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Coastal marine and in-river migration behaviour of adult sockeye salmon en route to spawning grounds

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ABSTRACT: Although behaviour and physiology of the reproductive migration of Pacific salmon *Oncorhynchus* spp. have been studied for the upriver migration, equivalent information for the coastal marine migratory phase has been difficult to obtain. Acoustic acceleration transmitters equipped with pressure sensors provide a tool to study swimming activity and migration depth of salmon in both marine and fresh water. Ocean migrating sockeye salmon *O. nerka* bound for the Fraser River, British Columbia (Canada), were intercepted approximately 200 km from the river entrance, tagged and tracked as they crossed several acoustic receiver lines in coastal waters and the lower Fraser River. Acceleration data were converted to swim speed using an existing statistical model. Data from 55 tagged fish revealed that swim speed and depth varied among migratory locales. Migration difficulty (freshwater migration distance and elevation to natal stream) was related to swim speed in the marine environment. Some of the variability in swim speed and depth was explained by diel and tidal cycles. In the marine environment, average (±SEM) swim speed estimate was ~1.23 body lengths (BL) s^{-1} at an average depth of 13 ± 0.058 m (range = 0–171 m), whereas the average swim speed in the river was significantly higher at ~1.57 BL s^{-1} at an average (±SEM) depth of ~9 ± 0.018 m (range = 0–21 m). Consistent with the physiological literature, coastal migrating fish were swimming near metabolically optimal speeds (0.9–1.2 BL s^{-1}). Overall this study demonstrates that using acoustic accelerometer transmitters can provide valuable insights into behaviour of homing sockeye salmon in both marine and freshwater environments.

KEY WORDS: Accelerometer · Behaviour · Sockeye salmon · Swim speed · Telemetry

INTRODUCTION

Migration is defined as the synchronous, directional, long-distance movement of a number of individuals of the same species between distinct environments (Endler 1977, Dingle 1996). Many of the longest and most challenging migrations are reproductive migrations, whereby individuals migrate great distances to assemble at sites of high-quality breeding and rearing habitat. One of the most renowned and remarkable reproductive migrations is that of the semelparous Pacific salmon (*Oncorhynchus* spp.), which migrate extraordinarily long distances (>1000 km) from ocean feeding grounds to their natal freshwater streams to spawn and die.

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Of the Pacific salmon, the migration biology of sockeye salmon *Oncorhynchus nerka* is one of the best understood, particularly for sockeye salmon destined for the Fraser River in British Columbia, Canada (Hinch et al. 2006). Physiological changes and sexual maturation have been observed as far away as 850 km from the Fraser River (Hinch et al. 2006, Crossin et al. 2009) and, within 300 km of the Fraser River, sockeye salmon stop feeding and complete the remaining migration and maturation on endogenous reserves (Hinch et al. 2006). Sockeye salmon encounter many challenges during their migration that can accelerate energy loss, cause physiological stress, impair reproductive maturation and lead to premature mortality (Cooke et al. 2004c, Hinch et al. 2006, 2012). For example, high river flows or high temperatures can cause migratory and spawning failure (reviewed by Martins et al. 2012). However, the influence of marine energy expenditure and behaviour on survival of migrating adults is not well known for most Pacific salmon (see Drenner et al. 2012).

Previous work tracking adult coastal migrating Pacific salmon has estimated average swim speeds at 1 body length (BL) s^{-1} for both adults (Madison et al. 1972, Stasko et al. 1976, Quinn 1988, Tanaka et al. 2001, Crossin et al. 2007) and outmigrating smolts (Welch et al. 2011). Adult sockeye salmon migrating through the Skeena River estuary were manually tracked, and ground speeds were recorded between 0.43 and 1.42 BL s^{-1} (Madison et al. 1972). A later study by Stasko et al. (1976) in Haro Strait found similar values, with sockeye salmon ground speeds varying between ~0.5 and 1.5 BL s^{-1}, an observation that was later replicated in the Queen Charlotte Islands, eastern Johnstone Strait and the northern Strait of Georgia by Quinn (1988) and Quinn et al. (1989). Together, these studies show that both smolt and adult sockeye salmon swim speeds may be close to 1 BL s^{-1} but are highly variable, both within and among individuals. More recent studies have calculated ground speed on a much coarser scale, by comparing the time between detections at distant arrays and have found that ground speed estimates are also close to 1 BL s^{-1} (Crossin et al. 2007). Environmental variables such as diel period and tidal cycle have been used to explain some variability, where individuals swim faster during the day and more slowly at night (Madison et al. 1972, Quinn et al. 1989). Physiological variables such as sex hormones, cortisol and gill physiology have also been used to attempt to explain variability in swim speeds with limited success (Cooke et al. 2006, Crossin et al. 2007, Miller et al. 2009). Much of the swim speed variability within the coastal migration phase has yet to be resolved on a fine temporal scale, and is thus difficult to explain using environmental variables.

Once at the Fraser River, sockeye salmon can remain in the Fraser River estuary for several days. Both osmoregulation (through Na/K ATPase expression) and sexual maturity (plasma testosterone concentrations) have been correlated with river entrance timing (Cooke et al. 2006, Crossin et al. 2007, 2009). Use of tidal flows to assist in migration through the estuary has been previously observed (Levy & Cadenhead 1995). Once in the Fraser River, adult sockeye salmon swim faster on average, between 1.0 and 1.9 BL s^{-1} depending on sex, river discharge and water velocity (Hinch & Rand 1998, Rand & Hinch 1998, Hinch et al. 2002, Hanson et al. 2008). Males have been observed to swim 1.3 times faster than females (118 cm s^{-1} compared to 89 cm s^{-1} for females; Hinch & Rand 1998), and fish swim more quickly during years of higher river discharge (Hanson et al. 2008) and in river reaches with higher flows (Hinch & Rand 1998).

Diel patterns in vertical distribution have been observed whereby individuals swim deeper during the day and shallower at night. This phenomenon has been observed in both the open ocean (Ogura & Ishida 1995) and freshwater lakes (Newell & Quinn 2005, Mathes et al. 2010, Roscoe et al. 2010). However, less evidence exists for this 'depth-seeking' behaviour during the coastal migration except in chum salmon *Oncorhynchus keta* observed diving to depths >100 m on the Japanese coast (Tanaka et al. 2001). Instead, sockeye salmon have a large vertical distribution above and below the thermocline (Quinn et al. 1989). Migrating sockeye salmon in Johnstone Strait and the Strait of Georgia (SOG) swim in the upper 30 m, above the thermocline and near the halocline. Pacific salmon have been documented undertaking vertical migrations, which involve quickly ascending to near-surface waters, and then returning to deeper waters, and may be an energy-saving strategy (Quinn et al. 1989, Tanaka et al. 2001). Vertical migrations appear to occur more often at night (Quinn et al. 1989) and are believed to aid in navigation, though whether fish are sampling surface waters for olfactory cues, or for other navigational cues (e.g. celestial or magnetic cues), is unknown. Generally, little evidence of 'depth-seeking' behaviours or vertical migrations has been collected for coastally migrating sockeye salmon.

There are ~50 genetically distinct populations of Fraser River sockeye salmon that migrate distances ranging from 50 to 1150 km from the river mouth to spawning areas. Populations exhibit differential body morphology and physiology that are related to the natural selective pressures exerted by migratory distance and difficulty (Crossin et al. 2004, Eliason et al. 2011). For example, coastal populations such as Weaver Creek or Harrison River swim shorter distances (~100 km) and enter the Fraser River later, when water velocity is lower. Their migration is easier compared to Chilko populations, which enter earlier when the river has higher flows, experience a broader range in water temperatures, swim farther (~1000 km, with an increase of 1200 m in elevation) and must pass Hell's Gate, a significant hydrological barrier (Hinch & Bratty 2000). Chilko fish tend to be more fusiform, have smaller eggs and are more efficient and better swimmers (i.e. broader aerobic scope and higher burst swim speeds, traits which are believed to be energy conservation adaptations for freshwater migrants; Crossin et al. 2004, Eliason et al. 2011). Studies which have examined marine migration swimming behaviour have rarely considered the role of population-specific adaptations on swim speed patterns (Crossin et al. 2007).

