

# Tracking wild sockeye salmon smolts to the ocean reveals distinct regions of nocturnal movement and high mortality

TIMOTHY D. CLARK,<sup>1,2,10</sup> NATHAN B. FUREY,<sup>2</sup> ERIN L. RECHISKY,<sup>3</sup> MARIKA K. GALE,<sup>4</sup> KEN M. JEFFRIES,<sup>5</sup>  
ASWEA D. PORTER,<sup>3</sup> MATTHEW T. CASSELMAN,<sup>2</sup> ANDREW G. LOTTO,<sup>2</sup> DAVID A. PATTERSON,<sup>6</sup> STEVEN J. COOKE,<sup>7</sup>  
ANTHONY P. FARRELL,<sup>8,9</sup> DAVID W. WELCH,<sup>3</sup> AND SCOTT G. HINCH<sup>2</sup>

<sup>1</sup>*Australian Institute of Marine Science, PMB 3, Townsville MC, Queensland 4810 Australia*

<sup>2</sup>*Pacific Salmon Ecology and Conservation Laboratory, Department of Forest and Conservation Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia V6T 1Z4 Canada*

<sup>3</sup>*Kintama Research Services, Ltd., 10-1850 Northfield Road, Nanaimo, British Columbia V9S 3B3 Canada*

<sup>4</sup>*Science Division, Freshwater Fisheries Society of BC, 34345 Vye Road, Abbotsford, British Columbia V2S 7P6 Canada*

<sup>5</sup>*Anatomy, Physiology & Cell Biology, and Wildlife, Fish & Conservation Biology, University of California, Davis, One Shields Avenue, Davis, California 95616 USA*

<sup>6</sup>*Fisheries and Oceans Canada, Science Branch, Pacific Region, School of Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia V5A 1S6 Canada*

<sup>7</sup>*Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental Science, Carleton University, 1125 Colonel By Dr., Ottawa, Ontario K1S 5B6 Canada*

<sup>8</sup>*Department of Zoology, University of British Columbia, 6270 University Blvd, Vancouver, British Columbia V6T 1Z4 Canada*

<sup>9</sup>*Faculty of Land and Food Systems, University of British Columbia, 2357 Main Mall, Vancouver, British Columbia V6T 1Z4 Canada*

**Abstract.** Few estimates of migration rates or descriptions of behavior or survival exist for wild populations of out-migrating Pacific salmon smolts from natal freshwater rearing areas to the ocean. Using acoustic transmitters and fixed receiver arrays across four years (2010–2013), we tracked the migration of >1850 wild sockeye salmon (*Oncorhynchus nerka*) smolts from Chilko Lake, British Columbia, to the coastal Pacific Ocean (>1000 km distance). Cumulative survival to the ocean ranged 3–10% among years, although this may be slightly underestimated due to technical limitations at the final receiver array. Distinct spatial patterns in both behavior and survival were observed through all years. In small, clear, upper-river reaches, downstream migration largely occurred at night at speeds up to 50 km/d and coincided with poor survival. Among years, only 57–78% of smolts survived the first 80 km. Parallel laboratory experiments revealed excellent short-term survival and unhindered swimming performance of dummy-tagged smolts, suggesting that predators rather than tagging effects were responsible for the initial high mortality of acoustic-tagged smolts. Migration speeds increased in the Fraser River mainstem (~220 km/d in some years), diel movement patterns ceased, and smolt survival generally exceeded 90% in this segment. Marine movement rates and survival were variable across years, with among-year segment-specific survival being the most variable and lowest (19–61%) during the final (and longest, 240 km) marine migration segment. Osmoregulatory preparedness was not expected to influence marine survival, as smolts could maintain normal levels of plasma chloride when experimentally exposed to saltwater (30 ppt) immediately upon commencing their migration from Chilko Lake. Transportation of smolts downstream generally increased survival to the farthest marine array. The act of tagging may have affected smolts in the marine environment in some years as dummy-tagged fish had poorer survival than control fish when transitioned to saltwater in laboratory-based experiments. Current fisheries models for forecasting the number of adult sockeye returning to spawn have been inaccurate in recent years and generally do not incorporate juvenile or smolt survival information. Our results highlight significant potential for early migration conditions to influence adult recruitment.

**Key words:** acoustic telemetry; British Columbia; Canada; Chilko Lake; Fraser River watershed, Canada; migration; Pacific salmon; predation.

Manuscript received 11 April 2015; revised 8 September 2015; accepted 22 September 2015; final version received 21 October 2015. Corresponding Editor: B. X. Semmens.

**Editors' Note:** Papers in this Invited Feature will be published individually, as soon as each paper is ready. Once the final paper

is complete, a virtual table of contents with links to all the papers in the feature will be available on the journal website.

<sup>10</sup>Present address: University of Tasmania and CSIRO Agriculture Flagship, Castray Esplanade, Hobart, Tasmania 7000 Australia. E-mail: timothy.clark.mail@gmail.com

## INTRODUCTION

Animal migrations have captivated naturalists and scientists for centuries. Whereas some migrations, such as those of African wildebeest (Thomson 1885, Talbot and Talbot 1963) and monarch butterflies (Riley 1878), are conspicuous and spectacular, others are visibly less conspicuous but no less impressive. The outmigration of anadromous sockeye salmon (*Oncorhynchus nerka*) smolts from natal freshwater rearing grounds to the ocean is an annual event that can include hundreds of millions of individuals from a single watershed and cover distances exceeding 1200 km (Groot et al. 1989, Groot and Margolis 1991). In contrast to terrestrial animals, the sockeye smolt migration can occur essentially unnoticed from a human perspective because it takes place underwater, often in fast-flowing and turbid rivers that are removed from human population centers. Once smolts commence their journey to the Pacific Ocean, they will not be seen in freshwater again until they return 2–3 yr later, usually to the location of their birth, for their single opportunity to reproduce prior to death.

The Fraser River watershed in British Columbia, Canada hosts some of the largest wild populations of sockeye salmon in the world. The impressive life cycle of sockeye salmon has been repeated in this watershed since the retreat of the last glaciers 9–13 ka ago (Ricker 1940, Stumpf et al. 2000). However, the trend over the last two decades has been a precipitous decline in numbers of returning adult Fraser River sockeye salmon from several large populations and general declines in productivity to levels below replacement. Amidst the general decline, the return of adult Fraser River sockeye in 2010 was the largest in a century, yet the reasons for this anomaly remain unclear (Cohen 2012). Fraser River sockeye are extremely valuable economically as part of large commercial and recreational fisheries, are important to First Nations culture and society, and are an iconic species to British Columbians. Arising from concerns for the long-term sustainability and conservation of sockeye salmon, the Prime Minister of Canada created a judicial inquiry (2009–2012) that identified critical knowledge gaps regarding the movement and survival of the out-migrating smolts (Peterman et al. 2010, Peterman and Dorner 2012). From 1960 to 1998, around 8–10% of migrating smolts from the Fraser River watershed survived to return to spawning grounds as adults, yet in recent years this figure has dropped to less than 5% (Irvine and Akenhead 2013). It remains largely unknown where and how smolts perish, which makes it difficult for fisheries managers to determine possible means of mitigating mortality or using this information in models to predict the number of returning adults.

With recent advances in the miniaturization of telemetry technology, and with the advent of large tracking networks like the Pacific Ocean Shelf Tracking (POST) network and the Ocean Tracking Network (OTN), it has become possible to tag and track Pacific salmon

smolts through freshwater and marine environments (e.g., Welch et al. 2004, 2008, 2009, 2011, Schreck et al. 2006, Chittenden et al. 2010, Cavallo et al. 2013). Most studies to date have examined hatchery-reared smolts, which are often morphologically, behaviorally, and physiologically distinct from wild smolts as hatchery practices are tailored to produce larger and fatter individuals (Piggins and Mills 1985, Levings et al. 1986, Poole et al. 2003, Huntingford 2004). Only one tracking study has examined the freshwater and early coastal out-migration of sockeye salmon smolts; Welch et al. (2009) acoustically tracked hatchery-reared individuals from the Cultus Lake population (a small Fraser River population) over a spatial scale of ~100 km in fresh water and then an additional ~400 km northward along the coast of mainland British Columbia. While significant mortality was documented across the ~500 km range (70–95%), which the authors largely attributed to predation, the broader applicability of the results remain uncertain because (1) the Cultus Lake population has a very short freshwater migration involving a narrow and highly modified stream that may have unusually high predator abundance, (2) the population is classed as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; *data available online*)<sup>11</sup> and thus represents only a tiny fraction of the sockeye biomass within the Fraser River system, and (3) there are significant unresolved questions concerning the applicability of survival and movement data from hatchery-reared fish to their smaller wild congeners.

Using acoustic telemetry tags and infrastructure to track small fish (e.g., Welch et al. 2002, 2009, Cooke et al. 2011a), the present research program was conducted to provide the first insight into the movements and survival of wild sockeye salmon smolts during their migration from natal rearing grounds to the open ocean. The Chilko Lake population was selected for the study (Fig. 1) because it has not been altered by hatchery production, smolt out-migrations and adult spawning have been monitored since the 1950s, it remains a major indicator population for management of Fraser River sockeye, and it is one of the largest sockeye populations in the Fraser River watershed, thereby contributing significantly to the resilience of the species in Canada and the productivity of the fishery (Lapointe 2010).

After hatching, pre-smolts of the Chilko population reside in Chilko Lake for 1–2 yr prior to undergoing smoltification and commencing their >1000 km outmigration to the open ocean; first through clear and shallow upper-river reaches of the Chilko and Chilcotin Rivers, continuing through the turbid and deeper mainstem Fraser River and estuary, and finally along the coastal marine environment as they head north into (eventually) the offshore Pacific Ocean. Some recent work combining DNA-based stock identification of sockeye smolts captured in ocean trawl surveys is

<sup>11</sup> [http://www.cosewic.gc.ca/eng/sct1/searchform\\_e.cfm](http://www.cosewic.gc.ca/eng/sct1/searchform_e.cfm)

