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Authors: Osgood, Geoffrey J., Kennedy, Laura A., Holden, Jessica J., and Hertz, Eric

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ARTICLE

Historical Diets of Forage Fish and Juvenile Pacific Salmon in the Strait of Georgia, 1966–1968

Geoffrey J. Osgood,* Laura A. Kennedy, Jessica J. Holden, and Eric Hertz
Department of Biology, University of Victoria, Post Office Box 3020, Station CSC, Victoria, British Columbia V8W 3N5, Canada

Skip McKinnell
Salmoforsk International Environmental Consulting, 2280 Brighton Avenue, Victoria, British Columbia V8S 2G2, Canada

Francis Juanes
Department of Biology, University of Victoria, Post Office Box 3020, Station CSC, Victoria, British Columbia V8W 3N5, Canada

Abstract

The Strait of Georgia, British Columbia, provides important feeding and rearing habitat for forage fish, such as Pacific Herring *Clupea pallasii* and Eulachon *Thaleichthys pacificus* as well as all species of North American Pacific salmon *Oncorhynchus* spp. during their juvenile out-migration. In recent decades, this region has undergone large-scale physical and biological changes. Pacific Herring and Pacific salmon populations have experienced dramatic population fluctuations, while Eulachon have failed to recover from precipitous declines in the 1990s. Archival records of stomach content data from the 1960s, collected primarily from juvenile Pacific salmon, Pacific Herring, and Eulachon, allowed us to investigate diet variability in these species 60 years ago. Consistent with contemporary reports, we found that all species except Eulachon had generalist diets. In contrast to recent studies finding that Pacific Herring are the most important fish prey, Eulachon were the most frequently consumed fish, occurring in 28% of all piscivorous fish stomachs. This suggests that Pacific Herring are an important component of some Pacific salmon diets now, but only because lipid-rich Eulachon are no longer available. Chinook Salmon *O. tshawytscha* and Coho Salmon *O. kisutch* had the most similar diets, in part because of their greater piscivory. Species, length, and month and year of capture showed some explanatory power in differentiating the diets of the fish, although they explained less than 10% of total diet variation. Historical data, such as those presented here, offer a unique opportunity to investigate temporal differences in foraging ecology, informing management on how changes in the Strait of Georgia ecosystem may impact the trophic interactions between species.

Estuarine and coastal marine environments are important foraging and rearing grounds for the early marine life stages of many fish species (Shepard 1981; Thorpe 1994; Duffy et al. 2010). In these habitats, juvenile fish experience more rapid growth and higher mortality than they do at other life stages (Willette et al. 2001; Beamish et al. 2010; MacFarlane 2010; Reum et al. 2013). Mortality in the early marine period is generally size selective, with larger individuals surviving at higher rates than smaller

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*Corresponding author: gjosgood@uvic.ca
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individuals (Sogard 1997; Beamish and Mahnken 2001; Duffy and Beauchamp 2011; Tucker et al. 2016). As growth rates may be largely modulated by changes in prey quantity and quality (Beauchamp 2009), the feeding ecology of juvenile fish in estuarine environments has the potential to impact their survival and recruitment. Furthermore, the study of fish diet is an important first step in understanding how natural variability and anthropogenic-induced environmental changes can affect species (Brodeur 1990; Duffy et al. 2010). Diet can be an important indicator of the ocean conditions that fish are experiencing (Thayer et al. 2014) and has been used as a tool to forecast survival (Daly et al. 2009; Schweigert et al. 2013).

The Strait of Georgia is a critical coastal marine ecosystem on the West Coast of North America for many species of fish, including Pacific salmon *Oncorhynchus* spp., Pacific Herring *Clupea pallasii*, and historically, Eulachon *Thaleichthys pacificus* (Perry and Masson 2013; Beamish and McFarlane 2014). Juveniles of all seven species of Pacific salmon rear within the Strait of Georgia during their out-migration to the Pacific Ocean, and this area is especially important habitat for juvenile Chum Salmon *O. keta*, Chinook Salmon *O. tshawytscha*, Pink Salmon *O. gorbuscha*, Sockeye Salmon *O. nerka*, and Coho Salmon *O. kisutch*. These economically, culturally, and ecologically valuable species, however, have experienced large fluctuations in population size between 1960 and the present (Beamish et al. 1995, 2012). Addressing concerns about the declining catch, large-scale Chinook and Coho Salmon hatchery operations were initiated in the 1980s (Preikshot et al. 2013). The abundance of Pacific Herring in the Strait of Georgia has also experienced dramatic changes, with the population collapsing in the late 1960s and being rebuilt in the intervening years (DFO 2005; Schweigert et al. 2010). Additionally, a nearly synchronous coastwide decline in Eulachon populations occurred in the 1990s. The endangered Fraser River Eulachon population has failed to recover (COSEWIC 2011). In addition to fluctuations in fish populations, the physical environment of the Strait of Georgia has also experienced increased coastal development and decadal-scale increases in sea surface temperature (Gower 2002; Masson and Cummins 2007) as well as earlier peak flows and increased temperatures from the Fraser River (Morrison et al. 2002). The impacts of these physical and biological changes on the trophic interactions among fish species are largely unknown.

Juvenile Pacific salmon, Pacific Herring, and Eulachon are epipelagic foragers with generalist tendencies (Brodeur 1990; Haegele 1997). While there can be considerable diel (Benkwitt et al. 2009), spatial (Brodeur et al. 2007), and temporal (Schabetsberger et al. 2003) variability in the diets of individual species, the five main species of Pacific salmon can be broadly split into two groups based on diet similarities. Coho and Chinook Salmon tend to become mainly piscivorous early in their marine residence (Daly et al. 2009). Conversely, Sockeye, Pink, and Chum Salmon are generally zooplanktivorous in their early marine residence, though Chum Salmon may consume more gelatinous zooplankton than other species (Brodeur 1990; Welch and Parsons 1993; but see Johnson and Schindler 2008). Pacific Herring and Eulachon are also generally zooplanktivorous, with diets that are more similar to those of juvenile Sockeye, Pink, and Chum Salmon (Haegele 1997; Yang et al. 2006). The diet studies on juvenile salmon, however, tend to be from later in their marine residence, i.e., when they have moved offshore and into the range of larger trawling vessels. For example, the minimum mean fork lengths for fish captured by these vessels were 79 mm for Pink Salmon and 166 mm for Coho Salmon (Brodeur et al. 2007). Though the focus has shifted to the early marine period in recent years, a historical record predating the large-scale changes to the Strait of Georgia has been lacking, despite its hypothesized importance to the overall survival of some salmon species (Landingham et al. 1998).

From 1966 to 1968, over 4,000 fish stomachs were sampled from the Fraser River plume region within the Strait of Georgia during spring and early summer. While many species were caught during that study, the focus of the stomach content sampling was on Pacific salmon, Pacific Herring, and Eulachon. Five species of Pacific salmon were caught in high enough numbers to be analyzed: Chum, Chinook, Pink, Sockeye, and Coho Salmon. The data from these 3 years provide a unique opportunity to explore historic juvenile Pacific salmon diets and the feeding habits of sympatric forage fish such as Pacific Herring and Eulachon. Despite stemming from perhaps the most comprehensive ecological survey of Strait of Georgia surface waters, these data have rarely been analyzed and reported in the primary (Barraclough and Fulton 1967) or secondary (Phillips and Barraclough 1978) literature.

