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The Bycatch Paradox: Incidental capture of native semi-aquatic vertebrates as a recovery signal during non-native fish eradication in high-mountain lakes

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ABSTRACT

Bycatch is generally regarded as an unintended negative consequence of wildlife exploitation. However, we hypothesized that, in the context of invasive species eradication actions, temporal changes in bycatch may provide indirect evidence of native fauna recovery. Here, we investigated bycatch dynamics in semi-aquatic vertebrates during multi-year removal campaigns of non-native fish in 31 high-mountain lakes across the Alps and Pyrenees. We predicted that, as fish densities declined, incidental captures of amphibians and semi-aquatic birds and mammals would increase due to competitive or predatory release. Our results supported this hypothesis for all amphibian species and for semi-aquatic birds, with bycatch events consistently increasing throughout the eradication process, whereas no clear pattern was detected for mammals. This general pattern contrasts with conventional fisheries, where bycatch is expected to decline with improved management. We refer to this pattern as the "Bycatch Paradox", in which bycatch increases during restoration processes, potentially reflecting native fauna recovery. Nevertheless, mitigating bycatch remains important, especially for threatened species.

1. Introduction

Bycatch, the incidental capture of non-target organisms, is a major consequence of wildlife exploitation, particularly in marine and freshwater fisheries (Lewison et al., 2004). It contributes to declines in multiple marine and freshwater taxa, including seabirds (Lewison and Crowder, 2003), turtles (Wallace et al., 2010; Midwood et al., 2015), marine mammals (Read et al., 2006), and non-target fish species (Oliver et al., 2015). Even in small-scale or recreational fisheries, unintentional captures can undermine sustainable management efforts (Dewhurst-Richman et al., 2020; Donlan and Wilcox, 2008; Dotson et al., 2009). Similar concerns frequently arise whenever wildlife trapping or removal is involved, such as in wildlife monitoring (Lane et al., 2010; Buchholz et al., 2011; Carpaneto et al., 2011) or invasive species management and pest control (Ferronato et al., 2014; Grocock et al., 2020; Ancillotto et al., 2024), where incidental captures are routinely recorded (Wade et al., 2021). As a result, bycatch remains a central issue in conservation biology and environmental policy (Soykan et al., 2008; MarFishEco, 2025).

However, invasive species control and eradication differ from most wildlife exploitation activities in that they are typically designed to achieve recovery of native species and habitats through sustained removal of alien species (Singh and Byun, 2023), rather than to harvest biological resources. Yet these frameworks rarely consider whether incidental capture may also carry information about restoration trajectories.

Eradication actions targeting non-native fish in high mountain lakes provide a particularly suitable system to explore this issue. These actions generally rely on the sustained, intensive use of gillnetting and fyke-netting over several years (Knapp and Matthews, 1998; Tiberti et al.,

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2021). Because these methods are not fully selective, incidental captures of semi-aquatic vertebrates such as amphibians, but also waterbirds and semi-aquatic reptiles and small mammals, are common (Tiberti et al., 2019; Sabás et al., 2026). Non-native trout and minnows strongly suppress native amphibians and other littoral vertebrates through predation and competition for shared food resources (Matthews et al., 2002; Epanchin et al., 2010; Bello et al., 2024). As fish densities decline during eradication, aquatic (e.g., benthic invertebrates) and semi-aquatic (e.g., amphibians) prey communities are expected to recover (Tiberti et al., 2019), which may subsequently facilitate the return of native semi-aquatic predators such as water shrews, dippers, and frog-eating snakes (Pope et al., 2008; Bello et al., 2024). This sequential response, can lead to a gradual increase in incidental captures, producing a pattern in which bycatch rises while species recover. We refer to this hypothetical pattern as the Bycatch Paradox, which contrasts sharply with conventional fisheries, where bycatch is typically expected to decline as management improves (Soykan et al., 2008).

Yet, despite their potential value, long-term bycatch trends have not been explicitly incorporated into monitoring frameworks, and their potential as early indicators of recovery remains unknown. In this study, we test the Bycatch Paradox, hypothesizing that temporal changes in bycatch may provide indirect evidence of native fauna recovery in non-native fish eradication actions. We therefore analyse multi-year bycatch data from high-mountain lakes in the Alps and Pyrenees undergoing non-native fish eradication, based on combined eradication records and independent ecological monitoring. We examine whether temporal changes in bycatch correspond to the progressive recovery of aquatic communities. We further explore the implications of the Bycatch Paradox for interpreting bycatch not only as a management concern, but also as a low-cost complement to standard recovery assessments embedded within routine eradication operations.

Within the context of our study system, fish eradication in high-mountain lakes is expected to benefit native semi-aquatic vertebrates (amphibians, semi-aquatic birds, and mammals), with this response potentially reflected in a parallel increase in their bycatch events. In relation to the study area and local biodiversity we expected bycatch of amphibians, semi-aquatic birds (e.g., white throated dippers *Cinclus cinclus*), and mammals (e.g., water shrews *Neomys fodiens*) to increase as a consequence of reduced predation pressure and increased invertebrate prey availability. In contrast, the response of the grass snake (*Natrix* sp.) was considered less predictable because of its opportunistic feeding on both fish and amphibians (Pope et al., 2008; Fig. 1).

2. Methods

2.1. Study lakes

This study is based on bycatch data collected from 31 high mountain lakes and ponds (hereafter referred to as lakes for simplicity) subjected to fish eradication between 2013 and 2025 in the Alps (Gran Paradiso National Park and Mont Avic Natural Park, Western Alps, Italy) and Pyrenees (Aigüestortes i Estany de Sant Maurici National Park and Alt Pirineu Natural Park, Catalonia, Spain; Site Naturel Classé des Camporelles, France) (Table 1). All sites are typical high-mountain lakes—ranging from 0.23 to 7.4 ha—characterized by cold temperatures, 4–9 months of annual ice cover, and elevations above 2000 m a.s.l., near or above the local timberline.

Introduced fish included both salmonids (brown trout *Salmo trutta* L. 1758; brook trout *Salvelinus fontinalis* Mitchill 1814; Arctic char *Salvelinus alpinus* L. 1758; rainbow trout *Oncorhynchus mykiss* Walbaum 1792) and small leuciscids (European minnow *Phoxinus* spp.; Table 1), which in our study area include at least *P. dragarum*, *P. csikii* and *P. septimaniae* (Suh, 2024). All lakes were treated using mechanical eradication methods (Tiberti et al., 2019; Pou-Rovira et al., 2019).

2.2. Eradication methods and measuring associated bycatch

Several annual permits for fish eradication were issued by the respective parks, and any bycatch represents an unintended consequence of these authorized activities. Non-target species were released

