Estimating Adult Pacific Salmon Energy Use in Coastal British Columbia and the Fraser River Estuary with Acoustic Accelerometer Transmitters

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Abstract

Energy depletion is a significant concern for animals that migrate long distances on fixed energy budgets. Migrating adult Fraser River sockeye salmon (*Oncorhynchus nerka*) cease feeding in the ocean and are entirely reliant on endogenous energy stores to successfully complete their subsequent freshwater migration and spawn. Most research on adult salmon energy use has focused on the riverine component of the migration, yet the coastal migration could be energetically costly, particularly in estuarine areas where temperatures can be warm and tidal currents turbulent. We compared the relative energetic costs of salmon migrations through coastal, estuarine, and riverine areas by tagging and tracking 38 adult sockeye salmon with acoustic tri-axial accelerometer transmitters for over 200 km along the British Columbian coast and through the Fraser River estuary. Accelerometer output was converted to temperature-specific rates of oxygen consumption. Oxygen consumption rates were twice as high in the riverine compared to coastal marine regions (including the estuary), driven largely by higher swim speeds. Oxygen consumption rates were also influenced by diel period, where energy use was higher during mid-day; however, we found no evidence that tidal cycles influenced energy use. Despite higher oxygen consumption rates in the Fraser River, cost of transport (kJ^{-1} kg^{-1} km) was highest in Seymour Narrows (a narrow coastal region with high tidal flushing), consistent with previous research showing this is a potentially challenging area for migrating salmon. Overall, we have demonstrated that coastal marine energy use is an important component of the spawning migration energy budget for Pacific salmon.

Keywords Accelerometer · Energy Use · Sockeye salmon · Telemetry

Introduction

Reproductive migrations are energetically costly and understanding how energy is allocated to specific activities is important for assessing sensitivity to environmental change (Lennox et al. 2016). Energy allocation during reproductive migrations is balanced among somatic maintenance, movement, and gamete production (Calow 1985). This is especially true in the case of capital breeders, which fuel migrations solely through endogenous energy reserves, and depletion of energy reserves may lead to an abandonment of that reproductive attempt, or death (Jönsson 1997), as well as

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for semelparous species, where failure to reproduce results in zero lifetime fitness (Patterson et al. 2004). Changes from historic environmental norms, such as alterations in temperature, destruction of critical stopover habitat, and in the case of aquatic migrations, alteration of flow regimes such as the installation of dams, can influence energy use, condition, and survival of migrants (Wilcove and Wikelski 2008). In particular, migratory fish may be especially sensitive to environmental change and anthropogenic disturbance (e.g. fishing pressure), as the energetic costs of disturbance are often highest at critical points in their life history (e.g. when diadromous fish aggregate in estuaries; McDowall 1999; Donaldson et al. 2011). Thus, understanding overall energetic requirements for migrations and how migration behaviour and environmental conditions influence these energy requirements is important for understanding the ecology of migrating species and informing conservation efforts (McDowall 1999; Lennox et al. 2016).

Despite the importance of understanding energetic requirements during sensitive life stages, estimating bioenergetics in free swimming fish remains a major challenge (Lucas et al. 1993; Cooke et al. 2016; Treberg et al. 2016). Biotelemetry and biologging enable remote observations of free ranging animals. When equipped with electromyogram or acceleration sensors, such devices can be used for estimating energy use and movement behaviours. Electromyogram (EMG) transmitters have been used to measure movement in free swimming animals, but are sensitive to placement in the musculature, so each tag needs to be individually calibrated, which is logistically challenging (Beddow and McKinley 1999; Brown et al. 2007). Biologgers equipped with acceleration sensors do not require individual calibration, though they do require methodological calibration (e.g. calibration based on tagging location, processing window, species, life stage). Biologgers can measure and store large quantities of acceleration values, but must be recovered and downloaded to obtain data, a serious logistical challenge for species with large home ranges or long distance migrations (reviewed in Cooke et al. 2016). Transmitters equipped with acceleration sensors do not require individual calibration or recovery of tags (i.e. to download logged data). Such devices measure acceleration in two or three axes, averaged over a set sampling interval, and transmit the data to a receiver where the data is stored. Unlike loggers which enable recording of vast quantities of data, acceleration values are only recorded when a tagged animal is within the range of a receiver. Thus, tagged animals must have a known home range or predictable movement patterns so receivers can be strategically placed. Accelerometer transmitters have successfully been used to measure activity and/or energy use in a variety of animals including cuttle fish (*Sepia officinalis* Payne et al. 2011), bonefish (*Albula vulpes* Brownscombe et al. 2017), and lake trout (*Salvelinus namaycush* Cruz-Font et al. 2016).

They have also been used to measure swim speed (Burnett, et al. 2014a, b; Wilson et al. 2014) and estimate aerobic and anaerobic metabolism (Burnett et al. 2014a, b) in migrating sockeye salmon (*Oncorhynchus nerka*), but have yet to be used to measure energy use in free-swimming salmon in the marine environment.

Many Pacific salmon (*Oncorhynchus* spp.) populations undertake arduous, energetically expensive reproductive migrations of greater than a 1000 km with elevation gains of over 1000 m which require several weeks to complete (Groot and Margolis 1991; Quinn 2005). Adult salmon cease feeding prior to river entry, with some beginning to fast hundreds of kilometers from the mouth of their natal river (Morash et al. 2013), becoming reliant on endogenous energy stores for the remainder of their spawning migration (Groot et al. 1995). As a result, body fat can be depleted by up to 75–95% between start and end of spawning migration (Idler and Clemens 1959, reviewed in Brett 1995). Due to their fixed endogenous energy allocation, salmon can be sensitive to changes in environmental conditions that increase energy costs above historical requirements. For example, during years when ocean feeding conditions are poor, returning adult sockeye salmon have lower than average somatic energy density (Crossin et al. 2004a, b), which can lead to increased risk of en-route (i.e. during migration) and pre-spawn mortality (Hinch et al. 1995, 2006; Crossin et al. 2004a, b). Understanding energy requirements of adult migrating salmon can help estimate sensitivity to energy exhaustion and inform estimates of en-route and pre-spawn mortality.

Climate-driven warming of rivers and higher flows increase the energetic requirements of freshwater migration and spawning, such that energy requirements may increasingly exceed somatic energy storage (Gilhousen 1980, 1990; Rand and Hinch 1998; Crossin et al. 2004a, b; Crozier et al. 2008; Macdonald et al. 2010). For example, climate warming has already increased peak summer water temperatures in the Fraser River by 2 °C since the 1950s (Patterson et al. 2007), contributing to large levels of en-route mortality in some years (Crossin et al. 2008; Mathes et al. 2010; Martins et al. 2011; Macdonald et al. 2012). For ectotherms, such as salmon, warming water temperatures increase standard metabolic rates, leading to increased oxygen consumption rates and energy use. In fact, standard metabolic rate increases exponentially with warming temperatures and can as much as double over a 10 °C temperature differential (Brett 1971; Fry 1971; Lee et al. 2003; Eliason et al. 2011; Eliason and Farrell 2016). Active metabolic rate also increases with temperature, albeit less dramatically than standard metabolic rate. As aerobic swimming activity increases, active metabolic rate can increase by three- to five-fold compared to when inactive. Accordingly, metabolic rate is influenced both by temperature and activity (Eliason and Farrell 2016).

Increased energy use over historic norms may have lethal or sublethal effects on individuals, as increased energy requirements during migration may leave less energy available for gamete production (Crossin et al. 2004a, b; Braun et al. 2013), and reduced maternal condition may result in reduced offspring quality (e.g. size, prolonged swim performance; Tierney et al. 2009; Braun et al. 2013; Sopinka et al. 2014). With increasing human impact on coastal and estuarine systems (Crain et al. 2009), quantifying animal energy use is a potentially powerful approach for understanding the ecological consequences of such anthropogenic activities.

