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ABSTRACT

Flow regime is a fundamental driver in fluvial ecosystems, shaping habitat structure and biodiversity, and sustaining ecological integrity. Fish respond to flow fluctuations but whether aspects of flow variability represent organism-level stressors is poorly understood. To find existing evidence of fluvial fish organism-level responses to flow variability (natural or anthropogenic), and whether it resulted in quantifiable stress (i.e. departure from homeostasis), we reviewed literature on the physiological responses of fish exposed to flow. Among 58 articles that we identified to be relevant to the research question, 40 reported whole-animal responses (tertiary responses to stress), 37 reported blood and tissue level changes (secondary responses to stress) and 18 reported neuroendocrine changes (primary responses to stress), exclusively or combined. Whole-animal responses (e.g. growth or disease resistance) were more commonly assessed due to their broader use in population and community dynamics studies. Due to their long-term character it was difficult to isolate flow variability as the only stressor and to understand the underlying mechanisms that culminated in a stress response. Our review indicates that flow variability can be a stressor for fish but it remains unclear if events such as floods or hydropeaking are inherently stressful per se. More experimentation is needed to find out if flow variability presents a stressor to fluvial fish, what thresholds trigger a stress response and to better understand the relative role of the different flow components. This knowledge can be used to define robust stress biomarkers (particularly for field studies) and propose adequate flow thresholds.

Introduction

In an ecological context, flow regime is a key driver of fluvial ecosystems shaping and controlling habitat structure, biodiversity composition and inherent ecological processes (Poff et al. 1997; Katopodis 2005; Allan and Castillo 2007; Naiman et al. 2008). The temporal and spatial character of flow components, including magnitude, frequency, duration, timing, and rate of change (Poff et al. 1997; Olden and Poff 2003) affects population and community dynamics, biotic interactions and short and long-term biological processes (Gasith and Resh 1999; Humphries et al. 1999; Freeman et al. 2001; Lytle and Poff 2004; Ugedal et al. 2008; Krimmer et al. 2011; Young et al. 2011). Flow is inherently variable, driven by geomorphology, landscape features (biotic and abiotic) and atmospheric processes (Black 1996; Gordon et al. 2004; Katopodis and Aadland 2006; Brown et al. 2011). Increasingly, anthropogenic pressures are contributing to changes in natural hydrological regimes (Vörösmarty et al. 2010) and are even aggravated in modified riverine systems. Examples of changes in the natural hydrograph include the release of artificial discharges from hydropower dams for electricity production (e.g. hydropeaking, Poff et al. 2003; Young et al. 2011), the extent and constant alteration of impervious surfaces in urban centres (Walsh et al. 2005), water abstraction for irrigation (Haddeland et al. 2006), and the installation of stormwater management facilities that rapidly move water off the landscape (Wanielista and Yousef 1993). Being constantly subjected to human alterations, pristine fluvial ecosystems are now rare (Allan and Castillo 2007). With the increasing demand for more efficient energy, food and clean drinking water, the consequent landscape alterations and the influence of climate change it is anticipated that river flows could be even more variable in the future (Arnell 1996; Rijsberman 2006; Hoekstra and Chapagain 2007). As a consequence, the continuous alteration of flow regime worsens the threats to biodiversity of rivers at a global scale (Nilsson et al. 2005; Dudgeon et al. 2006). Not surprisingly, freshwater fish are among the most threatened taxa on the planet (Bruton 1995).

Given the global interest in river restoration (e.g. Katopodis and Aadland 2006) and the ever increasing identification of optimal flow regimes in regulated rivers

(e.g. Katopodis 2005), it is not surprising that there is a vast body of research on how a variety of organisms, but especially fish, respond to flow dynamics (Poff and Zimmerman 2010). However, most of the research to date has focused on responses of fish populations and changes in assemblages (Murchie et al. 2008) rather than adopting a more mechanistic approach to understand if and how flow may result in organism-level stress. There already exists a rich history of research on how fish respond to different natural and anthropogenic stressors, such as temperature, salinity, hypoxia, as well as biotic and social interactions (e.g. predation, aggressive behaviour, reviewed in Fry 1971; Wendelaar Bonga1997; Barton 2002). Any real or perceived variation in these factors threatens the individual homeostasis and results in a stress response that acts as an adaptive mechanism to restore it (Barton 2002). Increasing the intensity of the stressor may compromise the capacity of the organism to respond with an adaptive mechanism, having consequent deleterious effects on the well-being of the fish (Barton 2002). The stress response begins by the recognition of a real or perceived threat by the central nervous system. Afterwards, a cascading set of endocrine responses involving chromaffin tissue and the hypothalamic–pituitary–interrenal axis is triggered, resulting in the physiological responses to stress (Barton 2002).These have been broadly grouped into primary and secondary; the first being associated to an initial neuroendocrine response, including changes in circulating stress hormone concentrations (adrenaline, noradrenaline and cortisol; Mazeaud et al. 1977). The secondary response is to physiological adjustments in metabolism, including changes in energetic metabolism, hydro-mineral balance, and cardio-vascular, respiratory and immune function (Barton 2002). Finally, tertiary responses include changes in whole-animal performance characteristics, like growth, reproduction, disease resistance and behaviour that may result directly or indirectly from primary and secondary responses (Barton 2002). These are generally indicative of long-term (chronic) stressors in opposition to the more immediate primary and secondary responses.

Flow variability, here referred to as the natural or anthropogenic changes in flow that have the potential to produce organism-level changes, is rarely considered or even mentioned in the context of environmental or ecological physiology. However, with the increasing alteration of flow regimes (Nilsson et al. 2005), it is necessary to understand the effects of these changes in organism-level mechanisms to identify the extent to which these are affected by flow and to effectively predict responses to flow variability (Nislow et al. 2004). It is essential to understand the complexity of the adaptive mechanisms to flow variability, because presumably the patterns in population level processes are driven by individual level differences in condition, health, energy levels, and physiological status (Calow

1989; Calow and Forbes 1998; Maltby 1999; Pankhurst 2011; Young et al. 2011).

The kinetics of cortisol is an example of a physiological mechanism that is broadly used to study the degree of stress experienced by fish (Barton and Iwama 1991; Wendelaar Bonga 1997). With proper experimental protocols it is possible to quantify the circulating levels of cortisol, either their resting levels (Gamperl et al. 1994) or after being affected by an external stimulus (e.g. swimming exercise, Zelnik and Goldspink 1981). Although we acknowledge the ecological effects of flow variability on fish in the river ecosystem (Poff and Zimmerman 2010), explaining if and how the severity of natural or modified flow conditions presents a challenge to fish, is poorly understood. There are examples of experimental protocols linking swimming activity with fish stress physiology (e.g. Zelnik and Goldspink 1981; Young and Cech Jr. 1993a, 1994a, 1994b); however they do not establish a relationship with the flow conditions experienced in the natural environment. Understanding the complexity of the adaptive mechanisms to flow variability would provide improved guidance for establishing biologically appropriate environmental flow solutions, whether using physiomimetic (i.e. nature-mimicking) approaches or habitat modeling (Katopodis 2005; Katopodis and Aadland 2006). To that end, this paper provides an overview of the evidence for organism-level responses of fluvial fish to flow fluctuations (natural or modified) and whether or not they produce a physiological response that can be measured and scaled to populations, communities and the ecosystem. The fluvial ecosystem will be the focus of this review because its ecological integrity depends on the dynamic equilibrium of its dimensions (longitudinal, lateral, vertical and temporal) and any disturbance, either anthropogenic or not, has the potential to disrupt the river continuum and to affect all ecological units, from organism to ecosystem (Vannote et al. 1980; Poff et al. 1997). Any study that has focused on fish species that spend part of their life-cycle in freshwater (both anadromous and catadromous species) was considered.

