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Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians

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Abstract

Numbers of successfully metamorphosing juvenile amphibians were tabulated at three wetlands in South Carolina, U.S.A. using terrestrial drift fences with pitfall traps. A relatively undisturbed Carolina bay was studied for eight years, a partially drained Carolina bay for four years, and a man-made borrow pit for three years. Annual production of juveniles at the undisturbed Carolina bay ranged from zero to 75,644 individuals of 15 species. Fewer individuals of fewer species typically metamorphosed at the borrow pit than at the undisturbed bay, with the least numbers at the partially drained Carolina bay. Both total number and species diversity of metamorphosing juveniles at each site each year showed a strong positive correlation with hydroperiod, *i.e.*, the number of days a site contained standing water that year. Data for one common anuran species and the most common salamander species were analyzed separately by multiple regression, in addition to the community analyses. For the mole salamander, *Ambystoma talpoideum*, hydroperiod was a significant predictor of the number of metamorphosing juveniles, but the number of breeding females was not. For the ornate chorus frog, *Pseudacris ornata*, the number of breeding females was a significant predictor of the number of metamorphosing juveniles, but hydroperiod was not. Variation in the dates of wetland filling and drying interacts with other factors to determine amphibian community structure and diversity. Either increasing or decreasing the number of days a wetland holds water could increase or decrease the number and species diversity of amphibians in and around a wetland.

Introduction

Many wetlands provide critical habitat for amphibian breeding and larval development. Carolina bays, elliptical-shaped wetlands found on the southeastern United States Atlantic Coastal Plain, are utilized by numerous species of amphibians (Gibbons and Semlitsch 1982; Sharitz and Gibbons 1982) and are one of the most important natural amphibian breeding sites in that physiographic province. In South Carolina, most amphibians breed during winter or spring, when ephemeral sites are most likely to contain standing water, but some species breed during the summer or autumn. Amphibians that breed in Carolina bays have an aquatic larval stage that typically lasts a few weeks to a few months. Most then metamorphose and emigrate from the bays to surrounding terrestrial habitats, where they are often fossorial (Semlitsch 1981, 1983, 1985; Caldwell 1987). Adults generally mi-

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grate annually from their terrestrial home ranges to breeding ponds and back again (Patterson 1978; Semlitsch 1983, 1985; Pechmann and Semlitsch 1986). Individuals often return to the same breeding sites each year (Martof 1953; Shoop 1965; Gill 1978; Semlitsch 1981). Thus, Carolina bays have a vital influence on the amphibian fauna of surrounding ecosystems and their importance extends well beyond the high-water line.

Amphibian populations may be regulated in either the larval stage, the adult stage, or both (Wilbur 1980). Man's activities and management practices in the land surrounding wetlands (Bennett *et al.* 1980; Brown 1980) as well as in the wetlands themselves (Shoop 1960; Semlitsch 1987) can affect these dynamics. This report examines natural variation among species, sites, and years in the diversity and abundance of metamorphosing juveniles as well as variation resulting from the impacts of man. Post-larval population dynamics extrinsic to the wetlands, although important, are not addressed.

In addition to fecundity, many other factors can affect the number of successfully metamorphosing amphibian juveniles produced per breeding female each year. These include biotic factors such as competition and predation (Brockelman 1969; Wilbur 1972; DeBenedictis 1974; Heyer *et al.* 1975; Morin 1983; Wilbur *et al.* 1983), abiotic factors such as seasonal pond drying (Licht 1974; Shoop 1974; Semlitsch 1983, 1987), and interactions between drying and biotic factors (Smith 1983; Wilbur 1987). In this paper we focus primarily on the influence of hydroperiod, *i.e.*, the length of time a site contains standing water during a year, in three wetlands that serve as amphibian breeding sites. Data from a relatively undisturbed Carolina bay, a Carolina bay with a man-altered hydroperiod, and a man-made wetland are used to examine the correlations between the hydroperiod of a site each year and the diversity and abundance of metamorphosing juveniles at that site that year.

