TWENTY-FIVE

Amphibian Population Cycles and Long-Term Data Sets

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The loss of biodiversity throughout the world is increasing at an alarming rate, with habitat destruction and fragmentation as the leading causes for extinction rates that are 100 to 1,000 times greater than pre-human levels (Pimm et al., 1995; Global Biodiversity Assessment, 1996; Chapin et al., 1998). Such losses are particularly evident among amphibian populations, which have disappeared or are declining in a wide range of environments (Wyman, 1990; Carey, 1993; Pounds and Crump, 1994; Blaustein and Wake, 1995; Vertucci and Corn, 1996; Lannoo, 1998b; Wake, 1998; Houlahan et al., 2000). Although most researchers agree that many amphibian populations are declining, there is debate about how to distinguish human-induced declines from natural population fluctuations (Pechmann and Wilbur, 1994; Sarkar, 1996). As with many species, amphibian populations are regulated by a variety of intrinsic and extrinsic factors that can create cyclic population fluctuations (see below). However, when compared to organisms such as insects (Hassell, 1986; Cappuccino and Price, 1995; Turchin et al., 1999) and small mammals (Krebs and Meyers, 1974; Krebs, 1992; Stenseth, 1993), there is a dearth of basic ecological information about the factors that underlie amphibian population cycles (see Green, this volume). This information is critical for determining whether the cause is manmade or natural and whether the effects are short-term or permanent (Pechmann et al., 1991; Pechmann and Wilbur, 1994; Sarkar, 1996).

Here we argue that systematic, long-term research on amphibian populations is necessary to provide basic information about the amplitude and frequency of natural fluctuations. Such baseline information is essential for posing and testing alternative hypotheses to explain declines in amphibian populations (e.g., Pounds et al., 1997). We review 20 years of research on a population of Arizona tiger salamanders *(Ambystoma tigrinum nebulosum)* at the Mexican Cut Nature Preserve (MCNP) in south-central Colorado. This review includes data that we have collected from 1989–99 (Wissinger and Whiteman, 1992; Whiteman et al., 1994, 1996; Whiteman, 1997; Wissinger et al., 1999a), and the work of other researchers from the previous 10 years (Dodson, 1982; Harte and Hoffman, 1989). The salamander population that we have been studying has fluctuated dramatically, but as with many studies (e.g., Crump et al., 1992; Laurance et al., 1996, 1997), fluctuations cannot be clearly linked to human impacts. We then consider which of the many possible hypotheses for population fluctuations are the most likely to explain the observed cycle of decline and recovery. Finally, we discuss the ability of long-term demographic studies to provide the background information necessary to distinguish natural fluctuations from human-induced declines.

Natural History of Mexican Cut Salamanders

Understanding the natural history of a species and the community within which it is embedded is fundamental for posing hypotheses about the factors that regulate population size. The population we study is isolated on a subalpine (3,500 m elevation) shelf that contains numerous adjacent open wetland basins. MCNP is owned by The Nature Conservancy and managed for low-impact ecological research by the Rocky Mountain Biological Laboratory (RMBL). MCNP has been the site of numerous ecological studies over the past three decades (e.g., Dodson, 1970, 1974, 1982; Sprules, 1972, 1974; Maly and Maly, 1974; Sexton and Bizer, 1978; Maly et al., 1980; Harte and Hoffman, 1989; Wissinger and Whiteman, 1992; Whiteman et al., 1994, 1996, 1999; Wissinger et al., 1996, 1999a,b; Whiteman, 1997; Bohonak, 1999; Bohonak and Whiteman, 1999).

The following summary of the natural history of the MCNP Arizona tiger salamanders is based on our long-term data set. In early summer (from late June to early July, depending on the year; Whiteman et al., 1999) metamorphic (terrestrial morphology, sexually mature) adults emigrate from terrestrial overwintering sites to breed in the largest permanent and semipermanent wetland basins. After breeding, these adults then migrate to semipermanent and seasonal basins, where they feed for 6–8 weeks before returning to the surrounding forest to overwinter (Whiteman et al., 1994). Eggs typically hatch in mid-July. Due to cold water temperatures and the short summer at this altitude, larval development is prolonged compared with lower-elevation populations, and metamorphosis occurs during the second or third summer. Thus, only larvae in permanent habitats or semipermanent habitats that do not dry can survive to successive summers (Wissinger and Whiteman, 1992). Many individuals forego metamorphosis and become sexually mature as larvae—i.e., become paedomorphic (larval morphology, sexually mature) adults (Whiteman, 1994a). Salamander life history stages are tied to wetland type. Permanent wetlands typically contain paedomorphic adults and several year classes of larvae that act as top predators within these ponds. Semipermanent and temporary basins typically contain metamorphic adults and hatchling larvae (Wissinger et al., 1999a). Semipermanent wetlands may have two cohorts during the summer after a year in which they retained water.