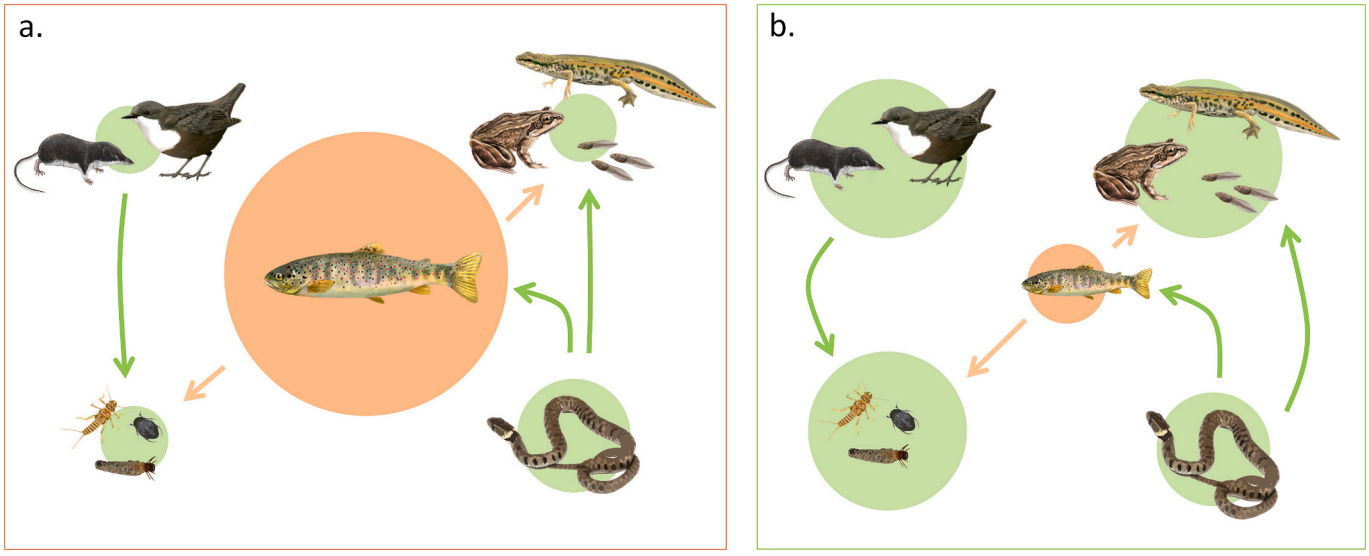


Fig. 1. Conceptual scheme of the expected effects of fish eradication/removal on taxa commonly affected by incidental captures in fyke-nets and gillnets, and on their prey, before (a) and during/after (b) fish eradication in high-mountain lakes. Increasing or decreasing circle diameters in panels a and b represent the expected population trends following fish eradication. Arrows indicate the main directional predator–prey trophic links between the introduced fish and their prey (red arrows) or between native species (green arrows). Different mechanisms are hypothesized to drive the trends in the depicted groups: fish (e.g., brown trout *Salmo trutta*) are expected to decrease as a direct consequence of active removal (Tiberti et al., 2021); amphibians (e.g., *Rana temporaria*) are expected to increase mainly due to reduced predation pressure (Tiberti et al., 2019; Miró et al., 2020); semiaquatic birds (e.g., white throated dippers *Cinclus cinclus*) and insectivore mammals (e.g., water shrews *Neomys* sp.) are expected to increase because of the rise in their invertebrate prey (Bello et al., 2024). Predictions for the semi-aquatic snakes (e.g., *Natrix* sp.) are less clear, and its circle was kept at a constant diameter: because semi-aquatic snakes in our study area feed on both fish and amphibians (Luiselli et al., 1997), their response to fish removal will likely depend on whether, and to what extent, they can shift from fish to frogs to meet their dietary needs (Pope et al., 2008; Stellati et al., 2019). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Main geographic and morphometric characteristics of the lakes treated for fish eradication, with summary information on target fish, number of fish removed (No. fish), sampling methods, and timing during which capture devices were active and bycatch data were collected. Target fish included European minnow *Phoxinus* spp. (PP), brown trout *Salmo trutta* (ST), brook trout *Salvelinus fontinalis* (SF), rainbow trout *Oncorhynchus mykiss* (OM), and Arctic char *Salvelinus alpinus* (SA). Reported methods include only those contributing to bycatch data collection (gillnetting, GN; fyke-netting, FN). Park name abbreviations were PNMA: Mont Avic Natural Park; PNGP: Gran Paradiso National Park; PNAESM: Aigüestortes i Estany de Sant Maurici National Park; PNAP: Alt Pirineu Natural Park; SNCC: Site Naturel Classé des Camporelles.

Lake	Park	Latitude N	Longitude E	Elevation	Area	Depth	Fish	No. fish	Methods		Timing
				(m)	(ha)	(m)			GN	FN	
Balena 2	PNMA	45.6379	7.5476	2564	1.7	4.0	PP	1689	1	1	2022–2025
Balena 3	PNMA	45.6396	7.5521	2570	0.4	3.8	PP	7661	1	1	2022–2025
Balena	PNMA	45.6396	7.5484	2564	1.7	5.8	PP	296,085	1	1	2022–2025
Cabana	PNAESM	42.5480	1.0390	2376	2.3	12	OM	585	1	0	2017–2019
Plan	PNAESM	42.6211	0.9296	2188	5.0	12	ST	508	1	0	2022–2025
Cap del Port	PNAESM	42.5336	1.0268	2521	7.4	31.7	ST	1693	1	0	2016–2021
Closell	PNAP	42.6828	1.2949	2074	0.7	3.7	PP	16,804	1	0	2014–2019
Coveta	PNAESM	42.5434	1.0357	2396	2.0	9.4	PP,ST,OM	164,551[a]	0	1	2022-2025
Dellui	PNAESM	42.5476	0.9477	2349	5.1	15	PP,ST	4289[b]	1	1	2022–2025
Dellui C	PNAESM	42.5533	0.9434	2314	1.1	6.2	PP,ST	4143[c]	1	1	2015–2025
Dellui N	PNAESM	42.5551	0.9426	2306	0.3	6.7	PP,ST	21,232[d]	1	1	2015–2025
Djouan	PNGP	45.5577	7.1787	2516	1.4	3.0	SF	1405	1	0	2013–2015
Dres	PNGP	45.4128	7.2240	2087	2.4	7.4	SF	15,221	1	0	2013–2016
Gargoles inferior	PNAESM	42.6166	0.9335	2299	2.1	9.8	ST	36	1	0	2022–2025
Herbier	SNCC	42.6117	2.0047	2220	0.7	1.6	SF	939	1	0	2022–2025
Leità	PNGP	45.4937	7.1322	2703	6.5	11.0	SF	6059	1	0	2023–2025
Leynir	PNGP	45.5077	7.1518	2746	4.5	21.1	SF	3442	1	0	2013–2016
Leita	PNMA	45.6434	7.5492	2537	1.4	7.5	PP,ST	180,421[e]	1	1	2022–2025
Llastra	PNAESM	42.5409	1.0333	2426	2.2	15.5	ST,OM	2142[f]	1	0	2022–2025
Miserino 2	PNGP	45.5847	7.4701	2666	0.2	3.0	SF	729	1	0	2022–2025
Miserino	PNGP	45.5832	7.4704	2667	4.2	9.9	SF	1850	1	0	2022–2025
Muanda	PNGP	45.5198	7.4358	2390	1.2	10.5	SF	1001	1	0	2022–2025
Muffet	PNMA	45.6379	7.6051	2076	0.8	4.5	ST	200	1	0	2023–2025
Muntanyó	PNAP	42.6726	1.0072	2205	5.0	14	PP,ST	133,028[g]	1	1	2022–2025
Naorte	PNAP	42.6898	1.3000	2150	3.9	14	PP	122,499	1	1	2015–2025
Nero Djouan	PNGP	45.5519	7.1687	2666	1.6	6.0	SF	201	1	0	2013–2015
Nero Miserin	PNMA	45.6049	7.5143	2551	1.7	5.8	SA,ST	72[h]	1	0	2023–2025
Rovinets	PNAP	42.6676	1.3346	2223	0.4	5.4	PP	5826	1	1	2016–2025
Subenuix	PNAESM	42.5721	0.9874	2194	2.6	11	SF	5213	1	0	2016–2021
Tres Estanys Mig	PNAP	42.6823	1.1841	2412	3.7	11	PP	163,505	1	1	2018–2025
Vernouille	PNMA	45.6338	7.5925	2145	0.5	3.6	PP	101,971	1	1	2022–2025

[a] 164,222 PP, 25 ST, and 304 OM.
[b] 85 PP, and 4204 ST.
[c] 3742 PP, 401 ST.
[d] 21,225 PP, and 7 ST.
[e] 180,799 PP, and 22 ST.
[f] 1004 ST and 1138 OM.
[g] 132,030 PP, and 998 ST.
[h] 70 SA, and 2 ST.

immediately after identification whenever possible, and all efforts were made to minimize handling time and reduce stress and mortality.