Methods

Study sites

The three wetlands are located within 5 km of each other on the U.S. Department of Energy's Savannah River Plant in Aiken and Barnwell Counties, South Carolina, U.S.A. The relatively undisturbed Carolina bay, Rainbow Bay, has an area of approximately 1 ha and a maximum water depth of 1.04 m. Two shallow ditches were dug through the bay before 1950, but these have filled in considerably and presumably have little effect on its current hydroperiod. The man-altered Carolina bay, Sun Bay, was originally about the same area and depth as Rainbow Bay. However, in 1978 prior to our study, a ditch was dug that partially drained Sun Bay and lowered the water level. The maximum depth of Sun Bay during the study period was 0.35 m. The third site was a man-made borrow pit, Bullfrog Pond, about 0.5 ha in size and with a maximum depth of 0.58 m. Bullfrog Pond was dug about 1955, and has since undergone secondary succession. Daily observations were made to record the dates of filling and drying and the duration each site contained standing water each year.

Vegetation was similar at all three sites. The deeper, center portions contained herbaceous plants such as bulrush (*Scirpus cyperinus*), knotweed (*Polygonum* sp.), cattail (*Typha latifolia*), rush (*Juncus repens*), spike rush (*Eleocharis* spp.), and grass (*Panicum* spp.). Shallower, less frequently inundated areas around the periphery were dominated by sweetgum (*Liquidambar styraciflua*) and buttonbush (*Cephalanthus occidentalis*). Deep, well-drained sandy soils planted with slash (*Pinus elliottii*) and loblolly (*P. taeda*) pines surrounded the sites. Wax myrtle (*Myrica cerifera*) and blackberry (*Rubus* sp.) were common in the understory around the edge of the sites.

Population monitoring

Amphibians migrating to and from the wetlands were captured using terrestrial drift fences with pitfall traps (Gibbons and Semlitsch 1982). A 50-cm-high aluminum flashing fence buried 10–15 cm in the ground completely encircled each site. Forty-liter pitfall traps were buried on each side of the fence at 10 m intervals. Traps were checked daily from 21 September 1978–30 September 1986 at

Rainbow Bay, 8 February 1979–24 June 1982 at Sun Bay, and 6 May 1980–18 August 1982 at Bullfrog Pond. All amphibians were identified, toe-clipped for future identification, and immediately released on the opposite side of the fence.

For most species this method provided a nearly complete census of the adults that entered each site every year to breed and of the number of larvae that successfully metamorphosed to the juvenile stage and emigrated to terrestrial habitats. Individuals of some species sometimes jumped or climbed over the fences (Gibbons and Semlitsch 1982). Trespass rates were probably greatest for climbing treefrogs (*Hyla* spp.) and large frogs such as bullfrogs (*Rana catesbeiana*) and Southern leopard frogs (*Rana utricularia*). Even for these species, however, few juveniles were able to cross the fence undetected. Trespass rates probably did not differ significantly among sites and years. Only one amphibian species found in the study areas, the lesser siren (*Siren intermedia*), is aquatic throughout its life cycle and was therefore not sampled by our terrestrial drift fences.

Statistical analyses

Data from each year at each site were treated as independent observations. Population counts were log-transformed. All analyses were performed using SAS® (SAS Institute Incorporated 1985). For the community-level analyses we first defined a hydrological year which differed from the calendar year. One site (Rainbow Bay) often filled in December and held water into the following calendar year. Any amphibian eggs and larvae present during December contributed to the next year's cohort of metamorphosing juveniles if they survived. December was therefore included with the following calendar year in hydroperiod counts. We calculated the Pearson product-moment correlation, pooling all sites, between the hydroperiod of a site and the total number of metamorphosing juvenile amphibians (all species combined) produced at that site during that year. The correlation between hydroperiod and species richness of juvenile amphibians was similarly calculated.

