Supporting Information S1–S5

This file contains the SI for:

'Towards a future without stocking: harvest and river regulation determine long-term population viability of migratory salmonids'

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S1.1 Figures

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Figure S1.7: Asymptotic population growth rate λ calculated from the projection matrix under different reductions of harvest mortality (rows) and dam passage mortality of spawners (columns). The latter is approximated as decreases in background mortality of below average-sized upriver spawners. White lines mark $\lambda = 1$ (solid) and $\lambda = 0.8, 0.9$ (dashed). Dam mortality of smolts is set to 0.

Figure S1.8: Asymptotic population growth rate λ calculated from the projection matrix under different reductions of harvest mortality (rows) and background mortality of below-dam spawners (columns). White lines mark $\lambda = 1$ (solid) and $\lambda = 0.8, 0.9, 1.1$ (dashed). Dam mortality of smolts is assumed to be unchanged.

S1.2 Tables

Table S1.1: Results from the analysis of mitigation measures in the absence of stocking.

[∗] Asymptotic population growth rate.

∗∗ Absolute difference relative to the the scenario with no mitigation measure.

S2 Vital Rate Estimation

S2.1 Estimating vital rates from data

All vital rates required for parameterising the IPM (Table 2) were either estimated from individual-based data or inferred from the literature, and their relationships with body size are plotted in Figures S2.1–S2.4.

We obtained estimates of size-dependent harvest and background mortality $(m_z^H \text{ and } m_{a,z}^O)$ and resulting survival probabilities $(S_{a,z})$ for adults spawning up- and downriver of the dam, as well as the probability of using the fish ladder (P_L) , from [Nater et al.](#page-34-0) [\(2020\)](#page-34-0). These estimates are based on a Bayesian mark-recapture model fit to 50 years of data. Intercepts (but not size-relationships) for all parameters were allowed to differ between wild-born and stocked individuals but estimates revealed basically identical harvest and background mortality and only slightly lower probability of using the fish ladder for stocked fish (Figure [S2.5,](#page-17-0) for a discussion of this lack of effect of hatchery origin see [Nater et al.](#page-34-0) [2020\)](#page-34-0).

As live recaptures of marked Hunder trout occur during biennial spawning runs, the mortality hazard rates and resulting survival probabilities in [Nater et al.](#page-34-0) [\(2020\)](#page-34-0) were estimated over a two-year interval based on body size at the beginning of the first year. To accommodate this for adult fish in the IPM, we assumed that spawners experience two years' worth of mortality while transitioning to the post-spawner stage, and that post-spawners have a survival of 1. As a consequence, the number and size-distribution of individuals in the post-spawner stage is not fully representative (but population growth is not affected by this). For calculating subadult survival, we rescaled m_z^H to a one-year interval and let it depend on current size every year. This assumption was sensible for subadults as they grow much faster than adults (and without reproduction costs), and as subadult background mortality was a free parameter (see below).

Annual growth functions for wild-born juveniles in the river and wild-born and stocked (sub)adults in the lake were parameterised using posterior means from a Bayesian growth model fitted to scale data from the Hunder trout [\(Nater et al.](#page-34-1) [2018;](#page-34-1) [2020\)](#page-34-0). In this model, the growth process is described as linear and size-independent during the river phase (size_{t+1} = size_t + h, where h is a fixed increment) and with a size-dependent von Bertalanffy curve including a cost of reproduction during the lake phase $(\text{size}_{t+1} = (\text{size}_{\infty} - \text{size}_{t})(1 - e^{-k}) * R$, where $\text{size}_{\infty} = \text{asymptotic size}$, k = growth rate, R = correction factor for growth post-maturation). The parameters k and size_∞ were estimated separately for stocked and wild-born individuals, resulting in growth trajectories for stocked trout that featured marginally larger growth increments at larger sizes (due to higher asymptotic size, Figure [S2.5\)](#page-17-0). The complete growth model additionally provided estimates of random individual, year, and residual process variation, and only the latter was used for predicting variation in size in the present IPM. The parameters of the river growth function were also used to describe the offspring size distribution, i.e. the size distribution of juveniles entering the population after completing their first year of river growth (size_{age1} = size_{hatching} + h).

