Analysis of three amphibian populations with quarter-century long time-series

Andrea H. Meyer^{1*}, Benedikt R. Schmidt² and Kurt Grossenbacher³

¹*Institut für Umweltwissenschaften, University of Zürich, Winterthurerstr. 190, CH-8057 Zürich, Switzerland (meyer1@uwinst.unizh.ch)*

²*Zoologisches Institut, University of Basel, Rheinsprung 9, CH-4051 Basel, Switzerland (schmidt@ubaclu.unibas.ch)*

³*Naturhistorisches Museum, Bernstrasse 15, CH-3005 Bern, Switzerland (kurt.grossenbacher@nmbe.unibe.ch)*

Amphibians are in decline in many parts of the world. Long time-series of amphibian populations are necessary to distinguish declines from the often strong fluctuations observed in natural populations. Time-series may also help to understand the causes of these declines. We analysed 23–28-year long time-series of the frog *Rana temporaria*. Only one of the three studied populations showed a negative trend which was probably caused by the introduction of fish. Two populations appeared to be density regulated. Rainfall had no obvious effect on the population fluctuations. Whereas long-term studies of amphibian populations are valuable to document population declines, most are too short to reveal those factors that govern population dynamics or cause amphibian populations to decline.

Keywords: density dependence tests; global amphibian decline; population fluctuations; population regulation; *Rana temporaria*; time-series

1. INTRODUCTION

Amphibians have been suspected to be in a global decline that goes beyond the overall biodiversity crisis (Blaustein & Wake 1990; Vitt *et al.* 1990; Wake 1991; Wake & Morowitz 1991; reviewed in Pechmann & Wilbur 1994). Indeed, an increasing number of studies have shown that many populations and species have disappeared from even seemingly pristine habitats within the last decades. Whereas it is clear that human activities such as habitat destruction or degradation and the introduction of exotic species may drive amphibian communities to local extinction (Blaustein & Wake 1990; Pechmann & Wilbur 1994), it was the strong decline or even disappearance of amphibian populations without any obvious human influence that caused concern among amphibian ecologists and conservationists (Blaustein & Wake 1990). It may be difficult, however, to distinguish population declines from natural fluctuations because amphibian populations may exhibit strong year-to-year fluctuations (Pechmann *et al.* 1991). What we therefore need are long time-series of amphibian populations. The analysis of such time-series would allow us to better identify actual population trends (Blaustein *et al.* 1994; Reed & Blaustein 1995) and may reveal some of the factors that govern the dynamics of amphibian populations, and ultimately determine population distribution and abundance. Here we report on the longest census study on amphibians we are aware of.

In Switzerland the common frog, *Rana temporaria*, reaches maturity at the age of 2–4 years, breeds annually and rarely grows older than 5 years (Ryser 1988). It is still Europe's most abundant frog although mass mortalities and declines have been reported for this (Cooke 1972; Gerlach & Bally 1992; Cunningham *et al.* 1993) and other European species (such as *Bufo bufo*: Semb-Johansson 1991, and *Hyla arborea*: Grossenbacher 1988). We recorded the breeding population size of three different populations of *R. temporaria* over the course of 23–28 years. This temporal range covered more than four turnovers of individuals (Connell & Sousa 1983). The populations lay in an agricultural landscape where there were no obvious changes in land use for several decades, which made them ideal to test for a possible decline caused by factors other than direct negative human impacts. Our data set enabled us to detect existing trends with higher statistical power than in previously published studies (Reed & Blaustein 1995; Hayes & Steidl 1997).

After assessing the population trends, we intended to gain insight into the driving forces of amphibian population dynamics. Therefore we concentrated on those biotic and abiotic factors that have been previously shown to affect amphibian populations: density and rainfall. There is strong evidence in the literature for density-dependent population regulation in amphibians (for examples, see Smith 1983; Van Buskirk & Smith 1991; Scott 1994; Berven 1995). We made use of newly developed statistical methods to test our data for density-dependent regulation within amphibian populations. Rainfall is an environmental factor that has been shown to affect breeding-population sizes of other amphibian species through its effect on breeding activity and past recruitment (see, for example, Semlitsch *et al.* 1996). We tested whether the

*Author for correspondence and address: Bundesamt für Statistik, Sektion Hochschulen und Wissenschaft, Holzikofenweg 8, CH-3003 Bern, Switzerland (andrea.meyer@bfs.admin.ch).

Figure 1. Location of the three population sites and the weather station.

amount of rainfall before and during the breeding season can explain the observed population fluctuations.