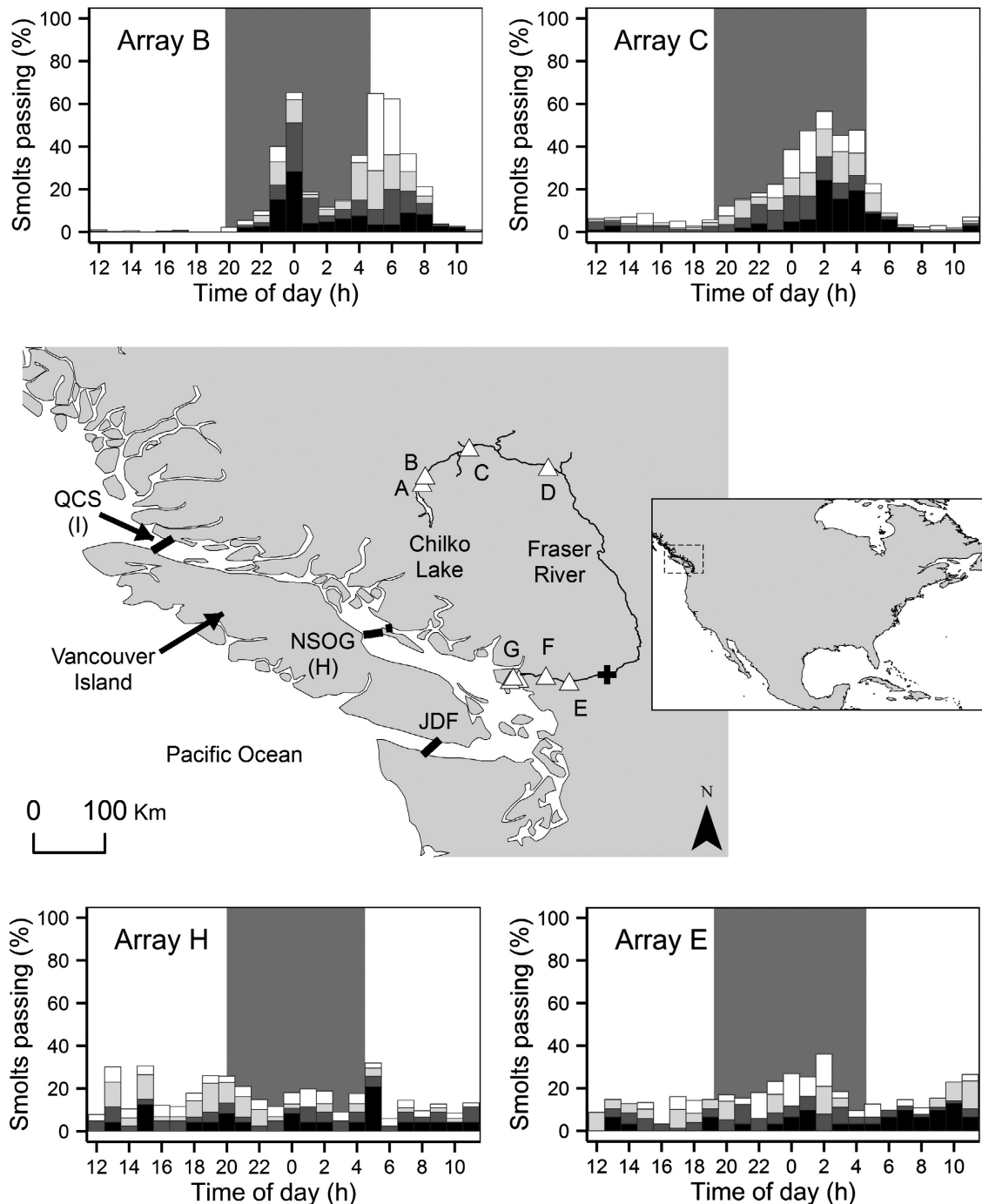


FIG. 1. Map of study area indicating Chilko Lake and the positions of acoustic receiver arrays (A–I). With the exception of Array G at the Fraser River mouth, each freshwater array was composed of five pairs of receivers (triangles indicate pairs) usually situated on either side of the river. Array G was composed of two pairs of receivers located at a similar distance from the release site with individual pairs deployed to monitor the various passage routes through the Fraser River estuary. In marine areas, the acoustic arrays were positioned as curtains and were composed of several receivers whose names reflect geographic locales: JDF Array, Juan de Fuca Strait (30 receivers); NSOG Array, Northern Strait of Georgia (27 receivers, Array H in this study); and QCS Array, Queen Charlotte Strait (24 receivers, Array I in this study). Four arrays were positioned in the Chilko/Chilcotin Rivers (Arrays A–D) and three arrays were positioned in the lower Fraser River (Arrays E–G). The cross indicates release location of transported smolts in 2013 upstream of Array E. Histogram panels illustrate the frequency of smolt detections as a function of time of day for four representative arrays. Dark hours are represented by gray shading in the background of each panel. Stacked bars illustrate data from 2010 (black), 2011 (dark gray), 2012 (light gray), and 2013 (white). All tag types and transport groups were pooled within year for each panel. Note that each year has a percentage of 100%, so the total cumulative percentage in each panel is 400%. Water temperature was typically 3–7°C at Array B, 7–11°C at Array C, 9–13°C at Array E, and 12–16°C in surface water at Array H.

available (Beacham et al. 2014a,b, Tucker et al. 2015), which shows the relative movement patterns of multiple stocks of sockeye after ocean entry. Our work is complementary in that it shows detailed information on rates of survival and migration speeds of individual smolts in both their freshwater and early ocean migration phases, both of which are difficult to replicate from catch data.

Our objectives were to assess migration rates through several different freshwater and marine migration segments over 4 yr, examine diurnal patterns of movement, and estimate segment-specific and overall survival levels. In 2 yr, we also experimentally tested the effects of predation on smolt migration using large-scale transfers of tagged fish (transportation) past identified mortality hot spots. Finally, we used controlled field and laboratory-based experiments involving survival, behavioral, and physiological assessments to further examine the effects of migratory locale (e.g., freshwater vs. saltwater), physiological state, and tagging on our interpretation of the field telemetry results. Effects of tagging and handling are infrequently assessed in smolt tracking studies (Drenner et al. 2012) and rarely investigated among multiple years for a single study (but see Rechisky and Welch 2010). Integrated linkages between telemetry and experimental biology, as reported here, are needed to best assess the endogenous and exogenous mechanisms responsible for patterns of wild animal survival during large scale migrations (Cooke et al. 2008).

## MATERIALS AND METHODS

### *Receiver infrastructure*

Extensive acoustic receiver infrastructure over a large spatial scale was required for this project (Fig. 1). Acoustic receivers (primarily VR2W and VR3; VEMCO, Bedford, Nova Scotia, Canada) were deployed at various check-points (termed “arrays”; Fig. 1) along the Chilko and Chilcotin Rivers, Fraser River, and coastal locales, at distances downstream of the release site. Array A (0 km; 51.62980° N, 124.13904° W) and Array B (14 km; 51.71568° N, 124.10628° W) were located in the Chilko River. Array C (80 km; 52.06659° N, 123.55384° W) was located in the Chilcotin River, <15 km from its confluence with the Chilko River. Array D (only in 2011 and 2012; 178 km; 51.82640° N, 122.56171° W) was also in the Chilcotin River, <20 km from the Fraser River confluence. Array E (599 km; 49.12326° N, 122.30035° W), Array F (627 km; 49.20155° N, 122.59584° W), and Array G (657 km; 49.16738° N, 122.93447° W) were all in the Fraser River (Fig. 1). Array G was composed of five pairs of receivers with each pair situated at similar distances from the release site to monitor the south and north arms of the Fraser River (see Welch et al. 2009). The region between Array E and Array G is considered estuarine herein. Acoustic arrays originally positioned by the Pacific Ocean Shelf Tracking (POST) project, and which have been maintained since 2012 by Canada’s

Ocean Tracking Network (OTN), were utilized to track the northward migration of the smolts in the marine environment at the Northern Strait of Georgia (NSOG; Array H; 804 km from release site), and the Queen Charlotte Strait (QCS; Array I; 1044 km from release site; Fig. 1). The Juan de Fuca Strait (JFS) Array (~860 km from release site) monitored southern movements around Vancouver Island to the open Pacific Ocean. Only three smolts were detected exiting to the Pacific Ocean via the JFS Array (all in 2011). These small sample sizes precluded us from including them in further analyses. Thus, herein we focus on the vast majority (>99%;  $n > 1850$ ) of smolts detected migrating northward along the east side of Vancouver Island (Fig. 1).

### *Smolt capture and tagging*

From 2010 to 2013 inclusive, smolts were captured between the end of April and the middle of May (Table 1). While most Chilko Lake sockeye smolts commence their migration to the ocean as 1-yr olds, up to 10% of the population can delay for a year and migrate as larger 2-yr olds. Survival to adulthood is the same in both age classes (Irvine and Akenhead 2013), so we focussed on 2-yr-old fish in the present study as 1-yr-old fish were generally too small to tag. Our goal each year was to track a minimum of approximately 200 smolts tagged with 69 kHz V7 acoustic tags and released at the point of capture. In 2 yr, additional fish (Table 1) were tagged and released as part of experimental transports detailed in *Materials and methods: Downstream transport experiments*, and we also tagged and released smaller 2-yr-old fish at the point of capture with 180 kHz V5 and V6 tags, but they could only be tracked to the mouth of the Fraser River because of the limited 180 kHz receiver infrastructure in marine waters. For all field and laboratory studies involving smolts, we followed animal use protocols (A08-0388 and A11-0215) approved by the University of British Columbia and the Canadian Council on Animal Care.

During the initial phase (first 1 km) of their downstream migration from Chilko Lake, migrating 2-yr-old smolts were collected at night (between 22:00 and 04:00) using a dip-net from a counting fence that extended across the Chilko River at the outlet from Chilko Lake that was operated by the Department of Fisheries and Oceans Canada (DFO) as a smolt enumeration site. Smolts were transported in river water to a flow-through holding tank. In preparation for surgical tag insertion, individual smolts were anaesthetized (100 mg/L MS222, 200 mg/L NaHCO<sub>3</sub>), then weighed (g) and measured (mm) for fork length (FL) before being placed supine on a surgery bench with the gills continuously irrigated with river water containing a low dose of anaesthetic (50 mg/L MS222, 100 mg/L NaHCO<sub>3</sub>). Condition factor was calculated as  $\text{weight (g)/FL (mm)}^3 \times 100000$  (Table 1). Tags were inserted into the body cavity through a 6–8 mm ventral incision (depending on tag



TABLE 1. Summary of acoustic-tagged sockeye smolts released across the four years of the study where tagging occurred with 5, 6, or 7 mm diameter tags (V5, V6, and V7, respectively).

Year	2010		2011			2012		2013	
Tag type	V7	V6	V7	V7	V7	V5	V7	V7	V7
Release group (Array)	Lake release (A)	Lake release (A)	Lake release (A)	Transport control (A)	Transport (C)	Lake release (A)	Lake release (A)	Lake release (A)	Transport (E)
Dates of release	2 May–9 May	29 April–10 May	29 April–10 May	1 May	3 May	22 April–16 May	22 April–16 May	26 April–29 April	8 May
No. smolts	199	200	254	85	104	199	386	203	229
Smolt mass (g)	17.3 ± 1.8	15.5 ± 3.2	17.9 ± 2.8	18.1 ± 4.5	17.4 ± 3.0	10.3 ± 2.4	14.0 ± 1.6	14.5 ± 1.2	14.3 ± 1.0
Smolt FL (mm)	130 ± 4	127 ± 8	133 ± 6	134 ± 9	133 ± 7	111 ± 8	123 ± 4	123 ± 3	123 ± 2
Condition factor	0.787 ± 0.002	0.743 ± 0.002	0.748 ± 0.002	0.747 ± 0.004	0.742 ± 0.004	0.753 ± 0.004	0.752 ± 0.003	0.779 ± 0.002	0.768 ± 0.002
Tag burden in air (% $M_b$ )	9.1 ± 0.9	6.8 ± 1.1	8.9 ± 1.2	9.0 ± 1.8	9.2 ± 1.5	6.5 ± 1.2	11.6 ± 1.2	9.7 ± 0.8	9.8 ± 0.6
Tag burden in water (% $M_b$ )	4.4 ± 0.4	3.4 ± 0.6	4.3 ± 0.6	4.3 ± 0.8	4.4 ± 0.7	3.2 ± 0.7	5.4 ± 0.6	5.2 ± 0.4	5.3 ± 0.3

*Notes:* Dates of release were always ~18–24 h after tagging. Values are means ± SD where relevant. Smolts in release group (A) released at tagging site. Transport (A) group released at the tagging site after ~2 h of round-trip road travel. Transport (C) group released just upstream of Array C after ~2 h of road travel. Transport (E) group released ~41 km upstream of Array E after ~10 h of road travel.  $M_b$  is body mass.

size), and the incision was closed with two interrupted monofilament sutures (Ethicon monocril 5-0 monofilament 3/8 circle reverse cutting 13 mm [P-3]; Wagner et al. 2011). Post-surgery, each smolt was given at least 10 min to recover in an aerated bucket of fresh river water before being placed into a large holding pen positioned in the Chilko River at a water depth of ~60 cm and with high-density foam providing cover on the water surface (swimming speed into the current was ~1–2 FL/s). Smolts were given 18–24 h to recover in the holding pen before a gate (30 × 30 cm) was opened during the night to allow the smolts to voluntarily leave the pen and continue their downstream migration. Negligible mortality (<1%) was observed while the fish were in captivity.

We used a range of sizes of acoustic tags across the four years of the study (V5-1H, V6-4L, or V7-2L transmitters; VEMCO, Bedford, Nova Scotia, Canada; see Table 1), but V7 tags (7 mm diameter, 22 mm long, 69 kHz) were used in all years. V5 tags (5 mm diameter, 12 mm long, 180 kHz) were implanted in 2012 into smolts ≥95 mm FL, V6 tags (6 mm diameter, 16.5 mm long, 180 kHz) were implanted in 2011 into smolts ≥115 mm FL, and V7 tags were implanted in all years into smolts ≥119 mm FL, with the exception of five smolts (109–118 mm FL) in 2012. For both field and laboratory studies, we assessed and reported tag burden in two ways: tag mass in air as a percentage of fish mass in air, and tag mass in water as a percentage of fish mass in air (e.g., Table 1). The former is a more common and traditional approach; however, it has been recommended that alternative metrics such as ours are useful to include (Brown et al. 1999, Jepsen et al. 2005). V7 tags were programmed to transmit an acoustic signal at random

intervals between 7 and 23 s for the first 14 d, and then at random intervals between 20 and 100 s thereafter (up until battery death at ~60 d). V7 tags transmitted at 69 kHz and could be detected on the receiver infrastructure in both freshwater and marine environments. V5 and V6 tags were programmed to transmit an acoustic signal at random intervals between 5 and 15 s, which was maintained until battery death for V6 tags (~24 d) and for 7 d for V5 tags. After 7 d, V5 tags transmitted at a random interval between 15 and 45 s until battery death (~40 d). The smaller V5 and V6 tags transmitted at 180 kHz and could not be detected on most of the receiver infrastructure in the marine environment. OTN upgraded some (eight of 29) receivers on the NSOG array (Array H) in 2012 with new dual frequency (69/180 kHz) VR4 receivers. Because of incomplete coverage, we did not assess survival or movement patterns based on V5 tags at this marine array, but we did use detections at Array H in 2012 to help assess 180 kHz detection efficiency at the previous Fraser River Array G. In 2011, prior to the deployment of dual frequency receivers on Array H, we used lower Fraser River Array G detections of V6 tags to estimate survival and detection efficiency at the upper Fraser River Array G receivers (separated by ~10 km).

#### *Travel time and migration rate*

Travel time (d) was calculated for each fish either from release to arrival at each array, or from arrival at one array until arrival at the next array along the migratory path. These estimates could only be made for smolts detected on both arrays bracketing the segment in question. Arrival was defined as the first detection on each

array. We then converted these travel times into travel rates (km/d), where distance was measured as the shortest in-water route between the arrays. Diel patterns in smolt migration were also investigated statistically, as outlined in Appendix S1.

