

EFFECTS OF LARVAL DENSITY DEPENDENCE ON POPULATION DYNAMICS OF *AMBYSTOMA OPACUM*

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ABSTRACT: Using data and insights derived from laboratory experiments, 9 yr of field experiments, and numerous observations of natural populations of the marbled salamander, *Ambystoma opacum*, we constructed a model to study the effects of larval density dependence on population dynamics. The model includes density-dependent larval survival and size at metamorphosis, density-independent survival in other stages, and size- and age-dependent terrestrial growth and reproduction. Terrestrial females are tracked individually. When survival in non-larval stages is high, equilibria are unstable, and high reproductive potential at low population densities leads to population dynamics with wide fluctuations. Density-dependent larval regulation, which decreases in intensity with decreasing survival in other stages, is much more sensitive to terrestrial survival than to egg survival. Density-dependent size at metamorphosis delays reproduction by as much as 3 yr and reduces average clutch size by as much as 70%. Applied to a natural population with low annual recruitment (range 0.7-7.9 metamorphs per breeding female over 9 yr), model results indicate that either high terrestrial survival ($>0.7 \text{ yr}^{-1}$) or immigration is required to maintain the population. The general sensitivity of the model population to terrestrial parameters underscores the importance of additional data on the demography of the terrestrial stages, as well as on processes controlling year-to-year variation in recruitment of larvae. This information is critical to understanding population regulation and to developing an adequate basis for conservation or management plans.

Key words: *Ambystoma opacum*; Amphibians; Complex life cycle; Density-dependence; Model; Population dynamics; Salamander

AMONG pond-breeding amphibians, density-dependent effects on the success of the larval stage are a common phenomenon (Wilbur, 1980). Although larval density dependence has been observed in nearly all species of the salamander genus *Ambystoma* that have been studied (Scott,

1990; Van Buskirk and Smith, 1991), its contribution to regulating the dynamics of natural populations remains poorly understood (Petranka, 1989; Scott, 1994; Van Buskirk and Smith, 1991; Wilbur, 1980). *Ambystoma* exemplifies some of the problems in understanding population dynam-

ics for amphibians generally. Dynamics of amphibian populations are known to be influenced by an interplay of competition, predation, abiotic conditions, and other factors such as parasitism (Pechmann et al., 1989, 1991; Wilbur, 1987). The complexity of the amphibian life cycle, which typically includes metamorphosis and a shift in habitat between the larval and adult stages, exacerbates the difficulties in evaluating the contribution of any single factor to the regulatory processes.

For *Ambystoma*, as well as for other amphibians, larval density influences growth and survival in the larval stage, duration of the larval period, and body size at metamorphosis (Cortwright, 1988; Petranka, 1989; Scott, 1990; Semlitsch 1987a,b; Smith, 1990; Stenhouse, 1985; Stenhouse et al., 1983; Van Buskirk and Smith, 1991). Delayed effects of larval density may also influence survival and reproduction of adults. In *A. opacum*, individuals reared at low larval densities generally reach reproductive maturity at earlier ages and larger sizes and exhibit higher survival to first reproduction than those reared at high larval densities (Scott, 1994). Similar effects have been demonstrated in other species of salamanders (paedomorphic *A. talpoideum*: Semlitsch, 1987a; paedomorphic *Notophthalmus viridescens*: Harris, 1987), as well as in anurans (*Rana sylvatica*: Berven, 1988, 1990; Berven and Gill, 1983; *Pseudacris triseriata*: Smith, 1987).

Experimental manipulations to test the effects of larval density dependence on dynamics of the entire population have been limited by the long life cycle of many amphibians and the difficulties in confining and censusing terrestrial stages (but see Pechmann, 1994, 1995). A model of population dynamics may serve as a complementary experimental system, limited in realistic details (Hairston, 1989) but potentially powerful in precision or generality. A model can be used to organize information about regulatory processes, to explore the influences of well quantified processes, and to evaluate potential importance of poorly quantified processes.

In this paper, we develop a stage-struc-

tured model for the marbled salamander (*Ambystoma opacum*) to study effects of larval density dependence on population dynamics. The model belongs to a large family of stage-structured models with density dependence (see Charlesworth, 1980, and Caswell, 1989, for introductions to these models). Our model is based on data and insights derived from laboratory experiments, 9 yr of field experiments, and numerous observations of natural populations. In the model, survival of larvae and body size at metamorphosis depend on larval density. Survival in the egg and terrestrial stages is density-independent. Adult growth and probability of breeding depend on body size and age, and clutch size depends on body size. The model tracks post-metamorphic females individually, to permit accounting for effects of variation in properties such as body size within a cohort.

In the analyses that we present here, we use the model first to estimate demographic properties of the salamander populations. We use it also as an experimental system to test the importance of processes that have been intensively studied only in the larval stage to dynamics of the entire population. We define conditions under which regulation by larval density-dependent processes may be strong and evaluate the contribution of density-dependent size at metamorphosis to the regulatory process. We consider the effect of variation in size at metamorphosis among individuals within a cohort on dynamics of the population. Finally, we use the model to test the plausibility of stage-specific survival rates estimated for a natural population. The analyses suggest which components of the model are important to producing a useful description of a natural population, where the observational basis for the model is weak, and what additional parameters should be included in future models.

