Food habits and marine survival of juvenile Chinook and coho salmon from marine waters of Southeast Alaska

LAURIE A. WEITKAMP¹,²,* AND MOLLY V. STURDEVANT³

¹National Marine Fisheries Service, Northwest Fisheries Science Center, Newport Research Station, 2032 SE OSU Dr., Newport, OR 97365, USA
²School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195, USA
³Auke Bay Laboratories, National Marine Fisheries Service, Alaska Fisheries Science Center, Ted Stevens Marine Research Institute, 17109 Pt. Lena Loop Rd., Juneau AK 99801, USA

ABSTRACT

Little is known about the food habits of juvenile Chinook (Oncorhynchus tshawytscha) and coho (Oncorhynchus kisutch) salmon in marine environments of Alaska, or whether their diets may have contributed to extremely high marine survival rates for coho salmon from Southeast Alaska and much more modest survival rates for Southeast Alaskan Chinook salmon. To address these issues, we documented the spatial and temporal variability of diets of both species collected from marine waters of Southeast Alaska during summers of 1997–2000. Food habits were similar: major prey items of both species included fishes, crab larvae, hyperiid amphipods, insects, and euphausiids. Multivariate analyses of diet composition indicated that the most distinct groups were formed at the smallest spatial and temporal scales (the haul), although groups also formed at larger scales, such as by month or habitat type. Our expectations for how food habits would influence survival were only partially supported. As predicted, Southeast Alaskan coho salmon had more prey in their stomachs overall [1.8% of body weight (BW)] and proportionally far fewer empty stomachs (0.7%) than either Alaskan Chinook (1.4% BW, 5.1% empty) or coho salmon from other regions. However, contrary to our expectations, coho salmon diets contained surprisingly few fish (49% by weight). Apparently, Alaskan coho salmon achieved extremely high marine survival rates despite a diet consisting largely of small, less energetically-efficient crustacean prey. Our results suggest that diet quantity (how much is eaten) rather than diet quality (what is eaten) is important to marine survival.

Key words: Chinook salmon, coho salmon, diets, marine ecology, marine survival, predator, prey, Southeast Alaska

INTRODUCTION

The ocean residence period for Pacific salmon (Oncorhynchus spp.) is largely viewed as a 'black box': mortality rates during this period are typically in excess of 95% (Bradford, 1995; Coronado and Hilborn, 1998) for reasons largely unknown. Most marine mortality is believed to occur during the first spring and summer in the ocean, when juvenile salmon are in coastal waters (Pearcy, 1992). During this period, ocean conditions are thought to regulate survival rates of salmon by controlling habitat characteristics such as temperature regimes, vertical mixing, prey availability, and competitor and predator abundances (Nickelson, 1986; Fisher and Pearcy, 1988; Hobday and Boehlert, 2001). For example, prey availability likely influences survival by influencing growth rates (Pearcy, 1992; Mortensen et al., 2000), which affects vulnerability to size-selective predation (Parker, 1971; Holtby et al., 1990; Moss et al., 2005) and determines acquisition of energy stores necessary to survive periods when prey availability is low (Beamish and Mahnken, 2001). However, how marine habitat characteristics as a whole translate into favorable or unfavorable survival is largely unknown. This poor understanding limits our ability to accurately predict how many salmon will survive the marine residence period and return to fresh water each year, frustrating managers of these culturally and commercially important species.

Little is known about the food habits or ecology of juvenile Chinook (Oncorhynchus tshawytscha) and coho (Oncorhynchus kisutch) salmon in marine habitats of Alaska because most studies in the region focus on the numerically dominant pink (Oncorhynchus gorbuscha) and chum (Oncorhynchus keta) salmon...
(Landingham et al., 1998; Boldt and Haldorson, 2002; Orsi et al., 2004; Moss et al., 2005). For example, the Southeast Alaska Coastal Monitoring (SECM) study documents the summer habitat use and early marine ecology of juvenile salmon in northern Southeast Alaska, with an emphasis on abundant pink and chum salmon (Orsi et al., 2000); the Chinook and coho salmon analyzed here for food habits were collected as part of this ongoing SECM study. Chinook and coho salmon exhibited species-specific habitat use within the study area. Chinook salmon were largely restricted to low-salinity inshore habitats at the eastern edge of the study area, whereas coho salmon catches were highest in the center of the study area in more saline strait habitats (Orsi et al., 2000). Juvenile Chinook and coho salmon also exhibited spatial segregation by origin: genetic analyses and recovered coded-wire tags indicated that salmon caught in strait and inshore habitats originated primarily from Southeast Alaska, whereas those caught in coastal waters originated south of Alaska; both groups included hatchery and wild fish (Orsi et al., 2000; Weitkamp, 2004; Morris et al., 2007). During the first 3 yr of the study (1997–99), the total catch of juvenile coho salmon (959 fish) was also approximately three times greater than that of Chinook salmon (278 fish), but was dwarfed by catches of juvenile pink (9357) and chum (7746) salmon (Orsi et al., 2000). The SECM study has also documented high variability in temperature, salinity, and zooplankton abundance and biomass associated with season and habitat type, with much less variation due to year (Orsi et al., 2000; Park et al., 2004; Sturdevant et al., 2004).

