

## **Poissons et Amphibiens ou Poissons ou Amphibiens?**

### **Aperçu des résultats d'études scientifiques récentes**

1. Les points essentiels en quelques mots	1
2. Récapitulatif des travaux de recherche	2
3. Recherches en Europe	7
4. Recherches en Amérique du Nord	15
5. Recherches dans un domaine particulier	33

Ce document de travail résume les résultats d'études scientifiques récentes qui traitent des interactions entre les poissons et les amphibiens. Les thèmes abordés en premier lieu sont l'impact des poissons sur la répartition, la dynamique des populations et l'abondance des amphibiens.

Ce récapitulatif se base sur des articles publiés dans des revues internationales, ce choix garantissant la qualité des travaux de recherche. Les copies de la plupart des articles cités (Format Adobe pdf) peuvent être obtenus auprès du **karch** ([info@karch.ch](mailto:info@karch.ch)).

### **1. Les points essentiels en quelques mots**

En résumé, ces travaux montrent que les poissons ont un fort impact négatif sur les amphibiens:

- Il y a moins souvent d'amphibiens dans les plans d'eau peuplés de poissons que dans des plans d'eau similaires dépourvus de poissons. S'ils sont présents, ils sont nettement moins abondants en présence de poissons. Seuls peu d'amphibiens, pour la plupart des espèces munies de glandes venimeuses cutanées, peuvent coexister avec les poissons.
- L'empoisonnement de plans d'eau naturellement dépourvus de poissons a un effet négatif sur les amphibiens, que ce soit sur leur présence ou leur abondance. L'impact est réversible si les amphibiens ont la possibilité de recoloniser le site une fois les poissons enlevés.
- L'empoisonnement de plans d'eau naturellement dépourvus de poissons peut avoir des conséquences allant bien au-delà du plan d'eau lui-même, car il peut aussi avoir un impact sur le réseau écologique terrestre environnant.
- L'empoisonnement de plans d'eau naturellement dépourvus de poissons peut modifier la structure génétique des populations d'amphibiens.
- L'empoisonnement de plans d'eau naturellement dépourvus de poissons peut véhiculer des agents pathogènes pour les amphibiens.

## 2. Récapitulatif des travaux

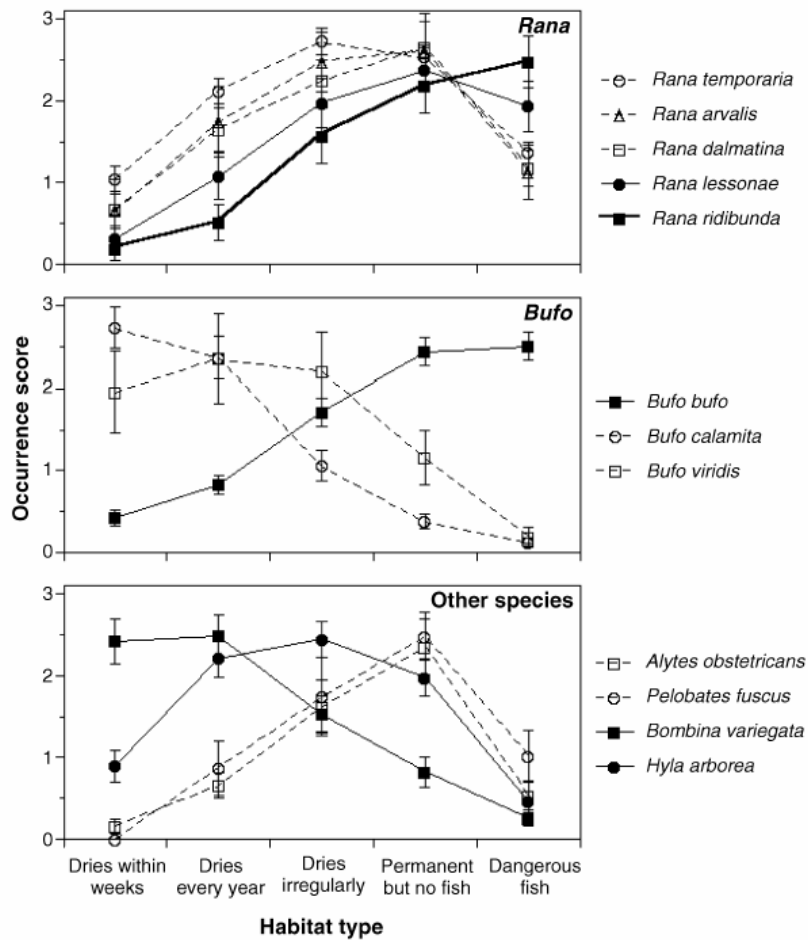
### 2.1. Critical literature review of the evidence for unpalatability of amphibian eggs and larvae. Gunzburger MS, Travis J 2005. JOURNAL OF HERPETOLOGY 39:547-571.

*Résultats importants:* Certaines larves d'amphibiens ne sont pas comestibles pour les poissons. Cependant, cette caractéristique est plutôt rare.

*Abstract:* We examined 142 papers, which contained 603 separate predator-prey trials, to investigate whether unpalatability is an important defense against predation for amphibian eggs and larvae. Although unpalatability is often cited as an antipredator defense, it was rarely demonstrated that 89% of the trials that we reviewed found prey to be palatable. The most extensively studied taxa, the genera *Bufo* and *Rana*, were diagnosed unpalatable at rates comparable to all other taxa. Diagnoses of unpalatability were not always consistent for a prey species across different predators and were influenced by experimental method. Despite these limitations and our conservative definition of unpalatability, several patterns emerged. First, across all taxonomic groups, eggs and hatchlings were unpalatable more often than mobile larval stages. Second, species that breed in temporary ponds were more likely to be palatable to fish predators than those that breed in permanent habitats. Third, fish and caudates were more likely to find amphibian prey unpalatable than insect predators. We conclude that unpalatability is rare, but when it occurs, it is a property of an ensemble (predator, prey, and alternative prey) and a life-history stage in a particular circumstance but is not a species-specific attribute. We suggest methods of experimentation that could strengthen future research on the palatability of amphibian eggs and larvae.

### 2.2. Habitat partitioning in European and North American pond-breeding frogs and toads. Van Buskirk J 2003. DIVERSITY AND DISTRIBUTIONS 9:399-410.

*Résultats importants:* La plupart des amphibiens, en particulier les espèces menacées figurant sur les Listes Rouges, préfèrent les plans d'eau dépourvus de poissons.



**Fig. 4** Habitat distributions of western European anuran tadpoles, as determined by the field observations of 40 herpetologists. Sample sizes range from 11 to 37 respondents per species.

**Abstract:** Distributions of species along a freshwater habitat gradient, ranging from ephemeral pools with few predators to permanent lakes with fish, have been used to infer how predation establishes trade-offs that promote ecological specialization. Larval anurans are said to support the trade-off model, but there are few comparable and quantitative habitat data available to assess this claim. I performed a survey of field biologists to evaluate the habitats of similar sets of species in the northern parts of Europe (40 respondents and 12 species) and eastern North America (30 respondents and 8 species), using a standard set of criteria. For six European species I also had quantitative field sampling data, and found close agreement between survey results and predator densities experienced by tadpoles in the field. Distributions of most species were restricted to only part of the habitat gradient, as expected under the trade-off model. The survey confirmed reports that North American *Rana* species replace one another along the gradient, but this was not true in Europe. European *Rana* were no different from the North American species in their seasonal and geographical overlap, so the absence of habitat partitioning in European *Rana* may result from interactions with other species or the special impact of glaciation in Europe. Habitats were unrelated to evolutionary relationships among species, suggesting that changes in habitat evolve quickly. The survey approach was

useful for comparing distributions of species, and for generating hypotheses about evolutionary responses to habitat gradients.

**2.3. Alien predators and amphibian declines: review of two decades of science and the transition to conservation. Kats LB, Ferrer RP 2003. DIVERSITY AND DISTRIBUTIONS 9: 99-110.**

*Résultats importants:* De nombreux travaux de recherche ont montré de façon convaincante que les poissons non autochtones dans une station sont responsables pour une bonne part du recul global des amphibiens. Les bases scientifiques sont suffisantes pour gérer les espèces invasives dont font partie plusieurs espèces de poissons dans certaines localités<sup>1</sup>.

*Abstract:* Over the last two decades, numerous studies have shown that alien predators contributed to amphibian population declines. Both experimental studies and correlative field surveys implicated alien species of fish, bullfrogs and crayfish as major contributors to amphibian population decline, and in some instances local extinction. Additional studies have demonstrated that alien predators also caused long-term changes in aquatic communities. Recent studies have examined the feasibility of removing alien predators, and provide some evidence that amphibian populations can recover. Applying information gained from past studies to the recovery of amphibian populations will be the challenge of future studies. International, national and local policies that regulate alien predators should be based largely on the body of scientific evidence already in the literature. Scientists need to be more involved with policy-makers to most effectively change laws that regulate alien predators.

**2.4. Effects of stocking-up freshwater food webs. Eby LA, Roach WJ, Crowder LB, Stanford JA 2006. TRENDS IN ECOLOGY & EVOLUTION 21:576-584.**

*Résultats importants:* Si les effets directs des introductions de poissons sont bien étudiés, ce n'est pas le cas de leurs conséquences sur les écosystèmes aquatiques et terrestres environnants (auxquelles on peut s'attendre).

*Abstract:* The establishment of exotic game fishes to enhance recreational fisheries through authorized and unauthorized stocking into freshwater systems is a global phenomenon. Stocked fishes are often top predators that either replace native top predators or increase the species richness of top predators. Many direct effects of stocking have been documented, but the ecosystem consequences are seldom quantified. New studies increasingly document how species and community shifts influence ecosystem processes. We discuss here how predator stocking might increase top-down effects, alter nutrient cycles and decrease links between aquatic and surrounding terrestrial ecosystems. As fisheries management moves beyond species-specific utilitarian objectives to incorporate ecosystem and conservation goals, ecologists must address how

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<sup>1</sup> Voir „Global Invasive Species Database“ de „Invasive Species Specialist Group“ de l'UICN, lequel mentionne entre autres *Salmo trutta* et *Oncorhynchus mykiss* parmi les 100 „worst invasive species“.  
<http://www.issg.org/database/species/search.asp?st=100ss&fr=1&str=>

common management practices alter food-web structure and subsequent ecosystem-level effects.

**2.5. The introduction of nonnative fish into wilderness lakes: Good intentions, conflicting mandates, and unintended consequences. Knapp RA, Corn PS, Schindler DE. ECOSYSTEMS 4:275-278.**

*Résultats importants:* Ce travail illustre les conflits d'intérêt des diverses institutions nationales concernées par les plans d'eau naturellement dépourvus de poissons. Il montre que l'empoisonnement n'a pas seulement un impact direct sur les espèces indigènes (prédation), mais également des effets sur les chaînes alimentaires des milieux terrestres environnants. Le travail montre aussi que l'écosystème perturbé par l'introduction de poissons ne peut pas toujours se rétablir, même si on élimine totalement les poissons non indigènes.

*Abstract:* Collectively, these papers indicate that the effects of widespread trout introductions into wilderness landscapes are not limited simply to direct effects on prey taxa, but instead can be transmitted throughout lake food webs and even beyond the shorelines of fish-containing lakes to fishless lakes. In addition, following fish removal, full recovery of ecosystem structure and function may not occur. These results pose a difficult challenge for fisheries and wilderness managers interested in better balancing the conflicting goals of maintaining nonnative fisheries in wilderness areas while also minimizing the effects of these fisheries on natural processes. If managers are to truly balance these often opposing goals, it is imperative that current fisheries management practices be evaluated in the context of their effects on ecosystem and landscape processes. It is our hope that this special feature will provide the impetus for such an evaluation and for the adoption of new management strategies to reduce the ecological impacts of nonnative fisheries in protected areas. (*Cet article n'a pas de résumé; ce sont les conclusions de l'étude.*)

**2.6. Principles for management of aquatic-breeding amphibians. Semlitsch RD 2000. JOURNAL OF WILDLIFE MANAGEMENT 64:615-631.<sup>2</sup>**

*Résultats importants:* Dans le cadre de la gestion de plans d'eau pour les amphibiens, il faut tenir compte du régime des eaux et veiller à ce qu'aucune population de poissons ne puisse s'établir.

*Abstract:* Coordinated efforts by ecologists and natural resource managers are necessary to balance the conservation of biological diversity with the potential for sustained economic development. Because some amphibians have suffered world-wide declines during the last 20 years, it is important to consider biologically based management strategies that will preserve local and regional populations. This paper provides a brief overview of potential threats to local and regional populations, the state of knowledge on population and landscape processes, and the critical elements needed for an effective management plan for amphibians. Local population dynamics and ecological connectivity of amphibian metapopulations must be considered in effective management plans. There are 3

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<sup>2</sup> Pas d'Adobe pdf disponible pour cet article.

critical factors to consider in a management plan (1) the number or density of individuals dispersing from individual wetlands, (2) the diversity of wetlands with regard to hydroperiod, and (3) the probability of dispersal among adjacent wetlands or the rescue and recolonization of local populations. Wetland losses reduce the total number of sites where pond-breeding amphibians can reproduce and recruit juveniles into the breeding population. Loss of small, temporary wetlands (<4.0 ha) may be especially harmful to amphibians because of their abundance and high species diversity. Alteration of wetlands, particularly hydrologic cycles, can severely impair completion of larval metamorphosis through either early pond drying (if hydroperiod is shortened) or through increased predation (if hydroperiod is lengthened or connections made with fish-infested lakes, rivers, or canals). Wetland loss also increases the distance between neighboring wetlands that is critical to metapopulation source-sink processes. Reduction in wetland density reduces the probability that populations will be rescued from extinction by nearby source populations. Local populations cannot be considered independent of source-sink processes that connect wetlands at the landscape or regional level. Further, the fragmentation of natural habitats from timber harvesting, agriculture, roads, drainage canals, or urban development impedes or prevents dispersal and decreases the probability of wetland recolonization. If our goal is to maintain or enhance present levels of amphibian diversity, then resource managers must incorporate critical elements into plans that protect population and landscape processes thereby maintaining viable populations and communities of amphibians.

