

**Effects of Abiotic Factors on Aquatic Macroinvertebrate
Compositions and Distributions in Ten Vernal Pools at UNDERC**

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Abstract

Vernal pools are among the most ancient and unique ecosystems found at UNDERC and many aquatic invertebrates have specialized adaptations for survival. Abiotic factors such as pH, dissolved oxygen concentration, conductivity, temperature, canopy cover, area, and hydroperiod combine to define the limitations experienced by aquatic life, both plant and animal. Our data suggest that there was a significant relationship of hydroperiod on genera richness and diversity. The area of the vernal pool also had a significant relationship with diversity suggesting that Island Biogeography Theory can be applied to vernal pools. Relationships were found between dissolved oxygen concentrations and with total number of invertebrates per min and total number of genera. Several more specific relationships were found; relationships of conductivity, maximum depth, and temperature with total Odonata genera were found. Relationships were also found between Heteropterans and both dissolved oxygen and pH. The results suggest that area, hydroperiod, and dissolved oxygen concentrations have the largest affect on the distribution and composition of aquatic invertebrates in vernal pools.

Introduction

Vernal pools are often viewed as obstacles of residential and commercial development because of their ephemeral nature and little utility for recreation. As a result, vernal pools were drained and endemic species lost until the Endangered Species Act of 1973 (Zedler 2003).

By definition, vernal pools are water-filled depressions that dry at least once a year and may alternate between dry and wet conditions (Keely and Zedler 1998). Innudation, either by rainfall or snow melt, during the time frame of germination of upland plants prevents their establishment and desiccation

prevents the establishment of most wetland flora (Keely and Zedler 1998). In connection with the prevention of wetland flora establishment, most vernal pools are heterotrophic and the major energy source is derived from detritus. Vernal pools colonized with a plant community in either the wet or dry phase are considered autochthonous (Graham 1998). Because vernal pools must dry by definition and are often isolated from permanent bodies of water, predation by fish is rarely a factor. Without fish predation, both aquatic invertebrate and amphibian species demonstrate increased survival (Zedler 2003, Keely and Zedler 1998).

The ephemeral nature of vernal pools is an obstacle for many groups of organisms. Many inhabitants have specialized adaptations in their physiology or life cycle. Several groups of habitat generalists colonize vernal pools but habitat specialists are the most successful (Brooks 2000). Studies revealed a wide array of highly specialized organisms that depend upon the abiotic and biotic characteristics of vernal pools for development and survival (Zedler 2003). Adaptations fall into three categories: escape of the habitat prior to desiccation, resistance to drying during a stage of the life cycle, or an actual life cycle specifically adapted to resist desiccation (Graham 1998).

Hydroperiod is defined as the number of days a vernal pool contains water. Many factors combine to affect the hydroperiod including geology and precipitation which are the most important. The hydroperiod of vernal pools has

been shown to have the greatest effect on the composition of aquatic invertebrates (Brooks 2000). The biotic factors affected by hydroperiod include species richness, invertebrate abundance, predator size, predator diversity and abundance, and invertebrate and amphibian reproductive success (Brooks 2000).

Studies have demonstrated hydroperiod to be strongly correlated with maximum volume (Brooks and Hayashi 2002). Even though area is related to hydroperiod volume, it is valuable to determine which factors are most important. Vernal pools have been related to the island biogeography theory because they are isolated ecosystems (Brooks 2000). Island biogeography theory states that as area increases, the diversity of organisms increases (Molles, Jr 2002). Area is strongly related to the diversity of microhabitats within a vernal pool (Brooks 2000). A greater diversity of habitats should support a greater diversity of macroinvertebrates. For example, species richness of aquatic beetles has been shown to increase with increasing pool area (Brooks 2000, Nilsson, Elmberg, and Sjoberg 1994).

Conductivity is an abiotic factor of vernal pools that may affect the composition of macroinvertebrates. Conductivity is the measure of dissolved ions and aquatic macroinvertebrates survive and reproduce more effectively in water with higher conductivity (Hellenthal personal communication).

pH is a factor that may influence the composition of aquatic invertebrates

because of its affect on a developing organism. Many orders of aquatic insects show tolerance to low pH except for Plecoptera. Studies have shown that no Plecoptera species can survive in a pH below 4 (Resh and Rosenberg 1984). No Plecopterans are expected to be found in our vernal pools. Other studies show that aquatic invertebrate species diversity and abundance will significantly decrease at and below a pH of 5.5 (Friday 1987). Other studies show that the breaking point is a pH of 5 (Resh and Rosenberg 1984). Because all of our pools are in a natural, unpolluted state, the relationship between pH and macroinvertebrate composition may be minimal.

