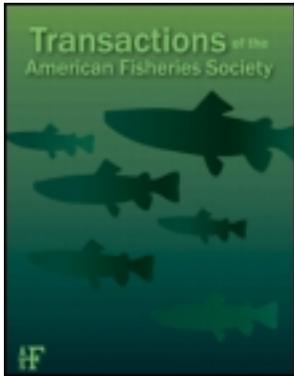


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## Transactions of the American Fisheries Society

Publication details, including instructions for authors and subscription information:

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

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Available online: 09 Jan 2011

To cite this article: Elizabeth A. Daly, Richard D. Brodeur & Laurie A. Weitkamp (2009): Ontogenetic Shifts in Diets of Juvenile and Subadult Coho and Chinook Salmon in Coastal Marine Waters: Important for Marine Survival?, Transactions of the American Fisheries Society, 138:6, 1420-1438

To link to this article: <http://dx.doi.org/10.1577/T08-226.1>

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## Ontogenetic Shifts in Diets of Juvenile and Subadult Coho and Chinook Salmon in Coastal Marine Waters: Important for Marine Survival?

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**Abstract.**—Successfully shifting to a more piscivorous diet may be an important factor in the growth and survival of juvenile coho salmon *Oncorhynchus kisutch* and Chinook salmon *O. tshawytscha* during their first summer in the northern California Current. Nonmetric multidimensional scaling and cluster analysis of diets by size showed several distinct groupings as the salmon grew during their first marine summer. These size-based diet differences were clearly driven by increased rates of piscivory for both species. Fish prey composition, feeding intensity, and fish prey–predator length ratios all significantly increased for coho salmon at approximately 240 mm fork length when they changed from diets dominated by juvenile rockfishes *Sebastes* spp., the larvae of crabs *Cancer* spp., and adult euphausiids to one of predominantly juvenile forage fish. As Chinook salmon grew, they gradually increased the proportional contribution (by weight) of fish prey in their diets—from 55% in the smallest length-class examined (80–100 mm) to 95% in the largest one (>375 mm). Chinook salmon fed in the same marine environments as coho salmon and consistently ate more and longer fish prey at a given size than coho salmon but had lower overall feeding intensity, perhaps owing to a higher level of prey selection. Relating subsequent interannual adult salmon returns to juvenile diets showed mixed results. During lower-survival years, coho salmon ate fewer and smaller fish prey, while subyearling Chinook salmon had less total food and more empty stomachs. We did not find consistent trophic patterns for yearling Chinook salmon in relation to their ultimate survival.

Ontogenetic diet shifts may be a mechanism to maximize fitness and survival for juvenile coho salmon *Oncorhynchus kisutch* and Chinook salmon *O. tshawytscha* in their first few months at sea. High predation pressure and size-selective mortality occurs during the early marine life history phase of juvenile salmonids (Moss et al. 2005). We also know that juvenile salmonids have high initial growth rates in the marine environment (Fisher and Pearcy 1988, 2005), coho salmon doubling in length in a few months (Brodeur 1991). This early rapid growth is thought to increase their chances of survival by reducing predation (Pearcy 1992; Trudel et al. 2007). High growth rates likely depend on intensive feeding (Weitkamp and Sturdevant 2008), which may also influence end-of-summer energy reserves and determine whether the salmon survive their first winter at sea (Beamish et al. 2004; Farley et al. 2007).

Coho and Chinook salmon in their first summer at sea in the northern California Current (NCC) eat a

mixture of small invertebrates and juvenile fish. Chinook salmon are generally more piscivorous than coho salmon (Brodeur and Pearcy 1990; Schabetsberger et al. 2003; Brodeur et al. 2007b; Baldwin et al. 2008). Coho and Chinook salmon undergo ontogenetic diet shifts, fish prey consumption increasing with salmon length (Brodeur 1991; Keeley and Grant 2001; Schabetsberger et al. 2003). The shift from a diet with numerous small invertebrate and fish prey to one of a few large fish prey could be critical to achieve the fast growth needed to avoid predators.

Keeley and Grant (2001) reviewed salmonid diet data from ocean, lake, and stream habitats and found that salmonids began feeding on fish prey at a smaller size in the marine environment compared with freshwater habitats. They concluded that the smaller size at onset of piscivory in ocean salmonids contributed to the greater growth potential in the marine habitats. Juvenile coho salmon in the ocean have the highest growth in length in the spring and early summer, and growth in weight in the fall (Fisher and Pearcy 2005). This early growth in skeletal length may assist in reducing predation pressure by size-selective predators, and the increase in bulk may assist

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Received November 25, 2008; accepted May 14, 2009  
Published online October 5, 2009

in overcoming potential food shortages in late fall and winter (Beamish and Mahnken 1999).

Ontogenetic shifts in prey type are driven, in part, by seasonal shifts in the prey available to juvenile and subadult coho and Chinook salmon, and there is a significant increase in amount of fish prey being consumed during their first marine summer as these salmon grow (Brodeur 1991). An overall increase in amount of fish prey consumed could signal an increase in preference of fish prey owing to physiological changes and demands, which could lead to enhanced growth and survival.

Brodeur (1991) examined ontogenetic diet shifts in juvenile salmon in the 1980s, and since that time there have been large changes in oceanographic conditions, fish communities (salmon and nonsalmon), hatchery production, and salmon diets and survival in the NCC (Emmett and Brodeur 2000; Brodeur et al. 2007a). This paper examines how the type of prey, stomach fullness, and size of prey change as juvenile and subadult coho and Chinook salmon grow during their first summer, and how these variables may have changed since Brodeur's 1980s study. Marine diet information is available for a broad size range of coho and Chinook salmon collected off Oregon and Washington from 1998 to 2003, enabling us to document changes in early marine feeding relative to size, month, and year, and also to identify any potential relationships with survival. We hypothesized that more larger or higher-quality prey are eaten in greater amounts during years of high survival compared with poor survival years, and that diets of small individuals may be important to our overall understanding of salmon dynamics because they have the highest risk of size-selective predation.

### Methods

**Fish collections.**—We collected juvenile salmonids off coastal Oregon and Washington in June and September 1998, and May, June, and September 1999–2003. We sampled with a 264 Nordic pelagic rope trawl along 5–10 transect lines, running perpendicular to shore, sampling stations along each transect extending from 3 to 50 km offshore (Figure 1; Fisher et al. 2007). The rope trawl, with a mouth opening 20 m deep and 30 m wide, was towed at the surface during daylight for 30 min at approximately 6 km/h (Brodeur et al. 2005). For each haul, captured salmon were identified to species, measured (fork length to the nearest 1 mm), individually tagged, and immediately frozen.

**Stomach analysis.**—In the laboratory, the field identifications of each salmon were verified, and each salmon was remeasured, weighed, and classified into life history stages of subyearling, yearling, and

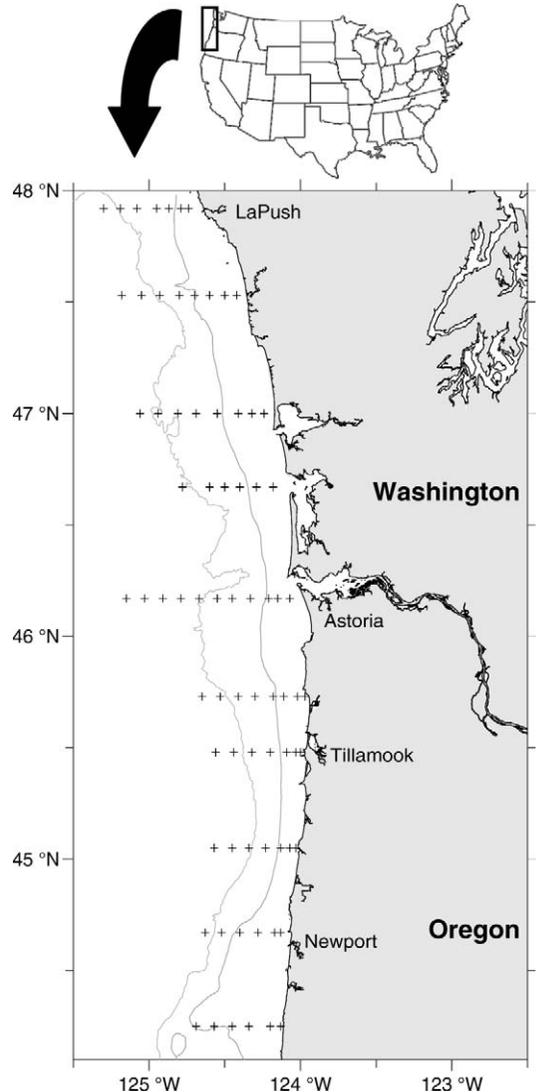


FIGURE 1.—Map showing the sampling transects off the coasts of Oregon and Washington where coho and Chinook salmon were collected by surface Nordic trawls; stations are marked with plus signs.

