River flow as a determinant of salmonid distribution and abundance: a review

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Abstract

River flow regime is believed to have a fundamental effect on riverine biota. It influences key aquatic processes, including levels of dissolved oxygen, sediment transport and deposition, water quality and habitat type and distribution. We review the impact of flow on the abundance and distribution of salmonid fishes in the context of developing approaches to regulating, setting and restoring river flow regimes as a means of conserving and managing populations. Flow can have direct impacts on salmonids, both through peak flow resulting in the washout of juveniles, and stranding of all life stages under low flow conditions. Salmonids can also be adversely affected through indirect effects of flow, from impacts on water temperature, dissolved oxygen condition, sediment deposition, and habitat availability. Early life stages, particularly eggs and larvae, appear particularly susceptible to the adverse impacts of flow, since they have a limited capacity for behavioral responses to altered flow conditions. A constraint to conservation and management efforts for salmonids is in selecting river flow targets at the catchment scale with confidence. Most studies linking flow with salmonid population processes are site specific, and may not be readily transferable to other sites. Despite this uncertainty, the requirement for catchment level flow targets has become critical as pressure on water resources has intensified, at the same time that salmonid populations have declined. Our proposal is that hypothesis-led analyses of broad scale long-term datasets are key to quantifying variability in fish abundance with respect to flow and informing flow modification field experiments. The water industry, conservation organizations, and environmental regulators are charged with collaboratively tackling the question of how to set, manage and restore river flow parameters, within the framework of the emerging science of hydroecology.

Keywords: ecological engineering, fish, hydroecology, management, model, restoration, salmon, trout

Introduction

River flow regimes influence a number of key aquatic processes, including levels of dissolved oxygen, sediment transport and deposition, water quality (through dilution and flushing), and habitat type and distribution (Poff et al., 1997; Richter et al., 1998; Bunn and Arthington, 2002). These processes influence the distribution and abundance of biota and flow regimes can thereby directly or indirectly determine the spatial and temporal distribution of fish (Jowett et al., 2005; Poff and Zimmerman, 2010). Human perturbation of flow, either by directly extracting water, regulating rivers using weirs and dams, or indirectly through patterns of land use, may affect fish populations and communities (Freeman et al., 2001; Cattanéo, 2005; Park et al., 2006; Benejam et al., 2010). Understanding the relationship between flow and fish abundance and distribution represents a key goal in aquatic ecology and fisheries management, and particularly in attempts to manage, restore and rehabilitate rivers for the benefit of aquatic communities (Richter et al., 2003; Souchon et al., 2008; Poff et al., 2010). Because of their ecological and commercial importance, salmonids have been the chief focus of the debate over flow management (Quinn, 2011; Milner et al., 2012).

In recognizing the dominant role of river flow on salmonids an additional consideration is the life-stages affected (Nislow and Armstrong, 2012). The direct and indirect effects of river flow will affect different salmonid life-stages in distinct and sometimes contrasting ways (Johnson et al., 1995; Malcolm et al., 2012; Milner et al., 1998; Nislow and Armstrong, 2012). The impacts of flow that act strongly on developing eggs (Steen and Quinn, 1999) may differ from those impinging on, for example, juveniles (Elliott et al., 1997) or migrating adults (Solomon and Sambrook, 2004). Impacts on different life-stages will depend on the timing and duration of low or high flow events (Bischoff and Wolter, 2001). High flows may have a profound effect on early life stages, whereas periods of low flow may interrupt the migration of adults. The flow requirements of salmonids have been reviewed (Quinn, 2011; Nislow and Armstrong, 2012).

The significance of flow for salmonids

The aim of this review is to summarize key scientific studies that demonstrate how river flow can influence the abundance of salmonid fishes, though where relevant, case studies using non-salmonid taxa are also included. A secondary goal is to identify which aspects of flow play the most significant role in shaping salmonid populations, and thereby, how this information might be used in river management, and rehabilitation and restoration of rivers for salmonids. The review focuses on salmonids because the bulk of studies that have addressed this question have concentrated on this family of fishes, a reflection of their economic and perceived ecological importance. Many salmonids are also of considerable conservation interest (Allendorf and Waples, 1996). Migratory salmonids occupy entire river catchments, from headwaters to estuaries, with each life stage having some dependency on the different habitat types potentially makes them particularly sensitive to river flow regime alteration. Salmonids have, consequently, been considered good ecological indicators of the impact of flow regime on ecosystems over a broad range of environmental scales (Milner et al., 2012).

Another feature of salmonid biology that makes them a valuable model in understanding the ecological impact of flow is the plasticity of their life-history traits in response to environmental variability (Klemetsen et al., 2003; Rieman and Dunham, 2000). Thus salmonids display wide intra- and interspecific variability in responses to flow variability, with the capacity to adapt to high-gradient upland streams and lowland rivers and estuaries (Beechie et al., 2006; Moore et al., 2012). While this feature of salmonid biology can serve to identify how flow regimes select for specific life-history traits, these adaptive responses also make it difficult to derive generic models of the impacts of flow, with contrasting results generated in different locations (Milner et al., 2012).

Describing river flow

Hydrologists typically use the term 'flow' to describe the volume of water that is discharged past a single point on a river. The flow regime of a river comprises flow magnitude, frequency, duration, timing and rate of change (Poff et al., 1997). Various numerical variables are used to describe mean, median, peak and low flow rates so that each of these components of water flow can be estimated (Poff et al., 1997; Shaw, 1988). Originally these descriptors were intended for river engineering or water resources management, driven by human population needs, such as flood alleviation or public water supply (Newson, 1994). Regulatory changes over time have shifted the emphasis of river and water resources management towards an ecological basis in order to meet the requirements of legislation, such as the EU Habitats Directive (European Commission, 1992) and the EU Water Framework Directive (European Commission, 2000). Consequently, the term 'environmental flow' has entered usage to denote the amount of flow required in a watercourse to maintain a healthy ecological state (Arthington et al., 2003; Gibbins et al., 2001; Acreman et al., 2008). The introduction of this term is problematic since quantifying ‘environmental flow’ is difficult for complex ecological systems, though it at least encapsulates an important concept. Despite these difficulties environmental flows are widely used to set abstraction limits and reservoir releases in river management and are typically defined in terms of departure from some baseline state, such as the ‘natural’ flow, itself a subjective concept since natural flows will naturally change in response to seasonal and climatic variation (for a full discussion see Poff et al., 1997). If the science and application of environmental flows is to develop, a better quantitative understanding of flow variability and biological response is required (Poff et al., 1997). For this review our goal is to evaluate the evidence for flow induced responses in salmonids, and identify the key aspects of those responses that appear relevant to the setting of environmental flows for salmonid management and as targets for restoration measures. For a recent review of terminology see Milner et al. (2011).

Part of the review outlines the processes that drive river flow so that their different scales and interactions can be placed in context when considering biological responses. This conceptual background is important to those with a biological or ecological background in order to gain some insight into the hydrological disciplines that tend to dominate river and water resources management. Transference can then be made to the rehabilitation of river ecology and restoration of natural features in engineered or degraded rivers. For brevity we employ the term ‘restoration’ to denote both river rehabilitation and restoration measures.

Determinants of river flow

The natural flow regimes of rivers can vary markedly depending on the sources and components of water runoff. Freeze (1972) partitioned the total runoff from a natural catchment into four component parts: channel precipitation, overland flow, interflow (subsurface flow), and groundwater flow (Freeze, 1972; Ward, 1974). Channel precipitation is that which falls directly onto the river water surface and represents the smallest component, since river surface area will make up only a small percentage of total catchment area. Overland flow is runoff that fails to infiltrate the substrate surface and is determined by the degree of soil saturation. Interflow occurs when water infiltrates the soil and moves laterally through the upper soil horizons to reach river channels. Precipitation that percolates through soils to the underlying waterbearing strata contributes to the groundwater flow component. Groundwater flow tends to lag behind rainfall events and is important in sustaining river flow during periods of little or no rain. The relative contribution of each of these components will determine the flow regime of a river. When these components are considered alongside other catchment characteristics, such as catchment size, rainfall pattern (spatial and temporal), geology, soil type and topography, an extensive range of river flow regimes will result (Ward, 1974; Newson, 1994; Poff et al., 1997). For example, upland rivers in northern Europe have a high runoff per unit area due to high rainfall and low evapotranspiration, combined with an impermeable geology, steep gradients and thin soils (Burt, 1992; Gilvear et al., 2002). They generally show marked flow peaks and troughs in response to periods of high and low rainfall due to short lag times between rainfall events and changes in river flow (Shaw, 1988). In contrast, lowland alluvial rivers will be influenced more by groundwater. As such, these show relatively more consistent and stable patterns of flow due to a damped response to rainfall and sustained flows in dry periods (Shaw, 1988). A further contrast is found in regions, such as North America, that experience significant precipitation in the form of snow, where river flow can be dominated by patterns of snowmelt. An assumption is that these varying patterns of flow will select for contrasting salmonid life histories, an assumption that appears to be justified (e.g. Elliott, 1995; Beechie et al., 2006).

