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

A Continuation Proposal Submitted to:

National Park Service
Capitol Reef National Park
Torrey, Utah 84775

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

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Principal Investigator, James W. Haefner

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Date


University Representative M.K. Jeppeson
Director, Contracts and Grants

23 Sept 88
Date

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I. Proposed Project Summary

It is proposed to pursue the most productive lines of research identified in the previous funding period. The combination of multiple linear regression and extensive surveys of pool attributes provided insights into possible mechanisms influencing macroinvertebrate species richness. We propose to continue this approach by improving the sampling design to permit quantitative analysis of variables other than species richness (e.g., total chlorophyll or zooplankton biomass).

Experimental results in the previous funding period emphasized trophic and predation relations between major components of the tinaja ecosystem. We will pursue a subset of these in the next funding period, but our major experimental component will be directed to competitive relations and the role of nutrients in structuring these communities. We plan a combination of small tub and whole-pool experimental manipulations.

II. Introduction and Previous Accomplishments

In October 1987, we initiated a study of 28 small pools in the Waterpocket Fold (Hall's creek) area of Capitol Reef National Park. Both descriptive surveys and manipulative experiments in small tubs were performed. Our major findings were reported in Haefner and Lindahl (1988) and include the following. The numerical abundance of major macroinvertebrate species was found to be influenced by many physical and chemical features of the pools, although no single factor can be said to have major importance. Abundance of primary consumers is severely limited by restricted primary productivity in the pools. An aquatic insect, the backswimmer Notonecta kirbiyi and the tadpole of the spadefoot toad (Scaphiopus intermontanus) are voracious predators on zooplankton including the large pothole crustaceans. When present, they are capable of cropping the consumer community to very low population levels. Use of the pools by livestock probably has no direct toxic effect as a result of ammonia additions. The most likely result of cattle use is eutrophication of the pools.

These results suggest that 2 phenomena are important agents in determining the distribution and abundance of species in the pools: nutrients and predators. Nutrient addition experiments indicate that the population sizes of most of the top predators (e.g. Notonecta kirbiyi) are limited by the food base. Our feeding experiments indicate that if prey and predators are present together, the predators have the potential to decimate quickly the prey population. There are, therefore, important but subtle effects on the population of the lower ranks of the foodweb from the timings of nutrient additions, re-hydration by rainfall, and the arrival of mobile predators. We propose to investigate these effects at the levels of community species composition, population dynamics of key prey species, and evolved life history characteristics of the major species present.

Using a combination of surveys and field manipulation experiments we propose to examine species-species relationships and the effects of abiotic factors. Our major goals fall into four areas:

1. The ecology of fairy shrimp
2. Competition between consumers and predators
3. The role of predators in rock pool population dynamics
4. Statistical analysis of abiotic factors

Thus, the overall objective is to develop an explanation for the dynamic properties of both low and high trophic levels in these communities.

III. Proposed Research

A. Pool Surveys

We intend to continue sampling 15-20 of the original 28 pools every 30 days, except in winter months. The choice of the pools will be made after a detailed examination of the data collected in the previous year and consultation with Park Service staff. The accuracy and usefulness of stepwise regression analysis (see Haefner and Lindahl, 1988) will be greatly improved if we have quantitative information samples of the macroinvertebrates rather than the presence/absence data. We intend to improve the rigor and detail of the biological component of this database. This requires that we reduce the number of pools studied.

We also intend to extend the analysis of species distributions by testing the effects of factors listed in Table 1 (Haefner and Lindahl 1988) such as shading, volume, isolation, etc. against quantitative macroinvertebrate and plankton species data.

Since the previous field season has given us the ability to identify invertebrates in the field without collecting or preserving them, we plan to design benthic samplers and do most the counting in the field.

We propose to design and build:

1. a passive live trap for crawling scavengers
2. a quantitative bottom grab for chironomids and infauna
3. a sweep net sampler for mid-water nekton
4. a seine net for fast-moving predators

This new equipment will be modifications of samplers currently used by limnologists.

B. The ecology of fairy shrimp

There are two points of view to explain the relative abundance of members of the class Branchiopoda. The first is that they are highly adapted to unique physical and chemical settings such as those found in temporary pools, and cannot live elsewhere. An alternative is that they only maintain their populations in situations where pools are temporary enough that predators are absent during some critical minimum time.

The Cottonwood and Willow Tanks system allows a test of the following two alternatives.

H0: Fairy shrimp are restricted to certain pools because they are physiologically adapted to the extreme conditions found there.

HA: Fairy shrimp are found only where their predators are absent.

We will test the null hypothesis in two ways by transplanting fairy shrimp to cages in replicate ponds. Individuals will be placed in a shallow plexiglas or screened box extending above the water surface. Predators will be excluded with a screened top. Survivorship will be compared to control cages in the "home" pool (i.e. pools N1 and W8, Haefner and Lindahl 1988, Table 1).

