Collaborative Fisheries Research in Support of Ecosystem-Based Salmon Management in Northern California

Final Report to California Sea Grant, Program Development Project No. R/FISH-212PD

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Abstract

The state of the Chinook salmon (*Oncorhynchus tshawytscha*) fishery in California is imperiled. One of the proposed mechanisms for recent population declines and fisheries closures is environmental variation having deleterious effects on prey availability and the ocean survival of Sacramento River fall Chinook (Lindley et al. 2009). To address this hypothesis, we analyzed collaborative fisheries research data (stomach samples obtained from commercial and recreational fisherman) on Chinook salmon diet in central California during the early-mid 1980s and mid 2000s. We compared this information with historic diet records for this population from 1955. Salmon diet composition changed significantly through time, with a decline in diet diversity. Specifically, previously important prey groups including juvenile rockfish (*Sebastes* spp.), krill (Euphausiidae), Pacific herring (*Clupea pallesi*) and market squid (*Loligo opalsecens*) were either greatly reduced or disappeared from the diet altogether. Conversely, Pacific sardine (*Sardinops sagax*), conspicuously absent from the diet (and environment) since the 1950s, became the second most important prey item in the 2000s. Northern anchovy (*Engraulis mordax*) remains an important prey item. The strongest correlation between salmon diet and environmental conditions was for local SST for all years in the study between 1955-2007. In the early 1980s, SST best explained salmon diet composition. While relationships were not significant in the mid 2000s, likely due to the short time period sampled, upwelling or the NPGO were the best descriptors of salmon diet variation. These physical pressure-state indicators have exhibited increasing trends and increasing variability through time and are indicative of the changing climate. Finally, we decomposed multiple prey variables into a univariate annual index and thus compared diet variation with the Sacramento Index (SI) of Chinook ocean abundance. We found a relationship between diet and the SI lagged by 2 years, potentially an indication of prey availability experienced by smolts after ocean entry (Figure 5). Collaborative fisheries research offers a means to track variation in salmonid diet with implications for understanding the connections between environmental variation, salmon survival, and declining fisheries in California.

Statement of Problem

California salmon are in state of crisis. Returns of fall run Sacramento River Chinook salmon (SRFC), the stock upon which the majority of fisheries in the region is based, were exceptionally low in 2007 and 2008, prompting fisheries closures for this stock from California to central Oregon in 2008 and 2009. The 2010 fishery was re-opened, but was severely restricted and few fish were caught. The Sacramento River population decline was not anticipated, and management agencies (Pacific Fisheries Management Council, PFMC; and California Department of Fish and Game, CDFG) are now attempting to develop better forecasting tools. In part, the National Marine Fisheries Service (NMFS, 2009) blamed "poor ocean conditions" in 2005 and 2006 for the population crashes in 2007 and 2008 as this stock spends ~2.5 years at sea. We sought to understand more about how "poor ocean conditions" affected the SRFC population by analyzing data available from Collaborative Fisheries Research programs in the region conducted in the early-mid 1980s (P. Adams et al. unpublished) and mid 2000s (J. Thayer and W.J. Sydeman, unpublished). We hypothesized that dietary indicators may provide insight into how ocean climate in 2005-2007 influenced salmon survival and run size in later years. This study may be useful for improving the predictive capabilities of salmon managers faced with increasing uncertainty in salmon populations in light of increasing ecosystem variability.

Background and Justification

Broad scale studies have clearly shown the influence of ocean conditions on salmon fisheries (Mantua et al. 1997). Effects of environment are most evident during the initial months of ocean life, when the salmon are small and susceptible to minor changes in prey availability and/or depredation. However, recent work has also shown that conditions during the year of return (escapement) are influential on growth and size at return, and the rate of maturation which is thought to determine the timing of spawning (Scheuerell & Williams 2005, Wells et al. 2007). While some diet data for adult salmon exists, food habits are typically not monitored over space and time in a standardized manner, and what data are available indicate tremendous year to year variation. Understanding the nature of salmon-climate relationships is therefore limited by the dearth of information on salmon diet, which are difficult and expensive to obtain by conventional means.