**2.7. Assessing the consequences of nonnative trout in headwater ecosystems in western North America. Dunham JB, Pilliod DS, Young MK 2004. FISHERIES 29:18-26**

*Résultats importants:* Cet article traite des conséquences biologiques et économiques de l'introduction de truites non autochtones. Les truites ont un impact négatif direct sur la plupart des espèces d'invertébrés et d'amphibiens. A cela s'ajoutent divers effets indirects comme par exemple la transmission de maladies.

*Abstract:* Intentional introductions of nonnative trout into headwater lakes and streams can have numerous effects on the receiving ecosystems, potentially threatening native species and disrupting key ecological processes. In this perspective, we focus on seven key issues for assessing the biological and economic consequences of nonnative trout in headwater ecosystems: (1) effects of nonnative trout can span multiple biological domains, (2) effects of nonnative trout can extend beyond waters where they are introduced, (3) nonnative trout do not travel alone, (4) not all habitats are equal, (5) ecosystems vary in their resistance and resilience to nonnative trout, (6) prioritization can improve management of nonnative trout, and (7) economic costs of recreational fisheries in headwater ecosystems can be substantial. Assessments that address these issues could provide more effective guidance for determining where recreational fisheries for nonnative trout are justified in headwater ecosystems and where they might be terminated to support other ecosystem values.

### 3. Recherches en Europe

#### 3.1. Effects of different predators on the survival and development of tadpoles from the hybridogenetic *Rana esculenta* complex. Semlitsch RD 1993. OIKOS 67:40-46. <sup>3</sup>

*Résultats importants:* En conditions expérimentales, les poissons sont responsables d'une très forte mortalité des têtards (supérieure à 99%), mortalité plus importante que celle due aux invertébrés prédateurs.

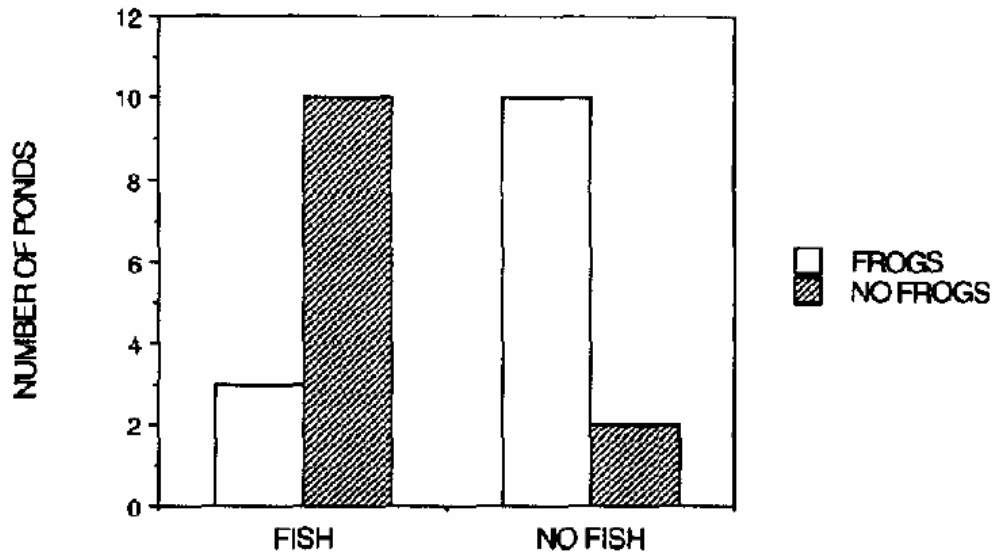
*Abstract:* I studied the effects of predation on two genotypes of tadpoles from the hybridogenetic *Rana lessonae*-*Rana esculenta* complex. Tadpoles were reared at two larval densities in artificial ponds with fish, newts, dragonfly larvae, and in a control with no predators. Survival was significantly reduced by the presence of predators, but was not differentially affected by larval density. Only 0.33% of the tadpoles survived with fish, 48.9% with newts, and 70.8% with odonates. Survival was highest (93.4%) in control ponds. Survival in ponds with fish, newts, and control ponds was not affected by genotype, however, in ponds with odonates the survival of *R. esculenta* was higher than that of *R. lessonae*. The higher survival of *R. esculenta* appeared to be correlated with lower activity of tadpoles. The percentage of survivors that metamorphosed was significantly affected by larval density, but not by predators or genotype of tadpole. Of the surviving tadpoles, 90.6% reared at high larval density and 96.4% reared at the low density metamorphosed. Metamorphs emerged larger in ponds with more intense predation and at low larval density. *Rana esculenta* tadpoles emerged sooner than those of *R. lessonae*. *Rana esculenta* hybrid tadpoles outperformed the parental species *R. lessonae* in days to metamorphosis. Results from my experiment suggest that the hybrid *R. esculenta* is equally or more successful than the parental species *R. lessonae* when reared with some aquatic predators. Differential activity of tadpoles is suggested as a possible mechanism accounting for the success of the hybrid.

#### 3.2. Does the presence of fish affect the distribution of tree frogs (*Hyla arborea*)? Brönmark C, Edenhamn P 1994. CONSERVATION BIOLOGY 8:841-845.

*Résultats importants:* Les rainettes occupent avant tout des plans d'eau dépourvus de poissons.

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<sup>3</sup> Pas d'Adobe pdf disponible pour cet article.



**Figure 1. Distribution of reproducing tree frogs in ponds with and without fish (n = 25). Open bars are ponds that had reproducing tree frogs during three years; cross-hatched bars are ponds with no recordings of tree frog presence.**

Abstract: --- <sup>4</sup>

3.3. Effects of widespread fish introductions on paedomorphic newts in Europe. Denoel M, Dzukic G, Kalezic ML 2005. CONSERVATION BIOLOGY 19:162-170.

*Résultats importants:* Là où des poissons ont été introduits, les Tritons alpestres pédomorphiques (= Tritons adultes conservant la morphologie et le mode de vie aquatique des larves) ont disparu.

*Abstract:* As a result of factors such as global warming, habitat destruction, and species introduction, amphibians are declining worldwide. No one, however, has analyzed the status of polymorphic amphibian species at a national or continental scale, although some local reports exist. Our aim was to report on the loss of intraspecific heterochrony as a loss to diversity in determining the consequences of fish stocking on European populations of paedomorphic newts. Paedomorphosis is a polymorphism in which larval traits are retained in the adult stage. We surveyed 39 paedomorphic populations of the alpine (*Triturus alpestris*) and palmate (*T. helveticus*) newts, all but one of which initially occupied fishless ponds and lakes in France, Italy, Slovenia, Bosnia, Montenegro, and Greece. Exotic fishes were found in 44% of the studied aquatic habitats, with a 100% presence in Montenegro. At all sites paedomorphs disappeared and metamorphs declined. Only fish explained these population changes because alternative factors such as drying were not significant. More catastrophi-

<sup>4</sup> Ce travail n'a pas de résumé.



cally, fish introductions occurred in habitats known to support the largest populations of newts and even some endemic subspecies. If management and legislative measures are not taken to stop fish stocking, protect paedomorphs as conservation units at national and international levels, and restore natural habitats, all the largest paedomorphic populations may disappear in the near future. Their disappearance would represent a loss of one of the rare, fascinating examples of intraspecific heterochrony.

**3.4. Multi-scale effect of landscape processes and habitat quality on newt abundance: Implications for conservation. Denoel M, Lehmann A 2006. BIOLOGICAL CONSERVATION 130:495-504.**

*Résultats importants:* Il y a moins souvent de Tritons palmés dans les plans d'eau peuplés de poissons que dans les plans d'eau similaires dépourvus de poissons. S'ils sont présents, ils sont nettement moins abondants en présence de poissons.

*Abstract:* Recent studies in population dynamics suggest that landscape processes and habitat quality. act at different scales on population abundances, but very few have modelled their simultaneous effects. However, at a time of large declines in natural populations, it is essential to understand such multivariate components. We tested the hypothesis that natural populations of palmate newts (*Triturus helveticus*) are affected on three scales: breeding patch (pond), habitat complementation (terrestrial cover), and metapopulation. structure (density of ponds, surrounding populations). We conducted our survey in 130 ponds from southern France (Larzac) and analysed data with generalized additive models (GAM). Two main novel results emerge from these models: (1) the three landscape scales have significant effects on newt abundance, with more newts in deep, vegetated ponds, devoid of fish and surrounded by wooded areas and inhabited ponds; (2) the quality of the surrounding breeding patches is of primary importance in determining the abundance at core sites in a complex way: high abundances are associated positively with high densities of inhabited ponds, but negatively with the number of surrounding ponds. Deforestation, invasive species and abandonment of ponds all have negative impacts on the persistence of palmate newt populations. Future studies should encompass landscapes at different scales and incorporate the habitat quality in surrounding sites to better understand population dynamics and. provide adequate conservation measures.

**3.5. Analysis of three amphibian populations with quarter-century long time-series. Meyer AH, Schmidt BR, Grossenbacher K 1998. PROCEEDINGS OF THE ROYAL SOCIETY OF LONDON SERIES B-BIOLOGICAL SCIENCES 265:523-528.**

*Résultats importants:* Une population de Grenouilles rousses (Widi) est en forte régression suite à l'introduction de Poissons rouges dans les étangs.

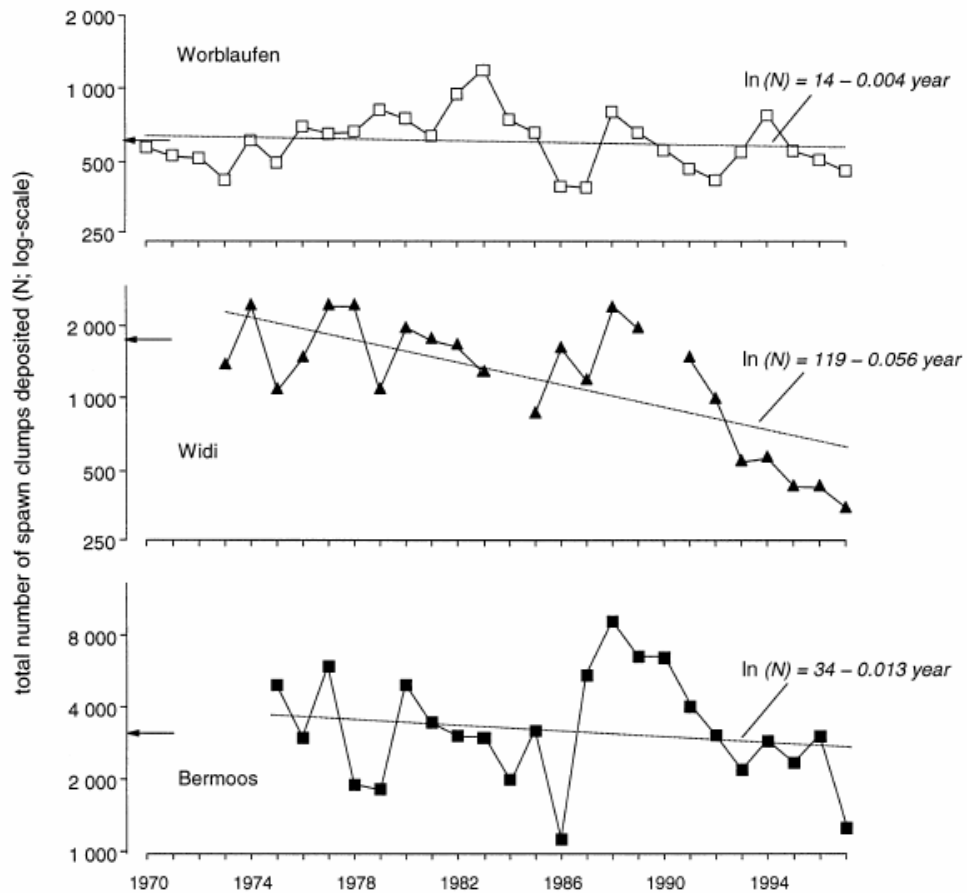


Figure 2. Temporal fluctuations of three populations of *R. temporaria*. The broken fitted lines refer to a model for simple linear regression, the slope and the intercept both being bootstrap estimates. The arrows point to the mean level of abundance ( $N_R$ ) to which the population tends to return, 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.

**Abstract:** 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.

**3.6. Predator complement determines the relative success of tadpoles of the *Rana esculenta* complex. Anholt BR, Negovetic S, Rauter C, Som C 2005. EVOLUTIONARY ECOLOGY RESEARCH 7:733-741.**

**Résultats importants:** La présence de poissons détermine l'abondance relative des têtards du complexe *Rana esculenta*. *Rana lessonae* est proportionnellement moins abondante que *Rana esculenta* en présence de poissons.

**Abstract:** Question: Does the identity of the apex predator in a system predict the relative success of closely related amphibian larvae?

Organisms: Larvae of the hybridogenetic european frog, *Rana kl. esculenta*, and its sexual host, *R. lessonae*.

Site: Three ponds supporting predatory fish and four ponds without fish but containing large invertebrate and amphibian predators in northern Switzerland.