Energetic modelling of freshwater energy use has been used to predict the risk of energy exhaustion in migrating adult salmon (Rand and Hinch 1998; Macdonald et al. 2010). However, these models are predicated on knowledge of fish condition and behaviour. For example, while there are some differences between male and female sockeye salmon energy use during upstream migration in the Fraser River of British Columbia (Idler and Clemens 1959), the primary driver of energy use patterns is swim speed, where river constrictions and turbulent flows result in milling and increases in energy use (Hinch et al. 1996; Hinch and Rand 1998). Salmon from populations with long migrations generally have higher densities of somatic energy, smaller eggs, and lower cost of transport than fish swimming shorter distances (Crossin et al. 2004a, b). Thus, salmon morphometrics and sex, as well as environmental conditions such as flow rate and water temperature, can influence energetic requirements for freshwater migration. Individual- (e.g. sex, mass), and population-level (e.g. morphometrics, fecundity) traits can affect energy efficiency and energy consumption during freshwater migrations, and therefore influence the sensitivity to sublethal effects or mortality from energy exhaustion. While there is substantial information on energy use during the freshwater migration of adult salmon (Idler and Clemens 1959; Gilhousen 1980; Hinch et al. 1996; Hinch and Rand 1998, 2000), much less is known about energy use during the coastal marine phase of the adult salmon spawning migration.

To estimate a complete energy budget for the non-feeding portion of the adult salmon migration, both freshwater and coastal marine energy use must be modelled, as coastal migrations could be energetically costly, particularly in estuaries given tidal processes that can lead to warm water temperatures and turbulent flows. Several populations of Fraser River sockeye delay their freshwater entry by milling, but not feeding, for up to 6 weeks in the estuary before initiating their upriver migration; a period of time that easily exceeds the duration of their freshwater migration (Cooke et al. 2004; English et al. 2005; Thomson and Hourston 2011; Wilson et al. 2014). This coastal non-feeding phase of the adult spawning migration could, therefore, represent a significant portion of the overall energy budget, but has received comparatively less attention than the freshwater migration

phase. A description of energy use during coastal migration in the period after feeding ceases but before entrance into the river, is required for complete understanding of spawning migration energy requirements, and to model how these may change under climate change. In this paper, we utilize behavioural and migratory information (Wilson et al. 2014), along with an established oxygen consumption calibration model developed from sockeye salmon carrying accelerometer transmitters swum in tunnel respirometers (Wilson et al. 2013), to assess energy use during the coastal marine migration of sockeye salmon tagged in coastal British Columbia, Canada and tracked through the Strait of Georgia and the lower Fraser River. Given the importance of activity and temperature to metabolic rates of salmon, we predict that areas with high hydraulic complexity, which can result in increased swimming speed, and/or migration in areas or times that have higher temperatures will have increased energy expenditure. Given that in river conditions are often warmer and have higher flows, we predict that oxygen consumption rates in the river will be higher than in the marine environment. For example, areas of constrictions (Hinch et al. 1996; Hinch and Rand 1998), higher tide heights (Levy and Cadenhead 1995; Wilson et al. 2014), day time (Wilson et al. 2014), and male salmon (Hinch and Rand 1998; Standen et al. 2002) have all been demonstrated to have increased activity-levels, which may translate to higher rates of oxygen consumption. Specifically, we examined how sex, fork length, array location, tide level, diel patterns, and migration difficulty influenced rates of oxygen consumption.

Methods

This study was part of a broader research program to use newly developed accelerometer transmitters to examine the coastal and estuarine migration of sockeye salmon. Two other studies have been published pertaining to this project. The first study calibrated accelerometer transmitters for use in predicting oxygen consumption rates and swim speed in sockeye salmon (Wilson et al. 2013). The second study explored migration and swimming behaviour of sockeye salmon in the Strait of Georgia and lower Fraser River (Wilson et al. 2014). This article uses the calibration of accelerometer transmitters from Wilson et al. (2013), and the acceleration values of tagged fish from Wilson et al. (2014), to predict energy use, cost of transport, and oxygen consumption rates during the coastal marine migration of sockeye salmon. The relevant methods and results from these previous studies are highlighted here to increase interpretability of this study, but for more information see methods of Wilson et al. (2013, 2014). The present study was conducted in accordance with the Canadian Council on Animal Care, as administered by both Carleton University (B10-08) and the University of British Columbia (A11-0215).

Transmitter Calibration

Acoustic accelerometer transmitters were previously calibrated to predict oxygen consumption rates and swimming speeds of sockeye salmon using Brett-style respirometers, and are reviewed here (see Wilson et al. 2013). Ten male and seven female Harrison River sockeye salmon (fork length (FL) 57.7–68.9 cm) were gastric tagged with acoustic accelerometer transmitters (VEMCO, Model V9A-2H, 69 Hz, 16×67 mm) before completing critical swimming speed tests in a Brett-style respirometer at different water temperatures (for swim protocol see Jain et al. 1997; Lee et al. 2003; for gastric tagging procedure see Bridger and Booth 2003; Dick et al. 2018). Fish were acclimated to water temperatures for 1 h before water velocity in the swim tunnel was steadily increased from resting (0.15 m s^{-1}) to the initial speed increment (0.65 m s^{-1}) over 15 min, and then increased by one speed increment (0.15 m s^{-1}) every 20 min until the fish stopped swimming and remained on the rear grid for > 10 s. After completing the swim test, the fish remained in the swim tunnel at a resting water velocity of 0.15 m s^{-1} for at least 1 h before the next critical swimming speed test (Jain et al. 1997; Farrell et al. 1998, 2003; Lee et al. 2003; MacNutt et al. 2004, 2006; Eliason, Wilson, et al. 2013a, b). Water temperatures were increased or decreased by no more than 4 °C per hour (Clark et al. 2008). We did not use the standard 14–30-day temperature acclimation period because A) wild Pacific salmon have a finite amount of energy stores and time before spawning and death, and their physiology changes rapidly throughout maturation and B) salmon can encounter rapid (natural) changes in temperature in both the freshwater and marine environment and are known to rapidly adjust to different temperatures (Eliason and Farrell 2016). Beyond salmon, other species have been shown to rapidly acclimate to new temperatures after 1–2 days (Klicka 1965; Barrionuevo and Fernandes 1998). Oxygen consumption rate and average acceleration were calculated during the last 10 min of each swim increment, when fish had established steady swimming. Acceleration was recorded using a portable acoustic hydrophone (VEMCO, VR100) that was inserted into the top of the swim tunnel. The acoustic accelerometer was programmed to measure acceleration in three axes at a 10 Hz sampling frequency and had a range of 0–4.901 m s^2. Three-dimensional acceleration was averaged over 10 s, converted to root mean squared acceleration (RMS $= (x^2 + y^2 + z^2)^{0.5}$) and transmitted to the receiver every 13–17 s. Oxygen consumption was measured at a rate of 1 Hz using dissolved oxygen probe (Mark IV Oxyguard probe, Point Four Systems, Richmond, BC, Canada), recorded using Windaq box (Dataq Instruments, Akron, OH, USA), and analysed using Labview software (National Instruments, TX, USA). Rate of oxygen consumption was calculated from the decrease in oxygen concentration over the last 10 min during each swim increment at each

temperature and standardized by body mass. Swim protocols were performed at six different temperatures (12, 14, 16, 18, 20, and 22 °C) for each fish. The order of the temperatures was randomised. Oxygen consumption rates were modelled using acceleration, sex, fork length and temperature, with individual fish ID as a random effect (Eq. 1, Fig. 1).

$$MO_2 = 0.22 \times \text{Temperature} + 4.39 \times \text{Acceleration}$$
$$- 0.05 \times \text{FL} + \begin{pmatrix} 0.61 & \text{Male} \\ 0 & \text{Female} \end{pmatrix} - 0.12 \quad (1)$$

