

## Habitat Segregation of *Ambystoma gracile* and *Ambystoma macrodactylum* in Mountain Ponds and Lakes, Mount Rainier National Park, Washington, USA

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**ABSTRACT.**—*Ambystoma gracile* (Baird) and *Ambystoma macrodactylum* Baird are common salamander species occupying key trophic positions in mountain ponds and lakes of Mount Rainier National Park (MORA). Based on amphibian surveys conducted in ponds and lakes in the northeast quadrant of MORA during the summers of 1993–1995, 20 sites were resampled in 1996 to document and evaluate distributions of the two species relative to site habitat characteristics. Distributions of larvae were assessed either by nearshore snorkel or visual encounter surveys of each study site. Twelve environmental variables representing pond and lake physical characteristics, water quality, and nutrient concentrations were measured. The occurrences at each site of three major habitat components (i.e., pond bottom firmness, coarse woody debris, and emergent/aquatic vegetation) were qualitatively estimated. Allotopic distributions of larval populations of both species were related to site elevation, maximum depth, organic content of bottom substrates, and surface area. *Ambystoma gracile* sites were larger, deeper, lower in elevation, had flocculent sediment higher in organic content, abundant coarse woody debris, and limited emergent/aquatic vegetation relative to *A. macrodactylum* sites. *Ambystoma macrodactylum* sites were smaller, shallower, higher in elevation, had firm sediments low in organic content, and had a greater occurrence of emergent/aquatic vegetation than did *A. gracile* sites. Two sites supported syntopic populations and exhibited many of the habitat characteristics observed at sites inhabited by each species. The distribution of each species in MORA was related to the interconnection between habitat characteristics of ponds and lakes and species life-history patterns and possibly interspecific interactions.

Life-history traits of ambystomatid salamanders can vary considerably, suggesting that these salamanders possess life-history strategies suitable for the diverse habitats they occupy (Semlitsch et al., 1990). For example, *Ambystoma jeffersonianum* (Green) and *Ambystoma maculatum* (Shaw) can be distributed syntopically, but they often occupy different habitats possessing characteristics related to differing behavioral and physiological requirements (Thompson and Gates, 1982). Different breeding habitats preferred by the stream and pond forms of *Ambystoma texanum* (Matthes) are thought to be a result of adaptation of stream forms to limited availability of ponds (Petranka, 1982). Populations of *A. texanum* also differ from populations of their sibling species, *Ambystoma barbouri* (Kraus and Petranka), in activity level, larval period, and timing of metamorphosis. These differences have been associated with water temperature and habitat duration (Maurer and Sih, 1996). The propensity to metamorphose in populations of *Ambystoma talpoideum* (Holbrook) has

been attributed, in part, to pond drying regime (Semlitsch et al., 1990), and pond permanence, as well as pond size and elevation, have been identified as contributing to the expression of several life-history patterns in montane populations of larval *A. macrodactylum* Baird (Kezer and Farner, 1955; Anderson, 1967; Howard and Wallace, 1985). Habitat characteristics such as water turbidity, firmness of pool bottom, and shoreline condition have also been related to the allotopic distributions of several ambystomatid salamander species (Thompson and Gates, 1982; Maurer and Sih, 1996).

*Ambystoma gracile* (Baird) and *A. macrodactylum* are common ambystomatid salamander species distributed throughout the Pacific Northwest. Both species occur in diverse habitats from sea level to approximately 2000–3000 m elevation on the west side of the hydrologic crest of the Cascade Mountains, and *A. macrodactylum* is also present on the east side of the Cascade Range (Nussbaum et al., 1983; Leonard et al., 1993; Corkran and Thoms, 1996). Larvae of *A. gracile* are typically found in permanent small shallow ponds to large deep lakes (Eagleson,

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1976; Corkran and Thoms, 1996) but have also been known to breed in semipermanent lentic habitats (Petranka, 1998). Montane populations of *A. macrodactylum* larvae can inhabit small seasonally ephemeral and permanent ponds, as well as large permanent lakes (Anderson, 1967; Howard and Wallace, 1985; Leonard et al., 1993). Presence and densities of aquatic macrophytes, coarse wood, and flocculent bottom sediments differ between montane ponds and lakes occupied by *A. gracile* and *A. macrodactylum* (Kezer and Farner, 1955; Anderson, 1967; Snyder, 1956; Petranka, 1998).

Larvae of *A. gracile* and *A. macrodactylum* develop more slowly in montane systems than in lower elevation habitats (Eagleson, 1976; Petranka, 1998) and exhibit life-history strategies in montane systems concordant with slower development (Kezer and Farner, 1955; Snyder, 1956; Anderson, 1967; Eagleson, 1976; Howard and Wallace, 1985). For instance, a large proportion of individuals in populations of *A. gracile* residing in mountain ponds and lakes never transform (Snyder, 1956; Efford and Mathias, 1969; Eagleson, 1976), resulting in a high frequency of neotenes (i.e., gilled adults) in montane populations (Duellman and Trueb, 1986). Neotenes of *A. gracile* can range in size from 65–105 mm snout-vent length (SVL; Nussbaum et al., 1983) and were found to average 80 mm SVL in a lake (1676 m elevation) in Mount Rainier National Park (Snyder 1956). Individuals that do transform can take up to three years before transformation occurs (Eagleson, 1976). Unlike *A. gracile*, neoteny does not occur in populations of *A. macrodactylum* (Nussbaum et al., 1983), and larvae can take from three to more than 48 months to transform depending on the type of lentic system they inhabit (Kezer and Farner, 1955; Anderson, 1967; Howard and Wallace, 1985). In relatively high-elevation lakes (e.g., 2470 m), larvae of *A. macrodactylum* can be as large as 47 mm SVL at metamorphosis, whereas in lower-elevation lakes (e.g., 420 m and 1140 m) larvae metamorphose at approximately 35–40 mm SVL (Howard and Wallace, 1983).