We used the same scale data to estimate smolting $(P_{smooth}(x))$ and maturation $(P_{mat}(x))$ probabilities. Both probabilities were described by binomial generalised linear mixed models with body size and sex as fixed effects and year as a random effect. Due to the presence of time trends, year and its interaction with body size were also included as linear predictors. For modelling the maturation probability $P_{mat}(x)$ of subadults in the lake, we further included an effect of origin (wild-born vs. stocked) on both the intercept and the size slope to capture lasting effects of hatchery-rearing, and a size-sex interaction effect to account for the size range at maturation being larger for males than females. We used the most parsimonious models as determined by AIC to make predictions for the IPM. The most parsimonious model for smolting probability included fixed effects of body size and its interaction with year, while the most parsimonious model for maturation probability was the full model (including all of the above effects). This model predicted a slightly narrower size-window for maturation in stocked than in wild-born individuals (Figure [S2.5\)](#page-17-0).

Fecundity $(F(x))$, defined as the number of eggs per female of a given size x, could also be estimated from data. The functional forms of positive relationships between fecundity and body size are well established for salmonids (Abée-Lund & Hindar [1990,](#page-32-0) [Fleming](#page-33-0) [1996\)](#page-33-0), and we here modelled $log(F)$ as a linear function of $log(x)$. Despite the sparsity of the data from our study system (16 data points from two years), the estimated relationship fell within the range reported for other populations of brown trout and Atlantic salmon (Figure S2.5). /addedWe assumed that origin (stocked vs. wild-born) did not influence fecundity.

For the remaining vital rates, most of which pertain to early life history $(S_0, S_j, S_{dam}, m_s^O)$, no data was available. We therefore obtained likely parameter values from published studies on brown trout and other salmonid species. We used identical parameter values for stocked and wild-born fish (where applicable). The details of the literature review, parameter inference, and a sensitivity analysis can be found in Appendix S3.

All analyses were run were run in R 3.5.2 [\(R Core Team](#page-34-2) [2018\)](#page-34-2). Generalised linear mixed models were fitted with version 1.1-17 of the lme4 package [\(Bates et al.](#page-32-1) [2015\)](#page-32-1).

S2.2 Vital rate functions under averaged conditions

We formulated vital rate functions for the IPM by setting parameters to the relevant mean estimates from frequentist models and means of the posterior distributions from Bayesian models.

For the present analyses, we built the IPM using vital rate functions representative of averaged environmental conditions. We defined these by setting the values of all standardised environmental covariates, random year effects, and random individual effects required to predict vital rates to 0. The prediction functions for river growth and smolting and maturation probability also included a time trend, and we here set the year to 1991, representing the median year of the study period $(1966-2016).$

Figure S2.1: Relationship of survival probabilities and body size (relevant ranges) for different life stages. S_j and S_{dam} are inferred from the literature and are therefore plotted as mean estimates without uncertainty (see Appendix S3). For S_s and S_a , solid lines represent predictions based on the posterior means while ribbons mark the 95% credibility intervals obtained from the Bayesian mark-recapture model [\(Nater et al.](#page-34-0) [2020\)](#page-34-0).

Figure S2.2: Relationship of overall and cause-specific mortality hazard rates and body size (relevant ranges) for different life stages. m_j and m_{dam} and m_s^O are inferred from the literature and are therefore plotted as mean estimates without uncertainty (see Appendix S3). For m^H and m_a^O , solid lines represent predictions based on the posterior means while ribbons mark the 95% credibility intervals obtained from the Bayesian mark-recapture model [\(Nater et al.](#page-34-0) [2020\)](#page-34-0).

Figure S2.3: Growth functions describing the relationship of current length and next length in the river- and lake phase of life. Solid lines represent predictions based on the posterior means obtained from the Bayesian growth model [\(Nater et al.](#page-34-1) [2018;](#page-34-1) [2020\)](#page-34-0).Ribbons mark the 95% credibility intervals under consideration of residual process variation. Random year- and individual variation are omitted. For the lake phase, growth is plotted separately for subadult individual, and mature individuals in a resting year (green, no cost of reproduction) and in a spawning year (orange, including cost of reproduction), respectively.

