Environmental Modelling and Software 120 (2019) 104494

Contents lists available at ScienceDirect

Environmental Modelling & Software

journal homepage: www.elsevier.com/locate/envsoft

Identification of salmon population bottlenecks from low flows in a hydro-regulated river

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ABSTRACT

Flow regime alterations from hydropower regulation may impact fish populations. Impacts can be characterized using methods for mapping bottlenecks for different species life stages. Improving the understanding of such bottlenecks could provide a basis for mitigation measures. An integrated modelling approach coupling a salmon population model (IB-salmon), a hydraulic 1D model (HEC-RAS) and a temperature model (Air2Stream) was used to identify the bottlenecks constraining the salmon population in a hydro-regulated river (Ljungan River, Sweden). This integrated approach evaluated changes in the salmon population under different low flow scenarios, involving potential dewatering of spawning sites, and the effect of restored spawning sites. Model results demonstrated that low discharges in winter and summer were potential hydrological bottlenecks for the salmon population, particularly in winter due to potential dewatering of spawning sites. Restoration of spawning sites increased salmon production under all scenarios, posing a potential counter measure against low flows.

1. Introduction

Hydropower production in northern Europe has an important and stabilizing role in the current and future Nordic energy system, and the “green shift” toward European renewable energies (Oecd/Iea, 2013). In 2016, the total installed capacity for hydropower in Sweden was 16 200 MW with an average annual production of 66 TWh (Flood, 2015), accounting for approximately half of the country's energy consumption. Shares in the energy system from Swedish and Norwegian hydropower play an important role in supporting decarbonisation in the Nordic countries (Oecd/Iea, 2013). The implementation of European legislation such as the Renewable Energy Directive (2009/28/EC) and the European Water Framework Directive (2000/60/EC), supporting agreed emission targets of greenhouse gases to reduce climate change while improving the quality of aquatic environments and sustaining biodiversity (Lindström and Ruud, 2017), implicitly necessitates a better understanding of how flows within regulated rivers can be used to sustain fish populations.

Sweden, a member state of the European Union, has approximately 1000–1200 water bodies including 670 km of regulated reaches (Johnsen et al., 2011) that are affected by hydropower regulation (Hav, 2015). Eighty-four percent of hydropower-affected reaches are inhabited by salmonid species () such as Atlantic salmon (*Salmo salar* L.) and sea trout (*Salmo trutta* L.), species with both high socio-economic interest and importance as indicator species for the quality of aquatic environments (Burger et al., 2015; Ignatius and Haapasaari, 2018). Thus, preserving sustainable populations of these species has an important political and management interest.

Atlantic salmon has a complex life cycle requiring different habitat characteristics at different life stages (Bardonnet and Baglinière, 2000; Armstrong et al., 2003) Reported challenges affecting Atlantic salmon populations in Swedish regulated rivers are related to anthropogenic migratory barriers such as hydropower dams, habitat loss and flow regulation (; Svensson, 2000; Rivinoja, 2005). Changes in water temperature due to regulation may also be an issue. Firstly, salmon survival, development, and growth is bound by temperature thresholds. Secondly, temperature affects fish migration, spawning and egg hatching (Olden and Naiman, 2010). Hydropower-induced reduction in water flows during summer in combination with higher air temperature will influence the salmon growth phase, while hydropower-induced changes in winter temperature will affect fish energy storage and potential for starvation (Heggenes et al., 2018). However, temperature impacts in Swedish regulated rivers may be reduced by the fact that they these rivers typically have hydropower systems with low-elevation dams that create upstream impoundments with little storage capacity (and therefore have less potential for storage-induced temperature

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https://doi.org/10.1016/j.envsoft.2019.104494
Received 1 March 2019; Received in revised form 21 July 2019; Accepted 25 July 2019

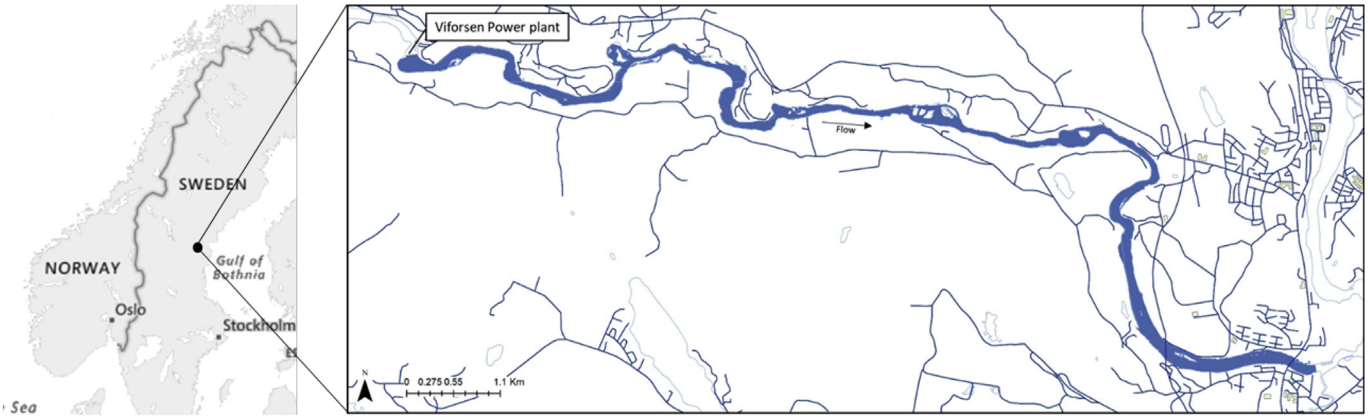

Fig. 1. The Ljungan River (62°18′23″N, 17°18′42″E), showing the extent of the modelled river reach, downstream of the Viforsen Power plant.

changes). Hydropower regulation may also cause reductions in water flow which will reduce the wetted area – the surface area of the river channel that is covered by water – and therefore reduce available salmon habitat. If winter flows are lower than in the previous spawning season, dewatering of spawning sites may lead to potential desiccation of eggs and stranding of juvenile salmon at spawning sites (Forseth and Harby, 2014; Johnsen et al., 2011). Furthermore, reductions in the magnitude and frequency of floods in regulated rivers may increase sand and silt deposition and reduce habitat quality (Barlaup et al., 2008), which may reduce the survival and fitness of juvenile salmon. Beside negative effects, hydro regulation may also positively impact salmon populations. In some cases, high winter flows due to high energy demand have been reported to increase the survival of juvenile salmon, and thus positively impact salmon smolt production in regulated rivers (Johnsen et al., 2011).

In light of the impacts produced in rivers from hydropower plants, the Water Framework Directive (WFD) alongside recommendations from Swedish national agencies (e.g. Swedish Agency for Marine and Water Management) are driving the implementation of mitigation measures in Swedish rivers regulated for hydropower (Lindström and Ruud, 2017). In some hydropower systems, run-of river impoundments may be owned by different hydropower companies, and therefore cooperation and coordination between stakeholders is motivated by the implementation of mitigation measures (Mrc, 2016). In recent years, different methods have been developed to identify bottlenecks – phenomena causing high mortality and having significant influence on fish population dynamics – and to assist the decision making process for implementing mitigation measures. Forseth and Harby (2014) published a guideline handbook for the diagnosis of bottlenecks and the design of mitigation measures in regulated salmon rivers. The handbook includes a definition for “hydrological bottleneck” because flow determines the extent of wetted area, and hydrological factors influence density-dependent growth and survival rates (see Milner et al., 2003) which are crucial to salmon populations. For example, a high flow will result in a large wetted area and fish will distribute over a large area with low densities; however, when flow decreases, wetted area will be reduced, fish densities will increase and density-dependent mortality may occur. Models combining hydrological and hydrodynamic factors can support the identification of hydrological bottlenecks. In addition, the combination of these models with biological modelling to predict changes in salmon populations has shown their potential to address a wide variety of impacts and bottlenecks in salmon populations and their implications for mitigation measures (Hedger et al., 2013a).