In this paper we ask the following specific questions.

1. Does the breeding population size decrease over the study period in the three populations?
2. Is there evidence for density-dependent regulation in the three populations?
3. Can the observed population fluctuations be explained by the amount of rainfall?

Finally, we will discuss the merits and possible limitations of analysing time-series of population abundances in the process of trying to understand global amphibian declines.

2. MATERIAL AND METHODS

(a) Study sites

The three sites at which the populations were monitored, Worblaufen (490 MAS), Widi (640 MAS), and Bermooos (550 MAS), and the nearest weather station at Bern-Liebefeld (570 MAS) are all situated near Bern, Switzerland (figure 1). Worblaufen covers the smallest area of the three sites. It consists of a series of relatively small ponds along the river Aare in an alluvial forest. Water levels are constant because these ponds receive water from nearby sources. Widi and Bermooos are fens. There is a large central pond in these fens, but frogs generally use shallow flooded parts of the fen in between *Carex* stands for spawning. The pond at Widi contains goldfish (*Carassius auratus*) of which a large population was observed in 1992 for the first time, but which had already been introduced a few years before. Bermooos covers the largest area of the three sites. Whereas the

water level of Bermooos can be artificially regulated, the hydrology and drying of shallow ponds depends on rainfall.

(b) Data recording

We counted the total number of spawn clumps deposited per year, during visits to each site three to nine times during the breeding season at intervals of 1 to 6 d (depending on spawning activity) to estimate breeding population size (Griffiths & Raper 1994). Population censuses began in 1970 (Worblaufen), 1973 (Widi), and 1975 (Bermooos) and we present data up to the year 1997. Data on rainfall were provided by the Swiss Meteorological Institute at Bern-Liebefeld.

(c) Data analysis

All analyses were done using the Genstat (release 3.2) software product (Payne *et al.* 1993).

(i) Analysis of population trend

We tested for temporal trends in population size by regressing breeding-population size against year of observation. Data were log-transformed before the analysis to meet the assumptions for regression analysis. The model thus assumes a constant annual rate (rather than absolute numbers) of population change which seems biologically meaningful (Hayes & Steidl 1997). Significances were obtained by randomization tests (see, for example, Edgington 1987), estimates for intercept and slope were obtained by a bootstrapping procedure (see, for example, Efron & Tibshirani 1993). In the case where a temporal trend was not significant at $\alpha=0.05$ we calculated how negative the slope must be, given the observed variance, to become significant with a power of 0.8 and $\alpha=0.05$ (Hayes & Steidl 1997 and Thomas 1997 discuss the use of retrospective power analyses for population trend analyses).

(ii) *Analysis of density dependence*

We used the test for statistically significant density-dependence (SSDD), developed by Dennis & Taper (1994), which compares the density-independent model

$$\ln(N_{t+1}/N_t) = a_0 + Z_t$$

with the density-dependent model

$$\ln(N_{t+1}/N_t) = a_1 + b_1 N_t + Z_t$$

where N_t and N_{t+1} are the population abundances at times t and $t + 1$, Z_t is a normally distributed random variable with a mean of 0 and a variance of σ^2 and a_0 , a_1 , and b_1 are constants. The model is suitable for data series with lengths like ours and was shown to work for species that live and reproduce in more than 1 year (Wolda & Dennis 1993).

The statistical test is based on a parametric bootstrapping likelihood ratio and tests for $b_1 = 0$ (null hypothesis) against $b_1 < 0$ (alternative hypothesis). If the null hypothesis is rejected (i.e. $b_1 < 0$) then the data are consistent with the hypothesis of density dependent population regulation (Dennis & Taper 1994).

We analysed the time-series of all populations for non-detrended as well as detrended data as even non-significant temporal trends make the detection of SSDD less likely (Holoak & Baillie 1996). To detrend the time-series data we used linear regression of the number of spawn clumps against year and then used the residuals for the test for SSDD (Holoak & Baillie 1996). At present it is not clear, however, how results based on detrended time-series data should be interpreted (B. Dennis, personal communication).

Because adults of *R. temporaria* reach maturity at the age of 2 to 4 years (Ryser 1988) and effects of density dependence at the larval stage would affect the adult population 2 to 4 years later, we wanted to test models that account for this delay (e.g. $\ln(N_{t+1}/N_t) = a_1 + b_1 N_t + b_2 N_{t-q} + Z_t$ or $\ln(N_{t+q}/N_t) = a_1 + b_1 N_t + Z_t$, where $q = 2, 3$ or 4). However, the analysis of time-series generated by using matrix models that incorporated density dependence at the larval and/or adult stage revealed that the model $\ln(N_{t+1}/N_t + Z_t) = a_1 + b_1 N_t$ detects SSDD at the larval stage as well whereas the other two 'delayed' models had low statistical power to detect density dependence at the larval and/or adult stage (A. H. Meyer & B. R. Schmidt, unpublished data).

