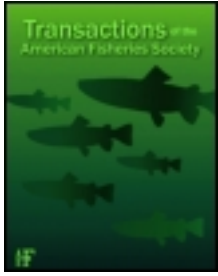


This article was downloaded by: [Michael H. H. Price]

On: 26 June 2013, At: 08:39

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Transactions of the American Fisheries Society

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/utaf20>

Prey Selectivity of Fraser River Sockeye Salmon during Early Marine Migration in British Columbia

Michael H. H. Price^{a b d}, Barry W. Glickman^a & John D. Reynolds^c

^a Department of Biology, University of Victoria, Post Office Box 3020, Station CSC, Victoria, British Columbia, V8W-3N5, Canada

^b Raincoast Conservation Foundation, Post Office Box 2429, Sidney, British Columbia, V8L-3Y3, Canada

^c Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, V5A-1S6, Canada

^d SkeenaWild Conservation Trust, 2115 22nd Avenue, Smithers, British Columbia, V0J-2N6, Canada

To cite this article: Michael H. H. Price, Barry W. Glickman & John D. Reynolds (2013): Prey Selectivity of Fraser River Sockeye Salmon during Early Marine Migration in British Columbia, Transactions of the American Fisheries Society, 142:4, 1126-1133

To link to this article: <http://dx.doi.org/10.1080/00028487.2013.799517>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

ARTICLE

Prey Selectivity of Fraser River Sockeye Salmon during Early Marine Migration in British Columbia

Michael H. H. Price*¹

Department of Biology, University of Victoria, Post Office Box 3020, Station CSC, Victoria, British Columbia V8W-3N5, Canada; and Raincoast Conservation Foundation, Post Office Box 2429, Sidney, British Columbia V8L-3Y3, Canada

Barry W. Glickman

Department of Biology, University of Victoria, Post Office Box 3020, Station CSC, Victoria, British Columbia V8W-3N5, Canada

John D. Reynolds

Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A-1S6, Canada

Abstract

Mortality of salmon during early marine life has long been thought to be a critical factor in limiting overall abundance. One of the key hypotheses proposed to explain the long-term productivity decline of Canada's iconic Fraser River Sockeye Salmon *Oncorhynchus nerka*, is deficient habitat conditions experienced during early marine life. Our study is a first step towards testing this hypothesis, with an aim of understanding food availability and prey choice of juvenile salmon early in their coastal migration. We investigated zooplankton density, diet composition, and foraging selectivity of juvenile Fraser Sockeye Salmon during the 2009 and 2010 migrations and determined whether the timing of their migration was related to feeding success. Sockeye Salmon diets showed high prey diversity and a preference for euphausiid, amphipod, decapod, terrestrial insect, fish, egg, and cumacean prey. Calanoid copepods, the most abundant available prey, were not strongly selected in either year. Zooplankton densities were highest in the tidally mixed Discovery Passage–Johnstone Strait area. The fish appeared to have an adequate prey resource pool during their early marine migration, and in the 2 years of our study we observed similar feeding success throughout the migration period. Importantly, we found no evidence of food limitations that might indicate that juveniles suffered food deprivation. Further research is needed to test the generality of these findings, including the potential impacts of warming ocean temperatures on the timing and availability of prey during migration.

Mortality of salmon during their early marine migration has long been thought to be an important factor limiting their overall abundance (Ricker 1976; Peterman 1982; Beamish et al. 2004). Marine survival of juveniles depends on their early marine growth (Farley et al. 2007; Duffy and Beauchamp 2011), and mortality is hypothesized to occur through interactions between

ocean conditions, food, and predation (Beamish and Mahnken 2001; Beamish et al. 2004).

Sockeye Salmon *Oncorhynchus nerka*, is an economically and culturally important species in the northeast Pacific. Populations of Sockeye Salmon inhabiting southern portions of their range are in decline (IUCN 2009), and those returning

*Corresponding author: pricem@citywest.ca

¹Present address: SkeenaWild Conservation Trust, 2115 22nd Avenue, Smithers, British Columbia V0J-2N6, Canada.

Received October 29, 2012; accepted April 18, 2013

to Canada's iconic Fraser River in particular may be experiencing multiple interacting stressors. The 2009 return of Sockeye Salmon to the Fraser River was the lowest in 50 years, prompting the Canadian government to launch a Can\$26 million Judicial Inquiry to investigate the cause of the decline and identify imminent threats to the survival of Sockeye Salmon (Cohen Commission 2012). Despite a substantial rebound by one year-class in 2010, there has been an overall decrease in productivity of most Fraser River Sockeye Salmon populations since the early 1990s (Peterman and Dorner 2012). Poor habitat conditions experienced during their early marine migration from the Fraser River is one of four hypotheses proposed to explain their recent decline (Peterman et al. 2010; Connors et al. 2012).

The Strait of Georgia, between British Columbia's Vancouver Island and mainland coast, is the primary migration corridor for Sockeye Salmon leaving the Fraser River (Groot and Cooke 1987; Welch et al. 2009, 2011; Price et al. 2011). This coastal sea receives emissions and waste discharge from the activities of several million people (Ross 2006). Aquatic species are exposed to the cumulative effects of pollution, fishing, habitat destruction, invasive species, and climate change (Johannessen and Macdonald 2009). Secondary production in the Strait of Georgia has been declining since 2001, and a change in the zooplankton assemblage may be underway (Johannessen and Macdonald 2009). Importantly, knowledge of the feeding habits and prey abundance for Fraser River Sockeye Salmon during their early migration is incomplete and antiquated, the most recent study having occurred during 1990–1993 (Haegele 1997), the beginning of the modern productivity decline for Fraser Sockeye Salmon.

