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ARTICLE

Early Ocean Life History of Harrison River Sockeye Salmon and their Contribution to the Biodiversity of Sockeye Salmon in the Fraser River, British Columbia, Canada

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Abstract

During a study of the early marine survival of Chinook Salmon *Oncorhynchus tshawytscha* and Coho Salmon *O. kisutch* in the Strait of Georgia from 1998 to 2010, moderate abundances of juvenile Sockeye Salmon *O. nerka* were observed to remain in the strait much longer than previously thought. In 2008, DNA stock identification showed that these juveniles were from the Harrison River, a population with a sea-type life history in which juveniles enter the ocean during the year of emergence from the gravel. Using information collected in 1998–2010, we describe the early ocean life and production of Harrison River sea-type Sockeye Salmon. Juveniles entered the Strait of Georgia from the Fraser River over an extended period, with most entering after mid-July—about 8 weeks later than lake-type juveniles, which had virtually all left the strait by that time. The September diets of sea-type juveniles were highly selective for hyperiid amphipods, which were not abundant in the zooplankton. Interaction with juvenile Pink Salmon *O. gorbuscha* during this early marine period was identified as potentially affecting the age structure of returning adults. Juvenile Sockeye Salmon remained in the strait until the fall and then moved offshore, where they remained until returning as age-3 or age-4 adults. There was a strong positive relationship between the September CPUE of juveniles in the Strait of Georgia and the total adult return of Harrison River Sockeye Salmon, indicating that total production in recent years was likely related to conditions in the strait. From 2005 to 2011, Harrison River Sockeye Salmon production exhibited a large increase in comparison with the total production of Sockeye Salmon in the Fraser River system. This recent increase in production of late-ocean-entering juveniles with a sea-type life history identifies the importance of managing for biodiversity of Sockeye Salmon populations within the Fraser River drainage.

Beginning in 1998, a study (Beamish et al. 2000) was conducted to determine the reasons for declining abundances of Chinook Salmon *Oncorhynchus tshawytscha* and Coho Salmon *O. kisutch* entering the Strait of Georgia in British Columbia (Figure 1). Juvenile Sockeye Salmon *O. nerka*,

Pink Salmon *O. gorbuscha*, and Chum Salmon *O. keta* were also studied, but funding limited the amount of effort available to study those three species. An intriguing observation during the study was that in some years, juvenile Sockeye Salmon were present at moderate abundances in the Strait of Georgia

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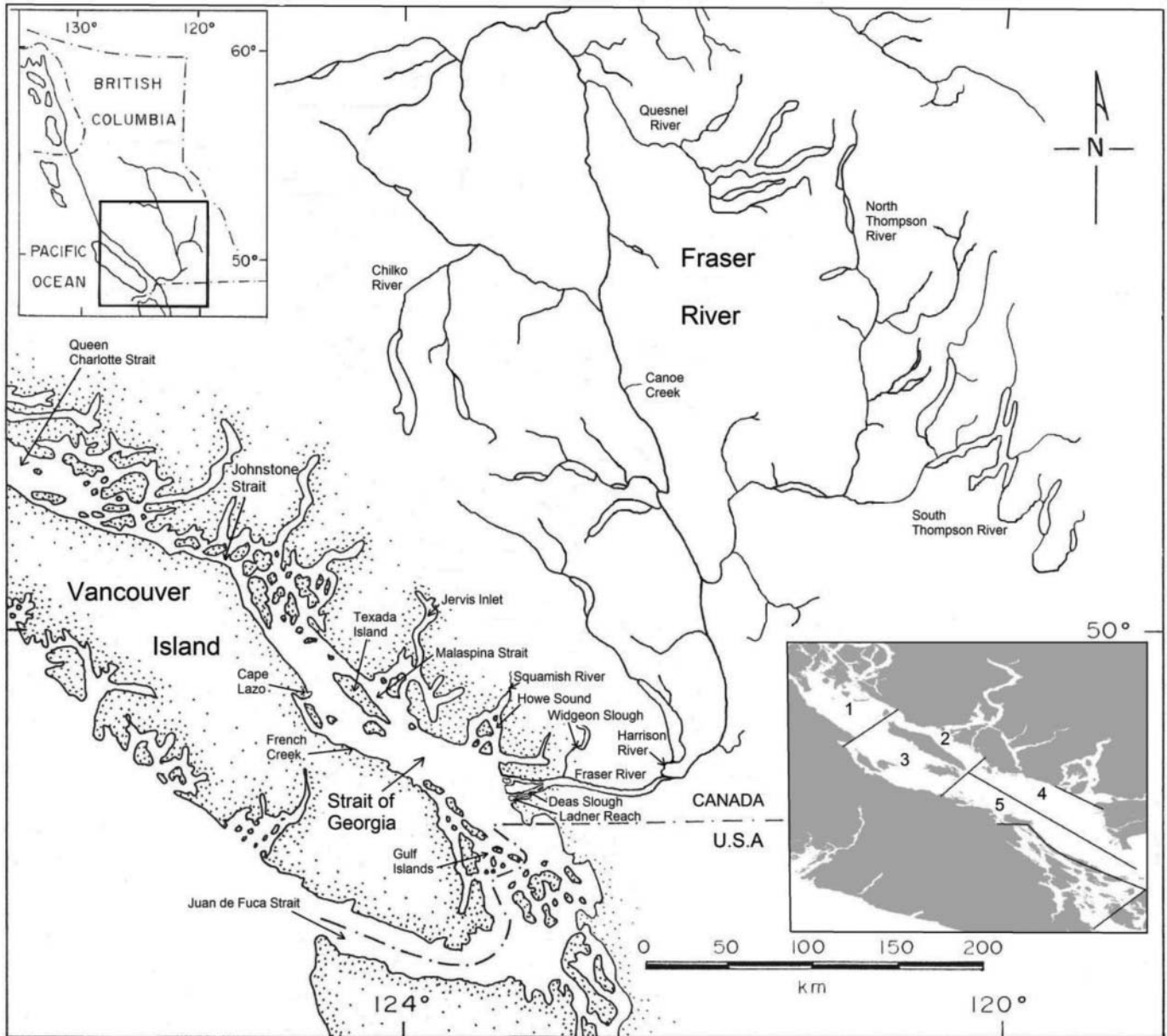


FIGURE 1. Location of the Strait of Georgia and the Fraser River watershed in British Columbia. Key locations are labeled (inset shows numbered areas in the strait that were used to report catches).

until the fall; this observation was in contrast to the prevailing interpretation that juvenile Sockeye Salmon leave the strait quickly after entering it in early spring (Healey 1980; Groot and Cooke 1987; Peterman et al. 1994). When funds for DNA analysis became available in 2008, it was discovered that almost all of the juvenile Sockeye Salmon sampled in September were from a population with a life history differing from that of essentially all other Sockeye Salmon populations in the Fraser River system (Figure 1).

Sockeye Salmon typically have a “lake-type” life history in which fry emerge from the gravel in a river and migrate to a lake, where they rear for 1–2 years before entering the ocean

(Foerster 1954; Burgner 1991). There is also a “sea-type” life history in which juveniles enter the ocean during the year of their emergence from the gravel; although this life history type is found throughout the distribution of Sockeye Salmon, it is generally rare (Schaefer 1951). Some biologists also recognize a “river-type” life history wherein fry do not enter a lake or ocean in their first year after emergence but instead remain in the natal river (Wood et al. 2008).

Gustafson et al. (1997) and Gustafson and Winans (1999) identified sea-type Sockeye Salmon populations from the Harrison River, southern British Columbia (Figure 1), to the Kamchatka Peninsula, Russia, with many of the sea-type

populations occurring in the Stikine and Taku River basins. The sea-type population from the Harrison River, located in the Fraser River drainage (Figure 1), was first reported by Gilbert (1914), who distinguished these fish as a separate population because the scales of returning adults lacked a freshwater annulus. In the Fraser River drainage, another, relatively small, population of sea-type Sockeye Salmon also occurs in Widgeon Slough; as we report later in this paper, the abundance of Widgeon Slough Sockeye Salmon is probably less than 1% of the Harrison River population's abundance. Gustafson and Winans (1999) reported that sea-type Sockeye Salmon were present in the Pitt River, but we have no evidence of their existence in this river or in our samples. Thus, unless otherwise specified, all sea-type Sockeye Salmon described here were assumed to be from the Harrison River.

