Declines in mean body size have been identified in a wide range 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 growth, age-at-maturity, and survival have also occurred among regions and species with disparate fishing pressures (REF), which suggests that large-scale environmental drivers may moderate interannual variation in traits such as body size. Given that reductions in body size may negatively impact fisheries via reduced per-capita productivity (REF) or altered community dynamics (REF), understanding the mechanisms that drive variation is of considerable interest. as a means of improving forecasts, understanding divergent dynamics among population aggregates, and by bounding expected levels of future productivity.

Both bottom-up and top-down drivers may regulate salmon body size via changes in growth during marine residence. For example, changes in sea surface temperature can influence metabolic rate (REF), as well as the quantity and quality of prey available to salmon (REF). Salmon growth and survival is often associated with indices such as the Pacific Decadal Oscillation, North Pacific Gyre Oscillation, and ENSO, which integrate environmental conditions over relatively large spatial and temporal scales (REF). Although population-level responses to these temperature indices are regionally coherent, they often vary across the species range with northern populations responding positively to temperature increases and southern populations the opposite (REF). Wind stress indices, such as ALPI 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).

While investigations into top-down effects are more limited, a growing body of evidence suggests that salmon growth or survival may be reduced when competitor abundance is high (REF). These effects may be driven by either con- or heterospecifics, with pink salmon receiving particularly close attention in recent years due to increases in hatchery production (REF). Generally the negative impacts of pink salmon appear to be strongest when incorporating relatively large aggregates of populations, which suggest competitive interactions occur during offshore residence when stocks are well mixed 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 traditionally profitable 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 competitor abundance (REF), presumably due to reduced opportunities for marine growth. Yet predicting these populations’ response to future, potentially more extreme, environmental conditions is difficult. Even with the relatively long time series (more than 50 years) available for many sockeye salmon populations, it is unclear whether they may exhibit non-linear responses to environmental conditions outside those observed in recent decades. Put more simply, are salmon dynamics normally regulated by factors such as sea surface temperature and competition or is this an artefact of rapid changes in these drivers in recent years?

To understand how sockeye salmon populations may respond to future conditions, we used a novel historical dataset to explore how they responded in the past. Specifically we used age-structured, individual length data collected between 1914 and 1946 to examine two Pacific salmon populations’ response to abiotic and biotic drivers prior to widespread increases in sea surface temperature and hatchery propagation. These data originated from extensively sampled nearshore fisheries targeting Nass River (northern British Columbia) and Rivers Inlet (central BC) sockeye salmon (*Oncorhynchus nerka*). Nass and Rivers Inlet are located close to the inflection point in a latitudinal gradient separating northern Pacific salmon systems that are currently in a phase of high productivity, from southern populations that have typically declined. Although both systems have exhibited reduced productivity in recent decades attributed to reduced marine survival, the proximate mechanism remains unclear.

are distributed relatively close to the latitudinal Additionally, we used data collected during the past twenty years in the Nass River to compare contemporary trends in body size to historical patterns.

*Methods*

*Salmon data*

We used size data of individual salmon collected from two different sources. The first were compiled from Nass River and Rivers Inlet commercial gillnet fisheries operating between 1914 and 1946. These fisheries occurred in nearshore waters, with data collected (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). The second, contemporary dataset included data collected in the Nass Rivers 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 using *x* nomenclature. For example, 1.2 individuals return to spawn 4 years after their parents spawn, having spent one year in the gravel, one year as a fry in freshwater, and two years at sea. 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 this included 1.2, 1.3, 2.2, and 2.3 individuals, while for Rivers Inlet 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 tested the performance of a suite of environmental variables as predictors of changes in body size. Three indices describe 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 (using 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 incorporated was the Aleutian Low Pressure Index (ALPI), which represents the relative intensity of the low-pressure system centered over the north Pacific during winter (REF). ALPI reflects the relative intensity of both winter storms (REF) and the position of westerly winds (REF) that 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 from the North Pacific Anadromous Fish Commission (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 likely overlap with sockeye salmon populations rearing in northern British Columbia (REF). 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). Catch data are necessarily an imperfect proxy for absolute abundance (REF), but they are the most complete index of abundance available for the historical sampling period. To maintain consistency between datasets we also used catch data as a covariate in the modern Nass analysis, though estimates of escapement as well as catch are now available.

*Statistical analyses*

Biological systems often exhibit non-linear responses to external forcing (REF). To account for this possibility, we used generalized additive models (GAM) to explore the relationship between body size, age-at-maturity, large-scale environmental indices, and density dependent effects. We constrained the modeled relationships to be linear, dome-shaped, or sigmoidal to by limiting each GAM’s parameter 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 or 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 that 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). To account for differences in size at return among age classes, we also included total age as a fixed effect. We did not include multiple environmental drivers in the same model since they were relatively strongly correlated with one another. 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 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).

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.