Rev Fish Biol Fisheries
https://doi.org/10.1007/s11160-024-09909-4

REVIEWS

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The environmental impact of hydropower: a systematic review of the ecological effects of sub-daily flow variability on riverine fish

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Received: 3 January 2024 / Accepted: 19 November 2024

Abstract Hydropower can help facilitate power grid decarbonization because it can respond to short-term changes in power demand and is comparatively more reliable than intermittent wind and solar. However, flexible hydropower operations can create rapid and abnormal fluctuations in downstream flow conditions, which can negatively impact aquatic ecosystems. Accordingly, we conducted a systematic review on the ecological effects of hydropower-driven sub-daily flow variability (SDFV) on riverine fishes. We reviewed and synthesized 109 articles relevant to fish-SDFV relationships from seven sources, most of which focused on Salmonids in North America and northern and western Europe and were published in the last 15 years. We found strong agreement in the literature that SDFV increases fish stranding risk, destabilizes habitat, and decreases production and diversity. We found moderate agreement that SDFV interrupts fish reproduction, increases or has no impact on condition, and prompts or discourages movement depending on local channel conditions. We found little to no agreement for relationships between SDFV and mortality, physiology, and behavior. The effects of SDFV on riverine fish ecology are intertwined in the complex suite of biotic and abiotic characteristics that structure aquatic ecosystems and are highly site-, species-, and life stage-specific. Assessments of the impact of SDFV on fish ecology should first characterize local habitat and channel quality and fish community composition to identify specific, measurable ecological outcomes to sustain or enhance, and then design mitigation strategies tailored to those ecological objectives.

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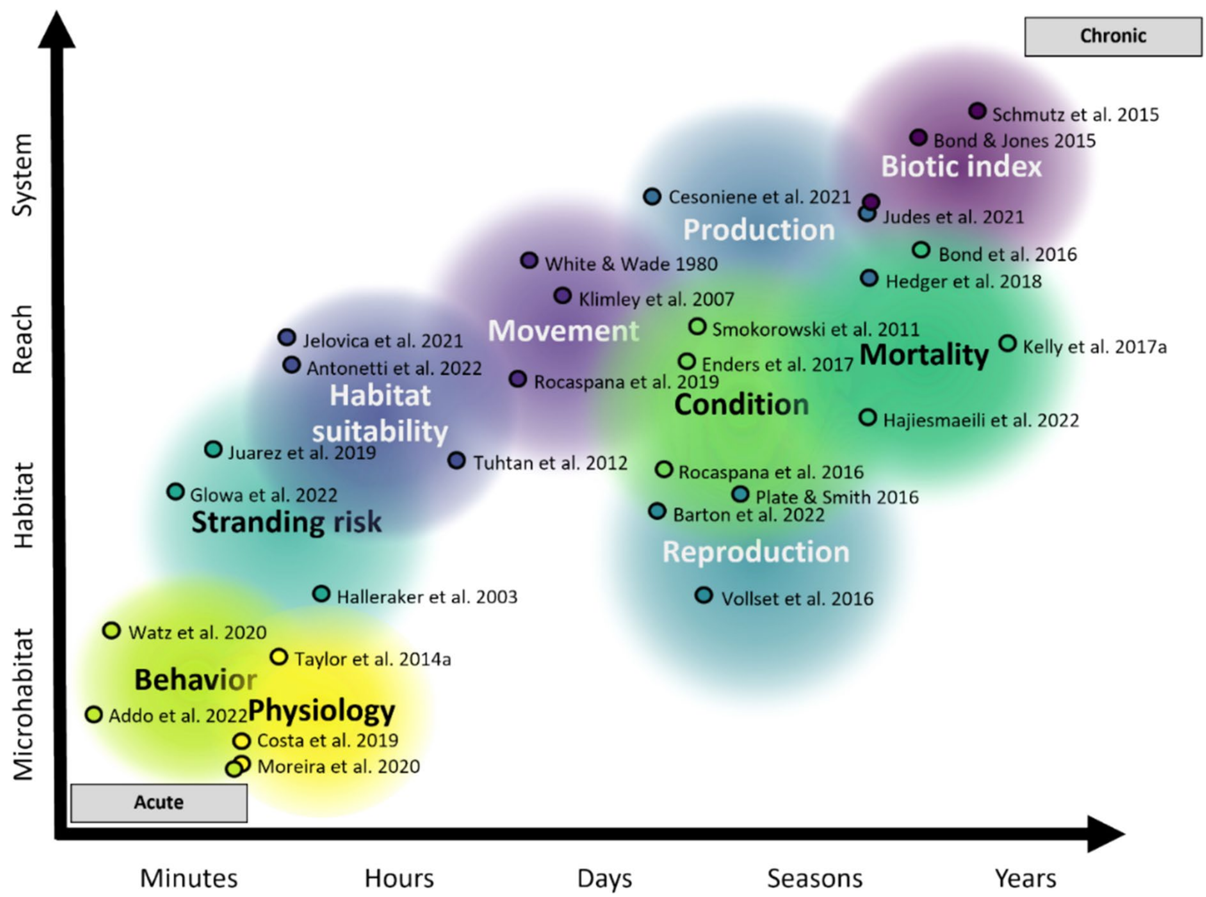
Graphical abstract



Keywords Hydropeaking · Fish · Regulated rivers · Flow regimes · Environmental mitigation · Short term flow fluctuation

Introduction

More than 80% of total global energy is produced from nonrenewable sources compared to less than 20% of energy produced from renewable sources and less than 5% from hydropower, geothermal, solar, and wind (IEA 2021). Shifting our energy production mix from mostly nonrenewable sources toward clean, low-carbon renewable sources can help mitigate the effects of global climate change by limiting the extent of atmospheric warming and protecting biodiversity (Riahi et al. 2022). Renewable energy production industries are growing rapidly around the world with renewable sources forecasted to account for nearly 40% of total global energy production by 2027 (IEA 2022). However, greater contribution of renewable energy sources to global energy portfolios means greater reliance on intermittent forms of renewable energy such as solar and wind which only generate power when environmental conditions are favorable (Schmutz et al. 2014). In fact, variable solar and wind energy are the greatest contributors to annual global energy capacity additions with greater net capacity additions during the late 2010s than any other energy source and record-breaking capacity additions for solar energy in 2023 (Blakers et al. 2019; IEA 2023). The increasing contribution of variable renewable energy to power grids presents a challenge to power producers tasked with meeting real-time power demands while maintaining power system security and stability (Mlilo et al. 2021).

Hydropower is a particularly promising form of renewable energy production that is well-poised to support decarbonization of the electric grid because it is a mature technology, has storage capabilities, can be dispatched quickly to meet grid demands when solar and wind production are not available, and consequently can support increased integration of variable renewable energy to global energy portfolios (Harby and Noack 2013; Smokorowski 2022). Unlike variable solar and wind energy, hydropower facilities are flexible; they can be powered up to generate power when demand is high and powered down when demand is low or can be met from other sources (e.g., wind and solar), and they can respond to variations in electricity demands in seconds to minutes. The increased reliability, economic, and power grid decarbonization benefits of real time power balancing services from flexible hydropower production have already driven substantially increased intra-day variability in dispatch and will continue to do so as more variable renewable energy comes online (Avesani et al. 2022; Jager et al. 2022; Marshall and Grubert 2022). The environmental consequences of these operational changes are poorly understood and underrepresented in hydropower operational optimization decisions.

Hydropower dams (as well as many nonpowered dams) provide myriad services to society, including hydroelectric power production and grid stability, recreational services (both upstream and downstream), flood control, water supply for agricultural, municipal, and industrial uses, and revenue for hydropower operators. To provide these services to meet societal needs, hydropower dams divert, store, or otherwise interrupt flow, which dramatically alters the characteristic dynamic flow patterns of a river both upstream and downstream from dams. A river's flow regime is characterized by flow patterns based on the magnitude, frequency, duration, timing, and rate of change of flows (Poff et al. 1997). Collectively, these flow regime components play a major role in structuring, supporting, and constraining ecological processes in rivers and streams (Palmer and Ruhi 2019; Poff and Ward 1989; Poff and Zimmerman 2010; Vannote et al. 1980). Generally, natural flow regimes in free-flowing, unregulated rivers follow seasonal, predictable patterns that create flow variability ranges that local aquatic organisms are adapted to withstand (Junk et al. 1989; Lytle and Poff 2004; Puffer et al. 2015). By comparison, flow regimes in regulated rivers, such as those dammed for hydropower production, may exhibit flow variability patterns with frequencies, magnitudes, durations, and/or rates of change that are dramatically different from natural systems, which may disrupt ecological processes from the organism to the community level (Bain et al. 1988; Judes et al. 2020; Taylor et al. 2012). There are many ways that humans modify rivers and alter flow regimes; in this study we focus on regulated flow regimes with unnatural degrees of sub-daily flow variability downstream from hydropower facilities.

Human alterations to natural flow regimes – including via hydropower dam construction and operation – are widely studied (Bain et al. 1988; Lytle and Poff 2004; Richter et al. 1996) and many different flow metrics have been derived to characterize and distinguish regulated flow regimes from natural flow regimes (e.g., Bakken et al. 2021; Bejarano et al. 2017; Bevelhimer et al. 2015). Hydropower dams employ many different modes of operation ranging from those that approximate natural flow regimes via matching downstream discharge with upstream inflow (i.e., run-of-river) to those that store and release water to maximize hydroelectric generation and create dramatically modified regulated flow regimes (e.g., hydropeaking), with potentially dramatic changes to flow in bypass reaches depending on specific project configuration (Greimel et al. 2016; Li and Pasternack 2021; McManamay et al. 2016a). Mode of operation is influenced by the physical characteristics of the dam and its storage and generation capacity, hydrology, local geography and river characteristics, power demand and market pricing, agency requirements, and legislative restrictions for environmental protection (McManamay 2014; Moreira et al. 2019; Poff and Hart 2002; Roni et al. 2023).

Hydropeaking is the mode of operation that has received the most research attention, perhaps because it ostensibly has the greatest environmental and economic impacts, although most hydropower modes of operation create regulated flow regimes that differ significantly from natural patterns (Zimmerman et al. 2010). Hydropeaking is variably defined in the scientific literature, but generally is conceptualized as an extreme form of load following where hydropower facilities operate flexibly in response to market demand for power by storing water when demand is low and releasing water during peak demand, which creates large and rapid fluctuations in both power production and downstream flow up to several times per day (Moog 1993; Sauterleute and Charmasson 2014). Hydropeaking is characterized by four distinct phases that include: (1) base flow during periods of no power production, (2) up-ramping to increase power production and flow, (3) continuous peak flow during highest power demand, and (4) down-ramping to reduce or cease power production and return to base flow (Costa 2019). Hydropeaking is one of the most common modes of operation of United States hydropower facilities, and is implemented by more than 30% of US hydropower dams and power plants (McManamay et al. 2016). Hydropeaking is an important component of decarbonized power grid reliability because it is the only low-carbon method of flexible power production (Smokorowski 2022). Although different modes of operation create different intensities of flow modification (Greimel et al. 2016; Zimmerman et al. 2010), regulated flow regimes generally exhibit diminished seasonal peak flows, extended periods of low flow, and much greater sub-daily flow variability relative to natural flow regimes (Hayes 2021).

Regulated flow regimes with reduced inter-annual flow variability and heightened sub-daily flow variability impact numerous downstream abiotic and biotic conditions including sediment and substrate, temperature, water chemistry, macroinvertebrate community composition, and riparian zone linkages (Antonetti et al. 2022; Hauer et al. 2018; Lagarrigue et al. 2002; Pulg et al. 2016). The direct effects of hydropower-induced sub-daily flow variability on fish ecology in regulated rivers is of particular importance to regulators, hydropower owners, and others involved in the hydropower regulatory process who are charged with balancing the cultural, economic, recreational, and intrinsic ecological values of fisheries and aquatic resources with the ability of flexible hydropower production to facilitate global renewable energy targets. Fish responses to sub-daily flow variability can be investigated as acute reactions to specific hydropeaking phases (e.g., stranding during down-ramping events) or as the cumulative result of chronic exposure to highly unstable environments (e.g., community composition between natural and regulated systems) using techniques ranging from laboratory experiments to field observations to model simulations. Similarly, the impacts of sub-daily flow variability on fish can range from negligible disruptions in behavior, physiology, or other life history processes to death or species extirpation. Previous reviews of relationships between hydropower production, flow regimes, and fish ecology have been restricted to specific groups of fishes (Hunter 1992), life stages (Hayes et al. 2019), or ecological outcomes (Harper et al. 2022; Nagrodski et al. 2012; Rytwinski et al. 2020), or have broadly reviewed all environmental, ecological, and social impacts of hydropeaking (Bipa et al. 2023). Consequently, there is a need for a systematic review to contextualize and synthesize reported relationships between hydropower flexibility and riverine fish ecology, characterize typical approaches and metrics used to study these relationships, and identify opportunities for future research directions.