Figure S2.4: Relationship of stage transition probabilities/fecundity and body size (relevant ranges) for different life stages. For P_{smolt} , P_{mat} , and F , solid lines represent mean predictions and ribbons mark the 95% confidence interval obtained from the linear (mixed) model fits. For P_L , solid lines represent predictions based on the posterior means while ribbons mark the 95% credibility intervals obtained from the Bayesian mark-recapture model [\(Nater et al.](#page-34-0) [2020\)](#page-34-0).

Figure S2.5: Origin-specific differences in size-dependent vital rates that were estimated with separate parameters for stocked (blue) and wild-born (wild) individuals. For m^H , $m^O_{a,u}$, $m^O_{a,d}$, P_L , and qL solid lines represent predictions based on the posterior means while ribbons mark the 95% credibility intervals obtained from Bayesian models. For P_{mat} solid lines represent mean predictions and ribbons mark the 95% confidence interval obtained from the linear (mixed) model fits. Unlike in Figure [S2.3,](#page-15-0) we here plot lake growth increment (instead of next size) to better illustrate the estimated difference due to origin.

Figure S2.6: Estimated relationship between fecundity and body size for the Hunder brown trout (red line, red circles $=$ data points) relative to other populations of *Salmo trutta* and *Salmo* salar (grey). Fecundity-size relationships for other populations were obtained from Abée-Lund $\&$ [Hindar](#page-32-0) [\(1990\)](#page-32-0), [Fleming](#page-33-0) [\(1996\)](#page-33-0), [Jonsson et al.](#page-33-1) [\(1996\)](#page-33-1), [Jonsson & Jonsson](#page-33-2) [\(1999\)](#page-33-2), [Heinimaa &](#page-33-3) [Heinimaa](#page-33-3) [\(2004\)](#page-33-3), [Moffett et al.](#page-34-3) [\(2006\)](#page-34-3).

S3 Inferring Unknown Vital Rates from Literature

S3.1 Meta-analysis of survival from literature

Several vital rates in the life cycle of the Hunder trout could not be directly estimated as no suitable data was available for the study population. All of these vital rates were related to survival (and underlying mortality hazard rates) early in the life cycle: early survival from egg to 1-year old (S_0) , annual juvenile survival (S_i) , dam passage survival of smolts (S_{dam}) , and annual background mortality hazard rate for subadults (m_s^O) . In order to parameterise the IPM, we therefore searched the literature for estimates of these vital rates from other salmonid species, and the results of this literature review are presented in Tables [S3.1](#page-19-2) and [S3.2,](#page-21-0) and Figure [S3.1](#page-20-0) (note that regarding subadults, we reviewed the literature for annual survival S_s , not just background mortality).

Table S3.1: Summary of literature review for early (S_0) , juvenile (S_i) , subadult (S_s) , and dam passage survival (S_{dam}) of salmonids. 90% and 50% ranges, median, and mean values are calculated using the lower and upper bounds of reported ranges from individual studies (see Table [S3.2\)](#page-21-0), and thus assume equal likelihood of all values between the lower and upper range boundaries. The exception is S_{dam} , where there is only one study and the mean based on the mean reported in that study.

IPM parameter Total range 90% range			50% range	Median	Mean
S_0	$0.009 - 0.140$			0.088	0.082
S_i	$0.025 - 0.750$	$0.050\hbox{--}0.700$	$0.230\hbox{--} 0.488$	0.322	0.353
S_{s}	$0.010 - 0.720$	$0.013\hbox{--} 0.693$	$0.100 - 0.450$	0.245	0.295
S_{dam}	$0.410 - 0.920$				0.750

For early survival S_0 , we directly used the mean value of 0.082 as calculated from three studies (assuming equal likelihood for all values between the reported lower and upper range limits). For juvenile survival, we assigned the mean survival value of 0.353 estimated from literature (and its equivalent mortality hazard rate) to individuals with a body size of 157mm, which is the average halfway size from age 1 to smolting (calculated from individual-level scale data, [Aass](#page-32-2) [et al.](#page-32-2) [2017\)](#page-32-2). As juvenile survival often increases with size in salmonids (e.g Al-Chokhachy $\&$ [Budy](#page-32-3) [2008,](#page-32-3) [Zabel & Achord](#page-35-1) [2004\)](#page-35-1), we then added a negative effect of body size on the log of juvenile mortality hazard rate. We calibrated this size effect such that the resulting size-survival relationship produced survival estimates aligning with the ranges reported in the literature (Table [S3.1\)](#page-19-2). The value for this size effect employed in the main model was −0.2.