Eradication actions were initiated at different times across sites and varied in duration depending on lake characteristics and target fish populations (Table 1, "Timing"), resulting in a mixture of completed and ongoing interventions. In 14 lakes, eradication has already been considered successful based on sustained zero captures for at least one year under constant and high capture effort, supported in several cases by longer periods without fish detections (Pou-Rovira et al., 2019; Tiberti et al., 2019, 2021). In the remaining lakes, operations started more recently and are still ongoing; however, by 2025 all systems showed either zero or >90% reduction in capture rates relative to the initial eradication phase, indicating strong progress towards eradication targets. Eradication methods followed different standardized protocols according to the target fish species. Salmonids were removed using intensive gillnetting, deployed year-round, either alone or in combination with shoreline electrofishing, whereas minnow populations (*Phoxinus* spp.) always required a combination of gillnetting, fyke-netting, and electrofishing (Table 1). The number of capture devices deployed was proportional to lake size (i.e., 15 gillnets per hectare and one fyke net every 10–15 m of shoreline). Nevertheless, capture effort was standardized within each lake category (salmonid- or minnow-invaded lakes) and analyses were conducted separately for captures in gillnets and fyke nets, and site-specific variation was accounted for in the statistical models (see Data analyses).

Bycatch was recorded during every inspection of passive capture devices—gillnets and fyke-nets—throughout the eradication process. Active methods such as electrofishing only resulted in temporary, non-lethal stunning of amphibians, with no actual capture of individuals. These events were not quantified as bycatch and were not systematically counted, due to their extremely brief and fully reversible nature. In contrast, passive capture devices (gillnets and fyke-nets) produced measurable bycatch, likely reflecting both their prolonged deployment (remaining active for years) and their non-selective mode of operation, which increases the likelihood of intercepting non-target species. Bycatch was therefore recorded during every inspection of gillnets and fyke-nets throughout the eradication process (Table 1). During each net-cleaning and fyke-net emptying event, all incidentally captured semi-aquatic, and terrestrial vertebrates were identified and counted. This included amphibians as well as semi-aquatic birds, reptiles, and mammals. For anuran amphibians, we also counted tadpoles and adults separately.

Since bycatch mortality can have relevant ethical and conservation implications, we estimated the lethality of bycatch events based on

survival at the moment of release, which was recorded for each individual in the Alps. Mortality data were not collected with the same level of detail and consistency in the Pyrenees, where in some cases only ranges of variation are available. Consequently, quantitative comparisons of bycatch lethality between regions should be interpreted with caution. In addition, sublethal effects were occasionally observed, primarily consisting of limb injuries in amphibians captured in gillnets and symptoms of drowning in amphibians captured in fyke nets. However, no systematic data collection was conducted for this aspect.

2.3. Linking bycatch to the monitoring of semi-aquatic vertebrates and of their prey

The study evaluates whether temporal variation in bycatch is associated with independent indicators of population recovery during fish eradication. Specifically, if bycatch reflects changes in the abundance of non-target species, increasing bycatch rates would be expected to covary with increasing abundance estimates obtained through independent monitoring. Less cryptic species, such as amphibians, reptiles, and white throated dippers, were surveyed using Visual Encounter Surveys (VES). This rapid assessment method involves walking along the lake shoreline and counting all adult individuals of the target species, as well as amphibian eggs and larvae (Crump and Scott, 1994). VESs were conducted between one and several times per year in each study lake throughout the fish eradication period. Originally designed to monitor herpetofauna (amphibians and semiaquatic snakes; Tiberti and von Hardenberg, 2012; Miró et al., 2020), VES was later (in 2022) expanded to include white throated dippers. Consequently, for amphibians and grass snakes, VES provides consistent monitoring data throughout the entire fish eradication period in all lakes. However, for dippers, VES data are missing for lakes treated for fish eradication prior to 2022. VESs provided information on the contrasting temporal trends of frogs and fish, which represent the primary prey of *Natrix* sp. (Luiselli et al., 1997; Stellati et al., 2019). Therefore, amphibian counts from VES were also used as an estimate of prey availability for grass snakes.

VES was largely ineffective for semiaquatic mammals, with only a single water shrew observation recorded throughout the study period. For such elusive species, trends in bycatch and responses to fish eradication were assessed primarily through indirect methods, focusing on the availability of their main prey resources, i.e., large benthic aquatic macroinvertebrates. We collected macroinvertebrate samples from 28 of the 31 study lakes (data were unavailable for Gargoles Inferior, Llastra, and Coveta; Table 1) to quantify prey availability for semi-aquatic insectivores throughout the fish eradication campaign. One or two samples were collected each summer during each reference period (Year 1 to Year $\geq$4). When multiple samples were available within the same period, counts were averaged. Macroinvertebrate sampling was largely consistent across lakes, although some records were incomplete: only one sampling period was available for Dellui and Cabana, whereas Muntanió and Tres Estanys Mig were sampled during three of the four sampling periods.

Macroinvertebrate sampling followed Knapp et al. (2001) and Osorio et al. (2022). Three littoral habitat types—sand (<2 mm), gravel (2–64 mm), and stony substrates ($\geq$64 mm)—were sampled using ten standardized 1-m sweeps per habitat with a D-frame net (25 × 20 cm, 0.5-mm mesh); in a few cases where one habitat type was absent, its ten sweeps were distributed equally between the other two habitat types, maintaining a constant sampling effort of 30 standardized sweeps per lake. Organisms were separated from detritus, preserved in 70% ethanol, and identified to family or genus following Campaioli et al. (1994). Each taxon was classified as either non-burrowing (epibenthic/nektonic) or burrowing, functional categories that reflect prey accessibility for both fish and semiaquatic predators. Non-burrowing taxa are more exposed than burrowing ones (Knapp et al., 2001; Tiberti et al., 2019; Bello et al., 2024).

To graphically represent the recovery in prey availability for semiaquatic insectivores, the composition of macroinvertebrate communities was depicted using a biplot from Principal Component Analysis (PCA), which identified changes in prey communities throughout the fish eradication process. The increase in prey availability was further represented by the growth trends of potential prey, particularly large non-burrowing macroinvertebrates and large benthic insects.

2.4. Data analyses

Trends in bycatch of common species or higher taxonomic/functional groups (pooled Amphibia, Anura, Caudata, Mammalia, and Aves; all semi-aquatic insectivores; Table 2) were analysed using generalized linear mixed models (GLMMs) with a negative binomial error distribution to account for count data and potential overdispersion. Analyses were performed in R (version 4.5.2; R Core Team, 2025) using the glmmTMB package (Magnusson et al., 2017).

Although negative binomial models can technically be fitted to sparse datasets, parameter estimates based on a limited number of informative events often exhibit low precision and reduced explanatory power. For this reason, models were fitted separately for bycatch recorded in gill nets and fyke nets, and only for species or higher taxonomic/functional groups with at least fifteen non-zero observations, a conservative threshold adopted to ensure minimum model robustness and stability of parameter estimation and avoid zero-inflation.

Bycatch records were aggregated by lake and eradication year prior to analysis. One year of eradication spans from the beginning of one field season to the beginning of the next, i.e., including the first check and clearing of nets and fyke-nets in the following ice-free season and accounting for the prolonged annual interruption caused by ice cover. For each taxon and gear type, the response variable consisted of the total number of bycatch individuals recorded within a lake during a given eradication year. Because the duration and timing of eradication activities varied among lakes from a minimum of three years of bycatch data to a maximum of eleven years (Table 1), to harmonize the temporal structure of the dataset, all observations from the fourth year onward were pooled into a single category (Year $\geq$4) for lakes with more than four years of data. This aggregation also reduced potential violations of linearity assumptions arising from the medium- to long-term stabilization of target species populations that often characterizes recovery dynamics.

