EXPERIMENTAL ECOLOGY OF FOOD WEBS: COMPLEX SYSTEMS IN TEMPORARY PONDS

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Abstract. A food web graphically represents the paths of nutrients and energy through the living components of an ecosystem and the context in which individuals exploit their prey and avoid their enemies. Temporary ponds are excellent arenas for the study of food webs because they are discrete communities that can be mimicked in containers that approach the realism of natural habitats. Artificial ponds permit repeatable initial conditions and sufficient replication of independent experimental units in complex experiments to test hypotheses about the control of structure and function in natural communities. I used a combination of observations of natural ponds, ''experimental natural history'' of artificial ponds in my study area, and controlled experiments in an array of 144 replicate ponds to develop, then test, hypotheses about how the structures of food webs are regulated.

Understanding food webs begins with population biology. Amphibians use the aquatic larval stage of their biphasic life cycle to exploit ephemeral opportunities for growth and development in temporary ponds. The regulation of population density and the fitness of individuals are determined by complex interactions among competition, predation, and uncertainty in the length of the time ponds retain water. Exponential models of density-dependent recruitment relate the number of metamorphs to the input of eggs into ponds without predators. Extensions of these models include interspecific competition and pre-

dation. The addition of predation to these systems has three effects. (1) Predators can reduce, even eliminate, prey. There are species-specific differences among co-occurring prey in their risks of predation, and these risks change with relative body sizes of predator and prey. (2) Individuals may evoke an inducible defense that reduces their risk by either decreasing active foraging or developing morphological adaptations, such as changes in the coloration and shape of tails. These defenses may entail costs in body size and timing of metamorphosis. (3) Finally, mortality due to predators may reduce competition, thereby benefiting the population of the prey by permitting individuals that escape predation to grow rapidly enough to escape drying ponds.

The order of arrival of species at breeding ponds has an impact on their own success as well as having a lasting impact on the success of species that arrive later. Such priority effects may result from size-specific changes in trophic connections or indirect effects between species mediated through the food web. Anurans can have strong effects on the partitioning of the flow of nutrients through the phytoplankton vs. the periphyton. This effect on partitioning of production can then have strong effects on zooplankton and insects. Salamanders can play the role of keystone, or critical, predators by affecting the structure of the assemblages of zooplankton and anurans that determine much of the dynamics of nutrient flows within food webs in temporary ponds.

INTRODUCTION

Food webs are a central, if not *the* central, idea in ecology. They represent known, or sometimes just suspected, trophic connections among taxa in ecological communities. These connections represent the paths of energy and nutrient flow through living organisms. The evolution of the morphology, physiology, behavior, and life history of individuals and the regulation of the density and spatial pattern of populations take place in the context of a food web as individuals respond and adapt to their intrasexual, intraspecific, and interspecific competitors, the defenses of their prey, and the adaptations of their own natural enemies. The food web may be the concept in ecology most widely appreciated by the general public because it is both a visual and an intuitive summary of much natural history. Food webs are represented by diagrams on the walls of nature centers and classrooms and in textbooks at all educational levels.

The food web is a useful departure point for the development of a predictive theory of community ecology. Such a theory would make projections about, for example, the consequence of the loss of a native species from an assemblage, or of the invasion of an assemblage by an exotic species. Food webs will also be important components of models that successfully predict the limits of productivity and the efficiency of transfer of energy and nutrients through ecosystems. Theoretical ecologists study the nature of food webs by asking such general questions as: What limits the length of food chains? What limits the number of species in a trophic level? Of what value is biodiversity? and the persistent conundrum, Does complexity beget stability? The answers to these questions, and the utility of food webs in a general ecological theory, depend to

a large extent on the validity of the assumptions that are made when a food web is constructed and employed as a vehicle for testing hypotheses.

Food webs have serious limitations, however, that are only now being understood.

1) Food webs are associated with a specific habitat, e.g., the food web of a lake, the food web of a forest, or the food web of a cave. Recent interest in landscape ecology and the ecology of metapopulations demands that we consider how adjacent habitats are ecologically connected. Highly mobile species, such as many large mammals, large marine fish, most birds, and the adults of many insects, become elements in several food webs as they move freely among habitats or habitat patches. Migratory species have a regular pattern of movement among food webs that may belong to adjacent communities or, in the case of many birds, habitats a hemisphere apart. Many species with complex life cycles are obligate members of two or more food webs during their ontogeny. Many marine taxa, for example, have a planktonic larval stage and a sedentary benthic or sessile adult stage attached to a hard substrate. All frogs with free-living larvae change at metamorphosis from a aquatic omnivorous tadpoles to a amphibious carnivorous adults. The role of such connections among food webs is a fruitful area for both theoretical and empirical research because the foraging of animals across ecotones may be an important biological mechanism linking elements of the mosaics of habitats that form landscapes.

2) Food webs are generally considered static structures with fixed trophic connections among taxa. Many species, however, change their trophic connections seasonally or ontogenetically by changes in morphology or behavior. Many larger turtles and lizards, for example, switch from being carnivores as juveniles to herbivores as adults, yet remain in the same commu-
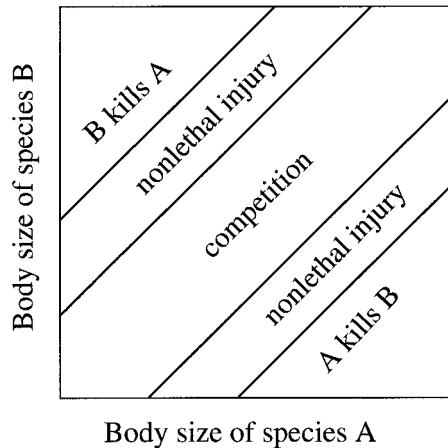
Fig. 1. Trophic connections may depend on differences in body size between taxonomically similar predatory taxa.

nity. Species may switch places as predator and prey as a result of different growth rates (Fig. 1; Morin 1983*a*, Wilbur 1988) as occurs in the guild of salamanders that live in the headwater streams of the Southern Appalachians (Resetarits 1988, Gustafson 1994).

3) Food webs present the illusion that only predator–prey interactions and exploitative competition are relevant to understanding community ecology. Chemical growth inhibitors, alleopathic agents, and behavioral interactions among species are examples of mechanisms of interference competition not apparent in food webs. Commensalism, cannibalism, facilitation, disease, and historical processes are also not represented in the traditional food web, although indirect commensalism and facilitation often can be inferred from trophic connections. Furthermore, the only indirect interactions that can be predicted from a food web are those that occur by trophic links. For example (Fig. 2), if predator A eats both B and C, but predator D eats only C, then A may have a beneficial effect on D because if A prefers to eat B, more C may be available for consumption by D. Loop analysis (Levins 1975) can be used to represent nontrophic connections among species, but it still hides much of the richness of mechanisms of species interactions.

4) Food webs are incomplete. A trophic connection between two taxa may be drawn based on a single anecdote or inference from morphology or the habits of related taxa. Such tenuous connections may then be given the same weight as a carefully documented connection representing the critical relationship between a predator and its primary prey that in turn is a dominant competitor in its trophic level. The nodes in a food web often reflect the interests and taxonomic competence of one ecologist. I, as a vertebrate ecologist, will identify the fish and amphibians in a pond by their species but may lump all suspended green things into

"phytoplankton," whereas a phycologist might attach a Latin binomial to all algae present in a pond but lump all the amphibian larvae as "tadpoles," or even worse, "pollywogs." The taxonomic and trophic resolution of a food web depends, of course, on why it was constructed. Food webs for modeling nutrient flows, for example, will tolerate more taxonomic lumping than ones designed to understand the context of coevolution.

5) Trophic connections are generally represented as binary rather than having some measure of importance associated with them. The information content of a food web is greatly enhanced if some measure of interaction strength can be associated with each trophic link. These measures might be rates of energy transfer if used in trophic dynamics or mortality rates if used in population dynamics.

Nevertheless, even with the above limitations (Cohen et al. 1993), food webs remain a valuable way of knowing how communities are organized and how a perturbation to one species may affect others. Food webs will remain a central idea in community ecology and conservation biology (Cohen 1978, Zaret 1980, Pimm 1982, DeAngelis 1992, Polis and Winemiller 1996). The experimental studies outlined in this paper may point to solutions to these deficiencies. My experiments that explicitly included the complexity of life cycles help forge the connections among communities and explicitly recognize that trophic connections change seasonally and ontogenetically. Assaying the condition of individuals at the conclusion of experiments, rather than just counting them, broadens the range of mechanisms that determine abundances beyond the predator–prey and exploitative interactions depicted in traditional food webs. It also broadens the representation of interactions from the binary presence or absence of trophic links to include quantitative measures of the importance of interactions. Finally, my attempt to broaden the taxonomic range of species manipulated and measured in experiments moves towards more complete understanding of interactions that regulate the structure of communities.

Temporary Ponds as Ecological Communities

I have used the food webs of temporary ponds to study general principles in population and community ecology. This research program was guided by obser-
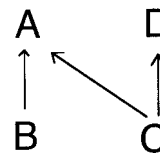

Fig. 2. Indirect effects can be inferred from a food web only by trophic connections. Species B may have an indirectly beneficial effect on species D because it provides food for the predator A which may therefore eat less of prey C which will then be available for the specialized predator D.

vational studies of natural history and the literature on the taxonomy and life histories of the amphibians, insects, and zooplankton that were found in my study area. An important source of ideas was an exercise in ''experimental natural history'' in which we placed 16 artificial ponds in a meaningful biogeographic design in the sandhills of the Inner Coastal Plain of North Carolina and observed community development for 12 yr (Travis and Wilbur 1984, H. M. Wilbur, *unpublished data*). During this study my students and I developed hypotheses about how species interact and then tested these conjectures with field experiments in which we manipulated initial conditions in an array of 144 experimental ponds in which we could follow the course of community structure throughout a season. My studies of the community ecology of temporary ponds have focused assemblages of insects and amphibians—both salamanders and anurans (frogs, toads, and treefrogs)—that dominate the local guilds (sensu Fauth et al. 1996) of predators and consumers. In this program, we used the experimental method to examine some of the assumptions of how complex systems are organized. My dual themes in this research program and in this paper are that complex questions require complex experiments and that experiments are the most direct way to address causal mechanisms. This theme of complexity has also been evident in other recent MacArthur papers (Schoener 1989, Levin 1992, Murdoch 1994, Vitousek 1994).

