Dietary overlap of juvenile fall- and spring-run chinook salmon, *Oncorhynchus tshawytscha*, in Coos Bay, Oregon

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Abstract–During the summer of 1987 in Coos Bay, Oregon, dietary overlap (Schoener index) between juvenile fall-run chinook salmon, *Oncorhynchus tshawytscha*, and an introduced stock of juvenile hatchery-reared spring-run chinook salmon was high (0.82), indicating the potential for competition for food between these two groups in times of food scarcity. Both groups consumed a variety of prey, including fishes, adult insects, algae, barnacle molts, gammarid and caprellid amphipods, and juvenile decapods. Diets of both salmon groups varied with fish size and capture location. Overlap was low (0.25–0.55) between the smallest juvenile fall chinook salmon (≤80 mm FL), for which insects were the predominant prey (26% by weight), and all other length groups of both fall and spring chinook salmon, for which fish were the predominant prey (49%–94% by weight). Dietary overlap between both salmon groups was high in the lower bay (0.82), where fish prey predominated in the diets, and was also high in the mid bay (0.75), where algae and barnacle molts predominated in the diets. Three pieces of evidence suggest that the introduced hatchery-reared spring chinook salmon did not outcompete fall chinook salmon for food: 1) both the median stomach fullness and the percentage of stomachs containing food was higher for fall chinook salmon than for spring chinook salmon, 2) the median stomach fullness of fall chinook salmon was as high in the period following releases of spring chinook salmon into the bay as in the period prior to the releases, and 3) food of high caloric density (i.e. fish prey) formed an equally high proportion of the diets of both salmon groups, indicating that the quality of food eaten by both was similar.

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Estuaries serve as rich feeding grounds and as refuges from predation for many juvenile subyearling fall-run (hereafter referred to as "fall") chinook salmon, *Oncorhynchus tshawytscha*, that reside in them for weeks or months before entering the ocean (Healey, 1980a, 1982, 1991; Myers, 1980; Kjelson et al., 1982; Myers and Horton, 1982; Simenstad et al., 1982). The survival of subyearling fall chinook salmon may be enhanced by extended residence in estuaries. Reimers (1973) reported that survival was greater among juvenile fall chinook salmon that resided in the Sixes River estuary from early summer through early fall than among those that quickly migrated through the estuary to the ocean in early summer.

Although there is much concern about the interaction between hatchery and wild stocks of salmon (Hilborn and Winton, 1993; Thomas and Mathisen, 1993; Winton and Hilborn, 1994), few reports document possible competition between groups of salmon for food in estuaries or the ocean. Peterman (1984) and Rogers and Ruggerone (1993) found negative correlations between size of sockeye salmon at different ages and their population and suggested that growth of sockeye salmon in the ocean was density dependent. Reimers (1973) and Neilson et al. (1985) found that the average growth rate of juvenile fall chinook salmon in the Sixes River estuary decreased during mid-summer when the population of juvenile salmon was high. Reimers (1973) attributed this drop in growth rate to intraspecific competition for limited food resources, leading to density-dependent growth, whereas Neilson et al. (1985), noting that the decrease in growth rate occurred during a period of increased abundance of the principal prey (*Corophium* sp.), suggested that lowered conversion efficiencies due to high temperatures in the estuary as well as intraspecific competition may have contributed to the drop in growth rate.

These studies suggest that releases of large numbers of hatchery salmon smolts into an estuarine basin could affect the native salmon in the system through competition for food in the estuary. The effect of competition on growth and survival of native fish would depend on several factors, among them the intensity and duration of the competition between the two groups. If the hatchery-reared fish eat different prey from that eaten by the wild fish, or if they move quickly through the estuary, their impact on the native fish may be relatively small. On the other hand, if the two groups have similar feeding behaviors and if hatchery fish reside in the estuary for a substantial period, then the effect of hatchery fish on the wild fish may be great.

Anadromous, Inc. operated a salmon-rearing and release facility on the North Spit of Coos Bay, Oregon in the 1980's. From this facility millions of smolts are released into the bay annually, principally large subyearling spring-run ("spring") chinook salmon, thus creating the potential for competition between these hatchery-produced spring chinook salmon and the native runs of fall chinook salmon in the Coos Bay drainage.

During the late spring and summer of 1987 we undertook a sampling program in the lower half of Coos Bay to study the use of the estuary by different groups of juvenile chinook salmon. In 1987 two groups of juvenile chinook salmon were present in Coos Bay: fall chinook salmon from the Coos and Millacoma River drainages (both wild fish and fish released by the Salmon and Trout Enhancement Program [STEP]) and spring chinook salmon released from the saltwater rearing pens of the Anadromous, Inc. facility, North Spit of Coos Bay (Fig. 1). About 400,000 STEP fall chinook salmon were released in tributaries of the Coos River between 30 April and 28 June at average fork lengths (FL) of between 48 and 94 mm, and over five million spring chinook salmon (123–156 mm FL) were released from the Anadromous, Inc. release facility on North Spit between 19 June and 1 October. In an earlier paper (Fisher and Pearcy, 1990) we reported on the distributions and residence times of juvenile spring and fall chinook salmon in the bay. In this paper we describe the food habits of these two groups, overlap in their diets, and the potential for competition for food between them.