NATURAL HISTORY AND DEMOGRAPHY OF *AMBYSTOMA OPACUM*

The marbled salamander, *Ambystoma opacum*, is found throughout much of the eastern United States (Conant and Collins,

1991). The terrestrial juveniles and adults live in soil and leaf litter and forage for insects and other invertebrates. In autumn, the adults migrate to ponds that are partially or completely dry and that are likely to refill later in autumn or in winter (Noble and Brady, 1933). Unlike most species of its genus, the adult marbled salamanders court and breed on land rather than in water (Krenz and Scott, 1994; Nussbaum, 1985). After breeding, the female lays eggs in a nest and often remains until the nest is inundated (Jackson et al., 1989; Noble and Brady, 1933; Petranka et al., 1982). The aquatic larvae prey mainly on aquatic microcrustaceans and insects (Petranka and Petranka, 1980; Stewart, 1956). After metamorphosis, the newly metamorphosed juveniles migrate from the pond margin to terrestrial habitats.

Populations of *A. opacum* have been studied on the United States Department of Energy's Savannah River Site (SRS) in Aiken and Barnwell counties, South Carolina for over 15 yr. Nest success (the percentage of eggs that survive to hatch and become free-swimming larvae) depends on the date and extent of pond filling. At Ginger's Bay, mean nest success in a year when the bay filled relatively late (3 January) was 20% (Jackson et al., 1989). Nest success of >80% has been observed for individual nests that are flooded by late November (D. E. Scott, unpublished data). Initial larval densities thus vary greatly from site to site and from year to year (Scott, 1990), depending on the number of breeding females, mean clutch size, nest success, and pond area. Larval densities ranging from <1–47 animals·m⁻² have been reported for natural populations (Scott, 1990). Low larval density promotes faster growth, larger body size at metamorphosis, shorter larval periods, and greater larval survival (Scott, 1990). In the study populations at SRS, the larval period is 3–6 mo, followed by metamorphosis and a terrestrial growth stage of 1–6 yr until reproductive maturity is reached (Scott, 1994). Larval survival values ranging from 0–93% have been estimated for enclosed natural populations on the SRS (Scott, 1990). Larval density is one of the primary

determinants of body size at metamorphosis. Snout–vent length at metamorphosis, which ranges from 26–54 mm for populations at SRS, is related to terrestrial survival and to size and age at first reproduction (Scott, 1994). Size at first reproduction, measured on marked individuals in natural populations at SRS, ranges from 45–66 mm (Scott, 1994). Clutch size, which is positively correlated with body size, may range from 30–200 eggs (Kaplan and Salthe, 1979; Scott, 1994). Terrestrial survival of adults, estimated from marked animals in natural populations, is about 50% per year (D. E. Scott, unpublished data). Maximum longevity for wild *A. opacum* in South Carolina is approximately 9–10 yr (D. E. Scott, unpublished data).

MODEL

The model of *Ambystoma opacum* includes egg, larval, terrestrial juvenile, and adult stages. The maximum life span is 10 yr, counting age from the time of oviposition. Duration of the egg stage is fixed at 0.2 yr, duration of the larval stage is fixed at 0.3 yr, and duration of the terrestrial juvenile stage is fixed at 0.5 yr. In the model, we consider females of age ≥ 1 yr to be adult, although the age at first reproduction is variable. Egg survival p_E is the probability of surviving the egg stage from egg laying to hatching; larval survival p_L is the probability of surviving the larval stage from hatching to metamorphosis; juvenile survival p_J is the probability of surviving the terrestrial juvenile stage from metamorphosis to the end of the first year; and adult survival p_A is the probability of surviving as a terrestrial adult from the beginning to the end of each subsequent year for years $i = 1$ to 9. Females may breed annually from age 2 yr to age 10 yr. Breeding occurs at the beginning of the year. The number of eggs in the clutch of eggs produced by the female of age i is C_i , and the probability of breeding is b_i .

Before specifying the forms of these relations and analyzing their effects on population dynamics, we consider a few general properties of such a model. For a population at equilibrium, each individual on

average produces enough offspring to replace itself. This condition of stationary population growth is represented in demographic terms by setting the equation for net reproductive rate R_0 equal to 1:

$$R_0 = \sum_{i=\alpha}^{\omega} l_i m_i = 1. \quad (1)$$

R_0 is the lifetime expectation of female offspring to a female, l_i is the probability that she survives from age 0 to age i , m_i is the number of female offspring that she produces at age i , and α and ω are the ages at first and last reproduction. Substituting the appropriate terms from the salamander model, we have

$$R_0 = \sum_{i=2}^{10} p_E p_L p_J p_A^{i-1} \frac{b_i C_i}{2} = 1. \quad (2)$$

Note that for each term in the summation, the survivorship term l_i is replaced by a string of stage-specific survival probabilities multiplied to yield the probability of surviving through each stage from laying of the egg to the end of year $i - 1$ (or the beginning of year i). The fecundity term m_i is replaced by the probability of breeding b_i multiplied by the clutch size C_i , which, assuming a 1:1 sex ratio, is divided by two to estimate the number of female offspring in each clutch.

Suppose that the salamander population is regulated by density-dependent survival in the larval stage, so that larval survival p_L depends inversely on the larval population N_L . We can re-arrange Equation 2 to examine larval survival at equilibrium:

$$\hat{p}_L = \frac{2}{p_E p_J \sum_{i=2}^{10} p_A^{i-1} b_i C_i}. \quad (3)$$

Larval survival may be interpreted as a measure of the intensity of density-dependent regulation. At equilibrium, larval survival depends inversely on survival in other stages and on clutch size. Decreasing survival in the egg, juvenile, or adult stages or decreasing fecundity will weaken density-dependent regulation by increasing larval survival at equilibrium.