From 1952 to 2005, Harrison River fish accounted for about 1.1% (on average) of the total Sockeye Salmon production in the Fraser River system (Figure 2A–C). However, from 2005 to 2011, Harrison River Sockeye Salmon represented an average of 6.9% of the total production, including an astonishing 27.9% in 2009 and 27.6% in 2011 (Figure 2C). Harrison River fry (age 0) are known to move downstream and grow in tidal sloughs of the Fraser River estuary (Dunford 1975; Levy and Northcote 1982; Macdonald 1984; Birtwell et al. 1987). Birtwell et al. (1987) identified Deas Slough and Ladner Reach in the lower Fraser River as rearing areas, but little else is known about the life history of Harrison River fish.

Schindler et al. (2010) identified the importance of life history diversity for Sockeye Salmon in Bristol Bay, Alaska. The portfolio effect provided by different life histories was shown to increase production of the populations by providing resilience in a changing environment. As the consequences of greenhouse-gas-induced climate change become more severe, it is expected that Sockeye Salmon production in the Fraser River drainage will decline (Healey 2011; Doney et al. 2012). However, an understanding of the early marine life history of Harrison River Sockeye Salmon may assist in determining whether these fish are better adapted to future changes in the Strait of Georgia, thus highlighting the importance of managing for Sockeye Salmon population biodiversity in the Fraser River drainage. Here, we use data that were available to describe the early marine life history of sea-type Harrison River Sockeye Salmon and show that recent “brood year strength” or total production is closely related to juvenile abundance in the Strait of Georgia during late summer. We also examine the impact of co-occurring juvenile Pink Salmon on the age at maturity of Harrison River Sockeye Salmon.

METHODS

Biological sampling.—Juvenile Sockeye Salmon were collected in the Strait of Georgia using a modified midwater trawl with a small-mesh cod end (Beamish et al. 2000; Sweeting

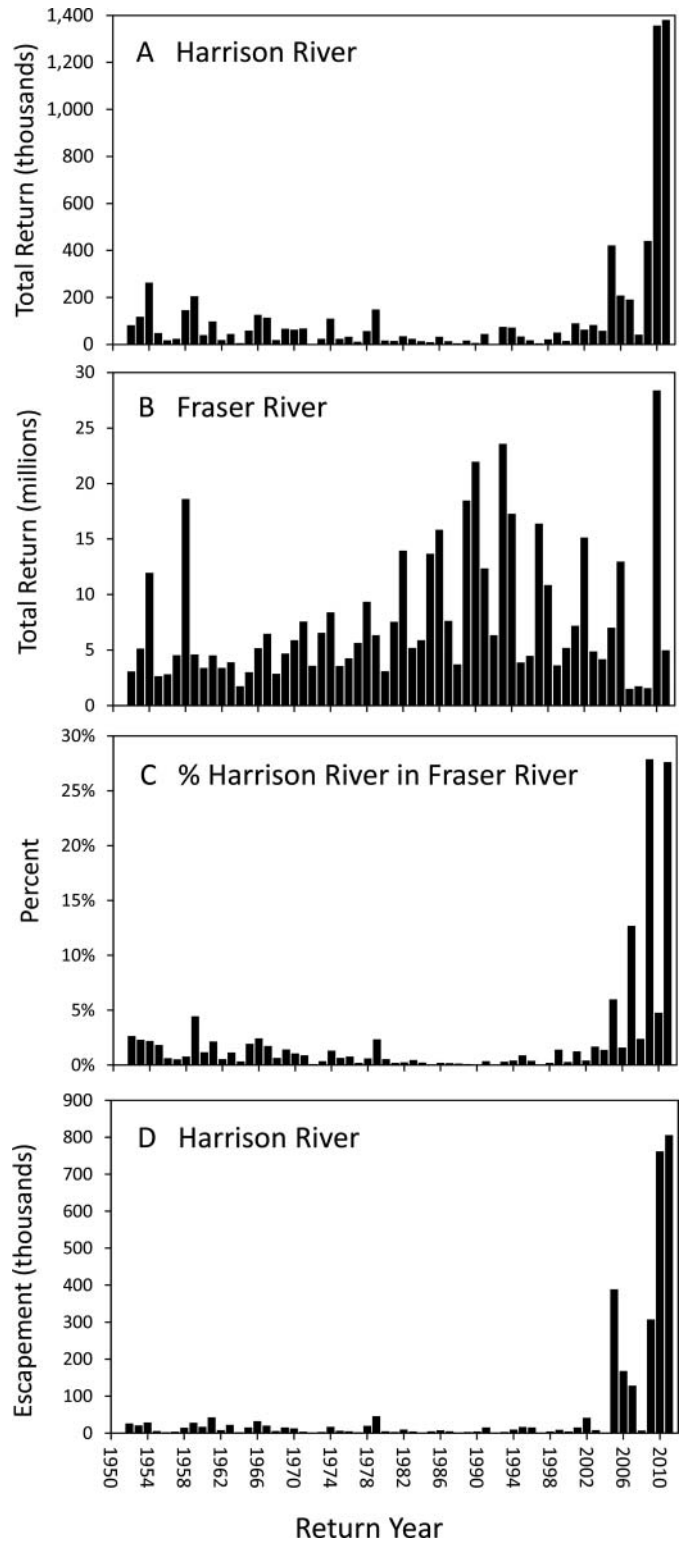


FIGURE 2. Returns and escapement of Sockeye Salmon for the years 1952–2011: (A) total return to the Harrison River, British Columbia; (B) total return to the Fraser River system; (C) percentage of Harrison River sea-type fish in the total Fraser River return; and (D) escapement of sea-type adults to the Harrison River (i.e., number of fish returning to the river in a single year).

et al. 2003). Trawling followed a standard track line that covered 93% of the strait's total area but did not include inlets or the Gulf Islands area (Figure 1). The net was fished at 15-m depth intervals from the surface, with most sets occurring in the uppermost 45 m. Deeper sets were occasionally made to determine whether juvenile Pacific salmon occurred at greater depths. Sets were generally 30 min, and vessel speed was between 2.3 and 2.6 m/s (4.5–5.0 knots). The average net opening was monitored using a scanner trawl eye mounted on the headrope and was approximately 15 m deep × 30 m wide but varied slightly depending on currents. Surveys took place during late June to early July and during September in 1998–2010. Fishing occurred outside the standard survey area (Howe Sound, Jervis Inlet, and Gulf Islands) in some years, and catches from those regions are presented separately to show the extent of juvenile Sockeye Salmon dispersal. Additional surveys sometimes occurred in other months; results from a February 2004 survey and a November 2008 survey are also included here. Juvenile Sockeye Salmon were measured for FL, and their stomach contents were examined and identified fresh at sea. The volume of stomach contents and the percentage contribution of individual prey types (identified to at least the family level) were estimated. All stomach contents were identified by the same person.

One sample of otoliths collected in September 2008 was examined for daily growth zones to determine the number of zones that formed in the ocean prior to the day of capture. All otoliths were mounted sulcus side up on petrographic slides by using thermoplastic cement (Aremco Crystalbond 509). A grinding wheel was used to polish each otolith until the primordia were visible. Two readers counted the zones independently and agreed upon a resolved interpretation of the number of freshwater and marine zones. The interpretation of growth zones required examination of different areas of the otolith section and the use of natural structures within the otolith to facilitate moving counts from one area to another. Freshwater zones on the otolith sections were closely spaced and were characterized by narrow translucent and opaque zones. Marine daily growth zones were wider and exhibited a more prominent translucent zone. The transition area between the freshwater and marine daily growth zones was relatively unstructured and bore no apparent growth zones. Marine growth zones were counted from (1) the first zone that formed closest to the transition area to (2) the outside edge of the otolith section.