subadult based upon length criteria from Pearcy and Fisher (1990). Stomachs were removed and placed in a 10% solution of formaldehyde for approximately 2 weeks, then rinsed with freshwater for 24 h before being transferred into a 70% solution of ethanol. We analyzed up to 30 stomachs of each species and life history stage from each haul. Stomach contents were identified to the lowest possible taxonomic category using a dissecting microscope. Prey were enumerated and weighed to the nearest 0.001 g. Lengths of fully intact prey (up to five individuals per prey taxa per

stomach) were measured to the nearest 0.1 mm (ocular micrometer) or 1 mm (stage micrometer), measurement sensitivity varying with the absolute size of the taxa being measured. Prey were grouped into 13 categories that consistently contributed to greater than 5% of salmon diets by weight: fish (unidentified fish prey and other fish prey that made up <5% of diet), northern anchovy *Engraulis mordax*, Pacific herring *Clupea pallasii*, Pacific sardine *Sardinops sagax*, whitebait smelt *Allosmerus elongatus* and other unidentified smelts (family Osmeridae), Pacific sand lance *Ammodytes hexapterus*, cottids, rockfish *Sebastes* spp., euphausiids, the larvae of crabs *Cancer* spp., other decapods (non-*Cancer* spp.), amphipods, copepods, and "other" (pteropods, mysids, polychaetes, gelatinous zooplankton, cephalopods, insects, and cirripede larvae). All diet analysis was based on percent weight of these prey categories. References in the text to "forage fish" collectively include northern anchovy, clupeids, and osmerids.

Although yearling and subyearling Chinook salmon length differences were observed (Figure 2B), we grouped the diets of both life histories together owing to similarity in size-specific diets, despite differences in assumed ages and timing of ocean entry.

**Statistical analysis.**—To examine size-related variations in coho and Chinook salmon diets, we grouped the salmon into 20-mm length bins (Table 1; Figure 2) regardless of month, year, or location of collection, and calculated percent diet composition based on the 13 prey categories for each 20-mm length bin for both coho and Chinook salmon; data were then transformed using the arcsine square root transformation to improve normality (Zar 1999). We evaluated changes in diet composition by fish size using two complimentary multivariate methods: nonmetric multidimensional scaling (MDS) ordination and hierarchical cluster analysis, using PRIMER software (Clarke and Warwick 2001). Both tests relied on matrices constructed from pairwise Bray–Curtis similarity indices of diet composition between the 20-mm size categories (Field et al. 1982). We found similar MDS ordination and cluster analysis results when using smaller (5-mm) and larger (50-mm) length bins.

Ordination and cluster analysis results showed that coho salmon diets in 20-mm length bins clustered into three groups (small: 100–240 mm; medium: 241–375 mm; large: >375 mm) and into four groups for Chinook salmon (extra small: 80–120 mm, small: 121–200 mm, medium: 201–300 mm, large: >300 mm; see Results). We used these larger categories (i.e., extra small, small, medium, and large) for size-based seasonal and interannual diet comparisons by month (May, June, September), and year (1998–2003). In

these analyses, individual salmon diets were nested by haul within the larger size categories; haul was included to account for potential within-haul correlation of diet composition. A minimum sample size of five hauls per factor was used. To test statistically whether there is a significant difference between factor groups, we used analysis of similarities (ANOSIM), a multivariate analog to analysis of variance (ANOVA), which is based on the matrix of pairwise Bray–Curtis similarity coefficients (Clarke 1993). The ANOSIM generates a global *R*-value, which ranges from 0 (no separation of groups) to 1 (complete separation of groups); statistical significance is determined by permutation (Clarke 1993). To assess which prey contributed to significant diet differences, we used similarity percentage breakdown analysis (SIMPER; Clarke and Warwick 2001). We listed only the prey that contributed to at least 10% of the diet dissimilarities.

To examine differences in the overall amount of food eaten, or feeding intensity, as salmon grew, we used the following index of feeding intensity (IFI):

$$\text{IFI} = (\text{stomach content weight}) \div (\text{total fish weight} - \text{stomach content weight}) \times 100.$$

The percentage of empty stomachs was also used to quantify feeding and was defined as any stomach with less than 0.05% IFI (Weitkamp and Sturdevant 2008). The Kruskal–Wallis test, a nonparametric alternative to ANOVA, was used to look at differences in median feeding intensity between salmon size-groups (Zar 1999).

To examine relative differences in size of fish and invertebrate prey consumed between salmon size-groups, we calculated prey–predator size ratios (total length of prey divided by fork length of salmon) for each prey fish and compared ratios between different-sized predators using a Kruskal–Wallis test (Zar 1999). We also used Kolmogorov–Smirnov two-sample test to evaluate for differences between coho and Chinook salmon prey–predator length ratios by 20-mm size bins. We examined whether prey length was dependent upon predator length for the dominant fish prey using least-squares regression and quantile regression for each 5% quantile (Scharf et al. 1998), using SAS software (SAS Institute 2005).

We also compared trophic habits of small juvenile salmon (100–240-mm coho salmon, 120–300-mm yearling Chinook salmon, and 120–220-mm subyearling Chinook salmon) in their first summer at sea with survival estimates from their adult returns in subsequent years under the assumption that most marine mortality influenced by food habits occurs when fish

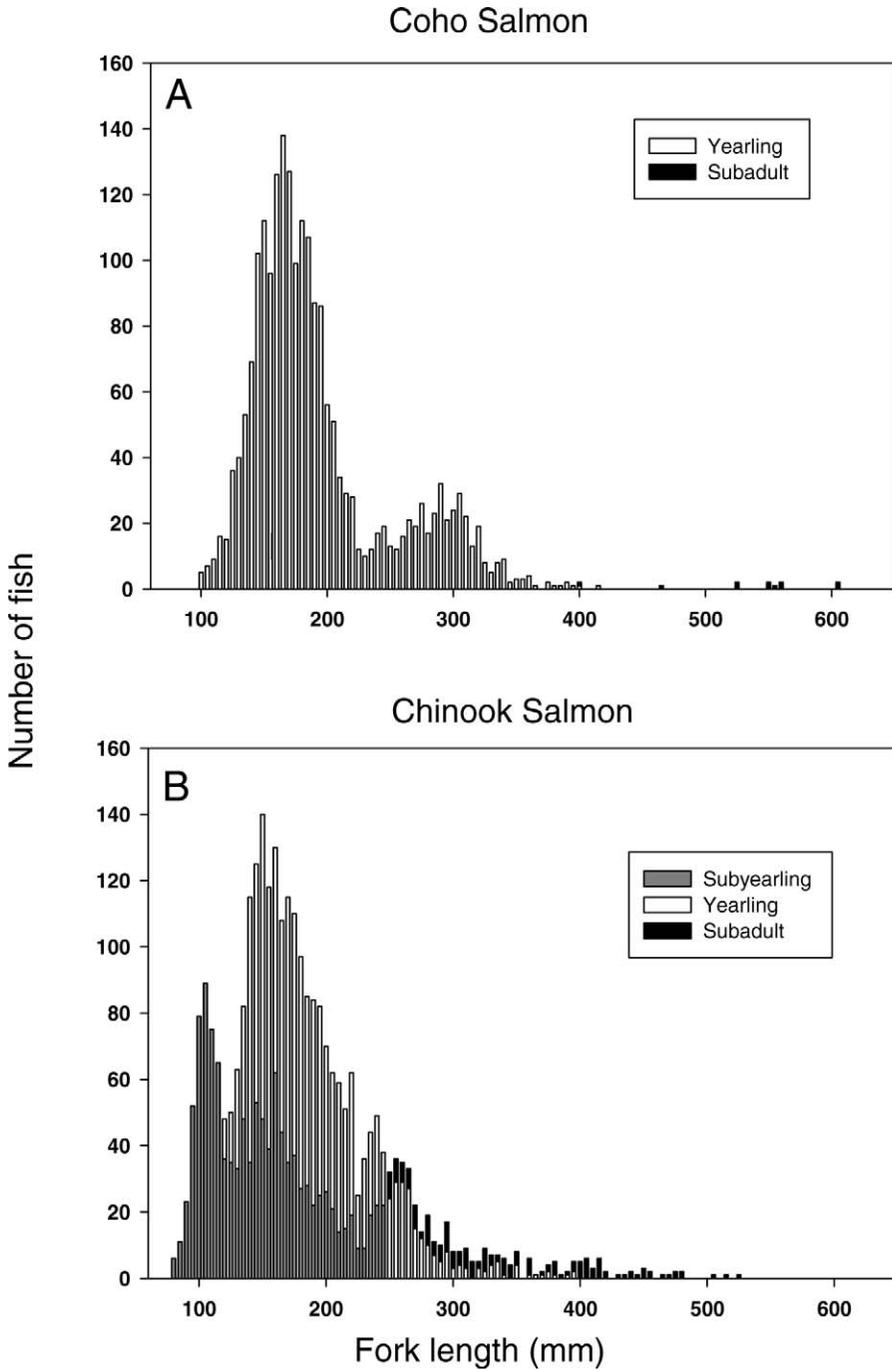


FIGURE 2.—Length frequency distributions for (A) the coho salmon and (B) the chinook salmon used in this study, by age-class or life history stage.