The natural history of temporary ponds

Each time a pond fills with water, a new episode in community ecology begins as species arrive to take advantage of the opportunity to complete the free-living aquatic stage of their life cycle. A flush of nutrients occurs as run-off water collects in the pond's basin and the nutrients from decomposition of the remains of plants and animals from the last time the basin held water are released into the new pond. As species colonize and individual plants and animals grow, many of these resources become locked up in living biomass or are exported as organisms complete the aquatic phase of their life cycle and leave the pond (Wilbur and Alford 1985). Competition may be low when the pond first fills, but as populations build and the demands of larger individuals for resources increase, some resources may become severely depleted and the strength of competition may increase to levels that prevent successful completion of the aquatic phase of the life history of many individuals (Wilbur 1987). Competition may be ameliorated by predation because many carnivores find that the flush of productivity when ponds fill supports dense, easily exploited populations of prey. The culling effects of predation may reduce competition and permit the survivors to grow rapidly enough to complete the aquatic stage of their life cycle and escape the ephemeral pond before it dries or freezes

(Wilbur 1987, Wilbur and Fauth 1990). A consequent theme in the population biology of organisms that exploit temporary ponds, such as amphibians, seems to be that selection has favored rapid colonization, rapid growth rates, and the ability to assay the triple risks of competition, predation, and desiccation and to have flexible mechanisms to terminate the aquatic phase of their life cycle by balancing the opportunities for growth with the risks of mortality when determining the optimal time of metamorphosis (Wilbur and Collins 1973, Werner 1986, Wilbur 1996). These broad generalizations are based on my observations of natural ponds, but nearly all have been explicitly tested in the experiments reviewed in this paper. I began these experiments during the period (1967–1971) when the ''balance of nature'' was widely believed to be manifested in equilibrium communities structured by competitive interactions. My earliest experiments (Wilbur 1972) convinced me that ecologists had a lot to learn about the nonequilibrium world of temporary ponds, where predation and competition interact with environmental uncertainty to determine relative abundances.

Temporary ponds can range from a few centiliters of water that support rich communities of micro-organisms, a few insects, and an occasional anuran tadpole in phytotelmata (Maguire 1971) such as the modified leaves of pitcher plants (Addicott 1974) and the bracts of heliconia (Seifert 1975), to treeholes (Chambers 1984, Juliano and Stoffregen 1994), to proper ponds ranging in area from several square meters to square kilometers in large playas and other shallow depressions. The temporal scale of drying episodes and the spatial scale of the basin of ponds are continua; my work, and this paper, are limited to ponds in the southeastern United States that dry, or winter-kill, frequently enough to preclude maintenance of populations of fish. Such ponds range in size from stump-holes as small as about a square meter to Carolina Bays of about a square kilometer. Some of the ponds we studied were formed by perched water tables on clay lenses in sandy soils, others were small Carolina Bays of uncertain origin (Savage 1982), and many had been dug as ''borrow pits'' during construction of roads, or as watering holes for wildlife.

Most of my field work was either in the second-growth, mixed pine and hardwood forests on clay soils of the Piedmont in Durham and Orange Counties, North Carolina; or the longleaf pine (*Pinus palustris*)–turkey oak (*Quercus laevis*)–wiregrass (*Aristida stricta*) savannas of the Carolina Sandhills of Scotland County, North Carolina and the similar habitats of the Lower Coastal Plain in the Green Swamp of Columbus and Brunswick Counties, North Carolina (Wells 1967). These ponds were visited in all seasons from the summer of 1974 until 1990; many ponds were sampled >50 times. Most visits included compiling a list of species

TABLE 1. Species of anurans observed calling in a single pond in Scotland County on 25 May 1976. Only eggs of species in boldface type regularly escape predation by newts and produce metamorphs.

Taxon	Adult female snout–ischium length (mm)	Clutch size	Egg size (mm)	Dispersion	Over-winter as larvae?
Pelobatidae					
Scaphiopus holbrookii	**60**	...	**1.7**	strings	no
Bufonidae					
Bufo terrestris	**68**	**2750**	**1.2**	strings	no
B. quercicus	26	557	1.2	files <10	no
Microhylidae					
Gastrophryne carolinensis	29	598	1.5	surface rafts	no
Ranidae					
Rana areolata	**92**	**7000**	**2.0**	submerged clumps	no
R. clamitans	**67**	**3000**	**1.5**	surface film	yes
R. virgatipes	**53**	**400**	**1.6**	submerged clumps	yes
R. sphenocephala	71	1253	2.1	submerged clumps	yes
Hylidae					
Acris gryllus	23	210	1.1	singly	no
Hyla andersonii	**42**	**900**	**1.3**	singly	no
H. chrysoscelis	**40**	...	**1.0**	surface rafts	no
H. femoralis	36	1056	1.1	surface rafts	no
H. gratiosa	54	...	1.0	singly	no
H. squirrella	**30**	**950**	**0.9**	singly	no
Pseudacris crucifer	34	755	**1.0**	singly	no
P. nigrita	26	...	1.0	submerged clumps	no
P. ocularis	17	101	0.8	singly	no

Note: Numbers in boldface type from Wright and Wright (1933). Ellipses indicate no available data.

of calling frogs and the animals we captured with seines or dipnets. Quantitative samples were taken in a few ponds using a 100×50 cm box sampler (Harris et al. 1988). These temporary, fish-free habitats support a diverse group of ~33 species of amphibians and a rich assemblage of >150 taxa of aquatic insects. Table 1 lists life history characteristics of the amphibians in our most frequently visited pond. The taxonomy and natural history of this fauna are known well enough to permit the construction of food webs and the proposition of hypotheses about the mechanisms that regulate their structure and function.

Experimental natural history

In 1977, an ensemble of 16 ponds was constructed in the Sandhills Game Management Area of Scotland County, North Carolina (Travis and Wilbur 1984). This area has longleaf pine–wiregrass–turkey oak savannas on broad flat divides of deep sandy soils separating steep valleys with seeps and creek bottoms supporting evergreen shrubs and small trees, such as *Ilex glabra, Lyonia lucida, Magnolia virginica, Persea palustris, Vaccinium corymbosum,* and *Pinus serotina,* characteristic of pocosin communities (Wells 1967). The ponds were arranged in four sets of four ponds each. Two of the sets were near small natural ponds; the other two sets were near small, permanent streams. Each set had two ponds close to the water supply at the edge of the pocosin vegetation in the mesic habitats bordering the pond or stream and two ponds were far from the water supply in the savanna. This design permitted a study of colonization as a function of distance from the source of colonists at two scales: the local scale of tens of meters within a set, and the regional scale of several kilometers between pond and stream areas. The purpose of this study was to document the assembly of communities, including the distribution and abundances of insects and amphibians in relation to the factors controlled by the experiment. My original intent was to use these descriptions to pose hypotheses about the mechanisms controlling the structure and function of food webs in natural temporary ponds and then to test these hypotheses by manipulating whole pond communities.

The experimental ponds were galvanized steel tanks 2.13 m in diameter and 0.61 m deep, painted with epoxy to prevent leaching of toxic metals from the galvanizing. Each tank was sunk flush with the surface of the ground and filled by pumping water from the nearby stream or pond. The water was passed through a coarse plankton net to remove macrofauna, but to permit an immediate inoculum of zooplankton, phytoplankton,

and other microorganisms. The ponds were then sampled at ~10-d intervals for 2 yr and then sporadically for the next 12 yr. A sample consisted of passing a D-shaped aerial insect net of ~1350 cm^2 once around the top of the tank and then passing a rectangular dip net 50 × 30 cm with 3-mm mesh once around the bottom of the tank. All amphibians and insects were counted, identified, and returned to the pond, except for the collection of taxonomic vouchers. It took three or four people 2 d to sample all 16 tanks. Later, complete censuses of these tanks without replacement (*unpublished data*) showed that our standard sample captured ~35% of all individuals in the tank averaged over all taxa of amphibians and insects (except small dipterans, such as *Chaeoborus,* chironomids, and culicids that were not efficiently retained by our nets). Assuming a binomial risk of capture per individual of 0.35, only populations with more than eight individuals are expected with 95% confidence to be represented by at least one individual in our sample.

We identified 135 taxa of aquatic insects, excluding chironomids, and found that 14 species of amphibians were able to complete the aquatic stages of their life cycles in these experimental ponds. A principal components analysis (PCA) was conducted of occurrences of 115 taxa (including the amphibians) in 272 samples selected from the complete collection of 660 samples with 135 taxa from the first two years of the study by choosing eight samples from each of the 16 tanks in each year matched by date between years. I used occurrence data rather than estimates of density because of the variance among taxa in body size and sampling characteristics. The PCA demonstrated that there was little structure to these assemblages as measured by occurrence data. The amount of variation explained by successive PCA axes fell monotonically with a shallow slope, as expected for an analysis of a large number of binary variables. The first three components accounted for ~21% of the variance in the occurrence matrix. It took 12 axes to include 50% of the variance. This stopping rule is an arbitrary (Jackson 1993), but useful, criterion for examining structure in this high-dimensional data set. These communities had many rare species; two-thirds of the 115 taxa occurred in 8 or fewer of the 272 samples and 20 taxa were only seen once. The PCA scores were approximately normally distributed variates with a mean of zero because each score was determined by many taxa, each with a small, additive effect. These scores were used as input to a multivariate analysis of variance to partition variation among the effects of time (year and season), location (geographical area of the four sets), source of colonists (stream or pond), and local habitat (savanna or pocosin). This is an analysis of the role of the environment rather than of species interactions in determining occurrence data. The experimentally controlled effects of time and location accounted for 79 and 48%, respec-

tively, of the variation in the PCA scores. Over all 12 components, temporal effects were ~1.6 times as great as spatial effects. Differences among years were strong. Within years, spatial effects were strong from late May to the middle of June when they accounted for 80–90% of the variance in principal component scores within sample dates, but weakened from July to late October when they accounted for ~40% of the variation in PCA scores within sample dates. Some species had strong seasonal patterns of occurrence that reflected their life histories. *Bufo terrestris* tadpoles, for example, were most common in early summer, whereas *Hyla femoralis* and *Gatrophryne* tadpoles were found only from mid to late summer. Two important libellulid dragonflies also differed seasonally. *Pantala flavescens* was found as naiads only in late summer and autumn, whereas naiads of *Libellula flavida* were most common in the early summer. Variance among the ponds increased through time. The Euclidean distance between samples in the occurrence space was greater in the second year than in the first year due to the increase in species richness. There was some evidence for ecological succession among the 50 most commonly sampled species with 5 species significantly more frequent in the first than in the second year and 9 species significantly more frequent in the second than the first year. Tadpoles of *Hyla femoralis* and *Gastrophryne carolinensis* and larvae of the dytiscid beetle *Thermonectus basilaris* and the libellulid dragonfly *Pantela flavescens* were significantly more widespread in the first year. These taxa were all observed to be rapid colonists of ephemeral natural ponds. The taxa more common in the second year included the small surface-feeding hemipteran *Microvelia americana,* nymphs of gerrids and notonectids, and adults of the nototectids *Notonecta irrorata* and *Buenoa* sp.