Salamanders at MCNP are keystone predators (Payne, 1966; Power et al., 1996) that have important impacts on the distribution and abundance of aquatic invertebrates (Dodson, 1970, 1974; Bohonak and Whiteman, 1999; Sprules, 1972; Wissinger et al., 1999a,b). Dietary analyses from stomach pumping indicate that most of the more than 100 species of aquatic invertebrates in these wetlands are consumed by one or more life history stages of salamanders (Whiteman et al., 1994, 1996; Wissinger et al., 1999a). Metamorphic adults specialize on fairy shrimp *(Branchinecta coloradensis)*, which comprise up to 99% of their diet. Larval stages exhibit an ontogenetic dietary niche shift in prey size and type, from small planktonic to larger benthic invertebrates. Large larvae and paedomorphic adults often cannibalize small larvae.

Fluctuations in Salamander Population Size at Mexican Cut

Over the past 20 years, estimates of the total size of the Arizona tiger salamander population (all life stages combined) at Mexican Cut have fluctuated from fewer than 200 to over 3,000 individuals (Fig. 25-1A). Although there are no quantitative census data from the 1970s, researchers working at that time report that salamanders were abundant and likely numbered in the thousands (S. Willey, S.I. Dodson, personal communication). We began marking individuals in 1989, including adults and larvae from the 1988 and subsequent cohorts. Through recapture censuses we have been able to estimate the population size, document the basic demography of the population, and detail the behavior of individuals (see Whiteman, 1997; Wissinger et al., 1999a).

During the early 1980s a population decline was documented by visual censuses (Harte and Hoffman, 1989). We now know that visual censuses considerably underestimate actual population sizes (unpublished data). However, given that the same methodology was used by Harte and Hoffman each year during the 1980s and based on the number of adults we found during the early 1990s, the general trend of decline was undoubtedly real. The decline abruptly ended in 1988 with the recruitment of over 3,000 juveniles into the population (Wissinger and Whiteman, 1992; Fig. 25-1A). From 1989–91 total population size totaled around 3,200 individuals, declined during 1992–93, and slowly increased from 1993–97 (Fig. 25-1). The number of adults also declined throughout the early 1980s, remained relatively constant during the latter part of that decade, then increased during the 1990s with the maturation of the 1988 and subsequent cohorts (Fig. 25-1). There is anecdotal evidence that similar fluctuations in population size have occurred before at MCNP. Long-term researchers at the RMBL who worked at MCNP recall similar boom and bust cycles in this population dating back to the 1940s (J. Cairns, S.I. Dodson, S. Willey, personal communication).

Hypotheses for Cyclic Population Fluctuations

Population fluctuations are common in nature (Varley et al., 1973; Myers, 1988; Royama, 1992; see examples in Hanski et al., 1993) and the causes of cyclic fluctuations have been the subject of considerable debate among ecologists (e.g., Murdoch, 1994; Turchin, 1995 and references therein). Underlying mechanisms for population cycles can be divided broadly into three categories: (1) fluctuations in the abiotic environment; (2) coupled oscillations associated with interspecific interactions; and (3) density-dependent regulation mechanisms within populations (Table 25-1). Historically, ecologists have most often associated population fluctuations with variation in abiotic factors such as climate (e.g., rainfall and temperature; Andrewartha and Birch, 1954; Kingsland, 1985). Variation in climate affects survival and reproduction (Stearns, 1992) and can be linked to both an initial fluctuation in population size and subsequent cycles related to demographic effects (e.g., Kalela, 1962; Stafford, 1971; Stacey and Taper, 1992; Woiwood and Hanski, 1992). Examples of amphibian fluctuations associated with natural climatic variation include the effects of drought (e.g., Pechmann et al., 1991; Semlitsch et al., 1996) and winterkill (typically due to oxygen depletion; e.g., Bradford, 1983) on recruitment.

Perhaps the best examples of regular cycles of population fluctuation are associated with interspecific interactions, especially predator-prey and parasite- or pathogen-host dynamics (e.g., Krebs and Myers, 1974; Anderson and May, 1980; Myers, 1988; Crawley, 1989; Hanski et al., 1993; Hudson et al., 1998). In some cases, prey and predator oscillations are truly coupled and mutually density-dependent. In other cases, predator numbers are determined by prey numbers that result from fluctuations in abiotic conditions (e.g., Dempster and Lakhani, 1979). Thus, it is useful to consider separately the degree to which a population is regulated by top-down (predators, parasites, pathogens), or bottom-up (prey, hosts, or their resources) processes (Harrison and Cappuccino, 1995). Populations can also be regulated by lateral or horizontal interactions such as interspecific competition and mutualism (Auerbach et al., 1995; Harrison and Cappuccino, 1995). Coupled oscillations among competitors ultimately can be driven by shifts in the abiotic environment that alternatively favor different competitors. Cyclic oscillations can also be facilitated by spatial dynamics (Kareiva, 1989) including metapopulation dynamics (Taylor, 1990, 1998; Hanski and Gilpin, 1997).