The population of larvae at equilibrium \hat{N}_L is calculated from larval survival at

equilibrium, the function relating larval survival to larval density (an example of such a function is described in the next section), and the area of larval habitat. Equilibrium numbers for populations in other stages, including terrestrial juveniles N_J and adults N_A , indexed by age class $i = 1$ to 10 yr, can then be calculated from the larval population at equilibrium:

$$\begin{aligned} \hat{N}_J &= \hat{p}_L \hat{N}_L \\ \hat{N}_1 &= p_J \hat{N}_J \\ \hat{N}_2 &= p_A \hat{N}_1, \text{ etc.} \end{aligned} \quad (4)$$

The dependency of the equilibrium population on other parameters of the growth model contrasts with the simple dependency of the equilibrium on the carrying capacity K in the familiar logistic growth model for a homogeneous population.

Density Dependence of Larval Survival and Size of Metamorphs

To describe the effect of larval density on survival of larval *A. opacum*, we combined results from large-scale field enclosures at three sites on the SRS over 6 yr (1986–1988: Scott, 1990; 1991–1993: D. E. Scott, unpublished data). The probability of larval survival from hatching to metamorphosis was high (median 0.7, range 0.4–0.95, $n = 21$ pens in seven experiments) at larval densities of 4–12 animals·m². The probability was low (median 0.25, range 0.05–0.4, $n = 12$ pens in four experiments) at larval densities of 30–41 animals·m². These data represent years that were favorable for larval survival, because the habitat remained inundated through the entire season for larval development. The response of larval survival to larval density D_L in animals·m² is represented in the function

$$\begin{aligned} p_L &= 0.410428 \arctan(1.5 - 0.1D_L) \\ &+ 0.596634 \\ &\text{for } D_L \leq 100 \\ p_L &= 0 \text{ for } D_L > 100 \end{aligned} \quad (5)$$

where $D_L = N_L/A$ and A is the area of the pond in m². This function is shown in Fig. 1A.

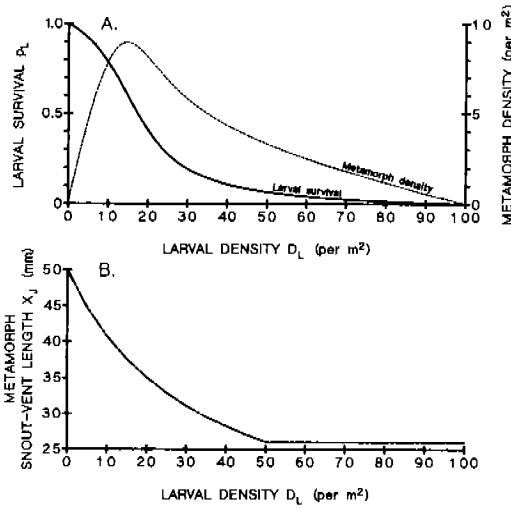


FIG. 1.—Larval density-dependence. (A) Larval survival is given by Equation 5; (B) snout-vent length at metamorphosis is given by Equation 6.

Data from larval density manipulations and natural populations (Scott, 1994) were used to estimate the relation between larval density and snout-vent length (SVL) X_j in mm of terrestrial juveniles immediately after metamorphosis:

$$X_j = \frac{1315}{(D_L + 33)} + 10.2$$

for $D_L \leq 50$

$$X_j = 26 \quad \text{for } D_L > 50. \quad (6)$$

This function is shown in Fig. 1B.

In the computer simulation, SVL at metamorphosis can be described by a normal distribution with mean $\mu = X_j$ and standard deviation (SD). The distribution is truncated above at $\mu + 2$ SD and below at $\mu - 2$ SD or the minimum length for metamorphs (26 mm), whichever is greater. Individual metamorphs are assigned values chosen at uniform probability intervals from the truncated normal size distribution. For *Ambystoma opacum* at Ginger's Bay, the mean of standard deviations for size at metamorphosis was 2.08 mm with range 1.83–2.37 mm for 8 yr when >20 metamorphs were measured. In simulations to test the effect of variation in size at metamorphosis among individuals

within a cohort, we set SD = 2.0 mm. In other simulations, we set SD = 0 mm to facilitate computation of statistics for the populations at equilibrium, such as equilibrium larval density \hat{p}_L from Equation 2.

Growth and Reproduction of Terrestrial Females

Although the essential feature of a demographic model is simply a schedule for survival and reproduction, incorporating size and growth into the model provides a way to compute the effects of age and of body size at metamorphosis on the breeding schedule and clutch sizes. After metamorphosis, the model tracks only female animals, under the assumption that the reproductive schedule is determined primarily by the age and size of the females. This assumption is termed demographic dominance of females (Charlesworth, 1980). Half of the metamorphosing larvae are assumed to be female. Sex ratios of larval *A. opacum* have not been measured. However, because sex determination appears to be controlled genetically, we have no basis for assuming that sex ratios are skewed (Scott, 1994).

Growth of terrestrial females depends on age and body size:

$$X_1 = 0.758 X_j + 19.9$$

$$X_2 = 0.937 X_1 + 7.36$$

$$X_3 = X_2 + 2.5$$

$$X_4 = X_3 + 1.5$$

$$X_i = X_{i-1} + 0.5 \quad \text{for } i \geq 5. \quad (7)$$

These relations were estimated from data on four large ($n > 1000$ metamorphs) cohorts of marked animals at Ginger's Bay (D. E. Scott, unpublished data). Snout-vent length X_i in mm is assessed at the beginning of the year, when breeding occurs. Growth curves determined from these equations are shown in Fig. 2.