Flexible hydropower operation can help support increased integration of variable renewable energy into global power grids as we look to decarbonize the power sector (Roni et al. 2023). However, flexible hydropower operation dramatically alters downstream flow regimes with potential consequences for aquatic ecosystems ranging in scale from acute impacts of discrete flow events on individual organisms to system-wide community impacts from chronic flow variability and in severity from minor to critical. Therefore, it is critical that we understand the relationship between sub-daily flow variability created by flexible hydropower production and fish ecological outcomes in downstream lotic environments to identify potential tradeoffs between power grid stability and ecological integrity and inform hydropower policy (Roni et al. 2023). Accordingly, we conducted a systematic review to summarize and synthesize the body of scientific knowledge on the full suite of reported ecological effects of sub-daily flow variability (SDFV) due to hydropower production (HPP) on freshwater fishes downstream of hydropower dams.

Methods

Primary question

What are the ecological effects of sub-daily flow variability due to hydropower production on riverine fish?

Our primary research question can be divided into population, exposure, and outcome (PEO) components (Table 1).

We conducted a systematic search and review of the peer-reviewed and gray literature pertaining to our research question generally following established systematic review guidelines (Foo et al. 2021; Haddaway et al. 2016; Moher et al. 2009, 2015). This iterative process consisted of (1) executing a search of the primary and gray literature in multiple databases, (2) pilot reviewing a subset of articles to develop inclusion-exclusion criteria and refine search strings, (3) screening titles and abstracts of initial search returns to remove duplicates and retain articles that met inclusion criteria, and (4) reviewing and summarizing the full text of the articles relevant to our research question.

Searching for articles

Published databases

The general relationship between fish and flow regimes has recently been comprehensively reviewed in a systematic map of the effects of flow regime changes on fish productivity (Rytwinski et al. 2020) and subsequent systematic review of the effects of hydropower-induced changes in flow magnitude on fish abundance and productivity (Harper et al. 2022). These reviews searched six online databases, one search engine, and 29 websites for articles published from 1900 to 2019 and collectively retrieved more than 1300 articles. We filtered their published databases for articles that featured hydropower-induced changes in flow magnitude, rate of change, and frequency over short time scales, including articles that referenced peaking or ramping operations. We pilot reviewed a subset ($N = 25$) of the filtered articles to develop a search string for subsequent online database searches and formalize explicit inclusion-exclusion criteria to apply during article screening.

Online databases

We developed a search string based on our research question using our pilot review, published strings from the systematic map and review, and iterative scoping searches of online databases (Harper et al. 2022; Rytwinski et al. 2020). The search string was designed to identify articles specific to sub-daily flow variability, was comprised of terms divided into three components of our research question, population, exposure, and outcome (PEO; Haddaway et al. 2016), and used Boolean operators and wildcards to account for multiple variations of each term (Table 2; Foo et al. 2021). We also specified terms to exclude from the search that were not relevant to our research question (e.g., aquaculture; Table 2). We used our search string to search Web of Science, Scopus, and ProQuest online databases for articles on the effects of sub-daily flow variability on fish ecology published from July 2017 (the search date of the published systematic map) and our search date of 22 December 2022.

Screening and reviewing articles

Inclusion-exclusion criteria

During the pilot review phase, we developed explicit inclusion-exclusion criteria to apply to articles identified in our search at two distinct levels: (1) title and abstract, and (2) full text. Our inclusion-exclusion criteria were closely tied to our research question and its individual components. Eligible populations included any fish species, population, guild, or community located in lotic freshwater systems. Fish could be migratory or resident, established nonnative or invasive species, and any life stage. Eligible exposures

Table 1 Components of the primary research question

Component	Description
Population	Fish in lotic environments
Exposure	Variability in flow in lotic systems due to hydropower production over short (24-hour or less) time scales
Outcome	Any measured or estimated metric of fish ecology in the context of flow variability

Table 2 Search string for online databases divided by research question component. This string was executed in the web of Science Online database on 22 December 2022. Boolean operators 'AND' and 'OR' perform searches that contain all or any bounding word(s), respectively. Specific phrases included in the search are bounded by quotations. Asterisk wildcards indicate searches for the root word preceding the asterisk and all variations of that word containing the root word and any number of additional letters. Dollar sign wildcards indicate searches for the root word preceding the sign and only one additional letter (e.g., dam or dams). Proximity operators (e.g., NEAR/0 or NEAR/1) indicate searches for bounding words within the specified number of words from each other regardless of order. This search string was adapted from Harper et al. (2022) with greater detail for exposure terms to capture articles that specifically examined sub-daily flow variability

Category	String
Population	((Fish*) AND ("Fresh water" OR Freshwater OR Stream$ OR River$ OR Fluvial OR "Hydro electric*" OR Hydroelectric* OR "Hydro dam*" OR Hydrodam* OR "Hydro power" OR Hydropower OR "Hydro" OR Dam$))
Exposure	((Flow OR Discharg*) AND ("Sub daily" OR subdaily OR "sub-daily" OR "Short term" OR shortterm OR "short-term" OR (Sudden NEAR/0 (increase OR decrease OR change OR shift)) OR ((Daily OR Hourly) NEAR/0 fluctuation*) OR ("hydro peaking" OR hydropeak* OR "hydro-peaking" OR dewater* OR strand* OR ((up OR down) NEAR/1 ramp*) OR "ramp rate" OR ramp)))
Outcome	(Productivity OR Growth OR Performance OR Surviv* OR Success OR Migrat* OR Passag* OR Reproduc* OR Biomass OR Stress* OR Disease$ OR Mortalit* OR Abundance$ OR Densit* OR Yield$ OR Recruit* OR "Ecological response" OR "Ecosystem response" OR "Biotic response")
Excluded	(mining OR "mine site" OR aquaculture OR "wastewater treatment" OR carbon)

included variability in flow in lotic systems over short (i.e., ≤ 24-hour) temporal scales. The target temporal scale for our research question was sub-daily variability; however, we also included articles that summarized flow variability at coarser (e.g., daily) time scales if the coarser temporal resolution described systems that exhibited variability at finer scales (e.g., articles that categorically compared fish ecological outcomes between regulated systems influenced by hydropeaking and natural systems). Eligible outcomes were any measured metric of fish ecology in the context of flow variability including growth, biomass, diversity, density, abundance, condition, survival, reproductive success, habitat use or suitability, stranding risk, or movement.

Our pilot review revealed considerable variability in study design in articles assessing – experimentally, observationally, or via model simulation – the effects of SDFV on fish. Accordingly, we did not explicitly account for article comparators (e.g., between regulated and unregulated reaches or before and after regulation in the same reach) in our search string. However, we developed comparator eligibility criteria to ensure that conclusions drawn from articles included in the review were based on legitimate comparisons within and/or between sites or time periods of differing sub-daily flow variability. Eligible comparators included differences between sites with regulated and natural flow regimes, within the same sites over time (e.g., before and after flow regime manipulation), between sites in the same longitudinal river network (e.g., up- and downstream from a dam), or experimental manipulations in artificial flumes designed to simulate hydropower-induced sub-daily flow variability. We also excluded articles for which a full-text version was not available in English and redundant articles that presented data analyzed in other articles in the database.

The focus of our review was on documenting direct relationships between fish ecological outcomes and sub-daily flow variability. However, we also wanted to capture articles that reviewed components of this relationship (and did not themselves directly measure outcomes) or developed metrics to characterize and distinguish regulated flow regimes with high sub-daily flow variability from natural flow regimes. Therefore, we expanded our inclusion-exclusion criteria beyond the specific components of our primary question to allow us to retain review and metric development articles relevant to SDFV-fish ecology relationships.

Screening articles

We combined the results of our published and online database searches into a single list of potentially relevant articles and removed duplicates. We used the inclusion-exclusion criteria to screen unique articles at the title and abstract level and downloaded eligible articles for full-text review to create our systematic review database. We anticipated that we would not be able to review every eligible article at the full-text level due to time constraints. Accordingly, we developed an SDFV-specific keyword search string comprised of keywords and phrases specific to sub-daily flow variability as informed by the pilot review (Table 3). We applied the keyword search string in Adobe Acrobat's Advanced Search function to identify instances of keywords in the full text of downloaded articles in our database and ranked and sequentially reviewed articles at the full-text level, prioritizing those with the most keyword instances ostensibly most relevant to our primary research question.

Full text review and article classification

Upon beginning the full-text review phase, we noted cited articles that were potentially relevant to our research question but that were not returned in our database searches. Additionally, a colleague shared a small handful of potentially relevant articles ($N=4$) which had not been returned in our database searches, but which were also cited in articles reviewed at the full-text level. We downloaded these articles, used the keyword search string to identify number of keyword instances, and placed them at the appropriate position in our database to be evaluated.

As we reviewed articles at the full-text level, we extracted information on year and type of publication, country where study was conducted, study species and life history stage, study type, and ecological outcome category. Because of the highly variable nature of the methods and approaches used to study the effects of SDFV on fish ecology across articles in our database, we also recorded qualitative descriptions of the metric(s) used to quantify SDFV (if reported), article objectives, and the reported relationship(s) between SDFV and fish ecology in each article. Publication type noted whether articles were articles published in peer-reviewed journals, academic theses or dissertations, government or agency reports (i.e., gray literature), or book chapters. For thesis chapter database entries that were also published in peer-reviewed journals, we downloaded and reviewed the peer-reviewed publications in lieu of the thesis chapter given that the former had benefited from peer review.

Many of the articles we reviewed investigated multiple species. Multi-species articles sometimes considered effects of SDFV on multiple species in parallel (i.e., on a species-specific outcome basis), sometimes considered SDFV effects on community composition (i.e., how many of each species is present), and sometimes both. For studies that considered outcomes for multiple species on a species-specific basis, we recorded the family of all species. For articles that considered outcomes for communities and reported specific results for certain species (e.g., fish community biomass and length-weight relationships for specific species; Judes et al. 2020; Smokorowski et al. 2011), we recorded the families of the species for which species-specific results were reported and also added a "community" classification. Articles that described the species identified in the communities but only reported community-level results were classified as community-only articles (e.g., Boavida et al. 2021; Česonienė et al. 2021; Glowa et al. 2022; Judes et al. 2022; Schmutz et al. 2014).

We also classified articles in our full-text database by study type, which was the primary method of scientific inquiry and data collection. Study types included experimental and field studies, model simulations, reviews, and metric development articles. Experimental studies were those which collected data via experimental stream flumes or channels (indoor or outdoor), or in experimental enclosures in natural systems where conditions could be controlled and the effects of one or two predictor variables could be isolated. Field studies were those which collected data

Table 3 Adobe Acrobat Advanced search keyword detection string used to prioritize full-text articles for review. Boolean search operators are described in Table 2

Adobe Acrobat Advanced Search keyword detection string
Sub daily flow OR subdaily flow OR short term flow OR shortterm flow OR hydro peaking OR hydropeaking OR peaking OR hourly power demand OR ramp OR ramp rate OR up ramp OR down ramp OR sudden increase OR sudden decrease OR sudden change OR hourly increase OR hourly decrease OR hourly change OR hourly fluctuat OR fluctuate hourly OR daily fluctuat OR fluctuate daily OR varies hourly OR varies daily OR dewater OR strand

by observation (or in some cases broad manipulation) in field settings, usually involving observing differences in fish outcomes between sites in regulated and natural systems or reaches. Model simulation articles simulated hydropeaking or other forms of sub-daily flow variability and compared fish outcomes between different flow scenarios without collecting empirical data. Review articles summarized the results of published articles without collecting new data or reporting novel empirical findings. Lastly, metric development articles focused on developing and testing flow regime metrics to differentiate hydropeaking flow regimes from natural flow regimes with little emphasis on fish outcomes. Some articles collected multiple types of data and were assigned multiple study classifications.

We classified each article by type of fish ecological outcome measured or estimated in the context of flow variability. Ecological outcome categories were identified during the pilot test review phase and refined during the full-text review phase. The ten identified ecological outcome categories were: (1) behavior, (2) physiology, (3) stranding risk, (4) habitat suitability, (5) movement, (6) reproduction, (7) condition, (8) production, (9) mortality, and (10) biotic index. Outcome categories were designed to capture the full range of fish responses to flow variability across a spectrum of hierarchical organization from intra-organism processes (e.g., physiology) to population- and community-level processes (e.g., production, biotic index). There are frequently different ways of investigating the same outcome in ecological studies, including the articles we reviewed. For instance, some studies calculate weighted usable area (WUA), others calculate habitat suitability maps, and others calculate hydraulic habitat suitability. Each of these response types relates to general habitat suitability for a fish species. Accordingly, we grouped articles with similar responses into single ecological outcome categories to facilitate result synthesis and manuscript organization. Categories were sufficiently broad to capture the varied ways researchers investigate flow impacts on fish, but not so broad as to obscure important differences between distinct fish responses (e.g., habitat suitability and movement). We explicitly defined outcome categories to account for conceptual overlap between outcomes such that each distinct SDFV-fish ecology relationship reported in reviewed articles was assigned to a single outcome (e.g., studies of spawning habitat quality were assigned to habitat suitability outcome and not reproduction outcome; Table 4).

