

Effects of density during freshwater and early marine rearing on juvenile sockeye salmon size, growth, and migration

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ABSTRACT: We tested for density-dependent effects on the body size, ocean entry date, growth rate, and migration speed of juvenile sockeye salmon *Oncorhynchus nerka* in 2 yr with contrasting competitor densities during freshwater residence (intraspecific), as well as the first 2 mo of marine residence (intra- and interspecific). Juvenile sockeye salmon entering the marine environment during a year with high competitor densities (conspecifics and 9 other pelagic species groups) were, on average, 11 % smaller and entered the ocean almost a week earlier. Differences between the high- and low-density years in entry size, but not entry date, were strongest in nursery lakes with high parental spawner abundance, consistent with density-dependent effects on freshwater growth. Mean daily growth rates of sockeye salmon during early marine residence did not vary between years after accounting for variation in ocean entry size and timing, even though the catch per unit effort of the most abundant juvenile salmon species increased more than 5-fold. However, juvenile sockeye salmon entering in the high-density year did migrate away from their ocean entry points significantly more rapidly (estimated ~40 % increase in body lengths per second). Our results suggest that juvenile sockeye salmon growth during early marine residence may not be strongly limited by competition and that shifts in migration speed or spatial distribution may buffer individuals from competitive interactions.

KEY WORDS: Density-dependent effects · Otolith microstructure · Growth · Migration · Competition · Body size · Phenology

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INTRODUCTION

The effect of competition on the dynamics of animal populations varies with the abundance of competitor populations and the ecosystem's carrying capacity. When abundances are high and resources are limited, intraspecific competition intensifies, often leading to increased mortality rates and reduced growth (Sinclair 1989). Yet identifying periods when individual traits are moderated by density can be compli-

cated by ontogenetic variation in ecological characteristics (e.g. body size, resource requirements, habitat use) that may influence competitive interactions (Ratikainen et al. 2008). Despite these difficulties, quantifying the strength of density dependence and its impact on population dynamics is important to support the sustainable use and conservation of animal populations (Hilborn & Walters 1992).

In salmon, intraspecific density-dependent effects during freshwater rearing are widely recognized.

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Large numbers of returning adult salmon can exceed the capacity of available spawning habitat, resulting in high rates of egg mortality due to nest superimposition (McNeil 1964). Similarly, high juvenile salmon abundance during freshwater rearing has been associated with slower growth (Foerster 1944, Schindler et al. 2005), displacement to suboptimal habitats (Gibson et al. 2008), altered downstream migration phenologies (Connor et al. 2013), and reduced survival (Jonsson et al. 1998).

Once salmon enter the marine environment, density-dependent effects can be relatively difficult to detect, particularly in highly migratory species or populations. Competitive interactions in the marine environment occur across large geographic areas and coincide with ontogenetic shifts in resource use (Brodeur et al. 2007, Hertz et al. 2016). Furthermore, the composition of marine communities varies across space and time (Orsi et al. 2007), altering the suite of species with which migrants interact. Despite these issues, length-at-age data and reconstructed growth

histories from spawners suggest that high densities of conspecifics (Peterman 1984) or other salmon species (Ruggerone et al. 2003, Ruggerone & Connors 2015, Debertin et al. 2017) may depress growth or survival, particularly during offshore residence. Similar density-dependent effects have been hypothesized to also occur early in marine life (Beamish et al. 2010), potentially resulting in size selective mortality and reduced spawner abundance (Beamish et al. 2004).

We examined the potential for density-dependent effects on a suite of individual traits during freshwater and early marine residence in juvenile sockeye salmon *Oncorhynchus nerka* originating from the Fraser River in British Columbia. After downstream migration, Fraser River sockeye salmon enter the Strait of Georgia, which lies between Vancouver Island and the British Columbia mainland and is connected to the northeast Pacific Ocean via Johnstone Strait in the north and Juan de Fuca Strait in the south (Fig. 1). Most Fraser River sockeye salmon migrate

north through the Strait of Georgia ecosystem over a 1–2 mo period (Preikshot et al. 2012, Freshwater et al. 2016b, Neville et al. 2016). Despite the relatively small size of the Strait of Georgia (6800 km²), hundreds of salmon populations enter and reside in this ecosystem for several months, resulting in high juvenile salmon densities (Groot & Margolis 1991).

Fraser River sockeye salmon populations exhibit substantial variation in interannual abundance (DFO 2014), which can be used to test for density-dependent effects. Particularly large differences in Fraser River spawner abundance were observed in 2009 and 2010. Spawner abundance in 2009 was exceptionally low (approximately 1 million fish), compared with a record high of 13 million estimated spawners in 2010. Juvenile sockeye salmon produced from these years largely entered the ocean during 2011 and 2012 (from 2009 and 2010 spawning, respectively) and catch per unit effort (CPUE) of juvenile sockeye salmon in the strait was consequently anomalously high in 2012 (Neville & Sweeting 2013). Additionally, density-dependent interactions in the strait may be magnified by the abundance of other pelagic fishes.

