Received Date : 20-Mar-2016
Revised Date : 07-Jul-2016
Accepted Date : 13-Jul-2016
Article type : Original Article

Interannual variability in the feeding and condition of subyearling Chinook salmon off Oregon and Washington in relation to fluctuating ocean conditions

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ABSTRACT

Chinook salmon (*Oncorhynchus tshawytscha)* is one of several economically-important species of salmon found in the Northeast Pacific Ocean. The first months at sea are believed to be the most critical for salmon survival, with the highest rate of mortality occurring during this period. Here, we examine interannual diet composition and body condition trends for late-summer subyearling Chinook salmon caught off Oregon and Washington from 1998 to 2012. Interannual variability was observed in juvenile salmon diet composition by weight of prey consumed. Juvenile subyearling Chinook salmon were mainly piscivorous, with northern anchovy (*Engraulis mordax)* being especially important, making up half the diet by weight in some years. Annual diets clustered into two groups, primarily defined by their proportion of invertebrate prey (14% versus 39% on average). Diet composition was found to influence adult returns, with salmon from high-invertebrate years returning in significantly larger numbers 2-3 years later. However, years that had high adult returns had overall lower stomach fullness and poorer body condition as juveniles, a counterintuitive result potentially driven by the enhanced survival of less fit individuals in better ocean conditions (top-down effect). Ocean conditions in years with a higher percentage of invertebrates in salmon diets were significantly cooler from May-August, and bottom-up processes may have led to a fall plankton community with a larger proportion of invertebrates. Our results suggest that the fall plankton community assemblage during this first fall may be critical in predicting adult returns of Chinook salmon in the Pacific Northwest.

Key words: Juvenile Chinook salmon, feeding, piscivory, body condition, ocean conditions

INTRODUCTION

Fish stocks around the globe are decreasing as the human footprint and the demand for seafood rise. Pacific salmon (*Oncorhynchus* spp.) are no exception, with 26 Evolutionary Significant Units (ESUs) in Oregon, Washington, California, and Idaho, USA. Of the 17 separate ESUs known to exist for Chinook salmon (*Oncorhynchus tshawytscha*) in the Pacific Northwest, seven are listed as threatened and two as endangered (Good *et al.*, 2005), including the threatened Snake River Chinook salmon population. Yet salmon remain a culturally and commercially important part of the Pacific Northwest. Deepening our understanding of the connections between the ocean environment, behavior, and survival of salmon during critical periods of their life cycle is crucial, especially in the face of warming effects from recent large-scale ocean anomalies and unusually strong El Niño-Southern Oscillation (ENSO) conditions (Wainwright and Weitkamp, 2013, Bond *et al.*, 2015, Leising *et al.*, 2015). The study of all stages of salmonid life history over multiple years is crucial to predicting adult returns, determining catch quotas, and managing the timing and number of hatchery releases.

Salmon are anadromous and spend up to one year post-hatching in freshwater before traveling to the ocean where they remain for 1-6 years before returning to their natal rivers to spawn. Salmon that migrate out to the ocean in their first year of life are termed "subyearlings." Residence times in each body of water, as well as migration paths once juveniles reach the coast, are highly variable between species and stock groups, and environmental and biological factors important to the survival of one stock may not apply to others (Tucker *et al.*, 2011, Fisher *et al.*, 2014, Weitkamp *et al.*, 2015). Typical ocean residencies of Chinook salmon are on the order of two to four years.

Studies suggest that the first few months at sea are the most critical part of the salmonid life cycle (Holtby *et al.*, 1990, Pearcy, 1992, Beamish *et al.*, 2004), although full explanations for high rates of juvenile mortality remain elusive. A plethora of environmental, biological, and physical factors are thought to play a role, and it is unclear whether bottom-up (prey-based) or top-down (predator-based) controls are more important. High mortality may be due to the "critical size, critical period" hypothesis (Beamish and Mahnken, 2001): during the first few months at sea, salmon are at high risk for size-selective predation, and fast-growing fish are more likely to survive than slow-growing fish (Duffy and Beauchamp, 2011). The faster a fish can grow, the less time it is a potential prey item for gape-limited predators (Moss *et al.*, 2005). The first months at sea may also represent a "critical period" when salmon must put away energy in fat storage to be able to survive the colder, less productive winter months (Beamish and Mahnken, 2001). The body condition of the fish is dependent upon individual growth rates, prey quantity, and prey quality, especially of the ichthyoplankton community (Auth, 2011, Daly *et al.*, 2013). The shift from feeding on invertebrates to larger, less numerous, but higher quality fish prey could be key to achieving the growth rate necessary for escaping predation and reaching the “critical size” for over-winter survival (Daly *et al.*, 2009).

Analysis of stomach contents to assess diet has been a standard practice in fish ecology for decades (Hyslop, 1980). The amount and type of food can potentially be used as a metric to assess a fish’s physical condition, extrapolate prey field composition, and enhance understanding of the link between diet, growth, and survival. Chinook salmon represent a relatively opportunistic species and exhibit a broad trophic spectrum during their first few months at sea. However, several groups stand out as important food sources, especially northern anchovy (*Engraulis mordax*), Pacific sand lance (*Ammodytes hexapterus*), rockfishes (*Sebastes* spp.), euphausiids, and crab megalopae (especially *Cancer* spp.) (Brodeur and Pearcy, 1990, Brodeur, 1991, Daly *et al.*, 2009, Wells *et al.*, 2012).

Oceanographic conditions during the spring and early summer have important consequences for salmon migrating out of the rivers months later (Malick *et al.*, 2015, Wells *et al.*, 2016). Sea surface temperature, a strong North Pacific high pressure system causing shelf upwelling, and certain macroscale climate oscillations have consequences for primary productivity and zooplankton density, with effects potentially lasting into the following year (Henson and Thomas, 2007, Wells *et al.*, 2012). Late or early upwelling or anomalously cool or warm ocean conditions could cause trophic mismatches between predators and the prey field (Chittenden *et al.*, 2010). The early plankton assemblage represents the forage base of the fish prey that Chinook salmon will eventually eat; i.e., early ocean conditions affect the prey of the prey of the juvenile salmon. Thus, oceanographic conditions prior to and during outmigration have the potential to affect juvenile salmon feeding behavior and body condition.

Here, we examine 1) whether Chinook salmon diets differ between years in composition and amount of food eaten; 2) if physical characteristics of the subyearlings (body condition, stomach fullness, and length) vary between years or with diet; 3) if oceanographic conditions at the time of ocean entry influence diet or physical characteristics of the fish; and 4) if adult returns can be predicted by oceanographic conditions, diet, or physical characteristics of the fish at the time of entry. As a result of genetic population analyses (Claiborne *et al.*, 2014, Teel *et al.*, 2015), we are further able to examine a subset of fish from the threatened Snake River population to determine whether there are feeding or physical disparities between this stock and other fall subyearling Chinook salmon caught concurrently.