Chinook and coho salmon in Southeast Alaska provide a unique opportunity to explore the relationship between diet and marine survival because many life history traits are similar, suggesting they are susceptible to the same suite of factors that affect their survival. For example, in Southeast Alaska both types of salmon enter the ocean as yearling or 2-yr-old (coho) smolts, at approximately the same size [70–100 mm fork length (FL)] and time (April–June; Halupka et al., 2000). However, their relative survival rates are quite different: coho salmon marine survival rates (for both hatchery and wild populations) averaged 15.2% during ocean entry years 1990–2000, whereas equivalent Chinook salmon survival rates averaged just 0.9% (Shaull et al., 2003; NSRRAA, 2005; PSMFC, 2006). These coho salmon survival rates are also exceptionally high compared to coho salmon from other areas (Shaull et al., 2007). During our period of interest (ocean entry years 1997–2000), marine survival rates for coho and Chinook salmon from Southeast Alaska averaged 12.5% and 1.1%, respectively. These rates don’t account for the longer lifespan and therefore higher natural mortality of Chinook salmon, and taking these factors into account (following Coronado and Hilborn, 1998) approximately doubles the estimated Chinook salmon survival rates. However, the adjusted survival rates are still far lower than those for coho salmon (Weitkamp, 2004). Consequently, comparison of food habits between Chinook and coho salmon within Southeast Alaska and with conspecifics in other regions allows us to explore whether diets may contribute to large survival differences between Chinook and coho salmon from Southeast Alaska. A forthcoming paper considers other possible mechanisms (e.g., growth, predation, competition) that could be responsible for the exceptionally high coho marine survivals.

If food habits are indeed important for survival, we predict that Southeast Alaska coho salmon will have more prey in their stomachs and consume prey that will maximize their net energetic intake compared to Chinook salmon in Southeast Alaska or coho salmon from other regions with lower survival rates (Emlen, 1966; Werner and Hall, 1974; Stephens and Krebs, 1986). Presumably, these prey would consist of large, high-energy food items (e.g., large fish) rather than small, low-energy items (e.g., small crustaceans; Davis et al., 1998); consumption of large prey may also decrease both necessary foraging time and predation risk (Clark and Levy, 1988; Walters and Juanes, 1993). By contrast, diet differences between Chinook salmon from Southeast Alaska and other regions should be less pronounced. In this study, we document food habits of Chinook and coho salmon collected in Southeast Alaska during the summers of 1997–2000. Our results provide new insight into salmon marine ecology in a little-studied area, and provide a unique opportunity to explore the possible role of food habits in the success of juvenile salmon in marine environments.

**MATERIALS AND METHODS**

**Collection of fish**

Juvenile Chinook and coho salmon were collected in 1997–2000 in Southeast Alaska as part of the annual SECM program (see Orsi et al., 2000, 2007; Fisher et al., 2007). Juvenile salmon were sampled during daylight hours in late June, July, August, and September at 19 stations grouped into three habitat types (inshore, strait, and coastal) based on similarities in physical characteristics and fish community composition (Fig. 1; Weitkamp, 2004). Fishing was conducted...
with a Nordic 264 rope trawl (18 m deep × 24 m wide mouth opening) towed at 1.5 m s⁻¹ for 20 min to sample fish in surface waters. This is the same trawl being used by other researchers to collect juvenile Pacific salmon in marine waters from the Gulf of Alaska to central California (Fisher et al., 2007). All collected fish were identified, counted, and measured to the nearest 1 mm FL, and juvenile salmon were individually tagged, bagged, and immediately frozen for later laboratory analysis. Concurrent oceano-graphic and biological sampling at all stations included conductivity, temperature, and depth (CTD) profiles, sea surface temperature and salinity measurements, ambient light intensities, and vertical and oblique plankton net hauls. Information on zooplankton and ichthyoplankton collected by these nets was not available to compare with diet composition, although previous studies have shown little correspondence between zooplankton abundance and juvenile Chinook and coho salmon diets (Landingham et al., 1998; Schabetsberger et al., 2003).

Laboratory analysis

In the laboratory, thawed juvenile salmon were re-measured (FL, mm) and weighed (total weight, g), and a maximum of 10 fish from each haul were randomly selected for stomach content analysis. Stomachs of juvenile salmon were extracted and fixed in 10% buffered formalin, and later transferred to 70% ethanol. Prey items in the stomachs of each fish were identified to a general taxonomic category or to species where practical; all individuals of each prey type were weighed together to the nearest 0.001 g to provide prey biomass estimates. Intact prey were measured in their largest dimension [nearest mm, total length (TL)] for comparison with predator length. No attempt was made to correct for shrinkage of prey items or loss of weight due to preservation; such changes were expected to be small (< 5% change in length or weight) and not unduly influence the findings presented here.

Stomach analysis metrics

Three types of data were collected as part of the stomach content analysis: (i) gravimetric diet composition, (ii) stomach fullness, and (iii) prey size. These measures were compared by species, month, year, habitat type, and fish size to determine how diets varied within and between species in time and space, using the metrics and methods described below.

@ 2008 The Authors, Fish. Oceanogr., 17:5, 380–395.
Diet composition was based on percent biomass of eight prey categories: fish, euphausiids, crab larvae, hyperiid amphipods, insects, miscellaneous crustacea (includes non-hyperiid amphipods, shrimp and hermit crab larvae, barnacles, copepods, and unidentified crustacea), other invertebrates (includes cephalopods, pteropods, and polychaetes), and non-food items (largely wood, conifer needles, seeds, and tree bark). For each juvenile salmon, diet composition was calculated as the biomass of each type of prey divided by the total biomass of all identifiable prey; this proportion was expressed as a percent by multiplying by 100. No corrections for loss of stomach material during digestion or sampling at different times of the day were made. Differences in percent contribution by prey category between all coho and all Chinook were explored using a Mann–Whitney test for difference in medians (Zar, 1984).

