

Fish stranding in freshwater systems: Sources, consequences, and mitigation

Alexander Nagrodski*, Graham D. Raby, Caleb T. Hasler, Mark K. Taylor, Steven J. Cooke

Fish Ecology and Conservation Physiology Laboratory, Department of Biology and the Institute of Environmental Science, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada

ARTICLE INFO

Article history:

Received 11 September 2011

Received in revised form

12 February 2012

Accepted 4 March 2012

Available online 4 April 2012

Keywords:

Fish stranding

Fish condition

Regulated rivers

Hydropower

Dewatering

ABSTRACT

Fish can become stranded when water levels decrease, often rapidly, as a result of anthropogenic (e.g., canal drawdown, hydropeaking, vessel wakes) and natural (e.g., floods, drought, winter ice dynamics) events. We summarize existing research on stranding of fish in freshwater, discuss the sources, consequences, and mitigation options for stranding, and report current knowledge gaps. Our literature review revealed that ~65.5% of relevant peer-reviewed articles were found to focus on stranding associated with hydropower operations and irrigation projects. In fact, anthropogenic sources of fish stranding represented 81.8% of available literature compared to only 19.9% attributed to natural fish stranding events. While fish mortality as a result of stranding is well documented, our analysis revealed that little is known about the sublethal and long-term consequences of stranding on growth and population dynamics. Furthermore, the contribution of stranding to annual mortality rates is poorly understood as are the potential ecosystem-scale impacts. Mitigation strategies available to deal with stranding include fish salvage, ramping rate limitations, and physical habitat works (e.g., to contour substrate to minimize stranding). However, a greater knowledge of the factors that cause fish stranding would promote the development and refinement of mitigation strategies that are economically and ecologically sustainable.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Fish stranding is any event in which fish are restricted to poor habitat as a consequence of physical separation from a main body of water. This phenomenon can occur in both lentic and lotic environments and is caused by natural and anthropogenic processes that generally result in rapidly falling water levels. Arguably, the majority of stranding research to date has emanated from hydropower studies that have typically focused on quantifying and reducing mortality of salmonids during hydropeaking operations (Cushman, 1985; Fig. 1). Comparatively little is known about non-salmonid species or in other contexts, and in general little is known about the factors that are associated with stranding, making it difficult to develop mitigation strategies. Nonetheless, there are other examples of stranding studies in the literature from freshwater systems around the globe (e.g., billabongs in Australia [Ward, 1998], ship wakes in navigation canals in Europe [Wolter et al., 2004]).

With increasing levels of aquatic habitat alteration (Richter et al., 1997) and increased management of flows and water levels

in freshwater systems (e.g., hydropower development [Bunn and Arthington, 2002; Nilsson et al., 2005], irrigation [Haag et al., 2010]), there is a need to understand the extent of stranding, the factors that contribute to stranding, and the consequences of stranding at various biological levels. Because fish stranding is a natural phenomenon in some systems (e.g., flood pulse concept; Junk et al., 1989), it may also play an important role in structuring aquatic systems (Junk et al., 1989) or even provide important sources of fish protein in developing countries (Martin et al., 2011). Despite the fact that fish stranding may be a significant issue, there is currently no synthesis of knowledge related to stranding in freshwater systems which makes it difficult to assess its relative threat to biodiversity or determine the need for mitigation strategies.

The objective of this paper is to generate a synthesis of knowledge related to the topic of fish stranding with a focus on freshwater systems. Specifically, we will: 1) characterize the literature on fish stranding using a quantitative literature review; 2) describe potential and documented sources of stranding; 3) summarize the factors affecting stranding rates; 4) discuss possible effects of stranding at organismal, population, community and ecosystem (including socio-economics) levels; 5) consider mitigation strategies that have been proposed and tested, and (6) identify knowledge gaps and suggest possible future research directions.

* Corresponding author. Tel.: +1 613 520 4377.

E-mail address: anagrodski@gmail.com (A. Nagrodski).



Fig. 1. Image of juvenile salmonids stranded downstream of a hydropeaking generating station. Photo credit: Fisheries and Oceans Canada.

2. Overview of fish stranding literature

To search for documented cases of anthropogenic and naturally caused fish stranding we used various combinations of the following search terms in both Web of Science and Google Scholar: fish, strand*, flood*, oxbow, drawdown, desiccation, ice dams, freshet, dewater*, fish kill, eggs, juvenile, alevin, redd, drought, irrigation, hydropeaking, floodway, vessel drawdown, and ship wake. In the existing technical and peer-reviewed literature we identified a number of documented sources of anthropogenic and naturally caused fish stranding. We also found incidental accounts and/or discussion of fish stranding in papers that were not explicitly focused on fish stranding. We focused on literature written in English so there is likely a bias towards work in developed countries. Moreover, although we consider the review of peer-reviewed materials to be exhaustive, non-peer reviewed sources such as technical reports were more difficult to identify and locate so are likely not fully represented. Furthermore, we are confident that the majority of fish stranding events are not documented in the literature. As authors, this was particularly evident to us in the spring of 2011 where there was extensive flooding in the Midwest and frequent media accounts of stranded fish being rescued by members of the public and resource management staff. It is unlikely that such events are formally documented outside of the media. We also acknowledge that this is a “mini-review” and in itself is not intended to be a detailed examination and summary of all available literature, rather it is a synthesis and overview of general patterns and concepts.

In total, we were able to find 116 papers relevant to fish stranding in freshwater systems – 78 peer-reviewed articles, 31 technical reports and 7 conferences or workshop symposia papers. Of the 116 papers, 21 studies were directly related to natural sources of fish stranding, while 93 focused on anthropogenic sources. The two remaining studies were categorized as both anthropogenic and natural sources of fish stranding. This classification was deemed appropriate as these studies simulated nonspecific dewatering events to make general inferences about both sources of stranding (Table 1). All 31 technical reports we found were concerned with human induced stranding events. The majority of the papers relevant to anthropogenic sources of fish stranding were related to variable flows downstream of hydroelectric dams (72 of 95; Table 1; see Fig. 2a,b). Other sources of anthropogenic fish stranding include water level management

Table 1

The proportion of studies focusing on the natural and anthropogenic sources of fish stranding, based on the peer-reviewed articles found by the authors during the literature review.

