PREDICTING POPULATION DYNAMICS
FOR THE HELLBENDER, *CRYPTOBRANCHUS ALLEGANIENSIS*:
USING POPULATION VIABILITY ANALYSIS (PVA)
AS A GUIDE FOR CONSERVATION

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PREDICTING POPULATION DYNAMICS FOR THE HELLBENDER, *CRYPTOBRANCHUS ALLEGANIENSIS*: USING POPULATION VIABILITY ANALYSIS (PVA) AS A GUIDE FOR CONSERVATION

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ABSTRACT

Cryptobranchus alleganiensis, the hellbender, is an elusive aquatic salamander species inhabiting the eastern, mountainous United States and Ozarks. In recent years, the hellbender has shown declines across portions of its range. Because of the long life-span of the hellbender, making predictions about how the population will respond to management practices over time can be difficult. Population viability analysis is one effective method of making predictions regarding likely population trends over time, and can be manipulated to include a wide range and wide variety of deterministic and stochastic factors that affect populations. In this study, available demographic data were combined with a range of factors that are likely affecting *C. alleganiensis* populations to examine potential population trends. Models considered both isolated populations and populations with dispersal abilities. *Cryptobranchus alleganiensis* proved fairly resilient to low-level negative factors, but was more susceptible to high-level factors. A trade-off appeared to exist between large isolated populations and small dispersing populations. Dispersal ability improved *C. alleganiensis* population health when multiple, high-level negative factors were acting on the populations, but when reproductive failure alone was the negative factor, a large isolated population resulted in greater total number of individuals across populations. Because of the uncertainty regarding actual causes of current *C. alleganiensis* declines, it is best to manage populations from a worst-case scenario to ensure adequate management strategies are employed.

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INTRODUCTION

Conservation biology is increasingly focused upon the urgent need to preserve the biodiversity of this planet. Unfortunately, while up to 400 species are lost per day (Mader 2002), humans are just beginning to understand the intricate interrelationships of organisms and how the presence or absence of one species may indicate the health of an entire ecosystem (Winter and Hughes 1997). Conservationists have emphasized setting aside tracts of land specifically for protection of endangered flora and fauna. The growing human population, however, inflicts its influence in and around the protected zones, leading to isolation and/or fragmentation. Declining populations necessitate an evaluation of the population status of species: how much can a population decline before it can no longer be sustained (Soule 1987, Meffe and Carroll 1999, Primack 2000, Akcakaya and Sjogren-Gulve 2000)?

Though extinctions and declines have occurred across many species groups, amphibian populations have been especially diminished in recent years (Wyman 1991, Blaustein et al. 1994, Greenspan 1998). Amphibians possess certain characteristics making them especially responsive to environmental change, including their occupation of both aquatic and terrestrial habitats, a thin, permeable epidermis, and the fact that juveniles feed at the base and adults near the top of the food web, exposing them to chemicals that could be bioconcentrated and biomagnified (Wyman 1990, Wake 1991). Therefore, amphibians are believed by many to be hypersensitive to environmental degradation and have been labeled “indicator” species by many scientists. Amphibian declines could be the first evidence of changes in air, water, soil, global climate, pollution levels, ultraviolet radiation, and habitat fragmentation (Wyman 1990, Wake 1991, Blaustein et al. 1994, Greenspan 1998).

The hellbender, *Cryptobranchus alleganiensis,* is an amphibian species that seems to be experiencing populations declines (Prosen 1999, Wheeler 1999). Although known to science for 200 years (Nickerson and Mays 1973), its status and some portions of its life history are still subject to speculation, in part because the hellbender is relatively difficult to observe across its entire lifetime (Iverson 1991). Examination of hellbender natural history suggests the need for further population studies.

Cryptobranchus alleganiensis **Natural History**

Cryptobranchus alleganiensis is a large, entirely aquatic salamander inhabiting cold, fast-flowing, high-gradient streams. *Cryptobranchus*, which has only one species, *alleganiensis,* belongs to the family Cryptobranchidae. Cryptobranchidae includes two extant genera, *Cryptobranchus*, and the Asiatic genus, *Andrias*. *Cryptobranchus. alleganiensis* has two subspecies, *C. a. alleganiensis*, the eastern hellbender, ranging from southern New York to Northern Alabama and in the Ozarks, and *C. a. bishopi*, the Ozark hellbender, which is limited to the Black River drainage and the North Fork of the White River drainage in the Ozark Mountains of Arkansas and Missouri (Nickerson and Mays 1973).

The name *Cryptobranchus* means "hidden gills" which can be misleading because *C. alleganiensis* actually does not possess gills beyond the early larval stages. Respiration is through extensively vascularized folds along the lateral line system, across which oxygen is acquired via capillary diffusion. This form of oxygen transfer limits *C. alleganiensis* to fast-moving streams with high dissolved oxygen content (Guimond and Hutchinson 1973, Guimond and Hutchinson, 1976) because the flow rate must be such that oxygen comes in contact with the hellbender at a fast enough rate for adequate diffusion to occur. Oxygen concentration would subsequently be expected to fall within certain limits to ensure that enough oxygen is present to create a diffusion-facilitating gradient.

Other than dissolved oxygen, the main factor determining suitability of habitat for *C. alleganiensis* is the geomorphological structure of the stream substrate (Nickerson and Mays 1973). Adult *C. alleganiensis* use large, flat rocks for cover and breeding sites. Data suggest that *C. alleganiensis* density is related to number of available cover rocks, with "one hellbender per rock" being a generally accepted rule (Smith 1907, Hillis and Bellis 1971, Nickerson and Mays 1973).

Reproduction in *C. alleganiensis*, unlike most other salamander species, occurs by external fertilization. Breeding is from late August to mid- November with seasonal differences related to environmental factors such as latitudinal variations in temperature (Dundee and Dundee 1965). Activity levels are markedly higher during the breeding season (Smith 1907, Peterson, 1987). Nests, prepared and defended by males, are found under flat rocks. Eggs are laid in gelatinous strands similar to the eggs of other externally fertilizing amphibians. *C. alleganiensis* exhibit polyspermy, the ability of the egg to be penetrated by multiple sperm, which is thought to ensure fertilization of all but a very few eggs (Smith 1912). Eggs hatch when embryos are 23 mm – 26 mm in length. Incubation lasts from 68 – 84 days (Bishop 1941). Juveniles lose their gills at 18 – 24 months of age and become sexually mature at 300 mm – 370 mm total length (Peterson 1985) or three to six years of age (Smith 1912, Bishop 1941, Nickerson and Mays 1973, Wheeler 1999).

Adult *C. alleganiensis* have few recognized predators. Those species presenting some threat are water snakes, turtles, large fish species, other *C. alleganiensis*, and humans (Nickerson and Mays 1973). *Cryptobranchus alleganiensis* commonly cannibalize both eggs and young (Smith 1912, Nickerson and Mays 1973, Peterson 1985). The main anthropogenic factors affecting *C. alleganiensis* are damming, channelization, pollution (Minton 1971, Nickerson and Mays 1973), habitat loss (Smith and Minton 1957), siltation (Minton 1971) and acidic mine drainage.

At this time, *C. alleganiensis* has not been listed as a species of concern by The International Union for Conservation of Nature (IUCN), The Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) or the U.S. Endangered Species Act. However, the U.S. Fish and Wildlife Service and several state agencies have afforded them such a status (Wheeler 1999). Additionally, researchers studying the species have expressed concern over the decline of adult and especially juvenile *C. alleganiensis* across their range (Peterson 1985, Prosen 1999, Wheeler 1999).

Juvenile declines were evident in a study by Peterson (1987) examining movement and sampling accuracy, in which he did not encounter many juvenile *C. alleganiensis*. Absence of juveniles followed a trend toward fewer juveniles seen in an earlier study (Peterson 1985) in which only one in four study populations had a significant number of juveniles. While *C. alleganiensis* populations are recognized to be normally dominated by large, slow-growing adults (Nickerson and Mays 1973, Peterson

1985, Prosen 1999, Wheeler 1999), the fact that Nickerson and Mays (1973), Taber (1975), and Peterson (1983) consistently located more juveniles within population surveys than recent studies conducted in the same region (Prosen 1999, Wheeler 1999), suggests justified concern regarding the health of *C. alleganiensis* populations.

Declines in the Prosen (1999) and Wheeler (1999) studies were not limited to juvenile *C. alleganiensis*. The purposes of these studies were to compare historical data with recent population data. Both determined that there was an overall decline in hellbender numbers within the Ozark study areas. While speculating that the declines could be a natural population cycle, both authors stated that normalcy of cyclic trends could not be determined due to the long life span of *C. alleganiensis*. The studies utilized historical data from the 1970's to the late 1990's, providing a partial look at only one generation. Studying multiple generations would be extremely time-consuming since *C. alleganiensis* live up to 30 years (Nickerson and Mays 1973b, Peterson 1985, Prosen 1999, Wheeler 1999). These possible declines, and the difficulty of studying *C. alleganiensis* across generations, suggests it would be valuable to simulate population behavior over time to determine how demographic changes within populations, as well as stochastic events, could impact population dynamics over several generations.

Population Viability Modeling

Several alternative strategies are available for modeling populations from a conservation perspective, of which the minimum viable population (MVP) and population viability analysis (PVA) are the most widely used. MVP has been used to determine the minimum requisite size of populations, below which populations were not expected to persist (Shaffer 1981). Use of MVP alone can create an unrealistic image of populations, because it suggests that populations will persist as long as they have a set number of individuals (Soule 1987). For this reason, though MVP is in use among some biologists, it is now more common to see population predictions in the form of a population viability analysis.

Population viability analysis incorporates life history parameters, along with deterministic and stochastic factors, to quantitatively assess extinction probability (Miller and Lacy 1999). PVA has been used on a variety of species including birds (Maguire et al. 1995), mammals (Forys and Humphrey 1999), and reptiles and amphibians (Miller and Lacy 1999). PVA has been used with increasing frequency to provide a guide for conservation management and research (Hamilton and Moller 1995). A useful PVA is one that identifies the relative severity of variable threats and outlines the efficacy of potential management strategies (Brook et al. 1997).

The deterministic factors causing population declines that can be modeled by PVA include over-harvesting, habitat loss, pollution, climate change, exotic competitors, predators, parasites, and diseases (Miller and Lacy 1999). Populations, and thus PVA models, are also affected by stochastic (random) events, which have been divided into four major groups by Shaffer (1981). These are demographic stochasticity, environmental stochasticity, genetic drift, and natural catastrophes. Demographic stochasticity involves random variation of birth rate, death rate, and sex ratios within populations. Environmental stochasticity arises from variation in reproduction and survival due to variability in environmental conditions. Genetic drift results from random change in allele frequencies within populations. Natural catastrophes are large-scale

(Peterson 1985, Peterson 1987, Prosen 1999, Wheeler 1999), scenarios were also performed with the incorporation of increased year one and year two mortality. Mortality following the predictions derived from the life table (Peterson 1985) was designated Basic mortality and was typical of a Type III survivorship curve with >99% mortality for year 0 , 14.3 – 26.3% mortality for year one, and 10 – 13.2% mortality for year two. All other mortality schedules had the same year zero mortality rates as in the Basic mortality schedule, but year one and year two mortality rates were varied. The 25% mortality schedule had a juvenile mortality rate of 25% for both year one and year two mortality. The 50% mortality schedule had a juvenile mortality rate of 50% for year one and year two mortality. The 75% mortality schedule had a juvenile mortality rate of 75% for year one and 50 % for year two mortality. In the 75% mortality schedule, the year two mortality was originally set at 75%, but this always resulted in unviable populations and so it was reduced to 50%. These hypothetical numbers were established to simulate how changes in juvenile mortality could affect population viability (Appendix B). The higher mortality estimates were based upon the few juveniles found in recent studies (Prosen 1999, Wheeler 1999) as compared to earlier work (Nickerson and Mays 1975, Taber 1975, Peterson et al. 1983). Other parameter estimates were based upon the means of parameter values found in the literature where those data were available (Appendix A).

A 100 year time frame was initially used to document population dynamics over multiple generations. While up to 200 years may be necessary to really grasp extinction time in longer lived organisms (Miller and Lacy 1999), a time frame greater than 100 years was considered unnecessary for the real model simulations because the populations showed definite trends toward either decline or equilibrium by the 100 year termination geological or climatic events such as hurricanes, earthquakes, or drought. Once deterministic and stochastic factors are identified, they are combined with life-history parameters and the PVA model is used to determine the probability of extinction and to identify appropriate management options. While the actual predictive ability of PVA has been questioned (Hamilton and Moller 1995, Brook et al. 1997), Brook et al. (2000) determined that PVA results approximated historical behaviors of actual natural populations.

For *C. alleganiensis*, whose population status is questionable, and for whom conducting a long-term study could take decades, PVA may be a useful means of predicting population trends over time and identifying the greatest threats to population persistence. An important feature of PVA is that it enables those studying populations to determine which specific factors seem to most affect the populations (Lacy 1993). From a conservation management perspective, until more data are available for making regionally specific predictions regarding management options, PVA might be the best currently available tool to provide a starting place for hellbender conservation management.

Another benefit of conducting a PVA is that trying to complete an accurate PVA requires a rigorous evaluation of the data for the target species. Even before the PVA results are finalized, deficient areas of data are exposed as the extensive data set required to create a PVA model is gathered. Data collection may reveal those areas that would benefit from further research. For example, population data pertaining to *C. alleganiensis* are limited due to difficulties collecting accurate information. In the Ozark region, a great deal of life history data exist (Nickerson and Mays 1973b, Peterson, 1985, Peterson 1987, Prosen 1999, Wheeler 1999), but data are less complete in other areas of the range of *C. alleganiensis*. Again, the life span of *C. alleganiensis* makes comprehensive life-history studies difficult to complete and multiple generation studies would take years. Further complicating matters are the still imperfect aspects of methodology. Locating and capturing *C. alleganiensis* is problematic and can potentially bias a sample (Peterson 1987), especially for juveniles whose size and less obvious cover choices make them especially elusive. Similarly, dispersal studies have just begun to provide a picture of the potentially elaborate metapopulation dynamics of *C. alleganiensis* (Wiggs 1977, Peterson 1987).

The goal of this study was to use PVA to simulate likely demographic scenarios to determine how changes in demographic parameters could influence long-term population dynamics of *C. alleganiensis*. Because the spatial arrangement of individuals, populations, and communities can play such an important role in population dynamics (Hanski 1998) and because it was not known to what extent dispersal ability could be vital to *C. alleganiensis* population health, effects of dispersal on *C. alleganiensis* populations were also modeled.

METHODS

Modeling Software

The PVA software, VORTEX (version 8.41-Miller and Lacy 1999), was chosen as the modeling software of this study for multiple reasons. VORTEX is an individual, rather than a cohort-based software program. *Cryptobranchus alleganiensis* is a long-lived organism of which a complete cohort study has yet to be accomplished, point. When preliminary extensions of the time span, to 200 years, were performed, no variation in final results occurred. Therefore, to keep output more manageable, 100 years was used as the baseline for real model scenarios. Because results were not clear by the 100 year termination point in dispersal models, these models were run for 200 years.

Scenarios Modeled

Once a model of the basic population parameters was established, it was necessary to manipulate various deterministic (e.g. over-harvesting and habitat loss) and stochastic (random) factors in the real models to determine how each parameter affected the dynamics of those populations. For the first scenarios, juvenile mortality schedules were manipulated (Table 1, Scenario 2). Juvenile mortality was manipulated by changing year one and year two mortality rates as previously described.

The next group of scenario manipulations involved the introduction of increased stochasticity. Although demographic and environmental stochasticity have not been quantified for *C. alleganiensis,* these risks were modeled as variable probabilities of occurrence. The stochastic events simulated changes in reproduction (Table 1, Scenario 3) and survivorship (Table 1, Scenario 4). Determining the level of stress from these factors which *C. alleganiensis* could withstand before exhibiting declines was considered valuable from a management perspective. Reproductive losses, which would be caused by inviability of eggs or loss of eggs before juveniles emerged, were modeled individually, and then in the presence of stochastic survivorship events (death of individuals across all age groups) creating a multifactor scenario (Table 1, Scenario 5).

necessitating the use of an individual based model. VORTEX is a widely used PVA modeling system. Though originally designed for use with mammals and birds, VORTEX has been adapted to accommodate the variable life histories of numerous species, making it suitable to a wider range of organisms, including reptiles and amphibians (Miller and Lacy 1999). VORTEX is used by the IUCN and the Species Survival Commission (SSC) for conservation purposes and has been shown to be a reasonably reliable means of predicting persistence over time (Brook et al. 2000).

VORTEX is a Monte Carlo simulation that models how deterministic and stochastic factors impact populations. It moves stepwise through various life table events (reproduction and mortality parameters) to dispersal parameters, carrying capacity, population growth rates, demographic stochasticity, environmental stochasticity, and catastrophes. Each "step" is assigned its own probability of occurrence, modeled as a constant or a random variable within a specific distribution (Figure 1). Performing many simulations based upon the same data set results in a representation of the range of fates a population may experience when faced with specified scenario (Miller and Lacy 1999).

Types of Models

Two groups of models were created during the *C. alleganiensis* PVA. The first group consisted of the "real" models and the second group was dispersal models. The parameters used in the real models were based on actual populations studied by Peterson (1985) in the Ozark region of Missouri. This was by far the most demographically explicit study containing a comprehensive look at *C. alleganiensis* populations. Wherever actual population data were available from within that study, they were used.

It was occasionally necessary to extrapolate data from other basic natural history sources such as Smith (1907, 1912) and Nickerson and Mays (1973) for general information such as age at sexual maturity. There were seven populations manipulated in the real models of this PVA, each given the name of the stream housing the study site: Big Piney 1, Big Piney 2, Eleven Point 1, Eleven Point 2, Spring River 1, Spring River 2, and Gasconade (Figure 2).

Dispersal within the real models was limited to mimic natural populations that were spatially discrete except for possible extremely low-level dispersal (one percent or less immigration into corresponding populations) from Big Piney 2 to Big Piney 1 and Spring River 1 to Spring River 2. In the real model populations, the Gasconade River had only one study site. Therefore, it was modeled as an isolated population. There was no estimated dispersal between Eleven Point 1 and Eleven Point 2 because the study sites were approximately 14 km apart, exceeding the lengthiest recorded movements of *C. alleganiensis* (Wiggs 1977). Movements in real models were limited to the upstream direction because Wiggs (1977) found *C. alleganiensis* primarily moved upstream: 63 of 67 movements, over a three-year period, were upstream. Peterson (1987) observed both upstream and downstream movements, but in populations which were immediately adjacent.

The second group of models, the "dispersal" models, were developed in an effort to determine whether or not dispersal plays an important role in preventing population declines and extinction events in *C. alleganiensis* populations. It is unknown from the Peterson (1985) study whether the populations studied were distinct populations or existed in the presence of smaller subpopulations, located in proximity to the populations

These events were also modeled along with a range of increased juvenile mortality as an interacting factor (Table 1, Scenario 6).

