

A future without stocking? The importance of  
harvest and river regulation for long-term  
population viability of migratory salmonids

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Running headline: Population viability without stocking

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# Abstract

1. Humans are influencing animal and plant populations both directly (e.g. through harvest) and indirectly by altering environments. For many exploited species, stocking with captive-bred individuals is a common strategy to mitigate negative human impacts and sustain populations over time. However, accumulating knowledge of negative side effects of stocking calls for quantification of consequences and exploration of sustainable alternatives.
2. Evaluating alternative management strategies using quantitative models is central to conservation. Here, we investigate the effects of several management strategies on a population of landlocked, migratory brown trout (*Salmo trutta*) inhabiting a large lake and spawning in a dammed river. We assess the population level consequences of terminating a long-term stocking programme and evaluate whether the loss of artificial recruitment may be compensated by changes in harvest regulations and/or river habitat improvement.
3. We build an integral projection model (IPM) classifying individuals by body size, life history stage, and location relative to the hydropower dam and parameterised it with 50 years of individual-based data supplemented with literature values. We first analyse the model to assess size, structure, and relative importance of different mortality components across life stages and locations in trout populations with and without stocking. We then investigate potential responses of an unstocked population to management actions involving different sets of harvest rules, reductions in dam passage mortality, and improvements of spawning habitat below the dam.

4. Our model predicts a strong population decline of 12–21% per year in the absence of stocking. This decline is largely attributed to high harvest mortality, and drastic reductions in fishing pressure thus necessary to ensure population viability without stocking. Reducing mortality associated with passage of the hydropower dam and restoring spawning areas has only small positive effects on population growth. Nonetheless, these mitigation measures can contribute to population viability when combined with changes in harvest regulations.
5. Intensely harvested populations may rely heavily on the addition of captive-bred individuals, and our results indicate that premature termination of stocking programmes can be detrimental without compensatory mitigation measures such as harvest reductions and habitat improvements. It is therefore crucial to collect necessary data and assess the impacts of alternative management strategies using quantitative models prior to making decisions.

## Keywords

dam, fishing, harvesting, hydropower, integral projection model, migratory salmonid, stocking, trout

## Sammendrag

1. Mennesker påvirker dyre- og plantepopulasjoner direkte (for eksempel via jakt og høsting) og indirekte via habitatendringer. For å begrense skadelige effekter av menneskelig påvirkning i høstede populasjoner, er det en vanlig strategi å sette ut oppdrettede individer. Det er viktig å kvantifisere konsekvensene av, og å utforske bærekraftige alternativer til oppdrett og utsetting, ettersom at det potensielt kan ha negative konsekvenser.
2. I naturvern er det sentralt å bruke kvantitative modeller for å evaluere forskjellige forvaltningsstrategier. I denne studien undersøker vi effektene av ulike forvaltningsstrategier for en populasjon av ørret (*Salmo trutta*) som holder til i en stor innsjø og gyter i en regulert elv. Vi ser på effekten av å stoppe et storstilt og langvarig utsettingsprogram av settefisk, og om tapet av den kunstige rekrutteringen kan kompenseres med andre tiltak som endringer i fiskeregler og/eller forbedring av elvehabitatet.
3. Vi utvikler en «integral projection model» (IPM) som klassifiserer individer basert på kroppsstørrelsen, livshistoriestadium, og hvor de befinner seg i forhold til demningen i elva, og tilpasser den med 50 år med individbasert data og litteraturverdier. Vi analyserer modellen både med og uten settefisk, og finner størrelsesstruktur og den relative viktigheten av forskjellige dødsårsaker i ulike livshistoriestadier og lokasjoner. Deretter ser vi på hvordan en populasjon uten tilførsel av settefisk kan bli påvirket av forvaltningstiltak som nye fiskeregler, reduksjon av dødelighet forbundet med passering av demningen, og forbedring av gyteområdene nedenfor demningen.

4. Modellen vår beregner at populasjonen vil reduseres med 12–21% årlig hvis utslipp av settefisk opphører. Den sterke nedgangen skyldes først og fremst en høy fiskedødelighet og en drastisk reduksjon i fiske er derfor nødvendig for å bevare ørrepopulasjonen uten settefisk. Redusert dødelighet forbundet med passering av demningen og forbedring av gyteområdene nedenfor demningen, har kun små positive effekter på populasjonen. Men sammen med endringer i fiskereglene, kan de to tiltakene bidra til en bærekraftig populasjon.
5. Sterkt høstede populasjoner kan være helt avhengige av en kontinuerlig tilførsel av oppdrettede individer, og våre resultater tilsier at uten kompensierende tiltak som for eksempel redusert fisketrykk og habitatforbedringer, kan en fremskyndet oppheving av et utsettingsprogram ha negative konsekvenser. Det er derfor viktig å samle inn nødvendige data og bruke kvantitative modeller for å vurdere konsekvensene av alternative forvaltningsstrategier før man tar en endelig avgjørelse.

# 1 Introduction

2 Human activities can have profound direct and indirect impacts on animal and  
3 plant populations (Hobbs & Huenneke 1992, Albuquerque *et al.* 2018). Direct  
4 impacts such as hunting, fishing, and forestry may alter the structure and viability  
5 of wild populations by imposing additional mortality on all or a selection of  
6 individuals (Reynolds *et al.* 2001). Indirect impacts are more diverse and encompass  
7 ecosystem alterations such as habitat destruction (Andren 1994) and climate  
8 change (Parmesan 2006). As human impacts have become key features of most  
9 contemporary ecosystems (Sanderson *et al.* 2002), quantifying their consequences  
10 for long-term population growth and persistence is crucial for management and  
11 conservation.

12 Stocking (or supplementation) programmes entail releasing captive-bred individuals  
13 into wild populations and are commonly used to counteract negative impacts  
14 of human disturbance, particularly in exploited populations (Laikre *et al.* 2010).  
15 Captive-bred individuals profit from elevated survival whilst in captivity, and their  
16 addition to natural populations effectively increases recruitment, leading to larger  
17 population sizes (Paquet *et al.* 2011). Populations reduced to critically low numbers  
18 have been saved from the brink of extinction by supplementation (Tallmon *et al.*  
19 2004, Hostetler *et al.* 2013), and long-term stocking programmes may be able to  
20 ensure the persistence of heavily exploited populations even if they have lost their  
21 capacity to reproduce naturally (e.g. through loss of recruitment habitat, Rogers  
22 *et al.* 2010, Ziegler *et al.* 2017, Johnston *et al.* 2018).

23 However, stocking programmes may have considerable adverse side effects, particularly

24 regarding the genetic integrity of wild populations (Laikre *et al.* 2010, Allendorf  
25 *et al.* 2013). For example, the introduction of captive-bred individuals can lead to  
26 loss of genetic variation through increased levels of inbreeding and breakdown of  
27 local adaptations in the wild population. These effects may be alleviated if the  
28 parents of stocked individuals originate from the wild population, but even then  
29 will genetic diversity decrease as a few parents will have disproportionately large  
30 contributions to the next generation (Ryman & Laikre 1991, Hansen *et al.* 2000).  
31 Furthermore, even a single generation of breeding in captivity may result in changes  
32 in gene expression that are passed on to offspring in wild populations (Christie *et al.*  
33 2016), and the introgression of hatchery genotypes may even make populations  
34 more vulnerable to environmental stressors such as climate warming (McGinnity  
35 *et al.* 2009).

