Freshwater and marine migration and survival of endangered Cultus Lake sockeye salmon (*Oncorhynchus nerka*) smolts using POST, a large-scale acoustic telemetry array

David W. Welch, Michael C. Melnychuk, Erin R. Rechisky, Aswea D. Porter, Melinda C. Jacobs, Adrian Ladouceur, R. Scott McKinley, and George D. Jackson

Abstract: Freshwater and early marine migration and survival of endangered Cultus Lake sockeye (*Oncorhynchus nerka*) salmon were studied using the Pacific Ocean Shelf Tracking (POST) array. Smolts were acoustically tagged in 2004–2007, and their migration was recorded within the lower Fraser River and coastal southern British Columbia waters. Most smolts showed rapid directional movement (swimming speeds of ~15–30 km·day^{-1}). Average exit time from the Fraser River was 4.0–5.6 days after release, and average residence time within the Strait of Georgia was 25.6–34.1 days. Most individuals migrated northward, generally close to the mainland coast. Survival rates, assessed using standard mark–recapture methods, were generally high during the downstream migration (50%–70%), except in 2005 when survival was <20%, possibly because of a late release. Marine survival rates were stable among years, between 10%–30% at a subarray sited 500 km away from the release site. Movement rates were similar to those of previously published work, but the POST array provided direct measurements of movement and estimates of survival and demonstrated the feasibility of establishing continental-scale acoustic arrays for management and conservation of marine species.

Résumé : Nous étudions la migration et la survie en eau douce et au début de la vie marine chez le saumon rouge (*Oncorhynchus nerka*) du lac Cultus, une forme menacée, à l'aide du réseau POST (« Pacific Ocean Shelf Tracking », surveillance de la plate-forme du Pacifique). Les saumoneaux ont été munis d'étiquettes acoustiques en 2004–2007 et leur migration enregistrée dans le Fraser inférieur et les eaux côtières de la Colombie-Britannique. La plupart des saumoneaux font des déplacements directionnels rapides (vitesses de nage ~15–30 km·jour^{-1}). Le temps moyen pour quitter le Fraser est de 4,0–5,6 jours après la libération et le temps moyen de résidence dans le détroit de Géorgie est de 25,6–34,1 jours. La plupart des individus migrent vers le nord, généralement près des côtes du continent. Les taux de survie, déterminés par des méthodes classiques de marquage et de recapture, sont généralement élevés durant la migration vers l'aval (50–70 %) excepté en 2005 où la survie était <20 %, probablement à cause d'une libération tardive. Les taux de survie en mer sont stables au cours des années, entre 10–30 % dans un sous-réseau situé à 500 km du point de libération. Les taux de déplacement sont semblables à ceux mentionnés dans des travaux antérieurs publiés, mais le réseau POST fournit des mesures directes des déplacements et des estimations de la survie. Notre étude démontre qu'il est possible d'établir des réseaux acoustiques à l'échelle continentale pour la gestion et la conservation des espèces marines.

[Traduit par la Rédaction]

Introduction

The management and conservation of salmon populations would be aided by a better understanding of the marine life-history phase (e.g., McKinnell et al. 2001; English et al. 2008; Lacroix 2008). The early marine stage is poorly studied relative to both the initial freshwater life-history phases (egg to fry, fry to smolt) and the very late marine and freshwater life-history phases of returning adults (e.g.,

D.W. Welch.[1] Kintama Research Corp, 10-1850 Northfield Rd., Nanaimo, BC V9S 3B3, Canada; School of Earth and Ocean Sciences, University of Victoria, Victoria, BC V8W 2Y2, Canada.
M.C. Melnychuk and E.R. Rechisky. Fisheries Centre, University of British Columbia, 2202 Main Mall, Vancouver, BC V6T 1Z4, Canada.
A.D. Porter, M.C. Jacobs, and A. Ladouceur. Kintama Research Corp, 10-1850 Northfield Rd., Nanaimo, BC V9S 3B3, Canada.
R.S. McKinley. The University of British Columbia, Department of Animal Science, 4160 Marine Drive, West Vancouver, BC V7V 1N6, Canada.
G.D. Jackson. University of Tasmania, Institute of Antarctic and Southern Ocean Studies, Private Bag 77 Hobart, Tasmania, 7001 Australia; Pacific Ocean Shelf Tracking Project (POST), Vancouver Aquarium, P.O. Box 3232, Vancouver, BC V6B 3X8, Canada.

[1]Corresponding author (e-mail: david.welch@kintama.com).

Groot and Margolis 1991). Although there are many estimates of overall survival for Pacific salmon (*Oncorhynchus* spp.) stocks based on outmigrating smolt numbers and the subsequent level of adult return some years later, it has not been possible to directly study survival at discrete periods during the marine portion of their life history. It is therefore difficult to pinpoint where major periods of mortality occur or understand their cause. Such information is necessary for understanding population dynamics and for making informed decisions for assisting the rebuilding of threatened and endangered populations of salmon.

The development and continued miniaturization of uniquely coded acoustic tags in the last decade holds the promise of allowing major advances in marine research (Voegeli et al. 1998, 2001; Heupel et al. 2006). Unlike radio waves, sound transmits effectively in both fresh and saline waters. Acoustic receivers can be arranged in line arrays or "curtains" (e.g., Lacroix and Voegeli 2000; Lacroix et al. 2005) placed in selected locations along potential migratory routes. In this way, it is possible both to track individuals seamlessly between the fresh and marine environments and to partition survival to understand where episodes of mortality occur.

This technology has formed the basis of the Pacific Ocean Shelf Tracking Project (POST) for tracking both juvenile (Welch et al. 2002, 2004; Melnychuk et al. 2007) and adult (e.g., Cooke et al. 2008) salmon, as well as other species (Welch et al. 2006; Lindley et al. 2008). The POST array is intended as a permanent continental-scale telemetry research platform for the entire west coast of North America, including major rivers. The component listening "curtains" (or subarrays) use Vemco VR-2 or VR-3 passive acoustic receivers (Amirix Systems Inc., Halifax, Nova Scotia) in precise geometries to enable a nearly complete census of acoustically tagged salmon as they cross each successive curtain. Although centered along the shelf in southern British Columbia waters, the array currently extends almost 900 km up the Columbia–Snake rivers in the United States and spans over 2500 km in geographic extent from the Columbia River to Graves Harbor, southeast Alaska (Haggan et al. 2009).

In this study, we used the POST array to study the migratory behaviour and survival of Cultus Lake sockeye (*Oncorhynchus nerka*) smolts over the 4-year period from 2004 to 2007. This sockeye population is genetically unique and has been studied since the 1920s (Ricker 2006). Between the 1920s and the 1960s, the number of returning adult Cultus sockeye averaged around 20 000. However, a rapid decline in the number of adult sockeye returning to spawn in the 1990s reduced the population to fewer than 100 (decreasing by 92% between 1991 and 2002; English et al. 2008), triggering a recommendation for an emergency listing of the population as endangered by the Committee on the Status of Endangered Wildlife in Canada in 2002 (Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2003). Although the federal government accepted the evidence, legal listing as endangered was not made because of the impact that the decision would have on commercial fisheries of other stocks of Fraser sockeye. (Cultus Lake sockeye are incidentally harvested during the late-run Fraser River sockeye fishery and fisheries closures would lead to eco-

nomic losses estimated to be on the order of $200 million; Government of Canada 2005.)

What is unclear is why marine survival decreased dramatically in the 1990s. COSEWIC (2003) listed the three primary causes of sockeye decline as overfishing and incidental harvest, high prespawning mortality, and low marine survival. Poor marine survival seems to be a feature shared by a number of salmonid stocks and other species in south and central coastal British Columbia waters (English et al. 2008), and the cause clearly warrants further investigation. The Cultus Sockeye Recovery Team states that "survival and distribution of Cultus sockeye in the Fraser River and nearshore marine areas have not been documented, thus resulting in a knowledge gap for this specific stock" (Cultus Sockeye Recovery Team 2005). It was thus of interest to explore how tracking migrating Cultus Lake sockeye smolts using the POST array might help to fill gaps in our understanding of where possible survival "bottlenecks" might occur.

The objectives of our study were to estimate survival and migratory behaviour of Cultus Lake sockeye smolts within the Fraser River and along their initial coastal migration. This work builds on our existing understanding from earlier investigations into the migration of Fraser River sockeye salmon (Groot and Cooke 1987; Groot and Quinn 1987; Groot et al. 1989).