Approaches to understanding river flow regime need to reflect the regional patterns. In the UK, the Institute of Hydrology developed the Base Flow Index (BFI) as a standard approach to apportioning the total river outflow to baseflow (Newson, 1994). The highest BFI scores relate to chalk and other porous limestone catchments, whilst the lowest corresponds to clay-dominated catchments (Table 1). This index provides hydrologists and water resource managers with a comparative guide to identify catchment types that are likely to be prone to low-flow conditions. In the USA, Reidy Liermann et al. (2012) developed a system of classification of rivers with relevance for the Pacific Northwest. Using a Bayesian mixture model they identified seven major classes of flow, a critical first step for setting flow requirements in the region. At a broader scale, Poff (1996) used the hydrological characteristics of relatively undisturbed rivers across continental USA to derive a river classification scheme that reflected patterns of flow variability among rivers. Attempts at a comparable hydromorphological assessment of European rivers have been less comprehensive (e.g. Raven et al., 2002; Downs and Gregory, 2014), though the EU Water Framework Directive now requires a status assessment of all water bodies.

Geomorphology

River flow patterns are dependent on the nature of the catchment through which they flow, which in turn is dictated by the underlying geology and topography and ultimately rainfall, the primary determinant of flow patterns (Helliwell et al., 2007). However, despite having similar controls, in terms of hydrology and geomorphology, river flow patterns may still diverge (Schumm, 1985). In addition to pattern diversity, Schumm (1985) noted that rivers also exhibit variation in their stability and resistance to erosion stemming from differences in bank and bed material and hydrological regimes. Nevertheless, the same controls operate at all scales from catchment and whole river at the broadest scale, to river reach at the medium scale, through to small scale processes such as in-channel features and sediment structure (Schumm, 1985; Newson and Newson, 2000). Geomorphological processes define both channel form and the controls on channel form, which ultimately determine channel change (Environment Agency, 1998). The interaction of flow with geomorphology, lithology and valley form are important elements in determining the physical habitat experienced by the biota living within a river (Poff et al., 1997; Newson and Newson, 2000), in particular determining bed scour depth, water velocity and depth, and inter-gravel flow for spawning salmonids and their eggs (Boughton et al., 2009).

Natural constraints on river flow

The four main runoff components to river flow (channel precipitation, overland flow, interflow and groundwater flow) are controlled through variations in climatic and catchment factors and their interaction (Ward, 1974; Shaw, 1988; Briggs et al., 1997). These controls are generic in that they influence both high and low river flow through their differing temporal and spatial variation and the nature of the interactions (Figure 1). Low river flows are natural phenomena that are ultimately dependent on a lack of rainfall and limited groundwater inputs. The main processes that sustain river flows in dry weather are storage and discharge from within the catchment consisting of groundwater and subsurface flow, storage in wetlands, lakes or snowmelt (Smakhtin, 2001). Patterns of low flows are determined by temporal variation in the magnitude of low flows, its variability, flow depletion and duration, along with spatial variations due to the regional distribution of rainfall, channel morphology, drainage network and catchment altitude and topography (Shaw, 1988; Briggs et al., 1997; Smakthin, 2001). In general terms, rivers in catchments with permeable geologies have a greater capacity to sustain river flows than rivers in impermeable catchments.

The processes that determine low flow conditions are similar to those that determine flood flow conditions (Figure 1). Again, variation in meteorological and terrestrial components will influence flooding seasonality, frequency, duration and intensity (Ward, 1974; Briggs et al., 1997). Flooding tends to have a seasonal pattern, for example, in northern Britain the majority of flood events (>78%) occur in the winter period between October to March, though they have been recorded at all times of year (Black and Werrity, 1997). Although flooding can be seasonal, flood conditions can also occur unpredictably and develop more quickly than low flow conditions, so can be seen as exerting greater influence on riverine communities (Junk et al., 1989; Poff et al., 1997).

Anthropogenic effects on river flow

Globally there are few riverine systems whose flow regime is unaffected by human activities (Ward, 1974; Petts, 1984; Sala et al., 2000). A range of human activities is capable of affecting rivers both through direct alteration of river channel habitats or through changes to hydrological and geomorphological processes, which ultimately alter river flow regimes (Poff and Allen, 1995). Dams and other hydraulic structures, agricultural and forestry practices, urbanization and water abstraction have the potential to alter river flow regimes and impact on river biota, including salmonid populations.

Water abstraction and impoundments

Impoundments and abstractions can lead to reduced annual and seasonal flow volumes. Groundwater abstractions can reduce the baseflow of rivers that depend upon this component of runoff to sustain flows during periods of low rainfall (Strevens, 1999; Weber and Perry, 2006). Additionally, headwater streams in high baseflow catchments can dry up, or their sources migrate downstream, thereby reducing habitat availability for fish and other organisms. The reduction of groundwater flow into rivers can also lead to thermal impacts on biota (Caissie, 2006). Salmonids have relatively exacting thermal requirements (Elliott, 1995; Wootton, 1998), with impacts on survival, growth, movement, migration and emergence (Caissie, 2006). In chalk streams in the southern UK, the reduction of relatively cool groundwater is recognized as a potential limiting factor for the survival of salmonids, especially when air and water temperatures are elevated (Solomon and Lightfoot, 2008). Similarly, rainbow trout (*Oncorhynchus mykiss*) in streams in Oregon, USA were dependent on cold water refugia created by upwelling groundwater to persist in warmer stream reaches (Ebersole et al., 2001).

Surface water abstraction can also reduce flow over a range of scales, from annual to daily, especially where large public water supply intakes are in operation. Large water intakes or diversions can disrupt the attractant flow for salmonids during downstream migration, leading to the entrapment of individuals and removal of significant numbers from the spawning population (Solomon, 1992; Aprahamian and Jones, 1997; Turnpenny et al., 1998). Other surface water intakes, for practices such as fish farming and watercress cultivation, tend not to affect the overall water resource budget as they return nearly all the water they use, though they can create river reaches that are depleted of flow and thus present habitat loss and potential barriers to migration for fish (Jones, 1990; Casey and Smith, 1994; Kelly and Karpinski, 1994). Fish farms can also degrade water quality and introduce pathogens to wild fish (Crisp, 1993). Reservoir operations can modify extensively the flow regime of rivers downstream, tending to reduce flow variability and aspects of the flow regime that play a role at specific life history stages (Gustard et al., 1987; Magilligan and Nislow, 2001; Pavlov et al., 2008). For example, flows that would normally transport fine sediment downstream, helping maintain hydromorphological conditions for biota, can be removed resulting in reduced sedimentation of river reaches below the dam. An outcome is coarsening of the substrate, termed 'bed armoring', which limits habitat availability, as well as increasing the risk of 'downcut' or channel erosion (Poff et al., 1997; Pulg et al., 2013; Osmundson et al., 2002). Natural low flow conditions can also be elevated by reservoir compensation flows, which may have been set without any ecological basis (Gustard et al., 1987; Acreman and Dunbar, 2004). Low flows may be needed during the period of emergence of larval salmonids to prevent washout and promote growth (Humphries and Lake, 2000).

Hydropeaking

Flow regulation and management for activities such as hydropower present fish downstream of the point of water release with a strikingly unnatural environment in terms of flow regime. The rapid increase in flows from dam releases (hydropeaking) are non-seasonal, frequent, of high magnitude and have varied duration (Lucas and Baras, 2001). Water released from dams may be at a lower or higher temperature than the river into which they are released. In some cases released water may be depleted in oxygen, in other cases supersaturated (Lucas and Baras, 2001).

