

# Hydropower-related pulsed-flow impacts on stream fishes: a brief review, conceptual model, knowledge gaps, and research needs

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**Abstract** The societal benefits of hydropower systems (e.g., relatively clean electrical power, water supply, flood control, and recreation) come with a cost to native stream fishes. We reviewed and synthesized the literature on hydropower-related pulsed flows to guide resource managers in addressing significant impacts while avoiding unnecessary curtailment of hydropower operations. Dams may release pulsed flows in response to needs for peaking power, recreational flows, reservoir storage adjustment for flood control, or to mimic natural peaks in the hydrograph. Depending on timing, frequency, duration, and magnitude, pulsed flows can have adverse or beneficial short and long-term effects on resident or migratory stream fishes. Adverse effects include direct impacts to fish populations due to (1) stranding of fishes along the changing channel margins, (2) downstream displacement of fishes,

and (3) reduced spawning and rearing success due to redd/nest dewatering and untimely or obstructed migration. Beneficial effects include: (1) maintenance of habitat for spawning and rearing, and (2) biological cues to trigger spawning, hatching, and migration. We developed a basic conceptual model to predict the effects of different types of pulsed flow, identified gaps in knowledge, and identified research activities to address these gaps. There is a clear need for a quantitative framework incorporating mathematical representations of field and laboratory results on flow, temperature, habitat structure, fish life stages by season, fish population dynamics, and multiple fish species, which can be used to predict outcomes and design mitigation strategies in other regulated streams experiencing pulsed flows.

**Keywords** Pulsed flow releases · Hydropower · Fish stranding · Downstream displacement

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## Introduction

Hydroelectricity is a critical element of a power-generation system because it provides flexible power for peak demand periods, has low production costs and makes minimal contributions to atmospheric CO<sub>2</sub> loading. The rivers, canals, dams, and reservoirs in a hydropower system are part of a broader multi-use water system providing water supply, flood control,

recreation, and other beneficial uses (McKinney 2003). However, there is substantial evidence that dams for hydroelectricity, water storage or flood control have negatively affected fish, amphibians, macroinvertebrates, and other aquatic biota (Barinaga 1996; Graf 1999; Holland 2001; Hunt 1988; Hunter 1992; Kingsford 2000; Petts 1984; Power et al. 1996). The effects of dams and reservoirs on downstream environments and their role in fragmentation of riverine networks are well documented. However, the specific effects of the associated pulsed-flow releases on stream fishes have not been reviewed in detail, or synthesized in a conceptual model that would allow managers to predict and mitigate the negative effects.

In the United States, there are over 70,000 working dams, most with a hydroelectric generation capacity of less than 5 MW (Koznick 2005). Some of the larger dams are federally owned and the rest are state or privately owned. These nonfederal dams are under the regulatory authority of the Federal Energy Regulatory Commission (FERC) which since 1935 has issued 1,009 licenses for terms of 30–50 years. Of these licensed hydroelectric projects, 550 are due for license renewal over 15 years from year 2000 (Moore et al. 2001). As such, the impacts of hydropower projects and pulsed flows on aquatic ecosystems are receiving increased scrutiny. We have four main objectives: (1) Review the international literature for the effects of pulsed flows on stream fishes; (2) Develop a conceptual model to predict the effects of different types of pulsed flow; (3) Identify gaps in knowledge; and, (4) Identify research activities to address these gaps. This information may then guide current licensing endeavors and encourage new research to allow a more thorough synthesis of pulsed flow effects. Ultimately, this will allow resource managers to prevent or mitigate significant negative impacts of pulsed flows while avoiding unnecessary curtailment of hydro-power operations due to a lack of knowledge.

#### Types of hydropower-related pulsed flows

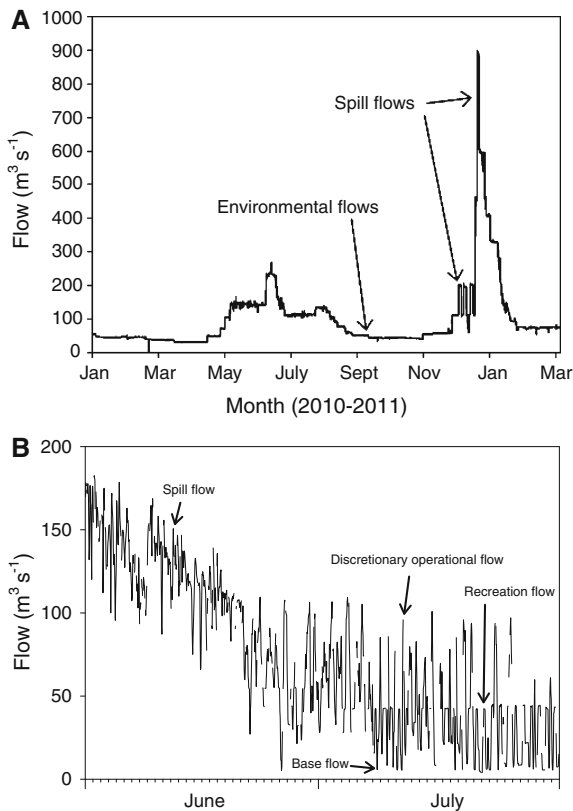
Hydropower-related pulsed flows can be classified into the following specific categories:

1. **Peaking flows:** Peaking pulsed flows occur regularly when water is typically held in a reservoir when electrical demand is comparatively low (e.g., at night) and released during periods of increased electrical demand (e.g., late afternoon). These large and relatively rapid (within minutes) flow changes may occur in a single daily cycle or in several cycles per day on weekdays, while release is minimal at other times (Cushman 1985).
2. **Load-following flows:** These are pulsed flows created when electricity is generated in response to immediate system load demands (Geist et al. 2008).
3. **Flushing flows:** Flushing pulsed flows can be classified as remedial flushing flows or maintenance flushing flows, and are discretionary flow releases usually timed with peaks in the natural hydrograph that can be used to remove sediment accumulations (Milhous 1990; Petts 1984). Timing, magnitude, frequency, and duration of releases are shaped to mimic naturally occurring pulses in the specific watershed.
4. **Spill flows:** Non-discretionary episodic events that result from natural snowmelt or precipitation that exceeds the regulated capacity of a given hydroelectric storage reservoir (Lundqvist et al. 2008).
5. **Recreation flows:** Discretionary flow releases that have varying schedules, magnitudes, frequencies, and duration. These flows are released for the purposes of kayaking, whitewater rafting, and/or other aquatic recreational activities (Daubert and Young 1981).
6. **Discretionary operational flows:** Discretionary flow releases that bypass out-of-service hydroelectric facilities so that downstream facilities can generate electricity (P. Kubicek, Pacific Gas and Electric Company, personal communication).

Dams may produce many types of flow pulses at different times of the year, and at different times of day (Fig. 1). Pulses often occur relative to a regulated minimum flow, or base flow that may be established to provide fish rearing habitat (Milhous 1990; Petts 1984; Reiser et al. 1989) or to provide cues for fish spawning (Nesler et al. 1988), hatching (Naesje et al. 1995) and migration (Ottaway and Clarke 1981; Ottaway and Forrest 1983).