36 Large-scale stocking programmes are common for economically valuable fish species  
37 such as salmonids (Laikre *et al.* 2010, Aas *et al.* 2018). Historically, many salmonid  
38 hatcheries and stocking programmes were established as political responses to  
39 demands for stable or increased harvest yields (Naish *et al.* 2007), and their potential  
40 effectiveness and risks were rarely assessed prior to implementation (Rogers *et al.*  
41 2010). Despite stocking representing but one of at least three distinct management  
42 actions for maintaining harvested fish populations, possible alternatives were often  
43 not considered either (Arlinghaus *et al.* 2016). The two main alternatives to stocking  
44 are 1) reducing fishing mortality through harvest regulations and 2) increasing  
45 natural production through improving and/or restoring the wild populations'  
46 habitat. The relative effectiveness of each management strategy depends on the  
47 wild population's reproductive capacity, the state of the habitat, and the total extent

48 of harvest (Rogers *et al.* 2010, Laikre *et al.* 2010, Arlinghaus *et al.* 2016).

49 At the core of optimising management of harvested populations lies the quantitative  
50 analysis of population dynamics and the assessment of the relative importance  
51 of underlying mechanisms (Lorenzen 2005). While the ultimate goal of stocking,  
52 habitat restoration, and harvest regulation pertains to the population level, management  
53 interventions in practice affect individuals. Exploring the potential outcomes of  
54 management thus requires understanding effects on individual's vital rates, and  
55 how these translate into population dynamics (Williams *et al.* 2002). Moreover,  
56 individual responses — and their importance for population-level patterns — often  
57 vary depending on factors such as developmental stage, age, and body size, and  
58 structured population models are necessary to account for that (Caswell 2001).

59 In the present study we develop a size-structured integral projection model (IPM,  
60 Ellner & Rees 2006) to investigate the effects of stocking, harvest, and river  
61 regulation on a population of landlocked, migratory brown trout (*Salmo trutta*).  
62 Many populations of large brown trout in Norway have declined over the last  
63 decades due to over-exploitation, hydropower production in spawning rivers, and  
64 habitat degradation (Museth *et al.* 2018). The study population has been subject  
65 to a large-scale compensatory stocking programme for over half a century, but  
66 concerns regarding negative impacts of hatchery supplementation have received  
67 more attention recently. While appropriate data for quantifying genetic effects of  
68 the stocking programme are not available, management authorities have recently  
69 suggested terminating the stocking programme to prevent further potential losses  
70 in genetic diversity. Here, we use the IPM parameterised with data collected over 50  
71 years to 1) assess population viability in the absence of stocking, 2) investigate the



72 relative importance of different mortality components across the entire life cycle, and  
73 3) explore to what degree changes in harvest regulations, reductions in dam passage  
74 mortality, and/or restoration of spawning- and recruitment areas compromised by  
75 hydropower production could compensate for the loss of captive-bred individuals.

## 76 **Materials and methods**

### 77 **STUDY SYSTEM AND DATA**

78 The study population of brown trout, commonly referred to as “Hunder trout”,  
79 inhabits Lake Mjøsa and its main inlet river, Gudbrandsdalslågen, in Eastern  
80 Norway. Despite being landlocked, Hunder trout closely resemble migratory sea  
81 trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) in terms of body size and  
82 life history (Aass *et al.* 1989, Figure 1). Adult Hunder trout spawn in the river  
83 in fall, and the eggs overwinter in loose gravel and hatch the following spring.  
84 Newly hatched trout spend 3–5 years in the river as juveniles before smolting and  
85 migrating downriver into the lake at an average length of 250 mm. After 2–3 years  
86 of piscivorous diet resulting in fast growth in the lake, they mature at an average  
87 length of 630 mm and migrate back up the river to spawn. Following the first  
88 spawning run, mature fish alternate between spawning and resting years, resulting  
89 in a biennial spawning cycle.

90 Due to a hydropower dam constructed in the river in the 1960s, the Hunder trout’s  
91 spawning and recruitment areas are clearly divided into an upriver section (above the  
92 dam), accessible for spawning trout via a fish ladder, and a downriver section (below  
93 the dam). The latter has restricted water flow and availability of suitable spawning  
94 sites, which may severely limit reproductive success and recruitment (Kraabøl  
95 2006). To compensate for expected adverse effects of the dam on production and  
96 harvest yield, a large-scale stocking programme was initiated immediately following  
97 dam construction (Aass 1993). After an initial experimental phase (1960s and 1970s,  
98 the stocking strategy was standardised in 1984. Since then, 20,000–40,000 2-year

99 old smolts with an average size of 200–240 mm have been released annually in  
100 several locations in the river (up- and downriver of the dam) and the lake. Stocked  
101 fish have constituted up to  $\sim 60\%$  of the spawning population in more recent years  
102 (Moe *et al.* 2019).

103 The Hunder trout population has been monitored extensively between 1966 and 2016.  
104 During this period, all adult trout ascending the fish ladder at the Hunderfossen  
105 dam were captured and individually marked. Marked trout were recaptured and  
106 reported both in the fish ladder during later spawning runs and by fishers following  
107 harvest. The resulting mark-recapture-recovery data spans 51 years and close to  
108 15,000 individuals. For around 8,000 of these individuals, additional individual-level  
109 data on growth histories and life history schedules (smolting and spawning events)  
110 has been obtained through sclerochronological analysis of scales collected in the fish  
111 ladder at marking. For detailed descriptions of data sets and sampling protocols  
112 see Aass *et al.* (2017) and Moe *et al.* (2019).

113 To supplement the long-term data sets, we collected a limited amount of individual-based  
114 data on fecundity during the spawning seasons of 2017 and 2018. Female trout were  
115 captured in the fish ladder, kept in pools until ready to spawn, and subsequently  
116 hand-stripped. For a total of 15 females (6 in 2017, 9 in 2018) we then measured  
117 body length and calculated the total number of eggs based on egg-weight estimates  
118 from three sub-samples of the total batch.

119 **SIZE-STRUCTURED POPULATION MODEL**

120 Based on the Hunder trout life cycle (Figure 1), we built an integral projection  
 121 model (IPM) structured by both life stage (representing life history stage and  
 122 spawning status) and body size (length, in mm). The model is female-based and  
 123 density-independent, and assumes that each year begins right after the trout  
 124 have begun their spawning migration and entered the river in late summer. The  
 125 transitions from life stages  $i$  in the current year  $t$  to life stages  $j$  in the next year  
 126  $t + 1$  are described by a projection matrix consisting of size-structured transition  
 127 kernels  $K_{ij}$ :

		<i>stage i (t)</i>					
		<b><i>Juv(u)</i></b>	<b><i>Juv(d)</i></b>	<b><i>Sub</i></b>	<b><i>Sp(u)</i></b>	<b><i>Sp(d)</i></b>	<b><i>PSp</i></b>
<i>stage j (t+1)</i>	<b><i>Juv(u)</i></b>	$K_{JJ}(x', x, u)$	0	0	$K_{SpJ}(x', x, u)$	0	0
	<b><i>Juv(d)</i></b>	0	$K_{JJ}(x', x, d)$	0	0	$K_{SpJ}(x', x, d)$	0
	<b><i>Sub</i></b>	$K_{JS}(x', x, u)$	$K_{JS}(x', x, d)$	$K_{SS}(x', x)$	0	0	0
	<b><i>Sp(u)</i></b>	0	0	$K_{SSp}(x', x, u)$	0	0	$K_{PSp}(x', x, u)$
	<b><i>Sp(d)</i></b>	0	0	$K_{SSp}(x', x, d)$	0	0	$K_{PSp}(x', x, u)$
	<b><i>PSp</i></b>	0	0	0	$K_{SpP}(x', x, u)$	$K_{SpP}(x', x, u)$	0

(1)

128 where  $x$  is the initial size prior to the growth season of the current year ( $t$ ) and  $x'$  is  
 129 the next size reached at the end of the current year's growth season (and therefore  
 130 also the initial size for the next year  $t + 1$ ). The indicator variables  $u$  and  $d$  denote  
 131 the location of juveniles and spawners as up- or downriver of the dam, respectively.  
 132 We also use  $z$  when referring to either location.

