Effects of environmental fluctuations on fish metabolism: Atlantic salmon *Salmo salar* as a case study

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Using Atlantic salmon *Salmo salar* parr as study species, recent findings are summarized on how (1) diurnal variations in water temperature affects standard metabolic rate, (2) shelter may reduce routine metabolic rate and (3) fluctuations of water speed affect the costs of activity. The results suggest that the accuracy of bioenergetics models can be hampered if the effects of environmental fluctuations are omitted. Incorporating environmental fluctuations into estimates and models of fish metabolism will not only improve the accuracy of energy budget calculations, but also have crucial management implications for conservation and improve the capacity to predict effects of climate change.

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INTRODUCTION

Metabolism is a key component in fish bioenergetics. Most of the knowledge on fish metabolic rates is derived from respirometric experiments conducted in the laboratory, where environmental complexity is minimized. Such studies have a great value to compare metabolic responses to different levels of, *e.g.* oxygen, salinity and toxicity. Fishes in their natural environment, particularly stream-dwelling species in northern climates, however, experience high temporal and spatial variations in environmental conditions with variable temperatures, heterogeneous habitat and complex flow fields. These variations may influence standard metabolic rate (SMR), routine metabolic rate (RMR) and the costs of activity of the fishes. Some recent respirometric studies have used controlled perturbations, such as temperature variations, cover and flow alterations, to explore their effects on metabolic rates.

Water temperature is one of the most important environmental variables influencing metabolic rates of ectotherms (Brett, 1971; Claireaux & Lagardere, 1999; Aas *et al.*, 2011). The effect of water temperature on fish metabolic rates has been widely studied. Traditionally, respirometric experiments are conducted with organisms that are acclimated to a constant water temperature for days to months, before measuring their

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metabolic rates (Hokanson *et al.*, 1977; Elliott & Hurley, 1997; Enders *et al.*, 2006). In their natural environment, however, both riverine and lacustrine fishes may experience intense water temperature variations, even on a daily basis. For example, during summertime, water temperature in streams can fluctuate by up to 15° C daily (Lynch *et al.*, 1984). In lakes, fishes may experience diurnal water temperature variations as a consequence of vertical migrations to search for prey or to avoid being preyed upon (Diana, 1983; Bevelhimer & Adams, 1993; Bertolo *et al.*, 2011).

Numerous studies suggested that physiological rates obtained at a constant water temperature might differ from those analysed under fluctuating temperatures with the same mean temperature (Malcolm *et al.*, 2004; Meeuwig *et al.*, 2004; Imholt *et al.*, 2011). Consequently, the physiological rates estimated using organisms adapted to constant water temperatures might not adequately represent the physiological rates of fishes inhabiting environments in which water temperature fluctuates on a daily basis.

Most studies on the effects of diurnal variations of water temperatures focused on growth rates (Hokanson *et al.*, 1977; Meeuwig *et al.*, 2004; Imholt *et al.*, 2011). Results from these studies have found growth to be increased (Biette & Geen, 1980), unaffected (Dickerson & Vinyard, 1999) or decreased (Meeuwig *et al.*, 2004; Imholt *et al.*, 2011) by diurnal water temperature variations. It has been hypothesized that the direction and the magnitude of the effect of water temperature variations may depend on the proximity of the mean experimental water temperature to the optimal water temperature of the study species for growth (Hokanson *et al.*, 1977). Growth has been found to increase with fluctuating water temperatures when the mean water temperature is below the optimal temperature, but to decrease when the mean temperature is above the optimal temperature (Jobling, 1997). Consequently, physiological responses to temperature variations may differ depending on whether the average experimental temperature is below, similar or above the optimal temperature for growth.