The impact of hydropeaking may vary among species and river types. Scruton et al. (2003) detected species-specific behavioral responses in salmonids. Atlantic salmon (*Salmo salar)* showed two distinct patterns during hydropeaking trials, fish either showed high site fidelity or moved substantial distances in response to water releases. In contrast, brook trout (*Salvelinus fontinalis*) moved more in relation to releases than to stable flows and also moved more at night in both stable and dynamic flow conditions. Valdez et al. (2001) investigated the effects of dam releases on the Colorado River and found little effect on the distribution, abundance or movement of native fish, proposing that the magnitude and duration of releases were insufficient to displace populations on this river. Hydropeaking has also been associated with strandings, with sudden reductions in flow leaving fish isolated in pools or on exposed substrate (Saltveit et al., 2001; Irvine et al., 2009).

Flood risk management

Mitigating flood risk is a major, though not exclusive, source of river engineering works (Smith and Winkley, 1996; Petts, 2009). Flood risk measures typically involve the straightening and resectioning of river channels to increase conveyance, and gravel removal to lower the riverbed and thereby increase channel capacity (Purseglove, 1988). Impediments to flow are also removed. Thus, boulders and woody debris are removed from the river channel, and riparian vegetation is cut back or removed altogether (Brookes et al., 1983; Harmon et al., 1986). Channelization and river clearance generate structurally simple and hydraulically efficient river channels that facilitate the rapid clearance of water from the floodplain (Brookes, 1985; Hodgson and O'Hara, 1994). These measures have the effect of intensifying the impact of high flows (Poff et al., 1997; Petts, 2009). In addition, the loss of structural complexity and refuge habitats through river modification serve to exacerbate the impact of high flows on fish. Loss of connectivity with the floodplain in particular has the effect of impeding access to low flow conditions, which may be critical spawning habitat or for early life stages (Junk et al., 1989; Poff et al., 1997). The overall impact of flood mitigation activities also tends to alter the ecological function of a river, and thereby fish populations (FAO, 1984; Poff et al., 1997; Pretty et al., 2003).

Land use

Riparian land use can influence river flow, primarily through modifying rates of runoff and introducing sediment. A study by Allan et al. (1997) demonstrated that while catchment level patterns of land use predicted runoff and sediment input, local scale land use was uncorrelated. Scale effects of land use have prompted a 'riverscape' approach to management, particularly of salmonids, but also of other fish taxa (Fausch et al., 2002). This approach recognizes that different physical processes that control river flow operate at different spatial scales (Figure 2).

Direct effects of flow on fish

River flow, either high or low, may have an impact on fish directly and may be felt differently at different life-stages (Nislow and Armstrong, 2012). Seasonally high flows and flooding are a dynamic but natural aspect of the character of a river's flow regime and play a critical role in determining the ecological integrity and biological productivity of rivers (Junk et al., 1989; Poff et al., 1997). Periods of low river flow are also natural and often strongly seasonal phenomena that create conditions in the river channel strikingly different to those under high flows. The proportion of high velocity and associated high energy areas are dramatically reduced during periods of low flow, and water depth in these areas tends to be shallow; conditions likely to have an effect directly on the movements and activities of fish (Solomon and Sambrook, 2004; Wissmar and Craig, 2004; Tetzlaff et al., 2008).

Biotic adaptations to flow

River biota exhibit adaptations to the natural heterogeneity of river systems and many organisms show adaptive resilience to a wide range of flows for example through morphological adaptations (suckers, claws or other mechanisms for holding fast in high flow), reproductive strategies (releasing eggs at particular flow events) and tactics to escape in space and time (migrating to specific locations during particular flow periods) (Lehtinen and Layzer, 1988; Southwood, 1988; Townsend and Hildrew, 1994; Vogel, 1994). Flood events may also have the effect of limiting the establishment of invasive species that lack adaptations for high flow conditions (Valdez et al., 2001). A negative impact on fish assemblages may occur when human activity modifies the pattern of river flow so that it deviates from its natural range (Petts, 2009). Human activity can alter variation in flow such that the frequency and duration of flood and drought events may be prolonged. In other circumstances, such as downstream of reservoirs, they may be eliminated altogether.

Effects of high flows

Fish production and growth may be linked to the extent of accessible floodplain (Junk et al., 1989), and nutrient inputs to rivers can be facilitated by high flows flushing adjacent floodplains during periods of high water discharge, thereby enhancing fish productivity (Bowes et al., 2005). In some taxa, spawning is directly related to flood cycles, enhancing reproductive success by creating spawning habitat and nursery areas (Wootton and Smith, 2015). However, the type of river channel and its location within a catchment can determine how floods drive productivity and biotic interactions. Low order streams may experience short and unpredictable flood events, with fish and other aquatic organisms having limited adaptations for using the aquatic/terrestrial transitional zone. Conversely more natural channels or higher order streams have a more predictable and longer flood pulse, with aquatic organisms showing adaptive strategies for utilizing the 'aquatic-terrestrial transition zone' (Junk et al., 1989) (Figure 2). Highly modified channels often preclude access to the transition zone. Fish that occupy rivers with prolonged and predictable floods often show adaptations to exploit the presence of seasonal floods and exhibit life history strategies that maximize their reproductive fitness (Langler and Smith, 2001; Zeug and Winemiller, 2008). Nevertheless, the seasonal timing, magnitude, duration and frequency of flood events will have different effects on the key life stages of fishes (eggs, larvae, juveniles and adult) (Wolter and Sukhodolov, 2008; Poff and Zimmerman, 2010; Konečná et al., 2009), and these are considered separately.

Fish in the early life stages (unhatched egg, embryo and larvae) have a limited capacity actively to seek out preferred habitats and so depend upon drift to transport them to an optimum environment that maximizes their rate of growth and development, and survival (Wolter and Sukhodolov, 2008). However, the timing of drift and the magnitude of displacement will have different optima among species (Reichard and Jurajda, 2007; Pavlov et al., 2008). Unusually large and un-seasonal floods may be detrimental to fish populations by transporting early life stages downstream away from optimum habitat (termed 'washout') or outside the river channel altogether (Fausch et al., 2001; Wolter and Sukhodolov, 2008). Conversely, the absence of natural periodic floods may fail to redistribute early life stages leading to elevated densities and competition (Zitek et al., 2004; Reichard and Jurajda, 2007). In some cases flood events may enable early stages to reach floodplain refugia, such as ponds, lakes or ditch systems necessary for them to complete development and/or avoid predation (Seddell et al., 1990; Tockner et al., 2000). In other cases flooding may enable young fishes to migrate down river and recruit to the adult population (Halls and Welcomme, 2004).

The early life stages of salmonids appear susceptible to major floods, despite a widespread view that their preferred river types are relatively high flow velocity environments compared with other freshwater fishes (Sukhodolov et al., 2009). During reproduction their eggs are deposited at an optimum depth in river gravels to minimize the risk of wash out, but sufficiently shallow to ensure adequate oxygenation for egg development and permit larval emergence (Crisp, 1989; Crisp and Carling, 1989). However, extreme floods that mobilize the substrate can damage eggs (Jensen and Johnsen, 1999), although such floods are relatively rare events. The impact of more regular spates are largely mitigated by the depth of egg deposition (Crisp, 1989) and composition and stability of spawning sites, termed 'redds' (Beard and Carline, 1991). Nevertheless, a degree of high flow is needed to promote flushing of fine sediment from gravels to maximize oxygen supply to eggs and embryos (O'Connor and Andrew, 1998; Jensen and Johnson, 1999; Levasseur et al., 2006), although if sediment input exceeds the transport and flushing capability of the river then gravel siltation is inevitable (O'Connor and Andrew, 1998). In addition to oxygen stress on eggs, fine sediment has the capability to entomb embryos and prevent emergence (O'Connor and Andrew, 1998; Jensen and Johnson, 1999). The emergence phase is seen as a critical one, with strong density-dependent mortality at this stage, but density independent factors, such as flooding, can also increase mortality substantially (Elliott, 2006). An adaptation to compensate for the negative effect of floods is that emergence is timed to coincide with a low probability of flooding (Fausch et al., 2001; Elliott, 2006; Lobon-Cervia, 2009). Experimental studies have shown that newly emerged salmonids are most sensitive to wash out, though their susceptibility declines over time, corresponding with an increase in body size and swimming ability (Heggenes and Traaen, 1988).

