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ORIGINAL PAPER

Simultaneous biologging of heart rate and acceleration, and their relationships with energy expenditure in free-swimming sockeye salmon (*Oncorhynchus nerka*)

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Abstract Monitoring the physiological status and behaviour of free-swimming fishes remains a challenging task, although great promise stems from techniques such as biologging and biotelemetry. Here, implanted data loggers were used to simultaneously measure heart rate (f_H), visceral temperature, and a derivation of acceleration in two groups of wild adult sockeye salmon (*Oncorhynchus nerka*) held at two different water speeds (slow and fast). Calibration experiments performed with individual fish in a swim tunnel respirometer generated strong relationships between acceleration, f_H, tail beat frequency and energy expenditure over a wide range of swimming velocities. The regression equations were then used to estimate the overall energy expenditure of the groups of fish held at different water speeds. As expected, fish held at faster water speeds exhibited greater f_H and acceleration, and correspondingly a higher estimated energy expenditure than fish held at slower water speeds. These estimates were consistent with gross somatic energy density of fish at death, as determined using proximate analyses of a dorsal tissue sample. Heart rate alone and in combination with acceleration, rather than acceleration alone, provided the most accurate proxies for energy expenditure in these studies. Even so, acceleration provided useful information on the behaviour of fish and may itself prove to be a valuable proxy for energy expenditure under different environmental conditions, using a different derivation of the acceleration data, and/or with further calibration experiments. These results strengthen the possibility that biologging or biotelemetry of f_H and acceleration may be usefully applied to migrating sockeye salmon to monitor physiology and behaviour, and to estimate energy use in the natural environment.

Keywords Accelerometer · Accelerometry · Biotelemetry · Bioenergetics · Fish · Metabolic rate · Metabolism · Oxygen consumption rate · Salmonids

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Introduction

The evolving disciplines of physiological ecology and conservation physiology (Wikelski and Cooke 2006) largely hinge on the capacity of scientists to measure the physiological status of free-roaming animals in the natural environment. While this is a particularly challenging task when studying active species of fish that can rapidly move large distances and often remain out of human sight, the integration of biology and electronic engineering offers great promise through techniques such as biologging and biotelemetry (Cooke et al. 2004b, 2005; Block 2005; Clark et al. 2008a, 2009).

The use of temperature and pressure sensors on biologging or biotelemetry devices has enabled the quantification of migration patterns, thermal and depth preferences (Block et al. 1998; Tanaka et al. 2001; Newell and Quinn 2005; Farrell et al. 2008), while the use of accelerometers, acoustic/radio/satellite tracking devices, and electromyogram (EMG) sensors has provided insight into fish activity levels and the rate of movement (Dewar et al. 1999; Tanaka et al. 2001; Hinch et al. 2002; Welch et al. 2002; Kawabe et al. 2003; Cooke et al. 2004c; Block 2005; Tsuda et al. 2006).

Stemming from a desire to quantify the energy turnover of free-swimming fishes, studies have utilised logged or telemetered variables as proxies for energy expenditure (Armstrong 1986; Lucas et al. 1993; Lucas 1994; Hinch and Rand 1998; Healey et al. 2003), and there are new potential proxies available that await trials in fish (e.g. Wilson et al. 2006). Indeed, variables directly linked with the oxygen transport cascade have been the focus of biologging and biotelemetry studies for many decades (Priede and Tytler 1977; Priede and Young 1977; Armstrong 1986, 1998; Laitinen and Valtonen 1994). While heart rate (f_H) has attracted much attention as a proxy for energy expenditure in many vertebrates (Butler et al. 2004; Clark et al. 2006; Green et al. 2009), it was previously considered of little value in fish because of the apparent ability of many fish species to alter cardiac stroke volume considerably and independently of f_H (Farrell 1996; Thorarensen et al. 1996). More recent studies, however, are proving that f_H can be of similar importance to regulating cardiac output in fishes as in other vertebrates (Altimiras and Larsen 2000; Schreer et al. 2001; Cooke et al. 2003; Clark et al. 2005, 2008a; Clark and Seymour 2006) as well as acting to indicate such things as feeding periods, stress and poor water quality (Heath and Hughes 1973; Milligan and Wood 1982; Laitinen and Valtonen 1994; Lucas et al. 1991).

Thus, rapid advancements in technology have increasingly enabled biologists to move to the natural environment to study aspects of the physiology and behaviour of wild fish. Lacking in most studies, however, are simultaneous recordings of multiple behavioural and physiological variables from the same individual. Clearly, augmenting our understanding of the physiological ecology of wild fish relies upon an increased knowledge of both the physiology and behaviour of the fish under the environmental conditions of interest. Furthermore, the measurement of multiple variables allows investigation into which proxies of energy expenditure may be most accurate.

The present study utilised a recently designed data logger for long-term simultaneous measurements of f_H, visceral temperature, and a derivation of acceleration in two groups of wild adult sockeye salmon (*Oncorhynchus nerka*) exposed to two controlled water velocities. Additionally, individual fish were swum at a range of water velocities in a tunnel respirometer to generate relationships between energy expenditure and the variables recorded by the data loggers. It was hypothesised that (1) while strong relationships may exist between energy expenditure and each of the measured variables (acceleration and f_H) over a wide range of swimming velocities, one variable in particular, or a combination of the variables, might provide the better proxy, and (2) f_H, acceleration and overall energy expenditure of fish held at higher water velocities would be greater than fish maintained at lower water velocities. While testing these hypotheses, the present study has become, to the best of our knowledge, the first to simultaneously measure f_H, acceleration and temperature of any animal species.

Materials and methods

Fish capture and handling

Wild adult sockeye salmon were intercepted during their upriver spawning migration from the ocean, approximately 140 km upstream of their freshwater entry point. Fish were corralled using a beach seine net deployed by a motorboat in the Harrison River, British Columbia, Canada, between 15 and 18 September 2008. Once in shallow water (40–50 cm), fish were individually dip-netted and either placed immediately into an anaesthetic bath containing tricaine methanesulfonate (MS-222; 100 mg l^{-1}) buffered with sodium bicarbonate ($NaHCO_3$; 200 mg l^{-1}) for immediate implantation of a data logger or temporarily held (mean 43 min; maximum 210 min) in a net pen ($L \times W \times D = 1.5 \times 1 \times 1.5$ m; positioned in the river at a water depth of about 70 cm) until they were required for data logger implantation. Fish capture procedures were repeated on 16 occasions over the 4-day period to obtain 28 salmon (13 males and 15 females; body mass = 2.4–4.2 kg; fork length (FL) = 59–72 cm), during which time ambient river water temperature ranged from 15.4 to 17.8°C.

