Regional Dynamics and the Status of Amphibians

Stephen J. Heenan; Robert T. M’Closkey


Stable URL:
http://links.jstor.org/sici?sici=0012-9658%28199610%2977%3A7%3C2091%3ARDATSO%3E2.0.CO%3B2-G

*Ecology* is currently published by The Ecological Society of America.

__________________________________________________________

Your use of the JSTOR archive indicates your acceptance of JSTOR’s Terms and Conditions of Use, available at http://www.jstor.org/about/terms.html. JSTOR’s Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/esa.html.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

__________________________________________________________

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.
REGIONAL DYNAMICS AND THE STATUS OF AMPHIBIANS

STEPHEN J. HECKMAN AND ROBERT T. M'CLOSKEY

Department of Biological Sciences, University of Windsor, Windsor, Ontario, Canada N9B 3P4

Abstract. Increasing attention is being devoted to the dynamics of interacting local populations of species, especially the role of changes in incidence that affect regional persistence. The status of species in a regional context may be determined more by metapopulation dynamics than by purely demographic birth and death processes. The contrast between local and regional views of species' persistence is illustrated today by discussion of the status of amphibians. The amphibian fauna may provide an important indicator of the impact of anthropogenic disturbance to wetland ecosystems. We assessed the status of 11 amphibian species in southwestern Ontario, Canada, by estimating species richness, changes in presence and absence, and incidence at 97 ponds from 1992 to 1994. We detected a significant reduction in amphibian species richness in one of three regions. This loss of diversity relative to the historical species complement is a consequence of the land use history. We observed surprisingly high turnover of species at ponds, with increased incidence varying from 0.07 to 0.29 species per pond per year, and decreased incidence ranging from 0.16 to 0.30 species per pond per year. The incidence of common species across years included both declines (leopard frog, Rana pipiens) and increases (American toad, Bufo americanus). For eight relatively rare species, losses exceeded gains between 1992 and 1993, but this pattern was reversed between 1993 and 1994. Understanding environmental factors that determine the status of species will require an expanded, large-scale view of groups of populations (metapopulations) and their spatial dynamics.

Key words: amphibian status; colonization; community dynamics; extinction; local vs. regional scale; metapopulations; population dynamics; species incidence; species persistence; species richness.

INTRODUCTION

Investigations of ecological processes within local communities have produced important insights into the proximate factors responsible for community structure. However, regional patterns in species diversity rarely can be understood solely by reference to local events (Ricklefs and Schluter 1993). Persistence of species at larger scales is determined by the dynamics of extinction, colonization, and migration among local populations (Gilpin and Hanski 1991). This contrast between regional and local processes has provided the basis for important theoretical and empirical studies in community ecology and conservation biology (Soulé 1986). Studies in metapopulation dynamics are also gaining prominence as a consequence of the increasing fragmentation of natural landscapes (Soulé 1987, Fiedler and Jain 1992).

Investigations of amphibian species are receiving considerable attention because of the proposed role of amphibians as indicators of ecosystem deterioration (Wake 1991). Many amphibian populations have distributions and spatial structure characteristic of metapopulations. These include their reliance on discrete breeding sites (ponds), use of terrestrial habitats (forest fragments) for hibernation and foraging by some species, and dispersal among sites at larger spatial scales.

Long-term studies at specific sites (Pechmann et al. 1991) are invaluable in providing detailed information on temporal variation in population size, the occurrence of recruitment failure, and demographic events proximally related to species' declines (Blaustein et al. 1994a). Virtually no information exists on large-scale changes in the incidence of amphibians (but see Stumpe 1987, Sjögren 1991). This view recognizes the potential importance of metapopulation structure and dynamics (Gilpin and Hanski 1991) in determining incidence and persistence of species on a regional scale.

In this paper, we report the results of an investigation of the status of amphibians in southwestern Ontario, Canada, showing both a significant reduction in species richness, relative to the historical species complement, and high turnover in species composition, as a consequence of changes in incidence at multiple spatial scales. Approximately half of the 11 species showed a change in status (either an increase or decrease in incidence) at wetland ponds over the duration of the study. Our results emphasize the importance of a geographical perspective on the occurrence of amphibians.

STUDY SYSTEM

The study area in southwestern Ontario has flat to rolling terrain, and the natural landscape has been highly altered by humans since the mid-1800s. Extensive forests and wetlands covered the area prior to European settlement, but by ~1850, maximum forest clearance for agriculture had occurred (Moss and Davis 1989).