## Materials and methods

Study site

Cultus Lake drains into the lower Fraser River via Sweltzer Creek, Vedder River, and Sumas River (Fig. 1). The total distance from the release site at the lake outflow to the mouth of the Fraser River is 100 km. Mean annual discharge of the Fraser River, which drains into the Strait of Georgia, is 3600 $m^3 \cdot s^{-1}$, with highest flows peaking in late June. Exit routes to the Pacific Ocean from the Strait of Georgia include Johnstone Strait and Queen Charlotte Strait to the north and the Strait of Juan de Fuca to the south (Fig. 1).

Smolt release groups

Hatchery-reared 1.5-year-old sockeye salmon smolts were surgically implanted with acoustic transmitters prior to release in 2004–2007. All smolts were from Cultus Lake stock. Those tagged in 2004, 2005, and 2007 were reared from wild adult returns. Those tagged in 2006 were from more complex origins because only 10 females were available for broodstock, which were taken from a total return of only 60 adults in the 2004 brood year. These smolts were produced from wild × wild parents (85%) or a mixture of hatchery-produced, naturally returning parents (one or both parents; 15%). Some of the 2006 matings also used cryopreserved sperm taken from wild adult males in 2002.

In 2004 (*n* = 100), sockeye smolts were reared at Rosewall Creek Hatchery on Vancouver Island, tagged, and then transported by helicopter to Cultus Lake for release. In 2005 (*n* = 376), 2006 (*n* = 200), and 2007 (*n* = 200), smolts were tagged at Inch Creek Hatchery (located near Cultus Lake) and then transported by truck to Cultus Lake for release. In all years except 2005, tagged fish were released in Sweltzer Creek at the outflow from Cultus Lake. A fence in Sweltzer

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Fig. 1. The southern British Columbia components of the POST array. The thick black lines indicate POST subarrays, which are formed by a linearly arranged sequence of independent receivers. Inserts provide details of the POST lines within the Fraser River and Cultus Lake and its outlets, along with mobile sampling locations in those areas (●). The bottom panel shows the array deployment within the Fraser River over the 4 years of the study. Subarray locations in the Fraser River differed between years and are identified by symbols and letters: ■ (A, B, D), 2004; ◆ (C, E), 2005; ▲ (C, F, G), 2006; ▼ (A, C, F, G), 2007.
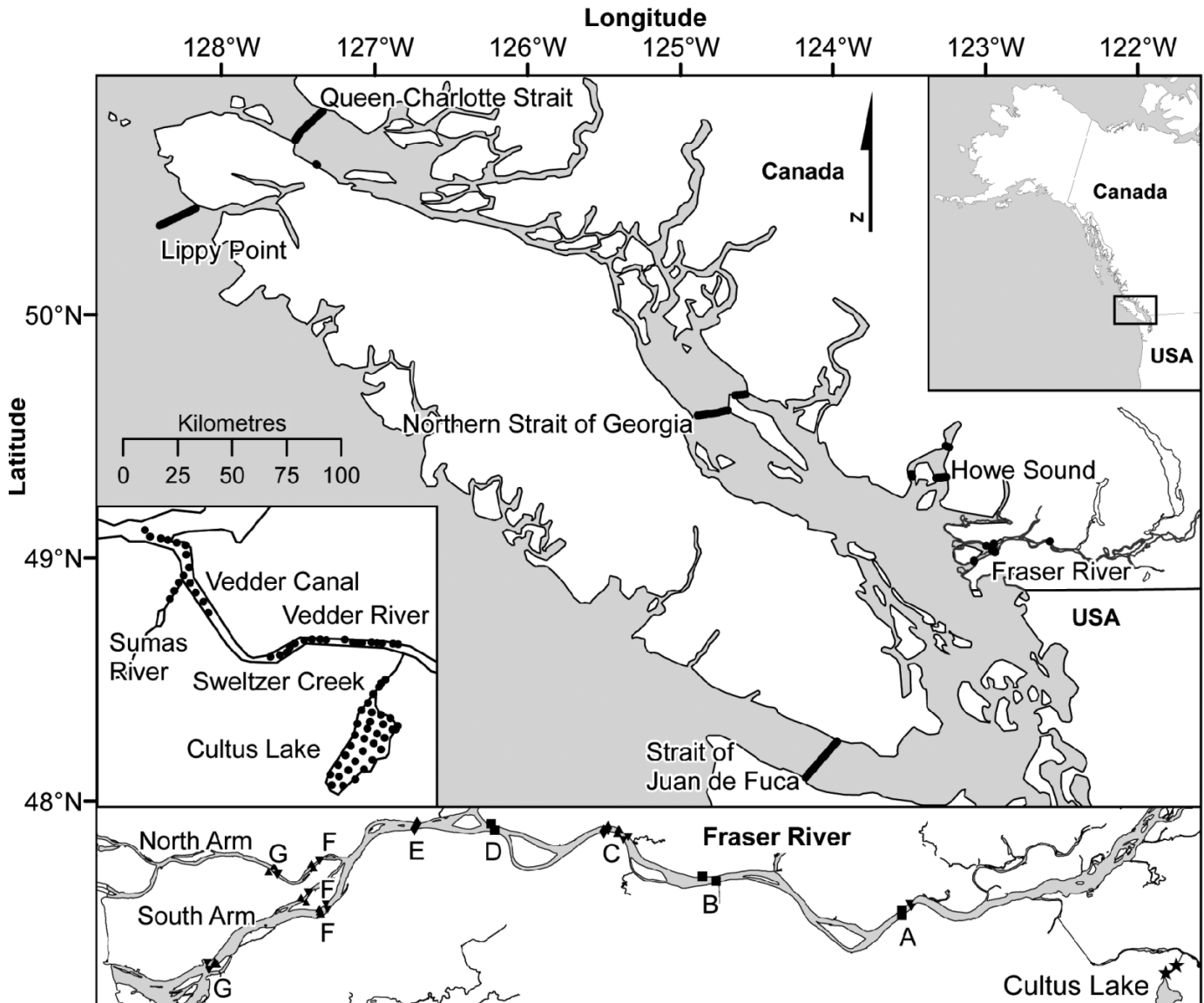
Creek upstream of the release site was in place each year until about 1 June to reduce the frequency of upstream movement into the lake. In 2005, fish were released in June after the fence had been removed, and therefore, they were released approximately 500 m downstream of the standard release site.

Average fork length (FL) of all Cultus Lake hatchery smolts tagged over the 4 years of the study ranged from 159 to 189 mm (Table 1). It should be noted that these hatchery-reared smolts were considerably larger than typical wild smolts (~100 mm), but currently available acoustic tags are too large for use in wild sockeye smolts.

Tag characteristics

Tags were programmed to transmit their acoustic codes at 69 kHz with a random time interval of 30–90 s between suc-

cessive transmissions (average 60 s). In 2004, we implanted Vemco V9-6L tags, which had projected life spans of >4 months. In 2005, we used a combination of V9-6L, V9-1L, and V9-2L tags (Table 1). The latter two models have an extended battery life because of their larger size. We programmed a "sleep" period that began on 22 July 2005 (V9-1L) or 1 December 2005 (V9-2L); during this time, acoustic transmission was terminated to reserve power for the 2007 return migration of any surviving adults. These tags were programmed to reactivate and begin transmission again on 30 June 2007, prior to the historic arrival time in the Strait of Georgia. The tags had sufficient projected reserve battery power to allow transmission to continue until at least 15 September 2007, after the time of expected adult entry into the Fraser River. The larger tags were implanted into larger smolts (see Table 1). In 2006 and 2007, we used

Table 1. Summary of Cultus Lake sockeye smolts tagged and released.[a]

				Fork length (mm)	
Year	Tag type[b]	Release date (UTC)	Number	Average	SD
2004	V9-6L	04 May 2004 (0330)	100	178	13
2005	V9-1L	09 June 2005 (0300)	92	172	5
	V9-2L	09 June 2005 (0300)	188	188	8
	V9-6L	09 June 2005 (0300)	96	159	5
2006	V9-1L	21 April 2006 (0100)	200	178	9
2007	V9-1L	16 May 2007 (2200)	200	189	8

Note: UTC, coordinated universal time; SD, standard deviation.

[a]Detailed data are available in the POST database (Pacific Ocean Shelf Tracking Project 2008).

[b]Tag dimensions: V9-6L tags are 21 mm × 9 mm and weigh 2.9 g in air; V9-1L tags are 24 × 9 mm and weigh 3.6 g in air; and V9-2L tags are 29 mm × 9 mm and weigh 4.7 g in air.

all V9-1L tags with 41–45 days of active transmission after release until their programmed sleep periods began on 1–4 June 2006 or 27–28 June 2007. The 2006 tags were programmed to reactivate between 18 April and 4 July 2008, whereas the 2007 tags should reactivate on 26 July 2009.