This is the first long-term study to focus exclusively on the feeding of fall subyearling Chinook salmon and their trophic responses to variable oceanographic conditions. It is also one of only a few to look at a large (>10 year) dataset on juvenile feeding habits. Prior long-term studies have focused on other species (Brodeur *et al.*, 2007a, Fergusson *et al.*, 2013) or on yearling Chinook salmon entering the ocean in early summer (Daly and Brodeur, 2015). This study further supplements the general body of knowledge on feeding ecology of salmon in the ocean. Past efforts have concentrated on spatial and geographical variations (Brodeur *et al.*, 2007b, Hertz *et al.*, 2015), differences between species (Brodeur, 1992, Schabetsberger *et al.*, 2003, Baldwin *et al.*, 2008, Weitkamp and Sturdevant, 2008, Daly *et al.*, 2009), and some interannual variation (Brodeur *et al.*, 2007a, Fergusson *et al.*, 2013, Thayer *et al.*, 2014).

METHODS

Data collection

Subyearling Chinook salmon were collected between September 19th and October 3rd from 1998-2012 from Newport, Oregon (44.6°N) to northern Washington (48°N) (Table 2). Sampling was conducted at nine transects oriented perpendicular to shore during daylight, extending from inshore to the continental shelf break (Fig. 1). A 264 Nordic pelagic rope trawl with a mouth opening 20 m deep by 30 m wide was used for sampling; the net was towed at 6 km/h for 30 minutes. Salmon were identified to species, measured (fork length to 1 mm), and immediately frozen. In the lab, salmon were re-identified, re-measured, and weighed (g). Salmon with lengths less than 250 mm were classified as subyearlings (Pearcy and Fisher, 1990). Genetic analyses were conducted on all fish using microsatellite DNA as described by Teel *et al.* (2015). Stomachs were removed and placed in either 10% formalin (1998-2007) or 20% Prefer (a formalin alternative used 2008-2012), for two weeks. Samples were then transferred to 70% ethanol prior to analysis. Up to 30 stomachs per haul were examined.

Stomach contents were analyzed under a dissecting microscope. Prey items were identified to the lowest taxonomic level possible, and intact fish prey were measured to the nearest millimeter. Individual taxa were blotted on absorbent paper and weighed to the nearest milligram. Prey items were classified into 64 different categories, but for analysis purposes, items were grouped into 12 general trophic groups. Groups were chosen if they made up >5% of the diet composition by weight for any given year. These categories were clupeids, engraulids, hexagrammids, osmerids, *Sebastes* spp., *Sardinops* spp., “miscellaneous fish” (unidentified and rare fish), amphipods, *Cancer* spp., euphausiids, *Vibilia* spp., and “other invertebrates”. The “other invertebrates” category consisted of non-*Cancer* spp. decapods, pteropods, copepods, insects, cumaceans, cephalopods, polychaetes, and less common miscellaneous zooplankton. Several of the categories were created by combining taxa (e.g., all crab species of the genus *Cancer*), which additively led to a >5% value by weight in at least one of the years. We also grouped all euphausiids together (primarily *Thysanoessa spinifera*, *Euphausia pacifica* and euphausiid material that were too digested to identify to species). Many common prey items retain certain distinct characteristics such as jaw shape, teeth, and eye size even after soft material is digested, facilitating identification in the lab. If a fish prey was not identifiable, it was grouped in with the “miscellaneous fish” category. Any salmon with solely non-biological prey items (e.g., wood, flotsam, feathers) or an empty stomach was removed from the diet composition analysis. We then calculated the average diet composition based on percent weight of each trophic group for each station within a year and for each year as a whole.

Statistical analysis

Interannual differences in average diet composition (by percent weight of prey consumed) were visually assessed using cluster analysis and tested for significant cluster differences with similarity profile (SIMPROF). A letter code denoting a specific cluster was then assigned to the average diet of every station within that group (i.e., the letter A was added to all stations in years that fell into cluster 1). To test for significant diet differences in more detail, a multivariate analysis of similarities (ANOSIM) was performed with station-averaged diets nested by cluster factors and based on a Bray-Curtis similarity matrix. All tests were considered significant if $P < 0.05$. To ascertain which prey categories were responsible for the significant differences between clusters, we ran a similarity percentage test (SIMPER). To visually represent interannual diet variability along with relationships to oceanographic variables, we created a principle coordinate ordination (PCO) based on a Bray-Curtis similarity matrix. In this analysis, the diet composition of each year was compressed into a numerical set of coordinates, with the percent of variability maximized along axis one.

We calculated the percent stomach fullness for each individual fish using the formula:

$$\text{Stomach fullness}=\frac{\text{Total stomach content weight}}{\text{Salmon weight-Total stomach content weight}} \qquad [1]$$

To assess differences in stomach fullness between cluster groups, we used an Analysis of Covariance (ANCOVA) test with length as a covariate. This adjustment for length of the fish was necessary, as previous research has shown that smaller salmon have the capacity to consume more food for their length than larger salmon (Daly *et al.*, 2009). Additionally, we calculated the percentage of empty stomachs for each year.

Body condition, a measure of how fat or thin the fish is for its length, was estimated as the residual from a length-weight regression, where lengths and weights were log-transformed to meet statistical assumptions of normality. This was calculated only for the 2,023 fish with recorded length and weights (117 did not have a weight measurement). Fish with positive condition values weighed more than expected for a given length, and vice versa. To examine for differences in fork length and body condition between yearly diet clusters, we used the Mann-Whitney test due to the non-normality of the data.

We examined whether diet composition (as represented by PCO1 values) affected subyearling stomach fullness, body condition, or length through regression analysis. We also used regression analysis to explore which of eight oceanographic variables influenced diet composition, stomach fullness, body condition, and length. We used oceanographic variables from 1998 to 2012, covering the period of this study (Table 1). The indices and their associated sources are:

1. Pacific Decadal Oscillation (PDO) values from the University of Washington JISAO (research.jisao.washington.edu/pdo/PDO.latest)
2. North Pacific Gyre Oscillation (NPGO) values from Emanuele Di Lorenzo (http://www.o3d.npgo/index.html)
3. Sea surface temperature (SST) measured at the NOAA Stonewall Banks buoy, located at 44.64°N 124.50°W (http://ndbc.noaa.gov/station_page.php?station=46050)
4. Northern Oscillation Index (NOI) values from NOAA's Pacific Fisheries Environmental Laboratory (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/NOIx/noix.html)
5. Multivariate El Niño-Southern Oscillation Index (MEI) from NOAA's Earth System Research Laboratory (htttp://www.esrl.noaa.gov/psd/enso/mei/)
6. Upwelling (UPI) for 45°N 125°W, from NOAA's Southwest Fisheries Science Center Environmental Research Division Live Access Server (las.pfeg.noaa.gov/LAS)
7. Columbia River outflow (COL), measured at Bonneville Dam (235 km upriver from the mouth of the Columbia River), from the US Army Corps of Engineers, Grant County Public Utility District, and the Oregon Department of Fish and Wildlife (http://www.cbr.washington.edu/dart/river.html)

To identify the time period over which oceanographic conditions best predicted subyearling diet composition and physical characteristics, we calculated several-month averages for the periods of May to August, June to August, and July to September for these eight oceanographic variables. We determined that the May to August interval most fully encompassed the spring period of prey field growth and the start of fall subyearling outmigration. We found this period to have the strongest relationships with diet composition, condition, stomach fullness, and length, and our results reflect solely this time period.

