Comparison of juvenile salmon diets in the Strait of Georgia and Puget Sound 1997-2006

R.M. Sweeting[1], R.J. Beamish[1] and C.A. Cooper[2]
[1]Pacific Biological Station, Nanaimo, BC
[2]Zotec Services, Nanaimo, BC

Abstract
Juvenile Pacific salmon (*Oncorhynchus* spp.) enter the ocean in early spring/summer. In the Strait of Georgia and Puget Sound, they generally spend several weeks to months rearing before migrating to other areas. During this time, growth and predation avoidance are major priorities. Interspecific competition for food and/or resources could be a limiting factor in survival over these initial months. This report will present the results of 9 years of summer (July) surveys in Puget Sound and the Strait of Georgia, during which stomach/diet data was collected for several thousand juvenile coho (*O. kisutch*), Chinook (*O. tshawytscha*) and chum (*O. keta*) salmon. In addition to examining similarities and differences in diet, the influence of size and environment will be discussed.

Introduction

Both Puget Sound and the Strait of Georgia are semi-enclosed, estuarine-driven inland seas (Figure 1) utilized by juvenile coho, Chinook and chum salmon as rearing habitat during the initial months of their marine existence. Their proximity to each other ensures that the local climate forcings (seasonal temperatures, winds, and onset of spring productivity) are similar. However, there are also differences, such as overall size, the domination of Fraser River freshwater input into the Strait of Georgia, and hatchery inputs. Of more interest is the superior marine survivals exhibited by coho and Chinook salmon stocks in Puget Sound compared to the Strait of Georgia. This paper will focus on differences in size, appetite and diet of juvenile coho, Chinook and chum salmon obtained from 10 years of surveys in July in Puget Sound and the Strait of Georgia.

Methods

Our surveys have been primarily conducted using the CCGS *W.E. Ricker*, a 180 m fisheries research vessel. We use a modified mid-water trawl that allows us to tow 5 knots at the surface (Beamish et al. 2000; Sweeting et al. 2003). Under these conditions, the net has an opening of 15 x 30 m. Thus, we stratify our effort by fishing at 15 m increments (0-15, 15-30, 30-45, 45-60), although the overall effort is strongly biased to the upper 30 m of the water column. Approximately 85-95% of coho and Chinook salmon, and 95-98% of chum salmon are captured in this upper layer (data not shown). Sets in the Strait of Georgia were typically 30 min in duration. Sets in Puget Sound ranged in duration from 5-20 min, in part due to much greater salmon densities and in part due to conservation concerns for Chinook and some chum salmon stocks.

Following identification and separation of each catch into various species, fish were counted and fork lengths measured (to the nearest mm) from either the total of small catches or a substantial subsample of large catches. Analysis of stomach contents is then immediately performed. Briefly, the stomach is removed at the cardiac and pyloric constrictions and the contents emptied into a clear Petrie dish. The gut cavity is rinsed with water, the total prey volume is estimated and the individual components identified. These stomach analyses have been performed by the same highly experienced and qualified person (C. Cooper) for the vast majority of these surveys. By conducting the analysis at sea the samples are fresh (making analysis easier) and the sample sizes are large. Prey items are categorized to the genus level in most cases. For analysis, diet items are combined into family-like groups.

Statistical analyses (ANOVA, T-tests) were conducted using Excel (Microsoft), with significance accepted at the 0.05% level. For diet overlap comparisons, the Horn Index (Horn 1966) was utilized. An index value of ≥ 0.60 was considered to indicate a similar diet, and ≥ 0.75 to indicate a very similar diet.

Figure 1. Map of Puget Sound and the Strait of Georgia, showing the Fraser River and other contributors to freshwater inflow. Outflow from both Puget Sound and the Strait of Georgia is via the Strait of Juan de Fuca. Survey track lines are shown in black for Strait of Georgia sets and dark blue for Puget Sound sets.

Results

A) Catch and Effort

Due to the differences in set duration between the two areas, catch data is converted to catch per unit effort (CPUE), which in this case is catch per hour of fishing (Table 1). As noted earlier, densities of juvenile salmon are significantly higher in Puget Sound than in the Strait of Georgia and this was reflected in the CPUE data. With the exception of 2006, CPUE of coho and Chinook salmon were always higher in Puget Sound, ranging from ~1.5- to 16-fold higher for coho, and from ~ 4- to 11-fold higher for Chinook (Table 1). The single extremely high CPUE for Chinook in the 2000 survey was a reflection of only 2 sets completed, due to conservation concerns and is most certainly an anomaly. Juvenile chum salmon exhibit a similar pattern, although perhaps not as consistent as observed with coho or Chinook. These differences in CPUE range from ~ 1.2- to 6-fold higher in Puget Sound. The CPUE for chum salmon was essentially equal for the two areas in 1998, 2001, 2005 and 2006 (Table 1). The very large CPUE for juvenile chum observed in 2004 was the result of a single 5-minute set conducted just north of the Tacoma Narrows, in which some 9,000 chum were captured. Removal of this set from the data decreases the survey CPUE to ~580 (Figure 2), still some 2-fold greater than the corresponding Strait of Georgia CPUE.