#### *Smolt detection and survival estimates*

A mark-recapture approach was used to estimate survival parameters of the acoustic-tagged smolts, where a recapture event was when an individual tag ID was detected at an acoustic receiver array. Estimates of survival ( $\phi$ ), detection probability ( $P$ ), and their associated variances were calculated using the Cormack–Jolly–Seber (CJS) model (and variants thereof) implemented in Program MARK (White and Burnham 1999) and RMark (Laake 2013) within a likelihood framework.

The analysis followed a series of steps. First, we screened the detection data and formed detection histories for each tagged individual. Second, we assessed goodness of fit (GOF) of the data to the models. Third, we estimated survival and detection probabilities using CJS models. In the years when we conducted downstream transport experiments (2011 and 2013), this included using CJS model selection to investigate the effect of treatment type on  $P$  in order to determine the structure of the model that provided the best estimates of  $\phi$  for each treatment type (our base model). Fourth, we calculated overall survival from release to each downstream detection site. In 2011 and 2013 we included two additional steps: we tested whether the act of transporting fish via truck affected subsequent survival, and finally, we compared the base model from the third step to models that represented hypotheses about the effects of release site on survival. Comprehensive details of all approaches, including specific details relating to the downstream transport experiments, are provided in Appendix S1. Assessments of GOF of the data to the models are given in Appendix S2.

#### *Downstream transport experiments*

We investigated the survival consequences of releasing smolts at different locations downstream of the Chilkol Lake outlet to determine whether high rates of initial mortality after release (as reported in Welch et al. 2009, and as discovered in the first year of the present study) could be associated with tag effects or reach-specific river conditions. In 2011, we included two release groups in addition to those released from the holding pen outlined previously (Table 1). One group (85 smolts) was held in a flow-through transport tank (1000 L; 7–8°C) for ~24 h post-tagging and then driven on a ~2 h round-trip (with water aeration) before being released at the same location as the holding pen. This group acted as a transport control for a subsequent group (104 smolts) that was held under the same conditions for ~24 h post-tagging and then transported ~2 h by road and released ~200 m upstream from Array C, 80 km downstream of the

holding pen release site. The timing of events was planned so that the transport control group (released at 01:40 on 1 May) migrated through Array C at a similar time to when the transported group was released near Array C (22:00 on 3 May). The difference in the median time of arrival at Array C was only 185 min for the two groups.

In 2013, we included one long-distance transport group (229 smolts) driven ~10 h by truck to the lower Fraser River and released 41 km upstream of Array E (~558 km downstream of the holding pen release site; Fig. 1). Smolts were transported under the same conditions as in 2011 before being released over a period of <10 min (at 16:05 on 8 May) along with an additional ~250 non-tagged smolts to produce a small school. As in 2011, the timing of release was planned such that the transported smolts should have migrated through the Fraser River estuary during a similar time period as many of those previously released in the Chilkol River. No transport control group was used in 2013.

#### *Tagging-effect experiments*

We held fish in field and laboratory tanks to monitor post-surgery survival (Table 2). These experiments were conducted opportunistically in 2010–2012 and specific holding times in freshwater and saltwater were dependent on availability of smolts, laboratory infrastructure, and available personnel. Therefore, the design each year varied, making direct statistical among-year contrasts difficult. Nevertheless, the results are important in helping to understand the mechanistic basis for the acoustic tracking data.

Identical tagging procedures to those described were used to implant dummy tags (identical in size, shape, and mass to real acoustic tags) into 28 smolts in 2010, 41 smolts in 2011, and 81 smolts in 2012. Along with non-tagged control fish (2010,  $n = 58$ ; 2011,  $n = 169$ ), sham-tagged fish (i.e., incision but no tag implantation; 2012,  $n = 59$ ), and anaesthetized-only fish (2012,  $n = 59$ ; Table 2), the dummy-tagged smolts were placed into 1000 L riverside tanks with flow-through river water. Subsequent treatment of the smolts varied between years to investigate different temporal patterns of survival in freshwater and saltwater. The smolts were held in the riverside tanks for 10–16 d in 2010, 7–8 d in 2011, or 1 d in 2012, before being transported ~13 h by truck (in 7–8°C river water) to the University of British Columbia (UBC), Vancouver, Canada. Smolts were then held in freshwater in the laboratory at 8–11°C for an additional 4 d (2010), 0 d (2011), or 12 d (2012) before being exposed to a saltwater transition that occurred within a few days (13–30 ppt/d; 11–13°C) for 13 d (2010), 81 d (2011), or 54 d (2012). Because free-migrating smolts could be feeding during their outmigration, the experimental fish were offered freeze-dried brine shrimp and commercial pellet food 1–2 times per day while being held at UBC. While some tagged and non-tagged fish

TABLE 2. Summary of tag-effect studies on captive smolts (means  $\pm$  SD where relevant).

Year	2010			2011			2012		
Tag/treatment	V6	V7	Control	V6	V7	Control	V6	Sham-tagged	Anaesthesia control
No. of smolts	13	15	58	16	25	169	81	59	59
Smolt mass (g)	15.5 $\pm$ 1.7	16.1 $\pm$ 1.4	16.7 $\pm$ 4.4	12.8 $\pm$ 0.6	17.2 $\pm$ 3.1	9.9 $\pm$ 1.5	10.0 $\pm$ 2.0	9.7 $\pm$ 1.4	9.4 $\pm$ 1.6
Smolt FL (mm)	126 $\pm$ 4	128 $\pm$ 4	127 $\pm$ 10	120 $\pm$ 2	133 $\pm$ 7	NA	111 $\pm$ 7	111 $\pm$ 5	110 $\pm$ 6
Condition factor	0.775 $\pm$ 0.003	0.768 $\pm$ 0.003	0.815 $\pm$ 0.004	0.741 $\pm$ 0.002	0.731 $\pm$ 0.005	NA	0.731 $\pm$ 0.004	0.709 $\pm$ 0.002	0.706 $\pm$ 0.002
Tag burden in air (% $M_b$ )	7.5 $\pm$ 0.8	9.1 $\pm$ 0.9	0	9.2 $\pm$ 0.6	9.3 $\pm$ 1.5	0	10.4 $\pm$ 2.0	0	0
Tag burden in water (% $M_b$ )	3.6 $\pm$ 0.4	4.7 $\pm$ 0.4	0	4.4 $\pm$ 0.2	4.5 $\pm$ 0.8	0	5.2 $\pm$ 1.0	0	0
Survival to 7 d post-tagging in freshwater	13/13 (100%)	15/15 (100%)	58/58 (100%)	16/16 (100%)	25/25 (100%)	168/169 (99%)	78/81 (96%)	59/59 (100%)	57/59 (97%)
Survival after 12 d in saltwater	8/13 (62%)	9/15 (60%)	54/58 (93%)	8/16 (50%)	10/25 (40%)	110/169 (65%)	43/81 (53%)	42/59 (71%)	36/59 (61%)
Survival after 20 d in saltwater	NA	NA	53/58 (91%)	5/16 (31%)	7/25 (28%)	99/169 (59%)	25/81 (47%)	38/59 (42%)	32/59 (54%)
Survival after 34 d in saltwater	NA	NA	52/58 (90%)	2/16 (13%)	5/25 (20%)	87/169 (51%)	16/81 (20%)	34/59 (58%)	24/59 (41%)

Notes: See text for all details, including tags and treatments. The experiment was not conducted in 2013. NA, not available.

did start to feed in captivity, it was clear that many fish did not commence feeding. Cumulative survival was calculated across all years at two time intervals (7 d in freshwater and subsequently after 12 d in saltwater) as these time points were shared among all years of investigation. In 2011 and 2012 (and only for non-tagged control fish in 2010), cumulative survival was additionally calculated for 20 d and 34 d in saltwater, which are similar to smolt migration times to Array H and I, respectively, in the marine environment. These laboratory values were compared to field estimates of survival from telemetry at similar times during the migration to aid in interpreting the field data. All surviving tagged and non-tagged smolts were sacrificed by cerebral percussion at the end of the holding period following approved animal care protocols.

An experiment was conducted in May 2011 to quantify the effects of tagging on burst swimming speed and duration of burst swimming (7–8°C). We chose these metrics as they can be proxies for susceptibility to predation (i.e., whether carrying a tag puts smolts at a higher risk of predation). The same procedures as those described previously were used to implant dummy tags (identical in size, shape, and mass to real V7-2L acoustic tags) into 16 smolts (134  $\pm$  3 mm; mean  $\pm$  SD) such that tag burden ranged between 5.9% and 10.7% (tag and fish mass in air). A control group of 18 smolts (129  $\pm$  2 mm; mean  $\pm$  SD) was caught at the same time and maintained in the same holding tanks but did not undergo the tagging procedure. All smolts remained in captivity for 4 d post-capture (2–3 d post-surgery for tagged smolts) before being assessed for maximum burst speed and duration of burst swimming (details in Appendix S1).

#### *Saltwater preparedness experiment*

A final laboratory study was conducted using non-tagged smolts captured at the fish fence to understand whether smolts were physiologically prepared for saltwater as soon as they commenced their migration from Chilko Lake (i.e., ~670 km prior to entering the marine environment). An ill-prepared ionoregulatory system is thought to be a potential cause of high smolt mortality as they transition from freshwater to marine areas (reviewed in Hinch et al. 2006). Preparedness was assessed using measurements of survival and blood plasma chloride levels (Houston 1959, Hoar 1988) following experimental saltwater exposure. All details are provided in Appendix S1.

## RESULTS

### *Movement patterns*

The migration of (non-tagged) smolts into the river from Chilko Lake occurred almost exclusively at night. Release times of acoustic-tagged smolts from the holding pen were influential to the temporal pattern of migration past Array B (Fig. 1), possibly because many smolts took several hours to make their way out of the holding pen. The smolts had reestablished almost exclusive nocturnal migration once they reached the Chilcotin River (Array C; one-sample *t* test, *df* = 3, *P* < 0.001; Fig. 1). Migration rates in each of these segments were limited to ~50 km/d across all 4 yr of the study (Fig. 2). Migration speeds in all years increased about three- to fourfold once fish entered the Fraser River (i.e., after Array D), reaching migration rates as fast as 220 km/d. We largely attribute

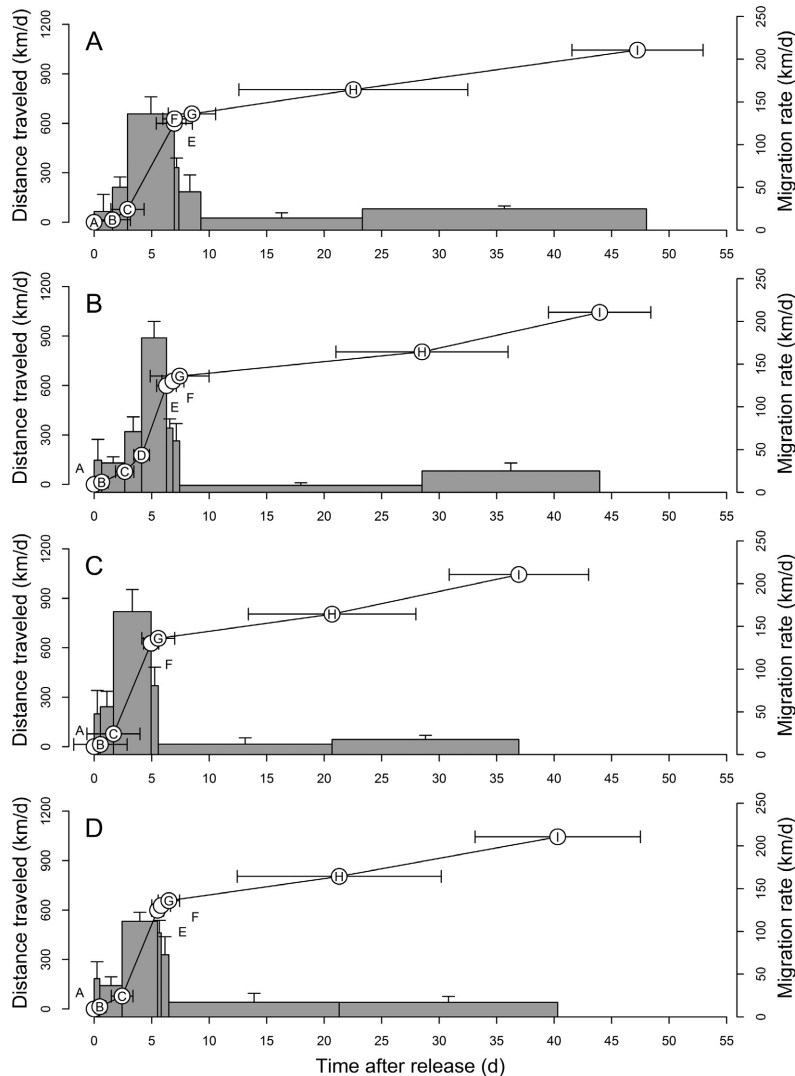


FIG. 2. Distance traveled (circles and black lines) and migration rate (gray bars) of sockeye salmon smolts across four years (2010–2013) following their release after being implanted with an acoustic tag. Values are mean  $\pm$  SD. Letters in or outside circle symbols represent receiver arrays. See Fig. 1 for specific locations of arrays. Note that migration rate for each segment could be calculated only for those smolts detected at consecutive receiver arrays.