In addition to the community-level analyses, we performed separate multiple regression analyses on data for one common anuran species, the ornate chorus frog (*Pseudacris ornata*), and the most common salamander species, the mole salamander (*Ambystoma talpoideum*). The number of metamorphosing juveniles produced at each site each year was treated as the dependent variable. The hydroperiod of a site and the number of females of that species that migrated to the site to breed that year were used as independent variables. A dummy variable for site was added to the model to factor out any differences among sites other than those in hydroperiod. The Pearson product-moment correlation between the two continuous independent variables, hydroperiod and number of breeding females, was calculated for both species.

We defined an appropriate hydrological year for calculating hydroperiod for each species, *i.e.*, that part of the year that oviposition and larval development has been observed to occur at these sites. This was 1 January through the date of first drying for *A. talpoideum*, and 1 January through either first drying or 30 June, whichever came first, for *P. ornata*. Similarly, adults of these species that migrate to their breeding site from October to December contribute to the next calendar year's cohort of metamorphosing juveniles. These adults were therefore counted with the following calendar year's breeding population to define an appropriate breeding year. Bullfrog Pond data from 1980 could not be used in the multiple regressions because population monitoring was begun too late in the breeding year to obtain estimates of breeding population sizes of *A. talpoideum* and *P. ornata*.

Results

Hydroperiod

Sites filled with water each winter (December–February) and dried during the spring or summer (April–September). Dates of filling and drying varied considerably among sites and years, depending on rainfall, temperature, and site characteristics (Table 1). Rainbow Bay (the undisturbed Carolina

Table 1. Dates of filling and drying and the number of days each site contained standing water each year, counted from 1 December of the previous calendar year through 30 November.

		1979	1980	1981	1982	1983	1984	1985	1986
Rainbow Bay	Date filled	8 Feb.	1 Dec.	12 Feb.	1 Jan.	10 Dec.	20 Dec.	6 Feb.	1 Dec.
	Date dried	3 Aug.	16 June	7 May	6 July	11 July	27 Sept.	4 Apr.	24 Apr.
	Date refilled	6 Sept.			10 July				
	Date redried				14 Sept.				
	Days containing water	263	198	85	254	214	282	58	145
Bullfrog Pond	Date filled		5 Jan.	20 Feb.	1 Jan.				
	Date dried		1 June	5 May	12 June				
	Days containing water		149	75	163				
Sun Bay	Date filled	8 Feb.	5 Jan.	12 Feb.	1 Jan.				
	Date dried	6 June	15 May	5 May	15 May				
	Days containing water	115	132	83	135				

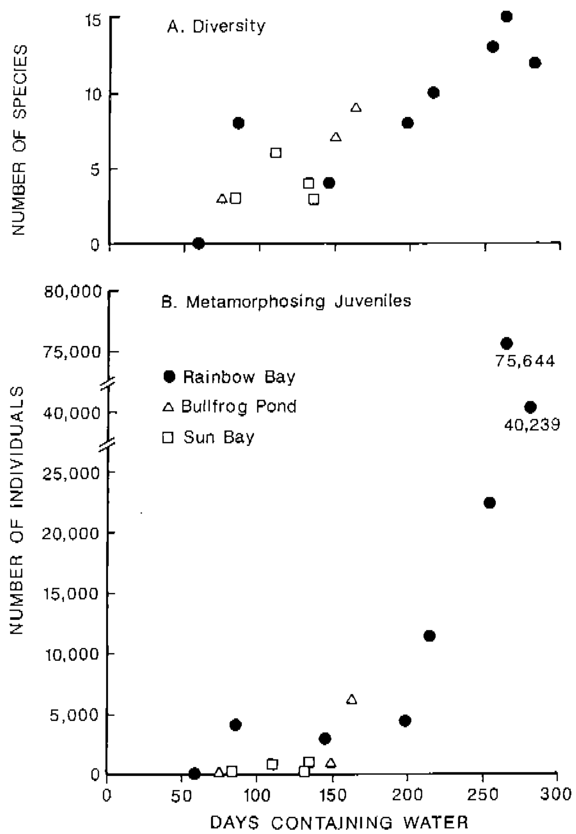

Fig. 1. Relationship between (A) number of species and (B) total number of individuals (all species combined) of metamorphosing juvenile amphibians produced at each site each year, and the number of days the site held water that year. Each data point represents one year at one site.