A number of methods have been used to examine locomotor behaviour, including estimating segment-specific movement rates using mark–recapture techniques with a variety of tag types (Peterson disc, passive acoustic and radio telemetry), and assessing fine-scale continuous movements and rates using active acoustic telemetry (Madison et al. 1972, Stasko et al. 1976, Quinn 1988), or stationary arrays (English et al. 2005, Crossin et al. 2007). However, these techniques assume that fish swim in a straight line and do not account for differences in swim speed associated with tidal influence, currents or vertical migrations. Thus, present estimates of swim speed may be conservative. Swim speeds can be approximated using electromyogram (EMG) radio transmitters (Cooke et al. 2004b), which more accurately measure swim speed by assessing tailbeat frequency, rather than inferring swim speed based on time and distance. However, EMG radio transmitters cannot be used in the marine environment as radio signals become attenuated (see Cooke et al. 2004b). Although acoustic EMG transmitters exist (Dewar et al. 1999, Lembo et al. 2008), they have not been widely adopted, and challenges remain with electrodes staying fixed in axial musculature over long migrations.

Development of accelerometer technology has provided new tools for studying the behaviour of marine animals. For example, in fish, acceleration can be used to derive swim speed principally by measuring acceleration associated with tailbeat oscillations (Kawabe et al. 2003a, Shepard et al. 2008). Accelerometer data loggers have been developed to record information on movement (e.g. 3-dimensional: overall dynamic body acceleration, ODBA; 2-dimensional: partial dynamic body acceleration, PDBA; Shepard et al. 2008) in a wide range of taxa (e.g. humans: Halsey et al. 2008; birds: Wilson et al. 2006, Green et al. 2009), including fishes (sharks: Gleiss et al. 2010; salmon: Clark et al. 2010, Tanaka et al. 2001, Kawabe et al. 2003a; flounder: Kawabe et al. 2003b; bonefish: Brownscombe et al. 2013). For example, accelerometer loggers have been successfully used to estimate swim speed in migrating adult chum salmon along the Japanese coast (Tanaka et al. 2001). However, as with all loggers, they have limited applicability for use in a natural environment where it is more difficult to retrieve loggers (Cooke et al. 2004a). More recently, acoustic transmitters have been developed that measure acceleration in 3 axes and then transmit a root mean square (RMS) acceleration to a receiver. These transmitters can also be fitted with pressure or temperature sensors, so information on depth can be collected. This technology has been used to monitor fine-scale movement patterns in great barracuda *Sphyraena barracuda* (O'Toole et al. 2010) and to estimate energy use of bonefish *Albula vulpes* (Murchie et al. 2011) and cuttlefish *Sepia apama* (Payne et al. 2011). Relationships between acoustic acceleration transmitter output and swim speed have recently been developed for sockeye salmon in laboratory respirometers (Wilson et al. 2013), enabling swimming speeds to be estimated for tagged free-swimming sockeye salmon. Here we used acceleration transmitters to characterize swimming behaviour of adult sockeye salmon as they migrate through a coastal portion of the marine migration phase, through the estuary and into the lower reaches of the Fraser River.

MATERIALS AND METHODS

Transmitter calibration

The linear mixed effect model that was used to estimate swim speed from accelerometer output was previously developed (Wilson et al. 2013). Briefly, 9 Harrison River adult sockeye salmon were collected from the Harrison River during their freshwater migration to natal spawning areas (6 males and 3 females; fork length, FL = 60.5–68.9 cm). Each fish was gastrically tagged with an accelerometer transmitter (VEMCO, Model V9A-2H, 69 kHz, 16 ×

67 mm) before completing a standard ramp critical swimming speed swim protocol using a Brett-style swim tunnel respirometer (fully described by Jain et al. 1997 and Lee et al. 2003). Water velocity was incrementally increased from a resting swim speed of 0.15 m s^{-1} up to 0.65 m s^{-1} (~50% of critical swim speed) over a 15 min period. Thereafter, the water velocity was increased by 0.15 m s^{-1} (~0.20 BL s^{-1}) every 20 min until the fish ceased swimming and remained on the rear grid for >10 s. Once a fish had fatigued, water velocity was decreased to 0.15 m s^{-1}, and the individual was allowed to recover for at least 1 h prior to the next trial. A portable acoustic hydrophone was inserted into the top of the swim tunnel, and the receiver unit (VR100, VEMCO) recorded acceleration data throughout each swim trial. Accelerometers measured acceleration in 3 axes for 10 s with a sampling frequency of 10 Hz. The RMS acceleration was calculated by averaging acceleration in all 3 dimensions using the equation $\text{RMS} = (x^2 + y^2 + z^2)^{0.5}$, transmitted every 13 to 17 s, and had a range of 0 to 4.901 m s^{-2}. Swim speed was corrected for blocking effect (Jones et al. 1974) and compared to mean acceleration during the last 10 min of each swim speed increment (see Fig. 2). A linear mixed effects model was used to describe the relationship between swim speed and acceleration using FL as a covariable, with subject ID as a random factor (to account for non-independence of data). The most parsimonious models were chosen based on a second-order information criterion (bias-corrected Akaike's information criterion, AICc; Sugiura 1978). Model parameters are presented in Table 1.

Table 1. *Oncorhynchus nerka.* Parameter estimates and significance of variables retained in model selection for the relationship between acceleration and swim speed for the 9 fish tagged for the laboratory study

Terms	Parameter estimate	p
Intercept	2.5560	0.0114
Fork length	−0.0358	0.0508
Acceleration	0.6250	<0.0001

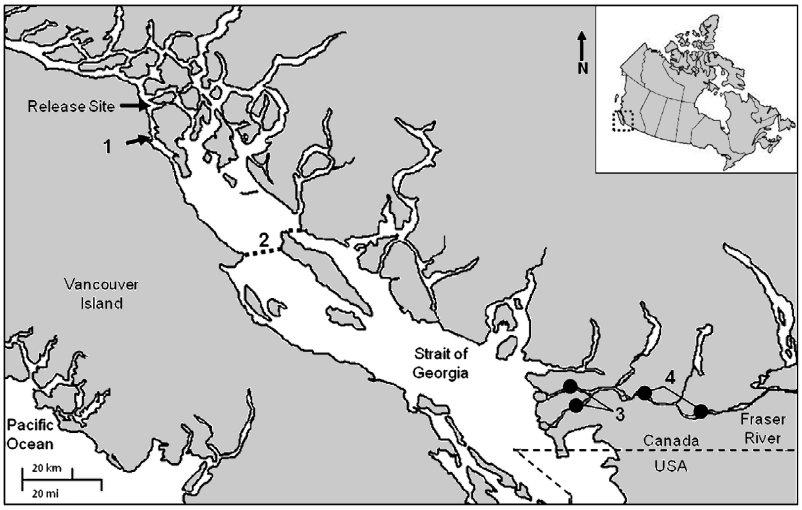

Fig. 1. Locations of acoustic receiver arrays throughout the Strait of Georgia (SOG) and lower Fraser River. 1: Seymour Narrows, 2: northern SOG (NSOG), 3: river entrance, 4: in river. Sockeye salmon were captured by trolling and were released in Rock Bay

Field site and receiver arrays

The present study was conducted in accordance with the University of British Columbia Animal Care Committee and guidelines of the Canadian Council on Animal Care, as administered by Carleton University (Animal Care no. B10–08) and the University of British Columbia (Animal Care no. A11–0215). Fifty-five sockeye salmon (FL = 51–70 cm) were caught by trolling in Rock Bay, Johnstone Strait (50° 20′ N, 125° 25′ W; Fig. 1) throughout 7 to 17 August 2012 (surface water temperature = 10–13°C). Once captured, fish were placed in a large flow-through tank and the trolling hook was removed. No more than 12 fish were held in the tank at any time. Fish were individually dip-netted out of the tank and placed in a V-shaped foam-lined trough, which was continuously refreshed with seawater. FL of fish was measured, and a tissue (<0.1 g) biopsy from the adipose fin was collected for population identification and stored at room temperature in 95% ethanol. The population of each sockeye salmon was identified using DNA analyses (Beacham et al. 1995, 2004). Tagging and biopsy samples were collected using protocols for the non-lethal anaesthetized sampling of sockeye salmon (see Cooke et al. 2005, 2006). A previous study by Cooke et al. (2005) showed no differences in behaviour or survivorship between tagged fish that were biopsied or not biopsied (Cooke et al. 2005). An accelerometer transmitter (VEMCO Model V13AP-1H, 69 kHz, 16 × 67 mm) was then gastrically inserted (Cooke et al. 2005). Accelerometers functioned the same as during the calibration experiment except that the V13AP tags transmitted every 20 to 70 s, alternating between acceleration and depth (in m), with a 3:1 ratio (i.e. A-A-A-D). The range of depth detected by these tags was 0–500 ± 2.0 m.

