Diet Comparisons Indicate a Competitive Interaction between Ocean Age-0 Chum and Coho Salmon

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Abstract: Systematic trawl surveys were conducted within the Strait of Georgia in June/July and September of 1997 and 1998. Stomachs of 2230 coho (*Oncorhynchus kisutch*) and 1558 chum (*O. keta*) ocean age-0 salmon were analysed. A large hatchery marking program was conducted for coho but not for chum salmon allowing us to compare diets of hatchery-marked and unmarked coho. There was almost complete diet overlap between hatchery-marked and unmarked coho throughout the seasons of both years. The seasonal patterns in diet composition illustrate that in early summer chum are potential competitors of coho in the Strait of Georgia. By late summer, chum are still competitors but they begin to feed upon gelatinous zooplankton. The implications of all diet comparisons are that chum and hatchery-reared coho are competitors of non-hatchery coho during their first marine summer. In the Strait of Georgia, the catch per unit effort indicates that chum salmon is two to four times more abundant than coho. If coho final brood year strength is determined via first summer growth and winter mortality (according to the critical-size-and-critical-period hypothesis), then the high abundance of chum and the overlap in chum and coho diets could explain, at least in part, the recent increase in natural marine mortality of coho.

INTRODUCTION

In the 1990s there has been a drastic decline in the marine survival of coho salmon (*Oncorhynchus kisutch*) in the Strait of Georgia (Beamish et al. 2000a). This has led to historic low returns of wild coho resulting in restrictions in fishing effort. Beamish and Mahnken (1999) proposed that coho brood year strength is determined in two major stages. The first stage is the commonly accepted early marine, predation based, mortality (Pearcy 1988). The second stage is based on the concept that to survive their first winter in the ocean, juvenile coho have to obtain enough food in summer to achieve a threshold amount of growth. This 'critical-size-and-critical-period' hypothesis is based on previous work which illustrated that mortality for juvenile coho reared in net pens increased greatly within the first fall through winter period (Mahnken et al. 1983) as a function of summer food intake.

Within the Strait of Georgia, there have been climate and ocean changes in the 1990s that have been linked to behavioural changes in coho (Beamish et al. 1999). Briefly, an increase in westerly winds and an increase in Fraser River discharge, led to changes in the estuarine circulation resulting in lower salinities and higher sea levels. Changes in estuarine circulation have implications for nitrate entrainment and primary productivity (St. John et al. 1993; Yin et al. 1997a, 1997b). These regional ecosystem changes were associated with changes in climate conditions in the North Pacific. Changes in oceanic conditions, such as those observed in the Strait of Georgia in the 1990s (Beamish et al. 1999), could affect the carrying capacity for coho. According to the critical-size-and-critical-period hypothesis, reduced first summer marine growth and increased mortality results from reduced food availability or increased intra- and interspecific competition or both. Higher abundance of competitors relative to coho abundance increases competition. Within the Strait of Georgia large numbers of chum salmon (*O. keta*) are released by hatcheries providing a potential source of increased interspecific competition. More obviously, hatchery released coho are sources of increased intraspecific competition for non-hatchery (wild) coho.

To the best of our knowledge, previous studies on juvenile coho or chum salmon diet composition have focused on fish that have survived their first ocean winter (i.e. ages greater than ocean age 0) and not on the early marine phase. Brodeur and Pearcy (1990) compared the diets of ocean age-0 coho, chinook (*O. tshawytscha*), chum and sockeye (*O. nerka*) caught off Oregon and Washington in 1980–1985.

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Unfortunately large-scale marking programs were not used by hatcheries during the 1980s and Brodeur and Pearcy (1990) were unable to compare diets between hatchery and non-hatchery coho. In the 1980s, coho marine survival was average and, on the basis of the critical-size-and-critical-period hypothesis, little intra- or inter-specific competition during the early marine phase would be expected. Brodeur and Pearcy (1990) observed low diet overlap among coho, chinook, chum and sockeye at the lowest taxonomic levels, but observed some similarities in major prey groups. Coho and chinook consumed teleosts and large zooplankton; and chum and sockeye had more diverse diets of smaller zooplankton. Similar observations were made by Landingham et al. (1998) for ocean age-0 salmon caught in southeastern Alaskan marine waters in 1983 and 1984. Within British Columbian waters Perry et al. (1996) investigated the diet of ocean age-0 chum salmon (and pink—*O. gorbuscha*) off the west coast of Vancouver Island during a single cruise in 1992. They did not compare chum (or pink) diets to coho, and their sample size for chum stomachs was small ($n = 261$), but they reported that chum mainly consumed larvaceans, euphausiids and calanoid copepods.

Given the recent declines in coho marine survival and the continued release of large numbers of hatchery coho and chum salmon into the Strait of Georgia during the 1990s, we decided to examine the diet composition of coho and chum salmon during their early marine phase to determine if there was potential intra- and inter-specific competition for food. Recent large-scale hatchery marking programs for coho salmon made diet comparisons between hatchery-marked and unmarked coho possible. Unfortunately, hatchery-reared chum were not marked. Our trawl surveys conducted in the Strait of Georgia provided large sample sizes ($n > 1000$) of ocean age-0 coho and chum salmon sufficient for diet overlap investigations. Here we report on the diet analyses conducted during surveys in the early- and late-summers of 1997 and 1998 for ocean age-0 coho and chum salmon caught throughout the Strait of Georgia.