For the dispersal models, because Wheeler (1999) suggested that reproductive failure could be the cause of decreased juvenile recruitment, total reproductive failure was introduced into the models (Table 2, Scenario 1). Factors such as large flow fluctuations and increased sedimentation at spawning sites can cause total reproductive failure in 90% of salmonids (Sando 1981). Because *C. alleganiensis* have similar spawning characteristics and utilize similar habitat as salmonids (Nickerson and Mays 1973, NMFS 1998), high rates of reproductive failure were modeled. To examine stochastically related reproductive failure, the probability that a population would suffer a total loss of reproduction was set at 90%, following the Sando (1981) salmonid findings, for all populations. A 90% chance of reproductive failure was used as a likely worst-case scenario for *C. alleganiensis* populations. Because of its unknown status, predicting worst-case scenario ensures that at least minimum conservation requirements are met. Additionally, because Peterson (1985) found more juveniles at one of four populations studied, 25% of the populations were modeled so that they would not experience large scale reproductive failure. This would also simulate the effect of a protected population providing a "source" for unprotected "sink" populations (Figure 4) as might exist in conservation settings (Pullium 1988).

A range of dispersal abilities (isolation, constant rate dispersal, and variable rate dispersal) were also combined with the survivorship losses and reproductive failures, to determine how interpopulational dispersal would change the population dynamics over time (Table 2, Scenario 2). Reproductive failure and survivorship losses were set being studied, though he did hypothesize that emigration was important in local population dynamics. A later study (Peterson 1987) observed emigration and immigration with 5 – 11% of *C. alleganiensis* being potential transients.

The dispersal models used data from the real models, but modified the number of interacting populations and dispersal rates between populations. The numbers of populations were four, eight,
and 16. One population (Big Piney 1, Spring River 1, Eleven Point 1, and Gasconade 1) was chosen from each stream site when examining four populations. First, all populations were modeled as if they were isolated. Simulations involving various multifactor threats and catastrophes affecting reproductive output were performed under the isolation assumption. Then, a new set of scenarios was modeled in which each of the four populations were assumed to have a 1% level of interpopulational interaction (emigration and immigration) with each of the other populations, which equaled 3% of the individuals at any one site dispersing at any given time over the course of the simulations. Again, these scenarios were manipulated with the different multifactor threats and reproductive losses potentially facing *C. alleganiensis* populations.

Increasing the numbers of populations to eight and 16 involved replicating some of the populations. For eight populations, each of the seven real model populations was used once, rather than doubling the four populations because this provided a greater variety of initial population sizes, which would be expected in natural populations. Also, using seven populations rather than four populations twice created a greater range of population parameters, lessening the chance that bias from any one population would be overly pronounced. The Gasconade population, because of its singularity, was used twice. For 16 populations, each of the seven real model populations was used twice except for the Gasconade population which was used four times.

The rates of dispersal were kept at the same level for eight and 16 populations: 3% of the individuals from any one population dispersing to the other populations at any given time across the course of the simulations. For eight populations the dispersal rate from one population to each of the other seven populations was 0.43% (e.g. 0.43% of the individuals from Big Piney 1 will disperse to Spring 1, 0.43% will disperse to Spring 2, etc.). For 16 populations, each population had a 0.2% dispersal rate to each of the other fifteen populations. The 3% dispersal scenarios were labeled *constant rate emigration dispersal.*

Dispersal was also modeled as a flat 1% from a given population to each of the other populations being modeled. For four populations, the proportion of individuals immigrating into each population remained at the same 3% level. For eight populations, the proportion of individuals immigrating was 7% (1% from a population to each of its seven counterparts). For 16 populations, immigration was set at 0.6% rather than 1% from a given population to each of its 15 associated populations, resulting in a total immigration rate of 9%. The 1% rate was not used because the total number of individuals leaving a single population would have exceeded the 5 – 11% predicted rate of dispersal for *C. alleganiensis* (Peterson 1987). The pattern of flat 1% (or 0.6%) dispersal which resulted in varying emigration rates was labeled *variable rate emigration dispersal.*

relatively low (10% chance of 75% reproductive failure and 10% chance of 20% survivorship losses). Finally, survivorship losses, reproductive failures and increased juvenile mortality were entered into the dispersal models, with reproductive failures and survivorship losses the same as above (10% chance of 75% reproductive failure and 10% chance of 20% survivorship losses) with the addition of 75% year one and 50% year two juvenile mortality .

Besides looking at dispersal and its effect upon the individual populations, the total number of individuals across populations, which is considered the metapopulation size, of the dispersal model populations was also examined. Metapopulation theory suggests that populations exist as larger entities inhabiting suitable patches across large, spatially connected areas (Hanski and Gilpin 1997) as opposed to one population existing as a unit within a single, isolated habitat patch. Metapopulation responses reflect the total numbers of individuals across habitat patches within a given area. Recent studies (Wiggs 1977, Peterson 1985, Peterson 1987) suggest that metapopulation dynamics are a factor in *C. alleganiensis* population dynamics.

RESULTS

Real Model Scenario Results

In the absence of negative factors, real model populations remained fairly stable over time (Figure 5). The introduction of increased juvenile mortality, reproductive failures, survivorship losses, and combinations of these factors, resulted in population declines of varying degrees. Low-level increases in juvenile mortality (25%) and low level reproductive failure (75% chance of 10% failure) caused the least amount of

Basic Population Parameters

For both real model and dispersal model scenarios, basic population parameters were established to form the groundwork of the PVA using data from literature and best approximations (Appendix A). These parameters included initial population sizes, fecundity, age at sexual maturity, and breeding characteristics. No real estimates of carrying capacity, K, could be derived from previous studies though it has been suggested that *C. alleganiensis* density is closely related to the geomorphological structure within the study area (Nickerson and Mays 1973, Peterson 1985). To establish the basic population parameters forming the basis of the PVA, it was decided that K would be set first at initial population size, then 10% above initial population size, and finally 10% below initial population size (Table 1, Scenario 1 a, b, c). When K approximated initial population size or was below initial population size, the populations showed an initial decline, followed by a stabilizing of the populations. When K was set 10% higher than initial population size, the population showed the greatest degree of stability over time. These results were reflected both within individual populations and in total numbers across all populations (Fig. 3 a, b, c). Because the populations were stable (mean number of individuals over time was approximately the same despite population fluctuations) at $K > N$ (initial), it was determined that for subsequent manipulations, the parameter value of K would be 10% above initial population size.

The mortality schedule was adapted from the Peterson (1985) life tables. VORTEX requires mortality to be input as a definite rate for each sex for each year up to the age of reproduction, and then as a mean mortality rate for adults. Because it is possible that mortality is higher than expected for juveniles in some populations isolated population experiencing increased juvenile mortality with the multiple, high-level negative factors was relatively high rates of decline in affected populations leading to eventual extinction (Figure 15 a, b, c).

Adding constant rate dispersal to scenarios with multiple negative factors resulted in declines in all populations with increased juvenile mortality and resulted in reduced to no declines in populations not experiencing increased juvenile mortality (Figure 16 a, b, c). Total number of individuals present across populations was lower when populations were isolated than occurred with constant rate emigration. (Figure 17). Total number of individuals across all populations was higher for constant rate emigration than for variable rate emigration after year 40 (Figure 18).

Throughout the scenarios the largest population (Spring River 1) was always one of the populations experiencing low-level negative factors. Therefore, the models were manipulated to examine the population responses to combined reproduction and survivorship losses with 75% juvenile mortality when the largest population was not assigned low-level negative factors. The results showed the same trends as seen when the largest population was not given high-level negative factors, but population sizes were smaller than occurred in the scenarios when the largest population was only experiencing low-level negative factors (Figure 19).

DISCUSSION

Juvenile Mortality

Increased juvenile mortality is a subject of concern to *Cryptobranchus* biologists (Prosen 1999, Wheeler 1999). As described earlier, it is difficult to grasp the actual negative change in population sizes over three generations (90 years) while the scenario with the greatest number of interacting factors (combination of reproduction and survivorship losses and juvenile mortality) caused the greatest declines across three generations. In all situations, increasing the magnitude of a negative factor imposed upon the population resulted in a greater rate of decline across three generations than when a lower-level factor was imposed.

Juvenile Mortality

Adjusting the *C. alleganiensis* juvenile mortality schedules (Table 1, Scenario 2) caused changes in population sizes over time (Table 3). Increasing year one and year two mortality to 25% (Figure 6a) had little effect on long–term population sizes except for the largest population (Spring River 1), which experienced a 25% decrease in number of individuals by year 90 as compared with the number of individuals at the start of the scenario.

Changing year one and year two mortality to 50% caused negative trends across almost all populations examined (Figure 6b). Again, the greatest proportional decline, 95% by the end of 90 years, was within the largest population. The Eleven Point populations showed stability with slight year-to-year fluctuations, but across all other populations a declining trend was evident.

The most severe mortality schedule was the 75% mortality schedule. This schedule predicted 75% mortality for year one and 50% mortality for year two juveniles. All populations experienced declines when this mortality schedule was imposed. Once more, the largest population experienced the greatest proportional declines, 92% by year

30 and 100% by year 90 (Figure 6c). Other populations were also decimated in this scenario, with a total of two of seven populations extinct by year 90 and another three populations experiencing more than a 93% reduction after 90 years than at the start of the simulation.

Because the largest populations were not expected to decline more rapidly than the smaller populations, it was necessary to determine whether these results originated from a problem in the modeling software, or if the results were an artifact of the data combinations of the Spring River 1 population. To test this problem, the initial population size of the affected population, which was 420 individuals, was changed to 160, the initial size of the Big Piney 1 population. The Big Piney 1 population was then assigned 420 individuals, based upon the initial size of the Spring River population. When scenarios involving these manipulated parameters were run, the largest population no longer experienced the greatest declines. The trend toward rapid decline was still in evidence with the Spring River 1 population even though it was no longer the largest population. Further examination revealed that the Spring River populations had higher mortality rates across all years compared to the other populations from year zero to year five (Appendix B). Scenarios in which the mortality schedule of Spring River population was modified to approximate that of the other populations were run for comparison and resulted in trends typical of the other stream sites, suggesting that the higher mortality rate across years in the Spring River population was the underlying factor causing increased rate of decline in response to additional negative factors. For the duration of the study, the mortality schedules found by Peterson (1985) were used despite the unexpected response to preserve the realism of the models.

severity of juvenile declines because of challenges faced when trying to accurately assess numbers of juveniles within study areas. Because of this lack of information, variable rates of juvenile mortality were modeled. As expected, the higher the rates of mortality for year 1 and year 2 juveniles, the more severe were the declines in population sizes over the course of the simulation time (Figure 5a, b, c). It is not unrealistic, in light of recent findings (Prosen 1999, Wheeler 1999) to predict that juvenile mortality could be as high as the 75 % for year one juveniles and 50 % for year two juveniles as modeled using the 75% mortality schedule (Appendix B), or even higher. Thus, the overall declines found in the Prosen (1999) and Wheeler (1999) studies would be expected if juvenile recruitment was extremely low.

These results suggest that it would be valuable to have an accurate means of determining numbers of juveniles within *C. alleganiensis* populations. Most studies, particularly in the Ozark region, have focused upon total *C. alleganiensis* numbers. It is likely that a study concentrating on juvenile capture and location could improve survey techniques and provide a more accurate estimate of juvenile *C. alleganiensis* numbers. Such information may be essential to the protection of *C. alleganiensis* populations because the models presented here suggest that juvenile *C. alleganiensis* mortality can play a large role in population dynamics.

Reproduction and Survivorship Losses

Stochastic events affecting survivorship and/or reproduction are common occurrences in natural populations (Hanski and Gilpin 1997, Miller and Lacy 1999). Therefore, it was not surprising to discover that low-level stochastic factors (Table 2, Scenario 3 a, b; Scenario 4a) had

Reproduction and Survivorship Losses

Population declines resulting from reproductive failures did not have a large, long-term impact on population size over time (Figure 7a, b, c) when the level and rate of occurrence were relatively low. When the level of loss was 75% with a 10% probability of occurrence (Figure 7a) or 80% with a 50% probability of occurrence (Figure 7b), no declines were seen. Increasing the incidence and severity of reproductive failure (90% loss with a 60% chance of occurrence) led to all populations experiencing declines (Table 4), with the largest population, Spring River 1, exhibiting greater declines than other populations (Figure 7c).

Survivorship losses due to stochasticity (Table 1, Scenario 4) also resulted in population declines over the course of the 100-year simulations (Table 5). When survivorship losses were 20% with a 10% probability of occurrence, declines greater than 10% by year 30 occurred in three (Spring 1, Spring 2, and Gasconade populations) of seven populations (Figure 8a). Increasing survivorship losses to 40% with a 10% probability of occurrence resulted in greater declines in population size with declines greater than 20% in four (Big Piney 2, Spring 1, Spring 2, and Gasconade populations) of seven populations (Figure 8b).

The interaction of stochastic survivorship and reproductive losses (Table 1, Scenario 5) increased the magnitude of declines resulting from a specific factor (Figure 9a). A 75% loss of reproduction with a 10% chance of occurrence had little impact upon populations when modeled without survivorship losses. When combined with a 20% survivorship loss, also with a 10% chance of occurrence, however, three (Spring 1, Spring 2, and Gasconade populations) of seven populations began to exhibit declines, with two of seven populations (Spring 1 and Spring 2) experiencing declines greater than 10% by year 30 (Figure 9). Increasing probabilities of occurrence beyond 10% and losses of reproduction and survivorship beyond 75% and 20% respectively, caused declines across all populations, with declines exceeding 50% by year 30 in five (Big Piney 1, Big Piney 2, Spring 1, Spring 2, and Gasconade populations) of seven populations (Table 6; Figure 9b).

Combining the multifactor scenario with various degrees of increased juvenile mortality (Table 1, Scenario 6) resulted in greater population declines (Figure 10 a, b, c) than when multifactor scenarios or increased juvenile mortality (Table 7 a, b, c) occurred in the absence of one another. When the multifactor scenario interacted with 25% juvenile mortality, notable declines in the three populations (Spring River 1, Spring River 2, and Gasconade populations) were seen, though declines were evident in all but the Eleven Point populations (Figure 10a). Adding a 50% juvenile mortality schedule to the multifactor scenario resulted in declines across all populations with extinction events seen in the Spring River 2 population (Figure 10b). 75% juvenile mortality compounded by multifactor catastrophes resulted in the greatest level of population declines with extinction events in four of seven populations by year 80 (Table 7; Figure 10c).

Dispersal Model Scenario Results

In the dispersal models, populations were either totally isolated from one another or had some degree of dispersal ability. In the dispersal models in which populations were isolated, those populations exposed to high level negative factors quickly began to little effect on the populations. This was especially the case for reproductive failures. *C. alleganiensis* has such a high mortality rate (Appendix B) from age 0 to age 1 (>99%) that low-level reproductive failures did not have a large impact upon the population as a whole. Population declines were only evident when there was a 60% chance of 90% reproductive failure (Figure 7c) or a 10% chance of 40% survivorship losses (Figure 8b).

It is commonly accepted that smaller populations are affected most by random events (Hanski and Simberloff 1997, Miller and Lacy 1999). It was thus unexpected that the largest population would be the one most impacted by the occurrence of random reproductive failures (Figure 7c), moderate survivorship losses (Figure 8a) and combinations of the two (Figure 9a). The initial population size of the largest population (420) was assigned to the data set of the Eleven Point population to determine whether the high rates of decline exhibited by the largest population resulted from the population size or from the data parameters. The result of this modification suggested that the trend toward large populations declining more rapidly than smaller populations resulted from the specific combination of parameters existing in the original data set rather than a problem with the simulation process itself. Examination of the data input parameters revealed that the largest population had higher mortality rates, even in those years unmanipulated, than the smaller populations for all age groups until the age of sexual maturity (Peterson 1985). Given the negative effects of juvenile mortality on these population models it was not surprising that the larger population experienced greater population declines than the smaller populations.

Because it was likely that stochastic reproductive and survivorship losses would be occurring along with increases in juvenile mortality, the two were combined with experience declines while those populations experiencing lesser degrees of negative factors remained relatively stable. Also with isolation, those populations experiencing high-level negative factors tended to become extinct with some extinctions occurring by year 60 and most occurring by year 90.

In the dispersal models in which dispersal did occur the general trend was a decline in all populations, with the greatest declines occurring in those populations experiencing high-level negative factors. In contrast to isolation scenarios however, when dispersal occurred, all populations persisted over time. The total number of individuals present across all populations varied in magnitude with isolation versus dispersal scenarios depending upon the number of populations and the negative factors imposed.

Isolation versus Dispersal and Reproductive Failure

When reproductive failure was the negative factor affecting populations (Table 1, Scenario 7), isolation resulted in extinctions of those populations experiencing high level reproductive failure. Whether there were four, eight or 16 populations, those populations experiencing high-level reproductive failure experienced declines of more than 75% by year 30. At least 50% of all populations were extinct by year 90 and all high-level factor populations were extinct by the end of the scenarios (Figure 11a, b, c). Populations with low-level negative factors imposed experienced slight to no decline (Table 8 a, b, c).

Enabling constant rate dispersal among populations with reproductive failure as the negative factor affecting populations resulted in declines of more than 40% by year 30 in all populations with the only exceptions being one (Eleven Point 1) of the eight population scenario which did not decline, and two populations in the 16 population scenario in which the Spring 3 population did not decline and the Gasconade population declined only slightly (Figure 12 a, b, c). Declines of populations experiencing high-level negative factors were relatively high (greater than 56% by year 30), but all populations persisted across the duration of the scenarios (Table 8 a, b, c).

Except for the 16 population scenario, the total number of individuals present across populations when populations were isolated was greater by year 60 than the total number of individuals present in scenarios with dispersal ability when emigration was constant (Figure 13), constant emigration involving 3% of individuals from any one population dispersing to the other populations at any given time across the course of the simulations. Constant rate emigration had greater total numbers of individuals across populations than when emigration was variable (Table 8 a, b, c), with variable rate emigration involving 1% of individuals from each population entering each of the other populations being modeled at any given time (Figure 14). Constant rate emigration resulted in higher numbers of individuals across populations by year 60 than all other variable rate emigration populations (Figure 14).

Isolation versus Dispersal and Multiple Negative Factors

Modeling populations with combined reproduction and survivorship losses imposed upon all populations and 75% mortality imposed upon three out of every four populations resulted in variable responses as a result of isolation or dispersal ability (Table 9 a, b, c). Isolation resulted in populations experiencing no increase in juvenile mortality showing little or no declines in population sizes over time. The result for those increases in juvenile mortality to determine how interacting factors might affect population dynamics. A 25% mortality schedule with reproduction and survivorship losses (Figure 10a) resulted in some declines, but they were of a lower magnitude than the declines resulting from a 50% (Figure 10b) or especially with a 75% mortality schedule combined with multifactor stochasticity, which was devastating for *C. alleganiensis* populations (Figure 10c). This was not an unexpected response. More negative factors influencing a population logically would result in greater population declines.

The multifactor/juvenile mortality scenarios likely represent the closest approximation to events that actually affect *C. alleganiensis* populations because it is probable that no single factor is causing declines in *C. alleganiensis* populations. Sedimentation from gravel mining, stream bank erosion, highway and bridge construction, and habitat degradation from development projects (Miller and Wilkerson 2000, Schultz 2000, Wilkerson 2000, Blanc 2001) affect the streams where the *C. alleganiensis* data used in this PVA were collected. Under similar anthropogenic impacts, salmonid populations have experienced reduced reproduction and survivorship and increased juvenile mortality (NMFS 1998). Increased sedimentation and habitat degradation are expected to cause nearly identical declines in *C. alleganiensis*, which live in similar habitats and require similar spawning substrate (Nickerson and Mays 1973).