Research approach

To find relevant literature on the physiological responses of fluvial fish to flow variability, we selected the electronic database Thomson Reuters Web of Science (https://apps.webofknowledge.com) and searched for articles published until the end of 2015. We first listed a set of possible keywords that in a second phase were combined and used as search strings in Web of Science. In the end we used the following search strings: (1) (flow OR flow NEAR/5 regime) + (fish*) + (stress* OR physiol*) NOT (marine OR estuar* OR aquaculture); (2) (flow* OR discharge OR "water level") + ("stress* response*" OR physiol*) + (stream*

OR river*) NOT (aquaculture OR marine OR estuar*) + (change* OR fluctuat* OR modif* OR reduct* OR regime* OR pulsed OR regulat*); (3) (flow* OR discharge OR "water level") + ("stress* response*" OR physiol* OR stress*) + (stream* OR river*) NOT (aquaculture OR marine OR estuar*) + (change* OR fluctuat* OR modif* OR reduct* OR regime* OR pulsed OR regulat*); refined by (fish*); (4) = to (3) and refined by: (fish* OR cyprini* OR salmonid*). For each search string, we screened the relevant titles and abstracts and for each article we screened the first 50 titles and abstracts of related articles. We only considered peer-reviewed documents. Additionally, we only selected English written documents. We have included relevant studies that considered the effects of flow variability on both growth and condition of fish, even if not indicated at any point of the study as a stressor. The Web of Science search results were quantitatively analysed to identify temporal and geographical trends, quantify the most used flow variability-organism-level responses, and determine the most common focal fish taxa to understand the adaptive mechanisms associated with the flow change. Flow-stress responses were classified in Primary (I), Secondary (II) and Tertiary (III), based on Barton's terminology (Barton 2002; Table 1). The qualitative analysis of how fluvial fish responded to flow variability at an organism-level, focused on natural and modified flow regimes, considering the role of flow as a driver of fluvial ecological integrity and the increasing severity of flow regulation.

Findings in flow variability-stress responses

Temporal and geographical trends according to flow regime studied

The use of physiological responses as fish performance indicators became more relevant since the nature-

Table 1. Fish responses to stress analysed in this review (adapted from Barton 2002), designated sub-categories and examples of studied responses found in the collected literature.

Type of responses to stress Sub-category	Examples of possible organism-level responses (changes)
Primary response (I)	
Corticosteroids	Blood cortisol
Catecholamine	Epinephrine, norepinephrine
Secondary response (II)	
Metabolic changes	Blood glucose; blood lactate; tissue glycogen; lipid metabolism; plasma pH
Cardio-respiratory system	Oxygen metabolism
Immune system	Haematocrit; antibody production
Ion-osmoregulation	Chloride; osmolality; potassium; sodium
Muscle activity	Physiological telemetry (e.g. electromyogram activity)
Tertiary response (III)	
Fitness	Lipid content
Reproductive success	
Growth	Otolith striping; body condition
Disease resistance	
Swimming behaviour	Aggression; foraging activity
Egg and larvae survival	

mimicking approach (Katopodis 2005) emerged as the natural flow regime paradigm and the recognition of its role as a key driver of the river ecosystem (Poff et al. 1997; Figure 1). This novel approach emerged given not only the importance of flow regime as a driver of the river ecosystem but also given the increasing extent of river regulation. This focus on the effects of flow dynamics at the individual level could be attributed to the need to understand individual level mechanisms to flow changes and how they would affect higher ecological units (Bunn and Arthington 2002; Poff and Zimmerman 2010).

We identified 58 relevant articles (Supplement 1) reporting whole- and sub-organismal responses according to flow variability features. The first studies reporting organism-level effects of flow variability were conducted in laboratory conditions where flow was manipulated to perform exercise training. This research approach aimed at optimizing fitness of hatchery-reared fish for conservation purposes, rather than attributing to flow variability a stressor effect
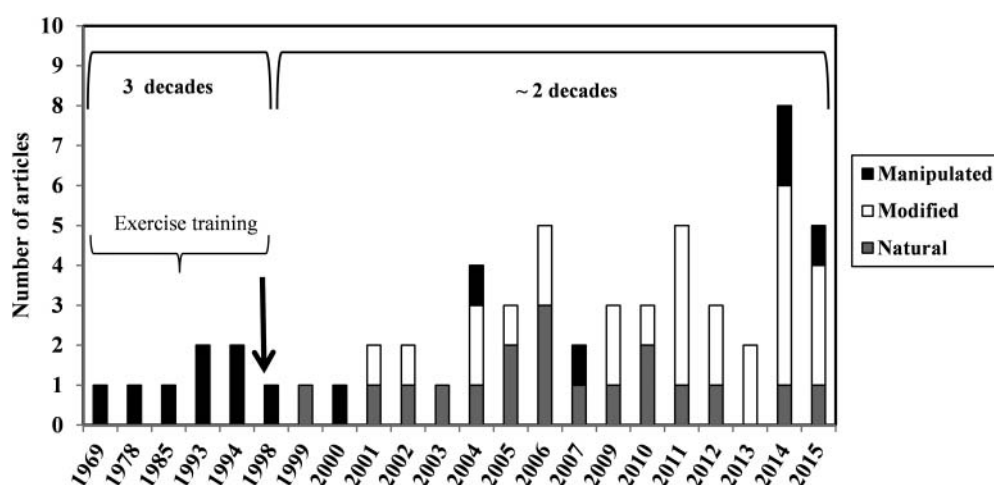
Figure 1. Temporal trends according to types of flow regime investigated. Manipulated – the research was conducted in laboratory conditions where flow was manipulated either in tanks, flumes or respirometers. Modified – the research was conducted in natural or controlled conditions that simulated altered flow regimes. Natural – The research was conducted in the natural environment under natural flow regime or in controlled conditions simulating the natural environment. The arrow indicates the year where "natural flow regime paradigm" was first described by Poff et al. (1997).

(Burrows 1964; Farlinger and Beamish 1978; Woodward and Smith 1985; Young and Cech Jr. 1993a, 1993b, 1994a 1994b; Figure 1). This line of investigation was prominent for three decades (Figure 1). Since then, fish fitness optimization by exercise training has been reviewed (Davison 1989, 1997) and its efficiency has been subsequently questioned (Brown et al. 2011). From the amassed literature, it was evident that most of the research focusing on organism-level responses occurred in the USA (28%) and Canada (27%), followed by Norway (14%), UK (9%) and China (9%). These results are not surprising because China ranks first among global hydropower producing countries, but lacks English written articles, while USA and Canada rank third and fourth place, respectively, and Norway ranks seventh (first in Europe) (IHA, 2015). Notably, 31% of the USA-based studies focused on exercise training and took place before the natural flow regime paradigm was described.

