Breeding-Site Characteristics of Pond-Breeding Amphibians at Whitehorse Ponds, Crater Lake National Park

By
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BREEDING-SITE CHARACTERISTICS FOR POND-BREEDING AMPHIBIANS AT WHITEHORSE PONDS, CRATER LAKE NATIONAL PARK

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Abstract. In the face of apparent amphibian population declines at global and regional scales, knowledge of the distribution and population dynamics of amphibians is becoming increasingly important. For pond-breeding amphibians, which require lentic habitats for egg-laying and for larval development, species patterns and population dynamics may be associated with the distribution and character of breeding sites. The purpose of this research was to examine the characteristics of pond-breeding sites for amphibians within a small and apparently undisturbed watershed, Whitehorse Ponds, in the Oregon Cascade Range. Predictions of species-patterns were based upon factors that may contribute to pond-insularity as suggested by island biogeography theory. Specifically, I examined associations between the species richness and relative abundance of breeding amphibians and the areal extent (site size), temporal extent (duration that water persists), habitat complexity (vegetation, substrate, water depth), and distribution of pond sites. Data collection for each site involved physical habitat characterization and amphibian sampling, which was comprised of basic pond (i.e., dip-netting) and funnel trapping surveys. Pond-breeding amphibians in their larval stages were detected in 7 (64%) of 11 sites. Species richness (1 salamander, 3 anurans) varied between 0 and 4 with method and site. Logistic regression revealed a significant association between water persistence and the number of larval species detected by netting, trapping, and incidental observations. There was a significant association between water persistence and the abundance of the salamander species (*Ambystoma* spp.) detected by trapping, but no association was found with netting. There were also significant associations between pond surface area and depth and between pond substrate class and sub-dominant substrate. The basic pond and funnel trapping surveys may detect different species, and it appears testing the effectiveness of the methods for inventory-level (e.g., species richness) and more intensive surveys (e.g., relative abundance) would be useful. The study suggests that insularity for breeding amphibians may occur at local and landscape scales. A metapopulation approach that balances local and landscape characters may be most appropriate in pursuing the notion of pond insularity and breeding amphibians.

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Finally, Kelly Christianson and Zoe Rickenbach, of the U.S. Forest Service, helped me pick my way through ArcView. I may still be plugging away at the GIS terminal today had they not interjected, saving the project from my computer-crashing capability.

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INTRODUCTION

Islands may be useful subjects of ecological study. They are visibly discrete (Adsersen 1995; MacArthur and Wilson 1967) with definable physical and biological characteristics (Wilcox 1980). Islands may encompass the fundamental processes, components, and interactions of ecological systems in simpler ways than continents (Vitousek et al. 1995) or oceans (MacArthur and Wilson 1967). Much of the early island population research focused on oceanic and land-bridge islands (e.g., Wallace 1881; Darwin 1859). More recently, mainland habitats have been described as insular, including terrestrial habitats (e.g., alpine mountaintops: MacArthur 1972) and aquatic habitats (e.g., temporary pools: March and Bass 1995). In particular, ponds may be ideal insular habitats upon which to base predictions of island biogeography. In the present study, I am interested in the potential effects of pond-insularity on the distribution, species richness, and abundance of pond-breeding amphibians.

Research has demonstrated two somewhat consistent species-patterns in island biogeography: 1) large islands tend to have more species than small islands; 2) near islands tend to have more species than far islands. The species-area relation appears to occur in many assemblages of organisms (Gotelli 1995; amphibians and reptiles: Darington 1957; land-birds: Gotelli and Abele 1982; deciduous forest birds: Preston 1960; stream invertebrates: March and Bass 1995). A factor hypothesized to contribute to the "area effect" (Gotelli 1995) is habitat diversity; large oceanic islands often have more complex topography than small oceanic islands (MacArthur and Wilson 1967), and this complexity may result in greater habitat heterogeneity (Gotelli 1995; MacArthur and Wilson 1967). The hypothesis follows that the more heterogeneous an island's habitat, the more species can potentially occupy the island (Wilcox 1980; MacArthur and Wilson 1967). The topography of an oceanic island may be analogous to the strata within a pond, and thus factors that may contribute to pond complexity (e.g., vegetation, substrate, water depth) might be associated with the number of amphibian species occupying a pond. Similarly, the size of a pond may be associated with its amphibian species richness.

The species-distance relation is not as well-documented (Shafer 1990; Williamson 1981). Nonetheless, faunal species richness of insular habitats may decrease with increasing distance from a source pool of organisms (e.g., bird species: Diamond 1972). The "distance effect" (Gotelli 1995) could be a result of relative dispersal rates; species with relatively slow rates of dispersal may not reach remote islands. As applied to pond-breeding amphibians, the distances between breeding sites may influence the amphibian species composition of ponds.

While area, complexity, and distance effects may occur for pond-breeding amphibians, lentic habitat may also encompass a temporal effect driven by water-level fluctuations. Ephemeral ponds are vulnerable to seasonal desiccation, and this might influence the species composition of such ponds; therefore, the seasonal length of time a pond holds water may be an additional factor to consider when examining amphibian species patterns of lentic habitat.

It is upon the premises of island biogeography that I formulate the following questions and hypotheses for pond-breeding amphibians:

1) *Is the areal and temporal extent of aquatic habitat associated with breeding amphibians?* I hypothesize that breeding species richness and abundance increases with site size and increases with the duration that sites retain water.

2) *Is aquatic habitat complexity associated with breeding amphibians?* I hypothesize that breeding species richness and abundance increases with pond strata contributing to physical habitat complexity and thus varies with substrate, water depth, and vegetation.

3) *Is the distribution of ponds associated with breeding amphibians?* I hypothesize remote sites have lower breeding species richness than proximal sites.

The above hypotheses are based upon physical phenomena of island biogeography but do not address the possible interactions of pond structural features. Interactions between pond depth, size, substrate, and other physical attributes may occur. An examination of associations among pond habitat variables may yield a more complete description of breeding-sites.

4) *Are there associations among habitat variables?* I hypothesize the following variables are associated: water depth, substrate type, surface area, and the duration that water is retained.

STUDY AREA

The study was conducted at Whitehorse Ponds within Crater Lake National Park in the Oregon Cascade Range physiographic province between 42° 52' and 42° 53' latitude. Elevations at the ponds range between 1920 and 1935 m. The ponds occur within a localized area (130 ha) in the southeast quadrant of the park on Whitehorse Bluff (map quadrants: T 31 S, R 5 E, Sections 14 and 15), and they appear to be relatively isolated from other aquatic habitats. The bluff is approximately 6 km southeast of Crater Lake and 39 m above the immediate landscape, and it appears to be composed of andesitic lava (Salinas et al. 1994). Apparently a result of low permeability of the bluff's geology, the ponds are located in topographic depressions in the lava with spill elevations ranging between 0.6 and 1.2 m above the invert elevations of the pond bottoms and are probably fed entirely by snow-melt (Salinas et al. 1994). A 1993 limnological study of Whitehorse Ponds (Salinas et al. 1994) suggests they are eutrophic and contain high amounts of organic material.

The number of ponds on the bluff that contain water may vary from year-to-year, but most ponds probably have persisted seasonally at least since visited by early naturalists (e.g., Farner and Kezer 1953). Kezer and Farner (1955) claim that "in June and July there are no less than 12 to 15 ponds of various sizes." More recently, Brandt (1992) and Salinas et al. (1994) identified 12 and 15 ponds, respectively.

The vegetation in and around the ponds appears to be diverse. Salinas et al. (1994) reports that 29 taxa of vascular plants were found in a day-long botanical survey of August 1993. Together, the dominant overstory tree, Shasta red fir (*Abies magnifica* var. *shastensis*), and the sub-dominant tree, mountain hemlock (*Tsuga mertensiana*), provide a nearly closed canopy over large areas of the bluff (Salinas et al. 1994); Salinas et al. (1994) identifies one additional fir and two pines on the bluff. Vascular plants also occur in the ponds themselves (Salinas et al. 1994): western quillwort (*Isoetes occidentalis*); small bur-weed (*Sparganium natans*); water sedge (*Carex aquatilis*); narrow-spiked reedgrass (*Calamagrostis inexpansa*); Drummond's rush (*Juncus drummondii*); broad-leaved twayblade (*Listeria convallarioides*); corn lily (*Veratrum viride*). Salinas et al. (1994) also lists understory vegetation on the bluff.

There is no evidence that Whitehorse Ponds have historically contained fishes.

METHODS

Data collection

A complete inventory (Fellers 1997; Thoms et al. 1997) of lentic habitats at Whitehorse Bluff was attempted between June and September 1996. Pond sites were identified using USGS topographic maps, hand-drawn maps published by previous studies (Brandt 1992; Salinas et al. 1994), and through field reconnaissance. Sites were flagged to aid in relocating, as most sites were visited multiple times in an attempt to measure temporal change (e.g., duration that sites retain water). During each visit, data collection involved physical habitat characterization and/or amphibian sampling.

Physical habitat data consisted of pond surface area and maximum depth, percent vegetation, and substrate type. Pond surface area (m^2) was obtained by pacing the water's edge and applying calculations for area; calculations were based on the m/pace for myself, and I verified my m/pace throughout the season. Maximum pond depth (m), as measured from the surface of the substrate to the water-level, was recorded to 1/100 m using a marked 1.50 m staff. The percentage of emergent vegetation in the pond relative to the surface area was estimated visually. Substrate in each pond was classified as soft or firm, referring to its relative consistency; dominant and sub-dominant substrate types, referring to relative areas of coverage, were categorized as silt, sand/gravel, or wood/tree-needles. The length of time that a pond held water was measured in weeks.

