

Food Habits of Juvenile Salmon in the Gulf of Alaska July–August 1996

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Abstract: Four species of juvenile salmon, pink (*Oncorhynchus gorbuscha*), sockeye (*O. nerka*), chum (*O. keta*), and coho (*O. kisutch*) salmon, were collected during July and August, 1996, using a midwater trawl in near surface waters of the Gulf of Alaska from Southeast Alaska to the Alaska Peninsula. Stomach contents of these salmon were examined to identify important prey items. Crustaceans, principally hyperiid amphipods and euphausiids, and fish were the primary prey. Decapod larvae, calanoid copepods, and pteropods were also commonly found in the juvenile salmon diets. The proportions of prey type varied by habitat and regions for each of the four salmon species examined. The variation in large prey types and the small proportion, 3%, of empty stomachs suggest that the availability of prey resources does not appear to be a limiting factor for production and growth of juvenile salmon examined in this study.

INTRODUCTION

In the past few years, considerable attention has been given to the diminished size of salmon in the North Pacific Ocean and Bering Sea (Helle 1989). This concern has prompted new studies of salmon diet and energetics, which are key to assessing the ocean's capacity to support recent levels in salmon production. Data on the similarity in diet between species, years, and areas provide insight into life history strategies such as ocean migrations, foraging behavior, and nutritional adaptations. Such studies enlarge our understanding of the trophic relations of salmonids in coastal and oceanic ecosystems of the North Pacific. They also provide data needed for models of salmon energetics and marine ecosystems.

Studies of feeding behavior and interspecific competition of juvenile salmon during marine residency can also provide insight on energy budgets and stock productivity. Changes in the abundance of inter- and intraspecific competitors can be reflected by changes in diet when prey resources are limiting for salmon (Tadokoro et al. 1996). Competition in foraging among species may suggest limited food resources and lower productivity (Healey 1978; Peterman 1984). At times, this competition may be limited to specific regions, time periods, and/or species. For example, earlier studies on juvenile salmon from waters in Southeast Alaska and northern British Columbia (Healey 1978; Landingham et al. 1998) showed that in some circumstances, the same major taxonomic prey shifted in proportions spatially and temporally between species; in other circumstances, diet overlap was apparent. Similarly, Peterson

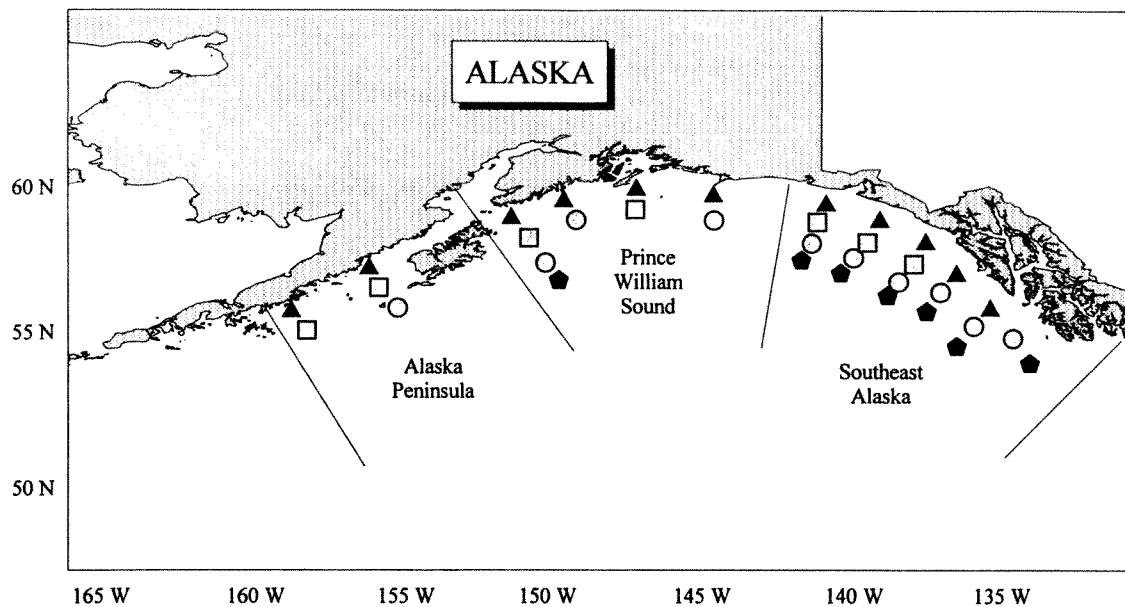
et al. (1982) and Brodeur et al. (1987) showed both diet overlap and similarity in feeding patterns for juvenile salmon off Oregon, suggesting a mixture of foraging strategies characterized by both prey availability or by prey selection.

This study describes the food habits of juvenile salmon taken in coastal waters of the Gulf of Alaska during July and August 1996. Diets of juvenile pink (*Oncorhynchus gorbuscha*), sockeye (*O. nerka*), chum (*O. keta*), and coho (*O. kisutch*) salmon are summarized and compared across four habitat types, extending from nearshore to oceanic waters, and across three regions from Southeast Alaska to the Alaskan Peninsula. The broad extent of the sampling area allows us to examine the diet characteristics of juvenile salmon as they enter coastal waters in Southeast Alaska and move north and westward along their migratory pathway. This pathway, with its changing current structure, continental shelf width and topography, nutrient inputs, and eddy activity, thus provides important insight into the plasticity of salmon foraging in diverse coastal habitats.