In this study we evaluate and identify bottlenecks that constrain an Atlantic salmon population in a hydropower regulated river in Northern Sweden, the Ljungan River. This study is based on a project collaboration between the county environment officer, national authorities, local and national NGO's and international research institutes. The motivation for this study was stakeholder concern regarding low release flows and the potential effect on the salmon population, in addition to an upcoming revision of the hydropower license which will include discussions concerning the establishment of a minimum flow. The project was established with an adaptive management approach (Walters, 1986) to ensure clear objectives, involvement from affected stakeholders, identification of bottlenecks for Atlantic salmon, and potential mitigation measures. The overall objective of this study is to identify hydrological bottlenecks in salmon smolt production in Ljungan River using an integrated approach. In addition, the effect on the salmon population of restoring spawning habitat as a mitigation measure is also investigated.

2. Materials and methods

2.1. Study area

This study was conducted in the Ljungan River, situated in Northern Sweden (Fig. 1). The Ljungan River is in total 399 km in length (Helcom, 2011) and is regulated for hydropower production through a cascade of 15 run-of-river (RoR) hydropower plants. Cascade systems are usually characterized by reservoirs with large storage capacity located at high altitude, followed by a series of RoR impoundments. These systems provide an effective way to enhance water resources utilization, maximize energy generation, optimize the regional water allocation, and mitigate possible flood events (Zhai et al., 2017; Shen et al., 2018; Ding et al., 2018). The lowermost hydropower plant in the Ljungan River is the Viforsen power plant, which has an installed capacity of 10 MW and an annual production of 79 GWh, and was designed to reduce rapid flow changes from upstream power plants. In the hydropower system, there is a minimum flow of 20 $m^3 s^{-1}$ specified by law for an upstream hydropower plant, but at Viforsen power plant there is no minimum flow specified by law. However, based on preliminary results from this project a local agreement has been established to maintain (when it is possible) a downstream minimum flow of 30 $m^3 s^{-1}$, particularly during winter. The annual average flow in the modelled reach in Ljungan River is 138 $m^3 s^{-1}$ (Table 1). Today, the Viforsen hydropower plant is the upstream barrier for anadromous fish species. The modelled river reach in this study comprised the 17 km lowermost part of the river system between Viforsen power plant and the estuary, the stretch available for supporting anadromous fishes such as Atlantic salmon.

The modelled river reach is dominated by glides and deep pools with intermittent riffles and rapids (Table 1). The modelled reach ranges from 40 to 280 m in width and has an average water depth of 3 m. The river bed is characterized predominantly by gravel and cobbles but also has areas with sand and boulders. The water normally has a high amount of humic substances, originating from pine forest and

Table 1
Characteristics of the modelled reach in Ljungan River (Alne, 2016; Kristofers, 2014). Flow characteristics were calculated for the hydrological time series from 1982 to 2015 provided by Statkraft AB Sweden.

Mean flow ($m^3 s^{-1}$)	Average min.flow winter ($m^3 s^{-1}$)	Average min.flow summer ($m^3 s^{-1}$)	1 day min.flow winter ($m^3 s^{-1}$)	1 day min. Flow summer ($m^3 s^{-1}$)	Average water T (C°)	Slope (%)	Average depth (m)	Riffles/glides (%)	Average substrate Size (m)
138 SD (± 85.98)	102 SD (± 37.06)	82 SD (± 60.19)	40 SD (± 2.88)	19 SD (± 2.51)	8 SD (± 7.80)	0.1	3	10/90	0.30

marsh areas within the catchment, which gives a brown colour to the water. The Ljungan River has a genetically unique Baltic Atlantic salmon population which is considered to be self-sustaining (Helcom, 2011). However, the stock abundance estimated from annual electro fishing demonstrates large year-to-year variation (Ices, 2015). Other fish species in the Ljungan River include sea trout (*Salmo trutta* L.) and grayling (*Thymallus thymallus* L.) among others.

2.2. Modelling approach

The main modelling approach was based on an integrated method that combined hydrological, hydraulic, and ecological components, initially presented in Adeva Bustos et al. (2017) but further developed in this study to include LiDAR data as a basis for hydraulic modelling. This integrated approach (Fig. 2) applies the salmon population model IB-salmon (see Hedger et al., 2013a) to calculate changes in smolt production as an indicator for changes in total salmon production in a selected river reach.

The approach in this project is built on the following steps. (1) IB-salmon was set up to simulate the Atlantic salmon population under present-day conditions. (2) A series of hypothetical scenarios were established which were used to simulate new populations with the IB-salmon model. Finally, (3) the change in smolt production, defined as percentage change from that produced under present-day conditions, for the different scenarios was analysed. As discharge, water temperature, proportion of dewatered area, spawning sites, parr carrying capacity and number of eggs are physical and biological factors controlling smolt production in IB-salmon, evaluation of how these changed according to scenario allowed us to identify the bottlenecks that constrained the salmon population.

2.2.1. IB-Salmon set-up

The Atlantic salmon population was simulated using the individual-based population model IB-salmon (see Hedger et al., 2013a for a description of the model design). IB-Salmon is designed to simulate the response of Atlantic salmon populations to changes in river discharge, water temperature and hydro-morphological characteristics. IB-salmon has been used to examine the effect of climate change (Hedger et al., 2013b; Sundt-Hansen et al., 2018), hydropeaking (Sauterleute et al., 2016; Hedger et al., 2018), and changes in long-term flow regimes and habitat modification (Adeva Bustos et al., 2017). The model simulates salmon population abundances across the salmon life cycle: parr (freshwater resident juveniles), smolts (salmon that are migrating to sea for the first time), sea resident, and returning adults. Processes in freshwater are modelled with a weekly time-step across the modelled reach which is compartmentalized into 50 m long river sections. Parr abundance is initially dependent on parr recruitment, which in turn is dependent on the spatial distribution and number of spawning sites. The maximum biomass of parr supported per section is the product of the parr carrying capacity ($g\ m^{-2}$) of the section and its total wetted area (which in turn is dependent on discharge). When the maximum biomass of a section is exceeded, excess parr migrate out of the section (i.e. density-dependent migration). A proportion of these migrating parr die, so density-dependent mortality is an implicit part of the model.