A panel of expert scientists recently recommended an ecological investigation of the Strait of Georgia to advance our knowledge of the state of Fraser Sockeye Salmon productivity (Peterman et al. 2010). Our study, a first step towards this goal, aimed to understand foraging behavior by juvenile Sockeye Salmon early in their migration at sea. We examined the prey assemblage, diet composition, and foraging selectivity of juvenile sockeye salmon. Furthermore, we investigated whether the timing of migration through the northern Strait of Georgia and southern Johnstone Strait is related to their feeding success and whether food limitations can be detected. More generally, our research attempted to shed light on a relatively unknown phase of salmon life histories, which may be related to productivity of populations.

METHODS

We collected 163 juvenile Sockeye Salmon from inland marine waters of northern Strait of Georgia and southern Johnstone Strait from May 24 to July 7, 2009, and 186 juveniles from May 14 to June 21, 2010 (Figure 1), as part of a broader ecological investigation (see Price et al. 2010, 2011). Each capture location was sampled weekly, and up to 10 juveniles per location per week were retained for diet analysis when

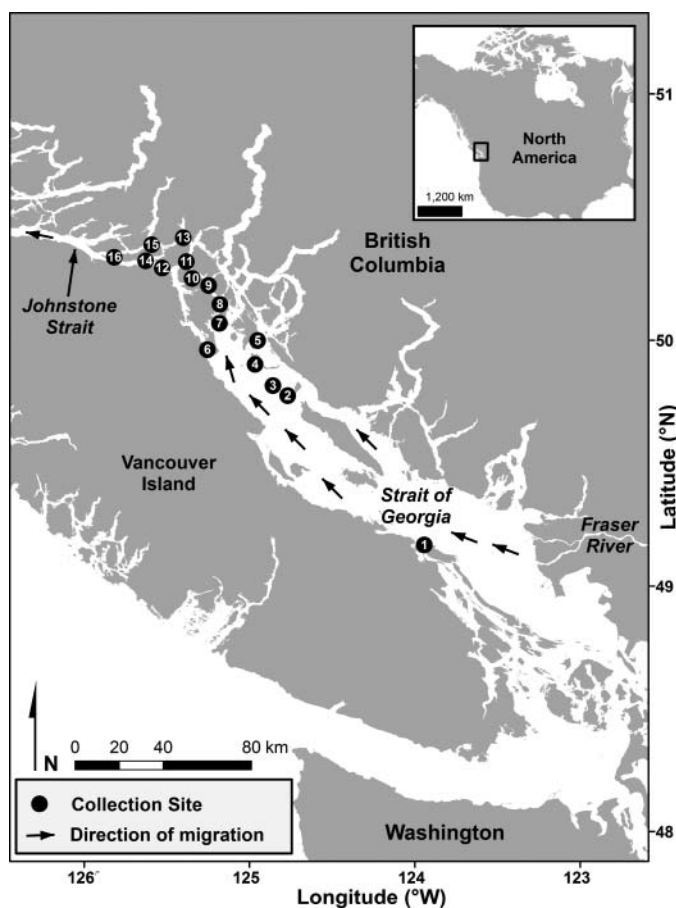


FIGURE 1. Study area of the Strait of Georgia and Johnstone Strait region of British Columbia's south coast showing the migration routes of juvenile Sockeye Salmon from the Fraser River and the sequentially numbered collection sites for those juveniles and zooplankton, as sampled during 2009 and 2010.

the number of fish caught at a site exceeded 50; we did not catch fish at some locations each week (Table 1). The northern Strait of Georgia and southern Johnstone Strait region hosts the largest juvenile Sockeye Salmon migrations on Canada's west coast (Groot and Cooke 1987), and our samples were collected throughout the main migration period of fish that originated from the Fraser River watershed (Welch et al. 2009, 2011; Price et al. 2011). Differences in sampling dates between years reflect differences in migration timing. Given the northbound migration of Sockeye Salmon through the study region, we did not catch fish at the most northern sites during the first 2 weeks, when fish were concentrated in the south, nor did we catch fish at the most southern sites during the final 2 weeks, once fish had migrated north. All fish collections occurred during daylight and crepuscular hours, which is reported to be the primary feeding time of juvenile salmon for this latitude and time of the year (Healey 1991; Landingham et al. 1998). We used a modified purse seine (70 m long, 10 m deep, 6 mm mesh) to capture the fish; after pursing the net, the catch was concentrated in the bunt of the seine, and fish were dip-netted out, euthanized by a swift

TABLE 1. Number of Sockeye Salmon stomachs collected during each sampling month in 2009 and 2010 by location (see Figure 1) and summary statistics (mean and SD in parentheses) for fish and oceanic variables.