Similarly for dam passage survival, we assigned the mortality hazard rate equivalent to the reported mean survival $(-log(0.75))$ to individuals with the average size at smolting of 250 mm, and added a log-linear size effect (value $= 0.05$) to it such that the resulting size-relationship closely resembled that reported in [Keefer et al.](#page-33-4) [\(2012\)](#page-33-4).

a) Annual juvenile survival

b) Annual subadult survival

Figure S3.1: Visualizations of the reported ranges for a) annual juveniles survival and b) annual subadult survival from the literature. Black lines represent the reported ranges, circles replace ranges when only single number estimates were reported, and grey numbers indicate the source as defined in Table [S3.2.](#page-21-0) Dashed lines mark the calculated mean values (red) and 50% ranges (blue) based on all sources.

Finally, for approximating annual survival of subadult Hunder trout, we combined estimates from literature with our model for harvest mortality. We assumed that subadults experienced the same size-dependent harvest mortality (m^H) as adults, and chose the intercept value for m_s^O for individuals of 437 mm (i.e. halfway size from smolting to maturation) such that combined with m^H for the same size added up to the mean subadult survival reported in the literature (0.295, Table [S3.1\)](#page-19-2). As for juvenile and dam survival, we then added a log-linear size effect on m_s^O to produce a size-survival relationship for subadults that produced survival estimates, consistent with what is commonly observed in the literature (Table [S3.1\)](#page-19-2). In the main model, background mortality hazard rates for individuals of size 437 mm was thus set to 0.62 with a log-linear size effect of -0.7 .

All of the here mentioned size-survival relationships are plotted in Figures S2.1 and S2.2. In the following, we present an analysis of sensitivity of model behaviour to the choice of specific values and size-relationships for early (S_0) , juvenile (S_i) , subadult (S_s) , and dam passage (S_{dam}) survival and mortality.

Table S3.2: Summary of information on early- (S_0) , juvenile- (S_j) , subadult- (S_s) , and dam passage survival (S_{dam}) of salmonids found in the Table S3.2: Summary of information on early- (S_0) , juvenile- (S_j) , subadult- (S_s) , and dam passage survival (S_{dam}) of salmonids found in the literature.

S3.2 Sensitivity analysis

We tested the effects of choosing different values from the range reported in the literature for the baseline survival/mortality in early life (S_0, m_0) , of juveniles (S_j, m_j) , of subadults $(S_s,$ via m_s^O , and of passing the dam on the smolt migration (S_{dam}) , as well as the strength of size-dependence in the latter three. The results of varying one parameter while keeping all others at the selected values (see previous section) are presented in Figure [S3.2.](#page-23-0) In general, the responses of asymptotic population growth rate λ were stronger to varying baseline mortality parameters than size effects, and whether or not the model assumed increased early mortality below the dam or not (below-dam penalty) did have little effect on the behaviour of the sensitivity. λ varied between 0.42 and 1.11, but only extreme values for baseline early- or juvenile mortality resulted in λ beyond the range 0.7–0.9. Variation in those two parameters also had the largest impacts on other population-level metrics including the stable stage distribution and within-stage average body size at equilibrium (results not shown). Among the tested parameters, baseline early and juvenile survival emerged as the most influential ones given the possible ranges reported in the literature. Nonetheless, substantial increases in both of them were necessary to produce a growing population even when assuming that there was no penalty for early survival below the dam (Figure [S3.3\)](#page-25-0).

