Alien fish eradication from high mountain lakes by multiple removal methods: estimating residual abundance and eradication probability in open populations.

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Complete List of Authors:	Tiberti, Rocco; Universita degli Studi di Pavia, Buchaca, Teresa; Spanish National Research Council, Centre for Advanced Studies of Blanes Boiano, Danny; National Park Service, Sequoia and Kings Canyon National Parks Knapp, Roland; University of California Pou Rovira, Quim; Sorello Tavecchia, Giacomo; Consejo Superior de Investigacion Cientifica, IMEDEA Ventura, Marc; Center for Advanced Studies of blanes, Limnology Unit Tenan, Simone; MUSE
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1 **Alien fish eradication from high mountain lakes by multiple removal methods: estimating residual**
2 **abundance and eradication probability in open populations.**

3
4 Rocco Tiberti^{1§}, Teresa Buchaca², Daniel Boiano³, Roland A. Knapp⁴, Quim Pou Rovira⁵, Giacomo
5 Tavecchia⁶, Marc Ventura², Simone Tenan^{7§}.

6
7 ¹ Water Research Institute - National Research Council (IRSA-CNR), Largo Tonolli 50, 28922 Verbania,
8 Italy.

9 ² Integrative Freshwater Ecology Group, Centre for Advanced Studies of Blanes (CEAB-CSIC), Accés Cala
10 St. Francesc, 14, 17300 Blanes, Catalonia, Spain.

11 ³ National Park Service, Sequoia and Kings Canyon National Parks, 47050 Generals Hwy, Three Rivers,
12 California 93271, USA.

13 ⁴ Sierra Nevada Aquatic Research Laboratory, University of California, Mammoth Lakes, California 93546
14 USA.

15 ⁵ Sorelló, Estudis al Medi Aquàtic, Parc Científic i Tecnològic de la Universitat de Girona 17003, Girona,
16 Spain.

17 ⁶ Animal demography and Ecology Unit (GEDA), IMEDEA (CSIC-UIB), c M. Marques 21, 07190 Esporles,
18 Spain.

19 ⁷ Institute of Marine Sciences, National Research Council (CNR-ISMAR), Arsenale, Tesa 104, Castello
20 2737/F, 30122 Venezia, Italy.

21 § RT and ST contributed equally to the paper

22
23 Correspondence author: Rocco Tiberti; IRSA-CNR, Largo Tonolli 50, 28922 Verbania, Italy; email:
24 rocco.tiberti@gmail.com

26 Abstract

27

- 28 1. Invasive alien species are among the most important threats to biodiversity. Plans for their eradication
29 have been implemented worldwide but estimating residual population size and eradication probability to
30 assess removal success is complicated by the imperfect detection of residual individuals.
- 31 2. Most methods to assess residual abundance and eradication probability rely on the often unrealistic
32 assumption that a population is closed to mortality and recruitment processes during the implementation
33 of removal actions. We extended existing removal models and developed a novel analytical approach to
34 estimate residual population size and derive eradication probability in open populations, while
35 accounting for multiple removal methods.
- 36 3. We apply this approach to 20 eradication projects in Europe and the United States that used mechanical
37 methods to return high mountain lakes to their original fishless condition.
- 38 4. The new removal model incorporates i) a mechanistic description of the ecological process underlying
39 survival and recruitment probabilities during the eradication period, and ii) the use of multiple,
40 concomitant removal methods (i.e., electrofishing, gillnetting, fyke-netting) at multiple sites
41 simultaneously.
- 42 5. We used a subset of “control” lakes where eradication success was confirmed by more than 5 years of
43 post-removal surveys to validate the model. For these lakes, eradication success, evaluated by whether
44 the 95% Bayesian credible interval for estimated residual population size encompassed values of less
45 than 2 individuals, was confirmed in 13 out of 15 lake-by-species case studies. In addition, the model
46 correctly assigned an eradication probabilities equal to 0 for the eradications that are still in progress.
- 47 6. *Synthesis and applications.* Our study provides insights into the dynamics of fish populations subject to
48 eradication in high mountain lakes of different countries. In addition, the analytical approach proposed
49 accounts for demographic processes and multiple removal methods in multiple sites and seasons. It can
50 represent an informative tool to estimate residual population size and eradication probability of alien
51 species to optimize eradication efforts and efficacy of conservation actions. The extension to open
52 populations makes the approach useful to evaluate long-term eradication plans.

53

54 **Keywords.** Adaptive management, Eradication success, High mountain lakes, Protected areas, Recovery,
55 Removal models.

56

57 **INTRODUCTION**

58

59 High mountain lakes are isolated ecosystems originally devoid of fish fauna, but introducing game fish (i.e.,
60 trout) and their live-baits (i.e., minnows) is very common and popular all over the world with dramatic
61 ecological consequences (Ventura et al., 2017). Due to the magnitude of the ecological impact and to the
62 global extent of fish introductions into mountain lakes, introduced fish are perhaps the most important threat
63 to mountain lake biodiversity (Knapp, Matthews, & Sarnelle. 2001). Recently, based on scientific evidence
64 and despite the popular appeal of fish stocking, officials and conservation-minded anglers have begun to take
65 action to mitigate the damage (Conniff, 2017). Several conservation projects in the United States (US)
66 (Knapp & Matthews 1998; Knapp et al., 2001; Vredenburg, 2004; Knapp, Boiano, & Vredenburg, 2007;
67 NPS, 2013), Canada (Parker, Schindler, Donald, & Anderson, 2001; Pacas & Taylor 2015), and Europe
68 (Tiberti et al., 2019; Toro et al., 2020) applied mechanical eradication methods to recover the native
69 biodiversity of high mountain lakes.

70 Even if biological invasions are an irreversible global process (IUCN, 2000), alien species
71 eradication is part of the general strategy to prevent biotic homogenization worldwide (Clout & Veitch
72 2002). The eradication of alien species can be achieved during the early stages of the invasions, before the
73 invaders uncontrollably spread (e.g., Bertolino & Genovesi 2003; Rout, Thompson, & McCarthy 2009;
74 Tavecchia et al. 2017) or when the invaders are constrained by ecological barriers within isolated habitat
75 patches (e.g., ecological islands) as it is the case for mountain lakes. However, even in these cases, both
76 under- and over-estimating the effort needed to eradicate alien species results in a waste of human and
77 economic resources. The cost of effort misjudgement is not only monetary. Inefficient plans can affect the
78 confidence of people and stakeholders in eradication actions. Also, underestimating the effort needed to
79 eradicate invasive species can lead to species re-invasion from residual individuals (Rout et al. 2009; Rout,
80 Kirkwood, Sutherland, Murphy, & McCarthy, 2014), whereas prolonging eradication actions would incur in
81 additive monetary and ecological costs. For example, Tiberti et al. (2019) observed a 30% increase of
82 bycatch mortality of non-target species attributable to a precautionary prolonging of the eradication efforts of

83 alien fish from a mountain lake. However, forecasting the optimal effort is a challenging task due to the
84 problem of imperfect detection and resulting uncertainty as to whether an invasive alien species has been
85 successfully eradicated or not (Rout et al. 2009, 2014). Multiple analytical approaches that account for
86 imperfect detection and allow estimation of residual population size are available in the ecological literature
87 (e.g. Davis et al., 2016, Dorazio, Jelks, & Jordan, 2005, Ruiz & Laplanche 2010, Sakamoto, Kumagai, &
88 Goka, 2017, Tenan et al., 2016). These approaches rely on the assumption that populations are closed to
89 births, deaths, emigration, and immigration during the removal period (Kéry & Royle, 2015, but see
90 Matechou et al. 2016 and Zhou, McCrea, Matechou, Cole, & Griffiths, et al. 2019). However, when
91 populations are sampled during multiple seasons, assuming population closure becomes unrealistic and can
92 lead to biased estimates.

93 We present a multi-season removal model that (i) allows the study population to be open to entries
94 (via local recruitment) and exits (via mortality) of individuals, (ii) accounts for multiple removal methods,
95 and (iii) quantifies the residual population size and the eradication probability of alien species during the
96 eradication process. We apply this analytical approach to real data from 20 high mountain lakes from which
97 eradication of alien fish was attempted using up to three mechanical methods (electrofishing, gillnetting, and
98 fyke-netting). We used data on the eradication of both introduced Salmonidae and Cyprinidae (i.e., minnows
99 *Phoxinus* sp.), whose use as live baits for trout fishing is causing widespread and impactful collateral
100 introductions, mainly in European mountains (Miró & Ventura, 2015). These data include a substantial part
101 of all the existing data on trout eradication and the totality of existing data on minnow eradication from
102 mountain lakes using mechanical methods, therefore representing a precious and varied source of
103 information. Our objective is to provide a realistic analytical approach to assess the eradication probabilities
104 and residual sizes of fish populations, on the basis of which to outline evidence-based guidelines on alien
105 fish eradication during the removal effort. By using data from multiple countries (US and Europe), including
106 lakes with different features (e.g., size, habitat complexity) and that target four alien fish species, we were
107 able to assess the large-scale application of our modelling approach.

108 MATERIALS AND METHODS

109 Data

110 Alien fish eradication data were collected between 1997 and 2018 in 20 lakes in three mountain ranges:
111 Sierra Nevada (California, US), Pyrenees (Catalonia, Spain), and Alps (Italy) (Table 1). All the study lakes

were originally fishless but were stocked during the 1900s or before (i.e., Lakes Dellui, Pyrenees; Miró & Ventura, 2013, 2015) with several fish species which established self-sustaining populations. Given their location at or above timberline, all lakes experience similar climatic conditions, but represent a wide range of abiotic and biotic characteristics, including elevation, latitude, surface area, depth, water chemistry, habitat complexity, and species of alien fish. These differences may influence the efforts needed to complete the eradication (Knapp & Matthews, 1998; Tiberti et al., 2019) and the required eradication methods (Table 2).

Fish were removed using intensive gillnetting, electrofishing, and fyke-netting (Table 2). Intensive gillnetting was used in all lakes and is the main eradication method for salmonids; a variable number of gillnets (usually > 10 nets ha^{-1}) were deployed continuously in each lake during the fish eradication period, including during winter ice-cover (further details in Knapp et al. 2007; Tiberti et al., 2019). Electrofishing in the littoral area (e.g., among littoral vegetation) was used in many lakes to support the eradication efforts and is the main eradication method along the inflowing and outflowing streams that are also inhabited by the introduced fish. Intensive fyke-netting was used together with electrofishing and gillnetting to remove minnows (*Phoxinus* sp., fam. Cyprinidae) from some lakes in the Pyrenees. In addition, a two-day rod-angling session substantially contributed to the decline of the population in L. Dres at the beginning of the eradication campaign (Tiberti et al. 2019), but rod-angling data were not included in the present article because this method was used only once. Similarly, captures obtained by the occasional electrofishing (i.e., less than 4 times per season) were not used. All the study lakes freeze during 6-9 months per year and fish were removed in the ice-free periods during multiple removal occasions. Removal date, species, and capture methods were recorded for each fish. Finally, the species-specific number of fish removed was summarized and modelled for each lake during each removal occasion in each season, within a robust design-type of data structure (Pollock, 1982) where multiple removal sessions (called secondary occasions) are nested within seasons (or primary occasions; from 01/09 to 31/08) (Fig. 1). Populations are assumed closed for the whole duration of each season, and individuals are assumed to enter or leave the population only between seasons, with local recruits born in the previous session available for capture from 01/09. A graphic description of the sampling and analytical concepts described above is reported in Figure 1, which is intended to drive the readers through the formulation of the removal model.

