# Stock-specific variability in productivity as a function of juvenile fish condition and abundance in freshwater[1]

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[1] The materials in this report represent in-progress research. As such, the contents of this report (unless previously published) are not to be cited without permission of the principal investigators and individual authors

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## EXECUTIVE SUMMARY

Previous Fisheries and Oceans Canada (DFO) research has examined relationships between successive brood lines of sockeye salmon (*Oncorhynchus nerka*) populations. Sockeye salmon populations can exhibit cyclic dominance, whereby the abundance of adult fish that return to fresh water in the dominant year can be several orders of magnitude greater than sub-dominant or off-cycle years, and this pattern persists through time (Ricker 1950; Ricker 1997). Multiple mechanisms have been invoked to explain this pattern of cyclic dominance.

Large spawning escapements produce a high abundance of juvenile sockeye salmon, which compete for resources throughout the freshwater life-cycle. Given a relatively constant lake productivity and habitat availability among years, competition for limited prey or habitat reduces energy uptake, growth, and energetic condition in offspring of larger broods. Indeed, the offspring produced by large escapements tend to be smaller and have lower survival than offspring produced by lower escapements. Cohort interactions, or delayed density dependent dynamics, can also affect juvenile condition and survival through longer term changes to the habitat, including trophic dynamics, or the build-up or predators or pathogens during the high abundance period (Ward and Larkin 1964; Larkin 1971; Levy and Wood 1992; Hume et al. 1996).

The current uncertainty in carrying capacity of different lakes can affect fishing opportunities for all sectors. Better understanding of the impact of different spawning escapement numbers on juvenile condition and survival of subsequent generations can help determine escapement planning. Perpetual low escapement causes low stock productivity, while high escapement indicates missed fishing opportunities with the possibility of no increase in smolt output or adult returns, due to greater competition among juveniles.

Among sockeye salmon rearing lakes in the Fraser River, there is substantial variation in elevation, thermal regimes, primary productivity, migration distance to sea, population spawner abundance, and size of out-migrating smolts. These observations stimulated the development of our SEF Proposal, *Stock-specific variability in productivity as a function of juvenile fish condition and abundance in freshwater.*

We identified four major objectives during the development of this project, as outlined in the original proposal:

1. Compare the utility of using energetic condition indices over traditional size metrics to examine the stock specific differences in smolt condition and variability in stock productivity and growth conditions within rearing lakes.

2. Explore the potential impact of high spawning escapement and cyclic dominance on the energetic condition and survival of juvenile sockeye at various life stages.

3. Research critical energy levels through evaluation of lipid and triglyceride stores, simple energy budgets, and explore other indices of critical energy that may be more sensitive that total lipid.

4. Explore whether fish physiological condition (lipid, genomic signatures) is a better indicator of future smolt to adult survival than smolt size metrics.

In order to address these objectives, we collected approximately 2,500 juvenile sockeye salmon from six populations in the Fraser River watershed, at important life-stages during the freshwater life-cycle, over ten years. The total body lipids of these fish were measured in the laboratory using gravimetric solvent extraction, modified from Higgs et al. (1995). Hydroacoustic and limnological surveys were conducted on the natal lakes to estimate abundance of juvenile sockeye salmon, photosynthetic rate, zooplankton standing crop, and to collect juvenile stomach contents. Ultimately, our goal was to determine if variation in juvenile sockeye salmon energetic condition is consistent with patterns of direct and delayed density dependence, related to high spawning escapements, and related to future survival.

The framework of this report consists of four chapters, each representing an independent paper addressing one of the four objectives outlined above:

1. Comparison of sockeye salmon smolt condition metrics across populations with different rearing habitats and migration routes
   V. Minke-Martin, D.A. Patterson, J.A. Hills, C. Storey, D. Selbie, and L. Pon

2. Evidence for density dependence and delayed density dependence from four condition metrics measured in juvenile sockeye salmon from six Fraser River rearing lakes
   V. Minke-Martin, D.A. Patterson, J.A. Hills, C. Storey, D. Selbie, and L. Pon

3. Evaluating minimum whole-body lipid values for survival in wild juvenile sockeye salmon collected from six rearing lakes in the Fraser River watershed
   V. Minke-Martin, D.A. Patterson, S. Wilson, K.A. Robinson, J.A. Hills, and C. Storey

4. The utility of percent total lipid for describing density dependent freshwater survival of sockeye salmon smolts using Ricker spawner-recruit models
   V. Minke-Martin, D.A. Patterson, and D. Braun

Below, we provide a review of the main conclusions across the four chapters, with specific references to the objectives outlined above.

## CHAPTER 1 EXECUTIVE SUMMARY

### RESULTS

- Energetic condition, as well as length, body weight, and condition factor, varied by population origin and sample year.
- Variation in energetic condition of Fraser sockeye smolts is greater among populations than across years within a population.
- Population-specific variability in energetic condition of smolts was reflective of variability in lake primary productivity and not migratory distance or lake size.

### DISCUSSION

- Differences in energetic data (i.e. percent total lipid) among populations suggests different trends in condition than length or weight alone. For example, smolts from Shuswap Lake are small and light, relative to smolts from other populations, but have proportionately higher levels of total lipid.
- Total lipid, in combination with other size metrics, may help to identify morphological differences between juveniles from different populations.
- All of the condition metrics we analyzed (length, weight, Fulton's condition factor, percent total lipid) were significantly positively related to lake primary productivity, suggesting that the magnitude of variation in juvenile condition caused by spawner abundance, and resulting juvenile densities, could be limited by bottom-up processes.

### MANAGEMENT IMPLICATIONS

Population and annual variation in energetic smolt condition are potential contributing sources of variation in population-specific estimates of productivity. Information on energetic status, independent of size metrics, is likely to be useful for understanding the mechanism behind current estimates of carrying capacity, and therefore setting spawning escapement targets.

### RECOMMENDATIONS

- Expand sampling to include other Fraser populations that would maximize the contrast in lake productivities, such as juveniles that rear in Fraser and Francois lakes.
- Create a measure of mean juvenile energetic condition, like the Fraser Index, which could be used to identify above- and below-average populations from samples taken from out-migrating smolts each year.
- Incorporate existing year-specific photosynthetic rate data from Cultus, Chilliwack, Quesnel, and Shuswap lakes to assess whether interannual variation accounts for additional variation in total lipid between years.
- Analyze existing juvenile sockeye salmon triacylglyceride (TAG) data to determine whether trends are consistent with those observed for total lipid.

## CHAPTER 2 EXECUTIVE SUMMARY

### RESULTS

- Significant negative relationships exist between EFS density and the length and weight of out-migrating smolts (i.e. direct density dependence).
- Significant negative relationships exist between the EFS density that gave rise to the previous brood and both condition factor and total lipid (i.e. delayed density dependence).
- Consistent patterns exist in total lipid levels across life-stages for different stocks, such as low levels during maximum summer growth period, maximum levels during fall (in preparation for overwinter), and lower levels in spring parr than out-migrating smolts.
- Interannual variability in fall fry condition is consistent with patterns of direct density dependent growth.

### DISCUSSION

- The overall density dependent and delayed density dependent responses were for models of pooled population data. More data points are needed to understand the relationship between EFS and smolt lipid levels at a population-specific level beyond Chilko.
- The ability to detect the negative relationships between EFS and length, weight, and condition factor for Chilko is likely the result of it being the only population with a long enough time series of data (10 years) and a distribution of spawning escapements across low to high abundance.
- Fall fry total lipid levels are important to over-winter survival; lower levels in dominant broods seen in Shuswap are likely impacting the abundance of age-1 sockeye salmon to out-migrate.
- Spring feeding, may be an important energy source for parr from some populations (Cultus, Shuswap) to achieve high body condition prior to out-migration as smolts.

### MANAGEMENT IMPLICATIONS

Spawning escapement levels can have direct influence on smolt condition metrics, suggesting both density dependent and delayed density dependent processes are occurring in the populations we sampled. However, samples sizes are currently too small to make large inferences to individual populations. There is recognition that freshwater limits to smolt quality are likely to influence management strategies to optimize productivity. More work is needed to understand the connection between quantity and quality of sockeye at distinct life stages in early freshwater environment, such as overwinter survival.

RECOMMENDATIONS

- Focus future sampling on populations at both low and high escapements (relative to $S_{max}$ capacity), in order to increase statistical power for parameterizing relationships between EFS density and juvenile energetic condition.
- Sample cohorts at multiple life-stages, in order to capture fluctuations in energetic condition that may be important to survival, such as paired sampling of fall fry and spring parr.
- Sample non-dominant cohorts at multiple life-stages, in order to establish population-specific baselines in energetic condition when direct density dependent and delayed density dependent processes are unlikely to be occurring.
- Analyze existing stomach content data to assess differences in feeding efficiency (i.e. relative fullness) and diet composition (i.e. prey switching) between juveniles in high and low abundance broods.
- Analyze existing lake zooplankton biomass and community composition data to assess the impact of high and low juvenile sockeye salmon biomass on food availability.
- Analyze existing juvenile sockeye salmon triacylglyceride (TAG) data to determine whether trends are consistent with those observed for total lipid.

## CHAPTER 3 EXECUTIVE SUMMARY

### RESULTS

- Distributions of energy content (i.e. percent total lipid) varied both across years and among populations.
- A 2% critical energy threshold was identified for sustained swim performance.
- Some populations (e.g. Chilko) and life-stages (e.g. summer fry and spring parr) consistently exhibit a relatively high proportion of individuals with total lipid levels below 2%, which may indicate population- or life-stage-specific critical thresholds.

### DISCUSSION

- The proportion of individuals in a cohort below the critical energy threshold was higher in high abundance broods, consistent with direct density dependence.
- The proportion of individuals in a cohort below the critical energy threshold was higher in populations that rear in less productive lakes.
- Variability in stocks in the portion of individuals at or near critical minimal energy levels is potentially predictive of future stock-specific marine survival.
- The critical energy value for sustained swimming provides one of the first physiological values that is relevant to the ecology of Fraser River sockeye salmon smolts.

### MANAGEMENT IMPLICATIONS

As more information becomes available on critical energy levels, it will be become possible to make risk determinations regarding the future survival of out-migrating smolts from more abundant stocks. This would require consistent sampling platforms, at either the lake outlet or lower Fraser River.

### RECOMMENDATIONS

- Focus future sampling on populations at both low and high escapements, relative to $S_{max}$ capacity.
- Utilize distributions or measures of spread, rather than mean values, to describe juvenile energetic condition, as similar mean values can come from cohorts with different proportions of fish below minimum energy levels.
- Study relationships between critical energy levels and burst swimming performance.
- Conduct experimental work on overwinter survival, in relation to water temperature and ration level, to identify the threshold energy levels for survival and smoltification.
- Analyze existing juvenile sockeye salmon triacylglyceride (TAG) data to determine whether trends are consistent with those observed for total lipid.

## CHAPTER 4 EXECUTIVE SUMMARY

### RESULTS

- Higher mean condition (i.e. total lipids) is associated with increased predicted survival to smolt out-migration and adult recruitment across low to high spawning escapements.
- There is a high correlation between Chilko and Cultus adult recruits per out-migrating smolt in broods from 2000-2011.

### DISCUSSION

- We created a proof of concept for incorporating mean total lipid data from out-migrating smolts into simple Ricker models, using small Chilko spawner-recruit dataset.
- Further collections of juveniles from a range of populations, over longer time series, would improve statistical power to make predictions about juvenile survival and the importance of energetic condition to population dynamics.
- It would be informative to apply the same analysis to Cultus data; however, uncertainty around EFS estimates makes it difficult to link spawner abundance with out-migrating smolt abundance and condition.

### MANAGEMENT IMPLICATIONS

Incorporating biological information, such as energetic condition, into traditional stock-recruit relationships has the potential to aid in pre-season run size forecasts. Similarly, if the shared co-variance in smolt-to-adult survival between Cultus and Chilko exists for other Fraser populations it has promise to better inform in-season run size estimates for populations with later adult migration timing.

### RECOMMENDATIONS

- Need to compare total lipid data to size metrics, with respect to smolt to adult survival, as there is potential to extend the relationship to brood years that predate energy work.
- Continue monitoring energetic condition in out-migrating smolts from Chilko Lake.
- Fit a linear model to the recruits per smolt and percent total lipid data, as the density dependent term in the Ricker model may not be suitable for the dynamics affecting survival of out-migrating smolts and sockeye salmon at sea.
- Fit models to recruits per smolt and percent total lipid data for both Chilko and Cultus populations to compare the importance of mean smolt condition to survival.
- Analyze existing juvenile sockeye salmon triacylglyceride (TAG) data to determine whether trends are consistent with those observed for total lipid.

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# Comparison of sockeye salmon smolt condition metrics across populations with different rearing habitats and migration routes

## INTRODUCTION

The sockeye salmon populations in the Fraser River watershed exhibit remarkable fluctuations in adult abundance, among both populations and years. Even highly abundant populations, whose peak returns exceed those of smaller populations by three or four orders of magnitude, can themselves vary by several orders of magnitude from year to year. Juvenile body condition is one factor that may underlie variation in adult returns, as individuals that leave rearing lakes in high condition are more likely to survive the downstream migration and transition to the marine environment. Smolt lipid reserves fuel migration and provide surplus energy if entry into the marine environment is mismatched with marine food supplies. Studies of coho, pink, and chum salmon suggest that survival from marine entry to adult return to fresh water is size-dependent, with greater mean smolt size yielding higher survival rates (Johnson 1970; Hager and Noble 1976; Bilton et al 1982; Kobayashi 1980). Some Fraser River sockeye salmon populations, including Cultus (Foerster 1954) and Chilko (Henderson and Cass 1991), have also exhibited increases in smolt-to-adult survival with increases in mean smolt size.

Juvenile growth and energy storage are limited by conspecific density related to habitat capacity. Sockeye salmon rearing lakes in the Fraser River watershed differ in seasonal food and habitat availability, caused by differences in latitude, elevation, size, depth, water chemistry, and adjacent land use. Variation in lake productivity can underlie population differences in juvenile size. Alternately, there may be a genetic basis to population-level differences in juvenile condition, driven by mortality associated with the energetic demands of the downstream migration and saltwater transition.

Our objective with this study was to determine if energetic status (total lipids as a percentage of total weight) and other condition metrics (length, weight, and condition factor) differed among out-migrating smolts from six different populations over multiple brood years. Additionally, we examined relationships between these condition metrics and measures of lake size (surface area), lake primary productivity (photosynthetic rate), and migration (distance and timing). We sampled fish from the populations that rear in Chilko Lake, Chilliwack Lake, Cultus Lake, Quesnel Lake, Seton and Anderson lakes, and Shuswap Lake, which vary in smolt abundance, lake size and productivity, and migration distance and timing.

We hypothesized that condition metrics would differ among populations, but that the ranked order of populations would be consistent for all of the condition metrics tested, such that the longest smolts would be in the best condition (i.e. greatest fat stores, heaviest, and highest condition factor). We predicted that smolts from larger and more productive lakes would have greater condition metrics values, due to greater habitat capacity and reduced conspecific competition. We also predicted greater condition metric values for smolts from populations

that migrate farther or leave lakes earlier, as these fish experience greater energetic demands from swimming and reduced opportunity to feed in fresh water. To determine whether habitat capacity or migratory preparedness is more important to smolt condition, we tested the relative effects of lake size, productivity, migration distance, and timing in a single statistical model.

## METHODS

### POPULATIONS

For this report, we collected juvenile sockeye salmon from populations that rear in six lakes in the Fraser River watershed. The location, limnology, and sockeye salmon population dynamics of each lake are described in some detail below, and lake attributes are compared in Table 1.

#### *Chilko Lake*

Chilko Lake (51°20'N, 124°05'W) is a cold, ultra-oligotrophic, sub-alpine lake, located on the eastern edge of the Coast Mountain Range at an elevation of 1172 m. The surface area of the lake is 185 $km^2$ (18,451 ha), and the mean and maximum depths are 123 m and 330 m. The lake has steep banks and limited littoral habitat. During winter, the lake temperature is 4°C. The growing season is May 1–October 31, with a seasonal average photosynthetic rate (PR) of 121 mg $C \cdot m^{-2} \cdot d^{-1}$ (Grant *et al.* 2011).

Most of the sockeye salmon in the population spawn in Chilko River, downstream of the lake outlet, with the remainder using gravel beaches throughout Chilko Lake (Hume *et al.* 1996). The Chilko population represents a major contributor to adult returns to the Fraser River in many years. During the years of the study (2005-2016), total spawners (and effective female spawners, EFS) was smallest in 2004, at 92,000 (49,000), and largest in 2010, at approximately 2,500,000 (1,180,000). The population does not have a regular four-year dominance cycle (Myers *et al.* 1997).

Smolts migrate into the Chilko River from mid-April until mid-May (median date: between April 26-May 5 in years 2006-2015); outmigrating smolts are enumerated by DFO using a counting fence with video monitoring. In some years, a relatively large proportion of parr remain in Chilko Lake for an additional year and outmigrate as two-year-old smolts (age 2+). In 2009, 2010, 2013, and 2014, 8–10% of outmigrating Chilko smolts were two-year-olds. The juvenile migration, from Chilko Lake to the Fraser River estuary, is 677 km.

*Chilliwack Lake*

Chilliwack Lake (49°03'N, 121°25'W) is a relatively cold, oligotrophic lake, located in the eastern Fraser Valley, at an elevation of 621 m. The surface area of the lake is 12 $km^2$ (1,187 ha), and the mean and maximum depths are 67 m and 121 m (Shortreed et al. 2001; Tunnicliffe et al. 2012). The seasonal mean photosynthetic rate of Chilliwack Lake is 101 mg $C \cdot m^{-2} \cdot d^{-1}$ (Grant *et al.* 2011).

Chilliwack Lake is the rearing lake for sockeye salmon populations that spawn in Dolly Varden Creek, a tributary, and in the lake itself. Escapements to Chilliwack Lake have been highly variable (Grant *et al*. 2011): 3,500 spawners (1,700 EFS) in 2014 to 126,000 spawners (79,000 EFS) in 2012. The dominant cycle line is the 2000 brood.

Sockeye salmon smolts leave Chilliwack Lake between mid-April and mid-May. Their migration through Chilliwack and Fraser rivers to the Strait of Georgia is 153 km.

*Cultus Lake*

Cultus Lake (49°03'N, 121°59'W), located in the eastern Fraser Valley, is a small lake of 6 $km^2$ (630 ha) at 46 metres above sea level. The lake is steep-sided, with a limited littoral area, and mean and maximum depths of 21 m and 44 m. Cultus Lake is productive, and the seasonal mean photosynthetic rate of 404 mg $C \cdot m^{-2} \cdot d^{-1}$ was the highest of the lakes studied (Grant *et al.* 2011). It has a highly developed catchment area, with residential, agricultural, and recreational land uses.

The sockeye salmon population that spawns in Cultus Lake has been assessed as Endangered by the Committee on the Status of Endangered Wildlife in Canada. From 1994 to 2016, the population declined 92% (COSEWIC 2003). During the study, escapements to Cultus Lake ranged from 892 spawners (19 EFS) in 2012 to 10,300 spawners (1,000 EFS) in 2010. A hatchery program supplements the wild population.

Sockeye salmon smolts migrate into Sweltzer Creek from mid-March until late May (median date: between April 7-30 in years 2007-2016), and the outmigration is enumerated by DFO using a counting fence. The juvenile migration, from the lake outlet to the Fraser River estuary, is 110 km.

*Quesnel Lake*

Quesnel Lake (52°30'N, 120°00'W) is an oligotrophic lake in the interior plateau of British Columbia, at an elevation of 725 m (Morton and Williams 1990). It is large, covering an area of 272 $km^2$ (26,090 ha), and deep, with mean and maximum depths of 158 m and 530 m. The lake has four arms, hereafter referred to as, West Arm, drained by the Quesnel River, Main Arm,

North Arm, and East Arm. The growing season is from May 1–October 31, and the lake has a seasonal mean PR of 130 mg $C \cdot m^{-2} \cdot d^{-1}$ (Grant *et al.* 2011).

The main spawning areas for sockeye salmon are in the Horsefly and Mitchell rivers, the largest tributaries to the lake, while additional spawning areas in small streams and along the lake shore support smaller numbers of fish (Hume *et al*. 1996). Returns to Quesnel Lake during the study were lowest in 2016, with 1,000 spawners (200 EFS), and highest in 2014, with 830,000 spawners (430,000 EFS). The dominant cycle line is the 2002 brood.

Juvenile sockeye salmon occupy the pelagic zone from July until October. The maximum estimated density of juveniles in Quesnel Lake is 6000 fry $ha^{-1}$, based on analysis of PR models and historic fry data by Hume *et al.* (1996). Smolts leave the lake in April and May and migrate 748 km to the Fraser River estuary.

*Seton and Anderson lakes*

Seton Lake (50°42'N, 122°08'W) and Anderson Lake (50°38'N, 122°24'W) are oligotrophic lakes in the rain shadow of the Coast Mountain Range, in southwestern British Columbia, at elevations of 237 m and 258 m, respectively. Seton Lake covers 25 $km^2$ (2,519 ha) and Anderson Lake covers 29 $km^2$ (2,844 ha). Both lakes are deep, with steep sides and limited littoral areas. The mean and maximum depths are 85 m and 151 m in Seton Lake and 140 m and 215 m in Anderson Lake. Anderson Lake is drained into Seton Lake by Portage Creek, a 3-km stream. Seton Lake also receives water via a hydropower diversion from Carpenter Lake, a reservoir in the adjacent Bridge River watershed. Flow from Seton Lake, through the Seton River, is controlled by the Seton Dam, which was built in 1956 and is located 800 m downstream of the lake outlet (Limnotek 2015). Anderson Lake is more productive than Seton Lake, with a photosynthetic rate of 303 mg $C \cdot m^{-2} \cdot d^{-1}$, compared to 233 mg $C \cdot m^{-2} \cdot d^{-1}$ (Grant *et al.* 2011).

Two populations of adult sockeye salmon spawn in the Seton-Anderson watershed: early summer run fish that return to Gates Creek, which flows into Anderson Lake, and late run fish that spawn in Portage Creek. The Portage Creek sockeye salmon were transplanted from the lower Adams River population in the early 20$^{th}$ century (Withler *et al.* 2000; Grant *et al.* 2011). The two populations are genetically distinct, with differently timed migration and spawning (Withler *et al.* 2000; Moreira 2014). The dominant cycle line for the Portage Creek population is 2002, and the Gates Creek sockeye population has not exhibited regular cyclic dominance since the late 1990s. The largest collective adult return to the system during the study was in 2010 (80,000 spawners; 33,000 EFS), and the smallest was in 2016 (8,800 spawners, 3,600 EFS). The majority of adult returns are to the Gates Creek population.

The majority of Gates Creek sockeye fry rear in Seton Lake, migrating through Portage Creek from mid-April to late-June as fry (Geen and Andrew 1961; Woodey 1975). Smolts leave Seton Lake in April and May, and the migration from the Seton Lake outlet above the Seton Dam, through the Seton and Fraser rivers to the Fraser River estuary, is 333 km.

*Shuswap Lake*

Shuswap Lake (50°00'N, 119°05'W) is a mesotrophic lake in the interior plateau of British Columbia, at an elevation of 347 m (Hume *et al*. 1995). The lake is roughly H-shaped, with four major arms: Main, Seymour, Anstey, and Salmon. A 1.5-km narrows at Sicamous separates Mara Lake from Salmon Arm. Little River drains the Main Arm of Shuswap Lake into Little Shuswap Lake, and sockeye salmon rear in Mara, Shuswap, and Little Shuswap lakes. The three-lake system is 330 $km^2$, but Mara and Little Shuswap were not routinely sampled, so an area of 300 $km^2$ (29,851 ha) was used. The mean and maximum depths of Shuswap Lake are 58 m and 171 m (Nidle and Shortreed 1996).

Shuswap Lake has a longer growing season (April 1–November 30) and warmer thermal regime than the other lakes in the study, with the exception of Cultus. The mean seasonal photosynthetic rate is 171 mg C $m^{-2}$ $d^{-1}$ (Grant *et al.* 2011)

Sockeye salmon return to a number of tributaries in the Shuswap lakes system, across two run timing groups: early summer and late. The early summer group returns predominantly to Scotch Creek, Eagle River, and Seymour River, while the majority of the late group spawns in Adams River and Lower Shuswap River. Spawning also occurs in other tributaries and along the shore (Grant *et al*. 2011). The smallest return during the study was 1,616 spawners (768 EFS) in 2016, and the largest was 8,947,869 spawners (3,753,548 EFS) in 2010.

Sockeye salmon fry occupy the pelagic zone from July until November (Hume *et al.* 1996), and the populations mix within and among lakes during rearing. Smolts leave the Shuswap system later than in other populations, outmigrating in May and June. The downstream migration is 497 km and is the most complex, following Little River into Little Shuswap Lake, the South Thompson River into Kamloops Lake, and the Thompson and Fraser rivers into the Strait of Georgia.

## JUVENILE FISH COLLECTION, TRANSPORT, AND STORAGE

Juvenile sockeye salmon (*Oncorhynchus nerka*) were collected from various locations across the Fraser watershed. Spring fry, summer fry, fall fry, spring parr and smolts, were collected across multiple years (2007-2017) using various capture methods, depending on the location and targeted life history stage (see Appendix A for details). Briefly, smolts were collected by beach seine, dip net, rotary screw trap, or incline plane trap from Chilko Lake, Sweltzer Creek, Chilliwack Lake, Little River, Quesnel River, Seton River, and the lower Fraser River at Mission. Spring fry were collected by beach seine from Quesnel River and Shuswap Lake. Summer fry Fall fry and spring parr were collected by lake trawl from Quesnel Lake, Shuswap Lake, Cultus Lake, and Chilliwack Lake (Appendix A: Table 1, Table 2). Following collection, fish were euthanized with an overdose of tricaine methanesulfonate (MS-222) prior to fork lengths (nearest mm) and

weights (nearest 0.01 g) being measured in the field. Individuals were wrapped in aluminum foil or individual whirl paks and frozen rapidly or on dry ice. A small subset was frozen on liquid nitrogen or placed in a -20°C freezer. The majority of fish caught by beach seine or dip net were transported to the Fisheries and Oceans research laboratory in West Vancouver ('West Van Lab') for long-term cold storage, although some samples were stored at the University of British Columbia in Vancouver or the Pacific Biological Station in Nanaimo, prior to transport to West Van Lab for analysis. The fish caught by lake trawl were stored at the Fisheries and Oceans research laboratory in Cultus Lake, prior to transfer to West Van Lab for analysis. For more detailed information on capture history and storage conditions for juvenile sockeye samples, see 'Appendix A: Sample collection 2007-2017.'

## GENETIC STOCK ASSIGNMENT

Genetic stock identification was performed on some groups of fish in this study. Fin tissue samples were taken from juvenile fish and stored in 95% ethanol or dry on Whatman paper and then transferred to the Pacific Biological Station in Nanaimo for analysis. Variation in microsatellite DNA was used to assign juvenile fish to population, following the procedures of Beacham et al. (2000a, 2000b). This information was used to distinguish sockeye from kokanee in Chilliwack mid-water trawls.

## LIFE-STAGE IDENTIFICATION

Assumptions regarding age assignments were made based on sampling location, sampling date, and size. The majority of juvenile fish had age assigned at the time of sampling. Age-1 or 2 fish caught in the river environment by seine net, dip net, or weir were called smolts. Sampling was conducted in June in Little River (Shuswap complex) and April or May for all other populations.

Age-2 smolts are larger than age-1 smolts. Chilko can have a high proportion of two-year-old smolts in some years (up to 10%), and these larger fish were generally noted as age-2 smolts at the time of sampling. Several additional fish in each population were identified as two-year-olds from population- and capture year-specific length-weight relationships, as the different age classes typically cluster separately.

## LIPID EXTRACTION AND CONSTITUENT ANALYSIS

Whole juvenile sockeye salmon (*Oncorhynchus nerka*) samples were removed from -80 $^{o}$C freezer storage and allowed to thaw at room temperature prior to taking fork length and weights measurements in the laboratory. Fish were cut into 8-10 pieces and placed in 50 ml Nalgene® tubes with two steel ball bearings and homogenized using a SPEX SamplePrep 2010 Geno/Grinder (SPEX, Metuchen, NJ, www.spexsampleprep.com) at 1500 rpm for two-minute intervals until completely homogenized.

Lipid extraction from homogenized tissue followed protocols developed by Bligh and Dyer (1959) with minor modifications (see: 'Appendix B: Lipid extraction and moisture ash' for detailed methods). Chloroform, methanol and water were added to a weighed subsample of homogenate (in 1:1:0.5 solvent ratios, respectively) and homogenized to form a biphasic layer of chloroform-lipid and methanol-water. The volume of the chloro-lipid layer was measured, prior to pipetting a known volume onto a pre-weighed tin boat and evaporating off the chloroform in an oven. The remaining lipid samples were then re-weighed and frozen for subsequent triglyceride analysis.

The percent lipid of the subsample was calculated using Eq. 1:

$$subsample\ \%\ lipid = \frac{extracted\ lipid\ wt.\ (g)}{subsample\ wt.\ (g)} * 100 \quad [1]$$

The weight of the total lipid in each fish was calculated using Eq. 2:

$$total\ lipid\ (g) = \frac{uncorr.\%\ lipid}{100\%} *\ whole\ fish\ wt._{thawed}\ (g) \quad [2]$$

Moisture lost from juvenile samples during storage was estimated and used to correct fish weights using procedures outlined in Appendix C.

## MIGRATION DISTANCE AND TIMING

Smolt marine migration distance was measured from a manually drawn path in Google Earth, which extended from the outlet of the most downstream lake in the system to the village of Steveston, British Columbia, in the Fraser River estuary. The path from Chilko Lake was measured from the northernmost end of the lake, at a location called 'the narrows.' At Chilliwack Lake, the migration was measured from the lake outlet into Chilliwack River. The Cultus Lake migration was measured from the outflow into Sweltzer Creek, upstream of the DFO counting fence. The path from Quesnel Lake was measured from the oulet of the West Arm of the lake into the Quesnel River. For Seton Lake-rearing sockeye salmon, the migration was measured from the downstream edge of Seton Lake, ~800 m upstream of the Seton Dam. For smolts from the Shuswap complex, the migration was measured from the outlet from the Main Arm of Shuswap Lake into Little River.

Paths were measured along the thalweg of the river, if it could be inferred from satellite imagery, and through the middle of lakes, where applicable. For populations that migrate through lakes, this is a minimum estimate, as circling may occur as smolts search for the lake outlet. Distances were rounded to the nearest kilometre.

Raw daily smolt outmigration totals from the counting fences on Chilko River and Sweltzer Creek were provided for years ranging from 2006 to 2016 by DFO Stock Assessment Division (T. Cone). For each population and year, the 50% migration date was determined as the day that the median fish passed through the fence.

## STATISTICAL ANALYSIS

Four juvenile condition metrics were each analyzed in two different statistical models. Model 1, the population model, tested for among-population differences in the condition metric of interest. Model 2, the rearing lake model, tested the relative importance of lake size (surface area), lake productivity (mean seasonal photosynthetic rate), outmigration timing (sampling date), and migration distance to the condition metric of interest. Model 1 and Model 2 both had four iterations, where the response variable was one of length (mm), wet weight (g), condition factor (Fulton's K), or total lipid (g per fish). A linear mixed effects model was fitted for each iteration, using the restricted maximum log-likelihood method (Zuur et al. 2010).

Brood year was included as a random effect in Model 1 and Model 2, to account for variation in juvenile condition among years. Population was included as a random effect in Model 2, to account for among-population variation not described by the fixed effects. In the iterations of Model 1 and Model 2 that examined total lipid, wet weight (g) was included as a fixed effect, to account for variation in lipid weight with fish size. Model 1 was fit with the function *lme*, from the 'nlme' package, and Model 2 was fit with the function *lmer*, from the 'lme4' package, which can accommodate crossed random effects (Bates, 2005; Bates & Sarkar, 2007).

To compare effect sizes in Model 2, lake surface area, photosynthetic rate, sampling date, and migration distance were centred by subtracting the mean and dividing by two standard deviations (Gelman 2008; Schielzeth 2010).

To ensure models did not violate statistical assumptions, residual plots from each model were visually examined (Zuur *et al.* 2009). Fish weight and total lipid were log transformed to improve normality and homoscedasticity of model residuals. The other variables were not transformed.

To determine whether each pairwise combination of populations differed for each condition metric, Model 1 was run six times for each response variable. Each time, a different population was treated as the model intercept, and the values of all other populations were estimated against it.

For each iteration of Model 2, candidate models were generated from all combinations of fixed effects and ranked by AIC values, using the 'MuMIn' package in R (Barton 2012). The model with the lowest $\Delta$AIC is the most parsimonious model describing the data, while the AIC weight is the probability that a given model is the most parsimonious one (Burnham and Anderson

2002). The models with cumulative AIC weights of $\geq 0.95$ were summed with the 'conditional average' method to generate coefficient estimates and 95% confidence intervals for explanatory variables (Burnham and Anderson 2002, Grueber et al. 2011).

In this report, raw data are presented as mean ± SD, and statistical significance was evaluated at 0.05. All statistical analyses were conducted with R software (version 3.2.2**,** R Core Team 2015).

## RESULTS

### MODEL 1:

Across condition metrics, populations were roughly consistent in their relative ranking, with Cultus and Seton having the highest values and Chilko near the lowest. A notable exception was Shuswap, which had the shortest and lightest fish on average, but the second highest mean condition factor and the third highest percent total lipid. Quesnel had intermediate length and weight but the lowest mean condition factor and percent total lipid. Within years, mean length and weight appeared to have similar trends, with populations ranking consistently by size (Figure 1). However, when tested statistically, populations clustered differently for each condition metric—with the exception of Cultus, which was significantly different from all others in length, weight, and percent total lipid.

#### *Smolt length*

Cultus Lake smolts had the largest mean fork-length of the populations studied, 102.2 mm (± 6.6 mm). This population differed significantly from all others (all $p < 0.001$). Chilko Lake and Chilliwack Lake smolts were not significantly different from each other ($t = 0.732$, $p = 0.464$), and had intermediate lengths (Chilko: 85.6 ± 10.4 mm, Chilliwack: 89.3 ± 9.1 mm). Smolts from Seton Lake and Quesnel Lake were slightly longer than Chilko and Chilliwack smolts (Seton: 90.9 ± 11.5 mm, Quesnel: 89.9 ± 6.6 mm), and did not differ significantly from each other ($t = 0.237$, $p = 0.813$). Shuswap Lake produced the shortest smolts on average (72.5 ± 10.9 mm) and their length differed significantly from all other populations (all $p < 0.005$). Smolt length data are summarized by population in Table 2 and by population and brood year in Tables 3a-3f. Model 1 results for statistical comparisons of smolt length by population are presented in Table 4.

#### *Smolt weight*

Cultus Lake smolts had the largest field weight of the populations studied (9.53 ± 1.97 g) and differed significantly from all other populations ($p < 0.001$). Smolts that reared in Seton Lake

were the next heaviest (6.12 ± 2.29 g) and differed significantly from all populations ($p < 0.001$), with the exception of Quesnel ($t = -0.969$, $p = 0.333$). The mean weight for Quesnel Lake smolts was 5.40 g (± 1.18 g), and they did not differ significantly from Chilliwack Lake smolts ($t = 1.797$, $p = 0.073$), which had an average weight of 5.63 g (± 1.73 g). Smolts that reared in Shuswap Lake were the lightest, with a mean weight of 3.57 g (± 1.79 g) and did not differ significantly from either Chilliwack Lake ($t = -1.262$, $p = 0.207$) or Chilko Lake smolts ($t = 0.347$, $p = 0.729$). Chilko Lake smolts had a mean weight of 4.86 g (± 1.84 g). Smolt weight data are summarized by population in Table 5 and by population and brood year in Tables 6a-6f. Model 1 results for statistical comparisons of smolt weight by population are presented in Table 7.

*Smolt condition factor*

Cultus Lake smolts had the highest mean condition factor of the populations studied (0.88 ± 0.07), but they were not statistically different from smolts that reared in Shuswap Lake (0.87 ± 0.10; $t = -0.332$, $p = 0.740$). Smolts from Seton Lake and Chilliwack Lake had intermediate condition factor (Seton: 0.78 ± 0.08, Chilliwack: 0.77 ± 0.05) and did not differ significantly from each other ($t = 0.283$, $p = 0.777$). Chilko Lake and Quesnel Lake smolts had the lowest mean condition factor across years (Chilko: 0.74 ± 0.06, Quesnel: 0.73 ± 0.03) and did not differ significantly between lakes ($t = -1.328$, $p = 0.185$). All other pairwise population comparisons were statistically significant ($p < 0.01$; see Table 10 for Model 1 results). Smolt condition factor data are summarized by population in Table 8 and by population and brood year in Tables 9a-9f.

*Smolt total lipid*

The raw total lipid data are presented as a percentage of body weight for each population and population by brood year (Table 11, Table 12a-12f). To facilitate fitting Model 1 to the lipid data, we compared total lipid weight, with fish weight as a covariate; the results of pairwise population comparisons are presented in Table 13.

Cultus Lake smolts had the highest total lipid content, as a percentage of body weight, of all the populations studied (4.96 ± 1.45%) and differed from all other populations in total lipid weight, after accounting for fish weight (all $p < 0.01$). Seton Lake smolts had the next highest percent total lipid of the populations studied (4.00 ± 1.85%) but did not differ significantly in total lipid weight from the smolts that reared in Shuswap Lake (2.88 ± 0.77%; $t = -1.696$, $p = 0.090$). The remaining three populations did not differ significantly from one another with respect to total lipid weight (Chilko and Chilliwack: $t = 0.806$, $p = 0.420$; Chilko and Quesnel: $t = 1.728$, $p = 0.084$; Chilliwack and Quesnel: $t = 1.322$, $p = 0.186$). Chilliwack Lake smolts had a mean total lipid of 2.77% (± 0.93), while Chilko Lake smolts had 2.69% (± 1.03%), and the smolts that reared in Quesnel Lake had 2.46% (± 0.80%).

MODEL 2:

Across the four iterations of Model 2 used to assess the relative importance of population-specific variables to the different condition metrics, there were strong relationships between explanatory and response variables. Lake productivity, measured as mean seasonal photosynthetic rate, had a significant positive relationship with smolt length, weight, and total lipid. The mixed effects model was a poor fit for the Fulton's condition factor data, and the null model was the only one in the confidence set. The values for lake area, lake productivity, and smolt migration distance are summarized for the six populations in Table 14.

*Smolt length*

The highest ranked model by AICc in the confidence set included all four explanatory variables from the global model and accounted for 56% of the variation in smolt length. In the averaged model, lake area had the largest magnitude effect (standardized coefficient = -4.89), although it was not statistically significant ($p = 0.065$). Lake productivity had a nearly equivalent opposite effect (standardized coefficient = 4.30), with lakes with higher photosynthetic rates producing larger smolts ($p = 0.008$). Smolts that were collected later (i.e. have later outmigration timing), relative to others in their cohort, were larger (standardized coefficient = 1.10), and this relationship was significant ($p = 0.011$). The model confidence set is presented in Table 16, and the coefficients for the averaged model are shown in Figure 2A.

*Smolt weight*

The top performing model in the confident set included lake productivity and capture date and accounted for 57% of variation in smolt weight. All four explanatory variables from the global model were represented in the averaged model of smolt weight. Lake productivity had the highest magnitude effect (standardized coefficient = 1.32), and the relationship was highly significant ($p < 0.001$). Smolts that were collected later (i.e. have later outmigration timing) were significantly heavier than those collected earlier in the year (standardized coefficient = 0.27, $p = 0.001$). Neither of the relationships between weight and lake area or migration distance were statistically significant (p: 0.19 and 0.80, respectively). The model confidence set is presented in Table 16, and the coefficients for the averaged model are shown in Figure 2B.

*Smolt condition factor*

None of the explanatory variables in the global model provided a better fit for the smolt condition factor data than the intercept alone, and the null model was the only model with a $\Delta$AICc value less than four, so no other candidate models were included in the confidence set.

The next best model (ΔAICc = 4.88) included lake productivity alone, and the two candidate models are compared in Table 16.

