*Science of the Total Environment*

# Hydropower impacts on reservoir fish populations are modified by environmental variation

Antti P. Eloranta [a,*], Anders G. Finstad [a,b], Ingeborg P. Helland [a], Ola Ugedal [a], Michael Power [c]

[a] Department of Aquatic Ecology, Norwegian Institute for Nature Research (NINA), P.O. Box 5685 Torgard, NO-7485 Trondheim, Norway

[b] Centre for Biodiversity Dynamics, Department of Natural History, NTNU University Museum, Erling Skakkes gate 47A, NO-7013 Trondheim, Norway

[c] Department of Biology, University of Waterloo, 200 University Avenue West, Waterloo, Ontario, Canada

E-mail addresses:
Antti P. Eloranta: antti.eloranta@nina.no
Anders G. Finstad: anders.finstad@ntnu.no
Ingeborg P. Helland: ingeborg.helland@nina.no
Ola Ugedal: ola.ugedal@nina.no
Michael Power: m3power@uwaterloo.ca

[*] Corresponding author: *E-mail address*: antti.eloranta@nina.no (A.P. Eloranta)

*Abbreviations:*
WLR, water level regulation; NDVI, normalized difference vegetation index; A, surface area; SD, shoreline development; SL, surrounding terrain slope; *FC*, fish community; *T*, mean July air temperature; *GS*, gillnet series; *ST*, stocking of brown trout.

# Abstract

Global transition towards renewable energy production has increased the demand for new and more flexible hydropower operations. Before management and stakeholders can make informed choices on potential mitigations, it is essential to understand how the hydropower reservoir ecosystems respond to water level regulation (WLR) impacts that are likely modified by the reservoirs' abiotic and biotic characteristics. Yet, most reservoir studies have been case-specific, which hampers large-scale planning, evaluation and mitigation actions across various reservoir ecosystems. Here, we investigated how the effect of the magnitude, frequency and duration of WLR on fish populations varies along environmental gradients. We used biomass, density, size, condition and maturation of brown trout (*Salmo trutta* L.) in Norwegian hydropower reservoirs as a measure of ecosystem response, and tested for interacting effects of WLR and lake morphometry, climatic conditions and fish community structure. Our results showed that environmental drivers modified the responses of brown trout populations to different WLR patterns. Specifically, brown trout biomass and density increased with WLR magnitude particularly in large and complex-shaped reservoirs, but the positive relationships were only evident in reservoirs with no other fish species. Moreover, increasing WLR frequency was associated with increased brown trout density but decreased condition of individuals within the populations. WLR duration had no significant impacts on brown trout, and the mean weight and maturation length of brown trout showed no significant response to any WLR metrics. Our study demonstrates that local environmental characteristics and the biotic community strongly modify the hydropower-induced WLR impacts on reservoir fishes and ecosystems, and that there are no one-size-fits-all solutions to mitigate environmental impacts. This knowledge is vital for sustainable planning, management and mitigation of hydropower operations that need to meet the increasing worldwide demand for both renewable energy and ecosystem services delivered by freshwaters.

**Keywords**: anthropogenic disturbance; hydroelectricity; lake ecosystem; population dynamics; renewable energy; salmonid

# 1. Introduction

Climate change, acidification and other environmental problems associated with the use of fossil fuels have increased the demand and the need for renewable energy sources worldwide (Dincer, 2000; IEA, 2012). Hydropower is among the most rapidly growing sources of renewable energy and high numbers of new hydropower plants are being constructed, particularly in Asia, Africa and Latin America (Winemiller et al., 2016). Simultaneously, the demand for more flexible energy generation and storage, e.g. to balance wind and solar power production, creates a need to adapt existing hydropower operations to new technologies and energy markets (Kumar et al., 2011; IEA, 2012). Although commonly considered as green energy, hydropower operations can cause severe environmental problems upstream and downstream of the power plant, including decreased habitat quality and quantity (Kumar et al., 2011; Zohary and Ostrovsky, 2011; Gibeau et al., 2016). Freshwaters and their shore zones provide vital aesthetic, cultural, economic and provisioning ecosystem services (Strayer and Findlay, 2010). Moreover, freshwaters are experiencing declines in biodiversity far greater than most other ecosystems (Dudgeon et al., 2006). To develop a transition towards sustainable renewable energy sources with minimal or predictable environmental consequences, knowledge-based, best practice management of hydropower operations that limit environmental impacts and associated societal conflicts are vital (e.g. Jager and Smith, 2008).

Reservoirs, upstream of hydropower production facilities, commonly have a water level regulation (WLR) regime that differs from natural water level fluctuations in terms of magnitude, frequency, duration and/or timing (Zohary and Ostrovsky, 2011; Hirsch et al., 2014; Fig. 1). Improved understanding of how these different WLR regimes can affect reservoir ecosystems and their biotic communities is a prerequisite for the sustainable development of hydropower operations. In reservoir ecosystems, the typical and most evident impacts of WLR are the impaired physical and biological status of the shallow littoral zone, which suffers from increased desiccation, freezing and erosion (Lindström, 1973; Carmignani and Roy, 2017; Hirsch et al., 2017). The altered physical and chemical conditions in hydropower reservoirs are typically reflected in the biotic communities ranging from primary producers to top predators (e.g. Hellsten and Riihimäki, 1996; Aroviita and Hämäläinen, 2008; Zohary and Ostrovsky, 2011). For instance, WLR has been observed to lead to decreased density and diversity of benthic invertebrates (Evtimova and Donohue, 2014), to a long-term decline in fish yield in several alpine reservoirs (Aass et al., 2004; Milbrink et al., 2011), and to a niche shift from littoral towards more pelagic resource use by fish (Freedman et al., 2014; Eloranta et al., 2016a). All the above-mentioned processes associated with WLR impacts can vary along gradients in reservoir morphometry, biological productivity and/or community composition. Although there is a growing body of evidence for hydropower impacts on reservoir ecosystems (see the reviews by Cott et al., 2008; Zohary and Ostrovsky, 2011; Carmignani and Roy, 2017; Hirsch et al., 2017), most previous studies are case-specific and often lack data on water levels. This has hampered prioritization of mitigation actions as well as the holistic governance of hydropower operations across different spatial scales (Hirsch et al., 2017).

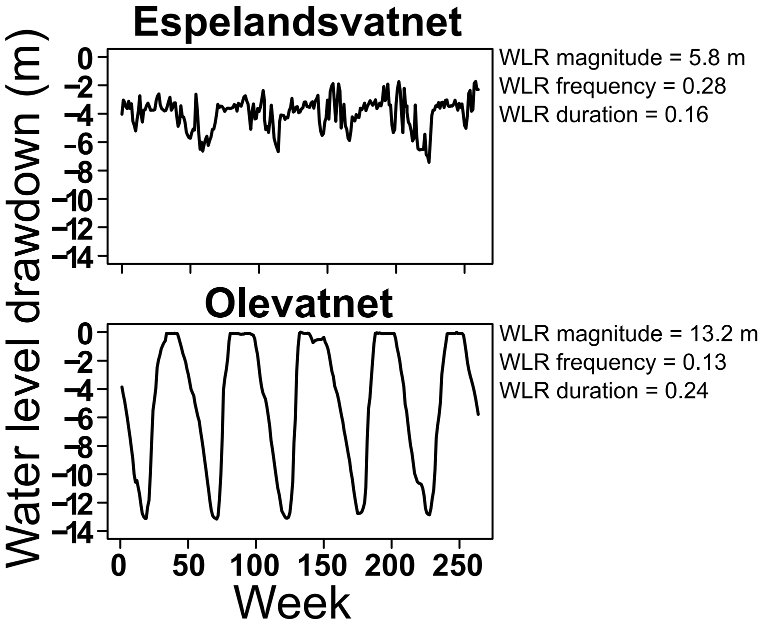


**Fig. 1.** Examples of contrasting five-year WLR patterns in two Norwegian hydropower reservoirs, plotted as the mean weekly deviance from the 10-year maximum water level. Espelandsvatnet (surface area 1.2 km$^2$) is subjected to frequent and irregular WLR, whereas more gradual, higher-magnitude WLR with extensive low water level periods occur in Olevatnet (surface area 2.4 km$^2$). Espelandsvatnet hosts a relatively dense population of small brown trout, whereas Olevatnet hosts a relatively low abundance of brown trout (density = 38 *versus* 2 fish 100 m$^{-2}$ night$^{-1}$; mean weight = 80 *versus* 181 g; mean length of mature females = 232 *versus* 355 mm).

Norway is among the largest hydropower producers in the world (Kumar et al., 2011; IEA, 2012). The high number of Norwegian reservoirs with variable environmental characteristics and operational regimes (WLR patterns), but species-poor communities, provides an under-utilized opportunity to evaluate hydropower impacts on reservoir fish populations and ecosystems. Such knowledge would facilitate science-based regulation and mitigation of hydropower operations, thereby helping to meet the demands for green energy and sustainable use of natural resources. To the best of our knowledge, no previous studies have utilized large datasets to investigate the environmental effects of hydropower operations varying in the magnitude, frequency and duration of WLR, or to test how these effects interact with reservoir environmental characteristics (cf. Carmignani and Roy, 2017; Hirsch et al., 2017).

Here, we study how hydropower operations (WLR) interact with environmental parameters to affect brown trout (*Salmo trutta*) populations in Norwegian reservoirs. The aim is to identify the key WLR-affected and natural environmental factors that control fish biomass, density, size, condition and maturation in hydropower reservoirs. Brown trout was chosen as the focal study species, because it is the dominant fish species in many Norwegian reservoirs and because generalist salmonids are known to reflect the overall productivity and changes in physical and biological status of lakes (e.g. Milbrink et al., 2011; Finstad et al., 2014). Moreover, public concerns are typically related to the potential negative impacts of hydropower operations on commercially and recreationally important fishes. A recent study of 283 Norwegian lakes demonstrated that brown trout were generally less abundant in lakes regulated for hydropower production, indicating negative impacts on recruitment and growth of this predominantly littoral fish species (Eloranta et al., 2016b). The effects of lake morphometric and climatic characteristics on brown trout abundance were also shaped by the local fish community structure likely due to competitive and predatory interactions (Eloranta et al., 2016b). Therefore, we hypothesize that hydropower induced WLR would have negative impacts on brown trout populations (i.e., decreased biomass, density, size and condition) but that the effects would be modified by natural environmental drivers, mainly fish community structure, lake morphometry and climatic conditions.

## 2. Material and methods

### 2.1. Fish data

As response variables for our analyses, we used data derived from fish surveys conducted in 102 Norwegian hydropower reservoirs in 1973–2009. The study reservoirs were originally natural lakes dammed for hydropower production and hence they do not include artificial or fluvial-like ecosystems with run-of-the-river power plants. From each reservoir, only fish data from a single sampling event performed in the late open-water season, i.e. between late July and early October, were included (see Eloranta et al., 2016b for more details). All reservoirs were fished with either standardized Nordic multi-mesh gillnets (30 × 1.5 m) with mesh sizes from 5 to 55 mm (Appelberg et al., 1995) or Jensen gillnet series consisting of eight nets (25 × 1.5 m) with knot-to-knot mesh sizes from 21 to 52 mm (Jensen, 1977). Salmonid food consumption and growth rates are density dependent and thus reduced population sizes are often associated with improved growth and condition of individuals (e.g. Amundsen et al., 2007; Persson et al., 2007). Therefore, we aimed to include data on brown trout that reflected different aspects of the fish populations and individuals within. The fish data obtained from all reservoirs included biomass, density and mean weight (wet mass, ± 1 g). For biomass and density, we used the total weight and number of brown trout caught per 100 $m^2$ gillnet area per night as proxies (Table 1). Brown trout biomass can reflect the overall biological productivity of the reservoir ecosystem (cf. Finstad et al., 2014), whereas density indicates recruitment success. Mean weight was used as a measure of population size structure. In addition, data on mean condition (estimated as Fulton's condition factor) and mean total length (± 1 mm) of mature female brown trout were obtained from subsets of the study reservoirs (Table 1). These variables were expected to reflect potential WLR impacts on the nutritional status and life history strategy of individuals. As presented in Table 1, the brown trout populations showed marked variation in estimated biomass (168–3706 g 100 m$^{-2}$ net night$^{-1}$), density (1–42 individuals 100 m$^{-2}$ net night$^{-1}$), mean weight (50–727 g), mean condition (0.88–1.22) and mean total length of mature females (220–367 mm). See Eloranta et al. (2016b) and references therein for more details of survey fishing methods and data sources.

**Table 1.** Summary table of the response and predictor variables included in the linear models. NDVI, normalized difference vegetation index; WLR, water level regulation.

| Parameter | *n* | Mean | SD | Min | Max |
|---|---|---|---|---|---|
| ***Response*** | | | | | |
| Biomass (g 100m$^{-2}$ night$^{-1}$) | 102 | 1168 | 761 | 168 | 3706 |
| Density (n 100m$^{-2}$ night$^{-1}$) | 102 | 10 | 9 | 1 | 42 |
| Mean weight (g) | 102 | 144 | 86 | 50 | 727 |
| Mean condition | 90 | 1.02 | 0.08 | 0.88 | 1.22 |
| Mean maturity length (mm) | 43 | 289 | 35 | 220 | 367 |
| ***Predictor*** | | | | | |
| Surface area (km$^2$) | 102 | 8 | 16 | 0.2 | 122 |
| Terrain slope (%) | 102 | 9.7 | 4.2 | 3.1 | 26.9 |
| Shoreline development | 102 | −0.04 | 0.27 | −0.54 | 0.75 |
| NDVI | 102 | 113 | 9 | 99 | 134 |
| Mean July air temperature (°C) | 102 | 8.7 | 2.7 | 3.5 | 14.6 |
| WLR magnitude | 102 | 18 | 15 | 1 | 76 |
| WLR frequency | 102 | 0.18 | 0.07 | 0.04 | 0.31 |
| WLR duration | 102 | 0.18 | 0.06 | 0.01 | 0.29 |

## 2.2. Environmental data

As predictor variables, we included measures of lake morphometry, productivity, climate, fish community composition and water level fluctuations (Table 1). The morphometric data included reservoir surface area (A, km$^2$), shoreline development (SD) and surrounding terrain slope (SL). To avoid autocorrelation associated with commonly used measures of lake shape (Wetzel, 2001), we estimated shoreline development as residuals from the linear regression between reservoir area and shoreline length, with negative and positive values indicating particularly circular and reticulate reservoirs. Terrain slope along the reservoir shoreline was used as a proxy for depth since no bathymetric data were available for most reservoirs. The estimate is given in percentages and has been successfully applied in previous studies on Norwegian lakes and fish populations (cf. Finstad et al., 2014; Eloranta et al., 2016b).

