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CHAPTER 9

Structure and Dynamics of an Amphibian Community

Evidence from a 16-Year Study of a Natural Pond

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I. INTRODUCTION

We examined 16 years of census data on the amphibians in a natural pond ecosystem under the paradigm that competition, predation, and disturbance are interacting mechanisms regulating the abundance and distribution of species at the local level. Although much evidence has been accumulated over the last

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25 years on the effects of each of these mechanisms and their interactions on particular species, few studies of amphibians have examined them within a whole natural community (but see Smith, 1983; Hairston, 1986). Most of our knowledge comes from detailed experimental studies of single or mixed species in cages or artificial pond communities (e.g., Brockelman, 1969; Jaeger, 1971; Wilbur, 1972, 1987; Morin, 1981, 1983a, 1987; Travis *et al.*, 1985a,b; Southerland, 1986; Van Buskirk, 1988; Wilbur and Fauth, 1990). Such experimental studies have provided a wealth of information on processes that may structure amphibian communities, and which can be used to generate a set of predictions to be tested in natural communities.

Numerous amphibian species use temporary ponds for a portion of their complex life cycle, primarily for mating, oviposition, and larval growth. During the nonbreeding season, most pond-breeding amphibians live in the terrestrial habitat surrounding a pond. In a typical year, adults migrate to the pond during favorable weather conditions to breed. Mating and oviposition usually occur in the pond, and then adults return to their terrestrial habitat. After hatching, the aquatic larvae feed, grow, and develop until metamorphosis, after which they emigrate as juveniles to terrestrial habitats.

Because of the high diversity of species and the high density of larvae in many ponds, species interactions and density dependence are likely to be important in population and community dynamics (Wilbur, 1980). Several excellent field studies have clearly demonstrated the primacy of density-dependent growth and survival in larval amphibians (e.g., Smith, 1983; Petranka and Sih, 1986; Petranka, 1989; Scott, 1990, 1994; Van Buskirk and Smith, 1991), yet there is little information on whether population regulation occurs only in the larval stage, the adult stage, or both and in which stages community structure is determined (Istock, 1967; Wilbur, 1980, 1996).

A species' use of ponds is constrained by the relationship between characteristics of the pond related to hydrological dynamics and by species characteristics such as physiological tolerances, genetic ability for local adaptation, and life-history requirements. Heyer *et al.* (1975) and Wilbur (1980, 1984) suggested that ponds that are extremely ephemeral (<30 days) or permanent (>1 year) are used by fewer species of amphibians than ponds with intermediate hydroperiods. If rapid drying and pond permanence are considered as two ends of a disturbance continuum, this is tantamount to suggesting that species diversity is maximized at intermediate levels of disturbance (Levin and Paine, 1974; Gibbons, 1976; Connell, 1978; Odum *et al.*, 1979). Pond drying may be viewed as an extreme disturbance for larval amphibians, as larvae may be killed if the pond dries before metamorphosis can occur. Likewise, pond permanence also severely affects larval amphibians by permitting many predators, such as fishes, to persist. In addition, ponds vary in hydroperiod not only across a spatial landscape but also temporally, so that species must cope with unpredictable annual fluctuations within a pond. Limitation on the use of a pond, once colonized, is determined by synchrony between the availability of water and the season of reproduction. Following successful mating and oviposition, species' characteristics such as larval requirements for food, temperature tolerance, predator avoidance, and length of the larval period all interact to determine larval success along the gradient of pond hydroperiod.

In communities of pond-breeding amphibians, predation and competition interact within the context of a disturbance gradient related to pond hydroperiod (Morin, 1981, 1983b; Smith, 1983; Wilbur, 1987; Werner and McPeek, 1994; Skelly, 1995). Because all salamanders (larval and adult) are carnivorous and frequently occur at high densities, they can exert strong predation pressure within the amphibian community (e.g., Morin, 1981), especially on small herbivorous tadpoles. Predatory salamanders can persist only in ponds with long hydroperiods, and predatory fish only in permanent ponds (occasionally they colonize temporary ponds after flooding). These predators can reduce or completely eliminate other species of salamanders or anurans with small vulnerable larvae or those without effective skin secretions or behaviors that reduce the chance of being eaten (e.g., Morin, 1986; Kats *et al.*, 1988; Lawler, 1989). In ponds with short hydroperiods that lack predatory fish or salamanders, explosive breeding species produce large numbers of fast developing larvae that compete for limited food through exploitative and interference competition, sometimes even switching from herbivory to carnivory and cannibalism (Collins and Cheek, 1983; Newman, 1989; Pfennig, 1990). Competition for food reduces growth and developmental rates, increasing the length of the larval period, and hence vulnerability to desiccation in a drying pond or exposure to predators in more permanent ponds (Wilbur, 1987, 1988; Wilbur and Fauth, 1990). Reduced growth and developmental rates also reduce body size at metamorphosis, which in turn may increase age at first reproduction and decrease size at first reproduction, survival to first reproduction, and fecundity (Berven and Gill, 1983; Smith, 1987; Berven, 1988, 1990; Semlitsch *et al.*, 1988; Scott, 1994).

Interactions between predation and competition have been demonstrated experimentally. For example, Morin (1981) showed that, in the absence of salamander predators, some anuran species whose larvae forage efficiently can outcompete other species and dominate in numbers. In the presence of salamander predators, however, competitively superior species may be preferentially eaten, allowing other competitively inferior species to increase in relative abundance. Wilbur (1987) also demonstrated that predation can ameliorate the effects of competition at high densities by removing larvae from the community and lowering effective density, thus allowing survivors to grow more rapidly and metamorphose before ponds dry.

We used the general results of the previously cited experimental studies on competition, predation, pond drying, and their interactions to generate a set of predictions. We then used the data we accumulated from a natural amphibian community during the past 16 years to examine these predictions:

1. Variation in breeding population sizes is related to the effects of environmental variation both on breeding activity and on past juvenile recruitment.
2. There are long-term trends in the breeding population sizes of some species and hence in community structure.
3. Pond hydroperiod is highly variable but is a significant predictor of the total numbers of metamorphosing juvenile amphibians and their species diversity.
4. Within each group of amphibians (salamanders and anurans), the density of competitors (potentially also predators, in the case of salamanders) is a significant predictor of the number of metamorphosing juveniles per breeding female.
5. The density of salamanders (predators) is a significant predictor of the number of metamorphosing anurans (prey) per breeding female.

Each of these predictions is related to general questions and themes of this volume. Predictions 1, 2, and 3 address the question of whether species composition and diversity change over time in the community. Predictions 1, 3, 4, and 5 are related to whether changes in the community can be predicted from changes in the environment. Predictions 4 and 5 address whether the effects of density compensation and predation can be detected by a correlative analysis of changes over time. In addition to the results of these predictions, we will discuss the consequences of our results for community structure and organization.

II. STUDY SYSTEM

A. The Pond

The study was conducted for 16 years (1979–1994) at Rainbow Bay in Barnwell County, South Carolina, on the U.S. Department of Energy's Savannah River Site. Rainbow Bay is a relatively undisturbed freshwater wetland known as a Carolina bay (Sharitz and Gibbons, 1982; Ross, 1987). Carolina bays are natural elliptical depressions that vary in size (long axis extremes from 50 m to 8 km; Sharitz and Gibbons, 1982) and in the degree to which they retain water. They serve as the primary breeding sites for many species of amphibians indigenous to the southeastern Atlantic Coastal Plain. Most Carolina bays are not connected to stream systems and thus are filled by rainfall and ground water recharge.

Rainbow Bay is a temporary pond with a surface area of approximately 1 ha and a maximum water depth of 1.04 m. The low, center portions of the pond are vegetated with rush (*Juncus repens*), spike-rush (*Eleocharis* sp.), bulrush (*Scirpus cyperinus*), panic grass (*Panicum verrucosum*), and knotweed (*Polygonum* sp.). Several pond cypress (*Taxodium ascendens*) also occur near the center. The periphery and higher portions of the pond are vegetated by buttonbush (*Cephalanthus occidentalis*), sweetgum (*Liquidambar styraciflua*), black gum (*Nyssa biflora*), water oak (*Quercus nigra*), Darlington oak (*Q. laurifolia*), and red maple (*Acer rubrum*). The understory around the edge of the pond consists of wax myrtle (*Myrica cerifera*), greenbriers (*Smilax* spp.), and blackberry (*Rubus* sp.). Prior to 1951, Rainbow Bay was surrounded by agricultural fields and pastures, but the area is now dominated by slash pine (*Pinus elliottii*) and loblolly pine (*P. taeda*) plantations (35–40 years old). This study site is not unusual in any obvious manner relative to other amphibian breeding ponds of its size in this region (Sharitz and Gibbons, 1982), except for its relatively undisturbed condition and protected status during the past 40 years. The 27 species of amphibians we observed in our study are representative of the diversity found in southern regions of the U. S. For example, Dodd (1992) collected 16 species of amphibians during a 6-year study at a small pond in the north Florida sandhills, and Wiest (1982) found 15 species of anurans during just one year in a series of temporary ponds in east-central Texas.