Background: *Rana esculenta* is a better competitor than *R. lessonae* in a wide range of conditions and is also a larger, more fecund frog than *R. lessonae*. Under most conditions, models predict competitive exclusion of *R. lessonae* followed by extinction of *R. lessonae*.

Methods: In the field, we measured the change in frequency of the two taxa from the larval stage to metamorphosis. In the laboratory, we measured the activity of the two taxa and measured their vulnerability to odonate predators.

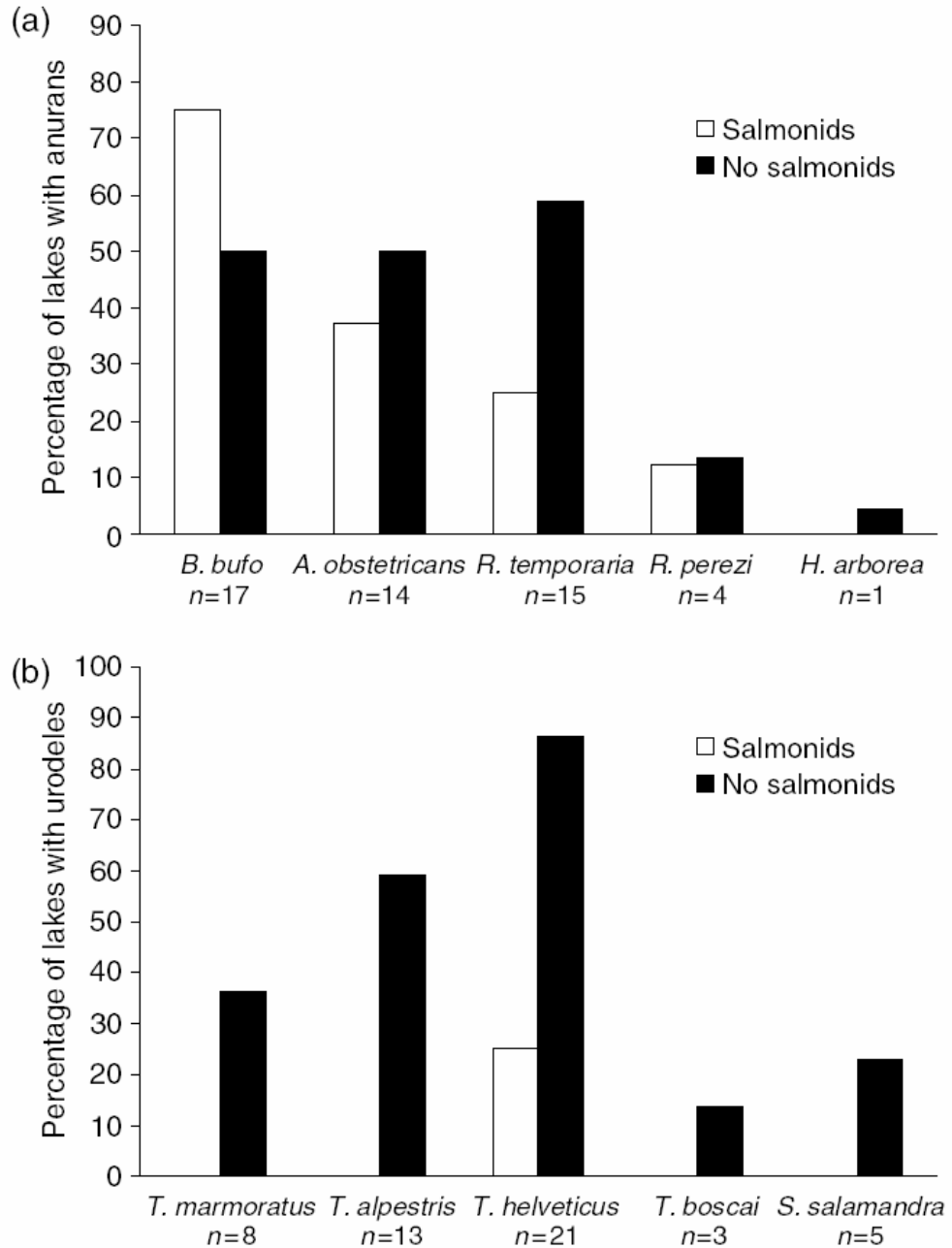
Conclusions: In the presence of fish, the frequency of *R. lessonae* declined relative to *R. esculenta* from the larval stage to metamorphosis. In the absence of fish and presence of other predators, the opposite was true. *Rana esculenta* was more active than *R. lessonae* and more vulnerable to predation. The two taxa are adapted to different predator complexes and the hybridogenetic system is maintained by occasional dispersal between dissimilar water bodies.

**3.7. Effect of salmonid introduction and other environmental characteristics on amphibian distribution and abundance in mountain lakes of northern Spain. Orizaola G, Brana F 2006. ANIMAL CONSERVATION 9:171-178.**

**Résultats importants:** L'introduction de Salmonidés dans les lacs de montagne réduit la chance de trouver 3 espèces de tritons. Cela n'a au contraire pas d'impact sur la présence du Crapaud commun et du Crapaud accoucheur. Il y a une tendance non statistiquement significative à la diminution chez la Grenouille rousse.

**Abstract:** Amphibians are currently experiencing a severe worldwide decline. Several factors, such as habitat alteration, climate change, emerging diseases or the introduction of exotic species, have been signalled as being responsible for the reduction of amphibian populations. Among these, the introduction of fish predators has been repeatedly indicated as a factor affecting the distribution of many species. The present study was developed to examine the effect of fish presence and other environmental factors on the distribution and abundance of amphibian species in mountain lakes of the Cantabrian Range in northern Spain. We found no effect of salmonid presence on the distribution and abundance of two widespread anuran species *Bufo bufo* and *Alytes obstetricans*, whereas *Rana temporaria* showed a non-significant tendency to be absent from salmonid-occupied lakes. However, the presence of introduced salmonids was the main negative factor explaining the distribution of the newt species *Triturus helveticus*, *Triturus alpestris* and *Triturus marmoratus*. The effect on these species is likely to be due to increased larval mortality, as adult and egg predation by fish, or oviposition avoidance by female newts has rarely been recorded. Fish removal and the creation of alternative

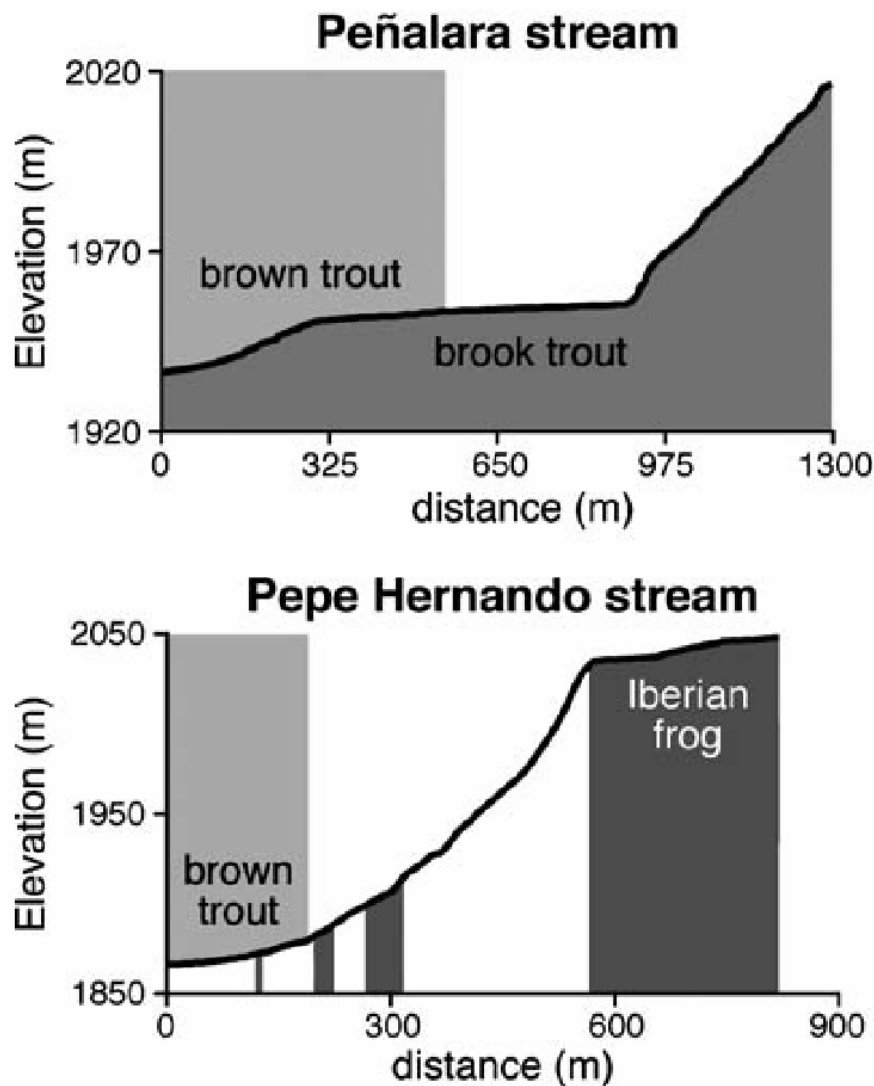
breeding habitats for amphibians are proposed as conservation measures to recover amphibian populations in the vicinity of fish-stocked lakes.



**Figure 1** Amphibian distribution (all stages considered) in lakes with or without the presence of fish predators. The total number of lakes where each species was found is indicated. (a) Anurans, (b) urodeles.

**3.8. Effects of introduced salmonids on a montane population of Iberian frogs. Bosch J, Rincon PA, Boyero L, Martinez-Solano I 2006. CONSERVATION BIOLOGY 20:180-189.**

*Résultats importants:* Dans un parc national espagnol, les grenouilles vivent dans les mêmes milieux que les truites qui ont été introduites. Les poissons tendent à repousser les grenouilles dans les habitats marginaux et les têtards ne cohabitent pas avec les truites.



*Figure 1. Stream profiles of the sampled sections of the studied streams of Peñalara Natural Park, indicating where tadpoles and salmonids are present. The gray blocks indicate the stream sections where tadpoles and salmonids are present*

**Abstract:** Amphibians are declining worldwide because of multiple factors, including human-mediated introduction of fishes into naturally fishless areas. Although several studies have focused on the effect of exotic fishes on native amphibians breeding in ponds or lakes, little is known about their effects on stream-breeding species. We studied the effects of introductions of native brown trout (*Salmo trutta*) and exotic brook trout (*Salvelinus fontinalis*) on the stream-breeding, endemic Iberian frog (*Rana iberica*) in a protected area in central Spain. We assessed occurrence patterns of tadpoles and salmonids and compared habitat use of the three species. We also determined experimentally whether chemical cues from salmonids elicited antipredator behavior in tadpoles. Finally, we assessed the relative influence of tadpole habitat preferences, differences in salmonid species, and invasion geography on tadpole occurrence. Despite widely overlapping habitat preferences, tadpoles and trout did not coexist, with the former restricted to fishless habitats. Tadpoles detected chemical cues from both trout species and reacted by decreasing their activity, although the response toward the native brown trout was stronger. The residual distribution of Iberian frogs in Penalarra is better explained by the geography of fish invasions than by the fish species involved. Measures such as fish extirpation from certain areas, aimed at recovering lost habitat and improving connectivity among remaining populations of Iberian frogs, seem critical for the species' long-term survival in central Spain.

**3.9. Amphibian diversity and nestedness in a dynamic floodplain river (Tagliamento, NE-Italy). Tockner K, Klaus I, Baumgartner C, Ward JV 2006. HYDROBIOLOGIA 565:121-133.**

**Résultats importants:** Dans une zone alluviale naturelle du Tagliamento, il y a une corrélation positive entre le nombre d'espèces d'amphibiens et la densité des poissons. Cela indique qu'il y a de nombreux secteurs, dans cette zone alluviale dynamique, qui ne conviennent ni aux amphibiens ni aux poissons.

**Abstract:** Amphibian distribution and assemblage structure were investigated along the last morphologically intact river corridor in Central Europe (Tagliamento). Thirteen taxa were identified with *Rana latastei* and *Bufo bufo* being the predominant species. In the main study reach, a 2 km(2) dynamic island-braided floodplain in the middle section of the river, 130 water bodies were delineated that were situated either in the active floodplain (82 sites) or in the adjacent riparian forest (48 sites). Results demonstrated that the active floodplain increased appreciably the available habitat for amphibians, despite frequent disturbances by floods or droughts. Amphibian richness within a given habitat was significantly correlated with distance from vegetated islands, fish density, and water temperature. In the active floodplain, species distribution was highly predictable, exhibiting nearly perfect nestedness, suggesting that selective colonisation and extinction processes predominated. The degree of nestedness was much higher than in the adjacent riparian forest or in regulated floodplains in Central Europe. Results clearly emphasise that amphibians can exploit the entire hydrodynamic gradient, except the main channel. In the active floodplain, vegetated islands and large woody debris are important, directly and indirectly, in maintaining both habitat and amphibian diversity and density in this gravel-bed river.

#### 4. Recherches en Amérique du Nord

**4.1. Reversing introduced species effects: Experimental removal of introduced fish leads to rapid recovery of a declining frog. Vre-denburgh VT 2004. PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE U.S.A. 101:7646-7650.**

*Résultats importants:* Des Salmonidés introduits dans des lacs de montagne ont été retirés de certains de ces lacs et laissés dans d'autres (lacs de contrôle). Les populations de grenouilles *Rana muscosa* ont très vite réagi en s'accroissant rapidement, à l'inverse des populations des lacs de contrôle qui restèrent petites. Cela montre deux choses: 1) La taille de la population d'amphibiens dépend de celle des prédateurs et 2) les effets de l'introduction des poissons sont réversibles.