(iii) *Analysis of rainfall data*

We tested whether the amount of rainfall affects breeding population size by regressing breeding population size against the total amount of rainfall during a specified period. The number of frogs breeding may depend on the amount of rainfall during the breeding season (Semlitsch *et al.* 1996). We therefore tested for the effect of the total amount of rainfall during 8, 16, 32, 64 and 128 d before the date spawning started (February or March; K. Grossenbacher, unpublished data). As frogs forage mostly during wet nights and females may not be able to acquire enough resources for egg production in a dry summer, we also tested for the effect of rainfall during the activity period of these frogs (from spawning to the end of October) in the year before breeding. Tadpoles may suffer density-independent mortality when the shallow parts of the fens (Widi and Bermos) dry up during summers when there has been low rainfall. In view of this, we finally tested for the effect of rainfall during the larval period (from spawning to the end of June). As the frogs in Switzerland reach maturity at 2–4 years-old we

expected the influence of rainfall to be delayed by 2 to 4 years if it affects population dynamics via effects on eggs or tadpoles.

Environmental factors acting on a larger scale may lead to synchronization of population dynamics. To assess this possibility we tested for correlated fluctuations among the log-transformed population sizes.

3. RESULTS

(a) *Population trend*

The breeding population size at Widi declined at a rate of ca. 5.6% per year ($R^2 = 0.50$, $p < 0.001$; figure 2). The other two populations showed no significant population decline ($R^2 = 0.02$ and 0.01 , $p = 0.48$ and 0.53 for Worblaufen and Bermos, respectively; figure 2). For these two populations, the smallest population decline detectable with a power of 0.8 and $\alpha = 0.05$, by using the observed residual variance (see Thomas 1997), was 1.9% per year for Worblaufen (i.e. slope of -0.019) and 5% per year for Bermos (i.e. slope of -0.050).

(b) *Density dependence of population regulation*

Tests for SSDD were done for the complete time-series of all three studied populations plus the time-series at Widi restricted to 1973–1989, the period when goldfish had not been introduced yet. Evidence for SSDD was found for the population at Widi whereas the test for SSDD was approaching significance at Worblaufen (table 1). Results did not differ greatly between detrended and non-detrended data, except for Widi when considering all years (i.e. 1973–1997). For the Bermos population we found no evidence for SSDD (table 1). Figure 2 shows the mean level of abundance N_R to which the populations tend to return when using non-detrended data ($N_R = -a_1/b_1$; Dennis & Taper 1994).

(c) *Influence of rainfall on population size*

The size of the breeding population was not significantly affected by the total amount of rainfall immediately before spawning (8, 16, 32, 64, and 128 d) in any of the three populations (table 2). Previous years' rainfall throughout the activity period was positively correlated with the size of the breeding population at Worblaufen, whereas no significant results were obtained for the other two populations (table 2). There was no significant relation between the amount of rainfall during the larval period 2–4 years before the breeding year and the size of the breeding population (table 2). Thus, without application of Bonferroni corrections, only one out of 27 tests on the effect of rainfall on population fluctuations was significant at $\alpha = 0.05$, a result that is expected by chance alone.

The population at Worblaufen was not significantly correlated with those of Widi or Bermos ($p > 0.2$ for both tests). However, there was a significant positive correlation between the sizes of the populations reproducing in the fens of Widi and Bermos ($r = 0.47$, $p = 0.031$).

4. DISCUSSION

(a) *Population trends versus natural fluctuations*

The length of the time-series allowed us to test for temporal trends with higher statistical power compared

Figure 2. Temporal fluctuations of three populations of *R. temporaria*. The broken fitted lines refer to a model for simple linear regression, the slope and the intercept both being bootstrap estimates. The arrows point to the mean level of abundance (N_R) to which the population tends to return, irrespective of whether the test for SSDD was significant or not (see §3b). For the Widi population, N_R is based on the period 1973–1989, i.e. before the start of the fish-mediated decline. No data were recorded at Widi in years 1984 and 1990.

with previously published studies on amphibian population trends (Reed & Blaustein 1995; Hayes & Steidl 1997; Thomas 1997). We found no evidence for a population decline in any of the three investigated *R. temporaria* populations that could not be attributed to local human interference. Whereas two of the three populations showed no negative trend at all, the decline observed for the third population at Widi could be explained by the introduction of goldfish at the end of the 1980s. Before this date there was no significant temporal trend (see figure 2) whereas between *ca.* 1989 and 1997 the population declined by *ca.* 20 % per year. Goldfish are known to prey heavily on tadpoles of *R. temporaria* (Glandt 1985) and could thus cause a population decline.

