

AN ABSTRACT OF THE THESIS OF

Brendan J. Brokes for the degree of Master of Science in Fisheries Science presented on October 7, 1999. Title: Habitat Segregation of Two Ambystomatids in Mountain Ponds, Mount Rainier National Park.

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Abstract approved: _____

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Ambystoma macrodactylum (long-toed salamander) and *A. gracile* (northwestern salamander) are two common salamander species occupying key trophic positions in mountain ponds of Mount Rainier National Park. The objective of this research was to document and evaluate the distributions and abundances of the two species, relative to habitat characteristics of ponds in the park.

Amphibian distributions and abundances were assessed in 20 ponds from June through September 1993 to 1996. Nutrient concentrations (total nitrogen, Kjeldahl-N, total phosphorus, and orthophosphate-P), habitat characteristics (surface area, depth, elevation, substratum organic content lost on ignition, amount of coarse woody debris, aquatic vegetation, and bottom firmness), and water quality (temperature, dissolved oxygen, alkalinity, conductivity, and pH) were measured.

Distinct habitat associations were found for each *Ambystoma* species. Ponds with one species only were different in surface area, maximum depth, substratum organic content, and elevation. Ponds with *A. macrodactylum* were small, shallow, high in elevation, and had firm sediments low in organic matter relative to *A. gracile* ponds. *Ambystoma macrodactylum* ponds typically contained little coarse woody debris relative to the amount of aquatic vegetation. *Ambystoma gracile* ponds were large, deep, low in

elevation, had flocculent sediment high in organic content, abundant coarse woody debris, and little aquatic vegetation relative to *A. macrodactylum* ponds. Two ponds supported reproducing populations of both species and exhibited habitat characteristics intermediate to the allopatric pond types. These findings suggest that habitat complexity plays an important role in the segregation of *A. macrodactylum* and *A. gracile*.

Habitat Segregation of Two Ambystomatids in Mountain Ponds,
Mount Rainier National Park.

by

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Habitat Segregation of Two Ambystomatids in Mountain Ponds, Mount Rainier National Park

INTRODUCTION

Ambystoma macrodactylum (long-toed salamander) and *Ambystoma gracile* (northwestern salamander), of the family Ambystomatidae, commonly breed in montane lakes and ponds on the western slopes and crest of the Cascade Range (Nussbaum et al., 1983; Leonard et al., 1993; Corkran and Thoms, 1996). These species can be quite numerous and occupy key trophic positions in aquatic and terrestrial systems (Blaustein et al., 1995; Holomuzki, 1986, 1989; Holomuzki and Collins, 1987). In the absence of fish, the two species are the top aquatic vertebrate predators in these ponds and lakes.

Ambystoma macrodactylum is the most widely distributed salamander taxon in Washington and Oregon. It inhabits a variety of habitats, including agricultural areas, humid forests, coastal ponds, subalpine and alpine meadows, mountain lakes and ponds, and sagebrush communities (Ferguson, 1961; Anderson, 1967; Howard and Wallace, 1985). It ranges from southeast Alaska, British Columbia, and western Alberta, to western Montana, Idaho, Washington, Oregon, and California (Nussbaum et al., 1983; Leonard et al., 1993; Corkran and Thoms, 1996). Across its range, *A. macrodactylum* breeds in slow-flowing streams, ponds, and lakes (ephemeral and permanent) from sea level to 2500 m elevation (Corkran and Thoms, 1996). Certain environmental factors appear to influence the life history and development of this species. The location of egg deposition varies with the availability of suitable attachment sites (Howard and Wallace, 1985). Egg cluster-size seems to vary with elevation and the occurrence of single eggs increases with increased elevation (Howard and Wallace, 1985; A. Blaustein, personal

communication). The length of the larval period is likewise influenced by elevation, ranging from three months at 1140 m to upwards of 48 months at elevations greater than 2100 m (Anderson, 1967; Howard and Wallace, 1985). In fishless mountain ponds and lakes at North Cascades National Park Service Complex (NOCA), Tyler et al. (1998) showed that *A. macrodactylum* larval densities were low in lakes with less than 0.045 mg/L total Kjeldahl-N, but increased in density with increasing concentrations of total Kjeldahl-N.

Neither paedomorphosis nor neoteny are known to exist in this species, yet Anderson (1967) and Sprules (1974a) suggested that *A. macrodactylum* may be paedogenic in high-elevation lakes that are deep and cold. Although *A. macrodactylum* has been observed to breed sympatrically with *A. tigrinum*, *Taricha granulosa*, and some anurans, there is no documented evidence of *A. macrodactylum* breeding sympatrically with *A. gracile* (Farner, 1947; Kezer and Farner, 1955; Efford and Mathias, 1969; Anderson, 1967, 1968; Neish, 1971; Taylor, 1984).

Ambystoma gracile is distributed from extreme southeastern Alaska and western British Columbia to northwestern California and is commonly encountered in mountain ponds and lakes of the Cascade Range and Olympic Mountains. It can be found from sea level to about 2000 m (Leonard et al., 1993; Corkran and Thoms, 1996). Terrestrial adults are found from moist lowland forests to subalpine forests, usually under the cover of rotting logs and bark. Adults breed in slow-flowing streams, semi-permanent and permanent ponds, and lakes (Nussbaum et al., 1983). Flocculent sediments, aquatic macrophytes, and woody debris are essential structural components of cover and egg attachment sites for *A. gracile* (Slater 1936; Snyder 1956; Taylor 1983b; Efford and

Mathias 1969; Petranka 1998). Eggs are laid in egg masses that usually range in number from 40 to 270 (Nussbaum et al., 1983). There is no evidence that *A. gracile* deposits solitary eggs. In lowland populations, most larvae metamorphose when approximately 12-14 months old (Snyder, 1956; Eagleson, 1976; Licht, 1975). Larvae in montane systems develop more slowly than do larvae in lowland systems, sometimes not metamorphosing in the third year (Sprules, 1974a; and Eagleson, 1976). Furthermore, the incidence of neoteny, or gilled adults, increases with elevation due to factors such as the stability of the environment and decreasing water temperatures (Sprules, 1974b; Eagleson, 1976; Petranka, 1998; Pough, 1998). Neoteny is common among montane *A. gracile* populations in Mount Rainier National Park (MORA) (Snyder, 1956), yet is uncommon in the low elevation (70 m) Little Cambell River in southwestern British Columbia (Licht, 1975). *Ambystoma gracile* breeds sympatrically with *T. granulosa* and some anurans (Efford and Mathias, 1969; Neish, 1971; Efford and Tsumura, 1973).

During the period from 1990 to 1995, amphibian surveys (Barbara Samora; unpublished park data) were conducted in Mount Rainier National Park to determine amphibian distributions, abundances, and species richness. These surveys suggested ostensible differences between the habitats utilized by *A. macrodactylum* and *A. gracile*. The goals of this research were to document and evaluate potential differences in the distributions and abundances of *A. macrodactylum* and *A. gracile* in fishless ponds, to document the apparent habitat segregation of *A. macrodactylum* and *A. gracile* and to assess the primary habitat characteristics of these systems. First, were there specific habitat differences between ponds with *A. macrodactylum* and *A. gracile*? Second, in

particular, were there differences in water quality, temperature, and nutrient concentrations between *A. macrodactylum* and *A. gracile* systems?

STUDY AREA

Mount Rainier National Park, located in southwestern Washington on the western slope of the Cascade Range (Figure 1), occupies 979.5 km² and ranges in elevation from approximately 533 m to 4392 m. The study area was located near Sunrise (park facilities) in the northeast corner of the park and included portions of Huckleberry Creek and Sunrise Creek basins that drained the Sourdough Mountains (Figure 2).

The study area was largely dominated by a relatively dry subalpine forest community due to the rain shadow effects of Mount Rainier. Subalpine fir (*Abies lasiocarpa*), mountain hemlock (*Tsuga mertensiana*), western redcedar (*Thuja plicata*), Alaska yellow cedar (*Chamaecyparis nootkatensis*), whitebark pine (*Pinus albicaulis*), and Pacific silver fir (*Abies amabilis*) account for the majority of the tree types found in the Huckleberry Creek and Sunrise Creek catchments (Franklin et al., 1988). The 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 to alpine wildflowers (Franklin et al., 1988).

The geomorphology of the area was created by volcanic activity from Mount Rainier. The Cascade Range upon which the volcano stands is older, being composed of a complex of sedimentary and igneous rocks approximately 20 to 60 million years old (Crandell, 1969). Ancestral eruptions of Mt. Rainier resulted in vast lava flows of gray andesite which resisted erosion and formed ridges and plateaus (e.g., Sourdough Mountains; Fiske et al., 1963). These andesitic flows and the previously existing

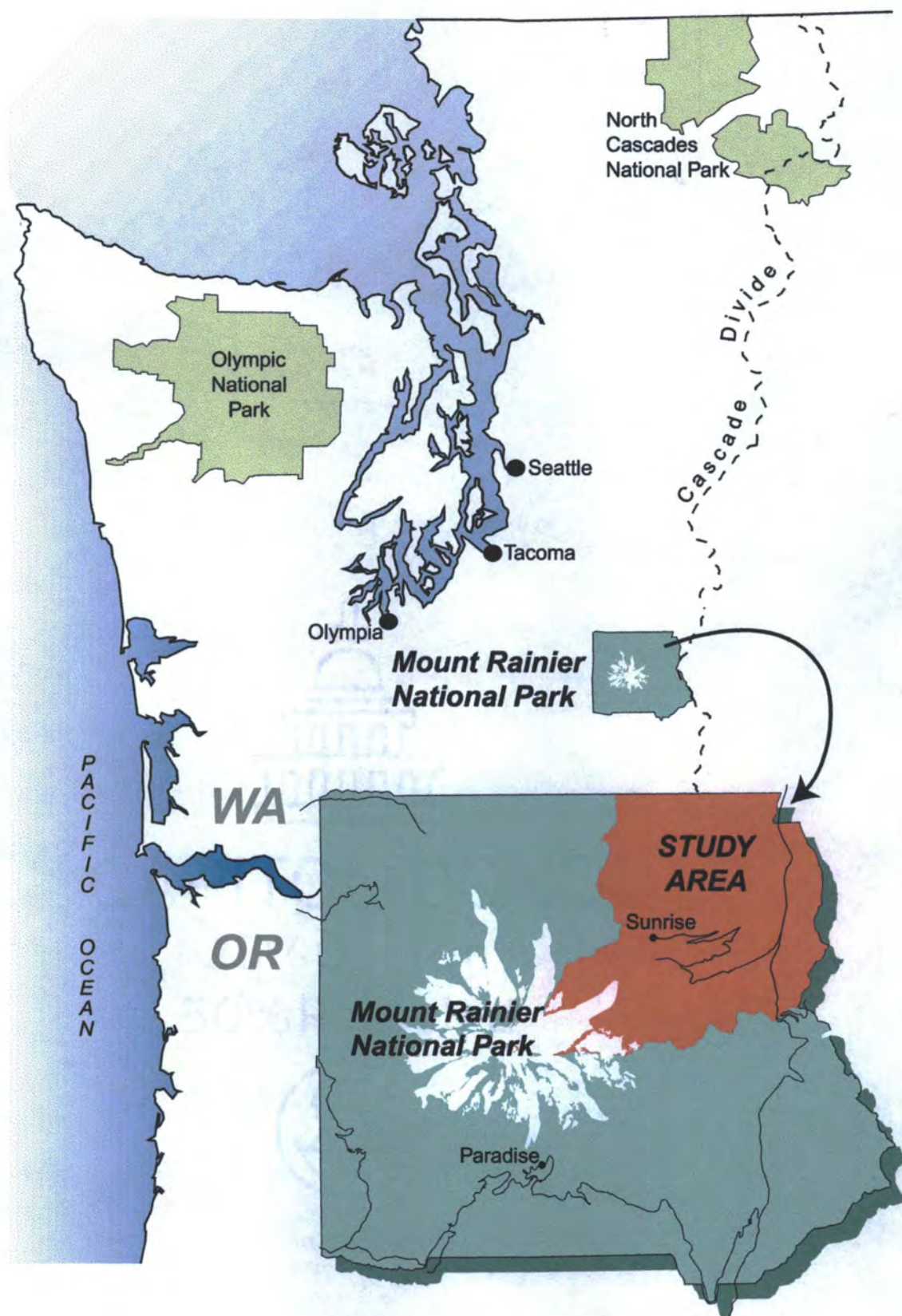


Figure 1. Location of study area in Mount Rainier National Park.

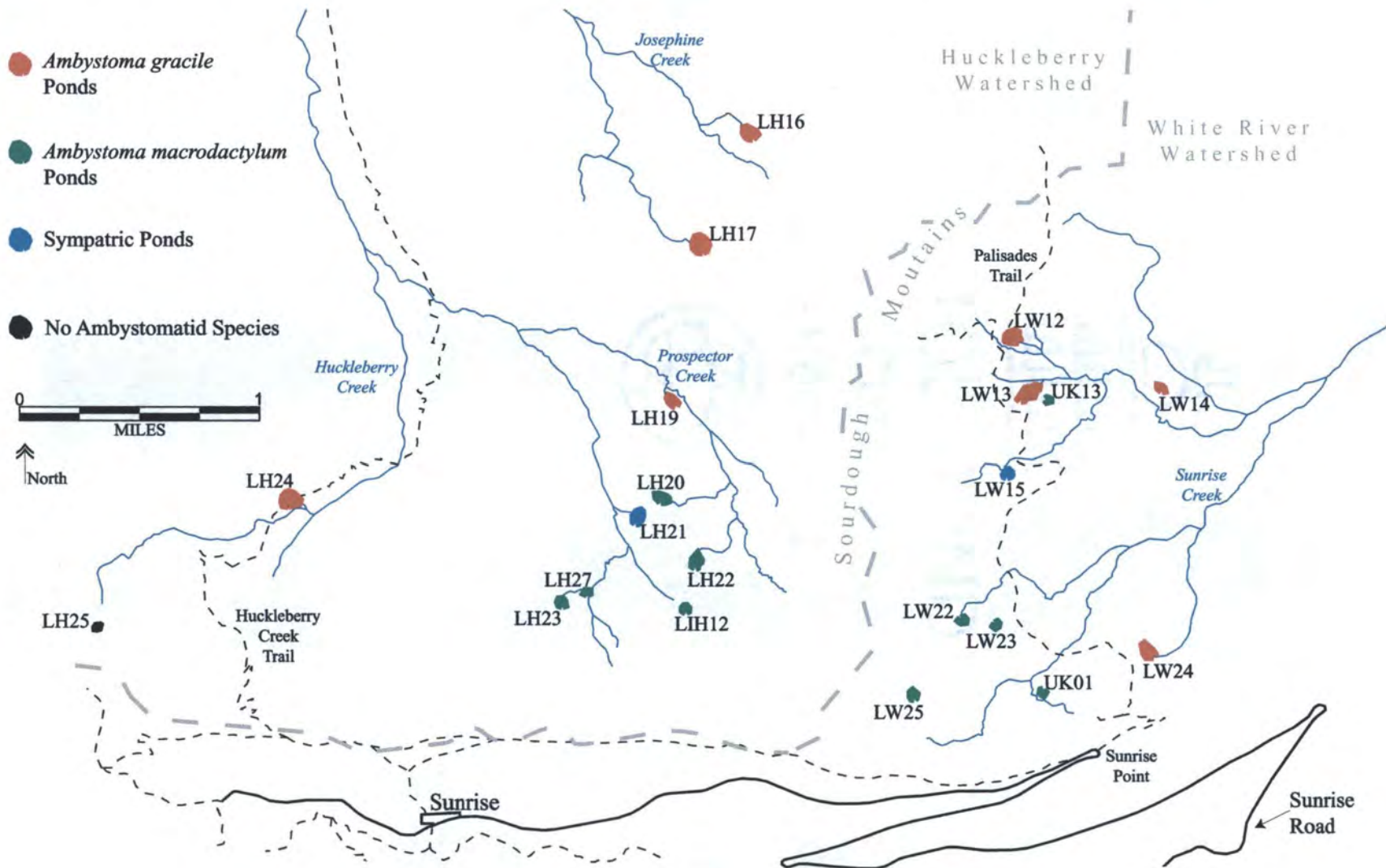


Figure 2. Distributions of Ambystomatid species and location of study ponds in Mount Rainier National Park.

granodiorite resulted in the relatively low buffering capacities of the lakes and ponds in these basins. Mount Rainier has erupted four times during the last 10,000 years, the most recent occurring 2,300 years ago (Mullineaux, 1974).