METHODS

Fish Collection

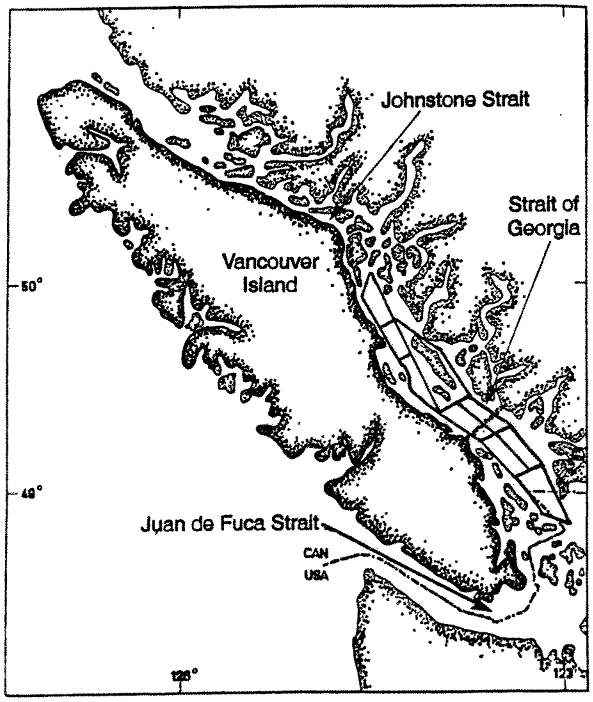
Four trawl surveys were conducted in June/July and September, 1997 and 1998, aboard the R/V *W. E. Ricker* (June 17–July 10, 1997, September 8–27, 1997, June 22–July 15, 1998, and September 8–16, 1998). Mechanical failure of the *W. E. Ricker* in September 1997, necessitated use of the fishing vessel *Frosti* to finish the survey (September 19–27). Beamish et al. (2000b) compared catch per unit effort between the two vessels and did not determine any significant differences. A midwater rope trawl (model 250/350/14) built by Cantrawl Pacific Limited, Richmond, B.C., was fished at a towing speed of approximately 5 knots. The net was held open with Model P USA Jet Doors that can be fished at the surface or any depth. The opening of the net was approximately 14 m deep by 30 m wide, and was estimated using a backwards-looking net sounder (Simrad FS3300). The net was towed approximately 3 boat lengths (180 m) from the stern. Specifications on the gear are outlined in Beamish et al. (2000b).

The ocean age-0 salmon used in this diet study were collected as part of a juvenile salmon abundance survey conducted throughout the Strait of Georgia (Fig. 1). Beamish et al. (2000b) provide details on the survey and sampling design. Briefly, fishing was conducted along track lines that formed a gridlike pattern and provided coverage for virtually all of the strait (Fig. 1). The first set of every day was always a surface tow, but thereafter sets were fished at randomly determined depths at the surface and at intervals of 15 m. Most salmon (> 80 %) were caught within the top 45 m, so catch per unit effort of each survey was expressed for all depths fished and for sets between 0–45 m.

Stomach Analyses

All diet analyses were conducted onboard from a random subsample of each catch. The forklength of each fish was measured to the nearest millimeter (mm) and weights to the nearest gram (g) were mea-

Fig. 1 Survey track lines throughout the Strait of Georgia.



sured when sea conditions permitted. Condition factor ($g{\cdot}cm^{-3}$) was calculated using available weight and forklengths. The cardiac and pyloric portions of each stomach were removed and the total volume of contents was estimated to the nearest 0.1 cc. The contents were flushed into a petrie dish in order to identify prey items. When necessary, 10x magnification was used to determine prey composition. Rather than count individual prey items, the relative contribution of a prey item to the overall stomach contents was estimated as a percentage of the total volume. This differs from the traditional numerical percentage approach to estimating the percentage ratio of contents, but it does allow for substantially more stomachs to be analysed. Prey were identified to the lowest taxonomic group possible, usually to order in invertebrates and to species in teleosts. The percentage of stomachs with each specific prey group was calculated for each survey for coho and chum. Prey were combined into major groups if overall that combination occurred in at least 3 surveys and in 5 % of the stomachs at least once. If prey groups did not meet this criterion, they were classed as "other". As we were interested in comparing coho and chum diets, we compiled a composite list of major prey groups for both species. We were also interested in comparing hatchery and non-hatchery coho diets, so the coho stomachs were reanalysed using these two categories. Empty stomachs were defined as containing less than 0.1 cc of all contents.