Post-larval juveniles and adults possess an enhanced capacity to navigate their way to preferred habitats, and to seek out refuges during peak flows (Wolter and Sukhodolov, 2008). This capacity suggests that the impact of flooding is likely to be felt less strongly at these stages, though the duration and magnitude of flooding will determine the impact, with unseasonal and exceptionally high flood events expected to have greatest impact. Jurajda et al. (2006) detected only minor effects on a cyprinid fish assemblage, and no significant change in fish density, in a tributary of the River Danube, immediately before and after exceptional summer floods during which river discharge peaked at 2000% of the long-term mean. Similarly, the displacement of barbel (*Barbus barbus*) by high summer flows in a UK river was followed by the fish homing back upstream to their former resident areas (Lucas, 2000). Notably, autumn displacement was more frequent and homing less frequent, suggesting a seasonal element to the effects of displacement (Lucas, 2000).

However, in some cases severe flood events have the potential drastically to reduce fish populations and increase the risk of local extinction. Sato (2009) measured dramatic declines (*c*. 98%) in a population of Japanese whitespotted char (S*alvelinus leucomaenis*) inhabiting mountain streams following a severe flood, with no sign of recovery two years after the event. In this case, flood flows were so severe that bank-side debris were mobilized, which had the impact of largely eliminating fish at a local scale and significantly changing the structure of the environment. This study highlights how isolated fish populations in lower order upland streams may be at greater risk of extinction from catastrophic flood events because fish are unable to move readily out of the main river channel in the way they often can in unregulated lowland rivers, and goes some way to supporting the flood-pulse concept (Junk et al., 1989). The flood-pulse concept posits that rivers and their floodplains comprise a single ecological and hydrological system with correlated responses to pulses in river discharge. Observations on stream-living marble trout (*Salmo marmoratus*) populations have revealed reductions of between 31% and 78% following severe flood events prior to spawning, but without long-term consequences to the population. The quick recovery of populations was possible because of a high intrinsic rate of population increase for this species, allowing the small number of reproductive individuals that survived a severe flood to successfully re-establish local populations (Vincenzi et al., 2008). Studies suggest that salmonid reproductive strategies show compensatory responses for dealing with extreme flows, at least within certain limits, which buffer effects at the population level.

Effects of low flows

In low flow conditions the overall volume of water in the river is substantially decreased, with a concomitant reduction in average depth and width of the river channel, which in turn will result in a net reduction in available habitat. This situation may present fish with the problem of obtaining access to preferred habitats for feeding, and the risk of oxygen stress.

When flow falls to the point that the risk of stranding or isolation become a serious threat fish rely on refugia habitat for survival until flow conditions improve. Refugia include areas of deeper water (Huntingford et al., 1999; Armstrong et al., 2003), which may include disconnected pools (Labbe and Fausch, 2000; Magoulick and Kobza, 2003). Davey and Kelly (2007) found refugia to be critical in enabling brown trout (*Salmo trutta*) to persist in a river with naturally intermittent flow in its middle reaches. They showed that brown trout (and other species) moved upstream as the stream dried, with sections subject to drying only slowly recolonized. Rates of colonization correlated negatively with increasing distance to refugia and the fish assemblage in sections susceptible to drying were quantitatively and qualitatively different to neighboring reaches. Davey and Kelly's (2007) findings suggest that river systems can exhibit similar ecological processes predicted from island biogeography theory (MacArthur and Wilson, 1967), with habitat colonization rates negatively correlated with distance from the source of colonizers. From an applied viewpoint this finding has implications for the way habitat quality and its connectivity along river corridors should be viewed and managed.

Intermittent rivers, those that only flow for some part of the year, are potentially important habitat for juvenile salmonids. In the western USA, intermittent rivers comprise over 65% of total river length and are a source of both spawning and nursery habitat. In a study of coho salmon (*Oncorhynchus kisutch*), Wigington et al. (2006) showed intermittent rivers to be key sites for the production of smolts, with juveniles able to persist in isolated pools between periods when river flow ceased.

In the case of predictable seasonal reductions in flow, fish may show adaptations that enable them to respond to the changed conditions, including dispersal (Pires et al., 1999). However, in many cases dispersal may be limited if there is too little water due to channel constriction (Crisp, 1989; Armstrong et al., 2003). Under the most extreme low flow conditions a river may comprise nothing more than a series of isolated pools. However, even if the river continues to flow as a discrete water body, the appearance of barriers such as gravel banks and boulders, that would be otherwise submerged, may impede fish movement.

A consequence of reduced low flows, then, will be elevated fish density, particularly if fish are unable to redistribute themselves. At high density fish may face a greater risk of hypoxia and possibly predation, including cannibalism (Smith and Reay, 1991). In addition, a number of population processes are density dependent. Thus, feeding and growth may be limited, while mortality rates would tend to increase. The transmission of pathogens is often strongly contingent on host density, especially if transmission is direct. In species that show territoriality or dominance hierarchies, which is frequently the case in salmonids, injuries and mortalities associated with aggression may also increase. The negative effects of low flow will depend on the extent of flow limitation, and also the period over which low flows occur. Elliott et al. (1997) noted that a juvenile year class of brown trout subjected to successive drought periods had lower growth rates and increased mortality, which was strongly linked to reduced densities of returning females. Summer droughts may not affect survival as much as low rainfall in spring and summer, or in summer and autumn, when low stream flows can be prolonged. The effects of low flow may also interact with other variables, notably temperature. Solomon and Lightfoot (2010) found correlations between poor salmon stock performance and reduced August flows, possibly linked to temperature effects on spawning migration. High water temperatures will exacerbate hypoxic effects resulting from low flow (Milner et al., 2003), while low winter flows may increase the risk of fish kills from freezing (Huusko et al., 2007). Notably Sabaton et al. (2008) demonstrated increases in the abundance of adult and juvenile brown trout when flows were restored to streams. Although increases in flow were not large, weighted usable area; i.e. available physical habitat, increased substantially in some rivers, suggesting that the impacts of low flow, and attempts to restore flow to rivers, are likely to be highly variable among rivers.

The negative impacts of low flow on fish may be especially damaging at the population level if they occur during periods of reproduction. Young stages have a limited capacity to avoid stranding, hypoxia or withstand periods of restricted ration (Wootton, 1998). However, the hyporheic zone may be utilized by the eggs and larvae of some species, and may not be unduly affected by low flows (Baxter and Hauer, 2000), but the risk to salmonids from egg desiccation can be considerable (Crisp et al., 1984; Milner et al., 2003). Furthermore, droughts have been identified as a main cause of severe reductions in the number of YoY salmonids with impacts on population size (Bell et al., 2000; Lobon-Cervia, 2009). These studies also demonstrate the resilience of populations where suitable in-channel habitat exists.

Effects of variable flow

While low and high flow rates can have an impact on salmonids, especially if these are of unusual magnitude or are unseasonal, another little understood impact is through increased variability in flow. Evidence from rivers subjected to pulsed water releases associated with hydropower generation (termed 'hydropeaking', see above) suggest that highly variable flows have negative effects on salmonids, especially on young stages. For example, Freeman et al. (2001) showed that high flow variability had a negative effect on juvenile fish by undermining habitat persistence. In a study of stream fish assemblages, Poff and Allan (1995) showed that the effect of a high coefficient of variation of flows generated fish communities distinct from those with low flow variation.

Even modest changes in flow can alter the behavior of territorial juvenile salmonids quite substantially. Juvenile salmonids usually rest on the substrate facing upstream under low flow conditions at a specific 'station'. From this point they collect food items that drift along the riverbed or in the water column and engage in aggressive behavior with neighboring territory holders (Jonsson and Jonsson, 2011). As flow increases they leave the substrate and swim more frequently in the water column. Here they can see and encounter neighbors more frequently, with a result that territory size increases, with a concomitant reduction in fish density (Kalleberg, 1958; Keenleyside, 1962).

In contrast, Heggenes et al. (2007) observed no difference in the home range size of brown trout (*S. trutta*) between channelized and natural river sections, and no consistent effects of abrupt changes in flow. The direct effects of flow on fish probably depend on local hydrological conditions, with optimal flows likely to be different in different sections of a catchment. Rosenfeld et al. (2007) proposed that habitat suitability for rainbow trout (*O. mykiss*) based on hydraulic geometry changed longitudinally along a river. Thus, optimal conditions for juvenile stages were predicted for smaller upstream sections, while those for larger fish were found downstream. These predicted patterns matched empirical data. A summary of stage-specific responses to flow variability is presented in Table 1.

