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[Article]

Ontogenetic Diet Shifts of Juvenile Chinook Salmon in Nearshore and Offshore Habitats of Puget Sound

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Abstract.—Marine growth and survival of juvenile Chinook salmon *Oncorhynchus tshawytscha* depend in part on the quality and quantity of prey consumed during this potentially critical life stage; however, little is known about the early marine diet of these fish or factors that affect the diet's variability. We examined the recent (2001–2007) dietary habits of Puget Sound, Washington, Chinook salmon (listed as threatened under the U.S. Endangered Species Act) during their first marine growing season (April–September). Juvenile Chinook salmon initially fed in nearshore marine habitats and then shifted to feed primarily offshore during July–September. Diet composition varied significantly among sampling regions (northern, central, and southern), habitats (nearshore, offshore), years, months, and fish size-classes. At nearshore sites, insects (all months) and gammarid amphipods (July) were dominant prey sources, whereas in offshore diets decapods (primarily crab larvae; July) and fish (September) were most important. Chinook salmon became increasingly piscivorous as they grew and ate fish with fork lengths up to 51% (nearshore) and 52% (offshore) of predator fork length. At nearshore sites, Chinook salmon fed mainly on larval and juvenile Pacific sand lances *Ammodytes hexapterus*; offshore, they primarily ate juvenile and older Pacific herring *Clupea pallasii*. Overall, Chinook salmon had more diverse diets and ate higher-quality prey (insects) in northern nearshore and central offshore waters, whereas Chinook salmon caught in the southern nearshore and northern offshore waters had a lower proportion of empty stomachs but ate lower-quality prey (crustaceans). Annual variation in the composition of offshore prey appeared to be determined early in the growing season, suggesting that environmental factors (e.g., climate) affecting marine productivity might produce strong interannual trends in marine survival of Puget Sound Chinook salmon. In addition, the importance of insects as high-quality prey highlighted the terrestrial link to the marine feeding of Chinook salmon and suggests that shoreline development and land use changes will affect feeding opportunities for these fish in Puget Sound.

The early marine life stages of Pacific salmon *Oncorhynchus* spp. experience some of the most rapid growth rates (LeBrasseur and Parker 1964; Healey 1979, 1982a; Mortensen et al. 2000) and highest mortality rates (Parker 1962; Royal 1962; Furnell and Brett 1986; Bradford 1995; Willette et al. 2001) compared with most other stages of the life cycle. Estuarine and coastal marine environments provide important foraging and rearing habitat for juvenile Pacific salmon (Shepard 1981; Simenstad et al. 1982; Thorpe 1994; Aitken 1998). Favorable early marine growth conditions are considered crucial as both larger size (Parker 1971; Blackbourn 1976; Healey 1982b; Ward et al. 1989; Henderson and Cass 1991) and faster growth have been associated with elevated overall marine survival for several salmon species (Holtby et al. 1990; Hargreaves 1997; Murphy et al. 1998; Tovey 1999; Beamish et al. 2004a; Moss et al. 2005; Cross et al. 2008). In Puget Sound, Washington, ocean-type Chinook salmon *O. tshawytscha* are currently listed as threatened under the U.S. Endangered Species Act (Myers et al. 1998; NMFS 1999). Poor marine survival

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is one factor contributing to the decline of this stock (Greene et al. 2005). As juveniles, Chinook salmon spend much of their first marine growing season in Puget Sound estuaries and offshore waters (Beamish et al. 1998). Therefore, recent declines in marine survival (Ruggerone and Goetz 2004) could reflect degraded rearing and foraging conditions during early marine life in Puget Sound.

Puget Sound Chinook salmon primarily exhibit an ocean-type life history, migrating to saltwater immediately after emerging from the gravel as fry or after spending up to several months rearing in freshwater. Most of these juveniles enter estuaries and occupy nearshore habitats primarily during the spring and early summer (Stober et al. 1973; Congleton et al. 1982; Simenstad et al. 1982; Brennan et al. 2004; Duffy et al. 2005; Beamer et al. 2006; Toft et al. 2007). By midsummer, most Chinook salmon transition from nearshore waters and are caught in large numbers in offshore habitats, where catches remain high at least through early fall (Beamish et al. 1998). Predation by fish, birds, and marine mammals is hypothesized to be responsible for most of the early marine mortality experienced by juvenile salmon (Parker 1971; Beamish and Mahnken 2001). Size at this stage is critical because it partially determines the level of predation risk posed by the many gape-limited predators (Sogard 1997; Juanes et al. 2002; Duffy and Beauchamp 2008). In addition, smaller fish may suffer higher predation mortality by employing riskier foraging strategies (Biro et al. 2005). Besides buffering the risk of predation, achieving a larger size enables Chinook salmon to begin eating a previously unavailable supply of energy-rich prey fishes. Incorporating high-energy prey into the diet can be critical for achieving the faster growth and increased lipid stores that are essential for surviving the winter (Post and Parkinson 2001; Sutton and Ney 2001; Beauchamp 2009).

Seasonal shifts in prey resources and water temperature can affect the potential growth rates of juvenile salmon. Poor-quality feeding areas, which vary over short and longer time frames, may result in increased susceptibility to predation due to poorer condition and smaller sizes of fish (Brodeur et al. 1992; Perry et al. 1996). The quality of feeding areas can also affect migration rates and residence times as salmon are believed to leave areas of poor food quality faster than when food is abundant (Simenstad and Salo 1980; Healey 1982b; Orsi et al. 2000). In Puget Sound, regional differences in environmental conditions (e.g., turbidity, salinity, and water temperature profiles) could affect the length and quality of early marine rearing of juvenile Chinook salmon, particularly in nearshore environments (Duffy et al. 2005). In addition, when food supply is limited, dietary overlaps among species and between hatchery and wild salmon may result in intra- and interspecific competition that would reduce growth rates and overall fish size (Fisher and Pearcy 1996; Sturdevant 1999).

Information on the diet of juvenile Chinook salmon in nearshore (Conley 1977; Fresh et al. 1978, 1981; Pearce et al. 1982; Parametrix, Inc. 1985; Duffy 2003; Brennan et al. 2004) and offshore (Fresh et al. 1981; Beamish et al. 1998) Puget Sound waters dates mainly to the 1970s, was not always collected or analyzed methodically, and may not represent the current situation. In the late 1970s, juvenile Chinook salmon in nearshore sublittoral waters ate primarily fish (Pacific herring *Clupea pallasii* and Pacific sand lances *Ammodytes hexapterus*) and brachyuran crab larvae during June and July and then consumed fish, insects, and polychaetes later in the summer (August; Fresh et al. 1981). In the late 1970s and 1990s, Chinook salmon became increasingly piscivorous (feeding mainly on Pacific herring) as they grew larger and were caught in offshore waters (Fresh et al. 1981; Beamish et al. 1998). The current status of prey resources in Puget Sound is unknown; however, Puget Sound is facing many of the problems seen in urbanized estuaries throughout the world, including widespread declines in fish, bird, and marine mammal populations (PSAT 2005). Recent declines in some Puget Sound forage fish populations—particularly Pacific herring (PSWQAT 2002)—may indicate a reduction in the supplies of energy-rich fish prey available for Chinook salmon. Similarly, increasing shoreline development and alteration of nearshore habitats may be altering prey abundance, diversity, and adequate feeding opportunities.

Puget Sound encompasses a wide variety of physical and environmental conditions. Localized differences among basins include the size and discharge of associated rivers, the degree of urbanization (e.g., altered habitats, pollutant loads), the magnitude of salmon runs, species composition, and proportion of natural versus hatchery salmon stocks. These differences likely affect the potential role and quality of these areas as rearing environments for juvenile salmon. Specifically, we expected diets of Chinook salmon to differ by (1) habitat (nearshore and offshore), (2) region (northern, central, and southern), (3) season (April–September), (4) year (2001–2007), and (5) fish size-class. Describing the feeding habits of Puget Sound Chinook salmon stocks during early marine life was an initial step towards understanding whether early marine feeding contributed to the recent declines and regional patterns in marine survival of these stocks (Ruggerone and Goetz 2004).

Methods

Study area.—Puget Sound is a deep, elongated glacial fjord composed of underwater valleys, ridges, and basins and has an average depth of 135 m. The maximum depth of 285 m occurs just north of Seattle in the large Main Basin. A shallow sill separates the Main Basin from the Southern Basin near the Tacoma Narrows. The Southern Basin receives less than 10% of the freshwater draining into Puget Sound, primarily from the Nisqually and Deschutes rivers and also from smaller rivers and streams (Burns 1985). Northeast of the Main Basin, the Whidbey Basin includes the waters of Possession Sound, Port Susan, Saratoga Passage, and Skagit Bay (Figure 1). The Whidbey Basin is fed by Puget Sound's two largest rivers, the Skagit and Snohomish rivers, and receives 60% of the freshwater entering Puget Sound (Burns 1985).

For this study, sampling was stratified by region and habitat. Sampling regions were defined as follows: (1) the northern region was north of Edwards Point and included the northern Main Basin, Admiralty Inlet, and southeastern Whidbey Basin; (2) the central region extended in the Main Basin from Edwards Point south to Tacoma Narrows; and (3) the southern region was located south of the Tacoma Narrows sill (Figure 1). These sampling regions included significant saltwater entry points for both wild and hatchery Chinook salmon, major freshwater inflows (Snohomish, Stillaguamish, Puyallup, Green, and Nisqually rivers), and marine rearing and migration corridors. Nearshore and offshore habitat types were defined primarily by the type of sampling gear used. Nearshore sites were sampled by floating beach seines, which cover the upper 2 m from shore out to a distance of approximately 33 m, targeting shallow sublittoral habitats in shoreline zones. Five to six nearshore sites were sampled in the northern and southern regions (Duffy et al. 2005), and 16 nearshore sites were sampled in the central region (Brennan et al. 2004). Open-water offshore sites (bottom depth generally > 30 m) were sampled by midwater rope trawl, which had an effective opening of 14×30 m (depth × width) when fishing (Beamish et al. 2000).

