

THE ECOLOGY OF SMALL POOLS IN
CAPITOL REEF NATIONAL PARK, UTAH

A Proposal Submitted to: National Park Service
Capitol Reef National Park
Torrey, Utah 84775

RFP #1350-7-0001

Principal Investigator: James W. Haefner
Department of Biology
Utah State University
Logan, Utah 84322-5305
(801) 750-3553

Project duration: September 15, 1987 - September 14, 1988

Amount Requested: \$10,000.00



Principal Investigator, James W. Haefner

8/24/87
Date



University Representative, M.K. Jeppesen
Director, Contracts & Grants

8/24/87
Date

TABLE OF CONTENTS

I. Project Summary	1
II. Description of Project	1
A. Literature Review	1
B. Capitol Reef Tinaja Habitats	3
C. Summary	4
III. Hypotheses to be Tested	5
IV. Methods and Analysis of Hypotheses	5
1. Hypothesis 1: Physical and Chemical Parameters	5
2. Hypothesis 2: Tolerance of Dessication	7
3. Hypothesis 3: Revival from Sediments	7
4. Hypothesis 4: Order of Arrival	8
5. Hypothesis 5: Effects of Livestock Use	8
6. Hypothesis 6: Effects of Predation	9
7. Hypothesis 7: Effects of Amphibian Tadpoles	9
V. Other Activities	9
VI. Time Schedule	11
VII. Calendar	12
VIII. Bibliography	13
Proposed Budget	
Budget Justification	
Vitae	

I. PROJECT SUMMARY

This is a one-year project with two goals: to conduct an extensive survey of biotic and abiotic attributes of temporary pools (tinajas) in Capitol Reef National Park and to test several hypotheses concerning factors which may influence the distribution and abundance of macroinvertebrate species. Permanent sampling sites will be chosen at Willow and Cottonwood tanks in the south part of the park, southwest of "The Post" on the Notom-Bullfrog road. Monthly samples will be taken to measure physical and chemical parameters of temporary waters as well as to enumerate major pool inhabitants. In the spring and summer of 1988, experiments will be conducted using artificial tanks at the site to evaluate the effects of arrival order of animals, livestock use, predation by insects, and tadpole presence.

II. DESCRIPTION OF PROJECT

Communities of organisms found in temporary aquatic habitats seem to have much in common world-wide. They contain small crustaceans found in few other habitats (fairy shrimps, clam shrimps, tadpole shrimps), microcrustaceans (copepods and cladocerans), as well as insect larvae. The first two groups tolerate the drying of their habitat by producing drought-resistant stages. The third escapes the drying of pools mainly by metamorphosis into a terrestrial adult.

An important feature is the remarkable speed with which these communities "develop". Within hours after a rain, even a small depression in the earth can be teeming with life.

Despite descriptions and surveys of potholes (Wiggins et al. 1980), very little is understood concerning the dynamic properties of the communities themselves. How are pools colonized? What limits the numbers and kinds of species that can survive in a pool? What are the physiological limitations of these species to heat, ion concentration, and tolerance of organic wastes? To what extent do nutrients stored in depressions provide a rapidly-mobilized nourishment source once a rainstorm fills them?

This is a proposal to develop a project to answer these questions in the tinaja habitats on the Waterpocket Fold area at Capitol Reef National Park. Although three years is anticipated for work on the project, the present proposal details the first year of study. Our approach will be to document the physical and chemical characteristics of the pools, survey the distribution and abundance of species among pools, then to test hypotheses concerning biological pattern found in the surveys. Thus, we will work on two levels at once, an entire waterpocket drainage and the dynamics of individual pools.

A. LITERATURE REVIEW

Although the aquatic habitats in question are widespread, experimental results are documented for only a few areas: Baltic Sea island rock pools (Pajunen 1982), granite outcrop pools in western Australia (Bayly 1982), rock pools in Malawi (McLachlan and Cantrell 1980) and temporary pools in southern Utah (Dodson 1987, and Lindahl 1977). For a general review, see Hartland-Rowe (1972).