Once tagging was completed, fish were returned to the tank and transported to the release sites. Four acoustic receivers (VEMCO Model VR2W) were set up ~10 km south of the release sites (Seymour Narrows; Fig. 2). Farther south (~70 km) of those acoustic receivers, fish passed the northern SOG (NSOG) line. Fish were next detected by receivers deployed throughout lower Fraser River (~200 km from NSOG, Fig. 2). Receiver range varies on a site-specific basis, but is typically between 500 and 1000 m.

Statistical analyses

DNA analysis identified 11 Fraser River populations amongst the tagged salmon (Weaver, Harrison, Pitt River, North Thompson, Gates Creek, Lower Adams, Birkenhead, Chilko, Stellako, Early Stuart, Bowron) and a non-Fraser River population (Klinaklini; a mainland population). Fraser River populations can be classified into run timing groups based on date of river entrance (Table 2). These populations can also be categorized based on the difficulty of their migration. Several 'migration difficulty indices' have been proposed, involving migratory distance, elevation, temperature, or combinations of these variables, which have been created for comparisons of freshwater migration behaviour in Fraser River sockeye salmon (e.g. Crossin et al. 2004, Eliason et al. 2011). We chose to use the one recommended by Crossin et al. (2004) that classifies populations based on 'work', defined as the distance of migration to the natal stream multiplied by the elevation multiplied by 0.001. Work represents the slope of migration, where the higher the value, the more difficult the migration. This resulted in values between 1 and 1000. We classified migratory 'work' into 3 categories of migration difficulty: values <100 = easy migrations, 100–200 = intermediate, and >200 = difficult (Table 2).

For the purposes of this study, all analyses were completed on RMS acceleration (which reflects tailbeat oscillations; see Wilson et al. 2013). After analyses, RMS acceleration was used to predict approximate swim speed in order to be comparable across studies, using a previously developed model (see Table 1). The linear mixed effects model used to predict swim speed was only accurate to ≤2.5 BL s^{-1}; therefore, detections of >2.5 BL s^{-1} were excluded from means (Wilson et al. 2013) but were included in the analyses. In this study, swim speed was defined as a measure of propulsive force rather than forward movement (Webb 1995). Ground speed was calculated by dividing the time between detection of an individual at 2 sequential receiver arrays by the distance between those arrays, and reflects a simple single vector trajectory of fish swimming based on distance travelled rather than tailbeat frequency (Table 3). Vertical migrations were defined as the fish occupying <2 m from the surface since tags are accurate to within ±2.5 m.

Statistical analyses were done using R 2.15.306 (R Development Core Team 2012) with 'nlme' (Pinheiro et al. 2013), 'AICcmodavg' (Mazerolle 2012) and 'multcomp' (Hothorn et al. 2008) packages. Data were tested for normality and homoscedasticity.

Table 2. *Oncorhynchus nerka.* Acoustic acceleration transmitters deployed in sockeye salmon, and migratory characteristics of the populations. NA: not applicable

Migration difficulty	Run timing group	Population	Migratory distance (D_M) (km)	Migratory elevation (E_M) (m)	Work (0.001 D_M E_M)	Number tagged
Easy	Late	Weaver	117	32	4	6
	Late	Harrison	121	10	1	1
	Early summer	Pitt River	78	10	1	1
	Other	Klinaklini	NA	NA	NA	1
Intermediate	Early summer	North Thompson	408	373	152	7
	Early summer	Gates Creek	364	280	102	4
	Late	Lower Adams	480	346	166	1
	Late	Birkenhead	268	495	133	2
Difficult	Summer	Chilko	642	1174	753	26
	Summer	Stellako	958	677	649	3
	Early Stuart	Early Stuart	1071	690	734	2
	Early summer	Bowron	1055	956	1009	1

Mixed effect models were used to determine how RMS acceleration and migration depth were influenced by tide, diel period, location and (due to collinearity) migration difficulty category, or run timing groups as predictor variables. Diel periods were described using the periodic terms sin(2π · hour/24) and cos(2π · hour/24). An interaction term was included for day of year and diel periodic terms. All 2-term interactions were included as potential explanatory variables. In addition, the random variables fish ID and fish ID nested with population were tested. All models contained fish ID as a random variable to account for repeated detections for each fish. The most parsimonious model for each response variable was chosen with a stepwise procedure based on minimizing the AICc (Burnham & Anderson 2002). Bonferroni post hoc tests with planned comparisons were used to examine differences in response variables across locations and within locations across migration difficulty index. Spearman's rank order correlation test was used to determine inter-individual variability in swim speed between locations. For this test, each fish was ranked by its swim speed relative to all other fish at each detection location, and rank was compared between sequential locations. Significance levels for all tests were $\alpha = 0.05$.

RESULTS

After analyses, mean RMS acceleration values were converted to swim speed estimates using the mixed effect models developed from the swim flume experiment which showed that swim speed and acceleration were positively correlated (Fig. 2). The final mixed effect model (ΔAICc = 0) used to estimate swim speed from acceleration included acceleration and fork length (Table 1). RMS acceleration values were used in 2 mixed effect models. The first mixed effect model included the terms marine (pooled data from the Seymour Narrows and NSOG arrays) and freshwater (pooled data from river entrance and in-river arrays). The marine/freshwater final model included environment (marine/river), tide and diel period. Bonferroni post hoc planned contrasts comparing swim speed between marine and freshwater sites showed that RMS accelerations were greater in the Fraser River (1.73 ± 0.02 m s^{-2}, 1.57 ± 0.50 BL s^{-1}) and lower in the marine environment (1.29 ± 0.01 m s^{-2}, 1.23 ± 0.43 BL s^{-1}; $p < 0.001$). A second mixed effect model was then created analysing each array separately. The most parsimonious (ΔAICc = 0) array-

Table 3. *Oncorhynchus nerka*. Summary of swimming behaviour for tagged sockeye salmon. Migration speed was determined by dividing distance and time between successive arrays. Tabulated values show means for all individuals, as well as by migration difficulty category (values in brackets: easy, intermediate, difficult, respectively). Tag losses may be due to capture in fisheries (2 tags were reported captured by local fishermen) or marine predators. NSOG: northern Strait of Georgia, RMS: root mean square, BL: body length, NA: not applicable

	Number of fish detected	Distance from release (km)	Mean RMS acceleration (m s^{-2})	Ground speed (BL s^{-1})	Mean swim speed (BL s^{-1})	Mean depth (m)	Range of depths (m)	Vertical migrations (% of detections <2 m)
Seymour Narrows	27 (5, 8, 14)	10	1.37 (1.39, 1.46, 1.32)	NA	1.32 (0.97, 1.35, 1.37)	26.9 (52.1, 16.4, 12.3)	0–171.9	42 (33, 48, 45)
NSOG	26 (5, 7, 14)	70	1.24 (1.06, 0.98, 1.61)	1.1	1.18 (0.84, 1.03, 1.52)	9.2 (12.7, 7.7, 7.3)	0–61.9	17 (9, 14, 28)
River entrance	16 (3, 4, 9)	200	1.61 (1.73, 1.32, 1.69)	1.02	1.49 (1.47, 1.22, 1.60)	8 (9.4, 6.1, 8.5)	0–20.9	17 (9, 29, 12)
In river	14 (2, 4, 8)	250	1.98 (1.84, 2.01, 2.01)	1.29	1.75 (1.51, 1.73, 1.82)	8.9 (8.2, 9.9, 8.5)	0–16.4	7 (10, 2, 9)

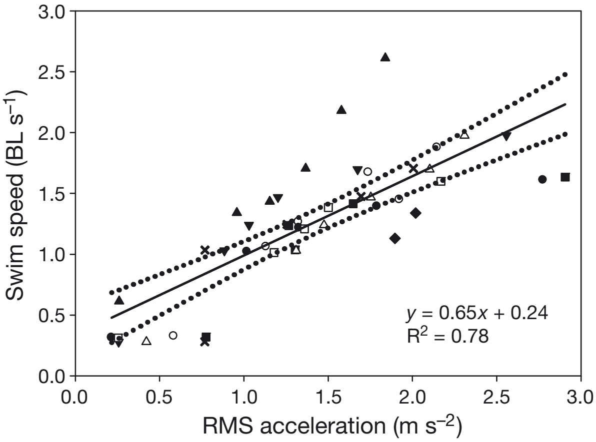

Fig. 2. *Oncorhynchus nerka.* Relationship between acceleration and swim speed at 14°C. Each symbol represents an individual (open symbols = females; closed symbols = males). Solid line: relationship for all fish. Dotted lines: 95% confidence intervals. BL: body length, RMS: root mean square. Data from Wilson et al. (2013)