Tags ranged in length between 10.0% and 16.7% of body length (mean ratios: V9-6L, 12.5%; V9-1L, 13.3%; V9-2L, 15.5%) and in mass between 2.4% and 9.6% of body mass (mean ratios: V9-6L, 5.5%; V9-1L, 5.1%; V9-2L, 5.9%). Tag–body size ratios of nearly all fish were below recommended limits for juvenile salmonids of 16% of length and 8% of weight (Lacroix et al. 2004).

Surgical techniques

Acoustic tags were surgically implanted into smolts following standard protocols (Welch et al. 2007). Smolts were sedated with 1 ppm metomidate HCl (Aquacalm; Syndel Laboratories Ltd., Qualicum Beach, B.C.) for a minimum of 10 min, and then 3–4 min prior to surgery, they were brought under full anaesthesia using 70 ppm Tricaine methanesulphonate (MS-222) mixed with a 140 ppm $NaHCO_3$ buffer. Gills were continuously irrigated during surgery using a purpose-built surgical table with recirculating water bath containing 50 ppm MS-222 (100 ppm $NaHCO_3$) flowing into the mouth. A tag was inserted into the abdominal cavity through a midventral line incision, which was closed using two to three polydioxanone monofilament sutures. Fish were then transferred to a recovery tank. Water baths were continually monitored for temperature and dissolved oxygen. All water baths were changed as needed to maintain dissolved oxygen levels between 8 and 11 ppm and to maintain water temperatures within 2 °C of ambient hatchery tank water. A water conditioner and mucous protectant (Vidalife; Syndel Laboratories Ltd.) was used in all water baths.

Animal care protocols were reviewed and approved annually by institutional animal care committees prior to all fieldwork. Sockeye smolts used in this study were surgically implanted at least 2 days prior to release to allow time for recovery from the anaesthetic and to monitor fish for signs of mortality, tag shedding, and abnormal swimming behaviour. No mortalities were observed. The release of tagged smolts in 2005 was several weeks later than in other years (Table 1) because an electrical failure at the hatchery resulted in the death of almost all surgically implanted smolts prior to their release. Logistical constraints resulted in the subsequent surgery and release of different fish much later

(early June 2005) than originally planned (Kintama Research Corp. 2005).

Hydrophone receiver deployments

Acoustic receivers were installed as single or paired units in the lower Fraser River at several locations downstream of the Sumas River confluence. Locations varied between years, with three lines and six receivers in 2004, two lines and four receivers in 2005, three lines (six sublines) and 12 receivers in 2006, and four lines (seven sublines) and 14 receivers in 2007 (Fig. 1).

Ocean detections were recorded in the northern Strait of Georgia (NSOG), Queen Charlotte Strait (QCS), and the Strait of Juan de Fuca (JDF) (Fig. 1). Two acoustic subarrays were also deployed in Howe Sound (HS), a coastal fjord 30 km north of the Fraser River mouth. In 2004 and 2005, Vemco VR2 receivers were used to construct all listening lines using receiver geometry calculated to provide a high probability of detection of any passing tagged smolts. These units were deployed in the spring and recovered in the fall at least 110 days after Cultus Lake sockeye smolts were released, well after the time that smolts were detected crossing ocean lines of receivers. In 2006, VR2 units on NSOG, QCS, and JDF lines initially deployed in the spring were replaced with permanent, year-round VR3 receiver lines during summer 2006. They were uploaded twice in 2007, once in the spring and once in the fall after outmigration. The NSOG and QCS lines remained relatively intact over the course of the study, with <10% loss of receivers per year, even when the more fragile VR2 deployment methodology was used. However, the JDF line was subjected to extensive shrimp bottom trawling and subsequent gear loss in 2004, with one-third of receivers not recovered. In other years, receiver loss was <10% on the JDF line.

Freshwater mobile tracking

To assess the potential for smolts to residualize in freshwater rather than migrate out to sea, we surveyed the number and location of smolts tagged with V9-2L or V9-6L tags in Cultus Lake, the Vedder and Sumas rivers, and Sweltzer Creek for 2 days in late July 2005 (Kintama Research Corp. 2005). We conducted two similar additional surveys in August 2007 to detect any "sleeper" tags (from residualized or dead fish) that were released in 2005 and turned back on in 2007 (Kintama Research Corp. 2008). The 2005 census would not have detected any of the V9-1L sleeper tags re-

leased that year as the survey was conducted 4 days after the tags would have turned off. Similarly, the 2007 survey would not have detected any tags released in 2007 as these surveys occurred during programmed sleep periods of tags.

On the first survey day of each year, we used a VR-2 deployed for 6–10 min at 31 fixed stations spaced approximately 500 m apart, covering approximately 95% of the Cultus Lake area. Two days later in 2005, a Vemco VR-28 mobile receiver was used to listen for tags while conducting sampling transects covering approximately 60% of the lake area. In 2007, 1 week after the first survey, we resampled the 31 fixed stations with VR-2 and VR-60 mobile receivers.

Additionally, a network of eight VR-2 receivers was deployed between October 2006 and October 2007 in Cultus Lake for a separate, unrelated study (C. Tovey, Fisheries and Oceans Canada, Pacific Biological Station, Hammond Bay Road, Nanaimo, British Columbia, unpublished data). These receivers detected several 2005 tags that had likely never left the lake and began transmitting again about 30 June 2007 following their sleep period and also several 2007 tags from fish that had residualized, died, or extruded tags in the lake (see Results).

To look for possible mortality locations in the first segment of the migration downstream of Sweltzer Creek (before the stationary Fraser River array), we spent 1 day in 2005 and 2 days in 2007 sampling in the rivers that connect Cultus Lake with the Fraser River. We walked along a 6 km stretch of the Vedder River downstream of the confluence with Sweltzer Creek and lowered a VR-2 receiver into the river at 19 stations, each separated by 200–500 m. In 2007, 600 m of Sweltzer Creek from the Vedder confluence upstream was also sampled. In the lower Vedder Canal, Sumas River, and approximately 2 km of the Fraser River downstream of the Sumas confluence, deeper water permitted tracking by boat. In 2005, we towed a VR-2 receiver and drifted or trolled across these areas, with a single pass being sufficient in the narrow Vedder and Sumas rivers and making three transects in the wider Fraser River section. In 2007, 15 fixed stations in the Vedder Canal and Sumas River were each sampled twice, 1 week apart.

Data analysis

We compiled a database of detections from the stationary receivers consisting of the dates, times, and geographical locations of the detection of each tag. First, we identified and excluded any detections likely to be false (owing to aliasing or tag collisions). Detections were excluded as false if they were detected only once on a line within a 30-min interval, had one or more other tags heard on the same receiver around the time of the suspect detection, and did not have supporting detections from other time periods or lines. Supporting detections are defined as a temporally consistent sequence of detections from release along the migration path. This screening excluded a small number of sporadic detections (0.03%), and the vast majority of the retained data consisted of multiple detections closely spaced in time on a given receiver or subarray. After eliminating suspect detections, we used these filtered data to estimate survival and detection probabilities, migration routes, and travel times and rates of tagged smolts.

Estimation of survival and detection probabilities are described in the next section (see below). To identify possible migratory pathways along the shelf or within the channel, we plotted the number of fish that were heard at each position on the line of acoustic receivers. Because individual fish are usually heard at more than one position on a line, we allocated a proportion of each fish to each of the receivers on which it was detected (i.e., if a fish was heard at three positions, each unit was allocated 0.33 of a fish). We used a χ^2 goodness-of-fit analysis to test if fish were distributed uniformly across the major ocean lines (i.e., each receiver as a separate category). We then grouped fish detected on adjacent receivers to identify broader migratory routes and increase the power of the test. Because the NSOG line is divided by an island, we grouped the fish heard on this line into east or west (i.e., two categories). The QCS line is not divided by an island, so to avoid arbitrarily defining east and west, we ran a series of χ^2 tests in which we grouped neighbouring receivers over an increasingly larger spatial extent (i.e., fewer categories in each test) up to a maximum of five receivers per group (representing potential migration routes ~4 km wide). When the number of receivers per group did not divide evenly, we dropped the receivers on the ends preferentially. We filled in gaps from lost receivers using arithmetic progression from neighbouring units. To test if individuals maintained a preferred migratory route between the NSOG line and the QCS line (240 km to the north), we ran a correlation analysis using the average distance from the mainland that each smolt was detected on each line. Travel times in each segment were measured as the difference between average travel times from release until the first detection of a tag on a line, for successive lines. Travel times from release to the mouth of the Fraser River and from the river mouth to the ocean lines were estimated using the furthest downstream line in the Fraser River each year. The segment distances used in travel rate estimation were measured with mapping software as shortest-route distances between lines of receivers, excluding landmasses.