The alternative hypothesis (HA) is that predators are important controllers of fairy shrimp abundance. To test this, we will divide pools N1, C4 and C6 in half with a mesh barrier. All Notonecta will be removed from one half, but allowed to colonize the other. Populations of the fairy shrimp will be censused at short intervals in all three ponds on both sides for the summer of 1989. Species densities will be compared using ANOVA with removal areas as the major treatment.

An interesting feature of crustacean ecology in these pools is that a larger fairy shrimp, Streptocephalus texanus is often found with aggressive predators, such as the backswimmer and spadefoot tadpole (Haefner and Lindahl 1988, Fig. 19). When several were placed in a dishpan with Notonecta kirbiyi, the shrimp was ignored. This contrasts sharply with N. kirbiyi behavior in the presence of Branchinecta lindahli (Haefner and Lindahl 1988, Fig. 29).

We never detected the two shrimp species together at the same time, although they did occupy the same pool on different dates.

We never found larvae or juveniles of Streptocephalus texanus in any of permanent pools, despite repeated plankton sampling every two weeks. They suddenly "appeared" in June, full sized. If they are inhabiting the deep areas of large pools until they are too big to be attractive to predators, we will detect this with the improved stratified sampling design and equipment.

C. Competition between pairs of consumers

The previous field season, among other tasks, stressed the experimental evaluation of predation in the pools. Another important biotic interaction that needs research is competition. During the course of the previous field season, we noted these facts:

1. Chlorophyll levels in the surveys of pools were always very low (.05-.07 mg/l) except for an occasional "bloom" in an isolated tank. This suggests that phytoplankton may be suppressed by the intense grazing of zooplankton.
2. Zooplankton levels were always low in all pools except in August, when notonectids are scarce and tadpoles are absent (Haefner and Lindahl, 1988, Fig. 18). When water from any source was used in any non-predation tub experiment (nutrient-enriched or not), zooplankton was abundant within a few days. This occurred as early as April. (See Haefner and Lindahl, 1988, Figs. 25 and 26.) This suggests that there is intense competition for microcrustaceans as prey.

Although it is puzzling why they both should be low, it does suggest that intense competition for resources could occur which would drive an inferior competitor to extinction in a particular pool.

We will test for competitive exclusion in situ by pairing the following species in cages inside pools:

1. Daphnia similis vs Diaphanosoma
2. Two species of chironomic larvae
3. Physa virgata vs Limnephilus atercus
4. Notonecta kirbiyi vs Scaphiopus intermontanus
5. Graptocorixa abdominalis vs Rhantus
6. Two species of dragonfly

We intend to measure growth rates and survival of treatment replicates (both species together) compared to controls (each species alone). Statistical analysis will be ANOVA.

D. The relationship between nutrients and colonization

During the course of the 1988 experiments, many replicates of "spiking" experiments were colonized by hundreds of Branchinecta lindahli. This occurred despite the following precautions: water was sieved through 110 micron mesh sieves, and no sediment was used. The tubs were covered with .5 mm nylon mesh. Untreated water was always nutrient-poor.

Further, the only tubs colonized were nutrient-enriched in some way. The most heavily colonized were those in which 1/2 strength algal growth medium was placed.

If eggs of Branchinecta are blown into pools, will they only develop in the presence of nutrients? If so, this would allow organisms to assess the "quality" of a pool for support of their food source. Areas with a previous "long-lived" pond could contain stored nutrients, whereas solid slickrock pools would have none. The null hypothesis is :

H₀: Colonization by Branchinecta lindahli is random with respect to nutrient concentration.

We will test this by placing experimental chambers containing six nutrient concentrations from a balanced algal culture medium (e.g., WC in Appendix 2 of Haefner and Lindahl 1988) in several areas at different times. We will count colonists as a function of nutrient levels. Because colonization is so variable, we will need a large number of replicates in this study. We will control the location of the chambers for distance from major sources of colonists.

If we are able to reject the null hypothesis, we will extend the test by manipulating several dry, temporary pools by pouring nutrient-poor water into them and measuring NO₃, PO₄ and SO₄ after 24 hrs. This will permit us to assess the relevance of our experimental protocol and choice of experimental nutrient concentrations.

E. Dispersal capabilities of crustaceans

An important assumption of island biogeography theory (MacArthur and Wilson 1967) is that colonization rates depend on the distance of the island to the source of colonists. We will test this theory in Capitol Reef tinajas. During the entire field season, replicate tubs will be placed known distances from a pool that has a consistent population of fairy shrimp when full. Differences in colonization rates will allow us to identify just how many propagules are available and where they accumulate.

F. Predation

We will evaluate the role of the predaceous diving beetle, Rhantus, by dividing three pools in half (C8, N2, and W5) with a "fence" of nylon screening. All beetles will be removed by hand from the predator free side. Any colonists will be removed when noted. This predator-free treatment will be compared to the controls (with the beetle) by counting copepod and cladoceran abundance. Other predators that may be evaluated in this manner are the two dragonfly species and the large black damselfly larva.