Besides temperature, cover and water speed also exert effects on metabolic rate. The availability of cover is essential to the survival of animals. Fishes search for shelter for numerous reasons such as protection against predators and harsh physical conditions (Valdimarsson & Metcalfe, 1998). Focusing the review particularly on parr of Atlantic salmon *Salmo salar* L. 1758, it has been shown that they compete for shelter (Kemp *et al.*, 2005) suggesting that cover is an important and limited resource (Armstrong & Griffiths, 2001). Direct avoidance of predation is generally thought to be the primary function of sheltering behaviour (Greenwood & Metcalfe, 1998; Valdimarsson & Metcalfe, 1998). Other benefits of cover for *S. salar* parr include its role as a refuge from high water speeds (Rimmer *et al.*, 1984; Heggenes *et al.*, 1993), from the negative effects of ice formation and movements, *i.e.* entrapment, stranding and potentially mortality (Heggenes *et al.*, 1993; Whalen *et al.*, 1999), and from exceedingly cold temperatures (Cunjak, 1988; Contor & Griffith, 1995). Furthermore, the use of shelter may allow fishes to reduce their metabolic rates. For example, cover can potentially reduce the energetic costs incurred by station-holding species in streams and rivers (Rimmer *et al.*, 1984). Exposure to predators has been shown to increase opercular beat rate (Metcalfe *et al.*, 1987) and heart rate (Höjesjö *et al.*, 1999; Johnsson *et al.*, 2001). Consequently, cover may allow the fish to reduce the metabolic rate by decreasing its exposure to predators. In addition, cover may replace the need for predator-avoiding mechanisms, such as camouflage or vigilance that may have associated metabolic costs (Millidine *et al.*, 2006).

Water speed affects energetic costs and its effect on metabolic rates has been widely studied (Brett, 1964; Boisclair & Tang, 1993). Measuring the oxygen consumption rate during respirometric experiments is the most direct measure of metabolic costs required for locomotion (Beamish, 1978). Typically, in these respirometric experiments, pumps and flow straighteners are used in the swim tunnel to minimize spatial and temporal flow heterogeneity (Bainbridge, 1958; Brett, 1964; Beamish, 1978). In their natural environment, stream-dwelling species experience intense and rapid fluctuations in water speed (10 fold changes of flow rate within seconds; Enders *et al.*, 2005). The turbulence may be an important factor influencing metabolic costs in these environments (Fausch, 1993; McLaughlin & Noakes, 1998). Yet, turbulence is not taken into account by either forced or spontaneous swimming models (Boisclair & Tang, 1993) and few studies have analysed the energetic costs of swimming in turbulent flow (Enders *et al.*, 2003; Taguchi & Liao, 2011; Roche *et al.*, 2014).

The aim of this review is to summarize key studies that have contributed to the physiological understanding of how the complex environment affects metabolic rate by focusing on the effects of (1) diurnal variations in water temperature on the standard metabolism, (2) cover on routine metabolism and (3) turbulence on the activity costs of *S. salar* parr. The focus of the review is *S. salar* parr because they occur in streams with daily fluctuating water temperatures, they are known to use interstitial spaces between the substratum as shelter (Cunjak, 1988) and they experience intense fluctuations in water speed. In addition, *S. salar* is a species of great importance for commercial, recreational and aboriginal fisheries (Aas *et al.*, 2011). Many populations in Canada are considered at risk by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Changes in the physical habitat are thought to be one of the limiting factors (COSEWIC, 2010). Climate changes in the northern hemisphere have already been observed as winters are getting shorter and annual average temperatures and intensity of precipitation have been increasing, which subsequently affects water temperature and also modifies habitat in streams and rivers (Schindler, 2001). As the influence of climate change and alterations of aquatic habitat modifies the temperature and flow patterns experienced by fishes in their natural environment (Malcolm *et al.*, 2004), it is predicted that climate change may reduce the range of suitable habitats particularly for cool water species (with a tolerance of $26 \cdot 5 – 29 \cdot 9°$ C) and cold-water species (with a maximum tolerance of $24 \cdot 3°$ C; Eaton & Scheller, 1996).