133  $K_{SpJ}(x', x, u)$  and  $K_{SpJ}(x', x, d)$  are the reproduction kernels upriver and downriver  
 134 of the dam respectively, and consist of the fecundity of a female of size  $x$  ( $F(x)$ ),  
 135 multiplied by 0.5 to represent only female offspring, the location-specific early  
 136 survival ( $S_{0,z}$ ) from egg to 1-year-old, and an offspring size distribution at age 1  
 137 independent of the mother's size ( $f(x')$ ). The production of offspring of size  $x'$  in  
 138 location  $z$  by females of size  $x$  is thus described as

$$K_{SpJ}(x', x, z) = 0.5F(x)S_{0,z}f(x') \quad (2)$$

139 All other kernels consist of survival and growth components, as well as pre- and/or  
 140 post-growth transition components (Table 1). For example, the kernel for the  
 141 transition from subadult to upriver spawner is defined as

$$K_{Sp}(x', x, u) = S_s(x)P_{mat}(x)g_L(x', x)P_L(x') \quad (3)$$

142 To become an upriver spawner within a year starting in late summer, a subadult  
 143 individual first survives ( $S_s(x)$ ) and matures ( $P_{mat}(x)$ , pre-growth stage transition)  
 144 depending on its current body size  $x$ . It then grows from size  $x$  to size  $x'$  before  
 145 the next late summer census ( $g_L(x', x)$ ), and subsequently uses the fish ladder  
 146 depending on its newly attained size  $x'$  ( $P_L(x')$ , post-growth stage transition). All  
 147 kernels and kernel components are defined in Tables 1 and 2. Survival probabilities  
 148 are expressed in terms of time-averaged mortality hazard rates (Ergon *et al.* 2018),  
 149 and estimation of vital rate functions is described in Appendix S2.

150 Using the kernel components of the projection matrix (1), the general IPM is

151 formulated by integrating over all sizes (Ellner & Rees 2006):

$$n_i(x', t + 1) = \sum_{j=1}^{\Omega} \int_L^U K_{ji}(x', x) n_j(x, t) dx \quad (4)$$

152 where  $n_j(x, t)$  is the density of individuals of size  $x$  in life stage  $j$  at time  $t$ ,  $\Omega$   
153 is the number of life stages, and  $L$  and  $U$  are the lower and upper size limits,  
154 respectively.

155 Here, we first build the IPM projection kernel for a size range from  $L = 0$  to  
156  $U = 1300$  mm and let all vital rate functions represent averaged environmental  
157 conditions (see Appendix S2, section S2.2). We then discretise the kernel by dividing  
158 the size range into 300 bins of 4.33 mm (an adequate resolution to obtain accurate  
159 results from our model). The resulting stage-by-size bin projection matrix forms  
160 the basis for all subsequent analyses.

## 161 SCENARIOS AND ANALYSES

### 162 Impact of the dam on reproduction

163 Potential reductions in recruitment below the dam (due to less available/suitable  
164 spawning areas) are important to consider when assessing population viability. In  
165 lack of empirical estimates of reproductive success above and below the dam, we  
166 adopted an explorative approach in which we introduced a “below-dam penalty” on  
167 early (= egg to 1-year-old) mortality downriver of the dam ( $m_{0,d}$ ). Specifically, we  
168 ran all of the following analyses for three scenarios: 1) no penalty ( $m_{0,d} = m_{0,u}$ ), 2)  
169 50% higher early mortality below the dam ( $m_{0,d} = 1.5 \times m_{0,u}$ , hereafter “moderate

170 penalty”), and 3) 100% higher early mortality below the dam ( $m_{0,d} = 2 \times m_{0,u}$ ,  
171 hereafter “high penalty”).

## 172 **Population dynamics under stocking**

173 To contrast population dynamics with and without stocking we extended the  
174 population model to include stocked smolt. These were added as individuals  
175 recruiting into the subadult stage with a given size distribution (see Appendix  
176 S4) via immigration at the same time as the wild-born fish enter this stage via  
177 smolting (Figure 1). Like their wild-born counterparts, stocked individuals may  
178 die while passing the dam depending on their size  $x$  (with probability  $1 - S_{dam}(x)$ )  
179 if released upriver, and survivors will then grow to size  $x'$  before the next census.  
180 The hatchery-to-subadult transition kernel for stocked fish released upriver ( $u$ ) and  
181 downriver ( $d$ ) of the dam are formulated as

$$K_{HS}(x', x, u) = S_{dam}(x)g_L(x', x) \quad (5a)$$

$$K_{HS}(x', x, d) = g_L(x', x) \quad (5b)$$

182 The next year’s size distribution of subadults is then given by

$$n_S(x', t + 1) = \sum_{j=1}^{\Omega} \int_L^U K_{jS}(x', x) n_j(x, t) dx + \int_L^U K_{HS}(x', x, u) n_H(x, u, t) dx + \int_L^U K_{HS}(x', x, d) n_H(x, d, t) dx \quad (6)$$

183 The first argument on the right-hand side of equation (6) represents all wild-born  
 184 juveniles smolting and becoming subadults, while the second and third argument  
 185 are the subadults that were released from the hatchery up- and downriver of the  
 186 dam respectively. We calculated the mean annual number of stocked smolt of size  
 187  $x$  released in location  $z$  ( $n_H(x, z, t)$ ) from annual smolt release reports (1984–2017,  
 188 see Appendix S4 for details). For projecting the population under stocking, we  
 189 further split the IPM into separate projection matrices for wild-born and stocked  
 190 individuals, each of which used origin-specific prediction functions for harvest  
 191 mortality, adult background mortality, lake growth, maturation probability, and  
 192 ladder usage probability.

193 Using this extended model, we were able to simulate the consequences of terminating  
 194 the stocking programme on population dynamics. We did this by first projecting  
 195 the population with stocking for 200 years (starting from the stable size-by-stage  
 196 distribution, Figure S1.1), and then continued the projection for another 200 years  
 197 without stocking.



## 198 **Sensitivity to mortality components**

199 We evaluated the sensitivity of population metrics ( $M$ ) to changes in the different  
200 mortality components. For  $M$ , we chose asymptotic population growth rate  $\lambda$   
201 for scenarios without stocking (the dominant right eigenvalue of the projection  
202 matrix, Caswell 2001) and equilibrium population size after 200 projection steps for  
203 scenarios with stocking. We calculated sensitivities using a perturbation approach:  
204 we added a small number  $a$  ( $= 1e^{-5}$ ) to one mortality hazard rate at a time, built  
205 the projection matrix (1) with the perturbed hazard rate, extracted the metric  
206 under perturbation ( $M_{pert}$ ), and compared it to the metric without perturbation  
207 ( $M_{orig}$ ). We then calculated sensitivity of  $M$  to the mortality hazard rate in question  
208 as  $\frac{M_{pert}-M_{orig}}{a}$ . Analogously, we calculated elasticities (= proportional sensitivities)  
209 as  $\frac{M_{pert}-M_{orig}}{aM}$  after multiplying mortality hazard rates by  $1 + a$ .

210 For stocked and unstocked populations, we separated the sensitivities to mortality  
211 hazard rates of up- and downriver juveniles and spawners to evaluate how the  
212 dam affected contributions. For stocked populations, we further distinguished the  
213 mortality components of stocked versus wild-born individuals.