Fish sampling.—Field sampling was designed to characterize the timing of nearshore and offshore habitat use, size structure, and diet of juvenile Chinook salmon in Puget Sound. At nearshore sites, we conducted beach seining (2 sets/site) biweekly during April–July and monthly during August and September in 2001 and 2002 at each northern and southern site (Duffy et al. 2005) and each central site (Brennan et al. 2004) using a floating beach seine (37.0 m long × 2.0 m high, with graded mesh from 6 mm at the cod end to 3 cm in the wings) according to standard estuarine fish sampling protocols (Simenstad et al. 1991). Additional beach seining was conducted at nearshore sites in the northern and southern regions during June–September 2003. Midwater trawling was conducted in the northern and central regions during 2-d cruises in July and September 2001–2007 (October was sampled instead of September in 2004 and no offshore sampling was done in 2003). Additional trawls were conducted in the southern region during July 2004 and in Hood Canal during September 2007. On average, 30 trawls were conducted per year. The average tow lasted 20 min at 4.4 knots (8.2 km/h), covering a distance of 1.45 nautical miles (2.69 km). Approximately two-thirds of the trawls sampled the upper 30 m of the water column, with occasional deeper tows ranging between 30 and 120 m. All sampling occurred during daylight hours.

Counts of all fish representing each species were recorded. Hatchery Chinook salmon were identified by adipose fin clips and coded wire tags (CWTs), while unmarked Chinook salmon were assumed to be of natural origin; however, some unknown proportion of these unclipped fish were of hatchery origin due to factors like incomplete tagging. Individual fork lengths (FLs; nearest 1 mm) and wet weights (nearest 0.1 g) were recorded for subsamples (at least 30 fish/species, when available). When possible (primarily in beach seine samples), fish were anesthetized with buffered tricaine methanesulfonate (MS-222), and gut contents were obtained using nonlethal gastric lavage and preserved in 10% buffered formalin or 95% ethanol for subsequent processing in the laboratory. Fish to be processed in the laboratory were first euthanized in an overdose of buffered MS-222 or with a sharp blow to the head and were then frozen.

Diet composition.—Stomach samples from a subset (5–10 fish/set, but all fish with CWTs) of juvenile Chinook salmon (and up to 10 of the larger age-1 and older Chinook salmon) caught at nearshore sites were examined in the laboratory. Under a dissecting microscope, invertebrate prey were separated into broad taxonomic categories, and fish prey were identified to species where possible. Blotted wet weights of individual fish prey and prey categories were recorded to the nearest 0.0001 g using an electronic scale. Stomach samples from offshore fish were processed on the boat immediately after capture. The fundic and cardiac portions of stomachs from all (or up to 30) of the Chinook salmon caught in a given tow were removed and examined by a single experienced individual. Using a 4× magnifying glass, this individual visually estimated the total volume of the stomach contents to the nearest 0.1 cm^3 and the proportional contribution of the major prey types

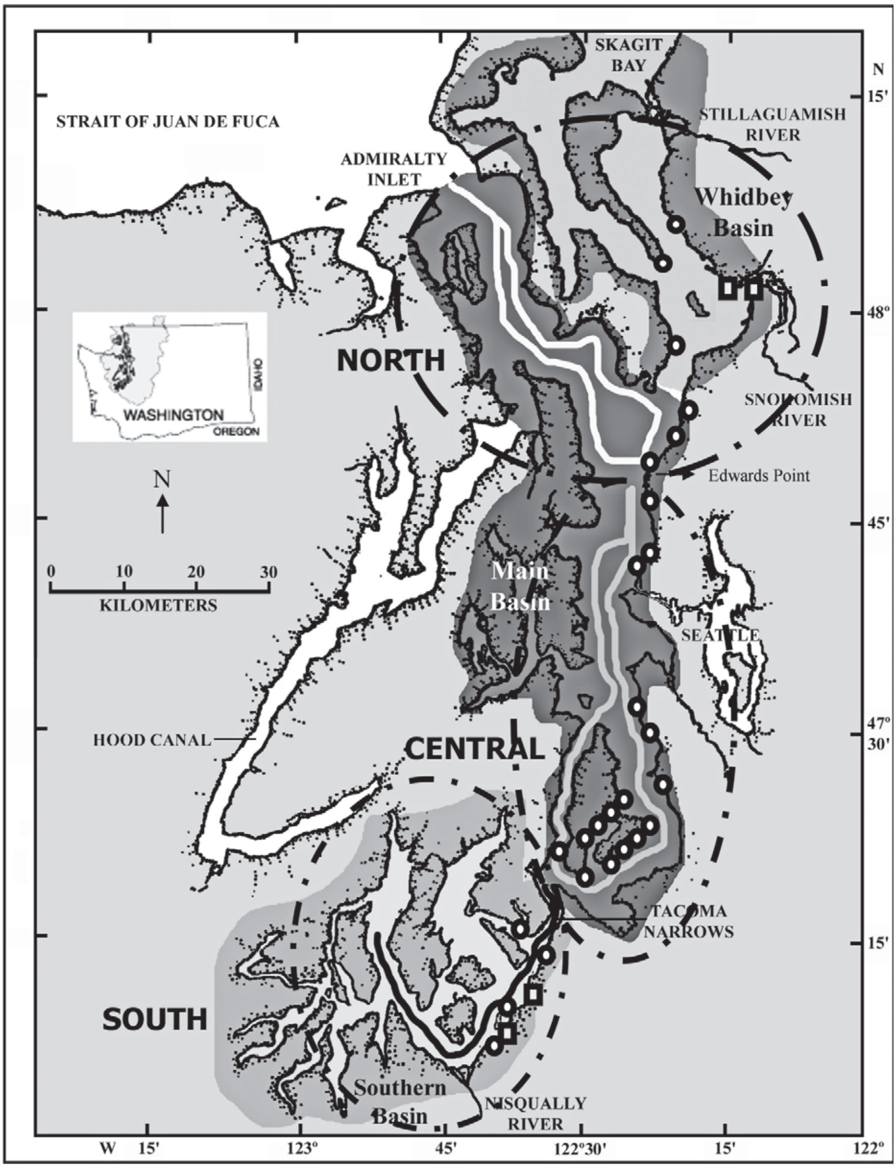

FIGURE 1.—Major basins, sampling regions, and sampling locations for juvenile Chinook salmon studies conducted in Puget Sound, 2001–2007. Shading indicates major basins (dark gray = Main Basin; medium gray = Whidbey Basin; light gray = Southern Basin). Ovals indicate north, central, and south sampling areas. Nearshore sites (circles) were sampled by beach seine during April–September of 2001 and 2002 (and June–September 2003 at northern and southern sites). Solid lines indicate typical routes surveyed by midwater trawl in northern (white line), central (gray line), and southern (black line) regions.

(Beamish et al. 2004b). When possible, individual fish prey lengths (FLs or total lengths depending upon the species) were measured from both nearshore and offshore samples.

Prey were grouped into broad taxonomic categories reflecting the dominant types: copepods (mostly calanoid copepods but also included harpacticoid copepods), decapods (primarily larval crab but also larval and adult shrimp), euphausiids, gammarid amphipods (hereafter, gammarids; both estuarine and marine species), hyperiid amphipods (hereafter, hyperiids), polychaetes (epibenthic and planktonic forms), barnacles (cyprids, nauplii, and exuviae), insects (including both terrestrial and aquatic insects [Insecta]

TABLE 1.—Gross energy density (J/g wet weight [ww]) values for prey eaten by juvenile Chinook salmon in Puget Sound.

Prey group	Energy density J/g (ww)	Sample area	Reference	Comments
Barnacles	2,045	Newport River estuary, North Carolina	Thayer et al. 1973	Barnacle larvae/exuviae
Copepods	2,625	North Pacific and Bering Sea	Davis et al. 1998	*Neocalanus cristatus*
Decapods	2,981	Bristol Bay	Davis 1993[a]	Crab zoea
Euphausiids	3,111	North Pacific and Bering Sea	Davis et al. 1998	*Thysanoessa* spp.
Fish	4,649	Washington; Alaska	Boldt and Haldorson 2002; Duffy 2003	Average of juvenile salmon, Pacific herring, and Pacific sand lance
Gammarids	4,408	Northwest Atlantic	Davis 1993[a]	Average for Gammarids and amphipods
Hyperiids	2,466	Bering Sea	Davis et al. 1998	July 1992–1995
Insects	5,311	Salmon River estuary, Oregon	Duffy 2003	Average of adult insects eaten by salmon
Polychaetes	3,186	Northwest Atlantic	Davis 1993[a]	Mean of two reported values

[a] Literature values are summarized in this reference.

as well as spiders [Arachnida] and water mites [Acari]), other invertebrates (rare and unidentifiable prey), and fish (including larval, juvenile, and adult forms). The proportional wet weight (nearshore; g) or volumetric (offshore; cm^3) contribution of each prey category was calculated individually for all nonempty stomachs. The energy density of each prey group was compiled (summarized from the literature; Table 1) to obtain an indication of prey quality (Armstrong et al. 2008).