1 Manuscript received 3 May 1995; revised 21 December 1995; accepted 20 January 1996.

2 Address correspondence to this author.
Before European settlement, aboriginal people used fire to maintain some areas as tallgrass prairie, but prairie covered only ≈2.4% of the study area (Bakowsky and Riley 1994). Present forest cover ranges from <1 to 80% in the study area. Large-scale drainage of wetlands to reclaim land for agriculture began around the 1880s. Wetlands in presettlement times covered 68.9% of the southern portion of the area and 23.1% of the northern portion (Snell 1987). Presently, wetlands cover from 2.9 to 10% of the study area. Much of the present wetland habitat consists of artificial ponds constructed for agricultural use. For the surveys, we used wetland regions that were based on physiographic characteristics such as geology, drainage, and vegetation (Anonymous 1984).

Three wetland regions in southwestern Ontario (Fig. 1) were the Essex Plain (5341 km², 58 ponds), Stratford Plain (9469 km², 27 ponds) and Grey–Bruce Uplands (7487 km², 12 ponds). We used ponds as local study units, rather than other types of wetlands, because they are easily delimited spatially, they may act as functional islands, and they provide a study system that can be analyzed on a geographic scale. In addition, they support the full regional complement of pond amphibian species occurring in southwestern Ontario. We define ponds as water bodies < 5 m deep. Of the ponds we studied, 87% were artificial, mean (±1 se) depth was 2.01 ± 0.111 m (range 0.27–5.00 m), area was 8339 ± 4265.2 m² (60.8–175 000 m²), and age was 30.4 ± 1.82 yr (1–113 yr). We located ponds using 1:50 000 scale topographic maps (Canada Department of Energy, Mines, and Resources), inquiries at Conservation Authorities, Provincial and National Parks, chance discovery, and information provided by private landowners. To avoid biased selection, all ponds to which we had access were included. We did not choose ponds based on initial observations. Thus, the suite of ponds studied should be a representative subset of the entire spectrum of ponds. We excluded small ephemeral pools, lakes, rivers, creeks, and ditches. Some of our ponds had the characteristics of swamps (wooded) and marshes (emergent vegetation). Ponds are the most common type of wetland in southern Ontario (Merendino et al. 1995).

FIELD PROCEDURES

We conducted pond surveys from the commencement of amphibian activity in late March to late July in each of three years (1992–1994), and proceeded from south to north to take advantage of the advancing spring weather. Searches involved from three to seven people intensively searching the perimeter to ≈10 m from the pond edge, and wading, canoeing, or rafting through the pond. We dipnetted through submerged vegetation and along the substrate for ≈15 min, depending on pond size and nature of the vegetation. If ponds were within or adjacent to wooded areas, we also searched underneath woody debris. We identified adult amphibians visually and by auditions of breeding calls. We identified larvae and eggs visually. On night surveys, we used spotlights.

Most ponds were visited on at least three occasions in spring and early summer of each year. On each occasion, both a day and a night survey were made for each pond. To test survey efficiency, we used two sites with well-known amphibian fauna and examined cumulative species richness over seven surveys. In both cases, species number did not increase between the second and seventh survey. We are confident that, with the effort and methods used, the surveys produced accurate species lists. A species was counted as present at a pond if any age class was identified. Conversely, a species was deemed absent if no age class was recorded at any time during that year.

RESULTS

Species richness

Thirteen amphibian species inhabit ponds within each wetland region of southwestern Ontario, thereby permitting comparisons of species richness and changes in incidence. The source pool of 13 amphibian species includes Pseudacris crucifer, P. triseriata, Hyla versicolor, Rana pipiens, R. sylvatica, R. palustris, R. clamitans, R. catesbeiana, Bubalus americanus, Notophthalmus viridescens, and Ambystoma maculatum. Two other species occurring in the species pool, but not observed by us in this study, are Hemidactylus scutatus and Ambystoma laterale-jeffersonianum complex salamanders.

Species richness differed among regions in southwestern Ontario, with Essex having significantly fewer species per pond than either Stratford or Grey–Bruce (Fig. 2). Differences among years were not significant
within regions. There was no evidence that reduced species richness in Essex could be attributed to differences among regions in pond characteristics. Ponds did not differ significantly among regions in age (F_{2,91} = 2.104, P = 0.128) or water depth (F_{2,94} = 2.528, P = 0.085). There were significant differences among regions in pond area (F_{2,94} = 8.286, P < 0.001), but there was no significant correlation between species richness and pond area (r = −0.005, P = 0.96). Acid precipitation can be ruled out as a factor affecting amphibian species richness, because pond water in southwestern Ontario is alkaline, hard, and well-buffered against pH change (Hecnarr 1996). However, there were significant differences among ponds in the amount of woodlands within 2 km (F_{2,94} = 80.325, P < 0.0001). Ponds in Essex had significantly less (Tukey’s hsd test) surrounding woodland (mean ± 1 se: 7.3 ± 6.4%) than either Stratford (40.0 ± 3.34%; P = 0.0001) or Grey–Bruce (41.5 ± 5.07%; P = 0.0001). Multiple regression (F_{4,89} = 17.359, P < 0.0001, R^{2} = 0.433) revealed significant association of woodlands (b’ = 0.33, t = 3.55, P = 0.001) and human population density (b’ = −0.21, t = −2.43, P = 0.017) with amphibian species richness. Amphibian species that are associated with woodlands (P. crucifer, N. viridescens, H. versicolor, R. sylatica, and Ambystoma spp.) had lower incidence in Essex (1–13%) than in Stratford and Grey–Bruce (3–70%) (Hecnarr 1996; Fig. 3).

