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**Investigating high seas foraging conditions for salmon in the North Pacific: insights from a 100 year scale archive for Rivers Inlet sockeye salmon**

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## Abstract

The high seas phase of Pacific salmon life history remains particularly data limited, and the potential implications of climate impacts on ocean productivity for salmon condition and reproductive success is poorly understood. We used carbon and nitrogen stable isotopes (SI) from salmon scales to reconstruct aspects of the marine environment experienced by Rivers Inlet sockeye salmon (*Oncorhynchus nerka*) over the last century (1915-2016). Time series of SI compositions of salmon scale showed a greater variability after 1950, probably linked to more dynamic high seas environmental conditions. However, climate indices (e.g., PDO, ENSO) did not explain the SI variability. We assessed the time series with respect to changes in food web dynamics, including shifting trophic baselines, changes in prey / salmon diet, and changes in salmon foraging location. A significant correlation ( $r=0.53$ ) between sea surface temperature and  $\delta^{13}\text{C}$  enabled us to define the area of potential salmon distribution in the open ocean for approximately 9 months prior to sampling. This method shows high potential for stock specific high seas distribution mapping that could be combined with prey isotope values to inform stock specific foraging experience.

**Résumé**

Très peu d'informations sont disponibles sur la phase pélagique des saumons, et les conséquences des variations climatiques via la productivité de l'océan sur la condition physique des saumons et leurs chances de reproduction sont mal comprises. On a utilisé les isotopes stables (IS) du carbone et de l'azote contenus dans les écailles de saumon pour reconstruire l'environnement expérimentées par les saumons en pleine mer pendant le siècle dernier (1915-2016). Les signatures isotopiques montraient une variabilité plus importante après 1950 surement dû à des conditions environnementales plus instables. La série temporelle a été interprétées en considérant différentes structures trophiques, mais aussi des changements dans la signature isotopique à la base de la chaîne trophique, dans le régime alimentaire des saumons, ou encore dans leurs distributions. Une corrélation significative entre la température de surface et le  $\delta^{13}\text{C}$  nous a permis de définir la région dans laquelle les saumons se situaient durant leurs 9 derniers mois passés en pleine mer. Cette méthode a montré un fort potentiel pour définir individuellement la distribution des stocks de saumons dans l'océan et devrait être couplée dans le futur avec des cartes de distribution de signatures isotopiques des proies pour permettre une meilleure compréhension des conditions expérimentées par les différents stocks.

## Introduction

After entering the marine environment, juvenile British Columbian (BC) sockeye salmon (*Oncorhynchus nerka*) are considered to move north and west through the coastal waters of Canada and Alaska, reaching the offshore waters of the Gulf of Alaska by the end of their first year at sea (French et al. 1976). They spend approximately 2-3 years foraging in the offshore waters of the Gulf of Alaska, where they put on up to 90% of their final adult body weight (Ishida et al. 1998), prior to migration back to their natal fresh waters to spawn (Burgner 1991). It is not unreasonable to expect that growth and survival of sockeye salmon stocks during the pelagic stage of their life cycle will impact long-term salmon production patterns. For example, salmon condition will determine their ability to reach their spawning grounds with enough reserves to spawn (Rand et al. 2006; Macdonald et al. 2010). Recent research has found that sockeye salmon recruitment is negatively impacted by pink salmon abundance through declines in sockeye productivity, length at age, and age at maturity (Ruggerone and Connors 2015). That study showed that the limited carrying capacity of the Northeast Pacific, combined with competition for food resources with species supported by hatcheries, may indeed limit BC sockeye productivity, and highlighted the importance of changing ocean conditions in the Northeast Pacific as a factor in salmon productivity.

During their pelagic phase, sockeye salmon encounter two major oceanic domains, the easterly flowing Subarctic current of the Transitional Domain, and Central Subarctic waters of the Alaska Gyre (Fig. 1) (Pearcy 1997). Both of these domains are characterized by high-nitrate, low-chlorophyll conditions where small phytoplankton cells dominate the base of the food web. However, these domains support diverse and dynamic prey assemblages of zooplankton and micronekton (Aydin et al. 2000; Kaeriyama et al. 2000, 2004). The geographical boundaries of

93 these domains and their species composition are affected by large scale climate processes. Several  
94 climate shifts have occurred during the past century, in 1925 and 1947 (Mantua et al. 1997), 1977  
95 and 1989 (Hare and Mantua 2000), possibly in 1999 (e.g., Batten and Welch 2004; Litzow 2006),  
96 and 2008 (Litzow and Mueter 2014). Such climate shifts alternate between “warm” or positive  
97 phases and “cold” or negative phases of the Pacific Decadal Oscillation (PDO). In a similar way,  
98 the Northeast Pacific Ocean has been affected by numerous El Niño/La Niña periods over the last  
99 century as described by Whitney and Welch 2002). During PDO positive phases (and El Niño  
100 events), the Gulf of Alaska experiences increased sea surface temperatures (SSTs) and decreased  
101 salinity levels, leading to shallower mixed layers and increased stratification. In contrast, negative  
102 PDO phases (and La Niña events) correspond with opposite ocean conditions in the Gulf of Alaska  
103 (Mantua and Hare 2002). Such variation in the physical properties of the offshore waters of the  
104 Gulf of Alaska have been associated with changes in light availability and nutrient supply for  
105 phytoplankton, leading to large fluctuations in primary production, which in turn would impact  
106 zooplankton and fish populations that mature in the high seas (Whitney and Freeland 1999).  
107 Warmer SSTs in the Gulf of Alaska have also been associated with changes in zooplankton  
108 community composition, for example, the intrusion of low lipid content southern species (Mackas  
109 et al. 1998; Batten and Welch 2004).

110 The current understanding of how these environmentally driven changes relate to salmon trophic  
111 ecology and production on the high seas remains limited. The costs and logistical difficulties of  
112 working on the high seas and of tagging/recovering fish operations have resulted in almost no  
113 stock specific information (Neave 1964; French 1976). Stable isotope (SI) analysis of returning  
114 adult tissues presents an approach that enables one to retrieve information on high seas salmon  
115 trophic ecology (e.g, trophic level, niche overlap) without requiring sampling in the open ocean

(Welch and Parsons 1993; Satterfield and Finney 2002). Stable isotope variations are influenced by changes in assimilation at the base of the food web, which is driven by several factors including  $\text{NO}_3^-$  availability or diazotrophy processes in the case of  $\delta^{15}\text{N}$  (e.g., Rau et al. 1998; Mompeán et al. 2013), and temperature or phytoplankton growth rates in the case of  $\delta^{13}\text{C}$  (e.g., Laws et al. 2002). Reconstructing long SI term series using salmon scales from archives has been shown to be useful for investigating the relationship between shifts in large scale climate conditions and salmon trophic ecology (Satterfield and Finney 2002; Johnson et Schindler 2012) and to determine high seas salmon distribution (MacKenzie et al. 2011).

In this study, we use a one hundred year scale time-series (1915-2016) to test how SI values can inform the long term response of salmon to changing ocean conditions. The scales used are from Rivers Inlet sockeye salmon, historically the third largest sockeye fishery in BC. This stock began to experience unstable returns in the 1970s before crashing in the 1990s, reaching a low of ~3,600 adult returns in 1999, down from an 80 year average of ~1 million (Walters et al. 1993; McKinnell et al. 2001). During the 2000s the stock recovered to 30 000-130 000 annual returns, but has remained below harvestable levels (200,000) despite the continued fishery closure. Post-collapse assessments indicate that there has been no decline in freshwater survival or pre-smolt production, pointing to marine survival as the driver (McKinnell et al. 2001). Climate driven changes in prey availability and / or quality in the high seas are one mechanism that may have impacted sockeye salmon growth and survival, and subsequent spawning success. Here we use the Rivers Inlet scale time series to test the relationship between high seas conditions experienced by maturing sockeye salmon and population declines, as a step towards understanding the importance of climate controls of high seas food webs to salmon production.