EFFECTS OF DIURNAL TEMPERATURE VARIATIONS ON SMR

SMR can be estimated as the oxygen consumption of a post-absorptive, non-feeding and inactive fish with no accumulated oxygen debt (Brett & Groves, 1979), and is synonymous with the minimum physiological cost of maintaining an organism alive. It has been recognized for many years that SMR is strongly affected by water temperature (Fry, 1971). Estimation of SMR at any specific water temperature is generally performed with organisms that are maintained at this temperature for extended periods of time. Using numerous SMR estimates obtained for a series of different water temperatures, models can be developed to describe the relationship between SMR and water temperature. The use of these models to predict SMR under natural environments assumes that water temperature variations are non-existent in such environments or that variations of water temperature have no effect on SMR (*i.e.* that there is no metabolic cost associated with adaptation to fluctuating water temperatures).
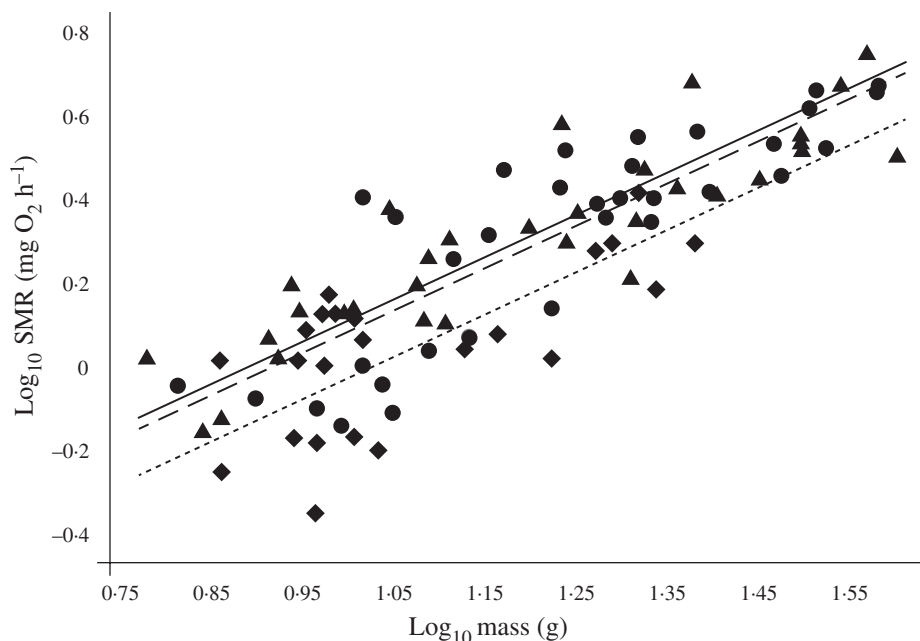
FIG. 1. Relationship between standard metabolic rate (SMR) of *Salmo salar* parr and body mass under constant thermal regime (20·0° C; ◆, ...; $y = 1·02x - 1·03$), medium variation thermal regime (mean ± S.D. of $20·0 ± 1·5°$ C; ●, _ _ ; $y = 1·02x - 0·91$) and high variation thermal regime (mean ± S.D. of $20·0 ± 2·5°$ C; ▲, ___; $y = 1·02x - 0·88$) from Beauregard *et al.* (2013).

The primary regulators of water temperature in streams and rivers are the volume and temperature of surface and ground-water influxes, the energy flux from solar radiation and air temperature; depending on the system, wind may affect the air to water temperature exchange (Vannote & Sweeney, 1980). The day–night variation in solar radiation causes diurnal variations in the water temperature of rivers (Vannote & Sweeney, 1980; Caissie, 2006). The observed variations between day and night can range from as little as 1° C up to 15° C (Constantz *et al.*, 1994; Johnson, 2004). To date, very few studies have quantified the effects of diurnal temperature variations on specific physiological mechanisms (Lyytikäinen & Jobling, 1998) and SMR has seldom been estimated for fishes experiencing diurnal temperature variations.

Beauregard *et al.* (2013) recently demonstrated that the SMR of *S. salar* parr is up to 34% higher for parr acclimated to a daily fluctuating thermal regime (mean ± S.D. = $20·0 ± 2·5°$ C) compared with parr acclimated to a constant thermal regime at the same mean temperature of 20·0° C (Fig. 1). At 20° C, these experiments were conducted above or near the optimal water temperature for growth for *S. salar* of *c.* 16° C and up to 20° C for some populations (Elliott, 1991; Elliott & Hurley, 1997; Jonsson *et al.*, 2001) and near the upper limit for feeding of 22·5° C (Elliott, 1991; Elliott & Hurley, 1997).