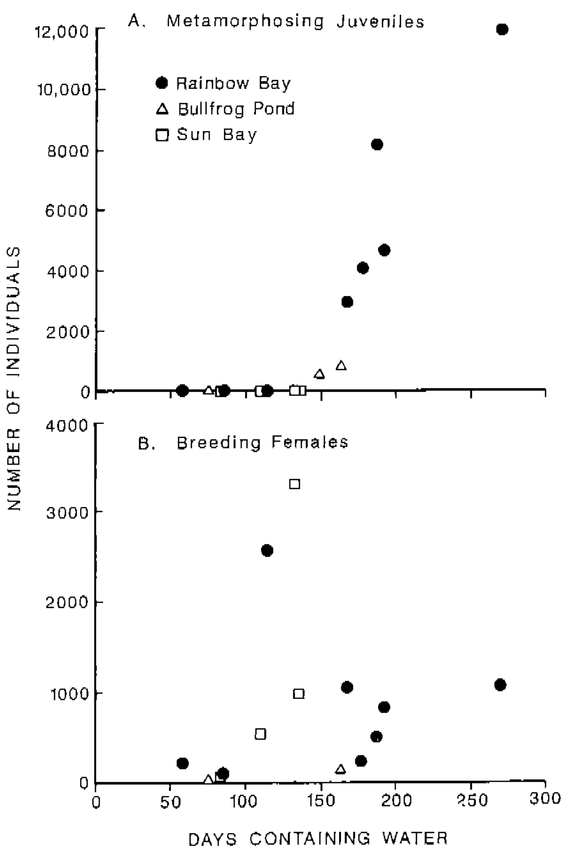

Fig. 2. Relationship between (A) number of juvenile *Ambystoma talpoideum* produced and (B) the number of breeding female *A. talpoideum* at each site each year, and the number of days the site held water that year from 1 January through first drying. Each data point represents one year at one site.

bay) held water for a longer period of time each year than Sun Bay (the ditched Carolina bay). Bullfrog Pond (the man-made wetland) was usually intermediate. However, the variation in hydroperiod at Rainbow Bay over the eight years it was studied was greater than the variation among sites in any particular year. Rainbow Bay held water for only 58 days in 1985, when it dried on 4 April, but held water for 282 days in 1984, when it did not dry until 27 September. Rainbow Bay dried, then refilled for an extended period in both 1979 and 1982 (Table 1). Once Bullfrog Pond and Sun Bay dried, they did not refill again until the next year during our study.

Community-level relationships

Most of the five salamander species and 11 anuran (frog and toad) species bred at each site each year, although breeding population sizes varied (see Appendix). The number of species that successfully produced any juveniles at each site in a given year was positively correlated with hydroperiod ($r = 0.88$, $p < 0.0001$; Fig. 1A), as was the total number (all species combined) of amphibian juveniles ($r = 0.84$, $p < 0.0001$; Fig. 1B). More juveniles of more species typically metamorphosed at Rainbow Bay than at Bullfrog Pond, and at Bullfrog Pond than at Sun Bay, following the hydroperiod rankings. The range of variation in amphibian recruitment observed at Rainbow Bay over eight years was greater than the variation observed among sites during the four years that other sites were also studied. No amphibian juveniles were produced at Rainbow Bay in 1985, whereas 75,644 individuals of 15 species were produced there in 1979, and 40,239 individuals of 12 species in 1984.