Variation in diet composition was explored using three complementary multivariate techniques: non-metric multi-dimensional scaling (MDS), hierarchical cluster analysis, and analysis of similarities (ANOSIM); all methods were run using PRIMER-E software (Clarke and Green, 1988). These analyses were conducted on resemblance matrices constructed using Bray-Curtis similarities on percent composition by weight of the eight prey categories listed above. Diet composition data were square root-transformed to downgrade dominant prey categories and provide the clearest patterns. However, the analyses were fairly insensitive to the type of transformation used (i.e., similar patterns resulted from both untransformed and natural log-transformed data). Similarly, ANOSIM and cluster analyses conducted with more prey categories (e.g., splitting the ‘fish’ category into four separate categories) produced comparable results to those presented here.

Both MDS and cluster analysis were used to explore the relatedness of groups of fish based on their diets. Salmon were grouped by species, month, habitat type, and year, and the mean diet composition for each group was calculated across all fish and square root-transformed; groups were eliminated from the analysis if \( N < 5 \) fish. Hierarchical agglomerative clustering employed group average linkage to combine groups into increasingly large clusters. The similarity profile (SIMPROF) algorithm was used to determine significant clusters by permutation.

ANOSIM, a multivariate analog to analysis of variance (ANOVA), was employed to explore the influence of four factors of interest on diet composition: species, month, year, and habitat type. In these analyses, haul (the sampling unit) was nested within the factor of interest with individual fish nested within each haul. This analysis produces global \( R \) statistics for both the factor of interest and the nested factor (haul), which range from 0 (no separation of groups) to 1 (complete separation of groups). The analysis was conducted by considering all fish together (Chinook and coho salmon combined) and separated by species. Where significant differences were found using ANOSIM, we used the similarity percentages procedure (SIMPER) to identify both differences between groups and the prey categories responsible for the differences (Clarke, 1993).

The size of prey relative to the size of the predator was estimated by dividing the maximum TL of intact prey by the predator FL. This ratio was then compared by broad prey type (invertebrate or fish) and predator species (juvenile Chinook or coho salmon) and differences were evaluated using linear regression, analysis of covariance (ANCOVA) with predator length as the covariate, or two sample \( t \)-tests (Sokal and Rohlé, 1995). To meet the requirements of normality, prey and predator length data were log-transformed, and ratios were transformed with square roots.

Stomach fullness was expressed as prey biomass relative to predator body weight (% BW), as:

\[
\text{% BW} = 100 \times \frac{\sum p_{bi}}{(BW - \sum p_{bi})}
\]

where \( p_{bi} \) is the biomass of each prey category \( i \), and \( BW \) is the total wet weight of the juvenile Chinook or coho salmon predator; this calculation includes a prey category for unidentified material. Fullness was only calculated on individuals with accurate whole body weights (fins of some fish were broken when frozen, preventing weight measurements), resulting in fewer fish available for fullness estimates than for diet composition. Stomach fullness was not adjusted to account for possible allometric changes in maximum meal size (e.g., Dunbrack, 1988); such changes were expected to be minimal (Weitkamp, 2004). Fish with a fullness of \(< 0.05\% \) BW were considered ‘empty.’ Differences in stomach fullness between groups were evaluated using either a Mann–Whitney test or two-way ANOVA on log-transformed data, followed by a Bonferroni test for differences between means when statistically significant differences were detected (Zar, 1984). Empty cells limited our ability to test more than two factors simultaneously. Species differences in the frequencies of empty stomachs were evaluated using a chi-squared \( (\chi^2) \) test (Zar, 1984). We did not examine the relationship between stomach fullness and environmental and biological parameters in this study because linear regressions performed by
Weitkamp (2004) indicated they were either not statistically significant \((P > 0.05)\) or not particularly informative \((r^2 < 0.06)\).

**RESULTS**

Food habits were analyzed for 208 juvenile Chinook and 519 juvenile coho salmon collected from marine waters of Southeast Alaska during the summers of 1997–2000 (Tables 1 and 2). These samples represent 50% of the Chinook and coho salmon caught during this 4-yr period; most salmon not analyzed for food habits came from large hauls \((N > 10)\) that were represented by a subsample. The mean size of both species increased during this summer period: juvenile Chinook \((157 \text{ mm FL}, 63 \text{ g})\) and coho salmon \((156 \text{ mm FL}, 47 \text{ g})\) collected in June were considerably smaller than those collected in September \((\text{Chinook}: 238 \text{ mm FL}, 196 \text{ g}; \text{coho:} 291 \text{ mm FL}, 309 \text{ g})\).

**Diet composition**

Juvenile Chinook and coho salmon captured in marine waters of Southeast Alaska consumed a wide variety of prey. The most commonly identified prey items for both salmon species were larval and juvenile fishes, particularly capelin \((\text{Mallotus villosus})\), Pacific sand lance \((\text{Amphodytes hexapterus})\), flatfishes \((\text{Pleuronectiformes})\), and walleye pollock \((\text{Theragra chalcogramma})\), as well as unidentified larval fishes. No juvenile salmon of any species were identified from the stomachs. Common invertebrate prey included Cancer spp. crab larvae (primarily \(\text{Cancer oreonensis}\)), hyperiid amphipods (most commonly \(\text{Themisto spp.}\)), juvenile and adult euphausiids (mainly \(\text{Thysanoessa raschii}\) and \(\text{Thysanoessa spinifer}\)), and a variety of other larval \((\text{e.g., shrimp, hermit crabs})\) and adult \((\text{e.g., isopods, copepods, gammarid amphipods})\) crustaceans. Larval and adult insects and several other types of invertebrates, including molluscs \((\text{cephalopods, pteropods})\) and polychaetes, were also identified in the stomachs. Chinook salmon stomachs also frequently included non-food items that were rare in coho salmon stomachs, primarily terrestrial plant material. Overall, the diets of Chinook salmon contained more fish \((65\% \text{ of prey weight})\) and non-food items \((1.2\%\) \text{respectively; Mann–Whitney} \(Z \geq 2.6, \ P < 0.01\); Table 1. Juvenile Chinook Salmon Food Habits in Southeast Alaska, 1997–2000, expressed as mean percent weight for major prey categories by habitat type and month across years. The salmon attribute information provided includes the number of fish caught and analyzed for diet composition and fullness, mean stomach fullness, and mean salmon size.