Table 1. Catch per unit effort (CPUE) (1 hour) for juvenile coho, Chinook and chum salmon captured in our July surveys from 1997 to 2006 in the Strait of Georgia (SoG) and in Puget Sound (PS). Note that no surveys were conducted in 2003.

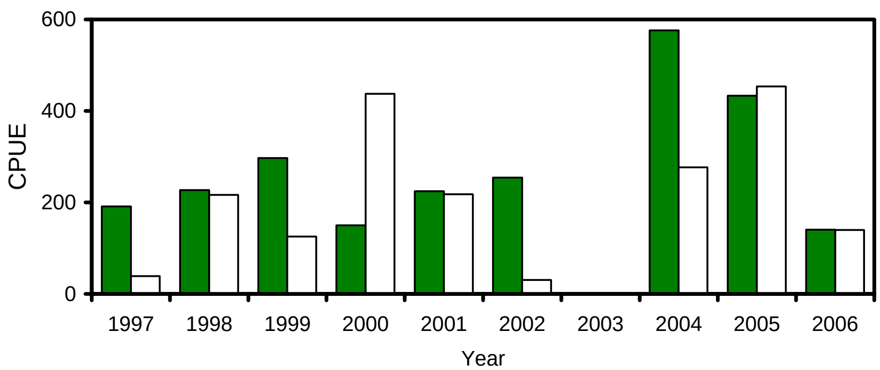
	COHO		CHINOOK		CHUM	
Year	SoG	PS	SoG	PS	SoG	PS
1997	18.55	288.9	46.6	542.1	39.07	191.3
1998	40.26	115.2	48.6	176.2	216.1	227.0
1999	41.46	289.2	38.9	393.6	125.1	297.0
2000	126.05	476.0	69.4	1656.0	437.5	150.0
2001	114.12	177.5	59.5	263.5	217.8	224.3
2002	43.10	392.4	42.8	474.7	30.5	254.3
2003			No survey			
2004	59.45	98.6	77.2	501.7	276.8	4571.5
2005	10.87	175.6	18.1	257.3	453.7	433.3
2006	102.90	7.6	86.9	46.9	139.6	140.7

B) Fork Lengths

Fork length has been proposed in many references throughout the literature as a critical factor in the early marine survival of juvenile salmon and teleosts in general. Briefly, it is considered that the major strategy of salmon upon entry to the marine environment is to grow large enough to escape the majority of predators within the ecosystem. Thus, we considered that greater marine survival in Puget Sound stocks may be reflected in larger average size of Puget Sound fish.

For coho salmon, this is generally the case (Table 2), with juvenile coho salmon captured in Puget Sound being significantly larger than their Strait of Georgia counterparts in 5 of the 9 years of the study, whereas the reverse was true only in two years (1998 and 2000). Average fork lengths were significantly larger for Strait of Georgia Chinook in 4 of the first 6 years of the study. Chinook captured in Puget Sound were larger than those in the Strait of Georgia in only one of these years (1998), but not significantly. However, Puget Sound juvenile Chinook were significantly larger than Strait of Georgia Chinook in the 2004, 2005, and 2006 surveys. The reasons for this reversal are unclear. Furthermore, if larger size is a strong correlate of early marine survival, then the increasing trend in average size observed in Chinook from both basins from 2002-2006 should be considered a positive trend. Juvenile chum salmon captured in Puget Sound have been significantly larger than those from the Strait of Georgia in all 9 years of the study, despite some limited sample sizes in the early Puget Sound surveys. Although the average fork length in 2006 was slightly smaller than the previous year, there does appear to be a general increasing trend in both regions since 2002, as observed for Chinook. However, there was no significant correlation between juvenile chum salmon fork length in July and marine survival in either region; and most of the correlations are, in fact, negative.

Figure 2. Catch per unit effort (CPUE) for juvenile chum salmon collected in Puget sound (green bars) and Strait of Georgia (white bars) in July surveys 1997 – 2006, with the removal of a single exceptional set in the July 2004 survey. No surveys conducted in 2003.