Although there are numerous studies that have shown the importance of predator-prey and competitive interactions among amphibians (see review by Wilbur, 1997), such interactions rarely have been linked to population fluctuations in nature. One exception is population fluctuations that apparently are associated with pathogen outbreaks (Kiesecker and Blaustein, 1997b; Laurance et al., 1996, 1997; Lips, 1999).

Fluctuations in populations that result from temporal or spatial variation in the abiotic environment and/or from interspecific interactions (described above) are considered to be extrinsic regulators of population size. In contrast, fluctuations related to some form of within-population, density-dependent mechanism (such as cohort effects, time lags associated with energy storage, intraspecific competition, cannibalism, and density-dependent dispersal; Denno and Peterson, 1995; Turchin, 1995) are considered to be intrinsic regulators. For species with isolated or fragmented populations, intrinsic regulators have become increasingly framed in the context of metapopulation dynamics (Levins, 1969, 1970; Hanski and Gilpin,

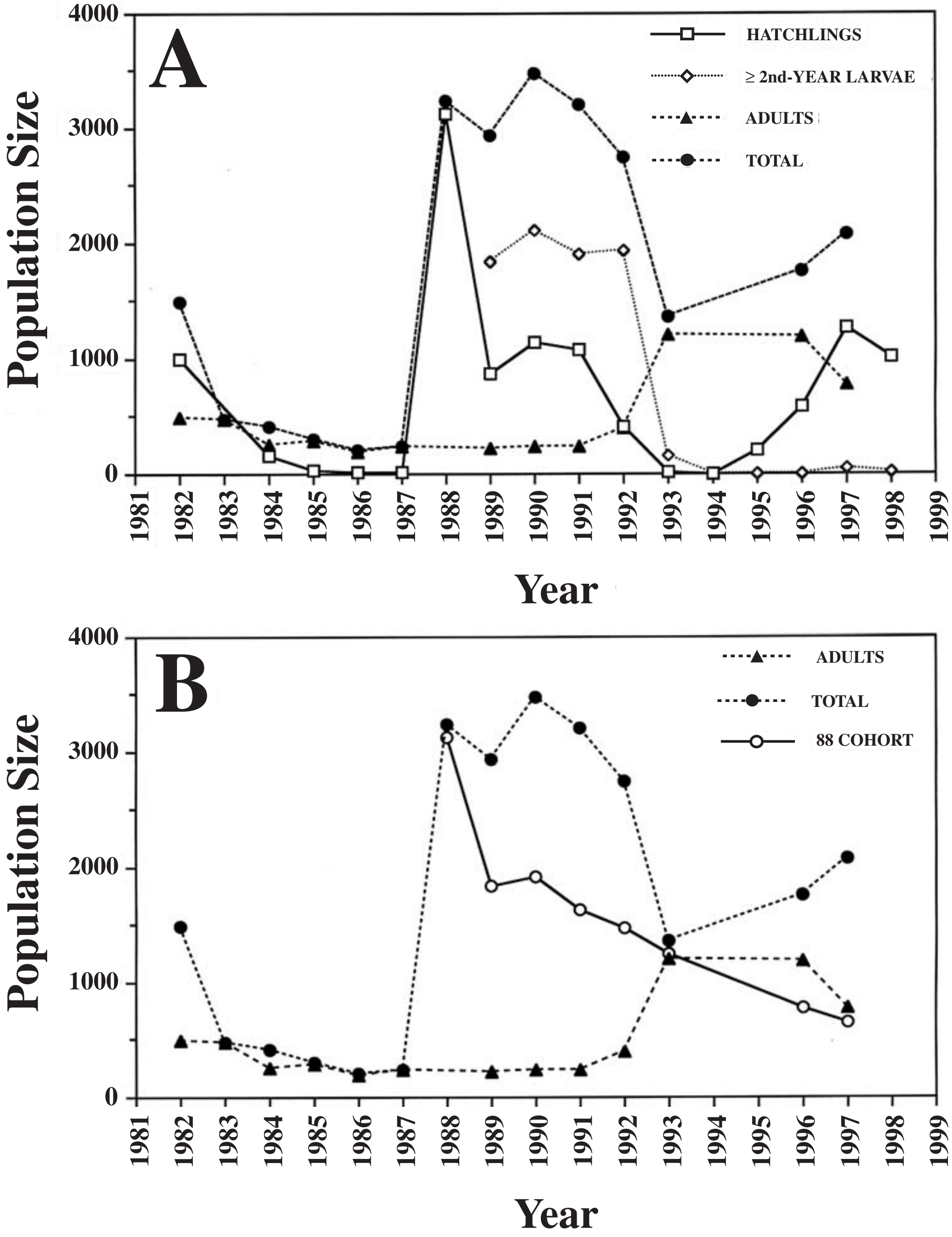


FIGURE 25-1 Population fluctuations of Arizona tiger salamanders from 1982–98 at the Mexican Cut Nature Preserve, based on life-history stage or cohort. Data from 1982–87 are from Harte and Hoffman (1989), which are based on visual counts and are therefore, likely underestimates of the true population size. **(A)** Population estimates of hatchlings, other larvae (2nd year and older), adults (paedomorphic and metamorphic adults combined), and total population size. **(B)** Impact of the 1988 larval cohort relative to the adult and total population size.

1997; Diffendorfer, 1998). Numerous studies on amphibians, particularly salamanders, provide evidence for the potential for intrinsic population regulation (e.g., Petranka and Sih, 1986; Van Buskirk and Smith, 1991; Scott, 1994), but there are few data to document the population outcomes of such regulation.

Evaluation of Alternate Hypotheses

Here we consider the degree to which these various potential causes fit the population fluctuations of salamanders at the MCNP study site. Due to the nature of these fluctuations, we are especially interested in the degree to which different mechanisms could be related to the genesis of large cohorts. We have the following three goals in mind for future study: (1) synthesize current observational and experimental data on population fluctuations to develop a predictive model; (2) use the model to identify the types of data that should be gathered during the course of a continued monitoring program; and (3) experimentally test hypotheses for the causes of these fluctuations.