Genetic stock composition.—Beginning in 2008, tissue samples from fins of juvenile Sockeye Salmon collected during the standard surveys were stored in a 95% solution of ethanol and were provided to the Molecular Genetics Laboratory at the Pacific Biological Station (Nanaimo, British Columbia). Tissue samples for DNA were also collected during the February 2004 and November 2008 surveys. In the laboratory, 14 microsatellites were surveyed with an Applied Biosystems, Inc. (ABI), 3730 Capillary DNA Sequencer (ABI, Foster City, California), and genotypes were scored with ABI GeneMapper

version 3.0 by using an internal lane sizing standard as detailed by Beacham et al. (2005). The North American portion of the 404-population baseline described by Beacham et al. (2014b) was used for estimation of stock composition and for individual identification. Sample analysis was conducted with a Bayesian procedure (BAYES) as outlined by Pella and Masuda (2001), with a modified, C-based version of the program (cBAYES; Neaves et al. 2005). In the analysis, eight 20,000-iteration Monte Carlo Markov chains of estimated stock composition were produced; initial starting values for each chain were set at 0.90 for a particular population, which was different for each chain, and equal prior probability was used for the remaining populations in the chain. Estimated stock compositions were considered to have converged when the shrink factor was less than 1.2 for the eight chains (Pella and Masuda 2001). The last 1,000 iterations from each of the eight chains were then combined; for each fish, the probability of originating from each population in the baseline was then determined. Individuals were assigned to the specific population with the highest estimated probability of correct assignment. Accuracy of estimated stock composition for Harrison River Sockeye Salmon was described by Beacham et al. (2005, 2014b): 91% of the Harrison River individuals in known-origin samples were correctly identified, even when another sea-type population from the Fraser River (Widgeon Slough; 100% accuracy) was included in the baseline.

Catch per unit effort in surveys and adult return numbers.—The catch of juvenile Sockeye Salmon from each set was standardized to 1 h. The CPUE was defined as the average catch from all standard survey sets conducted in the upper 45 m, as 99.8% of all juvenile Sockeye Salmon were caught from this depth zone. For comparison of the catch distribution, the survey area in the Strait of Georgia was subdivided into five regions (Figures 1, 3). Escapement (number of fish returning to the river in a single year) and total adult return (number of fish from a given brood year that were caught in fisheries or returned to the river as age-3 or age-4 adults) were estimated by the Pacific Salmon Commission (www.psc.org) through mixed-stock analysis of the catch and spawning ground escapement surveys (Grant and MacDonald 2013).

Interactions with Pink Salmon.—The Fraser River serves as one of the major systems for Pink Salmon production, but these fish spawn almost exclusively during odd-numbered years (Neave 1952). Consequently, Pink Salmon fry enter the Strait of Georgia during even-numbered years. The average estimated number of Pink Salmon fry entering the Strait of Georgia from 1984 to 2010 ranged from 350 to 625 million (Beamish et al. 2010); thus, hundreds of millions of juvenile Pink salmon are present in the Strait of Georgia during even-numbered years, whereas very few are present there during odd-numbered years. Relatively large abundances of juvenile Pink Salmon remain until September; during 1998–2008, the CPUE ranged from 26 to 80 fish/h (Beamish et al. 2010). This alternating pattern of abundances provides an opportunity to

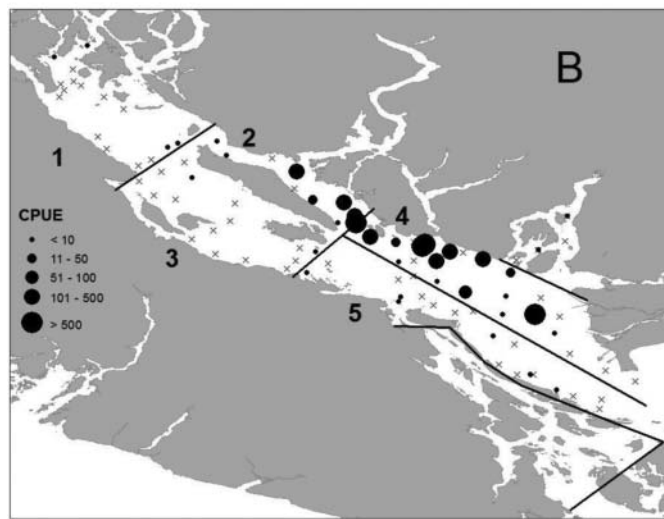
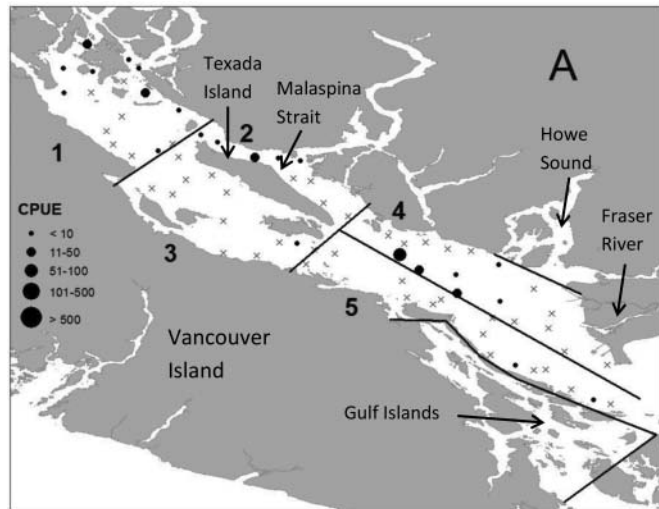


FIGURE 3. Examples of the trawl catch locations and CPUEs (fish/h) of juvenile Sockeye Salmon in the Strait of Georgia during (A) a low-catch year (2006) and (B) a high-catch year (2008). Catches in all years are summarized in Table 1. The strait was divided into five areas (Figure 1) to allow for a comparison of catches (\times = sets with a CPUE of 0 fish/h).

study competitive interactions between juvenile Pink Salmon and the Harrison River sea-type Sockeye Salmon. Age determinations were included in the information provided by the Pacific Salmon Commission.

Zooplankton analysis.—We examined linear relationships and nonparametric Spearman's rank correlations between amphipod percentages in the diets of juvenile Sockeye Salmon and the amphipod biomass in the Strait of Georgia from 1998 to 2010. Estimates of amphipod abundance in the major areas occupied by juvenile Sockeye Salmon during September were derived from 1998–2007 zooplankton data reported by Li et al. (2013); annual estimates of amphipod biomass and hyperiid amphipod biomass in the Strait of Georgia from 1998 to 2010 were obtained from Mackas et al. (2013). The results

of the two studies were compared by de-transforming the data from Li et al. (2013).

RESULTS

Ocean Entry Dates

Some otolith sections were unusable because daily growth zones were not distinguishable. Sections of otoliths from 38 juvenile Sockeye Salmon had daily growth zones of sufficient clarity to allow identification of the first ocean feeding date (capture date minus the number of daily ocean growth zones). Through DNA analysis, all of those individuals were identified as originating from the Harrison River. First ocean feeding occurred from June 6 to July 26 (Figure 4); the numbers of fish with first ocean feeding dates up to July 7 and those with dates after July 7 were equal.

Distribution and Catch in September

Juvenile Sockeye Salmon were captured throughout the Strait of Georgia during September in 1998–2010. In most years, the largest catch of juveniles was obtained from the strait's east side within area 4 below Texada Island (Figure 3A, B; Table 1). High catches were also obtained in Malaspina Strait (area 2) and the southern strait's west side (area 5) during some years (Table 1). The catch of juvenile Sockeye Salmon varied greatly among years, with smaller catches occurring in 1998, 2000, 2001, 2006, and 2010 (Figure 3A; Table 1). Larger catches of juveniles were obtained in 2002–2005 and 2007–2009 (Figure 3B; Table 1), and the CPUE began to increase in 2002 (Table 1).

In Howe Sound, the number of September trawling sets completed was four in 2008, five in 2009, and five in 2010 (Figure 1). The juvenile Sockeye Salmon CPUE in Howe Sound was 4.0 fish/h in 2008, 117.0 fish/h in 2009, and 54.8 fish/h in 2010. In Jervis Inlet, the number of September sets was eight in 2003, four in 2007, and eight in 2008 (Figure 1), yielding CPUEs of 2.8, 10.5, and 12.0 fish/h, respectively. During sampling at the Gulf Islands, the September CPUE was less than 1 fish/h in all years.