The first objective of the present study was to characterize the historical diets of the five species of Pacific salmon, Pacific Herring, and Eulachon. Based on contemporary findings, we hypothesized that these fish would be generalists early in their marine life with the exception of Eulachon, which may be more specialized (Yang et al. 2006). We expected the historical diets to differ in the abundance and identity of major fish prey given the changes to forage fish populations in recent years (Therriault et al. 2009); contemporary diets might show increased consumption of insects to compensate for the decreasing abundance of high-value fish prey (Duffy et al. 2010). Our second objective was to identify the major drivers of variation in diet. We hypothesized that fish diets would be influenced by species, size, month, and year. We expected greater similarity in the diets of Coho and Chinook Salmon than in those of other Pacific salmon species and that the diets of Pacific Herring and Eulachon would be more zooplanktivorous than those of Pacific salmon. We also expected fish to undergo ontogenetic diet shifts with increasing size. Temporally, we anticipated that fish diets would reflect seasonal changes in prey abundance (Mackas et al. 2013), while interannual differences in diet might be related to the odd–even cycle of juvenile Pink Salmon abundance (McKinnell and Reichardt 2012). Our objectives served to describe the historic diets of these fish species, an important step toward understanding how contemporary changes in the Strait of Georgia ecosystem may impact the trophic interactions between species.

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METHODS

Sampling.—Fish were caught by a surface trawl (6.1 m wide × 3 m high; total length including the cod end, 17.7 m) towed between two vessels with the headrope just breaking the surface at 208 sites in the Fraser River plume (Figure 1; Barraclough 1967). The mouth was held open with steel pipes that were weighted at the bottom. The tapering body was constructed of two sizes of knotless nylon mesh with stretched-mesh apertures of 5 and 2.5 cm. The cod end (1.8 m wide × 1.2 m high) was constructed of 1.3-cm stretched-mesh knotless nylon that tapered to a blunt end with a diameter of 76 cm. A 1.3-cm mesh trap located at the front of the cod end prevented fish from escaping. A standard Hensen plankton net (diameter, 73 cm; 0.35-mm mesh) was installed at the mouth of the cod end to capture smaller fish. At each station, the net was towed for 10 min at a speed of 3 knots (5.6 km/h), separated by a fixed distance of 45.7 m.

The fork lengths of major fish taxa were measured after we returned to the laboratory, but only subsamples were measured when the sample sizes were large (Barraclough 1967). For simplicity, we refer to captured fish as "juvenile" throughout, though we recognize that some of the smaller Pacific Herring and Eulachon would be more appropriately referred to as "larval." Though no records regarding preservation techniques were found, formalin was likely used given the techniques popular at the time. Prey were examined in the laboratory and identified to the lowest possible taxonomic group.

Data archaeology.—Although sampling was conducted in the Fraser River plume from 1966 to 1969 and in 1973, summary reports of this sampling were published in the Fisheries Research Board of Canada's Manuscript Series for only 1966 and 1967 (Barraclough 1967; Barraclough and Fulton 1967; Phillips and Barraclough 1978). When the Fisheries Research Board was disbanded in the early 1970s, the data were stored in an archive at the Pacific Biological Station, Nanaimo, British Columbia. Fortunately, the magnetic tapes were still readable in the late 1990s. The record formats had been lost, so the reconstruction began by decoding of the 80-byte "computer card images" by individuals that knew the coding and formatting practices that were typical during that era. Altogether, over 670,000 fish were caught in the Strait of Georgia during the five sampling years. The most abundant species in the records was Eulachon, mostly because of a few catches estimated to be up to 100,000 individuals that were made in a 10-min trawl. A total of 40,759 fish were measured for fork length and approximately 10% of those for body weight as well. Only the years with available stomach content data were used in this study (all of 1966 and 1967 and the early part of 1968).

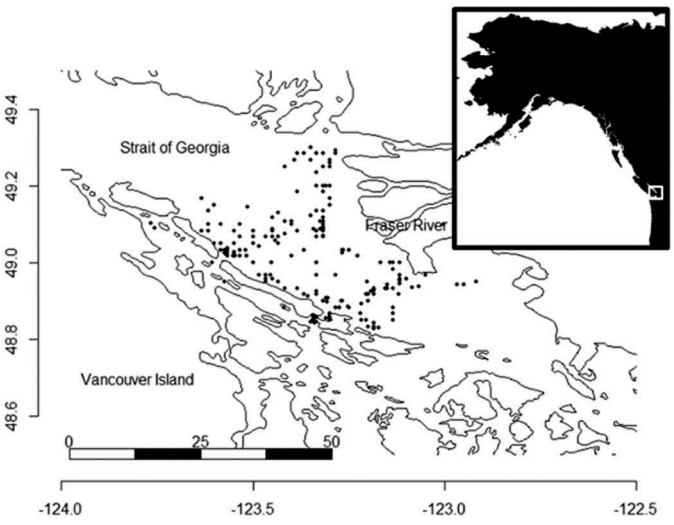


FIGURE 1. Map showing the sampling locations of the surface trawls (black dots) in the Strait of Georgia in which Pacific salmon, Pacific Herring, and Eulachon were collected in April–July 1966–1968.

Data analysis.—Mean fork length and the range in fork lengths were documented for each predator species. An ANOVA followed by a post hoc Tukey's honestly significantly different (HSD) test was used to test for differences in mean fork length among species, months, and years. Stomach contents were grouped into 16 taxonomic categories plus an "other" group consisting of cumaceans, isopods, pycnogonids, and mysids. The mean proportion of each prey class by its abundance in the diet of individual fish was calculated for qualitative comparisons among the different species. Within stomachs containing fish prey, the total proportion of each fish taxon was calculated as the fraction of the total number of fish prey consumed. The frequency of occurrence (FO) was calculated for each prey class as the number of stomachs containing that prey class divided by the total number of stomachs examined for that predator species. Individual fish prey species were also examined by calculating the FO within predator species containing fish prey. The FO for any important indicator species was also calculated by sampling month.

Given the potential influence of sampling month and year on the stomach contents of predators, an ANOSIM using Jaccard distance was run to compare diets between each of these two variables. An ANOSIM returns an R value ranging from –1 to +1, with +1 indicating a high degree of separation between the levels of a factor. To achieve comparable sample sizes, months were defined as April and May combined, June, and July. The results of these tests were used to determine which explanatory variables were important enough to include in further analyses. The Dufrêne–Legendre indicator (DLI) value of each prey group was subsequently calculated for the stomach contents of all predators by month in order to identify the important indicator species for each temporal group (Dufrêne and Legendre 1997). A threshold DLI value of 0.25 was suggested by Dufrêne and Legendre (1997) to define strong indicator species, but given the high variability and low DLI values found in this data set, strong indicator species were defined as those with a DLI value greater than 0.20 and a threshold of 0.15 defined indicator species of moderate importance (Espinoza et al. 2014).

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Jaccard similarity indices were calculated to compare prey composition among predator species diets. The Jaccard similarity index was first calculated and then averaged for predator diets by month. The index was then calculated a second time with all months pooled. The Jaccard index ranges from 0 (indicating similar compositions) to 1 (indicating dissimilar compositions). The DLI value of each prey group was also calculated for the stomach contents of predator species across months.