Because multiple factors are expected to be affecting *C. alleganiensis* populations, it would be useful to identify those factors having the greatest impact on rates of survival and reproduction, something that currently cannot be gathered from the data in the Ozark region, and to manage the population with those factors in mind. Until the time that those factors can be concretely identified, managing the species from a worst-case scenario may be the best conservation strategy. In the event that individual negative factors affecting populations cannot be identified, the range of factors modeled could provide a baseline for making predictions regarding potential population trends.

Dispersal and Population Responses

Peterson (1985) predicted that emigration and immigration were important to *C. alleganiensis* population dynamics. His 1987 study determined that dispersal rates of 5% to 11% were likely and suggested that dispersal is important to *C. alleganiensis* population dynamics (Peterson 1987). However, the results of this PVA study suggested that the effect of dispersal on population size may be much more complex than previously anticipated, with the outcome depending on the factors affecting the populations and the relative emigration and immigration rates. It is necessary to examine impacts from a metapopulation perspective (comparing isolation and variable rates of dispersal) to gain an understanding of the actual relationships of one population to another.

Isolation versus Dispersal and Reproductive Failure

When reproductive failure was the factor affecting populations, dispersal did not improve the total number of individuals present across populations except in the constant rate emigration scenario with 16 populations present. Isolated populations which experienced low-level reproductive failure, and subsequently persisted over time, showed

(Soule 1987). Increased juvenile mortality caused negative trends in population sizes and also, if severe, caused extinction in some populations. It has been suggested that juvenile mortality is most likely the factor affecting the populations utilized in this study (Prosen 1999, Wheeler 1999). Returning juvenile mortality to levels expected for healthy populations should decrease the magnitude of negative responses to other factors as well. Juveniles rely upon the interstices of gravel for both food and cover (Nickerson and Mays 1973). For salmonids, embryo survival is reduced with increases in the presence of fine sediments at spawning sites (Sando 1981, NMFS 1998). Invertebrates, which provide the bulk of juvenile *Cryptobranchus* diet, also depend upon the characteristics of stream substrate (Lampert and Sommer 1997). Sando (1981) stated that densities of benthic organisms were inversely correlated with sediment load, suggesting that food availability for juvenile *Cryptobranchus* would improve with *Cryptobranchus* habitat improvement. It follows that preserving natural geomorphological structure of stream substrate, which in *Cryptobranchus* habitat would consist of coarse gravel and large cover rocks or limestone shelves, (Nickerson and Mays 1973, Peterson 1985, Peterson 1987) would reduce juvenile mortality. Improvements to habitat quality through channel recovery processes can be accomplished in a time frame that is short compared to the life cycle of *Cryptobranchus* (Kanehl 1997). Thus, immediate positive responses of juvenile survivorship would be expected if *Cryptobranchus* juvenile mortality was found to be related to habitat and habitat protection/enhancement measures were enacted. In addition, studies focusing upon the identification of factors contributing to *Cryptobranchus* declines could use juvenile survival rates as early success indices, only slightly lower population sizes throughout the time of the scenarios than compared to their original size. This suggests that in most situations, high-level reproductive failure cannot be counteracted by increasing dispersal. In making management decisions, it must be determined whether having a few large populations, which are isolated and therefore subject to the dynamics of isolated populations (Soule 1987), or having more, smaller populations are going to be most beneficial to conservation of the species. In the simulations, a trade-off occurred between number of populations and population size in relation to dispersal versus isolation (Figure 11 a, b, c; Figure 12 a, b, c). When populations were isolated, the size of individual populations was higher than the population sizes when dispersal was occurring, but there were many fewer surviving populations. In the case of four populations, only the population that was not experiencing high-level negative factors persisted when populations were isolated, but that remaining population did not decline from its original levels. When dispersal was occurring, all of the populations persisted, but the number of individuals within populations was lower. This is analogous to the SLOSS (Single Large or Several Small) debate (Primack 2000) for the creation of reserves in which it must be determined whether the best strategy is to conserve a single large area, presumably minimizing edge-related mortality factors, or several small areas to reduce the risk of extinction should negative factors lead to extinctions in a single population. Deciding whether to preserve an isolated population (which represents a single large population) or to preserve the smaller dispersing populations (several small) depends on multiple spatial and land-use parameters (what is geographically feasible with the current land constraints) as well as historical population data and current population trends (what makes a healthy population?).

Constant rate emigration likely influenced the reproductive failure scenarios (Figure 12 a, b, c) because as the populations decline, constant emigration means fewer individuals will be dispersing to other populations. For example, if in the four population scenario, 100 individuals were present in a given year, then 3% of that 100 would be three individuals available from dispersal. If the subsequent year has only 80 individuals in the population, then 3% of the 80 would be 2.4 individuals. When populations are very small there will be years in which no individuals are available from other populations. Because of the reproductive failures imposed, the populations were in decline. Therefore, the numbers of individuals coming into the populations would decrease with each year of decline.

That low-level dispersal is favorable to maintaining populations is suggested by the results of 16 populations with constant rate dispersal that maintained higher population sizes (Figure 13). The more populations present, the greater the chance that an individual would be available to enter a population in any given year. In other words, populations will not have as many time periods in which they do not receive immigrants from other populations, as compared to scenarios with fewer populations. This is due to the number of populations experiencing only low-level negative factors, which was four for 16 populations (as compared to one in the four population scenarios and two in the eight population scenarios). Because there were four populations from which to receive a potential immigrant, fewer time periods would pass in which no immigrants entered a population. This also created a reciprocal relationship for the "source" populations, although conclusions about the long-term impact of increased juvenile survivorship on population structure would have to wait for a complete generation cycle.

Increased juvenile mortality may not be the only factor negatively affecting *C. alleganiensis* populations. It has been concluded that multiple factors are responsible for declines in salmonid stocks in the Pacific Northwest (Sando 1981, NMFS 1998). Both reproduction and survivorship have been linked to habitat quality in salmonids (NMFS 1988). While it is unclear whether one or multiple factors are affecting *C. alleganiensis* population dynamics, it can be predicted that habitat quality improvements could have a positive impact on *C. alleganiensis* populations.

There are several methods which could be used to improve habitat quality for both adult and juvenile *Cryptobranchus.* Channel recovery processes have traditionally focused on returning streams to their natural flow (Kanehl 1997). Though the Ozark area involved in this study has not experienced channelization on a large scale (Miller and Wilkerson 2000, Wilkerson 2000, Blanc 2001), using channel naturalization strategies to control flow fluctuations, which have caused reproductive failures in salmonids (Sando 1981), could be an appropriate management step in streams where channelization has altered habitat. Sedimentation could be eliminated using riparian buffer strips which serve as filters for particulate matter from runoff (Osborne and Kovacic 1993, Bren 1995, Coleman and Kupfer 1996). Buffer strips also serve to regulate water temperature (Osborne and Kovacic 1993, Coleman and Kupfer 1996) which is important to cold-water dwellers, like *Cryptobranchus.* Additionally, prohibiting construction of dams and the removal of current dams is an encouraged management step. Dams can completely alter the natural landscape of a region, changing lotic systems into lentic systems (Kanehl which also gained immigrants rather than only losing individuals to the "sink" populations.

The effect of degree of dispersal on population size over time was evident when using the variable emigration rate. The data involving variable rate emigration (which involved greater numbers of individuals dispersing between populations than occurred with constant rate emigration) suggest that increasing dispersal would not decrease the chance that small populations would decline further, because increasing dispersal (variable rate emigration) resulted in even fewer individuals across populations than with constant rate emigration (Figure 14). The result of variable rate emigration was fewer individuals across the populations for eight and 16 populations (Figure 14) than in constant rate emigration (Figure 15) in which emigration rate did not change for four populations with emigration pattern so the results were the same. Again, these populations were losing more individuals than they were gaining from other populations, resulting in population declines. The response of 16 populations exhibited a pattern similar to four and eight populations which were experiencing negative effects from dispersal. A trend toward lower population numbers for dispersal scenarios as compared to isolation scenarios occurred across all populations, regardless of number of individuals involved. The trend toward lower population numbers contrasted the greater population sizes seen for 16 populations with dispersal compared to isolation in the 16 populations of the constant emigration models. The contrasting trends may have resulted from the difference in numbers leaving each population. Total emigration from each population in the variable emigration rate when 16 populations were present rose from 3% (as in constant emigration) to 9%, a great increase in the number of individuals leaving for "sinks" where they would not likely be significant contributors to future generations (Pullium 1988).

Isolation versus Dispersal and Multiple Negative Factors

When moderate reproduction and survivorship losses were modeled with 75% juvenile mortality, the initial responses among individual isolated populations were similar to the responses seen when high level reproductive failure alone was the effector: those populations experiencing the negative factors declined to eventual extinction (Figure 15 a, b, c) while unaffected populations remained fairly stable.

In contrast, when dispersal involved a constant emigration rate, dispersal was beneficial to populations. Not only were the sizes of individual populations, regardless of the magnitude of negative factors, comparable (Figure 16 a, b, c), but the total number of individuals across populations with constant emigration rates was higher than for isolated populations (Figure 17), in contrast to what was observed for reproductive failure scenarios (Figure 13). The benefit of dispersal was highest for eight and 16 populations (Figure 17).

Within such scenarios, having eight populations with dispersal capabilities was more valuable than having eight or even 16 isolated populations, and having four populations with dispersal capabilities was almost as valuable as having eight isolated populations (Figure 17). This result could be extremely important from a conservation perspective. When land availability is not an issue, it would be much more feasible to protect eight populations and ensure their ability to intersperse than it would be to attempt to protect 16 isolated populations. It should be reemphasized that only four of those 16

1997). Often the areas downriver of the dam are no longer suitable for spawning of many fish (Bergstedt 1997) and would not be suitable for *Cryptobranchus*. Dam removal results in an increase in rocky substrate (Kanehl 1997) which would be of benefit to both adult and juvenile *C. alleganiensis.*

Habitat quality improvements would have to go beyond protecting an individual location within a stream. The results presented here suggest that dispersal could have a great impact on population dynamics. Isolated populations are theoretically at a greater risk of decline than metapopulations when faced with deterministic and stochastic variability. Yet some populations with dispersal resulted in decreases in population size, presumably when population growth was slower than the rate of emigration in source-sink metapopulations. This situation was especially evident when *C. alleganiensis* was experiencing high-level reproductive failure, as Wheeler (1999) speculated might be occurring in natural populations. High levels of reproductive failure as modeled for *C. alleganiensis* are realistic considering reproductive failure observed at those levels for salmonids which inhabit similar niches (Sando 1981).

The extreme levels of negative factors affecting some populations represent a conservation situation where one or more "protected" areas of habitat, such as might be found in a preserve, are surrounded by marginal habitat. The marginal habitat represents the "sinks" for the populations. Eventually, according to the predictions of these *C. alleganiensis* models, those populations that would otherwise be relatively healthy, experience declines due to the large numbers of individuals being lost to the "sinks". This suggests the necessity of approaching *C. alleganiensis* conservation from a landscape perspective in which the protection of all populations within a spatially isolated populations (the four populations not manipulated), persisted over time when the multifactor scenarios were imposed upon three of every four populations. The isolation simulations involving four populations demonstrated the uncertainty which would threaten the remaining four of 16 initial populations if they were isolated and later faced an increase in negative factors.

The conservation benefits of dispersal should be approached with caution. There appears to be a level of dispersal which, if exceeded in conditions with many patches of less-than-optimal habitat, could actually diminish *C. alleganiensis* populations. Population declines due to excessive dispersal would be expected to occur in situations where populations were losing too many individuals to "sink" populations which cannot reciprocate with any individuals from their own populations, as mentioned above. This became evident in the variable emigration models, which increased emigration in the eight and 16 population scenarios. Increasing emigration resulted in smaller metapopulation sizes over time (Figure 18). Populations with many individuals leaving could experience declines simply because they were serving as a "source" for other populations when population growth was slower than the rate of emigration. Further increasing emigration to "sink" populations, those experiencing high-level negative factors, would be expected to result in even smaller metapopulations or even extinction events over time.

Implications for Cryptobranchus Management and Research

From a conservation perspective, this PVA study supported the hypothesis that understanding population dynamics is imperative to maintaining a viable population dynamic region is considered. Certainly targeting individual populations for protection is important, but this PVA suggests that protecting a "source" population does not necessarily guarantee the viability of that population. For that reason, habitat quality improvements on a larger spatial scale would have to implemented in situations where dispersal has a negative effect on populations.

Determining which populations would actually benefit from protection must also be determined. Randomly selecting the population which is most convenient to human purposes, such as development projects, without fully considering the negative factors acting upon that population, may lead to the protection of populations which are doomed to extinction at the expense of a population which has a better chance of long-term viability. Because *C. alleganiensis* is long-lived, identifying the factors causing declines or determining whether or not a conservation strategy will be successful may not be evident for many years. If the reasons for declines in some populations are not known, then simply protecting a population by labeling a site as a preserve may not alleviate the reasons for declines. In this case, it would be better to protect those populations experiencing little or no decline because the chance of long-term persistence for populations experiencing low-level negative factors was shown to be more optimistic over time than for populations with high-level negative factors.

Deciding not to protect smaller dispersing populations in favor of isolated populations is another possible management strategy. The isolated populations remained stable as long as they were free from high levels of negative factors. Thus, conservation efforts could concentrate on protecting individual sites with healthy *C. alleganiensis* populations. This is unlikely to be an ideal conservation method given current *C.*

alleganiensis population declines (Prosen 1999, Wheeler 1999) and the degradation of suitable stream habitat by human impacts (Miller and Wilkerson 2000, Schultz 2000, Wilkerson 2000, Blanc 2001). Such a strategy seems unlikely to assure long-term viability of populations, since high levels of negative factors are probably already operating on *C. alleganiensis*.

Finally, to make truly informed decisions regarding management of this species, it is absolutely necessary to gather more reliable demographic data from multiple regions of its range. It is urgent that causes of population declines be concretely identified and, if possible, eliminated. The models suggested that population responses to negative factors vary according to the factors involved. Whether increasing dispersal abilities actually benefited populations was also variable. Therefore, incorrectly identifying the causes of population declines could negate the effectiveness of any conservation strategies imposed.

The longevity of *C. alleganiensis* makes total population responses to conservation difficult to quantify and makes reasons for declines more difficult to identify. Managing *C. alleganiensis* from a worst-case scenario, which would involve improvement or protection of habitat quality across metapopulation patches while monitoring juvenile numbers, is the currently the best means of ensuring that the species is adequately protected.

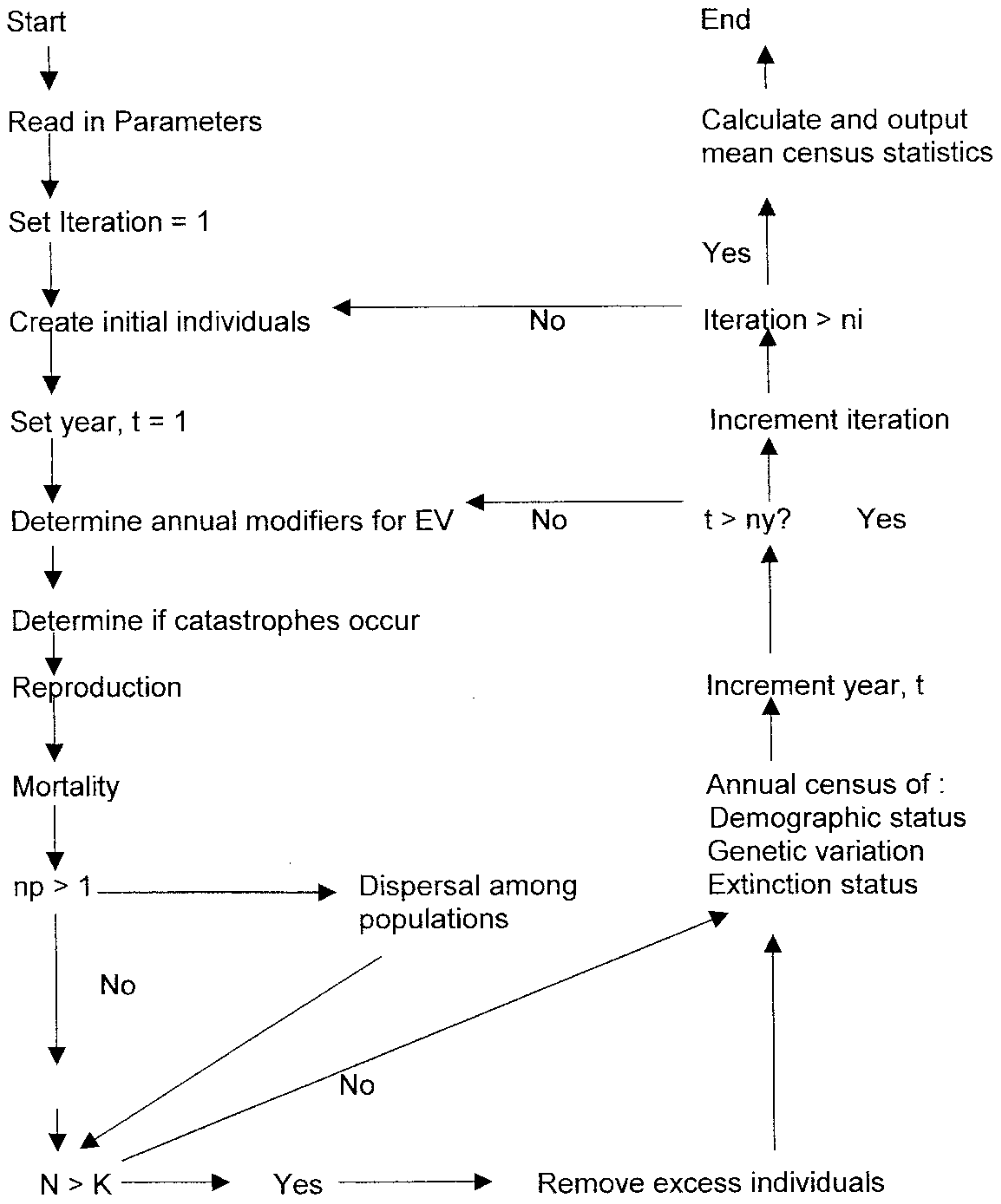


Figure 1 –Lacy 2000 (adapted). Flow chart showing methodology behind VORTEX PVA software. Arrows indicated direction of flow; t = year, EV = environmental variation, np = number of populations, N = population size, K = carrying capacity, ny = number of years simulated, ni = number of iterations.