#### Pulsed-flow effects on fishes

Hydropower-related pulsed flows can have many adverse and beneficial effects on resident or migratory stream fishes (Table 1). Adverse effects include



**Fig. 1** Examples of some types of hydropower-related pulsed flows. **a** Data from the lower American River, California USA, below Nimbus Dam. Data plotted are hourly flows from 1 January 2010 to 28 February 2011. Flows in September were released for salmon spawning downstream of Nimbus Dam. In December 2010 flows were repeatedly pulsed to approximately  $200 \text{ m}^3 \text{ s}^{-1}$  to lower Folsom Reservoir to the rule curve to prevent flooding, in anticipation of a large winter storm. This occurred during the Chinook salmon spawning period. A large, long duration pulse ( $>850 \text{ m}^3 \text{ s}^{-1}$ ) was released in late December to continue lowering the reservoir to prevent flooding, although there was a large risk of nest scouring. (Raw data from the California Department of Water Resources CDEC online database, for AFO (American River at Fair Oaks) gauge.) **b** Data are from Chili Bar Dam on the South Fork American River, California USA. Data plotted are hourly flows for June and July 2005. Flows in early June show the declining flows from the spring snowmelt. In late June through July flow releases were controlled to provide a minimum base flow of approximately  $5 \text{ m}^3 \text{ s}^{-1}$  for fish, regular  $40 \text{ m}^3 \text{ s}^{-1}$  recreational releases, and discretionary operational flows up to approximately  $100 \text{ m}^3 \text{ s}^{-1}$ . Note: Flow values were sometimes missing for periods of hours to days, resulting in the jagged (pixilated) appearance of the data line. (Raw data courtesy of Pacific Gas and Electric Company)

(a) stranding or lateral displacement of fishes along the changing channel margins; (b) downstream displacement of fishes; and (c) reduced spawning and

rearing success which may be due to redd dewatering and mistimed or obstructed migration. Beneficial effects include: (a) maintenance of habitat for spawning and rearing (e.g., by flushing fine sediments from gravel substrates) and (b) biological cues to trigger spawning, hatching, and migration. These beneficial pulsed flows may be permit requirements, to mitigate negative impacts of dams.

Adverse effects

Stranding

Stranding or lateral displacement of fish is defined as “the separation of fish from flowing water as a result of declining river stage” (Hunter 1992). There is an extensive literature on fish stranding, in comparison with other pulsed flow effects, so this section is correspondingly detailed.

Relatively sudden flow decreases (down-ramping) can strand fishes (e.g., in shallow side-channels or on gently sloping river bars) as water levels recede (Cushman 1985; Hunter 1992). Although stranding may affect only a small percentage of the fish population at a time, and may occur naturally, repeated flow fluctuations such as hydropower-related pulsed flows can cause cumulative mortalities that can result in a significant fish loss. Bauersfeld (1978) estimated a 1.5% fry loss per drawdown with a total loss of 59% of the salmon fry population for one season. Stranding can be classified into two categories: beach stranding, when fish flounder out of the water on the substrate; and entrapment, when fish are isolated in pockets of water (e.g., in potholes) with no access to the free-flowing surface water (Higgins and Bradford 1996; Hoffarth 2004; Hunter 1992). Stranding has been observed in several field studies (e.g., Bauersfeld 1978; Hamilton and Buell 1976; Olson and Metzgar 1987) and can result in desiccation, temperature stress, hypoxia, predation, and mortality of fish eggs, fry, juvenile, and sometimes adult fish (e.g., Becker et al. 1982; Hoffarth 2004; Hunter 1992) with consequent impacts on fish populations.

Becker et al. (1982) observed that eggs and fry were most vulnerable to high temperature stress when temperature rose to  $20\text{--}25^\circ\text{C}$  from an ambient river temperature of  $6^\circ\text{C}$ . Although some eggs can survive stranding if kept moist at appropriate temperatures, alevins are more vulnerable because they cannot

**Table 1** Effects of pulsed flows on fishes and the pulsed flow factors known to influence the effects, grouped by adverse or beneficial type of effect

Effect type	Effect	Pulsed flow factor	
Adverse	Stranding	Channel morphology	
		Substrate type	
		Down-ramping rate	
		Ramping range (amplitude, magnitude)	
		Critical flow	
		Frequency	
		Prior flow conditions	
		Duration of stranding	
		Timing (season, temperature, photophase)	
		Fish size	
		Fish species and source	
		Downstream displacement	Channel morphology
			Ramping range (amplitude, magnitude)
Timing (season, temperature, photophase)			
Fish size			
Reduced spawning	Ramping range (amplitude, magnitude)		
	Nest site dewatering		
	Ramping range (amplitude, magnitude)		
	Reduced rearing survival		
Indirect effects—food supply	Indirect effects—sediment scour, turbidity, decreased feeding		
	Indirect effects—physiological stress, gill abrasion		
Beneficial	Altered migration	Ramping range (amplitude, magnitude)	
	Habitat maintenance	Scour sediment and algae	
		Vegetation control	
	Spawning cues	Ramping range (amplitude, magnitude)	
	Hatching cues	Ramping range (amplitude, magnitude)	
	Migration cues	Ramping range (amplitude, magnitude)	
		Timing (season, temperature, photophase)	
		Fish size	

survive without intergravel flow as they use gills for oxygen uptake (Hunter 1992). Becker et al. (1982) observed many fish dying of temperature stress, oxygen depletion and predation before dewatering was complete. They reported high predation rates by birds and small mammals during fish stranding.

The following factors may affect fish stranding and subsequent mortality:

(a) Channel morphology: A river channel with many side channels, potholes, and low gradient bars has a much greater stranding potential than a river confined to a single channel with steep banks (Hunter 1992). Higher beach stranding occurs more frequently on gently sloping banks than on steeper

gravel bars (Adams et al. 1999; Bradford et al. 1995; Hunter 1992), especially with slopes that are <5% (Bauersfeld 1978; Beck and Associates 1989; Hunter 1992; Olson 1990; Pflug et al. 1989). In the Cowlitz River (California USA), most of the Chinook salmon (*Oncorhynchus tshawytscha*) fry stranding occurred on gravel bars of <2% slope (Bauersfeld 1978). Monk (1989) reported that in an experimental channel more Chinook salmon fry were stranded on 1.8% slopes than on 5.1% slopes.

Long side channels with intermittent water flows have great potential for fish entrapment, and unnatural fluctuations such as hydropower peaking flows will repeatedly trap fish fry, fingerlings, and smolts as

these areas are alternately flooded and dewatered (Hunter 1992; Olson 1990; Woodin 1984). Additionally, potholes can also trap fish as water recedes from river margins.

(b) Substrate type: Fish stranding has been observed in all types of substrate ranging from mud to boulder. Higher fish stranding rates occur in larger cobbles where water drains through rather than flowing off (Hunter 1992). Channels with low gradients usually have cobble and gravel substrates. More Chinook salmon and steelhead (*O. mykiss*) fry were stranded on cobble substrate than over small gravel because fry became trapped in pockets of water between cobbles (Monk 1989). Sandy areas with shallow depressions are prone to rapid percolation and may also cause fry stranding (CEC 2003). Beck and Associates (1989) reported increased fish stranding with coarse (>7.6 cm) substrates than in finer substrates. Bradford et al. (1995) concluded that stranding would be reduced if the substrates were more embedded. There are considerable variations in intergravel conditions during dewatering at different locations that affect egg and fry survival. Among these are: residual flow, moisture retention, temperature, gravel composition, and dissolved oxygen content (Becker and Neitzel 1985).