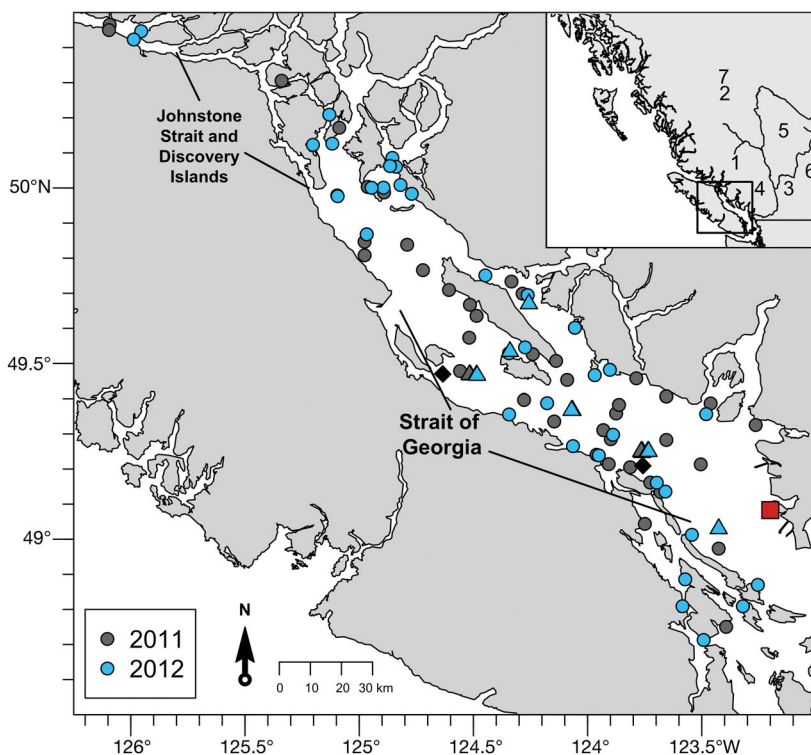


Fig. 1. Map of study area, the Strait of Georgia and Johnstone Strait, with inset showing southern British Columbia and Fraser River watershed. Sampling sites where otoliths were collected are shown by filled circles and the approximate ocean entry location of Fraser River sockeye salmon by the red square. Zooplankton sampling events and lighthouse locations where temperature data were collected, are shown as triangles and diamonds, respectively. Numbers in inset map represent approximate locations of lakes where sampled juveniles matured in freshwater: (1) Chilko, (2) Fraser, (3) Kamloops, (4) Lillooet, (5) Quesnel, (6) Shuswap, and (7) Stuart

Juvenile sockeye salmon in the Strait of Georgia co-occur with juvenile Fraser River pink salmon *O. gorbuscha* that compete for similar prey (Brodeur et al. 2007, Beamish et al. 2008, 2010). Pink salmon have biennial life cycles and are effectively absent as juveniles from the Strait of Georgia in odd years and are highly abundant in even years (Beamish et al. 2010, Neville & Sweeting 2013). Species such as juvenile chum salmon *O. keta* and Pacific herring *Clupea pallasii* also exhibit interannual variability in abundance (Rensel et al. 2010, Beamish et al. 2012), which may further moderate marine density-dependent interactions.

Although Fraser River sockeye salmon experience a common rearing environment in the Strait of Georgia, conditions during freshwater residence vary among populations within the watershed. Despite total spawner abundance in the Fraser River being extremely high in 2010, several populations experienced average or below average returns and low fry densities (DFO 2014). Therefore, although all Fraser River sockeye salmon populations experienced high competitor densities in the Strait of Georgia in 2012, freshwater density-dependent effects likely varied among nursery lakes.

The objectives of this study were to determine whether the body size, growth rate, and migratory phenology of juvenile sockeye salmon differed between 2011 and 2012, consistent with density-dependent effects during marine residence, while accounting for potential freshwater density-dependent effects. Although the conclusions that can be drawn with 2 yr of data are necessarily limited, these particular cohorts represent abnormally large differences in abundance that likely bracket the low and high densities that will be observed in this region. Preliminary analyses indicated juvenile sockeye salmon body size differed between 2011 and 2012 (Neville et al. 2013). Those results, coupled with the differences in spawner density between 2009 and 2010, provided some evidence for density-dependent growth; however, that preliminary analysis could not determine whether differences in body size were due to interactions occurring during freshwater or marine residence.

We predicted that size at capture (H1) and entry (H2) would be significantly greater and entry date significantly later (H3) in 2011 (low density) relative to 2012 (high density), particularly in lakes that had high densities of juveniles during freshwater residence. After accounting for these ocean entry effects, we hypothesized that growth rates for sockeye salmon would be greater in 2011 compared with

2012 (H4) due to density-dependent effects in the Strait of Georgia. Finally, as many species alter their movement patterns based on intra- or interspecific competitor density (Matthysen 2005, Chapman et al. 2012), we predicted that the mean migration speed of juvenile sockeye salmon would shift with increased competitor density (H5). Under conditions of reduced prey and limited potential growth, juvenile sockeye salmon may accelerate their migration speed within the Strait of Georgia to reach better feeding opportunities farther north. Alternatively, as migration speed is correlated with body size (Freshwater et al. 2016b), density-dependent reductions in body size may result in a coincident decrease in migration speed.

MATERIALS AND METHODS

Pelagic fish sampling and analysis

We captured juvenile salmon and other fishes throughout the Discovery Islands, Strait of Georgia, and lower Johnstone Strait (Fig. 1) in 2011 (18–31 May and 11–25 June) and 2012 (19 May–1 June and 11–25 June), using a purse seine fished from the F/V ‘Ocean Venture’. The areas fished are described in detail in Neville et al. (2013). To increase population-specific sample sizes, we also incorporated 11 individuals collected during mid-water surface trawls by the CCGS ‘W. E. Ricker’ in 2011 (24 June–1 July). Supplemental analyses indicated the inclusion of these samples did not change our conclusions (see the Supplement at www.int-res.com/articles/suppl/m579p097_supp.pdf). We randomly selected up to 30 juvenile sockeye salmon from each set to retain for sampling and the remaining individuals were identified to species, enumerated, and released. Immediately after capture, we recorded fork length, removed sagittal otoliths, and preserved tissue samples for genetic stock identification from all sampled fish. Individuals were assigned to spawning populations within the Fraser River using 14 microsatellite loci, with a 50% lower probability limit and an estimated 5% false assignment rate (Beacham et al. 2005). We restricted further analyses to populations that had at least 4 individuals captured in a sampling year. To meet this threshold, balance the dataset temporally, and account for common density-dependent effects during freshwater rearing, we aggregated several spawning populations by their shared, primary nursery lake or lake-complex. Population specific sample sizes and their assignment to different nursery lakes are shown in Table S1 in the Supplement.

We estimated the relative abundance of pelagic fishes that were captured during the purse seine surveys using CPUE (number of individuals captured per set). For this study, we restricted our analysis to species that were captured in at least 50 sampling sets across both years (183 and 194 sets completed in 2011 and 2012, respectively). We tested for differences between 2011 and 2012 in the total CPUE of all species, as well as the CPUE of individual species. A negative binomial generalized linear model (GLM) was used to test for differences in total CPUE because the summed catch data were over-dispersed. To test for species-specific differences in CPUE, we used zero-inflated Poisson GLMs, which simultaneously estimate the probability of a non-zero response using a binomial distribution with a logit link function and estimate the probability of observing a specific count using a Poisson distribution with a log link function. We fit capture year as a fixed parameter and estimated its effect on mean catch size, as well as the proportion of zero catches (for species-specific CPUE). We estimated parameters relative to 2012, i.e. negative estimates indicate that the probability of observing a zero catch (for zero-inflated model component) or observing a larger catch (for the count model component) was lower in 2012. We adjusted our significance tests for multiple comparisons of fish abundance using a false discovery rate (Benjamini et al. 2006). We fit zero-inflated Poisson GLMs in the *pscl* package (Zeileis et al. 2008) and conducted all statistical analyses using R version 3.2.2 (R Core Team 2017).