Study Region

Adult sockeye salmon return to the Fraser River using either the northern route through Johnstone Strait or the southern route through Juan de Fuca and Haro Straits, enter the Strait of Georgia and begin their upstream spawning migration into the Fraser River (Fig. 2). We intercepted adult sockeye salmon along their northern route, in the southernmost reach of Johnstone Strait in an area known as Discovery Passage (Fig. 2). This area is comprised of large and small islands, separated by deep, narrow channels. During changing tidal cycles, water rushes through these small channels creating violent currents and large eddies. After tagging, adult salmon migrated through a particularly deep, narrow channel (< 1 km wide) called Seymour Narrows, where currents can exceed 25 km h^{-1} (Fig. 2). Adult salmon generally passed the Seymour Narrows array 24 to 48 h after tagging (Fig. 2; Wilson et al. 2014). Seymour Narrows marks the end of the Discovery Passage which opens to the Strait of Georgia, a large inland sea between Vancouver Island and mainland British Columbia, around 40 km wide, 200 km long, with depths ranging from 155 to 400 m. The Strait of Georgia is split into the Northern Strait of Georgia, which extends from the Discovery Islands in the north to the southern tip of Texada Island, and the Southern Strait of Georgia, which extends south to the Juan de Fuca Strait (Fig. 2). The Northern Strait of Georgia is fully saline (28–30 ppt) with wind driven counterclockwise currents (Thomson 1981). Salmon arrived at the northern Strait of Georgia receiver array, which spans from the northern tip of Texada Island to Courtney, BC on Vancouver Island, ~ 100 to 120 h after tagging (Fig. 2). The southern Strait of Georgia is strongly influenced by the Fraser River discharge. Much of the southern Strait of Georgia is considered the Fraser River estuary, although the zone of freshwater influence changes throughout the year corresponding with changing freshwater discharge and prevailing winds. Generally, the region is stratified with warm, less dense freshwater dominating the first 10 m, and brackish water > 10 m (Thomson 1981). After detection at the Northern Strait of Georgia array, salmon passed through the remainder of the northern

Fig. 1 Relationship between oxygen consumption and acceleration output for sockeye salmon swimming at six different temperatures. Data from Wilson et al. 2013. (Color figure online)
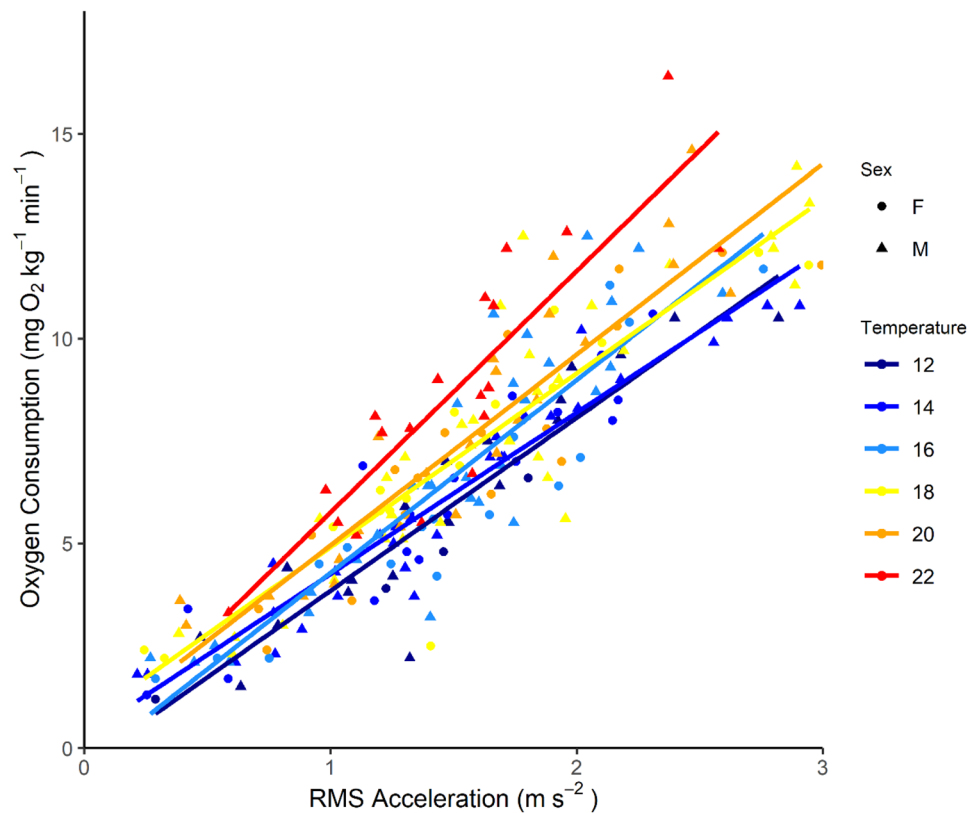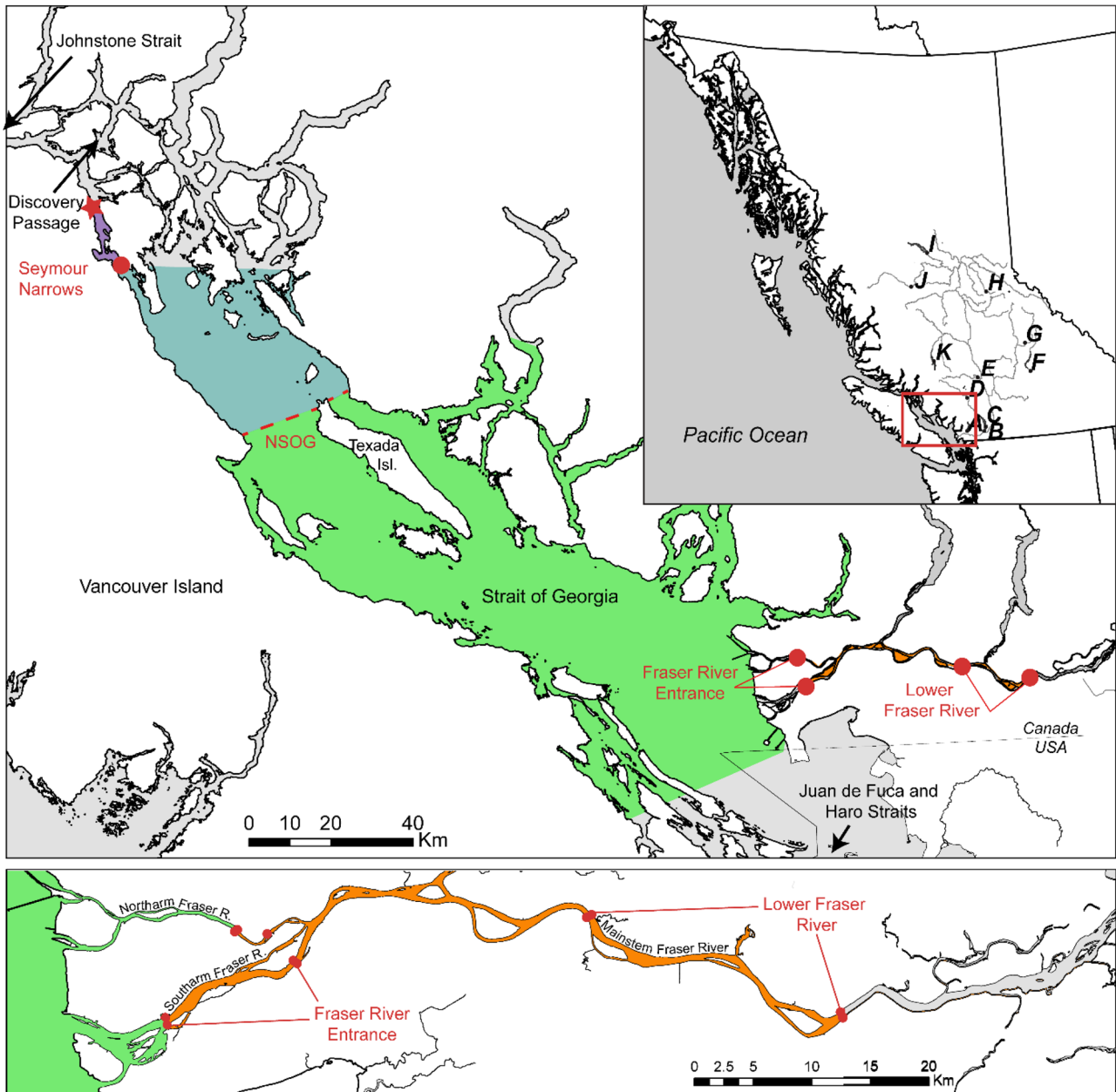

Strait of Georgia and the southern Strait of Georgia, finally entering one of the three arms the Fraser River where they were detected at the Fraser River Entrance array ~150–300 h after tagging (Fig. 2). This region of the Fraser River delta is shallow and salinity ranges depending on the tidal cycle. Salmon began their upstream migration and were detected in our last array, the Lower Fraser River array ~200–350 h after tagging (Fig. 2; Wilson et al. 2014). The last array is located near Mission, BC, and at the upstream-most tidal extent, marking the end of the Fraser River estuary and beginning of the freshwater upstream migration.