C) Stomach Volume ('appetite index')

Increasing size or growth infers input of energy to the animals, so the volume of prey in the stomach (i.e., stomach volume) was analyzed to assess possible relationships with growth and survival. Stomach volumes can be analyzed in two different ways: including or excluding empty stomachs (those stomachs with either no contents observed, or < 0.1 cc of prey). Since the trends were the same, average stomach volumes have been calculated excluding empty stomach data.

Juvenile coho salmon from both regions displayed complex patterns with no clear temporal trends (Figure 3A). Average stomach volumes in coho salmon from Puget Sound were significantly greater than those from Strait of Georgia in 4 of the 9 years, whereas the reverse was observed in 3 of the 9 years. There was a slight increasing trend over the 9 years of study. Juvenile Chinook salmon captured in the Strait of Georgia had significantly greater average stomach volumes compared to Puget Sound for 4 years (Figure 3B). There was an additional two years when Puget Sound volumes were larger but not significantly. There were no clear trends over time. Juvenile chum captured in Strait of Georgia consistently had greater volumes of prey than those from Puget Sound, except for the 2002 survey when the reverse was true (Figure 3C). Additionally, there was a strong increasing trend in stomach volume in the recent three years, in both regions.

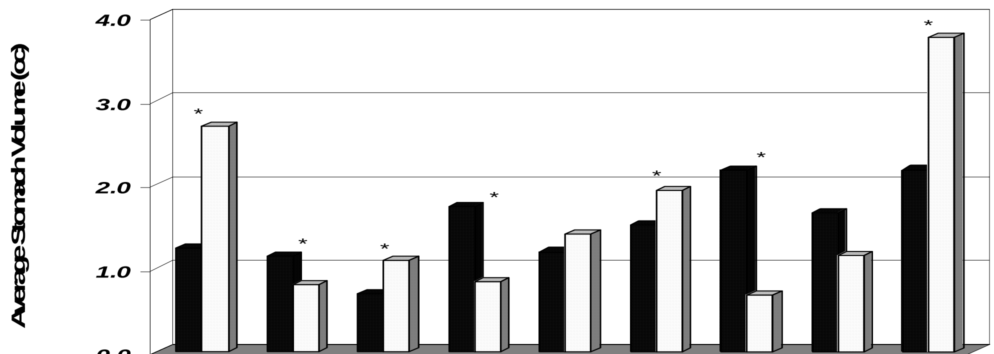
There was no difference in either total stomach volumes (i.e., including empty or near empty stomachs) or real stomach volumes (i.e., excluding empty and near-empty) (Table 3) when the results of the 9 surveys were combined (by species). There were, however, clear species differences, with coho salmon having the largest average volumes and chum salmon the least. In part, this may be related to size differences between the species, but diet choices may also contribute. It is important to re-emphasize that our effort was considerably different between the two regions, as noted by the different sample sizes (Table 4). The percentages of empty stomachs in Puget Sound coho and chum salmon were approximately twice that observed in the Strait of Georgia, whereas the number of juvenile Chinook salmon with empty stomachs was similar between the two regions. There were clear species differences, with coho salmon having the lowest percentages of empty stomachs and chum the highest. There was a negative relationship between the average volumes observed and the number of empty stomachs, with species having the lowest average volumes (chum) also having the highest percentage of empty stomachs.

Table 2. Average size (fork length, mm), standard deviation (SD), and sample size (N) for juvenile coho, Chinook, and chum salmon captured in July surveys in Puget Sound and the Strait of Georgia from 1997-2006. Asterisks denote significant differences in length (T- test, P ≤ 0.05) between regions in a given survey.

