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June 2016

This article was originally published at:

https://doi.org/10.1111/fog.12161

Citation for this paper:

Hertz, E., Trudel, M., Tucker, S., Beacham, T. D., Parken, C., Mackas, D., & Mazumder, A. (2016). Influences of ocean conditions and feeding ecology on the survival of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*). *Fisheries Oceanography,* 25(4), 407-419. https://doi.org/10.1111/fog.12161.

FISHERIES OCEANOGRAPHY

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Influences of ocean conditions and feeding ecology on the survival of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*)

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ABSTRACT

Recruitment variability in many fish populations is postulated to be influenced by climatic and oceanographic variability. However, a mechanistic understanding of the influence of specific variables on recruitment is generally lacking. Feeding ecology is one possible mechanism that more directly links ocean conditions and recruitment. We test this mechanism using juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) collected off the west coast of Vancouver Island, British Columbia, Canada, in 2000–2009. Stable isotopes of carbon (δ^{13}C), an indicator of temperature or primary productivity, and nitrogen (δ^{15}N), an indicator of trophic position, were taken from muscle tissues of genetically stock-identified salmon. We also collated large-scale climate indices (e.g., Pacific Decadal Oscillation, North Pacific Gyre Oscillation), local climate variables (e.g., sea surface temperature) and copepod community composition across these years. We used a Bayesian network to determine how ocean conditions influenced feeding ecology, and subsequent survival rates. We found that smolt survival of Chinook Salmon is predicted by their δ^{13}C value, but not their δ^{15}N. In turn, large-scale climate variability determined the δ^{13}C values of salmon, thus linking climate to survival through feeding ecology, likely through qualities propagated from the base of the food chain.

Key words: bottom-up, copepods, diet, North Pacific Gyre Oscillation, stable isotope, trophic

INTRODUCTION

Climate and ocean conditions influence the recruitment variability and early survival rates of many fish species (Aebischer *et al.*, 1990; Platt *et al.*, 2003; Ware and Thomson, 2005). However, the direct mechanisms underlying the linkages between climate and fisheries are not well-understood (Baumann, 1998) and relationships between environmental variables and recruitment often break down over time (Myers, 1998). In a period of rapid environmental change, understanding the mechanisms by which climate influences fisheries is important for both conservation and economic goals.

Pacific salmon (*Oncorhynchus* spp.) are an anadromous and semelparous species whose recruitment variability and survival have repeatedly been linked to climate. For example, the Pacific Decadal Oscillation (PDO) (Mantua *et al.*, 1997) and the North Pacific Gyre Oscillation (NPGO) (Kilduff *et al.*, 2015) are large-scale climate indices that both have been correlated with interannual variability in salmon recruitment. Numerous local-scale measures of ocean conditions have been similarly correlated with salmon recruitment, including upwelling (Wells *et al.*, 2007), alongshore current (Bi *et al.*, 2011a) and the timing of the spring bloom (Chittenden *et al.*, 2010). However, a mechanistic understanding of the intermediate steps between climate and recruitment is often lacking (Baumann, 1998; Malick *et al.*, 2015a).

There have been a variety of approaches used to link ocean climate to salmon survival. Linear regression models have been used between salmon survival and single selected climate variables (Bi *et al.*, 2011a; Tucker *et al.*, 2015a). Similarly, multiple climate variables can be reduced in dimensionality by procedures

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Received 25 November 2015
Revised version accepted 2 March 2016

doi:10.1111/fog.12161

such as principal component analysis, and then regressed against salmon survival (Greene *et al.*, 2005; Burke *et al.*, 2013). The limitation of these approaches, however, is that they do not consider the direct and indirect effects of different climate and ocean attributes. That is, climate variables do not directly influence recruitment: climate conditions indirectly influence more proximate factors such as the quality or quantity of prey, which then correlates with survival (Bi *et al.*, 2011a). These limitations have been previously addressed using path analysis and structural equation modelling (Wells *et al.*, 2007, 2008; Seo *et al.*, 2011), but these approaches require a long time-series of data that are unavailable to all but a few systems.

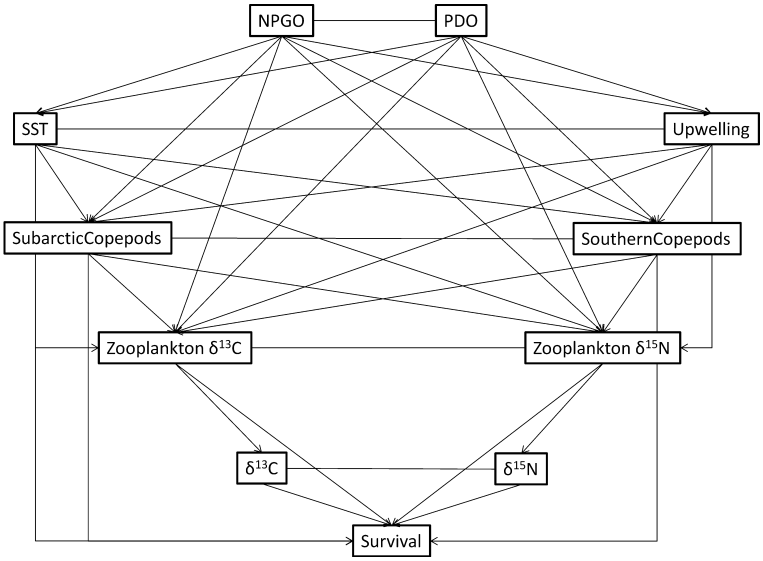
Bayesian networks are another potential tool to explore the linkages between climate and survival, yet this method has not received much interest until recently (Araujo *et al.*, 2013; Malick *et al.*, 2015a). Bayesian networks have advantages over other methods, as Bayesian Networks are flexible and allow for the incorporation of qualitative and quantitative variables, along with expert opinion (Amstrup *et al.*, 2008). This approach allows the elucidation of indirect and direct pathways, and can be implemented with less stringent data requirements than path analysis or structural equation modelling (Araujo *et al.*, 2013). Finally, Bayesian networks can be used to provide a probabilistic framework, in addition to hypothesis testing.