In temporary aquatic ecosystems, there is increased pressure on aquatic macroinvertebrates to reach the adult or desiccation-resistant stage before the pond dries. A study involving three species of Anisoptera showed that the rate of growth and development were higher for those individuals in the temporary habitat (Suhling et al. 2005). Because of their ectothermic nature the development of macroinvertebrates is affected by water temperature (Resh and Rosenberg 1984, Thorp and Covich 1991). Because water temperature and dissolved oxygen are inversely correlated, high water temperatures may decrease diversity and abundance of invertebrates.

Dissolved oxygen is one of the most important abiotic factors affecting invertebrate abundance and diversity (Thorp and Covich 1991). Many forms of lentic larvae can supplement atmospheric oxygen with dissolved oxygen. Oxygen

levels below 2 mg/L may decrease the fitness and chances of survival for many aquatic invertebrates. For example, Caddisfly larvae are especially vulnerable to decreased oxygen levels because their locomotion is restricted (Thorp and Covich 1991).

Given the review of the literature, I tested five hypotheses. First, genera richness, abundance, and diversity should be higher at sites with a longer hydroperiod. Second, genera diversity and richness should be higher at sites with greater area. Third, individual abundance and diversity should be higher at sites with higher concentrations of dissolved oxygen. Fourth, individual abundance should be higher at sites with higher conductivity. Fifth, individual abundance and diversity should be higher at sites with higher pH.

Materials and Methods

This study was conducted at the University of Notre Dame Environmental Research Center in the upper peninsula of Michigan in Gogebic County.

UNDERC is a 7500-acre, mostly contiguous mid-successional forested area.

Fifteen hundred acres are composed of kettle lakes or other large, water filled depressions, including vernal pools. These vernal pools differ in size, depth, surrounding habitat type, vegetative growth, pH, dissolved oxygen, conductivity,

temperature, light penetration and intensity, and hydroperiod (Lucero 2004, Klein 2002). The diversity of vernal pools at this site is convenient for the study of how different abiotic and biotic factors affect the distribution and composition of populations of aquatic macroinvertebrates. This area was subject to massive human disturbance (e.g., logging) in the early twentieth century and vernal pools were certainly affected. However, the area has been undisturbed for almost 80 years and the major effects have likely diminished.

Ten vernal pools were selected for this experiment and are identified as pools 5, 6, 7, 9, 10, J, K, N, P, and Wood Duck Pond. These pools were selected, in part, because past experiments have demonstrated the abiotic factors as diverse (Lucero 2004, Klein 2002).

The vernal pools were sampled three times in the time frame of May 17 to July 23. The first sampling period occurred between May 30th and June 4th. The second sampling period occurred on June 20th and June 21st. The third sampling period occurred on July 11th. All sampling was conducted from 10:00 a.m. to 4:00 p.m. Intense sunlight and dry atmospheric conditions characterized all sampling periods.

The relative areas of the ponds were first determined visually and then compared to data from Francl's bat studies (Francl personal communication). In an effort to keep sampling effort constant regarding pool surface area, pools were divided into 5 size classes, and pools within each size class were sampled for the

same amount of time; pools and sampling times are as follows: 250-500 m² for 30 min., 500-750 m² for 45 min., 750-1000 m² for 60 min., 1000-1250 m² for 75 min, and 1250-1500 m² for 90 min.

Two samplers collected invertebrates with dip nets sweeping the vegetation, along the bottom, and throughout the water column. Forceps were used to remove the invertebrates from the net and into jars of ethanol, which were later identified to genus. Care was taken to minimize disturbance in the habitat.

The length, width, and maximum depth were measured for each sampling period and area was calculated accordingly. pH was quantified using a pHep meter made by Hanna Instruments. Dissolved oxygen and temperature were quantified using an YSI 55 dissolved oxygen and temperature meter made by YSI Inc. Conductivity was quantified using a HI 9033 Multi-range conductivity meter made by Hanna Instruments. To determine pH, dissolved oxygen, conductivity, and temperature, five random places in the pond were chosen and the depth of the sensors was kept constant. True color was also quantified for the vernal ponds. Water samples were analyzed for true color in the lab with a spectrophotometer. A Spectronic Genesys 2 made by Spectronic Instruments was used for absorbance analysis. The wavelength was set at 455 nm. Hydroperiod was determined by the date at which the vernal pool remained dry for at least one week.