A multivariate regression tree (MRT) analysis was used to search for clustering in the prey item composition based on predator species and length as well as sampling month (De'ath 2002). This constrained clustering divides diets into two groups based on the single explanatory variable that best reduces the within-group sum of squares. This process is repeated on the resulting clusters to produce a tree based on recursive partitioning, with each split being based on the explanatory variable that best divides the clusters. The tree is then pruned via cross-validation relative error to determine the tree with best predicative ability. The most parsimonious tree within one standard error unit of the tree with the best predictive ability was chosen. Cross-validation relative error represents the ratio of variation unexplained by the tree to the total variation in the data and varies from 0 for perfect predictive trees to 1 for trees with poor predictors (De'ath 2002). The flexibility of this method allows for exploration of data with nonlinear patterns and interactions (De'ath 2002), and the method has been used to study forage fish diets (Garrido and Murta 2011). The DLI values of individual prey groups were estimated at the nodes of the tree to determine which items were most important in delineating clusters. The MRT was run on individual-level data since we were interested in using predator length, predator species, and month in explaining individual differences in diet. Because the particular trawl can also contribute to similarities in diet for fish caught together (Buckel et al. 1999), we performed two additional analyses to investigate the potential effects of nonindependence of the stomach samples. First, we repeated the MRT after pooling fish diets and averaging predator lengths by species within each trawl. This allowed us to investigate general clustering in the aggregate diets of fish caught together and how differences in these pooled diets are influenced by average predator size, month, and predator species among trawls. Second, we ran an MRT on the first four axes returned from an analysis of principal coordinates on the original, unpooled fish diets, in which the variation due to trawl was partialled out (removed). This analysis allowed us to explore individual-level variation in the diets of predators independent of trawl, but it is more difficult to interpret than the original MRT.

Finally, to investigate the variation in diets associated with predator species and predator length, a constrained analysis of principal coordinates (CAP) was run on the dissimilarity matrix of the Jaccard distances calculated between the stomach contents of individual predators, with prey groups coded as present/absent. The analysis was constrained by species and predator length after the effects of month and trawl had been partialled out.

All analyses were performed in the statistical language R. The ANOSIM and the CAP were run using the package *vegan* (Oksanen et al. 2014). The MRT was run using the package *mvpart* (De'ath 2014). The DLI analysis was done with the package *labdsv* (Roberts 2013).

RESULTS

Sample Sizes and Predator Fork Lengths

Pacific Herring was the most thoroughly sampled of the seven predator species, with a total of 511 stomachs being analyzed. Pacific Herring also exhibited the greatest size range (5–258 mm FL) (Table 1). The sample sizes for Coho Salmon and Chinook Salmon were much lower ($n = 60$ and 81 stomachs, respectively) than those of the other Pacific salmon species ($n > 200$) but these two species had the largest mean fork lengths of the Pacific salmon sampled (Table 1). Unlike Eulachon and Pacific Herring, all Pacific salmon sampled had fork lengths of 29 mm or more. There was large variability in both sample size and predator size among months for all seven species (Table 1). There were significant differences in mean fork length between species (ANOVA; $F = 73.645$, df = 6, 1,539, $P < 0.001$), months ($F = 55.768$, df = 2, 1,539, $P < 0.001$), and year ($F = 6.901$, df = 2, 1,539, $P < 0.001$). A post hoc Tukey's HSD test indicated that all species differed significantly in mean fork length ($P < 0.015$) with the exception of Pacific Herring and Chum Salmon ($P = 0.996$) and Chinook and Coho Salmon ($P = 0.12$).

Prey Groups and Accumulation Curves

Using all 21 broad taxonomic prey groups, our species accumulation curves for the stomach contents of Pink Salmon, Sockeye Salmon, Chum Salmon, and Pacific Herring reached asymptotes (defined as a slope of less than 0.5 between the last two points); those for Coho Salmon, Chinook Salmon, and Eulachon did not reach asymptotes (Figure 2).

Prey Abundance in Predator Diets

The diets of Sockeye, Chum, and Pink Salmon were primarily comprised of calanoid copepods, with average percentages ranging from 42% to 63% of stomach contents in the different species (Figure 3A). These species also fed on a diverse mixture of other prey, particularly insects, fish, amphipods, decapods, and larvaceans (Figure 3A). The diets of Coho Salmon and Chinook Salmon were primarily composed of insects, fish, and decapods, while calanoid copepods comprised smaller average percentages of individual stomach contents (11% and 20% in Coho Salmon and Chinook Salmon, respectively). Calanoid copepods made up the largest proportion of individual Pacific Herring and Eulachon stomach contents, accounting for 52% and 73%, respectively, on average. Cladocerans (99% of which were marine) provided the next largest contribution for these two predator species.

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TABLE 1. Number of stomachs sampled by month and year for each predator species as well as summary statistics for fork length and prey richness in the stomachs of fish sampled in the Fraser River plume, May–August 1966–1968. Prey richness is defined as the number of prey species groups and was calculated both as the total across all individuals sampled for a given predator species and the range of richness within individual stomachs for that species.

Variable	Month or statistic	Salmon species					Pacific Herring	Eulachon
		Sockeye	Chum	Pink	Coho	Chinook		
1966 stomachs	Apr	6	65	147	0	1	24	5
	Jun	13	4	7	4	33	48	22
	Jul	7	27	57	16	16	124	15
1967 stomachs	May	20	63	2	1	1	18	12
	Jun	30	47	3	21	12	93	31
	Jul	48	50	1	12	10	153	3
1968 stomachs	Apr	45	49	42	0	1	48	21
	May	34	9	5	6	7	11	0
Total stomachs		203	314	264	60	81	519	109
Fork length (mm)	Range	37–140	30–148	29–135	70–240	41–185	5–258	6–157
	Mean	84.5	61.7	51	126.8	110	63.4	33.4
	SD	19.7	28.8	27.2	34.2	28.9	55.6	32.2
Prey group richness	Total	14	18	14	14	12	18	9
	Range	1–8	1–8	1–7	1–6	1–5	1-–9	1–3

Frequency of Occurrence

Crustaceans were the most important prey assemblage by FO, with calanoid copepods, amphipods, decapods, and cladocerans occurring in 66, 23, 15, and 13% of all fish sampled, respectively (Table 2). Insects and fish were the next most important groups, occurring in 23% and 21% of all stomachs, respectively. Calanoid copepods had the highest FOs in all the predator species except Chinook and Coho Salmon, for which insects and fish were higher. Fish, insects, and decapods had high FOs in all the Pacific salmon species, as did euphausiids in Coho Salmon. The only prey group other than calanoid copepods that had a relatively high FO in Pacific Herring and Eulachon diets was cladocerans.

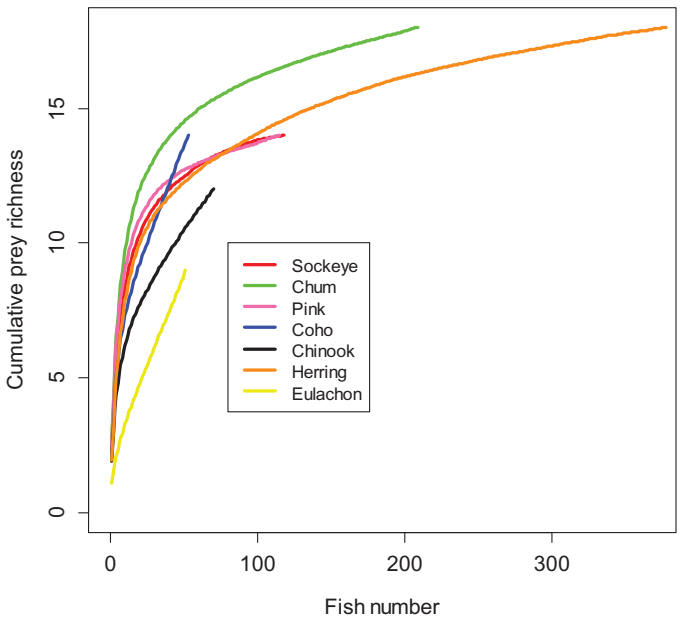


FIGURE 2. Species accumulation curves (based on the average of 10,000 permutations of fish number) for each of the seven predator species.