*Smolt total lipid*

Only two of the explanatory variables from the global model were represented in the averaged model of smolt total lipid. When the global model was dredged to produce all combinations of explanatory variables, fish weight was fixed in all models, to account for variation in the weight of total lipid with body size. The top model, which accounted for 90% of the variation in smolt total lipid, included fish weight and lake productivity. The relationship between total lipid and fish weight was positive and highly significant, indicating that heavier fish contain a greater mass of total lipid (standardized coefficient = 0.50, $p < 0.001$). Smolts from lakes with higher photosynthetic rates have greater total lipid mass, after accounting for smolt size (standardized coefficient = 0.16, $p < 0.001$). The model confidence set is presented in Table 16, and the coefficients for the averaged model are shown in Figure 2C.

## DISCUSSION

Our analysis confirmed that out-migrating smolts from different sockeye salmon populations in the Fraser River watershed differ in energetic status, as well as other condition metrics. The differences between populations across years appear to be greater than the differences between years within a population. The ranking of populations was relatively consistent across mean values of length, weight, Fulton's condition factor, and percent total lipid, with Cultus Lake-rearing smolts consistently in the best condition. Smolts from the Seton-Anderson system were also long, heavy, and had high condition factor and total lipid, relative to other populations. Conversely, smolts from Chilko consistently ranked low among populations. Most importantly, we observed that condition factor and total lipid convey additional information beyond length and weight alone. Although Shuswap fish are small, relative to juveniles from the other populations we examined, they are not in poor condition: Shuswap smolts were not statistically different from Cultus smolts in condition factor and Seton smolts in percent total lipid.

We determined that variation in habitat capacity explains more variation in smolt condition than measures of future migratory difficulty, such as migration distance. Although swimming longer distances should require greater energy stores, we did not observe a significant relationship between migration distance and total lipid. Indeed, the trend was opposite, with long distance migrants, like Chilko and Quesnel, having significantly lower lipid stores than smolts with shorter migrations, like Seton and Cultus.

Lake primary productivity is an important factor underlying smolt size and lipid content. Seasonal mean photosynthetic rate is a measure of phytoplankton availability to support the zooplankton community, which are the prey items for juvenile sockeye salmon. Much greater potential food availability in the most productive lake (i.e. Cultus) translates to greater surplus energy for growth or storage. Conversely, Chilko Lake is ultra-oligotrophic, with much less primary productivity to support bottom-up energy transfer to sockeye salmon, and the out-migrating smolts are relatively small, light, and low energy. Seton Lake, which has an inflow of glacial water from the Bridge River watershed for hydroelectric power production, has relatively high primary productivity but lower mean zooplankton biomass than nearly all Fraser River rearing lakes (422 mg dry wt·$m^{-2}$; Shortreed et al. 2001). However, the high lake turbidity provides visual protection from predation, and juveniles forage higher in the water column than juveniles Anderson Lake (Limnotek 2015), ultimately growing into some of the longest, heaviest, and most energy dense of the smolts we analyzed. Photosynthetic rate (PR) is used to model lake carrying capacity, and model results show good agreement with juvenile abundance (Fee *et al.* 1985; Downing *et al.* 1990; Grant *et al.* 2011).

Smolts from Cultus Lake had the best condition of all populations we studied, and this trend appears to be quite consistent through time. The population of sockeye salmon that rears in the highly productive lake is very small, and it is unlikely that it is approaching the carrying capacity, which would cause food limitation via competition within cohorts. However, if juvenile body condition were driving survival exclusively, we would expect higher adult returns to Cultus Lake. In Chapter 2, we examine density dependent dynamics and compare the abundances during the study years to carrying capacity estimates from PR models. In Chapter 4, we calculate adult recruits per smolt ratios for the Chilko and Cultus populations and assess the utility of including juvenile condition data in spawner-recruit relationships.

Juveniles in some populations may be feeding prior to outmigration, which would replenish lipid stores and provide an opportunity to increase in size, weight, and condition factor. The smolts collected later in the migration, relative to their population and brood, were longer and heavier, but this could also be caused by smaller fish leaving the lakes earlier. In Cultus Lake, warm temperatures and the absence of ice cover may support feeding throughout the winter. There is also a longer growing season in Shuswap Lake, relative to the higher elevation lakes in the study (i.e. Chilko, Chilliwack, and Quesnel), and smolts begin out-migrating later than in other systems, which may provide opportunities to feed. However, it is unknown whether growth is temperature- or ration-limited for spring parr in these populations; we assume that water is cold and prey are scarce in Chilko, Chilliwack, Quesnel, and Seton lakes in spring. To examine the effect of spring feeding on lipid stores, we examined the difference between mean total lipid in spring parr and smolts from the same cohort in Chapter 2.

Size metrics, like length and weight, are limited in comparing the condition of fish across populations, because they cannot account for morphological differences among populations. Fraser River sockeye salmon populations exhibit different morphologies at the juvenile life-stage (e.g. Weaver and Adams, Pon et al. 2007), which may relate to adaptations in swimming

ability. Percent total lipid provides additional information to distinguish between fish with higher weight to length ratios caused by morphology and body condition.

Further research into energetic differences between Fraser River sockeye salmon populations should disaggregate population groups that rear in the same lake, but have different population dynamics, such as early and late run timing groups in the Shuswap complex. Similarly, Gates Creek and Portage Creek populations have different migration timing (Hopkins et al. 2015), size and condition (D.A. Patterson, DFO Environmental Watch Program, unpublished data), adult escapement abundances, and rear across two lake systems. It would be useful for managers of Fraser River sockeye salmon populations to create a Fraser index to determine which juveniles are in the best condition, relative to other populations, each brood year.

TABLES

Table 1. Surface area, elevation, mean and maximum depth, seasonal mean photosynthetic rate, and distance to the Fraser River estuary for six sockeye salmon rearing lakes

| Lake | Surface area (ha) | Elevation (msl) | Mean depth (m) | Maximum depth (m) | Seasonal mean photosynthetic rate (mg C $m^{-2}$ $d^{-1}$) | Distance to Fraser estuary (km) |
|---|---|---|---|---|---|---|
| Chilko | 18,451 | 1172 | 123 | 330 | 121 | 677 |
| Chilliwack | 1,187 | 621 | 67 | 121 | 101 | 153 |
| Cultus | 630 | 46 | 21 | 44 | 404 | 110 |
| Quesnel | 26,090 | 725 | 158 | 530 | 130 | 748 |
| Seton | 2,519 | 237 | 85 | 151 | 233 | 333 |
| Anderson | 2,844 | 258 | 140 | 215 | 303 | 358 |
| Shuswap | 29,851 | 347 | 58 | 171 | 171 | 497 |

Table 2. Length data summaries by population

| Population | *n* | Mean | Median | Minimum | Maximum | $5^{th}$ quartile | $95^{th}$ quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| Chilko | 347 | 85.6 | 85 | 62 | 128 | 85 | 101 | 0.6 | 10.4 |
| Chilliwack | 210 | 89.3 | 90 | 59 | 119 | 90 | 106 | 0.6 | 9.1 |
| Cultus | 135 | 102.2 | 102 | 87 | 127 | 102 | 113.3 | 0.6 | 6.6 |
| Quesnel | 26 | 89.9 | 89.5 | 74 | 102 | 89.5 | 99.75 | 1.3 | 6.6 |
| Seton | 91 | 90.9 | 94 | 71 | 118 | 94 | 108.5 | 1.2 | 11.5 |
| Shuswap | 266 | 72.5 | 71 | 51 | 112 | 71 | 90.75 | 0.7 | 10.9 |

LENGTH DATA SUMMARIES BY POPULATION AND BROOD YEAR

Table 3a. Chilko smolts: length in mm

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2005 | 4 | 92.0 | 92.5 | 88 | 95 | 92.5 | 94.7 | 1.5 | 2.9 |
| 2006 | 7 | 83.6 | 84 | 78 | 92 | 84 | 89.9 | 1.8 | 4.8 |
| 2007 | 20 | 79.5 | 79 | 72 | 86 | 79 | 85.1 | 0.8 | 3.5 |
| 2008 | 20 | 95.2 | 91 | 74 | 128 | 91 | 126.1 | 3.6 | 16.1 |
| 2009 | 20 | 86.2 | 85 | 77 | 96 | 85 | 95.1 | 1.2 | 5.5 |
| 2010 | 42 | 75.9 | 76 | 62 | 88 | 76 | 85.0 | 0.8 | 5.1 |
| 2011 | 20 | 83.8 | 83.5 | 74 | 92 | 83.5 | 91.1 | 0.9 | 4.2 |
| 2012 | 79 | 97.2 | 97 | 82 | 106 | 97 | 104.1 | 0.5 | 4.7 |
| 2013 | 59 | 81.7 | 81 | 69 | 96 | 81 | 94.0 | 0.9 | 6.9 |
| 2014 | 56 | 79.4 | 76 | 64 | 104 | 76 | 96.5 | 1.2 | 9.1 |
| 2015 | 20 | 87.2 | 88.5 | 80 | 95 | 88.5 | 93.1 | 1.0 | 4.4 |

Table 3b. Chilliwack smolts: length in mm

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2012 | 100 | 84.4 | 84 | 59 | 99 | 84 | 94.0 | 0.7 | 6.6 |
| 2013 | 70 | 90.7 | 91 | 78 | 110 | 91 | 104.1 | 0.9 | 7.2 |
| 2014 | 20 | 98.1 | 96 | 83 | 114 | 96 | 114.0 | 1.8 | 8.1 |
| 2015 | 20 | 100.1 | 101 | 77 | 119 | 101 | 113.3 | 2.1 | 9.3 |

Table 3c. Cultus smolts: length in mm

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2007 | 20 | 100.3 | 99 | 90 | 110 | 99 | 110.0 | 1.4 | 6.4 |
| 2008 | 20 | 103.2 | 103.5 | 94 | 111 | 103.5 | 111.0 | 1.1 | 4.9 |
| 2009 | 20 | 105.3 | 105 | 93 | 114 | 105 | 114.0 | 1.2 | 5.3 |
| 2012 | 15 | 110.0 | 110 | 95 | 127 | 110 | 123.5 | 2.4 | 9.1 |
| 2013 | 20 | 97.3 | 97.5 | 87 | 111 | 97.5 | 104.4 | 1.2 | 5.5 |
| 2014 | 20 | 100.3 | 100.5 | 93 | 108 | 100.5 | 105.2 | 0.8 | 3.7 |
| 2015 | 20 | 101.3 | 101.5 | 94 | 110 | 101.5 | 109.1 | 1.0 | 4.4 |

Table 3d. Quesnel smolts: length in mm

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2013 | 2 | 111.5 | 111.5 | 107 | 116 | 111.5 | 115.6 | 4.5 | 6.4 |
| 2014 | 19 | 90.2 | 90 | 74 | 102 | 90 | 100.2 | 1.8 | 7.6 |
| 2015 | 7 | 89.3 | 89 | 85 | 94 | 89 | 92.8 | 1.0 | 2.7 |

Table 3e. Seton smolts: length in mm

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2010 | 21 | 75.2 | 75 | 71 | 80 | 75 | 78.0 | 0.5 | 2.1 |
| 2011 | 18 | 91.8 | 94.5 | 75 | 100 | 94.5 | 99.2 | 1.7 | 7.3 |
| 2012 | 12 | 98.6 | 98.5 | 93 | 104 | 98.5 | 104.0 | 1.0 | 3.4 |
| 2013 | 20 | 90.2 | 90 | 78 | 103 | 90 | 101.1 | 1.8 | 7.9 |
| 2015 | 20 | 102.7 | 100 | 93 | 118 | 100 | 113.3 | 1.6 | 7.1 |

Table 3f. Shuswap smolts: length in mm

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2010 | 195 | 69.3 | 69 | 51 | 95 | 69 | 84.0 | 0.7 | 9.2 |
| 2011 | 11 | 85.5 | 85 | 74 | 94 | 85 | 93.5 | 1.7 | 5.8 |
| 2014 | 60 | 80.5 | 79 | 61 | 112 | 79 | 100.0 | 1.4 | 10.9 |

Table 4. Coefficient estimates for all pairwise population comparisons of length of out-migrating smolts from six populations, generated from Model 1. The first population listed is the reference population, indicating the direction of the effect (e.g. 0.022 for Chilko:Chilliwack indicates that smolts from Chilko have lower mean length than smolts from Chilliwack). Bolded p-values indicate p<0.05.

| Pairwise population comparisons | Coefficient | Standard error | df | *t*-value | *p*-value |
|---|---|---|---|---|---|
| Chilko intercept | 85.947 | 1.804 | 1061 | 47.635 | 0.000 |
| Chilko:Chilliwack | 0.676 | 0.924 | 1061 | 0.732 | 0.464 |
| Chilko:Cultus | 14.796 | 0.728 | 1061 | 20.311 | **0.000** |
| Chilko:Quesnel | 6.224 | 1.882 | 1061 | 3.308 | **0.001** |
| Chilko:Seton | 6.697 | 0.896 | 1061 | 7.477 | **0.000** |
| Chilko:Shuswap | -3.242 | 0.914 | 1061 | -3.547 | **0.000** |
| Chilliwack intercept | 86.623 | 1.960 | 1061 | 44.191 | 0.000 |
| Chilliwack:Cultus | 14.120 | 1.024 | 1061 | 13.787 | **0.000** |
| Chilliwack:Quesnel | 5.548 | 2.018 | 1061 | 2.748 | **0.006** |
| Chilliwack:Seton | 6.021 | 1.137 | 1061 | 5.294 | **0.000** |
| Chilliwack:Shuswap | -3.918 | 1.220 | 1061 | -3.212 | **0.001** |
| Chilliwack:Chilko | -0.676 | 0.924 | 1061 | -0.732 | 0.464 |
| Cultus intercept | 100.743 | 1.849 | 1061 | 54.472 | 0.000 |
| Cultus:Quesnel | -8.572 | 1.919 | 1061 | -4.466 | **0.000** |
| Cultus:Seton | -8.099 | 1.012 | 1061 | -8.004 | **0.000** |
| Cultus:Shuswap | -18.038 | 1.068 | 1061 | -16.895 | **0.000** |
| Cultus:Chilko | -14.796 | 0.728 | 1061 | -20.311 | **0.000** |
| Cultus:Chilliwack | -14.120 | 1.024 | 1061 | -13.787 | **0.000** |
| Quesnel intercept | 92.171 | 2.547 | 1061 | 36.190 | 0.000 |

| | | | | | |
|---|---|---|---|---|---|
| Quesnel:Seton | 0.473 | 1.998 | 1061 | 0.237 | 0.813 |
| Quesnel:Shuswap | -9.466 | 1.982 | 1061 | -4.777 | **0.000** |
| Quesnel:Chilko | -6.224 | 1.882 | 1061 | -3.308 | **0.001** |
| Quesnel:Chilliwack | -5.548 | 2.019 | 1061 | -2.748 | **0.006** |
| Quesnel:Cultus | 8.572 | 1.919 | 1061 | 4.466 | **0.000** |
| Seton intercept | 92.644 | 1.930 | 1061 | 47.997 | 0.000 |
| Seton:Shuswap | -9.939 | 1.079 | 1061 | -9.208 | **0.000** |
| Seton:Chilko | -6.697 | 0.896 | 1061 | -7.477 | **0.000** |
| Seton:Chilliwack | -6.021 | 1.137 | 1061 | -5.294 | **0.000** |
| Seton:Cultus | 8.099 | 1.012 | 1061 | 8.004 | **0.000** |
| Seton:Quesnel | -0.473 | 1.998 | 1061 | -0.237 | 0.813 |
| Shuswap intercept | 82.705 | 1.946 | 1061 | 42.503 | 0.000 |
| Shuswap:Chilko | 3.242 | 0.914 | 1061 | 3.547 | **0.000** |
| Shuswap:Chilliwack | 3.918 | 1.220 | 1061 | 3.212 | **0.001** |
| Shuswap:Cultus | 18.038 | 1.068 | 1061 | 16.895 | **0.000** |
| Shuswap:Quesnel | 9.466 | 1.982 | 1061 | 4.777 | **0.000** |
| Shuswap:Seton | 9.939 | 1.079 | 1061 | 9.208 | **0.000** |

Table 5. Weight data summaries by population

| Population | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| Chilko | 347 | 4.86 | 4.49 | 1.76 | 13.47 | 4.49 | 8.16 | 0.10 | 1.84 |
| Chilliwack | 210 | 5.63 | 5.44 | 1.52 | 12.99 | 5.44 | 8.92 | 0.12 | 1.73 |
| Cultus | 134 | 9.53 | 9.38 | 5.80 | 17.59 | 9.38 | 12.89 | 0.17 | 1.97 |
| Quesnel | 26 | 5.40 | 5.40 | 2.73 | 7.45 | 5.40 | 7.36 | 0.23 | 1.18 |
| Seton | 91 | 6.12 | 6.67 | 2.66 | 12.67 | 6.67 | 9.81 | 0.24 | 2.29 |
| Shuswap | 266 | 3.57 | 3.21 | 1.05 | 12.52 | 3.21 | 6.49 | 0.11 | 1.79 |

WEIGHT DATA SUMMARIES BY POPULATION AND BROOD YEAR

Table 6a. Chilko smolts: wet weight in g

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2005 | 4 | 6.0 | 6.2 | 5.1 | 6.4 | 6.2 | 6.4 | 0.3 | 0.6 |
| 2006 | 7 | 4.8 | 4.8 | 3.8 | 6.0 | 4.8 | 5.8 | 0.3 | 0.7 |
| 2007 | 20 | 3.8 | 3.8 | 2.9 | 5.0 | 3.8 | 4.8 | 0.1 | 0.6 |
| 2008 | 20 | 6.3 | 5.1 | 2.7 | 13.5 | 5.1 | 13.4 | 0.8 | 3.6 |
| 2009 | 20 | 4.5 | 4.5 | 3.2 | 6.4 | 4.5 | 6.2 | 0.2 | 1.0 |
| 2010 | 42 | 3.3 | 3.2 | 1.8 | 4.9 | 3.2 | 4.2 | 0.1 | 0.6 |
| 2011 | 20 | 4.7 | 4.6 | 3.4 | 6.1 | 4.6 | 5.6 | 0.1 | 0.6 |
| 2012 | 79 | 7.0 | 6.9 | 3.9 | 9.2 | 6.9 | 8.5 | 0.1 | 1.0 |
| 2013 | 59 | 4.1 | 3.9 | 2.5 | 6.7 | 3.9 | 6.0 | 0.1 | 1.1 |
| 2014 | 56 | 3.8 | 3.4 | 1.9 | 8.1 | 3.4 | 6.3 | 0.2 | 1.3 |
| 2015 | 20 | 4.9 | 4.9 | 3.8 | 5.9 | 4.9 | 5.9 | 0.2 | 0.7 |

Table 6b. Chilliwack smolts: wet weight in g

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2012 | 100 | 4.7 | 4.6 | 1.5 | 7.2 | 4.6 | 6.3 | 0.1 | 1.0 |
| 2013 | 70 | 5.8 | 5.7 | 3.6 | 10.3 | 5.7 | 8.5 | 0.2 | 1.3 |
| 2014 | 20 | 7.2 | 6.5 | 4.1 | 11.7 | 6.5 | 11.0 | 0.4 | 1.9 |
| 2015 | 20 | 8.0 | 7.9 | 3.7 | 13.0 | 7.9 | 11.2 | 0.5 | 2.2 |

Table 6c. Cultus smolts: wet weight in g

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2007 | 20 | 9.6 | 9.3 | 6.6 | 12.9 | 9.3 | 12.4 | 0.4 | 1.9 |
| 2008 | 20 | 8.9 | 9.0 | 6.4 | 10.2 | 9.0 | 10.1 | 0.3 | 1.1 |
| 2009 | 20 | 10.2 | 10.4 | 6.8 | 13.7 | 10.4 | 12.9 | 0.4 | 1.8 |
| 2012 | 15 | 11.9 | 11.1 | 7.4 | 17.6 | 11.1 | 16.8 | 0.8 | 3.0 |
| 2013 | 20 | 8.2 | 8.0 | 5.8 | 12.6 | 8.0 | 10.3 | 0.4 | 1.6 |
| 2014 | 20 | 9.0 | 9.1 | 7.4 | 11.4 | 9.1 | 10.5 | 0.2 | 1.1 |
| 2015 | 20 | 9.4 | 9.4 | 7.9 | 11.4 | 9.4 | 11.4 | 0.2 | 1.1 |

Table 6d. Quesnel smolts: wet weight in g

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2013 | 2 | 10.8 | 10.8 | 9.9 | 11.7 | 10.8 | 11.6 | 0.9 | 1.2 |
| 2014 | 19 | 5.4 | 5.7 | 2.7 | 7.4 | 5.7 | 7.4 | 0.3 | 1.4 |
| 2015 | 7 | 5.3 | 5.3 | 4.7 | 6.1 | 5.3 | 6.0 | 0.2 | 0.5 |

Table 6e. Seton smolts: wet weight in g

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2010 | 21 | 3.1 | 3.1 | 2.7 | 3.6 | 3.1 | 3.6 | 0.1 | 0.3 |
| 2011 | 18 | 6.7 | 7.2 | 3.8 | 8.7 | 7.2 | 8.4 | 0.3 | 1.4 |
| 2012 | 12 | 7.0 | 7.1 | 6.0 | 8.5 | 7.1 | 8.0 | 0.2 | 0.7 |
| 2013 | 20 | 5.8 | 5.2 | 3.4 | 8.7 | 5.2 | 8.4 | 0.4 | 1.7 |
| 2015 | 20 | 8.5 | 7.9 | 6.7 | 12.7 | 7.9 | 11.3 | 0.4 | 1.6 |

Table 6f. Shuswap smolts: wet weight in g

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2010 | 195 | 3.0 | 2.7 | 1.0 | 7.1 | 2.7 | 5.2 | 0.1 | 1.2 |
| 2011 | 11 | 5.8 | 5.9 | 3.3 | 7.4 | 5.9 | 7.2 | 0.4 | 1.2 |
| 2014 | 60 | 5.0 | 4.9 | 1.9 | 12.5 | 4.9 | 9.2 | 0.3 | 2.2 |

Table 7. Coefficient estimates for all pairwise population comparisons of weight of out-migrating smolts from six populations, generated from Model 1. The first population listed is the reference population, indicating the direction of the effect (e.g. 0.022 for Chilko:Chilliwack indicates that smolts from Chilko have lower mean weight than smolts from Chilliwack). Bolded p-values indicate p<0.05.

| Pairwise population comparisons | Coefficient | Standard error | df | *t*-value | *p*-value |
|---|---|---|---|---|---|
| Chilko intercept | 1.539 | 0.063 | 1061 | 24.348 | 0.000 |
| Chilko:Chilliwack | 0.067 | 0.030 | 1061 | 2.238 | **0.025** |
| Chilko:Cultus | 0.662 | 0.024 | 1061 | 27.643 | **0.000** |
| Chilko:Quesnel | 0.189 | 0.064 | 1061 | 2.952 | **0.003** |
| Chilko:Seton | 0.255 | 0.030 | 1061 | 8.426 | **0.000** |
| Chilko:Shuswap | 0.012 | 0.036 | 1061 | 0.347 | 0.729 |
| Chilliwack intercept | 1.606 | 0.067 | 1061 | 23.828 | 0.000 |
| Chilliwack:Cultus | 0.594 | 0.032 | 1061 | 18.511 | **0.000** |

| | | | | | |
|---|---|---|---|---|---|
| Chilliwack:Quesnel | 0.122 | 0.068 | 1061 | 1.797 | **0.073** |
| Chilliwack:Seton | 0.187 | 0.037 | 1061 | 5.083 | **0.000** |
| Chilliwack:Shuswap | -0.055 | 0.044 | 1061 | -1.262 | 0.207 |
| Chilliwack:Chilko | -0.067 | 0.030 | 1061 | -2.238 | **0.025** |
| Cultus intercept | 2.200 | 0.064 | 1061 | 34.350 | 0.000 |
| Cultus:Quesnel | -0.473 | 0.064 | 1061 | -7.334 | **0.000** |
| Cultus:Seton | -0.407 | 0.033 | 1061 | -12.363 | **0.000** |
| Cultus:Shuswap | -0.649 | 0.039 | 1061 | -16.535 | **0.000** |
| Cultus:Chilko | -0.662 | 0.024 | 1061 | -27.643 | **0.000** |
| Cultus:Chilliwack | -0.594 | 0.032 | 1061 | -18.511 | **0.000** |
| Quesnel intercept | 1.728 | 0.088 | 1061 | 19.703 | **0.000** |
| Quesnel:Seton | 0.066 | 0.068 | 1061 | 0.969 | 0.333 |
| Quesnel:Shuswap | -0.177 | 0.070 | 1061 | -2.538 | **0.011** |
| Quesnel:Chilko | -0.189 | 0.064 | 1061 | -2.952 | **0.003** |
| Quesnel:Chilliwack | -0.122 | 0.068 | 1061 | -1.797 | 0.073 |
| Quesnel:Cultus | 0.473 | 0.064 | 1061 | 7.334 | **0.000** |
| Seton intercept | 1.793 | 0.067 | 1061 | 26.807 | 0.000 |
| Seton:Shuswap | -0.242 | 0.039 | 1061 | -6.139 | **0.000** |
| Seton:Chilko | -0.255 | 0.030 | 1061 | -8.426 | **0.000** |
| Seton:Chilliwack | -0.187 | 0.037 | 1061 | -5.083 | **0.000** |
| Seton:Cultus | 0.407 | 0.033 | 1061 | 12.363 | **0.000** |
| Seton:Quesnel | -0.066 | 0.068 | 1061 | -0.969 | 0.333 |
| Shuswap intercept | 1.551 | 0.070 | 1061 | 22.244 | 0.000 |
| Shuswap:Chilko | -0.012 | 0.036 | 1061 | -0.347 | 0.729 |
| Shuswap:Chilliwack | 0.055 | 0.044 | 1061 | 1.262 | 0.207 |
| Shuswap:Cultus | 0.649 | 0.039 | 1061 | 16.535 | **0.000** |
| Shuswap:Quesnel | 0.177 | 0.070 | 1061 | 2.538 | **0.011** |
| Shuswap:Seton | 0.242 | 0.039 | 1061 | 6.139 | **0.000** |

Table 8. Condition factor (Fulton's *k*) data summaries by population

| Population | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| Chilko | 347 | 0.74 | 0.74 | 0.53 | 0.98 | 0.74 | 0.83 | 0.00 | 0.06 |
| Chilliwack | 210 | 0.77 | 0.77 | 0.57 | 1.21 | 0.77 | 0.83 | 0.00 | 0.05 |
| Cultus | 134 | 0.88 | 0.88 | 0.64 | 1.37 | 0.88 | 0.97 | 0.01 | 0.07 |
| Quesnel | 26 | 0.73 | 0.73 | 0.67 | 0.80 | 0.73 | 0.78 | 0.01 | 0.03 |
| Seton | 91 | 0.78 | 0.77 | 0.54 | 1.00 | 0.77 | 0.89 | 0.01 | 0.08 |
| Shuswap | 266 | 0.87 | 0.86 | 0.57 | 1.83 | 0.86 | 0.99 | 0.01 | 0.10 |

CONDITION FACTOR (FULTON'S *K*) DATA SUMMARIES BY POPULATION AND BROOD YEAR

Table 9a. Chilko smolts: condition factor (Fulton's *k*)

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2005 | 4 | 0.77 | 0.75 | 0.75 | 0.82 | 0.75 | 0.81 | 0.02 | 0.04 |
| 2006 | 7 | 0.82 | 0.82 | 0.74 | 0.90 | 0.82 | 0.89 | 0.02 | 0.06 |
| 2007 | 20 | 0.75 | 0.76 | 0.69 | 0.83 | 0.76 | 0.80 | 0.01 | 0.04 |
| 2008 | 20 | 0.67 | 0.68 | 0.53 | 0.75 | 0.68 | 0.72 | 0.01 | 0.05 |
| 2009 | 20 | 0.70 | 0.70 | 0.62 | 0.78 | 0.70 | 0.75 | 0.01 | 0.04 |
| 2010 | 42 | 0.74 | 0.74 | 0.63 | 0.87 | 0.74 | 0.82 | 0.01 | 0.05 |
| 2011 | 20 | 0.79 | 0.79 | 0.72 | 0.91 | 0.79 | 0.88 | 0.01 | 0.05 |
| 2012 | 79 | 0.76 | 0.76 | 0.65 | 0.88 | 0.76 | 0.83 | 0.01 | 0.05 |
| 2013 | 59 | 0.75 | 0.75 | 0.63 | 0.86 | 0.75 | 0.83 | 0.01 | 0.05 |
| 2014 | 56 | 0.74 | 0.73 | 0.55 | 0.98 | 0.73 | 0.85 | 0.01 | 0.08 |
| 2015 | 20 | 0.74 | 0.73 | 0.68 | 0.79 | 0.73 | 0.78 | 0.01 | 0.03 |

Table 9b. Chilliwack smolts: condition factor (Fulton's *k*)

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2012 | 100 | 0.77 | 0.78 | 0.57 | 0.87 | 0.78 | 0.83 | 0.00 | 0.04 |
| 2013 | 70 | 0.77 | 0.77 | 0.67 | 1.21 | 0.77 | 0.84 | 0.01 | 0.07 |
| 2014 | 20 | 0.75 | 0.74 | 0.71 | 0.81 | 0.74 | 0.79 | 0.01 | 0.03 |
| 2015 | 20 | 0.78 | 0.78 | 0.73 | 0.84 | 0.78 | 0.82 | 0.01 | 0.03 |

Table 9c. Cultus smolts: condition factor (Fulton's *k*)

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2007 | 20 | 0.95 | 0.91 | 0.87 | 1.37 | 0.91 | 1.06 | 0.02 | 0.11 |
| 2008 | 20 | 0.81 | 0.81 | 0.74 | 0.89 | 0.81 | 0.88 | 0.01 | 0.05 |
| 2009 | 20 | 0.86 | 0.87 | 0.64 | 0.97 | 0.87 | 0.93 | 0.01 | 0.07 |
| 2012 | 15 | 0.88 | 0.87 | 0.78 | 0.97 | 0.87 | 0.94 | 0.01 | 0.05 |
| 2013 | 20 | 0.88 | 0.90 | 0.79 | 0.95 | 0.90 | 0.94 | 0.01 | 0.04 |
| 2014 | 19 | 0.89 | 0.89 | 0.83 | 0.98 | 0.89 | 0.94 | 0.01 | 0.04 |
| 2015 | 20 | 0.91 | 0.91 | 0.81 | 0.99 | 0.91 | 0.99 | 0.01 | 0.05 |

Table 9d. Quesnel smolts: condition factor (Fulton's *k*)

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2014 | 19 | 0.73 | 0.72 | 0.67 | 0.78 | 0.72 | 0.77 | 0.01 | 0.03 |
| 2015 | 7 | 0.75 | 0.74 | 0.69 | 0.80 | 0.74 | 0.79 | 0.01 | 0.04 |

Table 9e. Seton smolts: condition factor (Fulton's *k*)

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2010 | 21 | 0.74 | 0.73 | 0.59 | 0.89 | 0.73 | 0.83 | 0.01 | 0.07 |
| 2011 | 18 | 0.86 | 0.86 | 0.79 | 0.94 | 0.86 | 0.90 | 0.01 | 0.03 |
| 2012 | 12 | 0.73 | 0.74 | 0.66 | 0.79 | 0.74 | 0.79 | 0.01 | 0.04 |
| 2013 | 20 | 0.76 | 0.76 | 0.66 | 0.85 | 0.76 | 0.85 | 0.01 | 0.05 |
| 2015 | 20 | 0.79 | 0.78 | 0.54 | 1.00 | 0.78 | 0.92 | 0.02 | 0.09 |

Table 9f. Shuswap smolts: condition factor (Fulton's *k*)

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2010 | 195 | 0.85 | 0.84 | 0.57 | 1.83 | 0.84 | 0.97 | 0.01 | 0.10 |
| 2011 | 11 | 0.92 | 0.92 | 0.82 | 1.03 | 0.92 | 1.01 | 0.02 | 0.07 |
| 2014 | 60 | 0.91 | 0.92 | 0.70 | 1.12 | 0.92 | 1.04 | 0.01 | 0.07 |

Table 10. Coefficient estimates for all pairwise population comparisons of Fulton's condition factor of out-migrating smolts from six populations, generated from Model 1. The first population listed is the reference population, indicating the direction of the effect (e.g. 0.022 for Chilko:Chilliwack indicates that smolts from Chilko have lower mean condition factor than smolts from Chilliwack). Bolded p-values indicate $p<0.05$.

| Pairwise population comparisons | Coefficient | Standard error | df | *t*-value | *p*-value |
|---|---|---|---|---|---|
| Chilko intercept | 0.747 | 0.013 | 1058 | 56.968 | 0.000 |
| Chilko:Chilliwack | 0.022 | 0.006 | 1058 | 3.465 | **0.001** |
| Chilko:Cultus | 0.147 | 0.007 | 1058 | 20.093 | **0.000** |
| Chilko:Quesnel | -0.019 | 0.014 | 1058 | -1.328 | 0.185 |
| Chilko:Seton | 0.025 | 0.008 | 1058 | 2.964 | **0.003** |
| Chilko:Shuswap | 0.144 | 0.007 | 1058 | 19.666 | **0.000** |
| Chilliwack intercept | 0.770 | 0.014 | 1058 | 55.247 | 0.000 |
| Chilliwack:Cultus | 0.125 | 0.008 | 1058 | 14.810 | **0.000** |
| Chilliwack:Quesnel | -0.041 | 0.015 | 1058 | -2.759 | **0.006** |

| | | | | | |
|---|---|---|---|---|---|
| Chilliwack:Seton | 0.003 | 0.009 | 1058 | 0.283 | 0.777 |
| Chilliwack:Shuswap | 0.122 | 0.009 | 1058 | 13.602 | **0.000** |
| Chilliwack:Chilko | -0.022 | 0.006 | 1058 | -3.465 | **0.001** |
| Cultus intercept | 0.895 | 0.014 | 1058 | 63.624 | 0.000 |
| Cultus:Quesnel | -0.166 | 0.015 | 1058 | -10.858 | **0.000** |
| Cultus:Seton | -0.122 | 0.010 | 1058 | -12.092 | **0.000** |
| Cultus:Shuswap | -0.003 | 0.010 | 1058 | -0.332 | 0.740 |
| Cultus:Chilko | -0.147 | 0.007 | 1058 | -20.093 | **0.000** |
| Cultus:Chilliwack | -0.125 | 0.008 | 1058 | -14.810 | **0.000** |
| Quesnel intercept | 0.728 | 0.019 | 1058 | 38.548 | 0.000 |
| Quesnel:Seton | 0.044 | 0.016 | 1058 | 2.781 | **0.006** |
| Quesnel:Shuswap | 0.163 | 0.015 | 1058 | 10.894 | **0.000** |
| Quesnel:Chilko | 0.019 | 0.014 | 1058 | 1.328 | 0.185 |
| Quesnel:Chilliwack | 0.041 | 0.015 | 1058 | 2.759 | **0.006** |
| Quesnel:Cultus | 0.166 | 0.015 | 1058 | 10.858 | **0.000** |
| Seton intercept | 0.772 | 0.015 | 1058 | 52.250 | 0.000 |
| Seton:Shuswap | 0.119 | 0.009 | 1058 | 12.553 | **0.000** |
| Seton:Chilko | -0.025 | 0.008 | 1058 | -2.964 | **0.003** |
| Seton:Chilliwack | -0.003 | 0.009 | 1058 | -0.283 | 0.777 |
| Seton:Cultus | 0.122 | 0.010 | 1058 | 12.092 | **0.000** |
| Seton:Quesnel | -0.044 | 0.016 | 1058 | -2.781 | **0.006** |
| Shuswap intercept | 0.891 | 0.014 | 1058 | 62.525 | 0.000 |
| Shuswap:Chilko | -0.144 | 0.007 | 1058 | -19.666 | **0.000** |
| Shuswap:Chilliwack | -0.122 | 0.009 | 1058 | -13.602 | **0.000** |
| Shuswap:Cultus | 0.003 | 0.010 | 1058 | 0.332 | 0.740 |
| Shuswap:Quesnel | -0.163 | 0.015 | 1058 | -10.894 | **0.000** |
| Shuswap:Seton | -0.119 | 0.009 | 1058 | -12.553 | **0.000** |

Table 11. Percent lipid data summaries by population

| Population | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| Chilko | 347 | 2.69 | 2.39 | 1.01 | 8.37 | 2.39 | 4.68 | 0.06 | 1.03 |
| Chilliwack | 210 | 2.77 | 2.59 | 0.88 | 5.68 | 2.59 | 4.45 | 0.06 | 0.93 |
| Cultus | 134 | 4.96 | 4.91 | 1.79 | 8.58 | 4.91 | 7.64 | 0.13 | 1.45 |
| Quesnel | 26 | 2.46 | 2.22 | 1.17 | 5.28 | 2.22 | 3.83 | 0.16 | 0.80 |
| Seton | 91 | 4.00 | 3.63 | 1.30 | 8.95 | 3.63 | 7.42 | 0.19 | 1.85 |
| Shuswap | 266 | 2.88 | 2.78 | 1.41 | 5.49 | 2.78 | 4.28 | 0.05 | 0.77 |

PERCENT LIPID DATA SUMMARIES BY POPULATION AND BROOD YEAR

Table 12a. Chilko smolts: percent lipid (g total lipid / g wet weight)

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2005 | 4 | 2.53 | 2.37 | 1.86 | 3.53 | 2.37 | 3.41 | 0.38 | 0.76 |
| 2006 | 7 | 3.42 | 3.19 | 2.62 | 4.33 | 3.19 | 4.28 | 0.28 | 0.74 |
| 2007 | 20 | 2.84 | 2.79 | 1.36 | 5.99 | 2.79 | 4.17 | 0.23 | 1.04 |
| 2008 | 20 | 2.34 | 2.21 | 1.47 | 3.89 | 2.21 | 3.73 | 0.15 | 0.67 |
| 2009 | 20 | 2.73 | 2.32 | 1.64 | 4.97 | 2.32 | 4.57 | 0.23 | 1.03 |
| 2010 | 42 | 2.15 | 1.96 | 1.19 | 4.18 | 1.96 | 3.51 | 0.09 | 0.61 |
| 2011 | 20 | 2.47 | 2.25 | 1.44 | 4.52 | 2.25 | 3.73 | 0.19 | 0.86 |
| 2012 | 79 | 3.15 | 3.00 | 1.41 | 7.08 | 3.00 | 5.26 | 0.14 | 1.23 |
| 2013 | 59 | 2.55 | 2.20 | 1.63 | 6.56 | 2.20 | 4.74 | 0.13 | 0.97 |
| 2014 | 56 | 2.57 | 2.42 | 1.01 | 8.37 | 2.42 | 3.95 | 0.14 | 1.08 |
| 2015 | 20 | 2.82 | 2.78 | 1.75 | 4.41 | 2.78 | 4.09 | 0.17 | 0.74 |

Table 12b. Chilliwack smolts: percent lipid (g total lipid / g wet weight)

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2012 | 100 | 2.54 | 2.34 | 0.88 | 5.68 | 2.34 | 4.43 | 0.10 | 0.97 |
| 2013 | 70 | 2.95 | 2.89 | 1.61 | 4.72 | 2.89 | 4.21 | 0.08 | 0.69 |
| 2014 | 20 | 3.12 | 2.90 | 1.20 | 5.36 | 2.90 | 4.75 | 0.25 | 1.10 |
| 2015 | 20 | 2.93 | 2.69 | 1.71 | 5.38 | 2.69 | 4.48 | 0.23 | 1.01 |

Table 12c. Cultus smolts: percent lipid (g total lipid / g wet weight)

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2007 | 20 | 4.36 | 4.47 | 1.88 | 6.85 | 4.47 | 6.38 | 0.32 | 1.41 |
| 2008 | 20 | 5.19 | 5.09 | 3.43 | 7.76 | 5.09 | 7.62 | 0.24 | 1.05 |
| 2009 | 20 | 4.11 | 4.49 | 1.79 | 6.21 | 4.49 | 5.78 | 0.27 | 1.21 |
| 2012 | 15 | 5.06 | 4.77 | 3.20 | 6.65 | 4.77 | 6.61 | 0.30 | 1.16 |
| 2013 | 20 | 4.97 | 4.97 | 3.15 | 7.45 | 4.97 | 7.25 | 0.29 | 1.29 |
| 2014 | 19 | 5.59 | 5.68 | 2.65 | 8.58 | 5.68 | 8.26 | 0.44 | 1.91 |
| 2015 | 20 | 5.51 | 5.72 | 3.06 | 8.48 | 5.72 | 7.58 | 0.32 | 1.45 |

