

Abstract—We investigated the feeding ecology of juvenile salmon during the critical early life-history stage of transition from shallow to deep marine waters by sampling two stations (190 m and 60 m deep) in a northeast Pacific fjord (Dabob Bay, WA) between May 1985 and October 1987. Four species of Pacific salmon—*Oncorhynchus keta* (chum), *O. tshawytscha* (Chinook), *O. gorbusha* (pink), and *O. kisutch* (coho)—were examined for stomach contents. Diets of these fishes varied temporally, spatially, and between species, but were dominated by insects, euphausiids, and decapod larvae. Zooplankton assemblages and dry weights differed between stations, and less so between years. Salmon often demonstrated strongly positive or negative selection for specific prey types: copepods were far more abundant in the zooplankton than in the diet, whereas Insecta, Araneae, Cephalopoda, Teleostei, and Ctenophora were more abundant in the diet than in the plankton. Overall diet overlap was highest for Chinook and coho salmon (mean=77.9%)—species that seldom were found together. Chum and Chinook salmon were found together the most frequently, but diet overlap was lower (38.8%) and zooplankton biomass was not correlated with their gut fullness (% body weight). Thus, despite occasional occurrences of significant diet overlap between salmon species, our results indicate that interspecific competition among juvenile salmon does not occur in Dabob Bay.

Feeding ecology of juvenile Pacific salmon (*Oncorhynchus* spp.) in a northeast Pacific fjord: diet, availability of zooplankton, selectivity for prey, and potential competition for prey resources

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Juvenile salmon migrating into coastal waters face a variety of challenges as they adjust to a rapidly changing environment, such as outmigration timing, physiological acclimation, new prey fields, new predators, and competition for resources (Percy, 1992; Magnusson and Hilborn, 2003). High rates of natural mortality have been attributed to the ocean entry transition (Parker, 1971; Bax, 1983), yet we still have a poor understanding of the processes governing this mortality. Several mechanisms have been hypothesized—disruption of freshwater hydrological conditions, degradation of estuarine nursery conditions, and interannual variability of predator abundance and prey resources in the marine environment (Levings and van Densen, 1990; Willette, 2001; Logerwell et al., 2003).

Comprehensive management of salmon fisheries, including their conservation and recovery, requires detailed understanding of juvenile salmon ecology during this critical transition. Increased understanding of feeding relationships and potential density-dependent effects, such as diet overlap among co-occurring species and resource limitation could

allow for a more ecologically based approach for rebuilding threatened salmon stocks. Specifically, species interactions and their response to variability in prey resources could be important factors for predicting marine survival and the forecasting of adult returns (Logerwell et al., 2003).

Juvenile salmon have been documented feeding in a variety of habitats, including freshwater (Keeley and Grant, 2001; Hampton et al., 2006), estuaries (Healey, 1980; Murphy et al., 1988; Reese et al., 2009), and in the coastal ocean (e.g., Brodeur and Percy, 1990; Daly et al., 2009). Inland marine waters (e.g., bays, straits, sounds, fjords, etc.) have been characterized less frequently (Sturdevant et al., 2004; Romanuk and Levings, 2005; Saito et al., 2009). Like estuaries, these inland marine salmon habitats are more geographically and ecologically diverse than offshore habitats, and thus it may be more difficult to generalize about juvenile salmon feeding ecology in these areas.

Dabob Bay, a temperate marine fjord in Puget Sound, northwestern Washington, has been the site of numerous studies of plankton dynamics

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(e.g., Frost, 1988; Bollens et al., 1992a, 1992b; Frost, 2005 and references therein). Although these studies have provided extensive insight into zooplankton population dynamics and predator-prey interactions, none has specifically reported on the seasonality of zooplankton community composition from this area. Four juvenile salmon species reside in Dabob Bay temporarily during outmigration to the Pacific Ocean (Bollens and Frost, 1989): *Oncorhynchus keta* (chum), *O. tshawytscha* (Chinook), *O. gorbuscha* (pink), and *O. kisutch* (coho). Diets of these four species in the fjord have not been described. Feeding habits of juvenile chum salmon in neritic waters have been described for a nearby location in Hood Canal (Simenstad and Salo, 1980) and feeding habits of juvenile salmon in other nursery areas of Puget Sound have also been described (Simenstad et al., 1982; Duffy et al., 2005).

Much of our understanding of juvenile salmon feeding ecology in northeast Pacific marine waters has been based on detailed analyses of stomach contents, but

has been limited by a lack of corresponding analyses of prey fields. Some recent studies have identified the importance of prey selectivity as a factor in assessing the trophic ecology of salmon during early marine residence (Landingham et al., 1998; Schabetsberger et al., 2003). Furthermore, the highly variable diets demonstrated within and between studies indicate that temporal (seasonal, interannual, and interdecadal) and spatial scales of variability are important, and therefore pose a significant challenge for the design of field studies. The result has been an incomplete understanding of juvenile salmon response to dynamic zooplankton prey fields, particularly during one of the most critical life-history stages, i.e., the early ocean transition phase (Beamish and Mahnken, 2001).

Our objectives were 1) to investigate the diet composition of four salmon species (*Oncorhynchus* spp.) collected from two stations (nearshore-shallow and central-basin-deep) in Dabob Bay over three years and several seasons; 2) to determine salmon feeding selectivity (i.e., their diet in relation to prey availability); and 3) to explore potential resource competition among these species during their early marine residence.

Materials and methods

Fish collection and processing

Between May 1985 and October 1987 we sampled two stations in Dabob Bay, WA (47°45'–50'N lat., 122°50'W long.): a deep (190 m), central station, and a shallow (60 m), nearshore station 9 km apart (Fig. 1). Fish were sampled at night (just after dusk, i.e., when there was no apparent daylight) with two gear types: a midwater trawl with a mouth area of 81.0 m² (9.0×9.0 m), and a surface tow net with a mouth area of 18.3 m² (3.0×6.1 m) (see Bollens and Frost, 1989 for details). The midwater trawl was towed obliquely from a 50-m depth to the surface at a mean speed of 150 cm/s. Because of concerns about possible avoidance of this net by fish in the upper few meters of the water column (e.g., due to ship wake and propeller wash), we also deployed the surface tow net in the upper three meters of the water column, towed at a mean speed of 80 cm/s behind (50 m) and between (at a midpoint of 50 m) two different vessels (one vessel 5 m and one 15 m in length). Fish were collected at each station during each of four seasons (spring: April–May; early summer: June–July; late summer: August; and autumn: October) in each of three years (1985–87), except for spring of 1985, when no fish were collected (Table 1).