The objective of this paper was to describe the relationships between climate variability and survival of salmon, while explicitly taking into account the indirect pathways between them (Fig. 1). Specifically, we sought to fill in the intermediate steps separating large-scale climate variables from the local-scale processes that determine salmon growth and survival. We accomplished our objectives using a Bayesian network to relate climate variability and survival to a unique time-series of stable isotope values of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) in the Northern California Current (NCC) system in 2000–2009.

METHODS

The development of a Bayesian network to mechanistically link oceanic climate variability to survival requires a time series of climate variables, a measure of how these variables could influence survival through bottom-up or top-down processes, and estimates of survival rates. We thus modelled the interannual variability in the survival of Chinook Salmon in the Northern California Current as a function of climate variables that have previously been linked to growth or survival. We also determined the feeding ecology of juvenile

Figure 1. Possible links between climate variables, zooplankton community composition, feeding ecology and survival of west Coast of Vancouver Island (WCVI) juvenile Chinook Salmon from 2000–2009. Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO) and sea surface temperature (SST) are averaged over the period of May–September. Upwelling is the sum of the cumulative upwelling index at 51N 131W from January–June. $\delta^{13}C$ and $\delta^{15}N$ are the yearly isotopic values of juvenile Chinook Salmon in the fall. Survival is the yearly smolt survival rate of Robertson Creek Chinook Salmon.



Chinook Salmon (as indicated by stable isotopes of δ^{15}N and δ^{13}C), as this is one process that may link the bottom-up effects of climate to survival (Daly *et al.*, 2013). We hypothesized that variability in the δ^{15}N and δ^{13}C of juvenile salmon and zooplankton would be driven by climate variability, and would correlate with overall survival rates. Stable isotopes provide a longer-term, integrated indicator of diet (turnover time of muscle tissue ~1 month; Heady and Moore, 2013) when compared to the snapshot of diet contained in stomach contents. Generally, stable isotopes of nitrogen (δ^{15}N) provide an indicator of the trophic position (Post, 2002), whereas stable isotopes of carbon (δ^{13}C) can provide an indication of temperature (Newsome *et al.*, 2010; Hertz *et al.*, 2015), nutrient source (El-Sabaawi *et al.*, 2013) or primary productivity (Miller *et al.*, 2008; Oczkowski *et al.*, 2014).

We hypothesize that δ^{15}N will be positively related to survival as higher trophic-level fish prey are higher in energy content than lower trophic-level prey (Davis *et al.*, 1998; Pazzia *et al.*, 2002; Table S1). δ^{13}C could be either positively or negatively related to survival rates depending on which mechanisms are most important in driving interannual δ^{13}C values on the west Coast of Vancouver Island (WCVI). If SST is the primary factor driving interannual variability in δ^{13}C, then we would expect a negative relationship between δ^{13}C values of salmon and survival rates, as a warmer sea surface temperature (SST) is associated with a higher baseline δ^{13}C as a result of changes in the solubility of CO_2 (Newsome *et al.*, 2010; Hertz *et al.*, 2015). Warmer SSTs correspond with a copepod community that relates poorly to salmon growth and survival (Hooff and Peterson, 2006; Mackas *et al.*, 2007). Conversely, if productivity of phytoplankton is more important, than we would expect a positive relationship between δ^{13}C and survival as a higher δ^{13}C indicates higher primary productivity (Miller *et al.*, 2008; Oczkowski *et al.*, 2014) and a greater food supply for juvenile salmon (Ware and Thomson, 2005).

Study area

The NCC is a productive upwelling system off of the west coast of North America (Ware and McFarlane, 1989). Variability in local conditions such as SST and nutrients correlates with basin-scale indices such as the PDO, El-Nino Southern Oscillation (ENSO) and the NPGO (Peterson *et al.*, 2014). Interannual variability in zooplankton community composition also tracks these basin-scale indices (Hooff and Peterson, 2006; Keister *et al.*, 2011). A lipid-rich, subarctic copepod community dominates when PDO values are negative, ENSO values are negative and oceanic conditions are cooler with strong water transport from the north (Hooff and Peterson, 2006). Conversely, when PDO and ENSO values are positive, conditions become warmer, and large-scale transport brings a lipid-poor southern community of zooplankton onshore (Mackas *et al.*, 2007; Keister *et al.*, 2011). The subarctic and southern communities may differ in their value as a prey item to salmon, with subarctic copepods being large and lipid-rich compared with southern copepods (Lee *et al.*, 2006). Although juvenile salmon may not feed directly on these copepods, a higher lipid content in the base of the food web may lead to a lipid-rich food web that is passed onto juvenile salmon (Bi *et al.*, 2011b; Tucker *et al.*, 2015a). Finally, the NPGO is correlated with fluctuations in nutrients and salinity, which can drive variability in abundance of phytoplankton and higher trophic levels (Di Lorenzo *et al.*, 2008, 2009).