Initial biosampling and surgical implantation of data loggers

Following loss of equilibrium of the fish in the anaesthetic bath, a 2-ml blood sample was taken by caudal puncture into a heparin-coated vacutainer and stored on ice for subsequent processing. As opercular movements became weak, the fish was weighed, measured and then placed on a surgery bench, as described previously

(Clark et al. 2009). Chilled water containing a maintenance dose of anaesthetic (70 mg l^{-1} MS-222, 140 mg l^{-1} $NaHCO_3$) continuously irrigated the gills. The fish was first placed ventral side down to insert identification tags (Peterson discs; Floy Tag, http://www.floytag.com) into the dorsal tissue, and to take a sample of adipose fin tissue for subsequent population (=stock) identification using DNA analysis (Beacham et al. 2004a, b). The fish was then rolled into a supine position for implantation with a data logger (iLogR, mass 23 g in air; B.D. Taylor, La Trobe University, Melbourne, Australia). Methods of data logger implantation have been detailed previously (Clark et al. 2009). Briefly, a sterilised data logger was inserted into the visceral cavity through a 3-cm incision along the ventral midline, just anterior to the ventral fins and associated cartilage. The data logger was loosely sutured to the peritoneal wall and associated ventral tissue, and then the incision was closed with silk sutures and further sealed with *n*-butyl cyanoacrylate tissue adhesive (Vetbond™, 3M). The entire procedure took about 20 min. Sex was confirmed by gonadal examination during implantation of the data logger.

The data logger was pre-programmed to record the date, time and temperature every 10 min, immediately followed by a 10.14-s recording at 200 Hz (i.e. every 5 ms) of the acceleration in two dimensions (i.e. *X* and *Y* axes). To maximise data storage in the memory of the logger, the acceleration data were packaged as follows. The logger first calculated the absolute difference between the start and end value of each 5 ms sample interval for each axis, and then the values were cumulatively summed for each axis throughout the 10.14-s period (totalling 2,028 intervals per axis) to give a single *X* and a single *Y* value. Only these two values were archived to the memory of the data logger to provide an index of total acceleration in each axis throughout the measurement period. The position of the data logger within the visceral cavity was such that the *X* axis recorded lateral and dorso-ventral acceleration (including lateral acceleration associated with tail beats), and the *Y* axis recorded rostro-caudal acceleration and therefore any backward or forward acceleration. Fifteen of the 28 data loggers additionally measured the electrocardiogram (ECG) of the fish at 200 Hz during the same 10.14-s period for which acceleration data were obtained. The complete ECG trace over each 10.14-s period was stored to memory to allow subsequent viewing of the entire ECG waveform and ensure the accurate calculation of heart rate (f_H).

Following surgery, each fish was placed into a transport tank containing aerated freshwater and immediately taken to the Chehalis River Hatchery (<10-min drive), where it was placed into one of two holding raceways.

Holding raceways

The purpose of the raceway experiments was to expose two groups of fish to steady but different swimming challenges. The two rectangular holding raceways were constructed within a large outdoor concrete channel ($L \times W \times D = 50 \times 5 \times 2$ m) with flow-through river water at the Chehalis River Hatchery, in which water depth was maintained at about 50 cm. Each raceway ($L \times W = 7.5 \times 1$ m; wall height 1.5 m) was constructed using wooden boards along the outer lengths and plastic mesh at each end. The 'fast' raceway utilised the water inlet at the front of the concrete flow-through channel. The inlet water was directed down a stainless steel ramp ($L \times W = 3 \times 1$ m; angle $\sim 45°$) into and along the fast raceway, and it exited primarily at the rear but also at small unsealed gaps between the wooden boards along the length of the raceway. Water velocity ranged from 1.00 m s^{-1} at the front of the raceway to 0.30 m s^{-1} at the rear, with uniform flow across the width of the raceway. The 'slow' raceway, positioned 10 m further back in the concrete flow-through channel, had a uniform velocity of 0.15 m s^{-1} along its length. Fish were not offered food, as they had ceased feeding naturally several weeks earlier as they prepared for freshwater entry and spawning. On one occasion, a subsample of fish from each raceway ($N = 8$) was visually monitored for 5 min each to measure tail beat frequency (f_{TB}), with the aim to correlate values with measurements of acceleration from the data loggers.

There was large inter-individual variation in the rate of senescence of the fish used in the present study, which is normal during the final few weeks prior to spawning. Only fish that were in excellent physical condition were included in the data analyses (sample sizes given in text and in table and figure legends).

Respirometry

After at least a 3-day recovery period, individual fish that were in excellent physical condition were placed in a large (425 l) swim tunnel respirometer (Lee et al. 2003b; Steinhausen et al. 2008) for calibration experiments (only fish from the Weaver Creek population were used; see "Results"). A fish was dip-netted from a raceway in the evening and transported in an aerated freshwater bath to the respirometer (<1 min), where it recovered overnight at a water velocity of 0.25 m s^{-1} ($\sim$0.39 FL s^{-1}; swimming speeds were corrected for the solid blocking effect of each individual using the method described by Jones et al. 1974). The respirometer was equipped with an automatic ambient water flush pump set on a 30:30 min on:off cycle, which enabled automatic determinations of oxygen consumption rates ($\dot{M}O_2$) every other 30 min based on the

decline in oxygen saturation of the respirometer water as monitored continuously by an OxyGuard oxygen electrode (Mark IV, Point Four Systems, Richmond, Canada). Data were recorded at 1 Hz using LabChart software (ADInstruments, Sydney, Australia) and stored to a personal computer. Following overnight recovery, swimming speed was incrementally stepped up to a maximum of 1.02 m s^{-1} (~1.74 FL s^{-1}) using one increment of about 0.25 m s^{-1} every 1–2 h. This protocol allowed fish to reach steady-state conditions at each speed. The clear Perspex working section of the respirometer (diameter 25.4 cm, length 124.3 cm) was covered with black plastic to minimise visual disturbance of the fish, although three vertical strips of 2-cm width were left uncovered along the length of the working section to enable visual observations of the fish. The f_{TB} of each fish was quantified visually at several swimming speeds with the intention to correlate these data with the output of acceleration from the data loggers. Following the swim test, fish were lightly anaesthetised within the respirometer to ensure an easy removal and easy measurement of body mass, length, height, width and girth (the latter three were measured immediately anterior to the insertion of the dorsal fin). Fish were revived in their respective raceway, but data recorded to the data loggers were not analysed for the 24 h following the return of the fish to the raceway to ensure recovery from handling. Water temperature in the respirometer remained at 12.5 ± 1.0°C throughout the 2-week experimental period, and did not change by more than 1°C during any one experiment.