We also recorded the metrics or methods each article used to quantify SDFV (e.g., categorical comparisons between systems, discharge, SDFV metrics from the literature, etc.) and qualitative descriptions of article objectives and reported relationships between SDFV and fish ecological outcome. The relatively broad nature of our primary research question and wide range of methods and approaches used to assess SDFV-fish ecological outcomes in articles in our database precluded our ability to assess the validity or power of each article and conduct a quantitative synthesis. Accordingly, we qualitatively synthesized articles to describe general relationships observed between SDFV and riverine fish ecology and assess degree of article agreement regarding those relationships. Articles that did not meet each of the eligibility criteria at any point during the full-text review process were excluded with the reason (i.e., population, exposure, or outcome) noted.

Results

Results of literature search

Our literature search returned articles from seven sources: 238 articles from the published systematic map database (Rytwinski et al. 2020), 70 articles from the published systematic review database (Harper et al. 2022), 162 articles from Web of Science, 163 articles from Scopus, 44 articles from ProQuest, and 151 cited and shared articles. After removing duplicates and screening at the title and abstract level, 350 unique articles passed to full-text screening and review (Fig. 1). Of these 350 articles, 127 had fewer than 20 keyword instances and were classified as low relevance and 58 were deemed ineligible based on our inclusion-exclusion criteria and were excluded. We reviewed 109 relevant articles for summary and synthesis and were unable to review the remaining 56 articles due to time constraints. We reviewed articles in order of number of keyword occurrences, hence the 109 reviewed and synthesized articles are ostensibly more relevant to our primary research question than the 56 articles not reviewed. Of the 109 reviewed articles, 73 articles directly measured the relationship

Table 4 Ecological outcome category definitions, examples, and conceptual space-time details

Acute — Chronic

Outcome category	Scale of effect	Definition	Example papers (Figure 5)
Behavior	Microhabitat – habitat Minutes – hours	Any measure of fish swimming or foraging activity or inter- or intraspecific interactions	• Addo et al. 2022 • Moreira et al. 2020 • Watz et al. 2020
Physiology	Microhabitat – habitat Minutes – hours	Any measure of internal components of fish function or health	• Costa et al. 2019 • Moreira et al. 2020 • Taylor et al. 2014
Stranding risk	Habitat – reach Minutes – hours	Any measure of risk or rate of fish becoming stranded during dewatering events caused by rapid down-ramping	• Glowa et al. 2022 • Halleraker et al. 2003 • Juárez et al. 2019
Habitat suitability	Habitat – reach Hours – days	Any measure of habitat use, suitability, or availability for any life stage and activity including spawning	• Antonetti et al. 2022 • Jelovica et al. 2021 • Tuhtan et al. 2012
Movement	Habitat – reach Hours – seasons	Any measure of voluntary or involuntary movement of individuals, including number of individuals moving from one location to another	• Klimley et al. 2007 • Rocaspana et al. 2019 • White & Wade 1980
Reproduction	Habitat – reach Days – seasons	Any measure of reproductive activity or success, including measures of life stage-specific population metrics (e.g., YOY density)	• Bartoň et al. 2022 • Plate & Smith 2016 • Vollset et al. 2016
Condition	Habitat – system Seasons – years	Any measure of individual-level characteristics, including growth, length-at-age, body fat content, and sexual maturation	• Enders et al. 2017 • Rocaspana et al. 2016 • Smokorowski et al. 2011
Production	Reach – system Seasons – years	Any measure of population characteristics of a single species including abundance, density, or biomass	• Česonienė et al. 2021 • Hedger et al. 2018 • Judes et al. 2021
Mortality	Habitat – system Seasons – years	Any measure of mortality or survival not attributed to stranding risk or reproduction	• Bond et al. 2016 • Hajiesmaeili et al. 2022 • Kelly et al. 2017a
Biotic index	Reach – system Seasons – years	Any measure of species diversity, abundance, or biotic index	• Bond & Jones 2015 • Judes et al. 2021 • Schmutz et al. 2015

between sub-daily flow variability and at least one fish ecological outcome and the remaining 36 articles were reviews of relevant fish-flow relationships or focused on metric development to characterize and differentiate regulated flow regimes from natural flow regimes.

Article summary statistics

Our review returned articles that investigated SDFV-fish ecology relationships in 15 countries and one French territory. Most of the research in our database was conducted in North America and northwestern Europe. Specifically, Canada, the USA, Switzerland, Norway, and Austria are the five most-featured countries (Fig. 2). This area of inquiry is relatively new and rapidly expanding with greater than 90% of the articles in our database published in the last 15 years and at least five SDFV-fish ecology articles published per year in nine of the last ten years (Fig. 3a). Most entries in our full-text database were articles presenting original research in peer-reviewed scientific journals. The remaining entries were comprised of reviews, government reports, theses and thesis chapters, and book chapters (Fig. 3b). Articles in our full-text database reported results on fish species from 15 distinct families in addition to community-level results and included studies on all life stages of fish, from eggs to mature adults. Unsurprisingly, more than half of the articles investigated the effects of sub-daily flow variability on salmonid fishes. The next most popular fish families were Cyprinidae (10%) and Leuciscidae (9%), followed by community-level articles (7%) (Fig. 3c). For articles that reported specific metrics or methods used to describe or characterize SDFV, the most common metrics used were discharge ($N = 51$), suites of metrics developed to characterize SDFV in the literature (e.g., daily flow coefficient of variation or flow ratio, $N = 20$), lateral or vertical ramping rate (usually in the context of stranding or dewatering, $N = 12$), and categorical comparisons between regulated and unregulated reaches or systems ($N = 10$).

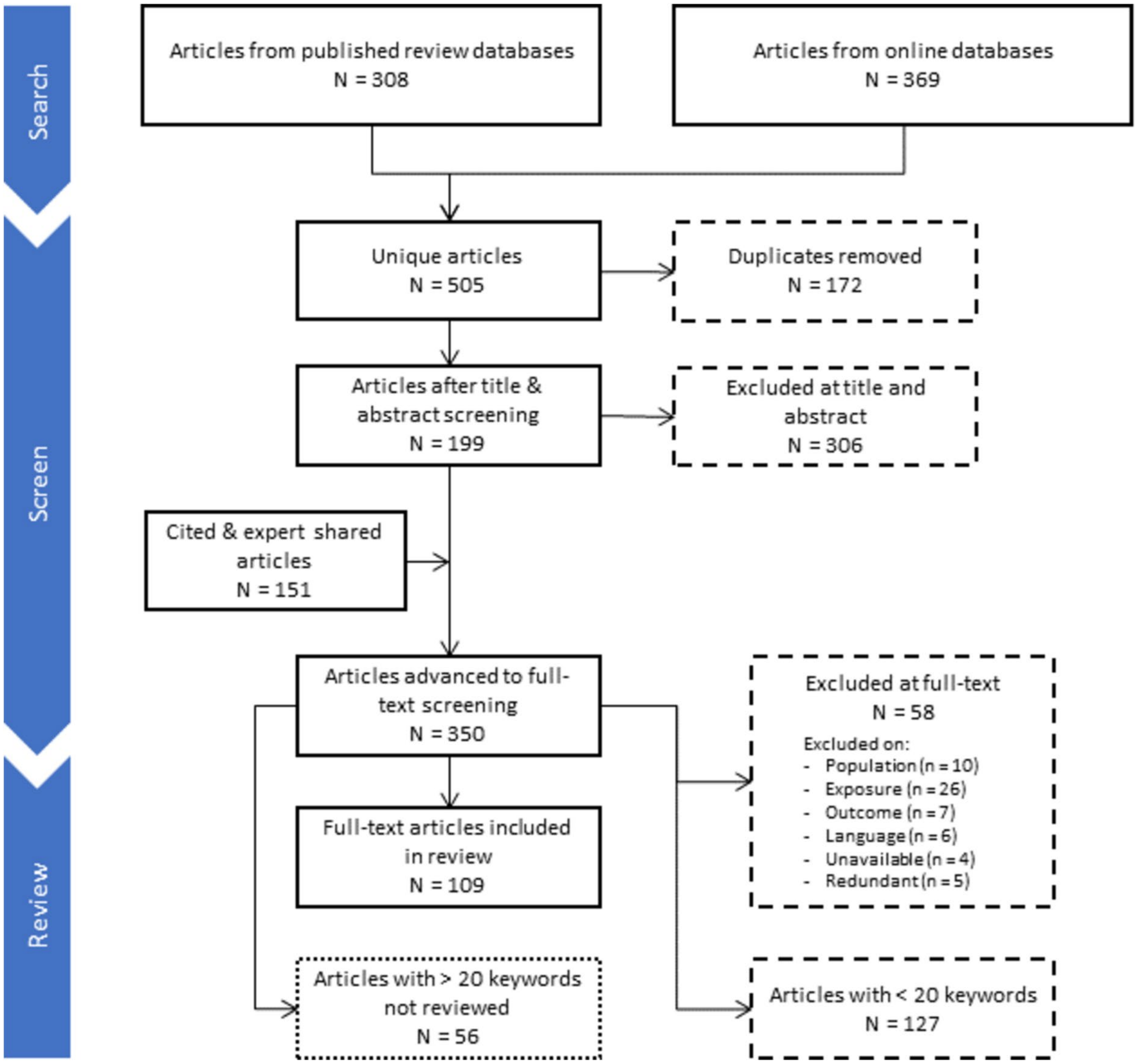


Fig. 1 Adapted ROSES flow chart of the systematic review search, filter, and article evaluation process. The six articles excluded based on language were written in French ($N = 3$) and German ($N = 3$)

The 10 ecological outcomes identified in the review are not perfectly distinct; rather, they can be conceptualized as partially overlapping response zones organized by the general temporal and spatial scales at which the effects of sub-daily flow variability on each outcome are realized (Fig. 5). For instance, some fish ecological outcomes are acutely affected by discrete flow variability events (e.g., physiological responses to up-ramping events as power generation increases); others are chronically affected by repeated exposure to highly variable flow environments (e.g., population productivity in regulated, hydropeaking flow regimes). We conceptually organized the ecological outcomes in our database articles in approximate order from acute (fine) to chronic (coarse) spatial and temporal response to SDFV and synthesize reported relationships below.

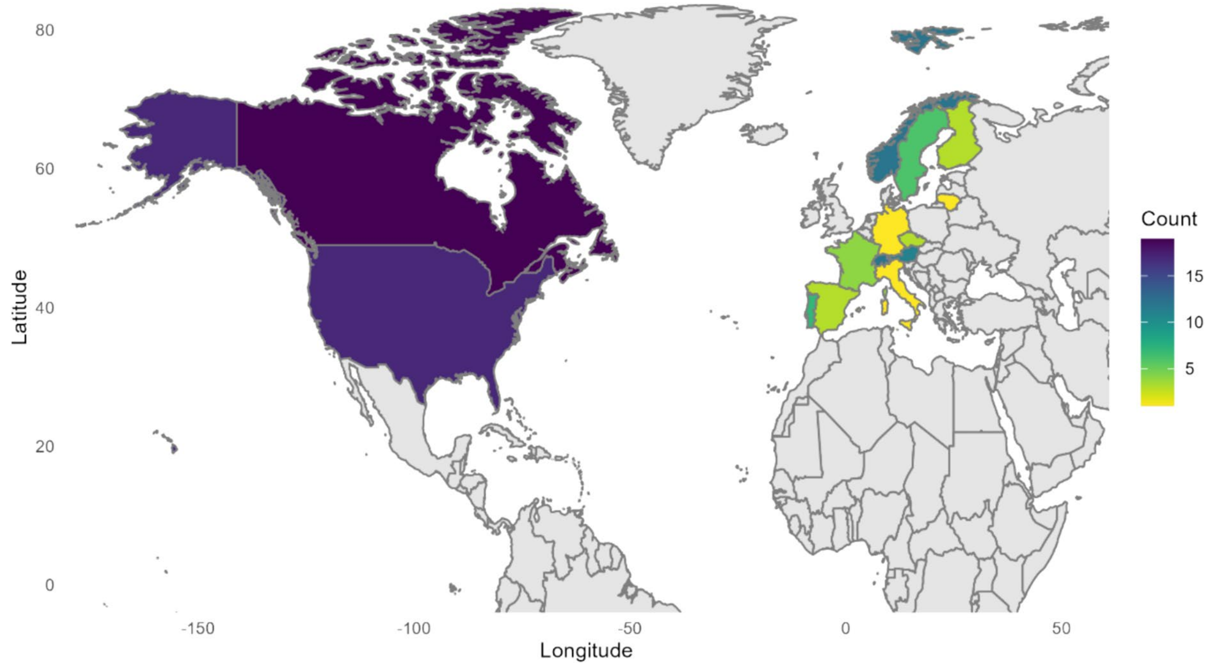


Fig. 2 Articles per country of research focus. Note: two articles are not depicted in this figure; one article in South Korea and another in the French island of Réunion in the western Indian Ocean. The map is focused on the northwestern hemisphere to maximize visible detail of the most-studied regions