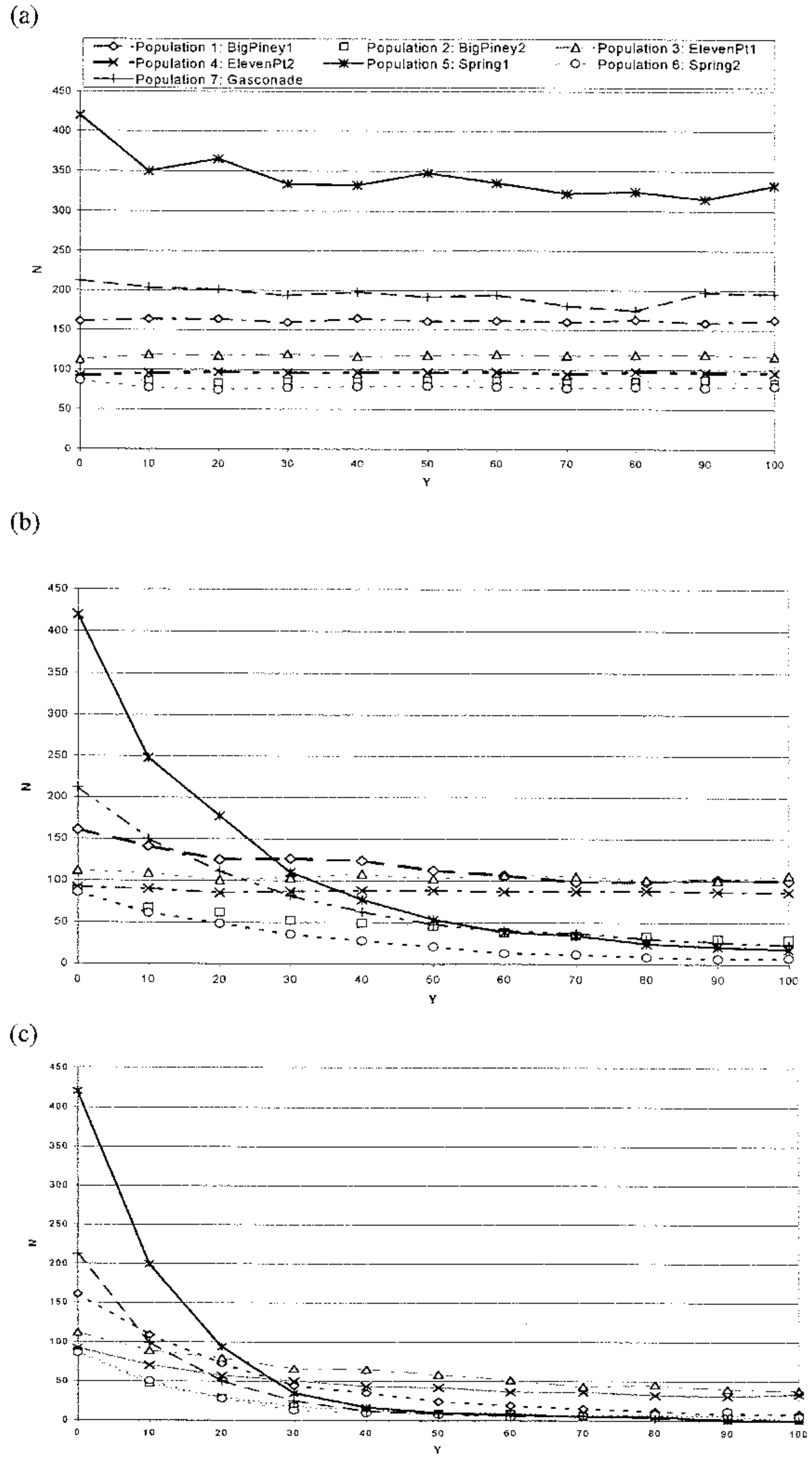


Figure 6 a, b, c – Responses of populations to changes in year one and year two juvenile mortality; (a) 25% year one and year two juvenile mortality, (b) 50% year one and year two juvenile mortality, (c) 75% year one and 50% year 2 juvenile mortality. N = population size, Y = year.

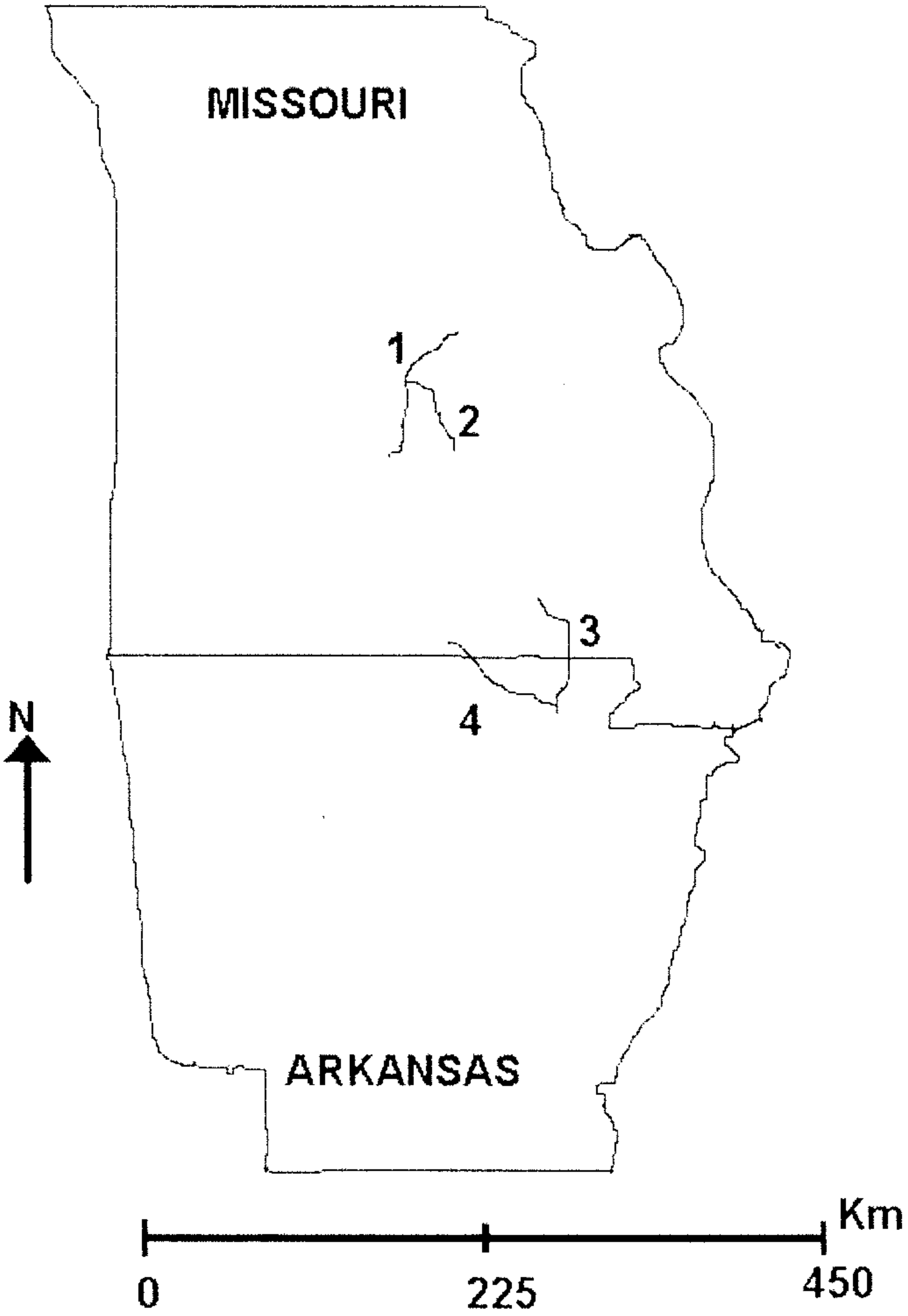


Figure 2 – Map showing relationship of streams containing study sites to one another. Streams are numbered; Big Piney River = 1, Gasconade River = 2, Eleven Point River = 3, Spring River = 4.

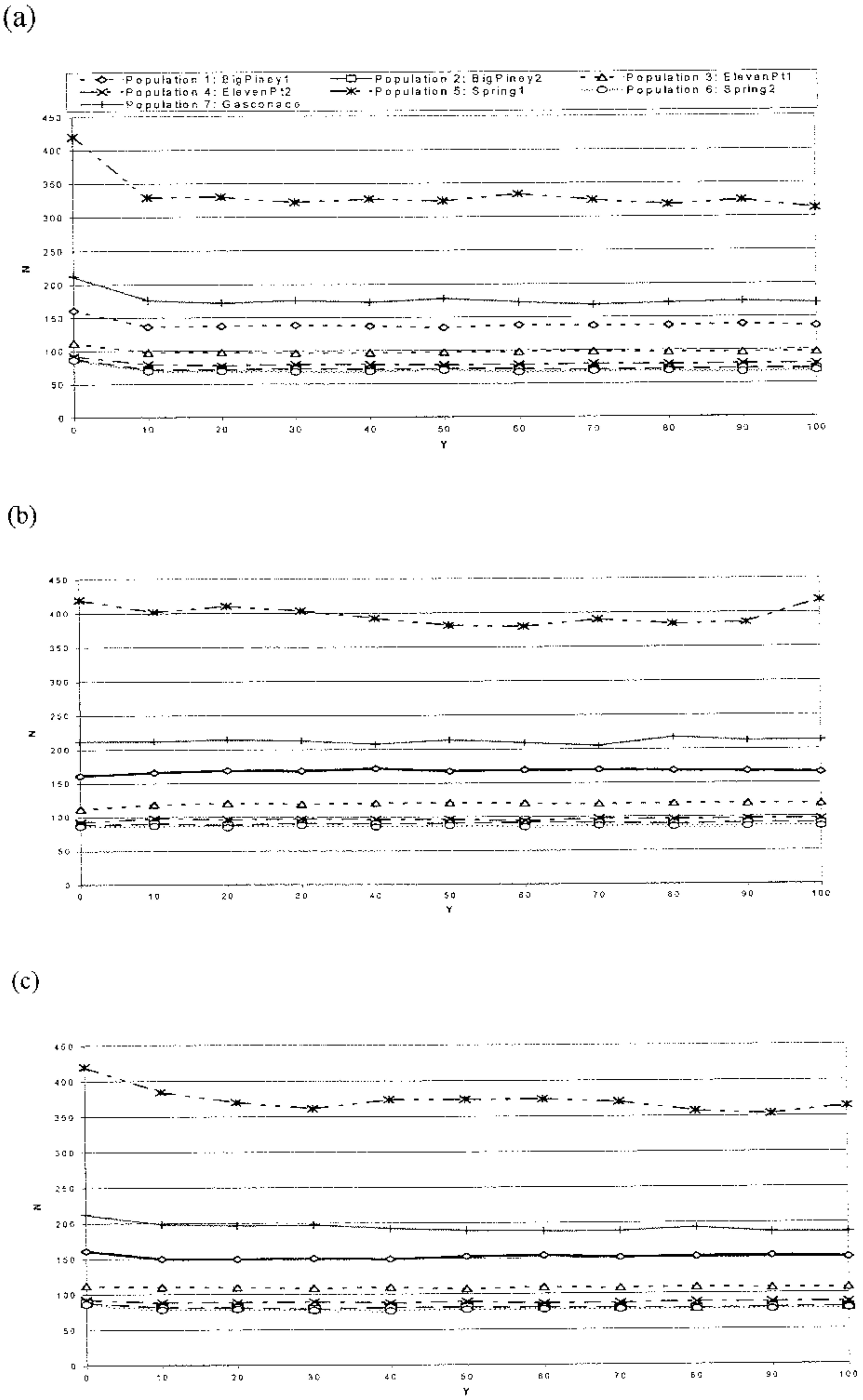


Figure 3a, b, c – Relationship of carrying capacity to initial population size and the subsequent impact on population stability over time; (a) carrying capacity is 10% lower than initial population size, (b) carrying capacity is 10% higher than initial population size, and (c) carrying capacity is equal to initial population size. N = population size, Y = year.

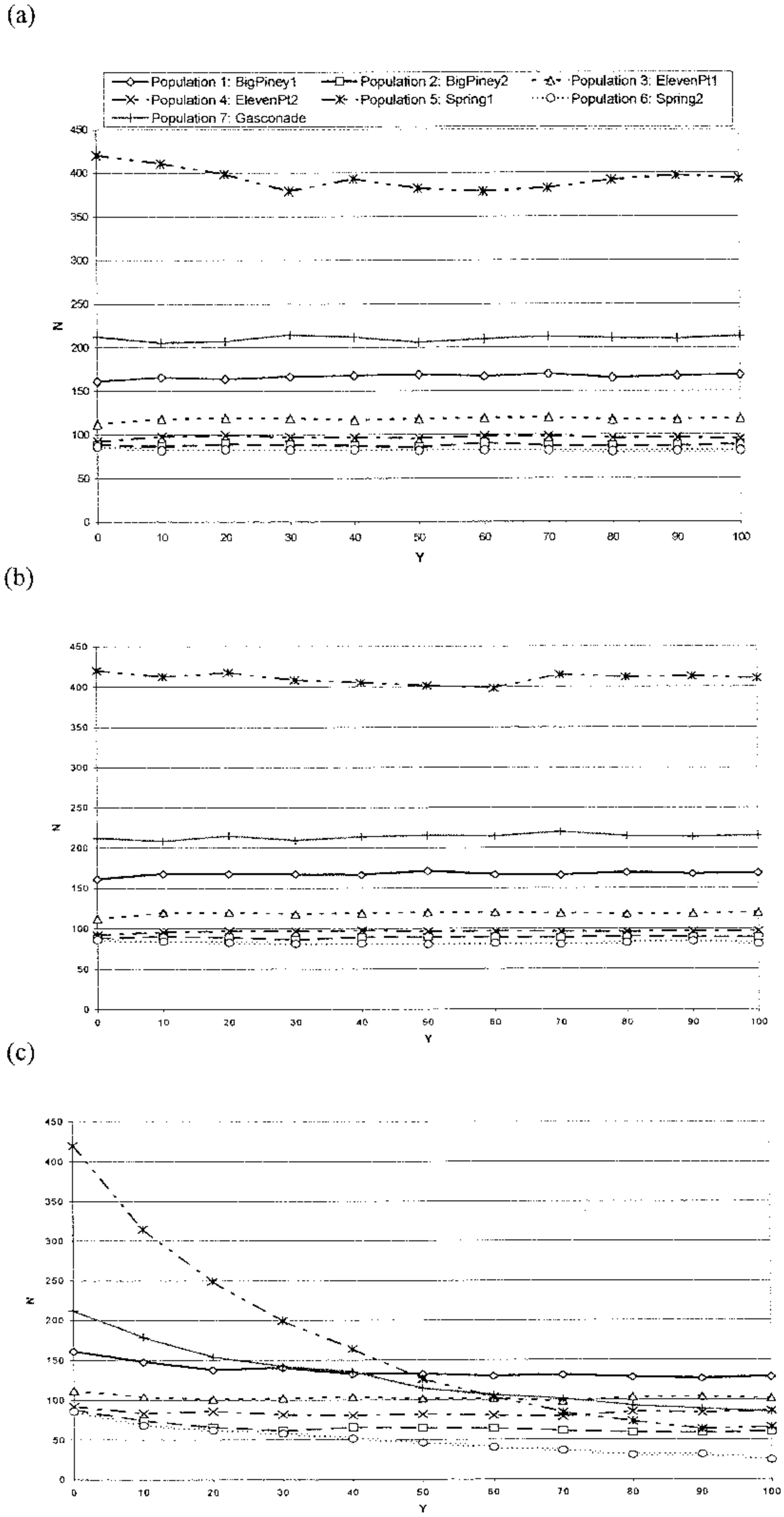


Figure 7 a, b, c – Population responses to variable degrees of incidence and severity of reproductive failure; (a) 10% chance of 75% reproductive failure, (b) 50% chance of 80% reproductive failure, (c) 90% chance of 60% reproductive failure. N = population size, Y = Year

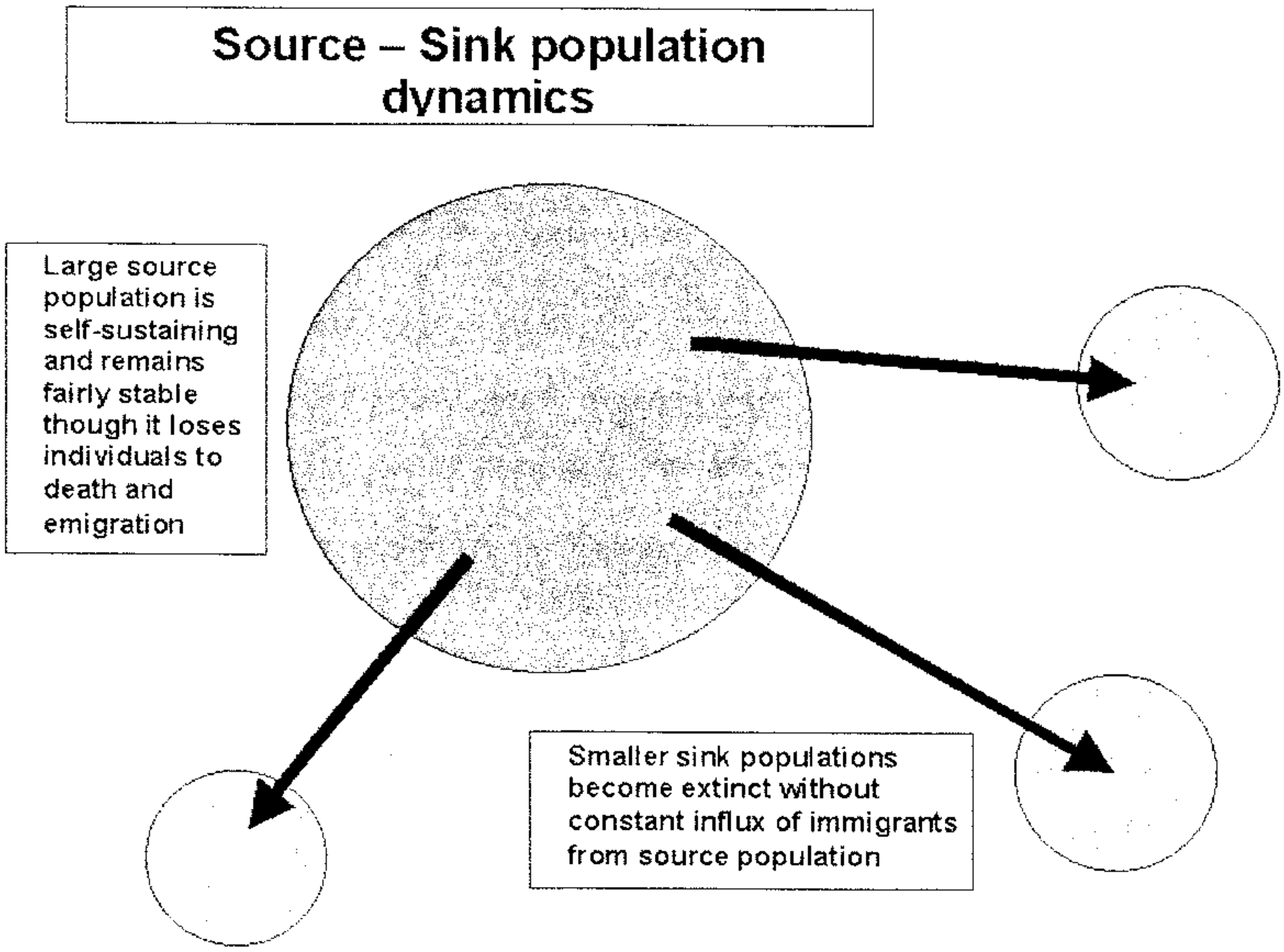


Figure 4 – Figure shows source-sink population dynamics.