In SYSTAT 11 a one-way ANOVA and a Tukey *post-hoc* test were used to analyze which pools were statistically different in reference to pH, dissolved

oxygen, conductivity, and temperature. A one-way ANOVA and a Tukey *post-hoc* test were also used to analyze differences in Shannon-Weiner diversity indices between ponds. A multiple linear regression was used to determine the effects of the abiotic factors on the biotic factors; rate of total number of individuals, total genera, rate of total number of individuals within the five orders, Trichoptera, Odonata, Diptera, Coleoptera, and Heteroptera, and genera richness.

Results

A total of 1508 aquatic invertebrates were collected and identified to genus. Five-hundred and ninety-one individuals in 21 orders were from the order Coleoptera, 288 individuals in 5 genera were from the order Diptera, 146 individuals in 10 genera were from the order Heteroptera, 251 individuals in 5 genera were from the order Trichoptera, and 382 individuals in 4 genera from the order Odonata (Table 7). The most common genera include: Dyticidae *Colymbetes* in the order Coleoptera, Libellulidae *Perithemis* and Lestidae *Lestes* in the order Odonata, Chaboridae *Chaborus* in the order Diptera, and Phryganeidae *Beothukus* in the order Trichoptera.

The pools that were sampled statistically differed among the four abiotic factors: pH, dissolved oxygen, conductivity, and temperature. The pools were the most different in pH and dissolved oxygen. The Shannon-Weiner indices differed

significantly and marginally for two vernal pools (Table 1). Vernal pool 10, with a low index value of 0.312, showed the most statistical difference and differed significantly from vernal pools 6, Duck, and P (Figure 5). The four pools with the greatest Shannon-Weiner indices were vernal ponds 6, J, P, and Duck. These four pools retained water throughout all three sampling time periods (Table 2). Vernal ponds 6, P, and Duck also had the largest areas for all of the vernal pools (Table 3).

Multiple linear regressions represent the bulk of statistical analysis for the data. Several relationships were found in the data for this experiment. The regression of hydroperiod on the biotic factors suggested that there is a significant and positive relationship of hydroperiod with Shannon-Weiner indices (linear regression; $p = 0.000015$, $R^2 = 0.5640$, $SE = 0.00127$) and also with the total number of genera collected (linear regression; $p = 0.01288$, $R^2 = 0.585$, $SE = 0.00991$).

The total number of genera throughout the vernal ponds did not vary much throughout the sampling periods but did vary between ponds. The data suggested that there is a significant and positive relationship of area with the total number of genera collected (linear regression; $p = 0.01003$, $R^2 = 0.447$, $SE = 0.00172$).

Dissolved oxygen showed a significant effect on invertebrates. Pools P, 6, 7, and Duck Pond show higher average dissolved oxygen concentrations. These ponds are statistically significant from most of the other ponds in dissolved

oxygen concentrations (Figure 1). The data shows a significant and positive relationship of dissolved oxygen with the total rate of individuals collected ($p = 0.006$, $R^2 = 0.287$, $SE = 0.087$).

pH is another factor hypothesized to affect the distribution of aquatic invertebrates. pH ranged from 4.58 to 6.34 across all pools. All pools but one, pool 6, had average pH values above 5.25 (Figure 2). Even with a more minimized range than expected, there is a significant and positive relationship of pH with total rate of Heteropterans collected ($p = 0.035$, $R^2 = 0.404$, $SE = 0.078$).

Dissolved oxygen also affected the distribution of Heteropterans. There is a significant and positive relationship of dissolved oxygen with total rate of Heteropterans collected ($p = 0.027$, $R^2 = 0.268$, $SE = 0.032$).

The order Odonata is the most affected of all orders analyzed in this experiment. Pools 5, 6, Duck, and 7 experienced only minimal changes in water depth while all other ponds completely dried or greatly receded (Table 2). There is a significant and positive relationship of maximum depth with total rate of Odonata collected ($p = 0.005$, $R^2 = 0.203$, $SE < 0.001$). The distribution of Odonatans also appears to be affected by conductivity. Conductivity values differed statistically among many of the vernal pools (Figure 4). There is a significant and inverse relationship of conductivity with total rate of Odonata collected ($p = 0.004$, $R^2 = 0.387$, $SE < 0.001$).

