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PRIMARY RESEARCH PAPER

Effects of water level regulation in alpine hydropower reservoirs: an ecosystem perspective with a special emphasis on fish

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Abstract Sustainable development of hydropower demands a holistic view of potential impacts of water level regulation (WLR) on reservoir ecosystems. Most environmental studies of hydropower have focused on rivers, whereas environmental effects of hydropower operations on reservoirs are less well understood. Here, we synthesize knowledge on how WLR from hydropower affects alpine lake ecosystems and highlight the fundamental factors that shape the environmental impacts of WLR. Our analysis of these impacts ranges from abiotic conditions to lower trophic levels and ultimately to fish. We conclude that the environmental effects are complex and case-specific and thus considering the operational regime of WLR (i.e. amplitude, timing, frequency, and rate of change) as well as the reservoir's morphometry, geology and biotic community are prerequisites for any reliable predictions. Finally, we indicate promising avenues for future research and argue that recording and sharing of data, views and demands among different stakeholders, including operators, researchers and the public, is necessary for the

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sustainable development of hydropower in alpine lakes.

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Water level regulation as a stressor caused by hydropower

Hydropower is amongst the largest and fastest growing sources of renewable energy worldwide and its environmental effects on aquatic ecosystems can be substantial. In the year 2014, hydropower plants with a net installed capacity of 1,171 GW provided 16% (3,906 TWh) of the world's electricity generation (IEA, 2016), and there is a global technical potential to more than triple that capacity (Kumar et al., 2011). Such development implies that a growing proportion of lakes will be influenced by hydropower operations in the years to come. Further, the operational regime of existing hydropower plants, and hence water level regulation in existing reservoirs, may be altered to meet future needs for more flexible energy generation and storage (Kumar et al., 2011; Solvang et al. 2014). The use of storage and pumped-storage reservoirs to balance volatile production by other renewable energies is also likely to increase in importance (Hirsch et al., 2016).

Many of the lakes influenced by the increase in hydropower production are essential to humans, since lake ecosystems provide 77% of the freshwater supply and other key ecosystem services (García Molinos et al., 2015). In relation to their size, lakes contribute disproportionally to global biodiversity and have a much higher number of endemic species threatened by extinction than terrestrial ecosystems (Collen et al., 2014). For a sustainable development, it is essential to be able to predict and minimize the potential environmental effects of both future alterations in the operational regime of existing reservoirs and the transformation of natural lakes into new reservoirs.

The most obvious and profound effect hydropower has on lake ecosystems is a change from natural water level fluctuations to regulated water levels. These water level regulations (henceforth termed WLR) often exceed and differ from natural fluctuations in terms of their combined amplitude, rate of change, and frequency (Hirsch et al., 2014) (Fig. 1). WLR are a stressor (sensu Adams, 2002) whose effects on lake ecosystems are still not well understood. Like other stressors, WLR can have both positive and negative impacts (e.g. Adams, 1990, 2002) whose eventuality needs to be properly accounted for in the assessment of environmental impacts. Regulation patterns vary greatly between reservoirs (e.g. Fig. 1). In some cases, the regulation amplitude may not exceed natural water level fluctuations, but still alter the timing, rate of change, and frequency of water level fluctuations. Natural water level fluctuations can also regulate the structure and function of lake ecosystems (Evtimova & Donohue, 2016) and thus natural variation should always be considered when monitoring, evaluating and predicting WLR impacts.

In this review, we seek to synthesize the current knowledge on the ecosystem effects of WLR in alpine storage and pumped-storage hydropower reservoirs. We specifically focus on hydropower reservoirs in alpine regions and thus exclude run-of-the-river systems as well as reservoirs built for other purposes, such as storing drinking and irrigation water. For consistency, all regulated lakes are termed reservoirs, independent of how the lake is dammed or regulated for hydropower production. Alpine regions, including the montane and subalpine regions, are characterized by a topography that allows for storage and release of water, and thus they are prime candidates for the development of hydropower (Hirsch et al., 2014). We particularly focus on the effects of WLR on fish, because fish populations are suitable sentinels for ecosystem change and they are well-studied species in food-web and lake ecology. As long-lived top predators, fish integrate the effects of environmental stressors both in time and space and they are socio-

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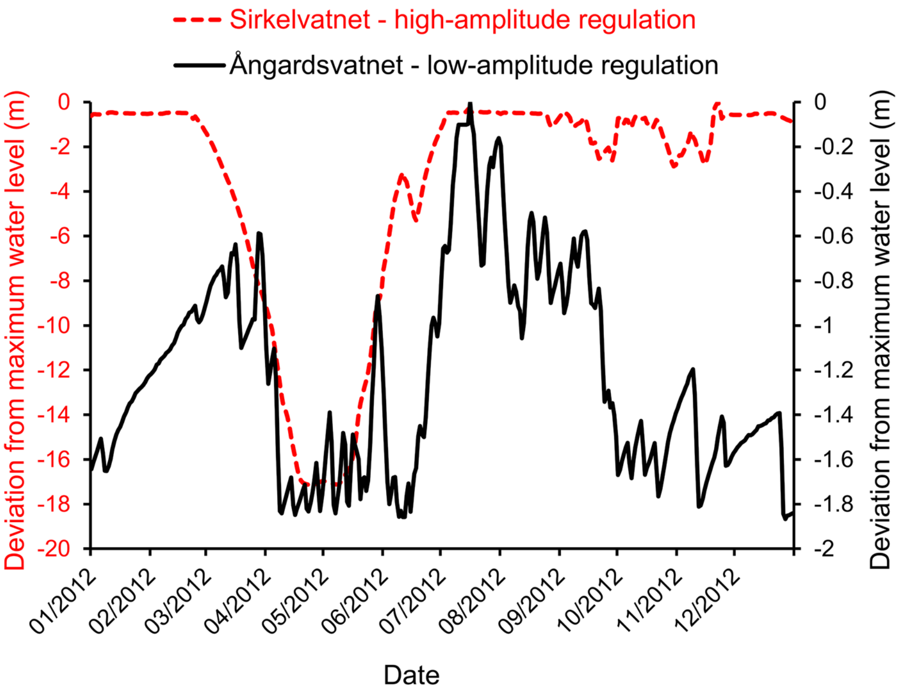