Amphibian surveys conducted in Mount Rainier National Park (MORA), Washington, between 1993 and 1995, indicated that larvae of *A. gracile* and *A. macrodactylum* were typically allotopic in their distributions and inhabited lentic systems with differing habitat characteristics. Based on these preliminary results, additional research was conducted in 1996 with the goal of enhancing our understanding of how distributions of these two salamander species were related to habitat characteristics of park ponds and lakes. Objectives of this research were to (1) document distributions of larvae of *A. gracile* and *A. macrodactylum* in study ponds and lakes

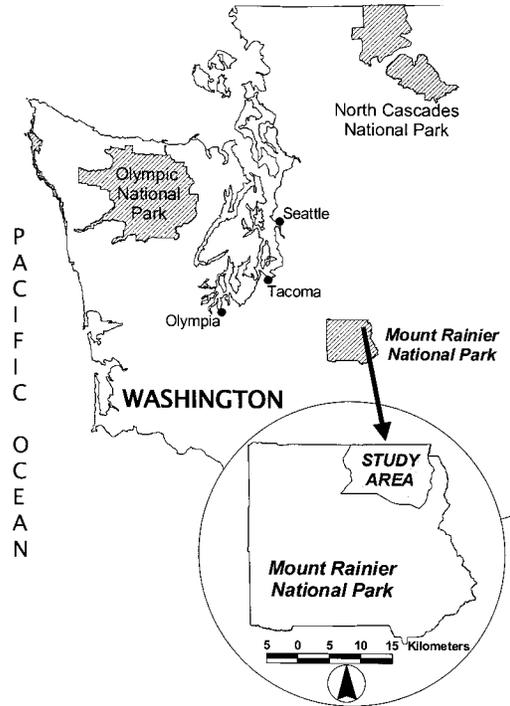


FIG. 1. Location of study area in Mount Rainier National Park (MORA), Washington.

and (2) identify and document differences in the selected habitat characteristics of study ponds and lakes inhabited by each species.

#### MATERIALS AND METHODS

**Study Area.**—The study area was located near Sunrise Point in the northeast portion of Mount Rainier National Park (Fig. 1) and included portions of Huckleberry Creek and Sunrise Creek basins that drain the Sourdough Mountains. A mosaic of relatively dry subalpine forest-meadow communities dominates these watersheds because of a rain shadow effect caused by Mount Rainier (elevation = 4393 m). Subalpine fir (*Abies lasiocarpa*), mountain hemlock (*Tsuga mertensiana*), western red cedar (*Thuja plicata*), Alaska yellow cedar (*Chamaecyparis nootkatensis*), whitebark pine (*Pinus albicaulis*), and Pacific silver fir (*Abies amabilis*) are the dominant tree species in these drainages (Franklin et al., 1988). The forest understory and meadows are dominated by a heath-shrub community composed mostly of huckleberries (*Vaccinium* spp.), heathers (*Phyllodoce* spp. and *Cassiope* spp.), fescues (*Festuca* spp.), sedges (*Carex* spp.), lush-herbaceous communities (*Valeriana-Veratrum* spp.), and various subalpine and alpine wildflowers (Franklin et al., 1988).

**Sites and Sampling Schedule.**—During the

TABLE 1. Physical characteristics of 20 fishless mountain ponds and lakes in the northeast quadrant of Mount Rainier National Park, 1996 (AM or M = *Ambystoma macrodactylum*; AG or G = *Ambystoma gracile*; VES = Visual Encounter Survey).

Lake	Species	Average no./100 m	Elevation (m)	Area (m <sup>2</sup> )	Depth (m)	Basin type	Survey
LH16	AG	26.0	1704	3170.00	2.10	Subalpine Forest	Snorkel
LH17	AG	5.3	1781	6169.00	1.94	Meadow	Snorkel
LH19	AG	58.5	1696	1376.00	0.88	Subalpine Forest	Snorkel
LH24	AG	21.9	1730	5854.00	2.43	Subalpine Forest	Snorkel
LW12	AG	31.4	1726	3748.00	2.14	Subalpine Forest	Snorkel
LW13	AG	1.8	1673	4338.30	2.60	Subalpine Forest	Snorkel
LW14	AG	2.2	1615	502.00	1.70	Subalpine Forest	VES
LW24	AG	27.8	1702	2640.00	3.64	Subalpine Forest	Snorkel
LH20	AM	196.0	1764	1742.00	0.71	Meadow	Snorkel
LH22	AM	14.0	1806	2038.00	0.70	Subalpine Forest	VES
LH23	AM	208.6	1843	980.00	1.30	Meadow	Snorkel
LH27	AM	159.4	1821	284.38	0.70	Meadow	VES
LH12	AM	1.0	1842	714.58	0.18	Meadow	VES
LW22	AM	137.2	1809	583.16	0.78	Meadow	Snorkel
LW25	AM	34.3	1909	940.00	0.41	Meadow	VES
LIW23	AM	69.1	1794	367.16	0.25	Meadow	VES
UK01	AM	129.8	1733	396.17	0.51	Meadow	VES
UK13	AM	211.3	1672	266.44	0.30	Meadow	VES
LH21	G > M	47.6 > 0.2	1757	2439.00	2.10	Subalpine Forest	Snorkel
LW15	M > G	80.8 > 18.7	1701	1033.52	0.80	Meadow	Snorkel

1993–1995 field seasons, larvae of *A. gracile* were found in 16 permanent, fishless ponds and lakes, and *A. macrodactylum* were found in 11 ephemeral and permanent fishless ponds and lakes. From this set of 27 sites, a subset of 22 ponds and lakes was selected for study in 1996. This subset included 11 sites selected randomly from the 16 sites inhabited by *A. gracile* as well as the 11 *A. macrodactylum* sites. Two of the 11 *A. gracile* ponds and lakes were dropped from the subset of study sites because of extremely difficult access. This left a final subset of 20 study sites (Table 1).