TABLE 1.—Mean fork length, wet weight, percent of fish in diets, sample sizes, and size-grouping for coho and Chinook salmon. Values in parentheses are SDs.

Species	Length-class	Fork length (mm)	Wet weight (g)	% Piscivory	Sample size				Size-grouping	
					May	Jun	Sep	Total		
Coho salmon	100–120	113.0 (5.7)	14.9 (2.6)	30.1	8	31	0	39	Small	
	121–140	132.7 (5.5)	23.6 (3.9)	51.7	71	84	0	155	Small	
	141–160	151.1 (5.5)	34.6 (5.4)	49.1	236	170	0	406	Small	
	161–180	170.1 (5.7)	51.0 (7.8)	64.0	158	361	1	520	Small	
	181–200	189.8 (5.8)	74.1 (9.9)	66.1	47	357	0	404	Small	
	201–220	209.5 (5.7)	103.7 (13.8)	65.2	21	148	4	173	Small	
	221–240	228.5 (5.8)	137.9 (15.7)	52.7	6	51	7	64	Small	
	241–260	250.1 (6.0)	189.5 (20.0)	77.9	4	21	42	67	Medium	
	261–280	271.2 (6.2)	243.4 (26.1)	74.9	1	4	85	90	Medium	
	281–300	291.7 (5.4)	302.0 (29.9)	84.8	0	5	103	108	Medium	
	301–375	321.2 (16.7)	411.4 (84.6)	79.1	0	1	169	170	Medium	
	376+	478.0 (93.3)	1,446.2 (697.5)	91.6	1	11	12	24	Large	
Total		198.7 (62.7)	123.1 (193.2)		553	1,244	423	2,220		
Chinook salmon	80–100	95.0 (4.6)	8.4 (1.3)	53.4	1	100	0	101	Extra-small	
	101–120	110.1 (5.6)	13.6 (2.5)	66.4	8	319	5	332	Extra-small	
	121–140	131.8 (5.8)	23.6 (4.1)	72.4	99	102	56	257	Small	
	141–160	150.7 (5.7)	36.8 (5.9)	78.5	253	90	190	533	Small	
	161–180	170.4 (5.9)	55.7 (8.3)	81.3	179	115	201	495	Small	
	181–200	190.3 (5.9)	79.8 (12.0)	79.2	150	102	108	360	Small	
	201–220	209.9 (6.0)	111.1 (14.0)	80.5	76	102	82	260	Small	
	221–240	229.8 (6.3)	147.7 (16.9)	84.7	45	74	65	184	Medium	
	241–260	249.9 (5.8)	197.2 (22.4)	90.6	42	30	99	171	Medium	
	261–280	268.9 (5.5)	250.9 (24.6)	86.7	25	22	70	117	Medium	
	281–300	290.7 (6.6)	312.6 (28.8)	89.4	8	22	35	65	Medium	
	301–375	331.7 (20.3)	483.1 (98.4)	70.4	1	53	36	90	Large	
	376+	424.8 (39.2)	1,033.4 (339.8)	96.2	0	41	22	63	Large	
	Total		184.9 (64.9)	110.8 (174.3)		887	1,172	969	3,028	

are still small (Pearcy 1992). We examined interannual variability in proportion of piscivory, feeding intensity, percent empty stomachs, and fish prey to predator length ratios of yearling coho and Chinook salmon and subyearling Chinook salmon in relation to their estimates of salmon survival to adults. Interannual changes in these variables were tested using a Kruskal–Wallis test followed by Dunn’s multiple comparison test when significant differences were detected ( $P < 0.05$ ). We did not test the percent of empty stomachs because only one data point is estimated per year. Owing to low sample sizes, this analysis excluded the year 1998, yearling Chinook salmon in September, and subyearling Chinook salmon in May or June.

Indices of salmon survival were from various sources. The marine survival of coho salmon in the Oregon Production Index (OPI) region was obtained by dividing adult and jack (precocious male) returns by the number of smolts released (PMFC 2008); the survival of yearling Chinook salmon was based on smolt-to-adult ratios (SARs) from Scheuerell and Williams (2005) and M. Scheuerell (Northwest Fisheries Science Center, personal communication); jack counts at Bonneville Dam (CBS 2008) served as our measure of the marine survival of subyearling Chinook salmon (Pearcy 1992). Survival year was adjusted to smolt outmigration year.

**Results**

*Ontogenetic Diet Composition*

Coho and Chinook salmon were caught in marine waters from central Oregon to northern Washington during 6 years (1998–2003), high spatial overlap occurring between the two species. The collections included yearling coho and Chinook salmon that were caught throughout the summer, whereas subyearling Chinook salmon were collected primarily in September. We analyzed diets of 5,248 juvenile to subadult coho and Chinook salmon caught in 411 hauls during May (except 1998;  $n = 1,440$ ), June ( $n = 2,416$ ), and September ( $n = 1,392$ ; Table 1).

Coho salmon were typically less piscivorous than Chinook salmon for the same size-groups, and the proportion of fish prey in coho and Chinook salmon diets generally increased with salmon size. Average proportions of total fish prey in coho salmon diets increased from 62.0% in the smallest (100–240 mm fork length [FL]) size-group, to 79.5% for medium (241–375 mm FL) and 91.6% fish prey for the largest coho salmon (>375 mm FL). Chinook salmon diets averaged 64.6% fish prey for extra-small (80–100 mm FL), 79.1% for small (101–220 mm FL), 86.5% for medium (221–300 mm FL), and 85.9% for large (>301 mm FL) size-groups.

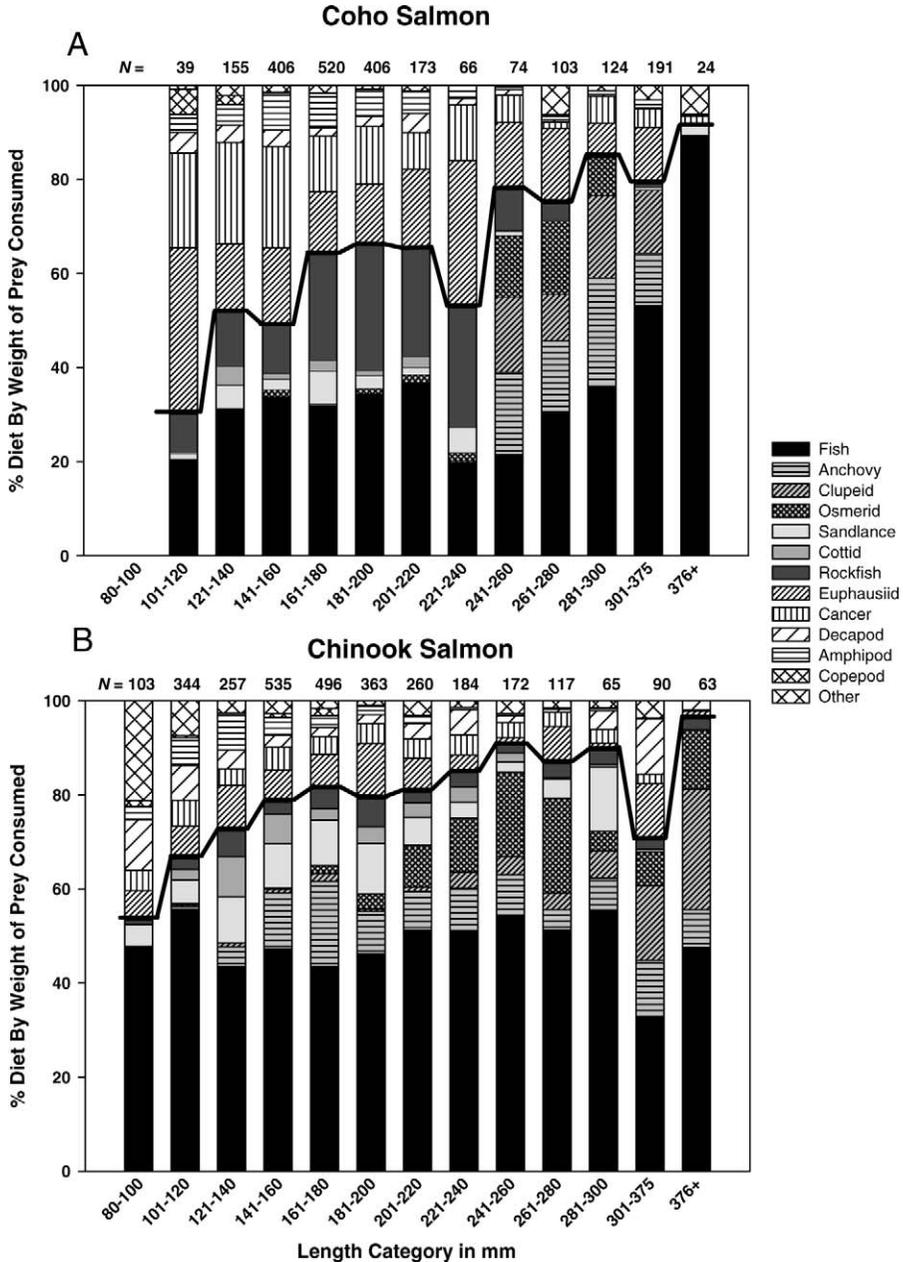


FIGURE 3.—Dominant prey categories in the diets of (A) coho salmon and (B) Chinook salmon, by 20-mm length-classes. Sample sizes are noted above the bars. The data below the dark line are for fish prey, and the line itself represents the piscivory trend.