	Number of studies	% of studies within anthropogenic/natural	% of studies overall
<i>Anthropogenic sources</i>			
Floodplain management	4	4.2	3.4
Hydropower operations	72	75.8	62.1
Irrigation operations	4	4.2	3.4
Vessel-induced drawdowns	8	8.4	6.9
Water diversion	4	4.2	3.4
Water level management	3	3.2	2.6
<i>Natural sources</i>			
Flood events	8	34.8	6.9
Dewatering events	14	60.9	12.1
Winter ice dynamics	1	4.3	0.9

(Mingelbier et al., 2008), irrigation operations (Kroger, 1973), water diversion (Becker et al., 1986), floodplain management (Jones and Stuart, 2008) and vessel-induced drawdowns (Pearson and Skalski, 2011). Natural sources of stranding include flooding (Sommer et al., 2005), droughts (Davey and Kelly, 2007) and winter ice dynamics (Prowse, 2001). While we were particularly interested in locating papers largely concentrated on fish stranding (62 of 116), we also sought literature that recorded incidental accounts of fish stranding in order to identify as many sources of stranding as possible (54 of 116). Most of the stranding focused literature (in both natural and anthropogenic causes) reported exclusively on the stranding of early life stages, such as eggs and alevins (12 of 62) and juvenile fish (22 of 62) as opposed to adults (3 of 62). The remainder of the studies ranged across multiple life stages and took a more general approach towards enumerating stranded fish (25 of 62). Of the 62 stranding-focused studies, 48 were field studies, 9 were lab studies, 3 used modeling approaches, and 2 were reviews.

Based on our search, the first paper to report on fish stranding was published by Heman et al. (1969). In this study, Heman et al. (1969) utilized a mid-summer reservoir drawdown as a management tool to help re-establish largemouth bass (*Micropterus salmoides*) populations in a lake dominated by smaller foraging fish. As water was lowered, stranding of shoreline fry, intermediate-sized fish and nests caused population reductions (Heman et al., 1969). Fish stranding research output has increased over time, particularly over the past decade (Fig. 3). Of the 78 articles published in peer reviewed journals, the most common outlets were North American Journal of Fisheries Management (16 of 77), River Research Application (9 of 77), Journal of Fish Biology (8 of 77), Hydrobiologia (7 of 77) and Transactions of the American Fisheries Society (7 of 77).

3. Sources of fish stranding

As noted above, our literature review revealed that the majority of fish stranding research is attributed to anthropogenic alteration of natural flow regimes. More specifically, rapid flow fluctuations downstream of hydropower facilities (e.g., hydropeaking and plant shutdowns; see Fig. 2a,b) were identified as being a common source of stranding (Cushman, 1985). Hydropeaking can drastically change river depths and available habitat, resulting in a flow regime that is significantly different from that of an undisturbed, natural flow regime. Subsequent dewatering can cause fish stranding in peripheral water bodies, or beaching on shoreline habitat (Hunter, 1992). For example, in a study evaluating fish stranding along a reach of the Nidelva River (Norway), researchers found that sudden reductions in river flow, caused by almost immediate power station shutdowns, increased stranding mortality among juvenile salmonids downstream of the hydropower facility (Saltveit

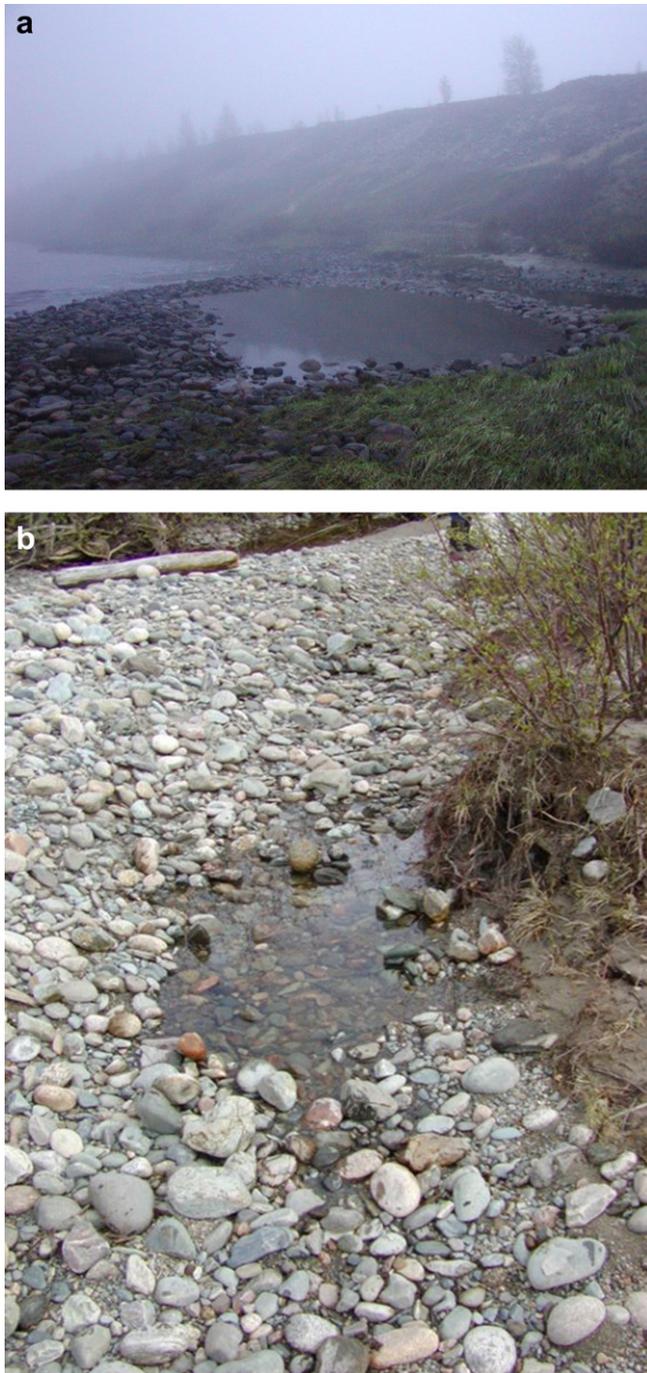


Fig. 2. a,b. Images of isolated pools that have the potential to strand fish downstream of a hydropeaking generating station. Photo credits: Fisheries and Oceans Canada.

et al., 2001). Meanwhile, during periods of peak energy usage, water released from hydropower facilities has the potential to cause shoreline drawdowns in the upstream reservoir and may also strand fishes. Bell et al. (2008) reported that salmonid fry (e.g. bull trout [*Salvelinus confluentus*], spring Chinook salmon [*Oncorhynchus tshawytscha*]) could commonly be observed stranded in Trail Bridge Reservoir, Oregon. In particular, researchers used extrapolation to estimate that 808 spring Chinook salmon fry and 444 brook trout (*S. fontinalis*) were stranded in the reservoir during spring 2006 (Bell et al., 2008).