Only four species had significantly different distributions between the pocosin and savanna habitats. Crayfish were in only one tank, resulting from a colonization by a berried (gravid) female of a tank at the edge of a pocosin in October 1978. Her offspring remained in the tank for the duration of the dates included in this analysis. Newts eventually colonized 10 of the 16 tanks and were significantly more frequent in the tanks near pocosins. A species of *Hydroporus* (Coleoptera: Dytiscidae) was found in all but one tank, but was most frequent in the upland tanks. One upland tank produced 17 of the 24 occurrences of naiads of the libellulid dragonfly *Libellula auropennis.*

The experimental ponds received species from a pool of probably >200 taxa, but relatively few species were frequently encountered and fewer still used the ponds to complete the aquatic stage of their life cycles. An annual cycle in species richness was superimposed on the longer term trend of a slow increase in the number of taxa. The annual maximum species richness occurred in early summer when each tank had about one-third

of the total number of taxa sampled in all 16 tanks on a given date. A few taxa occurred in predictable patterns with respect to season, age of the pond, and its location with respect to habitat and distance to nearest water source. Our data suggest that most species within a sample were transients and that predation by newts, dragonfly naiads, dytiscid beetles, and notonectids may have precluded their successful establishment in these structurally simple ponds. An interesting episode occurred when a 2-wk visit by an adult snapping turtle left a legacy of nutrients that affected the phytoplankton in one tank for months! In contrast to the insects that included many ephemeral species and much variation in occurrences, amphibian larvae appeared to have strong biotic interactions involving competition among anuran larvae and predation on them by odonate naiads and salamanders.

Differences among species in autecological characteristics, such as vagility, breeding phenology, and habitat selection, appear to be sufficient to explain much of the variation accounted for by the experimental design. In an observational study such as this, the importance of species interactions can only be inferred from correlations among taxa (Heyer et al. 1975) and only very strong interactions resulting in competitive exclusion or predator-mediated extinction are likely to be detected. I revisited the PCA results to look for correlations between the occurrences of a taxon and the score of each sample on the first principal axis (PC1). *Notophthalmus* and the hemipteran *Notonecta irrorata,* both generalized predators that occurred in roughly half the samples, had positive correlations between their occurrence and the PC1 score. All of the 20 species with occurrences having high negative correlations with PC1 scores are potential prey for at least one of these predators. The second principal component (PC2) had adults of predaceous insects (hemipterans and dytiscid beetles) on one side and frog and insect larvae on the other. The occurrence of *Notophthalmus* was not correlated with PC2 scores. The small dytiscid beetle *Laccophilus fasciatus* was found in most samples and thus was unimportant in the statistical analysis but may have had a strong biological role as a carnivore in both its larval and adult phases in these communities. The omnivorous corixids *Hesperocorixa* and *Sigara* were also common and successfully maintained large populations even in the presence of high densities of potential predators.

These rather crude analyses suggest the hypothesis that reproductive success of common taxa in the communities are strongly influenced by predation. The food web must be a complex network of shifting trophic connections determined by relative body sizes as well as taxonomy (Travis et al. 1985, Cronin and Travis 1986, Wilbur 1988). About 35 of the 50 most important species are predaceous beetles and odonate naiads. The broken-striped newt, *Notophthalmus viridescens dor-*
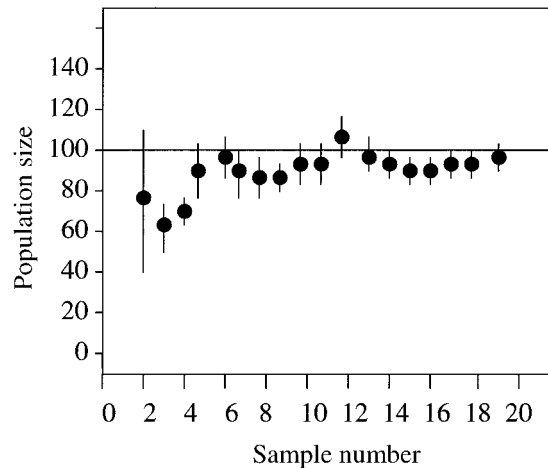

Fig. 3. Zippen estimates of the population size of newts in experimental ponds. Exactly 100 newts were added to the pond, allowed to disperse for an hour, and then sampled without replacement with equal effort. Dots indicate population estimates based on previous plus the current sample. Vertical lines indicate 95% confidence limits about the estimates.

salis, seems to be the critical species in these communities. Adults feed on zooplankton, aquatic insects, and any tadpole that is small enough for them to ingest. Larvae feed on zooplankton and chironomid larvae. Newts are also tightly correlated with the success of anurans in natural ponds in the Sandhills (Table 1). The role of newts as generalized predators of zooplankton and hatchling anuran larvae became a theme of our research program.

My original intention was to manipulate the food webs in these tanks set in natural habitats. A class exercise in which we released different densities of newts into a tank and then immediately tried to estimate their abundance changed my mind. The Zippen (1956) removal method of repeated sampling without replacement demonstrated that it would take ~10 of our standard samples to estimate the size of the newt population with a standard error <10% of the estimate (Fig. 3). This intensity of sampling was so disruptive to these simple communities that we decided against manipulating these tanks exposed to natural movements of insects and amphibians. Instead we began purchasing additional tanks to use as experimental ponds at the Duke Zoology Field Station where we could control colonization and experimentally study patterns and processes without repeatedly sampling the communities. Insects were not used in most of our later experiments because they were difficult to control in large, complex designs and, with the exception of odonates (Van Buskirk 1989, 1990), were not correlated strongly with the success of anuran larvae in experimental or natural ponds in the sandhills.

Artificial temporary ponds

Our use of tanks as mimics of temporary ponds in "experimental natural history" and in controlled experiments has several advantages and a few disadvantages (Wilbur 1989). A primary advantage is their price; each costs ~$100 fully outfitted with an adjustable standpipe and tightly fitted screen lid. This cost allowed us to buy enough tanks for complex experimental designs with sufficient replications of treatments to provide the statistical power necessary to examine subtle responses to treatments. The simple, uniform morphometry of the tanks made the experimental ponds very similar to one another, thus removing much of the variation among units that occurs in natural ponds or ones dug into natural substrates. The tanks could be emptied each year, repainted, and the ponds reconstituted to erase the effects of previous experiments, a nagging problem in the use of larger, more natural ponds (e.g., Hall et al. 1970). The small size of the tanks allowed us to rearrange them each year into an hexagonal array of blocks to minimize unexplained environmental differences within replicates of the current experimental design. A photograph of the array is published in the *Bulletin of the Ecological Society of America* (**76**:185). Standpipes were used to control water levels in each tank, making it possible to have ponds "dry" at predetermined schedules. A screened lid, tightly fitted over each pond, prevented colonization by unwanted species and retained the focal species, which therefore allowed us to control initial conditions and observe their consequences either at predetermined times when ponds were destructively sampled or by catching metamorphosed amphibians and insects as they emerged. This input–output approach eliminated the destructive effects of repeated sampling that we feared in our field study. The gain in realism and numerical precision of the effects of initial densities on survival and the timing and size at metamorphosis comes at a cost of learning less about mechanisms of interaction. We compensated by sacrificing replicate ponds to measure intermediate results in some experiments.

On the down side, these tanks are really just large tin cans. The straight sides preclude a naturally sloping "littoral" zone. This morphometry, however, approximates that of some rock pools (Smith 1983, Van Buskirk 1993) and stump holes. The sealed bottom prevents movement of groundwater into and out of the ponds, as occurs in rock pools and in some ponds perched on clay pans in sandy soils. The water depth of my ponds varied ~20 cm as precipitation exceeds evaporation on the scale of a few weeks throughout the year in North Carolina, with the exception of dry spells during July and August in some years (Clay et al. 1975). We controlled water level in the design of experiments. The small size of the tanks restricts the realism of their use as ponds towards the smaller end of the continuum of habitats used by amphibians and insects in the southeast.

Pearman (1991, 1993, 1995) explicitly studied the interaction between area and volume of habitat patches by controlling the size and shape of artificial ponds in factorial experiments that crossed three surface areas with three depths. He found that tadpoles of both *Bufo americanus* and *Rana clamitans* responded to these treatments. *Bufo* did better in shallow than in deep ponds. *Rana* survived less well, but metamorphosed at a larger size, in deeper ponds. When nutrients were manipulated in ponds of different depths and surface areas with constant volumetric densities of tadpoles (0.38 individuals/L), he found that survival was significantly more variable in smaller ponds and consistently lower in large ponds with low nutrient additions. Gascon and Travis (1992) found small effects of spatial scale when they varied depths of artificial ponds with two densities of *Rana* tadpoles and with or without predatory odonate naiads. These three experiments demonstrate that the configuration of habitat patches modify simple density-dependent competition within populations. The details of the experiments I am presenting are probably sensitive to the morphology of the experimental ponds, but I hope the general principles that I infer from them are robust. Scott's (1990) experiments with amphibian larvae in large enclosures in natural ponds and Pechmann's (1994) experiments in large artificial ponds help validate the use of mesocosms to mimic larger habitats.

Patricia Harris (1992) observed the trajectories of the zooplankton assemblages in 12 replicate tanks for 2 yr and found that the communities remained in about the same volume of the multivariate space describing the absolute abundances of species in spite of large differences in relative abundances. These results suggest that there are negative feedbacks among species that tend to regulate the structure of these assemblages. They further suggest that the differences observed between treatment combinations in our experiments are due to the treatments themselves rather than the compounding of small initial differences in the experimental ponds. Our use of three or more replicates of each treatment in randomized block designs is our insurance policy against such sensitivity to initial conditions obscuring the treatments used to test hypotheses.

On balance I believe these artificial ponds are fair mimics of small temporary ponds. Insects and amphibians colonize them readily, and the timing and body size at metamorphosis from experimental ponds correspond well to those for natural ponds. Our experiments attempted to have realistic backgrounds of nutrients and microorganisms in which subsets of the amphibian assemblage can be manipulated. Our use of natural pine straw as a substrate and of carefully randomized, repeated inoculation with zooplankton and water from natural ponds makes these ponds very good

mimics of the resource base for amphibians in natural, temporary ponds in the sandhills.

THE POPULATION AND COMMUNITY ECOLOGY OF ORGANISMS IN TEMPORARY PONDS

The mechanisms that determine community structure and the connections in food webs are determined by the population biology of the constituent species. Much of my work has focused on the responses of individuals to their environment and the consequences of these individual responses to species interactions and to the dynamics of populations. Early work in community ecology (Wilbur 1972) led to questions in population biology (Wilbur and Collins 1973, Wilbur 1976, 1977*a*, *b*, 1980) that then fed back to more studies in community ecology (Wilbur and Alford 1985, Wilbur 1987, 1988, Wilbur and Fauth 1990) and then to ecosystems (Leibold and Wilbur 1992).