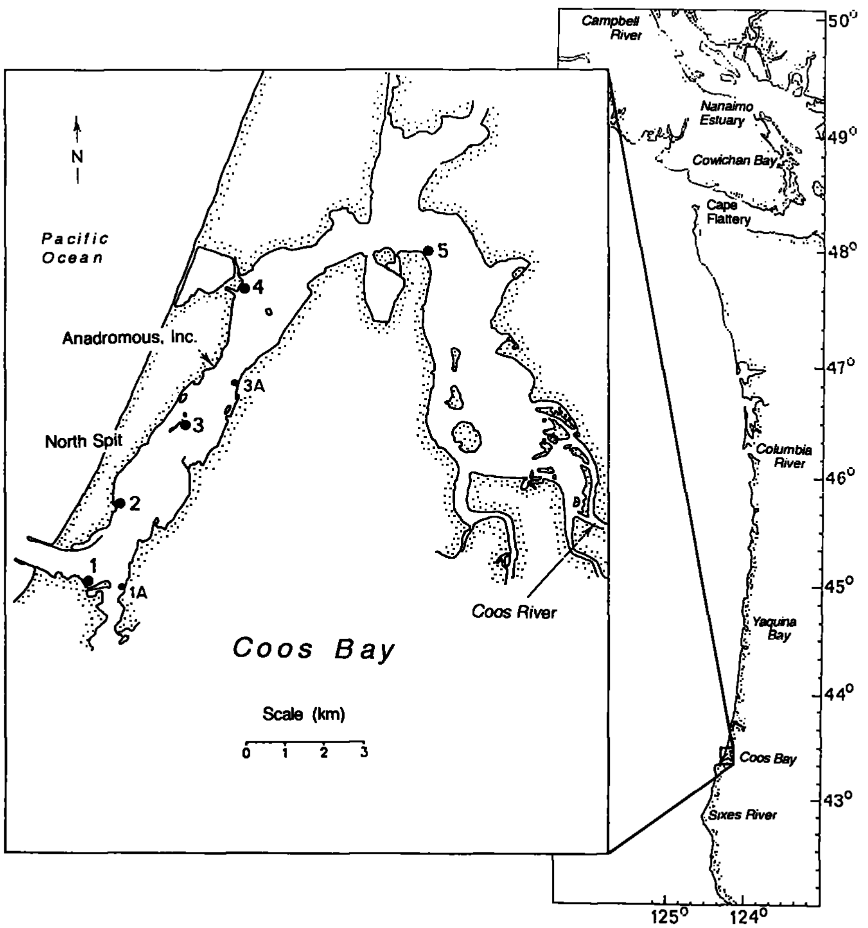

Figure 1

Map of Coos Bay, Oregon, showing the five stations sampled with beach seines in the summer of 1987. The lower bay and mid bays comprised stations 1–3 and 4–5 respectively.

Methods

Juvenile chinook salmon were caught by beach seine (60 m × 2.5 m with 19- and 13-mm mesh in the wings and bunt, respectively) at five locations on the margins of channels in the lower half of Coos Bay, Oregon, between late May and early October 1987 (Fig. 1). The substratum was sand at all but station 5, where it was a mixture of gravel fill and mud. At stations 2, 3, and 4, portions of eel grass beds were sampled during low tide. The area of Coos Bay we sampled was influenced strongly by the ocean and was highly marine in character with high salinities at all sampling sites, usually greater than 29 psu after mid-June. Water temperature (at 0.3 m depth) was fairly constant between May and October but increased with distance from the mouth, averaging 12.3°C at station 1 and 16.8°C at station 5 (Fisher and Pearcy, 1990).

Subsamples of juvenile chinook salmon caught in beach-seine sets were preserved in approximately 4% formaldehyde solution. Later, these were measured to the nearest mm FL and weighed to the nearest 0.01 g after excess moisture was removed by blotting. Stomachs were removed from 380 juvenile chinook salmon caught between 31 May and 4 September 1987 (Fig. 2). Stomach-content boluses were weighed to the nearest milligram after removing excess moisture by blotting. After weighing, they were preserved in 50% ethanol, then transferred to 75% ethanol.

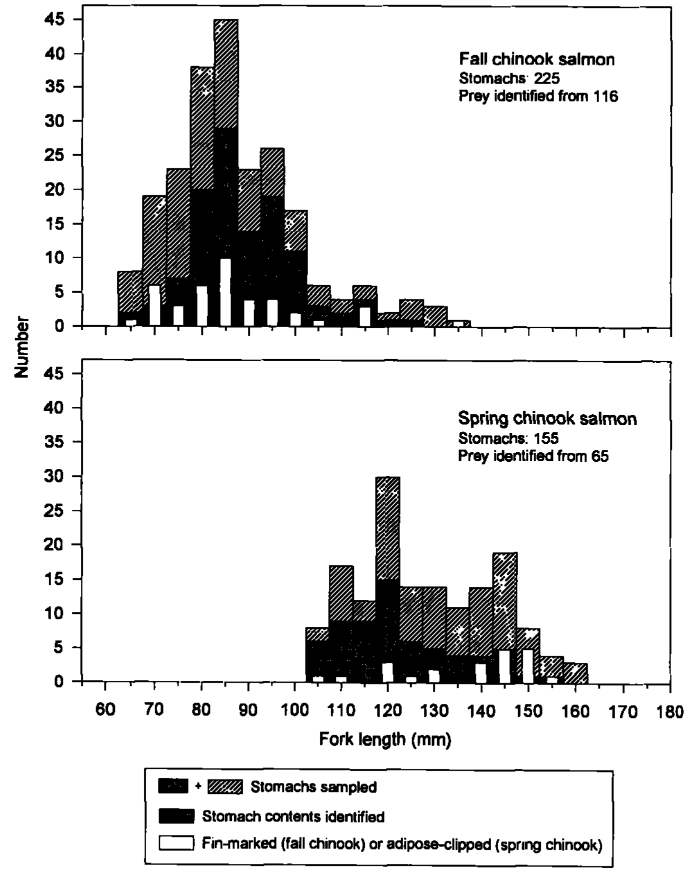

Figure 2

Length-frequency distributions of juvenile fish classified as fall and spring chinook salmon from which stomach samples were taken. Dark shading represents those stomach samples in which prey species were examined and identified. White bars in the upper and lower graphs represent numbers of fin-clipped STEP-reared fall chinook salmon and adipose clipped Anadromous, Inc.-reared spring chinook salmon, respectively.

At the time the stomach samples were obtained, the fish were examined for fin marks or for external parasites that could help to determine their origin. Most fish with clipped adipose fins also contained coded wire tags (CWT's) that identified them as spring chinook salmon produced at Anadromous, Inc. Fish with other fin clips were mainly STEP-reared fall chinook salmon released in freshwater tributaries of Coos Bay (Fisher and Pearcy, 1990).

