



# The potential impacts of migratory difficulty, including warmer waters and altered flow conditions, on the reproductive success of salmonid fishes



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## ABSTRACT

Climate change and urbanisation of watercourses affect water temperatures and current flow velocities in river systems on a global scale. This represents a particularly critical issue for migratory fish species with complex life histories that use rivers to reproduce. Salmonids are migratory keystone species that provide substantial economic value to ecosystems and human societies. Consequently, a comprehensive understanding of the effects of environmental stressors on their reproductive success is critical in order to ensure their continued abundance during future climatic change. Salmonids are capital breeders, relying entirely on endogenous energy stores to fuel return migration to their natal spawning sites and reproduction upon arrival. Metabolic rates and cost of transport en-route increase with temperature and at extreme temperatures, swimming is increasingly fuelled anaerobically, resulting in an oxygen debt and reduced capacity to recover from exhaustive exercise. Thermally challenged salmonids also produce less viable gametes, which themselves are affected by water temperature after release. Passage through hydrological barriers and temperature changes both affect energy expenditure. As a result, important energetic tradeoffs emerge between extra energy used during migration and that available for other facets of the reproductive cycle, such as reproductive competition and gamete production. However, studies identifying these tradeoffs are extremely sparse. This review focuses on the specific locomotor responses of salmonids to thermal and hydrological challenges, identifying gaps in our knowledge and highlighting the potential implications for key aspects of their reproduction.

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## 1. Introduction

Climate change has increased global surface temperatures and is predicted to continue to do so in the future, leading to more frequent hot and fewer cold temperature extremes, intensifying wet and dry seasons, warming the ocean, raising sea levels and affecting ocean circulation (IPCC, 2013). An increased extinction risk is projected especially for terrestrial and freshwater ecosystems, where climate change interacts with additional anthropogenic stressors (IPCC, 2014). Specifically, urbanisation (i.e., building of hydrosystems, removal of riparian vegetation, diversion of river flow for irrigation and hydroelectric power, thermal and chemical pollution) is affecting river systems worldwide, which has strong implications for the health and persistence of associated catchments and biomes (Nilsson et al., 2005). Increases in air temperatures directly affect river water temperatures (Hari et al., 2006; Isaak et al., 2011; van Vliet et al., 2011), altering freshwater ecosystems (IPCC, 2014) and decreasing suitable thermal habitats for aquatic

species (Hari et al., 2006; Wenger et al., 2011a,b), especially cold-adapted fish at the edge of their distribution (e.g. salmonids of the British Isles) (Graham and Harrod, 2009). Recent and future impacts of climate change and urbanisation on freshwater ecosystems force aquatic species to adapt to novel and intensified environmental challenges in order to persist (Isaak et al., 2011; Reed et al., 2011). As a response to increasing temperatures, many species perform poleward or altitudinal shifts in their geographical distribution to seek suitable thermal habitat (IPCC, 2014; Pörtner and Knust, 2007), while others fail to complete large scale migrations (Farrell et al., 2008), which leads to population collapses and local extinctions (Pörtner and Knust, 2007). Adaptation to climatic change and urbanisation represents a particularly critical issue for species with complex life histories, such as migratory fish, where the timing of life cycle transitions is finely tuned to environmental cues and affects subsequent life stages in radically different types of habitat (Crozier et al., 2008). Consequently, migratory fish are at increased risk of extinction compared to non-migratory fish (Cooke et al., 2008b and literature within; Hinch et al., 2005).

As ectothermic poikilotherms, most fish species are strongly affected by water temperature due to its effects on biochemical reactions (Angilletta et al., 2002). Thermal and hydrological conditions affect

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energetic demands and transport costs in fish (Enders et al., 2003, 2005; Rand et al., 2006; Salinger and Anderson, 2006) and they are crucial factors determining the initiation and success of migrations (Hinch et al., 2005). Low energy reserves at the onset of migration are likely to have significant negative effects on survival and fitness (Crossin et al., 2004), which is exacerbated by stressful migratory conditions such as elevated current flow velocity and water temperature (Rand et al., 2006). Energy depletion during migration inevitably reduces the energetic capital that is retained for subsequent activities, such as reproduction. Little, however, is known about the implications of successful passage through urbanised watercourses and at challenging temperatures on reproductive success upon completion of reproductive migrations (Nadeau et al., 2010).

Salmonids are an ideal model to understand the impacts of climate change and urbanisation on migratory fish physiology, behaviour and reproductive success. They are anadromous or potamodromous migrants moving between distinct habitats as juveniles in search of rich feeding grounds and again as adults when homing upriver to their natal spawning grounds (Groot and Margolis, 1991; Hinch et al., 2005; Jonsson and Jonsson, 2011; Quinn, 2005). Adult salmonids cease feeding upon commencing their spawning migration (Hinch et al., 2005; Kadri et al., 1995, 1997; Quinn, 2005) and their journey upriver is thus entirely fuelled by endogenous energy reserves (capital breeding) (Crossin et al., 2009). Efficient allocation and expenditure of their limited energy stores is of paramount importance (Crozier et al., 2008; Hinch et al., 2005; Mathes et al., 2010; Young et al., 2006), especially for populations that complete long and arduous migrations (Bernatchez and Dodson, 1987). Unsurprisingly, salmonids have evolved to be highly efficient swimmers (Eliason et al., 2013b). Increased water temperature (e.g. Farrell et al., 2008, Fig. 1), river discharge (e.g. Rand et al., 2006) or a combination of both (e.g. Keefer et al., 2004; Martins et al., 2012) can result in substantial increases in pre-spawning mortality.