Sea surface temperature and zooplankton data

Interannual differences in environmental conditions, such as temperature and prey availability, may influence marine growth or migratory behavior, confounding tests of density-dependent effects. To address this possibility, we estimated interannual differences in sea surface temperature using data collected by lighthouses at Chrome and Entrance islands. We also estimated interannual differences in prey availability using zooplankton data sampled during Fisheries and Oceans Canada (DFO) surveys that overlapped spatially and temporally (21 May–25 June in 2011 and 2012; Fig. 1) with juvenile salmon sampling events. Zooplankton samples were collected by a 0.56-m-diameter vertical bongo net with 236 μm mesh towed at depths from 39 to 400 m. For this study, we used samples that had been aggregated into broad taxonomic groups (typically order;

details in Mackas et al. 2013) and retained only taxa that have been commonly observed in juvenile sockeye salmon diets (Brodeur et al. 2007). We tested for interannual differences in seasonal increases in sea surface temperature with a linear model that included day of year, year, and their interaction as predictors. We tested for differences in the biomass of potential prey taxa between years using Mann-Whitney tests.

Abundance of effective female spawners

Estimates of juvenile sockeye salmon abundance within nursery lakes are unavailable for most Fraser River populations (DFO 2014). Instead we assessed differences in freshwater density-dependent effects using estimates of spawner abundance in the parental generation as a proxy for juvenile sockeye salmon densities in nursery lakes. Spawner abundance estimates are collected by DFO using a variety of techniques, including fence and tower counts, weir counts, and aerial and visual surveys (Grant et al. 2011, K. Benner, DFO, pers. comm.). These estimates are then converted to an estimate of effective female spawner (EFS) abundance using sex ratio and spawner success data collected during carcass surveys (Grant et al. 2011, DFO 2014). We calculated EFS abundance in 2009 (parents of 2011 juveniles) and 2010 (parents of 2012 juveniles) relative to mean EFS abundance (1974–2010). However, these data were highly skewed and dominated by several outliers. Therefore, we treated freshwater density-dependent effects as a categorical variable and classified it as present if EFS abundance was greater than mean EFS abundance plus 1 SD in 2010.

To estimate the effects of spawner density on competitive interactions between juveniles rearing in freshwater, it was necessary to aggregate EFS abundance data within a nursery lake system. Typically, spawner abundance is estimated at the scale of conservation units (CUs). CUs are management units that consist of spawning populations with a common life history type, rearing environment, and run timing (Holtby & Ciruna 2007, Grant et al. 2011). Each group of spawning populations that we aggregated by nursery lake for the otolith microstructure analysis belongs to a single CU (Table S1), but may rear in a lake or lake-complex sympatrically with CUs for which we do not have otolith samples. To provide an estimate of the maximum potential freshwater density-dependent effects juveniles may have encountered, we summed the spawner abundance for all

CUs that are likely to contribute fry to the nursery lake or lake-complex used by spawning populations for which we have otolith data. We provide details on the relationship between spawning populations, nursery lakes, and CUs, as well as how these aggregates were grouped, in Table S1.

Otolith microstructure analysis

We used otolith microstructure techniques to estimate individual size at ocean entry, ocean entry date, and marine growth rates (see Freshwater et al. 2015 for validation and details on sample preparation). We used cellSens Imaging Software (Olympus Scientific Solutions America) to measure otolith radius, marine entry check radius, and the number of daily increments formed after marine entry. We made all measurements dorsal and perpendicular to the otolith's anterior–posterior centerline and used the average of 3 sequential measurements, per otolith metric, for analysis. If an otolith was vateritic or damaged, if all measurements could not be completed, or if individual counts differed by more than 5 increments, that individual was excluded from subsequent analyses.

To estimate size at ocean entry, we used a linear regression (otolith radius vs. fork length) developed from a larger dataset of British Columbia sockeye salmon ranging in size from 66 to 209 mm and collected over 6 yr. We estimated entry fork length from marine entry check radii with both scale (i.e. hard structure) proportional and body proportional methods (Francis 1990), then used the mean of both as an estimate of fork length at ocean entry. Briefly, these methods assume a single relationship between otolith length and fish length by estimating either fork length (FL) as a function of otolith radius (OR) ($FL = 285.10 (\pm 4.85 \text{ SE}) \times OR - 76.20 (\pm 3.44 \text{ SE})$; $r^2 = 0.78$, $n = 920$; C. Freshwater, unpubl. data) or vice versa ($OR = 0.0027 (\pm 0.0004 \text{ SE}) \times FL + 0.37 (\pm 0.006 \text{ SE})$). Estimates of previous body size are then corrected for each individual's deviation from the average otolith-body size relationship. By taking the mean of both methods, we partially account for the possibility that variation among individuals may be due to either their somatic growth or their otolith growth deviating from the mean relationship within the population (Francis 1990).

We estimated daily marine growth rates by subtracting estimated size at ocean entry from size at capture, then dividing by the number of daily increments. We calculated 2 estimates of migration speed (defined here as the rate at which individual fish moved away

from their ocean entry point). For both, we first estimated migration distance as the linear distance (km) between the ocean entry point in the Fraser River estuary and capture location, after accounting for the Earth's curvature. We then divided the linear migration distance by the number of daily increments to estimate absolute migration speed. We converted migration speed in km d^{-1} to body lengths per second (bl s^{-1}) using estimates of fork length at ocean entry. Since we were primarily interested in how individual migratory effort may shift with changes in density, we focused on relative migration speed (i.e. bl s^{-1}), but analyses estimating changes in migration speed in km d^{-1} are presented in the Supplement.

We used generalized linear mixed effects models to examine differences in individual characteristics between years of low and high juvenile salmon abundance during early marine rearing. Specifically we tested that (1) size at capture, (2) size at ocean entry, (3) ocean entry date, (4) marine growth rates, or (5) marine migration speed did not significantly differ between 2011 and 2012. We tested hypotheses H1 to H3 using linear mixed effects models in the lme4 package (Bates et al. 2015), with sampling year and freshwater density-dependent effects (present or absent) as categorical fixed effects and random intercepts for each nursery lake to account for variation among rearing populations. To account for differences between years in ocean entry characteristics that may have been associated with freshwater rearing densities, we included an interaction term between the 2 fixed effects.