The encysted metacercarial stage of a strigeoid trematode parasite is common in the skin of juvenile salmonids found in freshwater tributaries of Coos Bay. These cysts are surrounded by a black pigment that can be seen easily without magnification (Amandi[1]). The presence of metacercarial cysts on the skin or fins of juvenile chinook salmon caught in Coos Bay appeared to be a reliable indicator that the fish originated in the freshwater tributaries of the bay. Cysts were present on 43% of known fall chinook salmon (fin-marked STEP fish or fish caught before the first release of spring chinook salmon) and on 71% of small fish <101 mm FL (>2SD below the mean FL of most release groups of spring chinook salmon by Anadromous, Inc.). Conversely, cysts were absent on adipose-clipped spring chinook salmon and found on only 13% of fish in the size range of the spring chinook salmon released by Anadromous, Inc. (≥101 mm FL). Fish >100 mm FL with cysts were probably native salmon or STEP-reared fall chinook salmon that attained these greater lengths through growth. On the basis of this evidence, we classified fish caught in Coos Bay as fall chinook salmon if they met *any* of

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[1] Amandi, T. 1995. Oregon Dep. Fish and Wildl., 516 Nash Hall, Oregon State Univ., Corvallis, OR 97331. Personal commun.

the following criteria: 1) they were caught before the first release of Anadromous, Inc. spring chinook salmon on 19 June; 2) metacercarial cysts were present on their skin or fins; 3) they had one of the STEP fin clips; or 4) they were ≤100 mm FL. Fish were classified as spring chinook salmon if they were ≥101 mm FL and did not meet any of the criteria for fall chinook salmon.

Stomach contents were examined and prey items identified to the lowest possible taxon from 116 fall chinook salmon and 65 spring chinook salmon collected between 29 June and 13 August 1987, the period of greatest overlap in the bay of the two groups (Fig. 2). Stomach contents from a single fall chinook salmon caught on 7 June were also examined.

Individual prey taxa in each stomach were weighed to the nearest 0.001 g after removing excess moisture by blotting. Those taxa that were too light to register on the scale (weight <0.0005 g), were assigned a weight of 0.0004 g. The estimated total weight of all food assigned this arbitrarily small value was only 0.05 g out of a total weight of 60.2 g for all taxa from all stomachs.

In the analyses of stomach contents, juvenile fall and spring chinook salmon were grouped by FL, by two collection areas ("lower bay," stations 1–3, and "mid-bay," stations 4–5) and by two sampling periods: 29 June to 17 July and 3–13 August. Within each class, the percent frequency of occurrence (FO) and percent by weight of each prey category in the diet was calculated. The percent by weight (p_i×100) of each prey category in each class was calculated as

$$100(p_i) = 100\left(\frac{\sum_{q=1}^{N} w_{iq}}{\sum_{q=1}^{N}\sum_{i=1}^{n} w_{iq}}\right), \qquad (1)$$

where w_{iq} is the weight of food category i in fish q, n is the number of food categories, and N is the number of fish in the class.

Dietary overlap between classes was calculated by using the Schoener overlap index (*ro*; Schoener, 1970; Wallace, 1981; Linton et al., 1981):

$$ro = 1 - \frac{1}{2}\sum_{i=1}^{n}\left|p_{ij} - p_{ik}\right|, \qquad (2)$$

where p_{ij} and p_{ik} are the proportions by weight of food category i (Eq. 1) in the diets of fish in classes j and k, respectively, and n is the number of food categories. Dietary overlap was calculated by using 14 categories of major prey and, because the overlap index is sensitive to the taxonomic resolution (Brodeur and Pearcy, 1992), it was also calculated by using the 86 lowest taxonomic levels identified (to genus or species in some cases). An overlap of ≥0.60 was considered significant (Zaret and Rand, 1971; Brodeur and Pearcy, 1992).

Results

Stomach fullness

The frequency distribution of stomach-content weight as a percentage of body weight ("stomach fullness") was skewed for both fall and spring chinook salmon (Fig. 3); therefore, nonparametric ranks tests were used to compare stomach fullness among different classes of fish. The median stomach fullness was higher for fall chinook salmon than for spring chinook salmon (2.4% vs. 1.2%, respectively; Mann Whitney (Wilcoxon) *W* test, *W*=11,630, $P<0.0001$). Stomachs were empty in a higher percentage of spring chinook salmon than of fall chinook salmon (16% vs. 1%), contributing to the difference in median stomach fullness of these two groups (Fig. 3).

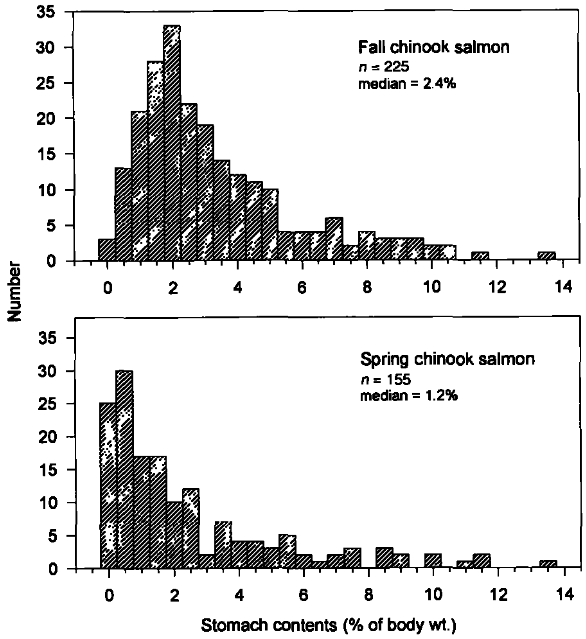

Figure 3

Frequency distributions of weight of stomach contents as a percentage of body weight for juvenile fall chinook salmon (top graph) and spring chinook salmon (bottom graph).

Range in stomach fullness was similar among fish of different lengths, and stomach contents weights of 8% of body weight or higher occurred in fish from 69 mm to 145 mm FL (Fig. 4). No significant difference in median stomach fullness was found among four FL classes (≤80 mm, 81–100 mm, 101–120 mm, and 121–140 mm) of fall chinook salmon (Kruskal-Wallace test, $P=0.09$). However, a significant difference in median stomach fullness was found among the three FL classes (101–120 mm, 121–140 mm, and ≥141 mm) of spring chinook salmon (Kruskal-Wallace test, $P=0.03$). Median stomach fullness was lowest (0.4%) for the largest spring chinook salmon (≥141 mm FL).