The probability of breeding b_i depends on age and body size:

$$b_i = a_i[0.129 \arctan(0.5X_i - 26.25) + 0.17]$$

for $i \geq 2$ and $X_i \geq 45 \quad (8)$

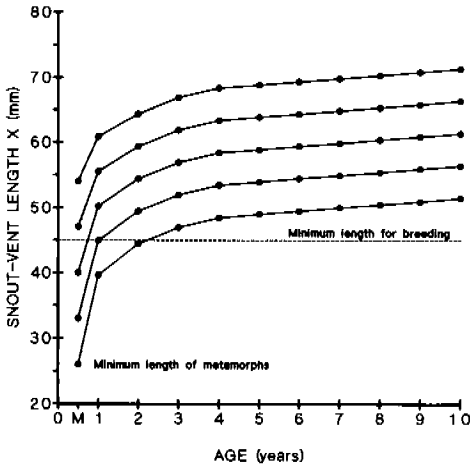


FIG. 2.—Growth curves for terrestrial females with various sizes at metamorphosis. Growth is given by Equation 7.

where the age factor a_i is 0.1 in the second year and 1.0 in subsequent years. This function was devised to approximate reproductive frequencies observed in three very large ($n > 4000$) groups of mixed-age females that were first captured as adults at Ginger's Bay (D. E. Scott, unpublished data). The value of the age factor a for females of age $i = 2$ yr is based on data in Scott (1994). Females of age $i = 1$ yr or length $X_i < 45$ mm do not breed. Clutch size depends on body size (Scott, 1994):

$$C_i = 7.45 X_i - 323 \quad (9)$$

(clutch size is rounded to the lower integer). These functions are shown in Fig. 3.

Computations

The model was implemented with computer programs written in Fortran. To compute larval survival and population sizes at equilibrium, Equations 3 and 4 were solved using schedules of survival and fecundity determined from the model (Equations 5–9). When size at metamorphosis depended on larval density, an iterative search procedure was used to solve Equation 3.

In the simulations, survival of each terrestrial female at the end of each year was determined by drawing a number from a uniform distribution over the interval [0, 1] and comparing it to the appropriate

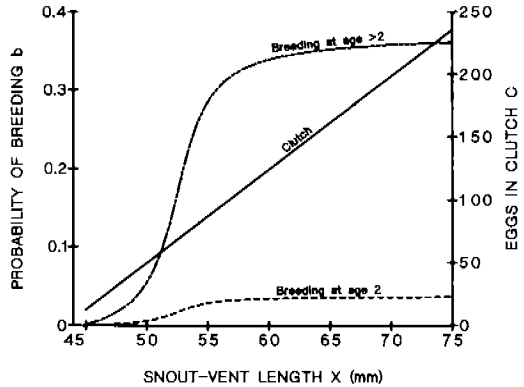


FIG. 3.—Probability of breeding and clutch size. Probabilities of breeding for females of age 2 yr and of age ≥ 2 yr are given by Equation 8. Clutch size is given by Equation 9.

probability. The fate of females eligible to breed was evaluated similarly. The programs accessed a pseudorandom number generator and other statistical subroutines of the IMSL/Stat Library.

Ginger's Bay

We set pond area in the model to 8000 m², the approximate area of Ginger's Bay when the pond is completely full. To simplify the analyses, we equated juvenile and adult survival. Based on the field data for nest success and adult survival at Ginger's Bay, we set egg and terrestrial survival at moderate levels ($p_e = p_j = p_A = 0.5$). We then compared results from computer simulations with field data for metamorphs and breeding females, which have been censused at a drift fence surrounding the pond for 9 yr (1987–1995: D. E. Scott, unpublished data). The yield of metamorphs, plotted against breeding females, was much higher for the model than for Ginger's Bay (median 3.0, range 0.7–7.9 metamorphs per breeding female). The average number of metamorphs is a product of the number of breeding females, average fecundity, egg survival, and larval survival. Assuming that egg survival was known less accurately than either average fecundity or larval survival, we adjusted egg survival in the model. A severe reduction, to $p_e = 0.04$, was required to bring the model results down into the range for

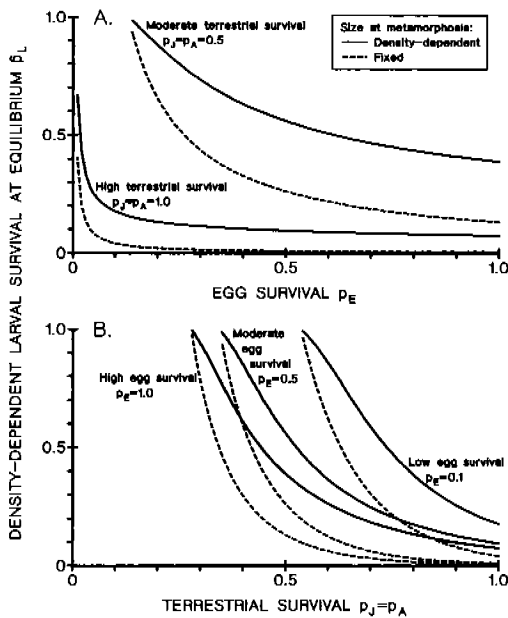


FIG. 4.—Larval survival at equilibrium. Values were calculated by solving Equation 3 with fixed ($X_J = 50$ mm) or density-dependent size at metamorphosis. Size at metamorphosis does not vary among members of a cohort ($SD = 0$ mm). Note that a curve for low terrestrial survival ($p_J = p_A = 0.1$) is omitted from (A) because equilibria with $\hat{p}_L \leq 1.0$ do not occur for any values of egg survival; thus the populations always decline to extinction.

the data from Ginger's Bay. For the population at Ginger's Bay, some of the reduction in survival probably occurred at the larval stage, rather than at the egg stage, but the field data provide no basis for partitioning the reduction between these stages.