Salamander Decline from Acidification

The 1980s decline in size of the MCNP salamander population was hypothesized to be related to acid precipitation (Harte and

TABLE 25-1

Summary of Hypotheses and Evidence for Population Fluctuations in Tiger Salamanders at the Mexican Cut Nature Preserve

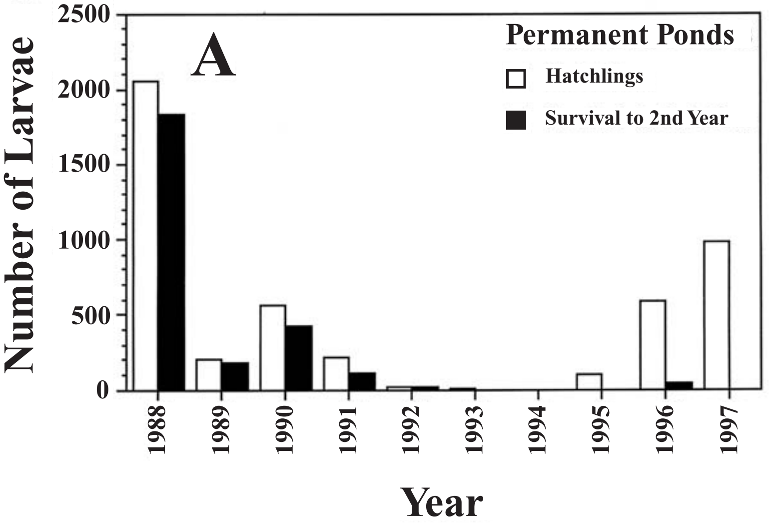
Hypothesis	*Evidence*	*References*
Human Effects		
Episodic acidification	indirect and weak inference for decline in 1980s; not observed in 1990s	Harte and Hoffman, 1989; Wissinger and Whiteman, 1992; Vertucci and Corn, 1996
Climatic Fluctuations		
Winter conditions	minimal winter mortality in some years apparently due to oxygen depletion; not clearly correlated with boom and bust cycles of recruitment	
Terrestrial conditions	inter-annual variation in migration of breeding adults; not clearly correlated with observed population fluctuation	Whiteman, 1997; Whiteman et al., 1999
Drought cycles and survival	annual variation in drying affects hatchling survival; not clearly correlated with observed population fluctuation	Wissinger and Whiteman, 1992; this chapter
Interspecific Interactions		
Predators	no evidence for linked fluctuations in egg predators (caddisflies and leeches); no evidence for linked fluctuations in larval predators (odonates and beetles); no known aquatic predators on paedomorphic or metamorphic adults; no information for predation on metamorphic adults in terrestrial environment	Wissinger et al., 1999a
Parasites and pathogens	no evidence for or against in this population; not correlated with population fluctuations	
Prey	over 100 species exploited; no clear temporal links with prey cycles	Wissinger et al., 1999a,b
Competitors	no evidence for interspecific competition; top predator in the system	Wissinger et al., 1999a
Intraspecific Effects		
Life history and cohort dynamics	lag-time associated with maturation and breeding frequency; life-table recruitment effects of large cohorts	Whiteman, 1994b, 1997
Density-dependent dispersal	isolated population—immigration/emigration unlikely	
Density-dependent growth	salamander growth is density-dependent potential effects on reproduction and mortality	Whiteman, 1994b; Whiteman et al., 1996 this chapter
Density-dependent resource abundance and time lags	benthic invertebrates have declined with rise of 1988 cohort; time lags may influence effects of resources on fluctuations	unpublished data; this chapter
Cannibalism	adults in large cohorts reduce survival of subsequent cohorts; could lead to long-term population cycles	this chapter