Since ocean entry size and phenology can influence the early marine growth (Freshwater et al. 2016a) and migration rate (Freshwater et al. 2016b) of juvenile sockeye salmon, we constructed additional mixed effects models that included entry size and phenology as covariates to test hypotheses H4 and H5. We did not believe that freshwater density-dependence would have an effect on marine growth or migration speeds after accounting for entry traits; therefore, we did not include this fixed effect or its interaction with capture year. To better interpret models that included covariates measured in different units, we centered and scaled entry size and entry date data (Schielzeth 2010). To meet normality assumptions, we log-transformed migration speed. We confirmed that explanatory variables were not collinear using variance inflation factors (the VIF of all explanatory variables was <2 ; $\text{VIF} <3$ indicates minimal collinearity). We also checked for adequate model fit by examining quantile–quantile plots and the distribution of residuals.

RESULTS

Pelagic fish abundance

The 10 most abundant taxa collected in the purse seine survey included: 5 species of juvenile Pacific salmon (sockeye salmon, pink salmon, chum salmon, Chinook salmon *Oncorhynchus tshawytscha*, and coho salmon *O. kisutch*), Pacific herring, kelp greenling *Hexagrammos decagrammus* and rock greenling *H. lagocephalus* (CPUE for both species were pooled), Pacific sand lance *Ammodytes hexapterus*, northern anchovy *Engraulis mordax*, and 3-spined stickleback *Gasterosteus aculeatus*. Total CPUE (i.e. catches of all zooplanktivorous fish species combined) was significantly greater in 2012 than 2011 (Table 1). This change in total abundance reflected increases in the abundance of nearly all the species we examined. The numbers of non-zero catches for juvenile sockeye salmon, pink salmon, and herring were significantly greater in 2012 than 2011 (Table 1, Fig. 2). After accounting for catches where no individuals were captured, CPUE for 8 of the 10 pelagic fishes (including all juvenile salmon species) was significantly greater in 2012 than 2011 (Table 1). Only Pacific sand lance and 3-spined stickleback CPUE were significantly lower in 2012 than 2011 (Table 1).

Sea surface temperature and zooplankton abundance

Sea surface temperature (SST) increased over the migratory period in both years (Fig. S1 in the Sup-

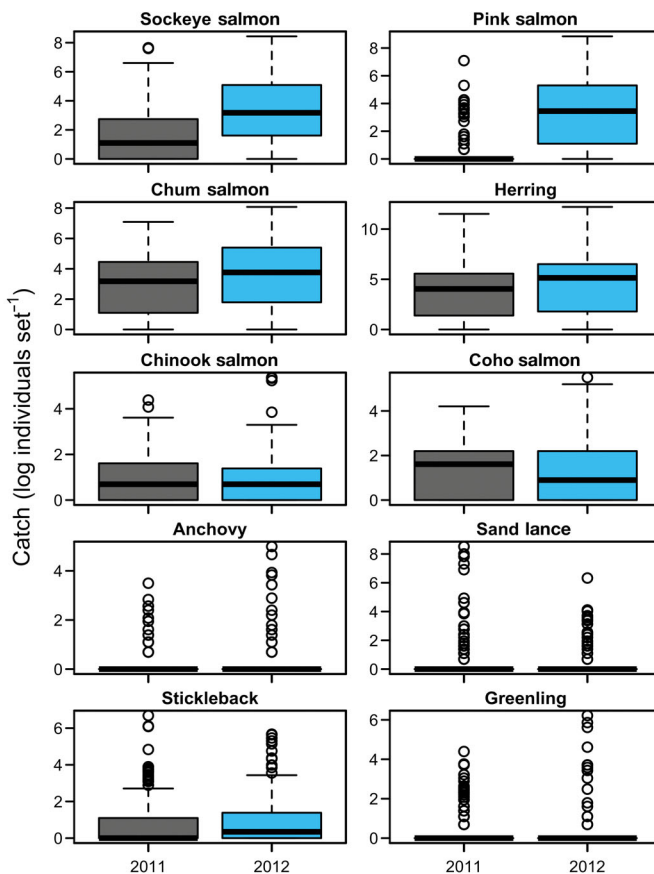


Fig. 2. Catch per unit effort (individuals per set, log transformed to improve readability) of pelagic fishes from Strait of Georgia purse seine surveys. There were 183 and 194 sampling sets in 2011 and 2012, respectively. Note that the scale of the y axis changes between taxonomic groups. Box plots show the median as a center line, the interquartile range as boxes, 150% of the interquartile range (or minimum and maximum values that fall within that range) as whiskers, and all data outside that range as circles

Table 1. Mean catch per unit effort (CPUE; individuals per purse seine set) during sampling surveys ($n_{2011} = 183$ sets; $n_{2012} = 194$ sets) and coefficients estimated from negative binomial (total CPUE) and zero-inflated (single species) Poisson regression models. p-values have been adjusted for multiple comparisons using a false discovery rate. Parameters were estimated relative to 2012, i.e. negative estimates indicate that the probability of observing a zero catch (for zero-inflated model component) or observing a larger catch (for the count model component) was lower in 2012. Species in which both model component coefficients were significant are bolded. na: not applicable

Species	Mean CPUE \pm SD		Zero-inflated model coefficients		Count model coefficients	
	2011	2012	Estimate \pm SE	p-value	Estimate \pm SE	p-value
Total	1277 \pm 7582	4454 \pm 22005	na	na	1.25 \pm 0.18	<0.005
Sockeye	49 \pm 239	323 \pm 760	-1.09 \pm 0.25	<0.005	1.61 \pm 0.01	<0.005
Pink	10 \pm 91	269 \pm 707	-2.68 \pm 0.26	<0.005	2.04 \pm 0.02	<0.005
Chum	73 \pm 161	209 \pm 451	-0.15 \pm 0.29	0.622	1.03 \pm 0.01	<0.005
Herring	1013 \pm 7572	3612 \pm 22052	-0.73 \pm 0.30	0.026	1.16 \pm 0.01	<0.005
Chinook	4 \pm 9	6 \pm 26	0.14 \pm 0.21	0.566	0.54 \pm 0.49	<0.005
Coho	7 \pm 10	10 \pm 27	0.20 \pm 0.23	0.450	0.39 \pm 0.04	<0.005
Anchovy	1 \pm 3	3 \pm 14	0.29 \pm 0.29	0.381	1.41 \pm 0.10	<0.005
Sand lance	104 \pm 611	5 \pm 42	0.52 \pm 0.29	0.099	-2.62 \pm 0.03	<0.005
Stickleback	14 \pm 76	11 \pm 40	-0.33 \pm 0.21	0.153	-0.43 \pm 0.03	<0.005
Greenling	2 \pm 8	8 \pm 49	0.63 \pm 0.31	0.062	1.95 \pm 0.06	<0.005

plement). Seasonal increases in SST from the beginning of the migratory period through mid-July were similar in both years and the effect of year, as well as the interaction between year and day of the year, were not significant ($\beta_{\text{year}} = -0.10 \pm 1.84$, $\beta_{\text{interaction}} = 0.00 \pm 0.01$; degrees of freedom = 194). A Mann-Whitney test indicated that the total biomass of potential prey items was not significantly different between 2011 and 2012 (Fig. S2). Similarly, there were no significant differences between years in the biomass of individual potential prey taxa (Fig. S2).

