990 and 1991. The phenology of salamander breeding, egg development, and larval hatching are superimposed on the pH data.

high alkalinity ponds (2/54 = 11%) (chi-square = 1.0, $P = 0.315$). In 1991, only 1 out of 254 eggs that we monitored was abnormal, and that egg occurred in a high ANC pond (L5).

Abundance, Survival, and Growth of Salamanders.—The estimated total number of hatchlings varied among years ranging from a high of 3126 in 1988 to a low of 870 in 1989 (Table 3). Two-way ANOVAs for the effects of ANC and pond permanence in each year and for the pooled data across all years revealed that the density of hatchlings in August did not differ between the high and low ANC drainages (pooled data $F = 0.31$, $P = 0.58$, df 1,36). However, across both years, the density of hatchlings was higher in semi-permanent than in permanent ponds ($F = 12.5$, $P < 0.001$, df 1,36). The two-way interaction (permanence × ANC) was not significant ($F = 0.69$, $P = 0.41$, df 1,36).

We also compared our estimates of larval survival from August of the first year to the following June as a function of ANC and pond permanence. Although we found no difference

TABLE 1. Two-way ANOVA for pond pH by date and ANC (low, high) in 1990 and 1991 at the Mexican Cut Nature Reserve.

Source of variation	Degrees of freedom	Mean square	F	P
		1990		
Main Effects				
Date	7	0.65	7.0	<0.001
ANC	1	6.06	65.9	<0.001
Interaction				
Date × ANC	7	0.18	1.9	0.07
Error	84	0.09		
		1991		
Main Effects				
Date	9	1.46	8.9	<0.001
ANC	1	0.38	282.5	<0.001
Interaction				
Date × ANC	9	0.07	1.8	0.08
Error	87	0.04		

in survival between the low and high ANC drainages ($F = 0.236$, $P = 0.632$, df 1,23), survival was dependent on hydroperiod. Across all cohorts (1988, 1989, 1990), survival was much higher in the permanent ponds than in semi-permanent ponds (Fig. 3; $F = 30.1$, $P < 0.001$, df 1,23). Over the three year period, the survival of first year larvae from August until the following June averaged 84% in the permanent ponds as compared to <2% in the semi-permanent ponds. From 1988 to 1990 nearly half of all first year larvae perished as a result of pond drying in autumn. Direct observations made in October, 1989 (S. Lohr, unpubl. obs.), and October, 1990 (C. Anderson, S. Wissinger, H. Whiteman, unpubl. obs.) revealed that larvae either died from desiccation or were preyed on by gray jays (*Perisoreus canadensis*) as the ponds dried in late October.

Because losses due to mortality are confounded by losses due to metamorphosis, we cannot reliably estimate survival of older larvae after July of their second summer of growth. However, we could compare body sizes (SVL) of third year larvae in permanent ponds with high vs. low ANC for the 1988 cohort in 1990, and for the 1990 cohort in 1991. For both the 1989 and 1991 cohorts, larvae were larger in low than in high ANC ponds (Fig. 4). We could not make this comparison for the 1989 cohort because recruitment was negligible in all but one of the permanent ponds (L1, see Fig. 3).

DISCUSSION

Salamander Survival and Acid Pulse.—During the 4 years of this study, the acid pulse associated with spring snowmelt at Mexican Cut

TABLE 2. Habitat conditions during salamander breeding and egg development at Mexican Cut in spring 1991. Single and multiple regression analyses for the effects of pond area, percent ice cover, pH, and temperature (C) on number of breeding metamorphs were not significant (all $P > 0.05$). The F statistics, significance values, and coefficients of determination below the table are from single regressions.

	2nd week of June adult metamorphs arrive at ponds					3rd–4th wk June deposit eggs		4th wk June to 3rd wk July embryo develop.	
Pond	Number of meta-morphs	Area (m^2)	% Ice cover	Temp. (6/18)	pH	Temp. (6/25)	pH	Temp. (7/15)	pH
L1	12	4647	95	3.1	6.49	10.0	6.72	19.5	6.83
L3	2	124	85	4.5	6.52	10.4	6.77	16.8	6.74
L5	3	1047	80	5.3	6.52	11.6	6.76	16.2	6.82
L6	3	195	0	10.5	5.93	15.3	6.05	16.0	6.03
L8	16	465	10	8.5	6.18	16.5	6.26	17.0	6.02
L9	12	593	5	10.5	6.17	16.0	6.27	18.7	6.09
L10	5	209	60	5.3	6.17	12.5	6.24	15.6	6.13
L11	9	197	10	8.0	6.10	13.4	6.21	17.0	6.12
L12	9	1708	25	10.0	6.24	16.8	6.26	17.7	6.11
Regression Statistics	F	1.62	1.02	0.45	0.46				
	P	0.33	0.35	0.72	0.64				
	r^2	0.61	0.12	0.21	0.13				