**Methods**

*Samples collection and preparation*

Rivers Inlet (RI) sockeye salmon scales have routinely been collected by DFO since 1912, for determination of stock age structure. Two scales were collected from individual fish at each of the major spawning rivers, and stored dry on gummed paper cards kept in a temperature controlled storage facility of the Schlerochronology Laboratory at the Pacific Biological Station. For the period 1915-2010, usually every 5 years, we selected between 20 and 30 scales, each representing an individual fish (Table 1). For the years 1915 through to 1970 as well as 1990, scales came from pre-spawn fish caught by gillnets during the commercial fishery between the months of June and August. For the years 1986, 1992 through to 2010 scales were collected from spawned dead/moribund fish sampled during routine stock assessments conducted by DFO during September-October. Scales were provided with fish age information, and mass and length until 1946. Condition factor was calculated for the fish as  $K_D = 100 W L^{-3}$ , where W is the mass in grams and L the length in cm.

Since 2011, approximately 100 sockeye salmon have been collected annually during the Wuikinuxv Nation food fishery. Fish are collected with gill nets as they enter the Wannock River during June-August and sampled for scale and muscle tissue. After sex determination, fish heads were cut off behind the gills and kept frozen at -20°C before being transferred to the University of British Columbia (UBC) laboratory for processing. Scales were removed from the skin covering the dorsal musculature posterior to the head. Wedges of muscle measuring approximately 1cm<sup>3</sup> were excised with a scalpel from the same area. Additionally, in 2013, scale and muscle were



collected from 78 spawned-out sockeye that were either moribund or freshly dead during surveys of three spawning creeks (Ashlum, Neechanz and Genesee).

#### *Measurement of stable isotopes*

Whole scales were soaked in deionized water. Any residue was removed from the surface of the scales using forceps. Scales were then dried at air temperature and stored in Eppendorf tubes prior to stable isotope analysis. Muscle tissues were oven-dried at 50°C for 24-48 h before being grounded to a fine powder with a mortar and pestle for SI analysis. Stable isotope analysis of scale and muscle tissue was performed at the IsoEnvironmental Laboratory (<http://www.isoenviro.co.za/>, Rhodes University, South Africa) and the Stable Isotope Facility (<http://isotopes.forestry.ubc.ca/>, UBC, Canada). Isotopic ratios are expressed in the following standard notation:

$$\delta X (\text{‰}) = (R_{\text{sample}} / R_{\text{standard}} - 1) \times 1000$$

where X is  $^{13}\text{C}$  or  $^{15}\text{N}$  and  $R_{\text{sample}}$  is the  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$  respectively.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were determined in parts per thousand (‰) relative to external standards of Vienna Pee Dee Belemnite and atmospheric nitrogen.

#### *Lipid correction in muscle and scale*

The carbon isotopic composition of individuals of the same age and from the same stock are expected to be quite constant based on the hypothesis that they feed on the same prey field. However, the lipid content may vary as a result of individual physiological differences and the

185 amount of lipid will affect  $\delta^{13}\text{C}$  values (e.g., Kiljunen et al. 2006), resulting in important inter-  
186 individual variation ( $\text{SD}=0.87$ ,  $n=96$ ). Lipid supplies will be depleted during the migration to the  
187 spawning ground and the reproductive processes in response to metabolic needs, resulting in a  
188 more similar SI values between individuals ( $\text{SD}=0.46$ ,  $n=78$ ). In order to compare SI values in  
189 scales and muscles, both dataset needed to be corrected for any lipid influence. The extensive  
190 sampling effort carried in 2013 on pre- and post-spawn fish was used to define the correction. We  
191 used the median  $\delta^{13}\text{C}$  distribution from post-spawn salmon muscles as a reference for a level of  
192 lipids considered as very low or null, and developed a logarithmic model based on C:N variation  
193 to correct the lipid effect in pre-spawn salmon ( $\Delta\delta^{13}\text{C} = a \cdot \ln(\text{C:N}) + b$ ,  $a=7.77$ ,  $b=-7.39$ ,  $r^2=0.82$ )<sup>1</sup>.  
194 Variation in scale C:N was observed for the period 1986 to 2013 (except 1990), with generally  
195 higher values than other periods (mean= 3.33, min= 2.93, max= 4.69 compared to mean= 2.74,  
196 min 2.56, max=2.89). While scales contain lipids (Grahl-Nielsen and Glover 2010), the amount is  
197 probably too small to affect the overall isotopic composition of the scales. Variations in scale C:N  
198 were therefore most likely due to remnant lipid deposits on the surface of the scales. A procedure  
199 similar to the one used to correct the muscles values was then applied with scale samples resulting  
200 in following parameter values,  $a=4.42$  and  $b=-4.66$  ( $r^2=0.81$  and  $n=78$ )<sup>2</sup>.  
201 Differences between muscle and scale isotopic values were investigated for 2011-2016 using  
202 Kruskal-Wallis tests (non-parametric test owing to heterogeneity of variance) and post hoc  
203 comparisons after removing outliers (outside of the 95% confidence interval; 10 and 21 out of 414  
204 for N and C respectively). All tests were performed with R (R Development Core Team 2018),  
205 Kruskal-Wallis using the function `kruskal.test` and post hoc using `dunnTest` (pckg FSA).

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<sup>1</sup> Fig. S1<sup>2</sup> Fig. S2

*Effect of anthropogenic carbon dioxide release*

The large amount of fossil fuel burned over the post-industrial era (after 1850) has increased the concentration of carbon dioxide in the atmosphere. This anthropogenic carbon dioxide is depleted in  $^{13}\text{C}$  and will affect the carbon isotopic composition in marine ecosystem through two processes: 1) decrease of  $\delta^{13}\text{C}$  in dissolved inorganic carbon (referred to as the Suess effect) (Gruber et al. 1999), and 2) an increase in aqueous  $\text{CO}_2$  concentration (Freeman and Hayes 1992). These affects need to be taken into account when comparing isotope values from the pre- and post- industrial periods, and for any multi-decadal time series. To quantify the effect of increased aqueous  $\text{CO}_2$  concentration on isotopic fractionation is a difficult task as it is determined by complex processes such as diffuse/active carbon uptake and leakage, and it will depend on nutrient concentrations, phytoplankton composition, cell size and geometry, and growth rates (Popp et al. 1988; Burkhardt et al. 1999; Riebesell et al. 2000; Hoins et al. 2016). This results in large uncertainties in correction values that vary substantially between studies. However, the total effect of increased aqueous  $\text{CO}_2$  concentration since the beginning of the industrial era seems to be negligible compared to the Suess effect (Misarti et al. 2009). Therefore, we chose not to attempt to quantify the effect of aqueous  $\text{CO}_2$  concentration directly but rather assumed that it was included in the model developed to correct from the Suess effect itself. Based on data presented in Gruber et al. (1999) and Hilton et al. (2006), and updated by Misarti et al. (2009), we developed an exponential model to correct carbon isotope values from the Suess effect:

$$\delta^{13}\text{C}^* = \delta^{13}\text{C} - a * e^{x*b}$$

where  $x$  is the number of years after 1850;  $b$  is equal to 0.027 to match the curve presented by Gruber et al. (1999) for change in  $\delta^{13}\text{C}$  in ocean for 1945-1997;  $a$  is a variable. We assumed here

that much of the long term trend in  $\delta^{13}\text{C}$  is due to Suess effect as SST has been shown to be quite stable over the last century in the middle of the Gulf of Alaska<sup>3</sup>. We fitted then this model to our data varying the  $\delta^{13}\text{C}$  baseline (SI value in 1850) and  $\alpha^4$ .