All lakes underwent annual visual inspections for possible fish reinvasions after the eradication actions (i.e., after the removal of the nets). Considering the high reproductive potential of both salmonids and

minnows, fish would take 2-3 generations to re-establish abundant populations (Cooper, 1962), making reinvasions clearly visible within 2-5 years after the removal of the last fish. We therefore identified a subset of 14 “control lakes” (15 lake-by-species eradication actions) where at least five years (5-19) had passed since the last fish capture and without subsequent observations of fish (Table 1). We validated our model with these control lakes where eradication success was confirmed by such a long period of post-removal monitoring. The remaining six lakes (8 lakes-by-species) are lakes from the Pyrenees where the eradication actions started later (2015-2016) and where the eradication is still in progress, or believed to be completed, but with a period of post-removal monitoring shorter than 5 years. For the control lakes, the estimated eradication probability is expected to be high - ideally close to 1.00 - and the residual population close to 0. For the remaining lakes, the estimated eradication probabilities and population sizes are expected to be more variable and to include some zero probability values for the lakes where the eradication is still in progress.

Modelling approach

We extended the original formulation of a the model for removal counts developed by Dorazio et al. (2005) to account for a two-stage (multi-season) temporal sampling scheme, where the population is assumed open between primary occasions (seasons in our case) but closed between secondary (i.e. within-primary) occasions as in a ‘robust design’ sampling scheme (Kendall, Nichols, & Hines, 1997; Pollock, 1982). Secondary occasions thus represent removal occasions, i.e. days during which fish were removed. Our open-population removal model provides estimates of population size at spatially distinct sites (i.e., lakes) by modelling population dynamics using two demographic parameters, recruitment (via reproduction, since immigration was absent in our case) and survival probability (Dail & Madsen, 2011) while accounting for imperfect detection (i.e. capture probability < 1) from removal counts only. The model is based on a state-space formulation (De Valpine & Hastings, 2002), namely a set of equations that specify the hidden ecological (or state) process, which is the target of our inference, and (conditional on the ecological process) the observation process, i.e., the stochastic mechanism that generated the data (i.e. the removal process; Royle & Dorazio, 2008). In this formulation, let $N_{i,t}$ be the unknown number of individuals of a certain species available to be captured (and removed) in population $i = 1, \dots, I$ (with $I = 23$, here represented by lake-by-species case studies), in season $t = 1, \dots, T_i$. Sampling yields vector y_{it} of the number of unique individuals of a certain species captured and removed from population i in season t . Animals are removed

during J_{TOT} secondary occasions (Fig. 1) for all sites, with $y_{i,t,j}$ denoting the number of individuals removed at site i (note that site is a lake-species combination) in season t and sampling occasion $j = 1, \dots, J_{TOT}$.

The number of animals removed is the result of two stochastic processes, (i) the state or ecological process which describes changes in time of local abundances ($N_{i,t}$) through births and deaths, and (ii) the observation process which links the observed individuals $y_{i,t,j}$ to the abundances. The state or ecological process is specified through the following distributional assumptions:

$$N_{i,1} \sim \text{Poisson}(\lambda_i) \quad (\text{for } t = 1) \quad \text{Eq. 1}$$

$$S_{i,t} \sim \text{Binomial}(N_{RES,i,t-1}, \omega_{i,t}) \quad (\text{for } t = 2, \dots, T) \quad \text{Eq. 2}$$

$$G_{i,t} \sim \text{Poisson}(\gamma_i N_{i,t-1}) \quad (\text{for } t = 2, \dots, T) \quad \text{Eq. 3}$$

$$N_{i,t} = S_{i,t} + G_{i,t} \quad \text{Eq. 4}$$

where λ_i is the expected abundance for population i during the first season ($t = 1$), $S_{i,t}$ is the number of individuals that survive from time $t-1$ to t and remain at the same site, $G_{i,t}$ is the number of individuals that were gained through local recruitment, $\omega_{i,t}$ is the apparent survival probability, γ_i is the arrival rate of individuals, and $N_{RES,i,t} = N_{i,t} - n_{TOT,i,t}$ denotes the residual population size after J_{TOT} removals (using one or multiple methods), with the total number of animals removed $n_{TOT,i,t} = \sum_{j=1}^{J_{TOT}} n_{i,t,j}$.

The observation process is expressed by conditioning on the total number of individuals removed ($n_{TOT,i,t}$) in each season and lake:

$$n_{TOT,i,t} \sim \text{Binomial}(1 - \pi_{0i,t}, N_{i,t}) \quad \text{Eq. 5}$$

with $\pi_{0i,t}$ representing the probability of not being captured, and the site-by-year-by-occasion specific number of removed individuals ($y_{i,t,j}$) described as follows:

$$y_{i,t,j} \sim \text{Multinomial}(\boldsymbol{\pi}_{i,t,j}^c, n_{TOT,i,t}) \quad \text{Eq. 6}$$

with probability vector $\pi_{i,t,j}^c$ composed of occasion-specific probabilities $\pi_{i,t,j}^c = \pi_{i,t,j} / (1 - \pi_{0,i,t})$, where $\pi_{0,i,t} = 1 - \sum_{j=1}^{J_{TOT}} \pi_{i,t,j}$. In other words, the number of individuals removed during each sampling occasion, lake and season ($y_{i,t,j}$) derives from the total number of individuals captured in each lake and season ($n_{TOT,it}$) and the related occasion-specific capture probabilities ($\pi_{i,t,j}^c$). We extended the classical single-removal method formulation to account for multiple method-specific probabilities of capture $p_m = \{pE, pG, pF\}$ (pE for electrofishing, pG for gillnetting, and pF for fyke-netting). The multinomial cell probabilities ($\pi_{i,t,j}$) were expressed as a function of capture probabilities as follows, depending on whether a removal method m was used (mUS) or not (mUN) during each sampling occasion j :

$$\pi_{i,t,j} = p_{mUS,i,t,j} (1 - p_{mUS,i,t,j})^{j-1} (1 - p_{mUN,i,t,j})^j \quad \text{for } j=1, \dots, J_{TOT}. \quad \text{Eq. 7}$$

We also used a removal operation matrix A , with dimension $I \times T_{max} \times J_{TOT}$ and with $T_{max} = \max(\mathbf{T})$, as a binary indicator denoting whether a specific type of removal sampling was carried out during each sampling occasion:

$$\pi_{i,t,j} = \pi_{i,t,j} A_{i,t,j}.$$

Capture probabilities can be expressed as a function of covariates to improve inference, such as the effect of seasonality:

$$\text{logit}(p_{*,i,t,j}) = \alpha_{p*,i} + \beta_{1,i} \text{date}_{i,t,j} + \beta_{2,i} \text{date}_{i,t,j}^2 \quad \text{Eq. 8}$$

with $p_* = \{pE, pG, pF\}$. In the general model we specified lake-specific time-invariant capture probabilities. However, for a subset of lakes we also tested whether the inclusion of seasonality in the observation model improved estimates of eradication probability (see below).

Duration of removal activity varied between 3 and 9 seasons (median 5) and it was ≥ 5 years for 14 over 23 lake-by-species case studies. In consideration of that, time-varying apparent survival was modelled with random time variation for lake-by-species sampled during more than five years and with fixed-time effects for lake-by-species sampled during shorter periods:

$$\text{logit}(\omega_{i,t}) = \alpha_{\omega,i} + \varepsilon_{i,t} \quad \text{with } \varepsilon_{i,t} \sim \text{Normal}(0, \sigma_{\omega}^2) \quad \text{for } T_i \geq 5 \text{ years} \quad \text{Eq. 9}$$

$$\text{logit}(\omega_{i,t}) = \alpha_{\omega,i} + \text{year}_{i,t} \quad \text{for } T_i < 5 \text{ years} \quad \text{Eq. 10}$$

Modelling survival using parameters in common across lake-by-species case studies, and thus using a single linear predictor for all case studies, is possible in this framework, as well as sharing parameters among lakes

224 or species only. However, given the diversity of conditions for each lake-by-species case study we decided
225 not to share parameters across lakes.

226 Arrival rate of individuals (γ_i) was modelled as a time-invariant lake-by-species parameter.

227 As a metric of successful eradication, we evaluated whether the 95% Bayesian credible interval (BCI)
228 for residual population size ($N_{RES,i}$) estimated in the final season of sampling encompassed values of < 2
229 individuals (for species with sexual reproduction and external egg fertilization, a single individuals cannot be
230 considered a population founder). In addition, lake, species and season-specific eradication probabilities
231 were derived in the model as the probability that residual population size $N_{RES,i,t} < 2$.

232 We used posterior predictive checks, summarized by the Bayesian p -value, to assessed model fit for
233 both the observed lake-by-season-by-occasion specific data ($y_{i,t,j}$) and the (observed) total number of
234 individuals removed ($n_{TOT,i,t}$), the two components of the observation process (see specific section in
235 Appendix A). We used Uniform(0,1) priors for survival intercepts on the probability scale (i.e. $\text{logit}^{-1}(\alpha_{\omega,i})$)
236 and the removal probabilities (pE, pG, pF), Uniform(0,10) priors for the arrival rates of individuals (γ_i) and
237 for the temporal random standard deviations for survival probability (σ_{ω}), and Normal(0,2.25) priors
238 (Guillera-Arroita, Kéry, Lahoz-Monfort., 2019) for the fixed year effects ($\text{year}_{i,t}$) and for the quadratic effect
239 of date ($\beta_{1,i}, \beta_{2,i}$) on removal probabilities. For further details on prior specification of model parameters, see
240 model code in Supporting Information.

241 Models were fitted using Markov chain Monte Carlo (MCMC) and results are based on 30,000 post
242 burn-in posterior samples (3 chains, thinning of 50, and burn-in of 2,000,000). To assess model convergence,
243 we used the Gelman–Rubin statistic, whose values were always < 1.1 thus indicating convergence (Brooks &
244 Gelman, 1998). The effective sample size was on average 17,370 among all parameters (see Appendix A,
245 Table S1 for further details). Models were implemented using program JAGS (Plummer, 2003) executed
246 from R (R Core Team, 2018) using R package jagsUI (Kellner, 2019).