Amphibian sampling involved a basic pond survey and/or an aquatic funnel trapping survey. The techniques for the basic pond survey (BPS) are similar to those of standardized protocols (Thoms et al. 1997; Fellers and Freel 1995). I approached each pond carefully, and while using binoculars to identify or locate amphibians, I encircled the site (Figure 1). Once encircled, I walked the water s edge and used a dip-net to capture amphibians (adults, larvae) seen, including any of those I may have previously spotted. I then waded in a zig-zag pattern within the pond itself, starting from one end; at regular intervals, I swept a dip-net through the water while wading. I measured the time of dip-netting (time of processing specimens not included), and this was used in the calculations of effort. I attempted to sample with equal effort all microhabitats in which I could safely walk. I often captured 1-3 cm of substrate with the dip-net, but I also tried to reduce the degree of disturbance to the substrate in and around the ponds. The presence of any evidence of fishes was noted.

In walking the water's edge and in dip-netting (Figure 1: steps 2 and 3), amphibians that were netted, seen in the water, or seen along the shoreline were counted as dip-net captures and were incorporated in the calculations of BPS abundance and species richness. Amphibians observed while encircling a site (Figure 1: step 1) or heard calling from the pond or shoreline during any part of the BPS were also considered BPS detections but were only included in the calculations of BPS species richness. Amphibians heard calling beyond the pond and immediate shoreline during a BPS and those observed or heard in the proximity of the study sites while not sampling were noted as incidental observations.

Funnel trapping surveys (FTS) that were conducted are similar to the habitat-based protocol of Adams et al. (1997). Minnow traps made of galvanized-steel hardware-cloth were utilized. The approximate number of traps/site used during a FTS was based on the pond surface area during that session (Adams et al. 1997). Traps were placed in the water so that a portion of the mesh was exposed to air to minimize mortality rates. I attempted to place the traps in equal proportions across the microhabitats at each site. All traps were set in the evening and checked the following morning. No bait was used in any of the trapping.

All netted and trapped individuals were identified using standard keys (e.g., Leonard et al. 1993; Nussbaum et al. 1983). Individuals were released where they had been captured, and care was taken to avoid recapturing individuals during any one survey.

Data analysis

The collected data was analyzed as one data set, corresponding to the entire length of the season. The data was subjected to a variety of analyses, which involved the calculations of species richness, relative abundance, and statistical measures of associations. Some of these metrics (e.g., species richness) were displayed graphically on GIS-based maps to visually assess spatial patterns.

Relative abundance and species diversity were calculated separately for each method

(BPS, FTS) and life-history stage (larvae, adult, larval and adult stages combined). Relative abundance for FTSs was calculated as *no. trap captures/trap-night* (Adams et al. 1997). Relative abundance for BPSs was calculated as *no. net captures/person-hour* (Fellers 1997).

Logistic regression was used in an attempt to develop models explaining the variation in observed species patterns (species richness, species relative abundance) and to address associations among habitat variables. One independent variable and one response variable was entered into each model. The statistical program Insight® (SAS 1996) was used to test each hypothesis (level of significance: $p \leq 0.05$). Logistic regression is particularly useful for the data collected in this study because both categorical variables (binary, ordinal) and continuous variables may be included in a model (SAS 1996; Agresti 1984). In addition, logistic regression is useful for small sample sizes with relatively large standard deviations (M.McDowell, statistician, pers. comm.). Statistical tests involving larval life-history stages were emphasized because it was assumed that the presence of a species it its larval form indicated the species had bred at a site.

RESULTS

A total of 11 wetland sites on Whitehorse Bluff were sampled (Figure 2) between 28 June and 05 September 1996. Over the course of the summer, *pond C* became a pond "complex" (Salinas et al. 1994); what had been a contiguous body of water at the beginning of the field season diverged into 4 "sub-ponds" by the end of the season, apparently a result of dropping water-levels. As the sub-ponds were created, each was sampled as a separate site. There was also evidence that 4 other sites were sub-ponds of 2 original ponds (*pond F*, *pond G*); although prior connectivity had not been confirmed visually for these 2 sites, such connectivity was assumed. As a result, data was collected for a total of 16 sites (8 pond sites, 8 sub-pond sites; Figure 3). Since sub-ponds appear to have been physically connected as pond complexes at one time during the 1996 breeding season, the sub-ponds are statistically-dependent samples (W.Jones, statistician, pers. comm.); therefore, sub-pond data was combined for each pond complex. Data was combined primarily using summations (e.g., the surface area for *pond C* was calculated as the sum of the surface areas of *sub-ponds* C_1, C_2, C_3, and C_4), but other methods of combining data was used depending on the type of data.

The BPS occurred at 9 of the 11 sites. Effort at all sites ($\text{Effort}_{\text{all}}$) varied between 0.17 and 3.00 person-hours, and effort at sites where ≥ 1 species was detected ($\text{Effort}_{\text{occupied}}$) ranged 0.67-3.00 person-hours (Table 1). Microhabitats ≤ 0.75 m were dip-netted, as this was the deepest depth at which I could safely traverse the ponds. Sites where the BPS occurred were sampled 1-2 times over the course of the summer.

The FTS occurred at 8 of the 11 sites. At the trapped sites, both $\text{Effort}_{\text{all}}$ and $\text{Effort}_{\text{occupied}}$ ranged 2-20 trap nights. The number of traps/site used during any one trapping session varied between 1 and 9, and traps were set as early as 1600 in the evening and checked as late as 1000 in the morning. Sites where the FTS occurred were sampled 1-3 times during the field season.

No evidence of fishes was found in any of the wetland habitats on Whitehorse Bluff.

Species richness

Species richness of pond-breeding amphibians (adults, larvae) varied between 0 and 4 with method and site (Table 2). A total of 5 species were detected: 1) *Ambystoma* spp. (possibly *A. macrodactylum* [Long-toed Salamander] or *A. gracile* [Northwestern Salamander]); 2) *Hyla regilla* (Pacific Treefrog); 3) *Bufo boreas* (Western Toad); 4) *Taricha granulosa* (Rough-skinned Newt); 5) *Rana cascadae* (Cascades Frog). The median species richness (adults, larvae) at Sites $_{\text{occupied}}$ (≥ 1 species detected) was 2 species.

A total of 4 species in an adult life-history stage and 4 species in a larval stage were detected. Both larval and adult stages of *Ambystoma* spp., *H. regilla*, and *B. boreas* were detected; *T. granulosa* was discovered only in its adult stage, and *R. cascadae* was found only in its larval stage. Trapping detected 1 species in its adult stage (*Ambystoma* spp.) and 2 species in their larval stage (*Ambystoma* spp., *H. regilla*). Trapping (adults, larvae) accounted for 2 (40%) of the 5 species detected among all methods and sites. Netting detected 3 species in adult (*Ambystoma* spp , *H. regilla*, *B. boreas*) and 4 species in larval stages (*Ambystoma* spp., *H. regilla*, *B. boreas*, *R. cascadae*). Netting (adults, larvae) accounted for 4 (80%) of the 5 total species detected. Incidental observations accounted for 3 of the species discovered in their adult stages (*H. regilla*, *B. boreas*, *T. granulosa*) and 1 species in its larval stage (*Ambystoma* spp.). Incidental observations (adults, larvae) accounted for 4 (80%) of the 5 total species.

Pond-breeding amphibians (adults, larvae) were detected in 7 (64%) of the 11 sites. *Ambystoma* spp. (adults, larvae) were found in all 7 of Sites $_{\text{occupied}}$; adult and larval stages of *Ambystoma* spp. were detected in 2 (29%) and 7 (100%) of Sites $_{\text{occupied}}$, respectively. *H. regilla* (adults, larvae) were detected in 4 (60%) of Sites $_{\text{occupied}}$; adult and larval stages of *H. regilla* were detected in 4 (57%) and 3 (43%) of Sites $_{\text{occupied}}$, respectively. *B. boreas* (adults, larvae) were found in 2 (29%) of Sites $_{\text{occupied}}$; the adult and larval stages were found at different sites. *T. granulosa*, found only in its adult stage, occurred at a single site (*pond C*). *R. cascadae*, found only in its larval form, was also detected at 1 site (*pond H*).

Trapping detected ≥ 1 species (adults, larvae) at 5 (63%) of 8 trapped sites; adults were trapped in 2 (25%) of the 8 sites, and larvae were trapped in 4 (50%) of the 8 sites. Netting yielded ≥ 1 species (adults, larvae) at 5 (56%) of 9 netted sites; adults and larvae were netted in 3

(33%) and 5 (56%) of the 9 sites, respectively. At least 1 species (adults, larvae) was observed incidentally in 4 of the 11 total sites; adults and larvae were incidentally-observed in 2 (18%) and 3 (27%) of the 11 sites, respectively.

Species Abundance

The number of amphibians detected varied among methods and species (Table 3). In absolute captures numbers, *Ambystoma* spp. (adults, larvae) was most abundant for all methods combined, comprising 775 (69%) of the 1126 total detections. *H. regilla* (adults, larvae) was the next most abundant, comprising 234 (21%) of all detections. *B. boreas*, *R. cascadae*, and *T. granulosa* made up 75 (7%), 41 (4%), and 1 (< 0.10%) of the remaining captures, respectively. Of all the methods, netting (adults, larvae) yielded the most detections with 936 (83%) of 1126 total detections. Trapping (adults, larvae) yielded 125 (11%) of all detections. Incidental observations (adults, larvae) accounted for 65 (6%) of all detections.