Life history adaptations

Many species of amphibians and insects use their complex life cycles to exploit temporary ponds (Wilbur 1980, 1990, Newman 1992). Amphibians are able to partition growth between the aquatic larval stage and the terrestrial juvenile stage (Wilbur and Collins 1973). Some taxa, such as toads (*Bufo*) and spadefoot toads (*Scaphiopus*), do most of their growing as terrestrial juveniles (Werner 1986); other taxa, such as the salamanders *Ambystoma talpoideum* and *A. tigrinum,* and some hylids, do most of their growing as aquatic larvae. Explosive breeders that exploit ephermal ponds, such as the spadefoot toad (*Scaphiopus holbrookii*), lay relatively large eggs that hatch within a day and can complete their larval period in <2 wk under optimal conditions. Frogs that breed in more nearly permanent ponds, such as bullfrogs (*Rana catesbeiana*), lay many small eggs and metamorphosis appears to occur at a target size, certainly modified by seasonal constraints, after a variable larval period of up to 3 yr in northern populations.

The optimal timing of metamorphosis is a complex problem in dynamic programming in which an individual has to time metamorphosis to maximize its reproductive potential in the face of uncertain benefits and costs of allocating time between the aquatic and terrestrial environments (Wilbur and Collins 1973, Ludwig and Rowe 1990, Rowe and Ludwig 1991). Species of amphibians that retain a complex life cycle vary greatly in the plasticity of the timing and size at metamorphosis (Wilbur and Collins 1973, Wilbur 1980, 1996, Werner 1986, Alford and Harris 1988, Newman 1988, 1994, Hensley 1993, Leips and Travis 1994). The phenotypic plasticity of the size and timing of metamorphosis makes for complex population dynamics of the larval stage of amphibians and insects in temporary ponds (Wilbur 1990, 1996).

Intraspecific density dependence

The life history adaptations to temporary environments exhibited by amphibians make them particularly sensitive to resource limitation and other aspects of intraspecific density. Intraspecific density dependence determines the survival of larvae in species that occur in small, temporary habitats, such as rock pools (Smith 1983, 1990, Van Buskirk 1990), in which there are few competing taxa and a low risk of predation. In these habitats, intraspecific competition may determine growth rate, which, in turn, determines how long it takes larvae to obtain the minimum size for metamorphosis that must be reached before the pond dries or freezes (Wilbur and Collins 1973). Population density interacts with nutrient levels via mechanisms that include interference and exploitation modes of competition (Wilbur 1977*b*).

Numerous studies in the laboratory and in field experiments with both frogs (e.g., Wilbur and Collins 1973, Wilbur 1976, 1977*a*, *b*) and salamanders (e.g., Wilbur 1972) have demonstrated density dependence in the timing and body size at metamorphosis. These in turn result in density-dependent survival during the larval period as a result of density-dependent growth rates. The season and body size at metamorphosis can carry over the density dependence of the larval period to the terrestrial juvenile and adult stages of the life cycle. Size at metamorphosis is an exponentially decreasing function of initial density of the population. At low density, many individuals metamorphose at a large size; at high densities most individuals metamorphose at what appears to be the minimum size threshold for successful metamorphosis. Survival is also an exponentially decreasing function of initial density, in part because as density is increased, reduced growth rate leads to a decreasing probability that an individual will obtain the minimum size threshold for metamorphosis before the pond dries or freezes. The mean length of the larval period increases exponentially with the initial density of the population. The distribution of larval periods within a cohort raised together has an exponential distribution as most individuals metamorphose near the minimum time, but some may have very long larval periods.

Population dynamics of cohorts of larvae can be modeled by exponential density dependence. The recruitment curve is

$$M_k = E_0 p \, \exp(-mE_0)$$

where M_k is the number of survivors that metamorphose after a larval period of k days, E_0 is the initial density of eggs laid in a pond, p is the density-independent survival during the larval period, and m is the coefficient of density dependence (Wilbur 1996; Fig. 4). Body size at metamorphosis (S) is also an exponential function of initial density,
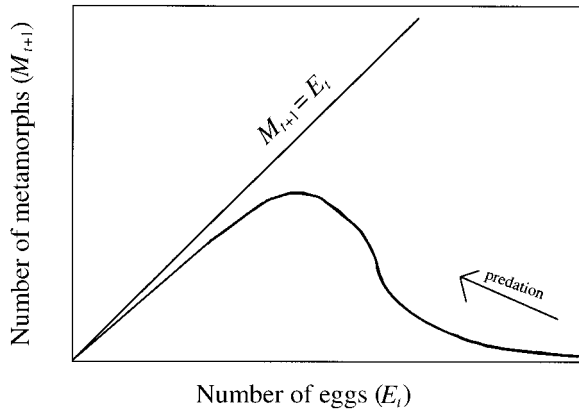
FIG. 4. Exponential recruitment curve relating the number of metamorphs to the initial density of eggs. One effect of predation early in the larval period is to reduce the effective density of tadpoles, pushing the population to the left up the right limb of the recruitment curve, as indicated by the arrow, thereby increasing the number of metamorphs.

$$S = b + c \exp(-aE_0)$$

where b is the minimum size for metamorphosis, and $b + c$ is the size of metamorphosis as density approaches zero. The rate of decrease in average size, S, with initial density, E_0, is controlled by the coefficient of density dependence, a. These exponential functions are the mean responses of individuals in replicated populations with different initial population densities. They mimic the results of experiments in enclosures in ponds (e.g., Wilbur 1972, 1976a, b, Wilbur and Collins 1973), in artificial ponds (e.g., Wilbur 1987), and in laboratory experiments (Wilbur 1977b, 1982, 1984). Within a population, the growth rates of individuals appear to be normally distributed, giving rise to lognormal distributions of body sizes (Wilbur and Collins 1973, Wilbur 1984). As the larval period proceeds, these distributions of body sizes become increasingly skewed as a few individuals grow rapidly, as if they were in low-density populations, but most individuals grow slowly. The coefficient of variation (standard deviation/mean) remains stable throughout the larval period, but populations started at high densities have greater variances in growth rates, generating more highly skewed size distributions later in the larval period. The physiological mechanisms generating these lognormal distributions of anuran larvae are incompletely understood. There is considerable evidence in some species (Adolph 1931, Rose 1960, Steinwascher 1978, Griffiths et al. 1993) that chemical growth inhibitors transmitted by microorganisms are responsible. Larger individuals, or water in which large individuals have been defecating, inhibit the growth of smaller individuals. Steinwascher (1978) identified the agent of inhibition in *Rana clamitans* as a yeast, but I suspect a more careful identification would reveal that it is a colorless ''green'' alga of the genus *Prototheca*

(Richards 1962, Griffiths et al. 1993). The mechanisms for the differential effect of inhibitors on small and large tadpoles are unknown. The relative importance of exploitation (direct competition for food) and interference (behavioral interactions and growth inhibitors) may vary among taxa (Wilbur 1976, 1977a, b). Growth inhibitors have not been convincingly demonstrated in natural populations (Petranka 1989b, Biesterfeldt et al. 1993).

An individual's body size and the timing of metamorphosis have long-term implications for its fitness (Brockelman 1969, Wilbur 1972, Emerson 1978, Berven and Gill 1983, Smith 1987, Semlitsch et al. 1988, Petranka 1989a, Berven 1990, John-Alder and Morin 1990, Pechmann 1994, Scott 1994, Newman and Dunham 1994, Goater 1994). Individuals that metamorphose at a large size have a high survival to maturity, may mature early, and may mature at a large body size and hence have a high fecundity. Individuals that escape risks in ponds by metamorphosing early at a small size are equipped less well for terrestrial life. They may have reduced scope for activity, and the allometry of limb development may make them less able jumpers than individuals that metamorphose after a longer larval period.

Pechmann (1994, 1995) studied these carry-over effects in two field experiments that are the first, to my knowledge, to follow individuals through metamorphosis to first reproduction in order to determine experimentally the consequences of density dependence in both stages of the life cycle. His studies also bridge the laboratory experiments used to test the exponential models of density dependence presented above to the dynamics of natural populations. He raised larvae at low and high initial population densities in ponds and then transferred metamorphs to large terrestrial enclosures with high and low population densities (Fig. 5). He repeated the study with the microhylid frog *Gastrophryne carolinensis,* an explosive breeder with filter-feeding tadpoles that can complete their larval period in <2 wk under good conditions, and with the salamander *Ambystoma talpoideum,* a less explosive breeder that takes several months to complete its larval period as an actively foraging predator of zooplankton, aquatic insects, and smaller amphibian larvae. He found that size at metamorphosis in *A. talpoideum* was smaller, age at first reproduction was later, and male survival from metamorphosis to first reproduction was lower in salamanders raised at high density as larvae. Neither juvenile density in the terrestrial habitat nor its interaction with density of the population of larvae in the aquatic habitat had statistically significant effects on demographic traits. These results suggest population regulation in this species may occur during the larval stage. This conclusion was consistent with the results of Scott (1994) for *Ambystoma opacum* larvae raised at controlled densities and followed as free-ranging meta-
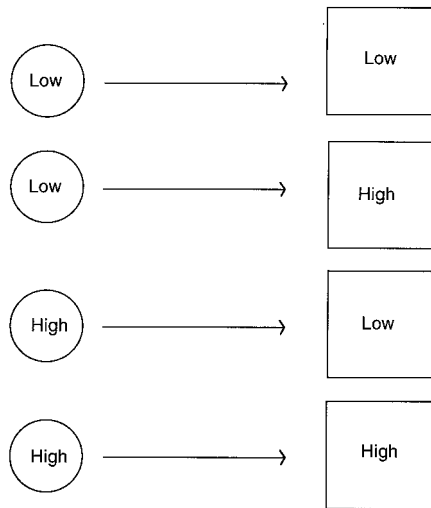
Fig. 5. Pechmann's design for studying the interaction between density dependence in the larval period in experimental ponds (circles) and the juvenile period in terrestrial enclosures (squares). Surviving metamorphs from different densities of larvae in ponds are transferred according to a randomized design to low or high densities in the terrestrial environments where they are allowed to mature.

morphs until maturity. In contrast, population regulation may be possible in both stages of the life cycle of *Gastrophryne carolinensis.* Survival and size at metamorphosis were lower and the larval period was longer in populations raised at high densities in the aquatic habitat. No individuals raised at high density as larvae survived to reproduction in the terrestrial habitat. Animals that were raised at low density as larvae responded in significantly different ways to the two population densities in the terrestrial juvenile stage. Survival from metamorphosis to first reproduction was lower, female size at first reproduction was smaller, and male age at first reproduction was later in the populations of juveniles raised at high density compared to populations raised at low densities in the terrestrial habitat. The implications of density dependence in both stages of a biphasic life cycle to population dynamics are explored in Wilbur (1996).