MATERIAL AND METHODS

Rope trawl surveys were conducted in near surface waters on the chartered fishing vessel F/V *Great Pacific*, a 38 m stern ramp trawler, in waters from Southeast Alaska to the Aleutian Islands in the North Pacific Ocean from 21 July to 22 August 1996 (Fig. 1; Carlson et al. 1996). The trawl was towed for five nmi at 5.0 knots in near shore (0–10 nmi offshore), shelf, slope (200 m depth contour), and oceanic waters (out to 60–120 nmi offshore). The net was 198 m long and was

Fig. 1. Sampling locations for juvenile salmon used in the diet analyses. Symbols represent the four habitat types: triangles – nearshore; squares – shelf; circles – slope; and hexagon – oceanic.



fished from the surface to a depth of approximately 18 m with a 52 m horizontal opening. The total catch of juvenile salmon in 1996 was 9,484, consisting of 4,701 pink, 1,932 chum, 1,405 coho, 1,414 sockeye, and 31 chinook (*O. tshawytscha*) salmon, and one steelhead (*O. mykiss*). A subsample of these fish was sorted, identified, and frozen whole for laboratory analysis of food habits. In the laboratory, each fish was measured to the nearest mm fork length, blotted dry, and weighed to the nearest 0.01 g. The stomach (from the pharynx to the pylorus) was removed and placed in a 7.5% formalin solution for 4–6 weeks, then transferred to 50% isopropyl alcohol for later analysis.

Data Collection

When available, 10 stomachs per species in each of four different habitats (near shore, shelf, slope, and oceanic) were selected and analyzed per transect. Relative stomach fullness was visually estimated and categorized using a scale of 1–6 (where 1 = trace, 2–5 = fullness in fourths, and 6 = distended stomachs). The state of digestion was noted as fresh, partially digested, or mostly digested. The stomachs were weighed to the nearest milligram, the contents removed, and then the stomachs were weighed empty. The contents were identified to major taxonomic groupings and enumerated. Larval and juvenile fish in the stomach contents were identified and measured (total length (TL)), when possible. Unidentifiable gelatinous material and incidental prey (barnacle cyprids, terrestrial insects, gammarids, and chaetognaths) were encountered in some of the stomachs. In

most cases these prey types occurred infrequently and were pooled into an “other” category.

Data Analysis

Stomach contents were identified to general taxa to provide a summary of diet composition. Comparisons of prey composition were made between species, habitat types and regions (off Southeast Alaska, Prince William Sound, and Alaska Peninsula). Prey weight data were predominantly used in the analyses as the importance of small prey such as oikopleura can be misrepresented when the data are reported as numerical or frequency percentages. Nevertheless, numerical and frequency of occurrence data were included in the tables for reader comparison. All three measures (number, weight, and frequency of occurrence) of each prey taxon were expressed as percentages.

Diet overlap by species and by area was estimated using the Schoener Index of Overlap, which is also known as the Percent Similarity Index (PSI; Schoener 1974). The PSI is computed as:

$$PSI_{jk} = \sum \min(p_{ij}, p_{ik}) = 1 - 0.5(\sum |p_{ij} - p_{ik}|),$$

where p is the proportion of the biomass of the i^{th} prey category in n taxonomic categories consumed by fish species (or habitat areas) j and k . Note that when prey are generalized into major taxa (as in this study), the PSI may overestimate diet similarity due to the use of summary prey categories; taxa used in a prey category identified from one species or area may not be the same taxa as those in that category collected from another species or area (Sturdevant et al. 1997).

RESULTS

Detailed analysis of stomach contents was performed on a total of 872 juvenile salmon (240 pink, 213 sockeye, 192 chum, and 227 coho salmon). Nearly all of the stomachs (97%) contained some food. Crustacean species most commonly encountered by the four juvenile salmon species within all habitats and regions were the euphausiid, *Thysannoessa spinifera*, and the common hyperiid, *Themisto pacifica*. Pteropods, mainly *Limacina helicina*, decapods, *Brachyura cancrivora* megalops, and *Calanus pacificus* copepods were also frequent prey in the diets. Of the various families of fish found in the diets (Table 1), 30-35 mm Osmerid larvae were the most abundant.

Southeast Alaska

Of the three survey areas in our study, fork lengths were notably smaller for juvenile salmon sampled from the southeastern Alaska transects. Pink salmon were smallest (89–182 mm, \bar{x} = 126 mm) followed by chum salmon (95–194 mm, \bar{x} = 128 mm), sockeye salmon (107–143 mm, \bar{x} = 143 mm), and coho salmon (111–279 mm, \bar{x} = 206 mm).

Nearshore waters

Euphausiids and fish were the two most important food items as measured by percent wet weight (Table 2). Pink and chum salmon fed primarily on euphausiids, whereas sockeye and coho salmon fed primarily on fish. Coho salmon had the least diverse diet with fish comprising over 93% of the prey weight; sockeye salmon had the most diverse diet that included euphausiids, hyperiid amphipods, and calanoid copepods as secondary food items.

Shelf waters

Euphausiids and calanoid copepods were two important food items (Table 2). Pink and chum salmon fed primarily on euphausiids, whereas sockeye salmon fed primarily on calanoid copepods and coho salmon fed primarily on fish. Coho salmon had the least diverse diet with fish comprising over 87% of the prey weight. Pink and chum salmon had the most diverse diet that included calanoid copepods and fish as secondary food items.