Accurately forecasting the number of returning adult fish is essential for establishing a sustainable fishery. Adult Chinook salmon return values are from Ruzicka *et al.* (2016), who back-calculated annual returns of adult Chinook salmon to Bonneville Dam (www.dbr.washington.edu/dar/adult_annual.html) to include both 2-year and 3-year returns. The adult return value for 2011 was 3.4 standard deviations above the long-term mean, and was not included in analysis. Using linear regression, we examined if any of the eight oceanographic variables, diet composition, body condition, stomach fullness, or length of the subyearling salmon could be used to predict the log-transformed adult return values. Snake River subyearling Chinook salmon are a threatened stock of fall Chinook salmon. We tested if the biological characteristics of this subset of fish differed from non-Snake River fall Chinook salmon subyearlings. Only stations where there were at least 3 Snake River fish and 3 non-Snake River fish were used. Diet differences were tested between the two groups at sampling station level using an ANOSIM test. Interannual differences in condition and length were examined using the Mann-Whitney test, and differences in stomach fullness were examined using the ANCOVA test.

RESULTS

Across all years, 4,581 subyearling Chinook salmon were caught, with an average fork length of 167.9 mm (±30.3 mm) (Table 2). 99.9% of subyearling salmon were found within 7 km of shore, although they were caught throughout the entire latitudinal range of the sampling grid.

Stomach analysis

In total, 2,140 stomachs were analyzed, with 93 of these being entirely empty. Subyearling Chinook salmon were highly piscivorous, with fish prey dominating their diets by percent weight in all years examined (Fig. 2). On average, fish prey made up 85.7% of diets. Juvenile salmon were especially dependent on juvenile northern anchovies (*Engraulis mordax)*, which made up an average of 33% of the total stomach composition by weight for all years. Northern anchovy were found in over a quarter of all stomachs examined (Appendix Table 1). Only two other prey taxa, Pacific herring (*Clupea pallasi*) and whitebait smelt (*Allosmerus elongatus*), made up more than 5% of the identifiable prey biomass consumed (Appendix Table 1).

Cluster analysis

Cluster analysis of annual diet composition revealed two major clusters that were significantly different based on SIMPROF test (Fig. 3). Years 1998, 2001-2008, and 2011 formed one cluster ("cluster A"), while 1999, 2000, 2009, 2010, and 2012 made up another ("cluster B"). The fine-scale station diet composition data nested within cluster A and B also revealed significant diet differences between the two clusters (ANOSIM; Global R = 0.207; P = 0.002). SIMPER analysis showed that the diets of cluster B had a significantly higher proportion of invertebrates than cluster A; on average, cluster A diets were made up of 14% invertebrates compared to 39% in cluster B. Although salmon were highly piscivorous in all years, cluster A was shown to contain significantly more juvenile forage fish such as northern anchovies, herring, and smelts (Fig. 2).

Annual changes in diet composition of subyearling Chinook salmon were aligned along axis 1 of the PCO analysis, which accounted for 61.8% of the diet variability (Fig. 4). Diet composition values for cluster A fell on the negative end of axis 1 of the PCO analysis. Diet composition values for cluster B, along with May-August Columbia River flow values, had positive values along axis 1.

Similar to diet composition, average stomach fullness also showed interannual variability (Fig. 5). Cluster B years were significantly less full than cluster A years (ANCOVA; P = < 0.0001). Stomach fullness was around 35% lower in cluster B years, and there were a higher percentage of empty stomachs (Fig. 5). In terms of length and body condition, salmon in cluster B were significantly shorter and in worse condition than those in cluster A (Kolmogorov-Smirnov; P = < 0.0001; Fig. 6). Diet composition negatively influenced stomach fullness (R^2 = 0.344; P = 0.03), body condition (R^2 = 0.311; P = 0.03), and length (R^2 = 0.309; P = 0.03). A negative correlation indicates that salmon consuming more invertebrates (i.e., those in cluster B) were less full, shorter, and in poorer condition.

Three of the eight oceanographic variables were found to influence diet composition: Pacific decadal oscillation (R^2 = 0.439; P = 0.01), May-August sea surface temperature (R^2 = 0.411; P = 0.01), and North Pacific gyre oscillation (R^2 = 0.299; P = 0.03). Diet composition had an inverse relationship with both PDO and SST: cooler ocean temperatures were associated with higher proportions of invertebrates in subyearling diets. Accordingly, most of the years in cluster A were found to have warmer sea surface temperatures and higher PDO values than those in cluster B, which generally had lower SST and PDO values. 2008 was the outlier in cluster A, with the lowest May-August average SST of the time series. 2009 was the exception among cluster B years. None of the eight oceanographic variables used directly influenced stomach fullness, body condition, or length (regression analysis, P > 0.05).

Snake River fall Chinook salmon diet characteristics and length were indistinguishable from non-Snake River salmon. There were 172 genetically identified Snake River fall Chinook salmon from 17 qualifying stations. Diet composition and stomach fullness did not differ from the rest of the subyearling salmon (ANCOVA; P > 0.05). The same was true for body condition and length (Mann-Whitney; P > 0.05). As with the complete September subyearling group, oceanographic variables did not have a significant effect on the stomach fullness, body condition, or length of Snake River juveniles (regression analysis, P > 0.05).

Relationship to Adult Returns

We evaluated whether physical characteristics of the subyearlings or oceanographic conditions at the time of ocean entry impacted adult returns. Adult returns were not influenced by stomach fullness, length, or body condition at the time of outmigration. However, returns of adult Chinook salmon were successfully predicted by diet composition (R^2 = 0.476; P = 0.006; Fig. 7). Interestingly, these were positive correlations – larger PCO values (representing the invertebrate-heavy diets of cluster B) correlated with significantly higher returns as adults.

Two oceanographic variables were found to strongly predict adult returns. These were sea surface temperature (R^2 = 0.414; P = 0.01) and Pacific decadal oscillation (R^2 = 0.423; P = 0.01). The negative relationship found between adult returns and ocean temperature indicates that salmon from cooler years returned in higher numbers 2-3 years later. Four out of the five years in cluster B had the highest adult returns of the time series; the exception was 2009. Cluster A had the lowest returns, aside from 2008.

DISCUSSION

Our analysis represents a synthesis of multiple years of data and contributes to our understanding of the importance of diet variability in salmon survival. We found that juvenile subyearling Chinook salmon from cluster B years ate more invertebrates and less fish than those from cluster A, although salmon from all years were still highly piscivorous. Juvenile salmon that entered the ocean in cluster B years were on average thinner for their length, had more empty stomachs, and had lower stomach fullness than those that entered in cluster A years. However, cluster B salmon returned as adults in significantly higher numbers than cluster A. Cluster A was generally associated with warmer ocean conditions based on PDO and SST; cluster B years had cooler ocean conditions. We established that the length and trophic habits of a threatened stock of subyearling Chinook salmon from the Snake River could be represented by the characteristics and habits of non-ESA listed subyearling salmon. This indicates that more abundant stocks could be used to evaluate the effects of oceanographic conditions on the threatened population.