The temperature of the vernal pool seems to have a large effect on the

distribution of Odonatans. Average temperatures differed from 15 to 20 °C (Figure 2). Water temperature differences among the pools were probably the result of percent canopy cover as it changes with time. There is a significant and direct relationship of temperature with total rate of Odonata collected ($p = 0.035$, $R^2 = 0.507$, $SE = 0.002$).

Discussion

According to the data, the diversity and distribution of aquatic invertebrates in vernal pools at UNDERC are influenced by several abiotic factors which had the greatest influence on genera abundance and richness. With this being a broad study of trends in invertebrate populations, it is not surprising that the most defining results were found in the broadest categories. Our data agreed with other work, implicating a significant relationship exists between hydroperiod and both genera richness and diversity (Brooks 2000). Invertebrates can effectively colonize vernal pools with longer hydroperiods (Brooks 2000). The types of organisms, rates of development, and reproductive success may be diminished in pools with short hydroperiods (Brooks and Hayashi 2002). Other biological factors influenced by hydroperiod include biomass, predator size, and amphibian reproductive success (Brooks 2000). It may be possible that aquatic

invertebrates are less adapted to desiccating habitats than to varying levels of other chemical abiotic factors.

Because of their isolated nature, vernal pools are considered as ecological islands and Island Biogeography Theory can be applied (Brooks 2000). As the area of the vernal pool increases, the total number of invertebrates and genera should increase (Molles Jr. 2002). There was no significant relationship between area and total numbers per min. of invertebrates collected. Dispersal mechanisms and behavioral adaptations may be responsible for equal density distributions among pools differing in area (Thorp and Covich 1991). However, there was a significant relationship between area and the total number of genera found. Area has been shown to be related to the number of microenvironments that exist (Brooks 2000). Increased microenvironments provide better opportunities for habitat specialists and an increase in diversity is very likely (Brooks 2000, Zedler 2003).

A significant and positive relationship existed between dissolved oxygen and the total rate of invertebrates collected. It is interesting to note that the three vernal pools with the highest concentrations of dissolved oxygen (pools 6, P, and Duck) were also heavily colonized with aquatic plant species. (Figure 1) It is also interesting to note that these three vernal pools had the highest Shannon-Weiner diversity indices (Figure 5). Oxygen derived from photosynthesis may have had an effect on species richness for these pools. In pools with a large density of

aquatic plants, dissolved oxygen may be saturated during the day and decrease substantially at night (Thorp and Covich 1991). Among the abiotic factors, dissolved oxygen along with salinity had the greatest affect on aquatic invertebrates (Thorp and Covich 1991). Dissolved oxygen is essential for most forms of developing aquatic invertebrates and higher concentrations seem to promote higher species diversity.

The data suggests that there is a relationship of the total number of Odonatans with conductivity, temperature, and maximum depth. A study on larval forms of a species of Odonata (*Tetragoneuria cynosura*) suggested that the development of the final instar is inversely related with temperature (Lutz 1974). Another study found that Odonata species have increased growth rates in vernal pools than in permanent water habitat (Suhling et al. 2005). Development for aquatic insects has an indirect relationship with temperature (Resh and Rosenberg 1984). Increased water temperatures may be affecting the time it takes for complete development among Odonata genera. Those ponds with very low temperature should have had increased genera richness of Odonata. However, our experimental data showed a direct relationship between temperature and numbers of Odonata individuals. It is possible that our average temperature readings were not broad enough to observe the true relationship. This developmental characteristic may also be limited to species within a genus or family. Other factors such as dissolved oxygen may have had a much stronger effect than

temperature. A larger sample size may reveal that there is an indirect relationship.

There were also significant inverse relationships with Odonata individuals and conductivity and maximum depth. I hypothesized a direct relationship between increased conductivity and increased number of invertebrates found. However, the data show that there is a relatively strong inverse relationship for Odonatans. Literature on the effects of conductivity was difficult to find and my hypothesis may not be based on enough experimental evidence. It is possible that internal osmotic conditions may differ between orders of aquatic invertebrates.

The data showed a significant inverse relationship with Odonata individuals on maximum depth. It is possible that increased depth allows for more effective navigation of predators. Species richness among predatory Dyticidae beetles has been found to increase with pond area (Nilsson et al. 1994). Because there usually is a direct relationship between depth and area, it may be possible that pools with increased depth have increased predation. (Brooks and Hayashi 2002) The majority of Odonata genera and individuals were found in vernal pools P, Wood Duck, and 6, all of which had moderately to dense layers of vegetation. The two obvious benefits of vegetative cover are increased dissolved oxygen concentrations and increased refugia.