Historically, salmon preyed upon a diverse prey field in the central California Current including zooplankton (euphausiid crustaceans or "krill"), juvenile rockfish, Northern anchovy, Pacific herring and market squid (Merkel 1957). During recent decades, however, ocean climate (DiLorenzo et al. 2005) and the pelagic food web have undergone substantial changes, and the food habits of salmon have undoubtedly been altered. For example, variations in krill (Brinton and Townsend 2003), a decrease in juvenile rockfish (Mills et al. 2007, Field et al. 2007) and an increase in anchovy (Litz et al. 2008) have been observed. These changes have resulted in variation in the diet and demography of other regional predators (marine birds) existing at the same trophic level as salmon (Sydeman et al. 2001, Abraham and Sydeman 2004, Sydeman et al. 2006, Thayer and Sydeman 2007, Mills et al. 2007, Wells et al. 2008, Sydeman et al. 2009, Field et al. in press).

Approach

We (re)initiated and analyzed data from a long-term Collaborative Fisheries Research (CFR) program targeting Chinook salmon food habits. Fortunately, our program included the focal years of 2005 and 2006, cited by NMFS as contributing to the recent SRFC run failures. The Pacific States Marine Fisheries Commission (PSMFC) and National Fish and Wildlife Foundation (NFWF) funded the 2005-2007 project in which Chinook salmon stomachs were collected during the spring and summer through collaboration with local fishers in central California. This was based on a project originally conceived and implemented by Pete Adams of the NOAA/NMFS/Southwest Fisheries Science Center. The original project started in the early 1980s but ended in 1999 (Mills et al. 2007). Notably, collaborative research with fishers has been recently identified as a priority for the California Ocean Protection Council (CA-OPC), so much so that they are establishing a new Collaborative Research Foundation through the PSMFC. We have analyzed the data that we and NMFS have collected in part to develop a better understanding of the value of this CFR program. We hope this report will demonstrate a compelling basis for a larger, long-term CFR program to enhance salmon population studies and management in California.

Objectives

Our objectives are to: (1) investigate Chinook salmon diet composition on a regional scale (central/ northern CA), (2) compare 2005-2007 data with previously published (Merkel 1957) and unpublished data (P. Adams/NMFS unpublished), (3) relate salmon food habits to indices of ocean climate in 1955, 1980-1986 and 2005-2007, (4) examine possible relationships between diet composition and salmon abundance indices, lagged appropriately, and (5) disseminate results to the management community (PFMC, NOAA/NMFS and CDFG).

Methodology

Chinook salmon stomachs were collected by commercial and recreational fishers in May-August between Monterey and Bodega Bay in central California from 1980-1986 and 2005-2007. Merkel (1957) studied Chinook salmon diet following similar methods in 1955. In the laboratory, we identified prey items to the lowest possible taxon. The contribution of each prey taxon to salmon diet was expressed as percent frequency of occurrence (%FO), and as a percentage of total estimated volume (%VOL*)* of prey ingested. As %FO and %VOL provide different insights into salmon feeding habits (Link 2004), we calculated an integrated index of composition, the geometric index of importance (GII; Assis 1996; Preti et al. 2008). The GII was expressed as: $\mathrm{GII}j = (\%\mathrm{FO}j + \%\mathrm{VOL}j) / \sqrt{n}$, where $\mathrm{GII}j$ = index value for the j-th prey category and n = the number of relative measures of prey quantities used in the analysis. Prey species or groupings were included in analyses if they contributed to 95% of salmon diet as measured by ranked cumulative percent frequency of occurrence. The Shannon-Weiner index of diversity calculated from %FO quantified changes in the food resource spectrum utilized by salmon over time: $H = -\sum p_i \ln p_i$, where p_i is the proportion by number represented by each prey category i (Mahe et al. 2007). Trends in diversity were measured using Spearman rank correlations weighted by sample size.

Inter-annual and decadal changes in diet composition were visualized using non-metric multidimensional scaling (MDS) conducted in PRIMER-E v6.0 (Clarke & Warwick 1994). To quantify similarity in diet composition between decades, one-way analysis of similarity

(ANOSIM) tests were performed to identify paired relationships (Bellegia et al. 2009, Daly et al. 2009). Similarity percentages (SIMPER) were used to identify which taxonomic categories characterized the diet composition and made the greatest contributions to dissimilarities.

To identify environmental variables that best explain temporal variation in salmon diet composition, the relationships between the salmon diet GII and normalized, log-transformed environmental variables were analyzed using the biota and environmental matching (BEST) procedure in PRIMER. This procedure iteratively compares the similarity matrices of diet data to environmental data and identifies the subgroup of environmental variables that has a greater weighted Spearman rank correlation (*rho*). Available measured ocean climate data for all time periods included regional SST at Southeast Farallon Island (Scripps Shore Station Program), upwelling indices averaged for 36□ and 39□N (www.pfeg.noaa.gov), and sea level (http://uhslc.soest.hawaii.edu). Integrated basin-scale indices used were the North Pacific Gyre Oscillation (NPGO; http://eros.eas.gatech.edu/npgo/data/NPGO.txt), Pacific Decadal Oscillation (PDO; http://jisao.washington.edu/pdo/PDO.latest), and Southern Oscillation Index (SOI; http://www.cgd.ucar.edu/cas/catalog/climind/soi.html). Anomalies were calculated by subtracting the climatological monthly means of time series (1950-2008) for each variable.