While the data collected in this study are from September, the same area is sampled in June, and the June biomass of potential prey for juvenile salmon is significantly related to the subsequent 2-year adult returns of fall Chinook salmon (Morgan *et al.*, 2015). This prey field index is primarily composed of invertebrates of younger stages than what subyearling Chinook salmon would typically consume. Peak outmigration time for subyearling Chinook salmon is in July (Weitkamp *et al.*, 2015); subsequently, fish caught in this study had potentially already survived multiple months at sea. By September, these salmon could be consuming fish prey, such as juvenile zero-age northern anchovies, that had directly benefited from the June biomass of potential prey. Together, these findings emphasize how bottom-up trophic processes may influence adult returns.

We found that salmon from cluster B years were in worse body condition than salmon in cluster A. This may be counterintuitive – one would expect that the increased upwelling in the generally cooler cluster B years would promote productivity on the shelf (Ware and Thomson, 2005), allowing salmon to grow faster. Further, cluster B salmon had significantly higher adult returns, when one would expect the fuller, larger cluster A salmon to return in larger numbers. It appears that the set of dynamics involved is much more complex than previously thought.

These results are consistent with those of a similar study (Daly and Brodeur, 2015) focusing on May and June, which determined that higher piscivory rates did not necessarily lead to better body condition of yearling Chinook salmon. However, this previous study found that yearling Chinook salmon collected in warmer years were in worse body condition than those from cool years, a result contradictory to the findings presented here. Changes in predator biomass and size-selective mortality between summer/fall and warmer/cooler ocean conditions could account for this disparity. Pacific hake (*Merluccius productus*) have been shown to feed on juvenile salmonids (Emmett and Krutzikowsky, 2008). Hake typically feed off Oregon and Washington in the summer months, particularly in warmer years. In average and cool ocean conditions, hake move south to California in the fall. In warmer ocean years, some hake may live in Pacific Northwest waters year-round (Benson *et al.*, 2002). Therefore, subyearling salmon that enter the ocean in June and July are subject to hake predation which may continue through September, particularly in years when fall ocean conditions are warmer than average. This could skew the average body condition of the surviving subyearling salmon for these years: the total number of survivors could be lower, potentially leading to decreased adult returns, but survivors would be in better body condition on average. This hypothesis agrees with the results presented here and by Daly & Brodeur (2015).

Two of the years sampled did not fit the general pattern of feeding clusters. The outmigration year of 2008 had anomalously high adult returns and cool ocean conditions while the diets fell within cluster A. 2009 had anomalously low returns several years later, with above average sea surface temperature; yet, diets fit into cluster B. Other factors besides food availability may have affected the survival of subyearling Chinook salmon in these years. The year 2008 was the coldest year in the time series, with strongly negative PDO values and low SST. This may have led to low numbers of fish predators in the Northern California Current (NCC) as observed by Litz *et al.* (2014). The low returns from outmigration year 2009 may be partially explained by the large numbers of large, piscivorous Humboldt squid (*Dosidicus gigas*) that were found off Oregon and Washington during this year (Litz *et al.*, 2011). Humboldt squid are tolerant of low dissolved oxygen and warm surface waters, and became a common predator off the Pacific Northwest in this year. The limited work completed on Humboldt squid diets has shown that squid do feed on salmonids, including Chinook salmon (Stewart *et al.*, 2014).

Adult returns may also have been caused by sea nettles (*Chrysaora fuscescens*), a large scyphozoan jellyfish that may be extremely abundant during warmer ocean conditions and some September cruises, particularly in 2009. This species has been shown to have negative impacts on subyearling Chinook salmon through indirect competition (Ruzicka *et al.*, 2016) which may have reduced adult returns several years later. Jellyfish predation upon zooplankton may divert food resources away from the prey eaten by juvenile salmonids (Ruzicka *et al.*, 2016).

Changes in prey availability may explain why subyearling Chinook salmon in cluster B years ate significantly more invertebrates than those in cluster A. Brodeur and

Morgan (2016) found that subyearling Chinook salmon diet composition both inside and outside of the Columbia River plume core differed from the plankton community makeup inside and outside of the plume, suggesting that juvenile salmon are selective in the types of prey they consume. We were not able to determine if the differences between the clusters were due to a) invertebrate prey being easier to catch, b) invertebrate prey being more numerous, or c) preferred fish prey being less numerous in some years. If the prey community was simply denser (but prey taxa were found in the same proportions in all years), salmon may preferentially consume invertebrates because they are generally slower and easier to catch than fish prey. Alternatively, invertebrates may be more abundant than fish prey during cool years, causing salmon to consume more invertebrates because they are more common. There is evidence that some typical invertebrate prey species, such as crab megalopae (*Cancer* spp.) and krill (euphausiidacea), are more abundant with low SST and negative PDO values (Feinberg and Peterson, 2003, Shanks, 2013).

A third possibility is that common fish prey of subyearlings are less abundant in cooler years. Some preferred fish prey species may have lower spawning success and survival in cool ocean years with strong upwelling, thus leaving juvenile salmon with a more limited pool of energy-dense fish prey to prey upon (Brodeur *et al.*, 2008, Daly *et al.*, 2010, Takahashi *et al.*, 2012). Climate events such as La Niña/El Niño have been shown to cause anomalous distributions of ichthyoplankton in the Northern California Current (Auth *et al.*, 2015). A key example of this is the northern anchovy, the most common fish taxa found in this analysis. Northern anchovy spawn in the Columbia River Plume where many of the salmon first enter the ocean. Anchovies have been found to spawn earlier and in a wider geographic range during warm and especially El Niño years, whereas osmerids (smelts) are more abundant in cool years (Brodeur *et al.*, 2008). The prey community in the summer/fall off Oregon is much less diverse than at other times of year, and northern anchovy, one of the few summer spawning species in the Northern California Current, can often be the dominant forage fish species during the summer (Brodeur *et al.*, 2008, Parnel *et al.*, 2008). Interannual variation in the timing and intensity of upwelling can result in delayed spawning of anchovy and slower growth rates (Takahashi *et al.*, 2012). This in turn alters the availability of this key prey taxon to subyearling Chinook salmon (Litz *et al.*, in review). Off Central California, (MacFarlane, 2010) found that northern anchovy were a critical prey of subyearling Chinook salmon emigrating from the San Francisco estuary and estimated that each salmon would need to consume three anchovies per day to sustain observed energetic gains and growth rates.

Daly and Brodeur (2015) found that prey species driving interannual differences in yearling Chinook salmon diets included several fish species (Pacific sand lance, flatfish, and rockfish) as well as invertebrates. Interestingly, while SST and PDO aligned with diet composition variation, Columbia River outflow was also found to be a significant abiotic factor affecting diet in yearling Chinook salmon. This demonstrates the possible importance of the freshwater environment for survival and growth of prey species in the spring and summer. Information on the summer and fall prey field composition is currently lacking.