Models included year since the start of eradication efforts (coded as a numeric variable ranging from 1 to 4, with year 4 representing the fourth year or all subsequent years when more than four years of data were available) as a fixed effect to test for temporal trends, and lake identity as a random intercept to account for repeated measures within lakes. To account for differences in sampling intensity among lakes and years, total sampling effort was included as an offset term, allowing bycatch counts to be interpreted on a per-unit-effort basis. Effort was expressed as trap-days (for fyke-nets) and net-days (for gillnets), calculated as the number of active traps or nets multiplied by the number of days they were deployed. For lakes with more than four years of data, effort values from year four to the final year of eradication were summed accordingly.

Model assumptions were evaluated by testing for overdispersion and zero-inflation using the *performance* package (Lüdecke et al., 2021). Model fit was quantified using marginal and conditional R^2 to distinguish the variance explained by fixed effects from that attributable to lake-level random effects. Model adequacy was further assessed through visual inspection of residual diagnostics.

3. Results

3.1. Bycatch composition

Bycatch composition primarily reflects biogeographic differences in species distribution, as some taxa occur in the Pyrenees but not in the

Table 2
Composition of bycatch recorded during fish eradication activities in 31 high mountain lakes from the Alps ($N = 15$) and Pyrenees ($N = 16$), broken down by capture method (FN = fyke-nets, data available from 13 lakes; GN = gillnets, data available from 30 lakes) and species or groups of species. For each species/group, the table reports the number of individuals captured per method (N), the number of positive counts (i.e. non-zero values; Pos. counts) per method, mortality rates per method in the Alps and Pyrenees, and frequency values, defined as the number of lakes where the species was recorded relative to the total number of surveyed lakes in each region and across the pooled dataset. A dash (–) indicates that the species was absent from that mountain region. Life stage is indicated where applicable: ad. = adult; l. = larva.

Groups		FN vs. GN	N	Pos. counts	Mortality (%)		Frequency		
					Alps	Pyrenees	Alps	Pyrenees	pooled
Amphibia	Pooled species[a]	FN	55,471	52	9	10–80	5/5	8/8	13/13
		GN	288	21	79	80–100	7/15	5/15	12/30
Anura	Pooled species, ad.	FN	10,492	51	9	10–80	5/5	8/8	13/13
		GN	201	18	79	80–100	7/15	5/15	12/30
	Pooled species, l.	FN	67,011	37	1	<1	4/5	7/8	11/13
		GN	0	0	0	0	0/15	0/15	0/30
	Common frog *Rana temporaria*, ad.	FN	9093	48	9	10–80	5/5	8/8	13/13
		GN	83	17	79	80–100	7/15	4/15	11/30
	Common frog *Rana temporaria*, l.	FN	25,692	32	1	<1	4/5	7/8	11/13
		GN	0	0	0	0	0/15	0/15	0/30
	Common midwife toad *Alytes obstetricans*, ad.	FN	52	4	–	100	–	1/8	1/8
		GN	0	0	–	0	–	0/15	0/15
	Common midwife toad *Alytes obstetricans*, l.	FN	1230	5	–	<1	–	2/8	2/8
		GN	0	0	–	0	–	0/15	0/15
	Spiny toad *Bufo spinosus*, ad.	FN	1347	20	–	10–80	–	7/8	7/8
		GN	118	1	–	80–100	–	1/15	1/15
	Spiny toad *Bufo spinosus*, l.	FN	40,089	18	–	<1	–	6/8	6/8
		GN	0	0	–	0	–	0/15	0/15
Caudata	Pooled species, ad. and l.[b]	FN	44,979	26	–	<1	–	7/8	7/8
		GN	87	5	–	80–100	–	3/15	3/15
	Pyrenean brook salamander *Calotriton asper*, ad. and l.[b]	FN	520	22	–	<1	–	7/8	7/8
		GN	1	1	–	0	–	1/15	1/15
	Palmate newt *Lissotriton helveticus*, ad. and l.[c]	FN	44,459	11	–	<1	–	3/8	3/8
		GN	86	4	–	80–100	–	3/15	3/15
Reptilia	*Grass snakes - Natrix* sp.	FN	46	8	33	78	1/5	2/8	3/13
		GN	14	5	100	100	1/15	1/15	2/30
Aves	*Pooled species*	FN	10	7	100	100	1/5	3/8	4/13
		GN	66	25	97	100	9/15	5/15	14/30
	White throated dippers *Cinclus cinclus*	FN	7	5	100	100	1/5	2/8	3/13
		GN	56	22	98	100	9/15	4/15	13/30
	Mullard *Anas platyrhynchos*	FN	3	2	–	100	0/5	2/8	2/13
		GN	10	4	90	100	1/15	3/15	4/30
Mammalia	Pooled species	FN	45	22	100	100	4/5	6/8	10/13
		GN	12	7	100	100	3/15	2/15	5/30
	Water shrews *Neomys* sp.	FN	38	19	100	100	4/5	5/8	9/13
		GN	10	6	100	100	3/15	1/15	4/30
	Iberian Desman *Galemys pyrenaicus*	FN	3	2	100	100	–	1/8	1/8
		GN	0	0	100	100	–	0/15	0/15
	Southern water vole *Arvicola sapidus*	FN	4	3	100	100	–	2/8	2/8
		GN	2	2	100	100	–	2/15	2/15
Insectivores	Pooled species	FN	48	23	100	100	4/5	7/8	11/13
		GN	66	24	98	100	10/15	4/15	14/30

[a] Anurans (100% adults) and caudates (95% adults).
[b] Approximatively 95% of caudata and palmate newts were adult individuals.
[c] Approximatively 80% of Pyrenean brook salamander were adult individuals.

Alps (Table 2). However, the bycatch was largely dominated by amphibians in both areas. A total of 55,471 and 288 adult individuals were captured in fyke-nets and gillnets, respectively, across most lakes, along with more than 67,000 tadpoles, which were exclusively captured in fyke-nets (Table 2). Other semi-aquatic species were consistently captured during eradication actions, although at much lower frequencies. These included 60 grass snakes (western grass snake *Natrix helvetica* in the Alps and viperine snake *N. maura* in the Pyrenees), 63 white throated dippers (*Cinclus cinclus*), and 48 European water shrews (*Neomys fodiens*) (Table 2). In addition, a few species were captured only sporadically, including 13 mallards (*Anas platyrhynchos*), six southern water voles (*Arvicola sapidus*) and three Iberian desmans (*Galemys pyrenaicus*) (Table 2). Although recorded in low numbers, these captures include species of high conservation concern, most notably the Iberian desman.

Since these are unstandardized totals, the contribution of each species to the total bycatch does not necessarily correspond to a comparable relative capture frequency among lakes. For example, some species that account for a high relative abundance in the bycatch, such as the palmate newt (*Lissotriton helveticus*), were recorded at only a few sites, whereas other species with lower relative abundance (e.g., *Neomys fodiens*) were captured across a large number of lakes.

Overall, fyke-nets exhibited higher bycatch for amphibians and small mammals, whereas gillnets contributed mainly to bird bycatch. Mortality varied markedly among taxonomic groups and capture methods. In fyke-nets, mortality was negligible in both Pyrenees and Alps for tadpoles, as well as for urodele amphibians in the Pyrenees, whereas higher mortality was observed for anuran amphibians and grass snakes. Noteworthily, the range mortality estimates for anuran amphibians in the Pyrenees (10–80%) were higher than mortality recorded in the Alps (9%; Table 2). Mortality associated with gillnets, although the number of individuals captured was very low, was approximatively 80–100% across adults of all amphibian taxa (Table 2). Mortality reached very high levels, or 100%, for all birds and mammals, irrespective of capture

method (gillnets or fyke-nets) (Table 2).

Bycatch also varied substantially among lakes, in addition to differences between fishing gears. Bycatch was observed in most lakes, except Nero-Djouan, Cabana, Cap del Port, Gargoles, Subenuix (Table 1). The composition of the bycatch differed among lakes: some lakes were dominated by amphibians, while others had a higher proportion of birds or small mammals, reflecting both local patterns of species abundance/distribution and the used eradication methods (gillnets or both gillnets and fyke-nets).