Table 4. *Oncorhynchus nerka.* Significance of variables and variable interactions for the linear mixed effects model of root mean square acceleration and depth of free-swimming fish. NSOG: northern Strait of Georgia, DOY: day of year

Description	Term	df	t	p
Acceleration				
Intercept	Intercept	4168	20.76	<0.001
Diel period	sin(2π · hour/24)	4168	−14.35	<0.001
	cos(2π · hour/24)	4168	1.16	0.246
Location	NSOG	4168	−11.60	<0.001
	River entrance	4168	2.17	0.030
	Seymour	4168	−10.94	<0.001
Migration category	Easy	32	−2.19	0.036
	Intermediate	32	−1.11	0.276
Tide	Tide	4168	−2.70	0.007
Diel period × DOY	cos(2π · hour/24) × DOY	4168	−2.63	0.009
	sin(2π · hour/24) × DOY	4168	−0.64	0.521
Location × Tide	NSOG × Tide	4168	4.12	<0.001
	River entrance × Tide	4168	−4.81	<0.001
	Seymour × Tide	4168	3.21	0.001
Location × Migr. category	NSOG × Easy	4168	1.53	0.126
	River entrance × Easy	4168	1.11	0.268
	Seymour × Easy	4168	10.43	<0.001
	NSOG × Intermediate	4168	−0.29	0.772
	River entr. × Intermediate	4168	−3.31	0.001
Depth				
Intercept	Intercept	1613	4.74	<0.001
Diel period	sin(2π · hour/24)	1613	2.08	0.037
	cos(2π · hour/24)	1613	−5.65	<0.001
Location	NSOG	1613	−2.18	0.029
	River entrance	1613	−0.31	0.754
	Seymour	1613	1.64	0.102
Migration category	Easy	32	−0.59	0.560
	Intermediate	32	−0.45	0.654
Diel period × DOY	cos(2π · hour/24) × DOY	1613	−3.14	0.002
	sin(2π · hour/24) × DOY	1613	0.45	0.648
Location × Migr. category	NSOG × Easy	1613	−2.39	0.017
	River entrance × Easy	1613	1.36	0.176
	Seymour × Easy	1613	7.89	<0.001
	NSOG × Intermediate	1613	0.99	0.322
	River entr. × Intermediate	1613	−1.43	0.152
	Seymour × Intermediate	1613	0.26	0.791

specific mixed effect model for RMS acceleration included diel period and an interaction between location and migration difficulty category and between location and tide (Table 4). Within the marine areas, swim speed was higher in Seymour Narrows than in the NSOG (Fig. 3A). Bonferroni post hoc planned contrasts comparing RMS acceleration between migration difficulty categories within each location showed that fish in the easy migration group had slightly higher RMS accelerations than fish with difficult migrations at Seymour Narrows ($z = -2.94$, $p = 0.039$) but did not differ from fish with intermediate migration difficulty ($z = -0.96$, $p = 1.000$). In the river entrance array, fish with difficult freshwater migrations had higher accelerations than fish with intermediate migrations ($z = 3.52$, $p = 0.005$) but did not differ from fish with easy migrations ($z = 1.55$, $p = 1.000$). There were no differences in RMS accelerations between fish with intermediate and fish with difficult migrations at Seymour Narrows ($z = -2.56$, $p = 0.125$) or between fish with intermediate and fish with easy migrations at the river entrance array ($z = -1.13$, $p = 1.000$). No differences in RMS accelerations were observed between any of the 3 migration difficulty categories at NSOG ($p > 0.05$).

Planned contrasts of each migration difficulty category across locations showed that fish with difficult migrations had RMS accelerations that were significantly higher in NSOG than in Seymour Narrows ($z = -5.76$, $p < 0.001$), significantly higher at the river entrance compared to NSOG ($z = -15.55$, $p < 0.001$) and highest in the river compared to the river entrance ($z = -6.84$, $p < 0.001$). Fish with intermediate and easy migrations had lower RMS accelerations in NSOG than in Seymour Narrows ($z = 5.80$, $p < 0.001$; $z = 10.83$, $p < 0.001$, respectively), and higher in the river entrance array compared to NSOG ($z = -3.98$, $p < 0.001$; $z = -9.67$, $p < 0.001$, respectively). Fish with intermediate migrations had the higher RMS accelerations in the river ($z = -12.15$, $p < 0.001$) compared to at the river entrance; however, RMS accelerations of fish with easy migrations did not differ between river entrance and in-river arrays ($z = -1.50$, $p = 1.000$). Compar-

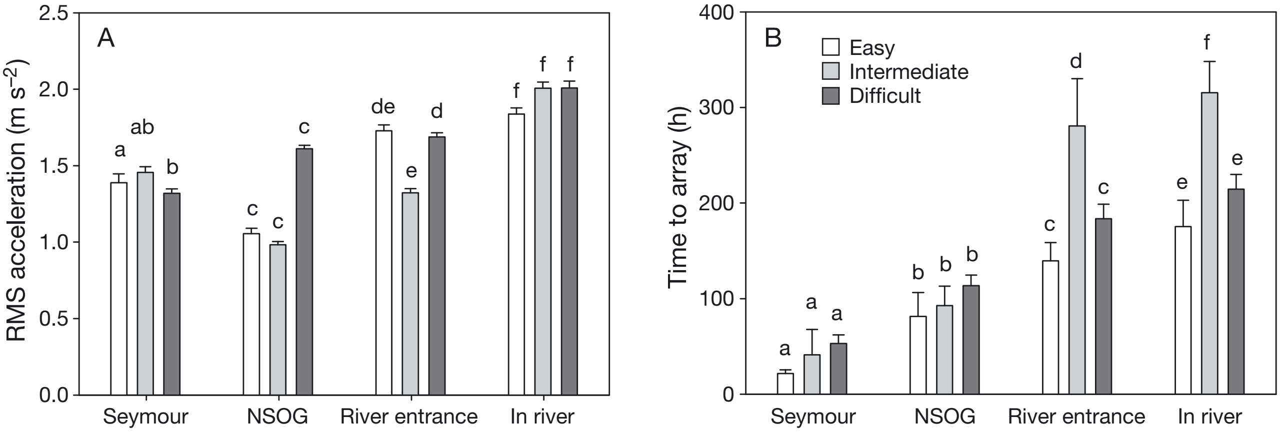

Fig. 3. *Oncorhynchus nerka.* Behavioural traits characterized for each migration difficulty category at each receiver array. (A) Root mean square (RMS) acceleration, (B) time to reach array from last site (i.e. release site to Seymour Narrows, Seymour Narrows to northern Strait of Georgia [NSOG]). Migration difficulty indicated by shading. Error bars represent SEM. Letters represent significant differences between migration difficulty groups ($\alpha = 0.05$)

isons of RMS accelerations during the day compared to night showed that RMS accelerations were not significantly different but slightly higher on average during the day than at night (1.54 ± 0.04 m s^{-2} [1.42 ± 0.49 BL s^{-1}] versus 1.48 ± 0.01 m s^{-2} [1.38 ± 0.46 BL s^{-1}], respectively; $t = 1.35$, df = 4530, $p = 0.175$).