Finally, we examined how fluctuations in salmon diet correspond to ocean abundance indices, such as the Sacramento Index (SI; http://www.pcouncil.org/salmon/salpre.html). We used principal components analysis (PCA) to identify the dominant relationships among prey groups and decompose multivariate data into a series of univariate indices that could be separately analyzed. Diet from the same year and with a 1-yr and 2-yr lag (as possible) was investigated using Spearman correlation. Diet from the same year reflects conditions experienced by returning adults, while diet lagged by 1-2 years reflects what sub-adults and age-0 or yearling fish may experience in the ocean, respectively. The SI extends back to 1983, so comparisons were made with the early-mid 1980s and mid 2000s diet data.

Results

Main prey of Chinook salmon included Northern anchovy, rockfish, krill, Pacific sardine, crab megalopae (*Cancer* spp.), Pacific herring and market squid (Table 1, Figure 2). Rockfish in particular were an important prey group in 1955 and during the 1980s. Species of rockfish included, in order of importance: shortbelly (*S. jordani*), widow (*S. entomelas*), splitnose (*S. diploproa*), chilipepper (*S. goodei*), blue (*S. melanops*), canary (*S. pinniger*), squarespot (*S. hopkinsi*), bocaccio (*S. paucispinis*), brown (*S. auriculatus*), olive (*S. serranoides*), and pygmy (*S. wilsoni*).

We did not observe significant differences in the proportion of empty stomachs or gut fullness between decades. However, Chinook salmon diet composition has changed drastically over the last half-century. Patterns in %FO and %VOL were similar. The GII, which combined %FO and %VOL data, revealed the decrease through time in dietary importance of rockfish, euphausiids, herring and squid, while sardine and anchovy increased in importance (Figure 2). Shannon-Weiner indices of diet diversity declined significantly through time (Spearman *rho* = -0.69, p = 0.02; Figure 3). There was, in fact, a wider spatial sampling range in 2005-2007, yet much lower diversity during these years.

Annual trends as visualized in an MDS plot indicated a state-like shift in salmon diet composition between decades, with the exception of 1985 and 1983, years of anomalously cold and warm conditions, respectively (Figure 4). The MDS analysis grouped 1985 with 1955, suggesting that similarities due to very cold SST may have been stronger than dissimilarities due to dietary changes between decades. However, there were no samples in July or August of 1985, which may have generated bias towards species normally found earlier in the season such as euphausiids and crab megalopae, which are also coincidentally representative of diet in colder years.

Quantitatively, differences in diet were significant between decades (ANOSIM: Global R statistic = 0.48, p = 0.01; Table 2). Pairwise tests revealed significant changes in diet from the 1980s to the 2000s. Diet also differed greatly between 1955 and the 1980s, and between 1955 and the 2000s, yet significance levels were high, likely due to only one year for comparison in the 1950s. Decreasing importance of rockfishes and euphausiids, and increasing importance of sardines and anchovies in the diet were largely responsible for decadal differences in diet composition (Table 2). The largest single contribution to diet differences was the decrease in rockfish from 1955 to the 2000s (35.3%). While 1955 was an exceptionally cold-water year, likely favoring rockfish spawning and survival, the decline of rockfish in the diet from the 1980s to the mid 2000s, when rockfish were completely absent, was still highly significant. A decline in herring contributed to 6% of the difference in diet composition from the 1980s to the 2000s. Alternately, the contribution of market squid to the diet was 9% of the variation between 1955 to the 1980s and 6% of the variation between 1955 to the 2000s.

Diet & ocean conditions. The strongest correlation between salmon diet and environmental conditions was indicated by local SST (*rho* = 0.32, p = 0.07; Table 3). For the early 1980s, SST also best explained variation in salmon diet (*rho* = 0.62; p = 0.11). Either upwelling or the NPGO exhibited the highest correlations with salmon diet in the mid 2000s, but these relationships were not significant, probably due to low sample size (p > 0.54).