*Abstract:* Amphibian population declines and extinctions are occurring even in the world's least impacted areas. The introduction and spread of nonnative predators is one of many proposed causes of amphibian declines. Correlational studies have shown a negative relationship between introduced fishes and declining amphibians, but little direct experimental evidence is available. This study experimentally manipulated the presence and absence of widely introduced salmonids rainbow trout (*Oncorhynchus mykiss*) and brook trout (*Salvelinus fontinalis*) to test the hypothesis that their introduction has contributed to the decline of the mountain yellow-legged frog (*Rana muscosa*). From 1996 to 2003, the introduced trout were removed from 5 lakes in a remote protected area of the Sierra Nevada, and 16 nearby lakes were used as controls, 8 with introduced trout and 8 without. To determine the vulnerable life stage, rainbow trout were placed in cages in three lakes containing amphibians. Removal of introduced trout resulted in rapid recovery of frog populations, and, in the caging experiment, tadpoles were found to be vulnerable to trout predation. Together, these experiments illustrate that introduced trout are effective predators on *R. muscosa* tadpoles and suggest (i) that the introduction of trout is the most likely mechanism responsible for the decline of this mountain frog and (ii) that these negative effects can be reversed.

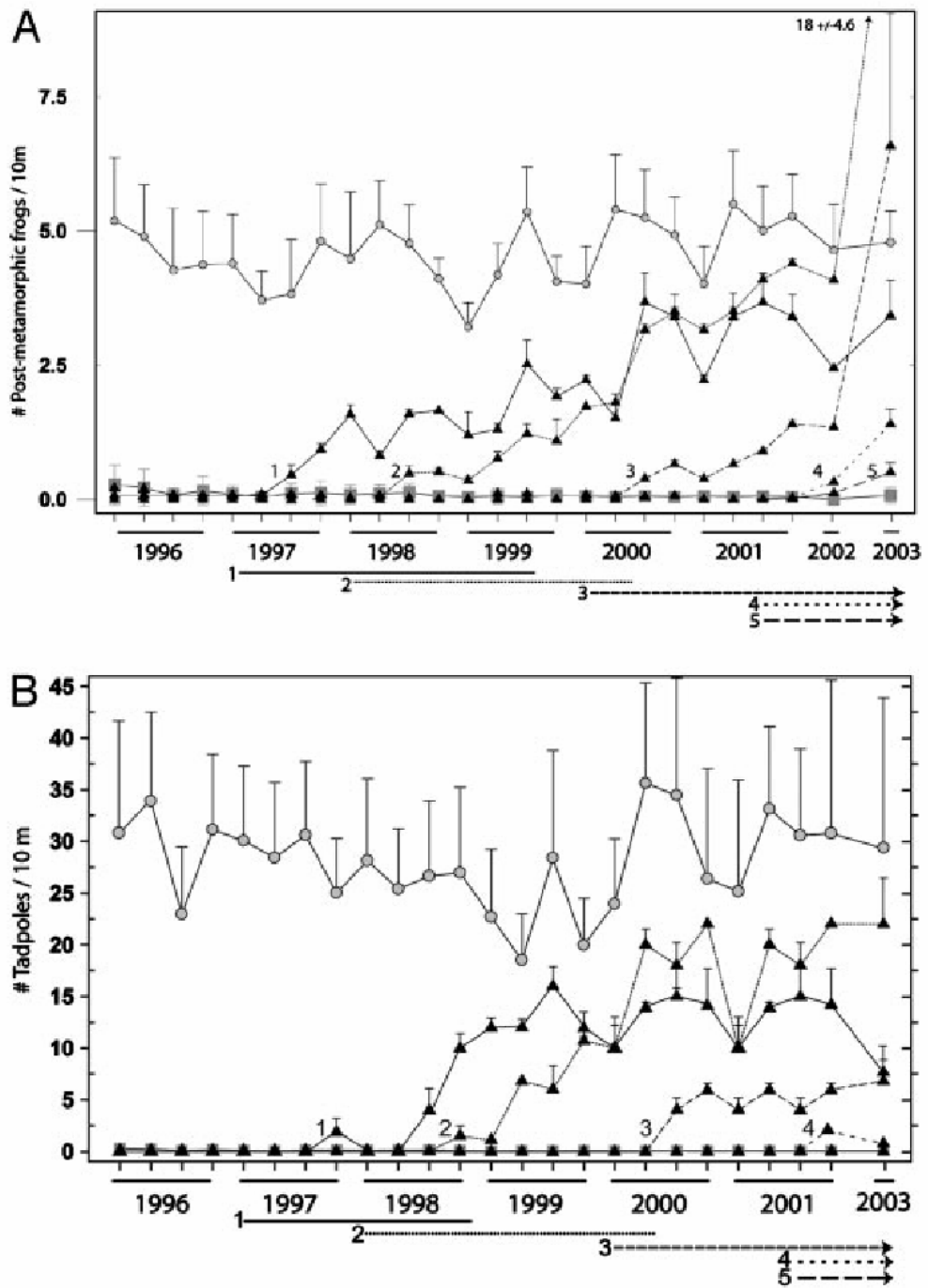


Fig. 3. Density (mean  $\pm$  SE) of postmetamorphic *R. muscosa* (A) and larval *R. muscosa* (B) in 21 lakes from 1996 to 2003. Filled triangles designate fish removal lakes ( $n = 5$ ); numbers correspond to lake numbers in Fig. 1. Shaded circles are fishless control lakes ( $n = 8$ ), and shaded squares are fish control lakes ( $n = 8$ ). Horizontal lines at the bottom of each figure indicate the trout removal period for each of the removal lakes, and numbers correspond to individual lake numbers. No tadpole counts were conducted in 2002.



**4.2. Responses of *Ambystoma gracile* to the removal of introduced nonnative fish from a mountain lake. Hoffman RL, Larson GL, Samora B 2004. JOURNAL OF HERPETOLOGY 38: 578-585.**

*Résultats importants:* Dans un lac de montagne, une population de salamandre s'est fortement accrue suite à l'éradication des Salmonidés. L'étude montre également un changement de comportement des Salamandres en présence des poissons.

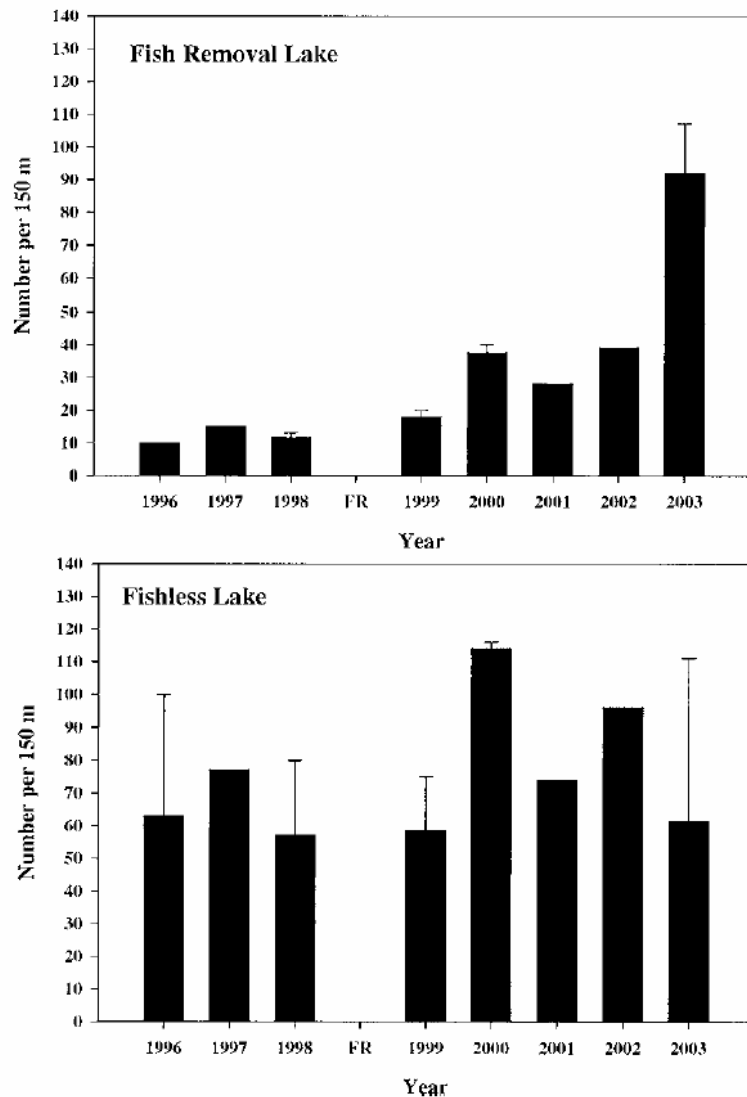


FIG. 1. Mean number of larvae/neotenes observed per year during day surveys in study lakes, 1996–2003. FR = Fish Removed and separates time intervals of fish presence in (1996–1998) and after all fish were removed from (1999–2003) the Fish Removal Lake. Error bars indicate standard error in years when two surveys were completed.

*Abstract:* Introduced, nonnative brook trout (*Salvelinus fontinalis*) were removed from a mountain lake in Mount Rainier National

Park, Washington, to examine the capacity of native *Ambystoma gracile* (Northwestern Salamander) in the lake to respond to the intentional removal of fish. Temporal trends ( $\Delta N$ ) were calculated for *A. gracile* larvae/neotene and egg mass relative abundances in the Fish Removal and an adjacent Fishless Lake. The diel and spatial patterns of *A. gracile* in the lakes were also enumerated during time-intervals of fish presence in and after fish removal from the Fish Removal Lake. Sixty-six fish were removed from the Fish Removal Lake. The  $\Delta N$ s for relative abundances in the Fish Removal Lake were positive for the study period and indicated that the number of larvae/neotenes and egg masses observed in the lake increased concurrent with the removal and extirpation of fish from the lake. Numbers of larvae/neotenes and egg masses observed in the Fishless Lake varied annually, but no overall positive or negative trends were evident during the study. *Ambystoma gracile* in the Fish Removal Lake, during fish presence, were predominantly nocturnal and located in the shallow, structurally complex near-shore area of the lake. After fish were removed, the number of *A. gracile* observed in the lake increased, especially during the day and in the deeper, less structurally complex offshore area of the lake. Fishless Lake *A. gracile* were readily observed day and night in all areas of the lake throughout the study. The *A. gracile* in the Fish Removal Lake behaviorally adapted to the presence of introduced fish and were able to recover from the affects of the fish following fish removal. This study underscores the important relationship between species life history and the variability of responses of montane aquatic-breeding amphibians to fish introductions in mountain lakes.

**4.3. Direct and indirect effects of predators on two anuran species along an environmental gradient. Werner EE, McPeck MA. 1994. ECOLOGY 75:1368-1382.**

*Résultats importants:* Dans un plan d'eau, les prédateurs (poissons et invertébrés) déterminent quels amphibiens peuvent se maintenir. Seules les espèces munies de glandes venimeuses cutanées peuvent coexister avec les poissons.

*Abstract:* This study examines direct and indirect interactions that influence the distribution of larvae of the bullfrog (*Rana catesbeiana*) and green frog (*R. clamitans*) along the environmental gradient of permanent to temporary ponds. The bullfrog is found in permanent ponds that typically contain fish, whereas the green frog is widely distributed along the gradient and is most successful in ponds where the bullfrog is absent. In a set of experimental ponds, bullfrogs were most abundant in ponds containing fish (bluegill, *Lepomis macrochirus*) and were rare in permanent ponds that lacked fish. In contrast, green frogs were most abundant in ponds that had been drained the previous fall, second most abundant in those that lacked fish, and sparse in ponds containing bluegill. When presence and absence of bluegill were experimentally manipulated in divided ponds, bullfrogs survived well in the presence of bluegill, whereas no individuals survived in the absence of bluegill. Green frogs survived in low numbers under both treatments with a tendency to better survivorship in the absence of bluegill. A series of laboratory choice experiments was conducted with three major predator types: the dragonfly larva *Anax junius*, the salamander *Ambystoma tigrinum*, and *L. macrochirus*.

Bullfrog larvae were more vulnerable to *Anax* and *Ambystoma* than were green frogs (because of higher activity levels), and green frogs were more vulnerable to bluegill than were bullfrogs (because tadpoles were less noxious). We argue that the high densities of bullfrogs found in the presence of bluegill reflect an indirect facilitation through two pathways: bluegill had strong negative effects on invertebrate and salamander predators of bullfrogs and on the green frog, which is a bullfrog competitor. The direct and indirect effects of these suites of predators appear to explain the differences in species abundances along the environmental gradient. Finally, we discuss the trade-offs at the individual level contributing to these differences in species performance along the gradient.

**4.4. Population decline of northern dusky salamanders at Acadia National Park, Maine, USA. Bank MS, Crocker JB, Davis S, Brotherton DK, Cook R, Behler J, Connery B 2006. BIOLOGICAL CONSERVATION 130:230-238.**

*Résultats importants:* L'introduction de poissons est l'une des causes de l'effondrement des effectifs d'une salamandre dans un parc national.