Fish Prey

A total of 21% of the stomachs analyzed contained fish prey (Table 2). The most important fish prey taxa by FO were Eulachon, Pacific Herring, Pacific Sand Lance, and rockfish (Table 3). In the stomachs containing fish, Eulachon were the most frequently found species in Pacific Herring (47%) and Sockeye Salmon (38%) (Table 3). Pacific Herring occurred most frequently in Chum Salmon (30%) and Pink Salmon (56%) stomachs. Pacific Sand Lances, on the other hand, were the most frequently occurring fish prey in Coho and Chinook Salmon (47% and 39%, respectively). Based on their abundance in predators' stomachs rather than their FO, Eulachon made up the largest proportion of total fish consumed by Chum Salmon (54%), Pink Salmon (47%), Chinook Salmon (55%), and Pacific Herring (70%) (Figure 3B). Eulachon, the most abundant fish caught in the trawls, also comprised a large proportion of fish prey in Sockeye Salmon stomachs (26%), though rockfish constituted the largest proportion for this predator (39%). Pacific Herring made up a substantial proportion of the fish prey in Chum (15%), Pink (45%), Coho (30%), and Chinook Salmon (13%) stomachs. Pacific Sand Lances, however, were the most consumed fish prey of Coho Salmon (45%).

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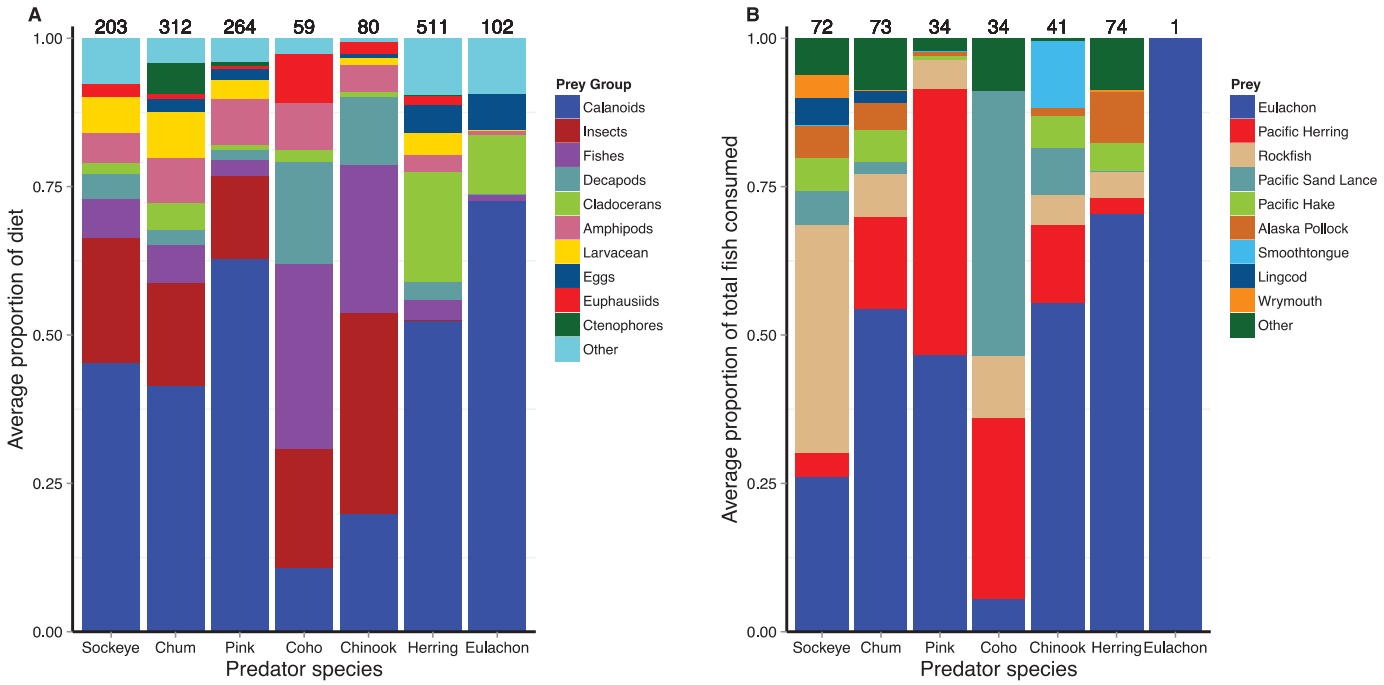


FIGURE 3. **(A)** Average proportion (by abundance) of each prey group in the stomachs of predator species and **(B)** average abundance of each fish prey species relative to the total number of fish prey consumed by predator species. The numbers at the tops of the bars are the sample sizes for the different predator species.

TABLE 2. Frequency of occurrence of prey groups in the stomachs of individual predator species and all predators pooled. The sample sizes for predators are indicated in parentheses. The "other" category includes cumaceans, isopods, pycnogonids, and mysids.

	Salmon species							
Prey group	Sockeye (203)	Chum (314)	Pink (264)	Coho (60)	Chinook (81)	Pacific Herring (519)	Eulachon (109)	Total (1,550)
Amphipods	0.369	0.338	0.269	0.317	0.136	0.137	0.009	0.228
Barnacles	0.025	0.035	0.049	0.017	0.000	0.071	0.064	0.048
Calanoids	0.640	0.650	0.807	0.217	0.272	0.701	0.734	0.662
Chaetognaths	0.074	0.057	0.076	0.033	0.000	0.002	0.000	0.036
Cladocerans	0.064	0.083	0.019	0.033	0.012	0.274	0.128	0.131
Ctenophores	0.000	0.083	0.011	0.000	0.000	0.002	0.000	0.019
Decapods	0.192	0.131	0.117	0.317	0.247	0.143	0.018	0.146
Eggs	0.005	0.045	0.042	0.033	0.012	0.073	0.064	0.048
Euphausiids	0.118	0.057	0.057	0.217	0.086	0.064	0.000	0.071
Fish	0.355	0.232	0.133	0.583	0.506	0.143	0.009	0.213
Insects	0.384	0.478	0.273	0.317	0.481	0.010	0.000	0.234
Larvaceans	0.172	0.143	0.049	0.000	0.012	0.067	0.009	0.084
Molluscs	0.044	0.010	0.000	0.017	0.025	0.094	0.009	0.042
Ostracods	0.138	0.073	0.038	0.017	0.000	0.114	0.018	0.079
Phytoplankton	0.000	0.006	0.000	0.000	0.000	0.023	0.055	0.013
Polychaetes	0.030	0.013	0.023	0.017	0.000	0.042	0.018	0.026
Other	0.015	0.022	0.004	0.033	0.025	0.015	0.018	0.016

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TABLE 3. Frequency of occurrence of fish prey species in the stomachs of individual predator species that contained fish and all predators pooled. The sample sizes for predators are indicated in parentheses.