Exercise training and respirometry studies revealed that fish velocity preferences were a determining factor influencing whole- and sub-organismal responses. Exercised (trained) salmonids showed accelerated maturation timing compared to fish in slack water (Patterson et al. 2004), and poecilids improved their sustained swimming performance (Sinclair et al. 2014). At a sub-organismal level, salmonids trained at low velocities after a bout of exhaustive exercise, experienced lower levels of plasma cortisol than fish recovering in still water (Milligan et al. 2000). However, centrarchids training at low-velocity after exhaustive exercise exhibited signs of physiological disturbance, absent in still water (Suski et al. 2007). Respirometry studies provided valuable insight on how different flow conditions associated with other environmental factors (e.g. predation, restricted ration, pollution) resulted in intensified competition with trade-offs between growth,

feeding and swimming activity (Gregory and Wood 1998), exerted selective pressure on swimming performance, morphology and plasticity (Fu et al. 2013, 2014, 2015), and increased tissue DNA damage due to exhaustive exercise (Aniagu et al. 2006).

Trends in organism-level responses investigated

From the 58 collected articles, 19 quantified a stress response directly linked with a flow feature (Figure 2). Conversely, in 39 of the collected articles there was not an evident cause-effect relationship between flow variability (natural or modified) and an actual measurable stress response. While focusing on unknown aspects of ecologically important species for conservation purposes, or on the metabolic costs associated with swimming activity, these studies provided fundamental knowledge about fish physiology by using novel approaches (e.g. exercise training, Burrows 1964; Young and Cech Jr. 1993a, 1994) and tools (e.g. respirometry, Gregory and Wood 1998). Thus, among the 31 articles that quantified a primary and/or secondary response (Figure 2, white bars), 12 aimed at understanding fish physiological performance under manipulated flow conditions that were not necessarily related with a particular hydrological regime.

From the articles with no evident link between a flow variability feature and a stress response, 20 addressed exclusively tertiary responses (Figure 3). This is probably rationalized by: (1) the difficulty in establishing causality between flow disturbance and a sub-organismal response in long-term studies, (2) the difficulty in measuring them in the natural environment, and (3) the transient nature of primary and secondary responses. Whole animal responses, such as growth and survival, are more commonly used to monitor fish population dynamics and community
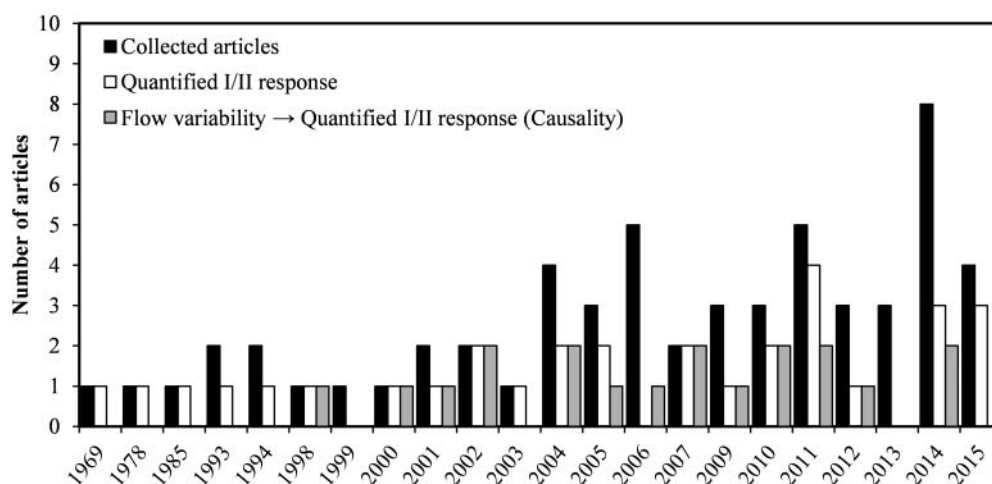
Figure 2. Temporal trend according to fish sub-organismal primary (I) and/or secondary (II) responses. From the 58 collected articles (black bars), 31 quantified a sub-organismal response, primary (I) and/or secondary (II), related to a flow feature variability (white bars) and of those, 19 found causality between flow variability (natural or modified) and a sub-organismal response (grey bars).
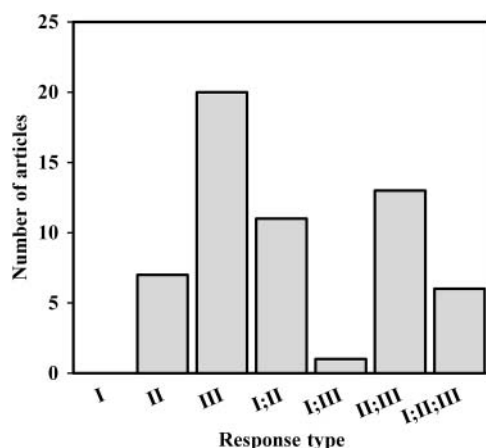
Figure 3. Number of assembled articles according to type of stress response studied. (I) Primary response to stress. (II) Secondary response to stress. (III) Tertiary response to stress.

structure and to assess the ecological status of the fluvial ecosystem. In opposition to primary and secondary responses, sampling protocols are not indicated to affect whole-animal responses and are easy to obtain. However, due to other confounding environmental factors, such as water temperature or water dissolved oxygen, and to biological factors, such as inter-specific interactions (e.g. predation, Sloman et al. 2001, 2002), attributing causality to flow variability could result in biased assumptions. Thus, to analyse short-term flow disturbances and to directly establish a link between an organism response and a flow feature, primary and/or secondary stress responses were preferred, being analysed in 38 articles. This is justified by the celerity of getting measurable responses, allowing causality with the flow disturbance of interest.

Notably, most of these studies focused on the ecologically and economically important salmonid family, with rainbow trout (*Oncorhynchus mykiss*) (7 of 58), brown trout (*Salmo trutta*) (7 of 58) and Atlantic salmon (*Salmo salar*) (7 of 58) as the most studied species. In addition to this, a significant amount of research has already been directed to identify flow requirements for specific life-cycle stages in salmonids (Signore et al. 2016). These fundamental studies can be used as references for future studies focusing on the potential stressful effects of flow variability in salmonids inhabiting highly modified fluvial ecosystems.

Responses in natural flow conditions

The inherent variability of natural flow regimes was investigated in 18 of the 58 collected articles with droughts (Sloman et al. 2001; Harvey et al. 2006; Maceda-Veiga et al. 2009; Balcombe et al. 2012), floods (Jensen and Johnsen 1999; Pottinger et al. 2011), flow increases (Sloman et al. 2002; Hackenberger et al. 2015), general features of flow variability (Nislow et al. 2004; Kemp et al. 2006; Teichert et al. 2010) and

turbulence (Enders et al. 2003, 2005; Sneddon et al. 2006) as the principal flow features of interest.