Two major themes can be discerned in these studies:

First, the size and age of a pool strongly influence species distribution patterns. Larger (by implication, older) pools have higher diversity, contain species which cannot tolerate dessication, and accomodate species which require more than a month to complete their life cycle. Characteristic members of these pool types are the genus Notonecta (backswimmers), the insect family Corixidae (boatman), Daphnia (a microcrustacean), the crustracean subclass Ostracoda (seed shrimps), various insect larvae, and predaceous beetles.

Smaller, shorter-lived pools are characterized by species which can tolerate complete pool drying for some part of their life cycle (fairy shrimp, clam shrimp, tadpole shrimp, some dipteran larvae, and algae). In addition, many terrestrial insects deposit their eggs in small pools, where the development of short-lived (i.e., 12-13 day) larvae can proceed without interference from aquatic predators: Dasyhela (a biting midge), mayflies, mosquitoes, and an occasional toad (genera are Bufo and Scaphiopus) or frog (Hyla arenicolor) fall into this category.

In general, the smaller the pool, the less likely it is to contain a predator, since few predaceous species can tolerate dessication.

Second, species often show negative and positive associations within pools of similar size. That is, species pairs are often found together (positive association) and certain pairs that can tolerate the same habitat are almost never found together (a negative association). A few species appear to have random associations with respect to all species.

These two generalizations are well-documented in Dodson (1987) and Lindahl (1977), although both studies are based only on presence-absence data acquired during a limited time period. The question of what factors are responsible for controlling the partitioning of species into available pools remains open.

Several attempts have been made to test the hypothesis that only dessication resistant species can live in very small pools. See Dodson (1987), and McLachlan and Cantrell (1980) for examples. Although these results suggest that species with a "cryptobiotic" stage can establish dominance in very small pools, these species often require benthic sediment and can be eliminated by chance colonization of large scavengers such as a clutch of tadpoles (McLachlan, 1985).

Chance colonization can play a role in determining community dominance. In the rain pools in Malawi, McLachlan (1985) and McLachlan and Cantrell (1980) demonstrated that water inhabited or conditioned by one species of non-cryptobiotic fly larva inhibited colonization of the cryptobiotic species. If both species colonize the pool, they compete for resources. The species which grows most rapidly monopolizes the food source, and a larger percentage of its members succeed in metamorphosing to the adult stage.

Bayly (1982) measured a few physical and chemical parameters in pools in Australia (depth of pool, salinity, pH) and made concurrent identifications of species (presence and absence only), but made no attempt to analyze of the results statistically.

Rather than assume physical chemistry alone is responsible for distributions of species, most biologists look to biotic interactions such as predation and competition to explain non-random assemblage patterns. Dodson (1985) was able to show (using laboratory feeding trials) that the biting midge Dasyhelela sublettei was excluded from large ponds by the predaceous backswimmer (genus Notonecta) and tadpole

shrimp (genus Triops). McLachlan and Cantrell (1980) suggest that ants can be a major predator on the cryptobiotic stage of midge larvae when the drying pool is still moist, and the midge has already become dormant.

Competition trials between two species of predatory corixids (water boatmen) in the Baltic islands (Pajunen, 1982) demonstrated that their resource use was completely overlapping. The larger predator seemed to have the competitive edge over the smaller one. The continued persistence of the smaller species in that area must be explained by some other trait that is superior to the larger species for a factor other than feeding.

In summary, the following biological features are known or suspected to influence the distribution and abundance of any particular aquatic species in temporary rock pool habitats: resistance to dessication, resistance to heat and dissolved chemicals, colonization ability, competitive status, susceptibility to predation, arrival order at pools, allelopathic interactions and even symbiotic associations. More than one organizing factor can be operating at any one time. Which ones occur and their relative importance are the subject of this proposal.