(c) Down-ramping rate: Down-ramping rate is the rate of water-flow reduction from a specific episode of flow fluctuation. Parasiewicz et al. (1998) reported that even with increased base flows and reduced peak flows in the lower reaches of Bregenzerach River (Austria), the fish biomass did not improve because the ramping rate was not changed. Fish-stranding incidents generally increase with increased down-ramping rate (Bauersfeld 1978; Bradford et al. 1995; Halleraker et al. 2003; Hunter 1992), but have little relation with up-ramping rate. In an artificial stream, juvenile brown trout (*Salmo trutta*) stranding significantly decreased when down-ramping rate was reduced from >60 cm h<sup>-1</sup> to <10 cm h<sup>-1</sup> (Halleraker et al. 2003). On the Sultan River (Washington USA), down-ramping rates ranging from <2.5 cm h<sup>-1</sup> in the summer to 15 cm h<sup>-1</sup> in spring and winter were required to protect steelhead and salmon fry (Olson 1990). In the upper Skagit River (Washington USA) Connor and Pflug (2004) observed greater protection of salmon fry (pink salmon *O. gorbuscha*, chum salmon *O. keta*, and Chinook salmon) from stranding

by reducing the annual number of ramping events and by reducing ramping during daytime, when fry are most vulnerable to stranding. Controlling ramping rate might be effective in reducing beach stranding but much less effective for pothole and side channel entrapment (Higgins and Bradford 1996; Hunter 1992). Higgins and Bradford (1996) suggested increasing flows before ramping down, to flush fish from potholes and then reduce flows before they have time to return.

It should be noted that in California, uncontrollable water-spill events occur (e.g., during storm events), but hydropower operators do not ramp up the flows before spill events nor ramp down when they get the system under control. Thus large amounts of water may be spilled on top of low and stable base flows, and then operators reduce flows down to base flows as quickly as possible to conserve stored water, resulting in very steep ramping rates (J. Canaday, California State Water Resources Control Board, pers. comm.).

For California streams with anadromous salmonids, stranding is less frequent at slower rates of dewatering. In the Pit River (California USA), down-ramping of the tail end of spill flows, instead of abrupt termination, was proposed to minimize stranding (Spring Rivers Ecological Sciences 2003). For the lower American River (downstream of Nimbus Dam, California USA), ramping flow rates of 2.8 m<sup>3</sup> s<sup>-1</sup> h<sup>-1</sup> or less at flows <113 m<sup>3</sup> s<sup>-1</sup> h<sup>-1</sup> were recommended to reduce stranding of steelhead (Snider et al. 2001). For the Klamath River (California USA), down-ramping rate recommendations ranged from 2.5 cm h<sup>-1</sup> (summer low flow, night) to 15 cm h<sup>-1</sup> (spring and winter, night). The summer rates were established to protect emergent steelhead fry, and the spring rates for salmon fry. It should be noted that stranding susceptibility is more related to the rate of water recession from the stream margins than the down-ramping rate per se (CEC 2003).

(d) Ramping range (amplitude): Ramping range, or magnitude of change, is the total change in water surface elevation resulting from a specific episode of flow fluctuation. The magnitude of change can determine gravel-bar exposure and, hence, will affect the potential for beach stranding. In some instances (e.g., alluvial streams), changes in water-surface elevation may increase the number of side channels and isolated bodies of water (e.g., potholes) and may

increase fish entrapment (Hunter 1992). Fry stranding studies on the Skagit River (Washington USA; Beck and Associates 1989; Woodin 1984) and on the Sultan River (Washington USA; Olson 1990) have shown that fry stranding in side channels and potholes was more related to ramping range than to down-ramping rate. Less incidence of entrapment occurs if the water depth over the top of the pothole is high (i.e., if the base flow is high) at the start of the down ramping (Beck and Associates 1989; Pflug et al. 1989) provided that there are not more potholes further up the side of the channel that would be flooded by increased water depth.

(e) Critical flow: Critical flow is the minimum operating discharge; that is, the minimum desired streamflow discharge from an ecological perspective. Stranding increases substantially when flow drops below the critical flow level because of exposure of gravel bars from which fry emerge may occur during periods of less than critical flows (Bauersfeld 1978; Fellers 1997; Hunter 1992; Olson 1990; Woodin 1984). On the Sultan River, a critical flow was established at  $8.5 \text{ m}^3 \text{ s}^{-1}$  (required minimum flow is  $5.7 \text{ m}^3 \text{ s}^{-1}$ ) below which down ramping must be at  $2.5 \text{ cm h}^{-1}$  to protect steelhead fry (Olson 1990). Additionally, intermediate flow ranges of 8.5–21 and 21–42  $\text{m}^3 \text{ s}^{-1}$  were established where faster down-ramping was allowed.

(f) Frequency of flow fluctuations: Repeated flow fluctuations can accumulate small losses from fry stranding and entrapment to a substantial cumulative loss (Bauersfeld 1978). Stranding rate was significantly reduced in pink, chum and Chinook salmon fry when the annual number of down-ramping events was reduced in the upper Skagit River (Connor and Pflug 2004; Washington USA).

(g) Prior flow conditions: A highly stable flow regime for a week or more prior to flow decline may increase fry stranding (Hunter 1992; Phinney 1974). Fry and juveniles can become accustomed to residing and feeding along stream margins during stable flows and, thus, are more likely to be stranded during down-ramping events (Hunter 1992). Hoffarth (2004) reported the use of prior weekday inflow to set weekday constraints to reduce fish stranding in Hanford Reach of the Columbia River (Washington USA). However, Olson (1990) reported that in the Sultan River there was no difference in beach

stranding among the 2-week, 4-day, and 1-day stable flow prior to reduced flows.

(h) Duration of stranding: Most fish do not survive out of water for >10 min. Thus, beach stranding is always fatal. Fish trapped in potholes and side channels can survive for hours, days, or under favorable conditions, months. However, many trapped fish experience predation, temperature stress, and/or oxygen depletion resulting in mortality, or very poor condition of surviving fish (e.g., Hoffarth 2004; Hunter 1992), with consequent impacts on fish populations.

(i) Timing of pulse: Small fry are present in streams only in certain seasons. Chinook, coho (*O. kisutch*), pink, and chum salmon fry emerge during late winter and early spring while steelhead emerge in late spring through fall (Olson 1990). Although fingerlings, smolts, and adults are vulnerable to stranding in other seasons, less restrictive flow-fluctuation criteria are often sufficient to protect them (Hunter 1992). Therefore, flow-fluctuation criteria may be most dependent on when fry are present. In the Skagit River in spring, Chinook salmon were most susceptible to pothole entrapment, followed by coho and chum salmon. However, in summer, coho salmon and steelhead were more susceptible than Chinook salmon (Beck and Associates 1989).

In the Nidelva River (Norway) higher incidences of Atlantic salmon (*S. salar*) and brown trout fry stranding were found during winter conditions (<4.5°C) compared with those at the higher water temperatures that occurred during late summer and early autumn, and may have resulted from lower fish activity and substrate-seeking behavior (Halleraker et al. 2003; Heggenes 1990; Saltveit et al. 2001). At winter water temperatures (<4°C) with a gravel substrate, many juvenile coho salmon and rainbow trout became stranded because they were concealed in the interstitial areas of the substrate and were reluctant to leave when water levels receded (Bradford et al. 1995). Bradford (1997) found that the stranding rate of juvenile salmonids was six times higher at 6°C than at 12°C and related this to the fact that the fish reside closer to the substrate at lower temperature. In the Hanford Reach of the Columbia River, Hoffarth (2004) used accumulated temperature units (ATU) to predict susceptibility of fall Chinook

salmon stranding. Based on data from 6 years, fish stranding susceptibility was reduced substantially above 1,400 ATU.