247 RESULTS

248 The number of fish removed and the eradication efforts (Table 2) varied greatly among lakes, with minnows
249 being particularly hard to eradicate and often constituting very abundant populations (Table 2; Fig. 2). In L.
250 Cony and L. Dellui Nord, only a few rainbow and brown trout respectively were removed, probably non-
251 reproductive individuals from recent stocking events or residual individuals from a sharp decline due to the
252 massive proliferation of the minnows. The number of removed fish reached zero in the last season of the

253 eradication period or earlier in 19 of the 23 lake-by-species removal studies (Table 2). Usually, most fish in
254 the populations were removed in the first 1-3 seasons (Table 2; Fig. 2, dotted line), producing a rapid decline
255 of the population sizes estimated by the model (Fig. 2, solid line).

256 In all the cases, the estimates of the residual population sizes indicated a rapid decline of the treated
257 populations (e.g., 58.3-99.8% decline at the end of the third season, 70.2-100% at the end of the fourth
258 season). As a measure of successful eradication, the 95% Bayesian credible interval (95% BCI) for the
259 estimate of residual population size in the last season of sampling encompassed values of < 2 individuals in
260 85% of the lake-by-species case studies (Table 3 and Fig. 2).

261 Considering the 14 control lakes (15 lake-by-species case studies) where eradication success was
262 confirmed by at least 5 years of post-eradication surveys, successful eradication was confirmed in 13 out of
263 the 15 removal studies (Table 3). For these case studies we expected an eradication probability close to 1.00
264 at the end of the study, but the average eradication probability was 0.57 ± 0.35 (mean $\pm$ SD). Despite that,
265 probability of eradication increased over the course of each lake-by-species eradication time series (Table 3).
266 The eradication probabilities and the residual population sizes in the Pyrenean lakes - where eradication
267 efforts started later - varied greatly (mean $\pm$ SD = 0.24 ± 0.43 ; Table 3), but as expected, was lower than for
268 control lakes. This is because in some Pyrenean lakes the eradication was still incomplete (residual fish
269 captured during the last sampling season) and the eradication probability equal to 0 (Table 2 and 3).

270 In 11 lake-by-species case studies the 95% BCI for the estimate of residual population size
271 encompassed values of < 2 individuals before the last season of sampling (Table 3). Therefore, on the basis
272 of model estimates, and as supported by empirical data, in some of these case studies the eradication effort
273 could have been stopped earlier. Not in all cases, because efforts cannot be stopped if a second species is still
274 to be eradicated, such as in L. CON, DEM, and DEN (Tables 2 and 3). An earlier stop of the eradication
275 effort in the remaining eight lakes would have led to a shortening of the eradication actions of 245 days on
276 average. On the same basis, the model would have suggested continuing eradication in seven lake-by-species
277 case studies ($Er=0$; Table 3). As mentioned above, two of these case studies (DRE and CON) are control
278 lakes, where eradication has been confirmed, while the remaining five case studies are Pyrenean lakes still in
279 the process of eradication.

280 The lower eradication probabilities and larger residual populations were usually recorded in Pyrenean
281 lakes containing minnows. In these lakes, minnows were very abundant and less catchable than salmonids, as

282 indicated by the lower method-specific capture probabilities (Table 4). For example, gillnetting probability is
283 about six times smaller for minnows (median= 0.01) than for salmonids (median=0.06), which may
284 underline the need to use more gillnets or alternative removal methods, i.e., electrofishing and fyke-netting.
285 These alternative removal methods are generally not essential to eradicate salmonids, but are the most
286 efficient removal methods for minnows. More generally, capture probabilities varied more under gillnetting
287 than the other methods (Figure 3). In addition, the inclusion of seasonality on the removal method-specific
288 probabilities did not substantially improve estimates of eradication probability, except for the L. Leynir case
289 for which eradication probability in the last year of sampling increased from 0.253 (in the general model) to
290 0.850. However, a successful eradication by the last year of sampling was estimated under both models
291 (Figure S1 in Appendix A).

292 Our model also provides some important population parameters such as recruitment and survival
293 probabilities which may influence the site-specific eradication efforts and enable evaluations/corrections of
294 ongoing eradication programs. Recruitment probability (γ_i) ranged, on average, from a minimum of 0.003 for
295 the rainbow trout population in L. UB3 to a maximum of 0.23 for the minnow population in L. Dellui Nord,
296 and was generally higher for minnows (mean= 0.150, 95% BCI 0.091-0.227) than for salmonids (mean=
297 0.079, 0.003-0.198) (Figure 3). Temporal random standard deviation of apparent survival probability (σ_w) for
298 lakes sampled during long periods (≥ 5 years) varied, on average, from 3.314 (for minnows from L. Naorte) to
299 8.523 (for brook trout from L. Dres), suggesting substantial variation of survival probability during the
300 different study periods (Figure S2 in Appendix S1). This was also evident in year-specific survival estimates
301 for lakes sampled for short periods (Figure S2 in Appendix S1).

302 **DISCUSSION**

303 Our study provides insights into the eradication process of alien fish from 20 high mountain lakes (23 lake-
304 by-species cases) in the US and Europe by multiple removal methods. We developed an analytical approach
305 for estimating residual population size and eradication probability while accounting for population dynamics
306 (via recruitment and mortality) and imperfect detection. Mountain lakes represent an interesting system
307 because they are often closed to new colonization but not to local recruitment and their original state can be
308 successfully recovered after eradication of alien species (Knapp et al. 2001; Tiberti et al., 2019). Many fish
309 eradication efforts to date have been motivated by an interest in recovering native amphibians (Vredenburg
310 et al., 2004; Knapp et al., 2007; Knapp et al., 2016). However, eradications have the potential to produce

311 broad ecosystem benefits, including the recovery of aquatic invertebrate communities (Knapp et al., 2001;
312 Tiberti et al., 2019), trophic state (Schindler, Knapp, & Leavitt, 2001), and the ecological connection with
313 surrounding terrestrial habitats (Epanchin, Knapp, & Lawler, 2016).

314 Eradication of alien species is part of a general strategy to counteract biotic homogenization worldwide
315 (Clout & Veitch, 2002) and promote ecosystem recovery. Because little guidance on eradication methods
316 and outcomes is available in the scientific literature, decisions by environmental managers regarding a
317 specific eradication projects are often based on limited information (Drolet, Locke, Lewis, & Davidson,
318 2014; Pullin, Knight, Stone, & Charman, 2004). A major challenge for environmental and conservation
319 scientists is to promote evidence-based environmental management by providing environmental managers
320 with tools that incorporate data and adaptive management in the decision-making process (Sutherland &
321 Freckleton, 2012). We developed our model as a tool providing evidence-based guidelines on alien species
322 eradication. By extending existing removal models, our objective in this study was to provide a more
323 realistic analytical approach to estimate residual population size during the eradication effort of alien fish
324 than spanned multiple seasons and thus must account for population openness. Such an approach can assist
325 managers in optimizing resources and avoiding additional costs associated with ending an eradication effort
326 too early in the process (resulting in eradication failure) or continuing the eradication effort after eradication
327 is in fact complete. The model also allows the inclusion of multiple mechanical (non-chemical) removal
328 techniques used simultaneously. In the next paragraphs we discuss separately the applications of our model
329 to the specific case of alien fish in mountain lakes and its applications to alien species management in
330 general.

331 **Model applications and decision analysis for fish eradications**

332 Estimates of the residual population size, method-specific capture probabilities, and demographic parameters
333 (e.g., recruitment) from the model we propose can be used during the eradication i) to decide when to end
334 eradication effort, ii) to better analyse the feasibility of an eradication action already started (e.g., given the
335 available capture devices and resources), and iii), in general, for a rational allocation of the eradication
336 efforts (e.g., planning the field surveys and preferred removal methods). Users must account for the fact that
337 a minimum of three sampling seasons are required to estimate survival, otherwise other static (i.e. single
338 season) removal models are recommended (e.g. Dorazio, Jelks, & Jordan, 2005, Kéry & Royle, 2015, but see
339 Matechou et al. 2016 and Zhou, McCrea, Matechou, Cole, & Griffiths, et al. 2019).

Residual population size and eradication probability. In the absence of quantitative methods supporting decision analysis, an ad hoc “wait and see” strategy is often adopted to decide when the eradication efforts can be stopped, while the eradication strategy (e.g., number of capture devices and sessions) exclusively depends on expert advices and available resources. During the waiting period, eradication efforts continue to ensure that no fish remain, and the duration of this period can vary among studies, from one summer to 1–2 years (Knapp & Matthews, 1998; Knapp et al., 2007; Tiberti et al., 2019; Daniel Boiano, personal communication). Reappearance of fish at eradication sites after this period has never been reported (see Tiberti et al., 2019 and references therein), which denote the good predictive abilities of experts, usually achieved thanks to their direct engagement in eradication actions and on the prolonged observation of the treated lakes. However, the variable duration of this monitoring period can result in significant unnecessary costs. Our model allows the estimation of residual population size (and the derived eradication probability) that provides a consistent and defensible basis for decisions regarding when to end eradication efforts. In this regard, model results usually match the expert predictions (i.e., population size dropped down to <2 in the last season) or perform slightly better, indicating that eradication were already completed in the seasons before the end of the actions (Table 3). In the latter case, deciding the end of eradication efforts based on the model estimates would have helped in saving resources. The fact that model results on the eradication end date match the expert predictions suggests that model output is realistic and crude removal data can be used to monitor eradication actions, i.e., eradication trends can be evaluated even when the experts are not in the field and fieldwork is delegated to less experienced personnel (e.g., park wardens, volunteers, field crews, etc.). This would provide further economic advantages in terms of personnel costs and increase the replicability of well-designed eradication actions where specific technical experiences and knowhow are not available.

Considering the control lakes where eradication success was confirmed by several years of surveys following the capture of the last fish, eradication probability estimates were lower than expected. However, for the last year of sampling, the 95% Bayesian credible interval for the estimate of residual population size encompassed values lower than two individuals in most cases and the estimated population sizes were very low in all the control lakes, suggesting eradication success. In addition, by using an endpoint of <2 individuals remaining, our approach may be conservative because it does not take into account the possible consequences of an Allee effect at low population sizes (Liebhold & Bascompte, 2003). Allee effects refer to

a decline in individual fitness at low population size or density, and often lead to population extirpation when population size or density falls below a minimum level. If Allee effects are strong, in theory complete eradication could be achieved by reducing populations below a minimum number, rather than capturing all individuals. However, for mountain lakes and introduced fish, we believe that Allee effects play a minimal role in the eradication process and, based on our experience, the eradication of alien fish populations from mountain lakes is achieved only after the removal of all fish.

Population parameters and method-specific capture probabilities. Apart of the eradication probability, our model provided estimates of the residual population, survival and recruitment, and method-specific capture probabilities which may be used in an adaptive management framework to evaluate the eradication actions, adjust the eradication efforts and minimize unnecessary costs. In this regard, one advantage of our model is to provide specific lake-by-species survival and recruitment estimates, and lake-by-species removal probabilities for each removal method (Fig. 3). These parameters can provide valuable information for evaluating how the eradication actions proceed and, at the same time, an early-warning to correct insufficient eradication strategies. Examples of the latter include increasing the eradication efforts when the removal probabilities are very low or relaxing the efforts when removal probabilities are high enough to achieve the eradication within the projected date. In a similar way we showed that minnow eradication requires the use of a plurality of methods due to the low removal probability by gillnets alone. In general, if recruitment is high (e.g., ≈ 0.2) and capture probability is low, eradication is expected to become harder. However, it is not clear how much time and field-work could be saved using such parameters to adapt the eradication strategies.