Data on averaged Normalized Difference Vegetation Index (NDVI) and mean July air temperature ($T$, °C) were used as proxies for lake productivity and climate, respectively (see Finstad et al. 2014 for a detailed description). In brief, NDVI data were obtained as monthly averages (1992–1993) at 480 m resolution from the US Geological Survey Eurasia Land Cover Characteristics database (http://edc2.usgs.gov./glcc/). Mean July temperatures were extracted for the lake surface using normal (long-term average for the period 1961–1990) temperature grids at 1 km resolution obtained from the Norwegian Meteorological Institute (Tveito et al., 2000). Reservoir altitude (ranging from 24 to 1477 m a.s.l.) was not included as a predictor variable due to its high negative correlation with NDVI ($r = –0.64$) and mean July air temperature ($r = –0.98$). Furthermore, the effects of altitude on water temperature and productivity in Norwegian lakes are shaped by the large latitudinal gradient, ranging here between 59–64°N. For example, lakes at the same altitude are generally much colder and less productive at high latitudes as compared to low latitudes.

Fish community ($FC$), measured as the presence or absence of sympatric fish species, was included as an explanatory variable to test for the potential effects of interspecific interactions on brown trout populations. Brown trout was the only fish species present in 69 of the study reservoirs. In most sympatric fish communities, brown trout coexisted with minnow (*Phoxinus phoxinus*; $n = 23$), Arctic charr (*Salvelinus alpinus*; $n = 18$), perch (*Perca fluviatilis*; $n = 9$) and/or whitefish (*Coregonus lavaretus*;

*n* = 6), the first two species being both potential competitors and prey fishes for brown trout (e.g. Museth et al., 2007; Helland et al., 2011; Sánchez-Hernández et al., 2017).

## 2.3. Water level data

The water level data for the selected reservoirs were obtained from a database managed by the Norwegian Water Resources and Energy Directorate (www.nve.no; Table 1, Fig. 1). Prior to calculation of WLR metrics, all daily water level values were transformed to weekly mean values because only weekly water level measurements were available for a large number of reservoirs (*n* = 38). Only reservoir water level data from a maximum of ten years prior to test fishing were included. This time period is sufficiently long to capture WLR impacts on adult brown trout of catchable size that typically vary in age between 3 and 10 years. In some cases (*n* = 20), some years were excluded from the 10-year time series due to poor or missing water level data. We calculated WLR metrics that were expected to affect brown trout populations and captured the important aspects of the WLR phenomenon (e.g. Olden and Poff, 2003): (1) maximum regulation amplitude; (2) relative proportion of weeks with a sudden rise or drop in water level; and (3) the relative proportion of weeks with exceptionally low water levels. Combined these variables capture the magnitude, frequency and duration aspects of WLR impacts on reservoir resident fishes and are henceforth termed as: (1) WLR magnitude, (2) WLR frequency, and (3) WLR duration (Table 1). The metrics for WLR frequency and duration were computed using the relative instead of the absolute number of weeks because of the varying lengths of time series data from each of the study reservoirs. Corresponding to the problem of choosing parameters for describing river flow regimes (e.g. Olden and Poff, 2003), the choice of parameters here was intended to explain the dominant proportion of statistical variation in the larger set of possible WLR metrics and to minimize potential multicollinearity within the considered dataset.

For each reservoir, the WLR magnitude was calculated as the difference between the observed maximum and minimum weekly water levels. The WLR frequency was calculated as the relative proportion of weeks when absolute weekly water level change showed a peak (i.e., sudden rise or drop), using the findPeaks function in the quantmod package v. 0.4-7 (Ryan, 2016) in R v. 3.3.0 (R Core Team, 2016). The WLR duration was calculated as the proportion of weeks when the water level was below a defined low water level threshold. The threshold was measured as one standard deviation subtracted from the long-term average water level (i.e., mean – 1SD). The WLR magnitude metric was expected to indicate how much of the littoral zone was affected by WLR. The WLR frequency metric was expected to reflect the incidence of WLR, with peaking WLR likely having negative impacts on brown trout and their littoral prey organisms. In contrast, the WLR duration metric was expected to capture the temporal aspects of WLR since it reflects the duration of the low water level period and the length of time that only a fraction of the whole lake littoral zone is wetted and inhabitable for littoral organisms, including brown trout. Overall, the 102 study reservoirs showed marked variation in hydropower operations, with the maximum regulation amplitude (WLR magnitude) ranging from 1–76 m and the relative proportion of weeks with a sudden drop or rise in water level (WLR frequency) or exceptionally low water level (WLR duration) ranging from 0.04–0.31 and 0.01–0.29, respectively (Table 1).

Prior to modelling, brown trout biomass, density and mean weight, reservoir area and WLR magnitude were ln-transformed to normalize the data (Fig. A1). All variables were standardized to zero mean and one unit standard deviation to facilitate comparison of parameter coefficients and the evaluation of explanatory variable importance in the models.

## 2.4. Statistical modelling

We tested for the responses of brown trout populations to different WLR patterns, reservoir morphometric and climatic characteristics by model comparison using the MuMin package v. 1.15.1 (Barton, 2015) in R v. 3.3.0 (R Core Team, 2016). Each initial full model included one of the brown trout population characteristics as the response variable and one of the three WLR metrics, the reservoir characteristics (A, SD, SL, NDVI and fish community) as well as the two-way interactions between the WLR metric and the different reservoir characteristics as explanatory variables (Table 1). Since there were no clear top-ranked candidate models (Table B1), we applied Akaike weight-based averaging over the 95% confidence model set (i.e., cumulative AIC weights of models ≥0.95) to estimate coefficients for the candidate models as well as their 95% confidence intervals. The relative influence (RI) of each variable was given as the summation of AIC weights across all models including that variable in the 95% confidence model set (Johnson and Omland, 2004). Fish community (*FC*), gillnet series [*GS*; Nordic ($n$ = 43) *versus* Jensen ($n$ = 59)], brown trout stocking [*ST*; absent ($n$ = 55) *versus* present ($n$ = 47)] and mean July air temperature (*T*) variables were regarded as controlling variables (*sensu* Freckleton 2002) that *a priori* were assumed to have an effect on our response variables (see Eloranta et al., 2016b). The main effect of these variables were entered as fixed variables and retained in all compared candidate models to make the model selection more tractable. Mean July air temperature (*T*) was not included in the two-way interactions due to its high correlation with NDVI ($r$ = 0.72;

Fig. A1) but was entered as an explanatory variable to account for potential temperature effects not captured by NDVI.

We also tested for potential quadratic relationships between WLR metrics and brown trout population responses by comparing models with linear and quadratic terms to models with only linear terms. Some evidence ($\Delta$AIC = -4.5) was found for a quadratic, U-shaped relationship between WLR magnitude and brown trout density. This was also evident with visual inspection of the data (Fig. 2). No other evidence was found to support quadratic relationships between any of the other considered variables ($\Delta$AIC > –1.6). When modelling the effects of WLR magnitude on brown trout density the final models included only linear terms of WLR magnitude. Thus, quadratic terms were *a priori* excluded for parsimony to restrict the number of explanatory variables and avoid unnecessary complexity.

Finally, we conducted statistical testing and visual inspection of final model residuals. There was no evidence for non-normality, heteroscedasticity, nonlinear relationships or spatial autocorrelation, except in one reservoir where exceptionally large brown trout (mean weight = 727 g) caused slightly non-normal residual distributions for mean weight models. Exclusion of this reservoir did not change the modelling results and therefore it was retained in all analyses.

## 3. Results

Brown trout populations showed different responses to the magnitude, frequency and duration aspects of WLR. While the WLR magnitude (Table 2) and WLR frequency (Table 3) had notable impacts, WLR duration had no significant effects on brown trout (Table C1, Fig. A1). The WLR impacts were most evident when using brown trout density and condition as measures of population status and occasionally when using biomass (Table C1, Fig. A1). In contrast, we found no clear effects of WLR on brown trout mean weight or female maturity length, although brown trout tended to become smaller with increasing WLR frequency (Table C1, Fig. A1).

### 3.1. WLR magnitude effects

We found support for our hypothesis that WLR affects brown trout populations, with some WLR effects modified by local conditions (Table 2, Fig. 2a–e). The effects of WLR magnitude on brown trout biomass, density and condition were modified by the reservoir morphometry and fish community composition (Table 2, Fig. 2a–e). Overall, reservoir morphometry interacted with WLR magnitude when using biomass (Fig. 2a), density (Fig. 2c–d), or mean condition (Fig. 2e) as a measure of brown trout population status, although morphometric characteristic (e.g. area, shoreline development) that modified the measured biological response varied (Table 2). Contrary to the hypothesized negative impacts, brown trout biomass increased with WLR magnitude in reservoirs with large surface area (Fig. 2a). Correspondingly, the positive relationship between WLR magnitude and brown trout density was particularly evident in reservoirs with complex shorelines (Fig. 2c) and large surface area (Fig. 2d). Fish community composition had a stronger interacting effect on brown trout density than the reservoir morphometric characteristics (Table 2). Brown trout density increased with increasing WLR magnitude in allopatric reservoirs, whereas the opposite pattern was observed in reservoirs inhabited by sympatric fishes (Fig. 2b, Table 2). Finally, the negative relationship between WLR magnitude and brown trout condition was particularly evident in deep reservoirs with steep terrain slope (Fig. 2e).

**Table 2.** Summary of the water level regulation (WLR) magnitude effects on brown trout populations. The results are based on model averaging of fixed effects in the 95% confidence model set (cumulative AIC weights $\geq 0.95$) with brown trout biomass, density and mean condition as response variables and WLR magnitude and reservoir environmental characteristics as predictor variables. Parameter estimates (on standardized scale) are interpretable as effect size because they describe changes in units of standard deviation of the original variable. Standard error (SE), relative importance (IR) and 95% confidence intervals (CI) for each parameter are shown, with significant parameters highlighted in bold. Besides WLR magnitude, the predictor variables included reservoir area (A, ln-transformed), shoreline development (SD), terrain slope (SL), Normalized Difference Vegetation Index (NDVI, ln-transformed) and their two-way interactions with WLR magnitude, as well as fish community composition (*FC*), gillnet series (*GS*), stocking of brown trout (*ST*), and mean July air temperature (*T*) as fixed explanatory variables.

***WLR magnitude effects on brown trout***

| Parameter | Estimate | SE | IR | -95% CI | +95% CI |
|---|---|---|---|---|---|
| **Biomass** | | | | | |
| **Intercept** | **0.44** | **0.20** | **-** | **0.04** | **0.84** |
| WLR | 0.19 | 0.15 | 0.91 | -0.10 | 0.49 |
| A | 0.08 | 0.13 | 0.74 | -0.17 | 0.33 |
| SD | -0.13 | 0.11 | 0.69 | -0.34 | 0.08 |
| SL | 0.03 | 0.12 | 0.33 | -0.21 | 0.27 |
| NDVI | 0.00 | 0.19 | 0.40 | -0.37 | 0.37 |
| **WLR:A** | **0.25** | **0.10** | **0.66** | **0.04** | **0.45** |
| WLR:SD | 0.23 | 0.12 | 0.52 | 0.00 | 0.47 |
| WLR:SL | 0.01 | 0.10 | 0.07 | -0.19 | 0.21 |
| WLR:NDVI | 0.19 | 0.15 | 0.19 | -0.10 | 0.48 |
| WLR:*FC* | -0.46 | 0.34 | 0.47 | -1.13 | 0.22 |
| *FC* | -0.27 | 0.31 | 1.00 | -0.89 | 0.36 |
| *T* | 0.10 | 0.17 | 1.00 | -0.24 | 0.45 |
| *GS* | -0.49 | 0.28 | 1.00 | -1.05 | 0.06 |
| *ST* | -0.25 | 0.25 | 1.00 | -0.74 | 0.24 |
| **Density** | | | | | |
| **Intercept** | **0.57** | **0.18** | **-** | **0.22** | **0.91** |
| **WLR** | **0.29** | **0.13** | **1.00** | **0.03** | **0.55** |
| A | 0.01 | 0.11 | 0.93 | -0.20 | 0.23 |
| **SD** | **-0.20** | **0.09** | **0.99** | **-0.38** | **-0.03** |
| SL | 0.04 | 0.10 | 0.52 | -0.16 | 0.25 |
| NDVI | -0.04 | 0.17 | 0.42 | -0.38 | 0.29 |
| **WLR:A** | **0.25** | **0.09** | **0.91** | **0.08** | **0.43** |
| **WLR:SD** | **0.29** | **0.10** | **0.97** | **0.09** | **0.49** |
| WLR:SL | 0.13 | 0.09 | 0.31 | -0.04 | 0.31 |
| WLR:NDVI | 0.18 | 0.15 | 0.20 | -0.11 | 0.47 |
| **WLR:*FC*** | **-0.74** | **0.29** | **0.96** | **-1.32** | **-0.17** |
| *FC* | -0.42 | 0.27 | 1.00 | -0.95 | 0.11 |
| *T* | 0.16 | 0.15 | 1.00 | -0.14 | 0.47 |
| ***GS*** | **-0.73** | **0.24** | **1.00** | **-1.21** | **-0.25** |
| *ST* | -0.36 | 0.21 | 1.00 | -0.77 | 0.06 |
| **Mean condition** | | | | | |
| Intercept | 0.23 | 0.23 | - | -0.23 | 0.68 |
| WLR | -0.28 | 0.16 | 1.00 | -0.61 | 0.04 |
| A | 0.12 | 0.13 | 0.60 | -0.15 | 0.38 |
| SD | -0.08 | 0.10 | 0.41 | -0.28 | 0.13 |
| SL | 0.15 | 0.15 | 0.81 | -0.14 | 0.44 |
| **NDVI** | **0.52** | **0.21** | **0.96** | **0.09** | **0.94** |
| WLR:A | -0.18 | 0.11 | 0.36 | -0.40 | 0.05 |
| WLR:SD | -0.04 | 0.12 | 0.11 | -0.28 | 0.20 |
| **WLR:SL** | **-0.22** | **0.10** | **0.72** | **-0.41** | **-0.03** |
| WLR:NDVI | -0.08 | 0.15 | 0.30 | -0.37 | 0.21 |
| WLR:*FC* | 0.03 | 0.32 | 0.27 | -0.61 | 0.67 |
| *FC* | -0.32 | 0.33 | 1.00 | -0.98 | 0.33 |
| ***T*** | **-0.71** | **0.24** | **1.00** | **-1.19** | **-0.24** |
| *GS* | -0.30 | 0.32 | 1.00 | -0.93 | 0.33 |
| *ST* | -0.12 | 0.26 | 1.00 | -0.64 | 0.40 |