The combination of very low egg survival and moderate terrestrial survival caused the model population to decline to extinction. The lowest level of terrestrial survival at which persistence occurred was just above $p_J = p_A = 0.662$. For the comparisons with Ginger's Bay, we set terrestrial survival to a value slightly above this minimum ($p_J = p_A = 0.7$, model G1) or to a high value ($p_J = p_A = 1.0$, model G2).

RESULTS

In the model of population dynamics for *Ambystoma opacum*, larval survival is determined directly by larval density, thus

indicating the strength of larval density dependence. The equilibrium value for larval survival, given by Equation 3, depends on survival in other stages, as well as on fecundity. Egg and terrestrial survival are independent of population density in the larval stage or any other stage. Reducing terrestrial survival from a high ($p_J = p_A = 1.0$) to a moderate ($p_J = p_A = 0.5$) level (Fig. 4A) has a stronger effect on larval survival at equilibrium than does reducing egg survival from a high to a moderate level (Fig. 4B).

Through its effect on size at metamorphosis, larval density dependence influences reproductive traits as well as larval survival. We measured this effect by comparing larval survival at equilibrium between models with density-dependent and fixed size at metamorphosis. We fixed size at metamorphosis at its maximum of 50.0 mm, the value given by Equation 6 at $D_L = 0$. With density-dependent size at metamorphosis, the smaller sizes at metamorphosis cause reductions in fecundity and delays in reproduction. The result is greater survival of larvae at equilibrium with density-dependent size at metamorphosis than with fixed size at metamorphosis (Fig. 4). In the most extreme case, with $p_E = p_J = p_A = 1.0$, \hat{p}_L increases from 0.004–0.07. First reproduction is delayed, on average, from 4.5–7.8 yr. The average size of breeding females drops from 66.6–50.7 mm, with a corresponding decrease in average clutch size from 173–54 eggs. Equilibrium population structure is also altered. For this example, density-dependent size at metamorphosis cuts the equilibrium larval density in half (from 93.4–47.8 animals·m⁻²) and increases the terrestrial population by nine-fold.

To study dynamical properties of these models, we used 100-yr trajectories of populations initiated with 4000 eggs in a pond of 8000 m². This initial population is far from the size and structure at equilibrium under any conditions. Mean size at metamorphosis is density-dependent (Equation 6) with $SD = 0.0$ mm. We illustrate population trajectories of female metamorphs and female adults for combinations of high, moderate, or low egg survival ($p_E = 1.0$,

TABLE 1.—Demographic characteristics for model populations of *Ambystoma opacum*. The exponential model assumes no density dependence, the value for larval survival is fixed, and values of other summary statistics are density-independent. The intrinsic rate of increase, r , is calculated from a discrete time formulation of the renewal equation. Models A–F, G1, and G2 have density-dependent larval survival and size at metamorphosis; values for larval survival and other summary statistics are calculated at equilibrium, if it exists. Net reproduction R_0 (Equation 2) is given for the exponential model; R_0^* , a measure of net reproduction at low population density, is given for the models with density-dependent larval survival. R_0^* is net reproduction R_0 (defined as in Equation 2, but not equated to unity) evaluated at $p_L = 1.0$ (from Equation 5 with $D_L = 0$).

Model	p_L	p_A	p_L or \bar{p}_L	R_0 or R_0^*	Metamorph SVL (mm)	First reproduction		Average clutches (per female metamorph)	
						SVL (mm)	Age (yr)		
Exponential $r = 1.28 \text{ yr}^{-1}$	1.0	1.0	1.000	248.0	50.0	65.4	4.49	163.8	2.87
A	1.0	1.0	0.073	248.0	26.5	50.5	7.49	53.4	0.51
B	0.5	1.0	0.094	124.0	27.6	51.2	7.34	58.5	0.72
C	0.1	1.0	0.177	24.8	30.6	52.9	6.40	70.9	1.53
D	1.0	0.5	0.387	7.7	34.7	53.9	3.65	78.3	0.06
E	0.5	0.5	0.559	3.8	37.1	55.3	3.47	89.0	0.08
F†	0.1	0.5	1.000	0.8	50.0	64.2	3.30	155.7	0.10
G1									
Ginger's Bay	0.04	0.7	0.927	1.3	45.2	61.2	3.71	133.6	0.39
G2									
Ginger's Bay	0.04	1.0	0.282	9.9	33.0	54.1	5.57	79.9	2.09

† Values of \bar{p}_L and other summary statistics are approached as population declines to 0.

0.5, or 0.1) and high or moderate terrestrial survival ($p_j = p_A = 1.0$ or 0.5). We omit cases with low terrestrial survival because, even with high egg survival, the populations decline rapidly to extinction.

