Declines in mean body size have been identified in a number of exploited fishes, including several Pacific salmon species (REF). Declines in body size within fishes are often attributed to the removal of larger individuals in size-selective fisheries (REF) or reduced individual growth due to unfavorable environmental conditions (e.g. altered prey community, increased competition) (REF). In the case of Pacific salmon, evidence suggests that high exploitation in selective fisheries (e.g. gill nets) may have resulted in a gradual decline in mean size in certain regions (REF). However, coherent changes in growth, age-at-maturity, and survival have also occurred among regions and species with disparate fishing pressures (REF), suggesting large-scale environmental drivers can moderate interannual variation in ecological traits in body size.

Pacific salmon growth and mortality rates during ocean residences are high, as well as variable. As a result, size at recruitment, and ultimately population productivity (REF), will be correlated with environmental conditions at sea. For example, increases in sea surface temperature can accelerate metabolic rates (REF), as well as alter the quantity and quality of prey available to salmon in specific regions (REF). Salmon growth and survival is often associated with indices such as the Pacific Decadal Oscillation, North Pacific Gyre Oscillation, and El Nino Southern Osicillation, which integrate environmental conditions over relatively large spatial and temporal scales (REF). Wind stress indices, such as the Aleutian Low Pressure Index or upwelling metrics, may also be correlated with salmon growth by moderating nutrient transport to surface layers during winter and early spring, prior to phytoplankton blooms (REF). Although population-level responses to environmental indices are regionally coherent, they often vary across species ranges, with northern and southern populations exhibiting opposite responses to a common signal (REF).

Salmon growth or survival may be influenced by top-down, as well as bottom-up, effects, predominantly via competitive interactions during ocean residence (REF). Negative density-dependent effects have been attributed to conspecifics (REF); however, competition between various salmon species and pink salmon has received particularly close attention due to dramatic increases in hatchery production (REF). Although evidence of density dependence is mixed, generally the negative impacts of pink salmon appear to be strongest when incorporating relatively large aggregates of populations. Therefore the effects of competition are thought to be strongest during the last year of marine residence when many stocks are widely distributed in the North Pacific (REF).

Sockeye salmon spawning in British Columbia (i.e. the southern portion of the species’ range) have been the focus of much of this previous research due to widespread declines in productivity that have negatively impacted commercial fisheries (REF). On the whole, the size and productivity of these populations appears to decline with warmer ocean temperatures (REF), weaker Aleutian lows (REF), and greater pink and sockeye salmon abundance (REF), presumably due to reduced opportunities for marine growth. Yet the long-term response of ecological systems to environmental drivers is often non-linear and apparently strong correlations can break down over time. Even with the relatively long time series (more than 50 years) available for many sockeye salmon populations, it is unclear how they will respond to novel environmental conditions that are likely to arise as climate change effects strengthen.

To explore how relationships between environmental drivers and salmon characteristics have varied through time, we used a novel historical dataset encompassing a larger range of environmental conditions than typically considered. We used age-structured, individual length measurements collected between 1914 and 1946 from Nass River (northern British Columbia) and Rivers Inlet (central BC) sockeye salmon (*Oncorhynchus nerka*) to test a series of hypotheses. First, did sockeye salmon exhibit differences in body size that are consistent with bottom-up and top-down effects, prior to widespread increases in sea surface temperature and hatchery enhancement efforts? Although long-term trends in Pacific salmon body size have been previously examined, these analyses rarely extend to the early 20th century and often lack data on age composition. By accounting for individual differences in freshwater and marine age, we could control for trends in age structure that may confound common tests for changes in mean body size. These age data also allowed us to test a second hypothesis that individuals rearing at sea for different lengths of time respond differently to shared environmental drivers, a relationship that would be consistent with age-specific spatial distributions. Finally, we used a contemporary, age-structured dataset from the Nass River to explore how associations between body size, the physical environment, and competitor abundance may have changed through time.