Ecological outcome syntheses

Behavior (N = 3)

We classified articles that measured fish swimming or foraging activity or inter- or intra-specific interactions in the context of sub-daily flow variability as behavior outcome articles (Table 4). Behavior was the least-studied response in our review (*N* = 3) and was studied exclusively in laboratory experiments (Fig. 4). Investigations of the relationship between fish behavior and SDFV generally conceptualized behavior as being acutely affected by discrete flow variability events (Fig. 5). Peaking flows during hydropeaking simulations in experimental flumes caused adult Iberian barbel (*Luciobarbus bocagei*) to significantly increase use of shaded velocity refugia (Moreira et al. 2020). Conversely, increasing flows to simulate hydropeaking caused juvenile European grayling (*Thymallus arcticus*) to exhibit greater swimming activity and become more isolated relative to stable flow, especially in sub-optimal, homogenous habitat conditions (Watz et al. 2020). Atlantic salmon (*Salmo salar*) and Brown trout (*Salmo trutta*) fry swimming activity and aggressive interactions did not differ significantly between stable and fluctuating flow treatments or high and low flow treatments, though more fry of both species were visible swimming above the substrate at low flows compared to high flows (Addo et al. 2022). Collectively, these limited lines of evidence suggest that the effects of sub-daily flow variability on fish behavior are species-, life stage-, and habitat-specific, potentially prompting fish to use refugia or substrate as shelter from high flows or increase swimming activity in search of better habitat and reducing inter-individual interactions. However, the limited number of articles in this outcome category and their corresponding low agreement precludes us from drawing strong conclusions about the general relationship between flow variability and fish behavior.

Physiology (*N* = 5)

We classified articles that measured internal components of fish function and health as physiology outcome articles (*N* = 5; Table 4). The relationship between physiology and sub-daily flow variability

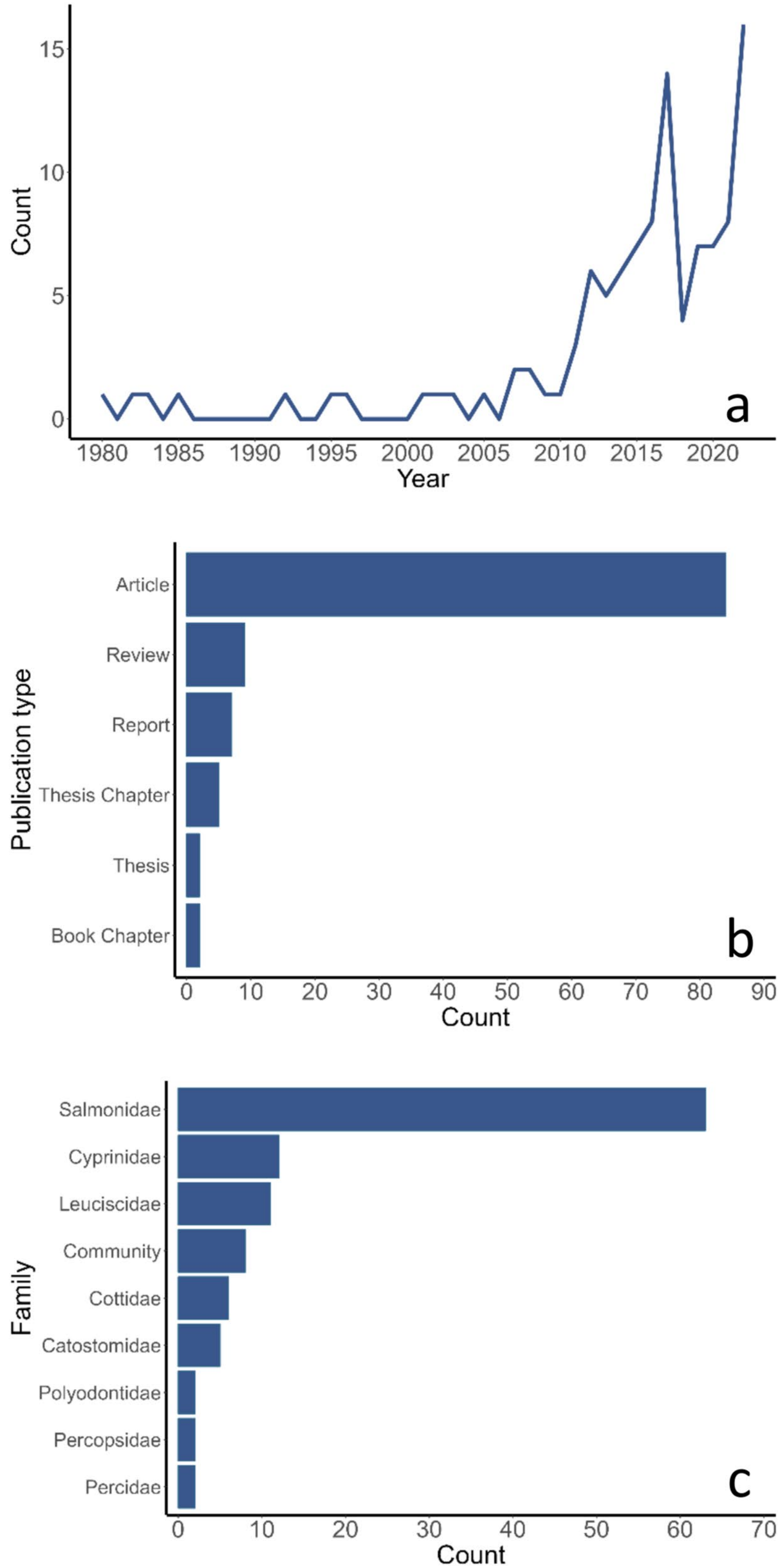


Fig. 3 Articles per year of publication (a), publication type (b), and fish family (c). Note: Fish families that were featured in only one article and are not displayed in the figure are Centrarchidae, Esocidae, Gobiidae, Bogionidae, Hiodontidae, Nemacheilidae, and Oxudercidae

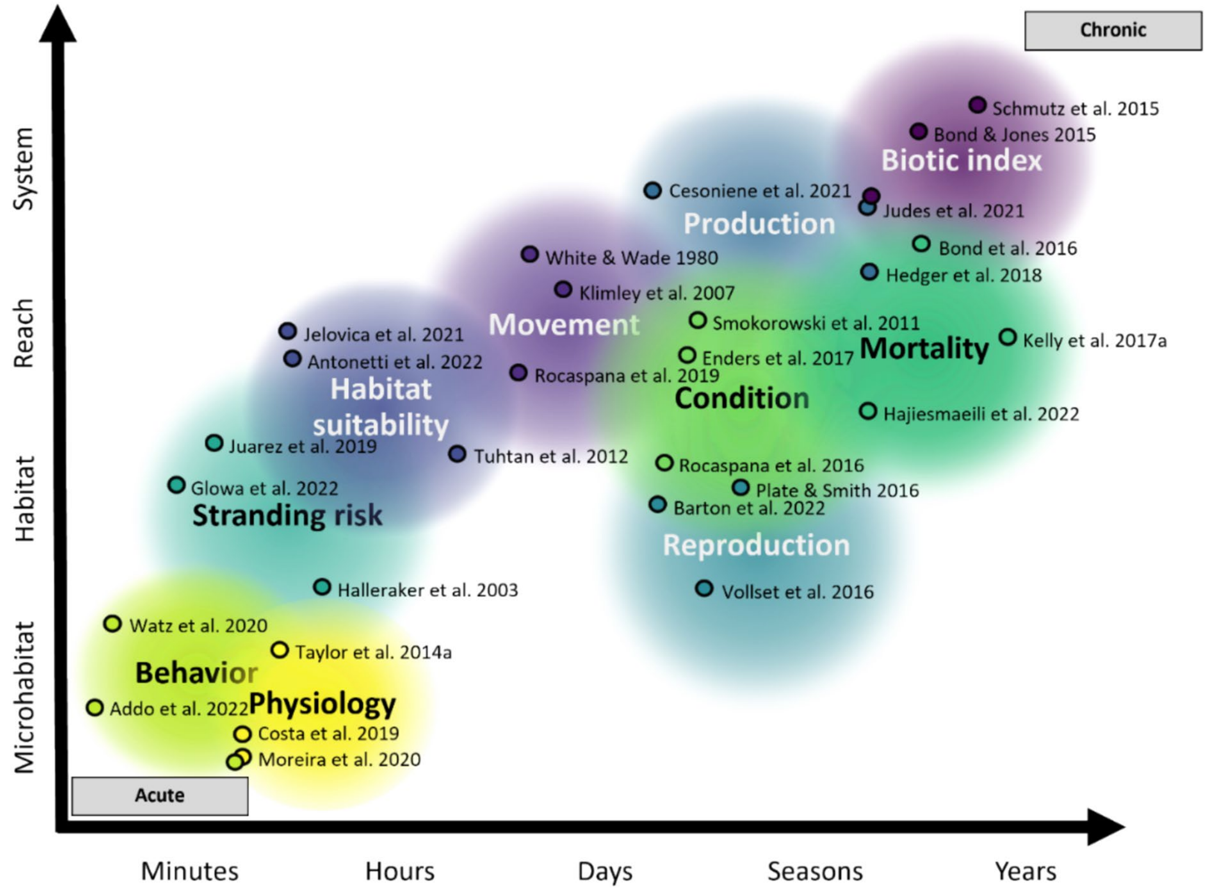
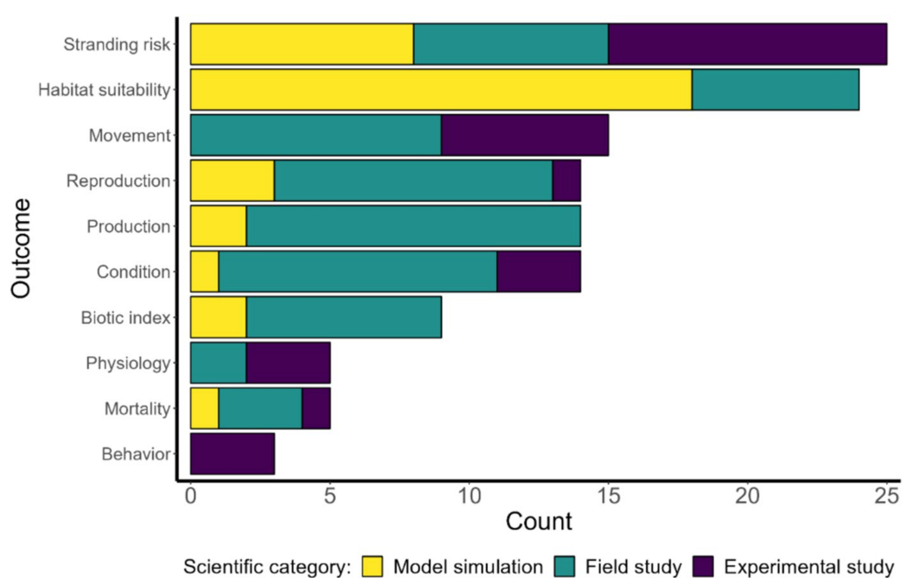


Fig. 4 Articles per ecological outcome category, grouped by study type. Note: count of each ecological outcome in this figure does not align exactly with number of articles featuring each outcome because some outcomes were investigated via multiple study types within the same article

Fig. 5 Conceptual figure of the temporal and spatial scale at which the effects of sub-daily flow variability are realized per ecological outcome category with three example database articles plotted per outcome. Fuzzy edges of each outcome category emphasize that the temporal and spatial extents of each outcome category are not definitive



was investigated by database articles via a blend of laboratory experiments and field studies with fish physiology generally theorized as responding acutely to discrete changes in flow over fine scales of space and time (Figs. 4 and 5). Laboratory experiments in artificial stream channels have shown that Iberian barbel (*Luciobarbus bocagei*) stress responses were significantly elevated during peak flow hydropeaking simulations, but that muscle activity remained unchanged or was reduced relative to base flows, perhaps due to fish using velocity refugia during high flow events (Costa et al. 2018). However, additional experiments on the same species have shown that stress response can be significantly greater at base flow than peak flow due to group refuge use, and refuge shape or quality can significantly increase swimming muscle activity irrespective of flow conditions by prompting fish movement (Costa et al. 2019). Moreira et al. (2020) found no significant difference in stress response on Iberian barbel muscle activity between flow conditions. Taylor et al. (2012) found that stress responses of Mountain whitefish (*Prosopium williamsoni*) significantly increased with mean discharge and within-hour change in discharge but observed that elevated blood cortisol levels were well within the range of pre-stress values for other salmonids and were not biologically meaningful.