3.2. Bycatch dynamics

Bycatch responses to eradication-year progression showed several increasing patterns consistent with our hypothesis. Among amphibians, most common taxa/groups exhibited significant increases in bycatch with advancing eradication years in both fyke-nets and gillnets (Fig. 2; Tables 3 and 4). Beyond amphibians, support for the study hypothesis was mainly driven by bycatch recorded in gillnets, where insectivorous vertebrates—particularly birds and white throated dippers—showed significant positive temporal trends (Table 4). By contrast, although mean bycatch in fyke-nets increased over time, these trends were not statistically significant for mammals, water shrews, or insectivores as a group (Table 3).

Effect sizes (β ± SE) varied among taxonomic groups and between gear types (Tables 3 and 4; Fig. 2). In fyke-net models, effect sizes for amphibians were positive and often larger for caudates and larval stages, whereas adult anurans showed weaker responses; non-amphibian groups exhibited consistently small and non-significant effects (Table 3). In gillnet models, temporal effects were consistently positive for amphibians (β = 0.59–0.75), indicating strong increases in bycatch over time; white throated dipper, birds and insectivores showed smaller but still significant positive effects (β ≈ 0.40–0.44), suggesting slower temporal increases.

Effect sizes were consistent between gillnets and fyke nets, with no evidence of divergent temporal trends between gear types. Differences in statistical significance across gears likely reflect differences in capture efficiency and precision of the estimates rather than biological discrepancies, as effect directions and magnitudes were broadly similar across models.

The inclusion of lake identity as a random effect in the models explicitly accounts for among-lake heterogeneity. Across models, marginal R^2 values were low (0.000–0.096), whereas conditional R^2 values were markedly higher (0.027–0.827; Tables 3 and 4), indicating that variation among lakes accounted for a substantial proportion of the

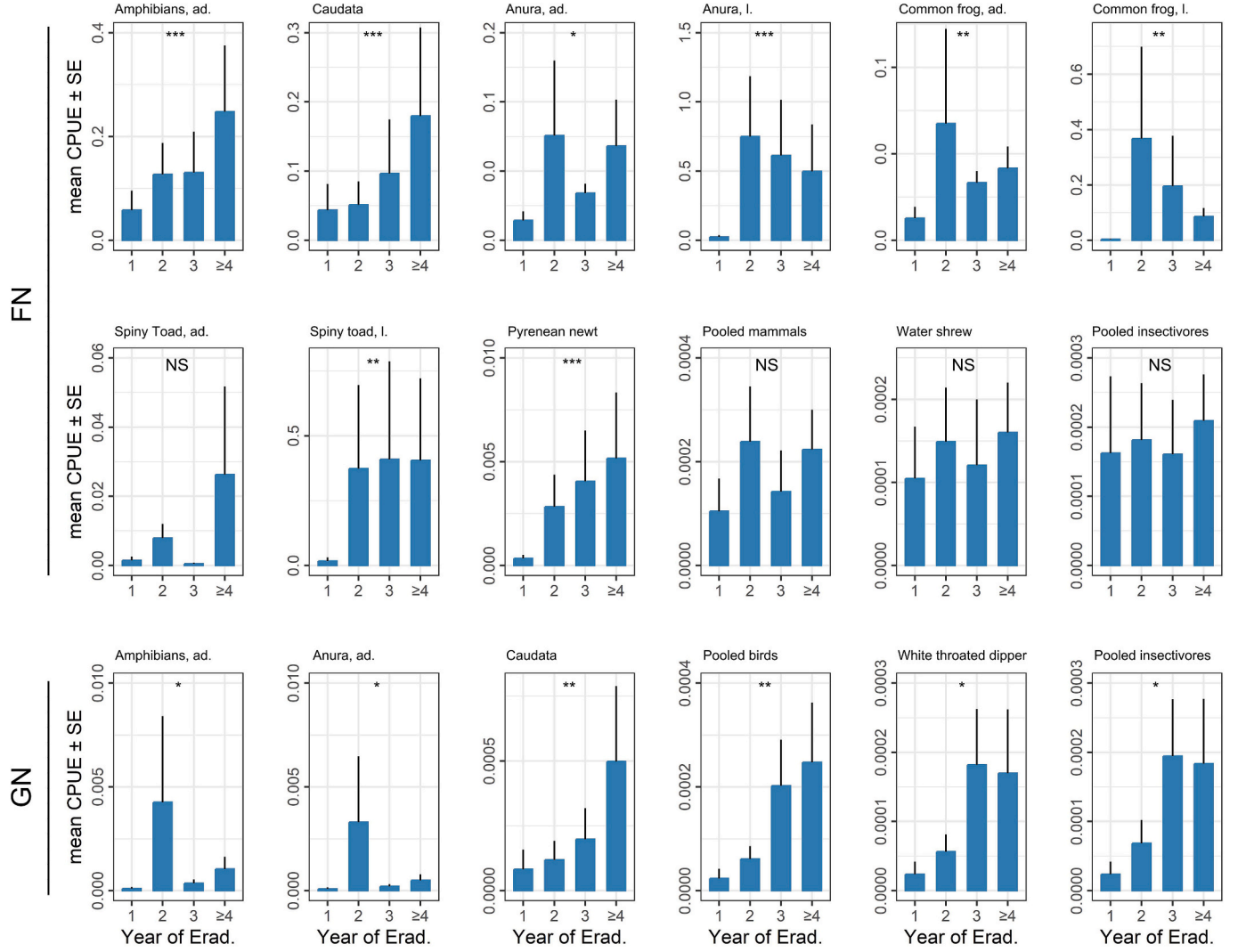


Fig. 2. Annual bycatch rates of semi-aquatic vertebrates corrected for sampling effort during fish eradication activities in high mountain lakes using fyke-nets (FN; upper rows, data from 13 lakes) and gillnets (GN; lower row, data from 30 lakes). Bycatch values are expressed as Capture Per Unit Effort, i.e., number of captures per standardized unit of effort (capture per net- or fyke-net-days). Bars represent mean CPUE ± SE across lakes. Levels of statistical significance of the effect of year on bycatch, as estimated by generalized linear mixed models (Tables 3 and 4), are indicated as NS (not significant), * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$).

Table 3
Summary of generalized linear mixed models (GLMMs) fitted to bycatch counts of several vertebrate groups captured in fyke nets used for fish eradication operations in up to 13 high-mountain lakes. Models used a negative binomial distribution with lake included as a random intercept.

Model	Covariates	β ± SE	z-Value	p	R^2c	R^2m
Pooled amphibians	Intercept	−4.00 ± 0.43	−9.22	<0.001	0.245	0.052
(52 obs, from 13 lakes)	Year	0.48 ± 0.07	6.57	**<0.001**		
Pooled caudata	Intercept	−4.57 ± 0.81	−5.66	<0.001	0.682	0.096
(32 obs, from 8 lakes)	Year	0.58 ± 0.11	5.04	**<0.001**		
Pooled anura, ad.	Intercept	−4.03 ± 0.33	−12.14	<0.001	0.112	0.016
(52 obs, from 13 lakes)	Year	0.22 ± 0.09	2.35	**<0.05**		
Pooled anura, l.	Intercept	−3.60 ± 0.65	−5.57	<0.001	0.703	0.070
(52 obs, from 13 lakes)	Year	0.48 ± 0.12	4.05	**<0.001**		
Common frog, ad.	Intercept	−4.34 ± 0.33	−13.17	<0.001	0.267	0.071
(52 obs, from 13 lakes)	Year	0.25 ± 0.09	2.77	**<0.01**		
Common frog, l.	Intercept	−4.16 ± 0.64	−6.50	<0.001	0.308	0.094
(52 obs, from 13 lakes)	Year	0.51 ± 0.16	3.26	**<0.01**		
Spiny toad, a.	Intercept	−4.43 ± 0.69	−6.38	<0.001	0.027	0.000
(32 obs, from 8 lakes)	Year	0.46 ± 0.21	−0.11	0.91		
Spiny toad, l.	Intercept	−3.92 ± 1.03	−3.82	<0.001	0.827	0.051
(32 obs, from 8 lakes)	Year	0.47 ± 0.15	3.06	**<0.01**		
Pyrenean brook newt	Intercept	−7.59 ± 0.79	−9.60	<0.001	0.315	0.041
(32 obs, from 8 lakes)	Year	0.49 ± 0.14	3.45	**<0.001**		
Mammals	Intercept	−9.58 ± 0.58	−16.47	<0.001	0.072	0.005
(52 obs, from 13 lakes)	Year	0.20 ± 0.18	1.11	0.27		
Water shrew	Intercept	−9.65 ± 0.61	−15.72	<0.001	0.073	0.002
(52 obs, from 13 lakes)	Year	0.14 ± 0.20	0.70	0.48		
Insectivores	Intercept	−9.26 ± 0.56	−16.68	<0.001	0.062	0.001
(52 obs, from 13 lakes)	Year	0.09 ± 0.19	0.51	0.61		

Bold values indicate that the effect of Years from the start of the eradication was statistically significant ($P < 0.05$).