While informative, this study was conducted with fish collected from one given river and maintained at one average acclimation temperature. Among-population variations of the response of routine metabolism (Galarowicz & Wahl, 2003), growth rate (Jonsson *et al.*, 2001), critical thermal maxima and heat shock protein gene

expression (Fangue *et al.*, 2006; Healy & Schulte, 2012) to water temperature suggest that populations of a given species may react differently to diurnal temperature variations. Few studies have evaluated the effects of different thermal regimes in their environment of origin on among-population differences in SMR (Garland & Adolph, 1991; Lahti *et al.*, 2002).

Consequently, Oligny-Hébert *et al.* (2015) studied if *S. salar* parr originating from rivers that possess different thermal regimes have a similar response to diurnal temperature variations. More precisely, the authors tested the hypothesis that SMR of parr, living in rivers with different mean and day and night variations of water temperature in the summer, had similar responses to daily variations of water temperature. The study indicated that both, the mean water temperature at which experiments were conducted and the rivers from which fish originate, influence the effect of diurnal water temperature variations on the SMR of parr. Interestingly, SMR estimated at 15° C for fish held under a fluctuating thermal regime of $15 \cdot 0 \pm 2 \cdot 5°$ C (mean $\pm$ S.D.) was not significantly different from that estimated for fish held under a constant thermal regime of 15° C, irrespective of the river from which fish originated. SMR estimated at 20° C for fish originating from the warmer river and held under a fluctuating thermal regime of $20 \cdot 0 \pm 2 \cdot 5°$ C (mean $\pm$ S.D.) were 34% higher than that estimated for fish held under a constant water temperature of 20° C. In contrast, SMR of parr from the cooler river held under the same fluctuating thermal regime had SMR that were 8% lower than that of fish held under a constant water temperature of 20° C. These results are consistent with findings from previous studies suggesting that water temperature variations may have different physiological effects depending on the proximity of the mean water temperature to the optimal growth temperature (Hokanson *et al.*, 1977; Jobling, 1997).

The response of SMR of *S. salar* parr to diurnal variations of water temperature appears to vary between populations originating from different rivers (Oligny-Hébert *et al.*, 2015). The fluctuating thermal regime of $15 \cdot 0 \pm 2 \cdot 5°$ C (mean $\pm$ S.D.) had no statistically significant effect on the SMR of parr from two rivers in eastern Canada, the Ouelle River (a warm river subjected to important diurnal variations of water temperature; mean $\pm$ S.D. water temperature in July 2012: $22 \cdot 1 \pm 3 \cdot 9°$ C; Oligny-Hébert *et al.*, 2015) and the Cascapedia River (a cool river in which diurnal variations of water temperature are modest; mean $\pm$ S.D. temperature in July 2012: $16 \cdot 0 \pm 1 \cdot 4°$ C; Oligny-Hébert *et al.*, 2015). In contrast, the fluctuating thermal regime of $20 \cdot 0 \pm 2 \cdot 5°$ C significantly increased SMR of Ouelle River fish, but decreased SMR of Cascapedia River fish. Water temperature above 22·5° C lead to parr stop feeding (Elliott, 1991; Elliott & Hurley, 1997), seek thermal refuges (Cunjak *et al.*, 2005) and switch from a territorial to a schooling behaviour (Breau *et al.*, 2007). Breau *et al.* (2011) have shown that parr markedly augment the use of anaerobic metabolism (increase in muscle and blood lactate) when water temperature increases from 22 to 24° C. These physiological and behavioural reactions have been described as responses to a thermal stress (Grutter & Pankhurst, 2000). Parr from the Ouelle River, which frequently face summer water temperatures above the critical limit of 22·5° C [under the fluctuating thermal regime of $20 \ 0 \pm 2 \cdot 5°$ C (mean $\pm$ S.D.), fish faced water temperature of 22·5° C for 3 h per day]. have apparently maintained or developed the capacity to recourse to aerobic metabolism at a water temperature of *c.* 22·5° C. In contrast, parr from the Cascapedia River may rarely face water temperatures above this critical thermal limit. Consequently, these parr may not possess the same capacity as the parr from the
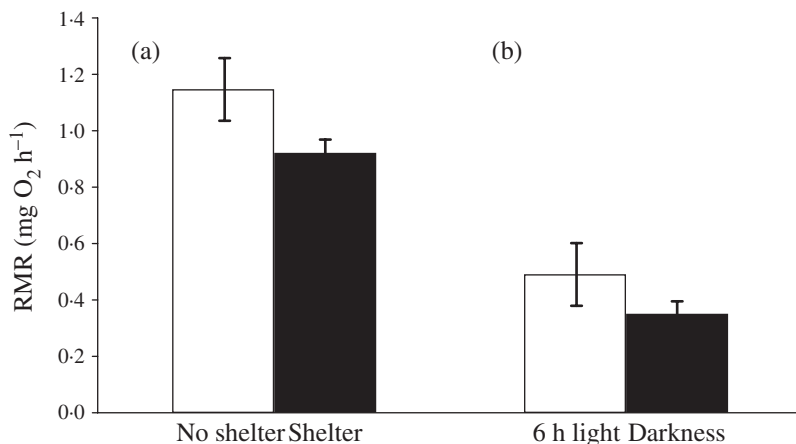
FIG. 2. (a) Comparison of mean ± s.e. routine metabolic rate (R_{RM}) of 4 g *Salmo salar* parr in the absence (□) and presence (■) of a single shelter at 10° C (Millidine *et al.*, 2006). (b) Mean ± s.e. RMR of 17 g *S. salar* parr reared in 6 h light (□) or darkness (■) at 1·3° C by Finstad *et al.* (2004).