Fishes can also be stranded by large, momentary shoreline drawdowns caused by ship wakes in navigation channels. Though

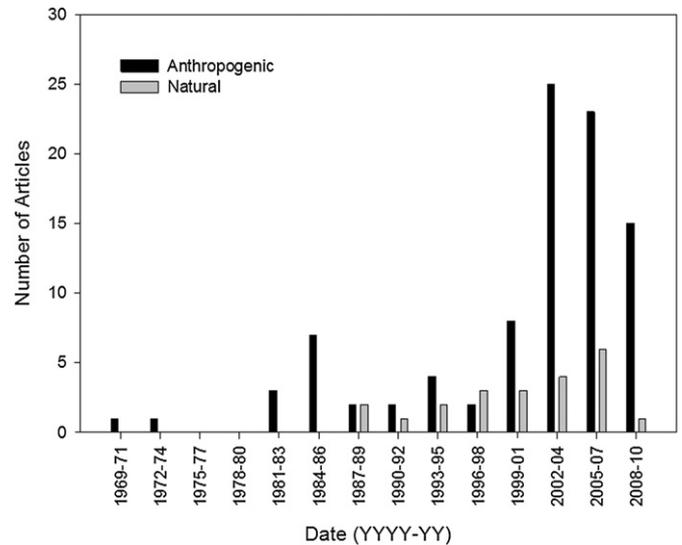


Fig. 3. Temporal trends of stranding related publications in freshwater that are focused on natural versus anthropogenic sources.

navigational canals can be valuable transportation corridors, boat wakes and subsequent swash from large vessels are sometimes a source of fish mortality (Adams et al., 1999; Pearson and Skalski, 2011). Adams et al. (1999) found that the behavioral responses of fish during navigational canal dewatering events determined the likelihood that they would become stranded. Species favoring littoral, backwater habitats generally moved out during periods of drawdown (either through self-propulsion or passive drift) whereas young fish residing in the main-channel exhibited positive rheotaxis, leaving them more susceptible to stranding (Adams et al., 1999). As inland navigational corridors become further developed through processes such as dredging, shoreline embankment and straightening, there may be additional impacts on fish survival, as alterations that ease vessel passage produce artificial environments that can further increase stranding risk (Wolter and Arlinghaus, 2003).

Another area where anthropogenic practices can lead to fish stranding events is during deepwater rice cultivation, occurring primarily in tropical and subtropical regions (Fernando, 1993). In particular, as most deepwater rice is grown under flood conditions, within inundated waters, a wide range of indigenous fish species are commonly found to inhabit rice fields. In these cases, fish can be found to actively enter rice fields or intentionally stocked in efforts to contribute to integrated farming practices (Coche, 1967; Fernando, 1993). Nevertheless, regardless of entry, fish stranding can occur as rice fields are dynamic environments, where the aquatic phase is temporary and seasonal (Fernando, 1993). During dry periods, fish are forced to survive in resting stages or in refuges however fish stranding events do occur as fish can become trapped in desiccated pools.

Several studies examined the effects of natural disturbance regimes such as flooding, droughts and winter ice dynamics (e.g., Bell et al., 2001; Brown et al., 2001; May and Lee, 2004). Although natural disturbance regimes can lead to fish mortality, they are a necessary component of a functional freshwater ecosystem (Resh et al., 1988; Ward, 1998). For example, the life cycle of the curimba (*Prochilodus lineatus*) is completely dependent on floodplain lagoons during early emergence and maturation before the later stages of development and growth in deeper waters (Agostinho and Zalewski, 1995). Sommer et al. (2005) determined that despite the increased risk of stranding- seasonal floodplains provide valuable rearing habitat for Chinook salmon. Freshwater

landscapes can naturally possess braided channels, sinuous watercourses, side tributaries, sloughs, seasonal floodplains, freshets and flood fringes that can occasionally form billabongs, oxbows and other ephemeral wetlands as a result of meandering watercourse pathways (Ward, 1998). While the formation of these natural features can be valuable, as they can serve as essential habitat for reproduction, development and growth of juveniles, these features have potential lethal or sub-lethal consequences for fishes (Sargent and Galat, 2002).

Sudden drawdowns experienced during naturally occurring, drought-like conditions can leave fish susceptible to stranding (Rayner et al., 2009). Processes such as ice formation, ice break-up and seasonal flooding can also impact fish assemblages; colder temperatures can cause changes in fish activity levels, which can leave fish susceptible to stranding (Brown et al., 2001). During winter, the accumulation of anchor ice, along a riffle in a river, can create ice dams that can cause upstream flooding, downstream dewatering and fluctuations in stream flow which can obstruct movement into side channels (Maciolek and Needham, 1952). Once the whole water mass reaches freezing point, anchor ice will readily form and increase the potential for fish to become stranded in dewatered pools and side channels. Likewise, while ice jams have similar impacts on fish assemblages, ice jams are formed during a buildup of surface ice which occurs during river breakup (Brown et al., 2001). Nevertheless, while the formation of ice can have potentially lethal implications on fish, the presence of ice can also insulate fish from cold temperatures as well as provide protection from predators (Maciolek and Needham, 1952).

4. Factors influencing fish stranding

Understanding the factors that influence fish stranding may help managers assess the potential for fish stranding in a given water body and/or strategies for mitigation. Abiotic factors that can influence fish stranding include water flow rate, water temperature, water quality, wetted history, seasonality, light conditions, time of day, bathymetric morphology, and substrate characteristics (Table 2; Saltveit et al., 2001; Halleraker et al., 2003; Irvine et al., 2009). In general, there appears to be a consensus that reduced water flow, gently sloped shorelines, heavily structured littoral zones, cooler water temperatures, abrupt water levels changes and poor water quality are conditions that increase the likelihood of fish stranding events (Hunter, 1992; Saltveit et al., 2001; Halleraker et al., 2003; Irvine et al., 2009). Inevitably, some contradictory findings do exist in the literature. For example, while many studies report stranding potential increases during rapid water level fluctuations (e.g. Hunter, 1992; Irvine et al., 2009), Bell et al. (2008) were unable to find a difference between numbers of stranded salmonid fry within Trail Bridge Reservoir during small and large water level fluctuations. Bathymetric properties such as channel aggradation (the process of sediment transport altering streambed configuration) can influence water availability and stranding potential. May and Lee (2004) reported that where riverbed substrate was porous, surface flow was intermittent, thus causing stranding of juvenile salmonids in drying channels or pools. Other studies have reported that heavily structured shorelines and riverbeds composed of large debris, cobbles and potholes, can impede fish movement and lead to stranding during shoreline drawdown (Chapman and Kramer, 1991; Bradford, 1997; Bell et al., 2008). Downstream of hydropower generation, the magnitude, frequency, duration and sequencing of ramping rates are the abiotic factors most commonly dictating rates of fish stranding (Poff et al., 1997; Scruton et al., 2008). A common finding has been that more rapid flow fluctuations have a greater potential to strand fishes downstream of hydropower facilities (Hunter, 1992; Bradford,

Table 2

Major abiotic and biotic factors that influence stranding potential, with key findings from published studies.