Location or measure	2009			2010	
	May	June	July	May	June
1	0	0	0	6	0
2	0	0	0	10	0
3	0	0	0	10	0
4	0	0	0	10	0
5	2	0	0	0	0
6	12	0	0	0	0
7	10	10	0	8	0
8	0	10	10	10	10
9	0	0	0	18	20
10	0	20	0	0	0
11	0	0	9	0	19
12	0	20	0	0	0
13	0	20	0	0	10
14	0	20	0	0	30
15	0	10	0	0	10
16	0	10	0	0	15
Fork-length (cm) ^a	10.8 (1.8)	10.4 (1.2)	10.6 (1.5)	10.2 (1.1)	11.6 (1.3)
Mass (g) ^a	14.3 (9.0)	12.1 (4.2)	13.1 (5.9)	13.0 (3.0)	15.2 (5.2)
Temperature (°C) ^b	14.0 (1.0)	11.2 (1.0)	10.6 (0.6)	11.2 (0.9)	11.1 (1.7)
Salinity (‰) ^b	28.3 (0.8)	29.3 (1.2)	29.2 (0.6)	28.4 (1.0)	28.4 (1.9)

^aSample size equaled the number of stomachs sampled in 2009 and was 93 in 2010.

^bSample size was 12 in 2009 and 18 in 2010.

blow to the head, and placed immediately in 1-L bottles containing a solution of 7% formalin in seawater. In the laboratory, individual fish were weighed and measured (fork length) prior to removing stomachs. Sea surface temperature and salinity were recorded during each sampling event via a YSI-30 SCT meter.

Stomach contents were examined using a Wild M-7 dissecting microscope, weighed to the nearest 0.01 g (wet weight), and divided into taxonomic categories. The percentages per taxonomic category for major components of each stomach were estimated visually. We used a feeding index (I_F) as a measure of foraging success, expressed as the percentage of body weight consisting of food items, which standardizes for differences in body size:

$$I_F = M_{sc}(M)^{-1}100,$$

where M_{sc} is the mass of the stomach contents (g), and M is fish mass (g; Farley et al. 2007).

We used relative abundance (A) as the primary metric to rank prey taxa, expressed as percent contents:

$$A = A_{i,f} \left(\sum_{f=1} A_{i,f} \right)^{-1} 100,$$

where $A_{i,f}$ is the total of prey category i in the f th Sockeye Salmon stomach sampled for diet analysis (Farley et al. 2007).

We also calculated the frequency of occurrence of each major prey group (F), expressed as a percent, and calculated as:

$$F = O(S)^{-1}100,$$

where O is the occurrence of a prey item (in numbers), and S is the number of samples examined (fish stomachs or zooplankton). Finally, we examined prey selectivity by juvenile Sockeye Salmon using the electivity index (E_i):

$$E_i = (r_i - p_i)/(r_i + p_i),$$

where r_i is the numerical proportion of the i th taxon in the stomachs; and p_i is the proportion of the same taxon in the environment (Ivlev 1961; see below). The electivity values provide a species-specific measure of prey selection by allowing a comparison of stomach contents to available prey. Values for E_i range from -1 to $+1$, where $+1$ indicates the highest selectivity (i.e., present in the diet, but never in the zooplankton samples), and -1 indicates lowest selectivity (i.e., never in the diet, but present in the zooplankton samples).

We also collected 16 zooplankton samples at Sockeye Salmon locations in 2009 and 20 in 2010 using a plankton

net (1 m diameter, 125- μ m mesh) towed vertically from a depth of 20 m. This should encompass the main depths where juveniles feed. For example, Landingham et al. (1998) showed that juvenile Sockeye Salmon more often select prey from surface waters than at a depth of 50 m. Zooplankton samples from each location were placed in 1-L bottles containing a 10% formalin–seawater solution. In the laboratory, plankton samples were decanted into a sieve stack of 1 mm, 500 μ m, and 150 μ m and rinsed with water to remove formalin. The filtrate was rinsed with ethanol and concentrated in a centrifuge. Subsamples of the concentrated zooplankton were examined with a counting slide under a compound microscope to determine the relative abundance of zooplankton taxa. Zooplankton density (D_z) was calculated for 2010 only, using the formula $D_z = A_i/V$, where A_i is the total abundance of zooplankton per sample and V is the corresponding volume to pass through the plankton net, where $V = \pi r^2 d$, r being the radius of the plankton net, d is the distance of the tow measured with a RIGO flowmeter. Density was not calculated for zooplankton collected at the most southerly site in our study area (location 1, Figure 1), nor for any collections in 2009, because we lacked flowmeter data.

We tested whether zooplankton density in 2010 depended on latitudinal distance and sampling date via multiple regression. Distance was set to zero (0) for the southernmost collection site

with density data (location 2, Figure 1), and all other sites were measured (km) from this reference location using the shortest linear distance by sea. Sampling day was set to 1 for the first collection of zooplankton in 2010, and all other subsequent days were counted sequentially. We also tested via linear regression whether foraging success depended on migration timing in each year (2009 and 2010), where migration day was set to 1 for the first collection of stomachs in a given sampling year and all other subsequent days were counted sequentially. Because the number of stomachs collected and examined at each sampling location over time was not equal, we averaged the feeding index for each sampling event. We transformed feeding index data using an arcsine square-root function to correct for unequal variances and nonnormality, and we performed all analyses in R version 2.15.0 (R Development Core Team 2012) using the lme4 package.

RESULTS

Juvenile Sockeye Salmon were significantly larger on average in fork length ($t = 5.96$, $df = 193$, $P < 0.001$) and mass ($t = 4.06$, $df = 178$, $P < 0.001$) in 2010 than in 2009 (Table 1). Calanoid copepods were the most abundant group in plankton samples both years (66.4% in 2009 and 71.0% in 2010), followed by barnacle larvae (12.2% in 2009 and 17.1% in 2010); frequency of occurrence for both groups

TABLE 2. Zooplankton samples and juvenile Sockeye Salmon diet items identified during 2009 and 2010 surveys; percent abundance (A) is the number of individuals of a given taxon divided by the total number of individuals of all taxa sampled, and frequency of occurrence (F) is the percentage of all samples in which that taxon occurred. Sample size (n) is the number of plankton and stomach samples collected in each year.