*Abstract:* We investigated and reviewed the current and historic distribution of northern dusky salamanders (*Desmognathus fuscus fuscus*) in Acadia National Park (ANP), Maine, USA during 1938-2003. Historical data indicate that northern dusky salamanders were once widespread and common in ANP. We conducted intensive surveys for stream salamanders during 2000-2003 and observed only two adult northern dusky salamanders on one stream. No eggs or larvae were observed. Although the cause of the observed population decline is unknown, we identify multiple potential stressors including stocking of predatory fishes, fungal pathogens, substrate embeddedness, and widespread pollution (i.e., from atmospheric pollutants) of surface waters at ANP. Our data suggest that ANP streams may no longer be suitable for northern dusky salamanders. This investigation is the first to document the decline of a stream dwelling amphibian species in a national park (i.e., areas that are not subject to obvious habitat loss or major changes in land use) with widespread mercury contamination of its surface waters.

**4.5. Resistance and resilience of alpine lake fauna to fish introductions. Knapp RA, Matthews KR, Sarnelle O 2001. ECOLOGICAL MONOGRAPHS 71:401-421.**

*Résultats importants:* La composition de la faune des lacs de montagne est fortement modifiée par l'introduction de poissons. Si les poissons disparaissent, la faune originale pourra à nouveau s'installer pour autant qu'elle soit présente dans les environs et qu'elle ait la possibilité de recoloniser le site.

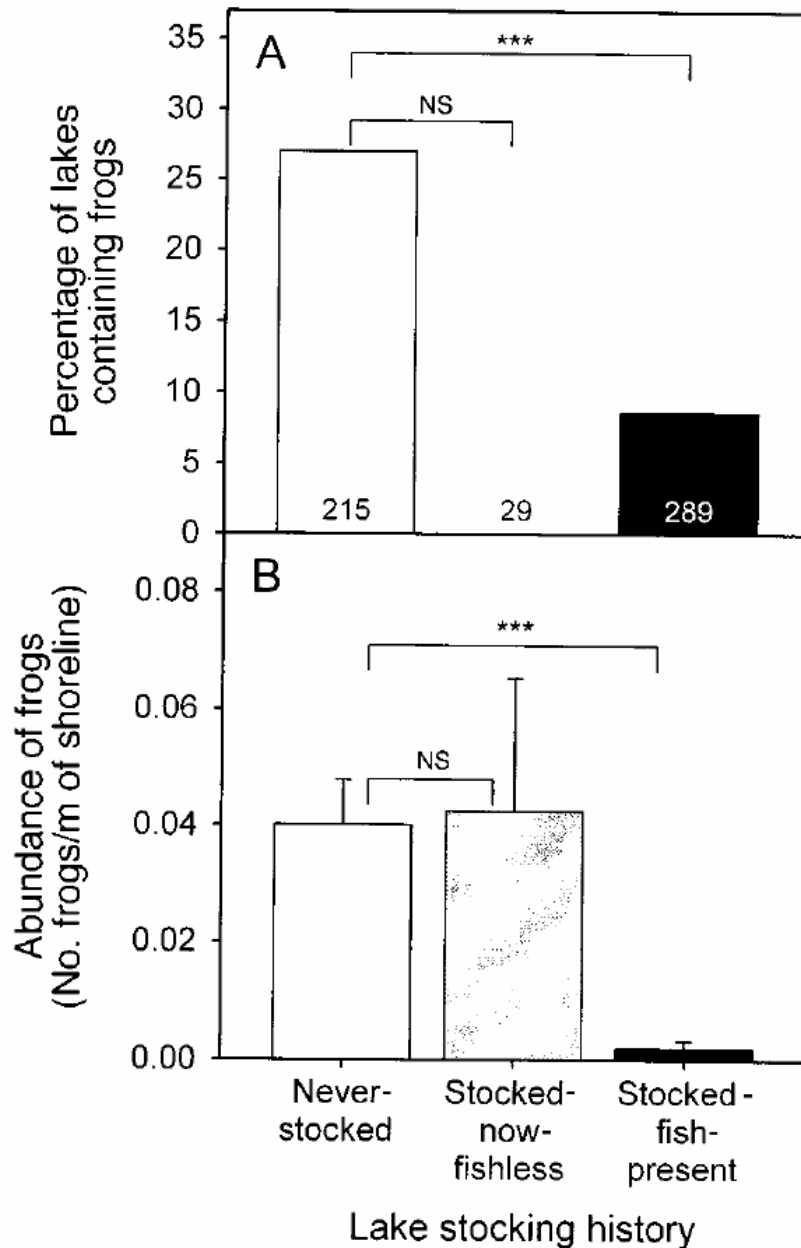


FIG. 2. (A) Percentage of never-stocked lakes (open bars), stocked-now-fishless lakes (gray bars), and stocked-fish-present lakes (black bars) containing mountain yellow-legged frog larvae. (B) The abundance of mountain yellow-legged frog larvae in never-stocked, stocked-now-fishless, and stocked-fish-present lakes. Abundance was measured as the number of larvae/m of shoreline and is expressed as  $\log_{10}(\text{abundance} + 1)$ . Bars indicate means + 1 SE. Sample sizes for each lake type are given inside the respective bar in (A). Lines and associated symbols connecting each bar provide the results of pairwise chi-square tests: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; NS, not significant ( $P > 0.05$ ).

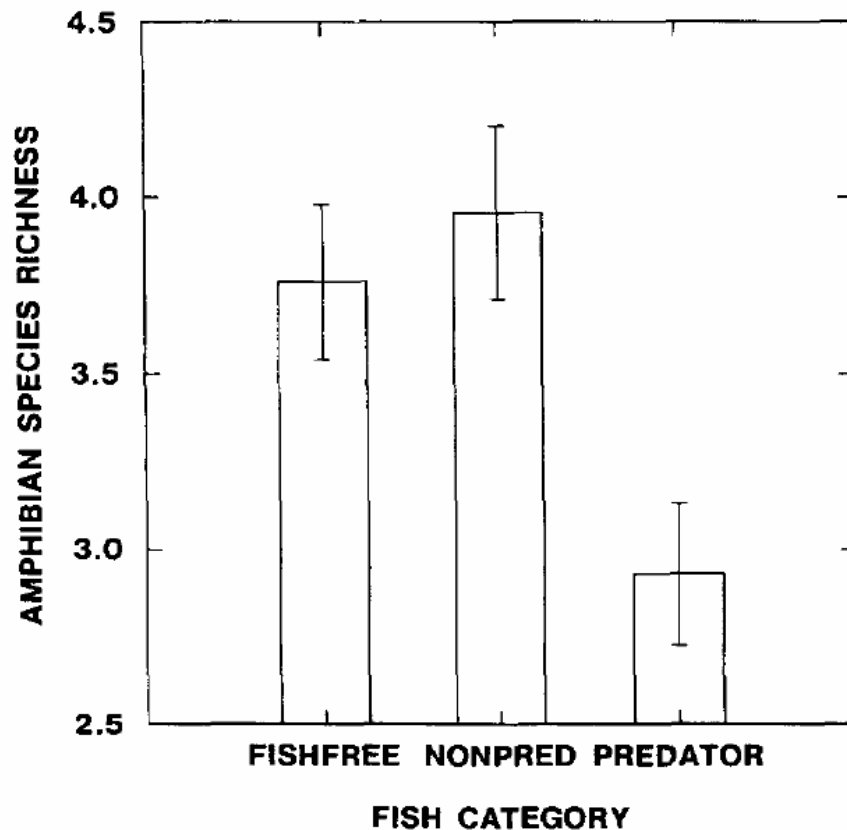
*Abstract:* This paper reports on the response by amphibians, benthic macroinvertebrates, and zooplankton in naturally fishless alpine lakes to fish introductions and subsequent fish disappearance. We assessed resistance (the degree to which a system is altered when the environment changes) by comparing faunal distribution and abundance in lakes that have never been stocked with fish vs. the distribution and abundance in lakes that have been stocked and still contain fish. We assessed resilience (the degree and rate of a system's return to its previous configuration once the perturbation is removed) by comparing faunal distribution and abundance in lakes that were stocked at one time but have since reverted to a fishless condition (stocked-now-fishless lakes) vs. the distribution and abundance in lakes that have never been stocked. We quantified recovery rates and trajectories by comparing faunal assemblages of stocked-now-fishless lakes that had been fishless for 5-10, 11-20, and >20 yr.

Faunal assemblages in the study lakes had low resistance to fish introductions, but in general showed high resilience. The mountain yellow-legged frog (*Rana muscosa*), conspicuous benthic macro invertebrates, and large crustacean zooplankton (>1 mm) were dramatically reduced in distribution and abundance by fish introductions but generally recovered to predisturbance levels after fish disappearance. Inconspicuous benthic invertebrate taxa, small crustacean zooplankton (<1 mm), and rotiferan zooplankton (<0.2 mm) were either unaffected by fish or increased in the presence of fish. For both the benthic macroinvertebrate community and the zooplankton community as a whole, fish disappearance was followed by a steady change away from the configuration characteristic of fish-containing lakes and toward that of lakes that had never been stocked. Both communities remained markedly different from those in never-stocked lakes 5-10 yr after fish disappearance and converged on the configuration of never-stocked lakes only 11-20 yr after fish disappearance.

Recovery was likely facilitated by the winged adult stages of many benthic macroinvertebrates, resting eggs of zooplankton, and nearby source populations of frogs. However, many frog populations have disappeared since the time that lakes in this study reverted to a fishless condition, and the viability of zooplankton egg banks should decline in fish-containing lakes over time. As a result, faunal resilience may be lower in lakes that revert to a fishless condition today than is suggested by the results of our study. These findings have important implications for the restoration of alpine lake ecosystems.

**4.6. The effects of predatory fish on amphibian species richness and distribution. Hecnar SJ, M'Closkey RT 1997. BIOLOGICAL CONSERVATION 79:123-131.**

*Résultats importants:* Le nombre d'espèces d'amphibiens est inférieur dans les plans occupés par des poissons prédateurs que dans les plans d'eau sans poissons ou avec des poissons non prédateurs.



**Fig. 1.** Amphibian species richness at ponds (mean  $\pm$  1 SE) among fish categories in southwestern Ontario.

*Abstract:* Amphibian communities at 178 ponds across southwestern Ontario, Canada, were studied to determine if presence of predatory fish was related to altered amphibian species richness or distribution on a geographic scale. Ponds are an important amphibian habitat in the study area and many have been stocked with fish. Surveys conducted over three years were used to construct amphibian species lists for individual ponds. Species richness and presence/absence were compared among ponds classified by the type of fish present. Amphibian species richness was significantly lower at ponds having predatory fish present than at non-predatory, or fish-free, ponds. Not all amphibian species were negatively affected by the presence of predatory fish. Those having either large bodies or clutch size co-occurred with predatory fish more frequently than those with small bodies or clutch size. Introduction of predatory fish by humans has likely resulted in altered amphibian species assemblages and reduced community diversity on a geographic scale.

**4.7. Sub-alpine amphibian distributions related to species palatability to non-native salmonids in the Klamath mountains of northern California.** Welsh HH, Pope KL, Boiano D 2006. *DIVERSITY AND DISTRIBUTIONS* 12:298-309.

*Résultats importants:* Le but de cette étude portant sur 728 plans d'eau alpins était d'évaluer l'impact de l'introduction de

poissons non autochtones sur les amphibiens. Les amphibiens ont été séparés en deux groupes: ceux qui ne sont pas comestibles en raison de leur venin cutané et ceux qui sont mangés par les poissons. Les amphibiens à la peau toxique coexistent souvent avec les poissons, à l'inverse des autres espèces, rarement observées en présence des poissons.

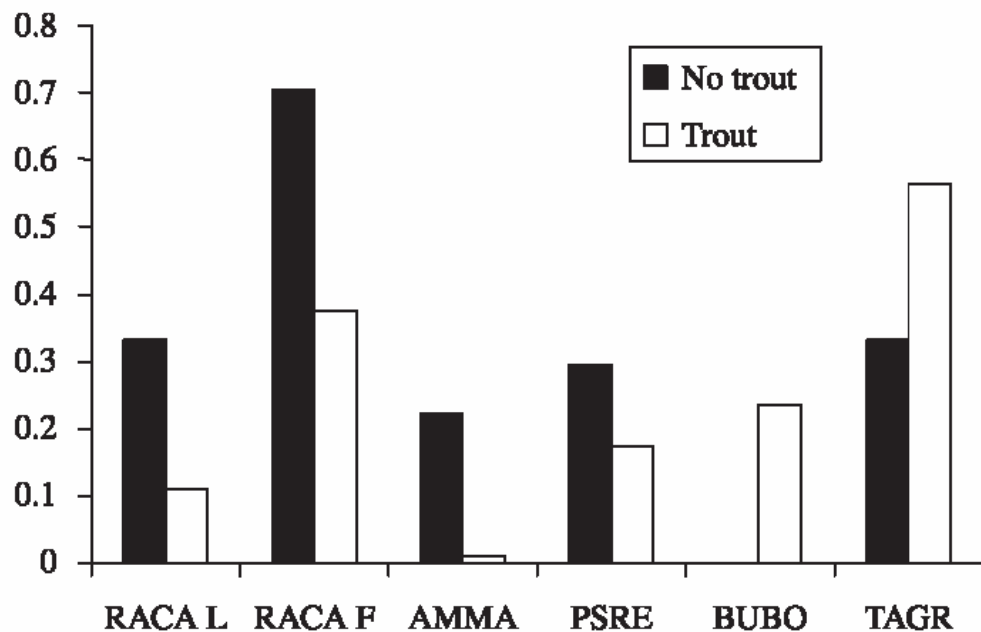


Figure 2 Proportion of water bodies greater than 2 m deep with amphibian species occupancy. Water bodies are categorized by whether trout were absent ( $N = 27$ ) or present ( $N = 191$ ). RACA L is *Rana cascadae* larvae, RACA F is post-metamorphic *R. cascadae* (adults and sub-adults), AMMA is *Ambystoma macrodactylum*, PSRE is *Pseudacris regilla*, BUBO is *Bufo boreas*, and TAGR is *Taricha granulosa*.