As measured in capture numbers, larvae were more abundant than adults across all methods and species. Larvae comprised 928 (99%) of the 936 netting captures, 122 (98%) of the 125 trapping captures, and 60 (92%) of the 65 incidental observations. In particular, *Ambystoma* spp. was the most abundant larvae, comprising 107 (88%) of 122 trapped larvae (Figure 4) and 604 (65%) of 928 netted larvae (Figure 5); all incidentally-observed larvae were *Ambystoma* spp. Adult forms of *Ambystoma* spp. constituted 3 (100%) of 3 trapped and 1 (13%) of 8 netted larvae. *H. regilla*, the next most abundant larvae, comprised 15 (12%) of 122 trapped larvae and 210 (23%) of 928 netted larvae. Adult *H. regilla* were not detected by trapping, but 6 (75%) of 8 netted and 3 (60%) of 5 incidentally-observed adults were *H. regilla*. *B. boreas* comprised 73 (8%) of 928 netted larvae and 1 (13%) of 8 adult netting captures. Neither adult nor larval forms of *B. boreas* were trapped; however, 1 (20%) of 5 incidentally-observed adults was a *B. boreas*. The larval form was the only life history stage of *R. cascadae* that was detected and made up 41 (4%) of 928 larvae netting captures.

Relative abundance indices were highly variable between methods, species, and life-history stages (Table 4). Among all species and life stages, trapping indices at sites ranged 0-12 captures/trap-night. Across all sites (Total $_{\text{all}}$), relative abundance (adults, larvae) as measured by trapping ranged from 0 captures/trap night for *B. boreas* and *R. cascadae* to 2.3 captures/trap-night for *Ambystoma* spp; however, trapping did not occur in the sites where *B. boreas* and *R. cascadae* had been detected by netting. Total$_{\text{all}}$ as measured by trapping (adults, larvae) yielded 0.31 captures/trap-night for *H. regilla*. Trapping relative abundance (adults, larvae) across all occupied sites (≥ 1 species detected, Total$_{\text{occupied}}$) ranged from 0 captures/trap-night for *B. boreas* and *R. cascadae* to 3.06 captures/trap-night for *Ambystoma* spp.; Total$_{\text{occupied}}$ for *H. regilla* was measured at 0.42 captures/trap-night. The only species trapped in its adult stage was *Ambystoma* spp. (Total$_{\text{all}}$ = 0.06, Total$_{\text{occupied}}$ = 0.08). Total$_{\text{all}}$ for the larvae of *Ambystoma* spp. and *H. regilla*, the 2 species whose larvae were trapped, was 2.2 and 0.31 captures/trap-night, respectively. Total$_{\text{occupied}}$ for the larvae of *Ambystoma* spp. was 2.97 captures/trap-night and for *H. regilla* larvae was 0.42 captures/trap-night.

Netting indices at sites ranged 0-226.9 captures/person-hour among all species and methods. Total$_{\text{all}}$ for netting (adults, larvae) ranged from 3.90 captures/person-hour for *R. cascadae* to 57.6 captures/person-hour for *Ambystoma* spp.; Total$_{\text{all}}$ for *B. boreas* and *H. regilla* measured 7.0 and 21.4 captures/person-hour, respectively. Total$_{\text{occupied}}$ for netting (adults, larvae) varied between 5.07 for *H. regilla* and 74.8 captures/person-hour for *Ambystoma* spp.; Total$_{\text{occupied}}$ (adults, larvae) for *B. boreas* and *H. regilla* was measured by netting as 9.15 and 26.7 captures/person-hour, respectively. No *R. cascadae* adults were netted, but Total$_{\text{all}}$ for adults of *Ambystoma* spp., *H. regilla*, and *B. boreas* was measured by netting as 0.10, 0.57, and 0.10 captures/person-hour, respectively. Total$_{\text{occupied}}$ for netted adults was 0.12 for *Ambystoma* spp., 0.74 for *H. regilla*, and 0.12 captures/person-hour for *B. boreas*. Total$_{\text{all}}$ for netted larvae ranged from 3.90 for *R. cascadae* to 57.5 for *Ambystoma* spp.; Total$_{\text{all}}$ for netted larvae was 7.0 captures/person-hour for *B. boreas* and 20.0 for *H. regilla*. Total$_{\text{occupied}}$ (adults, larvae) for *R. cascadae*, *B. boreas*, *H. regilla*, and *Ambystoma* spp. was 5.07, 9.02, 26.0, and 74.7 captures/person-hour, respectively.

There was also between-site variability for the relative abundance indices. As the most widely distributed species, the trap rate for *Ambystoma* spp. (adults, larvae) at sites ranged 0-12 captures/trap-night, and its net rate ranged 0-226.9 captures/person-hour; the greatest capture rates for *Ambystoma* spp. occurred at *pond G* for both netting and trapping. Trap and net rates for *H. regilla* (adults, larvae) ranged 0-1.3 captures/trap-night and 0-120 captures/person-hour between sites, respectively. The greatest net rate (adults, larvae) for *H. regilla* occurred at *pond H*, and its greatest trap rate occurred at *pond G*. The net rate across the sites ranged 0-109 captures/person-hour for *B. boreas* and 0-23.4 captures/person-hour for *R. cascadae*; neither *B. boreas* nor *R. cascadae* were detected by trapping.

Physical Habitat

Habitat characteristics also differed between sites (Table 5). Maximum surface areas ranged from 9 m^2 (*pond K*) to 1028 m^2 (*pond C*) with a mean of 170 m^2 (standard deviation s = 291). *Pond C* alone accounted for 53% of the total surface areas for all sites combined. Maximum depths ranged 0.29-0.75 m (mean = 0.46, $s = 0.16$). The deepest depth (0.75 m, *pond C*) reflects the deepest point I could physically measure. The maximum length of time water was present varied between 4 and >11 weeks (median = 5). 4 (37%) of 11 sites contained ≥0.10 m of water the last day of the field season (05 September) and were considered as having persisted >11 weeks; the most frequent water duration measurement was >11 weeks. 5 (45%) of 11 sites maintained water ≤5 weeks. The most frequent substrate consistency class was soft and for dominant and sub-dominant substrate types was silt and wood/tree-needles, respectively.

During the 1996 field season, vegetation characteristics in and around the ponds appeared to be highly variable between sites. Although not measured, the degree of canopy closure seemed to be much greater for some ponds than for others, with some sites exposed to sunlight for much of the daylight hours and others exposed to relatively little sunlight. In addition, the abundance of aquatic plants appeared to highly variable between ponds, and the maximum percentage of emergent vegetation ranged 1% (*pond C*) to 95% (*pond I*) with 5 sites ≤5% and 5 sites ≥55% vegetation.

Statistical Associations

Logistic regression revealed a significant association (Score Test $p \leq 0.05$) between water persistence and the number of larval species detected by netting, trapping, and incidental observations (Table 6). There was a moderate association ($p = 0.0686$) between water duration and larval species richness as measured for all methods combined. Larval species richness detected incidentally was significantly associated with depth ($p = 0.0203$) and moderately associated with surface area (0.0653). While not statistically significant, there was also a moderate association between larval species richness detected by trapping and the percentage of emergent vegetation ($p = 0.0912$).

There were fewer significant associations between measures of relative abundance and habitat variables (Table 7). There was a significant association between water persistence and the abundance of *Ambystoma* spp. detected by trapping ($p = 0.0399$), but no such association was found with netting ($p = 0.1113$). *Ambystoma* spp. showed no significant associations with any of the other habitat metrics. *B. boreas*, as detected by netting, was mildly associated with depth ($p = 0.0826$).

Measures of statistical associations among habitat variables produced some patterns (Table 8). Maximum surface area and maximum depth were significantly associated, regardless of which was the response and independent variable. There was a moderate association between depth (response variable) and substrate class ($p = 0.0861$) and between depth (independent variable) and dominant substrate ($p = 0.0882$). Associations between substrate class and sub-dominant substrate were also significant, regardless of which was the response and independent variable. There was a moderate association between substrate class (independent) and water persistence ($p = 0.0775$). An association of the same caliber ($p = 0.0704$) occurred between vegetation (independent) and sub-dominant substrate (response).

Species Distribution

Upon visual assessment, the amphibian species richness does not appear to be associated with the spatial distribution of the ponds, but there may be some patterns. For adult and larval stages combined, *Ambystoma* spp. and *H. regilla* appear to be the most widely distributed of the 5 species (Figure 6). *Ambystoma* spp. (adults, larvae) occurred in all sites where *H. regilla* (adults, larvae) were found. *B. boreas* (adults, larvae), detected at 2 sites, were found in the northern and southern portions of the study area. *R. cascadae* and *T. granulosa* were the least widely distributed, and each was found at a separate site. *Pond D* and *sub-pond* G_2, 2 of the 5 sites where no species (adults, larvae) were detected, occurred adjacent to ponds or sub-ponds that contained 1-3 species. Since all of the study sites are relatively proximal for pond-breeding amphibians, the distribution of $\text{sites}_{\text{occupied}}$ (adults, larvae) and sites in which no species were found appears to be random. Nonetheless, when adults and larvae are combined the 3 pond complexes (*pond C*, *pond F*, *pond G*) contained 4 (80%) of the 5 species detected.

Similar patterns are apparent when examining the distribution of species found in their larval stages (Figure 7). The larvae of *Ambystoma* spp. is the most widely distributed and occurred at all sites in which *H. regilla* larvae occurred. *R. cascadae*, which was only found in its larval stage, occurred at 1 site (*pond H*). *B. boreas* larvae also occurred at a single sub-pond (F_2). Unlike when adults and larvae are combined, larvae were found in only 3 of the 4 sub-ponds in the *pond C* complex. In addition, *Ambystoma* spp. was the only larvae detected in the 3 sites at the western flank of the study area (*pond I*, *pond J*, *pond K*), the most spatially isolated of the study sites.