Juvenile salmon ocean entry characteristics, growth, and migration speed

Of the 204 juvenile sockeye salmon that were sampled for otoliths, 180 met the criteria required for inclusion in the analysis. Genetic stock identification indicated these individuals originated from 7 nursery lake systems (Fig. 1; Table S1 summarizes the number of samples per population and nursery lake within a year). Based on estimates of EFS abundance in 2010 (the 2012 parental generation), we identified juveniles migrating from Chilko and Shuswap lakes as having a high probability of experiencing freshwater density-dependent effects (EFS abundance in 2010 greater than long term mean plus 1 SD). EFS

abundance in the 5 remaining lakes in 2010 and in all 7 lakes in 2009 (2011 parental generation) was low and individuals were unlikely to experience density-dependent effects (Table S2 in the Supplement).

After accounting for variation among nursery lakes, juvenile salmon captured in the high abundance year (2012) were smaller than those collected in 2011 (mean $FL_{2011} = 106.8$ mm, mean $FL_{2012} = 94.2$ mm). However, the interaction between year and freshwater density was significant in the size at capture model (Table 2), indicating nursery lakes with high spawner abundance in 2010 had a greater difference in marine size between years (Table 2). Juvenile sockeye salmon outmigrating in the high abundance year were also approximately 10 mm smaller at ocean entry (equivalent to a 40–45% difference in mass) and exited the river almost 1 wk earlier on average (Figs. 3 & 4). The interaction between year and freshwater density was significant in the entry size, but not the entry date, model. Therefore, differences in entry size between years were significantly greater in nursery lakes with large 2010 returns, while differences between years in entry date were relatively uniform among lakes (Table 2, Figs. 3 & 4).

Smaller juveniles typically had faster mean growth rates than those that entered at a larger size; however, this effect was not statistically significant

Table 2. Estimated effect sizes of predictor variables from linear mixed models. Fixed effects include freshwater density dependence (absent or present) and year (low marine densities in 2011 or high in 2012). Negative interactions indicate smaller size or earlier entry in 2012 in nursery lakes that also experienced freshwater density-dependent effects in that year. Continuous variables in growth and migration speed models were centered and scaled prior to fitting. Significant effect sizes (95% confidence intervals do not overlap with 0) are shown in bold type. bl: body lengths

Modeled response	Predictor	Effect size	95% confidence interval
Capture size (mm)	Freshwater density- dependence	7.13	−1.44 – 16.33
	Year	0.26	−5.03 – 5.48
	Interaction	−27.75	−35.96 – −19.40
Entry size (mm)	Freshwater density-dependence	−3.46	−17.54 – 10.01
	Year	−4.33	−8.73 – 0.14
	Interaction	−18.48	−24.57 – −12.02
Entry date (day of the year)	Freshwater density- dependence	−0.85	−10.60 – 9.03
	Year	−5.36	−8.55 – −1.96
	Interaction	−0.57	−5.44 – 4.70
Growth (mm d ^{−1})	Entry size	−0.02	−0.06 – 0.01
	Entry date	0.06	0.03 – 0.09
	Year	0.01	−0.05 – 0.08
Migration speed (log bl s ^{−1})	Entry size	0.14	0.04 – 0.25
	Entry date	0.21	0.11 – 0.30
	Year	0.35	0.15 – 0.57

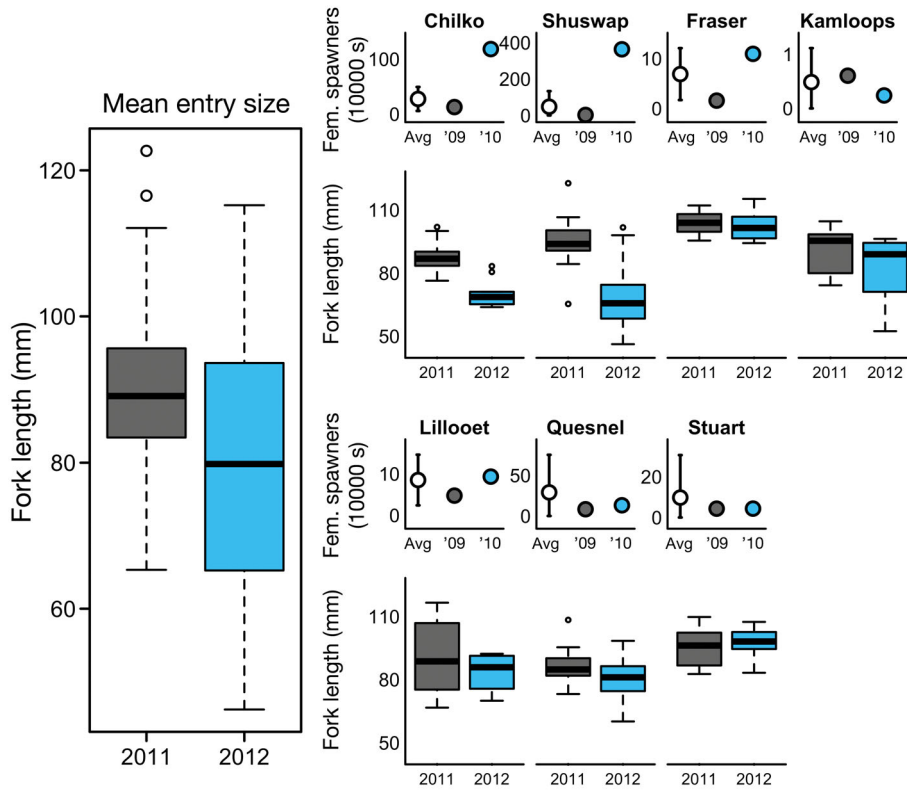


Fig. 3. Estimates of ocean entry size from otolith microstructure for juvenile sockeye salmon captured in 2011 (gray) and 2012 (blue) and effective female spawner abundance in parental generations. Overall estimates of entry size are shown in left-most panel and nursery lake-specific estimates are shown in the second and fourth rows. Dot plots in first and third rows represent effective female spawner abundance from 1973 to 2010 with 95% confidence interval (white), as well as in 2009 (gray) and 2010 (blue). Note that the y-axis scale for spawner abundance figures changes between lakes. Box plots show the median as a center line, the interquartile range as boxes, 150% of the interquartile range (or minimum and maximum values that fall within that range) as whiskers, and all data outside that range as circles