For each section, parr abundance was simulated at a weekly time step as a basis for calculation of annual smolt production. Model inputs were data on the Atlantic salmon population (used in estimating parr carrying capacity, and in validating model results) and data on the river habitat. Data on the juvenile Atlantic salmon population were obtained from Västernorrlands County. Abundance data for age 0 + parr and age 1–4 + parr were collected from electrofishing surveys at 14 sites within the Ljungan River conducted in August–October in the period 1988–2015 (92 sample sites in total). Body length data were obtained from 5930 parr captured downstream of Viforsen from 1988 to 2016 in August (N = 884), September (N = 4116) and October (N = 930). Body lengths showed a bimodal distribution corresponding to 0 + age

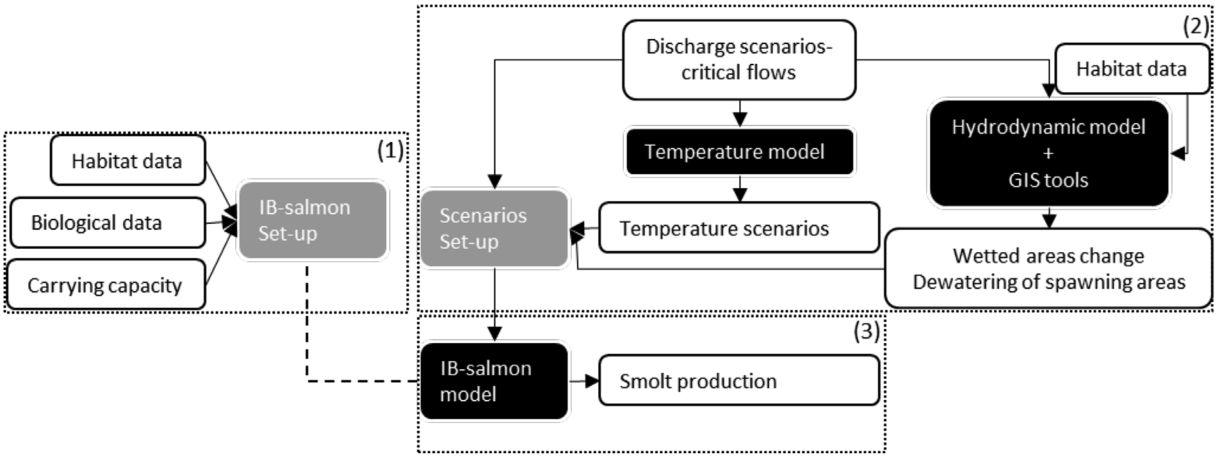

Fig. 2. Modelling procedure steps. Black elements indicate models, white elements indicate inputs and outputs, and grey elements indicate set-ups.

group (length < 95 mm) and 1–2+ age group (length ≥ 95 mm). Parr abundances and body lengths simulated by the model were compared with those observed using Mann-Whitney U-tests to validate the model simulation.

Physical habitat data were obtained from surveys conducted by Uni Research in 2014 (Skoglund et al., 2015). Habitat data used in the population model included the spatial distribution of spawning sites (which controlled the recruitment of parr) and the spatial distribution of shelter – a key determinant of parr carrying capacity (see Foldvik et al., 2017). The parr carrying capacity of each section was calculated by (i) establishing a relationship between observed maximum parr biomass (from electrofishing data) and shelter density, and (ii) applying this relationship throughout the watercourse. From electrofishing data, the maximum total biomass of parr at each station was determined. This was considered to be a conservative estimate of the biomass that each station could support. Using data on shelter density for each section, carrying capacity was assigned to all sections in the river based on their respective shelter densities (derived from Skoglund et al., 2015).

2.2.2. Scenario set-up

The scenario-specific inputs needed in IB-salmon were discharge, temperature, wetted area and spawning habitat availability. Temperature and wetted areas changes were modelled using hypothetical discharges, and spawning habitat availability was dependent on wetted areas changes.

2.2.2.1. Discharge and temperature. The weekly average discharge, calculated from observed discharge data from Ljungan River for the period 1982–2015 provided by Statkraft AB Sweden, was used for the generation of river discharge scenarios. The one day minimum flow registered was 19 $m^3 s^{-1}$ during summer, and 40 $m^3 s^{-1}$ during winter. As the chief objective was to identify potential hydrological bottlenecks related to salmon production within the context of the established minimum flow agreement of 30 $m^3 s^{-1}$ downstream of Viforsen, five hypothetical scenario groups were created (Fig. 3) based on the following criteria: i) *Baseline*, defined as the weekly average discharge and used for comparison to the other scenarios, ii) *Historical*, defined as unregulated flow conditions (obtained from the Swedish Meteorological and Hydrological Institute (Smhi, 2018)), iii) *Summer 30*, the hypothetical case of releasing the minimum flow during summer, iv) *Winter 30*, the hypothetical case of releasing the minimum flow during winter, and (v) *Summer 19*, the hypothetical case of releasing a flow during summer of 19 $m^3 s^{-1}$, equivalent to the minimum flow that has been observed during summer. In order to reduce stochasticity from the biological model, each discharge scenarios used the same intra-annual discharge pattern for every year of the simulation.

Water temperatures were dependent on discharge scenarios. Air2Stream, a hybrid statistical-physical model (Toffolon and Piccolroaz, 2015; Piccolroaz et al., 2016) that included a lumped heat budget model was used to model the water temperatures based on the given discharge scenario. Input data on air temperature from a gauge at Sundsvall airport (2202 Råsta) was provided by the Swedish Transport Administration (Trafikverket, 2018). Adjustments were made based on linear regression for low summer flows not occurring in the calibration data.

2.2.2.2. Wetted area changes and spawning location. A hydraulic model was set up for the modelled river stretch to evaluate changes in wetted area and the possible dewatered areas. The hydraulic model includes 340 cross sections for use in the hydrodynamic model HEC-RAS 5.0 (Hec, 2016). The cross sections were extracted from a digital elevation model (DEM) using HEC-GeoRAS 4.3 in ArcGIS 10.5 (Esri, 2016) with a mean distance between transects of 50 m, corresponding to the resolution of the IB-salmon model. The bathymetry data used to construct the DEM were derived from an airborne LiDAR bathymetry (ALB) survey carried out with the RIEGL VQ-880 G scanner (Riegl, 2014) on September 2nd' 2015. The LiDAR data had an accuracy of 0.07 m for planar coordinates, and a mean vertical accuracy of 0.03–0.04 m (Alne, 2016). As the ALB technique is sensitive to dissolved organic material and air bubbles, water column areas with no information may occur (Alne, 2016). Therefore, areas lacking bathymetry data were mapped using a Sontek RiverSurveyor M9 Acoustic Doppler Profiler (ADCP) (Sontek, 2016). Bathymetry data from the LiDAR and the ADCP were combined to produce the final DEM using an empirical Bayesian kriging interpolation method in ArcGIS. Changes in wetted area were simulated using a 1D modelling approach, with the selected discharge scenarios used as the upstream boundary condition and normal depth used as the downstream boundary condition. Changes in the wetted area were obtained from the model at each cross section for the eight discharge scenarios. Validation of the model was done by calibrating the observed water line (from LiDAR data) with the simulated water line in the model (from HEC-RAS 1D). Dewatered areas and potential dewatered spawning sites were identified using a quasi 2D model created from post-processing of the hydrodynamic results in HEC-GeoRAS 4.3.