Juvenile Chinook Salmon and zooplankton collection

Juvenile Chinook Salmon were collected in the fall (October–November) of 2000–2009 off of the WCVI in British Columbia, Canada. A research vessel or commercial fishing vessel towed a 28 × 16 m rope trawl for 30 min at approximately 5 knots (9.8 km h^{-1}) and up to 30 juvenile Chinook Salmon were taken from the resulting tows (Tucker *et al.*, 2011, 2012). Fish were measured, weighed and a skin sample was removed from the operculum for genetic stock identification (Beacham *et al.*, 2006; Tucker *et al.*, 2011, 2012). Fish that were genetically identified to have a >80% probability of originating from the WCVI were retained for this study. Juvenile Chinook Salmon tend to remain off the WCVI until at least after their first ocean winter, unlike many other stocks and species (Trudel *et al.*, 2009; Tucker *et al.*, 2011, 2012), which simplifies determining the oceanic conditions that they experience.

Bulk zooplankton samples were collected via an oblique tow towed at 1–2 knots (2000–2001) or vertical bongo tow (2002–2009) to 150 m or within 10 m of the ocean floor. Samples were size-fractionated on the research vessel, and the smallest size fraction (0.25–1.0 mm) was used for stable isotope analysis. Because of the seasonal shifts in the zooplankton isotopes off WCVI (El-Sabaawi *et al.*, 2012), we averaged the spring (May–June) and fall (October–November) values, to reflect the changes in the baseline that juvenile Chinook Salmon experience with equilibration to oceanic isotopes.

Stable isotope analysis

The preparation of juvenile Chinook Salmon for stable isotope analysis varied slightly (oven-dried whole fish versus freeze-dried muscle tissue), so we mathematically-corrected samples (Fig. S1). All samples were ground to a fine powder using a heavy-duty Wig-L-Bug grinder, packed into tin capsules, and were run on a Thermo Delta IV Isotope Ratio Mass Spectrometer (University of Victoria, Victoria, British Columbia). Stable isotope values of δ^{15}N and δ^{13}C are expressed in the delta notation

$$\delta^{15}\mathrm{N} \quad \text{or} \quad \delta^{13}\mathrm{C} = [(R_{\mathrm{sample}}/R_{\mathrm{standard}}) - 1] \times 1000 \tag{1}$$

where R is ^{15}N : ^{14}N or ^{13}C : ^{12}C for the sample or a standard. The standard for δ^{15}N was atmospheric nitrogen whereas the standard for δ^{13}C was Vienna Peedee Belemnite. An internal standard had a standard deviation of ~0.2‰. All samples of salmon and zooplankton were mathematically lipid-corrected according to Post *et al.* (2007), as differences in the amount of lipid between samples can affect δ^{13}C values.

Physical and biological variables

To determine how ocean conditions affect the δ^{15}N and δ^{13}C values of juvenile Chinook Salmon and their smolt survival rates, we reviewed literature sources to determine which variables are likely to influence feeding ecology and survival of juvenile Chinook Salmon in the NCC. Although many of the climate variables we chose covary, each represents different processes operating at different scales. In addition to the time integrations of climate variables listed below, we also tested integrations of the NPGO, PDO and SST from January–June, and annual means of these variables, to determine whether different time lags displayed different interrelationships.

Pacific Decadal Oscillation index

The PDO is the first principal component of the North Pacific SST variation north of 20°N (Mantua *et al.*, 1997). Positive PDO values correspond with warm temperatures and a southern copepod community in the NCC (Mackas *et al.*, 2007; Peterson *et al.*, 2014). We calculated the mean PDO value from May–September of each year, representing the period of ocean residence from ocean entry to just before our sampling (Trudel *et al.*, 2007). Data were retrieved online from http://research.jisao.washington.edu/pdo/.

NPGO

The NPGO index is the second principal component of sea surface height anomaly across the North Pacific (Di Lorenzo *et al.*, 2008, 2009). NPGO values represent gyre circulation in the North Pacific, and have been correlated with fluctuations in nutrients and salinity in the NCC (Di Lorenzo *et al.*, 2008, 2009). Similar to the PDO, NPGO values were also averaged from May to September, capturing the oceanic conditions that juvenile Chinook Salmon experience before our sampling.

SST

Sea surface temperature values were taken from the Amphitrite Lighthouse data (http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.html). Monthly values were averaged over the same period as the NPGO and PDO to capture conditions before and during outmigration and early ocean residence.

Upwelling

Upwelling was assessed using the Bakun upwelling index from Pacific Fisheries Environmental Laboratory data (ftp://orpheus.pfeg.noaa.gov/outgoing/upwell/monthly/upindex.mon). Higher values of this index reflect stronger upwelling events. The station used for WCVI was located at 51°N 131°W. The sum of monthly averages was used from January–June, representing a measure of cumulative upwelling before and during salmon outmigration.

Copepod anomalies

In the NCC, there are two predominant zooplankton species communities. The 'northern' or subarctic copepod community is comprised of subarctic or boreal copepod species, whereas the 'southern' copepod community is made up of subtropical copepod species (Mackas *et al.*, 2007). These communities tend to vary out-of-phase with each other, with northern copepods being more abundant with negative PDO and ENSO values (Mackas *et al.*, 2007). We used the annual biomass anomalies developed by Mackas *et al.* (2001) and recently updated by Tucker *et al.* (2015a) to describe this variability.

Survival

The smolt survival rate of an indicator stock, Robertson Creek, was used as a proxy for marine survival across all WCVI stocks, as other WCVI stocks are generally expected to experience similar ocean conditions, distribution and survival (Tucker *et al.*, 2011, 2012; but see Tucker *et al.*, 2015b). The smolt survival rate of Robertson Creek was determined via an annual cohort analysis using coded-wire-tag data from recoveries in escapement and fisheries (Magnusson and Hilborn, 2003; Pacific Salmon Commission, 2012). Smolt survival rates were logit-transformed.

