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Estimates of vital rates and predictions of population dynamics change along a long-term monitoring program

Simone Vincenzi[1] | Dušan Jesenšek[2] | Alain J. Crivelli[3]

[1]Institute of Marine Sciences, University of California, Santa Cruz, California

[2]Tolmin Angling Association, Most na Soci, Slovenia

[3]Station Biologique de la Tour du Valat, Arles, France

Correspondence
Simone Vincenzi, Institute of Marine Sciences, University of California, Santa Cruz, 110 Shaffer Rd., Santa 8 Cruz, CA 95060.
Email: simon.vincenz@gmail.com

ABSTRACT

Despite the widespread recognition of the importance of monitoring, only a few studies have explored how estimates of vital rates and predictions of population dynamics change with additional data collected along the monitoring program. We investigate how estimates of survival and individual growth, along with predictions about future population size, change with additional years of monitoring and data collected, using as a model system freshwater populations of marble (*Salmo marmoratus*), rainbow (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta* L.) living in Western Slovenian streams. Fish were sampled twice a year between 2004 and 2015. We found that in 3 out of 4 populations, a few years of data (3 or 4 sampling occasions, between 300 and 500 tagged individuals for survival, 100–200 for growth) provided the same estimates of average survival and growth as those obtained with data from more than 15 sampling occasions, while the estimation of the range of survival (i.e., the difference, over all sampling occasions considered, between maximum and minimum survival estimated in a sampling occasion) required more sampling occasions (up to 22 for marble trout), with little reduction of uncertainty around the point estimates. Predictions of mean density and variation in density over time did not change with more data collected after the first 5 years (i.e., 10 sampling occasions) and overall were within 10% of the observed mean and variation in density over the whole monitoring program.

KEYWORDS

conservation, long-term monitoring, population dynamics, vital rates

1 | INTRODUCTION

The estimation of vital rates and life-history traits and how they vary with habitat and population factors are crucial both for our understanding of population dynamics, risk of extinction, and evolution of traits in natural populations, and for informing management strategies in conservation programs (Frederiksen, Lebreton, Pradel, Choquet, & Gimenez, 2014; Letcher et al., 2015; Smallegange & Coulson, 2013). To understand how variation in vital rates and life histories of organisms among individuals and through time emerge and how that variation contributes to population dynamics and risk of extinction, we typically need long-term monitoring studies that include contrasting environmental conditions (Elliott, 1994), longitudinal data (Thomson, Cooch, & Conroy, 2009), and statistical models that can tease apart environmental and biological contributions to the observed temporal (and spatial, in case of meta-populations or multiple populations) variation in vital rates, life histories, and population dynamics (Letcher et al., 2015).

When the goal is informing management strategies for the conservation of species, monitoring is the process of collecting information about state variables (e.g., abundance, size, and vital rates) at different points in time and space for

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Simone Vincenzi no longer works at the Institute of Marine Sciences, University of California, Santa Cruz, at the time of final submission detecting changes in those variables through time, over space, and among individuals (Gerber, Beger, McCarthy, & Possingham, 2005). The purpose of a scientific investigation should drive model formulation and the type and amount of data collected (Elderd & Miller, 2016). It follows that defining "long-term" for monitoring is always context-dependent and often challenging, since how long the monitoring of natural populations must be carried out depends on the generation time and longevity of the organisms, the characteristics of the environment in which the species lives, and the goals of the monitoring program. For conservation programs, sufficient knowledge to address most practical problems related to conservation and management of endangered species will usually be obtained within a few years or generations of the monitored species, after which the cost of monitoring should begin outweighing the expected benefits with regard to management strategies and overall decision making (Possingham, Fuller, & Joseph, 2012).

Within a population, habitat factors—both extrinsic (e.g., weather, food) and intrinsic (e.g., population density, type of competition among organisms)—and their interaction, determine a large part of the temporal variation in vital rates, in recruitment, and population size, age-, and size-structure (Jonsson & Jonsson, 2011). If the fundamental parameters of an ecological system are constant, that is, if habitat factors vary little through either time or space, then we rarely need long-term monitoring for learning in the context of conservation biology (Possingham et al., 2012). On the other hand, highly stochastic environments such as those characterized by the occurrence of extreme events (Vincenzi, 2014) require decades-long monitoring to capture the effects of extreme events on vital rates, life histories, population dynamics, and risk of population extinction (Vincenzi, Mangel, Jesensek, Garza, & Crivelli, 2017). Besides, serendipitous findings and an appreciation of the effects of subtle variation in life histories in natural populations of long-lived species on individual and population processes may only come after many years of monitoring, although one might expect new knowledge to be gained in ever decreasing increments (Possingham et al., 2012). Lastly, especially for small populations, many years of data may be necessary to reduce the uncertainty around the estimation of vital rates due to sample size effects (Reynolds, 2012).

Only a few studies have investigated how estimates of vital rates and predictions of population dynamics change with additional data collected through the monitoring program, and what are the minimum or—when factoring in the costs in money and time of monitoring— optimal years of monitoring or amount of data collected for estimating vital rates and predicting population dynamics (Caughlan & Oakley, 2001). For instance, Gerber et al. (2005) studied how long we should monitor the recovery of an over-fished stock to determine the fraction of that stock to reserve; they found that the optimal monitoring time frame is rarely more than 5 years. After 5 years, the expected benefit of reduced uncertainty about the parameters of the system was negligible compared to the expected gain from earlier exploitation.

In the present study, we investigate how estimates of survival and body growth, along with predictions about future population size, change with additional years of data collected from monitoring programs. We use as a model system freshwater populations of marble (*Salmo marmoratus*), rainbow (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta* L.) living in Western Slovenian streams. These trout populations have been monitored (tag-recapture) since 2004 as part of the ongoing conservation program for the endangered marble trout (Crivelli, Poizat, Berrebi, Jesensek, & Rubin, 2000).

We estimated average and time-specific survival probabilities and average growth trajectories for each year of sampling, that is, with cumulative tag-recapture data up to 2006, 2007, and so on up to 2014, and then used models of population dynamics to study how predictions of mean population size and its temporal variation change with additional years of sampling data. Due to the similarity of the monitored species (all belonging to the family *Salmonidae*) and their restricted geography (Western Slovenia), our results are more descriptive than prescriptive. We encourage the undertaking of similar analyses by other conservation scientists and practitioners, with the objective of providing general guidelines on the minimum duration of monitoring programs, amount of data collected, or individuals tagged and recaptured for goals ranging from the estimation of vital rates to prediction of population dynamics and risk of extinction.

2 | MATERIAL AND METHODS

2.1 | Study area and species description

We estimated survival probabilities and growth trajectories, and predicted population dynamics for the marble trout (*Salmo marmoratus*) populations of Lower Idrijca [LIdri_MT] and Upper Idrijca [UIdri_MT] (Vincenzi, Mangel, et al., 2016), rainbow trout (*Oncorhynchus mykiss*) population of Lower Idrijca [LIdri_RT] (Vincenzi et al., 2019), and brown trout (*Salmo trutta* L.) population of Upper Volaja [UVol_BT] (Vincenzi, Jesenšek, & Crivelli, 2018). In LIdri, marble trout [LIdri_MT] live in sympatry with rainbow trout [LIdri_RT] (Vincenzi, Crivelli, Jeseňsek, Rossi, & De Leo, 2011; Vincenzi et al., 2019). Both UIdri_MT and UVol_BT live in allopatry. LIdri_RT was created in the 1960s (Vincenzi et al., 2019) and UVol_BT in the 1920s (Vincenzi et al., 2018) by stocking rainbow and brown trout, respectively. Both populations have been self-sustaining since their creation.