For some species the incidence of stranding is affected by photophase (i.e., day/night). At night, Chinook salmon fry are less dependent on substrate for cover and therefore less vulnerable to stranding (Connor and Pflug 2004; Hunter 1992; Olson and Metzgar 1987; Woodin 1984). However, steelhead fry were observed to be less vulnerable during the day (Olson 1990; Olson and Metzgar 1987), although Monk (1989) and Pflug et al. (1989) did not find any difference in steelhead fry stranding during the day and night. For juvenile rainbow trout and coho salmon, the incidence of stranding during cold winter conditions was lower (<10%) at night than during the day (30–80%). Bradford et al. (1995) noted that during spring and summer, juvenile coho salmon and rainbow trout (*O. mykiss*) exhibited less burrowing behavior during the day and thus, stranding rate was reduced. Similarly, in the Nidelva River, Atlantic salmon and brown trout fry were less likely to be stranded at night than during the day because they were more active at night (Halleraker et al. 2003; Heggenes et al. 1993; Saltveit et al. 2001). When temperatures were >9°C, higher stranding rates were observed at night for both species. Halleraker et al. (2003) recommended dewatering in darkness at all times of year to reduce stranding of salmonids, especially for brown trout. However, Olson (1990) and Pflug et al. (1989) reported that in the Sultan and Skagit Rivers during the summer, the incidence of steelhead fry stranding during the day was no different from during the night.

(j) Fish size: Juvenile fish are more vulnerable to stranding than are adults. Salmonid fry that have just absorbed the yolk sac and have recently emerged from the gravel are the most vulnerable because they are poor swimmers and seek refuge along stream margins (Hunter 1992). Once salmon fry grow to 50–60 mm, stranding vulnerability is reduced substantially (Bauersfeld 1977, 1978; Hoffarth 2004; Hoffarth et al. 2003; Hunter 1992; Hvidsten 1985; Olson 1990; Olson and Metzgar 1987; Woodin 1984). For steelhead, vulnerability is reduced once the fry reach 40 mm (Beck and Associates 1989; Hunter 1992; Olson and Metzgar 1987; Pflug et al. 1989). Larger juveniles are more likely to inhabit deeper

pools, glides, overhanging banks, and mid-channel habitats where they are less vulnerable to stranding and entrapment (Campbell and Neuner 1985; Hunter 1992; Irvine 1986). Salamunovich (2004a) documented 224 fish stranded in the North Fork Feather River (California USA) following recreational pulsed flow releases during June-to-October 2002. Over 92% of the stranded fish were post-larval cyprinid and catostomid fry that were less than 25 mm in length. The stranding peak occurred during June and July when the fry were abundant along the stream margins. However, Salamunovich concluded that stranding was not a significant source of mortality.

Increased minimum incubation flows improved redd protection, and reduced down-ramping events during daytime greatly reduced stranding of salmon fry (Chinook, pink, and chum salmon) in the upper Skagit River (Connor and Pflug 2004). In an artificial stream, the stranding rate of age-0+ brown trout fry (<50 mm FL) was twice as high as that of the larger fry (>75 mm FL) during rapid dewatering during daytime (Halleraker et al. 2003).

(k) Fish species and source: Fish stranding is related to the behavioral response of fishes to receding levels. Species that occur in littoral and backwater areas that either swim with the current or passively drift with the current are less likely to be stranded. While they may swim or drift up into newly flooded areas during a pulse, they will swim or drift back toward the main channel with receding water, while the young of main-channel fishes that are positively rheotactic are more likely to swim against the flow of receding water and become stranded (Adams et al. 1999).

Most fish-stranding studies have focused on salmonids not only because most salmon and trout are popular game species, but also because their fry stages are known to be more vulnerable to stranding than those of other species found in the same streams (Hunter 1992). When salmonid fry emerge from gravel, they tend to seek the shallow waters near the shoreline increasing the probability of stranding during pulsed flows. Hunter (1992) stated that Chinook salmon and steelhead are more vulnerable because they have comparatively long residence times in streams, whereas pink and chum salmon

tend to migrate to salt water shortly after emergence. He also stated that while coho salmon are also vulnerable, they prefer to spawn and rear in streams that are too small for hydropower development.

Among salmonid fry, some species are more susceptible to stranding than others, depending on the stream site. For example, chum and pink salmon fry were more vulnerable to stranding than Chinook salmon fry in the Skagit River (Beck and Associates 1989; Pflug et al. 1989; Woodin 1984), but not in the Sultan River (Olson 1990), potentially because of the preference of chum and pink salmon for higher water velocities and their tendency to migrate rapidly downstream after emergence (Olson 1990). Coho salmon were more vulnerable to pothole entrapment than Chinook salmon in both rivers (Beck and Associates 1989; Olson 1990; Pflug et al. 1989). In the Sultan River, steelhead and Chinook salmon fry had similar vulnerability to stranding (Olson 1990). In the Campbell River (British Columbia, Canada), extensive coho salmon stranding has been observed (Hamilton and Buell 1976). Bradford et al. (1995) observed that coho salmon fry were up to ten times more vulnerable to stranding than were rainbow trout. Finally, in the Nidelva River, 3.8 times as many Atlantic salmon fry were stranded as were brown trout fry (Hvidsten 1985).

Moyle and Baltz (1985) found that microhabitat preferences are species-specific. Because different species make use of flood-plain habitats to varying degrees, some species are more likely to enter habitats where they may become stranded later (Ross and Baker 1983). For example, 29% of hardhead (*Mylopharodon conocephalus*) and 17% Sacramento suckers (*Catostomus occidentalis*) in a laboratory experiment became stranded, but none of the rainbow trout did (Klimley et al. 2005). In addition to differential incidences of stranding for different species of fish, there may be differential incidences for natives versus non-natives. In the lower Putah Creek (California USA), native fishes tended to prefer faster streamflow, colder temperatures, and less pool habitat than non-natives and were less likely to get stranded (Marchetti and Moyle 2001).

In the Nivelda River, fewer hatchery-reared Atlantic salmon were stranded compared to wild fish (Saltveit et al. 2001). Hatchery-reared fish did not seem to seek shelter immediately after stocking and, therefore, were less vulnerable to stranding.

In contrast, Bell et al. (1976) observed that in the Columbia and Snake Rivers (Washington USA), hatchery rainbow trout were more susceptible to stranding than were wild stocks.

#### *Downstream displacement*

Downstream displacement of small fishes has been well documented; for example, juvenile coho salmon that stay in streams through winter periods when floods are common (Bell et al. 2001; Giannico and Healey 1998; Shirvell 1994). PIT-tagged juvenile coho salmon moved, mostly in the downstream direction, between 10 and 1,992 m (mean: 517 m) after a 5-year flood in Prairie Creek (California USA), where base flow was  $0.56 \text{ m}^3 \text{ s}^{-1}$ , flood discharge was about  $5.6 \text{ m}^3 \text{ s}^{-1}$ , and peak flood discharge was  $8.8 \text{ m}^3 \text{ s}^{-1}$  (Bell et al. 2001). The higher recapture rates of young coho salmon in more hydraulically protected habitat types (alcoves and backwaters), compared with those in main-channel pools, probably reflects the value of these off-channel habitats in minimizing the downstream displacement of fishes (Bell et al. 2001). Heggenes (1988) concluded that coarse substrate acted as a velocity shelter for brown trout and prevented displacement when discharge was increased 4–100 times (up to  $350 \text{ l s}^{-1}$ ) in a small stream. Brown trout  $< 67 \text{ mm}$  were more susceptible to downstream displacement than larger trout.