Ocean Tagging

Adult sockeye salmon were intercepted during their coastal migration, tagged with acoustic accelerometer transmitters and subsequently detected at several arrays in order to track energy use during coastal and estuarine migration (see Wilson et al. 2014). Adult sockeye salmon (28 males, 25 females, and 1 unknown; FL = 51–70 cm) were caught by troll fishing in Johnstone Strait (50° 20'N, 125° 25'W; Fig. 2), August 7th–17th, 2012. Captured fish were placed in a foam-lined V-shaped trough where they were gastrically tagged with acoustic accelerometer transmitter (VEMCO Model V13AP-1H, 69 kHz, 16 × 67 mm), fork length (FL) was measured, and a small tissue sample was collected for genetic population identification (Beacham

et al. 1995, 2005). A blood sample was taken from the caudal vasculature for sex determination using a vacutainer tube (4 mL, sodium–heparin anticoagulant, BD, NJ; 21 G, 11/2' long syringe; BD, NJ). The blood sample was placed in an ice-water slurry for < 30 min and then centrifuged for 5 min at 1500 rpm (Clay Adams Compact II Centrifuge, Becton-Dickson; Sparks, MD). Plasma was separated and flash frozen in liquid nitrogen and transferred to an ultra-cold freezer where they were stored at -80 °C until analysis. Radioimmunoassay was used to measure testosterone and 17b-estradiol levels in the thawed samples, and were used to determine sex (McMaster et al. 1992). Accelerometers had the same programming as tags during calibration (10 Hz sampling frequency averaged over 10 s) with the exception that these tags transmitted every 20–70 s, randomly. Fish could subsequently be detected at four acoustic receiver arrays along their migration route: Seymour Narrows, Northern Strait of Georgia, Fraser River Entrance and Lower Fraser River (Fig. 2). A commercial fishery occurred after tagged fish were released and we estimate several fish were captured. Of the 54 fish tagged only 38 fish (16 females, 22 males) were detected after the first 24 h post tagging (Wilson et al. 2014). Data presented here are for those 38 fish. Range of detection of acoustic signals by our receivers varied between 500 and 1000 m depending on conditions at each deployment site (Welch et al. 2003).

Fig. 2 Array locations throughout the Northern Strait of Georgia (top) and the lower Fraser River (bottom). Each array (Seymour Narrows, Fraser River Entrance, Lower Fraser River) is marked by a red dot and the northern Strait of Georgia array is marked by a dashed red line. Approximate tagging location is marked by the red star. Each region is coloured; purple: tagging to Seymour Narrows, blue: Seymour Narrows to Northern Strait of Georgia, green: Northern Strait of Georgia to Fraser River Entrance, orange: Fraser River Entrance to Lower Fraser River, *Inset:* Letters denote genetically distinct populations of sockeye salmon that were tagged in this study. A—Pitt River, B—Weaver Creek, C—Harrison River, D—Birkenhead River, E—Gates Creek, F—Lower Adams River, G—North Thompson River, H—Bowron Lake, I—Stuart Lake, L—Stellako Lake, K—Chilko Lake. (Color figure online)

Statistical Analyses

We used a previously developed relationship between acceleration and rate of oxygen consumption (Eq. 1; Wilson et al. 2013) to predict oxygen consumption rates throughout coastal migration and then used a mixed effect modelling approach to examine factors that may influence oxygen consumption rates. We used RMS acceleration, water temperature, sex, and FL (Eq. 1) to predict oxygen consumption rates for fish detected at four receiver arrays. Temperature data collected from migrating sockeye salmon from the previous year showed that migrating adult sockeye salmon experience

an average water temperature of 11.2 °C (min = 8.4 °C, max = 20.5 °C) through our study area (Drenner et al. 2014). Daily min, mean, and maximum river temperatures (available from Environmental Watch Program of Fisheries and Oceans Canada) were matched with the dates that salmon were detected at each in-river array. RMS acceleration values were recorded at receiver sites. Note that RMS acceleration values > 3.0 m s^{-2} were excluded from this study as they were not predictive of oxygen consumption (see Wilson et al. 2013). RMS acceleration values correlate with both activity levels and energy use (Wilson et al. 2013), we refer to both throughout this manuscript. During the calibration experiment RMS acceleration values > 3.0 m s^{-2} were observed during burst swimming behaviour, and thus represent anaerobiosis. Since the calibration model was predicated on direct measurement of oxygen consumption, it can only model aerobic swimming behaviours. Anaerobic burst swimming results in excess post-exercise oxygen consumption (EPOC) which would add to overall energy use (Lee et al. 2003), and has be linked to negative survival outcomes if exhibited frequently (Burnett et al. 2014a, b). Therefore, our measurements of energy use are conservative, as they do not account for EPOC; however, RMS acceleration values > 3.0 m s^{-2} were rarely observed (< 4.5% of all detections, Table 1).

Using this information, we were able to predict average oxygen consumption rates at each receiver location for min, mean and max temperatures experienced during migration, as well as energy use and cost of transport in the migratory areas between arrays (Table 1). Predicted oxygen consumption rate estimates were bootstrapped using 1000 iterations to estimate 95% confidence intervals. Minimum, mean, and maximum estimates of oxygen consumption rates (derived from min, mean and maximum water temperatures) and their 95% confidence intervals were used to estimate oxygen consumption for each migratory area. Our swim tunnel respirometry measurements captured whole animal MO$_2$ and we assumed that while most of the oxygen uptake was directed toward swimming, some proportion was also allocated to body maintenance and gonadal development (MO$_2$ costs of gonad development are unknown; Eliason and Farrell 2016). We assumed that gonad development and maintenance costs were similar between migratory areas and were likely similar to fish used during the calibration. Fish that were used during the calibration were captured just upstream from the tidally influenced section of the Fraser River, and therefore were captured at a similar migration stage and time of year as the tagged and released fish. The calibration was completed in freshwater, such that any differences in oxygen consumption due to saltwater (e.g. osmoregulation) are not accounted for in our modelling. Evidence showing increased metabolic cost in salt water is mixed, with findings ranging from 0 to 70% increase, such that oxygen consumption rates may not reflect osmoregulatory costs (Morgan and Iwama 1998;

Wagner et al. 2006; Ern et al. 2014; Hvas et al. 2018). However, differences in metabolic rates between salt and freshwater may not be driven solely by changes in salinity, as fish are simultaneously undergoing rapid physiological transitions, including gonadal development and sexual maturation, which could explain the high variation in observations. Rather than apply a saltwater correction based on a single, small study, we assumed that oxygen consumption is the same in both freshwater and saltwater. However, we did simulate possible rates of saltwater oxygen consumption based on freshwater oxygen consumption rates and swim speeds from Wagner et al. (2006) and confirmed our approach is robust to modest differences in freshwater and saltwater oxygen consumption rates (See Fig. S1 for results).

Migratory area-specific energy use (kJ kg^{-1}) during migration was calculated by converting oxygen consumption rates (mg O$_2$ kg^{-1} min^{-1}) to kJ kg^{-1} h^{-1} (1 mg O$_2$ = 815.55 Joules; Brett 1995) and multiplying by the time it took to migrate through each area between arrays (time of first detection at each array minus the time of first detection at the previous array). We also calculated cost of transport (mg O$_2$ kg^{-1} km^{-1}) by dividing the regional energy use by the distance between each array. For example, one fish travelled between the Seymour Narrows array and the NSOG array, a distance of 70 km, in ~ 30 h. Mean rate of oxygen consumption at the NSOG array was 1.93 mg O$_2$ kg^{-1} min^{-1} therefore mean energy use for the Seymour–NSOG region was 56.4 kJ kg^{-1} with a cost of transport of 0.81 mg O$_2$ kg^{-1} km^{-1}. This assumes that conditions experienced at each line are reflective of the previous environment they travelled through. It is important to note that the receiver placement in Seymour Narrows may have resulted in an overestimate of cost of transport, and total energy use in the following region, as the area is geomorphically diverse leading to complex tidal flows and hydraulic conditions that may not be broadly representative. We estimated cost of transport for the migratory areas between arrays (time of tagging to detection at Seymour Narrows array, Seymour Narrows to NSOG, NSOG to Fraser River entrance, Fraser River entrance to Lower Fraser River array; Fig. 2).

