

25 **ABSTRACT**

26 Climate change is expected to alter future temperature and discharge regimes of rivers. These
27 regimes have a strong influence on the life history of most aquatic river species, and are key
28 variables controlling the growth and survival of Atlantic salmon. This study explores how the
29 future abundance of Atlantic salmon may be influenced by climate-induced changes in water
30 temperature and discharge in a regulated river, and investigates how negative impacts in the
31 future can be mitigated by applying different regulated discharge regimes during critical
32 periods for salmon survival. A spatially explicit individual-based model was used to predict
33 juvenile Atlantic salmon population abundance in a regulated river under a range of future
34 water temperature and discharge scenarios (derived from climate data predicted by the Hadley
35 Centre's Global Climate Model (GCM) HadAm3H and the Max Plank Institute's GCM
36 ECHAM4), which were then compared with populations predicted under control scenarios
37 representing past conditions. Parr abundance decreased in all future scenarios compared to the
38 control scenarios due to reduced wetted areas (with the effect depending on climate scenario,
39 GCM, and GCM spatial domain). To examine the potential for mitigation of climate change-
40 induced reductions in wetted area, simulations were run with specific minimum discharge
41 regimes. An increase in abundance of both parr and smolt occurred with an increase in the
42 limit of minimum permitted discharge for three of the four GCM/GCM spatial domains
43 examined. This study shows that, in regulated rivers with upstream storage capacity, negative
44 effects of climate change on Atlantic salmon populations can potentially be mitigated by
45 release of water from reservoirs during critical periods for juvenile salmon.

46 **1. INTRODUCTION**

47 Climate change is expected to modify thermal and hydrological regimes of rivers, with
48 uncertain consequences for aquatic species (Knouft & Ficklin, 2017). In the Northern

49 Hemisphere, climate models have predicted an increase in air temperature and winter
50 precipitation, but a decrease in summer precipitation (IPCC, 2007; Schneider *et al.*, 2013).
51 For Southern Norway, run-off is expected to increase in winter, but decrease in summer
52 (Schneider *et al.*, 2013). Episodes of low summer discharges are expected due to longer
53 periods with low precipitation and lower levels of ground water in summer (Hanssen-Bauer *et*
54 *al.*, 2015). The projected changes in temperature and discharge (IPCC 2007), i.e. increased
55 temperatures and changed discharge patterns, may have detrimental effects on aquatic
56 organisms inhabiting rivers because both temperature (Angilletta *et al.*, 2002) and discharge
57 regimes influence important life history traits of many aquatic species, such as growth and
58 mortality (Heino *et al.*, 2009).

59 The Atlantic salmon life cycle is divided into two phases: the juvenile phase, which takes
60 place in freshwater; and the adult phase, which largely takes place in the ocean. For juvenile
61 salmon in the river, the temperature and discharge pattern are key parameters for survival and
62 growth. The water temperature will affect the speed of physiological and biochemical
63 reactions of this poikilothermic (cold-blooded) organism (Angilletta *et al.*, 2002). Salmon
64 growth is strongly influenced by temperature (Forseth *et al.*, 2001) and size determined by
65 growth is an important factor for juvenile survival (Einum & Fleming, 2007). The stage when
66 juveniles migrate from the river to the ocean as smolts is also largely determined by size
67 (Metcalf, 1998) and therefore strongly influenced by water temperature. The discharge
68 determines the wetted area of the river, depending on the river profile, with the wetted width
69 of a “U”-shaped cross section changing less with changing discharge than a “V”-shaped cross
70 section. The wetted area of the river controls the river’s carrying capacity, but carrying
71 capacity is also dependent on habitat quality for juvenile salmon, i.e. shelter availability is of
72 great importance (Finstad *et al.* 2009). The wetted area strongly influences density-dependent

73 mortality in early life-stages, a common bottleneck for salmon abundance in rivers (Einum *et*
74 *al.*, 2006). Thus, water temperature and discharge drive fundamental biological mechanisms,
75 both at the individual- and population level.

76 Atlantic salmon has been in a long-term decline in most of its distribution area, both in terms
77 of the number of populations and in terms of abundance in freshwater as well as the marine
78 environment (Hindar *et al.*, 2011; Windsor *et al.*, 2012; ICES 2013). In Norway,
79 approximately 30% of rivers with salmon stocks are affected by hydropower development,
80 with effects on salmon stocks ranging from extirpation to modest reductions in abundance or
81 even positive effects (Hvidsten *et al.*, 2015). Environmental flow practices in regulated rivers
82 are commonly dominated by a defined constant minimum discharge value for winter and a
83 higher constant value for summer (Alfredsen *et al.*, 2012). These values are often exceeded,
84 but cannot be lower. In a majority of regulated river systems, water masses are commonly
85 stored in reservoirs during periods of high run-off and released in periods when electricity is
86 required, usually in winter. Thus discharge regimes may be adjusted, which often leads to
87 increased winter discharges and reduced spring floods in Norwegian rivers, compared to
88 unregulated rivers. In a few documented cases, hydropower developments have increased
89 smolt abundance in parts of the river (Ugedal *et al.* 2008) or total smolt abundance, in both
90 cases due to increased water discharge during winter (Hvidsten *et al.*, 2015). Active
91 management of river discharge patterns in regulated watercourses may therefore represent a
92 rare case of effective mitigation of negative climate change effects on fish populations (Piou
93 & Prevost, 2013).

94 The current study explores how the future abundance of Atlantic salmon may be influenced
95 by climate-induced changes in water temperature and discharge in a regulated river, and how
96 negative impacts of climate change may be mitigated by implementing different minimum

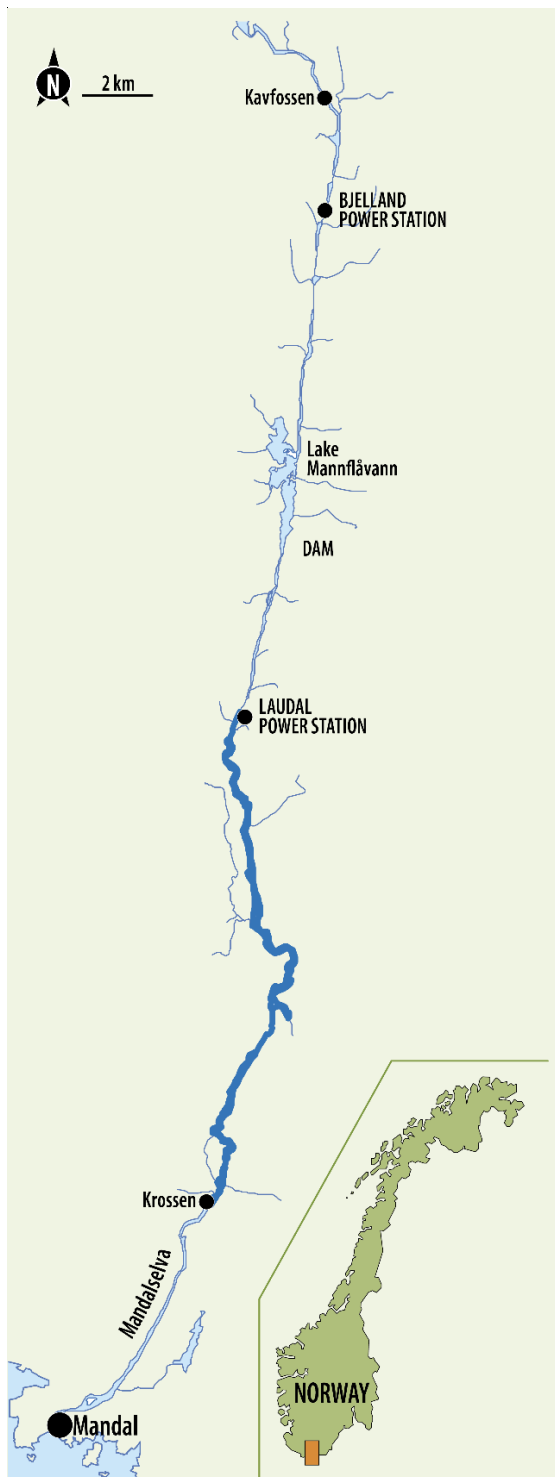
97 discharge regimes during critical periods. A spatially-explicit individual-based model is used
98 to predict population abundance under future climate regimes for comparison to abundance
99 under control (past) regimes, with a focus on how the discharge regime affects wetted area
100 and consequently carrying capacity. The effect of climate change on salmonid freshwater
101 abundance has been examined in previous studies (Battin *et al.*, 2007, Hedger *et al.*, 2013b,
102 Leppi *et al.*, 2014), but this is to the authors' knowledge the first study to include minimum
103 discharge regime scenarios, implemented as mitigation strategies for climate change, into the
104 model pathway.