Fig. 1 Daily water levels in heavily regulated Lake Sirkelvatnet and slightly regulated Lake Ångardsvatnet, Norway. The data illustrates different regulation patterns in reservoirs, with a more drastic but gradual winter drawdown in Sirkelvatnet as compared to generally minor, but relatively rapid, water level fluctuations in Ångardsvatnet. Note that the values for Ångardsvatnet are presented on a secondary *y*-axis with a smaller range of water levels. The water level data were extracted from the Hydra II database maintained by the Norwegian Water Resources and Energy Directorate

economically relevant because they deliver important cultural and provisioning ecosystem services to humans (Holmlund & Hammer, 1999; Adams, 2002).

Previous reviews by Baxter (1977), Cott et al. (2008), and Zohary & Ostrovsky (2011) have greatly advanced our knowledge of WLR impacts on reservoir ecosystems. However, we still lack a holistic ecosystem perspective of the effects of WLR, ranging from abiotic factors to the higher food-web levels. The immediate responses of reservoir ecosystems to WLR are alterations in abiotic (physical and chemical) characteristics, which ultimately shape the abundance and structure of the biotic community. Changes in the biotic community may in turn have significant feedbacks on the abiotic environment. However, each reservoir has its unique abiotic and biotic characteristics and finding any universal responses of reservoir ecosystems to WLR is a challenging task. For instance, based on unpublished data from 67 Norwegian reservoirs (Fig. 2), fish yield shows no clear response to WLR amplitude (i.e. difference between the highest and lowest water level), although the reservoirs are situated in a geographically restricted area and host only allopatric brown trout (*Salmo trutta* L.). The lack of a relationship illustrates the complexity of, and potential interactions between, natural and anthropogenic processes that may mask or shape WLR impacts even in species-poor alpine reservoirs. Hence, for improved monitoring and mitigation of hydropower impacts, it is necessary to disentangle the ecologically and hydrologically most relevant measures of WLR that connect the hydropower operations to key abiotic and biotic impacts. Examples of WLR measures include the amplitude, timing, frequency and rate of change of water level fluctuations (Bakken et al., 2016) and the relative proportion of affected littoral habitat (Hirsch et al., 2016). Reliable predictions and evaluations of WLR impacts should be case-specific and acknowledge the natural variation and complexity of reservoir ecosystems. Still, a synthesis of the potential impacts, mechanisms and confounding factors related to WLR, as well as large-scale studies separating WLR impacts from natural variation, would be invaluable for the development of environmentally friendly hydropower operations in alpine lakes.

Rather than attempting an exhaustive literature survey on selected issues of WLR, the aim of this review is to provide an integrative view of WLR impacts on alpine reservoir ecosystems and particularly on fish. We provide a structured review of which factors should be considered when aiming to understand the environmental effects of WLR in alpine reservoirs, and indicate which factors are well

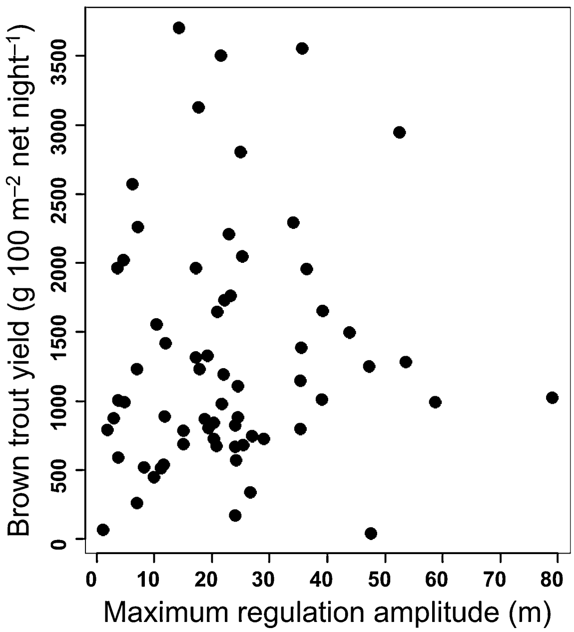

Fig. 2 Brown trout yield (in grams per 100 m^2 of multi-mesh gillnet per night) from standardized survey fishing (see Eloranta et al., 2016a for more details) conducted in 67 Norwegian reservoirs that differ in regulation amplitude (i.e. maximum difference between the highest and the lowest water level). The reservoirs are considered highly comparable as they are located within a geographically limited area and they host brown trout as the only fish species. The results from linear ($F_{1,65} = 0.177$, $P = 0.675$) and non-linear ($F_{2,64} = 0.457$, $P = 0.636$) models, the latter including linear and quadratic terms of regulation amplitude, indicate non-significant relationships

understood and which are understudied. We start by considering WLR as an anthropogenic stressor on ecosystems from an abiotic perspective. Thereafter, we describe how WLR can affect the ecosystem from the bottom of the food chain up to higher trophic levels. Focusing on fish, we seek to explore which complex mechanisms lie behind the observed environmental effects of WLR. We close by identifying promising avenues for future research on how to tackle the complexity of WLR effects, arguing that such research should form the basis for sustainable development of hydropower.