Type	Factor	Influence
Abiotic	Water flow rate	Faster reductions in flow cause increased stranding potential (Hunter, 1992) Conditioning reductions prior to operational reductions (in a hydropower context) reduce the probability of fish stranding (Irvine et al., 2009)
	Water temperature	Increased stranding potential at lower water temperatures (Saltveit et al., 2001)
	Water quality	As water quality declines, overall fish health declines (Evans, 2007)
	Wetted history	Longer periods of wetted history increase stranding potential (Irvine et al., 2009)
	Seasonality	Stranding potential is highest during the winter (Heggenes and Saltveit, 1990)
	Time of day/light conditions	Contradictory results in literature: some reports found stranding potential highest during the day due to concealment behavior (e.g., Bradford et al., 1995; Halleraker et al., 2003) while others found the opposite (e.g. Bradford, 1997)
	Bathymetric morphology	Greater stranding potential in areas with backchannels, gradually sloping bars and potholes (Bradford et al., 1995) Stranding potential is lower in areas with minimal shelter, fine substrate and few resting places for fish (Halleraker et al., 2003)
Biotic	Substrate characteristics	Suitable cover and substrate composition are not major factors dictating stranding during rapid dewatering events, however, during slow drawdowns these are major controlling factors (Saltveit et al., 2001)
	Fish morphology	It has been suggested that smaller fish become stranded first as a result of competition (Saltveit et al., 2001)
	Life stage	Young of year were affected more severely than older juveniles (Saltveit et al., 2001)
	Fish behavior	Species and life stage specific

1997; Halleraker et al., 2003). It should be noted that sometimes fish can survive stranding. For example, Saltveit et al. (2001) found fish alive, buried in substrate, hours after a stranding event. They suggested that in some cases, groundwater inflow may play an important role in fish survival (Saltveit et al., 2001).

The factors affecting fish stranding rates can vary depending on the cause of stranding in question. As inland navigational waterways are developed, fish assemblages become exposed to physical forces such as wave turbulence, drawdown, dewatering, backwash, and return currents, that are all factors which make fish more susceptible to stranding in littoral areas (reviewed in Wolter and Arlinghaus, 2003). An average vessel-induced dewatering period lasts approximately 2–3 min; however as vessel passage becomes more frequent, effects on ecosystems can become more pronounced (Holland, 1987). The severity of vessel-induced draw-down events, for fishes, is dictated by vessel characteristic (type, size, load, velocity, direction, draft and position), site characteristics (channel cross-section, river flow and current velocity) and wave characteristics (i.e. tidal stage height; Adams et al., 1999; Pearson and Skalski, 2011). Moreover, the ability of fish to resist stranding associated with these factors is largely based on life-stage, and depends on the swimming ability of the individual, which is based on factors such as: size, body shape, fin form, muscle function and swimming biomechanics (reviewed in Wolter and Arlinghaus, 2003).

Stranding rates are species- and life-stage specific, being largely dependent on factors such as size, swimming capacity, and other behavioral traits (e.g., Bradford, 1997). Different fish species exhibit

different activity patterns, prefer different microhabitats, and undergo different seasonal and daily spatial niche shifts (Heggnes and Saltveit, 1990; Heggnes, 1996). For example, coho salmon (*Oncorhynchus kisutch*) are more likely than rainbow trout (*Oncorhynchus mykiss*) to become stranded in artificial stream channels with cool water temperatures and gravel substrate (Bradford et al., 1995). Mature sockeye salmon migrating to spawning locations can sometimes strand themselves as they attempt to move through progressively shallow water until they can no longer swim (Quinn and Buck, 2001). Size is the key factor in stranding rates for mature migrating salmon, with larger fish being more susceptible to behavioral stranding and subsequent mortality (Quinn and Buck, 2001). Tramer (1977) observed in a study of stream fish survival in small shrinking pools, that the vast majority of mortality occurred during daytime hours, before complete pool dewatering. Fish species with subterminal/ventral mouths and lacking swim bladders (e.g., johnny darter, *Etheostoma nigrum*) had the highest mortality rates, as they were unable to access the thin oxygenated surface water near the air-water interface (Tramer, 1977). Therefore in general, while habitat characteristics are important in predicting survivorship, fish morphology can influence tolerance levels.

Eggs and early life stages are particularly susceptible to stranding following dewatering. Eggs are often laid in areas that experience frequent dewatering. Furthermore, earlier life stages have a reduced swimming capacity compared their more mature cohorts (Dabrowski et al., 1986). While cleavage eggs and embryos are relatively tolerant, the survival of both eleutheroembryos and alevins (egg sac fry) are severely impacted by dewatering events (Neitzel and Becker, 1985). This variation among life stages in survival is because of differences in respiratory systems. Following the development of functional gill structures, eleutheroembryos and alevins require a more constant supply of oxygenated water than do earlier life stages (Becker et al., 1983).

5. Consequences of fish stranding

The biological outcomes of fish stranding on individual fish described in the literature range from negligible sub-lethal impacts to direct mortality. However, the consequences of stranding (presumably via mortality of individuals) at the population-, community- and ecosystem-level have not been studied. Although a stranding event that leads to mortality of a fish is not of benefit to that individual, the fish may be a key food source for some shoreline dwelling animals (e.g., birds of prey, scavenging mammals, etc.) and invertebrates or serve as a source of riparian nutrients. As such, fish stranding could have cascading effects on community composition as well as the food web dynamics within ecosystems. We were unable to find much work on quantifying the socio-economic costs of stranding events; however, there are tools available for estimating financial loss associated with fish kill events (La and Cooke, 2011). Given that few studies have examined the systems level consequences of stranding, we focus on individual-level effects (both lethal and sublethal) with several examples of possible population-level consequences.

Stranding mortality (Fig. 4) occurs for a variety of reasons, with the most obvious being complete dewatering such that the fish is unable to respire and becomes desiccated (Evans, 2007). Death can also occur as a result of lack of dissolved oxygen (i.e., hypoxia or anoxia) or rapid fluctuations in water temperature (e.g., cold shock; Donaldson et al., 2008) that can occur in small temporary pools. In the winter, fish can become trapped in ice leading to mortality (Brown et al., 2001). Predation is presumably quite common and is a source of mortality for fish in temporary pools (Quinn and Buck, 2001). Moreover, when fish are stranded, they may be subject to easy capture and harvest by humans which in many cases is illegal,



Fig. 4. Image of dead fish found stranded associated with water level drawdown for water management. Photo credit: Cooke Lab, Carleton University.

but in developing countries can yield important protein. The extent to which that occurs is unknown.