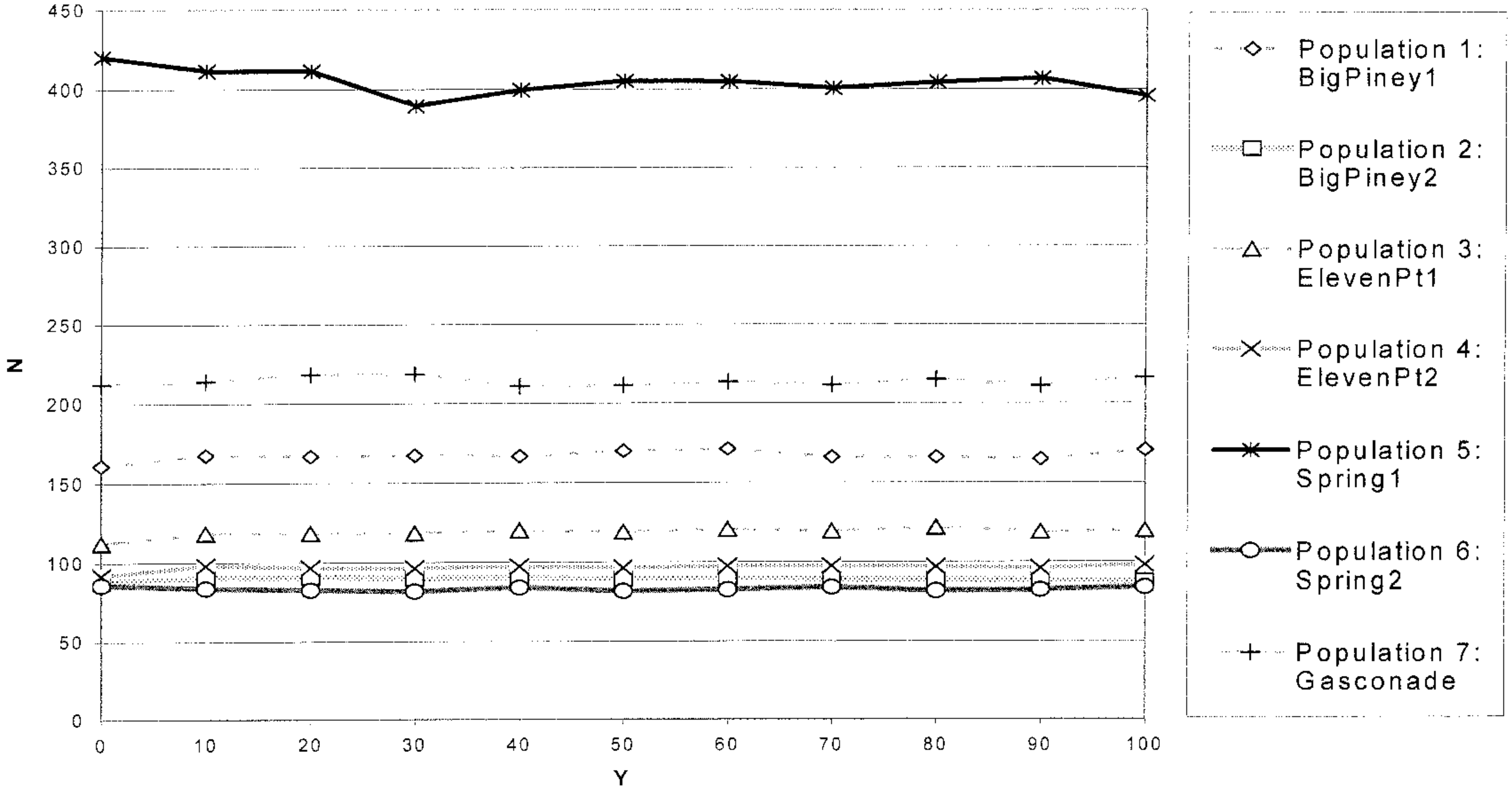


Figure 5 – Population trend resulting from input of basic life-history and demographic data for each population; N = population size, Y = year.

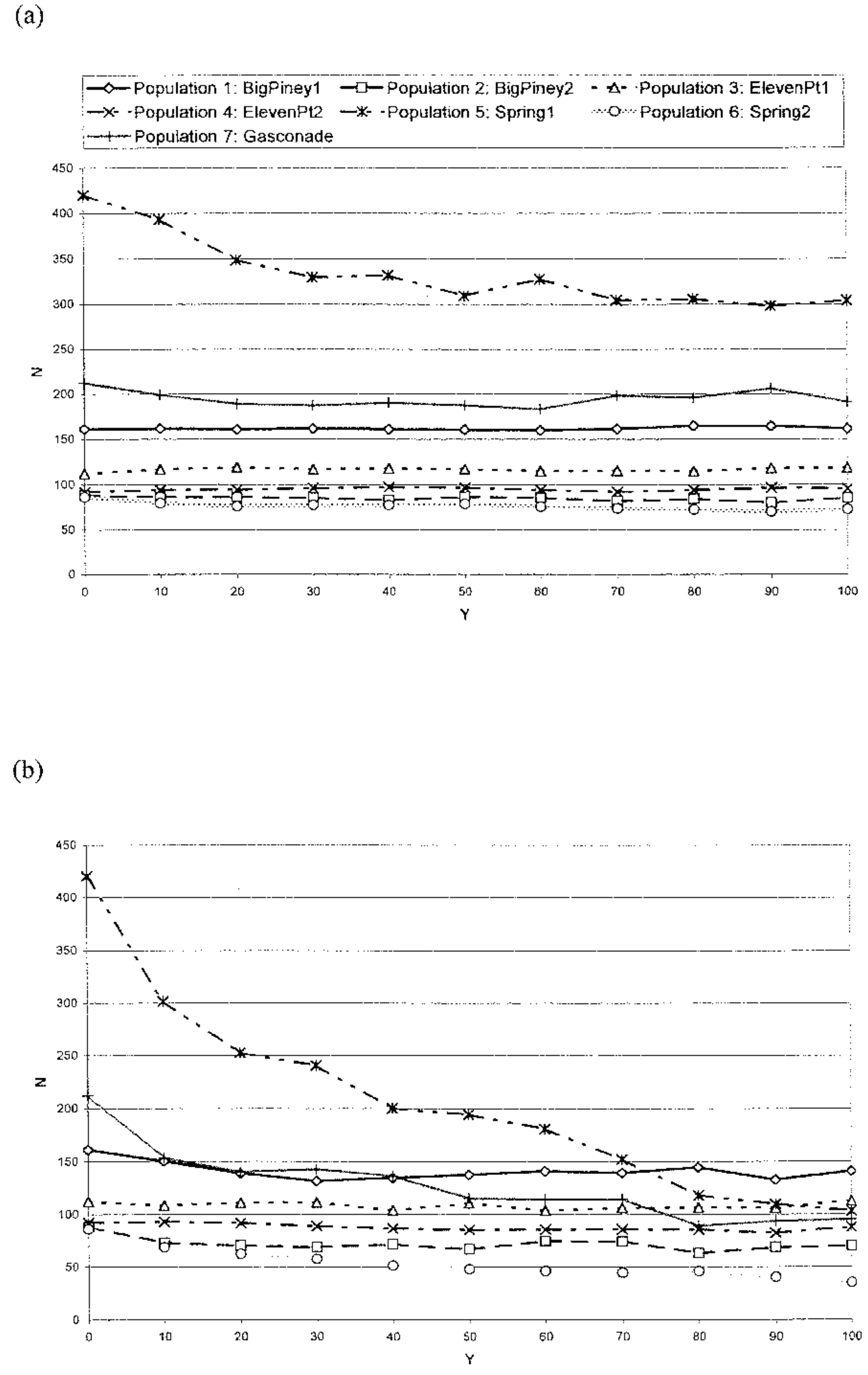
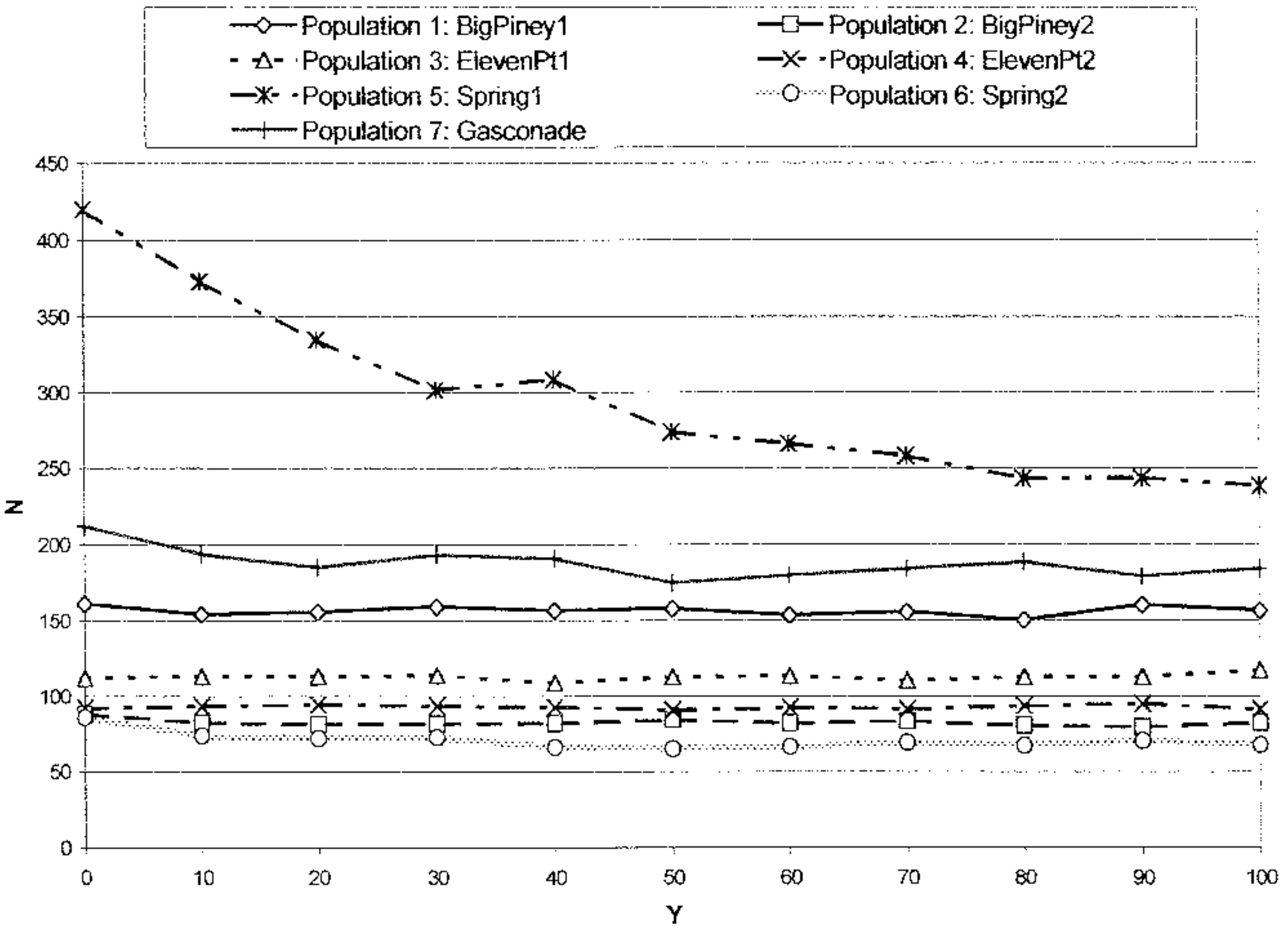


Figure 8 a, b – Population trends in response to (a) 10% chance of 20% survivorship loss and (b) 20% chance of 40% survivorship loss. N = population size, Y = year.

(a)



(b)

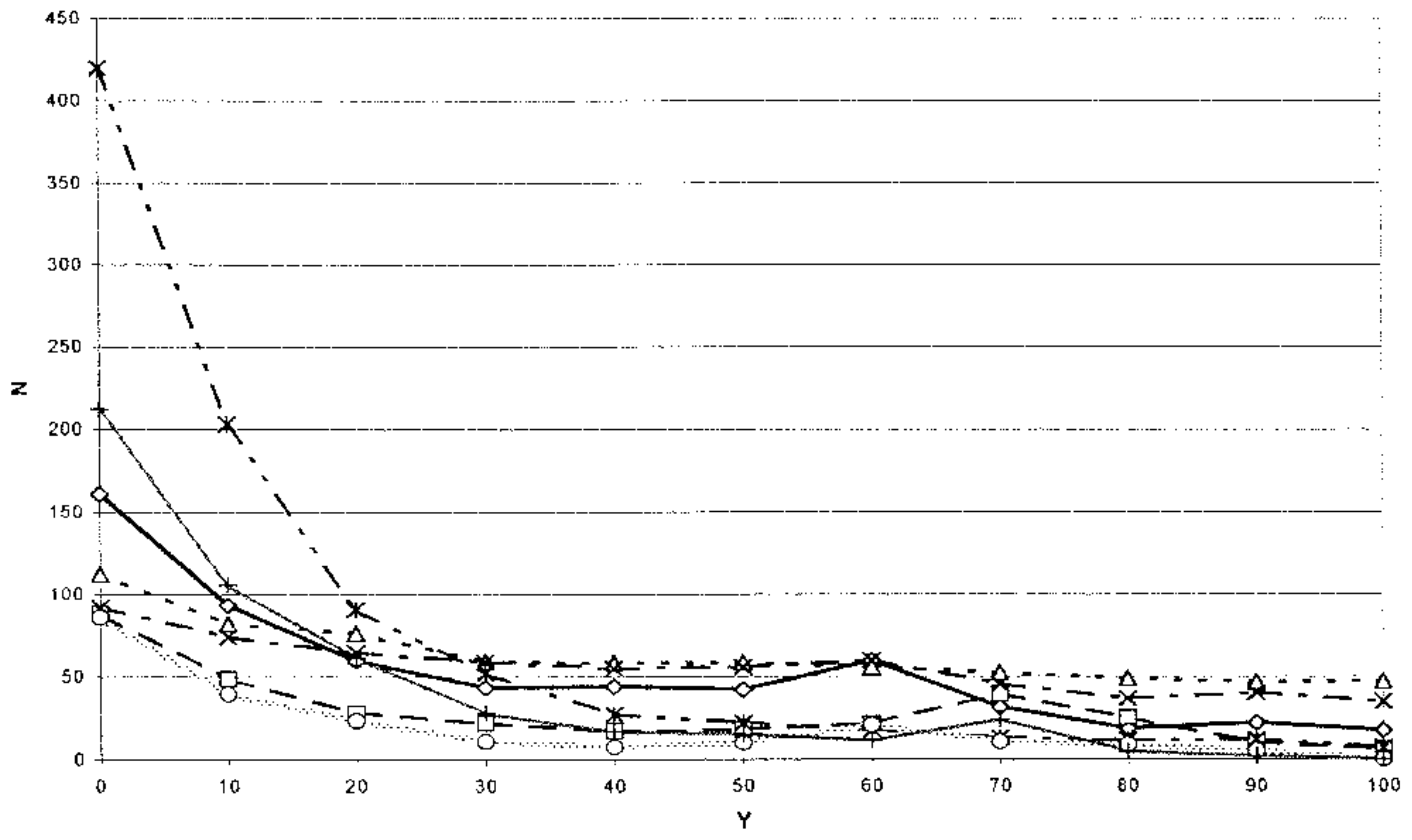


Figure 9 a, b – Population trends in response to (a) 10% chance of 20% survivorship losses and 75% reproductive failure (b) 30% chance of 30% survivorship loss and 90% reproductive failure. N = population size, Y = year.

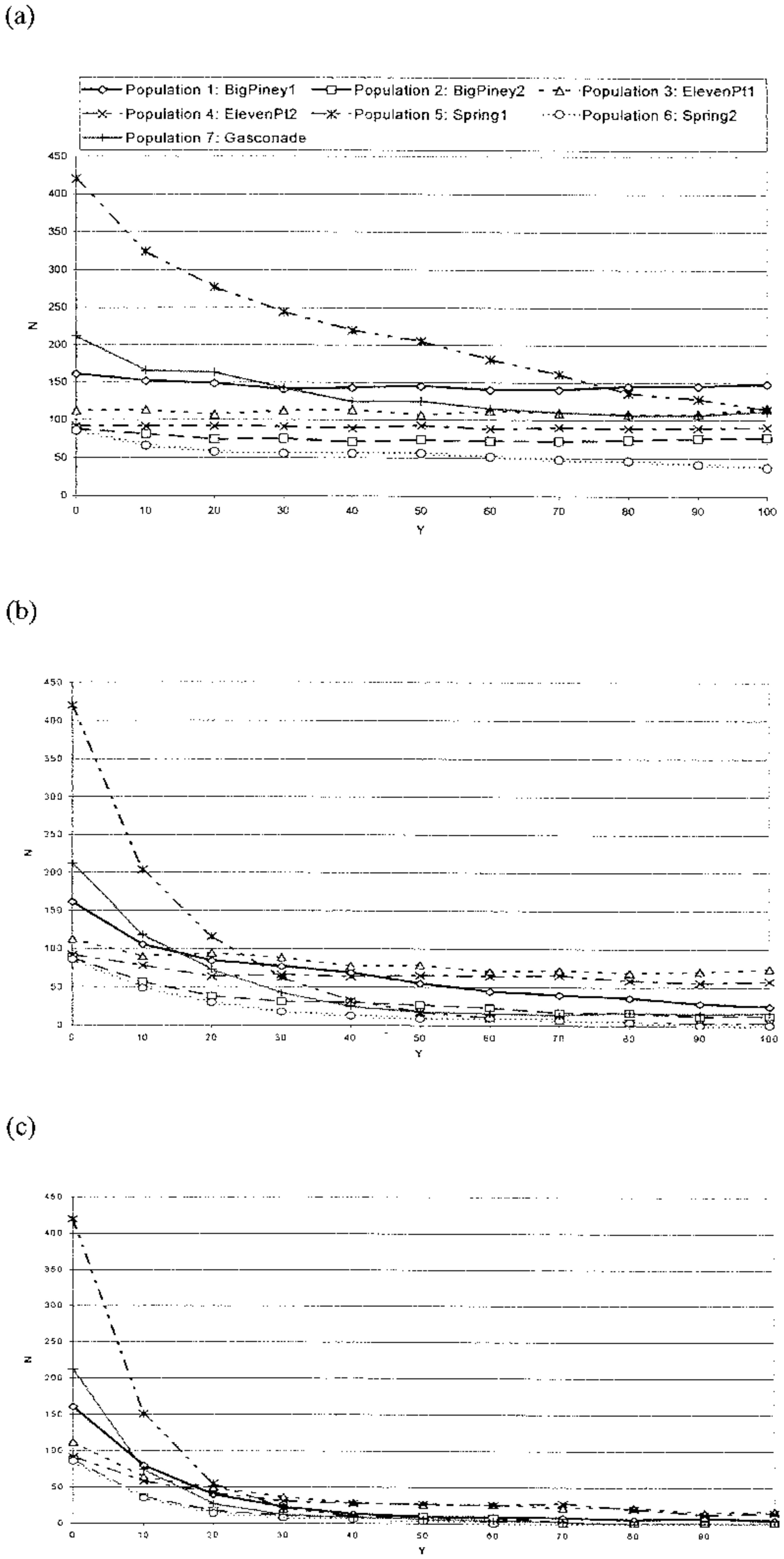


Figure 10 a, b, c – Combined survivorship losses and reproductive failures with increased juvenile mortality; (a) 25% year one and year two juvenile mortality, (b) 50% year one and year two juvenile mortality, (c) 75% year one and 50% year 2 juvenile mortality. N = population size, Y = year

