The Residence Time of Juvenile Fraser River Sockeye Salmon in the Strait of Georgia

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ARTICLE

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Abstract

Mortality in the early marine period in a particular habitat is related to the severity of the factors causing mortality and the time that juvenile Pacific salmon *Oncorhynchus* spp. spend in the habitat. Juvenile sockeye salmon *O. nerka* produced in the Fraser River rear in the Strait of Georgia immediately upon leaving freshwater. We used catches from trawl and purse seine surveys to develop two estimates of their average residence time in the Strait of Georgia and present a third estimate which pertains to Chilko Lake smolts in particular. The average time between the entry of the last 1% of juvenile sockeye salmon into the Strait of Georgia and the departure of the last juveniles was 54 d. The average time between the point when the maximum number of juvenile sockeye salmon entered the Strait of Georgia and the point when the maximum abundance in the strait occurred was 43 d. Individuals from the Chilko Lake population were shown to spend a minimum of 31–43 d in the Strait of Georgia, indicating that an average residence time of about 43–54 d is plausible.

The fishery for Fraser River sockeye salmon *Oncorhynchus nerka* is probably the most important fishery on Canada's Pacific coast because of its combined social and economic effects. The catch of Fraser River sockeye salmon is shared with the United States, as some returning adults move through U.S. waters before entering the Fraser River (Figure 1). The United States and Canada established an international commission in 1937 (Roos 1991) to ensure that fishing was sustainable and to provide information that could be used to apportion the catch between the two countries. Since 1937, there have been many issues and challenges in managing the fishery, culminating in 2009 when the lowest adult return in recorded history surprised everyone. It was apparent that survival in the ocean was poor, as the number of smolts entering the ocean in 2007 was exceptionally large (Beamish et al. 2012, this volume; Thomson et al. 2012, this volume) and these individuals would have primarily returned to spawn in 2009.

Relatively little attention has been paid to the early marine life history of sockeye salmon from the Fraser River (Foerster 1968; Burgner 1991). This paucity of attention reflected the belief that freshwater processes and mortality from fishing were the major influences on sockeye salmon production. As a consequence, there was relatively little information about the early marine life history of Fraser River sockeye salmon with which to assess the reasons for the poor return in 2009.

Studies of Pacific herring *Clupea pallasii* and other species of Pacific salmon *Oncorhynchus* spp. in the Strait of Georgia showed that there was exceptionally poor survival and growth (Beamish et al. 2012; Thomson et al. 2012) in the spring of 2007, when most sockeye salmon returning in 2009 entered the ocean as juveniles. It was likely that extremely anomalous ocean conditions in the Strait of Georgia in 2007 affected the growth and survival of Pacific herring, coho salmon *O. kisutch*, Chinook salmon *O. tshawytscha*, and chum salmon *O. keta*
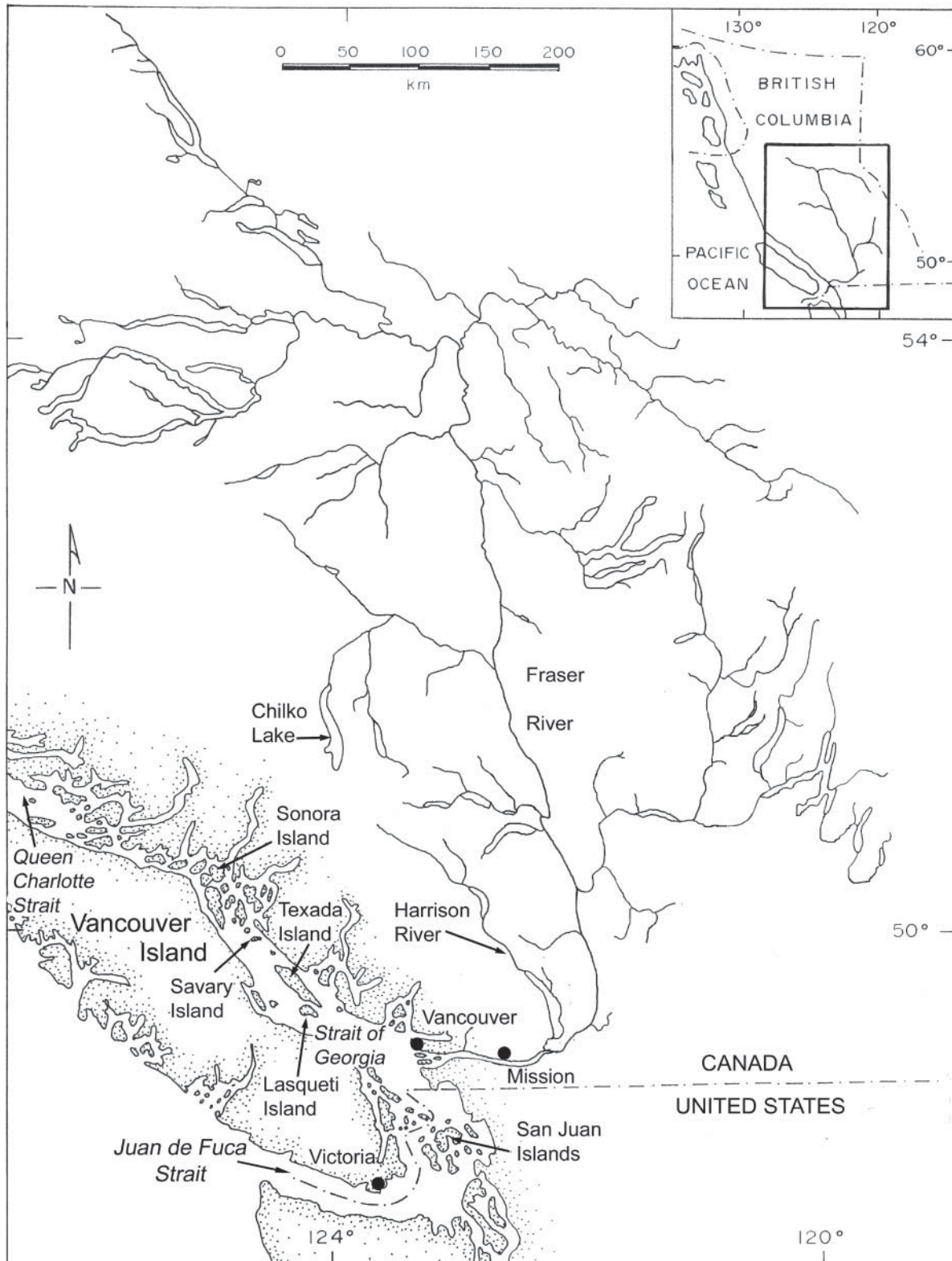
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FIGURE 1. Map of British Columbia showing the Fraser River watershed and places named in the article.