The effects of these flow features were addressed by analysing changes in whole-animal performance characteristics, namely growth (Jensen and Johnsen 1999; Nislow et al. 2004; Harvey et al. 2006; Kemp et al. 2006), lipid content (Kemp et al. 2006), behaviour (Sloman et al. 2001; Sunardi and Manatunge 2005; Sunardi et al. 2007; Kemp et al. 2006; Sneddon et al. 2006), body condition (Balcombe et al. 2012), survival (Jensen and Johnsen 1999; Harvey et al. 2006; Nadeau et al. 2010) and disease incidence (Maceda-Veiga et al. 2009; Hockley et al. 2014). Assessing primary and secondary responses to stress was rarer, with corticosteroid concentrations (Sloman et al. 2001; Pottinger et al. 2011), metabolic changes (Nadeau et al. 2010; Pottinger et al. 2011) and changes in the cardio-respiratory system (Enders et al. 2003, 2005) as the main indicators of stress. The use of biomarkers as secondary responses was also used in biomonitoring programmes to assess pollutant dissemination in streams with different hydrological regimes (Hackenberger et al. 2015).

Droughts have been reported to reduce fish condition, particularly when drought conditions were prolonged and when recent flow was absent (Balcombe et al. 2012), and to increase disease incidence due to favourable conditions for parasitic multiplication (low water level combined with suitable water temperatures; Maceda-Veiga et al. 2009). Salmonids grew less when experiencing reduced mean summer discharges in field experiments (Nislow et al. 2004; Harvey et al. 2006) and when subjected to decreasing discharges and high fish densities in artificial streams mimicking seasonal flow variability (Teichert et al. 2010). Simulated drought conditions resulted in significant changes in the stability of the dominance hierarchies of salmonids (Sloman et al. 2001) and poecilids (Sneddon et al. 2006), suggesting that hierarchical structure was stronger in undisturbed flow conditions. When integrating whole-animal performance alterations with sub-organismal responses, the results were somewhat inconclusive; plasma cortisol levels were characteristic of unstressed fish (<10 ng/ml; Pankhurst 2011) and liver glycogen did not differ significantly in comparison to control conditions (Sloman et al. 2001).

Floods had diverse effects on the growth and survival of fish, varying with species and life stage (Jensen and Johnsen 1999). Simulated high flow conditions resulted in decreased growth and poorer condition of cyprinids (Sunardi et al. 2007). However, when combining growth rate and lipid composition as responses to high flow conditions, juvenile salmonids either grew slower with no apparent effects on lipid composition or experienced lower lipid composition (higher energetic costs) with no apparent effect on growth (Kemp et al. 2006). These studies suggest that using solely

growth (body weight measurements on a temporal scale) or body condition as responses to simulated high flow conditions might generate biased assumptions (Kemp et al. 2006). For example, when combining whole-animal performance changes (social behaviour) with sub-organismal responses (cortisol), researchers found that the hierarchical structure of salmonids exposed to spates in experimental tanks was disrupted (Sloman et al. 2002). The plasma cortisol levels were consistent with these findings and were significantly higher in comparison to the control group (Sloman et al. 2002). In another experiment, salmonids were exposed in their final migration stage to fast velocity treatments which resulted in impaired physiological condition, shown by increased energetic costs (Nadeau et al. 2010).

Studies that used an integrated approach by assessing both whole-animal changes (tertiary responses to stress) and sub-organismal indicators (primary and secondary responses to stress) highlighted the importance of adding diverse indicators of stress, other than growth or body condition, to assess fish performance under flow variability (Sloman et al. 2001, 2002; Kemp et al. 2006). Not only is it relevant to add diverse indicators of the stress-axis, but also to include different components of flow, for example, turbulence. Turbulent conditions are common in rivers inhabited by salmonids which prefer fast-flowing waters, and when used to estimate their activity metabolism, turbulence negatively affected swimming costs (Enders et al. 2003, 2005).

Not all organism-level responses indicate causality between the stressor (flow variability) and the response under investigation. For example, Sloman et al. (2001) assessed the three types of responses to stress (primary, secondary and tertiary responses), finding no effect of the environmental perturbation on primary and secondary stress responses. A possible explanation was the timing that the blood samples were taken, which might have been inadequate to demonstrate a stress response. However, manipulating fish for blood removal more than one time during the same experiment could present an additional stressor that could confound conclusions about the stress response (Sloman et al. 2001).

Extreme hydrological regimes have been investigated as mechanisms of pollutant dissemination (Pottinger et al. 2011; Hackenberger et al. 2015). Although hydrological regime fluctuations were an additional stressor to fish, indicated by the significant variations in cortisol and glucose levels, the explaining mechanisms remained unclear (Pottinger et al. 2011). Interestingly, fish inhabiting fast-flowing waters affected by pollution were more susceptible to incurring increased stress as demonstrated by an increase in oxidative stress and DNA damage (Aniagu et al. 2006; Balcombe et al. 2012; Hackenberger et al. 2015). In respirometer experiments where fish were subjected to increasing water velocities, the higher swimming activity resulted in higher oxygen consumption rates (e.g. Enders et al. 2003; 2005). Higher fish swimming activity may result in an enhanced antioxidant potential (increasing enzymatic and non-enzymatic processes) (López-Cruz et al. 2010), thus if a riverine system is affected by pollution and unpredictable fluctuating or pulsed flows, the fish susceptibility to incur oxidative stress has the potential to increase.

Most of these aforementioned studies examined extreme flow features, some of which may only be comparable to catastrophic floods or droughts in natural systems. Natural flow disturbances like the more frequent floods and droughts are intrinsic components of pristine fluvial ecosystems exerting an adaptive pressure over organisms (Lytle and Poff 2004). These events are often critical for life-history stages, such as migration and reproduction, and although they are demanding they are not necessarily stressful (Pankhurst 2011). In fact, eliminating these natural disturbances has potential stressful effects on fish by affecting life-cycle events, such as reproduction or growth (Lytle and Poff 2004; Balcombe et al. 2012).

It is certain that different rates of natural disturbances result in increased primary and secondary responses and if they become chronic they can cause adverse effects on growth, disease resistance and behaviour. However, to identify the relationship between natural disturbances and the resultant stress response in the natural environment, is still a challenge (Pottinger et al. 2011); this is further complicated by the effects of confounding environmental variables that cannot be controlled (Harvey et al. 2006; Pankhurst 2011) and may compromise the feasibility of the entire experimental design.

Responses in modified flow conditions

A considerable amount of scientific effort has been directed to evaluate the effects of modified flow regimes in riverine fish (Murchie et al. 2008; Souchon et al. 2008). Still, the organism-level mechanisms explaining the effects of flow modifications in fluvial fish are poorly understood (Taylor et al. 2012).

The effects of modified flow regime were investigated in 26 of the 58 articles collected. Flow modifications associated with dams were of primary concern, either to address the effects of pulsed flows on swimming activity (Geist et al. 2005; Cocherell et al. 2011b; Taylor et al. 2012), growth (Korman and Campana 2009; Finch et al. 2015), survival (Korman et al. 2011; Fisk II et al. 2013) and endocrine processes (Flodmark et al. 2002; Taylor et al. 2012), or the effects of fishway passage efficiency on migration (Pon et al. 2009a; Cocherell et al. 2011a; Burnett et al. 2014).