There was an inverse relationship between Heteropterans and pH. My hypothesis stated that abundance should increase with increasing pH. This result showed the opposite relationship. Because most Heteropterans are semiaquatic, it

is possible that their hemelytra and exoskeleton serve as protection. There were no larval forms of Heteroptera found at any of our vernal ponds. Many lentic species of Heteroptera fly to streams to overwinter. One suborder of heteropterans inhabit the surface of the water and may exploit habitats other invertebrates cannot (Thorp and Covich). It is possible that the above characteristics allow individuals to be less exposed to pH.

There was also a direct relationship between Heteropterans and dissolved oxygen supporting my third hypothesis. Dissolved oxygen is one of the most important chemical factors for most aquatic and semi-aquatic invertebrates. Heteropterans have had impacts on mosquito populations and dissolved oxygen may be more related to their food source than themselves (Thorp and Covich 1991).

Abiotic factors appear to affect the distribution of invertebrates but there are other factors involved. Intraspecific and interspecific competition for resources may also limit the distribution of certain groups of invertebrates. Predator-prey dynamics is another possible factor. Many inhabitants of vernal pools are well developed for the abiotic parameters. This could be one reason why these data showed no R^2 values greater than 0.50 (Dunson 1991). It is important to understand that there are many factors that could be involved all at once. To understand the distribution of aquatic invertebrates in vernal pools means to understand all factors and the interactions that could take place.

Vernal pond 10 during the second sampling period had approximately 5-10 cm of water depth. We sampled the pond and realized that because caddisfly cases float, there was a huge sampling bias as we collected almost 700 individuals. This data was excluded from statistical analysis. Improvements for this experiment need to address hydroperiod. Ponds with very minimal amounts of water should not be sampled as many of the invertebrates burrow in the mud with decreased water depth. Future experiments could determine the effects of predatory-prey relationships or intraspecific and interspecific competition for resources. Such a project would aid in determining which factors interact together and which are the most important.

Tables

Table 1. Statistical values for a one-way ANOVA for four abiotic factors and the Shannon-Weiner diversity

F-ratio	132.24	62.31	90.00	27.88	4.48
Statistic	pH	DO	Conductivity	Temperature	SW Index
P – value	<0.001	<0.001	<0.001	<0.001	0.005
DF	40	40	40	40	15

Table 2. Maximum depths for the three sampling periods.

Vernal Pond	Depth 1	Depth 2	Depth 3
5	33	34	31
6	36	28	22
7	31	65	42
9	18	5	0
10	17	0	0
J	21	19	10
K	38	34	0
N	45	35	0
P	24	28	11
Duck	31	30	31

Table 3. Vernal pool area for the three sampling periods.

Vernal Pond	Area 1	Area 2	Area 3
5	95.45	94.5	24.5
6	1224	999	858
7	69.92	117	88
9	307.5	2.5	0
10	180	0	0
J	121.18	40.66667	36
K	154	85.05	0
N	69.35	44.72	0
P	153.6	166.75	96
Duck	255.3	205.8	54

Table 4. Average values for the abiotic factors of all of the vernal ponds with standard errors.

Vernal Pond	pH	DO (mg/L)	Conductivity	Temperature (C)
5	6.34 +/- 0.02	0.882 +/-0.13	57.86 +/-1.12	15.04 +/-0.14
6	4.58 +/- 0.10	2.818 +/-0.23	43.62 +/-4.44	18.1 +/-0.80
7	5.32 +/- 0.02	2.35 +/-0.10	35.26 +/-0.27	17.12 +/-0.27
9	5.4 +/- 0.06	1.214 +/-0.06	61.3 +/-3.22	19.0 +/-0.27
10	5.28 +/- 0.02	1.362 +/-0.19	63.66 +/-1.82	19.18 +/-0.11
J	5.84 +/-0.04	0.962 +/-0.04	102.58 +/-1.70	20.04 +/-0.44
K	6.1 +/- 0.03	0.87 +/-0.10	68.4 +/-2.62	17.18 +/-0.18
N	5.96 +/-0.02	0.798 +/-0.08	63.7 +/-0.88	15.94 +/-0.31
P	6.06 +/-0.05	4.111 +/-0.41	33.48 +/-1.62	16.22 +/-0.12
Duck	5.38 +/-0.02	3.254 +/-0.17	37.498 +/-0.54	21.02 +/-0.28

Table 5. Shannon-Weiner Indices and the associated averages and standard errors.