#### *Data analysis*

A set of parameters was defined to test the relationships between climatic indices, hydrological time-series, or salmon stock and C and N isotopic composition (Table 2). A limited number of climatic indices cover our entire study period. The PDO consists of updated standardized values derived as the leading principal component of monthly SST anomalies in the North Pacific Ocean, poleward of 20°N. El Nino Southern Oscillation (ENSO) is the average sea surface temperature anomaly in the region bounded by 5°N to 5°S, from 170°W to 120°W. The North Pacific Index (NPI) is the area-weighted sea level pressure over the region 30°N 65°N, 160°E-140°W. We also used Extended Reconstructed Sea Surface Temperature (ERSST v4, Huang et al. 2015). The SST minimum was calculated as defined by Aydin et al, 2000, to delimit squid distribution. Sockeye salmon catch (<http://www.pac.dfo-mpo.gc.ca/stats/comm/ann/index-eng.html>) and escapement (NuSEDS V2.0 database) were provided by DFO.

To test for associations between environmental variability and stable isotope values, we correlated (Pearson correlation)  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  time series with all of the indices described above. Different combinations were used, including lagging indices and averaging them over different periods of

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<sup>3</sup> Fig. S3

<sup>4</sup> Fig. S4

time (see Table 2) to account for potential delays between climate change and changes in salmon isotope values, as well as the integration time of isotopic composition in salmon scales.

### *Trophic structure and nitrate concentration*

Stable isotope data on potential prey items and suspended particulate organic matter (SPOM) were obtained from existing studies to inform food web structure in the NE Pacific. Isotope data for SPOM, copepods, pteropods, euphausiids, amphipods and chaetognaths were from samples collected between May 1991 and May 1993 at Ocean Station Papa (OSP) (Wu et al. 1997, 1999) and for squid from samples collected during spring and summer of 1992 and 1994 from the continental shelf of the Gulf of Alaska (Hobson et al. 1997). Gonatid squid (*Berryteuthis anonychus*) sampled in the continental shelf may be expected to be enriched in  $\delta^{15}\text{N}$  compared to the same squids sampled in the oceanic stations (assuming similar trophic level). Thus, the  $\delta^{15}\text{N}$  values of gonatid squid collected in the continental shelf were not directly comparable to the  $\delta^{15}\text{N}$  values of sockeye salmon prey collected at OSP. We compared the  $\delta^{15}\text{N}$  values of copepods sampled on the shelf together with the squids (Hobson et al. 1997) versus copepods sampled at the oceanic stations (Wu et al. 1999). The copepods sampled in the shelf were enriched in  $^{15}\text{N}$ , with  $\delta^{15}\text{N}$  values 2.66 ‰ higher than offshore. This coastal / offshore gradient was shown to be quite stable through the year (Chiba et al. 2012). We then applied this offset to the  $\delta^{15}\text{N}$  values of squid sampled in the shelf to estimate the equivalent oceanic  $\delta^{15}\text{N}$  values. Trophic levels (TL) were estimated assuming an average increase in  $\delta^{15}\text{N}$  of 3.4 ‰ between two adjacent TLs (Post 2002). There is an inverse relationship between surface nitrate concentration  $\text{NO}_3^-$  and the  $\delta^{15}\text{N}$  of SPOM (Rau et al. 1998). A decrease in surface nitrate concentration is expected to confer an increase in

$\delta^{15}\text{N}$  at the base of the food web, and this will subsequently be transferred up the food chain to salmon. Therefore, information on surface  $\text{NO}_3^-$  is needed for a more accurate interpretation of the variability observed in the nitrogen stable isotope time-series. A comprehensive  $\text{NO}_3^-$  time series recorded at OSP for the period 1990-2016 (3 samples per year) was facilitated by DFO.

## Results

### *Isotopic relationship between muscle and scale tissue*

Differences between muscle and scale isotope values were relatively constant over time and between individuals for both carbon (lipid corrected) and nitrogen (Fig. 2). The mean difference for the period 2011-2016 was  $0.56 \pm 0.22$  and  $-3.45 \pm 0.34$ , for nitrogen and carbon respectively. However, 2014 differed significantly from the average for  $\delta^{15}\text{N}$ , and 2011 and 2015 for  $\delta^{13}\text{C}$ . Four and five-year-old fish sampled from 1915 to 1990 showed very comparable distributions of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  with values being slightly lower for 5-year-old fish,  $-0.10$  and  $-0.18$  ‰ for N and C respectively (Fig. 3). Three year-old fish showed a significantly higher values, only 4 samples were available for this year class, all collected in 1965. No trend was found between the condition factor of the fish (pre-1946) and  $\delta^{15}\text{N}$ , neither for 4- nor 5-year old fish (Fig. 4). Both year classes had a similar average condition factor,  $1.23 \pm 0.12$ ,  $n=53$  for 4-year-old and  $1.27 \pm 0.10$ ,  $n=119$  for 5-year-old.

$\delta^{15}\text{N}$  from salmon scales showed a stable pattern until the 1950's with values mainly ranging between  $9.47$  and  $9.78$  ‰, with the exception of 1920 ( $10.25$  ‰) (Fig.5). Values increased to  $11$  ‰ during the second half of the century, with the exception of lower values at the beginning of

the 1990's. The  $\delta^{13}\text{C}$  values, corrected for Suess effect, showed no trend. The  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values showed high interannual variability for the 2010-2016 period, for which data were available for every year. The  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  time series were not correlated with each other, or with the climate and squid indices. However,  $\delta^{13}\text{C}$  was correlated with SST from OSP leading us to explore spatially the strength of the correlation using reconstructed SST for 1915-2016.

The spatial correlation between  $\delta^{13}\text{C}$  and SST averaged from March of the year before maturation (yr-1) to May of the maturation year was highest in the southern part of the northeast pacific (Fig. 6). Correlation was stronger for SST averaged from September yr-1 to May ( $r=0.53$ ,  $p<0.01$  vs  $r=0.44$ ,  $p=0.035$ ,  $n=23$ ) with maximum values shifting slightly toward the coast. Similarly, we found a negative, but non-significant, correlation between  $\delta^{15}\text{N}$  and  $\text{NO}_3^-$  concentration, which was strongest for the nitrates averaged from Sep<sub>yr-1</sub> to May than from Mar<sub>yr-1</sub> to May ( $r=-0.50$ ,  $p=0.13$  vs  $r=-0.32$ ,  $p=0.36$ ,  $n=10$ ).

Available isotope data for potential sockeye salmon prey and SPOM collected at OSP (except squid, see Methods) from 1991-1993 allowed us to establish a trophic hierarchy (Fig. 7). The trophic chain spanned three trophic levels (TLs) with SPOM as the baseline (TL 1) and sockeye salmon as the top predator (TL 3). Euphausiids, copepods, amphipods and gonatid squids were the second level, while pteropods could be considered as TL 1.5 and chaetognaths TL 2.5.