Marble trout is a freshwater salmonid fish of high conservation concern, due to its restricted geographical distribution and the risk of hybridization with alien brown trout. Only eight natural and two re-introduced populations of genetically pure marble trout remain, all in streams in the river basins of Soca, Baca, and Idrijca in Slovenia, persisting above barriers that have prevented the upstream movement of brown trout or marble-brown trout hybrids (Vincenzi, Mangel, et al., 2016). Marble trout spawn in November–December. Marble trout females typically reproduce at age 3 and older, and at a minimum size of 200 mm, and males age 2 and older.

Freshwater resident brown trout live in well-oxygenated waters. Depending on growth and life histories, resident brown trout achieve sexual maturity anywhere from 1 to 10 years. In the Northern Hemisphere, the usual time for breeding in most populations is between November and January and brown trout may spawn over several years.

Rainbow trout is a north Pacific species (Gall & Crandell, 1992). Rainbow trout in the Adriatic basin of Slovenia typically start spawning at age 1 (current authors, unpublished data), spawn over several years, and grow much faster in size than brown and marble trout.

2.2 | Sampling

Populations were sampled bi-annually in June and September. The first sampling for LIdri_MT, LIdri_RT, and UIdri_MT was in June 2004 and in September 2004 for UVol_BT. Sampling protocols are described in greater details in Vincenzi, Mangel, et al., 2016) and Vincenzi et al. (2018). If captured fish had length $L > 115$ mm, and had not been previously tagged or had lost a previously applied tag, they received a Carlin tag (Carlin, 1955), and age was determined by reading scales. Fish are 0+ (juveniles) in the first calendar year of life, 1+ in the second year and so on. Sub-yearlings of marble, rainbow, and brown trout are smaller than 115 mm in June and September, so fish were tagged when at least aged 1+. The adipose fin was also removed from all fish captured for the first time (starting at age 0+ in September), including those not tagged due to small size at age 1+. Therefore, fish with intact adipose fin were not sampled at previous sampling occasions at age 0+ or 1 + .

We estimated density of fish older than 0+ using a two-pass removal protocol (Carle & Strub, 1978) as implemented in the (R Development Core Team, 2014) package FSA (Ogle, 2015). Total stream surface of the monitored area (1,084, 1,663 and 746.27 m^2 for LIdri, UIdri and UVol, respectively) was used for the estimation of fish density (in fish ha^{-1}).

2.3 | Statistical analysis of survival and growth

Our goal was to investigate how estimates of (a) average and time-specific survival probabilities and (b) average body growth and (c) predictions of population dynamics change with each additional year of sampling data, where Y_f is the last year of monitoring/data collection in September. As simulations of population dynamics often prevent the use of null-hypothesis testing, and multiple comparisons increase the "researcher degrees of freedom," including the choice of convenient hypotheses to test (Gelman & Loken, 2013), we present and discuss our results on variation in survival, growth and population dynamics from a qualitative point of view, that is, without formal null-hypothesis testing.

For each population, the first models were estimated with $Y_f = 2005$, that is, using data up to from September 2005. For the analysis of survival, we used both June and September data, while for the analysis of growth we used only September data.

2.3.1 | Survival

Two relevant probabilities can be estimated from a capture history matrix: ϕ, the probability of apparent survival, and p, the probability that an individual is captured given that it is alive (Thomson et al., 2009). We used the Cormack–Jolly–Seber (CJS) model as a starting point for the analyses (Thomson et al., 2009). We tested the goodness-of-fit of the CJS model with the program Release (Burnham, Anderson, White, Brownie, & Pollock, 1987). We modeled the seasonal effect (*Season*) as a simplification of full-time variation, by dividing the year into two periods: June to September (*Summer*), and September to June of the following year (*Winter*). Since length of the two intervals (*Summer* and *Winter*) was different (3 and 9 months), we estimated probability of apparent survival on an annual scale.

To compare model results when different data were used, models tested included either only the constant term (i.e., average apparent survival over all the sampling intervals) or sampling occasion. For probability of capture p, following Vincenzi, Mangel, et al., 2016) we tested models with either *Age*, *Season*, *Cohort* or sampling occasion as predictors, along with the capture model with no predictors (i.e., constant probability of capture).

For each population, we used Akaike Information Criterion (AIC) for model selection (Akaike, 1974). For each Y_f, we obtained average survival probabilities over the whole sampling period (2004 to Y_f) and for each sampling interval from the respective best models of (a) average over the whole sampling period 2004 to Y_f and (b) for each sampling interval from 2004 to Y_f. We carried out the analysis of survival using the package *marked* (Laake, Johnson, & Conn, 2013) for R (R Development Core Team, 2014).

2.3.2 | Growth

The standard von Bertalanffy Growth Function (vBGF; von Bertalanffy, 1957) is

$$L(t) = L_\infty \left(1 - e^{-k(t - t_0)}\right) \tag{1}$$

where L_∞ is the asymptotic size, k is a coefficient of growth (in $time^{-1}$) and t_0 is the (hypothetical) age at which length is equal to 0.

In the vast majority of applications of the vBGF, L_∞, k and t_0 have been estimated at the population level starting from cross-sectional data, without accounting for individual heterogeneity in growth due to genetic, environmental and stochastic factors. However, when data include measurements on individuals that have been sampled multiple times, failing to account for individual variation in growth may lead to biased estimations of asymptotic size and mean length-at-age (Vincenzi, Crivelli, Munch, Skaug, & Mangel, 2016; Vincenzi, Mangel, et al., 2014).

In the present study, we used the formulation of the vBGF specific for longitudinal data of Vincenzi, Mangel, et al. (2014), in which L_∞ and k may be allowed to be a function of shared predictors and individual random effects. However, in this study, we limited our analyses to models including only the intercept (i.e., the overall mean) and individual random effects, that is, we did not include group effects (e.g., sex, cohort). In the estimation procedure, we used a log-link function for k and L_∞, since both parameters must be non-negative. We set:

$$\begin{cases} \log\left(k^{(ij)}\right) = \alpha_0 + \sigma_u u_{ij} \\ \log\left(L_\infty^{(ij)}\right) = \beta_0 + \sigma_v v_{ij} \\ t_0^{(ij)} = \gamma_0 \end{cases} \tag{2}$$

where $u \sim N(0, 1)$ and $v \sim N(0, 1)$ are the standardized individual random effects, σ_u and σ_v are the standard deviations of the statistical distributions of the random effects, i is the individual. Since the growth model operates on an annual time scale (i.e., the use of multiple data points per individual within a year would require a different growth model) and more data on tagged fish were generally available in September of each year, we used September data for modeling lifetime growth.

Models were fitted with the Automatic Differentiation Model Builder (ADMB), an open-source statistical software package for fitting nonlinear statistical models (Fournier et al., 2012). ADMB can fit generic random-effects models (module ADMB-RE) using an Empirical Bayes approach using the Laplace approximation (Skaug & Fournier, 2006).