The abiotic framework of water level regulation

WLR effects on whole ecosystems often arise from fundamental changes in the physical and chemical characteristics of the reservoirs, such as in bottom structure, temperature and water quality (e.g. Baxter, 1977; Zohary & Ostrovsky, 2011). These abiotic changes can affect fish directly e.g. via desiccation and freezing of eggs (Gaboury & Patalas, 1984), or indirectly e.g. via altered abundance and composition of potential food resources (Cott et al., 2008). In this section, we briefly summarize the main effects of WLR on the abiotic characteristics of alpine reservoirs, focusing on the most important factors that may ultimately affect fish and the whole reservoir ecosystem.

Erosion and reservoir succession

The most visual WLR impacts occur in the littoral zone—normally delineated as the shallow area with enough solar radiation at the bottom for photosynthesis (Wetzel, 2001; Cantonati & Lowe, 2014)—where desiccation, freezing and erosion commonly lead to physical and biological deterioration of the riparian and shallow bottom areas (Fig. 3A). Within the regulation zone, erosion by wave action and ice scouring removes fine particles and renders the substratum unstable, whereas the deeper bottom areas are subjected to increased sedimentation rate due to flushed fine particles. The coarse bottom substrate, like gravel, is often covered by fine particles, like sand and silt, which decreases the bottom surface area and interstices available as habitats for littoral organisms (e.g. Hellsten, 1998; Zohary & Ostrovsky, 2011). One fundamental factor to consider when evaluating, monitoring and mitigating environmental effects of WLR is the reservoir succession. WLR and potential flooding of originally dry land areas typically increases physical erosion of the riparian zone, as well as internal and external loading of dissolved nutrients, carbon and pollutants. Hence, the reservoir water quality decreases (Fig. 3C, D; Baxter, 1977; Hellsten, 1998; Cott et al., 2008, Dieter et al., 2015) and in some cases so does the quality of fish for human consumption (French et al., 1998). The potential increase in availability of autochthonous and allochthonous resources may lead to increased biological production at the early succession of the reservoir. This phase is typically followed by trophic depression when organic matter and nutrients are exhausted or rendered unavailable by silting (Baxter, 1977; Rydin et al., 2008; Milbrink et al., 2011).

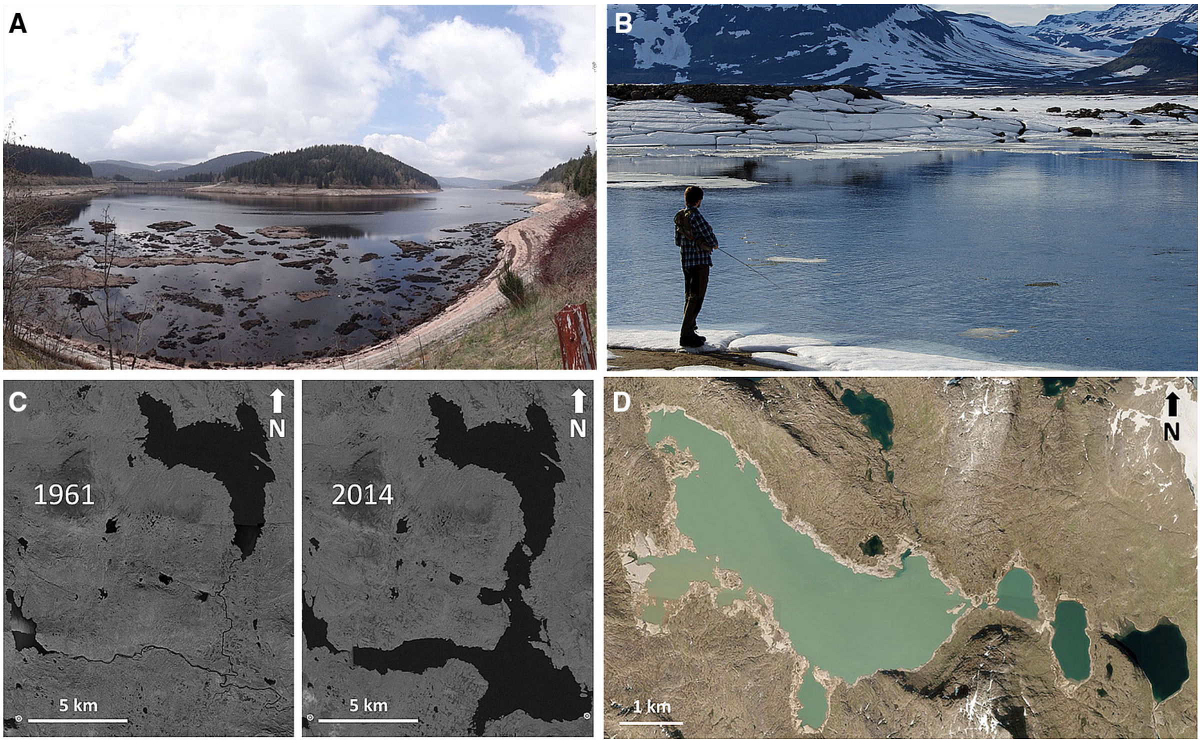

Fig. 3 (**A**) Water level regulation for hydropower production can lead to a severely impaired littoral zone as in the Schluchsee reservoir in the German Schwarzwald Highlands. (**B**) During winter, water level fluctuations can break up ice formation, as illustrated here from the Eldrevatn reservoir in Sogn og Fjordane, Norway. (**C**) The water levels in small lakes frequently exceed the natural levels when the lake is dammed and transformed into a hydropower reservoir. Here, the effect is illustrated with aerial photos taken before (1961) and after (2014) the construction of the Nesjøen dam (River Nea, Sør-Trøndelag, Norway). Flooding the valley below Lake Essandsjøen up to the upper water level of the lake created a continuous reservoir with surface water levels between 723 and 731 m.a.s.l. (**D**) An aerial photograph illustrating how WLR influences lake shoreline and water turbidity in the Langvatn reservoir in Nordland, Norway (maximum regulation amplitude 42 m). The small lakes north and east from the Langvatn reservoir are not subjected to unnatural shoreline erosion and resuspension of silt and thus have undisturbed littoral zones and clear water. Source of aerial photographs (**C**, **D**): www.kart.finn.no. Picture credits: Philipp Hirsch: (**A**); Nils Roar Sælthun: (**B**)