## Discussion

In this study, we present a time series of salmon scale stable isotope (SI) values spanning over a century (1915-2016). The reconstruction of this unprecedented time series allowed us to describe for the first time the long-term variability pattern in salmon SI. The long-term trend in Rivers Inlet

sockeye salmon  $\delta^{15}\text{N}$  was characterized by a shift in the 1950's to generally higher and more variable values for the latter half of the 20th century. While the long-term trend in  $\delta^{13}\text{C}$  was difficult to interpret due to the Suess effect, we found a significant relationship with SST allowing us to estimate the most likely area of salmon distribution in the open ocean. No other significant relationships were found between RI sockeye salmon SI values and large-scale climate indices or other hydrographical indices. However, the observed high variability in the carbon and nitrogen stable isotope values of the salmon time series suggests that there were substantial short-term changes in the environmental conditions experienced by high seas foraging salmon (Fig. 5). Similar high inter-annual variability has been observed in other studies (Satterfield and Finney 2002, Johnson et Schindler 2012). Three main processes may account for the variability observed in adult sockeye SI values: (1) changes in oceanographic conditions in their foraging regions that shift the SI baseline, (2) temporal changes in their diet and/or trophic position, and (3) changes in their foraging location.

#### *Changes in the SI baseline*

During the past decades, the upper ocean in the Northeast Pacific has undergone a series of changes in physical and chemical properties in response to large-scale climate shifts related to El Niño/La Niña cycles (Whitney et al. 1998). For example, during the 1989 La Niña, winter waters at OSP were relatively cool, saline and nitrate rich. However, with the onset of the 1991 El Niño period, winter waters at OSP were more saline by 0.3, warmer by over 2°C and nitrate depleted by 30% (Whitney et al. 1998). The variations observed in the isotope data of RI sockeye salmon scales could be linked to these major changes in oceanographic conditions through changes in nutrient



concentrations over a large region of the Gulf of Alaska. An inverse relationship is generally observed between surface  $\text{NO}_3^-$  and the  $\delta^{15}\text{N}$  of particulate organic matter (Rau et al. 1998). The variability in salmon  $\delta^{15}\text{N}$  may therefore reflect  $\text{NO}_3^-$  availability at the base of the food web: for example, low  $\text{NO}_3^-$  would lead to an increase in the  $\delta^{15}\text{N}$  of the trophic baseline which would be transferred up the food chain to salmon. We observed such a relationship between  $\delta^{15}\text{N}$  in salmon scales and  $\text{NO}_3^-$  concentration recorded at OSP for 1990-2016. At longer time scales however, sockeye salmon  $\delta^{15}\text{N}$  and PDO do not appear to be correlated. Comparing  $\delta^{15}\text{N}$  and PDO values during two periods of relative stability for both time series,  $\delta^{15}\text{N}$  values were lower for 1925-1946 (positive PDO phase) than 2000-2013 (negative PDO phase) suggesting that the PDO was not the main driver of long term SI variability.

#### *Diet/trophic variability*

Sockeye salmon in the Gulf of Alaska are known to prey on a wide variety of organisms, from large mesozooplankton (e.g., copepods) to micronekton such as squid and myctophids (LeBrasseur 1966; Pearcy et al. 1988; Kaeriyama et al. 2004). Changes in the isotopic values of RI sockeye salmon may result from changes in diet or from prey items themselves shifting foraging trophic level. With regard to prey diet shifting, the omnivorous copepod *Neocalanus plumchrus* will shift feeding strategy depending on ambient phytoplankton availability (Kobari et al. 2003). For example, during nitrate depleted periods, *Neocalanus* may shift from a diet dominated by phytoplankton to a one dominated by microzooplankton. This would be expected to result in a lengthening of the food chain, leading to an increase of both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  transferred up the food chain, although a recent study shows that this increase is moderate (Gutiérrez-Rodríguez et al.

2014). Unfortunately, little data are available on the interannual variability of copepod and squid specific SI values (Chiba et al. 2012), which inhibits examination of the link between changes in copepod/squid and salmon SI values.

Kaeriyama et al. (2004) studied salmon diets from 1994 to 2000 in the different oceanic domains of the Gulf of Alaska and found that although salmon can feed across many different trophic levels by switching their diets, gonatid squid (*Berryteuthis anonychus*) were the preferred prey of sockeye salmon. The northern limit of the core squid distribution can be defined using the minimum in SST located at the southern border of the Alaskan Gyre (Aydan et al. 2000). While salmon sampled in the Subarctic Current feed almost exclusively on squid, salmon from the Alaskan Gyre had more variability in their diet, shifting from gonatid squid to copepods depending on the year (Kaeriyama et al. 2004). The reconstruction of the food web based on samples from the early 1990's (Fig. 7) shows a difference in  $\delta^{15}\text{N}$  of 3.06 ‰ between RI sockeye salmon and squid and 4.18 ‰ between salmon and copepods. This would support the hypothesis of a diet mainly comprised of squid, assuming the generally accepted trophic enrichment in  $\delta^{15}\text{N}$  of 3.4 ‰ between trophic levels (Post 2002).

A shift in salmon diet over our time series from one source to another should be traceable using  $\delta^{15}\text{N}$  values as gonatid squid are situated at a higher trophic level than copepods (Fig. 7). The average scale  $\delta^{15}\text{N}$  values was roughly 1 ‰ lower for the period 1915-1946 compared to 2000-2016, which could imply a diet shift from copepods to a greater proportion of squid in recent years. The former years were characterized by the SST minimum having an average location of 53.65 °N, while during the latter years the SST minimum was located further south at 52.80 °N. Given that squid would be expected to occur further north during 1915-1946, the lower isotope values during these years are contradictory. This result suggests that RI sockeye salmon were mainly

distributed in the Subarctic current or further south, and thus were able to maintain a diet mainly consisting of squids independently of the SST minimum location, and that others processes were driving the change in  $\delta^{15}\text{N}$ .

### *Salmon foraging location on the high seas*

Pacific salmon are a highly migratory species that spend multiple years foraging widely in the North Pacific Ocean. The ocean migration of BC stocks of sockeye salmon is hypothesised to move counter clockwise, south in winter and north in summer, following the currents of the Alaskan Gyre (Burgner 1991). The difficulty of sampling in the open ocean has resulted in very little information about salmon species location, while stock specific locations are largely unknown. Recently, a new method has emerged to track animal location based on carbon SI values and it has been applied successfully to Atlantic salmon (MacKenzie et al. 2011). The method is based on the correlation between seawater temperature and  $\delta^{13}\text{C}$ . This correlation can be explained by the increased solubility of  $\text{CO}_2$  at lower temperatures and correspondingly increased availability of  $^{12}\text{C}$  which algal cells preferentially use in metabolic processes (Burkhardt et al. 1999; Freeman and Hayes 1992). We applied this approach to track RI sockeye salmon location at sea. The area with the strongest and significant correlation was located in the southern limit of the distribution range estimated from fishery catch report (Fig. 1 and 6). This is crucial information as changes in large spatial scale oceanographic features, such as the latitudinal location of the Subarctic current delimiting the separation between the transitional domain and the Alaskan Gyre (Fig. 1), will substantially affect the environment experienced by salmon. The proposed feeding area for RI sockeye salmon suggest, however, that this specific stock spends the last nine months of their

pelagic phase in the middle of the Transitional domain where they would encounter more stable prey composition. This is consistent with the result from the trophic analysis and the change in  $\delta^{15}\text{N}$  that were pointing toward a RI sockeye salmon diet mainly comprised of squids.