Diet & survival. Principal Component Analysis was conducted for salmon diet in the 1980s, in the 2000s, and for all years of the study combined (Table 4). $PC1_{diet}$ explained between 48 – 80% of the variance in these analyses, and suggested a switch between main prey, either anchovy/sardine or rockfish/krill between years.

Salmon diet was related to the SI lagged by 2 years (Spearman's *rho* = 0.63, p = 0.06), potentially an indication that the forage fish prey field experienced by smolts during the year of ocean entry was important to survival and runs years later (Figure 5). Excluding data in 1985, due to limited sampling in May-June only, did not improve this or other relationships of diet to the SI.

Discussion

Historic records of Chinook salmon diet in the central-northern California region (Merkel 1957, and others summarized therein) suggest high diet diversity, with substantial inter-annual variation. Similar to this information, we observed that a diverse array of prey were consumed and that the proportion of prey types in the diet varied annually, but we also found declining diet diversity through time, and that some prey species decreased or completely disappeared from the diet. The absence of previously important prey species, herring for example, may have implications for prey switching of these generalist predators, and may have had, or are having, demographic consequences by affecting survival at sea. This is one of the most important findings of our study.

Over the past half century, there has been considerable variation in marine conditions of the California Current. A strong La Niña event characterized 1955 (NOAA-CIRES Climate Diagnostic Center) when Merkel conducted his sampling. Between 1977 and 1998, the California Current was in a warm and relatively unproductive phase. One of the strongest El Niños on record occurred in 1982-1983, followed by a brief period of cool La Niña conditions (Lluch-Belda et al. 2005). The major 1982-1983 El Niño produced SST anomalies of +1–2.5°C, and deepened the inshore thermocline by as much as 50m (Simpson 1992). Since the mid 1990s, California Current conditions have been particularly variable. The strong 1997-1998 El Niño was followed by four years of cool La Niña-like conditions, which contributed to productive ocean conditions. However, in late 2002, oceanographic conditions again reversed, and warm conditions prevailed for the next four years. Warm ocean conditions in 2005-2006 were not causally related to El Niño, yet unusual atmospheric blocking may have resulted in poor upwelling-favorable winds and correspondingly warm SST (Sydeman et al. 2006, Schwing et al. 2006, Goericke et al. 2007). Subsequently, 2006–2007 began with moderate El Niño conditions and low upwelling values (Kaplan et al. 2009, McClatchie et al. 2008).

Salmon numbers in the Pacific Northwest have generally followed suite (Koslow et al. 2002). While the SI and CVI abundance estimates do not extend back to 1955, numbers since 1970 were lower after warm, unproductive periods and increased during cool, productive ones.

We found relationships between the diet of Chinook salmon and varying oceanographic conditions. Direct studies of prey species support these findings. For example, lower growth was reported in widow and yellowtail (*S. flavidus*) rockfish during the warm ocean conditions of the 1982-1983 El Niño, relative to that found in other years between 1980-1987 (Woodbury 1999). Brinton and Townsend (2003) reported a higher abundance of euphausiids such as *E. pacifica* off California during La Niña events and declines during El Niños. Anomalously warm conditions in 2005-2006 were associated with a decrease in cold-water euphausiids, and, as a likely consequence, productivity of central California seabirds, foraging at the same trophic level as salmon, was extremely depressed (Sydeman et al. 2006, Goericke et al. 2007). Forage fish numbers in the California Current in 2005 and 2006 were amongst the lowest of a nine-year time series (Goericke et al. 2007), and abundance remained low in 2007 (McClatchie et al. 2008). The years 2005-2007 also had the lowest rockfish catches in a 28-year record (Field et al. in press).

Specifically, we observed links between Chinook diet and local SST over all years in the study between 1955-2007. However, on a decadal basis, the strongest environmental relationships with diet in the mid 2000s were different than those observed in the 1980s, indicative of the changing climate. While not significant, likely due to the short time period sampled, the NPGO and upwelling were the best descriptors of diet in the 2000s. These physical pressure-state indicators have exhibited increasing trends and increasing variability through time (Sydeman & Thompson 2010), while Chinook diet diversity has decreased. The NPGO emerges from analyses of anomalies of Northeast Pacific sea-surface height (Di Lorenzo et al. 2008). Positive values indicate a strong North Pacific gyre and advective transport from the north into the California Current. Many NPGO 'events' since 1975 seem to have been more extreme or had a longer duration than those earlier in the time series (Sydeman & Thompson 2010). Correspondingly, variance in the NPGO in the 1990s and 2000s was greater than earlier in the time series. The upwelling index at latitude 39°N also showed a significant, though shallow, increase through time (Sydeman & Thompson 2010).