Size-based diets of the smallest coho salmon were commonly composed of juvenile rockfish, the larvae of crabs, and adult euphausiids. These invertebrate prey decreased as the proportions of forage fish (northern anchovy, clupeids, and osmerids) increased as coho salmon grew (Figure 3A). Clear size-based diet differences were identified using MDS and cluster

analysis (Figure 4A) for coho salmon. However, when we tested for significant differences between size-based diets, the ANOSIM results revealed only weak separation between small and medium coho salmon diets (global  $R = 0.055$ ,  $P = 0.002$ ; Table 2), but strong diet differences between haul groups (global  $R = 0.327$ ;  $P = 0.001$ ). This finding suggests that coho salmon of

TABLE 2.—Analysis of similarity (ANOSIM) test results of significant ( $P < 0.05$ ) differences in coho salmon diet composition by size, month, and year. Prey contributing to significant diet differences were identified by similarity percentage (SIMPER) analysis. Prey that contributed more than 10% (single asterisks) or more than 15% (double asterisks) to diet dissimilarity are indicated; ns = not significant; ID = insufficient data to run analyses.

Comparison	ANOSIM		SIMPER					
	R	p	Fish	Anchovies	Clupeids	Osmerids	Sand lance	Cottids
<b>Coho salmon</b>								
<b>Size</b>								
Small and medium	0.055	0.002	**					
Small and large		ns						
Medium and large		ns						
<b>Month</b>								
Small (May, Jun)	0.127	0.001	**					
Large (Jun, Sep)		ns						
<b>Year</b>								
Small, May (1999–2003) <sup>a</sup>	0.574	0.001	**					*
Small, Jun (1998–2003) <sup>a</sup>	0.608	0.001	**					*
Medium, Sep (1998–2003) <sup>b</sup>	0.417	0.001	**	*	*			
Large (1998–2003)		ns						
<b>Chinook Salmon</b>								
<b>Size</b>								
Extra small, small, medium, and large <sup>a</sup>	0.241	0.001	**					
<b>Month</b>								
Extra small	ID							
Small (May, Jun, Sep) <sup>a</sup>	0.409	0.001	**					*
Medium (May, Jun, Sep) <sup>a</sup>	0.321	0.001	**					*
Large (Jun–Sep)	0.23	0.001	**		*			
<b>Year</b>								
Extra small, May (1999–2003)	ID							
Extra small, Jun (1998–2003) <sup>c</sup>	0.252	0.001	**					
Extra small, Sep (1998–2003)	ID							
Small, May (1999–2003) <sup>d</sup>	0.081	0.01	**				**	*
Small, Jun (1998–2003)		ns						
Small, Sep (1998–2003)		ns						
Medium, May (1999–2003)		ns						
Medium, Jun (1998–2003)		ns						
Medium, Sep (1998–2003) <sup>e</sup>	0.055	0.05	**	*	*	**		
Large, May (1999–2003)		ns						
Large, Jun (1998–2003)		ns						
Large, Sep (1998–2003)		ns						

<sup>a</sup> All pairs significantly different.

<sup>b</sup> All pairs significantly different except (1998, 1999) and (1998, 2003).

<sup>c</sup> The following pairs were significantly different: (1998, 2000), (1998, 2001), (1998, 2003), (2000, 2001), (2000, 2003), (2001, 2003), and (2002, 2003).

<sup>d</sup> The following pairs were significantly different: (1999, 2000), (1999, 2003), (2001, 2002), and (2001, 2003).

<sup>e</sup> The following pairs were significantly different: (1998, 2003), (1999, 2000), (1999, 2002), (1999, 2003), (2001, 2002), and (2001, 2003).

various sizes were opportunistic predators and ate similar prey within a haul (where they were caught), which appeared to be stronger than size-based feeding preferences.

Chinook salmon consistently ate Pacific sand lance, cottids, forage fish, and small amounts of rockfish and invertebrates (Figure 3B). The MDS and cluster analysis of size-based diet composition grouped Chinook salmon into four distinct size categories (Figure 4B). Chinook salmon also became increasingly piscivorous as they grew, but unlike coho salmon, Chinook salmon had strong size-based diet differences

for all sizes (global  $R = 0.241$ ,  $P = 0.001$ ; Table 3), as well as between haul diet differences (global  $R = 0.240$ ;  $P = 0.001$ ). Chinook salmon maintained strong size-based feeding habits even when they were caught at the same location (haul). Varying proportions of fish contributed to diet differences between all size categories (SIMPER results, Table 3).

*Ontogenetic Seasonal and Interannual Patterns*

Ontogenetic diets of coho and Chinook salmon displayed both monthly and interannual changes in prey composition, although the patterns were species

TABLE 2.—Extended.

Comparison	SIMPER						
	Rockfish	Euphausiids	Crabs	Decapods	Amphipods	Copepods	Other
<b>Coho salmon</b>							
<b>Size</b>							
Small and medium		**	**				
Small and large							
Medium and large							
<b>Month</b>							
Small (May, Jun)		**	**				
Large (Jun, Sep)							
<b>Year</b>							
Small, May (1999–2003) <sup>a</sup>		*	**	*	**		
Small, Jun (1998–2003) <sup>a</sup>	*	**	**	*	**		*
Medium, Sep (1998–2003) <sup>b</sup>		*	*		*		*
Large (1998–2003)							
<b>Chinook Salmon</b>							
<b>Size</b>							
Extra small, small, medium, and large <sup>a</sup>		*	*	*	*		*
<b>Month</b>							
Extra small							
Small (May, Jun, Sep) <sup>a</sup>		*	*	*	*		
Medium (May, Jun, Sep) <sup>a</sup>			*	*			
Large (Jun, Sep)		*	*	*			
<b>Year</b>							
Extra small, May (1999–2003)							
Extra small, Jun (1998–2003) <sup>c</sup>		*	*	**	**		**
Extra small, Sep (1998–2003)							
Small, May (1999–2003) <sup>d</sup>		**	**	*			
Small, Jun (1998–2003)							
Small, Sep (1998–2003)							
Medium, May (1999–2003)							
Medium, Jun (1998–2003)							
Medium, Sep (1998–2003) <sup>e</sup>		*	**	*			*
Large, May (1999–2003)							
Large, Jun (1998–2003)							
Large, Sep (1998–2003)							

specific. Small coho salmon ate significantly more fish prey and crab larvae in May and more adult euphausiids in June, although the overall diet differences between the 2 months were weak (global  $R = 0.127$ ,  $P < 0.001$ ; Table 2). In contrast, small, medium, and large Chinook salmon diets clearly changed monthly. Small Chinook salmon ate more fish and Pacific sand lance in May, and more northern anchovy larvae in September (global  $R = 0.409$ ;  $P < 0.001$ ). Medium Chinook salmon ate more Pacific sand lance in May, and more fish and northern anchovy (larvae and juveniles) in September (global  $R = 0.321$ ;  $P < 0.001$ ). Finally, large Chinook salmon monthly changes were primarily due to more fish and clupeids being eaten in September (global  $R = 0.230$ ,  $P < 0.001$ ; Table 3). For the three sizes, June diets were a

transition between May and September, declines occurring in May fish types and increases in September fish.

Small coho salmon had strong interannual changes in their diets for all pairs of years. Interannual diet changes were primarily due to increases in the amounts of fish (2002), crab larvae (2001, 2003), euphausiids (June 2000 only), and amphipods in 2000 (May global  $R = 0.574$ , June global  $R = 0.608$ ,  $P < 0.001$ ; Table 2). Medium coho salmon diets also showed strong interannual differences owing to elevated proportions of fish (1998 and 2000–2001), northern anchovy (2002), and clupeid (2000) prey (global  $R = 0.417$ ,  $P < 0.001$ ; Table 2). In contrast with coho salmon, we found weak or nonexistent interannual diet changes for Chinook salmon diets (Table 3). Only extra small

TABLE 3.—Analysis of similarity (ANOSIM) test results of significant ( $P < 0.05$ ) differences in Chinook salmon diet composition by size, month, and year. Prey contributing to significant diet differences were identified by similarity percentage (SIMPER) analysis. Prey that contributed more than 10% (single asterisks) or more than 15% (double asterisks) to diet dissimilarity are indicated; ns = not significant.

