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Changes in California Chinook salmon diet over the past 50 years: relevance to the recent population crash

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ABSTRACT: Salmon are affected by variation in ocean productivity; thus, improved understanding of mechanisms behind variability in ocean survival should help management of these ecologically and economically important populations. Based on a cooperative fisheries research program, we compared central California Chinook salmon *Oncorhynchus tshawytscha* adult food habits from spring and summer in the mid-2000s with historical records from 1955 and the 1980s. Diet diversity decreased through time, and was particularly low in May and June of the 2000s. Previously important prey, including juvenile rockfish *Sebastes* spp., krill Euphausiidae, Pacific herring *Clupea pallesi* and market squid *Doryteuthis opalsecens,* declined or disappeared from the diet, while Pacific sardine *Sardinops sagax* became very important prey in the 2000s; anchovy *Engraulis mordax* remained important throughout the study. Diet composition was correlated with regional mid-water trawls of prey abundance and also with local sea surface temperature (SST). Diet composition was related to the Sacramento Index of fall-run Chinook ocean abundance with a lag of 1 or 2 yr, and reflected the importance of prey availability during the second ocean year and smolt ocean-entry period, respectively. Spring is peak ocean entry for fall-run Chinook smolts, so declining prey diversity (specifically in May and June in the mid-2000s) may be related to recent population crashes. Seasonally, winter and fall diet data further demonstrated the significance of temporal variation in specific prey. This study highlights the importance of marine predator–prey interactions at an appropriate temporal resolution for understanding salmonid population dynamics.

KEY WORDS: Chinook salmon · Diet diversity · Diet composition · Seasonal variation · Decadal variation · Prey availability · SST

INTRODUCTION

Fisheries operate within a complex array of species interactions and environmental effects, yet many of these processes and their effects on fish populations remain poorly understood. Recently, some salmonid populations in the northeast Pacific Ocean, including Chinook salmon *Oncorhynchus tshawytscha* in California, USA, coho salmon *O. kisutch* along the west coast of North America, and sockeye salmon *O. nerka* in British Columbia, Canada, have experienced dramatic changes in abundance over very short time periods, leading to both conservation concerns and socioeconomic impacts (Koslow et al. 2002, Lindley et al. 2009, Thomson et al. 2012). Specifically, Sacramento River fall-run Chinook salmon declined well below the Pacific Fisheries Management Council's escapement conservation goal of 122 000 to 180 000

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spawners in 2007 (88 000 fish) and 2008 (66 000 fish; Lindley et al. 2009), effectively shutting down the fishery.

'Ocean conditions' have been highlighted as a factor explaining salmon population variability, but often it is unspecified which aspects of the oceanic environment (physical or biological) are causally related to variation in survival and returns. While numerous studies have shown strong correlations to hydrographic conditions (e.g. Mantua et al. 1997, Botsford & Lawrence 2002, Scheuerell & Williams 2005), such analyses do not provide a mechanistic understanding of change. One of the proposed mechanisms for the recent variation is a 'bottom-up' (nutrient-driven) effect of ocean primary productivity on prey availability (Wells et al. 2012). While some work has been done on the diet of juvenile Chinook salmon (MacFarlane & Norton 2002, Daly et al. 2009), few data are available on the food habits of adults, and what data are available indicate tremendous year-to-year variation in diet (Hunt et al. 1999, Daly et al. 2009). Understanding the nature of variation in salmon survival at sea is therefore limited by the dearth of long-term information on salmon diet, which is difficult to obtain by conventional means (standardized surveys).

Historically, salmon prey in the central California Current (CC) included krill, juvenile rockfish, and anchovy (Merkel 1957). During recent decades however, ocean climate and the pelagic community have undergone substantial changes (DiLorenzo et al. 2005, Harding et al. 2011) and food habits of salmon may have been altered. For example, interannual variations in krill (Lavaniegos & Ohman 2007), a decrease in adult and juvenile rockfish (Field et al. 2010), the recovery of the California sardine (Hill et al. 2011), and variable numbers of anchovy (although a general decline since the 1980s; Litz et al. 2008, Fissel et al. 2011) have been observed. These changes in forage base have resulted in demographic effects on other predators existing at the same trophic level as salmon (e.g. marine birds; Sydeman et al. 2006, Thayer & Sydeman 2007).

Here, through a collaborative fisheries research program involving commercial and recreational fishers, we investigated long-term variability in adult Chinook salmon diet, and related this to historical information as well as changes in the ocean environment. Our specific objectives were to (1) summarize and compare salmon diet between decades (mid-1950s, early to mid-1980s, mid-2000s) for the central California region, on the scale of months to decades; (2) compare these diet data with conditions in the environment, including ocean conditions and prey availability as indexed by mid-water trawl surveys of various prey species; and (3) examine how salmon diet relates to central California salmon abundance indices.

MATERIALS AND METHODS

Salmon diet

Prey composition and temporal changes in the diet of adult Chinook salmon in central California were determined through stomach content analysis from May through August (spring-summer) of 1980 through 1986, and 2005 through 2007, and compared with May through August data available from 1955 (Merkel 1957). Salmon stomachs were largely obtained in the Gulf of the Farallones (Fig. 1; approximately Point Reyes [37° 60′ N, 123° 1′ W] to Pillar Point [37° 32′ N, 122° 30′ W]) from commercial passenger fishing vessels (CPFV) and a few commercial

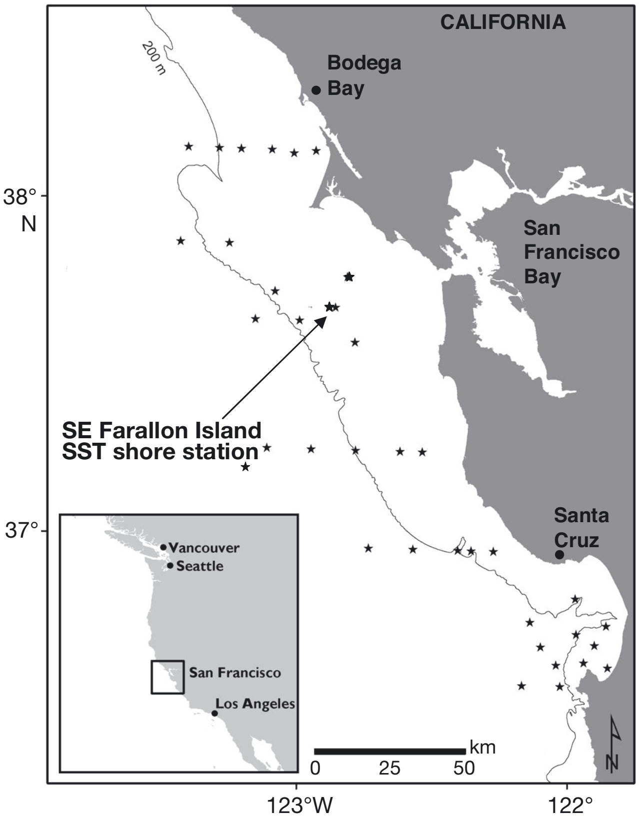

Fig. 1. Study area in the central California Current System. Stars represent National Marine Fisheries Service trawl stations, from which an index of prey availability was developed and compared with salmon diet for the years 1983–1986, and 2005–2007

vessels using trolling gear in 1955 (Merkel 1957), 1980 to 1986 (Larson 1987; P. Adams, NMFS, unpubl. data), and 2005 to 2007 (this study; see Tables S1–S3 in the Supplement at www.int-res.com/articles/suppl/m498p249_supp.pdf).