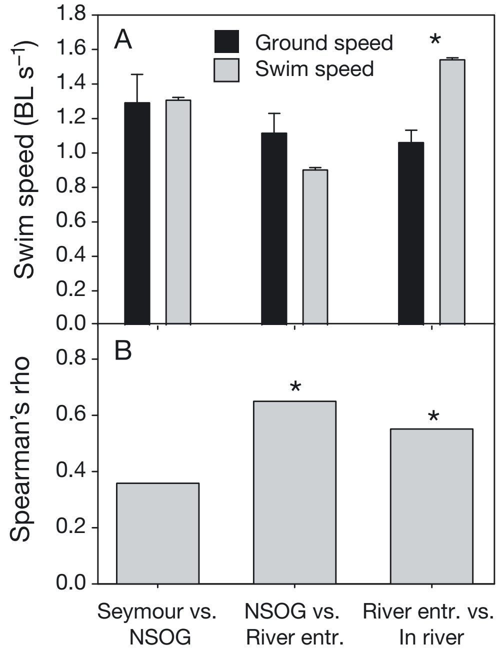

Fig. 4. *Oncorhynchus nerka.* (A) Ground speed and swim speed calculated using acceleration transmitters; BL: body length; error bars represent SEM. (B) Consistency of swim speeds between Seymour Narrows and northern Strait of Georgia (NSOG), NSOG and river entrance, and river entrance and in-river arrays. (*) Significantly different ($\alpha = 0.05$)

Higher RMS accelerations were not associated with faster time to arrival at each array (Fig. 3B). Fish from all 3 migration groups reached the Seymour Narrows and NSOG arrays in the same amount of time after release. However, fish from the intermediate migration category took longer to arrive at the river entrance array (Fig. 3B). Ground speed (the distance between arrays divided by the time required to swim between arrays) was compared with swim speeds calculated from RMS acceleration. Post hoc Bonferroni planned comparisons of the mixed effect model of location and speed estimate (ground speed versus swim speed) showed that only in-river estimates of swim speed were significantly higher than ground speed (1.54 BL s^{-1} [2.67 m s^{-1}] versus 1.06 BL s^{-1} [1.86 m s^{-1}], respectively, $z = 6.55$, $p < 0.0001$; Fig. 4A). Spearman rank order correlation was significant across consecutive locations (NSOG to river entrance: $\rho = 0.65$, $s = 238$, $p = 0.008$; river entrance to in-river: $\rho = 0.55$, $s = 204$, $p = 0.043$; Fig. 4B), but not Seymour to NSOG ($\rho = 0.36$, $s = 622$, $p = 0.145$). Furthermore, traces of 3 fish swimming at each location demonstrate that swimming was different between individuals but steady, with little intra-individual variability (Fig. 5).

The most parsimonious model (chosen by AICc) for describing depth included diel period and an interaction between location and migration difficulty category (Table 4). Planned contrasts within each array showed that fish with easy migrations swam significantly deeper in Seymour Narrows than fish with difficult migrations ($z = -4.51$, $p = 0.0001$) and intermediate migrations ($z = -4.38$, $p = 0.0002$). Fish from all 3 migration difficulty categories swam at the same depth within NSOG, river entrance, and in-river

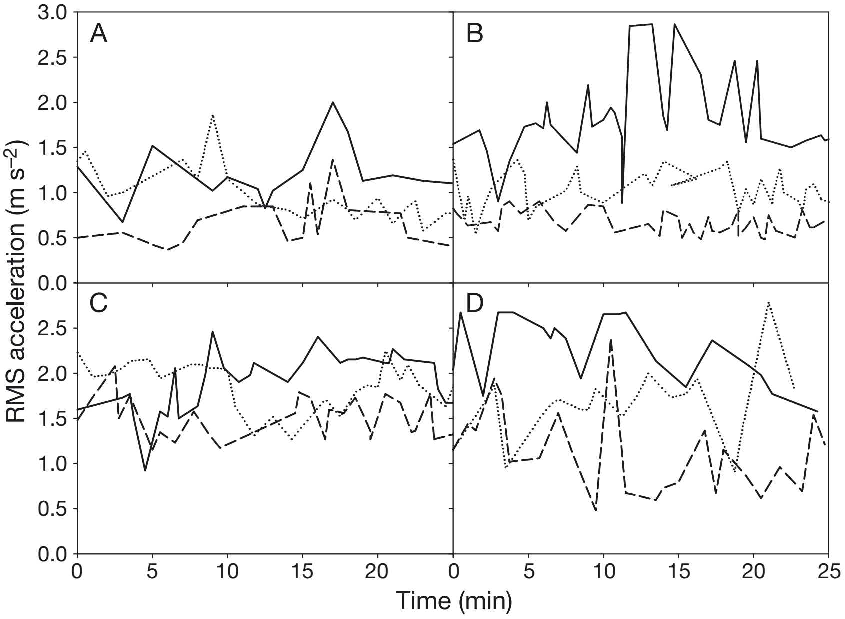

Fig. 5. *Oncorhynchus nerka.* Trace of root mean square (RMS) acceleration for 3 individual sockeye salmon at (A) Seymour Narrows, (B) northern Strait of Georgia (NSOG), (C) river entrance, and (D) in river. Each line type represents a different individual

arrays ($p > 0.05$; Fig. 6). Planned contrasts were also conducted comparing each migration difficulty category across all array sites. Fish with easy and difficult migrations swam deeper in Seymour Narrows than in NSOG ($z = 19.52$, $p < 0.0001$ vs. $z = 3.86$, $p = 0.002$), but no difference in swimming depth between Seymour Narrows and NSOG occurred for fish with intermediate migration difficulty ($z = 2.08$, $p = 0.794$). Fish with easy migrations swam shallower at the river entrance than at NSOG ($z = -6.21$, $p < 0.0001$), but fish with intermediate and difficult migrations swam at similar depths ($z = 1.82$, $p = 1.00$ vs. $z = -2.19$, $p = 0.600$). Once in-river, all fish swam at similar depths ($p > 0.05$; Fig. 6).

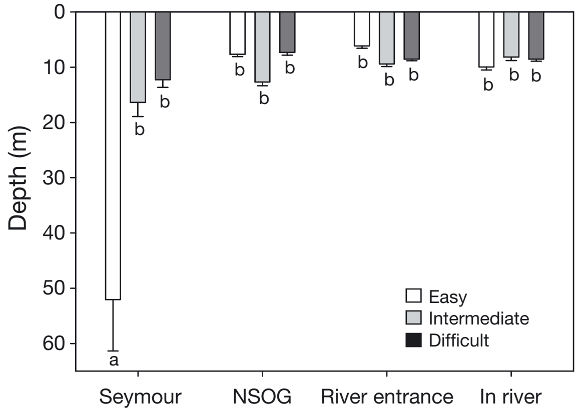

Fig. 6. *Oncorhynchus nerka.* Swimming depth for each migration difficulty category at each receiver array (see Fig. 7). Migration difficulty indicated by shading. Error bars represent SEM. Letters represent significant differences between migration difficulty groups ($\alpha = 0.05$)

Range in migration depth was the greatest in Seymour Narrows, and lower at NSOG (Table 3). In the river, range in migration depth was similar at both the river entrance and in-river arrays (Table 3). Detections of fish <2 m from the surface were considered vertical migrations. Vertical migrations, in percentage of detections <2 m at a receiver array, were highest in Seymour Narrows (42%), lower for NSOG and river entrance (17%) and lowest in-river (7%). Examples of traces of fish migration depths were reported over a 25 min continuous period of transmitted fish depth information (Fig. 7).

DISCUSSION

A linear mixed effect model was developed using Brett-style swim tunnels and was used to predict swim speed in free-swimming adult migrating salmon based on RMS acceleration. We found that RMS acceleration (and swim speeds) in the marine environment (Seymour Narrows and NSOG) were slower than in the river, consistent with the notion that river swim speed would increase in response to the increase in water velocity. Diel period was also retained in the marine/freshwater model, suggesting that diel period influenced RMS acceleration, and thus swim speed. The second mixed effect model which examined migration difficulty and receiver location included diel period, tide, receiver location and migration difficulty. Variability in RMS acceleration was related to diel period, where RMS acceleration (and swim speed) was slightly higher during the day, concurrent with the findings of Madison et al. (1972). In their study, diel period strongly influenced swim speeds likely because their fish were staging for river entrance into the Skeena River, rather than in the SOG or entering the turbid Fraser River. Tide was a significant, albeit minor, predictor of RMS acceleration, which was not surprising, as Stasko et al. (1976) found that despite the strong tidal influence of the coastal migration routes, salmon did not use tidal currents, but rather swam in a directed route

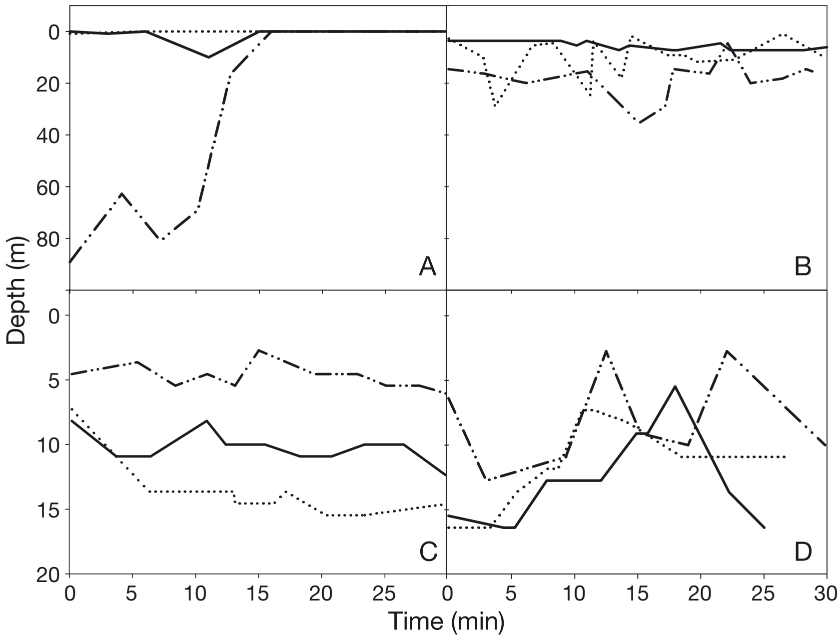

Fig. 7. *Oncorhynchus nerka.* Trace of depth of swimming for 3 individual sockeye salmon at (A) Seymour Narrows, (B) northern Strait of Georgia (NSOG), (C) river entrance, and (D) in river. Each line type represents a different individual

independent of flow. Tide was retained within the model as an interaction between tide and location. This suggests that salmon used tides in selective areas, such as Seymour Narrows, which is strongly tidally influenced, but not in other areas.