Figure S3.2: Response of asymptotic population growth rate (λ) to varying the parameters inferred from literature (sizes in title brackets represent sizes to which intercept parameters pertain). Colour represents the applied penalty on early survival below the dam relative to above: none (black), 50% higher (blue), and 100% higher (red). Dashed grey lines mark the selected values. (Figure continues on next page.)

Figure S3.2: *(continued)* Response of asymptotic population growth rate (λ) to varying the parameters inferred from literature (sizes in title brackets represent sizes to which intercept parameters pertain). Colour represents the applied penalty on early survival below the dam relative to above: none (black), 50% higher (blue), and 100% higher (red). Dashed grey lines mark the selected values.

Asymptotic growth rate

Figure S3.3: Response of asymptotic population growth rate (λ) to simultaneously varying baseline early- and juvenile survival (model without below-dam penalty). Blue indicates $\lambda < 1$ while red indicates $\lambda > 1$. Combinations where $\lambda > 1$ are additionally marked with red stars.

S4 Quantification of Stocking

The stocking programme for the Hunder trout has been going on for half a century, and stocked fish make up a considerable part of the population (up to $\sim 60\%$ of the spawning population in more recent years, [Moe et al.](#page-34-8) [2020\)](#page-34-8). In the 1960s and 1970s, there were large inter-annual differences in number, age, and average size of released hatchery fish in an attempt to experimentally assess and optimise the stocking programme. From 1984 onward the stocking strategy became more uniform, consisting of usually 20,000–40,000 2-year old smolts with an average size of 20–24 cm released in several locations in the river and the lake.

We obtained annual smolt release reports from 1985–2017 Eidsiva Vannkraft AS who operate the Hunder trout hatchery and coordinate the stocking programme. These reports detail the total number of hatchery-reared Hunder trout smolt released in different locations in the river Gudbrandsdalslgen and lake Mjøsa. We summed the number of released smolt in location upriver and downriver of the Hunderfossen dam for each year, and from that calculated the mean annual number of released smolt above the dam (11,909) and below the dam (15,111). Dividing those numbers by 2 gave estimates for the mean annual number of female released smolts (assuming an even sex ratio for the hatchery). For a subset of batches of released smolt, counts were provided not just for the entire batch but also for four discrete size classes: < 15 cm, $15-20$ cm, $20-24$ cm, > 24 cm. We used this information to approximate a continuous size distribution by assigning a representative size to each discrete size class $(140, 170, 220, 250 \text{ mm})$ and repeating each representative size by the number of individuals within the corresponding size class. The calculated mean (201.9 mm) and standard deviation (26.7 mm) of the approximated size distribution were then used to simulate the size distribution of stocked smolt entering the population.

In 10 out of 32 years, additional batches of 1-year old trout were released alongside the regular 2-year old smolt. These small fish likely have very low survival following release, and we thus omitted them from the present analyses.

S5 Exploration of compensatory density dependence

Compensatory density dependence in early life is well documented in fish and may prevent extinction through improved recruitment and lower juvenile mortality at low population sizes [\(Lorenzen](#page-34-9) [2005,](#page-34-9) [Rose et al.](#page-34-10) [2001\)](#page-34-10). In the case of the Hunder trout, substantial decreases in both early and juvenile mortality would be needed to prevent population decline (Figure [S3.3\)](#page-25-0), making it unlikely that density feedbacks in early life alone would be sufficient to ensure the future of an ecologically functional and sustainably harvestable population without stocking. Nonetheless, compensatory recruitment may contribute to protecting the population from extinction, and may affect the efficiency of different management strategies.

A comprehensive analysis of the impacts of density feed-backs on population viability and efficiency of management strategies is beyond the scope of this paper. Nonetheless, we here present some preliminary results from analyses using an extension of our model including compensatory density-dependence in early (= first-year, from egg to 1-year old) and juvenile mortality. Notably, no data from the Hunder trout system were available to quantify either of these parameters (SI S3) and – by extension – the strength and form of density dependence affecting them. We therefore adopted an exploratory approach, assuming a proportional effect of changes in population density on mortality hazard rates. This is commonly done, for example in Beverton-Holt and Ricker stock recruitment models. Specifically, we assumed that early mortality in any year t post-stocking was decreased/increased by the same factor as the number of spawning adults in year $t-1$ differed from the number of spawning adults that had been present at equilibrium with stocking. We made an analogous assumption for juvenile mortality, but here used changes in the number of juveniles rather than adults to inform the degree of decrease/increase in mortality. Density feedbacks were included separately for the upriver and downriver spawning grounds.