Salmon were measured (fork length, FL), capture location was logged via GPS, and stomachs were removed and either immediately frozen or put on ice and then frozen or stored in formalin upon return to port. Stomach contents were identified to the lowest possible taxon using a dissecting microscope if necessary, and complete prey items were measured and weighed. When necessary, prey hard parts (primarily otoliths and cephalopod beaks) were identified using atlases (Clarke 1986, Harvey et al. 2000) and reference collections (NMFS Southwest Fisheries Science Center; L. Spear and P. Pyle, PRBO Conservation Science; M. Weise, University of California Santa Cruz; J. Harvey, Moss Landing Marine Laboratory). Otoliths and cephalopod beaks were counted and a minimum number of individuals was determined for each stomach sample using the larger number of left or right, similar-sized otoliths of each fish taxon, or upper or lower cephalopod beaks.

Diet analysis

Contribution of each prey taxon to salmon diet was expressed as percent frequency of occurrence (%FO), number of prey (%N), and total volume (%VOL) of prey ingested. Empty guts, or those containing no prey, were not considered in the estimates of %FO. Prey size classes were summarized for the most abundant prey types, anchovy and juvenile rockfish.

The Shannon-Wiener 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.

As %FO, %N and %VOL provide different insights into salmon feeding habits (see Tables S1–S3 in the Supplement), the geometric index of importance (GII) was calculated to integrate these (Assis 1996). The GII was expressed as: $\mathrm{GII}_j = (\%\mathrm{FO}_j + \%\mathrm{N}_j + \%\mathrm{VOL}_j)(\sqrt{n})^{-1}$, where GII_j = index value for the j-th prey category and n = the number of relative measures of prey quantities used in the analysis. This diet index was converted to percentages to facilitate comparisons, and %GII was used for all further analyses. Proportional GII data were logit-transformed to spread out data near the boundaries of 0 and 1 (Warton & Hui 2011).

Main prey species or groupings were included in further analyses if they contributed to 95% of salmon diet as measured by ranked cumulative percent frequency of occurrence. Based on cumulative prey curves for each spring-summer period in all years, the number of samples required to represent main prey was 83 samples among years and 33 samples among months. Sample size among years was sufficient and ranged from 134 to 1250 (Table S1 in the Supplement). Sample size among months ranged from 29 to 388 (Table S4 in the Supplement; excluding 4 months with low sample sizes: 1983_{Aug} n = 3, 1984_{Aug} n = 10, 2006_{Jul} n = 18, 2007_{Aug} n = 9). Months with sample size <20 were included in a multidimensional scaling (MDS) plot for visualization purposes. These months were also included and excluded in further analyses to determine their effect. Months with sample sizes only slightly lower than generally required (1980_{May} n = 29, 2006_{Aug} n = 29) were included because prey curves calculated for these specific year-month combinations indicated that lower sample sizes would have been sufficient (i.e. 1980_{May} = 17 samples min., 2006_{Aug} = 8 samples min.). Low sample sizes did not represent lack of sampling effort, but rather low numbers of salmon captured during those months.

PRIMER-E (v6.1.5, 2006; Primer-E) was used for diet matrix comparisons. STATA-SE statistical software (v.11.0, 2009; StataCorp LP) was used for principal component analysis (PCA) and comparisons of diet with sea surface temperature (SST) and abundance indices.

Temporal comparisons

Inter-decadal and within-season changes in diet composition were visualized using a non-metric MDS plot. Plots were based on triangular matrices of Bray-Curtis similarities of the GII for each prey species. Stress values were calculated to give an indication if, and to what extent data were distorted (or scattered). Stress values less than 0.10 were regarded as being unlikely to result in misinterpretation of the data (Clarke & Warwick 2001).

To quantify similarity in diet composition among decades, spring-summer data were sub-sampled either by month (to examine annual differences) or by day (to examine monthly differences; this excluded 1955 from analyses). Similarity matrices were constructed from the GII using the Bray-Curtis similarity coefficient, and 1-way analysis of similarity (ANOSIM) tests were performed to identify any paired relationships (Daly et al. 2009). Similarity percentages (SIMPER) were used to identify which taxonomic categories made the greatest contributions to any dissimilarity.

Monthly %VOL data from February to April and September to November of 1955 and 1980–1986 were summarized to give insight into the winter and fall diet of Chinook.

Diet and environment

Prey availability in the salmon habitat was estimated from surveys of the National Marine Fisheries Service (NMFS). NMFS conducts mid-water trawls for juvenile rockfish (Fig. 1) from May to June each year, with information also collected on a range of other fishes and pelagic invertebrates (Bjorkstedt et al. 2011). Surveys began in 1983, and station locations were standardized in 1986 (hence low trawl sample sizes in 1983, 1984 and 1985). Methodology is available in Ralston & Howard (1995) and Field et al. (2007). RELATE matrix rank correlations were used to quantify similarities in logit-transformed salmon diet composition (%N; annual value for May and June only) and the log-transformed annual mean catch rates from NMFS surveys as representative of prey availability for northern anchovy, juvenile rockfish, Pacific sardine, Pacific herring, and market squid (1983 to 1986 and 2005 to 2007). Specifically, RELATE is a Mantel-type test of the null hypothesis by permutation; a Spearman rank correlation coefficient is computed between the corresponding elements of 2 triangular similarity matrices and the statistical significance derived by Monte Carlo permutation procedure (Somerfield et al. 2002).

We used PCA to identify the dominant relationships among salmon prey groups and decompose multivariate data into a series of univariate measures that could be separately analyzed. As SST is known to influence salmon survival (Koslow et al. 2002, Mueter et al. 2002), we compared local SST against changes in salmon diet as a potential mechanism for variation in survival. SST was obtained from the Southeast Farallon Island shore station (37.7° N 123.0° W, http://shorestation.ucsd.edu/active/index_active.html; representative of SST in the larger GOF region, Thayer et al. 2008). Anomalies were calculated by subtracting the climatological monthly mean from 1950 to 2008. Annual mean SST from May through August was compared against the principal component values of spring-summer salmon diet using linear regression.

Diet and abundance

We examined how fluctuations in salmon diet correspond to salmon survival as measured by the Sacramento Index (SI; 1983 to 2007) of ocean abundance for the fall-run Chinook salmon in central California. Samples in the 1980s and 2000s were almost exclusively Sacramento River fall-run Chinook (O'Farrell et al. 2013); although there is no way to confirm this for 1955 samples, they were captured during the same months in the same region. Relationships of the principal component values of diet and the SI with a 0 yr, 1 yr and 2 yr lag were investigated using logistic regression. Diet from the same year reflects conditions experienced by returning adults, and diet from lagged years may reflect what juveniles experienced in the ocean.

RESULTS

Annual diet composition

Main prey of Chinook salmon included northern anchovy, juvenile rockfish, euphausiid krill, Pacific sardine, crab megalopae *Cancer* spp., Pacific herring and market squid (Fig. 2, Tables S1–S3 in the Supplement).

Empty stomachs (0% gut fullness) were encountered in each year of sampling, but when comparing values for May–August across all years of the study, percentages of empty stomachs were higher in 2005–2007 (Table S1). Regardless of how we defined 'empty' (i.e. 0% gut fullness or 1% which contained trace amounts of prey), this pattern did not change; therefore, we do not believe this measure was biased by different researchers or slightly different methodologies. Most prey in the 'unknown fish' category for 2005 to 2007 were either anchovy or sardine, indistinguishable due to missing heads and/or the degree of digestion, not unknown species. Therefore, this would not have altered the observed patterns of identified prey, except to potentially increase the importance of sardine and anchovy in the diet in the 2000s, strengthening differences between decades.