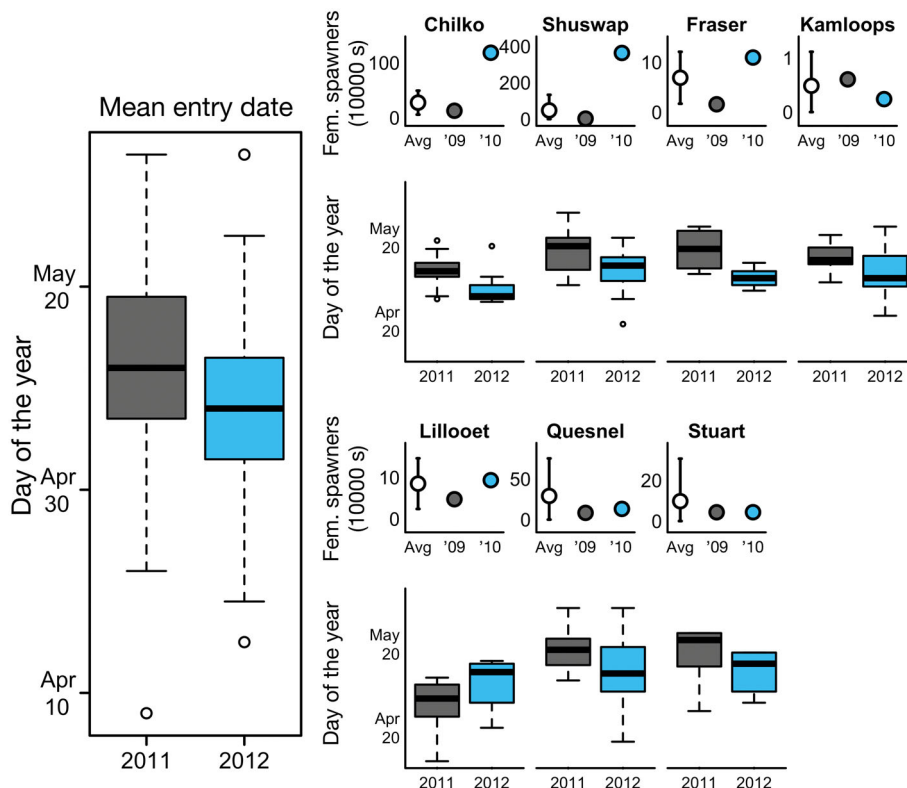


Fig. 4. Estimates of ocean entry date from otolith microstructure for juvenile sockeye salmon captured in 2011 (grey) and 2012 (blue) and effective female spawner abundance in parental generations. Overall estimates of entry size are shown in left-most panel and nursery lake-specific estimates are shown in the second and fourth rows. Dot plots in first and third rows represent effective female spawner abundance from 1973 to 2010 with 95% confidence interval (white), as well as in 2009 (gray) and 2010 (blue). Note that the y-axis scale for spawner abundance figures changes between lakes. Box plots show the median as a center line, the interquartile range as boxes, 150% of the interquartile range (or minimum and maximum values that fall within that range) as whiskers, and all data outside that range as circles

(Table 2, Fig. 5a). Conversely, growth was significantly and positively correlated with ocean entry timing (Table 2). Individuals entering in the latter half of the season grew up to 0.5 mm d^{-1} more than those in the first (Table 2, Fig. 5b). After accounting for variation in entry size and entry date between years, there was no significant difference in marine growth rates between the low and high abundance years (Table 2, Fig. 5; mean $\text{growth}_{2011} = 0.81 \text{ mm d}^{-1} \pm 0.22 \text{ SD}$, mean $\text{growth}_{2012} = 0.80 \text{ mm d}^{-1} \pm 0.16 \text{ SD}$).

Migration speed (bl s^{-1}) was correlated with both entry size and timing (Fig. 6). Larger juveniles had a significantly greater migration speed than smaller

individuals (Fig. 6a, Table 2) and juveniles that entered late in the year had a significantly greater migration speed than those entering early in the year (Fig. 6b, Table 2). After accounting for these relationships, individuals entering the ocean in the high abundance year had a significantly greater migration speed than juveniles entering when densities of fish competitors were low (Fig. 6, Table 2). After accounting for the effect of entry size and date, juveniles in 2012 had a mean migration speed 40 % greater than those entering in 2011. Here we present parameter estimates from a model estimating changes in relative migration speed (i.e. bl s^{-1}); however, when we

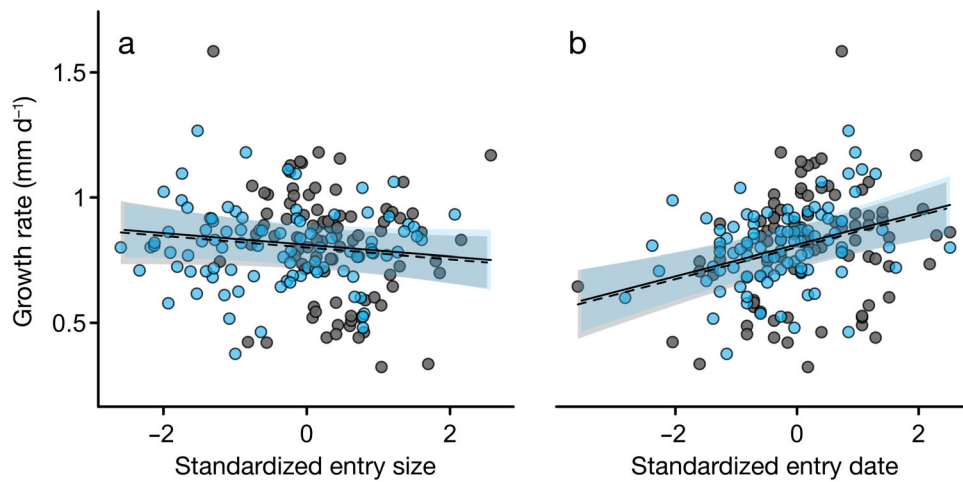


Fig. 5. Estimated mean daily growth rate of juvenile sockeye salmon as a function of (a) entry size and (b) date showing data from a low (gray) and high (blue) abundance year. Shaded regions represent the 95 % prediction intervals of the linear mixed effects model for each year (low density, blue; high density, grey). Prediction intervals incorporate variation among nursery lakes and are calculated holding model covariates at their mean value. Note that x-axis values have been centered and scaled