Demographic characteristics for these populations (models A–F) are summarized in Table 1. For comparison, we include a form of the model with density-dependent constraints removed, so that population growth is exponential. For populations with density dependence, R_0^* predicts behavior of the population when displaced away from equilibrium (Caswell, 1989; Charlesworth, 1980). For $R_0^* < 2.72$, the equilibrium is locally stable, and, over time, the population will approach it; for $R_0^* > 2.72$, however, the equilibrium is not necessarily unstable. Although breeding may begin at age 2, the average age at first reproduction is > 3 yr for all of these populations. Average age at first reproduction decreases with increasing size at metamorphosis (as seen in the series of models A–C and D–F); it also decreases with decreasing terrestrial survival, which reduces the number of older primiparous females (compare the exponential model with model F). The upper limit to the average

number of clutches per female metamorph (2.87) is given by the value for the exponential model. As a consequence of the smaller sizes at metamorphosis, the average number of clutches in the models with high terrestrial survival (models A–C) is reduced by 47–82% from this upper limit. Reducing terrestrial survival to a moderate level (models D–F) lowers the average number of clutches by about an order of magnitude further, despite the larger sizes at metamorphosis.

The populations with high terrestrial survival (models A–C in Fig. 5) exhibit trajectories with wide fluctuations that do not damp. The parameter R_0^* (Table 1) is one to two orders of magnitude greater than 2.72 in these cases. With high terrestrial and egg survival (model A), the population becomes extinct after two cycles, at year 28. The width of the fluctuations and R_0^* decrease as egg survival decreases. The models with moderate terrestrial survival exhibit trajectories with undamped but small fluctuations (model D), virtually smooth approach to equilibrium (model E), or fairly smooth decline to extinction (model F). R_0^* is only slightly above 2.72 for model E. Dynamics of the populations

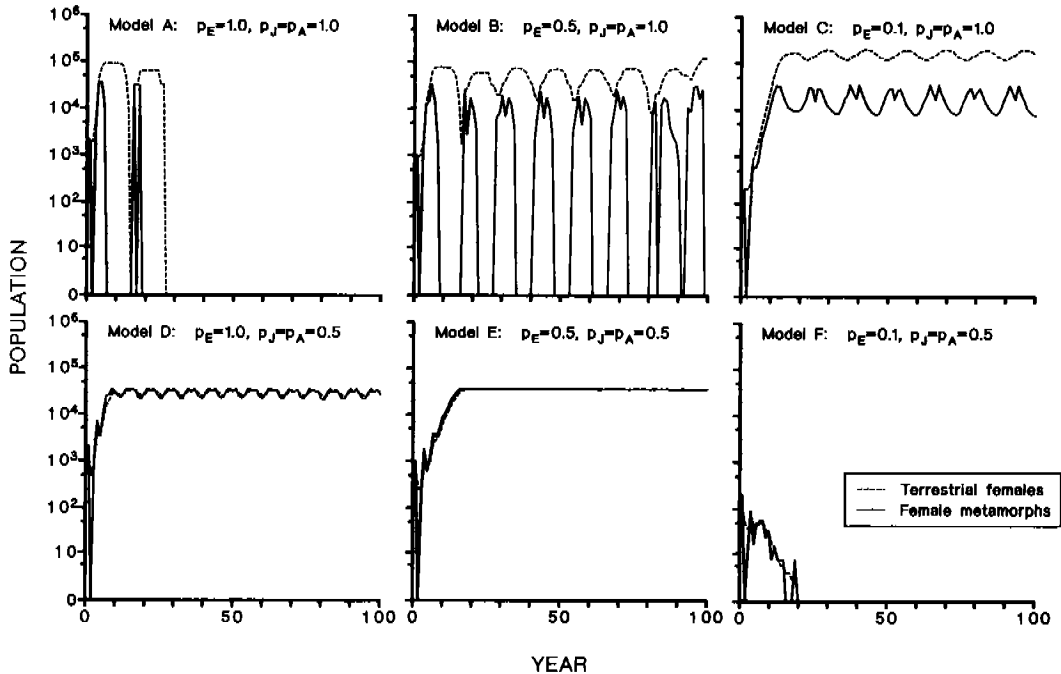


FIG. 5.—Dynamics of populations with density-dependent size at metamorphosis. Size at metamorphosis does not vary among members of a cohort ($SD = 0$ mm). Female metamorphs were censused at age 0.5 yr, the beginning of the juvenile stage. Terrestrial females were censused at beginning of each year. Each computer simulation was initiated with a population of 4000 eggs in a pond of 8000 m² area.

are sensitive to the exact form of the function describing larval density dependence. However, the general trends in the dynamics, such as wide or narrow fluctuation, remained similar when the function describing larval density-dependence was modified (results not shown).

The effect of variation in size at metamorphosis among individuals within a cohort was tested by comparing populations between simulations with ($SD = 2.0$ mm) and without ($SD = 0$ mm) this variation. If this variation has little effect, then, given identical initial populations, the dynamics of these populations should be similar, and their population sizes should remain highly correlated over time. For models A-F, the coefficient of determination for the correlation between populations of female metamorphs with $SD = 2.0$ mm and with $SD = 0$ mm over a 100-yr simulation ranges from $r^2 = 0.006$ (model A) to $r^2 \approx 1.0$ (model E). Two examples are shown in Fig. 6. The coefficient of determination is

related inversely to R_0^* ($r = -0.926$, $n = 6$, $P < 0.05$).