Genetic Stock Composition

The DNA samples collected during July surveys from 2008 to 2010 identified very few (0–5%) Harrison River Sockeye salmon from the standard survey area (Table 2). In contrast, juvenile Sockeye Salmon collected from Howe Sound (i.e., outside the standard survey area) during July in 2008–2010 were mostly (70–99%) Harrison River fish (Table 2). By September, the percentages of Harrison River Sockeye Salmon in the Strait of Georgia resembled the percentages observed in Howe Sound during July (Table 2). In 2008, the small percentage (2%) of

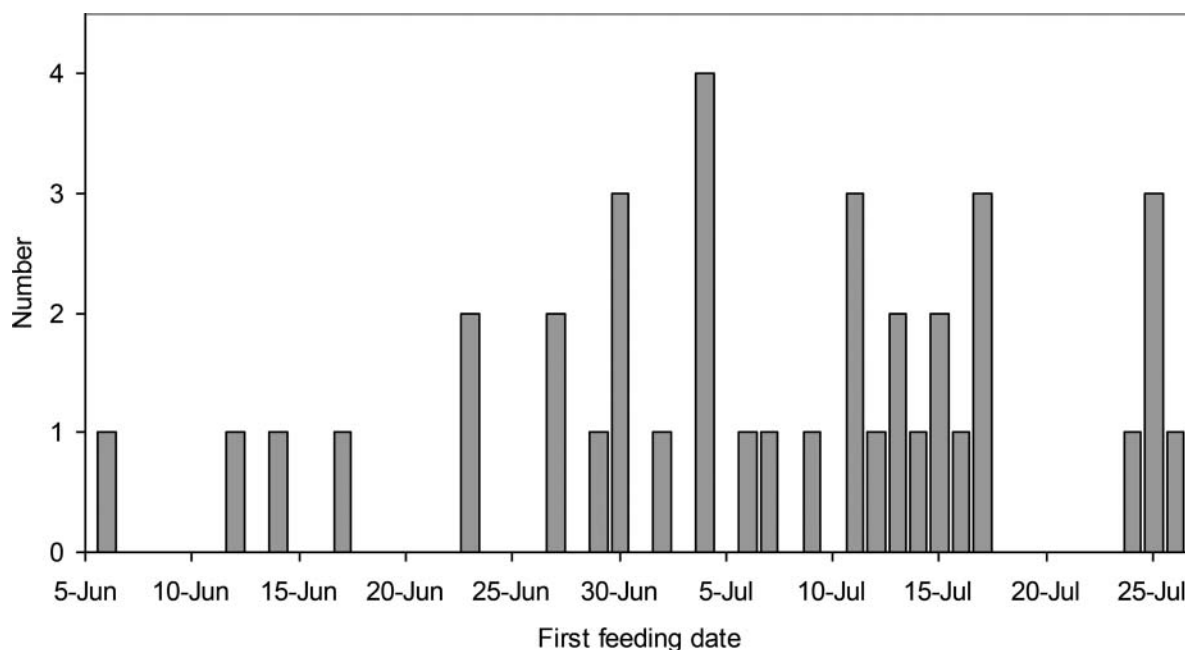


FIGURE 4. First ocean feeding date (estimated from otolith daily growth zones) for Harrison River Sockeye Salmon juveniles that were sampled from the Strait of Georgia during September 2008.

non-Harrison-River Sockeye Salmon was identified as originating from Widgeon Slough (the other sea-type population) and from the Quesnel River in the Fraser River drainage. In 2009, four non-Harrison-River fish were collected, and all were from the Fraser River drainage. In

2010, 18 of the sampled fish were from systems other than the Harrison River, including six locations in the Fraser River drainage (one individual from Widgeon Slough); five of the fish were from Lake Washington in Washington State (Table 3).

TABLE 1. Juvenile Sockeye Salmon CPUE (fish/h) in September trawl surveys conducted within the Strait of Georgia (sampling areas are shown in Figures 1 and 4) during 1998–2010. The number of sets is given in parentheses. The CPUE data are from the standard survey and do not include catches obtained from Jervis Inlet, Howe Sound, or the Gulf Islands region.

Year	Area					Average CPUE for all trawls
	1	2	3	4	5	
1998	0.4 (9)	10.8 (8)	0.5 (16)	7.5 (23)	3.7 (22)	4.5 (78)
1999	0.7 (11)	20.7 (6)	2.7 (15)	36.0 (22)	5.6 (20)	14.4 (74)
2000	1.0 (10)	1.5 (8)	0.8 (20)	1.9 (17)	2.4 (27)	1.6 (82)
2001	0.4 (9)	1.2 (10)	0.4 (19)	5.0 (23)	1.9 (23)	2.2 (84)
2002	0.6 (7)	2.8 (7)	0.8 (17)	59.6 (19)	46.2 (23)	30.2 (73)
2003	1.6 (10)	9.5 (4)	3.4 (18)	121.3 (23)	10.9 (23)	40.1 (78)
2004	0.6 (7)	37.5 (8)	8.2 (15)	26.9 (20)	23.9 (14)	20.3 (64)
2005	0.4 (10)	3.1 (7)	1.8 (6)	40.7 (24)	33.1 (16)	24.5 (63)
2006	3.6 (15)	4.7 (9)	0.2 (11)	8.6 (17)	0.4 (16)	3.7 (68)
2007	1.1 (7)	5.0 (8)	0.2 (12)	129.9 (17)	72.4 (19)	57.9 (64)
2008	0.7 (15)	99.7 (9)	0.5 (16)	332.9 (24)	1.3 (20)	105.9 (84)
2009	0.6 (10)	12.0 (8)	0.1 (14)	59.0 (26)	12.2 (17)	24.5 (75)
2010	1.1 (11)	0.0 (6)	0.7 (15)	3.3 (25)	0.4 (15)	1.5 (72)
Average CPUE	1.1	17.4	1.6	65.9	16.3	25.8
Total number of sets	163	98	194	279	256	990

TABLE 2. Origin of juvenile Sockeye Salmon sampled from trawl catches obtained in the Strait of Georgia and Howe Sound during 2008–2010, as determined by analysis of 14 microsatellite loci (DNA sample size = number of fish sampled).

Location	Date	DNA sample size	Percentage Harrison River origin	Percentage non-Harrison-River origin
Strait of Georgia	Jun 27–Jul 16, 2008	167	5	95
	Jun 26–Jul 7, 2009	140	0	100
	Jul 3–12, 2010	157	4	96
Howe Sound	Jul 21, 2008	89	99	1
	Jul 5, 2009	38	92	8
	Jul 7, 2010	33	70	30
Strait of Georgia	Sep 13–24, 2008	129	98	2
	Sep 16–25, 2009	110	96	4
	Sep 10–23, 2010	52	65	35

Fork Lengths

The mean FL of juvenile Sockeye Salmon in the September catch varied from 118 mm (SD = 15.3) in 2002 to 132 mm (SD = 14.1) in 2010 (Figure 5). The DNA samples collected during September 2008 and 2009 indicated that fish in the FL sample were virtually all from the Harrison River. Normal curves fitted to the FL distributions indicated that the distributions for 2001 and 2005 were bimodal. Mean FLs of the smaller and larger modes were 125 mm (SD = 9.6) and 183 mm (SD = 10.8) in 2001 and were 151 mm (SD = 14.3) and 196 mm (SD = 8.6) in 2005. Harrison River Sockeye Salmon in the 2010 sample (identified using DNA) were significantly smaller (mean = 143 mm FL, SD = 13.4; *t*-test: $P < 0.05$) than fish that originated from a mixture of lake-type stocks (mean = 168 mm FL, SD = 21.5; Table 3).

Juvenile Sockeye Salmon that were captured in Howe Sound during September had average FLs of 112 mm (SD = 9.9) in 2008, 116 mm (SD = 8.5) in 2009, and 127 mm (SD = 11.4) in 2010. The average FLs of Sockeye Salmon captured in Jervis Inlet were 140 mm (SD = 4.7) in 2003, 135 mm (SD = 9.2) in 2007, and 112 mm (SD = 8.3) in 2008. During the

July 2008 survey, the average FL of the 258 juvenile Sockeye Salmon captured from Howe Sound was 69 mm (SD = 7.5), which was significantly smaller (*t*-test: $P < 0.05$) than the average FL (106 mm; SD = 11.0) of the 1,239 juveniles captured during the standard survey in the Strait of Georgia at the same time.

February 2004 and November 2008 Sampling

During February 11–13, 2004, 34 Sockeye Salmon were captured in a trawl that was fished just off the bottom at 45–60-m depth in an area off the northeastern coast of Vancouver Island (between French Creek and Cape Lazo; Figure 1). The FL of those juveniles ranged from 205 to 270 mm and averaged 235 mm (SD = 12.5). Ages were not determined, but FLs indicated that the fish were spending their first winter in the Strait of Georgia. Analysis of DNA was conducted for 33 fish, five of which were identified as Harrison River Sockeye Salmon.