Examples of population-level relationships

Data for the most abundant salamander species, *Ambystoma talpoideum*, showed that past a threshold amount of time, the number of juveniles that metamorphosed generally increased with hydroperiod, the number of days a site held water during the oviposition and larval development period (Fig. 2A). No juvenile *A. talpoideum* were produced during two of eight years at Rainbow Bay, one of three years at Bullfrog Pond, and all four study years at Sun Bay. Although breeding population sizes varied, at least some females (minimum $n = 28$, Bullfrog Pond 1981) entered each site each year to breed (Fig. 2B). The two continuous independent variables used in the multiple regression, hydroperiod of a site and the number of breeding females, were not significantly correlated ($r = 0.47$, $p = 0.0922$). The multiple regression model explained 90% of the variance in the total number of juvenile *A. talpoideum* produced at each site during each year. Hydroperiod of a site was a significant predictor of juvenile number, but the number of breeding females and site were not (Table 2).

Compared with the salamander, numbers of metamorphosing *Pseudacris ornata* (Fig. 3A), a

Table 2. Summary of multiple regression analyses for the number of juveniles produced at each site during each year of study for two species, using site, the number of days a site contained water during their oviposition and larval development period, and the number of breeding females as independent variables. Values are for Type III sums of squares.

	Complete model	Site (dummy variable)	Days	Females
A. talpoideum	$F = 19.32$ $p = 0.0002$	$F = 3.81$ $p = 0.0632$	$F = 43.73$ $p < 0.0001$	$F = 3.30$ $p = 0.1025$
P. ornata	$F = 4.01$ $p = 0.0387$	$F = 0.00$ $p = 0.9968$	$F = 1.32$ $p = 0.2810$	$F = 8.79$ $p = 0.0159$

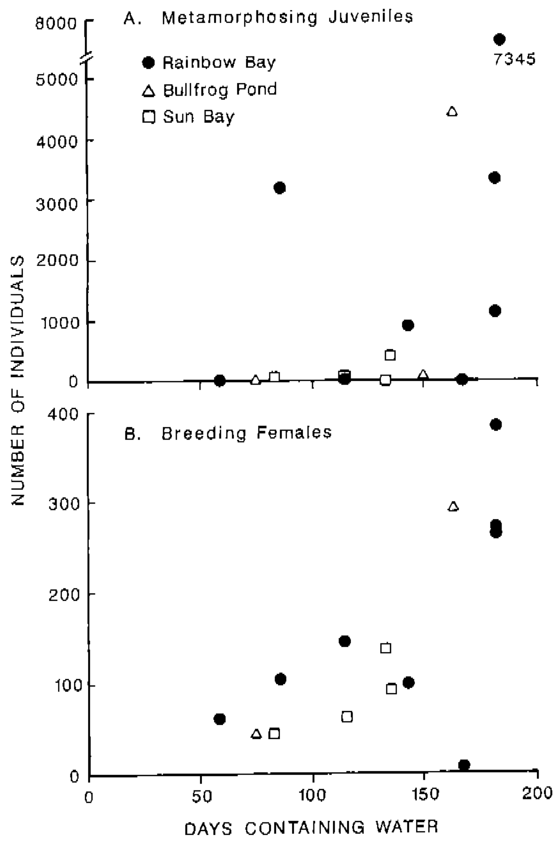

Fig. 3. Relationship between (A) number of juvenile *Pseudacris ornata* produced and (B) the number of breeding female *P. ornata* at each site each year, and the number of days the site held water that year from 1 January through 30 June or first drying. Each data point represents one year at one site.

common frog species, were not as strongly related to hydroperiod. Some *P. ornata* metamorphosed at each site each year it was studied except during 1980 and 1985 at Rainbow Bay. The number of breeding female *P. ornata* (Fig. 3B) was not significantly correlated with hydroperiod ($r = 0.42$, $p = 0.1365$). The multiple regression model explained 64% of the variance in numbers of metamorphosing *P. ornata*. The number of breeding female *P. ornata* was a significant predictor of the number of juveniles produced at each site during each year, but hydroperiod and site were not (Table 2).