was either negligible or occurred prior to salamander breeding and embryo development. This conclusion was reached independently during the same period by J. Harte (unpubl. obs.). This is in contrast to several years during the period from 1982–1988 when pH dropped to 5.0 or lower in both high and low ANC ponds (Harte and Hoffman, 1989). The exact timing of snowmelt relative to egg deposition is critical because pH minima are typically reached during the earliest phases of snowmelt when most of the chemical constituents in the snowpack are released (Denning et al., 1991). In 1989, 1990, and 1991, egg deposition occurred at the end of the snowmelt period at Mexican Cut and pH levels in the snowmelt entering the ponds (5.8–6.0) were higher than those shown to have a negative effect on embryo development (Harte and Hoffman, 1989). The moderate levels of pH near the end of the melt season at Mexican Cut are consistent with the idea that late-season runoff is unlikely to acidify surface waters because most of the chemical constituents are lost from the snowpack earlier in spring (Denning et al., 1991).

During our study, metamorphic salamanders did not preferentially select among the 10 breeding ponds based on ANC or pH, and there was no significant difference in egg survival between high and low alkalinity ponds. This was not surprising for 1989 and 1991, when pond pH was always greater than 6.0 during this vulnerable period of the life cycle. Although recruitment was lowest in these two years (Table 3), pH values during breeding and egg development were always greater than those that result in significant egg mortality in toxicity tests (≤ 5.7; Harte and Hoffman, 1989). In 1990, a relatively strong recruitment year, pH values in the low ANC ponds dropped briefly to between 5.5–5.7, but we could not detect any effect on egg mortality. During our study it did

TABLE 3. Population sizes of *A. tigrinum* at the Mexican Cut Nature Preserve during 1988–1991. The population total in 1988 does not include metamorphs which had emigrated to the terrestrial environment before our first census in August of that year. Data prior to 1990 are based on the number of collected animals + visual estimate of the numbers not caught. Most values for 1990 and 1991 are based on Lincoln-Peterson mark-recapture censuses (see text).

	Larvae				Adults		
	Hatchlings	2nd yr	3rd yr	≥4th yr	Paedom.	Metam.	Total
1988	3126			41*	>64		>3231
1989	870	>1841	—	—	104	108	2923
1990	1137	180	1916	—	111	123	3467
1991	905	443	79	1377	109	114	3027

* Year class inferred from Fig. 2 of Harte and Hoffman (1989) which indicates no recruitment in 1986 and 1987.

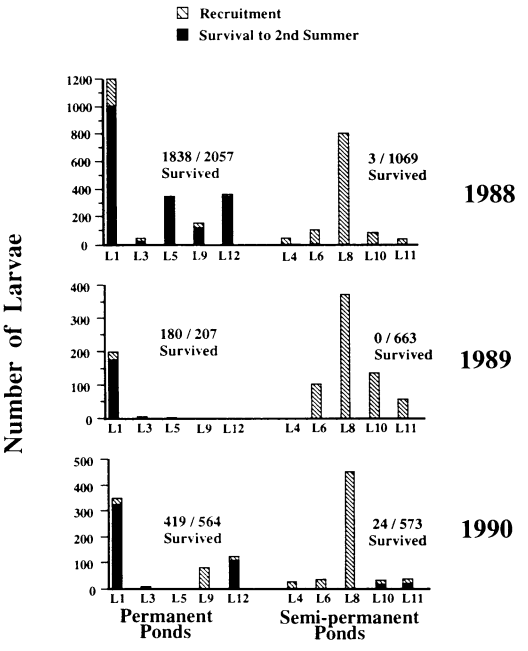

FIG. 3. Survival of first year salamander larvae in permanent vs. semi-permanent ponds at the Mexican Cut Nature Reserve. Recruitment (hatched bars) is based on total number of hatchlings counted in early August. Number surviving is based on second year larvae captured in each pond in June of the following year (open bars).

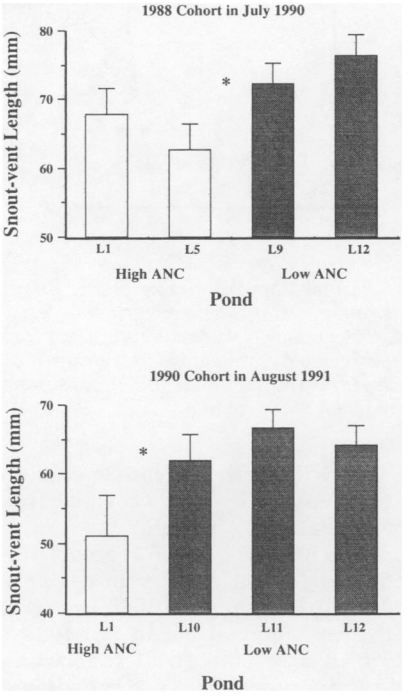

FIG. 4. Effect of ANC on the size of one and two year old larvae at Mexican Cut. The overall ANOVA was significant for the 1988 cohort in July 1990 ($F = 232.43$, $P < 0.001$, df 3,536). The overall ANOVA was significant for the 1990 cohort in August 1991 data ($F = 59.5$, $P < 0.001$, df 3,139). Tukey's a posteriori compromise test indicated that the mean snout-vent length of larvae in each of the low ANC ponds was significantly larger (*) than that in the high ANC ponds.