Last, we found relationships between diet composition and an index of salmon abundance, the Sacramento Index (SI). $PC1_{diet}$ explained 28% of the variation in observed SI for years in the study between 1981-2007. Age of California Chinook salmon return to natal rivers is not invariant, but rather relates to environmental conditions and growth, at least in terms of whether they return at age 2, 3, or 4 (Wells et al. 2007). We observed correlations of diet with the SI lagged by 2 years, suggesting an effect of the forage fish prey field in the year of ocean entry. Most Chinook originating from California rivers remain within California Current waters (Wells et al. 2007). Studies suggest that Chinook commonly remain near their natal systems before the first ocean winter (Beamish et al. 2004, MacFarlane et al. 2005), potentially migrating farther as they age, but they may also reside near their source during the second growth season (Wells et al. 2007). Salmon smolts from the SRFC run typically enter the ocean in spring (April-May; hatchery release), which corresponds nicely with our May-June adult diet sampling.

Other studies relating inter-annual adult salmon returns to juvenile diets during a similar time period to our study showed mixed results. Brodeur et al. (2007) and Daly et al. (2009) examined juvenile coho and Chinook diet off Oregon and Washington in the 1980s versus 1998-2003. The expectations of Daly et al. (2009) that juvenile salmon would feed on larger prey, more quality prey such as fish, and have higher stomach fullness in high survival years than low survival years were not entirely supported by the data. During lower-survival years, they found that coho salmon ate fewer and smaller fish prey, and subyearling Chinook salmon consumed less total food and had more empty stomachs, yet no consistent trophic patterns for yearling Chinook salmon in relation to their ultimate survival were seen. We did not observe a similar pattern for adult Chinook. Empty stomachs and gut fullness did not differ between decades, despite a dramatic difference in survival.

Even though the mechanisms are not yet well understood, most of the salmon forage species which declined during our study - rockfish, herring and squid - are heavily exploited, with current bans or restrictions on fishing based on conservation concerns. As key forage for an already imperiled and extremely important economic species such as salmon, managers may want to be more conservative. Food web models have been used to demonstrate that the widespread application of maximum sustainable yield (MSY) single-species management strategies could lead to detrimental impacts on higher trophic level species when applied to a broad assemblage of lower trophic level, forage species (Walters et al. 2005).

Conclusions

This study represents successful implementation of a Collaborative Fisheries Research program with local commercial and recreational fishers. The data we have presented on Chinook diet composition indicates decadal variation due to ocean conditions, and that variation in diet may determine survival and returns/run size years later. Overall, diet diversity declined over the study, as ocean conditions have gotten warmer and more variable, and several previously important prey species have been greatly reduced or disappeared from the diet altogether. SRFC abundance has recently declined substantially, especially in 2007-2009 which may be tracked back to the low diet diversity in 2005-2007. This suggests that the forage fish community is not as diverse as it once was, and that prey-switching in salmon is now constrained. The observed relationship between diet composition and the Sacramento Index (SI) at a lag of 2 years suggests that prey availability during the year of ocean entry is key to smolt survival.

Dissemination of findings

We have disseminated our findings to the public, NMFS, CDFG, and PFMC, at the annual salmon ecology meeting at NMFS/SWFSC in April 2010, at the annual state of the salmon meeting at Sonoma County Water Agency in April 2010, and to the PFMC Salmon Technical Team. Results will be detailed for a publication in *Fisheries Oceanography.*

Implications for CFR Program Development

This program development project forms the foundation for a larger Cooperative Fisheries Research (CFR) project centered around the influence of climate and food web dynamics on the ocean ecology of salmon, including effects on survival and returns. In this project, we have shown that collaboration with local fishers is possible and results in excellent scientific data. CFR allows for data collection on key issues in fisheries science without increasing mortality rates above that allowed by the fishery (i.e., no additional research sampling). While providing good data, the educational and outreach value of CFR should also not be underestimated. Our project thus far has served to strengthen communication between fishers and researchers towards the common goal of maintaining healthy marine ecosystems and salmon populations in central California. Finally, while this project was focused on the SRFC there is strong co-variation in salmon responses to temporal environmental variability along the entire west coast (Botsford and Lawrence 2002). Therefore, it is reasonable to suggest that an expansion of this project to other salmon species and regions of the California Current would be successful. A larger program may include partners from NMFS, CDFG, Sonoma County Water Agency, National Park Service (Point Reyes National Seashore, Golden Gate National Recreation Area), Oregon State University, University of Washington, and the OPC and PSMFC’s new Collaborative Research Foundation. This new foundation will begin with a focus on California, but under the Tri-State Governor’s Agreement, support for this type of research in Oregon and Washington will hopefully soon follow, covering PSMFC’s wider jurisdiction. We have had preliminary discussions with researchers from Oregon State University, who could currently obtain potential funds for this type of collaborative fisheries research through Oregon Sea Grant. The National Park Service is seeking collaborators in the areas of climate change response and ocean and coastal resource stewardship, and has expressed interest in a project involving coho salmon in northern California. The Sonoma County Water Agency is tasked with improving salmonid resources in the Russian River and its tributaries in central California, and as mentioned above, hosts an annual state of the salmon meeting. This program could enhance community involvement in salmon studies and management by providing more information on mechanisms linking ocean climate to salmon survival. We are enthusiastic about continuing to develop a CFR program to study the food habits of salmonids and other fish in the California Current.