Two summer-breeding species, the Eastern narrow-mouthed toad, *Gastrophryne carolinensis*, and the pine woods treefrog, *Hyla femoralis*, deserve special mention. They successfully produced juveniles only after a site dried, then refilled for a number of weeks during their breeding season, as did Rainbow Bay in 1979 and 1982 (1979 juveniles: $n = 6$ *G. carolinensis*, $n = 13$ *H. femoralis*; 1982 juveniles: $n = 185$ *G. carolinensis*, $n = 20$ *H. femoralis*). No juveniles of these species were produced in other years at Rainbow Bay or any year at Bullfrog Pond and Sun Bay, when the sites held water continually during the summer or dried before summer.

Discussion

Amphibian larvae must grow to a critical minimum body size before they can metamorphose to the terrestrial, juvenile stage (Wilbur and Collins 1973). If a site dries before an individual reaches this threshold size, a larva will desiccate (Shoop 1974, Smith 1983, Semlitsch 1983, 1987), or become easy prey for predators such as raccoons and birds (Stangel 1983). In 1985 Rainbow Bay dried on 4 April before any amphibians could metamorphose and emigrate from the site. The longer Rainbow Bay, Bullfrog Pond, and Sun Bay held water each year, the greater the number of amphibians that were able to metamorphose, and the greater the number of species for which at least one juvenile metamorphosed. Very early drying denied later-breeding species such as the Southern toad (*Bufo terrestris*) the opportunity to even oviposit at a site. Salamanders such as *Ambystoma talpoideum* require a longer aquatic larval period than do most species of anurans, including *Pseudacris ornata*, although there can be considerable variation among individuals within a population. Hydroperiod was a better predictor of the number of metamorphosing juveniles for *A. talpoideum* than for *P. ornata* because hydroperiod was more often limiting for the former at these sites.

Ditching reduced the number of days that Sun Bay held water each year, and thereby reduced the diversity and abundance of metamorphosing juvenile amphibians. Some species, including *A. talpoideum*, will likely become extinct at Sun Bay due to lack of juvenile recruitment. Since *A. talpoideum* spend most of the year in terrestrial habitats as far as several hundred meters away from their breeding site (Semlitsch 1981), this loss may affect surrounding ecosystems as well. Species such as *P. ornata* that require a shorter larval development period probably can persist at Sun Bay in spite of the ditching, but population sizes may be reduced.

Bullfrog Pond was intermediate to Rainbow Bay and Sun Bay in terms of hydroperiod as well as in diversity and numbers of metamorphosing juvenile amphibians. Although dug originally as a borrow pit, Bullfrog Pond fortuitously provides amphibians with a man-made breeding site. This suggests that loss or degradation of breeding sites such as Sun Bay could be mitigated under certain conditions by building nearby replacement wetlands, as is sometimes required by law. If Bullfrog Pond had been dug larger and deeper, it would hold water longer each year and probably be more similar to Rainbow Bay in terms of juvenile amphibian production. However, since many amphibian species are philopatric, returning to the same breeding site year after year, colonization of new man-made wetlands may be slow. The degree of isolation from other similar sites can also affect the colonization rate of man-made habits by herpetofauna (Szaro and Belfit 1986).

Clearly, hydroperiod can influence the structure and dynamics of wetland amphibian communities. However, often factors not addressed in this paper may be equally or more important. Competition among amphibian larvae can reduce growth rates, prolong larval periods, and increase the chance that a larva will desiccate before it can metamorphose (Semlitsch 1987; Wilbur 1987). Predation can reverse the outcome of competition among larval amphibians (Morin 1983) or completely eliminate species from ponds (Smith 1983; Stenhouse 1985). Inasmuch as hydroperiod was presumably correlated with mean water depth, mean water volume, and mean area inundated at a site during the year, indirect effects of hydroperiod on mean larval densities or food resources may have been important, in addition to its direct effect on the amount of time available for egg and larval development.

Extrapolation of our data might lead one to conclude that permanent ponds provide the best amphibian breeding sites. However, because the number of predators, including other amphibians, insects, and particularly fish, is usually greater in permanent ponds and wetlands, these usually support a lower density and diversity of amphibians than ephemeral sites (Heyer *et al.* 1975; Wilbur 1984, personal observations). Ephemeral sites also are often more productive in terms of food resources for amphibians, as fluctuations in water level enhance primary productivity (Odum 1969).