Diet Composition and Overlap

Any unidentifiable material resulting from excessive digestion was excluded from analysis. We used three measures of importance for each of the major prey groups of coho and chum salmon. Percent frequency of occurrence (%F.O.) was the percentage of stomachs containing at least one prey item. The proportion of contents importance (%C) was the average percentage of the individual volume of stomach contents that were made up of a prey group. The total volume importance (%V) was the percentage ratio of the total volume of the prey item consumed by all fish to the total volume of all prey items consumed by all fish. Pinkas et al. (1971) introduced the Index Relative Importance (IRI) which is calculated as a linear combination of a prey's numerical importance, volumetric importance and frequency of occurrence. We did not count individual prey items for calculating numeric importance and were unable to calculate IRI according to Pinkas et al. (1971). However, we used a modified index of relative importance (RI) such that;

$$RI = \%F.O. \times (\%C + \%V) \qquad (1)$$

Both indices (IRI and RI) relate how much of a prey item an individual fish eats, how many fish eat that prey item and, overall, how much that prey contributes to the total amount of food consumed by all fish examined. Similar to IRI (Pinkas et al. 1971), RI also ranges from zero, when a prey item is not present at all, to 20,000 when a prey item is consumed as a monodiet (i.e. %F.O., %C and %V all measure 100%). We expressed RI as a percentage (%RI) for easier comparison of relative prey item importance and used three-way graphs to indicate which measures of diet (%F.O., %C or %V) were most influential in the determination of %RI. Cortés (1997) proposed that the percent index of relative importance and three-dimensional graphical representations of the diet measures used to calculate the index be used as standardized measures in dietary analyses.

To estimate diet overlap between coho and chum, we calculated the Morisita-Horn index of overlap (Horn 1966);

$$O = \frac{2\sum_i^n p_{ij}\, p_{ik}}{\sum_i^n p^2{}_{ij} + \sum_i^n p^2{}_{ik}} \qquad (2)$$

where n = total number of prey item groups

p_{ij} = proportion of prey item used by coho

p_{ik} = proportion of prey item used by chum

The Morisita-Horn index was calculated separately for total volume importance (%V) and index of relative importance (%RI) as the measurements of proportion of prey items. The overlap index varies between 0 (no overlap) and 1.0 (complete overlap). We considered values ≥ 0.6 to reflect significant overlap. We used %V since it reflects an overall contribution and is not influenced by small prey items unless they are consumed often and in large quantities. We used the %RI since it is a composite measurement that provides an integrated expression of diet.

Hatchery-marked vs. Unmarked Coho

In 1997 and 1998, approximately 50 and 60% respectively of coho released from hatcheries into the Strait of Georgia were marked by a fin clip or by a coded wire tag insertion (Beamish et al. 1998). In order to identify potential intra-specific competition between hatchery and non-hatchery coho, the three measures of prey importance (%F.O., %C and %V) along with the corresponding %RI were calculated for hatchery-marked and for unmarked coho as above. The Morisita-Horn index of overlap was also calculated to measure overlap between hatchery-marked and unmarked coho diets.

RESULTS

A total of 2,230 coho stomachs and 1,558 chum stomachs were examined. The catch per unit effort within the top 45 m for chum was approximately two to four times higher than that for coho (Table 1). For coho, condition in early-summer 1998 and late-summers 1997, 1998 were similar, but in early-summer 1997 was lower than in the other three periods (ANOVA F = 3.61, $p = 0.01$, Table 1). The condition of chum in early-summer 1998 was higher than in early-summer 1997, and condition in both years increased by late-summer though was not different between years (ANOVA F = 15.95, $p < 0.0001$, Table 1). Coho were always larger and in better condition (ANOVA F = 23.52, $p < 0.0001$) than chum.

The mean percentage of coho stomachs containing prey items was 87.7% with survey percentages ranging from 76.9 (late-summer 1998) to 95.1% (late-summer 1997). Generally, the percentage of stomachs containing prey items in late summer was lower than in early summer. The opposite was true for chum, though there was less variability across surveys. The mean percentage of chum stomachs containing prey items was 86.9% with a range of 83.2% in early-summer 1997 to 90.6% in late-summer 1998. In each survey, at least 85% of all the coho and chum stomachs examined contained identifiable prey items. The stomachs of chum in early-summer 1997 were an exception since the percentage was 75.9%. The main focus during that survey was coho salmon, so chum stomachs were not processed quickly. The mean volume (cc) contained in stomachs was always higher in coho than in chum (Table 1).

The most frequently occurring prey items in coho stomachs were amphipods (gammariids and hyperiids), decapods, euphausiids and teleosts—primarily sandlance (*Ammodytes hexapterus*) and herring (*Clupea harengus*) (Table 2). For chum, the predominant prey items were chaetognaths, calanoid copepods, hyperiid amphipods, decapods, euphausiids and ctenophores (Table 3).

Table 1. Summaries for each survey. For each species, the total number of sets in which that species was caught, the total number caught, the catch per unit effort (CPUE) for all sets (and sets between 0–45 m only), and the total number of stomachs examined are denoted by survey. Based on the number of stomachs examined, the percentage of stomachs containing prey items and the percentage of stomachs containing items that were identifiable are listed. For all fish whose stomachs were examined, forklength, weight and condition factor are also listed.