Annual precipitation at Paradise, located in the southwest portion of the park (Figure 1), has averaged over 43 cm during the period from 1939 – 1996. The annual depth of the snowpack has ranged from 8 m (1939 - 40) to 28.5 m (1970 - 1971), and the annual depth of the snowpack has averaged 15.9 m (1920 - 1996, MORA records). Sunrise, however, received significantly less precipitation than Paradise, but the exact amount was not known because snowpack depth was not recorded on the eastside of the Park. In the Sunrise area, snowfall has typically begun in late September, with occasional snowstorms in August and early September. The snowpack typically has disappeared by mid-June at elevations of 1375 m and above, with some higher-elevation lakes not thawing until mid-August.

A herd of approximately 1000 elk (*Cervus elaphus*) inhabited the eastern half of the park. Many of the shallow ponds were used heavily by the elk as water sources. The elk caused considerable physical disturbance by wading in the ponds, and also urinated and defecated in the ponds.

During the 1993, 1994, and 1995 field seasons in the Sunrise Creek and Huckleberry Creek catchments, 11 ephemeral and permanent ponds were inhabited by *A. macrodactylum* and 16 permanent ponds were inhabited by *A. gracile*. *Ambystoma macrodactylum* and *A. gracile* embryos were observed in six ponds (LH19, LH21, LW12, LW13, LW15, and LW24).

From this set of 27 ponds, the 11 ponds inhabited predominantly by *A. macrodactylum*, and nine randomly selected ponds inhabited predominantly by *A. gracile* were sampled in 1996 (Table 1). The ponds were ice-free for a relatively short period during summer (i.e., early July until mid-September). All systems were fishless.

Table 1. Physical characteristics of twenty fishless mountain ponds in the northeast quadrant of Mount Rainier National Park, 1996.

| M /G ^a | Lake | Elevation (m) | Area (m ²) | Depth (m) | Basin (vegetation) |
|-------------------|--------------------|------------------|---------------------------|--------------|-----------------------|
| G | LH16 | 1704 | 3170.00 | 2.10 | Forest |
| G | LH17 | 1781 | 6169.00 | 1.94 | Meadow |
| G | LH19 | 1696 | 1376.00 | 0.88 | Forest |
| M | LH20 | 1764 | 1742.00 | 0.71 | Meadow |
| G>M | LH21 ^b | 1757 | 2439.00 | 2.10 | Forest |
| M | LH22 | 1806 | 2038.00 | 0.70 | Forest |
| M | LH23 | 1843 | 980.00 | 1.30 | Meadow |
| G | LH24 | 1730 | 5854.00 | 2.43 | Forest |
| M | LH27 | 1821 | 284.38 | 0.70 | Meadow |
| M | LIH12 ^c | 1842 | 714.58 | 0.18 | Meadow |
| G | LW12 | 1726 | 3748.00 | 2.14 | Forest |
| G | LW13 | 1673 | 4338.30 | 2.60 | Forest |
| G | LW14 | 1615 | 502.00 | 0.70 | Forest |
| M>G | LW15 ^b | 1701 | 1033.52 | 0.80 | Meadow |
| M | LW22 | 1809 | 583.16 | 0.78 | Meadow |
| G | LW24 | 1702 | 2640.00 | 3.64 | Forest |
| M | LW25 | 1909 | 940.00 | 0.41 | Meadow |
| M | LIW23 ^c | 1794 | 367.16 | 0.25 | Meadow |
| M | UK01 | 1733 | 396.17 | 0.51 | Meadow |
| M | UK13 | 1672 | 266.44 | 0.30 | Forest |

^{a)} M Indicates allopatric *A. macrodactylum* pond.

G Indicates allopatric *A. gracile* pond.

^{b)} Indicates sympatric pond.

^{c)} Indicates ephemeral pond.

METHODS

Sampling Schedule

The primary focus of the field work was to document: (1) salamander species richness, life history stage, distribution, and abundance; (2) pond water quality and nutrient concentrations; and (3) pond morphology and habitat characteristics, including the abundance of aquatic vegetation, the abundance of coarse woody debris, and the relative firmness and organic content of sediments (hardpan scale or HP). Study ponds were sampled as soon as possible after ice-out in July, 1996. A second sampling took place during August. From 1993 - 1995 some ponds also were sampled from June - September (unpublished park data).

Salamander Distributions and Abundances

Salamander distributions and abundances were assessed either by snorkel surveys or visual encounter surveys where systems were too shallow to snorkel. Generally, two people were involved in both techniques. Snorkeling was accomplished by swimming transects to determine the species and number of adults, larvae, and egg masses. Due to pond size variation, standardized transect lengths were not practical. The lengths and locations of pond transects were determined by estimating the percentage of various nearshore habitat types around each pond (i.e., vegetated, sandy, woody debris, talus), then selecting transect lengths proportional to these percentages in the appropriate locations. Individual larvae fleeing from within transect boundaries were included in the tally. When the snorkeler was in the water, the second individual followed closely (3 m

maximum) to record data and enumerate salamanders in the areas too shallow for the snorkeler to access. Salamander numbers were expressed as the number of individuals or egg masses per 100 m of shoreline. The nearshore area was snorkeled to a depth of approximately 1 m (or diver's reach). The snorkeler sorted and searched, in a zigzag pattern, through all potential cover (capable of being safely moved) for salamanders in the nearshore habitat (Tyler et al., 1998). The snorkeler carried a dive light and dipnet to aid in searching and species identification. Salamanders, upon disturbance, often burrowed deeply into the soft, flocculent bottoms and rendered further observations impossible (Taylor, 1983b). All animals associated with substrate, as well as free-floating individuals, were recorded.

The entire shorelines of small ponds were surveyed when possible, but time constraints prevented surveying the entire shorelines of large ponds. A minimum of 100 m was surveyed at each pond with a perimeter measurement greater than 100 m. The minimum and maximum individual transect lengths were 32.0 m and 193.7 m, respectively.

Visual encounter surveys were performed by searching for salamanders while slowly walking/wading the shoreline and nearshore areas, in a zigzag pattern, to a depth of approximately 0.7 m. If the nearshore area was narrow (2 - 3 m) one surveyor walked/waded the pond's edge while the other recorded data, and performed the collection of other data (e.g. pH, D.O., etc.). If the nearshore area exceeded 2 - 3 m in width, or aquatic vegetation was densely distributed, two surveyors worked in tandem approximately 2 - 3 m apart. The surveyors carried dipnets for capturing salamanders to aid in species identification.

Based on field experience, pond depth was the primary criterion used to determine which survey technique was employed at each site. In ponds less than 0.5 m deep, snorkeling was not possible because the diver was unable to remain buoyant. Although pond depths of 0.5 – 0.7 m were sufficient to maintain buoyancy, the diver's movements increased turbidity in the water column thereby reducing visibility and biasing the number of salamanders observed. Therefore, salamander relative abundance was sampled by visual encounter surveys in ponds less than 0.7 m deep, and snorkeling was used in ponds equal to or greater than 0.7 m deep.

A comparison of snorkel surveys and visual encounter surveys was conducted to evaluate the two techniques. Each technique was performed at three locations (LH20, LH23, and LH27; Table 1). These ponds were deep enough to sample by snorkeling, but because the habitat complexity of these ponds was similar to systems routinely surveyed by visual encounter survey, they served as appropriate comparison sites.

Inherent biases exist in all sampling methodologies, and it should be noted that combining data, gathered from two survey techniques (snorkeling and visual encounter surveys), could present certain biases. Generally, when small and shallow ponds (i.e., $< 2000 \text{ m}^2$, and $< 0.7 \text{ m}$, respectively) were visually surveyed, the observer viewed up to one-half the pond width from one shore, and the other half from the opposite shore, thereby having effectively surveyed the entire area of the pond. All these data were used in the analysis. However, the numbers of salamander larvae enumerated by snorkeling the deep water areas ($> 2 \text{ m}$) of large ponds ($> 2000 \text{ m}^2$) were not included in the pond-to-pond comparisons because: 1) small larvae ($< \text{approximately } 25 \text{ mm}$, total length) were difficult to detect; and 2) small larvae were difficult to accurately identify to species.

Therefore, the numbers of salamander larvae enumerated in large ponds, relative to each species, were possibly underestimated. Large ponds also contained relatively more woody debris than small ponds (Table 2), and even though snorkelers sorted and searched through all potential cover for larvae, this could also affect survey counts.

Ambystoma macrodactylum are diurnal (Anderson, 1967; Petranka, 1998), whereas, *A. gracile* can be diurnal or nocturnal (Efford and Mathias, 1969; Sprules, 1974a; Branch and Altig, 1981; Taylor, 1983b; and Petranka, 1998). Tyler et al. (1998) found no differences in abundance between day and night surveys for *A. macrodactylum*. Analyses are based on day surveys; thus the abundances of *A. gracile* are probably underestimated.

Salamander species identification was based on characteristics presented by Nussbaum et al. (1983), Leonard et al. (1993), Corkran and Thoms (1995), and Stebbins (1985). In cases in which larval identities were in question, they were captured and reared in a park laboratory until positive species identification were possible.

Pond Physical Characteristics

Pond surface areas were determined by digitizing 7 1/2-min. USGS topographic maps into Geographical Information System (GIS) software (ARC-Info and ARC-View). Surface areas were expressed in meters squared (m^2) because of the relatively small size of these ponds. Maximum depth (± 0.1 m) was recorded each time a pond was sampled. Changes in water lines and new additions or losses in cover/habitat (e.g. downed trees or log jams) were documented on bathymetric maps and through photography at each

sampling. Pond elevations were determined from field altimeter readings and 7 1/2-min. USGS topographic maps.

Substratum Samples

Bottom substrate samples were taken in August from 20 ponds in order to determine the organic content in the different sediment types found in these systems. Samples were collected by forcing a bevel-ended section of PVC pipe (3.5-inch diameter) into the sediments (approximately 25 cm), capping the ends, and extracting approximately two liters of bottom substrate. The sample was allowed to settle for 10 minutes before pouring off excess water, and then transferred to dark Nalgene™ bottles and frozen. They were thawed and desiccated in an oven (24 hrs.) to remove any remaining water and then weighed. The resulting dry samples were then ashed in a muffle furnace for 20 minutes (550° C), transferred to a desiccator for final cooling, then re-weighed. The resulting weight was subtracted from the dry weight to determine the organic content of the sediments (loss-on-ignition or LOI).

Categories of Three Qualitative Measures

Three qualitative “measures” were developed for visually estimating and characterizing nearshore and offshore habitats (Table 2): coarse woody debris (CWD, all sizes); aquatic vegetation (VEG), and pond bottom firmness (hardpan measure, HP). The aquatic vegetation scale included vegetation that was attached to the substratum and freely floating in the water column. The hardpan (HP) scale was created by walking a

Table 2. Qualitative habitat categories used in estimating the abundances of coarse woody debris (CWD), aquatic vegetation (VEG), and pond bottom firmness (HP) for the 20 study ponds.

| Category | Measure / Characteristics | Ponds | | | |
|----------|--|----------------------|----------------------|--------------|---------------|
| CWD | | | | | |
| 1 | Woody debris covering < 10 % of the shoreline or bottom, occasionally none; usually composed of smallest size classes. | LH27 | LH12 | LIW23 | LW25 |
| 2 | Woody debris covering 11 - 25 % of the shoreline or bottom; composed of mixed size classes, tending toward smaller sizes. | LH20 LW22 | LH22 UK01 | LW14 UK13 | LW15 |
| 3 | Woody debris covering 26 - 49 % of the shoreline or bottom; composed of mixed size classes, tending toward larger size classes. | LH17 LW24 | LH19 | LH21 | LH23 |
| 4 | Woody debris covering > 50 % of the shoreline or bottom; composed mostly of larger size classes. | LH16 | LH24 | LW12 | LW13 |
| VEG | | | | | |
| 1 | Aquatic vegetation may cover < 2 % of water surface and nearshore areas, occasionally none. | LH23 | LH27 | | |
| 2 | Aquatic vegetation may cover between 2 - 9 % of water surface and nearshore areas. | LH17 LW13 | LH21 LW24 | LH24 LW25 | LW12 |
| 3 | Aquatic vegetation may cover between 10 - 29 % of water surface and nearshore areas. | LH16 | | | |
| 4 | Aquatic vegetation may cover > 30 % of water surface and nearshore areas. | LH19 LW14 UK01 | LH20 LW15 UK13 | LH22 LW22 | LH12 LIW23 |
| 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); predominantly found in forested systems. | LH24 | LW12 | LW13 | LW14 |
| 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); predominantly found in forested, or partially forested, systems. | LH16 | LH17 | LH19 | LW24 |
| 3 | Sandy, or muddy sediments, firm with little flocculent material (thin layer, 1 -2 cm, if present); gray to light brown in color; typical in shallow ponds (< 1 m), found in meadowed systems. | LH21 | LW15 | LW22 | UK13 |
| 4 | Very firm hardpan, sand dominated, no flocculent organic matter visible; light to dark gray in color; typical in shallow ponds (< 1 m), found in meadowed systems. | LH20 LH12 | LH22 LIW23 | LH23 LW25 | LH27 UK01 |

pond's perimeter and probing every 3 - 4 m to estimate the relative firmness of the pond bottom substrates.