Table 12d. Quesnel smolts: percent lipid (g total lipid / g wet weight)

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2014 | 19 | 2.44 | 2.23 | 1.38 | 5.28 | 2.23 | 3.09 | 0.18 | 0.77 |
| 2015 | 7 | 2.52 | 2.20 | 1.17 | 3.92 | 2.20 | 3.81 | 0.36 | 0.94 |

Table 12e. Seton smolts: percent lipid (g total lipid / g wet weight)

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2010 | 21 | 2.16 | 1.94 | 1.30 | 3.39 | 1.94 | 3.15 | 0.14 | 0.62 |
| 2011 | 18 | 4.83 | 4.99 | 2.04 | 8.00 | 4.99 | 7.40 | 0.46 | 1.95 |
| 2012 | 12 | 4.82 | 4.76 | 2.18 | 6.82 | 4.76 | 6.63 | 0.37 | 1.28 |
| 2013 | 20 | 3.88 | 3.59 | 1.65 | 8.29 | 3.59 | 6.34 | 0.37 | 1.65 |
| 2015 | 20 | 4.81 | 4.24 | 2.18 | 8.95 | 4.24 | 7.74 | 0.40 | 1.77 |

Table 12f. Shuswap smolts: percent lipid (g total lipid / g wet weight)

| Brood year | *n* | Mean | Median | Minimum | Maximum | 5th quartile | 95th quartile | SE | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2010 | 195 | 2.84 | 2.70 | 1.41 | 5.49 | 2.70 | 4.24 | 0.06 | 0.78 |
| 2011 | 11 | 2.79 | 2.76 | 1.81 | 4.14 | 2.76 | 3.85 | 0.20 | 0.65 |
| 2014 | 60 | 3.03 | 3.00 | 1.50 | 4.93 | 3.00 | 4.53 | 0.10 | 0.77 |

Table 13. Coefficient estimates for all pairwise population comparisons of percent total lipid of out-migrating smolts from six populations, generated from Model 1. The first population listed is the reference population, indicating the direction of the effect (e.g. 0.022 for Chilko:Chilliwack indicates that smolts from Chilko have lower mean percent total lipid than smolts from Chilliwack). Bolded p-values indicate $p<0.05$.

| Pairwise population comparisons | Coefficient | Standard error | df | *t*-value | *p*-value |
|---|---|---|---|---|---|
| Chilko intercept | -4.033 | 0.050 | 1057 | -80.561 | 0.000 |
| Chilko:Chilliwack | -0.024 | 0.030 | 1057 | -0.806 | 0.420 |
| Chilko:Cultus | 0.459 | 0.039 | 1057 | 11.790 | **0.000** |
| Chilko:Quesnel | -0.116 | 0.067 | 1057 | -1.728 | 0.084 |
| Chilko:Seton | 0.296 | 0.039 | 1057 | 7.529 | **0.000** |
| Chilko:Shuswap | 0.221 | 0.032 | 1057 | 6.951 | **0.000** |
| Chilko:field wt | 1.233 | 0.029 | 1057 | 42.123 | **0.000** |
| Chilliwack intercept | -4.057 | 0.056 | 1057 | -72.432 | 0.000 |
| Chilliwack:Cultus | 0.482 | 0.041 | 1057 | 11.652 | **0.000** |

| | | | | | |
|---|---|---|---|---|---|
| Chilliwack:Quesnel | -0.092 | 0.069 | 1057 | -1.322 | 0.186 |
| Chilliwack:Seton | 0.319 | 0.042 | 1057 | 7.557 | **0.000** |
| Chilliwack:Shuswap | 0.245 | 0.039 | 1057 | 6.304 | **0.000** |
| Chilliwack:Chilko | 0.024 | 0.030 | 1057 | 0.806 | 0.420 |
| Chilliwack:field wt | 1.233 | 0.029 | 1057 | 42.123 | **0.000** |
| Cultus intercept | -3.575 | 0.072 | 1057 | -49.758 | 0.000 |
| Cultus:Quesnel | -0.574 | 0.073 | 1057 | -7.914 | **0.000** |
| Cultus:Seton | -0.163 | 0.047 | 1057 | -3.455 | **0.001** |
| Cultus:Shuswap | -0.237 | 0.047 | 1057 | -5.064 | **0.000** |
| Cultus:Chilko | -0.459 | 0.039 | 1057 | -11.790 | **0.000** |
| Cultus:Chilliwack | -0.482 | 0.041 | 1057 | -11.652 | **0.000** |
| Cultus:field wt | 1.233 | 0.029 | 1057 | 42.123 | **0.000** |
| Quesnel intercept | -4.149 | 0.082 | 1057 | -50.778 | 0.000 |
| Quesnel:Seton | 0.411 | 0.074 | 1057 | 5.589 | **0.000** |
| Quesnel:Shuswap | 0.337 | 0.069 | 1057 | 4.860 | **0.000** |
| Quesnel:Chilko | 0.116 | 0.067 | 1057 | 1.728 | 0.084 |
| Quesnel:Chilliwack | 0.092 | 0.069 | 1057 | 1.322 | 0.186 |
| Quesnel:Cultus | 0.574 | 0.073 | 1057 | 7.914 | **0.000** |
| Quesnel:field wt | 1.233 | 0.029 | 1057 | 42.123 | **0.000** |
| Seton intercept | -3.738 | 0.064 | 1057 | -58.551 | 0.000 |
| Seton:Shuswap | -0.074 | 0.044 | 1057 | -1.696 | 0.090 |
| Seton:Chilko | -0.296 | 0.039 | 1057 | -7.529 | **0.000** |
| Seton:Chilliwack | -0.319 | 0.042 | 1057 | -7.557 | **0.000** |
| Seton:Cultus | 0.163 | 0.047 | 1057 | 3.455 | **0.001** |
| Seton:Quesnel | -0.411 | 0.074 | 1057 | -5.589 | **0.000** |
| Seton:field wt | 1.233 | 0.029 | 1057 | 42.123 | **0.000** |
| Shuswap intercept | -3.812 | 0.051 | 1057 | -74.200 | 0.000 |
| Shuswap:Chilko | -0.221 | 0.032 | 1057 | -6.951 | **0.000** |
| Shuswap:Chilliwack | -0.245 | 0.039 | 1057 | -6.304 | **0.000** |
| Shuswap:Cultus | 0.237 | 0.047 | 1057 | 5.064 | **0.000** |
| Shuswap:Quesnel | -0.337 | 0.069 | 1057 | -4.860 | **0.000** |
| Shuswap:Seton | 0.074 | 0.044 | 1057 | 1.696 | 0.090 |
| Shuswap:field wt | 1.233 | 0.029 | 1057 | 42.123 | **0.000** |

Table 16. Model 2 confidence model sets (models with cumulative Akaike weights ≥ 0.95) from multimodal inference of variables influencing sockeye salmon smolt condition metrics, along with the null model.

| Response | Model | K | logLik | AICc | ΔAICc | $w_i$ | $r^2$ |
|---|---|---|---|---|---|---|---|
| Length | PR + lake area + migration distance + capture date | 4 | -3864.3 | 7744.8 | 0.00 | 0.64 | 0.5647 |
| | PR + lake area + capture date | 3 | -3867.1 | 7748.3 | 3.51 | 0.11 | 0.5638 |
| | *Null:* intercept | 0 | -3876.9 | 7761.7 | 17.0 | 0.00 | |
| Weight | PR + capture date | 2 | -2081.0 | 4174.0 | 0.00 | 0.39 | 0.5746 |
| | PR+ capture date + lake area | 3 | -2080.3 | 4174.8 | 0.76 | 0.27 | 0.5759 |
| | PR + capture date + migration distance | 3 | -2080.9 | 4175.9 | 1.92 | 0.15 | 0.5749 |
| | PR + capture date + lake area + migration distance | 4 | -2080.3 | 4176.7 | 2.68 | 0.10 | 0.5753 |
| | *Null*: intercept | 0 | -2090.8 | 4189.5 | 15.6 | 0.00 | |
| Fulton's condition factor | *Null*: intercept | 0 | 1331.4 | -2654.8 | 0.00 | 0.84 | |
| | PR | 1 | 1330.0 | -2649.9 | 4.88 | 0.07 | |
| Total lipid | Fish weight + PR | 2 | -315.7 | 643.5 | 0.00 | 0.61 | 0.9090 |
| | Fish weight | 1 | -317.7 | 645.5 | 1.96 | 0.23 | 0.9069 |
| | *Null*: intercept | 0 | -810.7 | 1629.4 | 985.93 | 0.00 | |

*Note:* K = number of parameters in the model, logLik = model log likelihood, ΔAICc = difference in AICc from top model, $w_i$ is the AICc model weight, $r^2$ = adjusted-$r^2$.

FIGURES

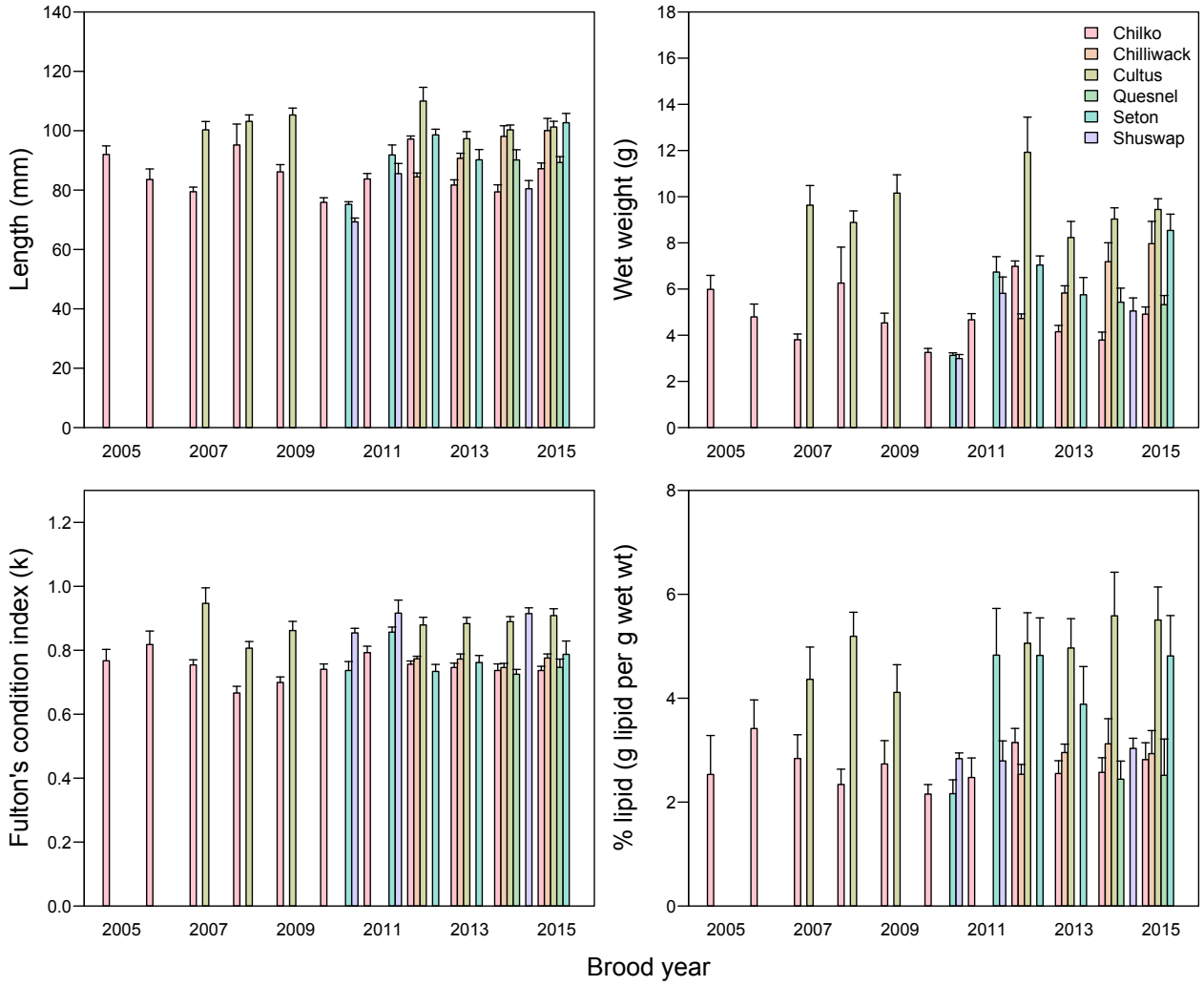


Figure 1. Mean length (mm), wet weight (g), Fulton's condition factor (k), and percent lipid (g lipid per g wet weight) for out-migrating sockeye salmon smolts from six populations collected from 2005 to 2015 brood years. The error bars show standard error.

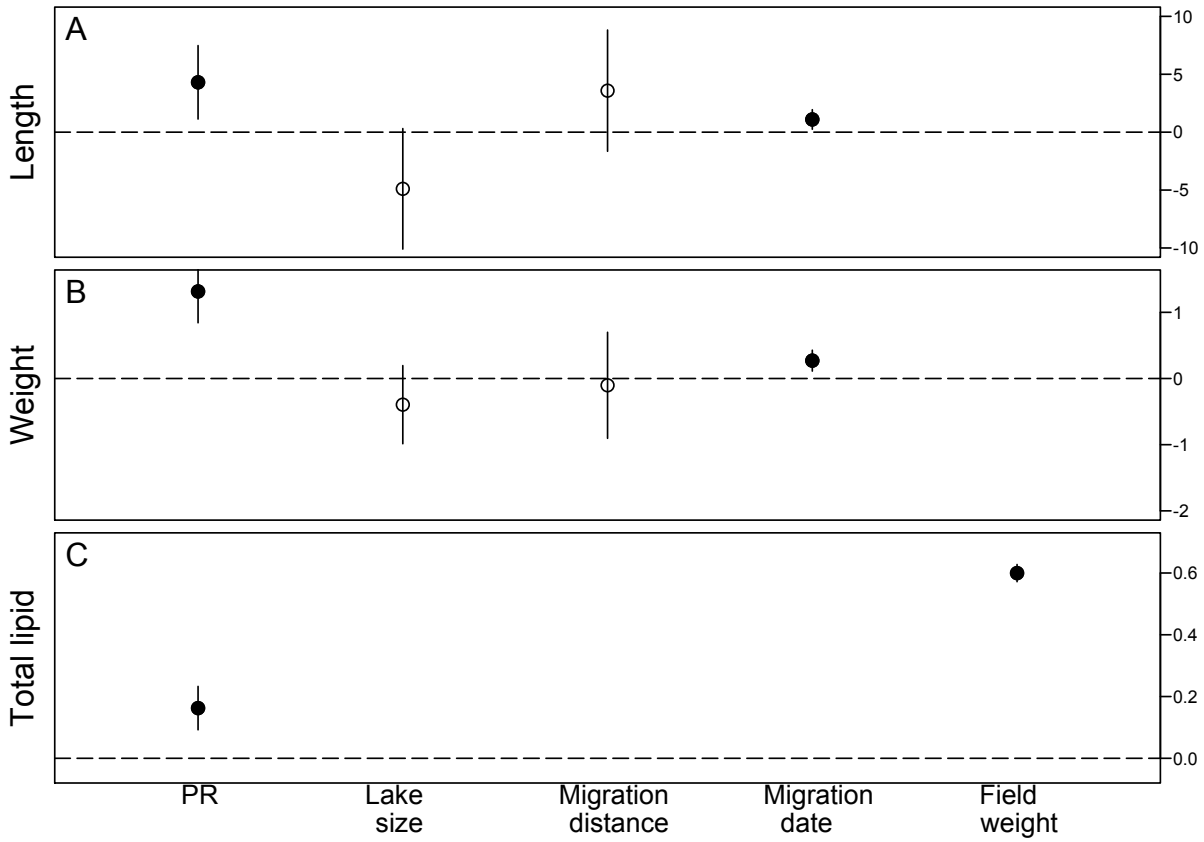


Figure 2. Standardized coefficients (mean=0, standard deviation=1) with 95% confidence intervals (CI) for models describing (A) length (mm), (B) weight (g), and (C) percent total lipid (g total lipid per g wet weight) of out-migrating sockeye salmon smolts from six populations collected from 2005 to 2015 brood years. Filled circles indicate explanatory variables with a significant effect ($p < 0.05$) on the relevant condition metric.

# Evidence for density dependence and delayed density dependence from four condition metrics measured in juvenile sockeye salmon from six Fraser River rearing lakes

## INTRODUCTION

Sockeye salmon populations can exhibit cyclic dominance, whereby the abundance of adult fish that return to fresh water in the dominant year can be several orders of magnitude greater than sub-dominant or off-cycle years, and this pattern persists through time (Ricker 1950; Ricker 1997). Sockeye salmon from the Fraser River watershed generally rear for one year in fresh water and spend more than two years at sea, returning to spawn as four-year-olds (age-$4_2$). A small proportion of fish spend an additional year in freshwater, returning to spawn as five-year-olds (age-$5_2$). Each spawning stream supports a population that is comprised of four cycle lines, or broods. Many Fraser River sockeye salmon populations exhibit a four-year abundance cycle, with the dominant year of high numbers of spawners followed by the sub-dominant year, with a much smaller number of spawners, and two off-cycle years with relatively few spawners (Ricker 1997). Other populations experience dramatic fluctuations in adult returns, without the consistent four-year pattern of cyclic dominance, and some populations have experienced changes to the dominant cycle line in recent decades. The mechanisms that underlie and enforce these patterns of cyclic dominance are still not well understood but typically centre on density-dependent and delayed density-dependent processes (e.g. Ricker 1950; Ward and Larkin 1965; Myers et al. 1997).

Large spawning escapements produce a high abundance of juvenile sockeye salmon, which compete for resources throughout the freshwater life-cycle. Given a relatively constant lake productivity and habitat availability among years, competition for limited prey or habitat reduces energy uptake, growth, and energetic condition in offspring of larger broods (Mazumder and Edmundson 2002; Schindler et al. 2005). Hence, the offspring produced by large escapements should tend to be smaller and have lower survival than offspring produced by lower escapements. This direct density-dependence survival would in theory create higher recruits per spawner in off-cycle years, causing the collapse of cyclic dominance without some other mechanism, such as higher exploitation rate on non-dominant years. Cohort interactions, or delayed density dependent dynamics, can also affect juvenile condition and survival (Levy and Wood 1992). For example, very high densities of fry and parr produced by dominant escapements may overgraze the lake zooplankton community, diminishing the food supply for successive juvenile cohorts (Hume et al. 1996) or produce a lag effect of increased predator densities (Ward and Larkin 1964; Larkin 1971). The debate between whether different Fraser sockeye populations are best represented by a Ricker type model (i.e. density-dependence – no cohort interaction) versus a Larkin-type model (i.e. assumes cohort interaction) continues today. In this chapter, we make predictions regarding different fish condition metrics using both model approaches.

Of concern to fisheries managers are situations when very low escapements fail to produce enough adult returns, or when high spawning escapements produce an abundance of juveniles that exceeds the carrying capacity of the rearing lake. In the former, suppressed spawner-recruit values can seriously impeded recovery efforts and jeopardize mixed stock fishing opportunities. In the latter case, missed fisheries opportunities are unlikely to increase fry output or adult returns, due to density dependent decreases in condition or survival in the rearing environment (Hume et al. 1996), having a negative effect on current and future harvest levels.

To better understand the relationship between escapement and sockeye salmon energetic condition in fresh water, we collected juveniles from multiple freshwater life-stages in six rearing lakes in the Fraser River watershed. The spawning escapements of populations that rear in Chilko, Chilliwack, Cultus, Quesnel, Seton, and Shuswap lakes can vary in abundance by several orders of magnitude. We hypothesized an inverse relationship between spawning escapement and juvenile length, weight, Fulton's condition factor, and total lipid when escapement exceeded the lake-specific rearing capacity (i.e. $S_{max}$), consistent with the direct density dependence in the Ricker model. We also examined support for the Larkin model, the potential for dominant broods to negatively affect fish condition in the subsequent sub-dominant line. Additionally, we described seasonal changes in juvenile total lipid content in fresh water, which may indicate the timing of bottlenecks in survival at high densities.

## METHODS

### POPULATIONS

For this report, we collected juvenile sockeye salmon from populations that rear in six lakes in the Fraser River watershed. The location, limnology, and sockeye salmon population dynamics of each lake are described in some detail below, and lake attributes are compared in Chapter 1, Table 1.

#### *Chilko Lake*

Chilko Lake (51°20'N, 124°05'W) is a cold, ultra-oligotrophic, sub-alpine lake, located on the eastern edge of the Coast Mountain Range at an elevation of 1172 m. The surface area of the lake is 185 $km^2$ (18,451 ha), and the mean and maximum depths are 123 m and 330 m. The lake has steep banks and limited littoral habitat. During winter, the lake temperature is 4°C. The growing season is May 1–October 31, with a seasonal average photosynthetic rate (PR) of 121 mg $C \cdot m^{-2} \cdot d^{-1}$ (Grant *et al.* 2011).

Most of the sockeye salmon in the population spawn in Chilko River, downstream of the lake outlet, with the remainder using gravel beaches throughout Chilko Lake (Hume *et al.* 1996). The Chilko population represents a major contributor to adult returns to the Fraser River in many

years. During the years of the study (2005-2016), total spawners (and effective female spawners, EFS) was smallest in 2004, at 92,000 (49,000), and largest in 2010, at approximately 2,500,000 (1,180,000). The population does not have a regular four-year dominance cycle (Myers *et al.* 1997).

Smolts migrate into the Chilko River from mid-April until mid-May (median date: between April 26-May 5 in years 2006-2015); out-migrating smolts are enumerated by DFO using a counting fence with video monitoring. In some years, a relatively large proportion of parr remain in Chilko Lake for an additional year and outmigrate as two-year-old smolts (age 2+). In 2009, 2010, 2013, and 2014, 8–10% of outmigrating Chilko smolts were two-year-olds. The juvenile migration, from Chilko Lake to the Fraser River estuary, is 677 km.

*Chilliwack Lake*

Chilliwack Lake (49°03'N, 121°25'W) is a relatively cold, oligotrophic lake, located in the eastern Fraser Valley, at an elevation of 621 m. The surface area of the lake is 12 $km^2$ (1,187 ha), and the mean and maximum depths are 67 m and 121 m (Shortreed et al. 2001; Tunnicliffe et al. 2012). The seasonal mean photosynthetic rate of Chilliwack Lake is 101 mg $C \cdot m^{-2} \cdot d^{-1}$ (Grant *et al.* 2011).

Chilliwack Lake is the rearing lake for sockeye salmon populations that spawn in Dolly Varden Creek, a tributary, and in the lake itself. Escapements to Chilliwack Lake have been highly variable (Grant *et al*. 2011): 3,500 spawners (1,700 EFS) in 2014 to 126,000 spawners (79,000 EFS) in 2012. The dominant cycle line is the 2000 brood. Sockeye salmon smolts leave Chilliwack Lake between mid-April and mid-May. Their migration through Chilliwack and Fraser rivers to the Strait of Georgia is 153 km.

*Cultus Lake*

Cultus Lake (49°03'N, 121°59'W), located in the eastern Fraser Valley, is a small lake of 6 $km^2$ (630 ha) at 46 metres above sea level. The lake is steep-sided, with a limited littoral area, and mean and maximum depths of 21 m and 44 m. Cultus Lake is productive, and the seasonal mean photosynthetic rate of 404 mg $C \cdot m^{-2} \cdot d^{-1}$ was the highest of the lakes studied (Grant *et al.* 2011). It has a highly developed catchment area, with residential, agricultural, and recreational land uses.

The sockeye salmon population that spawns in Cultus Lake has been assessed as Endangered by the Committee on the Status of Endangered Wildlife in Canada. From 1994 to 2016, the population declined 92% (COSEWIC 2003). During the study, escapements to Cultus Lake ranged from 892 spawners (19 EFS) in 2012 to 10,300 spawners (1,000 EFS) in 2010. A hatchery program supplements the wild population.

Sockeye salmon smolts migrate into Sweltzer Creek from mid-March until late May (median date: between April 7-30 in years 2007-2016), and the outmigration is enumerated by DFO

using a counting fence. The juvenile migration, from the lake outlet to the Fraser River estuary, is 110 km.

*Quesnel Lake*

Quesnel Lake (52°30'N, 120°00'W) is an oligotrophic lake in the interior plateau of British Columbia, at an elevation of 725 m (Morton and Williams 1990). It is large, covering an area of 272 $km^2$ (26,090 ha), and deep, with mean and maximum depths of 158 m and 530 m. The lake has four arms, hereafter referred to as, West Arm, drained by the Quesnel River, Main Arm, North Arm, and East Arm. The growing season is from May 1–October 31, and the lake has a seasonal mean PR of 130 mg $C \cdot m^{-2} \cdot d^{-1}$ (Grant *et al.* 2011).

The main spawning areas for sockeye salmon are in the Horsefly and Mitchell rivers, the largest tributaries to the lake, while additional spawning areas in small streams and along the lake shore support smaller numbers of fish (Hume *et al*. 1996). Returns to Quesnel Lake during the study were lowest in 2016, with 1,000 spawners (200 EFS), and highest in 2014, with 830,000 spawners (430,000 EFS). The dominant cycle line is the 2002 brood.

Juvenile sockeye salmon occupy the pelagic zone from July until October. The maximum estimated density of juveniles in Quesnel Lake is 6000 fry $ha^{-1}$, based on analysis of PR models and historic fry data by Hume *et al.* (1996). Smolts leave the lake in April and May and migrate 748 km to the Fraser River estuary.

*Seton and Anderson lakes*

Seton Lake (50°42'N, 122°08'W) and Anderson Lake (50°38'N, 122°24'W) are oligotrophic lakes in the rain shadow of the Coast Mountain Range, in southwestern British Columbia, at elevations of 237 m and 258 m, respectively. Seton Lake covers 25 $km^2$ (2,519 ha) and Anderson Lake covers 29 $km^2$ (2,844 ha). Both lakes are deep, with steep sides and limited littoral areas. The mean and maximum depths are 85 m and 151 m in Seton Lake and 140 m and 215 m in Anderson Lake. Anderson Lake is drained into Seton Lake by Portage Creek, a 3-km stream. Seton Lake also receives water via a hydropower diversion from Carpenter Lake, a reservoir in the adjacent Bridge River watershed. Flow from Seton Lake, through the Seton River, is controlled by the Seton Dam, which was built in 1956 and is located 800 m downstream of the lake outlet (Limnotek 2015). Anderson Lake is more productive than Seton Lake, with a photosynthetic rate of 303 mg $C \cdot m^{-2} \cdot d^{-1}$, compared to 233 mg $C \cdot m^{-2} \cdot d^{-1}$ (Grant *et al.* 2011).

Two populations of adult sockeye salmon spawn in the Seton-Anderson watershed: early summer run fish that return to Gates Creek, which flows into Anderson Lake, and late run fish that spawn in Portage Creek. The Portage Creek sockeye salmon were transplanted from the lower Adams River population in the early 20$^{th}$ century (Withler *et al.* 2000; Grant *et al.* 2011). The two populations are genetically distinct, with differently timed migration and spawning (Withler *et al.* 2000; Moreira 2014). The dominant cycle line for the Portage Creek population is 2002, and the Gates Creek sockeye population has not exhibited regular cyclic dominance since

the late 1990s. The largest collective adult return to the system during the study was in 2010 (80,000 spawners; 33,000 EFS), and the smallest was in 2016 (8,800 spawners, 3,600 EFS). The majority of adult returns are to the Gates Creek population.

The majority of Gates Creek sockeye fry rear in Seton Lake, migrating through Portage Creek from mid-April to late-June as fry (Geen and Andrew 1961; Woodey 1975). Smolts leave Seton Lake in April and May, and the migration from the Seton Lake outlet above the Seton Dam, through the Seton and Fraser rivers to the Fraser River estuary, is 333 km.

*Shuswap Lake*

Shuswap Lake (50°00'N, 119°05'W) is a mesotrophic lake in the interior plateau of British Columbia, at an elevation of 347 m (Hume *et al*. 1995). The lake is roughly H-shaped, with four major arms: Main, Seymour, Anstey, and Salmon. A 1.5-km narrows at Sicamous separates Mara Lake from Salmon Arm. Little River drains the Main Arm of Shuswap Lake into Little Shuswap Lake, and sockeye salmon rear in Mara, Shuswap, and Little Shuswap lakes. The three-lake system is 330 $km^2$, but Mara and Little Shuswap were not routinely sampled, so an area of 300 $km^2$ (29,851 ha) was used. The mean and maximum depths of Shuswap Lake are 58 m and 171 m (Nidle and Shortreed 1996).

Shuswap Lake has a longer growing season (April 1–November 30) and warmer thermal regime than the other lakes in the study, with the exception of Cultus. The mean seasonal photosynthetic rate is 171 mg C $m^{-2}$ $d^{-1}$ (Grant *et al.* 2011)

Sockeye salmon return to a number of tributaries in the Shuswap lakes system, across two run timing groups: early summer and late. The early summer group returns predominantly to Scotch Creek, Eagle River, and Seymour River, while the majority of the late group spawns in Adams River and Lower Shuswap River. Spawning also occurs in other tributaries and along the shore (Grant *et al*. 2011). The smallest return during the study was 1,616 spawners (768 EFS) in 2016, and the largest was 8,947,869 spawners (3,753,548 EFS) in 2010.

Sockeye salmon fry occupy the pelagic zone from July until November (Hume *et al.* 1996), and the populations mix within and among lakes during rearing. Smolts leave the Shuswap system later than in other populations, outmigrating in May and June. The downstream migration is 497 km and is the most complex, following Little River into Little Shuswap Lake, the South Thompson River into Kamloops Lake, and the Thompson and Fraser rivers into the Strait of Georgia.

## JUVENILE FISH COLLECTION, TRANSPORT, AND STORAGE

Juvenile sockeye salmon (*Oncorhynchus nerka*) were collected from various locations across the Fraser watershed. Spring fry, summer fry, fall fry, spring parr and smolts, were collected across multiple years (2007-2017) using various capture methods, depending on the location and

targeted life history stage (see Appendix A for details). Briefly, smolts were collected by beach seine, dip net, rotary screw trap, or incline plane trap from Chilko Lake, Sweltzer Creek, Chilliwack Lake, Little River, Quesnel River, Seton River, and the lower Fraser River at Mission. Spring fry were collected by beach seine from Quesnel River and Shuswap Lake. Summer fry Fall fry and spring parr were collected by lake trawl from Quesnel Lake, Shuswap Lake, Cultus Lake, and Chilliwack Lake (Appendix A: Table 1, Table 2). Following collection, fish were euthanized with an overdose of tricaine methanesulfonate (MS-222) prior to fork lengths (nearest mm) and weights (nearest 0.01 g) being measured in the field. Individuals were wrapped in aluminum foil or individual whirl paks and frozen rapidly or on dry ice. A small subset was frozen on liquid nitrogen or placed in a -20°C freezer. The majority of fish caught by beach seine or dip net were transported to the Fisheries and Oceans research laboratory in West Vancouver ('West Van Lab') for long-term cold storage, although some samples were stored at the University of British Columbia in Vancouver or the Pacific Biological Station in Nanaimo, prior to transport to West Van Lab for analysis. The fish caught by lake trawl were stored at the Fisheries and Oceans research laboratory in Cultus Lake, prior to transfer to West Van Lab for analysis. For more detailed information on capture history and storage conditions for juvenile sockeye samples, see 'Appendix A: Sample collection 2007-2017.'

## HYDROACOUSTIC ABUNDANCE ESTIMATES

Hydroacoustic surveys were conducted on Cultus, Chilliwack, Quesnel, and Shuswap lakes to estimate the abundance and density of fry or parr and collect juvenile samples using a mid-water trawl. Generally, years with dominant and subdominant cohorts were surveyed. Cultus Lake was consistently sampled once in spring (March or April), summer (June-September), and fall (October or November) from 2005 to 2015. Chilliwack Lake was surveyed in summer (July or August) and fall (November) in 2009, 2010, 2013, and 2014. Quesnel Lake was sampled in summer (August) and fall (September) in 2006, fall (September or October) in 2007 and 2010-2015, and spring (March) in 2015. See Table 1 for a summary of sampling dates and hydroacoustic estimates.

Prior to sampling, lakes were split into multiple sections depending on the size of each lake. Within these sections, a minimum of seven hydroacoustic transects perpendicular to the long-axis of the lake were established. At least one midwater trawl was completed within each section of the lake, with both trawls and hydroacoustic surveys taking place at night (see MacLellan and Hume 2010 for further details).

Prior to 2010, hydroacoustic abundance and density estimates were grouped as juvenile *Oncorhynchus nerka*, which includes fish from the anadromous (sockeye salmon) and non-anadromous (kokanee) populations. Some lakes have a potentially high number of kokanee, which are indistinguishable from juvenile sockeye on the echosounder. Since 2010, juvenile kokanee and sockeye were distinguished using otolith strontium and calcium isotope ratios from juveniles collected by mid-water trawl (MacLellan and Hume, 2010). Because lakes in the study area are typically low in strontium, it is used as a marine signature; higher strontium to

calcium ratios indicate offspring from anadromous parents. Confirmed sockeye salmon juveniles were stored, as described above, and analyzed for energetic condition, as described below, and the ratio of juvenile sockeye salmon to kokanee was used to discriminate hydroacoustic abundance estimates.

For Chilliwack Lake collections, sockeye salmon and kokanee were distinguished using genetic stock identification. Fin tissue samples were taken from juvenile fish and stored in 95% ethanol or dry on Whatman paper and then transferred to the Pacific Biological Station in Nanaimo for analysis. Variation in microsatellite DNA was used to assign juvenile fish to population, following the procedures of Beacham et al. (2000a, 2000b).

## LIFE-STAGE IDENTIFICATION

Assumptions regarding age assignments were made based on sampling location, sampling date, and size. The majority of juvenile fish had age assigned at the time of sampling. Trawl surveys were conducted by the DFO Lakes Program in the summer (July or August) and fall (September–November) to target age-0 sockeye salmon. Spring trawl surveys (February–May) were conducted to target age-1 sockeye salmon, with additional June surveys for age-1 sockeye salmon in Shuswap Lake. Age-0 fish, called offshore or pelagic fry, were considered summer or fall fry, depending on month of sampling. Age-1 fish caught by trawl were considered spring parr. Age-0 fish caught in the river environment by seine or dip net were called onshore fry. Age-1 or 2 fish caught in the river environment by seine net, dip net, or weir were called smolts. Sampling was conducted in June in Little River (Shuswap complex) and April or May for all other populations.

Age-2 smolts are larger than age-1 smolts. Chilko can have a high proportion of two-year-old smolts in some years (up to 10%), and these larger fish were generally noted as age-2 smolts at the time of sampling. Several additional fish in each population were identified as two-year-olds from population- and capture year-specific length-weight relationships, as the different age classes typically cluster separately.

## LIPID EXTRACTION AND CONSTITUENT ANALYSIS

Whole juvenile sockeye salmon (*Oncorhynchus nerka*) samples were removed from -80 $^{o}$C freezer storage and allowed to thaw at room temperature prior to taking fork length and weights measurements in the laboratory. Fish were cut into 8-10 pieces and placed in 50 ml Nalgene® tubes with two steel ball bearings and homogenized using a SPEX SamplePrep 2010 Geno/Grinder (SPEX, Metuchen, NJ, www.spexsampleprep.com) at 1500 rpm for two-minute intervals until completely homogenized.

Lipid extraction from homogenized tissue followed protocols developed by Bligh and Dyer (1959) with minor modifications (see: ‘Appendix B: Lipid extraction and moisture ash’ for

detailed methods). Chloroform, methanol and water were added to a weighed subsample of homogenate (in 1:1:0.5 solvent ratios, respectively) and homogenized to form a biphasic layer of chloroform-lipid and methanol-water. The volume of the chloro-lipid layer was measured, prior to pipetting a known volume onto a pre-weighed tin boat and evaporating off the chloroform in an oven. The remaining lipid samples were then re-weighed and frozen for subsequent triglyceride analysis.

The percent lipid of the subsample was calculated using Eq. 1:

$$subsample\ \%\ lipid = \frac{extracted\ lipid\ wt.\ (g)}{subsample\ wt.\ (g)} * 100 \quad [1]$$

The weight of the total lipid in each fish was calculated using Eq. 2:

$$total\ lipid\ (g) = \frac{uncorr.\%\ lipid}{100\%} *\ whole\ fish\ wt._{\ thawed}\ (g) \quad [2]$$

Moisture lost from juvenile samples during storage was estimated and used to correct fish weights using procedures outlined in Appendix C.

## LAKE PRODUCTIVITY AND CARRYING CAPACITY ESTIMATES

The estimates of photosynthetic rate and lake rearing capacity used in this chapter were taken from Grant et al. (2011, Appendix 4, Table C). In that document, the authors state that limnological data are multiyear seasonal means, incorporating data collected monthly, between May and October, for up to ten years. We used the 2009 estimate of photosynthetic rate for Chilko Lake, because it was the most recent unfertilized data point. Chilliwack and Cultus lakes were three-year mean values, Seton Lake was a four-year mean value, and we used the post-2003 five-year mean photosynthetic rate for Quesnel Lake. Photosynthetic rate data are used to model rearing capacity of nursery lakes, predicting the maximum biomass and abundance of sockeye salmon smolts and the number of spawners that would produce them (i.e. $S_{max}$; Hume et al. 1996). Grant et al. (2011) present a PR model that accounts for the presence of competitor species when estimating lake rearing capacity for sockeye salmon juveniles (Cox-Rogers et al. 2010).

To determine the lake rearing capacity in units of effective female spawners per hectare, we halved the $S_{max}$ values from the PR model, presented by Grant et al. (2011), assuming 100% spawning success in female sockeye salmon. These values were then divided by the surface area of the relevant lake or lakes (Table 2). For the Seton-Anderson system, the $S_{max}$ values for Gates Creek and Portage Creek populations were added, divided by two to approximate the

number of females, then divided by the sum of the lake surface areas, to account for shared rearing habitat between the two populations (Table 2).

## SMOLT AND SPAWNER ENUMERATION

Daily and cumulative annual smolt outmigration totals from the counting fences on Chilko River and Sweltzer Creek were provided for years ranging from 2006 to 2016 by DFO Stock Assessment Division (Tracy Cone, DFO Annacis Island).

Escapement data was determined from near final spawning ground estimates for individual spawning streams for years 1938 to 2016, which were provided by DFO Stock Assessment Division (T. Cone). The number of effective female spawners (EFS) was tallied by six stock groupings, based on natal rearing lake (Chilko Lake, Chilliwack Lake, Cultus Lake, Quesnel Lake, Seton Lake, and Shuswap Lake).

## STATISTICAL ANALYSIS

The same four condition metrics were analyzed as in Chapter 1: juvenile length (mm), weight (g), condition factor (Fulton's *k*), and total lipid (g per fish). As in Chapter 1, each time total lipid was analyzed, fish wet weight (g) was included as a covariate, to account for variation in lipid mass with fish mass. A linear mixed-effects model was fitted to three different datasets, with an iteration for each of the four condition metrics. Model 1, the spawner to smolt model, compared the density of effective female spawners (EFS $ha^{-1}$) to the condition of their offspring at the smolt life-stage to assess density dependent effects. Model 1 also included a term to assess delayed density (i.e. inter-cohort) effects: the density of effective female spawners in the year prior to the parents' cohort ($EFS_{prev}$ $ha^{-1}$).

Model 2, the fry and parr model, assessed density dependent dynamics during lake residency by comparing hydroacoustic estimates of juvenile density (juveniles $ha^{-1}$) to the condition of juveniles sampled from the cohort during the hydroacoustic survey.

Model 3, the smolt model, compared estimates of out-migrating smolt density (smolt $ha^{-1}$) from the Chilko and Cultus counting fences to the condition of smolts sampled during the out-migration. A term was included in Model 3 to assess the effect of delayed density dependent dynamics on smolt condition: the density of smolts that out-migrated in the previous cohort ($smolt_{prev}$ $ha^{-1}$).