Diet of Chinook salmon has changed over the last half-century. Shannon-Wiener indices of spring-summer diet diversity declined significantly through

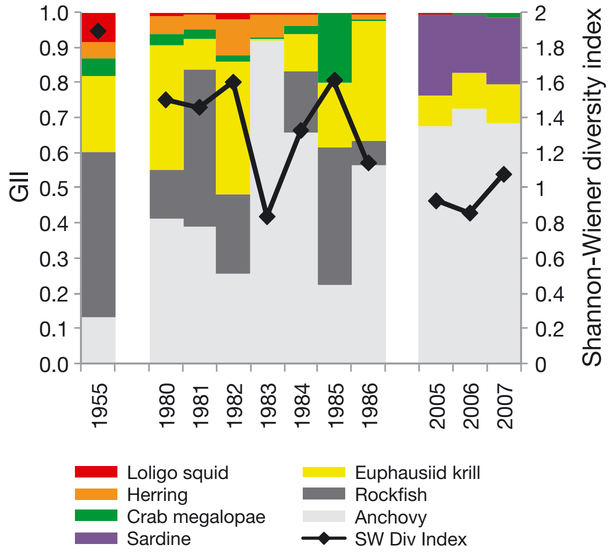

Fig. 2. *Oncorhynchus tshawytscha.* Chinook salmon diet in summer of 1955, 1980–1986 and 2005–2007, as represented by the geometric index of importance (GII). Annual Shannon-Wiener indices of diversity (SW Div Index) are overlaid

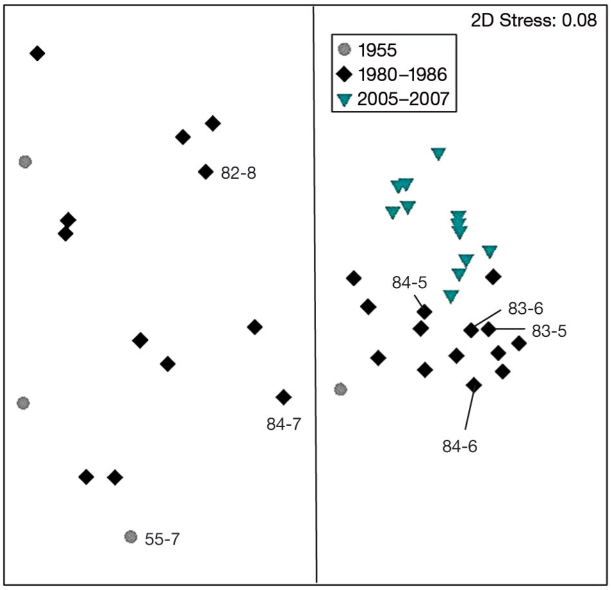

Fig. 3. Multi-dimensional scaling (MDS) ordination of Chinook salmon diet composition based on monthly Bray-Curtis similarity indices of geometric index of importance (GII) for the years 1955, 1980–1986, and 2005–2007. In general, data for May and June fall on the left side of the plot and July and August on the right side. Data points outside of this general pattern are labeled (yr-mo), with the exception of the mid-2000s

time (Spearman rho = –0.69, $p < 0.02$; Fig. 2). There was a slightly wider spatial sampling range of salmon in 2005 to 2007 (Supplementary methods in the Supplement), yet much lower diversity during these years.

In general, rockfish, krill, herring and squid in Chinook salmon diet have decreased, while sardine and anchovy have increased in importance (Fig. 2). Juvenile rockfish were very important in salmon spring-summer diet in 1955 and during the 1980s; however, they were completely absent from the mid-2000s diet. In the 1980s, species of *Sebastes* (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*. Krill was also well-represented in 1955 and in the 1980s. Herring and cancer megalopae, while still often important in the diet in 1955 and the 1980s, were barely detected in the 2000s or not at all. Sardine was not present in the diet at all until the mid-2000s.

Time trends as visualized in an MDS plot indicated a shift in salmon spring-summer diet composition through time (Fig. 3). The 1980s data points (SIMPER similarity = 47 %) clustered on the left side of the MDS plot were generally from the months May and June (and contained more juvenile rockfish and krill), while those on the right side were from July and August (and contained more anchovy and to a lesser extent, herring). There were no samples in July or August of 1985, and a few exceptions to the early/late summer pattern (see labeled months in Fig. 3). Overall, the MDS plot showed the monthly samples in 1955 fairly distant from each other, representing diet differences between months (SIMPER similarity = 43 %), contrasting with closely clustered samples in the 2000s (SIMPER similarity = 84 %). Diet in all months sampled in the 2000s was basically reduced to a dominance of anchovy, seen only in August and sometimes July in other decades. This also reflects the diminishing diversity indices observed through time.

Changes in spring-summer diet were also significant between decades (Table 1). Pairwise tests revealed significant differences for 2 out of 3 combinations of decades; the third was almost significant at $p < 0.07$ (1980s vs. 2000s). To test robustness, excluding months with low sample sizes only strengthened the results of the global and pairwise tests.

Decreasing importance of rockfish and krill, and increasing importance of sardine and anchovy in the diet were largely responsible for differences in decadal spring-summer diet composition (Table 1). The largest single contribution to diet differences was the

Table 1. Analysis of similarity (ANOSIM) test results of differences in Chinook salmon summer diet composition (geometric index of importance, GII) among decades (1950s, 1980s, 2000s). Contributions of main prey types to diet differences were identified by similarity percentage (SIMPER) analysis

	ANOSIM		SIMPER							Mean
	R	p	Rockfish	Anchovy	Euphausiid krill	Sardine	Loligo squid	Herring	Crab megalopae	dissimilarity
Global test	0.23	0.02								
Pairwise tests										
1955 vs. 1980s	0.24	0.035	35.8	27.0	20.0	n/a	6.9	4.1	6.3	63.0
1955 vs. 2000s	0.97	0.001	36.9	24.3	15.0	8.9	6.1	3.9	4.9	77.8
1980s vs. 2000s	0.13	0.068	18.3	31.4	22.4	17.6	0.7	6.2	3.5	50.5

decrease in juvenile rockfish through time. Market squid comprised 6 and 7% more of the diet in 1955 than in the 1980s or 2000s, respectively. A decline in herring accounted for 6% of the difference in diet composition between the 1980s and 2000s. Note that herring are not a large part of the summer diet of Chinook salmon, yet a decline was still evident. Historically, herring were much more important in the winter diet (Fig. 4).

Seasonal diet

Monthly examination of salmon diet was possible in spring-summer months for all 3 decades, and in winter and fall for 1955 and the 1980s (Fig. 4). Herring, squid and anchovy were historically present in the diet year round, although herring appeared to be most important in winter, squid in spring, and anchovy in fall. Appearing only seasonally, krill were most important in spring and rockfish in summer. This changed as herring was reduced in winter diet in the 1980s (no data were available for winter 2000s) and absent from summer diet in the 2000s (Fig. 4a). The importance of rockfish shifted temporally to earlier summer in the 1980s, and rockfish were completely absent in the 2000s (Fig. 4b). Squid was greatly reduced in spring diet in both the 1980s and 2000s and somewhat reduced in fall diet in the 1980s (no data were available for fall 2000s; Fig. 4c). Krill were at least as important or more important in diet in the 1980s compared to 1955, yet reduced in the 2000s (Fig. 4d). From 1955 to the 1980s, consumption of anchovy increased in spring to summer while consumption decreased in the fall (Fig. 4e). In the 2000s,