B. Sampling Technique

We sampled the amphibians migrating to and from Rainbow Bay using a terrestrial drift fence with pitfall traps (Gibbons and Bennett, 1974; Shoop, 1974; Gill, 1978). The pond was encircled by a drift fence of aluminum flashing (440 m long, 50 cm high, buried 10–15 cm deep in the ground). Pitfall traps (40-liter buckets) were buried inside and outside the fence flush to the ground and next to the fence at 10-m intervals (Gibbons and Semlitsch, 1982). These traps were checked daily from 21 September 1978 through 1 July 1994. All amphibians were identified, toe-clipped for future identification, and immediately released on the opposite side of the fence. For many species, this sampling technique provided a nearly complete annual census of the number of breeding adults and of juvenile recruitment. Adults of species that are proficient climbers (e.g., treefrogs) or jumpers (e.g., bullfrogs) could trespass the fence without being captured (Gibbons and Semlitsch, 1982; Dodd, 1991; R.D.S., J.H.K.P. personal observation); however, few juveniles of these species were able to cross the fence undetected. Species for which nearly all adults trespassed the drift fence were excluded from data analyses. For the remaining species, we assumed that variation among years in trespass rates was random and therefore unlikely to systematically bias annual comparisons or to create biased trends over time.

C. Data and Statistical Analyses

Census data for 13 amphibian species and hydrological data for the pond (Tables I and II) were used in this study. The other 14 species collected at Rainbow Bay were excluded from the data analyses because they reproduced too infrequently (or not at all) at the study site, were represented only by a few adults, or could not be censused by the drift fence. We treated data for each year as an independent observation and used years as replicates in all analyses. Data for juvenile recruitment each year were independent because the pond dried annually, which separated larval dynamics into discrete episodes. Data for breeding population sizes were not strictly independent because some individuals were present during more than one year, and because numbers in one year may be affected (positively or negatively) by the numbers available to produce offspring in previous years. Hydrological dynamics in each year also may be influenced by hydrological dynamics in previous years. In addition, temporal autocorrelation of environmental variables such as rainfall and temperature may compromise the independence of breeding population sizes and hydrological data among years.

We defined the amphibian reproductive year as 1 September through 31

TABLE I The 13 Species of Amphibians Breeding at Rainbow Bay Selected for the Study

Species	Breeding season	Females		Metamorphs	
Caudata					
Ambystoma opacum	Sept.–Dec	3,426	(.08)	27,908	(.13)
Ambystoma talpoideum	Sept.–Apr	10,638	(.25)	43,528	(.20)
Ambystoma tigrinum	Nov.–Mar	362	(.01)	2,536	(.01)
Eurycea quadridigitata	Aug.–Jan	7,282	(.17)	3,902	(.02)
Notophthalmus viridescens	Sept.–May	10,833	(.26)	43,208	(.20)
Anura					
Bufo terrestris	All year	816	(.02)	693	(<.01)
Gastrophryne carolinensis	May–Oct	3,072	(.07)	2,930	(.01)
Pseudacris crucifer	Nov–Apr	2,499	(.06)	9,245	(.04)
Pseudacris nigrita	Nov–Apr	318	(.01)	237	(<.01)
Pseudacris ornata	Nov–Apr	1,592	(.04)	19,182	(.09)
Rana clamitans	All year	106	(<.01)	2,214	(.01)
Rana utricularia	All year	605	(.01)	56,225	(.26)
Scaphiopus holbrooki	All year	197	(<.01)	3,483	(.02)
Totals (all species)		41,776		216,251	

Note. Breeding season of each species was defined by the earliest and latest months breeding adults were captured during the study period. Relative abundance according to the number and the proportion (in parentheses) of captures over 16 years is indicated for all 13 species. The total of all species includes six uncommon species that represent a combined total of less than 1%.

TABLE II Dates of Filling and Drying and the Number of Days That Rainbow Bay Contained Standing Water, i.e. the Hydroperiod, for Each Year

	Year															
	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
Date filled	8 Feb	6 Sep	12 Feb	1 Jan	10 Dec	20 Dec	6 Feb	30 Nov	12 Dec	24 Apr	9 Apr	8 Dec	11 Oct	29 Dec	22 Nov	28 Jan
Date dried	3 Aug	16 Jun	7 May	6 Jul	11 Jul	27 Sep	4 Apr	24 Apr	3 Jun	26 Apr	28 Apr	4 Apr	5 Nov	18 May	25 Jun	17 May
First hydroperiod	177	285	85	187	214	283	58	146	174	3	20	118	391	142	216	110
Date refilled	6 Sep	18 Jun	8 Jun	10 Jul				20 Aug	19 Jun		2 May	22 Aug		9 Jun		
Date redried		27 Jun	22 Jun	14 Sep				24 Aug	25 Jun		5 May	21 Sep		8 Jul		
Second hydroperiod	30	10	15	67				5	7		4	31		30		

Note. To correspond with the amphibian reproductive year, fillings that occurred after 1 September were included with the following calendar year. The period 6 September–5 October 1979 was included in both the 1979 and the 1980 hydroperiods because the pond held water continuously from 6 September 1979 to 1980 and was used by both summer- and autumn-breeding species during this period.

August of the following calendar year based on the natural phenology of species. Rainbow Bay filled and dried more than one time during some years. To account for the effect of hydrological dynamics on all 13 species, we calculated the first, second, and total hydroperiods for each year (Table II). First hydroperiod was defined as the number of days the pond held water (i.e., visible standing water in the center of the basin) from date of first filling following 1 September to the date of first drying. Second hydroperiod was defined as the number of days from second filling to second drying. Total hydroperiod was defined as the sum of first and second hydroperiods. We used Pearson product-moment correlations to examine the relationships between rainfall and first, second, and total hydroperiods. Correlations were also performed between total hydroperiod and the total number of metamorphosing juveniles as well as their species richness. Data used in the Pearson product-moment calculations were log-transformed.

The influence of rainfall during a species breeding season and the number of metamorphosed juveniles in previous years on the number of breeding females was analyzed using simple and partial Spearman's rank correlations. For most species, the number of metamorphs in the previous two years was used in these correlations because most individuals reached reproductive maturity and could participate in breeding activities at two years of age. However, if most metamorphs matured at one year of age, then only metamorphs in the previous year were used. Kendall's partial rank correlation between female breeding population size and year was calculated to test for trends in breeding population sizes over time for each species, after correcting for rainfall during the species' breeding season. Significance levels for the Kendall's partial correlations were calculated from the quantile estimates of Maghsoodloo (1975).

Potential predictors of the number of metamorphosed juveniles produced per breeding female were analyzed separately for each species using a Tobit regression model for left-censored data (Tobin, 1958; SAS Institute, Inc., 1990). The Tobit model was used because the number of juveniles produced per female was zero (left-censored) for many observations. For salamanders, both simple and partial regression coefficients were calculated using first hydroperiod, initial larval density of the species, and pooled initial larval density of all other salamanders (potential competitors or predators) as predictor variables. For anurans, simple and partial regression coefficients were calculated using first hydroperiod, initial larval density of the species, pooled initial larval density of all other anurans (potential competitors), and pooled initial larval density of all salamanders (potential predators) as predictor variables.

In 1988 and 1989, first hydroperiod at Rainbow Bay was only 3 days and 20 days, respectively. Little or no breeding occurred during these 2 years; therefore they were deleted from the Tobit regression analyses. We assumed that in other years all females present at the pond oviposited. For anurans, the initial density of larvae could only be approximated by the density of breeding females (total number divided by the volume of the pond) because average fecundity was not available for each species. For salamanders, larval density was calculated from the number of breeding females of each species multiplied by their average estimated egg number and then divided by the volume of the pond. We used the volume of the pond on the same date each year (1 March) because of the difficulty of standardizing larval density at the same stage of development for all species. This procedure may have under- or over-estimated the initial larval densities of some species and hence the impact of density in our analyses of species interactions. *Gastrophryne carolinensis* was excluded from Tobit analyses because its larvae were not consistently present in the pond at the same time as those of the other anurans and salamanders analyzed. The number of juvenile *B. terrestris, P. nigrita,* and *S. holbrooki* produced per breeding female was not analyzed by Tobit regression because these species produced juveniles in too few years (2–3) for the regressions to be informative. These three species, however, were included in the calculation of heterospecific anuran density for analyses of other species.