B. CAPITOL REEF TINAJA HABITATS

The organisms that inhabit the Hall's Creek drainage in Capitol Reef National Park have been collected by Lindahl (1977) in 1977 during three summer visits. Her observations of the tinaja areas indicate the following distributional patterns and questions of general ecological interest:

1. Fairy Shrimps

Two species of anostrocan crustaceans (fairy shrimps) occur in the pools, Streptocephalus texanus and Branchinecta lindahli. Both are abundant but never co-occur in the same tank or grouping of tanks. Three hypotheses can account for this: (a) each species is competitively superior in different physical or chemical settings, (b) the competitively superior species cannot colonize the drainages where the inferior species is found, (c) whichever species arrives first in a pothole area excludes potential invasion of the other.

2. Amphibians

Six species of amphibians were found in the Hall's Creek drainage in 1977. Of these, two (Woodhouse and southwestern toads) place eggs exclusively and (in June of 1977) abundantly in streamside pools. The leopard frog is limited to the large plunge pools at the ends of deep side canyons. The remaining three species (red-spotted toads, great basin spadefoot, and canyon treefrog) all deposit large clutches in single pools high on the waterpocket fold. A low percentage (1-2%) of the pools were used for this purpose in 1977.

Several studies are suggested by this pattern. Are differences in communities of streamside pools and the sandstone tinajas attributable to the high densities of southwestern toad tadpoles that are restricted to lower elevation streamside pools? McLauchlan (1981) has demonstrated such an effect in African rock pools.

It is not unusual to find a dry pool with several hundred flattened, dehydrated tadpole remains, all having failed to reach metamorphosis before the pool dried. Insect larvae are likely to meet the same fate. To what extent do these rich packets of nutrients contribute to the success, biomass, and diversity of the next aquatic

community to develop at that site?

3. Livestock Use

At Willow and Cottonwood tanks, cow winter use of the tanks appeared to be limited to the lowest and largest tanks. These tanks were characterized by the largest species diversity, greatest algal abundance, and smallest sizes of aquatic species (microcrustaceans), mayfly larvae, damselfly larvae. To what extent do cows alter the aquatic habitat? Do urine, feces, and/or trampling influence the aquatic community? To what extent do these large tanks serve as reservoirs for species which use the smaller tanks when they contain water? If cows influence the survivorship of species in large tanks, to what extent does this determine the availability of colonists for dispersal to the larger tank drainage system?

4. Lower Pools

What limits the following species to lower-elevation pools? Physa virgata (a pulmonate snail), the planorbid snail Helisoma trivolvis, the damselfly larva of Argia, Archilestes Ishnura and Hyponeura, the amphipod Hyaella azteca, the giant leech Haemopsis grandis, Lethocerus the giant water bug, all caddisfly larvae and the predaceous diving beetle, Acilius sp.

5. Predator Partitioning

Two similar families of predators, backswimmers (e.g. Buenoa sp. and Notonecta sp.), and water boatmen (e.g. Graptocorixa sp., Corisella sp. and Neocorixa sp.) are never found in the same habitats. The former inhabit lower elevation pools and the latter the slickrock temporary ponds. Does competition or differential toleration of physical characteristics explain this pattern?

In summary, many questions of community and population ecology can be addressed in this setting. All studies to date suffer from two shortcomings: first, they tend to be a "snapshot" view, a one-time collection of facts, and, second, very little rigorous statistical analysis has been applied to the experimental results. It is likely that short-term events (freezing, thunderstorms) are important. It is possible that important populations inhabit the potholes and were not seen when these field collections were made.

C. SUMMARY

This proposal intends to create a dynamic explanation of community composition. The three-year study will focus on a hierarchical set of questions and hypotheses on two scales: the whole region (repeated surveys) and individual tinajas (field experiments). First, we will ask, "What are the seasonal and area-wide patterns of abundance of major macroinvertebrate species in a large number of tinajas?" At the same time we will ask, "How variable are the physical and chemical attributes of the aquatic habitats?" Repeated sampling of marked pools will be undertaken. Statistical analysis of these data will indicate the extent of dependence of species on specific physical and chemical ranges. For patterns which cannot be explained by random distribution into ponds or physical tolerance, explanatory hypotheses will be constructed and tested (see below).