Comparison	ANOSIM		SIMPER				
	<i>R</i>	<i>p</i>	Fish	Anchovies	Clupeids	Osmerids	Sand lance
<b>Size</b>							
Extra small, small, medium, and large <sup>a</sup>	0.241	0.001	**				
<b>Month</b>							
Small (May, Jun, Sep) <sup>a</sup>	0.409	0.001	**				*
Medium (May, Jun, Sep) <sup>a</sup>	0.321	0.001	**				**
Large (Jun, Sep)	0.23	0.001	**		*		
<b>Year</b>							
Extra small, Jun (1998–2003) <sup>b</sup>	0.252	0.001	**				
Small, May (1999–2003) <sup>c</sup>	0.081	0.01	**				**
Small, Jun (1998–2003)		ns					
Small, Sep (1998–2003)		ns					
Medium, May (1999–2003)		ns					
Medium, Jun (1998–2003)		ns					
Medium, Sep (1998–2003)		ns					
Large, May (1999–2003)		ns					
Large, Jun (1998–2003)		ns					
Large, Sep (1998–2003)		ns					

<sup>a</sup> All pairs significantly different.

<sup>b</sup> The following pairs were significantly different: (1998, 2000), (1998, 2001), (1998, 2003), (2000, 2001), (2000, 2003), (2001, 2003), and (2002, 2003).

<sup>c</sup> The following pairs were significantly different: (1999, 2000), (1999, 2003), (2001, 2002), and (2001, 2003).

Chinook salmon in June had interannual differences with increases in amounts of fish (2002), decapod larvae (2003), amphipods (2000), and “other” prey (1998) in their diets (global  $R = 0.252$ ,  $P < 0.001$ ; Table 3). Large coho salmon did not show significant seasonal or interannual diet changes.

Prey changes were numerous from year to year and did not show much coherence between coho and Chinook salmon. There were a few years where both salmon consumed similar prey at higher levels, such as more fish prey in 2002, “other” prey in 1998, amphipods in 2000, and Pacific sand lance in 2002 (Tables 2, 3). This pattern may reflect an overlap in diets owing to higher abundances of the prey items, or in the case of the El Niño summer of 1998, the absence of the normal prey community (Lluch-Belda et al. 2005).

*Ontogenetic Feeding Intensity and Percent Empty Stomachs*

Patterns of feeding intensity were quite different between coho and Chinook salmon. Overall, coho salmon had a higher average IFI (1.3%) than Chinook salmon (0.9%), and only for the largest size-class did Chinook salmon (1.0%) have higher feeding intensity than large coho salmon (0.3%). Coho salmon exhibited a peak feeding intensity in their medium size-class (1.4%), and as Chinook salmon grew, they had little

variability in their size-based feeding intensity (Figure 5B). Coho and Chinook salmon both had an increase in percent empty stomachs as they became larger and more piscivorous (Figure 5).

Coho salmon had a peak in feeding intensity (1.9%) between the lengths of 241–260-mm FL, the size associated with a shift towards more forage fish in their diets (Figure 5A). Medium coho salmon ate significantly more food by weight than small coho salmon, and both sizes ate more than the large coho salmon (Kruskal–Wallis test:  $P < 0.001$ ; Figure 5A). The mean percentage of empty stomachs was highest for the largest coho salmon size-class (45.8%; Figure 5A).

Chinook salmon exhibited a relatively consistent feeding intensity as extra-small, small, and large Chinook salmon averaged 1.0% IFI, whereas medium Chinook salmon were significantly lower and averaged 0.8% (Kruskal–Wallis test:  $P < 0.001$ ). The lower intensity in medium fish coincided with a peak in forage fish consumption (Figure 5B). The smallest Chinook salmon had the lowest percentage of empty stomachs (10.5%) and highest mean feeding intensity, indicating greater potential for high growth when they first enter the ocean environment compared with other groups. Like coho salmon, the largest Chinook salmon had the highest percentage of empty stomachs (17.6%; Figure 5B).

TABLE 3.—Extended.

Comparison	SIMPER							
	Cottids	Rockfish	Euphausiids	Crabs	Decapods	Amphipods	Copepods	Other
			<b>Size</b>					
Extra small, small, medium, and large <sup>a</sup>			*	*	*	*		*
			<b>Month</b>					
Small (May, Jun, Sep) <sup>a</sup>			*	*	*	*		
Medium (May, Jun, Sep) <sup>a</sup>			*	*	*			
Large (Jun, Sep)			*	*	*			
			<b>Year</b>					
Extra small, Jun (1998–2003) <sup>b</sup>			*	*	**	**		**
Small, May (1999–2003) <sup>c</sup>	*		**	**	*			
Small, Jun (1998–2003)								
Small, Sep (1998–2003)								
Medium, May (1999–2003)								
Medium, Jun (1998–2003)								
Medium, Sep (1998–2003)								
Large, May (1999–2003)								
Large, Jun (1998–2003)								
Large, Sep (1998–2003)								

#### Ontogenetic Prey Size Relationships

Based on ratios of fish prey lengths to salmon fork lengths, both coho and Chinook salmon ate longer fish prey as they grew (mean prey predator ratios = 0.18 and 0.20, respectively). The average size of fish prey consumed by coho salmon was fairly consistent for salmon 100–240 mm in length, but increased substantially starting at 241–260 mm (Figure 6A), owing mainly to the consumption of large forage fish prey. When grouped into larger size categories, medium coho salmon had the highest fish prey–predator length ratio (0.20; Kruskal–Wallis test:  $P < 0.001$ ). In contrast, Chinook salmon gradually increased their fish prey–predator length ratio and did not have an area of substantial increase resembling the coho salmon pattern. Instead, extra-small and large Chinook salmon had significantly higher fish prey-to-predator length ratios (0.21) than medium Chinook salmon (0.19; Figure 6B). Chinook salmon had a significantly higher fish prey–predator length ratio (Kolmogorov–Smirnov test:  $P < 0.001$ ) than coho salmon at most sizes, coho salmon eating significantly larger fish prey only after reaching 281–300 mm FL.

Both species showed increasing size of fish prey consumed with increasing predator size (Figure 7;  $P < 0.0001$ ). The ratio between prey and predator lengths was slightly higher in coho salmon (0.27) than Chinook salmon (0.21), but the slopes were not significantly different. As seen with the predator–prey ratios, there is a dramatic increase in the size of the

largest prey eaten by coho salmon larger than 240 mm FL owing mainly to the consumption of large forage fish prey.

#### Relationship to Survival

Marine survival rates between coho and Chinook salmon varied by species and age-class: coho salmon survival rates were high in 2000 (OPI = 4.6%) and 2002 (OPI = 4.1%), and low in 1999 (OPI = 2.4%), while both yearling and subyearling Chinook salmon had high rates in 2000 (SAR = 3.8 and 74,496 jacks, respectively) and low rates in 2003 (SAR = 0.6% and 38,557 jacks, respectively), high survival for yearlings occurring in 1999 (SAR = 3.8%) as well (Table 4).

Our expectations that salmon would feed on larger prey, more quality prey such as fish, and have higher stomach fullness in high survival years than low survival years was not entirely supported by the data. Trophic habits of coho salmon for these contrasting survival years revealed that in 2002, a high survival year, coho salmon ate significantly more fish prey than any other year (Dunn's multiple range test:  $P < 0.0001$ ), and that 1999, the lowest survival year examined, had the least amount of total fish prey eaten. Coho salmon ate the shortest fish prey relative to their length in the low survival of 1999 (Kruskal–Wallis:  $P = < 0.0001$ ). Subyearling Chinook salmon, in the low survival year of 2003, had the lowest overall feeding intensity (0.5%), about half that of 2000 (0.9%; Table 4). Also in 2003, 25% of their stomachs were empty. Yearling Chinook salmon had substantially