We first projected the population following termination of stocking under several different assumptions for compensatory density dependence, namely including scenarios in which density feedbacks affected only early mortality, or early and juvenile mortality, as well as different strengths of the density feedbacks (proportional change in density multiplied by 1, 0.75, and 0.5). The results are plotted in Figure [S5.1.](#page-28-0)

Figure S5.1: Population trajectories following termination of stocking at $t = 50$ assuming compensatory density dependence in early and juvenile mortality (solid lines) or early mortality only (dashed lines), with strength of density feedbacks proportional to 1 (purple), 0.75 (pink), and 0.5 (orange) times the change in density relative to equilibrium density (of spawners and juveniles, respectively) under stocking.

In the rather unlikely scenario that compensatory density dependence only affected early mortality, density feedbacks prevented population decline when assuming 1:1 proportionality (purple dashed line in Figure [S5.1a](#page-28-0)). However, this was accompanied by a shift in population structure towards a higher proportion of small, young individuals. As a result, the number of trout of harvestable size ($>= 500mm$) was still predicted to decrease substantially following termination of stocking (Figure [S5.1b](#page-28-0)). Under all other combinations of assumptions, both the total population size and

the number of harvestable individuals was predicted to decrease substantially.

It may seem counter-intuitive that density feedbacks have a stronger impact on total population size when they only apply to early mortality, as opposed to early and juvenile mortality. However, this is a consequence of density-dependence being mediated by different segements of the population (i.e. spawner density affects early mortality, and juvenile density affects juvenile mortality). In scenarios with density feedbacks only in early mortality, survival from egg to juveniles increases quickly as spawner numbers decline. This, in turn, results in substantial increases in total population size due to more abundant juveniles and density effects will only start suppressing population growth once those new, big cohorts become spawners and start increasing early mortality again via spawner density. When juvenile mortality is also density-dependent, on the other hand, the density-feebacks in early and juvenile mortality interact, resulting in faster feedbacks that can counter-act each other.

The presence of density feedbacks modified the impact of different mitigation strategies in the absence of stocking (Figures [S5.2](#page-30-0) and [S5.3\)](#page-31-0). In all scenarios besides the "no harvest" scenario, population sizes stabilised at a lower level than under stocking, both with regards to the total number of individuals (Figure [S5.2a](#page-30-0)) and number of individuals >= 500 mm (Figure [S5.2b](#page-30-0)). Analogous to scenarios involving the density-independent model (Figure 4), harvest-slot limits were predicted to yield the best results (largest remaining population sizes). However, compared to density-independent simulations, protecting only small individuals from harvest was predicted to be more efficient than protecting only large individuals. The "no harvest" scenario resulted in population cycles around a total population size similar to the stocking period (Figure [S5.2a](#page-30-0)), but a relatively lower number of individuals \geq = 500 mm (Figure [S5.2b](#page-30-0)). The relative outcomes of the different mitigation strategies were similar under different assumptions about habitat quality below the dam, but remnant population sizes were lower relative to stocking-period levels when habitat quality was poorer (Figure [S5.3\)](#page-31-0).

Figure S5.2: Trajectories of the entire population (a) and all individuals \geq = 500 mm (b) following termination of stocking and initiation of mitigation measures at $t = 50$. The underlying assumptions are no penalty to recruitment below the dam, and density dependence in early and juvenile mortality with a strength of 0.75 times the change in density relative to equilibrium under stocking.

measures at $t = 50$. The underlying assumptions are no penalty to recruitment below the dam Figure S5.3: Population trajectories following termination of stocking and initiation of mitigation (a), 50% (b) and 100% higher early mortality below the dam, as well as density dependence in early and juvenile mortality with a strength of 0.75 times the change in density relative to equilibrium under stocking.

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