Diets of ocean-type juvenile Chinook salmon were the focus of the analysis, and monthly habitat-specific length frequency histograms were used to distinguish the age-0 fish (nearshore: $\leq$130 mm FL in April–June, $\leq$200 mm FL in July–September; offshore: $\leq$230 mm FL in July, $\leq$300 mm FL in September–October) from older and stream-type Chinook salmon. Summary information was compiled for the age-0 Chinook salmon diet information from nearshore (Table 2) and offshore (Table 3) habitats. We calculated monthly (April–September) average diet proportions for age-0 Chinook salmon by habitat (nearshore and offshore), region (northern, central, southern, and Hood Canal), and year (2001–2007).

Statistical analyses.—We initially used multivariate analysis of variance (multivariate ANOVA) tests (Zar 1999) to determine the effects of factors that were expected to influence (arcsine transformed; Zar 1999) diet proportions of juvenile Chinook salmon. These included temporal factors like year (2001–2007) and month (April–September), spatial factors like region (northern, central, southern) and habitat (nearshore and offshore), and ontogenetic factors like size-class (small, medium, and large). These initial results were screened for only those effects and prey categories that showed significant main effects or interaction terms after Bonferroni correction for multiple comparisons, and subsequent analyses were conducted on each prey category individually by using ANOVA (Zar 1999). All analyses were performed using the Statistical Package for the Social Sciences version 11.5.0 (SPSS, Inc., Chicago, Illinois).

Interhabitat analysis.—To test our hypothesis that diet composition would vary by habitat (nearshore versus offshore) due to ontogenetic shifts in feeding and differences in available prey, we compared diet proportions of Chinook salmon at sizes (small: 70–129 mm FL; large: 130–199 mm FL) that were caught concurrently in both habitats during July and September of 2001 and 2002 in the northern and central regions. We categorized month (July or September) as a covariate to reduce the influence of seasonal variability (Table 4).

Intrahabitat analysis.—We hypothesized that within each habitat, Chinook salmon diet proportions would vary spatially and temporally due to differences in prey composition and would vary with predator size due to prey availability (e.g., ability of the predator to capture the prey). To test this hypothesis, we compared diet proportions at nearshore sites across years (2001, 2002), months (April–September), regions (northern, central, and southern), and size-classes (small: $<$70 mm FL; medium: 70–129 mm FL; large: 130–199 mm FL). We then compared diet proportions at offshore sites across years (2001–2007 excluding 2003), months (July or September/October), regions (northern, central; northern, central, and southern for July 2004; northern, central, and Hood Canal for September 2007), and size-classes (small: $<$130 mm FL; medium: 130–199 mm FL; large: 200–299 mm FL; Table 4).

Piscivory.—The proportions of fish in the diets of all sizes of Chinook salmon were pooled over all regions and plotted separately for nearshore and offshore habitats to examine ontogenetic shifts in piscivory. We grouped Chinook salmon into size-classes ($<$70, 70–129, 130–199, 200–299, 300–399, and $\geq$400 mm FL) by habitat (nearshore, offshore), and we used one-way ANOVA to examine shifts in piscivory in relation to Chinook salmon size. The FLs of measured prey fish were compared graphically with the FLs of Chinook

TABLE 2.—Summary of diet samples for age-0 Chinook salmon (by month and year) caught by beach seine in nearshore areas of Puget Sound, 2001–2002 (FL = fork length).

		2001						
Region	Variable	Apr	May	Jun	Jul	Aug	Sep	Total
North	Stomachs (*N*)	13	51	19	91	24	8	206
	Percent empty	8	4	0	1	0	0	2
	Percent with fish	0	8	0	7	8	38	7
	Mean FL (mm)	65.1	78.3	85.2	98.5	109.7	152.5	93.5
	Length range	51–81	39–110	61–106	81–150	95–168	123–196	39–196
Central	Stomachs (*N*)		13	89	77	97	38	314
	Percent empty		0	12	5	4	3	6
	Percent with fish		15	2	12	11	11	9
	Mean FL (mm)		83.5	86.3	105.5	124.7	130.6	108.1
	Length range		72–104	70–121	84–148	95–195	110–172	70–195
South	Stomachs (*N*)		85	32	48	5	5	175
	Percent empty		2	0	2	0	0	2
	Percent with fish		4	6	0	0	0	3
	Mean FL (mm)		85.9	90.3	108.7	126.0	128.6	95.3
	Length range		65–115	58–120	80–138	106–177	118–137	58–177

salmon (including fish caught in 2003 and during crepuscular periods in May 2002) to examine size limits (gape limitation) and prey size selectivity.

Diel feeding.—All sampling occurred during daylight hours, which may have caused some gear avoidance and a potential bias in the diet composition. To examine potential diel differences in feeding patterns, we sampled nearshore sites in northern and southern regions over a 24-h sequence during the peak juvenile Chinook salmon migration period in May 2002 (1 d/region; Duffy 2003). To examine diel feeding chronologies, we multiplied the ratio of the wet weight of the gut contents to the whole body weight (less the weight of the gut contents) by 100 to get a measure of feeding intensity (Brodeur et al. 2007).

Results

Diet Composition

Interhabitat analysis.—Chinook salmon at offshore sites were consistently larger than those sampled concurrently at nearshore sites. In 2001–2002, the average FLs of Chinook salmon (with nonempty stomachs) at offshore sites were larger than at nearshore sites by 19–30 mm in July and by 29–44 mm in September (except for northern sites in 2001; Tables 2, 3). In offshore waters, the proportion of Chinook salmon that had eaten fish (5–29%) averaged higher than the proportion at nearshore sites, but the frequency of empty stomachs was also higher offshore (Tables 2, 3).

Seasonal diet composition differed significantly between nearshore and offshore habitats (Table 4), among regions, and among size-classes but did not differ among years (Table 4). Overall, Chinook salmon ate significantly more insects, gammarids, and barnacles at nearshore sites (Figures 2, 3) and more decapods and copepods in offshore habitats (Table 5; Figures 4, 5). Chinook salmon also ate more fish in offshore habitats, particularly during September (Figures 2, 5), although this difference was not statistically significant (Table 5). Adult insects and forage fish (Foy and Paul

TABLE 3.—Summary of diet samples for age-0 Chinook salmon caught by midwater trawl during July and September (*October in 2004) in offshore areas of Puget Sound, 2001–2007 (FL = fork length).

		July						
Region	Variable	2001	2002	2004	2005	2006	2007	Total
North	Stomachs (*N*)	17	28	92	56	30	44	267
	Percent empty	12	18	1	13	13	0	7
	Percent with fish	0	11	10	4	47	11	12
	Mean FL (mm)	127.5	127.2	140.3	147.0	164.5	148.0	143.5
	Length range	113–154	103–179	108–224	109–221	126–226	125–190	103–226
Central	Stomachs (*N*)	17	83	147	174	163	161	745
	Percent empty	0	34	34	35	12	14	24
	Percent with fish	0	1	0	1	19	0	5
	Mean FL (mm)	122.9	114.8	128.0	138.4	146.9	128.6	133.1
	Length range	88–152	86–166	97–230	102–230	94–208	102–207	86–230

TABLE 2.—Extended.

		2002						
Region	Variable	Apr	May	Jun	Jul	Aug	Sep	Total
North	Stomachs (*N*)		31	14	70	16	5	136
	Percent empty		13	0	9	0	0	7
	Percent with fish		3	0	7	19	20	7
	Mean FL (mm)		83.2	74.4	87.4	102.9	132.0	88.5
	Length range		52–128	51–88	60–111	81–119	110–175	51–175
Central	Stomachs (*N*)		35	110	99	72	56	372
	Percent empty		3	4	9	7	5	6
	Percent with fish		20	8	2	7	5	7
	Mean FL (mm)		94.9	93.1	98.5	106.7	121.0	101.54
	Length range		75–115	72–138	80–144	86–162	100–171	72–171
South	Stomachs (*N*)	5	47	42	12	13	6	125
	Percent empty	0	0	2	0	8	0	2
	Percent with fish	40	9	12	8	8	0	10
	Mean FL (mm)	75.4	89.8	90.4	97.3	116.9	138.8	95.3
	Length range	69–88	67–115	76–123	78–120	96–170	112–180	67–180

1999; Table 3) were the highest quality prey eaten by Chinook salmon, with average energy density values close to 5,300 J/g of wet weight—almost double the energy densities of the primary invertebrate prey (planktonic crustaceans like decapods: ~3,000 J/g; Table 1).

Intrahabitat analysis: nearshore.—At nearshore sites (Figures 2, 3), diets consisted primarily of insects, crustaceans, other miscellaneous invertebrates, and fish; diet composition varied significantly among months, sampling regions, and size-classes but not among years (Table 4). Insects (primarily dipterans and hymenopterans, but also lepidopterans, aphids, coleopterans, and trichopterans) and, to a lesser degree, gammarids were a key part of the diet during all months (Figures 2, 3). Hyperiids were significantly more dominant in diets during the summer (August), whereas polychaetes and euphausiids were more prevalent in April–June diets, when the abundance of juvenile Chinook salmon peaked at nearshore sites (Table 5; Figures 2, 3). Rarer prey items (grouped as "other invertebrates") included isopods, cumaceans, ostracods, caprellid amphipods, and molluscs.