Blood analyses

Haematocrit (Hct) of the initial caudal blood samples was determined using micro-capillary tubes spun at 10,000×*g* for 7 min, haemoglobin concentration ([Hb]) was determined using a handheld haemoglobin analyser appropriately calibrated for fish blood (HemoCue 201+, http://www.hemocue.com; Clark et al. 2008b), and mean corpuscular haemoglobin concentration (MCHC) was calculated as [Hb]/(Hct/100). Remaining whole blood was spun at 7,000×*g* for 7 min, and then the plasma was collected in Eppendorf tubes and stored in liquid nitrogen prior to being transferred to a −80°C freezer for subsequent analyses. Plasma measurements were made of cortisol (Neogen ELISA with Molecular Devices Spectramax 240pc plate reader), lactate, glucose (YSI 2300 stat plus analyser), osmolality (Advanced Instruments 3320 freezing point osmometer), chloride (Haake Buchler digital chloridometer), sodium and potassium (Cole-Parmer, model 410 single channel flame photometer) (see Farrell et al. (2001) for further details). The hormones testosterone and 17β-estradiol were assayed in duplicate after appropriate dilution and ether extraction (enzyme-linked immunosorbent assay, Neogen Co., Lexington, KY) to quantify the level of reproductive maturation of each fish.

Post-mortem measurements

All fish were killed upon the completion of the data logging period using a sharp blow to the head, and body mass and length were measured. The data logger was retrieved and subsequently downloaded to a personal computer using a custom-built interface. In addition, a cube of muscle tissue (mean mass 156 ± 7 g) was removed from the dorsal left side of the fish between the pectoral fin and the dorsal fin for proximate analysis. Energy density of the sample was calculated on the basis of 39.5 kJ g^{-1} of fat and 23.6 kJ g^{-1} of protein (this method provides an accurate index of whole body gross somatic energy density; D.A. Patterson, Canadian Department of Fisheries and Oceans, unpublished data).

Data handling and statistics

The text file from each data logger was imported into the software program LabChart (ADInstruments, Sydney, Australia) for subsequent analyses. The date and time records from the data logger were used to link archived data with field notes and respirometry data. A rate-meter function was applied to the ECG data to calculate instantaneous f_H, and all data were inspected manually to ensure correct values. The *X* and *Y* values from the accelerometer were summed, and the resulting value is herein termed 'acceleration activity' (AA), with no specific units. Rates of oxygen consumption (mg O_2 min^{-1} kg^{-1}) were converted to rates of energy expenditure (J min^{-1} kg^{-1}) assuming 1 mg O_2 is used per 14.1 J of energy expended (Elliott and Davison 1975; Brett and Groves 1979). All statistical analyses were performed in the programs SigmaStat (Build 3.01.0, Systat Software Inc.), SigmaPlot (Build 10.0.1.2, Systat Software Inc.), and SPSS (Build 16.0, SPSS Inc.). Data were log-transformed where necessary to satisfy tests for normality. Statistical differences between sexes were examined for (1) daily mean f_H and daily mean AA within each raceway (two-way repeated measures ANOVA; $P > 0.253$), (2) f_H, AA, f_{TB} and rate of energy expenditure at defined swimming speeds in the tunnel respirometer (repeated measures ANOVA; $P > 0.200$), and (3) caudal blood samples taken at the time of instrumentation (*t* tests and ANOVA; Table 1). Significant sex-specific differences were found only for some blood variables, and so male and female data for all other variables were combined for subsequent analyses.

Table 1 Mean (±SEM) and ranges for mass, fork length, and all blood variables for two populations of sockeye salmon (*Oncorhynchus nerka*) at the initial caudal sampling

	Male		Female	
	Weaver	Harrison	Weaver	Harrison
N	5	8	10	5
Mass (kg)	3.5 ± 0.2 (2.4–4.1)	3.5 ± 0.2 (2.9–4.1)	3.1 ± 0.1 (2.5–4.2)	2.9 ± 0.1 (2.7–3.3)
Fork length (cm)	67 ± 2 (59–72)	68 ± 1 (63–72)	64 ± 1 (59–70)	64 ± 1 (61–67)
[Hb] (g l^{-1})	91.0 ± 8.6 (61.0–108.2)	83.4 ± 3.5 (75.2–101.3)	96.0 ± 3.4 (76.0–113.5)	84.0 ± 4.5 (71.2–94.4)
Hct (%)	48.9 ± 4.1 (36.9–61.5)	40.8 ± 2.8^{A} (30.8–57.1)	51.7 ± 2.4^{A} (36.4–68.9)	42.0 ± 3.5 (34.2–51.5)
MCHC (g l^{-1})	185 ± 7 (165–210)	207 ± 9 (177–247)	188 ± 6 (161–227)	203 ± 10 (177–228)
Cortisol (ng ml^{-1})	110 ± 33^{A} (10–194)	161 ± 57^{B} (17–487)	431 ± 72^{AB} (59–782)	363 ± 77 (99–578)
17β-Estradiol (ng ml^{-1})	0.18 ± 0.01^{BD} (0.15–0.24)	0.12 ± 0.01^{AC} (0.08–0.15)	2.58 ± 0.10^{AB} (2.03–3.21)	2.24 ± 0.12^{CD} (1.89–2.57)
Testosterone (ng ml^{-1})	40.5 ± 14.3 (22.0–111.5)	14.5 ± 5.5^{A} (3.0–50.8)	69.6 ± 9.5^{AB} (1.2–116.7)	26.9 ± 6.4^{B} (13.8–49.1)
Glucose (mmol l^{-1})	6.53 ± 0.57 (4.29–7.80)	5.77 ± 0.60 (3.97–9.04)	5.16 ± 0.33 (2.37–6.54)	5.45 ± 0.76 (3.69–7.50
Lactate (mmol l^{-1})	11.4 ± 2.6 (3.4–19.8)	8.0 ± 1.6 (4.2–17.2)	13.9 ± 1.6 (4.1–20.5)	11.8 ± 3.1 (5.3–23.0)
Cl^{-} (mmol l^{-1})	128.7 ± 0.6 (126.1–129.7)	129.9 ± 2.0 (120.5–137.2)	126.6 ± 2.1 (112.5–141.0)	133.9 ± 1.6 (129.0–138.6)
Na^{+} (mmol l^{-1})	158.3 ± 1.1 (154.7–161.0)	155.9 ± 2.1 (145.1–165.2)	157.2 ± 2.8 (141.7–174.0)	159.4 ± 1.7 (154.2–164.7)
K^{+} (mmol l^{-1})	0.70 ± 0.43 (0.20–2.81)	2.02 ± 0.47 (0.20–3.52)	1.23 ± 0.64 (0.20–8.19)	0.54 ± 0.16 (0.25–1.11)
Osmolality (mOsm kg^{-1})	333.3 ± 6.4 (315.5–351.5)	316.1 ± 4.1 (301.5–334.5)	324.1 ± 7.9 (272.5–361.3)	330.2 ± 4.8 (315.5–345.0)