We propose also to continue our laboratory studies of the foraging rates and characteristics of Notonecta kirbiyi on its important prey species (e.g., Branchinecta lindahl). Additional hypotheses to be tested are:

1. Prey do not concentrate in complex habitat areas (simulated macrophytic stems) in the presence of predators.
2. Predators forage optimally when given the choice between large and small prey.
3. There is a threshold complexity of habitat below which predators forage as if habitat were present.

These hypotheses will be tested in the laboratory or in small tubs in the Cottonwood drainage according to the availability of predators and prey. The protocol will follow that of the Notonecta kirbiyi foraging experiments in Haefner and Lindahl (1988). We will also attempt to raise Notonecta kirbiyi in the laboratory so as to increase the time over which experiments may be performed.

Hypothesis 1, above, will be tested by performing the foraging studies in tubs in which one half has a complex habitat (simulated stems) and the other without stems. In addition to counting the number of kills per minute, we will also record the time the predator spends in each habitat (open and complex), as well as the number of prey in each habitat.

Hypothesis 2 will be tested by presenting Notonecta kirbiyi with two prey simultaneously: the larger Branchinecta lindahl and the smaller Daphnia magna. These tests will be performed in tubs with no complex habitat, 100% complex habitat, and 50% open/50% complex.

Hypothesis 3 will be tested by repeating the experiments in Haefner and Lindahl (1988) with different densities of complex habitat.

G. Anuran responses to their own densities

The composition of the community in a particular pool depends on the "decisions" made by individuals. For mobile, mature individuals (e.g. adult

Notonecta kirbiyi) the decision to be made is whether to stay or leave a drying pool. For immature individuals of species whose adults can leave the pool (e.g., tadpoles) a physiological "decision" is made as to whether to devote internal resources to body growth (to better survive as a tadpole), or towards maturation to the adult form that is capable of leaving the pool. Thus, we would like to know if tadpoles respond to nutrient limitation by prolonging the time to metamorphosis (and obtaining a large body size) or metamorphosing early at a smaller size.

Three densities of Bufo punctatus in 9 tubs will be given equal rations (1 tubifex pellet per day) over a period of several weeks. We will measure survivorship, mean time to metamorphosis, and mean size at metamorphosis. From these data, we will determine the tradeoffs for survival faced by B. punctatus in these small, temporary pools.

IV. Summary of Hypotheses to be Tested:

1. H0: Abiotic factors alone account for variation seen in macroinvertebrate abundance.
2. H0: Fairy shrimp are restricted to certain pools because they are physiologically adapted to them.
3. H0: Fairy shrimp are restricted to some pools by the absence of predators
4. H0: Daphnia (or other competitor) is driven to local extinction by Diaphanosoma (or other counterpart) by its superior use of resources.
5. H0: Streptocephalus outcompetes Branchinecta for resources and drives it to local extinction.
6. H0: Branchinecta is not limited to colonization of ponds with dissolved nutrients in them.
7. H0: Branchinecta embryos are rehydrated and develop in the location of sediments of a previous population.
8. H0: Prey do not concentrate in complex habitat areas (simulated macrophytic stems) in the presence of predators.
9. H0: Predators forage optimally when given the choice between large and small prey.
10. H0: There is a threshold complexity of habitat below which predators forage as if habitat were present.

V. Statistical Analyses

For the analysis of survey data, we will use multivariate analysis (e.g. cluster analysis, Dodson 1987) and multiple regression. The experimental, competition, predation, and nutrient addition studies will be analyzed with analysis of variance (ANOVA, a method similar to linear regression for use with independent variables that are not continuous).

VI. Time Schedule

1. Oct 1988 - Feb 1989: Write and submit to peer reviewed journals two papers from 1987-1988 field season. Complete analysis of any samples and chlorophyll measurements remaining from 1987-1988 field season.
2. Feb 1989 - Mar 1989: Design and construct sampling equipment.
3. April 1989: Initiate surveys on 15-20 pools that continue to end of funding period.
4. May 1989 - July 1989: Predation and Branchinecta lindahli experiments.
5. May 1989 - July 1989: Competition experiments.
6. June 1989 - Sept 1989: Nutrient/colonization experiments.
7. Aug 1989 - Sept 1989: Analyze data.
8. September 30, 1989: Final report due.

VII. Participation of park employee in field and lab work.

We anticipate the use of a seasonal or permanent park employee for approximately 2 days per month. This person, to be assigned by the Park Resource Specialist, will participate in survey sampling, data analysis, and taxonomic identification.

VIII. References

- Dodson, S.I. 1987. Animal assemblages in temporary desert rock pools: aspects of the ecology of Dasyhelea sublettei (Diptera: Ceratopogonidae). J. N. Amer. Bethol. Soc. 6:65-71.
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