	Survey Date			
	1997		1998	
	Early-summer	Late-summer	Early-summer	Late-summer
Number of sets	69	128	85	95
COHO SALMON				
Number of sets with species	31	98	57	73
Number caught	524	2277	1235	1326
CPUE all depths	14	37	28	29
(0–45 m)	(19)	(44)	(43)	(35)
Number of stomachs examined	272	652	573	733
Percentage of stomachs with prey items	94.5	84.1	95.1	76.9
Percentage of stomachs with identifiable items	98.9	91.1	100.0	98.4
Mean (stdev) volume (cm^3) in stomachs examined	1.10 (1.43)	1.22 (2.91)	0.99 (1.39)	1.52 (3.33)
Mean (stdev) forklength (mm) of fish examined	166 (31)	246 (23)	180 (24)	242 (34)
Mean (stdev) weight (g) of fish examined	64 (33)	175 (50)	74 (38)	181 (77)
Mean (stdev) condition factor (x 10^2) of fish examined	1.14 (0.19)	1.22 (0.45)	1.19 (0.14)	1.22 (0.21)
CHUM SALMON				
Number of sets with species	37	78	43	68
Number caught	1086	4869	4804	3789
CPUE	28	78	105	82
(0–45 m)	(41)	(93)	(160)	(101)
Number of stomachs examined	191	260	408	699
Percentage of stomachs with prey items	83.2	85.4	88.2	90.6
Percentage of stomachs with identifiable items	75.9	86.9	98.8	93.0
Mean (stdev) volume (cm^3) in stomachs examined	0.16 (0.35)	0.37 (0.53)	0.26 (0.31)	0.74 (0.88)
Mean (stdev) forklength (mm) of fish examined	121 (26)	191 (25)	126 (15)	186 (15)
Mean (stdev) weight (g) of fish examined	20 (14)	76 (27)	21 (8)	73 (15)
Mean (stdev) condition factor (x 10^1) of fish examined	0.92 (0.21)	1.13 (0.17)	1.01 (0.11)	1.15 (0.45)

Table 2. The percentage of coho salmon stomachs containing specific prey items. Parentheses are used to denote the lowest taxon group identified. Bold denotes phylum or subphylum of invertebrates. Teleosts were identified to species (in parentheses) except for the family Agonidae and for larval fish.

	1997		1998	
	Early-summer	Late-summer	Early-summer	Late-summer
Annelida				
(Hirudinea)		0.15		
Arthropoda				
(Insecta)	0.74	5.37	0.87	0.68
(Chaetognatha)			0.17	0.82
Tunicata				
(Oikopleuridae)				0.27
Crustacea				
(Cirripedia)				0.41
Copepoda				
(Calanoida)		2.61	2.44	1.64
(Harpacticoida)			0.17	
Amphipoda	1.47 undesignated			1.23 undesignated
(Gammaridea)	1.47	19.94	2.62	25.51
(Hyperiidea)	2.21	27.61	45.90	50.34
(Decapoda)	72.79	11.04	82.02	13.37
(Euphausiacea)	7.72	43.40	27.75	31.24
(Ostracoda)				0.14
(Mysidacea)				0.82
(Ctenophora)		0.15		
Mollusca				
Cephalapoda				
(Octopoda)	0.36			0.14
(Teuthoidea)			0.17	
Gastropoda				
(Opisthobranchia)				0.27
Unidentified invertebrate		0.46		0.27
Teleosts				
(Agonidae)		0.15		
Ammodytidae				
(*Ammodytes hexapterus*)	15.07	0.31	3.14	0.55
Clupeidae				
(*Alosa sapidissima*)			0.17	
(*Clupea harengus*)	10.07	3.53	8.38	3.27
Embiotocidae				
(*Cymatogaster aggregata*)				0.14
Gadidae				
(*Merluccius productus*)				0.14
Salmonidae				
(Oncorhynchus nerka)		0.15		
(*O. tshawaytscha*)		0.31		
Larval fish	2.21		0.70	
Unidentified fish	6.25	7.06	8.55	2.86

Table 3. The percentage of chum salmon stomachs containing specific prey items. Parentheses are used to denote the lowest taxon group identified. Bold denotes phylum or subphylum of invertebrates. Teleosts were identified to species (in parentheses) except for larval fish.

	1997		1998	
	Early-summer	Late-summer	Early-summer	Late-summer
Annelida				
(Polychaeta)			0.25	6.01
Arthropoda				
(Insecta)	2.56	0.77		
(Chaetognatha)		2.69	20.10	7.87
Tunicata				
(Oikopleuridae)			9.80	2.00
Cnidaria				
(Scyphozoa)	2.56	2.69		1.00
Crustacea				
(Cirripedia)				0.14
Copepoda				
(Calanoida)	2.56	6.54	10.54	3.29
(Cyclopoida)		0.38		
(Harpacticoida)			0.25	
Amphipoda				
(Gammaridea)		1.92		1.14
(Hyperiidea)	15.90	42.69	67.65	49.07
(Decapoda)	28.21	5.38	19.36	2.58
(Euphausiacea)	7.69	18.07	20.34	9.87
(Ostracoda)			0.25	
(Mysidacea)				

continued...