By operating on two levels at once, we intend to define the "metapopulation" scale for individual macroinvertebrate and amphibian species (sensu Gill, 1979). This is the geographic area in which a population can be considered stable. It is the

size of the habitat necessary to insure that at least some pools will contribute sufficient colonists to the next generation that the a population will persist in that area.

Tinajas are small enough on a human scale to allow manipulation of environmental variables to a greater extent than is possible in other aquatic habitats such as lakes and streams. This allows ecologists to test many hypotheses and analyze results with statistical rigor. The short life spans of tinaja inhabitants allows survivorship data to be accumulated rapidly. We intend to use the the results of these studies as a basis for a larger proposal directed toward other granting agencies.

III. HYPOTHESES TO BE TESTED

The following null hypotheses will be tested in the order listed. Timing may depend on the availability of organisms for tests.

EXTENSIVE SURVEY STUDIES

1. $H(0)$: Physical and chemical habitat characteristics alone determine which species will be present in tinaja communities.

LABORATORY EXPERIMENTS

2. $H(0)$: Resistance to duration of dessication determines which species will be found in small tinajas.
3. $H(0)$: Species which can survive in the pool's benthic sediment determine the composition of the next season's inhabitants.

FIELD MANIPULATION EXPERIMENTS

4. $H(0)$: Order of arrival of primary consumers determines which species will be successful in individual potholes.
5. $H(0)$: Livestock use does not affect community composition in individual potholes.
6. $H(0)$: The presence of predators does not affect community composition in individual potholes.
7. $H(0)$: The presence of amphibian tadpoles does not affect community composition in potholes.

IV. METHODS AND ANALYSIS OF HYPOTHESES

1. HYPOTHESIS 1. PHYSICAL AND CHEMICAL PARAMETERS

A. METHODS

In the Willow and Cottonwood Tanks areas of the Hall's Creek drainage, thirty pools will be chosen for permanent abiotic and biotic monitoring. Fifty pools will be monitored if time permits. At least three sets of five pools will be vertically

adjacent to one another so that rainwater flooding will connect all five pools in a sequential manner. This will allow us to determine the extent of colonization as a result of runoff from higher pools. The tanks to be sampled will be marked for temporary identification and mapped for future reference.

At sixty-day intervals in the cold months and at thirty day intervals in warmer/wetter months, water samples and non-destructive macroinvertebrate samples will be taken. See the timetable chart for the dates of these samples. We intend to measure the following physical and chemical parameters at each interval:

1. Pool size: depth, surface area, volume, distance to permanent pool
2. Benthic Sediment: depth, grain size
3. Temperature
4. Turbidity
- 5.* Particulate organic matter
7. Dissolved organic matter
8. pH
9. Chlorophyll a
10. Nitrate nitrogen
11. Ammonia nitrogen
12. Orthophosphate
13. Dissolved oxygen

All parameters except that designated by the * will be taken in the field using a Hach kit adapted for field use. Particulate organic matter will be measured in the lab at U.S.U. using equipment that cannot be adapted for field conditions. All analyses will be based on colorimetric and titration techniques using standard methods (APHA 1985).

Temperature, oxygen, and ammonia profiles will be made during several seasons at higher frequency (e.g. every four hours), to determine the degree of fluctuations the organisms experience.

Each pool will be sampled for living organisms on the same dates. Large organisms such as tadpoles can be counted directly. Smaller organisms such as young fairy shrimp and cladocerans will be sampled, preserved, and counted later in the laboratory. Stratified sampling may be necessary if some species cluster on the edges of ponds.