Changes in climate over the next few decades may cause a shift in the types of fish prey consumed by salmon of all ages. This is indicated in the 50-year time series examined by (Thayer *et al.*, 2014), which found that certain fish (sardine, anchovy) became more prominent in juvenile salmonid diets in warmer ocean conditions as other taxa (rockfish, herring) declined in abundance. We did not see a similar trend among the juvenile Chinook salmon off Oregon and Washington examined here, with our variation exhibiting a more oscillatory trend between years; however, as climate and ocean conditions continue to change, an overall shift in juvenile salmon diets may become apparent. Based on these results, anticipated ocean warming in the future may have a negative impact on the health of Chinook salmon populations through increased numbers of predators and/or competitors, or a less diverse or sparser prey field, all of which may eventually lead to decreased adult returns. Long-term dietary studies across highly variable ocean conditions such as this one continue to be important, especially in the face of a changing and perhaps more variable future climate.

ACKNOWLEDGEMENTS

We are indebted to many scientists, boat crews, and sampling teams for their work on this project. Greg Hutchinson and Robert Schabetsberger assisted with the dietary analyses. David Teel kindly allowed us access to the genetic data that identified the Snake River fish. We appreciate the insightful comments provided by Drs. William Pearcy, Rich Zabel, Brian Burke, and an anonymous reviewer for comments on earlier versions of this manuscript. Funding was provided to the first author by the National Oceanic and Atmospheric Administration through the Ernest F. Hollings Scholarship, The Bonneville Power Administration and the Northwest Fisheries Science Center provide financial support for collection, analyses, and logistics.

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FIGURE LEGENDS

Figure 1. Stations sampled during most of the years examined (white dots). Subyearling Chinook salmon were generally found inshore of the red line, generally less than 20 km from shore (Teel *et al*. 2015).

Figure 2. The average diet composition by weight of subyearling Chinook salmon caught in September of 1998-2012. The twelve major trophic categories are shown at right. Fish categories are colored; invertebrate categories are grayscale. Note that fish prey dominates by percent weight, with overall average piscivory rate denoted by solid horizontal line. Years boxed in orange represent "cluster A" years; years boxed in blue represent "cluster B" years.

Figure 3. SIMPROF cluster analysis for subyearling Chinook salmon diets by year, with the two emergent groups highlighted. Years in cluster A are in orange; cluster B are in blue.

Figure 4. Principal coordinate analysis of annually averaged diet composition for subyearling Chinook salmon. Each year is a numerical representation of its average diet composition by weight with diet variation maximized along axis 1 with 61.8% of variation is explained. Cluster A is denoted by orange colors; cluster B is denoted by blue. Oceanographic variables averaged over May-August that most closely follow axis 1 are responsible for a large part of the variation seen in diets.

Figure 5. Index of stomach fullness (bar plot with standard error bar) and percentage of empty stomachs (solid line) for juvenile subyearling Chinook salmon by year. Overall average stomach fullness is represented by dashed horizontal line. Cluster A years and cluster B years are highlighted.

Figure 6. Interannual body condition of subyearling Chinook salmon by year. Body condition residuals greater than zero represent fish fatter for their length than would be expected; values less than zero indicate fish thinner than expected. Annual box plots

include the 5th and 95th percent outliers. Dashed horizontal line represents average of all subyearling Chinook salmon. Cluster A years and cluster B years are highlighted.

Figure 7. Regression of lagged adult subyearling Chinook salmon return data versus diet variability as represented numerically by PCO1 values. The slope is significantly different from zero (P = 0.006). The value for 2011 was considered a strong outlier (+3.4 standard deviations above the mean) and was omitted from the analysis (see text).

Table 1. Four-month (May through August) averages of oceanographic variables and adult returns from Ruzicka *et al*. 2016 used in the regression analyses by year. See methods for explanation of variables and their sources, see text.

Year	PDO	MEI	COL	NOI	NPGO	SST	UPI	2 & 3 Year Adult Returns
1998	0.21	0.83	249.62	0.31	0.27	14.94	-30.77	145466
1999	-0.90	-0.57	277.78	0.06	1.58	13.26	-34.96	334683

2000	-0.59	-0.15	202.28	-0.06	1.83	13.90	-19.26	446109
2001	-0.71	0.16	118.89	0.33	1.93	13.37	-20.49	136804
2002	-0.17	0.79	239.45	-0.47	1.23	13.63	-23.24	245402
2003	0.85	0.09	209.69	-0.65	0.92	14.47	-25.40	240508
2004	0.55	0.45	202.25	0.06	0.52	15.12	-16.93	118959
2005	0.99	0.51	187.14	-0.60	-1.24	14.25	-11.19	96838
2006	0.31	0.45	247.03	-0.55	-0.28	14.09	-12.69	305148
2007	0.32	-0.25	201.93	0.53	1.05	13.92	-5.92	125562
2008	-1.52	-0.15	256.91	-0.25	1.52	12.94	-0.37	423048
2009	-0.41	0.76	210.42	-0.33	0.43	14.05	-12.53	143186
2010	-0.48	-0.71	209.23	1.66	1.17	13.01	-36.63	541009
2011	-1.17	-0.31	344.88	0.16	1.05	13.12	-13.44	1010318
2012	-1.40	0.83	307.42	0.85	1.73	13.48	-24.60	484391

Table 2. Sampling dates, sample sizes of total subyearling Chinook salmon caught and those examined for diet analysis, and mean fork length (± standard deviation) of salmon examined for diet analysis.

Year	Cruise Dates	Total Salmon Caught	Stomachs examined	Average fork length (mm)
1998	Sept. 20-29	192	104	183.9 (±27.6)
1999	Sept. 21- Oct. 1	491	218	177.8 (±32.2)
2000	Sept. 21-28	80	50	160.2 (±25.8)
2001	Sept. 20-29	457	108	193.4 (±37.4)

2002	Sept. 26- Oct. 3	358	200	169.7 (±30.8)
2003	Sept. 26- Oct. 3	104	78	193.1 (±28.9)
2004	Sept. 22-29	80	30	170.9 (±32.1)
2005	Sept. 21-28	339	267	162.3 (±17.7)
2006	Sept. 20-28	488	282	174.1 (±27.5)
2007	Sept. 22-28	264	187	156.9 (±24.5)
2008	Sept. 23- Oct. 1	639	291	174.5 (±33.6)
2009	Sept. 22-29	33	33	176.3 (±28.5)
2010	Sept. 21-28	257	85	157.2 (±20.4)
2011	Sept. 19-26	590	107	180.4 (±34.9)
2012	Sept. 22-29	209	100	174.5 (±31.6)
	Total	4581	2140	

Appendix Table 1. Detailed diet information on all juvenile Chinook salmon examined in this study.