Acknowledgements

We sincerely thank P. Adams/NMFS for his foresight, contributions, and interpretation of the 1980s data. PRBO Conservation Science provided fiscal and administrative support and laboratory facilities for this project in 2005-2007. Special thanks to all the hard work and long hours of S. Acosta who visited field sites, conducted lab analyses and managed data. The field and lab contributions of biologist K. Lindquist and interns S. Rhoades and A. Groesbeck were also invaluable during this period. Finally, we acknowledge the financial support of PSMFC, NFWF, NMFS, and California Sea Grant for making this synthesis possible.

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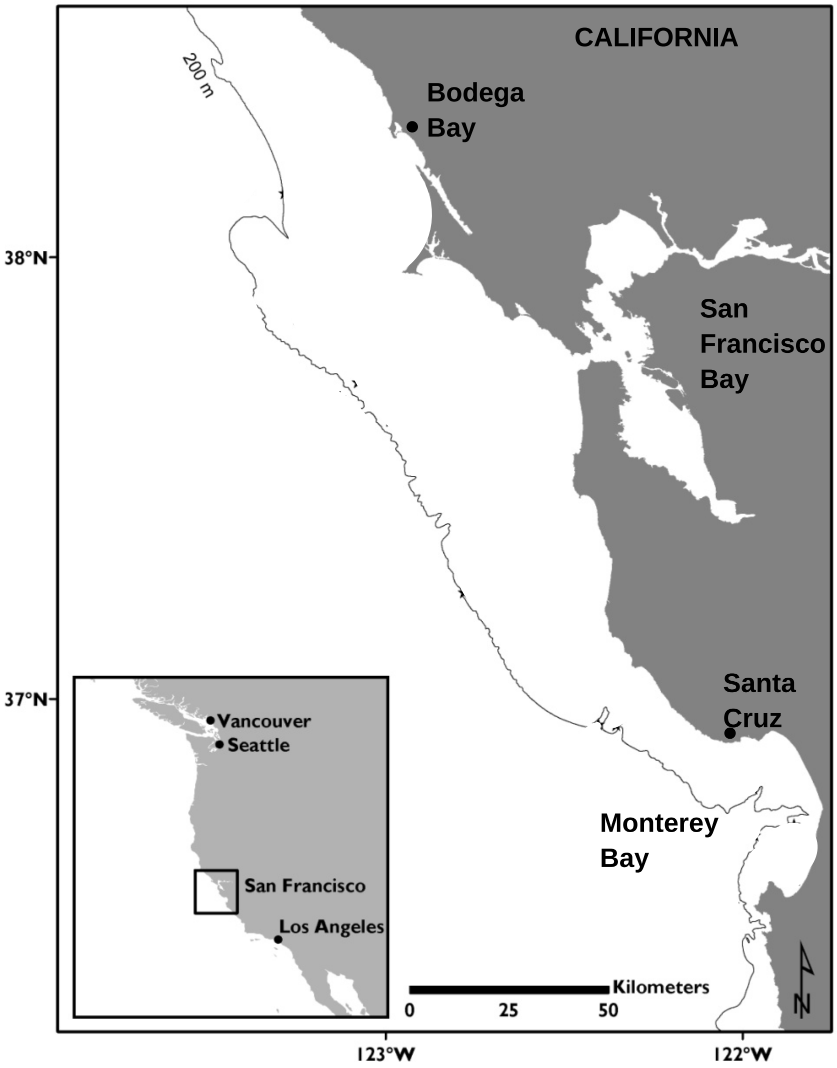

Figure 1. Map depicting study area in the central California Current System. See text for details.