Statistical analysis

To identify which physical and biological variables influence the feeding ecology and smolt survival of juvenile Chinook Salmon, we used a Bayesian network. Bayesian networks can infer dependence between variables in a network, allowing the structure and relationships between variables to be determined (Nagarajan *et al.*, 2013). Although we limited the fit of our models to linear relationships, in principle, nonlinear relationships between variables could also be taken into consideration. Bayesian networks graphically represent joint probability distributions of selected variables. Every random variable X_i depends directly only on its parents $\prod_{X_i}$ where, for continuous variables (Scutari, 2010)

$$f(X_1,\ldots,X_v)=\prod_{i=1}^{v} f\left(X_i \middle| \prod_{X_i}\right). \qquad (2)$$

Model selection algorithms first learn the structure of the Bayesian network, then subsequently estimate the parameters of local distribution functions.

We determined how interannual variability in basin-scale climate indices, local biological and physical oceanographic variables and the feeding ecology of juvenile Chinook Salmon ultimately influenced smolt survival. There are several methods that can be used to learn Bayesian networks, each with benefits and drawbacks (Bøttcher and Dethlefsen, 2003; Scutari, 2010). We used a score-based hill-climbing algorithm with an uninformative prior distribution (Scutari, 2010). The hill-climbing algorithm assigns scores to each candidate network and maximizes the score with a heuristic search algorithm (Scutari, 2010; Mori and Saitoh, 2014).

The directionality of nodes was limited so that large-scale variables could influence local-scale variables, but not the opposite. For example, NPGO could influence SST, but the path from SST to NPGO was not allowed (Fig. 1; Table S1). Climate variables were also not allowed to influence directly the δ^{13}C or δ^{15}N values of salmon, or survival rates, as the effects of these large-scale variables would be mediated through effects on lower trophic levels (i.e., zooplankton isotopes) and other climate variables (Table S1). The only exception to this is SST, which was allowed to influence survival directly, by altering the distribution and abundance of predators (Hinch *et al.*, 1995). All network analyses were implemented in R (R Core Team, 2012) with the associated *bnlearn* R package (Scutari, 2010). We used partial correlation coefficients to determine the strength of network paths (Zar, 1999) using the *ppcor* R package (Kim, 2015).

We repeated all analyses with size-corrected data as well, as slight interannual variation in timing of sampling could influence results. To correct for size, we fitted a logistic model to the δ^{15}N or δ^{13}C data (δ_{X_i}; where x is either C for carbon or N for Nitrogen) from individual juvenile Chinook Salmon, i, as a function of weight

$$\delta_{X_i}=\frac{\propto}{1+e^{\frac{\beta-w_i}{\theta}}} \qquad (3)$$

where $\propto$ is the asymptotic isotopic value, w_i is the weight of each fish at capture, and β and θ are scaling parameters (Hertz *et al.*, 2015). This model was separately fit to the δ^{15}N and δ^{13}C data as a function of weight. The yearly average of the residual variation was used as a variable in modelling (hereafter $\delta^{15}N_{\text{residual}}$ and $\delta^{13}C_{\text{residual}}$). This correction was necessary as some years (e.g., 2002) captured fish were larger, and more equilibrated with the oceanic baseline than other years (Fig. S2).

We also tested the sensitivity of the best model to determine whether or not the results were driven primarily by a single year, as there were only 10 years available for analysis, Thus, for the sensitivity analysis, we excluded one year at a time and repeated model runs.

RESULTS

Stable isotope analysis was performed on a total of 555 juvenile Chinook Salmon that were captured during the fall of 2000–2009. Yearly sample size ranged from 8 juvenile Chinook Salmon in 2000 to 282 in 2007. The yearly average δ^{15}N value was lowest in 2007 at 13.1‰ and highest in 2002 at 14.6‰ (Table 1). There was a slightly wider range in average δ^{13}C value, with 2009 having the lowest value at −17.4‰ and 2000 having the highest at −15.6‰. Correcting yearly samples for body size effects ($\delta^{15}N_{\text{residual}}$ and $\delta^{13}C_{\text{residual}}$) reordered the results somewhat for both δ^{15}N and δ^{13}C (Fig. S2). Survival rates of Chinook Salmon varied by an order of magnitude and were lowest in 2005 at 0.006 and highest in 2002 at 0.07.

Table 1. Interannual variability in survival and feeding ecology of juvenile Chinook Salmon

Year	Survival	δ^{13}C	δ^{15}N
2000	0.058	−15.6	14.1
2001	0.042	−16	13.3
2002	0.072	−15.7	14.6
2003	0.030	−15.8	14
2004	0.051	−16.4	14.3
2005	0.0064	−17.3	13.5
2006	0.031	−17.1	13.2
2007	0.0082	−17.1	13.1
2008	0.050	−16.9	13.2
2009	0.010	−17.4	13.5

We observed a wide range in ocean conditions over the study period. The mean SST (March–June) varied from 9.6°C in 2002 to 11.5°C in 2005 (Fig. 2). For the PDO, 2000–2002 and 2008–2009 were 'cold' years indicated by negative values, whereas 2003–2007 were positive, 'warm', years. NPGO, Southern Copepod Anomaly and Subarctic Copepod Anomaly all showed large variability as well (Fig. 2; Tucker *et al.*, 2015a). The seasonal-averaged mean values of zooplankton for δ^{15}N ranged from 8.5‰ in 2002 to 10.0‰ in 2005, and from −19.8‰ in 2007 to −18.0‰ in 2001 for δ^{13}C (see Table S2, for data by season). There were significant linear correlations between some large- and local-scale climate variables and δ^{15}N and δ^{13}C (Fig. 3). For example, δ^{13}C was strongly correlated with yearly NPGO and zooplankton δ^{13}C, whereas NPGO was also correlated with SST and PDO (Fig. 3).