Prey Taxa	**% of Prey Weight**	**% of Prey Number**	**% Freq. Occ.**
Polychaeta			
Unidentified Polychaeta	0.121	0.116	0.935
Mollusca			
Gastropoda			
Limacina spp.	0.019	0.368	0.654
Unidentified Pteropoda	0.006	0.560	0.980
Cephalopoda			
Enteroctopus dofleini	0.057	0.021	0.187
Octopus rubescens	0.088	0.026	0.187
Unidentified Teuthida	0.039	0.026	0.234
Unidentified Cephalopoda	0.028	0.011	0.093
Arthropoda			
Copepoda			
Euchirella rostrata	0.016	0.505	0.467
Calanus marshallae	0.051	2.336	1.589
Euchaeta spp.	0.163	6.229	0.421
Pseudocalanus spp.	<0.001	0.026	0.047
Acartia spp.	<0.001	0.021	0.047
Unidentified Calanoida	0.005	0.289	0.467
Unidentified Copepoda	0.002	0.174	0.654
Cirripedia			
Unidentified Cirripedia, molt	0.021	0.174	0.841
Unidentified Cirripedia, larvae	0.007	0.037	0.234
Mysida			
Alienacanthomysis macropsis	0.032	0.263	0.374
Neomysis kadiakensis	0.013	0.016	0.140
Neomysis rayii	0.011	0.021	0.187

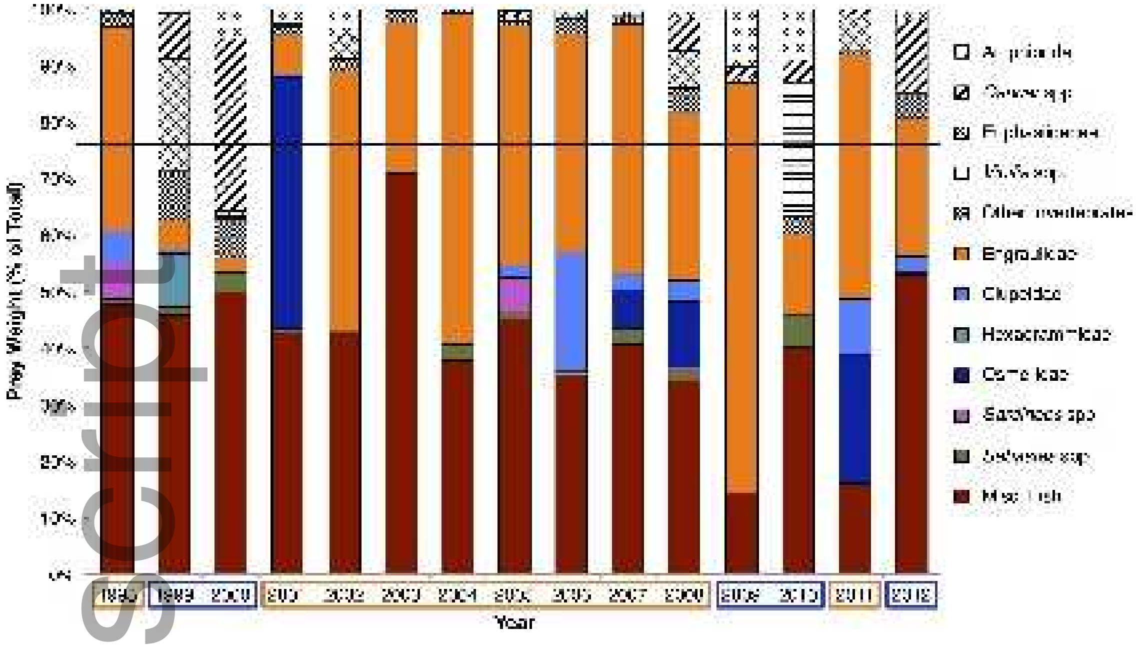
Unidentified Mysida	0.012	0.074	0.467
Cumacea			
Diastylopsis dawsoni	0.016	0.200	0.093
Diastylis spp.	<0.001	0.005	0.047
Unidentified Cumacea	0.086	0.716	1.262
Isopoda			
Synidotea berolzheimeri	0.006	0.032	0.187
Gnorimosphaeroma oregonensis	0.007	0.011	0.093
Idotea fewkesi	0.004	0.011	0.047
Unidentified Isopoda	0.012	0.150	0.980
Amphipoda			
Atylus tridens	0.162	0.584	1.542
Arthropoda (continued)			
Unidentified Gammaridae	0.044	0.289	1.916
Hyperia medusarum	0.590	1.173	5.748
Hyperoche medusarum	0.415	9.723	6.636
Themisto pacifica	0.060	1.242	2.150
Primno spp.	<0.001	0.016	0.140
Primno brevidens	0.002	0.021	0.187
Primno macropa	<0.001	0.011	0.093
Vibilia pyripes	0.051	0.452	0.093
Unidentified Vibiliidae	0.223	2.625	2.056
Unidentified Hyperiidae	0.381	2.615	8.692
Caprella anomala	0.009	0.053	0.187
Caprella equilibra	0.002	0.016	0.140
Caprella natalensis	0.002	0.016	0.093
Caprella verrucosa	0.007	0.079	0.374
Metacaprella anomala	<0.001	0.005	0.047
Unidentified Caprellidea	0.045	0.484	2.944
Unidentified Amphipoda	0.016	0.079	0.561

Euphausiacea			
Euphausia pacifica	0.986	1.594	1.916
Thysanoessa spinifera	1.443	1.936	3.598
Unidentified Euphausiidae	0.410	0.942	3.505
Decapoda			
Unidentified Pandalidae	0.049	1.989	1.822
Unidentified Caridea	0.040	0.020	0.100
Unidentified Crangonidae	0.509	4.651	2.103
Unidentified Paguridae	0.006	0.253	1.215
Pachycheles pubescens	0.023	0.542	0.280
Unidentified Porcellanidae	0.130	5.077	2.570
Cancer antennarius/gracilis	0.032	1.073	1.449
Cancer magister	0.371	1.336	4.159
Cancer oregonensis/productus	1.762	17.757	15.280
Cancer spp.	0.117	0.737	2.944
Neotrypaea californiensis	0.014	0.011	0.093
Hemigrapsus oregonensis	<0.001	0.016	0.093
Pachygrapsus spp.	<0.001	0.011	0.093
Unidentified Grapsidae	<0.001	0.005	0.047
Pinnixa spp.	0.009	0.058	0.374
Unidentified Pinnotheridae	0.006	0.074	0.327
Lophopanopeus spp.	<0.001	0.016	0.140
Lophopanopeus bellus	<0.001	0.016	0.093
Unidentified Xanthidae	<0.001	0.005	0.047
Unidentified megalopae	0.090	0.650	2.240
Arthropoda (continued)			
Unidentified Crustacea	0.243	0.605	3.598
Insecta			
Psocoptera	0.001	0.063	0.093
Hemiptera	<0.001	0.005	0.047

Coleoptera	<0.001	0.005	0.047
Diptera	0.005	0.063	0.280
Ichneumonidae	<0.001	0.005	0.047
Hymenoptera	0.002	0.089	0.187
Plecoptera	<0.001	0.011	0.047
Pterygota	0.019	0.563	0.421
Unidentified Insecta	0.876	7.434	9.019
Arachnida			
Unidentified Araneae	0.003	0.042	0.327
Unidentified Arachnida	<0.001	0.005	0.047
Chaetognatha			
Sagitta elegans	<0.001	0.011	0.093
Unidentified Chaetognatha	0.002	0.021	0.140
Chordata			
Osteichthyes			
Clupea pallasii	5.231	0.205	1.495
Unidentified Clupeidae	0.812	0.121	0.654
Engraulis mordax	33.069	5.840	27.850
Sardinops sagax	1.037	0.137	0.841
Allosmerus elongatus	5.164	0.158	0.935
Unidentified Osmeridae	2.000	0.226	1.168
Microgadus proximus	0.002	0.005	0.047
Sebastes spp.	1.063	0.452	2.804
Sebastes diploproa	0.041	0.021	0.140
Sebastes elongatus	0.032	0.011	0.093
Sebastes proriger	0.056	0.016	0.093
Unidentified Scorpaenidae	0.015	0.005	0.047
Ophiodon elongatus	0.514	0.068	0.421
Agonopsis vulsa	0.002	0.011	0.047
Xeneretmus latifrons	<0.001	0.005	0.047
Unidentified Agonidae	0.001	0.011	0.047