Prey species	Salmon species					Pacific Herring (74)	Eulachon (1)	Total (331)
	Sockeye (72)	Chum (73)	Pink (35)	Coho (35)	Chinook (41)			
Eulachon	0.375	0.137	0.294	0.029	0.195	0.473	1.000	0.278
Pacific Hake *Merluccius productus*	0.069	0.082	0.029	0.000	0.024	0.257	0.000	0.097
Pacific Herring	0.083	0.301	0.559	0.206	0.317	0.162	0.000	0.239
Lingcod *Ophiodon elongatus*	0.056	0.041	0.000	0.000	0.000	0.000	0.000	0.021
Other	0.194	0.301	0.265	0.265	0.049	0.216	0.000	0.218
Walleye Pollock *Gadus chalcogrammus*	0.167	0.096	0.059	0.000	0.024	0.081	0.000	0.085
Rockfish *Sebastes* spp.	0.097	0.164	0.235	0.147	0.122	0.135	0.000	0.142
Pacific Sand Lance *Ammodytes hexapterus*	0.139	0.068	0.000	0.471	0.390	0.014	0.000	0.145
Northern Smoothtongue *Leuroglossus schmidti*	0.014	0.000	0.029	0.000	0.049	0.027	0.000	0.018
Dwarf Wrymouth *Cryptacanthodes aleutensis*	0.125	0.014	0.000	0.000	0.000	0.014	0.000	0.033

Month and Year Effects

An ANOSIM revealed high similarity ($R = –0.0055$, $P = 0.86$) in stomach contents among years but less similarity across months ($R = 0.18$, $P = 0.001$); thus years were combined for analysis. Calanoid copepods, fish, and insects all had relatively high FOs (>0.15) over all of the months sampled. The FO of calanoid copepods, however, declined from 0.91 in April and May to 0.42 in July. Cladocerans and decapods had higher FOs in June and July than in April and May (see Table S.1 in the supplement to this article). A DLI analysis revealed that calanoid copepods were the only strong indicator species differentiating stomachs sampled in different months (DLI value = 0.44), with cladocerans being a moderately important indicator for diets in June (0.14) and decapod crustaceans for diets in July (0.15).

Predator Species Effects: Jaccard Dissimilarity

In terms of monthly averages, the similarity of diets was high among all species except Eulachon (Table 4; for a breakdown by month, see Table S.2). For example, Chum, Pink, and Sockeye Salmon had Jaccard similarity indices ranging from 0.68 to 0.82. The diets of Chinook and Coho Salmon were also similar to each other (0.72). Pacific Herring diets were most similar to those of Chum, Pink, and Sockeye Salmon (0.62–0.68). When the Jaccard similarity indices were calculated using data pooled over all months, however, the diets of all species became highly similar (Table 4). The analysis comparing pooled predator species' diets resulted in no important indicator prey species.

Multivariate Regression Tree Analysis

The most parsimonious tree had five terminal leaves and explained only 13.1% of the variation in diets. The cross-validated relative error was 0.877, indicating that predator species, predator length, and month were generally poor predicators of diet variability (Figure 4). Predator length (<36.5 mm or ≥36.5 mm) was the primary variable separating the diets of individual fish, explaining 6.20% of the diet variation. Approximately 60% of Pacific Herring and Pink Salmon and 76% of Eulachon stomachs were classified into the smaller length class. Of the other Pacific salmon, only 16% of Chum Salmon were sorted into this group. The split, therefore, generally separated the smaller Pink Salmon, Pacific Herring, and Eulachon from the larger Sockeye, Chum, Coho, and Chinook Salmon. Month then separated both predator length clusters, explaining 1.64% of the total variation in the stomach contents of the smaller fish and 3.08% of that of the larger fish. For the smaller fish, stomach contents in April and May clustered separately from those observed in June and July. Conversely, for larger fish, July diets were clustered separately from those of fish caught in April, May, and June. Within the cluster of larger fish caught in July, a final split (explaining 2.22% of diet variation), separated the five Pacific salmon species from Pacific Herring and Eulachon.

Although all prey species except the "other" category were statistically significant indicators for the terminal leaves of the MRT ($P < 0.05$ from a permutation test with 10,000 permutations), all DLI values for these leaves were relatively small, ranging from only 0.051 to 0.29. The strong indicator prey species (DLI values ≥0.2) delineating predator diets within the five terminal leaves were calanoid copepods, insects, and decapods. Cladocerans, fish, and ostracods were also relatively important indicator species, with DLI values ≥0.15. Calanoid copepods were the primary indicator species for the smaller predators, with an indicator value of 0.45, while fish prey (DLI = 0.33) were the primary indicator for the cluster comprising larger predators. Amphipods (DLI = 0.28), decapods (0.21), and insects (0.28) were also important indicators of this larger predator group. Within both the small-

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TABLE 4. Jaccard similarity indices between the stomach contents of predator species calculated (1) by month (April–May, June, and July) and then averaged (monthly average) and (2) for all months combined (pooled over all months).

Type of average	Species	Chum Salmon	Pink Salmon	Sockeye Salmon	Chinook Salmon	Coho Salmon	Pacific Herring
Monthly	Pink Salmon	0.68					
	Sockeye Salmon	0.82	0.73				
	Chinook Salmon	0.41	0.39	0.45			
	Coho Salmon	0.52	0.51	0.53	0.72		
	Pacific Herring	0.68	0.64	0.62	0.38	0.49	
	Eulachon	0.29	0.32	0.28	0.18	0.23	0.41
Pooled over all months	Pink Salmon	0.79					
	Sockeye Salmon	0.79	0.88				
	Chinook Salmon	0.55	0.59	0.69			
	Coho Salmon	0.79	0.76	0.88	0.59		
	Pacific Herring	0.95	0.75	0.75	0.52	0.75	
	Eulachon	0.65	0.53	0.61	0.44	0.61	0.70

(0.56) and large-predator (0.54) clusters, calanoid copepods served as an indicator of diets observed earlier in the spring. Cladocerans, on the other hand, were indicative of summer (June and July) diets for the smaller predators (0.34), while decapod prey were indicators for July diets within the larger-predator size cluster (0.28). Within this final cluster, comprised of larger predators that were caught in July, insects (0.47) and fish (0.25) were the primary indicator species of Pacific salmon diets, while decapods (0.27) and calanoid copepods (0.40) were the primary indicators of Pacific Herring and Eulachon diets. Ostracods (0.25) and amphipods (0.22) were also indicative of Pacific Herring and Eulachon diets in July (Figure 4).

The results were qualitatively similar and explained a similar percentage of the variation in diets (19%) when the data were analyzed with trawl taken into consideration (Figure S.1). The relative importance of predator species increased (explaining 6.9% of the total variation) and the importance of month declined (explaining 4.2% of the variation), allowing for some species-specific diet shifts according to season to be seen. The overall patterns and conclusions remain unchanged, as length still determined the first split and the same species were determined to be indicators (Figure S.1). When we used the same explanatory variables to run an MRT on the first four axes obtained from an analysis of principal coordinates (in which the variation attributable to trawl was partialled out), predator diets also separated in a similar way based on predator species and length (Figure S.2). The diets of Pacific Herring and Eulachon were still distinguished from those of Pacific salmon, although length became more important than month in separating them.

Constrained Analysis of Principal Coordinates

Constrained variation comprised only 9.72% of the total variation, while month and trawl (which were partialled out) explained 31.78%. The variance explained by predator species and predator length (pseudo-F = 31.683, df = 7, 1,335, P = 0.001) was significant based on a permutation test with 1,000 permutations.