We also tested whether there were noticeable differences in vBGF models when estimating model parameters using a standard nonlinear regression fitting routine with no random effects (*nls* function in R) or using ADMB-RE. We carried out this analysis to determine whether the fitting of a random-effects model is recommended even when only mean growth trajectories at the population level are needed, thus in the case when the fitting of a standard non-linear regression model may represent a theoretically viable procedure.

2.4 | Population dynamics

We simulated population dynamics of marble, rainbow and brown trout using individual-based models that include the most critical vital rates for the population dynamics for salmonids, that is, reproduction, juvenile survival (from 0+ to 1+), and survival of fish older than 0+.

Previous studies on the same marble (Vincenzi, Mangel, et al., 2016)), rainbow (Vincenzi et al., 2019), and brown trout (Vincenzi et al., 2018) populations have found that recruitment in all these populations was driving most of the variation in population density of fish older than juveniles. Investigations in fish farms have suggested minimum size for gonad development and reproduction in marble trout (~200 mm) and rainbow trout (~150 mm). However, pedigree reconstruction in four marble trout populations, including LIdri_MT and UIdri_MT (Vincenzi et al., 2017; Vincenzi et al., 2019), and in the rainbow trout population of Lower Idrijca (LIdri_RT) (Vincenzi et al., 2019), showed that marble and rainbow trout can occasionally reproduce at smaller sizes, and reproductive success as number of juveniles produced appears to be independent of parents' size. Thus, for simulating recruitment (i.e., density of 0+ in September) in the model of population dynamics, we did not use the model of growth and the model of size-dependent fecundity. Instead, we used the stock-recruitment Generalized Additive Models (GAM, Wood, 2006) of Vincenzi, Mangel, et al., 2016) for marble and rainbow trout and of Vincenzi et al. (2018) for brown trout. These GAM models are in the form:

$$R(t) = Pop + s(D_s(t-1)) \tag{3}$$

where $R(t)$ is recruitment at year t, Pop is the salmonid population, $D_s(t-1)$ is the density of potential spawners at year $t-1$, and s is the nonlinear function linking spawners to recruitment.

Early survival, and in particular the first overwinter survival, is the major bottleneck for population size in freshwater salmonids (Vincenzi, Satterthwaite, & Mangel, 2012). Many years of data, and possibly data from multiple populations spanning a wide range of densities (Imre, Grant, & Cunjak, 2005), are necessary to estimate density-dependent survival early in life (from 0+ to 1+). In our model of population dynamics, we used for marble trout the model of density-dependent early survival developed in Vincenzi, Mangel, et al., 2016). For both marble trout populations, density-dependent survival early in life $\sigma_{0-1}$was modeled as:

$$\log\left(\sigma_{0-1}\right) = \alpha + \beta \log\left(D_{\geq 1+}\right) \tag{4}$$

where $D_{\geq 1+}$is the density of fish of age 1+ and older when juveniles are in the first year of their life.

For rainbow and brown trout, we randomly (i.e., we did not model autocorrelation) drew at each year of the simulation of population dynamics a value from the discrete set of estimated early survival probabilities reported in (Vincenzi et al., 2019) for rainbow trout and in Vincenzi et al. (2018) for brown trout.

For modeling survival of fish older than juveniles, we used the population-specific, time-varying survival probabilities estimated in this study. For each population, we simulated 100 years of population dynamics using survival probabilities estimated with final year of sampling $Y_f = 2006, 2008, 2010, 2012$ or 2014. At each time step of the simulation of population dynamics, a survival probability was randomly drawn from the *logit* distribution of estimated survival probabilities, and Bernoulli trials were used to determine whether an individual survived or not. Since UVol_BT is a source-sink system (Vincenzi et al., 2018), we also modeled the influx of brown trout from the source population by doubling the number of fish in each cohort after the first overwinter survival (Vincenzi et al., 2018).

For each replicate, we recorded (a) mean density of fish older than 0+ over simulation time, and (b) the coefficient of variation (CV) of population density of fish older than 0+ over simulation time. Since freshwater salmonid populations living in Western Slovenia are at contemporary risk of extinction only after the occurrence of extreme climate events such as flash floods or debris flows (Vincenzi et al., 2017; Vincenzi et al., 2018), we did not include population extinction as response variable, as the risk of population extinction would almost entirely depend on the modeled intensity and frequency of extreme events (Vincenzi et al., 2008).

For an ensemble of realizations (100 replicates for a fixed set of parameters), we computed: (a) mean and 2.5 and 97.5% quantiles of mean density of fish older than 0+ over simulation time; (b) mean and 2.5 and 97.5% quantiles of CV of density of fish older than 0+ over simulation time.

3 | RESULTS

Results are fully reproducible. Data and R code are at https://github.com/simonevincenzi/Limit_sampling.

Estimates of population densities were variable throughout the time in all four trout populations, with the highest coefficient of variation (CV) for LIdri_RT (0.60) and the lowest for UVol_BT (0.17) (Figure 1).

Previous work has found no or minor effects of population density, water temperature, body size or sex on survival in marble trout (Vincenzi, Mangel, et al., 2016). For $Y_f > 2006$ (i.e., after 6 sampling occasions for marble and rainbow trout, and 5 for brown trout), average survival was