In the best Bayesian Network, smolt survival of Chinook Salmon was strongly and positively related to their δ^{13}C value, and also less strongly related to the Subarctic Copepod Anomaly (Fig. 4). The strong relationship between the δ^{13}C value of salmon and survival was influenced by climate variables: NPGO directly and indirectly influenced the δ^{13}C value of zooplankton, which was, in turn, strongly correlated with the δ^{13}C value of salmon. Years with a high NPGO value also had a high Chinook Salmon δ^{13}C (via zooplankton δ^{13}C values), and correspondingly high survival rates. The direct effects of SST on zooplankton δ^{13}C values (and thus salmon δ^{13}C) appeared to be negligible as a direct link between these variables was not supported in the best model (Fig. 4), and the weak, direct correlation between these variables was in the opposite direction than it would be expected to be if this was the primary driver (Fig. 3). Thus, the link between climate and δ^{13}C could either be mediated via copepod community structure or variables that we were unable to consider here such as primary productivity or nutrients. Zooplankton δ^{15}N was strongly related to the southern copepod community anomaly, which was influenced by the PDO. Size-correcting the isotopes of juvenile Chinook Salmon, or altering the time-lag of climate variables, did not

Figure 2. Time series of selected environmental variables.

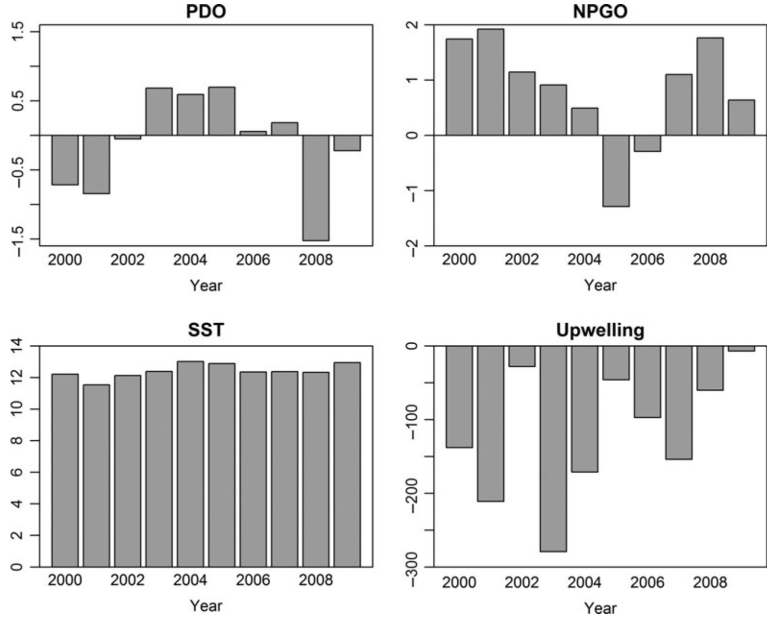


Figure 3. Pairplot of variables used in the Bayesian Network. Lower half panels show scatter plots of data, and upper panels show correlation values between variables. Font size scales with strength of the correlation. ** refers to significance at the $P < 0.001$ level, and * is significant at $P < 0.01$. All other correlations are $P > 0.05$. See Fig. 1 caption for abbreviations.