105 **2. MATERIAL AND METHODS**

106 **2.1 Study area**

107 The study river, the River Mandalselva (58.2°N, 7.5°E), is one of the largest rivers in southern
108 Norway. The river is 115 km long and is regulated with seven hydropower stations and
109 several reservoirs (Ugedal *et al.*, 2006). Atlantic salmon and brown trout (*Salmo trutta* L.) can
110 migrate from the sea 47 km upstream to the natural waterfall of Kavfossen (Fig. 1). The mean
111 discharge at the outlet of the most downstream hydropower station (Laudal) is 88 m³ s⁻¹;
112 average lowest daily discharges range between 18.6 m³ s⁻¹ during summer (Jul-Sep) and 33.1
113 m³ s⁻¹ during winter (Jan-Mar) (Ugedal *et al.*, 2006). The Mandal system has a total storage
114 capacity of 358 million m³ (NVE Atlas, <https://atlas.nve.no>), providing the opportunity to
115 store water from extra winter precipitation and to release this water in drier periods of the
116 year.

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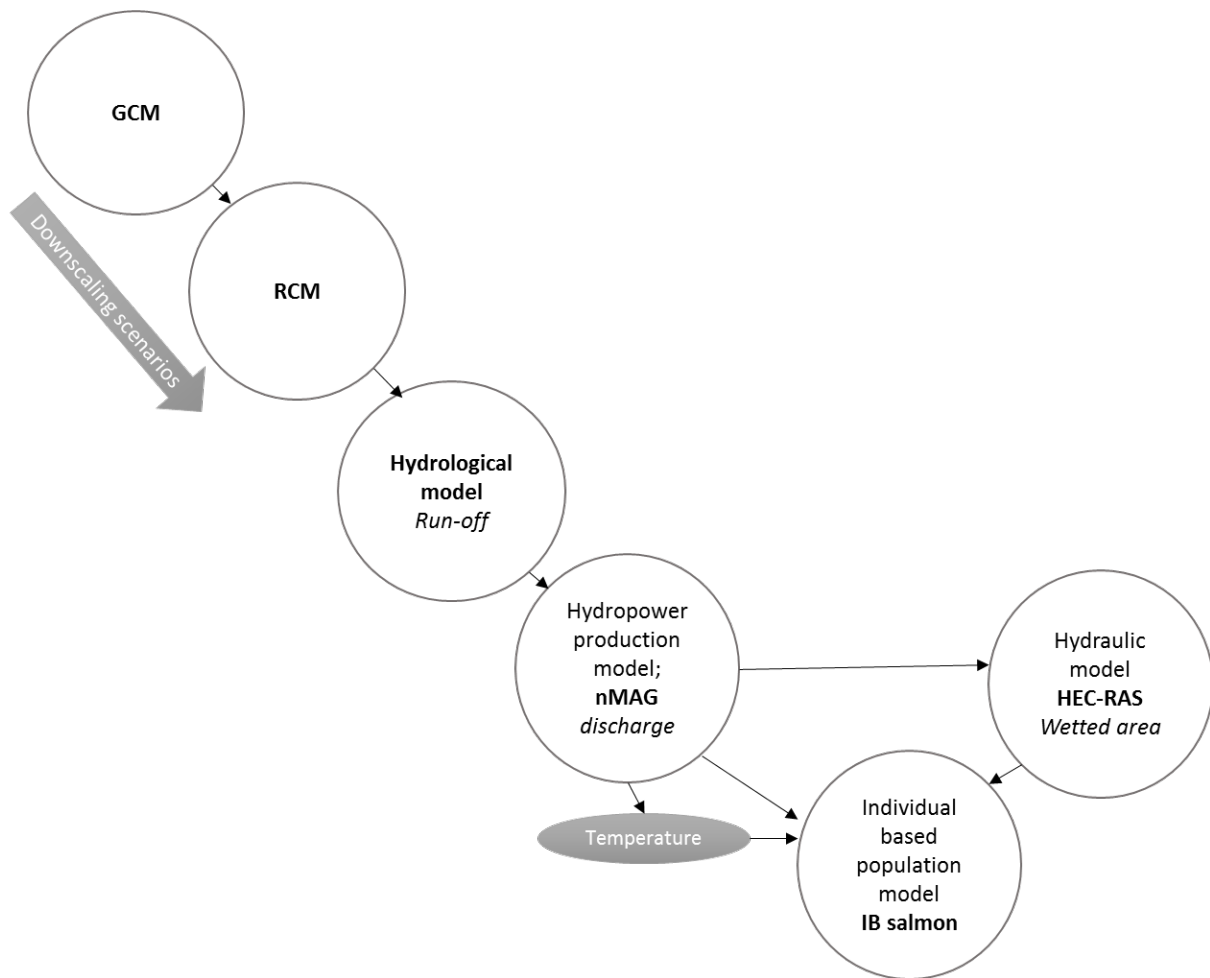
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119 **Fig. 1. River Mandalselva with the modelled stretch of the river marked with a thick**
 120 **blue line, from the outlet of Laudal Power station and downstream to Krossen (start of**
 121 **the tidal zone).**

122 In the beginning of the 20th century, the salmon fisheries in the river were highly productive,
123 but acidification during the 1960s extirpated the original salmon population. However, liming
124 was initiated in 1997 and a new salmon stock, resulting from strayers from other rivers and
125 the release of eggs and fry from a stock in a nearby river, rapidly increased in size. The catch
126 peaked at 10 tonnes in 2001. The present salmon stock in the river is a genetic blend, with
127 likely weak or no links to the original stock (Hesthagen *et al.*, 2010).

128 **2.2 Modelling procedure**

129 Water temperature and discharge (and consequently wetted area) in the regulated stretch
130 downstream of the Laudal hydropower station – stretching downstream 20 km from the outlet
131 of the station (upstream distance = 20.5 km) to the start of the tidal zone (upstream distance =
132 700 m – were generated for selected climate scenarios using a modelling hierarchy (Fig. 2).
133 Coarse-scale predictions of air temperature and precipitation from Global Climate Models
134 (GCMs) were downscaled using a Regional Climate Model (RCM) to provide finer-scale
135 predictions (spatial resolution = 1 km²) of air temperature and precipitation across the
136 catchment encompassing the Mandalselva. These data were used to determine the
137 hydrological regime of the catchment using a hydrological model. Given that the Mandalselva
138 is regulated and the hydraulic properties of the river are influenced by hydropower operation
139 as well as the hydrological regime, outputs from the hydrological model were used in a
140 hydropower production model, to provide water temperature and discharge. A hydraulic
141 model was then used to derive weekly wetted area, a critical component of the individual-
142 based population model, from the discharge data.



143

144 **Fig. 2. The model pathway from downscaling of the Global Climate Model (GCM), via a**
 145 **Regional Climate Model (RCM), to hydrological-, hydropower- and hydraulic- models,**
 146 **and finally down to the individual-based population model, IB-salmon.**

147

148 **2.3 Global Climate Model (GCM) and Regional Climate Model (RCM)**

149 Climate data used in this study were provided by the Norwegian Meteorological Institute
 150 DNMI (Engen-Skaugen *et al.*, 2008). These data were derived from predictions from the
 151 Hadley Centre's HadAm3H GCM and the Max Plank Institute's ECHAM4 GCM. Scenarios
 152 used were both for (1) future climates, the SRS A2 (high CO₂) and B2 (low to medium CO₂)
 153 emission scenarios (2071-2100), and (2) a control climate, SRS CN (1960-1990) (Table 1).

154 These scenarios are used by the DNMI to evaluate the future climate in Norway. The SRS A2
155 and B2 emission scenarios are described in the IPCC Fourth Assessment Report (IPCC 2007)
156 and represent the climate forcing through CO₂ emissions for specific scenarios of future
157 development of the world (IPCC SRES 2000), and are respectively similar to the RCP 8.5 and
158 RCP 6.0 scenarios used in the IPCC Fifth Assessment Report (IPCC 2014) (see van Vuuren &
159 Carter, 2014). GCM data were at a 55 × 55 km regional domain (spatial resolution) for the
160 HadAm3H model, and at both this domain and a finer domain (25 × 25 km) for the ECHAM4
161 model. GCM predictions of temperature and precipitation were then downscaled to a finer
162 resolution (grid of 1 km² cells) by the DNMI using the Regional Climate Model (RGM)
163 HIRHAM (Christensen et al. 2007; May 2007) which was bias adjusted based on observations
164 of local climate (Engen-Skaugen, 2007). The use of data from different GCMs with different
165 spatial domains allowed the investigation of how prone predictions of salmon population
166 abundance were to the climate model outputs on which the analyses were based.