Ouelle River and at water temperatures between 20·0 and 22·5° C. Cascapedia River fish may supplement their vital activities with anaerobic metabolism to maintain their vital physiological functions.

EFFECTS OF COVER ON RMR

Although most respirometric studies work with transparent swim chambers, few studies have actually included cover into the experimental design of respirometric experiments (Finstad *et al.*, 2004; Millidine *et al.*, 2006). Millidine *et al.* (2006) observed that *S. salar* parr without access to a shelter had substantially higher RMR, averaging a 30% increase in RMR in the absence of shelter [Fig. 2(a)]. Fish with higher RMR also had a darker colouration, which is thought to be associated with a physiological stress response (Suter & Huntingford, 2002) leading to increased metabolic rates.

Although *S. salar* parr sought shelter when first introduced into the experimental set-up, once they had settled during the measurements, they rested adjacent to the shelter space rather than hiding inside it (Millidine *et al.*, 2006). Consequently, the decreased RMR appears to be related to the decreased stress associated with the presence of a shelter rather than the actual use of the shelter. The availability of shelter affects metabolism even when light and activity levels remain unchanged. Therefore, RMR may vary, independent of nutritional state or activity levels, solely because of changes in the physical structure of the abiotic environment.

Simulated shelter (due to 24 h darkness) also reduced the RMR of *S. salar* parr by 30% compared with parr in 6 h of light per day [Fig. 2(b); Finstad *et al.*, 2004]. Several factors may contribute to the lower RMR in darkness. The effect of light on melatonin secretion leads to an increase in RMR mediated by the pineal gland (Wendelaar Bonga, 1993). This could have caused the lower RMR in darkness. There may also have been

differences in the activity levels between the fish held at different light levels that were not monitored by Finstad *et al.* (2004).

EFFECTS OF TURBULENCE ON ACTIVITY COSTS

Activity costs are often estimated using respirometry models developed from forced swimming experiments, in which fish swim against a flow of constant speed (Brett, 1964). Forced swimming models obtained using a procedure that minimizes flow heterogeneity may not represent the costs of swimming in rivers characterized by turbulence and by a wide range of instantaneous flow rates. Very few studies have been conducted to estimate the costs of swimming in turbulent flow (Enders *et al.*, 2003; Taguchi & Liao, 2011; Roche *et al.*, 2014).