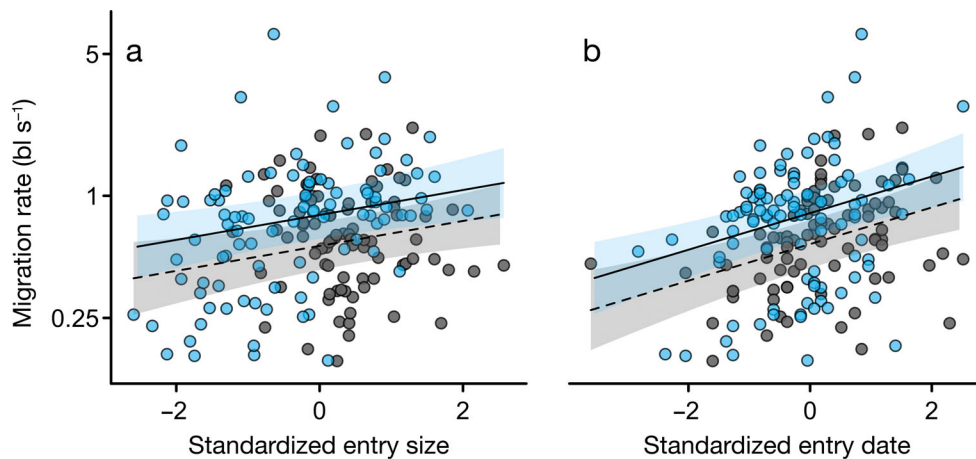


Fig. 6. Estimated mean migration speed of juvenile sockeye salmon as a function of (a) entry size and (b) date showing data from a low (gray) and high (blue) abundance year. Shaded regions represent the 95 % prediction intervals of the linear mixed effects model for each year (low density, blue; high density, grey). Prediction intervals incorporate variation among nursery lakes and are calculated holding model covariates at their mean value. Note that x-axis values have been centered and scaled and that the y axis has been log-transformed. bl: body lengths

modeled absolute migration speed (km d^{-1}) as the response, all parameters remained significant and the patterns were qualitatively similar (Table S3 and Fig. S3 in the Supplement).

DISCUSSION

Competition among and within Pacific salmon species during offshore residence is associated with decreased survival, growth, and size at maturity (Ruggerone et al. 2003, Ruggerone & Connors 2015, Debertin et al. 2017). In this study, we used 2 yr characterized by large differences in the abundance of juvenile Pacific salmon and other pelagic species to test for density-dependent effects in sockeye salmon during the first weeks of marine residence. Juvenile sockeye salmon were significantly smaller at capture during the high abundance year (2012) and exhibited consistent differences in ocean entry characteristics. After accounting for variation among nursery lakes, juveniles sampled during the high abundance year were significantly smaller at ocean entry and outmigrated from freshwater earlier in the year. Differences between years in entry size were correlated with density-dependent effects during freshwater rearing (e.g. Martinson et al. 2008, Rich et al. 2009), while shifts in entry phenology were not. While we did not observe a significant difference in mean daily growth rate between high and low abundance years, juvenile sockeye salmon that entered when densities were high moved away from their ocean entry points at significantly greater rates.

Fraser River sockeye salmon entering the Strait of Georgia in 2012 experienced a considerably higher density of potential competitors than individuals entering the previous year. Mean CPUE of juvenile sockeye salmon increased more than 6-fold between 2011 and 2012. We also observed large increases in the abundance of juvenile pink salmon and chum salmon, species with diets similar to that of sockeye salmon (Brodeur et al. 2007) and potential competitors (Ruggerone & Nielsen 2004, Beamish et al. 2010). Moreover, we found little evidence that the abundance of other zooplanktivorous species decreased to buffer the community from greater juvenile pink and sockeye salmon abundance. The CPUE of Pacific herring, the dominant pelagic forage fish in the Strait of Georgia (Orsi et al. 2007), was significantly greater in 2012 than 2011. Young-of-the-year herring CPUE also increased more than 6-fold in 2012 (Boldt et al. 2015). Juvenile coho salmon and Chinook salmon CPUE was also significantly greater in 2012 than

2011. While estimates of Pacific sand lance and 3-spined stickleback abundance showed an opposite pattern, it is unlikely that the lower CPUE of these 2 species in 2012 compensated for increases in the abundance of the other 8 species given their low abundance relative to other pelagic fish species. We note, however, that our estimates only reflect the abundance of diurnal finfishes and do not account for potential differences between years in the abundance of jellyfish or taxa with diel vertical migrations. Jellyfish in particular may compete with zooplanktivorous fishes for common prey, resulting in lower salmon survival (Ruzicka et al. 2016).

Although the abundance of juvenile sockeye salmon competitors was high throughout the Strait of Georgia in 2012, density-dependent effects during freshwater residence likely varied among nursery lakes due to differences in the abundance of EFS. We assumed individuals rearing in systems with exceptionally high EFS abundances (i.e. Chilko Lake and the Shuswap Lake complex) experienced density-dependent effects, while juveniles in other nursery lakes did not. We recognize that EFS abundance is an imperfect proxy for freshwater rearing densities, but feel previous studies justify its use here. The relationship between spawner and juvenile abundance has been modeled for Quesnel, Chilko, and Shuswap lakes (DFO 2014). In each lake, a standard Ricker stock–recruit relationship between EFS and the abundance of sockeye salmon fry provides reasonably strong predictive power ($R^2 = 0.4\text{--}0.8$; DFO 2014). Although these models indicate per capita productivity is reduced when spawner abundance is high, there is still substantial variability in fry abundance (DFO 2014). Fry and smolt abundance estimates indicate that 2012 juvenile abundance in Chilko and Shuswap lakes was the third highest and highest on record, respectively, while the abundance of Quesnel juveniles was below average (DFO 2014).