Median stomach fullness of fall chinook salmon was fairly constant during the study period, both before and after spring chinook salmon were released into the bay. No short-term decreases in stomach fullness of fall chinook salmon were associated with individual releases of spring chinook salmon, except for the 4 August release (Fig. 5). Conversely, median stomach fullness of spring chinook salmon was low immediately following releases of large numbers of spring chinook salmon from the Anadromous, Inc. facility, especially the 4 August and the August 31–3 September releases (Fig 5).

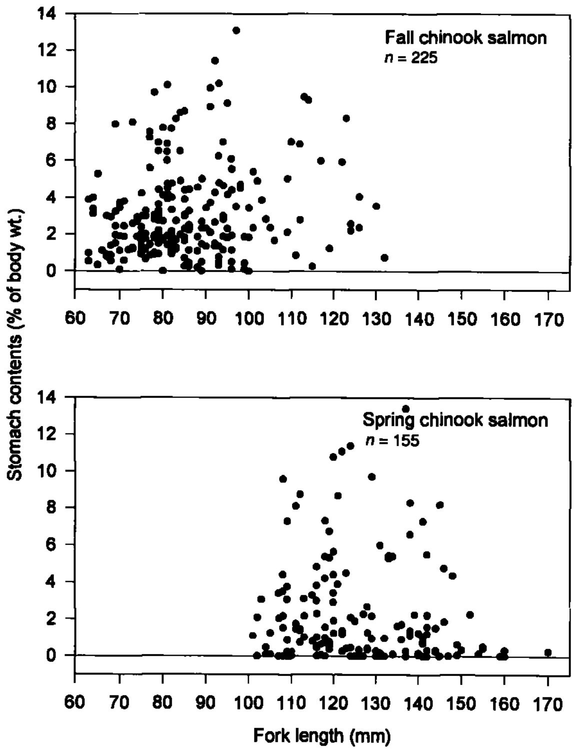

Figure 4

Weight of stomach contents as a percentage of body weight versus fish length for juvenile fall chinook salmon (top graph) and spring chinook salmon (bottom graph).

Diets of fall and spring chinook salmon

Percent FO and percent by weight of fourteen major prey categories from stomachs of juvenile fall and spring chinook salmon are summarized in Table 1. By weight, juvenile or larval fish were dominant prey of both fall and spring chinook salmon, representing 64% and 65% of the total weight of stomach contents, respectively. The fish prey of fall chinook salmon were juvenile smelt, unidentified fish remains, *Ammodytes hexapterus*, juvenile *Sebastes* sp., and an unidentified cottid, representing 41%, 10%, 8%, 6%, and <1% of stomach-content weight, respectively. Fish prey of spring chinook salmon were similar: juvenile smelt, *Ammodytes hexapterus*, unidentified fish remains, and *Sebastes sp.*, accounted for 49%, 13%, 3%, and <1% of stomach-content weight, respectively.

Other prey categories accounted for much smaller fractions of stomach-content weights of the two groups of juvenile chinook salmon. Of the nonfish prey, insects and plants (mainly algae) composed the largest fractions by weight in stomachs of fall chinook salmon (8% and 7%, respectively), whereas plants (mainly the algae *Ulva* sp. and *Enteromorpha* sp.) and barnacle molts composed the largest fractions by weight in stomachs of spring chinook salmon (16% and 12%, respectively; Table 1).

The most numerous insects[2] in fall chinook salmon stomachs were adults of terrestrial taxa (61% of the total) and adults of taxa having aquatic or semiaquatic larvae (36% of the total). Larvae and pupae composed only 3% of the total number of individuals. Adults in the orders Diptera, Hemiptera, Homoptera, Pscoptera, Hymenoptera, Coleoptera, and Trichoptera accounted for 33%, 23%, 15%, 10%, 7%, 6%, and 2% of the total number of insects in fall chinook salmon stomachs, respectively. The most numerous taxa in these insect orders (and their percentages of total insect numbers) were midges (Chironomidae; 25%), plant bugs (Miridae; 22%), aphids (Aphididae; 11%), book and bark lice (10%), parisitoid wasps (5%), rove beetles (Staphylinidae; 4%), and caddis flies (2%), respectively.

Although insects were a much larger fraction by weight of the diet of fall chinook salmon than of the diet of spring chinook salmon (8% vs. 1%, respectively, Table 1), they occurred frequently in stomachs of both salmon groups (80% and 60%, respectively). Many of the same insect taxa were consumed by both fall

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[2] The different insect taxa were not weighed separately, but individuals of each taxon were counted.