During the marine portion of migration, adult sockeye salmon exhibited higher RMS acceleration values and swim speeds in the Seymour Narrows array, compared with NSOG. Seymour Narrows is the narrowest portion of Johnstone Strait, and tidal currents are much stronger than in other regions. The higher RMS acceleration values relative to NSOG were therefore not surprising. Swim speeds determined from RMS acceleration were close to 1 BL s^{-1} in NSOG, which supports previous estimates of swim speed for that region reported for both adults (Quinn 1988, Quinn et al. 1989, Crossin et al. 2007) and smolts (Welch et al. 2011), and in other coastal areas (Tanaka et al. 2001). RMS acceleration values and thus swim speeds were higher in the river than in the marine environment, and highest in the in-river array, away from tidal influence. Previous studies have shown that salmon use tidal flows to assist in migration through the estuary (e.g. Levy & Cadenhead 1995). However, tide-mediated swimming speeds were not observed in our study.

Swim speeds through the in-river array were 1.7 BL s^{-1} on average, which was similar to swim speeds calculated from EMG telemetry observations in more upstream regions of the river (Hinch & Rand 1998). In EMG-based river studies, swim speed largely depended on sex, river discharge and water velocity, with males swimming 1.3 times faster than females (Hinch & Rand 1998), fish swimming faster during years of higher river discharge (Hinch & Rand 2000) and faster through river reaches with higher water velocities (Hinch & Rand 1998). The in-river array used in this study was approximately 100 km downstream of where the previous EMG estimates of swim speeds were collected, thus suggesting that fish swim speeds were relatively consistent throughout the lower Fraser River.

Sockeye salmon populations have different morphological, behavioural physiological adaptations to cope with their different freshwater migratory experiences (Crossin et al. 2004, Eliason et al. 2011). With telemetry, Crossin et al. (2007) observed population-specific differences in marine and lower Fraser River travel speeds. While studies generally make comparisons among populations or run-timing groups, we discovered that freshwater migration difficulty, rather than population or run-timing group, was a better predictor of marine swimming behaviour. Thus adaptations that contributed to differences among populations in swim performance and energy conservation during Fraser River migrations (Crossin et al. 2004, Eliason et al. 2011) appeared to also be influential for migrations in the marine environment. These findings are the first evidence in anadromous fish that marine swim speeds are influenced by physiological, morphological and behavioural traits important for successful completion of freshwater migrations.

In the vicinity of the Seymour Narrows array, fish with easy river migrations had lower RMS acceleration values and swam significantly slower than fish with difficult migrations, which pass Hell's Gate (a significant migratory challenge farther upstream). However, this trend was not observed in the NSOG array. Differences in migratory behaviour were again apparent in the river, as individuals with intermediate migrations had lower RMS accelerations than fish of other migration difficulty categories. Interestingly, although all fish appeared to have similar RMS accelerations and swim speeds, fish with intermediate migrations entered the river later than fish with easy or difficult migrations. The time taken to arrive at both Seymour Narrows and NSOG receiver arrays was similar between groups, so swim speed alone cannot explain the discrepancies in arrival at the river entrance array. Either fish with these migrations swam slower after NSOG (where there are no receivers), or, more likely, these fish held outside of the mouth of the Fraser River, a phenomenon that has been previously observed (Cooke et al. 2004c, Crossin et al. 2007).

Traditionally, ground speeds in the SOG have been inferred by dividing the distance between detections by the elapsed time between detections. This method assumes that fish swim in a straight line and does not account for differences in swim speed due to tidal influence and currents. We calculated ground speed and compared it to swim speeds calculated from RMS acceleration and found that at marine sites (Seymour Narrows and NSOG), swim speed was not different from ground speed. This demonstrated that sockeye salmon migrate in a very directed manner, with few deviations. Once in the river, swim speed was much faster than ground speed, which was expected since fish were swimming against strong river currents. This method also showed that swim speeds within the SOG were close to 1 BL s^{-1}, consistent with previous measurements of ground speed in SOG (Quinn 1988, Quinn et al. 1989, Crossin et al. 2007), as well as fish manually tracked in the Skeena River estuary (Madison et al. 1972) and Haro Strait (Stasko et al. 1976).

Each individual's RMS accelerations were generally consistent across sites. Fish that had higher RMS acceleration values (higher swim speeds) relative to others at NSOG generally had higher RMS acceleration values throughout marine coastal and in-river migration. This trend was not apparent between Seymour Narrows and NSOG arrays, which could be a result of the complex flows of Seymour Narrows. This finding is supported by a study by Hanson et al. (2008), who found that ground speed was not consistent within individuals or in areas of complex flows, although this study was conducted farther upriver (~100 km) than the current study. English et al. (2005) showed that swim speeds appeared to be consistent within individuals once the fish had reached the Thompson River (~300 km from the Fraser River mouth). Our data show that RMS acceleration (and swim speeds) were consistent with respect to other fish throughout coastal ocean migration (except in Seymour Narrows) and into the most downstream reaches of the Fraser River; the fastest swimming fish were consistently the fastest across geographic range. Inter-individual variability has often been observed in salmon. Some individuals swim more aggressively, while others tend to follow microcurrents (Stasko et al. 1976). Physiology has been used to explain some of this inter-individual variability (Hinch & Rand 1998, Crossin et al. 2007, Hanson et al. 2008). This variability was observed in the traces of 3 representative swimming sockeye salmon. Generally, traces of RMS acceleration values at receiver sites showed that within an individual, swimming appeared consistent, with only 5% of detections exceeding 2.5 BL s^{-1}. This was similar to a study by Quinn (1988), who observed sockeye salmon swimming consistently, with 17% of detections at what he considered 'bursting speeds'. The consistency of swimming at 1 BL s^{-1} supports previous findings that salmon minimize energetic costs by swimming at close to optimal swim speed (0.9 to 1.2 BL s^{-1}; Brett 1995).

The most parsimonious mixed effect model showed that diel period influenced migration depth. In Seymour Narrows, migration depth exhibited strong diel patterns, where fish swam much deeper during the day. However, this trend was not as strong throughout the rest of migration. Fish swam deepest in Seymour Narrows, which has generally greater water depths and has a stronger tidal influence compared to the rest of the coastal migration (250 m water depths in some areas, compared to an average of 150 m in NSOG). Fish arrived at the Seymour Narrows array <24 h after release, which suggested that short-term tagging effects may have influenced depth. However, previous studies have shown that tagging does not appear to affect behaviour (Davidsen et al. 2013). This area also has more marine predators, so depth-seeking behaviour may have represented an anti-predation mechanism. Migration depths at NSOG, river entrance and in-river arrays were similar (8 to 12 m). The relative difficulty implied by the migration difficulty category was also a predictor of migration depth, with fish with easy migrations swimming the deepest in Seymour Narrows, compared to fish with intermediate and difficult migrations. Similar to swim speed, migration depth varied considerably between individuals. Interestingly, depth traces showed that fish were swimming more closely to the surface than previous studies, which found that sockeye salmon swim in the upper 30 m but avoided warm surface waters (Quinn et al. 1989). Vertical migrations were defined as the fish occupying <2 m from the surface since tags are accurate to within ±2.5 m. Frequent vertical migrations were observed with fewer vertical migrations closer to the Fraser River. Frequent vertical migrations are believed to aid in navigation (Quinn et al. 1989). Thus decreasing the frequency of vertical migrations with decreasing distance to the Fraser River could have been due to increased strength of navigational cues. Alternatively, fish may be actively avoiding predators in Seymour Narrows. In the river, fewer vertical migrations may have been a result of habitat selection, since the current is typically faster near the surface, and thus would require more energy to swim at the surface.