The first canonical axis explained 73% of the constrained variation but only 10.5% of the total variation in predator diets. This axis, in particular, separated Pacific Herring and Eulachon, which had mean negative scores, from the Pacific salmon species, which had mean positive scores (Figure 5A). Prey that loaded positively on this axis were fish, decapods, amphipods, ctenophores, insects, chaetognaths, and euphausiids. Calanoid copepods, cladocerans, molluscs, eggs, and barnacles loaded negatively on this axis (Figure 5B).

The second canonical axis explained 19% of the constrained variation, or 2.7% of the total variation. This axis partly separated Chum, Pink, and Sockeye Salmon, which had mean positive scores, from the larger Coho and Chinook Salmon, which had mean negative scores. Insects loaded strongly and positively onto the second axis, along with cladocerans and larvaceans. Fish, decapods, euphausiids, amphipods, calanoid copepods, and ostracods loaded negatively on this axis (Figure 5B). Phytoplankton loaded somewhat strongly onto both axes but were rare in the diets. Predator size was associated with both axes: larger fish were associated with fish, decapod, amphipod, and euphausiid prey, which loaded positively on the first canonical axis and negatively on the second.

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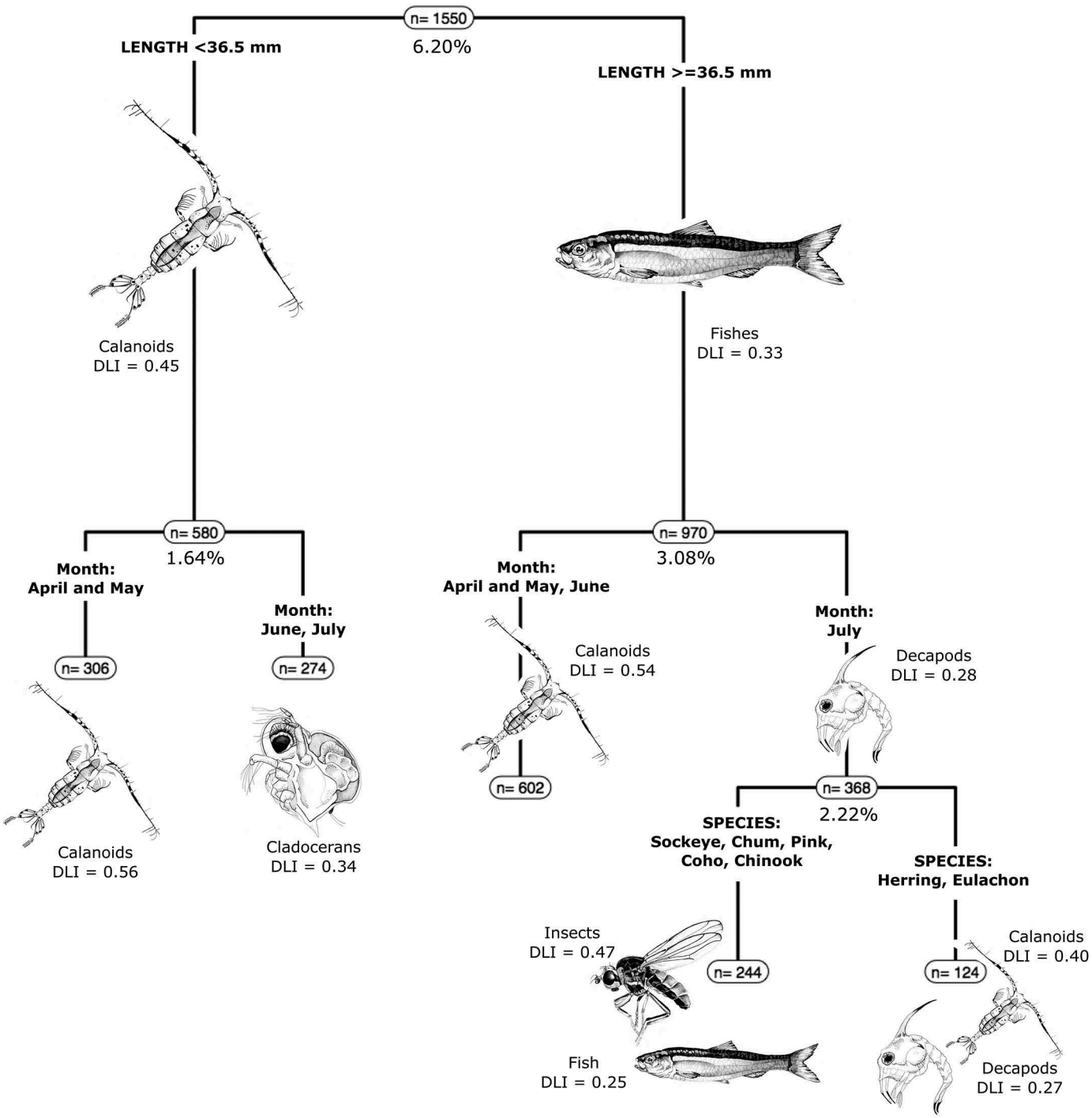


FIGURE 4. Multivariate regression tree showing the discriminating explanatory variables and important indicator species (DLI > 0.15) in the stomach contents of juvenile Pacific salmon, Pacific Herring, and Eulachon. The percentages at the nodes are the percentages of the total variation explained by the different splits. Sample sizes (*n*) are also given for the different groups produced by the splits. Only the one or two most important indicator species are illustrated here. See text for more details. (Images courtesy of J. Holden.)

DISCUSSION

This study provides the first detailed analysis of Pacific salmon and forage fish feeding ecology in the Strait of Georgia from an era before major changes occurred, including large-scale hatchery release programs (Beamish et al. 1997), shifting climate–ocean conditions (McFarlane et al. 2000), declines in secondary production (Mackas et al. 2013), and the collapse of Eulachon populations (COSEWIC 2011).

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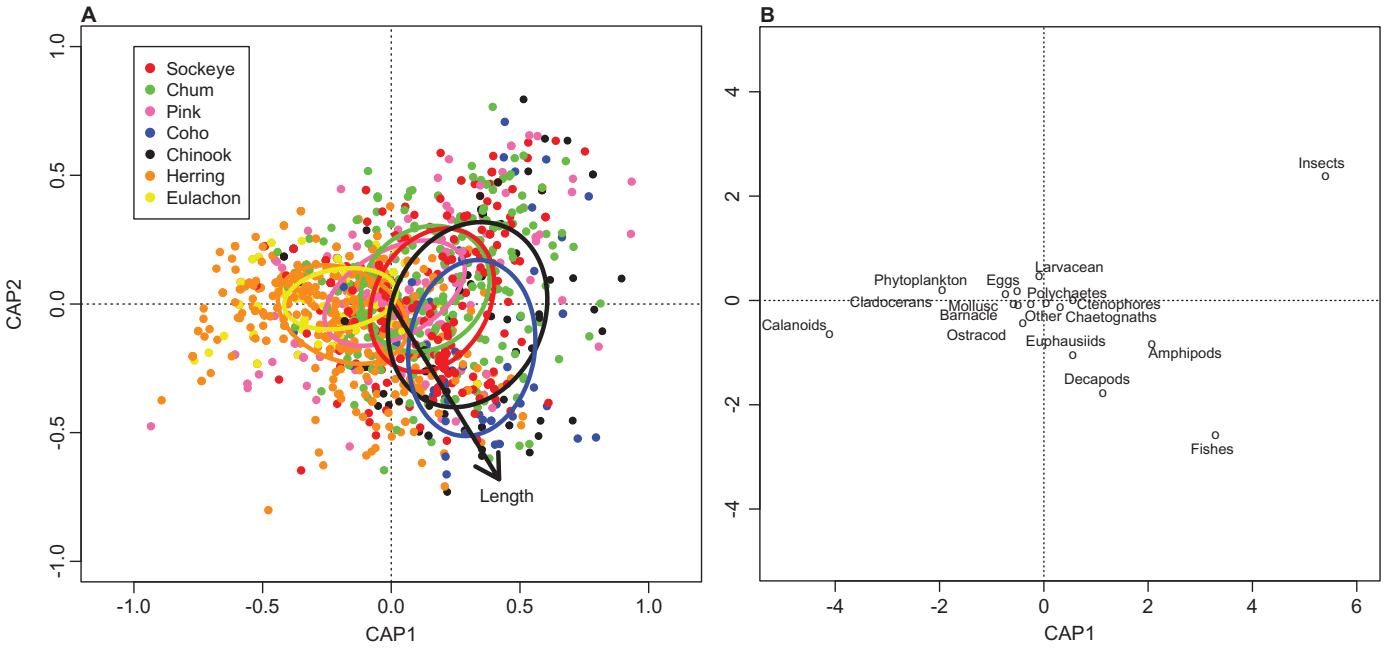