Liparis spp.	0.010	0.005	0.047
Unidentified Cyclopteridae	0.077	0.110	0.140
Artedius fenestralis	0.003	0.016	0.047
Leptocottus armatus	0.005	0.011	0.093
Dasycottus setiger	0.005	0.016	0.047
Unidentified Cottidae	0.130	0.247	1.449
Osteichthyes (continued)			
Anoplopoma fimbria	0.259	0.005	0.047
Unidentified Syngnathidae	<0.001	0.005	0.047
Ammodytes hexapterus	0.081	0.011	0.093
Ronquilus jordani	0.037	0.011	0.093
Glyptocephalus zachirus	0.017	0.005	0.047
Isopsetta isolepis	0.004	0.005	0.047
Pleuronichthys coenosus	0.003	0.011	0.093
Unidentified Pleuronectidae	0.073	0.058	0.514
Unidentified Osteichthyes	38.328	9.670	60.561
Unidentified material	1.947	1.882	17.009
Number of stomachs examined		2140	
Number of empty stomachs		93	
Mean fork length (mm)		167.9	
Fork length range (mm)		113-240	

fog_12180_f1.tiff



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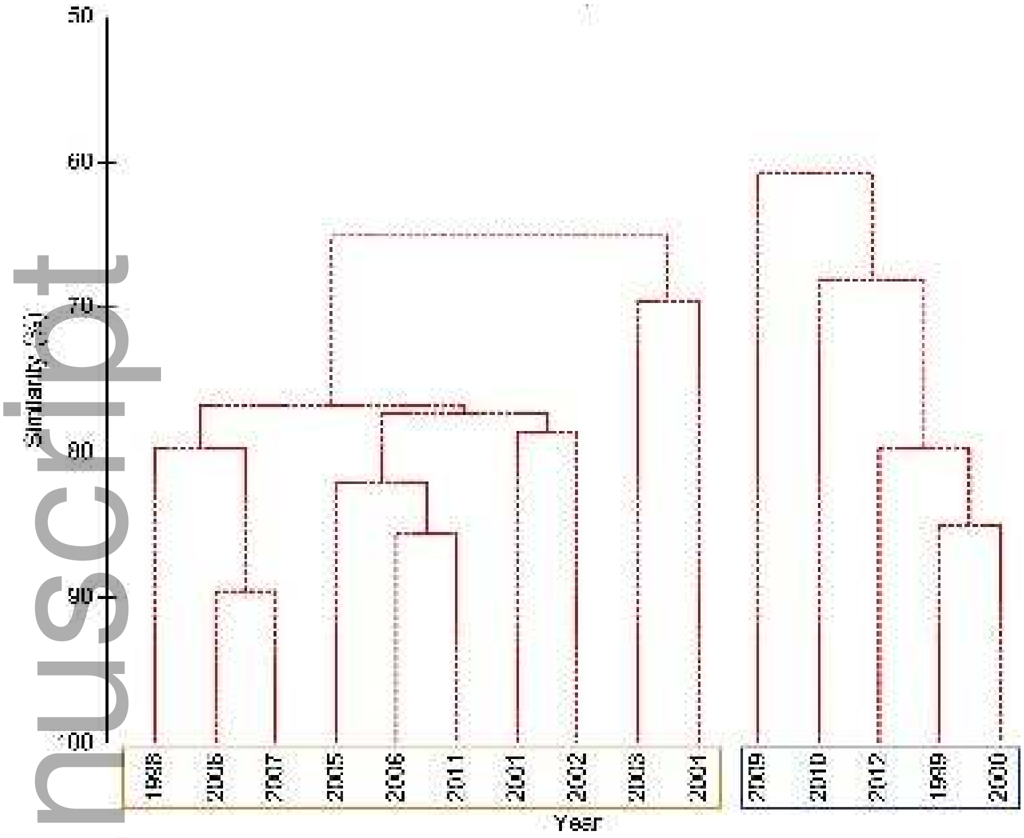

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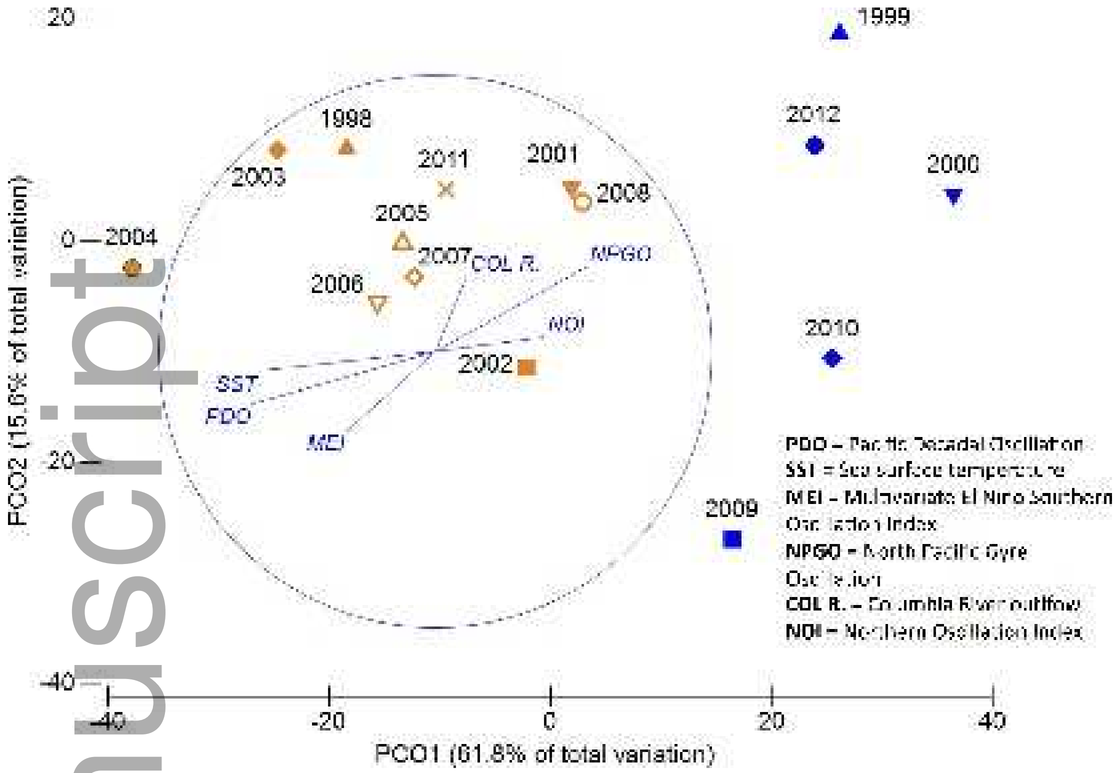