<table>
<thead>
<tr>
<th>Prey category</th>
<th>Coastal</th>
<th>Strait</th>
<th>Inshore</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fishes</td>
<td>70.2</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Euphausiids</td>
<td>0.0</td>
<td>88.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Crab larvae</td>
<td>12.6</td>
<td>2.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Hyperiid amph.</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Insects</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Misc. crust.</td>
<td>17.2</td>
<td>10.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Other invert.</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Nonfood</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Chinook salmon attributes</th>
<th>Coastal</th>
<th>Strait</th>
<th>Inshore</th>
</tr>
</thead>
<tbody>
<tr>
<td>(N) caught</td>
<td>4</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>(N) diet comp.</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>(N) fullness</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>No. empty</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Mean FL</td>
<td>226</td>
<td>279</td>
<td>226</td>
</tr>
<tr>
<td>Mean wt.</td>
<td>154</td>
<td>279</td>
<td>154</td>
</tr>
<tr>
<td>Mean fullness*</td>
<td>0.90</td>
<td>0.97</td>
<td>0.95</td>
</tr>
<tr>
<td>Mean stom. wt.†</td>
<td>1.47</td>
<td>2.68</td>
<td>0.50</td>
</tr>
</tbody>
</table>

\(N\), sample size; FL, fork length \((\text{mm})\); Wt., weight \((\text{g})\).

*Fullness is expressed as \% of body weight.

†Mean stomach weight is the average weight of stomach contents \((\text{g})\).
Fig. 2). Conversely, coho salmon consumed more crab larvae (30% versus 8%) and hyperiid amphipods (4.5% versus 3.2%) than Chinook salmon did ($Z \geq 4.3, P < 0.01$).

Temporal and spatial variation in diet composition indicated several trends common to both species (Tables 1 and 2, Fig. 2). For example, insect consumption was high in early summer and in inshore habitats, crab larvae consumption was high in midsummer, and euphausiid consumption was high in September. We also noted species-specific trends, such as low fish and high crab larvae consumption by coho salmon in mid-summer and consistently high fish consumption by Chinook salmon regardless of month or habitat type (Fig. 2).

Results from the three complementary multivariate analyses used to explore variation in diet composition were generally in agreement, indicating high similarity in diets between species and years, with only limited separation by habitat type or month. For example, the six distinct clusters produced by the cluster analysis (labeled A–F in Fig. 3) each contained both Chinook and coho salmon, and generally represented diets in a particular month and/or habitat type, but not year. In the clearest examples, cluster E contained both species collected in inshore habitats in June [when insect consumption was high (39%) and fish consumption was modest (34%)], whereas cluster F contained fish from strait habitats in September 2000 (when euphausiids composed over 69% of diets). Diet composition was well represented by the MDS analysis (stress = 0.13) and showed separation between fish collected from inshore and strait habitats and (to a lesser degree) by month, but not by species or year (data not shown).

The ANOSIM test only indicated differences in diet composition by month, regardless of the fish considered (all salmon, coho only, or Chinook only; Table 3). However, in all ANOSIM comparisons, haul was statistically significant and formed better-separated groups than the factor of interest (i.e., haul $R$ exceeds factor $R$; Table 3). Accordingly, although diets consistently varied at large temporal (month) scales, the most distinct groups (with the highest within-group similarity) were formed by fish caught together in the same haul. The SIMPER procedure identified fish (mean contribution 31%), crab larvae (25%), and euphausiids (16%) as the prey categories that contributed the most to these

Table 2. Juvenile coho salmon food habits in Southeast Alaska, 1997–2000, expressed as mean percent weight for major prey categories by habitat type and month across years. The salmon attributes information provided includes the number of fish caught and analyzed for diet composition and fullness, mean stomach fullness, and mean salmon size.

<table>
<thead>
<tr>
<th>Prey category</th>
<th>Coastal</th>
<th>Strait</th>
<th>Inshore</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fishes</td>
<td>85.7</td>
<td>74.7</td>
<td>62.7</td>
</tr>
<tr>
<td>Euphausiids</td>
<td>0.0</td>
<td>1.7</td>
<td>7.1</td>
</tr>
<tr>
<td>Crab larvae</td>
<td>0.7</td>
<td>23.6</td>
<td>11.0</td>
</tr>
<tr>
<td>Hyperiid amph.</td>
<td>0.0</td>
<td>0.0</td>
<td>7.1</td>
</tr>
<tr>
<td>Insects</td>
<td>13.1</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Misc. crust.</td>
<td>0.5</td>
<td>0.0</td>
<td>3.0</td>
</tr>
<tr>
<td>Other invert.</td>
<td>0.0</td>
<td>0.0</td>
<td>9.1</td>
</tr>
<tr>
<td>Nonfood</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