167

168 **Table 1. Overview of Global Climate Models (GCM), emission scenarios, spatial**
 169 **resolutions of GCM output data, and scenarios simulations used with the individual-**
 170 **based model (IBM).**

GCM	Emission scenario	Domain	Spatial resolution (km)	IBM scenario name
HadAm3H	A2 + control	RegClim	55 × 55	Had.Reg.A2
				Had.Reg.CN
HadAm3H	B2 + control	RegClim	55 × 55	Had.Reg.B2
				Had.Reg.CN
ECHAM4	B2 + control	RegClim	55 × 55	ECHAM.Reg.B2
				ECHAM.Reg.CN
ECHAM4	B2 + control	NorAcia/NorClim	25 × 25	ECHAM.Nor.B2
				ECHAM.Nor.CN

171

172 **2.4 Hydrological model**

173 Downscaled temperature and precipitation predictions from the RCM were used as input to a
 174 hydrological model to predict water inflows along the complete watercourse of the
 175 Mandalselva. Hydrological modelling was performed in the open source model platform
 176 ENKI (Kolberg & Bruland, 2012). This gridded model simulates inflow based on
 177 meteorological inputs (temperature and precipitation) and catchment characteristics
 178 (elevation, soil water storage, distribution of sub-catchments and river network). The model

179 interpolates temperature and precipitation across the catchment using Inverse-Distance
180 Weighting and Kriging, respectively. Soil-moisture and surface runoff (from excess soil
181 moisture) are then calculated using the response function developed for the Hydrologiska
182 Byråns Vattenbalanavdelning (HBV) model. To achieve a better model of soil moisture and
183 surface runoff, the model includes an evaporation routine based on the routine in LandPine
184 model (Rinde, 2000) and a snow accumulation/snowmelt routine (see Kolberg *et al.*, 2006).
185 The former reduces soil moisture and runoff (particularly in the summer); the latter introduces
186 a lag in soil moisture and runoff by storing precipitation as snow during winter, and releasing
187 this in spring. The model is calibrated for individual sub-catchments within the entire
188 catchment by setting the model to run for one individual sub-catchment at a time and
189 validating with the remaining catchments (iterating with the Shuffled Complex Evolution
190 Method, with Nash Sutcliffe's efficiency criteria (Nash & Sutcliffe, 1970)).

191

192 **2.5 Hydropower production model**

193 The hydropower production discharge in the river was simulated using the nMAG model
194 (Killingtveit & Sælthun, 1995; Killingtveit, 2004) based on inputs from the hydrological
195 model. The nMAG model simulates hydropower operations for whole systems consisting of
196 hydropower stations, reservoirs and transfers, and predicts river discharge among other
197 variables. A model of the hydropower system with all reservoirs and power stations in the
198 Mandalselva was used (Fjeldstad *et al.*, 2014) and the operational strategy of the power
199 system was kept unchanged among the climate scenarios. Water temperature downstream of
200 the Laudal hydropower system was found from regression equations based on observed water
201 temperature, air temperature, production discharge and simulated inflow. Water temperature

202 in the modelled watercourse, T_w , was calculated by weighting the temperature contributions
 203 from natural inflow and the reservoir immediately upstream (Equation 1):

$$T_w = \frac{Q_{in}}{Q_{tot}}T_{in} + \frac{Q_{res}}{Q_{tot}}T_{res} \quad (1)$$

204 where T_{in} and T_{res} are water temperatures from natural inflow and the reservoir respectively,
 205 Q_{in} and Q_{res} are the respective discharges, and Q_{tot} is the total discharge. Water temperatures
 206 in the natural inflow and in the reservoir were estimated from regression relationships
 207 established with air temperature, T_a (Equation 2 and 3).

$$\begin{cases} T_{in} = 0.5 & T_a < -3 \\ T_{in} = 0.0658T_a^2 + 0.5287T_a + 1.5707 & -3 \geq T_a \leq 1 \\ T_{in} = 0.9567T_a - 0.8926 & T_a > 1 \end{cases} \quad (2)$$

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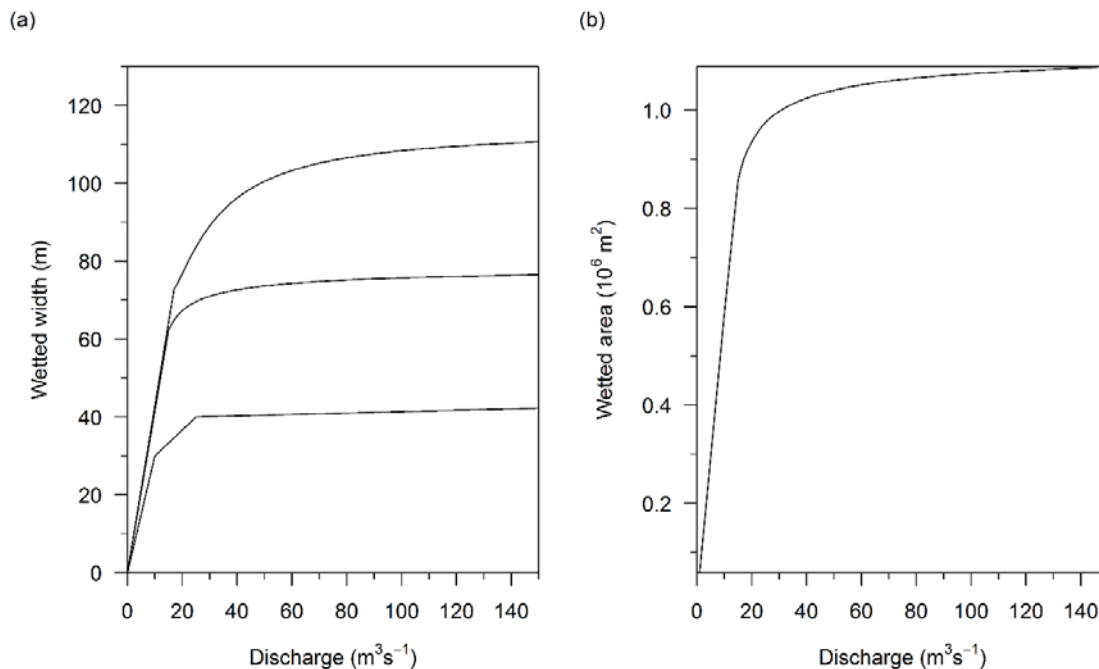
$$\begin{cases} T_{res} = 0.13 & T_a < -6 \\ T_{res} = 0.0567T_a^2 + 0.5117T_a + 1.5617 & -6 \geq T_a \leq 1 \\ T_{res} = 1.0324T_a + 1.1685 & T_a > 1 \end{cases} \quad (3)$$

209

210 **2.6 Hydraulic model**

211 In order to estimate the relationship between discharge and wetted area in the modelled
 212 stretch, the HEC-RAS[®] (2008) hydraulic model was applied. This model can simulate
 213 discharges within rivers, for both steady-flow surface profiles, and 1-D and 2-D unsteady flow
 214 conditions. The HEC-RAS model was used to determine discharge – wetted width
 215 relationships for each of three stations with different channel profile characteristics
 216 representative of the modelled stretch of the river: channel profiles were more “U”-shaped,
 217 more “V” shaped, and intermediate between these two. The model was calibrated with field

218 observations of water level measurements in each station at a single discharge by varying the
 219 Manning's roughness coefficient (0.020 – 0.095) until the model prediction matched field
 220 observations. 1-D steady-state simulations were then performed at various discharges to
 221 establish discharge – wetted width curves (Fig 3a). Curves were extrapolated for discharges
 222 outside of the validated discharge range of the HEC-RAS simulations. The discharge – wetted
 223 width curves of the three stations were then transferred to the 50 m long river sections with
 224 corresponding channel profiles (determined by aerial photography) and scaled by the ratio
 225 between the maximum wetted width of the 50 m section in question (again, determined by
 226 aerial photography) and the maximum wetted width of the respective station. This enabled the
 227 estimation of the discharge – wetted width relationship for each section throughout the entire
 228 modelled stretch of the river. The wetted area of each section was calculated by multiplying
 229 the section wetted width by the section wetted length (50 m), giving a highly non-linear
 230 relationship between discharge and total wetted area in the modelled watercourse (Fig 3b).



231
 232 **Fig. 3. Relationship between discharge and (a) wetted width in the HEC-RAS stations,**
 233 **and (b) total wetted area in the modelled watercourse.**

234

235 **2.7 Atlantic salmon population model**

236 An individual-based modelling (IBM) approach was used to predict the impact of climate
237 change and mitigation measures on population abundances (expressed in this study as total
238 number of individuals within the modelled stretch) and changes in life history characteristics
239 of Atlantic salmon within the modelled watercourse. This approach was used because several
240 aspects of the processes affecting the salmon population would have been difficult to
241 parameterize using population differential equations (see DeAngelis and Grimm, 2014). For
242 example, changes in mortality resulted from changes in wetted area, which operate at a
243 spatially local level. Local changes in wetted area depend on local carrying capacity, local
244 river profile, local habitat quality and local parr biomass, and also the spatial configuration of
245 different carrying capacities, channel widths and biomass. Running an IBM allowed
246 population characteristics to dynamically emerge from heuristic functions that were well
247 parameterized at the spatially local and individual level.