Outreach and communication. The social dimension inherent to invasive species management is a factor of pivotal importance (Estévez, Anderson, Pizarro, & Burgman, 2015) and the outputs of our model can be also used for public education, communication to the public and stakeholders, and project reporting. Eradicating alien fish from mountain lakes is also a matter of public opinion and social context, which are an integral part of the eradication efforts and which should be taken into account to avoid social opposition and sabotage. Providing updated estimates of the residual population sizes as well as of the eradication probability could be a powerful communication tool. The ability of providing quantitative data during long eradication processes could maintain the confidence of the public and stakeholders and avoid conflicts.

Strengths, limits and broad applicability of the modelling approach

Our model accounts for demographic processes and multiple removal methods in multiple sites and seasons and can be useful to evaluate long-term eradication plans. The multi-site framework used here not only allows the simultaneous estimation of eradication success in different populations, but also permits the inclusion of site-specific covariates. This allows testing of hypotheses about factors affecting demographic rates and capture probabilities across sites. In addition, when ecologically sensible, sharing parameters across sites can facilitate inference for sites with limited amounts of information. In theory, there is no limit to the number and combination of removal methods that can be applied and modeled at single sites. However, we note that large variability of removal methods across sites or site-by-species combinations, as was the case in the current study, can make it hard to identify a single adequate model structure for all site-by-species cases. In this situation, users may opt for a single-site formulation of the model. The model formulation we used allows for a mechanistic description of the ecological process by distinguishing between survival and recruitment parameters. Modeling survival, recruitment, and detection probabilities as a function of covariates may help to reduce unmodeled heterogeneity in parameters, improve precision in parameter estimates (e.g., large uncertainty in survival probabilities in Fig. 3), and limit potential bias in the eradication probability estimates (e.g., Link, Schofield, Barker, & Sauer, 2018, Barker, Schofield, Link, & Sauer, 2018, Kéry 2018). The lack of appropriate covariates for demographic and removal rates may have limited our inference, leading in some cases to underestimated average eradication probabilities (i.e., overestimated residual population sizes) for some sites. We however note that eradication probability increases above zero only when the credible interval of the posterior distribution for the residual population size estimate encompasses the threshold number of individuals below which eradication success is assumed (2 in the current study). Furthermore, eradication probability does not reach values close to one until most of the associated posterior density includes values equal or lower than the defined threshold number. Large uncertainty around the residual population size estimate can thus limit eradication probability to values that never get close to one. In consideration of that, we suggest evaluating whether or not credible intervals for residual population size estimates include the threshold number of individuals below which eradication success is assumed. This metric provides a useful measure of eradication likelihood throughout the eradication process, including the first years/seasons when the number of individuals is still large and eradication probabilities equal zero. The analytical framework presented here can be applied to a variety of eradication studies as well to alien species control, to evaluate residual population sizes. Future work should

consider extending the current multi-site multi-method removal framework to a fully open removal model (Matechou et al., 2016), to overcome the need for defining periods of demographic closure, and the incorporation of lake-specific heterogeneity in removal rates by inclusion of lake-specific covariates (Laplanche, Leunda, Boithias, Ardaíz, & Juanes, 2019). Also the model can be applied to other disciplines such as pest control in agricultural and epidemiological studies. Finally, although the model can be fit using software widely-used by quantitative ecologists (R and JAGS), the community of conservationists and environmental managers would greatly benefit by the development of a routine that allows their application through a user-friendly interface (see Drolet et al., 2014).

Efficient allocation of resources to manage invasive species is needed to optimize conservation and economic benefits (Epanchin-Niell, Haight, Berc, Kean, & Liebhold, 2012). Our model for estimating the probability of alien fish eradication and residual population size has general applicability to a wide range of alien plants, animals, and pathogens. When adequate eradication data are available, our model can be applied to guide the decisions of conservationists and environmental managers regarding when eradications are complete and for adopting corrective measures to increase the probability of eradication when eradication actions are still in progress. Evaluating eradication success is critical to minimize the risk of failed eradication and to save effort and resources spent on unnecessary eradication efforts (i.e., effort expended after the last fish has been captured). With minimal conceptual adjustment it may also be used for different conservation issues, e.g., to predict the probability of extinction of native species or in wildlife management.

445

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452 **AUTHOR CONTRIBUTION**

R.T. and S.T. conceived the research idea and wrote the paper; R.T., T.B., D.B., R.A.K., Q.P.R., and M.V. provided the eradication data. All the authors edited the paper.

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DATA AVAILABILITY STATEMENT

Raw eradication data from this study will be available via the Figshare Repository (doi:
[10.6084/m9.figshare.13242293](https://doi.org/10.6084/m9.figshare.13242293))

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582 **Tables**583 **Table 1.** Main characteristics of the fish eradication study lakes.

Lake-ID	Lake	Area	Latitude N	Longitude E	Elevation m a.s.l.	Surface ha	Depth m	Fish species
AB4 ^c	-	SEKI (Sierra Nevada, US)	-	-	3403	12.3	18.5	OM
CON ^c	-	SNF (Sierra Nevada, US)	-	-	3492	1.5	3.2	OM SF
DEP	Cap de Port	PNAESM (Pyrenees, Spain)	42°32'10''	01°01'36''	2521	7.4	31.7	ST
DEM	Dellui Mig	PNAESM (Pyrenees, Spain)	42°33'12''	00°56'36''	2314	1.1	6.2	PH ST
DEN	Dellui Nord	PNAESM (Pyrenees, Spain)	42°33'18''	00°56'33''	2306	0.4	6.7	PH ST
DJO ^c	Djouan	PNGP (Alps, Italy)	45°33'27''	07°10'43''	2515	1.2	3.0	SF
DRE ^c	Dres	PNGP (Alps, Italy)	45°24'45''	07°13'25''	2088	2.1	7.4	SF
KNO ^c	-	SNF (Sierra Nevada, US)	-	-	3358	3.4	5.5	OM
LEY ^c	Leynir	PNGP (Alps, Italy)	45°30'28''	07°09'08''	2747	4.5	21.1	SF
MAR ^c	-	SNF (Sierra Nevada, US)	-	-	3583	3.1	7.8	OM
NAO	Naorte	PNAP (Pyrenees, Spain)	42°41'23''	01°20'05''	2150	3.9	14.0	PH
NER ^c	Nero	PNGP (Alps, Italy)	45°33'06''	07°10'07''	2671	1.4	6.0	SF
NOG ^c	-	SNF (Sierra Nevada, US)	-	-	3516	1.7	5.0	SF
PB1 ^c	-	SEKI (Sierra Nevada, US)	-	-	3509	3.7	25.0	SF
ROV	Rovinets	PNAP (Pyrenees, Spain)	42°40'3''	01°20'05''	2223	0.4	5.4	PH
SL1	-	SEKI (Sierra Nevada, US)	-	-	3410	1.2	6.0	SF
SUB	Subenuix	PNAESM (Pyrenees, Spain)	42°35'34''	00°59'14''	2194	2.6	11.0	SF
UB3 ^c	-	SEKI (Sierra Nevada, US)	-	-	3450	3.1	15.0	OM
UL2 ^c	-	SEKI (Sierra Nevada, US)	-	-	3213	1.5	5.7	OM
UP1 ^c	-	SEKI (Sierra Nevada, US)	-	-	3500	3.3	15.0	OM

584 Lake-ID: lake identification code, superscript “c” indicate control lakes, i.e., lakes with at least 5 years of post-
585 eradication monitoring and without observations of fish; Area - SNF: Sierra National Forest; Area - SEKI: Sequoia and
586 King Canyon National Parks; Area - PNGP: Gran Paradiso National Park; Area - PNAESM: Aiguestortes and Estany de
587 Saint Maurici National Park; Area - PNAP: Alt Pireneu National Park; Fish species - SF: brook trout *Salvelinus*
588 *fontinalis*; Fish species - ST: brown trout *Salmo trutta*; Fish species - OM: rainbow trout *Oncorhynchus mykiss*; Fish
589 species - PH: minnow *Phoxinus* sp. We do not report the names and coordinates of the lakes from the US, because here
590 there is a risk that such information would be used to sabotage the fish removals (i.e., fish restocking).

Table 2. Summary of the methods, timing, effort, and results of the eradication actions. The year of removal of the last fish (Year last fish) is reported only for the control lakes, where at least 5 years of post-eradication monitoring confirmed the action success. No. of removal sessions listed per removal method (GN – EF – FN) are provided as an estimate of the eradication efforts.

Lake-ID	Fish species	No. of removed fish per season									No. tot.	Removal Methods	No. of sessions	Start year	Year last fish
		Season 1	Season 2	Season 3	Season 4	Season 5	Season 6	Season 7	Season 8	Season 9					
AB4	OM	765	789	373	117	15	0	0	-	-	2059	GN	54 - 0 - 0	2012	2016
CON	OM	7	0	0	0	-	-	-	-	-	7	GN	41 - 0 - 0	2000	2002
	SF	221	368	43	0	-	-	-	-	-	632	GN	41 - 0 - 0	2000	2000
DEP	ST	77	623	908	92	14	-	-	-	-	1714	GN EF FN	57 - 32 - 8	2015	-
DEM	PH	1260	2222	217	4	0	-	-	-	-	3703	GN EF FN	51 - 64 - 66	2015	-
	ST	218	182	1	0	0	-	-	-	-	501	GN EF FN	51 - 64 - 66	2015	-
DEN	PH	7382	7511	1922	4187	223	-	-	-	-	21225	GN EF FN	57 - 82 - 86	2015	-
	ST	4	0	0	0	0	-	-	-	-	4	GN EF FN	57 - 82 - 86	2015	-
DJO	SF	1320	85	0	0	-	-	-	-	-	1405	GN (EF)	39 - 5 - 0	2013	2014
DRE	SF	3153	9833	397	0	0	-	-	-	-	13383	GN EF (RA)	83 - 38 - 0	2013	2015
KNO	OM	386	172	10	3	0	0	-	-	-	571	GN	39 - 0 - 0	1997	2001
LEY	SF	1126	2180	134	2	0	0	-	-	-	3442	GN (EF)	57 - 6 - 0	2013	2016
MAR	OM	258	58	17	0	-	-	-	-	-	333	GN	22 - 0 - 0	1997	2000
NAO	PH	39319	23137	12860	6568	1922	-	-	-	-	83806	GN EF FN	86 - 79 - 92	2015	-
NER	SF	177	22	2	0	-	-	-	-	-	201	GN	30 - 0 - 0	2013	2015
NOG	SF	387	85	0	-	-	-	-	-	-	485	GN	38 - 0 - 0	2000	2002
PB1	SF	1503	1321	1045	858	15	0	-	-	-	4742	GN	53 - 0 - 0	2009	2013
ROV	PH	4490	703	477	36	-	-	-	-	-	5706	GN EF FN	41 - 25 - 60	2016	-
SL1	SF	816	702	362	0	0	-	-	-	-	1880	GN (EF)	70 - 3 - 0	2001	2003
SOU	SF	3294	1647	30	0	-	-	-	-	-	4971	GN EF FN	62 - 12 - 13	2016	-
UB3	OM	1422	969	415	0	0	-	-	-	-	2806	GN	41 - 0 - 0	2005	2007
UL2	OM	156	354	17	25	15	5	6	0	0	572	GN	83 - 0 - 0	2001	2007
UP1	OM	517	109	2	0	-	-	-	-	-	628	GN	18 - 0 - 0	2009	2010

Lake-ID: lake identification code; Fish species - SF: brook trout *Salvelinus fontinalis*; Fish species - ST: brown trout *Salmo trutta*; Fish species - OM: rainbow trout *Oncorhynchus mykiss*; Fish species - PH: minnow *Phoxinus* sp.; Removal method – GN: gillnetting; Removal method – EF: electrofishing; Removal method – FN: fyke-netting; Removal methods in brackets were used only on a few occasions (i.e., less than 4 times per season) and capture data from these removal methods were not used to estimate the eradication probability.