not appear that the difference in ANC between drainages has any effect on survival or recruitment. This is consistent with Harte and Hoffman (1989) who found that recruitment during their study was similarly low in both high and low ANC ponds.

The 4-fold differences in recruitment we observed in just four years at this study site are similar to those reported in other *Ambystoma* populations (Pechmann et al., 1991). This year-to-year variability in recruitment cannot be attributed to variability in either the timing or intensity of an acid pulse which was absent in all years. Although we do not completely understand the underlying cause(s) for the observed variability in recruitment, our mark-recapture data for individually marked adults suggest it may depend in part on the number of metamorphs that return to the ponds to breed in a given year. Year-to-year variation in breeding population sizes in other *Ambystoma* populations appears to be in part related to the occurrence of favorable temperature and rainfall conditions during migration from the terrestrial habitats where adults overwinter (Tanner et al., 1971; Sexton et al., 1990; Pechmann et al., 1991; see also Wyman, 1991). High-altitude amphibian populations face especially harsh (cold and dry) abiotic conditions as compared to those in mesic environments at lower elevations. Thus, it is possible that year-to-year variation in the size of the breeding population, and hence recruitment, at Mexican Cut may depend largely on weather conditions during spring migration.

There is considerable evidence that eggs are the most acid-sensitive stage in amphibian life cycles, but in some cases habitat acidification has been demonstrated to negatively affect survival and growth in other life stages (see reviews by Pierce, 1985; Freda, 1986; Freda et al., 1991). In this population, we have as yet not detected any patterns in the survival and/or growth of older larvae or paedomorphs that suggest they are being negatively affected by acidification.

Hydroperiod and Larval Recruitment.—Larvae require a minimum of 14 months to metamorphose at this altitude (Whiteman and Wissinger, unpubl. data), so pond drying at any time

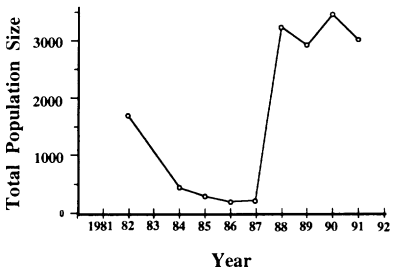

FIG. 5. Total population size of the salamander *Ambystoma tigrinum nebulosum* over a ten-year period at the Mexican Cut Nature Reserve. Data for 1982–1987 are calculated as the sum of hatchlings and adults given in Harte and Hoffman (1989); those for 1988–1991 are taken from Table 3.

of the year will result in year-class failure for that pond. Despite this risk, a considerable proportion of hatchling recruitment (1988, 34%; 1989, 74%; 1990, 50%; 1991, 66%) occurs in ponds that might or might not dry in a given year depending on autumnal rainfall. Because all or most of these ponds dried in fall 1988, 1989, and 1990, nearly half of all the larvae that hatched and survived their first growing season perished in autumn. Thus, our data suggest that hydroperiod had a greater impact on the demographics of this population during 1988–1991 than the effects of episodic acidification. Because recruitment in this population appears to be critically dependent on pond drying, this population may be especially sensitive to changes in evaporation and/or precipitation that might accompany global warming.

10-Year Trends in Population Size.—Combining the population data presented in this paper with those of Harte and Hoffman (1989) provides 10 years of census data from which to assess trends in salamander population size at Mexican Cut (Fig. 5). These data suggest that total population size fell dramatically from 1982–1988, but recovered during 1988–1992 with no net change in the size of the population over the 10 year period. A caveat is that the amplitude of this fluctuation may be exaggerated by differences in sampling techniques. Harte and Hoffman's (1989) data are based on visual census which we found to underestimate population sizes to varying degrees in different ponds as compared to the mark-recapture and total capture censuses we conducted (S. Wissinger, H. Whiteman, and S. Willey, unpubl. obs.).

The question remains as to what factor(s) underlie year-to-year variation in recruitment and whether the decrease in population size during the 1980s was due to a series of severe acidic pulses associated with snowmelt or to some other factor or combination of factors. Our results and those of previous studies emphasize that (1) year-to-year changes in hydroperiod associated with drought can underlie fluctuations in amphibian species that breed in semi-permanent habitats (Pechmann et al., 1991); and (2) such fluctuations can confound inferences made about the effects of anthropogenic causes of amphibian decline.