Fish collected with the midwater or surface trawls were sorted and counted, and the catch was weighed by species, lengths were measured, and then individuals of five predetermined size (fork length [FL]) classes (≤49 mm, 50–74 mm,

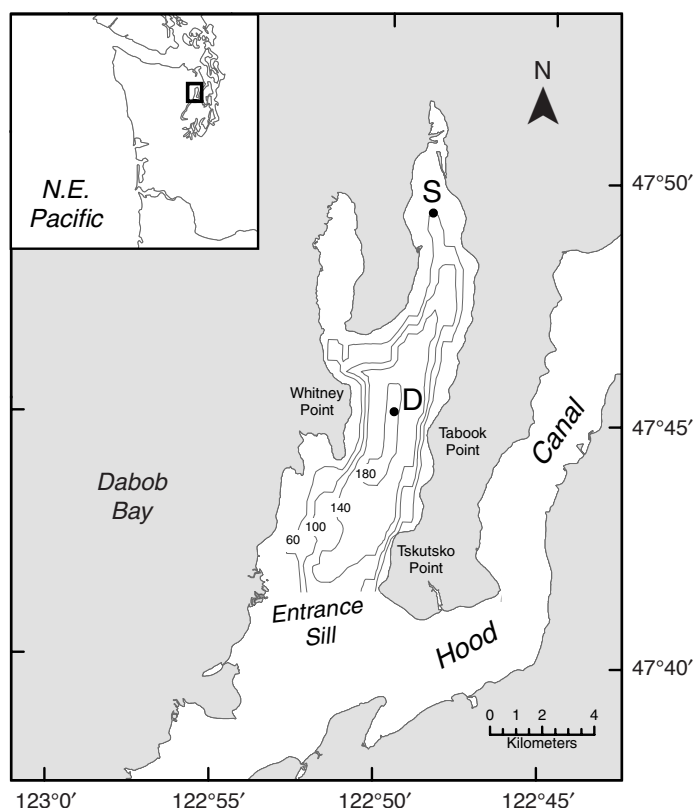


Figure 1

Map of Dabob Bay, Washington. Four species of juvenile Pacific salmon—chum (*Oncorhynchus keta*), Chinook (*O. tshawytscha*), coho (*O. kisutch*), and pink (*O. gorbuscha*)—and zooplankton were sampled at two stations between April 1985 and October 1987 to examine salmon diet, zooplankton availability, feeding selectivity, and potential competition for prey. D=location of the deep (190-m) central bay station, and S=the location of the shallow (60-m) nearshore station.

Table 1

Number of juvenile Chinook (*Oncorhynchus tshawytscha*), chum (*O. keta*), coho (*O. kisutch*), and pink (*O. gorbuscha*) salmon stomach samples and zooplankton samples collected during 12 visits to each of two stations in Dabob Bay, Washington, 1985–87. Sampling dates are grouped by year within season, number of samples for the deep (D, 190 m) station are indicated on the left and those for the shallow (S, 60 m) station indicated on the right. Diet samples were pooled from midwater trawl and surface trawl collections at each station for each date or dates; duplicate zooplankton samples were collected at each station on each date by vertical hauls of plankton nets. Fish samples were not collected in spring of 1985.

Season and sampling dates	Number of juvenile salmon stomachs								Number of zooplankton samples	
	Chinook		Chum		Coho		Pink		D	S
	D	S	D	S	D	S	D	S		
Spring										
1985									2	2
30 Apr and 29 May 1986	0	0	16	15	0	0	3	7	2	2
6–7 May 1987	0	0	6	10	0	0	0	0	2	2
Subtotal	0	0	22	25	0	0	3	7	6	6
Early summer										
19–20 Jun 1985, 24–25 Jun 1985, 26 Jul 1985	5	10	14	9	0	0	0	0	2	2
4–5 Jun 1986	4	3	10	4	5	1	0	0	2	2
17–18 Jun 1987, 13 Jul 1987	3	5	0	14	1	2	0	0	2	2
Subtotal	12	18	24	27	6	3	0	0	6	6
Late summer										
19–20 Aug 1985, 26–27 Aug 1985	4	5	10	12	0	0	0	0	2	2
12 Aug 1986, 14 Aug 1986	5	7	7	3	0	0	0	0	2	2
19–20 Aug 1987	11	6	7	0	1	0	0	0	2	2
Subtotal	20	18	24	15	1	0	0	0	6	6
Autumn										
7–9 Oct 1985	0	6	5	0	0	0	0	0	2	2
22 Oct 1986	6	10	7	0	0	0	0	0	2	2
14–15 Oct 1987	29	3	3	0	0	0	0	0	2	2
Subtotal	35	19	15	0	0	0	0	0	6	6
Total	67	55	85	67	7	3	3	7	24	24

75–99 mm, 100–149 mm, ≥ 150 mm) were removed and 0.5–3.0 cc of undiluted formaldehyde were injected into their gut cavity to halt digestion. Each fish was then stored in dilute (5%) formalin-seawater solution. Fish from both trawl types were combined to yield a representative sample of fish residing in the upper 50 m of the water column at night. Subsequently, each fish was weighed (g, wet weight) and measured in the laboratory, and its stomach excised. Stomach contents were weighed (wet weight), digestion stage was recorded, and then prey were identified to the lowest possible taxon (often to species), and enumerated and weighed (wet weight) by category. Diet composition was summarized as the normalized average percent prey biomass ([biomass of taxonomic group]/[total weight of stomach – the weight of the unidentified portion of the stomach contents]). A total of 294 salmon stomachs were examined; six were empty and were not considered further.

For ease of comparison, we pooled the original 122 prey taxa observed into 13 categories that made up at

least 10% of any one fish's total normalized prey biomass. Data were stratified by salmon species and size class, season, and station across the three years pooled. In most cases the pooled data were a good representation of the three individual years of data, but in some cases there were interesting interannual differences, as discussed below.

Collection and processing of zooplankton

Zooplankton collections were made at the two stations within 1–2 hours of the fish trawls by using a 1-m² mouth opening and 333- μ m mesh multiple net sampler (Frost, 1988) in 1985 and 1986 and a 1-m diameter mouth opening and 216 μ m mesh Puget Sound net (Research Nets Inc., Seattle) (Miller et al., 1977) in 1987. Duplicate zooplankton samples were collected at each station and on each date (Table 1). A subsample (collected with a Stempel pipette) of 1–2% of the animals was taken and the species were enumerated and

identified for all dates and stations at which fish were collected. Identification of gelatinous animals was generally poor because of their damage during collection. Abundances (densities) were calculated from the subsample counts and volumes (m^3) of water filtered (as measured by a flow meter). Data from different depth strata were weighted by the size (height, m) of the depth strata and then averages for the upper 50 m were computed. Zooplankton community composition was described by station by using the data from duplicate zooplankton tows to compute average abundances for each taxonomic group for each of four seasons (spring, early summer, late summer, and autumn) over the three years studied (1985–87). Dry weights (g/m^2) for zooplankton $\geq 216 \mu\text{m}$ were measured as described in Bollens et al. (1992b).

For ease and clarity of presentation of the zooplankton compositional data, the category “other Copepoda” that is used in presenting juvenile salmon gut contents was partitioned into several subcategories, i.e., the genera *Oithona*, *Metridia*, and *Pseudocalanus*. In addition, several taxonomic groups that were common in salmon gut contents were rarely or never observed in the zooplankton samples (e.g., Insecta and Araneae, Cephalopoda, Teleostei, and Ctenophora) and were therefore placed into the “other” category for characterizing zooplankton community composition.

Data analysis

We estimated interspecific diet overlap between co-occurring juvenile salmon species on the basis of biomass of prey in common, using Schoener's (1970) percent similarity index (PSI):

$$PSI_{x,y} = 100 \left(1 - 0.5 \left(\sum |P_{x,i} - P_{y,i}| \right) \right), \quad (1)$$

where $P_{x,i}$ = percent biomass of food category (i) in the stomach of species x ; and

$P_{y,i}$ = percent biomass of food category (i) in the stomach of species y .

We first pooled the prey biomass data by size class for each salmon species. PSI calculations were made for the subset of samples with a minimum of three stomachs per species. We examined intraspecific spatial variation in diet by calculating the PSI of juvenile salmon between the two stations. PSI values $\geq 60\%$ were considered significant (Brodeur and Pearcy, 1992; Landingham et al., 1998).