III. HYDROPERIOD

A. Annual Dynamics

The dates of filling and drying of Rainbow Bay, and hence hydroperiod, varied greatly from year to year (Table II). First filling most often occurred in the winter between November and February and corresponded to the peak reproductive season for many species of amphibians. The earliest date of filling during the study was 6 September (1979, following a hurricane) and the latest was 24 April (in 1988). There was a strong positive relationship between cumulative annual rainfall (1 September–31 August) and first hydroperiod ($r = 0.76$, $P = 0.0006$, $n = 16$) as well as total hydroperiod ($r = 0.57$, $P = 0.02$, $n = 16$). The second hydroperiod was not significantly correlated with cumulative annual rainfall ($r = -0.16$, $P = 0.5594$, $n = 16$). Second fillings occurred when heavy rains fell during the summer (e.g., 1990), or when moderate rains fell shortly after the pond dried for the first time (e.g., 1982).

B. Relationship to Species Diversity and Reproductive Success

The number of species that produced metamorphosed juveniles increased significantly each year with the total hydroperiod ($r = 0.84$, $P < 0.0001$, $n = 16$,

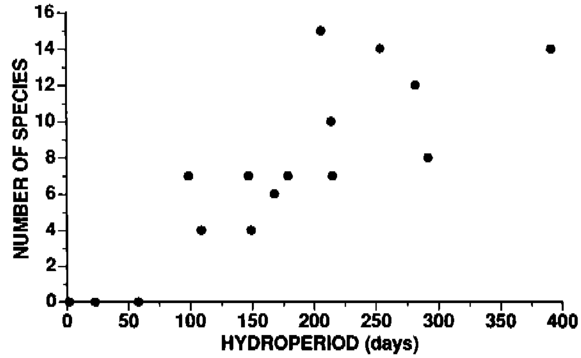


FIGURE 1. Relationship between the diversity of metamorphosing juvenile amphibians and total hydroperiod at Rainbow Bay. Each data point represents 1 year from 1979 to 1994.

Fig. 1). In addition, the total number of larvae metamorphosing (pooling all species) increased directly with total hydroperiod at Rainbow Bay ($r = 0.83, P < 0.0001, n = 16$, Fig. 2). Longer hydroperiods allowed a greater diversity of seasonally reproducing species to breed in the pond. Longer hydroperiods also permitted a greater number of larvae the opportunity to reach the critical size to initiate metamorphosis (Wilbur and Collins, 1973) and hence allowed more juveniles of more species to be recruited into terrestrial adult populations.

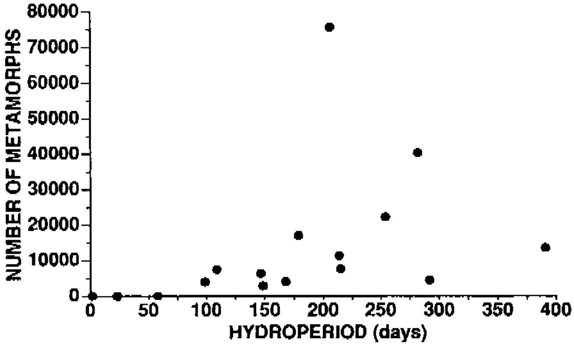


FIGURE 2. Relationship between the number of metamorphs of 13 amphibian species and total hydroperiod at Rainbow Bay. Each data point represents 1 year from 1979 to 1994.

IV. ANNUAL VARIATION IN BREEDING POPULATIONS

For each species, the number of breeding females varied by two or three orders of magnitude among the 16 years (Figs. 3 and 4). It is important to note that the drift fence with pitfall traps only captures those adults migrating to the pond to breed, which may not represent the entire adult population. Variation in breeding population sizes can result from the effects of climatic conditions on migratory activity, as well as from demographic factors (and fence trespass for some species). For some species, variation in breeding population size was related more to rainfall (a climatic factor) than to juvenile recruitment in the previous years (a demographic factor), whereas variation for other species was more related to juvenile recruitment (Table III). Breeding population size was significantly positively correlated with rainfall during the breeding season for two species of amphibians: the salamander *A. talpoideum* and the anuran *B. terrestris.* One additional species of salamander, *A. opacum,* also showed the same relationship after partial correlations were performed to remove the effects of the number of metamorphs produced in previous years (Table III). The partial correlation of rainfall and breeding population size was nearly significant ($P = 0.06$) for *A. tigrinum* and *S. holbrooki.*

We assume that rainfall affects the conditions available for some species to migrate successfully from the terrestrial environment to the pond and that more rainfall allows more individuals to reach the pond (Packer, 1960; Hurlbert, 1969; Gibbons and Bennett, 1974; Sinsch, 1990). For example, adult *A. talpoideum* migrate only at night and during or shortly after periods of rain; individuals do not migrate on nights without rain (Semlitsch, 1985a; Semlitsch and Pechmann, 1985). In addition, the positive correlation between rainfall and pond hydroperiod (Section III.A.) suggests that rainfall could provide amphibians with a predictive cue to the presence of water in the pond and to how long it will remain. Adults may forego breeding migrations if it is likely that there is no water in the pond or that the pond may dry before larvae are able to metamorphose. Climatic limitation was reflected more generally for other species by the observation that in the driest years (1981, 1985, 1988, and 1989) almost all species had few or no breeding females due to drought conditions (Table II, Figs. 3 and 4). The reduction of breeding females was unlikely an exclusive effect of mortality during these dry periods because large numbers of previously marked females were recaptured during the year or two following such droughts. This suggests that the reduction of breeding females is an effect of climatic limitation on migratory activity, or on food resources and the acquisition of energy for reproduction, or both.

The breeding population size of a species may vary widely due to fluctua-

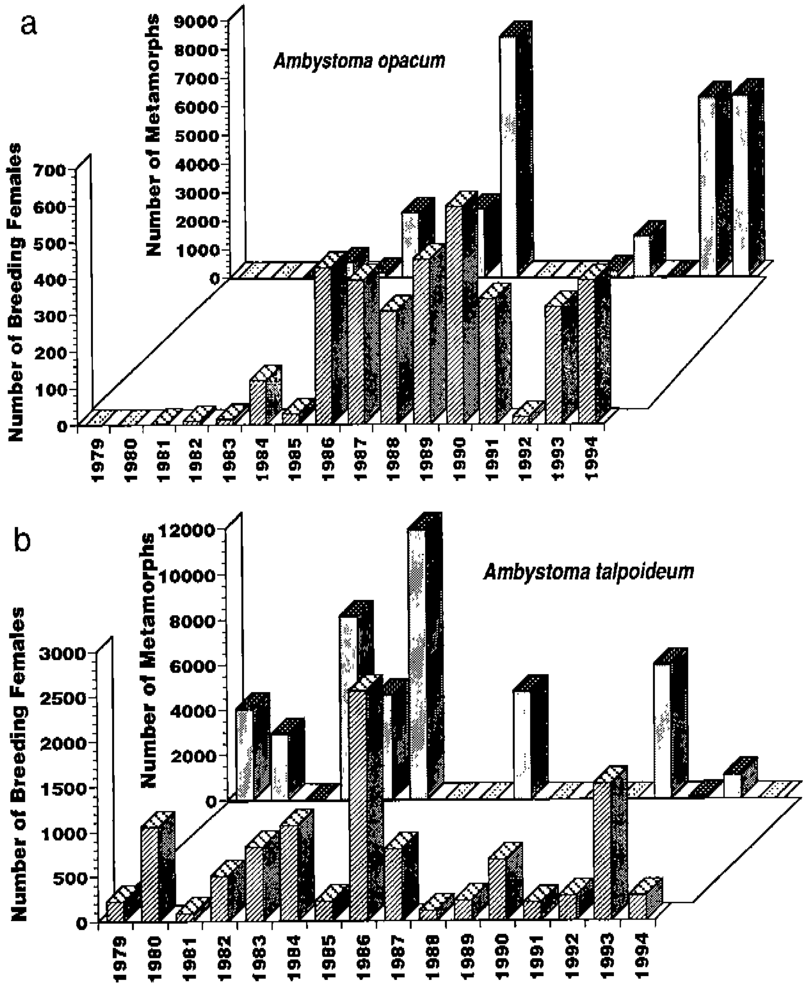
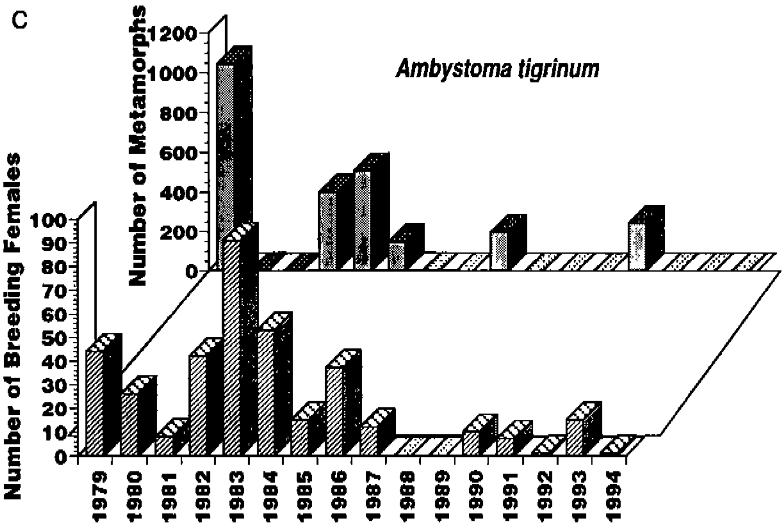