Table 3. continued.

	1997		1998	
	Early-summer	Late-summer	Early-summer	Late-summer
(Ctenophora)		36.15	3.92	47.78
Mollusca				
Gastropoda				
(Opisthobranchia)		1.92		2.43
Unidentified invertebrate				0.14
Teleosts				
Ammodytidae				
(*Ammodytes hexapterus*)	0.51			
Clupeidae				
(*Clupea harengus*)	8.72	0.38		
Larval fish	2.05	3.15	0.98	0.14
Unidentified fish	4.10		0.25	

Early-summer 1997

In the early-summer of 1997, the top three important prey items for coho, as measured by %RI, were decapods, teleosts and euphausiids (Fig. 2A). Important prey items for chum were decapods, teleosts and amphipods (Fig. 2B). The relative importance of decapods in coho was influenced by both %V and %C, while the decapod relative importance in chum was mainly influenced by %C (Fig. 2B). Amphipod %RI in chum diets was influenced by %F.O. and %C (Fig. 2B). The diet overlap between coho and chum in early-summer 1997 was large i.e. approximately 0.8 (Fig. 3).

Late-summer 1997

In September 1997, the top three important prey items for coho were euphausiids, amphipods and teleosts (Fig. 4A). The relative importance of amphipods was primarily influenced by %F.O. and %C. Ctenophores replaced teleosts as important prey items for chum and the order of the top three important prey items was slightly different than for coho: amphipods, ctenophores and euphausiids (Fig. 4B). Unlike that for coho, the relative importance of amphipods was influenced by %F.O., %C and %V. The diet overlap measured by %V was moderate, though overlap measured by %RI was greater than 0.6 (Fig. 3).

Early-summer 1998

Generally, coho diet was less varied than chum (Fig. 5A). Two different prey items dominated the diet of coho and chum with decapods largely important for coho and amphipods largely important for chum (Fig. 5B). The relative importance in both cases was influenced by all three diet measurements (Fig. 5). Unlike early-summer of the previous year, teleosts were not a major component of chum diet. The overlap in coho and chum diets was very small i.e. < 0.3 (Fig. 3).

Fig. 2. Three-way plot of percentage frequency of occurrence (%F.O.), percent total volume (%V) and percent contents (%C) for each major prey item for a) coho and b) chum in early-summer 1997. The area contained within each prey item box represents the index of relative importance (i.e. %F.O. (%C + %V)).

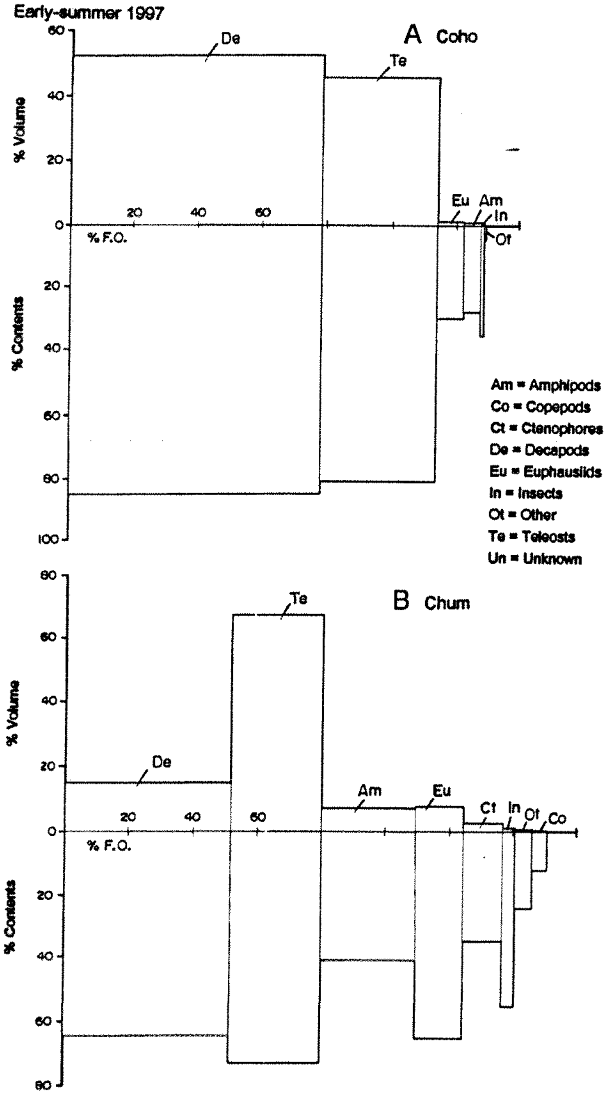


Fig. 3 Coho and chum diet overlap measured by the Morisita-Horn Index for proportion of total volume (vertical stripes) and for percentage index of Relative Importance (horizontal stripes). An overlap index value greater than 0.60 is generally considered to reflect significant overlap.