Indirect effects of flow on fish

River morphology

River and water resource management tends to focus solely on the direct impacts of flow (Petts, 2009). However, flow is often simply a surrogate for a more complex interaction between channel morphology, water depth and flow that underpins the availability of habitat for river biota (Brooker and Graynoth, 2008). Changes to river flow regime can result in changes to both habitat quantity and quality at a range of scales. Because fish migrate among different 'meso' and 'micro' scale habitats there is potential for effects of flow at the population level (Pavlov et al., 2008). Consequently, an understanding of the role of river morphology during different salmonid life stages is important if flow effects are to be understood. Experimental addition and removal of boulders in the Little Southwest Miramichi River by Dolinsek et al. (2007) showed that the presence of boulders significantly increased juvenile Atlantic salmon (*S. salar*) density, though not of non-salmonid species. The presence of coarse woody debris has also been shown to have a positive effect on juvenile salmonids, primarily by diversifying flow conditions and thereby enhancing feeding opportunities and providing refuges from high flow conditions (Harmon et al., 1986; Roni et al., 2008; Hafs et al., 2014).

Temperature

The energy budgets of fish are driven strongly by water temperature (Rankin and Jensen, 1993; Wootton, 1998), which is negatively correlated with flow rate (e.g. Webb et al., 2003). Therefore there are potential consequences of reduced or enhanced flow rates for fish bioenergetics, and ultimately on the survival of certain life stages indirectly through their effect on water temperature (Wootton, 1998). Water temperature also plays a major role in controlling the upstream migration of some salmonids (Quinn et al., 2007; Moore et al., 2012).

Sediment

The rate of transport of sediment is a function of flow, with the greatest volumes of material transported during flood events (Walling and Webb, 1992; Kondolf, 1997; Lenzi and Marchi, 2000). Land management activities, particularly agriculture but also forestry, mining, road construction, effluent discharge, and urban sources, can all result in elevated sediment inputs to watersheds (Henley et al., 2000; Walling and Webb, 1992). Sediment inputs are not wholly rainfall dependent, and so can occur when their impact may be most ecologically damaging (Marks and Rutt, 1997), though rainfall will ultimately determine the rate and volume of sediment transport into and along the river channel. Catchment and river type can also influence sediment transport and deposition processes (Lenzi and Marchi, 2000).

Increased sedimentation and turbidity leads to decreased primary production that can cascade through trophic levels (Osmundson et al., 2002). The avoidance of turbid waters has been observed in juvenile coho salmon *O. kisutch,* arctic grayling *Thymallus arcticus*, and rainbow trout *O. mykiss* (Newcombe and Jensen, 1996). The negative effects of suspended particles have been observed on juvenile and adult stages in fishes through gill damage (Berg and Northcote, 1985), and reduced feeding rates (Waters, 1995; Argent and Flebbe, 1999). Perhaps, the biggest impact on salmonid production, though, is likely to come from sedimentation affecting oxygen supply and uptake by eggs (see below). A meta-analysis of the impact of sediment on egg to juvenile survival in four species of Pacific salmon by Jensen et al. (2009) showed coho salmon to be most vulnerable and chum salmon least susceptible, while Chinook salmon and migratory rainbow trout showed intermediate sensitivity.

While the transport of large amounts of sediment resulting in fine sediment intrusion is associated with moderate to high flows (Wood and Armitage, 1997), low winter flows at times of low rainfall and icy conditions, can also result in the infiltration of sediment into spawning redds (Levasseur et al., 2006). A consequence is that natural sediment inputs that occur during high flow events can result in less severe ecological effects than at times of low flow (Marks and Rutt, 1997). Hence although periods of high rainfall increase the input of sediment to a river, the effects can be partly be mitigated by dilution and mobilization of sediment under high flow conditions while, counterintuitively, low flow conditions can result in siltation of the river channel (Wood and Armitage, 1997).

Dams have the effect of removing all but the finest suspended sediment, resulting in sediment-depleted water. A common outcome is increased coarsening or 'armoring' of the riverbed, which can limit habitat availability for aquatic invertebrates on which juvenile salmonids feed. Loss of coarse sediment also creates a riverbed that may be unsuitable for spawning by adults (Poff et al., 1997).

Oxygen

Well-oxygenated water is important for all salmonid life stages (Armstrong et al., 2003; Hendry et al., 2003). Oxygen availability is especially important during egg development, since at this life stage the fish are unable to show a behavioral response to low levels of dissolved oxygen. Fine sediments have multiple impacts on the supply of oxygenated water to developing salmonid eggs and alevins (Crisp, 1996; Grieg et al, 2005a). Fine sediments can limit interstitial flow velocities, while organic sediment has the effect of depleting dissolved oxygen levels (O'Connor and Andrew, 1998; Acornley and Sear, 1999; Grieg et al, 2005a). Clay particles create low permeability seals on the surface of salmonid eggs, greatly reducing rates of oxygen consumption (Grieg et al, 2005b).

Dissolved oxygen concentration and water flow are often correlated, and the relationship between flow and dissolved oxygen availability often confounds links between flow and other variables (Downes, 2010). Low summer flows and elevated temperatures in rivers are associated with reductions in dissolved oxygen concentration. These effects occur through reduced oxygen solubility and an elevation in oxygen consuming processes at higher temperatures. At low flow rates water turbulence is also reduced, which limits re-aeration of oxygen-depleted water. Fish growth and activity increase with a rise in temperature to an optimum, at which point they become increasingly constrained by oxygen availability (Jonsson and Jonsson, 2009). Reduced oxygen levels can also lead to greater susceptibility to disease (Johnson et al., 2009), and to a reduction in migration into freshwater by salmonids (Solomon and Sambrook, 2004).

Pollutants, nutrients, BOD

Water quality can be a limiting variable for salmonid population productivity. Efforts to rehabilitate rivers for salmonids and other fishes may not be fully realized if water quality is limiting (Ormerod, 2003). River flow exerts an effect on water chemistry through a dilution effect (Webb and Walling, 1992). High flow rates may also mitigate the anoxic effects of organic pollutants. Reduced flow conditions tend to exacerbate the impacts of pollutants (Smakhtin, 2001), which can be further aggravated at elevated water temperatures when pollutants tend to have greater toxicity (Alabaster and Lloyd, 1982; Mason, 2002). Episodic pollution events without adequate dilution, during periods of limited flow, have the greatest impact and can lead to ecosystem degradation (McCahon and Pascoe, 1990).

Aquatic and riparian vegetation

Indirect impacts of river flow on salmonids can come through effects on other components of the river community, particularly instream and riparian vegetation. Instream, but particularly riparian tree cover, is important in providing shade and thereby plays a role in water temperature regulation (Eklöv et al., 1999). Vegetation can additionally enhance the production of macroinvertebrates (Robinson at al., 2002; Gowan and Fausch, 2002), an important food supply for salmonids that can determine their local distribution

(Kawaguchi and Nakano, 2001). Coarse woody debris is recognized as an important component of habitat structure. It functions by regulating sediment transport, effects debris and sediment accumulation, and dissipates energy by impeding flow and providing refuges for fish and invertebrates (Van Kirk and Benjamin, 2001).

Productivity and bioenergetics

Rate and variance of river flow can influence rate of food delivery to salmonids, primarily in the form of drifting invertebrates that are of either terrestrial or aquatic origin (Kawaguchi and Nakano, 2001). The energetic costs of holding station in a river to feed influences fish energy expenditure, as does water temperature, thus the impact of flow can influence salmonids through the structure and balance of their energy budgets. Field studies with salmonids have shown that those in fast currents attain higher food consumption rates than those in slower currents but experience lower growth rates through greater energy expenditure (Tucker and Rasmussen, 1999).

Managing river flow

Directly or indirectly river flow can influence different aspects of salmonid life cycles, as well as being important to other river biota. Other reviewers have viewed the evidence base as inconsistent, with scientific testing lacking (Milner et al., 2011), and to a degree this is true. Nevertheless, the current review provides sufficient evidence to implicate river flow as an appropriate variable for ecologically-based river management and restoration, though this approach has rarely been used in practice. Traditionally, river flow management has been the realm of hydrologists and river engineers principally concerned with reducing flood risk while improving, or at least maintaining, water supply infrastructure (Shaw, 1988; Newson 1994). However there has been growing recognition of the importance of setting environmental flows, with over 250 different procedures now employed in at least 20 countries (Dunbar et al., 2012).

How are environmental flows established?