Nineteen of the 20 study sites were sampled twice during the 1996 field season. The first three-week sampling period began as soon as possible after ice-out in early July, and the second sampling period was conducted in August. The order in which sites were sampled was determined without regard to salamander species present at each site. During each sampling period, each site was surveyed for salamanders, habitat characteristics, and water quality. LIW23 was only sampled in July because it was dry in August. LH16 and LH17, although sampled twice for salamanders, were sampled only in July for water chemistry and nutrients because the ponds were muddy in August caused by disturbance associated with elk wading in the ponds.

*Salamander Surveys.*—Snorkeling and visual encounter surveys were used to verify which salamander species was present at each study

site. These methods have been used in past research (see Thoms et al., 1997; Tyler et al., 1998) and care was taken to use each method as efficiently and effectively as possible. Snorkel surveys were conducted at 12 sites from 0.71–3.64 m deep (mean = 1.78 m; Table 1). Snorkeling was used at these sites because it was determined that this method could be used without decreasing snorkeler visibility caused by disturbance of the pond or lake bottom. Visual encounter surveys (VES) were used at eight sites from 0.18–1.7 m deep (mean = 0.44 m; Table 1). It was determined that in these ponds a snorkeler would disturb the bottom, greatly diminishing water clarity and, therefore, the snorkeler's ability to observe and identify larvae. Although all VES were performed in the nearshore area of each site (i.e., from the shoreline to approximately 2 m offshore), care was taken to also visually inspect the deeper parts of these relatively shallow systems.

VES was more likely to be used at shallow sites with *A. macrodactylum* than at sites with *A. gracile* (Table 1). This created a relatively strong correlation and potential bias between survey method and species presence. In our experience, VES was effective for determining the presence/absence of salamander species in the nearshore areas of shallow ponds, as well as for observing and identifying larvae in the deeper parts of these ponds. Snorkeling was effective for observing and identifying larvae in the nearshore and offshore areas of deeper ponds and

lakes. Therefore, we chose to use the method best suited for each site relative to the constraints imposed by site depth and the potential for diminished water clarity and found each method to be equitable and effective for identifying species presence in study sites.

Snorkel surveys were accomplished by swimming transects parallel to the shoreline of a pond or lake. Because of variation in pond/lake sizes, standardized transect lengths were not practical. Lengths and locations of transects were determined by estimating the percentage of various nearshore habitat types around each pond and lake (i.e., vegetated, sandy, woody debris, talus) and then selecting transect lengths proportional to these percentages in the appropriate locations. For instance, if it was estimated that two-thirds of a site's nearshore area was covered by woody debris and one-third by talus, then of 100 m of shoreline snorkeled, 67 m would be in areas with woody debris and 33 m in areas with talus. The nearshore area was snorkeled to a depth of approximately 1 m (or diver's reach) and a maximum width of approximately 2 m from the shoreline. The snorkeler searched through all potential nearshore cover (capable of being moved) for salamanders.

Visual encounter surveys were performed by searching for salamanders while slowly walking the shoreline and nearshore areas of a study site in a zigzag pattern (Thoms et al., 1997). If the nearshore area was narrow (2–3 m), one surveyor walked the edge of a site while the other recorded data. If the nearshore area either exceeded 2–3 m in width or emergent and/or aquatic vegetation was densely distributed, two surveyors worked in tandem approximately 2–3 m apart.

*Species Identification.*—Species identification was based on characteristics presented by Nussbaum et al. (1983), Stebbins (1985), Leonard et al. (1993), and Corkran and Thoms (1996). In cases where the species identity of individual larvae was in question, the larvae were captured with dip nets and reared in aquaria at a park laboratory until positive species identifications were possible.

*Environmental Variables.*—Four physical variables were determined for each site. Surface area (m<sup>2</sup>) was determined by digitizing 7.5-min U.S. Geological Survey (USGS) topographic maps into GIS software (ARC-Info<sup>™</sup> and ARC-View<sup>™</sup>). Maximum depth was recorded each time a site was sampled by dropping a weighted line to the pond/lake bottom at locations along three line transects across the width of the pond/lake and one line transect across the pond/lake length. Site elevation was determined either from field altimeter readings or 7.5-min USGS topographic maps. At the end of

the field season in August, bottom substrate samples were collected from all sites and used to determine organic content of sediment. Samples were collected approximately 1 m from shore by forcing a bevel-ended section of a 9 cm diameter PVC pipe about 25 cm into the sediments, capping the pipe ends, and extracting about 2 liters of bottom substrate. The sample was allowed to settle for 10 min before pouring off excess water and then transferred to dark polyethylene bottles and frozen. Later, samples were thawed and desiccated in an oven for 24 h to remove any remaining water. The resulting dry samples were weighed and then ashed in a muffle furnace for 20 min at 550°C, transferred to a desiccator for final cooling, and then reweighed. The ashed weight was subtracted from the dry weight to determine organic content of the sediments and was expressed as percent loss on ignition (LOI; Wetzel and Likens 2000).