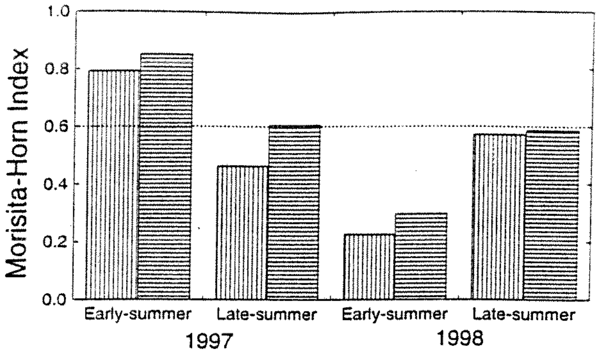


Fig. 4. Three-way plot of percentage frequency of occurrence (%F.O.), percent total volume (%V) and percent contents (%C) for each major prey item for a) coho and b) chum in late-summer 1997. The area contained within each prey item box represents the index of relative importance.

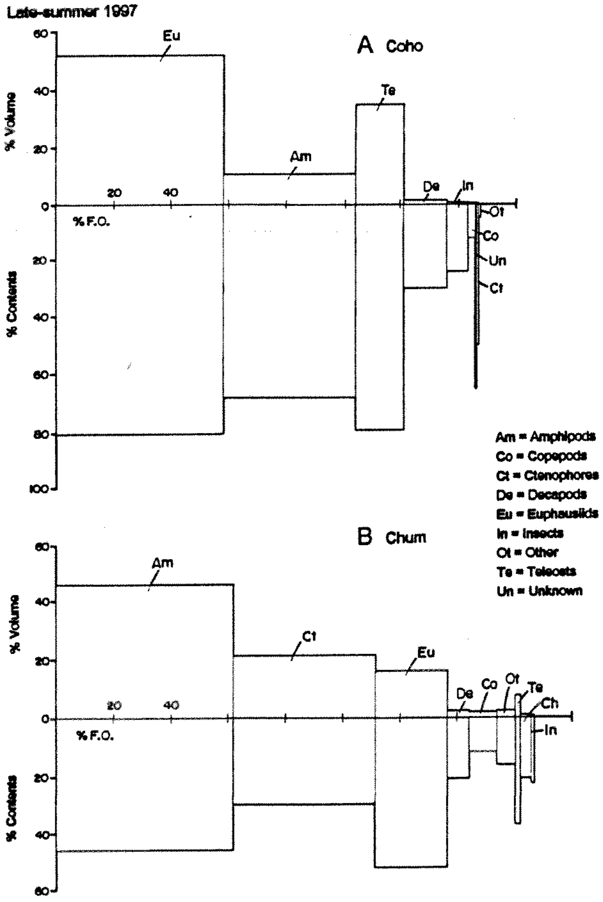
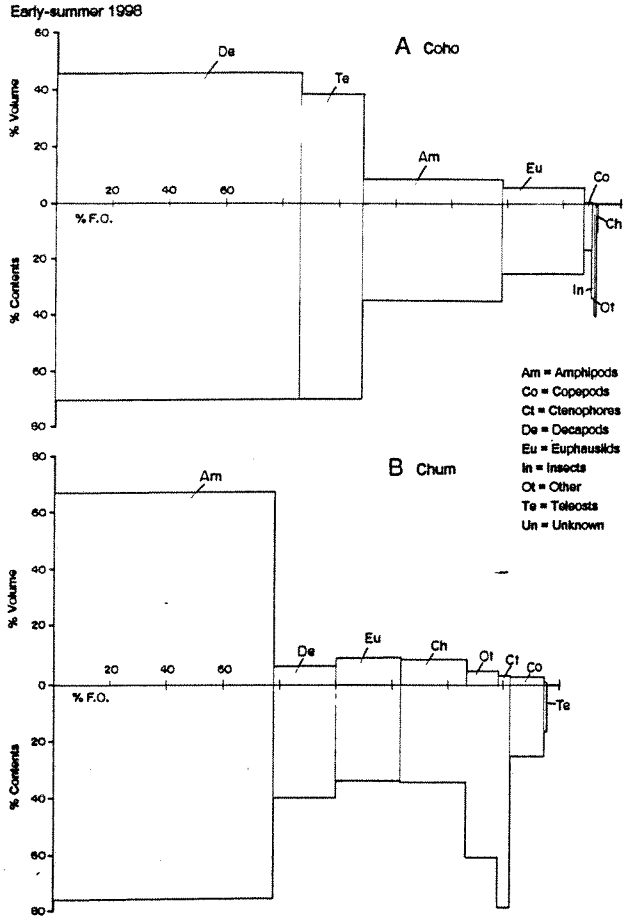