Prey selectivity by juvenile salmon species was examined by using Ivlev's (1961) electivity index (E_i):

$$E_i = (r_i - p_i) / (r_i + p_i), \quad (2)$$

where E_i = the electivity index;

r_i = the numerical proportion of the i^{th} taxon in the stomachs; and

p_i = the proportion of the same taxon in the environment.

The electivity values provide a species-specific measure of prey selection by allowing a comparison of salmon gut contents to available prey. Values for E_i range from -1 to 1 , where 1 indicates the highest selectivity (i.e., present in the diet, but never in the zooplankton samples), and -1 indicates lowest selectivity (i.e., never in the diet, but present in the zooplankton samples). We summarized these observations as average species-specific electivity scores for all size classes, seasons, and years combined to compare selection across salmon species.

We compared juvenile salmon gut fullness (% body weight) and zooplankton abundance (dry weight) at each station, as well as each salmon species' gut fullness between the two stations, using Spearman's rank correlations (Zar, 1999). The difference in mean zooplankton abundance (dry weight) between the two stations was tested by using a Mann-Whitney U test (Zar, 1999).

Results

Juvenile salmon diet

Juvenile salmon in Dabob Bay showed species-specific patterns of occurrence throughout the April–October time period across years. In general, more and smaller juvenile salmon were caught at the nearshore shallow station during spring and early summer, and more and larger juvenile salmon were caught at the central-bay deep station during late summer and autumn. Chum salmon were most prominent during the spring and early summer, whereas Chinook salmon were caught more frequently later in the year, particularly at the deep station (190 m). All four salmon species were predominantly planktivorous, although there were some exceptions as described below. Because of the greater occurrence of chum and Chinook salmon diet samples, our analyses were focused on these two species.

Juvenile chum salmon

Chum salmon exhibited striking ontogenetic and spatial variation in diets, including a tendency for fish < 100 mm FL to consume more insects and larvaceans and those > 100 mm to consume more amphipods and decapod larvae. At the deep station in late spring, euphausiids were the dominant prey type by weight (Fig. 2). Small (≤ 49 mm) fish also consumed insects, arachnids, and copepods other than *Calanus pacificus*, whereas larger fish (75–99 mm) consumed high percentages of teleosts (primarily unidentified species), hyperiid amphipods, and decapod larvae. The single fish of the 50–74 mm size range captured during early summer at the deep station consumed mostly insects and arachnids, whereas fish between 75 and 150 mm consumed predominantly larvaceans and hyperiids. The single large fish (≥ 150 mm) contained exclusively euphausiids. In late summer at the deep station, fish 100–149 mm consumed mostly hyperiid amphipods, whereas fish ≥ 150 mm consumed

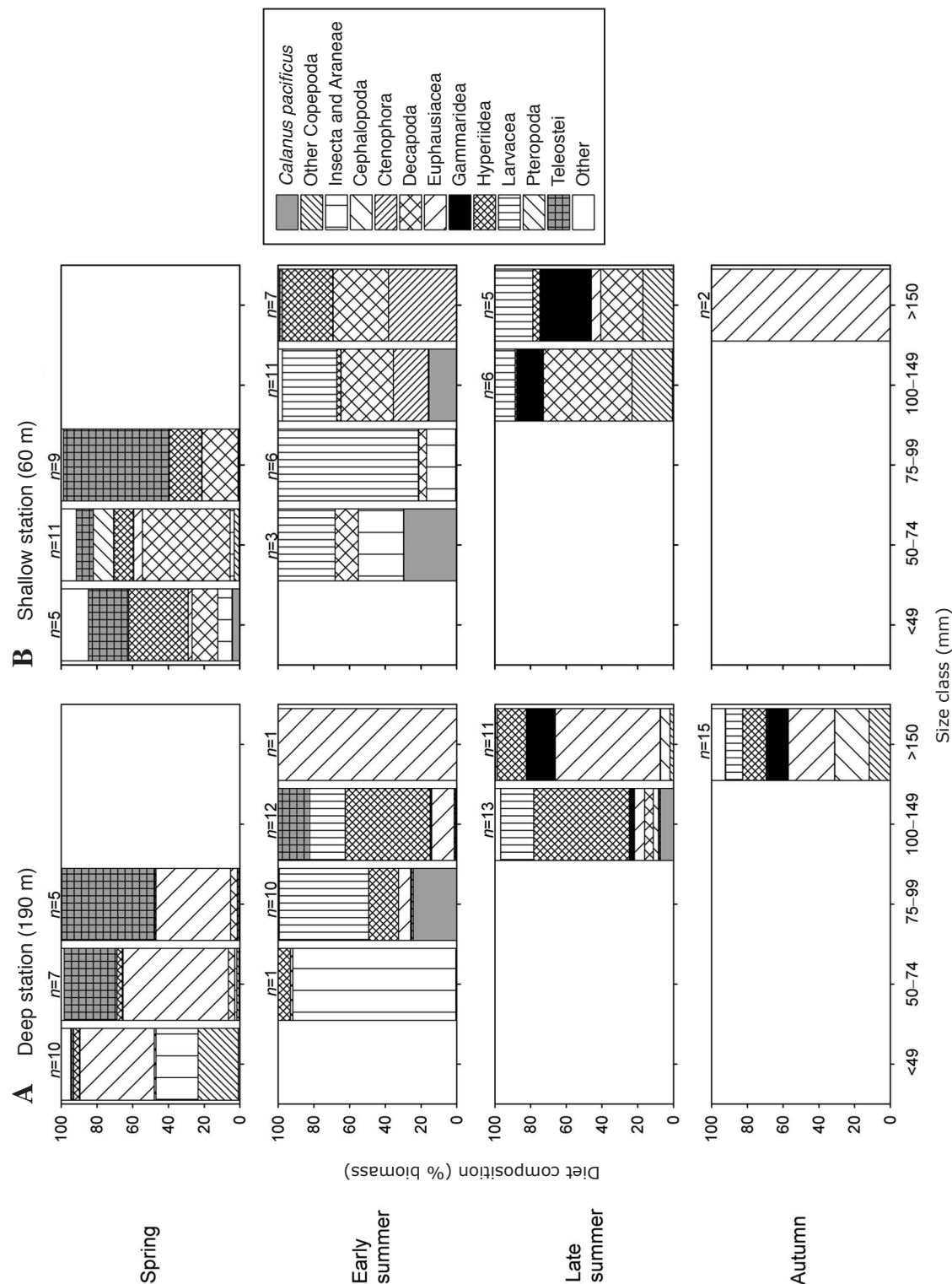


Figure 2 Stomach contents of juvenile chum salmon (*Oncorhynchus keta*) caught at the deep station (A) and shallow station (B) of Dabob Bay, Washington, during different seasons. Collections were made with a midwater trawl and a surface tow net at each station on each date. Data were pooled over three years (1985–87) for each season and calculated as the normalized biomass of each taxonomic group.