Table 1. May–August totals, by year, for number of Chinook salmon stomachs sampled, percent of empty stomachs, and number of prey by group.

	1955	**1980**	**1981**	**1982**	**1983**	**1984**	**1985**	**1986**	**2005**	**2006**	**2007**
N	387	245	425	544	397	465	265	269	1250	184	134
Empty stomachs	9%	38%	22%	33%	39%	20%	12%	27%	20%	23%	24%
N. anchovy	57	213	390	389	717	936	235	364	1757	259	167
***Sebastes* spp.**	212	117	1186	667	0	478	1222	87	0	0	0
Euphausiids	97	13666	2259	25263	8	10272	6698	18101	10769	4065	1663
P. sardine	0	0	0	0	0	0	0	0	327	36	20
***Cancer* megalopae**	29	68	1636	1098	2	204	10428	7	106	0	45
P. herring	18	12	24	189	27	34	0	4	0	0	0
Market squid	32	2	4	13	1	1	0	2	5	0	0
other crustaceans	3	8	5	3	74	3	3	0	4	0	0
other cephalopods	9	1	3	3	1	3	4	2	0	0	0
other invertebrates	0	4	29	0	2	1	0	0	0	0	0
other fish	48	4	4	3	17	163	14	5	13	8	2
unknown fish	129	60	314	82	51	18	6	17	848	108	99
unidentified	0	0	2	0	0	0	0	0	16	0	1

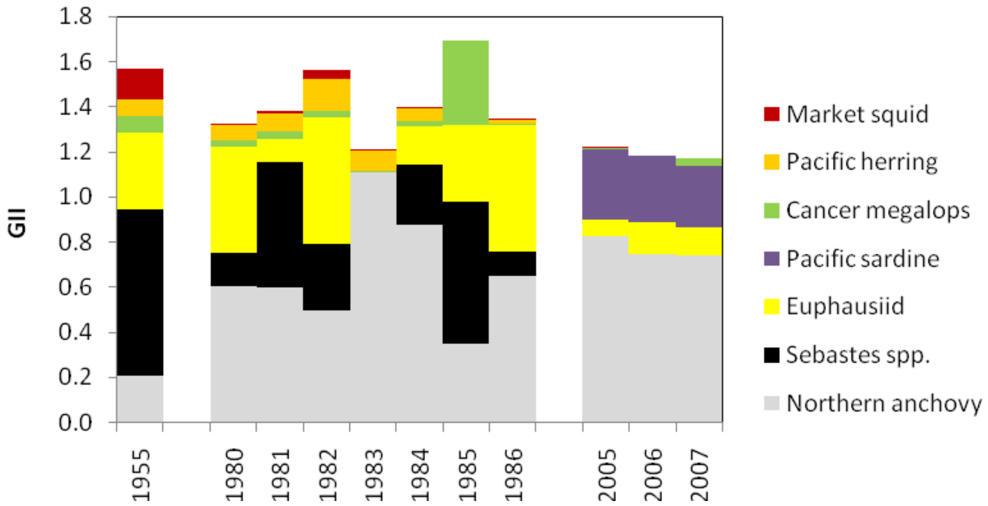

Figure 2. Geometric index of importance (calculated from %FO and %Vol) for prey in Chinook salmon diet between 1955-2007.

Figure 3. Shannon-Weiner indices of diversity for Chinook salmon diet 1955-2007.