Interspecific competition

Competition from other species is easily added to the model of intraspecific density dependence (Wilbur 1982, Wilbur and Fauth 1990). Ideas derived from my experiments on intraspecific competition (density dependence) were used to design experiments to elucidate the nature of interspecific competition. Competition was highly asymmetric in a laboratory study of two sympatric species of tree frogs (Wilbur 1982). Although the two species overlap in their use of ponds, *Hyla gratiosa* tends to occur in larger ponds whereas *Hyla femoralis* occurs in smaller, more ephemeral ponds. *Hyla gratiosa* had a very strong negative effect on *H. femoralis* but was unaffected by it. Such asym-

metries are to be expected if interference (such as chemical inhibition or behavioral dominance) between species is the principal mode of interaction or if there is a large difference in body size, activity, or the niche of one species is included in that of another. Werner (1992) found asymmetric competition between *Rana pipiens* and *Rana sylvatica* and suggested that the superiority of *R. pipiens* was due to its greater activity rather than interference mechanisms. Other experiments with larvae of ambystomatids, newts, and sirens suggest that competition in larval salamanders of roughly the same body size in ponds is dominated by exploitation of food (Wilbur 1972, Fauth et al. 1990, Fauth and Resetarits 1991) and is thus more symmetric than in frog larvae. This generalization about pond-breeding salamanders is in sharp contrast to my current research with terrestrial and amphibious plethodontid salamanders that live near streams and use behavioral interference mechanisms that generate highly asymmetrical competitive relationships. I studied two aspects of interspecific competition, historical effects and higher order interactions, to test common assumptions made when representing interactions among species by a food web.

Historical effects

The time of arrival at a pond may be crucial to the reproductive success of a female; individuals that lay eggs early give their offspring an initial size advantage over competitors because the interaction between two individuals within a guild may depend as much on body size as on taxonomy, especially if exploitation or aggression are the modes of interaction (Wilbur 1988). The timing of reproduction in pond-breeding amphibians may be largely a function of the terrestrial biology of the adults because in spite of this apparent advantage to early arrival, ponds typically have a predictable succession of species (Murphy 1963; H. M. Wilbur, *personal observation*). Frogs that are able to tolerate freezing temperatures, such as *Pseudacris crucifer* and *Rana sylvatica* (Storey 1990), and are able to migrate at low temperatures (John-Alder et al. 1988) can begin breeding even before ice has completely left ponds. Other species, such as *Hyla versicolor* and *Rana catesbeiana,* grow and mature eggs in the spring before breeding.

The order of arrival of species at a pond can affect success of their larvae. We tested this hypothesis by manipulating the length of time a pond was established before tadpoles were added (Wilbur and Alford 1985) and the order in which they were added (Alford and Wilbur 1985, Alford 1986; Fig. 6). *Hyla chrysoscelis* had much more rapid development and metamorphosed at a larger size with higher survival when introduced into ponds that had been filled 15 d before eggs were introduced as compared with ponds that had been filled for 80 d. We interpreted this result as a function of the availability of suspended phytoplankton in the newer
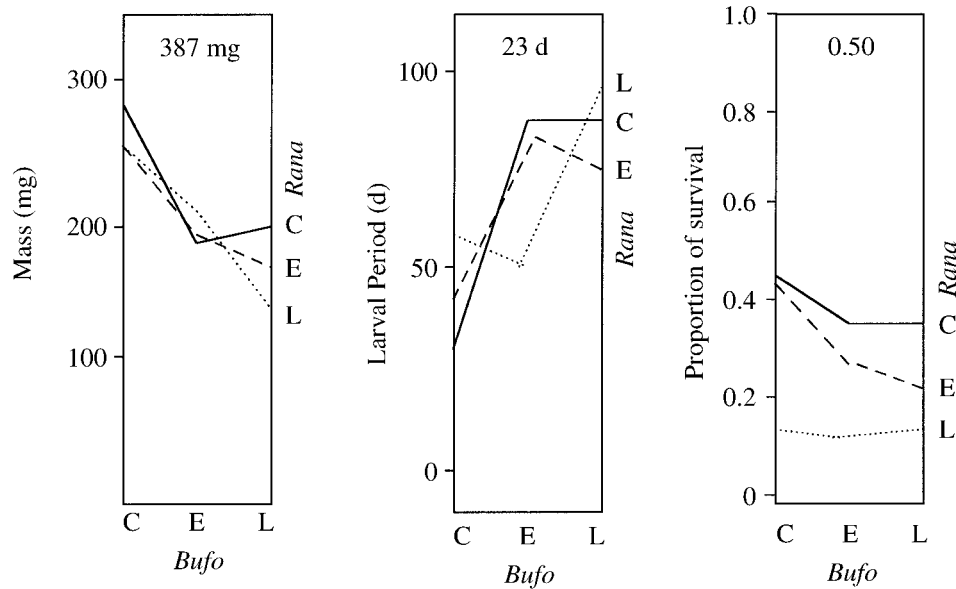
FIG. 6. Responses of *Hyla chrysoscelis* to initial conditions in experimental ponds. The three panels depict the mean response of three replicate populations to 10 initial conditions. The number at the top of the panel is the performance of *Hyla* in newly filled ponds that had neither *Bufo* nor *Rana* added. The solid line connects the response of *H. chrysoscelis* added to ponds that had been filled for 80 d when *Rana* were never added (C) across the treatments in which *Bufo* was never added (C), added early (E), or added late (L). The dashed line connects the *Bufo* treatments when *Rana* was added early (E). The dotted lines connect the *Bufo* treatments when *Rana* was added late (L). Differences between early and late treatments demonstrate priority effects.

ponds as compared with the older ponds in which nutrients were locked up in filamentous algae that could not be processed efficiently by the tadpoles. In other ponds in this experiment, the order of arrival of *Rana sphenocephala* and *Bufo americanus* tadpoles was important in the competitive interaction between them as well as their effect on *Hyla chrysoscelis* that were added 68 d after the first larvae had been introduced and after all *Bufo* had metamorphosed (Fig. 6). These persistent effects probably result from the impact of each species on the resources of the other species. A difference in 6 d in the time of arrival of *Rana* and *Bufo* had effects that lasted throughout the summer. Morin (1987*b*) also demonstrated strong competition between temporally separated species. These studies of historical effects help make sense of the temporal succession of species in natural ponds. It would be interesting to test the hypothesis that summer-breeding frogs are trapped between competition with species that are able to breed in the spring and the threat of desiccation in late summer.

The studies of historical effects were expanded by Ross Alford (1986) to include seven relative times of introduction of *Rana palustris* and *Bufo americanus*. To our surprise, there was no effect of the order of breeding on the outcome of the larval period. These two species co-occur frequently in farm ponds and scour ponds along streams in the Piedmont of North Carolina. Perhaps they have coevolved or otherwise differentiated in a way that has reduced competition to low, and to us undetectable, levels in contrast to the interaction we observed in the earlier experiment with *Rana sphenocephala,* a species that occurs less frequently with *Bufo americanus.*

The importance of the coevolutionary history of sympatic species is also an area ripe for more experiments. Food webs provide a framework for addressing many of these issues. Fauth (1990*a*), for example, studied the differences in interactions between allopatric and sympatric populations of two species of salamanders of the genus *Ambystoma* in common garden experiments designed to detect coevolution. He found evidence that *A. opacum* is a more efficient predator and stronger competitor in populations with a history of interaction with *A. maculatum* than in allopatric stocks. The taxonomically diverse amphibian fauna and the varied associations of species offer a plethora of possibilities for experiments on coevolution.

Historical effects are well documented in terrestrial plant communities, such as the successional sequence from old field to pine to hardwood forests on the Piedmont of the Carolinas (Billings 1938, Keever 1950, Bormann 1953, Christensen 1977, Christensen and Peet 1981). Fields used as pastures and those used for row crops have differences in vegetation a century after abandonment. Sutherland's (1978, Menge and Sutherland 1987) classic studies of the colonization of hard substrates by marine invertebrates on the Carolina coast

and Tanner et al.'s (1996) work on coral reefs also demonstrate the role of history in competitive interactions. The role of history in the dynamics of food webs has also been documented in the rocky intertidal community of the Pacific Northwest by Paine (1966, 1980, 1994, Paine and Levin 1981) and Dayton (1971).

Historical effects are one form of nonadditive interaction because the interaction between two species that arrive at a pond late in the season may depend on the effect of earlier species on the community. The additivity of species interactions has generally been discussed in the context of species interacting contemporaneously.

Additivity of interactions

The issue of nonaddititive effects remains a rich area for experimental studies of the mechanisms of interactions between taxa (Wootton 1993, Kareiva 1994). Competition in multispecies assemblages is nonadditive in ambystomatid salamanders (Wilbur 1972) such that predictions based on studies of two species are sensitive to the presence or absence of a third species in experimental assemblages. This lack of additivity probably results from the nonlinear effects of density dependence within species, as outlined above, as well as the mixture of exploitative and interference modes of interaction between species. Fauth (1990a) found similar nonadditive effects in a taxonomically more diverse assemblage of a toad (*Bufo americanus*), and three salamanders (larvae of *Ambystoma opacum* and *A. maculatum* and adults of *Notophthalmus virdescens*) that occur in vernal ponds in the mixed deciduous forests of the North Carolina Piedmont.

Community saturation

Classic questions in the heyday of niche theory (e.g., Hutchinson 1959, MacArthur and Levins 1967, Levins 1968 or as revisited by Rosenzweig 1995) were: Why are there so many species? and What limits the similarity of coexisting species? A central idea was that niche space was finite and there was a limit to the packing of species; therefore, a community could become saturated with species if competition is the mechanism controlling community structure. The question of whether communities are saturated was studied by biogeographers (e.g., MacArthur and Wilson 1967) and played a role in the concept of the taxon cycle (Wilson 1961, Ricklefs and Cox 1972). Other evidence came from the ecology of invasions in which exotic species were thought to competitively displace elements of native biotas. Interest in studies of niche saturation and what makes communities invadable should see a revival as conservation biologists re-ask these classic questions with a new urgency. This reawakening should not be constrained, however, by the assumption implicit in most studies of niche packing in the 1960s and 1970s

that natural communities are closed and at competitive equilibrium.

I tested the hypothesis that the native assemblage of three small species of pond-breeding *Ambystoma* was ecologically saturated by introducing a fourth species of the genus into enclosures in a pond. Three small species, *Ambystoma maculatum, A. laterale,* and *A. tremblayi,* coexist in ponds on the E. S. George Reserve in southeastern Michigan. Sometimes a larger, fourth species, *A. tigrinum* (Collins and Wilbur 1979), also occurs in these ponds. *Ambystoma texanum* reaches the northern limit of its range in Ann Arbor south of the George Reserve. There was no evidence from my experiment (Wilbur 1972) that the endemic community was saturated; *A. texanum* was able to invade the native assemblage, at least in the cages that I was using to study interactions among the native species. In this modest experiment with low statistical power, the invader had an equal effect on the three native species, evidence that competition among species was not linearly ordered along a single niche axis.