Slope waters

Hyperiid amphipods and euphausiids were the two most important food items consumed in this habitat (Table 2). Pink salmon fed primarily on hyperiid amphipods, sockeye and chum salmon fed primarily

Table 1. List of prey organisms recorded from examination of the stomach contents of juvenile pink, sockeye, coho, and chum salmon in July–August 1996. Listed are prey types which were identified and categorized into general taxa categories. Genera and species are listed where positive identification was possible. This list includes prey that was encountered infrequently.

| | |
|---------------------------------|--------------------------|
| Gastropoda | Decapoda |
| Pteropoda | Brachyura |
| <i>Limacina helicina</i> | (Cancridae) |
| <i>Clione</i> sp. | (Majidae) |
| <i>Clio</i> sp. | Anomura |
| | (Paguridae) |
| Cephalopoda | (Lithodidae) |
| <i>Gonatus</i> sp. | Pandalidae |
| Insect | Hyperiidea |
| Diptera | <i>Themisto pacifica</i> |
| | <i>Hyperoche</i> sp. |
| | <i>Primno</i> sp. |
| Calanoida | Chaetognatha |
| <i>Calanus pacificus</i> | <i>Sagitta elegans</i> |
| <i>Calanus marshallae</i> | |
| <i>Epilabidocera longipedes</i> | Larvaceans |
| <i>Metridia pacifica</i> | <i>Oikopleura dioica</i> |
| <i>Eucalanus bungii</i> | |
| <i>Neocalanus</i> sp. | Osteichthyes |
| <i>Centropages abdominalis</i> | Hexagrammidae |
| <i>Pseudocalanus</i> sp. | Gadidae |
| <i>Acartia</i> sp. | Osmeridae |
| Cirripedia | Salmonidae |
| <i>Lepas</i> sp. | Cottidae |
| Euphausiacea | |
| <i>Thysannoessa spinifera</i> . | |
| <i>T. raschii</i> | |
| <i>Euphausia pacifica</i> | |

on euphausiids, and coho salmon fed primarily on fish. Hyperiid amphipods were also important for sockeye salmon and euphausiids important to pink salmon. Sockeye salmon had the most diverse diet that included calanoid copepods and fish as well as hyperiids and euphausiids.

Oceanic waters

Euphausiids were most important in this habitat for pink, sockeye, and coho salmon, whereas chum salmon consumed primarily gelatinous material (Table 2). Pink salmon had the least diverse diet, followed by chum salmon.

Prince William Sound

Average fork lengths of juvenile salmon sampled from Prince William Sound Alaska transects generally increased in comparison to Southeast Alaska. Pink salmon were smallest (102–196 mm, \bar{x} = 126 mm) followed by chum salmon (55–263 mm, \bar{x} = 137 mm), sockeye salmon (89–263 mm, \bar{x} = 137 mm), and coho salmon (132–345 mm, \bar{x} = 232 mm).

Table 2. Summary of prey consumed by juvenile salmon caught in trawls off Southeast Alaska, 21–28 July 1996: %N, percent by number; %W, percent by wet weight; and %FO, percent frequency of occurrence. Unidentified gelatinous and incidental prey are combined into an "Other" category. Prey weight data reported in the text are in bold type.