The distribution of adult species detected appears to reflect the fewer number of sites in which adults were found (Figure 8). The greatest species richness of adults occurred in the *pond C* complex, which contained *Ambystoma* spp., *H. regilla*, *B. boreas*, and *T. granulosa*. Not including pond complex sub-ponds, no adult species were found in 6 of the 10 other sites. Unlike in the larval stages, *Ambystoma* spp. and *H. regilla* occurred together in only 1 site (*pond C*). *Ambystoma* spp. was the only adult species found at the most 3 westerly sites. *H. regilla* was the only adult found at the most southern site (*pond H*).

DISCUSSION

The MacArthur-Wilson model (MacArthur and Wilson 1967) was one of the first attempts to explain species patterns on islands and was the basis for most of the hypotheses addressed in this study. Although developed and tested on oceanic islands, the model has been applied more widely (Vitousek et al. 1995). The MacArthur-Wilson, or equilibrium (Gotelli 1995), model attributes the number of species occupying an island to a balance between the rates of species immigration and extinction (Gotelli 1995; Diamond 1967; MacArthur and Wilson 1967), and it assumes there is a permanent "source" pool of species that can potentially occupy an island, a "sink" (Gotelli 1995). The model predicts that an island is constantly losing and gaining species, while the island's species richness is relatively constant (Gotelli 1995; Wilcox 1980). The model theorizes that extinction rates decrease with increasing population sizes (Diamond 1972), and large islands tend to have large population sizes. Large islands generally have complex topography, and the theory follows that the more heterogeneous an island's habitat, the more species can potentially occupy the island (Wilcox 1980; MacArthur and Wilson 1967). The model further predicts that immigration rates decrease with increasing distance from a permanent source pool of species due to random dispersal (Diamond 1972).

In this study, I examined the potential effects of insularity on pond-breeding amphibians. Since lentic habitat appears to have insular characteristics, I conceptualized that ponds may effectively function as islands for breeding amphibians, especially for the larvae of pond-breeders. I hypothesized that the distribution, species richness, and abundance of pond-breeding amphibians displays patterns consistent with those found in studies of insular ecology and thus varies with the areal extent, habitat complexity, and spatial distribution of pond breeding sites. The seasonal length of time ephemeral ponds hold water was also examined because hypothetically the longer a pond contains water, the more species can potentially occupy it; this is analogous to an area effect but on a temporal scale.

The study occurred at Whitehorse Ponds, a relatively isolated watershed that contains 12-15 ponds which have apparently existed on Whitehorse Bluff at least since visited by early naturalists (e.g., Farner and Kezer 1953). The bluff, which has a steep rock face along its northern edge, appears to be relatively far from other known pond sites. Together, the bluff's rock face and its distance from other pond sites may be indicative of limited immigration and emigration of amphibians between the bluff and the immediate landscape. Whitehorse Ponds are relatively proximal (within 0.50 mile^2) with no apparent barriers to migration among the ponds themselves, and this supports the assumption that all the ponds are available for amphibians breeding on the bluff.

While lentic habitat appears to have insular characteristics, Whitehorse Ponds as an aggregate also displays insularity relative to the surrounding landscape. Insularity may be apparent at both local and landscape scales.

Local Scale Insularity

This study examined the potential effects of pond insularity at local breeding sites. Various associations occurred that were significant ($p \leq 0.05$; e.g., depth and incidental richness) and somewhat significant ($p \leq 0.10$; e.g., surface area and incidental richness, depth and abundance of *B. boreas*, vegetation and trapping richness). However, the only associations that were consistent across methods, suggesting the existence of a pattern, involved the length of time ponds held water.

Water duration was significantly associated with breeding species richness for netting, trapping, and incidental observations (Table 6). These associations support the notion that sites which hold water longer enable greater species occupation, but the data may be biased toward sites in which water persisted for a relatively long time because such sites were sampled more times than sites that dried early (Table 9). Amphibians may be associated with water duration for biological reasons, and there might be habitat qualities characteristic of sites that contain water a relatively long time to which amphibians may,be tied. Water duration was somewhat, though not significantly, associated with substrate consistency class (Table 8; $p = 0.0775$); however, I found no associations between water persistence and any of the other habitat metrics. As a result, the data suggests there may be a real relationship at Whitehorse Ponds between species richness and the length of time sites hold water. Future research examining this temporal effect may consider:

1) refining methods of species and habitat data collection; 2) collecting data at a finer temporal scale; 3) analyzing the relative effectiveness and biases of the BPS and FTS; 4) doing parallel studies in other isolated watersheds. Rowe and Dunson (1995) claim that the "hydroperiod" for ephemeral ponds varies between years; therefore, another area for future research as related to insularity is the influence of year-to-year variability of the hydroperiod on the insularity and species composition of ponds.

The only species whose larval abundance was significantly associated with water duration was *Ambystoma* spp. (Table 7). *Ambystoma* spp. was virtually the only species found in its larval stage during all sample weeks (Table 10). The presence of *Ambystoma* spp. at a large number of sites over much of the season may reflect a reproductive strategy, as the species may saturate all available wetland habitats in an area. *R.* cascadae, *B. boreas*, and *T. granulosa* on the other hand, were each found in only one site, and this may be indicative of greater site-specificity. *Ambystoma* spp. was the most commonly captured larvae (Figure 4; Figure 5), but since it was detected by all methods its presence and abundance does not appear to reflect a bias in the methods; however, it may be conducive to being detected in such surveys (e.g., less wary to survey activity). Research which examines the effectiveness of the methods for each species would be useful.

In addition to the biases in the methods themselves, biases may have resulted from the sample frequency and effort. Frequency (Table 9) and effort of sampling (Table 1) at each site was not consistent for each collection phase (habitat characterization, amphibian sampling). In fact, 3 of the 11 ponds were not discovered until week 7 of the field season, and after that point they were only trapped. The other 8 sites were visited up to 4 of the first 5 weeks but not subsequently sampled until week 7 or 10; no amphibians were sampled weeks 6-8. Effort $_{\text{all}}$ for trapping, which ranged 2-20 trap nights, had a standard deviation $s = 6$; Effort $_{\text{occupied}}$ ranged 0.17-3.00 person-hours ($s = 0.90$). The extent of the ranges in effort might be attributed to the variability in the size and permanence of the sites (e.g., surface area for *pond B* = 11 m^2 and water persisted 3 weeks; surface area for *pond C* = 1028 m^2 and water persisted >11 weeks). It may be difficult to compare the effectiveness between methods with the data in this study because there were 5 sites that were either netted or trapped but not both. For instance, trapping did not occur in the sites where *B. boreas* and *R. cascadae* had been detected by netting, and this does not permit a complete analysis of the effectiveness of the methods for these 2 species.

The MacArthur-Wilson model may help explain species patterns of insular habitats, but it fails to integrate the possible influence of population dynamics. Intra- and interspecific interactions (e.g., competition and predation) influence population size (Gotelli 1995) and community composition. Previous studies suggest that the extent of an ephemeral pond's hydroperiod can determine the reproductive strategy, recruitment, growth, and the timing and size of metamorphosis of amphibians (see Rowe and Dunson 1995). In turn, this may influence the species composition of a site. In light of the potential effects of the hydroperiod, tests measuring species-habitat associations may actually be measuring characters that result from amphibian biology rather than amphibian ecology. Nonetheless, associations do not necessarily reflect causal relationships, and it is still appropriate to measure and discuss such associations; however, less weight may be given to associations between species and habitat because of these possible physiological changes driven by water fluctuations.

The MacArthur-Wilson model, which explains some physical interactions, does not address biological interactions. In fact, a recognition of the importance of interactions between physical and biological factors (Adsersen 1995) has helped direct contemporary island population research toward metapopulation approaches.

Landscape Scale Insularity

While the local scale may be important, Whitehorse Ponds as a whole could be one component of a larger system rather than a system of its own.

A "metapopulation" (Levins 1969) was originally conceptualized as a population of populations (Hanski and Simberloff 1997). This narrow view has been largely replaced by the broader view that metapopulations comprise "any assemblage of discrete local populations with migration among them" (Hanski and Simberloff 1997), and this migration influences local population dynamics. A metapopulation approach recognizes that factors external to localized structural features (e.g., area, complexity, hydroperiod) can influence island populations. Nonetheless, local habitat conditions may play an integral role in local population dynamics, and island populations, which may comprise local populations of metapopulations, may be subject to both island habitat conditions and the spatial assemblage of island habitats (i.e., local and landscape scale influences).

These theories of insular ecology have been more recently incorporated into reserve designs. Most reserves are not isolates but rather samples of a larger habitat (Preston 1962). Preston (1962) noted that these samples contain more species per unit area than do isolates and attributed this to greater rates of immigration due to the proximity of adjacent habitat; Shafer (1990) suggests that the greater number of immigrants enables a larger number of species, each represented by relatively few individuals, to occupy the reserve. While there are distinctions between samples and isolates, the establishment of reserves must confront the issues of reserve size, distance to other reserves, and the overall assemblage of reserves. Large reserves, having fewer extinctions than small reserves, theoretically protect the most species. However, extinction rates are species-specific (Gotelli 1995), and Shafer (1990) suggests that "extinction-prone species" (Terborgh 1974) must be identified so that reserves can be designed to accommodate vulnerable species. Reserves based entirely upon the MacArthur-Wilson model predictions, which focuses primarily on physical habitat, may fall short in protecting such species because the model does not account for other critical factors that influence island populations. On the other hand, by stressing connections between island habitats in our land management, we could be ignoring important local characters of the islands themselves, such as size, complexity, and other habitat features.