If a fish survives being stranded, it is important to consider that a range of sub-lethal impacts are possible which will reduce the overall fitness of the individual. Dewatering has implications for habitat quality and stream ecology as it alters physiochemical properties (i.e., dissolved oxygen, ionized ammonia and turbidity) and food availability (Kushlan, 1974; Sargent and Galat, 2002). As water quality declines, fish can be exposed to acute and chronic levels of environmental hypoxia, resulting in lethal or sub-lethal impacts (Sabo et al., 1999). In the absence of an adequate supply of dissolved oxygen, the efficiency of metabolic processes essential during life activities (e.g. standard metabolism, locomotory activity, feeding, predator avoidance, growth and reproduction) becomes impaired (Evans, 2007). Dewatering can also alter fish behavior. Stradmeyer et al. (2008) reported that while feeding declined during dewatering events, the highest ranked dominant fish would monopolize an isolated refuge pool, forcing the remaining fish to adopt cryptic, stationary behaviors. In large fish communities supporting a number of fish species, some prey fish may actually avoid or exclude themselves from a particular refuge due to the presence of a predator (Magoulick and Kobza, 2003). Predator avoidance behaviors, exhibited by some prey fish, can occasionally be maladaptive as avoidance of refuge pools can leave prey fish more susceptible to stranding events (Magoulick and Kobza, 2003).

High rates of fish stranding mortality among early life stages can potentially impact recruitment (Kohler et al., 1993; Smith et al., 2007). Juvenile fishes inhabiting systems with low or fluctuating water levels generally exhibit reduced daily food consumption (energy intake), stunted somatic growth rates, reduced growth efficiency and altered nearshore distributions and habitat use, in contrast to fish in stable aquatic environments (Flodmark et al., 2004; Korman and Campana, 2009). Many riverine fishes, including Cyprinidae (minnows), Catostomidae (suckers), Centrarchidae (sunfish), Esocidae (pike), Salmonidae (salmonids), Acipenseridae (sturgeons) and Polyodontidae (paddlefish) are vulnerable to hydrologic fluctuations, as they rely on shallow, lithophilic areas for spawning and nest construction (e.g., Kohler et al., 1993; Grabowski and Isely, 2007). Fish stranding events may also impact fish populations by causing nest abandonment, home range reductions and a loss of habitat connectivity (Stradmeyer et al., 2008; Korman and Campana, 2009). However, in some instances, fish repeatedly exposed to rapid water level

fluctuations have been found to learn the necessary behaviors to avoid becoming stranded (Odling-Smee and Braithwaite, 2003).

6. Mitigation strategies

One of the most common mitigation methods for fish stranding are manual salvage efforts (Fig. 5), typically associated with planned anthropogenic water-level lowering events (e.g., canal drainings, hydropower plant shutdowns). Such efforts are labour intensive, expensive, and not sustainable in the long-term, particularly for more regular water level fluctuations such as downstream from peaking hydropower facilities. Higgins and Bradford (1996) reported on the effectiveness of fish salvage to reduce the impacts of hydropeaking and estimated a cost-benefit ratio of 10:1. However, if fish salvage effort is supported by volunteered labour and gear, and focused on areas of high fish abundance, fish salvages should be effective for mitigating stranding mortality in some systems. From 2007 to 2010, volunteers have assisted with the salvage of fish that were stranded as a result of winter canal draining in an historic canal system in Ottawa, Canada, providing an opportunity to engage stakeholders in an adaptive management experiment intended to reduce stranding (Cooke, Unpublished Data).

Where fish stranding is caused by hydropeaking (e.g., Bednarek and Hart, 2005; Weber et al., 2007), one strategy that has been evaluated is the control of ramping rates. Generally, more gradual ramping rates have almost universally been identified as having a reducing effect on stranding rates for juvenile salmonids (Bradford, 1997; Halleraker et al., 2003). As such, hydropower ramping rates tend to be prescribed by regulatory agencies, although in some cases there can be unexpected deviations from plans and ramping rates are not always based on empirical data from that system. Indeed, caution should be taken with the application of generic prescribed regulated flow regimes as each system has unique site-specific characteristics (Jones and Stuart, 2008). Arthington et al. (2006) expressed concern that a growing number of dammed facilities are operating under simple, static hydrological “rules of thumb”, i.e., not providing flow variability that simulates natural hydrology. In some cases certain flows or operating conditions may be prescribed in an effort to minimize stranding but there may be other more serious consequences on riverine function and productivity associated with maintaining muted hydrographs in an attempt to save fish from stranding. In efforts to rehabilitate regulated flow regimes,



Fig. 5. Image of electrofishing to salvage fish stranded in temporary pools following reduction in river flows associated with planned works at a hydropower facility. Photo credit: Guy Martel, BC Hydro.

“flushing floods” have been used as a method of restoring spawning habitat and improving fisheries potential (Ortlepp and Mürle, 2003). While flushing floods have potential to improve food resources and spawning habitat, floods can cause stranding and mobilize sediment, causing damage to the gills and mucous layers of fish (Ortlepp and Mürle, 2003). For hydropower managers, flow rates are the most easily manipulated variable and the most well understood in the context of fish stranding. More extreme, but rather effective approaches include physical works such as re-profiling of river beds and channels to remove potential stranding pools, but again there is potential for negative consequences that may not be balanced by the reduction in stranding. For infrequent planned reductions in water flow, some attempts have been made to use fences to exclude fish from areas where stranding is known to occur. In general there is sufficiently little known about the ecosystem-level consequences of stranding versus potential mitigation strategies to inform management actions.

In some cases, the importance of flow rate (ramping rate) is secondary, or highly dependent on other abiotic factors. Seasonal and diel patterns in light intensity and temperature are two such factors that should be considered when implementing mitigation strategies (Saltveit et al., 2001; Irvine et al., 2009). Both in winter and during daylight hours, juvenile salmonids tend to seek cover in substrate and have reduced willingness to move (Saltveit et al., 2001). While these findings are based on studies with juvenile salmonids, these behavioral patterns (cover seeking, predator avoidance) are common among many juvenile fishes (Magoulick and Kobza, 2003). Therefore, in most cases, an appropriate mitigation strategy may be to ramp down during night hours and more slowly during winter than in summer.

‘Conditioning flows’ may be an appropriate strategy for mitigating stranding in side channels or pools in hydropeaking systems (i.e., the practice of rapidly decreasing and then rapidly increasing river flows within one hour of a planned major flow reduction; Irvine et al., 2009). By creating learned behavior in juvenile fishes to emigrate to deeper water during flow reduction, this new procedure may be an effective mitigation strategy, particularly for decreasing stranding in side-channels or pools (see Irvine et al., 2009).

Fish stranding mortality from drawdowns in irrigation canals and other canal systems can be substantial (Baumgartner et al., 2007; Haag et al., 2010). In some systems, the simplest way to reduce the stranding of fish in these systems is to prevent fish from entering the canals using screens at intake points (Baumgartner et al., 2007; Haag et al., 2010). Small fish and larval stages tend to be most likely to enter smaller irrigation canals, making fine mesh screens necessary (Baumgartner et al., 2007). However, installing and maintaining such screens can be costly. Another option for irrigation canal managers is to avoid drawing water into canals during periods of high larval abundance to avoid entrainment in canal reaches that will later become dewatered (Baumgartner et al., 2007). Fish salvages are also sometimes used to reduce stranding losses in canal systems.