Change in incidence

The lack of significant differences in species richness among years belies the high turnover of species within and among regions (Fig. 4). Changes in incidence are measurable features of amphibians at the level of individual ponds. We represented these changes as the mean number of events (gains or losses) at each pond divided by species richness, and took the mean for the ponds within each region. We divided the 97 ponds into nine subregions (four in Essex, three in Stratford, two in Grey–Bruce) that provided estimates of changes in incidence (Fig. 4). Subregions were defined as clusters of ponds at the watershed scale. Mean (±1 se) nearest-neighbor distance between sampled ponds was 1.5 ± 0.61 km, mean distance between subregions was 12.0 ± 1.72 km, and mean distance between regions was 63.8 ± 24.85 km.

Increase in incidence varied from 0.07 to 0.29 species per pond per year, although the increase in incidence of the total amphibian fauna did not differ significantly among regions (Fig. 4). Decrease in incidence varied between 0.16 and 0.30 species per pond per year, and was significantly different among regions for 1992–1993 (Fig. 4).

Differences among species

At the level of individual species, changes in incidence varied substantially (Fig. 5). Of the three most
common amphibian species, the leopard frog (*R. pipiens*, 58% incidence) showed a large decrease (23%) in incidence between 1992 and 1993, but a much smaller decrease (5%) between 1993 and 1994. The American toad (*B. americanus*, 50% incidence) showed an increase in incidence (17%) between 1992 and 1993, and no change between 1993 and 1994. The green frog (*R. clamitans*, 78% incidence) showed a slight gain (1%) between 1992 and 1993, and a decrease in incidence (14%) between 1993 and 1994 (Fig. 5). For the eight rarer species (1–24% incidence), there was a net decrease in incidence, with losses occurring more frequently (n = 18) than gains (n = 4) (Fig. 5A) between 1992 and 1993. This pattern was reversed between 1993 and 1994 (Fig. 5B), with gains (n = 24) exceeding losses (n = 14). Regional patterns in changes in species’ incidence are shown in Table 1. Although about half of the species showed no change in incidence (Fig. 5), the three regions showed a net loss of incidence between 1992 and 1993, and a net gain between 1993 and 1994.

Subregional (watershed scale) patterns of changes in incidence of the three most common species are shown in Fig. 6. For individual species, changes in incidence differed among the nine subregions. From 1992 to 1993, *Rana clamitans* decreased in two, increased in one, but showed no net changes in the other six subregions. *Rana pipiens* decreased in seven, increased in one, and showed no change in one subregion. *Bufo americanus* decreased in two, increased in four, and...
Fig. 6. Mean changes in incidence of the three most common amphibian species by subregion in southwestern Ontario between 1992–1993 and 1993–1994. Open bars represent increased incidence, and closed bars represent decreased incidence. The status of a particular species in a subregion can be assessed by the difference between the increases and decreases. Increased incidence exceeded 1.0 in three cases (B. americanus in Albuna and Parkhill; R. pipiens in Albuna) in which the number of new ponds occupied exceeded the number occupied in the previous year. The number of ponds surveyed were: Amherstburg (12), Albuna (17), Harrow (18), Ojibway (11), Allan Park (4), McGregor Point (8), Bayfield (11), Hay Township (9), and Parkhill (7).
showed no net change in three subregions. From 1993 to 1994, *Rana clamitans* decreased in four, but showed no net change in the other five subregions. *Rana pipiens* decreased in three, increased in four, and showed no net change in two subregions. *Bufo americanus* decreased in two, increased in three, and showed no net change in four subregions.