Turbulence may be perceived as a partly random, partly structured, temporal variation of flow velocity at one point in space (Kirkbride, 1993). It may also be perceived as the spatial heterogeneity of flow velocities at a given time (Bradshaw, 1985). In a gravel-bed river, natural flow conditions comprise realistic flow structures such as temporal successions of fast and slow-moving flow events extending over the whole water column [Fig. 3(a); Buffin-Bélanger *et al.*, 2000] that last from 0·5 to 5·0 s and occur at 5–30 s intervals [Fig. 3(b); Roy *et al.*, 1999; Enders, 2003]. To describe the intensity of flow-rate fluctuations, a few different time-averaging variables may be used such as s.d. of the flow rate (u_{SD}), turbulence intensity (I_T, s.d. of the flow speed divided by the mean flow speed) or turbulent kinetic energy [E_{TK}; g cm^{-1} s^{-2}, which was calculated as: $E_{TK} = n^{-1} \sum_{i=1}^{n} 0.5\rho \left(u_i'^2 + v_i'^2 + w_i'^2 \right)$, where n is the number of instantaneous flow-rate fluctuations, ρ (g cm^{-3}) is the water density and u_i', v_i' and w_i' (cm s^{-1}) represent the instantaneous flow-rate fluctuation of the three speed components].

Pavlov *et al.* (2000) observed a decrease in sustained and critical swimming speeds with an increase of I_T for two lowland species, gudgeon *Gobio gobio* (L. 1758) and roach *Rutilus rutilus* (L. 1758), which indicates that the energy expenditures may increase with I_T. In respirometric experiments, Enders *et al.* (2003) assessed the activity costs of *S. salar* parr in turbulent flow conditions. During the experiments, fish swam continuously for 6 h under turbulent flows characterized by mean flow speeds of 18 and 23 cm s^{-1} and s.d. of flow speed of 5 and 8 cm s^{-1}. The results demonstrated that, with an increase in u_{SD} from 5 and 8 cm s^{-1}, activity costs increased by 1·3 to 1·6 fold [Fig. 3(c)]. Comparing these results with traditional forced swimming models highlighted that activity costs are actually 1·9 to 4·2 fold higher than those measured under minimized flow heterogeneity. This increase in activity costs with turbulence was especially dramatic for trials conducted at higher mean flow speeds (Enders *et al.*, 2005). The analyses suggested that models in which both the mean and the s.d. of flow speed are explicitly represented are needed to adequately estimate activity costs in turbulent flows. Consequently, activity cost models for *S. salar* parr swimming in turbulent flow using u_{SD}, I_T and ET_K, respectively, were developed that especially account for the effects of speed fluctuations in turbulent environments. In these models, considerable 14% of the variability in activity costs was explained by the respective turbulence metrics (Enders *et al.*, 2005). Similar results have been described for labriform shiner surfperch *Cymatogaster aggregata* Gibbons 1854 swimming in steady *v.* fluctuating flow (Roche *et al.*, 2014). Activity costs in highly fluctuating flow were on average 25·3% higher than in steady flow.
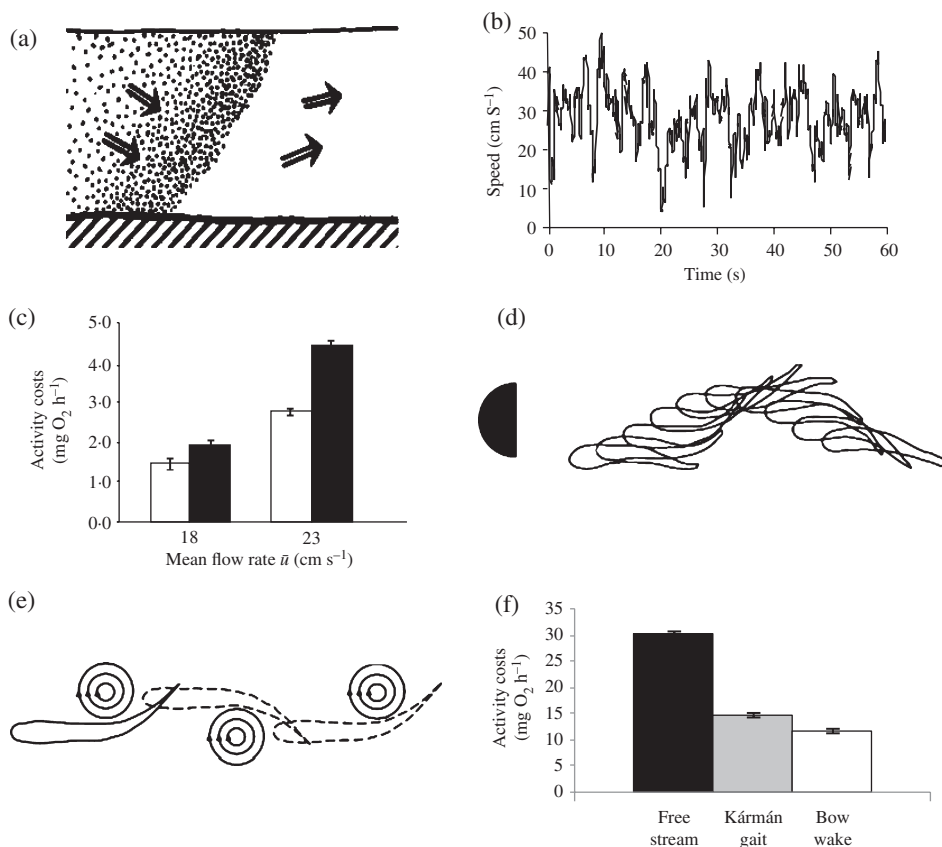
FIG. 3. (a) Side view illustration of the passage of high and low-speed flow wedges in a gravel-bed river in which *Salmo salar* parr occur. The high-speed flow wedge is orientated towards the river bed, whereas the low-speed flow wedges rises to the water surface; modified from Buffin-Bélanger *et al.* (2000). (b) Speed time series measured in the focal point of an *S. salar* parr; from Enders (2003). (c) Activity costs of 10 g *S. salar* parr at 15° C under four fluctuating flow conditions defined by the mean flow speed ($\bar{u}$) and the S.D. of flow speed (u_{SD}) from Enders *et al.* 2003. Low turbulence conditions (u_{SD} of 5 cm s^{-1}; □, ± 95% C.I.) and high turbulent conditions (u_{SD} of 8 cm s^{-1}; ■, ± 95% C.I.) are represented. (d) Plan view silhouette of a 10 cm *Oncorhynchus mykiss* swimming in a Kármán vortex street created by a 5 cm diameter cylinder (Liao *et al.*, 2003). In comparison with fish swimming in free flow, Kármán-gaiting fish display lower tail-beat frequency and higher tail-beat amplitude. (e) Plan view schematic highlighting the importance of vortex size and orientation on swimming performance (Lacey *et al.*, 2012). Only vortices of a certain size relative to the fish length and of vertically orientation enable fish to Kármán gait. (f) Mean ± S.E. activity costs of *O. mykiss* (107 g body mass) at 15° C in free stream flow of 3·5 body lengths s^{-1} (■, + 95% C.I.), Kármán gaiting (■, ± 95% C.I.) and entraining in the bow wake (□, ± 95% C.I.) by Taguchi & Liao (2011).