Stranding mortality from ship wakes in navigation canals has been the subject of relatively little research. Work to date has indicated that more gradually sloped shorelines can reduce the likelihood of stranding because wave action dissipates as it moves through shallower water (Wolter et al., 2004). Additionally, creating more heterogeneous and structured shoreline habitat in canals provides small fishes with cover so they can avoid the physical forces of ship wakes (Wolter and Arlinghaus, 2003).

7. Knowledge gaps and future research directions

To date, research on hydropeaking systems has served as the basis for the majority of the knowledge on fish stranding. However,

many questions remain and today, particularly in the context of hydropower, regulators and utilities continue to struggle with identifying the magnitude and consequences of stranding as well as identifying potential mitigation strategies (Table 3). One of the more fundamental questions that still exists is whether the extent of fish stranding has whole-population impacts and is thus of concern to resource managers (Table 3). This void is likely a reflection of the difficulty in estimating total stranding mortalities as a proportion of population size. Accurately enumerating stranded fish can be particularly difficult, especially while considering variation in stranding potential across developmental stages and habitat types. Moreover, predators can rapidly remove stranded (dead or alive) fish and thus make enumeration over large areas difficult. Researchers could address the population-level issue indirectly by determining whether anthropogenic fish stranding rates are significantly different from those in otherwise comparable natural systems (Table 3). This would be best accomplished using simple surveys, monitoring of flow regimes, and microcosm experiments (e.g., Bradford, 1997) with paired comparisons of natural and non-natural systems. Such research would serve to answer the persistent question of whether fish stranding is a significant concern for resource managers.

There are a number of fish stranding research needs in non-hydropower systems. For example, in navigation canals, there is opportunity to explore different constructed channel morphologies or even boat design to minimize stranding. In irrigation systems there is need to explore different types of screens, guidance technologies, and best-practices for minimizing entrainment and later stranding. In all systems, there is a need to better understand the seasonal aspects of stranding. Further, stranding research has failed to investigate the sub-lethal consequences of fish stranding. However, difficulties lie in assessing and enumerating the number of fish that experience sub-lethal conditions associated with stranding events. Brief, seemingly harmless incidences of stranding that result in no immediate mortality may have substantial impacts

Table 3

Examples of research questions and knowledge gaps associated with stranding research. Research needs specific to mitigation are excluded from this table but covered in the text.

Individuals	Stress responses	What physiological changes are a direct consequence of stranding?
		Do the physiological changes associated with stranding result in mortality?
	Behavioral responses	What stimuli are most closely linked to fish movement during stranding?
		Are groups of fish more likely to be stranded, or less likely?
Growth rates	What seasonal effects exist?	
	Are growth rates of fish altered by frequency of stranding events?	
Morphology	How does body shape influence individual stranding potential?	
Population	Recruitment	Does higher stranding risk for juvenile fishes shape species abundance and persistence of populations?
	Population size	Can increased stocking mitigate fish mortality due to stranding?
		What is the contribution of stranding to population growth?
Evolutionary dynamics	Can stranding be a selection pressure in particular systems?	
Community	Food web	What is the importance of stranded fish to shoreline predators and scavengers?
	Species interactions	Can predation/competition lead to higher stranding rates?
	Diversity	Are areas with higher rates of stranding mortality less or more diverse?

and result in long-term fitness consequences for individual fish (e.g., reduced feeding opportunities, restriction of available spawning habitat). Future research could also assess the importance of fish stranding to shoreline predators and scavengers that may have some level of dependence on stranded fish in their diets.

As in some other areas of fisheries research, the majority of the published research has focused on salmonids of the Pacific Northwest. It follows that managers would benefit from a more robust understanding of mortality factors for stranding sources other than hydropeaking and in non-salmonid systems. Indeed, river regulation is occurring around the world (Nilsson et al., 2005) and it is unlikely that data generated for salmon smolts will be relevant to fish in sub-tropical rivers. Meanwhile, managers of hydropower systems that resemble those studied in the literature should take advantage of the knowledge that has been generated by using an adaptive management approach to mitigation. Such management approaches should combine experimental management with monitoring and, where possible, use rapid and inexpensive means of assessment (e.g., visual surveys).

Fish stranding research efforts should attempt, where possible, to combine field observations and experimentation with laboratory experiments and modeling exercises to better understand the population-level consequences of stranding, factors associated with stranding, and mitigation options. We also recognize that stranding from the perspective of the fish represents a complex interaction of various and interacting sensory cues such as water velocity, temperature, dissolved oxygen, and turbidity, among others. As such, it would be useful to understand how sensory systems of fish respond to these various and interacting cues which could identify additional potential mitigation strategies. Use of decision frameworks and other decision support tools may also be useful for helping managers to understand and manage sources of uncertainty. Additional perspectives could be gained through human dimension surveys intended to quantify the socio-economic costs of stranding and stakeholder perspectives towards different mitigation options. To date, stranding research papers have lacked true replication. For example, there have been no research programs studying stranding in a hydropeaking context using multiple systems in a comparative framework.

8. Synthesis and conclusion

Our review identified that stranding occurs as a result of both natural and anthropogenic causes although it is difficult to use primary literature to understand and quantify the relative frequency of stranding events and their causes as most accounts of stranding do not find their way into journals. The factors associated with stranding are diverse and in general poorly understood. Indeed, it is most likely that when stranding occurs in a given system, the extent of stranding is dictated by the complex interaction of a variety of biotic and abiotic factors. Quite simply, there is insufficient literature available to enable a rigorous examination and few predictive models available to assist with decision support. We hope the recommendations in this paper will help to guide future fish stranding research and generate interest among managers and scientists and close the knowledge gaps we have identified. Without knowledge of the population-level consequences of fish stranding, managers lack the impetus to design and implement fish stranding mitigation strategies. From a basic perspective, aquatic ecologists would benefit from an improved understanding of how stranding impacts the structure and function of populations, communities and ecosystems. Such knowledge is essential to inform debate about conflicting values (e.g. minimizing stranding vs. habitat diversity and flow variability) and thus the choice of appropriate mitigation strategies that embrace natural river processes.

Acknowledgements

Our team is supported by the Canada Research Chairs Program, the Ontario Ministry of Research and Innovation, Parks Canada, Fisheries and Oceans Canada (Center of Expertise on Hydropower Impacts on Fish), and the Natural Sciences and Engineering Research Council of Canada through the HydroNet Strategic Network Project. We thank Karen Smokorowski and Brent Mossop for assisting with finding appropriate photos.