FIGURE 3. The annual numbers of breeding females and of metamorphosing juveniles for five species of salamanders ((a) *A. opacum*, (b) *A. talpoideum*, (c) *A. tigrinum*, (d) *E. quadridigitata*, and (e) *N. viridescens*) at Rainbow Bay. Bars represent the total numbers collected in pitfall traps at the drift fence for each year from 1979 to 1994.

tions in juvenile recruitment; if recruitment rate is high and variable relative to adult survival rate, terrestrial density dependence is weak, and population dynamics are determined at the local pond or are synchronous at nearby ponds from which individuals may immigrate. Past juvenile recruitment and breeding population sizes also may be strongly correlated because of long-term


c
Ambystoma tigrinum
Number of Metamorphs
0
200
400
600
800
1000
1200
Number of Breeding Females
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10
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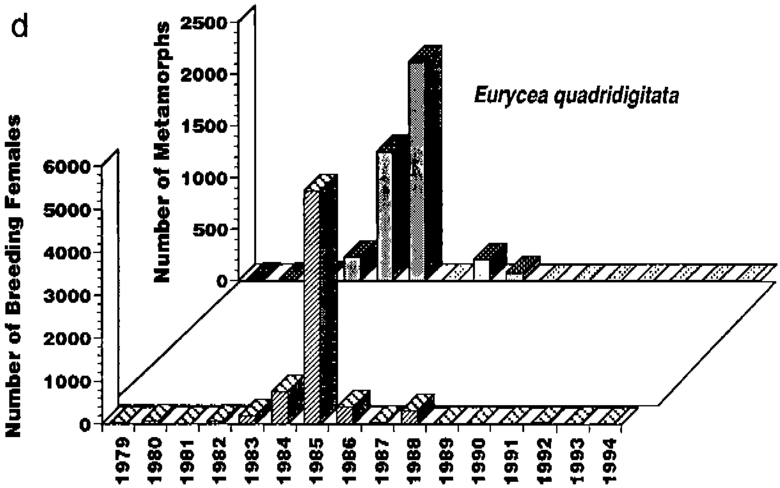
d
Eurycea quadridigitata
Number of Metamorphs
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500
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1500
2000
2500
Number of Breeding Females
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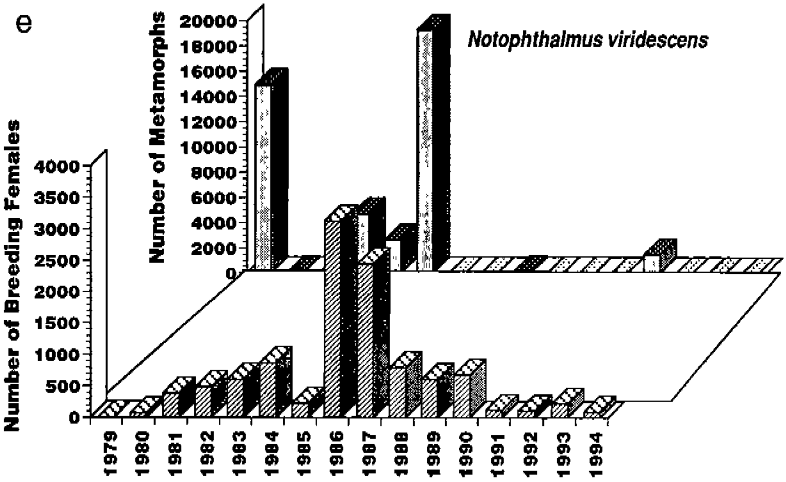
e
Notophthalmus viridescens
Number of Metamorphs
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2000
4000
6000
8000
10000
12000
14000
16000
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20000
Number of Breeding Females
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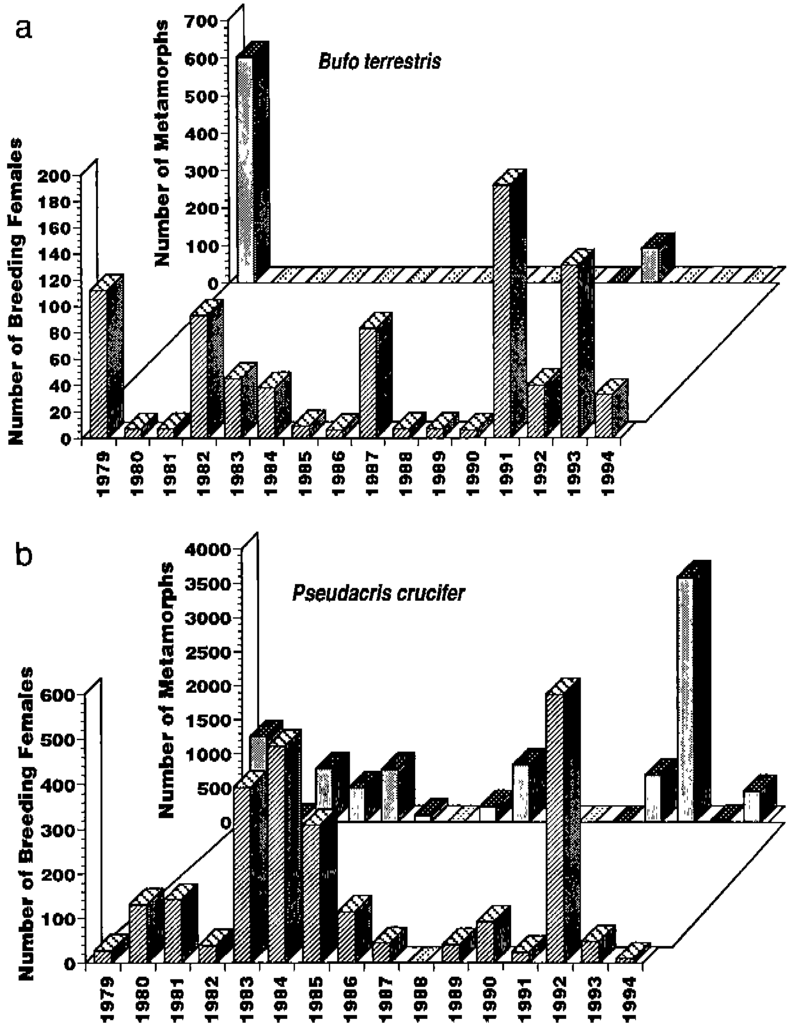
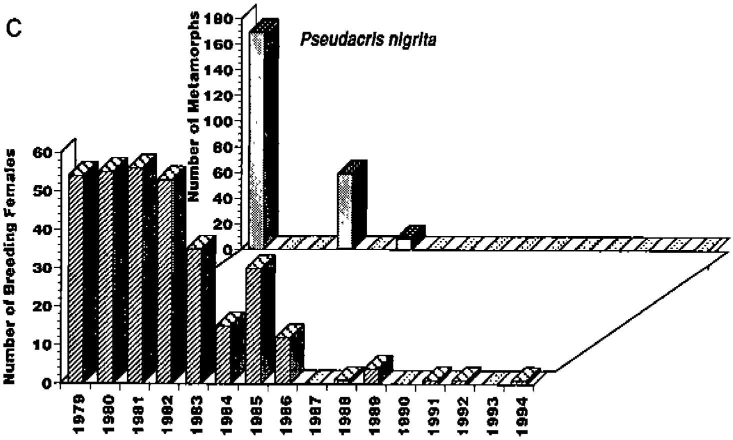


FIGURE 4. The annual numbers of breeding females and of metamorphosing juveniles for eight species of anurans ((a) *B. terrestris*, (b) *P. crucifer*, (c) *P. nigrita*, (d) *P. ornata*, (e) *R. clamitans*, (f) *R. utricularia*, (g) *S. holbrooki*, and (h) *G. carolinensis*) at Rainbow Bay. Bars represent the total numbers collected in pitfall traps at the drift fence for each year from 1979 to 1994.