Field studies on salmonids have shown that Bull trout (*Salvelinus confluentus*) swimming muscle activity significantly increases with total flow magnitude but is unaffected by within-hour flow variability (Taylor et al. 2014). A study of Mountain whitefish (*P. williamsoni*) in the same system revealed that swimming muscle activity increased significantly with mean hourly discharge but was unaffected by short-term flow fluctuations, despite large within-hour changes in flow (920 m3/s; Taylor et al. 2012). Much of the variation in swimming muscle activity was not explained by discharge, suggesting that fluctuating flows are not more energetically costly for these salmonids than stable flows (Taylor et al. 2012, 2014). Collectively, these articles suggest that increasing flows can increase physiological stress responses and swimming activity in fish but that these stress responses generally are not biologically meaningful, and fish seem to be good at finding velocity refugia to avoid excessive swimming during high flow events. These limited lines of evidence suggest that sub-daily flow variability does not strongly impact fish physiology.

Stranding risk ($N=21$)

We classified articles that evaluated risk or rate of fish becoming stranded during dewatering events caused by rapid down-ramping as stranding risk outcome articles (Table 4). This phenomenon was studied via a balance of field studies, lab experiments, and model simulations, and was the most-studied outcome in our review ($N=21$; Fig. 4). Stranding risk generally is impacted by SDFV during discrete down-ramping events that occur within habitats and reaches over minutes to hours (Fig. 5). There is general literature consensus that young fish are at risk of becoming stranded during down-ramping events and that stranding risk is influenced by many factors including down-ramping rate, time of day, season, local habitat-scale and reach-scale channel morphology, fish life stage, substrate composition, and baseline flow conditions.

Führer et al. (2022) found that larval Common nase (*Chondrostoma nasus*) stranding risk was greatest (in order of decreasing effect importance) in habitats with shallow bank slopes (2%) at night for the youngest larval stages during rapid down-ramping rates; bank slope was the most influential variable and steep bank slopes (5%) negated the effect of the second most important variable, time of day (Führer et al. 2022). Down-ramping rate has been shown to be a weaker influence on stranding probability relative to much stronger effects of temperature and substrate size (Glowa et al. 2022). Time of day and temperature (or season) may interact to influence stranding rates based on species life history. During the winter when many juvenile salmonids are least active, down-ramping during the day (also a period of reduced activity) can significantly increase stranding frequency relative to down-ramping during the night, and time of day is less important for stranding risk during the summer when juvenile salmonids are more active (Bradford et al. 1995; Saltveit et al. 2001). Stranding risk was greater during rest periods at night than during daytime feeding for juvenile European grayling (*Thymallus thymallus*), especially in heterogenous habitat types with isolated small pools, but was reduced by decreased ramping rates (Auer et al. 2017). Halleraker et al. (2003) found that cold water temperatures, coarse substrate, shallow bank slopes, high flow, and greater numbers of trout parr increased the probability of stranding for trout fry.

In addition to local, habitat-scale channel characteristics, reach-scale channel morphology strongly influences fish stranding risk by regulating the extent to which fish habitat becomes disconnected from the river channel during varying discharge levels. Channels with point bars are relatively insensitive to down-ramping events and provide juvenile fish with stable habitat across a spectrum of discharges compared to alternating gravel bars which may actually worsen stranding risk during down-ramping events (Hauer et al. 2014). Braided river channels provide complex habitats suitable for many different life stages of fish and offer protection to young life stages during high flows; however, these channel types also create habitat pockets that become disconnected from the main channel and strand fish as flow decreases (Vanzo et al. 2016).

Baseline flow conditions and connectivity to other sources of flow also can be important determinants of stranding risk. High base flows during wet years or side channel connectivity to mainstems may result in less habitat becoming dewatered during rapid down-ramping events relative to low flows during dry years or in nearby mainstems, and the severity of these effects is mediated by local channel morphology (Moreira et al. 2020b; Plate and Smith 2016; Tuhtan et al. 2012). Shifting hydropower operation policy to discourage salmonids from spawning in marginal habitat that is frequently dewatered during normal operations has not been effective (Plate and Smith 2016; Smith 2007). Finally, frequency of down-ramping events also may affect stranding risk whereby fish that become habituated or acclimated to pulsed flows are less likely to become stranded (Halleraker et al. 2003; Klimley et al. 2007). However, it also is possible that fish exhibit high inter-individual differences in stranding risk and susceptible individuals are removed from the population during initial dewatering events resulting in reduced population stranding rate in subsequent dewatering events (Halleraker et al. 2003).

In addition to time of day, season, channel morphology, and baseline flow conditions, slow down-ramping rates may reduce stranding risk of juvenile and adult fish by providing more time for fish to shift from spawning or rearing stream margin habitats to stream channels as water levels recede (Bradford et al. 1995; Burman et al. 2021; Halleraker et al. 2003; Smith 2007). Slower down-ramping rates (e.g., 5 cm/hr versus 15 cm/hr) also may reduce the longitudinal impact of hydropeaking downstream, although this is strongly impacted by channel morphology (Juárez et al. 2019). Fish stranding due to rapid down-ramping events is potentially the most severe effect of hydropeaking (Tonolla et al. 2017), and may extend throughout entire populations by reducing juvenile survival such that compensatory density-dependent mortality is impacted, potentially dampening or exacerbating the population-level effects of stranding depending on the season and species (Hedger et al. 2018).

Fish stranding due to dewatering events in rapid down-ramping hydropeaking phases does not necessarily result in mortality. A series of experiments on multiple developmental stages of Rainbow trout (*Oncorhynchus mykiss*) and Chinook salmon (*Oncorhynchus tshawytscha*) revealed that salmonid egg developmental phases can survive dewatering for several days at a time provided temperatures remain above freezing and humidity remains near 100%, but alevin phases with gill-dependent respiration cannot survive more than a few hours of dewatering (Becker et al. 1982, 1983, 1986). Subzero temperatures and/or dry conditions significantly increase mortality of dewatered eggs (Casas-Mulet et al. 2015).

There is consensus among the stranding risk articles in our database that rapid down-ramping phases of hydropeaking negatively impact downstream fish communities by increasing the probability that individuals become stranded in isolated pools of water away from river channel habitat. Furthermore, the literature agrees that stranding probability is a complex function of down-ramping rate, habitat- and reach-scale channel morphology, season, time of day, baseline flow conditions, presence of other life stages or conspecifics, species-specific life history, and frequency or regularity of down-ramping events. Fish are most likely to become stranded during periods when they are least active, and stranding risk is exacerbated by local habitat heterogeneity and reach-scale channel morphology. For juvenile salmonids, which are the most-studied group for stranding risk, stranding tends to be worse during the day and in colder temperatures in coarse substrate with many interstitial spaces for juveniles to take shelter from fast velocities and hide from predators, and in stream segments with shallow stream bank slopes that result in rapid and substantial decreases in stream wetted width as water levels recede during down-ramping. Rapid down-ramping rates exacerbate stranding risk by giving fish limited time to react to receding water levels and return to permanently wetted river channels. Strategies to mitigate the effects of hydropeaking on fish must consider the full suite of biotic and abiotic characteristics known to influence stranding risk of juvenile fish for maximum efficacy.

Habitat suitability ($N=20$)

We classified articles that evaluated elements of habitat use, stability, or availability for any life stage and any activity (including spawning) as habitat suitability outcome articles (Table 4). This was the second most studied phenomenon in our database ($N=20$) and articles primarily evaluated habitat suitability using model simulations (Fig. 4). The effects of sub-daily flow variability on fish habitat suitability generally are realized over habitats or reaches over the timespan of hours to days (Fig. 5), and are dependent on season, species, life stage, local channel morphology, and downstream distance from the generating station.

Hydropeaking reduces overall habitat suitability by creating unpredictable flow conditions that decrease the quality of habitat within a given reach or shift the locations of suitable habitat, even when high discharge during peaking events increases the total habitat area available to fish (Person 2013). The severity of the effects of sub-daily flow variability on fish habitat suitability and stability are dependent on river morphology and fish life stage, with greater and more rapid impacts in homogeneous than heterogeneous habitats (Boavida et al. 2015; Choi et al. 2017) and stronger effects on juveniles than adults (Jelovica et al. 2022). As flow increases during hydropeaking, fish may be forced to move from central locations in stream channels to stream margins to remain in suitable habitat and avoid high flows (Boavida et al. 2015; Judes et al. 2022). During peak flows, fish may be forced to occupy habitats near stream margins that provide refuge from high flows compared to low flow periods when they otherwise would occupy habitats nearer the thalweg better suited for feeding (Boavida et al. 2021). For instance, peak flow phases during hydropeaking concentrated juvenile Brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) into suboptimal feeding habitats with potentially negative consequences for growth and predation (Hajiesmaeili et al. 2022). Juvenile fish that remain in suboptimal habitats in the channel during peak flow and do not shift to stream margins may exhibit reduced growth during important summer feeding seasons (Korman and Campana 2011). Less mobile organisms such as benthic macroinvertebrates and certain life stages of frogs may be less capable of moving as suitable habitat locations shift between high and low flow phases and therefore may be more strongly impacted by hydropeaking, and these effects could impact trophic relationships and contribute to species decline or extirpation (Judes et al. 2022; Kupferberg et al. 2012).

Sub-daily flow variability can change stream lateral width and depth in short periods of time. Shifts in the location or quality of suitable habitat during hydropeaking are strongly influenced by habitat- and reach-scale channel morphology. Habitat suitability in reaches with shallow-sloped banks is more sensitive to increasing discharge than in reaches with steeply sloped banks and the same flow modification can have different impacts on habitat suitability in reaches with different morphologies (Holzapfel et al. 2017; Tuhtan et al. 2012). Braided river reaches are more resilient to hydropeaking than channelized reaches because high channel complexity provides greater overall suitability and refugia under a wide range of flows (Antonetti et al. 2022; Boavida et al. 2015; Person et al. 2014). In some cases, braided river reaches may exhibit increases in total useable habitat during high flows due to increases in wetted area across shallow bank slopes at peak flow when suitable habitat shifts laterally from the thalweg to stream margins (Judes et al. 2022; Valentin et al. 1996). In reaches that have been channelized or otherwise simplified, increasing discharge can severely limit total usable habitat area for fish (Person 2013). Reaches with steep bank slopes may exhibit little or no increase in habitat area between base and peak flow due to minimal changes in stream width and marginally suitable habitats at base flow may become unsuitable at peak flow (Hauer et al., 2017).

Different life stages have different habitat requirements and flow conditions that provide suitable habitat for one life stage (e.g., adults) might not provide suitable habitat for other life stage (e.g., juveniles).

For instance, high-flow phases of hydropeaking provide maximum useable habitat area for adult Iberian barbel (*Luciobarbus bocagei*), and low-flow phases provide more suitable habitat for juveniles (Boavida et al. 2020). Peak flow phases of hydropeaking may increase habitat suitability for spawning adults but decrease suitable habitat for young-of-the-year who require shallow, low flow habitats at stream margins (Person 2013). Increasing discharge decreased habitat suitability for both juvenile Brown trout (*S. trutta*) and adult European grayling (*Thymallus thymallus*) but was worse for juvenile trout (Jelovica et al. 2022; Valentin et al. 1996). Suitable feeding habitat for juvenile Brown trout (*S. trutta*) was limited to base flows of hydropeaking flow cycles when feeding conditions and macroinvertebrate prey availability were greatest (Holzapfel et al. 2017).