#### *Role of high seas ecosystems in Rivers Inlet sockeye decline*

The causes for decline of the RI sockeye salmon population are still under debate. The approach used in this study provided insights into the potential role of high seas ecosystems in affecting salmon condition during the pelagic phase. The observed shift in  $\delta^{15}\text{N}$  around the 1950's may have been a precursor to the decline to come. However, based on our dataset, we were not able to directly relate the decline of RI sockeye with a shift in the SI baseline or a change in diet. This may have been due in part to the difficulty in teasing apart the combined effects of the processes affecting salmon SI values over different spatio-temporal scales. The  $\delta^{15}\text{N}$  values, which were quite stable before 1950, became more variable thereafter, pointing to a more variable environment. Given that salmon appear to rely heavily on squid availability during their last year at sea (LeBrasseur 1966), further investigation into *Berryteuthis anonychus* ecology and population dynamics (Ushikawa et al. 2004) would be beneficial to understanding salmon condition when maturing and their ability to successfully reach the spawning grounds.

#### *Standardizing $\delta^{13}\text{C}$ time series*

An understanding of the relationship between muscle- and scale-derived stable isotope values is important for the interpretation of scale isotopic results. Turnover rates of muscle carbon and

nitrogen are believed to be around 3 months (Sakano et al. 2005; Jardine et al. 2004) and C and N SI thus provide information for this period of time. It is recommended to isolate the last annuli of each scale when information on the last growing season are targeted (Hutchinson 2006). However, the whole scale also has a SI value strongly influenced by the last fast growing period of the fish due to the increasing surface of the layer formed when the scale gets larger (Trueman and Moore 2007). Our result shows a quite constant difference in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between muscle and scales during the period 2011-2016, which supports a comparable time integration period between muscles and scales, or at least that both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values are mainly influenced by the last fast growing season. Furthermore, the best correlation between  $\delta^{13}\text{C}$  and SST, and  $\text{NO}_3^-$  and  $\delta^{15}\text{N}$  was found for Sep yr-1 to May, supporting an integration time of approximately 9 months. The average difference between the  $\delta^{13}\text{C}$  of muscle and scales in this study was similar to that observed in a previous study (-3.45 ‰ - this study; -3.72 ‰ - Satterfield and Finney 2002). Our results also suggest that the Suess effect should be taken into account and that constant  $\delta^{13}\text{C}$  values over a certain amount of time can be the result of a balance between the Suess effect (increasing  $^{12}\text{C}$  replete  $\text{CO}_2$  concentration in the water column) and increasing temperature (decreasing solubility of  $\text{CO}_2$ ). Cumulative Suess correction difference was estimated from our model to be 2.03 ‰ from pre-industrial time to 2016, and 1.90 ‰ over our study period (1915-2016). These values fall in the higher end of the range found in the literature, which is what we would expect as our dataset span until 2016 and the phenomena is amplifying every year. The rate of change of  $\delta^{13}\text{C}$  in surface water due to the Suess effect is estimated to be between -0.014 and -0.025 ‰  $\text{yr}^{-1}$  in recent decades, with higher values in areas without strong mixing processes (Grubber et al. 1999; Quay et al. 2003). Overall, we think that long term trend in  $\delta^{13}\text{C}$  values should be interpreted with caution as

they will be strongly influenced by the correction model applied and the parameter setting. It also limits the comparison between  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ .

#### *Recommendations for future studies*

Isotopic composition is a powerful tool to investigate links between ocean productivity and salmon condition, providing information on both the structure of food webs (e.g., food chain length, linkages) and the processes that may be supporting them (e.g., mixing, increased atmospheric  $\text{CO}_2$ ). There are however some limitations that should be dealt with to obtain meaningful interpretations. Changes in climate over large scales can result in variation in the SI baseline values that will shift salmon SI values without necessarily reflecting a change in salmon diet. New efforts should be encouraged to collect SI data for lower trophic levels (plankton and micronekton) in the North Pacific. Furthermore, spatial variation in the SI values of lower trophic levels needs to be mapped (e.g., Isoscapes; Graham et al. 2010), to inform regional food web dynamics that can be compared against stock specific salmon distributions.

The temporal resolution of the time series also matters because both C and N SI values may vary strongly from one year to the next. It can be argued that five year frequency data would allow one to track the same stock as it corresponds to one generation for most RI salmon. However, special events, such as unusual age distribution, show that care needs to be taken when doing so. In general, high temporal resolution (yearly) time series are necessary to disentangle the different components of climate change and their direct and indirect effects.

A critical gap in our understanding of salmon dynamic is the actual distributions of salmon in the high seas. Identification of salmon location in the pelagic realm is critical to be able to detail the

relationship between ocean environment and salmon condition, and to understand differences in stock dynamics. The method used in this study, based on correlation between  $\delta^{13}\text{C}$  and SST showed very promising results and as such should be developed further in the future. Based on our preliminary findings we recommend that  $\delta^{13}\text{C}$  time series should first be corrected for the Suess effect and lipid content, and that a SST integration time window of nine months gives the strongest correlation when using the entire scale. The next step would be to expand this method to additional stocks / populations to investigate differences in distributions and changes over time. If different salmon populations distribute differently on the high seas, each may experience a unique set of environment conditions and be impacted differently by environmental changes.

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Draft

**Figure captions**

Fig. 1 Schematic diagram indicating the two main major oceanic domains encounter by sockeye salmon. Sea surface temperature minimum as defined by Aydin et al. 2000 is used to determine the latitudinal squid distribution index. The southern limit of sockeye distribution is inferred from 1956-83 INPFC salmon research operation (see Burgner 1991).

Fig. 2. Averaged differences ( $\pm$  SD) in  $\delta^{13}\text{C}$  (open squares) and  $\delta^{15}\text{N}$  (open triangles) measured in salmon muscle and scale for 2011-2016. The number of samples analyzed for each year is indicated ( $n$ ).

Fig. 3. Boxplot of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  as a function of salmon age. Based on salmon sampled during 1915-2010. The number of samples analyzed for each age is indicated ( $n$ ). 3-, 4- and 5-year-old fish correspond to age 1.1, 1.2 and 1.3 fish in commonly used European system.

Fig. 4.  $\delta^{15}\text{N}$  values as a function of the condition factor for 4 year old (age 1.2; black dots) and 5 year old (age 1.3; open squares) salmon. Based on salmon sampled during 1915-1946.

Fig. 5. Long term distribution of  $\delta^{15}\text{N}$  (top) and  $\delta^{13}\text{C}$  (bottom) mean ( $\pm$  SD), based on salmon scales for the period 1915-2016.  $\delta^{13}\text{C}$  series has been corrected from Suess effect. Escapement (open bar) and catch (black bar) data are displayed. Approximate averaged historical catch (before 1950) are indicated (grey dashed line).



Fig. 6. Proposed feeding area for Rivers Inlet sockeye salmon based on the strength of the correlation between  $\delta^{13}\text{C}^*$  and modeled SST averaged over 15 (top) and 9 (bottom) months before salmon migration back to the river.

Fig. 7. Mean ( $\pm$  SD) nitrogen stable isotope ratios from sockeye salmon prey and suspended particulate organic matter (SPOM) collected between May 1991 and May 1993 at Ocean Station Papa; squid samples taken during spring and summer of 1992 and 1994 from the continental shelf of the Gulf of Alaska; and from RI sockeye salmon scales collected in 1992. Sample sizes given in parentheses.