Water Quality Variables

Alkalinity, conductivity, and pH samples were taken at a depth of 1 m below the surface, except in ponds less than 1 m deep, where samples were taken at one half the maximum depth. Alkalinity and conductivity were analyzed in a park laboratory within 24 hours of sampling. Alkalinities were determined by the Gran titration method (Gran, 1952) and expressed in microequivalents / liter ($\mu\text{eq/L}$). Conductivities were measured with a Hach™ conductivity meter and were expressed in $\mu\text{mhos/cm}$, or $\mu\text{S/cm}$, at 25° C. Measurements of pH were made in the field soon after the water samples were taken using a Hach™ field pH meter that was calibrated and checked at each sampling site.

On each sampling date, water temperature and dissolved oxygen were recorded at 1 m intervals beginning at the surface to a depth of 1 m off the bottom using a YSI™ dissolved oxygen meter. In ponds less than 1 m deep, these data were recorded at the surface and at one half the maximum depth.

Spot temperatures also were taken on each sampling date with a hand-held thermometer at 1 m below the surface, or at one half the maximum depth for ponds less than 1 m deep. In addition to spot temperature readings, Hobo™ temperature loggers were placed in nine ponds (July 7 - Sept. 10, 1996). The temperature loggers were set to record data at 16-minute intervals for a duration of 20 days. The temperature loggers were then removed, downloaded (Boxcar and Logbook 2.0+), and replaced in the

field until the end of the field season (20 days). Raw temperature logger data were converted into daily maximum, minimum, and mean temperatures (Appendix 1).

Nutrient samples were collected from 17 ponds in August at 1 m below the surface (or at half the maximum depth as above), filtered using heat-treated 0.45 μm methyl-cellulose filters, and frozen until processed. The samples were analyzed for Kjeldahl-N (TKN), total nitrogen, orthophosphate-P, and total phosphorus by the Cooperative Chemical Analytical Laboratory (CCAL) in the Forest Sciences Laboratory at Oregon State University.

With the exceptions of the shallow systems recently disturbed by elk, the Secchi disk was visible on the bottom of all ponds in the study. In ponds utilized by elk just prior to sampling, water transparency was reduced to 10-15 cm, rendering amphibian censuses impossible during these sampling periods.

Statistical Analyses

Several statistical tests were used to analyze data. The level of significance in all tests was $\alpha = 0.05$. Environmental variables were averaged over the years sampled resulting in an average annual measurement. Nonparametric Mann-Whitney (MW-U) tests were used to test for differences in water chemistry, nutrient, and physical characteristics between *A. gracile* ponds and *A. macrodactylum* ponds. K-Means clustering (Heintze, 1992) was used to group the 20 study ponds based on four significant variables (surface area, maximum depth, LOI, and elevation) identified by the Mann-Whitney tests.

Logistic regression (SAS, 1997) was used to develop prediction models of the probability of salamander occurrence, given environmental variables. Logistic regression creates models from a binary distribution which, in this study, was the presence ($y = 1$) or absence ($y = 0$) of a salamander species. Explanatory variables were discrete (CWD, VEG, and HP) and continuous (remaining quantitatively measured variables).

Generalized logistic regression models take the form:

$$\ln(\text{odds of occurrence}) = \ln(p/1-p) = \beta_0 + \beta_1 X_1 + \dots + \beta_p X_p$$

where p = probability of a salamander occurring, $X_1 \dots X_p$ are explanatory variables.

Significance of the models was determined by computing exact probabilities under a null hypothesis using Fisher's Exact Test, rather than relying on approximation. In this case, the response was the presence or absence of *A. macrodactylum* or *A. gracile*. This test was used to identify if a relationship existed between a given categorical variable (i.e., CWD, VEG, and HP) and the presence or absence of *A. macrodactylum* or *A. gracile*. The p-value expressed how likely that relationship was, based on the random assignment of the response to the categories.

RESULTS

Survey Techniques

To examine potential biases in survey methods, salamander larvae were enumerated in three ponds by snorkeling as well as by visual encounter surveys. This comparison resulted in relatively minor differences in the number of *A. macrodactylum* larvae observed (Table 3).

Table 3. A comparison of two survey techniques used in three MORA mountain ponds. *Ambystoma macrodactylum* larvae expressed as numbers per 100 m of shoreline.

| Pond | Snorkel Survey | Visual Encounter Survey |
|------|----------------|-------------------------|
| LH20 | 201.6 | 188.3 |
| LH23 | 202.0 | 194.0 |
| LH27 | 102.0 | 117.0 |

Pond bathymetry and water transparency biased snorkel counts in the large-deep ponds (i.e., $> 2000 \text{ m}^2$ and $> 2 \text{ m}$, respectively). In LW12, LW13, LW24, LH17, and LH24 many of the large *A. gracile* larvae ($> 50 \text{ mm}$ snout-vent length or SVL) occupied deep areas of the ponds (outside the diver's reach), and therefore, were not tallied during the near-shore snorkel transects. Because of this potential bias, salamander abundances were probably underestimated in these systems.

General Observations of Larval Salamander Abundance and Distribution

Salamander populations at the 20 sample sites were designated allopatric *A. macrodactylum*, allopatric *A. gracile*, or sympatric. An allopatric population was defined by the presence of only one species of salamander larvae in a pond. A pond was

designated sympatric if larvae of both species were present. Although adults and embryos of both species were found at five sites (LH16, LH19, LH24, LW12, and LW24), if larvae of only one species were observed, a pond was designated allopatric. Sympatric populations were found in LH21 and LW15, where larvae of both species were observed. Abundances of *A. macrodactylum* larvae were higher in LW15 and lower in LH21 than were *A. gracile* larvae. Because one of the species always outnumbered the other when sympatric, the analysis of the environmental variables was simplified into two pond types, *A. macrodactylum* ponds and *A. gracile* ponds.

The average number of larvae per 100 meters of shoreline in allopatric *A. macrodactylum* ponds (average = 116.1, n = 10) was higher than in allopatric *A. gracile* ponds (average = 21.9, n = 8; MW-U, p = 0.021) (Table 4). In sympatric ponds, the average number of *A. macrodactylum* larvae (40.5 / 100 m, n = 2) was not significantly higher than the number of *A. gracile* larvae (33.2 / 100 m, n = 2; MW-U, p = 1.000).

Pond Physical Characteristics

Pond area, depth, and elevation appeared to play a role in the distribution and abundance of the two ambystomatids. *Ambystoma macrodactylum* ponds were significantly smaller in area, shallower in depth, and higher in elevation than were *A. gracile* ponds (Table 5).

Table 4. Averages (1993 - 1996) of abiotic and biotic variables for 20 mountain ponds in the northeast quadrant of Mount Rainier National Park. Data include loss-on-ignition (LOI), dissolved oxygen (D.O.), pH, alkalinity (Alk.), conductivity (Cond.), total Kjeldahl-N (TKN), total nitrogen (TN), total phosphorus (TP), orthophosphate-P (PO₄), *A. gracile* larvae (G-larvae), and *A. macrodactylum* larvae (M-larvae).

| M / G ^a | LAKE | LOI (%) | D.O. (mg/l) | pH | Alk. (µeq/l) | Cond. (µmhos/cm @ 25° C) | TKN ^d (mg/l) | TN ^d (mg/l) | TP ^d (mg/l) | PO ₄ ^d (mg/l) | G-larvae (no./ 100m) | M-larvae (no./ 100m) |
|--------------------|--------------------|------------|----------------|------|-----------------|--------------------------------|----------------------------|---------------------------|---------------------------|--|----------------------------|----------------------------|
| G | LH16 | 25.08 | 8.12 | 6.74 | 156.26 | 16.76 | ** | ** | ** | ** | 26.0 | 0 |
| G | LH17 | 31.18 | 8.56 | 8.27 | 300.56 | 31.81 | ** | ** | ** | ** | 5.3 | 0 |
| G | LH19 | 36.55 | 7.28 | 6.73 | 92.70 | 13.63 | 0.658 | 0.660 | 0.024 | 0.005 | 58.5 | 0 |
| M | LH20 | 18.29 | 6.70 | 6.66 | 42.18 | 6.25 | 0.435 | 0.438 | 0.019 | 0.003 | 0 | 196 |
| G>M | LH21 ^b | 30.27 | 7.17 | 6.80 | 116.49 | 12.10 | 0.174 | 0.175 | 0.006 | 0.002 | 47.6 | 0.2 |
| M | LH22 | 7.44 | 7.65 | 6.63 | 40.50 | 13.32 | 0.379 | 0.380 | 0.014 | 0.002 | 0 | 14.0 |
| M | LH23 | 13.06 | 7.65 | 5.88 | 67.51 | 5.20 | 0.070 | 0.074 | 0.011 | 0.001 | 0 | 208.6 |
| G | LH24 | 54.59 | 7.15 | 6.87 | 143.58 | 15.70 | 0.273 | 0.260 | 0.010 | 0.003 | 21.9 | 0 |
| M | LH27 | 13.18 | 7.38 | 6.86 | 97.28 | 11.99 | 0.100 | 0.100 | 0.007 | 0.001 | 0 | 159.4 |
| M | LIH12 ^c | 8.27 | 8.05 | 5.84 | 23.34 | 5.80 | 0.420 | 0.431 | 0.035 | 0.002 | 0 | 1.0 |
| G | LW12 | 53.78 | 7.09 | 6.08 | 9.59 | 4.25 | 0.170 | 0.171 | 0.005 | 0.001 | 31.4 | 0 |
| G | LW13 | 66.13 | 7.57 | 7.07 | 100.66 | 15.19 | 0.115 | 0.115 | 0.008 | 0.002 | 1.8 | 0 |
| G | LW14 | 41.66 | 7.15 | 6.37 | 102.46 | 13.40 | 0.364 | 0.365 | 0.007 | 0.002 | 2.2 | 0 |
| M>G | LW15 ^b | 13.57 | 8.65 | 6.79 | 154.00 | 17.67 | 0.229 | 0.230 | 0.006 | 0.003 | 18.7 | 80.8 |
| M | LW22 | 18.60 | 8.37 | 6.44 | 80.34 | 13.03 | 0.329 | 0.330 | 0.017 | 0.003 | 0 | 137.2 |
| G | LW24 | 18.00 | 8.31 | 6.37 | 54.05 | 5.67 | 0.149 | 0.150 | 0.006 | 0.003 | 27.8 | 0 |
| M | LW25 | 7.12 | 8.00 | 6.36 | 40.40 | 9.57 | 0.538 | 0.540 | 0.022 | 0.003 | 0 | 34.3 |
| M | LIW23 ^c | 24.21 | 7.50 | 5.86 | 14.65 | 5.23 | ** | ** | ** | ** | 0 | 69.1 |
| M | UK01 | 9.16 | 7.96 | 6.83 | 138.53 | 19.94 | 0.243 | 0.256 | 0.006 | 0.002 | 0 | 129.8 |
| M | UK13 | 41.87 | 6.80 | 6.00 | 36.98 | 9.32 | 0.894 | 0.895 | 0.052 | 0.015 | 0 | 211.3 |

^{a)} M Indicates allopatric *A. macrodactylum* pond.

G Indicates allopatric *A. gracile* pond.

^{b)} Indicates sympatric pond.

^{c)} Indicates ephemeral pond.

^{d)} ** No samples taken.

Table 5. Fifteen environmental variables used to compare *A. macrodactylum* systems with *A. gracile* systems (n = 8; Standard Errors in parentheses).

| Environmental Variable | <i>A. macrodactylum</i> Ponds | | <i>A. gracile</i> Ponds | | MW-U Test |
|--|-------------------------------|---------------------|-------------------------|---------------------|-----------|
| | Average | Range | Average | Range | P |
| Surface Area (m ²) | 849.60 (177.26) | 266.44 - 2038.00 | 3359.60 (631.63) | 502.00 - 6169.00 | 0.002* |
| Maximum Depth (m) | 0.60 (0.09) | 0.18 - 1.30 | 2.1 (0.29) | 0.70 - 3.64 | 0.007* |
| Elevation (m) | 1790 (20.67) | 1672 - 1909 | 1709 (16.07) | 1615 - 1781 | 0.014* |
| LOI (%) | 15.9 (3.06) | 7.1 - 41.9 | 39.7 (5.24) | 18.0 - 66.1 | 0.002* |
| pH | 6.26 | 5.84 - 6.86 | 6.57 | 6.08 - 7.07 | 0.087 |
| Alkalinity (µeq/l) | 66.88 (13.93) | 14.65 - 154.00 | 119.59 (26.99) | 9.59 - 300.56 | 0.074 |
| Conductivity (µmhos/cm @ 25°C) | 10.67 (1.52) | 5.20 - 19.94 | 14.28 (2.63) | 4.25 - 31.81 | 0.239 |
| Dissolved Oxygen (mg/l) | 7.70 (0.18) | 6.70 - 8.65 | 7.60 (0.19) | 7.09 - 8.56 | 0.569 |
| T Max ^a (°C) | 19.24 (0.88) | 16.81 - 22.21 | 16.47 (1.10) | 12.90 - 19.61 | 0.309 |
| T Min ^a (°C) | 12.41 (0.78) | 10.20 - 14.08 | 13.52 (0.60) | 11.66 - 14.91 | 0.083 |
| Range of Daily T Variance ^a (°C) | 6.83 (1.54) | 3.44 - 12.01 | 3.44 (0.60) | 2.00 - 4.70 | 0.146 |
| TN (mg/l) | 0.367 (0.075) | 0.074 - 0.895 | 0.271 (0.072) | 0.115 - 0.660 | 0.380 |
| TKN (mg/l) | 0.364 (0.075) | 0.070 - 0.894 | 0.272 (0.072) | 0.115 - 0.658 | 0.380 |
| TP (mg/l) | 0.019 (0.005) | 0.006 - 0.052 | 0.009 (0.003) | 0.006 - 0.024 | 0.107 |
| PO ₄ (mg/l) | 0.004 (0.001) | 0.001 - 0.015 | 0.002 (0.0005) | 0.001 - 0.005 | 0.961 |

Substratum Samples

Bottom sediments of *A. gracile* ponds had a higher percentage of organic matter, expressed as percent lost on ignition (LOI), than did *A. macrodactylum* ponds (Table 5). The average LOI for the sympatric ponds, LH21 (30.3 %) and LW15 (13.6 %), approximate the average values of the respective allopatric *A. macrodactylum* and *A. gracile* ponds.