Water temperature and ice conditions

In addition to physical habitat alterations in the littoral zone, WLR typically influences water temperature and ice conditions (Fig. 3B). Ice cover may become unstable, break or not form at all if the amplitude or frequency of WLR are high. Further, water temperature and ice cover are strongly connected and if WLR reduces the ice cover, this can lead to changes in the thermal regime of the reservoir such as earlier warming and mixing in spring (Gebre et al., 2014). WLR-induced changes in temperature profiles, ice-cover stability and water quality are particularly evident in pumped-storage reservoirs, where water is transferred between a lower and an upper reservoir, which may have drastically different water qualities and temperatures (Potter et al., 1982; Bonalumi et al., 2011, 2012). For instance, a study of a North American reservoir found that pumped-storage operations facilitated heat exchange between water layers (i.e. vertical temperature differences decreased from 13°C to 7°C), expanded the epilimnion depth and delayed the thermal stratification (Potter et al., 1982). The depth of the turbine tunnel(s) likely influences how the reservoir's temperature profile, ice-cover stability and water qualities are affected by WLR (Bonalumi et al., 2012). More specifically, if the outflow turbine tunnel is located in the deep hypolimnion, the relative loss of heat from the system during a drawdown is low in summer, but high in winter. Conversely, if the turbine tunnel is located in the epilimnion, relatively cold surface water is discharged in winter and relatively warm water in summer. There is limited empirical evidence (but see Bonalumi et al., 2012), but it is likely that pumped-storage operations have minor impacts on temperature profiles if hypolimnetic water with relatively constant temperature is transferred between the lower and upper reservoirs.

Oxygen concentration and water clarity

The effect of WLR on temperature and ice cover may indirectly change other abiotic conditions such as the oxygen concentrations in different water layers and light attenuation (Cott et al., 2008). Most alpine reservoirs are oligotrophic and have a well-oxygenated water column all year round. In contrast, more eutrophic reservoirs may suffer from winter anoxia due to the discharge of oxygenated surface water through the turbines during winter drawdown (Cott et al., 2008). The light attenuation within the water column can also be severely affected by WLR because of increased resuspension of fine particles (e.g. clay, silt or humus, Fig. 3D). The resulting decrease in water clarity can cause light limitation of primary production and reduce secondary production in the reservoir (cf. Borgstrøm et al., 1992; James & Graynoth, 2002; Karlsson et al., 2009; Finstad et al., 2014). However, recent research suggests that, in some cases, availability of well-oxygenated habitat rather than light and food resources may become the principal factor controlling secondary production in lakes (Craig et al., 2015).

Effects depend on the reservoir's operational regime and morphometry

As evident from the above, the effects of WLR in reservoirs are not easily generalizable in terms of which type of WLR triggers which type of abiotic response. However, two fundamental and tightly linked, yet poorly studied, predictors are evident: the operational regime (the extent and temporal pattern of WLR, as exemplified in Fig. 1), and the reservoir's morphometry and geology. The difference between the highest and lowest water level determines how deep and large bottom areas are exposed to WLR impacts, including desiccation, freezing and erosion via ice scouring, waves and wind (Hellsten, 1998). Correspondingly, the temporal pattern (timing, frequency and rate of change) of WLR influences physical, chemical and biological impacts (Marttunen et al., 2006; Cott et al., 2008; Zohary & Ostrovsky, 2011). For instance, water level drawdowns expose bottom areas to desiccation and wind erosion during open-water periods and to freezing and ice scouring during ice-cover periods. Raising water levels may increase input of allochthonous nutrients and organic matter, including invertebrate prey for fish, during open-water periods, and decrease ice-cover stability during cold seasons (e.g. Baxter, 1977). Organisms and life-stages varying in size, mobility and sensitivity show different responses to WLR (see "Effects on lower trophic levels"). Small, sessile or highly specialized taxa and life-stages are generally more vulnerable than large, mobile or more generalist taxa and conspecifics. Hence, the operational regime largely shapes the degree and nature of WLR impacts on different levels of biological organization.

WLR may have drastically different impacts on reservoirs that differ in morphometry (i.e. area, depth and shoreline complexity) or geology. Lake morphometry determines several fundamental limnological factors, such as habitat availability and productivity (Wetzel, 2001; Vadeboncoeur et al., 2008; McMeans et al., 2016). Lakes with complex (dendritic) shorelines and gentle slopes generally have larger littoral zones and experience more complex mixing processes compared to lakes with simple shorelines and steep shores. Although steep and circular lakes have larger proportions of pelagic and profundal habitats, WLR can still have severe environmental impacts, particularly if the entire littoral habitat is disturbed (Marttunen et al., 2006). Lakes formed on, or surrounded by, loose substrates such as peatland or clay soils are likely more sensitive to WLR-induced changes in water quality than those based on solid bedrock. For instance, several alpine reservoirs in Norway have very turbid water due to high resuspension of silt from the sediment to the water column, which is still evident decades after the onset of hydropower operations (Fig. 3D; Eloranta et al., 2016b). Such potential changes in light penetration and nutrient availability ultimately affect biological productivity, ranging from primary producers up to top predators, both in the littoral and pelagic food-web compartments (Wetzel, 2001; Vadeboncoeur et al., 2008; Karlsson et al., 2009). Hence, the reservoir's operational regime, morphometry and geology are all essential factors that determine how

WLR affects reservoir ecosystems. Next, we discuss in more detail how the WLR-induced changes in abiotic conditions influence different trophic levels in the littoral and pelagic food-web compartments.