248 **Model functions**

249 The IBM used (IB-salmon) (Hedger *et al.*, 2013a, Hedger *et al.*, 2013b; Sauterleute *et al.*,
250 2016) is a spatially-explicit model designed for predicting population characteristics of the
251 freshwater stage of juvenile Atlantic salmon, but also models sea survival and the return of
252 surviving adults from the sea. The model has a time-step interval of one week, with the river
253 divided into a series of 50 m sections. Individual life-history traits (growth, smoltification
254 timing, fecundity, mortality) and other characteristics (location, migration) are modelled using
255 empirical functions (Hedger *et al.*, 2013a, Hedger *et al.*, 2013b). Life-stages modelled as
256 individual elements are parr (juveniles in the river), smolts (parr that have smoltified, which
257 then migrate to sea), sea resident adults, and returning adults (adults that have returned to the

14

258 river to spawn). The main input parameters of the model are wetted area (dependent on
 259 channel profile and discharge), water temperature, spawning location and area, and parr
 260 carrying capacity. At the beginning of a simulation, annual egg deposition is read from a file,
 261 and binned into sections according to relative spawning habitat quality. Later when a full age-
 262 distribution of spawning adults has returned, eggs are deposited in sections as a function of
 263 spawning female abundance and body mass in which the spawning female was born. The
 264 weekly parr growth is determined using a Ratkowsky-type model (Ratkowsky *et al.*, 1983)
 265 parameterized with experimental data on growth/temperature relationships for Norwegian
 266 Atlantic salmon juveniles (Jonsson *et al.*, 2001) (Equation 4).

267

$$\left\{ \begin{array}{ll} M_t = M_{t-1} & T < T_L \text{ or } T > T_U \\ M_t = \left(M_{t-1}^b + b \left(\frac{d(T - T_L)(1 - e^{g(T - T_U)})}{100} \right) \right)^{(1/b)} & T \geq T_U \text{ \& } T \leq T_U \end{array} \right. \quad (4)$$

268 where M is the individual body mass for time t , T is the weekly mean temperature, T_L and T_U
 269 are lower and upper temperatures for growth, and b , d and g are parameters of the model.

270 Body length, L , is predicted from body mass every week, using a power function relationship
 271 (Equation 5).

$$L = \left(10^5 M / 0.84 \right)^{1/3} \quad (5)$$

272 The annual smoltification probability (applied in week of year 20), SP , is estimated for each
 273 individual as a logistic function of body length, L (Equation 6).

$$\begin{cases} SP = \frac{e^{(p1+(p2 \times L))}}{1 + e^{(p1+(p2 \times L))}} & \text{if } L \leq 250 \\ SP = 1 & \text{if } L > 250 \end{cases} \quad (6)$$

274 where $p1$ and $p2$ are parameters of the model.

275 Parr density dependent mortality in any given section is dependent on the total biomass of
 276 parr within that section (the sum of individual body masses of all parr in the section) and the
 277 total carrying capacity of the section (the total biomass that can be supported, which is the
 278 product of the carrying capacity per unit area and the total wetted area of the section). If the
 279 biomass within a section exceeds the total carrying capacity, surplus parr are forced to migrate
 280 out of the section: they may either migrate to a new section or experience mortality (density
 281 dependent mortality) (Equation 7).

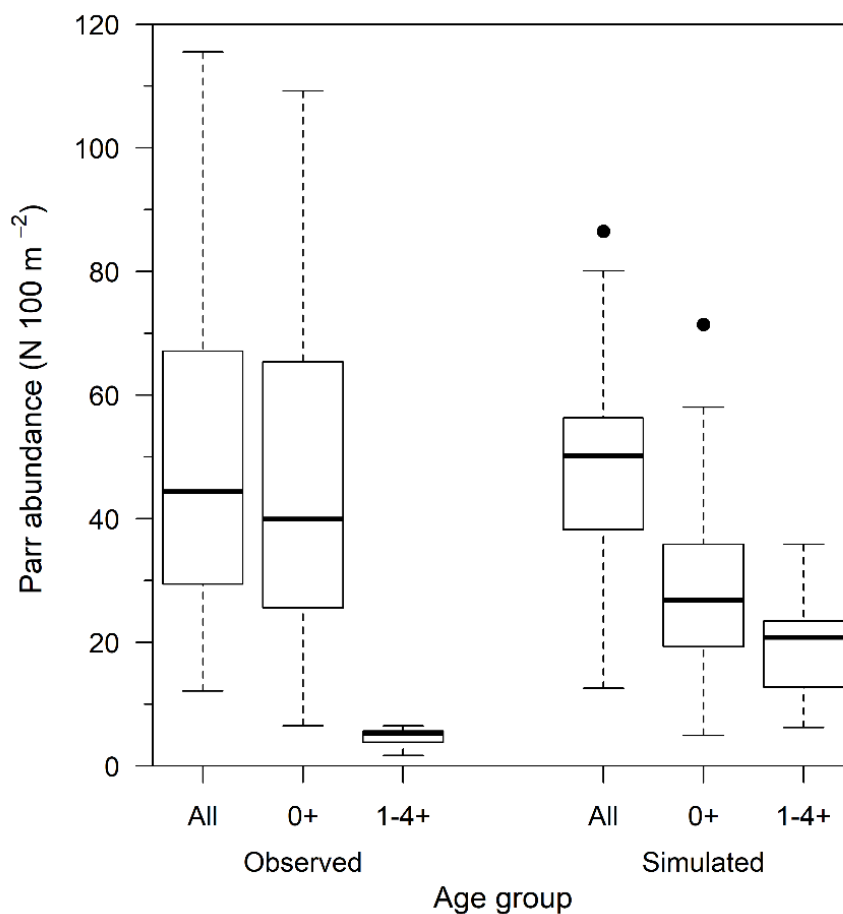
$$\begin{cases} B_{s,t} = B_{s,t-1} & B_{s,t-1} < K \\ \begin{cases} D_{s,t} = s(B_{s,t} - K) \\ B_{s,t} = K + D_{s+1,t-1} \end{cases} & B_{s,t-1} \geq K \end{cases} \quad (7)$$

282 where B is the total parr biomass (g m^{-2}) within the section, s , at time, t , D is the total parr
 283 biomass (g m^{-2}) of individuals that disperse out of the section and survive, K is parr carrying
 284 capacity (g m^{-2}) and s is the parr survival probability. Density dependent mortality may
 285 increase if the section biomass increases (due to body mass growth or an increase in
 286 abundance via recruitment or immigration) or the total carrying capacity of the section
 287 decreases due to a decrease in the wetted area.

288 **Parameterizing and running the model in the Mandalselva**

289 The model was parameterized to run on a part of the river stretching 20 km downstream from
 290 the outlet of the most downstream hydropower station (Fig. 1). Discharge into this stretch of
 291 the river is regulated by the hydropower operator: with water entering from a turbine output

292 and from an upstream bypass (minimum discharges of 3 m s⁻¹ and 1.5 m s⁻¹ in summer and
 293 winter respectively). The minimum discharge was manipulated in future scenarios to study the
 294 effect of mitigation measures. The model was parametrized and validated using available data
 295 on electrofishing juvenile densities (Fig. 4) and juvenile size at age (based on electrofishing at
 296 seven stations in October/ November, yearly from 2002 – 2010, Norwegian Environment
 297 Agency), and smolt abundance at age (see Ugedal et al. 2006). Habitat quality of each section
 298 in the modelled stretch was based on field surveys of substrate type and size, spawning habitat
 299 and shelter measurements (Finstad et al. 2007). Spawning habitat was determined from survey
 300 data. A spawning habitat quality index, varying between zero (no spawning) and one
 301 (maximum spawning), was used to allocate the initial egg deposition at start of simulations to
 302 the different sections.



303

304 **Fig. 4. Observed parr abundance and age distribution from electrofishing juvenile**
305 **densities compared to simulated parr abundance and age distribution from the salmon**
306 **abundance model (IB salmon).**

307 The model was run with a “burn-in” time of 10 years to allow for the simulation of a salmon
308 population, followed by 40 years of simulation to provide output data on the population. The
309 burn-in-time is used to create stable population processes (see Williams *et al.*, 2017) – in the
310 case of IB-salmon, this involved generating an age- and size-specific population distribution
311 from an initial estimate of egg deposition. Predictions from the burn-in time were excluded
312 from the analysis. For analysis of the effect of changes in climate scenarios and discharge
313 regimes on population abundance, one population was simulated per set of parameter values.

314 Given that the IBM included probabilistic functions, generated populations abundances would
315 vary according to simulation, even with the same set of parameter values. However, a
316 preliminary analysis of simulations showed that the effect of stochasticity in generated output
317 was small. For example, when running ten separate simulations for each of the climate
318 scenarios, the coefficient of variation (CV) for annual smolt abundance was always less than
319 0.2% for each climate scenario. This CV was negligible in comparison to the difference in
320 smolt abundance between different climate scenarios.

321

322 **2.8 Mitigation in future climates**

323 In order to explore potential mitigation measures for climate change and how these would
324 affect juvenile abundance, simulations were run with the implementation of minimum
325 discharge regimes during summer weeks (week 20-40). Summer discharges in most future
326 scenarios were less than those of the corresponding control scenarios (see Table 2). Therefore,

327 regulating discharges so that they were greater than what would occur naturally during this
328 period allowed for comparing potential mitigation measures for climate change. Five
329 summertime minimum discharge regimes were examined: 2, 4, 6, 8 and 10 m³ s⁻¹. These
330 minimum discharge regimes are sustainable from the high storage capacity of the
331 Mandalselva system.