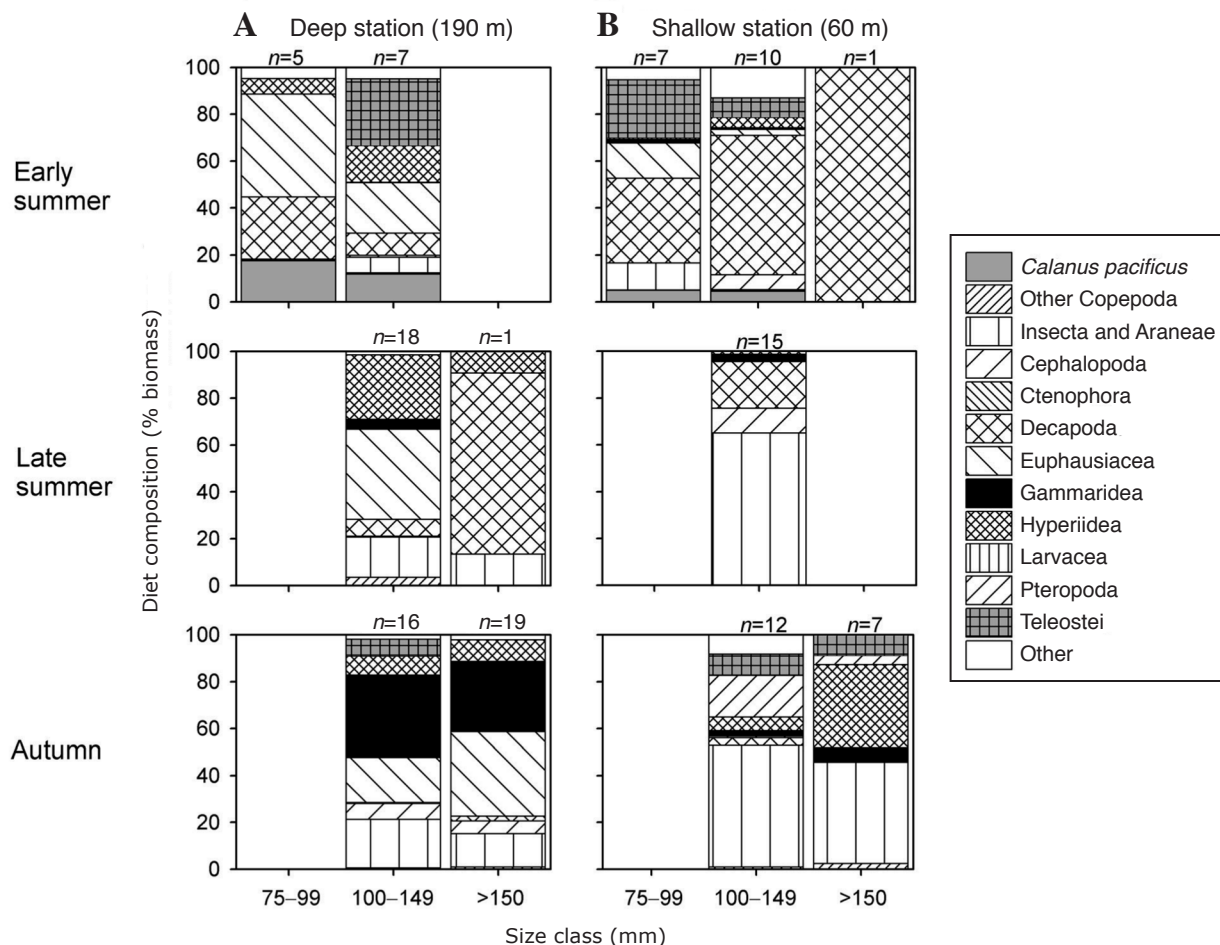


Figure 3

Stomach contents of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) caught at the deep station (A) and shallow station (B) of Dabob Bay, Washington, during different seasons. Collections were made with a midwater trawl and a surface tow net at each station on each date. Data were pooled over three years (1985–87) for each season and calculated as the normalized biomass of each taxonomic group.

mostly euphausiids, and the remainder consumed mainly gammarid and hyperiid amphipods. In autumn, the diet of fish ≥ 150 mm from the deep station was composed more evenly of several prey categories, including euphausiids, copepods other than *C. pacificus*, gammarid and hyperiid amphipods, larvaceans, and cephalopods.

In contrast, prey of chum salmon < 150 mm at the shallow station were more varied, and few euphausiids were present (Fig. 2B). Teleosts and larvaceans, however, were represented in similar proportions to those at the deep station. Larger chum salmon (> 100 mm) sampled in early summer were the only group that consumed relatively large amounts of ctenophores; the remainder of their prey consisted mainly of decapod larvae and hyperiids. During late summer at the shallow station, chum salmon consumed decapod larvae, gammarid amphipods, copepods other than *C. pacificus*,

and larvaceans. Large fish (≥ 150 mm) collected in autumn fed almost entirely on euphausiids.

Juvenile Chinook salmon

There was substantial variation in Chinook salmon diets across size classes, seasons, and stations. At the deep station during early summer, euphausiids constituted a large proportion of the diet of Chinook salmon between 75 and 99 mm (Fig 3A). Fish 100–149 mm consumed a more evenly distributed mix of prey, dominated by teleosts and euphausiids. In late summer, fish 100–149 mm at the deep station consumed mostly hyperiid amphipods and euphausiids. In autumn, fish > 100 mm at the deep station consumed mostly gammarids, euphausiids, insects, arachnids, cephalopods, and hyperiids.

At the shallow station in early summer, decapod larvae dominated the diet of Chinook salmon ≥ 75 mm (Fig. 3B). During both late summer and autumn, insects and arachnids dominated the diets of all three size classes of Chinook salmon, but in autumn, those Chinook salmon >150 mm also consumed hyperiid amphipods.

Diet of other salmon species

Fewer diet samples were available for juvenile pink and coho salmon than for juvenile chum and Chinook salmon. Diet samples of pink salmon were available only for small fish (<49 mm) in spring. At the deep station these fish contained about 50% euphausiids, and gammarids, copepods other than *C. pacificus*, insects, and arachnids made up the other 50%. At the shallow station, their diet included a variety of prey consisting mainly of teleosts, pteropods, copepods other than *C. pacificus*, and fewer insects, decapod larvae, gammarids, and "others." The "others" in this case were mostly bivalves, whereas the "others" for the co-occurring juvenile chum salmon were mostly chaetognaths.

A few juvenile coho salmon were also caught at the two sample stations. At the deep station, diet of coho salmon 100–149 mm consisted primarily of decapod larvae and euphausiids, and a single larger (>150 mm) coho salmon consumed mostly decapod larvae in early summer and another large coho, only gammarid amphipods in late summer. At the shallow station, three coho salmon were caught in June: one (75–99 mm) consumed about 75% "other" taxa (mostly the ostracod *Euphilomedes*), and the two other fish consumed almost exclusively decapod larvae (like the five co-occurring Chinook salmon).