Table 4
Summary of generalized linear mixed models (GLMMs) fitted to bycatch counts of several vertebrate groups captured in gillnets used for fish eradication operations in up to 30 high-mountain lakes. Models used a negative binomial distribution with lake included as a random intercept.

Model	Covariates	β ± SE	z-Value	p	R^2c	R^2m
Pooled amphibians	Intercept	−10.37 ± 1.04	−9.94	<0.001	0.357	0.037
(114 obs, 30 lakes)	Year	0.59 ± 0.25	2.34	**<0.05**		
Pooled anura, ad.	Intercept	−11.22 ± 1.23	−9.15	<0.001	0.364	0.052
(114 obs, 30 lakes)	Year	0.72 ± 0.28	2.57	**<0.05**		
Common frog, ad.	Intercept	−13.60 ± 1.35	−10.04	<0.001	0.515	0.039
(114 obs, 30 lakes)	Year	0.75 ± 0.22	3.36	**<0.001**		
Birds	Intercept	−11.20 ± 0.72	−15.51	<0.001	0.245	0.052
(114 obs, 30 lakes)	Year	0.46 ± 0.17	2.62	**<0.01**		
White throated dipper	Intercept	−11.11 ± 0.73	−15.17	<0.001	0.162	0.018
(114 obs, 30 lakes)	Year	0.40 ± 0.19	2.13	**<0.05**		
Insectivores	Intercept	−11.11 ± 0.66	−16.81	<0.001	0.165	0.022
(114 obs, 30 lakes)	Year	0.44 ± 0.17	2.59	**<0.01**		

Bold values indicate that the effect of Years from the start of the eradication was statistically significant ($P < 0.05$).

explained variance. This pattern is consistent with the marked among-lake differences in bycatch composition and occurrence described above.

No evidence of overdispersion or zero-inflation was detected, and model residuals did not show systematic patterns indicative of model misspecification, supporting the adequacy of the negative binomial specification.

For grass snakes, the limited number of positive events (Table 2) prevented us from testing for temporal trends. However, several bycatch events occurred already during the first year of eradication, indicating that the presence of fish (and the reduced availability of amphibians) may not constitute an exclusion factor. Bycatch continued throughout the study period, indicating snake persistence despite incidental mortality (Table 2).

3.3. Changes in populations and prey communities along the eradication process

Descriptive data from VESs indicate an increase in both frequency of occurrence and the abundance of amphibians over time (Fig. 3a–c). No consistent temporal pattern is observed for *Natrix* populations in the four lakes where this species occurs (Fig. 3d). For white throated dipper monitoring data suggest a possible increase in probability of occurrence over time (Fig. 3e).

Concerning prey, as noted above, amphibian populations increased, potentially compensating for the loss of fish in the diet of grass snakes. The PCA indicates that benthic macroinvertebrate communities were initially relatively similar across lakes (small year 1 ellipse encompassing two-thirds of the samples) but became increasingly heterogeneous over time (larger ellipses; Fig. 4a). This pattern is consistent with increasing divergence in macroinvertebrate community composition during the study period. Such changes coincide with an increase in the availability of potential prey for semi-aquatic insectivores (white throated dipper, water shrew, and Pyrenean desman), particularly non-burrowing macroinvertebrates and large benthic insects (Fig. 4b–c).

4. Discussion

4.1. Bycatch as a signal of recovering lakes

The bycatch probabilities of several common semi-aquatic vertebrates increased during non-native fish eradication in high-mountain

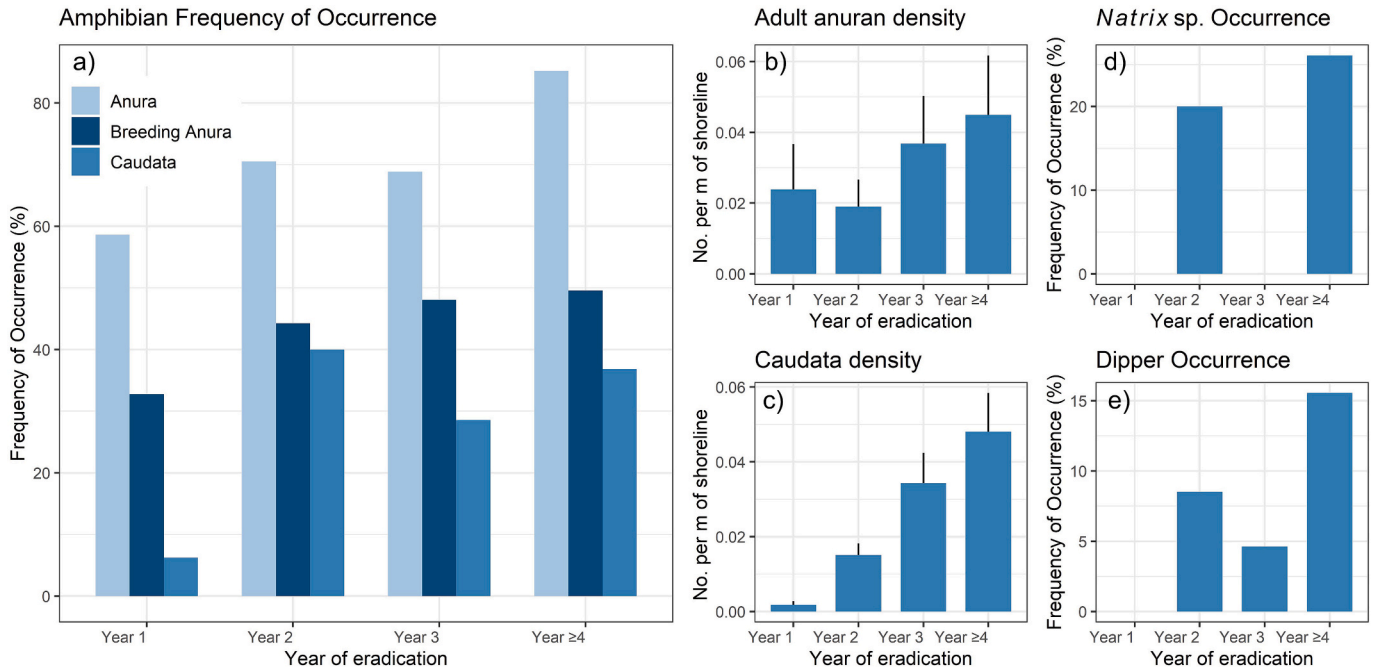


Fig. 3. Visual Encounter Survey (VES) monitoring data along the eradication period: Panel a): frequency of occurrence of anuran amphibians and of their eggs/larvae (indicating reproduction), and caudata; Panel b): mean number of adult anurans per meter of shoreline, with error bars representing the Standard Error; Panel c): mean number of adult caudata per meter of shoreline, considering only VESs from Pyrenean lakes, where Caudata are present; Panel d): frequency of occurrence of snakes (*Natrix* sp.), considering only VESs from four lakes (MUF, NAO, ROV, VER; Table 1) where *Natrix* are known to occur; Panel (e) frequency of occurrence of white throated dippers (*Cinclus cinclus*).