*Methods*

*Salmon data*

The individual size data we used for our analyses originated from two sources. Historical data were collected from Nass River and Rivers Inlet commercial gillnet fisheries operating between 1914 and 1946. These fisheries occurred in nearshore waters (specific locations), with data collected by (x). Returning adult sockeye salmon were sampled weekly and individual fork length (mm), weight (g), and sex were recorded. Although sampling occurred regularly from mid-June to late August in the majority of years, we excluded a subset of years due to insufficient sampling (Nass: 1915, 1920, 1922, 1924, 1938, 1945; Rivers Inlet: 1924, 1945). Contemporary data were collected from the Nass River fishwheel test fishery, operated by the Nisga’a First Nation between 1994 and 2017. Individuals were sampled daily and length and sex recorded. To account for differences in sampling location that would influence estimates of return timing, we assumed that individuals took seven days to travel from marine fishery locations to the fish wheel. This assumption is consistent with the Pacific Salmon Foundation’s Northern Boundary Sockeye Salmon run reconstruction model (REF).

Individual salmon were aged and scale annuli characteristics were used to distinguish between freshwater and marine residence. Subsequent references to specific age classes follow *x* nomenclature, e.g. 1.2 individuals spend one year in the gravel, one year as a fry in freshwater, and two years at sea, returning to spawn four years after the brood year. Although a relatively large number of age classes were recorded, we constrained our analysis to dominant ages, i.e. those that were observed in every year in the historical dataset. For the Nass we included 1.2, 1.3, 2.2, and 2.3 individuals, while for Rivers Inlet we retained only 1.2 and 1.3 individuals. Historical age data were generated by *x*, while contemporary aging analyses were conducted by Fisheries and Oceans Canada (1994-2004) or Alaska Department of Fish and Game (2005-2017) schlerochronology lab.

*Environmental data*

We used a statistical modeling approach to test for relationships between variation in body size and a suite of environmental variables. Three of these indices represent variation in sea surface temperature. First, we incorporated monthly averages of raw sea surface temperature generated by… Interannual variability in sea surface temperature is often correlated with changes in the community composition of lower trophic levels (REF), as well as the growth and survival salmon (REF). We also included monthly indices of the Pacific Decadal Oscillation (PDO), the first principal component of variability in sea surface temperature in the Pacific Ocean poleward of 20°N (Mantua *et al.* 1997), retrieved from research.jisao.washington.edu/pdo/. The PDO captures long-term temperature trends, with positive anomalies frequently co-occurring with El Nino events (REF), as well as reduced salmon survival in southern regions and the opposite pattern among northern populations (REF). We generated a third monthly index using the second principal component of sea surface temperature variability poleward of 20°N (based on the raw sea surface temperature data described above). Although not commonly used, this final index represents variation in temperature independent of the PDO that could represent anomalies with substantial biological impacts. We calculated the average value of each temperature index from March to June, which corresponds to the period when returning Pacific salmon gain the largest portion of their growth (REF; Brett paper cited by Skip 1995?).

The final abiotic covariate we tested was the Aleutian Low Pressure Index (ALPI), representing the relative intensity of the winter low-pressure system centered over the north Pacific (REF). ALPI reflects the relative intensity of winter storms (REF) and the position of westerly winds (REF), which appear to moderate biological productivity by altering the phenology of spring upwelling events (REF). Since ALPI is defined as the area (km2) in the North Pacific Ocean with mean seasonal (December to March) sea level pressure less than or equal to 100.5 kPa, it is provided as an annual index by default.