(Beamish et al. 2012) and thus that these conditions would also affect juvenile sockeye salmon. The anomalous conditions consisted of high rainfall and river runoff combined with low hours of sunshine and low surface salinity. Delayed changes to summer wind patterns also resulted in the retention of these low-salinity waters in the strait (Thomson et al. 2012). Because the residence time of juvenile sockeye salmon in the Strait of Georgia was uncertain, it was not known whether they were exposed to the anomalous conditions long enough to be affected in the same way as the other species. Thus, an estimate of average residence time was necessary to determine the reasons for the poor marine survival of the Fraser River sockeye salmon smolts that entered the Strait of Georgia in 2007. The objective of this study was to use catches from trawl and purse seine surveys for juvenile sockeye salmon in the Strait of Georgia and counts of sockeye salmon smolts in the Fraser River to estimate the average residence time of juvenile sockeye salmon in the Strait of Georgia.

Residence time can refer to the time that any particular juvenile Pacific salmon spends in the Strait of Georgia or any other habitat. However, for a species that migrates out of the strait there needs to be a clearer understanding of residence time, especially as it pertains to populations. A few studies have estimated the residence time of sockeye salmon juveniles in the Strait of Georgia, but no strict definitions are employed by any of these (Groot and Cooke 1987; Peterman et al. 1994; Welch et al. 2009). In these studies, it is implied that residence time is the time the average sockeye salmon juvenile spends migrating through the Strait of Georgia. The results from historical field research suggest a residence time of 25–34 d, whereas modeling estimates yield a wider range of 14–38 d (Table 1). Concepts of residence time do exist for freshwater, but these have tended to focus on relatively limited geographic scales and employ mark–recapture techniques, e.g., English et al. (1992) and Manske and Schwartz (2000). Estimates of residence time derived from tracking individuals implanted with acoustic tags have been produced for Atlantic salmon *Salmo salar* in a fjord (Dempson et al. 2011). Similar research has been conducted in the Strait of Georgia with sockeye salmon juveniles (Welch et al. 2011). However, the size of the acoustic tags makes them suitable only for juveniles that have matured for two winters in freshwater after fry emergence. The vast majority of emigrating

juvenile sockeye salmon migrate to the ocean 1 year earlier (Hume et al. 1996; Bradford et al. 2000) and are too small to be acoustically tagged. Because of the large relative area of the Strait of Georgia and the lack of marking data, other methods were required to estimate the residence time of sockeye salmon juveniles in the strait. The definition of residence time should consider that there are ocean entry dates, ocean exit dates and maximum abundance dates. Ocean entry and exit dates should relate to the movement of a percentage of the population to avoid the outlier effects of early and late migrants. We proposed two definitions of average residence time according to the data available. In one analysis, we considered the dates for the portion of the population that was last to enter the Strait of Georgia and the last to leave. We also considered the span of time between the date of maximum abundance in the strait (the day when the largest number of juvenile sockeye salmon were in the Strait of Georgia, as determined from trawl survey data) and the date when the maximum number entered the Strait of Georgia (as determined from smolt count data at Mission, about 60 km upstream from the mouth of the Fraser River). Our definitions were developed to use existing data from transects across the northern Strait of Georgia each day from about mid-May to mid-July. The maximum of a distribution of a standardized daily catch would be the maximum abundance date. There may also be components of the population that have different behaviors and life history strategies. For example, larger and older smolts which enter the marine environment after two winters in freshwater, after fry emergence, may migrate faster out of the Strait of Georgia, resulting in shorter average residence times than for other juveniles. Thomson et al. (2012) noted that the juvenile sockeye salmon that migrated earlier into Hecate Strait were consistently larger fish.

METHODS

The data used in our analysis were derived from four sources: trawl surveys of juvenile salmon in the Strait of Georgia conducted between 1997 and 2010 (Beamish et al. 2012), purse seine surveys conducted on juvenile salmon in the Strait of Georgia in 2011, sockeye salmon smolt migration timing past Mission, British Columbia (Figure 1) from 1998 to 2008 (D. Patterson, Fisheries and Oceans Canada, personal communication), and counts of sockeye salmon smolt migration from Chilko Lake (Figure 1) during 1986–2011 (T. Cone, Fisheries and Oceans Canada, personal communication). Descriptions of the juvenile salmon trawl survey program and sampling protocols are outlined in Beamish et al. (2000) and Sweeting et al. (2003). The intermediate section of the net had meshes ranging from 20 to 160 cm, and the cod end mesh was 10 cm with a 1-cm liner. Data from the 2011 purse seine survey were collected from May 18 to May 31. The purse seine was 280 m long and 9 m deep. The net was fished from the commercial fishing vessels *Ocean Venture* and *Franciscan* with set locations selected

TABLE 1. Estimates of residence time obtained by previous studies. Note that the estimate for Groot and Cooke (1987) is not explicitly stated in their paper but is calculated as their estimated swimming speed (6–7 km/d) divided by the approximate distance from the mouth of the Fraser River to the northern limit of the Strait of Georgia.

Source	Estimate of residence time (d)
Welch et al. (2009)	25.6–34.1
Peterman et al. (1994)	14–38
Groot and Cooke (1987)	25.7–30
Healey (1980)	20–30

TABLE 2. Daily average CPUE for sockeye salmon juveniles in the Strait of Georgia trawl surveys, 1997–2010. The mean daily CPUE for the entire period is shown in the far right column; it was calculated by summing all CPUE estimates by set for each day and then dividing by the total number of sets available across years.

Date	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	Mean
Jun 27												150.4	22.0		137.6
Jun 28												76.0	135.3		105.6
Jun 29												97.0			97.0
Jun 30		25.8	2.0									33.8	183.0		59.0
Jul 1		14.0	121.4									0.5	62.6		51.8
Jul 2		28.0	49.3			11.0						33.1	41.1		35.7
Jul 3		67.5	12.9			4.6						9.1	16.9	9.3	16.0
Jul 4		6.5	0.6			5.0		574.6				0.6	5.7	6.0	90.7
Jul 5		6.7	0.3			19.3		4.6					6.7	1.4	6.7
Jul 6	1.3	0.3	1.1			3.3		20.5				2.4	4.0	7.7	5.9
Jul 7	2.0	0.0	12.3		99.0			17.3					1.0	4.4	28.9
Jul 8	8.0	0.0	1.4		16.9	3.8		16.0			3.6			2.0	6.8
Jul 9	3.7	92.0			58.3	10.0		8.8		4.0	3.7			0.6	19.0
Jul 10				0.0	9.3	2.3		13.0			2.2			8.8	6.4
Jul 11					12.0	0.3		0.5		0.3	6.9			13.0	4.2
Jul 12					3.1			4.5		9.7	3.7			2.7	4.8
Jul 13			11.7	21.7				2.0		0.3	0.3				7.5
Jul 14			11.4	25.5					9.1	9.7	0.6				9.9
Jul 15			10.8	36.0					1.8	0.0	0.0			4.0	12.3
Jul 16			1.7						20.0	19.5					15.1
Jul 17			2.7						10.6						7.4
Jul 18			24.7						6.9						15.8
Jul 19			0.0						15.4	0.3					5.8
Jul 20			1.0						11.7	0.0					5.5
Jul 21									0.9						0.9

throughout the Strait of Georgia. The length measurements in all samples were fork lengths.