**Abstract:** The goal of this study was to examine how introduced trout influence the distributions and abundances of a sub-alpine amphibian assemblage whose members display a variety of different life-history and defence strategies. Our study was conducted in the sub-alpine lentic habitats of three wilderness areas that form the core of the Klamath-Siskiyou Bioregion of northern California, a biodiversity 'hotspot' that supports the highest diversity of sub-alpine, lentic-breeding amphibians in the western USA. These wilderness areas contain no native fishes, but all have been populated with non-native trout for recreational fishing. Five of the eight amphibian species that occur in this region were sufficiently common to use in our study; these included one that breeds in both temporary and permanent waters and is palatable to fish (Pacific treefrog, *Pseudacris regilla*), two that breed primarily in permanent waters and are unpalatable to fish (western toad, *Bufo*

*boreas*, and rough-skinned newt, *Taricha granulosa*), and two that breed primarily in permanent waters and are palatable to fish (Cascades frog, *Rana cascadae*, and long-toed salamander, *Ambystoma macrodactylum*). Based on life histories and predator defence strategies (i.e. palatable or not), we predicted that the three palatable species would likely be negatively correlated with introduced trout, but with *P. regilla* less impacted because of its use of both temporary and permanent waters. We predicted that *B. boreas* and *T. granulosa* would not be significantly correlated with introduced trout due to the lack of any predator/prey interactions between them. We surveyed 728 pond, lake, or wet meadow sites during the summers of 1999-2002, using timed gill-net sets to measure trout occurrence and relative density, and visual encounter surveys to determine amphibian presence and abundance. We used semiparametric logistic regression models to quantify the effect of trout presence/absence and density on the probability of finding amphibian species in a water body while accounting for variation within and among the various lentic habitats sampled. The distributions of *P. regilla*, *A. macrodactylum* and *R. cascadae* were strongly negatively correlated with trout presence across all three wilderness areas. *Ambystoma macrodactylum* was 44 times more likely to be found in lakes without fish than in lakes with fish. *Rana cascadae* and *P. regilla* were 3.7 and 3.0 times more likely, respectively, to be found in fishless than fish-containing waters. In contrast, the two unpalatable species were either uncorrelated (*T. granulosa*) or positively correlated (*B. boreas*) with fish presence. We found that the relative density of fish (catch per unit effort) was negatively correlated with the combined abundances of the three palatable amphibians, and also with both the length and the condition of the fish themselves. Our results are consistent with a compelling body of evidence that introduced fishes greatly alter the aquatic community structure of mountain lakes, ponds, and wet meadows.

**4.8. Wetland restoration for amphibians: Should local sites be designed to support metapopulations or patchy populations? Petranka JW, Holbrook CT 2006. RESTORATION ECOLOGY 14:404-411.**

*Résultats importants:* Plusieurs espèces d'amphibiens évitent les plans d'eau habités par des poissons. Dès qu'un plan d'eau est colonisé par des poissons, toute la population d'amphibiens peut gagner un autre site de reproduction dépourvu de poissons.

*Abstract:* Pond-breeding amphibians have been characterized as having metapopulation structure, and a goal of many local restoration projects is to establish viable metapopulations. However, recent studies suggest that metapopulation organization is unlikely at the local level because of high dispersal rates between neighboring ponds. Although many amphibians avoid ovipositing in habitats that pose high predation risk to their offspring, the spatial scale of avoidance is poorly resolved for natural systems and could involve wholesale movements between ponds. To determine the scale of avoidance, we monitored annual habitat use by the Wood frog (*Rana sylvatica*), American toad (*Bufo americanus*), and Spotted salamander (*Ambystoma maculatum*) at a restoration site in western North Carolina, U.S.A. Wood frogs consistently used most fish-free ponds, but rapidly curtailed use following fish invasions. American toads rarely used the same



breeding site from year to year, and adults strongly avoided ovipositing in habitats with predatory Wood frog tadpoles. Spotted salamanders exhibited a predator avoidance response to fish that was weaker than the predator avoidance response of anurans. Our data indicate that the spatial scale of predator avoidance by ovipositing amphibians often exceeds that of an individual pond and that the focal species at this site are organized as patchy populations rather than as metapopulations. At local restoration sites, ponds that are placed in spatial arrays to create metapopulations may not accomplish their goal and may limit the extent to which ovipositing adults can express an adaptive antipredator behavior. We discuss an alternative design that is more likely to enhance the long-term persistence of local populations.

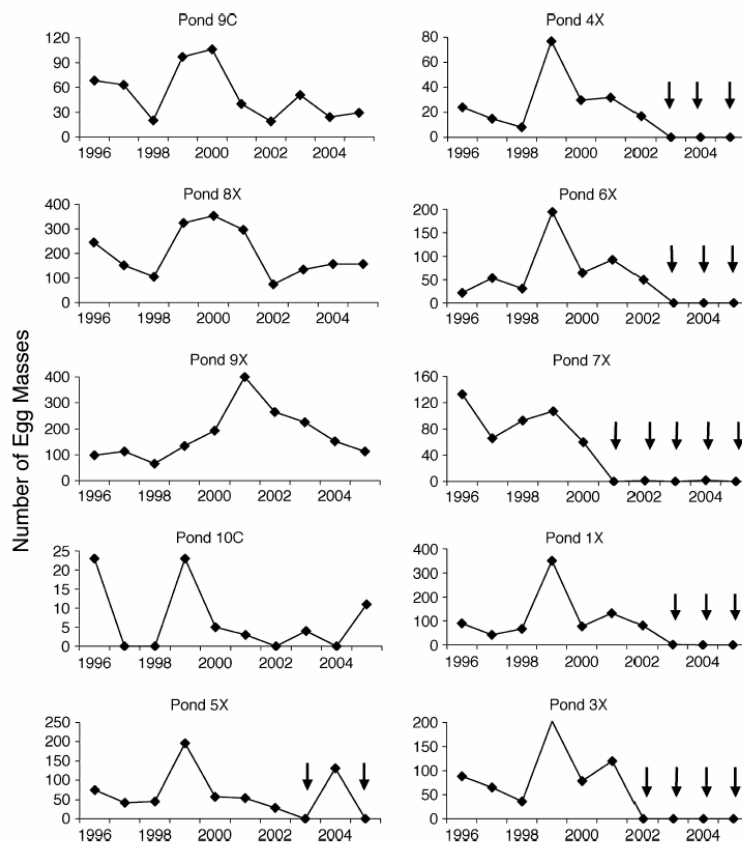


Figure 1. Number of egg masses deposited annually by *Rana sylvatica* in study ponds. Data are shown for 10 ponds that were monitored from 1996 to 2005. Arrows indicate years when fish were present at the time of breeding.

**4.9. Effects of nonnative fish and habitat characteristics on lentic herpetofauna in Yosemite National Park, USA. Knapp RA 2005. BIOLOGICAL CONSERVATION 121:265-279.**

*Résultats importants:* Cette étude porte sur plus de 2600 plans d'eau. Elle montre que les amphibiens occupent avant tout les plans d'eau dépourvus de Salmonidés non autochtones dans la station et introduits (à l'exception des espèces d'amphibiens toxiques pour les poissons). La répartition des serpents semi-aquatiques est quant à elle corrélée avec celle des amphibiens: si les amphibiens sont absents en raison de la présence de poissons introduits, les serpents sont également absents.

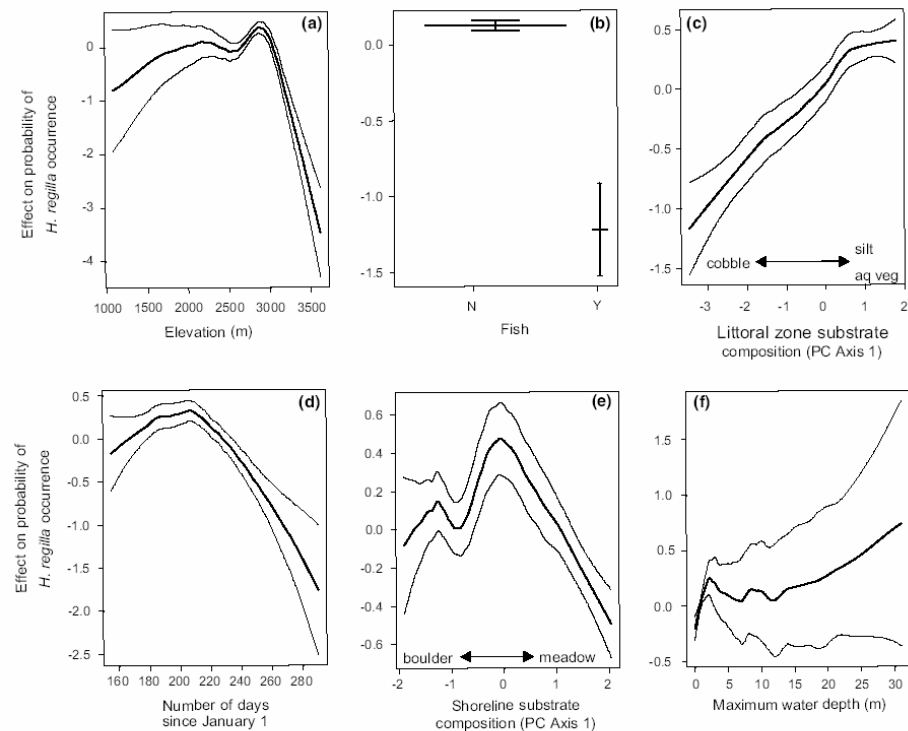


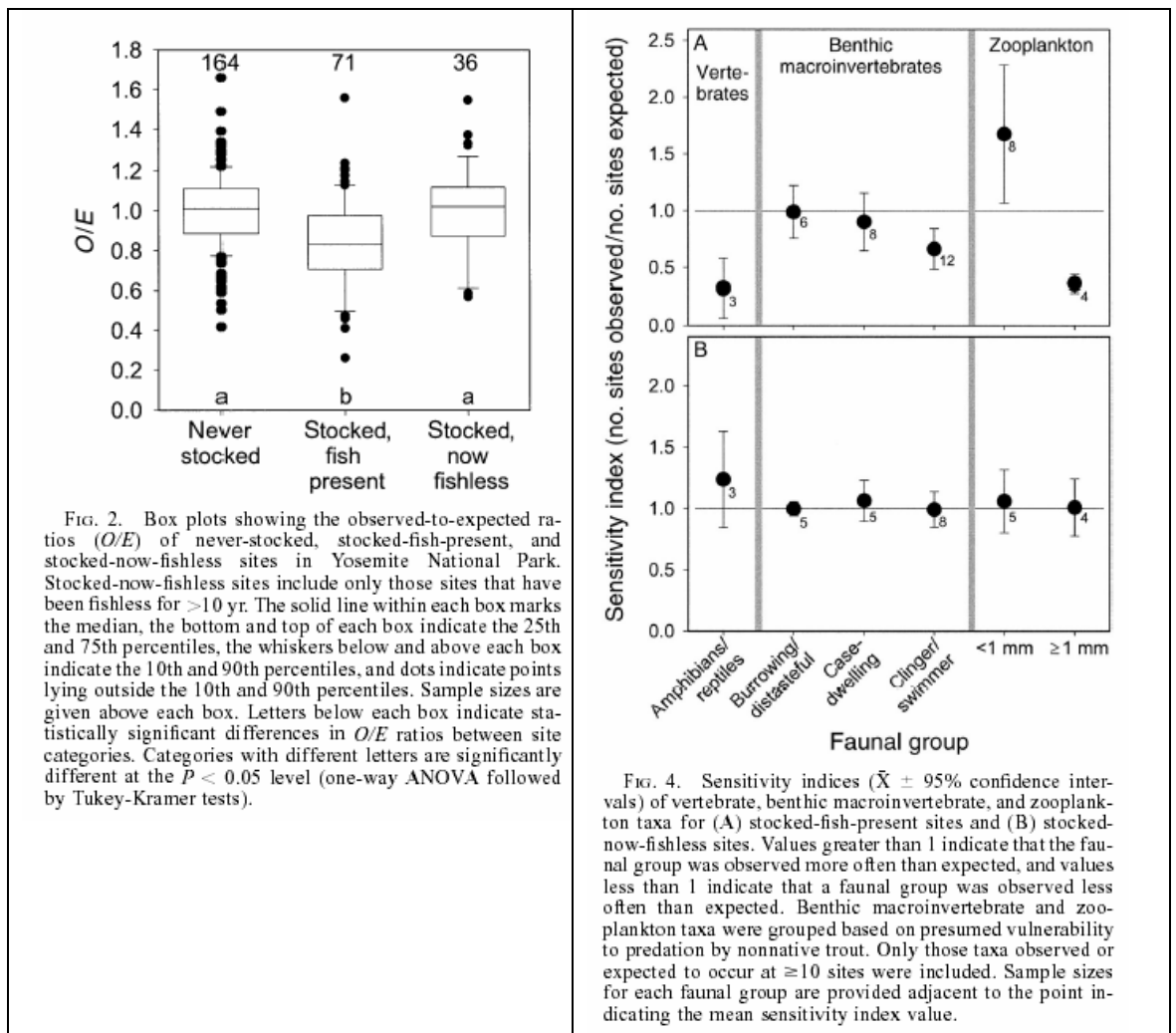
Fig. 4. Estimated effect of each of the highly significant ( $P \leq 0.01$ ) predictor variables (including approximate 95% confidence intervals) on the probability of occurrence by *Hyla regilla*, as determined from the generalized additive model (span = 0.5). Variables are (a) elevation, (b) presence/absence of nonnative trout, (c) littoral zone substrate composition, (d) the number of days since January 1, (e) shoreline substrate composition, and (f) maximum water depth. Variables are displayed in order of decreasing importance.