NOTE: See text for explanation and discussion of potential interactions among hypotheses.

Hoffman, 1989, 1994). Harte and Hoffman (1989) conducted field experiments using salamander eggs from a nearby habitat and found that pH levels similar to those in the MCNP ponds during snowmelt resulted in reduced egg survival. Although Harte and Hoffman (1989) never monitored the survival of eggs in the ponds themselves, they speculated that episodic acidification during snowmelt in spring was a likely cause of the decline in this population. The recruitment boom in 1988 and subsequent years led us to question the acid pulse-egg mortality hypothesis. For this hypothesis to be correct, acid pulses must occur when eggs are present. During our study, acid pulses always occurred between late May and early June, but always rebounded to circumneutral levels by late June to early July when female salamanders deposited their eggs. Eggs monitored in the field had low mortality that did not vary with pH levels (Wissinger and Whiteman, 1992; unpublished data). Furthermore, *A. tigrinum* are known to be relatively acid-tolerant (Whiteman et al., 1995; Kiesecker, 1996), although geographic variation in pH tolerance can occur (see review by Rowe and Freda, 2000). In short, because of the temporal disparity between acid pulses and egg deposition, we rejected the acid pulse hypothesis as a cause of MCNP population declines (Wissinger and Whiteman, 1992; Vertucci and Corn, 1994, 1996).

Climate and Population Fluctuations

The hypotheses suggesting that climatic fluctuations affect reproduction and/or survival of one or more life history stages in



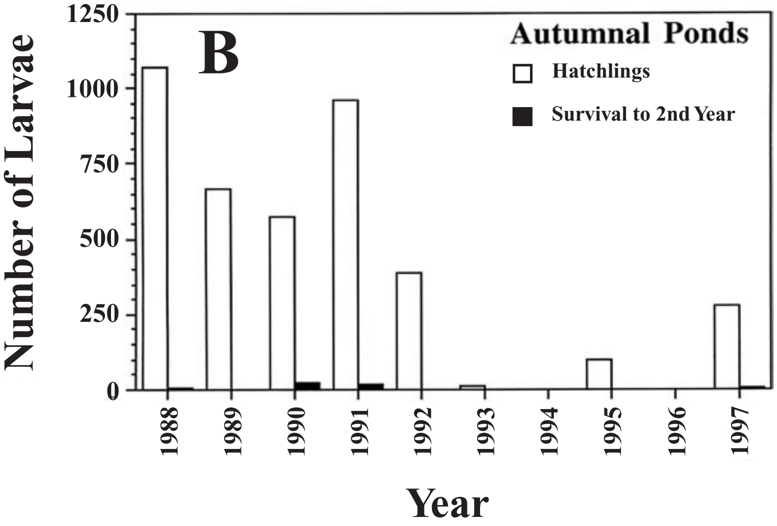


FIGURE 25-2 Larval recruitment at the Mexican Cut Nature Preserve, 1988–98 in permanent **(A)** and semipermanent **(B)** ponds. Open bars represent estimated hatchling production, and dark bars represent estimates of hatchlings surviving to their second year.

this population are supported by data showing that population variation is related to pulses in juvenile recruitment or mortality. Several abiotic factors could be simultaneously affecting different life stages of this species and subsequently leading to such fluctuations. First, as has been shown in many ambystomatids (Douglas, 1979; Semlitsch and Pechmann, 1985; Phillips and Sexton, 1989; Semlitsch et al., 1996), there is considerable year-to-year variation in the number of metamorphic adults that enter MCNP ponds during breeding migrations. Our data show that not all metamorphic females breed every year and that there is considerable variation in the proportion of females that breed in a particular year (Whiteman, 1997). We have not yet determined the causes or even correlates (factors could include variation in snowpack, timing of snowmelt, and invertebrate abundance during the previous year) of this variation, but it is likely that it is driven to some degree by environmental variability.