Similar letters indicate significant differences within each row (ANOVA, $P < 0.05$)

Results

Initial biosampling

DNA analyses revealed two distinct spawning populations in the experimental fish: Harrison sockeye (8 males, 5 females) and Weaver Creek sockeye (5 males, 10 females). Higher testosterone concentrations in Weaver sockeye suggested a more advanced state of sexual maturation compared with Harrison sockeye, while cortisol and 17β-estradiol were higher in females than males (Table 1). Aside from a higher Hct in Weaver females compared with Harrison males (Table 1), none of the other variables measured in this study showed significant effects of population or sex.

Grouped fish in raceways

Periodic visual observations indicated that the fish generally remained unagitated throughout the experimental period, and shifting of position within the group was seldom vigorous. The fish in the fast raceway typically remained in the rear one-third of the raceway where water velocities were 0.30–0.55 m s^{-1}, which were two to five times faster than the slow raceway. An example of the data obtained from the data loggers is presented in Fig. 1. These continuous recordings revealed that periods of vigorous activity (as indicated by elevated AA) were indeed occasional but more frequent in the fast raceway (e.g. bottom trace of Fig. 1).

Two-way repeated measures ANOVA (with 'day' and 'raceway' as factors) revealed significant differences between raceways for each of f_H ($P = 0.049$) and AA ($P < 0.001$). As anticipated, fish swimming in the fast raceway exhibited significantly higher f_H and AA than fish swimming in the slow raceway (Fig. 2). Frequency histograms revealed that the fish in the slow raceway spent most (~55%) of their time at f_H between 35 and 44 beats min^{-1}, whereas the fish in the fast raceway maintained higher, more variable rates, with only about 32% of their time at f_H between 35 and 44 beats min^{-1}. Frequency histograms for AA illustrate similar results, where the distribution of data for fish in the fast raceway is right-shifted (i.e. higher AA) in comparison with fish in the slow raceway (Fig. 2). While AA of fish in both raceways was maintained independent of natural fluctuations in water temperature, f_H was temperature-dependent (Fig. 2). The effects of natural water temperature changes on daily mean f_H are illustrated in Fig. 3 for fish in each raceway.

Swim tunnel calibrations

A strong exponential relationship existed between f_{TB} and AA as individual fish swam progressively faster in the tunnel respirometer (Fig. 4). Concomitant with the increase in AA with swimming speed were increases in f_H and the rate of energy expenditure. Strong linear relationships were established between the rate of energy expenditure and each of AA and f_H (Fig. 5). A repeated measures stepwise multiple linear regression, conducted on those fish for

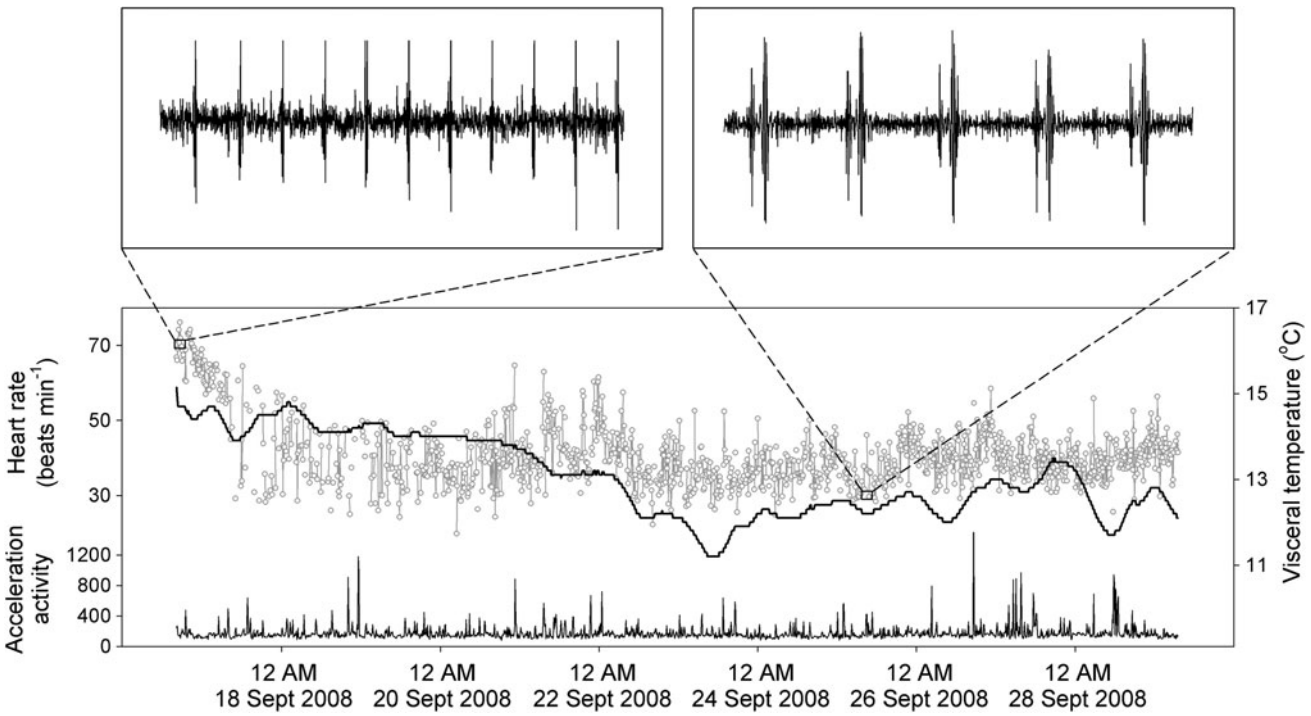

Fig. 1 Representative traces for a male Weaver Creek sockeye salmon (*Oncorhynchus nerka*) of visceral temperature, heart rate and acceleration activity over approximately a 12-day period in the fast raceway. *Top panels* display raw electrocardiogram (ECG) data from the time points indicated by *small rectangles*