## 214 **Mitigation measures in the absence of stocking**

215 Termination of stocking results in a loss of artificial recruitment and other mitigation  
216 measures may be necessary to compensate for this. As a first step towards evaluating  
217 the potential of compensatory mitigation measures, we explored the effect of  
218 four different harvest strategies: 1) no harvest ( $m^H = 0$ ), 2) minimum size limit  
219 protecting small individuals ( $m^H = 0$  for  $x < 500$  mm), 3) maximum size limit

220 protecting large individuals ( $m^H = 0$  for  $x > 700$  mm), and 4) harvest slot regulation  
221 to protect both small and large individuals ( $m^H = 0$  for  $500 < x < 700$  mm). We  
222 evaluated the viability of the trout population under these four strategies by looking  
223 at responses of  $\lambda$  and long-term projections after stocking is terminated.

224 Next, we explored the population response to decreases in total harvest mortality  
225 (all sizes) ranging from 0 to 100% reduction in combination with a second type of  
226 mitigation measure: reducing the dam mortality of smolts and/or adult spawners  
227 on their downriver migration. For the dam mortality of smolts we compared an  
228 unperturbed scenario (no change in  $m_{dam}$ ) to a scenario where all smolts survived  
229 dam passage ( $m_{dam} = 0$ ). For upriver spawners, we used a different approach since  
230 dam mortality is not an explicit parameter in our population model but contained  
231 in the estimate of adult background mortality ( $m_{a,u}^O$ ). With currently available  
232 data, it was impossible to determine what part of the estimated  $m_{a,u}^O$  is due to  
233 passing the dam. However, Nater *et al.* (2019) suggested that the high mortality of  
234 smaller above-dam spawners may be due to the dam, as they are more likely to  
235 enter the turbines on their downriver migration. With that in mind, we designed  
236 exploratory scenarios of reduced dam mortality of upriver spawners by reducing the  
237 increase of  $m_{a,u}^O$  with body size for smaller than average ( $x < 670$  mm) individuals  
238 by 0–100%. We then built projection matrices and calculated  $\lambda$  for the range of  
239 possible combinations of harvest- and adult dam mortality (= 2601 scenarios; each  
240 mortality reduction ranging from 0 to 100 % at 2% intervals). We then repeated  
241 these calculations for  $m_{dam} = 0$ .

## 242 Results

### 243 Population dynamics with and without stocking

244 With stocking in place, the population was projected to converge towards a  
245 stable equilibrium population size, which depended strongly on the severity of the  
246 below-dam penalty on early survival (Figure 2). In the absence of stocking, the  
247 population declined rapidly towards extinction irrespective of whether reproductive  
248 output below the dam was penalised or not (Figure 2). Here, the long-term growth  
249 rate  $\lambda$  took values of 0.882 when assuming no below-dam penalty, 0.824 with a  
250 moderate below-dam penalty, and 0.783 with a severe below-dam penalty. With or  
251 without stocking, juveniles made up the largest part of the population (84–97%).  
252 The higher the below-dam penalty, the larger was the proportion of juveniles up-  
253 relative to downriver of the dam, and subadults and small spawners made up a  
254 larger segment of the population when stocking was included (Figure S1.1).

### 255 Relative importance of mortality components

256 In general, harvest mortality had the largest effect on modelled population dynamics.  
257 The sensitivity of equilibrium population size (with stocking) and  $\lambda$  (without  
258 stocking) to harvest mortality was twice that of the next-ranking component,  
259 subadult background mortality ( $m_s^O$ , Figure 3). With higher below-dam penalty,  
260 changes in other mortality components (particularly  $m_{0,u}$  and  $m_{j,u}$ ) became relatively  
261 more influential and even outweighed harvest mortality when proportional changes  
262 (elasticities) were considered (Figure S1.3a). The dynamics of stocked populations  
263 were more sensitive to mortality of stocked than wild-born individuals (Figure

264 S1.2). As a consequence, harvest and subadult background mortality — the two  
265 mortality components applying to the large number of stocked fish after their  
266 release — were relatively more important (Figures 3a and S1.3a). The dynamics  
267 of wild populations, conversely, were more sensitive to contributions from natural  
268 recruitment (i.e.  $m_0$  and  $m_j$ ), particularly when considering proportional changes  
269 (Figures 3b and S1.3b).

## 270 **Response to mitigation measures**

271 Mitigation measures involving changes in harvest regulations had strong impacts  
272 on population viability in the absence of stocking (Figure 4). Completely abolishing  
273 harvest led to a  $\sim 25\%$  increase in  $\lambda$  irrespective of below-dam penalty (Table  
274 S1.1). This resulted in a growing population when there was either no (Figure 4a)  
275 or only a moderate below-dam penalty (Figure S1.4). Sparing only a part of the  
276 population based on their body size had smaller impacts, leading to  $\sim 11\%$  higher  
277  $\lambda$  when both small ( $>500$  mm) and large ( $>700$  mm) individuals were protected.  
278 Sparing large individuals was more efficient when there was no below-dam penalty,  
279 whereas sparing small individuals had a larger effect when recruitment below the  
280 dam was compromised (Table S1.1). Mitigation measures protecting all or only  
281 large individuals further resulted in higher proportions of large-sized individuals  
282 within populations (Figure 4b).

283 Scenarios involving proportional decreases in harvest mortality revealed that even  
284 in the best case (i.e. no below-dam penalty) a reduction of harvest mortality  
285 by 54–58% was necessary to ensure population viability (Figure 5). Assuming a  
286 moderate below-dam penalty, the population was viable in the absence of stocking

287 only if total harvest was reduced by at least 84–88% (Figure S1.5b). Finally, if the  
288 below-dam penalty was severe, even completely abolishing harvest was insufficient  
289 to sustain the population (Figure S1.5c). Simultaneous decreases in dam mortality  
290 of spawners had only small effects, but combined measures led to higher  $\lambda$  than  
291 harvest measures alone. Additionally reducing dam mortality of smolts to 0 had  
292 only minor effects, increasing  $\lambda$  by 0.63% (no below-dam penalty) to 2.09% (severe  
293 below-dam penalty, Figure S1.6).<sup>‡</sup>

## 294 Discussion

295 We used an integral projection model structured by body size and life stage to  
296 study the dynamics of a population of brown trout exposed to multiple human  
297 activities: long-term stocking with captive-bred individuals, intensive harvest, and  
298 river regulation. Our model projections indicated that current levels of exploitation  
299 are only possible due to the large-scale stocking programme, and that its termination  
300 may lead to a population crash. As harvest of subadult and adult individuals was  
301 the key driver of population dynamics, drastic reductions in harvest were found  
302 necessary to ensure long-term population viability without stocking.

303 With regular stocking, the trout population stabilised at an equilibrium size which  
304 depended strongly on the number of stocked fish and the capacity for natural  
305 recruitment below the dam (Figure 2). Without stocking, the population was  
306 unable to persist and was projected to disappear in less than 50 years in the  
307 best scenario, thus closely resembling the dynamics of other landlocked salmonids  
308 exposed to multiple human disturbances (Whelan & Johnson 2004, Brown *et al.*  
309 2013). Post *et al.* (2003) noted that populations of landlocked migratory salmonids  
310 can only tolerate low levels of harvest due to their slow life histories, and the present  
311 study supports this by revealing a strong sensitivity to harvest relative to other  
312 sources of mortality (Figure 3). The fundamental link between the speed of life  
313 history and vulnerability to harvest is well established for fish in general (Hutchings  
314 & Reynolds 2004), as well as for other taxonomic groups (Reynolds *et al.* 2001),  
315 and is a consequence of populations being unable to naturally replace the older,  
316 larger individuals targeted by harvest fast enough. In agreement with this, our  
317 sensitivity analysis also showed that without stocking, mortality components across

318 the entire life cycle were highly influential (Figures 3b and S1.3b). Population  
319 dynamics with stocking, on the other hand, were driven predominantly by harvest  
320 and background mortality of subadults (Figure 3a). This mirrors the fact that in  
321 the stocked population, newly released subadults represent the majority of the  
322 recruitment and make up a considerable part of the population (Figures S1.6 and  
323 S1.7).