332 **Table 2. The summary statistics (median, min, max and range) of discharge (m³s⁻¹) in**
 333 **control (1961-1990) and future scenarios (2070-2100), for all years and for the summer**
 334 **period (week 20-40).**

Scenarios	All year				Summer period (week 20-40)			
	Median	Min	Max	Range	Median	Min	Max	Range
Control (1961-1990)	64.6	2.4	445.0	442.6	53.1	2.4	260.0	257.6
	67.7	1.8	490.0	488.2	52.4	1.8	311.3	309.6
	66.4	2.4	462.5	460.1	55.0	2.4	267.2	264.8
Future (2070-2100)	61.37	0.61	347.5	346.9	12.5	0.6	116.5	115.9
	60.33	1.5	521.83	520.33	18.5	1.5	197.6	196.1
	75.03	3.08	499.21	496.13	38.4	3.1	374.8	371.7
	64.84	1.08	390.41	389.33	21.5	1.1	198.2	197.1

335

336 **3. RESULTS**

337 **3.1 Climate change in future scenarios**

338 *3.1.2 Hydraulic predictions*

339 Water temperature increased under all future scenarios (Had.Reg.A2, Had.Reg.B2,
 340 ECHAM.Reg.B2 and ECHAM.Nor.B2) compared to the control scenarios (Fig. 5, Table 3).
 341 The Had.Reg.B2 scenario showed a slightly lower mean temperature during summer weeks
 342 than the Had.Reg.A2 scenario, but one that was still several degrees higher than the control
 343 scenario.

344 **Table 3. Mean water temperatures (°C) in the control (1961-1991) and future climate**
 345 **scenarios (2071-2100).**

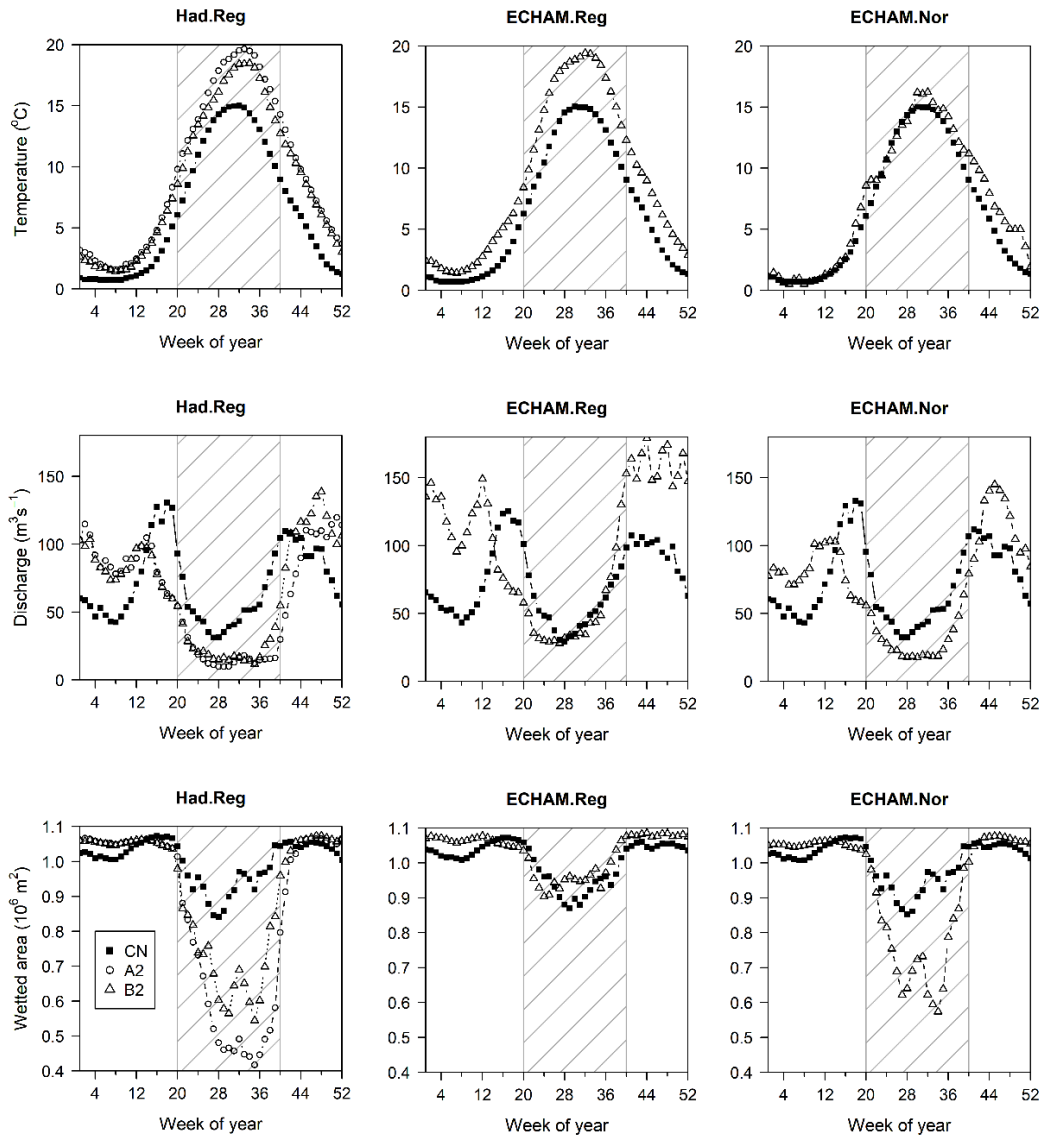
Scenarios	Global circulation models	Temperature (°C)
Control	Had.Reg.CN	6.25 (SD ± 5.16)
Control	ECHAM.Reg.CN	6.27 (SD ± 5.16)
Control	ECHAM.Nor.CN	6.27 (SD ± 5.14)
Future	Had.Reg.A2	9.05 (SD ± 5.76)
Future	Had.Reg.B2	8.48 (SD ± 5.52)
Future	ECHAM.Reg.B2	8.66 (SD ± 5.76)
Future	ECHAM.Nor.B2	8.89 (SD ± 5.16)

346

347 Winter discharges in all future scenarios were greater than in the corresponding control
348 scenarios. In contrast, the spring flood was reduced in all future scenarios compared to the
349 control, and occurred a few weeks earlier in the year. Discharges in the summer months of
350 June, July and August were lower in the future scenarios than in the control scenarios (Fig. 5).
351 Of the future scenarios, the ECHAM.Reg.B2 scenario predicted a higher discharge in summer
352 than the future Had.Reg.A2, Had.Reg.B2 and ECHAM.Nor.B2 scenarios.

353 In summer, wetted area was considerably reduced in the future scenarios Had.Reg.A2,
354 Had.Reg.B2 and ECHAM.Nor.B2. In contrast, wetted area predicted under the
355 ECHAM.Reg.B2 scenario, did not change considerably compared to the control scenario.
356 (Fig. 5).

357



358

359 **Fig. 5. Modelled mean weekly water temperature, discharge and wetted area in the**
 360 **control (1961-1991) and future (2071-2100) scenarios. Curves show mean weekly values**
 361 **across all output years of the simulation: control scenarios (filled squares); A2 scenarios**
 362 **(circles); and B2 scenarios (triangles). Hatched areas show the summer season.**

363

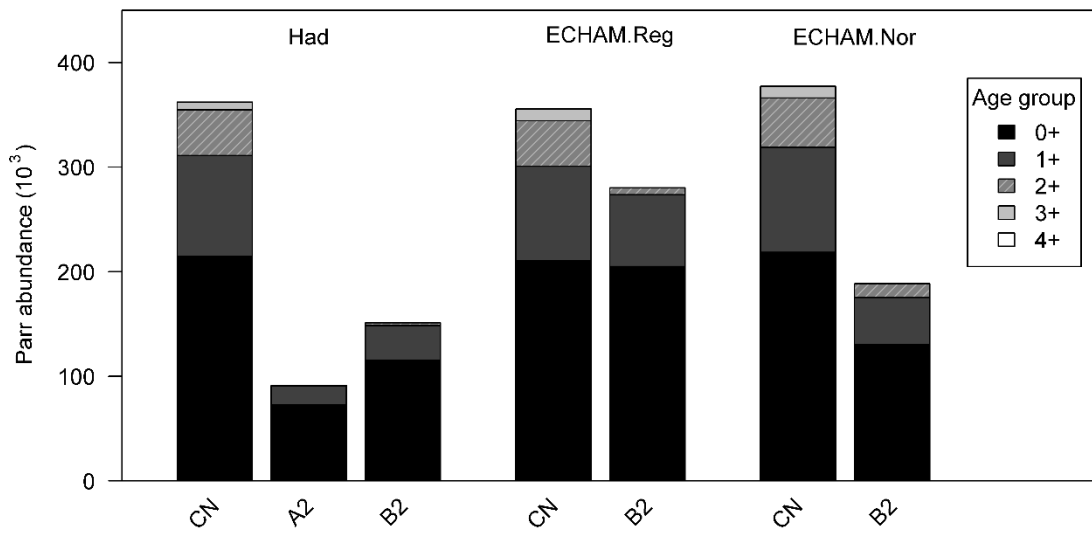
364 *3.1.2 Salmon population predictions*

365 Parr abundance decreased in all future scenarios, compared to the respective control scenarios
366 (Fig. 6 a). This reduction was, however, small in the ECHAM.Reg.B2 scenario. Because of
367 changes in age at smoltification and subsequent emigration to sea, the age composition in all
368 future scenarios shifted towards younger parr in comparison to the control scenarios. In the
369 future scenarios, the 3+ and 4+ juvenile age class (in years) disappeared and a very small
370 proportion of 2+ was left, compared to the control scenarios.