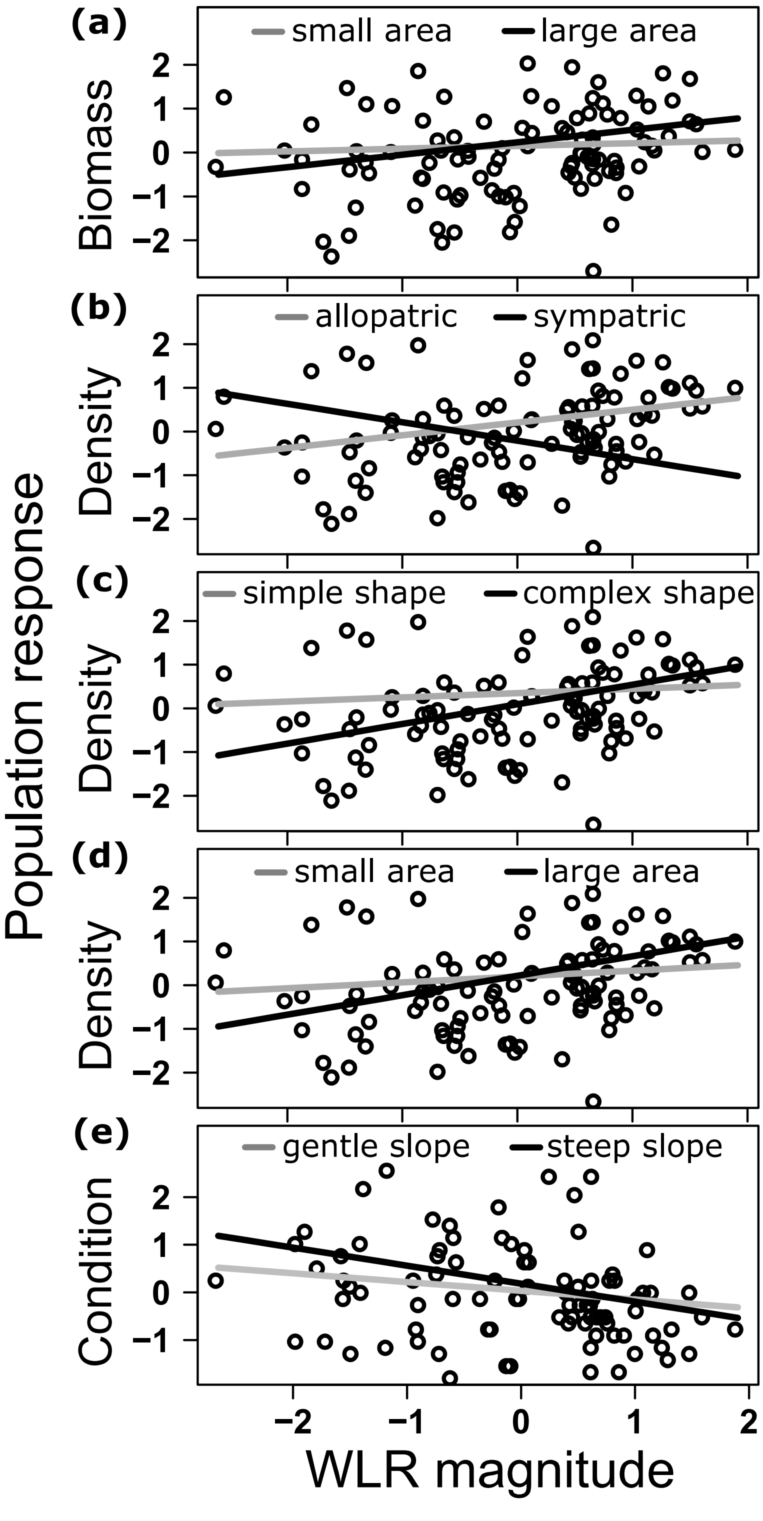


**Fig. 2.** The responses of brown trout (a) biomass, (b–d) density, and (e) condition to increasing water level regulation (WLR) magnitude. The lines present predicted regression values (parameter estimates in Table 2) for the significant two-way interactions, plotted after rerunning the final model using the first (grey line) and third (black line) quartiles of the explanatory variable interacting with WLR magnitude. The interacting explanatory variables include:

reservoir surface area (a & d), fish community composition (b), shoreline development (c) and terrain slope (e). Allopatric and sympatric refer to fish communities without or with coexisting fish species, respectively, whereas terrain slope is a proxy for reservoir depth. All modelled and presented data are standardized to have a mean of zero and a standard deviation of one. See Methods for more details of the used response and explanatory variables.

### 3.2. WLR frequency effects

The WLR frequency had significant effects on brown trout density and condition, and the impacts were not modified by the reservoirs' environmental characteristics (Table 3). Specifically, increasing WLR frequency was associated with increasing density (Fig. 3a) but decreasing condition of brown trout (Fig. 3b). When using mean condition as a measure of population status, other environmental variables like temperature and NDVI influenced brown trout more than either WLR magnitude or WLR frequency (see the parameter estimates in Table 2 and 3). In addition, gillnet series had a strong effect on brown trout density estimates (Table 2 and 3), because Nordic survey nets generally captured more brown trout than Jensen gillnet series.

**Table 3.** Summary of the water level regulation (WLR) frequency effects on brown trout populations. The results are based on model averaging of fixed effects in the 95% confidence model set (cumulative AIC weights $\geq 0.95$) with brown trout density and mean condition as response variables and WLR frequency as well as reservoir environmental characteristics as predictor variables. Parameter estimates (on standardized scale) are interpretable as effect size because they describe changes in units of standard deviation of the original variable. Standard error (SE), relative importance (IR.) and 95% confidence intervals (CI) for each parameter are shown, with significant parameters highlighted in bold. Besides WLR frequency, the predictor variables included reservoir area (A, ln-transformed), shoreline development (SD), terrain slope (SL), Normalized Difference Vegetation Index (NDVI, ln-transformed) and their two-way interactions with WLR frequency, as well as fish community composition (*FC*), gillnet series (*GS*), stocking of brown trout (*ST*), and mean July air temperature (*T*) as fixed explanatory variables.

***WLR frequency effects on brown trout***

| Parameter | Estimate | SE | IR | -95% CI | +95% CI |
|---|---|---|---|---|---|
| **Density** | | | | | |
| **Intercept** | **0.50** | **0.18** | **-** | **0.15** | **0.85** |
| **WLR** | **0.26** | **0.12** | **0.99** | **0.02** | **0.50** |
| A | 0.06 | 0.11 | 0.37 | -0.15 | 0.27 |
| SD | -0.11 | 0.09 | 0.59 | -0.29 | 0.07 |
| SL | 0.15 | 0.11 | 0.59 | -0.07 | 0.36 |
| NDVI | 0.04 | 0.19 | 0.63 | -0.34 | 0.41 |
| WLR:A | 0.07 | 0.11 | 0.30 | -0.15 | 0.29 |
| WLR:SD | 0.11 | 0.08 | 0.10 | -0.05 | 0.28 |
| WLR:SL | 0.05 | 0.10 | 0.17 | -0.15 | 0.25 |
| WLR:NDVI | 0.22 | 0.12 | 0.48 | -0.02 | 0.46 |
| WLR:*FC* | -0.26 | 0.28 | 0.39 | -0.81 | 0.28 |
| *FC* | -0.42 | 0.24 | 1.00 | -0.89 | 0.06 |
| *T* | 0.01 | 0.18 | 1.00 | -0.34 | 0.36 |
| ***GS*** | **-0.53** | **0.25** | **1.00** | **-1.04** | **-0.03** |
| *ST* | -0.26 | 0.22 | 1.00 | -0.69 | 0.17 |
| **Mean condition** | | | | | |
| **Intercept** | **0.47** | **0.22** | **-** | **0.05** | **0.90** |
| **WLR** | **-0.44** | **0.13** | **1.00** | **-0.70** | **-0.18** |
| A | 0.12 | 0.12 | 0.51 | -0.12 | 0.37 |
| SD | -0.06 | 0.10 | 0.37 | -0.26 | 0.14 |
| SL | 0.12 | 0.14 | 0.46 | -0.16 | 0.40 |
| **NDVI** | **0.48** | **0.19** | **0.97** | **0.10** | **0.86** |
| WLR:A | -0.11 | 0.12 | 0.17 | -0.35 | 0.14 |
| WLR:SD | -0.03 | 0.10 | 0.09 | -0.22 | 0.17 |
| WLR:SL | -0.09 | 0.11 | 0.15 | -0.31 | 0.14 |
| WLR:NDVI | -0.04 | 0.12 | 0.27 | -0.29 | 0.21 |
| WLR:*FC* | -0.20 | 0.25 | 0.34 | -0.70 | 0.29 |
| *FC* | -0.10 | 0.28 | 1.00 | -0.66 | 0.47 |
| ***T*** | **-0.51** | **0.21** | **1.00** | **-0.93** | **-0.09** |
| ***GS*** | **-0.73** | **0.30** | **1.00** | **-1.32** | **-0.14** |
| *ST* | -0.31 | 0.26 | 1.00 | -0.83 | 0.21 |

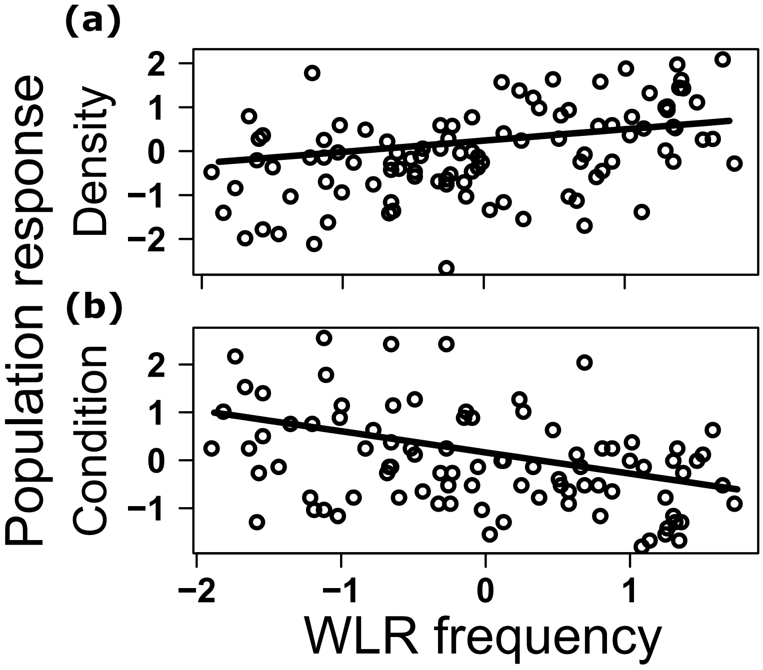


**Fig. 3.** The responses of brown trout (a) density and (b) condition to increasing water level regulation (WLR) frequency. The lines present predicted regression values for the significant main effects (parameter estimates in Table 3). All modelled and presented data are standardized to have a mean of zero and a standard deviation of one. See Methods for more details of the used response and explanatory variables.

## 3. Discussion

Our results demonstrate that hydropower induced WLR can have different impacts on brown trout populations depending on the reservoirs' environmental characteristics and regulation pattern. These findings have important implications for the management of environmental impacts of hydropower operations in reservoirs. Among the natural environmental characteristics included, reservoir morphometry and the presence of other fish species had the clearest effects on how brown trout were influenced by WLR. Hence, together with WLR patterns, these natural factors should be considered when targeting and mitigating hydropower impacts at local and wider geographical scales.

### 3.1. Fish community and reservoir morphometry effects

Our results accord with previous studies demonstrating the significant effects of lake morphometry, fish community composition and climatic conditions on the abundance, growth and niche use of salmonid populations (e.g. Finstad et al., 2014; Eloranta et al., 2015; 2016b). Specifically, brown trout biomass and density responded differently to increasing WLR magnitude depending on reservoir morphometry and fish community. In essence, our findings suggest that brown trout populations are least vulnerable to negative WLR impacts in reservoirs that are relatively large and host only brown trout. Such reservoir ecosystems likely provide sufficient habitat and food resources for brown trout, unlike small or multispecies reservoirs where the carrying capacity is limited and/or alternative niches can be restricted or dominated by coexisting fishes. In heavily regulated reservoirs that have impaired littoral zone and sympatric fish communities, superior competitors can exclude brown trout from the less affected pelagic and profundal food and habitat resources. For example, Arctic charr and whitefish are efficient users of pelagic zooplankton and profundal benthic invertebrate resources (e.g. Eloranta et al., 2011, 2013) and are probably less sensitive to impaired littoral habitat quality and productivity in hydropower reservoirs (e.g. Lindström, 1973; Hirsch et al., 2017). In sympatric communities, these species likely dominate the pelagic and profundal niches in reservoirs with extensive regulation zone (i.e., high WLR magnitude), whereas in allopatric communities brown trout can utilize all available habitat and food resources and are able to better adapt to the environmental conditions as altered by WLR.

Lake morphometry (i.e., size, depth profile and shoreline development) determine several fundamental properties of the ecosystem, including the availability and productivity of habitats, as well as linkages between them (e.g. Wetzel, 2001; Schindler and Scheuerell, 2002; Vadeboncoeur et al., 2008). These factors, in turn, shape the structure and function of lake food webs and the niche use of individuals and populations (Eloranta et al., 2015; McMeans et al., 2016). Our results provide evidence that lake morphometry also plays an important role in modifying the impacts of hydropower induced WLR on reservoir fish populations. The interactive effects of WLR magnitude with reservoir morphometry are likely associated with the overall ecosystem size and resource availability. The extent of the littoral zone tends to decrease with lake surface area and depth but increase with shoreline complexity (Wetzel, 2001; Vadeboncoeur et al., 2008). Therefore, in large reservoirs, brown trout populations may find alternative food resources or naturally utilize less-affected pelagic habitats and prey (see Eloranta et al., 2015 and McMeans et al., 2016 for examples of how other salmonids shift towards a pelagic or piscivorous niche with increasing lake area). While our results generally contrast with the frequently observed direct negative impacts of WLR on reservoir biota (see Carmignani and Roy, 2017 and Hirsch et al., 2017 and references therein), the interactive effect of WLR magnitude with reservoir depth on brown trout condition points to indirect WLR impacts. Deep lakes with steep bottom slopes are usually unproductive due to limited resuspension of nutrients and organic matter from the sediment (Wetzel, 2001). Increasing littoral zone slope has also been noted to have negative effects on fish populations (Randall et al., 1996), implying that reservoirs with steep terrain slope will be more negatively affected by increasing WLR magnitude as was found here. Deep reservoirs are, therefore, likely more significantly affected because WLR will influence a higher percentage of the littoral zone which itself accounts for a smaller proportion of the reservoir area and primary production as compared to shallow reservoirs (Vadeboncoeur et al., 2008). In other words, deep reservoirs have naturally limited littoral resources, which might increase the susceptibility of large littoral benthic organisms and benthivorous brown trout to increasing WLR magnitude.