Insects were significantly more dominant in diets from the northern and central regions than in southern diets, whereas Chinook salmon in the southern region ate significantly more euphausiids and hyperiids (Table 5) and consistently had the lowest proportion of empty stomachs (<2%; Table 2). Hyperiids were significantly more prominent in diets of Chinook salmon in the southern and central regions, as well as overall in the diets of the largest Chinook salmon (130–199 mm FL; Table 5).

The largest age-0 Chinook salmon also ate significantly more fish (Table 5), but the proportion of the population that had eaten fish was more consistent at northern and central sites (7–9%) than at southern sites (3–10%; Table 2). Chinook salmon fed mainly on larval and juvenile Pacific sand lances, but other fish prey included pink salmon *O. gorbuscha* and chum salmon *O. keta* (at northern and southern sites), surf smelt *Hypomesus pretiosus* (northern), Pacific herring

TABLE 3.—Extended.

		September						
Region	Variable	2001	2002	2004*	2005	2006	2007	Total
North	Stomachs (*N*)	75	105	26	50	30	79	365
	Percent empty	5	10	27	10	53	5	13
	Percent with fish	31	47	23	20	27	13	29
	Mean FL (mm)	154.0	160.7	180.9	195.3	172.8	169.3	168.4
	Mean FL (mm)	96–253	121–250	142–252	165–226	134–221	143–207	96–253
Central	Stomachs (*N*)	87	151	115	171	124	127	775
	Percent empty	10	13	27	11	15	10	14
	Percent with fish	11	15	13	11	28	2	14
	Mean FL (mm)	165.6	165.3	192.8	178.7	189.3	160.1	175.3
	Length range	127–297	123–300	129–282	135–248	126–278	135–190	123–300

TABLE 4.—Results from multivariate analysis of covariance (MANCOVA) and multivariate analysis of variance (MANOVA) tests examining the effects of habitat (nearshore [near]; offshore [off]), sampling region canal (N = north, C = central, S = south, Hd = Hood Canal), years (2001–2007), months (April–September, where 4 = April and 9 = September; 10 = October, for 2004 only), and size-classes (fork length [FL]: sm = small, md = medium, lg = large) on the diet of juvenile Chinook salmon in Puget Sound. Degrees of freedom (df) are listed for both hypothesis (Hyp) and error terms.

Factor	Levels	Hyp df	Error df	Wilks' lambda	*F*	*P*
	Habitat MANCOVA					
Month (covariate)	7, 9	11	844	0.94	5.08	0.00
Habitat	Near, off	11	844	0.82	16.94	0.00
Year	2001, 2002	11	844	0.98	1.63	0.09
Region	N, C	11	844	0.93	5.44	0.00
Size-class	Sm (FL < 130 mm), lg (130–199 mm FL)	11	844	0.94	5.04	0.00
	Nearshore MANOVA					
Year	2001, 2002	9	1,200	0.99	1.85	0.06
Month	4–9	45	5,371	0.91	2.50	0.00
Region	N, C, S	18	2,400	0.96	2.92	0.00
Size-class	Sm (FL < 70 mm), md (70–129 mm FL), lg (130–199 mm FL)	18	2,400	0.98	1.64	0.04
	Offshore MANOVA					
Year	2001–2007 (except 2003)	45	7,728	0.88	4.83	0.00
Month	7, 9 (2004: 7, 10)	18	3,454	0.97	3.26	0.00
Region	N, C (Jul 2004: N, C, S) (Sep 2007: N, C, Hd)	9	1,727	0.97	6.53	0.00
Size-class	Sm (FL < 130 mm), md (130–199 mm FL), lg (200–299 mm FL)	18	844	0.89	11.03	0.00

(central), shiner perch *Cymatogaster aggregata* (northern and central), bay pipefish *Syngnathus leptorhynchus* (northern), and sculpins (Cottidae; northern and southern). Stomachs of Chinook salmon that contained fish averaged (mean ± SE) 1.7 ± 0.5 prey fish/stomach, with a maximum of 20 (larval) fish/stomach.

Intrahabitat analysis: offshore.—Overall, the diets of pelagic Chinook salmon were dominated by crustaceans, insects, and fish (Figures 4, 5), but the relative importance of different prey taxa varied by year, month, sampling region, and size-class (Table 4). Decapods were the most important offshore prey in July (Table 5), particularly during 2001–2004, but they were somewhat less important during 2005–2007 as the contributions of hyperiids, insects, euphausiids, and fish increased (Figure 4). Fish, gammarids, and euphausiids were more important components of offshore diets in September than in July (Table 5). Overall, Chinook salmon in September fed on a more diverse mix of prey types (Figure 5). Decapods, euphausiids, and hyperiids were consistently important, while rarer prey items, including ostracods and larval octopus, occasionally contributed substantially to the diet (Figure 5).

Decapods (almost exclusively crab larvae), euphausiids, and fish were significantly more important prey items in the northern region than in the central region (Table 5; Figures 4, 5), whereas copepods, gammarids, hyperiids, insects, and polychaetes represented a significantly larger proportion of the offshore diet in the central region (Table 5) as well as in the diets of the smaller size-classes of Chinook salmon (Table 5). The proportion of empty stomachs was higher in the central region than in the northern region, particularly during July (Table 3).

Additional spatial variability was found in offshore diets. In July 2004, Chinook salmon caught in the southern region (mean ± SE, 124 ± 4 mm FL; $n = 28$) ate decapods at a proportion similar to that of Chinook salmon in the northern region (and significantly greater than that of Chinook salmon in the central region); Chinook salmon in the southern region consumed a significantly lower proportion of amphipods relative to Chinook salmon in the central region (Table 5). In September 2007, Chinook salmon caught in Hood Canal (164 ± 1 mm FL; $n = 79$) ate a significantly higher proportion of fish and insects and significantly lower proportion of gammarids than did Chinook salmon in the northern and central regions (Table 5).

As in the nearshore habitat, Chinook salmon feeding offshore ate a significantly higher proportion of fish as predator size-class increased (Table 5). Piscivorous Chinook salmon in offshore waters fed mainly on juvenile and older Pacific herring, followed by Pacific sand lances. Other fish prey included surf smelt, bay pipefish, quillfish *Ptilichthys goodei*, and larval and juvenile fishes representing various families (Osmeridae, Myctophidae, Agonidae, Cottidae, Sebastidae, and Pleuronectidae). Fish made up the greatest proportion of the July diets in 2006, when Chinook salmon were larger on average than in the other years (Figure 4). Piscivorous Chinook salmon contained an average of 1.21 ± 0.03 fish/stomach (mean ± SE), with a maximum of 4 fish/stomach.

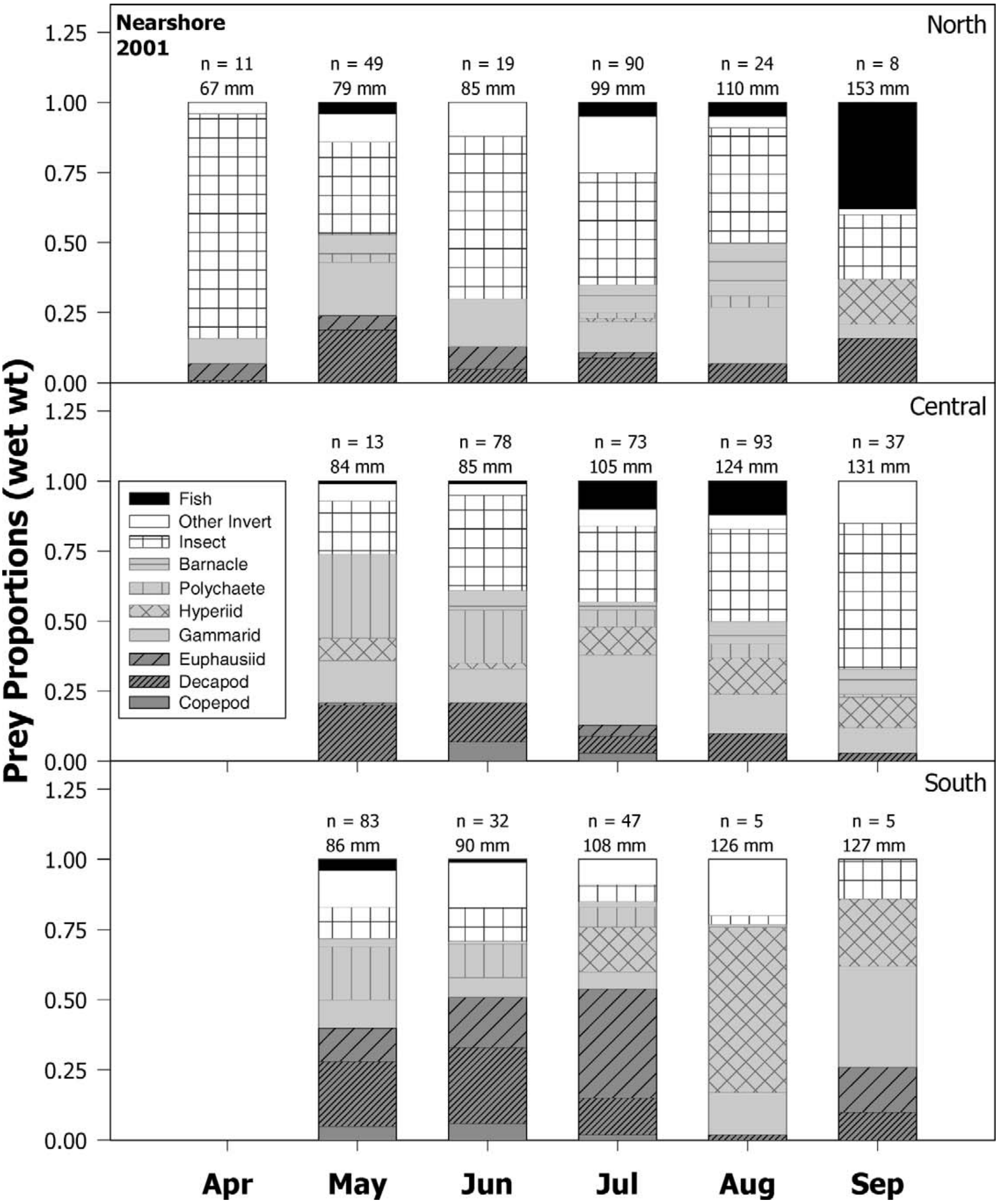

FIGURE 2.—Monthly nearshore marine diet composition (in wet-weight [wt] proportions of each prey category; invert = invertebrate) for age-0 Chinook salmon in northern (upper panel), central (middle panel), and southern (bottom panel) regions of Puget Sound during 2001. Sample size and average fork length are listed above each bar.