Demographic characteristics for models G1 and G2 (the forms of the model with egg survival adjusted to fit the data for Ginger's Bay) are summarized in Table 1. Note that the plot of metamorphs against breeding females is a form of stock-recruitment curve (Fig. 7A). Terrestrial survival in model G1 is just above the minimum for persistence of the population; terrestrial survival in model G2 is high. Equilibrium is reached at 6640 breeding females and 34,144 metamorphs for model G1 and at 57,944 breeding females and 55,552 metamorphs for model G2. Even the lower equilibrium values exceed the 9-yr maxima of 4268 breeding females (in 1987) and 20,014 metamorphs (in 1994) at Ginger's Bay. These and other equilibrium results are sensitive to terrestrial survival (compare models G1 and G2 in Table 1). At the egg survival value required to approximate the reproductive success of breeding

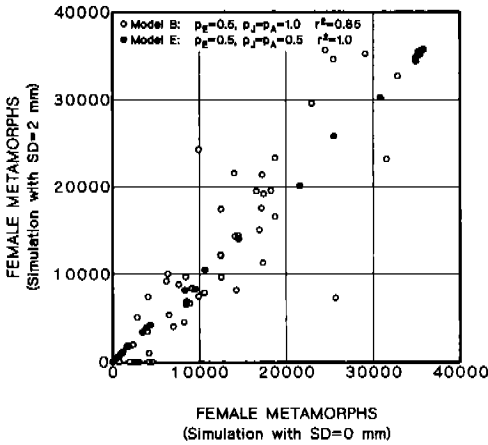


FIG. 6.—Comparison of dynamics for populations with (SD = 2 mm) and without (SD = 0 mm) variation in size at metamorphosis among individuals within a cohort. Size at metamorphosis is density-dependent. Correlations were made for numbers of female metamorphs from 100-yr simulations, each initiated with a population of 4000 eggs in a pond of 8000 m² area.

females in the pond, the model does not generate wide fluctuations in populations, even with high terrestrial survival (model G2). This result is not sensitive to the partitioning of reduced survival between the egg and the larval stages.

Over the range of breeding population sizes observed at Ginger's Bay, the model shows a weak effect of larval density dependence, as indicated by the modest decline in size at metamorphosis with increasing numbers of breeding females (Fig. 7B). This result is fairly sensitive to the partitioning of reduced survival between the egg and larval stages: an increase in egg survival, combined with a decrease in larval survival by a density-independent factor, produces a steeper decline in metamorph SVL with numbers of breeding females.

DISCUSSION

A model is necessarily a simplification of what we know. The population model for the salamander *Ambystoma opacum* incorporates stage structure and larval density dependence of both survival and size at metamorphosis. Larval density influences reproduction through effects on body size. Other demographic parameters are assumed to be independent of population density and invariant with time. The model is built from a firm understanding of the timing of the main transitions in the life-history, and the evidence for all of the

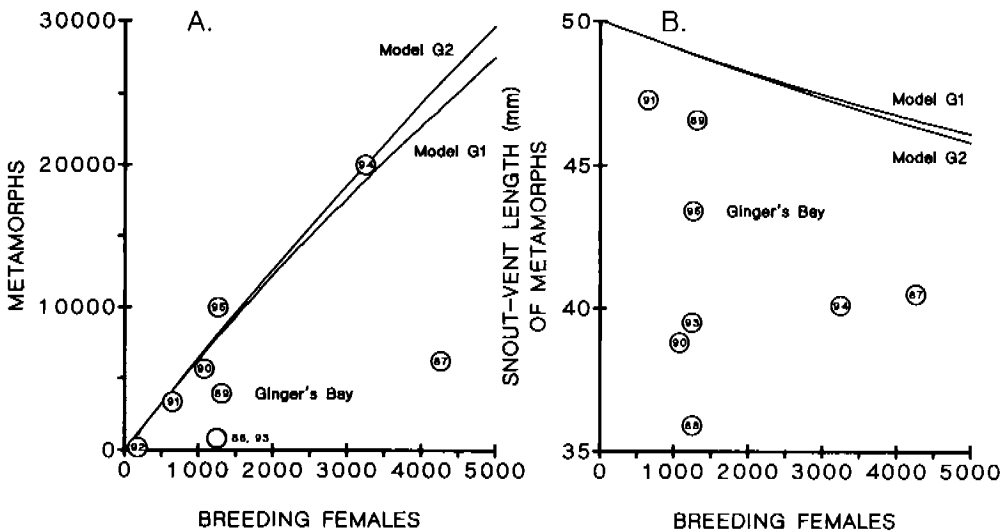


FIG. 7.—Populations and metamorph sizes of *Ambystoma opacum* at Ginger's Bay compared with trajectories generated by models G1 and G2. Mean metamorph length was unavailable for the population at Ginger's Bay for 1992. Each computer simulation was initiated with a population of 4000 eggs in a pond of 8000 m² area.

relations in the model is strong. Some relations, such as size-specific fecundity, are quantified with precision. Others, such as breeding probabilities and larval density dependencies, represent patterns or major features abstracted from more variable sets of data. In general, growth and fecundity are easier to measure than survival, and thus reproduction is understood better than mortality.

Inconstancy of natural conditions, at least for salamander populations, is typical. Thus, neither the equilibrium states nor nonequilibrium dynamics of a model with time-invariant parameters, such as the one that we present here, may be expected to describe fully the dynamics of populations that we observe in nature. However, the model provides a basis for organizing demographic information to evaluate the reproductive potential of the natural population, the intrinsic capacity for fluctuation driven by density-dependent processes, and the sensitivity of these properties to alterations of the parameters. Our model also provides a basis for designing more complicated or detailed models for specific applications, such as studying the effects of year-to-year variation in pond hydroperiod on juvenile recruitment.