FIGURE 5. Results of the constrained analysis of principal coordinates (CAP) of the Bray–Curtis distance between fish diets scored as the presence/absence of prey using species, fork length, and month of capture as explanatory variables and partialling out the variation due to year and trawl: **(A)** scaling = 1 biplot of the individual scores of the predator species on the first two axes of the CAP with 95% confidence ellipses calculated from standard deviations of their CAP scores, with the tip of the arrowhead indicating the biplot score for the constraining variable length; **(B)** scaling = 2 biplot showing the prey species scores of the CAP on the first two axes.

Overall, the feeding habits of the five sympatric species of Pacific salmon, Pacific Herring, and Eulachon were dynamic, varying with predator species, predator size, and sampling month. While these variables had a statistically detectable influence, all generally failed to explain more than 10% of the variation in diets. The remaining variation may be due to sampling design, other biological effects, and individual-level variation reflective of the very generalist diets of these species. Environmental drivers such as the small-scale patchiness of prey likely contributed additional variation, especially since trawl explained 32% of the variation in the CAP. Individual-level variation in foraging between conspecifics could also be a source of variation, as has been reported in other fish diet studies (Araújo et al. 2007, 2011).

Our results indicate that the five species of Pacific salmon in our study exhibited a large degree of generalism and overlap in their diets during early marine residence in April–July 1966–1968. Larger Chum Salmon and Pacific Herring in particular consumed a diverse mixture of species. It is possible, however, that these species were partitioning resources at a finer scale than we were able to detect with our relatively course taxonomic resolution. Eulachon, on the other hand, had a more specialized diet.

Due to the small sample sizes for some species, we were unable to consider interactions between species, size, and month. The sample sizes, especially those for Chinook and Coho Salmon, may not have been sufficient to fully describe the diets of such opportunistic species. Despite the low sample sizes, however, the diets of these two salmonids were consistent with expectations.

Predator Species and Length

The MRT and CAP both identified the diets of the five Pacific salmon species studied as being somewhat distinct from those of Pacific Herring and Eulachon. The greatest similarity occurred between the diets of Chum, Pink, and Sockeye Salmon (Table 4), an overlap frequently reported in the literature (Auburn and Ignell 2000; Kaeriyama et al. 2004; Zavolokin and Efimkin 2007). Such overlap suggests the potential for competition under food-limited conditions, such as might occur owing to a mismatch in timing between out-migrating Pacific salmon and the spring phytoplankton bloom (Chittenden et al. 2010). Year, however, did not have much of an effect in the ANOSIM despite fork length differences between years and the inclusion of 2 years of high (1966 and 1968) and 1 year of low (1967) juvenile Pink Salmon abundance. This suggests that a higher abundance of juvenile Pink Salmon did not significantly alter the diets of the other juvenile fish that we studied. The diets of Chum, Pink, and Sockeye Salmon were primarily comprised of calanoid copepods (Figure 3A; Table 2) and thus could be particularly susceptible to declining abundances of calanoid copepods in the Strait of Georgia (Mackas et al.

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2013). Chum Salmon, however, consumed higher frequencies of ctenophores than did the other Pacific salmon. The importance of gelatinous zooplankton in the diet of Chum Salmon has been noted previously in adults across different regions (Brodeur 1990; Welch and Parsons 1993), but not early in marine life. The ability to exploit this food source may become increasingly advantageous as anthropogenic gelatinous zooplankton (e.g., *Aurelia aurita*) blooms become more prominent (Purcell et al. 2007).

Despite both species' failing to reach an asymptote in the accumulation curves (Figure 2), we observed high similarity between Chinook Salmon and Coho Salmon diets (Table 4), a pairing common in other studies (Kaeriyama et al. 2004; Bollens et al. 2010; Cook and Sturdevant 2013). Chinook Salmon diets, however, contained somewhat more insects and calanoid copepods than those of Coho Salmon. Based on a comparison of contemporary diets in Puget Sound with those in the 1970s, Duffy et al. (2010) also identified insects as key, high-quality prey for Chinook Salmon, speculating that insects have become increasingly important as the prevalence of fish prey has decreased. Our results indicate that both prey types played an important role in the Strait of Georgia as far back as the 1960s.

The diets of Pacific Herring and Eulachon overlapped with those of the Pacific salmon species but were still distinct. The first axis of the CAP, for instance, divided most of the Pacific salmon from the Pacific Herring and Eulachon, largely based on the lack of insects in the stomachs of the latter two species (Figure 5A, B). While similar to the diets of Sockeye, Chum, and Pink Salmon, Pacific Herring diets were more distinct from those of Coho and Chinook Salmon (Table 4). Eulachon had the most unique diet among the predator taxa examined (although our diet characterization may have been incomplete: see Figure 2). While the MRT and CAP tended to group Eulachon with Pacific Herring, a preference for primarily calanoid copepods and cladocerans resulted in its specialized diet. Yang et al. (2006) also identified Eulachon as a specialist in the Gulf of Alaska. Such specialization, combined with recent declines in copepod abundance within the Strait of Georgia (Mackas et al. 2013), may have contributed to Eulachon population declines and the poor recovery of this species (Clavel et al. 2011; Gallagher et al. 2015).

Predator size also distinguished diets. The second axis of the CAP separated the insectivorous diets of smaller Pacific salmon from the piscivorous diets of larger Pacific salmon. This separation likely reflects both ontogenetic diet shifts as well as diet differences among species, particularly between the larger Chinook and Coho Salmon and the smaller Chum, Pink, and Sockeye Salmon. The MRT identified predator length as the most important variable distinguishing the diets of the predators, dividing them into clusters of smaller and larger fish (node at 36.5 mm FL). This node essentially divides the Pacific Herring, Eulachon, and smaller Pink Salmon from the larger Sockeye, Chum, Coho, and Chinook Salmon. Cladocerans, molluscs, and eggs distinguish Pacific Herring and Eulachon diets from those of the Pacific salmon, although some of the differences may have arisen from the higher proportion of small Pacific Herring and Eulachon in the data set compared with the juvenile Pacific salmon. Consistent with this hypothesis, cladocerans, molluscs, and eggs were not important indicator species for the Pacific Herring and Eulachon cluster within that of the larger predators identified by the MRT.