Our results indicate that brown trout density and condition were the most evident population responses to WLR impacts. In general, population density reflects recruitment success, whereas condition indicates nutritional status of individuals within the populations (Wootton, 1998). These two population characteristics are typically highly correlated because increased population sizes are often associated with reduced growth and condition of individuals and *vice versa* (e.g. Amundsen et al., 2007; Persson et al., 2007). While no significant negative correlations between brown trout density and condition were observed in our dataset, our results demonstrate that increasing WLR frequency (i.e., peaks in absolute weekly water level change) can be associated with increased population density but decreased mean condition of brown trout. The positive effect of WLR frequency on brown trout density was unexpected, particularly when considering the negative impacts of water level peaking on riverine fish and ecosystems (e.g. Young et al., 2011; Hauer et al, 2017). However, reservoir brown trout often spawn in inlet streams and/or deep areas, which can facilitate high population recruitment even when the shallow littoral zone is heavily impacted by WLR (Brabrand et al., 2002). It is also possible that increased WLR frequency leads to a replacement of large benthic invertebrates (e.g. large crustaceans, molluscs and insect larvae) with less profitable small-sized taxa (see Carmignani & Roy, 2017 for examples of benthic invertebrate responses to WLR), which could explain the poorer condition of brown trout in reservoirs subjected to high WLR frequency. In addition, substantial and unpredictable fluctuations in water level may increase direct physiological stress

(Flodmark et al., 2002), thereby reducing the condition of fish in reservoirs subjected to high WLR frequency.

### 3.2. Study limitations and applications

We found marked effects of WLR magnitude and frequency on brown trout abundance and condition. Hence, it seems that the most important hydropower impacts on reservoir brown trout are related to how much and how often the littoral zone and biota are affected (cf. White et al., 2011). In contrast, the temporal aspects of WLR do not appear crucial given there were no clear effects of WLR duration on brown trout populations. While findings here have important implications for the management of environmental impacts of hydropower operations in reservoirs, some of the results should be interpreted with caution due to the nature of survey fishing data and possible unrevealed interactions between fish, reservoir and water level data. For instance, the fish data were obtained from single sampling occasions at each reservoir and do not consider potential seasonal dynamics or long-term changes in fish populations resulting e.g. from climatic effects or succession of the reservoir ecosystem. Hence, long-term monitoring studies could reveal more explicitly hydropower induced alterations in reservoir ecosystem and fish population status (see e.g. Aass et al., 2004; Milbrink et al., 2011). The relatively high catches of brown trout in reservoirs subjected to high water level fluctuations may be a sampling artefact resulting from WLR-driven increases of fish movement and an associated higher catchability of fish. Increased movement needs further investigation, but via increased energetic demands, it could also partly explain the observed poorer condition of brown trout in reservoirs with high WLR frequency. Moreover, how a given reservoir is regulated for hydropower production is often highly dependent on its location and morphometry. For instance, reservoirs with high WLR magnitude tend to be located at high altitudes and are therefore subjected to low ambient temperatures and terrestrial inputs (Fig. A1, Table 1). Lastly, it should be noted that our study focuses on regulated lakes and hence the findings may not hold in run-of-the-river hydropower reservoirs with distinct riverine, transitional and lacustrine zones (Wetzel, 2001; Kumar et al., 2011).

Our results provide fundamental knowledge and insights into the complex interactions between anthropogenic and natural drivers affecting reservoir fishes and ecosystems. We found that hydropower operations can have various and somewhat unexpected impacts on reservoir fish populations, as illustrated by the positive and interacting effects of WLR magnitude on brown trout biomass and density. Therefore, when designing management policies to meet the future demands for renewable energy, biogeographic, climatic, socio-political and other relevant gradients should be considered to appropriately balance energy generation needs and goals for minimizing environmental impacts and social conflicts (DeRolph et al., 2016). As noted here, one of the complicating factors for hydropower management and policymaking is the dynamic nature of the causal interactions between drivers of hydropower operations and ecosystem impacts. Hydropower operations are long-term investments that need to adapt to changes in markets, regulations and production capacity, all of which can alter the way that the reservoir water levels are regulated. Moreover, climate change driven alterations of precipitation patterns will directly influence hydropower operations e.g. in terms of magnitude, timing and predictability of water level changes, but also the reservoir ecosystem and fish e.g. via changes in water temperature and quality as well as in potential for successful invasions of undesirable species.

## 4. Conclusions

To increase renewable energy capacity and at the same time reduce the overall negative impacts on ecosystems and their related services, it is essential to identify waterbodies in which new or altered hydropower operations should be either avoided or conducted. To this end, our study provides important insights to the factors that need to be considered in sustainable planning, management and mitigation of hydropower development, including variation in the reservoirs' abiotic and biotic characteristics as well as in the operational regimes (i.e., WLR patterns). For reservoirs formed by damming lakes, our results suggest that those with restricted littoral zones (i.e., steep slope), sympatric fish communities and/or high WLR frequency are most vulnerable to negative WLR impacts on brown trout nutrition and condition. However, it is important to note that conclusions drawn regarding WLR impacts depend on the complicated interactions among environmental variables that can, in some instances, produce unexpected effects, such as the positive correlation between brown trout biomass and WLR magnitude in reservoirs with large surface area. Our results demonstrate that no single solution exists to mitigate environmental impacts even with the set of regulated lakes studied here. Accordingly, applying a more holistic reservoir management that includes consideration of local conditions, hydrological alterations and possible habitat restorations that improve habitat quantity and quality for resident fish and overall ecosystem status, is a prerequisite for the environmentally and socio-economically sustainable development of hydropower production.

## Competing interests

The authors have no competing interests.

## Data Accessibility

Data from the manuscript will be archived in the Dryad Digital Repository (http://datadryad.org/) on acceptance of the manuscript for publication.

## Acknowledgements

We thank Sigrid Skoglund for compiling fish population data. This work was supported by the Research Council of Norway [grant numbers 228714, 193818]. The funder had no involvement in the study design; in the collection, analysis and interpretation of the data; in the writing of the report; or in the decision to submit the article for publication.

# References

Aass, P., Jensen, C.S., L'Abée-Lund, J.H., Vøllestad, L.A., 2004. Long-term variation in the population structure of Arctic charr, *Salvelinus alpinus*, and brown trout, *Salmo trutta*. *Fisheries Manag. Ecol.* 11, 125–134.

Amundsen, P.-A, Knudsen, R., Klemetsen, A., 2007. Intraspecific competition and density dependence of food consumption and growth in Arctic charr. *J. Anim. Ecol* 76, 149–158.

Appelberg, M., Berger, H.M., Hesthagen, T., Kleiven, E., Kurkilahti, M., Raitaniemi J. & Rask, M., 1995. Development and intercalibration of methods in nordic freshwater fish monitoring. *Water Air Soil Poll.* 85, 401–406.

Aroviita, J., Hämäläinen, H., 2008. The impact of water-level regulation on littoral macroinvertebrate assemblages in boreal lakes. *Hydrobiologia* 613, 45–56.

Barton, K., 2016. MuMIn: Multi-Model Inference. R package version 1.15.6. https://CRAN.R-project.org/package=MuMIn

Brabrand, Å., Koestler, A.G., Borgstrøm, R., 2002. Lake spawning of brown trout related to groundwater influx. *J. Fish Biol.* 60, 751–776.

Carmignani, J.R., Roy, A.H., 2017. Ecological impacts of winter water level drawdowns on lake littoral zones: a review. *Aquat. Sci.* 79, 803–824.

Cott, P.A., Sibley, P.K., Somers, W.M., Lilly, M.R., Gordon, A.M., 2008. A review of water level fluctuations on aquatic biota with an emphasis on fishes in ice-covered lakes. *J. Am. Water Resour. As.* 44, 343–359.

DeRolph, C.R., Schramm, M.P., Bevelhimer, M.S., 2016. Predicting environmental mitigation requirements through the integration of biophysical and socio-political geographies. *Sci. Total Environ.* 566–567, 888–918.

Dincer, I., 2000. Renewable energy and sustainable development: a crucial review. *Renew. Sust. Energ. Rev.* 4, 157–175.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., … Sullivan, C.A., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.* 81, 163–182.

Eloranta, A.P., Siwertsson, A., Knudsen, R. & Amundsen, P.-A., 2011. Dietary plasticity of Arctic charr (*Salvelinus alpinus*) facilitates coexistence with competitively superior European whitefish (*Coregonus lavaretus*). *Ecol. Freshw. Fish* 20, 558–568.

Eloranta, A.P., Knudsen, R. & Amundsen, P.-A., 2013. Niche segregation of coexisting Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) constrains food web coupling in subarctic lakes. *Freshwater Biol.* 58, 207–221.

Eloranta, A.P., Kahilainen, K.K., Amundsen, P.-A., Knudsen, R., Harrod, C., Jones, R.I., 2015. Lake size and fish diversity determine resource use and trophic position of a top predator in high-latitude lakes. *Ecol. Evol.* 5, 1664–1675.

Eloranta, A.P., Sánchez-Hernández, J., Amundsen, P.-A., Skoglund, S., Brush, J.M., Henriksen, E.H., Power, M., 2016a. Water level regulation affects niche use of a lake top predator, Arctic charr (*Salvelinus alpinus*). *Ecohydrology* 10, e1766.

Eloranta, A.P., Helland, I.P., Sandlund, O.T., Hesthagen, T., Ugedal, O., Finstad A.G. 2016b. Community structure influences species’ abundance along environmental gradients. *J. Anim. Ecol.* 85, 273–282.

Evtimova, V.V., Donohue, I., 2014. Quantifying ecological responses to amplified water level fluctuations in standing waters: an experimental approach. *J. Appl. Ecol.* 51, 1282–1291.

Finstad, A.G., Helland, I.P., Ugedal, O., Hesthagen, T., Hessen, D.O., 2014. Unimodal response of fish yield to dissolved organic carbon. *Ecol. Lett.* 17, 36–43.

Flodmark, S.E.W., Urke, H.A., Halleraker, J.H., Arnekleiv, J.V., Vøllestad, L.A., Poléo, A.B.S., 2002. Cortisol and glucose responses in juvenile brown trout subjected to a fluctuating flow regime in an artificial stream. *J. Fish Biol.* 60, 238–248.

Freckleton, R.P., 2002. On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *J. Anim. Ecol.* 71, 542–545.

Freedman, J.A., Lorson, B.D., Taylor, R.B., Carline, R.F., Stauffer Jr., J.R., 2014. River of the dammed: longitudinal changes in fish assemblages in response to dams. *Hydrobiologia* 727, 19–33.

Gibeau, P., Connors, B.M., Palen, W.J., 2016. Run-of-river hydropower and salmonids: potential effects and perspective on future research. *Can. J. Fish. Aquat. Sci.* 74, 1135–1149.

Hauer, C., Siviglia, A., Zolezzi, G., 2017. Hydropeaking in regulated rivers – from process understanding to design of mitigation measures. *Sci. Total Environ.* 579, 22–26.

Helland, I.P., Finstad, A.G., Forseth, T., Hesthagen, T., Ugedal, O., 2011. Ice-cover effects on competitive interactions between two fish species. *J. Anim. Ecol.* 80, 539–547.

Hellsten, S., Riihimäki, J., 1996. Effects of lake water level regulation on the dynamics of aquatic macrophytes in northern Finland. *Hydrobiologia*. 340, 85–92.

Hirsch, P.E., Eloranta, A.P., Amundsen, P.-A., Brabrand, Å., Charmasson, J., Helland, I.P., … Yang, H., 2017. Effects of water level regulation in alpine hydropower reservoirs: an ecosystem perspective with a special emphasis on fish. *Hydrobiologia* 794, 287–301.

IEA, 2012. Hydropower. International Energy Agency, Paris. http://dx.doi.org/10.1787/9789264189201-en

Jager, H.I., Smith, B.T., 2008. Sustainable reservoir operation: can we generate hydropower and preserve ecosystem values? *River Res. Appl.* 24, 340–352.

Jensen, K.W., 1977. On the dynamics and exploitation of the population of brown trout, *Salmo trutta*, L., in Lake Øvre Heimdalsvatn, southern Norway. *Rep. Inst. Freshw. Res. Drottningholm* 56, 18–69.

Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. *Trends Ecol. Evol.* 19, 101–108.

Kumar, A., Schei, T., Ahenkorah, A., Caceres Rodriguez, R., Devernay, J.-M., Freitas, M., … Liu, Z., 2011. Hydropower, in: Edenhofer, O., Pichs-Madruga, R., Sokona, Y., Seyboth, K., Matschoss, P., Kadner, S., … von Stechow, C. (Eds), IPCC Special Report on Renewable Energy Sources and Climate Change Mitigation. Cambridge University Press, United Kingdom and New York, pp. 437–496.

Lindström, T., 1973. Life in a lake reservoir: fewer options, decreased production. *Ambio*, 2, 145–153.

McMeans, B.C., McCann, K.S., Tunney, T.D., Fisk, A.T., Muir, A.M., Lester, N., … Rooney, N., 2016. The adaptive capacity of lake food webs: from individuals to ecosystems. *Ecol. Monogr.* 86, 4–19.

Milbrink, G., Vrede, T., Tranvik, L.J., Rydin, E. 2011. Large-scale and long-term decrease in fish growth following the construction of hydroelectric reservoirs. *Can. J. Fish. Aquat. Sci.* 68, 2167–2173.

Museth, J., Hesthagen, T., Sandlund, O.T., Thorstad, E.B., Ugedal, O., 2007. The history of the minnow *Phoxinus phoxinus* (L.) in Norway: from harmless species to pest. *J. Fish Biol.* 71 (Supplement D), 184–195.

Olden, J.D., Poff, N.L., 2003. Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. *River Res. Appl.* 19, 101–121.

Persson, L., Amundsen, P-A., De Roos, A.M, Klementsen, A., Knudsen, R., Primicerio, R., 2007. Culling prey promotes predator recovery—alternative states in a whole-lake experiment. *Science* 316, 1743–1746.

Peterson, B.G., Carl, P., 2014. PerformanceAnalytics: Econometric tools for performance and risk analysis. R package version 1.4.3541.

Randall, R.G, Minns, C.K., Cairns, V.W., Moore, J.E., 1996. The relationship between an index of fish production and submerged macrophytes and other habitat features at three littoral areas in the Great Lakes. *Can. J. Fish. Aquat. Sci.* 53, 35–44.

R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Ryan, J.A., 2016. quantmod: Quantitative Financial Modelling Framework. R package version 0.4-7. https://CRAN.R-project.org/package=quantmod

Sánchez-Hernández, J., Eloranta, A.P., Finstad, A.G., Amundsen, P.-A., 2017. Community structure affects trophic ontogeny in a predatory fish. *Ecol. Evol.* 7, 358–367.

Schindler, D.E., Scheuerell, M.D., 2002. Habitat coupling in lake ecosystems. *Oikos* 98, 177–189.