In summary, the results of this paper do not support the hypothesis that episodic acidification has been a primary cause of mortality in the Mexican Cut salamander population during the 1988–1991 seasons. During this period the acidic pulse from snowmelt was either benign, or occurred prior to salamander embryo development. Our data suggest that a natural or anthroprogenically-induced change in hydroperiod is as viable a working hypothesis as acidification for explaining the trends in this population during the past ten years.

We want to emphasize that these conclusions are based on short-term data and should be viewed in the context of the need for long-term population monitoring of populations that breed in acid-sensitive watersheds (Pechmann et al., 1991, Freda et al., 1991). Our chemistry data imply that many ponds at Mexican Cut remain poorly buffered and have decreased slightly in average pH during the past two decades (Dodson, 1982). Because of its small size, this unique sub-alpine population of *A. t. nebulosum* will be especially vulnerable to any human-induced regional or global change in climate, and the population should continue to be monitored closely.

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APPENDIX 1 Water chemistry in the ponds of the lower shelf of Mexican Cut in 1991 during the open water season at Mexican Cut. Acid-neutralizing capacity (ANC) values were obtained by Acid Rain Analysis System Gran titration (Kramer, 1982; USEPA, 1987), and values generally corresponded well to alkalinity as calculated as the difference in the bases and acids.

				[μeq/L]								Sum	Sum	Diff. =	
Pond	Date	pH	[μS/cm]	CA	MG	NA	K	NH_4	CL	NO_3	SO_4	bases	acids	alkal.	ANC
A. Ponds in high alkalinity drainage															
L1	5/31	6.48	20.95	138.72	35.07	13.38	7.93	3.22	10.61	2.52	26.28	195.11	39.40	155.71	165.90
	6/6	6.43	34.62	204.74	53.91	10.66	4.02	1.66	3.98	1.63	33.83	273.33	39.44	233.89	246.60
	6/11	6.87	34.89	181.94	44.65	10.41	11.62	1.00	10.27	0.00	34.94	248.62	45.20	203.41	208.40
	6/18	6.49	27.47	172.80	50.90	6.91	3.15	0.61	2.34	0.44	36.85	233.77	39.63	194.14	190.20
	6/25	6.72	35.90	215.27	66.20	8.14	4.62	1.05	3.78	0.00	54.05	294.23	57.83	236.40	241.60
	7/1	6.91	39.17	230.64	70.27	8.94	3.46	1.44	4.29	0.00	52.91	313.31	57.19	256.12	254.40