One definition of average residence time for sockeye salmon in the Strait of Georgia was the time between the last smolts exiting the Fraser River and the last exiting the Strait of Georgia. We determined the last exit date using a linear fit to the daily average CPUE values for each juvenile salmon trawl survey year. The date at which the line crossed the x-axis in a given year was the exit date for that year (Table 2). We transformed the catch data into catch per unit effort (CPUE) by standardizing trawl set durations to 1 h (i.e., catch per hour of effort). We used the resulting declining trend of these average daily CPUEs for each year to estimate the exit dates of juvenile sockeye salmon from the Strait of Georgia. Although there were high catches at the end of the surveys in 1998 and 2001, these observations were not included in the calculation of the mean exit dates.

In order to calculate the date at which juvenile sockeye salmon entered the strait we used counts of sockeye salmon smolts sampled by a smolt trap at Mission in the lower Fraser River. These count data were converted to a cumulative form using the summed proportion of the population that had entered the strait, as indicated by a logistic growth curve

$\text{Sum}_d = [k \cdot (P_0 \cdot e^{r \cdot d})] / [(k + P_0 \cdot e^{r \cdot d}) - 1];$

Sum_d = total population past Mission on day n;

k = maximum value of the logistic curve, i.e., 100% of the population;

r = the rate of increase in abundance;

P_0 = starting number, i.e., approaching zero; and

d = time in days.

The cumulative proportion of migrating smolts that had exited the Fraser River and entered the Strait of Georgia daily was estimated with Microsoft Excel Solver to minimize the sum of squared differences between the observed and predicted daily cumulative abundances by optimizing r and P_0 with k set to 100, i.e., 100% of the fish being in the strait. This methodology was used to estimate the time required for the smolts to migrate past Mission in a typical year by fitting logistic curves to individual years of available data (1998, 2000, 2002, 2004, 2006, and 2008). The smolt trap was operated only in even-numbered years, as the principal objective of the sampling was to estimate the abundance of migrating pink salmon *O. gorbuscha* juveniles, and juvenile pink salmon migrate downstream in the

Fraser River only in even-numbered years. Because the logistic fit to the data asymptotically approaches 100, we used the date at which 99% of smolts had passed Mission from the fitted data as the date the "last" smolt had entered the Strait of Georgia.

To determine the Fraser River exit date (at a point downstream from Mission), we lagged the cumulative passage of smolts past Mission by 1 d. A model developed by Crittenden (1994) suggested that a total migration time of 7 d was required for smolts to travel from Chilko Lake in the middle portion of the drainage to the mouth of the Fraser River. Because the distance from Mission to the mouth of the Fraser River represents one-seventh of the distance, we reasoned that 1 d should elapse between a smolt moving past the Mission site and leaving the river.

Another definition of average residence time was the time between the average date of maximum juvenile abundance at the Mission site (plus 1 d) and the average date of estimated maximum smolt abundance in the Strait of Georgia. In both 1997 and 2010, we conducted a portion of our trawl surveys in the Strait of Georgia in early May, when juvenile sockeye salmon began entering the Strait of Georgia. We used the data from these two surveys to estimate a maximum CPUE date in the Strait of Georgia. This maximum CPUE date was compared with the date at which the maximum number of smolts was estimated to have entered the Strait of Georgia. The long-term average was used because the trap at Mission was not operated in 1997 and data were not available for 2010.

DNA analysis (Beacham et al. 2005) was used to identify sockeye salmon smolts from Chilko Lake in the 2008 and 2009 trawl surveys. As the estimated transit time from Chilko Lake to the Strait of Georgia is 7 d (Crittenden 1994) and the dates of leaving the lake are known, we were able to estimate the exit times of the Chilko Lake population from the Fraser River. Using DNA analysis and the dates when Chilko Lake juveniles were collected in the Strait of Georgia, we identified the number of days that they had been resident in the Strait of Georgia.

RESULTS

Residence Time Using Exit Dates from the Fraser River and the Strait of Georgia

The daily average CPUE typically declined during the trawl surveys (Table 2; Figure 2). The trend in the long-term average daily CPUE was very similar to a negative logistic curve ($R^2 = 0.84$). Linear trend analysis of annual daily CPUEs (Table 2) indicated that CPUE values of 0 occurred between July 4 and July 22, with a mean date of July 12 (Figure 2). Because the estimated date of 0 CPUE was highly correlated to the dates on which the survey was conducted, the overall mean of July 12 was used as the exit date for all years in subsequent analysis, with July 4 and July 22 constituting the minimum and maximum dates.

Observed smolt abundances at Mission indicated that the migration period occurred over 4–5 weeks (Figure 3). The average maximum daily abundance at Mission occurred on May 4
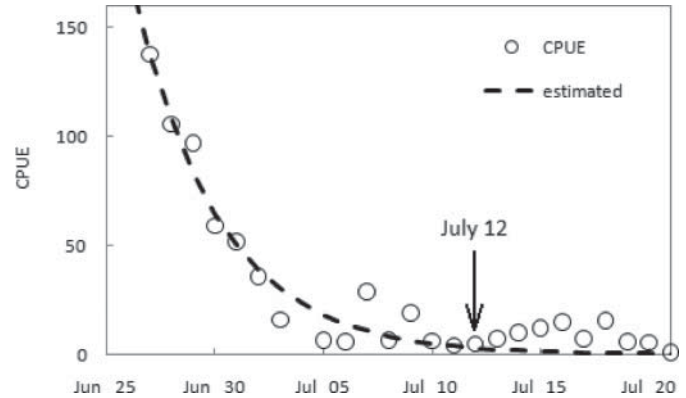

FIGURE 2.   Average juvenile sockeye salmon CPUE in the Strait of Georgia for each calendar day averaged over 12 years of trawl survey data. The dashed line shows the fit of the logistic model (estimated; $R^2 = 0.84$). The arrow identifies the average exit date of July 12.

(Figure 4a), which was identical to the date of the average maximum daily abundance of smolts migrating out of Chilko Lake (Figure 4b). The long-term average cumulative passage of smolts by Mission closely followed a logistic estimation ($R^2 = 0.97$; Figure 5). Cumulative abundance past Mission for each year also closely followed a logistic curve ($R^2 = 0.85, 0.96, 0.98, 0.99, 0.98,$ and 0.98 for 1998, 2000, 2002, 2004, 2006, and 2008, respectively). Annual variation ranged from a minimum of 19 d for passage in 2000 to a maximum of 48 d for passage in 2004 (Figure 3). With the 1-d lag from Mission to the mouth of the Fraser River, exit dates from the Fraser River ranged from May 14 in 1998 to May 28 in 2002, with a mean exit date of May 19 (Table 3). With the mean exit day from the Strait of Georgia of July 12 and the year exit dates in Table 3, average annual residence times ranged from 45 to 59 d, with a mean residence time of 54 d (Table 3).