Whole-animal changes were the most common stress indicators while investigating the effects of modified flows in fish. For example, higher egg incubation mortalities were reported during fluctuating flows in large regulated rivers (Korman et al. 2011), in dewatering experiments performed in the natural environment (Casas-Mulet et al. 2015) and in experimentally controlled conditions (Fisk II et al. 2013). Growth was also negatively affected by hydropeaking conditions in YOY salmonids in large regulated rivers (Korman and Campana 2009) and in juvenile salmonids in controlled experiments under stable low-flow and constant flow fluctuations (Flodmark et al. 2004). Some contradictory results have been reported for salmonids under simulated hydropeaking conditions. For example, growth and foraging were optimized in stable high flows in fiberglass tanks (Flodmark et al. 2004) while in an artificial stream no effects on growth or aggression were found (Flodmark et al. 2006). Surprisingly, in an adaptive management programme at a dam on the Colorado River, juvenile cyprinid growth was lower in more natural steady flows in comparison to hydropeaking flows (Finch et al. 2015). However, purposed controlled floods resulted in higher chances of survival and growth in YOY salmonids (Korman et al. 2011), highlighting the interspecific differences in responses to flow. Although these studies reinforce the need to set hydropower plant production operational measures to meet fish species flow requirements, the approximation of modified flow regimes to natural regimes does not always result in improved fish performance and the objectives of flow regulation should be carefully considered prior to development and implementation of a flow regime strategy.

The effects of pulsed flows as triggers of primary and secondary stress responses in fish were firstly investigated in an artificial stream by Flodmark et al. (2002). In this study, the velocity ranges and flow depths were characterized in detail, minimizing the effects of confounding environmental variables and allowing causality inferences between water velocities and stress responses. Interestingly, the highest plasma cortisol levels in brown trout (*Salmo trutta*) were reported for the short duration down ramping events (2 h), suggesting that the fish were experiencing an acute stress, but after six and twelve hours, plasma cortisol returned to pre-exposure levels (Flodmark et al. 2002). In the long-term seven-day experiment, after four days of flow fluctuations, no plasma cortisol response was observed, suggesting habituation to the stressor (Flodmark et al. 2002). The time of exposure to stressors has different implications on fish, ranging from habituation to compensation or exhaustion (Flodmark et al. 2002). Compensation occurs when after a repeated exposure to the flow fluctuation the fish adjusts physiologically or behaviourally (e.g. velocity refuging); exhaustion occurs when the stress-axis

has been stimulated to a degree where a down-regulation of the system occurs and the fish are unable to react to the flow fluctuation (Schreck 2000). In some cases when animals are exposed repeatedly to a stressful stimulus, stress responses are attenuated and the stimulus ceases to be considered a stressor (Schreck 2000).

Flodmark et al. (2002) reported no changes in blood glucose levels, suggesting that using solely blood glucose as a stress indicator might mask other responses and lead to inaccurate assumptions. Such studies could be strengthened by integrating quantitative behaviour metrics that would support behavioural assumptions according to the cortisol results. For example, in a study integrating behaviour and physiological telemetry (electromyogram (EMG) activity), the discharge duration, frequency and magnitude had a significant positive effect on the swimming activity and cortisol levels of a salmonid in a hydropeaking reach (Taylor et al. 2012). Although there was a significant increase in cortisol concentrations, they corresponded to typical values of unstressed fish (<10 ng/ml; Pankhurst 2011) and lactate loads were not indicative of fish swimming anaerobically. In addition, there was a considerable amount of variance that remained unexplained, possibly due to other environmental variables or inter and intra-specific variables that could not be controlled. In a controlled experiment simulating dewatering during down ramping, a salmonid moved ∼ 2.5 times more in comparison to the reference channel although blood cortisol levels, blood glucose and energy stores did not persist over time after the stimulus (Krimmer et al. 2011). Short-term elevated levels of cortisol have also been reported in laboratory dewatering experiments but were also followed by rapid habituation (Arnekleiv et al. 2004). These findings suggest that either the flow regime imposed was not stressful or the target species became habituated to the disturbance (Flodmark et al. 2002; Arnekleiv et al. 2004). Either way, knowing the flow thresholds (magnitude, duration, frequency and rate of change) that might produce a stress response in fish is difficult. In addition, the water level changes that occur during the dewatering stage or the flooding that occurs during the pulsed flow cycles might result in contradictory conclusions; increased stress during dewatering (e.g. Flodmark et al. 2002) and small home ranges coupled with lower swimming costs during flooding (e.g. Cocherell et al. 2011b). However, it is necessary to find out whether flow variability represents an actual stress and if it does, to use bioindicators that effectively quantify the stress response and to define effective flow variability mitigation strategies. High flows may characterize fishway entry and passage and are usually associated with anaerobic conditions, increasing the susceptibility of migratory fish to stress (Burnett et al. 2014). Additionally, when moving through some fishways at large dams, fish may be

subjected to fatigue-recovery cycles (Pon et al. 2009b; Cai et al. 2014, 2015). Although the anaerobic conditions associated with high attraction flows explained in part the higher mortalities of salmonids after passage success (Burnett et al. 2014), physiological indicators (plasma cortisol, lactate and glucose, haematocrit, and ionic status) were not indicative of stress or exhaustive exercise within the operational range studied for the same fish in the same dam (Pon et al. 2009a). In sturgeon, there was a significant increase in corticosteroid levels (plasma cortisol) and metabolic changes (haematocrit, pH, osmolality and lactate) in an experimental fishway, but 24 hours post-experiment, indicator values returned to pre-stress levels (Cocherell et al. 2011b). Apparently, to efficiently enter and surpass these obstacles, fish have to negotiate under anaerobic conditions and, depending on flow intensity and individual characteristics (e.g. life stage, condition), the responses to stress might be different and sometimes contradictory.

Physiological telemetry (e.g. EMG activity) was a common (7 of 26) tool used to estimate the energetic costs associated with exposure to daily pulsed flows (estimate of aerobic swimming-muscle activity of free-swimming fish). These high flow fluctuations were indicated to increase the energetic costs of mountain whitefish (*Prosopium williamsoni*; Taylor et al. 2012), rainbow trout (*Oncorhynchus mykiss*; Cocherell et al. 2011b) and white sturgeon (*Acipenser transmontanus*; Geist et al. 2005) at different discharge magnitudes and rates of change (Table 2). When calibrated to swimming speed (respirometry), these studies demonstrated that oxygen consumption increased with swimming speed. In contrast with Taylor et al. (2012), there was no evident flow-stress response (Geist et al. 2005; Cocherell et al. 2011b) and overall free-swimming fish speed was lower than their individual critical swimming speeds (Cocherell et al. 2011b), with no indication of exhaustive exercise. Apparently, above a certain threshold there was a decrease in swimming speed (Cocherell et al. 2011b) and telemetry results revealed a small home range where movements were restricted by high flows with minimal longitudinal movements during the increased pulsed flows (Geist et al. 2005; Cocherell et al. 2011b). The small home range during the pulses was explained either by the higher habitat availability caused by inundation (Cocherell et al. 2011b) or the duration of the low-flow period, reducing the time required to search for new habitats (Geist et al. 2005). The reluctance to change lateral position in response to sudden increases in flow has been demonstrated in experimental studies performed with juvenile fish (Vehanen et al. 2000; Kemp et al. 2003; Vilizzi and Copp 2005), suggesting that in these highly modified environments fish species perform restricted movements.