	7/15	6.83	38.05	225.10	76.63	9.23	3.94	2.99	4.01	0.00	62.00	314.90	66.01	248.89	254.50
	8/16	7.28	31.90	218.41	70.44	4.52	1.96	1.33	1.47	0.00	61.30	295.33	62.76	232.57	236.90
	9/15	7.17	29.48	178.34	56.55	1.13	1.30	1.28	2.03	0.13	53.18	237.32	55.34	181.98	199.50
	10/15	7.01	29.80	220.46	70.36	2.82	2.06	1.11	2.28	0.00	66.34	295.70	68.62	227.08	202.80
L2 (frozen 5/31-6/18)															
	6/25	6.80	35.57	211.63	64.56	7.63	3.65	1.28	2.82	0.00	53.13	287.46	55.96	231.51	238.40
	7/15	6.65	35.26	206.94	68.86	8.44	4.38	0.67	3.53	0.00	56.59	288.62	60.12	228.50	228.90
	8/16	7.20	32.20	219.76	69.80	4.82	3.87	3.66	2.88	0.00	29.46	298.25	32.34	265.91	264.90
	9/15	7.02	28.15	173.80	56.83	0.84	1.50	0.83	2.26	0.00	50.45	232.97	52.71	180.27	180.60
	10/15	6.55	25.84	188.77	62.32	2.74	2.08	1.44	2.76	0.00	53.28	255.92	56.04	199.87	157.80
L3 (frozen 5/31-6/11)															
	6/18	6.52	28.33	169.26	49.57	6.96	3.06	0.67	2.34	0.00	37.75	228.85	40.09	188.76	186.80
	7/1	6.77	35.79	212.82	65.28	9.04	6.47	0.72	6.68	0.00	53.59	293.61	60.28	233.34	238.00
	7/15	6.74	39.68	240.67	79.98	9.50	4.16	2.22	4.01	1.21	56.59	334.31	61.81	272.50	275.70
	8/16	7.19	30.80	220.61	69.98	3.36	2.05	1.77	1.47	0.00	45.76	296.00	47.23	248.77	222.00
	9/15	7.00	19.69	158.78	52.08	0.78	1.53	0.00	2.26	0.00	47.33	213.17	49.58	163.59	160.10
	10/15	6.90	30.89	220.56	52.77	3.68	2.92	1.28	3.24	0.00	84.62	284.93	87.86	197.07	192.70
L4 (frozen 5/31-6/11)															
	6/18	6.52	28.76	169.76	49.10	7.27	3.52	1.28	2.82	0.44	38.21	229.65	41.46	188.19	187.80
	7/1	6.80	35.25	213.87	64.55	7.93	3.36	0.50	2.82	0.00	52.70	289.71	55.52	234.19	236.80
	7/15	6.66	39.68	244.26	79.65	8.40	3.19	1.88	2.59	1.66	55.03	335.50	59.29	276.21	278.40
	8/16	6.86	31.10	221.96	70.69	5.13	4.53	4.82	4.03	0.00	45.76	302.30	49.80	252.51	228.20
	9/15	7.01	27.34	163.32	53.70	0.94	1.53	0.50	2.26	0.00	48.89	219.50	51.14	168.35	168.40
	10/15	6.72	31.48	221.21	73.37	2.58	2.58	2.22	3.72	0.00	84.18	299.74	87.90	211.84	197.20
L5	5/31	6.40	12.95	67.07	20.48	5.99	5.80	6.32	3.98	8.27	13.68	99.33	25.93	73.40	80.40
	6/6	5.88	9.11	36.56	11.78	7.71	4.85	3.83	4.43	4.29	16.64	60.90	25.35	35.55	34.40
	6/11	6.82	33.96	186.03	48.50	7.93	4.15	1.94	3.24	2.37	40.41	246.61	46.03	200.58	202.00
	6/18	6.52	27.68	162.52	44.29	6.59	3.19	0.55	2.57	0.94	44.10	216.60	47.60	169.00	168.10