Survival rate estimation

We used the fully time varying Cormack–Jolly–Seber model (CJS) for live recaptures and variants thereof to simultaneously estimate survival (φ) and detection (p) probabilities in each segment of the migration. To do so, we first determined the detection history of individual fish at each receiver (i.e., recapture) line along the migration path. Sockeye smolts were detected on two to four detection lines in the Fraser River (depending on year) and then on two lines in the ocean (NSOG and QCS) for a total of five, six, or seven detection sites. Only two fish in 2005 and six fish in 2007 were detected on the JDF line, but these were pooled with the QCS detections for the final digit of the CJS tag capture histories to represent exit from the Strait of Georgia system.

The final survival probability is confounded with detection probability at the final line (QCS–JDF), essentially because there is no more distant location at which the ratio of detected to undetected tags can be assessed. To isolate these factors, we estimated an overall detection probability for the NSOG line (p_{NSOG}) across all four years of the study and as-

sumed this value for the QCS and JDF lines in all years. This approach is reasonable because all three lines had similar receiver geometry during the study period. We used a shorter, three-digit capture history involving release, NSOG recapture, and QCS recapture to more accurately estimate the mean and variance of p_{NSOG}. This estimate of p is the fraction of smolts detected on the QCS line that were also detected on NSOG. Our estimate of p_{NSOG} was for V9 tags from all populations of salmon smolts tagged under POST in 2004–2007 that crossed this line, not just Cultus Lake sockeye. This pooling was done because sample sizes of some populations crossing ocean lines were small and thus population-specific p estimates were highly variable. No consistent seasonality pattern was observed in population-specific p_{NSOG} estimates when compared with their average run timing across this line, so pooling was justified. Further, model selection criteria showed 99.9% support, as measured by Akaike weights, for a model in which species, populations, and years were pooled in a set of four other models involving less pooling of species-, population-, and year-specific estimates of p_{NSOG}. With years pooled, a single estimate of p_{NSOG} was generated and then applied to QCS and JDF as a fixed value in each year. To avoid underestimating uncertainty in the survival estimate for the final migration segment due to fixing this value, survival rates were also calculated by fixing the detection probabilities of QCS and JDF at the lower and upper 95% confidence limits of p_{NSOG}; this bounded a range of uncertainty for the final stage survival estimate and thus the total migration survivorship estimates (Fig. 2).

After assuming fixed values for the final stage detection probabilities, we used the full capture histories in a CJS live recaptures-only model implemented with program MARK (White and Burnham 1999) through RMark (Laake and Rexstad 2007) to estimate φ in river and ocean segments, as well as p on river lines in each year.

Our approach involved two main steps. (*i*) To determine whether survival was best described, on average, as a function of body size, migration distance, and (or) average travel time, we tested several candidate models. We first combined all 4 years in a capture-history data set and assigned "year" as a group covariate. Combining years allowed us to constrain the slope of survival vs. one such covariate to be consistent among years (while permitting intercepts to differ). For example, we constrained the relative survival difference of a big smolt and a small smolt to be equal among years in logit space, even though particular body sizes or overall survival at a particular body size could differ among years.

We considered eight candidate models (Table 2) using this combined data set. Detection probabilities in all models were line-specific and year-specific, $p_{(time \times year)}$, where the "time" factor represents recapture locations at receiver lines. One survival model was the classic time-varying CJS model, $\varphi_{(time \times group)}$, with separate segment-specific survival estimates for each of the 4 years. Another model incorporated the additive effect of body size as an individual covariate into the CJS model. The other six models involved minimum migration distance or average travel time group covariates to replace the freely varying segment-specific estimates. These constrained models, some of which included body size as a covariate, involved fewer parameters. Some allowed for sep-

Fig. 2. Survivorship estimates from release to exit from the Strait of Georgia system for different assumed detection probabilities on the final Queen Charlotte Strait (QCS) and Strait of Juan de Fuca (JDF) lines. The mean and lower and upper 95% confidence limits of northern Strait of Georgia (NSOG) detection probabilities, p, are assumed for QCS and JDF detection probabilities. Error bars show 95% confidence limits on resulting survivorship estimates.
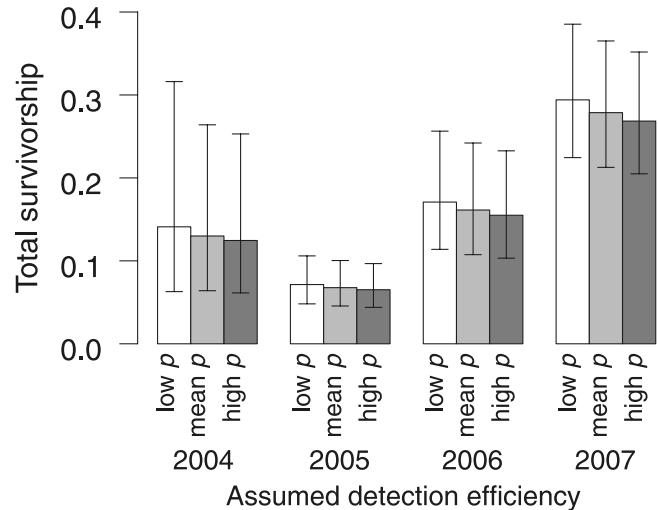
arate effects of in-river and ocean segments of distance or travel time on survival, and others were further constrained without this multiplicative habitat effect. We estimated a variance inflation factor $(\hat{c})$ to compensate for overdispersion, or extra-binomial variation, in estimated probabilities (Burnham et al. 1987). We estimated $\hat{c}$ (= 1.3325) using the deviance ratio method in MARK's goodness-of-fit bootstrapping routine assuming the general CJS model, $\varphi_{(time \times year)} p_{(time \times year)}$. QAIC$_c$ values, corrected for extra-binomial variation and sample sizes, were computed for model comparison.

For step *ii*, once we determined the best-supported models on average from the eight models described above, we analyzed the 4 years independently so that we could estimate the extra-binomial variation, $\hat{c}$, for each year of the study. By estimating $\hat{c}$ annually, the variance around each of the estimated probabilities is specific to the variation observed within that year (and not all years combined). Using the bootstrapping routine again, we estimated $\hat{c}$ for the fully time varying CJS models as 1.73, 0.59, 1.44, and 1.28 in 2004–2007, respectively. The $\hat{c}$ value estimated at <1 in 2005 was set to 1 (Cooch and White 2007). These $\hat{c}$ values were used to expand standard errors of real parameter estimates and values in the variance–covariance matrix.

The top two candidate models had almost equal support and together had nearly 100% of the support within the set of eight models considered, and therefore we considered only these two models for each individual year. We computed model-averaged parameter estimates for φ and p at each segment or detection station for that year. For each sequential receiver station, we calculated survivorship from release to that point as the product of segment-specific φ estimates. We used the delta method to calculate the variance of this product.

Table 2. Model selection results for recaptures-only survival probability estimates.[a]

Model	No. of parameters	$QAIC_c$	$\Delta QAIC_c$	Akaike weight
$\varphi_{(\text{time}\times\text{year}+\text{body})}p_{(\text{time}\times\text{year})}$[b]	43	2284.5	0.0	0.52
$\varphi_{(\text{time}\times\text{year})}p_{(\text{time}\times\text{year})}$	42	2284.6	0.1	0.48
$\varphi_{(\text{TravTime}+\text{habitat}\times\text{year}+\text{body})}p_{(\text{time}\times\text{year})}$[b,c]	28	2309.1	24.6	0.00
$\varphi_{(\text{TravTime}+\text{habitat}\times\text{year})}p_{(\text{time}\times\text{year})}$	29	2309.3	24.8	0.00
$\varphi_{(\text{distance}+\text{habitat}\times\text{year}+\text{body})}p_{(\text{time}\times\text{year})}$	28	2394.2	109.8	0.00
$\varphi_{(\text{distance}+\text{habitat}\times\text{year})}p_{(\text{time}\times\text{year})}$	29	2394.2	109.8	0.00
$\varphi_{(\text{TravTime}+\text{year})}p_{(\text{time}\times\text{year})}$	24	2441.7	157.2	0.00
$\varphi_{(\text{distance}+\text{year})}p_{(\text{time}\times\text{year})}$	24	2465.1	180.6	0.00

[a]AIC values are adjusted for small sample sizes and extra-binomial variation with $\hat{c} = 1.3325$.

[b]Time in models refers to segment- or line-specific probabilities, whereas TravTime is a group covariate and refers to average travel time of the population in a particular segment of the migration.

[c]Habitat in models means that the intercept between survival and either distance or travel time was allowed to differ in river and ocean segments. Models with an interaction term added so that the slope was also allowed to differ (TravTime×habitat and distance×habitat) were also tested, but these reduced AIC by less than 2, so the incorporation of the extra parameter was not supported.