All these studies highlight the importance of integrating tools, for example swimming activity with physiological indicators, to effectively evaluate modified flows at the organism-level. However, the limitations related to experimental design, namely study location or experiment type (natural or manipulated laboratory flow conditions) are known and have to be considered. In field experiments, external factors and biotic and abiotic interactions occur and cannot be controlled, whereas in laboratory conditions fish might not exhibit their full genetic potential. In natural conditions, the difficulty in observing fish behaviour individually inevitably leads to assumptions that have not been experimentally verified, such as compensation behaviour (searching for "flow refuging") during high flows and foraging or social interactions during low flows. Although laboratory studies have the advantage to eliminate other confounding natural or anthropogenic factors, confinement does not provide optimal conditions to express whole-fish performance. Furthermore, fish swimming abilities can vary widely for a single or group of species which demonstrate performance similarity, such as subcarangiform or anguilliform swimmers (Katopodis and Gervais 2016). The different fish morphologies and swimming hydrodynamics result in diverse swimming performances and consequently in energetic discrepancies (Sfakiotakis et al. 1999; Pettersson and Hedenström 2000). These additional constraints in both laboratory and natural conditions might justify the low number of articles that focus on organism-level responses to flow variability. Certainly, integrated approaches that measure both whole-animal performance and physiological responses provide more insight (Taylor et al. 2012). The resultant findings would provide useful guidelines for water managers to define flow requirements according to species and life-stage, propose hydropower plant operational measures or to design effective fishways.

Biomarkers for flow variability

Environmental physiologists have been struggling to understand and quantify the effects of flow variability on fish physiology. However, it is essential to evaluate the validity of the physiological responses as adequate indicators of a flow disturbance and whether or not they can be used as reference values to address the potential of a flow disturbance to cause a stress response in fish. The value of stress physiology as a tool to evaluate the impact of natural or anthropogenic disturbances on a specimen is well known (Pankhurst 2011); additionally, fish are highly susceptible to disturbance (Poff and Zimmerman 2010), thus they can be used as potential sentinel organisms to quantify the extent to which a certain flow disturbance can cause a physiological response (Pottinger et al. 2011). Not surprisingly, salmonids were the most studied group (32 of 58) and were mainly studied to assess the effects of

Table 2. Studies that analysed a specific flow feature and quantified a stress response. Flow features were separated according to natural or modified flows. Flow features and stress indicator thresholds are indicated. (I), (II), (III) – primary, secondary and tertiary stress-axis responses, respectively. (s.d.) standard deviation; (Hct) haematocrit; (SMR) standard metabolic rate; (MEL) metabolic energy loss; (GSH) glutathione; (SOD) superoxide dismutase; (HSI) haepatosomatic index; (TBF) tail beat frequency. Studies performed under controlled conditions simulated natural and/or modified flow regime.

A: Natural

Flow feature	Author	Taxa	Experiment type	Flow feature threshold	Measured responses to stress	Indication of stress
Spates	Sloman et al. (2002)	Salmonidae	Experimental flume	Water velocity: 0.84±0.05 m/s	(I)Plasma cortisol; (II)HSI; (III)Growth	Plasma cortisol: ↑25.75±8.70 ng/ml HSI ↓ 0.87±0.04
Flow increase	Sunardi et al. (2007)	Cyprinidae	Tank	Riffle 0.11±0.072 m/s; Pool 0.02± 0.037 m/s	(II)SMR,MEL; (III)Growth, Condition	↑ Energetic costs
Drought	Sloman et al. (2001)	Salmonidae	Tank	↓ 37% (Water level)	(I)Plasma cortisol; (II)Gill epithelial chloride cell density, Interrenal nuclear areas; (III)Growth	Absence of dominance hierarchy
Low/high	Harvey et al. (2006)	Salmonidae	Artificial stream	↓ 75%–80% (Water level)	(II)Growth	↓ 8.5 fold
	Nadeau et al. (2010)	Salmonidae	Experimental raceways	Fast velocity: 0.38–0.39 m/s; Slow velocity: 0.10–0.12 m/s	(II)Plasma osmolality, Lactate, Glucose, Hct, Chloride, Potassium, Sodium, Gill ATPase, GSE, Concentration of lipid water, protein, ash	↑ Lactate and Glucose; ↓ GSE Hct Osmolality; Chloride; Sodium
Turbulence	Enders et al. (2003)	Salmonidae	Respirometer	Water velocity: Mean 0.18, 0.23 m/s; s.d. 0.05, 0.08 m/s	(II)Swimming costs (Oxygen metabolism)	Swimming costs: ↑ 1.3–1.6 fold Oxygen Consumption: 1.46–4.42 mg O₂/h (1.4–4.3 times SMR)
	Enders et al. (2005)	Salmonidae		Water velocity: Mean 0.18, 0.23 and 0.40 m/s; s.d. 0.05,0.08 and 0.10 m/s	(II)Swimming costs (Oxygen metabolism)	Swimming costs: ↑ 9.3 fold

B: Modified pulsed flows

Flow feature	Author	Taxa	Experiment type	Flow feature threshold	Measured responses to stress	Indication of stress
	Krimmer et al. (2011)	Salmonidae	Artificial stream	↓ 50%–75% in 4h	(I)Plasma cortisol; (II) Plasma glucose, Bioenergetics; (III) Growth	↑ 2.5 fold of small scale movement; ↓ body mass condition; No indication of stress according to (I) and (II)
	Cocherell et al. (2011b)	Salmonidae	River/respirometer	5–35 m³/s(weekdays); 5- >45 m³/s (weekends)	(II) Swimming costs (Oxygen consumption)	> 44 m³/s: ↓ swimming speed and activity
	Flodmark et al. (2002)	Salmonidae	Artificial stream	Discharge – water velocity 190 dm³/s - 0.26–0.33 m/s; 40 dm³/s – 0.09–0.13 m/s	(I) Blood cortisol; (II) Blood glucose	Blood cortisol:59.4±35.3 ng/ml (2h-down ramping); 61.3±26.8 ng/ml (1 day-daily cyclical fluctuations)
	Geist et al. (2005)	Acipenseridae	River/respirometer	Pulsed 192–836 m³/s; high 442–629 m³/s; Low 275–284 m³/s	(II)Swimming costs (Oxygen consumption)	↑ Oxygen consumption: 140.2–306.5 mg O₂ /kg/h (attributed to water temperature and light levels)
	Taylor et al. (2012)	Salmonidae	River	Hourly discharge: mean: 621 m³/s; Range: 0–1770 m³/s	(I) Plasma cortisol; (II) Blood lactate	Plasma cortisol: ↑ 1.60 ± 0.09 ng/ml
Flow increase	Aniagu et al. (2006)	Cyprinidae	Experimental flume	Water velocity: 0.2 m/s every 15 min	(II)DNA damage; (II)Antioxidant status: GSH and SOD	DNA damage: 25% tail DNA in exercised fish; DNA strand breaks: % 22 in exercised gills; oxidative stress
Drought	Arnekleiv et al. (2004)	Salmonidae	Artificial stream	Water velocity: 0–0.64 m/s; Water depth: 10–50 cm	(I)Plasma cortisol; (II)Blood glucose	No stress indication to dewatering
Fishway	Burnett et al. (2014)	Salmonidae	Fishway passage	Discharge: 1.2±2.0×10⁻³ m³/s; Water velocity: 1.7–2.1 m/s; Head tank discharge: 0.88 m³/s	(II) Oxygen consumption	↑ Anaerobic metabolism
	Cocherell et al. (2011a)	Acipenseridae			(I)Plasma cortisol; (II)Hct, plasma pH Osmolality, Chloride, Ion concentration; Lactate,Glucose	↑Plasma cortisol: 78.5±14.5 ng/ml Lactate: 5.77 ±2.11 ng/ml Hct: 28.0±1.5%; ↓ pH:7.75±0.02 post swimming (24h)
	Pon et al. (2009a)	Salmonidae		Discharge: intermediate –12.7 m³/s High – 15.8 m³/s; Low – 11.0 m³/s	(I)Plasma cortisol (II)Plasma lactate, Glucose Ions, Osmolality, Hct	No indication of stress or exhaustive exercise
Low/high	Young et al. (2010)	Osmeridae	Fish screen	Approach: 0; 0.06; 0.10; 0.15 m/s; Sweeping: 0; 0.31; 0.62; m/s	(I)Plasma cortisol; (II) Hct, pH	↑ Plasma cortisol: ↑Approach velocities and ↑ Sweeping velocities – range ~ 150–500 ng/ml