which all of AA, f_H, visceral temperature and energy expenditure were measured simultaneously ($N = 11$), resulted in the following equation (standard error, SE, in parentheses):

$$\begin{aligned}\text{Energy expenditure (J min}^{-1}\text{ kg}^{-1}) &= -43.762(\text{SE} = 8.712) + 0.068(\text{SE} = 0.008)\text{AA} \\ &\quad + 1.513(\text{SE} = 0.198) f_H, \end{aligned} \quad (1)$$

where $P < 0.001$ and the standard error of the estimate = 10.267 ($r^2 = 0.650$ after the stepwise inclusion of AA, $r^2 = 0.818$ after the additional inclusion of f_H, while the inclusion of visceral temperature did not significantly improve the relationship possibly because of the small range examined, i.e. 11.5–13.5°C). Subsequently, the regression equations determined during the respirometry calibrations (Eq. 1 and other equations presented in Fig. 5) were used to estimate the rates of energy expenditure of the grouped fish.

Energy expenditure of grouped fish in raceways

Estimates of energy expenditure of the fish in the raceways, based on each of f_H, AA, and a combination of the two variables (i.e. Eq. 1), are illustrated in Fig. 6. For the slowly swimming fish, the mean estimated rates of energy expenditure were similar across the experimental period (28.8 ± 3.7, 29.2 ± 0.7, 24.1 ± 2.4 J min^{-1} kg^{-1}, respectively). However, for the fast swimming fish, significant differences were apparent among the energy expenditure estimates from each of the algorithms (50.6 ± 5.3, 36.4 ± 0.8, 42.4 ± 3.7 J min^{-1} kg^{-1}, respectively). These values were largely influenced by the fact that (1) estimates based on Eq. 1 were largely governed by f_H because AA within each raceway showed little variation, and (2) f_H was temperature-dependent but AA was not, which is most evident throughout the first half of the experimental period (Figs. 3, 6).

Proximate analyses of gross somatic energy density revealed a significantly higher value for slowly swimming fish at death (5.04 ± 0.15 MJ kg^{-1}; $N = 13$) in comparison with fish in the fast raceway (4.68 ± 0.11 MJ kg^{-1}; $N = 15$; $P = 0.039$). The absolute difference between raceways (0.36 MJ kg^{-1}) corresponded to a 23.8 J min^{-1} kg^{-1} higher rate of energy expenditure of fast swimming fish across the experimental period. This value is remarkably consistent with the difference in energy expenditure between raceways as estimated from logging of f_H alone (21.8 J min^{-1} kg^{-1}) or in combination with AA (18.3 J min^{-1} kg^{-1}), but not for AA alone (7.2 J min^{-1} kg^{-1}). Thus, these agreements point to f_H, and f_H in combination with AA, as being reliable proxies for energy expenditure in grouped adult wild salmon.

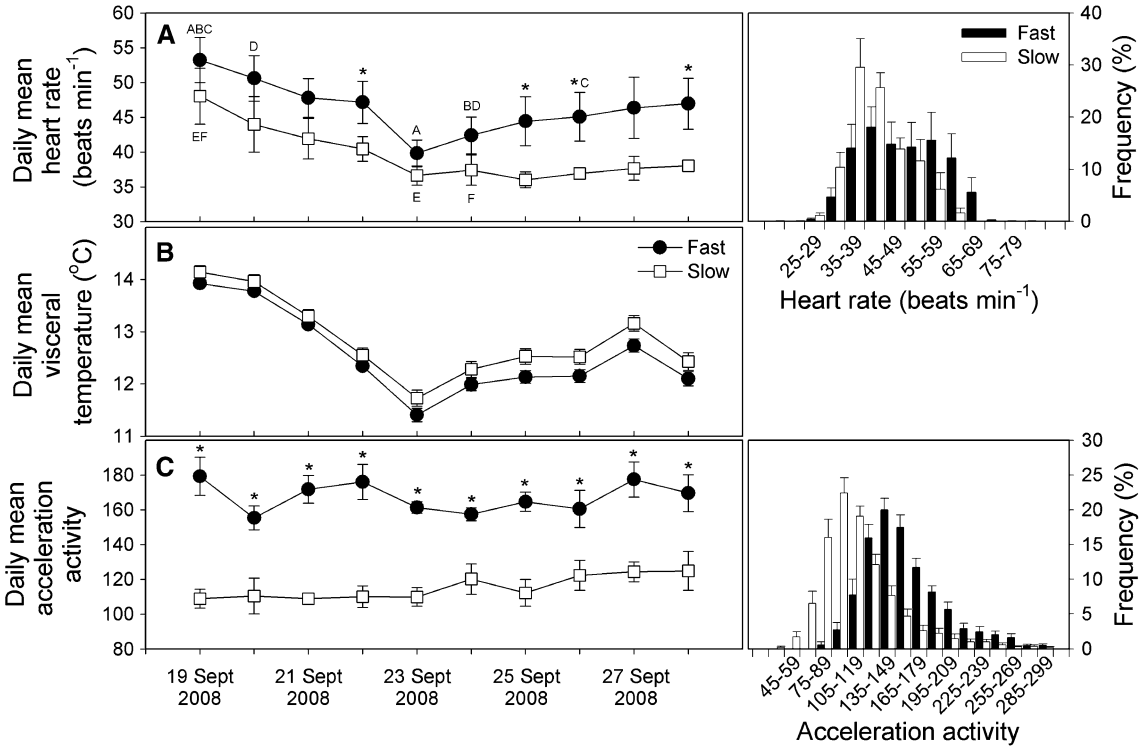

Fig. 2 **a** Daily mean heart rate ($N = 9$–14), **b** daily mean visceral temperature ($N = 12$–17) and **c** daily mean acceleration activity ($N = 12$–17) (±SEM) of sockeye salmon (*Oncorhynchus nerka*) in fast (*filled symbols*) and slow (*open symbols*) holding raceways over 10 days. *Asterisks* indicate significant differences between raceways within each day (no differences existed for visceral temperature), while *similar letters* denote differences across days within a raceway (*no letters* given for visceral temperature, as differences existed across all days except between 25 and 26 September, 24 and 28 September, and 22 and 26 September). Also presented are frequency histograms (mean ± SEM) for heart rate and acceleration activity to highlight the differences in frequency distributions between fish in the fast and slow raceways