| Prey taxon | Pink | | | Sockeye | | | Chum | | | Coho | | |
|--------------------|---------|-------------|------|---------|-------------|------|---------|-------------|------|---------|-------------|------|
| | %N | %W | %FO | %N | %W | %FO | %N | %W | %FO | %N | %W | %FO |
| Near shore | | | | | | | | | | | | |
| Hyperideia | 14.9 | 14.5 | 60.0 | 17.6 | 10.6 | 60.0 | 1.6 | 0.4 | 42.5 | 0.7 | 0.0 | 10.0 |
| Euphausiacea | 6.0 | 64.9 | 43.3 | 20.0 | 27.3 | 55.0 | 2.9 | 74.9 | 55.0 | 12.4 | 4.4 | 32.0 |
| Calanoida | 6.7 | 9.2 | 43.3 | 24.0 | 12.9 | 60.0 | 1.3 | 2.5 | 32.5 | 0.0 | 0.0 | 0.0 |
| Fish | 2.2 | 6.1 | 30.0 | 26.1 | 45.9 | 50.0 | 1.5 | 9.8 | 35.0 | 6.1 | 93.6 | 72.0 |
| Decapoda | 1.1 | 2.8 | 43.3 | 1.9 | 2.6 | 20.0 | 1.0 | 6.7 | 22.5 | 45.1 | 1.8 | 42.0 |
| Pteropoda | 14.3 | 1.5 | 63.3 | 10.3 | 0.7 | 20.0 | 5.2 | 1.3 | 57.5 | 32.5 | 0.1 | 24.0 |
| Larvaceans | 53.8 | 1.1 | 33.3 | 0.0 | 0.0 | 0.0 | 86.4 | 4.1 | 45.0 | 2.3 | 0.0 | 2.0 |
| Other | 1.0 | 0.0 | 26.7 | 0.0 | 0.0 | 0.0 | 0.1 | 0.4 | 5.0 | 1.0 | 0.0 | 3.0 |
| Number of stomachs | | (30) | | | (20) | | | (40) | | | (50) | |
| Shelf | | | | | | | | | | | | |
| Hyperideia | 0.8 | 1.4 | 30.0 | 0.3 | 0.2 | 20.0 | 0.7 | 0.2 | 33.3 | 0.7 | 0.0 | 10.0 |
| Euphausiacea | 2.2 | 39.0 | 30.0 | 15.8 | 25.0 | 35.0 | 2.1 | 48.4 | 46.7 | 10.8 | 9.3 | 40.0 |
| Calanoida | 33.0 | 31.3 | 73.3 | 73.4 | 72.5 | 95.0 | 16.6 | 20.6 | 76.7 | 0.0 | 0.0 | 0.0 |
| Fish | 4.9 | 22.7 | 3.3 | 0.4 | 0.8 | 15.0 | 3.8 | 23.2 | 23.3 | 3.0 | 87.8 | 95.0 |
| Decapoda | 0.1 | 0.2 | 6.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 3.3 | 0.6 | 0.2 | 30.0 |
| Pteropoda | 23.1 | 4.0 | 90.0 | 9.9 | 0.8 | 80.0 | 6.2 | 1.4 | 76.7 | 84.5 | 0.7 | 45.0 |
| Larvaceans | 35.7 | 1.2 | 20.0 | 0.0 | 0.0 | 0.0 | 70.2 | 3.0 | 30.0 | 0.0 | 0.0 | 0.0 |
| Other | 0.1 | 0.2 | 3.3 | 0.2 | 0.7 | 8.0 | 0.3 | 0.2 | 10.0 | 0.2 | 2.0 | 5.0 |
| Number of stomachs | | (30) | | | (20) | | | (30) | | | (20) | |
| Slope | | | | | | | | | | | | |
| Hyperideia | 43.9 | 61.1 | 75.0 | 27.7 | 21.8 | 75.0 | 64.6 | 39.1 | 63.3 | 3.1 | 0.0 | 22.0 |
| Euphausiacea | 5.4 | 17.1 | 62.5 | 22.2 | 39.7 | 62.5 | 7.2 | 48.6 | 43.3 | 20.6 | 28.4 | 32.0 |
| Calanoida | 6.4 | 12.5 | 50.0 | 11.4 | 12.7 | 40.0 | 8.9 | 3.2 | 46.7 | 0.0 | 0.0 | 0.0 |
| Fish | 0.1 | 0.6 | 12.5 | 2.6 | 15.9 | 32.5 | 0.6 | 1.0 | 23.3 | 3.7 | 62.3 | 74.0 |
| Decapoda | 0.6 | 2.0 | 35.0 | 1.3 | 2.5 | 22.5 | 1.2 | 1.8 | 26.7 | 1.9 | 0.8 | 34.0 |
| Pteropoda | 43.4 | 6.6 | 72.5 | 34.0 | 2.9 | 77.5 | 17.0 | 1.1 | 50.0 | 70.2 | 0.9 | 48.0 |
| Squid | 0.0 | 0.0 | 0.0 | 0.0 | 3.7 | 5.0 | 0.0 | 0.0 | 0.0 | 0.5 | 7.5 | 22.0 |
| Other | 0.2 | 0.1 | 7.5 | 0.7 | 0.8 | 14.0 | 0.5 | 5.2 | 6.7 | 0.0 | 0.0 | 0.0 |
| Number of stomachs | | (40) | | | (40) | | | (30) | | | (50) | |
| Oceanic | | | | | | | | | | | | |
| Hyperideia | 16.9 | 4.8 | 93.3 | 6.8 | 4.5 | 78.0 | 62.7 | 7.1 | 91.7 | 0.7 | 0.1 | 37.0 |
| Euphausiacea | 25.8 | 82.1 | 50.0 | 47.7 | 70.6 | 80.0 | 0.9 | 2.2 | 41.7 | 53.6 | 72.2 | 44.4 |
| Calanoida | 13.9 | 4.0 | 40.0 | 19.0 | 17.5 | 55.0 | 2.6 | 3.0 | 16.7 | 0.0 | 0.0 | 0.0 |
| Fish | 0.8 | 6.8 | 16.7 | 2.3 | 4.5 | 35.0 | 2.1 | 6.5 | 50.0 | 2.7 | 23.2 | 55.6 |
| Decapoda | 0.7 | 0.6 | 40.0 | 0.2 | 0.3 | 20.0 | 0.7 | 1.8 | 16.7 | 3.3 | 1.0 | 29.6 |
| Pteropoda | 41.3 | 1.3 | 30.0 | 23.2 | 1.6 | 50.0 | 25.5 | 2.9 | 83.3 | 38.7 | 0.5 | 81.5 |
| Other | 0.6 | 0.5 | 10.0 | 0.7 | 1.0 | 5.0 | 5.9 | 76.6 | 45.0 | 1.0 | 3.0 | 7.4 |
| Number of stomachs | | (30) | | | (40) | | | (12) | | | (27) | |
| | n = 130 | | | n = 120 | | | n = 112 | | | n = 147 | | |

Nearshore waters

Euphausiids and decapod larvae were the two most important food items (Table 3). Pink, sockeye, and chum salmon fed primarily on euphausiids, and coho salmon fed primarily on fish. Hyperiid amphipods were of secondary importance for pink and chum salmon, whereas decapod larvae were found in the stomachs of sockeye, chum, and coho salmon. Larvaceans were also important for chum salmon, and euphausiids were fed upon by coho salmon. Pink salmon had the least diverse diet with euphausiids comprising over 75% of the prey weight.

Shelf waters

Fish were the most important food item for juvenile salmon, followed by euphausiids and hyperiid amphipods (Table 3). Sockeye and coho salmon fed primarily on fish, pink salmon on euphausiids, and chum salmon on hyperiid amphipods. Fish were also very important to pink and chum salmon. Sockeye salmon consumed the least diverse diet with fish comprising over 84% of the prey weight.