Water chemistry variables were measured at each site on the same day but before salamander surveys. Water samples for measuring pH, alkalinity, and conductivity were collected from a depth of 1 m below the pond/lake surface using a Van Dorn bottle, although in sites < 1 m deep samples were taken at one half maximum depth. Field measurements of pH were made soon after water samples were collected using a Hach<sup>™</sup> field pH meter that was calibrated at each sampling site. Alkalinity and conductivity were determined in a park laboratory within 24 h of sampling. Alkalinity was measured by the Gran titration method (Gran, 1952) and expressed in microequivalents/liter (μeq/L). Conductivity was measured with a Hach<sup>™</sup> conductivity meter and expressed in μmhos/cm at 25°C. Dissolved oxygen was recorded at 1-m intervals beginning at the surface to a depth of 1 m off the pond/lake bottom using a YSI<sup>™</sup> dissolved oxygen meter. In ponds < 1 m deep, dissolved oxygen was recorded at the surface and at one-half maximum depth.

Nutrient samples were collected from 17 of the 20 study sites within a two-week period in August. Water samples were collected from 1 m below the pond/lake surface (or at half maximum depth as above) and filtered using 0.7 μm prewashed Watman<sup>™</sup> GF/C filters. Samples were frozen until processed. Three sites could not be sampled for nutrients in August: LIW23 was dry, and LH16 and LH17 were muddied by suspended sediments caused by elk wading in the ponds prior to planned sampling. The 17 samples were analyzed for total nitrogen, total Kjeldahl nitrogen (TKN), total phosphorus, and orthophosphate-P (PO<sub>4</sub>) by the Cooperative Chemical Analytical Laboratory (CCAL) in the Forest Sciences Laboratory at Oregon State University.

TABLE 2. Qualitative categories used in estimating the habitat characteristics of study ponds.

Category	Measure/Characteristics
Pond Bottom Firmness (HP)	
1	Very soft, readily penetrable, thick flocculent layer (0.7–1.0 m); organic detritus dominated (needles, small woody debris, and CPOM), usually dark brown to almost black in color; no sand visible; typical of deep ponds (1.0–4.0 m); primarily found in forested basins.
2	Soft, moderate to thick flocculent layer (0.1–0.7 m); dark brown in color, no sand visible; typical of deep ponds (1.0–4.0 m); primarily found in forested or partially forested basins.
3	Sandy or muddy sediments; firm with little flocculent material (thin layer of 1–2 cm if present); gray to light brown in color; typical in shallow ponds (< 1 m); found in meadow basins.
4	Very firm hardpan, sand dominated with no flocculent organic matter visible; light to dark gray in color; typical in shallow ponds (< 1 m); found in meadow basins.
Coarse Woody Debris (CWD)	
1	Woody debris covering < 10% of the shoreline or bottom, occasionally none; usually composed of smallest size classes.
2	Woody debris covering 11–25% of the shoreline or bottom; composed of mixed size classes, tending toward smaller sizes.
3	Woody debris covering 26–49% of the shoreline or bottom; composed of mixed size classes, tending toward larger sizes.
4	Woody debris covering > 50% of the shoreline or bottom; composed mostly of larger size classes.
Emergent/Aquatic Vegetation (VEG)	
1	Aquatic vegetation may cover < 2% of water surface and nearshore areas, occasionally none.
2	Aquatic vegetation may cover 2–9% of water surface and nearshore areas.
3	Aquatic vegetation may cover 10–29% of water surface and nearshore areas.
4	Aquatic vegetation may cover > 30% of water surface and nearshore areas.

*Qualitative Habitat Scales.*—Three qualitative scales were developed for visually estimating and characterizing nearshore and offshore habitats (Table 2). The coarse woody debris (CWD) scale included all sizes of woody debris. The emergent/aquatic vegetation (VEG) scale included vegetation that was attached to substra-

tum or freely floating in the water column. The site bottom firmness (HP) scale was estimated by probing the bottom of a site's nearshore area between 70 and 100 cm from shore. This was done every 3–4 m along a site's perimeter and was used to estimate the relative firmness of bottom substrates.

*Statistical Analysis.*—Number Cruncher Statistical Systems 2000 (NCSS 2000; Hintze 1998) was used to analyze physical, water chemistry, and nutrient variables of 17 ponds and lakes. Because water chemistry and nutrient variables were not measured in August for LIW23, LH16, and LH17, they were not included in the statistical analyses of environmental variables. The level of significance for all analyses was  $\alpha = 0.05$ . Water chemistry variables and maximum depth were measured twice in 1996. The 1996 average water chemistry measurements were compared to average values determined between 1993 and 1995. Because no differences in average values were apparent for any of the water chemistry variables, the variables were averaged over the years sampled resulting in an average annual measurement for each variable. Maximum depth was expressed as the average of the 1996 measurements.

Data were initially screened using the multivariate normal procedure to determine whether the 12 environmental variables were normally distributed. Because seven of the variables were found to not be normally distributed, logistic regression with forward variable selection was chosen to examine the relationship between environmental variables and two binary response variables (i.e., presence of *A. gracile*; presence of *A. macrodactylum*; NCSS 2000; Hintze, 1998). This analysis consisted of separating the environmental variables into three groups (i.e., physical, water chemistry, and nutrients) and calculating a regression model based on the relationship between each binary response variable and each environmental variable group. K-Means clustering algorithm was then used to group sites based on the environmental variables determined by logistic regression to be important in creating significant regression models for the presence-absence of both salamander species (NCSS 2000; Hintze, 1998). In this process, site characteristics rather than salamander species were responsible for the association of sites with one another and the grouping of sites into clusters. The nonparametric Spearman Correlation was used to investigate the correlative relationship between elevation, area, maximum depth, LOI, and the three qualitative habitat scales.

## RESULTS

The 1996 larval salamander surveys confirmed that eight of the 20 study sites had al-

TABLE 3. Presence of salamander larvae and the mean and median measurements of physical variables for ponds and lakes in each of three clusters. Cluster variables were pond and lake elevation, maximum depth, and LOI (i.e., loss on ignition or organic content of bottom sediments). Elevation and maximum depth in m; LOI in % and area in m<sup>2</sup>. (A.m. = *Ambystoma macrodactylum*; A.g. = *Ambystoma gracile*).