We used differences in salmon abundance among years and nursery lakes to test for the presence of density-dependent effects during both freshwater and marine residence. As previously observed by Neville et al. (2013), juvenile sockeye salmon captured at sea were significantly smaller in 2012 relative to 2011. We determined that shifts in size were mirrored by differences in ocean entry traits. The mean size of individuals at ocean entry in 2012 was approximately 10 mm smaller than those in 2011, while mean ocean entry date was approximately 1 wk earlier. The interaction between high EFS abundance and capture year had a significant, negative effect on entry size, indicating that differences in

ocean entry size were greatest in Chilko Lake and the Shuwap Lake complex. This evidence of freshwater density-dependent effects is supported by data suggesting below-average early freshwater survival and juvenile salmon body mass preceding the 2012 outmigration in these 2 systems (DFO 2014). Although ocean entry date was significantly advanced in the high abundance year (2012), the interaction between year and high EFS abundance was not significant, indicating that this shift was relatively uniform across nursery lakes. Interannual variation in outmigration phenologies within sockeye salmon populations may be more strongly linked to regional environmental drivers, such as temperature or flow (Achord et al. 2007), than juvenile densities.

After accounting for the effect of entry size and date, sockeye salmon that outmigrated during the high abundance year (2012) did not grow at a significantly different rate from those captured in the low abundance year (2011). Evidence suggests competitive interactions among Chinook salmon are moderated by estuarine habitat quality (David et al. 2016). Since productivity in the Strait of Georgia appears to be predominantly regulated by bottom-up mechanisms (Preikshot et al. 2013), juvenile sockeye salmon may only experience density-dependent growth in years with poor environmental conditions. This result is also consistent with evidence from returning spawners that the effects of offshore competition outweigh interactions during the first ocean year (e.g. Ruggerone & Connors 2015).

Individual characteristics at ocean entry had mixed effects on growth. For instance, individuals that entered later in the year grew more rapidly than those entering earlier. Greater growth later in summer may be linked to increases in zooplankton prey availability between May and July (Mackas et al. 2013), which occur 1–2 mo after the initial spring phytoplankton bloom in early April (Allen & Wolfe 2013). Conversely, growth was weakly and negatively correlated with ocean entry size. Although this relationship was not significant, similar growth rates across size classes and between years indicate smaller-bodied salmonids remain capable of growing quickly (reviewed in Marco-Rius et al. 2012), even when competitor densities are high.

Despite similar growth rates, we observed significant increases in migration speed in the high-density year. Consistent with previous observations (Freshwater et al. 2016b), the migration speed of juvenile sockeye salmon within a given year was strongly correlated with ocean entry characteristics—individuals that were larger or that entered later in the year

migrated away from their ocean entry points at a significantly greater rate. After accounting for variation in entry timing and date, juvenile sockeye salmon that entered the ocean during the high abundance year migrated at a significantly greater rate than those in 2011 (~40 % faster in bl s^{-1}). Shifts in migration speed are consistent with previous evidence that juvenile salmon migratory patterns are influenced by local conditions. For example, the marine distribution of Columbia River chinook salmon is linked to dynamic environmental conditions such as sea surface temperature and primary productivity that moderate geospatial cues (Burke et al. 2013). Both the spatial distribution of high CPUE sampling sites (Neville et al. 2013) and the probability of non-zero sockeye salmon catches were greater in 2012, suggesting increases in mean migration speed were linked to greater dispersal within the Strait of Georgia. However, given the data that can be collected from otoliths (i.e. mean linear distance travelled per day), we cannot exclude the possibility that individuals also migrated out of the Strait of Georgia more rapidly. Regardless, either greater dispersal to local habitats or a more rapid migration is consistent with individuals altering their movement patterns to reduce competitive interactions (Matthysen 2005, Chapman et al. 2012) and may have contributed to stable growth rates between years.

We recognize that our analysis would benefit from a greater number of sampling years, spanning a greater range of observed densities. However, we believe this study's broad conclusions remain valid. First, alternative time series of juvenile salmon abundance (Neville & Sweeting 2013), as well as the abundance of spawners in the parental generations (DFO 2014), suggest that 2011 and 2012 represented anomalously low and high density years. Since these years likely represent reasonable lower and upper bounds of juvenile abundance in the Strait of Georgia, they should also provide a realistic threshold for density-dependent effects. A second issue is that differences between years in conditions unrelated to salmon abundance may have confounded our tests for density-dependent effects. While we cannot reject this possibility conclusively, both 2011 and 2012 exhibited comparable seasonal increases in sea surface temperature and were cooler than the long-term average (Masson 2013), conditions that are generally considered favorable for juvenile salmon survival in British Columbia (DFO 2014). We also did not detect significant differences in the biomass of potential prey taxa between years. Although we were unable to complete a detailed examination of differ-

ences in prey quality between years, the Strait of Georgia zooplankton community does not periodically shift to lipid-poor species and species diversity remains fairly stable interannually (Mackas et al. 2013). The years we observed also did not exhibit anomalously high or low zooplankton biomass relative to previous long-term averages (Mackas et al. 2013), indicating foraging conditions throughout the strait were probably fair.

Overall, our findings indicate sockeye salmon out-migrating during a year of exceptionally high juvenile salmon and pelagic finfish abundance exhibited consistent differences in size associated with shifts in ocean entry characteristics, not differences in marine growth. Despite many million more juvenile salmon rearing in the Strait of Georgia, we did not observe lower growth rates in 2012. Conversely, juvenile sockeye salmon migrated from ocean entry points significantly more quickly in the high abundance year. Faster travel speeds or greater dispersal throughout the Strait of Georgia may buffer juvenile salmon from competitive interactions in nearshore environments and stabilize growth rates. We emphasize, however, that the conclusions that can be drawn with 2 yr of survey data are limited, particularly given that 2011 and 2012 both appeared to be relatively optimal for Pacific salmon growth and survival. If rearing conditions are poor (e.g. high temperatures, mismatch between ocean entry and prey), density-dependent effects on early marine growth may become more severe (Levin et al. 2001). We also note that we predominantly relied on estimates of species abundance from diurnal surveys designed to target juvenile salmon and our ability to accurately characterize the pelagic community may be limited. To better understand potential density-dependent effects during marine rearing, future studies should examine years representing a greater range of environmental conditions and juvenile densities. Replicating investigations into growth during discrete stages of the migratory period and expanding surveys to sample a larger range of potential competitors will provide important information as to how different population and species assemblages may compete for shared prey resources.

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