Average Residence Time Using Time between Maximum Abundance of Smolts in the River and Juveniles in the Strait of Georgia

The average maximum daily abundance of smolts at Mission occurred on May 4 (Figure 4a). The average for all populations was identical to the average maximum abundance of smolts

TABLE 3.   Estimated residence times of juvenile sockeye salmon in the Strait of Georgia using Fraser River exit dates derived from Mission data in 1998, 2000, 2002, 2004, 2006, and 2008 and an average exit date from the Strait of Georgia of July 12.

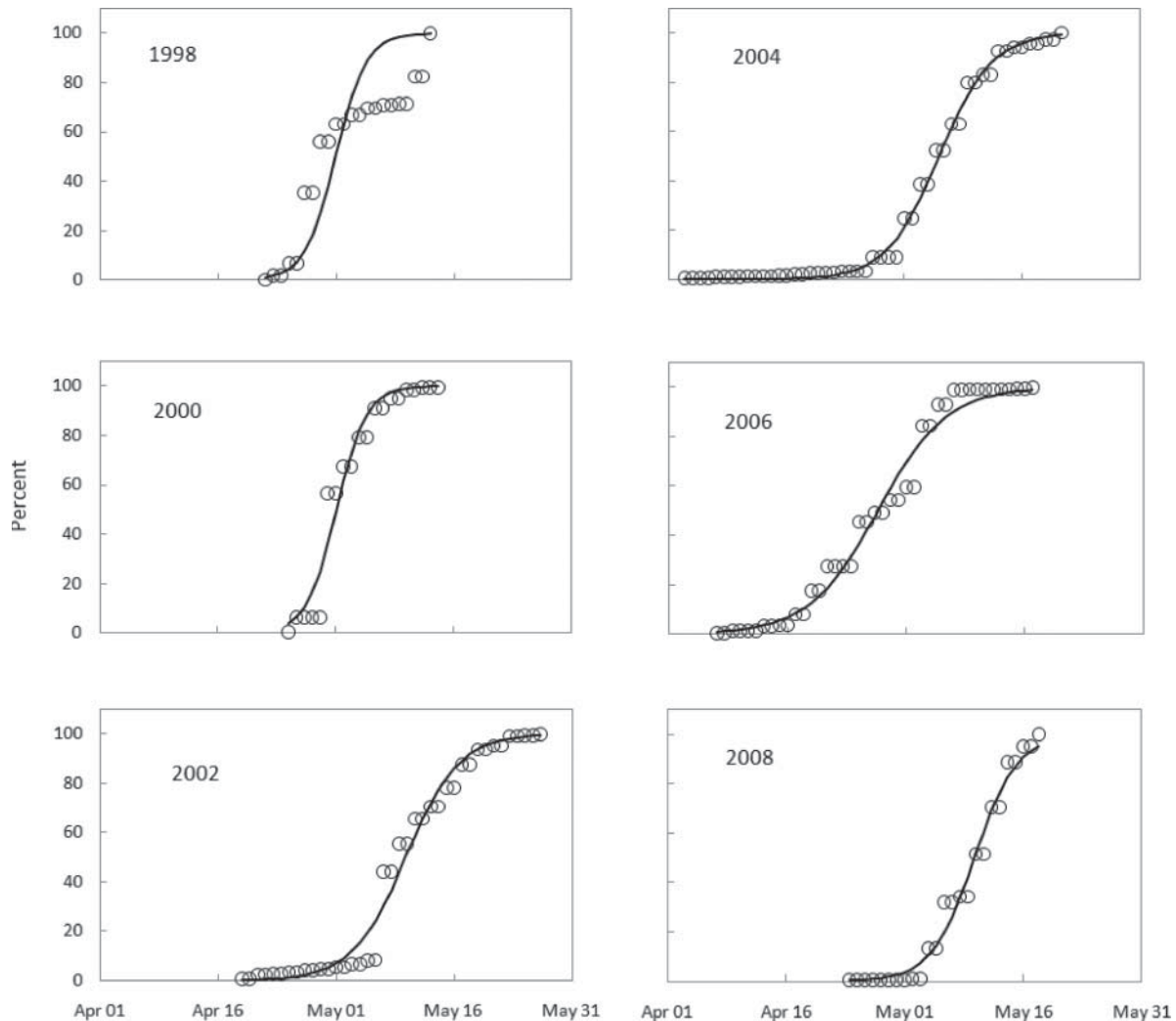| Fraser River exit date	Average residence time (d)
May 14, 1998	59
May 15, 2000	58
May 28, 2002	45
May 22, 2004	51
May 18, 2006	55
May 19, 2008	54

FIGURE 3.   Cumulative abundance of sockeye salmon smolts at Mission in 1998, 2000, 2002, 2004, 2006, and 2008 (circles) fitted to logistic curves.

leaving Chilko Lake (Figure 4b), even though Chilko Lake was approximately 600 km upstream from Mission. A parabola fitted to the daily CPUEs in 1997 and 2010 indicated that maximum abundance in the strait occurred on June 15 in 1997 and June 19 in 2010, with an average of June 17 (Figure 6). The number of days between these dates and a Fraser River maximum abundance date of May 5 resulted in average residence times of 41 and 45 d, with an average of 43 d (Figure 7).

2011 Purse Seine Survey

A purse seine survey was conducted from May 18 to May 31, 2011, that completed 91 sets (Figure 8). Sets made on May 18–19 along the eastern side of the southern Strait of Georgia captured juvenile sockeye salmon (Figure 8). However, virtually no juvenile sockeye salmon were captured in the 43 sets north of this area from May 20 to May 25. Juvenile sockeye salmon were found along the western side of Texada Island in the May 26–27 sets, but none were found along the eastern side of Vancouver

Island (Figure 8). Juvenile sockeye salmon were found from May 28 to May 31 on the eastern side of Vancouver Island in the southern Strait of Georgia.