In order to simulate the effect of spawning site availability, four spawning site conditions were combined with the discharge scenario groups (Fig. 4): *Present, NewSpawn, Dewatered,* and *New. Sp-Dew*. The present-day spatial distribution of Atlantic salmon spawning areas identified by the river survey conducted by Uni Research was included in the IB-salmon model as the *Present* condition. The *NewSpawn*

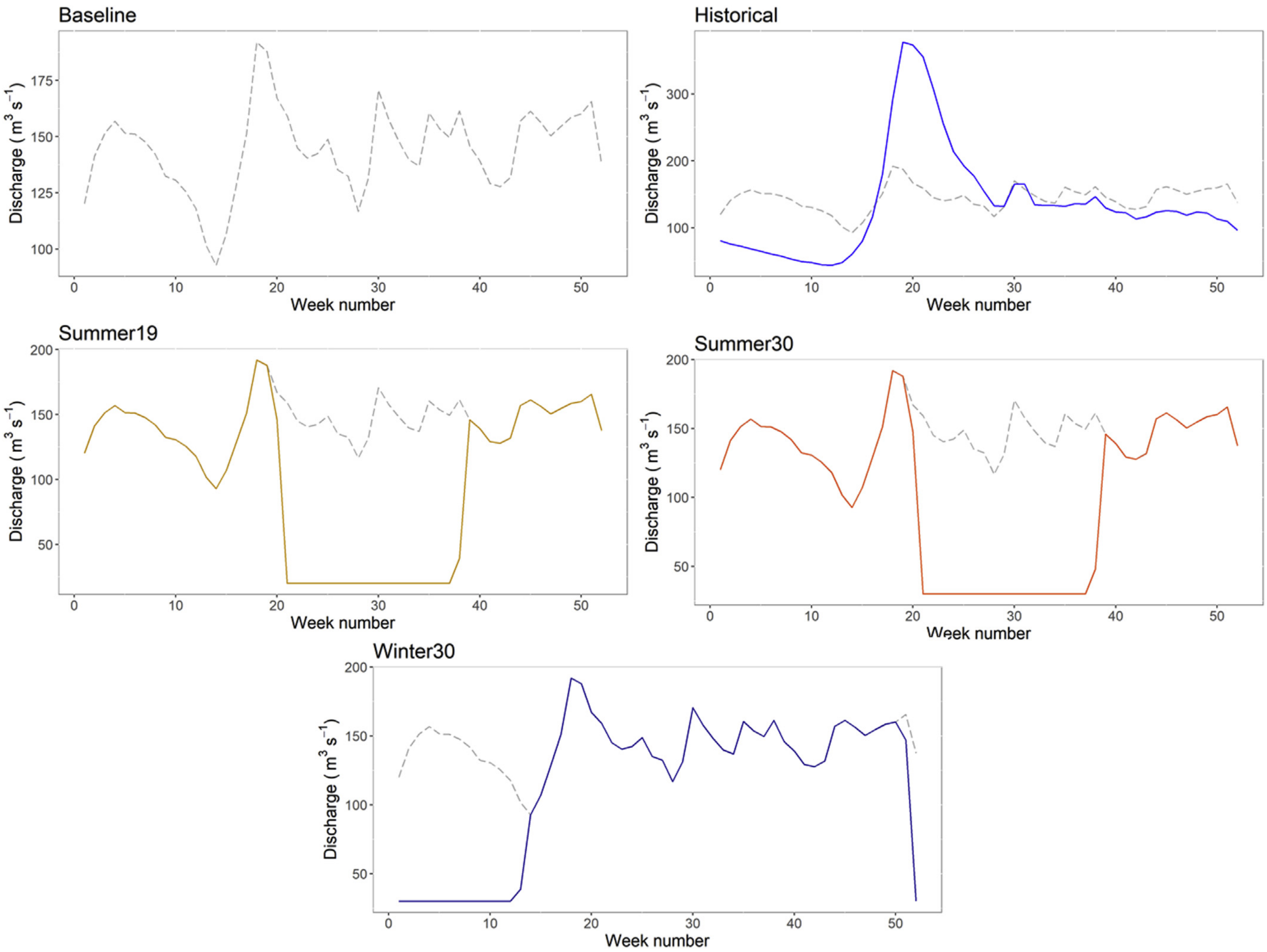

Fig. 3. Intra-annual pattern for each hypothetical discharge (solid line) alongside that of the Baseline scenario group (dashed line).

condition was based on the *Present* condition but had an additional four restored spawning sites, involving an increase in spawning area of 11%. The *Dewatered* condition involved certain spawning sites being rendered ineffective due to desiccation of the spawning site centres during low discharge. Existing and restored spawning areas were evaluated in each discharge scenario to identify those that were dewatered between spawning and egg hatching using a quasi 2D model created from post-processing of the hydrodynamic results in HEC-GeoRAS 4.3. The dewatered situation was included in all discharge scenarios except the *Baseline* scenario group (where winter flows were higher than during the spawning season) and the *Summer 19* and *Summer 30* scenario group (where eggs had hatched by the time the conditions of these scenarios would have applied). Finally, the *New. SpDew* condition including the four new spawning sites (from the *NewSpawn* condition) but also considered those that were dewatered (from the *Dewatered* condition).

2.2.3. Parameterising IB-salmon

Outputs from scenarios were used as inputs in the IB-salmon population model. Population dynamics were simulated for 34 years, corresponding to the number of years of available discharge data in the *Baseline Present* scenario. To obtain a full age-distribution of spawning adults in the model, the first ten years of each simulation were used as a burn-in period and the latter 24 years were used to analyse the smolt production under the different scenarios. Smolt production from the hypothetical scenarios were compared with that of the *Baseline Present* scenario (average observed flow scenario under present-day spawning) to determine the relative effects of the scenario conditions.

3. Results

3.1. Simulated population validation

The salmon population model simulated a population abundance that was similar to that observed for both 0 + parr (Mann-Whitney *U* test, W = 223, p = 0.87) and 1–4+ parr (Mann-Whitney *U* test, W = 148, p = 0.08) (Fig. 5, left panel). The salmon population model also generated similar body length distributions to those observed (Fig. 5, right panel), with 0 + parr being approximately 65–70 mm in length, and 1–2 + parr being approximately 120–135 mm. However, there were marginally significant differences between simulated and observed lengths (0 + parr, W = 117, p-value = 0.011; 1–2+ parr, W = 310, p-value = 0.016).

3.2. Hec-RAS model calibration

Simulated water surface elevations showed strong agreement with those observed from the water line on the day of the ALB survey, indicating that the model was valid to simulate the alternative scenarios (Fig. 6). Mean vertical errors were 0.13 m and 0.14 m for the left and right bank respectively, with a minimum and maximum vertical error of [0.001–0.9 m] for both banks calculated without outliers.