Taxon	Zooplankton samples				Stomach content samples			
	2009 ($n = 16$)		2010 ($n = 20$)		2009 ($n = 162$)		2010 ($n = 186$)	
	A (%)	F (%)	A (%)	F (%)	A (%)	F (%)	A (%)	F (%)
Copepoda	66.4	100.0	71.0	100.0	49.9	76.7	32.1	83.9
Brachyura	12.2	100.0	17.1	100.0	0.1	32.5	0.4	24.2
Oikopleura	9.1	100.0	0.6	100.0	10.2	39.9	4.4	22.0
Euphausiacea	2.2	100.0	1.6	83.3	16.6	66.3	21.2	62.9
Cnidaria	2.8	88.9	1.7	100.0	0.0	0.0	0.0	0.0
Cladocera	3.2	87.5	1.2	94.4	0.1	18.0	0.1	16.7
Cyclopoida	0.5	50.0	1.9	88.9	0.0	0.0	0.0	0.0
Harpacticoida	1.8	56.3	0.2	16.7	0.0	0.0	0.0	0.0
Polychaeta	0.6	100.0	1.4	100.0	0.0	0.0	0.0	0.0
Echinodermata	0.7	81.3	1.7	77.8	0.0	0.0	0.0	0.0
Mollusca	0.1	12.5	0.3	38.9	0.0	0.0	0.0	0.0
Pteropoda	0.2	18.8	0.4	77.8	0.1	9.8	0.7	25.3
Decapoda	0.1	6.4	0.4	66.7	5.7	33.7	13.1	45.7
Other	0.0	50.0	0.4	77.8	0.0	0.0	0.0	0.0
Amphipoda	0.1	0.0	0.2	0.0	7.5	50.3	15.5	67.7
Insecta	0.0	0.0	0.0	0.0	2.9	15.3	0.4	5.9
Fish	0.0	0.0	0.0	0.0	2.9	12.9	11.0	15.1
Cumacea	0.0	0.0	0.0	0.0	2.1	9.8	0.1	3.8
Eggs	0.0	0.0	0.0	0.0	2.1	3.7	1.1	3.8

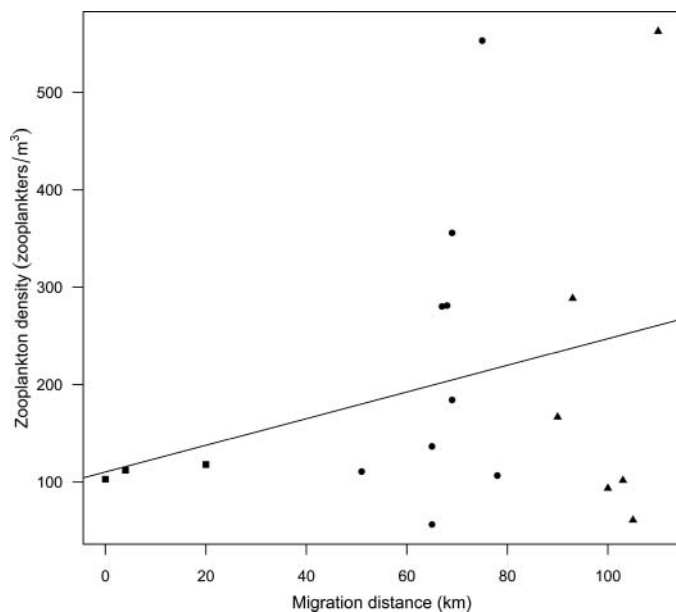


FIGURE 2. Distribution of zooplankton density (zooplankters/m³) in relation to distance 0 (site location 2 on Figure 1), during May to June 2010, where squares are sites 2–4, circles are sites 5–11, and triangles are sites 12–16.

was 100% (Table 2). Remaining zooplankton were much less abundant in each year. The combined group, “other” in 2009 included several fish larvae and the marine ectoparasite *Caligus clemensi*. Multiple regression analysis showed that distance north ($\beta = 6.750$, $P = 0.035$; Figure 2) significantly predicted zooplankton density, but sampling day did not ($\beta = -6.225$, $P = 0.116$; the overall model fit was $R^2 = 0.202$).

Juvenile Sockeye Salmon ate a high diversity of prey across the study area (Table 2). Of 67,246 food items identified, calanoid copepods were the most common item in both abundance and frequency of occurrence for 2009 and 2010; euphausiids were the second most consumed prey in both years (in numerical terms). An adult female sea louse, *C. clemensi*, was found in a Sockeye Salmon stomach in 2010. Despite the large prey diversity, juvenile Sockeye Salmon in both years consistently and strongly selected for euphausiid, amphipod, decapod, terrestrial insect, fish, egg, and cumacean prey ($E_i > 0.75$); they routinely selected against brachyuran and cladoceran prey (Figure 3). Calanoid copepods, the most abundant available prey, were not strongly selected for in either year. Although foraging success did not differ between migration years ($t = 0.947$, $df = 240$, $P = 0.345$), the percentage of empty stomachs was higher in 2009 (3.1%) than in 2010 (0.0%); foraging success remained relatively constant over the migration period, both in 2009 ($R^2 = -0.043$, $df = 15$, $P = 0.568$) and 2010 ($R^2 = -0.027$, $df = 20$, $P = 0.514$; Figure 4).