**Abstract:** Nonnative fishes have been introduced into naturally fishless mountain lakes worldwide, often with negative consequences for native fauna. In this study, I used data collected during a census of native herpetofauna, normative trout, and habitat characteristics at all lentic water bodies in Yosemite National Park ( $n = 2655$ ) to quantify the effect of trout introductions and habitat on the distribution of four amphibian species and two reptile species. Impacts of trout on amphibians and reptiles were characterized using generalized additive models that included as predictor variables fish presence/absence, amphibian presence/absence (only in models for the two reptile species), elevation, water depth, littoral zone and shoreline substrate composition, relative survey date, and location. All species showed significant associations with habitat characteristics, and elevation and water depth appeared particularly important in influencing distributions. In addition, distributions of the mountain yellow-legged frog (*Rana muscosa*) and Pacific treefrog (*Hyla regilla*) were strongly negatively associated with the presence of nonnative trout while those of the Yosemite toad (*Bufo canorus*) and Sierra newt (*Taricha torosa sierrae*) were unrelated to trout presence. The distribution of the mountain garter snake (*Thamnophis elegans elegans*) was strongly negatively associated with the presence of normative trout and positively associated with the presence of native amphibians. Regression results for the Sierra garter snake (*Thamnophis couchi couchi*) were similar except that the direct effect of nonnative trout was considerably weaker. Together, these results indicate that trout introductions have re-

sulted in considerable alteration of Yosemite's herpetofauna. Long-term studies will be necessary to determine whether removal of normative trout populations, where possible, would allow these impacts to be partially reversed.

**4.10. Fauna of Yosemite National Park lakes has low resistance but high resilience to fish introductions. Knapp RA, Hawkins CP, Ladau J, McClory JG 2005. ECOLOGICAL APPLICATIONS 15:835-847.**

*Résultats importants:* La faune des plans d'eau naturellement dépourvus de poissons est sensible à l'empoisonnement. Les amphibiens réagissent très fortement. Si on enlève les poissons, la faune originelle se rétablit rapidement.



**Abstract:** The ratio of the number of taxa observed at a site to that expected to occur in the absence of anthropogenic impacts (O/E) is an ecologically meaningful measure of the degree of faunal alteration. We used O/E ratios to describe the response by amphibian, reptile, benthic macroinvertebrate, and zooplankton taxa in originally fishless lakes in Yosemite National Park to the introduction and subsequent disappearance of nonnative fish. To quantify resistance (the degree to which a system is altered when

the environment changes) and resilience (the degree to which a system returns to its previous configuration once the perturbation is removed), we compared O/E ratios between lakes that were never stocked, were previously stocked and still contained fish, or were previously stocked but had reverted to a fishless condition. On average, stocked- fish-present sites had 16% fewer taxa than never-stocked sites (O/E = 0.84 vs. 1.00, respectively). This statistically significant difference in O/E ratios indicates that native fauna had relatively low resistance to fish introductions. Resistance was inversely related to fish density and elevation, and directly related to water depth. Vulnerability to impacts of trout predation differed markedly between faunal groups, being high for amphibians, reptiles, conspicuous benthic invertebrates, and zooplankton and low for inconspicuous benthic invertebrates. O/E ratios in stocked-now-fishless sites were significantly higher (1.00) than those in stocked-fish-present sites and were not significantly different from those in never-stocked sites, indicating that this fauna had high resilience. For stocked-now-fishless sites, the relationship between the O/E ratio and the number of years since fish disappearance indicated that taxonomic composition recovered to closely resemble that of never-stocked lakes in less than two years following fish disappearance. Collectively, these result's indicate that despite strong effects of an introduced predatory fish on community structure, these systems recover quickly and predictably following fish removal.

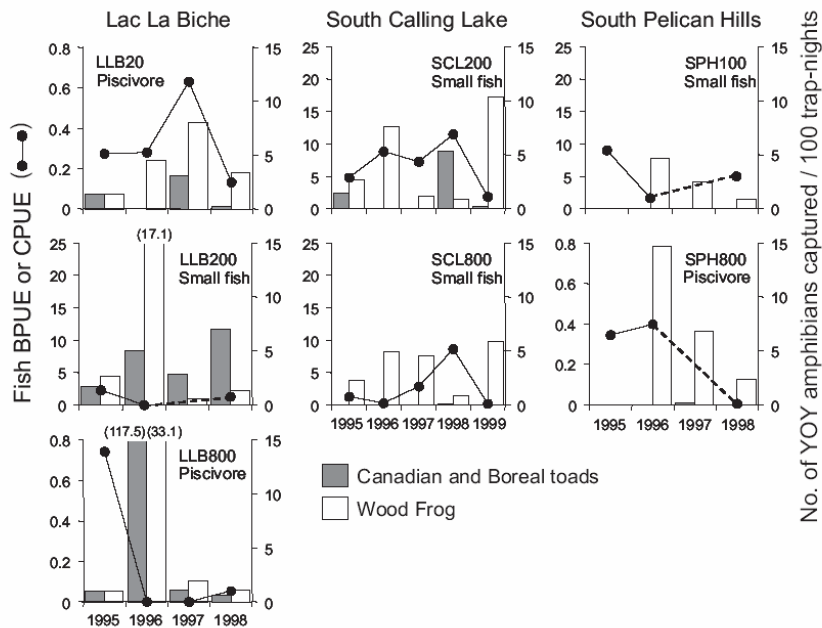
**4.11. Indirect effects of fish winterkills on amphibian populations in boreal lakes. Eaton BR, Tonn WM, Paszkowski CA, Danylchuk AJ, Boss SM 2005. CANADIAN JOURNAL OF ZOOLOGY 83:1532-1539.**

*Résultats importants:* Si un hiver rigoureux tue les poissons dans les lacs canadiens, ces lacs produisent beaucoup plus de jeunes amphibiens que la normale les années suivantes.

*Abstract:* We exploited fish winterkills in small, boreal Alberta lakes to determine if anuran amphibians respond to large but natural changes in fish densities. Eight large declines in fish abundance occurred in seven lakes over a 5 year period, while major increases in fish abundance, reflecting recovery after winterkill, were recorded 5 times. Summer pitfall trapping of young-of-the-year (YOY) Wood Frogs (*Rana sylvatica* LeConte, 1825) and Boreal (*Bufo boreas boreas* Baird and Girard, 1852) and Canadian (*Bufo hemiophrys* Cope, 1886) toads indicated that frog abundance responded consistently to such large changes in fish abundance, but especially if fish communities were dominated by small-bodied species (sticklebacks and minnows). As well, changes in YOY Wood Frog and fish abundance were negatively correlated; YOY Wood Frogs were as much as 7.7 times more abundant after winterkills than in non-winterkill years. These increases in metamorphs did not result from an increased immigration of breeding adults to winterkill lakes, suggesting instead that larval survival was greater. Higher abundance of YOY Wood Frogs and toads was associated with smaller body size at metamorphosis. Despite this apparent reduction in individual growth, abundance of juvenile frogs remained significantly elevated 1 year after winterkill. In contrast to Wood Frogs, YOY toads tended to respond positively to recoveries of small-fish populations. Because anuran amphibians can respond to fish winterkill, and because winterkill is a frequent natural disturbance,

small fish-bearing lakes can serve as important breeding habitat for amphibians in Alberta's boreal forest.

Fig. 1. Abundance of fish and young-of-the-year (YOY) Wood Frog (*Rana sylvatica*) and toads (Boreal, *Bufo boreas boreas*, and Canadian, *Bufo hemiophrys*, toads combined) from the seven study lakes in three regions of boreal Alberta. Fish communities are classified as being dominated by larger, piscivorous species or by small species. Abundance estimates for fish are in biomass per unit effort (BPUE, kg-h<sup>-1</sup>; piscivores) or catch per unit effort (CPUE, number of fish captured-h<sup>-1</sup>; small fish); amphibian estimates are in CPUE (numbers / 100 trap-nights). Amphibians were not sampled at the SPH lakes in 1995; fish were not sampled in 1997 at LLB200 or the SPH lakes.



4.12. Pond permanence and the effects of exotic vertebrates on anurans. Adams MJ 2000. ECOLOGICAL APPLICATIONS 10:559-568.

Résultats importants: Des expériences menées dans des plans d'eau temporaires et permanents montrent que la survie des têtards est supérieure dans les plans d'eau temporaires. Les poissons réduisent à zéro la survie des têtards.

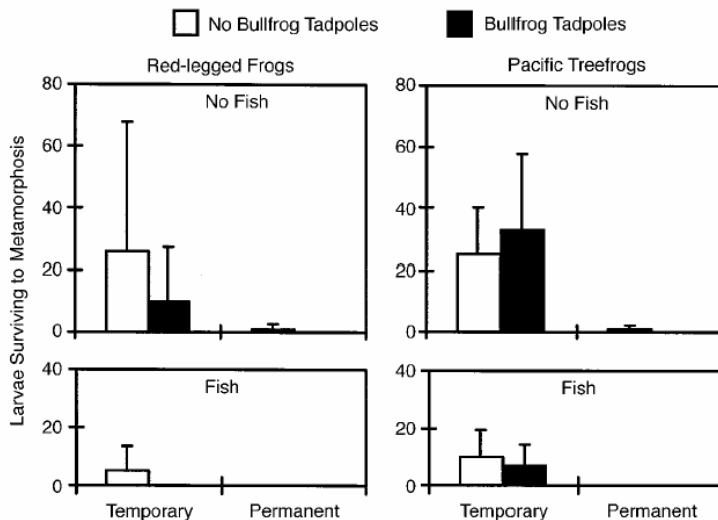
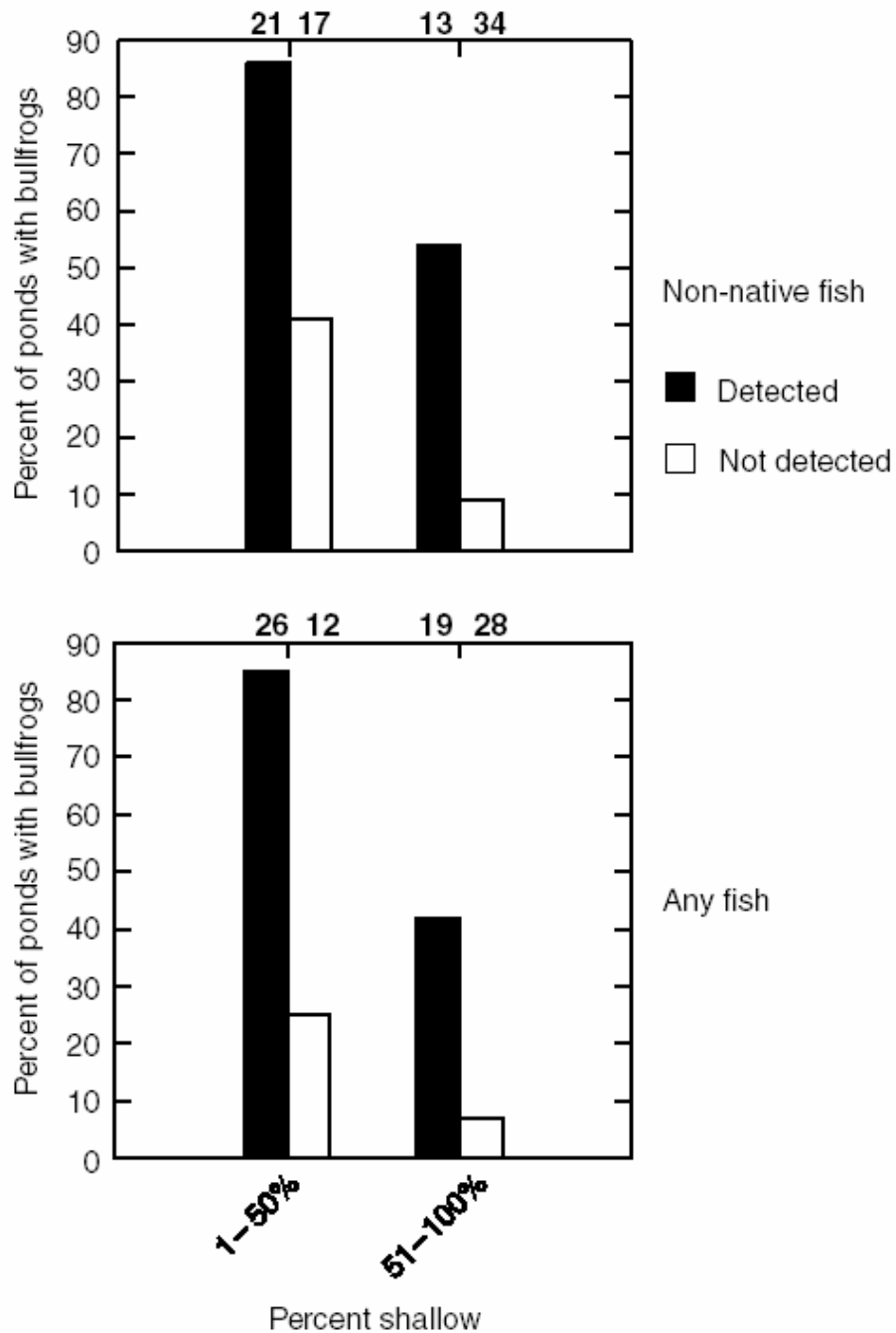


FIG. 2. Number of larvae surviving to metamorphosis (mean and 1 SD) at three permanent and three temporary ponds in Experiment 1.