Categories of Three Qualitative Measures

Allopatric *A. macrodactylum* ponds ranked the lowest on the CWD scale (1 and 2), and *A. gracile* ponds ranked the highest (3 and 4; Table 2). Allopatric *A.*

macrodictylum ponds ranked the highest (3 and 4) on the HP scale, and allopatric *A. gracile* ponds ranked the lowest (1 and 2). The CWD and HP values of ponds supporting sympatric salamander populations (i.e. LH21 and LW15) were intermediate to both allopatric pond types (i.e. *A. macrodictylum* ponds and *A. gracile* ponds). Although the VEG classifications were more variable, allopatric *A. macrodictylum* ponds generally ranked higher on the VEG scale (3 and 4) than did allopatric *A. gracile* ponds (1 - 3).

Water Quality Variables

There were no differences in the average alkalinity, conductivity, pH, and dissolved oxygen between *A. macrodictylum* ponds and *A. gracile* ponds (Table 5). Although no significant temperature differences were found between *A. macrodictylum* ponds and *A. gracile* ponds (Table 5), a general summary of temperature logger data demonstrated that >50% of the average daily temperature maximums and ranges of *A. macrodictylum* ponds tended to exceed those of *A. gracile* ponds and conversely, >50% of the average daily temperature minimums of *A. macrodictylum* ponds tended to be lower than those of *A. gracile* ponds (Figure 3). Thermal stratification did not occur in any of the study ponds. No differences in nutrients (i.e. TN, TKN, TP, PO₄) were found between the *A. macrodictylum* (n = 10) and *A. gracile* (n = 7) ponds (Table 5).

Cluster Analysis

Of the fifteen environmental variables examined (Table 5), four variables (surface area, maximum depth, LOI, and elevation) were significantly different between the *A. macrodictylum* and the *A. gracile* ponds. Based on these variables, K – Means clustering

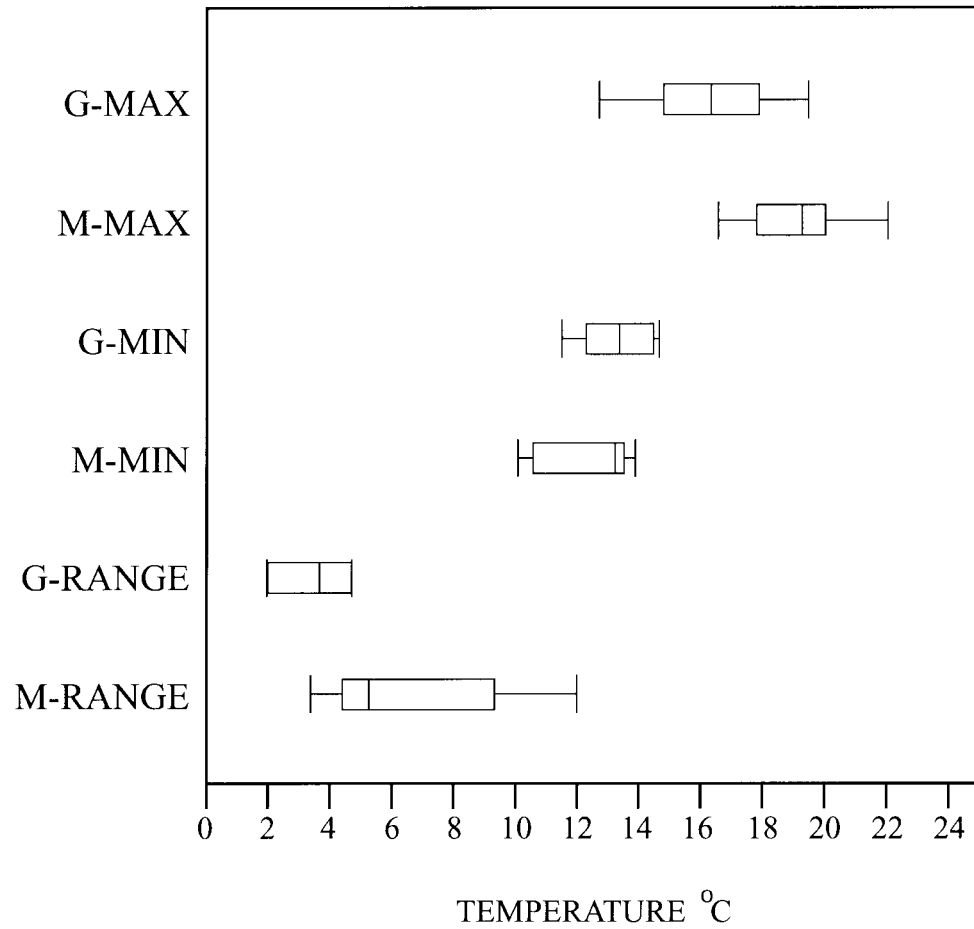


Figure 3. Average daily maximum, minimum, and range for all temperature logger data in *A. gracile* (G) and *A. macrodactylum* (M) ponds (n=9; 7/30/96 - 9/10/96).

Table 6. K - Means clustering results for four environmental variables in 20 mountain ponds in the northeast quadrant of Mount Rainier National Park.

| Cluster | Ponds | Surface Area (m ²) | Depth (m) | LOI (%) | Elevation (m) |
|---------|--|-----------------------------------|--------------|---------------|------------------|
| 1 | LH20 LH22 LW22 LH23 LIW23 LH27 LW25 LIH12 UK01 | 893.94 (618.79) ^a | 0.62 (0.33) | 13.26 (5.99) | 1813.44 (50.31) |
| 2 | LH19 LW14 LW15 UK13 | 794.49 (503.22) | 0.67 (0.26) | 33.41 (13.46) | 1671.00 (39.42) |
| 3 | LH16 LH21 LW24 | 2749.67 (377.64) | 2.61 (0.89) | 24.45 (6.16) | 1721.00 (31.19) |
| 4 | LH17 LH24 LW12 LW13 | 5027.33 (1168.79) | 2.28 (0.29) | 51.42 (14.62) | 1727.50 (44.12) |

^{a)} Numbers in parentheses = one standard deviation.

grouped the ponds into a four-cluster model ($p < 0.001$; Table 6). The model expressed minimum variability between ponds within each cluster and indicated clear differences between the four clusters. Cluster one included nine *A. macrodactylum* ponds. These ponds had small surface areas, shallow depths, and sediments with low organic content, and occurred at high elevations. Cluster two contained one *A. macrodactylum* pond (UK13), two *A. gracile* ponds (LH19 and LW14), and one of the two ponds supporting sympatric populations of both species (LW15) which clearly was dominated by *A. macrodactylum* (Table 4). The ponds in this cluster were characterized by small surface areas, with relatively shallow depths, low elevation, and bottom sediments with a relatively high organic content. The third cluster contained two *A. gracile* systems (LH16 and LW24) and the other pond supporting a sympatric salamander population (LH21). *Ambystoma gracile* clearly dominated LH21 (Table 4). Cluster four contained four *A. gracile* systems (LH17, LH24, LW12, and LW13). Clusters three and four shared some environmental characteristics (i.e., depth and elevation), but differences in surface area and the organic content of the bottom sediments were significant, which placed them in separate clusters. Relative to the other clusters, these ponds had the largest surface areas (average = 2749.7 and 5027.3 m², respectively) and the greatest depths (average = 2.61 and 2.28 m, respectively). The average elevations of the third and fourth clusters lay between the first and second clusters.

Logistic Regression

Logistic regression was used to incorporate the three categorical variables (CWD, VEG, and HP) into the analysis. The regression identified no significant relationships

between these three variables and the presence of either species. However, single parameter logistic regression models identified significant relationships between the presence of either *A. macrodactylum* or *A. gracile* and pond surface area ($p = 0.024$), depth ($p = 0.032$), LOI ($p = 0.020$), and elevation ($p = 0.023$) (Table 7). The relationship between the logistic regression coefficients and the explanatory variables in question is interpreted by making statements about odds. For example, the odds of finding *A. gracile* in any system, given a 30 percent increase in LOI, were estimated to be approximately 82 times higher (95% C.I.: 1.97 to 3441.97) than the odds of finding *A. macrodactylum* in that same system. The single parameter models also may be used to predict the likelihood, or odds, of *A. gracile* or *A. macrodactylum* occurring in any system by inserting the value in question (e.g., the given variable's mean value from these data) into the appropriate model. The likelihood of *A. gracile* occurring in other systems with similar habitat characteristics is far greater than if the systems exhibit habitat characteristics similar to those of *A. macrodactylum* systems (Table 8).

Fisher's Exact Test

Further examination of these variables was achieved using Fisher's Exact Test, a method of testing for association. CWD and HP were identified as variables that could predict the association of either *A. macrodactylum* or *A. gracile* with a given variable in the study ponds. In other words, there was a high likelihood that *A. macrodactylum* was associated with a HP value of three to four, and there was a high likelihood that *A. gracile* was associated with a HP value of one to two ($p < 0.001$). Similarly, there was a high likelihood that *A. macrodactylum* was associated with a CWD value of one to two, and

Table 7. A summary of logistic regression results. Response variable is the presence of *A. gracile*; signs in regression structure reverse for the presence of *A. macrodactylum*.

| Variable | Regression structure (η) | DF | Standard Error | Pr > Chi-Squared Dist. |
|-----------------|--|----|----------------|------------------------|
| Depth | = - 4.317 + 3.725 (Depth) | 1 | 1.734 | 0.032 * |
| Area | = - 3.253 + 0.002 (Area) | 1 | 0.001 | 0.024 * |
| Elevation | = 42.396 - 0.024 (Altitude) | 1 | 0.011 | 0.029 * |
| LOI | = - 3.934 + 0.147 (LOI) | 1 | 0.064 | 0.020 * |
| D.O. | = 2.270 - 0.323 (D.O.) | 1 | 0.809 | 0.690 |
| Alkalinity | = - 1.570 + 0.016 (Alkalinity) | 1 | 0.010 | 0.117 |
| pH | = - 13.757 + 2.065 (pH) | 1 | 1.313 | 0.116 |
| Conductivity | = - 1.409 + 0.098 (Conductivity) | 1 | 0.0834 | 0.238 |
| TKN | = 0.360 - 2.285 (TKN) | 1 | 2.676 | 0.393 |
| TN | = 0.403 - 2.413 (TN) | 1 | 2.700 | 0.371 |
| TP | = 1.038 - 109.495 (TP) | 1 | 80.254 | 0.173 |
| PO ₄ | = - 0.009 - 117.916 (PO ₄) | 1 | 208.852 | 0.572 |

* Significance at $\alpha = 0.05$.

there was a high likelihood that *A. gracile* was associated with a CWD value of three to four ($p < 0.001$). The variable VEG was not associated with the presence of either species ($p = 0.175$).

Table 8. Estimations of the likelihood of the occurrence of *A. gracile* in any given site, based on single parameter models, using average values of the variables for *A. gracile* ponds ($n = 9$) and *A. macrodactylum* ponds ($n = 11$).

| Variable | Average | Odds |
|---|---------|-------|
| <i>A. g.</i> Surface area (m ²) | 3360 | 32:1 |
| <i>A. m.</i> Surface area (m ²) | 850 | 0.2:1 |
| <i>A. g.</i> Depth (m) | 2.0 | 23:1 |
| <i>A. m.</i> Depth (m) | 0.6 | 0.1:1 |
| <i>A. g.</i> LOI (%) | 40 | 7:1 |
| <i>A. m.</i> LOI (%) | 16 | 0.2:1 |
| <i>A. g.</i> Elevation (m) | 1709 | 4:1 |
| <i>A. m.</i> Elevation (m) | 1790 | 0.2:1 |

DISCUSSION

This study demonstrated that the segregation of *A. macrodactylum* and *A. gracile* in MORA ponds was associated with differences in microhabitats, substratum, and environmental and pond morphological characteristics. Small, shallow ponds (average surface area and depth = 849.5 m² and 0.6 m, respectively) with bottom substratum low in organic content (average = 15.9 % LOI) supported allopatric *A. macrodactylum* populations. These ponds were characteristically firm-bottomed, abundant in aquatic vegetation, and low in coarse woody debris. Conversely, ponds that were large in surface area (average = 3359.6 m²), deep (average = 2.1 m), and with substratum high in organic content (average = 39.7 % LOI) supported allopatric *A. gracile* populations. These ponds were characteristically soft-bottomed (flocculent), supported moderate amounts of aquatic vegetation, and abundant coarse woody debris. Ponds supporting sympatric populations exhibited intermediate characteristics.

These results were similar to those of Thompson and Gates (1982) in western Maryland, who showed that some “pools” were used exclusively by *A. maculatum*, some pools by *A. jeffersonianum*, and other pools by both species for breeding. They demonstrated habitat differences between the three pool types. Pools that supported both species were low in elevation, large, and sustained abundant aquatic vegetation. Topographic location (upland or bottomland) and the pool’s water regime (slowly flowing or standing) was a strong indicator as to whether *A. maculatum* and *A. jeffersonianum* occurred sympatrically or allopatrically. Based on the present work, a conceptual model supported by the cluster analysis was developed to provide a

framework for evaluating the distribution of *A. macrodactylum* and *A. gracile* in the northeast quadrant of MORA (Figure 4). Alpine ponds (e.g., LH25) appeared to support neither species (unpublished park data). Nine small and shallow ponds found in subalpine meadows (left side of model) with firm bottoms, relatively abundant aquatic vegetation, virtually no coarse woody debris, and bottom sediments with low organic content were inhabited by *A. macrodactylum*. Six large, deep ponds (right side of model) found in the subalpine forest with moderately abundant VEG, abundant CWD, relatively soft bottoms, and the highest average LOI were inhabited by *A. gracile*. However, two ponds (LH21 and LW15) supported both species.

LW15 supported sympatric populations of the two ambystomatids, yet *A. macrodactylum* were dominant based on their greater abundance relative to *A. gracile* (Table 4). Near the edge of the pond the substratum was firm, low in organic content, and covered by emergent sedges and grasses as in allopatric *A. macrodactylum* ponds. Near the center of the pond, however, was a small and relatively deep “hole” (2 - 3 m by 0.80 - 1.0 m) that contained coarse woody debris. Large *A. gracile* larvae inhabited this hole, but were not observed in the shallows, whereas small larvae and hatchlings of both species utilized the shoreline vegetation. *Ambystoma macrodactylum* eggs or egg clusters were typically laid in the shoreline vegetation and rarely found in, or near, the hole. Only occasionally were adult *A. macrodactylum* observed in the hole.