	No. of lakes	A.m. only	A.g. only	Both species	Elevation	Depth	LOI	Area
Cluster 1	8	8	0	0				
Mean					1815.9	0.66	11.9	959.8
Median					1815.0	0.70	11.1	827.3
Cluster 2	5	0	4	1				
Mean					1717.6	2.58	44.5	3803.9
Median					1726.0	2.43	53.8	3748.0
Cluster 3	4	1	2	1				
Mean					1671.0	0.67	33.4	794.5
Median					1684.0	0.75	39.1	767.7

lotopic larval *A. gracile* populations, 10 sites had allotopic larval *A. macrodactylum* populations, and two sites had syntopic larval *A. gracile* and *A. macrodactylum* (Table 1). The average observed abundances for *A. gracile* ranged from 1.8–58.5 larvae per 100 m, and average observed abundances for *A. macrodactylum* populations ranged from 1.0–211.3 per 100 m. Seven of the eight (87.5%) allotopic *A. gracile* sites were in forested subalpine basins, whereas nine of the 10 (90%) allotopic *A. macrodactylum* sites were in subalpine meadows.

Logistic regression of the three environmental variable groups (i.e., physical, water chemistry, and nutrients) with presence-absence of larvae of *A. gracile* as the binary response variable in 17 study sites identified two significant models. Site elevation and maximum depth were selected as the physical variables responsible for creating one of the models ( $N = 17$ ,  $R^2 = 0.6267$ ,  $\chi^2 = 23.51$ ,  $P = < 0.0001$ ). Total phosphorus (TP) and orthophosphate-P ( $PO_4$ ) were the nutrient variables selected in creating the second model ( $N = 17$ ,  $R^2 = 0.3993$ ,  $\chi^2 = 9.30$ ,  $P = 0.009$ ). No significant model was created using water chemistry variables. When elevation, maximum depth, TP, and  $PO_4$  were used to generate a logistic regression model, elevation and maximum depth were selected over TP and  $PO_4$  ( $N = 17$ ,  $R^2 = 0.6267$ ,  $\chi^2 = 23.51$ ,  $P = < 0.0001$ ). This indicated that site elevation and maximum depth were the most important environmental variables associated with the presence-absence of *A. gracile*.

One significant logistic regression model was created for the three environmental variable groups and presence-absence of *A. macrodactylum*. Site elevation, maximum depth, and percent loss on ignition (LOI) were selected as important physical variables in this model ( $N = 17$ ,  $R^2 = 0.6924$ ,  $\chi^2 = 22.07$ ,  $P = < 0.0001$ ). No signif-

icant models were created for water chemistry or nutrient variables and presence-absence of *A. macrodactylum*.

Site elevation, maximum depth, and percent LOI were then used to cluster the 17 study sites. The three cluster-level was selected for analysis. Eight of the nine allotopic *A. macrodactylum* sites were placed into Cluster 1. The sites in this cluster had the highest mean and median elevations; were relatively shallow with mean and median maximum depths  $< 1$  m; had the lowest mean and median percents LOI; and were relatively small in surface area (i.e., mean and median areas  $< 1000$  m<sup>2</sup>; Table 3, Fig. 2). Cluster 2 was dominated by *A. gracile* sites. Four of the five sites in this cluster had allotopic *A. gracile*, and one syntopic site (LH21) had substantially more observed *A. gracile* than *A. macrodactylum* (Tables 1,3). The sites in this cluster were intermediate in elevation to the sites in Clusters 1 and 3; had the deepest mean and median maximum depths (i.e.,  $> 2$  m); were highest in mean and median percents LOI; and were four to five times larger in surface area than the sites in Clusters 1 and 3 (Table 3, Fig. 2). Four sites were placed into Cluster 3. Two of the sites were populated by *A. gracile*, one site had allotopic *A. macrodactylum*, and one site was syntopic where the observed number of *A. macrodactylum* was over four times greater than the observed number of *A. gracile* (Tables 1,3). The mean and median elevations of the sites in Cluster 3 were the lowest of the three clusters (Table 3, Fig. 2). These sites were also relatively shallow, second highest in mean and median percents LOI, and smallest in mean and median surface areas (i.e.,  $< 800$  m<sup>2</sup>) compared to the other sites (Table 3, Fig. 2).

Habitat characteristics of sites based on the four qualitative categories defining the proportional occurrence of pond bottom firmness (HP), coarse woody debris (CWD), and emer-