Trawl surveys of the Gulf Islands region, the southern Strait of Georgia, and Howe Sound occurred during November 2008. The Gulf Islands region was surveyed on November 17–18, and 23 sets captured 108 juvenile Sockeye Salmon (CPUE = 10.3 fish/h) with an average FL of 149 mm (SD = 12.6). The results of DNA analysis showed that 98% of the fish originated from the Harrison River; of the remaining fish, one was from Widgeon Slough (sea-type life history) and one was from the Chilko River. On November 19 and 21, the southern Strait of Georgia was surveyed with 14 sets, capturing 103 juvenile Sockeye Salmon (CPUE = 15.8 fish/h). The average FL of juveniles in the southern strait (150 mm; SD = 9.54) was similar to that of fish captured in the Gulf Islands region; 96% of the fish originated from the Harrison River. One of the two non-Harrison-River fish was from Widgeon Slough. Nine sets were made in Howe Sound on November 20, but no Sockeye Salmon were captured.

TABLE 3. Population composition and mean FL (SD in parentheses) of 52 juvenile Sockeye Salmon sampled from trawl catches in the Strait of Georgia during September 2010. All populations except Lake Washington (Washington State) are located in British Columbia.

Population	Sample size	Mean FL (mm)
Harrison River	34	142.9 (13.4)
Pitt River	4	154.3 (12.1)
Dolly Varden Creek	4	181.5 (15.4)
Fennell Creek	2	190.0 (43.8)
Chilko Lake	1	150
Narrows Creek	1	171
Widgeon Slough	1	126
Lake Washington	5	171.8 (6.4)

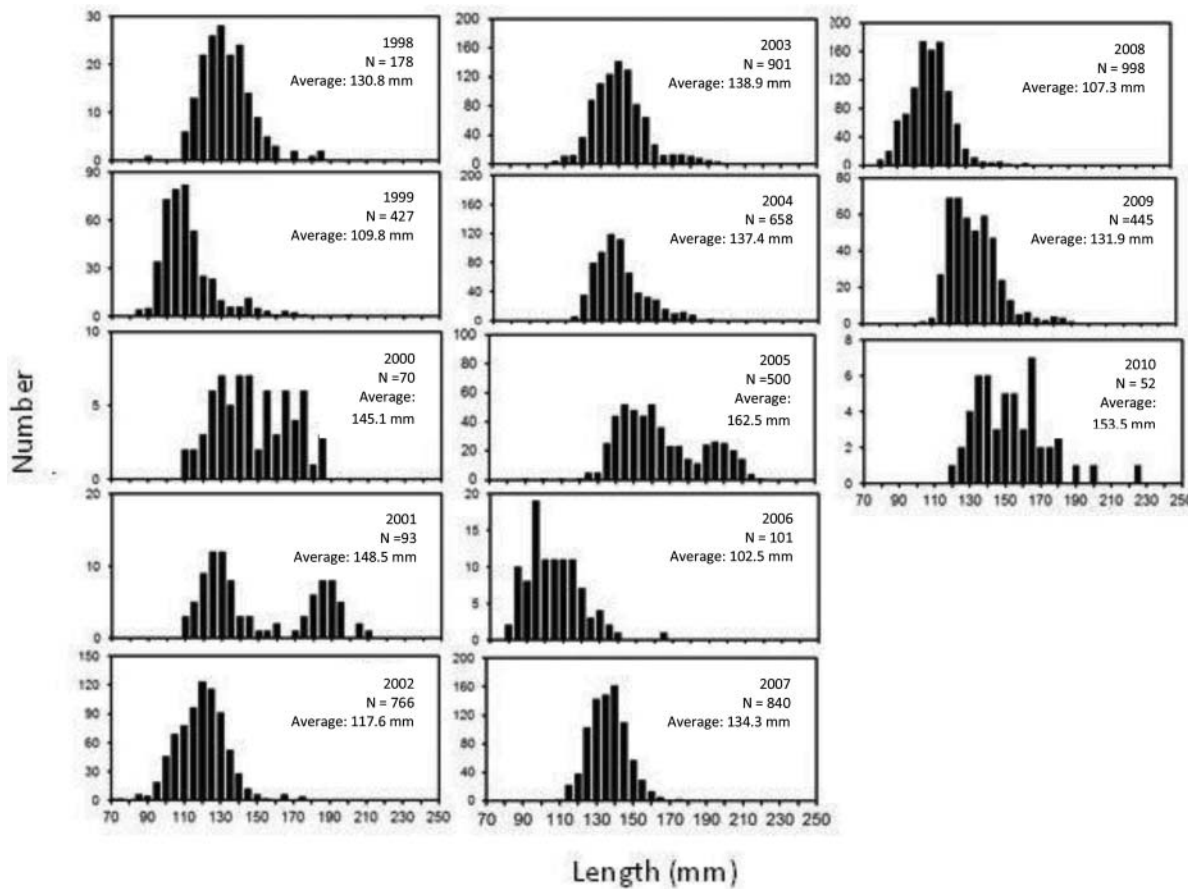


FIGURE 5. Length frequency distributions (FL, mm) and sample sizes of juvenile Sockeye Salmon that were captured in the Strait of Georgia during September of 1998–2010.

Relationship between Catch per Unit Effort and Total Return

The total return of Harrison River Sockeye Salmon was low until 2005 (Figure 2A). Beginning in 2005, there was generally a large increase in total return and escapement (Figure 2A, D). The increase in production also generated an increase in the Harrison River population's percentage contribution to the total return of all Fraser River Sockeye Salmon (Figure 2B, C). We detected no relationship between Sockeye Salmon escapement to the Harrison River in a given year (1997–2009) and the CPUE of juvenile Sockeye Salmon rearing in the Strait of Georgia during September of the next year ($R^2 = 0.00$; Figure 6A). Beginning in 1998, there was a weak linear relationship between the escapement and total return for a given brood year ($R^2 = 0.16$; Figure 6B). We also detected a weak linear relationship between juvenile CPUE and average FL ($R^2 = 0.11$); the relationship was slightly weaker ($R^2 = 0.09$) when individuals from the larger FL distributions in 2001 and 2005 were removed. A strong positive linear relationship was observed between September CPUE and the total

return for the corresponding brood year ($R^2 = 0.85$; Figure 6C).

Ages of Returning Adults

For ocean entry years 1977–2008, the percentage of age-4 fish in the escapement exceeded the percentage of age-3 fish for 20 of the 32 years (Figure 7A). When the comparison was by brood year (which includes two return years) instead of return year (which includes two brood years), the percentage of age-4 fish exceeded the percentage of age-3 fish for 22 of the 32 years. For ocean entry years 1977–1989, the number of years in which age-4 fish exceeded age-3 fish for a given brood year was approximately equal. After 1989, the percentage of age-4 fish exceeded the percentage of age-3 fish in all but 3 years (Figure 7B). After 1989, the age-4 percentage in the escapement oscillated such that the percentage for a given brood year was greater than that for the preceding or subsequent brood year when entry into the Strait of Georgia occurred during an even-numbered year (Figure 7B). This oscillation was most apparent for ocean entry years 1996–2006 (Figure 7B).