We used a model comparison approach to determine which set of factors best explained rates of oxygen consumption throughout coastal and estuarine migration. We used rate of oxygen consumption at mean marine and freshwater temperatures (11.2 °C and 18.8 °C, respectively), and did not complete repeated tests at other temperatures or for other energy units because oxygen consumption rates did not vary strongly across temperatures (Fig. 1, Table 1) and cost of transport and regional energy use were calculated from rates of oxygen consumption. Multiple testing of the same data will inflate Type II error rate (Bolker 2008). We used a combination of factors based on *a prior* hypotheses including sex, fork length, array location, tide

Table 1 Summary of energy use estimates for accelerometer-tagged sockeye salmon migrating past acoustic receivers located throughout coastal BC and the Fraser River (See Fig. 1 for locations) and regional energy use and cost of transport between arrays

	Sample size (M/F)	Fork-length (cm) (SE)	Acceleration (m s^{-2}) (% Detections > 3 m s^{-2})	Time to first detection (hrs) (SE)	Distance from tagging (km)	Predicted MO$_2$ (mg O$_2$ kg^{-1} min^{-1}) (95% CI)* ‡			Cumulative energy use (kJ kg^{-1}) (95% CI) ‡ †			Cost of transport (mg O$_2$ kg^{-1} km^{-1}) (95% CI) ‡**		
						Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Seymour Narrows	31 (17/15)	58.5 (0.87)	1.34 (1.3)	51 (6)	10	4.69 (2.83, 7.04)	5.20 (3.24, 7.66)	7.18 (4.82, 10.03)	219.34 (134.65, 326.46)	242.71 (153.31, 354.04)	332.07 (225.22, 460.77)	1483.97 (907.02, 2217.12)	1648.91 (1038.20, 2410.50)	2260.18 (1523.99, 3145.84)
NSOG	26 (15/11)	62.5 (1.16)	0.92 (0.3)	110 (11)	70	3.33 (1.88, 5.29)	3.76 (2.19, 5.82)	5.41 (3.45, 7.87)	341.95 (184.65, 557.65)	388.86 (218.28, 616.46)	571.77 (354.87, 845.84)	169.25 (95.61, 267.74)	191.45 (112.42, 294.93)	275.08 (175.67, 398.84)
Fraser River Entrance	16 (9/7)	57.7 (0.78)	1.48 (2.9)	199 (19)	200	7.58 (5.18, 10.46)	7.61 (5.21, 10.50)	7.66 (5.24, 10.57)	1331.57 (902.73, 1849.30)	1337.25 (907.78, 1855.42)	1345.57 (912.88, 1868.19)	205.67 (141.18, 283.08)	207.04 (142.34, 284.67)	208.29 (143.10, 286.19)
Lower Fraser River	14 (9/5)	57.2 (0.87)	1.90 (4.4)	231 (23)	250	9.68 (6.89, 12.96)	9.71 (6.92, 12.98)	9.79 (6.97, 13.10)	1873.23 (1328.28, 2514.45)	1877.72 (1333.54, 2518.22)	1891.85 (1341.56, 2538.28)	76.87 (55.13, 102.36)	77.31 (55.43, 102.89)	77.70 (55.76, 103.36)

* MO$_2$ predicted based on 8.4 °C, 11.2 °C, and 20.5 °C representing min, mean and maximum ocean temperatures (Drenner et al. 2014) and Lower Fraser water temperatures 18.6 °C, 18.8 °C, and 19.0 °C representing minimum, mean and maximum temperatures (data from Environmental Watch Program of Fisheries and Oceans Canada) experienced during the days salmon were migrating in the lower river

‡ Calculated values based on model predictions. 95% confidence intervals have been used for these predictions to better reflect model uncertainty

† Predicted cumulative energy use was calculated using oxygen consumption rates multiplied by the time to first detection at each array (regional energy use), added to all previous regional energy use estimates. Thus cumulative energy use represents the energy used up until that array. For example, cumulative energy use for the Northern Strait of Georgia is the energy used between release to the Seymour Narrows array, added to the energy used between the Seymour Narrows array and the Northern Strait of Georgia array

** Cost of transport (COT) was calculated from predicted MO$_2$ at each array multiplied by the travel time between arrays, divided by the distance between arrays. Thus COT represents regional COT estimate between arrays. For example, COT for Seymour Narrows is actually the COT between tagging and Seymour Narrows array

level, diel patterns and migration difficulty (see Wilson et al [2014]). Migration difficulty level was determined by 'work' (migration distance x elevation), where work < 100 was considered an easy migration, 100 − 200 an intermediate migration, and > 200 was considered a difficult migration (Crossin et al. [2004a], [b]). Each sockeye salmon was identified to population using DNA analyses (Beacham et al. [1995], [2005]) and assigned a level of migration difficulty based on migration length and elevation (Crossin et al. [2004a], [b]) (Table S1). Tide height was retrieved from station 8074; Fisheries and Oceans Canada, Tides and Water Levels archive and diel pattern was modeled using $\sin(2\pi \bullet \text{hour}/24) + \cos(2\pi \bullet \text{hour}/24) + \sin(2\pi \bullet \text{hour}/24)$ x DOY + $\cos(2\pi \bullet \text{hour}/24)$ x DOY, where DOY was the year-day, and hour was the hour of the day in a 24-h cycle. Migratory difficulty level, sex, fork length, tide height, and diel period were included as they have been shown to influence migratory behaviours including swim speed, and thus could influence energy use estimates (Crossin et al. [2004a], [b]; Wilson et al. [2014]). For example, Levy and Cadenhead ([1995]) found that sockeye salmon use tidal cycles to assist in starting upstream migration, and several studies have found that male adult sockeye salmon used more energy than females to move the same distance (Hinch and Rand [1998]; Standen et al. [2002]). Fish ID was included as a random intercept. All *a priori* model combinations were tested (Table S2). The most parsimonious model was chosen using Akaike Information Criterion, corrected for small sample sizes (AICc), where models with < 2 ΔAIC were considered the top models (Burnham and Anderson [2004]). All variables had variance inflation factors (VIFs) less than 2 (Table [3]) demonstrating that variables were not collinear with other independent variables in the model. Since AICc is known to overfit models, we report the top model as the model with the fewest parameters, and parameters that have 95% confidence intervals that do not cross zero in the top model set (Bolker [2008]; Arnold [2010]; Harrison et al. [2018]). Bonferroni post hoc tests with planned comparisons were used to further investigate the effect of array site on oxygen consumption rate. Significance levels for this test were α = 0.05. Statistical analyses were completed using R (v. 3.5.2; R Core Team [2018]) and GUI RStudio (v. 1.1.463) using packages 'nlme' (Pinheiro et al. [2018]) and 'AICcmodavg' (Mazerolle [2017]). Rate of oxygen consumption was square-root transformed to achieve residual normality and homoscedasticity.

Results

We used the previously developed calibration model (Eq. [1]) to predict energy use of adult sockeye salmon from transmitted RMS acceleration values at arrays along their migration route through the Strait of Georgia and lower Fraser River. RMS acceleration was lower in the marine (Seymour Narrows, NSOG arrays), compared to the riverine (Fraser River Entrance, Lower Fraser River arrays) environment, 1.04 ± 0.68 m s^{-2} (mean $\pm$ SD) and 1.61 ± 0.68 m s^{-2}, respectively. Given the lower RMS acceleration and lower water temperatures, it was not surprising that oxygen consumption rates were generally lower in the marine ($MO_{2\ temp8.4}$ = 3.7 (2.1, 5.8) mg O$_2$ kg^{-1} min^{-1}, $MO_{2\ temp11.2}$ = 4.2 (2.5, 6.3) mg O$_2$ kg^{-1} min^{-1}, $MO_{2\ temp20.5}$ = 5.9 (3.8, 8.5) mg O$_2$ kg^{-1} min^{-1}; mean (5%, 95% CI)) compared to riverine environments ($MO_{2\ temp18.6}$ = 8.2 (5.7, 11.2) mg O$_2$ kg^{-1} min^{-1}, $MO_{2\ temp18.8}$ = 8.2 (5.7, 11.2) mg O$_2$ kg^{-1} min^{-1}, $MO_{2\ temp19.0}$ = 8.3 (5.8, 11.3) mg O$_2$ kg^{-1} min^{-1}; Table S3). Additionally, rates of oxygen consumption varied strongly by migratory area and time of day (Table [1], Fig. [3]).