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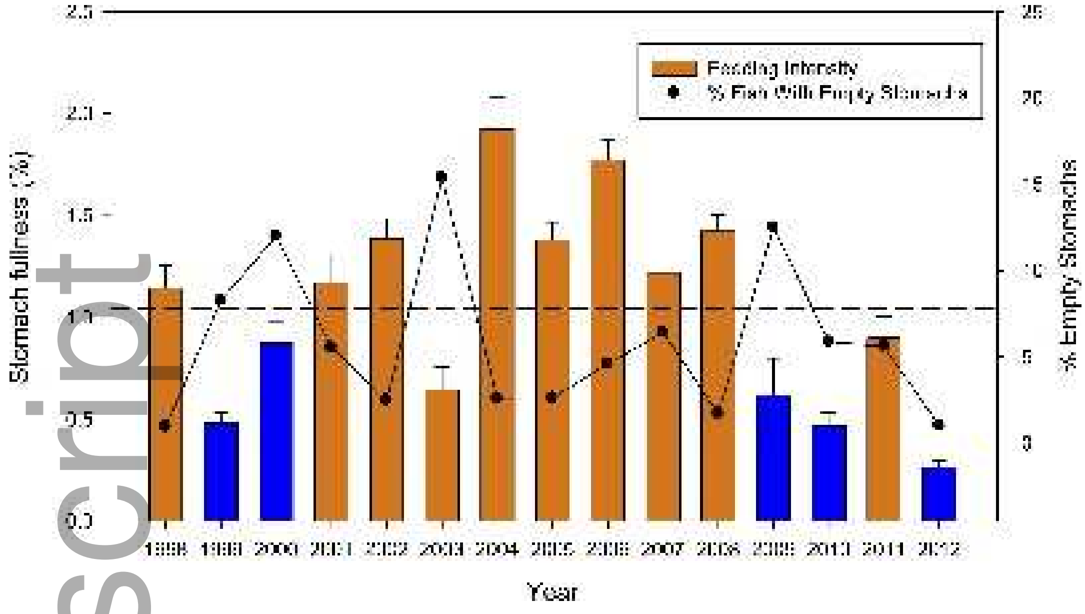

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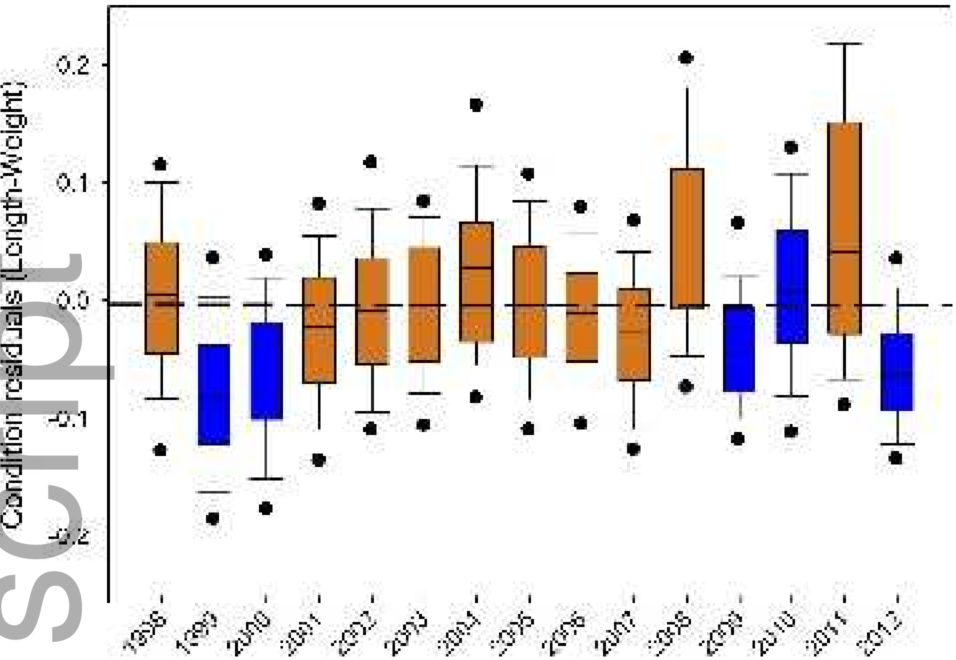

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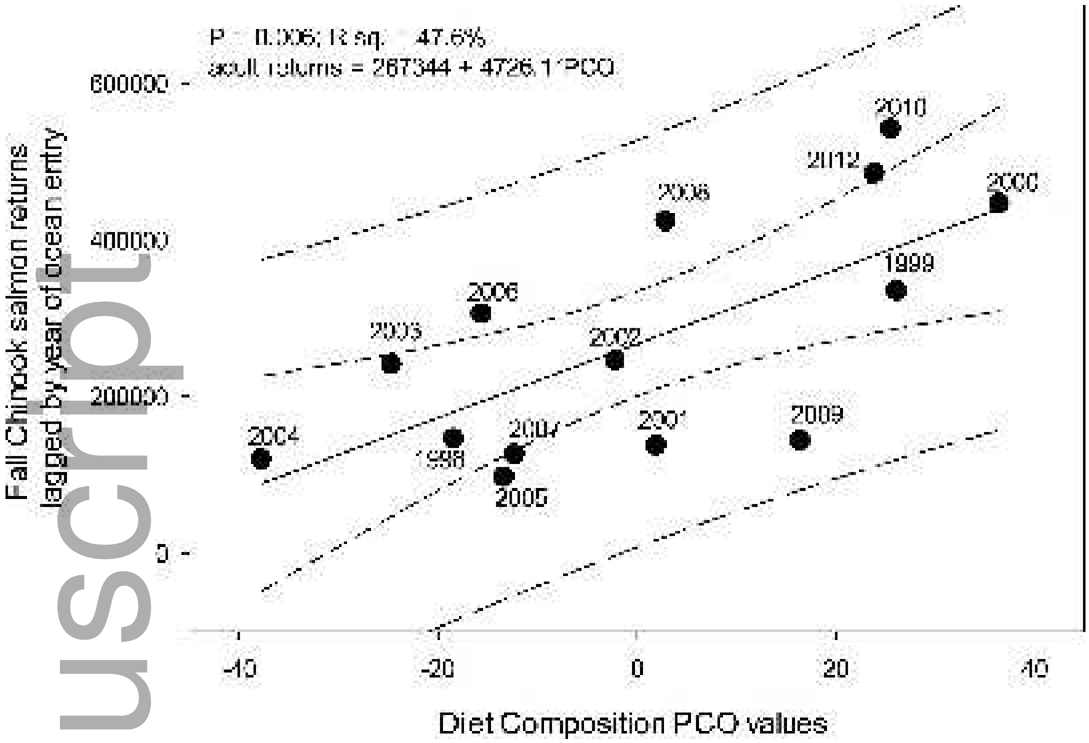

fog_12180_f7.tiff