The following types of organisms will be identified and counted:

1. amphibian larvae
2. all macroinvertebrates, including larval and adult forms, instars
3. large multicellular algae
4. unicellular and microscopic algae (on a restricted basis)
5. vascular plants

B. ANALYSIS

The density of each species will be compared to the levels of each abiotic parameter to determine whether there is a positive correlation, a negative correlation or no correlations with the abiotic value in question. This is simple correlation analysis. Multivariate analyses using simultaneous consideration of all parameter values with all species densities will demonstrate which parameter values are the

most important.

Chi-square tests of association for all possible pairs of species will indicate where there are positive and negative associations. The method uses presence/absence data and a 2 x 2 Contingency Table (Grieg-Smith 1983) and the Model 1 G-statistic as a test of significance (Sokal and Rohlf 1981).

To find out what groupings of species are found together, and if tanks tend to group into physical and chemical "types", cluster analysis will be performed using the Group Average Method (Wishart 1978).

Further statistical analyses will be undertaken depending on patterns revealed by the above analysis. The data set will be large by the end of the sampling period and can be divided in many ways by choosing subsets of the pools and correlating any two sets of measurements. For example, we could ask, how impoverished in species is the lower end of a vertical string of pools compared to those at the top? Do pools with high particulate organic matter reach a higher density of individuals than those with low particulate organic matter?

2. HYPOTHESIS 2. TOLERANCE OF DESSICATION

A. METHODS

Living macroinvertebrates will be collected from tinajas in the fall and taken to the lab at Utah State. Thirty individuals of each species will be placed separately in aquaria containing mud from the bottom of pools. The aquaria will be allowed to air dry for six or more time intervals (e.g. 12, 24, 48, etc. hours). At the end of each trial, the containers will be flooded. Live animals will be counted to determine how many organisms have survived the interval. For each time interval measurement, a new batch of individuals will be used.

B. ANALYSIS

Differences in survivorship among species will be plotted over time, indicating the standard errors for mean survivorship at each time interval. Real differences between means on single dates will be evaluated using a one-way analysis of variance, (Sokal and Rohlf 1981).

3. HYPOTHESIS 3. ABILITY TO BE REVIVED FROM BOTTOM SEDIMENTS

A. METHODS

Replicate cores of bottom sediments will be taken from marked dried pools of two different sizes during the fall. In the lab at U.S.U., flooding conditions will be simulated, and individuals which emerge alive will be counted. Emergence numbers will be compared between pools of different sizes. This species list will be compared to the lists in the communities that actually develop in the pools during the next rain event.

B: ANALYSIS

Organisms which emerge from rehydrated sediments of small ponds will be counted and compared to the numbers emerging from pools of large size using correlation

analysis. This analysis will allow us to predict which drying pools will store populations of organisms and which will not.

A comparison of the artificially revived pool species list will be made with actual pool species lists the next summer.

4. HYPOTHESIS 4. ORDER OF ARRIVAL OF PRIMARY CONSUMERS

A. METHODS

This and the remaining three hypotheses will be addressed using twenty-five artificial pools, plastic laboratory tanks which simulate average potholes in size, depth and sediment characteristics. Each treatment or control group will consist of five replicate tanks, arranged in a randomized block design in the field.

By the spring of 1988, the identity of the numerically dominant primary consumers will be known. Based on the field notes of Lindahl (1977), they will probably be the two species of anostracan fairy shrimps, Streptocephalus and Branchinecta, the larva of the mayfly Baetis and the mosquito Aedes. Equal biomasses of each of these species will be placed in the four treatment replicates after counting of individuals. Distilled water will be placed over sediment in the control.

At the end of seven, fifteen, and thirty days, samples of each pool will be counted for abundance of all macroinvertebrates.

If an effect of inhibition or facilitation of colonization using the live animals can be shown, the experiment will be repeated using only water conditioned by each presumed competitor. Results will be harvested in the same manner.