Table 3. Eradication probability by lake and season, and summary statistics for residual population size at the end of the last sampling season (N_{RES} with 95% Bayesian credible interval – 95% BCI). Whether eradication can be considered completed ($Er=1$) or not ($Er=0$) is assumed to depend on the 95% CRI of the residual population size at the last year of sampling which may encompass values < 2 individuals ($Er=1$) or not ($Er=0$). When the 95% BCI encompassed values < 2 individuals already before the last sampling season, the eradication probability is marked in bold.

Lake-ID	Species	Season									Er	N_{RES} median (95% BCI)
		1	2	3	4	5	6	7	8	9		
AB4 ^c	OM	0.00	0.00	0.00	0.00	0.00	0.31	0.72			1	0 (0-6)
CON ^c	SF	0.00	0.00	0.00	0.01						0	20 (3-63)
CON ^c	OM	0.39	0.83	0.97	0.98						1	0 (0-1)
DEM	PH	0.00	0.00	0.00	0.00	0.03					1	6 (1-14)
DEM	ST	0.00	0.00	0.25	0.74	0.89					1	0 (0-4)
DEN	PH	0.00	0.00	0.00	0.00	0.00					0	1562 (1427-1733)
DEN	ST	0.31	0.86	0.96	0.98	0.98					1	0 (0-1)
DEP	ST	0.00	0.00	0.00	0.00	0.00					0	59 (36-100)
DJO ^c	SF	0.00	0.00	0.23	0.74						1	0 (0-6)
DRE ^c	SF	0.00	0.00	0.00	0.00	0.00					0	10 (4-36)
KNO ^c	OM	0.00	0.00	0.00	0.30	0.89	0.95				1	0 (0-2)
LEY ^c	SF	0.00	0.00	0.00	0.00	0.00	0.25				1	4 (0-22)
MAR ^c	OM	0.00	0.00	0.00	0.41						1	2 (0-7)
NAO	PH	0.00	0.00	0.00	0.00	0.00					0	9884 (9412-10355)
NER ^c	SF	0.00	0.00	0.36	0.82						1	0 (0-4)
NOG ^c	SF	0.00	0.00	0.03							1	13 (1-41)
PB1 ^c	SF	0.00	0.00	0.00	0.00	0.00	0.50				1	2 (0-11)
ROV	PH	0.00	0.00	0.00	0.00						0	35 (21-52)
SL1 ^c	SF	0.00	0.00	0.00	0.50	0.78					1	0 (0-6)
SOU	SF	0.00	0.00	0.00	0.02						0	15 (2-76)
UB3 ^c	OM	0.00	0.00	0.00	0.70	0.87					1	0 (0-4)
UL2 ^c	OM	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.36	0.68	1	1 (0-6)
UP1 ^c	OM	0.00	0.00	0.44	0.88						1	0 (0-3)

ID: lake identification code, superscript “c” indicates “control” lakes; Fish species - SF: brook trout *Salvelinus fontinalis*; Fish species - ST: brown trout *Salmo trutta*; Fish species - OM: rainbow trout *Oncorhynchus mykiss*; Fish species - PH: minnow *Phoxinus* sp.

613 **Table 4.** Posterior estimates (mean, standard deviation, and percentiles) of method-specific daily removal
614 probabilities for Salmonids and Cyprinids.

Removal method	Fish group	Removal probability				
		Mean	SD	2.5%	50%	97.5%
Gillnetting	Salmonidae	0.095	0.103	0.010	0.058	0.437
	Cyprinidae	0.014	0.013	0.003	0.009	0.038
Electrofishing	Salmonidae	0.034	0.041	0.000	0.025	0.137
	Cyprinidae	0.027	0.013	0.018	0.020	0.052
Fikenetting	Salmonidae	0.026	0.042	0.000	0.007	0.137
	Cyprinidae	0.024	0.020	0.011	0.013	0.060

615
616

617 **Figures**
618

619 **Fig. 1** Vignette of the main concepts and components of the model formulation. The vignette is
620 based on the real gillnetting data and model estimates from L. Leynir (Italian Alps) where brook
621 trout was eradicated.
622

Figure 2. Year-specific estimates of residual population size (black solid line) for each lake-by-species removal study (shown in the title of each panel; species codes as in Table 1), and the total number of fish removed each season (i.e., field data; blue dotted line). Vertical lines represent 95% Bayesian credible intervals for the estimates.

630 **SUPPORTING INFORMATION**

631 The following Supporting Information is available for this article online:

632 Appendix A. Details on parameter estimates.

633 Appendix B. Tutorial for preparing the data and running the general removal model.

Fig. 1 Vignette of the main concepts and components of the model formulation. The vignette is based on the real gillnetting data and model estimates from L. Leynir (Italian Alps) where brook trout was eradicated.

115x112mm (300 x 300 DPI)

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Figure 2. Year-specific estimates of residual population size (black solid line) for each lake-by-species removal study (shown in the title of each panel; species codes as in Table 1), and the total number of fish removed each season (i.e., field data; blue dotted line). Vertical lines represent 95% Bayesian credible intervals for the estimates.

Figure 3. Recruitment and removal probabilities for each lake-by-species removal study (Table 1). Vertical lines represent 95% Bayesian credible intervals for the estimates.

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APPENDIX A. Details on parameter estimates.

Alien fish eradication from high mountain lakes by multiple removal methods: estimating residual abundance and eradication probability in open populations.

R Tiberti, T Buchaca, D Boiano, RA Knapp, Q Pou Rovira, G Tavecchia, M Ventura, S Tenan

Table S1. Average and median effective sample size among the main groups of parameters. The latter can vary by lake, species, and in time. Parameter notation includes the one used in the supplementary R and JAGS code, and the corresponding notation in the different equations reported in main text.

Parameter			ESS	
Model code notation	Mathematical notation	Equation #	Mean	Median
lambda	λ	1	18216.26	17557.0
gamma	γ	3	11446.04	7351.0
mean_omega	$\text{logit}^{-1}(\alpha_{\omega})$	9	14698.35	11800.0
sd_omega	σ_{ω}	9	24618.21	30000.0
year_effect_omega	year	10	18296.66	24143.0
pE0	pE	7	21905.57	30000.0
pG0	pG	7	15168.74	15307.0
pF0	pF	7	20463.65	24318.0
Nres	N_{RES}	2	15665.25	13440.5
N	N	1, 3-4	15665.25	13440.5
S	S	2, 4	14054.81	10241.0
G	G	3-4	15290.98	13554.0

Figure S1. Effect of seasonality on removal probabilities for the L. Leynir case study.

Figure S2. Estimates of average survival probability for the group of lake-by-species case studies where removal effort lasted for more than five years ($T \geq 5$) and for the group of lake-by-species case studies with shorter sampling periods ($T < 5$; see Table 1 for case study names). Vertical lines represent 95% Bayesian credible intervals for the estimates. Average survival probabilities are given on the probability scale; temporal random standard deviations of survival (σ_w , Eq. 9 in the main text) are on the logit scale.

Goodness-of-fit

We used the Bayesian p -value as a summary of posterior predictive checks (Gelman et al. 1996) to evaluate the fit of two model components, i) the observed lake-by-season-by-occasion specific data ($y_{i,t,j}$) (observation part of the model, Eq. 6 in the main text), and the (observed) total number of individuals removed ($n_{TOT,i,t}$) (abundance part of the model, Eq. 5 in the main text). We used the Freeman-Tukey statistic as discrepancy measure, $\sum(\sqrt{y} - \sqrt{E[y]})^2$ (with $E[y]$ representing the expected value for the data), and compared the posterior distribution of that statistic with the posterior distribution of the statistic for a new dataset simulated from the posterior distribution. We chose the Freeman-Tukey statistic since it obviates the need to pool cells with small expected values and it is insensitive to unstable results due to small expected cell frequencies (Kéry & Royle, 2015), a problem we foresaw with observed lake-by-season-by-occasion specific data ($y_{i,t,j}$). The Bayesian p -value is the probability of getting a more extreme value of the test statistic under the Null hypothesis of a fitting model. Given that the null distribution of Bayesian p -values is not uniform, we cannot say that a Bayesian p -value outside the interval 0.025-0.975 represents a significant lack of fit (Kéry & Royle, 2015). However, a model that fits the data will have a value not too close to 0 or 1. We performed posterior predictive checks and calculated the Bayesian p -value separately for the group of lake-by-species case studies where removal effort lasted for more than five years and for the group of lake-by-species case studies with shorter sampling periods. This choice was supported by the fact that i) the survival model differed for the two groups (despite being incorporated in the same global model for all lake-by-species case studies), and ii) no parameters were shared across lake-by-species case studies. The Bayesian p -value for the observation part of the model ($y_{i,t,j}$) was 0.1 for both groups of lake-by-species case studies, and the Bayesian p -value for the abundance part of the model was 0.61 and 0.63 for the lake-by-species case studies with a longer and shorter removal period, respectively. Even if judging model fit through posterior predictive checks and Bayesian p -values is qualitative, we can see that the fit of the observation part of the model (observed lake-by-season-by-occasion specific data) is poor but the abundance part of the model provides an adequate fit of the data. The poor fit for the observation part of the model, i.e. data for specific removal occasions, can be due to the lack of appropriate covariates to inform estimates of removal rates. However, we were not interested in predicting the number of fish removed at specific sampling occasion, rather we were mainly interested in estimating population size of eradicated species, a parameter which is directly related to the abundance part of the model (Eq. 5 in the main text) that fits the total number of individuals removed in each season of each lake-by-species case study.