Residence Times for Chilko Lake Juvenile Sockeye Salmon in the Strait of Georgia

Smolts from Chilko Lake sockeye salmon entered the Strait of Georgia from May 4 to May 24 in 2008 and from April 27 to May 26 in 2009 (Figure 9). DNA stock identification analysis of the samples in the trawl catch, including catches in the Gulf Islands, identified 6 (2%) of the 251 juveniles analyzed as Chilko Lake fish in 2008 and 74 (39%) of the 192 juveniles analyzed in 2009. The average length of these juveniles was 112 mm (SD, 10.0) and 114 mm (SD, 9.5) in 2008 and 2009, respectively. In 2008 the 6 fish were captured from June 24 to June 28, and in 2009 the 74 fish were captured from June 25 to July 1. If these fish were the last to enter the Strait of Georgia and would have left immediately had they not been captured, the juveniles could
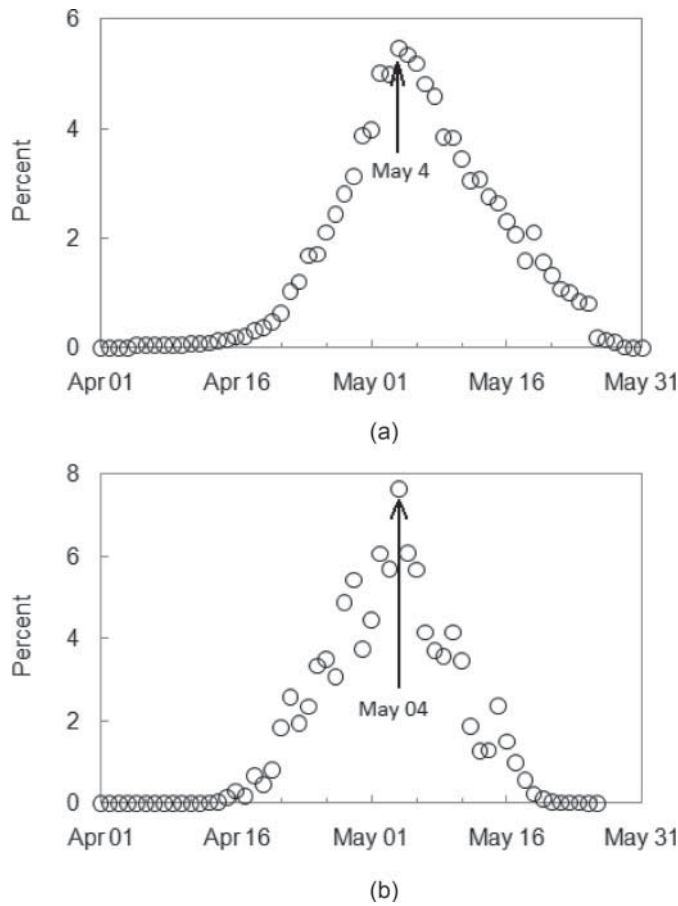
(a)

(b)

FIGURE 4. **(a)** Average daily percentage of downstream-migrating sockeye salmon smolts at Mission, 1976–2008 (Patterson, personal communication), and **(b)** average daily percentage of sockeye salmon smolts leaving Chilko Lake, 1986–2009 (Cone, personal communication). The arrows identify the maximum averages on May 4.
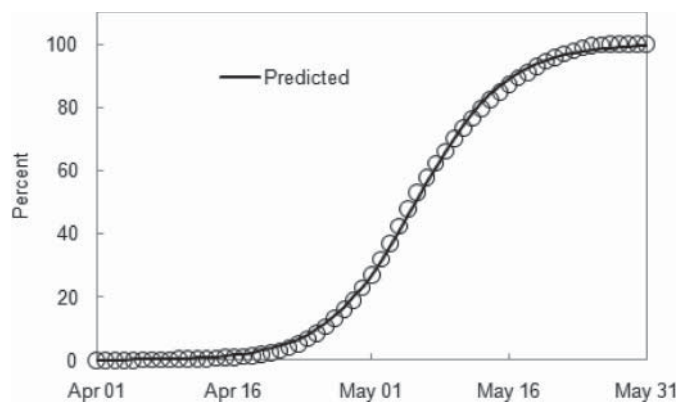

FIGURE 5. Average cumulative daily abundance of sockeye salmon smolts at Mission, 1998–2008, fitted to a logistic approximation.
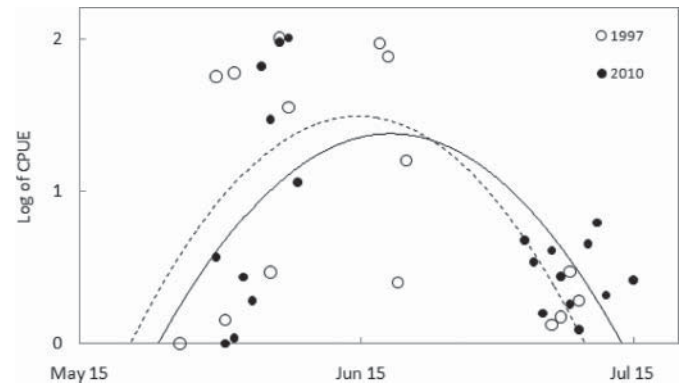

FIGURE 6. Daily average CPUE of juvenile sockeye salmon in the trawl surveys in 1997 and 2010 fitted to parabolas.

have been in the Strait of Georgia 31–35 d in 2008 and 37–43 d in 2009.

DISCUSSION

Average Residence Time

We developed two definitions of residence time to estimate the time that juvenile sockeye salmon spent in the Strait of Georgia. The approach using the time between the entry of the last smolts into the Strait of Georgia and the departure of the last ones from the strait resulted in an estimate of 54 d for residence time. The second approach of using the time between the entrance of the maximum number of sockeye salmon smolts into the Strait of Georgia and the occurrence of the maximum abundance of juveniles in the strait resulted in an estimate of 43 d for residence time. The estimate of the maximum number of smolts leaving the Fraser River used counts that were extensive and that most likely provided a reliable estimate of the average date of maximum smolt abundance. The estimate of the maximum juvenile abundance within the Strait of Georgia may suffer in that there were only 2 years when surveys occurred in
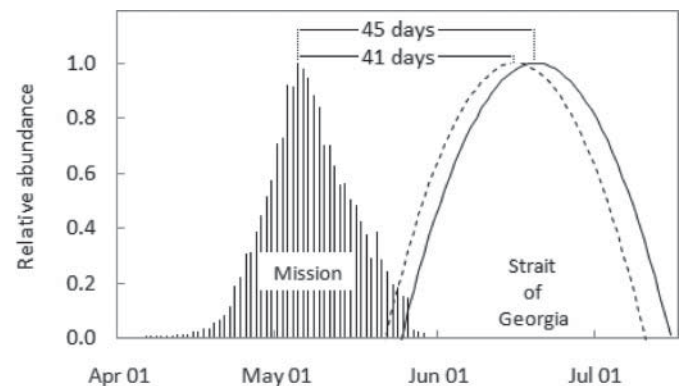