Strayer, D.L., Findlay, S.E., 2010. Ecology of freshwater shore zones. *Aquat. Sci.* 72, 127–163.

Tveito, O.E., Førland, E.J., Heino, R., Hanssen-Bauer, I., Alexandersson, H., Dahlström, B., … Westman, Y., 2000. Nordic temperature maps. *DNMI Klima* 9, 1–55.

Vadeboncoeur, Y., Peterson, G., Vander Zanden, M.J., Kalff, J., 2008. Benthic algal production across lake size gradients: interactions among morphometry, nutrients, and light. *Ecology* 89, 2541–2552.

Wetzel, R.G., 2001. Limnology: lake and river ecosystems. Academic Press, San Diego, California.

White, M.S., Xenopoulos, M.A., Metcalfe, R.A., Somers, K.M., 2011. Water level thresholds of benthic macroinvertebrate richness, structure, and function of boreal lake stony littoral habitats. *Can. J. Fish. Aquat. Sci.* 68, 1695–1704.

Winemiller, K.O., McIntyre, P.B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., … Sáenz, L., 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science* 351, 128–129.

Wootton, R.J., 1998. Ecology of teleost fishes, second ed. Kluwer Academic Publishers, Dordrecht, The Netherlands.

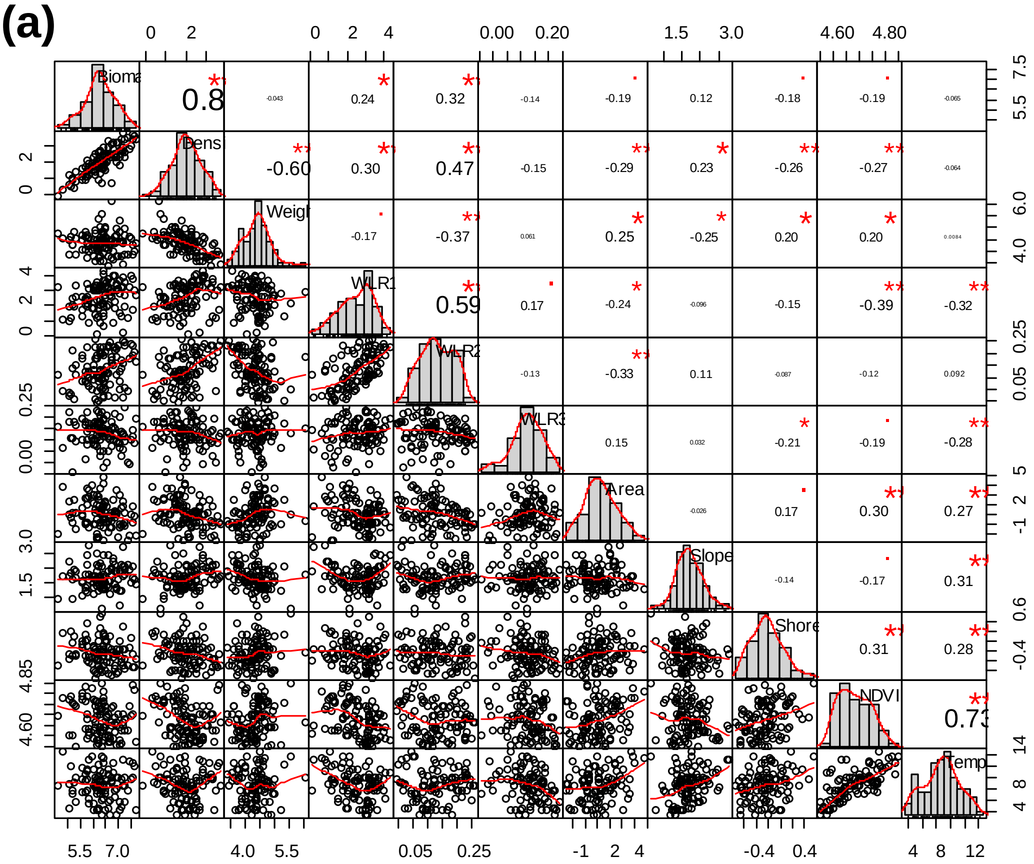
Young, P.S., Cech Jr., J.J., Thompson, L.C., 2011. Hydropower-related pulsed-flow impacts on stream fishes: a brief review, conceptual model, knowledge gaps, and research needs. *Rev. Fish Biol. Fisher.* 21, 713–731.

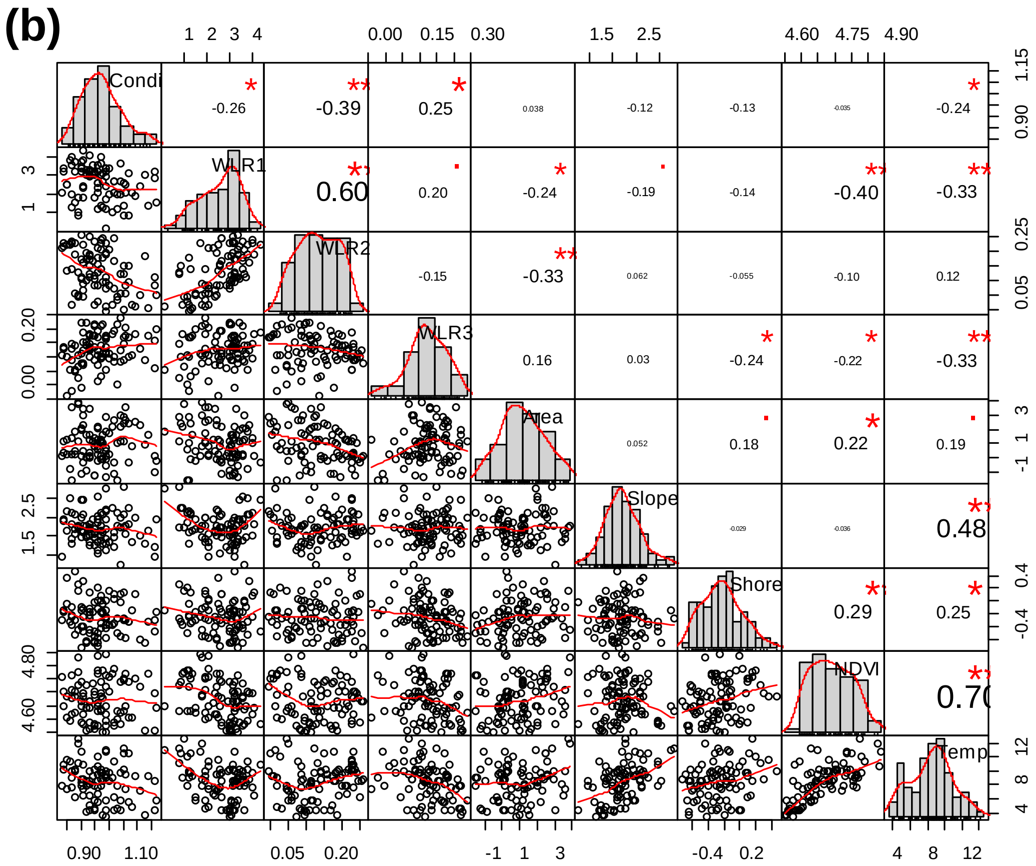
Zohary, T., Ostrovsky, I., 2011. Ecological impacts of excessive water level fluctuations in stratified freshwater lakes. *Inland Waters* 1, 47–59.

# Appendices

**Fig. A1.** Frequency distributions of and pairwise Pearson correlations between the response and explanatory variables included in the modelling based on data from: (a) all 102 reservoirs with data for brown trout biomass, density and mean weight; (b) 90 reservoirs with data for brown trout mean condition; and (c) 43 reservoirs with data for mean total length of mature females. WLR1, WLR2 and WLR3 refer to the metrics describing magnitude, frequency and duration aspects of water level regulation, respectively. The graphics are drawn in R using chart.Correlation function in PerformanceAnalytics package v. 1.4.3541 (Peterson & Carl 2014; [https://CRAN.R-project.org/package=PerformanceAnalytics](https://CRAN.R-project.org/package=PerformanceAnalytics)).

**(a)**




(b)
Condi
WLR1
WLR2
WLR3
Area
Slope
Shore
NDVI
Temp
-0.26
-0.39
0.25
0.038
-0.12
-0.13
-0.035
-0.24
0.60
0.20
-0.24
-0.19
-0.14
-0.40
-0.33
-0.15
-0.33
0.062
-0.055
-0.10
0.12
0.16
0.03
-0.24
-0.22
-0.33
0.052
0.18
0.22
0.19
-0.029
-0.036
0.48
0.29
0.25
0.70
1 2 3 4
0.00 0.15 0.30
1.5 2.5
4.60 4.75 4.90
0.90 1.10
0.05 0.20
-1 1 3
-0.4 0.2
4 8 12
1.15
0.90
0.25
0.05
3
1
0.20
0.00
2.5
1.5
0.4
-0.4
4.80
4.60

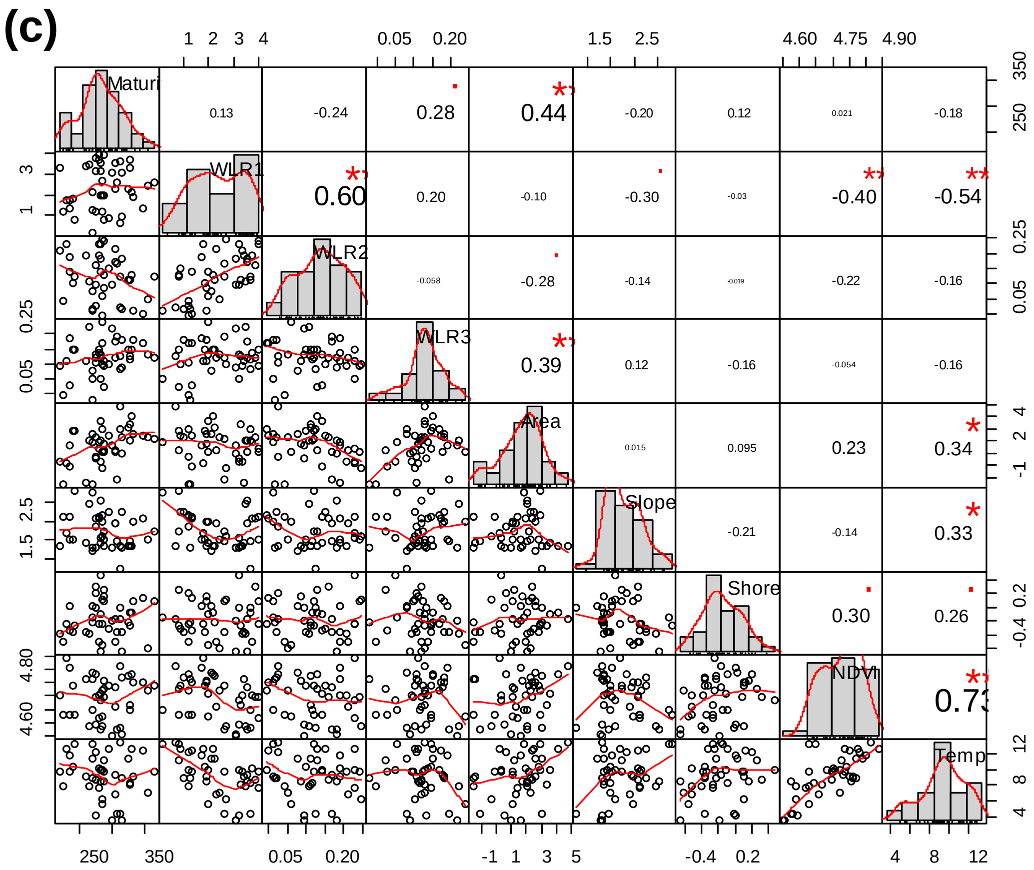

(c)
Maturi
WLR1
WLR2
WLR3
Area
Slope
Shore
NDVI
Temp
0.13
-0.24
0.28
0.44
-0.20
0.12
0.021
-0.18
0.60
0.20
-0.10
-0.30
-0.03
-0.40
-0.54
-0.058
-0.28
-0.14
-0.019
-0.22
-0.16
0.39
0.12
-0.16
-0.054
-0.16
0.015
0.095
0.23
0.34
-0.21
-0.14
0.33
0.30
0.26
0.73
1 2 3 4
0.05 0.20
1.5 2.5
4.60 4.75 4.90
250 350
-1 1 3 5
-0.4 0.2
4 8 12

**Table B1.** Model selection tables of brown trout (a) biomass, (b) density, (c) mean weight, (d) mean condition, and (e) maturation size (i.e., mean total length of mature females) against water level regulation (WLR) patterns and other explanatory variables including: reservoir area (A, ln-transformed), shoreline development (SD), terrain slope (SL), Normalized Difference Vegetation Index (NDVI, ln-transformed) and their two-way interactions with the given WLR metrics (magnitude, frequency and duration), as well as fish community composition (*FC*), gillnet series (*GS*), stocking of brown trout (*ST*), and mean July air temperature (*T*) as fixed explanatory variables. The tables show parameter estimates for model terms included in the models, AIC, AIC difference from best model (delta), and Akaike weights (weights). The top ten candidate models are shown.