References

- Gelman, A., Meng, X. L., & Stern, H. (1996). Posterior predictive assessment of model fitness via realized discrepancies. *Statistica Sinica*, 733-760.
- Kéry, M., & Royle, J. A. (2015). *Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 1: Prelude and Static Models*. Academic Press.

Appendix B. Tutorial for preparing the data and running the general removal model.

Alien fish eradication from high mountain lakes by multiple removal methods: estimating residual abundance and eradication probability in open populations.

R Tiberti, T Buchaca, D Boiano, RA Knapp, Q Pou Rovira, G Tavecchia, M Ventura, S Tenan

Hereafter we provide a step-by-step tutorial for running the model in R and for extracting the useful information from the model output.

1. Download R and JAGS

The code to run the model is written in R (<https://cran.r-project.org/>) language, and program JAGS (<http://mcmc-jags.sourceforge.net/>) is called from R for the Markov Chain Monte Carlo (MCMC) simulations. Both programs can be freely downloaded at the links mentioned above.

2. Prepare your data or import example data from our study

Organize your data in a table using one of the commonly available spreadsheets, e.g., OpenOffice or Excel. Our removal model works on site-by-species cases study (e.g., in a lake there could be two fish species to be eradicated); each row represent a removal session; data have to be filled into 9 columns:

- Column 1: “site_id”: this is a unique identifier of the site (e.g., the name of the lake, an identification code, or a number). Make sure the site name of a site is always written in the same way. If different sites were under treatment, you can add them here.
- Column 2: “date”: this is the date of the removal sessions (dd/mm/yyyy).
- Column 3-5: “method1”, “method2”, “method3”; data from different removal methods can be integrated in the model (e.g., electrofishing, gillnetting, fyke-netting). There is not a limit to the number of removal methods that can be added; the present example include up to three removal methods, but new columns can be added with minimal and intuitive changes to the script of the model. Write “1” if the specific removal method was used in the removal session; “0” if not.
- Column 6-8: “no_method1”, “no_method2”, “no_method3”; number of individuals (e.g., alien fish) removed using method1, method2 and method3.
- Column 9: “species”; alien species to be removed; you can add an identification code (e.g., ST is *Salmo trutta*; Fig. S1).

In Fig. 1 we provide an easy example of a datasheet based on the removal data of alien fish from two mountain lakes. Raw eradication data from our study is available via the Figshare Repository (doi: [10.6084/m9.figshare.13242293](https://doi.org/10.6084/m9.figshare.13242293)), and can be used as example data to run the model.

	A	B	C	D	E	F	G	H	I
1	site	date	method1	method2	method3	no_method1	no_method2	no_method3	species
2	Marmot	28/09/1997	0	1	0		48		OM
3	Marmot	29/09/1997	0	1	0		103		OM
4	Marmot	30/09/1997	0	1	0		25		OM
5	Marmot	01/10/1997	0	1	0		22		OM
6	Marmot	06/10/1997	0	1	0		34		OM
7	Marmot	07/10/1997	0	1	0		0		OM
8	Marmot	09/10/1997	0	1	0		8		OM
9	Marmot	10/10/1997	0	1	0		3		OM
10	Marmot	20/08/1998	0	1	0		15		OM
11	Marmot	01/10/1998	0	1	0		34		OM
12	Marmot	06/07/1999	0	1	0		8		OM
13	Marmot	19/08/1999	0	1	0		16		OM
14	Marmot	22/09/1999	0	1	0		16		OM
15	Marmot	02/10/1999	0	1	0		0		OM
16	Marmot	14/10/1999	0	1	0		0		OM
17	Marmot	04/07/2000	0	1	0		0		OM
18	Marmot	29/07/2000	0	1	0		1		OM
19	Marmot	29/09/2000	0	1	0		0		OM
20	Marmot	30/09/2000	0	1	0		0		OM
21	Marmot	05/10/2000	0	1	0		0		OM
22	Marmot	07/10/2000	0	1	0		0		OM
23	Marmot	25/10/2000	0	1	0		0		OM
24	De Port	09/08/2015	1	0	0	77			ST
25	De Port	20/06/2016	1	0	0	155			ST
26	De Port	10/08/2016	1	0	0	211			ST
27	De Port	18/08/2016	0	1	0		48		ST
28	De Port	19/08/2016	0	1	0		44		ST
29	De Port	20/08/2016	0	1	0		53		ST
30	De Port	22/08/2016	0	0	1			6	ST
31	De Port	23/08/2016	0	1	1		6	1	ST
32	De Port	24/08/2016	0	1	1		34	2	ST
33	De Port	25/08/2016	0	1	0		28		ST
34	De Port	26/08/2016	0	0	1			1	ST
35	De Port	30/08/2016	0	1	0		22		ST
36	De Port	31/08/2016	0	1	0		12		ST
37	De Port	01/09/2016	0	1	0		9		ST
38	De Port	06/09/2016	0	1	0		26		ST
39	De Port	07/09/2016	1	1	0	82	7		ST
40	De Port	08/09/2016	1	1	0	36	36		ST
41	De Port	09/09/2016	1	1	0	10	30		ST

Figure S1 Example of the datasheet. Methods from 1 to 3 represent electrofishing, gillnetting and fyke-netting; when a certain method was used (cell value =1), the number of removed fish was added (e.g., in Lake Marmot only gillnetting was used, in Lake de Port a combination of removal methods was used). Species-OM: rainbow trout *Oncorhynchus mykiss*; species-ST: brown trout *Salmo trutta*.

3. Save your data in CSV

Save your data as Comma Separated Values (CSV); use “,” as separator; below the file is named “EradicationData.csv”. To run the model, we provide data from our case study, but you should be able to adapt the scripts to your needs with minimal R competences.

4. Import data

You can copy and paste the following commands (note that strings in green and starting with “#” do not run any command; they represent further short explanations of what the commands in red do):

```
# Set your working directory and load the data
setwd("/your/path/") # e.g., setwd("C:/Users/MyLaptop/Desktop")
d <- read.table(file="EradicationData.csv",sep=";",header=T)
```

5. Load needed packages

At this stage, be sure that your laptop has internet connection. To upload all the needed packages, copy and paste the following commands (a window with many national repositories will appear; we used Italy, but all options should work):

```
install.packages("data.table"); library(data.table)
install.packages("reshape2"); library(reshape2)
install.packages("abind"); library(abind)
install.packages("jagsUI"); library(jagsUI)
```

6. Prepare the data to be used in the R and JAGS model

Now data need some adjustments to be used in the R and JAGS model (please note that some of the following commands works for example data from our case study; read comments in green for further explanations):

```
# from lake names to lake-by-species names, to account for multiple species sampled in the same
lake (in our case study we had multiple species in Lakes Cony, Dellui Mig and Dellui Norte;
adapt the script to your case study)

d$lakeSP <- factor(ifelse(d$site=="Cony"|d$site=="Dellui Mig"|d$site=="Dellui
Norte",paste0(d$site,"_",d$species),as.character(d$site)))

# set date, day of year, year and month
d$dates <- as.Date(d$date,format='%d/%m/%Y', origin = "1900-01-01")
d$dayofyear <- as.numeric(format(d$dates, format = '%j'))
d$year <- as.numeric(format(d$dates, format = '%Y'))
d$month <- as.numeric(format(d$dates, format = '%m'))

# fix some errors in the data
d <- d[-which(d$year==2019),]

# from year to season: account for the fact that we assume recruits are available to capture
from Sept 1st
d$yearClosure <- ifelse(d$month>=9,d$year+1,d$year)

# number of lake-by-species case studies
nLakes <- length(unique(d$lakeSP))

# total number of seasons
d_lakeBYyear <- ifelse(table(d$lakeSP,d$yearClosure)>0,1,0)
nYears_tot <- rowSums(d_lakeBYyear)
```

```

# check number of occasions per case study; the following commands are based on the library
"data.table"

d_occBYlakeBYyear <-
setDF(setDT(d)[, .(nDayofyear=uniqueN(dayofyear),nDates=uniqueN(dates)), .(lakeSP,yearClosure)])
max_Rep_lake <- tapply(X=d_occBYlakeBYyear$nDates,INDEX=d_occBYlakeBYyear$lakeSP,FUN=max)

# occasions and seasons numbered sequentially
d$occasion <- ave(as.numeric(d$dates), list(d$lakeSP,d$yearClosure), FUN = seq_along)
d$start_year <- ave(d$yearClosure,d$lakeSP,FUN=min)      # first year of activity
d$yearNum <- d$yearClosure-d$start_year+1

# method-specific removal frequencies; the following commands are based on the library
"reshape2"

d$no_elecNum <- as.numeric(d$no_method1)
d$no_gillNum <- as.numeric(d$no_method2)
d$no_fikeNum <- as.numeric(d$no_method3)

melted_d <-
melt(d,id.vars=c("lakeSP","occasion","yearNum"),measure.vars=c("no_elecNum","no_gillNum","no_fikeNum"),variable.name = "method")

# 4D array
d_4D_n <- xtabs(value ~ ., melted_d[,c("lakeSP","yearNum","occasion","method","value")])

# derive removal activity array
d$electrofishing2<- as.numeric(d$method1)
d$gillnetting2 <- as.numeric(d$method2)
d$fikenetting2 <- as.numeric(d$method3)

melted_d_activity <-
melt(d,id.vars=c("lakeSP","occasion","yearNum"),measure.vars=c("electrofishing2","gillnetting2","fikenetting2"),variable.name = "method")
d_4D_act <- xtabs(value ~ .,
melted_d_activity[,c("lakeSP","yearNum","occasion","method","value")])

# day of year for removal occasions
melted_d_dates <-
melt(d,id.vars=c("lakeSP","occasion","yearNum"),measure.vars=c("dayofyear"),variable.name =
"method")

```



```

d_4D_dayofyear <- xtabs(value ~ ., melted_d_dates[,c("lakeSP","yearNum","occasion","value")])
yDAY_tot <- d_4D_dayofyear

# get 3D arrays for removal frequencies and method-specific activity; the following commands are
# based on the library "abind"
yOBS_tot <- abind(d_4D_n[,,,1],d_4D_n[,,,2],d_4D_n[,,,3],along=3)
yCONTROL_tot <- abind(d_4D_act[,,,1],d_4D_act[,,,2],d_4D_act[,,,3],along=3)

# save data for the model
save(
  d_4D_n,
  d_4D_act,
  nLakes,
  nYears_tot,
  max_Rep_lake,
  yOBS_tot,
  yCONTROL_tot,
  yDAY_tot,
  file="multiLake_removal.RData",
  ascii=T)

load("multiLake_removal.RData") # load data

ncap<-rowSums(yOBS_tot,dim=2) # year-specific total number of removed individuals for each
lake-by-species study

ncapTOT <- rowSums(ncap,na.rm=T) # total number of removed individuals for each lake-by-species
study

priorN1 <- cbind(ncapTOT,round(ncapTOT*1.5)) # upper bound for initial population size
(specified in the JAGS model)

# reorder data based on duration of the removal period: first lake-by-species studies with >=5
seasons of data (suffix "Long") and then those with a shorter sampling period ("Short")
# and derive some quantities with new lake-by-species order