Piscivory

There appeared to be a length threshold associated with the onset of piscivory for Chinook salmon in nearshore (70 mm) and offshore (130 mm) habitats (Figure 6); fish that exceeded these thresholds became increasingly piscivorous as they grew larger (Table 6; ANOVA: nearshore $F = 85.02$, $P < 0.01$; offshore $F = 290.02$, $P < 0.01$). Chinook salmon ate fish with FLs

TABLE 5.—Results from analysis of variance (ANOVA) examining the effects of year, month, region, habitat, and size-class on proportions of prey groups in the diet of juvenile Puget Sound Chinook salmon. See Table 4 for definition of codes for levels in each factor (ns = not significant).

		Barnacles		Copepods		Decapods		Euphausiids	
Factor	df	*F*	Relationship	*F*	Relationship	*F*	Relationship	*F*	Relationship
					Habitat				
Habitat	1	9.56[b]	Near > off	6.83[b]	Off > near	137.88[b]	Off > near	0.51	ns
Year	1	0.25	ns	0.02	ns	2.88	ns	0.55	ns
Region	1	0.00	ns	10.05[b]	C > N	9.59[b]	N > C	1.59	ns
Size-class	1	2.05	ns	0.17	ns	7.92[b]	Sm > lg	1.35	ns
Month[c]	1	0.16	ns	2.84	ns	31.19[b]	7 > 9	0.15	ns
					Nearshore				
Year	1	0.04	ns	0.03	ns	0.26	ns	0.43	ns
Month	5	0.45	ns	0.94	ns	0.96	ns	3.70[b]	5 > 8, 9
Region	2	1.21	ns	0.95	ns	1.09	ns	10.06[b]	S > N, C
Size-class	2	0.93	ns	0.44	ns	1.27	ns	2.83	ns
					Offshore				
Year	1	0.36	ns	2.03	ns	3.66[a]	2001 > 2005	4.71[b]	2005 > all years (except 2006)
Month	5	1.39	ns	1.19	ns	59.63[b]	7 > 9, 10	16.34[b]	9 > 7, 10
Region	2	0.94	ns	5.14[a]	C > N	29.24[b]	N > C	4.75[a]	N > C (Sep 2007; N > C, Hd)
						32.79[b]	(Jul 2004; N, S > C)	11.51[b]	
						15.31[b]	(Sep 2007; Hd, N > C)		
Size-class	2	0.32	ns	3.61[a]	Sm > lg	18.39[b]	Sm > md > lg	0.44	ns

[a] $P < 0.05$.
[b] $P < 0.01$.
[c] Covariate.

that were up to 51% (nearshore) and 52% (offshore) of predator FL (Figure 7). At nearshore sites, Chinook salmon fed mainly on larval and juvenile Pacific sand lances (FL was 5–43% of predator FL); offshore, they primarily ate juvenile and older Pacific herring (15–52% of predator FL). Other nearshore fish prey included juvenile pink salmon, chum salmon, and Chinook salmon (5–33% of predator FL), shiner perch (18–34% of predator FL), bay pipefish (32–51% of predator FL), and threespine sticklebacks *Gasterosteus aculeatus* (14–18% of predator FL). Offshore fish prey also included Pacific sand lances (17–43% of predator FL), smaller Chinook salmon (29–42% of predator FL), and other larval and juvenile fishes (estimated as <15% of predator FL).

Diel Feeding

In May 2002, we were able to track the diel feeding chronology of juvenile Chinook salmon at nearshore sites in southern Puget Sound. Gut fullness levels suggest that Chinook salmon fed most actively during mid-day (Figure 8A). Euphausiids were a dominant part of peak daytime diets but were absent from stomach contents at other times. Decapods and copepods were the dominant prey items at dusk and dawn, respectively (Figure 8B).

Discussion

Juvenile Chinook salmon in Puget Sound exhibited diverse diets that varied among habitats, regions, seasons, and years. The current diet composition is similar to what was reported in the late 1970s (Fresh et al. 1981) but indicates an increased importance of insects, especially earlier in the season, and a reduction in the prevalence of fish in the diet, although this may be partly due to differences in study design and reporting. In general, Chinook salmon are opportunistic feeders, taking advantage of the local forage base and availability of prey (Beamish et al. 2003). The consistent appearance of several key prey items in the Puget Sound diets (e.g., insects, Pacific herring, crab larvae) suggests either that these prey were abundant and consistently available or that Chinook salmon have specific dietary preferences. To evaluate the status of foraging conditions for Chinook salmon, we need to examine both the quantity and quality of their historic versus contemporary diets in the context of spatial, temporal, and ontogenetic variability. Feeding intensity and proportion of empty stomachs give us an indication of the quantity of feeding. However, factors including the time of day (particularly for larger fish) and tide (particularly for nearshore fish) can have a large

TABLE 5.—Extended.

Fish		Gammarids		Hyperlids		Insects		Polychaetes	
F	Relationship	*F*	Relationship	*F*	Relationship	*F*	Relationship	*F*	Relationship
				Habitat					
1.91	ns	4.75[a]	Near > off	0.30	ns	49.60[b]	Near > off	0.22	ns
1.15	ns	0.22	ns	0.12	ns	4.71	2002 > 2001	0.01	ns
10.26[b]	N > C	1.55	ns	8.70[b]	N > C	9.92[b]	C > N	4.10[a]	C > N
28.09[b]	Lg > sm	1.26	ns	8.85[b]	Lg > sm	2.05	ns	0.01	ns
1.75	ns	1.32	ns	2.52	ns	13.26[b]	7 > 9	0.23	ns
				Nearshore					
3.51	ns	0.68	ns	8.86[b]	2001 > 2002	0.18	ns	1.08	ns
0.97	ns	2.37[a]	4 > 6, 7	11.41[b]	8 > all months	4.65[b]	7, 9 > 5	2.60[a]	6 > 9
8.97[b]	C > S	2.73	ns	6.68[b]	C, S > N	16.38[b]	N, C > S	0.23	ns
24.00[b]	Lg > sm, md	1.05	ns	4.71[b]	Lg > sm, md	0.08	ns	0.66	ns
				Offshore					
19.42[b]	2006 > all years (except 2002)	2.44[a]	2005 > 2001	9.54[b]	2007 > all years (except 2005)	2.11	ns	0.19	ns
28.64[b]	9 > 7	9.23[b]	9 > 7	1.21	ns	0.29	ns	0.11	ns
13.95[b]	N > C (Sep 2007; Hd > N, C)	10.05[b]	C> N	9.62[b]	C > N	29.13[b]	C > N	21.81[b]	C > N
23.02[b]		8.28[b] 30.06[b]	(Jul 2007; C > N, S) (Sep 2007; C, N > Hd)	8.77[b]	(Jul 2004; C > N, S)	6.57[b]	(Sep 2007; Hd > N, C)	21.81[b]	C > N
118.44[b]	Lg > md > sm	3.08[b]	Md > Sm	6.31[b]	Md < lg	6.27[b]	Sm, md > lg	0.76	ns

influence on the stomach fullness; thus, these metrics should be interpreted cautiously. Specific characteristics of the prey (e.g., nutritional value and handling time) give a measure of the quality of foraging conditions in a particular region or habitat, although this information is not always readily available. We used energy density as an indicator of the relative quality of individual prey items (Table 1). However, these values should also be interpreted cautiously as they were primarily values from the literature and they included prey sampled in different geographical areas or average values from comparable species.

The most striking differences in diet composition and feeding intensity at nearshore sites occurred regionally between the northern and southern Puget Sound sampling sites. The dominance of largely terrestrial insects in diets at northern sites differed markedly from the largely planktonic crustacean-dominated diets at southern sites, while diets at central sites were intermediate between those at northern and southern sites. Adult insects are high-quality prey, with energy densities almost double those of most planktonic crustacean prey (Table 1). Kaczynski et al. (1973) reported a similar regional difference for chum salmon and pink salmon in the early 1970s; diets were more diverse at Port Susan (northern), including insects, mysids, and copepods, whereas diets at Anderson Island (southern) consisted almost entirely of copepods. The greater proportion of neustonic drift insects at northern sites was probably a result of substantially greater freshwater flow into that region, which was apparent in the lower surface salinities at northern sites than at southern sites (Duffy et al. 2005). Other sources of insects that may differ between sampling areas are fallout from riparian habitats (Simenstad et al. 1982) and transportation by wind (Cheng and Birch 1978; Hardy and Cheng 1986; Pathak et al. 1999) from vegetation in wetlands and uplands.