324 The high sensitivity of population dynamics to harvest (Figure 3), and the fact  
325 that harvest mortality — unlike most other types of mortality — can be targeted  
326 by management intervention directly, make harvest regulations a key mechanism  
327 for ensuring population viability. Given the assumptions of the current model, we  
328 found that the total harvest mortality of fish of all sizes would have to be reduced  
329 by 54–100% (depending on natural recruitment capacity) to sustain a population  
330 without stocking in the long run (Figures 5, S1.8 and S1.9). At the same time, this  
331 would lead to higher proportions of ecologically valuable, large-sized individuals  
332 in the population (Figure 4b, Whelan & Johnson 2004, Ohlberger *et al.* 2014). In  
333 practice, however, reductions in total harvest mortality of such magnitude would  
334 likely have to be achieved by drastically limiting not only each individual fisher’s  
335 catch (e.g. with bag limits) but also the total fishing effort (e.g. by restricting the  
336 number of fishers, Post *et al.* 2003). Policy interventions such as these, which place  
337 strong limitations on fishers’ activity, tend to be faced with strong opposition and  
338 may thus be hard to implement and enforce (Arlinghaus *et al.* 2002). This is likely  
339 also the case for the fishery of the Hunder trout, which not only has a long history  
340 (Aass & Kraabøl 1999) but is also very popular today. Alternatives to policies aiming  
341 for drastic reductions of total harvest include size limits and catch-release fishing

342 (Gwinn *et al.* 2015, Cooke & Schramm 2007). Harvest scenarios employing minimum  
343 (500 mm) or maximum (700 mm) size limits led to similar increases in population  
344 growth rate in our model (Figure 4a) but were unable to prevent the population  
345 from declining if harvest pressure remained unchanged beyond the limit. Combining  
346 minimum and maximum size limits, while still insufficient to achieve viability in  
347 the presented projections, increased population growth rates substantially. Harvest  
348 slot limits have proved to be a valuable option to meet conservation targets while  
349 ensuring fisher satisfaction in other systems (by maintaining the presence of large,  
350 harvestable individuals in the population, Gwinn *et al.* 2015, Arlinghaus *et al.* 2010),  
351 and may thus be worth considering, especially in combination with policies reducing  
352 total harvest. However, just like catch-and-release fishing (which is becoming more  
353 popular in our study system), their efficiency depends strongly on hooking mortality  
354 and thorough study and evaluation are needed prior to implementation (Post *et al.*  
355 2003, Cooke & Schramm 2007).

356 The effects of stocking and harvest on the modelled Hunder trout population  
357 are intricately linked to hydropower production in the river and we investigated  
358 potential synergistic effects with two consequences of river regulation: compromised  
359 spawning and rearing habitat below the dam (represented by recruitment penalties)  
360 and additional mortality of smolts and upriver spawners associated with passing  
361 the dam on the downriver migration. Increasing recruitment penalties below the  
362 dam resulted in lower population sizes and growth rates and altered the relative  
363 importance of up- and downriver reproduction (Figures 3 and S1.3). Consequently,  
364 the value of mitigation strategies reducing dam mortality also depended on the  
365 recruitment penalty below the dam (Figures S1.8–S1.10). When early survival was



366 assumed independent of spawning location, population dynamics were more sensitive  
367 to mortality of eggs, juveniles, and spawners downriver of the dam. Mitigation  
368 measures improving dam survival of upriver smolts and spawners thus had very  
369 little effect. This was a direct consequence of highly fecund, large individuals  
370 being much more likely to spawn below the dam (Figure S2.4, Nater *et al.* 2019).  
371 When assuming compromised downriver recruitment due to river regulation, on the  
372 other hand, large individuals spawning below the dam lost a large portion of their  
373 reproductive output. Recruitment above the dam and the survival of smolts during  
374 the downriver migration ( $S_{dam}$ ) thus became relatively more influential (Figures 3),  
375 and population persistence in the absence of stocking was more likely when not  
376 only harvest but also dam mortality of smolts and spawners were reduced (Figures  
377 S1.8–S1.10). Ensuring self-sustainability of the Hunder trout population in the  
378 long-run may thus require mitigation of not just harvest but also other human  
379 disturbances, as has been shown previously for Atlantic salmon (Gibson *et al.*  
380 2009), Chinook salmon (*Onchrorhynchus tshawytscha*, Kareiva *et al.* 2000), and the  
381 entire salmonid assemblage in the Upper Great Lakes (Whelan & Johnson 2004).  
382 In our study system, measures for mitigating negative impacts due to hydropower  
383 production could involve 1) increasing the number of large trout spawning upriver  
384 of the dam by improving the fish ladder, 2) reducing smolt and spawner dam  
385 mortality by installing safer downstream passages (Fjeldstad *et al.* 2018), and 3)  
386 restoring, protecting, and enhancing spawning habitat in the river (Trussart *et al.*  
387 2002, Rubin *et al.* 2004).

388 Using a structured demographic model, we were able to investigate the potential  
389 effects of different management actions on population dynamics of the Hunder trout.

390 Our general insights could be refined by extending the model in several ways. In lack  
391 of individual-based data for much of the early life history, several vital rates in the  
392 model were derived from literature. While our general conclusions were robust to the  
393 choice of literature parameters (Appendix S3), efforts to collect population-specific  
394 data on egg, juvenile, and subadult mortality would greatly enhance our model's  
395 ability to make robust quantitative predictions. In this context, consideration of  
396 density-dependent effects may also be important. Compensatory density dependence  
397 in early life (recruitment, juvenile survival) is well documented in fish (Lorenzen  
398 2005, Rose *et al.* 2001). While unlikely to prevent population collapse in the  
399 absence of stocking, compensatory density dependence may prevent extinction at  
400 low population sizes and modify the outcome of mitigation measures in declining  
401 populations. The outcome of some mitigation measures may also be affected by  
402 density-dependent harvest dynamics: fishers may change their effort and behaviour  
403 in response to fish population size and this can impact the effects of changes in  
404 fishing regulations (e.g. Post *et al.* 2003). Accounting for density-dependent effects  
405 in both early life and harvest may thus improve our mechanistic understanding of  
406 this and similar systems and their responses to human activity, in particular at  
407 low population size, and we see appropriate extensions of the present model as a  
408 promising future direction. Finally, the model presented here focused exclusively  
409 on the demographic consequences of stocking vs. not stocking. The biggest concern  
410 regarding stocking programmes and the main argument for their termination,  
411 however, is the associated loss of genetic variation (Laikre *et al.* 2010). Changes in  
412 genetic variation can be modelled alongside demographic mechanisms in integrated  
413 models (e.g Coulson *et al.* 2015, Willoughby & Christie 2019). Adopting such an  
414 approach for the Hunder trout would be beneficial for quantifying past and future

415 impact of stocking on genetic variation. It could also aid in developing strategies  
416 for enhancing stocking practices to minimise negative genetic and demographic  
417 impacts (Araki & Schmid 2010) and for weighing different stocking practices against  
418 compensatory mitigation measures (Johnston *et al.* 2018, Arlinghaus *et al.* 2002,  
419 Janowitz-Koch *et al.* 2018).