DISCUSSION

Our study contributes novel insight into some important biotic conditions faced by Canada’s Fraser River Sockeye Salmon

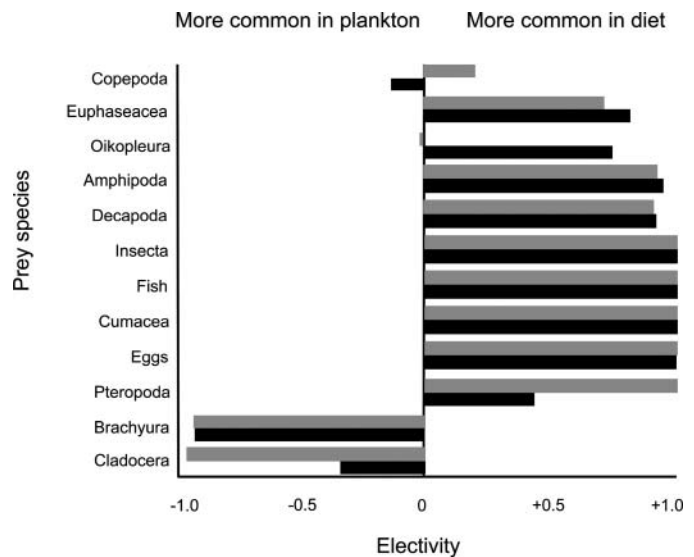


FIGURE 3. Electivity scores (a species-specific measure of prey selection) for primary prey species identified in juvenile Sockeye Salmon stomachs during 2009 (grey bars) and 2010 (black bars).

during an assumed critical period of marine migration. Prey were more plentiful in the north, and although juvenile Sockeye Salmon consumed a high diversity of zooplankton, they showed strong preferences for particular prey. Importantly, their foraging success was high in both years and consistent throughout the migration period.

Our finding that zooplankton are predominated by copepods confirms previous observations in this region (Legare 1957; Harrison et al. 1983) and further north in British

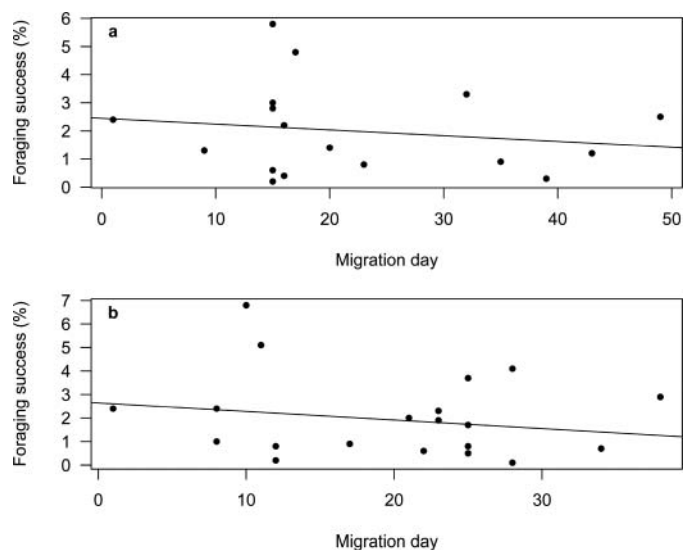


FIGURE 4. Foraging success, expressed as percent body weight of stomach contents in relation to the migration of juvenile Sockeye Salmon through the study region in (a) 2009 and (b) 2010. Migration day is the number of days since the first stomach collection in a given year. Regression analysis was not significant for 2009 ($P = 0.568$) or 2010 ($P = 0.514$).

Columbia and Alaska (Landingham et al. 1998). Zooplankton abundance was not spatially uniform, however. For example, zooplankton density at southern locations 2–4 (Figure 1) averaged 111 zooplankters/m³, and increased to an average of 223 zooplankters/m³ in the northern tidally mixed Discovery Passage and Johnstone Strait region (locations 5–16), where there was also more variability among sites. Although there have been few studies of zooplankton in our study area (i.e., northern Strait of Georgia and southern Johnstone Strait), phytoplankton densities during spring in the Strait of Georgia are highest at both the mouth of the Fraser River (south of where we sampled) and at the approach of Johnstone Strait. These are areas where the most complete mixing of freshwater and seawater occurs (Hutchinson and Lucas 1931; Stockner et al. 1979; Parsons et al. 1981; Harrison et al. 1983). Mixing of waters may promote the up-welling of nutrients and increase productivity. Therefore, rather than indicating a trend of increasing zooplankton abundance along the entire Vancouver Island migration route, the spatial variation we observed in zooplankton density may best reflect differences in oceanographic properties and productivity between the stable two-layer Strait of Georgia and the tidally mixed Discovery Passage–Johnstone Strait area. It may also partly explain the rapid migration of juvenile Sockeye Salmon through the Strait of Georgia (i.e., 26 km/d; Welch et al. 2009, 2011).

Juvenile Sockeye Salmon migrating through the Strait of Georgia and Johnstone Strait consumed zooplankton almost exclusively, as opposed to fish or eggs, which we also recorded in small numbers. Prey diversity was high, consisting of more than 12 higher taxa in both years, which matches previous studies in the Strait of Georgia and other regions of the northeast Pacific (Healey 1980, 1991; Brodeur and Pearcy 1990; Landingham et al. 1998). Despite the large numbers of species consumed, our results show evidence of selectivity for particular prey. Sockeye Salmon routinely selected for euphausiid, amphipod, decapod, terrestrial insect, fish, egg, and cumacean prey, and avoided abundant brachyuran and cladoceran prey. Calanoid copepods, the most abundant and consumed prey, were not selected out of proportion to their availability in either year. Calanoid copepods have been described as a major diet item for juvenile salmon generally but are not considered preferred prey (Pearcy 1992), and Sockeye Salmon have been shown to avoid numerically predominant copepods elsewhere (Landingham et al. 1998).