modified flow regimes (17 of 26). Growth was the most studied indicator of whole-animal performance to changes in flow regimes, whether they were natural (7 of 18) or modified (6 of 26) flows. Yet, relatively few studies determined if there was a stress response to a defined flow variability stimulus (but see Table 2).

Short-term responses to stress were most commonly quantified by determining plasma cortisol concentration, as a primary response, and swimming costs, measured by oxygen consumption or blood lactate, as a secondary response (Table 2). Cortisol concentration was directly associated with the studied threshold of flow variability, and increasing swimming costs, measured by oxygen consumption, were associated with fast water velocities (Table 2). Haematocrit and osmolality were negatively linked with the flow stimulus and plasma glucose and lactate concentrations were more variable and difficult to interpret (Table 2).

Although there is enough evidence that basal cortisol levels in wild teleosts are usually <10ng/ml (Pankhurst 2011) or even <5 ng/ml (Pickering and Pottinger 1989), what these baseline values represent when considering the environmental factor "flow" has been scarcely assessed. Additionally, translating these values to thresholds according to environmental flow requirements is unknown. The main constraints to identify these thresholds reside in inherent characteristics of the fluvial ecosystem and the species under study and in the sampling procedure (fish handling and time interval between flow disturbance exposure and sample collection). Apparently there is no method that eliminates sampling stress to estimate short-term primary and secondary responses to stress (Arnekleiv et al. 2004; Pankhurst 2011). To minimize the effect of handling and external confounding factors, authors have suggested the use of calibration curves by conducting blood sampling for analysis only once at the end of the experiment, in experimental and reference fish, thus avoiding fish behaviour disturbance throughout the analysis (Sloman et al. 2001; Krimmer et al. 2011). Establishing credible resting or baseline data for unstressed fish in the wild is difficult but of critical importance to understand how the same endocrine variables might change in relation to processes where the primary driver may not be the response to a stressor (Pankhurst 2011).

Studies analysing fish swimming activity demonstrated that increases in water velocity resulted in higher energetic costs (Table 2), particularly when combined with other environmental factors such as temperature or predation (Gregory and Wood 1998; Enders et al. 2003, 2005; Nadeau et al. 2010). Considering the definition of energetic cost, i.e. the necessary energy to transport one body mass by one unit distance (Schmidt-Nielsen, 1972), and fish inter- an intra-specific characteristics (e.g. morphology, Fu et al. 2013, 2014; predation, Sloman et al. 2001), it makes sense

that increasing water velocities result in higher oxygen consumption rates and that these changes could represent a transient stress response. The challenge is in finding the minimum cost of transport given a determined water velocity, i.e. the optimal swimming speed (U_{opt}), and the maximum cost of transport given the maximum velocity that the fish can sustain, i.e. the critical swimming speed (U_{crit}). Studies using respirometers, where swimming speeds were a proxy for energy expenditure, or exercise training, where water velocity was a proxy for fitness optimization, also demonstrated that water velocity increments resulted, respectively, in higher swimming costs (Gregory and Wood 1998; Fu et al. 2015), but also in improved fitness (Woodward and Smith 1985; Young and Cech Jr. 1993a, 1994a 1994b). These studies analysed the swimming costs associated with increases in water velocity (respirometers) or in fitness improvement by confinement in constant flow conditions (exercise training) and demonstrated that increasing water velocities resulted in sub-organismal responses (changes in plasma cortisol, glucose, lactate) and whole-animal performance changes (growth, swimming behaviour) that could compromise the full expression of the fish genetic potential. The intensity of the manipulated stimulus (duration, frequency, magnitude, rate of change) together with individual fish fitness were indicated to be the main factors influencing fish whole-animal performance and endocrine responses that in the natural environment would be translated in diversified swimming behaviours such as habituation, compensation and/or exhaustion (Flodmark et al. 2002). Using these experimental approaches to simulate flow variability conditions that fish would encounter in the natural environment, would provide valuable insight on the energetic costs associated with both optimal and critical swimming performance. This resultant knowledge can be applied for the design of mitigation measures that maximize habitat heterogeneity and optimize the fish chances of seeking velocity shelters and widening the lateral and longitudinal range of movements by increasing habitat connectivity which is particularly important during the up- and down-ramping in highly regulated rivers.

Conclusions

Scientists and water managers worldwide have been struggling to define effective water management guidelines that optimize environmental flow regimes, thus increasing the sustainability and ecological integrity of the fluvial system (e.g. Katopodis 2005; Souchon et al. 2008; Jones 2014). At an individual scale, scientific effort has been dedicated to identify fish flow requirements at critical life stages, such as rearing or migrating to spawn and forage, with particular emphasis given to salmonid

species (Enders et al. 2009; Fenkes et al. 2016; Signore et al. 2016), or to swimming behaviour (Liao 2007).

Fluvial fish are evolved to live in environments with variable flow but are adapted for certain flow conditions. Flow variation can therefore represent a potential stressor for fish in conditions beyond their optima. This review summarized the growing body of research reporting the impacts of flow variability at an organism-level. Natural and anthropogenic flow variability presents a potential stressor to fish, demonstrated by the changes in physiological processes and/or whole-animal performance characteristics. Increased levels of blood cortisol (primary response), changes in oxygen metabolism and increased levels of blood glucose and lactate (secondary responses) were some of the most relevant indications that changes in flow components contribute to a transient short-duration stress. These results were more evident under pulsed flow scenarios (e.g. Flodmark et al. 2002) and in the highly unstable flow conditions occurring in fishway entry and passage (e.g. Cocherell et al. 2011a) where the cortisol levels increased 6–8-fold in comparison to the reference value for unstressed fish. These endocrine changes may be followed by habituation or compensation, indicating that fish trigger adaptive mechanisms aiming at re-establishing homeostasis. When the organism can no longer maintain homeostasis, critical life-stages such as reproduction, foraging, escaping from predators or migrating, can be compromised. For example, under hydropeaking scenarios larval survival was negatively affected (Casas-Mulet et al. 2015). Thus, under severe flow conditions the energetic cost associated with swimming activity increases (e.g. Geist et al. 2005; Sunardi et al. 2007) and less energy will be directed to those critical processes.