## 420 **Conclusion**

421 Large-scale stocking programmes have been used to sustain and supplement  
422 populations for decades, but the practice is increasingly called into question due  
423 to its potential negative impacts on the genetic integrity of wild populations. The  
424 results of this study indicate that termination of a long-term stocking programme  
425 may lead to the rapid collapse of a population of landlocked, migratory brown trout,  
426 unless accompanied by appropriate mitigation measures. Specifically, we found that  
427 drastic reductions in harvest pressure, possibly accompanied by improvements of  
428 natural spawning habitats, and enhanced survival while passing a hydroelectric dam  
429 were required to sustain the population in the long run. Our study highlights the  
430 need to quantify the effects of terminating stocking on population dynamics prior  
431 to changing policy and illustrates the large potential of structured demographic  
432 models for this purpose.

## 433 **Authors' contributions**

434 All authors were involved in conception of ideas; CN, AR, YV and AV collected  
435 data; CN, YV, ØL, and MWS designed methodology; CN and MWS analysed  
436 demographic data; CN performed population model analyses and led manuscript  
437 writing. All authors contributed critically to drafts and gave final approval for  
438 publication.

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443 Oppland) and Frank Hansen (Hunderfossen hatchery) for providing smolt release  
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445 discussions leading up to this paper.

## 446 **Data accessibility**

447 Data will be made available on Dryad.

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## 612 **Supporting information**

613 The following supporting information is available for this publication: Appendices  
614 S1–S4.

615 **Figures**

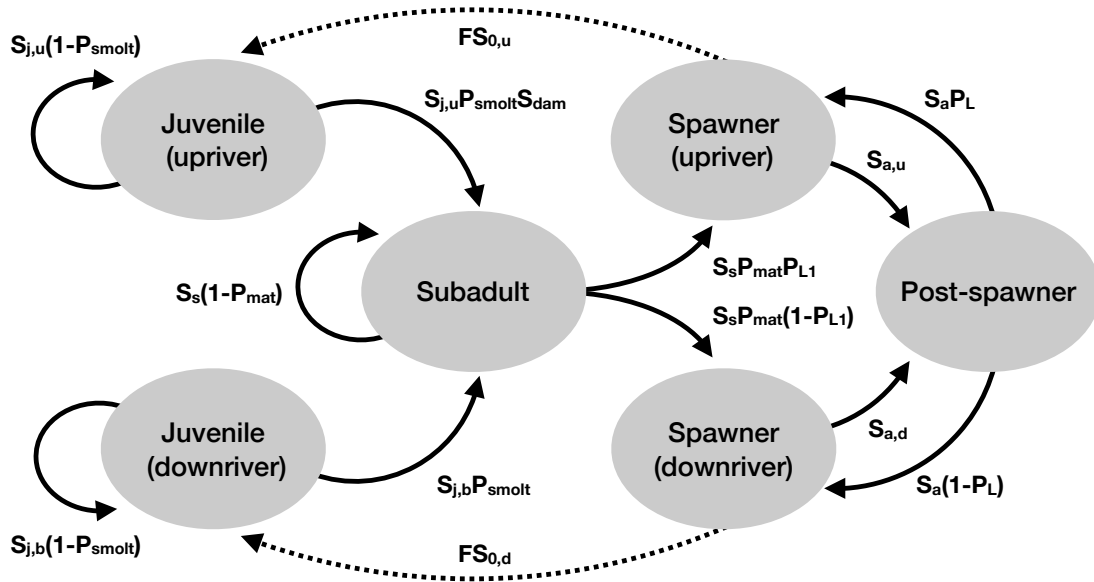


Figure 1: Life cycle of the Hunder trout as formulated in the IPM. Arrows represent the possible annual transitions from the start of the spawning migration in year  $t$  to the start of the spawning migration in year  $t + 1$ . Arrows are annotated with transition probabilities based on various vital rates (see Table 2).

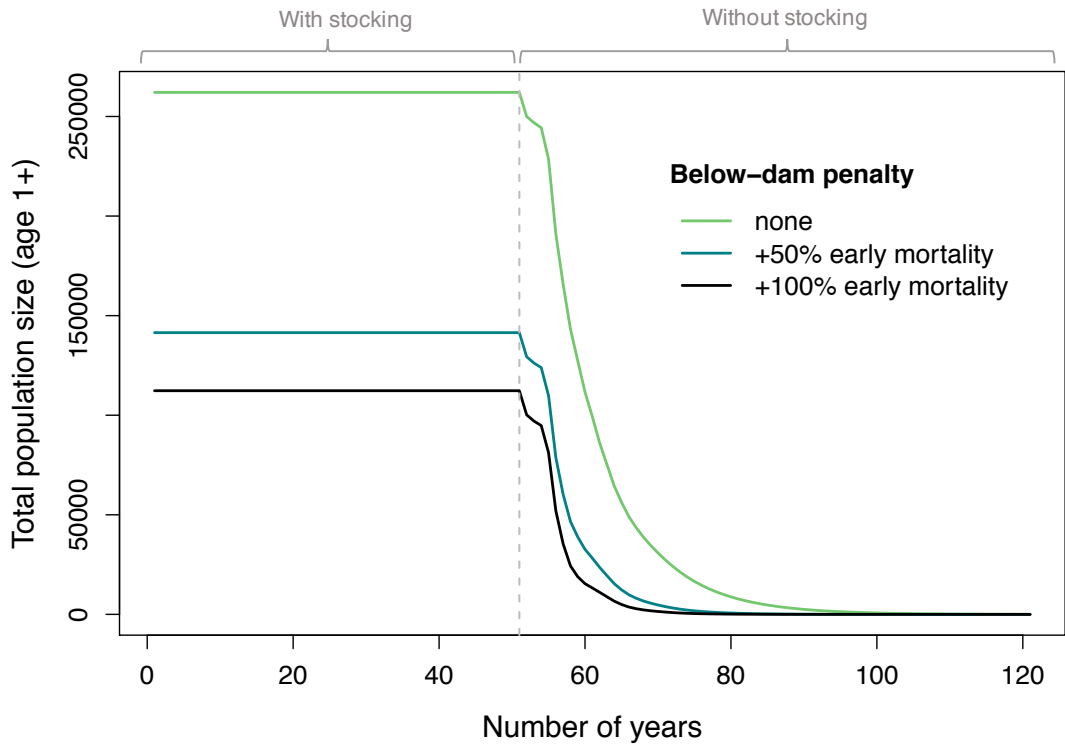
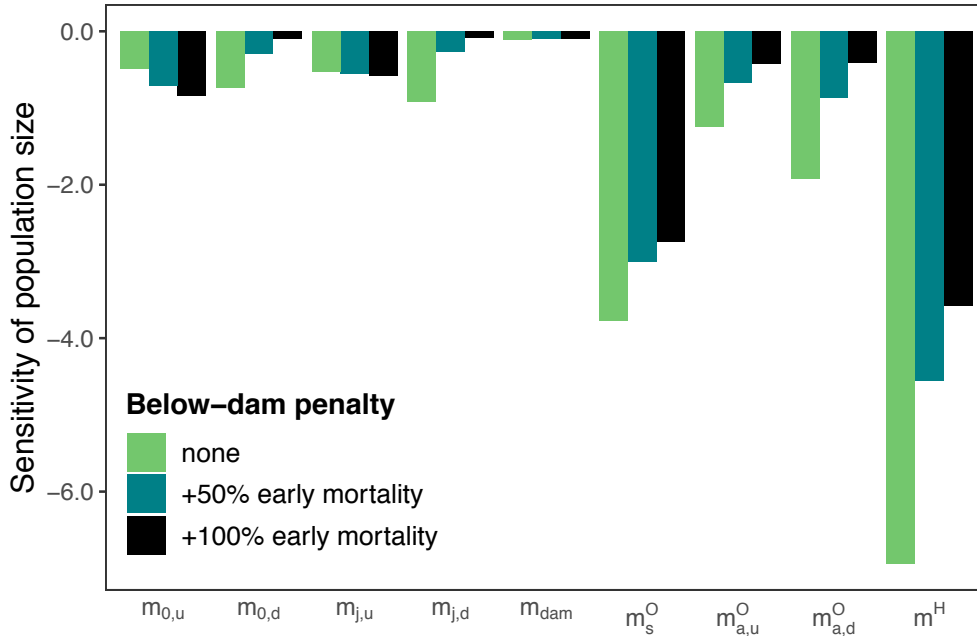


