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EFFECT OF INTRODUCED FISH ON AMPHIBIAN ASSEMBLAGES IN MOUNTAIN LAKES OF NORTHERN SPAIN

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We have analyzed the effect of introduced fish on amphibian assemblages in mountain lakes of the Cantabrian range (Asturias and León; northern Spain), by comparing amphibian species richness, abundance and diversity in lakes occupied by introduced fish and in those without fish. Amphibian species numbers were significantly lower in lakes inhabited by fish, both considering the absolute mumber and the values corrected for the effect of the main correlates of the species richness (shore extent and altitude). Amphibian abundance (all species and stages pooled) and diversity also tended to be lower in lakes inhabited by fish as compared with the fishless ones. Direct predation by fish, for which we present evidence in our studied lakes, is likely to be the main cause for the reported amphibian depletion, although recognition by adult amphibians of chemical cues from predatory fish and subsequent avoidance of habitats with fish for reproduction could also be contributory.

INTRODUCTION

The herpetological literature of the past decade provides evidence that amphibian populations are undergoing a rapid decline. Changes in environmental factors such as ultraviolet radiation or pH of breeding sites, infectious outbreaks, severe droughts and pollution, among others, were implicated as possible factors in explaining the "amphibian decline" (Barinaga, 1990; Wake, 1991; Dunson, Wyman & Corbett, 1992; Crump, Hensley & Clark, 1992; Blaustein, 1994; Márquez, Olmo & Bosch, 1995). However, there is still an open question about whether the decline actually represents a particular phenomenon in amphibians or whether it follows the general biodiversity crisis related to anthropogenic causes (Pechmann, Scott, Semlitsch, Caldwell, Vitt & Gibbons, 1991; Beebee, 1992; Pechmann & Wilbur, 1994; Travis, 1994). Further, population sizes of some amphibians are known to fluctuate dramatically, so the evaluation of population changes was difficult in most cases because of the lack of long-term census data (Pechmann *et al*., 1991; Crump *et al*., 1992; Dunson *et al*., 1992; Travis, 1994). Despite a number of uncertain issues, the recent spread of studies on amphibian population dynamics and conservation has provided evidence that complex life cycles and especially the vulnerability of larval stages make amphibians very sensitive to environmental stress (Sadinski & Dunson, 1992; Blaustein, 1994), so their conservation requires increased effort in studying particular populations and identifying potential threats.

Predation by introduced fish and perhaps by other aquatic vertebrates (e.g. *Rana catesbeiana*, Hayes & Jennings, 1986) has been reported as a certain cause for reduction in local amphibian populations (Macan, 1966; Honegger, 1978; Bradford, 1989; Aronsson & Stenson, 1995), even leading to virtual extinction (Bradford, 1991). This effect can be particularly risky in the case of metapopulations comprising a number of local populations, each associated with isolated breeding ponds, as this situation makes the balance between local extinction and recolonization critical for amphibian population persistence (Bradford, 1991; Pechmann & Wilbur, 1994). Successful reproduction in large pools and lakes is likely to be a key factor, because they can provide the source stocks for recolonization (Pulliam, 1988; Travis, 1994), but such large permanent pools were frequently fish-stocked for commercial or recreational purposes, thus threatening amphibian populations on a wider scale. The purpose of this study was to elucidate whether fish introductions affected amphibian species richness and abundance in a chain of permanent mountain lakes lying within a 150 km west to east strip in the Cantabrian Mountains (northern Spain).

METHODS

We selected 16 large and permanent pools or lakes (listed in Table 1), ranging from 1070 to 1750 m in elevation, 200 to 1850 m in perimeter, and 2.0 to 50.3 m in maximum depth. The occurrence of fish was determined by visual observation of individual specimens or signals, such as waves of surface feeding. Electrofishing from the lake shore and immediately adjacent reaches of tributaries (for lakes 1, 2, 7, 8, 9, as numbered in Table 1), catches with gillnets (7, 8, 9), and examination of fish caught by fishermen (2, 5, 6, 8, 9) allowed species identification. Additional information was provided by the freshwater fisheries authorities of Asturias and León. Fish presence was determined in nine out of 16 lakes (species in Table 1), mainly originating from repeated stocking since the earliest decades of the present century (Terrero, 1951). Lake Ercina was categorized as having fish because of reports of repeated stocking with several species, mainly rainbow trout (Muñoz, 1967). As this lake had a

TABLE 1. Occurence of fish and amphibians in lakes of the Cantabrian Mountains range (northern Spain). Numbers in parentheses indicate species location according to the following lake identifications: 1- Ercina, 2- Enol, 3- Lillo, 4- Isoba, 5- Embalse de Valle, 6- Lago del Valle, 7- Cerveriz, 8- La Cuerva, 9- Calabazosa, 10- La Mesa, 11- Arbás, 12- Muniellos (Isla), 13- Muniellos (Candanosa), 14- Ubales, 15- Ausente, 16- Bueno. Asterisks in fish list indicate possible native populations.