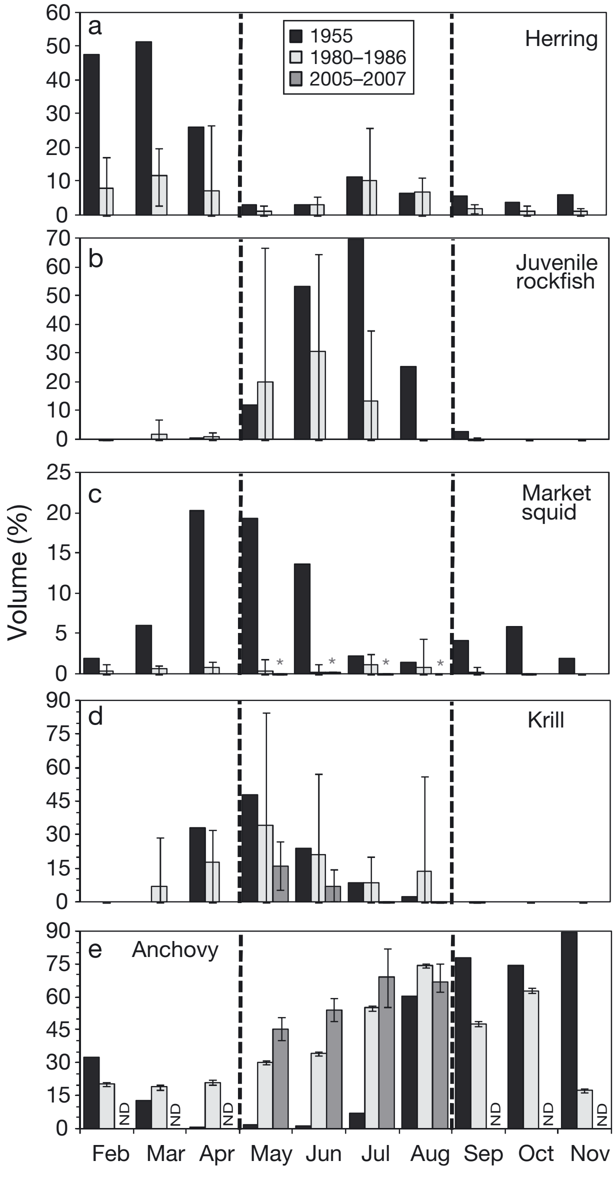

Fig. 4. *Oncorhynchus tshawytscha.* Monthly percent volume of forage species in Chinook salmon diet in 1955, 1980–1986, and 2005–2007: (a) herring, (b) juvenile rockfish, (c) market squid, (d) krill, and (e) anchovy. Error bars for 1980–1986 and 2005–2007 denote maximum and minimum annual percent volume in each time period. Dashed lines indicate Mar–Aug for which data were collected in all study periods (including 2005–2007). ND: no data were available for that period (Feb–Apr and Sep–Nov 2005–2007). *'trace' amounts of a specific prey

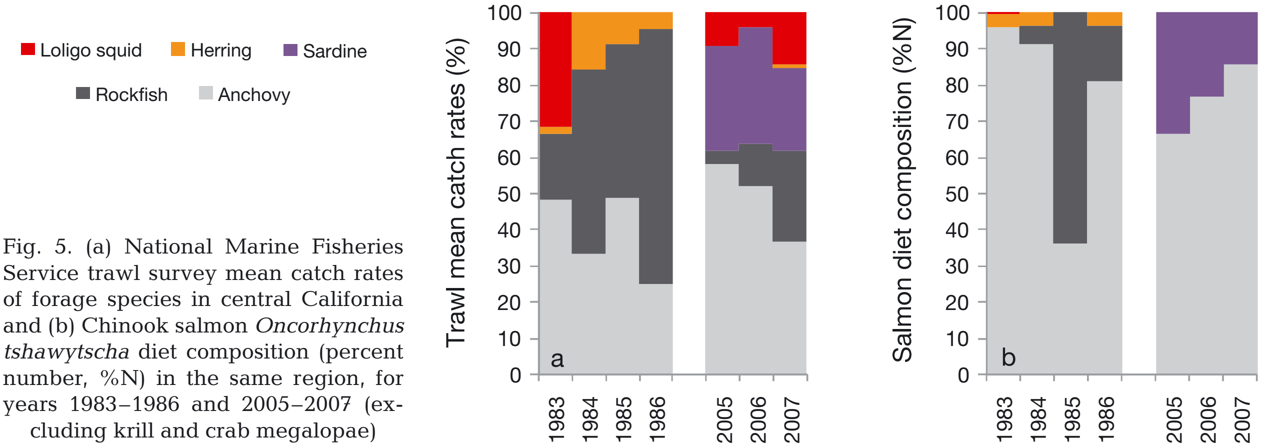

Fig. 5. (a) National Marine Fisheries Service trawl survey mean catch rates of forage species in central California and (b) Chinook salmon *Oncorhynchus tshawytscha* diet composition (percent number, %N) in the same region, for years 1983–1986 and 2005–2007 (excluding krill and crab megalopae)

the importance of anchovy greatly increased in summer diet. Sardine, which were absent in previous decades, also appeared in summer diet in the 2000s.

Prey size classes

Rockfish in spring-summer salmon diet in the 1980s ranged in size from 5 to 137 mm FL (mean of approximately 50 mm), while anchovy ranged from 5 to 175 mm (mean of approximately 100 mm). There were no rockfish sampled in salmon diet in the mid-2000s, but anchovy ranged from 78 to 170 mm (mean = 123 mm). Merkel (1957) did not distinguish prey size classes for spring-summer; summaries instead spanned February to November with rockfish ranging from 25 to 191 mm (including older fall fish of this spring-spawning species) and anchovy from 51 to 165 mm FL.

Diet and environment

An annual index of prey availability from NMFS mid-water trawls in May and June was available starting in 1983, and was significantly positively correlated with prey observed in the salmon diet in only May and June (rho = 0.62, p = 0.03); particularly anchovy, rockfish and sardine (Fig. 5). A large proportion of anchovy was observed in both trawls and salmon diet, as well as presence of sardine in the 2000s which was conspicuously absent from both in the 1980s. Rockfish was present in both trawls and diet in the 1980s. Salmon consumed substantially more rockfish in 1985 than was evident in trawls, while the opposite was true in 1984 and 1986. Trawls sampled small amounts of rockfish in the El Niño Southern Oscillation (ENSO) year of 1983 and the mid-2000s, but salmon diet did not reveal any rockfish during those years.

From a PCA of salmon diet, $PC1_{diet}$ explained 58 % of the variance in diet, while $PC2_{diet}$ explained 23 % of the variance (Fig. 6). $PC1_{diet}$ was an ordination of

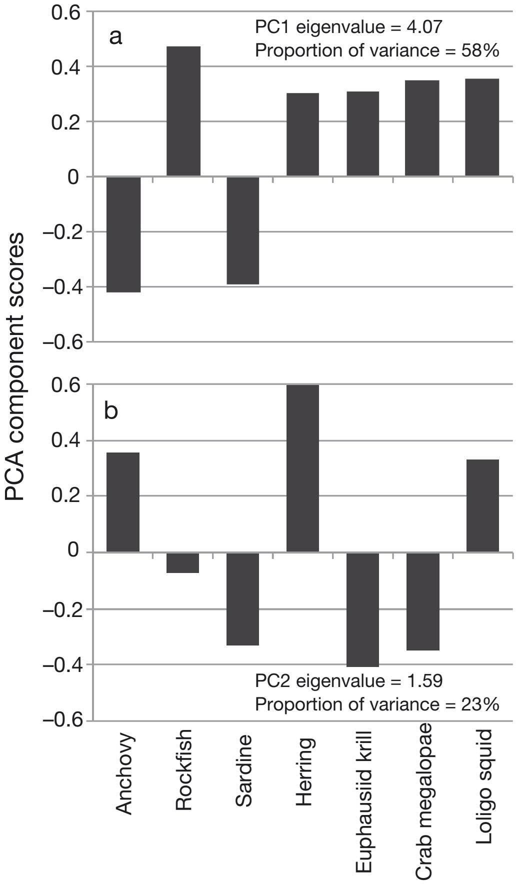

Fig. 6. Principal component analysis (PCA) (with eigenvalue, variance, and factor loadings) results for (a) PC1 and (b) PC2 for the main prey groups of Chinook salmon based on the GII diet index (for 1955, 1980–1986, 2005–2007)

diet from rockfish-krill-herring (high PC1) to sardine-anchovy (low PC1). $PC2_{diet}$ loaded anchovy, herring and squid positively and sardine, krill and crab negatively.