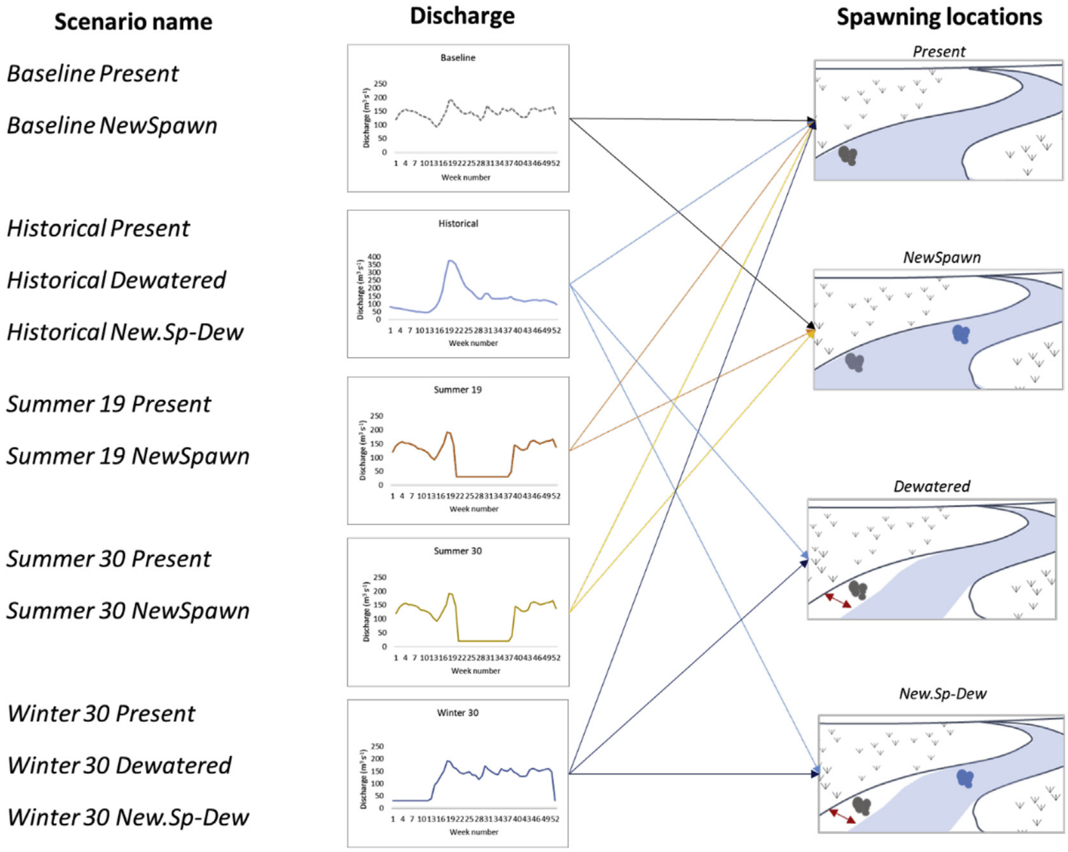

Fig. 4. Scenarios names, discharge and spawning sites (grey circles, for present spawning sites, blue circles for new spawning sites, and red arrow for dewatering process). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.3. *Wetted area changes and dewatering of spawning sites*

Little reduction in wetted area occurred until the river discharge fell below 110 $m^3 s^{-1}$. In addition, all spawning sites were covered at a discharge of 110 $m^3 s^{-1}$. Therefore, a discharge of 110 $m^3 s^{-1}$ was used for the comparison of results regarding wetted area change and dewatering of spawning sites. Reducing discharge below this caused a decrease in wetted area and a consequent increase in dewatered spawning habitat (Fig. 7). Below a discharge of 20 $m^3 s^{-1}$, wetted area was reduced by 35% and spawning sites were reduced by 25%. The four new spawning sites were found to be covered in all the discharge scenarios.

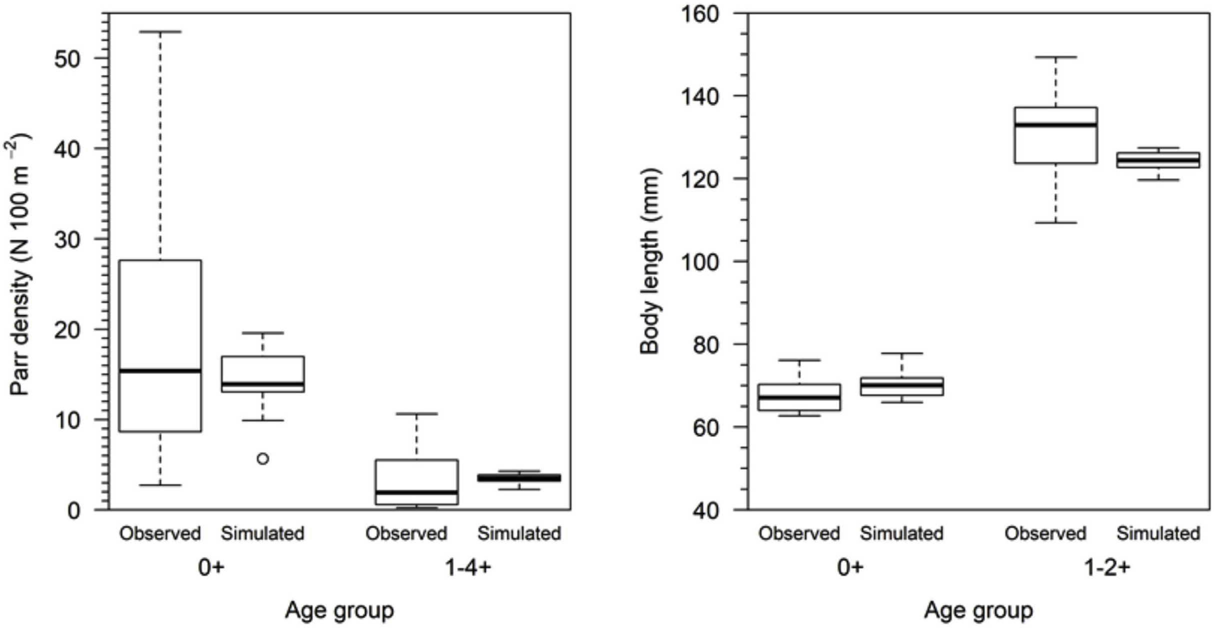

Fig. 5. Observed and simulated mean annual parr densities (left panel) and body lengths (right panel).

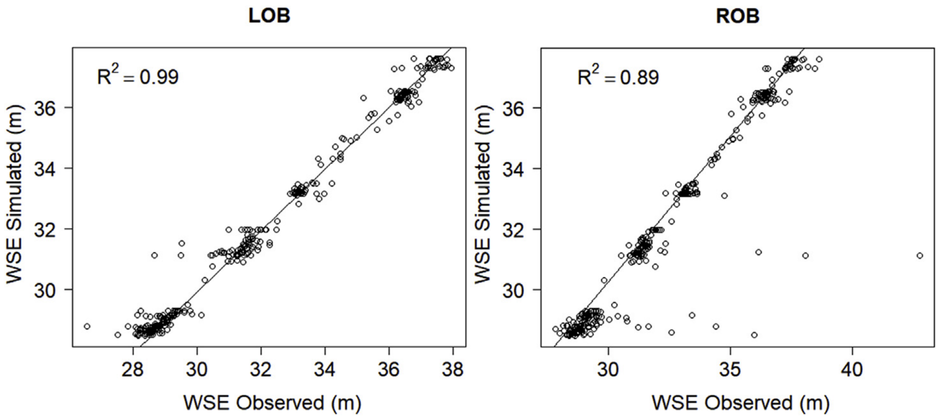

Fig. 6. Observed versus simulated water surface elevations for the left bank (left panel) and right bank (right panel).

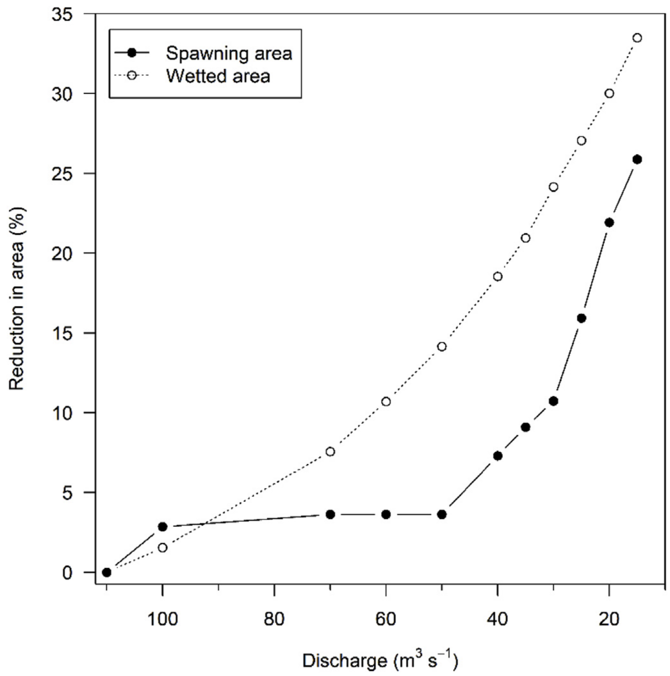

Fig. 7. The effect of a reduction in discharge from the minimum discharge (110 m^3 s^{-1}) required to cover all possible spawning habitat on the reduction in wetted and spawning area.