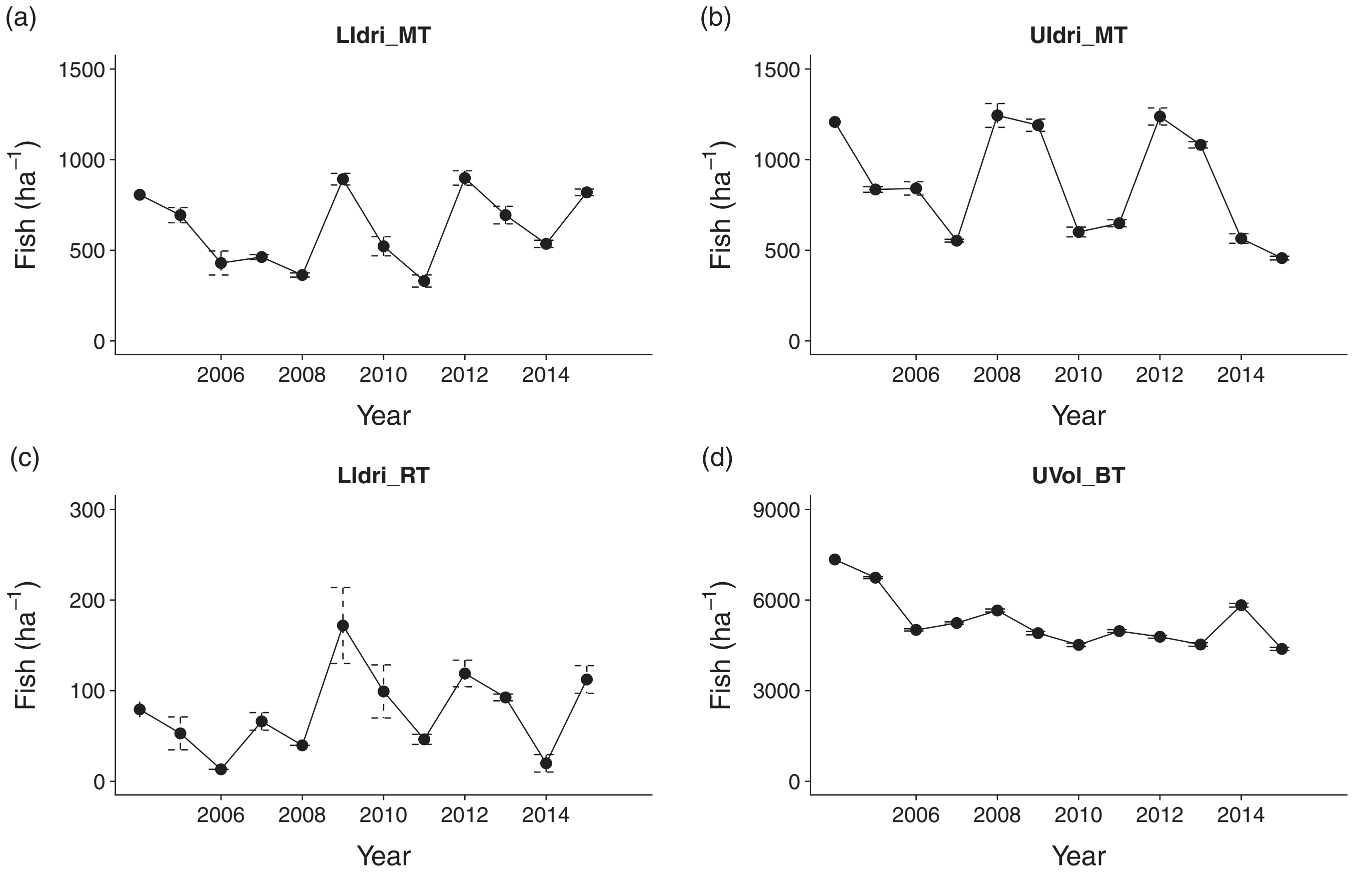

FIGURE 1 Estimated density from observation data over time ± 95% confidence intervals (individuals older than 0+ in September of each year) of marble trout in lower (LIdri_MT), (a) and upper (UIdri_MT), (b) Idrijca, rainbow trout in lower Idrijca (LIdri_RT), (c) and brown trout in upper Volaja (UVol_BT), (d). Coefficients of variation of point estimates of population density between 2004 and 2015 were 0.60 (LIdri_RT), 0.17 (UVol_BT), 0.35 (UIdri_MT) and 0.33 (LIdri_RT). Scales on the y-axis are different as estimated densities of rainbow trout and brown trout are much lower and higher, respectively, than those of marble trout

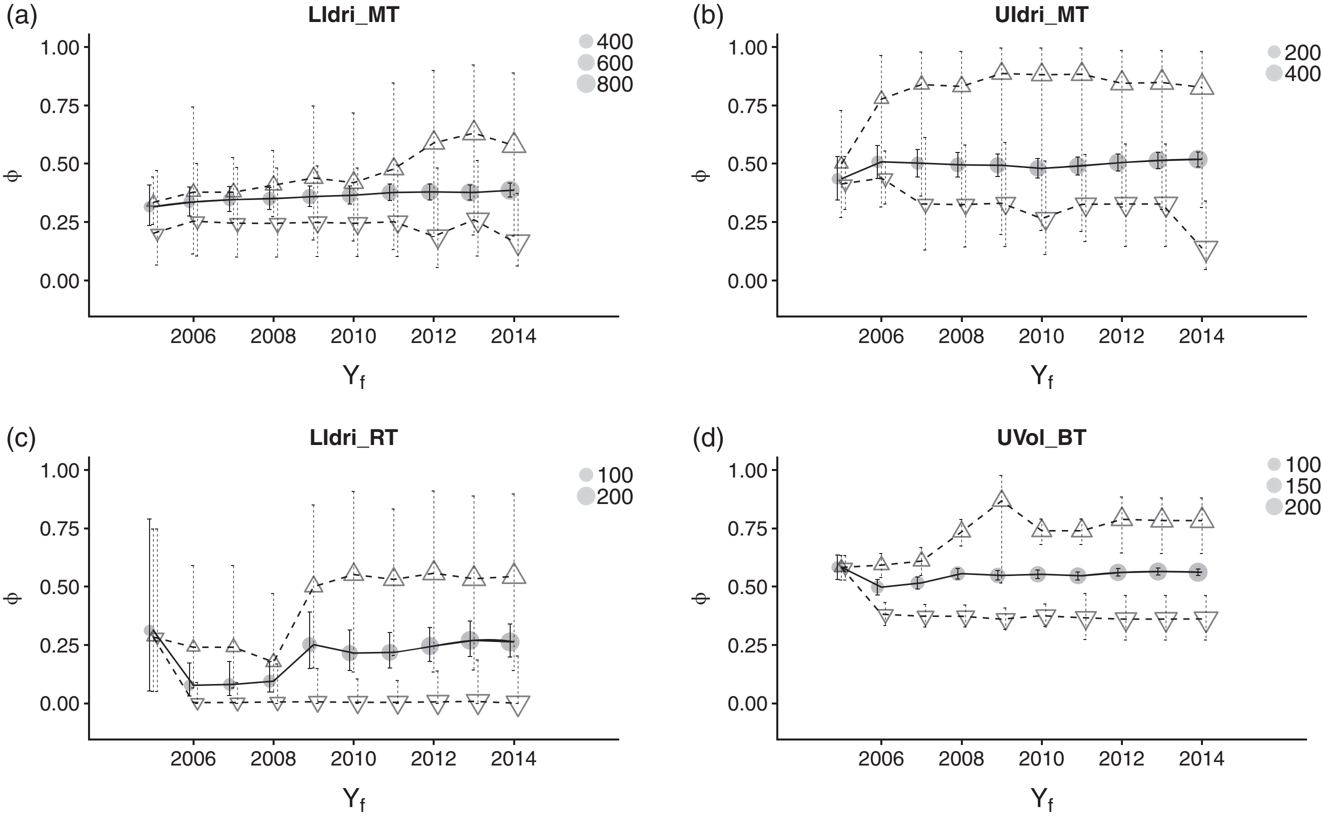

FIGURE 2 Point estimates ±95% confidence intervals for average survival (circle), highest (up triangle) and lowest (down triangle) survival for a sampling interval for different last year of sampling Y_f for marble trout in lower (LIdri_MT, (a) and upper Idrijca (UIdri_MT), (b), rainbow trout in lower Idrijca (LIdri_RT), (c), and brown trout in upper Volaja (UVol_BT), (d). Symbol size represents sample size

constant for LIdri_MT, UIdri_MT, and UVol_BT (Figure 2). For LIdri_RT, average survival was constant for $Y_f > 2009$ (i.e., after 12 sampling occasions). The distance between point estimates of maximum and minimum time-varying survival probabilities increased through time, but the 95% CI of maximum and minimum survival probabilities overlapped for each Y_f, except in UVol_BT (Figure 2).

von Bertalanffy growth function models fitted with standard nonlinear regression (i.e., without accounting for individual variability in growth) show estimates of asymptotic size that are typically greater than those obtained with random-effects models (Figure 3). In LIdri_MT, the greater asymptotic size when estimating model parameters without using random-effects was caused by long-lived individuals that were bigger-at-age than shorter-lived individuals (Figure 3). In LIdri_RT and UVol_BT, the estimates of asymptotic size when using models with or without random effects were basically the same at any point in time (Figure 3). The estimates of asymptotic size when using the random-effects vBGF did not change with Y_f, when Y_f was >2005 (Figure 3). For all populations, estimates of parameters in vBGF models with individual random-effects with $Y_f = 2006$ or 2014 described the same average growth trajectories (Figure 4).