CONCLUSION

A metapopulation approach to species patterns of insular habitats integrates physical and biological interactions, and it is one description of the insularity of Whitehorse Ponds in Crater Lake National Park. The MacArthur-Wilson model explains species patterns of local insular habitat conditions, but it does not address the possible influence of an island's position within a larger context. While metapopulations may also influence island populations, metapopulations may be difficult to delineate because they may lack the physical discreteness of islands. Additionally, the local habitat conditions of an island may play an integral role in local population dynamics. Understanding the breeding-site characteristics of pond-breeding amphibians in a small watershed may be a step in understanding the amalgamation of insular ecology at local and landscape scales.

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FIGURES

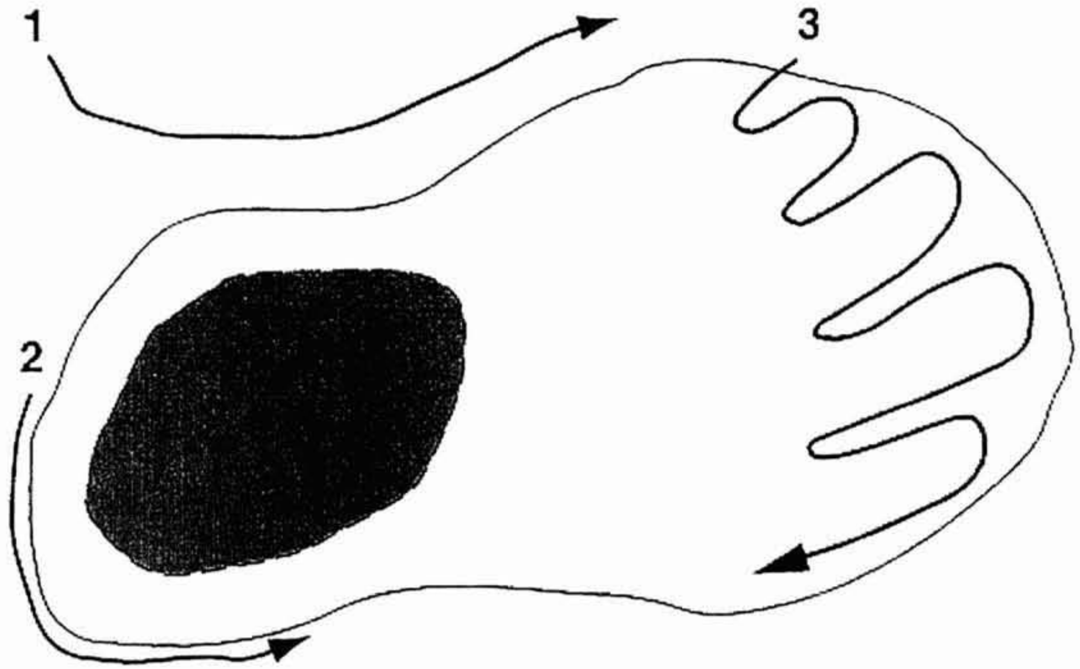

Figure 1. Typical basic pond survey pattern 1) encircle site; 2) walk water's edge; 3) dip-net the site while wading.

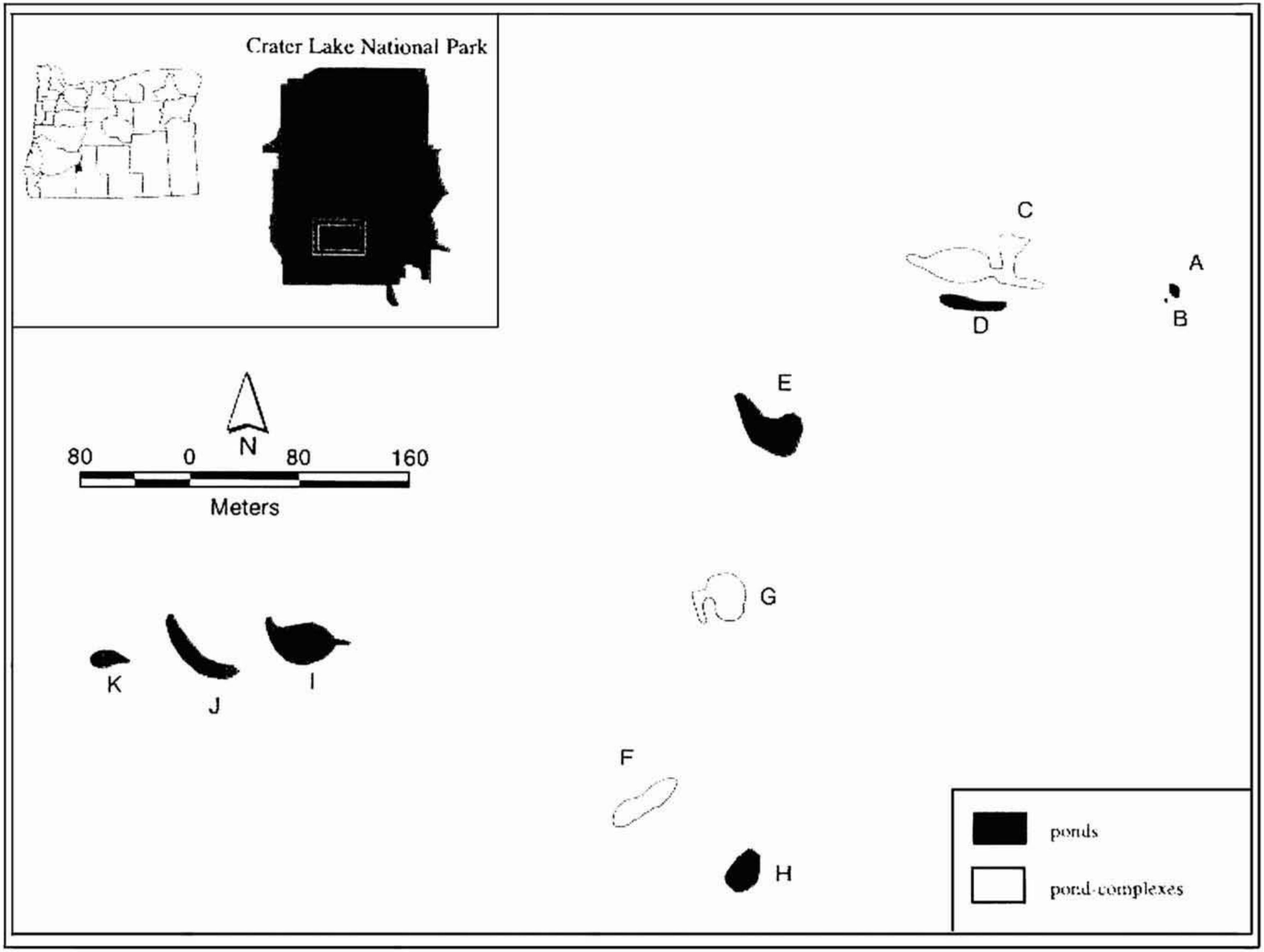

Figure 2. Whitehorse Ponds study sites, depicting ponds and pond-complexes prior to divergence of complexes. Crater Lake National Park, OR

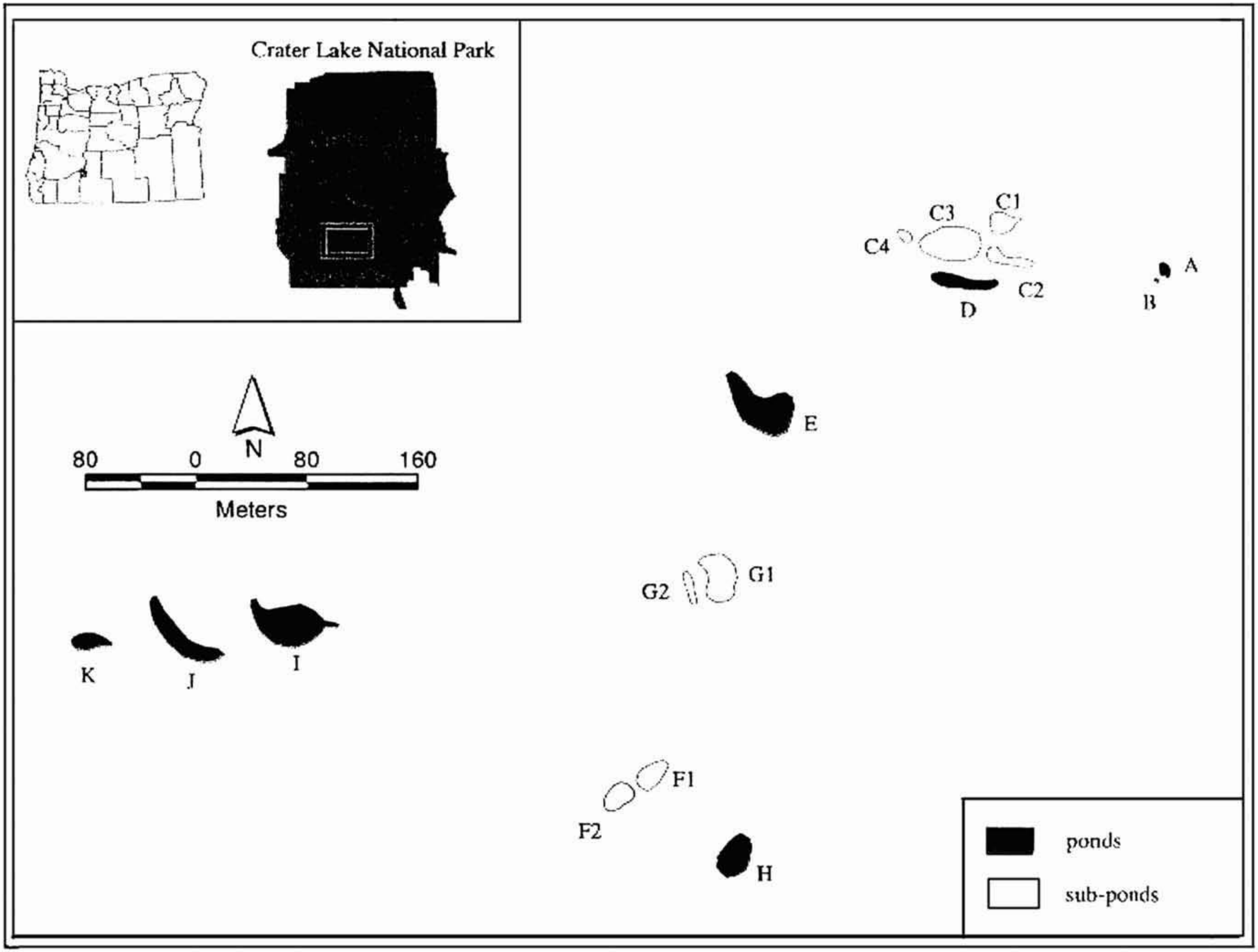

Figure 3 Whitehorse Ponds study sites, showing divergence of pond-complexes. Crater Lake National Park, OR.