Second, as in other populations (Pechmann et al., 1991; Rowe and Dunson, 1995), at MCNP there is variation in the survival of larvae depending on whether or not semipermanent wetlands dry (Fig. 25-2B; Wissinger and Whiteman, 1992). Why salamanders continue to deposit eggs in semipermanent habitats in the face of this mortality is probably related to the food-resource benefits of exploiting these habitats in wet years. Larvae that metamorphose from semipermanent habitats are often much larger and in better condition than those from permanent basins (Whiteman et al., unpublished data). However, our data do not show a correlation between recruitment over the entire population and basin drying; wetlands dried in several of the largest recruitment years (e.g., 1988 and 1990) and remained wet in some years with low recruitment (e.g., 1992, 1993, and 1995). Thus, while drying has a strong effect on recruitment in individual semipermanent wetlands (Fig. 25-2B), drying alone does not provide a sufficient explanation for the observed patterns of fluctuation in the overall population.

Third, there is considerable variation across years in mortality among larvae and paedomorphic adults in permanent wetlands. In some years, large numbers of dead animals are observed in the ponds in early spring after snowmelt. Measurements taken through the ice suggest that this mortality is related to low oxygen levels during winter (a classic winterkill scenario; see Bradford, 1983; Lannoo, 1998c; Larson, 1998). Such winter mortality could kill large numbers of paedomorphic adults generated by boom cohorts (see below), but is not likely to drive the variability that produces boom cohorts (also see Vertucci and Corn, 1996). This is true in part because paedomorphic adults are male-biased in this population and paedomorphic females breed less frequently than metamorphic females (Whiteman, 1997), so paedomorphic egg production is not as important to cohort production as metamorphic reproduction (see below). Thus, winter mortality might contribute to the decline phase of salamander population cycles, but in and of itself is not sufficient to initiate these cycles. Because there is some evidence that smaller larvae are more susceptible to winter mortality than larger ones (Whiteman et al., unpublished data), it is also possible that winter conditions could play a role in lengthening population cycles by reducing the size of larval cohorts, and thus their impact on population dynamics.

Interspecific Interactions

Cyclic fluctuations in population size can be the result of interactions with competitors, predators, parasites, pathogens, prey, or hosts (Table 25-1). Several of these population interactions are unlikely explanations for the fluctuations that we have observed in this population. As described above, Arizona tiger salamanders are the top predators in this system and large larvae and adults are unlikely to be regulated by top-down processes related to predation. Salamander eggs are eaten by caddisfly larvae and leeches, while odonate and dytiscid beetle larvae consume hatchling larvae. However, the overall effect of these predators on salamander mortality appears to be minimal (Wissinger et al., 1999a). Thus, we currently have no evidence that the fluctuations in this population are predator induced (Table 25-1).

We currently have no evidence that parasites and pathogens are important in this system. However, because parasites often underlie cyclic population fluctuations in vertebrate hosts (e.g., Anderson and May, 1980; Dobson and Hudson, 1992; Ranta, 1992; Sait et al., 1994; Poulin, 1995; Hudson et al., 1998), we recognize the importance of testing this hypothesis. We also have no evidence for competitor-induced cycles. None of the top invertebrate predators (beetles, odonates) that are likely to compete with larvae have fluctuated during the ten years of our study (Wissinger, unpublished data). Finally, while there have been changes in the overall abundance of prey taxa during our study (see below), there have been no obvious patterns of fluctuation in species that dominate the diets of metamorphic adults (fairy shrimp), paedomorphic adults and older larvae (immature stages of dipteran flies, caddisflies, and beetles), or hatchlings (cladocerans and copepods).

Life History and Cohort Dynamics

The observed population fluctuations at MCNP could be related to the effects of large cohorts on population demography. Several types of demographic mechanisms are known to lead to cyclic population fluctuations. First, because female sexual maturation in this population requires a minimum of three years, and usually four to six years (Whiteman, 1994b; unpublished data), there is a time-lag in reproduction. Thus the contribution of a large or small cohort to annual recruitment will lag behind the appearance of that cohort. Maturation varies by morph with metamorphic females breeding approximately one to two years earlier than paedomorphic females. Furthermore, metamorphic females breed every 1.8 years on average, whereas paedomorphic females breed every 2.4 years (Whiteman, 1994b, 1997). When metamorphic and paedomorphic females from the same cohort converge in reproduction (as they might at ages 6, 11, and 13), one could expect recruitment booms followed by a slow decline in population size on a twelve to nineteen-year cycle. Second, this is a long-lived species, and a single cohort can have long-term demographic impacts. The large 1988 cohort has dominated the Mexican Cut population over the past 12 years (Fig. 25-1B). Major changes in population size due to mortality have all been associated with the events that affect the 1988 cohort (e.g., winter mortality). However, no reproductive pulses associated with this cohort have been documented.