Another feature of turbulent flows is vortices that occur when flow passes over obstacles resulting into vortex shedding. To describe the periodicity of the vortices, spectral analysis of the speed time series can give an estimation of the frequency of the shedding. Flow passing a D-shaped cylinder produces a periodical vortex shedding known as Kármán vortex street [Fig. 3(d); Liao *et al.*, 2003]. When flow speed and cylinder diameter, and consequently the frequency of the vortex shedding and the wavelength (spacing and size of the vortices), are adjusted to the tail-beat frequency

and the body length, it is possible for a fish to Kármán gait [Fig. 3(e); Liao *et al.*, 2003; Lacey *et al.*, 2012]. The Kármán gait motion is characterized by a lower tail-beat frequency and larger lateral body amplitudes and curvatures than observed for fish swimming in free stream flow of the same speed.

The study showed that adult rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) Kármán gaiting behind an obstacle use the energy of these vortices to maintain their position in the turbulent flow while reducing their muscle activity (Liao *et al.*, 2003). This indicates that activity costs of fish using vortices that occur in turbulent flows may be lower than in the absence of such vortices. Taguchi & Liao (2011) confirmed with respirometric experiments that fish Kármán gaiting in a vortex street have 47% lower activity costs than individuals swimming in free stream flow [Fig. 3(f)]. Furthermore, fish are often observed to entrain on an obstacle, taking advantage of reduced speeds associated with the flow-field downstream of the obstacle, referred to as bow wake. In respirometric experiments, it has been confirmed that entrainment reduces the activity costs of fish in comparison to free stream flow and Kármán gaiting (Cook & Coughlin, 2010; Przybilla *et al.*, 2010; Taguchi & Liao, 2011).