FIGURE 7. Difference between the timing of the average maximum abundance of sockeye salmon smolts exiting the Fraser River and their maximum abundance in the Strait of Georgia in 1997 (dotted line) and 2010 (solid line).
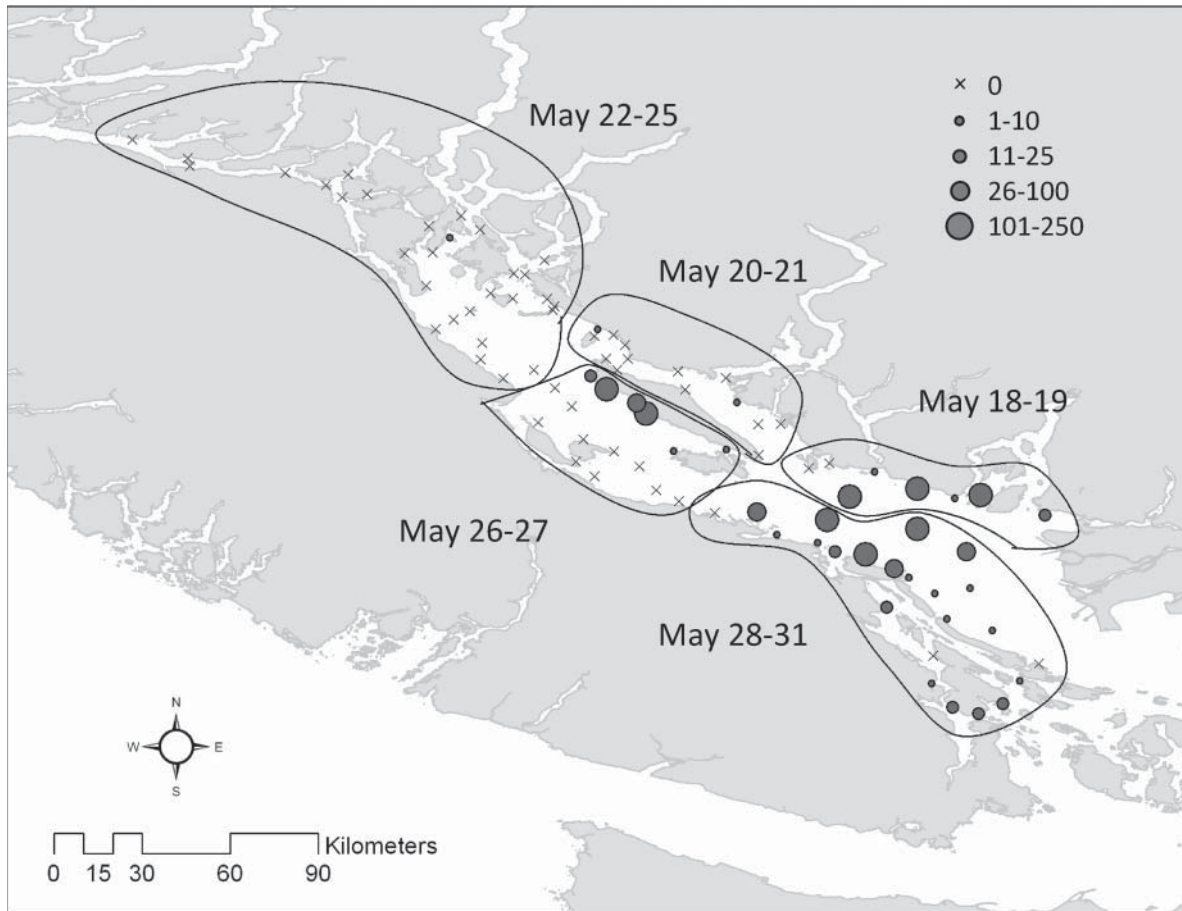
FIGURE 8.   Catches of juvenile sockeye salmon in the purse seine survey in the Strait of Georgia from May 18 to May 31, 2011.

early June and there was the large variation in the average daily CPUE.

The extensive purse seine survey conducted in mid to late May 2011 found virtually no Fraser River sockeye salmon juveniles in the northern Strait of Georgia between May 18 and

FIGURE 9.   Cumulative percentages of sockeye salmon smolts entering the Strait of Georgia in 2008 and 2009 using the smolt counts at Chilko Lake and allowing 7 d for them to enter the strait.

May 23. This purse seine survey, therefore, provided no evidence of any sockeye salmon having either migrated relatively quickly through the Strait of Georgia or dispersed throughout the strait. In purse seine surveys conducted up to May 31, 2011, only four sockeye salmon juveniles were caught north of Texada Island and these were all more than 150 mm in length. Additional information from work reported in Groot et al. (1985) and from the 1997 and 2010 early trawl surveys indicated that the maximum abundance in the Strait of Georgia occurred in mid-June.

The average length of sockeye salmon sampled south of Texada Island was 110 mm, 22 mm longer than the average length of 88 mm for smolts leaving Chilko Lake in 2011 (Cone, personal communication). We interpret the average length and the catches in the southern strait to indicate that most of the juvenile sockeye salmon were in the Fraser River or the southern Strait of Georgia at the end of May 2011.
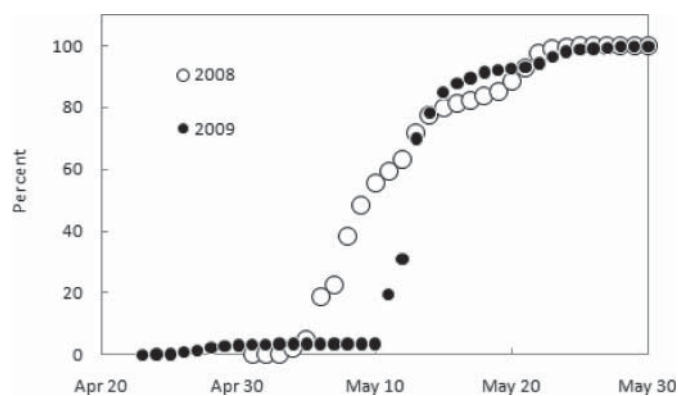
Other Estimates of Residence Time

In the early 1980s a purse seine survey was employed to identify the distribution of juvenile sockeye salmon in the Strait of Georgia in the spring (Groot et al. 1985). We reanalyzed their

TABLE 4. Daily average numbers of sockeye salmon juveniles per set in the 1982, 1983, and 1984 surveys conducted by Groot et al. (1985) in the northern, central, and southern basins of the Strait of Georgia.

	May				Jun			
Date	South	Central	North	Total	South	Central	North	Total
1	0.2			0.2	22.1		49.8	71.9
2				0.0	63.0			63.0
3	0.1			0.1	0.6			0.6
4	0.5			0.5	166.4			166.4
5	117.8			117.8	47.6		82.8	130.4
6	0.0			0.0	2.5			2.5
7	0.0			0.0			31.2	31.2
8	0.4			0.4		46.4	3.3	49.7
9	332.5			332.5		5.8		5.8
10	0.2			0.2		1.3		1.3
11	94.3			94.3		38.0		38.0
12		6.5		6.5		367.9		367.9
13	0.1			0.1		1.1	116.9	118.0
14	0.0			0.0	0.1			0.1
15	16.4			16.4	1.0			1.0
16	150.5			150.5	0.3			0.3
17	4.7			4.7				0.0
18	0.1			0.1				0.0
19	190.2			190.2		49.4		49.4
20	0.4			0.4		55.1		55.1
21	0.0			0.0			0.9	0.9
22	178.8			178.8			2.0	2.0
23	0.0	0.3		0.3			3.6	3.6
24		94.6		94.6				0.0
25		95.0		95.0			1.7	1.7
26	21.4		48.2	69.6			0.3	0.3
27				0.0				0.0
28	3.0			3.0				0.0
29		0.3		0.3				0.0
30	92.8	81.2	18.3	192.3				0.0
31	124.5		134.4	258.9				

data (Groot and Cooke 1987) and combined the data for 1982–1984 into three zones: south (Victoria to Lasqueti Island), central (Lasqueti Island to Savary Island), and north (Savary Island to Sonora Island). Juvenile sockeye salmon catches were converted to the number caught per set for each zone. Our reanalysis showed that the abundance of juvenile sockeye salmon remained high in the southern strait into early June and in the central strait until mid-June (Table 4). The highest daily catch was in the central strait on June 12, which is similar to our estimated date of average maximum abundance (June 17) for the combined years 1997 and 2010. These data indicated that very few juveniles were observed in the central and northern portions of the strait until late May or early June.