APPENDIX 1 Continued

Pond	Date	pH	[μS/cm]	[μeq/L] CA	MG	NA	K	NH_4	CL	NO_3	SO_4	Sum bases	Sum acids	Diff = alkal.	ANC
	6/25	6.76	32.87	190.62	50.04	9.31	6.43	1.55	6.37	0.69	54.82	256.40	61.89	194.51	197.50
	7/1	6.88	41.04	246.86	64.75	9.30	5.64	1.88	5.58	0.00	57.94	326.54	63.53	263.01	262.90
	7/15	6.82	42.01	263.17	76.31	7.23	2.02	2.99	2.59	0.00	62.38	348.72	64.97	283.75	295.90
	8/16	6.85	29.70	222.01	64.58	1.30	0.94	2.00	1.21	0.00	57.03	288.82	58.24	230.58	206.90
	9/15	6.97	20.32	146.86	42.42	0.81	2.16	0.83	4.17	0.00	52.01	192.25	56.19	136.07	132.60
	10/15	6.99	31.98	228.19	61.84	2.55	1.72	2.05	3.72	0.00	85.49	294.31	89.21	205.09	197.50
L18 (frozen 5/31-6/18)															
	6/18	6.70	31.36	185.38	32.13	5.36	4.30	0.50	2.82	10.79	82.55	227.17	96.16	131.00	136.00
	6/25	6.83	36.76	221.36	54.86	8.63	9.32	2.27	7.95	0.00	64.75	94.17	72.71	221.46	226.20
	7/1	6.82	38.73	233.78	56.33	8.29	3.66	0.33	1.97	0.00	67.52	302.06	69.50	232.57	224.70
	7/15	7.03	41.08	258.13	69.68	10.49	5.29	2.55	6.32	1.21	50.78	343.60	58.31	285.29	292.40
	8/15	7.00	34.60	265.97	67.39	4.41	2.64	2.49	1.47	0.00	25.57	340.41	27.03	313.38	300.40
	9/15	6.88	26.32	168.61	46.53	0.17	2.52	0.72	5.39	0.00	57.47	217.82	62.85	154.97	153.60
	10/15	7.06	32.37	229.99	62.34	2.58	7.37	2.49	7.05	0.00	73.29	302.28	80.34	221.94	221.00
B. Ponds in low alkalinity drainages															
L6	5/31	5.81	10.66	52.20	16.51	8.66	6.23	1.22	2.59	1.63	25.03	83.60	29.25	54.35	44.20
	6/6	5.72	19.91	50.65	16.21	7.94	4.74	0.72	2.82	2.52	26.28	79.54	31.61	47.93	41.70
	6/11	5.95	9.53	50.55	12.39	6.63	2.78	0.50	2.34	1.94	17.32	72.36	21.60	50.76	38.60
	6/18	5.93	8.79	41.05	13.07	8.93	6.15	1.72	5.73	0.00	19.65	69.20	25.38	43.82	39.20
	6/25	6.05	10.57	55.29	16.14	9.77	7.28	2.05	5.92	0.00	21.26	88.47	27.18	61.29	49.30
	7/1	6.26	11.88	62.38	18.43	10.15	6.31	1.77	6.43	0.00	16.93	97.27	23.36	73.91	54.80
	7/15	6.03	11.06	60.73	18.51	8.70	4.89	3.38	4.68	0.00	17.89	92.83	22.57	70.26	61.90
	8/16	6.41	9.01	62.38	19.04	5.03	4.17	2.05	3.33	0.00	11.20	90.62	14.53	76.09	58.70
	9/15	6.51	9.76	56.89	17.69	6.49	5.75	0.67	5.61	0.00	15.30	86.82	20.92	65.91	55.20
	10/15	6.49	9.99	69.76	22.23	8.09	8.36	1.39	7.53	0.00	18.88	108.43	26.42	82.02	57.90
L7 (frozen 5/31-6/11)															
	6/18	6.20	9.24	48.40	14.57	7.91	5.50	0.89	3.53	0.00	16.95	76.38	20.47	55.91	48.60
	6/25	6.09	10.77	56.49	16.46	8.65	6.78	1.72	5.70	0.69	18.20	88.37	24.59	63.78	58.60
	7/1	5.99	13.41	73.90	20.64	9.23	5.15	1.28	5.36	0.00	10.45	108.92	15.81	93.11	79.20
	7/15	6.10	11.02	61.58	17.64	8.90	8.88	4.44	4.91	0.00	7.83	97.01	12.74	84.27	75.60
	8/16	6.42	11.69	73.05	19.23	3.14	6.02	1.22	6.09	0.00	22.34	101.45	28.43	73.02	76.80
(dry 9/15-10/15)															
L8	5/31	6.01	8.03	16.17	6.67	3.86	2.62	24.06	5.58	31.71	2.35	29.31	39.64	−10.33	17.30
	6/6	5.78	5.73	15.35	4.69	2.60	2.46	7.10	2.37	12.24	7.39	25.10	22.00	3.10	11.00
	6/11	5.96	7.53	38.48	9.58	4.73	3.06	0.89	3.72	3.24	11.47	55.85	18.44	37.41	29.40
	6/18	6.18	6.90	34.29	11.16	5.15	3.38	0.78	2.34	0.94	13.76	53.98	17.04	36.94	33.10
	6/25	6.26	8.41	41.81	12.84	6.84	5.93	2.33	3.89	0.00	14.76	67.41	18.65	48.76	45.70