B. ANALYSIS

At the end of each time step, comparisons will be made among treatments of the numbers of each species counted. One-way analysis of variance for each species will be conducted, using each seeded tank type and control as treatment. Comparisons will be made for each species colonizing at each time interval.

HYPOTHESIS 5. EFFECTS OF LIVESTOCK USE

A. METHODS

In April, before the date of livestock removal from the park, experimental assessment of three aspects of livestock use will be made: urine addition, feces addition, and trampling. All artificial pools will be filled with water containing natural tank organisms from an "average" pool. Treatments (in replicate) will consist of: ammonia added (to simulate urine), feces added, sediment turbation (to simulate trampling), and a combination of all three. The control will consist of artificial pools without treatment.

In addition to counting all organisms at the end of the 15-30 day experiment, chlorophyll a and ammonia nitrogen will be measured at the beginning and on all sampling dates.

B. ANALYSIS

Comparisons of numbers of individuals of different species will be made using one-way analysis of variance; each treatment will constitute one source of variation (Sokal and Rohlf 1981). Differences in density, diversity, chlorophyll a, and ammonia nitrogen among treatment will also be made using this form of analysis.

HYPOTHESIS 6. EFFECTS OF PREDATION

A. METHODS

A study of the effect of predation on pothole communities will be conducted in May or June, depending on the time required for earlier experiments. Four species of major predators will be added to treatment tanks: the water boatman Graptocorixa, the predaceous diving beetle, Agabus, water striders, Gerris (with a screen to prevent escape), and Somatochlora a larval dragonfly. Equal biomasses of these predators will be added to each tank. After 15-30 days, the pools will be emptied and all invertebrate organisms enumerated. Predation treatments will be compared to a control.

B. ANALYSIS

One-way analysis of variance for each colonizing species will be performed using predator species as treatment (source of variation).

HYPOTHESIS 7. EFFECTS OF AMPHIBIAN TADPOLES

A. METHODS

To each of the three treatment tanks, a different species of amphibian larva will be added. To the fourth, all three species will be pooled. The tadpole species are: the red-spotted toad (Bufo punctatus), the great basin spadefoot (Scaphiopus intermontanus), and the canyon treefrog (Hyla arenicolor).

As in the previous experiments, the effect of differences in community will be detected by counting organisms that survive the treatment and compare species abundance in treatment tanks to controls.

B. ANALYSIS

Analysis will be the same as hypothesis 6, using tadpole species as the source of variation.

V. OTHER ACTIVITIES

Three major activities will take place during this year that do not fall under the heading of hypothesis testing.

First, an attempt will be made in the field to construct an enclosure for livestock around a single pond. This task will enable us to design the best possible apparatus for the next field season (second year of study) when attempts will be made to construct replicate livestock enclosures in the field. Sampling of the enclosed

pool will be more casual than the marked pools, since statistical analyses cannot be done on a single pool. Construction and maintenance of such an enclosure will require the cooperation of the Park Service and grazing leaseholders. We will ask the assistance of the Park Service for help at the appropriate time.

Second, a survey will be done while cattle are present to discover which tanks the cattle are using, how high they are willing to climb to get to water, and the extent to which they are seen urinating in, defecating in, and trampling sediment in pools.

Third, experiments will be conducted during the rainy summer months when it is anticipated that competition among macroinvertebrates is the most intense and major colonization events take place. These experiments will be set up in July and August and harvested in August and September (see chart below). Since the final report on this project is due on August 30, it will not be possible to include the results of these studies in that report. Results will appear in the report of the next year's project.