Using time-varying fish survival probabilities estimated at different Y_f had little effects on predictions of mean population density (Figure 5) and on its coefficient of variation (Figure 6). The simulated mean densities were within 10% of the observed mean densities for all trout populations for all Y_f (Figure 5). The only exception was UVol_BT, for which the simulated mean densities with $Y_f = 2006$ were 20% lower than the observed mean density over 2004–2015. CV of density from simulations was lower than the observed CV over 2004–2015 for LIdri_MT, and similar to the observed CV for the other trout populations (Figure 6).

4 | DISCUSSION

Effective conservation of species requires the estimation of variation in vital rates and life-history traits and an understanding of the determinants of the observed variation. Then, vital rates and life histories estimated from focal data, findings from published literature, and controlled experiments should be integrated into models of population dynamics for prediction and evaluation of scenarios of population dynamics, evolution of traits, and management strategies (Elderd & Miller, 2016; Evans, Holsinger, & Menges, 2010). However, how long the monitoring programs informing those models should go on is often unclear.

In the present study, we investigated how estimates of vital rates and predictions of population dynamics change along the monitoring program with the collection of more

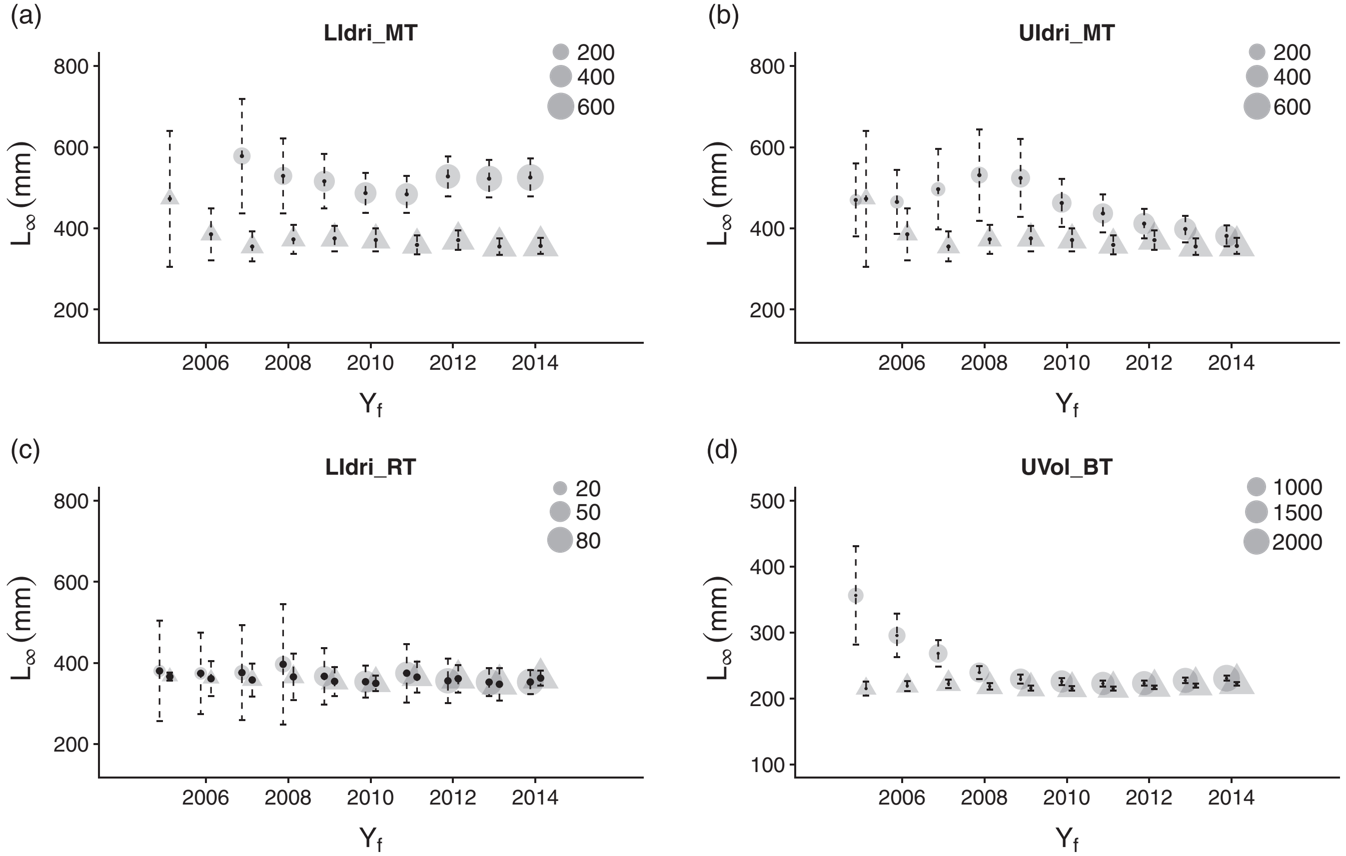

FIGURE 3 Point estimates ±95% confidence intervals (95 CI) for asymptotic size L_∞in the von Bertalanffy growth function estimated using standard nonlinear regression (circle) or the random-effects model (triangle) for different last year of sampling Y_f for marble trout in lower (LIdri_MT), (a) and upper Idrijca (UIdri_MT), (b), rainbow trout in lower Idrijca (LIdri_RT), (c), and brown trout in upper Volaja (UVol_BT), (d). Size of symbols is proportional to the number of unique individuals in the data set. For LIdri_MT, the estimate of asymptotic size when using standard nonlinear regression techniques with $Y_f = 2005$ and 2006 (not shown) were (mean [95% CI]): 1,818 mm [(−1899)-5,535] and 1,555 mm [(−577) − 3,688], respectively

data. We found that in 3 out of 4 populations, a few years of data (3 or 4 sampling occasions, close to the generation time of marble trout and ~1.5 times the generation time of rainbow and brown trout) provided the same estimates of average survival and growth as those obtained by more than 15 sampling occasions, while the estimation of the range of survival probabilities (i.e., ideally the distribution of survival probabilities over time, more often the difference between maximum and minimum survival) required, as expected, more sampling occasions (up to 22 for marble trout), with little reduction of uncertainty around the point estimates. Predictions of mean density and variation in density over time did not change with more data after the first 5 years (i.e., 10 sampling occasions) and were within 10% of the observed mean and variation in density over 11 years.