There was a significant negative correlation of SST from May through August with $PC1_{diet}$ for all years of the study ($\beta = -2.07$, $R^2 = 0.50$, $p = 0.01$; Fig. 7), but not with $PC2_{diet}$ ($\beta = 0.24$, $R^2 = 0.02$, $p = 0.70$). By decade, annual values of $PC1_{diet}$ were correlated with SST in the early 1980s ($\beta = -2.63$, $R^2 = 0.76$, $p = 0.01$), but not in the mid-2000s ($\beta = -0.32$, $R^2 = 0.43$, $p = 0.54$).

Diet and abundance

$PC1_{diet}$ was significantly related to the SI lagged by 2 years corresponding to the smolt ocean entry period (Logarithmic regression: $R^2 = 0.65$, $p = 0.02$; Fig. 8a), and lagged by 1 year corresponding to the second ocean year ($R^2 = 0.31$, $p = 0.02$), but not without any lag ($R^2 = 0.08$, $p = 0.30$). Below ~10 % of the maximum value of $PC1_{diet}$, effects on salmon were highly negative. $PC2_{diet}$ was not correlated to any of the SI datasets when the outlier 1985 was included (Fig. 8b). However, sampling in 1985 was conducted in May and June only; excluding this point resulted in a highly significant relationship between $PC2_{diet}$ and the SI lagged by 2 years ($R^2 = 0.67$, $p = 0.03$).

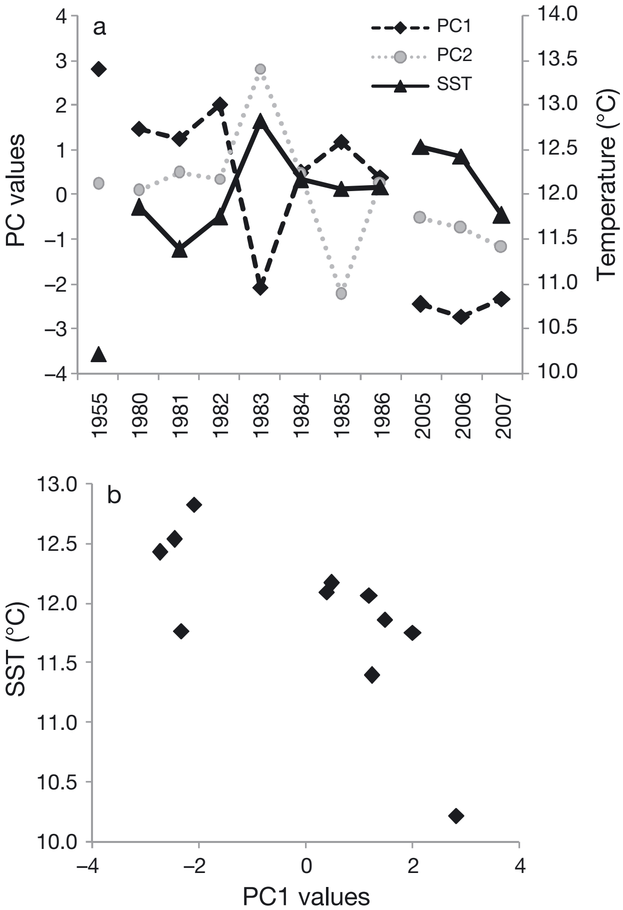

Fig. 7. (a) Changes in PC1 and PC2 of salmon diet and May–August sea surface temperature (SST) through time, and (b) relationship of PC1 against SST

DISCUSSION

There are a number of studies linking oceanographic variability to salmon production, but many of these lack analysis of underlying mechanisms driving salmon dynamics. We focused on salmon diet as one of these mechanisms, revealing correlations of diet with oceanographic variables and also with salmon production in the region. We interpret this as salmon production tracking environmental changes through diet, although the observed relationships are of course also possible due to covariance in response to an additional shared driver, as of yet unknown. Multiple aspects of diet are likely important to salmon growth and survival, including food abundance, diet diversity, and seasonal availability.

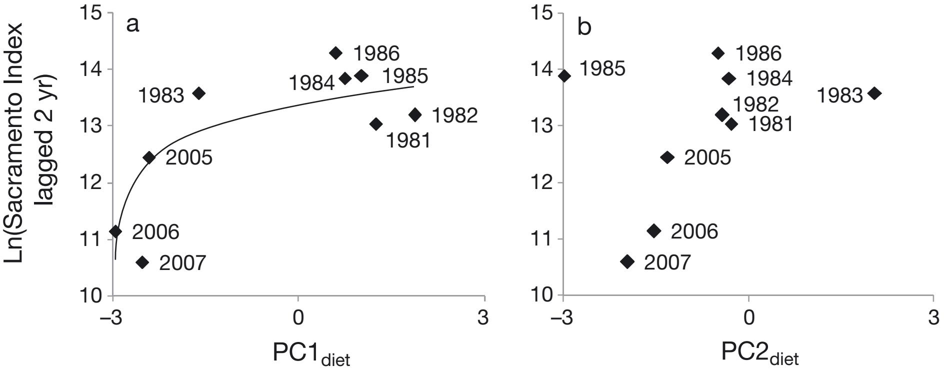

Fig. 8. Relationship between (a) PC1 or (b) PC2 of geometric index of importance (GII) for Chinook salmon diet in May–August, and the Sacramento Index (SI) lagged by 2 years (for 1982–1986, and 2005–2007, years for which the SI was available). PC1 trendline depicts logarithmic regression

Diet links environment to salmon abundance

Over the past 3 decades, physical and biological oceanographic conditions have varied greatly in continental shelf waters of the CC. There was a strong La Niña in 1955, a period of very cool and productive ocean conditions (strength compared to 1999; Wolter & Timlin 1998). Between 1977 and 1998, the northern CC was in a warm and relatively unproductive phase; during this period salmon numbers in this region declined. One of the strongest ENSO events on record occurred in 1982–83 (Wolter & Timlin 1998), followed by a short La Niña event. The 1982–83 ENSO produced SST anomalies of +1.0 to 2.5°C, deepened the inshore thermocline by as much as 50 m, and affected biota in mid-latitude coastal areas of the North Pacific (Simpson 1992). Since the mid-1990s, conditions in the northern CC have been particularly variable, with the 1997–98 ENSO followed by 4 years of La Niña events. During these cool, productive La Niña years, northeast Pacific salmon rebounded. However, in late 2002, oceanographic conditions again reversed, and warm conditions prevailed for the next 4 years. Except for 2003, this period was not characterized by ENSO; instead, the positioning of the North Pacific High and latitude of the North Pacific Current may have been stronger influences (Sydeman et al. 2006, 2011). This recent warm phase coincided with a decline in adult return rates of both coho and Chinook salmon (Peterson & Hooff 2006).