The wider range of predator sizes among the Pacific Herring that we sampled, and the consequently high variability in their stomach contents, likely facilitated both the similarities and differences noted between Pacific Herring and the other six predator species in our analyses. The lower end of the size range of Pacific Herring, for instance, overlapped with that of Eulachon, while larger Pacific Herring were more comparable in length to the larger Pacific salmon. When smaller (<30-mm FL) Pacific Herring and Eulachon were removed, the conclusions from the CAP did not change substantially (Figure S.3). The MRT did change somewhat, with different variables being responsible for the splits, but similar species groupings were observed overall (Figure S.4). The lack of a strong influence by the small fish on the CAP, in combination with the similarity in the resulting clusters obtained from both MRTs, indicates that the differences observed were not solely related to differences in size.

Sampling Month

The Strait of Georgia is characterized by strong seasonality in primary productivity, particularly in the late winter and early summer (Mackas et al. 2013). During early summer, large, nutritious calanoid copepods play an important role in the diets of juvenile Pacific salmon (Bi et al. 2011). Consistent with these seasonal productivity differences, we found significant differences in stomach contents between sampling months. Based on their FO, calanoid copepods were more common in spring than in summer diets, while cladocerans and decapods had greater FOs later in the summer. Furthermore, sampling month defined a node within both size clusters of the MRT. Not surprisingly, calanoid copepods were indicative of diets observed earlier in the spring for both size clusters. Seasonal changes in diet have been reported in many other studies (Brodeur et al. 2007; Duffy et al. 2010) and suggest either ontogenetic shifts associated with changes in size and morphology or simply shifts in prey abundance (Nunn et al. 2012). Given the generalist diet observed in the Pacific salmon from our study and the dynamics of the Strait of Georgia, the diet shifts observed here were likely a result of changes in prey availability. For example, our data set includes high numbers of calanoid copepods during the spring, which coincides with the peak abundance of calanoid copepods in the Strait of Georgia in that season (El-Sabaawi et al. 2010). *Neocalanus plumchrus*, the dominant calanoid copepod in this region (El-Sabaawi et al. 2010), occurs at high densities in the Fraser River plume during the spring before completing its life cycle and migrating into deeper waters in late May and June

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(Mackas et al. 2013), presumably beyond the prey field of epipelagic-foraging juvenile fish. Still, ontogenetic shifts may be partially responsible for the changes in diet, given the length differences that we observed in predator species among months.

Fish Prey

This data set provides a unique record of fish prey in Pacific salmon, Pacific Herring, and Eulachon diets prior to recent declines in Eulachon populations (COSEWIC 2011) and the rebuilding of Pacific Herring stocks (DFO 2005). The role of Pacific Herring and Eulachon in the diets of predators was of particular interest because they were the most important prey in this study. Historical records showing the high prevalence of Eulachon in Pacific salmon diets are noteworthy because Eulachon are higher in lipids than are other common salmon prey (Anthony et al. 2000). The high consumption of Eulachon by the Pacific salmon in our data set—in contrast to their low importance in contemporary studies (Duffy et al. 2010; Beamish et al. 2012)—suggests that the loss of this energy-rich food has caused shifts in the feeding ecology of Pacific salmon that may have implications for their growth and survival rates.

A particularly important limitation to our study is that predator size, species, and month of capture were all confounded with one another, which makes disentangling the effects of each factor difficult. The differences in species and month, for example, could correspond to differences in length, given that nearly all predator species differed significantly in mean fork length, as did fish sampled in the early spring from those sampled in the summer. Furthermore, the small sample sizes for Chinook Salmon, Eulachon, and Coho Salmon and their failure to reach an asymptote in the species accumulation curves suggest that the sampling was not sufficient to fully describe the diets of these species.

Another caveat to consider in interpreting our results pertains to our metric for quantifying diet. A variety of metrics, each with its own advantages and drawbacks, have been used to describe the diets of fish, including percent by number, weight, and volume as well as frequency of occurrence (Chipps and Garvey 2007). Most studies of the diets of juvenile salmon use percent by volume or weight (e.g., Brodeur et al. 2007), but due to the nature of our data we were limited to using abundance or frequency of occurrence. Baker et al. (2014) argued that frequency of occurrence might be preferable to other metrics in many cases because of the unquantifiable and potentially significant error associated with the aforementioned methods of analyzing stomach content data. Given that our findings suggested groupings in the diet overlap of juvenile Pacific salmon species similar to those reported in the literature, we do not believe that our use of FO data greatly influenced our results.

Additionally, the MRT did not consider the lack of independence for fish caught in the same trawl, which could affect the relative importance of our explanatory variables in the MRT. However, the conclusions did not change drastically when diets were aggregated at the trawl level. Furthermore, when the variation due to trawl was first removed by an analysis of principal coordinates, the MRT run on the resulting axes still distinguished fish diets by species and predator length, as had the original MRT. This once again suggests that predator length and species are important factors influencing diets, with Pacific Herring and Eulachon having diets that are distinct from those of Pacific salmon. Month may be a less important factor and is confounded with trawl; this may be the reason why it did not define any clustering in predator diets once the variation due to trawl was removed. We ultimately used the results of the original MRT to present the full range of variation in the data because its interpretation is more intuitive while being consistent with the overall results of analyses that account for the nonindependence of fish from the same trawl. Furthermore, because the goals of the MRT were exploratory, we did not draw conclusions from a statistical test based on a probability distribution, for which the independence of the samples would be more important (De'ath 2002).

Hypotheses and Future Work

The diets of the Eulachon, Pacific Herring, and five species of Pacific salmon that we studied indicate that the historical food web in the Fraser River plume had strong interconnections. Such overlap could have had interesting implications for Pacific salmon growth and survival in light of the physical and biological changes that have occurred in the Strait of Georgia ecosystem since the 1960s. Increasing sea surface temperature in the strait, for example, has been associated with increased feeding rates among Pacific salmon (Daly and Brodeur 2015), potentially reflecting increased energy demands. But less availability of prey items high in energy content (such as euphausiids, copepods, and amphipods), coupled with a rise in gelatinous zooplankton (Davis et al. 1998; Li et al. 2013), compounds the pressures on Pacific salmon to meet their energy demands. A comparison of contemporary diets with those in the historical data could be useful for discerning how these changes have influenced fish foraging. Another major change in the Strait of Georgia that could have influenced the diets of these fish is the decline of the Fraser River population of Eulachon. Eulachon were the most abundant fish species caught in this study and the most abundant fish prey found in predator stomachs. The loss of such a high-quality prey item could have had consequences for the trophic interactions of the remaining predator species. We postulate that the larger role of Pacific Herring in contemporary Pacific salmon diets is a response to the declines in Eulachon availability.

Comparing historical diet overlap and prey availability with contemporary competition in the Strait of Georgia in light of the biotic and abiotic changes to this important rearing ground could be an important avenue for future studies. Of particular interest is the relative impact of these changes on juvenile Pacific salmon

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species, given that Chum Salmon readily utilize gelatinous zooplankton, a specialization that may be advantageous under contemporary conditions. The availability of baseline historical records in the Strait of Georgia makes these types of comparisons possible and may provide insight into ecosystem-scale changes. Such comprehensive data sets, spanning long time intervals, can facilitate ecosystem-based science and help inform management responses to long-term fluctuations in populations.

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