To provide a more complete picture of the factors that affect juvenile condition, the statistically significant explanatory variables from Model 2 (the rearing lake model) in Chapter 1 were included in the models in this chapter. For example, lake photosynthetic rate and migration date (i.e. Julian day of collection) were included in each model of juvenile length, along with the measures of fish density described above. To compare effect sizes between rearing lake

attributes and measures of fish density, continuous explanatory variables were centred (mean subtracted) and standardized (divided by two standard deviations; Gelman 2008; Schielzeth 2010).

In Model 1, all populations were pooled, and population and collection year were included as random effects, to account for variation in condition among populations and years that was not captured by the fixed effects. Model 1 was also fitted to the data from each population separately, to identify differences in population dynamics. Chilliwack and Quesnel were not modeled individually, as we had only two years with both condition and escapement data for Chilliwack and no overlap in condition and escapement data for Quesnel. The pooled population model was fit with the function *lmer*, from the 'lme4' package, which can accommodate crossed random effects (Bates, 2005; Bates & Sarkar, 2007), and the individual population models were fit with the function *lme*, from the 'nlme' package. The pooled and individual population models for length are shown below.

$$length \sim PR + Julian\ day + EFS + EFS_{prev} + (1 \mid population) + (1 \mid collection\ year)$$

$$length \sim Julian\ day + EFS + EFS_{prev} + (1 \mid collection\ year)$$

In Model 2, only data from Chilliwack, Cultus, Quesnel, and Shuswap were included, as hydroacoustic surveys were not conducted in Chilko or Seton lakes. Population, brood year, and life-stage were included as random effects. The model was not fit to individual populations, as there were not enough years with survey data for the recommended minimum of five levels per random effect (Zuur et al. 2009). Model 2 was fit with the function *lmer*, to accommodate crossed random effects (Bates, 2005; Bates & Sarkar, 2007). The pooled population model for length is shown below.

$$length \sim PR + Julian\ day + juvenile\ density + (1 \mid population) + (1 \mid collection\ year) + (1 \mid life - stage)$$

Model 3 was fit to data from Chilko and Cultus separately, as the populations differ substantially in out-migrating smolt density and two was an insufficient number of levels to estimate the random effect of population (Zuur et al. 2009). The individual population models were fit with the function *lme*, from the 'nlme' package. The structure of the model for length is shown below.

$$length \sim Julian\ day + out - migration\ density + out - migration\ density_{prev} + (1 \mid collection\ year)$$

To ensure models did not violate statistical assumptions, residual plots from each model were visually examined (Zuur *et al.* 2009). Fish weight and total lipid were log transformed in each model that assessed total lipid, to improve normality and homoscedasticity of model residuals. The other response variables were not transformed.

For each iteration of the Model 1 and Model 2 pooled population models, candidate models were generated using maximum likelihood from all combinations of fixed effects and ranked by AIC values, using the 'MuMIn' package (Barton 2012). Fish wet weight was fixed in all models with total lipid as the response variable. The model with the lowest $\Delta$AIC is the most parsimonious model describing the data, while the AIC weight is the probability that a given model is the most parsimonious one (Burnham and Anderson 2002). The models with cumulative AIC weights of $\geq 0.95$ were summed with the 'conditional average' method to generate coefficient estimates and 95% confidence intervals for explanatory variables (Burnham and Anderson 2002, Grueber et al. 2011).

In this chapter, raw data are presented as mean ± SD, and statistical significance was evaluated at 0.05. All statistical analyses were conducted with R software (version 3.2.2**,** R Core Team 2015).

## RESULTS

Across populations, we found evidence of density dependent and delayed density dependent effects on the four condition metrics examined. In general, these effects were detected in the statistical models where data from all populations were pooled, rather than those that modeled data from each population separately, which was likely due to the limited number of collection years for some individual populations.

Chilko was the only individual population that exhibited density dependence. There was a negative relationship between effective female spawners and the length, weight, and total lipid of their offspring at the smolt life-stage.

### MODEL 1: RELATIONSHIPS BETWEEN EFFECTIVE FEMALE SPAWNER DENSITY AND SMOLT CONDITION

Across populations, out-migrating smolts were shorter and weighed less at higher densities of effective female spawners (EFS), when among-population and inter-annual differences in length and weight were accounted for. Lake photosynthetic rate and migration date (i.e. Julian day of capture) were positively correlated with both length and weight, in the pooled population versions of Model 1 (Figure 1A, Figure 1B). There was no effect of EFS on smolt total lipid or Fulton's condition factor, but lake photosynthetic rate had a positive relationship with both condition metrics (Figure 1C, Figure 1D). As in Chapter 1, smolts with greater mass had a greater mass of total lipid, and the relationship was highly significant (Figure 1D).

Out-migrating smolts were longer and heavier when EFS density was high in the cohort prior to their parents ($EFS_{prev}$; Figure 3A, Figure 3B), a positive delayed density effect. However, $EFS_{prev}$ density had a negative effect on total lipid (Figure 3D), such that out-migrating smolts had

lower lipid levels when the previous spawning cohort was large. The confidence set of models describing the effects of EFS and $EFS_{prev}$ on the four condition metrics are presented in Tables 3-6.

At the individual population level, Model 1 found negative effects of EFS density on length, weight, and total lipid for smolts out-migrating from Chilko Lake. There was no effect of migration date on weight or length in Chilko smolts (Table 7). Conversely, early out-migrating smolts from Cultus Lake were smaller than those that began the migration later, after accounting for differences in size among years (Table 8). This was also true of smolts out-migrating from Shuswap Lake (Table 10). There was no evidence that the density of EFS or $EFS_{prev}$ affected any measure of condition in smolts that reared in Cultus, Seton, and Shuswap lakes (Tables 8-10).

## MODEL 2: RELATIONSHIPS BETWEEN CONSPECIFIC DENSITY AND JUVENILE CONDITION

In Model 2, we evaluated the relationship between hydroacoustic estimates of fry or parr density and the condition of juveniles sampled at the same time period. Across populations, life-stages, and years, there was no relationship between conspecific density and juvenile length or weight (Figure 6A, Figure 6B). Lake photosynthetic rate was found to have a negative relationship with length and a positive relationship with weight, while collection date (i.e. Julian day) had a positive relationship with both condition metrics (Figure 6A, Figure 6B). However, higher conspecific densities were related to significantly lower Fulton's condition factor and total lipid in juveniles during lake residency. Photosynthetic rate was not significantly related to Fulton's condition factor, nor total lipid (Figure 6C, Figure 6D).

## MODEL 3: RELATIONSHIPS BETWEEN OUT-MIGRATING SMOLT DENSITY AND SMOLT CONDITION

The last of the three datasets that we analyzed for density and delayed density dependent dynamics was the annual smolt out-migration counts from the Chilko River and Sweltzer Creek counting fences. There was no relationship between the density of out-migrating smolts and any of the four condition metrics in either population, with the exception of a negative effect of the density of the previous cohort of out-migrating smolts on Fulton's condition factor in Cultus smolts (Table 11, Table 12).

## CHANGES TO PERCENT LIPID WITHIN FRESHWATER LIFE-STAGES

For brood-years where juvenile sockeye salmon were collected from the rearing lake as spring, summer, and fall fry and as spring parr and smolts, we were able to characterize a pattern of fluctuations in total lipid content during the freshwater residency. We observed that the percent total lipid was generally highest in the fall, and that the magnitude of difference

between lipid values in summer and fall fry was greatest for fish from non-dominant cohorts (e.g. Shuswap: Figure 7**;** all populations: Chapter 3, Tables 1-6). Spring fry generally had higher percent total lipid than summer fry, and there was a substantial decline in percent total lipid over winter (i.e. from fall fry to spring parr). In some populations (e.g. Cultus and Shuswap; Figure 7), the percent total lipid increased from the time when the cohort was sampled in the lake (i.e. as spring parr) to a few months later, when fish had exited or were exiting the lake (i.e. as smolts). In several populations, the mean percent total lipid value of out-migrating smolts was relatively consistent across years (e.g. Shuswap, Figure 7; Chilliwack, Figure 8). Juveniles from Cultus Lake did not appear to follow the same pattern as fish in other lakes. Mean lipid values of fall fry were not substantially higher than other life-stages, and mean lipid values in smolts were often higher than in spring parr, although there were few years where the same brood was collected at both life-stages (Chapter 3, Table 3).

## DISCUSSION

Our analysis of density dependence in sockeye salmon populations examined three different time-steps where competition might negatively affect juvenile condition: spawner to smolt, within life-stages in rearing lakes, or between out-migrating smolts. Greater statistical power in analyses of pooled population data (i.e. spawner to smolt and within life-stages in lakes) likely contributed to our ability to detect significance at these time-steps.

Higher densities of effective female spawners produced shorter and lighter out-migrating smolts, after accounting for differences in length and weight among populations and brood years. This provides support for the bottom-up trophic dynamics hypothesis that high competition within the large cohorts of juveniles produced by high spawner densities reduces surplus energy for growth. The negative relationship between EFS and smolt size is consistent with previous results from Chilko, Quesnel, and Shuswap populations (Hume et al. 1996). Although EFS had a larger effect on length and weight, lake photosynthetic rate was significantly positively correlated with all four condition metrics in the spawner to smolt models. Within the spawner to smolt models at the individual population level, there were few significant relationships between EFS density and juvenile condition and these only occurred for Chilko broods. Smolts in the cohorts produced by higher spawner densities were shorter, lighter, and had lower levels of total lipid per gram of body weight. It is not surprising, given the dataset, that we did not observe density dependence in other populations. Chilko was the population with the longest time series of data on smolt total lipid (eleven years) and the only population to experience multiple spawning escapements above $S_{max}$, the number of spawners that produces the maximum number of juveniles the lake can sustain. The photosynthetic rate model uses habitat capacity to infer juvenile production, so we would not expect to see reduced juvenile condition at spawning escapements considerably below $S_{max}$, when food is readily available. Our results are consistent with Hume et al. (1996), who observed that lakes like Chilko and Quesnel, despite having relatively low primary productivity, have the capacity to support larger sockeye salmon populations. Although we had lipid data for the 2010 and 2014

cohorts produced by two enormous returns to the Shuswap complex, we had only one low abundance brood for comparison. In this way, our sampling strategy of opportunistically collecting juveniles from dominant and sub-dominant returns somewhat limited our inferences about density dependent dynamics. We recommend targeting juveniles from off-cycle cohorts, where capture is possible, for evaluation of smolt condition at low and intermediate densities of EFS.

There was limited evidence for delayed density dependence. In the pooled population spawner to smolt model, out-migrating smolts had significantly lower lipid levels if the spawning escapement prior to their parents' was large. We hypothesize that this occurs when a cohort is large enough that high feeding pressure alters the lake trophic dynamics substantially enough to affect food availability for the subsequent brood. However, it is unclear why length and weight were significantly positively correlated with density of EFS in the previous year. To better understand how sockeye salmon population dynamics affect zooplankton communities in rearing lakes, it will be necessary to incorporate annual data on zooplankton density and juvenile stomach contents into these analyses. Preliminary exploration of stomach content data found that overconsumption of *Daphnia sp.*, the preferred and most energy efficient prey species, by the dominant 2012 brood in Chilliwack Lake caused the 2013 brood to switch to feeding on copepods (*Diaptomous sp.*; L. Pon, unpublished data). In dominant years, *Daphnia* densities can be 60% lower in Shuswap and Quesnel lakes, with juvenile sockeye salmon instead feeding on *Eubosmina, Diacyclops,* and *Leptodiatomus* species (Hume et al. 1996; Shortreed et al. 2001).

As in Chapter 1, the positive relationships between migration date and smolt length for Cultus and Shuswap populations suggested that parr in these lakes are feeding prior to out-migration. Indeed, examining fluctuations in mean total lipid among life-stages revealed that out-migrating smolts from Cultus and Shuswap lakes had higher lipid values than spring parr collected from the same cohort just weeks earlier. This is unusual; physiological characteristics used to distinguish smolts from parr in Atlantic and Pacific salmon and steelhead include lower body total lipid and condition factor (Wedermeyer et al. 1980). Stomach content data will inform further conclusions about the prevalence of feeding among spring parr within all six lakes.

Fall fry had the highest lipid densities of all freshwater life-stages. Allocation of surplus energy to storage in the fall increases the likelihood of over-winter survival, during periods of low food availability (Post and Parkinson 2001). Summer fry had relatively low total lipid values, which may be indicative of high competition as juveniles move offshore, or allocation of all surplus energy to growth, in order to store larger quantities of lipid in the fall. For broods where we had both fall fry and spring parr samples, we observed declines in total lipid, consistent with metabolism of stored lipid during winter months. Between fall and spring, juvenile length increased, which could be explained by winter growth or mortality of the smallest fish, which have the lowest probability of over-winter survival (Post and Parkinson 2001).

In these analyses we encountered what Grant et al. (2011) called the "non-one-year-old *nerka* problem." Many analyses of sockeye salmon populations do not account for age-$5_2$ fish, which

remain in fresh water for an additional year before out-migrating. These fish contribute to difficulties in quantifying juvenile competition, as EFS numbers do not account for them during their second year in the lake. We collected two-year-old smolts from several populations, though Chilko was the only one with more than a few per year. As we suspected that condition on out-migration would reflect the most proximal rearing conditions, we included two-year-old smolts with the one-year-old smolts from the following brood, which would have been conspecifics during their second year in fresh water. Perhaps the overlap of two-year-olds across brood years mutes the effect of density dependence on the condition metrics of interest. We can only make inferences about why some age-1 parr do not out-migrate; perhaps smoltification cannot occur or reverses if juveniles have not reached a threshold size or condition. Large Atlantic salmon parr turned silvery earlier than small fish, after experiencing a thermal trigger for smoltification (Johnston and Eales 1970). If smoltification is size-dependent, there should be a density-dependent relationship between juvenile abundance and the ratio of one- to two-year-old smolts, which could be studied further. In this chapter, samples sizes were too small for meaningful comparison of condition between one- and two-year-old smolts.

Future analysis of these datasets should consider the contribution of kokanee to measures of juvenile density. In some populations, such as Chilliwack, during off-cycle years, kokanee are estimated to comprise up to 80% of the juvenile *O. nerka* population (Hume et al. 1994), though that estimate is likely to be high, based on recent hydroacoustic survey data (L. Pon, pers. comm.). Estimates of kokanee fry abundance have been incorporated as competitors into PR models of lake carrying capacity (see Grant et al. 2011). We could improve our analysis of within lake density dependent dynamics by using a total *nerka* density, rather than sockeye density alone, since kokanee and sockeye population dynamics are likely to be interlinked through habitat capacity.

The implications of our results are likely to be important for bioenergetics and growth models of species that predate on sockeye salmon. Large seasonal fluctuations in fry and parr lipid content could substantially impact the energy budget of predator species throughout the year.

TABLES

Table 1. Summary of hydroacoustic survey estimates of juvenile sockeye salmon abundance in Chilliwack, Cultus, Quesnel, and Shuswap lakes between 2010 and 2015. Juvenile life-stage indicates age-0 (fry) or age-1 (parr) targeted. Density is the abundance estimate divided by lake surface area (see Table 2, below).

| Rearing Lake | Survey date | Juvenile life-stage | Abundance | Density (juveniles per ha) | Confidence Interval |
|---|---|---|---|---|---|
| Chilliwack | 2010-08-10 | summer fry | 120062 | 101 | 0.19 |
| Chilliwack | 2010-10-12 | fall fry | 56013 | 47 | 0.20 |
| Chilliwack | 2013-07-30 | summer fry | 3119635 | 2627 | 0.32 |
| Chilliwack | 2013-10-22 | fall fry | 1805473 | 1521 | 0.17 |
| Chilliwack | 2014-07-30 | summer fry | 511170 | 431 | 0.49 |
| Chilliwack | 2014-10-20 | fall fry | 245378 | 207 | 0.15 |
| Cultus | 2010-11-02 | fall fry | 222285 | 353 | 0.28 |
| Cultus | 2011-06-28 | summer fry | 497259 | 789 | 0.21 |
| Cultus | 2011-10-25 | fall fry | 487251 | 773 | 0.23 |
| Cultus | 2012-04-03 | spring parr | 164519 | 261 | 0.28 |
| Cultus | 2012-07-23 | summer fry | 234762 | 373 | 0.58 |
| Cultus | 2012-10-30 | fall fry | 495688 | 787 | 0.23 |
| Cultus | 2013-04-09 | spring parr | 113945 | 181 | 0.28 |
| Cultus | 2013-07-08 | summer fry | 133636 | 212 | 0.26 |
| Cultus | 2013-11-04 | fall fry | 440722 | 699 | 0.29 |
| Cultus | 2014-07-03 | summer fry | 683960 | 1085 | 0.21 |
| Cultus | 2014-10-28 | fall fry | 406958 | 646 | 0.20 |
| Cultus | 2015-03-31 | spring parr | 59980 | 95 | 0.29 |
| Cultus | 2015-07-15 | summer fry | 775902 | 1231 | 0.62 |
| Cultus | 2015-11-04 | fall fry | 486926 | 773 | 0.15 |
| Cultus | 2014-04-02 | spring parr | 20972 | 33 | 0.21 |
| Quesnel | 2010-09-14 | fall fry | 13635392 | 523 | 0.24 |
| Quesnel | 2011-09-20 | fall fry | 24970095 | 957 | 0.29 |
| Quesnel | 2012-09-17 | fall fry | 6427365 | 246 | 0.22 |
| Quesnel | 2014-09-23 | fall fry | 15426032 | 591 | 0.38 |
| Quesnel | 2015-03-17 | spring parr | 11675222 | 448 | 0.32 |
| Quesnel | 2015-09-21 | fall fry | 70826120 | 2715 | 0.50 |
| Shuswap | 2011-08-02 | summer fry | 192915949 | 6463 | 0.16 |
| Shuswap | 2011-10-20 | fall fry | 186627751 | 6252 | 0.15 |
| Shuswap | 2012-08-13 | summer fry | 16798824 | 563 | 0.21 |
| Shuswap | 2012-10-15 | fall fry | 11176047 | 374 | 0.19 |
| Shuswap | 2015-08-10 | summer fry | 188593304 | 6318 | 0.15 |
| Shuswap | 2015-10-05 | fall fry | 129200513 | 4328 | 0.20 |

Table 2. The total spawning escapement predicted to produce the maximum number of juveniles per lake ($S_{max}$), predicted by a photosynthetic rate (PR) model that accounts for competitor abundance, rearing lake surface area (in hectares), and the density of effective female spawners (EFS per hectare) estimated to produce the maximum number of juveniles per lake. The EFS density values assume 100% spawning success and an equal ratio of male to female spawners.

| Rearing Lake | Adjusted PR model predicted escapement ($S_{max}$)[1] | Lake surface area (ha) | Effective female spawners (EFS per ha) |
|---|---|---|---|
| Chilko Lake | 483,000 | 18,451 | 13.1 |
| Chilliwack Lake | NA | 1,187 | NA |
| Cultus Lake | 85,000 | 630 | 67.4 |
| Quesnel Lake | 1,115,000 | 26,090 | 21.4 |
| Seton-Anderson system total | 474,000 | 5,363 | 44.2 |
| Seton Lake | 188,000 | 2,519 | 37.3 |
| Anderson Lake | 286,000 | 2,844 | 50.3 |
| Shuswap Lake | 1,900,000 | 29,851 | 63.6 |

[1]Values from Grant et al. (2011, p. 83).

Table 3. The confidence set of mixed-effect models, with cumulative AIC weights ≥ 0.95, with combinations of fixed effects used to describe delayed density dependent effects on length (mm) in smolts. The number of effective female spawners (EFS) for the brood prior to the parent generation ($EFS_{prev}$) was divided by lake area to give a density per hectare. Photosynthetic rate (PR, mg $C \cdot m^{-2} \cdot d^{-1}$) was a multi-year seasonal mean for each lake. Julian date was the day of year that each smolt was collected. Random effects of collection year and population were included in all models.

| Response | Model | K | logLik | AICc | ΔAICc | $w_i$ | $r^2$ |
|---|---|---|---|---|---|---|---|
| length | $EFS_{prev}$ + EFS + PR + Julian date | 8 | -4270.6 | 8557 | 0.00 | 0.93 | 0.55 |
| | $EFS_{prev}$ + EFS + PR | 7 | -4274.6 | 8563 | 5.95 | 0.05 | 0.55 |
| | *Null*: intercept | | -4353.7 | 8715 | | | |

*Note:* K = degrees of freedom, logLik = model log likelihood, ΔAICc = difference in AICc from top model, $w_i$ is the AICc model weight, $r^2$ = $r^2$ value from 'dredge'.

Table 4. The confidence set of mixed-effect models, with cumulative AIC weights ≥ 0.95, with combinations of fixed effects used to describe delayed density dependent effects on field weight (g) in smolts. The number of effective female spawners (EFS) for the brood prior to the parent generation ($EFS_{prev}$) was divided by lake area to give a density per hectare. Photosynthetic rate (PR, mg $C \cdot m^{-2} \cdot d^{-1}$) was a multi-year seasonal mean for each lake. Julian date was the day of year that each smolt was collected. Random effects of collection year and population were included in all models.

| Response | Model | K | logLik | AICc | ΔAICc | $w_i$ | $r^2$ |
|---|---|---|---|---|---|---|---|
| weight | EFS + Julian date + PR + $EFS_{prev}$ | 10 | -2726.9 | 5474 | 0.00 | 0.75 | 0.45 |
| | EFS + Julian date + PR | 9 | -2729.3 | 5477 | 2.62 | 0.20 | 0.45 |
| | *Null*: intercept | | -2789.6 | 5587 | | | |

*Note:* K = degrees of freedom, logLik = model log likelihood, ΔAICc = difference in AICc from top model, $w_i$ is the AICc model weight, $r^2$ = $r^2$ value from 'dredge'.

Table 5. The confidence set of mixed-effect models, with cumulative AIC weights ≥ 0.95, with combinations of fixed effects used to describe delayed density dependent effects on condition factor (Fulton's *k*) in smolts. The number of effective female spawners (EFS) for the brood prior to the parent generation ($EFS_{prev}$) was divided by lake area to give a density per hectare. Photosynthetic rate (PR, mg $C \cdot m^{-2} \cdot d^{-1}$) was a multi-year seasonal mean for each lake. Random effects of collection year and population were included in all models.

| Response | Model | K | logLik | AICc | ΔAICc | $w_i$ | $r^2$ |
|---|---|---|---|---|---|---|---|
| Condition | $EFS_{prev}$ + PR | 6 | 1416.4 | -2821 | 0.00 | 0.44 | 0.42 |
| factor | $EFS_{prev}$ | | 1414.7 | -2819 | | | |
| | $EFS_{prev}$ + PR + EFS | | 1416.6 | -2819 | | | |
| | $EFS_{prev}$ + EFS | | 1415.1 | -2818 | | | |
| | *Null*: intercept | | -2789.6 | -2811 | | | |

*Note:* K = degrees of freedom, logLik = model log likelihood, ΔAICc = difference in AICc from top model, $w_i$ is the AICc model weight, $r^2$ = $r^2$ value from 'dredge'.

Table 6. The confidence set of mixed-effect models, with cumulative AIC weights ≥ 0.95, with combinations of fixed effects used to describe delayed density dependent effects on log-transformed total lipid (g) in smolts. Log-transformed fish field weight (g) was fixed as a covariate in all models. The number of effective female spawners (EFS) for the brood prior to the parent generation ($EFS_{prev}$) was divided by lake area to give a density per hectare. Photosynthetic rate (PR, mg $C \cdot m^{-2} \cdot d^{-1}$) was a multi-year seasonal mean for each lake. Random effects of collection year and population were included in all models.

| Response | Model | K | logLik | AICc | ΔAICc | $w_i$ | $r^2$ |
|---|---|---|---|---|---|---|---|
| log (total lipid) | log(fish wt.) + PR + $EFS_{prev}$ | 7 | -372.3 | 759 | 0.00 | 0.58 | 0.81 |
| | log(fish wt.) + PR + $EFS_{prev}$ + EFS | 8 | -372.2 | 760 | 1.83 | 0.23 | 0.81 |
| | log(fish wt.) + PR + EFS | 7 | -374.1 | 762 | 3.46 | 0.10 | 0.81 |
| | log(fish wt.) + PR | 6 | -375.2 | 763 | 3.73 | 0.10 | 0.81 |
| | *Null*: intercept | | -932.9 | 1874 | | | |

*Note:* K = degrees of freedom, logLik = model log likelihood, ΔAICc = difference in AICc from top model, $w_i$ is the AICc model weight, $r^2$ = $r^2$ value from 'dredge'.

Table 7. Summaries of mixed effects model (Model 1, spawner to smolt) used to describe delayed density dependent effects on condition metrics, length (mm), weight (g), condition factor (Fulton's *k*), and total lipid (g total lipid per g wet weight), of out-migrating smolt collected from Chilko River. EFS is the density of effective female spawners and previous EFS is the density of effective female spawners that gave rise to the previous brood.

| Response | Explanatory variable | Coefficient | Standard error | *df* | t-value | p-value |
|---|---|---|---|---|---|---|
| length | EFS | -26.09 | 9.46 | 8 | -2.76 | 0.02 |
| | $EFS_{prev}$ | 10.82 | 5.63 | 8 | 1.92 | 0.09 |
| | Julian date | 1.96 | 2.66 | 371 | 0.72 | 0.46 |
| weight | EFS | -6.86 | 3.34 | 8 | -2.05 | 0.07 |
| | $EFS_{prev}$ | 1.75 | 1.95 | 8 | 0.90 | 0.39 |
| | Julian date | 0.21 | 0.74 | 391 | 0.28 | 0.78 |
| condition | EFS | 0.03 | 0.06 | 8 | 0.45 | 0.67 |
| factor | $EFS_{prev}$ | 0.04 | 0.03 | 8 | 1.15 | 0.28 |
| total lipid | EFS | -0.40 | 0.13 | 8 | -3.00 | 0.02 |
| | $EFS_{prev}$ | -0.11 | 0.08 | 8 | -1.50 | 0.17 |
| | log(fish wt.) | 1.08 | 0.05 | 391 | 23.42 | <0.001 |

Table 8. Summaries of mixed effects model (Model 1, spawner to smolt) used to describe delayed density dependent effects on condition metrics, length (mm), weight (g), condition factor (Fulton's *k*), and total lipid (g total lipid per g wet weight), of out-migrating smolt collected from Sweltzer Creek. EFS is the density of effective female spawners and previous EFS is the density of effective female spawners that gave rise to the previous brood.

| Response | Explanatory variable | Coefficient | Standard error | *df* | t-value | p-value |
|---|---|---|---|---|---|---|
| length | EFS | -65.35 | 99.09 | 3 | -0.66 | 0.56 |
| | $EFS_{prev}$ | -41.12 | 60.01 | 3 | -0.69 | 0.54 |
| | Julian date | 10.70 | 2.73 | 3 | 3.92 | 0.03 |
| weight | EFS | -10.73 | 23.44 | 3 | -0.46 | 0.68 |
| | $EFS_{prev}$ | -3.38 | 13.78 | 3 | -0.25 | 0.82 |
| | Julian date | 3.18 | 0.65 | 3 | 4.92 | 0.02 |
| condition | EFS | 0.55 | 2.25 | 4 | 0.24 | 0.82 |
| factor | $EFS_{prev}$ | 0.98 | 1.42 | 4 | 0.69 | 0.53 |
| total lipid | EFS | 6.15 | 5.97 | 4 | 1.03 | 0.36 |
| | $EFS_{prev}$ | 4.64 | 3.71 | 4 | 1.25 | 0.28 |
| | log(fish wt.) | 1.50 | 0.15 | 126 | 9.74 | <0.001 |

Table 9. Summaries of mixed effects model (Model 1, spawner to smolt) used to describe delayed density dependent effects on condition metrics, length (mm), weight (g), condition factor (Fulton's *k*), and total lipid (g total lipid per g wet weight), of out-migrating smolt collected from Seton River. EFS is the density of effective female spawners and previous EFS is the density of effective female spawners that gave rise to the previous brood.

| Response | Explanatory variable | Coefficient | Standard error | *df* | t-value | p-value |
|---|---|---|---|---|---|---|
| length | EFS | 15.94 | 18.55 | 1 | 0.86 | 0.55 |
| | $EFS_{prev}$ | 439.71 | 203.53 | 1 | 2.16 | 0.28 |
| | Julian date | -78.24 | 53.40 | 1 | -1.47 | 0.38 |
| weight | EFS | 3.71 | 1.85 | 1 | 2.00 | 0.29 |
| | $EFS_{prev}$ | 80.43 | 19.86 | 1 | 4.05 | 0.15 |
| | Julian date | -13.39 | 5.29 | 1 | -2.53 | 0.24 |
| condition | EFS | 0.03 | 0.13 | 2 | 0.23 | 0.84 |
| factor | $EFS_{prev}$ | 0.75 | 0.67 | 2 | 1.12 | 0.38 |
| total lipid | EFS | 0.08 | 0.40 | 2 | 0.19 | 0.86 |
| | $EFS_{prev}$ | 3.17 | 2.18 | 2 | 1.45 | 0.28 |
| | log(fish wt.) | 1.55 | 0.17 | 89 | 8.94 | <0.001 |

Table 10. Summaries of mixed effects model (Model 1, spawner to smolt) used to describe delayed density dependent effects on condition metrics, length (mm), weight (g), condition factor (Fulton's *k*), and total lipid (g total lipid per g wet weight), of out-migrating smolt collected from Little River. Previous EFS is the density of effective female spawners that gave rise to the previous brood.

| Response | Explanatory variable | Coefficient | Standard error | *df* | t-value | p-value |
|---|---|---|---|---|---|---|
| length | $EFS_{prev}$ | 14.70 | 4.12 | 1 | 3.56 | 0.17 |
| | Julian date | 5.40 | 1.35 | 284 | 4.00 | <0.001 |
| weight | $EFS_{prev}$ | 3.22 | 0.74 | 1 | 4.37 | 0.14 |
| | Julian date | 0.92 | 0.28 | 282 | 3.28 | 0.001 |
| condition factor | $EFS_{prev}$ | -0.01 | 0.02 | 1 | -0.32 | 0.80 |
| total lipid | $EFS_{prev}$ | -0.15 | 0.03 | 1 | -5.29 | 0.12 |
| | log(fish wt.) | 1.19 | 0.04 | 282 | 32.34 | <0.001 |

Table 11. Summaries of mixed effects model (Model 3, out-migrating smolts) used to describe delayed density dependent effects on condition metrics, length (mm), weight (g), condition factor (Fulton's *k*), and total lipid (g total lipid per g wet weight), of out-migrating smolt collected from Chilko River. Density is the number of co-migrating smolts and previous density is the number of out-migrants in the previous brood, divided by lake surface area.

| Response | Explanatory variable | Coefficient | Standard error | *df* | t-value | p-value |
|---|---|---|---|---|---|---|
| length | density | 4.58 | 6.11 | 6 | 0.75 | 0.48 |
| | $density_{prev}$ | -13.87 | 7.99 | 6 | -1.74 | 0.13 |
| | Julian date | -9.59 | 7.37 | 396 | -1.30 | 0.19 |
| weight | density | 1.07 | 1.14 | 6 | 0.93 | 0.39 |
| | $density_{prev}$ | -3.11 | 1.45 | 6 | -2.14 | 0.08 |
| | Julian date | 1.17 | 1.80 | 396 | 0.65 | 0.52 |
| condition | density | 0.06 | 0.03 | 6 | 2.26 | 0.07 |
| factor | $density_{prev}$ | -0.04 | 0.03 | 6 | -1.17 | 0.29 |
| total lipid | density | -0.07 | 0.09 | 6 | -0.77 | 0.47 |
| | $density_{prev}$ | -0.07 | 0.11 | 6 | -0.62 | 0.56 |
| | log(fish wt.) | 1.09 | 0.04 | 416 | 24.75 | <0.001 |

Table 12. Summaries of mixed effects model (Model 3, out-migrating smolts) used to describe delayed density dependent effects on condition metrics, length (mm), weight (g), condition factor (Fulton's *k*), and total lipid (g total lipid per g wet weight), of out-migrating smolt collected from Sweltzer Creek. Density is the number of co-migrating smolts and previous density is the number of out-migrants in the previous brood, divided by lake surface area.

| Response | Explanatory variable | Coefficient | Standard error | *df* | t-value | p-value |
|---|---|---|---|---|---|---|
| length | density | -36.83 | 89.36 | 3 | -0.41 | 0.71 |
| | $density_{prev}$ | 18.25 | 18.73 | 3 | 0.97 | 0.40 |
| | Julian date | -12.06 | 0.80 | 182 | -15.06 | <0.001 |
| weight | density | -8.54 | 20.85 | 3 | -0.41 | 0.71 |
| | $density_{prev}$ | 3.74 | 4.37 | 3 | 0.86 | 0.46 |
| | Julian date | -2.18 | 0.20 | 182 | -10.67 | <0.001 |
| condition | density | 0.13 | 0.16 | 3 | 0.85 | 0.46 |
| factor | $density_{prev}$ | -0.12 | 0.04 | 3 | -3.24 | 0.048 |
| total lipid | density | 0.36 | 2.53 | 3 | 0.14 | 0.89 |
| | $density_{prev}$ | -0.19 | 0.54 | 3 | -0.36 | 0.74 |
| | log(fish wt.) | 1.27 | 0.07 | 181 | 17.83 | <0.001 |

FIGURES

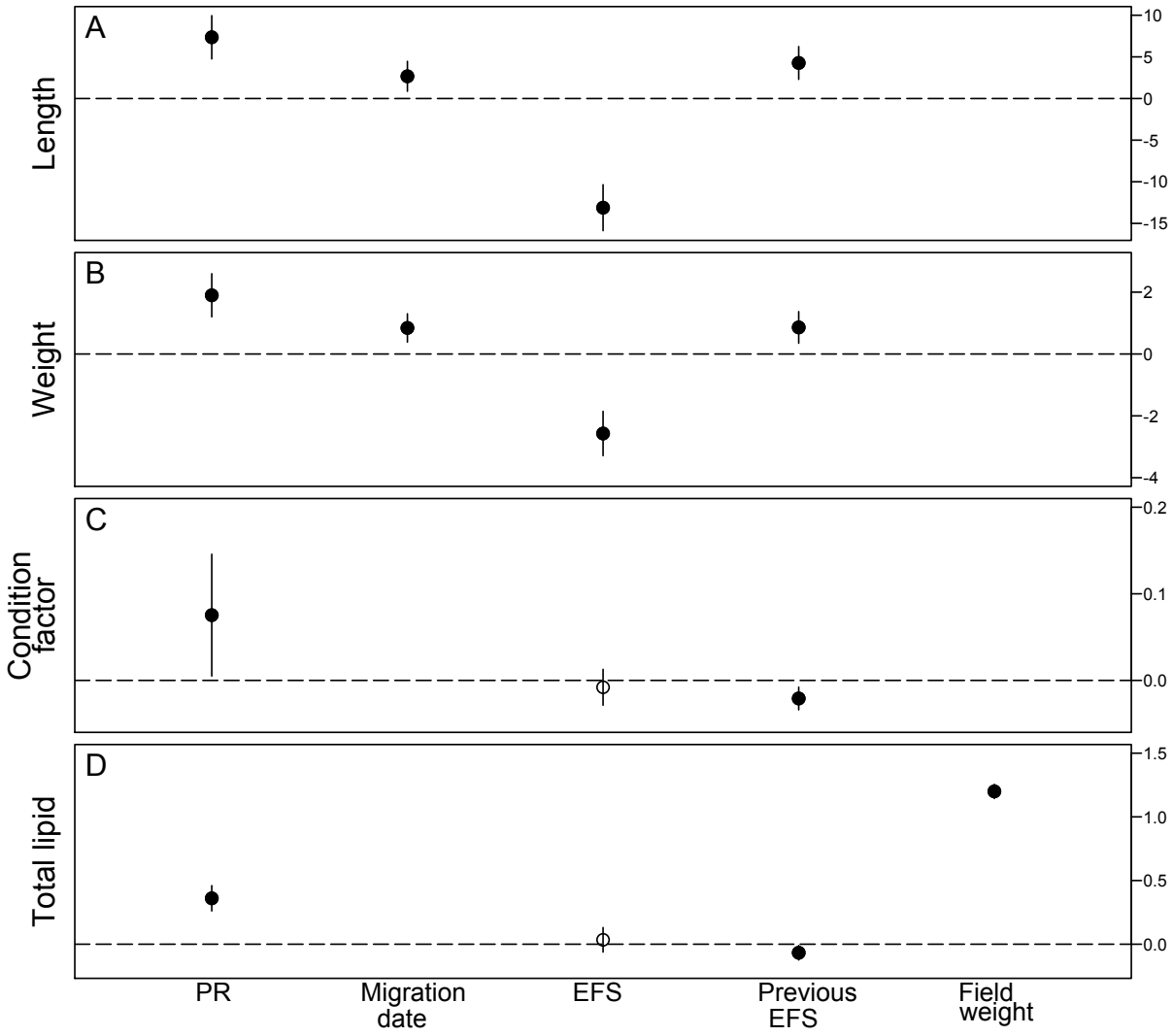


Figure 1. Model averaged standardized coefficients (mean=0, standard deviation=1) with 95% confidence intervals (CI) for models describing (A) length (mm), (B) weight (g), and (C) percent total lipid (g total lipid per g wet weight) of out-migrating sockeye salmon smolts from Chilko River, Sweltzer Creek, Seton River, and Little River. Filled circles indicate explanatory variables with a significant effect ($p < 0.05$) on the relevant condition metric.

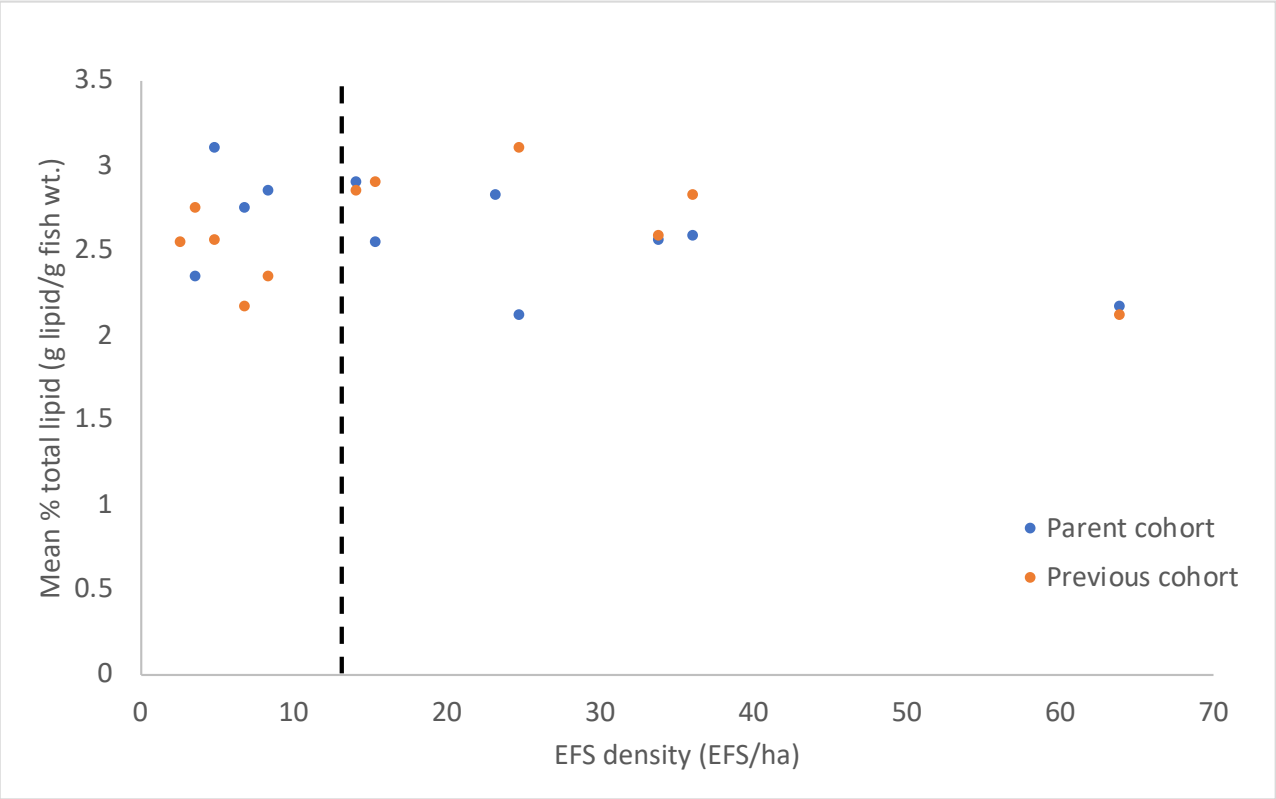


Figure 2. The relationship between the average % total lipid (g lipid per g fish wt.) of one- and two-year-old out-migrating smolts and the number of effective female spawners (EFS per hectare of rearing lake) of their parent cohort (blue dots) and the previous spawning cohort (orange dots). Smolts were collected from the counting fence in the Chilko River in 2007-2017. The vertical dashed line at 13.1 EFS per hectare is the approximate EFS density that would produce the maximum number of juveniles from Chilko Lake (i.e. the lake rearing capacity, from the PR model).