There may be interactions among the seasonal timing of pulsed flows, the life-history stage of fish present, and the relative magnitude of pulses compared with normal flows for that time of year. For example, field-study data show that some juvenile salmonids seek faster currents during their transformation from a freshwater parr to a seawater-capable smolt (McDonald 1960, Meehan and Siniff 1962). Similarly, in laboratory experiments, juvenile coho salmon preferred faster currents ( $0.1\text{--}0.3 \text{ m s}^{-1}$ ) during their springtime parr-smolt transformation (Katzman et al. 2010).

With the exception of emigrating juvenile salmonids, the longitudinal displacement of larger fish seems less likely due to their increased swimming performance compared with that of smaller fishes (Flagg and Smith 1982; Thorpe and Morgan 1978; Webb 1971; Webb et al. 1999) unless there are velocity refuges that are more accessible to smaller-sized fish (Chun et al. 2010; Thompson et al. 2010).



Numerous field studies found no consistent effect of sudden, extreme peaking flows (ranging from 0.15 to  $>200 \text{ m}^3 \text{ s}^{-1}$ ) on area use or movements by adult trout and salmon (Bunt et al. 1999; Gido et al. 2000; Heggenes et al. 2007; Scruton et al. 2005). Similarly, domestic rainbow trout in the South Fork American River (California USA), with SL  $> 25$  cm, were not forced downstream by daily pulsed flow increases from 5 to  $>40 \text{ m}^3 \text{ s}^{-1}$ . (Cocherell et al. 2010). Because many river fishes (e.g., members of the family Cyprinidae, the minnows and carps) may have less aerobic (red) muscle than trout (Bainbridge 1960, 1962), downstream displacement of larger minnows and suckers might be anticipated with a pulsed flow. For example, Sacramento suckers fitted with radio transmitters were displaced an average of 2 km downstream after a flow pulse in the Mokelumne River (California USA) in 2003 (Jeffries et al. 2005).

In 2002 and 2003, Salamunovich (2004a, b) examined displacement of stream fishes in the Rock Creek-Cresta reaches of the North Fork Feather River due to recreational pulsed flows ( $28\text{--}46 \text{ m}^3 \text{ s}^{-1}$ ) from June to October (base flow was about  $5.7\text{--}8.5 \text{ m}^3 \text{ s}^{-1}$ ). He concluded that local fish populations were tolerant of short-term, elevated-flow events because there were similar counts of fish numbers before and after the recreational pulsed flow releases. However, fish were not marked or tagged so it is possible that fish in the study area prior to the pulsed flows were displaced downstream, but that fish from upstream were displaced down into the study area, replacing the fish observed before the pulsed flows.

Thompson et al. (2010) investigated the response of fish to a 1-day pulse flow release from Camino Dam on Silver Creek, a tributary of the South Fork American River. Flows in the Camino Reach of Silver Creek were increased from a base flow of  $0.5 \text{ m}^3 \text{ s}^{-1}$  to a peak of  $18.5 \text{ m}^3 \text{ s}^{-1}$  by midday, and decreased back to base levels. One rainbow trout and six brown trout were radio-tagged and tracked prior to, during, and after the pulsed flow. Six tagged fish were observed in the reach prior to the pulsed flow and remained in the reach during and after the pulsed flow. In snorkel surveys of a 300-m study reach before and after the pulse, counts of young-of-the-year trout were 26% lower after the pulse, and counts of juvenile trout were 9% lower, while counts of adult trout were 12% higher, suggesting that most trout were able to remain in the study reach during the

pulse, but that smaller trout may be more vulnerable to displacement.

#### *Reduced spawning*

Ramping range has the potential to significantly affect fish spawning behavior. Hamilton and Buell (1976) observed that Chinook salmon in the Campbell River repeatedly started and abandoned redds before completion because of high flow fluctuations. Hunter (1992) stated that adult Chinook salmon may be discouraged by flow fluctuations and thus move to less desirable, more crowded locations. However, Chapman et al. (1986) reported Chinook salmon abandoning redds when the water level receded, but returning to complete them when the water level increased. Nelson (1986) demonstrated that the lowest production of yearling brown trout in Beaverhead River (Montana USA) occurred when water flows were intentionally reduced to  $3.15\text{--}13.22 \text{ m}^3 \text{ s}^{-1}$  to conserve water for irrigation season (October 16 to April 14), then increased to  $8.55\text{--}24.63 \text{ m}^3 \text{ s}^{-1}$  during the irrigation season (April 15–October 15). These flow fluctuations were suspected to have disrupted spawning. In the lower Columbia River (Washington USA), load-following flows caused temperature and vertical hydraulic gradient variations within the chum and Chinook salmon spawning areas. These gradients altered the cues each species uses to select redd sites, presumably leading to salmon spawning segregation and reduced incubation success (Geist et al. 2008).

#### *Nest site dewatering*

Under certain conditions, hydropower-related flow fluctuations may cause nest site dewatering, especially as a result of load-following operations (McMichael et al. 2005). Bauersfeld (1978) reported that high discharge in the Columbia River encouraged spawning of Chinook salmon at flow levels that could not be maintained, resulting in dewatering of eggs when flow subsided to the legal minimum of  $1,020 \text{ m}^3 \text{ s}^{-1}$ . Attempts to discourage spawning by briefly reducing flows at night were not effective because of lack of spawning area at low flows. Additionally, flow fluctuations resulted in superimposition of multiple poorly constructed redds at different water levels that could not withstand scouring. In the Savannah River (Georgia USA), Grabowski and Isely (2007) observed

that over 50% the nest sites of robust redhorse (*Moxostoma robustum*) on a main-channel gravel bar were completely dewatered or left in near zero-flow conditions for several days.

Many studies have demonstrated that salmonid eggs can survive for weeks in dewatered gravel if they are moist (at least 4% moisture by weight) and are not subjected to extreme temperatures or predation (Becker et al. 1982, 1983; Becker and Neitzel 1985; Reiser and White 1983). The high survival of dewatered eggs is due to good oxygen transport brought about by influx of air into the substrate interstitial spaces. If the water is stagnant, the eggs will die because of low oxygen content caused by biotic degradation (Reiser and White 1983).

#### *Reduced rearing survival*

Although salmonid eggs can survive dewatering for weeks, newly hatched alevins are less tolerant and may die within 4–10 h of dewatering (Becker and Neitzel 1985; Becker et al. 1982, 1983; Neitzel and Becker 1985; Reiser and White 1983), with consequent impacts on fish populations. Weyers et al. (2003) demonstrated that emergent larval catostomid suckers exposed to 4 and 12 h pulsed, high-velocity water flows of  $>36 \text{ cm s}^{-1}$  had significantly lower survival and growth than those that were not exposed to high flows. They explained that few larvae were able to swim up and inflate their gas bladders when water velocity was high. Larvae that attempted to do so were caught in the high flows and died. Delay or failure in gas-bladder inflation decreased larval fish survival. Growth rates of the surviving fish were reduced by 2% (4 h pulse) and 5% (12 h pulse) compared to those at low flows of  $<0.75 \text{ cm s}^{-1}$ .