Differences in the proportion of Chinook salmon with empty stomachs may indicate regional differences in prey supply and availability. Chinook salmon in the southern region had the lowest proportion of empty stomachs, suggesting a more constant availability of prey. Annual and seasonal variability in the proportion of empty stomachs was highest in the northern region, which suggests that feeding conditions in this region were highly variable. For Chinook salmon using the nearshore habitat, feeding conditions appeared to be limited by the patchy availability of high-quality prey in the northern region, while at southern sites the fish had access to a lower-quality but more consistent and potentially abundant source of food. Accordingly, prey resources in the northern region are probably linked more to environmental variables (e.g., freshwater flow and wind) and terrestrial factors (e.g., extent of riparian and upland vegetation), whereas the prey resources in

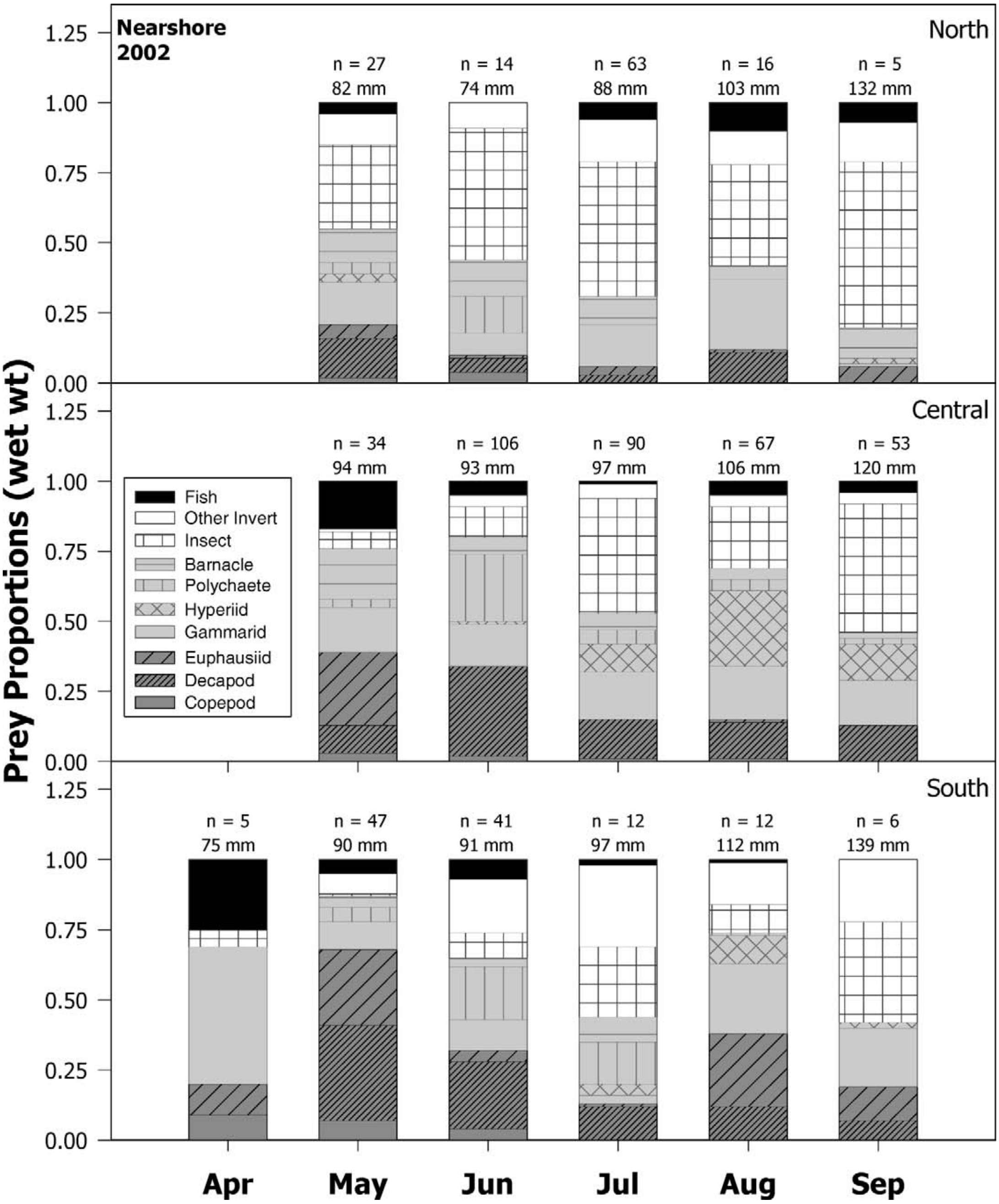

FIGURE 3.—Monthly nearshore marine diet composition (in wet-weight [wt] proportions of each prey category; invert = invertebrate) for age-0 Chinook salmon in northern (upper panel), central (middle panel), and southern (bottom panel) regions of Puget Sound during 2002. Sample size and average fork length are listed above each bar.

the southern region appear to be more marine in origin and are probably linked to environmental variables that control plankton production (e.g., climate).

In the offshore habitat, the diet composition of Chinook salmon was more diverse in fall (September–October) than in summer (July) and was more diverse in the central region than in the northern region. Decapods (primarily brachyuran crab larvae) were the

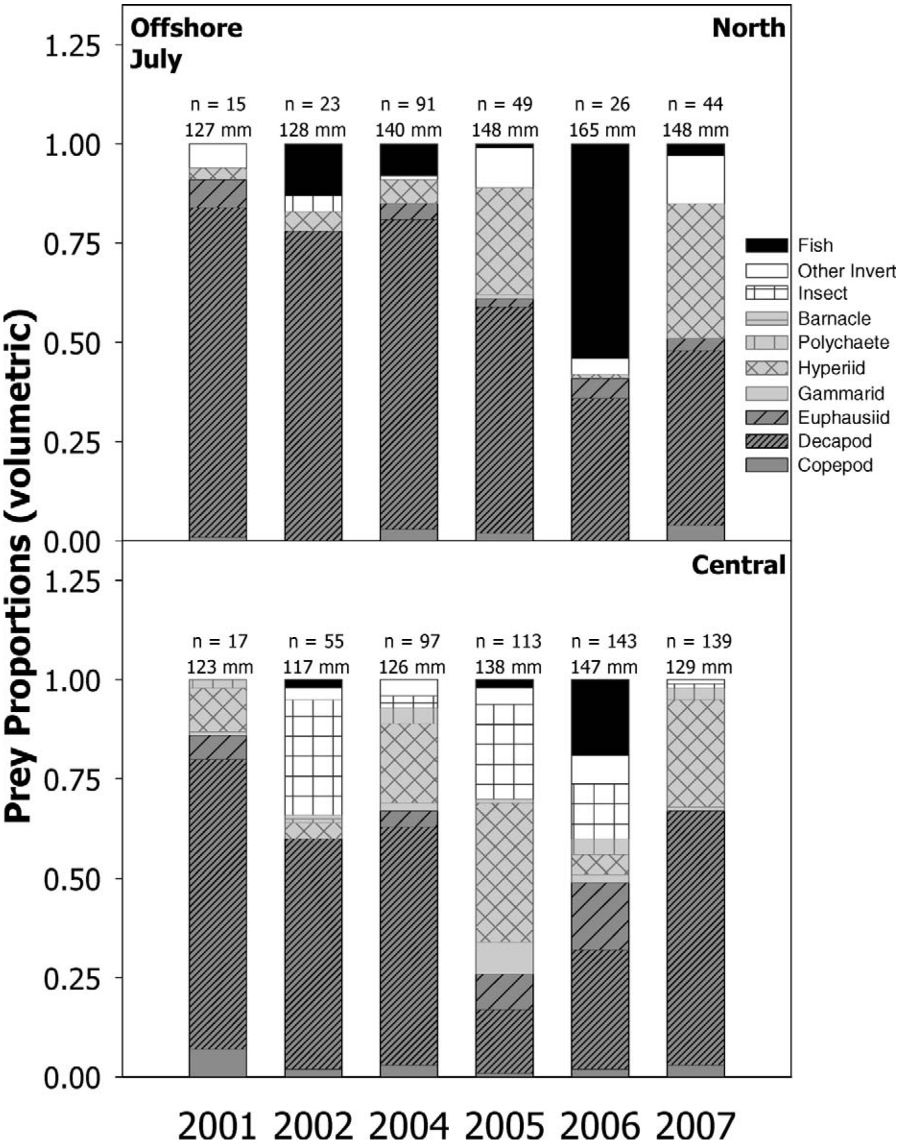

FIGURE 4.—Offshore marine diet composition (in volumetric proportions of each prey category; invert = invertebrate) for age-0 Chinook salmon in northern (upper panel) and central (lower panel) regions of Puget Sound during July 2001–2007. Sample size and average fork length are listed above each bar.

most important component of the diets in both regions during July. Crab larvae were also a major component of the July diets of other juvenile salmon species (in particular, coho salmon *O. kisutch*) and forage fishes (Fresh et al. 1981; R. J. Beamish, unpublished data). The abundance of larval crab prey and the availability of alternative prey resources may substantially affect the quality of summer feeding conditions for juvenile Chinook salmon (and probably coho salmon and forage fishes) in Puget Sound. The lower proportion of crab larvae in 2004–2005 diets and the greater variability in the diet composition at central sites suggest either that larval crab production was lower in those years or that Chinook salmon were opportunistically taking advantage of higher-energy prey items (e.g., insects at central sites in 2001–2004 and fish in 2006) when such items were available. The greater variability in the diet composition at central sites could also suggest that prey resources were more dynamic and unpredictable than in northern offshore waters.