Juvenile salmon gut fullness in relation to zooplankton abundance

Juvenile salmon gut fullness (% body weight) was not related to zooplankton abundance (dry weight) (Fig. 4; Spearman's rank correlation, $P>0.05$). For all four species of salmon, gut fullness was generally greater in spring and early summer and declined somewhat during late summer and autumn (chum salmon at the deep station in 1985 was an exception to this). In contrast, zooplankton dry weight at the deep station peaked in the fall, and minima occurred in the spring. At the shallow station, peaks in zooplankton dry weight tended to occur in the summer, and less pronounced minima occurred in spring and autumn. Zooplankton dry weight was substantially greater at the deep station than at the shallow station ($P<0.001$, Mann-Whitney *U* test; Zar, 1999), generally by one order of magnitude. Some of this difference may have been due to the three-fold greater water column depth at the deep station, whereas a generally larger part of this difference was due to greater abundances of large-body zooplankton in the deep station samples. In addition, no significant correlation was found for individual salmon species' gut

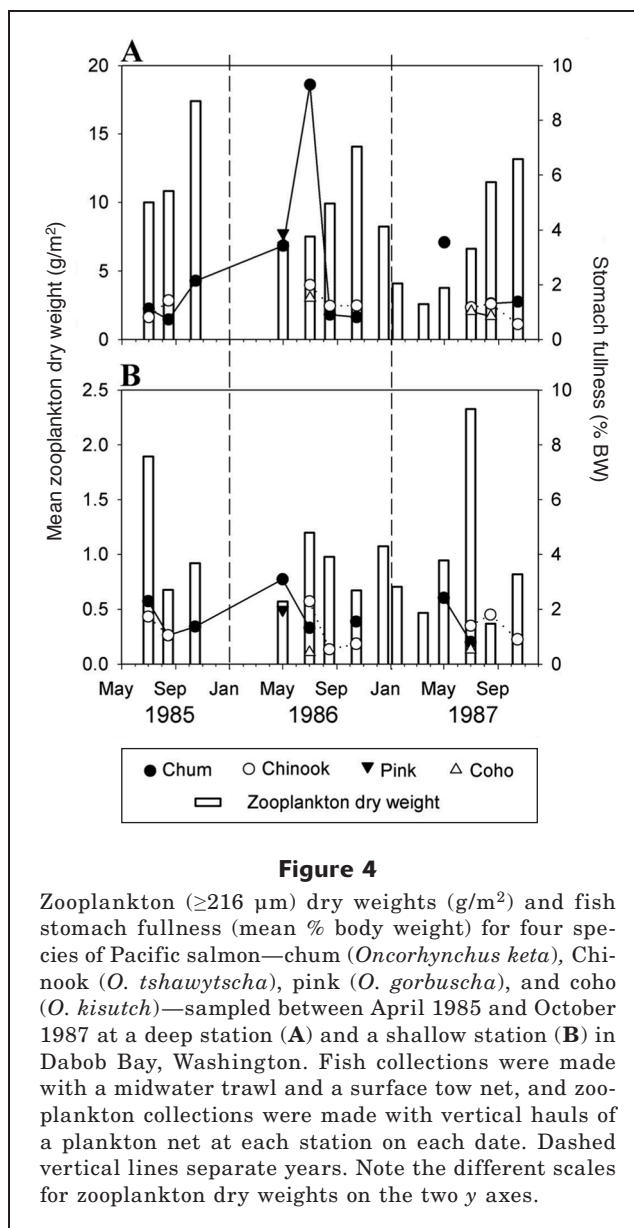


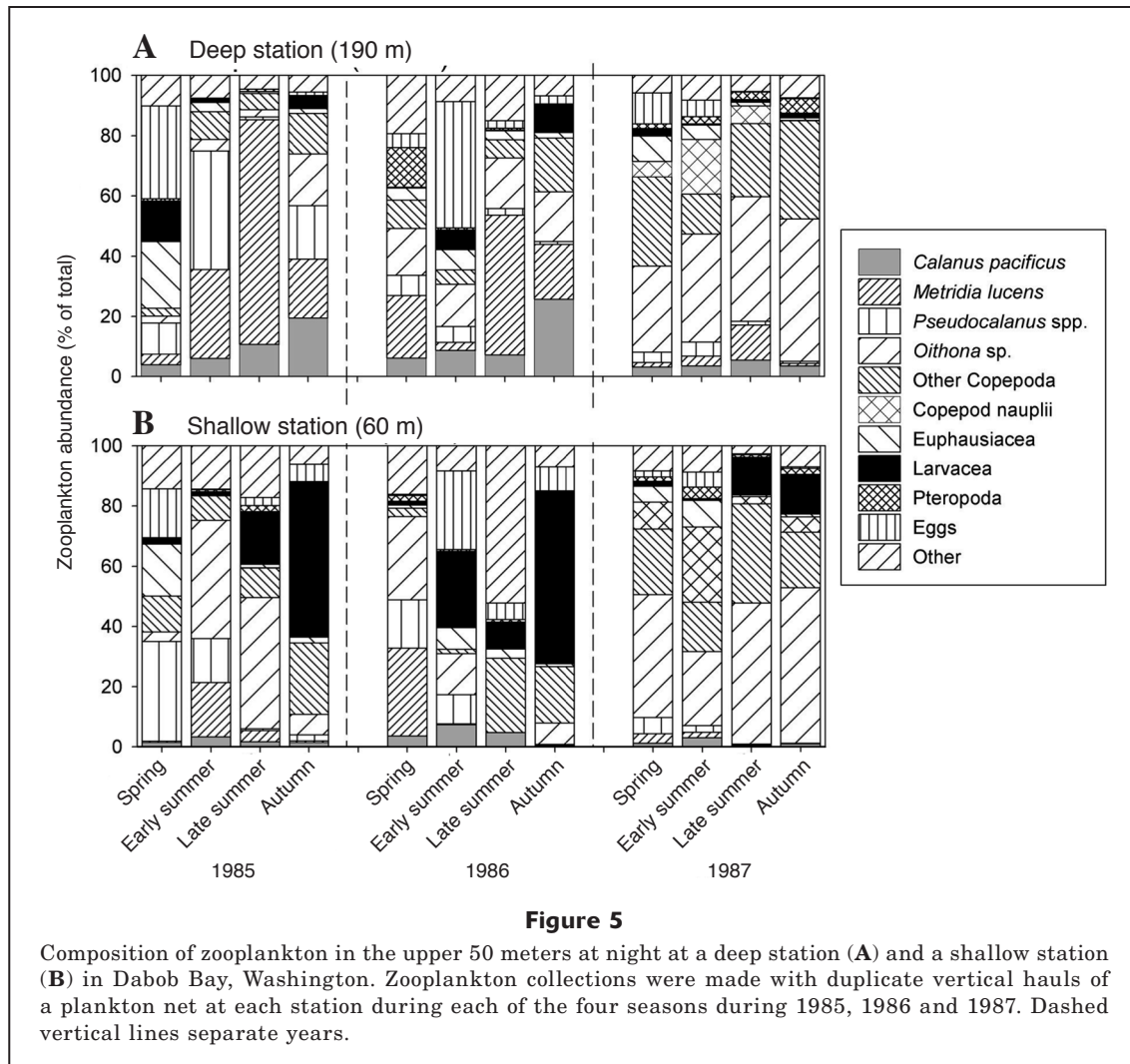
Figure 4

Zooplankton (≥ 216 μm) dry weights (g/m^2) and fish stomach fullness (mean % body weight) for four species of Pacific salmon—chum (*Oncorhynchus keta*), Chinook (*O. tshawytscha*), pink (*O. gorbuscha*), and coho (*O. kisutch*)—sampled between April 1985 and October 1987 at a deep station (A) and a shallow station (B) in Dabob Bay, Washington. Fish collections were made with a midwater trawl and a surface tow net, and zooplankton collections were made with vertical hauls of a plankton net at each station on each date. Dashed vertical lines separate years. Note the different scales for zooplankton dry weights on the two y axes.

fullness at the two different stations (Spearman's rank correlation, $P>0.05$; Zar, 1999).