Figure 2: Projection of the Hunder trout population with (up to year 50 = dashed line) and without stocking, and assuming either no below-dam penalty (green), or below-dam penalties of 50% (blue) and 100% (black) higher early mortality.

**a) Population with stocking**



**b) Population without stocking**

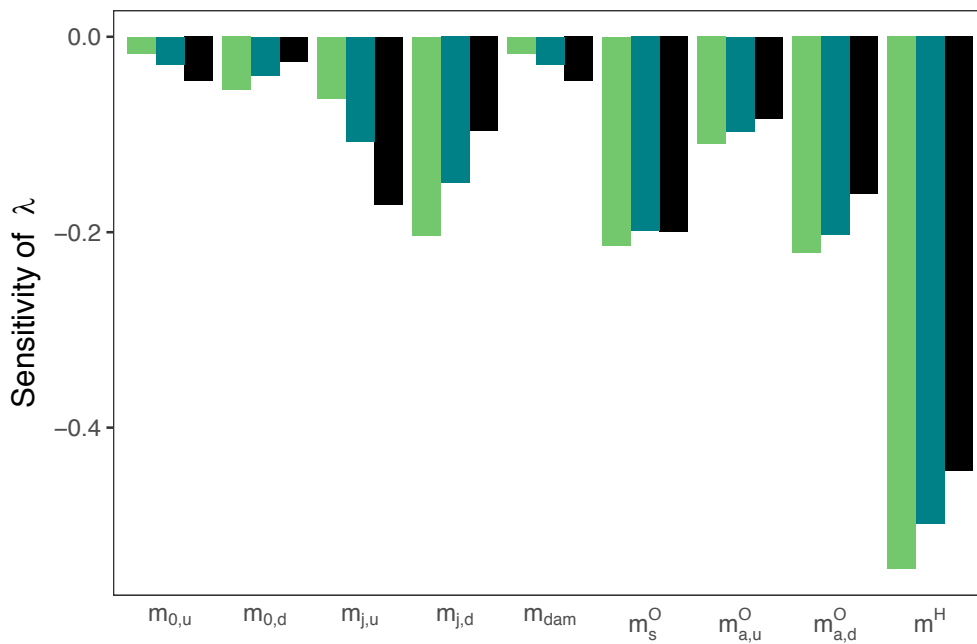


Figure 3: Sensitivity of a) equilibrium population size in a population with stocking and b) asymptotic population growth rate  $\lambda$  in a population without stocking to different mortality hazard rates (see Table 2).

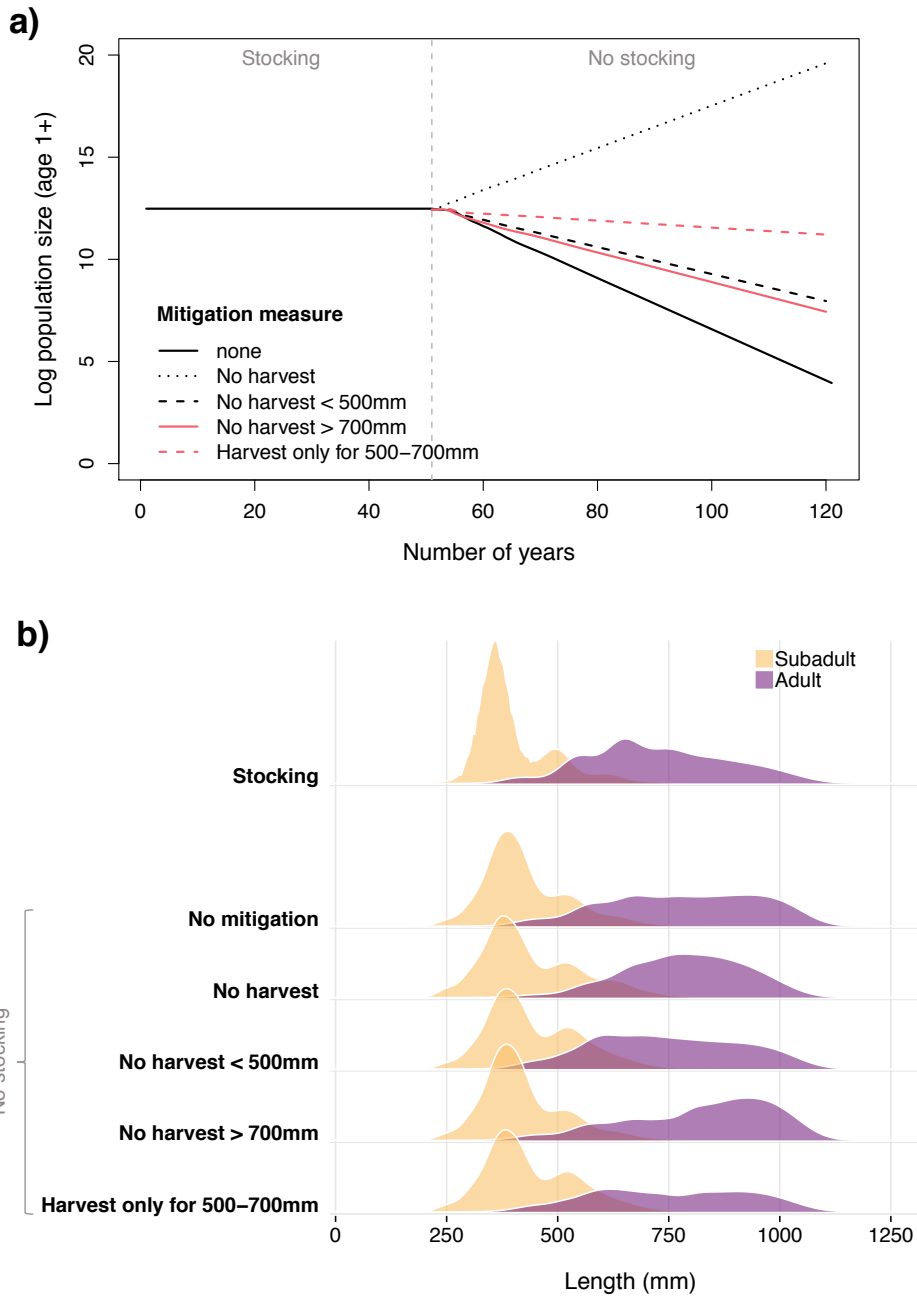


Figure 4: Projection of a) trout population size (log-scale) and b) size distributions within subadult and adult stages (spawners and post-spawners) with and without stocking and complimentary mitigation measures (no below-dam penalty). Size distributions in b) are scaled to sum to 1 within stages, representing relative, not total, density.