We used model competition to determine the top explanatory predictors of the rate of oxygen consumption at average marine and riverine temperatures. Possible model parameters included tide height, diel period, array location, population specific migration difficulty, sex, and size. Parameters included in the top model were size, diel period, and array location, and all significantly affected rates of oxygen consumption (95% confidence intervals did not include 0, Tables [2], [3]; Bolker [2008]). Array location was also strongly related to rate of oxygen consumption, with the highest rates in the Lower Fraser River, followed by the Fraser River Entrance, and Seymour Narrows—fish detected at the NSOG array had the lowest mean oxygen consumption rate (Tables [1], [3]). Oxygen consumption rates were the highest during daylight hours, between 5AM and 5PM (Fig. [3]B). Size had the weakest effect on oxygen consumption rates— larger fish had slightly lower rates of mass-specific oxygen consumption (60.0 ± 5.3 cm; Table [3]). Tide height was included in the top model set (< 2 ΔAIC) but not in the top model (Table [2]). Migration difficulty and sex were not present in the top explanatory model set.

Despite lower rates of oxygen consumption, cost of transport (COT) was much higher in the marine environment compared with the riverine environment, especially in Seymour Narrows (Tables [1], S3). Cumulative energy use of adult salmon during the 250 km coastal and lower river migration was estimated to be 1877 kJ kg^{-1} (1333.54 kJ kg^{-1}, 2518.22 kJ kg^{-1}; 95% CI), based on average temperatures (Table [1]). The most energetically expensive region (highest energy use) during the migration was for the region between the Northern Strait of Georgia to the Fraser River entrance (Table [1], Fig. [4]). Importantly, these estimates are possibly conservative, as they do not account for potential differences in metabolic rate between salt and fresh water, or from energy used during anaerobic metabolism.
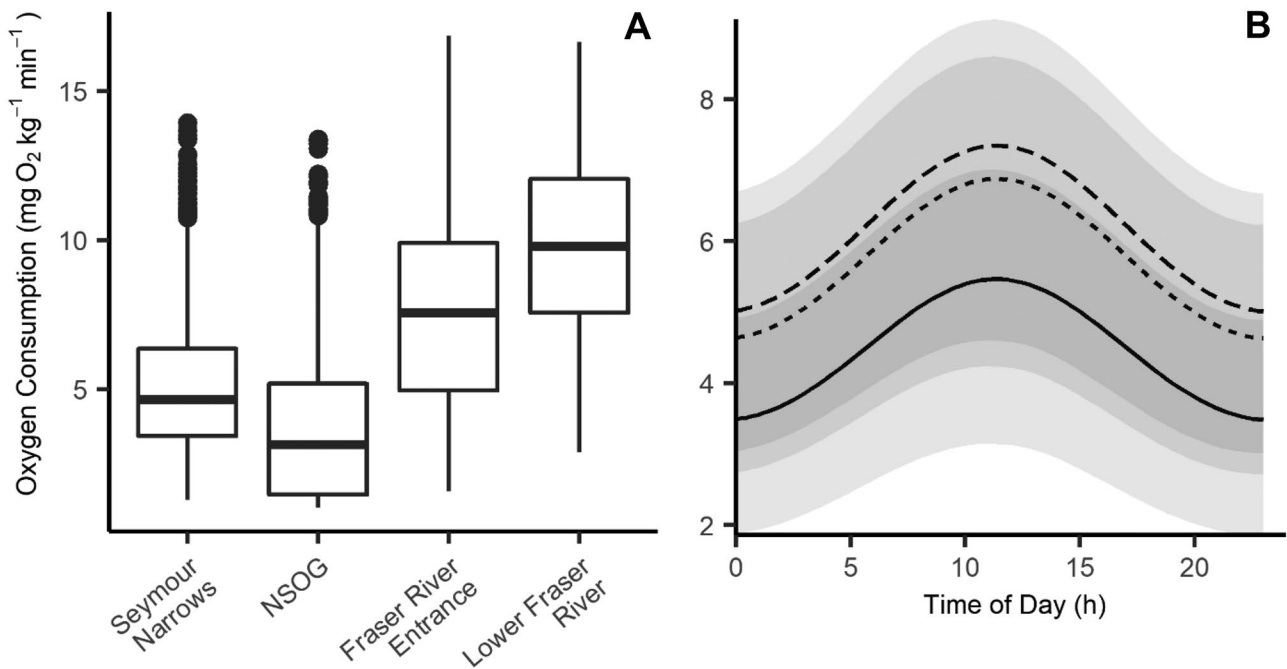
Fig. 3 Predicted oxygen consumption rates based on top model for migrating adult sockeye salmon by A) Array location. Lines in box and whisker plot represent 95% confidence interval, and box represents 25, 50 and 75% quantiles. X-axis labels are ordered by distance from tagging, shortest to longest distance. And B) Time of day.

Shaded region is 25th and 75th quantiles, solid line is for a large fish (75th quantile, FL = 64.5 cm), dotted line represents a median sized fish (FL = 58.0 cm) and dashed lined represents small fish (25th quantile, FL = 56 cm)

Discussion

Tagging of adult salmon with MO_2 calibrated accelerometer transmitters revealed marked differences in total energy use, cost of transport, and rates of oxygen consumption in distinct migratory areas during their final transition from a coastal marine to a freshwater riverine environment. This study furthers our understanding of the bioenergetics of the remarkable spawning migrations of Pacific salmon in estuaries. Energy use varied strongly by location where oxygen consumption rates were over two times higher in the riverine environment compared to the marine environment. Energy use also varied by migratory area as well as by fish size and diel period, with smaller fish, and fish migrating during mid-day, having higher rates of mass-corrected oxygen consumption. We have shown that accelerometer transmitters can be used to observe patterns of energy use in salmon.

Notwithstanding the limitations noted here, we also provide the first estimates of coastal marine energy use and oxygen consumption, which for some populations could represent a significant portion of their overall energy budget.

Indeed, mean energy use estimated during the region between Seymour Narrows and the Lower Fraser River was 1877 kJ kg^{-1}, which is comparable to some population's total upstream migration costs. For example, Harrison River sockeye salmon migrate an additional ~ 30 km upstream of our last receiver array, such that > 90% of their non-feeding migration is in the marine environment. Gilhousen (1980) estimated that the in-river migration of adult Adams River sockeye salmon (~ 500 km freshwater migration; ~ 400 m elevation) utilized ~ 1500 kJ kg^{-1}, meanwhile, for Chilko Lake sockeye salmon (~ 650 km freshwater migration; ~ 1200 m elevation), freshwater energy use could be as much as ~ 4500 kJ kg^{-1} for a three week freshwater

Table 2 Top model results for model set ΔAIC < 2 estimating oxygen consumption of free-swimming adult sockeye salmon

Model	Parameter	Δ AIC	AIC ω
Fork Length + Detection Location + Diel period + Tide	12	0	0.51
Fork Length + Detection Location + Diel period + Tide + Sex	13	1.95	0.19
Fork Length + Detection Location + Diel period	11	1.97	0.19

*Diel period was estimated by $\sin(2\pi \cdot h/24) + \cos(2\pi \cdot h/24) + \sin(2\pi \cdot h/24) \times DOY + \cos(2\pi \cdot h/24) \times DOY$