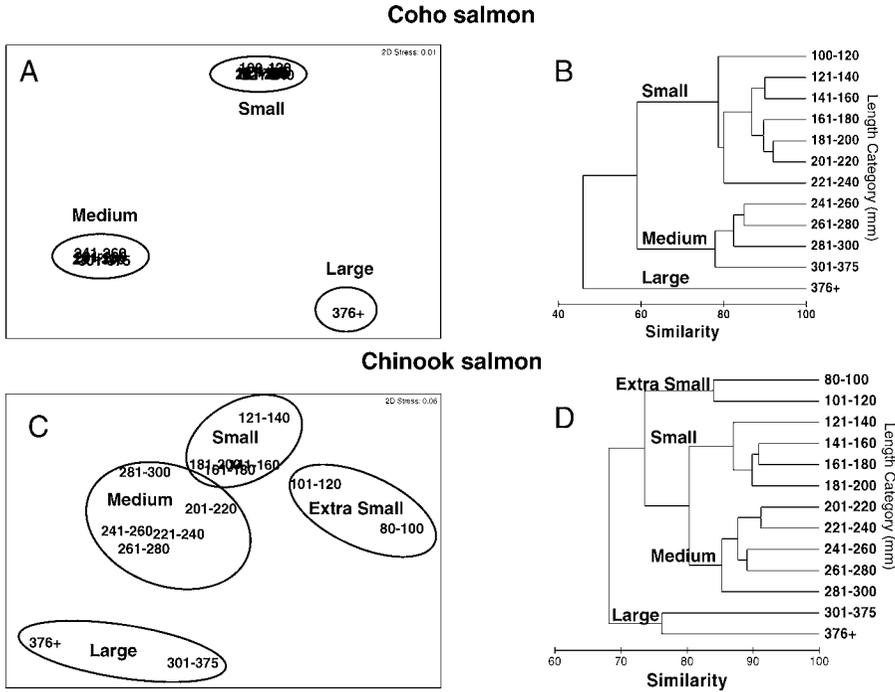


FIGURE 4.—Nonmetric multidimensional scaling ordination (left panels) and cluster analysis (right panels) of the diets of (A)–(B) coho salmon and (C)–(D) Chinook salmon, by 20-mm length-classes.

higher SAR levels in 1999 and 2000 than the extremely low survival year of 2003, yet we found little evidence of more favorable trophic indices between these years (Table 4).

Better trophic habits were not found consistently during higher survival years. We did not find a relationship between coho salmon survival and total amount of food eaten as there was little interannual variability in this index (Table 4). We also found the highest amounts of percent empty stomachs for coho salmon in 2002, a year of high survival and piscivory. Yearling Chinook salmon had their highest feeding intensity level in their worst survival year of 2003 and the highest percentage of empty stomachs (10.2%) in their peak survival year of 1999. Average fish prey–predator ratios for yearling Chinook salmon were highest in 1999, but they were not statistically different than 2003 (Kruskal–Wallis test:  $P = 0.003$ ). Subyearling Chinook salmon consumed significantly more total fish prey in their lowest survival year of 2003 (91.3%) than in 2000 (30.0%; Kruskal–Wallis test:  $P < 0.0001$ ; Table 4).

In summary, coho salmon were more piscivorous and ate longer fish in their higher survival years, subyearling Chinook salmon had fewer empty stomachs and higher amounts of food in their better survival

years, and we found mixed results with yearling Chinook salmon during their variable survival years.

**Discussion**

Clear ontogenetic increases in piscivory occurred in juvenile coho and Chinook salmon during their first marine summer in the NCC. As the salmon grew, their diets changed from a mixture of invertebrate and smaller fish prey to diets primarily composed of larger fish prey, Chinook salmon being more piscivorous than coho salmon. These results are consistent with those of previous studies (Peterson et al. 1982; Beacham 1986; Brodeur 1991). Chinook salmon maintained more consistent size-based feeding habits even when caught together in the same salmon haul, while coho salmon were more opportunistic predators (different size coho salmon typically eating similar prey when caught together). Most sizes of coho salmon exhibited a higher feeding intensity than Chinook salmon, which is similar to recent work by Weitkamp and Sturdevant (2008), but in contrast to findings in Brodeur (1992) for diets in the 1980s when coho and Chinook salmon feeding intensities were not significantly different from each other.

As coho salmon increased in length, their diets markedly shifted to include forage fish prey, and we

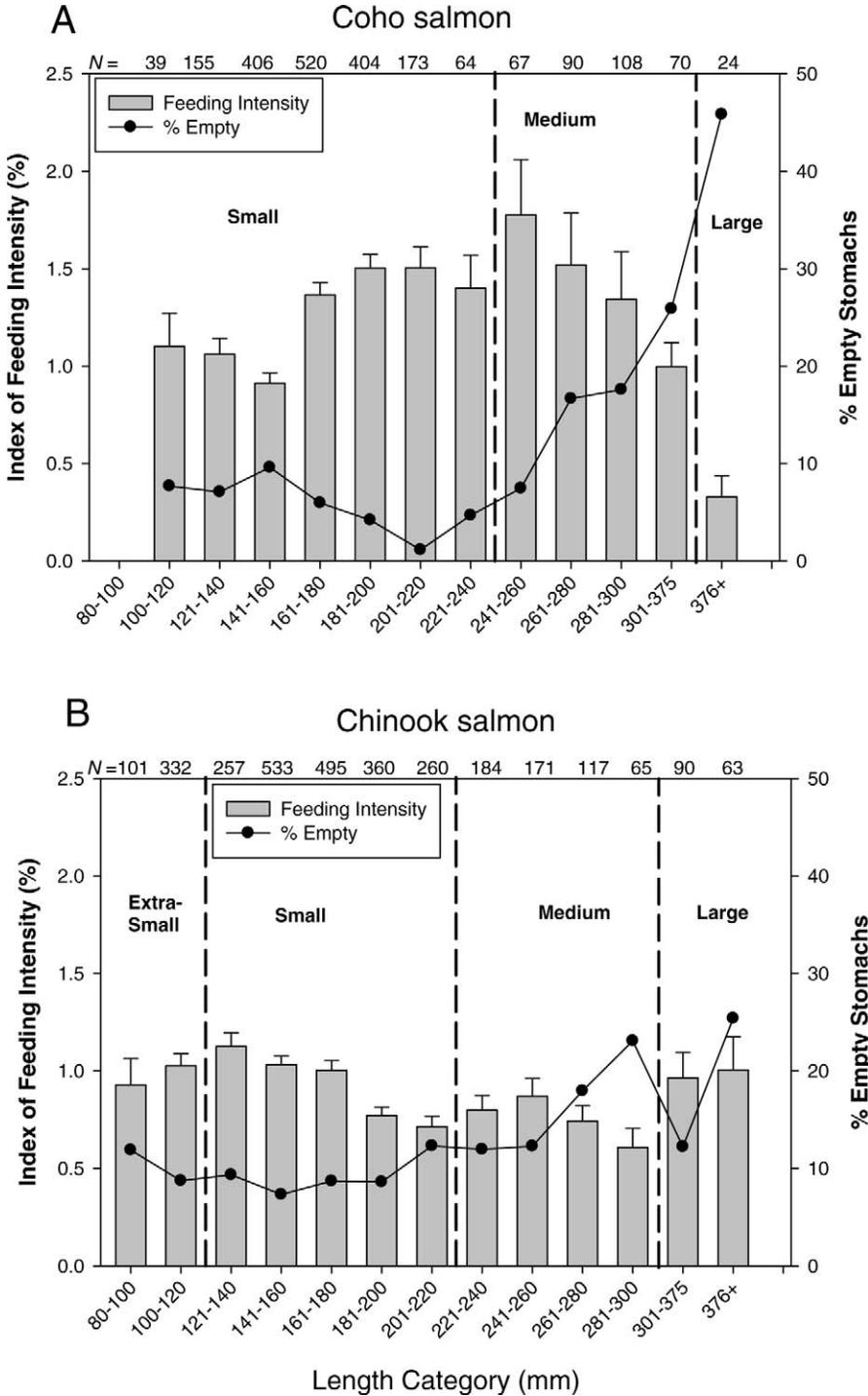


FIGURE 5.—Indices of feeding intensity and percentages of empty stomachs for (A) coho salmon and (B) Chinook salmon. Sample sizes are noted above the bars; the thin vertical lines represent SEs. The dashed lines separate the major size-groups.