Overall, SST explained a large amount of variability in Chinook diet composition in our study, which was not surprising given the effect of SST on the vertical and horizontal distribution and abundance of pelagic schooling prey species. Other studies along the northeast Pacific have also found that salmon production is more strongly linked to local oceanographic processes such as SST than to basin-scale indices (Mueter et al. 2002). Chinook salmon diet in our study exhibited a strong correlation with SST in the mid-1980s, but not as much in the mid-2000s. ENSO/La Niña events with related SST signals were strong in 1955 and the early 1980s. Generally warmer SST were observed between 2005 and 2007 in the central to northern CC (García-Reyes & Largier 2012), although ENSO mechanisms were not evident (Sydeman et al. 2011). Our MDS analysis showed that diet composition in the mid-2000s had changed most notably (relative to previous decades) in May and June. The declining diet diversity, and specifically the lack of intra-annual variability in 2000s may explain why the relationship between diet and SST broke down during this period. $PC1_{diet}$, to which SST was linked, appeared to reflect a continuum of cool-water species (rockfish, krill, herring) to warmer-water species (anchovy, sardine), as well as changes in diversity (higher under cooler conditions), given the remarkably similar pattern between the Shannon-Wiener index of diversity and $PC1_{diet}$ through time.

Both $PC1_{diet}$ and $PC2_{diet}$ were significantly correlated with a lagged SI of ocean abundance for fall-run Chinook, indicating different aspects of diet that influence salmon abundance. The interpretation of $PC2_{diet}$ was not clear, but may represent spatial availability of prey. Anchovy, herring, and squid loaded positively on $PC2_{diet}$, while krill, crab megalopae and to a lesser extent sardine loaded negatively. A spatial study in the larger Gulf of the Farallones region since 1990 shows that anchovy and squid have generally been found on the continental shelf and to the south, and krill *Euphausia pacifica* and sardine were found further offshore, largely along the shelf-break (Santora et al. 2012).

The relationship of $PC1_{diet}$ with the SI lagged by both 1 and 2 years potentially indicates the importance of diet to ocean-entry smolts and second-ocean-year fish. Juvenile Chinook salmon eat larval and juvenile stages of fish as well as krill and other small micronekton (MacFarlane & Norton 2002, Daly et al. 2009). Specifically in the Gulf of the Farallones, MacFarlane & Norton (2002) found that at least half, if not more, of the diet of smolts was fish, with krill and crab megalopae making up most of the remainder. Fish in smolt diets, when constrained to ocean catches in the same region and solely during the same months (May through August), were comprised largely of anchovy (mean size 67 mm, range 30 to 97mm), Pacific herring (mean size 60 mm, range 50 to 70 mm) and rockfish (mean size 36 mm, size range 13 to 70 mm) (B. MacFarlane unpubl. data), representing somewhat smaller individuals but with considerable overlap with the prey sizes we observed in adult diet. Chinook smolts from the Sacramento fall run typically enter the ocean in late spring or early summer (Lindley et al. 2009), which overlapped with our adult salmon diet sampling period (May through August). Therefore, adult salmon diet could be a reasonable index of ocean prey availability for smolts and subadults in this region. As suggested by many studies, the timing and availability of prey may be important for salmon survival (Chittenden et al. 2010, MacFarlane 2010, Wells et al. 2012). Diet is related to survival of salmon in general through abundance and nutritive content of food, and also specifically for smolts through growth rates (to attain larger size and avoid predation; Beamish & Mahnken 2001, Daly et al. 2009).

The one year in our study that did not quite fit the relationship between salmon diet composition and the lagged SI was 1983 — a strong ENSO year. Salmon abundance in the year of return was higher than expected for such a negative $PC1_{diet}$ score (more anchovy than rockfish in the diet). However, anchovies in salmon diet in 1983 consisted of smaller size classes, with roughly 10% smaller than 20 mm (compared to no more than 3% of anchovies <40 mm in other years in the 1980s), sizes much more accessible as smolt prey than the typical anchovies observed (means of ≥100 mm). $PC1_{diet}$ may possibly be interpreted as containing an element of prey size importance to salmon as well.

Other studies relating salmon returns to diets during a similar time period to our study showed mixed results. Daly et al. (2009) examined inter-annual and seasonal ontogenetic diet shifts in juvenile salmon off Oregon and Washington in the 1980s versus the late 1990s and early 2000s (1998 to 2003). Daly et al.'s (2009) expectations that juvenile salmon would feed on larger, higher quality prey such as fish, and have higher stomach fullness in high survival years were somewhat but not entirely supported by their data. During lower-survival years, coho salmon ate fewer and smaller fish prey, while ocean-entry year Chinook salmon had less total food and more empty stomachs. Interestingly, Daly et al. (2009) also documented a sharp increase in the percent of empty stomachs between the 1980s and the 1999 to 2003 period, consistent with what we observed between the early 1980s and the mid-2000s. Yet no consistent trophic patterns for larger Chinook salmon in relation to their ultimate survival were seen in that study.

Regionally, a recent 10 yr study (1997 to 2006) linked central California Chinook salmon returns with krill abundance in the year of ocean entry, and juvenile rockfish abundance in the year of return (Thompson et al. 2012). While diet in our study was significantly related to 2 yr lagged returns (ocean entry year) and 1 yr lagged returns (second ocean year), we saw no relationship in the year of return.

Spatio-temporal heterogeneity of food resources

Diet diversity declined significantly in our study between 1955 and the mid-2000s. A diet dominated by rockfish in summer 1955 and containing herring, krill, squid, crab and anchovy changed to include more anchovy in the mid-1980s, but switched to a diet dominated by anchovy in the mid-2000s. Granted, 1955 (n = 1, i.e. a single year, but the only historical data available) was an anomalously cool and productive year, likely favoring rockfish spawning and survival; although a significant decline of rockfish in the diet still occurred between the early 1980s (n = 7 years) and mid-2000s (n = 3 years, when rockfish were completely absent). This switch from juvenile rockfish to anchovy has been observed in other predator species in the central CC (e.g. rhinoceros auklet *Cerorhinca monocerata* and common murre *Uria aalge*; Sydeman et al. 2001, Thayer & Sydeman 2007). There are alternative reasons why diet could have become increasingly dominated by anchovy (and sardine) — either scarcity of other prey, or super-abundance of anchovy (and sardine). The former, however, seems more parsimonious. Poor conditions in 2005–2007 resulted in the lowest levels of juvenile rockfish abundance in a 25 yr time series (Field et al. 2010, although abundance has subsequently increased; Bjorkstedt et al. 2011). In 2005–2007, the trawl survey also exhibited low squid and krill abundances and positive but not overly abundant anchovy and sardine (Bjorkstedt et al. 2011). The trawl surveys were a good index of salmon prey availability as shown by the significant correlation between diet and survey in our study (1983–1986, 2005–2007); similar results were reported from the 4 years of overlap between the trawl results and diet in the 1980s only (Larson 1987). Bio-acoustic and modeling data also showed significant decrease of krill abundance in 2005–2006, with spatial distribution shifting south away from the Gulf of the Farallones (Santora et al. 2011, Dorman et al. 2011) — consistent with reduced krill occurrence in salmon diet during those years.

Salmon rely on a diverse array of prey resources not only due to inter-annual variability, but also because of intra-annual variability in each one. Merkel (1957) stressed this point. The timing of spawning of herring (winter; Watson & Sandknop 1996), squid (spring, with smaller pulse in fall; Fields 1965), krill (spring-summer; Feinberg & Peterson 2003), and rockfish (spring-summer; Ralston & Howard 1995) in the CC coincides with higher occurrences of these species in salmon diet. Prey appearing to be 'subdominant' in diet composition at an annual scale may be more important on a seasonal or monthly scale due to changing availability — herring being a case in point (see Fig. 4). Overall, in addition to a decline in diet diversity through the study period, diet changed the most with respect to composition in May and June — a period previously dominated by rockfish and krill, and the time during which Chinook smolts from the Sacramento fall run typically enter the ocean. Both the reduced abundance of specific prey types and required prey size classes may have negatively impacted ocean-entry smolts in May and June of the mid-2000s and could be related to population crashes observed several years later, as also indicated by Wells et al. (2012), who focused their analysis on interactions between ocean-entry smolts and variability in krill abundance.