Coho salmon attributes

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>N caught</td>
<td>12</td>
<td>30</td>
<td>39</td>
<td>24</td>
<td>467</td>
<td>431</td>
<td>132</td>
<td>46</td>
<td>20</td>
<td>10</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>N diet comp.</td>
<td>7</td>
<td>9</td>
<td>33</td>
<td>18</td>
<td>164</td>
<td>134</td>
<td>94</td>
<td>38</td>
<td>13</td>
<td>7</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>N fullness</td>
<td>6</td>
<td>9</td>
<td>27</td>
<td>13</td>
<td>151</td>
<td>120</td>
<td>82</td>
<td>36</td>
<td>12</td>
<td>7</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>No. empty</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Mean FL</td>
<td>193</td>
<td>205</td>
<td>271</td>
<td>301</td>
<td>156</td>
<td>206</td>
<td>232</td>
<td>286</td>
<td>135</td>
<td>186</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Mean wt.</td>
<td>92</td>
<td>103</td>
<td>272</td>
<td>348</td>
<td>47</td>
<td>104</td>
<td>151</td>
<td>294</td>
<td>28</td>
<td>79</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Mean fullness</td>
<td>2.71</td>
<td>1.86</td>
<td>1.34</td>
<td>1.63</td>
<td>2.15</td>
<td>1.54</td>
<td>1.51</td>
<td>1.83</td>
<td>2.02</td>
<td>1.02</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Mean stom. wt.</td>
<td>2.70</td>
<td>1.61</td>
<td>3.34</td>
<td>5.42</td>
<td>0.92</td>
<td>1.52</td>
<td>2.06</td>
<td>5.12</td>
<td>0.49</td>
<td>0.74</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

N, sample size; FL, fork length (mm); Wt., weight (g).

*Fullness is expressed as % of body weight.

†Mean stomach weight is the average weight of stomach contents (g).

ANOSIM differences based on month or haul. Taken together, these multivariate analyses indicate that diet composition was influenced to a greater degree by month and habitat type than by species or year; however, the greatest influence occurred at the smallest spatial and temporal scale: the haul.

Figure 2. Overall prey composition (percent weight) of juvenile Chinook (left) and coho salmon (right) diets during 1997–2000, showing mean diets for all salmon (top), and grouped by month (middle) and habitat type (bottom). Samples sizes are provided.

Prey length

The relationship between prey TL and juvenile salmon FL was examined for a subset of 160 Chinook and 359 coho salmon prey collected across all years, months, and habitats (Fig. 4). This prey–predator length ratio was strongly influenced by prey type and less so by predator species. For example, the mean ratio for invertebrate prey (0.06) was significantly lower than that of fish prey (0.19; ANCOVA, $F = 309$, $P < 0.01$) and was independent of both juvenile salmon species and salmon size (both species combined, $r^2 < 0.01$, $F = 0.1$, $P > 0.1$). By contrast, the size of fish prey increased with salmon size ($r^2 = 0.22$, $F = 115$, $P < 0.01$) and at similar rates for both species (ANCOVA, $F = 1.1$, $P > 0.1$), although the mean size of fish prey consumed by juvenile Chinook exceeded that of juvenile coho salmon (ANCOVA, $F = 8.2$, $P < 0.05$). Within fish prey species, a significantly higher prey–predator length ratio (mean = 0.65; two-sample $t = 11.6$, $P < 0.01$) was observed for quillfish (*Ptilichthys goodei*; Fig. 5), an extremely filiform species observed in the stomachs of several juvenile salmon. This prey–predator length ratio is the highest reported for juvenile Chinook and coho salmon in captive or natural settings (Weitkamp, 2005).

Stomach fullness

Stomach fullness (prey biomass as % BW) was estimated for a subset of 175 Chinook and 465 coho salmon caught in marine waters of Southeast Alaska (Tables 1 and 2). Stomach fullness was extremely variable, even for fish caught in the same haul (L. Weitkamp, unpublished data). Overall, stomach fullness for juvenile Chinook salmon (mean = 1.4%...
BW) was 22% lower than that of coho salmon (mean = 1.8% BW, Mann–Whitney Z = 3.6, P < 0.05; Fig. 5). Empty stomachs (< 0.05% BW) occurred almost 10 times more frequently in juvenile Chinook salmon (5.1% of stomachs) than in coho salmon (0.7%; χ² = 55.2, P < 0.05). Most empty Chinook salmon stomachs occurred in inshore habitats, whereas empty coho salmon stomachs were restricted to strait and coastal habitats (Tables 1 and 2).

Variability in stomach fullness examined by month, year, and habitat type indicated similar patterns for both Chinook and coho salmon. In comparisons that considered two of these factors at once, fullness differed significantly by month but not by year or habitat type (Fig. 5). In particular, stomach fullness was greatest in June for both Chinook (1.9% BW) and coho salmon (2.2% BW), whereas July and August values were significantly lower (0.9–1.1% BW for Chinook, 1.5% BW for coho; two-way ANOVA F ≥ 3.2, P < 0.05). With respect to habitat type, Chinook salmon fullness in inshore habitats was significantly greater in June than in other months (one-way ANOVA, F = 6.8, P < 0.05), but did not differ in strait habitats by month (F = 1.2, P > 0.10). Coho salmon fullness was greatest in June in both strait and inshore habitats (one-way ANOVA, F = 4.8, P < 0.05) but did not differ in coastal habitats (F = 1.5, P > 0.10).