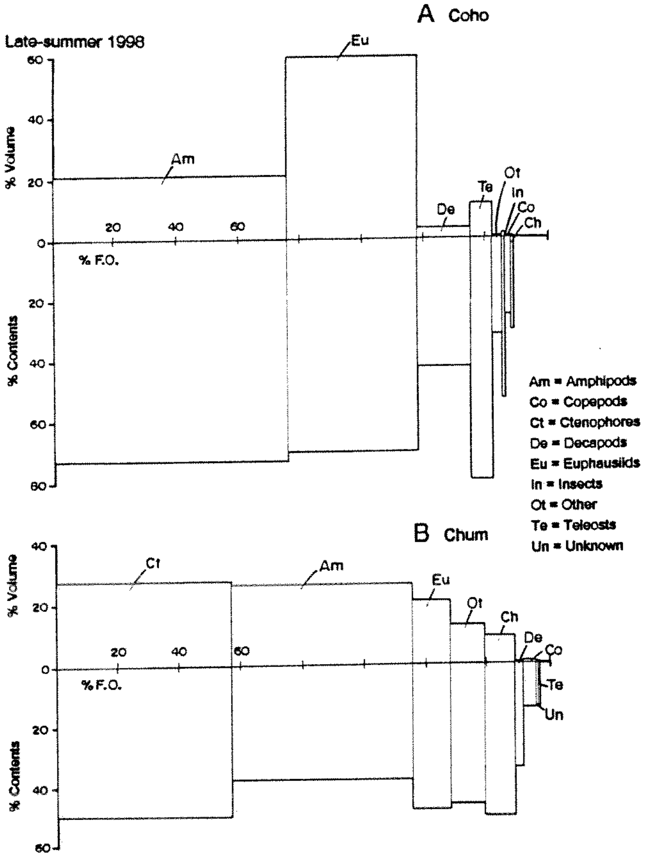
Fig. 5. Three-way plot of percentage frequency of occurrence (%F.O.), percent total volume (%V) and percent contents (%C) for each major prey item for a) coho and b) chum in early-summer 1998. The area contained within each prey item box represents the index of relative importance.



Late-summer 1998

For coho, the top three prey items in late-summer 1998 were amphipods, euphausiids and decapods (Fig. 6A), %C influenced the %RI values for amphipod and decapod prey groups. The higher %F.O. for decapods gave this prey group a higher %RI than teleosts which had a high %C. For chum, ctenophores, amphipods and euphausiids were the top three prey items, though chaetognaths and other prey were closely matched to euphausiids (Fig. 6). The %RIs of these prey groups were influenced by all three diet importance measurements. The overlap between chum and coho was only slightly lower than 0.60 (Fig. 3).

Fig. 6. Three-way plot of percentage frequency of occurrence (%F.O.), percent total volume (%V) and percent contents (%C) for each major prey item for a) coho and b) chum in late-summer 1998. The area contained within each prey item box represents the index of relative importance.



Hatchery vs. Non-hatchery Marked Coho

There were no differences between length, weight or mean volume consumed of hatchery-marked or unmarked coho except for late-summer 1998 when hatchery-marked coho were longer (ANOVA F = 463.73, $p < 0.0001$) and heavier (ANOVA F = 205.08, $p < 0.0001$) than unmarked coho (Table 4). Despite these differences in length and weight, there was no difference in condition factor between hatchery-marked and unmarked coho during any of the surveys (ANOVA F = 1.62, p = 0.12, Table 4).

For all four surveys, the top three prey items for hatchery-marked and unmarked coho were the same as those identified above for all coho. There were no differences between the rankings of all prey items based on %RI. The overlap in diet between marked and unmarked coho was close to complete for all four surveys (Fig. 7).

DISCUSSION

The major items in the diet of coho were similar in the early-summer of 1997 and 1998 and there was a general similarity in the diets in the late-summer, although the percentages differed slightly. Chum diets varied between years for the early-summer, with teleosts important in 1997 and not important in 1998. Chum switched to ctenophores in late-summer. The early-summer 1997 diet comparison between coho and chum showed that diet overlap can be quite high. The early-summer 1998 diet comparison illustrates that diet overlap can also be quite low. This implies that potential interspecific competition may at times also be high or low. Changes in oceanic conditions and carrying capacity or changes in relative abundance of competitors might alter the degree of diet overlap and competition in different seasons and years.

Diet composition studies from previous decades or on salmon older than ocean age 0, have shown that coho are mainly piscivorous and that chum feed mainly on small zooplankton and gelatinous zooplankton (Brodeur and Pearcy 1990; Perry et al. 1996; Tadokoro et al. 1996; Landingham et al. 1998). We have illustrated that chum may not begin feeding on gelatinous zooplankton until late in their first ocean summer. More importantly, we have illustrated that some major prey of chum, such as teleosts, are similar to coho. Possibly the presence of particular prey items in a diet (e.g. teleosts in chum diets) is an indication of a lower availability of preferred prey items.