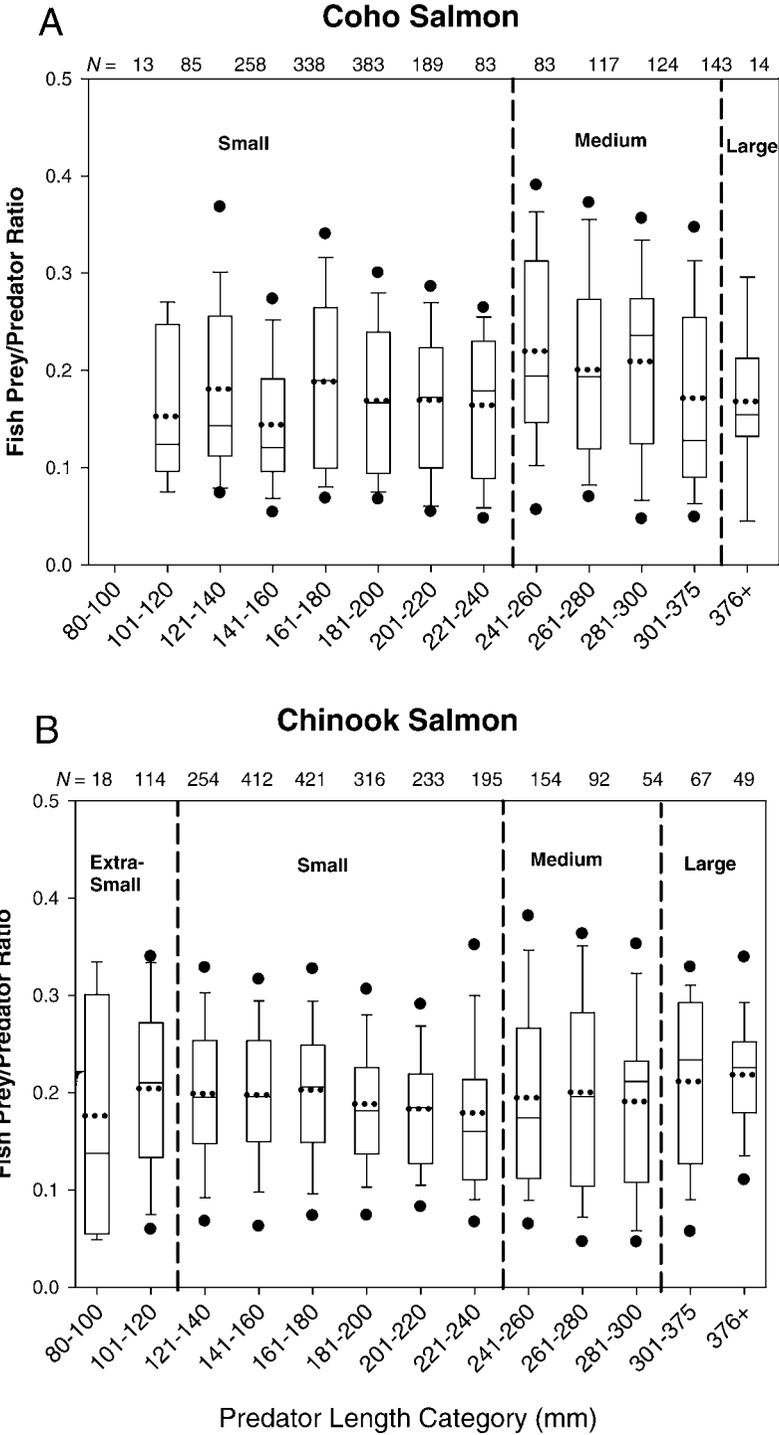


FIGURE 6.—Fish prey–predator length ratios for (A) coho salmon and (B) Chinook salmon. Shown are box plots with the medians (solid lines in the boxes), means (dotted lines within the boxes), 25th and 75th percentiles (lower and upper ends of the boxes), 10th and 90th percentiles (error bars), and 5th and 95th percentiles (points) for each year. Sample sizes are noted above the box plots. The dashed lines separate the major size-groups.

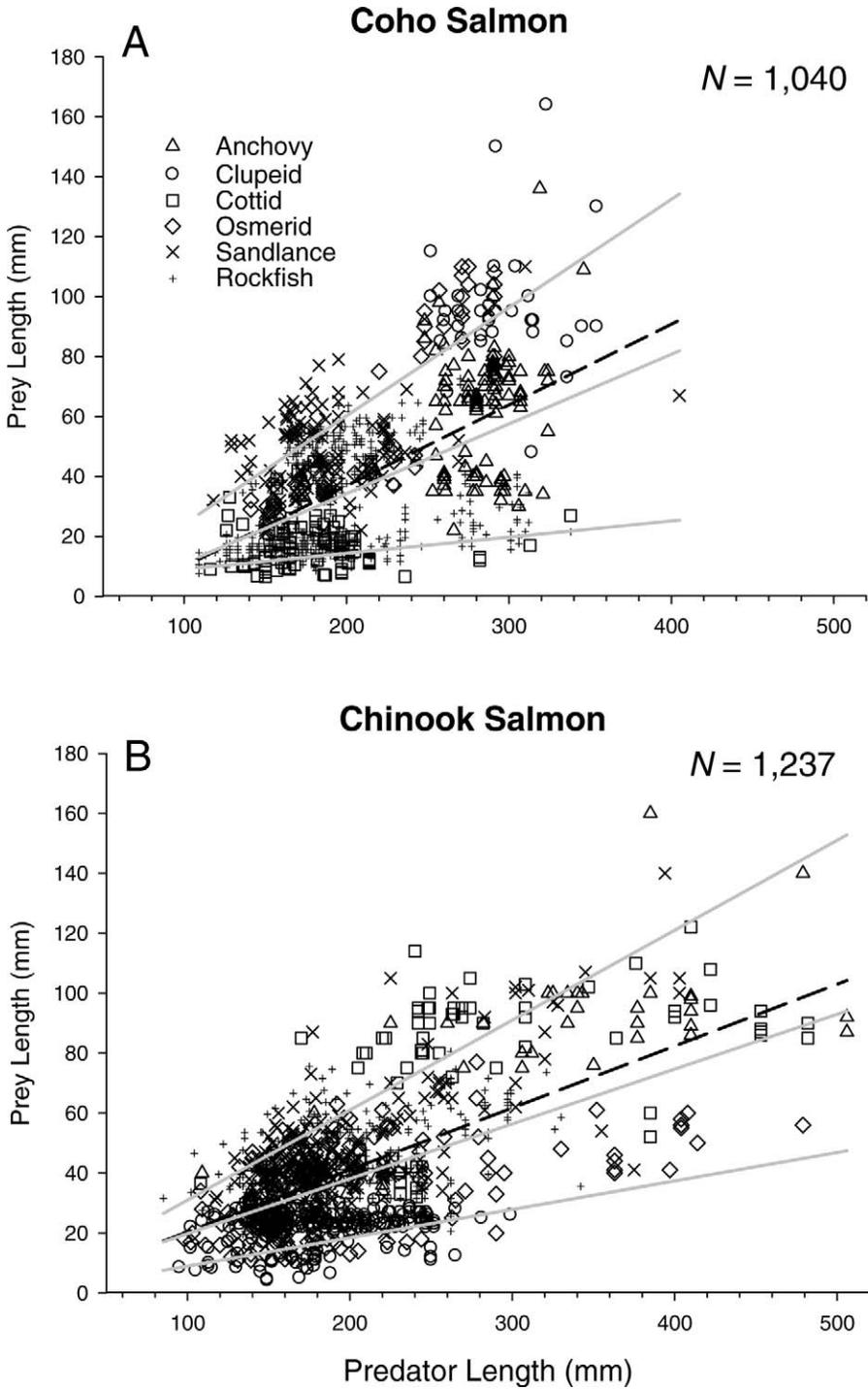


FIGURE 7.—Relationships between predator length and that of the dominant fish prey found in the stomachs of (A) coho salmon and (B) Chinook salmon. Also shown are the best-fit linear regressions (dashed lines) and the 5, 50, and 95% quantile regressions (the lower, middle, and upper gray lines, respectively) for all fish prey species combined.

TABLE 4.—Survival estimates and percent fish in diets, percent feeding intensity, percent empty stomachs, and fish prey–predator length ratios for yearling coho and Chinook salmon and subyearling Chinook salmon in 1999–2003. *P*-values from Kruskal–Wallis tests and significant year pairs from Dunn’s multiple comparison test are listed.

Smolt migration year	Survival (%) <sup>a</sup>	Total fish (%)	Feeding intensity (%)	Empty stomachs (%)	Fish prey : predator
<b>Coho salmon (100–240 mm, all months)</b>					
1999	2.4	37.1	0.9	6.0	0.13
2000	4.6	24.1	1.2	5.5	0.20
2001	2.7	43.4	1.4	6.7	0.21
2002	4.1	63.0	1.4	7.7	0.16
2003	2.8	42.3	1.3	4.1	0.15
<i>P</i> -value		<0.0001	0.03	No test	<0.0001
Significant annual pairs		2002 > all years; all years > 2000 except 1999	None found		2000 and 2001 > 2002 > 2003 and 1999
<b>Yearling Chinook salmon (120–300 mm in May and Jun)</b>					
1999	3.8	67.3	0.8	10.2	0.19
2000	3.2	50.0	1.0	7.0	0.18
2001	2.2	71.5	0.7	7.7	0.16
2002	2.3	75.6	0.8	7.5	0.18
2003	0.6	71.5	1.1	6.9	0.17
<i>P</i> -value		<0.0001	0.01	No test	0.003
Significant annual pairs		All year > 2000	2003 and 2002 > all years		1999 and 2002 > 2001
<b>Subyearling Chinook salmon (120–220 mm in Sep)</b>					
1999	55,538	48.1	0.6	12.3	0.23
2000	74,496	30.0	0.9	15.6	0.18
2001	40,179	62.2	0.8	11.1	0.17
2002	47,601	81.0	1.5	4.8	0.24
2003	38,557	91.3	0.5	25.0	0.26
<i>P</i> -value		<0.0001	<0.0001	No test	<0.0001
Significant annual pairs		2003 and 2002 > all years; 2001 > 2000	2002 > all years		2003 and 2002 > 2001

<sup>a</sup> Jack counts for subyearling Chinook salmon.

also saw corresponding increases in feeding intensity and prey–predator length ratios. The principal size-based trophic changes in coho salmon may be driven by their physical ability to consume forage fish prey, and our data suggests that this shift occurs when coho salmon are larger than 240 mm. Similar size-based increases in piscivory were seen for coho salmon collected in the 1980s (Brodeur 1991), although there was not a sharp increase in amount or size of fish consumed as seen in the present study. The physical ability of coho salmon to consume large fish prey in late summer may substantially increase their chances to survive over the winter, when prey resources would be reduced (Beamish and Mahnken 1999).