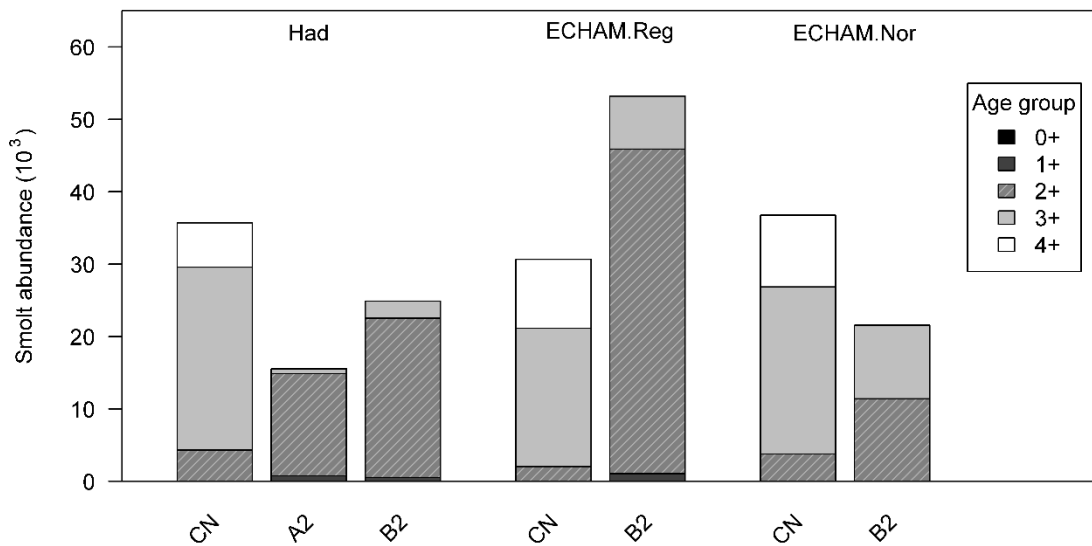
371 Smolt abundance in three of the future scenarios – Had.Reg.A2, Had.Reg.B2 and
372 ECHAM.Nor.B2 – was less than in the respective control scenarios (Fig. 6 b). However,
373 smolt abundance in the ECHAM.Reg.B2 scenario was greater than in the respective control
374 scenario. The age composition of smolts changed in all future scenarios, with age shifting
375 towards a year younger compared to smolts in the control scenarios. The majority of smolts in
376 the future scenarios were 2+, compared to 3+ and 4+ in the control scenarios.

377 The weekly density dependent mortality of parr (as a proportion of the total parr abundance)
378 was inversely correlated with wetted area and was highest during the summer period in all
379 future climate scenarios, when the wetted area was predicted to be small (Fig. 7). Future
380 scenarios with greater summertime reduction in wetted area (HAD scenarios) caused greater
381 density dependent mortality than scenarios with smaller summertime reductions in wetted
382 area (ECHAM scenarios).

(a)



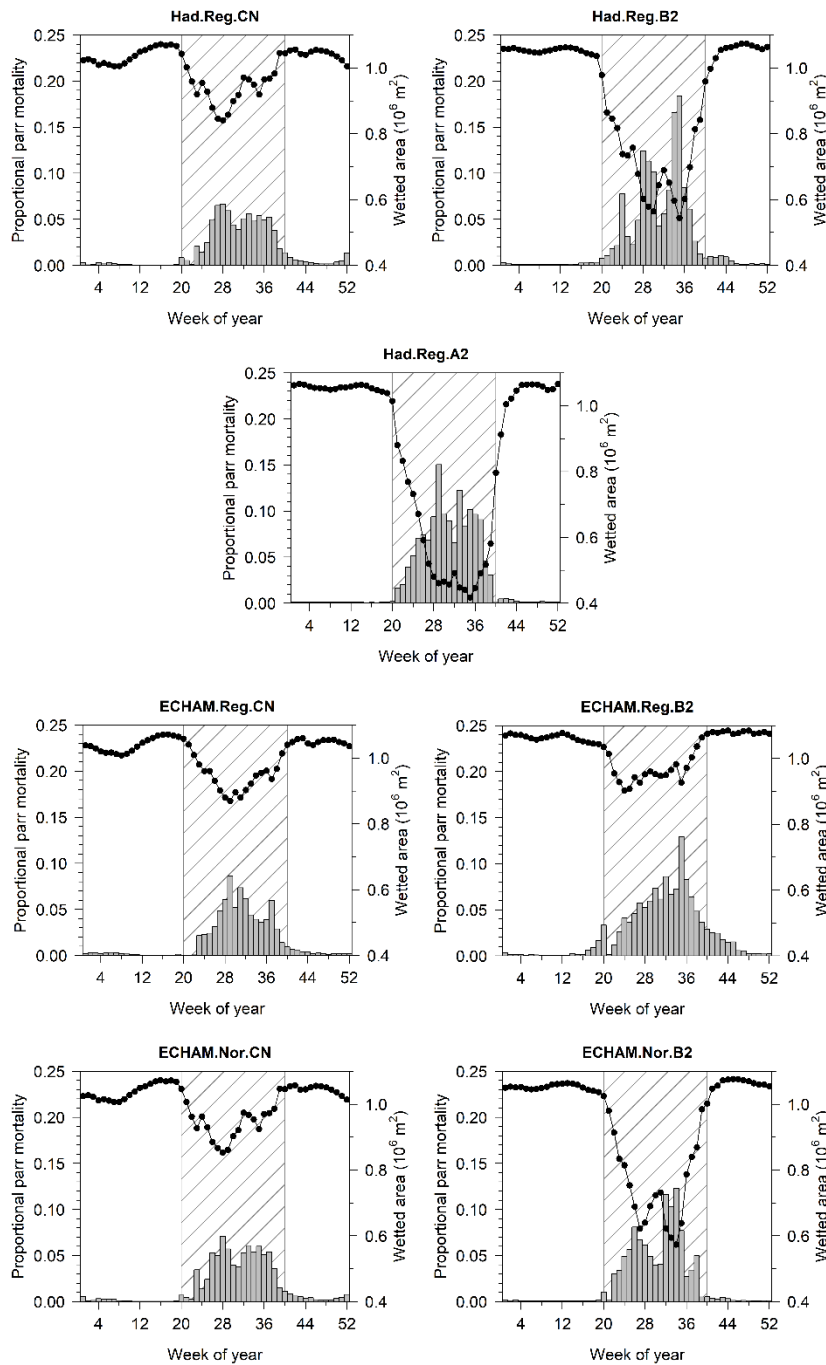
(b)



383

384 **Fig. 6. Mean parr abundance (a) and smolt abundance (b) according to age (0+, 1+, 2+,**

385 **3+, 4+) in the control (1961-1991) and future (2071-2100) scenarios.**



386

387 **Fig. 7. Mean weekly density dependent mortality of parr (proportion of the total weekly**
 388 **parr abundance) and the corresponding weekly wetted area in the control (1961-1990)**
 389 **and future (2071-2100) scenarios. Barplots and curves show mean weekly values across**
 390 **all output years of the simulation. Hatched areas show the summer season.**