```

```

lakesLong <- which(nYears_tot>=5) # 14 lake-by-species studies

lakesShort <- which(nYears_tot<5)

max_Rep_lake_RE <- max_Rep_lake[c(which(nYears_tot>=5),which(nYears_tot<5))],]

yOBS_tot_RE <- yOBS_tot[c(which(nYears_tot>=5),which(nYears_tot<5))],]

yCONTROL_tot_RE <- yCONTROL_tot[c(which(nYears_tot>=5),which(nYears_tot<5))],]

nYears_tot_RE <- nYears_tot[c(which(nYears_tot>=5),which(nYears_tot<5))],]

ncap_RE <- ncap[c(which(nYears_tot>=5),which(nYears_tot<5))],]

priorN1_RE <- priorN1[c(which(nYears_tot>=5),which(nYears_tot<5))],]

# reordered year-specific observed total number of removed individuals for each lake-by-species
study

ncap_obs_RE <- ncap_RE
for(i in 1:nrow(ncap_RE)){
  if(nYears_tot_RE[i]<9){ncap_obs_RE[i,(nYears_tot_RE[i]+1):ncol(ncap_obs_RE)] <- NA}
}

```

7. Run the model

```

# JAGS model code
cat("
model {
#-----LONG PERIOD LAKES
for(i in 1:nLakesLong){
# Priors
  lambda[i] ~ dunif(lower_priorN1[i],upper_priorN1[i])
# survival
  for(t in 1:(nYears[i]-1)){

```

```

        logit(omega[i,t]) <- omega0[i] + eps_omega[i,t] # could also have covariates
here

        eps_omega[i,t] ~ dnorm(0,tau_omega[i])
    }
    tau_omega[i] <- pow(sd_omega[i], -2)
    sd_omega[i] ~ dunif(0,10) # temporal random variation in survival
    omega0[i] <- log(mean_omega[i]/(1-mean_omega[i]))
    mean_omega[i] ~ dunif(0, 1)

    # recruitment
    gamma[i] ~ dunif(0,10)

    # removal probabilities
    pE0[i] ~ dunif(0, 1)
    pG0[i] ~ dunif(0, 1)
    pF0[i] ~ dunif(0, 1)
}

# Likelihood
for(i in 1:nLakesLong){
    # 1.First year
    # 1.1.Abundance model first year
    N[i,1] ~ dpois(lambda[i])
    # residual population
    Nres[i,1] <- N[i,1]-ncap[i,1]
    # 1.2. Observation model: removal
    # probability of capture during jth removal (with first method)
    for(j in 1:nReps1){
        mu_tmp[i,1,j] <- pE[i,1]*((1-pE[i,1])^(j-1))*((1-pG[i,1])^j)*((1-pF[i,1])^j)
        mu[i,1,j] <- mu_tmp[i,1,j]*yCONTROL_tot[i,1,j] # goes to zero if no activity
performed
    }
    # probability of capture during jth removal (with second method)
    for(j in (nReps1+1):nReps2){
        mu_tmp[i,1,j] <- pG[i,1]*((1-pG[i,1])^(j-nReps1-1))*((1-pE[i,1])^(j-
nReps1))*((1-pF[i,1])^(j-nReps1))
        mu[i,1,j] <- mu_tmp[i,1,j]*yCONTROL_tot[i,1,j] # goes to zero if no activity
performed
    }
    # probability of capture during jth removal (with third method)

```

```

    for(j in (nReps2+1):nRepsTot){
      mu_tmp[i,1,j] <- pF[i,1]*((1-pF[i,1])^(j-nReps2-1))*((1-pE[i,1])^(j-
nReps2))*((1-pG[i,1])^(j-nReps2))
      mu[i,1,j] <- mu_tmp[i,1,j]*yCONTROL_tot[i,1,j] # goes to zero if no activity
performed
    }
    # probability of NOT being captured Pr(00000000)
    pi0[i,1] <- 1-sum(mu[i,1,1:nRepsTot])
    # probability of being captured in one of the nRepsTot occasions
    pcap[i,1] <- 1-pi0[i,1]
    pcap1[i,1] <- max(0.00001,pcap[i,1])
    for(j in 1:nRepsTot){
      muc[i,1,j] <- mu[i,1,j]/pcap1[i,1]
    }
    # the conditional multinomial
    y[i,1,1:nRepsTot] ~ dmulti(muc[i,1,1:nRepsTot], ncap[i,1])
    # model for the observed count of uniques
    ncap[i,1] ~ dbin(pcap1[i,1],N[i,1])
    # 2 Other years -----
    for(t in 2:nYears[i]) {
      # 2.1.Abundance model
      S[i,t-1] ~ dbin(omega[i,t-1], Nres[i,t-1])
      G[i,t-1] ~ dpois(gamma[i]*N[i,t-1]) # per-capita recruitment, 'autoreg'
      N[i,t] <- S[i,t-1] + G[i,t-1]
      # residual population
      Nres[i,t] <- N[i,t]-ncap[i,t]
      # 2.2. Observation model: removal
      # probability of capture during jth removal (with first method)
      for(j in 1:nReps1){
        mu_tmp[i,t,j] <- pE[i,t]*((1-pE[i,t])^(j-1))*((1-pG[i,t])^j)*((1-
pF[i,t])^j)
        mu[i,t,j] <- mu_tmp[i,t,j]*yCONTROL_tot[i,t,j] # goes
to zero if no activity performed
      }
      # probability of capture during jth removal (with second method)
      for(j in (nReps1+1):nReps2){

```

```

        mu_tmp[i,t,j] <- pG[i,t]*((1-pG[i,t])^(j-nReps1-1))*((1-pE[i,t])^(j-
nReps1))*((1-pF[i,t])^(j-nReps1))

        mu[i,t,j] <- mu_tmp[i,t,j]*yCONTROL_tot[i,t,j] # goes to zero if no
activity performed

    }

    # probability of capture during jth removal (with third method)
    for(j in (nReps2+1):nRepsTot){

        mu_tmp[i,t,j] <- pF[i,t]*((1-pF[i,t])^(j-nReps2-1))*((1-pE[i,t])^(j-
nReps2))*((1-pG[i,t])^(j-nReps2))

        mu[i,t,j] <- mu_tmp[i,t,j]*yCONTROL_tot[i,t,j] # goes to zero if no
activity performed

    }

    # probability of NOT being captured Pr(00000000)
    pi0[i,t] <- 1-sum(mu[i,t,1:nRepsTot])

    # probability of being captured in one of the nRepsTot occasions
    pcap[i,t] <- 1-pi0[i,t]
    pcap1[i,t] <- max(0.00001,pcap[i,t])

    for(j in 1:nRepsTot){

        muc[i,t,j] <- mu[i,t,j]/pcap1[i,t]

    }

    # the conditional multinomial
    y[i,t,1:nRepsTot] ~ dmulti(muc[i,t,1:nRepsTot], ncap[i,t])

    # model for the observed count of uniques
    ncap[i,t] ~ dbin(pcap1[i,t],N[i,t])

}#t

    # Removal method-specific detectabilities
    for(t in 1:nYears[i]) {

        pE[i,t] <- pE0[i] # could also have covariates here
        pG[i,t] <- pG0[i] # could also have covariates here
        pF[i,t] <- pF0[i] # could also have covariates here

    }

}#i

#-----SHORT PERIOD LAKES
for(i in (nLakesLong+1):nLakes){

# Priors

    lambda[i] ~ dunif(lower_priorN1[i],upper_priorN1[i])

```

```

    for(t in 1:(nYears[i]-1)){
      logit(omega[i,t]) <- omega0[i] + year_effect_omega[i,t] # could also have
covariates here
    }
    omega0[i] <- log(mean_omega[i]/(1-mean_omega[i]))
    mean_omega[i] ~ dunif(0, 1)
    # corner constraint
    year_effect_omega[i,1] <- 0
    for(t in 2:nYears[i]){
      year_effect_omega[i,t] ~ dnorm(0,(1/(2.25^2)))
      # year-specific omegas 2:nYears[i]
      mean_omegaYY[i,t] <- 1/(1+exp(-omega0[i]-year_effect_omega[i,t]))
    }
    mean_omegaYY[i,1] <- mean_omega[i]
    gamma[i] ~ dunif(0,10)
    pE0[i] ~ dunif(0, 1)
    pG0[i] ~ dunif(0, 1)
    pF0[i] ~ dunif(0, 1)
  }
# Likelihood
for(i in (nLakesLong+1):nLakes){
  # 1.First year
  # 1.1.Abundance model first year
  N[i,1] ~ dpois(lambda[i])
  # residual population
  Nres[i,1] <- N[i,1]-ncap[i,1]
  # 1.2. Observation model: removal
  # probability of capture during jth removal (with first method)
  for(j in 1:nReps1){
    mu_tmp[i,1,j] <- pE[i,1]*((1-pE[i,1])^(j-1))*((1-pG[i,1])^j)*((1-pF[i,1])^j)
    mu[i,1,j] <- mu_tmp[i,1,j]*yCONTROL_tot[i,1,j] # goes to zero if no activity
performed
  }
  # probability of capture during jth removal (with second method)
  for(j in (nReps1+1):nReps2){
    mu_tmp[i,1,j] <- pG[i,1]*((1-pG[i,1])^(j-nReps1-1))*((1-pE[i,1])^(j-
nReps1))*((1-pF[i,1])^(j-nReps1))

```

```

        mu[i,1,j] <- mu_tmp[i,1,j]*yCONTROL_tot[i,1,j] # goes to zero if no activity
performed
    }

    # probability of capture during jth removal (with third method)
    for(j in (nReps2+1):nRepsTot){

        mu_tmp[i,1,j] <- pF[i,1]*((1-pF[i,1])^(j-nReps2-1))*((1-pE[i,1])^(j-
nReps2))*((1-pG[i,1])^(j-nReps2))

        mu[i,1,j] <- mu_tmp[i,1,j]*yCONTROL_tot[i,1,j] # goes to zero if no activity
performed
    }

    # probability of NOT being captured Pr(00000000)
    pi0[i,1] <- 1-sum(mu[i,1,1:nRepsTot])

    # probability of being captured in one of the nRepsTot occasions
    pcap[i,1] <- 1-pi0[i,1]

    pcap1[i,1] <- max(0.00001,pcap[i,1])

    for(j in 1:nRepsTot){

        muc[i,1,j] <- mu[i,1,j]/pcap1[i,1]

    }

    # the conditional multinomial
    y[i,1,1:nRepsTot] ~ dmulti(muc[i,1,1:nRepsTot], ncap[i,1])

    # model for the observed count of uniques
    ncap[i,1] ~ dbin(pcap1[i,1],N[i,1])

    # 2 Other years -----
    for(t in 2:nYears[i]) {

        # 2.1.Abundance model

        S[i,t-1] ~ dbin(omega[i,t-1], Nres[i,t-1])

        G[i,t-1] ~ dpois(gamma[i]*N[i,t-1]) # per-capita recruitment, 'autoreg'

        N[i,t] <- S[i,t-1] + G[i,t-1]

        # residual population

        Nres[i,t] <- N[i,t]-ncap[i,t]

        # 2.2. Observation model: removal

        # probability of capture during jth removal (with first method)

        for(j in 1:nReps1){

            mu_tmp[i,t,j] <- pE[i,t]*((1-pE[i,t])^(j-1))*((1-pG[i,t])^j)*((1-
pF[i,t])^j)

            mu[i,t,j] <- mu_tmp[i,t,j]*yCONTROL_tot[i,t,j] # goes to zero if no
activity performed