For Chinook salmon, we saw higher proportions of fish appearing in their diets at a much smaller predator size and earlier in the summer than for coho salmon. Chinook salmon appeared to be a more piscivorous and selective predator than coho salmon, consistent with the earlier observations (Brodeur 1991). Chinook salmon consistently ate significantly larger fish prey relative to body length than coho salmon for most size-classes. These results are in contrast with those for

juvenile coho and Chinook salmon in the 1980s, when coho salmon ate significantly longer prey for their length (Brodeur 1991). Another notable difference between the two study periods was that we saw an almost doubling in percent empty stomachs between the 1980s (5.4% and 6.4%) for both coho and Chinook salmon, respectively (Brodeur 1992) and our study period (9.1% and 10.4%, respectively). Since the 1980s, there have been oceanographic changes, declines in groundfish stocks, and changes to the pelagic nekton community (Emmett and Brodeur 2000), all of which likely influenced quantity of food resources available for young salmon. Unfortunately, we lack data on interannual variability in abundance of prey (especially juvenile fish) available to these salmon as this stage is difficult to sample quantitatively in either plankton nets or our large-mesh trawls. It is possible that smaller fish larvae collected in plankton nets during winter and early spring, during their peak period of occurrence (Brodeur et al. 2008), may function as a surrogate for early summer juvenile fish abundance. Annual abundance estimates in the winter and early spring of key salmon prey prior to the marine

migration of salmon could be of interest to managers for predicting future returns based on feeding conditions available to young salmon.

Along with oceanographic changes, there have been dramatic changes in both salmon abundances and stock composition between the two periods for both coho and Chinook salmon. Numerous wild and hatchery populations are now protected under the U.S. Endangered Species Act, and there have been substantial declines in Oregon coast hatchery production for both species (Weitkamp et al. 1995; Myers et al. 1998; PFMC 2008). These population changes could affect salmon behavior and trophic habits in numerous ways, such as changes in foraging behavior, prey preference, and size and timing of ocean entrance.

Chinook salmon were consistently more piscivorous than coho salmon. Fish are the highest caloric quality food consumed by coho and Chinook salmon, and would maximize growth potential over lower-quality prey such as crustaceans (Davis et al. 1998). Chinook diets that are higher in caloric value may explain the difference in stomach fullness between coho and Chinook salmon, in which coho salmon generally ate more food than Chinook salmon but of presumably lower quality. Similar tradeoffs between diet quality and quantity were also observed for juvenile coho and Chinook salmon in marine waters of southeast Alaska (Weitkamp and Sturdevant 2008). Lower stomach fullness may also have been indicative of Chinook salmon diet preferences and increased fish prey selectivity, which would restrict the overall amount of prey available to them (Healey 1980). Chinook salmon also appear to exhibit lower annual growth rates than coho salmon (Trudel et al. 2007), which may possibly reduce the need for prey consumption, resulting in lower stomach fullness.

Ontogenetic feeding behaviors were different between the two salmon species even at the individual station level. We clearly found three different size-based feeding patterns for coho salmon in both ordination and cluster analyses results (neither of which included haul), yet the ANOSIM test (which did include haul) indicated little grouping in ontogenetic diets but substantial grouping by haul effects. High similarity of salmon diets caught together in the same haul has been documented in previous studies (Brodeur et al. 2007a; Weitkamp and Sturdevant 2008). In contrast, Chinook salmon had both significant size-based feeding when caught together in a net haul and between-haul diet differences. This suggests a stronger ontogenetic selection of prey occurred at the haul level for Chinook salmon and less so for coho salmon.

Ontogenetic feeding changes may be driven, in part, by seasonal and interannual shifts in prey availability.

Diets of small coho and Chinook salmon are primarily made up of age-0 juveniles of winter-spawning taxa such as rockfish, Pacific sand lance, cottids, and osmerids (Richardson and Pearcy 1977; Brodeur et al. 2008). They also consume larvae of crabs that generally spawn in winter (Lough 1975) and adult euphausiids that move onto the shelf in the spring and summer (Gómez-Gutiérrez et al. 2005). By midsummer, some common taxa, such as rockfish, cottids, and many flatfishes, begin to settle to demersal habitats and are thus unavailable to pelagic salmon by September. For larger coho and Chinook salmon (>240 and 220 mm FL, respectively) in September, prey were predominantly the juvenile pelagic species available at this time, such as northern anchovy, Pacific herring, and osmerids. Small prey such as amphipods, euphausiids, and decapod larvae were still abundant in September as seen in the diets of small Chinook salmon (<220 mm FL), but showed decreased representation of prey such as cottids and rockfish and increases in larval anchovy that were spawned in summer (Litz 2008).

In comparing the diets of smaller salmon early in their marine residence with corresponding survival indices, we hypothesized that larger or higher-quality prey (fish) would be eaten in greater amounts during years of high survival compared with poor survival years. As predicting marine survival of salmon to adults is complicated by many factors seen in the ocean environment (Pearcy 1992; Hobday and Boehlert 2001; Weitkamp and Sturdevant 2008), the limited ability for our trophic data, over a short time scale, to correspond with survival indices may have demonstrated aspects of bottom-up influences on salmon survival. Oceanographic, bottom-up, and top-down processes affecting juvenile salmon fluctuate on a seasonal, interannual, and decadal basis in a complex, interrelated manner (Francis et al. 1998).

Top-down predation pressure and bottom-up food availability, along with oceanographic processes, may play a confounding role in interannual differences in survival of juvenile salmon. For example, in summer 2003, there were good feeding conditions—high amounts of quality food (fish prey) and low percentages of empty stomachs for both yearling coho and Chinook salmon; however, there was not a corresponding rise in their ultimate survival. Warmer ocean conditions in 2003 may have led to an early high abundance of predators moving onto the shelf, which suggests high predation on juvenile salmonids that year (Emmett et al. 2006). Even though we observed good feeding conditions in 2003, higher than usual predation may have caused excessive losses to juvenile salmon in 2003. In some years, food quality may play an

important role in ultimate survival of juvenile salmon. During the year of highest survival for yearling Chinook salmon (1999), we did not see higher stomach fullness, but we did find significantly more Pacific sand lance, a fish prey of high lipid value (Hislop et al. 1991; Robards and Piatt 1999). MacFarlane and Norton (2001) showed that juvenile Chinook salmon utilize lipids for early growth once they reach the marine environment, so consuming fish high in lipids early in the summer could have greatly improved their survival.

The relationships between interannual survival and diet differences appeared to be clearer for yearling coho and subyearling Chinook salmon than for yearling Chinook salmon. However, we note that the indices of survival for both salmon species themselves are only estimates mainly for hatchery fish with unknown error, so the presence or lack of association between feeding and survival is merely suggestive at this time. Associating early marine trophic habits of juvenile coho and Chinook salmon with their survival is likely to be complex, requiring the inclusion of additional factors to assist in our understanding of this relationship. For example, we have an incomplete understanding of coho and Chinook salmon prey field abundances, distribution, and quality, which may hinder our understanding of the mechanisms linking trophic habits with salmon survival. This information could provide insights into prey selection and assist in defining what constitutes good and poor feeding conditions for juvenile salmon.

### Acknowledgments

We thank the many National Oceanic and Atmospheric Administration and Oregon State University personnel who assisted in the field collections and laboratory dissections of the salmon. Jackie Noskov, Robert Schabetsberger, Carolyn Knight, and Rob Boley assisted with the analyses of the diets. Ed Casillas, Robert Emmett, Rebecca Baldwin, and three anonymous reviewers provided comments on earlier drafts of this manuscript. Many thanks to Cheryl Morgan for database management, and Susan Hinton for organizing our field collections. Funding was provided by the Bonneville Power Administration and the U.S. Global Ocean Ecosystems (GLOBEC) Northeast Pacific Program. This is contribution 636 of the U.S. GLOBEC Program. Reference to trade names does not imply endorsement by the U.S. Government.

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