Mitigation strategies to reduce the effects of hydropeaking on habitat suitability should consider species life histories and local channel morphology. Decreasing the down-ramping rate can reduce the impact of hydropeaking on fish habitat by slowing the rate at which habitat is lost via reductions in wetted width and reducing overall habitat loss longitudinally (Juárez et al. 2019). Similarly, increasing frequency of hydropeaking can reduce the amount of spawning habitat that becomes dewatered during low flows but also reduce overall suitable spawning habitat by creating suboptimal depth and velocity conditions for spawning (Burman et al. 2021). Alternatively, if depth, velocity, and substrate remain suitable for fish to complete spawning under the entire range of flow conditions created by hydropeaking, then habitat suitability mitigation might not be needed (Tonolla et al. 2017). The relationship between habitat suitability and hydropeaking is strongly dependent upon river morphology and if morphological conditions are poor (e.g., channelized reaches) flow mitigation measures will be largely ineffective (Holzapfel et al. 2017; Person 2013; Person et al. 2014; Tuhtan et al. 2012). The intensity of the effects of hydropeaking decreases with downstream distance from the generating station and the degree of longitudinal attenuation is related to morphology (Burman et al. 2021; Juárez et al. 2019; Valentin et al. 1996).

Natural flow variability is widely recognized as being an important driver of ecological processes in natural systems, including maintaining critical habitat form and function for riverine fish (Junk et al. 1989; Poff and Ward 1989; Resh et al. 1988). However, increasing discharge during up-ramping and peak flow phases of hydropeaking generally has a negative effect on fish habitat quantity, quality, and overall suitability (Hajiesmaeili et al. 2022; Jelovica et al. 2022; Tuhtan et al. 2012; Valentin et al. 1996). There is consensus among the habitat suitability outcome articles in our database that increasing flows destabilize, shift, or otherwise reduce the quality and/or quantity of suitable fish habitat, that these effects are most severe for juvenile fish in homogeneous, channelized habitats, and that the effects of hydropeaking on habitat suitability decrease with increasing downstream distance from the source of flow variability. Mitigation strategies aimed at reducing the negative impacts of hydropeaking on fish habitat suitability should consider the role that local morphology plays in attenuating or exacerbating the effects of flow variability on fish habitat and should attempt to create flows that will provide seasonally appropriate suitable habitats for all life stages of a given species within the natural range of flow variability of a given system.

Movement ($N = 14$)

We classified articles that evaluated the distance or number of voluntary or involuntary fish movements using telemetry, mark-recapture, or experimental flumes as movement outcome articles ($N = 14$, Table 4). Fish movement was evaluated by articles in our full-text database using a mix of field studies and laboratory experiments and was not assessed using model simulations (Fig. 4). Fish movement in response to sub-daily flow variability generally occurs within reaches or between systems and at timescales of hours to days to seasons (Fig. 5).

Adult Rainbow trout (*Oncorhynchus mykiss*) and Mountain whitefish (*Prosopium williamsoni*) shifted locations within river reaches during hydropeaking to occupy lower velocity refugia (i.e., pools or eddies) but did not move significant distances up- or downstream in response to pulsed flows (White and Wade 1980). High discharge during hydropeaking decreased the likelihood of Bull trout (*Salvelinus confluentus*) movement in the Columbia River and changes or peaks in discharge did not displace Bull trout downstream (Taylor et al. 2013). Neither Rainbow trout (*O. mykiss*) nor Brown trout (*Salmo trutta*) moved significantly up- or downstream in response to pulsed flows in a California stream or hydropeaking simulations in an experimental flume (Klimley et al. 2007). Conversely, Brown trout (*S. trutta*) moved significantly more and had larger home ranges in a hydropeaked river reach relative to a reference reach, potentially because hydropeaking increased the distance between complementary habitats required for Brown trout life history (Rocaspana et al. 2019). North American paddlefish (*Polyodon spathula*) moved upstream in response to increasing discharge, but upstream movements were much greater for flood mitigation than hydropeaking operation, potentially because the former produced greater discharge increases that cued upstream movement (Lallaman 2012). Sub-daily flow variability created by hydropeaking operations 12 km upstream of Asp (*Leuciscus aspius*) spawning grounds caused spawning individuals to move to downstream sections of the spawning ground, potentially interrupting crucial spawning processes (Bartoň et al. 2022).

Hydropeaking simulations in experimental flumes caused fish to move from free swimming at base flows to upstream velocity refugia during high flows (Costa et al. 2018, 2019). In another set of experiments, European grayling (*Thymallus thymallus*) made fewer position changes during up-ramping events compared to stable base flow before and after peak flows (Watz et al. 2020). In some cases, movement due to high flow variability may not be voluntary. Nighttime up-ramping and peaking flows significantly increased downstream movement of juvenile European grayling (*T. thymallus*) in experimental flumes, especially in heterogeneous habitat types (Auer et al. 2017). Increased drift rates at night were attributed to reduced grayling activity and a shift to shallow habitats during this period, and downstream drift rates significantly decreased when up-ramping rates were reduced (Auer et al. 2017). Similarly, increasing discharge increased larval Sicydiinae goby drift rates and decreased duration of diadromous migration, though this likely was offset by increased larval mortality in high flows (Lagarde et al. 2018).

The relationship between sub-daily flow variability and fish movement is dependent on season. Juvenile Atlantic salmon (*Salmo salar*) moved greater distances during the summer with the greatest rate and magnitude of flow change, and home range sizes tended to be largest during summer and smallest during winter (Scruton et al. 2008). Similarly, juvenile Atlantic salmon (*S. salar*) moved significantly greater distances in summer than in winter, regardless of time of day and hydropeaking flow condition, and most movements were upstream suggesting movement was voluntary (Scruton et al. 2005). Hydropeaking did not affect juvenile Atlantic salmon (*S. salar*) movement during winter experiments, but significantly increased movement in summer experiments both during daytime hydropeaking and at night after peak flow periods (Puffer et al. 2015). The relationship between sub-daily flow variability and movement also is dependent on time of day, with greater movement observed during night than day (Auer et al. 2017; Puffer et al. 2015; Scruton et al. 2008).

The movement articles reviewed in our full-text database report two distinct fish responses to sub-daily flow variability. At fine scales (i.e., between habitats), fish seem to take shelter in nearby refugia at the onset of high flows and then resume swimming freely once stable flows resume (e.g., Costa et al. 2018; Watz et al. 2020; White and Wade 1980). At coarse scales (i.e., within reaches), fluctuating flows may prompt fish to move to seek complementary habitats to complete life histories (e.g., Lallaman 2012; Rocaspana et al. 2019). Generally, articles moderately agree that fluctuating flows due to hydropeaking are not displacing fish downstream (but see Auer et al. 2017; Lagarde et al. 2018) and that movement in response to sub-daily flow variability is dependent on season and time of day, with most movement observations occurring during periods of increased activity (summer, night).

Reproduction ($N=10$)

We classified articles that evaluated reproductive activity or success outside of the context of habitat use and stranding, including articles that measured a life stage-specific population metric (e.g., young-of-the-year density) for the explicit purpose of evaluating reproductive success, as reproduction outcome articles ($N=10$, Table 4). Examples of reproduction metrics measured or estimated in reproduction outcome articles in our full-text database include egg-to-hatch survival (Harnish et al. 2014), young-of-the-year density (YOY; Person 2013), egg dislodgement (White and Wade 1980), and adult spawning behavior (e.g., number of redds or active spawners per unit area; Smith 2007). The relationship between fish reproduction and sub-daily flow variability was investigated predominately via field studies and model simulations (Fig. 4) and generally occurs between habitats and reaches and over days to seasons (Fig. 5).

There was no significant difference in Brown trout (*Salmo trutta*) egg-to-hatch survival or YOY density between naturally flowing and hydropeaking river reaches despite unstable spawning habitat conditions created by hydropeaking (Person 2013). However, subsequent investigations in a nearby channelized river revealed lower egg survival and YOY density in hydropeaked reaches relative to natural reaches, suggesting that channel morphology plays an important role in tempering or exacerbating the effects of sub-daily flow variability on riverine fish (Person 2013). High flows during hydropeaking can significantly decrease egg density in spawning grounds by dislodging eggs from the substrate and depositing them in low flow stream margins, where they are potentially at greater risk of dewatering during subsequent low flow events (Bartoň et al. 2021; White and Wade 1980). Installing flow deflectors to reduce high hydropeaking flows in spawning areas can significantly increase egg density in protected areas (Bartoň et al. 2022), but the practicality and efficacy of this mitigation strategy is highly site specific. Model simulations estimated that fish reproduction – measured via abundance of juvenile Brown trout (*S. trutta*) – was in poor condition in a hydropeaking flow regime and did not predict that it would improve in response to a proposed retention basin mitigation strategy (Tonolla et al. 2017).

Studies of the relationship between flow and Chum salmon (*Oncorhynchus keta*) spawning in a side channel of the Fraser River in Canada indicate that operating power generation stations to dissuade spawning activity in marginal habitat that becomes dewatered during low flow shutdowns does not work. Brief low flow periods during generation station shutdowns caused spawning salmon to rapidly retreat to deeper water but did not deter spawning activity as the number of active spawners was greater during the low flow period than before, and spawners returned to incomplete redds abandoned during low flows to complete spawning as flow increased (Smith 2007). Embryo survival was the same between marginal, dewatered spawning habitat and non-marginal, never-dewatered spawning habitat despite significantly greater embryo density in the non-marginal habitat (Plate and Smith 2016).

Low flows during rapid down-ramping events downstream of a hydropeaking dam in Norway differentially affected spawning activity of two salmonids. Down-ramping caused spawning Atlantic salmon (*Salmo salar*) to temporarily retreat to deeper water before returning to complete nest building during subsequent up-ramping events, whereas smaller spawning Brown trout (*S. trutta*) were able to remain in spawning grounds during low flows (Vollset et al. 2016). Despite low flow periods disrupting Atlantic salmon (*S. salar*) spawning activity, total nest mortality remained very low indicating that fluctuating flows may interrupt spawning behavior but not significantly impact egg viability (Vollset et al. 2016). Hydropeaking mitigation strategies aimed at protecting the youngest life stages of Chinook salmon (*Oncorhynchus tshawytscha*) in the Pacific Northwest, USA, via decreasing marginal spawning habitat availability during spawning periods and limiting the magnitude of discharge fluctuations during emergence and early rearing resulted in dramatic improvements in egg escapement, pre-smolt abundance, and egg-to-pre-smolt survival probabilities (Harnish et al. 2014).

Measured or estimated reproduction outcomes in our database should be interpreted in the context of stranding risk, production, and habitat suitability outcomes given substantial overlap between these categories (e.g., many stranding risk outcome articles evaluated egg survival during periods of dewatering). Nonetheless, there is moderate agreement among reproduction outcome articles in our database that sub-daily flow variability interrupts riverine fish reproduction, but likely does not substantially impact the viability of eggs that are not dislodged during peaking flows. Mitigation strategies tailored for specific life stage of species at specific sites can be effective at protecting riverine fish reproduction.

Condition ($N = 14$)

We classified articles that measured individual-level body or size characteristics as affected by sub-daily flow variability as condition outcome articles ($N = 14$, Table 4). Most of these articles collected data via field studies, though there were a few laboratory experiments and one model simulation (Fig. 4). The effects of sub-daily flow variability on condition generally are realized between habitats, reaches, and systems on timescales of seasons to years (Fig. 5).

Model simulations and laboratory experiments on the relationship between sub-daily flow variability and fish condition suggest that regulated flow regimes depress condition metrics. Model simulations of multiple hydropeaking scenarios predicted that hydropeaking reduces juvenile Atlantic salmon (*Salmo salar*) and Brown trout (*Salmo trutta*) growth relative to a hypothetical natural flow regime (Hajiesmaeili et al. 2022). Laboratory experiments that expose fish to hydropeaking flow pulses in experimental stream flumes suggest that the relationship between flow variability and condition is dependent on species, season, and competition. For instance, simulated hydropeaking flows in experimental flumes significantly reduced growth of juvenile Brown trout (*S. trutta*) but did not affect Atlantic salmon (*S. salar*) growth (Addo et al. 2022). Similar experiments have shown that fluctuating flows significantly reduce body mass and fat in juvenile Atlantic salmon (*S. salar*) relative to stable flows, but that this effect is only evident in the summer (Puffer et al. 2015). Other experiments have shown that the effects of hydropeaking on juvenile Atlantic salmon (*S. salar*) growth are outweighed by stronger effects of inter- and intraspecific competition (Puffer et al. 2017).

Field studies of the relationship between flow variability and condition tell a somewhat different story. Comparisons between a hydropeaking river and a nearby naturally flowing river in Ontario, Canada revealed that fish condition metrics (e.g., annual growth rate, length-at-age, condition, field metabolism) for Longnose dace (*Rhinichthys cataractae*), Slimy sculpin (*Cottus cognatus*), Trout-perch (*Percopsis omiscomaycus*), and Brook trout (*Salvelinus fontinalis*) were the same or significantly greater in the hydropeaking river (Bond et al. 2016; Kelly et al. 2015, 2017a, b; Smokorowski et al. 2011). Other field studies have shown no significant difference in growth rates or conditions of multiple species between hydropeaking and natural flow regime sites, but significantly greater fullness in hydropeaking site individuals (Enders et al. 2017; Lagarrigue et al. 2002; Rocaspana et al. 2016). In contrast, Korman and Campana (2011) found that juvenile Rainbow trout (*Oncorhynchus mykiss*) grew significantly more during periods of stable flow than when exposed to hydropeaking, likely because peaking flows limited their access to productive stream margin habitat. In tailwaters across the western United States, negative correlations between Rainbow trout (*O. mykiss*) and Brown trout (*S. trutta*) length and high daily fluctuations in flow were outweighed by stronger negative relationships with intra- and inter-specific competition (e.g., catch rates of conspecifics, new adult cohort strength; Dibble et al. 2015).