```

```

    }

    # probability of capture during jth removal (with second method)
    for(j in (nReps1+1):nReps2){
        mu_tmp[i,t,j] <- pG[i,t]*((1-pG[i,t])^(j-nReps1-1))*((1-pE[i,t])^(j-
nReps1))*((1-pF[i,t])^(j-nReps1))

        mu[i,t,j] <- mu_tmp[i,t,j]*yCONTROL_tot[i,t,j] # goes to zero if no
activity performed
    }

    # probability of capture during jth removal (with third method)
    for(j in (nReps2+1):nRepsTot){
        mu_tmp[i,t,j] <- pF[i,t]*((1-pF[i,t])^(j-nReps2-1))*((1-pE[i,t])^(j-
nReps2))*((1-pG[i,t])^(j-nReps2))

        mu[i,t,j] <- mu_tmp[i,t,j]*yCONTROL_tot[i,t,j] # goes to zero if no
activity performed
    }

    # probability of NOT being captured Pr(00000000)
    pi0[i,t] <- 1-sum(mu[i,t,1:nRepsTot])

    # probability of being captured in one of the nRepsTot occasions
    pcap[i,t] <- 1-pi0[i,t]
    pcap1[i,t] <- max(0.00001,pcap[i,t])
    for(j in 1:nRepsTot){
        muc[i,t,j] <- mu[i,t,j]/pcap1[i,t]
    }

    # the conditional multinomial
    y[i,t,1:nRepsTot] ~ dmulti(muc[i,t,1:nRepsTot], ncap[i,t])

    # model for the observed count of uniques
    ncap[i,t] ~ dbin(pcap1[i,t],N[i,t])
}#t

# Removal method-specific detectabilities
for(t in 1:nYears[i]) {
    pE[i,t] <- pE0[i] # could also have covariates here
    pG[i,t] <- pG0[i] # could also have covariates here
    pF[i,t] <- pF0[i] # could also have covariates here
}
}#i
}

",fill=TRUE,file="multilake_DM_GeomRecr2a.txt")

```



```
# JAGS data
```

```
bugs.data <- list(y=yOBS_tot_RE,nLakes=dim(yOBS_tot_RE)[1],

nRepsTot=dim(yOBS_tot_RE)[3],nReps1=dim(yOBS_tot_RE)[3]/3,nReps2=dim(yOBS_tot_RE)[3]*2/3,
               nYears=nYears_tot_RE,ncap=ncap_RE,yCONTROL_tot=yCONTROL_tot_RE,
               lower_priorN1=priorN1_RE[,1],upper_priorN1=priorN1_RE[,2],
               nLakesLong=length(lakesLong)
               )
```

```
# Initial values
```

```
N_inits <- ncap_RE+50
for(i in 1:nrow(ncap_RE)){
  if(nYears_tot_RE[i]<9){N_inits[i,(nYears_tot_RE[i]+1):ncol(N_inits)] <- NA}
}
Si <- N_inits[,-1]
Si <- ifelse(is.na(Si),NA,50)
Gi <- N_inits[,-1]-Si
N_inits2 <- N_inits
N_inits2[,-1] <- NA

inits <- function(){list(lambda=round(priorN1_RE[,1]*1.2),
                          S=Si,G=Gi,
                          N=N_inits2
                          )}
```

```
# Define parameters to be monitored (see Table S1 in Appendix A for a correspondence between
names of monitored parameters and equations in the main text)
```

```
parameters <- c("lambda","gamma","mean_omega","sd_omega","mean_omegaYY","year_effect_omega",
               "pE0","pG0","pF0","Nres","N","S","G")
```

```
# Parameters to be monitored for the Goodness-of-fit tests only
```

```
# parameters <- c("lambda","gamma","omega","Nres","muc","pcap1","N")
```

```
# load package to call JAGS from R; the following commands are based on the library "jagsUI"
```

```

# MCMC settings (this can take time to run; consider changing MCMC settings in relation to your
data and computer RAM)

n.adapt  <- 10000
n.burnin <- 200000
n.iter   <- 250000
thin     <- 50
chains   <- 3

# run the model

out <- jags(data = bugs.data,
            inits = inits,
            parameters.to.save = parameters,
            model.file = "multilake_DM_GeomRecr2a.txt",
            n.chains = chains,
            n.adapt = n.adapt,
            n.iter = n.iter,
            n.burnin = n.burnin,
            n.thin = thin,
            parallel=T)

# mean effective sample size per group of parameters

cbind(unlist(lapply(out$n.eff,mean,na.rm=T)),unlist(lapply(out$n.eff,median,na.rm=T)))

##### Goodness-of-fit tests (for details see specific section in Appendix A)
# objects needed

y=yOBS_tot_RE

# nLakes

nRepsTot=dim(yOBS_tot_RE)[3]
nYears=nYears_tot_RE
ncap_RE
nLakesLong=length(lakesLong)

```

```

nLakesShort=length(lakesShort)

nsamples=out$mcmc.info$n.samples

# get arrays from JAGS output

lambda <- out$sims.list$lambda # [nLakes]
gamma <- out$sims.list$gamma # [nLakes]
omega <- out$sims.list$omega # [nLakes,max(nYears[])-1]
Nres <- out$sims.list$Nres # [nLakes,max(nYears[])]
muc <- out$sims.list$muc # [nLakes,max(nYears[]),nRepsTot]
pcap1 <- out$sims.list$pcap1 # [nLakes,max(nYears[])]
N <- out$sims.list$N # [nLakes,max(nYears[])]

# create empty objects to be filled

y.new <- array(NA, dim=c(nsamples,nLakes,max(nYears[]),nRepsTot))
ncap.new <- array(NA, dim=c(nsamples,nLakes,max(nYears[])))
e1 <- resid1 <- resid1.new <- resid1RSS <- resid1.newRSS <- array(NA,
dim=c(nsamples,nLakes,max(nYears[]),nRepsTot))
e2 <- array(NA, dim=c(nsamples,nLakes,max(nYears[])))
e2[, ,1] <- lambda
S_exp <- G_exp <- array(NA, dim=c(nsamples,nLakes,max(nYears[])-1))
resid2 <- resid2.new <- resid2RSS <- resid2.newRSS <- array(NA,
dim=c(nsamples,nLakes,max(nYears[])))
ft1.data <- ft1.new <- ft2.data <- ft2.new <- vector(mode = "numeric", length = nsamples)
ft1.dataRSS <- ft1.newRSS <- ft2.dataRSS <- ft2.newRSS <- vector(mode = "numeric", length =
nsamples)

# Code for deriving test statistics

for(iter in 1:nsamples){
  for(i in 1:nLakes){
    for(t in 1:nYears[i]) {

      # the conditional multinomial

```

```

        y.new[iter,i,t,1:nRepsTot] <- rmultinom(n=1, size=ncap_RE[i,t],
        prob=muc[iter,i,t,1:nRepsTot])

        # model for the observed count of uniques

        ncap.new[iter,i,t] <- rbinom(n=1, size=N[iter,i,t],
        prob=pcap1[iter,i,t])
    }#t
  }#i
}#iter
for(i in 1:nLakes){
  for(t in 1:nYears[i]) {
    for(j in 1:nRepsTot){
      e1[,i,t,j] <- muc[,i,t,j] * ncap_RE[i,t]

      # Freeman-Tukey

      resid1[,i,t,j] <- (sqrt(y[,i,t,j])-sqrt(e1[,i,t,j]))^2
      resid1.new[,i,t,j] <- (sqrt(y.new[,i,t,j])-sqrt(e1[,i,t,j]))^2

      # RSS (not used)

      resid1RSS[,i,t,j] <- (y[,i,t,j]-e1[,i,t,j])^2
      resid1.newRSS[,i,t,j] <- (y.new[,i,t,j]-e1[,i,t,j])^2
    } #j
  }#t
}#i
for(i in 1:nLakes){
  for(t in 2:nYears[i]){

    # 2.1.Abundance model

    S_exp[,i,t-1] <- omega[,i,t-1] * Nres[,i,t-1]
    G_exp[,i,t-1] <- gamma[,i] * N[,i,t-1]
    e2[,i,t] <- S_exp[,i,t-1] + G_exp[,i,t-1]
  }
}

```

```

for(i in 1:nLakes){
  for(t in 1:nYears[i]) {

    # Freeman-Tukey

    resid2[,i,t] <- (sqrt(ncap_RE[i,t])-sqrt(e2[,i,t]))^2
    resid2.new[,i,t] <- (sqrt(ncap.new[,i,t])-sqrt(e2[,i,t]))^2

    # RSS (not used)

    resid2RSS[,i,t] <- (ncap_RE[i,t]-e2[,i,t])^2
    resid2.newRSS[,i,t] <- (ncap.new[,i,t]-e2[,i,t])^2
  }
}#i

# derive the Freeman-Tukey statistic and the Bayesian p-values based on duration of the removal
period: first lake-by-species studies with >=5 seasons of data (suffix "Long") and then those
with a shorter sampling period ("Short")

ft1.dataLong <- apply(resid1[,1:nLakesLong,,],c(1,2),sum,na.rm=T)
ft1.newLong <- apply(resid1.new[,1:nLakesLong,,],c(1,2),sum,na.rm=T)
ft2.dataLong <- apply(resid2[,1:nLakesLong,],c(1,2),sum,na.rm=T)
ft2.newLong <- apply(resid2.new[,1:nLakesLong,],c(1,2),sum,na.rm=T)

# Bayesian p-values

mean(ft1.newLong>ft1.dataLong)
mean(ft2.newLong>ft2.dataLong)

ft1.dataShort <- apply(resid1[, (nLakesLong+1):nLakes,,],c(1,2),sum,na.rm=T)
ft1.newShort <- apply(resid1.new[, (nLakesLong+1):nLakes,,],c(1,2),sum,na.rm=T)
ft2.dataShort <- apply(resid2[, (nLakesLong+1):nLakes,],c(1,2),sum,na.rm=T)
ft2.newShort <- apply(resid2.new[, (nLakesLong+1):nLakes,],c(1,2),sum,na.rm=T)

# Bayesian p-values

mean(ft1.newShort>ft1.dataShort)

```

```
mean(ft2.newShort>ft2.dataShort)
```