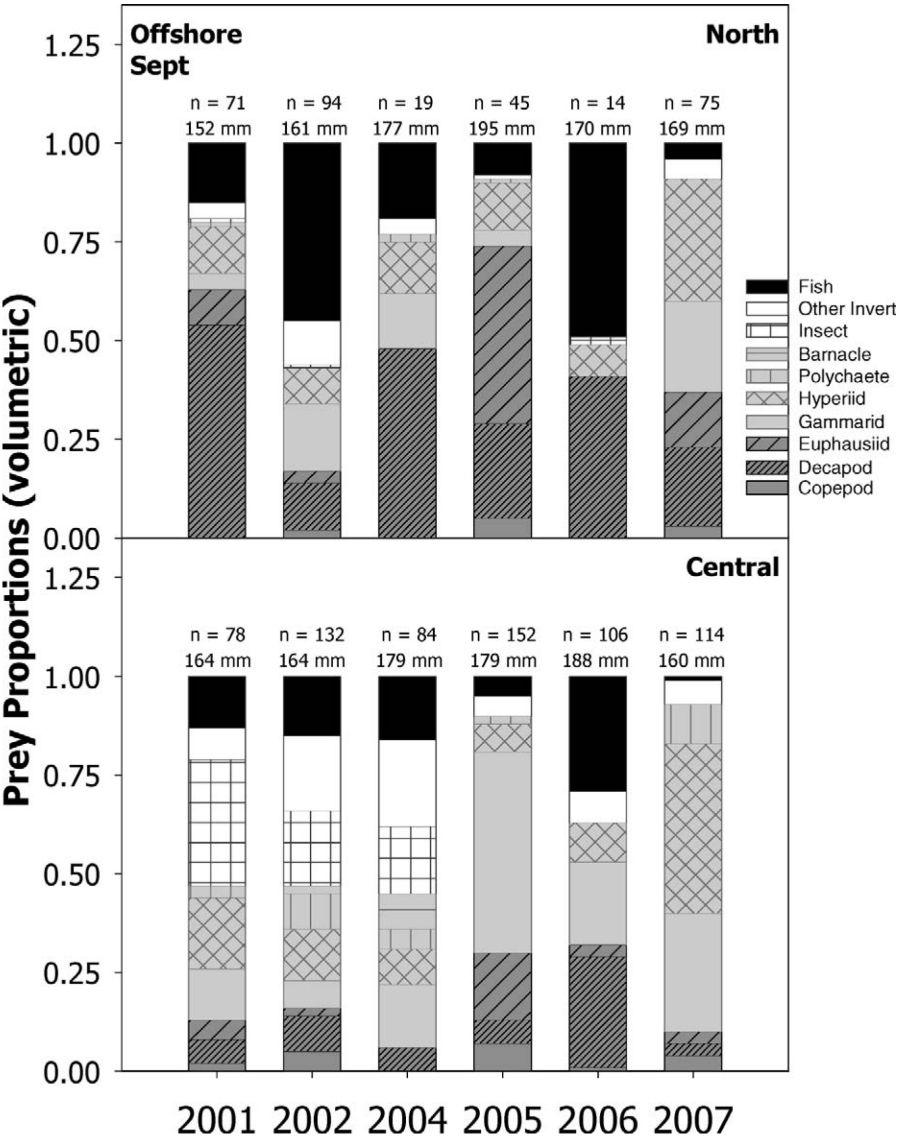

FIGURE 5.—Offshore marine diet composition (in volumetric proportions of each prey category; invert = invertebrate) for age-0 Chinook salmon in northern (upper panel) and central (lower panel) regions of Puget Sound during September 2001–2007 (in 2004, sampling was conducted in October instead of September). Sample size and average fork length are listed above each bar.

Regional differences in feeding intensity were also apparent in the late 1970s, when yearling Chinook salmon caught by purse seine in the central region showed a higher proportion of empty stomachs (36% versus 15%) and lower gut fullness (2.8 versus 3.7 on a qualitative scale, where 1 = empty and 7 = full) than those caught in the southern region (Fresh et al. 1981). Overall, annual shifts in the offshore diets appeared to be consistent among regions and seasons. For instance, in 2002, 2004, and 2006, fish prey made up a higher proportion of the diets in both regions, and this trend persisted between summer and fall (irrespective of size differences among consumers), as did the importance of hyperiids in 2007 diets. This suggests that the composition of prey available offshore in Puget Sound may be established by or before early summer.

It was difficult to separate temporal effects from size- and habitat-based shifts because these factors generally covaried with time. The most apparent size-based dietary shifts related to the onset of piscivory. In

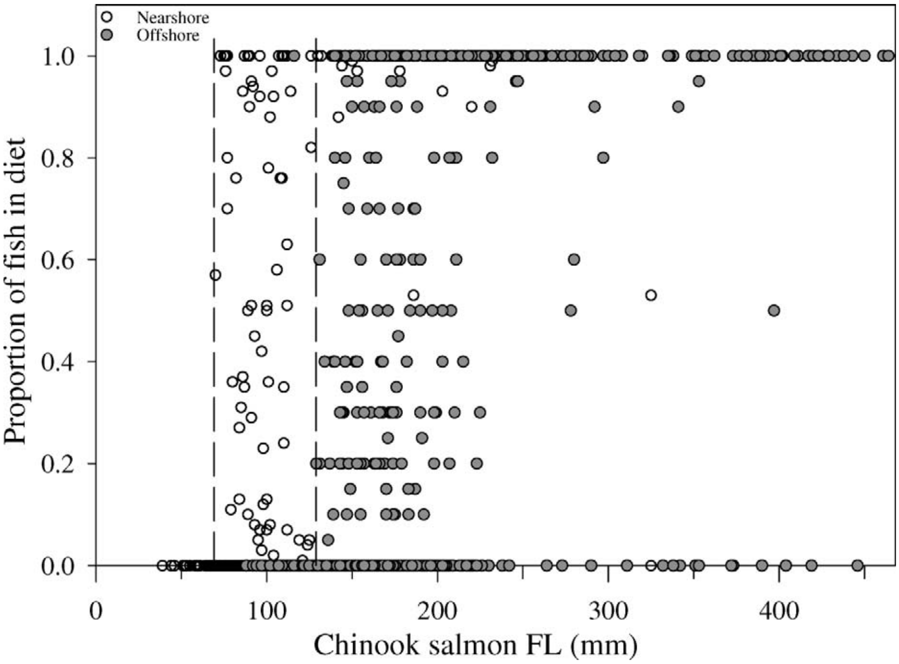

FIGURE 6.—Proportional contribution of fish prey (by wet weight in nearshore samples [open circles] or by volume in offshore samples [gray circles]) to the diets of Puget Sound Chinook salmon in relation to predator fork length (FL). Chinook salmon were collected nearshore by beach seine in 2001–2002 (northern, central, and southern regions: $n = 1{,}354$) and offshore by midwater trawl in 2001–2007 (northern and central regions: $n = 1{,}886$).

all regions and habitats, fish prey appeared in the Chinook salmon diets only above a certain predator size threshold (~70 mm FL nearshore and 130 mm FL offshore) and the proportion of fish in the diet increased as fish grew, which reflects gape limitations, swimming speed, and the size range of available prey. In laboratory conditions, Chinook salmon consumed salmon prey with lengths that were up to 40–47% of predator FL (Pearsons and Fritts 1999). Chinook salmon off the coast of Washington and Oregon consumed fish of lengths that were as much as 50% of predator length, although the average prey fish size was 20% of predator length (Brodeur 1990). In Puget Sound, Chinook salmon at both nearshore and offshore sites ate fish with lengths that were up to 52% of predator FL, and these Chinook salmon tended to have more than one fish in their stomachs (offshore: up to 4 fish/stomach; nearshore: up to 20 fish/stomach).

As in the late 1970s (Fresh et al. 1981), Chinook salmon in our study were highly piscivorous, especially as subadults and adults, and Pacific herring continued to be the predominant prey fish. Chinook salmon also occasionally preyed upon juvenile salmon, including conspecifics. At nearshore sites, juvenile Chinook

TABLE 6.—Mean proportion of fish in the diets of Chinook salmon (based on prey wet weight for nearshore habitat, and prey volume for offshore habitat) caught in Puget Sound by beach seine at nearshore sites (April–September 2001–2002) and by midwater trawl in offshore waters (July, September, and October 2001–2007). Data from all sampling regions are included and organized by size-classes (fork length [FL]; mm) to show ontogenetic shifts in piscivory.