This suggests that salmon may be vulnerable to the loss of one or several key prey resources, especially if this comes during a critical period of the season. Rockfish (excluding shortbelly rockfish *S. jordani* and a few other species), herring and market squid — 3 of the 4 salmon prey types which declined significantly during our study — are commercially exploited. Periods of exploitation match decreases of these species in salmon diet. The California herring fishery underwent a dramatic resurgence from 1972 to 1980 (Spratt 1981), and the herring population is currently thought to be depressed with significant age-class truncation (CDFG 2011a). The market squid fishery in California grew substantially from the mid-1970s to the 2000s (CDFG 2011b). Although the main fishery for market squid occurs off southern California, there is also a smaller fishery in central California. Many rockfish populations (e.g. widow, etc.) were overexploited in the 1990s leading to low population sizes, although some unexploited rockfish populations such as the shortbelly rockfish also declined (Field et al. 2007). A combination of overexploitation and ocean conditions may have contributed to low availability for predators (Field et al. 2010). Anchovy and sardine, which increased in importance in the diet as these other species declined, are also commercially important. Increased future climate variability, such as greater inter-annual variation in ENSO (Lee & McPhaden 2010) could lead to still greater sensitivity between climate and fishing effects, resulting in greater variability in the forage base for dependent predators (Shelton & Mangel 2011).

As key forage for an ecologically vulnerable and economically important species such as Chinook salmon, it may be prudent to take a more conservative approach to fishing allowances for these prey species. Modeling studies have suggested that if all species are fished at maximum sustainable yield (MSY), yield of higher trophic-level species decreases as the lower trophic-level species decline (Walters et al. 2005, Smith et al. 2011). In the case of salmon, forage includes mid-trophic small pelagic fishes (anchovy, sardine, herring), juveniles of larger higher-trophic fish (rockfish), and low to mid-trophic invertebrates (krill, market squid). Although existing management measures for coastal pelagic species include some consideration of forage needs (MacCall 2009, PFMC 2011), they are not based on comprehensive assessments of such needs, nor are they coordinated across management entities (e.g. state and federal agencies) to ensure some stability among multiple populations of forage species.

Species-rich communities are thought to produce more temporally stable ecosystem services, termed the 'portfolio' or stabilizing effect. Salmon population diversity has been shown to stabilize variability in returns (Schindler et al. 2010, Carlson & Satterthwaite 2011). We suggest that a similar argument can be invoked for salmon prey. For Sacramento River Chinook, not only has population-level diversity decreased (the population is currently predominantly hatchery fish), but prey diversity has declined as well. Both of these factors have likely contributed to reduced and more variable Chinook salmon abundance and return rates. Therefore, in addition to direct salmon management, efforts to better understand and manage salmon prey are imperative.

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LITERATURE CITED

Assis CA (1996) A generalized index for stomachs analysis in fish. Sci Mar 60:385–389

➤ Beamish RJ, Mahnken C (2001) A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog Oceanogr 49:423–437

Bjorkstedt EP, Goericke R, McClatchie S, Weber E and others (2011) State of the California Current 2010–2011: regional variable responses to a strong (but fleeting?) La Niña. CCOFI Rep 52:36–69

➤ Botsford L, Lawrence CA (2002) Patterns of covariability among California Chinook salmon, coho salmon, dungeness crab, and physical oceanographic conditions. Prog Oceanogr 53:283–305

➤ Carlson SM, Satterthwaite WH (2011) Weakened portfolio effect in a collapsed salmon population complex. Can J Fish Aquat Sci 68:1579–1589

CDFG (California Department of Fish and Game) (2011a) Final supplemental environmental document Pacific herring commercial fishing regulations (Sections 163, 1631, 1635, and 164, Title 14, California Code of Regulations). SCH No. 98052052, CDFG, Sacramento, CA

CDFG (California Department of Fish and Game) (2011b) Review of selected California fisheries for 2009: coastal pelagic finfish, market squid, ocean salmon, groundfish, highly migratory species, dungeness crab, spiny lobster, spot prawn, Kellet's whelk, and white seabass. CCOFI Rep 52:13–35

Chittenden CM, Jensen JL, Ewart D, Anderson S and others (2010) Recent salmon declines: a result of lost feeding opportunities due to bad timing? PLoS ONE 5:e12423

Clarke MR (1986) A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E, Plymouth

Daly EA, Brodeur RD, Weitkamp LA (2009) Ontogenetic shifts in diets of juvenile and subadult coho and Chinook salmon in coastal marine waters: important for marine survival? Trans Am Fish Soc 138:1420–1438

Di Lorenzo E, Miller AJ, Schneider N, McWilliams JC (2005) The warming of the California Current: dynamics and ecosystem implications. J Phys Oceanogr 35:336–362

Dorman JG, Powell TM, Sydeman WJ, Bograd SJ (2011) Advection and starvation cause krill (*Euphausia pacifica*) decreases in 2005 Northern California coastal populations: implications from a model study. Geophys Res Lett 38:L04605, doi:101029/2010GL046245

Feinberg LR, Peterson WT (2003) Variability in duration and intensity of euphausiid spawning off central Oregon, 1996–2001. Prog Oceanogr 57:363–379

Field JC, Dick EJ, Key M, Lowry M and others (2007) Population dynamics of an unexploited rockfish (*Sebastes jordani*) in the California Current. In: Heifetz J, DiCosimo J, Gharrett AJ, Love MS, O'Connell VM, Stanley RD (eds) Biology, assessment, and management of north Pacific rockfishes. Alaska Sea Grant Rep AK-SG-07-01, Fairbanks, AK, p 451–472

Field JC, MacCall AD, Bradley RW, Sydeman WJ (2010) Estimating the impacts of fishing on dependent predators: a case study in the California Current. Ecol Appl 20: 2223–2236

Fields WG (1965) The structure, development, food relations, reproduction, and life history of the squid, *Loligo opalescens* Berry. Fish Bull Calif Dep Fish Game No. 131, Scripps Institution of Oceanography, San Diego, CA

Fissel BE, Lo NCH, Herrick SF (2011) Daily egg production, spawning biomass and recruitment for the central subpopulation of northern anchovy 1981–2009. CCOFI Rep 52:116–129

García-Reyes M, Largier JL (2012) Seasonality of coastal upwelling off central and northern California: new insights, including temporal and spatial variability. J Geophys Res 117:C03028, doi:10.1029/2011JC007629

Harding JA, Ammann AJ, MacFarlane RB (2011) Regional and seasonal patterns of epipelagic fish assemblages from the central California Current. Fish Bull 109:261–281

Harvey JT, Loughlin TR, Perez MA, Oxman DS (2000) Relationship between fish size and otolith length for 62 species of fishes from the eastern north Pacific Ocean. NOAA Tech Rep NMFS 150

Hill KT, Crone PR, Lo NCH, Macewicz BJ, Dorval E, McDaniel JD, Gu Y (2011) Assessment of the Pacific sardine resource in 2011 for US management in 2012. Stock assessment and fishery evaluation. NOAA National Marine Fisheries Service, La Jolla, CA. Available at www.pcouncil.org/wp-content/uploads/F2b_SUP_ATT8_2011_Pacific_Sardine_Assessment_FINAL_Draft1.pdf

Hunt SL, Mulligan TJ, Komori K (1999) Oceanic feeding habits of Chinook salmon, *Oncorhynchus tshawytscha*, off northern California. Fish Bull 97:717–721