Evidence for the interaction between hydroperiod and predation is suggested by our data for *Hyla femoralis* and *Gastrophryne carolinensis*. These two species successfully produced juveniles only when Rainbow Bay dried, then subsequently refilled, during their breeding season. Predation by insect and salamander larvae or desiccation probably eliminated their eggs and larvae in other years at Rainbow Bay and all years at other sites. When a pond dries, these aquatic predators are killed or forced to metamorphose. *Hyla femoralis* and *G. carolinensis* were most likely able to breed successfully after Rainbow Bay refilled because of this reduction in predators.

Although hydroperiod is only one of many factors affecting wetland amphibian communities, it is especially important from a management viewpoint since man's activities often alter wetland hydrologic cycles. Increasing or decreasing the number of days a wetland holds water, or the number of times it dries then refills, could increase or decrease the number and species diversity of amphibians in and around a wetland. Ditching reduced the diversity and number of metamorphosing juvenile amphibians at Sun Bay, but turning it into a permanent pond might have been equally detrimental, particularly if it were then colonized by fish. Heyer *et al.* (1975) and Wilbur (1984) predicted that tadpole species diversity would be highest at intermediate values along a pond ordination axis that included pond size, duration, primary productivity, and structural complexity. A number of authors have suggested that diversity or productivity in many different communities is maximized at intermediate levels of disturbance, *e.g.* Levin and Paine (1974), Gibbons (1976), Connell (1978), and Odum *et al.* (1979). If pond drying is viewed as a disturbance, these models are similar to those of Heyer *et al.*

(1975) and Wilbur (1984) and may be generally applicable to amphibian communities.

Hydroperiod can affect the size at and time of metamorphosis in amphibians, in addition to its effects on the diversity and number of metamorphosing individuals (Semlitsch 1987; Semlitsch *et al.* 1988). Size at and time of metamorphosis can in turn affect adult fitness-related traits, such as age and size at first reproduction (Smith 1987; Semlitsch *et al.* 1988).

Finally, the high variation among years in numbers of metamorphosing juvenile amphibians at a single site deserves emphasis. About two-thirds of the *A. talpoideum* and *P. ornata* juveniles produced at Rainbow Bay during the eight years of study were produced during only two of those years. A two or three year study of a wetland amphibian population could thus lead one to mistake natural fluctuations in numbers for a long-term population decline. Variation in hydroperiod and both diversity and numbers of metamorphosing juvenile amphibians at Rainbow Bay over eight years was greater than the differences among sites in any single year. Therefore any short-term comparison among sites could be very misleading. Separating natural variation from changes due to man's activities, *e.g.* ditching, can be a difficult task. Long-term field studies coupled with well-designed, controlled experiments are indispensable to an understanding of population and community dynamics, the impacts of man, and how best to preserve species diversity in wetland amphibian communities.

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Appendix

List of amphibian species that bred at Rainbow Bay, Sun Bay, and Bullfrog Pond on the Savannah River Plant, South Carolina, U.S.A., during the study.

Anura	Frogs and toads
Bufo terrestris	Southern toad
Gastrophryne carolinensis	Eastern narrow-mouthed toad
Hyla crucifer	spring peeper
Hyla femoralis	pine woods treefrog
Hyla gratiosa	barking treefrog
Pseudacris nigrita	Southern chorus frog
Pseudacris ornata	ornate chorus frog
Rana catesbeiana	bullfrog
Rana clamitans	bronze frog
Rana utricularia	Southern leopard frog
Scaphiopus holbrooki	Eastern spadefoot toad
Caudata	Salamanders
Ambystoma opacum	marbled salamander
Ambystoma talpoideum	mole salamander
Ambystoma tigrinum	tiger salamander
Eurycea quadridigitata	dwarf salamander
Notophthalmus viridescens	red-spotted newt