The observed or predicted relationship between sub-daily flow variability and condition is dependent upon the method of inquiry used to investigate the relationship. Laboratory experiments and model simulations suggest that variability generally negatively affects condition, whereas field studies suggest that condition may be unaffected or even improved by sub-daily flow variability. One potential explanation for observed positive relationship between flow variability and condition is increased prey availability during pulsed flows, which apparently offsets any additional energy expenditures incurred by individuals in fluctuating flow regimes (Bond et al. 2016; Kelly et al. 2015, 2017b; Lagarrigue et al. 2002; Rocaspana et al. 2016). Model simulations and laboratory experiments did not account for prey subsidies at higher flows. In cases where fish condition and hydropeaking were negatively correlated, this relationship was tempered by season (Puffer et al. 2015), life stage (Korman and Campana 2011), or better explained by intra- and interspecific interactions than hydraulic metrics (Dibble et al. 2015; Puffer et al. 2017). There is moderate agreement among articles in our database that individuals downstream from hydropeaking dams may exhibit the same or better condition than individuals in natural flow regimes, likely because increased food resources outweigh the energetic costs associated with living in highly variable flow regimes.

Production ($N=13$)

We classified articles that evaluated population-level characteristics of a single species – including abundance, density, biomass, or other metrics related to the total number of individuals at a given time and place – as production outcome articles ($N=13$, Table 4). Two articles used model simulations to assess the relationship between fish production and sub-daily flow variability; the remainder used field studies (Fig. 4). The effects of sub-daily flow variability on production generally are realized across reaches and systems on timescales of seasons to years (Fig. 5).

Models simulating the effects of sub-daily flow variability on fish productivity generally predict that hydropeaking negatively influences productivity via life stage-specific mechanisms but that these effects can be somewhat ameliorated by compensatory density-dependent mortality or mitigation strategies. Hydropeaking model simulations significantly reduced abundance of young life stages of Atlantic salmon (*Salmo salar*) via stranding; these effects propagated throughout the population and were cumulative over time resulting in suppressed abundances of each life stage, with greater population-level impacts from hydropeaking in the spring and winter due to reduced compensatory effects of density-dependent mortality (Hedger et al. 2018). Additional model simulations predicted fish productivity was unsatisfactory in the existing hydropeaking flow regime but could be improved if basin flow dampening mitigation strategies were adopted for peaking retention, which would reduce stranding rates of juvenile trout and increase macroinvertebrate biomass (Tonolla et al. 2017).

A long-term field study of 45 stream reaches in France revealed that non-hydropeaking seasonal high flows had greater effects on species-specific densities than low intensity hydropeaking and that the effects of pulsed flows were dampened by habitat connectivity and heterogeneity (Judes et al. 2020). Fish abundance and biomass were significantly reduced downstream of some small hydropower plants with low intensity hydropeaking in Lithuania relative to upstream reference sites, but these results were only observed at 20% of the evaluated power plants and were not explained by any of the potential predictor variables (Česonienė et al. 2021). European grayling (*Thymallus thymallus*) biomass was significantly reduced in low- and normal-intensity hydropeaking rivers in Austria and sites with the highest biomass had the low down-ramping rates and flow fluctuation amplitudes (Hayes et al. 2021).

The effects of sub-daily flow variability on fish production are dependent on life stage and season. For instance, juvenile Brown trout (*S. trutta*) were significantly less abundant downstream from a hydropeaking dam relative to an upstream reference site, likely due to high hydropeaking intensity and frequency during autumn and winter resulting in unfavorable conditions for juveniles (Saltveit et al. 2020). In another field study, Brown trout (*S. trutta*) density and biomass were significantly lower downstream of a hydropeaking dam relative to an upstream reference site, and the downstream hydropeaking site had an imbalanced population size structure with few younger individuals (Rocaspana et al. 2016). There were similar imbalances in population size structure for several fish species in a Canadian river, with fewer younger individuals in hydropeaking sites downstream of a dam relative to an upstream reference site in Canada (Enders et al. 2017). Lagarrigue et al. (2002) also observed reduced biomass and density of Brown trout (*S. trutta*) in a site influenced by hydropeaking, which was primarily driven by fewer juveniles.

Conversely, fish biomass was not significantly different between hydropeaking and naturally flowing rivers in Canada, potentially due to ramping rate and minimum discharge restrictions (17% of maximum discharge; Smokorowski et al. 2011). Hydropeaking flow pulses can increase the abundance of specific life stages during seasons when high flows are important for certain life cycle activities (e.g., salt water migration of goby larvae; Lagarde et al. 2018). A long-term analysis of trout recruitment in 29 tailwaters in the western United States revealed that Brown trout (*S. trutta*) recruitment was significantly negatively correlated with hydropeaking and high flow whereas Rainbow trout (*Oncorhynchus mykiss*) recruitment was more closely correlated with seasonal flow patterns (Dibble et al. 2015). In a Canadian field study, sculpin biomass was significantly greater in hydropeaking rivers relative to naturally flowing rivers, and sculpin density shifted longitudinally within the hydropeaking rivers; these patterns were attributed to shifts in invertebrate prey availability (Bond and Jones 2015).

Collectively, these articles strongly agree that fish production – expressed via biomass, density, abundance, or other metrics – likely is suppressed by sub-daily flow variability largely via reduced numbers of younger life stages in flow regimes with high-intensity hydropeaking. Fish populations in hydropeaking rivers are smaller and/or less balanced relative to populations in natural flow regimes because small fish have low tolerance to fast, highly variable flow. In cases where production was not strongly correlated with flow, hypothesized reasons are effective mitigation strategies (Smokorowski et al. 2011), low hydropeaking intensity or fish adaptation to fluctuating flows (Česonienė et al. 2021; Judes et al. 2020), and increased prey availability (Bond and Jones 2015).

Mortality (N = 5)

We classified articles that evaluated elements of mortality or survival not attributed to stranding risk or reproduction as mortality outcome articles (*N* = 5, Table 4). Mortality due to sub-daily flow variability was one of the lesser-studied phenomena in our review, and was predominately investigated via field studies, with one model simulation and laboratory experiment each (Fig. 4). Mortality is impacted by sub-daily flow variability from habitats to systems at timescales of seasons to years (Fig. 5).

Mortality due to sub-daily flow variability is species-specific. Annual survival for Longnose dace (*Rhinichthys cataractae*) and Slimy sculpin (*Cottus cognatus*) was significantly lower in a hydropeaking river relative to a naturally flowing river, but Trout-perch (*Percopsis omiscomaycus*) survival was unchanged (Bond et al. 2016; Kelly et al. 2017a). Fluctuating flow treatments to simulate hydropeaking in experimental flumes resulted in significantly greater juvenile Brown trout (*Salmo trutta*) mortality relative to stable flow treatments, but juvenile Atlantic salmon (*Salmo salar*) mortality did not differ between treatments (Addo et al. 2022). Individual-based model simulations predicted the opposite trend for these same species – reduced survival due to increased predation risk of juvenile Atlantic salmon (*S. salar*) in hydropeaking scenarios relative to the natural baseline flow scenario but unchanged juvenile Brown trout (*S. trutta*) survival (Hajiesmaeili et al. 2022). Finally, increased discharge during hydropeaking events increased the mortality of Red-tailed goby larvae (*Sicyopterus lagocephalus*) en route to the ocean to complete their life history (Lagarde et al. 2018), although increases in discharge decreased travel time to the ocean, which is beneficial for this species. The limited number of mortality articles in our database and their variability of reported results preclude our ability to draw strong conclusions about the relationship between sub-daily flow variability and mortality, but generally suggest that that survival or river fishes is lower in systems with high flow variability and magnitude relative to stable, naturally flowing systems and that these effects are species-specific.

Biotic index (*N* = 8)

We classified articles that evaluated the abundance or richness of species at a given site as biotic index outcome articles (*N* = 8, Table 4). Biotic indices were assessed primarily via field studies (Fig. 4). Biotic indices are impacted by sub-daily flow variability within reaches or systems across seasons and years (Fig. 5). Fish diversity was lower and more variable at hydropeaking sites relative to reference sites, and diversity was strongly negatively impacted in higher order, channelized reaches with frequent peaking events and rapid ramping rates (Schmutz et al. 2014). Fish diversity was lower in a hydropeaked site relative to an upstream reference site, potentially due to low habitat heterogeneity at the hydropeaked site which was unable to support a diverse array of species across a fluctuating flow regime (Boavida et al. 2015). Fish communities were less diverse downstream of small hydropower plants across Lithuania, but community indices were more strongly influenced by river depth and area downstream of the dams than flow or ramping rate (Česonienė et al. 2021).

Fish communities immediately downstream from hydropeaking dams are less diverse than communities further downstream or at upstream or nearby reference sites and were primarily composed of generalist species tolerant of hydropeaking (Bond and Jones 2015; Enders et al. 2017; Smokorowski et al. 2011). In other cases, fish assemblages were more strongly impacted by stream size than low intensity hydropeaking, with headwater streams favoring trout and lower elevation, larger streams favoring cyprinids (Judes et al. 2020). A model simulation estimated that fish community structure was in moderate condition under an existing hydropeaking regime and that it would not be improved under retention basin mitigation strategies (Tonolla et al. 2017).

The biotic index articles in our database strongly agree that sub-daily flow variability depresses fish community diversity. Sites downstream from hydropeaking facilities tend to support less diverse fish communities, likely as a complex combination of highly variable flow regimes, broad-scale river characteristics like network position (i.e., higher versus lower order) and stream size and depth (Česonienė et al. 2021; Judes et al. 2020; Schmutz et al. 2014), and local channel morphology and habitat heterogeneity (Boavida et al. 2015). Mitigation strategies to improve fish community diversity in the context of variable flow regimes should consider whether downstream habitat morphology and river characteristics will support additional diversity beyond generalist species.

Articles not reviewed

We were unable to review 56 articles in our database due to time constraints and we did not review an additional 127 articles due to low keyword counts. It is possible that several of the articles we were unable to review due to time constraints may have investigated low-studied ecological outcomes in our review (e.g., physiology and behavior) and thus substantially influenced our conclusions. Similarly, it is possible that some of the 127 articles not reviewed due to low keyword count may have been relevant to our review. To estimate the effects of these omissions, we randomly selected 50% ($N=29$) of the articles not reviewed due to time constraints and 10% ($N=13$) of the low-relevance articles and recorded the country where the study was conducted, as well as the fish family and ecological outcome category.

For the subsample of articles omitted due to time constraints, eight would have been excluded based on population ($N=1$), exposure ($N=5$), or outcome ($N=2$). Of the remaining 21 articles, one was a review and the remaining 20 predominately assessed ecological outcomes that were well-represented in our review: two assessed stranding risk ($N=21$ stranding risk articles in the review), three assessed habitat suitability ($N=20$), five assessed movement ($N=14$), three assessed condition ($N=14$), three assessed production ($N=13$), two assessed reproduction ($N=10$), and four assessed biotic index ($N=8$) (recall that single articles can report multiple outcomes). Of the low-studied outcomes in the database, these omitted articles would have contributed one additional article each to mortality ($N=5$), physiology ($N=5$), and behavior ($N=3$). None of the omitted articles would have contributed information on a fish family not already included in the review, although one article would have added information from one additional country (India). For the subsample of articles omitted due to low keyword count, ten would have been excluded based on exposure. The remaining three assessed condition, biotic index, and production for fish families and countries already represented in the review.

Discussion

Our systematic review of 109 articles on the relationship between sub-daily flow variability due to hydropower production on riverine fish ecology suggests that highly variable flows over short timespans negatively impact fish in rivers in many ways. There is literature consensus that sub-daily flow variability increases stranding risk, destabilizes habitat, decreases population production, and decreases diversity. There was moderate agreement among articles in our database that sub-daily flow variability interrupts – but does not drastically impair – reproduction, increases or does not affect condition, and prompts different movement responses based on life-history requirements and local habitat conditions. Finally, few articles in our database investigated the relationship between flow variability and mortality, physiology, and behavior, and those that did reported relationships that were inconsistent or not biologically meaningful.