	COHO			CHINOOK			CHUM		
Year	SoG		PS	SoG		PS	SoG		PS
1997	159.2 (22.5) (N = 520)	*	208.0 (23.9) (N = 846)	140.3 (33.8) (N = 1585)	*	130.7 (23.9) (N = 1405)	121.5 (25.6) (N = 907)	*	131.9 (17.1) (N = 504)
1998	172.8 (23.3) (N = 1219)	*	166.9 (19.0) (N = 350)	120.8 (36.9) (N = 1411)		124.1 (29.5) (N = 157)	122.9 (15.0) (N = 1206)	*	133.0 (16.4) (N = 348)
1999	167.6 (22.3) (N = 1639)	*	196.5 (23.1) (N = 160)	139.0 (37.4) (N = 1664)	*	131.4 (16.8) (N = 643)	115.8 (19.4) (N = 1227)	*	139.5 (16.5) (N = 325)
2000	199.8 (23.4) (N = 3360)	*	193.5 (21.6) (N = 198)	143.7 (36.9) (N = 1994)		143.4 (22.7) (N = 289)	127.9 (18.0) (N = 2609)	*	142.7 (17.5) (N = 20)
2001	184.5 (21.0) (N = 2957)	*	196.2 (25.1) (N = 418)	146.0 (32.3) (N = 2211)	*	127.7 (21.9) (N = 557)	130.4 (17.5) (N = 2192)	*	141.3 (20.3) (N = 189)
2002	168.6 (22.7) (N = 1887)	*	185.7 (23.8) (N = 567)	136.2 (28.8) (N = 1984)	*	117.6 (20.9) (N = 1089)	114.6 (15.2) (N = 1067)	*	122.3 (16.1) (N = 213)
2003					No survey				
2004	178.9 (28.2) (N = 2257)		179.7 (19.9) (N = 275)	119.9 (37.0) (N = 3073)	*	125.0 (17.2) (N = 1915)	123.4 (25.1) (N = 2915)	*	151.9 (16.2) (N =1302)
2005	190.9 (24.3) (N = 414)	*	196.5 (22.5) (N = 412)	134.4 (26.8) (N = 641)	*	137.4 (18.4) (N = 876)	153.4 (14.3) (N = 2692)	*	164.6 (16.8) (N = 716)
2006	194.0 (23.7) (N = 2327)		191.3 (26.8) (N = 203)	131.0 (36.7) (N = 2586)	*	145.1 (26.4) (1032)	141.0 (26.4) (N = 1968)	*	158.3 (20.2) (N = 473)

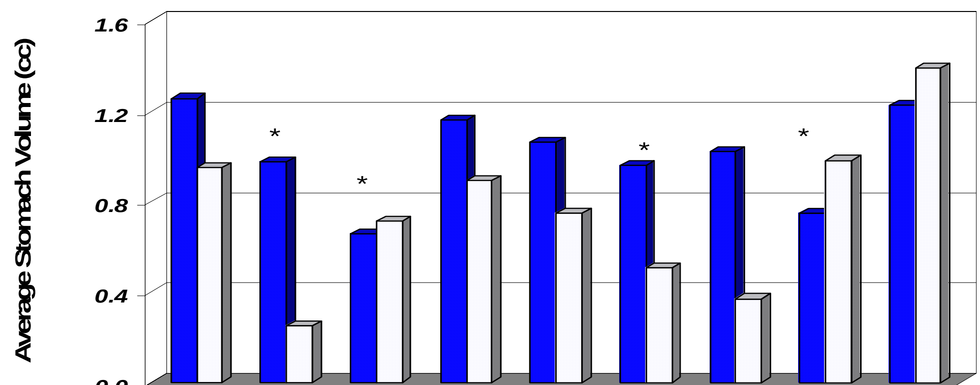
Figure 3. Average prey volumes (cc) for juvenile coho (A), chinook (B), and chum (C) salmon captured in July surveys in Puget Sound (solid bars) and the Strait of Georgia (open bars) from 1997-2006. The average volume is shown across the bottom. Asterisks denote a significant difference (T-test, P ≤ 0.05) between the two regions in a given survey. No surveys in 2003.

A



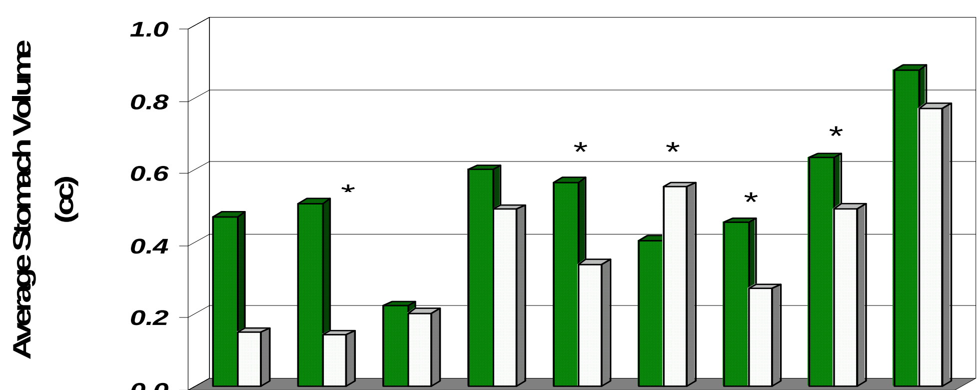
	1997	1998	1999	2000	2001	2002	2004	2005	2006
■ Strait of Georgia	1.24	1.14	0.69	1.73	1.19	1.51	2.17	1.66	2.18
□ Puget Sound	2.69	0.80	1.09	0.83	1.40	1.93	0.68	1.15	3.76

B



	1997	1998	1999	2000	2001	2002	2004	2005	2006
■ Strait of Georgia	1.25	0.97	0.66	1.16	1.06	0.96	1.02	0.75	1.23
□ Puget Sound	0.95	0.25	0.71	0.89	0.75	0.51	0.37	0.98	1.39

C



	1997	1998	1999	2000	2001	2002	2004	2005	2006
■ Strait of Georgia	0.47	0.51	0.22	0.60	0.57	0.40	0.45	0.63	0.88
□ Puget Sound	0.15	0.14	0.20	0.49	0.34	0.55	0.27	0.49	0.77

Table 3. Average stomach volumes (cc), sample size (N), and empty stomachs (%) observed in combined July surveys from 1997-2007 (no 2003 survey) for juvenile coho, Chinook and chum salmon in Puget Sound and the Strait of Georgia. Asterisks denote a significant difference between the two regions (T-test, $P \leq 0.05$).