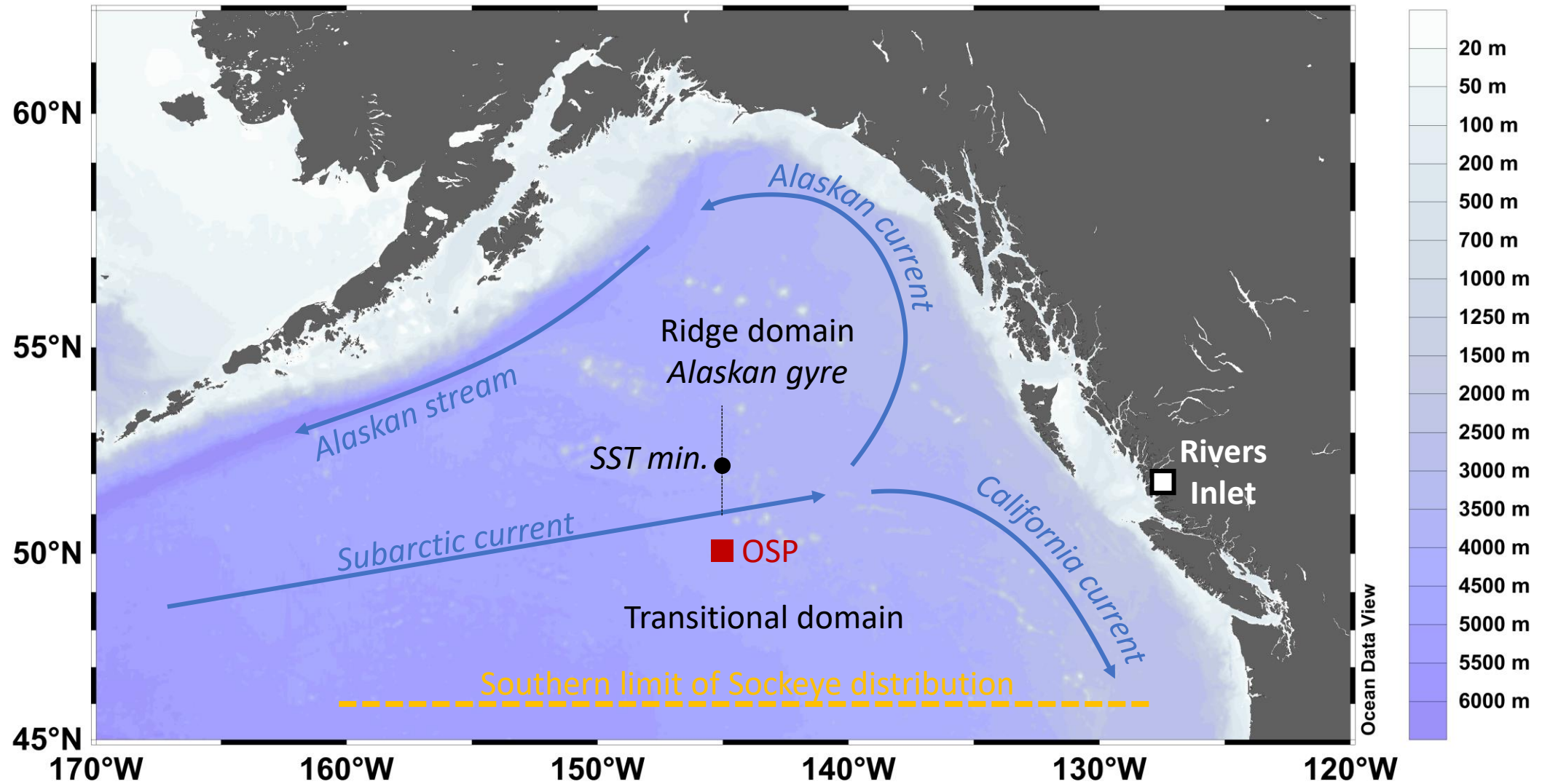
Fig. S1. (a) C:N and  $\delta^{13}\text{C}$  in muscles from sockeye salmon collected in Rivers Inlet in the fjord (pre-spawn) and on the spawning ground (post-spawn) in 2013. (c) Model used to correct from lipid effect based on C:N.  $\delta^{13}\text{C}$  reference value for  $\Delta\delta^{13}\text{C}$  calculation is the median of  $\delta^{13}\text{C}$  distribution in scales of post-spawn sockeye salmon.

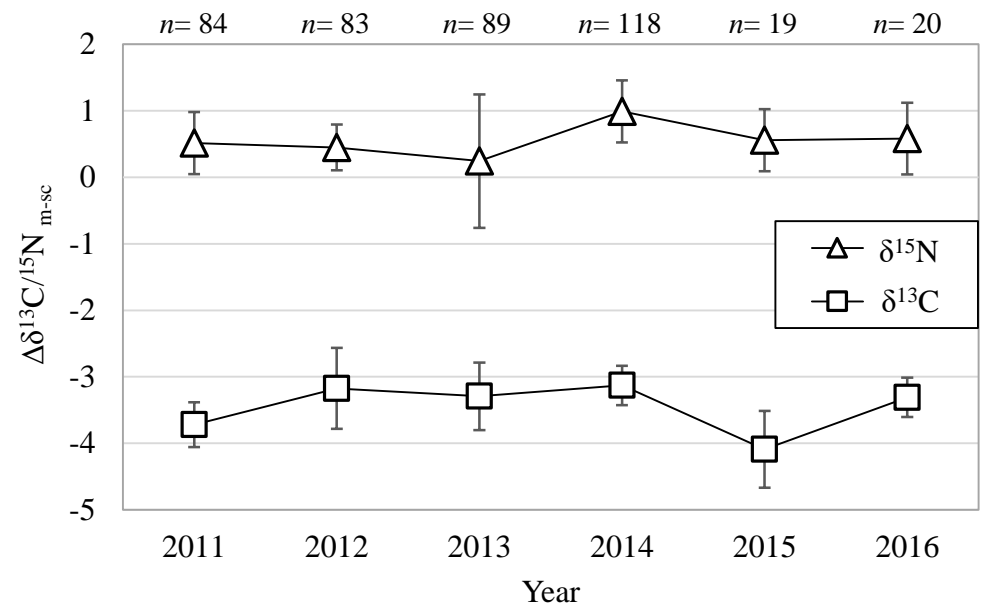
Fig. S2. Model used to correct for remnant lipids on sockeye salmon scales, based on an extensive sampling effort carried out in 2013.  $\delta^{13}\text{C}$  reference value for the  $\Delta\delta^{13}\text{C}$  calculation is the median of a batch of scales ( $n=69$ ) with a C:N expected for clean scale (median= 2.61).