Reasons for the selectivity of prey by juvenile Sockeye Salmon observed in our study are not clear. Salmonids are considered opportunistic drift feeders (Everest and Chapman 1972; Filbert and Hawkins 1995) that will consume visually obvious prey within a certain size range (Brodeur et al. 2003). But even within a particular size range, preferences are evident. For example, juvenile Sockeye Salmon migrating along British Columbia's north coast consumed a disproportionate number of large prey; small copepods were ignored relative to their abundance (Healey 1991; Landingham et al. 1998). Large prey should be easier to detect and more profitable than

small prey. This could explain the high selectivity shown in our study for amphipods: large, but limited prey, with relatively high gross energy (as per prey energy estimates in Tanasuchuck and Routledge 2011). The small size and low gross energy of brachyura may also explain why Sockeye Salmon in our study consistently selected against them, despite their high abundance. Confusing this rather simplistic interpretation, however, is the strong selectivity in 2010 for oikopleura, which are small and have the lowest estimated energy content of prey available to juvenile Sockeye Salmon (Tanasuchuck and Routledge 2011). Thus, the diet of Sockeye Salmon is undoubtedly a combination of prey abundance and preference, and we agree with Healey (1991) that, "The complex of factors underlying a particular diet cannot be fully sorted out in a descriptive study such as this."

This is the first report of Sockeye Salmon preying on *C. clemensi*. This is a common external parasite of Atlantic Salmon *Salmo salar*, in open-net salmon farms in the region, and on wild juvenile Sockeye Salmon (Korman 2011; Price et al. 2011). Our finding of adult *C. clemensi* in a Sockeye Salmon stomach and at sea suggests either a dispersal mechanism that may involve adult transfer between hosts (see Connors et al. 2008; Costello 2009) or simply the dislodgement of abundant lice in the study region from hosts and subsequent opportunistic capture.

Predictions of climate warming effects on Fraser River Sockeye Salmon include changes in the abundance and distribution of prey in the Strait of Georgia, which could result in a timing mismatch between nearshore productivity and migrating juvenile salmon (Healey 2011). In a recent study involving the northern Strait of Georgia region in 2009, zooplankton abundance was highest between mid-May and June and peaked during the first week of June (Chittenden et al. 2010). Juvenile Coho Salmon *O. kisutch*, which entered the marine environment of this region during the peak bloom period, had significantly higher survival rates than fish that began marine migration before or after this period (Chittenden et al. 2010). Our observations since 2007 suggest that the peak migration timing of Fraser River Sockeye Salmon through northern Strait of Georgia–southern Johnstone Strait is during the first 2 weeks in June. Prey were abundant during this time, and foraging success remained relatively unchanged, which suggests that fish may not be experiencing a trophic mismatch during their early marine migration, at least during the 2 years of our study. Importantly, the question remains as to whether this apparent resource abundance for juveniles relates to improved marine survival and consistent adult returns in subsequent years, as was shown for Coho Salmon outmigrating in 2009. Preliminary estimates suggest that productivity (recruits per spawner) for the 2009 and 2010 outmigration of Fraser River Sockeye Salmon smolts was above average compared to the modern low productivity era post-1993, but equal to and slightly below the long-term average (1956–2010), respectively (M. Lapointe, Pacific Salmon Commission, personal communication).

Juvenile Sockeye Salmon did not experience severe food limitations during the years of our study. Despite significantly

larger fish in 2010 than in 2009, foraging success was similar between years and averaged 1.9% for the 2 years of our study. These are the highest recorded for Sockeye Salmon during their first summer at sea and comparable with other juvenile salmon for this region and elsewhere. Juvenile Sockeye Salmon examined along British Columbia's north coast showed an average feeding index between 0.3% (July 1986) and 0.5% (July 1987); levels considered at the time to indicate food limitations (Healey 1991). Concomitantly, averages for Chum Salmon *O. keta*, Chinook Salmon *O. tshawytscha*, and Coho Salmon in the Strait of Georgia (0.73–1.15%; Healey 1980), and Coho Salmon in Oregon and Washington (1.2–2.7%; Fisher and Percy 1988) were reported as evidence for an adequate food supply (Healey 1991).

The low percentage of juveniles with empty stomachs (3.1% in 2009, and 0.0% in 2010) further suggests that food limitation (if present during the years of this study) was not widespread. Haegele (1997) showed that on average 32% of juvenile Sockeye Salmon had empty stomachs during 1990–1993 in the Strait of Georgia (a high of 75% in 1993), which was the beginning of reduced returns of Sockeye Salmon to the Fraser River (Connors et al. 2012). Beamish et al. (2012) reported that about 40% of juvenile Sockeye Salmon in the Strait of Georgia had empty stomachs in 2007 and speculated that subsequent marine survival was affected, although this was based on a sample size of 65 fish. That same study, however, showed that about 40% of Sockeye Salmon in 2004 had empty stomachs, as did about 20% in 2009; yet no link was made with these years to food limitations. One plausible explanation for the lower empty stomach rates that we report for 2009 compared to those reported by Beamish et al. (2012) is that the Sockeye Salmon we examined were captured further north, whereas Beamish et al. (2012) may have captured fish as far south as the mouth of the Fraser River. Alternatively, perhaps we were just sampling the survivors of food-deprived fish that may have been preyed upon. This is an inherent difficulty in interpreting any study. The principal unanswered questions for future work are: (1) whether juveniles grow fast enough to minimize size-related predation mortality, (2) whether or not there is a critical period in the early life history, and (3) whether or not it occurs in the Strait of Georgia.