References

- Adams, S.R., Keevin, T.M., Killgore, K.J., Hoover, J.J., 1999. Stranding potential of young fishes subjected to simulated vessel-induced drawdown. *Transactions of American Fisheries Society* 128, 1230–1234.
- Agostinho, A.A., Zalewski, M., 1995. The dependence of fish community structure and dynamics on floodplain and riparian ecotone zone in Parana River, Brazil. *Hydrobiologia* 303, 141–148.
- Arthington, A.H., Bunn, S.E., Poff, N.L., Naiman, R.J., 2006. The challenge of providing environmental flow rules to sustain river ecosystems. *Ecological Applications* 16, 1311–1318.
- Baumgartner, L.N., Reynoldson, N., Cameron, L., Stanger, J., 2007. The Effects of Selected Irrigation Practices on Fish of the Murray–Darling Basin. NSW Department of Primary Industries Narrandera Fisheries Centre, Narrandera NSW, p. 92.
- Becker, C.D., Neitzel, D.A., Charlike, D.W., 1986. Survival data for dewatered rainbow trout (*Salmo gairdneri* Rich.) eggs and alevins. *Journal of Applied Ichthyology* 3, 102–110.
- Becker, C.D., Neitzel, D.A., Abernethy, C.S., 1983. Effects of dewatering on Chinook salmon redds: tolerance of four development phases to one-time dewatering. *North American Journal of Fisheries Management* 3, 373–382.
- Bednarek, A.T., Hart, D.D., 2005. Modifying dam operations to restore rivers: ecological responses to Tennessee River dam mitigation. *Ecological Applications* 15, 997–1008.
- Bell, E., Duffy, W.G., Roelofs, T.D., 2001. Fidelity and survival of juvenile coho salmon in response to a flood. *Transactions of the American Fisheries Society* 130, 450–458.
- Bell, E., Kramer, S., Zajanic, D., Aspittle, J., 2008. Salmonid fry stranding mortality associated with daily water level fluctuations in Trail Bridge reservoir, Oregon. *North American Journal of Fisheries Management* 28, 1515–1528.
- Bradford, M.J., 1997. An experimental study of stranding of juvenile salmonids on gravel bars and inside channels during flow decreases. *Regulated Rivers: Research and Management* 13, 395–401.
- Bradford, M.J., Taylor, G.C., Allan, J.A., 1995. An experimental study of the stranding of juvenile coho salmon and rainbow trout during rapid flow decreases under winter conditions. *North American Journal of Fisheries Management* 15, 473–479.
- Brown, R.S., Power, G., Beltaos, S., 2001. Winter movements and habitat use of riverine brown trout, white sucker and common carp in relation to flooding and ice break-up. *Journal of Fish Biology* 59, 1126–1141.
- Bunn, S.E., Arthington, A.H., 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30, 492–507.
- Chapman, L.J., Kramer, D.L., 1991. The consequence of flooding for the dispersal and fate of poeciliid fish in an intermittent tropical stream. *Oecologia* 87, 299–306.
- Coche, A.G., 1967. Fish culture in rice fields a world-wide synthesis. *Hydrobiologia* 30, 1–44.
- Cushman, R.M., 1985. Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. *North American Journal of Fisheries Management* 5, 330–339.
- Dabrowski, K.R., Kok, L.Y., Takashima, F., 1986. How efficiently do fish larvae and juveniles swim? *Comparative Biochemistry and Physiology A* 85, 657–661.
- Davey, A.J.H., Kelly, D.J., 2007. Fish community responses to drying disturbances in an intermittent stream: a landscape perspective. *Freshwater Biology* 52, 1719–1733.
- Donaldson, M.R., Cooke, S.J., Patterson, D.A., Macdonald, J.S., 2008. Cold shock and fish. *Journal of Fish Biology* 73, 1491–1530.
- Evans, D., 2007. Effects of hypoxia on scope for activity and power capacity lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries and Aquatic Sciences* 64, 345–361.
- Fernando, C.H., 1993. Rice field ecology and fish culture – an overview. *Hydrobiologia* 259, 91–113.
- Flodmark, L.E.W., Vøllestad, L.A., Forseth, T., 2004. Performance of juvenile brown trout exposed to fluctuating water level and temperature. *Journal of Fish Biology* 65, 460–470.
- Grabowski, T.B., Isely, J.J., 2007. Effects of flow fluctuations on the spawning habitat of a riverine fish. *Southeastern Naturalist* 6, 471–478.
- Haag, J.J., White, J.S., Logan, M., February 2010. 2009 Fish Survey in Recently Dewatered Western Irrigation District Canals. Western Irrigation District by Quality Environmental Consulting Ltd., Edmonton, Alberta.
- Halleraker, J., Saltveit, S.J., Harby, A., Arnekleiv, J.V., Fieldstad, H.-P., Kohler, B., 2003. Factors influencing stranding of wild juvenile brown trout (*Salmo trutta*) during rapid and frequent flow decreases in artificial stream. *River Research and Application* 19, 589–603.
- Heggnes, J., Saltveit, S.J., 1990. Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon (*Salmo salar* L.) and brown trout (*S. trutta* L.) in a Norwegian river. *Journal of Fish Biology* 36, 707–720.
- Heggnes, J., 1996. Habitat selection of brown trout (*Salmo trutta*) and young Atlantic salmon (*S. salar*) in streams: static and dynamic hydraulic modeling. *Regulated Rivers: Research and Management* 12, 155–169.
- Heman, M.L., Campbell, R.S., Redmond, L.C., 1969. Manipulation of fish populations through reservoir drawdown. *Transactions of the American Fisheries Society* 2, 293–304.
- Higgins, P.S., Bradford, M.J., 1996. Evaluation of a large-scale fish salvage to reduce the impacts of controlled flow reduction in a regulated river. *North American Journal of Fisheries Management* 16, 666–673.
- Holland, L.E., 1987. Effect of brief navigation related dewatering on fish eggs and larvae. *North American Journal of Fisheries Management* 7, 145–147.
- Hunter, M.A., 1992. Hydropower flow fluctuations and salmonids: a review of the biological effects, mechanical causes and options for mitigation. Technical Report No. 119, Department of Fisheries, State of Washington.
- Irvine, R.L., Oussoren, T., Baxter, J.S., Schmidt, D.C., 2009. The effects of flow reduction rates on fish stranding in British Columbia, Canada. *River Research and Application* 25, 405–415.
- Jones, M.J., Stuart, I.G., 2008. Regulated floodplains—a trap for unwary fish. *Fisheries Management and Ecology* 15, 71–79.
- Junk, W.J., Bayley, P.B., Sparks, R.E., 1989. The flood pulse concept in river-floodplain systems. In: Dodge, D.P. (Ed.), *Proceedings of the International Large River Symposium (LARS)*. Canadian Special Publication of Fisheries and Aquatic Sciences, Ottawa, Canada, pp. 110–127.
- Kohler, C.C., Sheenan, R.J., Sweatman, J.J., 1993. Largemouth bass hatching success and first-winter survival in two Illinois reservoirs. *North American Journal of Fisheries Management* 13, 125–133.
- Korman, J., Campana, S.E., 2009. Effects of hydropeaking on nearshore habitat use and growth of age-0 rainbow trout in a large regulated river. *Transactions of the American Fisheries Society* 138, 76–87.
- Kroger, R.L., 1973. Biological effects of fluctuating water levels in the Snake River, Grand Teton National Parks, Wyoming. *American Midland Naturalist* 89, 478–481.
- Kushlan, J.A., 1974. Effects of a natural fish kill on the water quality, plankton, and fish population of a pond in the Big Cypress Swamp, Florida. *Transactions of the American Fisheries Society* 112, 236–243.
- La, V.T., Cooke, S.J., 2011. Advancing the science and practice of fish kill investigations. *Reviews in Fisheries Science* 19, 21–33.
- Maciolek, J.A., Needham, P.R., 1952. Ecological effects of winter conditions on trout and trout foods in Convict Creek, California, 1951. *Transactions of the American Fisheries Society* 81, 202–217.
- Magoulick, D.D., Kobza, R.M., 2003. The role of refugia for fishes during drought: a review and synthesis. *Freshwater Biology* 48, 1186–1198.
- Martin, S., Lorenzen, K., Arthur, R.I., Kaisone, P., Souvannalangsy, K., 2011. Impacts of fishing by dewatering on fish assemblages of tropical floodplain wetlands: a matter of frequency and context. *Biological Conservation* 144, 633–640.
- May, C.L., Lee, D.C., 2004. The relationship among in channel sediment storage, pool depth, and summer survival of juvenile salmonids in Oregon coast range streams. *North American Journal of Fisheries Management* 24, 761–774.
- Mingelbier, M., Brodeur, P., Morin, J., 2008. Spatially explicit model predicting the spawning habitat and early stage mortality of Northern pike (*Esox lucius*) in a large system: the St. Lawrence River between 1960 and 2000. *Hydrobiologia* 601, 55–69.
- Neitzel, D.A., Becker, C.D., 1985. Tolerance of eggs, embryos, and alevins of Chinook salmon to temperature changes and reduced humidity in dewatered redds. *Transactions of the American Fisheries Society* 114, 267–273.
- Nilsson, C., Reidy, C.A., Dynesius, M., Revenga, C., 2005. Fragmentation and flow regulation of the world's river systems. *Science* 308, 405–408.
- Odling-Smee, L., Braithwaite, V.A., 2003. The role of learning in fish orientation. *Fish and Fisheries* 4, 235–246.
- Ortlepp, J., Mürle, U., 2003. Effects of experimental flooding on brown trout (*Salmo trutta* fario L.): the River Spöl, Swiss National Park. *Aquatic Science* 65, 232–238.
- Pearson, W.H., Skalski, J.R., 2011. Factors affecting stranding juvenile salmonids by wakes from ship passage in the lower Columbia River. *River Research and Application* 27 (7), 926–936.
- Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegard, K.L., Richter, B.D., Sparks, R.E., Stromberg, J.C., 1997. The natural flow regime. *BioScience* 47, 769–784.
- Prowse, T.D., 2001. River-ice ecology. *Journal of Cold Regions Engineering* 15, 17–33.
- Quinn, T.P., Buck, G.B., 2001. Size- and sex-selective mortality of adult sockeye salmon: bears, gulls, and fish out of water. *Transactions of the American Fisheries Society* 130, 995–1005.
- Rayner, T.S., Jenkins, K.M., Kingsford, R.T., 2009. Small environmental flows, drought and the role of refugia for freshwater fish in the Macquarie Marshes, arid Australia. *Ecology* 2, 440–453.
- Resh, V.H., Brown, A.V., Covich, A.P., Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B., Wissmar, R.C., 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7, 433–455.
- Richter, B.D., Baumgartner, J.V., Wigington, R., Braun, D.P., 1997. How much water does a river need? *Freshwater Biology* 37, 231–249.
- Sabo, M.J., Bryan, C.F., Kelso, W.E., Rutherford, D.A., 1999. Hydrology and aquatic habitat characteristics of a riverine swamp: II hydrology and the occurrence of chronic hypoxia. *Regulated Rivers: Research & Management* 15, 525–542.