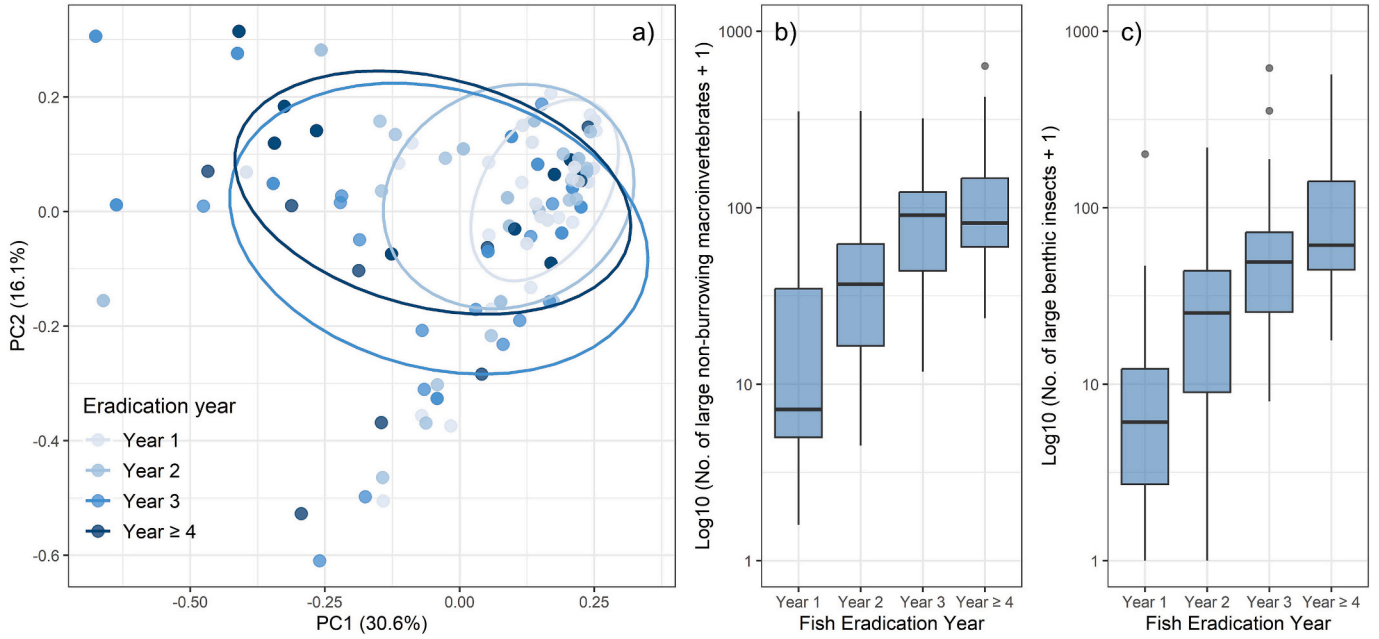


Fig. 4. Macroinvertebrate community composition and prey availability for semiaquatic insectivores during fish eradication. (a) Principal Component Analysis (PCA) of littoral macroinvertebrate communities across 28 lakes, with points representing the first two principal components (PC1 and PC2) and ellipses indicating 67% concentration per eradication year. (b) Boxplots showing log10-transformed abundance of large non-burrowing macroinvertebrates, and (c) of large benthic insects, the main prey for semiaquatic insectivores like the white throated dipper (*Cinclus cinclus*) and water shrews (*Neomys* sp.) across eradication years.

lakes. This pattern was observed for all common amphibian species and groups, as well as white throated dippers and insectivores captured in gillnets. These increases occurred in parallel with increases in their populations, in their occurrence, or in the abundance of their prey, as indicated by independent monitoring data (Figs. 3 and 4). The pattern was consistently observed across multiple species and lakes in both the Pyrenees and the Alps. These results support the hypothesis that bycatch data reflect the recovery of semi-aquatic vertebrates promoted by the eradication of introduced fish from high-mountain lakes. Such recovery may take the form of population growth, as observed in amphibians, or increased use of lake by semiaquatic insectivores, likely driven by greater prey availability, as observed for white throated dippers.

Importantly, during eradication campaigns, mitigation measures were frequently implemented to reduce bycatch for ethical and conservation reasons, such as relocating particularly problematic gillnets or fyke-nets, or installing protective grids at the entrance of some fyke-nets to prevent the entry of the desman (see next section for further considerations on the conservation concerns associated to bycatch on threatened species). Although such mitigation actions could be viewed as reducing methodological consistency, they demonstrate, beyond our primary commitment to conservation, that the observed increases in bycatch are conservative and likely underestimate the true magnitude of recovery in the target taxa. We therefore believe that this strengthens, rather than weakens, the inference drawn from our results.

While the recovery of amphibians confirms expectations (Knapp et al., 2007; Tiberti et al., 2019; Miró et al., 2020), providing an ideal and well-studied context for a direct test of our hypothesis, the patterns observed for birds and insectivores extend this mechanism to less-studied taxa. Evidence of fish impacts on non-amphibian vertebrates, such as snakes, dippers, and shrews, remains comparatively scarce (Matthews et al., 2002; Epanchin et al., 2010; Bello et al., 2024). The observed increases in bycatch probabilities for white throated dippers and insectivores as a group therefore represent a novel finding that warrants further interpretation. Current evidence suggests that these increases may be driven by enhanced prey availability following fish removal (Epanchin et al., 2010; Bello et al., 2024), which could attract more insectivores to lakes or increase the frequency and duration of their use of these habitats.

From a conservation perspective, this study provides valuable insights into the effects of fish presence and removal on semi-aquatic vertebrates in high-altitude lakes. Such studies are particularly useful because they focus on protected, emblematic, or charismatic species (Bello et al., 2024). Including protected species enables access to dedicated conservation funding and helps build a more compelling narrative for decision-makers. Furthermore, the potential of semi-aquatic vertebrates to serve as flagship species can mobilize public awareness for subtle but ecologically important conservation issues, such as the impact of introduced fish in high-altitude lakes, where large-scale ecological effects may not be immediately visible in such otherwise scenic environments.

Importantly, caution is warranted when generalizing these findings, as they are likely typical of high-mountain lakes and semiaquatic vertebrates impacted by fish. In high-mountain lakes, introduced fish function as novel apex predators and exert pervasive impacts (Knapp et al., 2001). Other lake types, in particular lowland lakes, may show weaker or different responses to alien fish removal because of more complex food webs and the natural presence of native fish communities. Caution is also warranted because restoration responses may differ among taxa. For example, the patterns observed for amphibians and white throated dippers may not apply to grass snakes. Because grass snakes are not typical prey of fish, have a generalist diet that includes both amphibians and fish (Stellati et al., 2019), and exhibit slower life-history traits, their response to fish eradication may differ from that of other semi-aquatic vertebrates. Indeed, the frequent co-occurrence of grass snakes with non-native fish, together with the absence of clear trends in either incidental captures or independent monitoring data, suggests that fish exert weaker pressure on grass snakes than on taxa such as amphibians. This interpretation underscores the importance of considering complex trophic interactions when interpreting bycatch data (Pope et al., 2008). In addition to its opportunistic diet on both fish and frogs, *Natrix* is characterized by low mobility and dispersal capacity, low population density, long lifespan, and relatively low reproductive potential. These life-history traits make the species potentially vulnerable to even moderate levels of bycatch, which could threaten its local persistence. However, the continued presence of *Natrix* throughout the eradication period represents an encouraging indication that mechanical fish eradication operations can be conducted safely, even for species with contrasting reproductive strategies and dispersal abilities.