Table 3 Parameter estimates for models with ΔAIC < 2 estimating oxygen consumption of free-swimming adult sockeye salmon

| Model	Description	Parameter	df	Parameter Estimate	95% Confidence Interval	VIF[1]
Model 1	**Intercept**	**Intercept**	**19,455**	**5.67**	**3.7, 7.6**	**NA**
	Size	**Fork Length**	**35**	**-0.04**	**-0.079, -0.0091**	**1.00**
	Detection Location	**Seymour Narrows**	**19,455**	**-0.80**	**-0.84, -0.77**	**1.58**
		NSOG	**19,455**	**-0.99**	**-1.02, -0.97**	
		Fraser River Entrance	**19,455**	**-0.29**	**-0.31, -0.27**	
	Tide	Tide	19,455	0.01	-0.000085, 0.023	1.96
	Diel Period	**sin(2 $\pi \cdot$ h/24)**	**19,455**	**0.04**	**0.033, 0.056**	**1.39**
		cos(2 $\pi \cdot$ h/24)	**19,455**	**-0.24**	**-0.25, -0.23**	**1.31**
	Diel Period x DOY	**sin(2 $\pi \cdot$ h/24) x DOY**	**19,455**	**-0.0040**	**-0.0054, -0.0026**	**1.01**
		cos(2 $\pi \cdot$ h/24) x DOY	**19,455**	**-0.0017**	**-0.0029, -0.0004**	**1.05**
Model 2	**Intercept**	**Intercept**	**19,455**	**5.75**	**3.8, 7.8**	**NA**
	Size	**Fork Length**	**35**	**-0.046**	**-0.082, -0.0090**	**1.00**
	Detection Location	**Seymour Narrows**	**19,455**	**-0.80**	**-0.84, -0.77**	**1.58**
		NSOG	**19,455**	**-0.99**	**-1.02, -0.97**	
		Fraser River Entrance	**19,455**	**-0.29**	**-0.31, -0.27**	
	Diel Period	**sin(2 $\pi \cdot$ h/24)**	**19,455**	**0.04**	**0.033, 0.056**	**1.39**
		cos(2 $\pi \cdot$ h/24)	**19,455**	**-0.24**	**-0.24, -0.22**	**1.31**
	Diel Period x DOY	**sin(2 $\pi \cdot$ h/24) x DOY**	**19,455**	**-0.0040**	**-0.0054, -0.0026**	**1.01**
		cos(2 $\pi \cdot$ h/24) x DOY	**19,455**	**-0.0017**	**-0.0029, -0.00042**	**1.05**
	Tide	Tide	19,455	0.01	-0.00011, 0.023	1.96
	Sex	Sex	35	0.03	-0.24, 0.31	1.17
Model 3 (Top Model)	**Intercept**	**Intercept**	**19,455**	**5.69**	**3.74, 7.64**	**NA**
	Size	**Fork Length**	**35**	**-0.04**	**-0.079, -0.0089**	**1.00**
	Detection Location	**Seymour Narrows**	**19,455**	**-0.79**	**-0.82, -0.79**	**1.08**
		NSOG	**19,455**	**-0.98**	**-1.00, -0.95**	
		Fraser River Entrance	**19,455**	**-0.28**	**-0.31, -0.26**	
	Diel Period	**sin(2 $\pi \cdot$ h/24)**	**19,455**	**0.04**	**0.03, 0.05**	**1.05**
		cos(2 $\pi \cdot$ h/24)	**19,455**	**-0.23**	**-0.24, -0.22**	**1.02**
	Diel Period x DOY	**sin(2 $\pi \cdot$ h/24) x DOY**	**19,455**	**-4.0×10^{-3}**	**-0.0053, -0.0026**	**1.00**
		cos(2 $\pi \cdot$ h/24) x DOY	**19,455**	**-1.6×10^{-3}**	**-0.0028, -0.00037**	**1.05**

Bold values indicate terms that have 95% confidence intervals that do not cross zero

[1]VIF = variance inflation factor

migration (Gilhousen 1980; Rand and Hinch 1998). Thus, when accounting for energy use during estuarine phase, marine migration could account for between 23 and 35% of the total energy used during spawning migration and holding at spawning grounds across populations. Marine conditions experienced after salmon cease eating should be considered when modelling energy budgets of adult salmon during their spawning migration given the high overall contribution to the total energy budget. Hitherto, this has often been an understudied area for salmon bioenergetics with efforts either focused on the high seas (Hinch et al. 1995) or the riverine phase of migration (Idler and Clemens 1959; Gilhousen 1980, 1990; Hinch et al. 1996; Hinch and Rand 1998, 2000; Rand and Hinch 1998; Standen et al. 2002; Crossin et al. 2004a, b; Crozier et al. 2008; Burnett et al. 2014a, b).

We found differences in energy use across locations within the riverine and marine environments. Oxygen consumption rates in the marine environment were higher in Seymour Narrows, compared to the Northern Strait of Georgia but were similar across the two in-river arrays in tidally influenced areas of the river. Temperature and RMS acceleration were the two main variables used to predict oxygen consumption rates. The differences in oxygen consumption rates between the two marine sites were likely driven by differences in behaviour (i.e. activity levels), rather than differences in temperature. Whereas temperature was estimated to be the same in both regions (11.2 °C) and did not contribute to observed differences in oxygen consumption rates, Wilson et al. (2014) found that RMS acceleration was higher in Seymour Narrows than in the Northern Strait of Georgia, indicating swim speeds were higher in this region.

Fig. 4 Energy use for each region between arrays along the migration of free-swimming adult sockeye salmon. Regional energy use was estimated from oxygen consumption rates at each array and the time spent in each region. Lines in box and whisker plot represent 95% confidence interval, and box represents 25, 50, and 75% quantiles
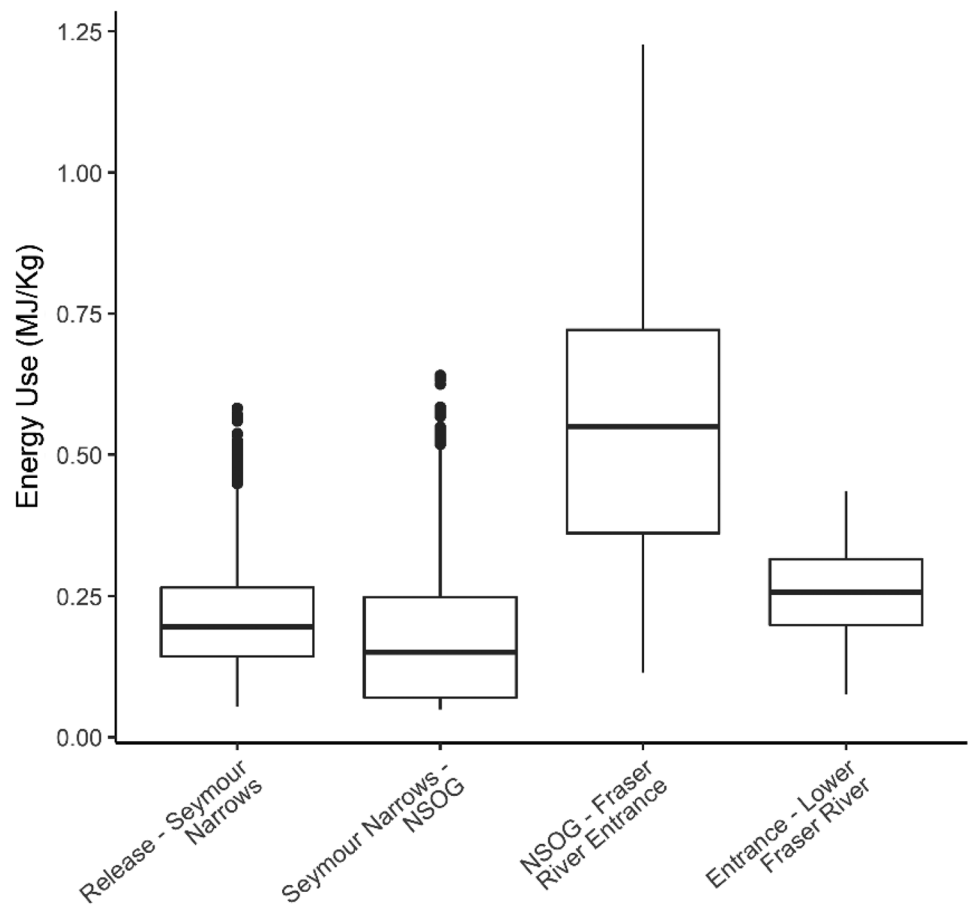
In fact, Wilson et al. (2014) found that swim speed estimates in Seymour Narrows were > 20% higher than in the Northern Strait of Georgia. Seymour Narrows is a narrow region with strong currents driven by high tidal flushing. The complexity and strength of currents in this region, and resultant higher swim speeds likely drove the higher oxygen consumption rates we observed in Seymour Narrows compared to the Strait of Georgia. On the other hand, oxygen consumption rates for the two in-river arrays (Fraser River entrance and lower Fraser River arrays) were similar to each other but higher than even Seymour Narrows. Indeed, oxygen consumption rates were 2.5–3 times higher in riverine arrays compared to the arrays in the marine environment. These differences are due to both higher freshwater temperatures (mean freshwater temperature was 18.8 °C compared to an estimated marine temperature of 11.2 °C (based on Drenner et al. 2014)), as well as the higher activity rates (RMS acceleration was 60% higher in freshwater compared to marine) observed by Wilson et al. (2014). Given the weak effect of river temperatures between 12 and 18 °C, in the calibration model (Fig. 1), it is not surprising that activity, rather than temperature, drove oxygen consumption rates. However, at temperatures approaching the critical temperature (i.e. above 20 °C), temperatures have a much stronger