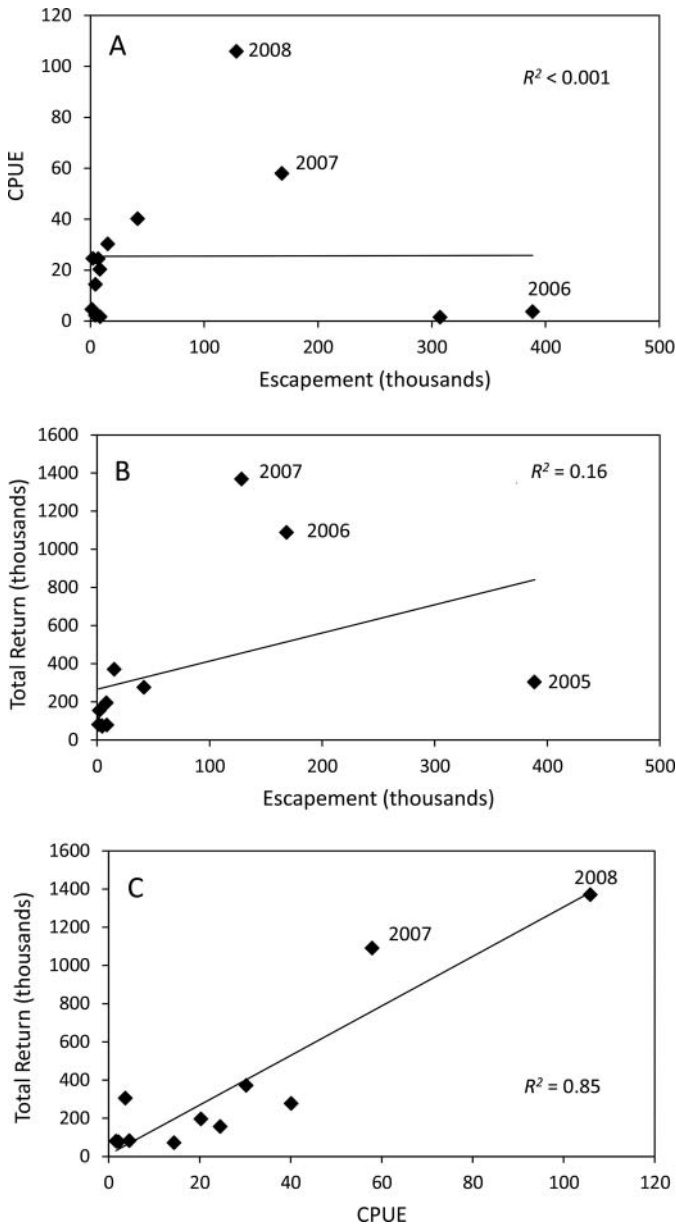


FIGURE 6. Relationships between returns, escapement, and CPUE of Harrison River Sockeye Salmon: (A) escapement (number of fish returning to the river in a single year) and juvenile CPUE during September trawl surveys conducted in the next year (1998–2010; ocean entry years are shown); (B) escapement in 1997–2007 and the total brood year return of age-3 and age-4 individuals produced by that escapement (escapement years are shown); and (C) CPUE and the total return of the brood year that produced the CPUE (1998–2008; ocean entry years are shown). For example, juveniles captured via trawling in 2007 were from the 2006 brood year and would have returned as adults in 2009 and 2010 (age 3 and 4).

Diets

Hyperiid amphipods were the major diet item based on analysis of 2,208 stomachs from juvenile Sockeye Salmon collected during September in 1998–2010 (Table 4). Amphipods averaged 60.5% of the total volume of diet items, ranging

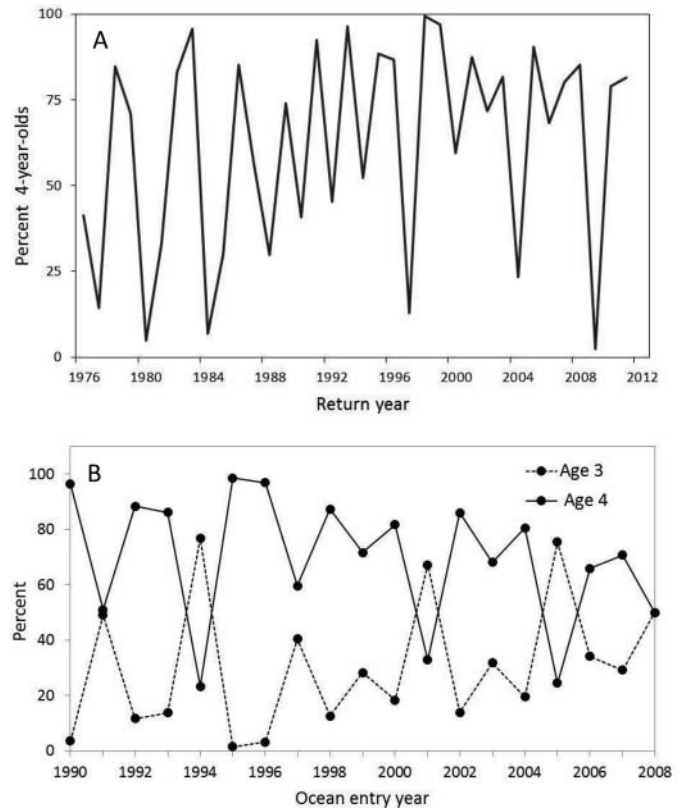


FIGURE 7. (A) Percentage of age-4 Sockeye Salmon returning to the Harrison River, 1976–2010 (age-4 fish were from two brood years); and (B) percentage of Harrison River Sockeye Salmon returning at age 3 (solid line) or at age 4 (dashed line) for brood years 1989–2007 (ocean entry years 1990–2008).

from a low of 33.5% (in 2007) to a high of 81.0% (in 2005). Hyperiid amphipods comprised the bulk of the amphipod component of the September diets, averaging 99.5% of the amphipod volume over the period 1998–2010. Gammarids made up the remaining small percentage (also, one caprellid was found in a single stomach over the 13 years). The dominant hyperiid species in the diet was *Primno abyssalis* (~75% of hyperiid volume) and *Themisto pacifica* (~25% of hyperiid volume).

The next most common diet category (by volume) was the “other” group, averaging 25.5% over the 13 years of study. The “other” category comprised a diverse range of organisms, including calanoid copepods, *Oikopleura*, chaetognaths, insects, polychaetes, and fish. Calanoid copepods were observed during all 13 years, averaging 21.8% in frequency of occurrence but only contributing an average of 8.7% of the total dietary volume. *Oikopleura* and chaetognaths were observed during 12 of the 13 years, making up 8.6% and 2.2% of the total volume, respectively; *Oikopleura* was found in 15.8% of the stomachs examined, and chaetognaths were observed in 8.3% of the stomachs. Insects were found in the stomach contents during 9 of the 13 years but were always present in less than 10% of the stomachs, and they only

TABLE 4. Diet composition (% of total volume) based on analysis of stomach contents from juvenile Sockeye Salmon sampled via trawling in the Strait of Georgia during September of 1998–2010.

Year	Prey group				Number of stomachs examined
	Amphipods	Decapods	Euphausiids	Other	
1998	65.8	1.6	4.1	28.5	135
1999	72.9	5.7	1.9	19.7	153
2000	69.2	1.9	5.0	23.9	36
2001	60.0	4.5	18.8	16.7	66
2002	41.4	0.6	14.1	43.8	200
2003	63.7	1.5	5.5	29.3	258
2004	65.1	2.0	14.8	18.1	331
2005	81.0	3.6	5.6	9.8	208
2006	69.3	8.8	15.9	6.0	103
2007	33.5	5.4	6.8	54.4	302
2008	61.5	0.7	10.6	27.2	207
2009	48.2	11.3	15.6	24.9	165
2010	55.2	1.0	14.4	29.4	44
Average	60.5	3.7	10.2	25.4	
SD	13.1	3.3	5.6	12.7	

contributed 1.7% of the total volume, on average. Polychaetes were observed during 8 of the 13 years, averaging 2.4% occurrence and 1.4% of the diet volume. A number of other organisms (*Clione*, ctenophores, gastropods, harpacticoids, *Limacina*, mysids, juvenile octopus, ostracods, and pteropods) also were included in this catch-all category, but none exhibited any consistency or large volume in the diet. Euphausiids (primarily *Euphausia pacifica*) comprised the third most common category. Together, amphipods, euphausiids, and “other” contributed approximately 96% of the average dietary volume. Decapods (primarily crab megalopae and zoeae) made up 3.7% of the overall diet volume. The contribution of juvenile or larval fish to the September diet was minimal, as this prey type was observed during only 4 of the 13 years and represented only 0.4% of the dietary volume.

Both linear regression and nonparametric Spearman’s rank correlation showed a positive relationship between amphipod biomass in the Strait of Georgia and the proportional contribution of amphipods to the diets of juvenile Sockeye Salmon. The biomass of all amphipods in the strait during September of 1998–2007 (Li et al. 2013) and the annual biomass of hyperiid amphipods in the strait during 1998–2010 (Mackas et al. 2013) exhibited positive linear relationships with the corresponding proportions in the diet, although not significantly so ($R^2 = 0.01$, $P = 0.80$ for the data from Li et al. 2013; $R^2 = 0.08$, $P = 0.35$ for the data from Mackas et al. 2013; Figure 8A, B). Spearman’s rank correlation also confirmed a weakly positive relationship (correlation coefficient $\rho = 0.39$ for the data from Li et al. 2013; $\rho = 0.22$ for the data from Mackas et al. 2013).