**(a)**

***Biomass against WLR amplitude***

| I | WLR1 | A | SD | SL | NDVI | WLR1:A | WLR1:SD | WLR1:SL | WLR1:NDVI | WLR1:*FC* | T | K | AIC | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.39 | 0.27 | 0.05 | -0.17 |  |  | 0.26 | 0.24 |  |  | + | 0.15 | 12 | 280.116 | 0 | 0.09 |
| 0.46 | 0.13 | 0.09 | -0.14 |  |  | 0.21 | 0.19 |  |  |  | 0.18 | 11 | 281.352 | 1.236 | 0.048 |
| 0.54 | 0.13 | 0.13 |  |  |  | 0.23 |  |  |  |  | 0.1 | 9 | 281.842 | 1.726 | 0.038 |
| 0.38 | 0.27 | 0.05 | -0.17 |  | -0.02 | 0.26 | 0.25 |  |  | + | 0.17 | 13 | 282.093 | 1.977 | 0.033 |
| 0.39 | 0.27 | 0.05 | -0.17 | 0 |  | 0.26 | 0.24 |  |  | + | 0.15 | 13 | 282.114 | 1.998 | 0.033 |
| 0.38 | 0.34 | 0.05 | -0.16 |  | -0.03 | 0.25 | 0.22 |  | 0.18 | + | 0.14 | 14 | 282.128 | 2.012 | 0.033 |
| 0.38 | 0.1 |  | -0.13 |  |  |  | 0.24 |  |  |  | 0.13 | 9 | 282.167 | 2.051 | 0.032 |
| 0.51 | 0.21 | 0.11 |  |  |  | 0.27 |  |  |  | + | 0.08 | 10 | 282.609 | 2.493 | 0.026 |
| 0.51 | 0.13 | 0.13 | -0.1 |  |  | 0.24 |  |  |  |  | 0.13 | 10 | 282.671 | 2.555 | 0.025 |
| 0.47 |  |  |  |  |  |  |  |  |  |  | 0.03 | 6 | 282.824 | 2.708 | 0.023 |

***Biomass against WLR frequency***

| I | WLR2 | A | SD | SL | NDVI | WLR2:A | WLR2:SD | WLR2:SL | WLR2:NDVI | WLR2:*FC* | T | K | AIC | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.35 | 0.16 |  |  |  |  |  |  |  |  |  | 0.01 | 7 | 282.597 | 0 | 0.072 |
| 0.47 |  |  |  |  |  |  |  |  |  |  | 0.03 | 6 | 282.824 | 0.227 | 0.064 |
| 0.33 | 0.16 |  | -0.08 |  |  |  |  |  |  |  | 0.02 | 8 | 283.895 | 1.297 | 0.038 |
| 0.45 |  |  | -0.08 |  |  |  |  |  |  |  | 0.04 | 7 | 284.173 | 1.576 | 0.033 |
| 0.39 | 0.17 | 0.07 |  |  |  |  |  |  |  |  | -0.01 | 8 | 284.194 | 1.597 | 0.032 |
| 0.33 | 0.17 |  |  | 0.06 |  |  |  |  |  |  | -0.02 | 8 | 284.222 | 1.624 | 0.032 |
| 0.34 | 0.19 |  |  |  |  |  |  |  |  | + | 0 | 8 | 284.497 | 1.9 | 0.028 |
| 0.45 |  |  |  | 0.05 |  |  |  |  |  |  | 0 | 7 | 284.539 | 1.942 | 0.027 |
| 0.5 |  | 0.06 |  |  |  |  |  |  |  |  | 0.01 | 7 | 284.582 | 1.985 | 0.027 |
| 0.35 | 0.16 |  |  |  | 0 |  |  |  |  |  | 0.01 | 8 | 284.597 | 1.999 | 0.027 |

***Biomass against WLR duration***

| I | WLR3 | A | SD | SL | NDVI | WLR3:A | WLR3:SD | WLR3:SL | WLR3:NDVI | WLR3:*FC* | T | K | AIC | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.46 | -0.26 |  |  |  |  |  |  |  |  | + | -0.04 | 8 | 281.965 | 0 | 0.051 |
| 0.44 | -0.16 |  |  |  |  |  |  |  |  |  | 0 | 7 | 282.101 | 0.136 | 0.048 |
| 0.47 |  |  |  |  |  |  |  |  |  |  | 0.03 | 6 | 282.824 | 0.86 | 0.033 |
| 0.41 | -0.17 |  | -0.11 |  |  |  |  |  |  |  | 0.02 | 8 | 282.9 | 0.935 | 0.032 |
| 0.53 | -0.27 | 0.1 |  |  |  |  |  |  |  | + | -0.06 | 9 | 283.185 | 1.22 | 0.028 |
| 0.51 | -0.18 | 0.11 |  |  |  |  |  |  |  |  | -0.02 | 8 | 283.219 | 1.255 | 0.027 |
| 0.44 | -0.27 |  |  | 0.08 |  |  |  |  |  | + | -0.08 | 9 | 283.227 | 1.262 | 0.027 |
| 0.44 | -0.26 |  | -0.08 |  |  |  |  |  |  | + | -0.02 | 9 | 283.245 | 1.281 | 0.027 |
| 0.42 | -0.17 |  |  | 0.08 |  |  |  |  |  |  | -0.03 | 8 | 283.5 | 1.535 | 0.024 |
| 0.52 | -0.14 | 0.12 |  |  |  | 0.11 |  |  |  |  | -0.04 | 9 | 283.727 | 1.762 | 0.021 |

**(b)**

***Density against WLR amplitude***

| I | WLR1 | A | SD | SL | NDVI | WLR1:A | WLR1:SD | WLR1:SL | WLR1:NDVI | WLR1:*FC* | T | K | AIC | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.55 | 0.32 | 0 | -0.21 | | | 0.26 | 0.29 | | | + | 0.18 | 12 | 247.031 | 0 | 0.249 |
| 0.6 | 0.25 | 0.03 | -0.2 | 0.05 | | 0.26 | 0.3 | 0.11 | | + | 0.15 | 14 | 248.386 | 1.355 | 0.126 |
| 0.54 | 0.32 | 0.01 | -0.2 | 0.05 | | 0.25 | 0.28 | | | + | 0.15 | 13 | 248.618 | 1.587 | 0.113 |
| 0.52 | 0.32 | 0 | -0.22 | | -0.06 | 0.26 | 0.29 | | | + | 0.22 | 13 | 248.823 | 1.792 | 0.102 |
| 0.62 | 0.3 | 0.04 | -0.2 | 0.01 | -0.06 | 0.24 | 0.29 | 0.18 | 0.23 | + | 0.15 | 16 | 248.893 | 1.862 | 0.098 |
| 0.52 | 0.36 | 0 | -0.21 | | -0.06 | 0.25 | 0.27 | | 0.1 | + | 0.2 | 14 | 250.038 | 3.008 | 0.055 |
| 0.59 | 0.25 | 0.03 | -0.2 | 0.04 | -0.02 | 0.26 | 0.3 | 0.11 | | + | 0.16 | 15 | 250.376 | 3.345 | 0.047 |
| 0.54 | 0.32 | 0 | -0.2 | 0.05 | -0.01 | 0.25 | 0.28 | | | + | 0.16 | 14 | 250.614 | 3.583 | 0.041 |
| 0.54 | 0.36 | 0 | -0.2 | 0.04 | -0.03 | 0.25 | 0.27 | | 0.09 | + | 0.16 | 15 | 251.92 | 4.889 | 0.022 |
| 0.55 | 0.2 | | -0.19 | | | | 0.3 | | | + | 0.13 | 10 | 252.633 | 5.602 | 0.015 |

***Density against WLR frequency***

| I | WLR2 | A | SD | SL | NDVI | WLR2:A | WLR2:SD | WLR2:SL | WLR2:NDVI | WLR2:*FC* | T | K | AIC | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.45 | 0.33 | | | | -0.08 | | | | 0.29 | + | 0.08 | 10 | 253.639 | 0 | 0.031 |
| 0.49 | 0.23 | | -0.15 | | | | 0.13 | | | | 0.11 | 9 | 253.744 | 0.105 | 0.029 |
| 0.48 | 0.24 | | | 0.14 | | | | | | | -0.03 | 8 | 253.842 | 0.203 | 0.028 |
| 0.52 | 0.21 | | | 0.17 | 0.09 | | | | 0.16 | | -0.06 | 10 | 253.9 | 0.261 | 0.027 |
| 0.48 | 0.31 | | | 0.13 | 0.05 | | | | 0.25 | + | -0.05 | 11 | 254.016 | 0.377 | 0.026 |
| 0.44 | 0.34 | | -0.12 | | -0.05 | | 0.12 | | 0.25 | + | 0.11 | 12 | 254.12 | 0.481 | 0.024 |
| 0.43 | 0.33 | | -0.1 | | -0.08 | | | | 0.27 | + | 0.1 | 11 | 254.289 | 0.65 | 0.022 |
| 0.47 | 0.23 | | -0.12 | 0.1 | | | 0.11 | | | | 0.05 | 10 | 254.449 | 0.81 | 0.021 |
| 0.52 | 0.24 | | | | | | | | | | 0.04 | 7 | 254.472 | 0.834 | 0.02 |
| 0.49 | 0.24 | | -0.12 | | | | | | | | 0.06 | 8 | 254.489 | 0.85 | 0.02 |

***Density against WLR duration***

| I | WLR3 | A | SD | SL | NDVI | WLR3:A | WLR3:SD | WLR3:SL | WLR3:NDVI | WLR3:*FC* | T | K | AIC | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.6 | -0.19 | | -0.12 | 0.13 | | | | | | | 0 | 9 | 256.156 | 0 | 0.039 |
| 0.63 | -0.17 | | | 0.15 | | | | | | | -0.03 | 8 | 256.16 | 0.003 | 0.039 |
| 0.62 | -0.17 | | -0.14 | | | | | | | | 0.06 | 8 | 256.436 | 0.279 | 0.034 |
| 0.69 | -0.18 | | | 0.22 | 0.19 | | | | | | -0.18 | 9 | 256.926 | 0.77 | 0.026 |
| 0.65 | -0.2 | | -0.11 | 0.19 | 0.17 | | | | | | -0.13 | 10 | 257.183 | 1.026 | 0.023 |
| 0.66 | -0.15 | | | | | | | | | | 0.04 | 7 | 257.211 | 1.055 | 0.023 |
| 0.79 | -0.22 | 0.13 | | 0.25 | 0.25 | | | | | | -0.26 | 10 | 257.261 | 1.104 | 0.022 |
| 0.66 | -0.21 | 0.09 | -0.12 | 0.13 | | | | | | | -0.03 | 10 | 257.299 | 1.143 | 0.022 |
| 0.69 | -0.19 | 0.09 | | 0.15 | | | | | | | -0.06 | 9 | 257.318 | 1.162 | 0.022 |
| 0.61 | -0.17 | | | 0.16 | | | | -0.07 | | | -0.04 | 9 | 257.503 | 1.347 | 0.02 |

**(c)**

***Mean weight against WLR amplitude***

| I | WLR1 | A | SD | SL | NDVI | WLR1:A | WLR1:SD | WLR1:SL | WLR1:NDVI | WLR1:*FC* | T | K | AIC | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| -0.53 | | | | -0.16 | | | | | | | -0.02 | 7 | 273.504 | 0 | 0.066 |
| -0.57 | | | | | | | | | | | -0.09 | 6 | 274.202 | 0.698 | 0.047 |
| -0.58 | | | | -0.21 | -0.15 | | | | | | 0.09 | 8 | 274.898 | 1.394 | 0.033 |
| -0.52 | | | 0.07 | -0.14 | | | | | | | -0.03 | 8 | 274.972 | 1.469 | 0.032 |
| -0.57 | 0.06 | | | -0.16 | | | | -0.13 | | | -0.01 | 9 | 275.024 | 1.52 | 0.031 |
| -0.54 | | | 0.09 | | | | | | | | -0.11 | 7 | 275.187 | 1.684 | 0.029 |
| -0.54 | -0.01 | | | -0.14 | | | | -0.14 | | + | 0.03 | 10 | 275.19 | 1.686 | 0.029 |
| -0.52 | -0.03 | | | -0.16 | | | | | | | -0.02 | 8 | 275.424 | 1.921 | 0.025 |
| -0.53 | | 0.01 | | -0.16 | | | | | | | -0.02 | 8 | 275.501 | 1.997 | 0.024 |
| -0.52 | -0.03 | | 0.11 | -0.1 | | | -0.18 | -0.16 | | + | -0.03 | 12 | 275.799 | 2.295 | 0.021 |

***Mean weight against WLR frequency***

| I | WLR2 | A | SD | SL | NDVI | WLR2:A | WLR2:SD | WLR2:SL | WLR2:NDVI | WLR2:*FC* | T | K | AIC | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| -0.39 | -0.19 | | | -0.16 | | | | | | | 0.01 | 8 | 272.24 | 0 | 0.055 |
| -0.44 | -0.18 | | | | | | | | | | -0.07 | 7 | 273.309 | 1.07 | 0.032 |
| -0.53 | | | | -0.16 | | | | | | | -0.02 | 7 | 273.504 | 1.264 | 0.029 |
| -0.43 | -0.16 | | | -0.2 | -0.09 | | | | -0.14 | | 0.05 | 10 | 273.528 | 1.288 | 0.029 |
| -0.44 | -0.19 | | | -0.22 | -0.15 | | | | | | 0.12 | 9 | 273.549 | 1.309 | 0.028 |
| -0.38 | -0.19 | | 0.07 | -0.15 | | | | | | | -0.01 | 9 | 273.675 | 1.435 | 0.027 |
| -0.41 | -0.17 | | 0.12 | | | | -0.13 | | | | -0.13 | 9 | 273.817 | 1.577 | 0.025 |
| -0.39 | -0.18 | | 0.1 | -0.13 | | | -0.11 | | | | -0.06 | 10 | 273.983 | 1.744 | 0.023 |
| -0.4 | -0.16 | | | -0.17 | | | | | | + | 0 | 9 | 274.11 | 1.87 | 0.021 |
| -0.41 | -0.19 | | | -0.16 | | | | 0.03 | | | 0 | 9 | 274.129 | 1.889 | 0.021 |

***Mean weight against WLR duration***

| I | WLR3 | A | SD | SL | NDVI | WLR3:A | WLR3:SD | WLR3:SL | WLR3:NDVI | WLR3:*FC* | T | K | AIC | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| -0.53 | | | | -0.16 | | | | | | | -0.02 | 7 | 273.504 | 0 | 0.071 |
| -0.57 | | | | | | | | | | | -0.09 | 6 | 274.202 | 0.698 | 0.05 |
| -0.58 | | | | -0.21 | -0.15 | | | | | | 0.09 | 8 | 274.898 | 1.394 | 0.035 |
| -0.52 | | | 0.07 | -0.14 | | | | | | | -0.03 | 8 | 274.972 | 1.469 | 0.034 |
| -0.52 | 0.06 | | | -0.17 | | | | | | | 0 | 8 | 275.008 | 1.504 | 0.033 |
| -0.54 | | | 0.09 | | | | | | | | -0.11 | 7 | 275.187 | 1.684 | 0.031 |
| -0.5 | -0.02 | | | -0.16 | | | | | | + | -0.04 | 9 | 275.303 | 1.799 | 0.029 |
| -0.53 | | 0.01 | | -0.16 | | | | | | | -0.02 | 8 | 275.501 | 1.997 | 0.026 |
| -0.57 | -0.02 | | | -0.24 | -0.23 | | | | | + | 0.12 | 10 | 275.867 | 2.363 | 0.022 |
| -0.56 | 0.04 | | | | | | | | | | -0.08 | 7 | 275.984 | 2.48 | 0.02 |