	Nearshore			Offshore		
Size-class (FL, mm)	*n*	Mean proportion fish	SD	*n*	Mean proportion fish	SD
<70	42	0.00	0.00			
70–129	1,152	0.03	0.16	356	0.00	0.06
130–199	135	0.24	0.42	1,406	0.10	0.27
200–299	18	0.66	0.48	156	0.62	0.46
300–399	7	0.65	0.47	38	0.75	0.43
≥400				42	0.88	0.33

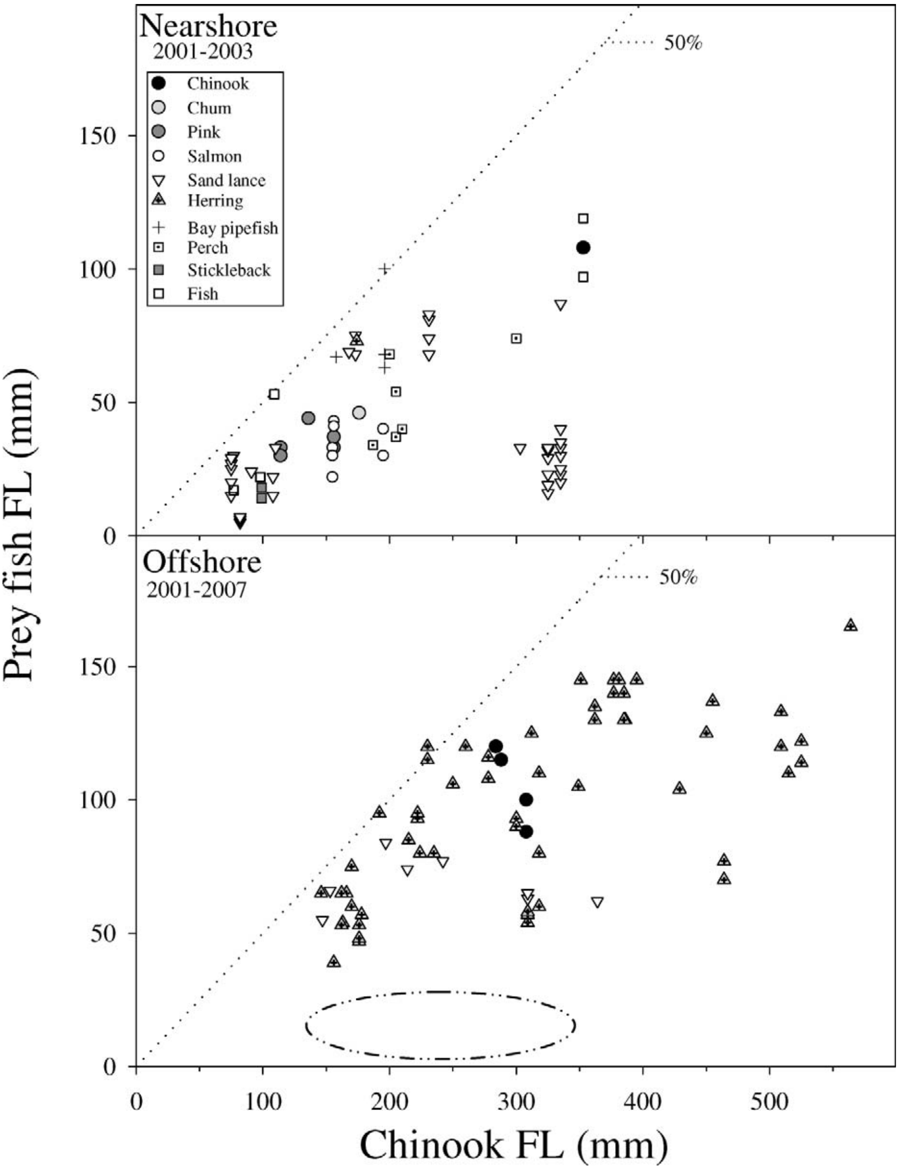

FIGURE 7.—Relation between the fork length (FL) of Puget Sound Chinook salmon (nearshore: $n = 31$ fish; offshore: $n = 34$ fish) and the FLs of consumed fish prey of different species (nearshore: $n = 93$ prey fish; offshore: $n = 73$ prey fish). Chinook salmon were collected nearshore by beach seine in 2001–2003 (northern and southern regions; upper panel) and offshore by midwater trawl in 2001–2007 (northern and central regions; lower panel). The dotted oval represents the likely size distribution of larval fish eaten by Chinook salmon in offshore waters (larval prey fish measurements were not available). Reference lines indicate prey FLs that are 50% (dotted) of predator FL. Prey types depicted are Chinook, chum, and pink salmon; other salmon; Pacific sand lance; Pacific herring; bay pipefish; shiner perch; threespine stickleback; and other fishes.

salmon mainly consumed pink salmon and chum salmon. Offshore, the only salmon species found in the stomachs of larger subadult Chinook salmon were juvenile Chinook salmon. Chinook salmon subadults have also been reported as occasional predators of juvenile salmon in the Pacific Ocean (Fresh et al. 1981; Brodeur 1990). Overall, it appears that Chinook salmon consume the most abundant and available fish prey (within the predator's gape limits and ability to capture; Fresh et al. 1981). While Pacific herring continue to be the most abundant pelagic forage fish in Puget Sound, there have been serious concerns over

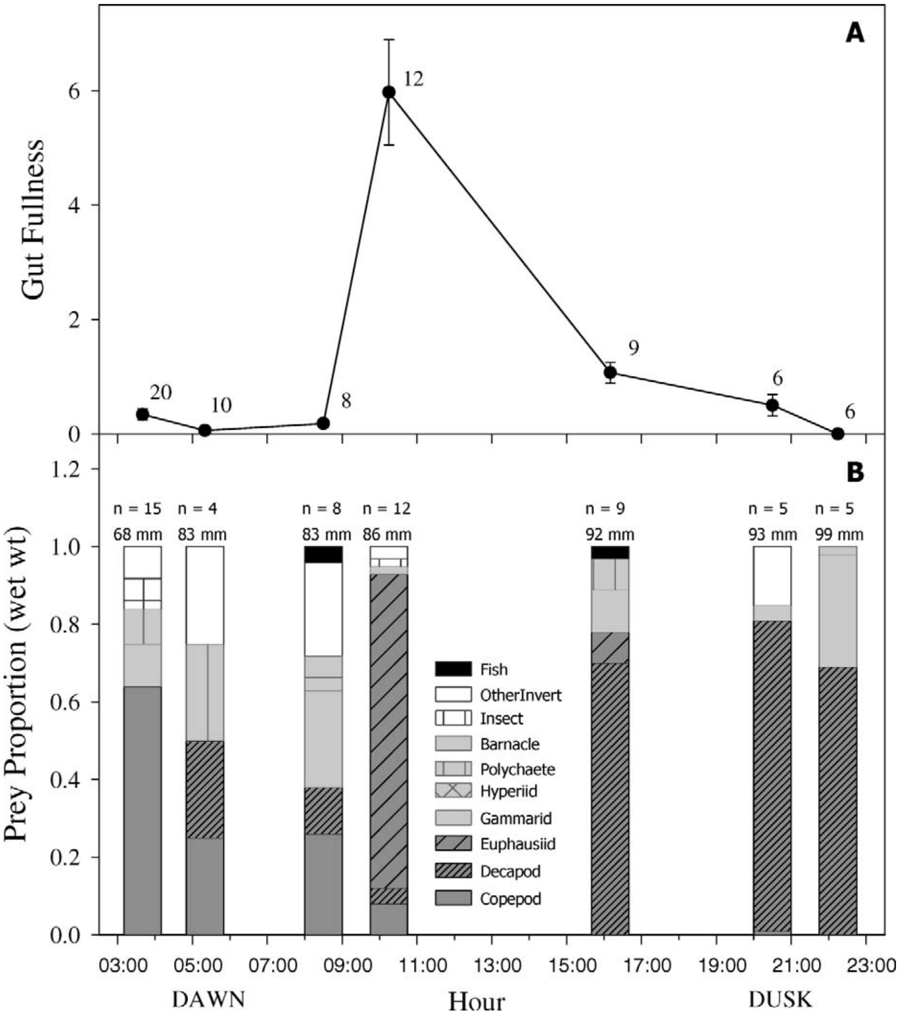

FIGURE 8.—Feeding chronology of age-0 Chinook salmon captured over a 24-h diel sampling period at nearshore sites in southern Puget Sound during May 2002: **(A)** gut fullness in percent body weight (mean ± SE; sample size is given above each data point) and **(B)** diet composition in wet weight (wt) proportions of major prey categories (invert = invertebrate; sample size and average predator fork length are indicated above each column).

recent declines in this species (PSWQAT 2002). Declines in Pacific herring stocks may doubly affect Chinook salmon by (1) reducing the quality of feeding conditions in Puget Sound and (2) potentially reducing a species that may act as a buffer to predation by larger salmon and many other species (birds, fish, and marine mammals). Further investigation into the current status of Puget Sound forage fish stocks (especially Pacific herring) and their trophic linkages to Chinook salmon is important for uncovering the mechanisms behind declines in Puget Sound Chinook salmon.

In Puget Sound, recent feeding conditions for juvenile Chinook salmon ranged from high quality yet variable to consistent but lower quality, and these differences were linked to region and habitat. In the northern region, nearshore feeding conditions appear to be more closely linked to terrestrial processes, and Chinook salmon from this region may be more vulnerable to increased shoreline modifications and development-driven loss of vegetation than those from the southern region, where feeding conditions are determined more by marine plankton availability. However, for Chinook salmon in offshore environments, moving into the northern region could provide a more consistent, higher-quality feeding environment than the central region. A northward shift might also encourage earlier migration towards the Pacific Ocean if foraging success at this stage translates to higher survival. In addition, the present study suggests that annual variation in the composition and quality of prey eaten by juvenile Chinook salmon in Puget Sound is determined early in the growing season, which may translate to strong annual patterns in marine survival. A greater understanding of the mechanisms limiting survival (i.e., predation, starvation, and disease) and the conditions that mediate them (i.e., prey resources and environment) during and subsequent to this critical early marine life history stage is necessary to improve marine survival forecasts and aid recovery plans for Puget Sound Chinook salmon.

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