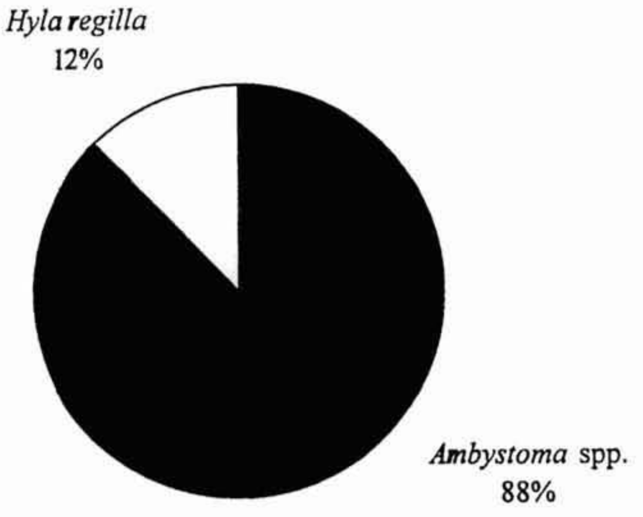

Figure 4. Larval species composition for funnel trapping surveys.

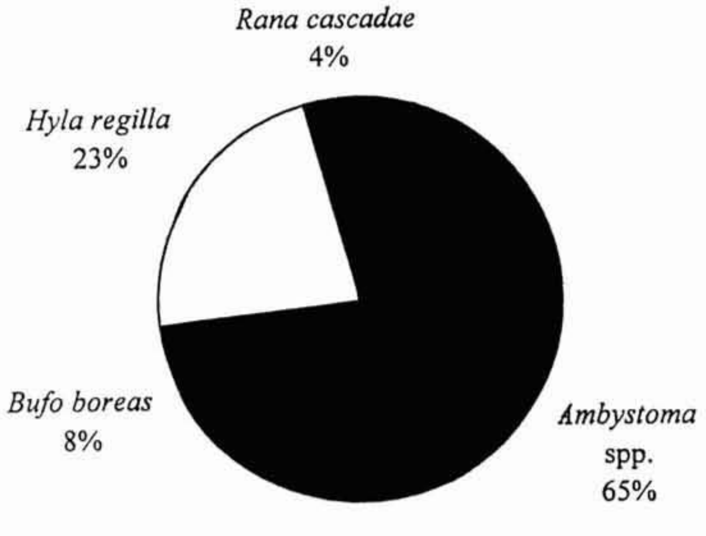

Figure 5. Larval species composition for netting surveys.

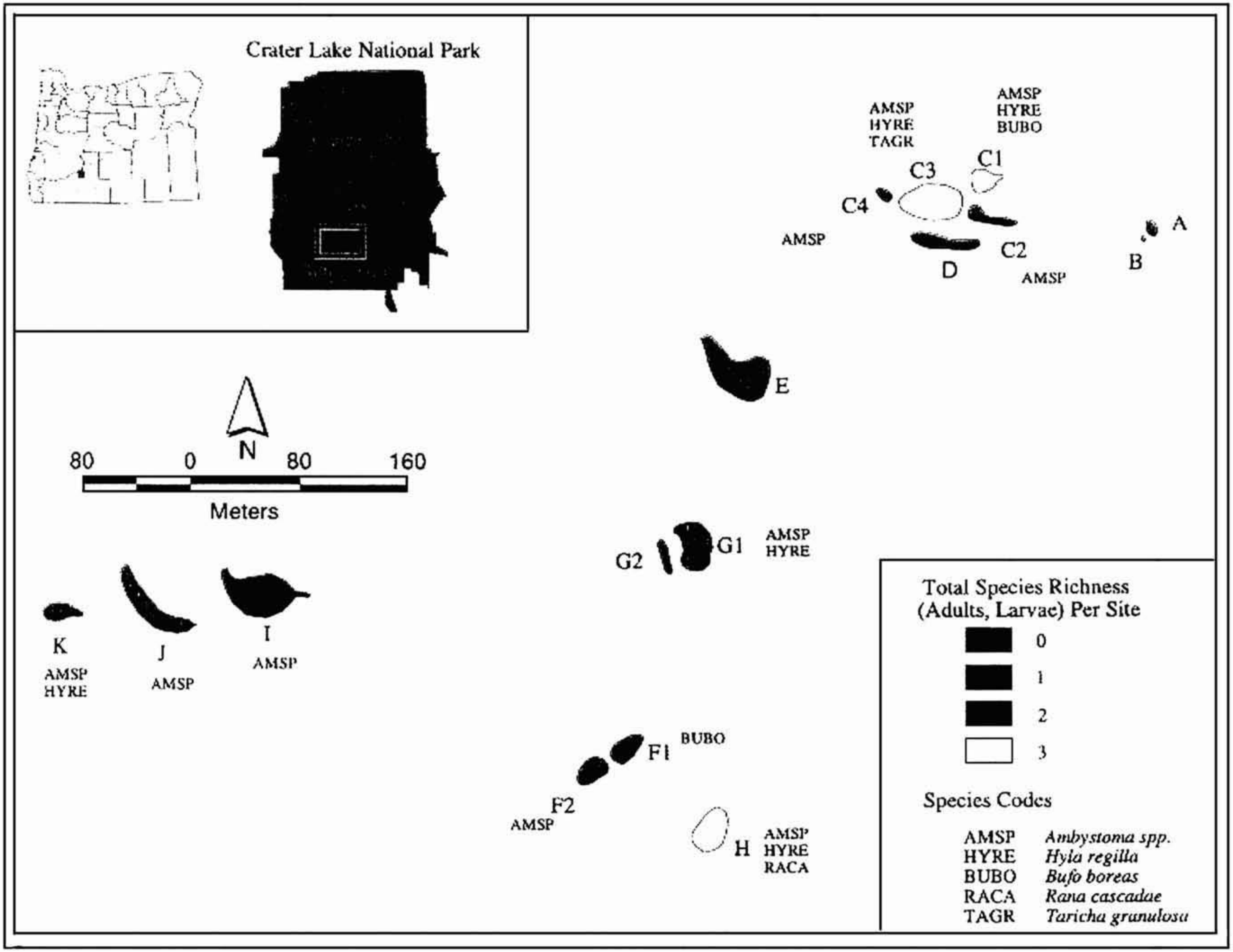

Figure 6 Total species richness (adults, larvae) at ponds and pond-complexes as detected across all methods (BSP, FTS, incidental observations). Whitehorse Ponds, Crater Lake National Park, OR.