The model used to calculate swim speed from acceleration output has some limitations. Swim speed was determined from RMS acceleration using a previously developed model (Wilson et al. 2013). This model was developed in fresh water and as there is a slight difference in density between fresh water and saltwater, this may result in some error in swim speed calculations. The accelerometer measures acceleration, mostly driven by tailbeat frequency. Thus actual swimming speeds may be slightly slower than calculated (due to increased force required to move through a denser medium), but given variability in swim speed, such a bias would probably be very modest and would not influence overall patterns of swimming behaviour. Additionally, the fish used to develop the model were slightly larger (57 to 68 cm) than the fish in this study (51 to 70 cm) and were from the Harrison River (easy migration category). As a result, the small differences in size and body morphology may have influenced swim speed as locomotor effort. More fusiform fish have lower drag to overcome, so differences in swim speed may have led to an underestimation of swim speed. Smaller fish have slightly higher acceleration values than larger fish, according to the swim speed–acceleration prediction model. As a result, the swim speeds of the smaller fish in this study may have been overestimated. However, the FL variable was a very minor predictor, and this is not likely to strongly influence swim speeds. The equation is only accurate within the range of 0.5 to 2.5 BL s^{-1} (Wilson et al. 2013). Generally, these limitations were avoided by analysis of RMS acceleration (rather than predicted swim speed), but may have influenced estimated swim speeds. Approximately 95 to 98% of detections at each site fell within the calibrated range of the swim speed model. Therefore, we believe that the data generated from the model and presented here are an accurate representation of the majority of swim speeds exhibited by migrating sockeye salmon. Finally, the swim speed–acceleration prediction model was developed in a swim flume, where some behaviours could not be observed (i.e. fast turns and dives). These behaviours may influence swim speed estimates; however, accelerometer transmitters use an on-board filter designed to minimize the impacts of body movements that are not directly involved with thrust. This is similar to the filters used in ODBA and PDBA, where it was found that the sway axis remained the most influential axis both in swim tunnels and in ponds (where fast turns could occur; Gleiss et al. 2010). Diving may also influence swim speed estimates. However, the depth data showed that the tagged sockeye salmon swam fairly consistently with few dives, so the error associated with diving is likely small.

The swim speed estimates determined in this study are comparable to estimates of swim speed from other more traditional methods (i.e. acoustic, disc, radio) showing that sockeye salmon swim at ~1 BL s^{-1} in the SOG. However, use of measurements of swim speed from accelerometers yields more insight into behaviour, individual variability and population differences for a poorly described region (coastal transition zone). In more constricted areas such as Johnstone Strait and the Fraser River, salmon swim faster due to increased water velocity. Our study also supports previous work that suggests sockeye salmon swim in a directed route, with little deviation throughout the coastal approach, until fish reach the mouth of the Fraser River. The overall difficulty of migration to the spawning ground for a given population is an important predictor of both swim speed and migration depth for sockeye salmon. In the future, this work could be expanded to increase sample sizes and further examine why differences in swimming speed relative to migration difficulty exist (i.e. physiology) and look at success (i.e. survival to spawning grounds). Finally, we found that individual swim speeds were consistent between sites, but significant inter-individual variance in swim speed and migration depth remains unexplained. Future work should examine swimming behaviour in the context of energy use in coastal migration and how this behaviour influences survival and reproductive investment. This represents the first study to use accelerometers to measure swim speed in both marine and freshwater environments.

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LITERATURE CITED

➤ Beacham TD, Withler RE, Wood CC (1995) Stock identification of sockeye salmon by means of minisatellite DNA variation. N Am J Fish Manag 15:249–265

➤ Beacham TD, Lapointe M, Candy JR, McIntosh B and others (2004) Stock identification of Fraser River sockeye salmon (*Oncorhynchus nerka*) using microsatellites and major histocompatibility complex variation. Trans Am Fish Soc 133:1106–1126

Brett JR (1995) Energetics. In: Groot C, Margolis CL, Clarke WC (eds) Physiological ecology of Pacific salmon. University of British Columbia Press, Vancouver, p 3–68

➤ Brownscombe JW, Thiem JD, Hatry C, Cull F, Haak CR, Danylchuk AJ, Cooke SJ (2013) Recovery bags reduce post-release impairments in locomotory activity and behaviour of bonefish (*Albula* spp.) following exposure to angling-related stressors. J Exp Mar Biol Ecol 440:207–215

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York, NY

➤ Clark TD, Sandblom E, Hinch SG, Patterson DA, Frappell PB, Farrell AP (2010) Simultaneous biologging of heart rate and acceleration, and their relationships with energy expenditure in free-swimming sockeye salmon (*Oncorhynchus nerka*). J Comp Physiol B Biochem Syst Environ Physiol 180:673–684

➤ Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Wolcott TG, Butler PJ (2004a) Biotelemetry: a mechanistic approach to ecology. Trends Ecol Evol 19:334–343

➤ Cooke SJ, Thorstad E, Hinch SG (2004b) Activity and energetics of free-swimming fish: insights from electromyogram telemetry. Fish Fish 5:21–52

➤ Cooke SJ, Hinch SG, Farrell AP, Lapointe M and others (2004c) Early-migration and abnormal mortality of late-run sockeye salmon in the Fraser River, British Columbia. Fisheries 29:22–33

➤ Cooke SJ, Crossin GT, Patterson DA, English KK and others (2005) Coupling non-invasive physiological assessments with telemetry to understand inter-individual variation in behaviour and survivorship of sockeye salmon: development and validation of a technique. J Fish Biol 67: 1342–1358

➤ Cooke SJ, Hinch SG, Crossin GT, Patterson DA and others (2006) Physiology of individual late-run Fraser River sockeye salmon (*Oncorhynchus nerka*) sampled in the ocean correlates with fate during spawning migration. Can J Fish Aquat Sci 63:1469–1480

➤ Crossin GT, Hinch SG, Farrell AP, Higgs DA, Lotto AG, Oakes JD, Healey MC (2004) Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. J Fish Biol 65:788–810

➤ Crossin GT, Hinch SG, Cooke SJ, Welch DW and others (2007) Behaviour and physiology of sockeye salmon homing through coastal waters to a natal river. Mar Biol 152:905–918

➤ Crossin GT, Hinch SG, Cooke SJ, Cooperman MS and others (2009) Mechanisms influencing the timing and success of reproductive migration in a capital breeding semelparous fish species, the sockeye salmon. Physiol Biochem Zool 82:635–652

➤ Davidsen JG, Rikardsen AH, Thorstad EB, Halttunen E and others (2013) Homing behaviour of Atlantic salmon (*Salmo salar*) during final phase of marine migration and river entry. Can J Fish Aquat Sci 70:794–802

➤ Dewar H, Deffenbaugh M, Thurmond G, Lashkari K, Block BA (1999) Development of an acoustic telemetry tag for monitoring electromyograms in free-swimming fish. J Exp Biol 202:2693–2699

Dingle H (1996) Migration: the biology of life on the move. Oxford University Press, Oxford

➤ Drenner SM, Clark TD, Whitney CK, Martins EG, Cooke SJ, Hinch SG (2012) A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. PLoS ONE 7:e31311

➤ Eliason EJ, Clark TD, Hague MJ, Hanson LM and others (2011) Differences in thermal tolerance among sockeye salmon populations. Science 332:109–112

Endler JA (1977) Geographical variation, speciation and clines. Princeton University Press, Princeton, NJ

➤ English KK, Koski WR, Sliwinski C, Blakley A, Cass A, Woodey JC (2005) Migration timing and river survival of late-run Fraser River sockeye salmon estimated using radiotelemetry techniques. Trans Am Fish Soc 134: 1342–1365

➤ Gleiss A, Dale J, Holland K, Wilson R (2010) Accelerating estimates of activity specific metabolic rate in fishes: testing the applicability of acceleration data loggers. J Exp Mar Biol Ecol 385:85–91

➤ Green JA, Halsey LG, Wilson RP, Frappell PB (2009) Estimating energy expenditure of animals using the accelerometry technique: activity, inactivity and comparison with the heart-rate technique. J Exp Biol 212:471–482