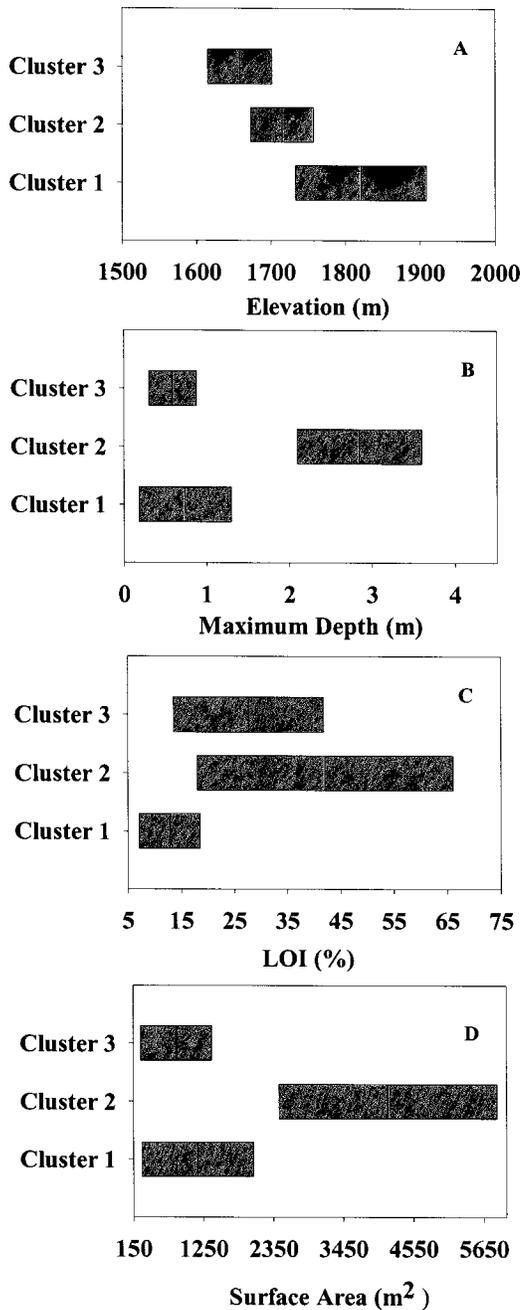


FIG. 2. Ranges for ponds and lakes in each of three clusters: (A) elevation; (B) maximum depth; (C) percent organic content of bottom sediments (LOI); and (D) surface area. Vertical line within bar identifies the mean.

gent/aquatic vegetation (VEG; Table 2) varied between clusters (Table 4). Sites in Cluster 1, with allotopic larval *A. macrodactylum* populations, had a firm HP with limited flocculent-or-

TABLE 4. The percent of ponds and lakes in each cluster assigned to each of four qualitative categories of three major habitat components.

Habitat characteristic and qualitative category	Cluster 1	Cluster 2	Cluster 3
1. Bottom Firmness			
Thick Flocc—very soft	0	60	25
Flocc—soft	0	20	25
Sand/little Flocc—firm	12.5	20	50
Sand—very firm	87.5	0	0
2. Coarse Woody Debris			
< 10% shoreline and bottom	37.5	0	0
11–25% shoreline and bottom	50	0	75
26–49% shoreline and bottom	12.5	40	25
> 50% shoreline and bottom	0	60	0
3. Emergent/Aquatic Vegetation			
< 2% surface and nearshore	25	0	0
2–9% surface and nearshore	12.5	100	0
10–29% surface and nearshore	0	0	0
> 30% surface and nearshore	62.5	0	100

ganic material and  $\leq 25\%$  of the shoreline and bottom of seven of eight sites contained CWD. In five of these sites, VEG was present in  $> 30\%$  of the surface and nearshore area of each site. In Cluster 2, the four allotopic *A. gracile* sites had soft bottom substrates containing flocculent-organic material, whereas the HP of the one syntopic *A. gracile*–*A. macrodactylum* site was relatively firm with small amounts of flocculent material. Relatively high amounts of CWD were observed along the shoreline and bottom of all of the sites in this cluster, and all sites were located in forested subalpine basins. Limited amounts of VEG were observed in Cluster 2 sites. In the two Cluster 3 sites with *A. macrodactylum* (one allotopic, one syntopic), HP was firm with little flocculent-organic material, the presence of CWD was limited to from 11–25% of the shoreline and bottom of each site, and VEG was relatively abundant. The HP of the two allotopic *A. gracile* sites in this cluster was soft with thick flocculent-organic material, a relatively moderate amount of CWD was present at each site, and VEG was abundant.

Elevation, area, LOI, maximum depth, and the three qualitative habitat scales were found to be variously correlated (Table 5). There were strong negative correlations between elevation and LOI, and HP with LOI, maximum depth, and CWD. Strong positive correlations were calculated for elevation and HP, area and maximum depth, and CWD with area, LOI, and maximum depth. All other correlations were low to moderate. Overall, these variables, especially area, maximum depth, CWD, and VEG, were not as strongly correlated with elevation as anticipated because the increase in elevation from the lowest

TABLE 5. Correlations between seven variables used to describe habitats of MORA ponds and lakes inhabited by larvae of *Ambystoma gracile* and *Ambystoma macrodactylum* (LOI = loss on ignition; Depth = maximum depth; HP = bottom firmness; CWD = coarse woody debris; VEG = emergent/aquatic vegetation).

	Elevation	Area	LOI	Depth	HP	CWD
Area	-0.1495					
LOI	-0.7255	0.3873				
Depth	-0.2948	0.8084	0.5504			
HP	0.7636	-0.4919	-0.8692	-0.6364		
CWD	-0.4524	0.7672	0.7043	0.8773	-0.7137	
VEG	-0.3148	-0.3216	-0.0668	-0.4198	0.0680	-0.3351

study site (1615 m) to the highest site (1909 m) was small (294 m) relative to potential differences in elevation among sites in the Cascade Mountains of the Pacific Northwest.

The physical and habitat characteristics of the three sites not used in the statistical analysis were similar to the characteristics of sites in Clusters 1 and 2. LIW23, with allotopic *A. macrodactylum*, was similar to sites in Cluster 1. This site, although having a relatively moderate LOI of 24.2 %, was high in elevation (1794 m), very shallow (maximum depth = 0.25 m), and quite small (surface area = 367.2 m<sup>2</sup>). The pond had a very firm bottom substrate (4 on the HP qualitative category scale), limited coarse wood (1 on the CWD qualitative category scale), and abundant emergent/aquatic vegetation (4 on the VEG qualitative category scale). The two allotopic *A. gracile* sites, LH16 and LH17, were similar to the sites in Cluster 2. Both sites were quite large (3170 m<sup>2</sup> and 6169 m<sup>2</sup>, respectively) and had maximum depths approximately 2 m. LOI was moderate (25.1 % and 31.2 %, respectively) and their elevations were 1704 m and 1781 m, respectively. These were sites with soft, flocculent-organic bottom substrates (2 on the HP qualitative category scale); high to moderate presence of CWD (4 and 3, respectively, on the CWD qualitative category scale); and moderate amounts of emergent/aquatic vegetation (3 and 2, respectively, on the VEG qualitative category scale).