Fig. 3. Survivorship relative to cumulative distance migrated for acoustically tagged Cultus Lake sockeye. Vertical bars represent 95% confidence intervals; 2004, ■; 2005, ◆; 2006, ▲; 2007, ▼. NSOG, northern Strait of Georgia; QCS, Queen Charlotte Strait.
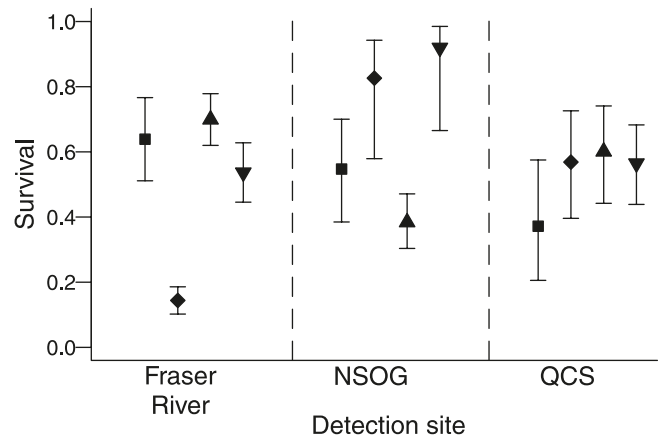

Fig. 4. Segment-specific survival estimates for acoustically tagged Cultus Lake sockeye from release to the lower Fraser River, lower Fraser River to northern Strait of Georgia (NSOG), and NSOG to Queen Charlotte Strait (QCS), 2004–2007. Vertical bars represent 95% confidence intervals; 2004, ■; 2005, ◆; 2006, ▲, 2007, ▼.
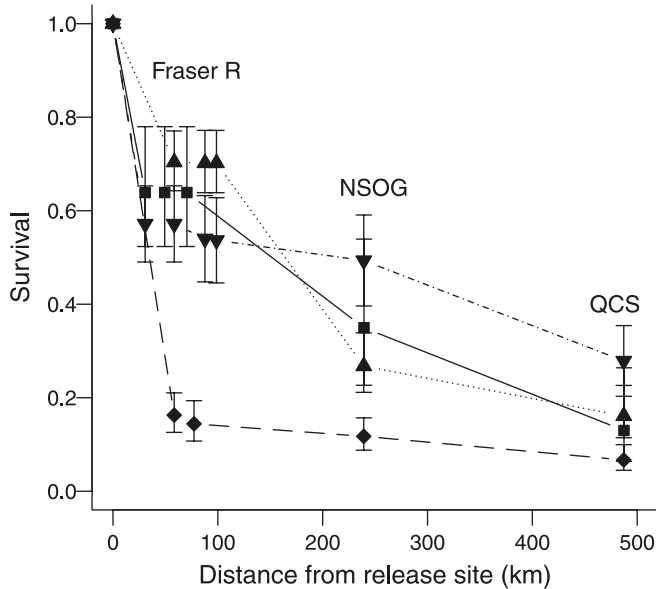
Results

Survival estimates

Model selection

Of the eight survival models evaluated across all years, the strongest support was found for two models: the fully time varying CJS model (with year- and segment-specific estimates); and the fully time varying CJS model that incorporated body size as an individual covariate (Table 2). These two models had essentially equal support, as seen in their Akaike weights. These models differed by a single parameter, so the small difference in AIC suggests little support for the larger model overall. However, when analyzed separately, 2004 and 2006 had somewhat more support for the model incorporating body size ($\Delta QAIC_c > 3$), so these models were both used for averaging the year-specific esti-

mates. The six models with migration distance or average travel time constraints had fewer parameters but had much poorer fits (as measured by the overall likelihood of each model), so had little support from the data within the model set.

Survival probability estimates

With each year analyzed separately, the model-averaged estimates of the top two models (Table 2) show decreasing survivorship over the first 500 km of the juvenile salmon migration (Fig. 3). The "low p" (or "high p") estimates reported show the estimated survivorship to exit from the Strait of Georgia system assuming that the value of p_{QCS} is set to the lower (or upper) 95% confidence interval of p_{NSOG} rather than the mean estimate (Fig. 2; see Materials and methods). Because this bounded range of survivorship estimates is relatively small (compared with yearly differences, for example), and because much mortality occurred before the final segment, our survivorship estimates appear to be fairly robust to uncertainty in p_{QCS}.

The 2005 cohort stands out with markedly lower mean

Table 3. Migratory behaviour categories for Cultus Lake sockeye in 2004 to 2007.

Migration behavior	2004	2005	2006	2007
North (direct)	21(21.0)	37 (9.8)	40 (20)	69 (34.5)
North through HS	9 (9.0)	6 (1.6)	13 (6.5)	8 (4.0)
South	0	2 (0.5)	0	6 (3.0)
Milling on NSOG	0	5 (1.3)	5 (2.5)	5 (2.5)
Milling on QCS				1 (0.5)
Milling on JDF		1 (0.27)		1 (0.5)
Milling on Fraser	0	0	10 (5.0)*	1 (0.5)
Residualization in Cultus Lake	Not surveyed	17 (4.5)	Not surveyed	12 (6.0)

Note: The first number in each column is the number of fish detected. The number in parentheses indicates the percentage of fish detected in relation to all fish released that year. Milling is defined as being detected either for >24 h on a line or (on Fraser River lines) downstream, upstream, and then downstream again. HS, Howe Sound; NSOG, northern Strait of Georgia; QCS, Queen Charlotte Strait; JDF, Strait of Juan de Fuca.

*Five of these 10 fish were detected downstream, upstream, then downstream again. Three of these five were subsequently heard on ocean lines and two were not; we suspect that these two tags may have been in seals. The remaining five fish were heard on a Fraser River line for >24 h (3 fish) or moved between subarrays within stations F or G (Fig. 1), thereby requiring upstream travel (2 fish).

Table 4. Residualization and initial downstream migration surveys of Cultus Lake and the rivers that connect it to the Fraser River.

Detection year	Tag year	Cultus Lake	Sweltzer Creek	Vedder River	Lower Vedder Canal	Lower Sumas River	Fraser River
Mobile surveys							
2005	2005	13	NA	0	0	2	0
2007	2005	6	0	0	0	0	NA
	2007	NA	NA	NA	NA	NA	NA
Number of 2005 tags heard in both years							
		NA	5	NA	0	0	0	NA
Additional tags heard in DFO survey (not heard in either mobile survey)							
2007	2005	7	NA	NA	NA	NA	NA
	2007	12	NA	NA	NA	NA	NA

Note: NA, not applicable. Sweltzer Creek was not surveyed in 2005, and the Fraser River was not surveyed in 2007.

survival (0.12) compared with the other years, especially in the freshwater component of the migration where survival was less than one-third that of the other years (0.5–0.7). Taken across all years, mean survivorship to the northern Strait of Georgia ranged from 0.1 to 0.5, whereas survivorship to the final line in Queen Charlotte Strait ranged from 0.07 to 0.28 (Fig. 3).

Survivorship to the outer lines was probably underestimated in 2006 and possibly in 2007. Smolt tags in 2006 were programmed to shut off between 1 and 4 June (and to begin retransmitting 2 years later during the adult return migration), but some surviving outbound smolts may not have crossed the QCS line before the tag's transmissions were stopped. The mean date of first crossing the QCS line was 25 May (0216 hours), but a few fish ($n = 3$) were still detected on 1–2 June. The likelihood that a few fish crossed the line after their tags were turned off is also supported by the date of crossing the NSOG line: the mean crossing date was 8 May (1052 hours) for fish that were detected on QCS ($n = 30$), and 10 May (2311 hours) for fish not detected on QCS ($n = 24$). Individuals late in crossing the NSOG line thus also tended to be the individuals not detected on QCS. Similarly, tags in 2007 were programmed to shut off around 27–28 June, and a few fish were still detected on the QCS line between 20 and 25 June. Thus, some slower-moving smolts could have crossed the QCS line undetected; four of

the five tags last detected on the NSOG line (between 10 and 17 June) were not detected on the QCS line. However, the potential effect of a premature shutdown of active transmission is likely to have little effect on the overall estimate of survival to QCS, as the majority of detected animals reached the QCS line at least 2 days prior to tag shutdown (27 of 30 detected survivors in 2006; 43 of 44 detected survivors in 2007).

Segment-specific survival estimates (Fig. 4) provide a way to directly assess Cultus Lake smolt survival in various segments of their migration path. The markedly lower freshwater survival in 2005 stands out. However, the 2005 cohort had relatively early high marine survival, indicating that the reduced survival observed in freshwater did not persist in the ocean. The Fraser–NSOG segment survival for 2006 indicated significantly lower marine survival (despite high freshwater survival that year) compared with both the 2005 and 2007 cohorts. There were no marked trends in marine survival within the NSOG–QCS segment other than the slightly lower (and more uncertain) value measured in 2004, and there was considerable overlap in all 95% confidence intervals.