Effects on lower trophic levels

Littoral zone

The lake littoral zone is typically the most diverse and productive area (Vadeboncoeur et al., 2002; Cantonati & Lowe, 2014), particularly in oligotrophic, clear-water lakes (Karlsson & Byström, 2005; Ask et al., 2009; Hampton et al., 2011). Hence, WLR-induced disturbance to the littoral zone commonly decreases biological productivity and diversity in the whole reservoir ecosystem (Fig. 4). Freezing, desiccation and direct physical stress associated with WLR often decrease the abundance and diversity of littoral sessile macrophytes and benthic algae (e.g. Hellsten & Riihimäki, 1996; Mjelde et al., 2013; Evtimova & Donohue, 2014, Hirsch et al., 2016). These changes at the bottom of the food web are often reflected in higher trophic levels (i.e. benthic invertebrates and fish) via reduced food and habitat resources (e.g. Grimås, 1964, 1965; Aroviita & Hämäläinen, 2008; Milbrink et al., 2011). Recent empirical studies provide further evidence that WLR can reduce littoral primary production (Hirsch et al., 2016) and induce a pelagic niche shift by generalist fish (Eloranta et al., 2016a).

The species richness of benthic invertebrates is commonly reduced due to WLR, because sensitive taxa are lost and only more tolerant taxa remain (Smith et al., 1987; Aroviita & Hämäläinen, 2008; White et al., 2011). Sensitive taxa typically cannot escape or endure unfavourable conditions, or they suffer from mismatched life-history events as natural water levels turn into WLR. These taxa often include important fish food resources, such as large crustaceans, molluscs and insect larvae (Grimås, 1964, 1965; Aass, 1969; McEwen & Butler, 2010). While the species richness of benthic invertebrates decreases due to WLR, the densities of tolerant taxa might increase (Furey et al.,

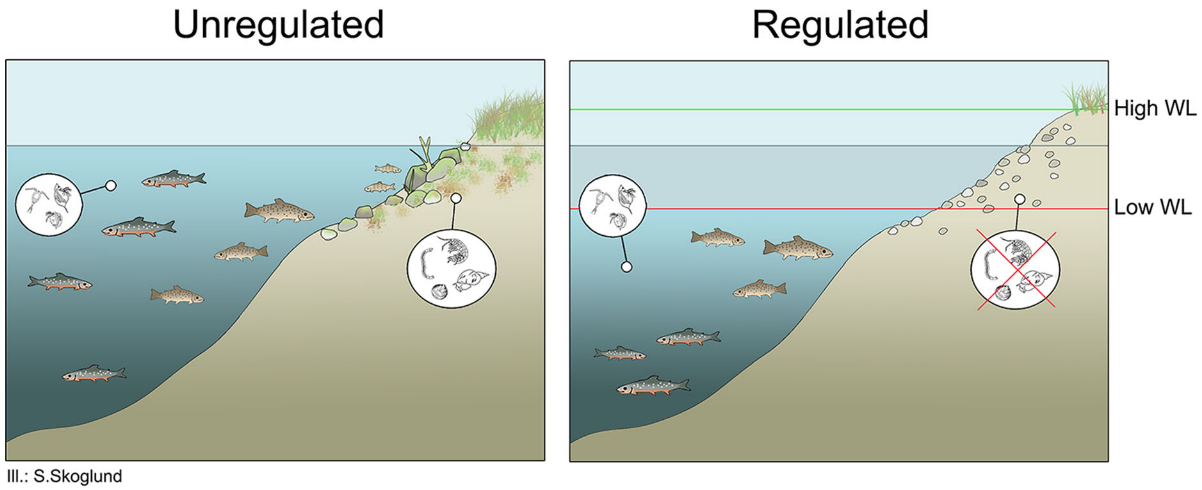

Fig. 4 Schematic illustration of how WLR influences lower trophic levels and fish in reservoirs. The littoral food-web compartment is affected by a loss of primary producers and a subsequent change in community composition and density of primary consumers. Sessile taxa become replaced by taxa that can move faster or have physiological adaptations or resting stages that survive desiccation and freezing. The effects of WLR on the pelagic food-web compartment are less straightforward because pelagic organisms are less impacted by rising or falling water levels as they can simply 'move' with the water level. However, zooplankton communities can be indirectly affected by WLR. For example, nutrient dynamics, water retention time and other abiotic conditions such as water clarity can cause changes in predator–prey dynamics in the pelagic food-web compartment. Many fish species use the littoral zone as feeding, spawning or nursery grounds, but WLR can make the habitat unavailable when water levels fall or become unsuitable as a result of macrophyte loss or increased substrate siltation. Due to the reduced littoral resources, competitive interactions among fish change. Species and individuals that are better in exploiting pelagic or profundal resources gain a competitive edge over littoral specialists. Picture credit: Sigrid Skoglund. Drawings of benthic invertebrates and zooplankton: Pekka Antti-Poika

2006; Thompson & Ryder, 2008). The tolerant taxa predominantly found in alpine reservoirs include chironomids and oligochaetes, as well as other taxa with physiological or life-cycle adaptations for desiccation and freezing (i.e. diapause stages, cocoons, and ephippia) (Grimås, 1964, 1965; Palomäki & Koskeniemi, 1993; Valdovinos et al., 2007). Overall, the general pattern is a decreased biomass and hence availability of large-sized benthic invertebrate prey for fish.