Table 3. Summary of prey consumed by juvenile salmon caught in trawls off shore from Prince William Sound, Alaska, 29 July to August 3, 1996: %N, percent by number; %W, percent by wet weight; and %FO, percent frequency of occurrence. Unidentified gelatinous and incidental prey are combined into an "Other" category. Prey weight data reported in the text are in bold type.

| Prey taxon | Pink | | | Sockeye | | | Chum | | | Coho | | |
|--------------------|------|-------------|-------|---------|-------------|-------|------|-------------|------|------|-------------|------|
| | %N | %W | %FO | %N | %W | %FO | %N | %W | %FO | %N | %W | %FO |
| Near shore | | | | | | | | | | | | |
| Hyperidea | 49.3 | 16.9 | 63.3 | 41.3 | 9.8 | 65.0 | 56.9 | 13.1 | 56.7 | 2.0 | 0.2 | 37.5 |
| Euphausiacea | 19.8 | 75.9 | 73.3 | 32.9 | 68.5 | 75.0 | 16.3 | 41.9 | 56.7 | 28.3 | 26.0 | 47.5 |
| Calanoida | 8.1 | 2.8 | 36.7 | 2.2 | 0.5 | 15.0 | 1.0 | 0.3 | 20.0 | 2.0 | 0.2 | 12.5 |
| Fish | 0.2 | 0.2 | 16.7 | 0.1 | 0.8 | 10.0 | 0.3 | 0.2 | 16.7 | 3.0 | 52.3 | 62.5 |
| Decapoda | 2.4 | 3.8 | 66.7 | 21.6 | 20.2 | 55.0 | 13.9 | 12.4 | 43.3 | 62.8 | 21.3 | 90.0 |
| Pteropoda | 8.6 | 0.1 | 53.3 | 0.9 | 0.0 | 15.0 | 1.7 | 0.0 | 23.3 | 0.7 | 0.0 | 12.5 |
| Larvaceans | 10.6 | 0.0 | 20.0 | 0.0 | 0.0 | 0.0 | 6.5 | 31.3 | 6.7 | 0.0 | 0.0 | 0.0 |
| Other | 0.9 | 0.4 | 13.0 | 1.1 | 0.2 | 5.0 | 3.5 | 0.9 | 10.0 | 1.0 | 0.2 | 7.0 |
| Number of stomachs | | (30) | | | (20) | | | (30) | | | (40) | |
| Shelf | | | | | | | | | | | | |
| Hyperidea | 14.9 | 6.6 | 93.3 | 25.0 | 4.3 | 80.0 | 83.6 | 39.3 | 83.3 | 13.9 | 1.4 | 43.3 |
| Euphausiacea | 9.5 | 47.3 | 56.7 | 1.6 | 0.6 | 33.3 | 3.9 | 16.5 | 66.7 | 1.0 | 1.1 | 20.0 |
| Calanoida | 6.0 | 3.7 | 40.0 | 1.3 | 0.3 | 23.3 | 3.5 | 2.3 | 36.7 | 0.0 | 0.0 | 3.3 |
| Fish | 3.5 | 36.4 | 43.3 | 21.0 | 84.7 | 63.3 | 3.5 | 38.8 | 60.0 | 12.5 | 59.2 | 60.0 |
| Decapoda | 0.5 | 0.5 | 33.3 | 1.1 | 0.5 | 30.0 | 1.5 | 1.9 | 53.3 | 56.3 | 11.4 | 53.3 |
| Pteropoda | 65.3 | 3.2 | 56.7 | 47.4 | 0.9 | 50.0 | 3.1 | 0.2 | 43.3 | 13.6 | 0.1 | 30.0 |
| Other | 0.9 | 0.4 | 6.7 | 0.4 | 8.7 | 6.0 | 0.8 | 0.1 | 6.7 | 2.4 | 0.3 | 10.0 |
| Number of stomachs | | (30) | | | (30) | | | (30) | | | (30) | |
| Slope | | | | | | | | | | | | |
| Hyperidea | 85.7 | 40.2 | 100.0 | 39.6 | 5.7 | 90.0 | 91.3 | 74.9 | 95.0 | 1.7 | 0.1 | 20.0 |
| Euphausiacea | 3.0 | 30.1 | 95.0 | 57.9 | 94.0 | 100.0 | 2.4 | 22.0 | 95.0 | 92.5 | 8.7 | 90.0 |
| Calanoida | 2.2 | 13.6 | 65.0 | 0.0 | 0.0 | 0.0 | 1.1 | 0.4 | 45.0 | 0.6 | 0.0 | 10.0 |
| Fish | 0.2 | 3.2 | 50.0 | 0.5 | 0.2 | 60.0 | 0.2 | 0.5 | 45.0 | 3.5 | 91.0 | 60.0 |
| Decapoda | 0.6 | 7.6 | 30.0 | 0.0 | 0.0 | 0.0 | 1.0 | 1.8 | 40.0 | 1.8 | 0.3 | 30.0 |
| Pteropoda | 8.0 | 3.8 | 80.0 | 1.6 | 0.0 | 30.0 | 3.8 | 0.3 | 85.0 | 0.0 | 0.0 | 0.0 |
| Other | 0.2 | 1.4 | 15.0 | 0.3 | 0.0 | 10.0 | 0.3 | 0.0 | 10.0 | 0.0 | 0.0 | 0.0 |
| Number of stomachs | | (20) | | | (10) | | | (20) | | | (10) | |
| Oceanic | | | | | | | | | | | | |
| Hyperidea | 15.5 | 9.3 | 100.0 | - | - | - | - | - | - | - | - | - |
| Euphausiacea | 0.0 | 0.2 | 10.0 | - | - | - | - | - | - | - | - | - |
| Calanoida | 1.4 | 3.9 | 60.0 | - | - | - | - | - | - | - | - | - |
| Fish | 0.7 | 9.2 | 30.0 | - | - | - | - | - | - | - | - | - |
| Decapoda | 2.7 | 36.8 | 80.0 | - | - | - | - | - | - | - | - | - |
| Pteropoda | 79.6 | 49.3 | 100.0 | - | - | - | - | - | - | - | - | - |
| Other | 0.0 | 0.5 | 10.0 | - | - | - | - | - | - | - | - | - |
| Number of stomachs | | (10) | | | (0) | | | (0) | | | (0) | |
| | | n = 90 | | | n = 60 | | | n = 80 | | | n = 80 | |