Community composition of zooplankton

Zooplankton communities (upper 50 m at night) were numerically dominated by copepods at both stations (Fig. 5). The most striking contrast between our zooplankton composition and our juvenile salmonid diet composition was the far greater abundance of copepods in the zooplankton. Substantially different seasonal patterns in zooplankton community composition were observed between stations during 1985 and 1986, but not in 1987. At the deep station, the greatest species richness was typically observed during early spring, whereas two species—*Metridia lucens* and *Calanus pacificus*—dominated



in summer and autumn. In contrast, *Oithona* sp. and larvaceans dominated the shallow station in summer and autumn. In 1987, however, zooplankton community composition between the two sites was remarkably similar (Fig. 5) and was dominated by *Oithona* sp. and "other Copepoda" (predominantly unidentified stages 1 and 2 calanoid copepodites) throughout the entire sampling period.

Electivity indices for juvenile salmon

All salmon species consistently and strongly selected for insect, arachnid, and cephalopod prey ($E_i > 0.75$) and routinely selected against *Calanus pacificus*, copepods other than *C. pacificus*, ctenophores, larvaceans and pteropods ($E_i < -0.25$). All salmon species except pink salmon typically selected for decapod prey ($0.25 < E_i < 0.75$; both caridean shrimp and brachyuran crab larvae were present in the spring, but brachyurans dominated the decapod prey in summer). Hyperiid amphipods and teleosts were generally selected for by chum and Chinook salmon

($0.25 < E_i < 0.75$) but were consumed in proportion to their relative abundance or were selected against by coho and pink salmon ($-0.75 < E_i < 0.25$). Euphausiids were generally neutrally selected ($-0.25 < E_i < 0.25$). However, electivity scores varied substantially within a given salmon species. For example, in 26 Chinook salmon diet samples, electivity indices for euphausiid prey ranged from -1.0 to 0.99 (data not shown), but were not consistently related to predator size, season, or prey abundance.

Important ontogenetic changes in prey-selection behavior were revealed by size-specific electivity values (Fig. 6). For instance, smaller size chum salmon strongly avoided larvacean prey, whereas larger chum (> 75 mm) showed roughly neutral or positive selectivity. Similarly, small (75–99 mm) Chinook salmon tended to avoid gammarid amphipods, whereas larger individuals (> 100 mm) tended to select gammarids. Also, smaller Chinook salmon individuals tended to consume *Calanus pacificus* at rates proportional to their abundance in the environment, but the larger Chinook salmon strongly avoided these prey. In general, it seemed that larger fish

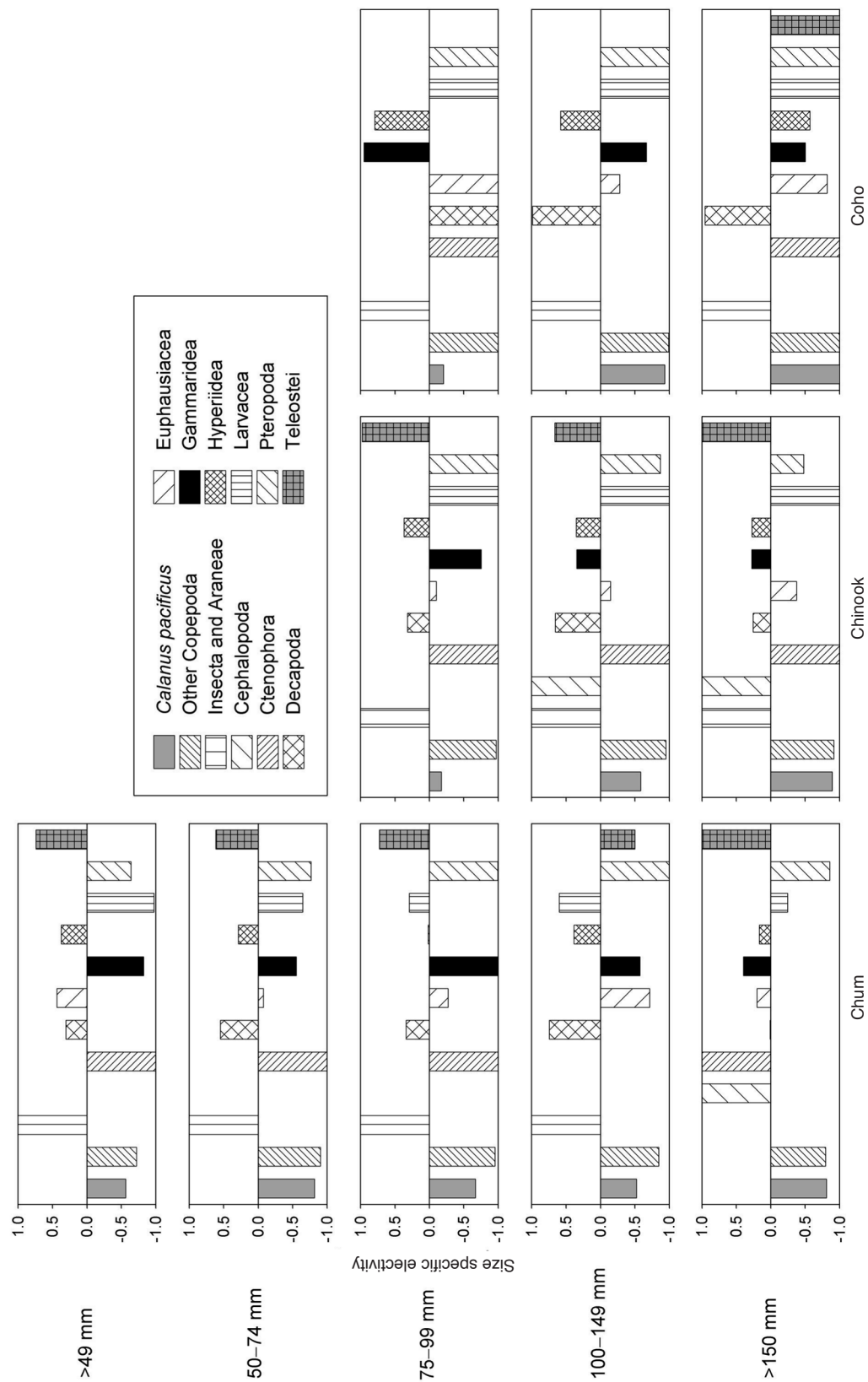


Figure 6 Size-specific (mm fork length) electivity indices (E_i) for chum (*Oncorhynchus keta*), Chinook (*O. tshawytscha*), and coho (*O. kisutch*) salmon at Dabob Bay, Washington. Fish collections were made with a midwater trawl and a surface tow net, and zooplankton collections were made with vertical hauls of a plankton net at each station on each date. Electivity indices were pooled over all seasons (early spring to autumn), both stations (190-m and 60-m deep), and years (1985–87).

selected for larger prey. However, prey selection by coho and pink salmon showed little ontogenetic variation, although we had far fewer data for these taxa to make a definitive statement. Patterns of prey selectivity were fairly similar between stations for each juvenile salmon species, although there were occasionally some differences, e.g., for 100–149 mm Chinook salmon, which selected euphausiids at the deep station but avoided them at the shallow station.