**(d)**

***Mean condition against WLR amplitude***

| I | WLR1 | A | SD | SL | NDVI | WLR1:A | WLR1:SD | WLR1:SL | WLR1:NDVI | WLR1:*FC* | T | K | AIC | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.14 | -0.22 | | | 0.16 | 0.5 | | | -0.22 | | | -0.7 | 10 | 242.67 | 0 | 0.084 |
| 0.24 | -0.26 | 0.09 | | 0.16 | 0.58 | -0.17 | | -0.19 | | | -0.84 | 12 | 243.265 | 0.594 | 0.062 |
| 0.12 | -0.22 | | -0.09 | 0.15 | 0.5 | | | -0.23 | | | -0.67 | 11 | 243.868 | 1.198 | 0.046 |
| 0.13 | -0.2 | | | 0.17 | 0.52 | | | -0.25 | -0.1 | | -0.73 | 11 | 243.96 | 1.29 | 0.044 |
| 0.25 | -0.24 | 0.1 | | 0.16 | 0.54 | | | -0.2 | | | -0.74 | 11 | 243.995 | 1.325 | 0.043 |
| 0.14 | -0.21 | | | 0.16 | 0.5 | | | -0.22 | | + | -0.7 | 11 | 244.656 | 1.986 | 0.031 |
| 0.23 | -0.26 | 0.09 | -0.07 | 0.15 | 0.57 | -0.17 | | -0.19 | | | -0.81 | 13 | 244.656 | 1.986 | 0.031 |
| 0.39 | -0.43 | 0.16 | | | 0.45 | -0.19 | | | | | -0.7 | 10 | 244.749 | 2.079 | 0.03 |
| 0.23 | -0.24 | 0.08 | | 0.17 | 0.59 | -0.17 | | -0.21 | -0.07 | | -0.85 | 13 | 244.882 | 2.211 | 0.028 |
| 0.11 | -0.2 | | -0.09 | 0.16 | 0.52 | | | -0.26 | -0.11 | | -0.7 | 12 | 245.035 | 2.365 | 0.026 |

***Mean condition against WLR frequency***

| I | WLR2 | A | SD | SL | NDVI | WLR2:A | WLR2:SD | WLR2:SL | WLR2:NDVI | WLR2:*FC* | T | K | AIC | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.43 | -0.48 | | | | 0.4 | | | | | | -0.41 | 8 | 240.728 | 0 | 0.063 |
| 0.41 | -0.39 | | | | 0.42 | | | | | + | -0.46 | 9 | 241.29 | 0.563 | 0.048 |
| 0.54 | -0.48 | 0.13 | | | 0.45 | | | | | | -0.47 | 9 | 241.404 | 0.676 | 0.045 |
| 0.43 | -0.47 | | | 0.13 | 0.51 | | | | | | -0.55 | 9 | 241.684 | 0.956 | 0.039 |
| 0.56 | -0.46 | 0.14 | | 0.14 | 0.57 | | | | | | -0.62 | 10 | 242.169 | 1.441 | 0.031 |
| 0.41 | -0.48 | | -0.07 | | 0.4 | | | | | | -0.4 | 9 | 242.211 | 1.483 | 0.03 |
| 0.51 | -0.49 | 0.1 | | | 0.45 | -0.12 | | | | | -0.49 | 10 | 242.298 | 1.57 | 0.029 |
| 0.51 | -0.39 | 0.11 | | | 0.46 | | | | | + | -0.5 | 10 | 242.333 | 1.605 | 0.028 |
| 0.44 | -0.47 | | | | 0.41 | | | | -0.06 | | -0.43 | 9 | 242.374 | 1.646 | 0.028 |
| 0.42 | -0.39 | | | 0.1 | 0.5 | | | | | + | -0.56 | 10 | 242.679 | 1.951 | 0.024 |

***Mean condition against WLR duration***

| I | WLR3 | A | SD | SL | NDVI | WLR3:A | WLR3:SD | WLR3:SL | WLR3:NDVI | WLR3:*FC* | T | K | AIC | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.2 | 0.09 | | | | 0.34 | | | | 0.15 | + | -0.43 | 10 | 251.124 | 0 | 0.076 |
| 0.15 | 0.04 | | | | 0.3 | | | | | + | -0.44 | 9 | 251.3 | 0.176 | 0.07 |
| 0.04 | 0.02 | | | | | | | | | + | -0.28 | 8 | 252.456 | 1.331 | 0.039 |
| 0.2 | 0.23 | | | | 0.41 | | | | 0.21 | | -0.42 | 9 | 252.481 | 1.356 | 0.039 |
| 0.2 | 0.08 | | | 0.1 | 0.42 | | | | 0.14 | + | -0.54 | 11 | 252.654 | 1.53 | 0.036 |
| 0.16 | 0.02 | | | 0.11 | 0.39 | | | | | + | -0.55 | 10 | 252.733 | 1.609 | 0.034 |
| 0.22 | 0.03 | 0.08 | | | 0.33 | | | | | + | -0.47 | 10 | 252.868 | 1.744 | 0.032 |
| 0.24 | 0.08 | 0.05 | | | 0.36 | | | | 0.14 | + | -0.46 | 11 | 252.95 | 1.825 | 0.031 |
| 0.2 | 0.09 | | 0 | | 0.34 | | | | 0.15 | + | -0.43 | 11 | 253.122 | 1.998 | 0.028 |
| 0.15 | 0.04 | | 0.01 | | 0.3 | | | | | + | -0.44 | 10 | 253.294 | 2.17 | 0.026 |

**(e)**

***Mean maturity length against WLR amplitude***

| I | WLR1 | A | SD | SL | NDVI | WLR1:A | WLR1:SD | WLR1:SL | WLR1:NDVI | WLR1:*FC* | T | K | AIC | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| -0.58 |  | 0.41 |  |  |  |  |  |  |  |  | -0.35 | 7 | 111.468 | 0 | 0.158 |
| -0.54 |  | 0.43 | 0.1 |  |  |  |  |  |  |  | -0.35 | 8 | 112.927 | 1.458 | 0.076 |
| -0.5 |  | 0.44 |  |  | 0.13 |  |  |  |  |  | -0.42 | 8 | 113.108 | 1.64 | 0.069 |
| -0.57 |  | 0.41 |  | -0.05 |  |  |  |  |  |  | -0.32 | 8 | 113.329 | 1.861 | 0.062 |
| -0.58 | -0.04 | 0.42 |  |  |  |  |  |  |  |  | -0.36 | 8 | 113.407 | 1.938 | 0.06 |
| -0.45 |  | 0.46 | 0.1 |  | 0.14 |  |  |  |  |  | -0.44 | 9 | 114.501 | 3.033 | 0.035 |
| -0.53 | -0.07 | 0.44 | 0.11 |  |  |  |  |  |  |  | -0.37 | 9 | 114.742 | 3.274 | 0.031 |
| -0.6 | -0.06 | 0.39 |  |  |  | -0.11 |  |  |  |  | -0.39 | 9 | 114.783 | 3.315 | 0.03 |
| -0.54 |  | 0.43 | 0.09 | -0.03 |  |  |  |  |  |  | -0.34 | 9 | 114.888 | 3.42 | 0.028 |
| -0.49 | -0.05 | 0.45 |  |  | 0.13 |  |  |  |  |  | -0.44 | 9 | 115.019 | 3.551 | 0.027 |

***Mean maturity length against WLR frequency***

| I | WLR2 | A | SD | SL | NDVI | WLR2:A | WLR2:SD | WLR2:SL | WLR2:NDVI | WLR2:*FC* | T | K | AIC | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| -0.58 |  | 0.41 |  |  |  |  |  |  |  |  | -0.35 | 7 | 111.468 | 0 | 0.085 |
| -0.44 | -0.02 | 0.42 |  |  | 0.2 |  |  |  | -0.26 |  | -0.4 | 10 | 112.703 | 1.235 | 0.046 |
| -0.6 | 0.17 | 0.37 |  |  |  |  |  |  |  | + | -0.36 | 9 | 112.809 | 1.341 | 0.043 |
| -0.54 |  | 0.43 | 0.1 |  |  |  |  |  |  |  | -0.35 | 8 | 112.927 | 1.458 | 0.041 |
| -0.5 |  | 0.44 |  |  | 0.13 |  |  |  |  |  | -0.42 | 8 | 113.108 | 1.64 | 0.037 |
| -0.57 |  | 0.41 |  | -0.05 |  |  |  |  |  |  | -0.32 | 8 | 113.329 | 1.861 | 0.033 |
| -0.55 | -0.05 | 0.41 |  |  |  |  |  |  |  |  | -0.34 | 8 | 113.338 | 1.87 | 0.033 |
| -0.58 | -0.11 | 0.36 |  |  |  | -0.18 |  |  |  |  | -0.33 | 9 | 113.411 | 1.943 | 0.032 |
| -0.56 | 0.17 | 0.36 |  | -0.12 |  |  |  |  |  | + | -0.3 | 10 | 113.987 | 2.519 | 0.024 |
| -0.38 | -0.04 | 0.44 | 0.1 |  | 0.21 |  |  |  | -0.26 |  | -0.41 | 11 | 114.054 | 2.586 | 0.023 |

***Mean maturity length against WLR duration***

| I | WLR3 | A | SD | SL | NDVI | WLR3:A | WLR3:SD | WLR3:SL | WLR3:NDVI | WLR3:*FC* | T | K | AIC | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| -0.58 |  | 0.41 |  |  |  |  |  |  |  |  | -0.35 | 7 | 111.468 | 0 | 0.129 |
| -0.54 |  | 0.43 | 0.1 |  |  |  |  |  |  |  | -0.35 | 8 | 112.927 | 1.458 | 0.062 |
| -0.5 |  | 0.44 |  |  | 0.13 |  |  |  |  |  | -0.42 | 8 | 113.108 | 1.64 | 0.057 |
| -0.57 |  | 0.41 |  | -0.05 |  |  |  |  |  |  | -0.32 | 8 | 113.329 | 1.861 | 0.051 |
| -0.6 | -0.12 | 0.34 |  |  |  | -0.19 |  |  |  |  | -0.32 | 9 | 113.365 | 1.897 | 0.05 |
| -0.59 | -0.01 | 0.42 |  |  |  |  |  |  |  |  | -0.35 | 8 | 113.46 | 1.992 | 0.048 |
| -0.45 |  | 0.46 | 0.1 |  | 0.14 |  |  |  |  |  | -0.44 | 9 | 114.501 | 3.033 | 0.028 |
| -0.54 |  | 0.43 | 0.09 | -0.03 |  |  |  |  |  |  | -0.34 | 9 | 114.888 | 3.42 | 0.023 |
| -0.54 | 0.01 | 0.42 | 0.1 |  |  |  |  |  |  |  | -0.35 | 9 | 114.925 | 3.457 | 0.023 |
| -0.5 | -0.02 | 0.45 |  |  | 0.13 |  |  |  |  |  | -0.43 | 9 | 115.081 | 3.613 | 0.021 |

**Table C1.** Summary result for model averaging of fixed effects in the 95% confidence model set (cumulative AIC weights ≥ 0.95) with different brown trout population characteristics (i.e., biomass, density, mean weight, mean condition and mean length of mature females) as response variables and WLR metric as well as reservoir environmental characteristics as predictor variables. Parameter estimates (on standardized scale) are interpretable as effect size because they describe changes in units of standard deviation of the original variable. Standard error (SE), relative importance (IR.) and 95% confidence intervals for each parameter are shown, with significant parameters highlighted in bold. The predictor variables included reservoir area (A, ln-transformed), shoreline development (SD), terrain slope (SL), Normalized Difference Vegetation Index (NDVI, ln-transformed) and their two-way interactions with the given WLR metrics (magnitude, frequency and duration), as well as fish community composition (*FC*), gillnet series (*GS*), stocking of trout (*ST*), and mean July air temperature (*T*) as fixed explanatory variables.