Koslow JA, Hobday A, Boehlert GW (2002) Climate variability and marine survival of coho salmon (*Oncorhynchus kisutch*) off the coast of California, Oregon and Washington. Fish Oceanogr 11:65–77

Larson RJ (ed) (1987) Progress in rockfish recruitment studies. Administrative Report T-87-01, Southwest Fisheries Center, National Marine Fisheries Service, Tiburon, CA

Lavaniegos BE, Ohman MD (2007) Coherence of long-term variations of zooplankton in two sectors of the California Current system. Prog Oceanogr 75:42–69

Lee T, McPhaden MJ (2010) Increasing intensity of El Niño in the central-equatorial Pacific. Geophys Res Lett 37: 14603, doi:10.1029/2010GL044007

Lindley ST, Grimes CB, Mohr MS, Peterson W and others (2009) What caused the Sacramento River fall Chinook stock collapse? NOAA Tech Memo NMFS NOAA-TM-NMFS-SWFSC-447

Litz MN, Emmett RL, Heppell SS, Brodeur RD (2008) Ecology and distribution of the northern subpopulation of northern anchovy (*Engraulis mordax*) off the US West Coast. CCOFI Rep 49:167–182

MacCall AD (2009) A short scientific history of the fisheries. In: Checkley, D, Alheit J, Oozeki Y, Roy C (eds) Climate change and small pelagic fish. Cambridge University Press, Cambridge

MacFarlane RB (2010) Energy dynamics and growth of Chinook salmon (*Oncorhynchus tshawytscha*) from the Central Valley of California during the estuarine phase and first ocean year. Can J Fish Aquat Sci 67:1549–1565

MacFarlane RB, Norton EC (2002) Physiological ecology of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California. Fish Bull 100:244–257

Mahe K, Amara R, Bryckaert T, Kacher M, Brylinski JM (2007) Ontogenetic and spatial variation in the diet of hake (*Merluccius merluccius*) in the Bay of Biscay and the Celtic Sea. ICES J Mar Sci 64:1210–1219

Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. Bull Am Meteorol Soc 78: 1069–1079

Merkel TJ (1957) Food habits of the king salmon, *Oncorhynchus tshawytscha* (Walbaum), in the vicinity of San Francisco, California. Calif Fish Game 43:249–270

Mueter FJ, Ware DM, Peterman RM (2002) Spatial correlation patterns in coastal environmental variables and survival rates of salmon in the north-east Pacific Ocean. Fish Oceanogr 11:205–218

O'Farrell MR, Mohn MS, Palmer-Zwahlen ML, Grover AM (2013) The Sacramento Index (SI). NOAA Tech Memo NOAA-TM-NMFS-SWFSC-512

Peterson WT, Hooff RC (2006) Relationships between interannual and decadal changes in the Pacific Decadal Oscillation (PDO), zooplankton community structure, and coho and Chinook survival in the coastal ocean off the Pacific Northwest. EOS Trans Am Geophys Union 87 (Abstract)

PFMC (Pacific Fisheries Management Council) (2011) Coastal pelagic species fishery management plan as amended through Amendment 13. Pacific Fishery Management Council, Portland, OR

Ralston S, Howard DF (1995) On the development of year-class strength and cohort variability in two northern California rockfishes. Fish Bull 93:710–720

➤ Santora JA, Ralston S, Sydeman WJ (2011) Spatial organization of krill and seabirds in the central California Current. ICES J Mar Sci 68:1391–1402

➤ Santora JA, Field JC, Schroeder ID, Sakuma KM, Wells BK, Sydeman WJ (2012) Spatial ecology of krill, micronekton and top predators in the central California Current: implications for defining ecologically important areas. Prog Oceanogr 106:154–174

➤ Scheuerell MD, Williams JG (2005) Forecasting climate-induced changes in the survival of Snake River spring/summer Chinook salmon (*Oncorhynchus tshawytscha*). Fish Oceanogr 14:448–457

➤ Schindler DE, Hilborn R, Chasco B, Boatright CP, Quinn TP, Rogers LA, Webster MS (2010) Population diversity and the portfolio effect in an exploited species. Nature 465: 609–612

➤ Shelton AO, Mangel M (2011) Fluctuations of fish populations and the magnifying effects of fishing. Proc Natl Acad Sci USA 108:7075–7080

➤ Simpson JJ (1992) Response of the southern California Current system to the mid-latitude North Pacific coastal warming events of 1982–1983 and 1940–1941. Fish Oceanogr 1:57–79

➤ Smith ADM, Brown CJ, Bulman CM, Fulton EA and others (2011) Impacts of fishing low-trophic level species on marine ecosystems. Science 333:1147–1150

➤ Somerfield PJ, Clarke KR, Olsgard F (2002) A comparison of the power of categorical and correlational tests applied to community ecology data from gradient studies. J Anim Ecol 71:581–593

Spratt JD (1981) Status of the Pacific herring, *Clupea harengus pallasii*, resource in California, 1972 to 1980. Fish Bull Calif Dep Fish Game 171:1–107

➤ Sydeman WJ, Hester MM, Thayer JA, Gress F, Martin P, Buffa J (2001) Climate change, reproductive performance, and diet composition of marine birds in the southern California Current system, 1969–1997. Prog Oceanogr 49:309–329

Sydeman WJ, Bradley RW, Warzybok P, Abraham CL and others (2006) Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: unusual atmospheric blocking? Geophys Res Lett 33:L22S09, doi: 101029/2006GL026736

Sydeman WJ, Thompson SA, Field JC, Peterson WT and others (2011) Does positioning of the North Pacific Current affect downstream ecosystem productivity? Geophys Res Lett 38:L12606, doi:101029/2011GL047212

➤ Thayer JA, Sydeman WJ (2007) Spatio-temporal variability in prey harvest and reproductive ecology of a piscivorous seabird, *Cerorhinca monocerata*, in an upwelling system. Mar Ecol Prog Ser 329:253–265

➤ Thayer JA, Bertram DF, Hatch SA, Hipfner MJ, Slater L, Sydeman WJ, Watanuki Y (2008) Forage fish of the Pacific Rim as revealed by diet of a piscivorous seabird: synchrony and relationships with sea surface temperature. Can J Fish Aquat Sci 65:1610–1622

➤ Thompson SA, Sydeman WJ, Santora JA, Black BA and others (2012) Linking predators to seasonality of upwelling: using food web indicators and path analysis to infer trophic connections. Prog Oceanogr 101: 106–120

➤ Thomson RE, Beamish RJ, Beacham TD, Trudel M, Whitfield PH, Hourston RAS (2012) Anomalous ocean conditions may explain the recent extreme variability in Fraser River sockeye salmon production. Mar Coast Fish 4: 415–437

➤ Walters CJ, Christensen V, Martell SJ, Kitchell JF (2005) Possible ecosystem impacts of applying MSY policies from single-species assessment. ICES J Mar Sci 62: 558–568

➤ Warton DI, Hui FKC (2011) The arcsine is asinine: the analysis of proportions in ecology. Ecology 92:3–10

Watson W, Sandknop EM (1996) Clupeidae: herrings. In: HG Moser (ed) The early stages of fishes in the California Current region. CalCOFI Atlas No. 33, Allen Press, Lawrence, KS, p 159–171

➤ Wells BK, Santora JA, Field JC, MacFarlane RB, Marinovic BB, Sydeman WJ (2012) Population dynamics of Chinook salmon *Oncorhynchus tshawytscha* relative to prey availability in the central California coastal region. Mar Ecol Prog Ser 457:125–137

➤ Wolter K, Timlin MS (1998) Measuring the strength of ENSO events: How does 1997/98 rank? Weather 53:315–323

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