We used catch estimates of sockeye and pink salmon captured throughout the northeast Pacific to test for con- and heterospecific density dependent effects, respectively, on sockeye salmon size-at-return. For the historic sampling period (1914-1946), we used catch data from the International Pacific Fisheries Commission (REF). For the modern sampling period (1994-2015), we used data curated by the North Pacific Anadromous Fish Commission (REF). Although the offshore distributions of most Pacific salmon stocks remain poorly understood, it is likely that there is substantial overlap of species ranging from northern Washington to western Alaska (REF). Unfortunately catch records for British Columbia and Washington do not begin until 1925. Therefore, we used catches in Alaska in the year of return as a proxy for the total number of sockeye or pink salmon maturing in the Gulf of Alaska that year. Alaskan stocks are often numerically dominant in the North Pacific and Alaskan catch was strongly correlated (insert correlation) with total catch when data were available for all three regions. However to test the sensitivity of our results to this assumption we completed a supplementary analysis restricted to years when catch data were available from BC and WA (Supplementary Material). We recognize that catch data are an imperfect proxy for abundance (REF), but they are the most complete index available for historical sampling periods. To assess whether our results were biased by the use of catch data, rather than estimates of total run size (i.e. catch plus escapement), we completed a second sensitivity analysis comparing catch and run size estimates as covariates in the modern Nass analysis.

*Statistical analyses*

Biological systems often exhibit non-linear responses to external forcing (REF). To account for this possibility, we used generalized additive models (GAMs) to explore the relationship between body size, age-at-maturity, large-scale environmental indices, and competitor abundance. We constrained the modeled relationships to be linear, dome-shaped, or sigmoidal by limiting each GAM’s parameters’ effective degrees of freedom to three (REF). Given differences in the timing of sampling events, as well as the possibility that the importance of environmental drivers varies in time and space, we analyzed each of the three datasets (i.e. Nass historical (NH), Rivers Inlet historical (RH), and Nass modern (NM)) separately. For each dataset, we fit a suite of models, which contained up to one abiotic driver (e.g. temperature, PDO, PC2, or ALPI) and one index of salmon abundance (pink, sockeye, or total) (Table 1). We did not include multiple environmental drivers in the same model since they were relatively strongly correlated with one another. To account for differences in size at return among age classes, we also included each age class (i.e. unique combination of freshwater and marine age) as a fixed effect. Since fish collected in the same year cannot be considered independent samples, we used generalized additive mixed models, an extension of GAMs that can incorporate various correlation structures and estimated a random intercept for each sampling year. We identified the most parsimonious model using an information theoretic approach, selecting the model with the lowest Akaike information criterion adjusted for small sample sizes (AICc; REF). We evaluated the performance of more complex models that accounted for temporal autocorrelation among years via an AR1 process; however these models were not favored by model selection (the AICc score was not minimized) and we did not detect evidence of autocorrelation in the residuals of any of the top ranked models (Supplementary Information).

*Results*

Trends in mean body size varied among watersheds, sampling periods, and age classes (Figure 2). During the historical period (1914-1946), mean body size increased in the oldest Nass ocean age classes (1.3 and 2.3), while younger ocean age classes (1.2 and 2.2) in the Nass and all age classes in Rivers Inlet exhibited declines or no trend in mean size. Furthermore, we found strong support that size at return was correlated with both physical and biological environmental variables, and that these effects varied among specific age classes (Table 1).

In all three datasets Alaskan pink salmon catch was a better predictor of sockeye body size than Alaskan sockeye catch or the cumulative Alaskan catch of both species (Table 1; Figure 3). In the historical datasets these effects were relatively variable – pink salmon catch had weak, but generally negative effects on the body size of younger ocean age fish from both watersheds, but curvilinear or weak positive effects on older ocean age classes (Figure 3). Conversely, the relationship between body size and pink salmon catch was uniformly negative in the modern Nass dataset (Figure 3).

The most parsimonious abiotic driver identified by model selection varied among datasets, but was always a temperature index rather than ALPI. In the Rivers Inlet dataset body size co-varied most strongly with PDO with either age class exhibiting opposite and curvilinear responses to positive temperature anomalies. The Nass historical dataset was more strongly correlated with raw temperature data than the three environmental indices. Size at return was generally positively correlated with increasing temperature. As in Rivers Inlet, however, these patterns were strongly linked to ocean age, with older ages exhibiting a weak linear response and younger ages a relatively strong, but curvilinear effect.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M. & Francis, R.C. (1997) A pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society,* **78,** 1069-1079.