VI. TIME SCHEDULE

MONTH	SURVEY SAMPLE (HYP. 1)	SET UP EXP.	FINISH EXP.	PROGRESS REP.	OTHER
SEPT. 87					order Hach kits, chem.
OCT. 87	X	dessication resistance (Hyp.2)	dessication resistance (Hyp.2)		try cow enclosure species i.d.
NOV. 87					
DEC. 87	X	sediment emergence (Hyp.3)	sediment emergence (Hyp.3)	X	
JAN. 88					
FEB. 88	X	order of arrival (Hyp. 4)			quantify livestock use
MAR. 88	X(*)				
APR. 88	X	livestock use (Hyp.5)	order of arrival (Hyp. 4)	X	
MAY 88	X(*)		livestock use (Hyp.5)		
JUN. 88	X	predation effect (Hyp.6)	livestock use (Hyp.5)		
JUL. 88	X	tadpole effect (Hyp.7)	predation effect (Hyp.6)		
AUG. 88	X	competition (for next yr)	tadpole effect (Hyp. 7)	X (final)	
Sept. 88	X	livestock enclosure	competiton exp.		

(*) Park Employee samples on this date

VII. CALENDAR

SURVEY SAMPLES (Hyp.1) * * * (*) * (*) * * * *

EXPERIMENTS

```

DESSICATION (H.2)          *****
EMERGENCE (H.3)            *****
ORDER OF ARRIVAL           *****
    (H.4)
LIVESTOCK USE               *****
    (H.5)
PREDATION (H.6)            *****
TADPOLE (H.7)              *****
COMPETITON                  *****
COLONIZATION                *****
CATTLE EXCLOSURE           *****

```

REPORTS	X	X	X (FINAL)
---------	---	---	-----------

DATE	SEPT 1987	OCT	NOV	DEC	JAN 1988	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP
------	--------------	-----	-----	-----	-------------	-----	-----	-----	-----	-----	-----	-----	-----

VIII. BIBLIOGRAPHY

- APHA. 1985. Standard Methods for the Examination of Water and Wastewater. Joint Publication of American Public Health Association, American Water Works Association, and Water Pollution Control Federation at American Public Health Association, Washington, D.C.
- Bayly, I. A. E. 1982. Invertebrate fauna and ecology of temporary pools on granite outcrops in Southern Western Australia. Australian Journal of Marine and Freshwater Research. 33:599-606.
- Dodson, S. I. 1987. Animal assemblages in temporary desert rock pools: aspects of the ecology of Dasyhelea sublettei (Diptera: Ceratopogonidae). J. N. Am Benthol. Soc. 6:65-71.
- Gill, D. 1979. The metapopulation ecology of the Red-Spotted Newt, Notophthalmus viridescens (Rafinesque). Ecological Monographs 48:145-166.
- Greig-Smith, P. 1983. Quantitative plant ecology. Studies in ecology, Volume 9. University of California Press, Berkeley.
- Hartland-Rowe, R. 1972. The limnology of temporary waters and the ecology of Euphyllipoda. Essays in Hydrobiology. R. B. Clark and R. J. Wootan (eds), James Townsend and Sons: Exeter p.15-31.
- Lindahl, A. 1977. A faunal survey of Hall's Creek, Capitol Reef National Park and Glen Canyon National Recreation Area. Ms. 37p.
- McLachlan, A. J. 1981. Interaction between insect larvae and tadpoles in tropical rain pools. Ecological Entomology 6:175-182.
- McLachlan, A. J. 1985. What determines the species present in a rain-pool? Oikos 45:1-7.
- McLachlan, A. J. and M. A. Cantrell. 1980. Survival strategies in tropical rain pools. Oecologia (Berlin) 47:344-351.
- Pajunen, V. I. 1982. Replacement analysis of non-equilibrium competition between rock pool corixids (Hemiptera, Corixidae). Oecologia (Berlin) 52:153-155.
- Sokal, R. S., and F. J. Rohlf. 1981. Biometry. 2nd edition. Freeman and Co., San Francisco.
- Wiggins, G. B., R. J. Mackay, and I. M. Smith. 1980. Evolutionary and exological strategies of animals in annual temporary pools. Archiv fur Hydrobiologie, Supplement 58:97-206.
- Wishart, D. 1978. Clustan users manual. 3rd edition. Edinburgh University.