In conclusion, juvenile Fraser River Sockeye Salmon appeared to have an abundant prey resource pool while migrating through south-coast British Columbia during the 2 years of this study. This was matched by consistently high foraging success in both years. Ocean conditions vary widely from year to year; hence, we cannot say anything about the 2007 cohort, which returned in exceptionally low numbers 2 years later. We also cannot say anything about future migrations and subsequent survival. Rather, further progress in linking oceanic conditions to survival of salmon will require comprehensive annual monitoring of both the fish and their prey during this assumed critical phase of their life cycle.

ACKNOWLEDGMENTS

We thank the late S. Bergh, as well as F. Campbell, T. Campbell, C. Carr-Harris, J. Eriksson, A. Rosenberger, and Raincoast Conservation Foundation for technical and in-kind support, and R. Tanasichuck, D. Welch, the Associate Editor, and an anonymous reviewer for helpful suggestions that greatly improved the manuscript. This work was supported by Mountain Equipment Co-op Environment Fund, the Tom Buell Endowment Fund, the Pacific Salmon Foundation, a Natural Sciences and Engineering Research Council of Canada (NSERC) Industrial Postgraduate Scholarship to M.H.H.P., and a NSERC Discovery Grant to J.D.R.

REFERENCES

- Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography* 49:423–437.
- Beamish, R. J., C. Mahnken, and C. M. Neville. 2004. Evidence that reduced early marine growth is associated with lower marine survival of Coho Salmon. *Transactions of the American Fisheries Society* 133:26–33.
- Beamish, R. J., C. Neville, R. Sweeting, and K. Lange. 2012. The synchronous failure of juvenile Pacific salmon and herring production in the Strait of Georgia in 2007 and the poor return of Sockeye Salmon to the Fraser River in 2009. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 4:403–414.
- Brodeur, R. D., K. W. Myers, and J. H. Helle. 2003. Research conducted by the United States on the early life history of Pacific salmon. *North Pacific Anadromous Fish Commission Bulletin* 3:89–131.
- Brodeur, R. D., and W. G. Percy. 1990. Trophic relations of juvenile Pacific salmon off the Oregon and Washington coast. *U.S. National Marine Fisheries Service Fishery Bulletin* 88:617–636.
- Chittenden, C. M., J. L. A. Jensen, D. Ewart, S. Anderson, S. Balfry, E. Downey, A. Eaves, S. Saksida, B. Smith, S. Vincent, D. Welch, and R. S. McKinley. 2010. Recent salmon declines: a result of lost feeding opportunities due to bad timing? *PLoS ONE* [online serial] 5:e12423.
- Cohen Commission. 2012. Commission of inquiry into the decline of Sockeye Salmon in the Fraser River. Cohen Commission, Final Report. Available: <http://www.cohencommission.ca/en/FinalReport/> (January 2013).
- Connors, B. M., D. C. Braun, R. M. Peterman, A. B. Cooper, J. D. Reynolds, L. M. Dill, G. T. Ruggione, and M. Krkosek. 2012. Migration links ocean-scale competition and local ocean conditions with exposure to farmed salmon to shape wild salmon dynamics. *Conservation Letters* 5:304–312.
- Connors, B. M., M. Krkosek, and L. M. Dill. 2008. Sea lice escape predation on their host. *Biology Letters* 4:455–457.
- Costello, M. J. 2009. How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. *Proceedings of the Royal Society of London B* 276:3385–3394.
- Duffy, E. J., and D. A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 68:232–240.
- Everest, F. H., and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile Chinook Salmon and steelhead trout in two Idaho streams. *Journal of the Fisheries Research Board of Canada* 29:91–100.
- Farley, E. V., J. M. Murphy, M. Adkison, and L. Eisner. 2007. Juvenile Sockeye Salmon distribution, size, condition and diet during years with warm and cool spring sea temperatures along the eastern Bering Sea shelf. *Journal of Fish Biology* 71:1145–1158.
- Filbert, R. B., and C. P. Hawkins. 1995. Variation in condition of Rainbow Trout in relation to food, temperature, and individual length in the