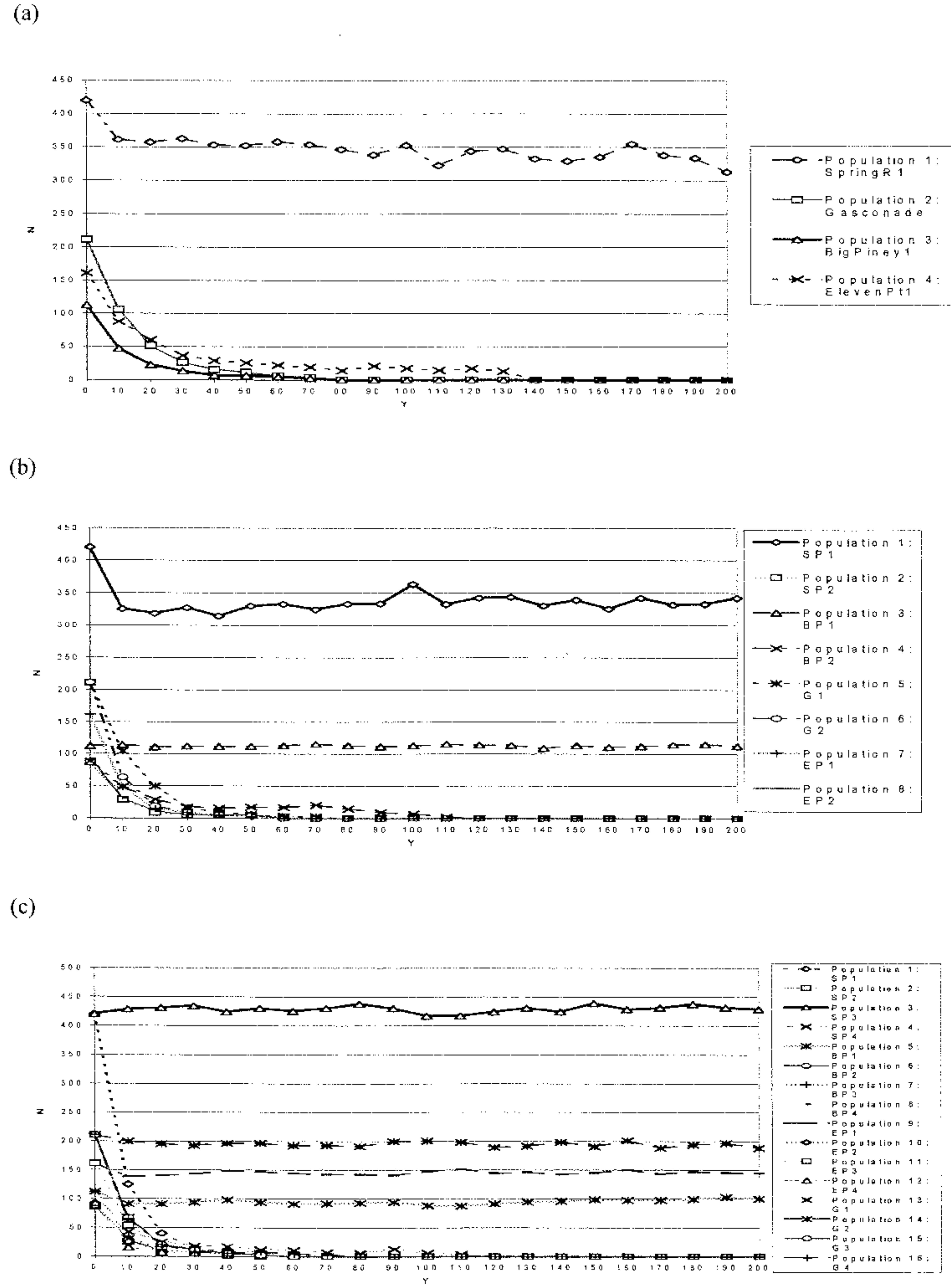


Figure 11 a, b, c – Four, eight, and 16 populations isolated from one another, 75% of populations experience high-level reproductive failure (100% chance of 90% reproductive failure) while 25% of populations experience low-level reproductive failure (10% chance of 75% reproductive failure); (a) four populations, (b) eight populations (c) 16 populations, N = population size, Y = year, SP = Spring River, BP = Big Piney River, EP = Eleven Point River, G = Gasconade River.

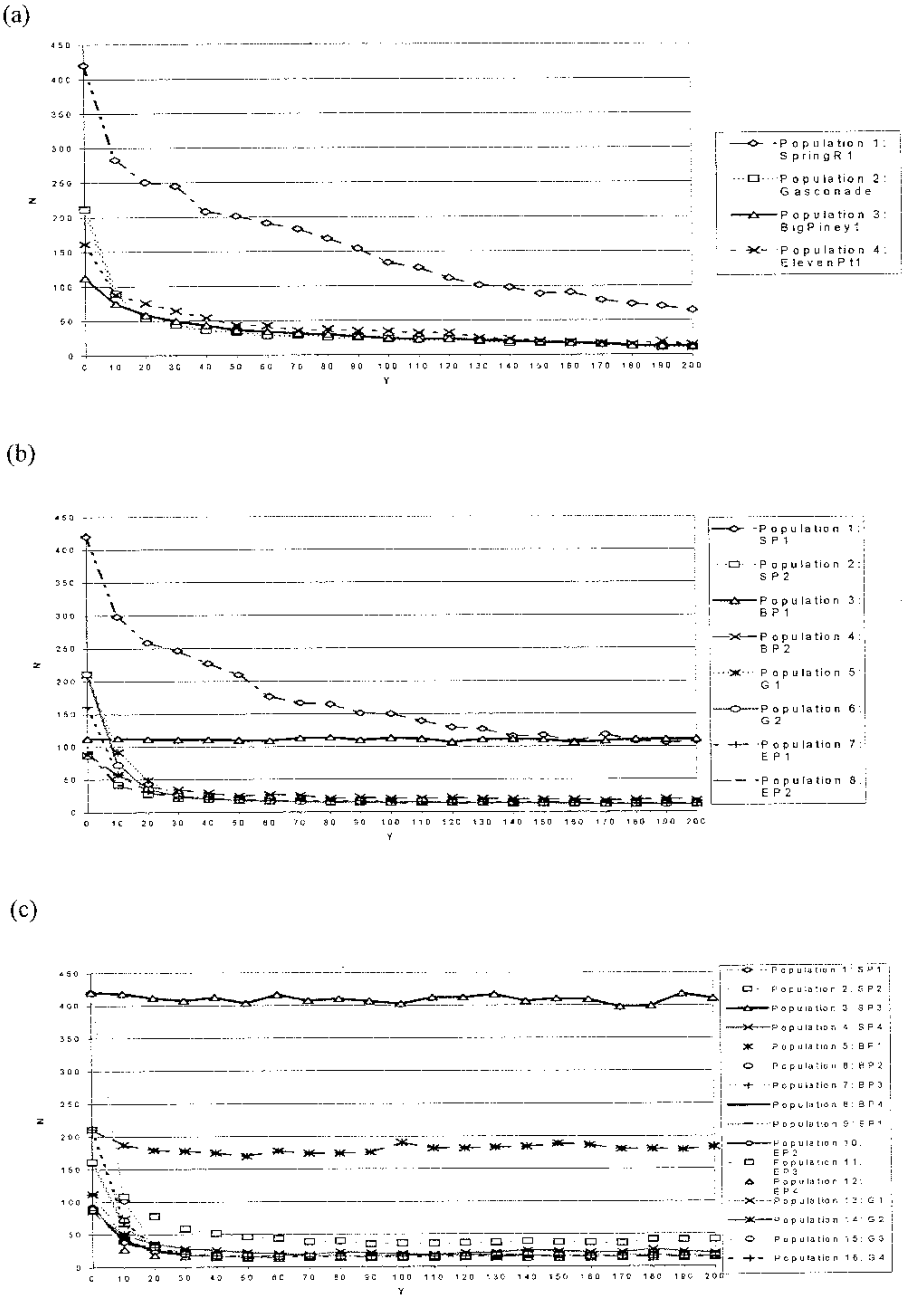


Figure 12 a, b, c – Four, eight, and 16 populations with constant rate emigration, 75% of populations experienced high-level (100% chance of 90% failure) reproductive failure while 25% of the populations experienced low-level (10% chance of 75% failure) reproductive failure. Legend shows name of each population with an assigned symbol and line-pattern indicating the trend line associated with the population's response to the parameters imposed over the course of the simulation; (a) four populations, (b) eight populations, (c) sixteen populations, N = population size, Y = year, SP = Spring River, BP = Big Piney River, EP = Eleven Point River, G = Gasconade River.

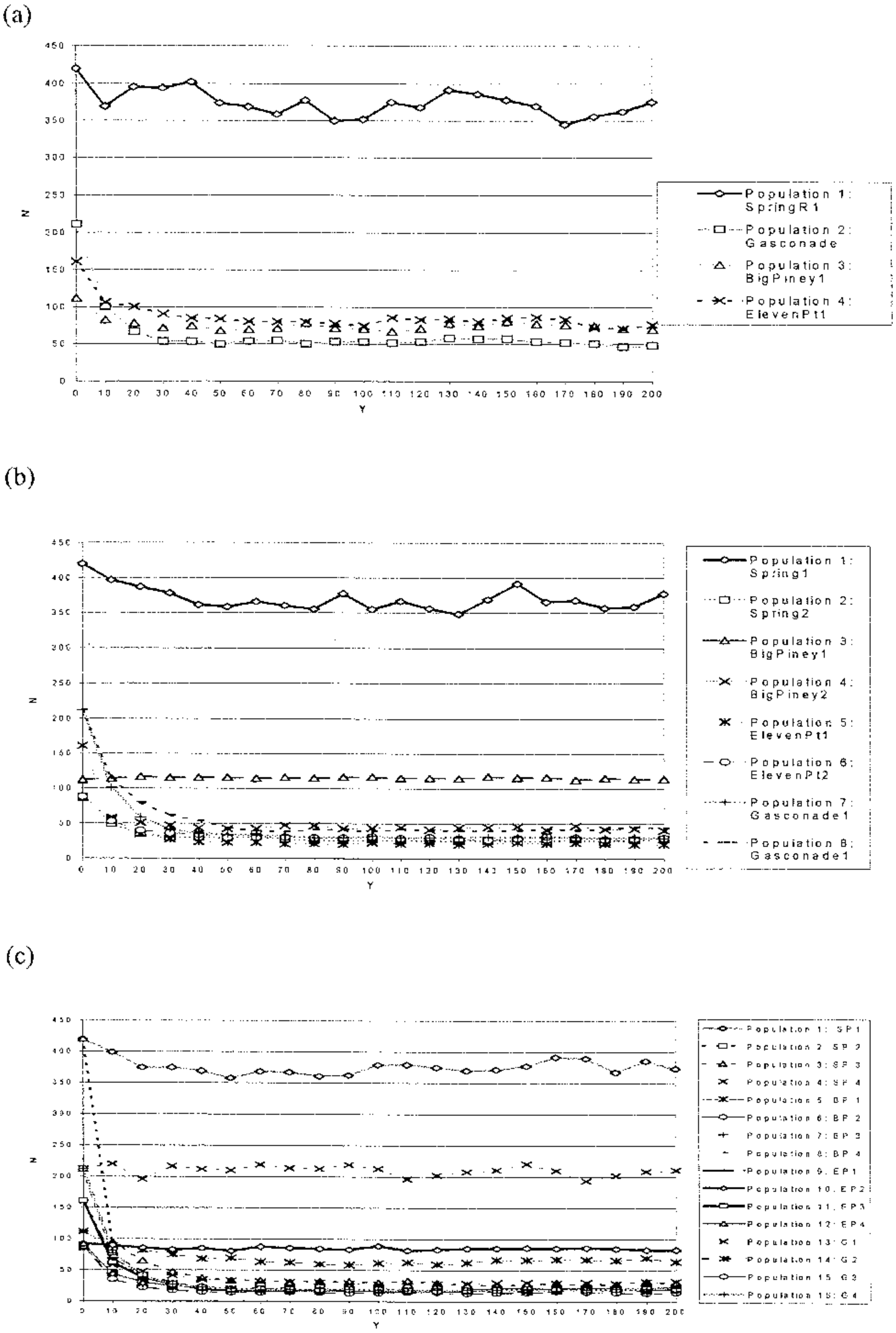


Figure 16 a, b, c – Four, eight, and 16 populations with constant rate emigration; 75% of populations experienced high-level survivorship losses and reproductive failures in the presence of 75% year one and 50% year two juvenile mortality, while 25% of the populations experienced low-level survivorship losses and reproductive failures in the presence of 75% year one and 50% year two juvenile mortality, (a) four populations, (b) eight populations, (c) 16 populations. Legend shows name of each population with an assigned symbol and line-pattern indicating the trend line associated with the population's response to the parameters imposed over the course of the simulation; N = population size, Y = year, SP = Spring River, BP = Big Piney River, EP = Eleven Point River, G = Gasconade River.

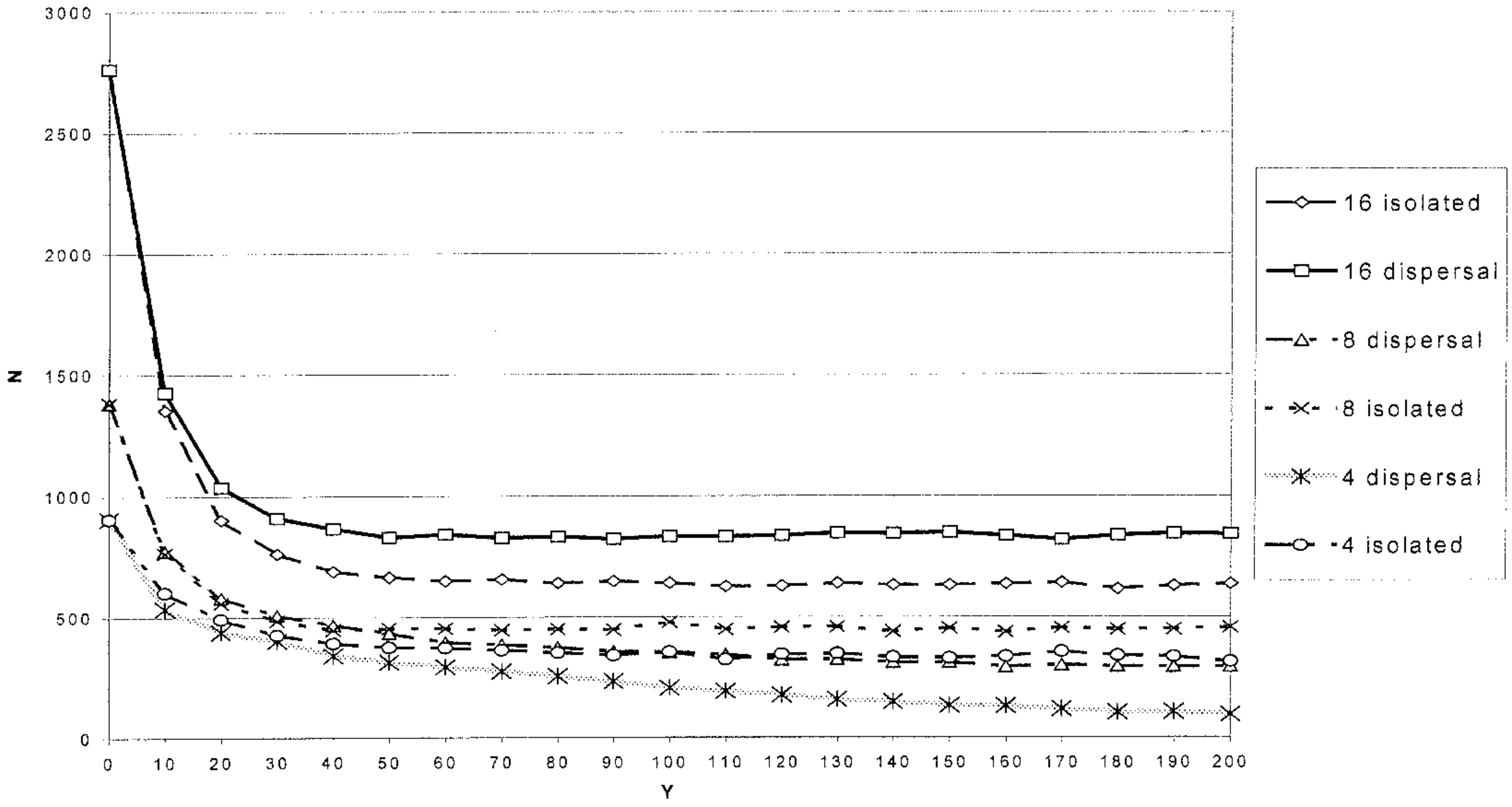


Figure 13 – Effect of dispersal ability on number of individuals across populations when 75% of populations in population group are experiencing high-level (100% chance of 90% failure) reproductive failure and 25% of populations in population group are experiencing low-level (10% chance of 75% failure) reproductive failure. Subpopulations composing population groups are either isolated from one another or have constant rate emigration. Legend shows number of subpopulations composing population group as well as dispersal designation. N = population size, Y = year.

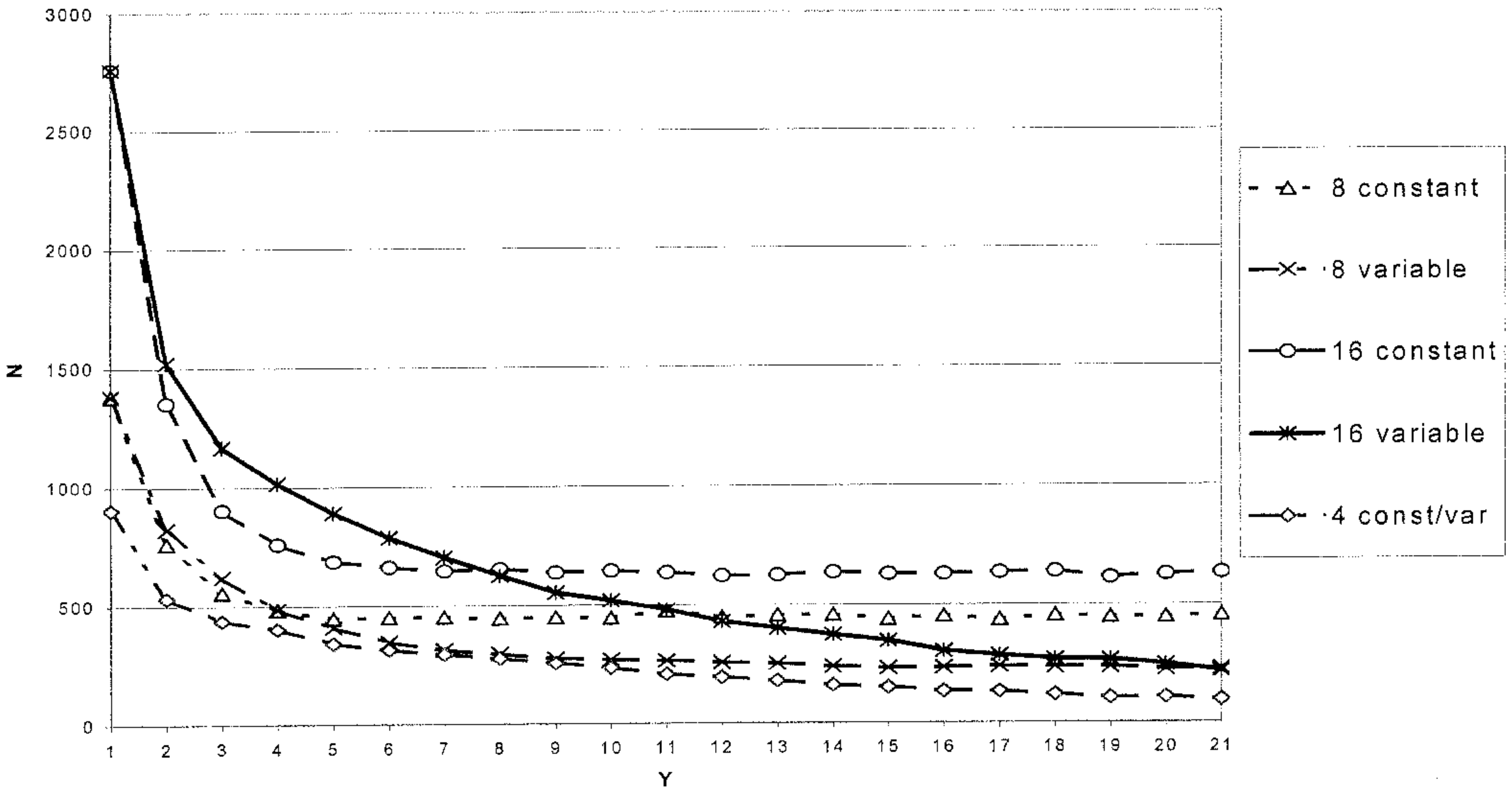


Figure 14 – Effect of degree of dispersal on number of individuals across populations when 75% of populations are experiencing high-level reproductive failure (100% chance of 90% failure) and 25% of populations are experiencing low-level reproductive failure (10% chance of 75% failure). Populations are grouped by dispersal ability and number of subpopulations making up the population group. Population groups have constant rate or variable rate emigration. Legend shows number of subpopulations composing population group and dispersal designation; N = population size, Y = year.