Juvenile salmon diet overlap

Juvenile salmon diets rarely overlapped significantly. Diet overlap for the most frequently co-occurring ($n=11$ hauls) species, chum and Chinook salmon, ranged from 10.5% to 66.8%, and averaged 38.3%. PSI was significant only on June 1985 and August 1987, when both species consumed euphausiids, hyperiid amphipods, and *C. pacificus*. We observed the greatest diet overlap between coho and Chinook salmon, which both ate decapod prey in June 1986 and 1987, for an average PSI of 77.9%. Diet similarities varied for the other juvenile salmon species and were based on only one or two co-occurrences. For juvenile chum and coho salmon, the PSI was only 10.8%; for juvenile pink and chum salmon, the PSI was 58.9% in April 1986.

Salmon diets also varied spatially; however, the PSI was not significant for any of the 13 intraspecific comparisons between stations, and averaged only 26.5%. Chinook salmon PSI was approximately 30% ($n=7$), and that of chum ($n=5$) and pink ($n=1$) salmon was <20%.

Discussion

Juvenile salmon diets, zooplankton abundance and composition, and salmon feeding selectivity in Dabob Bay exhibited considerable spatial, seasonal, and interannual variability. Some notable patterns and trends were nevertheless evident, and provide important implications for our understanding of feeding ecology and potential resource competition among juvenile salmon as they migrate from nearshore environments to more open waters.

Food resources and salmon gut fullness

Dramatic differences in the zooplankton communities between the deep water and nearshore stations occurred in two of three years. The most striking difference was the greater biomass of zooplankton, often an order of magnitude higher, at the deep station compared to the shallow station (Fig. 4; Bollens et al., 1992b), primarily because of the greater abundance of large, vertically migrating zooplankton at the deeper station (e.g., euphausiids and large calanoid copepods). Because zooplankton biomass represents a measure of overall food abundance (although see below for an alternative interpretation), we expected to see differences in gut fullness

between the two stations if juvenile salmon were food limited and did not often migrate between the sites (a distance of 9 km). However, despite this large difference in prey resources between sites, we found no evidence for fuller salmon guts at the deep station. In addition, different zooplankton communities were consistently observed between stations (Fig. 5), which could explain the low diet overlap of each salmon species between stations (mean PSI=27%).

Gut fullness can be a useful indicator of feeding success. However, gut fullness does not account for potential differences in prey nutritional quality (Brodeur, 1992; Armstrong et al., 2008). Given equal gut fullness, feeding success may be greater for fish that consumed a larger proportion of high quality prey than were eaten by congener species. We observed very high gut fullness (9% of body weight) in juvenile chum salmon during early summer 1986, but much of the diet was composed of low-quality food items such as larvaceans. Data on prey quality would enhance future comparisons of juvenile salmon diets and gut fullness.

Electivity patterns and ontogeny

The nearshore feeding ecology of the earliest marine stages of juvenile salmon <100 mm has been studied well in the past (e.g., Kaczynski et al., 1973; Sturdevant et al., 1996), and juvenile salmon feeding ecology, species-specific feeding preferences, and prey selection for fish >100 mm in length captured in highly variable nearshore coastal environments have been examined in more recent studies (Moulton, 1997; Landingham et al., 1998; De Robertis et al., 2005; Armstrong et al., 2008). Ours is one of few studies where larger juvenile fish from transitional inland marine habitats have been examined (Willette, 2001; Sturdevant et al., 2004; Armstrong et al., 2008).

A variety of zooplanktivorous fish select prey disproportionate to their abundance in the environment (e.g., Lazzaro, 1987; Gerking, 1994). For salmon and other fishes, these patterns have been attributed to multiple factors, including: prey size (Brodeur, 1991); prey pigmentation or other visual indicators (Peterson et al., 1982; Schabetsberger et al., 2003); and vertical migration behavior of predator and prey (Bollens and Frost, 1989; Viitasalo et al., 2001). Our three-year study of juvenile salmon feeding in Dabob Bay provides additional evidence that juvenile chum, Chinook, coho, and pink salmon exhibit ontogenetic shifts in prey size selection and that they select for larger and more visually conspicuous prey. Previous studies showed that diel vertical migration is an important mediator of planktivore trophic interactions in Dabob Bay (e.g., Bollens and Frost, 1989; Frost and Bollens, 1992; Bollens et al., 1993).

Juvenile salmon in Dabob Bay used a diverse prey field and demonstrated species-specific prey preferences. Chum and Chinook salmon both highly preferred insects, cephalopods, decapod larvae, hyperiid amphipods,

and teleost prey. Coho and pink salmon both strongly selected for insects, whereas decapod larvae were important to the former and gammarid amphipods to the latter. Our study supports the importance of insect prey to young juvenile salmon in transitional environments (Moulton, 1997; Romanuk and Levings, 2005; Weitkamp and Sturdevant, 2008).

The diet of juvenile chum salmon further differed from the other salmon species by the abundance of larvaceans (primarily *Oikopleura* sp.) in their gut contents, and their consumption of ctenophores. These observations are consistent with other reports (Simenstad and Salo, 1980; Black and Low, 1983; Landingham et al., 1998) and may be related to anatomical gut specialization, which enables chum salmon to assimilate prey items that other salmon cannot digest (Welch, 1997; Arai et al., 2003).

Calanoid copepods have been described as a major diet item for juvenile salmon generally (Pearcy, 1992), and for chum and pink salmon specifically (Godin, 1981; Sturdevant et al., 2004). However, despite a diverse and abundant assemblage of copepod species in Dabob Bay, copepods only represented a modest component of our salmon diets and were particularly limited to smaller predators. Instead, juvenile salmon in Dabob Bay were found more often feeding on numerically less abundant macrozooplankton such as euphausiids, hyperiid amphipods, and decapod larvae. Similarly, Peterson et al. (1982) showed that juvenile coho and Chinook salmon off Oregon fed more on hyperiid amphipods than on the numerically dominant copepods. These results support the results from other studies that indicate that salmon are more likely to feed on larger, more visible prey items (Healey, 1980; Schabetsberger et al., 2003), in which case abiotic factors (e.g., light intensity and turbidity) and biotic processes (e.g., vertical migration and predator evasion behavior) will be important variables that will help determine stomach fullness and feeding success.

Ontogenetic diet thresholds for juvenile salmon at approximately 80 mm, before which teleost prey are less important, have been indicated by other studies (Brodeur, 1991; Keeley and Grant, 2001). In contrast, our electivity results provide evidence that teleost prey were strongly selected for by small (<75 mm) chum and pink salmon during spring, when fish larvae may have been particularly small (Bollens et al., 1992a; Fulmer and Bollens 2005). Simenstad and Salo (1980) found that juvenile chum salmon transitioned from nearshore habitats with epibenthic food sources to neritic habitats with pelagic and nektonic food sources when they reached approximately 45–55 mm FL. In other studies, seasonal variability in salmon gut contents has been attributed to ontogenetic shifts in feeding preferences or feeding behavior (Beacham, 1986; Brodeur, 1991; Daly et al., 2009). Similarly, our results indicate that small chum, Chinook, and coho salmon select small prey, then larger prey as the fish develop. Small Chinook and coho salmon selected *Calanus pacificus* roughly in

proportion to its abundance, but other copepods were avoided. Similarly, only small coho salmon selected gammarid and hyperiid amphipods. In contrast, only large Chinook salmon selected for gammarids. Thus, both species-specific and ontogenetic shifts in prey preference were observed.

Our diet and electivity results should be interpreted cautiously because our samples were pooled across broad size, temporal, and spatial scales, and because of limitations associated with sample sizes, net sampling biases, and pooling of prey species and life history stages. For example, the range of euphausiid electivity values observed may be due to the pooling of euphausiid species and life-history stages, potentially obscuring euphausiid prey selection patterns observed in other studies (Schabetsberger et al., 2003).