- Green River, Utah. Transactions of the American Fisheries Society 124: 824–835.
- Fisher, J. P., and W. G. Pearcy. 1988. Growth of juvenile Coho Salmon (*Oncorhynchus kisutch*) off Oregon and Washington, USA, in years of differing coastal upwelling. Canadian Journal of Fisheries and Aquatic Sciences 45:1036–1044.
- Groot, C., and K. Cooke. 1987. Are the migrations of juvenile and adult Fraser River Sockeye Salmon (*Oncorhynchus nerka*) in near-shore waters related? Canadian Special Publication of Fisheries and Aquatic Sciences 96:53–60.
- Haegele, C. W. 1997. The occurrence, abundance, and food of juvenile herring and salmon in the Strait of Georgia, British Columbia. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2390.
- Harrison, P. J., J. D. Fulton, F. J. R. Taylor, and T. R. Parsons. 1983. Review of the biological oceanography of the Strait of Georgia: pelagic environment. Canadian Journal of Fisheries and Aquatic Sciences 40:1064–1094.
- Healey, M. C. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia. Pages 203–229 in W. J. McNeil and D. C. Himsforth, editors. Salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis.
- Healey, M. C. 1991. Diets and feeding rates of juvenile pink, chum, and Sockeye Salmon in Hecate Strait, British Columbia. Transactions of the American Fisheries Society 120:303–318.
- Healey, M. C. 2011. The cumulative impacts of climate change on Fraser River Sockeye Salmon (*Oncorhynchus nerka*) and implications for management. Canadian Journal of Fisheries and Aquatic Sciences 68:718–737.
- Hutchinson, A. H., and C. C. Lucas. 1931. The epilhalassa of the Strait of Georgia: salinity, temperature, pH and phytoplankton. Canadian Journal of Research 5:231–284.
- IUCN (International Union for the Conservation of Nature). 2009. Pacific Sockeye Salmon (*Oncorhynchus nerka*) added to IUCN red-list. Available: <http://www.iucnredlist.org/apps/redlist/details/135301/0>. (August 2011).
- Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut.
- Johannessen, S. C., and R. W. Macdonald. 2009. Effects of local and global change on an inland sea: the Strait of Georgia, British Columbia, Canada. Climate Research 40:1–21.
- Korman, J. 2011. Summary of information for evaluating impacts of salmon farms on survival of Fraser River Sockeye Salmon. Cohen Commission, Technical Report 5A, Vancouver.
- Landingham, J. H., M. V. Sturdevant, and R. D. Brodeur. 1998. Feeding habits of juvenile Pacific salmon in marine waters of southeastern Alaska and northern British Columbia. U.S. National Marine Fisheries Service Fishery Bulletin 96:285–302.
- Legare, J. E. H. 1957. The qualitative and quantitative distribution of plankton in the Strait of Georgia in relation to certain oceanographic factors. Journal of the Fisheries Research Board of Canada 14:521–552.
- Parsons, T. R., J. Stronach, G. A. Borstad, G. Louttit, and R. I. Perry. 1981. Biological fronts in the Strait of Georgia, British Columbia, and their relation to recent measurements of primary productivity. Marine Ecology Progress Series 6:237–242.
- Pearcy, W. G. 1992. Ocean ecology of North Pacific salmonids. University of Washington Press, Seattle.
- Peterman, R. M. 1982. Nonlinear relation between smolts and adults in Babine Lake Sockeye Salmon (*Oncorhynchus nerka*) and implications for other salmon populations. Canadian Journal of Fisheries and Aquatic Sciences 39:904–913.
- Peterman, R. M., and B. Dorner. 2012. A widespread decrease in productivity of Sockeye Salmon (*Oncorhynchus nerka*) populations in western North America. Canadian Journal of Fisheries and Aquatic Sciences 69:1255–1260.
- Peterman, R. M., D. Marmorek, B. Beckman, M. Bradford, N. Mantua, B. E. Riddell, M. Scheuerell, M. Staley, K. Wieckowski, J. R. Winton, and C. C. Wood. 2010. Synthesis of evidence from a workshop on the decline of Fraser River sockeye. Report to the Pacific Salmon Commission, Vancouver.
- Price, M. H. H., A. Morton, and J. D. Reynolds. 2010. Evidence of farm-induced parasite infestations on wild juvenile salmon in multiple regions of British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 67:1925–1932.
- Price, M. H. H., S. L. Proboszcz, R. D. Routledge, A. S. Gottesfeld, C. Orr, and J. D. Reynolds. 2011. Sea louse infection of juvenile Sockeye Salmon in relation to marine salmon farms on Canada's west coast. PLoS ONE [online serial] 6:e16851.
- R Development Core Team. 2012. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Ricker, W. E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and non-catch mortality caused by fishing. Journal of the Fisheries Research Board of Canada 33:1483–1524.
- Ross, P. S. 2006. Fireproof killer whales (*Orcinus orca*): flame-retardant chemicals and the conservation imperative in the charismatic icon of British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 63:224–234.
- Stockner, J. G., D. D. Cliff, and K. R. S. Shortreed. 1979. Phytoplankton ecology of the Strait of Georgia, British Columbia. Journal of the Fisheries Research Board of Canada 36:657–666.
- Tanasichuck, R. W., and R. Routledge. 2011. An investigation of the biological basis of return variability for Sockeye Salmon (*Oncorhynchus nerka*) from Great Central and Sprout lakes, Vancouver Island. Fisheries Oceanography 20:462–478.
- Welch, D. W., M. C. Melnychuk, J. C. Payne, E. L. Rechisky, A. D. Porter, G. D. Jackson, B. R. Ward, S. P. Vincent, C. C. Wood, and J. Semmens. 2011. In situ measurement of coastal ocean movements and survival of juvenile Pacific salmon. Proceedings of the National Academy of Sciences of the USA 108:8708–8713.
- Welch, D. W., M. C. Melnychuk, E. L. Rechisky, A. D. Porter, M. C. Jacobs, A. Ladouceur, R. S. McKinley, and G. D. Jackson. 2009. Freshwater and marine migration and survival of endangered Cultus Lake Sockeye Salmon (*Oncorhynchus nerka*) smolts using POST, a large-scale acoustic telemetry array. Canadian Journal of Fisheries and Aquatic Sciences 66:736–750.