In LH21, the other pond that supported sympatric salamander populations (Table 4), *A. gracile* larvae clearly outnumbered *A. macrodactylum* larvae. As in LW15, nearshore margins of LH21 were shallow and covered with aquatic vegetation. LH21 differed from LW15 in that a large, deep “trough” (8 - 10 m by 2 m) ran along the east-

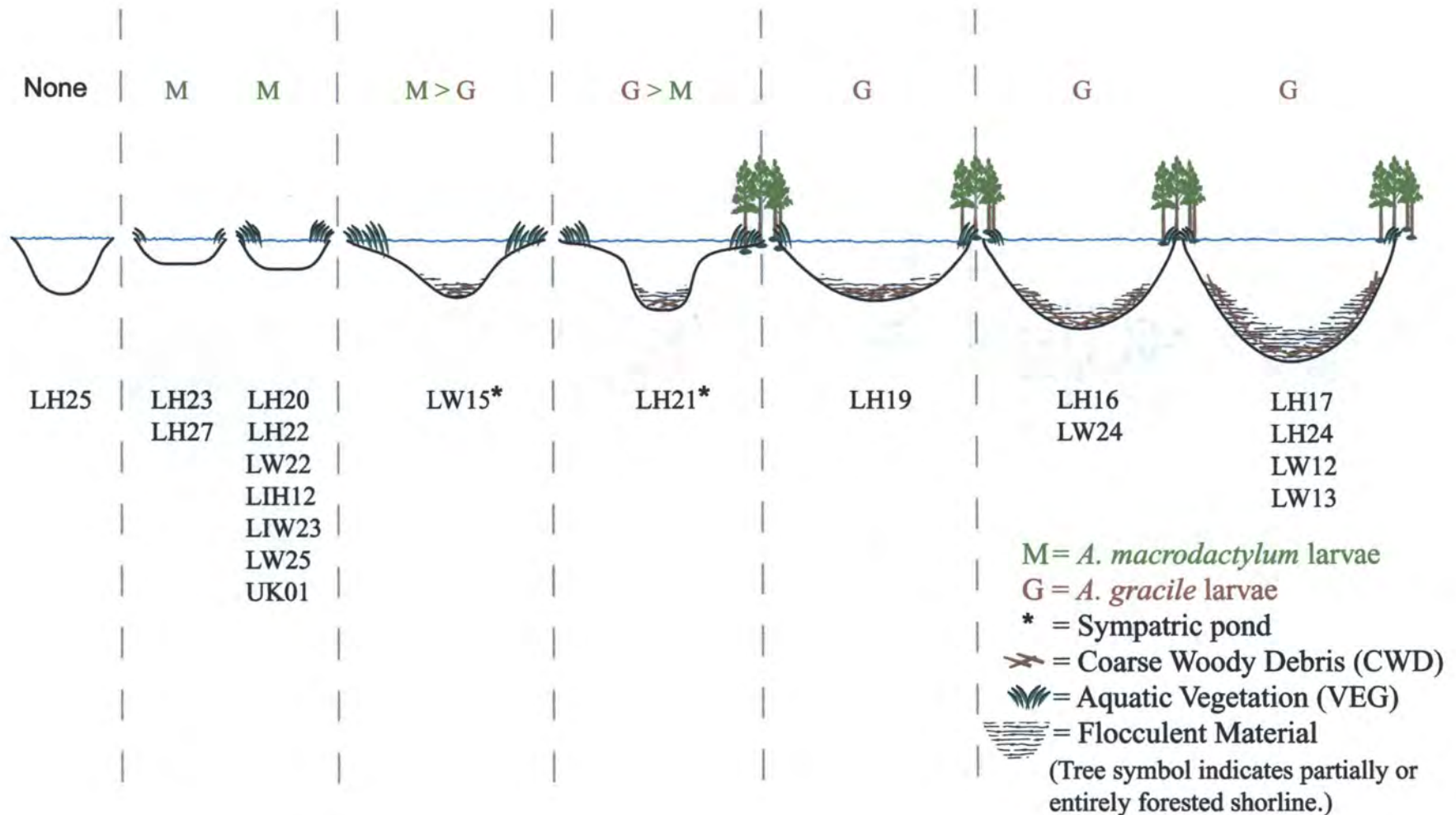


Figure 4. A conceptual model, based on K-Means clustering, depicting habitat characteristics of ponds in the study area. Ponds are listed directly below the diagram that best describes their habitat characteristics.

west axis. Flocculent material surrounded and filled the trough. Most of the large woody debris in the pond was located in this area. Large *A. gracile* larvae were regularly observed in the trough, yet rarely in the shallows. Conversely, *A. macrodactylum* larvae were found in the vegetated shallows and were rarely observed in the deeper regions.

The high LOI (36.5 %) and low HP (2) in LH19 were consistent with other allopatric *A. gracile* ponds, yet LH19 was small and shallow (Table 1). Although adult *A. macrodactylum* were found along the shoreline of LH19 (personal observation), and up to 830 embryos were counted during one survey (7/20/96), no larval *A. macrodactylum* were observed during snorkeling. The available refugia appeared to be sufficient to harbor developing *A. macrodactylum* hatchlings (VEG = 4). Predation by large *A. gracile* larvae may explain why *A. macrodactylum* larvae were not observed (Hoffman and Larson, in press).

Two ponds, LW14 and UK13, exhibited unique habitat characteristics that were not representative of the other ponds in the study area and hence, were excluded from the generalized conceptual model. Both ponds appeared to be in late successional stages. LW14 was an allopatric *A. gracile* pond located in a small clearing, and was characterized by sparse CWD, abundant VEG, and a thick, flocculent bottom composed of 41.6 % organic matter. The depth of algal mats, rooted and emergent macrophytes, and flocculent material in LW14 exceeded one meter. This tangle of vegetation, detritus, and some large woody debris provided excellent refuge for salamanders, and possibly a substantial temperature buffer. When the open water depth of 0.7 m (Table 4) was considered in addition to the depth of the flocculent and organic material, this pond more closely modeled other allopatric *A. gracile* systems. UK13 also was located in a small

clearing surrounded by dense subalpine forest. UK13 was a small, shallow allopatric *A. macrodactylum* pond characterized by darkly stained water (tannins), high nutrient levels (TKN = 0.894 mg/l), high organic content to the bottom sediments (LOI = 41.9 %), and abundant aquatic vegetation. This system contrasted sharply with nearby deeper and larger systems (LW12 and LW13) that exhibited well-defined shorelines, large pelagic areas, less aquatic vegetation and hence, appeared to be in earlier successional stages. Though the LOI value in UK13 approximated the mean LOI value of an *A. gracile* pond, the small size and very shallow depth of UK13 were consistent with other allopatric *A. macrodactylum* ponds.

The qualitative habitat measures (HP, CWD, and VEG) combined with certain aspects of basin morphology provided a visual representation of the relationship between certain habitat characteristics and the distribution of the two salamander species (Figure 5). The “typical” mountain pond inhabited by *A. macrodactylum* was found in subalpine meadows, small, shallow, low in CWD, and firm bottomed. Conversely, the “typical” mountain pond inhabited by *A. gracile* was found in the subalpine forest, large, deep, high in CWD, and flocculent bottomed. Accordingly, the ponds that supported successful breeding populations of both salamander species shared habitat characteristics of both types of systems. These two sympatric ponds (LW15 and LH21) were located at ecotones between forest and meadow and hence, could be termed transitional basins. These ponds were deep enough to collect flocculent material which provided cover and possibly a temperature buffer for *A. gracile*, contained sufficient CWD that served as *A. gracile* egg mass attachment sites, yet vegetated and shallow nearshore areas provided refuge, and presumably warmer temperatures, for developing *A. macrodactylum* larvae.

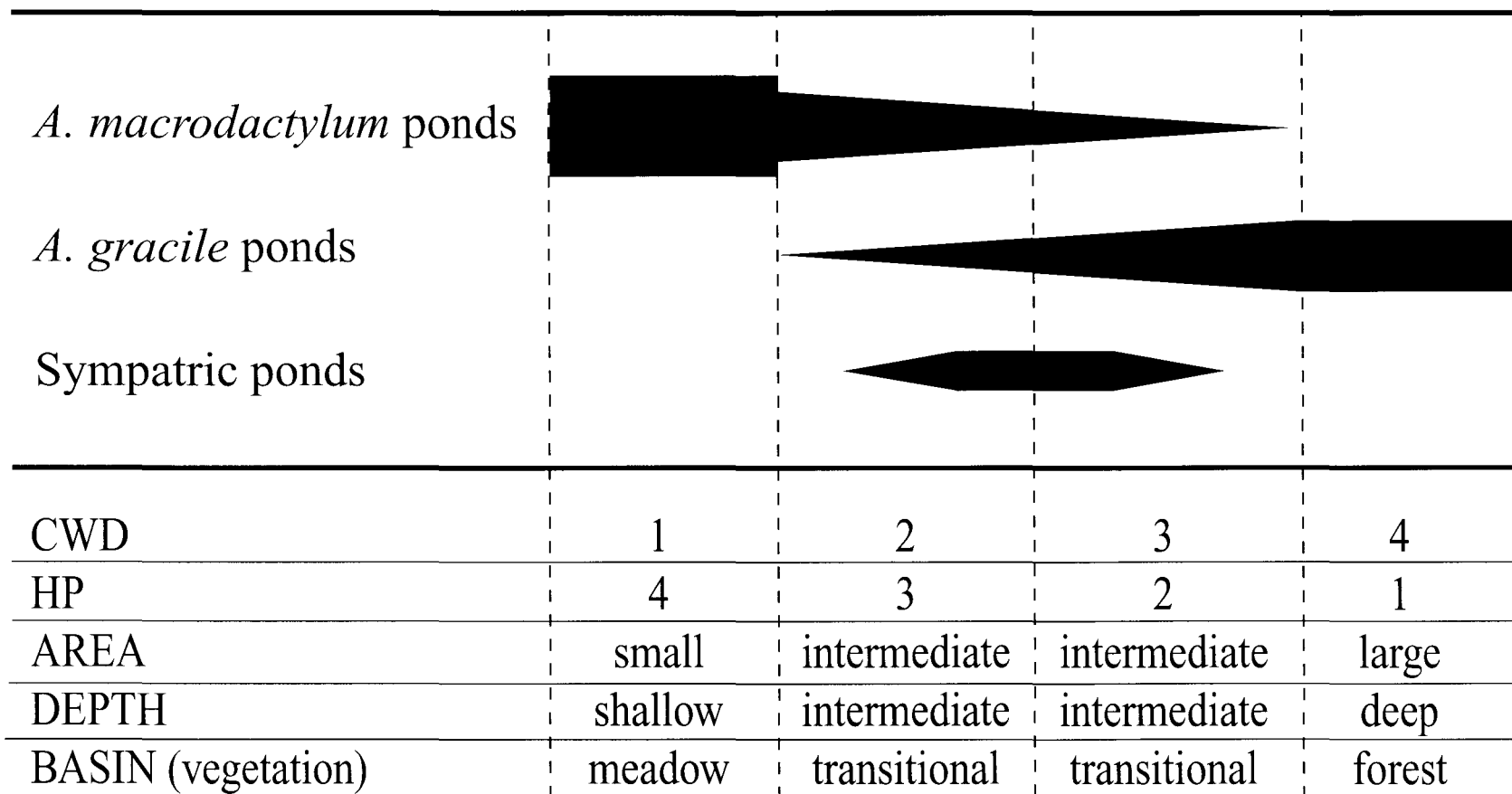


Figure 5. A conceptualized relationship between salamander species distribution and five habitat characteristics for 20 mountain ponds in Mount Rainier National Park. Increased bar thickness approximates increased number of ponds satisfying the below criteria.

Figure 5 demonstrates the linearity of the categorical variables CWD and HP. A relatively constant, incremental, and linear change in CWD and HP was evident in the "transition" from the allopatric *A. macrodactylum* ponds to the allopatric *A. gracile* ponds (Figure 5). The VEG category was highly variable and therefore not included in Figure 5. However, as the sympatric ponds demonstrated, aquatic vegetation was influential in determining species distribution and abundance (Thompson and Gates, 1982).

Therefore, the results of this study illustrated that habitat structure and complexity played a role in the distribution and physical segregation of the two species. Given sufficient habitat complexity, sympatry was observed. As these ponds appeared to have a tendency towards allopatry, spatial and temporal (*A. gracile* nocturnal activity) segregation may provide the necessary mechanisms allowing sympatry. Snorkeling LW15 and LH21 revealed that large *A. gracile* larvae occupied deep areas, whereas the vegetated shallow margins provided refuge for developing *A. macrodactylum* larvae. Similar habitat partitioning has been documented in other regions of MORA (three ponds in Elysian Fields, two in Berkeley Park, three in the Golden lakes, and other lakes in the Huckleberry drainage, personal observation). Other researchers also have documented habitat partitioning, or spatial segregation, in lakes with co-occurring salamander populations (Anderson and Graham, 1967; Neish, 1971; Holomuzki, 1986; Thompson and Gates, 1982; Taylor, 1984; Slater, 1936; Efford and Mathias, 1969). Competition and predation among ambystomatids have been shown to regulate salamander populations (Efford and Mathias 1969; Thompson and Gates, 1982; Taylor 1983a; Taylor 1984; Holomuzki and Collins, 1987; Semlitsch 1987; Petranksa and Thomas, 1995), and

habitat partitioning may serve as a mechanism to reduce these effects (i.e., larval mortality, personal observation).

Cannibalism is known in at least three ambystomatids: *A. m. columbianum*, *A. opacum*, and *A. tigrinum* (Pfennig and Collins, 1993; Walls and Roudebush, 1991; Walls et al., 1993; Walls et al., 1996). *Ambystoma m. columbianum* cannibalistic morphs have been documented in a high-elevation ephemeral pond in the south-central Cascade Range (Walls et al., 1993), but these morphs were not observed in MORA. The lack of previously documented *A. gracile* cannibalism in natural systems has been attributed to the more stable habitats (i.e., permanent ponds) in which *A. gracile* are typically found (Walls et al., 1996). Laboratory cannibalism in *A. gracile* had not been documented, yet researchers suspected it may occur (Sprules, 1974b). However, field experiments in the northeast quadrant of MORA revealed large *A. gracile* larvae cannibalizing hatchlings as well as, in a separate experiment, consuming *A. macrodactylum* hatchlings (Hoffman and Larson, in press). Therefore, the presence of larger, overwintering *A. gracile* larvae during the hatching of *A. macrodactylum* embryos offers a potential explanation for the lack of *A. macrodactylum* larvae in LH19 and LW14. This explanation was reinforced by the observation of allopatric *A. macrodactylum* larvae in small, ephemeral "satellite" ponds (elm wallows) adjacent to LW14.