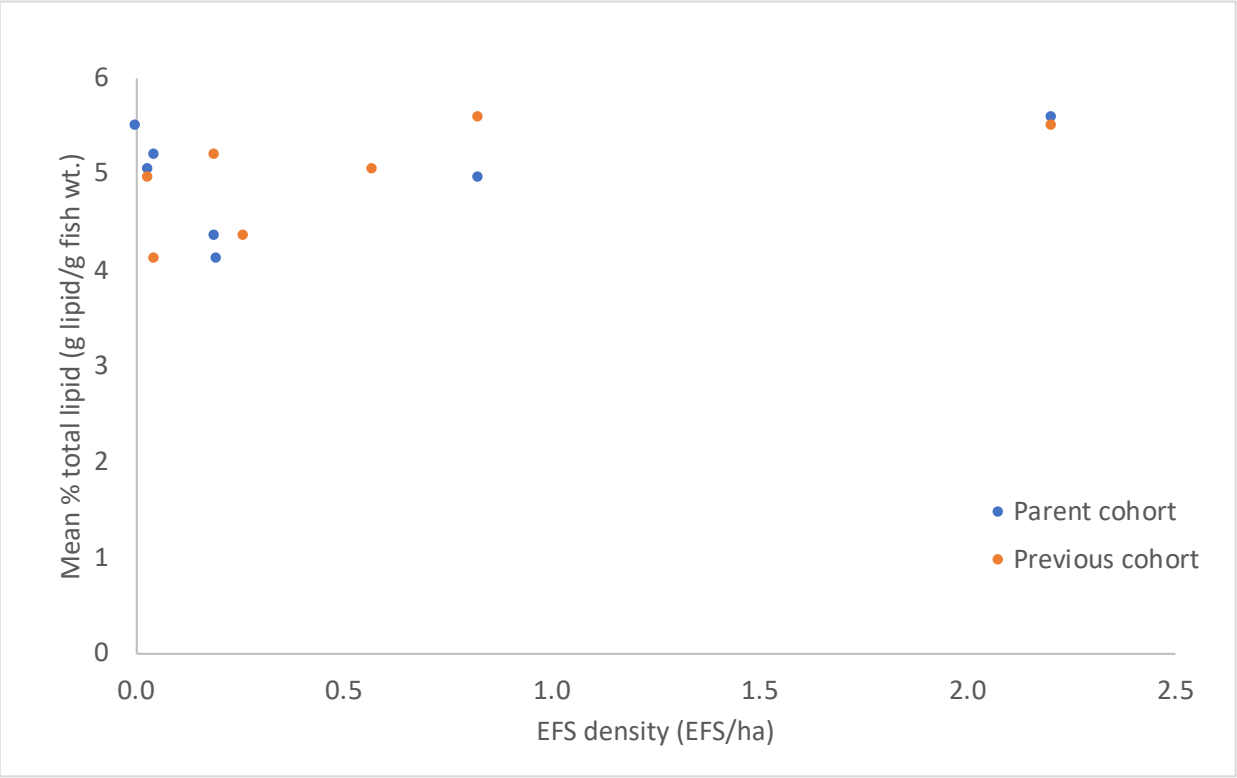


Figure 3. The relationship between the average % total lipid (g lipid per g fish wt.) of one- and two-year-old out-migrating smolts and the number of effective female spawners (EFS per hectare of rearing lake) of their parent cohort (blue dots) and the previous spawning cohort (orange dots). Smolts were collected from the counting fence in Sweltzer Creek, downstream of Cultus Lake, in 2009-2011 and 2014-2017. The density of EFS that would produce the maximum number of juvenile sockeye salmon from Cultus Lake (i.e. the lake rearing capacity, from the PR model) is approximately 67.4 EFS per hectare, which is beyond the range of the x-axis.

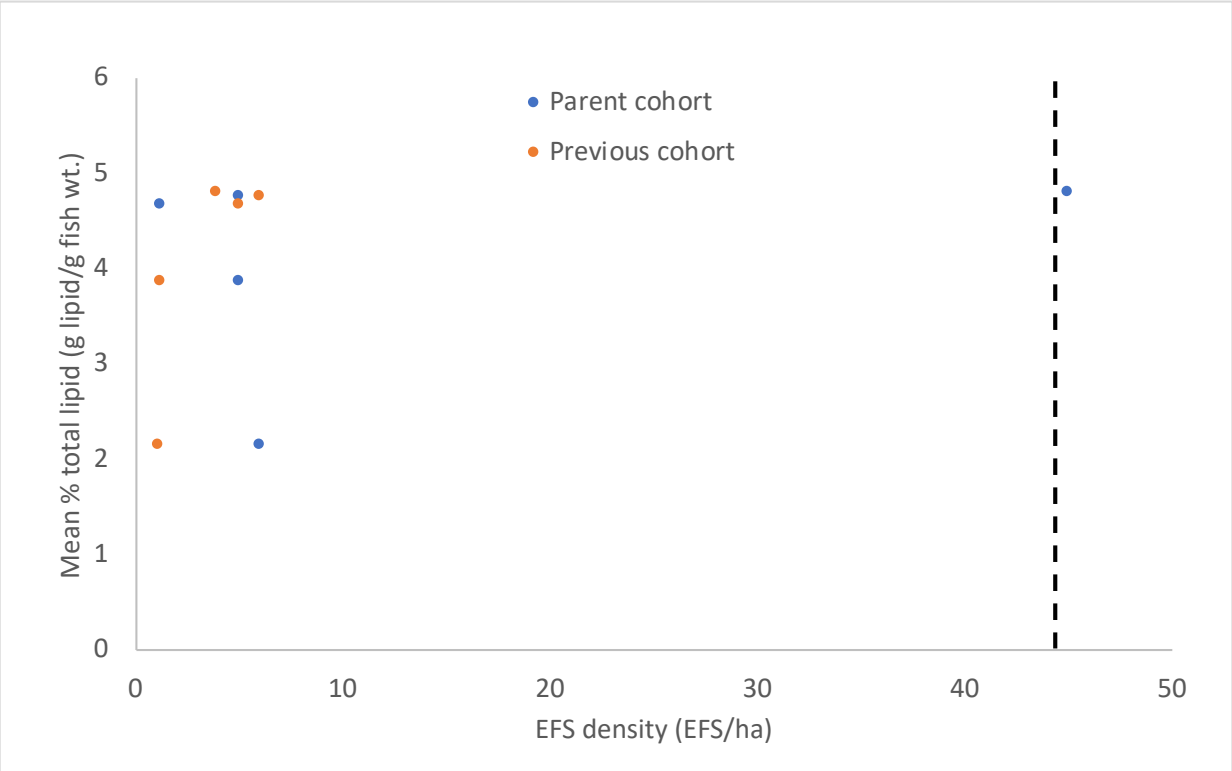


Figure 4. The relationship between the average % total lipid (g lipid per g fish wt.) of one- and two-year-old out-migrating smolts and the number of effective female spawners (EFS per hectare of rearing lake) of their parent cohort (blue dots) and the previous spawning cohort (orange dots). Smolts were collected from a rotary screw trap or an incline plane trap in the Seton River in 2012-2015 and 2017. The vertical dashed line at 44.2 EFS per hectare is the approximate EFS density that would produce the maximum number of juveniles from the Seton-Anderson system (i.e. the lake rearing capacity, from the PR model).

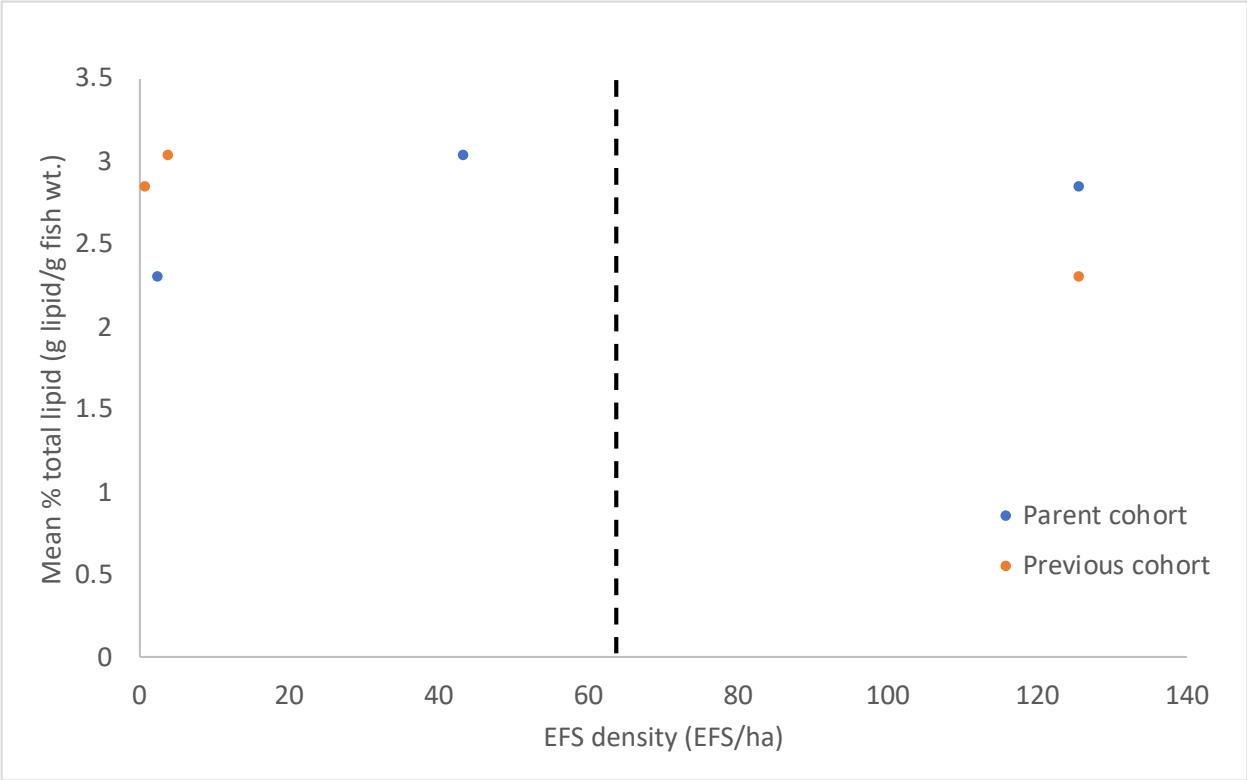


Figure 5. The relationship between the average % total lipid (g lipid per g fish wt.) of one- and two-year-old out-migrating smolts and the number of effective female spawners (EFS per hectare of rearing lake) of their parent cohort (blue dots) and the previous spawning cohort (orange dots). Smolts were collected from Little River, downstream of the Shuswap Lake outlet, in 2012, 2013, and 2016. The vertical dashed line at 63.6 EFS per hectare is the approximate EFS density that would produce the maximum number of juveniles from the Shuswap Lake system (i.e. the lake rearing capacity, from the PR model).

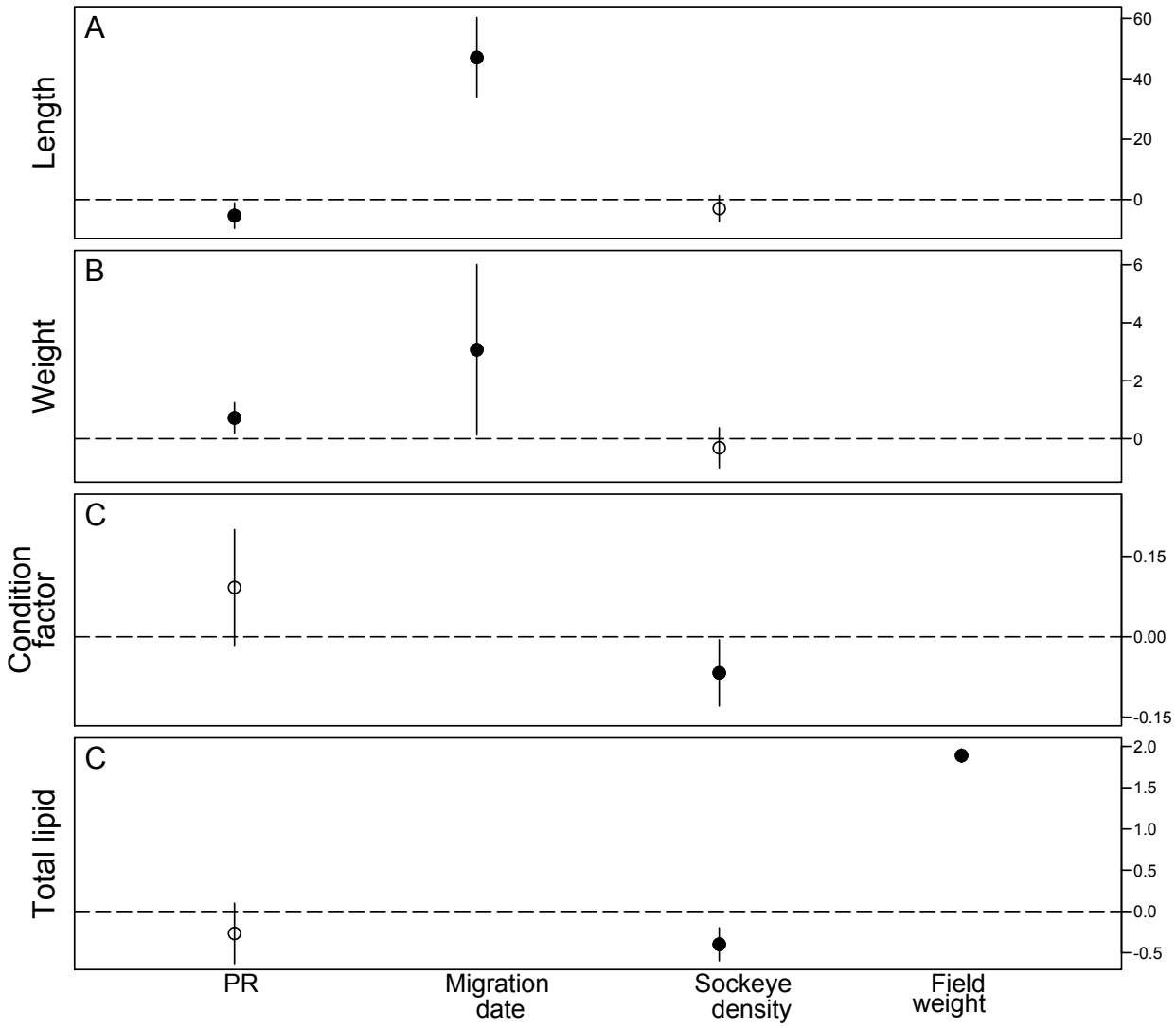


Figure 6. Model averaged standardized coefficients (mean=0, standard deviation=1) with 95% confidence intervals (CI) for models describing (A) length (mm), (B) weight (g), and (C) percent total lipid (g total lipid per g wet weight) of juvenile sockeye salmon (spring fry, summer fry, fall fry, and spring parr) from Cultus, Quesnel, Seton, and Shuswap lakes. Filled circles indicate explanatory variables with a significant effect ($p < 0.05$) on the relevant condition metric.

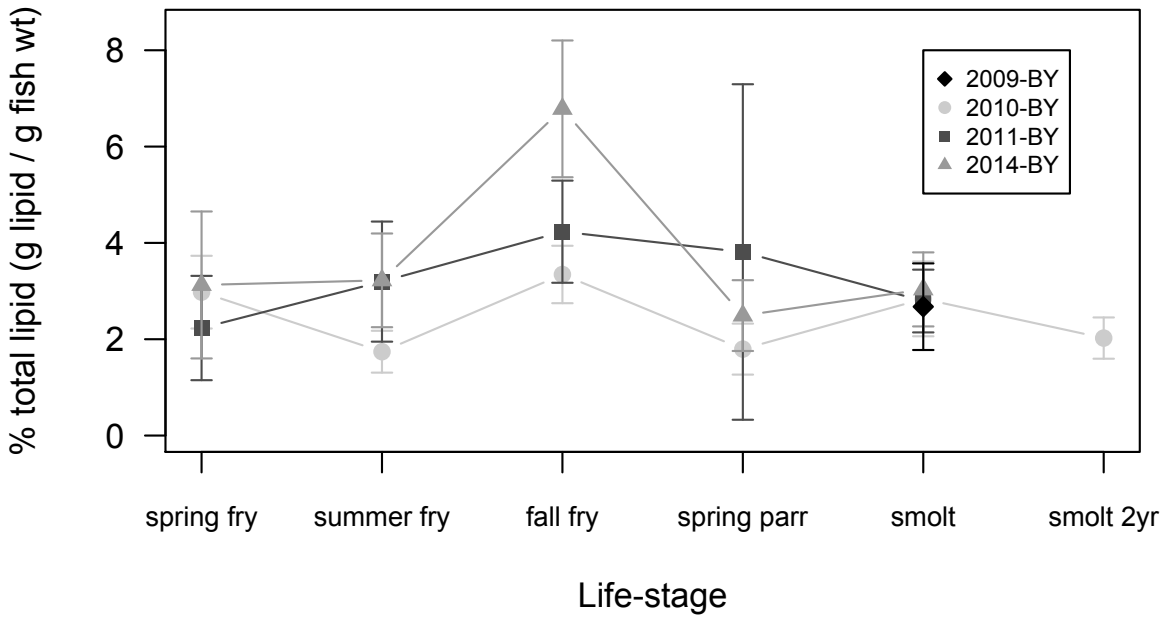


Figure 7. Mean and standard deviation of percent total lipid of juvenile sockeye salmon from brood years 2009-2011 and 2014 collected from Shuswap Lake and Little River at multiple life-stages.

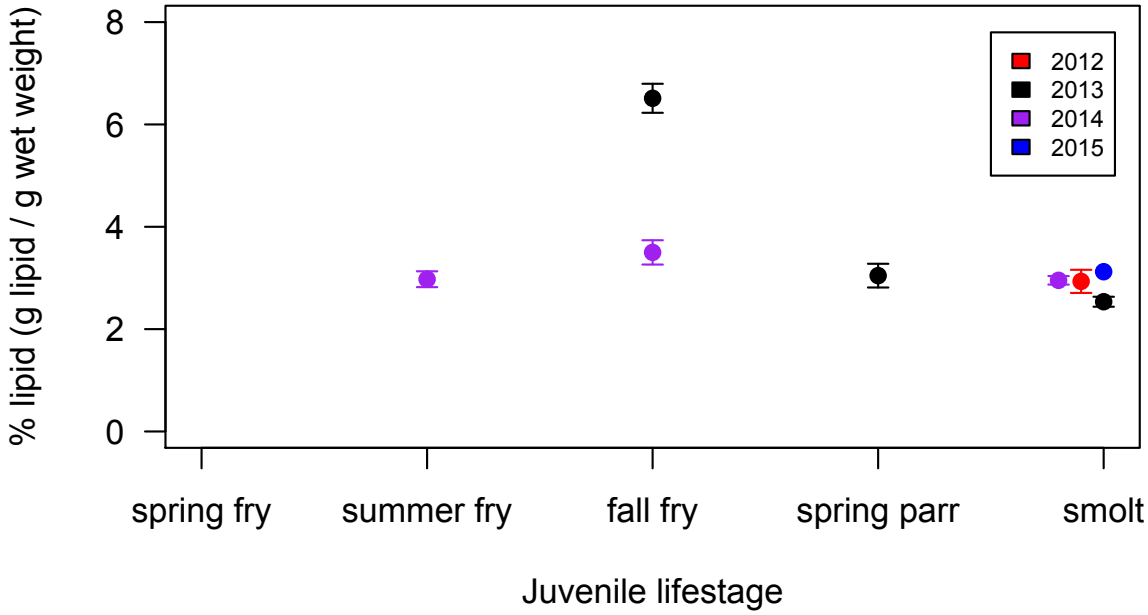


Figure 8. Mean and standard error of percent total lipid of juvenile sockeye salmon from brood years 2012-2015 collected from Chilliwack Lake and Chilliwack River at multiple life-stages.

# Evaluating minimum whole-body lipid values for survival in wild juvenile sockeye salmon collected from six rearing lakes in the Fraser River watershed

## INTRODUCTION

Surplus energy beyond an organism's basal metabolic demand can be allocated to activity, growth, or storage. Lipid is a readily available source of endogenous energy during periods of low food availability. However, not all lipids in a fish's body are storage lipids that can be metabolized for survival, activity, or growth. A portion of a fish's total lipids is essential to physiological structure and function, including lipids in the phospholipid bilayers that forms cell walls. Therefore, there is a minimum quantity of total lipids (i.e. storage and structural lipids) necessary to support basal metabolism and sustain life. In fishes, triacylglycerides (TAG) are the primary form of storage lipid (Hendersen and Tocher, 1987; Sheridan 1988).

Individuals within a population of fish differ in their relative quantity of stored lipids, due to physiological and behavioural differences in metabolic rates, feeding, and habitat use. The proportion of the population in the poorest condition (i.e. with the lowest lipid stores) will have a higher risk of mortality than others in the cohort during periods of low food availability, which can occur at multiple life-stages. Food is typically scarce during winter months, as cold temperatures and ice cover on lakes reduces photosynthesis and zooplankton production. Greater energy stores in the fall are associated with higher probability of over-winter survival (Post and Evans 1989; Shuter and Post 1990; Johnson and Evans 1991; Schultz and Conover 1997).

Low food availability can also occur during the growing season if there is a high abundance of conspecifics are competing for limited prey. Some sockeye salmon populations in the Fraser River experience dramatic fluctuations in cohort sizes on a four-year cycle, with one brood several orders of magnitude larger than the other three cycle lines that rear in the same lake.

Additionally, sockeye salmon undergo long juvenile and adult migrations that are fueled entirely by endogenous energy stores. In migrating adults, energy density has been positively associated with survival to spawning grounds (Cooke et al. 2006). A recent holding study on Chilko Lake sockeye salmon smolts suggested that two percent of a fish's total mass is the minimum total quantity of lipid necessary to sustain swimming activity (S. Wilson, pers. comm.). Although sockeye smolts can survive at lower levels of total lipids with very minimal activity, impairment of feeding, predator avoidance, and migration would jeopardize survival (S. Wilson, pers. comm.). Gardiner and Geddes (1980) found similar fat content threshold of 2% for stream salmonids overwinter.

Our objective with this study was to assess evidence for an energetic threshold for survival in juvenile sockeye salmon sampled from six different populations over multiple brood years. In

particular, we examined the distribution of percent total lipid values for fall fry and spring parr, to assess over-winter changes in energetic status, and smolts, to assess migratory preparedness. We also assessed differences in the distribution of percent total lipid values between high and low abundance cohorts. We sampled fish from the populations that rear in Chilko Lake, Chilliwack Lake, Cultus Lake, Quesnel Lake, Seton and Anderson lakes, and Shuswap Lake, which differ in lake productivity, juvenile abundance (see Chapter 2), and juvenile energetic status (see Chapter 1).

We predicted that smolts from populations that rear in less productive lakes (i.e. with lower photosynthetic rates) would have a greater proportion of individuals with total lipid values below 2%, across life-stages. We predicted that a greater proportion of spring parr would have total lipid values below 2% than fall fry in the same brood, as lipid would be metabolized through the winter and low condition individuals may die. We also predicted that the proportion of juveniles with percent total lipid values below 2% would be greater in high abundance cohorts.

## METHODS

### POPULATIONS

For this report, we collected juvenile sockeye salmon from populations that rear in six lakes in the Fraser River watershed. The location, limnology, and sockeye salmon population dynamics of each lake are described in some detail below, and lake attributes are compared in Chapter 1, Table 1.

#### *Chilko Lake*

Chilko Lake (51°20'N, 124°05'W) is a cold, ultra-oligotrophic, sub-alpine lake, located on the eastern edge of the Coast Mountain Range at an elevation of 1172 m. The surface area of the lake is 185 $km^2$ (18,451 ha), and the mean and maximum depths are 123 m and 330 m. The lake has steep banks and limited littoral habitat. During winter, the lake temperature is 4°C. The growing season is May 1–October 31, with a seasonal average photosynthetic rate (PR) of 121 mg $C \cdot m^{-2} \cdot d^{-1}$ (Grant *et al.* 2011).

Most of the sockeye salmon in the population spawn in Chilko River, downstream of the lake outlet, with the remainder using gravel beaches throughout Chilko Lake (Hume *et al.* 1996). The Chilko population represents a major contributor to adult returns to the Fraser River in many years. During the years of the study (2005-2016), total spawners (and effective female spawners, EFS) was smallest in 2004, at 92,000 (49,000), and largest in 2010, at approximately 2,500,000 (1,180,000). The population does not have a regular four-year dominance cycle (Myers *et al.* 1997).

Smolts migrate into the Chilko River from mid-April until mid-May (median date: between April 26-May 5 in years 2006-2015); out-migrating smolts are enumerated by DFO using a counting fence with video monitoring. In some years, a relatively large proportion of parr remain in Chilko Lake for an additional year and outmigrate as two-year-old smolts (age 2+). In 2009, 2010, 2013, and 2014, 8–10% of outmigrating Chilko smolts were two-year-olds. The juvenile migration, from Chilko Lake to the Fraser River estuary, is 677 km.

*Chilliwack Lake*

Chilliwack Lake (49°03'N, 121°25'W) is a relatively cold, oligotrophic lake, located in the eastern Fraser Valley, at an elevation of 621 m. The surface area of the lake is 12 $km^2$ (1,187 ha), and the mean and maximum depths are 67 m and 121 m (Shortreed et al. 2001; Tunnicliffe et al. 2012). The seasonal mean photosynthetic rate of Chilliwack Lake is 101 mg $C \cdot m^{-2} \cdot d^{-1}$ (Grant *et al.* 2011).

Chilliwack Lake is the rearing lake for sockeye salmon populations that spawn in Dolly Varden Creek, a tributary, and in the lake itself. Escapements to Chilliwack Lake have been highly variable (Grant *et al*. 2011): 3,500 spawners (1,700 EFS) in 2014 to 126,000 spawners (79,000 EFS) in 2012. The dominant cycle line is the 2000 brood.

Sockeye salmon smolts leave Chilliwack Lake between mid-April and mid-May. Their migration through Chilliwack and Fraser rivers to the Strait of Georgia is 153 km.

*Cultus Lake*

Cultus Lake (49°03'N, 121°59'W), located in the eastern Fraser Valley, is a small lake of 6 $km^2$ (630 ha) at 46 metres above sea level. The lake is steep-sided, with a limited littoral area, and mean and maximum depths of 21 m and 44 m. Cultus Lake is productive, and the seasonal mean photosynthetic rate of 404 mg $C \cdot m^{-2} \cdot d^{-1}$ was the highest of the lakes studied (Grant *et al.* 2011). It has a highly developed catchment area, with residential, agricultural, and recreational land uses.

The sockeye salmon population that spawns in Cultus Lake has been assessed as Endangered by the Committee on the Status of Endangered Wildlife in Canada. From 1994 to 2016, the population declined 92% (COSEWIC 2003). During the study, escapements to Cultus Lake ranged from 892 spawners (19 EFS) in 2012 to 10,300 spawners (1,000 EFS) in 2010. A hatchery program supplements the wild population.

Sockeye salmon smolts migrate into Sweltzer Creek from mid-March until late May (median date: between April 7-30 in years 2007-2016), and the outmigration is enumerated by DFO

using a counting fence. The juvenile migration, from the lake outlet to the Fraser River estuary, is 110 km.

*Quesnel Lake*

Quesnel Lake (52°30'N, 120°00'W) is an oligotrophic lake in the interior plateau of British Columbia, at an elevation of 725 m (Morton and Williams 1990). It is large, covering an area of 272 $km^2$ (26,090 ha), and deep, with mean and maximum depths of 158 m and 530 m. The lake has four arms, hereafter referred to as, West Arm, drained by the Quesnel River, Main Arm, North Arm, and East Arm. The growing season is from May 1–October 31, and the lake has a seasonal mean PR of 130 mg $C \cdot m^{-2} \cdot d^{-1}$ (Grant *et al.* 2011).

The main spawning areas for sockeye salmon are in the Horsefly and Mitchell rivers, the largest tributaries to the lake, while additional spawning areas in small streams and along the lake shore support smaller numbers of fish (Hume *et al*. 1996). Returns to Quesnel Lake during the study were lowest in 2016, with 1,000 spawners (200 EFS), and highest in 2014, with 830,000 spawners (430,000 EFS). The dominant cycle line is the 2002 brood.

Juvenile sockeye salmon occupy the pelagic zone from July until October. The maximum estimated density of juveniles in Quesnel Lake is 6000 fry $ha^{-1}$, based on analysis of PR models and historic fry data by Hume *et al.* (1996). Smolts leave the lake in April and May and migrate 748 km to the Fraser River estuary.

*Seton and Anderson lakes*

Seton Lake (50°42'N, 122°08'W) and Anderson Lake (50°38'N, 122°24'W) are oligotrophic lakes in the rain shadow of the Coast Mountain Range, in southwestern British Columbia, at elevations of 237 m and 258 m, respectively. Seton Lake covers 25 $km^2$ (2,519 ha) and Anderson Lake covers 29 $km^2$ (2,844 ha). Both lakes are deep, with steep sides and limited littoral areas. The mean and maximum depths are 85 m and 151 m in Seton Lake and 140 m and 215 m in Anderson Lake. Anderson Lake is drained into Seton Lake by Portage Creek, a 3-km stream. Seton Lake also receives water via a hydropower diversion from Carpenter Lake, a reservoir in the adjacent Bridge River watershed. Flow from Seton Lake, through the Seton River, is controlled by the Seton Dam, which was built in 1956 and is located 800 m downstream of the lake outlet (Limnotek 2015). Anderson Lake is more productive than Seton Lake, with a photosynthetic rate of 303 mg $C \cdot m^{-2} \cdot d^{-1}$, compared to 233 mg $C \cdot m^{-2} \cdot d^{-1}$ (Grant *et al.* 2011).

Two populations of adult sockeye salmon spawn in the Seton-Anderson watershed: early summer run fish that return to Gates Creek, which flows into Anderson Lake, and late run fish that spawn in Portage Creek. The Portage Creek sockeye salmon were transplanted from the lower Adams River population in the early $20^{th}$ century (Withler *et al.* 2000; Grant *et al.* 2011). The two populations are genetically distinct, with differently timed migration and spawning

(Withler *et al.* 2000; Moreira 2014). The dominant cycle line for the Portage Creek population is 2002, and the Gates Creek sockeye population has not exhibited regular cyclic dominance since the late 1990s. The largest collective adult return to the system during the study was in 2010 (80,000 spawners; 33,000 EFS), and the smallest was in 2016 (8,800 spawners, 3,600 EFS). The majority of adult returns are to the Gates Creek population.

The majority of Gates Creek sockeye fry rear in Seton Lake, migrating through Portage Creek from mid-April to late-June as fry (Geen and Andrew 1961; Woodey 1975). Smolts leave Seton Lake in April and May, and the migration from the Seton Lake outlet above the Seton Dam, through the Seton and Fraser rivers to the Fraser River estuary, is 333 km.

*Shuswap Lake*

Shuswap Lake (50°00'N, 119°05'W) is a mesotrophic lake in the interior plateau of British Columbia, at an elevation of 347 m (Hume *et al*. 1995). The lake is roughly H-shaped, with four major arms: Main, Seymour, Anstey, and Salmon. A 1.5-km narrows at Sicamous separates Mara Lake from Salmon Arm. Little River drains the Main Arm of Shuswap Lake into Little Shuswap Lake, and sockeye salmon rear in Mara, Shuswap, and Little Shuswap lakes. The three-lake system is 330 $km^2$, but Mara and Little Shuswap were not routinely sampled, so an area of 300 $km^2$ (29,851 ha) was used. The mean and maximum depths of Shuswap Lake are 58 m and 171 m (Nidle and Shortreed 1996).

Shuswap Lake has a longer growing season (April 1–November 30) and warmer thermal regime than the other lakes in the study, with the exception of Cultus. The mean seasonal photosynthetic rate is 171 mg C $m^{-2}$ $d^{-1}$ (Grant *et al.* 2011)

Sockeye salmon return to a number of tributaries in the Shuswap lakes system, across two run timing groups: early summer and late. The early summer group returns predominantly to Scotch Creek, Eagle River, and Seymour River, while the majority of the late group spawns in Adams River and Lower Shuswap River. Spawning also occurs in other tributaries and along the shore (Grant *et al*. 2011). The smallest return during the study was 1,616 spawners (768 EFS) in 2016, and the largest was 8,947,869 spawners (3,753,548 EFS) in 2010.

Sockeye salmon fry occupy the pelagic zone from July until November (Hume *et al.* 1996), and the populations mix within and among lakes during rearing. Smolts leave the Shuswap system later than in other populations, outmigrating in May and June. The downstream migration is 497 km and is the most complex, following Little River into Little Shuswap Lake, the South Thompson River into Kamloops Lake, and the Thompson and Fraser rivers into the Strait of Georgia.

## JUVENILE FISH COLLECTION, TRANSPORT, AND STORAGE

Juvenile sockeye salmon (*Oncorhynchus nerka*) were collected from various locations across the Fraser watershed. Spring fry, summer fry, fall fry, spring parr and smolts, were collected across multiple years (2007-2017) using various capture methods, depending on the location and targeted life history stage (see Appendix A for details). Briefly, smolts were collected by beach seine, dip net, rotary screw trap, or incline plane trap from Chilko Lake, Sweltzer Creek, Chilliwack Lake, Little River, Quesnel River, Seton River, and the lower Fraser River at Mission. Spring fry were collected by beach seine from Quesnel River and Shuswap Lake. Summer fry Fall fry and spring parr were collected by lake trawl from Quesnel Lake, Shuswap Lake, Cultus Lake, and Chilliwack Lake (Appendix A: Table 1, Table 2). Following collection, fish were euthanized with an overdose of tricaine methanesulfonate (MS-222) prior to fork lengths (nearest mm) and weights (nearest 0.01 g) being measured in the field. Individuals were wrapped in aluminum foil or individual Whirlpaks and frozen rapidly on dry ice. A small subset was frozen on liquid nitrogen or place in a -20C freezer. The majority of fish caught by beach seine or dip net were transported to the Fisheries and Oceans research laboratory in West Vancouver ('West Van Lab') for long-term cold storage, although some samples were stored at the University of British Columbia in Vancouver or the Pacific Biological Station in Nanaimo, prior to transport to West Van Lab for analysis. The fish caught by lake trawl were stored at the Fisheries and Oceans research laboratory in Cultus Lake, prior to transfer to West Van Lab for analysis. For more detailed information on capture history and storage conditions for juvenile sockeye samples, see 'Appendix A: Sample collection 2007-2017.'

## LIFE-STAGE IDENTIFICATION

Assumptions regarding age assignments were made based on sampling location, sampling date, and size. The majority of juvenile fish had age assigned at the time of sampling. Trawl surveys were conducted by the DFO Lakes Program in the summer (July or August) and fall (September–November) to target age-0 sockeye salmon. Spring trawl surveys (February–May) were conducted to target age-1 sockeye salmon, with additional June surveys for age-1 sockeye salmon in Shuswap Lake. Age-0 fish, called offshore or pelagic fry, were considered summer or fall fry, depending on month of sampling. Age-1 fish caught by trawl were considered spring parr. Age-0 fish caught in the river environment by seine or dip net were called onshore fry. Age-1 or 2 fish caught in the river environment by seine net, dip net, or weir were called smolts. Sampling was conducted in June in Little River (Shuswap complex) and April or May for all other populations.

Age-2 smolts are larger than age-1 smolts. Chilko can have a high proportion of two-year-old smolts in some years (up to 10%), and these larger fish were generally noted as age-2 smolts at the time of sampling. Several additional fish in each population were identified as two-year-olds from population- and capture year-specific length-weight relationships, as the different age classes typically cluster separately.

## LIPID EXTRACTION AND CONSTITUENT ANALYSIS

Whole juvenile sockeye salmon (*Oncorhynchus nerka*) samples were removed from -80 °C freezer storage and allowed to thaw at room temperature prior to taking fork length and weights measurements in the laboratory. Fish were cut into 8-10 pieces and placed in 50 ml Nalgene® tubes with two steel ball bearings and homogenized using a SPEX SamplePrep 2010 Geno/Grinder (SPEX, Metuchen, NJ, www.spexsampleprep.com) at 1500 rpm for two-minute intervals until completely homogenized.

Lipid extraction from homogenized tissue followed protocols developed by Bligh and Dyer (1959) with minor modifications (see: 'Appendix B: Lipid extraction and moisture ash' for detailed methods). Chloroform, methanol and water were added to a weighed subsample of homogenate (in 1:1:0.5 solvent ratios, respectively) and homogenized to form a biphasic layer of chloroform-lipid and methanol-water. The volume of the chloro-lipid layer was measured, prior to pipetting a known volume onto a pre-weighed tin boat and evaporating off the chloroform in an oven. The remaining lipid samples were then re-weighed and frozen for subsequent triglyceride analysis.

The percent lipid of the subsample was calculated using Eq. 1:

$$subsample\ \%\ lipid = \frac{extracted\ lipid\ wt.\ (g)}{subsample\ wt.\ (g)} * 100 \quad [1]$$

The weight of the total lipid in each fish was calculated using Eq. 2:

$$total\ lipid\ (g) = \frac{uncorr.\ \%\ lipid}{100\%} *\ whole\ fish\ wt._{\ thawed}\ (g) \quad [2]$$

Moisture lost from juvenile samples during storage was estimated and used to correct fish weights using procedures outlined in Appendix C.

## SMOLT AND SPAWNER ENUMERATION

Daily and cumulative annual smolt outmigration totals from the counting fences on Chilko River and Sweltzer Creek were provided for years ranging from 2006 to 2016 by DFO Stock Assessment Division (Tracy Cone, DFO Annacis Island).

Escapement data was determined from near final spawning ground estimates for individual spawning streams for years 1938 to 2016, which were provided by DFO Stock Assessment Division (T. Cone). The number of effective female spawners (EFS) was tallied by six stock

groupings, based on natal rearing lake (Chilko Lake, Chilliwack Lake, Cultus Lake, Quesnel Lake, Seton Lake, and Shuswap Lake).

## TOTAL LIPID THRESHOLDS

In order to compare the distributions of percent total lipid values within populations, brood years, and life-stages, we quantified the number of poor condition fish in each cohort. Poor condition fish were those with a percent total lipid value below the thresholds of 1.8, 2.0, and 2.2 g total lipid per g body weight. We then calculated the proportion of fish in each cohort that fell within the tail of the distribution, using Eq. 1 below for each threshold value:

$$Proportion < 2.0\% = \frac{\sum juveniles\ with\ total\ lipid < 2.0\%}{\sum all\ juveniles\ in\ cohort} * 100 \quad [1]$$

## RESULTS

In general, smolts from Chilko Lake had lower energetic status than smolts from other populations, which was evident when comparing distributions of percent total lipid values (Figures 1-9). A larger proportion of individual fish within cohorts from Chilko Lake were below the lipid thresholds of 1.8%, 2.0%, and 2.2% than cohorts of fish that reared in other lakes. There was a single year (2006) when none of the one-year-old smolts from Chilko Lake had percent lipid values below 2.0%, and the sample size for this cohort was just seven fish (Table 1). Across 2005-2015 brood years, between 15.0% and 52.4% of the one-year-old smolts sampled had total lipid values below 2.0% (Table 1). Highly abundant broods, like 2010, 2013, and 2014 (from 1,180,000, 620,000, and 670,000 effective female spawners, respectively), had a large proportion of one-year-old smolts with total lipid values lower than 2% (52.4%, 23.7%, and 26.8% of smolts collected, respectively), but these were not the only broods where greater than 20% of fish had total lipids below 2% (Table 1). We did not sample juveniles younger than the smolt life-stage from Chilko Lake.