Our reported survival estimates depend on the simultaneously estimated detection probabilities at the various subarrays (or listening lines) that we deployed. Detection probabilities on individual receiver lines in the Fraser River

Fig. 5. Distribution of migrating acoustically tagged Cultus Lake sockeye on the northern Strait of Georgia lines: (*a*) 2004; (*b*) 2005; (*c*) 2006; (*d*) 2007. Each numbered bar represents a receiver in the line. If a fish was heard on multiple receivers, that individual's detection was allocated equally across all receivers on which it was detected. The 0% above receiver 8 in 2004 indicates that this receiver was not operational during the time when the fish were crossing the line. Receiver 23 in 2007 was not recovered.
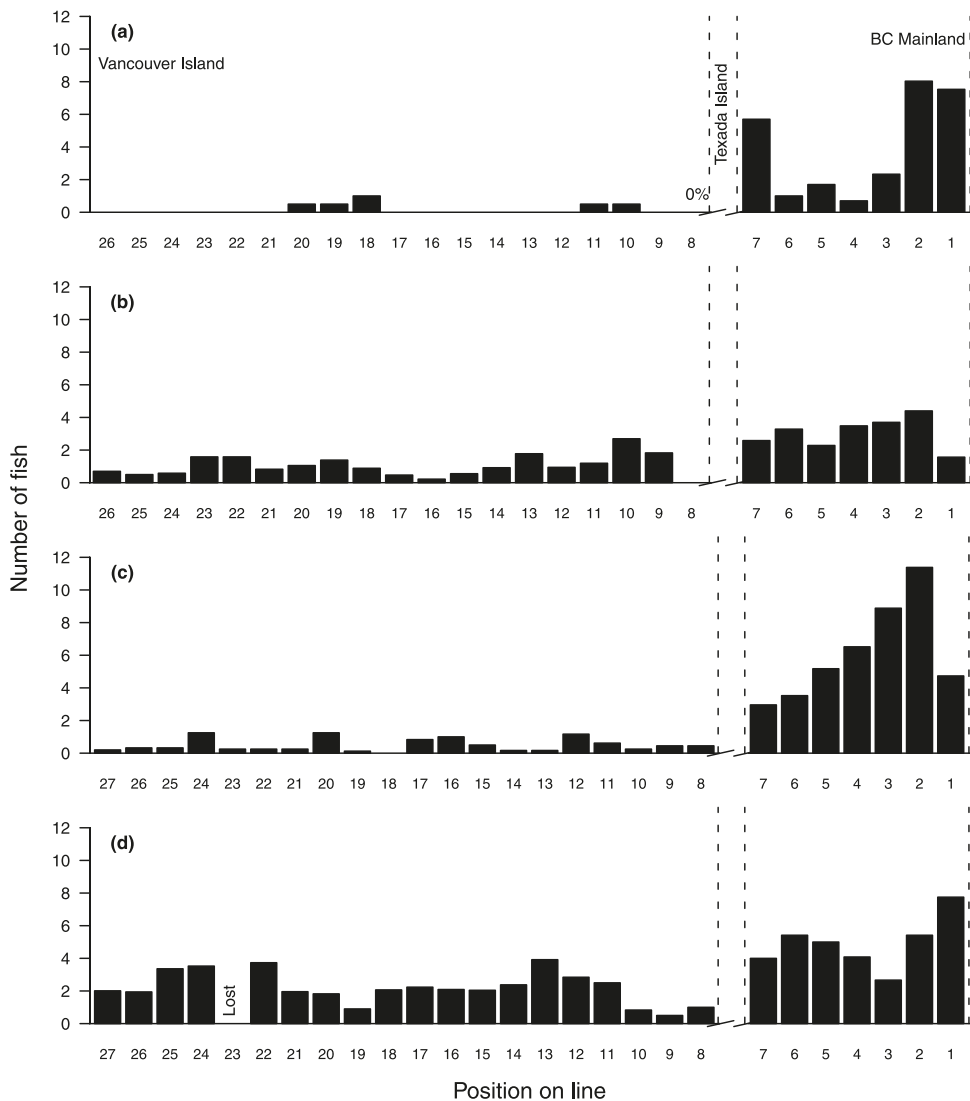
(p_i) ranged from 14% to 98% across all years (average of 64%). Taking the product of $(1 - p_i)$ for all Fraser River lines in each year results in the probability of a smolt crossing all Fraser lines without being detected (Melnychuk et al. 2007). This value (2004, 0.7%; 2005, 23%; 2006, 0.03%; 2007, 7.8%) is the nondetection rate for the Fraser River subarray as a whole; thus, in most years, aggregated detection probabilities for the lower Fraser River subarray exceeded 90%. Detection probabilities on the NSOG line averaged 90% (range 85%–93%). As discussed earlier, this value was assumed for the QCS–JDF lines, as the geometry of these subarrays is very similar.

Migration behaviour

Cultus Lake sockeye displayed four predominant migratory behaviours (Table 3). Northward migration in the ocean was the most common behaviour observed, which accounted for 9.8%–34.5% of all released fish each year. These fish

migrated quickly out of the Fraser River and then had a directed migration crossing the NSOG and QCS lines. Migration north but first entering Howe Sound prior to heading across the two northern lines of NSOG and QCS occurred in 1.6%–9% of all released fish each year. Only eight fish, two (0.5% of released fish) in 2005 and six (3% of released fish) in 2007, were ever detected swimming south from the Fraser River (Table 3). However, it should be noted that one-third of the receivers on the JDF line were lost in 2004, so it is possible that some fish migrated south through these gaps and were not detected in 2004. Two of the six fish crossing the JDF line in 2007 were also detected later on the Lippy Point line (Fig. 1). There was some evidence of fish milling within the Fraser River and in the vicinity of ocean lines (Table 3).

Some tagged fish moved upstream after release in Sweltzer Creek into Cultus Lake (Tables 3 and 4) during both of the years in which freshwater surveys were conducted (4.5%

Fig. 6. Distribution of migrating acoustically tagged Cultus Lake sockeye on the Queen Charlotte Strait line: (*a*) 2004; (*b*) 2005; (*c*) 2006; (*d*) 2007. Each numbered bar represents a receiver in the line. If a fish was detected on multiple receivers, that detection was allocated across all receivers on which it was detected. The 0% above receivers 22 and 23 in 2007 indicates that these receivers were not operational during the time when the fish were crossing the line. Receiver 24 in 2006 was not recovered.
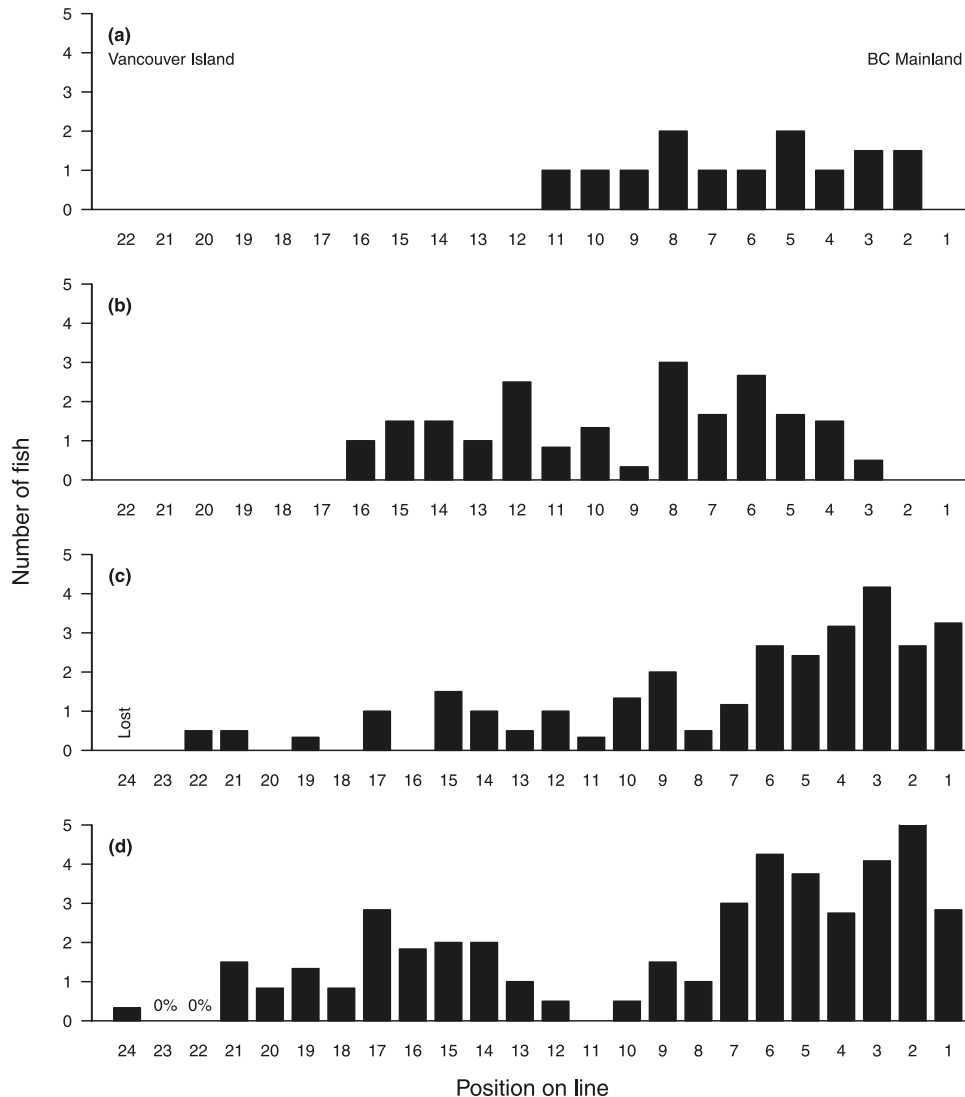
in 2005 and 6.0% in 2007). After this initial upstream movement, fish could have remained within Cultus Lake without migrating out of freshwater, died in the lake, or shed their tags in the lake. Four of the 12 fish detected in the 2007 surveys were detected at the same stations as in 2005, which suggests that these were probably tags lying on the lake bottom. It is unclear whether the tags only detected on a single survey were present in moving (and therefore surviving) sockeye, but this seems likely for at least some tags.