Our trawl survey in late June and early July caught juveniles that were at the end of their migration out of the Strait of Georgia.

We did observe that some of these fish were from Chilko Lake. As we know when these smolts entered the Strait of Georgia, we know the last ocean entry date, which indicates that the Chilko Lake fish had been in the Strait of Georgia at least 31 d in 2008 and 37 d in 2009 (and if they were some of the first to arrive in the ocean, it would be longer). We recognize that these are not estimates of an average residence time for the population, but the estimates indicate that juveniles from one population remain in Strait of Georgia for a minimum of 31–37 d.

Although residence time has not previously been defined, one interpretation of the movement of Fraser River sockeye salmon juveniles through the Strait of Georgia has been that the migration is relatively rapid and directed. For example, Clemens (1951) noted that Fraser River sockeye salmon smolts migrated through the Strait of Georgia and went to the open sea by the

southern route through Juan de Fuca Strait (Figure 1). Clemens (1951) reported that in beach seine surveys around the San Juan Islands between July 3 and August 8, 1950, no sockeye salmon juveniles were observed. He hypothesized that this could be due to the fish already having passed the sampling sites, implying a short residence time or a residence time even shorter than for the pink, chum, and Chinook salmon that were sampled. Despite its reliance on only negative evidence, the short residence time–southern migration route hypothesis was accepted by most researchers (Foerster 1968). More intensive surveys summarized in Healey (1980) also supported the suggestion that sockeye salmon smolts exited the Strait of Georgia by Juan de Fuca Strait with an estimated total time for transiting the Strait of Georgia of 20–30 d.

As mentioned above, Groot and Cooke (1987) suggested that the juvenile sockeye salmon exited through the north end of the Strait of Georgia, with a residence time of 30 d. Peterman et al. (1994) used a smolt migration model that included the effects of wind, tides, and Fraser River flow to estimate a mean residence time of 24 d. They did not define mean residence time per se, but their work implied an estimation of the time for individuals to transit the strait and they gave consideration to relevant physical influences.

Welch et al. (2009) estimated a residence time of 25.6–34.1 d in the Strait of Georgia. Because the average size of juveniles in the Strait of Georgia in all of our surveys was considerably smaller than the size of juveniles tagged by Welch et al. (2009, 2011), it is highly probable that the smaller juveniles that represent most of the fish in the population reared for a longer period in the Strait of Georgia. The average length of the 7,919 sockeye salmon smolts sampled in our trawl surveys from 1997 to 2010 was 115 mm (SD, 18.9). The average length of the 282 sockeye salmon juveniles sampled in the 2011 purse seine survey was 105 mm, 10 mm smaller than the average length observed in the trawl catches. However, individuals larger than 150 mm in the purse seine catch accounted for only 2.3% of all juveniles sampled. As the mean length of individuals acoustically tagged by Welch et al. (2009, 2011) was about 180 mm, these acoustically tagged juveniles were larger than about 98% of the fish sampled in our surveys. Thus, the residence time in the Strait of Georgia of the larger, acoustically tagged fish was likely to be less than that of the majority of individuals in the strait.

Our results are more consistent with a movement model that involves a degree of dispersion of sockeye salmon smolts into the Strait of Georgia, either as a result of innate behavior, physical forcing in the marine environment, or both. We observed that relatively large abundances of juvenile sockeye salmon migrate into the Gulf Islands, as reported by Healey (1980). In some years they remain in the area to the end of June and early July, when they probably migrate north out of the Strait of Georgia. This behavior identifies a residence pattern of spreading out within the Strait of Georgia while migrating north.

One consequence of the model's estimating residence times from Fraser River exit date to Strait of Georgia exit date is that in years when sockeye salmon smolts passed Mission rapidly, early, or both the estimated residence times were longer because of the fixed July 12 Strait of Georgia exit date. This may explain why the exit date estimate of average residence time is longer than the maximum-to-maximum estimate. Some sea-type sockeye salmon remain longer (Beamish et al. 2012), but the general decline in the abundance of juveniles identified in this study indicated that virtually all lake-type juveniles were out of the Strait of Georgia by July 12 in an average year.

Another factor influencing the exit date residence time model is the assumption that the cumulative abundance of sockeye salmon smolts at Mission is an indication of the passage of all Fraser River populations. For example, in 1998 there was a bimodal distribution of the emigrating smolts which reflected Chilko Lake emigration data from Chilko Lake a few days earlier. Furthermore, the Chilko Lake smolt counts in 1998 showed that emigration continued for several days after the counting at Mission was over; thus, the apparently 100% cumulative abundance may not have been achieved.

These residence time estimates make no attempt to capture the migration timing and duration of Harrison River sockeye salmon smolts. Many life history characteristics of this population are distinct from those of other Fraser River sockeye salmon. Most Fraser River sockeye salmon migrate to sea in the spring after spending one or two winters in freshwater after fry emergence. Harrison River sockeye salmon smolts migrate to sea later in the calendar year after having spent only the winter after their brood year in freshwater (Beamish et al. 2010). One consequence of this behavior may be some of the anomalously high catches seen in CPUE data from early July onwards. The only way to exclude Harrison fish from our data set would be through genetic analysis, and this was not possible except in 2008 and 2009. Beamish et al. (2012) considered a scenario that excluded catches of smaller fish in order to assess the impact of Harrison sockeye salmon in the data from the trawl survey.

Early Marine Residence and Mortality

Field work on pink salmon smolts suggested that in the first weeks of ocean life daily mortality was 2% to 4% per day (Parker 1968). Unfortunately, no comparable work has been conducted on sockeye salmon smolts during their early marine life history. As discussed for coho salmon juveniles in Lander and Henry (1973), mortality is likely highest when the juvenile salmon first enter the marine environment. For sockeye salmon juveniles in the Strait of Georgia, then, we can infer that the longer they are in the strait the more likely it is that processes there help determine total marine survival. When conditions in the strait are poor, such as in 2007 (Thomson et al. 2012), the early marine mortality in the Strait of Georgia would be large on any migrating salmonids and be magnified by the length of their residence time. This inference is consistent with the conclusions

reported by Mueter et al. (2002b) that physical oceanographic conditions encountered during the first few months at sea were associated with variations in the marine production of pink, chum, and sockeye salmon. Mueter et al. (2002a) also showed that changes in upwelling, sea surface temperature, and sea surface salinity near the point of ocean entry of stocks of pink, chum, and sockeye salmon were most closely related to changes in their marine production.