Pulsed flows may affect fish indirectly, through effects on food supplies. Benthic macroinvertebrates comprise the principal food source of both migratory and resident fish populations in streams (Briggs 1950). Their density, biomass and species diversity are negatively affected by high flow fluctuations (Cushman 1985, Shaw and Richardson 2001). High flow fluctuations can also cause scouring, resulting in high suspended solids. The combination of high flow fluctuations and high content of suspended solids can devastate invertebrate communities (Petts 1984; Shaw and Richardson 2001) and can in turn reduce fish growth (Svanback and Eklov 2002).

Another negative effect on fish growth may occur indirectly through the effect of pulsed flows on sediment pulsed duration (Shaw and Richardson 2001). Sediment pulsed duration is the period of time for which the sediment is disturbed by events (pulsed flows, rain, thunderstorm) or activities (riparian timber harvesting, cattle movement) in streams. Shaw and Richardson (2001) observed that rainbow trout growth over a 19-day period was negatively correlated with pulse duration. The authors concluded that fine sediment caused impaired vision leading to reduced prey capture success and increased metabolic costs from physiological stress, and that these two factors were more important than decreased invertebrate richness and abundance. Physiological stress in young fish may result from decreased respiratory capabilities through gill abrasion (Berg and Northcote 1984) and reduced interstitial dissolved oxygen (Scrivener and Brownlee 1989).

#### *Altered migration*

Under certain circumstances, hydropower-related pulsed flows can affect fish migration. In the Snake River, migrations of juvenile steelhead generally occurred later than those of Chinook salmon and usually coincided with maximum stream flow. Reduced river flows can cause a significant number of steelhead to stop migrating (Raymond 1979), with consequent effects on fish populations. In contrast, Montgomery et al. (1983) concluded that the onset of migration runs for Atlantic salmon, brook trout (*Salvelinus fontinalis*), longnose sucker (*C. catostomus*), white sucker (*C. commersoni*), and lake chub (*Couesius plumbeus*) coincided with declining water levels and flows.

#### *Beneficial effects*

##### *Habitat maintenance*

Pulsed flows known as remedial flushing flows may be used to scour sediment and algae and to remove fines and sands within the affected stream beds below the dam (Milhous 1990; Petts 1984). They can also be used to offset a perturbation resulting from an improper land-use activity or natural catastrophic events such as landslide or slump (Reiser et al. 1989). These are short-term fluctuations (e.g., from approximately  $0.6$  to  $5\text{--}9 \text{ m}^3 \text{ s}^{-1}$ ) over a period of about

15 min to successfully scour sediment and algae from below the dam (Petts 1984). Similarly, maintenance flushing flows may be used for channel and fish-habitat maintenance (Milhous 1990; Reiser et al. 1989), not only for substrate management but also for vegetation control. These flows usually occur on an annual basis and are sometimes intended to keep fines and sand from being deposited, and/or to remove them from the surface of the stream bed (Milhous 1994), and also to maintain the riparian corridor, such as prevention of vegetation encroachment by removing most new seedlings.

### *Spawning cues*

Flow pulses with high spikes can act as spawning cues for some fishes. In the Yampa River (Colorado USA), Nesler et al. (1988) observed that in five cases during 1983–1986, the spawning peaks of Colorado pikeminnow (*Ptychocheilus lucius*) were associated with pulsed flows of 27–71 m<sup>3</sup> s<sup>-1</sup> that occurred over 2–3 days during late June to late July, suggesting that major flow spikes in early summer may be used as an environmental cue to stimulate substantial spawning. However, water project operators are cautioned against the timing of large flow releases that may act as spawning cues for fishes at the wrong time.

### *Hatching cues*

High flow pulses can also act as environmental cues for the hatching of some fish eggs. For example, in the River Lagen (Norway), increased water discharge during spring floods acted as the primary cue for the start of hatching and drift of European vendace (*Coregonus albula*) and whitefish (*Coregonus lavaretus*). Because they use flow pulses as a cue for the start of hatching, fish larvae are sensitive to artificial changes in stream flow (Naesje et al. 1995). Hydropower-related pulsed flows can also assist in distribution of hatched pelagic fish (Brismar 2002).

### *Migration cues*

Flow augmentation in some rivers during the summer months has been suggested as a means to improve migration success of juvenile fishes, particularly salmonid smolts, but results to date are mixed. Studies conducted in the Columbia River did not show

compelling evidence that migration of subyearling Chinook salmon, steelhead, and sockeye salmon (*O. nerka*) was affected by changes in river flow (Giorgi et al. 1997). However, in experimental channels, McPhee and Brusven (1976) demonstrated that a 17-fold flow fluctuation caused 60% of the Chinook salmon fry to emigrate. Irvine (1986) found that Chinook salmon emigration was increased by fluctuating discharge when flows were increasing and mean water velocity exceeded 30 cm s<sup>-1</sup> at the peak of the cycle, but the emigration was observed only at night and in the first 2–3 weeks following the emergence of the fry. Ottaway and Clarke (1981) concluded that rainbow trout fry are more likely to move downstream in response to increases in water velocity just after the swim-up stage and thereafter become less affected by flow fluctuations. In another experimental channel study, Ottaway and Forrest (1983) observed a positive correlation between brown trout fry movement and mean water velocity, especially when the flow increase was abrupt. They also found increased downstream movement as fish entered the free-feeding stage.

Water flow rate is most frequently cited as the primary factor controlling the rate of upstream migration of salmonid spawners, although temperature and photophase may modify it (see review by Banks 1969). The correlation between salmonid migration and flow rate is highest in small streams which have rapid runoff, a fairly short spawning season, and in species with little overlapping of year classes on the spawning beds.

## **Synthesis and conceptual model of pulsed flow effects**

We have described a range of adverse effects of hydropower-related pulsed flows on resident or migratory stream fishes, summarized in Table 1. A majority of studies have focused on salmonids, although we found literature describing effects on six non-salmonid species. There is currently a large body of knowledge on stranding (lateral displacement) and considerable information on downstream displacement. There is some evidence of reduced spawning and rearing success related to nest site dewatering and untimely or obstructed migration, with consequent effects on fish populations. There have also been important findings on some beneficial uses of well-managed

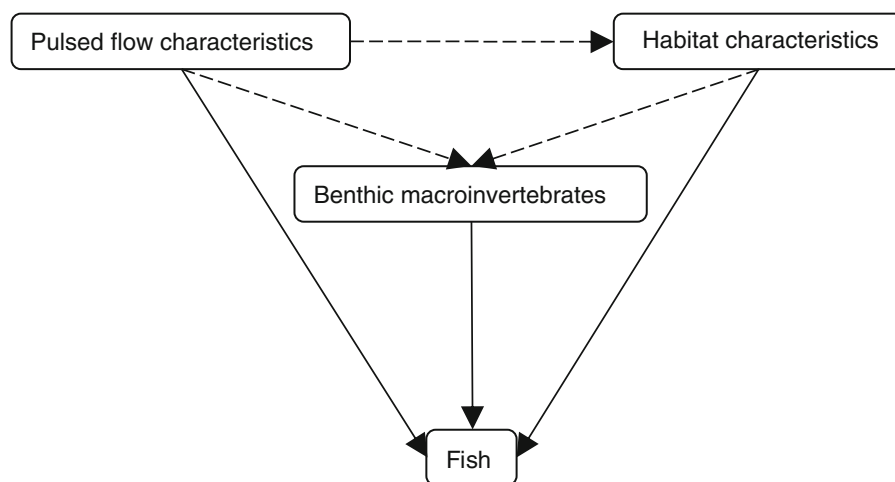
pulsed flows, such as the maintenance of habitat for spawning and rearing, and biological cues to trigger spawning and hatching, while effects on juvenile emigration are uncertain. This information should be useful in ongoing FERC re-licensing efforts.