#### DISCUSSION

Eighteen of 20 populations of larval *A. gracile* and *A. macrodactylum* surveyed in this study were distributed allotopically in two watersheds in the northeast quadrant of MORA, and inhabited ponds and lakes with different habitat characteristics. *Ambystoma gracile* inhabited large, deep lakes and ponds in forested subalpine basins at elevations relatively lower than ponds inhabited by *A. macrodactylum*. Each *A. gracile* study site was inhabited by large neotenes (i.e., gilled adults) that ranged in size from approximately 80 mm SVL to  $\geq$  94 mm SVL, and accounted for a relatively large proportion of the

individuals observed at these sites (RLH, pers. obs.; MORA unpubl. data). Neotenes also appeared to be responsible for most, if not all of the reproductive effort in these ponds since terrestrial *A. gracile* adults were rarely to occasionally observed in or near the ponds. *Ambystoma gracile* lakes and ponds had soft, flocculent bottoms high in organic content, contain abundant coarse woody debris, and low to moderate amounts of emergent/aquatic vegetation. *Ambystoma macrodactylum* inhabited small, shallow ponds in subalpine meadows at elevations relatively higher than *A. gracile*. These ponds had firm bottom substrates low in organic content, relatively low amounts of coarse wood, and abundant emergent/aquatic vegetation.

There are exceptions to these general trends. Two *A. gracile* sites, LH19 and LW14, although similar to other *A. gracile* sites in elevation, basin-type, high organic content of bottom substrates, and relative presence of coarse wood, were small in size compared to the other *A. gracile* ponds and lakes (Table 1). LH19 was also the shallowest *A. gracile* site, yet deeper than all but one *A. macrodactylum* pond (Table 1). The *A. macrodactylum* pond UK13, although quite small and shallow (Table 1), differed from the other *A. macrodactylum* ponds by having a bottom substrate with high organic content (i.e., LOI = 42%) that was similar to the average LOI of the allotopic *A. gracile* ponds in Cluster 2 (Table 3). Larvae occurred syntopically in two ponds (i.e., LH21 and LW15). Habitat characteristics of sites with allotopic populations of each species were present in each of these ponds. In LH21, *A. gracile* larvae outnumbered *A. macrodactylum* larvae (Table 1). The nearshore margins of LH21 were shallow and covered with emergent/aquatic vegetation, while a large, deep "trough" (8–10 m long by 2 m wide) was present in the middle of the pond. This "trough" was surrounded by and filled with flocculent-organic material (LOI = 30.3%) and coarse woody debris. *Ambystoma gracile* larvae were common in the "trough," yet rare in the shallows, whereas *A. macrodactylum* larvae were observed primarily in the vegetated shallows of the pond. The dominant species in

LW15 was *A. macrodactylum* (Table 1). The substrate near the edge of this pond, where *A. macrodactylum* larvae and hatchlings of both species were typically observed, was firm, low in organic content (LOI = 13.6%), and covered by emergent sedges and grasses as in other allotopic *A. macrodactylum* ponds. Near the center of the pond, however, was a small (2–3 m long by 0.80–1.0 m wide) and relatively deep “hole” with a soft, flocculent bottom and coarse woody debris. This “hole” was inhabited by large bodied larvae of *A. gracile*.

The general restriction of larvae of *A. gracile* in MORA to permanent large, deep, soft-bottomed lakes in forested subalpine basins can be explained, in part, by developmental and reproductive patterns of montane *A. gracile*. Larvae in montane populations develop more slowly than larvae in ponds and lakes at lower elevations (Eagleson, 1976), and the proportion of gilled adults (i.e., neotenes) in populations increases with increasing elevation (Snyder, 1956; Eagleson, 1976; Titus and Gaines, 1991). Individuals in montane populations may metamorphose during their third year, but a large proportion of individuals spend their lives in ponds and lakes without transforming (Snyder, 1956; Eagleson, 1976). In ponds at sea level, larvae typically metamorphose within one to two years after hatching (Snyder, 1956). Although time and length of oviposition varies between low- and high-elevation *A. gracile*, reproductive strategies of the populations are similar. In particular, females always attach their single, firm, globular, gelatinous egg masses to sturdy support structures such as stalks of aquatic plants and reeds, cattails, twigs and limbs, and the small branches of fallen trees (Slater 1936; Watney 1941; Knudsen 1960; Petranka 1998), with limbs and branches being primary attachment sites in the MORA populations (RLH, pers. obs.). These structures are common and abundant in lakes and ponds in forested subalpine basins, but their presence decreases in lakes and ponds in subalpine meadows and alpine basins.

Inhabiting permanent, hydrologically stable and relatively deep lentic systems enhances the ability of slow developing larvae of *A. gracile* in populations dominated by gilled adults (i.e., neotenes) to survive potentially harsh and lethal montane winter and summer climatic conditions. The winter cover of montane ponds and lakes is composed of ice, snow, and slush, creating a complex stratigraphic structure that episodically freezes, melts, floods, and refreezes through the winter (Catalan, 1989; Felip et al., 1999). MORA ponds and lakes are typically covered by thin surface ice, slush, and thick snowpack (i.e.,  $\geq 3$  m deep) for approximately seven to nine months per year (Larson, 1973). Under

these conditions, many shallow ponds would be filled with ice, slush, and snowpack to the pond bottom, and water temperatures would be quite cold. In deeper ponds and lakes, unfrozen water would be present between the pond or lake bottom and the bottom of the snowpack layer and surface ice (Larson, 1973; RLH, pers. obs.). This column of water as well as the relatively thick layer of flocculent material might act as an insular layer covering the bottom of deeper ponds and provide a winter retreat for larvae of *A. gracile* during periods of reduced larval activity or winter dormancy. During periods of summer drought, small, shallow ponds can dry relatively quickly (i.e. from 1–2 months; Girdner and Larson, 1995). Because larvae of *A. gracile* in montane populations cannot typically develop and transform this rapidly (Snyder, 1956), they would not survive pond drying.