Species-specific flow ranges have been defined from scientific assessments, particularly for salmonid species given dewatering conditions (Sloman et al. 2001, Harvey et al. 2006, Krimmer et al. 2011) and velocities (e.g. 0.35 m/s; Flodmark et al. 2002, Nadeau et al. 2010). However, specific flow components, such as duration, magnitude, frequency and rate of change, together with external biotic and abiotic factors are still strong limitations to find flow thresholds that present real stressors to fish. What remains unclear is the extent to which changes in those flow components trigger a stress response or allow habituation and compensation (e.g. Flodmark et al. 2002) to avoid long-term effects.

Future research directions

There is a clear imbalance in the number of studies examining whole-animal performance and sub-organismal stress responses to flow variability, favouring the first, although there is a diverse set of physiological indicators and measuring tools that can be integrated for such studies. The lack of research focusing on short-term stress-axis responses might be attributable to the difficulty in establishing a direct association between the flow component affecting the fish and the indicator response. According to the studies conducted so far, the reported reasons explaining this reluctance include the time it takes between stimulus duration and sample collection, the external environmental factors that cannot be controlled and the facilities where the experiment occurs (field or laboratory). When addressing the effects of flow variability at an organism-level, sentinel species should be proposed not only as indicators of whether or not flow presents a stressor but by exposing them to increasing flow stimulus and determine the threshold that results in a potential response. These species could also be used to monitor mitigation measures and perform adaptive management (Adams and Ham 2011). Additionally, studies that bridge the gap between individual responses (whole and sub-organismal) and populations, communities and the fluvial ecosystem are necessary (e.g. Sloman et al. 2001, 2002; Harvey et al. 2006). Considering the role of flow regime as a driver of fish life-history adaptations, future research should be directed in finding robust biomarkers that not only link the effects of flow disturbances at the individual level to populations but that could also be included in conservation and environmental management policy (Cooke and O'Connor 2010).

According to the diverse physiological tools available to quantify how flow variability affects fish behaviour, it is difficult to choose the most reliable and robust for assessing the potential for a stress response. Because there already exists an accepted concentration for plasma cortisol as an indicator of unstressed teleost fish, this was the elected short-term stress response and it was used in 16 of the 58 collected articles. To establish valid baseline values for unstressed wild fish associated either with natural flow dynamics (Sloman et al. 2001; Krimmer et al. 2011), or according to the fluvial ecosystem conditions that they inhabit, it is essential to have a comparable reference value, as long as the sampling techniques are minimally invasive to reduce handling stress, and external factors that otherwise could not be explained, are eliminated (Arnekleiv et al. 2004, Finch et al. 2015).

It is essential to integrate effective measuring tools to quantify the effects of flow variability and adequate indicators of a stress response, to avoid inaccurate assumptions that would otherwise result in the implementation of costly mitigation measures that would not improve the fluvial system. For example, changing operation procedures in hydropower production plants to achieve a more natural flow regime did not result in increased fish growth and revealed to be counterproductive (Finch et al. 2015). In this study, growth was

the only functional indicator used and it could be supported by utilizing other fish fitness indicators associated, for example, with swimming costs (e.g. lipid metabolism, oxygen consumption) and even endocrine indicators of stress (plasma cortisol) or exhaustive exercise (plasma lactate). Physiological telemetry is a promising tool to address how flow disturbances induce organism-level responses in the wild (Cocherell et al. 2011b; Hasler et al. 2012, 2014; Taylor et al. 2012, 2013, 2014). Taylor et al. (2012) combined EMG responses with primary stress responses and although the results on whether the pulsed flows were contributing to a stress response were not conclusive, quantifying the available types of stress responses prevented inaccurate assumptions that could otherwise result in the implementation of unnecessary mitigation measures. Using behavioural metrics supported by direct observation or using small scale movement tracking technologies (accelerometry) could also be alternatives to provide evidence on how flow affects individual-level performance. These are particularly relevant, as the fast changes occurring downstream of a hydro-power plant seem to induce only small scale movements in fish (Krimmer et al. 2011). The combination of acceleration models with oxygen metabolism has demonstrated how the extreme flow conditions which are sometimes associated with fishway entrance and passage can be stressful to fluvial fish performing spawning migrations (Burnett et al. 2014; Table 2). Understanding the effects on movement patterns and small scale habitat preferences seems to be an important research focus aiming at promoting effective flow management in these highly fluctuating environments. Finally, these could be added to powerful statistical modelling to make predictions of future scenarios (e.g. Cocherell et al. 2011a 2011b; Taylor et al. 2013).

Other aspects of flow variability research requiring further attention include how flow behaves according to the interface of the fish body and fins (Liao 2007) and how the body shape correlates with swimming performance and other ecological parameters (Fu et al. 2013; Katopodis and Gervais 2016). Although this line of investigation does not address flow variability as a potential stressor in isolation, it increases the awareness of the selective pressure that flow variability can exert on fish phenotype and increase the individual potential to benefit from flow variability to reduce the swimming costs associated with the increasingly higher fluctuating flow environments (Fu et al. 2013). Using experimental protocols that are able to quantify endocrine responses without handling stress (Zelnik and Goldspink, 1981), combine them with protocols to analyse fish swimming energetics (e.g. Taguchi and Liao, 2011; Fu et al. 2013, 2014) and experimental studies that simulate flow variability conditions that fish would encounter in the natural environment (e.g. Sloman et al. 2001,2002; Fu et al. 2014, 2015) could be

a valuable experimental approach that would explain if and how those flow constraints do actually represent a stressor to fish and to understand the adaptive mechanisms to flow variability.

Establishing experimental facilities in the fluvial system, either by installing cages (Hackenberger et al. 2015) or creating artificial streams (Casas-Mulet et al. 2015) to investigate both natural and highly modified flow conditions was effective in demonstrating the negative effects of pulsed events in the physiological condition of adult fish and in hatching success and larval survival, respectively. By using experimental facilities in the wild it was possible to isolate environmental variables, eliminate the challenges of confinement and to establish an association between flow variability and an organism-level stress response. Notably, even in confinement, fluvial fish were capable of expressing swimming behaviour identical to natural conditions, (e.g. dominance hierarchies, Sloman et al. 2001, 2002; foraging, Flodmark et al. 2004), and responses to stress typical of unstressed wild fish have been reported. However, as confinement hinders the capacity of a fish to fully express its performance potential, the possiblity of performing experiments in the natural environment should always be considered during the critical phase of experimental design (Patterson et al. 2004). There is certainly a need for large ecohydraulic experimental flumes or stream channels where flow can be manipulated over relevant time-scales. Knowing that these experiments aim at answering local and regional scale problems related to flow modifications (e.g. Taylor et al. 2012; Casas-Mulet et al. 2015), their outcome can function as groundwork to assess flow modification problems at the river catchment scale.

Although this review emphasizes the difficulty in isolating environmental variables when analysing stress responses to flow (Sloman et al. 2001; Harvey et al. 2006; Krimmer et al. 2011), and thus in determining the real basis for the physiological response, field experiments conducted in natural or highly modified flow regimes demonstrated that extreme flow conditions (e.g. floods, droughts, dewatering and pulsed flows) presented potential stressors to fluvial fish.

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