Pelagic and profundal zone

While the effects of WLR on littoral communities are frequently studied, there is limited empirical evidence of how WLR influences pelagic planktonic and profundal benthic organisms in alpine reservoirs. These organisms and habitats are likely less affected since they are usually not exposed to the direct physical disturbance associated with WLR (Spitale et al., 2016; Fig. 4), except increased sedimentation and turbidity due to flushing of fine particles from the regulation zone (Fig. 3D). However, reduced littoral habitat and food resources can increase predatory interactions in the pelagic food-web compartment and thereby alter the structure and stability of entire lake food webs (Tunney et al., 2014; McMeans et al., 2016). WLR-induced changes in water quality (e.g. turbidity, nutrients and oxygen concentration) and temperature can alter the abundance and composition of phytoplankton and zooplankton communities (Baxter, 1977; Zohary & Ostrovsky, 2011). WLR can also reduce habitat availability if the profundal zone suffers from WLR-induced anoxia (Cott et al., 2008). Zooplankton responses to WLR in alpine reservoirs may be driven by bottom-up processes, but this remains unstudied because the few published studies focus on reservoirs in other climatic zones (e.g. Gal et al., 2013; Simoes et al., 2015). However, one study in a subarctic Newfoundland reservoir found that zooplankton biomass, which increased approximately 19-fold during 11 years after impoundment, was not correlated with increased nutrient or resource availability (i.e. bottom-up processes) but instead with increased retention time and hence decreased washout of zooplankton (Campbell et al., 1998). Based on stable hydrogen isotope data from ten reservoirs in central Virginia, zooplankton may rely strongly on allochthonous (terrestrial) resources, but zooplankton allochthony may not be related to the reservoir age despite successional reduction of the terrestrial particulate organic matter pool (Emery et al., 2015). In essence, as discussed in the following section and exemplified by recent research (Eloranta et al., 2016b; Hirsch et al., 2016), the potential shift from littoral towards more pelagic primary and secondary production can ultimately control the abundance, growth, niche use and competitive interactions among fish populations in alpine reservoirs (Fig. 4).

Effects on fish

Compared to abiotic factors and lower trophic levels, the ecology of fish and trophic interactions among and within fish species are well studied in alpine lakes and reservoirs. Here, we summarize three main processes that affect fish when natural water level fluctuations change into WLR: (1) The most obvious and direct effects are changes in spawning success and population recruitment that result from the degradation or loss of suitable spawning and nursing grounds, ultimately increasing egg and fry mortality. (2) Further, WLR indirectly affects fish production and overall fish biomass through changes in the reservoir's overall productivity. In general, fish biomass may increase following increased availability of allochthonous and autochtonous organic matter and nutrients due to WLR, but decrease as the reservoir's succession enters the stage of trophic depression. (3) Finally, the relative changes in the reservoir's littoral and pelagic food-web compartments can have cascading and feedback food-web effects. As resources change, competitive and predatory relationships among and between fish species and their resources are rearranged. All such trophic interactions occur under a specific set of aforementioned abiotic conditions (e.g. water clarity and ice cover) which are dependent on WLR and can influence competitive and predator–prey relationships.

Fish spawning and population recruitment

Many alpine fish species are dependent on suitable littoral spawning or nursery grounds. Thus, a temporal match between water levels and the timing of spawning or development of early life stages may be crucial for the reproductive success of fish in reservoirs. How exactly fish are affected depends on the species' spawning season and habitats (Gertzen et al., 2012; Linløkken & Sandlund, 2016). Physical deterioration of littoral spawning grounds due to flushing, erosion, drying and freezing of the littoral zone is detrimental for both littoral spring- and autumn-spawning fishes (Kahl et al., 2008). For example, the eggs and juveniles of autumn-spawning salmonids like brown trout, Arctic charr (*Salvelinus alpinus* L.) and kokanee (*Oncorhynchus nerka* Walbaum) have been found to be exposed to drying or freezing due to water level drawdown in late spring (e.g. Aass, 1986; Modde et al., 1997; Brabrand et al., 2002). Recruitment in a population of the shallow-water spawning European whitefish (*Coregonus lavaretus* L.) was negatively affected by the combination of early ice-off and low water levels in late April (Linløkken & Sandlund, 2016). At the same time, the reduction in the whitefish population appeared to have resulted in increased recruitment of the competitor vendace (*C. albula* L.). Similar observations have been noted in other European reservoirs, where extensive water level drawdown in late winter or early spring can disturb the juvenile survival of autumn-spawning coregonids (Sutela et al., 2002; Winfield et al., 2004).

Studies on fish that depend on suitable littoral areas for nest building in spring suggest that WLR may result in non-optimal nest placement or nest abandonment, which ultimately impairs recruitment (Clark et al., 2008). In contrast, WLR and flooding of vegetated riparian areas may provide profitable spawning and nursery habitats for littoral spring-spawning fishes (Miranda et al., 1984; Miranda & Lowery, 2007). Indeed, higher than normal water levels during the spawning period have been associated with dominant year-classes of spring-spawning pike (*Esox lucius* L.) and roach (*Rutilus rutilus* L.) populations in lowland reservoirs (Kahl et al., 2008), but similar recruitment studies for alpine reservoirs are largely lacking (except recent work by Linløkken & Sandlund, 2016). In some cases, prolonged water level drawdowns that coincide with spawning and growing periods can have positive effects on resident fish populations: decreased population size due to recruitment failure can result in increased growth rates in the surviving recruits due to reduced intra-specific competition (Heman et al., 1969; Eloranta et al., 2016b). In alpine reservoirs, some species may also adapt their spawning behaviour to compensate for the loss of spawning habitat by utilizing inlet streams, or by shifting spawning grounds below the regulation zone. For example, in a reservoir in southwestern Norway, a strong reduction in brown trout recruitment was predicted prior to the start of hydropower operations in 1969, because in-lake spawning occurred on littoral grounds within the regulation zone (Rosseland, 1964). However, brown trout maintained high recruitment success by spawning below the drawdown limit, where eggs did not suffer from desiccation (Brabrand et al., 2002). Correspondingly, the older Ringedal reservoir in western Norway (regulated since 1908) is dominated by a dense population of brown trout although there are no inlet rivers available for spawning (Borgstrøm et al., 1992). In summary, WLR may have direct negative effects on fish that rely on the littoral zone as a spawning ground (Sutela & Vehanen, 2008), but whether such effects are reflected in the growth of cohorts, and ultimately population biomass, depends on the species and local reservoir conditions.