DISCUSSION

Ocean Entry

We used DNA stock identification to show that Harrison River Sockeye Salmon were rarely found in open waters of the Strait of Georgia before mid-July. During the period up to and including mid-July, lake-type juveniles, which dominate the Fraser River Sockeye Salmon populations, were resident in the Strait of Georgia (Preikshot et al. 2012). In fact, virtually all lake-type juvenile Sockeye Salmon had left the Strait of Georgia by mid-July. The otolith daily growth zone study was only conducted in a single year; however, it indicated that first feeding in the ocean occurred from June 6 to July 26 for individuals caught during September in the strait’s open areas, thus supporting the observation that Harrison River fish enter the ocean later than lake-type fish. We also showed that (1) first feeding occurred before most of the juveniles appeared in trawl catches in the open waters of the strait and (2) ocean entry extended over a period of at least 2 months. Birtwell et al. (1987) reported that juveniles from the Harrison River were 31–33 mm FL and first arrived in the Fraser River estuary as early as late April, with most occurring there between June 6 and July 4. The late-April FLs of those juveniles (Birtwell et al. 1987) were about one-half the size of the Harrison River Sockeye Salmon captured from the Strait of Georgia and Howe Sound during July (present study), indicating considerable estuarine growth before the fish exit into more open-ocean areas. Small numbers of juveniles that were most likely sea-type fish occurred in the river as late as October (Birtwell et al. 1987), showing that movement into the Strait of Georgia is prolonged and can take place over about 6 months. Thus,

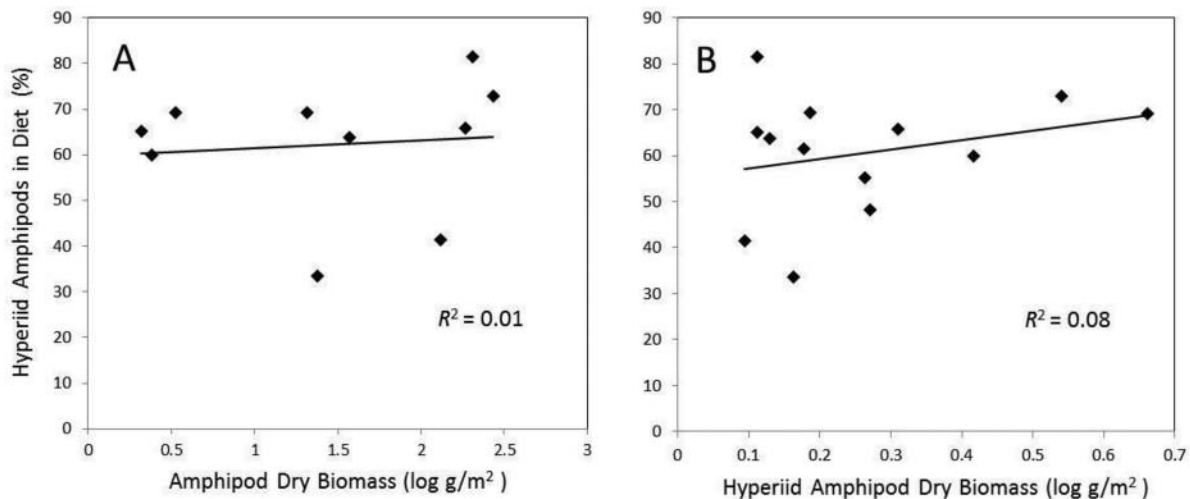


FIGURE 8. Relationships between the percentage contribution (by volume) of hyperiid amphipods to the diets of juvenile Harrison River Sockeye Salmon sampled from the Strait of Georgia and (A) dry biomass of amphipods in zooplankton samples collected from the strait during September 1998–2007; or (B) average annual dry biomass of hyperiid amphipods sampled in the strait during 1998–2010.

most of the Harrison River Sockeye Salmon enter the open-ocean areas within the survey area after about mid-July—approximately 8 weeks later than the average entry time for lake-type Sockeye Salmon and after virtually all of the lake-type juveniles have left the strait (Preikshot et al. 2012). Ocean entry of the sea-type Sockeye Salmon also occurs over a longer period than that of lake-type fish.

After leaving the estuary, juvenile Sockeye Salmon from the Harrison River were commonly found in Howe Sound (Table 2). By September, 65–99% of the juvenile Sockeye Salmon captured in the Strait of Georgia were from the Harrison River, and they were found throughout the strait; the largest concentrations occurred on the strait's east side, including Jervis Inlet. Stockner et al. (1979) reported that the east side of the strait had high levels of plankton production due to advection of phytoplankton from the productive boundary waters to the southwest and the resupply of nutrients via periodic deepwater mixing events.

The Squamish River (Figure 1) flows into Howe Sound and is one of the largest rivers in British Columbia. Like the Fraser River, it is fed mainly by snowmelt, resulting in maximum discharge during early summer (Thomson 1981) at approximately the time that the Harrison River juvenile Sockeye Salmon begin leaving the Fraser River (i.e., late June and early July). The movement of these juveniles into Howe Sound may reflect a preference for low-salinity water. The preference of sea-type juveniles for lower-salinity areas early in their life and after colonizing rivers is believed to have led to the development of the lake-type life history, as proposed by Gustafson et al. (1997). Thus, due to a preference for low salinity and possibly the presence of abundant prey, the Harrison River juveniles initially migrate into Howe Sound in a manner analogous to the migration of lake-type fry into a lake.

Residence Time in the Strait of Georgia

Preikshot et al. (2012) proposed that the average residence time of the lake-type life history in the Strait of Georgia was 43–54 d, with a minimum of 31–43 d. If most Harrison River Sockeye Salmon are in the strait by the end of July and if most are gone by November, then their average residence time could be about 4 months, or two to three times longer than the average residence time for lake-type Sockeye Salmon. The catches of Harrison River juveniles in southern areas of the Strait of Georgia during November 2008 and their absence from Howe Sound indicate that the juveniles were probably leaving the strait at the south through the Strait of Juan de Fuca. Beacham et al. (2014a) reported that in the fall, Harrison River juveniles were caught off the west coast of Vancouver Island and in the Queen Charlotte Strait area, suggesting that the fish exited the Strait of Georgia via northern and southern pathways but with perhaps a preference for the southern route (i.e., Strait of Juan de Fuca). We caught ocean age-1 Harrison River Sockeye Salmon in the northern Strait of Georgia during winter 2004, indicating that some individuals overwintered in the strait and were probably exiting through Johnstone Strait.

Determination of Total Production

The positive relationship between juvenile Sockeye Salmon CPUE and the total return for a brood year identified the Strait of Georgia as an ocean habitat that has likely had a major influence on total production in recent years. This interpretation was consistent with the poor relationships between a brood year's escapement and either its trawl CPUE or its total return, indicating that the juvenile abundance (CPUE) in September probably was more related to conditions within the Strait of Georgia than to the size of the spawning population. The relationships in Figure 6 (A, B) could follow a Ricker-

type curve that would identify density dependence in the total production trends. We found little evidence of density dependence in the relationship between CPUE and either total return (Figure 6C) or average FL, and the time series was relatively short; therefore, we compared trends by using linear regressions. However, an important issue with the comparison of CPUE and total returns, escapement, or average FL is that during some years, the stock composition in the Strait of Georgia may include stocks other than Harrison River Sockeye Salmon, as was demonstrated by the DNA analysis for 2010 and the bimodal FL distributions in 2001 and 2005 (Table 2; Figure 5). In contrast, when the CPUE of juvenile Sockeye Salmon was large (2008 and 2009), virtually all of the juveniles were from the Harrison River (Table 2). We speculate that in years characterized by low September CPUE, there may be larger percentages of non-Harrison-River Sockeye Salmon. Until more stock-specific information is collected, it is possible only to conclude that recent conditions in the Strait of Georgia were likely a major contributor to the improved production.

It is possible that freshwater survival was exceptionally high during the years that we observed a large September CPUE in the Strait of Georgia; if so, then escapement would not be an index of smolt abundance. We have no measure of freshwater survival; however, if freshwater survival improved for the sea-type life history, it apparently did not improve—or failed to improve at the same level—for the lake-type life history, as evidenced by the increased percentage of Harrison River individuals in the total return of Sockeye Salmon during recent years. Furthermore, Irvine and Akenhead (2013) demonstrated that Sockeye Salmon smolts from Chilko Lake (Fraser River drainage) had a declining survival trend from 1992 to 2008 but with no indication of an increasing abundance trend over the same period. Thus, we believe that a site-specific change in freshwater survival is unlikely to explain the strong relationship between juvenile CPUE in the Strait of Georgia and the total return of Harrison River Sockeye Salmon.