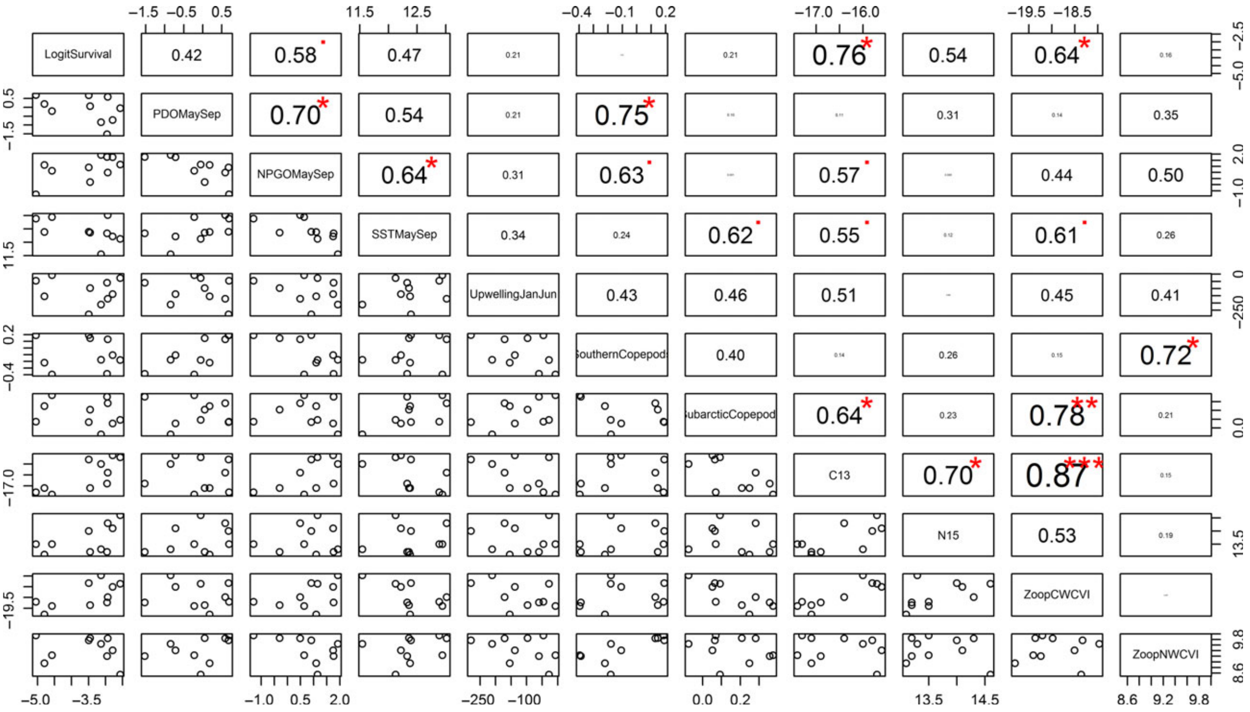
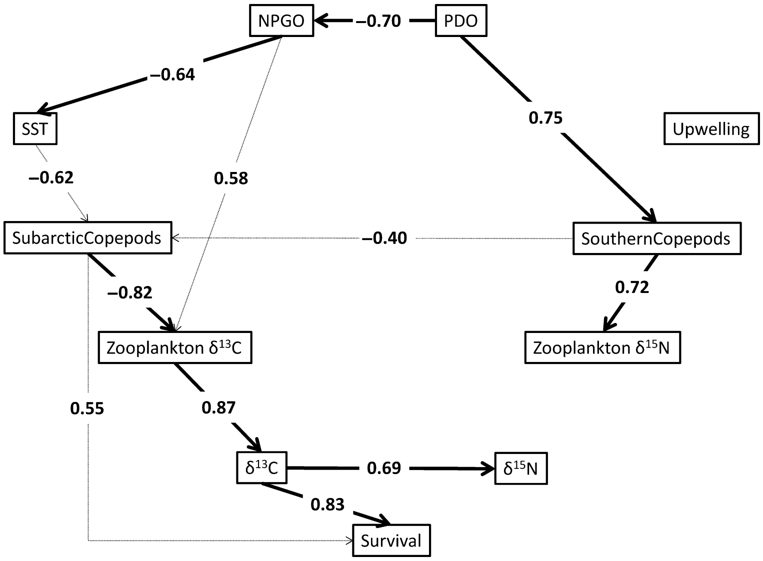


Figure 4. Bayesian network that best represents the data after a hill-climbing algorithm using raw isotopic values for juvenile Chinook Salmon. Numerical values show partial regression coefficients. Solid, thick lines are significant at $P < 0.05$ (Legendre, 2000; Kim, 2015), whereas thin, dashed lines are $P > 0.05$. See Fig. 1 caption for node abbreviations.



appreciably change the network structure, mainly altering the weak links between climate variables (Figs. S3–S5). The sensitivity analysis also indicated that the model was robust to leaving years out of the analysis, with the same general model structure maintained regardless of the year removed (Figs. S6–S15).

In all sensitivity analysis models except for '2009', the strongest link to salmon survival was via δ^{13}C; when 2009 was removed, the path to survival went via zooplankton δ^{13}C rather than salmon δ^{13}C (Fig. S15).

DISCUSSION

Climate dynamics have repeatedly been implicated in driving interannual variability in the recruitment of fish populations, yet the mechanisms linking climate to recruitment are opaque (Baumann, 1998). Here, using a Bayesian network, we show a possible mechanism linking climate to recruitment for Chinook Salmon off the WCVI.

Linking climate to stable isotopes and survival

We observed a strong, positive relationship between the δ^{13}C during the first growing season and the smolt survival of Chinook Salmon. This demonstrates how large-scale climate variability can affect the survival of Chinook Salmon by mediating feeding ecology, and is thus one step further than previous approaches as we are simultaneously examining multiple intermediate steps between climate and survival. Specifically, when the NPGO was positive, δ^{13}C values were enriched, and survival rates of Chinook Salmon were enhanced.

While we have shown that δ^{13}C may be useful as a leading indicator for survival rates, it is still somewhat difficult to determine the relative importance of shifts in baseline δ^{13}C values versus shifts in zooplankton species composition. We can, however, suggest that SST was not the primary driver of baseline δ^{13}C variability, as there was no direct link between these variables in the best model (Fig. 4), and the weak correlation between these variables was not in the hypothesized direction. On a continental-scale, SST is correlated with differences in zooplankton and salmon δ^{13}C values (Hertz *et al.*, 2015), but other mechanisms are likely driving the interannual patterns we observed here.

One possibility is that δ^{13}C of zooplankton, and subsequently salmon, serves as an indicator of ecosystem productivity available for juvenile salmon. There are two different paths that lead to zooplankton δ^{13}C: one directly from NPGO, and one leading from NPGO → SST → Subarctic Copepods → zooplankton δ^{13}C. The direct path from NPGO could be the result of shifts in nutrient sources leading to higher primary productivity (and subsequent δ^{13}C) in years with a higher NPGO (Di Lorenzo *et al.*, 2008, 2009). However, we were unable to assess directly primary productivity in this study (*see Limitations and future directions*). The path leading from NPGO to δ^{13}C through SST and the zooplankton community structure could also be related to differences in primary productivity since δ^{13}C of zooplankton is modulated at the phytoplankton level. Other possible explanations include species or size differences in phytoplankton (Laws *et al.*, 1997; Popp *et al.*, 1998) that are associated with differences in water transport by the NPGO. Future research should further explore these mechanisms underlying interannual variability in δ^{13}C.