		COHO	CHINOOK	CHUM
Puget Sound				
	Sample size	922	1,032	576
	Average Volume[a]	1.4	0.6	0.2
	`% Empty	14.4	25.7	36.1
Strait of Georgia				
	Sample size	5,644	6,560	3,482
	Average Volume[a]	1.4	0.8	0.4
	% Empty	14.4	25.7	18.3

[a] – average volume does not include empty stomachs in the calculations.

Table 4. Horn index analysis of dietary overlaps between juvenile coho, Chinook and chum salmon captured in July surveys from 1997-2006 in Puget Sound and the Strait of Georgia. An index value ≥ 0.60 is considered to denote significant overlap.

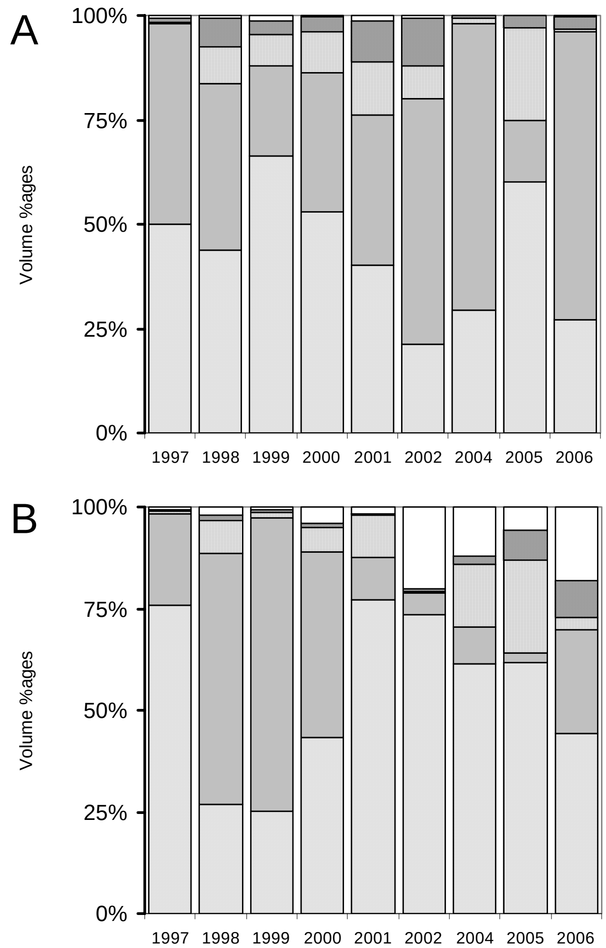
	Puget Sound			Strait of Georgia		
	COHO	CHINOOK	CHUM	COHO	CHINOOK	CHUM
COHO	1.00			1.00		
CHINOOK	0.79	1.00		0.86	1.00	
CHUM	0.44	0.35	1.00	0.15	0.22	1.00

D) Diet analysis

We combined prey items into 5 major categories: 1) Amphipods, mostly hyperids, but also gammarids; 2) Decapods, consisting primarily of juvenile stages (zoea and megalops) of crab and shrimp; 3) Euphausiids; 4) Teleosts, primarily (75-80%) juvenile herring, but also sandlance, smelts, juvenile rockfish, and other small pelagic fishes; and 5) Other, a catch-all category consisting of minor (< 1-2%) prey items, including copepods, chaetognaths, insects, mysids, oikopleura, polychaete worms, seaweed, unknown or unidentifiable items, and items too digested to be categorized. For juvenile chum salmon, a sixth category was utilized – Ctenophores, which for the other two salmon species were included in the "Other" category.

Decapods and teleosts are the two major diet items of juvenile coho salmon in both Puget Sound and Strait of Georgia (Figure 4AB). There was a greater proportion of decapods and reduced levels of teleosts in the diets Puget Sound coho salmon. This may reflect the lower abundances of herring in Puget Sound. Years when decapods were lowest in proportion in Strait of Georgia coho salmon were years when they were at their highest levels in Puget Sound coho. Nonetheless, decapods and teleosts comprised 75-95% of the stomach volume in both regions. Amphipods and Euphausiids dominated the remainder of dietary items observed in coho stomachs. There was no clear trend over time in either region for any diet category.