| | *WLR magnitude* | | | | | *WLR frequency* | | | | | *WLR duration* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Parameter | Estimate | SE | IR | -95% CI | +95% CI | Estimate | SE | IR | -95% CI | +95% CI | Estimate | SE | IR | -95% CI | +95% CI |
| **Biomass** | | | | | | | | | | | | | | | |
| **Intercept** | **0.44** | **0.20** | **-** | **0.04** | **0.84** | 0.38 | 0.20 | - | -0.01 | 0.78 | **0.47** | **0.18** | **-** | **0.11** | **0.83** |
| WLR | 0.19 | 0.15 | 0.91 | -0.10 | 0.49 | 0.18 | 0.13 | 0.73 | -0.07 | 0.42 | -0.22 | 0.12 | 0.86 | -0.46 | 0.03 |
| A | 0.08 | 0.13 | 0.74 | -0.17 | 0.33 | 0.07 | 0.12 | 0.35 | -0.17 | 0.31 | 0.11 | 0.12 | 0.43 | -0.13 | 0.35 |
| SD | -0.13 | 0.11 | 0.69 | -0.34 | 0.08 | -0.08 | 0.10 | 0.38 | -0.28 | 0.12 | -0.09 | 0.10 | 0.40 | -0.29 | 0.12 |
| SL | 0.03 | 0.12 | 0.33 | -0.21 | 0.27 | 0.06 | 0.12 | 0.33 | -0.17 | 0.29 | 0.09 | 0.12 | 0.40 | -0.14 | 0.32 |
| NDVI | 0.00 | 0.19 | 0.40 | -0.37 | 0.37 | 0.03 | 0.19 | 0.35 | -0.35 | 0.40 | 0.05 | 0.20 | 0.32 | -0.34 | 0.45 |
| **WLR:A** | **0.25** | **0.10** | **0.66** | **0.04** | **0.45** | 0.08 | 0.12 | 0.07 | -0.16 | 0.32 | 0.08 | 0.11 | 0.13 | -0.14 | 0.30 |
| WLR:SD | 0.23 | 0.12 | 0.52 | 0.00 | 0.47 | 0.07 | 0.10 | 0.08 | -0.12 | 0.26 | -0.01 | 0.12 | 0.09 | -0.26 | 0.23 |
| WLR:SL | 0.01 | 0.10 | 0.07 | -0.19 | 0.21 | 0.03 | 0.11 | 0.06 | -0.19 | 0.25 | -0.07 | 0.11 | 0.11 | -0.29 | 0.14 |
| WLR:NDVI | 0.19 | 0.15 | 0.19 | -0.10 | 0.48 | 0.15 | 0.13 | 0.12 | -0.11 | 0.40 | 0.02 | 0.11 | 0.06 | -0.19 | 0.23 |
| WLR:*FC* | -0.46 | 0.34 | 0.47 | -1.13 | 0.22 | -0.11 | 0.26 | 0.21 | -0.63 | 0.40 | 0.27 | 0.22 | 0.40 | -0.16 | 0.70 |
| *FC* | -0.27 | 0.31 | 1.00 | -0.89 | 0.36 | -0.39 | 0.27 | 1.00 | -0.93 | 0.16 | -0.47 | 0.27 | 1.00 | -1.00 | 0.07 |
| *T* | 0.10 | 0.17 | 1.00 | -0.24 | 0.45 | 0.00 | 0.16 | 1.00 | -0.32 | 0.32 | -0.04 | 0.17 | 1.00 | -0.37 | 0.29 |
| *GS* | -0.49 | 0.28 | 1.00 | -1.05 | 0.06 | -0.36 | 0.27 | 1.00 | -0.90 | 0.17 | -0.43 | 0.27 | 1.00 | -0.95 | 0.10 |
| *ST* | -0.25 | 0.25 | 1.00 | -0.74 | 0.24 | -0.20 | 0.25 | 1.00 | -0.70 | 0.31 | -0.25 | 0.24 | 1.00 | -0.74 | 0.24 |
| **Density** | | | | | | | | | | | | | | | |
| **Intercept** | **0.57** | **0.18** | **-** | **0.22** | **0.91** | **0.50** | **0.18** | **-** | **0.15** | **0.85** | **0.67** | **0.17** | **-** | **0.34** | **1.00** |
| **WLR** | **0.29** | **0.13** | **1.00** | **0.03** | **0.55** | **0.26** | **0.12** | **0.99** | **0.02** | **0.50** | -0.20 | 0.10 | 0.91 | -0.39 | 0.00 |
| A | 0.01 | 0.11 | 0.93 | -0.20 | 0.23 | 0.06 | 0.11 | 0.37 | -0.15 | 0.27 | 0.11 | 0.11 | 0.44 | -0.11 | 0.32 |
| **SD** | **-0.20** | **0.09** | **0.99** | **-0.38** | **-0.03** | -0.11 | 0.09 | 0.59 | -0.29 | 0.07 | -0.12 | 0.09 | 0.55 | -0.30 | 0.06 |
| SL | 0.04 | 0.10 | 0.52 | -0.16 | 0.25 | 0.15 | 0.11 | 0.59 | -0.07 | 0.36 | 0.18 | 0.11 | 0.72 | -0.04 | 0.40 |
| NDVI | -0.04 | 0.17 | 0.42 | -0.38 | 0.29 | 0.04 | 0.19 | 0.63 | -0.34 | 0.41 | 0.17 | 0.20 | 0.43 | -0.23 | 0.57 |
| **WLR:A** | **0.25** | **0.09** | **0.91** | **0.08** | **0.43** | 0.07 | 0.11 | 0.30 | -0.15 | 0.29 | 0.02 | 0.09 | 0.10 | -0.16 | 0.21 |
| **WLR:SD** | **0.29** | **0.10** | **0.97** | **0.09** | **0.49** | 0.11 | 0.08 | 0.10 | -0.05 | 0.28 | 0.01 | 0.10 | 0.13 | -0.19 | 0.21 |
| WLR:SL | 0.13 | 0.09 | 0.31 | -0.04 | 0.31 | 0.05 | 0.10 | 0.17 | -0.15 | 0.25 | -0.07 | 0.09 | 0.22 | -0.26 | 0.11 |
| WLR:NDVI | 0.18 | 0.15 | 0.20 | -0.11 | 0.47 | 0.22 | 0.12 | 0.48 | -0.02 | 0.46 | -0.01 | 0.09 | 0.09 | -0.18 | 0.17 |
| **WLR:*FC*** | **-0.74** | **0.29** | **0.96** | **-1.32** | **-0.17** | -0.26 | 0.28 | 0.39 | -0.81 | 0.28 | 0.06 | 0.19 | 0.24 | -0.33 | 0.44 |
| *FC* | -0.42 | 0.27 | 1.00 | -0.95 | 0.11 | -0.42 | 0.24 | 1.00 | -0.89 | 0.06 | **-0.57** | **0.24** | **1.00** | **-1.04** | **-0.10** |
| *T* | 0.16 | 0.15 | 1.00 | -0.14 | 0.47 | 0.01 | 0.18 | 1.00 | -0.34 | 0.36 | -0.07 | 0.19 | 1.00 | -0.44 | 0.30 |
| ***GS*** | **-0.73** | **0.24** | **1.00** | **-1.21** | **-0.25** | **-0.53** | **0.25** | **1.00** | **-1.04** | **-0.03** | **-0.70** | **0.24** | **1.00** | **-1.19** | **-0.22** |
| *ST* | -0.36 | 0.21 | 1.00 | -0.77 | 0.06 | -0.26 | 0.22 | 1.00 | -0.69 | 0.17 | -0.36 | 0.22 | 1.00 | -0.78 | 0.07 |
| **Mean weight** | | | | | | | | | | | | | | | |
| **Intercept** | **-0.54** | **0.18** | **-** | **-0.89** | **-0.19** | **-0.43** | **0.19** | **-** | **-0.81** | **-0.06** | **-0.53** | **0.17** | **-** | **-0.87** | **-0.20** |
| WLR | -0.03 | 0.14 | 0.66 | -0.30 | 0.24 | -0.18 | 0.12 | 0.85 | -0.41 | 0.06 | 0.02 | 0.12 | 0.63 | -0.23 | 0.26 |
| A | 0.00 | 0.12 | 0.30 | -0.23 | 0.24 | -0.01 | 0.11 | 0.30 | -0.24 | 0.21 | -0.02 | 0.12 | 0.30 | -0.25 | 0.22 |
| SD | 0.09 | 0.10 | 0.42 | -0.11 | 0.29 | 0.09 | 0.10 | 0.45 | -0.11 | 0.29 | 0.10 | 0.10 | 0.42 | -0.10 | 0.30 |
| SL | -0.16 | 0.11 | 0.70 | -0.39 | 0.06 | -0.18 | 0.11 | 0.65 | -0.40 | 0.05 | -0.18 | 0.12 | 0.66 | -0.41 | 0.05 |
| NDVI | -0.10 | 0.21 | 0.34 | -0.51 | 0.32 | -0.06 | 0.21 | 0.45 | -0.47 | 0.35 | -0.13 | 0.22 | 0.37 | -0.56 | 0.30 |
| WLR:A | -0.06 | 0.10 | 0.05 | -0.27 | 0.14 | 0.00 | 0.11 | 0.05 | -0.23 | 0.22 | 0.07 | 0.11 | 0.06 | -0.16 | 0.29 |
| WLR:SD | -0.14 | 0.12 | 0.14 | -0.38 | 0.09 | -0.12 | 0.09 | 0.18 | -0.30 | 0.07 | -0.07 | 0.13 | 0.08 | -0.32 | 0.19 |
| WLR:SL | -0.14 | 0.09 | 0.30 | -0.31 | 0.04 | 0.01 | 0.10 | 0.14 | -0.19 | 0.22 | 0.02 | 0.10 | 0.11 | -0.18 | 0.23 |
| WLR:NDVI | 0.05 | 0.15 | 0.06 | -0.24 | 0.34 | -0.16 | 0.12 | 0.21 | -0.40 | 0.07 | 0.03 | 0.10 | 0.06 | -0.18 | 0.23 |
| WLR:*FC* | 0.38 | 0.28 | 0.33 | -0.18 | 0.94 | 0.03 | 0.26 | 0.23 | -0.48 | 0.55 | 0.31 | 0.22 | 0.34 | -0.12 | 0.73 |
| *FC* | 0.30 | 0.29 | 1.00 | -0.27 | 0.87 | 0.20 | 0.26 | 1.00 | -0.32 | 0.72 | 0.30 | 0.26 | 1.00 | -0.21 | 0.81 |
| *T* | -0.01 | 0.18 | 1.00 | -0.36 | 0.34 | -0.02 | 0.18 | 1.00 | -0.38 | 0.34 | -0.02 | 0.18 | 1.00 | -0.38 | 0.34 |
| ***GS*** | **0.69** | **0.26** | **1.00** | **0.17** | **1.22** | **0.58** | **0.26** | **1.00** | **0.06** | **1.10** | **0.68** | **0.26** | **1.00** | **0.17** | **1.19** |
| *ST* | 0.32 | 0.23 | 1.00 | -0.14 | 0.78 | 0.22 | 0.24 | 1.00 | -0.26 | 0.70 | 0.29 | 0.23 | 1.00 | -0.18 | 0.75 |
| **Mean condition** | | | | | | | | | | | | | | | |
| Intercept | 0.23 | 0.23 | - | -0.23 | 0.68 | **0.47** | **0.22** | **-** | **0.05** | **0.90** | 0.18 | 0.21 | - | -0.24 | 0.59 |
| WLR | -0.28 | 0.16 | 1.00 | -0.61 | 0.04 | **-0.44** | **0.13** | **1.00** | **-0.70** | **-0.18** | 0.08 | 0.15 | 0.97 | -0.23 | 0.38 |
| A | 0.12 | 0.13 | 0.60 | -0.15 | 0.38 | 0.12 | 0.12 | 0.51 | -0.12 | 0.37 | 0.07 | 0.14 | 0.37 | -0.21 | 0.34 |
| SD | -0.08 | 0.10 | 0.41 | -0.28 | 0.13 | -0.06 | 0.10 | 0.37 | -0.26 | 0.14 | 0.00 | 0.11 | 0.33 | -0.23 | 0.22 |
| SL | 0.15 | 0.15 | 0.81 | -0.14 | 0.44 | 0.12 | 0.14 | 0.46 | -0.16 | 0.40 | 0.10 | 0.16 | 0.40 | -0.22 | 0.42 |
| **NDVI** | **0.52** | **0.21** | **0.96** | **0.09** | **0.94** | **0.48** | **0.19** | **0.97** | **0.10** | **0.86** | 0.39 | 0.21 | 0.85 | -0.03 | 0.81 |
| WLR:A | -0.18 | 0.11 | 0.36 | -0.40 | 0.05 | -0.11 | 0.12 | 0.17 | -0.35 | 0.14 | -0.08 | 0.14 | 0.11 | -0.35 | 0.19 |
| WLR:SD | -0.04 | 0.12 | 0.11 | -0.28 | 0.20 | -0.03 | 0.10 | 0.09 | -0.22 | 0.17 | 0.07 | 0.14 | 0.09 | -0.22 | 0.36 |
| **WLR:SL** | **-0.22** | **0.10** | **0.72** | **-0.41** | **-0.03** | -0.09 | 0.11 | 0.15 | -0.31 | 0.14 | 0.06 | 0.11 | 0.11 | -0.17 | 0.28 |
| WLR:NDVI | -0.08 | 0.15 | 0.30 | -0.37 | 0.21 | -0.04 | 0.12 | 0.27 | -0.29 | 0.21 | 0.16 | 0.11 | 0.47 | -0.05 | 0.38 |
| WLR:*FC* | 0.03 | 0.32 | 0.27 | -0.61 | 0.67 | -0.20 | 0.25 | 0.34 | -0.70 | 0.29 | 0.51 | 0.26 | 0.76 | -0.01 | 1.02 |
| *FC* | -0.32 | 0.33 | 1.00 | -0.98 | 0.33 | -0.10 | 0.28 | 1.00 | -0.66 | 0.47 | 0.33 | 0.30 | 1.00 | -0.27 | 0.93 |
| ***T*** | **-0.71** | **0.24** | **1.00** | **-1.19** | **-0.24** | **-0.51** | **0.21** | **1.00** | **-0.93** | **-0.09** | **-0.46** | **0.22** | **1.00** | **-0.90** | **-0.02** |
| *GS* | -0.30 | 0.32 | 1.00 | -0.93 | 0.33 | **-0.73** | **0.30** | **1.00** | **-1.32** | **-0.14** | -0.41 | 0.32 | 1.00 | -1.04 | 0.22 |
| *ST* | -0.12 | 0.26 | 1.00 | -0.64 | 0.40 | -0.31 | 0.26 | 1.00 | -0.83 | 0.21 | -0.13 | 0.27 | 1.00 | -0.66 | 0.41 |
| **Mean maturity length** | | | | | | | | | | | | | | | |
| Intercept | -0.55 | 0.30 | - | -1.16 | 0.07 | -0.51 | 0.32 | - | -1.15 | 0.13 | -0.56 | 0.30 | - | -1.17 | 0.05 |
| WLR | -0.05 | 0.20 | 0.52 | -0.45 | 0.35 | 0.02 | 0.21 | 0.75 | -0.41 | 0.45 | -0.04 | 0.20 | 0.61 | -0.44 | 0.36 |
| **A** | **0.42** | **0.16** | **0.98** | **0.10** | **0.74** | **0.41** | **0.16** | **0.99** | **0.08** | **0.73** | **0.41** | **0.17** | **0.98** | **0.05** | **0.76** |
| SD | 0.10 | 0.15 | 0.36 | -0.20 | 0.41 | 0.10 | 0.15 | 0.37 | -0.20 | 0.40 | 0.08 | 0.15 | 0.34 | -0.23 | 0.39 |
| SL | -0.03 | 0.16 | 0.31 | -0.35 | 0.30 | -0.05 | 0.17 | 0.33 | -0.39 | 0.30 | -0.01 | 0.17 | 0.35 | -0.36 | 0.34 |
| NDVI | 0.14 | 0.26 | 0.33 | -0.39 | 0.67 | 0.16 | 0.26 | 0.47 | -0.37 | 0.69 | 0.15 | 0.27 | 0.34 | -0.41 | 0.71 |
| WLR:A | -0.10 | 0.16 | 0.16 | -0.43 | 0.22 | -0.12 | 0.16 | 0.26 | -0.45 | 0.20 | -0.18 | 0.16 | 0.28 | -0.50 | 0.14 |
| WLR:SD | -0.05 | 0.16 | 0.05 | -0.38 | 0.27 | -0.03 | 0.14 | 0.07 | -0.32 | 0.26 | 0.11 | 0.18 | 0.06 | -0.26 | 0.48 |
| WLR:SL | -0.11 | 0.14 | 0.06 | -0.39 | 0.17 | -0.07 | 0.19 | 0.07 | -0.46 | 0.33 | -0.18 | 0.16 | 0.11 | -0.51 | 0.15 |
| WLR:NDVI | 0.04 | 0.19 | 0.04 | -0.36 | 0.43 | -0.25 | 0.16 | 0.24 | -0.57 | 0.08 | 0.07 | 0.16 | 0.06 | -0.25 | 0.40 |
| WLR:*FC* | -0.12 | 0.40 | 0.13 | -0.93 | 0.69 | -0.36 | 0.35 | 0.33 | -1.06 | 0.35 | -0.15 | 0.38 | 0.18 | -0.93 | 0.63 |
| *FC* | 0.02 | 0.37 | 1.00 | -0.74 | 0.78 | 0.00 | 0.35 | 1.00 | -0.71 | 0.70 | 0.05 | 0.33 | 1.00 | -0.63 | 0.73 |
| *T* | -0.39 | 0.22 | 1.00 | -0.84 | 0.07 | -0.37 | 0.23 | 1.00 | -0.83 | 0.08 | -0.37 | 0.23 | 1.00 | -0.84 | 0.11 |
| *GS* | 0.52 | 0.35 | 1.00 | -0.20 | 1.23 | 0.45 | 0.37 | 1.00 | -0.31 | 1.21 | 0.54 | 0.36 | 1.00 | -0.18 | 1.27 |
| *ST* | 0.41 | 0.31 | 1.00 | -0.21 | 1.04 | 0.37 | 0.31 | 1.00 | -0.26 | 1.00 | 0.45 | 0.31 | 1.00 | -0.19 | 1.08 |