Fish species (lake number)	Amphibian species (lake number: water)/(surrounding land)
Salmo trutta (2,3*, 4,5*, 6,8,9)	*Chioglossa lusitanica* (13)/
Salvelinus fontinalis (9)	*Salamandra salamandra* /(6)
Oncorhynchus mykiss (1?,3)	*Triturus alpestris* (1,8,10,13,14,16)/(6,7,8,9)
Phoxinus phoxinus (2,6,7,8,9)	*Triturus boscai* (12,13)/
Tinca tinca (2)	*Triturus helveticus* (1,11,12,13,14,15,16)/(2,4,8,9)
Rutilus arcasii (4)	*Triturus marmoratus* (11)/
	Alytes obstetricans (1,11,15,16)/(1,2,5,6,9,10)
	Bufo bufo (1,10,13,14,16)/(1,5,6,7,8,9,10,11,16)
	Rana iberica /(1,7)
	Rana perezi (4)/(3)
	Rana temporaria *(6,7,8,9,10,11,12,14,15,16)/* *(4,5,6,7,8,9,10,11,12,16)*

comparatively rich amphibian fauna, we have maintained the classification, although its status is uncertain at the present time, to make the tests conservative with respect to acceptance of differences in amphibian presence and abundance between lakes with fish and without fish.

The lakes shared the potential amphibian fauna (listed in Table 1), and all the samples were taken in a two week period in early July 1995, to avoid excessive among-lakes heterogeneity in the phases of the reproductive cycle. The presence of amphibians was assessed by searching the shoreline for larvae and metamorphosed individuals, surveys were extended into the surrounding land up to 500 m from the shoreline. In addition, four to six representative sampling points were chosen in each lake to determine and count larval amphibians, and so obtain figures of abundance and diversity. Abundance relative to shore length was log $(x+1)$ transformed to achieve normality (Kolmogorov-Smirnov, $P<0.05$) and to avoid the log 0 indetermination. Diversity of larvae was computed by Simpson's index ($D=1/p_i^2$; see Pianka, 1973).

RESULTS

Amphibian species richness, including larval and adult stages sampled in the water, was significantly lower in lakes inhabited by fish, both considering absolute species numbers (Fig. 1; range, mean species number, SD, for lakes without fish: 3-5, 4.00, 0.82, $n=7$; for lakes with fish: 0-4, 1.22, 1.30, $n=9$; $t=4.92$, $P<0.001$). Values were corrected for differences in shore extent (ANCOVA, with lake perimeter as the covariate; $F_{1,15}=26.57$, $P<0.001$), or altitude ($F_{1,15}=16.44$, $P=0.001$), the main correlates of amphibian species number. Differences in the numbers of amphibian species within the 500 m surrounding the lakes, although showing the same trend, were not statistically significant (range and mean and SD, for lakes without fish: 3-5, 4.29 0.76; for lakes with fish: 1-6, 3.67 1.58; $t=0.95$, $P=0.358$).

Lakes with fish tended to exhibit lower amphibian abundance (all species and stages pooled) than the fishless ones, but this difference was at the limit of statistical significance ($t=2.13$, $P=0.051$). Across lakes, amphibian abundance was significantly correlated with the extent of the shallow platform (less than 0.5 m in depth; $r=0.659$, $P=0.006$; see Fig. 2). Thus, we used this covariate to further examine the effect of fish presence on amphibian abundance. This resulted in a slight reduction of the effect of fish presence ($F_{1,15}=3.92$,

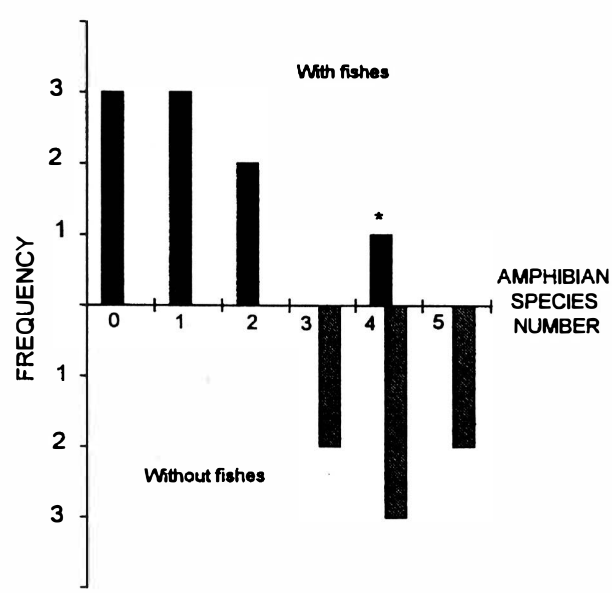

FIG. 1. Frequency distributions of amphibian species number (all stages considered) within the water for lakes with fish and without fish. The asterisk indicates the position of lake Ercina, whose classification was considered uncertain (see text).