increases or decreases in total population size. There were four species that showed a significant positive correlation between the number of breeding females and metamorphs produced in previous years: *A. opacum*, *E. quadridigitata*, *P. nigrita*, and *P. ornata*. The correlation was nearly significant ($P = 0.06$) for *A. tigrinum* (Table III). Correlations for all five of these species c


Pseudacris nigrita
Number of Metamorphs
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Number of Breeding Females
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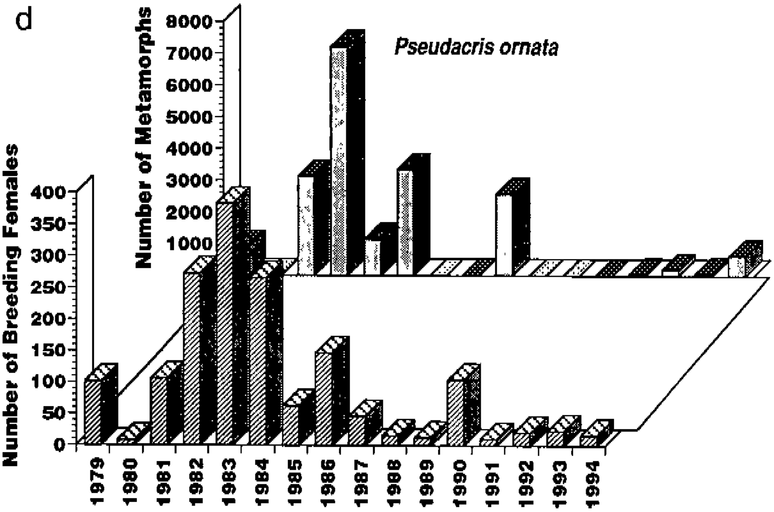
Pseudacris ornata
Number of Metamorphs
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Number of Breeding Females
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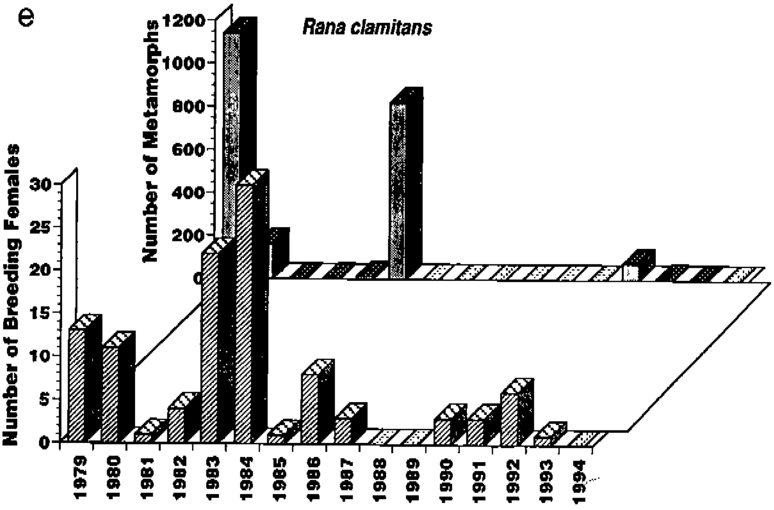
Rana clamitans
Number of Metamorphs
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Number of Breeding Females
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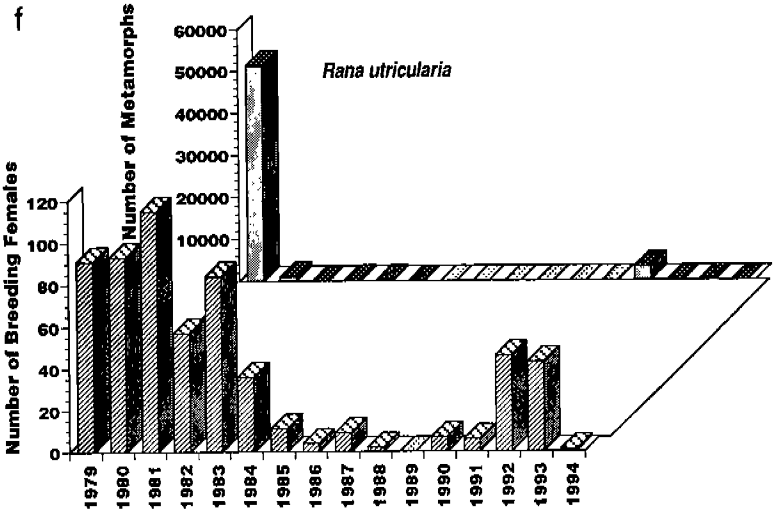
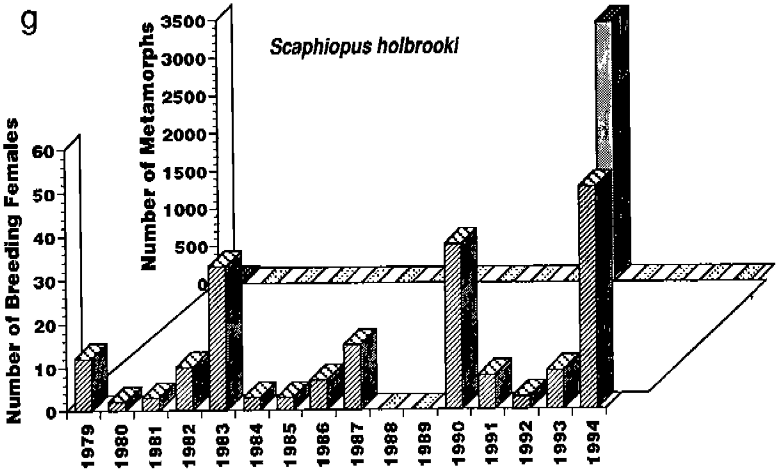
1993
1994


f
Rana utricularia
Number of Metamorphs
60000
50000
40000
30000
20000
10000
Number of Breeding Females
120
100
80
60
40
20
0
1979
1980
1981
1982
1983
1984
1985
1986
1987
1988
1989
1990
1991
1992
1993
1994


g
Scaphiopus holbrooki
Number of Metamorphs
3500
3000
2500
2000
1500
1000
500
0
Number of Breeding Females
60
50
40
30
20
10
0
1979
1980
1981
1982
1983
1984
1985
1986
1987
1988
1989
1990
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1993
1994

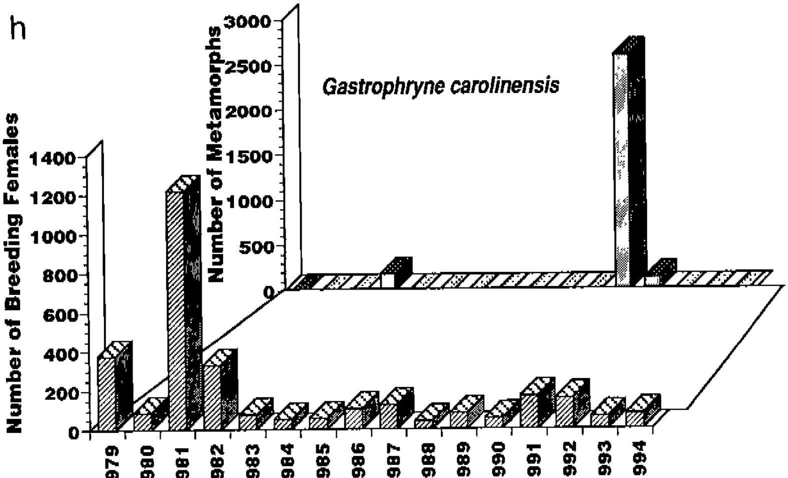
h
Gastrophryne carolinensis
Number of Metamorphs
3000
2500
2000
1500
1000
500
0
Number of Breeding Females
1400
1200
1000
800
600
400
200
0
1979
1980
1981
1982
1983
1984
1985
1986
1987
1988
1989
1990
1991
1992
1993
1994

TABLE III **Summary of the Spearman Partial (and Simple) Rank Correlations of the Number of Breeding Females with Cumulative Rainfall during the Species' Breeding Season and the Number of Metamorphs in Previous Years (See Methods)**