Slope waters

Euphausiids and hyperiid amphipods were the two most important food items (Table 3). Pink, and chum salmon fed primarily on hyperiids, coho salmon fed primarily on fish, and sockeye salmon fed primarily on euphausiids. Euphausiids were also important prey for pink and chum salmon, and calanoid copepods were

consumed by pink salmon. Diets of sockeye and coho salmon were dominated by one prey type.

Oceanic waters

Diet information was only available for pink salmon collected from this habitat. Pteropods were the most important food item followed by decapod larvae (Table 3).

Alaska Peninsula

Data collected off the Alaska Peninsula were limited to examinations of juvenile pink salmon from shelf and slope waters and sockeye salmon from nearshore and shelf waters (Table 4). Average fork lengths for pink salmon (84–170 mm, \bar{x} = 120 mm) were similar to Southeast Alaska, while sockeye salmon (147–229 mm, \bar{x} = 185 mm) were considerably larger.

Nearshore waters

Diets of sockeye salmon consisted of decapod larvae, fish, and euphausiids.

Shelf waters

Hyperiid amphipods followed by euphausiids were important prey for pink salmon; decapod larvae followed by fish were important prey for sockeye salmon.

Oceanic waters

Pink salmon fed primarily upon hyperiid amphipods and decapod larvae.

Diet Overlap Among Species and Regions

Diets of pink and chum salmon were the most closely related; they had the highest similarity indices in four of the seven habitats with complete diet information (Table 5). The low correlation between pink and chum salmon in oceanic waters off Southeast Alaska arose from the high consumption of gelatinous species by chum salmon there. The most dissimilar diets occurred between coho and either pink or chum salmon. Sockeye diets were similar to diets of all other species, partially due to their lack of specialization in foraging as shown by the wide variety of prey items contained in their stomachs.

Coho salmon had the largest diet overlap in nearly all habitats and geographical areas where they fed consistently on fish (Tables 6 and 7). Percent similarity indices for coho salmon averaged 60.1 across all the habitats, which means that on the average over 60% of the prey biomass in their stomachs was similar among areas. Sockeye and chum salmon were the most diverse foragers with diet overlap indices averaging 37% across all habitats. Much of the spatial dissimilarity in chum diets resulted from the occasional occurrence of gelatinous prey items, or larvaceans in their stomachs (Tables 2–4).

Table 4. Summary of prey consumed by juvenile salmon caught in trawls off the Alaska Peninsula, 4–9 August, 1996: %N, percent by number; %W, percent by wet weight; and %FO, percent frequency of occurrence. Unidentified gelatinous and incidental prey are combined into an "Other" category. Prey weight data reported in the text are in bold type. Data for chum and coho salmon from the Alaska Peninsula were unavailable.

| Prey taxon | Pink | | | Sockeye | | | Chum | | | Coho | | |
|--------------------|--------|-------------|-------|---------|-------------|-------|-------|----|-----|-------|----|-----|
| | %N | %W | %FO | %N | %W | %FO | %N | %W | %FO | %N | %W | %FO |
| Near shore | | | | | | | | | | | | |
| Hyperideia | - | - | - | 2.2 | 1.2 | 42.5 | - | - | - | - | - | - |
| Euphausiacea | - | - | - | 79.9 | 19.8 | 56.5 | - | - | - | - | - | - |
| Calanoida | - | - | - | 0.4 | 0.2 | 47.8 | - | - | - | - | - | - |
| Fish | - | - | - | 0.1 | 31.4 | 30.4 | - | - | - | - | - | - |
| Decapoda | - | - | - | 16.5 | 47.0 | 91.3 | - | - | - | - | - | - |
| Pteropoda | - | - | - | 0.2 | 0.0 | 17.4 | - | - | - | - | - | - |
| Other | - | - | - | 0.5 | 0.5 | 17.3 | - | - | - | - | - | - |
| Number of stomachs | (0) | | | (23) | | | (0) | | | (0) | | |
| Shelf | | | | | | | | | | | | |
| Hyperideia | 98.7 | 72.5 | 100.0 | 83.5 | 7.1 | 80.0 | - | - | - | - | - | - |
| Euphausiacea | 0.2 | 18.9 | 40.0 | 0.7 | 6.6 | 40.0 | - | - | - | - | - | - |
| Calanoida | 0.8 | 6.3 | 70.0 | 0.1 | 0.1 | 10.0 | - | - | - | - | - | - |
| Fish | 0.0 | 0.0 | 0.0 | 0.7 | 22.0 | 60.0 | - | - | - | - | - | - |
| Decapoda | 0.0 | 1.9 | 10.0 | 14.7 | 64.1 | 100.0 | - | - | - | - | - | - |
| Other | 0.2 | 0.4 | 40.0 | 0.4 | 0.0 | 20.0 | - | - | - | - | - | - |
| Number of stomachs | (10) | | | (10) | | | (0) | | | (0) | | |
| Slope | | | | | | | | | | | | |
| Hyperideia | 93.9 | 79.6 | 100.0 | - | - | - | - | - | - | - | - | - |
| Euphausiacea | 0.3 | 0.5 | 50.0 | - | - | - | - | - | - | - | - | - |
| Calanoida | 0.3 | 0.3 | 40.0 | - | - | - | - | - | - | - | - | - |
| Decapoda | 5.3 | 19.5 | 70.0 | - | - | - | - | - | - | - | - | - |
| Other | 0.2 | 0.1 | 10.0 | - | - | - | - | - | - | - | - | - |
| Number of stomachs | (10) | | | (0) | | | (0) | | | (0) | | |
| | n = 20 | | | n = 33 | | | n = 0 | | | n = 0 | | |