- Saltveit, S.J., Halleraker, J.H., Arnekleiv, J.V., Hardy, A., 2001. Field experiments on stranding in juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) during rapid flow decreases caused by hydropeaking. *Regulated Rivers: Research & Management* 17, 609–622.
- Sargent, J.C., Galat, D.L., 2002. Fish mortality and physicochemistry in a managed floodplain wetland. *Wetlands Ecology and Management* 10, 115–121.
- Scruton, D.A., Pennell, C., Ollerhead, L.M.N., Alfredsen, K., Stickler, M., Harby, A., Roberson, M., Clarke, K.D., LeDrew, L.J., 2008. A synopsis of 'hydropeaking' studies on the response of juvenile Atlantic salmon to experimental flow alteration. *Hydrobiologia* 609, 263–275.
- Smith, B.M., Farrel, J.M., Underwood, H.B., Smith, S.J., 2007. Year-class formation of upper St. Lawrence River northern pike. *North American Journal of Fisheries Management* 27, 481–491.
- Sommer, T.R., Harrell, W.C., Nobriga, M.L., 2005. Habitat use and stranding risk of juvenile Chinook salmon on a seasonal floodplain. *North American Journal of Fisheries Management* 25, 1493–1504.
- Stradmeyer, L., Hojesjo, J., Griffiths, S.W., Gilvear, D.J., Armstrong, J.D., 2008. Competition between brown trout and Atlantic salmon parr over pool refuges during rapid dewatering. *Journal of Fish Biology* 72, 848–860.
- Tramer, E.J., 1977. Catastrophic mortality of stream fishes trapped in shrinking pools. *American Midland Naturalist* 97, 469–478.
- Ward, J.V., 1998. Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation* 83, 269–278.
- Weber, C., Peter, A., Zanini, F., 2007. Spatio-temporal analysis of fish and their habitat: a case study on a highly degraded Swiss river system prior to extensive rehabilitation. *Aquatic Sciences* 69, 162–172.
- Wolter, C., Arlinghaus, R., Sukhodolov, A., Engelhardt, C., 2004. A model of navigation-induced currents in inland waterways and implications for juvenile fish displacement. *Environmental Management* 34, 656–668.
- Wolter, C., Arlinghaus, R., 2003. Navigation impacts on freshwater fish assemblages: the ecological relevance of swimming performance. *Reviews in Fish Biology and Fisheries* 13, 63–89.