**4.13. Indirect facilitation of an anuran invasion by non-native fishes. Adams MJ, Pearl CA, Bury RB 2003. ECOLOGY LETTERS 6:343-351.**

*Résultats importants:* Une espèce de grenouille invasive, capable de cohabiter avec les poissons en raison de sa toxicité, ne peut s'établir que dans les plans d'eau occupés par des espèces invasives de poissons.

*Abstract:* In many permanent ponds throughout western North America, the introduction of a variety of exotic fish and bullfrogs (*Rana catesbeiana*) correlates with declines in native amphibians. Direct effects of exotics are suspected to be responsible for the rarity of some native amphibians and are one hypothesis to explain the prevalence of amphibian declines in western North America. However, the prediction that the permanent ponds occupied by exotics would be suitable for native amphibians if exotics were absent has not been tested. I used a series of enclosure experiments to test whether survival of northern red-legged frog (*Rana aurora aurora*) and Pacific treefrog (*Hyla regilla*) larvae is equal in permanent and temporary ponds in the Puget Lowlands, Washington State, USA. I also examined the direct effects of bullfrog larvae and sunfish. Survival of both species of native anuran larvae was generally lower in permanent ponds. Only one permanent pond out of six was an exception to this pattern and exhibited increased larval survival rates in the absence of direct effects by exotics. The presence of fish in enclosures reduced survival to near zero for both native species. An effect of bullfrog larvae on Pacific treefrog larval survival was not detected, but effects on red-legged frog larvae were mixed. A hypothesis that food limitation is responsible for the low survival of native larvae in some permanent ponds was not supported. My results confirm that direct negative effects of exotic vertebrates on native anurans occur but suggest that they may not be important to broad distribution patterns. Instead, habitat gradients or indirect effects of exotics appear to play major roles. I found support for the role of permanence as a structuring agent for pond communities in the Puget Lowlands, but neither permanence nor exotic vertebrates fully explained the observed variability in larval anuran survival.



**Figure 1** Comparison of pond occupancy by breeding populations of bullfrogs at 85 ponds in the Willamette Valley, OR, USA. The Y-axis is the percentage of ponds in the indicated category where we detected breeding populations of bullfrogs. Sample size is shown above each column.

**Abstract:** Positive interactions among non-native species could greatly exacerbate the problem of invasions, but are poorly studied and our knowledge of their occurrence is mostly limited to plant-pollinator and dispersal interactions. We found that invasion of bullfrogs is facilitated by the presence of co-evolved non-native fish, which increase tadpole survival by reducing predatory macroinvertebrate densities. Native dragonfly nymphs in Oregon, USA caused zero survival of bullfrog tadpoles in a replicated field experiment unless a non-native sunfish was present to reduce dragonfly density. This pattern was also evident in pond surveys where the best predictors of bullfrog abundance were the presence of non-native fish and bathymetry. This is the first experimental evidence of facilitation between two non-native vertebrates and supports the invasional meltdown hypothesis. Such positive interactions among non-native species have the potential to disrupt ecosystems by amplifying invasions, and our study shows they can occur via indirect mechanisms.

**4.14. Amphibian occurrence and aquatic invaders in a changing landscape: Implications for wetland mitigation in the Willamette Valley, Oregon, USA. Pearl CA, Adams MJ, Leuthold N, Bury RB 2005. WETLANDS 25:76-88.**

**Résultats importants:** Dans une vallée de l'Oregon, la répartition des espèces indigènes d'amphibiens est négativement corrélée avec celle des poissons non indigènes. Les poissons indigènes n'influencent guère la répartition des amphibiens.

**Abstract:** Despite concern about the conservation status of amphibians in western North America, few field studies have documented occurrence patterns of amphibians relative to potential stressors. We surveyed wetland fauna in Oregon's Willamette Valley and used an information theoretic approach (AIC) to rank the associations between native amphibian breeding occurrence and wetland characteristics, non-native aquatic predators, and landscape characteristics in a mixed urban-agricultural landscape. Best predictors varied among the five native amphibians and were generally consistent with life history differences. Pacific tree frog (*Pseudacris regilla*) and long-toed salamander (*Ambystoma macrodactylum*) occurrence was best predicted by the absence of non-native fish. Northern red-legged frog (*Rana a. aurora*) and northwestern salamander (*Ambystoma gracile*) were most strongly related to wetland vegetative characteristics. The occurrence of rough-skinned newts (*Taricha granulosa*), a migratory species that makes extensive use of terrestrial habitats, was best predicted by greater forest cover within 1 km. The absence of non-native fish was a strong predictor of occurrence for four of the five native species. In contrast, amphibians were not strongly related to native fish presence. We found little evidence supporting negative effects of the presence of breeding populations of bullfrog (*Rana catesbeiana*) on any native species. Only the two *Ambystoma* salamanders were associated with wetland permanence. Northwestern salamanders (which usually have a multi-year larval stage) were associated with permanent waters, while long-toed salamanders were associated with temporary wetlands. Although all the species make some use of upland habitats, only one (rough-skinned newt) was strongly associated with surrounding landscape conditions. Instead, our analysis suggests that within-wetland characteristics best predict



amphibian occurrence in this region. We recommend that wetland preservation and mitigation efforts concentrate on sites lacking non-native fish for the conservation of native amphibians in the Willamette Valley and other western lowlands.

**4.15. Development of expectations of larval amphibian assemblage structure in southeastern depression wetlands. Snodgrass JW, Bryan AL, Burger J 2000. ECOLOGICAL APPLICATIONS 10:1219-1229.**

*Résultats importants:* Ce travail catégorise les sites de reproduction d'amphibiens (plans d'eau) et met en évidence 4 types. La catégorisation se base principalement sur le régime de l'eau, à savoir si un plan d'eau s'assèche plus ou moins longtemps ou jamais. Un seul type de plan d'eau occupé par des amphibiens, quelques espèces spécialisées seulement, contient des poissons.

*Abstract:* We surveyed larval amphibians and fish in 25 relatively pristine depression wetlands on the upper Atlantic coastal plain of South Carolina to examine relationships among hydroperiod length, fish presence/absence and larval amphibian assemblage structure. Our goals were to test the application of general models of lentic community structure to Southeastern depression wetlands and to develop expectations of larval amphibian assemblage structure at reference sites. Amphibian species richness showed a unimodal pattern along a hydroperiod gradient, with wetlands that contained water for 8-10 mo/yr having the highest species richness. Wetlands that contained water for longer periods (i.e., dried only during severe drought) often contained fish and had relatively low amphibian species richness. Most species occurred along a restricted portion of the hydroperiod gradient, and some species were found almost exclusively in wetlands with fish. Associations among the occurrence of species led to relatively discrete breaks in assemblage structure along the hydroperiod gradient. Canonical correspondence analysis of catch-per-unit-effort data identified four groups of wetlands with similar assemblage structure: (1) short (drying in spring), (2) medium (drying in summer), and (3) long (drying in fall or semi-annually) hydroperiod wetlands without fish; and (4) long hydroperiod wetlands with fish. Our results suggest that general models of community structure in lentic systems are applicable to southeastern isolated wetlands and should form the basis for developing expectations of larval amphibian assemblage structure in these systems.

## 5. Recherches dans un domaine particulier

**5.1. Molecular evidence for historical and recent population size reductions of tiger salamanders (*Ambystoma tigrinum*) in Yellowstone National Park. Spear SF, Peterson CR, Matocq MD, Storfer A 2006. CONSERVATION GENETICS 7:605-611.**

*Résultats importants:* Chez les salamandres, l'introduction de poissons peut conduire à un goulet d'étranglement génétique (bottleneck).

*Abstract:* Population declines caused by natural and anthropogenic factors can quickly erode genetic diversity in natural populations. In this study, we examined genetic variation within 10

tiger salamander populations across northern Yellowstone National Park in Wyoming and Montana, USA using eight microsatellite loci. We tested for the genetic signature of population decline using heterozygosity excess, shifts in allele frequencies, and low ratios of allelic number to allelic size range (M-ratios). We found different results among the three tests. All 10 populations had low M-ratios, five had shifts in allele frequencies and only two had significant heterozygosity excesses. These results support theoretical expectations of different temporal signatures among bottleneck tests and suggest that both historical fish stocking, recent, sustained drought, and possibly an emerging amphibian disease have contributed to declines in effective population size.

**5.2. Transfer of a pathogen from fish to amphibians. Kiesecker JM, Blaustein AR, Miller CL 2001. CONSERVATION BIOLOGY 15:1064-1070.**

*Résultats importants:* L'introduction de poissons peut avoir comme conséquence la transmission d'agents pathogènes mortels pour les amphibiens. Les poissons sont des vecteurs de maladies fongiques.

*Abstract:* Ecological studies of exotic species focus primarily on hole invaders directly affect particular resident species. In contrast, little is known about the indirect effects of introduced species on native communities, including how pathogens may be spread by introduced species. We provide evidence suggesting that introduced fish may serve as a vector for a pathogenic oomycete, *Saprolegnia ferax*, that has been associated with embryonic mortality of amphibians in the Cascade Mountains of Oregon, U.S.A. In laboratory, experiments, mortality induced by *S. ferax* was greater in western toad (*Bufo boreas*) embryos exposed directly to hatchery-reared rainbow trout (*Oncorhynchus mykiss*) experimentally infected with *S. ferax* and hatchery-reared trout not experimentally infected than in control embryos. Embryos also developed significant *S. ferax* infections when raised on soil that was exposed to trout experimentally infected with *S. ferax*. Furthermore, toad embryos exposed to *S. ferax* isolated from sites where *Saprolegnia* outbreaks are common experienced higher mortality than embryos exposed to *S. ferax* isolated from sites where *Saprolegnia* outbreaks have not occurred. Given the widespread practice of introducing hatchery-reared fishes, we suggest that fish used in stocking programs could be an important vector for diseases responsible for amphibian losses.

**5.3. Molecular characterization of iridoviruses isolated from sympatric amphibians and fish. Mao JD, Green DE, Fellers G, Chinchar VG 1999. VIRUS RESEARCH 63:45-52.**

*Résultats importants:* Des virus présents chez les poissons peuvent infecter les amphibiens.

*Abstract:* Iridoviruses infect invertebrates (primarily insects and crustaceans) and ectothermic vertebrates (fish, amphibians, and reptiles). Identical, or nearly identical viruses, have been isolated from different animals within the same taxonomic class, indicating that infection by a given virus is not limited to a single species. Although inter-class infections have been documented following experimental infection with vertebrate iridoviruses, it is not clear whether such infections occur in nature.

Here we report the isolation of apparently identical iridoviruses from wild sympatric fish (the threespine stickleback, *Gasterosteus aculeatus*) and amphibians (the red-legged frog, *Rana aurora*). Viruses isolated from sticklebacks (stickleback virus, SBV) and from a red-legged frog tadpole (tadpole virus 2, TV2) replicated in fathead minnow (FHM) cells and synthesized proteins which co-migrated with those of frog virus 3 (FV3). Following restriction endonuclease digestion of viral DNA with *Hind* III and *Xba* I, gel analysis showed that the profiles of SBV and TV2 were identical to each other and distinct from FV3. Using oligonucleotide primers specific for a highly conserved region of the iridovirus major capsid protein, a 500 nucleotide DNA fragment was amplified from SBV and TV2. Sequence analysis showed that within this 500 nucleotide region SBV and TV2 were identical to each other and to FV3. Taken together these results provide the first evidence that iridoviruses naturally infect animals belonging to different taxonomic classes, and strengthen the suggestion that fish may serve as a reservoir for amphibian viruses or vice versa.

**5.4. Evidence for emergence of an amphibian iridoviral disease because of human-enhanced spread. Jancovich JK, Davidson EW, Parameswaran N, Mao J, Chinchar VG, Collins JP, Jacobs BL, Storfer A. 2005. MOLECULAR ECOLOGY 14:213-224.**

*Résultats importants:* Des analyses génétiques montrent qu'un nouveau virus infectant les amphibiens s'est largement répandu par le biais soit d'appâts pour les poissons (salamandres), soit de Salmonidés non indigènes introduits.

*Abstract:* Our understanding of origins and spread of emerging infectious diseases has increased dramatically because of recent applications of phylogenetic theory. Iridoviruses are emerging pathogens that cause global amphibian epizootics, including tiger salamander (*Ambystoma tigrinum*) die-offs throughout western North America. To explain phylogeographical relationships and potential causes for emergence of western North American salamander iridovirus strains, we sequenced major capsid protein and DNA methyltransferase genes, as well as two noncoding regions from 18 geographically widespread isolates. Phylogenetic analyses of sequence data from the capsid protein gene showed shallow genetic divergence (< 1%) among salamander iridovirus strains and monophyly relative to available fish, reptile, and other amphibian iridovirus strains from the genus *Ranavirus*, suggesting a single introduction and radiation. Analysis of capsid protein sequences also provided support for a closer relationship of tiger salamander virus strains to those isolated from sport fish (e.g. rainbow trout) than other amphibian isolates. Despite monophyly based on capsid protein sequences, there was low genetic divergence among all strains (< 1.1%) based on a supergene analysis of the capsid protein and the two noncoding regions. These analyses also showed polyphyly of strains from Arizona and Colorado, suggesting recent spread. Nested clade analyses indicated both range expansion and long-distance colonization in clades containing virus strains isolated from bait salamanders and the Indiana University axolotl (*Ambystoma mexicanum*) colony. Human enhancement of viral movement is a mechanism consistent with these results. These findings suggest North American salamander *Ranaviruses* cause emerging disease,

as evidenced by apparent recent spread over a broad geographical area.

Benedikt Schmidt, 16. Januar 2007