4.2. The Bycatch Paradox

The *Bycatch Paradox* refers to the idea that, within the context of invasive species removal and ecological restoration, bycatch can serve as a valuable ecological signal rather than merely an undesirable outcome, as it is generally considered in conventional fisheries. In this context, bycatch may function both as an operational indicator of restoration progress and as evidence of food-web reassembly. For example, increased bycatch of amphibians may reflect population recovery following fish removal, whereas increased bycatch of white throated dippers may indicate the re-establishment of trophic links previously disrupted by introduced fish, such as those connecting large benthic insects to semi-aquatic insectivores.

A concept related to the Bycatch Paradox has been explored in studies that use bycatch as a monitoring tool for data-limited species (e.g., marine mammals; Meager and Sumpton, 2016). However, in the absence of a clearly defined restoration framework aimed at improving the conservation status of the affected species, interpreting temporal trends in bycatch remains challenging, as changes may reflect multiple, often confounding ecological and anthropogenic processes.

Variation in bycatch should be therefore interpreted in relation to population trends—whether positive or negative—which may reflect conservation actions, natural demographic processes, or anthropogenic pressures, including population declines directly caused or exacerbated by bycatch itself. For example, an increase in the reproductive success of seabirds on islands where non-native rats have been actively eradicated is likely to lead to a rise in bycatch of these species in off-shore fisheries (Donlan and Wilcox, 2008), making efforts to reduce bycatch events potentially unrealistic, frustrating, and misleading if interpreted without context. In these cases, bycatch data must be interpreted alongside or as a proxy of population trends: paradoxically, a low number of incidental captures could signal concern, while a high number may indicate recovery.

If a population is recovering, bycatch management should realistically aim for the growth of bycatch to occur at a rate lower than that of population increase, rather than treating an increase in bycatch as inherently negative. In conclusion, bycatch data can be misleading or uninformative if interpreted without considering population trends, and we invite integrating bycatch into conservation monitoring frameworks as an informative ecological signal. In this context, when planning conservation interventions, acknowledging the potential occurrence or even a temporary increase in bycatch should not be perceived as a weakness to justify, downplay, or conceal. On the contrary, transparent reporting of incidental captures, combined with adaptive mitigation measures, can improve the ecological interpretation of management outcomes and help strengthen the credibility of conservation actions.

4.3. Bycatch as a conservation issue and rapid response to conservation-relevant bycatch

While our results highlight the potential of bycatch as an indicator of ecological recovery, bycatch should nevertheless continue to be regarded as an undesirable outcome of fish eradication campaigns. Efforts should therefore be made to minimize bycatch, monitor it to ensure that it remains within acceptable levels, implementing corrective measures when necessary.

For the vast majority of cases, bycatch involved species and methods with low associated mortality, and the observed incidental captures did not prevent clear population increases, as evidenced both by bycatch data and independent monitoring. This general consideration applies to all amphibians in our study area, whose positive demographic responses overwhelmingly compensate for any mortality caused by capture devices (e.g., Miró et al., 2020). However, caution is warranted before generalizing this conclusion to all habitats and species.

With regard to habitat characteristics, the difference in amphibian mortality in fyke nets between the Alps and the Pyrenees (Table 2)

suggests that mortality may depend on local environmental conditions, as Pyrenean lakes sampled with fyke nets are generally at lower elevations and lower latitudes than Alpine sites (Table 1), resulting in warmer summer conditions that may increase metabolic stress and reduce oxygen availability for trapped individuals.

In contrast, species-specific conservation status can fundamentally alter acceptable levels of bycatch mortality. In a recent fish eradication effort aimed at protecting a threatened, micro-endemic, and highly endangered subspecies of high-mountain newt (*Mesotriton alpestris inexpectatus*), any level of mortality associated with gillnetting was deemed excessively risky (Bernabò et al., 2023). Consequently, the eradication plan allows only methods expected to entail negligible mortality for newts, such as fyke-nets.

In other cases, particularly for birds and mammals with higher dispersal ability and variable susceptibility to gillnets or fyke-nets, increases in bycatch may not reflect true population growth. For instance, white throated dippers may be attracted to the lakes undergoing fish eradication due to higher prey availability and consequently spend more time in the area, making them more susceptible to capture independent of any local population trend. In such situations, lakes under restoration actions may temporarily function as ecological traps, where increasingly attractive conditions elevate capture risk. Nevertheless, the conservation status of these species, both locally and globally, does not raise immediate concern (BirdLife International, 2018; Hutterer et al., 2016), nor does the mortality associated with eradication activities. In these cases, although immediate population increases cannot be taken for granted, long-term benefits, such as the availability of previously inaccessible foraging habitats, are expected to enhance population density and fitness for future generations, thereby compensating for temporary losses.

A special and illustrative case is the incidental capture of desman (*Galemys pyrenaicus*). Although this species was rarely caught, its endangered conservation status (Aymerich and Gosàlbez, 2018; Quaglietta et al., 2024) means that the loss of even three individuals in a single lake represents a serious event. Unlike amphibians, and similar to dippers, incidental captures of desman cannot be interpreted as intrinsically positive, as there is no evidence from independent monitoring that population increases occurred. A cautious interpretation therefore suggests that incidental captures may have caused a net population loss, not readily compensated by recruitment. Unlike dippers or water shrews, the precarious conservation status of the desman prevents us from assuming that the long-term benefits of eradication actions will offset short-term losses and ultimately eliminate the concern. The incidental capture of highly threatened species should always be included in a formal risk assessment, or, if not possible (e.g., because of knowledge gaps), addressed immediately as soon as the issue arises, through adaptive management of eradication interventions. In our case, desman captures were unforeseen due to: 1) the lack of previous experience indicating its presence in nearby lakes subject to similar eradications, 2) the limited knowledge of desman use of lentic habitats, which were previously assumed to be marginal habitats for the desman (Aymerich and Gosàlbez, 2018), and 3) the absence of previous reports of desman in the lake area targeted by the intervention. Therefore, a risk for this species could not have been anticipated by the project staff. Following the first desman capture, awareness of the issue was raised, but it was considered an exceptional and non-replicable event. After the second incident, involving two individuals simultaneously, an adaptive management response was immediately implemented. Protective nylon nets were installed at fyke-net entrances in areas with potential desman presence, with mesh large enough to allow fish to enter but preventing desman access. This corrective measure effectively halted further desman bycatch. Importantly, these incidents provided critical new insights into desman habitat use and distribution in the study area, advancing ecological knowledge, and established a new biosecurity standard for eradication actions in habitats hosting threatened semi-aquatic species, advancing conservation techniques. This case highlights that even low levels of mortality in rare or threatened species warrant careful ethical and conservation consideration, as well as prompt corrective action.

Invasive species are already recognized as threats to the desman, particularly the American mink, and potential impacts of invasive crayfish (*Procambarus clarkii* and *Pacifastacus leniusculus*) have also been highlighted (Quaglietta et al., 2024). Yet, no studies have addressed whether invasive fish might negatively affect desman by competing for the same prey, despite evidence that other semi-aquatic insectivores, such as water shrews (Bello et al., 2024) or white throated dippers (present study), respond to similar trophic pressures. Addressing this knowledge gap, a comparative study of desman presence in lentic and lotic habitats, invaded or uninvaded by non-native fish and integrated with prey availability data, could clarify ecological impacts and inform conservation strategies.

CRediT authorship contribution statement

Rocco Tiberti: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Lucia Bello:** Writing – review & editing, Writing – original draft, Investigation, Data curation, Conceptualization. **Teresa Buchaca:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Funding acquisition. **Anna Corapi:** Writing – review & editing, Investigation. **Giorgia Mattioli:** Writing – review & editing, Investigation. **Víctor Osorio:** Writing – review & editing, Investigation. **Quim Pou Rovira:** Writing – review & editing, Investigation, Funding acquisition. **Ibor Sabás:** Writing – review & editing, Investigation. **Marc Ventura:** Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

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Data availability

Data will be made available on request.

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