391

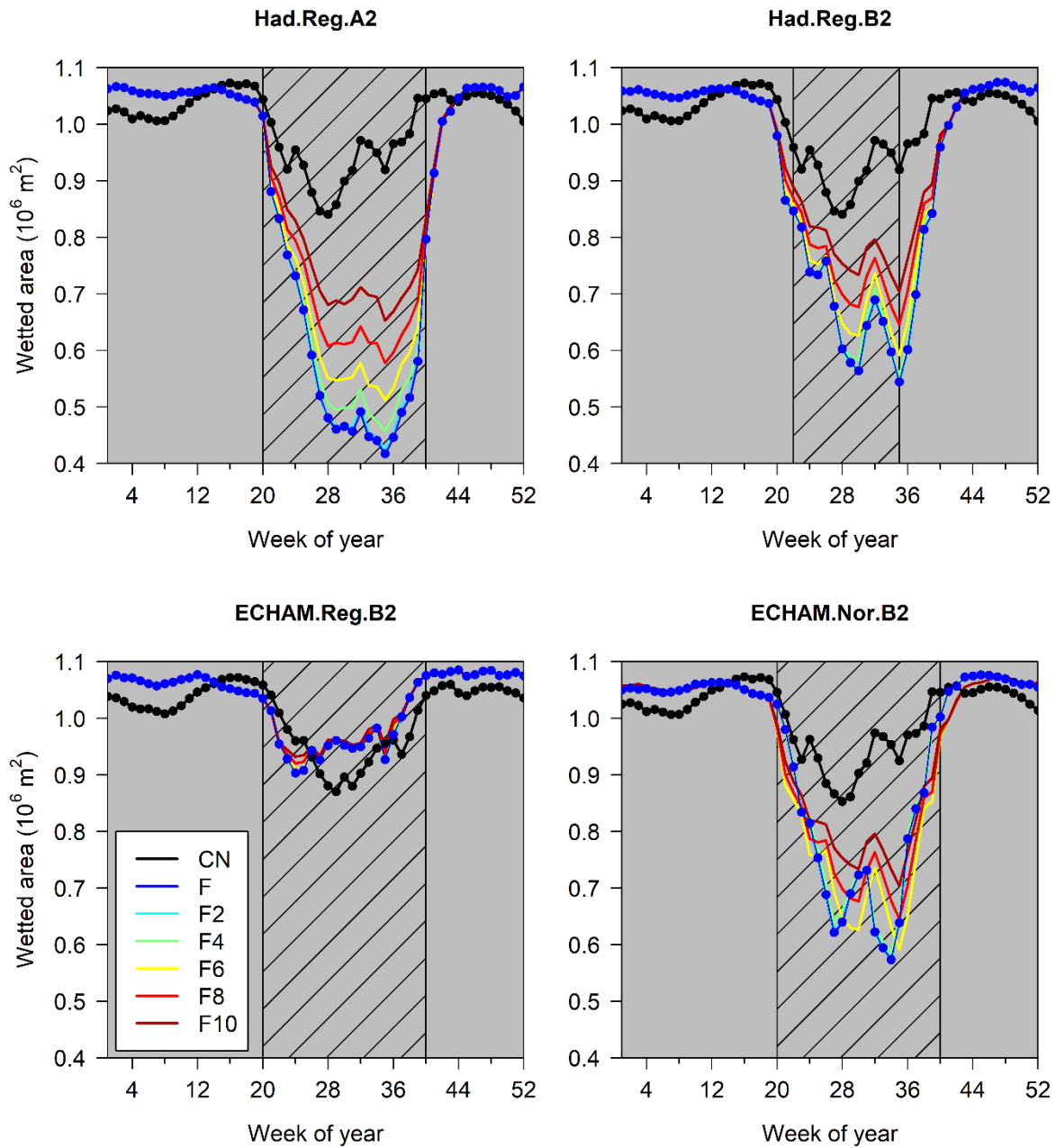
392 **3.2 Mitigation of climate change**

393 *3.2.1 Discharge and wetted area*

394 Discharges in the future scenarios were reduced during summer weeks, particularly in
395 projection Had.Reg.A2, Had.Reg.B2 and ECHAM.Nor.B2, and less so in the
396 ECHAM.Reg.B2 scenario. Implementation of minimum discharge regimes (from 2 to 10 m³ s⁻¹)
397 ¹⁾ increased summer wetted area for the Had.Reg.A2, Had.Reg.B2 and ECHAM.Nor.B2
398 scenarios (Fig. 8). The effect was strongest for the Had.Reg.A2 where summer wetted areas
399 increased from $\approx 4.5 \times 10^6$ m² under conditions of no assigned minimum discharge to $\approx 7 \times 10^6$
400 m² under a minimum discharge of 10 m³ s⁻¹. In contrast, implementation of minimum
401 discharge regimes had little effect on wetted areas for the ECHAM.Reg.B2 scenario during
402 summer months due to summer discharges in this scenario being greater than those assigned
403 in the minimum discharge regimes.

404 *3.2.2 Parr and smolt abundance*

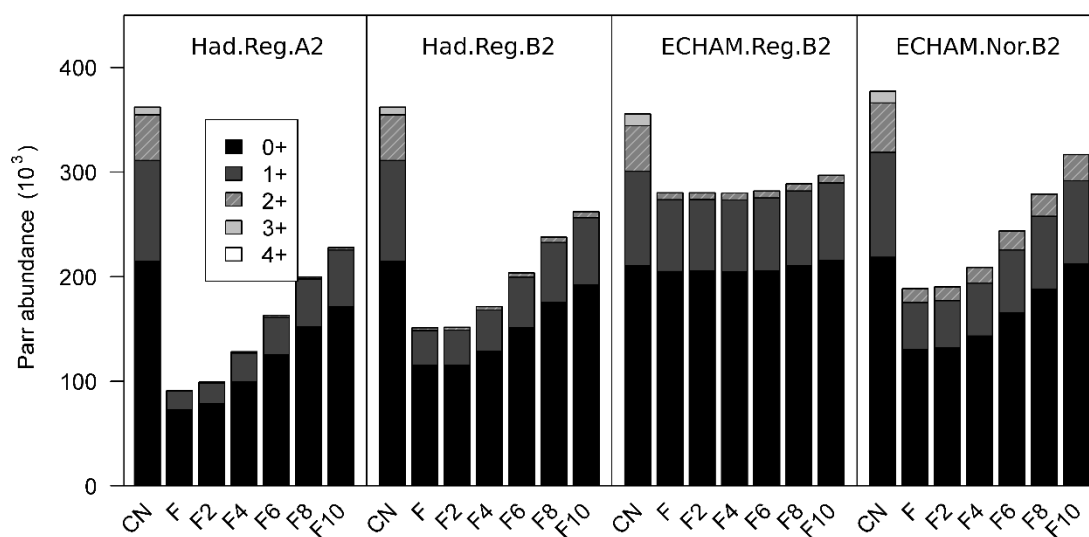
405 When running the IBM with a range of different minimum discharge regimes, parr and smolt
406 abundance increased with increasing minimum discharge in all scenarios except for the
407 ECHAM.Reg.B2 scenario (Fig. 9). The increase in abundance of both parr and smolt occurred
408 when minimum discharge in summer was 4 m³ s⁻¹ or greater. The ECHAM.Reg.B2 scenario
409 was not strongly influenced by the different minimum discharge regimes because the
410 predicted discharge in summer was higher than that assigned in the minimum regimes.



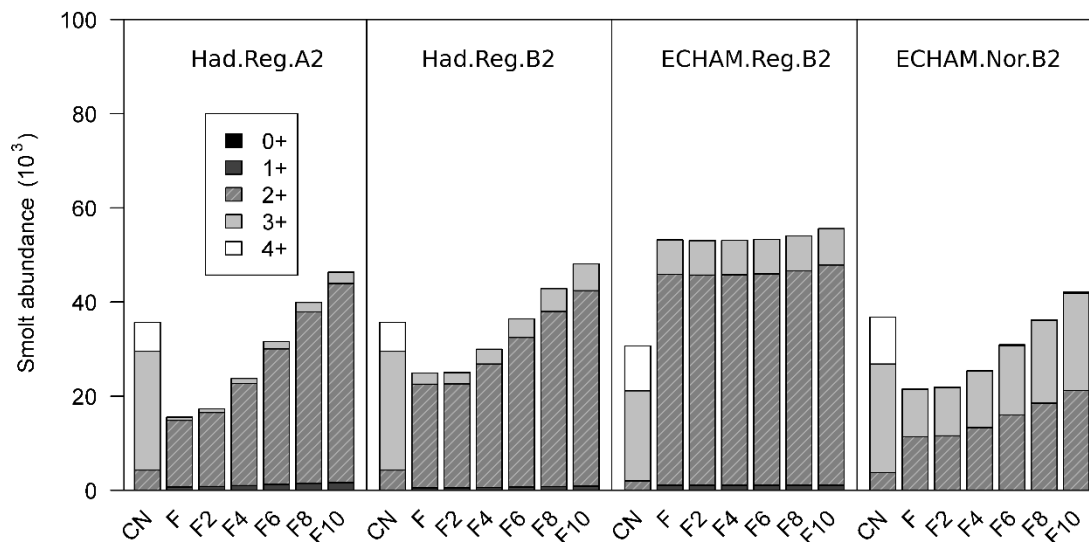
411

412 **Fig.8. Mean weekly wetted area in the control (1961-1990) and future (2071-2100)**
 413 **scenarios with a minimum discharge in week of year 20 - 40 of 2, 4, 6, 8 and 10 m³s⁻¹ in**
 414 **the future scenarios. Curves show mean weekly values across all output years of the**
 415 **simulation. Hatched areas show the summer season.**

(a)



(b)



416

417 **Fig. 9. Mean parr abundance (a) and smolt abundance (b) according to age (0+, 1+, 2+,**
418 **3+, 4+) in the control (1961-1990) and future (2071-2100) scenarios, with a minimum**
419 **discharge in week 20-40 of 2, 4, 6, 8 and 10 m³s⁻¹ in the future scenarios.**

420

421

422 **4. DISCUSSION**

423 **4.1 Effect of climate scenarios on future freshwater salmon abundance**

424 In this study, the effect of future climate change on an Atlantic salmon population in a
425 regulated river was modelled, and bottlenecks for salmon abundance in future climates were
426 identified. This study suggests that the abundance of Atlantic salmon in future climates will
427 decrease for the region modelled, and elucidates mechanisms important for regulation of
428 juvenile Atlantic salmon individuals. Low water discharge in summer was identified as a
429 possible bottleneck, and simulation of different minimum discharge regimes showed that
430 changes in river regulation may be a possible mitigation measure. The exact change in
431 Atlantic salmon abundance depended on the GCM and GCM domain used to supply
432 predictions of air temperature and precipitation, so further advances in GCM modelling are
433 required to increase the robustness of the prediction of how any given Atlantic salmon
434 population will respond to climate change.