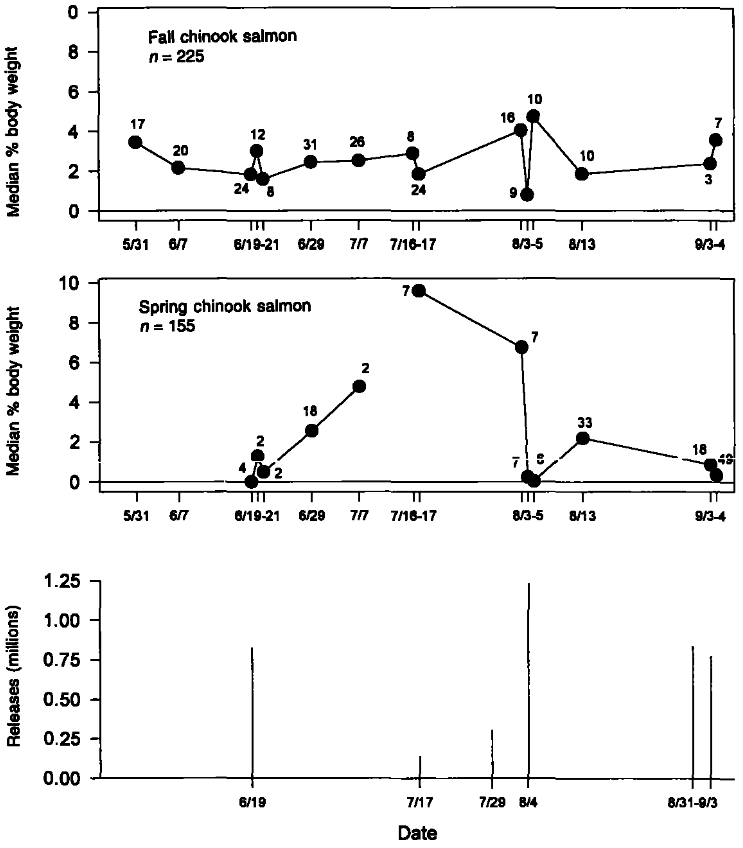

Figure 5

Median weight of stomach contents as a percentage of body weight by sampling date for fall chinook salmon (top graph) and spring chinook salmon (middle graph). Numbers indicate sample size. Numbers of spring chinook salmon released into Coos Bay by Anadromous, Inc. on different dates are also shown (bottom graph).

and spring chinook salmon. The most numerous insects from spring chinook salmon stomachs were chironomids (31%), book and bark lice (23%), aphids (9%), tipulids (crane flies, 8%), and plant bugs (4%).

Other prey categories that occurred frequently in stomachs of both fall and spring chinook salmon were barnacle molts (47% and 51%, respectively), algae and other plant material (46% and 68%), gammarid amphipods (41% and 43%), fishes (40% and 37%), and crab larvae (27% and 35%). Isopods, caprellid amphipods, nonanomuran or nonbrachyuran decapod larvae, spiders, unidentified arthropods, and molluscs were less common, occurring in 14% or fewer of stomachs

Gammarid amphipods were a moderately important component of the diet of fall chinook salmon (4% by weight), but were less important in the diet of spring chinook salmon (only 1% by weight). A variety of gammarid species were eaten by fall chinook salmon, the most abundant were *Jassa* spp. unidentified gammarids, *Megalorchestia pugettensis*, *Ischyrocerus* spp., *Atylus tridens*, and *Corophium* spp. (2.0%, 0.6%, 0.3%, 0.2%, 0.2%, and 0.1% of total food weight respectively).

Dietary overlap between juvenile fall and spring chinook salmon, according to the relative weights (Eq. 2) of the 14 major food categories (Table 1), was high (0.82), owing largely to the predominance of fish prey in diets of both groups. Diet overlap based on relative weights of prey identified to the lowest possible taxonomic level (86 categories of varying taxonomic level) was lower but still relatively high (0.66).

Diets by fish length

Insect prey were relatively more important and fish prey were relatively less important in the diet of the

Table 1

Percentage by weight and frequency of occurence (in parentheses) of fourteen major food categories in stomachs of juvenile fall-run and spring-run chinook salmon caught in 1987 in Coos Bay. Numbers in brackets are sample sizes.

Food category	Fall chinook salmon [116]	Spring chinook salmon [65]
Cirripedia molts	5 (47)	12 (51)
Isopods	<1 (9)	<1 (11)
Caprellid amphipods	1 (14)	<1 (11)
Gammarid amphipods	4 (41)	1 (43)
Brachyuran, anomuran larvae	2 (27)	2 (35)
Other decapod larvae	<1 (8)	<1 (2)
Crustacean fragments	5 (20)	1 (25)
Araneae	<1 (14)	<1 (5)
Insects	8 (80)	1 (60)
Other arthropods	<1 (6)	<1 (2)
Molluscs	<1 (4)	<1 (12)
Teleosts	64 (40)	65 (37)
Algae, plants	7 (46)	16 (68)
Other material	4 (43)	2 (55)

Table 2

Percentage by weight and frequency of occurence (in parentheses) of fourteen major food categories in stomachs of different size groups of fall and spring chinook salmon caught in 1987 in Coos Bay. Numbers in brackets are sample sizes.

	Fall chinook salmon FL (mm)			Spring chinook salmon FL (mm)		
Food category	≤80 [32]	81–100 [73]	≥101 [11]	101–120 [39]	121–140 [19]	≥141 [7]
Cirripedia molts	9 (63)	5 (45)	3 (18)	22 (62)	9 (42)	<1 (14)
Isopods	<1 (9)	<1 (10)	0	<1 (10)	<1 (16)	0
Caprellid amphipods	1 (9)	1 (18)	0	<1 (8)	<1 (16)	<1 (14)
Gammarid amphipods	4 (44)	5 (42)	<1 (18)	1 (51)	1 (37)	<1 (14)
Brachyuran, anomuran larvae	7 (25)	2 (32)	0	1 (28)	2 (42)	3 (57)
Other decapod larvae	<1 (13)	<1 (7)	0	0	<1 (5)	0
Crustacean fragments	11 (22)	6 (22)	0	2 (23)	1 (32)	<1 (14)
Araneae	<1 (13)	<1 (16)	0	<1 (5)	<1 (5)	0
Insects	26 (94)	7 (81)	1 (36)	1 (69)	<1 (63)	0
Other arthropods	<1 (13)	<1 (4)	0	0	<1 (5)	0
Molluscs	1 (6)	<1 (4)	0	<1 (5)	<1 (26)	<1 (14)
Teleosts	18 (9)	62 (45)	94 (91)	49 (31)	68 (32)	91 (86)
Algae, plants	12 (56)	7 (42)	2 (36)	20 (72)	18 (63)	4 (57)
Other material	11 (59)	4 (38)	<1 (27)	4 (59)	<1 (42)	2 (71)

smallest fall chinook salmon (≤80 mm FL) than in the diets of the other length groups of both fall and spring chinook salmon. Insect prey made up 26% of food by weight in stomachs of the smallest fall chinook salmon (Table 2). The insect fraction of the diet dropped to 7% and 1% for larger fall chinook salmon 81–100 mm FL and ≥101 mm FL, respectively, and was ≤1% for all length groups of spring chinook salmon. Fish made up only 18% by weight of the diet of fall chinook salmon ≤80 mm FL, but 62% and 94% by weight of the diet of fall chinook salmon 81–100 mm FL and ≥101 mm FL, respectively, and between 49% and 91% by weight of the diet of spring chinook salmon.