The proportion of Chilliwack Lake smolts with total lipid levels below 2.0% ranged quite broadly among the years that we sampled. Nearly 40% of smolts from the 2012 dominant brood had total lipid levels below 2.0%, while the proportions were lower for the sub-dominant and off-cycle broods (2013-2015: 5.7%, 10.0%, and 20.0%; Table 2, Figure 3). Spring parr collected from the 2012 brood had a lower distribution of lipid values (30% of fish below 2.0%) than the cohort did in the previous fall (0% of fish below 2.0%; Table 2). However, there were fall fry with total lipid values below 2.0% collected from the sub-dominant brood (2013-by: 6.7% of fish, n=15).

We observed very few out-migrating smolts from Cultus Lake with total lipid levels below 2.0%. Of the smolts collected from the 2007 and 2009 broods, 5% of each had total lipid values less

than 2.0%; in all other years, the proportion was zero (Table 3, Figure 4 vs. Figure 5). In the 2014 brood, the only one for which we had both fall fry and spring parr samples, neither distribution had values below 2.0% (Table 3).

The one-year-old smolts that we collected from two broods in Quesnel River had relatively few fish with lipid levels below the 2% threshold (15.8% and 14.3% of fish in 2014 and 2015, respectively; Table 4, Figure 6). Spring parr had higher total lipid values than fall fry from the 2013 brood (0.0% and 3.4% of fish collected, respectively; Table 4). A high proportion of the spring fry that we collected from the abundant 2014 brood had total lipid levels below 2% (i.e. 64.7%; Table 4).

In general, smolts from Seton Lake had higher energetic status than smolts from the other populations (Figures 1-9). Like smolts that out-migrated from Cultus Lake, few broods had any individuals with total lipid levels below the threshold. Of the smolts we collected from the 2010 dominant brood, 57.1% had total lipid values less than 2.0%, while 15% percent of the smolts from the 2013 brood also had total lipid levels below the threshold (Table 5, Figure 7).

Across the brood years and life-stages that we sampled from Shuswap Lake, the only life-stage without any fish below 2.0% total lipid was fall fry, which had minimum total lipid levels of 2.2%, 2.7%, and 4.1% in 2010, 2011, and 2012, respectively (Table 6; Figures 8 and 9). Spring parr had among the largest proportions of fish with total lipid values less than 2.0% of any life-stage sampled (74.1%, 34.2%, and 30% of fish sampled in 2010, 2011, and 2012; Table 6; Figures 8 and 9). We observed a decrease in the proportion of fish with lipids below 2.0% from spring parr collected from Shuswap Lake to one-year-old smolts collected from Little River in all three brood years (Table 6). In the dominant 2010 brood, a high proportion of summer fry had lipid levels below the 2.0% threshold (i.e. 73% of fish; Figure 8). The following spring, a high proportion of the spring fry we collected from the subdominant 2011 brood also had lipid levels below 2.0% (i.e. 53.6% of fish; Table 6).

## DISCUSSION

In some populations, life-stages, and brood years, we observed extremely high proportions of juvenile sockeye salmon with total lipid levels below 2%. Two percent of body weight has been recently be identified through empirical studies as a minimum quantity of total lipids to support prolonged swimming activity of Chilko sockeye salmon smolts (S. Wilson, pers. comm.), and thus is a possible threshold for survival in wild, free-swimming smolts. Lower levels of 1.6% body lipid are also suggested to be critical value to actually sustain life, but it would seem unlikely for fish in the wild to get to these levels without succumbing to predation.

In Chapter 1 of this report, we observed that smolts from populations that rear in lakes with lower mean seasonal photosynthetic rates had lower quantities of total lipid, relative to body weight, than smolts from more productive lakes. Indeed, the distributions that we examined in

the present chapter spanned low total lipid values for smolts from Chilko Lake, relative to smolts from Seton and Cultus lakes, and greater proportions of smolts with values below 2%. However, for Chilko, Chilliwack and Shuswap lakes, density dependent and delayed density dependent dynamics likely also contributed to higher proportions of juveniles with low total lipid levels.

For Chilko Lake smolts, we did not observe a strong effect of density dependence at intermediate numbers of effective female spawners. The 2013 and 2014 broods, which both had greater than 600,000 EFS, did not have markedly lower lipid values. However, density dependent and delayed density dependent dynamics at high EFS (i.e. greater than 1,000,000) likely contributed to a high proportion of smolts from the 2010 brood having low total lipid levels. Fifty-two percent of one-year-olds collected in 2012 had lipid levels below 2% (n=42 collected), while 50% and 85% of one- and two-year-old smolts collected the following year had below-threshold quantities of total lipid (n=20 and n=20 collected, respectively). We would expect lower downstream survival in the 2010 and 2011 broods, if the 2% total lipid threshold observed in laboratory swimming experiments of Chilko Lake smolts is transferable to free-swimming smolts.

There was evidence from other populations to support our prediction that there would be a greater proportion of below 2% total lipid values in juveniles from high abundance cohorts.

In the Shuswap population complex, almost 75% of summer fry sampled from the dominant 2010 brood had less than 2% total lipid, compared to approximately 15% of summer fry from the subdominant 2011 brood. For 2010-by summer fry, lower lipid levels reflect lower food availability in Shuswap Lake at fry densities of approximately 6500 fry per hectare in August 2011, compared to 600 fry per hectare in August 2012 (L. Pon, unpublished data). Summer fry from all cohorts in Shuswap Lake may be maximizing growth at the expense of storage, as larger fish have a greater capacity to store lipid during the fall, and greater lipid stores increase likelihood of over-winter survival (Post and Parkinson 2001). Surprisingly, the estimate of fry density in Shuswap Lake in October 2011 was only 3% smaller (~6300 fry per hectare; L. Pon, unpublished data), yet none of the fall fry collected at that time had lipid values below 2%. Rather than very high mortality among the lowest condition fish, this suggests a dramatic increase in energy allocation to lipid storage across the cohort between August and October. Indeed, fall fry are clearly maximizing energy allocation to lipid storage across brood years, as they had the highest percent total lipid values of any life-stage that we sampled. Additionally, we can conclude that total lipid levels of 2% body weight are adequate to sustain wild, free-swimming fry, and the threshold for survival must be lower.

Interestingly, the spring fry of the subdominant 2011 brood had very low lipid levels: over half of the fish we collected from the littoral zone in Shuswap Lake were below the 2% threshold. Food availability in spring of 2012 was likely very low in Shuswap Lake, due to over-grazing of the zooplankton community during the previous growing season and over the winter months by the very abundant dominant brood. Until May and June, when smolts leave Shuswap Lake, age-

1 parr continued to affect food availability for age-0 fry, but by August, juvenile densities had substantially decreased, and summer fry lipid levels had increased.

Fall fry in Cultus Lake do not consistently have the highest lipid levels of life-stages within a brood year, as they do in Chilliwack and Shuswap lakes. Energy storage maximization in fall would be unnecessary for over-winter survival if lake conditions support juvenile sockeye salmon feeding year-round in Cultus Lake. The climate is milder, so the lake does not ice over, the growing season begins earlier, and there may not be adequate sockeye salmon abundance to graze down the zooplankton standing crop each season. For several broods, we observed that lipid levels increased, relative to body size, from spring parr to smolt, which would indicate that juveniles are at least feeding prior to out-migration.

Examining distributions of total lipid values increased our understanding of the relative energetic condition of juvenile sockeye salmon, among life-stages, brood years, and populations. Small differences between mean values do not fully represent the potentially large differences in the proportion of a cohort near or below lipid threshold values for swimming activity or survival. Cohorts in relatively poor condition may experience higher migration mortality as smolts; identifying populations and broods at greater risk of high downstream mortality would be useful for managers in forecasting adult sockeye salmon returns.

TABLES

Table 1. Summary of total lipid values, expressed as a percentage of fish wet weight for all brood years and life-stages of juvenile sockeye salmon collected from Chilko River. The percentage of each cohort with total lipid values below 1.8%, 2.0%, and 2.2% is shown.

| Brood year | Life-stage | *n* | Percent total lipid (g total lipid/g wet wt.) | | | | Percent of cohort below total lipid threshold | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Mean | Minimum | Maximum | SD | 1.8% | 2.0% | 2.2% |
| 2005 | smolt | 4 | 2.5 | 1.9 | 3.5 | 0.8 | 0.0 | 25.0 | 50.0 |
| 2005 | smolt 2yr | 3 | 1.7 | 1.6 | 1.7 | 0.1 | 100.0 | 100.0 | 100.0 |
| 2006 | smolt | 7 | 3.4 | 2.6 | 4.3 | 0.7 | 0.0 | 0.0 | 0.0 |
| 2007 | smolt | 20 | 2.8 | 1.4 | 6.0 | 1.0 | 15.0 | 15.0 | 25.0 |
| 2007 | smolt 2yr | 20 | 3.3 | 1.8 | 5.4 | 1.2 | 10.0 | 10.0 | 30.0 |
| 2008 | smolt | 20 | 2.3 | 1.5 | 3.9 | 0.7 | 15.0 | 40.0 | 50.0 |
| 2009 | smolt | 20 | 2.7 | 1.6 | 5.0 | 1.0 | 15.0 | 20.0 | 35.0 |
| 2010 | smolt | 42 | 2.2 | 1.2 | 4.2 | 0.6 | 19.0 | 52.4 | 71.4 |
| 2010 | smolt 2yr | 20 | 1.7 | 1.3 | 2.7 | 0.3 | 70.0 | 85.0 | 95.0 |
| 2011 | smolt | 20 | 2.5 | 1.4 | 4.5 | 0.9 | 30.0 | 50.0 | 50.0 |
| 2011 | smolt 2yr | 10 | 2.7 | 1.0 | 4.0 | 1.1 | 20.0 | 30.0 | 30.0 |
| 2012 | smolt | 79 | 3.1 | 1.4 | 7.1 | 1.2 | 10.1 | 21.5 | 30.4 |
| 2012 | smolt 2yr | 1 | 2.2 | 2.2 | 2.2 | NA | 0.0 | 0.0 | 0.0 |
| 2013 | smolt | 59 | 2.6 | 1.6 | 6.6 | 1.0 | 5.1 | 23.7 | 49.2 |
| 2013 | smolt 2yr | 2 | 2.5 | 2.3 | 2.7 | 0.3 | 0.0 | 0.0 | 0.0 |
| 2014 | smolt | 56 | 2.6 | 1.0 | 8.4 | 1.1 | 10.7 | 26.8 | 39.3 |
| 2015 | smolt | 20 | 2.8 | 1.7 | 4.4 | 0.7 | 5.0 | 15.0 | 25.0 |

Table 2. Summary of total lipid values, expressed as a percentage of fish wet weight for all brood years and life-stages of juvenile sockeye salmon collected from Chilliwack Lake and Chilliwack River. The percentage of each cohort with total lipid values below 1.8%, 2.0%, and 2.2% is shown.

| Brood year | Life-stage | *n* | Percent total lipid (g total lipid/g wet wt.) | | | | Percent of cohort below total lipid threshold | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Mean | Minimum | Maximum | SD | 1.8% | 2.0% | 2.2% |
| 2012 | fall fry | 20 | 6.5 | 4.6 | 8.3 | 1.3 | 0.0 | 0.0 | 0.0 |
| 2012 | spring parr | 40 | 3.0 | 1.0 | 6.0 | 1.5 | 25.0 | 30.0 | 30.0 |
| 2012 | smolt | 100 | 2.5 | 0.9 | 5.7 | 1.0 | 22.0 | 37.0 | 44.0 |
| 2013 | summer fry | 20 | 3.0 | 2.0 | 4.4 | 0.7 | 0.0 | 0.0 | 20.0 |
| 2013 | fall fry | 15 | 3.5 | 1.7 | 5.0 | 0.9 | 6.7 | 6.7 | 13.3 |
| 2013 | smolt | 70 | 3.0 | 1.6 | 4.7 | 0.7 | 1.4 | 5.7 | 12.9 |
| 2014 | smolt | 20 | 3.1 | 1.2 | 5.4 | 1.1 | 10.0 | 10.0 | 15.0 |
| 2015 | smolt | 20 | 2.9 | 1.7 | 5.4 | 1.0 | 15.0 | 20.0 | 25.0 |

Table 3. Summary of total lipid values, expressed as a percentage of fish wet weight for all brood years and life-stages of juvenile sockeye salmon collected from Cultus Lake and Sweltzer Creek. The percentage of each cohort with total lipid values below 1.8%, 2.0%, and 2.2% is shown.

| Brood year | Life-stage | n | Percent total lipid (g total lipid/g wet wt.) | | | | Percent of cohort below total lipid threshold | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Mean | Minimum | Maximum | SD | 1.8% | 2.0% | 2.2% |
| 2007 | spring parr | 28 | 4.7 | 1.8 | 7.7 | 1.5 | 3.6 | 3.6 | 3.6 |
| 2007 | smolt | 20 | 4.4 | 1.9 | 6.8 | 1.4 | 0.0 | 5.0 | 10.0 |
| 2008 | smolt | 20 | 5.2 | 3.4 | 7.8 | 1.1 | 0.0 | 0.0 | 0.0 |
| 2009 | fall fry | 25 | 5.3 | 1.6 | 10.5 | 2.4 | 16.0 | 16.0 | 16.0 |
| 2009 | smolt | 20 | 4.1 | 1.8 | 6.2 | 1.2 | 5.0 | 5.0 | 10.0 |
| 2011 | spring parr | 20 | 2.9 | 1.4 | 5.0 | 1.1 | 20.0 | 20.0 | 25.0 |
| 2012 | smolt | 15 | 5.1 | 3.2 | 6.7 | 1.2 | 0.0 | 0.0 | 0.0 |
| 2013 | smolt | 20 | 5.0 | 3.1 | 7.5 | 1.3 | 0.0 | 0.0 | 0.0 |
| 2014 | fall fry | 20 | 4.7 | 2.7 | 8.1 | 1.6 | 0.0 | 0.0 | 0.0 |
| 2014 | spring parr | 16 | 4.3 | 2.5 | 6.5 | 1.3 | 0.0 | 0.0 | 0.0 |
| 2014 | smolt | 19 | 5.6 | 2.7 | 8.6 | 1.9 | 0.0 | 0.0 | 0.0 |
| 2015 | smolt | 20 | 5.5 | 3.1 | 8.5 | 1.4 | 0.0 | 0.0 | 0.0 |

Table 4. Summary of total lipid values, expressed as a percentage of fish wet weight for all brood years and life-stages of juvenile sockeye salmon collected from Quesnel Lake and Quesnel River. The percentage of each cohort with total lipid values below 1.8%, 2.0%, and 2.2% is shown.

| Brood year | Life-stage | n | Percent total lipid (g total lipid/g wet wt.) | | | | Percent of cohort below total lipid threshold | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Mean | Minimum | Maximum | SD | 1.8% | 2.0% | 2.2% |
| 2013 | fall fry | 59 | 6.5 | 1.7 | 15.4 | 2.9 | 1.7 | 3.4 | 8.5 |
| 2013 | spring parr | 56 | 7.1 | 4.0 | 10.9 | 1.5 | 0.0 | 0.0 | 0.0 |
| 2013 | smolt 2yr | 2 | 4.0 | 2.3 | 5.8 | 2.5 | 0.0 | 0.0 | 0.0 |
| 2014 | spring fry | 17 | 1.7 | 0.7 | 2.9 | 0.6 | 58.8 | 64.7 | 70.6 |
| 2014 | fall fry | 59 | 5.7 | 2.2 | 8.3 | 1.5 | 0.0 | 0.0 | 1.7 |
| 2014 | smolt | 19 | 2.4 | 1.4 | 5.3 | 0.8 | 5.3 | 15.8 | 42.1 |
| 2014 | smolt 2yr | 1 | 1.8 | 1.8 | 1.8 | NA | 100.0 | 100.0 | 100.0 |
| 2015 | smolt | 7 | 2.5 | 1.2 | 3.9 | 0.9 | 14.3 | 14.3 | 42.9 |
| 2016 | spring fry | 5 | 2.4 | 1.6 | 3.0 | 0.6 | 20.0 | 20.0 | 40.0 |

Table 5. Summary of total lipid values, expressed as a percentage of fish wet weight for all brood years and life-stages of juvenile sockeye salmon collected from Seton River. The percentage of each cohort with total lipid values below 1.8%, 2.0%, and 2.2% is shown.

| Brood year | Life-stage | n | Percent total lipid (g total lipid/g wet wt.) | | | | Percent of cohort below total lipid threshold | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Mean | Minimum | Maximum | SD | 1.8% | 2.0% | 2.2% |
| 2010 | smolt | 21 | 2.2 | 1.3 | 3.4 | 0.6 | 33.3 | 57.1 | 61.9 |
| 2010 | smolt 2yr | 2 | 4.2 | 3.2 | 5.3 | 1.4 | 0.0 | 0.0 | 0.0 |
| 2011 | smolt | 18 | 4.8 | 2.0 | 8.0 | 1.9 | 0.0 | 0.0 | 5.6 |
| 2011 | smolt 2yr | 2 | 3.8 | 3.7 | 3.8 | 0.1 | 0.0 | 0.0 | 0.0 |
| 2012 | smolt | 12 | 4.8 | 2.2 | 6.8 | 1.3 | 0.0 | 0.0 | 8.3 |
| 2013 | smolt | 20 | 3.9 | 1.6 | 8.3 | 1.7 | 5.0 | 15.0 | 20.0 |
| 2015 | smolt | 20 | 4.8 | 2.2 | 8.9 | 1.8 | 0.0 | 0.0 | 5.0 |

Table 6. Summary of total lipid values, expressed as a percentage of fish wet weight for all brood years and life-stages of juvenile sockeye salmon collected from Shuswap Lake and Little River. The percentage of each cohort with total lipid values below 1.8%, 2.0%, and 2.2% is shown.

| Brood year | Life-stage | n | Percent total lipid (g total lipid/g wet wt.) | | | | Percent of cohort below total lipid threshold | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Mean | Minimum | Maximum | SD | 1.8% | 2.0% | 2.2% |
| 2009 | spring parr | 20 | 2.7 | 1.3 | 4.9 | 0.9 | 10.0 | 15.0 | 30.0 |
| 2010 | spring fry | 139 | 3.0 | 1.5 | 5.5 | 0.8 | 2.9 | 5.8 | 16.5 |
| 2010 | summer fry | 30 | 1.7 | 1.1 | 2.9 | 0.4 | 53.3 | 73.3 | 86.7 |
| 2010 | fall fry | 30 | 3.3 | 2.2 | 4.4 | 0.6 | 0.0 | 0.0 | 0.0 |
| 2010 | spring parr | 58 | 1.8 | 1.0 | 3.5 | 0.5 | 56.9 | 74.1 | 82.8 |
| 2010 | smolt | 195 | 2.8 | 1.4 | 5.5 | 0.8 | 4.6 | 13.8 | 23.6 |
| 2010 | smolt 2yr | 20 | 2.0 | 1.0 | 2.9 | 0.4 | 25.0 | 35.0 | 70.0 |
| 2011 | spring fry | 97 | 2.2 | 0.9 | 4.9 | 1.1 | 48.5 | 53.6 | 58.8 |
| 2011 | summer fry | 30 | 3.2 | 1.5 | 6.6 | 1.2 | 6.7 | 13.3 | 23.3 |
| 2011 | fall fry | 30 | 4.2 | 2.7 | 6.0 | 1.1 | 0.0 | 0.0 | 0.0 |
| 2011 | spring parr | 38 | 3.8 | 1.4 | 12.8 | 3.5 | 21.1 | 34.2 | 47.4 |
| 2011 | smolt | 11 | 2.8 | 1.8 | 4.1 | 0.7 | 0.0 | 18.2 | 18.2 |
| 2014 | spring fry | 7 | 3.1 | 1.5 | 6.0 | 1.5 | 14.3 | 28.6 | 28.6 |
| 2014 | summer fry | 25 | 3.2 | 1.5 | 5.3 | 1.0 | 4.0 | 12.0 | 12.0 |
| 2014 | fall fry | 20 | 6.8 | 4.1 | 9.5 | 1.4 | 0.0 | 0.0 | 0.0 |
| 2014 | spring parr | 20 | 2.5 | 1.3 | 4.2 | 0.7 | 15.0 | 30.0 | 40.0 |
| 2014 | smolt | 60 | 3.0 | 1.5 | 4.9 | 0.8 | 8.3 | 10.0 | 11.7 |

FIGURES

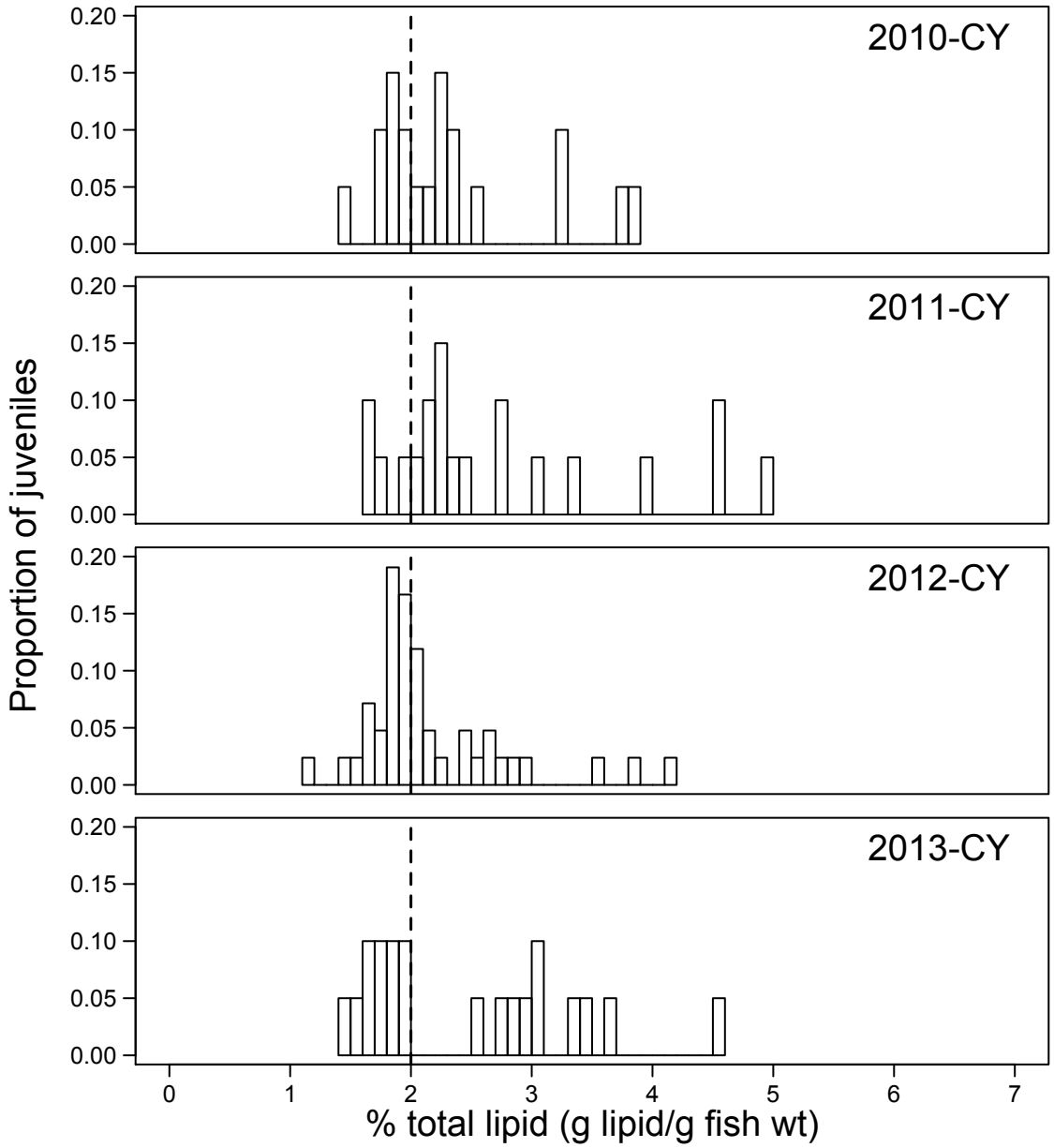


Figure 1. Distributions of lipid values (g total lipid per g fish wt.) for one- and two-year-old smolts that reared in Chilko Lake, collected from Chilko River in 2010 (n=40), 2011 (n=20), 2012, (n=42), and 2013 (n=40), respectively. The dashed vertical line indicates a potential total lipid threshold for survival at 2% of body weight.

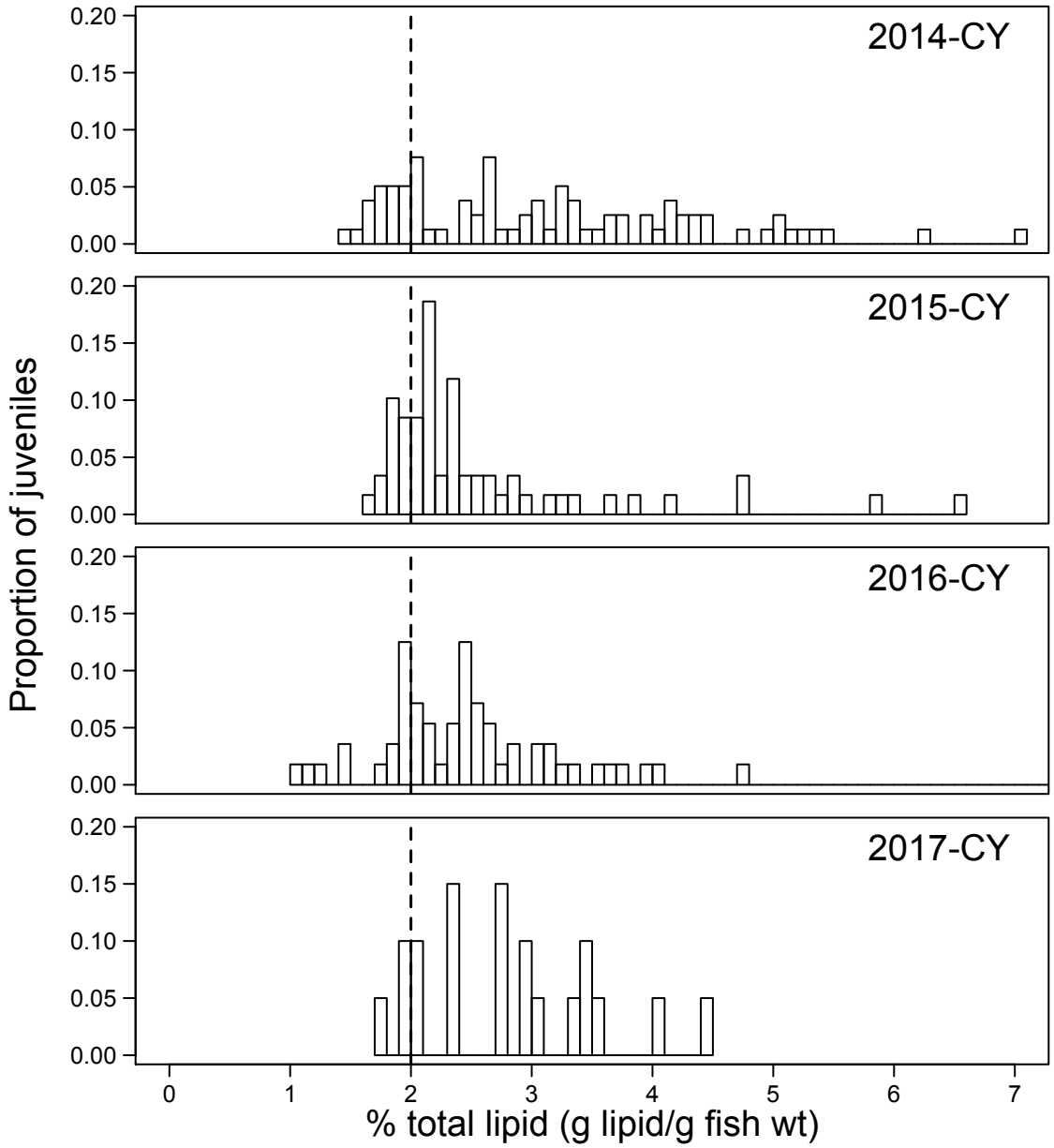


Figure 2. Distributions of lipid values (g total lipid per g fish wt.) for one- and two-year-old smolts that reared in Chilko Lake, collected from Chilko River in 2014 (n=89), 2015 (n=60), 2016, (n=58), and 2017 (n=20), respectively. The dashed vertical line indicates a potential total lipid threshold for survival at 2% of body weight.

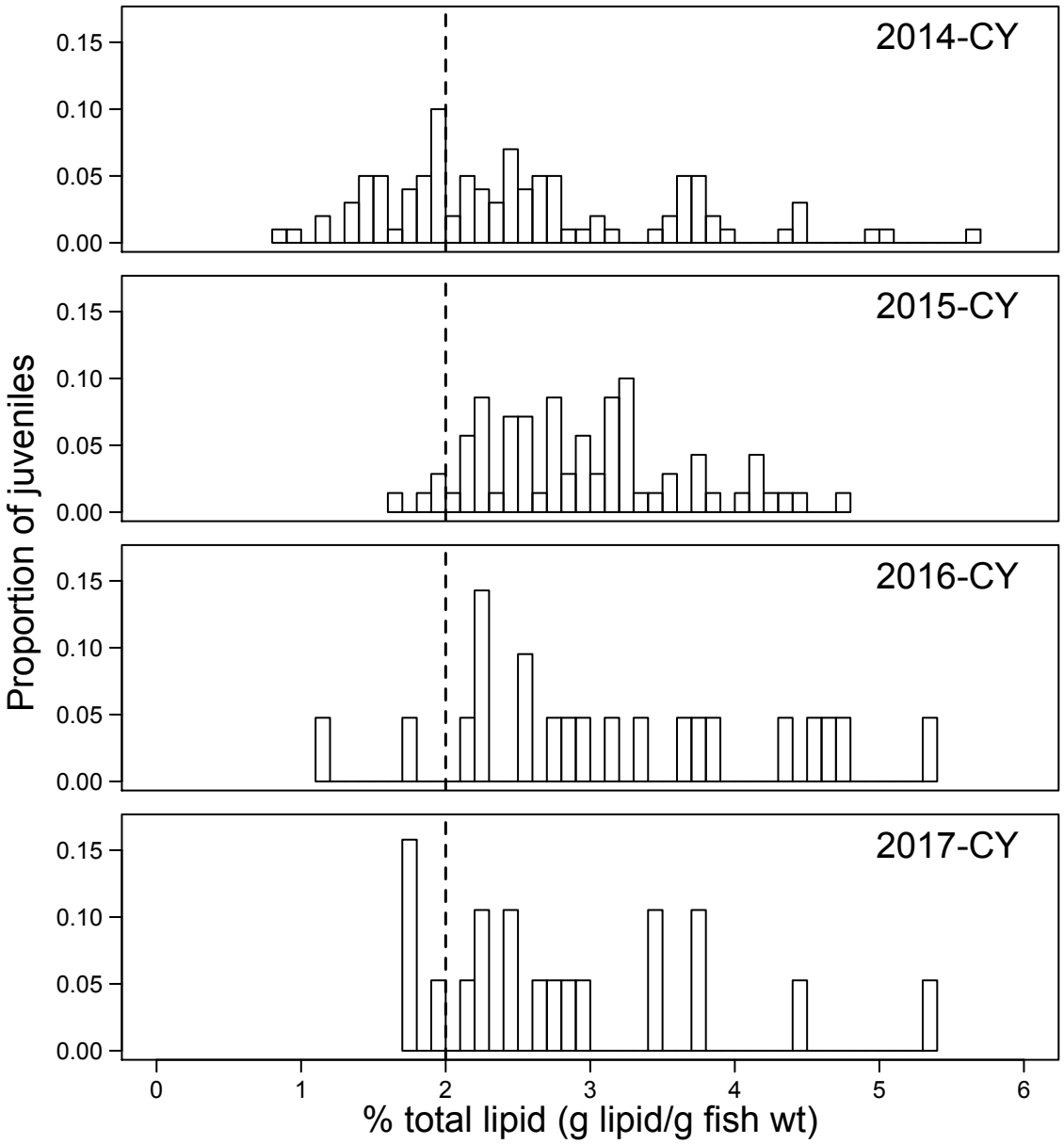


Figure 3. Distributions of lipid values (g total lipid per g fish wt.) for one-year-old smolts that reared in Chilliwack Lake, collected from Chilliwack River in 2014 (n=100), 2015 (n=70), 2016, (n=21), and 2017 (n=19), respectively. The dashed vertical line indicates a potential total lipid threshold for survival at 2% of body weight.

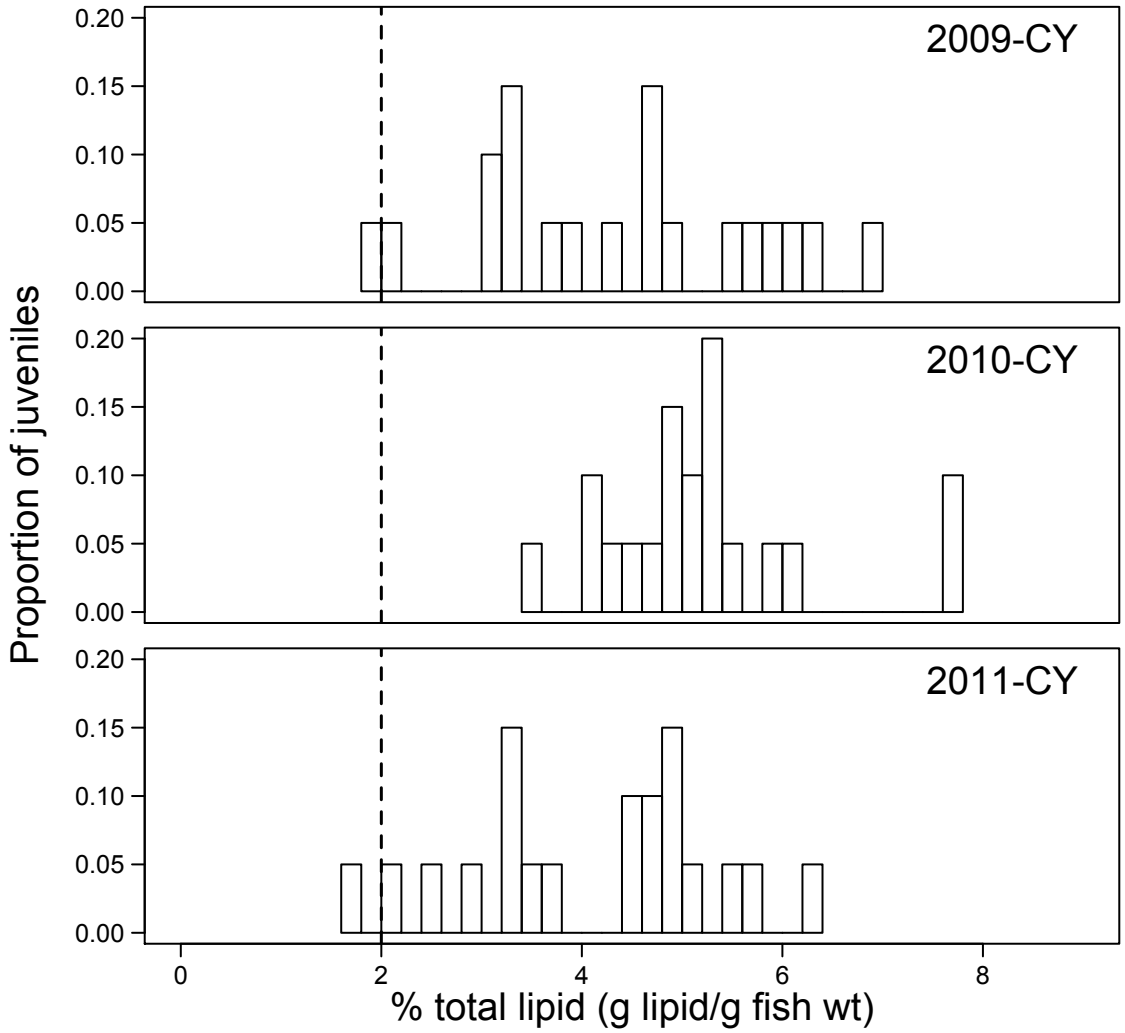


Figure 4. Distributions of lipid values (g total lipid per g fish wt.) for one-year-old smolts that reared in Cultus Lake, collected from Sweltzer Creek in 2009 (n=20), 2010 (n=20), and 2011 (n=20), respectively. The dashed vertical line indicates a potential total lipid threshold for survival at 2% of body weight.

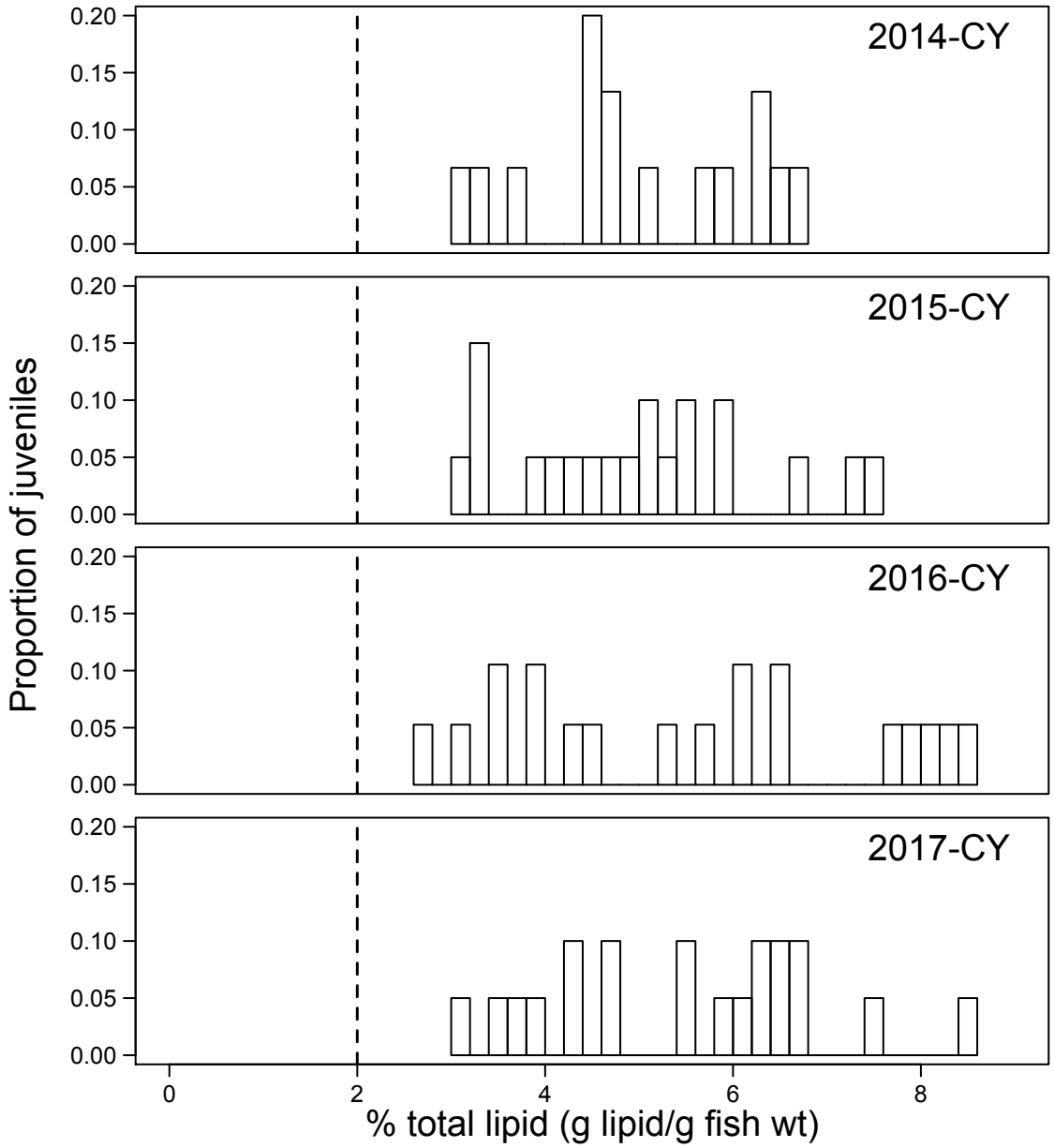


Figure 5. Distributions of lipid values (g total lipid per g fish wt.) for one-year-old smolts that reared in Cultus Lake, collected from Sweltzer Creek in 2014 (n=15), 2015 (n=20), 2016 (n=19), and 2017 (n=20), respectively. The dashed vertical line indicates a potential total lipid threshold for survival at 2% of body weight.