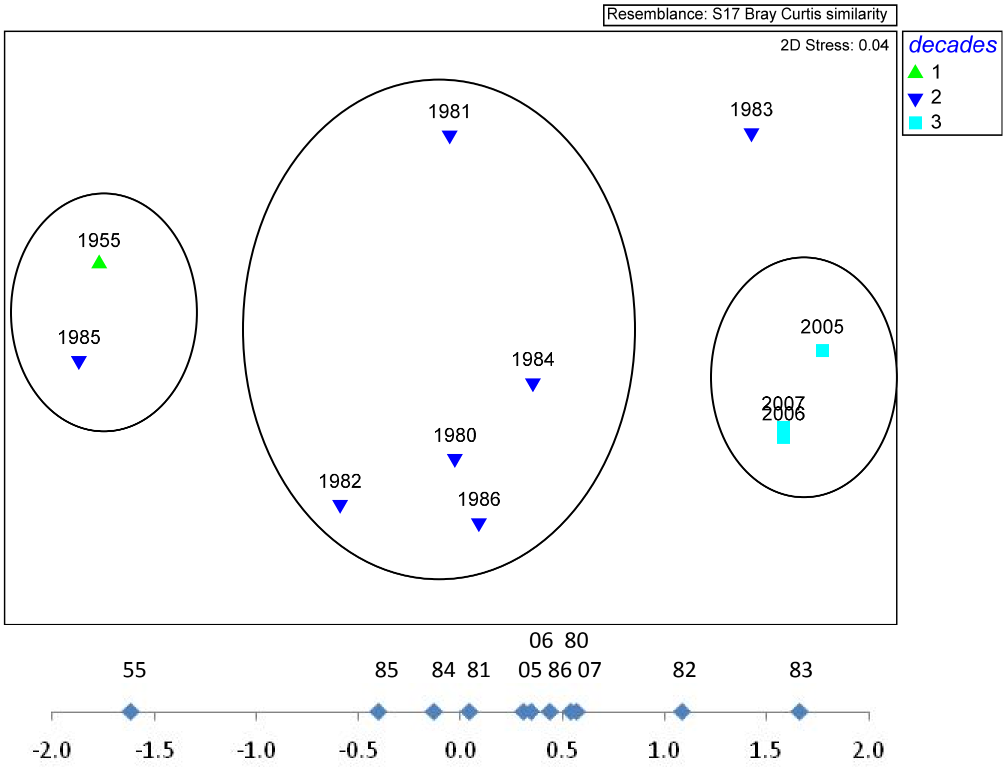

Figure 4. MDS ordination of Chinook salmon diet composition based on annual Bray-Curtis similarity index of GII (calculated from %FO and %Vol) for years between 1955-2007. Stress = 0.04; stress is a measure of goodness-of-fit for various possible MDS configurations; the smaller the stress, the better the fit. The bottom graph denotes the Multivariate ENSO Index (MEI) values for each 2-digit-labeled year.

Table 2. Analysis of similarity (ANOSIM) test results of significant (P < 0.05) differences in Chinook salmon diet composition by year. Percent prey contributions to significant diet differences were identified by similarity percentage (SIMPER) analysis.

		ANOSIM		SIMPER						
		R	Significance level%	Anchovy	Rockfish	Euphausiid	Sardine	Market squid	Herring	Cancer megalopae
	Global test:	**0.48**	**1.1**							
	Pairwise tests									
Years	**1955 & 1980s**	0.33	25	34.5	33.7	14.1		9.0		
	1955 & 2000s	1	25	26.9	35.3	10.9	14.1	6.3		
	1980s & 2000s	0.44	3.3	19.2	23.6	20.3	25.2		5.7	

Table 3. Results of the biota and environmental matching (BEST) correlation analysis for Chinook salmon diet composition and environmental factors (SST, sea level, upwelling, PDO, NPGO, SOI). Combinations of environmental factors, *k* at a time, yielding Spearman rank correlation coefficients (*rho*) between diet patterns and environmental data. Within each *k* category, parameter combinations are sorted according to their *rho* values.

Global test: p = 0.07

k	ρ	Best variable combinations			
1	0.322	SST			
3	0.264	SST	PDO	sea level	
2	0.254	SST	PDO		
4	0.252	SST	PDO	sea level	SOI
4	0.249	SST	PDO	sea level	NPGO
3	0.247	SST	sea level	NPGO	
2	0.242	PDO	sea level		
2	0.241	SST	sea level		
3	0.239	SST	PDO	SOI	
3	0.236	PDO	sea level	SOI	

Table 4. Principal Component Analysis including (eigenvalue, variance explained, and factor loadings for PC 1) that includes the main prey groups of Chinook salmon for time periods 1980-1986 (MRI 2); 2005-2007 (MRI 2); and all years (1955, 1980-86, 2005-07; MRI 3)

	1980-86 (MRI 1)	2005-07 (MRI 2)	**1955-2007 (MRI 3)**
Eigenvalue	2.860	3.980	**3.35**
Proportion of Variance	0.48	0.80	**0.48**
Anchovy	0.42	0.50	-0.47
Rockfish	-0.47	-	0.49
Euphausiid	-0.09	-0.43	0.35
Sardine	-	0.47	-0.40
Cancer megalopae	-0.54	0.72	0.27
Herring	0.44	-	0.24
Squid	0.33	0.25	0.36

Figure 5. Relationship between PC1 of Chinook salmon diet in May-August, and the Sacramento Index lagged by 2 years, for 1981-1986 and 2005-2007. Note that sampling in 1985 occurred only in May-June

and therefore may be biased towards prey occurring early in the season (e.g. euphausiids, crab megalopae).