Predation

Predation can be a density-dependent mortality agent sufficient to regulate prey population dynamics, but the presence of predators can also affect the behavior and morphology of prey. These induced defenses can reduce the risk of mortality from predation, although they may have costs with respect to escaping a drying pond. These costs may be mediated by the commitment of resources to a morphological defense or of foraging time to a behavioral defense and these costs may be paid by slow growth and hence a smaller size at metamorphosis or longer larval period. Predators can also have a positive effect by reducing the population density of prey, thereby promoting rapid growth, which in turn may allow individuals to escape an ephemeral habitat. Several of our experiments demonstrate that production of metamorphs may be enhanced by the mortality caused by predation (Wilbur 1984, 1987). Anholt and Werner (1995) showed that when food level was experimentally reduced, predation risk in *Rana catesbeiana* tadpoles increased because they became more active. These risks are also size specific when the predator is gape limited (Werner and Anholt 1996). The relative importance of these three effects of predation and interactions among them (mortality, cost of induced defense, and release from competition) needs more experimental investigation. Predators can cause mortality or nonlethal injury. Nonlethal injury that is density dependent and reduces fecundity or future survival can regulate population density (Harris 1989). Amphibians readily regenerate many lost body parts, such as tails and legs. A very high proportion of anuran tadpoles in many of our samples had tails in various stages of regeneration, a record of failed predation attempts (Morin 1985). Wilbur and Semlitsch (1990) test-

ed the hypothesis that there is a cost to the individual incurred by this mechanism of reducing mortality risk. We demonstrated a slight, but significant ($P = 0.02$), reduction in growth in tadpoles of *Rana catesbeiana* with 75% tail loss but not with 25 or 50% tail loss. Tadpoles of *Rana sphenocephala* with regenerating tails had a significant reduction in survival when exposed to predation by *Notophthalmus,* probably because loss of tails reduced acceleration, maneuverability, or precluded the defense of shedding the tail in subsequent encounters. Density-dependent tail loss can also occur through intraspecific aggression in populations of predaceous *Ambystoma* larvae (Petranka 1989*a*).

Some predators are ready and waiting for a pond to fill and the arrival of breeding by taxa of prey. Amphibian examples include *Siren intermedia,* a salamander that can aestivate entombed in the mud for more than a year. When the pond fills, *Siren* terminate their dormancy and can be actively foraging within a few hours of the first rain (*personal observation*). A less spectacular, but none-the-less potent, example is provided by newts, *Notophthalmus viridescens dorsalis,* that are able to retreat into mud cracks and burrows during dry spells and then emerge to forage terrestrially on nights when the risk of desiccation is low (*personal observation*). Both of these salamanders prey on amphibian eggs and hatchlings as well as aquatic insects. Newts are spectacularly efficient predators of amphibian eggs, including those of conspecifics (*personal observation*) and other salamanders, as well as anurans. The composition of the anuran populations in ponds can be affected by the time of arrival and departure of adult newts (Alford 1989). In one of my larger study ponds in the sandhills, 17 species of anurans (Table 1) have been heard calling on a single night in late May. Most of these species lay eggs in clumps but only those that lay them singly, *Acris gryllus, Pseudacris crucifer,* and *Hyla gratiosa,* regularly escape predation by newts and produce large numbers of metamorphs from this pond. Newts, and perhaps *Siren,* can be critical or keystone species in these communities because they can prey on anuran eggs and hatchlings.

Representatives of another group of predators arrive at newly filled ponds and lay eggs that develop into predaceous larvae. Salamanders of the genus *Ambystoma* are the most important amphibians within this group. If larvae of *Ambystoma tigrinum* escape predation by newts as hatchlings, they grow large enough to depress recruitment of newts by preying on newt larvae (Morin 1983*b*). *Ambystoma opacum* is especially efficient in ponds on the Piedmont because it anticipates the filling of ponds during fall rains. In early autumn adults migrate to ponds, court, and lay eggs in the dry basin. Females attend the eggs, usually until the nests are flooded and the larvae hatch. The larvae feed first on zooplankton, then remain in the

pond over the winter and are effective predators of amphibians that breed in the spring, such as *Pseudacris crucifer* and *Ambystoma maculatum* (Stenhouse et al. 1983, Chambers 1984; H. M. Wilbur, *personal observation*). The winter-breeding tiger salamander, *Ambystoma tigrinum,* can be an important predator (Wilbur 1972), although it is found in only a few ponds in my study area. Among insects, beetles (especially Dytiscids) and hemipterans (*Notonecta, Lethocerus,* and *Bellostoma*) are effective predators of small tadpoles. Adult *Lethocerus* can kill even adult salamanders and large *Ambystoma tigrinum* larvae (*personal observation*). The most effective predaceous insects in the sandhills, however, are dragonflies. The libellulid *Pantella flavescens* is as efficient as the most explosively breeding frogs at finding newly filled ponds. Although their eggs are small, *Pantella* larvae can quickly grow large enough to kill most amphibian larvae. This species is able to complete its larval period in 2 wk (*personal observation*), as rapidly as the fastest frogs. Aeshnids, such as *Anax junius,* are equally effective predators in larger ponds as *Pantella* is in smaller, more temporary, ponds.

A third group of predators is composed of widely foraging species that may visit ponds as they dry and the tadpoles become concentrated and easily caught. I have frequently seen snakes, such as *Nerodia erythrogaster,* herons, and raccoons feasting on tadpoles in drying ponds. This behavior may provide a windfall for the predators but is not likely to have an impact on the population dynamics of their prey as they were doomed to desiccation if they had not been eaten by these scavengers.

The relationship between predators and prey depends on the palatability of the prey to a specific predator and the ability of this predator to catch and ingest the prey; both may depend on relative body sizes. *Rana catesbeiana* and *R. clamitans* have different risks of predation when exposed to sunfish, dragonfly naiads, and salamander larvae (Werner and McPeek 1994). Adult *Notophthalmus viridescens dorsalis* are a keystone predator in temporary ponds in the Sandhills because they are highly efficient predators of eggs and small anuran larvae, especially those of the actively swimming competitive dominants, such as tadpoles of spadefoot toads, *Scaphiopus holbrookii* (Morin 1981, Wilbur 1987). Newts, however, have narrow heads and thus are gape limited so that they are only effective predators for the first few days of the larval period of most frogs and salamanders. Larval salamanders of the genus *Ambystoma* have much wider heads, grow as larvae, and are able to stay ahead of their growing anuran prey. Dragonflies, such as *Anax* and *Pantela,* hemipterans such as *Lethocerus,* and beetle larvae, such as *Dytiscus,* are able to capture, kill, and consume prey larger than themselves, making it difficult for tadpoles to obtain a size refuge.

Some tadpoles, such as *Bufo,* are protected by dermal toxins, but these may be effective only against vertebrate predators that chew their prey and may be ineffective against invertebrates that pierce and suck their prey, such as hemipterans. Behavioral mechanisms may also reduce the risk of predation. Tadpoles that breed in temporary ponds tend to be more mobile and hence more vulnerable to predation compared to species typical of permanent ponds (Woodward 1983, Wilbur 1987). Both anuran larvae (Morin 1986, Skelly 1992, Semlitsch and Reyer 1992, Smith and Van Buskirk 1995) and salamander larvae (Walls 1995) remain cryptic in the litter when they sense the risk of predation. Tadpoles that are able to coexist with fish survive by being toxic, distasteful (e.g., *Rana catesbeiana*), or by foraging in the extreme shallows where fish cannot feed (*Rana clamitans* and *Acris gryllus*).

Schooling has been reported in toads of the genus *Bufo* (Beiswenger 1975, 1977, Breden et al. 1982) and in spadefoots of the genus *Scaphiopus* (Richmond 1947, Bragg 1961, 1964, 1968). This schooling has been interpreted as an adaptation to crowding in species that have synchronized breeding and high fecundity, especially among filter feeders in ephemeral ponds (Richmond 1947, Wassersug 1973). The group is thought to be more efficient at finding food concentrations and getting the food into suspension. I (Wilbur 1987) observed schooling in *Scaphiopus holbrookii* tadpoles in response to predation in an experiment on the interaction between competition and predation. Schools were defined by tight aggregations in which individuals were within a centimeter of their nearest neighbor and most individuals were moving in the same direction. The 62 experimental ponds all also contained tadpoles of *Rana utricularia* that did not form schools. Hatchling *Scaphiopus* were added to ponds 4 d before the observations were made. The 12 tanks that had initial densities of four newts, 65 *Scaphiopus,* and 50 *Rana* had no surviving tadpoles of either frog species. The 12 tanks that had four newts and 260 *Scaphiopus* and 200 *Rana* had an average of 59.4 surviving *Scaphiopus* tadpoles, suggesting that newts were satiated at high densities. The schools that were observed were pure *Scaphiopus.* The null hypothesis of no association between schooling and the presence of newts (Table 2) was rejected by a Fisher exact test with $P = 0.000005$. The observations were repeated 5 d later and I found 5 of the 12 high-density populations of *Scaphiopus* had been eliminated by newts. The null hypothesis was again rejected ($P = 0.0000002$). These dense schools may serve as selfish herds (sensu Hamilton 1971) in which individuals have a lower risk of predation by joining a herd than by remaining a solitary target for predators (Black 1970).

The most remarkable adaptations to predation in tadpoles are the induced morphological defenses that have been found in several species of hylid tadpoles, such

TABLE 2. Association between the presence of adult newts (*Notophthalmus viridescens*) and the occurrence of schooling in *Scaphiopus holbrookii*. Data are presented as the number of populations observed in each condition 4 and 9 d after the *Scaphiopus* were introduced as hatchlings into the experimental ponds.

Adult newts	Day of observation	No. of populations observed	
		No schools	Schools
Absent	4	30	2
	9	32	0
Present	4	4	12
	9	1	10

as red tails and high tail fin in *Hyla chrysoscelis*: (McCollum 1993, McCollum and Van Buskirk 1996), high tailfins in *Pseudacris triseriata* (Smith and Van Buskirk 1995), and black tail tips in *Acris gryllus* (Caldwell 1982). McCollum (1993) found that *Hyla chrysoscelis* in ponds with *Anax junius* have wide tailfins with bright red coloration and strongly contrasting black spots. Tadpoles raised without the threat of predation have narrower tails and drabber coloration. The presence of *Anax* is all that is required to induce the ''turbo'' morph. Tadpoles with the induced morphology were able to accelerate faster when their swimming performance was compared in a flow tank with tadpoles raised in the absence of *Anax* larvae. These ''turbo tadpoles'' sustained fewer injuries than the ''plain tadpoles'' in feeding trials, but in the absence of predation survived less well, strong evidence that there is a cost to the induced defense. It has long been known that some species have morphological variation correlated with the occurrence of predators, but it was not known before McCollum's work that these were induced defenses rather than a genetic polymorphism.