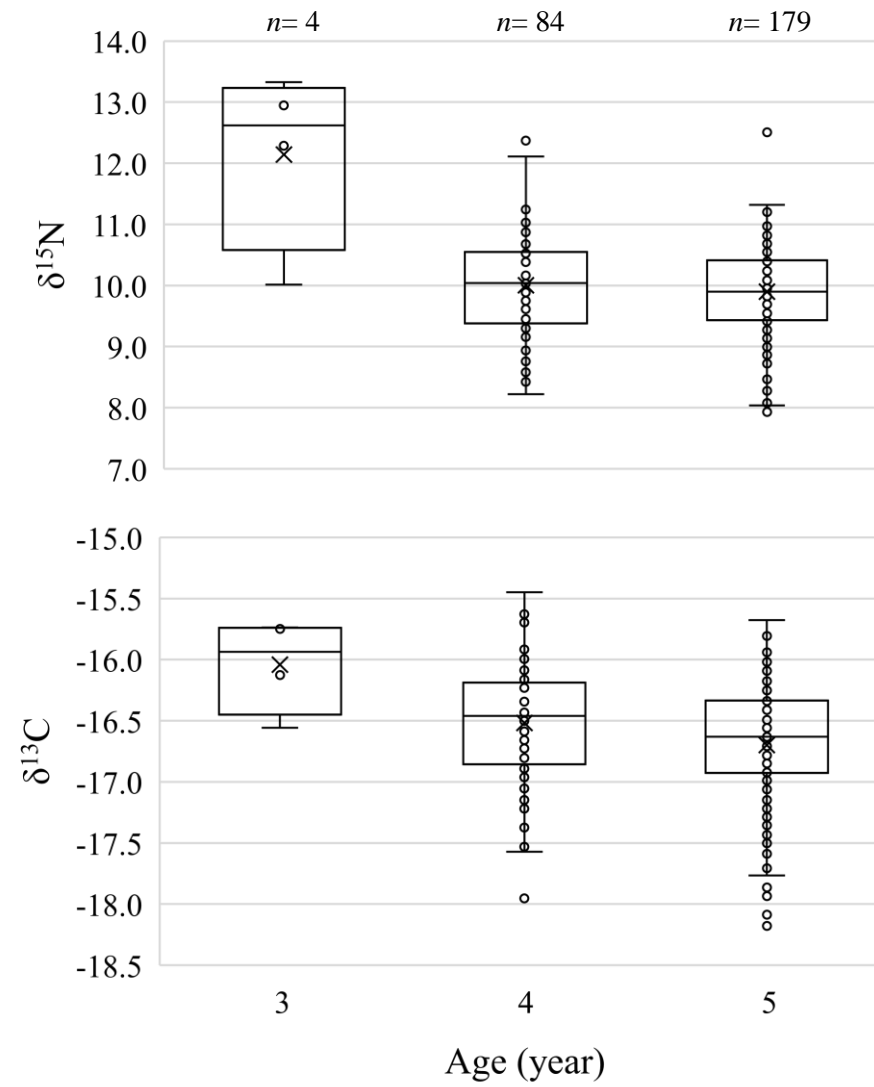
Fig. S3. Annual SST time series averaged for the area 48-56 °N and 152-136 °W for 1914-2016. Data are part of the Extended Reconstructed Sea Surface Temperature (ERSST v4) dataset.

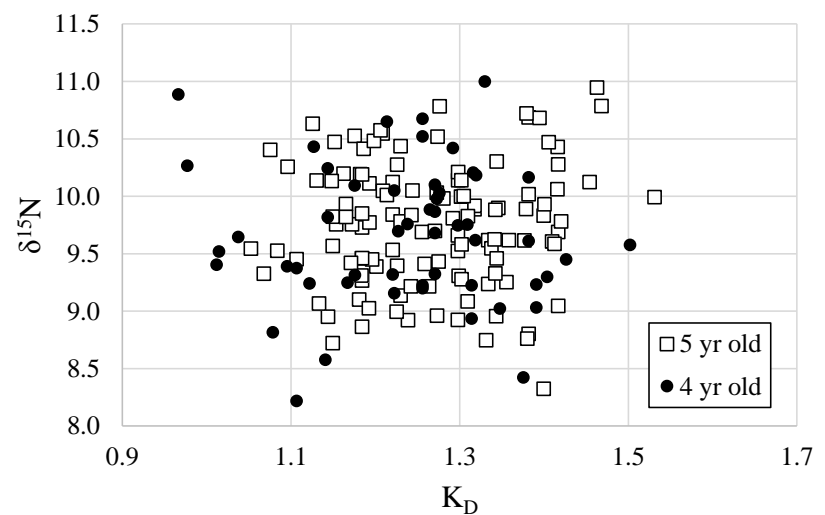
724 Fig. S4. Model used to correct  $\delta^{13}\text{C}$  data for the Suess effect. The shape of the curve defined by  
725 the parameter  $a$  was presented by Gruber et al. 1999 and adapted by Hilton et al. 2006.

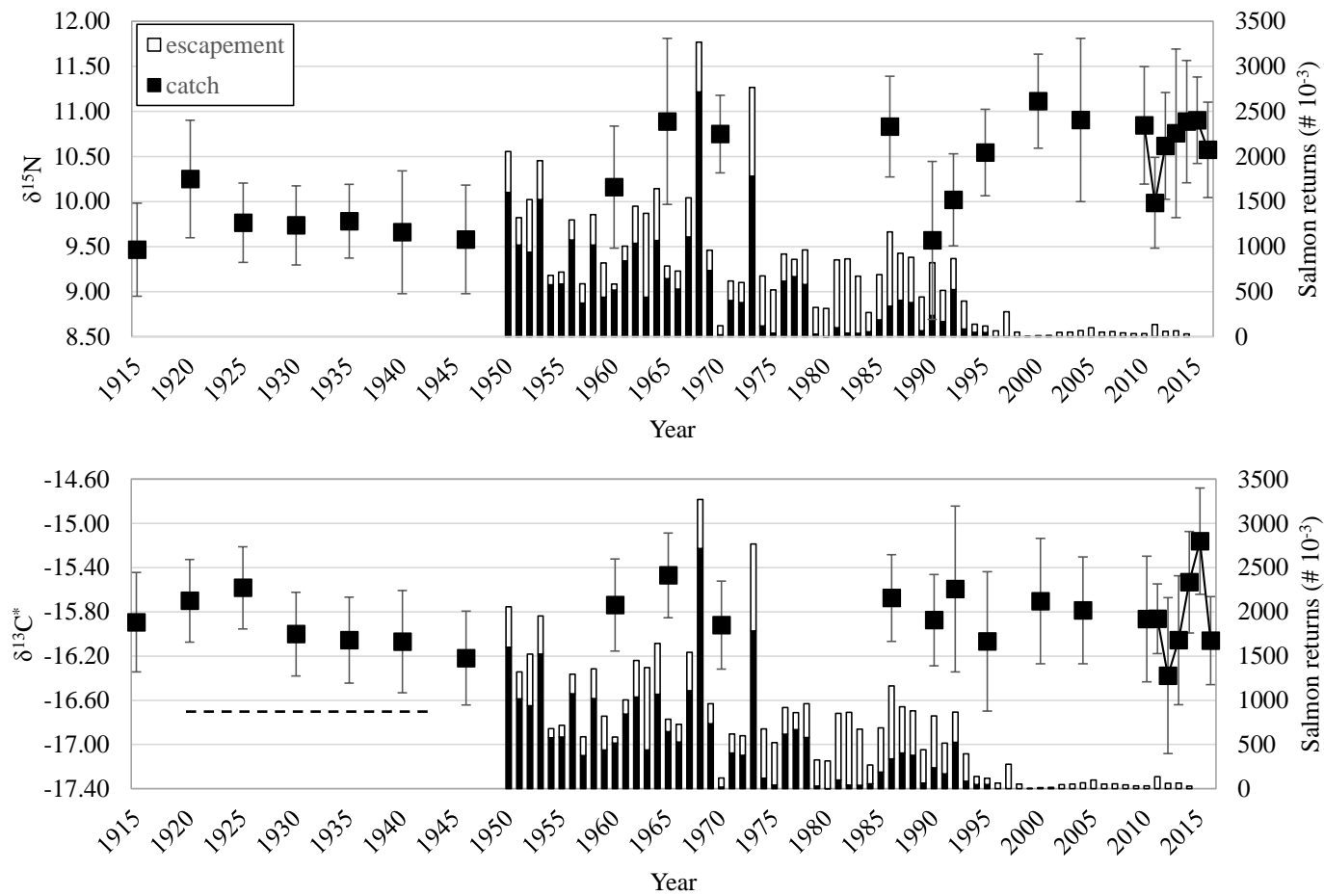
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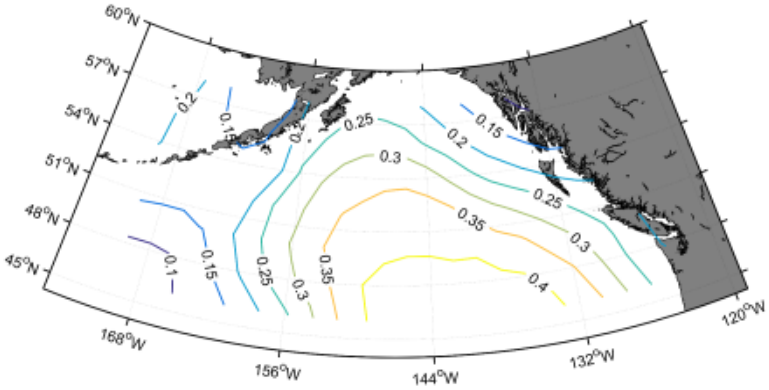