2006 Brood Year

During spring 2007, a synchronous failure of survival in juvenile Pacific Herring *Clupea pallasii* and Pacific salmon was observed in the Strait of Georgia (Beamish et al. 2012). Juveniles of those species accounted for almost 98% of fish sampled in the top 30 m during daytime in the spring (Beamish et al. 2012). The early marine survival of lake-type Sockeye Salmon from the Fraser River drainage was exceptionally poor during 2007, resulting in a historically low adult return for 2009 (Thomson et al. 2012). The cause of the poor survival and (for some species) poor growth was the anomalous weather (climate) and ocean conditions that produced a very shallow mixing layer (Thomson et al. 2012). The shallow mixing layer probably resulted in poor plankton production after the spring bloom and reduced the availability of prey for the

first-feeding juveniles (Beamish et al. 2012; Thomson et al. 2012). In contrast to the poor production of Pacific Herring and Pacific salmon that entered the Strait of Georgia during spring, the CPUE of Harrison River Sockeye Salmon juveniles in September 2007 was the second-highest CPUE observed in all trawl surveys during the study, and the subsequent total return of adults from the 2006 brood year (i.e., returning in 2009 and 2010) was the third highest in recorded history. The reason for the improved production of late-ocean-entering Harrison River juveniles was not determined, but we speculate that a return to more average weather and ocean conditions during summer 2007 (Thomson et al. 2012) resulted in better secondary plankton production as well as reduced competition and possibly reduced predation.

Age at Return and Interaction with Juvenile Pink Salmon

Most of the Harrison River Sockeye Salmon adults return at age 4, but a varying percentage of fish return at age 3. In the last two decades, there has been an imperfect but clearly recognizable pattern of more Sockeye Salmon returning at age 4 if, as juveniles, they had coexisted with juvenile Pink Salmon in the Strait of Georgia during even-numbered years (Figure 7B). The pattern is particularly apparent for brood years that entered the strait from 1996 to 2006. Competition for food or an interaction that reduces feeding efficiency may alter the energy balance (Duffy and Beauchamp 2011) in a way that changes the age at return for some individuals. An influence on the age at return would be a sublethal effect; there is evidence that large abundances of juvenile Pink Salmon can affect the survival of other Pacific salmon species. Many studies have identified the impacts of Pink Salmon on other species. For example, Ruggerone and Nielsen (2004) found that abundances of juvenile Pink Salmon from the Fraser River lowered the marine survival of juvenile Chinook Salmon in Puget Sound during even-numbered years. Smoker (1984) also identified an impact of Pink Salmon on Chum Salmon age at maturity. Recently, Scheuerell (2005) reported that the rate of growth between emergence and smoltification can affect the age at maturation in Chinook Salmon. Thus, competition with Pink Salmon could reduce prey availability, requiring the expenditure of more energy to find prey. An intriguing possibility is that a reduction in energy storage during the early marine stage could influence the processes that regulate the age at return 2–3 years after the juveniles leave the Strait of Georgia. However, the larger abundances of juvenile Pink Salmon during even-numbered years could lead to competition in areas outside of the Strait of Georgia, as proposed by Blackburn and Tasaka (1989). It is also possible that the effect of competition occurs both within and beyond the strait.

Diets

In the September surveys, amphipods represented 60.5% of the total volume of all gut contents, and the amphipod volume

consisted almost entirely (99.5%) of hyperiids. Thus, Harrison River Sockeye Salmon demonstrated strong feeding selectivity for hyperiid amphipods, specifically for *P. abyssalis*. However, amphipods only contributed an annual average of 8.2% to zooplankton biomass in the Strait of Georgia (Mackas et al. 2013). Hyperiid amphipods represented only 29.3% of the total amphipod biomass in the strait, and *T. pacifica* (rather than *P. abyssalis*) dominated the hyperiid biomass (Mackas et al. 2013). The dramatically different representation of *P. abyssalis* in the diets of juvenile Sockeye Salmon relative to its role in the zooplankton composition indicated that individual Sockeye Salmon were actively searching for *P. abyssalis*. *Primno abyssalis* is a relatively large hyperiid, with females in the Japan Sea ranging in size from 14 to 23 mm and males ranging from 7 to 9 mm (Ikeda 1995); in contrast, *T. pacifica* in the same area are rarely larger than 8 mm (Yamada et al. 2004). The size difference may be an important contributor to the difference in diet composition, as the larger *P. abyssalis* could make feeding more efficient for the young Sockeye Salmon. With no available time series data for *P. abyssalis*, we were able to show a weak positive relationship only between the amphipod percentage in the diet and the amphipod biomass in the zooplankton. Although the relationship was weak and nonsignificant, an increase in *P. abyssalis* abundance is a possible explanation for the improved production of Harrison River Sockeye Salmon, and the plankton sampling may have been inadequate for measuring the abundance of *P. abyssalis*. Schabetsberger et al. (2003) found that hyperiid amphipods were the dominant group consumed by juvenile Coho Salmon and Chinook Salmon in offshore areas of the Columbia River plume; they also found that juvenile Pacific salmon were highly selective for a particular species of hyperiid amphipod. Although that hyperiid species was not *P. abyssalis*, it was also less abundant than other species in the zooplankton. Using the report of Madin and Harbison (1977) that hyperiid amphipods are associated with gelatinous zooplankton, Schabetsberger et al. (2003) hypothesized that aggregations of gelatinous zooplankton may facilitate the feeding on hyperiid amphipods. We hypothesize that an increase in gelatinous zooplankton in the Strait of Georgia may be related to the improved production of hyperiid amphipods and, in turn, the increased productivity of Harrison River Sockeye Salmon.

The dynamics of amphipod production have not been well studied, but the pelagic amphipod *T. pacifica* in the Strait of Georgia is known to consume copepods, amphipods, cladocerans, and ostracods (Haro-Garay 2004) and to demonstrate a preference for copepods. Johannessen and Macdonald (2009) reported that surface chlorophyll fluorescence in the mid-strait region during 2003 was highest in April, but there were prominent spikes during June and August. The blooms during June and August would be secondary plankton blooms, as previously reported (Parsons and LeBrasseur 1970; Stockner et al. 1979; Harrison et al. 1983),

and could provide prey for amphipods. Johannessen and Macdonald (2009) proposed that future changes in climate would cause secondary plankton blooms to extend later into the summer and early fall, which could increase the availability of prey for amphipods and thus for juvenile Harrison River Sockeye Salmon. In summary, a key to understanding the reasons for the improved production of Harrison River Sockeye Salmon as well as understanding the impacts of a changing climate would be to study the population dynamics of amphipods in general—and *P. abyssalis* in particular—within the Strait of Georgia.

Biodiversity

The productivity of Harrison River Sockeye Salmon, as indicated by total returns, increased at a time that the survival of lake-type fish was declining (Peterman and Dorner 2012). The improved productivity could be related to a larger, more accessible supply of food in the strait as well as reduced predation in the early marine period due to the small size of the Harrison River juveniles. Predators that during May would normally feed on juvenile lake-type Sockeye Salmon entering the Strait of Georgia may have left the area, changed their functional response, or both. It may be relevant that small sub-yearling Chinook Salmon smolts from the South Thompson River (Figure 1) also enter the Strait of Georgia at about the same time as the Harrison River Sockeye Salmon, and they survive much better than the approximately 130 other Fraser River populations of Chinook Salmon, which enter the ocean 6–8 weeks earlier (Beamish et al. 2013).

The late-ocean-entering Sockeye Salmon from the Harrison River provide diversity to Sockeye Salmon production from the Fraser River and make the populations more resilient in a changing ocean environment. Hilborn et al. (2003) and Schindler et al. (2010) described how the preservation of biodiversity in an Alaskan Sockeye Salmon population has been attributed to the species' ability to persist and support fisheries in a changing climate. Not all populations have necessarily flourished at all times, but production has been maintained within the aggregate of populations. Hilborn et al. (2003) explained that this persistence was partly attributable to management strategies that did not necessarily focus on the most productive stocks but rather focused on an array of stocks. Healey (2009) discussed the resilient capacity of Pacific salmon in British Columbia and the importance of having management systems that support the inherent diversity of populations within a species. The recent improvement in production of Harrison River Sockeye Salmon may turn out to be an anomaly or may become an early example of structural changes in fish populations that will occur as climate change alters ocean ecosystems. Importantly, this new information about the ocean life of Harrison River sea-type Sockeye Salmon illustrates how much more we need to understand about the mechanisms regulating their ocean survival.

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