Pechmann *et al.* (1991) have shown that natural population fluctuations can easily be misinterpreted as declines, particularly if fluctuations are large relative to the length of the data set. Our results corroborate this conclusion.

Based on models developed by Cole (1951), Pechmann & Wilbur (1994) suggested that populations are likely to be in decline most of the time followed by short increases after high recruitment. We here provide empirical evidence for this prediction in amphibians. Despite an overall stability (except Widi after 1988), all populations showed negative population trends for most of the time that were generally followed by strong and short (i.e. 1–2 years) increases. The analysis of subsets of our time-series might thus have lead to the erroneous conclusion that the populations were in danger of going extinct (see, for example, periods 1970–1973, 1979–1981, 1983–1987, 1988–1992, and 1994–1997 at Worblaufen; figure 2).

Short-term simultaneous monitoring of several populations may also give a wrong impression about regional population trends as uncorrelated populations might happen to be synchronized over short periods. In our study all three populations were strongly declining from

Table 1. Results of tests for statistically significant density dependence in three populations of *R. temporaria* using the model ' $\ln(N_{t+1}) = a_1 + b_1 N_t + \zeta_t$ '

(Results are presented for non-detrended and for detrended time series. Number of bootstrap samples = 5000.)

	Worblaufen 1970–1997	Widi 1973–1997	Widi 1973–1989	Bermoos 1975–1997
before detrending	$a_1 = 0.46$ $b_1 = -7.6$ $\times 10^{-4}$ $\sigma^2 = 0.06$ $p = 0.090$	$a_1 = 0.33$ $b_1 = -2.5$ $\times 10^{-4}$ $\sigma^2 = 0.18$ $p = 0.315$	$a_1 = 1.34$ $b_1 = -7.4$ $\times 10^{-4}$ $\sigma^2 = 0.07$ $p = 0.003$	$a_1 = 0.50$ $b_1 = -1.5$ $\times 10^{-4}$ $\sigma^2 = 0.32$ $p = 0.141$
after detrending	$a_1 = 0.47$ $b_1 = -7.7$ $\times 10^{-4}$ $\sigma^2 = 0.06$ $p = 0.082$	$a_1 = 1.08$ $b_1 = -7.4$ $\times 10^{-4}$ $\sigma^2 = 0.16$ $p = 0.004$	$a_1 = 1.35$ $b_1 = -7.5$ $\times 10^{-4}$ $\sigma^2 = 0.08$ $p < 0.001$	$a_1 = 0.54$ $b_1 = -1.6$ $\times 10^{-4}$ $\sigma^2 = 0.33$ $p = 0.125$

Table 2. Regression of rainfall data against breeding population size for different ranges over which the rainfall totals were calculated

(Significance values were obtained by randomization tests.)

range over which rainfall data were calculated	Worblaufen	Widi	Bermoos
8 d before breeding	$R^2 = 0.01$, $p = 0.84$	$R^2 = 0.01$, $p = 0.87$	$R^2 < 0.01$, $p = 0.96$
16 d before breeding	$R^2 < 0.01$, $p = 0.86$	$R^2 = 0.06$, $p = 0.30$	$R^2 = 0.01$, $p = 0.72$
32 d before breeding	$R^2 = 0.02$, $p = 0.47$	$R^2 < 0.01$, $p = 0.96$	$R^2 = 0.02$, $p = 0.59$
64 d before breeding	$R^2 = 0.06$, $p = 0.25$	$R^2 = 0.01$, $p = 0.70$	$R^2 = 0.03$, $p = 0.48$
128 d before breeding	$R^2 = 0.01$, $p = 0.74$	$R^2 = 0.01$, $p = 0.67$	$R^2 = 0.10$, $p = 0.16$
activity period ^a of previous year	$R^2 = 0.16$, $p = 0.048$	$R^2 = 0.04$, $p = 0.38$	$R^2 = 0.14$, $p = 0.089$
larval period ^b 2 years before breeding year	$R^2 < 0.01$, $p = 0.98$	$R^2 < 0.01$, $p = 0.99$	$R^2 = 0.07$, $p = 0.24$
larval period ^b 3 years before breeding year	$R^2 = 0.02$, $p = 0.47$	$R^2 < 0.01$, $p = 0.75$	$R^2 = 0.07$, $p = 0.24$
larval period ^b 4 years before breeding year	$R^2 < 0.01$, $p = 0.75$	$R^2 = 0.01$, $p = 0.80$	$R^2 = 0.02$, $p = 0.50$

^aFrom spawning date to end of October.