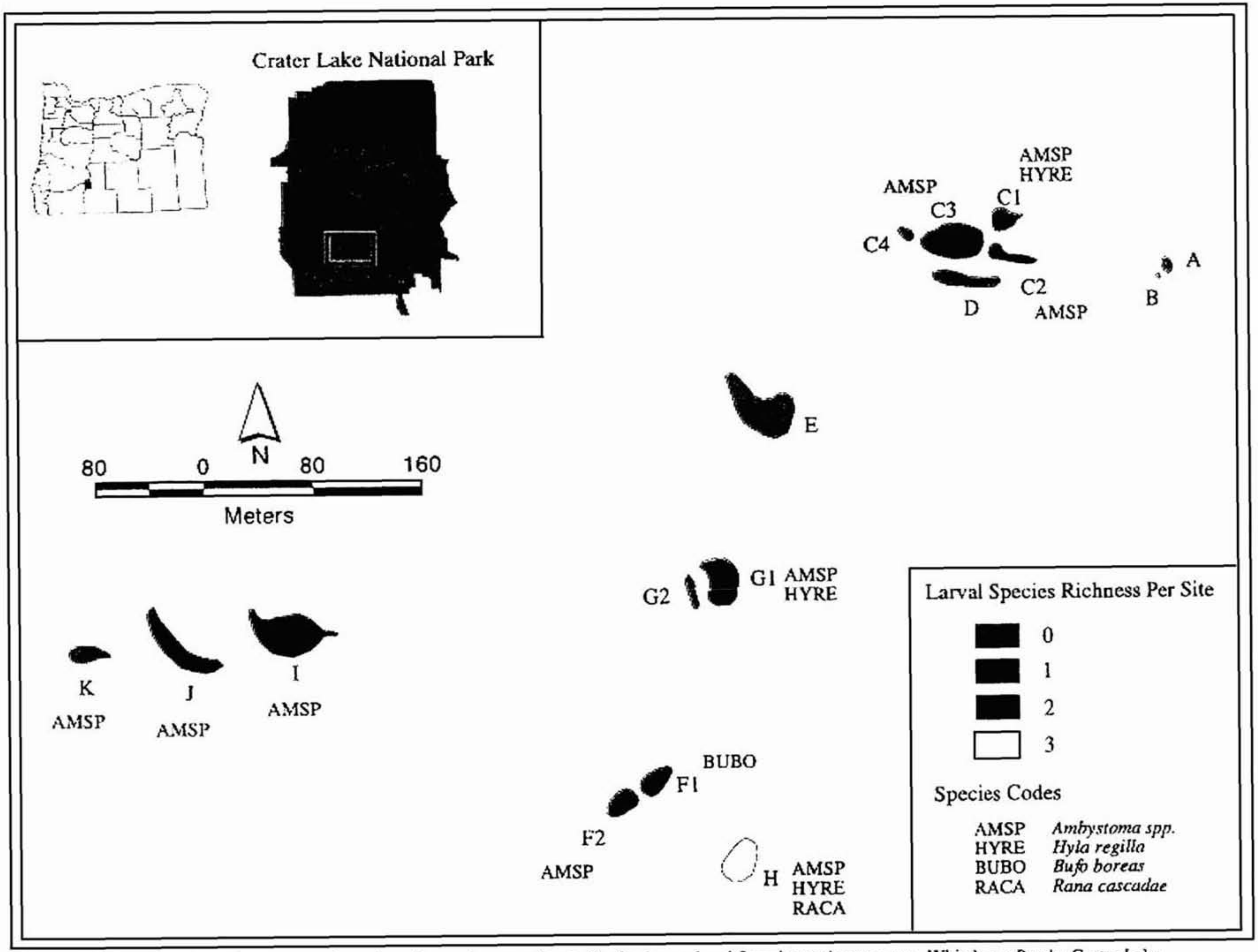

Figure 7. Larval species richness at ponds and pond-complexes as detected by basic pond and funnel trapping surveys. Whitehorse Ponds, Crater Lake National Park, OR.

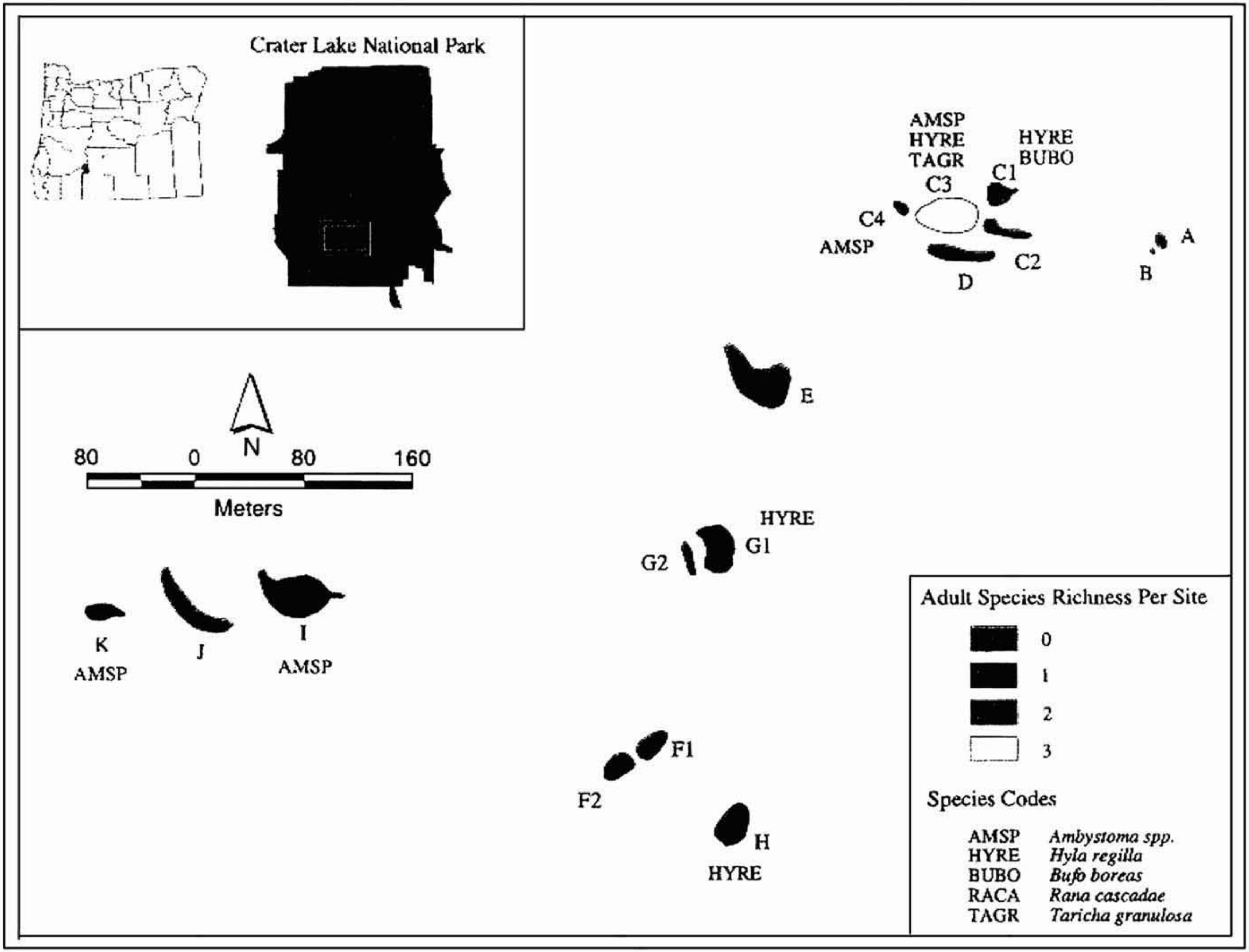

Figure 8. Adult species richness at ponds and pond-complexes as detected by basic pond and funnel trapping surveys. Whitehorse Ponds, Crater Lake National Park, OR.

TABLES

Table 1. Effort by method and site. Effort$_{all}$ = effort across all sites, Effort$_{occupied}$ = effort across occupied sites.

Site	Trapping (trap nights)	Netting (person-hours)
A	4	1.00
B	-	0.17
C	**20**	**3.00**
D	3	0.33
E	5	0.92
F	-	**0.67**
G	**4**	**1.92**
H	-	**1.75**
I	**5**	**0.75**
J	**5**	-*
K	**2**	-
Effort$_{all}$	48	10.51
Effort$_{occupied}$	36	8.09

* - not sampled

bold type indicates occupied sites (at least 1 species detected by method)

Table 2. Number of species detected with various sampling methods (funnel trapping, dip-netting, incidental observations) for each site. Species Codes: AMSP = *Ambystoma* spp.; HYRE = *Hyla regilla* ; BUBO = *Bufo boreas* ; TAGR = *Taricha granulosa* ; RACA = *Rana cascadae* .

	Trapping			Netting			Incidental Observations			All Methods		
Pond	Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total	Adults	Larvae	Total
A	0	0	0	0	0	0	0	0	0	0	0	0
B	-*	-	-	0	0	0	0	0	0	0	0	0
C	1 AMSP	2 AMSP HYRE	2 AMSP HYRE	3 AMSP BUBO HYRE	1 AMSP	3 AMSP BUBO HYRE	3 BUBO HYRE TAGR	1 AMSP	4 AMSP BUBO HYRE TAGR	4 AMSP BUBO HYRE TAGR	2 AMSP HYRE	4 AMSP BUBO HYRE TAGR
D	0	0	0	0	0	0	0	0	0	0	0	0
E	0	0	0	0	0	0	0	0	0	0	0	0
F	-	-	-	0	2 AMSP BUBO	2 AMSP BUBO	0	0	0	0	2 AMSP BUBO	2 AMSP BUBO
G	0	2 AMSP HYRE	2 AMSP HYRE	1 HYRE	2 AMSP HYRE	2 AMSP HYRE	0	0	0	1 HYRE	2 AMSP HYRE	2 AMSP HYRE
H	-	-	-	1 HYRE	2 HYRE RACA	2 HYRE RACA	0	1 AMSP	1 AMSP	1 HYRE	3 AMSP HYRE RACA	3 AMSP HYRE RACA
I	1 AMSP	0	1 AMSP	0	1 AMSP	1 AMSP	0	1 AMSP	1 AMSP	1 AMSP	1 AMSP	1 AMSP
J	0	1 AMSP	1 AMSP	-	-	-	0	0	0	0	1 AMSP	1 AMSP
K	0	1 AMSP	1 AMSP	-	-	-	1 HYRE	0	1 HYRE	1 HYRE	1 AMSP	2 AMSP HYRE
Total	1	2	2	3	4	4	3	1	4	4	4	5

* - not sampled

Table 3. Number of individuals of each species detcted by each sampling method.

	Trapping			Netting			Incidental Observations			
	Adult	Larvae	Total	Adult	Larvae	Total	Adult	Larvae	Total	Total
Ambystoma spp.	3	107	110	1	604	605	0	60	60	775
Bufo boreas	0	0	0	1	73	74	1	0	1	75
Hyla regilla	0	15	15	6	210	216	3	0	3	234
Taricha granulosa	0	0	0	0	0	0	1	0	1	1
Rana cascadae	0	0	0	0	41	41	0	0	0	41
Total	3	122	125	8	928	936	5	60	65	1126

Table 4. Relative abundance for species detected by netting and trapping surveys (*Ambystoma* spp.; *Bufo boreas*; *Hyla regilla*; *Rana cascadae)*. Trapping index = *captures/trap-night*; Netting index = *captures/person-hour*; $\text{Total}_{\text{all}}$ = relative abundance across all sites ($\text{Effort}_{\text{all}}$ = 48 trap-nights, 10.51 person-hours); $\text{Total}_{\text{occupied}}$ = relative abundance across occupied sites ($\text{Effort}_{\text{occupied}}$ = 36 trap-nights, 8.09 person-hours).