Species	Cumulative rainfall	Number of metamorphs
Caudata		
A. opacum	0.57*	0.86*
	(0.11)	(0.80*)
A. talpoideum	0.63*	0.43
	(0.58*)	(0.20)
A. tigrinum	0.55	0.63*
	(0.37)	(0.53)
E. quadridigitata	−0.20	0.63*
	(−0.25)	(0.66*)
N. viridescens	−0.16	0.45
	(−0.10)	(0.43)
Anura		
B. terrestris	0.76*	0.48
	(0.57*)	(0.44)
P. crucifer	−0.05	0.04
	(0.03)	(0.04)
P. nigrita	−0.32	0.73*
	(−0.27)	(0.72*)
P. ornata	0.30	0.62*
	(0.03)	(0.57*)
R. clamitans	0.24	0.24
	(0.37)	(0.32)
R. utricularia	0.21	0.33
	(0.11)	(0.40)
S. holbrooki	0.55	−0.10
	(0.48)	(−0.02)

Note. Significant correlation coefficients are indicated by an asterisk ($P < 0.05$). The two predictor variables were not significantly correlated for any species (all $P > 0.20$).

were significant after the effect of rainfall was removed by partial correlation (Table III). For *A. opacum, A. tigrinum,* and *P. nigrita,* these correlations may reflect significant trends in their population sizes over the course of the study (see following discussion). Caldwell (1987) suggested from mortality data that both *P. ornata* and *P. nigrita* were short-lived, which could increase their sensitivity to variation in juvenile recruitment. For some species the lack of a significant correlation between breeding population sizes and prior juvenile recruitment may have resulted from migration between Rainbow Bay and other nearby ponds. The presence of a breeding population of females at Rainbow Bay during most years despite infrequent juvenile recruitment, e.g., for *B. terrestris* and *S. holbrooki,* is consistent with this hypothesis. Three of the four lowest correlations between breeding population sizes and juvenile recruitment were for species whose adults frequently trespass the drift fence: *P. crucifer, R. clamitans,* and *R. utricularia.*

The breeding population sizes of five species exhibited significant correlations with year, i.e., significant trends over the time period of the study (Table IV). Correlations for these same five species were significant after adjusting for the effect of breeding season rainfall (Table IV). Both the simple and partial correlations with year were positive and significant for *A. opacum,* indicating an increase over time. No *A. opacum* bred at Rainbow Bay during the first two years of our study, but several hundred females bred during eight of the last nine years (Fig. 3). This suggests that *A. opacum* may have recently colonized or recolonized Rainbow Bay. Alternatively, its population may have fluctuated to a small size at the time our study began and then recovered without the necessity for recolonization.

Breeding population sizes of the other four species, *A. tigrinum, P. nigrita, R. clamitans,* and *R. utricularia,* decreased significantly during the period of our study (Table IV; Figs. 3 and 4). We attribute these decreases primarily to the lack of juvenile recruitment associated with extended drought conditions from 1985 to 1990 (Table II; Figs. 3 and 4). For *A. tigrinum* and *P. nigrita,* there was

TABLE IV Summary of the Trend Analysis Using Kendall's (Tau^{-b}) Rank Correlations of the Number of Breeding Females with Year, Cumulative Rainfall during the Breeding Season, and Partial Rank Correlations with Year after Removing the Effect of Rainfall

Species	Year	Rainfall	Year (correcting for rainfall)
Caudata			
A. opacum	0.58*	0.08	0.57*
A. talpoideum	0.03	0.47*	−0.03
A. tigrinum	−0.46*	0.28	−0.53*
E. quadridigitata	−0.23	−0.18	−0.21
N. viridescens	−0.15	−0.08	−0.14
Anura			
B. terrestris	−0.01	0.44*	−0.08
G. carolinensis	−0.22	0.20	−0.22
P. crucifer	−0.17	0.01	−0.17
P. nigrita	−0.72*	−0.18	−0.71*
P. ornata	−0.33	0.07	−0.35
R. clamitans	−0.39*	0.27	−0.45*
R. utricularia	−0.53*	0.03	−0.54*
S. holbrooki	0.15	0.33	0.11

Note. Significant correlation coefficients are indicated by an asterisk ($P < 0.05$). The two predictor variables were not significantly correlated for any species (all $P > 0.40$).

a significant partial correlation of breeding population size with past juvenile recruitment (Table III). It is also possible that the increase in *A. opacum* contributed to the decrease in the other four species, due to predation by its larvae on the other species larvae. There was a negative association between the density of heterospecific salamander larvae (all species pooled) and per-capita juvenile recruitment for three of the species that declined (see section V.; one species, *P. nigrita,* was not analyzed). Although the total density of salamander larvae (all species pooled) did not increase significantly over time (Kendall correlation with year = 0.27, $P = 0.17$, $n = 14$), *A. opacum* may be a particularly important predator because its larvae are usually the first present in the pond and initially larger in body size.

V. LARVAL SUCCESS: INTERACTIONS AMONG SPECIES AND WITH HYDROPERIOD

A. Salamanders

The simple Tobit regressions between the number of metamorphosing juveniles per breeding female and length of the first hydroperiod were significant for three of the five species of salamanders (Table V). After correcting for any linear effects of conspecific and heterospecific larval density, first hydroperiod was positively related to increased reproductive success only for *A. talpoideum.* For *A. tigrinum* and *N. viridescens,* the partial regression coefficient for hydroperiod was not significantly different from zero even though the simple regression coefficient was. This indicates that any effects of hydroperiod on these two species could not be separated from the effects of the other predictor variables. Hydroperiod was significantly correlated with one or both of the other predictor variables for all the salamander species (Table V). This may be, in part, because the other variables were larval densities calculated using 1 March pond volume, which was itself significantly correlated with pond hydroperiod (Spearman's rank correlation $r = 0.78$, $P < 0.001$).

A positive relationship of first hydroperiod with the number of metamorphs is most likely attributable to more time available to complete larval development. The species for which this relationship was weakest were the two autumn breeders, *A. opacum* and *E. quadridigitata* (Table V), both of which usually migrate to the pond and breed early in the season (September–November). Their larvae metamorphose earlier and are less affected by a short hydroperiod than those of species (*A. talpoideum, A. tigrinum,* and *N. viridescens*) that breed later in the season (i.e., winter or early spring; Table V).

The simple and partial Tobit regressions of the total number of metamorphs per female of a species with its initial larval density were significant only for

TABLE V Summary of the Tobit Regression Analyses for the Number of Metamorphosed Juveniles Produced Per Breeding Female of Five Salamander Species at Rainbow Bay

				Initial density	
	Non-censored (*N*)	Left-censored (*N*)	First pond hydroperiod	Same species	All other species
A. opacum	11	1	0.02 ± 0.05	−38.5 ± 178.8	−9.9 ± 12.2
			(0.04 ± 0.05)	(−139.7 ± 150.7)	(−12.8 ± 9.9)
A. talpoideum	10	4	0.07 ± 0.02*	−205.1 ± 37.7*	−17.2 ± 38.8
			(0.10 ± 0.03*)	(−222.3 ± 65.9*)	(−94.6 ± 74.9)
A. tigrinum	8	6	0.06 ± 0.04	−533.8 ± 1122.8	−140.2 ± 81.3
			(0.11 ± 0.04*)	(−1490.2 ± 923.0)	(−185.1 ± 83.6*)
E. quadridigitata	8	6	−0.02 ± 0.02	−48.3 ± 58.7	−2.8 ± 3.3
			(−0.01 ± 0.02)	(−50.2 ± 103.9)	(−1.9 ± 3.5)
N. viridescens	7	7	0.08 ± 0.05	17.2 ± 123.1	−193.9 ± 115.2
			(0.11 ± 0.05*)	(−114.4 ± 103.1)	(−207.4 ± 118.9)

Note. Partial regression coefficients are indicated ±1 SE. Corresponding simple regression coefficients are given in parentheses. Significance ($P < 0.05$) is indicated by an asterisk. There were significant ($P < 0.05$) Spearman rank correlations between the following pairs of predictor variables: hydroperiod and density of the same species (negative) for *A. talpoideum* and *N. viridescens*, hydroperiod and density of other species (negative) for all species, and density of the same species and of other species (positive) for *A. talpoideum*, *A. opacum*, *N. viridescens*, and *E. quadridigitata*.

A. talpoideum (Table V). The regression coefficients were negative and likely indicate density-dependent reproductive success. This species is abundant at Rainbow Bay (Table I), and it is likely to numerically and behaviorally dominate competitive relationships with other species as well as with itself (Semlitsch and Walls, 1993). Although the additional density effect of the other species also influenced *A. talpoideum* negatively, the regressions were not significant (Table V). The reproductive success of the other four species, *A. opacum, A. tigrinum, E. quadridigitata,* and *N. viridescens,* was not significantly affected by their own initial larval densities (Table V).