Fish biomass and overall productivity

When a lake is turned into a reservoir, the WLR-induced release of nutrients from sediments or newly flooded land may promote primary and secondary production (Rydin et al., 2008). Overall fish biomass may initially increase as autochthonous production increases and there is a higher availability of drifting littoral and terrestrial prey for larger consumers (Baxter, 1977; Milbrink et al., 2011). As the reservoir ages, nutrient input from the inundated land and the littoral zone commonly declines, and large-bodied and energetically profitable macroinvertebrate prey items may disappear. Smaller macroinvertebrates that are less energetically profitable for fish frequently start to dominate (McEwen & Butler, 2010) (Fig. 4). An overall reduction in nutrient load in the reservoir can result in a reduction in the pelagic resource base (Rydin et al., 2008; Milbrink et al., 2011). In combination with the more evident reduction in the littoral resource base, as well as potential recruitment failure, this often leads to an overall reduction in fish biomass as the reservoir's autochthonous production stabilizes below pre-damming levels (Aass, 1990; Aass et al., 2004; Milbrink et al., 2011). A recent study from 283 Norwegian lakes indicates that brown trout abundance is generally lower in regulated lakes as compared to unregulated lakes, even when natural variation in lake abiotic and biotic characteristics, as well as fish stocking activity, are taken into account (Eloranta et al., 2016b). However, as indicated by Enge & Kroglund (2011), fish yield in alpine reservoirs may not always respond negatively to WLR. This is likely because other natural (e.g. lake morphometry, climate and fish community composition) and anthropogenic (e.g. stocking and fishing) factors may partly compensate or mask the WLR impacts. Moreover, the results from alpine reservoirs contrast with observations from tropical reservoirs where fish yields are often positively affected by WLR (Kolding & van Zwieten, 2011).

Habitat use and interactions between fish

Because WLR leads to changes in availability of littoral and pelagic resources, they can further alter the competitive and predatory interactions between and among fish species (Fig. 4). A recent study from northern Norway demonstrated that WLR-induced recruitment failure and decline of littoral resources led to reduced population size and increased use of pelagic and profundal food and habitat resources by small Arctic charr (Eloranta et al., 2016b). Larger fish capable of adopting a predatory diet may simply switch to consuming fish as prey if littoral resources become less available (e.g. Eloranta et al., 2015). Species that are more specialized to either littoral or pelagic resources are likely more affected than less specialized species if resources overall become sparse or inaccessible and competition for resources increases. The complex interplay of competitive interactions is well illustrated by Arctic charr and brown trout (Lindström, 1973). Arctic charr and brown trout are the most common fish species inhabiting reservoirs located in European alpine areas. Brown trout is a more littoral specialized feeder and thus expected to be more vulnerable to WLR than Arctic charr, which can more effectively utilize pelagic and profundal food and habitat resources (Nilsson, 1961; Lindström, 1973; Eloranta et al., 2013). Studies from European alpine reservoirs show that both fish species can subsidize reduced littoral food resources by foraging on terrestrial prey during the summer season (Saksgård & Hesthagen, 2004; Eloranta et al., 2016b). However, Arctic charr include more pelagic prey in the diet, which releases it from competition for littoral resources (Nilsson, 1961; Gregersen et al., 2006; Eloranta et al., 2013). Competitive and predator–prey interactions can be further complicated by the establishment of introduced prey species. For example, after the opossum shrimp (*Mysis relicta* Lovén) was accidentally introduced through hydropower operation in a large Norwegian reservoir, Arctic charr shifted to feed predominantly on the new pelagic prey, whereas the diet of brown trout remained unchanged (Gregersen et al., 2006).

WLR can affect fish through more complex factors than mismatching water levels during spawning season and alterations in the littoral and pelagic food bases. One important abiotic condition that strongly influences trophic relationships, and eventually fish populations, is water clarity. Most fish are visual hunters and turbidity can greatly affect feeding efficiency and hence trophic relationships (Bartels et al., 2012). WLR-induced changes in ice cover also alter the visual conditions in the water and may affect feeding behaviour in fish and other organisms. For example, field and laboratory studies suggest that Arctic charr is generally a superior competitor over brown trout in colder and darker environments (Helland et al., 2011). Changes in turbidity following WLR can also affect predator–prey relationships among fish. For example, in alpine reservoirs in New Zealand, small benthic koaro (*Galaxias brevipinnis* Günther) were five times more abundant in places where WLR induced high turbidity, because turbid water provided protection from visually hunting salmonids (Rowe et al., 2003). This example demonstrates that WLR not only affects fish through alterations in resource availability, but also indirectly through alterations in the abiotic conditions under which resources are utilized.

Conclusions

Our review demonstrates that the environmental effects of WLR are complex and that abiotic and biotic factors can cause changes within the reservoir ecosystem that are hard to predict. Still, we can synthesize which factors determine the environmental effects of WLR (summarized in Table 1). We argue that these factors and their uncertainties must be addressed when scientist and practitioners are tailoring research programs and/or management plans for

Table 1 Summary of identified WLR effects, the mechanisms through which the effects take place, and confounding factors that can mask, alter and/or interact with the WLR effects