4.1 | Survival

Previous work has found cohort and time effects on the survival probabilities of freshwater salmonids living in Western Slovenian streams. As neither water temperature nor population density seemed to explain variation in survival, the observed variation might be ascribed to variation in flow rates, trophic conditions or other unobserved or unmeasured properties of the environment Vincenzi, Mangel, et al., 2016). Although due to the effects of sample size and of a fairly stable environment in Lower Idrijca, Upper Idrijca and Upper Volaja we expected the marginal effect of additional data to be increasingly smaller along the monitoring program, we found that even after 6–8 sampling occasions the estimates of average survival (both point estimates and confidence intervals) did not change with additional years of data. The only exception was the rainbow trout population of Lower Idrijca—the smallest of the four salmonid populations—, for which the estimates of average survival remained stable over time only after using data from 12 sampling occasions. In total, capture-recapture data from between 300 and 500 tagged fish were sufficient for stable estimates of average survival probabilities. Since newly tagged fish entered the data set at each sampling occasion, further studies will investigate how many complete life histories are needed to obtain stable estimates of average survival probabilities.

Due to small population sizes, the CIs of the estimates of maximum and minimum survival over a sampling interval overlapped in all populations except the brown trout population of Upper Volaja. In addition, while maximum survival is expected to have a ceiling determined by habitat conditions and the ecology of the species that can be estimated

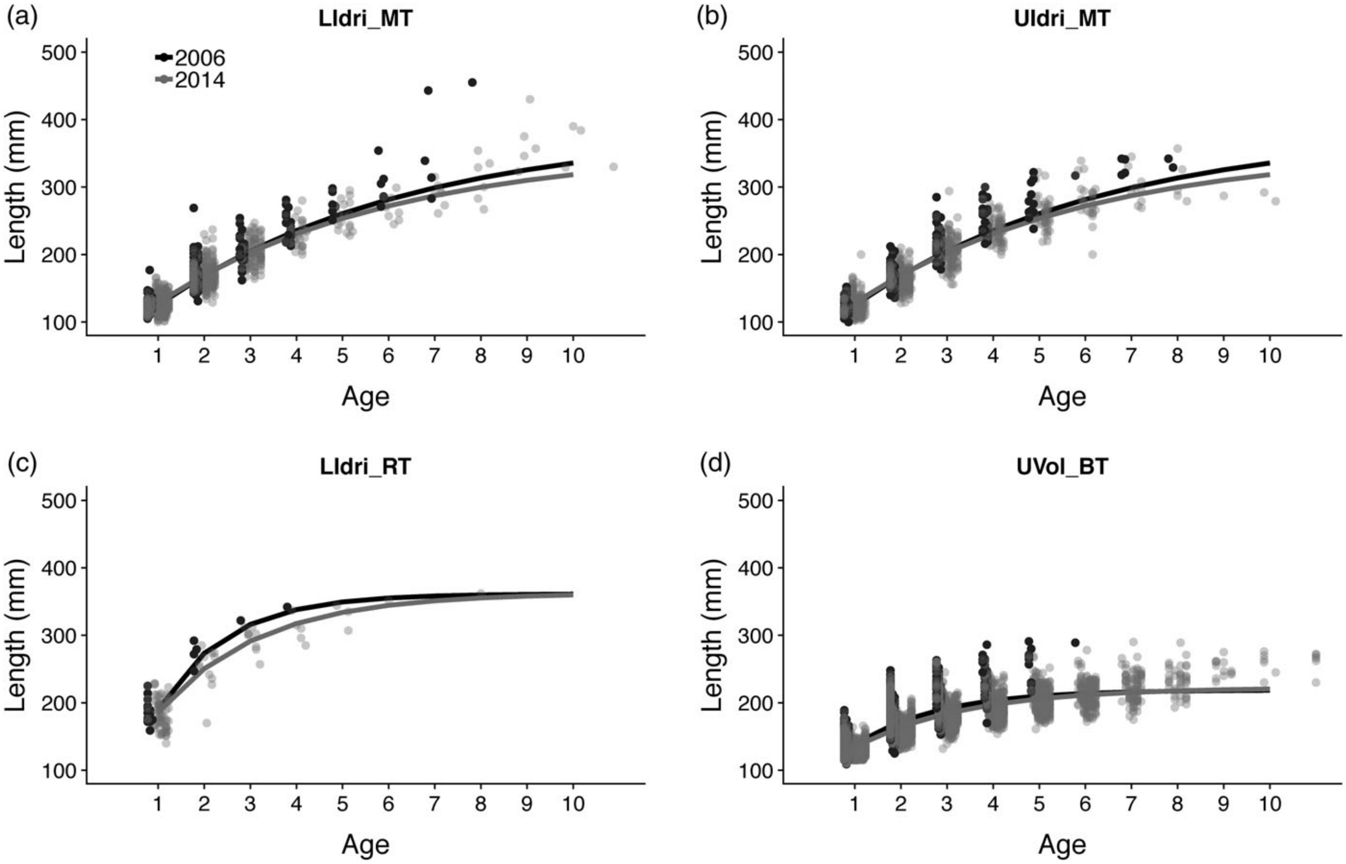

FIGURE 4 Average growth trajectories for body length estimated using the random-effects von Bertalanffy growth function models using data collected up to 2006 (black) and up to 2014 (gray) for marble trout in lower (LIdri_MT), (a) and upper Idrijca (UIdri_MT), (b), rainbow trout in lower Idrijca (LIdri_RT), (c), and brown trout in upper Volaja (UVol_BT), (d)

with a few years of data, the estimation of very low survival probabilities such as those caused by flash floods and debris flows Vincenzi, Mangel, et al., 2016) may require decades-long monitoring programs.

In our analyses, we imposed that data collection for all populations started on the first sampling occasion of the real monitoring program for the four trout populations. Other analyses could be run by maintaining the same length of the monitoring program (say, four sampling occasion), but setting an arbitrary sampling occasion as the first one (say, 2010 instead of 2004). For the two trout populations of Lower Idrijca, it might appear that by setting the first sampling occasions later on we would quickly capture the biggest difference between maximum and minimum survival probabilities. However, probability of capture and probability of survival at each sampling occasion are jointly estimated using all data available, and the presence of many degrees of freedom might bias the comparison of results when choosing different starting sampling occasions for the analyses. Regarding the former, the highest point estimate for maximum survival in a sampling occasion in Upper Volaja is larger with the end of sampling in 2009 than in 2010, although intuitively we would not expect the highest point estimate for maximum survival in a sampling occasion to ever decrease with more sampling occasions. For the latter, among others, sampling becomes more efficient over time as technicians and field workers "reliably locate" hiding spots and pools, and the probability of losing tags decreases with more practice in setting them.

The rainbow and marble trout populations showed greater fluctuation in population size than the brown trout population. Theoretically, and apart from the effects of extreme events, we would expect to need fewer sampling occasions to estimate the maximum difference between maximum and minimum survival in a sampling occasion in populations with smaller fluctuations in population size. Our results may appear to support the hypothesis; the rainbow trout population showed both the largest fluctuations in population size and the longest time to reach a semi-stable distance between maximum and minimum survival in a sampling occasion. However, the rainbow trout population is also that with the smallest numbers—which are expected to lead to a large coefficient of variation in population size—and smallest mean survival, thus, making it difficult to assume causality between non-stationarity of population size and time to reach a semi-stable distance between maximum and minimum survival in a sampling occasion.