➤ Halsey LG, Shepard ELC, Hulston CJ, Venables MC, White CR, Jeukendrup AE, Wilson RP (2008) Acceleration versus heart rate for estimating energy expenditure and speed during locomotion in animals: tests with an easy model species, *Homo sapiens.* Zoology 111:231–241

➤ Hanson KC, Cooke SJ, Hinch SG, Crossin GT and others (2008) Individual variation in migration speed of upriver migrating sockeye salmon in the Fraser River in relation to their physiological and energetic status at marine approach. Physiol Biochem Zool 81:255–268

➤ Hinch SG, Bratty JM (2000) Effects of swim speed and activity pattern on success of adult sockeye salmon migration through an area of difficult passage. Trans Am Fish Soc 129:604–612

➤ Hinch SG, Rand PS (1998) Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): role of local environment and fish characteristics. Can J Fish Aquat Sci 55:1821–1831

➤ Hinch SG, Rand PS (2000) Optimal swim speeds and forward assisted propulsion: energy conserving behaviours of up-river migrating salmon. Can J Fish Aquat Sci 57: 2470–2478

Hinch SG, Standen EM, Healey MC, Farrell AP (2002) Swimming patterns and behaviour of up-river migrating adult pink (*Oncorhynchus gorbuscha*) and sockeye (*O. nerka*) salmon as assessed by EMG telemetry in the Fraser River, British Columbia, Canada. Hydrobiologia 483:147–160

➤ Hinch SG, Cooke SJ, Healey MC, Farrell AP (2006) Behavioural physiology of fish migrations: salmon as a model approach. Fish Physiol 24:239–295

➤ Hinch SG, Cooke SJ, Farrell AP, Miller KM, Lapointe M, Patterson DA (2012) Dead fish swimming: a review of research on the early migration and high premature mortality in adult Fraser River sockeye salmon *Oncorhynchus nerka.* J Fish Biol 81:576–599

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50:346–363

Jain KE, Hamilton JC, Farrell AP (1997) Use of a ramp velocity test to measure critical swimming speed in rainbow trout, *Oncorhynchus mykiss.* Comp Biochem Physiol A Comp Physiol 117:441–444

Jones DR, Kiceniuk JW, Bamford OS (1974) Evaluation of the swimming performance of several fish species from the Mackenzie River. J Fish Res Board Can 31:1641–1647

Kawabe R, Kawano T, Nakano N, Yamashita N, Hiraishi T, Naito Y (2003a) Simultaneous measurement of swimming speed and tail beat activity of free swimming rainbow trout *Oncorhynchus mykiss* using an acceleration data-logger. Fish Sci 69:959–965

Kawabe R, Nashimoto K, Hiraishi T, Naito Y, Sato K (2003b) A new device for monitoring the activity of freely swimming flatfish, Japanese flounder *Paralichthys olivaceus.* Fish Sci 69:3–10

Lee CG, Farrell AP, Lotto A, MacNutt MJ, Hinch SG, Healey MC (2003) The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. J Exp Biol 206:3239–3251

Lembo G, Carbonara P, Scolamacchia M, Spedicato MT, Bjørnsen JE, Holand B, McKinley RS (2008) Introduction of a new physiological acoustic electromyogram transmitter. Fish Manag Ecol 15:333–338

Levy DA, Cadenhead AD (1995) Selective tidal stream transport of adult sockeye salmon (*Oncorhynchus nerka*) in the Fraser River estuary. Can J Fish Aquat Sci 52:1–12

Madison DM, Horrall RM, Stasko AB, Hasler AD (1972) Migratory movements of adult sockeye salmon (*Oncorhynchus nerka*) in coastal British Columbia as revealed by ultrasonic tracking. J Fish Res Board Can 29:1025–1033

Martins EG, Hinch SG, Cooke SJ, Patterson DA (2012) Climate effects on growth, phenology, and survival of sockeye salmon (*Oncorhynchus nerka*): a synthesis of the current state of knowledge and future research directions. Rev Fish Biol Fish 22:887–914

Mathes MT, Hinch SG, Cooke SJ, Crossin GT, Patterson DA, Lotto AG, Farrell AP (2010) Effect of water temperature, timing, physiological condition and lake thermal refugia on migrating adult Weaver Creek sockeye salmon (*Oncorhynchus nerka*). Can J Fish Aquat Sci 67:70–84

Mazerolle MJ (2012) AICcmodavg: model selection and multimodel inference based on (Q) AIC(c). R package version 1.25. Available at http://cran.r-project.org/web/packages/AICcmodavg/index.html

Miller KM, Schulze AD, Ginther N, Li S, Patterson DA, Farrell AP, Hinch SG (2009) Salmon spawning migration: metabolic shifts and environmental triggers. Comp Biochem Physiol D Genomics Proteomics 4:75–89

Murchie KJ, Cooke SJ, Danylchuk AJ, Suski CD (2011) Estimates of field activity and metabolic rates of bonefish (*Albula vulpes*) in coastal marine habitats using acoustic tri-axial accelerometer transmitters and intermittent-flow respirometry. J Exp Mar Biol Ecol 396:147–155

Newell JC, Quinn TP (2005) Behavioral thermoregulation by maturing adult sockeye salmon (*Oncorhynchus nerka*) in a stratified lake prior to spawning. Can J Zool 83:1232–1239

O'Toole AC, Murchie KJ, Pullen C, Hanson KC, Suski CD, Danylchuk AJ, Cooke SJ (2010) Locomotory activity and depth distribution of adult great barracuda (*Sphyraena barracuda*) in Bahamian coastal habitats determined using acceleration and pressure biotelemetry transmitters. Mar Freshw Res 61:1446–1456

Ogura M, Ishida Y (1995) Homing behavior and vertical movements of four species of Pacific salmon (*Oncorhynchus* spp.) in the Central Bering Sea. Can J Fish Aquat Sci 52:532–540

Payne NL, Gillanders BM, Seymour RS, Webber DM, Snelling EP, Semmens JM (2011) Accelerometry estimates field metabolic rate in giant Australian cuttlefish *Sepia apama* during breeding. J Anim Ecol 80:422–430

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2013) nlme: linear and nonlinear mixed effects models. R package version 3.1–113. Available at http://cran.r-project.org/web/packages/nlme/index.html

Quinn TP (1988) Estimated swimming speeds of migrating adult sockeye salmon. Can J Zool 66:2160–2163

Quinn TP, Terhart BA, Groot C (1989) Migratory orientation and vertical movements of homing adult sockeye salmon, *Oncorhynchus nerka*, in coastal waters. Anim Behav 37: 587–599

R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rand PS, Hinch SG (1998) Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): simulating metabolic power and assessing risk of energy depletion. Can J Fish Aquat Sci 55:1832–1841

Roscoe DW, Hinch SG, Cooke SJ, Patterson DA (2010) Behaviour and thermal experience of adult sockeye salmon migrating through stratified lakes near spawning grounds: the roles of reproductive and energetic states. Ecol Freshw Fish 19:51–62

Shepard ELC, Wilson RP, Quintana F, Gómez-Laich A and others (2008) Identification of animal movement patterns using tri-axial accelerometry. Endang Species Res 10: 47–60

Stasko AB, Horrall RM, Hasler AD (1976) Coastal movements of adult Fraser River sockeye salmon (*Oncorhynchus nerka*) observed by ultrasonic tracking. Trans Am Fish Soc 105:64–71

Sugiura N (1978) Further analysis of the data by Akaike's information criterion and the finite corrections. Commun Stat A Theory Methods 7:13–26

Tanaka H, Takagi Y, Naito Y (2001) Swimming speeds and buoyancy compensation of migrating adult chum salmon *Oncorhynchus keta* revealed by speed/depth/acceleration data logger. J Exp Biol 204:3895–3904

Webb PW (1995) Locomotion. In: Groot C, Margolis L, Clarke WC (eds) Physiological ecology of Pacific salmon. University of British Columbia Press, Vancouver, p 69–101

Welch DW, Melnychuk MC, Payne JC, Rechisky EL and others (2011) In situ measurement of coastal ocean movements and survival of juvenile Pacific salmon. Proc Natl Acad Sci USA 108:8708–8713

Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. J Anim Ecol 75: 1081–1090

Wilson SM, Hinch SG, Eliason EJ, Farrell AP, Cooke SJ (2013) Calibrating acoustic acceleration transmitters for estimating energy use by wild adult Pacific salmon. Comp Biochem Physiol A Mol Integr Physiol 164:491–498

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