Larval crab (anomuran and brachyuran) prey were a moderately important component of the diet of the two smallest length classes of fall chinook salmon (≤80 mm FL and 81–100 mm FL) and of the two largest length classes of spring chinook salmon (121–141 mm FL and ≥141 mm FL), representing 7% and 2%, and 2% and 3% of total food by weight, respectively (Table 2). However, crab larvae of various taxa and at different developmental stages were consumed by chinook salmon of different stock and length groups. The smallest fall chinook salmon (≤80 mm FL) fed mainly on porcellanid, pinnotherid, callianassid, and unidentified brachyuran zoea rather than on megalopae (95% zoea and 5% megalopae by weight), whereas larger fall chinook salmon (81–100 mm FL) fed more on megalopae than on zoea (69% vs. 31% by weight), and the large spring chinook salmon (≥121 mm FL) fed exclusively on megalopae, mainly large *Cancer magister* (72%), *Cancer oregonensis* (19%), and *Cancer* sp. (4%).

Gammarid amphipods were also a fairly important component of the diet of the small fall chinook salmon, representing 4% and 5% by weight for fish ≤80 mm FL and 81–100 mm FL, respectively, but were a less important component of the diets of the largest fall chinook salmon (≥101 mm FL) and spring chinook salmon (Table 2).

Dietary overlap, based on the 14 major prey categories was low (≤0.55) between the smallest fall chinook salmon (≤80 mm FL) and all other length categories of fall and spring chinook salmon (Table 3). This reflects the reduced relative importance of fish and the greater relative importance of insects and crab larvae in the diet of the smallest fall chinook salmon than in the diet of larger fish (Table 2). Excluding the smallest fall chinook salmon, diet overlap was high for eight of ten comparisons among length groups of fall and spring chinook salmon (Table 3).

Dietary overlap, in respect to the lowest identified taxa (86 categories) was also low between fall chinook salmon ≤80 mm FL and all other groups. Overlap among the other groups was generally higher than that with the small fall chinook salmon but was ≥0.60 for only four of the ten comparisons.

Diets by location

Dramatic differences in the diets of fall and spring chinook salmon were associated with where the fishes were caught in the bay. For both salmon groups, fish were a much more important component of the diet at lower-bay stations 1–3 than at mid-bay stations 4–5 (Table 4). Conversely, barnacle molts and algae made up a much larger fraction of stomach contents at mid-bay stations than at lower-bay stations (Table 4). Dietary overlap based on the 14 major food categories was high between fall and spring chinook salmon caught in the same areas of the bay but was low for all comparisons of salmon caught in the two different areas of the bay (Table 5). Dietary overlap based on the 86 lower taxonomic categories was also highest for fall and spring chinook salmon caught in the same area of the bay, but only for fish caught in the lower bay was the overlap value ≥0.60 (Table 5).

Table 3

Dietary overlap of different length groups of fall and spring chinook salmon. Overlap values based on 14 major food categories are in normal type and those based on 86 lower taxonomic categories are in italics. High overlap values (≥0.60) are in bold type.

		Fall chinook salmon FL (mm)		Spring chinook salmon FL (mm)		
		81–100	≥101	101–120	121–140	≥141
Fall chinook salmon FL (mm)	≤80	0.55	0.25	0.48	0.44	0.27
		0.36	*0.13*	*0.25*	*0.21*	*0.07*
	81–100	—	**0.68**	**0.70**	**0.79**	**0.70**
			0.56	*0.57*	***0.67***	*0.46*
	≥101	—	—	0.55	***0.74***	**0.94**
				0.35	***0.63***	***0.72***
Spring chinook salmon FL (mm)	101–120	—	—	—	**0.80**	0.56
					0.63	*0.32*
	121–140	—	—	—	—	**0.74**
						0.59

Diets by sampling period

Between two sampling periods (29 June–17 July and 3–13 August) moderate changes occurred in the proportions of the 14 major food categories in stomachs of both fall and spring chinook salmon. In stomachs of fall chinook salmon, the percentage by weight of insects, gammarid amphipods, and crab larvae was higher in the earlier than in the later period, whereas the percentage by weight of fish prey was higher in the later than in the earlier period (Table 6). In spring chinook salmon stomachs, barnacle molts and fish were more abundant in the earlier period than in the later period, whereas algae and crab larvae were more abundant in the later period than in the earlier period.

Despite these shifts in prey composition, diet overlap based on the 14 major prey categories was high for all comparisons of fall and spring chinook salmon caught in the two time periods (Table 7). However,

Table 4

Percentage by weight and frequency of occurrence (in parentheses) of fourteen major food categories in stomachs of fall and spring chinook salmon caught in 1987 in the lower (stations 1–3) and mid (stations 4–5) sections of Coos Bay. Numbers in brackets are sample sizes. Mean fork lengths (FL) of fish in each area are also shown.

	Fall chinook salmon		Spring chinook salmon	
Food category	Sta. 1–3 87 mm FL [90]	Sta. 4–5 88 mm FL [26]	Sta. 1–3 123 mm FL [39]	Sta. 4–5 118 mm FL [26]
Cirripedia molts	2 (39)	22 (77)	4 (33)	35 (77)
Isopods	<1 (4)	<1 (23)	<1 (8)	<1 (15)
Caprellid amphipods	1 (14)	1 (12)	<1 (15)	<1 (4)
Gammarid amphipods	4 (42)	2 (35)	<1 (33)	2 (58)
Brachyuran, anomuran larvae	2 (28)	6 (23)	2 (44)	1 (23)
Other decapod larvae	<1 (10)	0	<1 (3)	0
Crustacean fragments	6 (22)	3 (12)	1 (26)	1 (23)
Araneae	<1 (12)	<1 (19)	<1 (3)	<1 (8)
Insects	6 (76)	17 (96)	<1 (49)	1 (77)
Other arthropods	<1 (6)	1 (8)	0	<1 (4)
Molluscs	<1 (2)	1 (12)	<1 (13)	<1 (12)
Teleosts	71 (47)	14 (15)	79 (54)	24 (12)
Algae, plants	3 (37)	31 (77)	11 (56)	32 (84)
Other material	4 (44)	3 (38)	1 (54)	3 (58)

Table 5

Dietary overlap of fall and spring chinook salmon caught in the lower (stations 1–3) and mid (stations 4–5) sections of Coos Bay. Overlap values based on 14 major food categories are in normal type and those based on 86 lower taxonomic categories are in italics. High overlap values (≥0.60) are in bold type.