effect on oxygen consumption rates (Fry 1971; Eliason et al. 2011), but were rarely observed in our river temperature time series for 2012. Climate change-driven changes in river temperature could increase energy use of fish migrating through the lower Fraser River (Figure S1). Furthermore, increases in temperature could result in a collapse in aerobic scope, slower swim speeds, and an increased reliance on anaerobic metabolism to fuel swimming (Eliason et al. 2013a, b), which could increase migration duration and further exposure to higher temperatures, thus increasing the energy budget in a way that our model could not predict. Indeed, our modelling approach could not account for anaerobic metabolism resulting in EPOC. During single or infrequent short bursts, EPOC is likely small, not contributing much to overall energy use. However, during periods of long/multiple bursting EPOC could be higher, resulting in our model underestimating energy use (Lee et al. 2003). We rarely observed RMS acceleration values > 3.0 m s⁻² (bursting behaviour), but these acceleration values were observed more in riverine compared to marine environments and may mean our energy use estimates were conservative. Differences in oxygen consumption rates between the two marine migratory areas were driven by differences in locomotor activity, whereas differences between freshwater and marine

oxygen consumption rates appear related to both locomotor activity and temperature.

Cost of transport (energy use per km) and total energy use across areas was driven by behavioural differences among migratory areas. For example, whereas oxygen consumption rates were the lowest in the Northern Strait of Georgia, energy use was highest, since fish spent more time in this region. Moreover, outside of Seymour Narrows, this region had the highest cost of transport, even higher than in the Fraser River, where fish must actively migrate upstream. The region between the Northern Strait of Georgia array and the Fraser River Entrance array is the longest region (130 km) denoted in this study, and therefore the size of the region is a major contributor to the amount of energy used to migrate through this region. Additionally, migration rates in the Northern Strait of Georgia region were lower compared to swim speeds (from RMS acceleration) estimated by Wilson et al. (2014), supporting previous studies that have shown that some fish spend time in the region, potentially waiting for cues (e.g. tidal, temperature, diel), and refining their navigation (Levy and Cadenhead 1995; English et al. 2005; Crossin et al. 2009; Donaldson et al. 2009; Cooperman et al. 2010). Previous work has shown that while migration is directed during upstream migration in the Fraser River, some fish spend time in non-directed movements in the Strait of Georgia and Fraser River estuary (Quinn 1988; English et al. 2005; Cooperman et al. 2010; Drenner et al. 2012). Such non-directed migration behaviours increased regional energy use estimates and cost of transport for this region.

Other than detection location, diel period but not tide height or sex predicted energy use, which differs from the findings of other studies. Interestingly, sex did not appear important in our model estimating energy use for free-swimming fish. EMG transmitters have been used to estimate energy use of migrating sockeye salmon in the Fraser River revealing that males had three times higher cost of transport than females (Hinch and Rand 1998; Standen et al. 2002). Sex was a statistically significant predictor of oxygen consumption rates for the calibration model, but the effect size was small (Wilson et al. 2013). It is possible that behavioural differences compensated for the differences in metabolic rate between female and male fish. For example, whereas males had higher metabolic rates than females, they could have travelled more efficiently, thus decreasing the difference in energy use. However, this is unlikely, as a previous study found no obvious differences in swim speeds between males and females in these regions (Wilson et al. 2014). It is more likely that individual variation was higher than any sex-specific differences in metabolic rate. Similarly, there was no influence of tide height on energy use, though a previous study found there was an influence of tide height on activity levels, suggesting that additional activity from tide height did not significantly influence energy use (Wilson et al. 2014).

However, Wilson et al. (2014) found differences in activity levels over the day which could explain the higher energy use during daylight hours which we observed. It is unclear what was driving this pattern of increased energy use, but could be predator avoidance, or a result of attempts to navigate (Drenner et al. 2014). Our findings were consistent with those of Hinch and Rand (1998) who found that sockeye salmon that migrated through the lower Fraser River had relatively low cost of transport. However, fish moved through constricted reaches faster than other reaches, indicating that while momentarily energy intensive, these areas may not contribute strongly to overall energy use.

Interestingly, pending migration difficulty (i.e. what salmon would encounter throughout their population-specific migration) did not explain variability in energy use. It is known that populations with 'easy' migrations—those that migrate short distances with little elevation gain (e.g. Weaver Creek population) are larger bodied, less fusiform and start the upriver migration with less somatic energy reserves relative to populations with 'difficult' migrations (e.g. Chilko Lake population; Crossin et al. 2004a, b). Our study estimated oxygen consumption rates using a model built on RMS acceleration for sockeye salmon from the Harrison River which is a Fraser River population that has a short upriver migration with low migration difficulty. Metabolic rates differ among sockeye populations (Eliason et al. 2011) and therefore the Harrison River population metabolic rate may not be representative of populations that migrate longer distances, or at different times of the year (i.e. run timing groups; Eliason et al. 2013a, b). Indeed, the majority of fish that we tracked were from the Chilko Lake population which has one of the most difficult upriver migrations of all sockeye salmon (Crossin et al. 2004a, b; Eliason et al. 2011) and may have a more directed marine migration than several other Fraser populations (Hinch et al. 2012). Furthermore, since our model was calibrated with fish in freshwater, our results could be an underestimate of the total energy budget of the marine coastal migration. One study found adult sockeye salmon swimming in seawater may have as much as 30–70% higher rates of routine oxygen consumption, than fish in freshwater, but the seawater acclimated fish were swum 3 to 6 weeks earlier than the freshwater fish; thus, they had different maturation and energetic status (Wagner et al. 2006). Additionally, as commented above, this study did not account for excess post exercise oxygen consumption (EPOC), associated with anaerobic burst swimming. Burst swimming (RMS values > 3.0 m s^{-2}) beyond the range of calibration for aerobic metabolism only occurred 4.5% of the time. It was most common in the riverine environment and least common Strait of Georgia. Our understanding of EPOC costs as a function of burst duration and temperature, as well as our understanding of differences in oxygen consumption rates between salt and freshwater, are incomplete and warrant further study in order to be incorporated into energy estimates. While a starting

point, these modelled data only provide a single estimate of energy use in a highly variable environment (i.e. annual/seasonal changes in river flow, estuary salinity, and temperature), understanding energy use in different years would give a better indication of the variability. Further studies of different populations/run timing groups or across years would be important for understanding population-specific risk of energy exhaustion. Additionally, future work could pair accelerometer tagged fish, with proximate body composition of fish captured in regions near arrays following the migration schedule. This would enable further verification of this technique and a comparison across different populations. Nevertheless, our model represents a way to compare relative energy use among populations and sites, but our absolute estimates of energy use and cost of transport may be over estimated given the possibility that long distance migrating populations are more energetically efficient migrators (Gilhousen 1980).

In conclusion, the non-feeding coastal migration of adult salmon can add considerably to the energy budget of adult migration, with energy use varying regionally. We found that while oxygen consumption rates were higher in the Fraser River than in the marine environment, migratory area-specific energy use estimates were higher in the marine environment likely due, in part, to milling behaviours in the Fraser River estuary. Cost of transport was highest in the constricted Seymour Narrows region, suggesting that constrictions in the ocean environment can function similar to constrictions in a river which are known to elevate energy use and delay migrations (Hinch et al. 1996; Rand and Hinch 1998; Hinch and Bratty 2000). Thus, coastal marine energy use is an important and understudied component of overall salmon migration energy budget. The approach used here has value in assessing how fish respond to dynamic environmental conditions that often define coastal and estuarine systems (Dryer 1997). Moreover, given the extent of human development and impact on coastal and estuarine systems (Crain et al. 2009), the approach used here has value in identifying and predicting the energetic (and potential fitness) consequences of environmental change as well as restoration and provides new opportunities for using ecologically meaningful indicators (Whitfield and Elliott 2002; Borja et al. 2008). Accelerometer transmitters are a useful tool for measuring oxygen consumption rates in free-swimming animals and can add information to calculating energy budgets of migratory species.

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2148

Estuaries and Coasts (2022) 45:2134–2150

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