**DISCUSSION**

**General patterns**

Food habits of over 700 juvenile Chinook and coho salmon collected from marine waters of northern Southeast Alaska were analyzed to document how diets varied between species, across time, and in space. Diets of the two juvenile salmon species were similar regardless of the time or place fish were collected. Analysis of diet composition indicated that diets were most similar at the finest spatial and temporal scale – fish caught together in the same haul – followed by month and habitat type. Healey (1991) also observed the highest similarity in diets of juvenile pink, chum, and sockeye (Oncorhynchus nerka) salmon at the finest temporal and spatial scales. These results suggest diet variability in both Chinook and coho salmon is largely driven by prey availability rather than prey choice, consistent with their characterization as opportunistic visual predators both searching for the same types of prey (Beacham, 1986; Brodeur, 1991).

Chinook salmon generally consumed more and slightly larger fish prey than coho salmon, whereas coho consumed more crustacean prey (e.g., crab larvae and hyperiid amphipods). Assuming that fish prey are more energy-dense than crustacean prey (e.g., Davis...
et al., 1998; Boldt and Haldorson, 2002) this results in higher quality (i.e., energy-dense) diets for Chinook salmon than for coho salmon. However, some studies indicate that in some situations crustacean prey may have relatively high-energy density, whereas fish prey may have relatively low-energy density (e.g., Pearcy and Fife, 1981; Robards et al., 1999; Mazur et al., 2007), and many studies show strong species, age, temporal, or spatial differences in energy content for both fish and invertebrate prey (e.g., Davis et al., 1998; Paul and Paul, 1998; Payne et al., 1999; Anthony et al., 2000). Clearly, without estimates of actual prey energy densities from the study area across the season, it is impossible to determine whether Chinook or coho diets were more energy-dense. However, because coho salmon had higher overall stomach fullness than Chinook salmon (Fig. 5), they had much greater energy content per stomach than Chinook salmon, even if their diets were less energy-dense. In the extreme case, Chinook salmon would need diets that contained nearly twice the energy density of coho diets in September to obtain equivalent total energy (Pope et al., 2001) because coho stomachs contained almost twice as much prey weight per stomach (5.4 g) as Chinook stomachs (2.9 g).

This comparison obviously ignores the energy required to find, catch, consume, and digest prey, which may far outweigh the benefits of consuming particular high-energy prey (e.g., Graeb et al., 2004; Moss and Beauchamp, 2007). However, the greater fullness and lower frequency of empty stomachs in coho salmon that we observed, along with documented consistently high rate of feeding over 24 h throughout the season (Sturdevant et al., 2002), suggest that coho salmon in Southeast Alaska receive much greater benefit from a higher cumulative daily ration than do Chinook salmon.

**Predation on subyearling salmon**

Yearling coho salmon are known to prey upon subyearling salmon (primarily pink, sockeye, and chum salmon) in fresh water and shortly after entering marine environments (Parker, 1971; Hargreaves and LeBrasseur, 1985; Ruggerone and Rogers, 1992). However, no juvenile salmon were found in the stomachs of the Chinook and coho salmon we examined.

---

**Figure 5.** Whisker plots of stomach fullness [expressed as percent body weight (% BW)] for juvenile Chinook (left column) and coho salmon (right column) for all individuals combined (top), and by month (middle), and habitat type (bottom), pooled across years 1997–2000. Black circles connected by dotted lines represent the mean, black horizontal lines indicate the median, boxes represent the 25th and 75th percentiles, and whiskers indicate the upper and lower adjacent values. Adjacent values are the smallest and largest values that are within 1.5 times the interquartile range (the area indicated by the box) of the 25th and 75th percentiles (Sokal and Rohlf, 1995). Sample sizes are indicated.
despite the high abundance of juvenile pink and chum salmon caught with them in strait habitats (Orsi et al., 2000). Landingham et al. (1998) also observed no predation on subyearling salmon by juvenile Chinook and coho salmon in the same area in the early 1980s, despite even greater consumption of fish prey during this time (99% by weight).

This lack of predation is likely due to the relatively large size of juvenile pink and chum salmon during this stage of ocean residency (95–115 mm FL in June, 178–200 mm FL in September; J. Orsi, NMFS, USA, unpublished data). We estimate pink and chum salmon were 60–70% of the length of juvenile Chinook and coho salmon, similar to the earlier observations (Jaenicke and Celewycz, 1994; Landingham et al., 1998). Juvenile coho salmon consume subyearling salmon that are usually no more than 45% of their length (Hargreaves and LeBrasseur, 1985; Pearson and Fritts, 1999), whereas the size of prey fish we documented was typically < 25% of the predator size (Fig. 4), except for the extremely elongate quillfish (Weitkamp, 2005). Accordingly, it appears that by this stage of ocean residency, juvenile pink and chum salmon are no longer vulnerable to predation by yearling salmon because of their rapid marine growth rates.

Regional comparison of food habits

Throughout their geographic range, dietary weight of juvenile Chinook and coho salmon prey during their first summer in the ocean is dominated by juvenile and larval fish, with lower quantities of euphausiids, hyperiid amphipods, crab larvae, and other planktonic invertebrates. The diets of juvenile Chinook and coho salmon documented here for Southeast Alaska consisted of the same types of organisms (if not species) identified by earlier studies from the same area (Landingham et al., 1998; Auburn and Ignell, 2000) and for elsewhere in the North Pacific Ocean (Healey, 1980a; Emmett et al., 1986; Gorbatenko and Chuchukalo, 1989; Brodeur and Paeary, 1990). However, the amount of fish reported in these diets was highly variable across locations and years (Table 4). For example, reported values range from 99% in Southeast Alaska/northern British Columbia in the 1980s (Landingham et al., 1998) to < 1% in the Okhotsk Sea and Gulf of Farallones (Gorbatenko and Chuchukalo, 1989; MacFarlane and Norton, 2002). Mean values reported here for Southeast Alaska (65% by weight for juvenile Chinook, 49% for coho) are intermediate compared with the range of reported values (Table 4).