Predation can be a mixed blessing. There is intense selection on individuals to avoid predation, but most predators probably have a positive effect at the level of the population of tadpoles in temporary ponds (Wilbur 1984). If an individual is a survivor in a population subjected to predation, it may enjoy the benefits of reduced competition and grow rapidly enough to escape the pond before it dries or freezes. This interaction among competition, predation, and environmental uncertainty was the focus of one experiment (Wilbur 1987) and an implicit component of nearly all our work in temporary ponds. The large aggregations of breeding females of many species of frogs, and the high fecundity of each pair, means that most populations of pond-breeding anurans start far out on the right limb of the recruitment curve (Fig. 4). The action of predation is to push the population to the left, thereby causing it to climb the curve and produce more and larger metamorphs than they would in the absence of predation. A familiar analogy is the thinning of radishes to produce a few large individuals rather than many small ones.
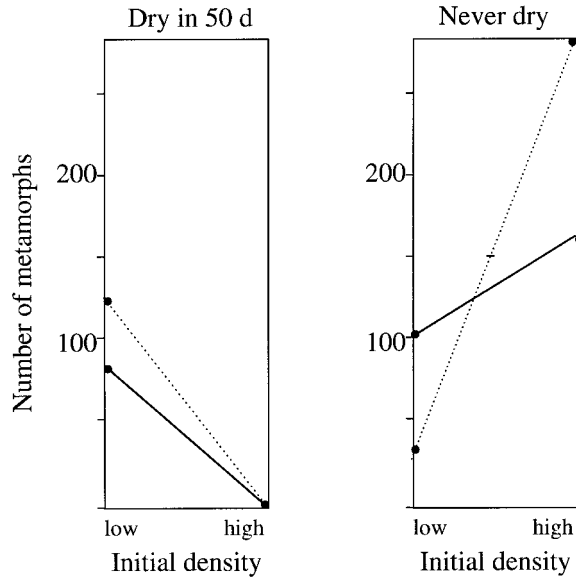
FIG. 7. The interaction among competition, predation, and environmental uncertainty in the success of *Bufo americanus* in experimental ponds. In ponds with high initial density with no predators (———), competition slows growth, resulting in low survival in ponds that dry early. Predation (········) reduces effective density, permitting rapid growth and successful escape from drying ponds. The crossing of the lines is a consequence of the interaction between competition and predation.

Counterexamples to the beneficial effects of predation include the case when newts consume the eggs of their prey before they hatch and several examples that we have observed of dragonflies eliminating tadpoles from small ponds. In spite of the beneficial effects of predation at the level of the population, male frogs will discriminate among ponds when establishing calling sites and females will lay their eggs preferentially in ponds without predators (Resetarits and Wilbur 1989, 1990). Habitat selection, synchronized breeding, scattering of eggs, high fecundity, and spatial complexity are all likely to be important mechanisms of either satiating predators or reducing the likelihood of predation.

Food Webs in Temporary Ponds

Notophthalmus viridescens dorsalis can act as a critical or keystone predator (sensu Paine 1969) in ponds by playing a role in determining the relative abundances of both zooplankton and anurans (Morin 1981, 1982, 1987*a*, Morin et al 1983, Wilbur et al. 1983, Fauth and Resetarits 1991, Leibold and Wilbur 1992). *Scaphiopus holbrookii* is the dominant anuran in the assemblage we have used in our experiments. This spadefoot toad is an explosive breeder that lays large eggs after exceptionally heavy rains that come with hurricanes, northeasters, and severe thunderstorms. Females may be able to breed any month of the year

if conditions are suitable. The eggs hatch within a day and the tadpoles are very active foragers. In Morin's experiments, *Scaphiopus* competitively dominated four other species of anurans, *Pseudacris* (*Hyla*) *crucifer, Rana utricularia,* and *Bufo terrestris. Scaphiopus* was the preferred prey of newts, probably because of their high activity and apparent lack of chemical defenses. *Scaphiopus* had low survival in ponds with newts and dominance passed to *Pseudacris.* We attempted to repeat Morin's experiment with a similar community in the same set of experimental ponds (Morin et al. 1983). Due to a difference between the years of these two experiments in the time of arrival of heavy rains, our experimental ponds had been set up several weeks before *Scaphiopus* eggs became available. In this period before anuran eggs were introduced, primary production became dominated by filamentous algae, an unsuitable food for *Scaphiopus. Scaphiopus* was not able to establish competitive dominance and did poorly in all treatments in this experiment. A third experiment (Wilbur 1987) repeated Morin's original result, again because *Scaphiopus* was introduced soon after the ponds were filled. This sequence of experiments demonstrates once again the role of initial conditions and history in determining the trajectory of a community.

This last experiment (Wilbur 1987) demonstrated the interaction between the mechanisms that structure communities in temporary ponds (Fig. 7). In ponds that hold water for a long time and do not have predators, an unlikely combination in nature, the relative
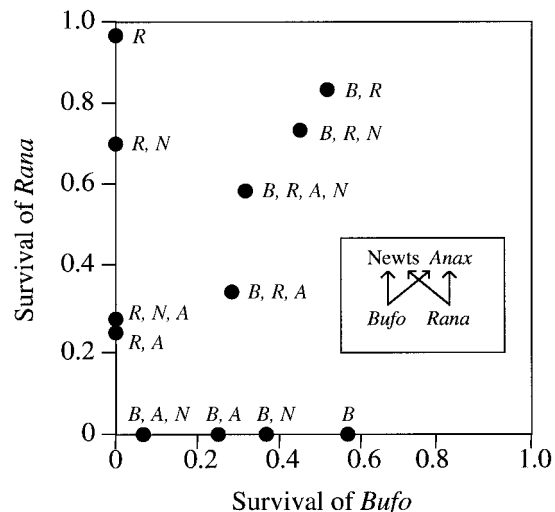

FIG. 8. The interaction between two predators, the newt (*N = Notophthalmus viridescens*) and naiads (*A = Anax junius*), on two anuran prey (tadpoles of *R = Rana sphenocephala* and *B = Bufo americanus*). The axes are the mean probabilities of survival of each species of tadpole. The labels by dots indicate which species were present in the ponds. Predator–prey relationships are represented by the food web.

abundance of metamorphs is determined by competition and the phenology of the anurans. If ponds without predators dry rapidly, a common occurrence in nature, relative abundances are determined by competition and the autecology of the species' responses to the environment. Differences in the success of species reflect variation in phenotypic plasticity that permits some species to accelerate metamorphosis as the pond dries (Wilbur 1987, Crump 1989, Newman 1989). When predators are present, the relative abundances of anurans are determined by the competitive abilities and the defenses of the tadpoles as well as their ability to initiate metamorphosis when the threat of desiccation increases. In the diversity of natural ponds, population regulation and the determination of relative abundances of metamorphs are determined by complex interactions among the life histories of the species, their defenses against predators, and their competitive abilities. It takes complex experiments to understand causal mechanisms in such complex systems.

Wilbur and Fauth (1990) studied the interaction between predation and competition in greater detail in a factorial experiment in which the occurrences of two predators, newts and *Anax,* were combined with the occurences of two species of prey, *Rana sphenocephala* and *Bufo americanus,* in a factorial design with all 16 treatments replicated 4 times (Fig. 8). This experiment was designed to test how well studies of systems with one and two species predicted the outcome of systems with three and four species. The design permitted estimation of the strength of competition between the two species of prey by comparing their performances when together with their performances when alone. *Rana* had a higher survival than *Bufo* when each was alone in the tanks. Each species affected the growth rate of the other when they were raised together. This competition was symmetrical with only a small reduction in survival in both species. The design permitted only a weak test of competition between the predators because there were only two individuals in each population of *Anax* and newts. The predators had small effects on one another when zooplankton was the only prey available. The risk of predation to each species of tadpole was determined by comparing their survival when alone to their survival when exposed to each predator. Newts had an equal effect on both species of anuran prey, reducing their populations by ~100 individuals compared to the control conditions when the each species of prey was raised alone. *Anax* had a stronger effect than newts on both species of tadpole. *Anax* had a greater effect on *Rana* than on Bufo, canceling the difference of survival in the control tanks and bringing the species to nearly equal abundance when subject to predation. There was strong evidence that *Bufo* perceived the risk of predation and initiated metamorphosis early and at a small size. There was no evidence of such a facultative response in *Rana,* which had a long larval period and was headed towards metamorphosis at a small size in the absence of predation. In the presence of newts, *Rana* that escaped predation were able to initiate metamorphosis early and at a large size.

These systems of one and two species were used to make predictions about survival and relative abundances expected in the systems with three and four species. The predicted survivorships were significantly smaller than the observed survival of both species of tadpoles. This is expected if the two predators either interfere with one another directly or if one predator causes a shift in the behavior of prey that affects its risk of encounter with the other predator. Fauth (1990*b*) favored this explanation for the nonadditive effects of crayfish and newts on *Hyla chrysoscelis* tadpoles. On the other hand, Travis et al. (1985) found an additive effect of predation by dragonfly naiads (*Tramea*) and salamander larvae (*Ambystoma opacum*) on *Hyla gratiosa.*

Again, it took a complicated experiment (16 treatments replicated 4 times in 64 tanks) to answer the complicated question of how well the study of pairs of species predict the behavior of multispecies assemblages. The implication of this study for community ecology is that food webs provide only a diagrammatic representation of trophic relationships. The nature and strength of interactions may depend on induced morphological changes and behavioral responses that are difficult to predict from studying species only in pairwise combinations. The limitations of using studies of pairs of species to predict relationships in multispecies assemblages depend on the level of accuracy desired (Vandermeer 1969). The elimination of species may be predicted successfully. Ranks of abundances may also be predicted with some success. Accurate predictions of absolute abundances, however, may require experiments even more complex than the one just described. After all, our experiment started each species with the same initial density when it was present ($n = 500$ prey, $n = 2$ predators). We did not manipulate the initial densities of each species or their relative abundances. The next step in complexity would have been a $3 \times 3 \times 3 \times 3$ factorial design requiring 81 treatments, for each species to be present at three initial densities. Such an experiment would demand 324 ponds for four replicates!

The last experiment demonstrates how factorial designs can be used to understand the mechanisms that determine the structure and function of food webs. It demonstrated that the pairwise study of species predicts the behavior of larger systems only in coarse detail. It is logistically difficult to extend such studies to include either multiple initial densities of the focal species to study nonlinearities in density dependence or to broaden the design to include additional species, because the number of units increases multiplicatively as factors or

levels are increased. Several solutions to this dilemma are possible.

One approach is to give up knowledge about some higher order interactions by using fractional factorial designs (Cochran and Cox 1957, Box et al. 1978, Mead 1988). This is a very attractive approach because it seems unlikely that the higher order interactions found by Wilbur (1972), Neill (1974), Wilbur and Fauth (1990), and Wootton (1993), will *dominate* the behavior of complex systems. I would favor this approach to address hypotheses about the presence and absence of species, such as issues of the saturation of natural communities, the consequences of extinctions and invasions, and the connectivity of food webs. A fractional design that gives up all but main effects and pairwise interaction terms would have allowed us to study interactions among five species with four replicates of each treatment with the same 64 ponds, a gain of only one species to balance the loss of the three-, four-, and five-way interactions. The relative gain increases with larger designs, but for my modus operandi, a study of eight species would have been the limit as all 144 ponds would be required.