^bFrom spawning date to end of June.

1988–1992 and an observer might have concluded that there is a regional decline, even though the decline only continued at Widi whereas the other two populations apparently recovered (figure 2).

(b) Factors governing population dynamics

The observed pattern of population fluctuations leads to the question: which factors govern the dynamics of these populations? We used Dennis & Taper's test (1994) to

detect density dependence in amphibian-population time-series. A significant result in this test means that a population fluctuates around a mean level of abundance (equivalent to N_R in figure 2) suggesting that the population is density regulated (Dennis & Taper 1994; Turchin 1995). Experiments and key factor analysis gave strong evidence for density dependence in amphibians (for examples, see Smith 1983; Van Buskirk & Smith 1991; Scott 1994; Berven 1995). Here, we found evidence for density-dependent population regulation (see table 1). The population at Widi appeared to be regulated by density before introduced fish caused its decline. Our test for SSDD was approaching significance for the population at Worblaufen whereas the population at Bermoos appeared to be unregulated. Longer time-series and time-series with regular fluctuations (i.e. a zigzag pattern) are more likely to reveal SSDD (Wolda & Dennis 1993; Turchin 1995). Dennis & Taper's test might thus lead to significant results for all three populations once more data become available.

Rainfall is an environmental factor that has been shown to affect breeding population sizes of other amphibian species through its effect on breeding activity and past recruitment (see, for example, Semlitsch *et al.* 1996). However, there was no evidence in any of the three studied populations that rainfall affected the observed population fluctuations. Yet, the fact that the sizes of the two populations breeding in the same type of habitat are correlated suggests that environmental factors acting at larger scales may affect the fluctuations of these populations in a similar, but mechanistically unknown, way.

5. CONCLUSIONS

Amphibian time-series serve to show the range of natural fluctuations that the population size of a particular species can exhibit and they can provide us with testable hypotheses concerning the population's past, present and possibly future behaviour, including population declines. Yet, our results show that it is not wise to rely solely on the analysis of time-series when trying to understand global amphibian declines. Amphibians have complex life cycles in which density-dependent regulation may occur at the larval, the juvenile and the adult stage. Tests that are currently available for SSDD do not indicate at which stage(s) regulation occurs. Each stage may also interact with density-independent environmental variables. This may result in highly complex dynamics and most available amphibian time-series' (Reed & Blaustein 1995) may be too short to give clear results when analysing them. Therefore, time-series of amphibian populations are of limited value if we try to understand the mechanisms that lead to the global amphibian declines we observe at present. Still, shorter time-series may be valuable when accompanied by detailed knowledge of the influence of predators, competitors, and environmental variables on reproduction and survival (see, for example, Semlitsch *et al.* 1996; Leirs *et al.* 1997), in particular when observations, experiments and theory can be combined.

We thank B. Anholt, T. Beebe, A. K. Holenweg, U. Reyer, B. Schmid, J. Van Buskirk, and an anonymous referee for valuable discussions and comments on the manuscript.