Ambystoma opacum has enormous reproductive potential, despite its late maturity. Without the constraints of density-dependent processes in the larval stage and density-independent processes in other stages, the population described by our model has a per capita growth rate of $r = 1.28 \text{ yr}^{-1}$, equivalent to 360% annually. In the terms of the model, density-dependent processes control what density-independent processes fail to control. Thus, adding density-independent mortality by reducing survival rates in either the egg or terrestrial (juvenile and adult) stages diminishes density-dependent regulation in the larval stage.

In one sense, this result is trivial; populations are regulated, density-dependently or density-independently, and neither salamanders nor any other form of life has yet smothered the globe with its reproductive potential. What is nonethe-

less interesting about the results from the model is that, within ranges estimated for natural populations of this species, egg survival and terrestrial survival have quantitatively different effects on both the intensity of larval density dependence at equilibrium and the nonequilibrium dynamics. Reducing egg survival to the levels observed for *A. opacum* at Ginger's Bay is insufficient to moderate the intensity of larval density dependence. Larval survival at equilibrium remains low, and the equilibria are unstable, with trajectories of growth from small initial populations leading to wide, undamped fluctuations. In contrast, reducing terrestrial survival to the levels estimated for the natural population substantially shifts behavior of the model population. Larval survival at equilibrium increases substantially, and fluctuations in the growth trajectory are small. From these results, we infer that strong larval density dependence is less likely to occur in populations with low terrestrial survival. The high reproductive capacity that causes strong larval density-dependent regulation also promotes fluctuating nonequilibrium dynamics. Thus, when strong density-dependent regulation can occur, its intensity will be likely to fluctuate over time, even in the absence of temporal variability in density-independent processes.

For *A. opacum*, our results indicate that delayed effects of larval density, modeled as consequences of density-dependent size at maturity, may have large demographic effects (e.g., a 3-yr increase in average age at first reproduction). Such effects seem to be widespread among animals with complex life cycles and are best-studied among insects (Prout and McChesney, 1985; Rodriguez, 1989), but they have usually been omitted from models of density-dependent population dynamics. In this model, the delayed effects of larval density on adult reproduction are large enough to shift the equilibrium points for the model quite substantially (Fig. 4). Effects of larval density on survival of terrestrial juveniles, which we did not include in the model, could further enhance these shifts.

Because body size often correlates

strongly with fitness in amphibians, variation in size among individuals within a cohort, as well as among cohorts, has become an important measure in studies of amphibian life-histories (Berven, 1988, 1990; Scott, 1994; Semlitsch et al., 1988). The results from the model for *A. opacum* indicate that variation in size at metamorphosis among individuals within a cohort can strongly influence dynamics of the population. The negative correlation between the effect on population dynamics and the parameter R_0^* suggests that its intensity may be directly related to population's capacity for growth at low population density. When this capacity for growth is high, the large additional labor of developing, testing, and running an individual-based computer model may be justified.

One of the striking features of the dynamics of *A. opacum* at Ginger's Bay is low reproductive success, measured in numbers of metamorphs produced by breeding females. The egg survival required to fit the model to the data from Ginger's Bay was much lower than the egg survival observed in marked nests (Jackson et al., 1989) or average embryonic survival of *A. opacum* observed in other studies (Petranka, 1990; Stenhouse, 1987). The low value of egg survival used in the model may account in part for reduced larval survival or fecundity in the natural population, but the field data do not allow us to distinguish among these possibilities. Whatever the causes for the low reproductive success, the consequence is that the model population requires moderately high terrestrial survival even to persist. Thus, the value of 50% annual survival estimated for terrestrial populations on the SRS (D. E. Scott, unpublished data) seems too low to sustain the population at Ginger's Bay. Unless breeding probabilities for the natural population are much higher than values in the model, we infer that persistence of the population at Ginger's Bay must depend on higher annual terrestrial survival, at least 70% according to the model, or on immigration from adjacent populations.

Another striking feature of the population dynamics at Ginger's Bay is the wide year-to-year fluctuation in numbers of animals and average sizes of metamorphs. This fluctuation is driven in part by variation in timing and extent of pond filling and drying (Scott, 1994). In years when the pond is small, the larvae are concentrated, and density-dependent processes are probably intensified. Survival and size at metamorphosis are lower when the pond dries early (Scott, 1990). As Petranka (1989) noted, the typical status of amphibian populations, relative to their equilibria, is not well characterized. If populations are usually held far below their equilibria, density-dependent factors may influence population dynamics strongly only during rare population eruptions or unusually dry years.

We can identify demographic processes that are critical to improving our understanding of salamander demography. Processes influencing the probability of breeding and controlling year-to-year variation in reproductive success of breeding females are obviously important. The sensitivity of the model to terrestrial parameters underscores the need for more observational data on juvenile and adult survival and dispersal; this sensitivity is common among long-lived vertebrate species (Congdon et al., 1994). Accurate estimates of demographic parameters are logistically more difficult to obtain for terrestrial stages than for aquatic stages of pond-breeding amphibians. However, for *A. opacum* and other species with terrestrial stages that are long in relation to the aquatic stage, these data are essential to understand population regulation, assess the potential effects of changes in land use or climate, and develop an adequate basis for conservation or management plans.

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