There was an interesting pattern between literature agreement and ecological outcome representation in our database articles. It is possible that the observed differences in relationships between ecological outcomes and sub-daily flow variability are due to differences in the number of articles per outcome in our database. However, observed differences in amount of literature agreement may also be a result of how different outcomes are quantified or predicted and ultimately affected by sub-daily flow variability. Stranding risk and habitat suitability were the most-studied outcomes in our database and there was consensus among articles for both outcomes regarding their relationships to sub-daily flow variability. Stranding risk is the most widely studied biological impact of sub-daily flow variability on riverine fish (Hunter 1992). Fish stranding occurs instantaneously in response to discrete down-ramping events and is readily observable in the field via direct or remote surveillance (e.g., Glowa et al. 2022; Saltveit et al. 2001) and relatively easily producible in experimental settings (e.g., Führer et al. 2022). Similarly, baseline knowledge of fish habitat requirements, typically known depth and velocity preferences, allow for relatively straightforward modelling approaches to simulate changes in quantity and arrangement of suitable habitat under a variety of real or hypothetical flow scenarios, which may or may not be validated by field observations (e.g., Antonetti et al. 2022; Judes et al. 2022).

By comparison, mortality, physiology, and behavior, the three least studied (and lowest agreement) outcomes in our database, are either difficult to precisely measure or diffuse by nature. Quantifying fish physiological responses in relation to flow variability requires precise control of flow in experimental settings and/or specialized techniques to measure physiological responses that are directly connected to the flow variable of interest and not biased by handling or other study artifacts (Costa et al. 2018; Taylor et al. 2012). Similarly, mortality attributed to sub-daily flow variability generally is realized at coarse spatial and temporal scales and it can be difficult to disentangle the effects of flow variability on mortality from other complex system dynamics when comparing regulated and natural flow regimes between different rivers (e.g., Bond et al. 2016; Kelly et al. 2017a). Lastly, fish behavior can take many forms including different types of foraging behavior or interactions with other individuals or their immediate environment. It is therefore unsurprising that behavior observations in our database were inconsistent given that articles recorded different behaviors of different species in different settings (Addo et al. 2022; Moreira et al. 2020b; Watz et al. 2020).

Movement, reproduction, production, condition, and biotic index were represented by eight to fourteen articles in our database and articles displayed strong to moderate agreement regarding relationships between sub-daily flow variability and respective outcomes. Reported relationships between these outcomes and sub-daily flow variability were almost always dependent on other covariates. For example, in addition to sub-daily flow variability, movement is dependent upon season and time of day (e.g., Auer et al. 2017; Scruton et al. 2008), reproduction is dependent on channel morphology (e.g., Person 2013), production is dependent on life stage (e.g., Saltveit et al. 2020), condition is dependent on competition (Dibble et al. 2015), and biotic index is dependent on broad scale river characteristics (e.g., Judes et al. 2020). Stranding risk and habitat suitability, the sub-daily flow variability-ecology relationships with the most agreement in the literature, also were strongly co-dependent on habitat complexity and channel morphology (e.g., Choi et al. 2017; Hauer et al., 2017). Consequently, anticipating the effects of sub-daily flow variability on riverine fish requires considering how underlying biological and environmental variables might temper or exacerbate fish response to varying flow.

Generalized protocols for evaluating sub-daily flow variability impacts

The effects of sub-daily flow variability on riverine fish ecology are inextricably intertwined in the complex suite of biotic and abiotic characteristics that structure and constrain aquatic ecosystems (Poff 1997; Poff et al. 1997). This complexity creates a degree of site-, species-, and life stage-specificity that makes it difficult to provide mitigation recommendations that apply to more than a handful of circumstances. Nonetheless, insight gained from this review can provide guidance for generalizing protocols to evaluate the effects of flow variability on riverine fishes to determine which (if any) ecological outcome to mitigate and which mitigation method might be most appropriate.

Mitigation measures can be generally classified into three categories: operational (i.e., measures that constrain hydropower facility operation to attenuate one or more elements of the flow phase), constructional (i.e., measures that modify or construct hydraulic infrastructure such as retention ponds or side channels to lessen flow variability or hydropeaking intensity of discharge into downstream reaches), and compensation (i.e., measures that construct point bars, create habitat complexity, or otherwise modify physical river characteristics to improve habitat and create refugia across the range of realized flows) measures (Bruder et al. 2016; Charmasson and Zinke 2011; Greimel et al. 2018). Selected mitigation measure(s) should be designed to maintain or enhance specific, measurable ecological outcome(s) at a given location (Bätz et al. 2022; Bruder et al. 2016). Accordingly, flow variability impact assessments should first characterize channel (e.g., channelized or braided) and/or habitat (e.g., simple or complex) conditions and fish community composition downstream from a flexible hydropower facility before selecting outcome-specific mitigation strategies.

Characterizing which species and life stages are present in a certain type of channel or habitat can inform which ecological outcome(s) are at potentially impacted by sub-daily flow variability, and, consequently, which mitigation measure(s) might best improve those outcomes (Greimel et al. 2018). For example, preventing the dewatering of spawning grounds and preserving nearshore rearing habitat of post-emergence juvenile salmonids in braided channels might involve operational mitigation strategies of raising minimum flow levels and minimizing the magnitude of flow variability during incubation and post-emergence periods (Harnish et al. 2014; Hayes et al. 2019). Mitigation measures that are designed to improve specific ecological outcomes may have no impact or may adversely impact others (Tonolla et al. 2017). Even extensive mitigation measures may be unsuccessful if they are misaligned with the target outcome or if underlying conditions are not conducive to outcome improvement (e.g., operational flow mitigation in severely degraded reaches; Holzapfel et al. 2017; Person et al. 2014; Tuhtan et al. 2012). Outcome-specific mitigation measures must be judiciously selected in the broader context of the targeted species or community such that any benefits from the selected strategies are not outweighed by negative impacts to other life stages of the species or the broader ecosystem. In summary, knowing the fish community composition and channel and habitat characteristics impacted by sub-daily flow variability can allow managers and regulators to leverage life history information to decide whether mitigation is appropriate, which ecological outcome(s) to prioritize, and which mitigation measure(s) are most likely to result in outcome improvement for the net benefit of the species or system. Strategies that seek to reduce the severity of one or more components of sub-daily flow variability (e.g., reducing ramping rates) without accounting for underlying complex system dynamics or focusing on species- or life stage-specific outcomes for fish may result in reduced power production without corresponding ecological improvements.

Review limitations and future research directions

Our systematic review was limited in a few ways. First, we were unable to review every article identified as potentially relevant during our search process and it is possible that some of the unreviewed articles present different depictions of sub-daily flow variability-fish ecological outcomes, which could shift our conclusions. However, this seems unlikely given that our assessment of a random subset of omitted articles did not reveal large numbers of articles investigating outcomes or fish families that were relatively underrepresented in our review, and that there was strong or moderate literature agreement for SDFV-outcome relationships for outcomes with at least eight observations. Furthermore, our conclusions generally align with syntheses and trends reported in other relevant reviews on similar topics (Bipa et al. 2023; Hayes et al. 2022; Melcher et al. 2017; Smokorowski 2022; Young et al. 2011). No systematic review captures all relevant articles, but we are confident that future reviews of this subject will build on our conclusions as new research becomes available. Our review also was biased toward articles written or translated into English. We are hopeful that this bias does not significantly impact our conclusions given that fewer than 2% of the 350 articles identified for full-text review were excluded due to language.

Lastly, our review largely focused on research conducted in North America and northwestern Europe on salmonids. This limitation is a function of the current state of this research area rather than our search strategy, which was not limited geographically. It is not surprising that much of the current body of research on hydropower-driven sub-daily flow variability has occurred in these regions given that Canada and the United States are among the top five hydropower producing countries in the world and Norway, Switzerland, and Austria produce most of their power from dams (IEA 2021; IHA 2021). Nonetheless, as global power balances shift toward low- or zero-carbon energy sources, we are hopeful that new research will highlight the ecological effects of hydropower in other parts of the world.

During our systematic review, we identified several promising areas for future research to advance our understanding of the complex relationship between hydropower and freshwater ecosystems. First, there is a need to better understand how hydropower-driven flow variability is exacerbated or attenuated by reach-scale channel morphology and local habitat complexity within peaking and bypass reaches, and how these effects extend longitudinally downstream from dams. Channel and habitat structure exert strong influence over the relationship between sub-daily flow variability and several ecological outcomes in our review. Complex habitats are less sensitive to flow fluctuations because they provide many different habitats under a range of flows; however, complexity also increases stranding risk during down-ramping by creating pockets where fish can become isolated from the main channel. Future research should leverage advanced sensing techniques (i.e., sonar and green LIDAR instruments) to characterize habitat at the resolution and scale relevant to riverine fish and quantify longitudinal relationships between habitat complexity, channel structure, and flow variability to better inform mitigation strategies.

Second, there is a need to better characterize flow variability due to hydropower production in the context of local and regional power grid demands. Many flow variability metrics have been developed to characterize and distinguish regulated flow regimes from natural flow regimes (e.g., Bejarano et al. 2017; Bevelhimer et al. 2015; Meile et al. 2010), including those that help differentiate different types of dam operation (Greimel et al. 2016; McManamay 2014; Zimmerman et al. 2010). However, most of this research remains disconnected from the decisions that drive hydropower operation schedules – the need to support power grid demand and respond to market trends for profitability. Future research should connect flow variability to energy markets (Hayes et al. 2023) by characterizing flow variability in the context of current and expected future power balances.

Third, our review evaluated the direct effects of sub-daily flow variability on the ecology of riverine fish without regard to whether studied populations were native or naturalized nonnative. Native and nonnative fishes respond differently to altered flow regimes (Gido et al. 2013; Propst and Gido 2004; Yard et al. 2011). Sub-daily flow variability due to hydropower production may create temperature, substrate, and flow conditions downstream that are advantageous to nonnative species at the expense of native species. Future research should explore the indirect effects of sub-daily flow variability on native species via shifting community composition, including how interspecific relationships might be expected to respond to mitigation measures in the context of a changing climate.

Finally, research on the ecological effects of sub-daily flow variability due to hydropower production has the unique opportunity to directly connect fish ecological outcomes (e.g., habitat suitability) to the full suite of services rendered by specific hydropower operational scenarios, including grid support and reliability, flood control, recreational opportunities, and hydropower owner profitability (Niu and Insley 2013; Person et al. 2014). If we want to use hydropower to help offset the severity of effects of global climate change while also maintaining downstream ecological integrity, we need to understand how different hydropower operation strategies will impact economic, social, and environmental outcomes (Bipa et al. 2023). Future research should harness expected ecological outcomes to financial outcomes, regional grid dynamics, power demand, and other services provided by hydropower (e.g., flood control) in the context of discrete hydropower operation policy to properly evaluate energy flexibility-environment trade-offs and to satisfy diverse sets of stakeholders. This is especially critical for enhancing the sustainability of regulated rivers in an uncertain future marked by a changing climate and rapid, concurrent shifts in energy production sources and methods.

Conclusion

Our systematic review of the ecological effects of sub-daily flow variability on riverine fish suggests that flexible hydropower production negatively impacts downstream fish from the organism to the community level. Hydropower operations can decrease fish production and diversity, interrupt reproduction, increase condition, prompt fish movement, increase stranding risk and decrease habitat stability. Flow variability impact assessments should characterize local fish community composition and channel and habitat morphology and resulting mitigation strategy decisions should be tailored to specific measurable ecological outcomes within the context of the broader population or community at a given site for greatest efficacy. Given that flexible hydropower plays a large and growing role in the ongoing shift to low- or zero-carbon power grids, it is critical that we continue to investigate the effects of sub-daily flow variability on aquatic ecosystems to optimize flexible hydropower production to meet societal needs and maintain or enhance downstream ecological integrity.

Acknowledgements This manuscript benefitted greatly from comments and suggestions from many individuals, including M. Fisher, B. Lawson, N. Miller, B. Lake, D. McCoskey, D. Steindorf, K. Colburn, B. Nasdor, and others. This work was supported by the U.S. Department of Energy (DOE), Office of Energy Efficiency and Renewable Energy, Water Power Technology Office (WPTO). The views expressed in the article do not necessarily represent the views of the DOE or the United States Government. Oak Ridge National Laboratory is operated for the DOE by UT-Battelle, LLC under Contract No. DE-AC05-00OR22725. Pacific Northwest National Laboratory is operated for the DOE by Battelle Memorial Institute under Contract DE-AC05-76RL01830.

Author contributions All authors contributed to the study conceptualization, design, and search string formulation. The literature search and data synthesis were conducted by B. Bozeman. The first draft of the manuscript was written by B. Bozeman and all authors contributed to subsequent manuscript drafts and approved the final manuscript.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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