3.4. *Changes in smolt production*

All scenarios under the *Present* spawning condition showed lower smolt production compared with *Baseline Present* scenario (average observed flow scenario under present-day spawning) (Fig. 8). Four scenarios showed higher smolt production than the *Baseline Present* scenario: *Baseline NewSpawn, Historical New. Sp-Dew, Summer 19 NewSpawn and Summer 30 NewSpawn.* No scenario showed higher production than *Baseline NewSpawn*, which produced 20% more smolts than *Baseline Present.*

Scenarios with lower average smolt production for the modelled river stretch also had lower smolt production per 50 m section (see Fig. 9, showing the two scenarios with lowest production – *Winter 30* and *Summer 19* – and the *Baseline* scenario). Results for *Summer 19* and *Winter 30* showed a general reduction in wetted area and in smolt production per section (Fig. 9) compared with *Baseline* scenario. Comparison of the three scenarios under *Present* conditions for spawning sites showed that some sections under the *Baseline Present* scenario were more productive than under *Summer 19* and *Winter 30 Present* scenarios.

Smolt production was greater in scenarios with additional spawning sites (*Summer 19 NewSpawn* and *Winter 30 New. Sp-Dew*) than in the respective scenarios without additional sites (*Summer 19 Present and Winter 30 Present*). However both scenarios (*Summer 19 NewSpawn* and *Winter 30 New. Sp-Dew)* showed lower smolt production than the Baseline scenario with new spawning sites (*Baseline NewSpawn*). Differences between smolt production under *Winter 30 Present* and *Winter 30 Dewatered* spawning conditions exhibited the effect of dewatering spawning areas being implemented, showing areas with no production under *Winter 30 Dewatered* compared with *Winter 30 Present.*

3.5. *Effect of temperature on salmon smolt production*

The simulated age distribution of smolts was scenario-specific. Scenario groups *Summer 19* and *Summer 30* with lower discharges and therefore high temperature in summer compared with the *Baseline* scenario caused smoltification at a younger age, and a resulting increase in the percentage of parr smoltifying as age group 1 + or 2 + rather than at older age groups (Fig. 10). The smolt age distribution did not depend on whether spawning habitat improvement had been made.

4. Discussion

Potential bottlenecks and the effect of restoring spawning sites were evaluated based on changes in smolt production obtained under different hydropower production scenarios. Results indicated that a low winter discharge (30 m^3 s^{-1}) could be the most critical bottleneck for smolt production in the Ljungan River due to a significant increase in dewatered spawning sites. It is important to notice that the hypothetical scenario in which the agreed minimum flow is released during winter is unlikely to happen considering past and current operational releases. However, results from low summer flows (which have been observed) indicated that reduced flow in summer is also a bottleneck for the smolt production. Results also indicate that low summer flows in combination with high water temperatures may lead to reduced smolt age, and thus could increase smolt production in the absence of other limiting factors such as wetted area. In addition, restoration of spawning sites as a mitigating action in regulated rivers can compensate for the potential negative effect of dewatered areas in spawning sites and be of vital importance in mitigating the effects from low discharges.

The 1D hydrodynamic model simulated water surface elevations that fitted those observed, indicating a robust hydraulic modelling of wetted area – key input data for the salmon population model. One dimensional models have also been shown to be computational efficient when large areas needs to be modelled for a range of river discharges, producing accurate results especially for wetted areas and water depths (Benjankar et al., 2015), supporting our work. Further, the quasi 2D

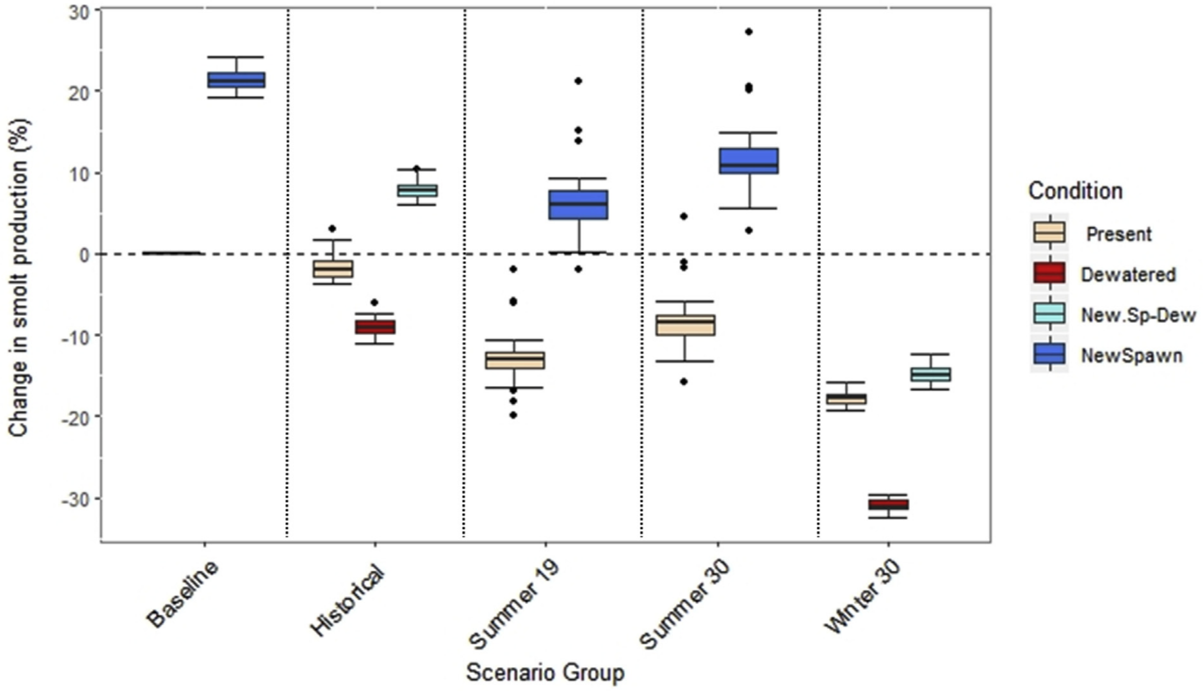

Fig. 8. Change in smolt production under each scenario with respect to the Baseline scenario. The bold line in each box is the median, the boxes shows the interquartile range (IQR), the whiskers 1.5 × IQR, and the circles show outliers. Raw mean numbers for each scenario are provided in Appendix Table A1.