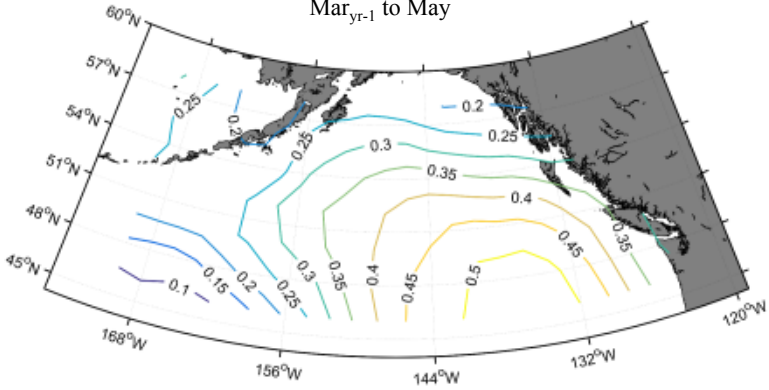








Mar<sub>yr-1</sub> to May



Sep<sub>yr-1</sub> to May



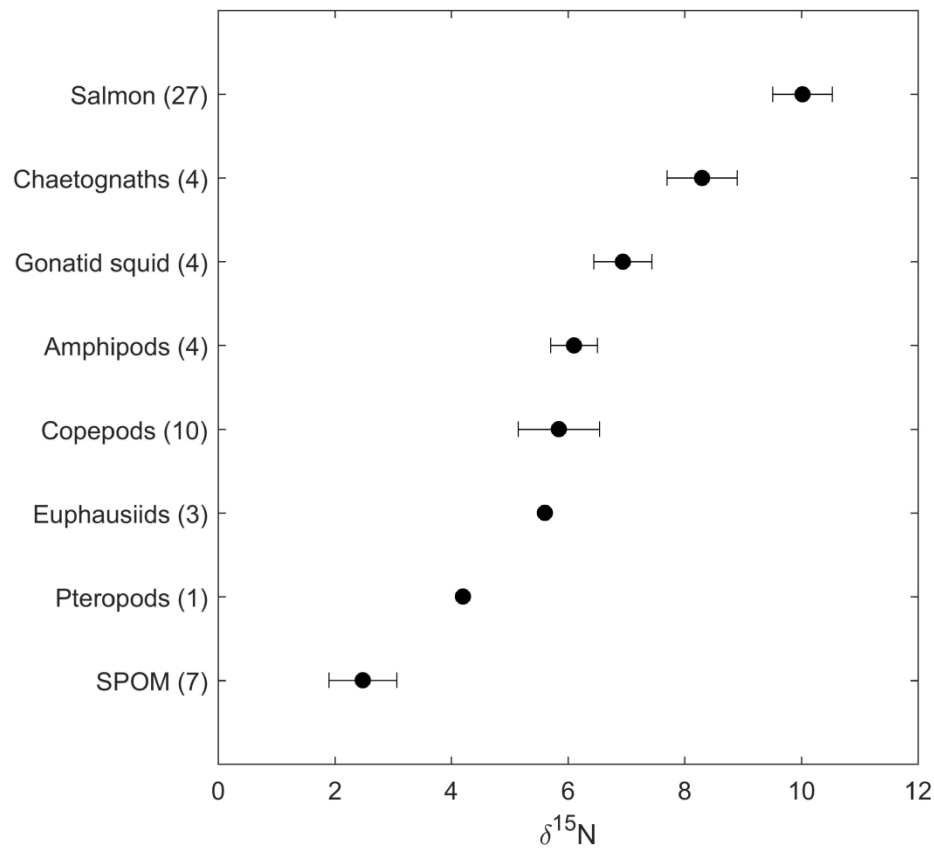


Fig. 7. Mean ( $\pm$  SD) nitrogen stable isotope ratios from sockeye salmon prey and suspended particulate organic matter (SPOM) collected between May 1991 and May 1993 at Ocean Station Papa; squid samples taken during spring and summer of 1992 and 1994 from the continental shelf of the Gulf of Alaska; and from RI sockeye salmon scales collected in 1992. Sample sizes given in parentheses.

1162x1075mm (72 x 72 DPI)

Table 1. Details of the scales time series used in this study. A: age, S: sex, W: weight, L: length

Sources	Years	Nbr. samples	Fish status	Additional information
DFO	1915	25	Pre-spawn	A; S; W; L
Commercial	1920	24	Pre-spawn	A; S; W; L
fisheries	1925	25	Pre-spawn	A; S; W; L
Jun-Aug	1930	25	Pre-spawn	A; S; W; L
	1935	25	Pre-spawn	A; S; W; L
	1940	25	Pre-spawn	A; S; W; L
	1946	25	Pre-spawn	A; S; W; L
	1960	25	Pre-spawn	A; L
	1965	25	Pre-spawn	A
	1970	25	Pre-spawn	A
	1990	25	Pre-spawn	A
DFO	1986	38	Spawned	A
Stock assessment	1992	27	Spawned	A; S; L
routine	1995	18	Spawned	A
Sep-Oct	2000	28	Spawned	A
	2004	28	Spawned	A
	2010	30	Spawned	A
Wuikinuxv Nation	2011	84	Pre-spawn	S; W; L
food fishery	2012	83	Pre-spawn	S
Jun-Aug	2013	89	Pre-spawn	S

	70	Spawned	S; L
2014	135	Pre-spawn	S; W; L
2015	20	Pre-spawn	S
2016	20	Pre-spawn	S
<i>Total</i>	944		

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Table 2. Summary of the parameters selected to attest of any relationship with changes in stable isotope signatures in BC sockeye salmon. Only variables covering the whole of the studied period were considered.

Parameter	Unit	Time windows	Source
PDO		9/15 months averaged 1 year averaged lagged 1 yr	JISAO, University of Washington
ENSO	°C	9/15 months averaged 1 year averaged lagged 1 yr	NINO 3.4; NOAA
NPI	hPa	9/15 months averaged	Trenberth and Hurrell 1994
SST	°C	9/15 months averaged	ERSST; Huang et al. 2017
Squid index	Latitude, °N	lagged 1 yr	Based on Aydin et al. 2000