Table 5. Percent similarity indices (PSI) of diet overlap between pairs of juvenile salmon species within habitat type and geographical area of capture.

| Region | Habitat | Diet Overlap Indices | | | | | |
|----------------------------|-----------|----------------------|-----------|-----------|--------------|--------------|-----------|
| | | Pink-Sockeye | Pink-Chum | Pink-Coho | Sockeye-Chum | Sockeye-Coho | Chum-Coho |
| Southeast Alaska (SE) | | | | | | | |
| | Nearshore | 47.4 | 78.7 | 12.4 | 43.4 | 52.2 | 16.1 |
| | Shelf | 58.3 | 85.4 | 33.1 | 47.6 | 11.5 | 33.5 |
| | Slope | 57.0 | 63.0 | 19.4 | 69.4 | 49.7 | 31.1 |
| | Oceanic | 85.7 | 18.9 | 80.7 | 17.1 | 77.0 | 13.3 |
| Prince William Sound (PWS) | | | | | | | |
| | Nearshore | 83.0 | 60.2 | 30.6 | 64.8 | 47.6 | 39.2 |
| | Shelf | 43.4 | 62.6 | 39.8 | 44.8 | 62.1 | 43.4 |
| | Slope | 36.0 | 79.3 | 12.3 | 27.9 | 9.0 | 9.6 |
| Alaska Peninsula (AP) | | | | | | | |
| | Shelf | 15.7 | | | | | |

Table 6. Percent similarity indices (PSI) of diet overlap between habitat types and areas for chum and coho salmon. The PSI measures the similarity in diet for chum and coho salmon among habitats and regions.

| Region | Habitat | Southeast Alaska | | | | Prince William Sound | |
|-------------|-----------|------------------|-------|-------|---------|----------------------|-------|
| | | Nearshore | Shelf | Slope | Oceanic | Nearshore | Shelf |
| Chum | | | | | | | |
| SE | Nearshore | | | | | | |
| | Shelf | 65.7 | | | | | |
| | Slope | 55.8 | 54.2 | | | | |
| | Oceanic | 15.1 | 13.6 | 21.4 | | | |
| PWS | Nearshore | 54.0 | 45.9 | 58.2 | 12.5 | | |
| | Shelf | 14.3 | 42.6 | 61.0 | 20.2 | 32.1 | |
| | Slope | 25.4 | 23.5 | 64.1 | 12.3 | 37.4 | 58.7 |
| Coho | | | | | | | |
| SE | Nearshore | | | | | | |
| | Shelf | 92.5 | | | | | |
| | Slope | 67.6 | 72.5 | | | | |
| | Oceanic | 28.7 | 33.2 | 52.9 | | | |
| PWS | Nearshore | 58.5 | 61.8 | 51.0 | 56.5 | | |
| | Shelf | 62.2 | 60.9 | 61.2 | 25.8 | 65.2 | |
| | Slope | 95.7 | 96.8 | 71.3 | 32.3 | 61.4 | 60.7 |

Table 7. Percent similarity indices (PSI) of diet overlap between habitat types and areas for pink and sockeye salmon. The PSI measures the similarity in diet for pink and sockeye salmon among habitats and regions.

| Region | Habitat | Southeast Alaska | | | | Prince William Sound | | | | Alaska Peninsula | | |
|-----------------------|-----------|------------------|-------|-------|---------|----------------------|-------|-------|---------|------------------|-------|------|
| | | Nearshore | Shelf | Slope | Oceanic | Nearshore | Shelf | Slope | Oceanic | Nearshore | Shelf | |
| Pink Salmon | | | | | | | | | | | | |
| SE | Nearshore | | | | | | | | | | | |
| | Shelf | 58.5 | | | | | | | | | | |
| | Slope | 44.9 | 35.9 | | | | | | | | | |
| | Oceanic | 81.7 | 52.9 | 28.5 | | | | | | | | |
| PWS | Nearshore | 85.3 | 43.9 | 39.2 | 84.8 | | | | | | | |
| | Shelf | 65.7 | 70.4 | 31.8 | 64.8 | 57.9 | | | | | | |
| | Slope | 61.3 | 52.7 | 76.3 | 44.5 | 54.3 | 47.7 | | | | | |
| | Oceanic | 23.8 | 19.1 | 22.7 | 18.1 | 16.8 | 23.8 | 25.3 | | | | |
| Alaska | Shelf | 41.6 | 27.0 | 86.5 | 28.7 | 40.9 | 30.1 | 67.7 | 15.7 | | | |
| | Slope | 18.1 | | 2.5 | | 64.0 | 6.6 | 21.6 | 8.0 | 49.0 | 29.7 | 75.3 |
| Sockeye Salmon | | | | | | | | | | | | |
| SE | Nearshore | | | | | | | | | | | |
| | Shelf | 39.6 | | | | | | | | | | |
| | Slope | 69.7 | 40.2 | | | | | | | | | |
| | Oceanic | 50.2 | 45.0 | 64.1 | | | | | | | | |
| PWS | Nearshore | 40.2 | 26.7 | 53.5 | 74.8 | | | | | | | |
| | Shelf | 52.3 | | 3.4 | | 23.3 | 11.9 | | 6.7 | | | |
| | Slope | 33.2 | 25.4 | 45.6 | | 75.3 | 74.4 | | 5.1 | | | |
| AP | Nearshore | 55.2 | 21.5 | 40.1 | 26.5 | 42.4 | 34.4 | 21.2 | | | | |
| | Shelf | 38.4 | 7.7 | 32.2 | 16.0 | 27.5 | 27.5 | 12.5 | | | | 76.9 |