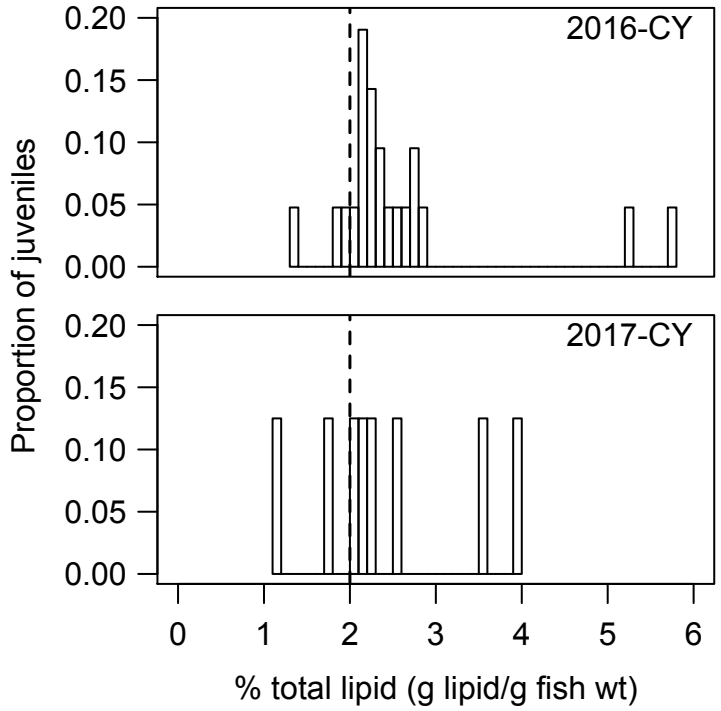


Figure 6. Distributions of lipid values (g total lipid per g fish wt.) for one- and two-year-old smolts that reared in Quesnel Lake, collected from Quesnel River in 2016 (n=21) and 2017 (n=8). The dashed vertical line indicates a potential total lipid threshold for survival at 2% of body weight.

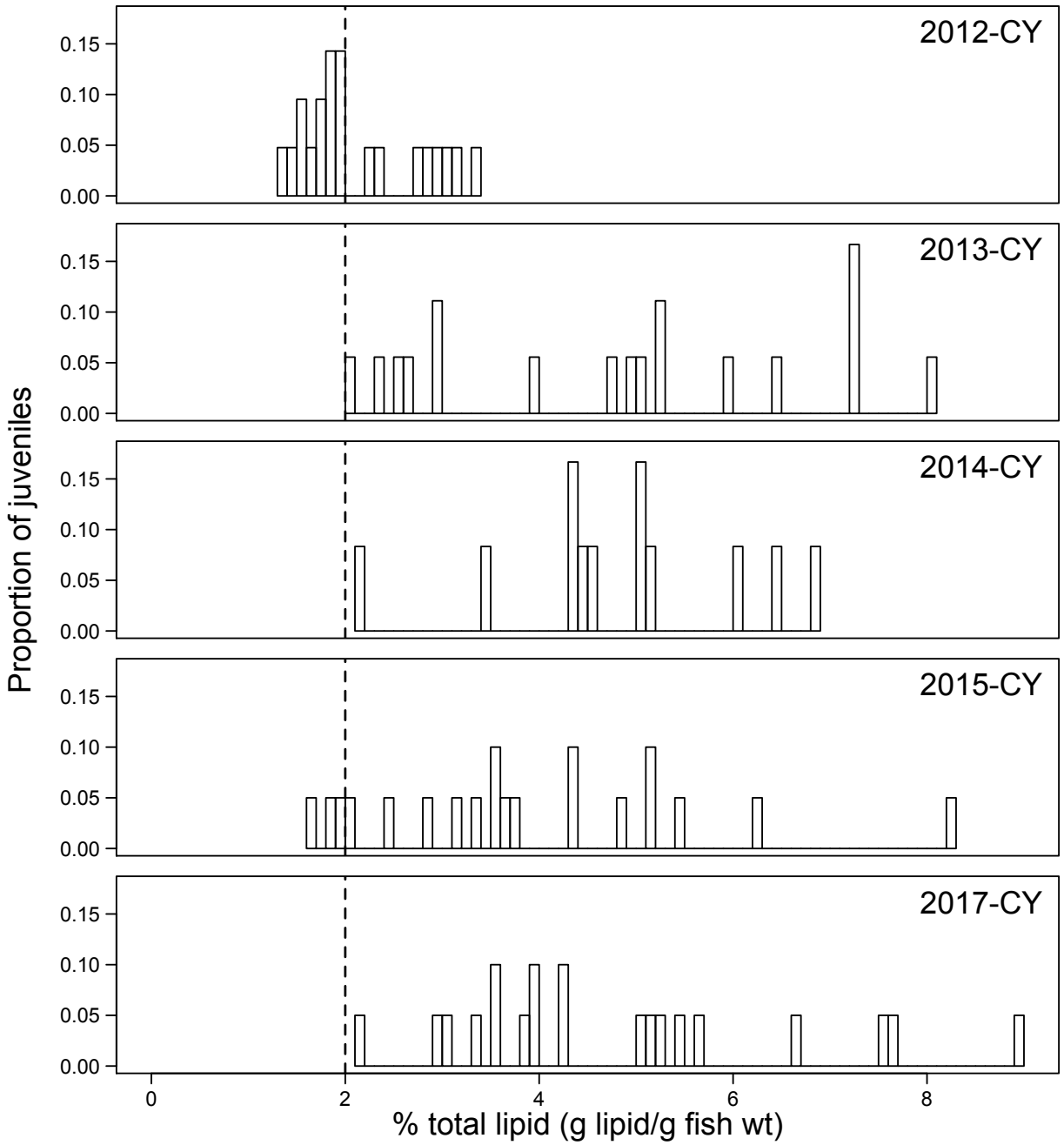


Figure 7. Distributions of lipid values (g total lipid per g fish wt.) for one- and two-year-old smolts that reared in Seton Lake, collected from Seton River in 2012 (n=21), 2013 (n=20), 2014 (n=14), 2015 (n=20), and 2017 (n=20). The dashed vertical line indicates a potential total lipid threshold for survival at 2% of body weight.

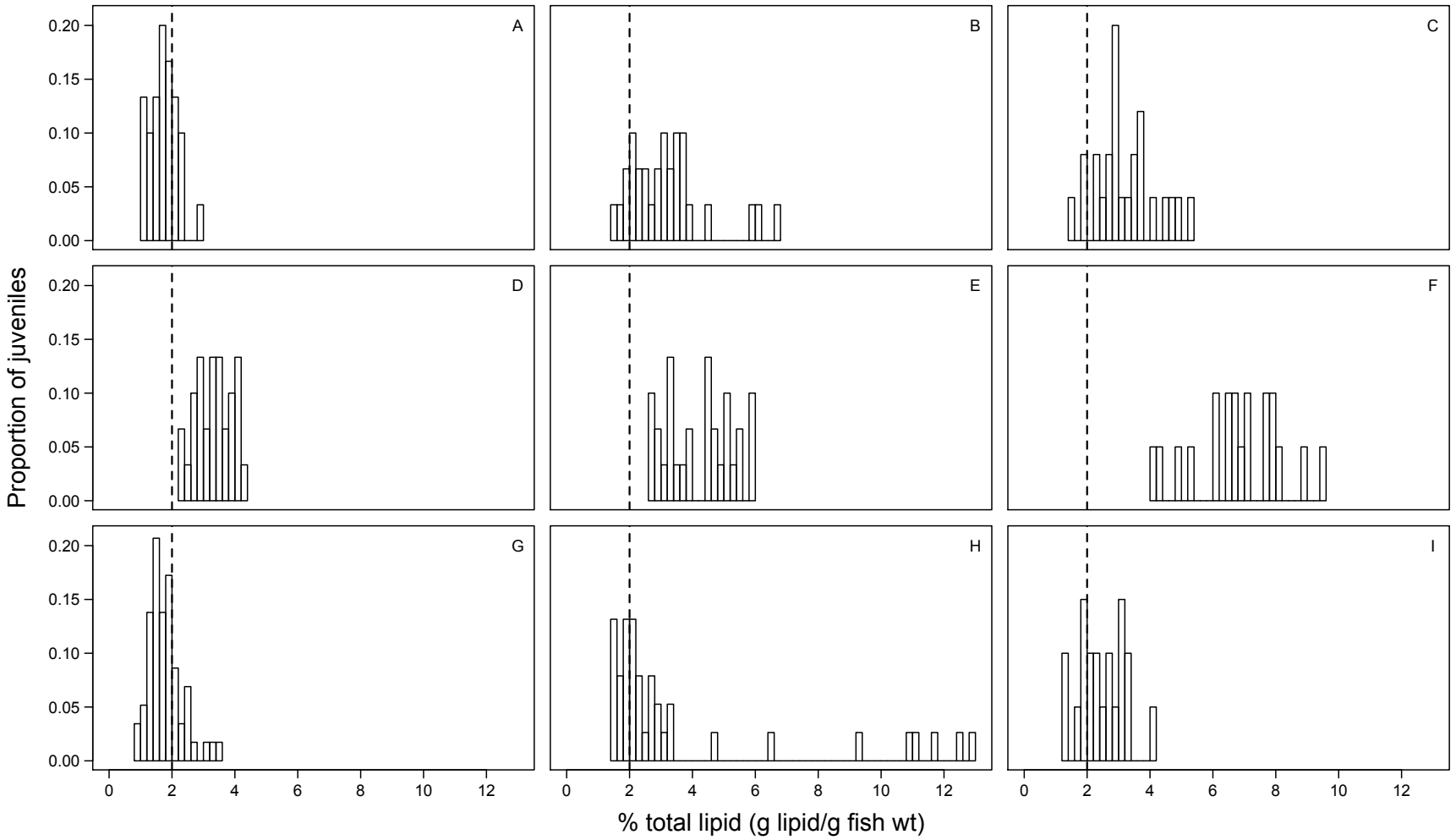


Figure 8. Distributions of lipid values (g total lipid per g fish wt.) for juveniles collected from Shuswap Lake. Summer fry (top row: n=30, n=30, n=30), fall fry (middle row: n=30, n=30, n=30), and spring parr (bottom row: n=58, n=38, n=30) are shown from brood years 2010 (left column), 2011 (middle column), and 2014 (right column), respectively. The dashed vertical line indicates a potential total lipid threshold for survival at 2% of body weight.

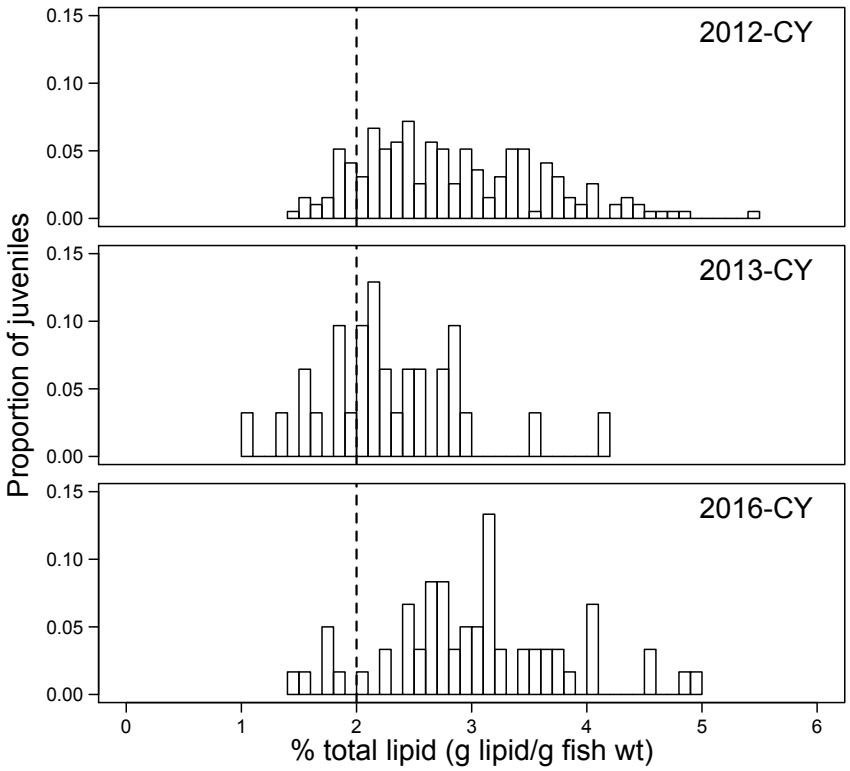


Figure 9. Distributions of lipid values (g total lipid per g fish wt.) for one- and two-year-old smolts that reared in the Shuswap Lake system, collected from Little River in 2012 (n=195), 2013 (n=33), and 2016 (n=60), respectively. The dashed vertical line indicates a potential total lipid threshold for survival at 2% of body weight.

# The utility of percent total lipid for describing density dependent freshwater survival of sockeye salmon smolts using Ricker spawner-recruit models

## INTRODUCTION

At high abundances, competition among juvenile sockeye salmon in the same nursery lake can limit food availability, causing reductions in size, body condition, and survival. In Fraser River sockeye salmon populations, variation in juvenile energetic condition among populations reflects the capacity of the rearing lake, and the density dependent dynamics caused by variation in population abundance. While extensive research has found increases in juvenile survival with length (e.g. Ricker 1959, Henderson & Cass 1993, Koenings et al. 1993, Bradford et al. 2001), we are not aware of studies that have assessed the importance of energetic condition to survival within the rearing lake or during downstream migration for sockeye salmon.

The sockeye salmon populations that rear in Chilko and Cultus lakes are both enumerated during the smolt out-migration using counting fences. Chilko is an indicator stock for the sockeye salmon populations in the broader Fraser River watershed, while Cultus is monitored because of its conservation status.

Since the late 2000s, the sockeye salmon population that spawn in Chilko Lake and River has experienced multiple spawning escapements above historical $S_{max}$, the spawner abundance that produces the maximum number of juveniles the rearing habitat can support. The $S_{max}$ value for Chilko Lake, estimated using decades of population spawner and recruitment data, is approximately 400,000 spawners, and the value estimated using with lake photosynthetic rate, a measure of habitat productivity, is approximately 483,000 spawners (Grant et al. 2011). In 2010, 2013, and 2014, total escapement counts (and effective female spawners) on spawning grounds in the Chilko River and Lake were approximately 2,460,000 (1,180,000 EFS), 1,240,000 (620,000 EFS), and 1,030,000 (670,000 EFS), respectively. In Chapter 2 of this report, we observed lower total lipid in out-migrating Chilko smolts from broods with higher EFS, after accounting for variation in smolt size.

In comparison, the sockeye salmon population that spawns in Cultus Lake has been assessed as Endangered by the Committee on the Status of Endangered Wildlife in Canada. From 1994 to 2016, the population declined 92% (COSEWIC 2003). The $S_{max}$ value estimated from spawner and recruitment data for Cultus Lake is approximately 80,000 spawners, and the $S_{max}$ value estimated using lake photosynthetic rate is 85,000 spawners (Grant et al. 2011). Since the late 2000s, the highest total spawning escapement to the lake was 10,300 spawners in 2010, with only 1,000 effective females. In 2014, the total escapement of 4,400 spawners included approximately 1,400 EFS. Evidently, the population has not approached the lake habitat carrying capacity in many years. In Chapter 1 of this report, we demonstrated that Cultus Lake juveniles are the longest, heaviest, and have the highest total lipid of all six sockeye salmon

populations that we assessed, after accounting for differences in body size. We did not observe a relationship between juvenile condition and spawner density in Chapter 2.

In this report, we used simple Ricker models to assess density dependent dynamics on survival of juveniles and adults from Chilko and Cultus lakes. We predicted a negative relationship between measures of maximum population growth rate [i.e. ln(smolts / EFS) or ln(recruits / EFS)] and EFS for Chilko and no relationship with EFS for Cultus. We also predicted a positive relationship between measures of maximum population growth rate and mean total lipid in out-migrating smolts. We expected to observe higher freshwater and marine survival (i.e. number of smolts per EFS and number of adult recruits per smolt) for Cultus than Chilko, as Cultus juveniles are in better condition.

## METHODS

### POPULATIONS

The location, limnology, and sockeye salmon population dynamics of Chilko and Cultus lakes are described in some detail below, and lake attributes are compared in Chapter 1, Table 1.

#### *Chilko Lake*

Chilko Lake (51°20'N, 124°05'W) is a cold, ultra-oligotrophic, sub-alpine lake, located on the eastern edge of the Coast Mountain Range at an elevation of 1172 m. The surface area of the lake is 185 $km^2$ (18,451 ha), and the mean and maximum depths are 123 m and 330 m. The lake has steep banks and limited littoral habitat. During winter, the lake temperature is 4°C. The growing season is May 1–October 31, with a seasonal average photosynthetic rate (PR) of 121 mg $C \cdot m^{-2} \cdot d^{-1}$ (Grant *et al.* 2011).

The Chilko population represents a major contributor to adult returns to the Fraser River in many years. Smolts migrate into the Chilko River from mid-April until mid-May (median date: between April 26-May 5 in years 2006-2015); outmigrating smolts are enumerated by DFO using a counting fence with video monitoring.

#### *Cultus Lake*

Cultus Lake (49°03'N, 121°59'W), located in the eastern Fraser Valley, is a small lake of 6 $km^2$ (630 ha) at 46 metres above sea level. The lake is steep-sided, with a limited littoral area, and mean and maximum depths of 21 m and 44 m. Cultus Lake is productive, and the seasonal mean photosynthetic rate of 404 mg $C \cdot m^{-2} \cdot d^{-1}$ was the highest of the lakes studied (Grant *et al.* 2011). It has a highly developed catchment area, with residential, agricultural, and recreational land uses.

A hatchery program supplements the wild population with fry released into the lake in the fall as well as a direct smolt release in the spring. Spawning behaviour is difficult to observe, because the wild population spawns in deep areas around the shores of the lake. Difficulty recovering carcasses limits accuracy and precision of EFS enumeration; the numbers we present are likely underestimates. Sockeye salmon smolts migrate into Sweltzer Creek from mid-March until late May (median date: between April 7-30 in years 2007-2016), and the outmigration is enumerated by DFO using a counting fence.

## JUVENILE FISH COLLECTION, TRANSPORT, AND STORAGE

Juvenile sockeye salmon (*Oncorhynchus nerka*) were collected from various locations across the Fraser watershed. Spring fry, summer fry, fall fry, spring parr and smolts, were collected across multiple years (2007-2017) using various capture methods, depending on the location and targeted life history stage (see Appendix A for details). Briefly, smolts were collected by beach seine, dip net, rotary screw trap, or incline plane trap from Chilko Lake, Sweltzer Creek, Chilliwack Lake, Little River, Quesnel River, Seton River, and the lower Fraser River at Mission. Spring fry were collected by beach seine from Quesnel River and Shuswap Lake. Summer fry Fall fry and spring parr were collected by lake trawl from Quesnel Lake, Shuswap Lake, Cultus Lake, and Chilliwack Lake (Appendix A: Table 1, Table 2). Following collection, fish were euthanized with an overdose of tricaine methanesulfonate (MS-222) prior to fork lengths (nearest mm) and weights (nearest 0.01 g) being measured in the field. Individuals were wrapped in aluminum foil or individual whirl paks and frozen rapidly or on dry ice. A small subset was frozen on liquid nitrogen or placed in a -20°C freezer. The majority of fish caught by beach seine or dip net were transported to the Fisheries and Oceans research laboratory in West Vancouver ('West Van Lab') for long-term cold storage, although some samples were stored at the University of British Columbia in Vancouver or the Pacific Biological Station in Nanaimo, prior to transport to West Van Lab for analysis. The fish caught by lake trawl were stored at the Fisheries and Oceans research laboratory in Cultus Lake, prior to transfer to West Van Lab for analysis. For more detailed information on capture history and storage conditions for juvenile sockeye samples, see 'Appendix A: Sample collection 2007-2017.'

## LIFE-STAGE IDENTIFICATION

Assumptions regarding age assignments were made based on sampling location, sampling date, and size. The majority of juvenile fish had age assigned at the time of sampling. Age-1 or 2 fish caught in the river environment by seine net, dip net, or weir were called smolts. Sampling was conducted in June in Little River (Shuswap complex) and April or May for all other populations.

Age-2 smolts are larger than age-1 smolts. Chilko can have a high proportion of two-year-old smolts in some years (up to 10%), and these larger fish were generally noted as age-2 smolts at the time of sampling. Several additional fish in each population were identified as two-year-olds

from population- and capture year-specific length-weight relationships, as the different age classes typically cluster separately.

## LIPID EXTRACTION AND CONSTITUENT ANALYSIS

Whole juvenile sockeye salmon (*Oncorhynchus nerka*) samples were removed from -80 °C freezer storage and allowed to thaw at room temperature prior to taking fork length and weights measurements in the laboratory. Fish were cut into 8-10 pieces and placed in 50 ml Nalgene® tubes with two steel ball bearings and homogenized using a SPEX SamplePrep 2010 Geno/Grinder (SPEX, Metuchen, NJ, www.spexsampleprep.com) at 1500 rpm for two-minute intervals until completely homogenized.

Lipid extraction from homogenized tissue followed protocols developed by Bligh and Dyer (1959) with minor modifications (see: 'Appendix B: Lipid extraction and moisture ash' for detailed methods). Chloroform, methanol and water were added to a weighed subsample of homogenate (in 1:1:0.5 solvent ratios, respectively) and homogenized to form a biphasic layer of chloroform-lipid and methanol-water. The volume of the chloro-lipid layer was measured, prior to pipetting a known volume onto a pre-weighed tin boat and evaporating off the chloroform in an oven. The remaining lipid samples were then re-weighed and frozen for subsequent triglyceride analysis.

The percent lipid of the subsample was calculated using Eq. 1:

$$subsample\ \%\ lipid = \frac{extracted\ lipid\ wt.\ (g)}{subsample\ wt.\ (g)} * 100 \quad [1]$$

The weight of the total lipid in each fish was calculated using Eq. 2:

$$total\ lipid\ (g) = \frac{uncorr.\ \%\ lipid}{100\%} *\ whole\ fish\ wt._{\ thawed}\ (g) \quad [2]$$

Moisture lost from juvenile samples during storage was estimated and used to correct fish weights using procedures outlined in Appendix C.

## SMOLT, RECRUIT, AND SPAWNER ENUMERATION

Daily and cumulative annual smolt outmigration totals from the counting fences on Chilko River and Sweltzer Creek were provided for years 2006 to 2016 by DFO Stock Assessment Division (Tracy Cone, DFO Annacis Island).

Recruitment data by brood year and age for Cultus and Chilko populations for years 1948 to 2015 was provided by Sue Grant (DFO Annacis Island).

Escapement data was determined from near final spawning ground estimates for individual spawning streams for years 1938 to 2016, which were provided by DFO Stock Assessment Division (T. Cone). The number of effective female spawners (EFS) was used for the stock groupings Chilko River (rears in Chilko Lake) and Cultus Lake (rears in Cultus Lake). Other spawning areas for stocks that rear in Chilko Lake, the South End Chilko Lake and Chilko Channel, were not counted during the years of the study.

RICKER MODELS

To model the population dynamics of the sockeye salmon populations that rear in Chilko and Cultus lakes, we used Ricker models of the form:

$$\ln(\frac{R_t}{S_t}) \sim a - b * S_t \quad [6]$$

Where R is the number of recruits in a cohort and S is the number of effective female spawners (EFS) that spawned the eggs that produced the recruits in brood year *t*. *a* is the intercept, which gives the maximum population growth rate when EFS is low. *b* represents the effect of spawner density on survival of the offspring in brood *t*, with larger values indicating greater density dependent dynamics.

We used two datasets to model populations dynamics. In the first, R was the number of out-migrating smolts in brood *t* counted in the smolt fence on Chilko River or Sweltzer Creek and S was the number of EFS that spawned the brood. In the second dataset, R was the total number of adult recruits in brood *t* and S was the number of EFS that spawned the brood. These simple Ricker models are given by Eq. 7 and Eq. 8:

$$\ln(\frac{smolts}{EFS}) \sim a - b * EFS \quad [7]$$

$$\ln(\frac{total\ recruits}{EFS}) \sim a - b * EFS \quad [8]$$

To assess the effect of the condition of out-migrating smolts in brood *t* on the maximum population growth rate, as measured in units of $\ln(\frac{R_t}{S_t})$, we used Ricker models with an additive effect of smolt percent total lipid. The effect of total lipid was added to both Eq. 7 and Eq 8, to produce the following models:

$$\ln\left(\frac{smolts}{EFS}\right) \sim a - b * EFS + percent\ total\ lipid_{smolt} \quad [9]$$

$$\ln\left(\frac{total\ recruits}{EFS}\right) \sim a - b * EFS + percent\ total\ lipid_{smolt} \quad [10]$$

## POPULATION PRODUCTIVITY

We used counts of EFS, out-migrating smolts, and total adult recruits for brood years 2000-2012 from Chilko to calculate two measures of population productivity for each brood year. Smolts per EFS is an index of freshwater survival, while recruits per smolt is an index of migration and marine survival. Smolts per EFS was calculated for brood year, *t*, using Eq. 11, and adult returns per smolt was calculated for brood year, *t*, using Eq. 12.

$$smolts\ per\ EFS = \frac{(smolts_t)}{(EFS_t)} \quad [11]$$

$$recruits\ per\ smolt = \frac{(total\ recruits_t)}{(smolt_t)} \quad [12]$$

# RESULTS

## RICKER MODELS

In the four Ricker models fit to data from Chilko brood years between 2005 and 2014, we observed negative relationships between the number of effective female spawners (EFS) and $\ln\left(\frac{smolts}{EFS}\right)$ and $\ln\left(\frac{recruits}{EFS}\right)$, indicating density dependence. Proportionally fewer recruits to the population (i.e. smolts or adults) were produced at higher EFS abundance (Table 1; Figure 1; Figure 2). Including the mean total lipid of out-migrating smolts as an additive term in the model produced small but positive coefficients (Table 1). The confidence intervals of coefficient estimates generated by both models crossed zero, so the effect of smolt total lipid on the maximum population growth rate is uncertain (Figure 3). Nonetheless, model predictions indicated better survival to smolt out-migration and to adult return when smolt total lipid values were high (Figure 1; Figure 2). From an EFS of 0.25 million, there would be approximately 30 million smolts, given low lipid values (two standard deviations subtracted from the multi-year mean) and approximately 45 million smolts, given high lipid values (two standard deviations added to the multi-year mean). At higher abundances of EFS, low and high lipid levels are associated with increasingly different numbers of smolts produced. From an EFS of 0.5 million, broods with low total lipid on average would have approximately 50 million out-

migrating smolts, while broods with high total lipid would have nearly 80 million. Although the data were sparse above 0.5 million, model predictions for low and high lipid levels began to converge (Figure 1). Similarly, model predictions suggested dramatically higher numbers of adult recruits for broods with high mean total lipid levels as smolts. For EFS of 0.25 million, low lipid levels in smolts were associated with fewer than 0.5 million recruits, while high lipid levels were associated with greater than 4 million recruits (Figure 2).

We were unable to fit models to the EFS data from Cultus, due to uncertainty in carcass enumeration. Furthermore, relating out-migrating smolt numbers to EFS data is misleading, as juveniles are stocked from the hatchery, prior to out-migration and we are unable at this time to separate the two contributing sources of data.

Despite fewer than ten data points in each model, the adjusted-$R^2$ values for the $\ln(\frac{smolts}{EFS})$ model was quite high (i.e. 0.55; Table 1). The parameters generated from the Ricker models are listed in Table 1.

## POPULATION PRODUCTIVITY

An average of 151 smolts were produced by each effective female spawner in Chilko (years: 2000-2012), and the number of smolts per EFS ranged from 49.2 to 277.9 (Table 2).
The ranges of adult returns per out-migrating smolt overlapped for the two populations (Chilko: 0.004-0.066, Table 2; Cultus: 0.007-0.053, Table 3), and interestingly there was a positive trend when the ratios were plotted against each other (Figure 4). The out-migrating smolts from Chilko Lake produced an average of 0.037 adult recruits (years: 2000-2011), and the smolts from Cultus Lake produced an average of 0.023 adult recruits (years: 2000-2011).

## DISCUSSION

This chapter demonstrates a proof of concept for incorporating percent total lipid data from out-migrating smolts into Ricker models assessing density dependence in Fraser River sockeye salmon populations. We chose to use Ricker rather than Larkin models to explore the relationships between effective female spawners (EFS) and $\ln(\frac{smolts}{EFS})$ and $\ln(\frac{returns}{EFS})$ for the population that rears in Chilko Lake, because in Chapter 2 of this report we did not find evidence of delayed density dynamics affecting smolt condition in Chilko Lake.

Although we had very few years of lipid data for out-migrating smolts from these populations and could only use a subset of the decades of spawner, smolt, and recruit data available, our Ricker models had reasonably high correlation coefficients. Adding the total lipid term decreased the fit of the $\ln(\frac{smolts}{EFS})$ model slightly but improved the fit of the $\ln(\frac{returns}{EFS})$ model substantially. The model predictions suggested that mean smolt energetic condition accounts

for important variation in recruitment to the smolt out-migration and adult recruit stages that is not accounted for by spawner abundance. Better body condition, and the resulting higher survival, likely occur during years of higher primary productivity in Chilko Lake, which more than compensated for the greater competition among conspecifics caused by higher EFS. The uncertainty around the coefficient estimates for total lipid is likely a result of creating models with so few data points, rather than the absence of an effect of energetic condition on survival. In particular, the $\ln(\frac{returns}{EFS})$ model has two fewer years of data and no points above 5 million recruits, so the predictions for high total lipid values should be treated with caution.

Cultus Lake has high primary productivity that translates in good condition smolts for those that survive. In Chapter 1 of this report, we observed that juveniles rearing in Cultus Lake are longer, heavier, and in better condition than juveniles from other rearing lakes (see Chapter 1 of this report). Evaluating a freshwater survival index, like the one that we calculated for Chilko juveniles in this chapter, would enrich our conclusions about the importance of condition to juvenile survival. Interestingly, although the $\ln(\frac{returns}{EFS})$ model predicted much higher survival to adult recruit for out-migrating Chilko smolts with high lipid values, the considerably higher condition smolts from Cultus Lake do not survive to adult recruit at higher rates than Chilko smolts, according to recruits per smolt values. The number of smolts surviving to adulthood is lower among cohorts from Cultus Lake, compared to Chilko Lake. Thus, any effect of juvenile condition on survival from lake exit to the adult recruitment stage is small, relative to other drivers. More effort will be needed to separate differences in survival between hatchery versus wild smolts.

There was large uncertainty in estimating the model parameters for Chilko $\ln(\frac{returns}{EFS})$, and this reflects the many factors that affect survival of sockeye salmon during downstream migration, marine residence, and spawning migration. The positive trend in the recruits per out-migrating smolt ratios for the 2000-2011 broods shows a lot of shared variation in smolt survival, suggesting that marine and migration conditions may be driving the magnitude of smolt to adult mortality, but not variability between populations. Both populations are experiencing similar drivers of mortality during these life-stages, which may include water temperature, marine food availability, or unaccounted-for fisheries.

This proof of concept suggests the potential for incorporating smolt condition information into stock-recruit relationships for Fraser River sockeye salmon populations. The enumeration of out-migrating smolts from Chilko and Cultus lakes makes these important populations for studying the relationships between smolt condition and both freshwater and marine survival. Additional data is necessary to assess the strength of these relationships, and we recommend that out-migrating smolts continue to be collected from these populations each year, to build a longer time series. In the future, with another decade of lipid data for out-migrating smolts, we recommend regressing lipid data against the residuals from Ricker models built with longer time series of spawner and recruit data, to determine of juvenile condition explains any additional variation in survival. A similar approach would be to assess whether smolt out-

migration abundance and mean total lipid values explain any variation in the residuals of the Fraser Index for the Chilko population.

TABLES

Table 1. Parameters from individual Ricker models $\ln(\frac{R}{S}) \sim \ln a - b * S$ fit to counts of effective female spawners (EFS), out-migrating smolts, and total adult recruits for Chilko brood years 2005-2014. Total lipid is the mean percent total lipid (g lipid per g wet weight) of smolts collected from each brood, which was included in a subset of models as an additive effect. Not all data were available for all years in the time series.

| Population | Response | Explanatory variables | Maximum population growth rate (*a*) | Density dependence (*b*) | Total lipid | *df* | Adj-$R^2$ |
|---|---|---|---|---|---|---|---|
| Chilko | ln(smolts/EFS) | EFS | 237.8 | -1.34 | - | 7[1] | 0.60 |
| Chilko | ln(smolts/EFS) | EFS + total lipid | 119.4 | -1.20 | 0.24 | 6[1] | 0.55 |
| Chilko | ln(recruits/EFS) | EFS | 7.9 | -1.38 | - | 5[2] | 0.08 |
| Chilko | ln(recruits/EFS) | EFS + total lipid | 0.1 | -0.61 | 1.48 | 4[2] | 0.22 |

[1] data from 2005-2012, 2014

[2] data from 2005-2011

Table 2. Counts of effective female spawners (EFS), out-migrating smolts, and total adult recruits (all in thousands) for Chilko brood years 2000-2012. The number of out-migrating smolts per EFS and the number of recruits per out-migrating smolt are shown.

| Brood year | EFS (thousands) | Out-migrating smolts (thousands) | Total recruits (thousands) | Smolts per EFS | Recruits per smolt |
|---|---|---|---|---|---|
| 2000 | 395.6 | 19475.4 | 452.1 | 49.2 | 0.023 |
| 2001 | 331.2 | 35710.9 | 1090.7 | 107.8 | 0.031 |
| 2002 | 215.1 | 19625.2 | 1225.5 | 91.3 | 0.062 |
| 2003 | 334.9 | 25060.2 | 351.2 | 74.8 | 0.014 |
| 2004 | 49.2 | 10974.2 | 422.1 | 223.1 | 0.038 |
| 2005 | 285.1 | 76507.9 | 300.0 | 268.4 | 0.004 |
| 2006 | 261.9 | 72782.9 | 4799.3 | 277.9 | 0.066 |
| 2007 | 156.5 | 25223.3 | 1073.3 | 161.2 | 0.043 |
| 2008 | 68.7 | 12115.5 | 511.0 | 176.3 | 0.042 |
| 2009 | 127.4 | 33837.8 | 1795.5 | 265.7 | 0.053 |
| 2010 | 1181.5 | 54972.2 | 2557.2 | 46.5 | 0.047 |
| 2011 | 457.7 | 43224.2 | 870.0 | 94.4 | 0.020 |
| 2012 | 90.8 | 11492.5 | - | 126.6 | - |

Table 3. Counts of out-migrating smolts and total adult recruits (all in thousands) for Cultus brood years 2000-2012. The number of recruits per out-migrating smolt are shown. Uncertainty in carcass enumeration limits the reliability of EFS data, so smolts per EFS are not presented.

| Brood year | Out-migrating smolts (thousands) | Total returns (thousands) | Returns per smolt |
|---|---|---|---|
| 2000 | 9.5 | 0.1 | 0.008 |
| 2001 | 13.7 | 0.2 | 0.015 |
| 2002 | 117.0 | 5.1 | 0.044 |
| 2003 | 98.6 | 0.7 | 0.007 |
| 2004 | 107.9 | 1.2 | 0.011 |
| 2005 | 97.9 | 0.9 | 0.009 |
| 2006 | 389.2 | 20.5 | 0.053 |
| 2007 | 340.1 | 12.4 | 0.036 |
| 2008 | 145.3 | 1.9 | 0.013 |
| 2009 | 174.1 | 2.6 | 0.015 |
| 2010 | 318.4 | 16.1 | 0.051 |
| 2011 | 119.8 | 1.6 | 0.013 |
| 2012 | 103.2 | - | - |

FIGURES

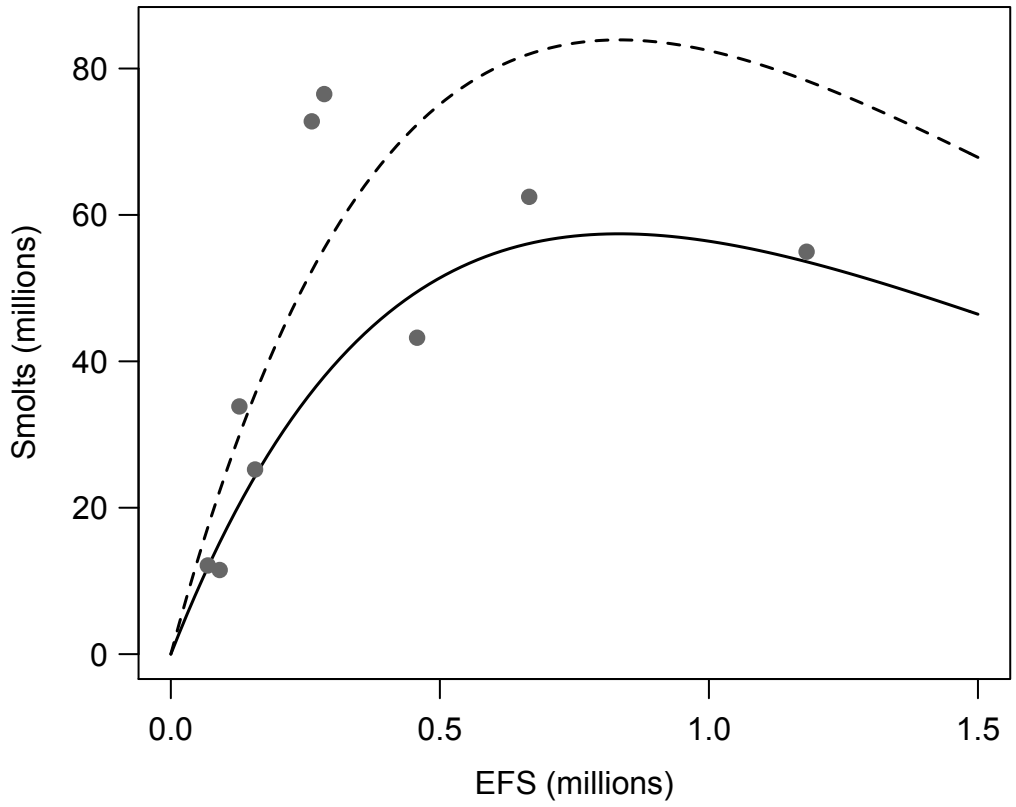


Figure 1. Predicted lines from the exponential form of the Ricker model $Smolts \sim a * EFS * e^{-b*EFS+total\ lipid_{smolt}}$, where parameter *a* is the exponentiated intercept and *b* is the slope from the Ricker model $\ln(\frac{Smolts}{EFS}) \sim \ln a - b * EFS + total\ lipid_{smolt}$. The grey dots show data for Chilko Lake sockeye salmon from brood years 2005-2012 and 2014 (n=9). The solid black line shows the relationship between effective female spawner (EFS) and smolt abundance, both in millions, given a low total lipid level of 1.9% (multi-year mean minus two standard deviations: 2.7% - 2*0.40%). The dashed line shows the relationship, given a high total lipid level of 3.5% (multi-year mean plus two standard deviations: 2.7% + 2*0.40%).