APPENDIX 1 Continued

Pond	Date	pH	[μS/cm]	[μeq/L] CA	MG	NA	K	NH_4	CL	NO_3	SO_4	Sum bases	Sum acids	Diff = alkal.	ANC
	7/1	5.99	8.75	45.49	13.59	6.09	5.27	1.44	3.41	0.00	8.29	70.44	11.70	58.74	43.90
	7/15	6.02	7.95	45.42	14.28	5.44	5.27	0.72	2.59	0.00	11.70	70.41	14.30	56.11	42.30
	8/16	5.84	6.35	42.64	13.12	2.09	2.96	3.10	2.62	0.00	7.33	60.81	9.95	50.86	35.90
	9/15	6.45	6.47	38.50	11.32	0.92	2.95	1.50	2.74	0.00	13.74	53.70	16.48	37.22	31.40
	10/15	6.46	8.20	48.67	14.82	5.07	13.16	1.33	3.72	0.00	20.20	81.72	23.92	57.80	42.30
L9	5/31	5.83	10.90	47.93	15.44	13.77	6.94	1.83	8.32	2.08	17.89	84.08	28.29	55.79	49.90
	6/6	5.64	10.25	49.88	15.27	8.38	3.23	0.28	3.27	2.52	17.89	76.75	23.67	53.08	43.90
	6/11	6.03	8.14	44.74	11.11	5.36	2.58	1.16	3.95	2.81	10.68	63.79	17.44	46.36	35.90
	6/18	6.17	7.04	35.62	11.73	5.08	2.70	0.44	2.09	0.00	12.87	55.14	14.95	40.18	35.80
	6/25	6.27	8.48	43.45	13.82	6.99	4.73	2.05	3.89	0.00	12.85	69.00	16.74	52.26	47.70
	7/1	6.11	8.87	45.52	14.64	6.70	4.13	0.67	4.51	0.00	6.50	70.99	11.01	59.98	47.10
	7/15	6.09	7.75	40.71	14.42	4.26	2.90	0.00	3.30	0.00	10.54	62.28	13.84	48.44	42.80
	8/16	5.85	5.60	33.81	11.62	0.17	1.38	2.49	1.92	0.00	7.70	46.99	9.62	37.36	32.80
	9/15	6.35	5.11	28.14	8.90	10.39	1.37	0.11	1.55	0.00	9.06	48.80	10.61	38.19	24.40
	10/15	6.37	7.08	43.30	15.62	3.75	8.39	2.61	2.76	0.00	11.06	71.06	13.82	57.24	42.20
L10 (frozen 5/31-6/6)															
	6/11	6.03	10.28	46.50	13.62	8.01	5.15	2.33	5.30	2.37	13.80	73.28	21.48	51.80	44.90
	6/18	6.17	7.66	38.12	12.83	5.69	3.15	1.00	2.34	0.00	14.22	59.78	16.56	43.22	40.30
	6/25	6.24	9.58	49.12	16.18	7.56	5.53	1.94	4.80	0.00	14.39	78.38	19.18	59.20	55.80
	7/1	6.16	10.18	52.50	16.75	7.75	6.24	0.11	5.13	0.00	6.85	83.23	11.98	71.24	57.80
	7/15	6.13	9.81	56.79	18.52	6.19	7.58	3.71	3.53	0.00	10.14	89.08	13.67	75.42	59.80
	8/16	6.36	3.98	22.61	8.18	1.02	2.39	0.11	2.88	0.00	1.50	34.20	4.38	29.82	25.10
	9/15	6.46	7.26	43.93	14.94	2.27	4.82	0.00	2.99	0.00	8.29	65.96	11.28	54.69	41.30
	10/15	6.37	7.78	51.15	17.87	4.52	9.35	1.66	4.68	0.00	10.18	82.90	14.86	68.03	41.90
L11	5/31	6.08	4.86	15.17	5.47	6.09	3.11	4.10	7.87	2.97	2.77	29.84	13.61	16.24	20.40
	6/6	5.64	8.23	35.33	8.92	4.80	5.38	0.00	3.98	7.39	11.18	54.43	22.54	31.89	26.40
	6/11	5.90	8.65	38.68	10.53	6.07	4.32	0.72	3.47	3.68	14.60	59.60	21.74	37.86	31.10
	6/18	6.10	6.71	31.55	11.30	4.79	2.97	1.22	1.86	0.44	12.41	50.61	14.71	35.90	32.60
	6/25	6.21	8.15	39.82	13.32	5.63	4.79	1.44	2.76	0.00	12.85	63.56	15.61	47.95	43.60
	7/1	6.02	8.68	43.52	14.17	5.73	5.94	0.00	3.86	0.00	5.41	69.36	9.28	60.08	45.70
	7/15	6.12	8.57	48.38	17.21	4.60	8.14	3.10	2.85	0.00	7.83	78.33	10.68	67.65	49.60
	8/15	6.51	8.99	51.10	17.30	6.62	9.37	5.27	7.56	0.00	3.04	84.38	10.60	73.79	52.60
	9/15	6.13	7.14	41.51	14.65	0.99	6.07	0.00	3.22	0.00	9.45	63.22	12.67	50.55	68.60
	10/15	6.32	9.12	52.69	18.25	5.93	15.98	4.16	8.97	0.00	11.49	92.86	20.46	72.39	45.30
L12	5/31	5.85	5.00	13.74	4.11	6.50	4.91	3.44	6.71	6.06	4.87	29.27	17.65	11.62	9.60
	6/6	5.90	5.37	19.63	5.81	3.72	2.03	1.39	2.59	6.06	9.49	31.19	18.15	13.04	15.00
	6/11	5.95	6.30	26.53	4.83	4.69	6.14	5.43	7.56	10.63	7.16	42.19	25.35	16.84	16.20
	6/18	6.24	6.95	32.95	11.22	4.88	2.89	3.66	2.34	0.00	11.06	51.95	13.40	38.55	40.80