		Fall chinook salmon	Spring chinook salmon	
		Sta. 4–5	Sta. 1–3	Sta. 4–5
Fall chinook salmon	Sta. 1–3	0.37	**0.82**	0.38
		0.28	***0.68***	*0.35*
	Sta. 4–5	—	0.35	**0.75**
			0.22	*0.47*
Spring chinook salmon	Sta. 1–3	—	—	0.43
				0.41

Table 6

Percentage by weight and frequency of occurrence (in parentheses) of fourteen major food categories in stomach of juvenile fall and spring chinook salmon caught during two time periods in 1987 in Coos Bay. Numbers in brackets are sample sizes. Mean fork lengths (FL) of fish caught during each time are also shown.

	Fall chinook salmon		Spring chinook salmon	
Food category	29 Jun–17 Jul 85 mm FL [89]	3–13 Aug 95 mm FL [26]	29 Jun–17 Jul 117 mm FL [26]	3–13 Aug 123 mm FL [39]
Cirripedia molts	6 (54)	3 (23)	17 (65)	8 (41)
Isopods	<1 (11)	0	<1 (4)	<1 (15)
Caprellid amphipods	1 (17)	<1 (4)	<1 (12)	<1 (10)
Gammarid amphipods	6 (47)	<1 (19)	1 (38)	1 (46)
Brachyuran, anomuran larvae	2 (29)	<1 (15)	1 (27)	2 (41)
Other decapod larvae	<1 (10)	0	0	<1 (3)
Crustacean fragments	9 (24)	<1 (8)	<1 (15)	2 (31)
Araneae	<1 (17)	<1 (4)	<1 (8)	<1 (3)
Insects	11 (84)	2 (65)	<1 (65)	1 (56)
Other arthropods	<1 (8)	0	<1 (4)	0
Molluscs	<1 (3)	<1 (8)	0	<1 (21)
Teleosts	51 (36)	84 (54)	73 (38)	58 (36)
Algae, plants	6 (45)	7 (50)	6 (62)	24 (72)
Other material	5 (47)	3 (31)	1 (38)	3 (67)

diet overlap based on the lowest identified taxa (86 categories) was low for all comparisons except that between fall and spring chinook salmon caught in the period 3–13 August. Although a variety of fish prey were eaten by both salmon groups during the earlier period, during the later period fish prey were nearly all juvenile osmerids.

Discussion

Potential for competition

The high dietary overlap values (Tables 3, 5, 7) between juvenile fall chinook salmon ≥81 mm FL and hatchery spring chinook salmon suggest that there is the potential for competition for food between these two groups in Coos Bay under conditions of food limitation. However, whether or not the two groups were competing for food in 1987 cannot be determined from dietary overlap alone. In fact, high dietary overlap may sometimes indicate a condition in which abundant food resources are shared between potential competitors rather than a condition in which there is competition for a resource in short supply (Zaret and Rand, 1971; Myers, 1980). Zaret and Rand (1971), in a study of tropical stream fishes, found that dietary overlap between species was high during the rainy season, when food resources were abundant, and low during the dry season, when food resources were scarce and when the different fish species targeted different prey.

We found little evidence in this study that the introduced hatchery-reared spring chinook salmon outcompeted native and STEP-reared fall chinook salmon for food. One potential result of competition for food between groups is a shift to less desirable prey in the diet of the weaker competitors (Hanson and Leggett, 1986). However, during the period when both fall and spring chinook salmon were in Coos Bay, calorically dense (high-quality) fish prey made up an equally large fraction by weight of the diets of both salmon groups (Table 1); i.e. fall chinook salmon were eating just as nutritious prey as that eaten by spring chinook salmon. Another potential result of competition is a decrease in growth rate (or average stomach fullness) of one or all of the competing groups (Reimers, 1973; Nielson et al., 1985; Hanson and Leggett, 1986). If spring chinook salmon outcompeted fall chinook salmon for food, the average stomach fullness of fall chinook salmon might be expected to drop following releases of the spring chinook salmon; this, however, did not occur. Stomach fullness of fall chinook salmon was equally high in the periods be-

Table 7

Dietary overlap of fall and spring chinook salmon during two time periods. Overlap values based on 14 major food categories are in normal type and those based on 86 lower taxonomic categories are in italics. High overlap values (≥0.60) are in bold type.

		Fall chinook salmon	Spring chinook salmon	
		3–13 Aug	29 Jun–17 Jul	3–13 Aug
Fall chinook salmon	29 Jun–17 Jul	**0.66** *0.26*	**0.67** *0.44*	**0.73** *0.32*
	3–13 Aug	—	**0.83** *0.49*	**0.73** ***0.70***
Spring chinook salmon	29 Jun–17 Jul	—	—	**0.75** *0.56*

fore and after spring chinook salmon were released into the bay (Fig. 5). In fact, stomach fullness of fall chinook salmon was usually higher than that of spring chinook salmon throughout the study period (Figs. 3 and 5). The low stomach fullness among spring chinook salmon following releases from the Anadromous, Inc. facility (Fig. 5) may reflect a delay in the start of feeding on natural prey by these hatchery fish. Paszkowski and Olla (1985) suggested that the inability of some hatchery fish to adapt to the natural environment may contribute to the poor survival of some groups of hatchery salmon. We conclude that the high dietary overlap between juvenile fall and spring chinook salmon indicates the potential for competition for food between these salmon groups in Coos Bay, but that in the summer of 1987 there was little evidence of actual food limitation or competition.