The results of this study indicate that the size, depth, and elevation of these systems may influence the expression of particular life history strategies. *Ambystoma macrodactylum* were observed in deeper systems throughout MORA, yet *A. gracile* were rarely observed in small and shallow (< 2000 m² area, < 1 m deep) mountain ponds, and never in ephemeral ponds. Although *A. gracile* has been documented to breed in

ephemeral systems, it more commonly breeds in permanent and hence, more stable water sources (Walls et al., 1996). As a pond dries, water temperatures increase, and larval densities and mortality rates become increasingly variable (Wilbur, 1987; Semlitsch, 1987; Semlitsch and Wilbur, 1988).

The number of *A. gracile* neotenes or paedomorphs generally increases with elevation (Snyder 1956; Sprules 1974a; Sprules 1974b; Eagleson 1976). In montane regions, subject to harsh terrestrial environments (severe temperature fluctuations, low humidity, and lack of suitable food or cover), facultative neoteny or paedogenesis provide a response adaptively advantageous over the standard, metamorphic, life history (Sprules, 1974a; Eagleson, 1976; Bizer, 1978; Sexton and Bizer, 1978; Whiteman, 1994). At high elevations, life history sequences (metamorphic or neotenuous/paedogenic) are generally governed by temperature, and warmer temperatures translate to faster metamorphosis at a smaller size (negative correlation between growth rate and size at metamorphosis) (Bizer, 1978). At low-elevations (So. Michigan), food abundance controls the timing of metamorphosis (Licht, 1991), and a positive correlation exists between growth rate and size at metamorphosis (Wilbur and Collins, 1973). Therefore, small shallow ponds that exhibit great temperature and hydrologic fluctuations potentially select for amphibians capable of expressing a metamorphic life history (i.e., *A. macrodactylum*), while ponds that are cooler, and exhibit a narrower range of temperature and hydrologic fluctuations select for amphibians that can express a neotenuous or paedomorphic life history (i.e., *A. gracile*).

At high elevations in MORA, some lakes are not inhabitable by any amphibians due to the short ice-free periods that allow insufficient time to complete their complicated

reproductive strategy (e.g., LH25). Below 10° C, where amphibian growth rates are exceedingly slow (Sexton and Bizer, 1978), these high-elevation ponds typically maintain low water temperatures year-round (LH25 was 6.2° C at 1 m on 21 Aug., 1996) and it is, therefore, unlikely that salamander larvae could attain the necessary size for metamorphosis or sexual maturity.

Nutrient concentrations also influence salamander abundance and distribution. Kjeldahl-N concentrations (≥ 0.045 mg/l) in high-elevation lakes in NOCA were found to function as an index of primary productivity which in turn, through food web linkages, influenced the density of *A. macrodactylum* in fishless systems (Tyler et al., 1998). In these lakes, *A. macrodactylum* densities increased above a "threshold" concentration ($\text{TKN} \geq 0.045$ mg/l). Nutrient concentrations in MORA lakes were greater than those in NOCA lakes, and no relationships were identified between Tyler et al.'s (1998) minimum threshold Kjeldahl-N concentration and the abundance or distribution of *A. macrodactylum* or *A. gracile*.

In summary, this research suggests that habitat variation and complexity in lentic ecosystems across this relatively small geographical area influenced the segregation of *A. macrodactylum* and *A. gracile* in the study ponds. Differences in surface area, depth, LOI, elevation, CWD, and HP significantly affected the distribution and dominance of *A. macrodactylum* or *A. gracile* in the high-elevation ponds and lakes of MORA. Habitat partitioning facilitated by the variation in pond bathymetry and the quantity and dispersion of aquatic vegetation also played a role in the distribution and abundance of these salamanders.

The model developed from this research predicts the colonization of all MORA ponds by *A. macrodactylum* in the absence of *A. gracile*. But in the presence of *A. gracile*, competition, predation, and environmental variables are apparent factors in determining the distribution and abundance of these two salamander species. The nearly ubiquitous occurrence of *A. macrodactylum* throughout a wide variety of habitats, west and east of the hydrologic crest of the Cascade Range, is likely due to the highly variable life history of this species (Kezer and Farner, 1955; Ferguson, 1961; Anderson, 1967; Nussbaum et al., 1983; Howard and Wallace, 1985; Petranka, 1998). The distribution of *A. gracile* is not as widespread as *A. macrodactylum*, although great variation in habitat use also exists across its geographic range. *Ambystoma gracile* do not occur east of the hydrologic crest of the Cascade Range and appear to be somewhat limited in distribution along the western slope of the northern portions of Washington's Cascade Range as well as interior British Columbia (see range maps: Nussbaum et al., 1983; Petranka, 1998). *Ambystoma gracile* generally occurred in all large, deep ponds in MORA (B. Samora, unpublished data), yet were relatively uncommon in ponds in NOCA (located in the northern Washington Cascade Range; Tyler et al., 1998). Furthermore, in the southern Cascade Range, *A. gracile* was documented breeding in tire ruts (D. Olson, personal communication). Further application of this model on lentic systems in MORA, and throughout the ranges of *A. macrodactylum* and *A. gracile*, may assist in the understanding of these relationships and, hence, aid in developing management decisions affecting salamander populations in the future.

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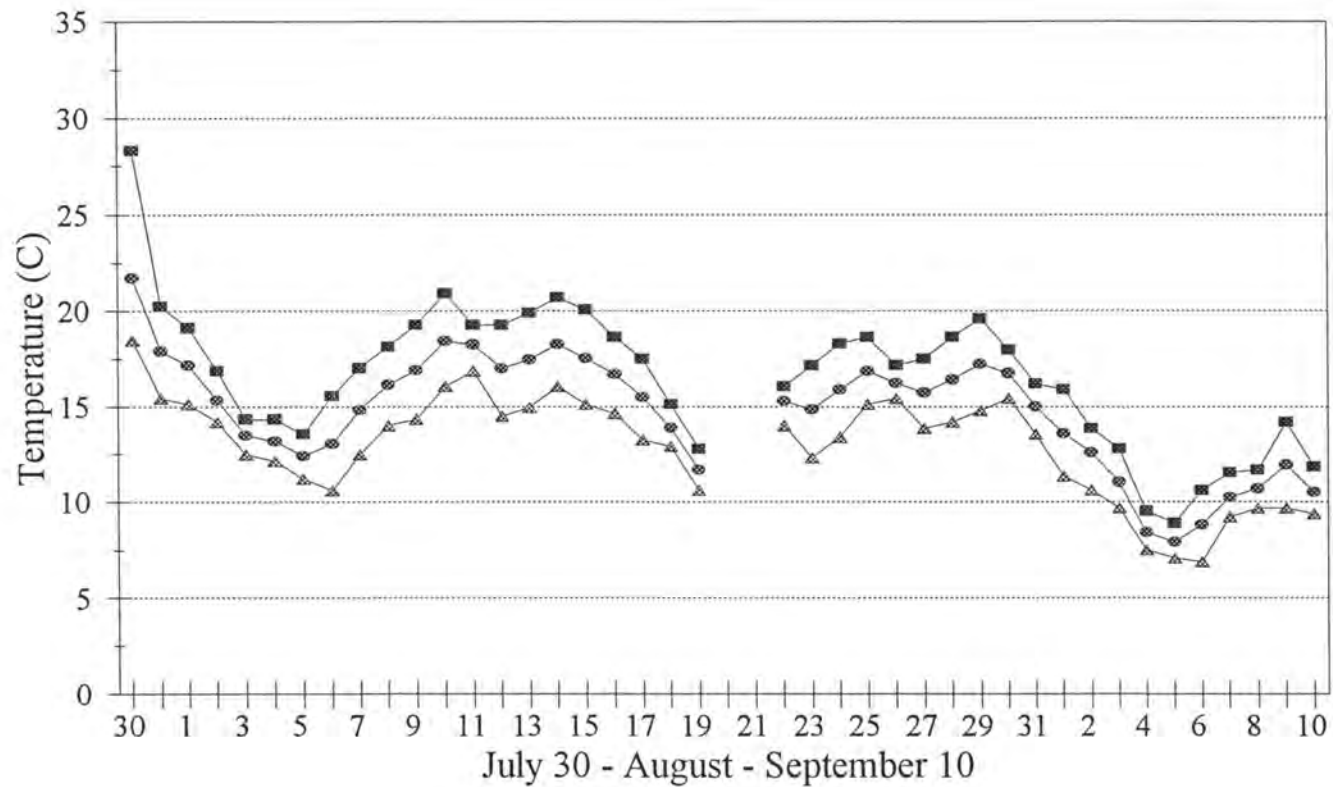
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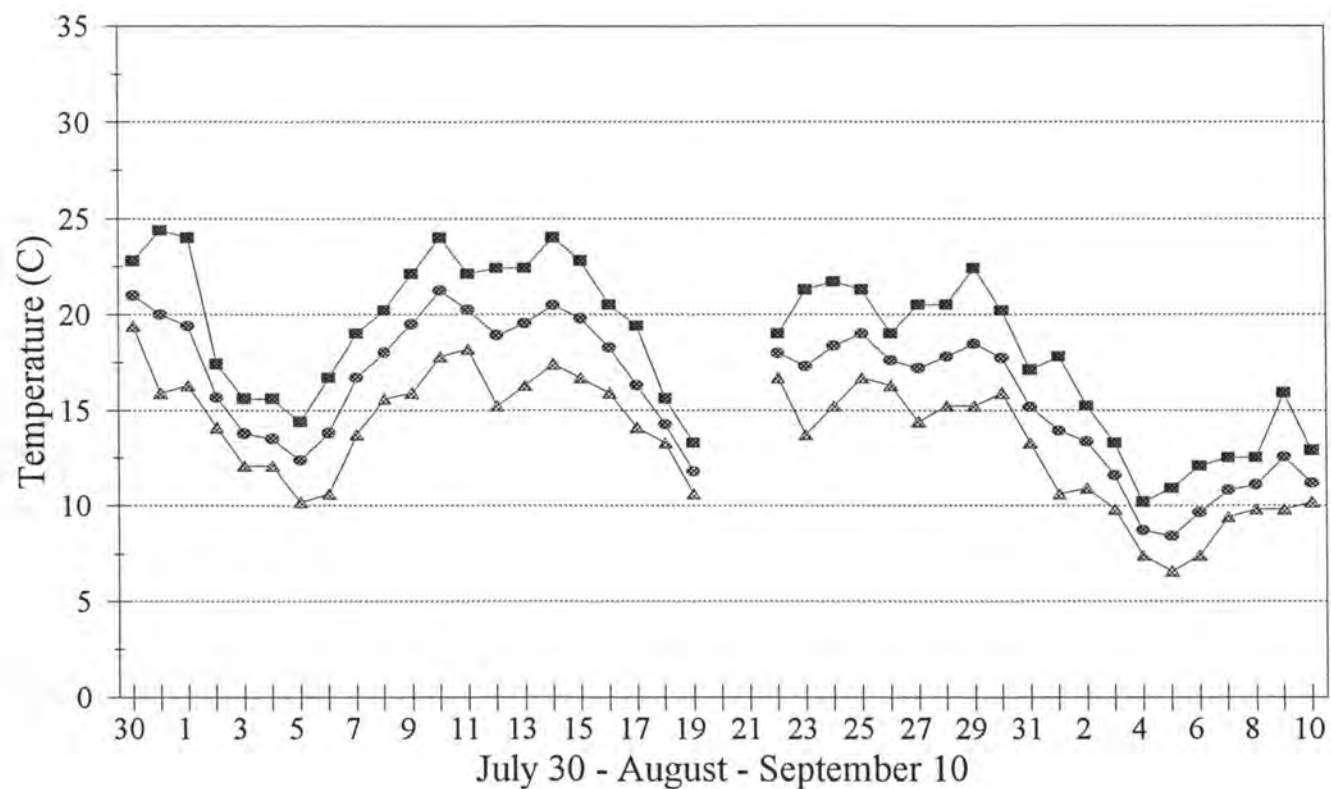
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APPENDIX



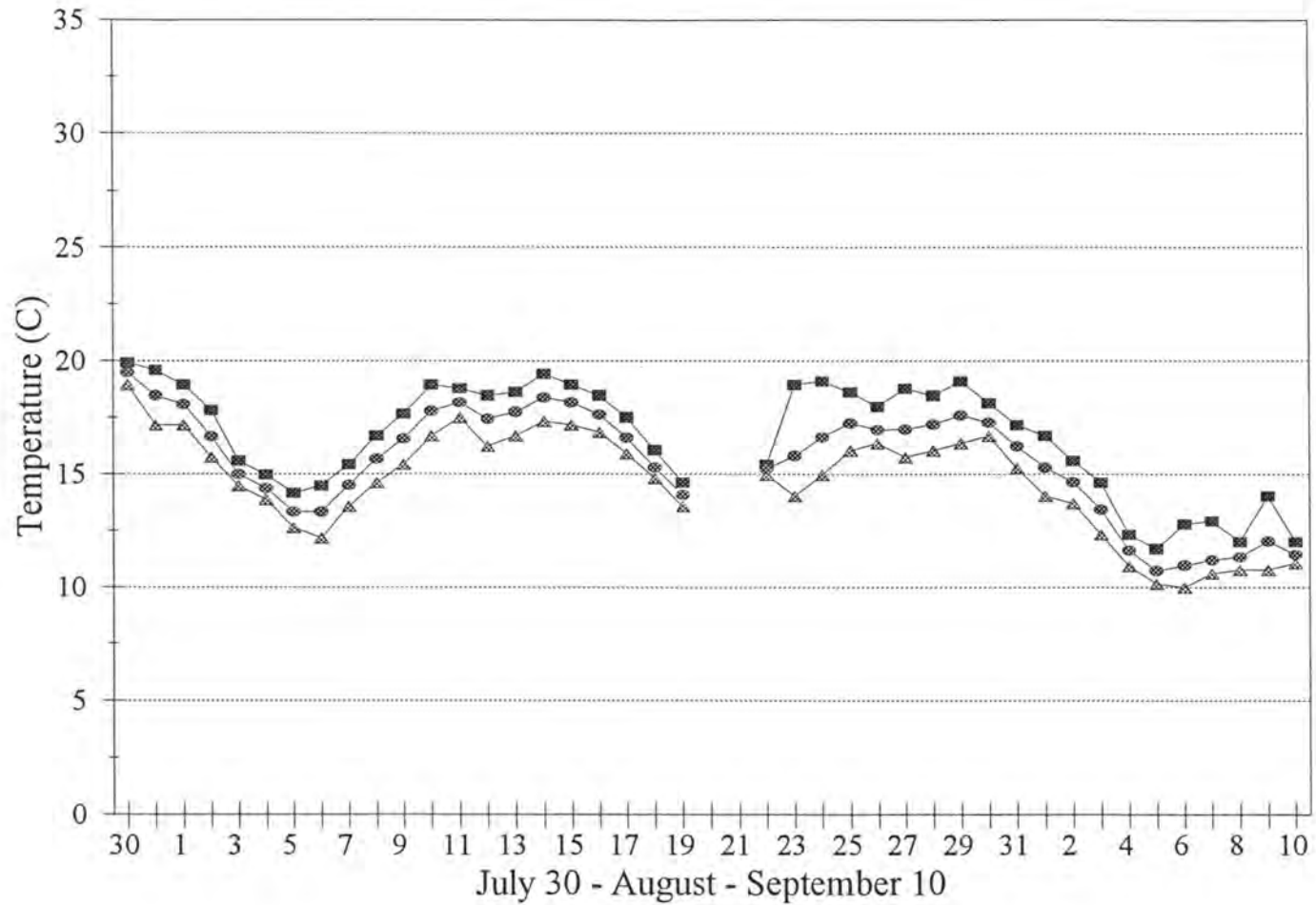
Average daily maximum, minimum, and mean temperatures in LH19 (July 30 - September 10, 1996).