Diet composition at any particular time reflects a trade-off between prey availability and feeding preference (Healey, 1980a). Accordingly, high variation in fish consumption likely results from variation in juvenile fish and/or invertebrate prey abundance, or preference differences. One of the largest obstacles to determining why fish consumption varies is effectively quantifying the abundances of larval and juvenile fishes (Schabetsberger et al., 2003). The correspondence between fish prey abundance based on Chinook and coho salmon stomach contents and plankton samples collected using standard zooplankton nets is typically quite low (Brodeur et al., 1992; Schabetsberger et al., 2003), especially in Southeast Alaska (< 17% similarity; Landingham et al., 1998). Consequently, the relative abundance of fish prey between and within the various study areas is not well documented. Clearly, better techniques to quantify fish prey abundances are needed.

It is unlikely that variation in fish consumption between studies is due to differences in diet preference. Laboratory feeding studies (e.g., Ivlev, 1961; Hart and Gill, 1992) and observations of juvenile salmon in marine environments (Suzuki and Fukuwaka, 1998) indicate that when hungry, fish eat a wider variety of prey, but as fish approach satiation they become highly selective and only eat preferred prey. Based on food habits of juvenile Chinook salmon in the Strait of Georgia, Healey (1980a) proposed that salmon preferred to eat fish but would eat other prey types when fish were not available. Juvenile Chinook and coho salmon from this study with the least amount of material in their stomachs consumed significantly less fish and more small invertebrates than individuals with higher stomach fullness (Weitkamp, 2004), consistent with Healey’s hypothesis.

Assuming that juvenile salmon diet preferences are constant, the large difference in the percent of fish in the diets reported here (≤ 65%) and the previous study (99%) from the same area in the 1980s (Landingham et al., 1998) suggests that juvenile and larval fish abundances in Southeast Alaska may have changed dramatically between the two time periods, although the species consumed were similar. The Gulf of Alaska ecosystem underwent a dramatic change in the late 1970s and early 1980s (Trites et al., 2007), including the near disappearance of capelin (the most common fish prey species in this study) after the mid-1980s (Anderson and Piatt, 1999; Hunt et al., 2002). Diets of salmon have been shown to respond to such ecosystem changes (Kaeriyama et al., 2004; Brodeur et al., 2007a), and the decline of fish in juvenile salmon diets between our study and the earlier one likely reflects a similar response to ecosystem changes. In addition, bioenergetic modeling of the study area (Icy Strait) during 2001 indicated that zooplankton were highly abundant despite large removals by abundant surface
predators (Orsi et al., 2004). It is unknown whether the current high productivity in Icy Strait is associated with a recent regime shift or with climate change (Park et al., 2004; Cooney, 2005; Litzow, 2006) but high availability of these small crustaceans (Park et al., 2004; Sturdevant et al., 2004; Fisher, 2006) likely explains their prominence in the Chinook and coho salmon diets reported here.

Many studies have also documented a shift toward greater fish consumption with increasing size of Chinook or coho salmon (Peterson et al., 1982; Beacham, 1986; Brodeur, 1991; Schabetsberger et al., 2003). No such shift was observed here: diets in September, when juvenile salmon were largest, did not typically contain more fish (Fig. 2), nor did larger salmon (independent of month caught) have more fish in their diets (L. Weitkamp, unpublished data). This lack of increasing piscivory at larger sizes again suggests that diets largely reflect prey availability rather than prey preferences.

Although the diet composition reported here is typical of other studies, the fullness estimates indicate that juvenile salmon from Southeast Alaska had high mean fullness and few empty stomachs compared to conspecifics elsewhere in the North Pacific Ocean. In studies that are directly comparable (those reporting arithmetic means of fullness based on percent body weight), fullness ranged from 0.6% to 2.4% BW (Table 4). By comparison, our fullness estimates (1.4% and 1.8% BW for Chinook and coho, respectively) were the second and third highest for Chinook and coho salmon, respectively. A comparison of the percent of empty stomachs among regions is even more striking (Table 4). The percent of empty Southeast Alaskan coho salmon stomachs (0.7%) was approximately an order of magnitude lower than found in any other study (5–15%), except the previous study from the same general area (0.6%; Landingham et al., 1998). The difference was less extreme but still notable for Chinook salmon in Southeast Alaska, which

Table 4. Comparison of reported percent weight of fish in diets, mean stomach fullness (% body weight) and percentage of empty stomachs for juvenile Chinook and coho salmon collected from marine habitats in the North Pacific Ocean. Chinook salmon smolt age (in years) is provided when reported.