A second approach is to embed complete factorial experimental designs within larger food web experiments in which the responses of unmanipulated species are included in the analyses. One approach is to manipulate one functional group, such as predators or grazers, and to observe the impact of the treatment on other functional groups. We have used this approach in experiments in which only amphibians were manipulated by the experimental design but zooplankton were also included in the analyses (Morin 1982, 1987*a*, Wilbur et al. 1983, Leibold and Wilbur 1992) or grazers were manipulated and producers were also included in the analyses (Harris 1992, Leibold and Wilbur 1992).

As reviewed above, newts act as keystone predators in determining the relative abundance of the zooplankton as well as the relative abundance of the anurans in our experimental ponds. Newts also appear to have a critical role in determining the occurrence of insects in the natural ponds of the Sandhills. The effect of newts on the dominant microcrustacean *Daphnia* also has an impact on how nutrients are made available to tadpoles. *Daphnia* is a well-known competitive dominant in zooplankton assemblages, apparently because of its efficiency at filter-feeding on suspended green algae (Leibold 1989). Predators that feed on zooplankton in ponds, such as fish (Brooks and Dodson 1965, Galbraith 1967) and newts (Wilbur et al. 1983, Morin 1987*a*, Leibold and Wilbur 1992), are size selective, preferentially feeding on *Daphnia,* thereby releasing smaller species of zooplankton from competition (Zaret 1980).

Leibold and Wilbur (1992 and *unpublished data*) did a series of experiments to test how the food web structure determined how the community responded
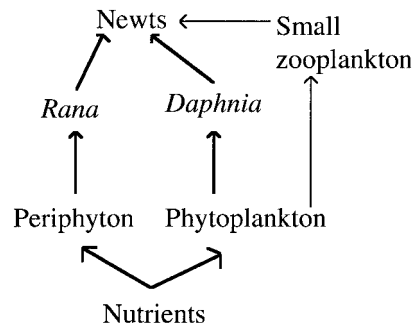

FIG. 9. Leibold and Wilbur (1992) added nutrients to food webs in which the presence and absence of newts (*Notophthalmus viridescens*), tadpoles (*Rana sphenocephala*), and the cladoceran *Daphnia* were controlled. The responses of all taxa were assayed.

to nutrient additions (Fig. 9). We manipulated the presence of *Daphnia, Rana sphenocephala,* and newts and added nutrients to these different food webs. A diverse assemblage of microorganisms, periphyton, phytoplankton, and small zooplankton was present in all of the experimental ponds. *Daphnia* was the competitive dominant within the zooplankton community. There was a significant interaction between the presence of *Rana* and *Daphnia* on their effects on nutrient flows. When *Rana* is absent, nutrients get locked up in periphyton, especially filamentous algae, which is a poor resource for most species of zooplankton, especially *Daphnia.* When *Rana* is present, they scrape all surfaces in the ponds preventing the dominance of periphyton. This releases nutrients that then are available to support phytoplankton, including *Daphnia.* The negative effects of the filter-feeding of *Rana* and sequestering of resources by their increased body mass are offset by the recycling of nutrients through their reduction of periphyton by scraping surfaces. When nutrients are added to the system in the presence of *Rana,* the zooplankton benefit directly. When nutrients are added in the absence of *Rana,* there was little response by the zooplankton because of the shift to dominance of production by periphyton.

Newts can also have a controlling influence through their impact on the *Rana* population. If newts cause the elimination or severe reduction in the density of hatchling *Rana,* ponds probably become dominated by filamentous algae. It would be instructive to extend our experiment by crossing a range of initial densities of *Rana* tadpoles and newts to disentangle the interaction between *Rana* as a controller of periphyton and newts as predators of both *Rana* and *Daphnia.*

Patricia Harris (1992) combined both approaches to complex designs in a series of experiments in which incomplete factorial designs were embedded in the food web of temporary ponds. She assayed the effect of manipulating four taxonomically diverse periphyton grazers, isopods (*Caecidotea obtusa*), amphipods

(*Crangonyx obliuus–richmondensis* complex), tadpoles (*Pseudacris triseriata*), and sphaeriid clams (*Sphaerium* sp.), in two-, three-, and four-species combinations on the periphyton and phytoplankton components of the community. She predicted that these grazers on the periphyton would indirectly benefit the phytoplankton due to competitive release among the producers. She also predicted that these taxonomically diverse grazers should compete for the common resource of available periphyton, itself a taxonomically rich assemblage.

Her experimental design used 48 tanks into which a diverse community of zooplankton, phytoplankton, periphyton, and microorganisms were introduced using carefully randomized inocula pooled from collections made in local temporary ponds in Durham and Orange Counties, North Carolina. The introduction of the grazers used an incomplete factorial design in four randomized spatial blocks, each being a complete replicate of the 12 treatments. The grazers were either not introduced so that she could study the control community with microorganisms alone, or the grazers were introduced in all six pairwise combinations, the four three-species combinations, and the one four-species combination. The relative abundance of phytoplankton in the different treatments was measured by fluorometry at 460 nm and the relative abundance of periphyton was measured by fluorometry of chlorophyll extracted from the assemblages that grew on plastic strips attached to the walls of the tanks.

The herbivores caused a significant reduction in their food source, the periphyton, and the predicted increase in phytoplankton. The periphyton was reduced more on the bottom litter than on the sides of the tanks, perhaps due to both the grazing habits of the herbivores and shading of the bottom by the dense bloom of phytoplankton that occurred when grazers were present. None of the effects of herbivores on each other were statistically significant after probability levels were adjusted for multiple comparisons, suggesting that interference mechanisms are not important and that food was not limiting numerical abundances of the herbivores during the 4-mo experiment.

These experiments lead to the question of how to define functional similarity. In a second experiment Harris (1992, 1995) manipulated three pairs of common species in temporary ponds. The members of each pair were similar autecologically but taxonomically diverse. The pairs included two predators (*Gambusia affinis,* a fish, and *Ambystoma maculatum* larvae, a salamander), two herbivorous snails (*Pseudosuccinea columella* and *Menetus dilatatus*) and two herbivorous tadpoles (*Bufo americanus* and *Pseudacris triseriata*). The effects of each treatment on the community were measured by the abundances of isopods (*Caecidotea obtusus*), amphipods (*Crangonyx obliquus–richmondensis*), the abundances of species manipulated by the treatments,

relative abundance within the zooplankton assemblage, the standing crop of phytoplankton measured fluorometrically, and the standing crop of periphyton measured by mass. The experiment had 5 replicates of each treatment and 10 replicates of the control ponds and ran for 6 m.

Harris (1992, 1995) found a negative correlation between the standing crops of periphyton and phytoplankton in the 10 control tanks, reinforcing the generalization that these two types of producers are in competition in our experimental systems. The fish, salamander, and the snail *Pseudosuccinea* had significant multivariate effects on their communities when compared with the controls. The other manipulated taxa did not cause the communities to differ from the control communities when corrected for multiple comparisons. Predators had different impacts than herbivores, causing reductions in isopods, amphipods, and the zooplanker *Diaptomus*. The fish had a greater effect on *Diaptomus* than the salamander larvae. The communities in tanks with snails did not differ from the communities in tanks with tadpoles in the omnibus test including all assay species. The univariate tests showed that snails and tadpoles had different effects on the phytoplankton and periphyton but not on the animals (zooplankton, amphipods, and isopods). A cluster analysis of treatment means based on the responses of all assayed species showed that the effects of the manipulated species were predicted a priori by their autecological similarity.

Harris's failure to find a significant effect of tadpoles on their food supply is in contradiction to our earlier results (Wilbur 1987, Leibold and Wilbur 1992). This is because she measured algal biomass only at the end of the experiment after most tadpoles had metamorphosed. An effect of tadpoles on phytoplankton was evident visually earlier in the experiment (P. Harris, *personal communication*). She concluded that the four herbivores are a single functional group with respect to their impact on the community and that indirect effects are damped and not nearly as strong as the direct effects of one species consuming another. Her results go against the prediction by Yodzis (1988) that small differences in interspecific interaction coefficients can have large effects on system dynamics in the fairly brief time scale of an episode of pond filling and drying.

Conclusions

Temporary ponds are excellent arenas for the study of community ecology. These small habitats are structurally simple enough to replicate with reasonable realism in inexpensive containers. This in turn permits the design of experiments with many units that can be distributed among many replicates of a few treatments to provide sufficient statistical power to test for small differences among treatments, or the units can be used

for complex designs of lower power. I have chosen to emphasize complex designs under the conviction that experimental ecology is at the stage in which we need to test assumptions of how we construct models of complex systems. I have found, for example, that the form of density dependence is more accurately modeled by the exponential function of the Ricker equation than by the linear function of the logistic equation. Another issue I have addressed is why linear-additive models, such as the community matrix (Levins 1968, May 1975), do not fully capture the complexities of multiple species competing for common resources. Behavioral and chemical mechanisms of interference and size-specific interactions as well as exponential density dependence can lead to these nonlinearities. Yet another issue is whether food webs are highly connected because diffuse competition spreads the effects of changes in resources across many competing species within a trophic level and predators have multiple alternative prey, or alternatively, communities are composed of subwebs loosely connected by rare top-order predators. Some of our experiments have approached the level of complexity at which these issues emerge. Our experiments on functional groups support the notion of highly connected webs. Our exercise in "experimental natural history" demonstrated that temporary ponds are dominated by a diverse assemblage of predators, but that the newt *Notophthalmus viridescens* is a critical or keystone species that can regulate the flow of nutrients through producers and the relative abundance of consumers in tightly controlled communities. The role of ontogenetic niche shifts in food webs, especially among species with complex life cycles, such as insects and amphibians, is still poorly understood. Ecologists tend to think of food webs as static structures that characterize a given community. In fact, our experiments have shown that size-structured interactions are constantly changing connections in food webs that include growing predators and prey. These seasonal shifts in trophic links make the interpretation of patterns observed in nature difficult without the power of experiments to test hypotheses about mechanisms. Adjacent communities may have mobile taxa that cross ecotones either continuously or during ontogenetic habitat shifts. These movements may link the food webs of adjacent communities, thus integrating ecosystems across larger landscapes. Food webs deserve a central role in ecology, but ecologists need to move away from a static concept of stable linkages among taxa to include some of the spatial temporal, and ontogenetic mechanisms that make actual food webs constantly changing tangles of trophic relationships.

These are all complex issues that are nearly impossible to evaluate through observation and correlations. As previously argued by Connell (1975) and Hairston (1989), it is far more efficient and less ambiguous to do experiments with the necessary complexity and replication to evaluate alternative views of how communities function than to try to draw strong inferences from observational studies or to rely on so-called "natural experiments" that lack randomly assigned controls.

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