If δ^{13}C is a measure of prey quantity or quality, then presumably the relationship between δ^{13}C and survival is indicative of interannual variability in feeding and growth rates. Faster growth is expected to reduce predation via size-selective mortality, under the assumption that bigger is better (Claiborne *et al.*, 2014; Tucker *et al.*, 2016). Thus, the hypothesized mechanism is that if a greater proportion of the population in a given year experience improved feeding ecology (high δ^{13}C), then growth rates will be higher, size-selective predation lower and survival enhanced. Thus, there are still missing links between the δ^{13}C that we measured in juvenile salmon and their survival rates.

In the Gulf of Alaska, it appears that a similar mechanism between δ^{13}C and survival may be operating for juvenile Pink Salmon (*Oncorhynchus gorbuscha*). A relationship was observed between the δ^{13}C of salmon and their survival rate (Kline *et al.*, 2008), although the direction of this relationship was negative, rather than positive as we observed. Differences in oceanography between regions are probably the reason underlying the different relationships: in the downwelling system of coastal Gulf of Alaska, the food supply of juvenile salmon appears to be related to the transport of offshore waters onshore via mesoscale eddies (Kline, 2009, 2010). When there is greater mesoscale eddy activity, more low-δ^{13}C zooplankton are transported nearshore where they are available for juvenile salmon (Kline *et al.*, 2008; Kline, 2010).

After controlling for the effect of salmon δ^{13}C on survival, we found a positive link between the subarctic copepod community and survival. In coastal Oregon and Washington, years with a high abundance of lipid-rich northern copepods tend to have a greater survival of salmon (Peterson and Schwing, 2003; Hooff and Peterson, 2006; Bi *et al.*, 2011a). This relationship is probably as a result of large-scale ocean transport (Keister *et al.*, 2011), and has been recently linked to the feeding ecology of juvenile salmon through the use of trophically transmitted parasites as diet tracers (Losee *et al.*, 2014). In our study, using independent methods, data and approach, we show that a similar process may also be operating off of WCVI.

Interestingly, the Bayesian network indicated that salmon δ^{13}C was a better predictor of smolt survival rates of Chinook Salmon than the zooplankton δ^{13}C. As it appears that large-scale climate variability influences salmon survival through bottom-up processes, a stronger relationship between zooplankton isotopes and salmon survival may have been expected. The longer isotopic integration time for juvenile Chinook Salmon (Weidel *et al.*, 2011; Vander Zanden *et al.*, 2015) may enable them to more effectively capture the interannual variability caused by large-scale climate indices than zooplankton (Hertz *et al.*, 2015). This suggests that attributes of the juveniles themselves, rather than indicators of climate or zooplankton variability, may be more effective in predicting survival. Alternatively, seasonal averaging or a spatial mismatch between zooplankton and salmon samples may have also weakened this relationship (Hertz *et al.*, *in press*).

We hypothesized that δ^{15}N and juvenile Chinook Salmon survival would be related, as an ontogenetic shift to fish prey may provide greater energy for growth and storage (Davis *et al.*, 1998; Pazzia *et al.*, 2002). We did not observe this relationship in either the size-corrected or raw model. Elsewhere, links between climate, ontogeny in diet and survival are also unclear. Off of the coast of Oregon, Daly *et al.* (2009) found that during low survival years, Coho Salmon (*Oncorhynchus kisutch*) consumed smaller and fewer fish and subyearling Chinook Salmon consumed less food overall. These authors found no consistent patterns for yearling Chinook Salmon (Daly *et al.*, 2009). Losee *et al.* (2014) used trophically-transmitted parasites to compare the diet of juvenile Coho and Chinook Salmon off coastal Oregon and found that the parasite community was influenced by climate variability, and associated with interannual survival rates. Of note with these different diet approaches, stomach contents only represent a snapshot of recently-consumed diet (~24 h) and may be biased by a difference in digestibility among prey items (Polunin and Pinnegar, 2002). Thus, longer-term indicators of diet such as stable isotopes or trophically transmitted parasites may provide a more suitable indication of diet and the differential oceanographic variables affecting it.

Limitations and future research

The environmental variables we used were chosen because of their correlation with salmon growth or production, either in the NCC or elsewhere. Other variables that we could have tested include primary productivity (Malick *et al.*, 2015b), the date of physical or biological spring transition (Logerwell *et al.*, 2003) and alongshore transport (Bi *et al.*, 2011a), but we were limited in the number of variables we could test given the brief nature of our time-series and the availability of data sources. Regardless, the variables chosen should encapsulate bottom-up processes that may influence the survival of juvenile Chinook Salmon in the NCC (e.g., Burke *et al.*, 2013).

Because of the ontogenetic niche shift that juvenile Chinook Salmon undergo early in their marine life (Brodeur, 1991; Hertz *et al.*, 2015), we also explored Bayesian networks that corrected yearly isotopic values for size using residuals from a non-linear curve. The relationship with survival is maintained whether or not $\delta^{13}C_{residual}$ or raw δ^{13}C values are used, and the resultant Bayesian Network is only slightly different when residual values are used. Specifically, a path from δ^{15}N of zooplankton to $\delta^{13}C_{residual}$ is supported in the best residual model, and the relationship between $\delta^{13}C_{residual}$ and survival is slightly weaker than raw δ^{13}C and survival (Fig. S3).