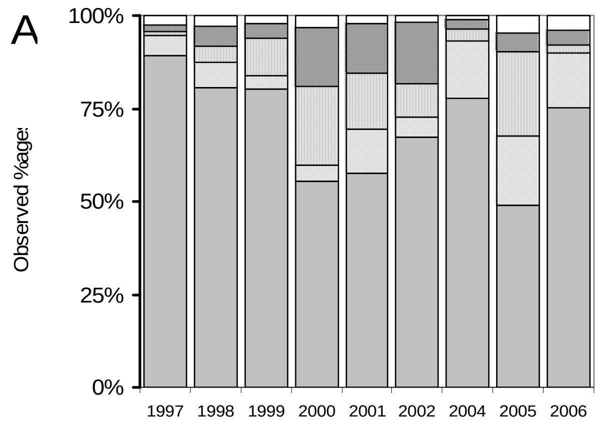
Figure 4. Diet breakdown, by percent volume by year, for juvenile coho salmon examined from July surveys in Puget Sound (A) and the Strait of Georgia (B) from 1997-2006. Prey groups are designated as follows: amphipods (cross-hatched), decapods (stippled), euphausiids (diagonal stripe), other (white) and teleosts (solid grey). See text for specific details. No survey in 2003.

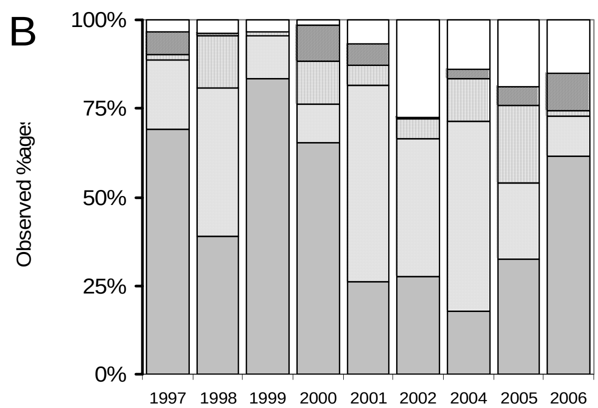


Juvenile Chinook in the Strait of Georgia clearly preferred teleosts (primarily juvenile herring) as their major diet item (Figure 5AB). Decapods, amphipods, and euphausiids made up the rest of the diet, with no clear trends or patterns. As noted earlier in the coho data, teleosts contributed much less to the diet in juvenile Chinook salmon caught in Puget Sound than for those caught in the Strait of Georgia, averaging 70% of the diet of the Strait of Georgia Chinook salmon (range: 48-89%) compared to 47% in Puget Sound diets (range: 17-83%). Decapods made up much of the remainder of the diet items in Puget Sound Chinook salmon, even dominating in 2001 and 2004. Amphipods and euphausiids also made up significant proportions of the Chinook salmon diet in both regions.

Amphipods, decapods, ctenophores and euphausiids made up the majority of diet items in juvenile chum salmon (Figure 6AB), with no group clearly dominating. Teleosts contributed a very minor amount to the diet of juvenile chum salmon (with the exception of 1997 in the Strait of Georgia, but this was a limited sample size and none were assayed in Puget Sound). There is also a considerable increase in the amount of Other category, particularly in the Puget Sound samples. It should be noted that ctenophores are a dominant food item in the diet of these fish and are also very rapidly degraded in the stomachs of fish (M. Arai, pers. comm.). Much of the Other category in both Puget Sound and Strait of Georgia juvenile chum is digested matter (averaging 47 and 50%, respectively), which we have concluded is primarily partially digested ctenophores.