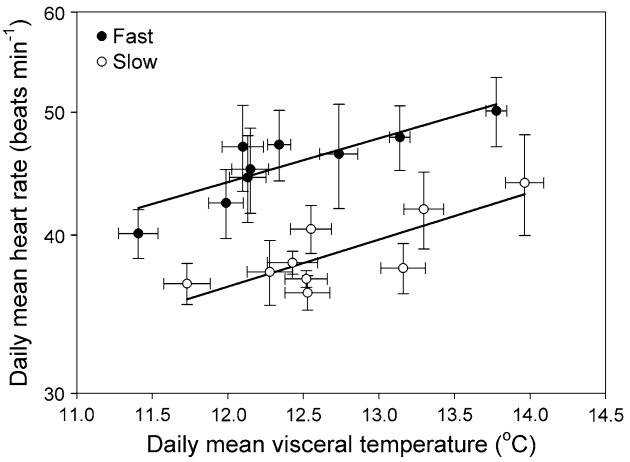

Fig. 3 Daily mean heart rate (f_H; logarithmic scale) as a function of daily mean visceral temperature (T_V) (±SEM) for sockeye salmon (*Oncorhynchus nerka*) in fast and slow holding raceways from midnight 20 September until midnight 29 September 2008. Regression lines for data from the fast and slow raceway, respectively, are described by: $f_H = 16.226\, e^{0.0830 T_V}$ ($r^2 = 0.756$, $P = 0.002$); and $f_H = 13.553\, e^{0.0825 T_V}$ ($r^2 = 0.628$, $P = 0.010$). Q_{10} values for heart rate between 11.5 and 14°C are 2.29 for the fast raceway, and 2.28 for the slow raceway. $N = 5$–7 for each raceway

Discussion

Heart rates and rates of oxygen consumption in salmonids

Biologging provides data from untethered fish in conditions where stress is minimised. Since stress elevates f_H in fishes, it is not surprising that the lowest f_H values measured here (~37 beats min^{-1} at 12°C) are among the lowest documented for any salmonid species at a comparable temperature (Figs. 3, 5; Altimiras and Larsen 2000; Clark et al. 2008c; Steinhausen et al. 2008). In the respirometry experiments, such low f_H corresponded with $\dot{M}O_2$ values (~1.4 mg min^{-1} kg^{-1}) among the lowest reported previously for other salmonids (Fig. 5; Lee et al. 2003b; Clark et al. 2008c; Eliason et al. 2008; Steinhausen et al. 2008). There is some evidence that grouped juvenile fish may maintain lower $\dot{M}O_2$ than when confined alone (e.g. Herskin and Steffensen 1998), yet increases in $\dot{M}O_2$ of grouped fish have also been documented (Sloman et al. 2000; Millidine et al. 2009). It was not possible to examine $\dot{M}O_2$ of groups of fish in the present study, although we

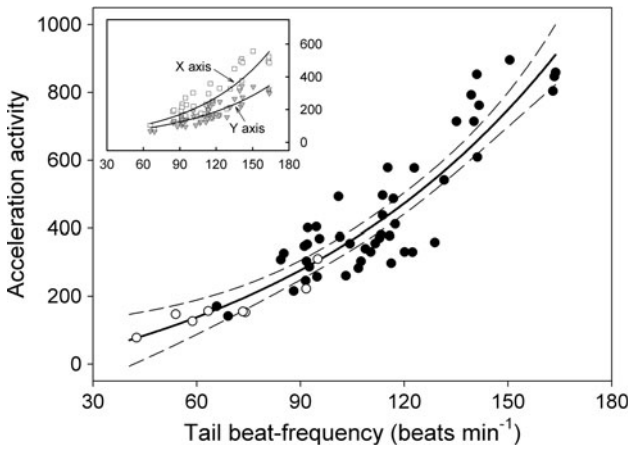

Fig. 4 Biologged acceleration activity (sum of *X* and *Y* acceleration) of Weaver Creek sockeye salmon (*Oncorhynchus nerka*) as a function of tail beat frequency (f_{TB}). Values were obtained from steadily swimming fish in a tunnel respirometer (*filled symbols*; 3–4 data points from each of $N = 14$ fish) and fish within raceways (*open symbols*; $N = 8$ fish). The exponential regression line was constructed using all data points and is described by: acceleration activity $= -199.385 + 169.766\, e^{0.0115 f_{TB}}$ ($r^2 = 0.85$; $P < 0.001$). *Dashed lines* are 95% confidence intervals. *Inset* illustrates the corresponding values of acceleration measured by the data loggers in each of the *X* (*squares*) and *Y* (*triangles*) axes while fish swam in the tunnel respirometer (two-parameter exponential regression lines are described by: *X* axis acceleration $= 39.957\, e^{0.016 f_{TB}}$, $r^2 = 0.69$; *Y* axis acceleration $= 35.697\, e^{0.014 f_{TB}}$, $r^2 = 0.79$)

believe that the likelihood of a decrease in $\dot{M}O_2$ related to grouping would be negligible in the large adult salmon used here.