**Discussion**

Our results emphasize two different aspects of the question of amphibian status. First, our surveys reveal the loss of regional species richness, an impact at the level of amphibian assemblages (Fig. 2). Because all regions share the same source pool of amphibians, and historical records (Weller and Oldham 1988, Oldham and Weller 1995) show all species to have been present, the lower diversity in Essex suggests a loss of amphibian species richness relative to its historical complement. Species associated with woodlands (*P. crucifer, N. viridescens, H. versicolor, R. sylvatica, and Ambystoma spp.*) (Johnson 1989, Conant and Collins 1991) have low incidence in Essex (Fig. 3) because of their dependence on forest habitat for hibernation and foraging. In addition, Essex has relicut assemblages of amphibians in which species richness is as high as that found anywhere in southwestern Ontario. Relictual “islands” in the Essex region include Rondeau Provincial Park (11 spp.), Walpole Island (10 spp.), and Point Pelee National Park (5 spp., formerly 11 spp.). These relictual “islands” are reserves that contain large forested tracts. There are also examples of relictual populations of species, such as *Ambystoma maculatum and Hyla versicolor*, that persist in isolated woodlots in Essex. This suggests that the lower species richness in Essex (Fig. 2) represents a recent loss of diversity rather than intrinsic differences in regional diversity between Essex and Stratford Grey–Bruce. Although habitat loss seems to be the most parsimonious explanation for species loss, an alternate hypothesis, probably not mutually exclusive, is agricultural chemical use. Heavy application of pesticides and fertilizer occurs across the entire study area, but the lack of forest cover in Essex would reduce any filtration effect on chemicals (Simmons et al. 1992, Phillips et al. 1993).

Second, there is surprisingly high population turnover within regions (Fig. 4) and at the level of individual species (Figs. 5 and 6), emphasizing the transiency and spatial dynamics of amphibians, apparent even over a short span of time. These questions of high turnover have not been explicitly addressed in studies to date (but see Sjögren 1991, Sjögren Gulve 1994). It is well known that recruitment patterns in many amphibians are temporally variable (Peckmann et al. 1991), dependent on age structure, and partly responsible for changes in occurrence at breeding ponds. Brief periods of synchronous breeding, absence of breeding, or use of different breeding sites in different years could have biased our estimates of changes in incidence. Nonetheless, many of our reported changes in presence and absence may represent local extinction and colonization of ponds. We think this is likely, given the permanence of the ponds, frequency and intensity of the surveys, site fidelity of amphibians (Sinsch 1990, Duellman and Trueb 1994), and our use of any life stage to indicate presence. In addition, the year-round use of ponds by some species (e.g., *R. clamitans and R. catesbeiana*) makes it highly unlikely that they would have been missed during the surveys. Both of those species showed substantial turnover and changes in incidence during the study period (Figs. 5 and 6).

Our surveys have revealed regional declines in the incidence of some species (*R. pipiens, R. catesbeiana*), and increases in others (*B. americanus*). Even species showing relatively little change in incidence have high turnover among ponds (*R. clamitans*). Virtually any subset of our ponds or species at a restricted set of ponds could show the gamut of changes in status, including decreased, increased, or no change in incidence. Ecological studies generally have been conducted at local scales; results obtained from small-scale investigations are dependent on which study sites are chosen for analysis of patterns (Ricklefs and Schluter 1993).

Amphibian species richness is ultimately determined by environmental factors that affect colonization and extinction. Recent attention has focused on several, more or less independent, hypotheses advanced to explain amphibian declines. Most hypotheses implicate either direct or indirect anthropogenic causes, and include pollution (acid rain, pesticides, fertilizers), habitat destruction (urbanization, agriculture), introduction of exotic predators, and global climate change (greenhouse effect, ozone holes) (Hayes and Jennings 1986, Berger 1989, Beebee et al. 1990, Phillips 1990, Wake and Morowitz 1991, Blaustein et al. 1994b, Pounds and Crump 1994). Evidence for many of the population declines is largely anecdotal and sometimes paradoxical, in that not all species are declining. Some species appear to be declining in pristine areas, and some regions are apparently unaffected (Barinaga 1990, Phillips 1990, Wyman 1990, Wake and Morowitz 1991).

Pond ecosystems may provide the framework for metapopulation structure and dynamics in many amphibian species (Gill 1978, Sjögren 1991, Blaustein et al. 1994a, Peckmann and Wilbur 1994, Sjögren Gulve 1994). Therefore, assessment of the status of amphibians requires an expanded, regional viewpoint. This approach is not a substitute for long-term studies at specific sites, but rather is a necessary complement to them. Specific environmental factors may explain the decline or loss of amphibians in particular cases (Corn and Fogleman 1984, Blaustein et al. 1994a, b), but the ultimate cause for large-scale loss may be reduced opportunities for colonization and increased frequency of extinction.

**Acknowledgments**

field and lab work. We thank the Ontario Ministry of Natural Resources and Parks Canada; the Ausable-Bayfield, Maitland Valley, Essex Region, and Saugeen Valley Conservation Authorities; and many private landowners for their continued cooperation and interest. Shirley Cramp prepared the manuscript copy. J. Pechmann and an anonymous reviewer made valuable comments on the manuscript. Funding was provided through a Natural Sciences and Engineering Research Council of Canada grant to R.T. M’Closkey.

LITERATURE CITED