The reviews of Acreman and Dunbar (2004) and Dunbar et al. (2012) summarized the different methods for establishing environmental flows into four main categories; look-up tables, desktop analysis, functional analysis, and hydraulic-habitat modeling (Table 3). These approaches encompass a wide range of scales and situations (Table 3), and both reviews concluded that these approaches should not be viewed in isolation, but should form part of a framework (and continuum of methods) where the application of a methodology is determined by factors such as cost, time, perceived environmental risk, availability of expertise, and scale of assessment (whole system through to single site or species). There is a tendency in setting environmental flows to select some aspect of the natural flow regime, for example mean flow or low flow, as a reference point (Richter et al., 1997, 1998, 2003; Poff et al., 2010). However, little reference is made to the ecological conditions associated with natural flows, possibly due to the confounding effects of other environmental pressures (Bunn and Arthington, 2002; Dunbar et al., 2012), and because few river systems worldwide are unaffected by human activity in some way (Richter et al., 1997; Lytle and Poff, 2004; Welcomme, 2008), which limits the opportunity for identifying the relationship between natural flow conditions and river ecology. Reference condition models, particularly the River Invertebrate Prediction and Classification System (RIVPACS) for macroinvertebrates, go some way to helping establish a reference community (Wright et al., 1998). However, the adequacy of such models within environmental flow setting is questionable where measured at-site variables (river depth, wetted width and substrate composition) are used for biological prediction, as these variables are likely to naturally vary in response to flow (Harrison et al., 2004). Where alternative variables can be used adequately, this may offer some opportunity to develop similar predictive models for fish communities. In the case of salmonids, and perhaps other river ecosystem components, returning to the natural flow regime may be not always be beneficial, especially in rivers where releases from reservoirs have altered flow significantly and populations appear to be benefitting (Milner et al., 2011). Thus, unnatural flow conditions can be envisaged, such as enhanced summer flows, that might significantly enhance survival and growth at critical periods that might otherwise limit population size or productivity (Nislow and Armstrong, 2012). A further consideration is the impact of a salmonid population that has been 'enhanced' through flow management on ecosystem function. Impacts are potentially detrimental, for example through elevated rates of predation, or might be relatively benign. In the case of lowland rivers in the UK, the majority of which have been highly modified (Brookes, 1988), the concept of what 'natural' means in the context of river flow regime is equivocal. Elsewhere, natural flow regimes may be less ambiguous (Pettit et al., 2001; Lytle and Poff, 2004; Propst and Gido, 2004). In situations where natural flow regime may be difficult to define, flow management might be targeted specifically at generating a temporal pattern of flow to create the conditions that maximize salmonid production. The challenge in this case is to identify what those flow conditions are.

Habitat management and restoration

It is widely acknowledged that a range of pressures affect riverine ecosystems, but there is also a view that given these pressures, it is habitat quality that limits ecosystem function (Ward et al., 2001; Giller, 2005). This view has led to efforts aimed at restoring or rehabilitating river habitat, and as a practice has gained in popularity in river and catchment management over several decades (Holmes, 1998; Ormerod, 2003; Palmer et al., 2005). The underlying principles employed takes account of the interaction between habitat and river flow by focusing on establishing site or reach scale in-channel features to create hydraulic complexity as guided by geomorphological processes (Kemp et al., 2000; Pretty et al., 2003; Harrison et al., 2004; Newson and Large, 2006; see Roni et al., 2008 for comprehensive review).

A common in-channel approach to targeting salmonid populations is to focus on the availability and quality of spawning gravels to ensure recruitment conditions are optimal. Spawning habitat rehabilitation is a widely used tool in European rivers in (Brown and Pasternack, 2009; Pederson et al., 2009; Vehanen et al., 2010). In North America, while the introduction of gravel in sediment-starved river systems has proven beneficial (Merz et al., 2004, 2005), the practice is not common (Roni et al., 2008). Whilst focusing on ensuring reproductive success makes some sense, efforts in this direction appear to have met with mixed or, in some cases, limited success. Pulg et al. (2013) examined the provision of gravel and its regular cleaning as a mechanism for restoring brown trout populations in regulated rivers. The positive effects appeared to be short-lived, which suggests that the maintenance of an appropriate flow regime to replenish spawning gravels and keep them free of fine sediment is a more sustainable approach. Salmonid spawning habitat is highly dependent upon the delivery of suitable spawning material from upstream to downstream reaches, and the use of hydraulic models may help determine the discharge required to renew the spawning substrate (Hauer et al., 2011). On balance, simply implementing a minimum flow regime alone as part of attempts at management or restoration is unlikely to rehabilitate salmonid spawning habitat, since the geomorphological processes needed to generate the desired physical habitat could be missing (Brown and Pasternack, 2008). In certain situations specific habitat types may be more critical than flow regime. Sukhodolov et al. (2009) showed that braided channels in alpine streams provide refugia for larval and juvenile fish during floods. However, many alpine rivers have lost their braided structure, so restoration of this habitat feature in this instance may represent the priority.

Other categories of river rehabilitation can address riparian rehabilitation, floodplain connectivity, road improvement, and nutrient enrichment (reviewed by Roni et al., 2008). Understanding the ecological benefits of rehabilitation works is important to guiding on-going river habitat management, and poor monitoring programs can be a handicap (Holmes, 1998; Hendry et al., 2003; Giller, 2005). Pederson et al. (2009) advocated an evaluation of gravel re-introduction for salmonids in Danish streams that acknowledged differences in habitat quality among reaches within a river system. To understand habitat quality in a quantitative manner requires a comprehensive monitoring design (Jähnig et al., 2009). One approach is the use of a Before/After, Control/Impact (BACI) design, but even this approach is not without limitations. For instance, it is a common feature of natural systems for populations at two sites to diverge or converge through time, even without an effect resulting from activities at the 'impact' site (Underwood, 1991). Vehanen et al. (2010) used the BACI approach three years prior and post restoration with an unmodified control. Streambed complexity increased, but no effects on brown trout stocks in rehabilitated areas were detected. Moreover 2+ and older age classes decreased in abundance. A severe drought after the scheme reduced densities of trout to a low level in all streams, overriding any beneficial local effects of rehabilitation. This finding suggests that large-scale regional factors may overwhelm local management efforts, and although suitable habitat exists, flow stress can severely limit restoration efforts.

River restoration is essentially based on a premise that if habitat conditions are suitable, the biota will respond positively, an approach termed the 'Field of Dreams hypothesis'; “if you build it, they will come.” (Palmer et al., 1997). Despite its obvious weaknesses, this approach is often advocated on the basis that a lack of knowledge in quantifying biological processes should not be a barrier to action. A more rational approach, what has been termed 'process-based restoration aims' (Beechie et al., 2010), is to employ habitat restoration and rehabilitation measures alongside the activities of ecologists that have both field and quantitative skills to design restoration measures, implement monitoring protocols and, what has hitherto been a significant omission, to devise appropriate statistical analyses to demonstrate ecological benefits.

What data and information would benefit environmental flow management?

A wide range of approaches to environmental flow setting exist worldwide, supported in part by research and expert opinion (Acreman et al., 2005; Roni et al., 2008; Dunbar et al., 2012; Milner et al., 2012). In the UK, attempts have been made to set environmental standards to meet the EU WFD by defining water abstraction limits to protect river systems and appropriate flow releases from reservoirs. These were established using a combination of site-specific data, expert opinion and stakeholder groups (Acreman and Ferguson, 2010). Many empirical studies worldwide have been conducted at a site-specific level, which provides useful detailed information but for only one or a few sites, so their transferability to unknown sites, or to a catchment scale is questionable (Petts, 2009; Acreman and Ferguson, 2010). Nevertheless widely applicable and generalized models are emerging. For example, Booker and Acreman (2007) analyzed data from 63 PHABSIM studies and found strong relationships between single measures of channel form and river hydraulics and the availability of habitat for target species. Estimates of physical habitat sensitivity to flow change from single measures were comparable with full PHABSIM predictions, albeit with greater uncertainty, though some ambiguity may be acceptable in a more risk-based flow setting framework. The modeling approach by Dunbar et al. (2010a,b) has also shown a generic biological response to flow change. A macroinvertebrate community index responded positively to low and high flow and interacted significantly with river channel modification whereby less modified sites had overall higher biotic index scores and appeared to be more resilient to flow reduction. This finding has implications for flow management and restoration by indicating the likely direction of ecological change in response to flow and habitat alteration. The value of this approach is that it can be applied to a range of sites where little or no biological data exist. Notably the models of Dunbar et al. (2010a,b) utilized existing river flow, river habitat and macroinvertebrate data, obtained from a well-established monitoring network of the Environment Agency. This approach tallies with the view of Petts (2009) who proposed that models that incorporate long-term data sets are needed so that population level responses can be predicted.