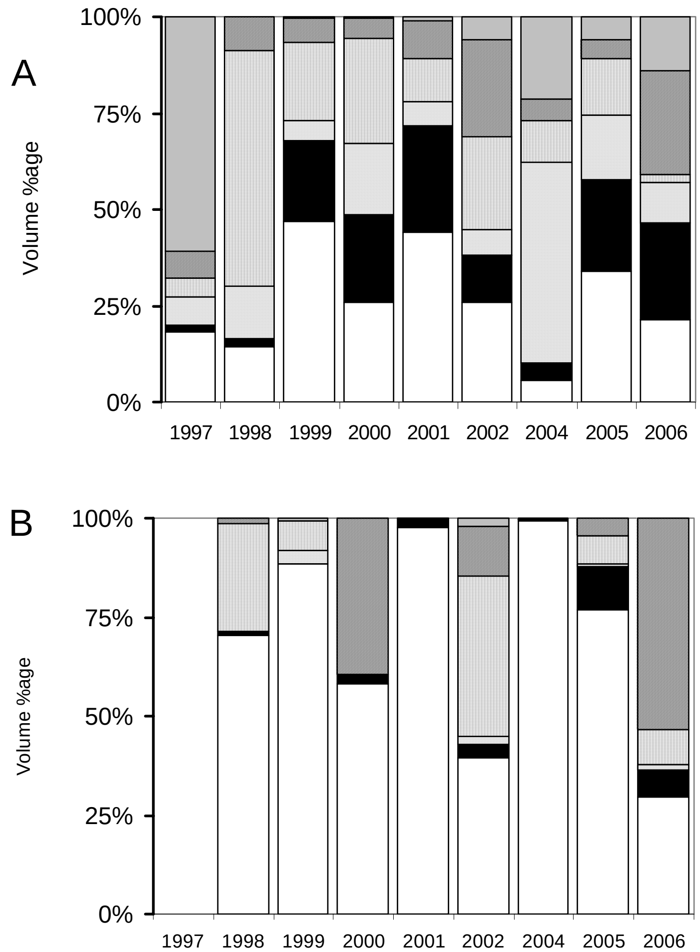
Figure 5. Diet breakdown, by percent volume by year, for juvenile Chinook salmon examined from July surveys in Puget Sound (A) and the Strait of Georgia (B) from 1997-2006. Prey groups are designated as follows: amphipods (cross-hatched), decapods (stippled), euphausiids (diagonal stripe) other (white) and teleosts (solid grey). See text for specific details. No survey in 2003.





Combining the results of all surveys, by species, demonstrates the diet differences between the three species of salmon (Figure 7). Analysis of the diet preferences across species, using the Horn Index method, shows that the diet of juvenile coho significantly overlaps that of juvenile Chinook in both Puget Sound and the Strait of Georgia (Table 4). Neither juvenile coho nor Chinook salmon showed significant dietary overlaps with juvenile chum salmon in either Puget Sound or the Strait of Georgia. This may reflect the focus on teleosts by juvenile coho and Chinook salmon in contrast to the near exclusion of small fishes from the juvenile chum salmon diet. A comparison of the diet patterns between the two regions clearly shows similarities in patterns and trends within the individual species, indicating a general trend both in the production of prey species and a common preference for prey items. Note that for these overlap comparisons, ctenophores are recombined into the Other category for juvenile chum salmon.

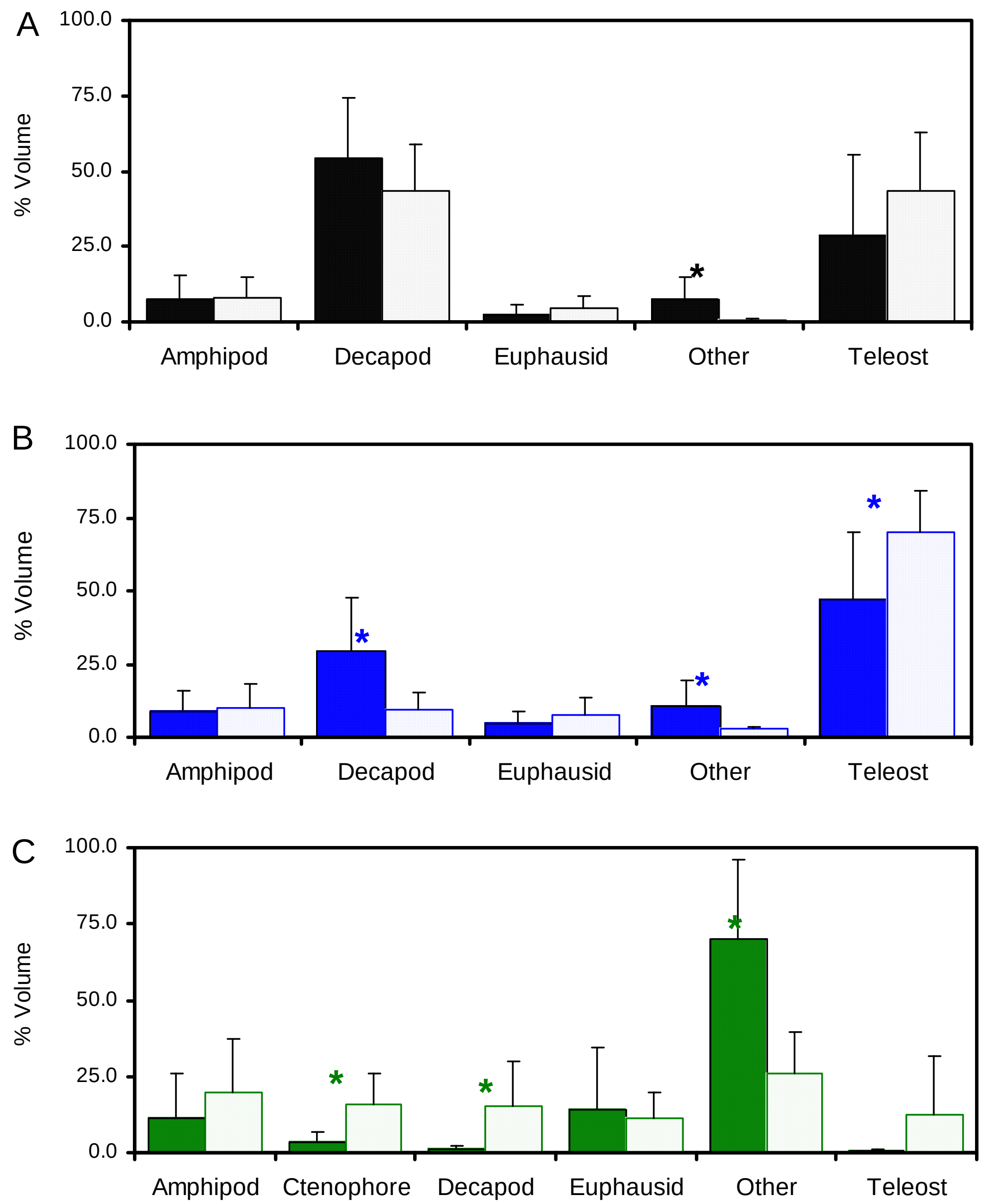
Figure 6. Diet breakdown, by percent volume by year, for juvenile chum salmon examined from July surveys in Puget Sound (A) and the Strait of Georgia (B) from 1997-2006. Prey groups are designated as follows: amphipods (cross-hatched), ctenophores (solid black), decapods (stippled), euphausiids (diagonal stripe), other (solid white) and teleosts (solid grey). See text for specific details. No survey in 2003, no PS data shown from 1997 (due to limited sample size).