these changes to a transition to non-stop downstream movement; smolt migration past Array E (one-sample  $t$  test,  $df = 3$ ,  $P = 0.34$ ; Fig. 1) and other lower Fraser River arrays was not dependent on time of day. Smolts typically arrived in the lower Fraser River 5–7 d following their release from the Chilko River holding pen (Fig. 2). There was no evidence that smolts delayed their migration as they moved through the freshwater/saltwater interface in the estuary (e.g., movement from Arrays F to G; Figs. 1 and 2), as migration through this segment was completed in 0.7–1.3 d at a rate of 43–83 km/d (Fig. 2). Smolts exited the Fraser River with mean travel times (SD) between  $5.1 \pm 0.4$  d (2012; the year of fastest migration) and  $8.4 \pm 0.4$  d (2010; the year of slowest migration) following their release from the holding pen in Chilko

River. Smolt migration through coastal marine waters occurred at rates of 10–25 km/d across years (Fig. 2) and was independent of time of day (Array H; one-sample  $t$  test,  $df = 3$ ,  $P = 0.76$ ; Fig. 1D). Migration rates were generally faster during the final marine segment (Array H–Array I) than during the initial segment between the river mouth and Array H (Fig. 2). Across years, smolts reached the furthest array (1044 km from release site) around 36–48 d post-release. The general patterns of movement in terms of time to migrate through freshwater, estuarine, and marine segments were very consistent across all the years (Fig. 2). Furthermore, V7-tagged fish that were transported downstream to bypass either the upper reaches (2011) or much of the freshwater migratory route (2013) migrated to subsequent arrays at speeds that



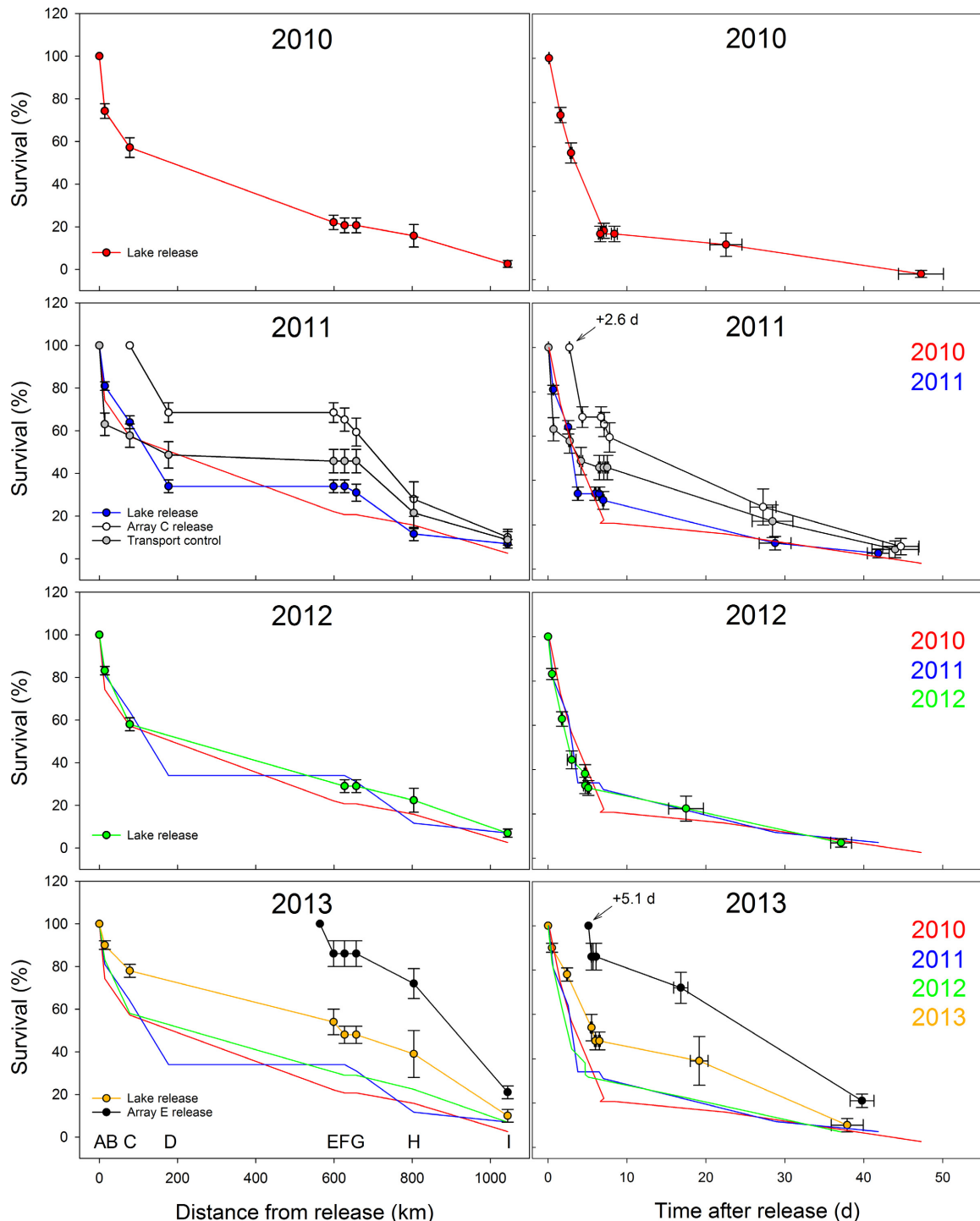


FIG. 3. Smolt survival ( $\pm$  SE) from V7-tagged fish as a function of distance travelled from release site (left-side panels) and time elapsed after release (right column) where years are represented in separate rows. SE was also assessed for time elapsed after release at each array. Array letters are provided at the bottom of the lower left panel. Colored circles and lines represent smolts released from the holding pen near Chilko Lake (red, 2010; blue, 2011; green, 2012; orange, 2013). Earlier years (lake releases only) are superimposed as colored lines on the panels of subsequent years for comparative purposes. Survival for the different release groups in 2011 (Array C release and the transport control group) and 2013 (Array E release) are presented and have been offset by 2.6 d and 5.1 d, respectively in the "Time after release" panels, to represent the mean time that lake-released smolts took to migrate from Chilko Lake to these locations. Array D was not deployed in 2010, and the lack of data at Array D (2012 and 2013) and Array E (2012) is due to equipment or detection efficiency issues. Array locations are identified on Fig. 1. Survival estimates for V5 and V6 tagged fish are in Tables 3 and 4.

were similar to those of fish released from Chilko Lake (right column, Fig. 3).

### *Survival patterns*

Over the first 14 km following direct release (i.e., not including transport control releases) from the lake (between Arrays A and B), survival ranged among tag types and years from 74% to 90% (Tables 3 and 4). During migration through the upper reaches of the study area (Array A to Array C; V7 tagged fish shown in Fig. 3) cumulative survival ranged from 57% to 78% across years (Table 3) and segment-specific survival between Array C and D was one of the lowest freshwater values in the study (e.g., 53% in 2011; Table 4). Segment-specific survival improved markedly during migration down the Fraser River mainstem (Array D–E) ranging 86–100% among years, and survival was even higher for migration through the estuary (Array E–G) with segment-specific values generally above 90% (Fig. 3; Table 4). Despite the high survival in the Fraser River mainstem and estuary, survival generally decreased again when smolts migrated through the coastal marine environment (Fig. 3). Segment-specific survival between the Fraser River mouth (Array G) and the first marine array (Array H) ranged from 38% to 83%, whereas survival between the two marine arrays (Arrays H–I) ranged between 19% and 61% (Table 4). Across years and tag types, smolts had an apparent survival of 3–10% over the 1044 km between release at Chilko Lake to the furthest marine array (Fig. 3; Table 3). Survival to the furthest array, however, may be somewhat better than estimated due to lower detection efficiency of the array or weakening acoustic power of the tags with time (see Appendix S3 for counts of detections per smolt at Arrays H and I). There were clearly some among-year differences in survival patterns, with 2013 having some of the best survival through most of the migration segments and 2010 having some of the poorest. Nonetheless, the among-year qualitative patterns of between-array survival were remarkably consistent (Fig. 3).

### *Transportation experiments*

Using model selection, we found that transportation by truck affected subsequent survival of smolts in 2011 (weight of  $AIC_c$  (Akaike's information criterion corrected for sample sizes) = 1; Appendix S4: Table A3), with survival of the transport control group being higher than the lake-released group in nearly all freshwater segments except for the first segment (Table 4). Cumulative survival to the Fraser River mouth (Array G) was 50% greater for the transport control group (Table 3). Thus, the process of physically transporting the smolts did not reduce smolt survival.

In 2011 and 2013, transported groups had similar (not higher) survival as their respective lake-released groups in common migration segments (Table 4). If the high levels of mortality observed in the lake-released smolts

between release and Array D were due to tag effects, we would have expected to see similarly high levels of mortality for the transported smolts immediately downstream after their releases near Arrays C and E. Instead, these results indicate that the high initial mortality in the lake-released smolts was caused by processes within the Chilko and Chilcotin Rivers, such as predation, and was not due to tag effects.

Transporting smolts downstream to avoid areas of high mortality had a positive effect on overall survival (Fig. 3; Table 3). In 2011, the effect of transportation on cumulative survival was substantial when measured to the Fraser River mouth (Array G), with survival nearly doubling relative to lake released fish (mean  $\pm$  SE: 59%  $\pm$  7% vs. 31%  $\pm$  4%, respectively). This advantage persisted to Array H, but some of the advantage was lost during the coastal marine migration (Array H–I) such that cumulative survival to the final Array I for transported fish was 10% ( $\pm$  4%) compared to 7% ( $\pm$  2%) for the lake-released fish. In 2013, transportation again nearly doubled survival to Array G (86%  $\pm$  6%) compared to lake-released fish (48%  $\pm$  4%), and the difference was maintained to the final Array I (21%  $\pm$  3% vs. 10%  $\pm$  3%, respectively).

We did find evidence of a tag burden effect on survival but only in 2012, as in that year the model including tag burden as a covariate had 77% of the  $AIC_c$  weight (Appendix S4). The tag burden beta parameter was negative (−8.3) and the associated confidence interval did not contain zero. Thus, fish with higher tag burdens experienced reduced survival in 2012. In that year, fish of taggable sizes were the smallest of all the years, and the tag burden effect was likely driven specifically by the V7 tagged fish, which had a mean tag burden in air of 11.6% (5.4% in water), the highest of all year and tag combinations (Table 1). Mean tag burden in air did not exceed 9.8% (5.3% in water) in any other year, and the average of all mean tag burdens in air across all years (excluding 2012) was 8.9% (4.5% in water). In 2011, the small V6 tags (similar tag burdens to the V5 tagged fish in 2012; Table 1) generated survival estimates that were generally indistinguishable from those of the V7-tagged fish at each freshwater array (Table 3). In-depth investigations of tag burden, including interactions with survival at an individual level, are the objectives of a companion study (E. L. Rechisky, *unpublished manuscript*).

### *Tagging-effect experiments*

Dummy-tagged fish and non-tagged control fish had mean ( $\pm$  SE) fatigue times (171  $\pm$  6 s vs. 164  $\pm$  7 s, respectively) and burst speeds (11.9  $\pm$  0.4 FL/s vs. 11.8  $\pm$  0.4 FL/s) that did not differ from each other ( $t$  tests,  $P = 0.405$  and  $P = 0.942$ , respectively), suggesting that at tag burdens <11% (in air) and 2–3 d after tagging, there was little effect of the surgical tag implantation and tag presence on the abilities of smolts to perform exhaustive burst swimming. Across the three

TABLE 3. Overall survival estimates (SE) of Chilko Lake sockeye smolts 2010–2013.

Year	Treatment type	Tag type	Array B (14 km)	Array C (80 km)	Array D (178 km)	Array E (599 km)	Array F (627 km)	Array G (657 km)	Array H (804 km)	Array I† (1044 km)
2010	Lake released	V7	0.74 (0.03)	0.57 (0.04)	‡	0.22 (0.03)	0.21 (0.03)	0.21 (0.03)	0.16 (0.05)	0.03 (0.01)
2011	Lake released	V7	0.81 (0.02)	0.64 (0.03)	0.34 (0.03)	0.34 (0.03)	0.34 (0.03)	0.31 (0.04)	0.12 (0.03)	0.07 (0.02)
2011	Transport Array C	V7	NA	NA	0.69 (0.05)	0.69 (0.05)	0.65 (0.05)	0.59 (0.07)	0.28 (0.08)	0.10 (0.04)
2011	Transport lake released	V7	0.63 (0.05)	0.58 (0.05)	0.49 (0.06)	0.46 (0.06)	0.46 (0.06)	0.46 (0.06)	0.22 (0.07)	0.09 (0.04)
2011	Lake released	V6	0.74 (0.04)	0.62 (0.04)	0.38 (0.04)	0.37 (0.05)	0.37 (0.05)	0.32 (0.05)§	¶	¶
2012	Lake released	V7	0.83 (0.02)	0.58 (0.03)	#	#	0.29 (0.03)	0.29 (0.03)	0.22 (0.06)	0.07 (0.02)
2012	Lake released	V5	0.83 (0.03)	0.68 (0.03)	0.44 (0.04)	0.38 (0.04)	0.36 (0.04)	0.34 (0.03)	¶	¶
2013	Lake released	V7	0.90 (0.02)	0.78 (0.03)	#	0.54 (0.06)	0.48 (0.04)	0.48 (0.04)	0.39 (0.11)	0.10 (0.03)
2013	Transport Array E	V7	NA	NA	NA	0.86 (0.06)//	0.86 (0.06)	0.86 (0.06)	0.72 (0.07)	0.21 (0.03)

*Notes:* Distances indicate the cumulative distance from the Chilko Lake release site. NA, not applicable. See Fig. 1 for array locations. Survival was not estimated to Array A because it was located at the release site.