Vernal Pond	1	2	3	Average	SE
5	0.8131	1.7344	0.8451	1.130	0.301
6	2.1011	2.1534	1.8156	2.023	0.104
7	0.7346	1.7749	1.0192	1.176	0.310
9	1.5619	1.1244		1.343	0.218
10	0.3116			0.311	
J	1.4592	1.6552	1.213	1.442	0.127
K	1.0982	0.8609		0.979	0.118
N	1.5579	1.0097		1.283	0.274
P	2.1251	1.7013	1.8597	1.895	0.123
Duck	1.7807	1.9311	1.944	1.885	0.052

Table 6. Values for multiple linear regressions

Rate of Total Individuals				
Factor	DF	F-ratio	p-value	R ²
DO	1	9.26	0.006	0.287
pH	1	2.50	0.128	
Conductivity	1	1.116	0.302	
Temperature	1	3.085	0.093	
Area	1	0.231	0.636	
Max Depth	1	0.231	0.636	
Regression	1	9.258	0.006	
Rate of Total Heteropterans				
Factor	DF	F-ratio	p-value	R ²
DO	1	5.63	0.027	0.268
pH	1	5.046	0.035	0.404
Conductivity	1	0.385	0.542	
Temperature	1	0.944	0.342	
Area	1	0.026	0.874	

Max Depth	1	0.079	0.781	
Regression	2	7.472	0.003	
<u>Total Odonata Individuals</u>				
DO	1	0.299	0.591	
pH	1	0.003	0.956	
Conductivity	1	10.151	0.004	0.387
Temperature	1	5.107	0.035	0.507
Area	1	0.359	0.556	
Max Depth	1	9.703	0.005	0.203
Regression	2	7.197	0.002	
<u>Shannon-Weiner Indices</u>				
DO	1	0.309	0.584	
pH	1	0.117	0.736	
Conductivity	1	1.801	0.193	
Temperature	1	0.0134	0.909	
Area	1	0.6452	0.4304	
Max Depth	1	0.101	0.7541	
Hydroperiod	1	29.762	<0.00001	0.564
Regression	2	29.762	0.000015	
<u>Total Number of Genera</u>				
Area	1	7.937	0.010	0.447
Hydroperiod	1	7.326	0.013	0.585
Regression	2	15.450	0.0000630	

Table 7. Total number of individuals and genera collected for five orders.

Order	Individuals	Genera
Coleoptera	591	21
Diptera	288	5
Heteroptera	146	10
Odonata	382	4
Trichoptera	251	5

Graphs

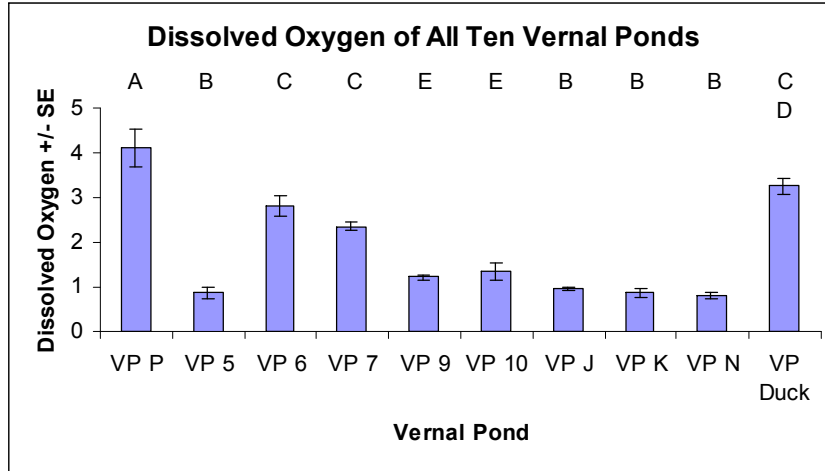


Figure 1. Average dissolved oxygen concentrations for all vernal pools with standard errors.