However, information about the behavioural and physiological mechanisms determining migratory success is still limited (Caudill et al., 2007; Cooke et al., 2008b). Salmonid migratory mass movements involve high concentrations of individuals following particular pathways (Lucas and Baras, 2001). This concentration of biomass can

provide crucial nutrients to otherwise often sparse environments, making them keystone species (Quinn, 2005). Additionally, salmonids are subject to intense commercial and recreational exploitation (Cooke et al., 2008b), creating substantial economic value. Understanding anthropogenic impacts on all aspects of their complex life histories is crucial in order to establish ways to manage their continued abundance and to preserve the ecosystem services they provide.

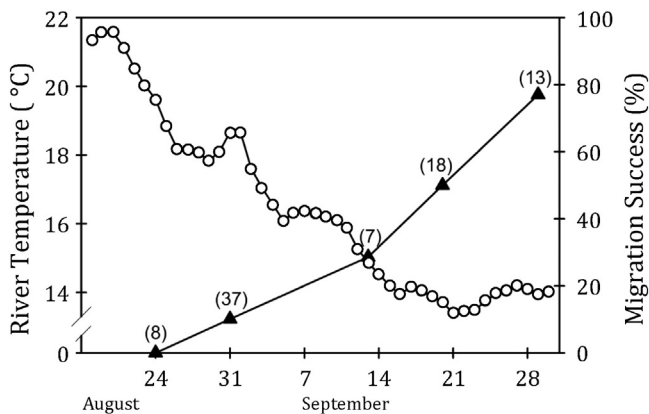
## 2. Behavioural, physiological and locomotor responses to migratory challenges

Salmonids have evolved to be highly efficient swimmers and can respond to environmental challenges en route with a variety of avoidance behaviours (e.g., thermal refuging (Mathes et al., 2010) or optimal path selection to avoid high flows (Standen et al., 2004)) and/or energy-minimizing migratory tactics (i.e., kinematic strategies such as burst-and-coast swimming (Videler and Weihs, 1982) or exploiting vortices (Liao et al., 2003; Taguchi and Liao, 2011)). However, thermal and velocity challenges strongly affect salmonid physiology, leading to non-aerobic fuelling of locomotion, anaerobiosis and energy loss when tolerance levels are transgressed (Lee et al., 2003a,b) (Fig. 2). The consequences are often lethal (pre-spawn mortality; e.g., Budy et al., 2002); however, sub-lethal consequences of energy depletion on subsequent reproductive success are highly likely, but seldom considered. The behavioural and physiological responses of salmonids to migratory challenges en route, as well as their physiological consequences and costs, are described in the following and are summarised in Fig. 3A and Table 1.

### 2.1. Behavioural plasticity in migratory tactics

In order to ensure that conditions at the spawning grounds are adequate for reproduction and subsequent offspring development, return migration timing and spawning date are highly conserved traits in salmonids (Crozier et al., 2008; Hodgson and Quinn, 2002; Mathes et al., 2010). However, in response to unusually high river temperatures, some species may advance (Cooke et al., 2008a; Juanes et al., 2004; Quinn and Adams, 1996), while others may postpone (Robards and Quinn, 2002) migration to avoid peak summer temperatures en route (Mathes et al., 2010). Salmonids can also respond to suboptimal water temperatures by delaying migration in cool thermal refuges (Berman and Quinn, 1991; Goniea et al., 2006; High et al., 2006; Hyatt et al., 2003). Thermal refuges include cold water tributaries, lateral ground-water seeps, deep pools and cold alcoves (Caissie, 2006); their location and temporal stability is highly variable (Dugdale et al., 2013) and their preservation will be key in the survivorship of salmonid stocks in the warming climate (Mathes et al., 2010). However, delaying migration through thermal refuging prolongs exposure to freshwater diseases and parasites, which is exacerbated by high water temperatures (Hari et al., 2006) and can contribute to pre-spawning mortality (reviewed by Hinch et al., 2012).

When encountering suboptimal thermal and flow conditions during migration, salmonids exhibit cost minimizing locomotor strategies. Burst-and-coast swimming, where bursts of fast swimming are in cyclic alternation with phases of coasting, in which the body is kept straight and motionless, can be an energetically advantageous strategy that allows fish to gain fast swimming speeds during short bursts while preventing the effects of fatigue by allowing metabolic recovery of muscle fibres during the coast phases (Videler and Weihs, 1982). Migrating fish can conserve energy by identifying and exploiting slow-velocity regions in the water column (Hinch and Rand, 2000; McElroy et al., 2012; Standen et al., 2004) as well as oncoming vortices created by objects in the stream (Liao et al., 2003; Taguchi and Liao, 2011) or by adjusting kinematic movement to maintain swimming efficiency during acute thermal and velocity challenges (Nudds et al., 2014). When confronted with high flow velocities that cannot be avoided, salmonids can adapt their migratory strategy from one of minimizing



**Fig. 1.** Changes in river temperature and migration success of Weaver Creek sockeye salmon, *Oncorhynchus nerka*, migrating through Harrison River, CA, in 2004. Lines and triangles denote survival rates (%); continuous line and circles denote water temperature (°C). Individual salmon were intercepted and fitted with radio transmitters; the number of tagged and released fish is shown in parentheses for each of five tagging dates (indicated by triangles). Mean ( $\pm$  95% confidence interval) entry dates are based on previous telemetry results showing migration rates of 25–36 km/d for tagged Weaver Creek sockeye salmon. Due to extremely high river temperatures in 2004, low overall migration success (30%) was observed. However, individual migration success increased with decreasing temperature and was highest (78%) for salmon sampled at the last tagging date; these fish delayed river entry by holding in the cooler estuary for several weeks and migrated when temperatures in the river had decreased. The results indicate the detrimental effects of early river entry at near critical water temperature. Redrawn with permission from Farrell et al. (2008).

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