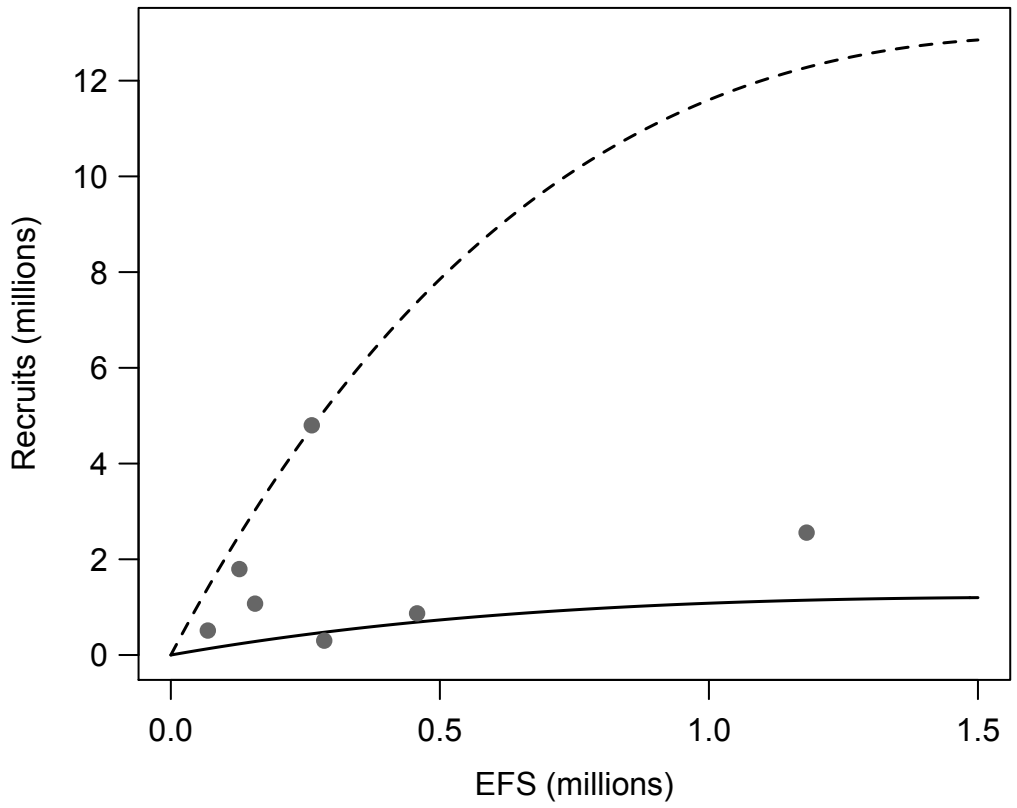


Figure 2. Predicted lines from the exponential form of the Ricker model $Recruits \sim a * EFS * e^{-b*EFS+total\ lipid_{smolt}}$, where parameter *a* is the exponentiated intercept and *b* is the slope from the Ricker model $\ln(\frac{Recruits}{EFS}) \sim \ln a - b * EFS + total\ lipid_{smolt}$. The grey dots show data for Chilko Lake sockeye salmon from brood years 2005-2011 (n=7). The solid black line shows the relationship between effective female spawner (EFS) and total recruit abundance, both in millions, given a low total lipid level of 1.9% (multi-year mean minus two standard deviations: 2.7% - 2*0.40%). The dashed line shows the relationship, given a high total lipid level of 3.5% (multi-year mean plus two standard deviations: 2.7% + 2*0.40%).

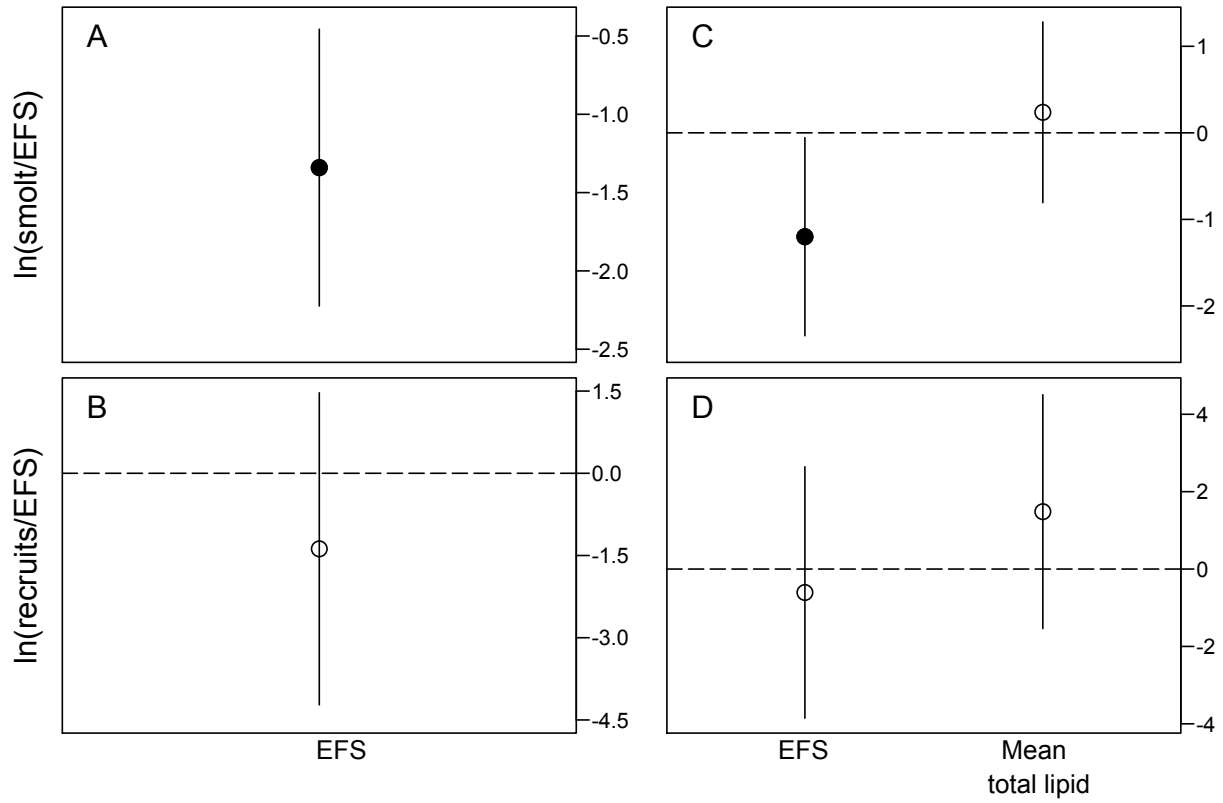


Figure 3. Unstandardized Ricker model coefficients with 95% confidence intervals (CI) for models describing $\ln(\frac{smolts}{EFS})$ for the Chilko Lake sockeye salmon population by (A) effective female spawners (EFS) alone and (C) with mean total lipid of out-migrating smolts and $\ln(\frac{recruits}{EFS})$ by (B) effective female spawners (EFS) alone and (D) with mean total lipid of out-migrating smolts. Filled circles indicate explanatory variables with a significant effect ($p < 0.05$) on the relevant condition metric.

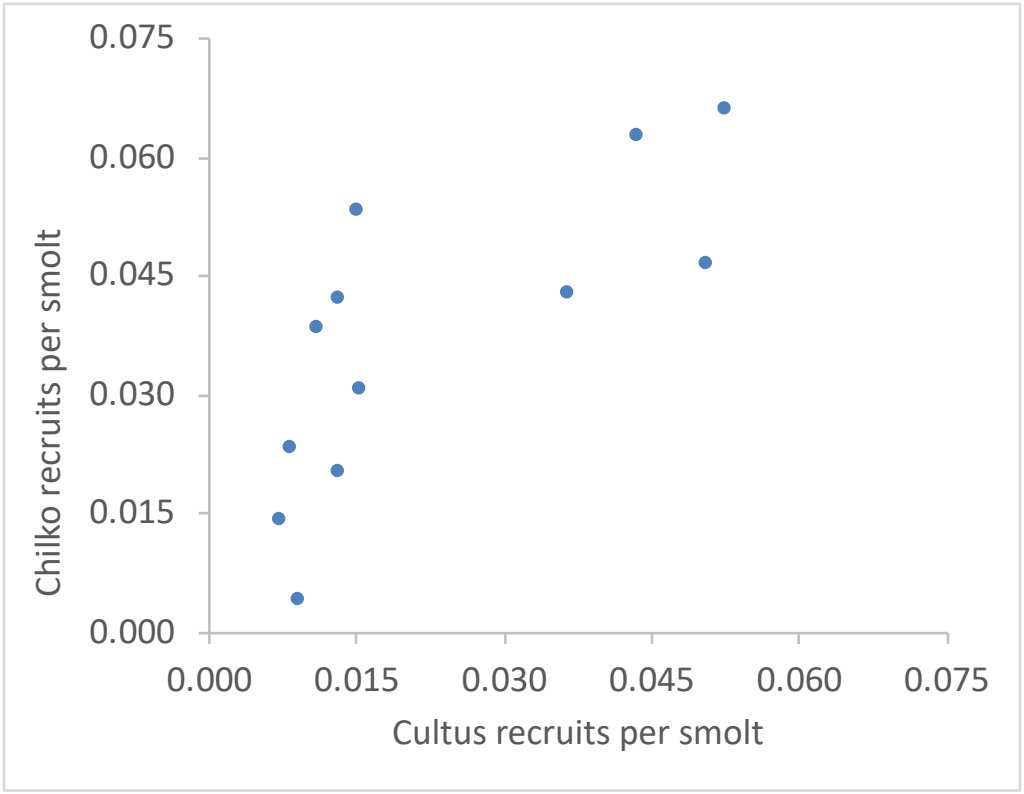

Figure 4. The relationship between the number of adult recruits produced per out-migrating smolt in the 2000-2011 broods from Chilko and Cultus lakes.

# Appendix A: Sample Collection

## COLLECTION, TRANSPORT, AND STORAGE OF JUVENILE SOCKEYE SALMON

Juvenile sockeye salmon (*Oncorhynchus nerka*) were collected across multiple years (2007-2017; n = 2475) and locations to analyze energetic condition (total body lipid and triglyceride content) across and among populations and life stages. Various capture methods were employed across the study system based on the location and life history stage being targeted. Smolts were collected using dip nets from a counting fence at Chilko Lake (2007-2017; beach seine used in 2015) and from Sweltzer Creek (2009-2011, 2014-2016), and by beach seine at the outlet of Chilliwack Lake (2013, 2014) and Little River (2012, 2013, and 2016). Dip nets and pole seines were used in the Quesnel River (2015-2017), while rotary screw traps and inclined plane traps were used to collect smolts in the Seton River (2012-2015, 2017). In the lower Fraser at Mission (2012), smolts were collected by rotary screw traps or incline plane traps. Near-shore fry (spring fry) were caught with beach seines from the Quesnel River (2015, 2017) and Shuswap Lake at Cruickshank Point (2011, 2012, and 2015). Several lake trawl methods were used to capture fry and parr in the pelagic zone, including large ("3x7"; towed up to 55 m depth) and smaller ("2x2"; towed up to 32 m depth) midwater trawl nets deployed from boats (MacLellan & Hume, 2010). Fall and summer fry were collected with such trawl nets towed through Quesnel Lake (in multiple locations; 2014, 2015), Chilliwack Lake (2013, 2014), Shuswap Lake (2011, 2012, and 2015) and Cultus Lake (2010, 2015), while spring parr were collected by trawl in Shuswap Lake (2011-2013, 2016), Chilliwack Lake (2014), Cultus Lake (2009, 2013, and 2016) and Quesnel Lake (2015). Freshwater trawls were typically paired with hydroacoustic surveys to estimate juvenile abundance of sockeye salmon and kokanee (both *Oncorhynchus nerka*) in rearing lakes (e.g. MacLellan & Hume, 2010). A sub-sample of fish were fin-clipped to separate the proportion of kokanee from sockeye using DNA stock ID methods or electrophoresis. Detailed capture information for the present report, including locations and sample sizes collected are presented in Tables 1 and 2.

Following capture, fish were immediately euthanized using an overdose of tricaine methanesulfonate (MS-222). Fork length (mm) and body mass (g) were recorded in the field prior to individuals being wrapped in aluminum foil or placed in individual whirl-pak bags and then rapidly frozen by being placed into a liquid nitrogen dewar (only possible with foiled wrapped fish), or placed on dry ice for transfer The majority of fish caught by beach seine or dip net were transported to the Fisheries and Oceans research laboratory in West Vancouver ('West Van Lab') for long-term cold storage at -80 C, although some samples were stored at the University of British Columbia in Vancouver or the Pacific Biological Station in Nanaimo, prior to transport to West Van Lab for analysis. The fish caught by lake trawl were stored at the Fisheries and Oceans research laboratory in Cultus Lake, prior to transfer to West Van Lab for analysis. Prior to 2013, some samples were placed in -20 $^{o}$C freezers; however, after 2013 samples were all stored at -80 $^{o}$C. Samples remained in ultra-cold storage until laboratory assessments, which included lipid extraction, moisture ash, and triglyceride analysis. Samples analyzed in the laboratory to date are summarized in Table 2.

Table 1. Sampling locations for juvenile sockeye samples collected, including number of samples collected, years of collection, and life stages.

| Sampling location | Approximate GPS co-ordinates | Years of collection | Life stages collected | Numbers of samples |
|---|---|---|---|---|
| Chilko fish fence | 51°37'33"N 124°08'31"W | 2007-2017 | Smolts (1- and 2-year) | 403 |
| Cultus Lake | 49°03'24"N 121°59'1"W | 2009, 2010, 2013, 2015, 2016, 2017 | Fall fry, spring parr, smolts | 135 |
| Sweltzer Creek (Cultus) | 49°04'44"N 121°58'37"W | 2009, 2010, 2011, 2014, 2015, 2016 | Smolts | 115 |
| Chilliwack Lake | 49°04'44"N 121°58'37"W | 2013, 2014 | Summer fry, fall fry, spring parr | 95 |
| Chilliwack Lake outlet | 49°05'5"N 121°27'35"W | 2014-2017 | Smolts | 210 |
| Mission (Lower Fraser) | 49°07'13"N 122°18'51"W | 2012 | Smolts | 312 |
| Shuswap Lake - Main Arm | 50°58'11"N 119°06'24"W | 2011, 2012, 2013, 2015, 2016 | Summer fry, fall fry, spring parr | 326 |
| Shuswap Lake - Cruickshank | 50°53'39"N 119°32'12"W | 2011, 2012, 2015 | Spring fry | 249 |
| Little River (Shuswap) | 50°52'5"N 119°35'30"W | 2012, 2013, 2016 | Smolts (1- and 2-year) | 288 |
| Seton River | 50°40'9"N 121°57'35"W | 2012, 2013, 2014, 2015, 2017 | Smolts (1- and 2-year) | 95 |
| Quesnel - East Arm | 52°35'25"N 120°33'4"W | 2014, 2015 | Fall fry, spring parr | 30 |
| Quesnel - Middle Arm | 52°31'26"N 121°09'53"W | 2014, 2015 | Fall fry, spring parr | 30 |
| Quesnel - North Arm | 52°41'38"N 120°54'54"W | 2014, 2015 | Fall fry, spring parr | 60 |
| Quesnel - West Arm | 52°32'14"N 121°31'34"W | 2014, 2015 | Fall fry, spring parr | 73 |
| Quesnel River | 52°50'29"N 122°13'25"W | 2015, 2016, 2017 | Spring fry, smolts (1- and 2-year) | 54 |
| | | | **Total:** | 2475 |

Table 2. Collection summary, including numbers of individuals collected by each brood year, collection location, life stages, and number of samples analyzed in the laboratory to date.

| | | | Brood year | | | | | | | | | | | | | Analyzed to date | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **System** | **Location** | **Life stage** | **2005** | **2006** | **2007** | **2008** | **2009** | **2010** | **2011** | **2012** | **2013** | **2014** | **2015** | **2016** | **Total** | **Lipid** | **Moisture Ash** | **TAG** |
| **Chilko** | Fish fence | smolt (1-year) | 4 | 7 | 20 | 20 | 20 | 42 | 20 | 79 | 59 | 56 | 20 | | 347 | 347 | 11 | 11 |
| | | smolt (2-year) | 3 | | 20 | | | 20 | 10 | 1 | 2 | | | | 56 | 56 | 6 | 6 |
| **Cultus** | Cultus Lake | Fall fry | | | | | 25 | | | | | 20 | | | 45 | 20 | 1 | 1 |
| | | Spring parr | | | 29 | | | | 20 | | | 16 | | | 65 | 36 | 3 | 3 |
| | | smolt | | | | | | | | | | | 20 | | 25 | 25 | 25 | 0 |
| | Sweltzer Creek | Spring parr | | | 20 | 20 | 20 | | | 15 | 20 | 20 | | | 115 | 15 | 1 | 1 |
| **Chilliwack** | Lake | Summery fry | | | | | | | | | 20 | | | | 20 | 15 | 1 | 1 |
| | Lake | Fall fry | | | | | | | | 20 | 15 | | | | 35 | 35 | 2 | 2 |
| | Lake | Spring parr | | | | | | | | 40 | | | | | 40 | 40 | 1 | 1 |
| | Outflow | Smolt | | | | | | | | 100 | 70 | 20 | 20 | | 210 | 210 | 4 | 4 |
| **Fraser** | Mission | Smolt | | | | | 5 | 307 | | | | | | | 312 | 307 | 3 | 3 |
| **Shuswap** | Lake - Main Arm | Summer fry | | | | | | 30 | 30 | | | 30 | | | 90 | 85 | 3 | 3 |
| | | Fall fry | | | | | | 30 | 30 | | | 30 | | | 90 | 80 | 3 | 3 |
| | | Spring parr | | | | | 20 | 58 | 38 | | | 30 | | | 146 | 135 | 4 | 4 |
| | Lake - Cruickshank Pt. | Spring fry | | | | | | 140 | 99 | | | 10 | | | 249 | 244 | 3 | 3 |
| | Little River | Smolt (1-year) | | | | | | 195 | 11 | | | 60 | | | 266 | 266 | 3 | 3 |
| | | Smolt (2-year) | | | | | | 22 | | | | | | | 22 | 20 | 1 | 1 |
| **Seton** | Seton River | Smolt (1-year) | | | | | | 21 | 18 | 12 | 20 | | 20 | | 91 | 93 | 6 | 6 |
| | | Smolt (2-year) | | | | | | 2 | 2 | | | | | | 4 | 2 | 1 | 1 |
| **Quesnel** | East Arm | Fall fry | | | | | | | | | 15 | | | | 15 | 0 | 1 | 1 |
| | | Spring parr | | | | | | | | | 15 | | | | 15 | 14 | 1 | 1 |
| | West Arm | Fall fry | | | | | | | | | 15 | 30 | | | 45 | 34 | 2 | 2 |
| | | Spring parr | | | | | | | | | 28 | | | | 28 | 14 | 1 | 1 |
| | North Arm | Fall fry | | | | | | | | | 15 | 30 | | | 45 | 14 | 2 | 2 |
| | | Spring parr | | | | | | | | | 15 | | | | 15 | 15 | 1 | 1 |
| | Middle Arm | Fall fry | | | | | | | | | 15 | | | | 15 | 0 | 1 | 1 |
| | | Spring parr | | | | | | | | | 15 | | | | 15 | 14 | 1 | 1 |
| | Quesnel River | Spring fry | | | | | | | | | | 20 | | 5 | 25 | 22 | 2 | 2 |
| | | Smolt (1-year) | | | | | | | | | | 19 | 7 | | 26 | 26 | 2 | 2 |
| | | Smolt (2-year) | | | | | | | | | 2 | 1 | | | 3 | 3 | 1 | 1 |
| | | **Total:** | 7 | 7 | 89 | 40 | 90 | 867 | 278 | 267 | 341 | 392 | 87 | 5 | **2475** | | | |

# Appendix B: Laboratory Analyses

## LIPID EXTRACTION AND CONSTITUENT ANALYSIS

Whole sockeye salmon (*Oncorhynchus nerka*) smolts were removed from -80$^{o}$C freezer storage and allowed to thaw at room temperature prior to measuring fork length and weight of each individual. Using a scalpel, fish were cut into 8-10 pieces prior to being placed in labelled 50 ml polypropylene copolymer Nalgene® tubes along with two steel ball bearings. Samples were ground using a SPEX SamplePrep 2010 Geno/Grinder (SPEX, Metuchen, NJ, www.spexsampleprep.com) at 1500 rpm for two-minute intervals until fully homogenized (up to 12 minutes total; typically 4-8 minutes). Following homogenization, samples were picked through to remove any non-homogenized pieces (bone, skin, scales etc.) leaving the best homogenate for lipid and moisture-ash analysis. Any excess sample was refrigerated in a 5 mL plastic vial until analysis was complete, then transferred to a -40$^{o}$C freezer.

Lipids were extracted from homogenized samples using the chloroform-methanol method, following Bligh and Dyer (1959) with minor modifications. Two 0.3 g (+/-0.015 g) replicate homogenate samples per individual were placed into 10 mL polypropylene vials containing two steel ball bearings. If 0.6 g of homogenate was not available because of low smolt weight, 0.2 g or 0.1 g replicates were used. For smolts less than 0.5 g, no replicate was used. Two 0.3 g olive oil standards were included with each analysis set of 10 fish to verify the lipid values (i.e. as references).

Extraction was performed using 1 mL chloroform: 1 mL methanol: 0.5 mL distilled water for every 0.1g of homogenate present. These volumes were added in a specific sequence to increase solubility of the lipid in chloroform (Smedes and Thomasen 1996). To each vial containing ~3.0 g of homogenate, 3 mL of chloroform and 1.5 mL of methanol were added then ground for two minutes at 1500 rpm. Next, 1.5 mL of chloroform was added and ground at 1500 rpm for 30 seconds. Finally, 1.5 mL of distilled water was added and ground for 30 seconds at 1500 rpm.

To remove suspended tissue, each replicate was filtered using a vacuum flask, funnel, and filter paper (Whatman 42.5 mm). The contents of the vacuum flask were decanted into 10 mL graduated cylinders and covered with tinfoil to prevent evaporation. A 1:1 mixture of methanol and chloroform was used to rinse the filter paper and vacuum flask ensuring maximum lipid retention. The solution fully separated into biphasic layers (within 2-3 minutes), with the water-rich methanol layer above, and chloro-lipid layer below. The volume of the chloro-lipid layer (*CHCl3 total*) was recorded prior to siphoning off the methanol layer.

A known volume of chloro-lipid from each replicate was pipetted (*CHCl3 pipetted*) into its own pre-weighed tin weigh boat, which were placed in an oven at 100$^{o}$C for 10 minutes to completely evaporate the chloroform. The lipid was weighed and percent lipid of each sample calculated following:

$$\% \text{ Lipid } = Lipid\ Weight \times \left[\frac{CHCl3\ pipetted}{CHCl3\ total} \times \frac{1}{sample\ weight}\right]$$

Replicates of homogenized tissue were placed into pre-weighed porcelain crucibles. Typically, 0.3 g of tissue per replicate (+/- 0.015 g) was used unless insufficient sample was available. Crucibles were placed in a convection oven (Cole-Parmer) at 100$^{o}$C for 12-16 hours to remove moisture from tissue. Crucibles were placed in a desiccator for 15 minutes, then weighed to determine dry mass and to calculate moisture content.

For ash analysis, the same pre-weighed crucibles were then placed within a tabletop muffle furnace (Cole-Parmer) at 600$^{o}$C for 2.25-2.5 hours to burn off all carbon sources, after which samples were allowed to cool for an hour within the oven. Crucibles were placed in a desiccator for 15 minutes then weighed to determine ash content. The remaining mass was the protein content of the subsample.

## TRIGLYCERIDE ANALYSIS

To measure triglyceride concentrations from extracted lipids, we used commercially available triglyceride colorimetric assay kits (Item 10010303, Cayman Chemicals, Ann Arbour, MI; www.caymanchem.com) using protocols outlined by the manufacturer (with minor modifications). These kits use enzymatic hydrolysis of triglycerides by lipase to produce free fatty acids and glycerol, and the resulting reaction can be measured using spectrophotometry to estimate triglyceride concentrations (Weber et al. 2003).

Triglyceride analyses was run with the chloro-lipid samples from the lipid extraction procedure (see: 'Lipid extraction and moisture ash' above) which were stored at -80 $^{o}$C. Prior to running the assay, all reagents and samples were allowed to thaw for at least 10 minutes at room temperature. Samples and the blank (100 μL of chloroform into an empty test tube) were vortexed, placed in labelled test tubes and dried under nitrogen gas ($N_2$) at ~15 psi for 10-15 minutes, or until the chloroform was fully evaporated from each tube. After drying, isopropanol (i.e. isopropyl alcohol) was added to each test tube, which was then covered with parafilm and briefly vortexed (15-20 seconds) until the lipid residue was fully dissolved. Volumes of isopropanol (i.e. dilution factors) varied depending on the lipid concentrations of samples. Test tubes were covered and allowed to reconstitute for at least an hour. Enzyme buffer was created by mixing sodium phosphate buffer and the enzyme mixture (provided with kit) together with de-ionized water following the manufacturer's protocols. Standards were performed as a serial dilution (ranging from 0 mg/dL to 200 mg/dL) in duplicate using isopropanol and the triglyceride standard (1000 mg/dL) provided with the assay kit. The standards allowed for the creation of a standard curve to calculate the triglyceride concentration of samples based on detected absorbance by spectrophotometry.

A 96-well solid plate was prepared by first adding 10 μL of standards into the first two columns (n = 16 wells) of the plate. For the remaining wells, up to 40 samples were loaded (10 μL per well) on each plate. Diluted enzyme buffer (150 μL) was added to each well, and then plates were shaken, covered, and allowed to incubate at room temperature for 15 minutes. Absorbance was then read at 530-550 nm using a FLUOstart Omega multimode microplate reader (BMG Labtech, Ortenberg Germany, www.bmglabtech.com).

Standards and samples were corrected by subtracting absorbance values by the average absorbance of the blanks. Triglyceride concentration was then calculated using the values obtained from the standard curve following the equation:

$$\text{Triglycerides } \left(\frac{\text{mg}}{\text{dL}}\right) = \left[\frac{(Corrected\ absorbance) - (y - int)}{Slope}\right]$$

Final triglyceride concentration was then calculated by multiplying the concentration by the dilution factor of isopropanol added to samples.

# Appendix C: Assessment Of Moisture Loss From Juvenile Sockeye Salmon Samples In Long-Term Cold Storage

## BACKGROUND AND OBJECTIVES

Long-term freezer storage of biological samples can result in sample degradation due to enzymatic lipid hydrolysis or oxidation (Auberg et al. 2005) and potential evaporative losses in water content. Both temperature and time are known to influence these aspects of samples in long-term cold storage (Burgaard and Jorgensen 2011); therefore, estimates of lipid and water content in samples taken from cold storage may not be reflective of their initial condition when collected in the field. To better understand how various storage parameters influence smolt sample quality, we collected sockeye smolts (*Oncorhynchus nerka*) and stored them at two different temperatures for time-periods up to two years, before applying standard laboratory methods to assess moisture loss and lipid concentrations.

The primary objective of this experiment was to assess how methods of long-term cold storage influence the constituents of salmonid samples used for lipid extraction and analysis. We were interested in comparing two methods of storage (-20 $^{o}$C and -80 $^{o}$C) to determine how storage time and temperature interact to influence estimated values of moisture and lipids in smolt samples. By estimating and correcting for the quantity of moisture lost from samples during storage, we aimed to improve our accuracy in estimating the lipid content of juvenile fishes *in vivo*.

## COLLECTION AND STORAGE METHODS

Sockeye salmon smolts (n = 155) were collected at the outflow of Shuswap Lake, British Columbia (i.e. Little River; 50.87N -119.58W) on May 19$^{th}$, 2016. All individuals were collected close to the shore by beach seine, euthanized via a lethal dose of tricaine methanesulfonate (MS-222), and measured for fork length and mass in the field prior to being frozen on dry ice. Frozen samples were then transported on dry ice to the Center for Aquaculture and Environmental Research in West Vancouver.

To experimentally test how freezer storage duration and temperature influence estimated lipid values in samples, frozen smolt samples were randomly assigned to one of two storage treatments one day after collection (May 20$^{th}$ 2016). Samples were either placed in a -20 $^{o}$C (n = 75), or -80 $^{o}$C freezer (n = 80) until subsequent laboratory analyses dates (Table 1).

## LABORATORY METHODS

Multiple laboratory sampling time periods were used to assess moisture and lipid contents of smolt samples. The first sampling period began 10-12 days after samples were placed in storage, with subsequent sampling periods occurring every six months afterwards. To date, ~80 % of samples have been analyzed in the laboratory, with only one more analysis period remaining (scheduled for May 2018).

On each sampling date, subsets of 15-20 smolts were randomly selected from each freezer storage type (Table 1) and allowed to thaw at room temperature prior to measuring mass in the laboratory. Gravimetric lipid extraction protocols followed those developed by Bligh and Dyer (1956) with minor modifications (see Appendix B for detailed description). Whole body smolt samples were homogenized using a SPEX SamplePrep 2010 Geno/Grinder (SPEX, Metuchen, NJ, www.spexsampleprep.com) in 50 ml polypropylene Nalgene® tubes with two steel ball bearings. To estimate moisture content of smolts, ~3.0 g of homogenized tissue from each individual was placed in pre-weighed crucibles and dried in an oven at 100°C for 12-20 hours. Crucibles containing dried samples were then removed from the drying oven, re-weighed, and placed in a furnace at 600°C for ~2.5 hours to determine ash content. The resulting data allowed for the estimation of percentages of carbon and water in homogenized tissues of smolt samples.

Two replicates were extracted from each homogenized sample using chloroform, methanol and distilled water at 1:1:0.5 parts, respectively. Two olive oil replicates were used as lipid standards. Samples were then filtered into 10 ml graduated cylinders, covered and allowed to separate into two layers. After biphasic layers formed, 1.5-2 ml of the chloro-lipid layer from each sample was pipetted onto pre-weighed aluminum dishes, while a 100 uL subsample was placed in glass culture tubes and frozen at -80 °C for future triglyceride analysis. Chloroform was evaporated from aluminum dishes by placing them in a drying oven at 100 °C for 5-10 minutes, and then dried weights were recorded to determine lipid content.

In October 2017, following analysis of the fourth group of fish, the percent difference between the wet weight measured in the field and the thawed weight measured in the lab was calculated for each fish using Eq. 1:

$$whole\ fish\ wt._{field-thawed} = \frac{whole\ fish\ wt._{field} - whole\ fish\ wt._{thawed}}{whole\ fish\ wt._{thawed}} * 100\% \quad [1]$$

The percent differences were plotted by storage time and fish size. The relationships differed by storage temperature, in that moisture loss was greater for fish stored at -20°C, within several days of storage. As the fish analyzed in this report were stored at -80°C, only the data from the fish stored at -80°C in the experiment are described.

We assumed that moisture loss would approach an asymptote over time. We also assumed that percent moisture loss would be greater for smaller fish, due to the higher surface area to volume ratio. We fit a linear model to the logarithm of percent difference between field and

thawed weights, as a function of the logarithm of storage time and the untransformed thawed weights. To determine which terms to include, we evaluated the fit of all possible combinations of the two explanatory variables using AIC.

$$\log\left(whole\ fish\ wt._{field-thawed}\right) \sim \log\left(storage\ time\ (d)\right) + whole\ fish\ wt._{thawed}\ (g) \quad [2]$$

## RESULTS AND DISCUSSION

Five of the smolts stored at -80°C were omitted from analysis due to measurement errors. For all five of the fish, the thawed weight measured in the lab was greater than the field weight, which we attributed to not allowing the balance to tare during field measurements. This left data from 60 smolts to fit the model.

The AIC table is presented in Table 2. As the full model presented in Eq. 2 was the most parsimonious model for the data, with the lowest $AIC_c$ score, it was used to calculate the difference between the field and thawed weights for each fish, based on storage time and thawed weight. The difference was added to the thawed weight to calculate a field weight that incorporated the moisture lost during storage. For comparison between measured and calculated field weights, see Figure 1. In addition to quantifying moisture lost during sample storage, the moisture loss equation was useful for calculating field weights for batches of fish that were missing field weight data, or where the data were likely to be inaccurate. Field conditions, including wind, rain, and boat movement can inhibit accuracy of scale readings. Furthermore, the balances used for field collections measure weight to two decimal places, while laboratory balances measure to four decimal places.

The moisture loss equation was used to calculate a field weight from the thawed weight of all juvenile fish collected from the six study populations (Eq. 3):

$$whole\ fish\ wt._{field\ calc.} = whole\ fish\ wt._{thawed} + \left[\frac{10^{[0.1725*\log(storage\ time)-(0.2111*whole\ fish\ wt._{thawed})+1.083]}}{100\%} * whole\ fish\ wt._{thawed}\right] \quad [3]$$

This calculated field weight was used for all subsequent analysis, except in a few situations, which are described below.

The percent lipid of all juveniles was corrected to the calculated field weight using Eq. 4:

$$corr.\%\ lipid = \frac{total\ lipid\ (g)}{whole\ fish\ wt._{\ field\ calc.}\ (g)} * 100\% \quad [4]$$

The percent water of each fish was corrected to its field weight using Eq. 5:

$$corr.\%\ water = \frac{water\ (g) + (\Delta\ whole\ fish\ wt._{\ field\ calc.-thawed}\ (g))}{whole\ fish\ wt._{\ field\ calc.}\ (g)} * 100\% \quad [5]$$

The relationship between fish size, storage time, and moisture loss was developed using data from 60 smolts with mean (± SD) thawed weight of 5.37 g (± 1.62 g, range: 2.84–9.61 g), which were stored between ten and 554 days. However, the juvenile sockeye salmon collected for the condition study have a wider range of sizes and storage periods. The moisture loss relationship shows good agreement across the range of sizes but overestimates moisture loss for fish less than 10g stored for long periods (i.e. >2000 days; Figure 2).

TABLES

Table 1: Freezer experiment study design, including sample sizes for each temperature treatment, as well as laboratory analyses dates.

| Storage Time | -20 sample size | -80 sample size | Lab Analysis Date |
|---|---|---|---|
| 0 (10 days) | 15 | 20 | May 30-June 2, 2016 |
| 6 months | 15 | 15 | Nov 17-Nov 23, 2016 |
| 12 months | 15 | 15 | May 8-May 11, 2017 |
| 18 months | 15 | 15 | Nov 20-Nov 24, 2017 |
| 24 months | 15 | 15 | To do: May 19, 2018 |
| **TOTAL** | **75** | **80** | |

Table 2. All possible combinations of explanatory variables used to describe percent different in field and thawed weights of smolts analyzed in the freezer experiment.

| Response | Model | K | logLik | AICc | $\Delta$AICc | $w_i$ | $r^2$ |
|---|---|---|---|---|---|---|---|
| log (fish wt. $_{field\text{-}thawed}$) | log(storage time) + fish wt. $_{thawed}$ | 2 | -44.3 | 97.4 | 0.00 | 0.997 | 0.50 |
| | fish wt. $_{thawed}$ | 1 | -51.2 | 108.8 | 11.43 | 0.003 | 0.33 |
| | log(storage time) | 1 | -55.4 | 117.3 | 19.88 | 0.000 | 0.20 |
| | *Null*: intercept | 0 | -61.2 | 126.6 | 29.26 | 0.000 | 0.00 |

*Note:* K = number of parameters in the model, logLik = model log likelihood, $\Delta$AICc = difference in AICc from top model, $w_i$ is the AICc model weight, $r^2$ = adjusted-$r^2$.

FIGURES

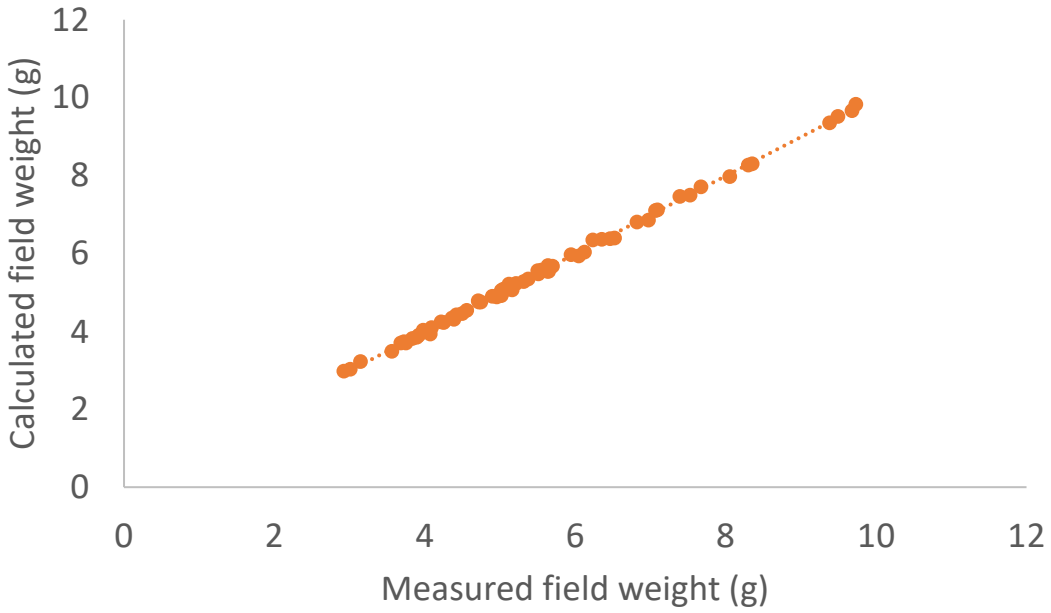


Figure 1. The relationship between the weight of Shuswap smolts (n=60) measured in the field and the weight calculated using Eq. 3, developed to correct for moisture lost during storage. Calculated field weight strongly approximates measured field weight ($y=1.00x-0.01$, $r^2=1.00$).

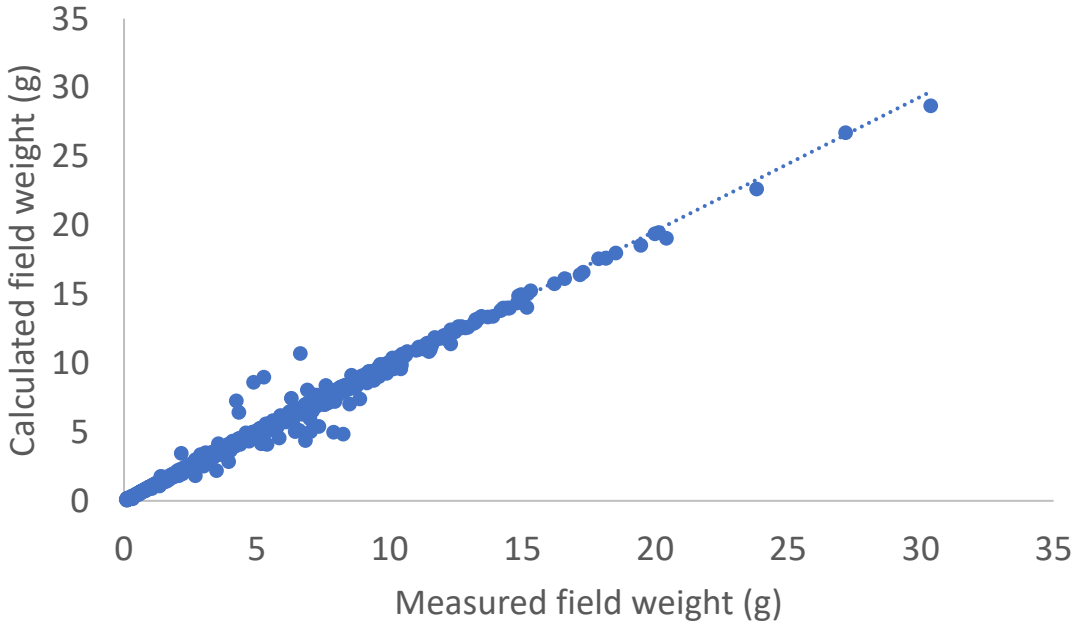


Figure 2. The relationship between the weight of juveniles (n=1747), from Chilko, Chilliwack, Cultus, Quesnel, Seton, and Shuswap, measured in the field and the weight calculated using Eq. 3, developed to correct for moisture lost during storage. Calculated field weight strongly approximates measured field weight ($y=0.98x+0.07$, $r^2=0.99$), with a few exceptions.