†We assumed a detection probability of 0.67 to estimate survival to the final array, yet survival to this array may be underestimated due to points raised in Appendix S3.

‡Array D was not deployed in 2010.

§For V6 transmitters, we split the array into two components: upper Fraser River mouth and lower Fraser River mouth; we then used the lower mouth receivers to estimate survival to the upper mouth.

¶V5 and V6 transmitters could only be detected on freshwater arrays.

#Too few tagged fish were detected to estimate survival to these arrays.

//These transported fish were released only 41 km upstream of Array E.

TABLE 4. Segment-specific (migration distances within segments) survival estimates (SE) for Chilko Lake sockeye smolts 2010–2013.

Year	Treatment type	Tag type	Migration segment (distance of segment)									
			Array A–B (14 km)	Array B–C (66 km)	Array C–D (98 km)	Array C–E (520 km)	Array D–E (421 km)	Array C–F (547 km)	Array E–F (28 km)	Array F–G (30 km)	Array G–H (147 km)	Array H–I (240 km)
2010	Lake release	V7	0.74 (0.03)	0.77 (0.05)	‡	0.39 (0.05)	‡	...	0.94 (0.08)	1 (0)	0.77 (0.23)	0.19 (0.10)
2011	Lake release	V6	0.74 (0.04)	0.83 (0.04)	0.62 (0.06)	...	0.97 (0.06)	...	1 (0)	0.88 (0.1)	†	†
2011	Lake release	V7	0.81 (0.02)	0.79 (0.03)	0.53 (0.05)	...	1 (0)	...	1 (0)	0.90 (0.11)	0.38 (0.1)	0.61 (0.18)
2011	Transport lake release	V7	0.63 (0.05)	0.91 (0.04)	0.84 (0.07)	...	0.94 (0.07)	...	1 (0)	1 (0)	0.47 (0.15)	0.41 (0.19)
2011	Transport Array C	V7	...	...	0.69 (0.05)	...	1 (0)	...	0.95 (0.05)	0.91 (0.09)	0.47 (0.14)	0.36 (0.15)
2012	Lake release	V5	0.83 (0.03)	0.82 (0.03)	0.65 (0.05)	...	0.86 (0.07)	...	0.96 (0.08)	0.94 (0.06)	†	†
2012	Lake release	V7	0.83 (0.02)	0.69 (0.03)	§	¶	¶	0.51 (0.05)	¶	1 (0)	0.77 (0.18)	0.31 (0.10)
2013	Lake release	V7	0.90 (0.02)	0.87 (0.03)	§	0.7 (0.07)	§	...	0.89 (0.1)	1 (0)	0.82 (0.23)	0.24 (0.09)
2013	Transport Array E	V7	...	...	...	...	0.86 (0.06)#	...	1 (0)	1 (0)	0.83 (0.1)	0.29 (0.05)

*Notes:* See Fig. 1 for array locations. Note that survival was only estimated for segments if array use, array performance, and tag type permitted. Survival was not estimated to Array A because it was located at the release site.

†V5 and V6 transmitters could only be detected in the freshwater migration segments.

‡Array D was not deployed in 2010.

§Too few tagged fish were detected at Array D to estimate survival.

¶Too few tagged fish were detected at Array E to estimate survival.

#These transported fish were released only 41 km upstream of Array E.

years in which we conducted holding studies to assess survival of tagged fish within freshwater (involving holding smolts in tanks streamside, during transport to a laboratory, and after transport at the laboratory), we found 96–100% survival after 7 d in controls and tagged fish in every instance (Table 2). This time period is significant as lake-released smolts in each year would have reached or even exited the Fraser River estuary by then. Once smolts were placed into saltwater, mortality started to occur in all of the treatments. Specifically, by day 12 across all years survival of dummy-tagged fish ranged from 40 to 62%; although not as pronounced, survival was also reduced in control fish (61–93%; Table 2). After 20 d in saltwater, survival was further reduced in the dummy-tagged groups (47% survival in 2012; 28–31% in 2011) and control groups (54% survival in 2012; 59% in 2011; 91% in 2010). This trend continued after 34 d in saltwater for both the control (41% survival in 2012; 51% in 2011; 90% in 2010) and dummy-tagged (20% survival in 2012; 13–20% in 2011) groups (Table 2).

#### *Saltwater preparedness experiments*

Saltwater preparedness was examined in a separate group of non-tagged congeners at Chilko Lake in 2011 that were ~660 km and ~5–8 d away from exiting the Fraser River estuary into the marine environment. Plasma chloride was used to assess osmoregulatory capacity at this early point in their migration. In a subset of smolts sampled immediately after capture from the Chilko River, mean ( $\pm$  SE) plasma chloride concentration was  $153 \pm 5$  mmol/L. For fish sampled after 24 h in either freshwater or saltwater, plasma chloride did not differ ( $143 \pm 6$  vs.  $156 \pm 2$  mmol/L, respectively;  $P = 0.058$ ). After 72 h, plasma chloride in freshwater fish tended to be lower than in saltwater fish ( $148 \pm 3$  vs.  $168 \pm 7$  mmol/L, respectively;  $P = 0.026$ ). However, plasma chloride levels in these two treatment groups at each time period were not statistically different from those of smolts sampled directly from Chilko River ( $P > 0.125$  in all cases). Importantly, survival was 100% in both the freshwater group (starting  $n = 24$ ) and the saltwater group (starting  $n = 30$ ) across the entire 4-d experimental period.

#### DISCUSSION

This acoustic-tagging study involves the largest spatial and temporal scale to date for assessing the survival and behavior of migrating wild sockeye salmon smolts and is one of the most extensive for any Pacific salmonid. We provide detailed quantitative information on survival and behavior over a >1000 km migration with replication over four consecutive years (i.e., the four yearly cohorts of this population). The survival and movement patterns were generally consistent across years even though different tag sizes and fish sizes were often involved. Survival from Chilko Lake to the final marine acoustic array was low and ranged ~3–10% during a migration period of 36–48 d.

There have been other acoustic-tagging studies assessing survival in freshwater and seawater for Pacific salmonid smolts, although most of them covered much shorter spatial scales and often primarily involved hatchery fish (except see Welch et al. 2011). In an acoustic-tagging study involving a hatchery population of Fraser River sockeye smolts, Welch et al. (2009) found that survival to the same final marine acoustic array as in the present study was somewhat higher (10–30%) than we report; however, their freshwater migration was relatively short (~100 km). In that study, the segment-specific survival of Cultus Lake smolts from Array G to Array H (range 55–92%) and from Array H to Array I (range 27–60%) was very similar to our Chilko Lake smolts despite the Cultus smolts being of larger size and of hatchery origin. In an acoustic-tagging study involving wild steelhead trout in the Napa River/Point Reyes system (located north of San Francisco Bay, California, USA), smolts exhibited higher overall survival (at least 30% higher than Chilko sockeye) from freshwater natal areas to final marine acoustic arrays, but the freshwater and marine distances travelled were much shorter than the present study (~34 km migration in freshwater and ~100 km migration in seawater; Sandstrom et al. (2013)). Similarly, relatively higher overall survival was found for acoustic-tagged hatchery steelhead trout and Chinook salmon in the Sacramento River/San Francisco Bay system (13.8–14.6% and 19.2–23.6%, respectively) over relatively short travel distances (156 km in freshwater, 51 km in seawater; Singer et al. 2013), yet monitoring over greater distances revealed much poorer overall survival in Chinook salmon (Michel et al. 2015). Rechisky et al. (2013) tracked Snake River spring Chinook smolts ~850 km to the Columbia River estuary and ~2500 km in total to southeast Alaska. Combined freshwater and river plume survival ranged 12–32% and coastal ocean survival averaged 10% to northwestern Vancouver Island, Canada, representing similar distances and survival rates as the Chilko smolts. Steelhead trout smolts acoustically tracked in the Green River/Puget Sound system, whose marine system shares the same local body of water as in our study (i.e., Puget Sound and Strait of Georgia are part of the Salish Sea), had overall survival levels similar to those in our study (9.7% and 3.6%, wild and hatchery fish, respectively), though survival was again only assessed over a relatively small spatial-scale (~39 km freshwater, ~170 km seawater; Goetz et al. 2015). Welch et al. (2011) annually (2004–2006) tracked wild steelhead from the Thompson River drainage in British Columbia to the Fraser River mouth, and then to the same marine Array I as in our study. Although their study animals were much larger than ours, they found overall survival to vary among years to a similar extent as for Chilko smolts (20–50% through freshwater, 15–40% through marine areas). In trying to make sense of diverse results among studies, and to put our broad spatial-scale results into context, focused attention needs to be placed on the relative differences that occur within specific freshwater and early coastal segments of the migration of Chilko Lake sockeye smolts.



### Freshwater migration

The present study revealed that a large component of the total loss of smolts that we documented occurred in freshwater. We are confident that the disappearance of smolts in freshwater was caused by mortality, and not technological issues, because the detection efficiencies of most of the receiver arrays in this area were high and there was no evidence of tag expulsion in any of our holding studies. Nearly all of the freshwater mortality (total freshwater migration exceeding 600 km distance) occurred in the Chilko and Chilcotin Rivers (~180 km), and among-year mortality levels were 22–43% in just the first 80 km. A recent study (Jeffries et al. 2014) suggests that a component of the large levels of mortality occurring in the clear and shallow waters downstream of our release site could be caused by physiological and/or immunological impairments. It is possible that an impaired physiological state could make smolts more prone to predation; however, we are not able to disentangle this possible linkage with our current data.

By transporting smolts in 2011 past the uppermost study reaches, we increased survival considerably (~20%) to the confluence of the Chilcotin and Fraser Rivers (i.e., to Array D), and this survival advantage persisted to the estuary. Smolts transported to the lower reaches of the Fraser River in 2013 incurred only nominal mortality to and through the estuary after release. Both transport experiments support the notion that the upper reaches of our study area were associated with a phenomenon causing high mortality that was not related to tag effects. Although levels of freshwater mortality varied among years, there was no clear among-year pattern to suggest that the duration of time spent in freshwater was associated with particularly high or low mortality levels (Fig. 3). Our results support evidence from others of relatively high freshwater mortality in tagged outmigrating smolts in the upper reaches of rearing rivers (Welch et al. 2011, Chase et al. 2013, Singer et al. 2013). One of the likely causes for such high levels of mortality in these upper reaches is predation by piscivorous fishes, birds, and mammals, which is thought to be a significant component of smolt mortality (Ruggerone and Rogers 1984, Heggenes and Borgström 1988, Mesa 1994, Collis et al. 2001, Evans et al. 2012, Hostetter et al. 2012, Cavallo et al. 2013). It was visually evident throughout the four years of the present study that a wide range of predators gathered near the Chilko Lake outlet (e.g., bull trout, *Salvelinus confluentus*; rainbow trout, *Oncorhynchus nerka*; mergansers, *Mergus* spp.; gulls, *Larus* and *Chroicocephalus* spp.; and river otters, *Lontra canadensis*) to target the large schools of smolts as they commenced their downstream migration in the shallow upper Chilko River. In fact, bull trout sampled in 2013 at the Chilko Lake outlet during smolt outmigration were found to feed nearly exclusively on sockeye smolts with individual fish

stomachs containing up to 69 smolts and regularly exceeding 20 smolts (Furey et al. 2015). Supporting the idea that this area had high levels of predation risk was the fact that sockeye smolts showed a clear preference for nocturnal movement in the earliest phase of their migration in the Chilko and Chilcotin Rivers, which are relatively clear and shallow. A preference for nocturnal migration has been documented in other juvenile salmon during downstream migration in clear waters (Ibbotson et al. 2011, Chapman et al. 2013, Chase et al. 2013, Michel et al. 2013) and is suggested in those studies to be indicative of a behavioral adaptation to minimize predation risk from visual predators.