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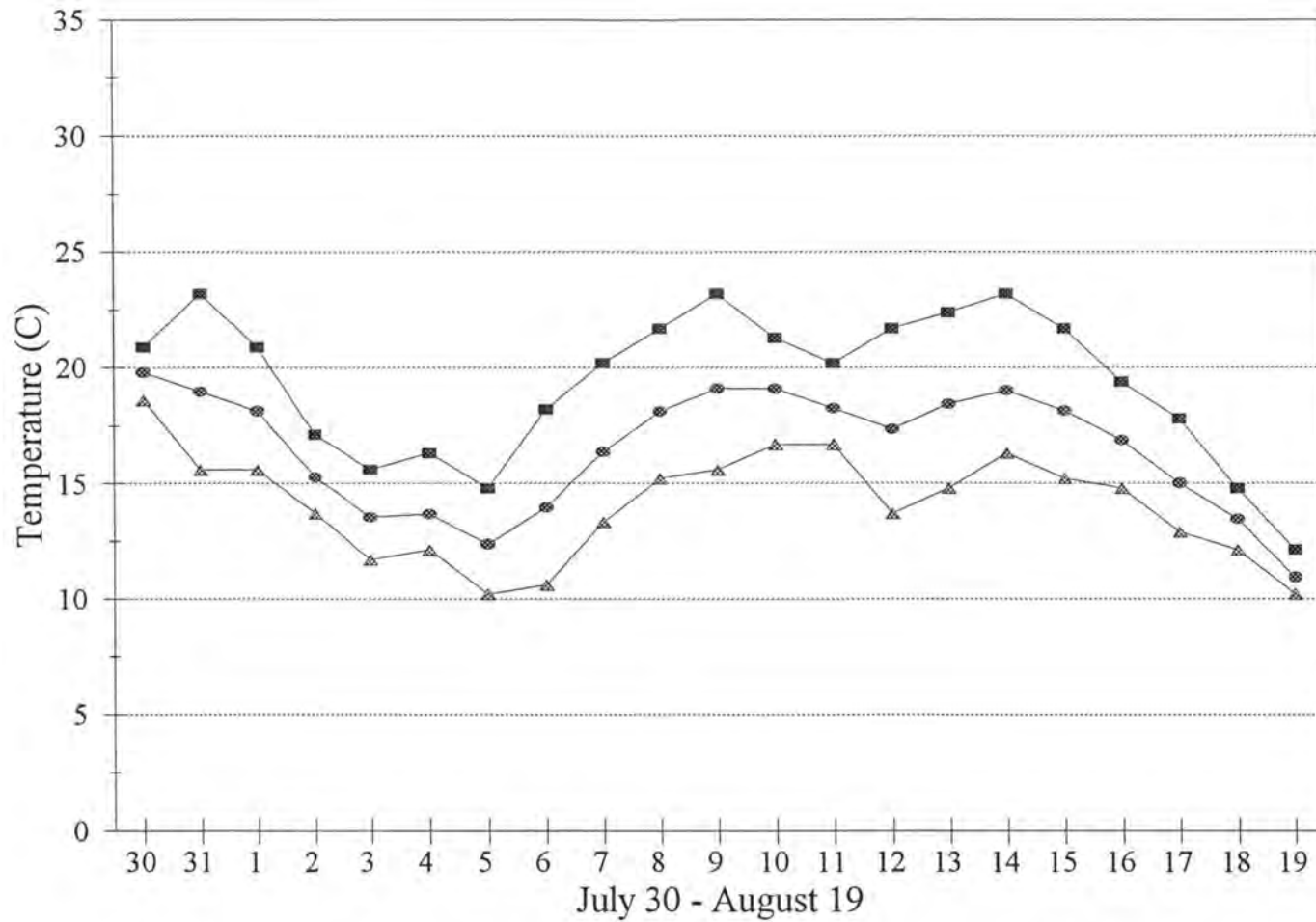
Average daily maximum, minimum, and mean temperatures in LH20 (July 30 - September 10, 1996).

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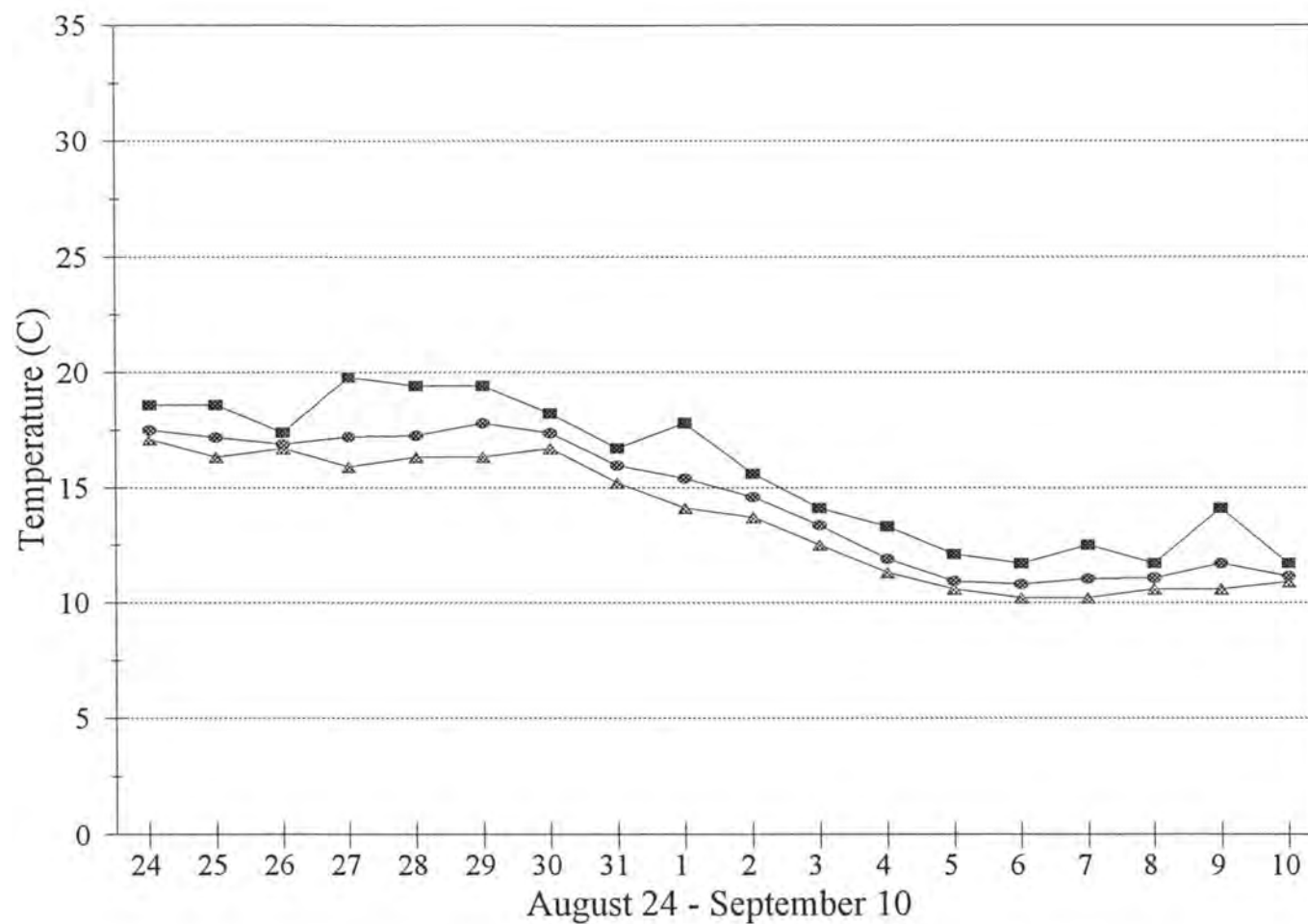
Average daily maximum, minimum, and mean temperatures in LH21
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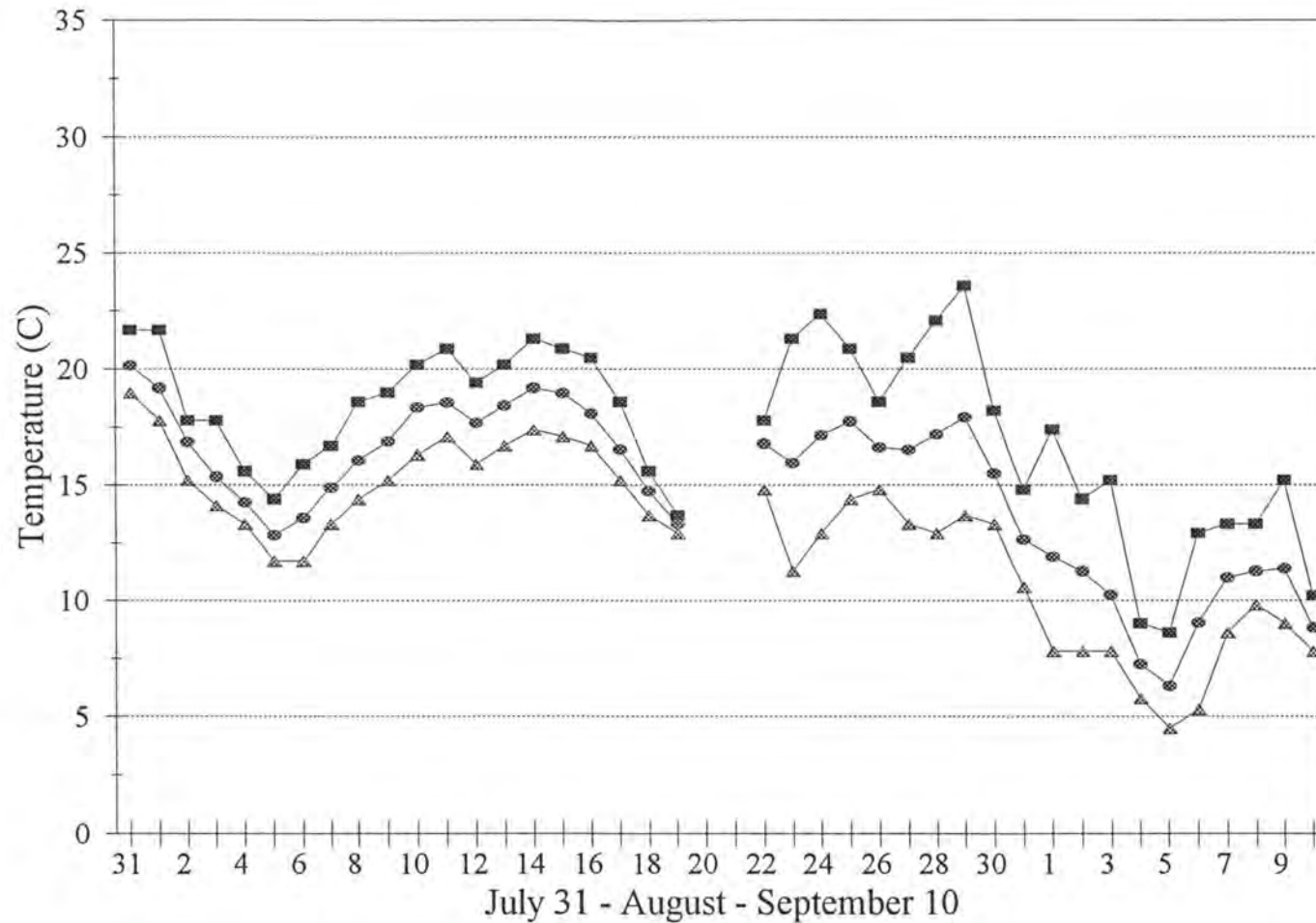
Average daily maximum, minimum, and mean temperatures in LH22
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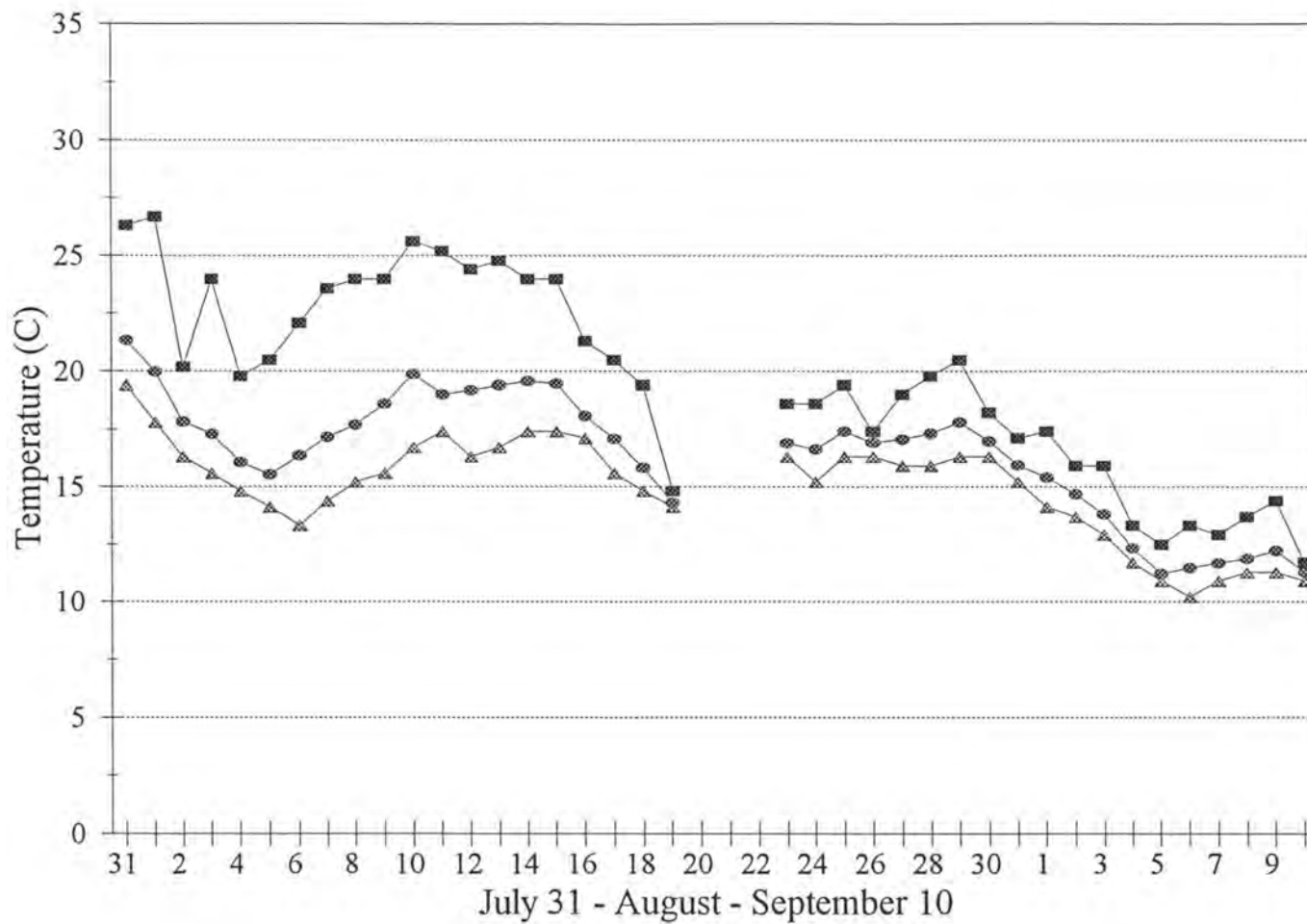
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(August 24 - September 10, 1996).