The Tobit analyses detected only weak evidence for negative interactions (competition or predation) among salamander species. The only significant Tobit regression for the number of metamorphosing juveniles per breeding female with the initial density of heterospecific larvae was the simple regression for *A. tigrinum* (Table V). The corresponding partial regression coefficient was smaller and not quite significant ($P = 0.08$). This suggests that any effects of heterospecific density on *A. tigrinum* were partially confounded with the effects of hydroperiod, with which heterospecific density was significantly correlated (Table V). Both the simple and partial Tobit regressions for heterospecific density effects on *N. viridescens* were nearly significant ($P = 0.08$ and $P = 0.09$, respectively). The weakest effects of heterospecific salamander density were again for the two species that breed the earliest in the season, *A. opacum* and *E. quadridigitata.* Early breeding reduces the temporal overlap between their larvae and those of other salamanders. In addition, it provides *A. opacum* and *E. quadridigitata* with a size advantage over other larvae.

B. Anurans

The simple coefficient for *R. utricularia* was the only positive, significant Tobit regression coefficient with first hydroperiod as a predictor of the number of metamorphosing juveniles per breeding female (Table VI). The simple coefficient was also nearly significant for *R. clamitans* ($P = 0.08$), but the corresponding partial regression coefficient was not significant for either species (Table VI). This suggests that any effect of hydroperiod on *R. utricularia* and *R. clamitans* could not be distinguished from the effects of other variables, two of which were significantly correlated with hydroperiod (Table VI). It is likely that longer hydroperiods would increase the number of metamorphs for these two species, because they have relatively long larval periods. Longer hydroperiods may have allowed more individuals to reach the critical size to initiate metamorphosis. Species such as *P. crucifer* have a shorter larval period (<45 days) and were unlikely constrained by hydroperiod in most years (i.e., except in 1985, 1988, and 1989; Fig. 4 and Table II).

TABLE VI Summary of the Tobit Regression Analyses for the Number of Metamorphosed Juveniles Produced Per Breeding Female of Four Anuran Species at Rainbow Bay

	Non-censored (*N*)	Left-censored (*N*)	First pond hydroperiod	Initial density		
				Same species	All other anurans	Salamanders
P. crucifer	13	1	−0.08 ± 0.06	−62297 ± 28593*	−46630 ± 53743	−8.7 ± 10.8
			(0.02 ± 0.05)	(−61299 ± 28729*)	(−65481 ± 43749)	(−14.7 ± 10.8)
P. ornata	12	2	−0.17 ± 0.05*	−29794 ± 85937	−62925 ± 25230*	−16.2 ± 13.5
			(−0.04 ± 0.06)	(−76312 ± 71277)	(−36154 ± 27176)	(−14.1 ± 12.1)
R. clamitans	8	5	−0.17 ± 0.10	9538474 ± 3675740*	−164589 ± 60104*	−574 ± 179*
			(0.21 ± 0.12)	(−1620982 ± 3934530)	(−96752 ± 51292)	(−456 ± 224*)
R. utricularia	10	4	−0.24 ± 0.68	−393941 ± 1665789	−500097 ± 375056	−3999 ± 1140*
			(1.52 ± 0.69*)	(−684877 ± 2278149)	(−734259 ± 379757)	(3980 ± 1149*)

Note. Partial regression coefficients are indicated ±1 SE. Corresponding simple regression coefficients are given in parentheses. Significance ($P < 0.05$) is indicated by an asterisk. There were significant ($P < 0.05$) Spearman rank correlations between the following pairs of predictor variables for all species: hydroperiod and density of other anurans (negative), hydroperiod and density of salamanders (negative), and density of other anurans and of salamanders (positive). Also, density of same species was significantly correlated with density of other anurans (positive) for *R. utricularia* and *P. ornata*, and with hydroperiod (negative) and density of salamanders (positive) for *P. ornata*.

There was a significant negative relationship between hydroperiod and per-capita juvenile recruitment of *P. ornata*, after correcting for the other predictor variables (Table VI). This means that *P. ornata* tended to do more poorly in years with long first hydroperiods. Rainbow Bay was more likely to fill early in these years (e.g., 1980, 1991), before the breeding season of *P. ornata*. Its tadpoles may therefore have been exposed to greater levels of competition and predation (from invertebrates and vertebrates) than in years when *P. ornata* bred shortly after the pond filled. It should be noted that *P. ornata* also did poorly in short-hydroperiod years when the pond dried early (e.g., 1985, 1990), suggesting that intermediate hydroperiods were the most favorable.

Second hydroperiod also may have affected juvenile recruitment of some species, but this was not formally analyzed here. The only large cohort of *S. holbrooki* metamorphs was produced in 1990 after Rainbow Bay dried and then refilled (Fig. 4; Table II). *Gastrophryne carolinensis* produced metamorphs only when Rainbow Bay refilled for at least several weeks during the summer after drying completely (1979, 1982, and 1990) or nearly drying (1991). In most other years Rainbow Bay did not hold water for an adequate period during the summer breeding season of *G. carolinensis*, or did so but did not dry first, and no metamorphs of this species were produced (Fig. 4; Table II).

Conspecific density was a significant predictor of the number of juveniles produced per breeding female for *P. crucifer* and *R. clamitans* but not for *P. ornata* or *R. utricularia* (Table VI). Both the simple and the partial regression coefficients were significant and negative for *P. crucifer*, suggesting that intraspecific competition reduced survival to metamorphosis in years that larval densities were high. Intraspecific density effects may have been more detectable for *P. crucifer* because its breeding population sizes at Rainbow Bay averaged larger than those for all other anurans except *G. carolinensis* (Table I). For *R. clamitans*, the simple regression coefficient for conspecific density was negative and not significant, whereas the partial coefficient was positive and significant (Table VI). This suggests that survival to metamorphosis of *R. clamitans* may have been facilitated by higher densities of conspecific larvae, after correcting for other factors.

The partial Tobit regression coefficients for heterospecific anuran density were negative and significant for *P. ornata* and *R. clamitans* (Table VI), while the corresponding simple coefficients were negative and not significant (but nearly so for *R. clamitans*; $P = 0.06$). This suggests that interspecific competition measurably reduced per-capita juvenile recruitment of these two species at Rainbow Bay, after accounting for the effects of other variables. Tobit regression coefficients for heterospecific anuran density were negative but not significant for *P. crucifer* and *R. utricularia* (Table VI), although the simple coefficient for *R. utricularia* was nearly significant ($P = 0.053$).

The simple and partial Tobit regressions for the initial density of salamander larvae with the number of metamorphosed juveniles per breeding female were significant for *R. clamitans* and *R. utricularia* (Table VI). The regression coefficients were negative and likely indicated predation by salamander larvae on the tadpoles. Per-capita juvenile recruitment of *P. crucifer* and *P. ornata* was not significantly affected by the density of salamander larvae (Table VI). These results are consistent with Morin's (1983a) experimental finding that salamander predation was greater on *R. utricularia* tadpoles than on *P. crucifer* tadpoles. Salamander predation on *P. ornata* eggs and tadpoles may be reduced because *P. ornata* usually breeds just after the pond fills, before larger salamander larvae are present in the pond. The negative relationship between salamander density and juvenile recruitment of *R. clamitans* that we observed is not consistent with Walters' (1975) observations that eggs and tadpoles of this species were unpalatable to adult *N. viridescens* and larval *Ambystoma*.

The relationship between second hydroperiod and juvenile recruitment observed for some anuran species at Rainbow Bay may be interpreted as evidence for the importance of interspecific interactions. The fact that *G. carolinensis* metamorphs were produced only after Rainbow Bay dried, then refilled, suggests that other species have negative effects on this species and that drying is necessary to eliminate predators or competitors (either amphibians or other taxa). Similarly, *S. holbrooki* produced a large number of metamorphs only in 1990, when Rainbow Bay refilled after drying.

VI. DISCUSSION AND CONCLUSIONS

Our 16-year study found that pond hydroperiod (disturbance) is a primary source of variation in community structure for this natural community of pond-breeding amphibians (*sensu* Menge and Sutherland, 1987). Larval competition and predation form other axes that are positioned along a continuum of hydroperiod, and the strength of their influence on the success of species is mediated by pond hydroperiod. Although hydroperiod, competition, and predation all had a detectable influence on the amphibian community at Rainbow Bay, the effects of these factors were often difficult to separate. Correlative analyses are less powerful for sorting out confounding factors (see a discussion of field data in Petranka and Sih, 1986) than manipulative experiments in replicated artificial ponds (e.g., Morin, 1983a; Wilbur, 1984, 1987). The predictor variables used were often themselves correlated. Furthermore, we lacked sufficient replication to test for statistical interactions among the variables, which may play an important role (Wilbur, 1987).