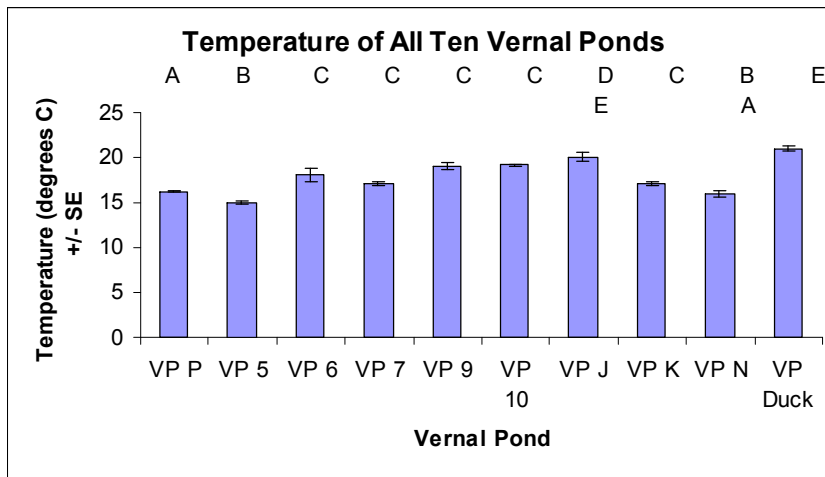


Figure 2. Average temperatures of all vernal pools with standard error.

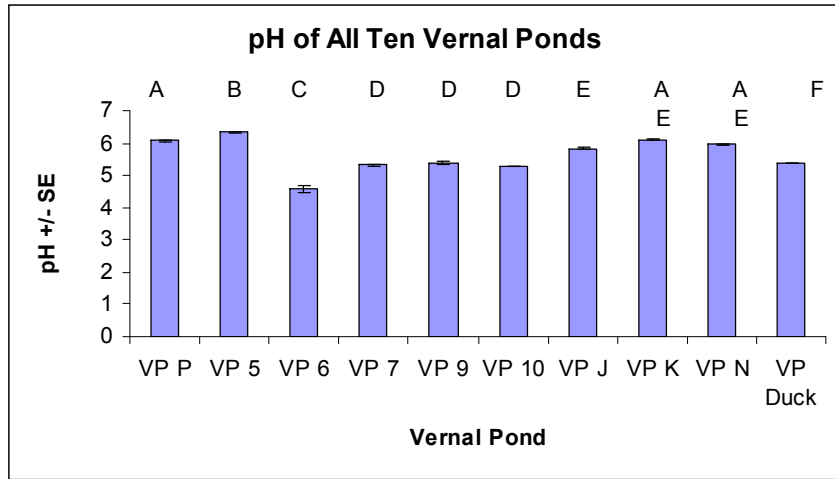


Figure 3. Average pH for all vernal ponds with standard error.

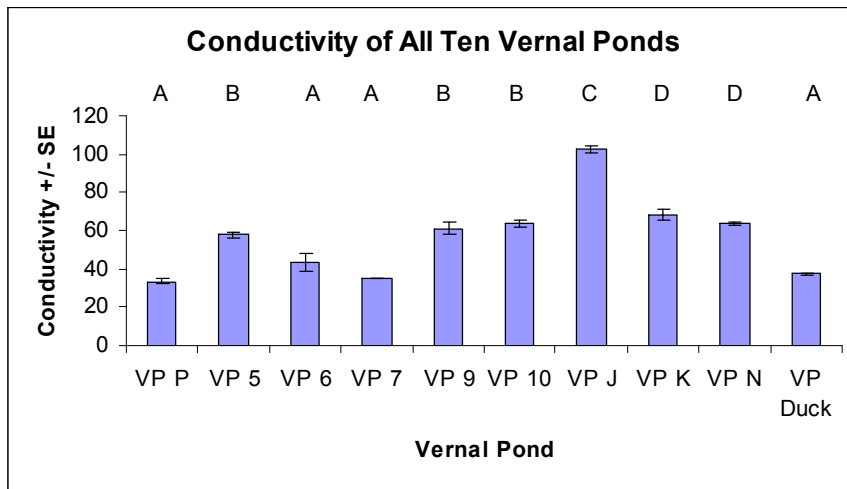


Figure 4. Average conductivity values for all vernal ponds with standard error.