4.2 | Growth

Estimates of body growth are fundamental for management. For instance, age-structured stock assessment methods are

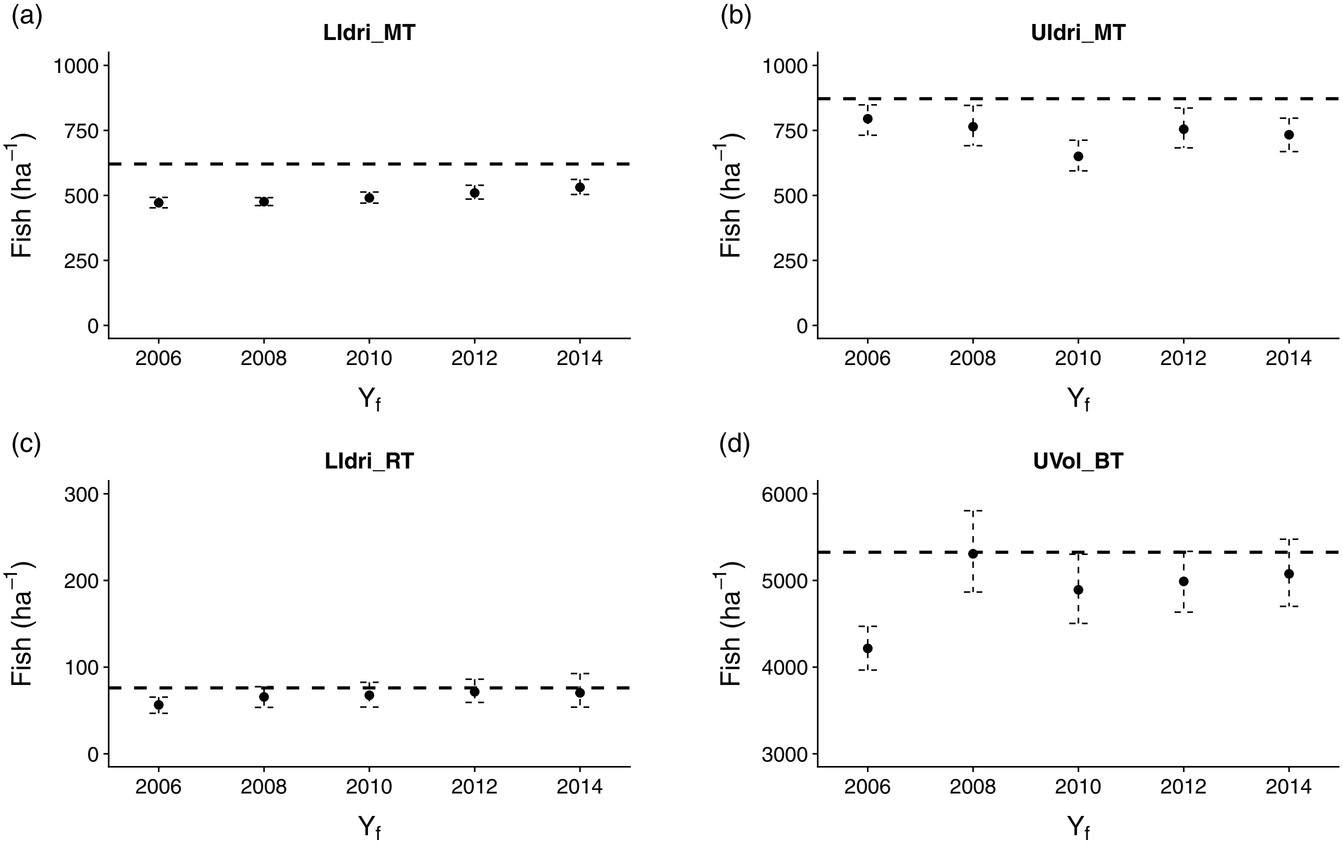

FIGURE 5 Observed mean population density of fish older than 0+ from 2004 to 2015 (horizontal dashed line) and mean and 2.5 and 97.5% quantiles of mean density of fish older than 0+ over simulation time for different last year of sampling Y_f for marble trout in lower (LIdri_MT), (a) and upper Idrijca (UIdri_MT), (b), rainbow trout in lower Idrijca (LIdri_RT), (c), and brown trout in upper Volaja (UVol_BT), (d). Scales on the y-axis are different as estimated densities of rainbow trout and brown trout are much lower and higher, respectively, than those of marble trout

based on sizes-at-age that are often derived from parameters of the von Bertalanffy growth model for that species (Katsanevakis & Maravelias, 2008). Size-at-age, which is the easiest-to-observe realization of the growth process, often varies considerably among individuals living in the same environment. In the four trout populations, the size of the smallest age-1 fish was ~50% of the size of the biggest age-1 fish.

Longitudinal data (e.g., tag-recapture) and random-effects models greatly facilitate the estimation of individual and group (i.e., sex, year-of-birth) variation in growth. In particular, for the two marble trout populations, we found that standard nonlinear regression (i.e., models without random-effects) provided estimates of asymptotic size that were consistently larger (up to $Y_f = 2014$ for marble trout in Lower Idrijca and up to $Y_f = 2012$, ~800 tagged fish, for marble trout in Upper Idrijca) than those provided by the random-effects vBGF models.

In marble trout, the primary type of intra-specific competition for resources seems to be interference competition for space (Vincenzi, Crivelli, et al., 2016), probably due to their high territoriality. In interference competition, bigger individuals (in the case of marble trout, those with access to better sites) reduce the access to resources, such as space and food, of smaller individuals, and may also live longer than smaller individuals. On the other hand, the estimates of asymptotic size using the random-effects vBGF models were little affected by the use of more data when 100 to 200 individuals of various ages were already included in the data set. Since the vBGF parameters can seldom be interpreted separately (Vincenzi, Mangel, et al., 2014), the analysis of the whole growth trajectories is crucial for understanding variation in growth. Also when examining whole growth trajectories, we found that the growth trajectories predicted by the random-effects vBGF models were almost identical when using data from 3 (100–200 individuals of various ages) or 11 years of monitoring.

4.3 | Population dynamics

Evans et al. (2010) found that parameter uncertainty was responsible for 50–64% of the variation in the stochastic growth rate of simulated populations of Florida scrub mint, despite data used to estimate vital rates was long term (20 years) and involved thousands of individuals across multiple populations. In our model of population dynamics, there were small differences between predicted densities when using data from 3 (6 sampling occasions) or 11 (22 sampling occasions); the only exception was the brown trout population of Upper Volaja. The low mean population density predicted for Upper Volaja when using data from 5 sampling occasions