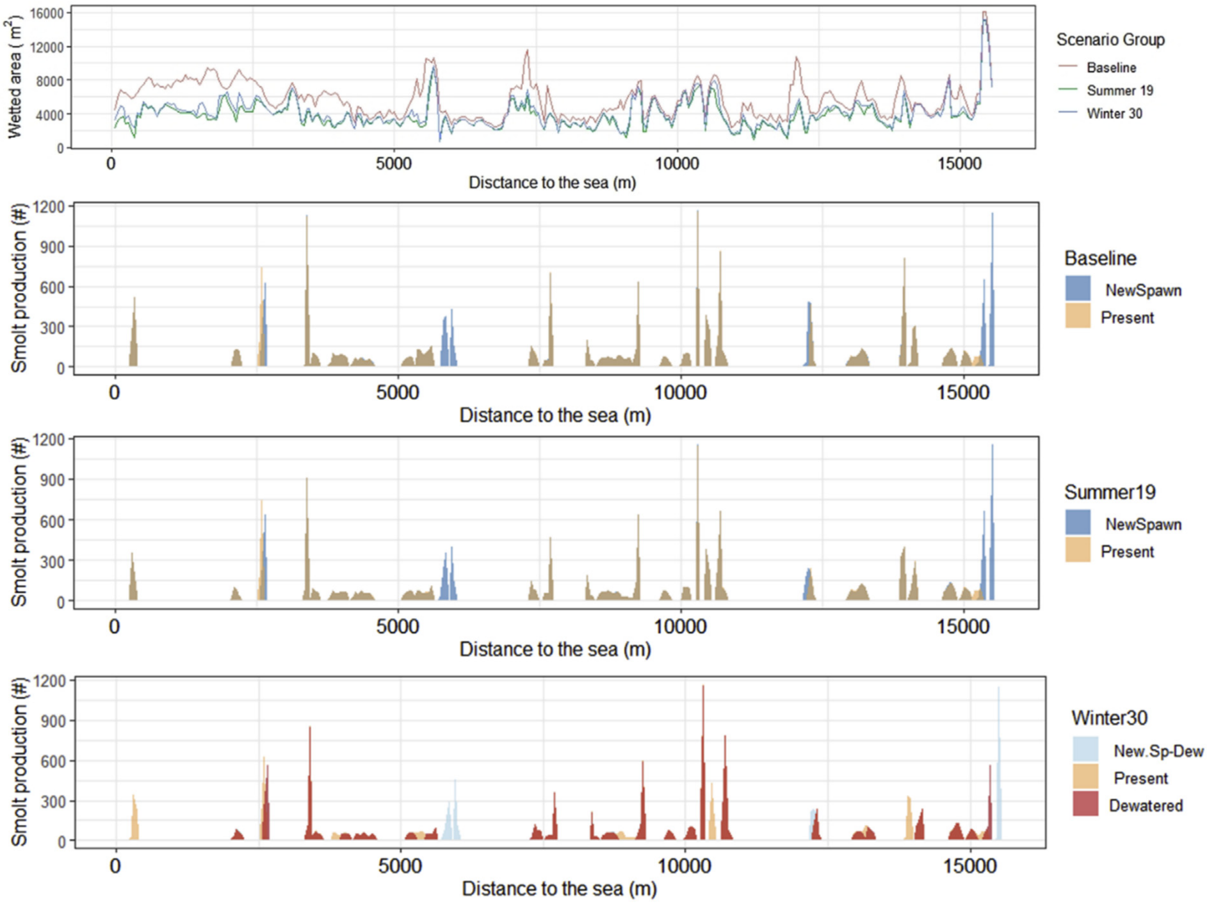

Fig. 9. Wetted area and smolt production per section of the modelled river reach under *Baseline*, *Summer 19* and *Winter 30* scenarios groups, see Fig. 4 for description of the scenario groups.

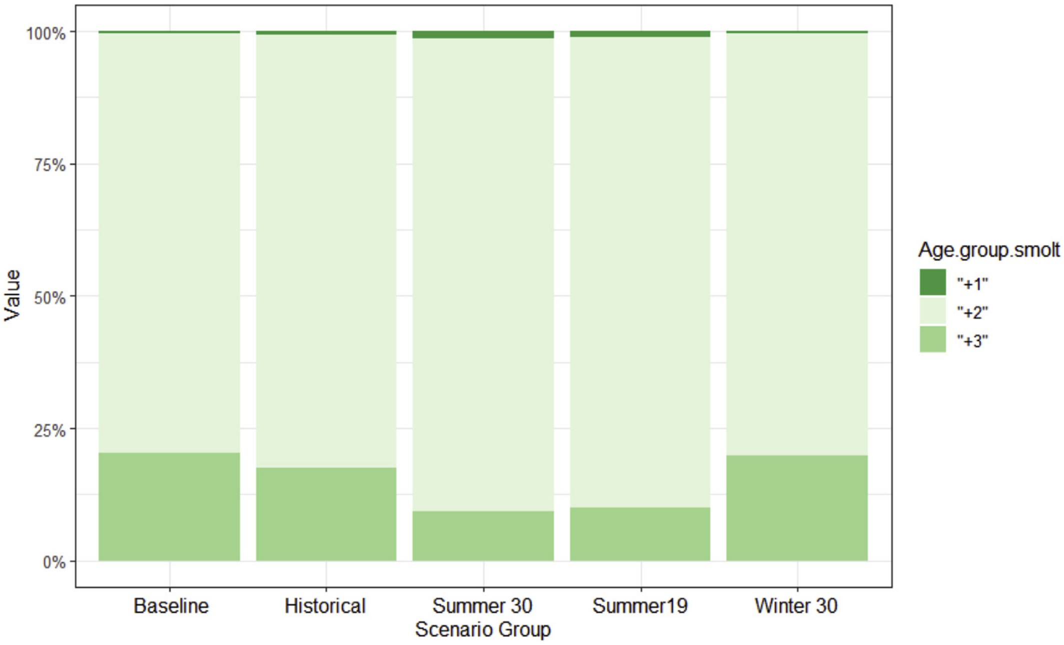

Fig. 10. Age distribution of smolt production under each scenario group.

model used in this study to evaluate dewatered spawning sites was shown to adequately predict dewatered areas. The results were also corroborated in stakeholder meetings, confirming both human perceptions and actual measured observations. Based on this, the integrated approach has shown the potential to adequately predict salmon population abundance and hydraulic conditions.

Model results demonstrated a sharp decrease in wetted areas during flows less than 30 $m^3 s^{-1}$. Under these conditions the proportion of dewatered spawning sites increased, meaning that the minimum flow of 30 $m^3 s^{-1}$ specified for the river is adequate and should be maintained in order to preserve sustainable populations of Atlantic salmon. A reduction in wetted area of 30% under *Winter 30 Present* decreased smolt production by 17%. The same percentage reduction in wetted area (30%) decreased smolt production for *Summer 30 Present* scenario by only 8%. Despite winter flows showing a lowered smolt production, scenarios with 19 $m^3 s^{-1}$ and 30 $m^3 s^{-1}$ discharge during summer also reduced smolt production. Therefore, winter and summer low flows might be considered as the two most important hydrological bottlenecks in Ljungan River, which is in agreement with Forseth and Harby (2014) and the results from Adeva Bustos et al. (2017). The findings of the current study can be explained by the increase in juvenile density-dependent mortality as a function of reduction in wetted area in the IB-salmon model (see Hedger et al., 2013a). Forseth and Harby (2014) also identified winter and summer wetted area as a factor influencing salmon population abundance. At the same time, comparing the *Historical* scenario group with the *Baseline* scenario group showed that an increase in the winter discharge due to regulation could result in increased wetted area and reduced juvenile mortality. These results are in agreement with Johnsen et al. (2011) who reported higher juvenile survival from higher and more stables winter flows in a Norwegian regulated river.