Pink salmon diets were used for spatial comparisons among regions because pink salmon occurred in all habitats and regions where juvenile salmon were encountered. When compared across habitats but within regions, pink salmon diets were more similar within Southeast Alaska (SE) than within Prince William Sound (PWS; Table 7). Comparisons between these two regions showed that diet consistency within a region was no greater than between regions. In fact, the highest diet overlap in these two regions was cross-regional, occurring between the nearshore habitats of SE and PWS.

DISCUSSION

Planktonic crustaceans were present in the diets of all four salmon species. Euphausiids were the primary food item for pink, sockeye, and chum salmon in most region/habitat strata. Hyperiid amphipods were the next most important crustacean, with decapod larvae, pteropods, and calanoid copepods being occasionally important in the diets. Fish, however, were the primary food item for coho salmon in nearly all cases and were often important to the other species, particularly in nearshore and shelf waters off Southeast Alaska and in shelf waters off Prince William Sound.

Despite the importance of euphausiids and fish in juvenile salmon diets, prey types still varied extensively by habitat and region, particularly for sockeye and chum salmon. Each one of the secondary food items, e.g., hyperiid amphipods, decapod larvae, etc., were occasionally very important, but it is unclear if these changes in importance were due to changes in prey availability, selection of particular prey within certain strata, or foraging competition.

We suspect that some combination of these three processes, particularly prey availability and prey selection, was found in our data. For example, prey selection in some form was apparent throughout our study area. Diet overlap rates between species were more often below 50% than above. In several strata, the diet overlap between coho salmon and other species even dropped below 10%. Many of these differences were due to the larger body size and distinct feeding behavior of coho salmon, who predominately fed on osmerid larvae, one of the largest prey items which typically ranged from 30 to 35 mm in length. Salmon, particularly coho salmon, are known both to feed opportunistically and to select prey on the basis of size, availability, and ease of capture (Ricker 1937; Brooks and Dodson 1965; Carlson 1976; Eggers 1978; Murphy et al. 1988). The piscivorous tendency of coho salmon may alleviate foraging competition with other species, lowering its diet overlap when large prey items are available. Size-selective foraging can also incur energetic advantages for the preda-

tor by increasing consumption for a given number of prey items.

Prey selection combined with prey availability may best explain the preponderance of gelatinous zooplankton in the chum diets collected from Southeast Alaska oceanic habitat, particularly given a selective preference for gelatinous taxa by chum salmon (Welch and Parsons 1993; Landingham et al. 1998). Alternatively, the incidence of gelatinous zooplankton could suggest competition between pink and chum salmon in this habitat (incurring prey switching); consumption of this energetically less favorable prey (Davis et al. 1998) has been shown to increase in areas of high pink salmon abundance (Tadokoro et al. 1996). There was little evidence, however, for a competitive feeding strategy – at least in some of the areas and habitats in our study. For instance, diet similarity of pink and chum salmon (the two most abundant species in the survey; Carlson et al. (1996) off Southeast Alaska was higher in the nearshore than the slope area, even though catch rates of these species were also highest nearshore.

Differences in prey among regions and habitats suggest the possibility that juvenile salmon feeding (particularly pink and chum salmon) was associated more with availability than with preference for specific organisms (e.g., LeBrasseur 1966). Pink salmon in Southeast Alaska consumed a much higher percentage of fish, one of the largest prey items, than pink salmon in Prince William Sound even though the Southeast Alaska pink salmon were smaller in size. Similarly, smaller chum salmon in nearshore waters of Southeast Alaska consumed a much higher percentage of fish than the larger chum salmon in shelf waters of the same region (see Carlson et al. (1996) for data on sizes of juvenile salmon by habitat type). We would have expected the opposite—that the larger fish would have an increased proportion of larger prey items—if feeding was predominately size-based; thus the data suggest the importance of prey availability in the diets of juvenile salmon migrating in the coastal GOA.

In summary, variations in foraging of juvenile salmon along the coastal waters of the northern Gulf of Alaska appear to be associated with both selection and availability of prey. The small proportion, 3%, of empty stomachs along with sustained high diet overlap indices in areas of high pink and chum salmon abundance suggest that the availability of prey resources does not appear to be a major limiting factor for production and growth of juvenile salmon examined in this study. A more definitive analysis of foraging strategy is beyond the scope of this study, however, as it would require joint analysis of stomach contents and prey availability (Landingham et al. 1998), the latter of which was not collected during the cruise. Further small-scale studies integrating data on feeding behavior,

prey size and abundance, growth, and energetics of juvenile salmon in coastal waters of the Gulf of Alaska would shed additional insight into salmon foraging tactics, particularly with respect to feeding and migration strategies and the growth potential of juvenile salmon during their first year at sea.

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