Another major caution concerns our ability to determine “available prey” with plankton nets. More mobile and larger nektonic prey, such as cephalopods and young fish, are able to avoid conventional plankton nets, with the consequence that electivity indices for these prey types would be biased upward. Conversely, small prey types that are unable to avoid the plankton net (e.g., small copepods) would be proportionately over-represented in the net samples, with the consequence that electivity indices for these forms would be biased downward. We recommend that further research be undertaken into adequately sampling macrozooplankton and micronekton (e.g., Gewant and Bollens, 2005), such that a broader and potentially more appropriate range of potential prey for fishes can be quantitatively sampled.

Several additional complicating factors should be considered when interpreting electivity indices. First, strongly positive electivity (e.g., $E_i=1.00$) often results from a rare presence of a species in the gut contents and a corresponding absence of that same species in the plankton. In some cases zero abundance in the plankton may be due to low-volume plankton hauls which under-sample the available prey field. Conversely, an E_i of -1.00 could result from a rare (but nonzero) occurrence of a species in the environment, combined with its absence from the gut contents, perhaps simply because of a low probability of encounter between predator and prey.

A final caution concerns the vertical resolution of sampling. Landingham et al. (1998) used both neuston and oblique plankton tows and showed that salmon diet most closely resembled that of the neuston assemblage. The upper 50 m were sampled with our sampling methods and therefore electivity values may have been biased. For example, if juvenile salmon are primarily feeding near the surface, abundant zooplankton (i.e., copepods) that are more deeply distributed may not fully be part of the “available” prey community. We recommend finer-scale, vertically resolved sampling of juvenile salmon and their potential prey in future studies.

Dabob Bay has been the site of numerous studies for which the interactions between planktivorous fishes and

the behaviors exhibited by their potential prey have been explored (Ohman, 1986; Frost, 1988; Bollens and Frost, 1989; Bollens et al., 1992a; Bollens et al., 1993). Field studies by Bollens and Frost (1989) indicated that abundances of actively feeding planktivorous fish (including *Oncorhynchus* spp.) are directly linked with the strength and timing of vertical migration exhibited by the copepod *Calanus pacificus*. Our results indicate that the adaptive response exhibited by species such as *Calanus pacificus* seems to be an effective mechanism for avoiding predation by species such as juvenile salmon. Thus, "available" prey items are not only those that are abundant or of the desired size, but those that are also available for visual detection. Availability may be affected by the prey's presence or absence from the photic zone, or by the presence of pigmentation that makes the prey more detectable visually. Most of the prey items that were consistently consumed by salmon in this study (e.g., euphausiids, hyperiid and gammarid amphipods, and decapod larvae) possess characteristically dark or large eyes. The ability of salmon to detect these potential prey items may be increased by heavy pigmentation, large body size, and their frequently noted association with the near surface layer (Lough, 1976; Peterson et al., 1982) where salmon typically feed.

Diet overlap and potential interspecific competition among salmon species

A variety of studies have relied on diet overlap as a primary indicator of potential resource competition between co-occurring species. Although there is little consensus among studies of salmon, diet overlap has been most frequently observed between Chinook and coho salmon in Oregon and Washington (Peterson et al., 1982; Emmett et al., 1986; Brodeur and Pearcy, 1990; Brodeur, 1991), and to a lesser extent between chum, pink, and sockeye salmon (*Oncorhynchus nerka*) in British Columbia and Southeast Alaska (Healey, 1980; Beacham, 1993; Landingham et al., 1998). Our results from Dabob Bay show the greatest spatial and temporal overlap between chum and Chinook salmon but also provide evidence only for resource partitioning (low diet overlap) between these two species, not necessarily competition (which would require resource limitation).

In contrast, our data show significant diet overlap between Chinook and coho salmon (average PSI=77.9%), supporting earlier reports of potential resource competition between these two species. Although Brodeur and Pearcy (1990) did not see evidence for significant overlap between four salmon species when all observations were combined, they observed significant overlap between Chinook and coho salmon during May and June, as well as during the 1983 El Niño. Likewise we found that significant overlap between Chinook and coho salmon occurred during June (of 1986 and 1987), largely because of the shared consumption of decapod larvae, which are visually conspicuous and seasonally abundant at this time of year. However, the co-occurrence of juvenile Chinook and coho in Dabob Bay was

less prominent than in coastal Oregon (Peterson et al., 1982; Brodeur and Pearcy, 1990; Brodeur and Pearey, 1992); however, our results are based on far fewer data.

Despite the co-occurrence of different juvenile salmon species in Dabob Bay, and the occasional occurrence of significant diet overlap between these species, we did not see any indication of food limitation. That is, there was never a significant relationship between stomach fullness and zooplankton biomass, as might be expected if food was limited. However, just as with the electivity indices discussed above, we caution that our vertical plankton net hauls may not adequately sample the potential prey of juvenile salmon. Testing for food limitation by correlating salmon stomach fullness and the abundance of potentially more appropriate prey (e.g., macrozooplanktonic, micronektonic, and neustonic prey) would prove interesting, but was not possible given our sampling method. Similarly, our comparison of zooplankton dry weights with salmon stomach wet weights complicates the interpretation of food limitation and potential competition because conversions from wet-weight to dry-weight would be expected to vary between prey taxa (e.g., between gelatinous and crustacean prey).

Resource limitation by juvenile salmon during their early marine transition may be influenced by several other factors not addressed in our study, including direct and indirect effects of hatchery production in the region (Quinn et al., 2005) and potential diet overlap with other zooplanktivores (Purcell and Sturdevant, 2001). Furthermore, zooplankton dynamics in temperate marine waters are clearly influenced by interannual (El Niño cycles) and interdecadal (Pacific Decadal Oscillation) scales of climate variability (Mackas et al., 2001; Hooff and Peterson, 2006) and there are important linkages to salmon survival during multiple life-history stages (Beamish and Bouillon, 1993; Logerwell et al., 2003). Although diet data from our three-year study could be averaged across years (as opposed to size classes, etc.), interannual climate factors cannot be overlooked. Indeed, based on a multivariate El Niño–Southern Oscillation index (MEI), 1987 ranks as a moderate to strong El Niño year (April–October MEI average=1.91), and likewise represents the most anomalous year of our study for seasonal plankton composition in Dabob Bay. This was particularly apparent at the deeper station, where the abundance of *Oithona* sp. and larvaceans seemed to be more characteristic of the shallow, nearshore station in 1985 and 1986. Mechanisms underlying the interannual variability of zooplankton composition in Dabob Bay warrant further exploration.

Our combination of detailed analyses of prey fields and fish diets is clearly only one approach to understanding juvenile salmon feeding ecology. Biochemical methods of studying energetics and feeding relationships (e.g., Johnson and Schindler, 2009) provide additional insight into juvenile salmon trophic dynamics. Studies across the variety of habitats encountered by salmon during their outmigration and early residence in marine environments will be necessary to fully un-

derstand species-specific responses to resource and environmental variability. Our results from Dabob Bay indicate that periodic high diet overlap between salmon species may occur. However, evidence of resource partitioning, especially between frequently co-occurring species (e.g., chum and Chinook salmon), combined with a lack of evidence for food limitation (although this should be more explicitly tested in the future), indicates that competition between juvenile salmon is unlikely to occur in this marine fjord.

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