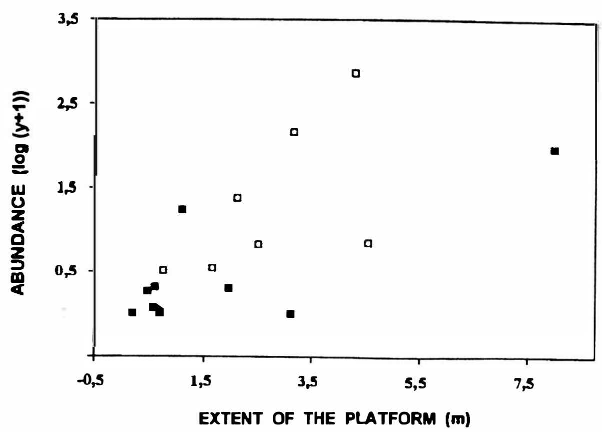

FIG. 2. Plot of the ratio [log (y+1) transformed] between amphibian abundance and lake perimeter versus the mean width of the shallow platform (less than 0.5 m in depth), for lakes without (empty squares) and with (black squares) fish.

P=0.069). Amphibian species diversity was not correlated with other habitat features (altitude, lake perimeter, depth, extent of the platform), but again tended to exhibit higher mean values for lakes without fish (1.40± 0.53 *vs.* 0.69± 0.76; t=2.06, P=0.059).

DISCUSSION

Choice of oviposition sites by breeding adults, development of chemical defences, rapid growth rates, and behavioural modifications by larval stages to reduce detection risk are common responses of amphibian populations evolved under intense predatory pressure (Petranka, Kats & Sih, 1987; Lawler, 1989; Resetaris & Wilbur, 1989; Holomuzki, 1995; Manteifel, 1995). Although subjected to modification by experience, such anti-predator behaviours have been shown to be inherited in some amphibian species (Semlitsch & Reyer, 1992). However, most amphibian species in our study area have evolved under conditions of limited fish predation. Mature individuals are aquatic only during the reproductive period, juveniles are mainly terrestrial, and egg and larval stages develop in small temporary ponds or isolated lakes of glacial origin not containing fish. Only two species (*Triturus boscai* and *Rana iberica*) reproduce regularly, in running waters inhabited by predatory fish, and frequently in small first-order reaches where juvenile brown trout are the only fish present. Therefore, specific avoidance, defence or escape mechanisms towards introduced predators (or towards high general levels of predation) are unlikely to be developed, although some generic predator recognition and avoidance behaviours can occur when amphibians are faced with unknown potential predators (Kats, Petranka & Sih, 1988; Manteifel, 1995; but see Aronsson & Stenson, 1995). In any case, the strong effect of introduced fish on amphibians in our study agrees with that expected in systems where prey and predators had no common evolutionary history (Thorp, 1986; Townsend & Crowl, 1991).

The scarcity of amphibians in habitats with predatory fish can be the result of direct predation on various stages of development, as repeatedly reported for both anurans and salamanders (e.g., Aronsson & Stenson, 1995; Manteifel, 1995; Resetaris, 1995). Analyses of stomach contents of fish from the Calabazosa lake (No. 9 in Table 1) sampled at the time of the amphibian survey provided evidence of amphibian consumption for the two most abundant and ubiquitous fish species in the study area. Despite the extreme scarcity of amphibians in this lake, two out of 12 brown trout examined contained identifiable remains of one larval salamander and three larval anurans, respectively; one out of 65 *Phoxinus phoxinus* did so; no amphibian remains were found in stomachs of 14 adult *Salvelinus fontinalis* (A. F. Ojanguren, pers. com.). Further evidence of fish predation on newts (*Triturus* sp.) and even the detection of a sudden decline of amphibians during the few years following the earliest salmonid introductions (by 1880) was reported for lake Enol (No. 2 in Table 1; Terrero, 1951). However, chemical-mediated recognition and subsequent avoidance by adult amphibians of habitats with fish for reproduction has been demonstrated for several amphibian species (e.g., Resetaris & Wilbur, 1989; Kats & Sih, 1992; Holomuzki, 1995) and could also be contributory to the reported impoverishment. In any case, the amphibian shortage relates to fish presence, and the final outcome is the almost complete disablement of large permanent pools or lakes for amphibian reproduction. Small temporary or unstable breeding-ponds are likely to exhibit high among-years variability and eventual failure in amphibian recruitment and so could be "sink habitats" (Pulliam, 1988), requiring regular immigration from more productive (or more constant in production) neighbouring source stocks. On the contrary, large pools or lakes in our study area are more stable over time and have large peripheral shallow areas suitable for amphibian reproduction (lake perimeter and extent of the shallow platform were positively correlated with species number and abundance), representing potential source stocks for colonization, and so being critical for population persistence.

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