The nocturnal migratory behavior in the upper study reaches of the Chilko River resulted in the slowest migration rates throughout the entire freshwater component (~30–50 km/d among years). Such a slow migration rate has been observed before for sockeye in clear water streams; smolts out-migrating in the Stamp and Somass Rivers on Vancouver Island only migrated at night, and total speed to complete their 25-km migration to the ocean was estimated from trapping to be about 60 km/d (Wood et al. 1993). Migration rates for Chilko smolts increased (80–100 km/d) as they progressed into the Chilcotin River. The Chilcotin is faster-flowing than the Chilko River, so fish could be passively carried downstream at higher rates during their nocturnal migration. Once in the Fraser River mainstem, the migration of Chilko sockeye smolts was continuous through day and night periods, and also extremely fast (e.g., 220 km/d in 2012 through the ~422-km migration segment between Arrays D and E). This has been observed in other large and turbid river systems; marked sockeye smolts that were released from hatcheries in the upper Columbia River accelerated their migration rates once they entered the Columbia River mainstem and showed no nocturnal migratory preference once in the mainstem (Anas and Gauley 1956). Although we did not measure water velocities during our study, surface water velocities assessed in the 1990s in July in the center of the river at several sites upstream of Array E recorded values ranging from 1 to 3 m/s (Hinch and Rand 1998). Discharge during the months of May (when our smolts were primarily migrating in the mainstem) and July are very similar to each other (peak flows occurring in June; *data available online*),<sup>12</sup> and the speed of the smolt migration in the present study (86–259 km/d) is consistent with the fish being passively carried downstream just under the surface of the water in the main current (see Crittenden 1994, Melnychuk et al. 2010, Mahoney et al. 2013). As a result, smolts typically arrived in the lower Fraser River in 5–7 d after release, which is consistent with travel times of non-tagged Chilko smolts caught in traps at Mission, British Columbia (near our Array E).

Our study included a series of laboratory and tank experiments aimed at understanding whether freshwater

<sup>12</sup> <http://bcrcf.env.gov.bc.ca>

survival was directly or indirectly compromised by the tagging procedures employed (e.g., see Adams et al. 1998), an approach rarely undertaken within large-scale telemetry projects (Cooke et al. 2011b). Nearly all smolts implanted with dummy tags survived 7 d in freshwater across years ( $\geq 96\%$  survival; Table 2). Acoustic-tagged smolts generally migrated from the release site to the estuary in less than a week; therefore, it is unlikely that direct tagging effects contributed substantially to freshwater mortality. Additionally, there was no evidence at 2–3 d post-surgery that tagging affected burst swimming speed or duration, suggesting that tagged fish should have been equally able to use this important behavior to avoid predation. This is consistent with experiments that showed similar predation rates by largemouth bass (*Micropterus salmoides*) on tagged and non-tagged juvenile Chinook salmon (*Oncorhynchus tshawytscha*; Anglea et al. 2004, Thompson et al. 2014).

Tag burden is also an important consideration when interpreting the mortality patterns. Although we tagged relatively large 2-yr-old smolts, the size of the smolts at migration relative to the tags available for use in this study meant that a proportion of the tagged fish, particularly those implanted with V7 tags, had tag burdens which exceeded some recommended limits from the literature. Brown et al. (2006) found that wild sockeye smolts with tag burdens less than 10.3% (in air) had critical swimming speeds largely unaffected by the presence of tags (they had  $\sim 5\%$  slower swimming speeds compared with non-tagged controls following a  $\geq 48$  h period after tag implantation). Collins et al. (2013) examined the effects of tag burden on prolonged burst swimming duration with hatchery-reared sockeye salmon in freshwater and found that median swim durations ( $\sim 90$  s) did not differ from control fish up to  $\sim 10\%$  tag burden (in air), although at  $\geq 8\%$  tag burden (in air), fish were not able to attain the maximum durations that were part of the experimental design (1200 s). In every year of our tracking study (except 2012 with V7 tags), acoustic-tagged smolts had mean tag burdens  $\leq 9.8\%$  (in air; 5.3% in water) and the average of all mean tag burdens in air across all years (excluding 2012) was 8.9% (4.5% in water; Table 1). Burdens for the V5 and V6 tagged fish were lower at  $< 7\%$  (in air;  $< 4\%$  in water). Our swim performance and survival-holding studies, however, showed no short-term tagging effects, and the survival patterns identified using smaller tags (i.e., V5 and V6 tags) were very similar to what we found with the larger V7 tags. For example, survival to the Fraser River mouth was nearly identical for V6 and V7 tagged smolts in 2011. Only in 2012 could our models detect an effect of tag burden with V7 tags (E. L. Rechisky, *unpublished manuscript*), a year we also released smolts with V5 tags (with almost half the tag burden of V7 tags), allowing a direct contrast in migration segment survival attributable to tag burden (Table 3). We contend that the general mortality patterns we have identified for the freshwater portion of the migration are not largely

attributable to tagging or tag burden effects, and we suggest that tag burden from the larger V7 tags had perhaps a 5–10% effect on overall freshwater survival of the relatively small smolts in 2012.

#### *Estuarine and early marine migration*

Despite the lack of diel patterns, migration rates slowed by 50% or more as smolts entered the estuary, likely owing to the fact that tidal influences could reduce passive transport relative to the Fraser River mainstem. Additionally, fish could be actively attempting to feed, which would require deviating from the main current of the Fraser River. Somass River sockeye smolts slowed their migration dramatically from 60 km/d to  $\sim 2$ –7 km/d as they entered the tidally influenced Barclay Sound on the west coast of Vancouver Island (Wood et al. 1993); the authors noted that this put the smolts at high vulnerability to predacious Pacific hake (*Merluccius productus*), spiny dogfish (*Squalus acanthias*), and walleye pollock (*Theragra chalcogramma*).

Mortality was relatively low ( $< 10\%$ ) as smolts transited through the estuary (Arrays E–G). Once smolts entered the marine environment in the Strait of Georgia, mortality to the first array (a distance of 147 km) increased, with higher levels in 2011 (segment-specific mortality, 53–62%) than in the other three years (segment-specific mortality, 17–23%). Generally, these levels were lower than those in the early phases of the freshwater migration (i.e., release through the first 80–178 km).

Migration to the final marine array (an additional 240 km from the previous array) was associated with high mortality that varied by a factor of two among years (segment-specific mortality, 39–81%). As with transit through freshwater, there was no obvious among-year pattern in the marine environment to suggest that migration duration influenced mortality levels (Fig. 3). It should be noted that our final estimates of survival to the final array (Array I) may be underestimated due to our limitations in understanding the detection efficiency at this location. If the detection efficiency of Array I is poorer than Array H (see Appendix S3), then our survival estimates may be underestimated.

Why smolts perish in their coastal migratory phase, in some years at high levels, could again be attributable to varying intensities of predation. Although we have no direct observations of predation intensity as we did in the upper reaches of the freshwater environment, it is well known that potential predators of juvenile salmon are abundant in the Strait of Georgia and could have large impacts on salmon smolt survival (Cohen 2012). Also of potential importance is that the dominant food for sockeye smolts in the Strait of Georgia (copepod zooplankton) have been experiencing steady declines in the recent decade accompanied by changing composition of the phytoplankton spring bloom; it is possible that Fraser sockeye smolts in recent years have not been able to gain weight during their early coastal migration,

putting them at higher risk of predation and starvation (reviewed in Beamish and Mahnken 2001, McKinnell et al. 2011, Cohen 2012). It has also been suggested that *Heterosigma akashiwo*, a red tide organism, may also impact smolt survival in some years (Rensel et al. 2010). How predation, harmful algal blooms, pathogens, and food availability vary among years in the coastal environment where Fraser River sockeye migrate, and how these factors contribute to determining the survival patterns we observed, should be the focus of future research.

As Chilko smolts passed northward through the Strait of Georgia, their migration rates were the slowest of all migratory segments in this study (10–20 km/d; 1–2 BL/s for a 12 cm smolt); these migration rates were very similar to those observed for hatchery-reared and larger-bodied Cultus Lake sockeye acoustically tracked through this same area from 2004 to 2007 (Welch et al. 2009, 2011), and residence time was similar to that estimated by Preikshot et al. (2012) when scaled for body size. Chilko smolt migration rates increased in most years (up to 30 km/d; also observed for tagged Cultus Lake smolts [Welch et al. 2009, 2011]) as they passed through the final study segment (Discovery Passage; Array H–I), where a narrowing of the coastlines leads to surface tidal currents which can exceed 43 km/d (~50 cm/s) in the direction that smolts are migrating (Foreman et al. 2012). In addition to the fact that smolts must actively swim through this area (McKinnell et al. 2011), it is possible that smolts may modify their behavior to take advantage of the variation in tides to increase their net migration speed. Finally, smolts may have grown larger by the time they entered the final migration segment and thus may be able to swim at higher absolute speeds.

It is a common belief that the transition to saltwater is physiologically stressful and hence a period of high mortality among smolting salmonids (Boeuf 1994, reviewed in Hinch et al. 2006). However, we demonstrated that non-tagged smolts had 100% survival when exposed to 35 ppt saltwater for 96 h immediately upon departing Chilko Lake, and their plasma chloride levels after 72 h in saltwater did not differ from levels measured in smolts caught directly from Chilko River. Despite this, within the first 12 d of saltwater exposure in laboratory holding studies, we observed some level of mortality in all of our treatments (Table 2). The mortality of dummy-tagged fish was consistently higher than controls, a trend that continued throughout 34 d in saltwater (Table 2). Mortality levels for tagged migrating smolts after they entered the marine environment assessed between Arrays G and H (18–28 d after tagging) were highest in 2011 (segment-specific mortality, 53–62% for the three V7 tagged groups). In all other years, mortality between Arrays G and H was stable at 17–23%; subsequent mortality to Array I, however, was lower in 2011 than in 2012. Collins et al. (2013) compared the survival of dummy-tagged and control hatchery-reared Cultus Lake sockeye smolts in the laboratory over 9 d in seawater after transitioning them as we did from freshwater;

in that study, the control and dummy-tagged groups did not differ in their response to saltwater (~3% mortality in both). These hatchery fish were bigger and with a higher condition factor (including thicker ventral tissue) than our wild smolts, which could account for the better immediate survival compared with our study. Therefore, we cannot rule out a potential interaction between seawater experience and tag presence in our laboratory studies with wild fish. Notably, we transitioned smolts from freshwater to 30 ppt saltwater, which may have been to a level much higher than they would typically experience during the first portions of their coastal migration (~15 ppt in May–July in the southern Strait of Georgia near the Fraser River; Thomson 1981). Additionally, we observed that many fish failed to feed in captivity during the holding experiments. Given these factors, and the large among-year differences we noted in both our laboratory experiments and in the field results, it is difficult to directly apply the experimental results and fully understand the potential role that tagging may play on marine patterns of mortality in Chilko smolts. If the mortality patterns of our tank-held, dummy-tagged animals are representative of the free-migrating population, marine survival will be higher than our estimates indicate. Much more work is required in this area to elucidate the drivers of among-year variability in survival and the interactions between tagging and saltwater survival.

#### *Management implications*

The Chilko Lake population of sockeye is one of the largest in the Fraser River watershed and is an important indicator for the >150 populations of sockeye salmon present in the watershed. It is unique in that the abundance of out-migrating smolts has been assessed continuously by the Department of Fisheries and Oceans Canada (DFO) using a weir and fence system since 1960; typically 10–30 million smolts emigrate annually (Irvine and Akenhead 2013). Among-year variability in smolt numbers and size has been used to help understand linkages between adult spawner abundance, lake productivity, and climate (Henderson and Cass 1991, Bradford et al. 2000, Irvine and Akenhead 2013). Forecasting the number of sockeye adults that will return to spawn in any given year is an important task for fisheries managers, as this information is used to allocate potential harvest between Canada and the USA (under the Pacific Salmon Treaty), and between Canadian fishers (e.g., First Nations, different commercial gear sectors, recreational fishers). For most Fraser River populations, forecasting is done using relationships between historical spawning stock sizes and recruitment, which are coarse measures that integrate mortality among numerous life stages. Thus, run-size forecast models contain large levels of uncertainty (Cohen 2012). Chilko sockeye smolt-to-adult survival data have been used to reduce some of the uncertainties in these models as they largely eliminate

the freshwater life history component (Cohen 2012). However, our results illustrate that even within the short-duration smolt stage, survival can vary from year to year, in both freshwater and marine environments; overall migration survival of lake-released smolts varied ~threefold among years to both the Northern Strait of Georgia (12–39%) and to the final marine array in Queen Charlotte Strait (3–10%). Smolt survival rates may be a useful tool that managers could utilize in their models to further reduce uncertainties in run size forecasts, thus requiring the integration of smolt-tagging studies as part of routine monitoring and fisheries stock assessments. Indeed, smolt-to-adult survival of Chilko Lake sockeye salmon in recent years has been generally <5% (dropping from 8–10% during 1960–1998; Irvine and Akenhead 2013), and the present study indicates that the early stages of smolt migration are influential to these patterns. Certainly, a better understanding of the among-year factors that contribute to variability in survival of migrating smolts (e.g., predator levels, temperatures, currents, food availability) could highlight drivers of smolt survival to further improve models for forecasting.