Density-Dependence, Resource Abundance, Time Lags, and Cannibalism

Birth rate, death rate, emigration, and immigration vary with population density, and time lags in the responses of these variables with respect to density can lead to cyclic fluctuations in population size. We do not suspect that density-dependent emigration or immigration is important in this extremely isolated population. There is experimental evidence for density-dependent reproduction and survival in amphibians (e.g., Wilbur, 1977a,b; Petranka, 1989c; Scott, 1990, 1994), but there are relatively few data from multiple cycles of fluctuation in natural populations. At MCNP, we have documented density-dependent growth both in larvae (Whiteman, 1994b) and adults (Whiteman et al., 1996). We have also found that the overall abundance of prey resources has decreased as the total biomass of the 1988 cohort has increased (Whiteman et al., unpublished data). Population fluctuations associated with density-dependent effects are most likely when there is a lag time between resource depression and a decline in reproduction and survival (May, 1976). For example, stored energy can sustain reproduction and survival in populations that leads to cycles of carrying capacity overshoot and subsequent declines (e.g., Goulden and Hornig, 1980). The potential for such time lags could be inferred by assessing changes in body fat or body condition with respect to the timing of food availability. For example, we found that metamorphic adults increase their body condition (mass per SVL) by feeding on fairy shrimp in semipermanent wetlands (Whiteman et al., 1996). Although the effect of these food resources on subsequent reproduction is unclear, fairy shrimp consumption may account for the reduced interval between breeding attempts in metamorphic females (Whiteman, 1997). This, in turn, should affect the overlap in breeding between the two morphs and thus produce a potential mechanism for boom cohorts (see above).

Cannibalism can give rise to population fluctuation cycles (Fox, 1975; Polis, 1981, 1988; reviews by Elgar and Crespi, 1992). At MCNP, large larvae and paedomorphic adults cannibalize small larvae (Wissinger et al., 1999a; Whiteman, unpublished data). Hatchlings avoid larger conspecifics by foraging at different times and in different microhabitats (Marcus and Whiteman, in preparation; Wissinger et al., unpublished data), and hatchling survival is greater in ponds without larger larvae (Whiteman et al., unpublished data). If cannibalism is a major source of hatchling mortality, then large cohorts such as the 1988 generation could reduce or eliminate recruitment in subsequent years. For example, second-year recruitment was high between 1988 and 1991 in permanent ponds when adult densities were low (Figs. 25-1A, 25-2A). As the number of paedomorphic adults increased from the maturation of the 1988 cohort, hatchling survival declined dramatically (1995–97). We cannot rule out that reduced resource abundance (see above) was responsible for this lack of recruitment success, but the ontogenetic diet shift that occurs in these salamanders (Wissinger et al., 1999a) suggests that competition between paedomorphic adults and hatchlings is unlikely to substantially reduce hatchling survival.

Cannibalism has been linked to cyclic fluctuations in population size in a variety of other stage-structured populations (e.g., Alm, 1952; Brinkhurst, 1966; Mertz and Robertson, 1970; Mertz, 1972; King and Dawson, 1973; Orr et al., 1990; Ruxton et al., 1992; Van Buskirk, 1992). The role of cannibalism in generating cyclic fluctuations in fish populations provides an intriguing model for the MCNP salamander population. Cannibalism by adult perch in large cohorts can reduce or completely eliminate subsequent recruitment for years. Cohort suppression is most likely to lead to long-term (10–15 years) population fluctuations in low nutrient habitats and in the absence of potential competitors (Le Cren, 1955, 1965; McCormack, 1965). Interestingly, MCNP is ultraoligotrophic and Arizona tiger salamanders are the lone vertebrate predator at the top of the food web (Wissinger et al., 1999a).

Lessons from MCNP for Population Regulation and Amphibian Conservation

In some cases of amphibian decline (e.g., habitat destruction), human causes are so obvious that alternative hypotheses only distract (e.g., Blaustein and Wake, 1995). In other cases, declines are not as easily linked to a specific causal agent and it is important to consider alternative explanations (Pechmann and Wilbur, 1994; Sarkar, 1996). For the latter situation, we must understand how to distinguish between true declines and population fluctuations. It is equally important, however, to determine the demographic warning signs of amphibian populations that are susceptible to decline.

Multiple Hypotheses and Key-Factor Analysis

The approach that we have taken loosely resembles a key factor analysis, a method that is often used for insect populations. A key factor analysis attempts to identify which of the many sources of mortality at different life history stages are the density-dependent (and therefore key) regulators of population size (Varley and Gradwell, 1960, 1970; Varley et al., 1973; Manly, 1977; Stiling, 1988; Yamamura, 1999).