435 Reduced parr abundance was found in all future climate scenarios in comparison to control
436 scenarios, although the reduction was small for the ECHAM.Reg.B2 scenario. Three out of
437 four climate scenarios (Had.Reg.A2, Had.Reg.B2 and ECHAM.Nor.B2) predicted reduced
438 smolt abundance, whereas the fourth (ECHAM.Reg.B2) predicted increased smolt abundance.
439 Climate outputs derived from the three climate scenarios – Had.Reg.A2, Had.Reg.B2 and
440 ECHAM.Nor.B2 – resulted in a strong reduction in wetted area during summer relative to the
441 respective control scenarios. Reduced wetted areas during summer caused increased density-
442 dependent mortality of juveniles, resulting in low parr abundances and reduced abundance of
443 smolts. In contrast, climate outputs from the ECHAM.Reg.B2 climate scenario resulted in
444 little change in summer-wetted area compared to the control scenario and consequently little
445 change in density dependent mortality. The model results therefore suggest that wetted area,

446 particularly during the summer months, regulates salmon abundance in the Mandalselva,
447 where long periods during summer with low discharge will represent a bottleneck for future
448 salmon abundance by increasing density dependent mortality. This result is consistent with
449 other studies, which have found discharge to be one of the most important factors regulating
450 the freshwater abundance of Atlantic salmon (Gibson & Myers, 1988; Ugedal *et al.*, 2008).
451 For example, Hvidsten *et al.* (2015) analysed field data of Atlantic salmon juvenile densities
452 and discharges from a 27 year time series and found that low discharges during both summer
453 and winter affected smolt abundance negatively. However, increased discharges in a future
454 climate may in other locations reduce salmon survival and future peak flows may increase
455 egg-to-fry mortality (Leppi *et al.* 2014).

456

457 "However, increased discharges in a future climate may in other locations reduce salmon
458 survival and future peak flows may increase egg-to-fry mortality

459 Parr abundance decreased in the ECHAM.Reg.B2 scenario compared to the control scenario,
460 but smolt abundances were still higher than in the control scenario. This can be explained by a
461 higher annual turnover of parr to smolt in the future scenarios. Age of smoltification is linked
462 to parr growth and body size (Økland *et al.*, 1993) and an increase in temperature will
463 increase growth rate (Forseth *et al.*, 2001) provided that there is no limitation to food supply.
464 Water temperatures in summer were higher in all future scenarios than in control scenarios.
465 This resulted in increased parr growth rates and reduced age at smolt migration (typically at
466 age 2+ rather than age 3+ in the control scenario). Smoltification at a younger age meant that
467 parr individuals were experiencing a shorter total period of parr density dependent mortality
468 (between parr recruitment and smoltification). For the ECHAM.Reg.B2 scenario this caused a
469 net increase in smolt abundance. For the other three scenarios, the magnitude of increased

470 density dependent mortality caused by the large reduction in wetted area cancelled out the
471 effect of the shorter period of density dependent mortality associated with earlier
472 smoltification, and caused reduced smolt abundance compared to the control scenarios. Thus,
473 this study shows that an increase in temperature in future climates in the study area has a
474 positive effect on the abundance of smolt, by shortening the time from hatching to
475 smoltification, that may or may not be cancelled by other negative effects of climate change.
476 A similar result, such as faster growth of parr (Beer & Anderson 2013) and younger smolt
477 ages due to fast growth, has also been shown by Hedger *et al.* (2013b) and Leppi *et al.* (2014).
478 Further, simulating future climate change in the southern distribution range of Atlantic
479 salmon, Piou & Prevost (2013) showed an increase in parr growth and population size, with
480 increased future river temperatures, but no change in smolt age. However, in the population
481 they studied Atlantic salmon smoltified as 1-year olds and a decrease in smolt age was thus
482 not possible. Nevertheless, in populations where Atlantic salmon smoltify from 2-years and
483 older, a relatively small increase in water temperature could have a potentially large influence
484 on smolt abundance. If a large proportion of parr is just below the size required for
485 smoltification in spring, a small increase in temperature could potentially have a large effect
486 on the annual turnover of smolts by enabling these to smoltify at a younger age.

487 This study contributes to the understanding of mechanisms influencing freshwater Atlantic
488 salmon populations under conditions of a climate-induced change in discharge and water
489 temperature. However, it is important to stress that the model presents a simplified
490 conceptualization of an Atlantic salmon population and does not contain all factors that may
491 influence the population. The results should be viewed as one possible outcome of climate
492 change, but with the notion that there are alternative possible outcomes if additional factors
493 are added or changed. The modelling in the current study focused on the freshwater phase,

494 and potential future climate changes in the marine phase were not studied. However, it is
495 likely that climate change also will affect the marine phase of the life cycle of Atlantic
496 salmon, particularly traits such as post-smolt growth, sea survival and the timing of spawning
497 migration (Jonsson & Jonsson, 2009) which may affect the subsequent population abundance
498 in the freshwater phase through determining the number and size distribution of returning
499 spawners.

500 **4.2 Mitigation of effect of climate change on freshwater salmon abundance**

501 In the three future scenarios that predicted the lowest wetted area (Had.Reg.A2, Had.Reg.B2
502 and ECHAM.Nor.B2), there was a strong positive influence on parr and smolt abundance
503 from implementing minimum discharge regimes. Parr and smolt abundance increased
504 correspondingly with an increase in minimum discharge from $2 \text{ m}^3\text{s}^{-1}$ up to $10 \text{ m}^3\text{s}^{-1}$. Thus,
505 increasing the minimum discharge during summer months had a positive long-term effect on
506 the abundance of Atlantic salmon smolt.

507 An unknown indirect effect of climate change in regulated rivers is the future demand for
508 energy. The hydropower production model nMAG was run in this study with the present
509 regulation pattern, which is a result of today's energy market and consumption pattern of
510 energy. However, this regulation pattern will probably change in the future to adapt to the
511 future climate conditions and energy demands. Such an adaptation may be to change the time
512 and pattern for when reservoirs are emptied, to reduce flood loss and spilling in winter. If
513 more winter water is stored in the future, it may be possible to use this water in summer, i.e.
514 as a mitigation measure to counteract the negative effects of very low discharges (and
515 correspondingly wetted area) in the abundance of Atlantic salmon smolts.

516 A general trend in future scenarios for Southern Norway is increased winter precipitation and
517 reduced summer precipitation (Schneider *et al.*, 2013). The fact that the Mandalselva is

518 regulated and has reservoir capacity to store water, may benefit the Atlantic salmon
519 population in a future climate because it allows for the possibility of releasing water from
520 reservoirs for the Atlantic salmon population in critical periods (see Piou & Prevost, 2013).
521 To use minimum discharge as a mitigation measure requires reservoirs with storage capacity.
522 Atlantic salmon is found in rivers that flow into the North Atlantic, in Europe and North
523 America. Within these continents, there are 3518 reservoirs listed in the FAO AQUASTAT
524 database (fao.org/NR/WATER/aquastat/main/index.stm), where 42 % have a storage capacity
525 above 100 million m³ and 21 % have a storage capacity of at least 300 million m³. These
526 numbers suggest that there is considerable storage capacity, although it is unknown how many
527 of these reservoirs are connected to rivers with Atlantic salmon populations and further how
528 many of these populations are in need of future mitigation measures. However, to compare
529 different river systems and mitigation measures, detailed knowledge of hydrology,
530 hydropower systems, channel hydraulics, and the local fish populations needs to be combined.
531 As an example, bottlenecks for other Atlantic salmon populations may not be the same as for
532 the population in the Mandalselva, depending on climate projections, the power system and
533 other local factors. For instance, future climate change projections for Western Norway
534 predict higher discharges from summer to winter (Hedger et al. 2013b) and in such systems a
535 low wetted area in summer may not be the bottleneck. In unregulated rivers and in regulated
536 rivers with a low reservoir capacity, it may be possible to implement other mitigation
537 measures, such as restoration of habitat, but such methods may not be as effective as direct
538 mitigation of hydrological impacts (in addition to other mitigation measures) (Battin *et al.*,
539 2007). However, this depends on the specific bottleneck for each fish population.

540 **5. CONCLUSION**

541 This study simulates how future climate change may result in reduced Atlantic salmon
542 abundance in rivers where discharge during summer is reduced. Reduced discharge may result
543 in reductions in wetted area, and consequent reductions in river carrying capacity. Lower
544 carrying capacities lead to reduced juvenile abundance. However, by simulating different
545 regulated minimum discharge regimes, this study also shows that regulated rivers with
546 reservoir capacity may contribute to future mitigation solutions for Atlantic salmon
547 populations by allowing for release of water from reservoirs during critical periods for
548 juvenile Atlantic salmon. These results are specific to the regional climate examined –
549 reduced summertime precipitation is not predicted for all parts of the world. However, this
550 simulation approach can be applied to regulated rivers in different regions to identify potential
551 bottlenecks in Atlantic salmon survival, enabling remediation strategies to be devised.

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556

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