We found high levels of mortality very early in the freshwater migration that were likely attributable to predation. Although a variety of other predators were observed in the Chilko River system, we suspect that bull trout play an important role (see Furey et al. 2015) given the large sizes of individual fish and high densities that we observed, the ease at which aboriginal fishers could catch them, the pristine nature of Chilko Lake, and the fact that recreational fishing pressure would be relatively light due to the distance from major population centers (Post et al. 2002). One interpretation of our results could be that increased fishing pressure on bull trout might benefit survival of sockeye smolts, but we would caution against such a conclusion. If predator populations and their influence on smolts have remained stable over time, then it is unlikely that predation in these landscapes has driven recent declines in sockeye populations. Furthermore, bull trout are a species of special concern in British Columbia (BC Conservation Data Centre 2014), they support First Nation subsistence and recreational fisheries, and they are highly susceptible to overfishing due to their slow growth and late age of reproductive maturity (Dunham et al. 2008). Management becomes difficult and complex when both prey and predator species are of economic and conservation interest (Marshall et al. 2015), and thus, further information on this relationship between bull trout and smolts should be obtained prior to any suggestion of bull trout population control.

Although the smolts in this study were released downstream of the fish fence, we observed large numbers of bull trout attracted to the schools of (non-tagged) smolts as they channeled through the counting gates (*unpublished data*). This may facilitate predation, although we have no information on what predation rates might be like in the absence of the fish fence. Certainly, the

transportation of smolts downstream, away from the fish fence and the clear water of the upper study area, benefited survival. Transportation to the lower Fraser River just upstream of the estuary (~558 km away from release) enhanced survival to the final marine array (survival was twice as high as lake-released fish) but whether this survival advantage would have persisted beyond the final array is unknown. Mass downstream transportation of smolts is a commonly used management tactic to increase smolt survival to the ocean in large river systems where smolts are moved around dams and high levels of predators (e.g., Williams et al. 2005). These programs usually involve loading thousands of fish onto barges and transporting them through hundreds of kilometers of reservoir. The use of barges in the upper Fraser River is not possible as the river flows freely with no dams (or reservoirs) on the mainstem and therefore smolts would have to be moved by truck, an infeasible method for large numbers of fish given the road conditions in the upper Chilko area. There are also several potential disadvantages for mass transportation as being a viable conservation strategy, including increased disease transmission among individuals during transport (Van Gaest et al. 2011) and impaired homing ability in transported fish when they return as adults (Keefer et al. 2008). Indeed, reduced adult return rates have been reported when hatchery and wild Chinook salmon smolts were transported down sections of the Columbia River (Williams et al. 2005); however, this difference does not appear to develop in the early marine phase (Rechisky et al. 2012) and may be related to timing of transportation (Muir et al. 2006).

## CONCLUSIONS

We investigated the survival and movement of wild Chilko Lake sockeye smolts during their >1000 km migration from freshwater rearing grounds to coastal Pacific Ocean environments. Spatial and qualitative patterns of mortality and migration rates were very consistent across years. Mortality was high in the upper-river reaches, which appears to be largely linked with predation despite behavioral adaptations of the smolts to avoid visual predators by migrating at night. Migration rates increased by up to threefold as smolts passed through the more turbid Fraser River, then slowed as smolts entered the estuary; mortality abated significantly through both areas. In all years, mortality levels again rose while migration rates slowed to their lowest levels as smolts entered the marine environment. Mortality levels through the final (and longest, 240 km) marine migration segment had the greatest among-year range (39–81%) out of all the migration segments we examined. The causes of such large among-year differences in marine survival are currently unclear but highlight the potential importance of early ocean conditions in determining the abundance of returning adult sockeye and the importance of telemetry information in population



forecasting. The smolt transport studies helped test hypotheses about mortality in freshwater environments, generated insights into mortality mechanisms, and confirmed that the majority of the post-release mortality is unlikely to be related to our tagging approaches. The tagging-effect studies provided extensive datasets to help understand the drivers of mortality-related behavioral patterns and the potential roles of handling and tagging, and they emphasize the importance of conducting appropriate controlled experiments to complement field tagging studies. Given the relatively larger interannual variability in marine survival and the paucity of information on direct mechanisms of marine mortality, we suggest that focused studies are now needed to assess how freshwater and marine predator levels, food availability, and abiotic features, such as temperatures and currents, are influencing year-to-year patterns of movement and survival. With better information of this kind, we can start to quantify critical environments in both freshwater and marine areas, and improve predictions of adult spawner returns.

#### ACKNOWLEDGEMENTS

We thank the Pacific Salmon Foundation (PSF, Brian Riddell) and anonymous donors to the PSF for purchase of some acoustic tags and for logistic support. DFO Canada provided additional tags and its Environmental Watch Program provided logistic support. Funding and infrastructure was also provided through the Canada Ocean Tracking Network, which was supported through the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Canada Foundation for Innovation. We are grateful to Fred Whoriskey and Sara Iverson at Dalhousie University for facilitating this research. NSERC Discovery grants to S. G. Hinch also supported this work. A. P. Farrell was supported by a Canada Research Chair. The Alfred P. Sloan and The Gordon & Betty Moore Foundation provided financial support for some of the marine components of the POST system. N. B. Furey was supported by a NSERC Vanier Graduate Scholarship. Marley Bassett and Collin Middleton provided valuable field assistance. We thank the Xeni Gwet'in First Nation for access to study sites. Dennis Klassen and DFO Chilko River Camp staff are thanked for providing accommodation and logistic support. Jennifer MacDonald and Mark Sekela from Environment Canada are thanked for providing environmental data from the Fraser River estuary as well as helping to deploy additional acoustic receivers in the estuary.

#### LITERATURE CITED

- Adams, N. S., D. W. Rondorf, S. D. Evans, J. E. Kelly, and R. W. Perry. 1998. Effects of surgically and gastrically implanted radio transmitters on swimming performance and predator avoidance of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 55:781–787.
- Anas, W. E., and J. R. Gauley. 1956. Blueback salmon, *Oncorhynchus nerka*, age and length at seaward migration past Bonneville Dam. U.S. Fish and Wildlife Service Special Scientific Report: Fisheries 185:46.
- Anglea, S. M., D. R. Geist, R. S. Brown, K. A. Deters, and R. D. McDonald. 2004. Effects of acoustic transmitters on swimming performance and predator avoidance of juvenile Chinook salmon. *North American Journal of Fisheries Management* 24:162–170.
- BC Conservation Data Centre. 2014. BC species and ecosystems explorer. BC Ministry of the Environment, Victoria, British Columbia, Canada.
- Beacham, T. D., R. J. Beamish, J. R. Candy, C. Wallace, S. Tucker, J. H. Moss, and M. Trudel. 2014a. Stock-specific migration pathways of juvenile sockeye salmon in British Columbia Waters and in the Gulf of Alaska. *Transactions of the American Fisheries Society* 143:1386–1403.
- Beacham, T. D., R. J. Beamish, J. R. Candy, C. Wallace, S. Tucker, J. H. Moss, and M. Trudel. 2014b. Stock-specific size of juvenile sockeye salmon in British Columbia waters and the Gulf of Alaska. *Transactions of the American Fisheries Society* 143:876–889.
- Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography* 49:423–437.
- Boeuf, G. 1994. Salmonid smolting: a pre-adaptation to oceanic environment. Pages 105–135 in G. C. Rankin and G. B. Jensen, editors. *Fish ecophysiology*. Chapman and Hall, London, UK.
- Bradford, M. J., B. J. Pyper, and J. S. Shortreed. 2000. Biological responses of sockeye salmon to the fertilization of Chilko Lake, a large lake in the interior of British Columbia. *North American Journal of Fisheries Management* 20:661–671.
- Brown, R. S., S. J. Cooke, W. G. Anderson, and R. S. McKinley. 1999. Evidence to challenge the “2% rule” for biotelemetry. *North American Journal of Fisheries Management* 19: 867–871.
- Brown, R. S., D. R. Geist, K. A. Deters, and A. Grassell. 2006. Effects of surgically implanted acoustic transmitters >2% of body mass on the swimming performance, survival and growth of juvenile sockeye and Chinook salmon. *Journal of Fish Biology* 69:1626–1638.
- Cavallo, B., J. Merz, and J. Setka. 2013. Effects of predator and flow manipulation on Chinook salmon (*Oncorhynchus tshawytscha*) survival in an imperiled estuary. *Environmental Biology of Fishes* 96:393–403.
- Chapman, E., et al. 2013. Diel movements of out-migrating Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*) smolts in the Sacramento/San Joaquin watershed. *Environmental Biology of Fishes* 96:273–286.
- Chase, R., N. Hemphill, J. Beeman, S. Juhnke, J. Hannon, and A. Jenkins. 2013. Assessment of juvenile coho salmon movement and behavior in relation to rehabilitation efforts in the Trinity River, California, using PIT tags and radiotelemetry. *Environmental Biology of Fishes* 96:303–314.
- Chittenden, C. M., M. C. Melnychuk, D. W. Welch, and R. S. McKinley. 2010. An investigation into the poor survival of an endangered coho salmon population. *PLoS ONE* 5:e10869.
- Cohen, B. 2012. Commission of Inquiry into the Decline of Sockeye Salmon in the Fraser River (Canada). B. I. Cohen commissioner. Minister of Public Works and Government Services Canada, Ottawa, Ontario, Canada.
- Collins, A. L., S. G. Hinch, D. W. Welch, S. J. Cooke, and T. D. Clark. 2013. Intracoeleomic acoustic tagging of juvenile sockeye salmon: swimming performance, survival, and post-surgical wound healing in freshwater and during a transition to seawater. *Transactions of the American Fisheries Society* 142:515–523.
- Collis, K., D. D. Roby, D. P. Craig, B. A. Ryan, and R. D. Ledgerwood. 2001. Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia River Estuary: vulnerability of different salmonid

- species, stocks, and rearing types. *Transactions of the American Fisheries Society* 130:385–396.
- Cooke, S. J., et al. 2008. Developing a mechanistic understanding of fish migrations by linking telemetry with physiology, behavior, genomics and experimental biology: an interdisciplinary case study on adult Fraser River sockeye salmon. *Fisheries* 33:321–338.
- Cooke, S. J., S. J. Iverson, M. J. W. Stokesbury, S. G. Hinch, A. T. Fisk, D. L. VanderZwaag, R. Apostle, and F. Whoriskey. 2011a. Ocean Tracking Network Canada: a network approach to addressing critical issues in fisheries and resource management with implications for ocean governance. *Fisheries* 36:583–592.
- Cooke, S. J., C. Woodley, M. B. Eppard, R. S. Brown, and J. L. Nielsen. 2011b. Advancing the surgical implantation of electronic tags in fish: a gap analysis and research agenda based on a review of trends in intracoelomic tagging effects studies. *Reviews in Fish Biology and Fisheries* 21:127–151.
- Crittenden, R. N. 1994. A diffusion model for the downstream migration of sockeye salmon smolts. *Ecological Modelling* 71:69–84.
- Drenner, S. M., T. D. Clark, C. K. Whitney, E. G. Martins, S. J. Cooke, and S. G. Hinch. 2012. A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. *PLoS ONE* 7:e31311.
- Dunham, J., et al. 2008. Evolution, ecology, and conservation of Dolly Varden, white spotted char, and bull trout. *Fisheries* 33:537–550.
- Evans, A. F., N. J. Hostetter, D. D. Roby, K. Collis, D. E. Lyons, B. P. Sandford, R. D. Ledgerwood, and S. Sebring. 2012. Systemwide evaluation of avian predation on juvenile salmonids from the Columbia River based on recoveries of Passive Integrated Transponder tags. *Transactions of the American Fisheries Society* 141:975–989.
- Foreman, M. G. G., D. J. Stucchi, K. A. Garver, D. Tuele, J. Isaac, T. Grime, M. Guo, and J. Morrison. 2012. A circulation model for the Discovery Islands, British Columbia. *Atmosphere-Ocean* 50:301–316.
- Furey, N. B., S. G. Hinch, A. G. Lotto, and D. A. Beauchamp. 2015. Extensive feeding on sockeye salmon *Oncorhynchus nerka* smolts by bull trout *Salvelinus confluentus* during initial outmigration into a small, unregulated, and inland British Columbia river. *Journal of Fish Biology* 86:392–401.
- Goetz, F. A., E. Jeanes, M. E. Moore, and T. P. Quinn. 2015. Comparative migratory behavior and survival of wild and hatchery steelhead (*Oncorhynchus mykiss*) smolts in riverine, estuarine, and marine habitats of Puget Sound, Washington. *Environmental Biology of Fishes* 98:357–375.
- Groot, C., and L. Margolis. 1991. *Pacific salmon life histories*. University of British Columbia Press, Vancouver, British Columbia, Canada.
- Groot, C., R. E. Bailey, L. Margolis, and K. Cooke. 1989. Migratory patterns of sockeye salmon (*Oncorhynchus nerka*) smolts in the Strait of Georgia, British Columbia, as determined by analysis of parasite assemblages. *Canadian Journal of Zoology* 67:1670–1678.
- Heggenes, J., and R. Borgström. 1988. Effect of mink, *Mustela vison* Schreber, predation on cohorts of juvenile Atlantic salmon, *Salmo salar* L., and brown trout, *S. trutta* L., in three small streams. *Journal of Fish Biology* 33:885–894.
- Henderson, M. A., and A. I. Cass. 1991. Effect of smolt size on smolt-to-adult survival for Chilkco Lake sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 48:988–994.
- Hinch, S. G., and P. S. Rand. 1998. Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): role of local environment and fish characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1821–1831.
- Hinch, S. G., S. J. Cooke, M. C. Healey, and A. P. Farrell. 2006. Behavioural physiology of fish migrations: salmon as a model approach. Pages 239–295 in K. A. Sloman, R. W. Wilson and S. Balshine, editors. *Behaviour and physiology of fish*. Elsevier, New York.
- Hoar, W. S. 1988. The physiology of smolting salmonids. Pages 275–343 in W. S. H. A. D. Randall, editor. *Fish physiology*. Academic Press, New York, New York, USA.
- Hostetter, N. J., A. F. Evans, D. D. Roby, and K. Collis. 2012. Susceptibility of juvenile steelhead to avian predation: the influence of individual fish characteristics and river conditions. *Transactions of the American Fisheries Society* 141:1586–1599.
- Houston, A. H. 1959. Osmoregulatory adaptation of steelhead trout (*Salmo gairdneri* Richardson) to sea water. *Canadian Journal of Zoology* 37:729–748.
- Huntingford, F. A. 2004. Implications of domestication and rearing conditions for the behaviour of cultivated fishes. *Journal of Fish Biology* 65:122–142.
- Ibbotson, A., W. C. Beaumont, and A. Pinder. 2011. A size-dependent migration strategy in Atlantic salmon smolts: small smolts favour nocturnal migration. *Environmental Biology of Fishes* 92:151–157.
- Irvine, J. R., and S. A. Akenhead. 2013. Understanding smolt survival trends in sockeye salmon. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 5:303–328.
- Jeffries, K. M., et al. 2014. Immune response genes and pathogen presence predict migration survival in wild salmon smolts. *Molecular Ecology* 23:5803–5815.
- Jepsen, N., C. Schreck, S. Clements, and E. B. Thorstad. 2005. A brief discussion on the 2% tag/bodymass rule of thumb. Page 295 in M. T. Spedicato, G. Lembo and G. Marmulla, editors. *Aquatic telemetry: advances and applications*. Proceedings of the Fifth Conference on Fish Telemetry held in Europe, Ustica, Italy, 9–13 June 2003.
- Keefer, M. L., C. C. Caudill, C. A. Perry, and S. R. Lee. 2008. Transporting juvenile salmonids around dams impairs adult migration. *Ecological Applications* 18:1888–1900.
- Laake, J. L. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep 2013-01. Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, Seattle, Washington, USA.
- Lapointe, M. 2010. Fry emergence and migration to sea. Page 189 in *Summit on Fraser River sockeye salmon: understanding stock declines and prospects for the future*. Simon Fraser University, Burnaby, British Columbia, Canada.
- Levings, C. D., C. D. McAllister, and B. D. Chang. 1986. Differential use of the Campbell River estuary, British Columbia by wild and hatchery-reared juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 43:1386–1397.
- Mahoney, J. E., J. A. Tadey, T. R. Whitehouse, C. Neville, and S. M. Kalyn. 2013. Evaluation of timing, size, abundance and stock composition of downstream migrating juvenile sockeye salmon in the lower Fraser River.
- Marshall, K. N., A. C. Stier, J. F. Samhouri, R. P. Kelly, and E. J. Ward. 2015. Conservation challenges of predator recovery. *Conservation Letters* 9:70–78.
- McKinnell, S. M., E. Curchitser, C. Groot, M. Kaeriyama, and K. W. Myers. 2011. The decline of Fraser River sockeye salmon *Oncorhynchus nerka* (Steller, 1743) in relation to marine ecology. PICES Advisory Report. Cohen Commission Technical Report 4. Vancouver, British Columbia, Canada.