The knowledge gained from pulsed flow studies provides material for the development of a conceptual model conducive to generalization to unstudied watersheds, and qualitative prediction of the effects of future pulsed flow regimes. Key pulsed flow characteristics include frequency, magnitude and duration. These characteristics together with season and photophase, as we show in a very basic model, may affect fishes directly, or may have indirect effects transmitted to fish through habitat characteristics or effects on food sources such as benthic macroinvertebrates (Fig. 2). The diagram shows a snapshot in time, but cumulative effects over time can be inferred and may be acute or chronic. For example, (1) a single, short pulse of large magnitude may produce acute direct effects on fishes; (2) repeated small-magnitude pulses may produce chronic direct effects (decreased feeding and growth); (3) repeated large-magnitude pulses may produce acute direct effects on fishes (downstream displacement of juvenile fishes, nest scour) as well as chronic indirect effects through negative effects to food supplies such as benthic macroinvertebrates (downstream displacement, decreased survival and production).

In practice, systems experiencing pulsed flows are more complex, so a decision-tree approach helps to predict the effects of different combinations of pulsed flow characteristics (Fig. 3). Choices regarding season (winter/spring vs. summer/fall), frequency (single or repeated), magnitude (small or large), duration (short or long), and photophase (day or night) of pulsed flows will determine the type of effect, and the species and life stages most likely to be affected. More negative effects are expected for pulsed flows that occur “out of season”, that is, less synchronized with the natural hydrograph, and more beneficial effects are anticipated for pulsed flows that occur during times when flow peaks would naturally happen in an unimpaired system.

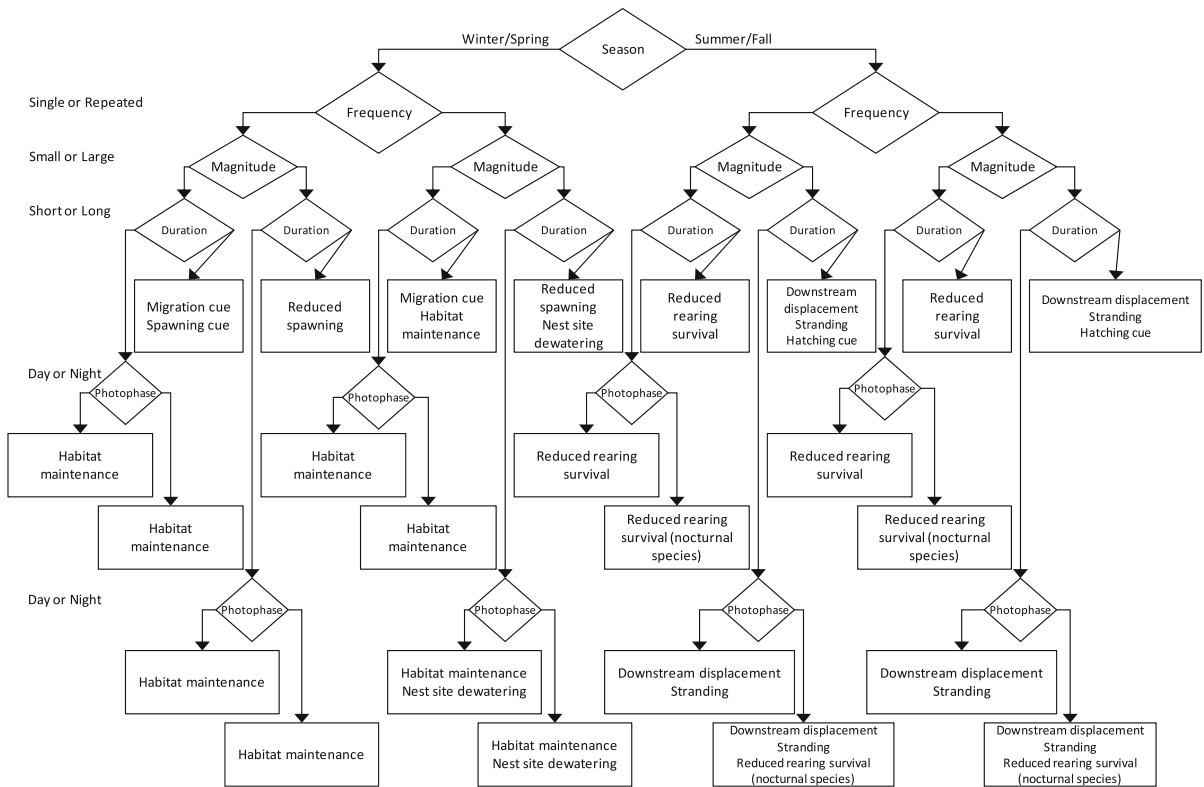
### Knowledge gaps and research agenda

The effects of pulsed flows have been studied for over 35 years. Researchers have observed effects on fish at all life stages, and generally more indication of negative effects than positive ones, with consequent effects on fish populations. This presents a dilemma for water managers. There is an implicit assumption in dammed watersheds that these systems will not have a wholly natural flow regime (Poff et al. 1997). For example, in California, government agencies have plans to allow salmon and steelhead to migrate



**Fig. 2** Simplified conceptual diagram of pulsed flow effects on fishes. *Solid lines* indicate direct effects on fish. *Dashed lines* indicate indirect effects on fish. Pulsed flow characteristics may

include season (winter/spring vs. summer/fall), frequency (single or repeated), magnitude (small or large), duration (short or long), and photophase (day or night)



**Fig. 3** Decision tree diagram for effects of different pulsed flows on fishes and fish habitat, for a model fish species that normally migrates and spawns in winter/spring. Pulsed flow characteristics influencing the potential effects of a pulse include: season (winter/spring vs. summer/fall), frequency (single, left side of pair, or repeated, right side of pair), magnitude (small or large), duration (short or long), and photophase (day or night). Long duration pulses are assumed to be greater than 1 d, so the photophase choice is omitted for this

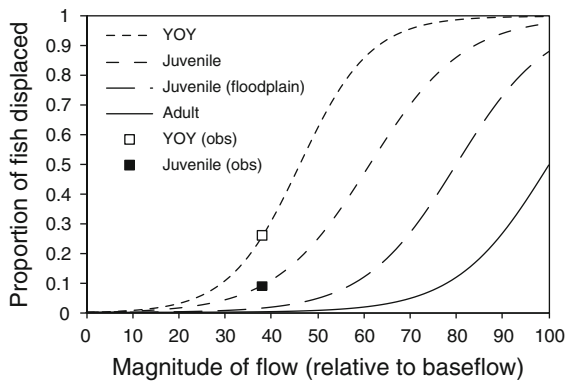
decision branch. *Diamonds* indicate decision points, and *rectangles* contain potential effects of a given decision branch. Note that the pulsed flow characteristics included in this figure are described qualitatively and that quantitative information for a particular dam and river would be necessary for decision-making. Also, this diagram includes a sub-set of characteristics that are commonly important, but other important characteristics likely vary between rivers and fish species

above several currently impassable large dams (NMFS 2009), but the upstream habitat is still affected by other smaller dams that may produce pulsed flows. It is likely that individual and population level effects will be of increasing severity in proportion to the degree of deviation from the natural hydrograph. This includes deviation both in terms of pulse magnitude and seasonal timing. This puts pulsed flows in potential conflict with stated goals of fish recovery and conservation.