APPENDIX 1 Continued

Pond	Date	pH	[μS/cm]	[μeq/L] CA	MG	NA	K	NH_4	CL	NO_3	SO_4	Sum bases	Sum acids	Diff = alkal.	ANC
	6/25	6.26	7.97	33.51	10.68	9.41	10.02	4.55	10.21	0.00	10.56	63.63	20.77	42.86	47.90
	7/1	6.14	6.14	30.45	10.30	5.69	2.49	0.61	3.41	0.00	2.89	48.94	6.31	42.63	34.10
	7/15	6.11	5.18	26.75	10.70	3.09	1.18	1.44	1.92	0.00	7.06	41.72	8.98	32.74	28.30
	8/16	6.52	8.13	52.20	17.72	3.99	5.62	5.49	3.33	0.00	5.00	79.53	8.33	71.20	50.90
	9/15	6.01	3.57	19.78	8.20	0.00	1.29	0.00	1.78	0.00	2.81	29.27	4.59	24.68	5.60
	10/15	6.11	4.00	26.39	10.75	0.03	1.45	1.28	1.58	0.00	5.83	38.62	7.41	31.21	16.90
L13 (frozen 5/31-6/11)															
	6/18	5.89	6.09	22.81	7.44	4.28	3.00	2.83	2.82	1.44	7.43	37.52	11.69	25.83	22.00
	6/25	6.01	6.21	25.52	8.45	4.53	5.29	2.05	3.89	0.00	5.98	43.79	9.87	33.92	28.90
	7/1	5.71	7.36	31.86	9.86	4.60	6.01	0.67	2.65	0.00	4.50	52.33	7.15	45.18	29.60
	7/15	5.69	7.31	36.11	12.08	2.19	3.35	3.22	1.66	1.21	3.56	53.73	6.43	47.29	27.70
	8/16	6.00	6.35	42.58	12.94	0.00	1.90	3.88	0.54	0.00	2.27	57.43	2.81	54.62	29.30
	9/15	6.94	26.62	167.12	54.19	0.87	1.75	0.00	2.26	0.00	48.89	223.93	51.14	172.79	164.00
	10/15	6.22	12.61	58.18	19.88	8.74	39.39	2.33	6.35	0.00	34.13	125.19	40.47	84.72	46.10
L14 (frozen 5/31-6/11)															
	6/18	6.07	6.40	25.80	7.91	2.31	4.62	3.44	2.34	2.42	6.54	40.63	11.30	29.34	31.30
	6/25	6.13	6.82	29.08	8.48	3.12	6.92	2.22	3.89	0.00	4.46	47.60	8.35	39.25	39.80
	7/1	6.02	9.86	30.70	9.49	3.91	6.89	0.28	3.78	0.00	2.96	50.99	6.74	44.25	38.70
	7/15	6.07	6.23	28.87	10.20	2.94	6.44	2.49	2.14	0.00	2.42	48.46	4.56	43.90	35.50
	8/16	6.42	5.72	36.95	10.99	0.17	4.67	4.05	0.76	0.00	0.71	52.77	1.47	51.30	40.20
	9/15	6.13	4.74	26.34	7.89	0.00	3.51	0.00	1.78	0.00	2.04	37.74	3.82	33.93	24.00
	10/15	6.12	4.55	28.89	9.08	1.27	4.64	0.00	2.06	0.00	1.92	43.88	3.97	39.91	22.60
L15 (frozen 5/31-6/11)															
	6/18	6.22	8.40	38.42	11.32	7.67	4.68	0.94	4.26	0.00	19.65	62.09	23.91	38.18	38.10
	6/25	6.13	10.13	48.01	13.22	10.54	9.56	0.33	7.45	0.00	17.95	81.33	25.39	55.94	48.80
	7/1	6.27	8.97	45.70	12.94	7.00	5.48	0.94	4.34	0.00	18.57	71.12	22.92	48.21	44.40
	7/15	6.21	9.65	56.74	15.81	7.02	10.28	0.50	4.46	0.76	10.14	89.85	15.35	74.49	54.30
	8/16	6.08	9.85	63.02	16.79	5.91	12.11	9.81	6.15	0.00	3.04	97.84	9.19	88.65	53.90
	9/15	6.10	10.48	60.23	17.25	4.62	8.30	0.00	8.01	0.00	22.34	90.39	30.35	60.04	54.60
	10/15	6.33	9.25	60.48	17.13	6.69	9.43	0.00	8.97	0.00	21.92	93.73	30.89	62.83	39.00
L16 (frozen 5/31-6/18)															
	6/25	6.99	32.00	187.62	50.63	10.03	7.51	2.44	6.60	0.00	22.78	55.80	29.38	226.42	241.90
	7/1	6.87	43.03	275.60	64.51	11.59	6.25	0.33	5.16	0.00	22.94	357.95	28.11	329.84	352.60

APPENDIX 1 Continued

Pond	Date	pH	[μS/cm]	[μeq/L] CA	MG	NA	K	NH_4	CL	NO_3	SO_4	Sum bases	Sum acids	Diff = alkal.	ANC
(dry 7/15–10/15)															
L17 (frozen 5/31–6/18)															
	6/25	6.41	9.75	50.20	18.61	4.76	4.29	3.33	3.22	2.50	12.85	77.85	18.56	59.29	66.30
	7/1	6.38	7.85	39.03	14.36	4.51	5.01	0.28	3.33	0.00	12.95	62.91	16.28	46.63	44.40
(dry 7/15–10/15)															
L19 (frozen 5/31–6/11)															
	6/18	5.91	8.91	34.09	10.13	8.99	6.72	3.83	4.99	0.44	8.35	59.93	13.78	46.15	45.00
	6/25	6.02	8.07	34.56	10.34	5.79	10.39	2.72	4.34	0.00	9.04	61.08	13.38	47.70	38.50
	7/1	6.19	10.99	57.49	16.51	8.61	2.41	0.61	2.43	0.00	24.49	85.02	26.91	58.11	43.60
	7/15	5.98	12.43	62.87	17.92	10.81	7.12	0.00	2.59	0.00	11.70	98.73	14.30	84.43	57.60
(dry 8/15–10/15)															