REFERENCES

- Berven, K. A. 1995 Population regulation in the wood frog, *Rana sylvatica*, from three diverse geographic localities. *Aust. J. Ecol.* **20**, 385–392.
- Blaustein, A. R. & Wake, D. B. 1990 Declining amphibian populations: a global phenomenon? *Trends Ecol. Evol.* **5**, 203–204.
- Blaustein, A. R., Wake, D. B. & Sousa, W. P. 1994 Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conserv. Biol.* **8**, 60–71.
- Cole, L. C. 1951 Population cycles and random oscillations. *J. Wildl. Manag.* **15**, 233–252.
- Connell, J. H. & Sousa, W. P. 1983 On the evidence needed to judge ecological stability or persistence. *Am. Nat.* **121**, 789–824.
- Cooke, A. S. 1972 Indications of recent changes in status in the British Isles of the frog (*Rana temporaria*) and the toad (*Bufo bufo*). *J. Zool.* **167**, 161–178.
- Cunningham, A. A., Langton, T. E. S., Bennett, P. M., Drury, S. E. N., Gough, R. E. & Kirkwood, J. K. 1993 Unusual mortality associated with poxvirus-like particles in frogs (*Rana temporaria*). *Vet. Rec.* **133**, 141–142.
- Dennis, B. & Taper, M. L. 1994 Density dependence in time series observations of natural populations: estimation and testing. *Ecol. Monogr.* **64**, 205–224.
- Edgington, E. S. 1987 *Randomization tests*. New York: Marcel Dekker, Inc.
- Efron, B. & Tibshirani, R. 1993 *An introduction to the bootstrap*. London: Chapman & Hall.
- Gerlach, G. & Bally, A. 1992 Das Grasfroschsterben in der Nord-Schweiz. *Schriftendr. Umwelt.* **192**.
- Glandt, D. 1985 Kaulquappen-Fressen durch Goldfische *Carassius a. auratus* und Rotfedern *Scardinius erythrophthalmus*. *Salamandra* **21**, 180–185.
- Griffiths, R. A. & Raper, S. J. 1994 How many clumps are there in a mass of frog spawn? *Br. Herpetol. Soc. Bull.* **50**, 14–17.
- Grossenbacher, K. 1988 Verbreitungsatlas der Amphibien der Schweiz. *Doc. faun. helvet.* **7**.
- Hayes, J. P. & Steidl, R. J. 1997 Statistical power analysis and amphibian population trends. *Conserv. Biol.* **11**, 273–275.
- Holyoak, M. & Baillie, S. R. 1996 Factors influencing detection of density dependence in British birds. I. Population trends. *Oecologia* **108**, 47–53.
- Leirs, H., Stenseth, N. C., Nichols, J. D., Hines, J. E., Verhagen, R. & Verheyen, W. 1997 Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. *Nature* **389**, 176–180.
- Payne, R. W., Lane, P. W., Digby, P. G. N. *et al.* 1993 *Genstat 5, release 3 reference manual*. Oxford: Clarendon Press.
- Pechmann, J. H. K., Scott, D. E., Semlitsch, R. D., Caldwell, J. P., Vitt, L. J. & Gibbons, J. W. 1991 Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* **253**, 892–895.
- Pechmann, J. H. K. & Wilbur, H. M. 1994 Putting declining amphibian populations into perspective: natural fluctuations and human impacts. *Herpetologica* **50**, 65–84.
- Reed, J. M. & Blaustein, A. R. 1995 Assessment of 'nondeclining' amphibian populations using power analysis. *Conserv. Biol.* **9**, 1299–1300.
- Ryser, J. 1988 Determination of growth and maturation in the common frog, *Rana temporaria*, by skeletochronology. *J. Zool.* **216**, 673–685.
- Scott, D. E. 1994 The effect of larval density on adult demographic traits in *Ambystoma opacum*. *Ecology* **75**, 1383–1396.
- Semb-Johansson, A. 1991 Declining populations of the common toad (*Bufo bufo* L.) on two islands in Oslofjord, Norway. *Amphibia-Reptilia* **13**, 409–412.
- Semlitsch, R. D., Scott, D. E., Pechmann, J. H. K., Gibbons, J. W. 1996 Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. In *Long-term studies of vertebrate communities* (ed. M. L. Cody & J. A. Smallwood), pp. 217–248. San Diego: Academic Press.
- Smith, D. C. 1983 Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royale, Michigan. *Ecology* **64**, 501–510.
- Thomas, L. 1997 Retrospective power analysis. *Conserv. Biol.* **11**, 276–280.
- Turchin, P. 1995 Population regulation: old arguments and a new synthesis. In *Population dynamics: new approaches and synthesis* (ed. N. Cappuccino & P. W. Price), pp. 19–40. San Diego: Academic Press.
- Van Buskirk, J. & Smith, D. C. 1991 Density-dependent population regulation in a salamander. *Ecology* **72**, 1747–1756.
- Vitt, L. J., Caldwell, J. P., Wilbur, H. M. & Smith, D. C. 1990 Amphibians as harbingers of decay. *BioScience* **40**, 418.
- Wake, D. B. 1991 Declining amphibian populations. *Science* **253**, 860.
- Wake, D. B. & Morowitz, H. J. 1991 Declining amphibian populations—a global phenomenon? *Alytes* **9**, 33–42.
- Wolda, H. & Dennis, B. 1993 Density dependence tests, are they? *Oecologia* **95**, 581–591.