Discussion

Current models of early marine survival of salmon generally conclude that faster growing fish are better able to escape the 'predation window', due to larger size, increased swimming speed, and different micro-habitat utilization. Average fork length in July of the first year in the ocean has, in fact, been successfully used to forecast marine survival of coho salmon in the Strait of Georgia (Sweeting, pers. comm.). For the juvenile salmon captured in these July surveys, predator avoidance is still a major concern and thus we considered that size, appetite and/or diet may reflect some of the differences in marine survival not only between species, but also within species and across regions.

Figure 7. Diet breakdown, by percent volume per group, for juvenile coho (A), Chinook (B), and chum (C) salmon captured in July surveys, combined for 1997-2006, from Puget Sound (dark, with white stippling) and Strait of Georgia (white, with dark stippling). Asterisks denote significant differences (T-test, P ≤ 0.05%) between Puget Sound and Strait of Georgia.



Clearly, the much higher CPUE in Puget Sound demonstrated the much greater population (or, at least, density) compared to the Strait of Georgia. The available evidence from coded wire tags shows that little if any emigration has occurred in either basin by this time and little movement between the two regions (see Beamish et al., in these proceedings). While there are some correlations between length and marine survival, no clear patterns emerge for any of the species. Thus, it would appear that size itself may not be an accurate predictor of juvenile salmon survival, although for Strait of Georgia coho it has proven to be very useful. Year-to-year variations in salmon abundance/size, predator abundance/size and prey abundance/size may interact to obscure overall correlations. Furthermore, shifts in climate and ocean conditions can also introduce variability outside the biological parameters discussed herein. Specific growth rates may be a better indicator, but such estimates are beyond this study.

Increases in size infer input of energy, or consumption of food. However, only chum salmon showed any clear correlations between average fork length and average volume of prey in the stomachs. Thus, the amount of prey found in the stomach at any time may not accurately reflect the growth status of an individual fish, but rather its individual feeding success for that day. Data from the surveys clearly shows species differences in average stomach volumes, but they agree with the fork length data only in a casual way.

If not the actual amount of food found in the stomach, then the type of food ingested may be critical to relating this to marine survival. Not only are there caloric differences between food items (e.g., a herring vs. an amphipod), but there may be clear cost: benefit considerations. Much of this is beyond the scope of the current study, but clearly different species of salmon are preying on different organisms within the aquatic water column. Most juvenile salmon are captured in surface tows, yet there are significant differences in their diets. This infers that juvenile salmon are selectively feeding within the common habitat.

Acknowledgements
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