Juvenile production for all species was virtually episodic, with large numbers of metamorphs being produced in only a small number (1–7 years) of the 16 years. Our data show that temporal variation may favor the reproductive success of different species in different years. Nevertheless, in many cases a good year for a species was also a good year for its competitors and predators. Our third prediction, that hydroperiod is a highly variable but still significant predictor of the number and diversity of metamorphosing amphibians at Rainbow Bay, was supported by the data. Relationships between species diversity and hydroperiod were suggested previously by Heyer *et al.* (1975) and Wilbur (1980, 1984). Their emphasis, however, was on spatial variation among ponds rather than temporal variation. Rapid pond drying often causes complete reproductive failure in amphibian species (e.g., Blair, 1957; Tevis, 1966; Shoop, 1974; Newman, 1987; Semlitsch, 1987). Early pond drying is sometimes viewed as an unusual or catastrophic event with little or no influence on community structure because of its seemingly random occurrence. Yet, early pond drying was not rare but rather a pervasive risk at Rainbow Bay. Although hydroperiod is systematically linked to rainfall, and rainfall can be viewed as random, its effects on community structure and dynamics are predictable. Over the 16 years of our study, 4 (25%) of the years (1981, 1985, 1988, and 1989) had short total hydroperiods (≤100 days), and complete or nearly complete reproductive failure occurred for most species. Although short hydroperiods were catastrophic for most species in these years, other species actually benefitted from pond drying followed by refilling in other years, presumably because it eliminated predators (both salamander and insect larvae), competitors, or both (e.g., *G. carolinensis*, *S. holbrooki* in Fig. 4; and *Hyla femoralis* in Pechmann *et al.*, 1989). Seven (44%) of the years (1979, 1980, 1982, 1983, 1984, 1991, and 1993) had long total hydroperiods (>200 days), which allowed species that breed late or have long larval periods to produce metamorphosed juveniles. Numbers and species diversity of metamorphosing juveniles were, on average, highest in these years. The remaining 5 years were intermediate in total hydroperiod (between 100 and 200 days). There was no clear indication that species diversity was maximized at intermediate hydroperiods as suggested by Heyer *et al.* (1975) and Wilbur (1980, 1984), probably because the extreme case of no pond drying did not occur at Rainbow Bay for comparison.

Juvenile recruitment of all species was limited by hydroperiod in the driest years. The Tobit regressions tested for a relationship between hydroperiod and per-capita juvenile recruitment above the estimated threshold hydroperiod for non-zero recruitment. Longer hydroperiods were significantly associated with increased recruitment for three of five salamanders and one of four anurans examined by the Tobit analyses. The positive effect of longer hydroperiods, however, could be separated from the effects of predation and competition only for the salamander *A. talpoideum*. Longer hydroperiods were associated with decreased recruitment of one anuran, *P. ornata*, after correcting for other variables.

Our fourth prediction, that the density of competitors affects the number of metamorphosing juveniles per breeding female, was supported for some species. There was evidence for intraspecific competition for one abundant salamander and one abundant anuran. There was evidence for facilitation in another anuran species. The number of metamorphosing juveniles was significantly affected by interspecific competition in two of four anuran species tested. The density of heterospecific salamander larvae had a significant effect on juvenile recruitment in only one of five salamander species, and this effect could not be statistically separated from that of hydroperiod.

Data from Rainbow Bay also supported our fifth prediction, that the density of salamander larvae is a significant predictor of per-capita juvenile recruitment for anurans. A significant negative relationship was detected for two of four anuran species analyzed, most likely due to predation by the salamander larvae on the anuran tadpoles. Thus, predation, competition, and hydroperiod all had detectable effects on the numbers of metamorphosing juvenile amphibians at Rainbow Bay.

Fluctuations in juvenile recruitment, the effects of rainfall on breeding migrations, and perhaps other factors resulted in wide fluctuations in breeding population sizes, affirming our first prediction. Annual variation, short-term trends, and long-term trends (our second prediction) all were observed during the course of our 16-year study. The result was that community structure, at least in terms of relative abundances, varied continuously. The breeding population size of *A. opacum* began at 0 and increased significantly during this period. No species were lost from Rainbow Bay during our study, but numbers of four species declined significantly, in some cases to very low levels. We view these long-term trends as prolonged natural fluctuations related to climatic variation, predation, competition, and other natural interacting factors. Some amphibian populations are reported to have declined or disappeared in isolated, protected areas around the world since the 1970s (Wake and Morowitz, 1990; Blaustein *et al.*, 1994). The concern is that these losses have resulted from undetected human impacts. Data from Rainbow Bay illustrated the difficulty of distinguishing declines due to human activities from natural fluctuations (Pechmann *et al.*, 1991).

Our analyses in this paper concentrated on the larval stage of the complex life cycle of amphibians. Population sizes and community diversity may also be affected by processes acting upon the terrestrial stages (Istock, 1967; Wilbur, 1980, 1996; Werner and Gilliam, 1984; Loreau and Ebenhoh, 1994; Pechmann, 1994). Local dynamics may also be influenced by immigration and emigration among ponds, i.e., by processes occurring at a metapopulational or regional level (Hanski and Gilpin, 1991; Ricklefs and Schluter, 1993). For example, *Ambystoma opacum* may have colonized or recolonized Rainbow Bay during our study. For some species the low frequency of successful reproduction observed at Rainbow Bay, coupled with a lack of correlation between juvenile recruitment and breeding population sizes, suggests that their persistence at this site may be aided by metapopulation "rescue effects" or "source-sink" processes (Brown and Kodric-Brown, 1977; Pulliam, 1988).

In conclusion, environmental variation resulted in striking changes in the relative abundances of amphibian species at Rainbow Bay, both from year to year and over the 16 years of the study. This community cannot be viewed as being in equilibrium; nevertheless, species interactions and density dependence play a significant role. We suggest that long-term results from Rainbow Bay can be generalized to other amphibian communities. Variation in breeding population sizes and larval success among years similar to that observed at Rainbow Bay has been observed at other ponds in our geographic region in short-term studies (Gibbons and Bennett, 1974; Semlitsch, 1983, 1985b; Pechmann *et al.*, 1989). Similarly high levels of variability are well-documented in natural amphibian communities across a wide range of geographic regions (e.g., Bannikov, 1948; Blair, 1961; Tevis, 1966; Heyer, 1973, 1979; Shoop, 1974; Gill, 1978; Wiest, 1982; Berven and Grudzien, 1990; Dodd, 1992). Thus, there is no reason to believe that our results are unique because of geographic region, pond type, or species diversity.

The critical step in equating the dynamics of various pond-breeding amphibian communities is to first position ponds along a hydroperiod gradient ranging from extremely ephemeral (e.g., desert pools) to extremely permanent (e.g., spring-fed ponds or bogs). The importance of competition among species, and predation by fish, salamanders, and aquatic insects, will then vary with hydroperiod. In addition, it is important to consider whether a pond's position on the gradient of hydroperiod is static or dynamic. Our long-term data on the hydroperiod of Rainbow Bay indicates that some ponds change position along this gradient annually, and thus, the effects of competition and predation on species are also dynamic.

A critical question is whether these processes affecting the persistence and relative abundance of species are predictable or random. Although rainfall and pond hydroperiod may be viewed as stochastic influences, our data show that they produced a predictable pattern, interacting with competition and predation. Species unable to cope with high frequencies of years unfavorable for reproduction may persist for short periods of time but, barring immigration, would certainly become extinct locally as mortality exceeded reproduction. Thus, regulation of community structure within a pond occurs through the predictable interaction of rainfall, hydroperiod, competition, and predation.

VII. SUMMARY

Our 16-year study of amphibians in a natural temporary pond found that hydroperiod is a primary source of variation in community structure. Larval competition and predation also have a detectable influence, but the strength of their influence on the success of species is mediated by pond hydroperiod. Although hydroperiod, competition, and predation all had a detectable influence on the amphibian community at Rainbow Bay, the effects of these factors were often difficult to separate. Juvenile production for all species was virtually episodic, with large numbers of metamorphs being produced in only a small number (1–7) of the 16 years. Although hydroperiod was highly variable, it was still a significant predictor of the number and diversity of metamorphosing amphibians at Rainbow Bay. Our data show that temporal variation may favor the reproductive success of different species in different years. Nevertheless, in many cases a good year for a species was also a good year for its competitors and predators. Juvenile recruitment of all species was limited by a short hydroperiod in the driest years. In years with longer hydroperiods, the density of competitors affected the number of metamorphosing juveniles per breeding female for some species. The density of salamander larvae was also a significant predictor of per-capita juvenile recruitment for anurans. A significant negative relationship was detected for two of four anuran species analyzed, most likely due to predation by the salamander larvae on the anuran tadpoles. These results indicate that community structure, at least in terms of relative abundances, varied continuously. However, regulation of community structure within a pond occurs through the predictable interaction of rainfall, hydroperiod, competition, and predation.

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