The present study is the first to measure f_H simultaneously with $\dot{M}O_2$ for untethered sockeye salmon across a broad range of swimming speeds. Similar to several previous studies on other species of fish (Armstrong 1986; Lucas 1994; Claireaux et al. 1995; Clark et al. 2005), there existed a strong relationship between f_H and $\dot{M}O_2$ (=energy expenditure rate) in sockeye salmon (Fig. 5). Although temperature had a marked effect on f_H (Fig. 3), there was no evidence of temperature influencing the intercept of the regression between f_H and $\dot{M}O_2$ for sockeye salmon over the narrow temperature range examined in the respirometry experiments (Fig. 5). This result is similar to those for other salmonids (Atlantic salmon, *Salmo salar*, Lucas 1994; rainbow trout, *Oncorhynchus mykiss*, T.D. Clark, unpublished data) and pike (*Esox lucius*, Armstrong 1986). In contrast, others have reported that water temperature [both short-term (acute) and long-term (acclimation)] does alter the intercept of the regression between f_H and $\dot{M}O_2$ in some fishes, including Atlantic cod (*Gadus morhua*, Claireaux et al. 1995) and Murray cod (*Maccullochella peelii peelii*, Clark et al. 2005). Given this potential interspecific diversity of the effect of temperature on the relationship between f_H and $\dot{M}O_2$, temperature should remain

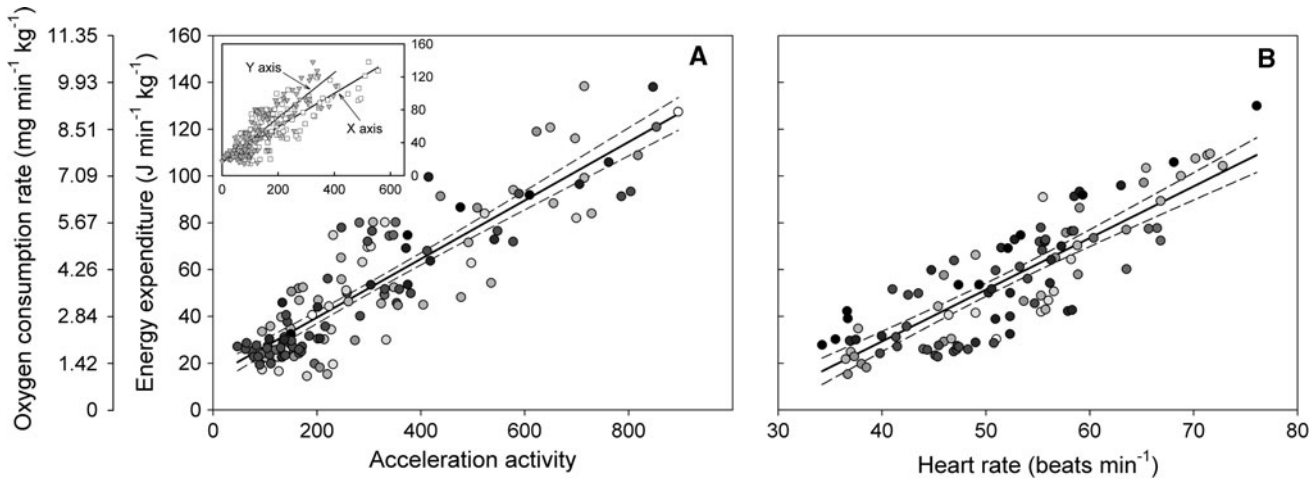

Fig. 5 Energy expenditure rate (=oxygen consumption rate) of Weaver Creek sockeye salmon (*Oncorhynchus nerka*) as a function of biologged **a** acceleration activity ($N = 14$; sum of *X* and *Y* acceleration) and **b** heart rate ($N = 11$) while swimming in a tunnel respirometer at temperatures ranging from 11.5°C (*white*) to 13.5°C (*black*). Regressions were determined using general linear models in which individual identity was a random factor and acceleration activity or heart rate was a covariate. The regression for acceleration activity (including standard errors (SE) in parentheses) is described by: energy expenditure = acceleration activity × 0.126 (SE = 0.006) + 14.632 (SE = 2.086) ($r^2 = 0.781$, $P < 0.001$, SE of estimate = 13.964); and the regression for heart rate is described by: energy expenditure = heart rate × 2.209 (SE = 0.142) − 59.081 (SE = 7.497) ($r^2 = 0.698$, $P < 0.001$, SE of estimate = 14.293). *Dashed lines* are 95% confidence intervals. *Inset* illustrates the corresponding values of acceleration measured by the data loggers in each of the *X* (squares) and *Y* (triangles) axes (regressions are described by: energy expenditure = *X* axis acceleration × 0.203 + 18.733, $r^2 = 0.712$; energy expenditure = *Y* axis acceleration × 0.274 + 15.313, $r^2 = 0.753$)