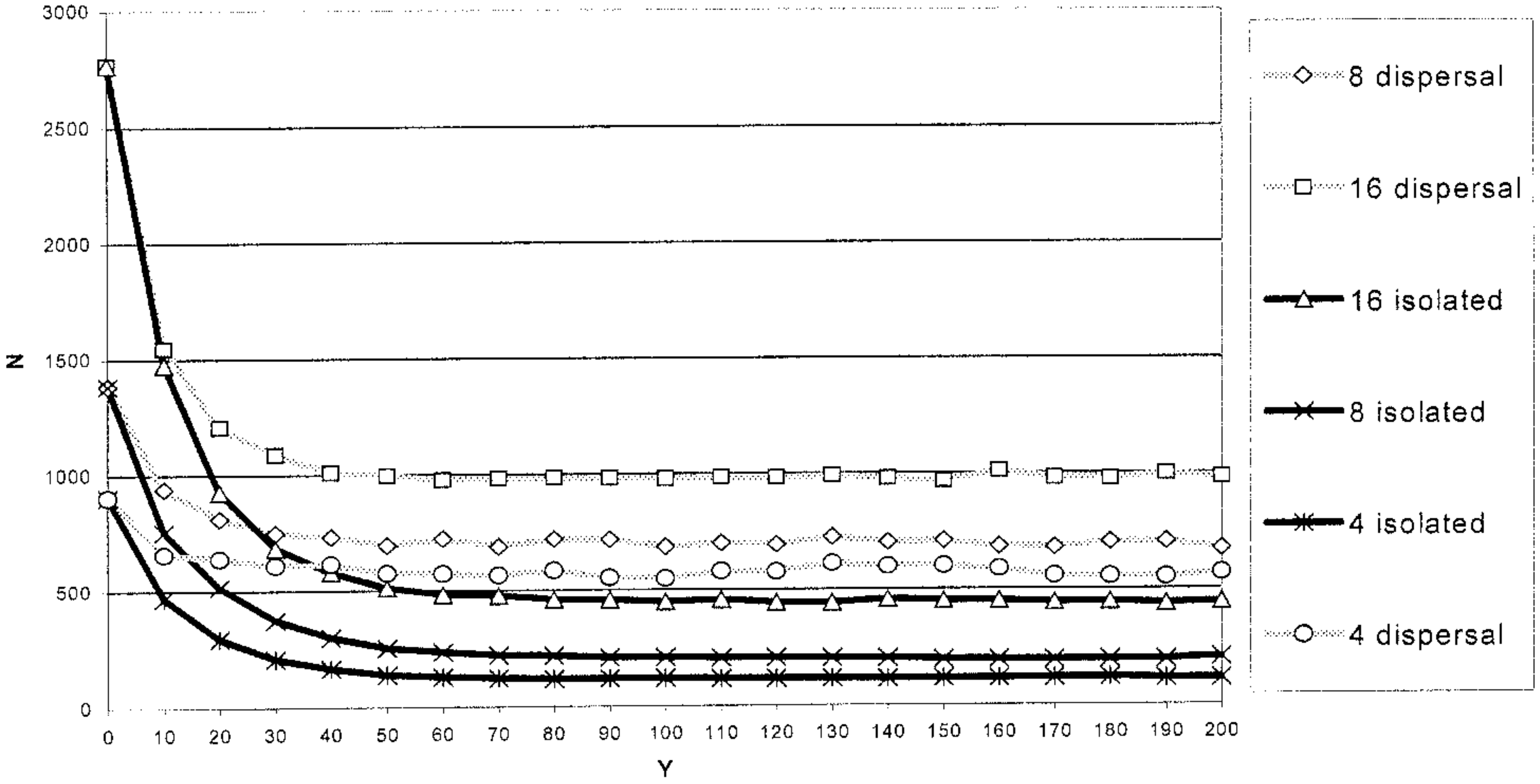


Figure 17 -- Total number of individuals across populations when 75% of populations experienced high-level survivorship losses and reproductive failures in the presence of 75% year 1 and 50% year 2 juvenile mortality, while 25% of the populations experienced low-level survivorship losses and reproductive failures in the presence of 75% year 1 and 50%year 2 juvenile mortality. Populations with dispersal ability have a constant rate emigration pattern of dispersal. Legend shows number of populations involved in the scenario and also designates whether the populations are isolated from one another or experience constant rate dispersal. Each group of populations is assigned a symbol and a line-pattern indicating the trend line associated with the population-group's response to the parameters imposed over the course of the simulation. N = population size, Y = year.

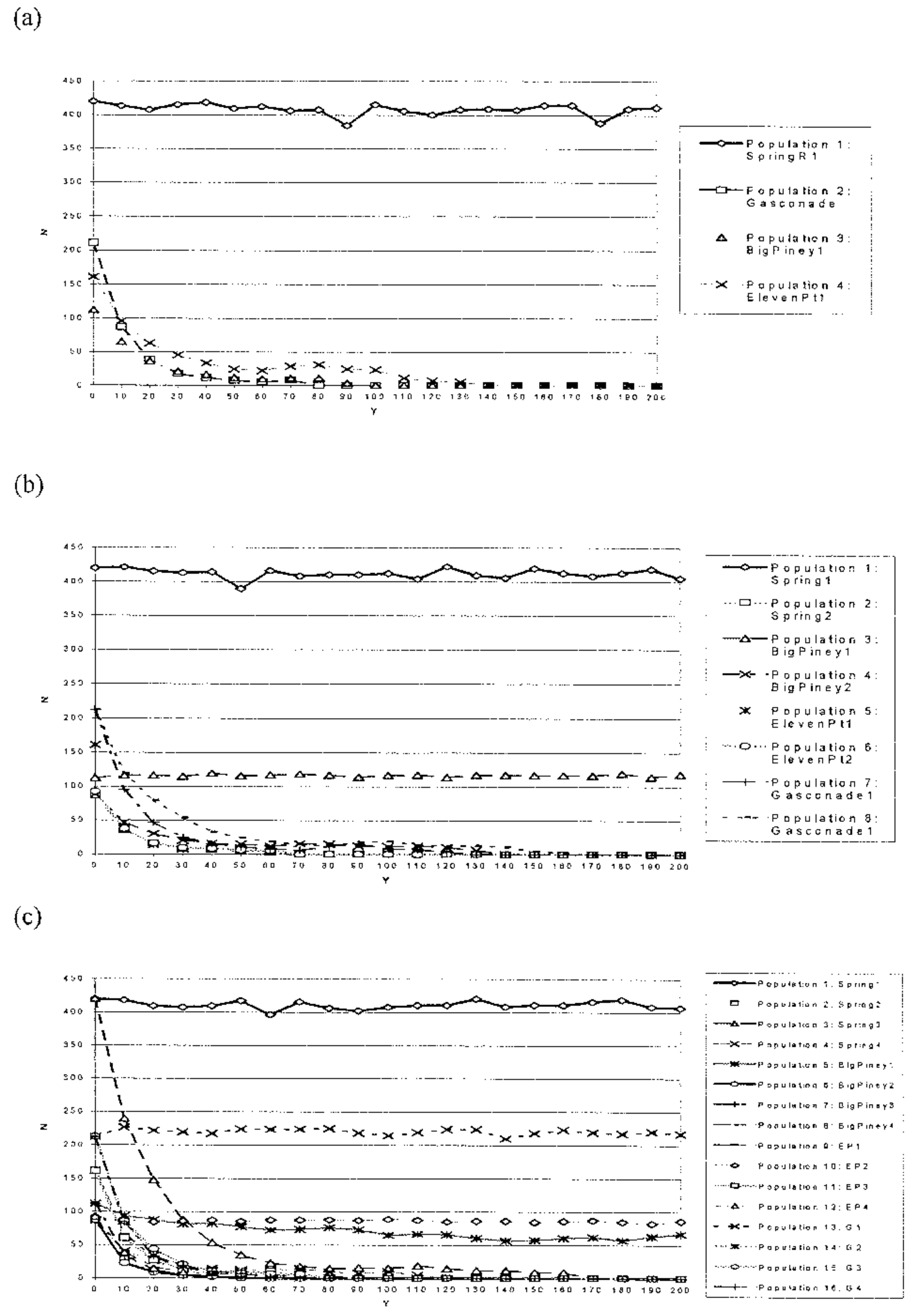


Figure 15 a, b, c – Four, eight, and sixteen populations isolated from one another, 75% of populations experienced high-level survivorship losses and reproductive failures in the presence of 75% year one and 50% year two juvenile mortality, while 25% of the populations experienced low-level survivorship losses and reproductive failures in the presence of 75% year one and 50% year two juvenile mortality. Legend shows name of each population with an assigned symbol and line-pattern indicating the trend line associated with the population's response to the parameters imposed over the course of the simulation. N = population size, Y = year, SP = Spring River, BP = Big Piney River, EP = Eleven Point River, G = Gasconade River.

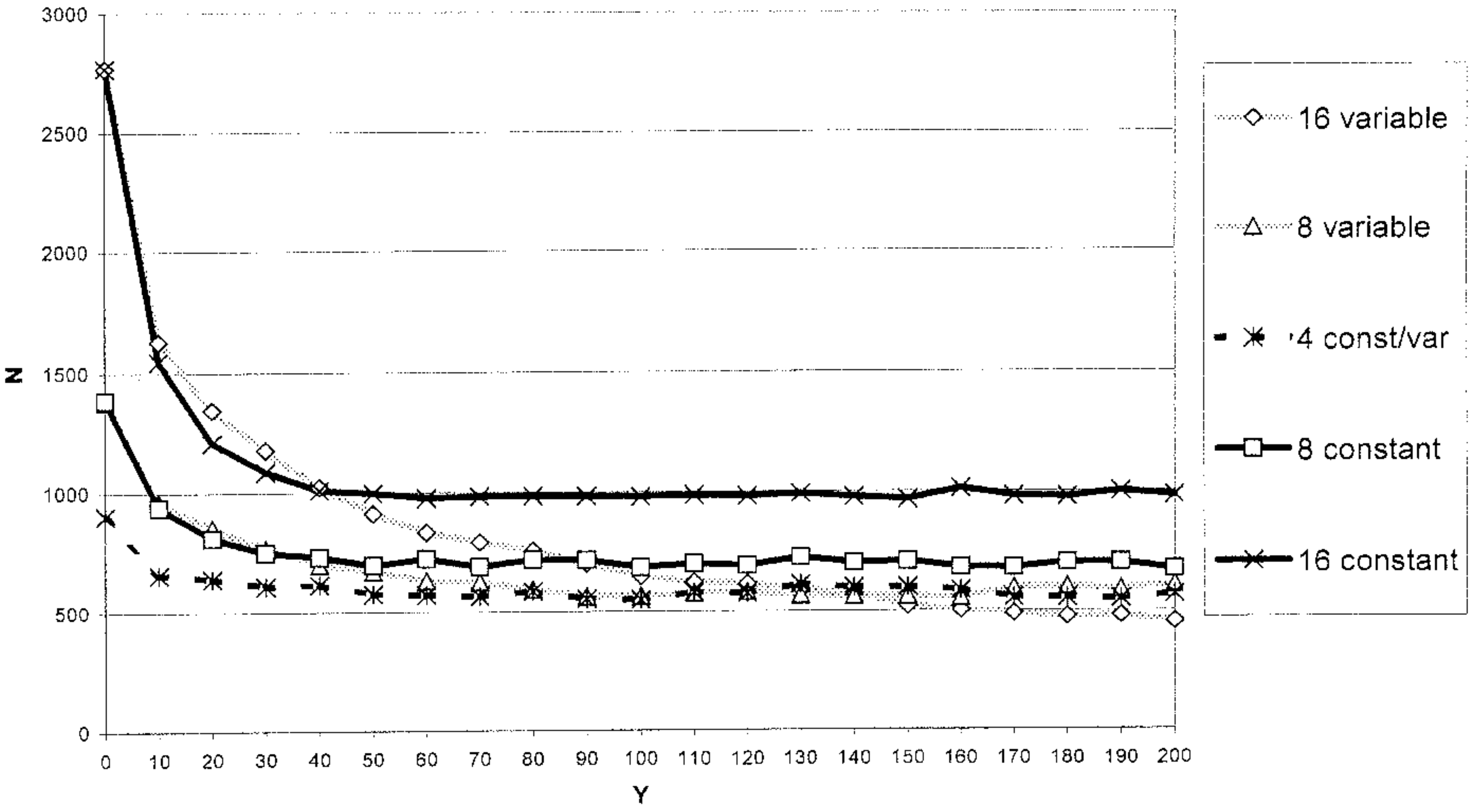


Figure 18 – Effect of degree of dispersal on number of individuals across populations when populations are experiencing combined survivorship losses and reproductive failures in the presence of 75% year 1 and 50% year 2 juvenile mortality. Populations are grouped by dispersal ability and number of subpopulations making up the population group. Population groups either have constant rate emigration or have variable rate emigration. Legend shows number of subpopulations composing population group and dispersal designation. N = population size, Y = year.

REAL MODELS	
SCENARIO	PARAMETERS MANIPULATED
(1) carrying capacity (Figure 3 a – c)	(a) K 10% above initial population size (b) K 10% below initial population size (c) K = initial population size
(2) mortality schedules (Figure 5, 6 a – c)	(a) Basic mortality (b) 25% year one and year two juvenile mortality (c) 50% year one and year two juvenile mortality (d) 75% year one and 50% year two juvenile mortality
(3) reproductive failures (Figure 7 a – c)	(a) 10% chance of 75% reproductive failure (b) 50% chance of 80% reproductive failure (c) 60% chance of 90% reproductive failure
(4) survivorship losses (Figure 8 a – b)	(a) 10% chance of 20% survivorship loss (b) 10% chance of 40% survivorship loss
(5) combined reproductive failures and survivorship losses (Figure 9 a – b)	(a) 10% chance of 75% reproductive failure 10% chance of and 20% survivorship losses (b) 30% chance of 90% reproductive failure and 30% chance of 30% survivorship losses
(6) combined reproductive failures, survivorship losses and increased juvenile mortality (Figure 10 a – c)	(a) reproductive failure, survivorship losses and 25% year one and year two juvenile mortality (b) reproductive failure, survivorship losses and 50% year one and year two juvenile mortality (c) reproductive failure, survivorship losses and 75% year one with 50% year two juvenile mortality

Table 1 – Table shows scenarios manipulated for Real models of *C. alleganiensis* PVA

DISPERSAL MODELS	
SCENARIO	PARAMETERS MANIPULATED
(1) Isolation and Reproductive Failure (Figure 11 a – c)	(a) Four populations: 75% of populations with 90% chance of 100% reproductive failure and 25% with 10% chance of 75% reproductive failure (b) Eight populations: 75% of populations with 90% chance of 100% reproductive failure and 25% with 10% chance of 75% reproductive failure (c) 16 populations: 75% of populations with 90% chance of 100% reproductive failure and 25% with 10% chance of 75% reproductive failure
(2) Constant rate emigration and Reproductive Failure (Figure 12 a – c)	(a) Four populations: 75% of populations with 90% chance of 100% reproductive failure and 25% with 10% chance of 75% reproductive failure (b) Eight populations: 75% of populations with 90% chance of 100% reproductive failure and 25% with 10% chance of 75% reproductive failure (c) 16 populations: 75% of populations with 90% chance of 100% reproductive failure and 25% with 10% chance of 75% reproductive failure
(3) Constant rate emigration versus Isolation and Reproductive Failure (Figure 13)	Number of individuals across populations when 75% of populations have a 90% chance of 100% reproductive failure and 25% of populations with 10% chance of 75% reproductive failure
(4) Constant rate emigration versus Variable rate emigration and Reproductive Failure (Figure 14)	Number of individuals across populations when 75% of populations have a 90% chance of 100% reproductive failure and 25% of populations with 10% chance of 75% reproductive failure
(5) Isolation and Multifactor Scenarios with Juvenile Mortality (Figure 15 a – c)	(a) Four populations: 75% of populations have 30% chance of 90% reproductive failure and 75% chance of 30% survivorship losses and 25% juvenile mortality (b) Eight populations: 75% of populations have 30% chance of 90% reproductive failure and 75% chance of 30% survivorship losses and 25% juvenile mortality (c) Sixteen populations: 75% of populations have 30% chance of 90% reproductive failure and 75% chance of 30% survivorship losses and 25% juvenile mortality

Table 2: Scenarios manipulated for Dispersal models of *C. alleganiensis* PVA

DISPERSAL MODELS CONTINUED	
SCENARIO	PARAMETERS MANIPULATED
(6) Constant rate emigration and Multifactor scenarios with Juvenile Mortality (Figure 16 a – c)	(a) Four populations: 75% of populations have 30% chance of 90% reproductive failure and 75% chance of 30% survivorship losses and 25% juvenile mortality (b) Eight populations: 75% of populations have 30% chance of 90% reproductive failure and 75% chance of 30% survivorship losses and 25% juvenile mortality (c) Sixteen populations: 75% of populations have 30% chance of 90% reproductive failure and 75% chance of 30% survivorship losses and 25% juvenile mortality
(7) Constant rate dispersal versus Isolation and Multifactor scenarios with Juvenile Mortality (Figure 17)	Number of individuals across populations when 75% of populations have a 30% chance of 90% reproductive failure and a 75% chance of survivorship losses and 25% juvenile mortality
(8) Constant rate emigration versus Variable rate emigration and Multifactor Scenarios with juvenile mortality (Figure 18)	Number of individuals across populations when 75% of populations have a 30% chance of 90% reproductive failure and a 75% chance of survivorship losses and 25% juvenile mortality
(9) Largest population is not "source" population	Isolation versus dispersal on number of individuals across populations when the source population does not have the largest population size

Table 2: continued

Table 3 – Table shows summary of results of mortality schedule manipulations. Each column shows the mean responses across populations for each scenario model with rate of positive or negative change in population size from initial size in parentheses. Results are shown on 30-year intervals for 90 years.