- Melnichuk, M. C., D. W. Welch, and C. J. Walters. 2010. Spatio-temporal migration patterns of Pacific salmon smolts in rivers and coastal marine waters. *PLoS ONE* 5:e12916.
- Mesa, M. G. 1994. Effects of multiple acute stressors on the predator avoidance ability and physiology of juvenile Chinook salmon. *Transactions of the American Fisheries Society* 123:786–793.
- Michel, C. J., A. J. Ammann, E. D. Chapman, P. T. Sandstrom, H. E. Fish, M. J. Thomas, G. P. Singer, S. T. Lindley, A. P. Klimley, and R. B. MacFarlane. 2013. The effects of environmental factors on the migratory movement patterns of Sacramento River yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*). *Environmental Biology of Fishes* 96:257–271.
- Michel, C. J., A. J. Ammann, S. T. Lindley, P. T. Sandstrom, E. D. Chapman, M. J. Thomas, G. P. Singer, A. P. Klimley, and R. B. MacFarlane. 2015. Chinook salmon outmigration survival in wet and dry years in California's Sacramento River. *Canadian Journal of Fisheries and Aquatic Sciences* 72:1749–1759.
- Muir, W. D., D. M. Marsh, B. P. Sandford, S. G. Smith, and J. G. Williams. 2006. Post-hydropower system delayed mortality of transported Snake River stream-type Chinook salmon: unraveling the mystery. *Transactions of the American Fisheries Society* 135:1523–1534.
- Peterman, R. M., and B. Dörner. 2012. A widespread decrease in productivity of sockeye salmon (*Oncorhynchus nerka*) populations in western North America. *Canadian Journal of Fisheries and Aquatic Sciences* 69:1255–1260.
- Peterman, R. M., et al. 2010. Synthesis of evidence from a workshop on the decline of Fraser River sockeye. Page 123 in *A Report to the Pacific Salmon Commission*. Vancouver, British Columbia, Canada.
- Piggins, D. J., and C. P. R. Mills. 1985. Comparative aspects of the biology of naturally produced and hatchery-reared Atlantic salmon smolts (*Salmo salar* L.). *Aquaculture* 45:321–333.
- Poole, W. R., D. T. Nolan, T. Wevers, M. Dillane, D. Cotter, and O. Tully. 2003. An ecophysiological comparison of wild and hatchery-raised Atlantic salmon (*Salmo salar* L.) smolts from the Burrishoole system, western Ireland. *Aquaculture* 222:301–314.
- Post, J. R., M. Sullivan, S. Cox, N. P. Lester, C. J. Walters, E. A. Parkinson, A. J. Paul, L. Jackson, and B. J. Shuter. 2002. Canada's recreational fisheries: the invisible collapse? *Fisheries* 27:6–17.
- Preikshot, D., R. J. Beamish, R. M. Sweeting, C. M. Neville, and T. D. Beacham. 2012. The residence time of juvenile Fraser River sockeye salmon in the Strait of Georgia. *Marine and Coastal Fisheries* 4:438–449.
- Rechisky, E. L., and D. W. Welch. 2010. Surgical implantation of acoustic tags: influence of tag loss and tag-induced mortality on free-ranging and hatchery-held spring Chinook (*Oncorhynchus tshawytscha*) smolts. Pages 69–94 in K. Wolf, J. O'Neal and W. Duvall, editors. *PNAMP special publication: tagging, telemetry and marking measures for monitoring fish populations*. Pacific Northwest Aquatic Monitoring Partnership.
- Rechisky, E. L., D. W. Welch, A. D. Porter, M. C. Jacobs-Scott, P. M. Winchell, and J. L. McKern. 2012. Estuarine and early-marine survival of transported and in-river migrant Snake River spring Chinook salmon smolts. *Nature Scientific Reports* 2:448.
- Rechisky, E. L., D. W. Welch, A. D. Porter, M. C. Jacobs-Scott, and P. M. Winchell. 2013. Influence of multiple dam passage on survival of juvenile Chinook salmon in the Columbia River estuary and coastal ocean. *Proceedings of the National Academy of Sciences* 110:6883–6888.
- Rensel, J. E. J., N. Haigh, and T. J. Tynan. 2010. Fraser river sockeye salmon marine survival decline and harmful blooms of *Heterosigma akashiwo*. *Harmful Algae* 10:98–115.
- Ricker, W. E. 1940. On the origin of kokanee, a fresh-water type of sockeye salmon. *Transactions of the American Fisheries Society, Canada* 34:121–135.
- Riley, C. V. 1878. On migratory butterflies. *Journal of Proceedings of the Academy of Science of St. Louis, Missouri* 3:cclxxiii–cclxxiv.
- Ruggerone, G. T., and D. E. Rogers. 1984. Arctic char predation on sockeye salmon smolts at Little Togiak River, Alaska. *Fishery Bulletin* 82:401–410.
- Sandstrom, P. T., T. Keegan, and G. Singer. 2013. Survival and movement patterns of Central California Coast native steelhead trout (*Oncorhynchus mykiss*) in the Napa River. *Environmental Biology of Fishes* 96:287–302.
- Schreck, C. B., T. P. Stahl, L. E. Davis, D. D. Roby, and B. J. Clemens. 2006. Mortality estimates of juvenile spring-summer Chinook salmon in the lower Columbia River and Estuary, 1992–1998: evidence for delayed mortality? *Transactions of the American Fisheries Society* 135:457–475.
- Singer, G. P., A. R. Hearn, E. D. Chapman, M. L. Peterson, P. E. LaCivita, W. N. Brostoff, A. Bremner, and A. P. Klimley. 2013. Interannual variation of reach specific migratory success for Sacramento River hatchery yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*). *Environmental Biology of Fishes* 96:363–379.
- Stumpf, A. J., B. E. Broster, and V. M. Levson. 2000. Multiphase flow of the late Wisconsin Cordilleran ice sheet in western Canada. *Geological Society of America Bulletin* 112:1850–1863.
- Talbot, L. M., and M. H. Talbot. 1963. The wildebeest in western Masailand, East Africa. *Wildlife Monographs* 12:3–88.
- Thompson, B. C., W. Porak, and M. S. Allen. 2014. Effects of surgically implanting radio transmitters in juvenile largemouth bass. *Transactions of the American Fisheries Society* 143:346–352.
- Thomson, J. 1885. *Through Masai Land*. Samson Low, Marston, Searle and Rivington, London, UK.
- Thomson, R. E. 1981. *Oceanography of inshore waters*. Department of Fisheries and Oceans, Vancouver, British Columbia, Canada.
- Tucker, S., et al. 2015. Coastal distribution and consequent factors influencing production of endangered Snake River sockeye salmon. *Transactions of the American Fisheries Society* 144:107–123.
- Van Gaest, A. L., J. P. Dietrich, D. E. Thompson, D. A. Boylen, S. A. Strickland, T. K. Collier, F. J. Loge, and M. R. Arkoosh. 2011. Survey of pathogens in hatchery Chinook salmon with different out-migration histories through the Snake and Columbia rivers. *Journal of Aquatic Animal Health* 23:62–77.
- Wagner, G. N., S. J. Cooke, R. S. Brown, and K. A. Deters. 2011. Surgical implantation techniques for electronic tags in fish. *Reviews in Fish Biology and Fisheries* 21:71–81.
- Welch, D. W., G. W. Boehlert, and B. R. Ward. 2002. POST-the Pacific Ocean salmon tracking project. *Oceanologica Acta* 25:243–253.
- Welch, D. W., B. R. Ward, and S. D. Batten. 2004. Early ocean survival and marine movements of hatchery and wild steelhead trout (*Oncorhynchus mykiss*) determined by an acoustic array: Queen Charlotte Strait, British Columbia. *Deep Sea Research Part II: Topical Studies in Oceanography* 51:897.
- Welch, D. W., E. L. Rechisky, M. C. Melnychuk, A. D. Porter, C. J. Walters, S. Clements, B. J. Clemens, R. S.

- McKinley, and C. Schreck. 2008. Survival of migrating salmon smolts in large rivers with and without dams. *PLoS Biology* 6:e265.
- Welch, D. W., M. C. Melnychuk, E. R. Rechisky, A. D. Porter, M. C. Jacobs, A. Ladouceur, R. S. McKinley, and G. D. Jackson. 2009. Freshwater and marine migration and survival of endangered Cultus Lake sockeye salmon (*Oncorhynchus nerka*) smolts using POST, a large-scale acoustic telemetry array. *Canadian Journal of Fisheries and Aquatic Sciences* 66:736–750.
- Welch, D. W., M. C. Melnychuk, J. C. Payne, E. L. Rechisky, A. D. Porter, G. Jackson, B. Ward, S. Vincent, C. C. Wood, and J. Semmens. 2011. *In situ* measurement of coastal ocean movements and survival of juvenile Pacific salmon. *Proceedings of the National Academy of Sciences USA* 108:8708–8713.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–139.
- Williams, J. G., S. G. Smith, W. D. Muir, B. P. Sandford, S. Achord, R. McNatt, D. M. Marsh, R. W. Zabel, and M. D. Scheuerell. 2005. Effects of the federal Columbia River power system on salmon populations. U.S. Department of Commerce, National Oceanographic and Atmospheric Administration, National Marine Fisheries Service, Silver Spring, Maryland, USA.
- Wood, C. C., N. B. Hargreaves, D. T. Rutherford, and B. T. Emmett. 1993. Downstream and early marine migratory behaviour of sockeye salmon (*Oncorhynchus nerka*) smolts entering Barkley Sound, Vancouver Island. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1329–1337.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1890/15-0632.1/supinfo>

## DATA AVAILABILITY

Data associated with this paper have been deposited in the OTN Data Portal: <http://dx.doi.org/10.14286/2015CLARKTCHILKO>