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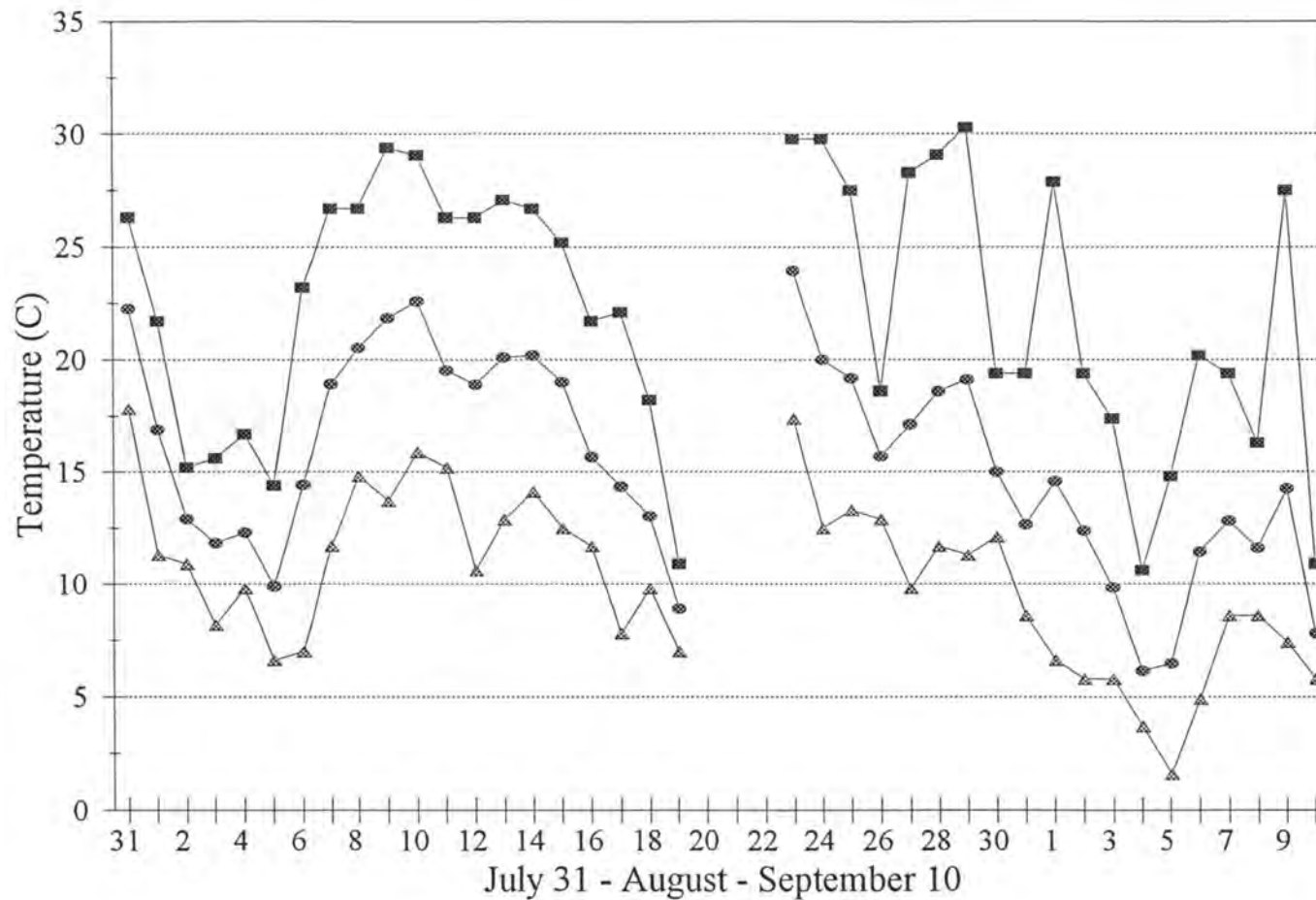
Average daily maximum, minimum, and mean temperatures in LW12
(July 31 - September 10, 1996).

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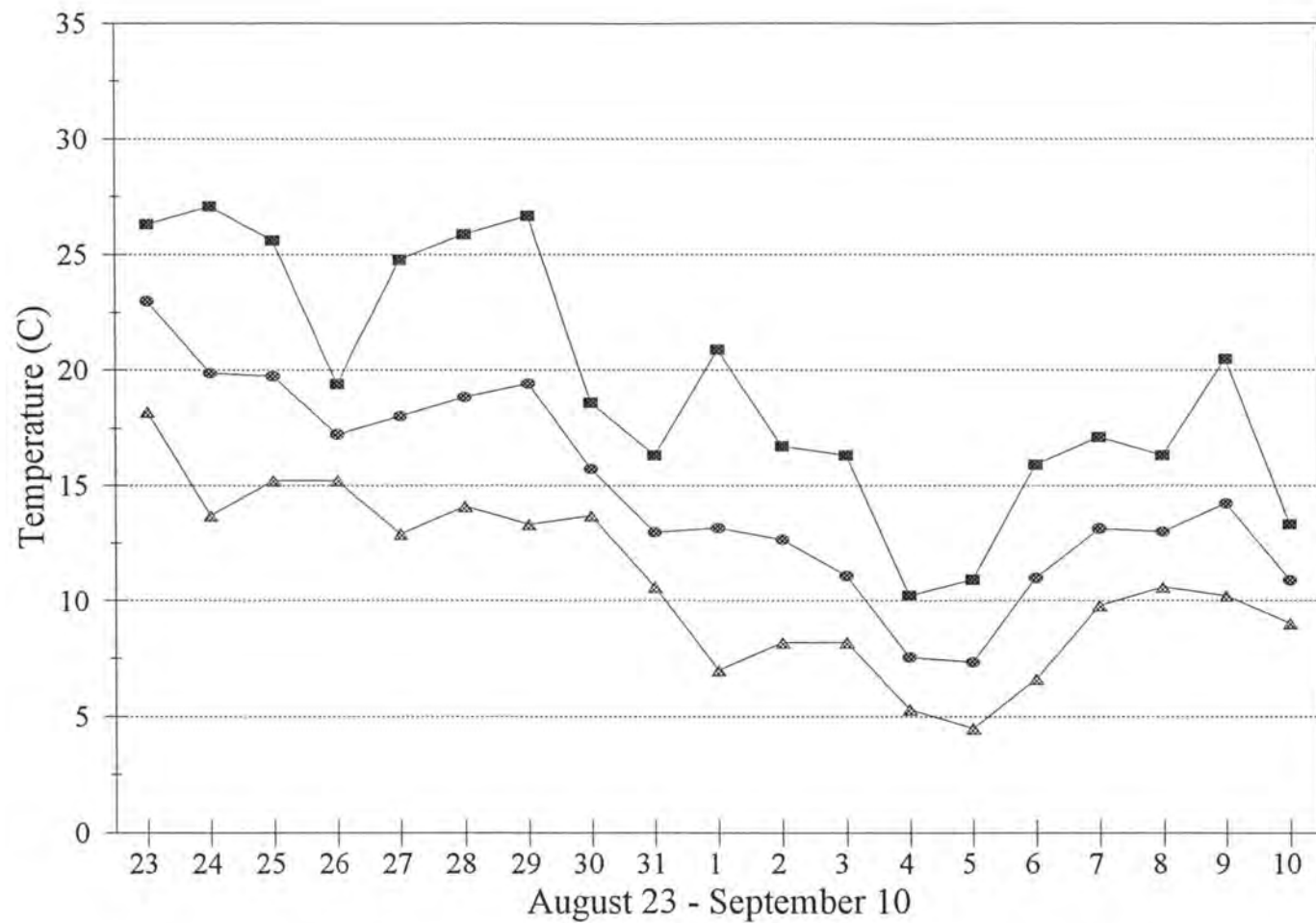
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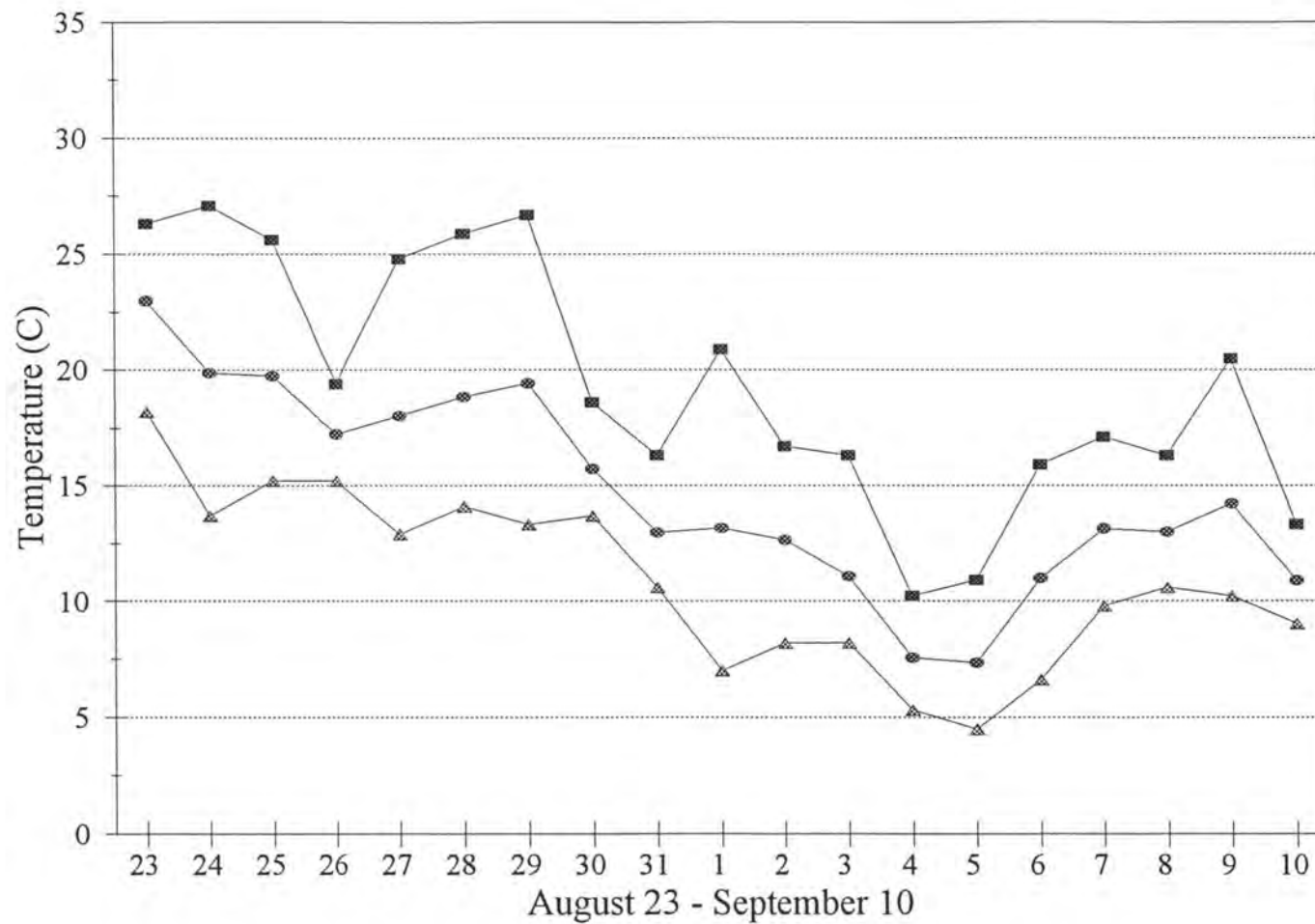
Average daily maximum, minimum, and mean temperatures in LW25
(July 31 - September 10, 1996).

—■— Maximum —▲— Minimum —●— Mean



Average daily maximum, minimum, and mean temperatures in UK01
(August 23 - September 10, 1996).

—■— Maximum —▲— Minimum —●— Mean



Average daily maximum, minimum, and mean temperatures in UK01
(August 23 - September 10, 1996).

—■— Maximum —▲— Minimum —●— Mean