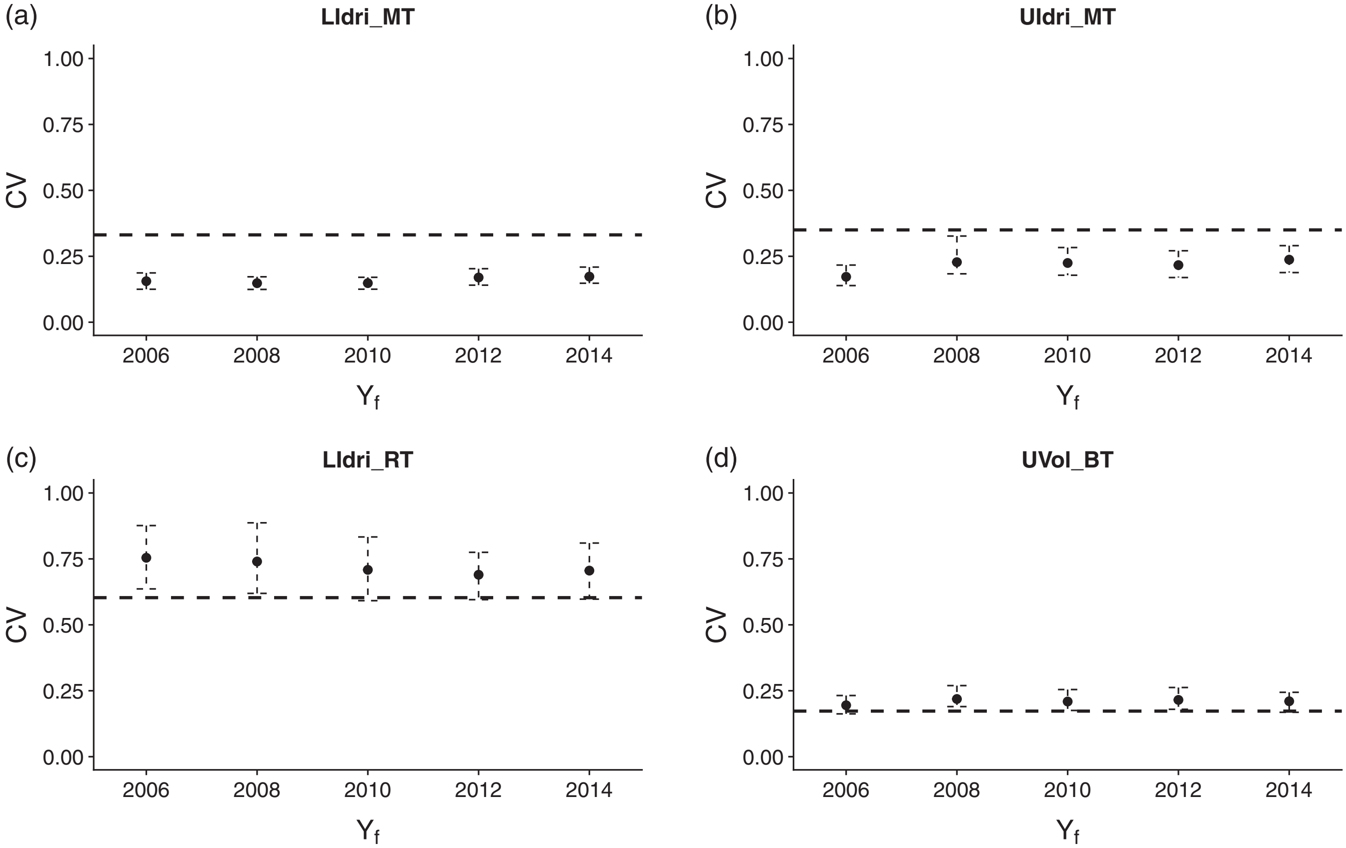

FIGURE 6 Observed coefficient of variation (CV) of density of fish older than 0+ from 2004 to 2015 (horizontal dashed line) and mean and 2.5 and 97.5% quantiles of coefficient of variation of density of fish older than 0+ over simulation time for different last year of sampling Y_f for marble trout in lower (LIdri_MT), (a) and upper Idrijca (UIdri_MT), (b), rainbow trout in lower Idrijca (LIdri_RT), (c), and brown trout in upper Volaja (UVol_BT), (d)

was due to low probabilities of survival in Upper Volaja between 2004 and 2007, whose inclusion in the model of population dynamics led to predictions of mean population size much lower than those provided by models parameterized with more data and more representative environmental conditions. As described in Vincenzi et al. (2018), high population densities in Upper Volaja 2004–2005, fast growth of fish born in early 2000s, and lower survival in the first years of sampling point to very low population densities in late 1990s and early 2000s, probably a consequence of an extreme climate event (e.g., flash flood or debris flow) that caused high fish mortalities. Thus, as in the case of the brown trout population of Upper Volaja, when the estimates of survival probabilities are not representative of the conditions typically experienced by individuals, model predictions can be inaccurate.

In our analyses, we only set survival probabilities as different among models for the same population. In our model of population dynamics, parameter uncertainty can be interpreted as a combination of both statistical uncertainty, which inevitably comes from parameter estimation, and process variability—i.e., the random draw at any time step of a survival probability can also represent variation in exogenous processes that determine variation in vital rates, and recruitment and early survival are both density-dependent.

However, the parameters with the most available data are not necessarily the parameters that have the biggest effect on model predictions. In some cases, empirical data may be lacking for parameters that can substantially alter model predictions. In our study, we were able to include a model of density-dependent early survival only in the models of population dynamics for the two populations of marble trout, since even more than 10 years of data were not sufficient to estimate parameters of similar models for brown trout and rainbow trout. Since in small populations early survival may almost entirely depend on environmental variables such as water temperature, trophic conditions, and water flow—whose year-to-year variation are intrinsically tough to predict—data on density and models of density-dependent survival may reach the limits of their (little) explanatory power after just a few years of monitoring. However, randomly drawing an early survival probability at each time step from the set of estimated probabilities did not seem to affect the accuracy of the predictions of mean population density. Then, for small populations living in highly variable environments, process variability of extreme events, such as stochastic variation in their timing and intensity, is often the major determinants of population dynamics (Vincenzi, Crivelli, et al., 2014). For instance, Evans et al. (2010) found that much of the variability in the population growth rate of simulated populations of Florida scrub mint resulted from process variability, such as random variation in fire history, year variation and demographic fates among replicates of population growth. Decades-long monitoring is needed to capture the statistical properties of extreme events and of their effects on vital rates and life histories. However, this additional data would rarely reduce the uncertainty of "useful" predictions of population dynamics for conservation, since those predictions heavily depend on the actual realizations of stochastic processes (i.e., a flood that wipes out a fish population might have a recurrence interval of 50 years, but in an interval of *n* years either occur or does not occur).

Models of recruitment dynamics were able to explain only a small part of the variability in recruitment (i.e., <30%). The relative balance between spawning stock size and environmental factors as determining recruitment in freshwater salmonids is still debated and probably context-specific (Einum, 2005; Nicola, Almodóvar, Jonsson, & Elvira, 2008). Recruitment in marble, rainbow and brown trout was highly variable over time; the marble and rainbow trout populations of Lower and Upper Idrijca were recruitment-driven, as indicated by the strong 1-year lagged correlation between density of older than newborn trout and density of newborns (Vincenzi, Mangel, et al., 2016; Vincenzi et al., 2019). In Upper Volaja, the absence of a correlation between density of older than newborn trout and density of newborns was caused by immigration of 0+ and 1+ from the source population (Vincenzi et al., 2018). Despite the uncertainty in recruitment models, the predictions of mean population density and variation of density over time were accurate.

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Authors contributions

SV conceived the ideas and designed methodology; AJC conceived and run the Marble trout Project and AJC and DJ collected the data; SV analyzed the data; SV and AJC led the writing of the manuscript. All authors gave final approval for publication.

DATA STATEMENT

Data and R code: https://github.com/simonevincenzi/Limit_sampling.

The file Readme.md in the repository describes each step of the reproducible analyses.

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