Science of the Total Environment 618 (2018) 313–322

Contents lists available at ScienceDirect

Science of the Total Environment

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

Hydropower impacts on reservoir fish populations are modified by environmental variation

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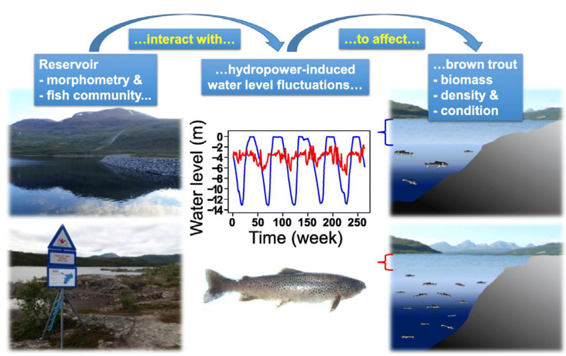
HIGHLIGHTS

- Hydropower impacts on reservoir ecosystems are relatively poorly known.
- Brown trout population status was modelled in 102 Norwegian hydropower reservoirs.
- Local conditions modified water level regulation (WLR) impacts on trout populations.
- Trout density increased but condition decreased with increasing WLR frequency.
- The findings are essential for management and mitigation of hydropower operations.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 25 September 2017
Received in revised form 25 October 2017
Accepted 26 October 2017
Available online xxxx

Editor: D. Barcelo

Keywords:
Anthropogenic disturbance
Hydroelectricity
Lake ecosystem
Population dynamics
Renewable energy
Salmonid

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,

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https://doi.org/10.1016/j.scitotenv.2017.10.268

management and mitigation of hydropower operations that need to meet the increasing worldwide demand for both renewable energy and ecosystem services delivered by freshwaters.

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., 2017; 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).

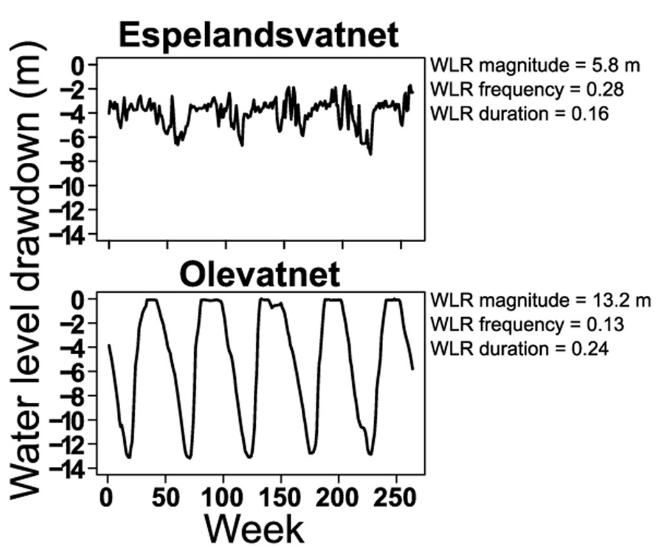

Fig. 1. Examples of contrasting five-year WLR patterns in two Norwegian hydropower reservoirs, plotted as the mean weekly deviance from the 10-year maximum water level. Espelandsvatnet (surface area 1.2 km^2) is subjected to frequent and irregular WLR, whereas more gradual, higher-magnitude WLR with 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