Distribution across receiver curtains

Because POST lines in the Strait of Georgia are bordered by land on both sides and because detection probabilities were high in all years, it was possible to explore the distribution of migrating smolts at sea and establish whether fish had preferred "migration highways". Smolts crossing the NSOG line (Fig. 5) showed a marked preference for the mainland route east of Texada Island in 2004 and 2006 ($p <$ 0.001) when compared with a uniform distribution across all receivers on the line (i.e., each receiver treated as a separate category in the χ^2 analysis). This preference was not evident in 2005 and 2007 ($p >$ 0.37). When fish were grouped according to whether they migrated on the east versus the west side of Texada Island (two categories; Texada Island splits the NSOG line into two sections), they showed a significant preference for the eastern channel (all years analyzed separately, $p \leq$ 0.001).

The distribution of smolts crossing the QCS line (Fig. 6) was not significantly different from uniform when each receiver was treated as a separate category in the χ^2 analysis (2005–2007 years tested separately, $p >$ 0.24; 2004 insufficient data). However, when the detections on neighbouring receivers were aggregated together (i.e., extending the spatial area and reducing the number of categories), the χ^2 tests became increasingly significant as the area of aggregation increased (Fig. 7). Fish showed significant preference for the eastern side of the Strait in 2004, 2006, and 2007 ($p =$ 0.04, $p <$ 0.001, $p =$ 0.002, respectively, over a 3.2 km extent) and

near-significant selection for the eastern–central channel in 2005 ($p = 0.11$).

A correlation analysis showed no relationship between where individuals crossed the NSOG line (estimated as the average distance from the B.C. mainland) and where they crossed the QCS line 240 km to the north ($r^2 = 0.04$–0.2; 2004–2007).

Travel rate and swimming speeds

Cultus Lake smolts exited the Fraser River in <6 days. The later-released fish in 2005 and 2007 travelled faster, with mean times to the river mouth of 4.1 and 4.0 days, respectively. The earlier-released fish in 2004 and 2006 took slightly longer to reach the river mouth (5.6 and 5.0 days, respectively). There was no clear pattern with release date and time taken to exit the Strait of Georgia across the QCS line. Average times from release to reaching the QCS line ranged from 25.6 to 34.1 days.

Travel rate was variable among years and for different sections of the migration route, with mean values ranging between 5 and 30 km·day^{-1} (Fig. 8; 0.46–1.8 body lengths (BL)·s^{-1}). Fish tagged in 2004 had the slowest migration rate in the Fraser River, with a mean speed of 15.5 km·day^{-1}. However, these fish had the fastest mean swimming rate in the marine sections when swimming directly to both the NSOG and QCS lines. The 2007 cohort had the fastest rate of movement out of the Fraser River (25.8 km·day^{-1}) but relatively slow rates in the ocean segment from the river mouth to either HS or NSOG. In most years, travel rates in the NSOG to QSC segment were faster than in other segments, around 26 km·day^{-1}.

Discussion

Survival

A significant constraint on salmon conservation and management is our poor understanding of mortality during different life-history stages after leaving freshwater. Poor marine survival has been implicated for the drastic decline of many salmon (McKinnell et al. 2001; Beamish et al. 2004; English et al. 2008) and steelhead (Ward 2000; Welch et al. 2000) stocks in southern B.C. This study presents a first step in monitoring both freshwater and early marine survival of endangered Cultus Lake sockeye during the initial stages of migration.

Survival rates during the freshwater migration phase were relatively stable among the years studied, at 50%–70% of migrating smolts (except 2005, when survival was <20%, possibly because of the very late release). However, given the relatively short distances that must be travelled to the mouth of the Fraser River (≤100 km), the short duration of the freshwater migration, and the absence of obvious impediments to travel such as dams, the specific survival levels observed are surprisingly low. Our results do seem consistent with freshwater survival estimates for other west coast salmon populations: Keogh River steelhead, 75% (Welch et al. 2004); Cheakamus River steelhead, 80% (Melnychuk et al. 2007); Thompson River steelhead, 30%; Thompson River Chinook, 23%; Snake River steelhead, 18%; and Snake River Chinook, 25% (Welch et al. 2008). The higher survival estimates are seen for smolts travelling much shorter

Fig. 7. Significance of a series of χ^2 goodness-of-fit tests obtained by grouping fish detected on neighbouring receivers. For spatial aggregations > 3 km (i.e., aggregating the data from four or more adjacent receivers), statistical support for significant spatial pattern on the Queen Charlotte Strait subarray is evident. 2004, ■; 2005, ◇; 2006, △; 2007, ▼.
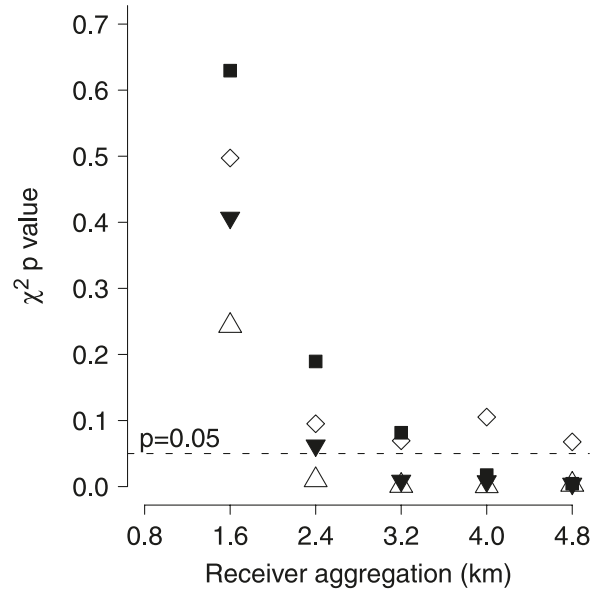

distances to the sea (ca. 0.3–16 km), and the lower survival estimates are for smolts travelling much farther to the sea (ca. 300–900 km); the Cultus sockeye results generally fall in the middle of this range.

Several factors may have caused the high freshwater mortality observed in 2005. First, these hatchery-reared fish were released much later than in other years because a power failure killed almost all of the smolts that were originally implanted (Kintama Research Corp. 2005). Later release times have been associated with poorer survival in other studies (Bilton et al. 1982), and the lower water levels in Sweltzer Creek during June compared with May might make the fish more susceptible to predators. (Three smolts were observed being taken immediately by birds after release that year.) Second, a fence normally sited in Sweltzer Creek to reduce the frequency of fish migrating back up into Cultus Lake was removed on 1 June 2005, which meant that some smolts could have migrated back upstream (however, the lake survey in 2005 revealed similar levels of residualization as in 2007 when the fence was in place).