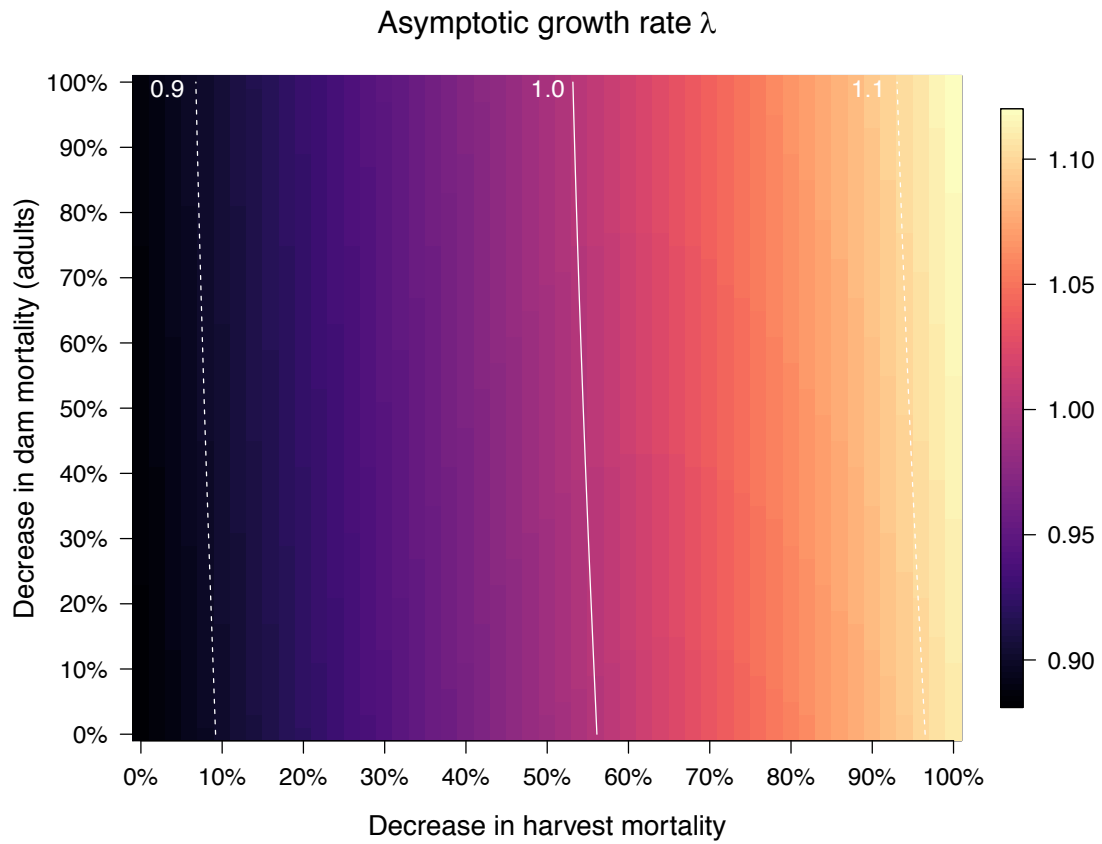


Figure 5: Asymptotic population growth rate  $\lambda$  calculated from the projection matrix (1) under different reductions of harvest mortality (rows) and dam mortality of adults (columns). The latter is approximated as decreases in background mortality of below average-sized above-dam spawners. White lines mark  $\lambda = 1$  (solid) and  $\lambda = 0.9, 1.1$  (dashed).

Table 1: Overview over the composition of all transition Kernels.

Stage transition	Transition kernel	Kernel composition
Juvenile-Juvenile	$K_{JJ}(x', x, u)$	$= S_{j,u}(x)[1 - P_{smolt}(x)]g_R(x', x)$
	$K_{JJ}(x', x, d)$	$= S_{j,d}(x)[1 - P_{smolt}(x)]g_R(x', x)$
Juvenile-Subadult	$K_{JS}(x', x, u)$	$= S_{j,u}(x)P_{smolt}(x)S_{dam}(x)g_L(x', x)$
	$K_{JS}(x', x, d)$	$= S_{j,d}(x)P_{smolt}(x)g_L(x', x)$
Subadult-Subadult	$K_{SS}(x', x)$	$= S_s(x)[1 - P_{mat}(x)](x)g_L(x', x)$
Subadult-Spawner	$K_{SS_p}(x', x, u)$	$= S_s(x)P_{mat}(x)(x)g_L(x', x)P_L(x')$
	$K_{SS_p}(x', x, d)$	$= S_s(x)P_{mat}(x)(x)g_L(x', x)[1 - P_L(x')]$
Spawner-Juvenile	$K_{S_pJ}(x', x, u)$	$= 0.5F(x)S_{0,u}f(x')$
	$K_{S_pJ}(x', x, d)$	$= 0.5F(x)S_{0,d}f(x')$
Spawner-Post-spawner*	$K_{S_pP}(x', x, u)$	$= S_{a,u}(x)g_L(x', x)$
	$K_{S_pP}(x', x, d)$	$= S_{a,d}(x)g_L(x', x)$
Post-spawner-Spawner**	$K_{PS_p}(x', x, u)$	$= S_{a,u}(x)g_L(x', x)P_L(x')$
	$K_{PS_p}(x', x, d)$	$= S_{a,d}(x)g_L(x', x)[1 - P_L(x')]$

\*  $S_{a,u}$  and  $S_{a,d}$  represent survival over 2 years.

\*\*  $S_{a,u}$  and  $S_{a,d} = 1$ .

Table 2: Summary of vital rates used in the population model. All functions for survival probabilities are formulated using time-averaged mortality hazard rates.

Model components	Vital rate*	Description*
Survival	$S_{j,z}(x)$	Survival probability of juveniles of size $x$ in location $z$ ; = $\exp[-m_{j,z}(x)]$
	$S_{dam}(x)$	Dam survival probability of smolts of size $x$ ; = $\exp[-m_{dam}(x)]$
	$S_s(x)$	Survival probability of subadults of size $x$ ; = $\exp[-(m^H(x) + m_s^O(x))]$
	$S_{a,z}(x)$	Survival probability of adults of size $x$ spawning in location $z$ ; = $\exp[-(m^H(x) + m_{a,z}^O(x))]$
	$m_{j,z}(x)$	Mortality hazard rate of juveniles of size $x$ in location $z$
	$m_{dam}(x)$	Dam mortality hazard rate of smolts of size $x$
	$m^H(x)$	Harvest mortality hazard rate of subadults and adults of size $x$
	$m_s^O(x)$	Background mortality hazard rate of subadults of size $x$
	$m_{a,z}^O(x)$	Background mortality hazard rate of adults of size $x$ spawning in location $z$
	Growth	$g_R(x', x)$
$g_L(x', x)$		Probability of subadults and adults of size $x$ to grow to size $x'$ in the lake
Pre-growth stage transition	$P_{smolt}(x)$	Smolting probability of juveniles of size $x$
	$P_{mat}(x)$	Maturation probability of subadults of size $x$
Post-growth stage transition	$P_L(x')$	Ladder usage probability of subadults and adults after having grown to size $x'$
Reproduction	$F(x)$	Fecundity of adults of size $x$
	$S_{0,z}$	Early (egg to juvenile) survival probability in location $z$ ; = $\exp[-m_0]$
	$m_{0,z}$	Early (egg to juvenile) mortality hazard rate in location $z$
	$f(x')$	Size distribution of recruits in fall

\*  $z$  denotes the location relative to the dam;  $z = u$  or  $z = d$  for up- and downriver, respectively.