YEAR	25% YEAR ONE AND YEAR TWO MORTALITY	50% YEAR ONE AND YEAR TWO MORTALITY	75% YEAR ONE AND YEAR TWO MORTALITY
0	167.29	167.29	167.29
30	151.7 (-0.09)	85.18 (-0.49)	35.91 (-0.78)
60	152.68 (-0.09)	61.18 (-0.63)	19.02 (-0.89)
90	149.88 (-0.10)	53.34 (-0.68)	16.58 (-0.90)

Table 4 – Table shows summary of results of reproductive failure manipulations. Each column shows the mean responses across populations for each scenario model with rate of positive or negative change in population size from initial size in parentheses. Results are shown on 30-year intervals for 90 years.

YEAR	75% CHANCE OF 10% REPRODUCTIVE FAILURE	80% CHANCE OF 50% REPRODUCTIVE FAILURE	90% CHANCE OF 60% REPRODUCTIVE FAILURE
0	167.29	167.29	167.29
30	163.54 (-0.02)	166.84 (-0.00)	112.21 (-0.33)
60	163.31 (-0.02)	166.50 (-0.00)	89.51 (-0.46)
90	165.10 (-0.01)	169.06 (+0.01)	79.60 (-0.52)

Table 7 – Table shows summary of results of reproductive failures combined with survivorship loss manipulations and increased year one and year two juvenile mortality. Each column shows the mean responses across populations for each scenario model with rate of positive or negative change in population size from initial size in parentheses. Results are shown on 30-year intervals for 90 years.

YEAR	REPRODUCTIVE FAILURE, SURVIVORSHIP LOSSES, AND 25% YEAR ONE AND YEAR TWO JUVENILE MORTALITY	REPRODUCTIVE FAILURE, SURVIVORSHIP LOSSES, AND 50% YEAR ONE AND YEAR TWO JUVENILE MORTALITY	REPRODUCTIVE FAILURE, SURVIVORSHIP LOSSES, AND 75% YEAR ONE WITH 50% YEAR TWO JUVENILE MORTALITY
0	167.29	167.29	167.29
30	123.13 (-0.26)	54.78 (-0.67)	20.35 (-0.88)
60	108.59 (-0.35)	33.85 (-0.80)	12.42 (-0.93)
90	99.22 (-0.41)	30.63 (-0.84)	11.43 (-0.93)

Table 5 – Table shows summary of results of survivorship loss manipulations. Each column shows the mean responses across populations for each scenario model with rate of positive or negative change in population size from initial size in parentheses. Results are shown on 30-year intervals for 90 years.

YEAR	10% CHANCE OF 20% SURVIVORSHIP LOSS	10% CHANCE OF 40% SURVIVORSHIP LOSS
0	167.29	167.29
30	150.40 (-0.10)	120.12 (-0.28)
60	148.44 (-0.11)	106.43 (-0.36)
90	147.44 (-0.12)	90.49 (-0.46)

Table 6 – Table shows summary of results of reproductive failures combined with survivorship loss manipulations. Each column shows the mean responses across populations for each scenario model with rate of positive or negative change in population size from initial size in parentheses. Results are shown on 30-year intervals for 90 years.

YEAR	10% CHANCE OF 75% REPRODUCTIVE FAILURE AND 10% SURVIVORSHIP LOSS	30% CHANCE OF 90% REPRODUCTIVE FAILURE AND 30% SURVIVORSHIP LOSS
0	167.29	167.29
30	145.09 (-0.13)	39.17 (-0.77)
60	136.21 (-0.19)	35.09 (-0.79)
90	134.43 (-0.20)	19.67 (-0.88)

Table 8 a, b, c – Table shows results of isolation versus various rates of dispersal when populations are exposed to reproductive failures. The table compares number of individuals across populations as well as showing the number of populations present throughout the first 90 years of the scenarios; (a) four, (b) eight, and (c) 16 populations.

(a)

		Total Numbers of Individuals Across all Populations at Given Year			**Total Number of Populations Present at a Given Year**		
Initial Number of Populations	**year**	**Isolation**	**Constant emigration**	**Variable emigration**	**Isolation**	**Constant emigration**	**Variable emigration**
4	0	904	904	904	4	4	4
	30	425.90	401.58	401.58	4	4	4
	60	371.84	294.26	294.26	4	4	4
	90	340.92	234.62	234.62	2	4	4

(b)

		Total Numbers of Individuals Across all Populations at Given Year			**Total Number of Populations Present at a Given Year**		
Initial Number of Populations	**year**	**Isolation**	**Constant emigration**	**Variable emigration**	**Isolation**	**Constant emigration**	**Variable emigration**
8	0	1381	1381	1381	8	8	8
	30	484.44	508.22	485.86	8	8	8
	60	452.00	394.48	312.96	5	8	8
	90	446.36	356.54	269.92	3	8	8

(c)

		Total Numbers of Individuals Across all Populations at Given Year			**Total Number of Populations Present at a Given Year**		
Initial Number of Populations	**year**	**Isolation**	**Constant emigration**	**Variable emigration**	**Isolation**	**Constant emigration**	**Variable emigration**
16	0	2762	2762	2762	16	16	16
	30	759.78	908.16	1015.78	16	16	16
	60	647.80	908.16	704.46	9	16	16
	90	646.82	820.08	520.64	4	16	16

Table 9 a, b, c – Table shows results of isolation versus various rates of dispersal when populations are exposed to reproductive failures, survivorship losses, and increased juvenile mortality. The table compares number of individuals across populations as well as showing the number of populations present throughout the first 90 years of the scenarios; (a) four, (b) eight, and (c) 16 populations.

(a)

		Total Numbers of Individuals Across all Populations at Given Year			**Total Number of Populations Present at a Given Year**		
Initial Number of Populations	**year**	**Isolation**	**Constant emigration**	**Variable emigration**	**Isolation**	**Constant emigration**	**Variable emigration**
4	0	904	904	904	4	4	4
	30	205.66	239.46	239.46	4	4	4
	60	128.86	176.14	176.14	4	4	4
	90	118.46	162.54	162.54	3	4	4

(b)

		Total Numbers of Individuals Across all Populations at Given Year			**Total Number of Populations Present at a Given Year**		
Initial Number of Populations	**year**	**Isolation**	**Constant emigration**	**Variable emigration**	**Isolation**	**Constant emigration**	**Variable emigration**
8	0	1381	1381	1381	8	8	8
	30	372.74	749.90	768.12	8	8	8
	60	235.16	723.68	631.56	8	8	8
	90	207.64	717.52	550.00	5	8	8

(c)

		Total Numbers of Individuals Across all Populations at Given Year			**Total Number of Populations Present at a Given Year**		
Initial Number of Populations	**year**	**Isolation**	**Constant emigration**	**Variable emigration**	**Isolation**	**Constant emigration**	**Variable emigration**
16	0	2762	2762	2762	16	16	16
	30	684.12	1086.98	1176.12	16	16	16
	60	480.80	977.30	834.50	12	16	16
	90	455.72	982.12	700.90	6	16	16

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Appendix A
Example of Input Parameters and Flow of Operation of the VORTEX model for basic population parameters*

Column 1: Parameter	Column 2: How derived
VORT_222.OUT ***Output Filename***	assigned
Y ***Graphing Files?***	graphs desireable
N ***Details each Iteration?***	not necessary
500 ***Simulations***	VORTEX listserv advice for statistically sound results
100 ***Years***	length of time required to see trends
10 ***Reporting Interval***	wanted population status every 10 years
0 ***Definition of Extinction***	all of one sex extinct
7 ***Populations***	Peterson 1985
N ***Inbreeding Depression?***	No data available
N ***EV concordance between repro and surv?***	Good years for reproduction not necessarily good years for survival
0.000000 ***Correlation of EV among populations***	no environmental correlation assigned between populations based on Peterson 1985
0 ***Types Of Catastrophes***	number of catastrophes
P ***Monogamous, Polygynous, or Hermaphroditic***	Bishop 1907, Nickerson and Mays 1973

5 ***Female Breeding Age***	Prosen 1999
5 ***Male Breeding Age***	Prosen 1999
30 ***Maximum Breeding Age***	Peterson 1985
50.000000 ***Sex Ratio (percent males)***	Nickerson and Mays 1973, Peterson 1985, Prosen 1999, Wheeler 1999
0 ***Maximum Litter Size (0 = normal distribution) *****	see manual (adapts to fecundity by assigning number of offspring/breeding at a later time
N ***Density Dependent Breeding?***	estimate
BigPiney1 BigPiney2 ElevenPt1 ElevenPt2 Spring1 Spring2 Gasconade	Peterson 1985
0 ***Lower Age For Dispersal***	All age groups no dispersal
30 ***Upper Age For Dispersal***	All age groups no dispersal
B ***DispersingSex: F, M, or Both***	Peterson 1987
100.000000 **Dispersal Survival (percent)**	estimated
1.000000 **Dispersal modifier**	estimated
0.000000 0.000000 0.000000 0.000000 0.000000 0.000000 from BigPiney1***	***Percent dispersal
1.000000 0.000000 0.000000 0.000000 0.000000 0.000000 from BigPiney2***	***Percent dispersal
0.000000 0.000000 0.000000 0.000000 0.000000 0.000000 from ElevenPt1***	***Percent dispersal

N	***All Males Breeders?***	Nickerson and Mays 1973, Peterson 1985
Y	***Answer--A--Known?***	
50.0	***Percent Males In Breeding Pool***	estimate at least half of males breed
Y	***Start At Stable Age Distribution?***	
161	***Initial Population Size***	Peterson 1985
177	***K***	Figures 3 a - c
5.0	***EV--K***	
N	***Trend In K?***	Did not assign downward trend
N	***Harvest?***	
N	***Supplement?***	
90.00	**breeding	Repeated above for each population
5.00	**EV-breeding	
408.080000	***BigPiney2: Mean Litter Size***	
48.780000	***BigPiney2: SD in Litter Size***	
99.753000	*FMort age 0	
0.147100	***EV	
17.567600	*FMort age 1	
5.098600	***EV	
11.475400	*FMort age 2	
1.342980	***EV	
10.000000	*FMort age 3	
1.417370	***EV	
8.642000	*FMort age 4	
0.897350	***EV	
8.000000	*Adult FMort	
3.000000	***EV	
99.753000	*MMort age 0	
0.147100	***EV	
17.567600	*MMort age 1	
5.098600	***EV	
11.475400	*MMort age 2	
1.342980	***EV	

0.000000 0.000000 0.000000 0.000000 0.000000 0.000000 ***Percent dispersal from ElevenPt2***	
0.000000 0.000000 0.000000 0.000000 0.500000 0.000000 ***Percent dispersal from Spring1***	
0.000000 0.000000 0.000000 0.000000 0.000000 0.000000 ***Percent dispersal from Spring2***	
0.000000 0.000000 0.000000 0.000000 0.000000 0.000000 ***Percent dispersal from Gasconade***	
90.00 **breeding	estimated
5.00 **EV-breeding	variation in breeding estimated
408.080000 ***BigPiney1: Mean Litter Size***	mean from literature
48.780000 ***BigPiney1: SD in Litter Size***	SD of above mean
99.753000 *FMort age 0	Next rows depict mortality from Peterson 1985
0.147100 ***EV	
17.567600 *FMort age 1	
5.098600 ***EV	
11.475400 *FMort age 2	
1.342980 ***EV	
10.000000 *FMort age 3	
1.417370 ***EV	
8.642000 *FMort age 4	
0.897350 ***EV	
8.000000 *Adult FMort	
3.000000 ***EV	
99.753000 *MMort age 0	
0.147100 ***EV	
17.567600 *MMort age 1	
5.098600 ***EV	
11.475400 *MMort age 2	
1.342980 ***EV	
10.000000 *MMort age 3	
1.417370 ***EV	
8.642000 *MMort age 4	
0.897350 ***EV	
8.000000 *Adult MMort	
3.000000 ***EV	

```
10.000000  *MMort age 3
1.417370  ***EV
8.642000  *MMort age 4
0.897350  ***EV
8.000000  *Adult MMort
3.000000  ***EV
N    ***All Males Breeders?***
Y    ***Answer--A--Known?***
50.000000    ***Percent Males In Breeding Pool***
Y    ***Start At Stable Age Distribution?***
88    ***Initial Population Size***
97    ***K***
5.000000    ***EV--K***
N    ***Trend In K?***
N    ***Harvest?***
N    ***Supplement?***
90.00  **breeding
5.00  **EV-breeding
408.080000  ***ElevenPt1: Mean Litter Size***
48.780000  ***ElevenPt1: SD in Litter Size***
99.543800  *FMort age 0
0.147980  ***EV
26.315800  *FMort age 1
5.098600  ***EV
13.214500  *FMort age 2
1.342980  ***EV
11.522600  *FMort age 3
1.417370  ***EV
9.767400  *FMort age 4
0.897350  ***EV
8.000000  *Adult FMort
3.000000  ***EV
99.543800  *MMort age 0
0.147100  ***EV
26.315800  *MMort age 1
5.098600  ***EV
13.214500  *MMort age 2
1.342980  ***EV
11.522600  *MMort age 3
1.417370  ***EV
9.767400  *MMort age 4
0.897350  ***EV
8.000000  *Adult MMort
3.000000  ***EV
N    ***All Males Breeders?***
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```
Y    ***Answer--A--Known?***
50.000000    ***Percent Males In Breeding Pool***
Y    ***Start At Stable Age Distribution?***
112    ***Initial Population Size***
123    ***K***
5.000000    ***EV--K***
N    ***Trend In K?***
N    ***Harvest?***
N    ***Supplement?***
90.00  **breeding
5.00  **EV-breeding
408.080000  ***ElevenPt2: Mean Litter Size***
48.780000  ***ElevenPt2: SD in Litter Size***
99.543800  *FMort age 0
0.147980  ***EV
26.315800  *FMort age 1
5.098600  ***EV
13.214500  *FMort age 2
1.342980  ***EV
11.522600  *FMort age 3
1.417370  ***EV
9.767400  *FMort age 4
0.897350  ***EV
8.000000  *Adult FMort
3.000000  ***EV
99.543800  *MMort age 0
0.147100  ***EV
26.315800  *MMort age 1
5.098600  ***EV
13.214500  *MMort age 2
1.342980  ***EV
11.522600  *MMort age 3
1.417370  ***EV
9.767400  *MMort age 4
0.897350  ***EV
8.000000  *Adult MMort
3.000000  ***EV
N    ***All Males Breeders?***
Y    ***Answer--A--Known?***
50.000000    ***Percent Males In Breeding Pool***
Y    ***Start At Stable Age Distribution?***
92    ***Initial Population Size***
101    ***K***
5.000000    ***EV--K***
N    ***Trend In K?***
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```
N     ***Harvest?***
N    ***Supplement?***
90.00  **breeding
5.00  **EV-breeding
408.080000   ***Spring1: Mean Litter Size***
48.780000   ***Spring1: SD in Litter Size***
99.866300  *FMort age 0
0.147980  ***EV
18.461500  *FMort age 1
5.098600  ***EV
11.006300  *FMort age 2
1.342980  ***EV
8.833900  *FMort age 3
1.417370  ***EV
8.527100  *FMort age 4
0.897350  ***EV
8.000000  *Adult FMort
3.000000  ***EV
99.866300  *MMort age 0
0.147100  ***EV
18.461500  *MMort age 1
5.098600  ***EV
11.006300  *MMort age 2
1.342980  ***EV
8.833900  *MMort age 3
1.417370  ***EV
8.527100  *MMort age 4
0.897350  ***EV
8.000000  *Adult MMort
3.000000  ***EV
N    ***All Males Breeders?***
Y    ***Answer--A--Known?***
50.000000     ***Percent Males In Breeding Pool***
Y    ***Start At Stable Age Distribution?***
420     ***Initial Population Size***
462     ***K***
5.000000     ***EV--K***
N    ***Trend In K?***
N     ***Harvest?***
N    ***Supplement?***
90.00  **breeding
5.00  **EV-breeding
408.080000   ***Spring2: Mean Litter Size***
48.780000   ***Spring2: SD in Litter Size***
99.866300  *FMort age 0
```

```
0.147980 ***EV
18.461500 *FMort age 1
5.098600 ***EV
11.006300 *FMort age 2
1.342980 ***EV
8.833900 *FMort age 3
1.417370 ***EV
8.527100 *FMort age 4
0.897350 ***EV
8.000000 *Adult FMort
3.000000 ***EV
99.866300 *MMort age 0
0.147100 ***EV
18.461500 *MMort age 1
5.098600 ***EV
11.006300 *MMort age 2
1.342980 ***EV
8.833900 *MMort age 3
1.417370 ***EV
8.527100 *MMort age 4
0.897350 ***EV
8.000000 *Adult MMort
3.000000 ***EV
N    ***All Males Breeders?***
Y    ***Answer--A--Known?***
50.000000    ***Percent Males In Breeding Pool***
Y    ***Start At Stable Age Distribution?***
86    ***Initial Population Size***
95    ***K***
5.000000    ***EV--K***
N    ***Trend In K?***
N    ***Harvest?***
N    ***Supplement?***
90.00 **breeding
5.00 **EV-breeding
408.080000  ***Gasconade: Mean Litter Size***
48.780000  ***Gasconade: SD in Litter Size***
99.844200 *FMort age 0
0.147980 ***EV
14.285700 *FMort age 1
5.098600 ***EV
10.000000 *FMort age 2
1.342980 ***EV
8.333300 *FMort age 3
1.417370 ***EV
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7.575800  *FMort age 4
0.897350  ***EV
8.000000  *Adult FMort
3.000000  ***EV
99.844200  *MMort age 0
0.147100  ***EV
14.285700  *MMort age 1
5.098600  ***EV
10.000000  *MMort age 2
1.342980  ***EV
8.333300  *MMort age 3
1.417370  ***EV
7.575800  *MMort age 4
0.897350  ***EV
8.000000  *Adult MMort
3.000000  ***EV
N    ***All Males Breeders?***
Y    ***Answer--A--Known?***
50.000000    ***Percent Males In Breeding Pool***
Y    ***Start At Stable Age Distribution?***
212    ***Initial Population Size***
233    ***K***
5.000000    ***EV--K***
N    ***Trend In K?***
N     ***Harvest?***
N    ***Supplement?***
N    ***AnotherSimulation?***
```

***it would be valuable to also consult the VORTEX manual for a greater understanding of what the parameters mean and how they are incorporated into the model.**

Appendix B

Age 0 to Age 4 mortality for each population under different scenarios

	Big Piney				**Eleven Point**				**Spring**				**Gasconade**			
Age	Basic	25%	50%	75%	Basic	25%	50%	75%	Basic	25%	50%	75%	Basic	25%	50%	75%
0	.9975	.9975	.9975	.9975	.9954	.9954	.9954	.9954	.9954	.9954	.9954	.9954	.9984	.9984	.9984	.9984
1	.1757	.2500	.5000	.7500	.1510	.2500	.5000	.7500	.2632	.2500	.2500	.2500	.1423	.2500	.5000	.7500
2	.1147	.2500	.5000	.7500	.1101	.2500	.5000	.7500	.1321	.2500	.5000	.7500	.1423	.2500	.5000	.7500
3	.1000	.1000	.1000	.1000	.0883	.0883	.0883	.0883	.1152	.1152	.1152	.1152	.8333	.8333	.8333	.8333
4	.0864	.0864	.0864	.0864	.0853	.0853	.0853	.0853	.0977	.0977	.0977	.0977	.0758	.0758	.0758	.0758