While the ultimate cause of variation in the survival of juvenile Chinook Salmon appears to be related to climate, the proximate causes of mortality are not well understood. Many previous studies have found linkages between ocean conditions and salmon survival throughout their range. The postulated mechanisms underlying these trends tend to be bottom-up (but see Hinch *et al.*, 1995; Emmett and Sampson, 2007) whereby climate conditions change the abundance, distribution, or type of prey available for juvenile salmon, but tests of these mechanisms have largely proven elusive. One remaining missing link is understanding the mediating effects of bottom-up forcing on top-down control. We know that interannual differences bottom-up processes can alter the growth and size distribution of juvenile salmon, but how top-down predation on salmon interacts with this variability is unknown (Tucker *et al.*, 2016). Predation and overwinter mortality, because of a lack of energy reserves, are speculated to be the largest proximate causes of mortality of juvenile salmon (Beamish and Mahnken, 2001). As the identity and abundance of salmon predators is largely unknown, it is also possible that the variation in climate could affect the survival of juvenile Chinook Salmon in a top-down manner (Emmett and Sampson, 2007) by changing the abundance or distribution of predators.

Although the response of oceanic ecosystems to climate change is uncertain, the variability in NPGO appears to have intensified in the late 20th century (Di Lorenzo *et al.*, 2009; Sydeman *et al.*, 2013, 2014).

This shift in variance has occurred concomitantly with a shift towards a greater ecological significance of the NPGO (Cloern *et al.*, 2010; Sydeman *et al.*, 2013; Kilduff *et al.*, 2015). As juvenile WCVI Chinook Salmon survival is related to the NPGO (through δ^{13}C), further shifts in the NPGO as a result of anthropogenic warming or natural climate variability could have a large impact on salmon returns. The location of WCVI relative to oceanic currents may also make this area highly responsive to climate change as WCVI is located at the very northern end of the California Current, near the transitional domain (Ware and McFarlane, 1989). The importance of upwelling versus downwelling varies considerably from year to year in relation to the position of the eastern subarctic current (Sydeman *et al.*, 2011), and could also be linked to changes in the NPGO.

Bayesian networks represent a powerful and flexible tool to forecast survival rates and elucidate links between climate variables, between climate variables and feeding ecology, and links between feeding ecology and survival. This method can be updated as more data (or nodes) become available and it provides some information about the missing middle between climate and survival of juvenile Chinook Salmon. All of the relationships between variables are still correlative, however, so the relationships may be expected to change with oceanic regime shifts, and shifts in climate drivers of survival. Regardless, this tool may prove to be useful for managers in that it is able to consider explicitly linkages between common drivers of survival.

In summary, we have demonstrated an environmental model that describes how climatic variability in the early marine life of juvenile Chinook Salmon influences feeding ecology, and by doing so alters overall survival rates. We have advanced knowledge beyond simple correlational mechanisms of climate impacts on survival and identified specific oceanographic variables related to survival rates of a population of Chinook Salmon.

ACKNOWLEDGEMENTS

We thank the numerous people who collected and processed the salmon and zooplankton in this study. We also thank the captains and crews of the CCGS *W.E. Ricker*, *F/V Frosti, and F/V Viking Storm* for field support. Cameron Freshwater provided helpful comments on an earlier draft of the manuscript. We thank NSERC, Fisheries and Oceans Canada, and Bonneville Power Administration for funding.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Mechanisms for hypothesized links between network nodes.

Table S2. Seasonal and annual variation in isotopic composition of zooplankton collected off the west coast of Vancouver Island. Note that δ^{13}C values are corrected for lipids according to Post *et al.* (2007). Stations located on the continental shelf were sampled in all seasons and years, while stations located in inlets and sounds were only sampled in 11 out of 20 season/year combinations.

Figure S1. Relationship between the freeze-dried muscle and oven dried whole fish isotopic signatures for carbon (left panel) and nitrogen (right panel). Each point is a single fish that has had separate processing done. Black lines represents the 1 : 1 line, while blue is the best fit model as determined by AICc values by comparing the fit of the best fit linear regression, to the 1 : 1 line (only shown if significantly different from 1 : 1 line).

Figure S2. Interannual variability in the relationships between δ^{15}N and weight of juvenile Chinook Salmon captured off of the west coast of Vancouver Island. Residual values of each individual juvenile Chinook Salmon were taken from the best fit curve (shown in black) and the average of these residual values were used as a predictor variable in the Bayesian Network.

Figure S3. Bayesian network that best represents the data after a hill-climbing algorithm for the size-corrected (residual) salmon isotope data. Numerical values show partial correlation coefficients. Solid, thick lines are significant at $P < 0.05$ (Legendre, 2000; Kim, 2015), while thin, dashed lines are $P > 0.05$. See Fig. 1 caption for node abbreviations.

Figure S4. Bayesian network that best represents the data after a hill-climbing algorithm with climate variables lagged over the period January–June. Numerical values show partial correlation coefficients. Solid, thick lines are significant at $P < 0.05$ (Legendre, 2000; Kim, 2015), while thin, dashed lines are $P > 0.05$. For clarity, partial correlation coefficients are only shown for significant paths. See Fig. 1 caption for node abbreviations.

Figure S5. Bayesian network that best represents the data after a hill-climbing algorithm with climate variables lagged annually. Numerical values show partial correlation coefficients. Solid, thick lines are significant at $P < 0.05$ (Legendre, 2000; Kim, 2015), while thin, dashed lines are $P > 0.05$. For clarity, partial correlation coefficients are only shown for significant paths, See Fig. 1 caption for node abbreviations.

Figures S6–15. Sensitivity analysis with years sequentially removed from the network. Bayesian networks that best represents the data after a hill-climbing algorithm. Numerical values show partial correlation coefficients. Solid, thick lines are significant at $P < 0.05$ (Legendre, 2000; Kim, 2015), while thin, dashed lines are $P > 0.05$. For clarity, partial correlation coefficients are only shown for significant paths. See Fig. 1 caption for node abbreviations.