The average juvenile sockeye salmon residence time in the Strait of Georgia may be longer than previously supposed (Table 1). Given the possibility of significant mortality occurring in the strait, current research could be extended to sample migrating smolts as they enter and exit the Strait of Georgia to provide more reliable estimates of residence time. Estimating abundances as juvenile sockeye salmon exit at the north end of the Strait of Georgia from mid-May to mid-July would also improve estimates of residence time. This combination of sampling would allow an estimate not only of the timing and duration of juvenile sockeye salmon migration through the strait but also an accurate estimate of stock-specific abundance and smolt mortality. By relating physical and biological changes in the strait to the total marine production of sockeye salmon, researchers would be able to provide improved scientific advice in managing this population, particularly in a changing environment.

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REFERENCES

Beacham, T. D., J. R. Candy, B. McIntosh, C. MacConnachie, A. Tabata, K. Kaukinen, L. Deng, K. M. Miller, R. E. Withler, and N. V. Varnavskaya. 2005. Estimation of stock composition and individual identification of sockeye salmon on a Pacific Rim basis using microsatellite and major histocompatibility complex variation. Transactions of the American Fisheries Society 134:1124–1146.

Beamish, R. J., K. L. Lange, C. M. Neville, R. M. Sweeting, T. D. Beacham, and D. Preikshot. 2010. Late ocean entry of sea type sockeye salmon from the Harrison River in the Fraser River drainage results in improved productivity. North Pacific Anadromous Fisheries Commission, Document 1283, Vancouver. Available: www.npafc.org. (April 2012).

Beamish, R. J., D. McCaughran, J. R. King, R. M. Sweeting, and G. A. McFarlane. 2000. Estimating the abundance of juvenile coho salmon in the Strait of Georgia by means of surface trawls. North American Journal of Fisheries Management 20:369–375.

Beamish, R. J., C. Neville, R. Sweeting, and K. Lange. 2012. The synchronous failure of juvenile Pacific salmon and herring production in the Strait of Georgia in 2007 and the poor return of sockeye salmon to the Fraser River in 2009. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 4:403–414.

Bradford, M. J., B. J. Pyper, and K. 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.

Burgner, R. L. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). Pages 1–118 *in* C. Groot and L. Margolis editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Clemens, W. A. 1951. The migration of Pacific salmon (*Oncorhynchus*). Transactions of the Royal Society of Canada 45:9–17.

Crittenden, R. N. 1994. A diffusion model for the downstream migration of sockeye salmon smolts. Ecological Modelling 71:69–84.

Dempson, J. B., M. J. Robertson, C. J. Pennell, G. Furey, M. Bloom, M. Shears, L. M. N. Ollerhead, K. D. Clarke, R. Hinks, and G. J. Robertson. 2011. Residency time, migration route and survival of Atlantic salmon *Salmo salar* smolts in a Canadian fjord. Journal of Fish Biology 78:1976–1992.

English, K. K., R. C. Bocking, and J. R. Irvine. 1992. A robust procedure for estimating salmon escapement based on the area-under-the-curve method. Canadian Journal of Fisheries and Aquatic Sciences 49:1982–1989.

Foerster, R. E. 1968. The sockeye salmon, *Oncorhynchus nerka*. Fisheries Research Board of Canada Bulletin 162.

Groot, C., and K. Cooke. 1987. Are the migrations of juvenile and adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in near-shore waters related? Canadian Special Publication of Fisheries and Aquatic Sciences 96:53–60.

Groot, C., K. Cooke, G. Ellis, and R. Bailey. 1985. Data record of juvenile sockeye salmon and other fish species captured by purse seine and trawl in the Strait of Georgia and Johnstone and Queen Charlotte straits in 1982, 1983, 1984, and 1985. Canadian Data Report of Fisheries and Aquatic Sciences 561.

Healey, M. C. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia. Pages 203–229 *in* W. J. McNeil and D. C. Himsworth, editors. Salmonid ecosystems of the North Pacific. Oregon State University Press and Oregon State University Sea Grant College Program, Corvallis.

Hume, J. M. B., K. S. Shortreed, and K. F. Morton. 1996. Juvenile sockeye rearing capacity of three lakes in the Fraser River system. Canadian Journal of Fisheries and Aquatic Sciences 53:719–733.

Lander, R. H., and K. A. Henry. 1973. Survival, maturity, abundance, and marine distribution of 1965–66 brood coho salmon, *Oncorhynchus kisutch*, from Columbia River hatcheries. U.S. National Marine Fisheries Service Fishery Bulletin 71:679–695.

Manske, M., and C. J. Schwartz. 2000. Estimates of stream residence time and escapement based on capture–recapture data. Canadian Journal of Fisheries and Aquatic Sciences 57:241–246.

Mueter, F. J., R. M. Peterman, and B. J. Pyper. 2002a. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. Canadian Journal of Fisheries and Aquatic Sciences 59:456–463.

Mueter, F. J., D. M. Ware, and R. M. Peterman. 2002b. Spatial correlation patterns in coastal environmental variables and survival rates of Pacific salmon in the northeast Pacific Ocean. Fisheries Oceanography 11:205–218.

Parker, R. R. 1968. Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. Journal of the Fisheries Research Board of Canada 25:757–794.

Peterman, R. M., S. G. Marinone, K. A. Thomson, I. D. Jardine, R. Crittenden, P. H. LeBlond, and C. J. Walters. 1994. Simulation of juvenile sockeye salmon (*Oncorhynchus nerka*) migrations in the Strait of Georgia, British Columbia. Fisheries Oceanography 3:221–235.

Roos, J. F. 1991. Restoring Fraser River salmon: a history of the International Pacific Salmon Fisheries Commission 1937–1985. Pacific Salmon Commission, Vancouver.

Sweeting, R. M., R. J. Beamish, D. J. Noakes, and C. M. Neville. 2003. Replacement of wild coho salmon by hatchery-reared coho salmon in the Strait

of Georgia over the past three decades. North American Journal of Fisheries Management 23:492–502.

Thomson, R. E., R. J. Beamish, T. D. Beacham, M. Trudel, P. H. Whitfield, and R. A. S. Hourston. 2012. Anomalous ocean conditions may explain the recent extreme variability in Fraser River sockeye salmon production. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 4:415–437.

Welch, D. W., M. C. Melnychuk, J. Payne, E. L. Rechisky, A. Porter, G. Jackson, B. Ward, S. Vincent, and J. Semmens. 2011. In situ measurement of coastal ocean movements and survival of juvenile Pacific salmon. Proceedings of the National Academy of Sciences of the USA 108:8708–8713. Available: http://www.pnas.org/content/early/2011/05/10/1014044108. (April 2012).

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.