<table>
<thead>
<tr>
<th>Location, years</th>
<th>Smolt age</th>
<th>N</th>
<th>% fish</th>
<th>Fullness</th>
<th>% empty</th>
<th>N</th>
<th>% fish</th>
<th>Fullness</th>
<th>% empty</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>SE Alaska, 1997–2000</td>
<td>1</td>
<td>206</td>
<td>65</td>
<td>1.4</td>
<td>5</td>
<td>519</td>
<td>49</td>
<td>1.8</td>
<td>1</td>
<td>This study</td>
</tr>
<tr>
<td>Coastal SE Alaska, 1996</td>
<td>–</td>
<td>0</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>70</td>
<td>69</td>
<td>–</td>
<td>–</td>
<td>Auburn and Iggel, 2000</td>
</tr>
<tr>
<td>Strait Georgia, BC, 1966</td>
<td>–</td>
<td>0</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>14</td>
<td>1</td>
<td>2.4</td>
<td>7</td>
<td>Barraclough and Fulton, 1968</td>
</tr>
<tr>
<td>Strait Georgia, BC, 1973–76</td>
<td>0 &amp; 1</td>
<td>203</td>
<td>46</td>
<td>0.9</td>
<td>–</td>
<td>534</td>
<td>32</td>
<td>1.0</td>
<td>–</td>
<td>Healey, 1980a,b</td>
</tr>
<tr>
<td>Strait Georgia, BC, 1997–98</td>
<td>–</td>
<td>0</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>2230</td>
<td>16*</td>
<td>0.9†</td>
<td>12</td>
<td>King and Beamish, 2000</td>
</tr>
<tr>
<td>WA/OR coast, 1980–84</td>
<td>1</td>
<td>840</td>
<td>86</td>
<td>–</td>
<td>6</td>
<td>1652</td>
<td>72</td>
<td>2.1</td>
<td>5</td>
<td>Fisher and Pearcy, 1988; Brodeur et al., 1992; Brodeur and Pearcy, 1990</td>
</tr>
<tr>
<td>WA/OR coast, 1980–85, 1998–2003</td>
<td>1</td>
<td>891</td>
<td>66</td>
<td>1.1</td>
<td>10</td>
<td>2845</td>
<td>71.3*</td>
<td>1.7</td>
<td>6</td>
<td>Schabetsberger et al., 2003; Brodeur et al., 2007a</td>
</tr>
<tr>
<td>Gulf of Farallones, 1997</td>
<td>0</td>
<td>23</td>
<td>50*</td>
<td>0.9</td>
<td>18</td>
<td>0</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>MacFarlane and Norton, 2002</td>
</tr>
<tr>
<td>Okhotsk Sea, 1985–86</td>
<td>1§</td>
<td>73</td>
<td>–</td>
<td>0.6</td>
<td>–</td>
<td>142</td>
<td>–</td>
<td>0.7</td>
<td>–</td>
<td>Gorbatenko and Chuchukalo, 1989</td>
</tr>
<tr>
<td>Kamchatka, 1974–75</td>
<td>1§</td>
<td>51</td>
<td>7</td>
<td>2.0</td>
<td>–</td>
<td>152</td>
<td>7</td>
<td>1.7</td>
<td>–</td>
<td>Karpenko, 1979</td>
</tr>
</tbody>
</table>

SE, Southeast; N, North; BC, British Columbia; WA, Washington; OR, Oregon; –, not reported.
*Estimated from graph.
†Assumes prey density of 1 g cm$^{-1}$.
§Chinook data from 2000 only.
Smolt age estimated from reported fish size.
had the second lowest rate of empty stomachs (Table 4). These comparisons between studies indicate that Southeast Alaskan habitats are quite productive not only for coho salmon, as anticipated, but also for Chinook salmon. Furthermore, comparisons of marine food habits of juvenile Pacific salmon along the West Coast of North America indicate high stomach fullness and few empty stomachs for all species of juvenile salmon (Chinook, coho, chum, pink, and sockeye) in Southeast Alaska compared to other regions (Brodeur et al., 2007b).

Food habits and marine survival

One objective of this study was to explore whether sufficient differences in food habits existed between Chinook and coho salmon in Southeast Alaska and other regions to explain the large differences in marine survival for the two species – exceptionally high survival for coho salmon and modest survival for Chinook salmon. Given their higher survival rates, we expected that coho salmon from Southeast Alaska would have more prey in their stomachs (higher fullness and few empty stomachs) and would have consumed prey types that optimized their net energetic intake, such as large fish (but certainly not small crustaceans), than either Chinook salmon from Southeast Alaska or coho salmon from other regions with lower marine survival rates. This expectation of more prey in coho salmon stomachs was corroborated. In fact, the most obvious diet difference between Chinook and coho salmon from Southeast Alaska was the quantity of food in their stomachs: Chinook stomach fullness was approximately 22% lower than that of coho salmon overall and Chinook salmon were nearly 10 times as likely to have an empty stomach as coho salmon. However, as discussed above, stomach fullness for both Chinook and coho salmon (as well as other Pacific salmon species; Brodeur et al., 2007b) from Southeast Alaska was high compared with that reported for other regions. By contrast, the percent of empty stomachs was extremely low for Alaskan coho salmon, the overwhelming majority (95%) of Chinook salmon had empty stomachs, and, although proportionally far fewer coho salmon had empty stomachs, the overwhelming majority (95%) of Chinook salmon had prey in their stomachs. If diet does, indeed, play a role in survival differences between Chinook and coho salmon, the differences are quite subtle, and may be difficult to detect when survival differences are less extreme.

ACKNOWLEDGEMENTS

We thank Auke Bay Laboratory personnel who participated in the research cruises and conducted initial laboratory analyses. We commend the command and crew of the NOAA ship John N. Cobb for their cooperation and performance throughout the cruises. We also thank the core members of the SECM team – Joe Orsi, Emily Fergusson, and Alex Wertheimer – for allowing L.W. to participate in cruises, study the Chinook and coho salmon collected, and share unpublished data. This manuscript was greatly improved by comments from C. Jordan, J. Zamon, J. Fisher, M. Mazur, and three anonymous reviewers.

REFERENCES