Allowing for the dewatered spawning sites in *Winter 30 Dewatered* resulted in a reduction of smolt production by 30%. This is related to the number of spawning sites being dewatered with a modelled minimum discharge of 30 $m^3 s^{-1}$. It is important to highlight however that groundwater effects on egg survival reported in previous studies (see Casas-Mulet et al. (2015) and Salveit et al. (2001)) were not considered in this study. Forseth and Harby (2014) indicated that a 7-day period with a minimum winter flow lower than the flow during the previous year's spawning period may be a bottleneck for the salmon population. In some years of the observed discharge regime of the Ljungan River, 7-day minimum flows in winter showed lower discharges than the previous spawning season, so this is a potential bottleneck. Reducing the flow during the spawning season to the minimum flow level during winter may therefore be an efficient mitigation measure to reduce mortality on eggs and the early life-stage of salmonids (see Casas-Mulet et al., 2016).

Lower river discharges also increased water temperature. Parr body mass growth was positively related with temperature and given that a critical body size was required for smoltification, higher temperatures led to earlier smoltification, with a consequent skewing of the parr age distribution to being composed of younger parr. This is consistent with the findings of Sundt-Hansen et al. (2018). Results in this study do not show large differences among the two summer scenario groups, which could be explained by the negligible temperature differences ($\approx 0.2\,^{\circ}C$) between them. Temperature increases in summer between summer scenario groups (*Summer* 19 and *Summer 30*) over those of the *Baseline* scenario group were approximately 3 °C. Increased temperatures could result in a shorter total period of parr density dependent mortality (between parr recruitment and smoltification) and thus could lead to higher smolt production. However, this effect can be cancelled out by the mortality produced by reduction in wetted areas as described by Sundt-Hansen et al. (2018).

Restoration of spawning sites are conventional compensation actions in regulated river systems. Such work has been demonstrated to be effective even under suboptimal depth and velocity conditions in five Norwegian rivers (Barlaup et al., 2008) and is widely applied from a cost-benefit approach. In Ljungan River, the hydrological bottlenecks identified under critical flows can be mitigated by restoring spawning sites. The increase in total spawning area resulted in elevated smolt production compared to the *Baseline* scenario group. This indicates that the availability of spawning sites can be a limiting factor for the population. Following the adaptive management approach, with a focus on objectives, actions, monitoring and evaluating, future monitoring in the Ljungan River will allow the evaluation of the efficiency of adding spawning sites based on experimental data. Total smolt production under the *Baseline NewSpawn* scenario was 21 000 smolts, similar to the 20 000 smolts predicted by Uusitalo et al. (2005) using a probabilistic salmon production capacity model built on expert knowledge, suggesting that the addition of spawning sites is an effective method of maximizing production. Our study also supports the importance of involving stakeholders with valuable local knowledge about the river in the planning phase, considering mitigation measures and adapting these to specific discharge levels to avoid dewatering in low flow conditions.

The addition of spawning sites may have positive effects on salmon production while dewatering may have negative effects. However, salmon production may also be affected by other factors, such as the spatial configuration of river habitat characteristics (Kocik and Ferreri, 1998; Poff and Huryn, 1998; Kim and Lapointe, 2011). In our model, dewatered areas in low discharges were found in segments with a wide range of salmon production potential. New spawning sites were added in segments classified as areas with moderate to large production potential. However, this classification could change when the spatial configuration of dewatered areas and new spawning sites is considered. Potential bottlenecks arising from a lack of spatial connection between spawning habitat (which would provide initial parr recruitment) and habitat with a high parr carrying capacity (which could potentially be dewatered) were simulated since the model implicitly simulates spatial processes via the density dependent emigration of parr from areas of high parr abundance.

This study contributes to the understanding of the constraints affecting an Atlantic salmon population in a Swedish regulated river system. It demonstrates the potential of using an integrating modelling approach that combines physical and biological components to identify possible bottlenecks and predict the effects of implementing mitigation measures. Furthermore, the cooperation between the stakeholders' group formed by the hydropower company, the county officer, national authorities, local and national NGO's and research institutes has benefitted the analyses in this study, providing useful inputs and data. The importance of involving stakeholders at an early stage in projects related to river restoration and preservation of environmental conditions is of vital importance and a success key, both from a perception point of view and from the value of incorporating local knowledge. The implementation of modelling scenarios conducted in this study could also be of benefit for hydropower mitigation measures and other projects requiring evaluation, as an alternative to long-term and costly monitoring studies.

5. Conclusion

In this study, low winter and summer discharges were identified as key hydrological bottlenecks because they reduced wetted area and increased juvenile Atlantic salmon density dependent mortality. In addition, winter low flows reduced juvenile Atlantic salmon recruitment via dewatering of spawning sites. The presently agreed upon specified minimum flow in Ljungan River (30 $m^3 s^{-1}$) was shown to be the critical flow in our analyses, and special attention should be paid to summer low flows to avoid flows below 30 $m^3 s^{-1}$. This study has shown the potential of integrating modelling tools – including a salmon population model and a hydraulic model – to investigate the response of a salmon population to modifications of discharge and spawning habitat. This approach can aid in identifying bottlenecks affecting fish populations and provide support for decisions on environmental mitigation measures. The method was developed for a specific river in this study but could be applied to other regulated rivers to investigate possible bottlenecks for Atlantic salmon populations and to predict the effect of implementing mitigation measures.

Acknowledgements

This work was supported by Norwegian University of Science and Technology (NTNU) under a strategic scholarship awarded to the Centre of Environmental Design of Renewable Energy funded by the Norwegian Research Council. In addition, Statkraft AB in Sweden has also financially supported this study. We would like to thank Johan Kristofers and Ingrid Alne (Department of Civil and Environmental Engineering, NTNU) for supporting us with background information about Ljungan River. We also thanks Angela Odelberg, Kenneth Ottosson, Leo Oras, Helge Skoglund, Björn Norell and the rest of the members in the stakeholders' group in Ljungan, for providing support, relevant data and help in corroborating and discussing the results presented in this study.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envsoft.2019.104494.

Appendix

Table A1
Smolt production (× 1000) statistics under each scenario with *Present, New.Sp-Dew* and Dewatered Conditions. * Indicate scenarios in which *NewSpawn* instead of *New.Sp-Dew* are considered.

		Baseline*	Historical	Summer 19*	Summer 30*	Winter 30
min	Present	14.56	14.08	12.69	13.33	12.08
	New.Sp-Dew	17.79	13.22	15.54	16.29	10.19
	Dewatered		15.48			12.29
max	Present	17.46	16.87	15.60	16.06	14.37
	New.Sp-Dew	21.37	15.66	19.08	19.34	12.00
	Dewatered		18.61			14.84
range	Present	2.90	2.79	2.91	2.73	2.29
	New.Sp-Dew	3.58	2.45	3.54	3.05	1.81
	Dewatered		3.13			2.55
sum	Present	392.24	385.73	342.01	360.23	322.71
	New.Sp-Dew	476.56	356.72	417.30	438.48	270.66
	Dewatered		423.17			334.29
mean	Present	16.34	16.07	14.25	15.01	13.45
	New.Sp-Dew	19.86	14.86	17.39	18.27	11.28
	Dewatered		17.63			13.93
std.dev	Present	0.78	0.66	0.59	0.56	0.59
	New.Sp-Dew	1.06	0.62	0.73	0.65	0.51
	Dewatered		0.80			0.67

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