Marine survival rates were also stable across years (including 2005) and were consistent with survival estimates for the nearby Cheakamus River steelhead (Melnychuk et al. 2007). The 2005 sockeye smolt outmigration year resulted in exceptionally poor adult returns coastwide in 2007 (Fisheries and Oceans Canada (DFO) 2008); however, our results for 2005 do not show a substantial difference between years in early ocean survival in the Strait of Georgia (SOG), which is consistent with independent information provided by a DFO SOG trawl survey for juvenile salmon (DFO 2008, p. 13). This could be explained by several possibilities. First, the SOG may have been insulated from events occurring more broadly on the west coast and thus higher mortality at sea could have occurred later, beyond

Fig. 8. Average travel rates for different sections of the migration route. Vertical bars represent 95% confidence intervals. 2004, ■; 2005, ◆; 2006, ▲; 2007, ▼; HS, Howe Sound; NSOG, northern Strait of Georgia; QCS, Queen Charlotte Strait.
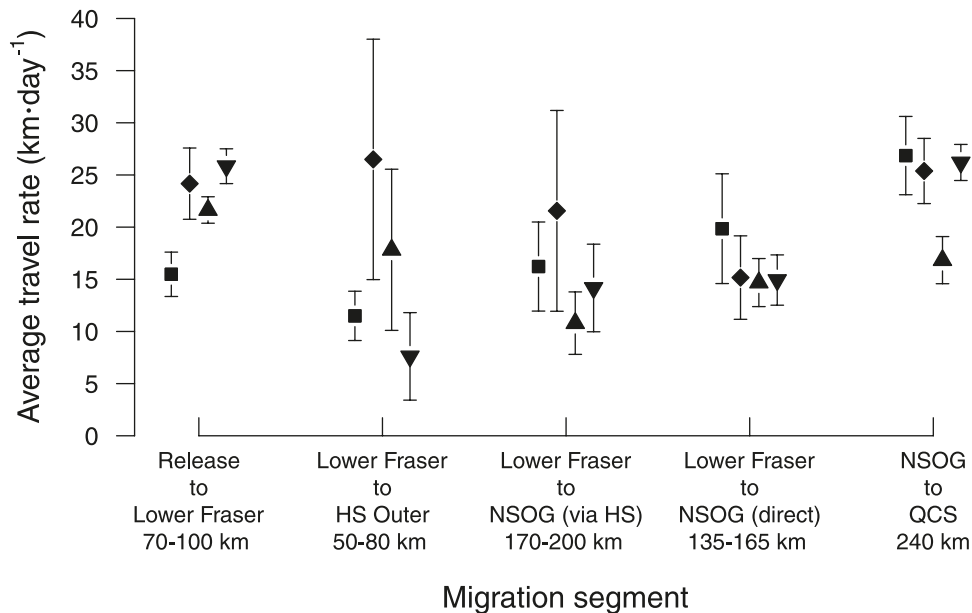
the SOG. Second, the low abundances of salmon smolts in the ocean in these other regions could also have been the result of poor downstream survival in other natal rivers. Third, the relatively high survival of Cultus Lake sockeye smolts through the Strait of Georgia system in 2005 may have been the result of the fittest individuals surviving the high freshwater mortality phase and thus migrating through the Strait of Georgia with relatively high survival.

Overall, survivals showed a relatively steady attrition with distance and do not indicate particular areas of higher mortality at the spatial resolution of this study. Unfortunately, we have no comparable data on baseline survival rates for the earlier period of much better adult returns that occurred prior to the deployment of POST in 2004.

It should be noted that the survival estimates presented here using the pilot phase of the POST array might not accurately represent survival in the overall Cultus Lake sockeye population. We sampled smolts that were about 50% longer than wild free-ranging smolts to accommodate the V9 acoustic tags that the "first generation" POST array was originally designed around in 2003. As salmon survival scales positively with size when considered over a wide range of sizes (McGurk 1996, 1999), we would expect that the survival of the wild (smaller) smolts to be potentially lower than what we measured here.

The survival estimates presented here may also be biased as a result of two confounding factors. First, total survival estimates reported for 2005 and 2007 are biased high as a result of overestimating survival in the segment from the river mouth to NSOG, due to the confounding factor of small numbers of fish swimming south after ocean entry in those years. However, as noted earlier, this bias is expected to be minor as only two fish were detected migrating south through Juan de Fuca in 2005 and only six fish were detected in 2007. Second, survival is actually a joint estimate of the probability of migration and survival. Residualization (nonmigration) in freshwater (either Cultus Lake or the

streams and rivers leading to the Fraser River mouth) is confounded with mortality during the downstream migration, so our reported survival estimates are biased low to some degree. However, the surveys carried out in 2005 and 2007 suggested a relatively low minimum residualization rate of between 5% and 6% of all tagged fish.

Migration highways

The POST lines (particularly those between the mainland and Vancouver Island) provide a unique means to identify whether salmon have preferred migration routes or "highways". Limited evidence suggests that specific "marine highways" may be as common under the ocean (e.g., Atlantic cod off Newfoundland; Rose 1993) as they are observed to be on land for mammals and birds. Our results for Cultus Lake sockeye confirm the importance of the Johnstone Strait migration pathway proposed for migrating juvenile Fraser River sockeye by Groot and Cooke (1987). These authors found that smolts predominantly move north in a directed migration with a preference for staying to the east side of the Strait of Georgia and Johnson Strait. Our results further extend the persistence of this migratory preference to Queen Charlotte Strait, some 500 km from the release site. As in our study, Groot and Cooke (1987) also found that Fraser River sockeye enter Howe Sound. The ecological reason for these migration routes in some years is unclear, as are the reasons for the interannual variation in saltwater distribution that we have documented with the array.

Cultus Lake sockeye displayed relatively rapid, directed movement once they commenced their downstream migration with little evidence of milling. Earlier work on sockeye salmon calculated average freshwater migration speeds of between 5.1 and 7.8 km·day^{-1} in lakes but up to 40 km·day^{-1} in the Columbia River (Burgner 1991). Our results indicated travel rates of between 15 and 25 km·day^{-1} for Cultus Lake sockeye. Obviously, river flow is an important influence on

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travel rate, although the results show that sustained travel rates of 10–30 km·day^{-1} were also achieved in the marine inshore environment. Thus continued rapid migration occurred without the influence of river flow. The faster downstream migration observed in 2005 and 2007 is likely related to release time, as river flow generally increases later in the season, exposing the 2005 and 2007 cohorts to greater stream flows.

The mean swimming speeds of Cultus sockeye smolts of 0.5–1.8 BL·s^{-1} in both freshwater and marine environments is comparable with results from acoustic tracking studies on other salmonids. Freshwater and marine swimming speeds of steelhead trout in southern British Columbia waters were found to be between 0.5 and 2.0 BL·s^{-1} (Welch et al. 2004; Melnychuk et al. 2007). In western Atlantic waters, Thorstad et al. (2007) recorded swimming speeds of 0.53 and 0.56 BL·s^{-1} for wild and hatchery Atlantic postsmolts, respectively (but only 0.06 BL·s^{-1} for brown trout postsmolts) in a Norwegian fjord.

The POST array

Our work represents the first direct estimates of survival and movement rates of sockeye (*Oncorhynchus nerka*) smolts during the freshwater and early marine phases of the migration period and demonstrates the utility of large-scale telemetry arrays for monitoring smolt migrations over repeated years. Acoustic technology, properly implemented, provides an essentially seamless monitoring system covering both freshwater and marine environments. It is thus possible to study salmon smolt migrations along the full length of their migration along the continental shelf as they move out of their natal stream. The POST array provides a level of resolution not previously available in marine studies and allows us to specify the speed, directionality, migration routes, and survival of tagged smolts with substantial precision even when using modest numbers of tagged smolts. Pinpointing areas of potentially elevated levels of mortality is of particular relevance to endangered stocks of salmon, as this can help direct research towards the most relevant parts of the life history.

The results from this study demonstrate that it is technically feasible to measure survival in both large river and coastal marine environments. Further miniaturization of the tags now allows smolts in the 100 mm TL range to be tagged, but at a substantially increased cost for operating an array of equivalent detection efficiency and thus statistical precision. However, a key point is that technical advances will thus likely allow future array designs to be extended to smaller fish and potentially resolve some of the limitations associated with only tagging larger smolts.

In summary, our study provides useful new data on Cultus Lake sockeye smolt migration and mortality during an important life-history period when the transition occurs from freshwater to marine life. The development of baseline data for salmon stocks can assist with managing them under climate change, not just by monitoring changes in survival, but also by allowing the formal testing of experimental hypotheses about the factors controlling salmon abundance. The POST array concept also provides a useful demonstration of the potential of continent-scale acoustic arrays for simultaneously monitoring a wide range of marine species for conservation and management. Such a concept is now being developed worldwide in the global initiative of the Ocean Tracking Network, which is establishing acoustic lines and arrays at strategic locations around the world (O'Dor et al. 2007). Developments like those reported here will help to incorporate biological observations into broader global ocean-observing systems.

Acknowledgements

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