A potential impediment to translating research results into flow management and restoration measures may be because appropriate expertise is fragmented across the disciplines of ecology, hydrology, geomorphology and civil engineering (Vaughan et al., 2009). An understanding of each field is needed to fully interpret results in order to make sound management decisions; a minimum requirement is that the essential ecological and morphological responses are understood in order to select suitable flow management methods (Jowett, 1997), and move to ecologically sustainable water management (Richter et al., 2003). However, this situation is changing with the recognition of the potential role of hydraulic-habitat modeling (Dunbar et al., 2012).

Long-term datasets and monitoring

For the management of many ecological systems it is necessary to employ a long-term perspective. Despite the general acceptance of this view, the availability of long-term data to support management remains conspicuously limited (Bayley and Li, 1992; Jackson and Füreder, 2006). Many studies tend to be undertaken over a 3-year time-scale, chiefly a consequence of the typical length of research funding awards, but long time-series data are considerably more valuable and have substantially helped advance our understanding of the temporal patterns of abundance (Elliott, 1995; Magurran, 2011). Furthermore, analyses of long-term datasets are more likely to identify spatial and temporal trends that are key to decision-making, something that short-term studies often fail to detect (Poff et al., 2010; Reidy Liermann et al., 2012). Protocols for detecting ecosystem perturbations require comprehensive time-series data for a suite of key indicators (Richter et al., 1996). For example, long-term studies of freshwater macroinvertebrates have improved our understanding of their inter-annual variation and cycles, biotic and abiotic interactions, and the effects of disturbance and recovery (Jackson and Füreder, 2006). It is important to undertake similar studies of long-lived species, such as salmonids, in order to improve our ecological knowledge, develop suitable models (Elliott, 1995), and detect long-term effects of human impacts on salmonid productivity (Ugedal et al., 2008). In this regard the environmental regulation bodies are in a unique position to adopt such an approach, and for salmonids they should be able to make best use of existing information from national monitoring programs (Milner et al., 2011), including measures of water quality ideally integrated with management strategies (see Poole et al., 2004 for discussion). Additionally, long-term hydrological datasets are often available for rivers supporting salmonids, and these can provide a detailed history of hydrological change to be considered alongside salmonid and habitat assessment data.

The potential of large datasets has to be considered against the adequacy of monitoring, since current approaches to data collection may be insufficiently specific to permit the confounding effects of autocorrelation between variables to be discerned. This limitation can be overcome to a degree when carrying out hypothesis-led data analyses and model validation, whilst accepting that in some instances monitoring improvements will be needed to ensure they are statistically robust (Milner et al., 2011). However, alterations to monitoring schemes are often viewed unfavorably by organizations that perform these functions; they see it as expensive and potentially render all previous data collection redundant. For salmonids, a parallel approach to the analysis of long-term datasets is needed that uses site-specific studies based upon agreed monitoring protocols so that adequate meta-analyses can be performed (Milner et al., 2011).

Conclusions

The direct and indirect effects of river flow will affect different fish life-stages in distinct ways but responses appear to be highly variable and attempts to generalize among salmonid species and hydrological regimes has proven problematic. Where river flow has a significant impact on salmonid distribution and abundance, its effects may be imposed over an extended period or over a series of short, but possibly extreme, episodes. Despite these highly variable effects upon salmonid populations, and other river biota, many environmental organizations around the world base their management decisions using relatively simple river discharge values (Acreman et al., 2008). This approach is unsurprising since many have invested significant resources in establishing river flow measurement networks. Additionally, biological monitoring networks have been established, principally in isolation from flow measurement networks, and mainly as a response to industrial pollution and the need to manage water quality. Research to date has shown biological response to flow, but causal links are opaque, possibly due to the correlation between river flow and other environmental variables. Furthermore, other factors that relate to river habitat quality and extent cannot be overlooked. Therefore, although there are developments in continuous simulation models which mean that gauged flows are not always required, the adequacy of the current network of flow and biological monitoring, together with data analysis capability represent a potential bottleneck to rational management measures and attempts at river restoration for salmonids, and should be reviewed and amended were possible.

Given the current paucity of long-term datasets tailored to salmonid management and restoration, there is a need to consider the value of existing datasets. Analyses applied to large datasets for macrophytes and invertebrates have demonstrated a range of periodicities in responses to river flow (Dunbar et al., 2010a,b; Acreman and Dunbar, 2011). Furthermore, long-term reductions in flow regime have coincided with reductions in fish populations, though population cycles or trends unrelated to hydrology cannot always be excluded (Bayley and Li, 1992; Acreman and Dunbar, 2011). Empirical models, exploiting long-term data to reveal generalized relationships between flow, habitat quality and macroinvertebrate communities, have been developed which could potentially be applied to assessing river discharge regimes and informing future water resources management (Dunbar et al., 2010a,b), at least in UK rivers for which these data are available. For salmonids there is a pressing need to develop generalized models of flow and habitat requirements that are transferable between river systems (Milner et al., 2011) and, possibly, species. In order to improve our understanding, and further develop such models, there is a requirement for empirical testing; possibly via adaptive management studies with a common design to ensure subsequent meta-analyses are statistically robust.

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Figure captions

Figure 1. Identical process controls, but contrasting conditions, leading to either flood flow or low flow in rivers. Modified from Briggs et al. (1997).

Figure 2. Conceptual model of physical and biotic processes operating at different spatial scales that influence riverine biota within controls imposed by underlying geology/lithology and geomorphology. Modified from Labbe and Fausch (2000).

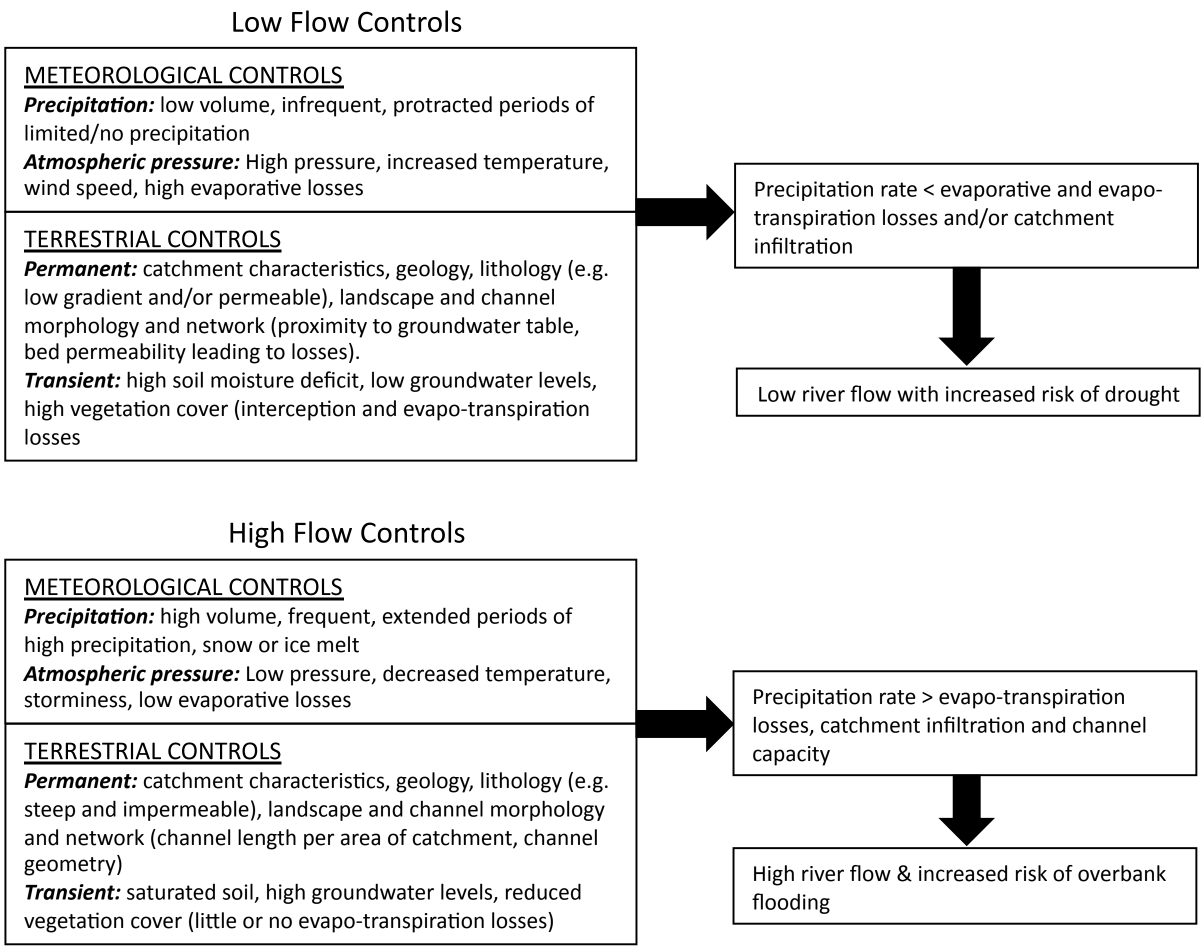
Low Flow Controls
METEOROLOGICAL CONTROLS
Precipitation: low volume, infrequent, protracted periods of limited/no precipitation
Atmospheric pressure: High pressure, increased temperature, wind speed, high evaporative losses
TERRESTRIAL CONTROLS
Permanent: catchment characteristics, geology, lithology (e.g. low gradient and/or permeable), landscape and channel morphology and network (proximity to groundwater table, bed permeability leading to losses).
Transient: high soil moisture deficit, low groundwater levels, high vegetation cover (interception and evapo-transpiration losses
Precipitation rate < evaporative and evapo-transpiration losses and/or catchment infiltration
Low river flow with increased risk of drought
High Flow Controls
METEOROLOGICAL CONTROLS
Precipitation: high volume, frequent, extended periods of high precipitation, snow or ice melt
Atmospheric pressure: Low pressure, decreased temperature, storminess, low evaporative losses
TERRESTRIAL CONTROLS
Permanent: catchment characteristics, geology, lithology (e.g. steep and impermeable), landscape and channel morphology and network (channel length per area of catchment, channel geometry)
Transient: saturated soil, high groundwater levels, reduced vegetation cover (little or no evapo-transpiration losses)
Precipitation rate > evapo-transpiration losses, catchment infiltration and channel capacity
High river flow & increased risk of overbank flooding