	WLR effects	Mechanisms	Confounding factors
Abiotic conditions	Altered temperature and oxygen conditions	Increased mixing, loss of oxygenated water	Reservoir morphometry, location of turbine tunnels
	Shorter ice-cover period	Weakened ice cover	Reservoir morphometry, location of turbine tunnels
	Altered water quality	Resuspension and leaching of inorganic and organic matter	Reservoir morphometry, geology and succession, location of turbine tunnels
Lower trophic levels	Decreased littoral production and diversity	Freezing, desiccation and physical alteration of shallow bottom areas	Reservoir succession, morphometry and geology
	Altered pelagic production and diversity	Changes in abiotic conditions and fish predation pressure	Reservoir succession, morphometry and geology, fish community composition
Fish	Successional change of fish abundance	Changes in lake productivity and food availability	Reservoir succession, fish community composition
	Altered intra- and inter-specific interactions	Changes in relative availability of littoral and pelagic resources	Reservoir morphometry, geology and succession, fish community composition

In all cases, the operational regime or how the water level is regulated for hydropower production (e.g. traditional vs. pump-storage operation, the amplitude, timing, frequency and rate of change of WLR) will strongly affect the abiotic and biotic conditions

specific reservoirs. Some of the factors we summarize (e.g. reservoir morphometry and operational regime) were rarely included in previous studies and should be addressed more thoroughly in future research. Furthermore, large-scale modelling studies across several lake and reservoir types and consistent recording, sharing and analysing of time-series data would provide fundamental insights into general WLR impacts. A more general understanding of WLR impacts would ultimately improve predictions of the environmental effects in reservoirs at the local level, something that is needed for the sustainable development of hydropower operations.

Consider temporal and spatial variation

As outlined above, the biological productivity and ecological status of a reservoir depends on how the reservoir is created (e.g. regulation of a previously natural lake versus a new reservoir filling previously dry land areas) and for how long the water level has been regulated for hydropower production. Most available research is based on single “snapshot” observations and thus the reservoir’s succession is rarely acknowledged (but see Rydin et al., 2008; Milbrink et al., 2011). Time-series analyses, including monitoring, paleolimnological and before-after-control-impact studies, as well as year-round studies conducted in multiple reservoirs would significantly improve our understanding of how WLR impacts are shaped by the reservoir’s succession as well as the seasonal fluctuations in abiotic and biotic conditions (Table 1). Moreover, experimental and reservoir-specific studies of WLR are needed to establish causality between different patterns of WLR and environmental effects, both abiotic and biotic. For example, fish recruitment and year-class-strength may vary naturally between years due to match or mismatch between spawning time and optimal environmental conditions. In reservoirs, recruitment variation results from interactions between natural inter-annual variations in climate and the operational regime of hydropower production, and the two processes must be disentangled to establish causality between WLR and changes in fish yields. Finally, as explained above and indicated in Table 1, reservoir morphometry and geology may largely determine, but also have complex interactions with, biotic factors, such as the loss of littoral primary production or fish spawning areas. Space-for-time studies may help to tackle this complexity, particularly if the WLR impacts are modelled across climatic, morphometric, and biotic community gradients from multiple reservoirs. Research considering both temporal and spatial variation is essential for identifying the most sustainable hydropower operations that maximize energy production with limited environmental impacts.

Integrate littoral and pelagic processes

To understand and minimize ecosystem-level impacts of WLR, both littoral and pelagic habitats and food-web compartments should be considered. Although the littoral habitat and biota may seem most vulnerable to WLR, it must be kept in mind that the apparently distinct habitats and food-web compartments interact strongly and ultimately determine the structure and stability of lake food webs (Vadeboncoeur et al., 2002; Tunney et al., 2014; McMeans et al., 2016). Modern stable isotope methods, such as compound-specific isotope analyses, isotopic labelling and analysis of multiple isotopes (e.g. C, N, H, S and O), can help to understand the resource use of different taxa and how WLR influence the structure (e.g. food-chain length) and function (e.g. littoral vs. pelagic energy flow to top consumers) of reservoir food webs (Layman et al., 2012; Middelburg, 2014; Eloranta et al., 2016b).

Acknowledge the complexity of fish life cycles

In our review, we assume that fish can serve as integrators of ecosystem changes, but effects seen in fish strongly depend on which life-stage of any given fish species is affected. Therefore, acknowledging that effects are life-stage dependent will help to improve our understanding of WLR effects in general. For example, the most directly established effect of WLR on fish may be the loss or provision of suitable spawning grounds. However, how changes in population recruitment triggered by WLR can affect the older life-stages via reduced intra- and inter-specific competition remains understudied. Future studies covering different fish life-stages are essential to determine the overall population-, community- and ecosystem-level effects of changing resource and habitat availability due to WLR.

Include the operational regime of the power plant

WLR depends on, and thus is as variable as, the operational regime of the hydropower plant. The operational regime for the hydropower plant typically changes in response to electricity prices, but could also be governed by science-based rules designed to required environmental standards (Smith et al., 2016; Kelly et al., 2017). Science-based regulation holds great potential to introduce a reasoned management approach to WLR aimed at mitigating environmental effects. However, understanding the causality between WLR patterns and environmental effects first requires an analysis of how the operational decisions to store or discharge water translate into WLR (Hirsch et al., 2014). Future scenarios of global energy systems predict that the share of renewable intermittent energies will increase and will change the WLR patterns (Solvang et al., 2014; Hirsch et al., 2016). The profitable development of hydropower will need to account for key environmental concerns to secure important ecosystem functions and services (Jager & Smith, 2008; Hirsch et al., 2014). In practice, this will require a better knowledge of the connections between the operational regime of WLR and its ecosystem-level impacts. Thus, knowledge of WLR impacts needs to build on a better understanding of both the operational regime as well as the environmental effects it causes. More specific predictions of causes and effects therefore require a system-specific assessment of both factors in concert. Here, the concept of environmental design of hydropower (Hellsten et al., 1996; Forseth & Harby, 2014) as well as early involvement of relevant stakeholders, including the hydropower companies, scientists, public and environmental agencies (Kumar et al., 2011; Nieminen et al., 2016), will be fundamental for the economically, environmentally and socially sustainable development of hydropower operations.

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