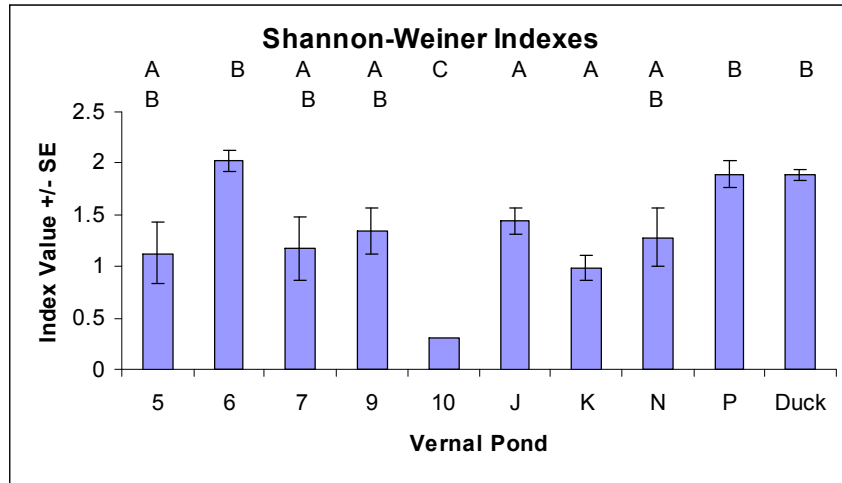


Figure 5. Average Shannon-Weiner diversity indices for all vernal ponds with standard error.

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Works Cited

- Brooks, Robert T. 2002. Annual and seasonal variation and the effects of hydroperiod on benthic macroinvertebrates of seasonal forest (“vernal”) ponds in central Massachusetts, USA. *Wetlands* **20** (4): 707-715.
- Brooks, R.T. and M. Hayashi. 2002. Depth-area-volume and hydroperiod relationships of ephemeral (vernal) forest pools in southern New England. *Wetlands* **22**: 2.
- Friday, L.E. 1987. The diversity of macroinvertebrate and macrophyte communities in ponds. *Freshwater Biology* **18**: 87-104.
- Graham, Tim B. 1998. Climate change and ephemeral pool ecosystems: Potholes and vernal pools as potential indicator systems. Pages 1 – 11. U.S. Department of the Interior, U.S. Geological Survey, Biological Resources Division.
<<http://geochange.er.usgs.gov/sw/impacts/biology/vernal/>>
- Graham, T.B. 2002. Survey of ephemeral pool invertebrates at Wupatki NM: an evaluation of the significance of constructed impoundments as habitat. *Hydrobiologia* **486** (1): 215-224.

- Keeley, J. E. and P.H. Zedler. Characterization and Global Distribution of Vernal Pools. 1998. C.W. Witham, E.T. Bauder, D. Belk, W.R. Ferren Jr., and R. Ornduff (Editors) Ecology, Conservation and Management of Vernal Pool Ecosystems-Proceedings from a 1996 Conference. California Native Plant Society. Sacramento, California. 1-14.
- <<http://www.werc.usgs.gov/seki/pdfs/keeley.pdf>> [October 1,2003]
- Klein, Lindsay. 2002. The biogeography of aquatic insects in vernal ponds in the upper peninsula of Michigan. The University of Notre Dame Environmental Research Library.
- Lucero, Joseph. 2004. Survey of invertebrate species in vernal ponds at UNDERC. The University of Notre Dame Environmental Research Library.
- Lutz, P.E. 1974. Effects of temperature and photoperiod on larval development in *Tetragoneuria Cynosura* (Odonata: Libellulidae). *Ecology* **55** (2): 370-377.
- Molles Jr., Manuel C. Ecology, Concepts and Applications. McGraw-Hill College. Jan. 2002.
- Nilsson, A.N., J. Elmberg, and K. Sjoberg. 1994. Abundance and species richness patterns of predaceous diving beetles (Coleoptera, Dytiscidae) in Swedish lakes. *Journal of Biogeography* **21** (2): 197-206.

Resh, V.H. and D.M. Rosenberg. 1984. The ecology of aquatic insects. Pages 56-67 and 519-531. Praeger Publishers.

Suhling F., G. Sahlen, J. Kasperski, and D. Gaedecke. 2005.

Behavioral and life history traits in temporary and perennial waters: comparisons among three pairs of sibling dragonfly species. *Oikos* **108** (3): 609-617.

Thorp, J.H. and A.P. Covich. 1991. Ecology and classification of North American freshwater invertebrates. Pages 22-36 and 597-627. Academic Press, Inc. Harcourt Brace Jovanich Publishers. New York, New York, USA.

Zedler, Paul H. 2003. Vernal pools and the concept of “isolated wetlands”. *Wetlands* **23** (3): 597-607