	Ambystoma spp.				*Bufo boreas*				*Hyla regilla*				*Rana cascadae*			
	Trapping		Netting		Trapping		Netting		Trapping		Netting		Trapping		Netting	
Pond	Adults / Larvae	Total	Adults / Larvae	Total	Adults / Larvae	Total	Adults / Larvae	Total	Adults / Larvae	Total	Adults / Larvae	Total	Adults / Larvae	Total	Adults / Larvae	Total
A	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0
B	-	-	0 / 0	0	-	-	0 / 0	0	-	-	0 / 0	0	-	-	0 / 0	0
C	0.1 / 0.35	0.45	0.33 / 12	12.3	0 / 0	0	0.33 / 0	0.33	0 / 0.5	0.5	1.3 / 0	1.3	0 / 0	0	0 / 0	0
D	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0
E	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0
F	-	-	0 / 186.6	186.6	-	-	0 / 109	109	-	-	0 / 0	0	-	-	0 / 0	0
G	0 / 12	12	0 / 226.9	226.9	0 / 0	0	0 / 0	0	0 / 1.3	1.3	0.52 / 0.52	1.1	0 / 0	0	0 / 0	0
H	-	-	0 / 0	0	-	-	0 / 0	0	-	0	0.57 / 119.4	120	-	-	0 / 23.4	23.4
I	0.2 / 0	0.2	0 / 10.7	10.7	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0	0 / 0	0
J	0 / 9.4	9.4	-	-	0 / 0	0	-	-	0 / 0	0	-	-	0 / 0	0	-	-
K	0 / 2.5	2.5	-	-	0 / 0	0	-	-	0 / 0	0	-	-	0 / 0	0	-	-
$\text{Total}_{\text{all}}$	0.06 / 2.2	2.3	0.10 / 57.5	57.6	0 / 0	0	0.10 / 7.0	7.0	0 / 0.31	0.31	0.57 / 20.0	21.4	0 / 0	0	0 / 3.90	3.90
$\text{Total}_{\text{occupied}}$	0.08 / 2.97	3.06	0.12 / 74.7	74.8	0 / 0	0	0.12 / 9.02	9.15	0 / 0.42	0.42	0.74 / 26.0	26.7	0 / 0	0	0 / 5.07	5.07

* - not sampled

Table 5. Habitat characteristics across all sites. Substrate Class: 1 = soft consistency, 2 = firm consistency; Substrate Type: 1 = silt, 2 = sand/gravel, 3 = wood/tree-needles.

						Substrate			
	Surface Area (sq m)		Depth (m)		Water Persistence	Class	Type (1, 2, 3)		Emergent Vegetation
Pond	Min	Max	Min	Max	(Weeks)	(1, 2)	Dominant	Sub-dominant	(Max %)
A	0	24	0	0.38	4	2	1	3	55
B	0	11	0	0.32	3	2	1	3	60
C	17	1028	0.17	0.75	>11*	1	3	2	1
D	0	86	0	0.47	4	1	3	1	15
E	0	234	0	0.62	5	1	1	2	5
F	0	55	0	0.22	5	1	1	2	77
G	0	158	0	0.4	10	2	2	3	1
H	0	96	0	0.62	10	1	3	3	60
I	163	163	0.52	0.52	>11	1	1	3	95
J	88	88	0.42	0.42	>11	1	3	1	5
K	9	9	0.29	0.29	>11	1	1	2	5
mean	25.18	177.45	0.13	0.46	n/a	n/a	n/a	n/a	34
s	52.64	290.66	0.20	0.16	n/a	n/a	n/a	n/a	35
median	0	88	0	0.42	5	1	1	2	15
mode	0	n/a	0	0.62	>11	1	1	3	5

* water persistence >11 weeks are sites that were not dry by last day of field season (05 September)

n/a = measures not applicable to that variable

Table 6. Logistic regression Score Test p-values measuring associations of habitat variables and larval species richness by method. H_0: no association between habitat variables and larval species richness.

				Substrate			
				Class	Type		
Method	Surface Area (Max)	Depth (Max)	Water Duration		Dominant	Sub-dominant	Vegetation (Max %)
Netting	0.7689	0.9183	0.0471	0.5582	0.4514	0.4202	0.6115
Trapping	0.1582	0.8267	0.0510	0.7003	0.2082	**	0.0919
Incidental	0.0653	0.0203	0.0288	0.2136	0.2636	0.2858	0.2890
*All Methods	0.2878	0.5380	0.0686	0.3715	0.2020	0.5503	0.8485

* combination of netting, trapping, and incidental observations

** no measure of association calculated: observed and predicted probabilities indistinguishable

Table 7. Logistic regression Score Test *p* -values measuring associations of habitat variables and larval relative abundance by method. *H* o: no association between habiat variables and larval relative abundance.

	Netting							Trapping						
				Substrate							Substrate			
	Surface Area (Max)	Depth (Max)	Water Duration	Class	Type		Vegetation (Max %)	Surface Area (Max)	Depth (Max)	Water Duration	Class	Type		Vegetation (Max %)
Species					Dominant	Sub-dominant						Dominant	Sub-dominant	
Ambystoma spp.	0.5538	0.4894	0.1113	*	0.7576	0.6796	0.8804	0.1269	0.6922	0.0399	0.5690	0.1317	0.3996	0.1049
H. regilla	0.6598	0.6535	0.1355	0.7077	0.1768	0.1969	0.7341	0.1028	0.3967	0.2914	0.2343	0.3267	0.3650	0.2725
B. boreas	0.5911	0.0826	0.5070	0.4533	0.3679	0.4913	0.2591	n/a	n/a	n/a	n/a	n/a	n/a	n/a
R. cascadae	0.6955	0.3383	0.3196	0.4533	0.1571	0.3896	0.5514	n/a	n/a	n/a	n/a	n/a	n/a	n/a

n/a = species not detected by method

* no measure of association calculated because observed and predicted probabilities indistingishable

Table 8. Logistic regression Score Test p-values measuring associations among habitat variables. H_0: no association between independent and response variables.

	Independent Variables						
				Substrate			
					Type		
Response Variables	Surface Area (Max)	Depth (Max)	Water Duration	Class	Dominant	Sub-dom.	Vegetation (Max %)
Surface Area (Max)	X	0.0057	0.1905	0.2844	0.2215	*	0.5195
Depth (Max)	0.0525	X	0.5501	0.0861	0.1529	0.6555	0.8522
Water Duration	0.1822	0.3015	X	0.0775	0.3720	0.5999	0.4357
Substrate Class	0.4071	0.2376	0.2017	X	0.2928	0.0488	0.7991
Dominant Substrate	0.1819	0.0882	0.2092	0.3370	X	0.1539	0.1451
Sub-dominant Substrate	0.5992	0.9436	0.9625	0.0376	0.1872	X	0.0704
Vegetation (Max %)	0.1031	0.3036	0.2725	0.8282	0.1967	0.2730	X

* no measure of association calculated because observed and predicted probabilities indistinguishable

Table 9. Frequency of sampling for each site by week. HAB = habitat characterization; BPS = basic pond survey; FTS = funnel trapping survey; x = sampled at least once in week; dry = pond dry, no subsequent sampling; found = when site discovered.

Pond and	Week									
Survey Type	1	2	3	4	5	6	7	8	9	10
A				dry						
HAB	x	-*	x							
BPS	x	-	x							
FTS	x	-	x							
B			dry							
HAB	x	-								
BPS	x	-								
FTS	-	-								
C										
HAB	x	-	x	x	x	-	x	-	x	x
BPS	x	-	-	-	-	-	-	-	-	-
FTS	x	-	-	-	-	-	-	-	-	-
D				dry						
HAB	x	-	x							
BPS	x	-	-							
FTS	x	-	-							
E					dry					
HAB	x	-	x	x						
BPS	x	-	-	-						
FTS	x	-	-	-						
F					dry					
HAB	-	-	x	x						
BPS	-	-	x	-						
FTS	-	-	-	-						
G										dry
HAB	-	-	x	-	x	-	-	-	-	
BPS	-	-	x	-	x	-	-	-	-	
FTS	-	-	-	-	x	-	-	-	-	
H										dry
HAB	-	-	x	-	x	-	-	-	-	
BPS	-	-	x	-	x	-	-	-	-	
FTS	-	-	-	-	-	-	-	-	-	
I							found			
HAB							-	-	x	x
BPS							-	-	-	x
FTS							-	-	x	-
J							found			
HAB							-	-	x	x
BPS							-	-	-	-
FTS							-	-	x	-
K							found			
HAB							-	-	x	x
BPS							-	-	-	-
FTS							-	-	x	-

* - not sampled

Table 10. Species richness per week as detected among all methods combined (BPS, FTS, incidental observations). Species Codes: AMSP = *Ambystoma* spp.; HYRE = *H. regilla*; BUBO = *B. boreas*; TAGR = *T. granulosa*; RACA = *R. cascadae;* dry = pond dry and no subsequent sampling. A = adult found; L = larvae found; A/L = adult and larval stages found.

Pond	Week							
	1	2	3	4	5	6 - 8	9	10
A	0		0	dry				
B	0		dry					
C	3 AMSP (A/L) HYRE (A) BUBO (A)		3 AMSP (L) HYRE (A) BUBO (A)	2 AMSP (A/L) HYRE (L)	3 AMSP (A/L) HYRE (L) TAGR (A)		AMSP (L)	AMSP (L)
D	0		0	dry				
E	0		0		dry			
F			2 AMSP (L) BUBO (L)		dry			
G			2 AMSP (L) HYRE (A/L)		2 AMSP (L) HYRE (L)			dry
H			1 HYRE (A/L)		1 RACA (L)			dry
I								1 AMSP (A/L)
J							1 AMSP (A/L)	
K							2 AMSP (A/L) HYRE (L)	