Furthermore, this review has revealed critical gaps in our understanding of pulsed flows. Researchers and managers still do not know with certainty how large a pulsed flow, relative to the natural seasonal flow, is likely to harm fish. Is it 10% or is it 80% more than natural? Presumably some alteration within the upper

range of the natural variance would be relatively safe. However, what about the effects of repeated pulses? How frequently can systems be pulsed before there are cumulative direct effects to fish, or indirect effects via habitat alteration?

The lack of quantitative understanding can be illustrated with the relationship between the magnitude of a pulsed flow, relative to the base flow, and the proportions of young-of-the-year, juvenile and adult fish that are displaced downstream (Fig. 4). As noted earlier, following a single, 1-d pulsed flow over 38 times the summer base flow, Thompson et al. (2010) observed 26% fewer young-of-the-year trout and 9% fewer juvenile trout, suggesting that the missing fish were probably displaced downstream. However, because this stream experienced a single



**Fig. 4** Hypothetical relationships between the magnitude of a pulsed flow, relative to the base flow, and the proportions of young-of-the-year, juvenile and adult fish that are displaced downstream. An additional curve is shown for juvenile fish in a stream where the pulsed flow can readily move out onto the floodplain. The actual shapes of these curves are largely unknown; the *square* symbols represent observed data points for rainbow trout and brown trout that experienced a single 1-d pulsed flow in a California stream (Thompson et al. 2010)

pulse, there is no information on the relationship between pulsed flow magnitude and downstream displacement over a wider range of magnitudes, and the form of such a relationship is unknown. In addition, channel morphology will affect the relationship; in streams where the increased flow can move out onto the floodplain, water velocities will be relatively lower than for a stream with constrained, steep banks, so a smaller proportion of fish would be displaced downstream.

In our review we have identified six key gaps in our knowledge of the effects of pulsed flows.

1. **Pulse type and life stage:** For most stream fish species we lack adequate relationships to determine the effects of different magnitudes, ramping rates, and timing (season and photophase) of pulsed flows on the abundance and longitudinal displacement of stream fishes at different life stages.
2. **Water quality and fish behavior:** While some studies have examined fish movement in response to pulsed flows, it is unclear to what degree pulsed flows affect water quality factors, such as water temperature or dissolved oxygen, in ways that influence behaviors such as predation and migration.

3. **Habitat complexity:** It is uncertain whether increased habitat complexity, such as presence of boulders, crevices in bedrock, or large wood, influences downstream displacement for different species and age classes, and over what magnitudes of pulse this complexity may reduce displacement. Channel morphology may interact with the effects of pulsed flows. For example, in a stream where the main channel connects to a large floodplain a given magnitude of pulse will result in lower instream velocities than in a stream constrained by steep, high banks.
4. **Habitat changes:** It is unclear whether relatively small, but repeated pulsed flows can alter instream habitat and have indirect effects on fishes. Repeated pulsed flows may alter channel morphology, sediment composition, or sediment transport, and in turn affect fish community structure.
5. **Long term, cumulative effects:** While individual short-duration, or small magnitude pulses may appear to have minimal effects on fishes, it is uncertain whether there may be thresholds, related to pulse duration or frequency, beyond which cumulative effects (adverse or beneficial) on fish and fish communities would be expected. For example, repeated small pulses may decrease feeding time, then growth, then species survival, and ultimately community composition.
6. **Mitigation:** Our lack of knowledge in the previously mentioned areas results in a lack of information on measures to mitigate the effects of pulsed flows. For example, could negative effects of pulsed flows be minimized through increase of habitat complexity (to provide shelter to small fish during pulses) and increased food availability or quality (to compensate for shorter feeding times)?

Our ability to predict and mitigate the effects of pulsed flows from hydropower projects on stream fishes would be improved by a clearer understanding of the mechanisms and relationships that underlie the effects. In response to this need we generated a research agenda with key topics to be addressed (Table 2). As far as possible, such studies should seek to develop broad quantitative relationships between pulsed flow characteristics and responses of particular species and life stages of fish.

**Table 2** Pulsed flow knowledge gaps and research needs

Knowledge gap	Research need
Pulse type and life stage	Determine the effects of different magnitudes, ramping rates, and timing (season and photophase) of pulsed flows on the abundance and longitudinal displacement of stream fishes at different life stages
Water quality and fish behavior	Determine whether pulsed-flow effects on water quality, such as water temperature or dissolved oxygen, influence behavioral factors such as predation and migration
Habitat complexity	Determine how habitat complexity influences longitudinal displacement for different species and age classes
Habitat changes	Compare geographically similar rivers that have a range of flow regimes, from unpulsed, to infrequently, and frequently pulsed and identify patterns in channel morphology, sediment composition, sediment transport, and fish community structure
Long term, cumulative effects	Identify thresholds (duration and frequency of pulsed flows) beyond which a specific effect (adverse or beneficial) on fish and fish communities would be expected
Mitigation	Evaluate effectiveness of existing mitigation measures, and develop improved mitigation measures, e.g., habitat improvement, increased food quantity or quality (e.g., riparian plantings to provide allochthonous inputs of terrestrial insects)

## Conclusions

Our review of the effects of pulsed flow effects on fishes provided adequate material for a conceptual model of these effects. The review also exposed knowledge gaps that hinder accurate predictions of pulsed flow effects, but prompted a research agenda to address these gaps.

We suggest that there is a clear need to move beyond our qualitative conceptual model to new quantitative approaches. We suggest that the synthesis needed is beyond the scope of individual field projects and requires an analytical framework that incorporates mathematical representations of flow, temperature, habitat structure, fish life stages by season, fish population dynamics (especially growth, reproduction, and mortality), and multiple fish species. We need to synthesize and integrate the results of field and laboratory studies into conceptual and mathematical models that will describe the physical and biological processes occurring with pulsed flows that can be used to predict outcomes in other regulated streams experiencing pulsed flows.

Models will need to be scaled to the pulsed flow effect in question, and it is unlikely that one model or set of models will be adequate for all pulsed flow scenarios. For example, stranding mortality could be modeled as a function of the relationship between body size and ramping rate versus the probability of stranding, taking into account interactive factors such as water flow and temperature. This could be accomplished by linking a watershed model with a

fish population dynamics model following the approach of Battin et al. (2007). For situations in which channel morphology and substrate are expected to be most influential, pulsed flow effects would be better addressed using a geomorphological model with detailed hydraulics components (Wheaton et al. 2010). A further advancement of this approach would be to include the addition of an economics model to allow consideration of the trade-offs between fish abundance, water storage, and profits from power generation. Initial models would have high uncertainty, but their development would reveal data gaps and pinpoint needs for research to complete the synthesis and provide improved predictive tools for managers.

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