Besides the predictability of the vortex shedding, the size of vortex (diameter) and its orientation (horizontal or vertical axis) in relation to the fish length and body undulation play an important role for swimming capacity (Tritico & Cotel, 2010). Experiments on creek chub *Semotilus atromaculatus* (Mitchill 1818) have demonstrated that individuals experiencing horizontally oriented vortices were influenced more than individuals in vertically oriented eddies. In addition, large vortices with low vorticity had no measurable effect on stability, whereas small vortices with high vorticity resulted in the fish losing its position. No respirometric study, however, has yet been conducted to confirm the implication of vortex size and orientation on activity costs.

IMPLICATIONS FOR BIOENERGETICS MODELLING

Fishes that inhabit streams and rivers may experience high variations in water temperature and high fluctuation in speed and dwell in complex habitats. Bioenergetics models have the potential to estimate the effects of such fluctuations on growth; however, bioenergetics components are traditionally modelled using fishes kept at constant water temperatures and speeds with minimized experimental complexity. This review is a compilation of studies that tested the hypotheses that diurnal water temperature variation increases SMR, that cover decreases RMR and that turbulence affects the costs of activity. The studies indicated that the traditional approach used to estimate and model components of the bioenergetics equation may substantially underestimate SMR of organisms that are subjected to temperature variations. Alternatively, habitat complexity and shelter decreased substantially the RMR. Chaotic fluctuations in water speed can increase activity costs (Enders *et al.*, 2003, 2005), whereas flows that produce temporally stable vortices can decrease activity costs (Taguchi & Liao, 2011).

Consequently, bioenergetics models aimed at estimating the costs of habitat use by fishes living in turbulent environments may require a description of behaviour, estimates of the mean flow speed and turbulence variables, and activity cost models in which the effects of the turbulence are explicitly represented. Activity cost models using the turbulence variables may provide estimates of the costs of habitat utilization by fish living in rivers that are more accurate than commonly used forced swimming models.

IMPLICATIONS FOR CLIMATE CHANGE

Climate change models predict increases in winter temperatures in the northern hemisphere (IPCC, 2007). Increase in water temperature will directly affect physiological process in ectothermic animals such as fishes (Schindler, 1997; Magnuson *et al.*, 2000). In addition, indirect effects of an increase in temperature may be reflected in changes in ice conditions. Small increases in temperature may induce thawing of ice-covered rivers. Ice cover, causing darkness in parr habitat, has been shown to affect RMR, growth and survival of stream-dwelling fishes in northern environments (Finstad *et al.*, 2004; Hedger *et al.*, 2013). Altering the environment during a critical period for survival may consequently have negative effect on the species sustainability.

CONCLUSIONS

In conclusion, to date, most metabolic rate models were developed using organisms acclimated to constant temperatures (Grøttum & Sigholt, 1998; Enders *et al.*, 2006). By conducting respirometric experiments and subsequently developing models assessing the energetics response of a specific species to different water temperatures when they are maintained under thermal regimes similar to those found in natural environments, SMR may be adequately estimated under natural conditions.

Fishes that inhabit streams and rivers may experience important fluctuations in water temperature and speed and dwell in complex habitat. Bioenergetics models have the potential to predict possible effects on growth due to these variations. Currently, most bioenergetics components are derived from laboratory studies in which organisms are subjected to constant water temperatures and speeds with minimized experimental complexity. The present review on *S. salar* parr summarized studies that analysed the effects of diurnal temperature variations on SMR, cover on RMR and turbulence on activity costs. The studies suggest that the current approach to obtain bioenergetics components may significantly underestimate SMR of fish that are experiencing diurnal temperature variations. By contrast, habitat complexity appears to decrease RMR considerably. Temporally predictable vortices that scale with fish length and orientation may decrease activity costs (Cook & Coughlin, 2010; Przybilla *et al.*, 2010; Taguchi & Liao, 2011), whereas intense chaotic fluctuations in velocity may significantly increase activity costs (Enders *et al.*, 2003, 2005; Roche *et al.*, 2014). Considering the dramatic effects environmental fluctuations may have on the metabolic rates of fishes, future respirometric experiments may want to include natural variability into the experimental design to obtain ecological relevant estimates.

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