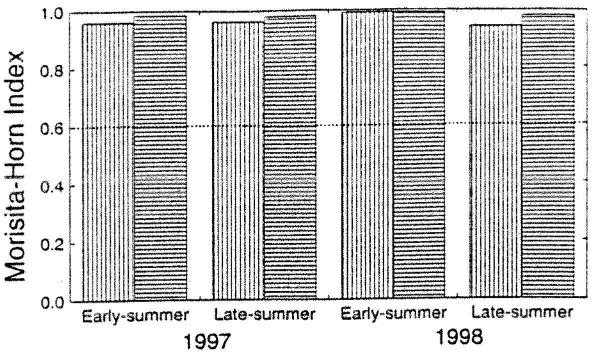
Hatchery released coho are likely strong competitors for non-hatchery coho in the Strait of Georgia. Our analysis here compared hatchery marked vs. unmarked fish, which does mean that hatchery-reared (but not marked) fish are likely included in the unmarked category. However, given the strong indication of diet overlap, it is likely that hatchery coho and non-hatchery coho diets are very similar. This has obvious implications for wild coho survival during periods when marine carrying capacity is low and the production of hatchery coho entering the ocean is higher than wild coho production.

Brodeur and Pearcy (1990) and Landingham et al. (1998) noted that larval and juvenile teleosts were present (but not dominant) in chum diets. Here, the diet overlap between chum and coho in early-summer 1997 was influenced by the dominance of teleosts (herring and larval fish) in the chum diet. In early-summer of the following year, teleosts were not dominant in chum diet and overlap with coho was low. In late-summer (1997 and 1998), diet overlap was moderate and influenced by the dominance of euphausiids and amphipods in both species' diet in both years. Though coho consumed gammariid am-

Table 4. Summaries for hatchery-marked (Mark.) and unmarked (Un.) coho caught and examined in each survey. Based on the number of stomachs examined, the percentage of stomachs containing prey items and the percentage of stomachs containing items that were identifiable are listed. For all fish whose stomachs were examined, forklengths, weights and condition factors are also listed.

	Survey Date							
	1997				1998			
	Early-summer		Late-summer		Early-summer		Late-summer	
	Mark.	Un.	Mark.	Un.	Mark.	Un.	Mark.	Un.
Number of stomachs examined	94	178	238	414	220	353	300	433
Percentage of stomachs with prey items	93.6	94.9	85.7	82.1	96.4	94.3	76.7	77.1
Percentage of stomachs with identifiable items	98.9	98.9	92.0	91.8	100.0	100.0	99.3	97.7
Mean (stdev) volume (cc) in stomachs examined	1.07 (1.38)	1.12 (1.47)	1.36 (3.81)	1.15 (2.24)	0.94 (1.20)	1.02 (1.50)	1.68 (3.50)	1.41 (3.20)
Mean (stdev) forklength (mm) of fish examined	162 (16)	169 (37)	247 (20)	246 (25)	179 (19)	180 (27)	249 (34)	237 (32)
Mean (stdev) weight (g) of fish examined	58 (18)	68 (39)	179 (53)	173 (49)	70 (25)	76 (44)	192 (70)	173 (81)
Mean (stdev) condition factor (x 10^1) of fish examined	1.12 (0.16)	1.15 (0.20)	1.22 (0.45)	1.22 (0.45)	1.18 (0.13)	1.19 (0.13)	1.22 (0.30)	1.22 (0.10)

Fig. 7 Hatchery-marked and unmarked coho diet overlap measured by the Morisita-Horn Index for proportion of total volume (vertical stripes) and for percentage index of Relative Importance (horizontal stripes). An overlap index value greater than 0.60 is generally considered to reflect significant overlap.



phipods, hyperiid amphipods were more common in coho and chum diets.

Our trawl survey allowed us to examine a large number of stomachs collected throughout the Strait of Georgia. We therefore, do not believe that our results were strongly biased by the sampling program. The exclusion of fish with empty stomachs and digested matter from diet analyses likely did not strongly bias the results since small percentages of stomachs were empty or contained digested matter.

The results presented here do support the hypothesis that diet overlap could have biological consequences if food resources were limited. In early-summer 1997 when diet overlap between coho and chum was high, the condition of coho was significantly lower than in early-summer 1998 when diet overlap was low. While the mean volume of prey consumed by chum is far lower than that consumed by coho, the catch per unit effort of chum is 2 to 4 times higher than that for coho. In early-summer 1998, overlap was low and coho condition was better than the previous year. Beamish and Folkes (1996) noted that in the 1990s, chum salmon within the Strait of Georgia appeared to remain within the ecosystem later in the year that in previous decades. In addition to the diet similarities and the large abundance of chum, the longer residence in the strait may increase competition. During the 1990s, changes in the Strait of Georgia ecosystem, carrying capacity and behaviour of chum, coupled with continued high release of hatchery-reared chum, may have resulted in increased inter-specific competition for coho. The critical-size-and-critical-period hypothesis suggests that inter-specific competition can partially account for the observed decline in coho marine survival if competition reduces the growth of an increasing number of coho such that their size is below the minimum size required to survive the first marine winter. The overlap in the diets of coho and chum during the summer growth period, and the higher abundance of chum compared to coho, is evidence (if the critical-size-and-critical-period hypothesis is valid) that chum juveniles could contribute to the marine mortality of coho.

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