A similar approach to population regulation in amphibians should be useful for distinguishing between anthropogenic declines and natural population fluctuations (c.f. Murdoch, 1994). At MCNP, we are in the process of evaluating the most likely hypotheses of population regulation by documenting a variety of key demographic variables at different population sizes. One result of this research will be an understanding of how salamander demography changes during a cycle, which will be used to pinpoint variables that can predict future cycles. For example, three variables appear to have a strong impact on MCNP Arizona tiger salamanders: age structure, age at maturity, and frequency of breeding. The interaction of these three variables (and the forces that influence them, such as variation in climate and cannibalism) might explain the boom and bust pattern we have observed. If similar basic demographic data were available for a presumed declining species, or a closely related congener, we would have valuable insight into whether true declines have occurred or if the species has an equilibrial life history, such as the Arizona tiger salamanders at MCNP. Unfortunately, such basic demographic data are not available for most amphibians (Duellman and Trueb, 1986; see also Pechmann and Wilbur, 1994).

We propose that similar multiple-hypothesis, key-factor studies be used across several representative taxa to identify alternative potential causes (and their interactions) for population fluctuations. Organisms should be sampled in areas with minimal human impacts so that baseline information can be collected from presumed healthy populations. Such analyses may provide insights into the mechanisms of population regulation, identify the variables most closely associated with fluctuations in each group or geographic domain, and potentially help predict the early warning signs of declining populations. We do not suggest that such data sets replace current conservation efforts. Instead, we are promoting the idea of sound scientific knowledge of amphibian population regulation to better understand and predict population fluctuations and declines.

There are several caveats to this approach. First, for organisms with complex life cycles, identifying a key factor in one life stage does not necessarily mean that factor regulates the overall population (Turchin, 1995). Second, population regulation can often be the result of several mechanisms that are simultaneously operating or are of varying importance at different stages of population cycles (Myers and Rothman, 1995). Third, factors can differ between locations within species (e.g., Berven, 1995), so intraspecific comparisons must be conducted with caution.

Long-Term Monitoring

Many studies have shown that understanding population fluctuations and their causes requires long-term population monitoring (e.g., Blaustein et al., 1994a; Semlitsch et al., 1996). Turchin (1995) suggests that the absence of evidence for population cycles is usually the result of a short-term data set—the longer we look, the more likely it is that we find evidence for fluctuations and their causes. The inherent cost to this approach is that if populations are truly declining, by the time it is clearly recognized it may be too late.

Another problem associated with long-term population monitoring is that causes will likely differ among species and habitats. For example, density-dependent dispersal is a likely hypothesis for fluctuations in many situations (reviewed by Denno and Peterson, 1995), but it is probably not important for an isolated population such as the one at MCNP. Similarly, although interspecific interactions are important in some amphibian communities (Wilbur, 1982; Stenhouse et al., 1983; Morin, 1986; Cortwright, 1988; Semlitsch et al., 1996; reviewed by Wilbur, 1997), they are unlikely to be important at our study site (one species, top generalist predator). However, the true utility of multiple, long-term studies is an understanding of how geographic and/or species-specific differences affect population fluctuations.

Computational Models and Ecological Experiments

One way to shorten the minimum time needed to understand the dynamics of population fluctuations is to develop predictive/computational models to transcend the long-term, real-time nature of the observed population fluctuations (see Sarkar, 1996). In collaboration with Dr. Ian Billick, we are using our basic demographic and ecological information to parameterize such models and determine what additional data will be necessary to test our hypotheses. For example, knowing the per capita effects of cannibalism on juvenile survival is important for testing the hypothesis that large cohorts can suppress recruitment and cause cyclic fluctuations. Similarly, the experimental manipulation of a particularly important food resource (e.g., fairy shrimp) would allow the inclusion of prey resources into a computational model predicting reproductive output. Incorporating a variety of such data into computational models will allow for the simultaneous testing of a subset of hypotheses that might operate alone or jointly to produce observed fluctuations. We agree with Sarkar (1996) that long-term monitoring in combination with the interim use of explicit and predictive models will help direct monitoring efforts. This, in turn, will allow researchers to maximize the collection of data most likely to be useful for the conservation and restoration of amphibian populations.

Summary and Conclusions

Our work with the MCNP Arizona tiger salamanders suggests a fluctuating population that is regulated by abiotic (pond hydroperiod) and biotic (resource abundance, life history, and cannibalism) factors. Although there is still much to learn about the interaction of these variables, a multiple-hypothesis, long-term demographic monitoring approach, when combined with planned models and experiments, should help predict future fluctuations and, perhaps, help understand cyclic phenomena in other species. Our results thus far suggest that similar approaches on relevant taxa throughout the globe will provide important and useful information for understanding amphibian population changes and the associated natural or anthropogenic factors that influence them.

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