Differences between smaller fall chinook salmon and larger hatchery spring chinook salmon in spatial distribution and duration of residence within estuaries may tend to minimize their competition for food. Small fish tend to occur in shallow, nearshore areas or in salt marshes, whereas large fish tend to occur in deeper channel areas (Healey, 1980a, 1991; Kjelson et al., 1982; Levings, 1982; Simenstad et al., 1982; McCabe et al., 1986; Macdonald et al., 1987). Larger juvenile chinook salmon also tend to spend less time in estuaries than do smaller fish (Myers, 1980; Simenstad and Wissmar, 1984; Fisher and Pearcy, 1990). Both these differences may tend to decrease competition for food between hatchery-reared and wild chinook salmon in estuaries if there is a large difference in their size. However, large releases of hatchery salmon smolts into an estuary may affect wild smolts detrimentally by attracting birds and other predators that prey on juvenile salmon (Emlen et al., 1990).

We did not investigate rates of secondary production in the bay, rates of exchange of prey between the adjacent ocean and the bay, the rations required by juvenile salmon to maintain optimum growth rates, or the fractions of available prey in the bay eaten by juvenile salmon and other potential competing species. Without such information it is difficult to assess the likelihood that the growth and survival of juvenile salmon was limited by food in Coos Bay in 1987. The lower half of Coos Bay is strongly influenced by the adjacent ocean (Burt and McAlister, 1959; Fisher and Pearcy, 1990). In a study of Yaquina Bay, an Oregon estuary with physical characteristics similar to Coos Bay, Myers (1980) suggested that much of the food for juvenile salmon residing in the bay was supplied by tidal exchange with the ocean. Undoubtedly, the productivity of the adjacent ocean has a strong influence on the capacity of Coos Bay to support juvenile chinook salmon.

Upper-bay and lower-bay gradients in diet

Between the mid and lower sections of Coos Bay the diet of juvenile fall chinook salmon shifted from predominantly drift insects, barnacle molts, and drift algae to predominantly marine fishes (Table 4). A similar increase in piscivory in the lower bay also occurred among spring chinook salmon (Table 4).

Shifts in the diet of juvenile chinook salmon as they move from the river, through the estuary, and to the ocean appear to be related to the changes in habitat and foraging behavior which occur as a consequence of growth and development. Macdonald et al. (1987) observed that large hatchery-reared chinook salmon were often found in deeper, more saline waters of the salt-wedge of the Campbell River estuary, whereas smaller wild chinook salmon were often found in the freshwater layer near the surface. Small fry and subyearling chinook salmon often use tidal marshes where they eat drift and emergent insects and epibenthic crustaceans (Kjelson et al., 1982; Simenstad et al., 1982; Levings et al., 1991; Shreffler et al., 1992), whereas, larger, yearling chinook salmon spend little time in salt marshes but quickly move to neritic habitats (Simenstad et al., 1982). When subyearling fish move to neritic habitats their diet shifts to fishes, decapod larvae, euphausiids, and drift insects (Simenstad et al., 1982). McCabe et al. (1986) observed that, in the Columbia River estuary, subyearling chinook salmon in pelagic areas were significantly larger than those caught in shallow intertidal habitats and that the prey of juvenile chinook salmon varied with season, habitat, and position in the estuary. Feeding behavior is also influenced by environmental factors, for example turbidity (Gregory and Northcote, 1993).

Diets of juvenile chinook salmon in freshwater reaches of river systems often are dominated by larval, pupal, or adult insects that are captured mainly in the drift at the surface or in the water column (Becker, 1973; Craddock et al., 1976; Sagar and Glova, 1987, 1988; Rondorf et al., 1990; Healey, 1991; Levings and Lauzier, 1991; Smirnov et al., 1994). Depending on season and habitat, both terrestrial insects as well as different developmental stages of aquatic insects can be important prey for chinook salmon in rivers (Rondorf et al., 1990; Levings and Lauzier, 1991). Insects are also important constituents of the diets of juvenile chinook salmon in many estuaries (Healey, 1980, a and b, 1982, 1991; Levings, 1982; McCabe et al., 1986; Kask et al., 1988; this study), particularly in fresh or brackish water tidal marshes (Kjelson et al., 1982; Levings et al., 1991; Shreffler et al., 1992).

Whereas insects are important prey in freshwater and upper estuaries, fishes are important prey of juvenile chinook salmon constituents in the lower reaches of estuaries as well as in marine, neritic or subtidal areas (Healey, 1980a; Myers, 1980; Kjelson et al., 1982; Simenstad et al., 1982; Argue et al., 1986; McCabe et al., 1986; Levings et al., 1991; Reimers et al.[3]; Nicholas and Lorz[4]). Fish prey are also predominant in the diets of juvenile chinook salmon in marine waters off Oregon and Washington (Peterson et al., 1982; Emmett et al., 1986; Brodeur and Pearcy, 1990, 1992; Brodeur et al., 1992), in the Gulf Islands area of the Strait of Georgia (Healey, 1980b), and in the Fraser River plume (St. John et al., 1992).

In Coos Bay, the increase in importance of marine fish in the diets of juvenile fall and spring chinook salmon at the lower-bay stations may reflect an upper-bay, lower-bay gradient in the abundance of fish prey. Juvenile osmerids, sandlance, and rockfish were the predominant fish prey of juvenile chinook salmon in Coos Bay. In Yaquina Bay, larval and juvenile stages of these species were present in peak abundances in plankton samples from the extreme lower-bay and offshore stations (Pearcy and Myers, 1974). Myers (1980) caught more species of fishes in the lower than in the upper section of Yaquina Bay and suggested that much of the food for juvenile chinook salmon residing in the bay was supplied by tidal exchange with the ocean. She also suggested that high temperatures in the upper bay inhibited movement of predominantly marine species into the upper bay. A similar mechanism may be operating in Coos Bay. In our beach-seine samples large juvenile and adult surf smelt were much more abundant at lower than at mid-bay stations (average catch per set was 2,290, 237, 108, 30, and 12 at stations 1, 2, 3, 4, and 5, respectively). If, as was the case in Yaquina Bay, smaller larval and juvenile smelt also are more abundant in lower Coos Bay, the increased consumption by juvenile chinook salmon of these fish prey in the lower bay may be a consequence of their greater density there.

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