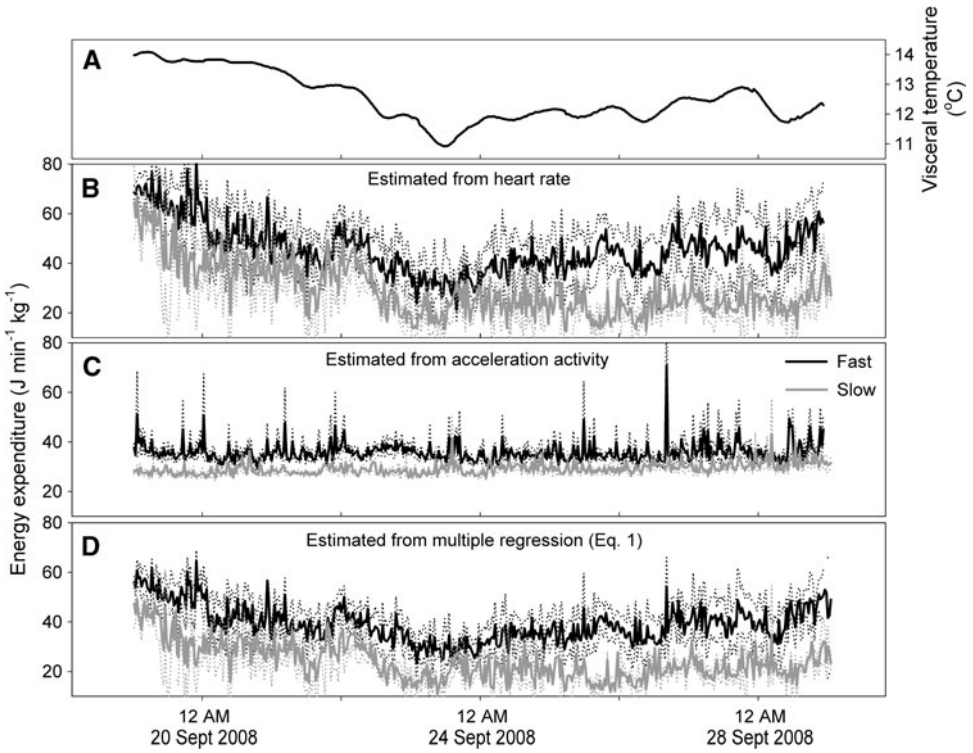

Fig. 6 **a** Visceral temperature and **b–d** rates of energy expenditure of sockeye salmon (*Oncorhynchus nerka*) while holding in the slow and fast raceways (*solid lines* are means, *dotted lines* are ± SEM), as estimated using regression equations for each of heart rate and acceleration activity (see Fig. 5), and a combination of the two (Eq. 1). The mean rates of energy expenditure across the experimental period **b** estimated from heart rate are 28.8 ± 3.7 J min^{-1} kg^{-1} for fish in the slow raceway and 50.6 ± 5.3 J min^{-1} kg^{-1} for fish in the fast raceway, **c** estimated from acceleration activity are 29.2 ± 0.7 J min^{-1} kg^{-1} for fish in the slow raceway and 36.4 ± 0.8 J min^{-1} kg^{-1} for fish in the fast raceway, and **d** estimated from Eq. 1 are 24.1 ± 2.4 J min^{-1} kg^{-1} for fish in the slow raceway and 42.4 ± 3.7 J min^{-1} kg^{-1} for fish in the fast raceway

an important variable whenever f_H is to be used as a proxy for energy expenditure over a broad temperature range.

Estimating rates of energy expenditure in fish

Energy turnover, and particularly how it is allocated to specific activities, is of central importance to understanding the physiological, behavioural and evolutionary ecology of organisms (McNamara and Houston 1996). This is becoming increasingly apparent with current trends in global climate change (Pörtner and Farrell 2008). Several methods have been developed to estimate the rates of energy expenditure in free-roaming fish and other vertebrates, with many of them focussed on using correlates of movement (e.g. acceleration, f_{TB}, EMG recordings from locomotory muscles) as indices of energy turnover (Hinch and Rand 1998; Lowe et al. 1998; Lowe 2002; Healey et al. 2003; Cooke et al. 2004c; Steinhausen et al. 2005; Clark et al. 2006; Wilson et al. 2006). Nevertheless, it is likely for several reasons that f_H was a more powerful proxy of energy expenditure than AA in the grouped fish in the present study.

First, it is well-established that energy expenditure of ectothermic animals is temperature-dependent, and therefore the temperature dependency of f_H is likely to provide a stronger correlation with energy expenditure than the temperature-independent AA (Fig. 6). Second, a brief bout of vigorous exercise (seconds to minutes) may utilise anaerobic metabolic pathways and consequently incur an oxygen debt that must be 'paid back' using aerobic pathways during the post-exercise recovery period (minutes to hours; Wood 1991; Lee et al. 2003a). While an increase in f_H is typical during the post-exercise recovery period to assist with oxygen debt recovery, correlates of fish movement such as AA are unlikely to correlate with oxygen transport because of the tendency for fish to resume low levels of activity while recovering from vigorous exercise. Indeed, this is likely to be the main cause of the apparent underestimate of energy expenditure based on AA in the fast swimming fish in the present study, given that these fish occasionally underwent short periods of vigorous exercise as they attempted to swim to the front of the raceway where water velocities were high (~1 m s^{-1}). Finally, it was f_H alone and in combination with AA, rather

than AA alone, that provided estimates of energy expenditure where the difference between raceways was most similar to the difference estimated using proximate analyses.

Thus, under the conditions examined in the raceways in the present study (i.e. fluctuating temperature, generally constant levels of activity interspersed with brief periods of vigorous exercise), it is concluded that f_H alone and in combination with AA provided better estimates of total energy expenditure than AA alone. This is likely to have been even further exacerbated if the fish were feeding throughout the experiment (sockeye salmon cease feeding naturally in the ocean prior to the spawning migration), as f_H can provide accurate estimates of energy expenditure during digestion (Lucas and Armstrong 1991; Lucas et al. 1991; Clark et al. 2008a; Eliason et al. 2008), whereas correlates of fish movement cannot. Nevertheless, AA proved useful in providing information on the behaviour and f_{TB} of the fish within the raceways and swim tunnel, and its strong relationship with energy expenditure (Fig. 5a) suggests that AA may prove to be a useful proxy under different circumstances, such as conditions of relatively constant temperature when non-digesting fish remain relatively active (e.g. sockeye salmon on the spawning ground; Clark et al. 2009). Alternatively, the lack of temperature dependency of AA could be rectified through the use of simultaneous measurements of temperature and the formulation of multiple regression equations. Continuous measurements of dynamic acceleration (i.e. excluding static acceleration due to gravity) such as 'overall dynamic body acceleration' (ODBA; Wilson et al. 2006; Halsey et al. 2009), rather than intermittent measurements of AA as used here, will additionally help to increase the efficacy of acceleration as a proxy for energy expenditure.

Conclusions

This study conducted simultaneous measurements of behaviour (AA) and physiology (f_H) from grouped fish, and highlighted some experiments that can be conducted under controlled conditions to ultimately quantify and maximise the information obtained from biologging and biotelemetry devices deployed in wild fish in the natural environment. For example, measurements of acceleration from wild fish that remain out of human sight (e.g. at depth, in turbid water, or at sea) may provide accurate estimates of f_{TB} following calibration of the relationship under more controlled conditions (e.g. Fig. 4; Gleiss et al. 2009).

The advent of biologging and biotelemetry devices that measure acceleration and f_H has provided new insight into the behaviour and physiological function of wild fish (Priede and Tytler 1977; Kawabe et al. 2003; Cooke et al. 2004a; Clark et al. 2008a, 2009). While the present study was concerned with the effects of swimming activity (and, to a lesser extent, water temperature) on AA and f_H, and how these variables interact with rates of energy expenditure, measurements of acceleration and f_H may also provide a useful tool for investigating the effects of stressful perturbations on the behaviour and physiology of fishes (e.g. predator/fisheries interactions; Laitinen and Valtonen 1994; Cooke et al. 2004a, b). Finally, with appropriate experiments to calibrate the interrelations between f_H and $\dot{M}O_2$ across a broad range of temperatures and activities, f_H scope models in combination with field f_H and temperature measurements may have greater utility than aerobic scope models (Wang and Overgaard 2007; Pörtner and Farrell 2008) in providing real-time information on the metabolic status of free-swimming fish in the natural environment.

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