Unlike *A. gracile*, *A. macrodactylum* inhabits diverse habitats throughout its range (Ferguson, 1961; Anderson, 1967; Nussbaum et al., 1983; Howard and Wallace, 1985; Leonard et al., 1993) and is considered the most adaptable and variable salamander species in the Pacific Northwest (Ferguson, 1961). This plasticity is seen in montane populations that express one of three life-history patterns, which vary according to the length of time to larval transformation and the size, elevation, stability, and permanence of the lentic system they inhabit (Kezer and Farner, 1955). Individuals in ephemeral and small shallow semipermanent ponds can develop in 80–90 days after hatching to metamorphose at relatively small size (e.g., approximately 25–30 mm SVL; Kezer and Farner 1955; Anderson 1967; Howard and Wallace 1985). In larger permanent ponds and lakes, individuals often metamorphose 14 months after hatching when they are approximately 38–47 mm SVL (Kezer and Farner 1955; Anderson 1967; Howard and Wallace 1985). Yet, in MORA, larvae of *A. macrodactylum* are restricted primarily to small shallow semipermanent and permanent ponds. We have often observed embryos and adults of *A. macrodactylum* in allotopic *A. gracile* ponds but have not detected *A. macrodactylum* larvae in these ponds. Conversely, we have not observed *A. gracile* egg masses or adults in allotopic *A. macrodactylum* ponds.

In the North Cascades National Park Service Complex (NOCA), approximately 150 km north of MORA, *A. gracile* do not occur east of the hydrologic crest of the Cascade Range. *Ambystoma macrodactylum* is the only salamander species found in ponds and lakes on this side of NOCA. In the absence of *A. gracile* and fish, *A. macrodactylum* larvae are able to inhabit diverse types of east side NOCA systems from small shallow ponds (e.g., 0.2-ha surface area and 1.2 m max-

imum depth) to large deep lakes (e.g., 4.1-ha surface area and 11.9 m maximum depth) ranging in elevation from 662–2033 m (T. Tyler, pers. comm.; NOCA unpubl. data). Habitat structure of these ponds and lakes is also diverse, ranging from sites with flocculent bottoms and coarse woody debris to sites with firm bottoms, rocky substrate, and little coarse wood (T. Tyler, pers. comm.; NOCA unpubl. data). On the west side of NOCA, allotopic *A. gracile* and *A. macrodactylum* populations generally inhabit systems similar to those inhabited by each species in MORA (Tyler et al., 1998; NOCA unpubl. data) although in the absence of *A. gracile*, *A. macrodactylum* larvae can also be found in relatively larger deeper west side NOCA ponds and lakes (NOCA unpubl. data). These results indicate that the habitat characteristics of ponds and lakes might not be solely responsible for the distributions of *A. macrodactylum* larval populations in MORA.

There is some circumstantial evidence that interspecific interactions between *A. gracile* and *A. macrodactylum* larvae could be partly responsible for the allotopic distributions of these species in MORA. Field experiments in the northeast quadrant of MORA showed that *A. gracile* larvae (58–94 mm SVL), when given the opportunity, will readily consume *A. macrodactylum* hatchlings (10–15 mm total length; Hoffman and Larson, 1999). This predation could potentially lead to the exclusion of *A. macrodactylum* larvae from ponds inhabited by *A. gracile* larvae. The local distributions of several other *Ambystoma* species (e.g., *A. maculatum*, *A. opacum* [Gravenhorst], and *A. talpoideum*) have also been shown to be partly affected by interspecific predatory and competitive interactions (Stenhouse et al., 1983; Stenhouse, 1985; Walls and Jaeger, 1987).

Complex and multidimensional patterns of environmental factors and conditions directly influence the distributions and persistence of species (Warren and Liss, 1980). Pond and lake elevation, maximum depth, size, percent organic content of pond and lake bottom, as well as the presence and amount of coarse woody debris and emergent/aquatic vegetation have been identified as environmental factors affecting the distributions of *A. gracile* and *A. macrodactylum* larval populations in MORA. Although the habitat characteristics of lentic systems inhabited by each species have previously been documented, differences between the habitat characteristics of montane ponds and lakes occupied by allotopic populations of these species have not been identified or compared at the landscape-level. Circumstantial and observational evidence also suggest that the distributions of the two species in MORA are additionally affected by interspecific interactions that have been shown to affect

the levels of coexistence and distributions of several *Ambystoma* species. Understanding the overall impact of these interactions on the distributions of *A. gracile* and *A. macrodactylum* larvae in MORA lakes and ponds will certainly require further investigation. The results of the present study provide additional support for the concept that the distributions and persistence of organisms and their capacity to adapt life-history strategies concordant with the dynamic physical and biological conditions of the environments they inhabit are intimately connected.

*Acknowledgments.*—The authors would like to thank B. Samora and Mount Rainier National Park for supporting and partially funding this research; the personnel at USGS Forest and Rangeland Ecosystem Science Center for their support and technical assistance; N. Leuthold for his outstanding assistance in the field; and D. Swinney for his GIS technical ingenuity and expertise.

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Accepted: 1 April 2002.