Fig. 1

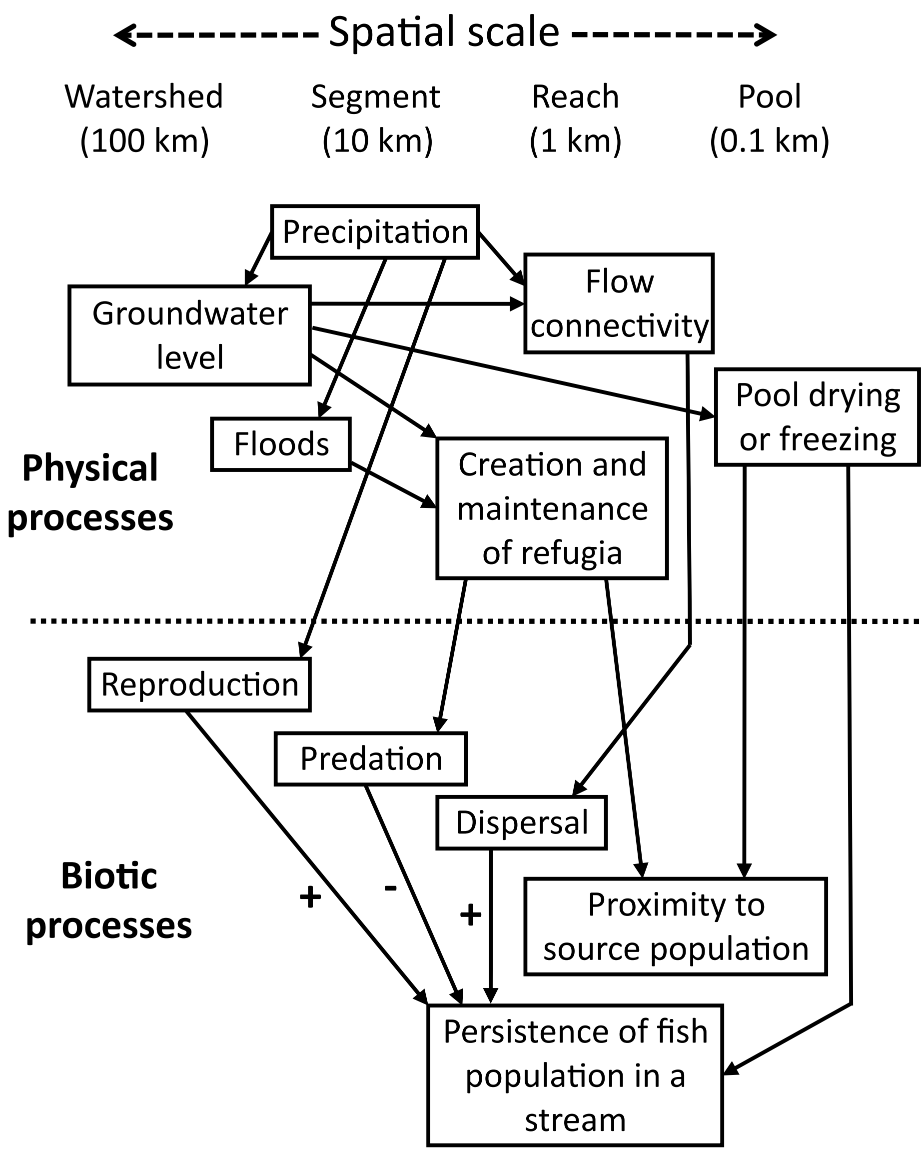
Spatial scale
Watershed (100 km)
Segment (10 km)
Reach (1 km)
Pool (0.1 km)
Precipitation
Groundwater level
Flow connectivity
Pool drying or freezing
Floods
Creation and maintenance of refugia
Physical processes
Reproduction
Predation
Dispersal
Proximity to source population
Biotic processes
+
-
+
Persistence of fish population in a stream

Fig. 2

Table 1. Life-stage specific impact of contrasting flow characteristics of salmonids among seasons (modified from Nislow and Armstrong, 2012) (NA = not applicable, ? = not known).

	Fry		Parr		Smolt	
Season	Low flow	High flow	Low flow	High flow	Low flow	High flow
Spring	Lower or higher survival	Lower survival	Reduced growth	?	Migratory delay and lower survival	Positive or negative depending on timing
Summer	Reduced growth	Reduced growth	Reduced growth	Increased shelter seeking	NA	NA
Autumn	NA	NA	Reduced growth	?	NA	NA
Winter	NA	NA	Positive or negligible effect on growth	Increased shelter seeking	NA	NA

Table 2. Effects of fine sediment on survival of embryonic stage of salmonids.

Sediment size/description	Effect	Reference
<0.063mm – 0.5mm Silts/clays – coarse sand	Reduced survival in egg stage	Julien and Bergeron (2006)
<0.125mm Silt and fine sand	>0.2% in redds leads to <50% embryo survival	Levasseur et al. (2006)
Clay sediment	Thin film on egg surface reduces oxygen exchange across membrane	Greig et al. (2005)
Fine sediment	>15% fine material in redds deleterious to survival	O'Connor and Andrew (1998)
0.43-0.85 mm	Reduced embryo survival with increased fine sediment. Emergent fry weight also reduced.	Argent and Flebbe (1999)

Table 3. Summary of environmental flow setting categories, example methods, scale of application, and type of situation employed. Adapted from Acreman and Dunbar (2004).

Method category	Example [Country]	Scale of application	Situation type
Look up table	Tennant (Montana) method [USA] Texas method [USA] Basque method [Spain]	Catchment	Scoping/planning
Desktop analysis	Range of Variability Approach (RVA) [USA & others] Resource Assessment and Management framework (RAM) [England and Wales]	Catchment/multiple or single sites	Planning/high level impact assessment
Functional analysis	Building Block Method (BBM) [South Africa and others] Expert Panel Assessment Method (EPAM) [Australia]	Multiple or single sites	Impact assessment
Hydraulic-habitat modeling	Instream Flow Incremental Method (IFIM)/ Physical Habitat Simulation (PHABSIM) [USA and others] Computer Aided Simulation model for Instream flow Requirements (CASIMIR) [Germany] River Simulation System (RSS) [Norway] Numerical habitat modeling (NHM) [Canada]	Multiple or single sites	Impact assessment River restoration (including flow regime)