Multi-decadal trends in body size of Puget Sound Chinook Salmon: Analysis of data from the Tengu Derby, a culturally unique fishery

Thomas P. Quinn1, Mark D. Scheuerell2, and James P. Losee3,4

1 School of Aquatic and Fishery Sciences, Box 355020, University of Washington

Seattle, WA 98195 USA

2 U.S. Geological Survey Washington Cooperative Fish and Wildlife Research Unit,

School of Aquatic and Fishery Sciences, Box 355020, University of Washington

Seattle, WA 98195 USA

3 Washington Department of Fish and Wildlife, 600 Capitol Way N. Olympia, WA 98501 USA

4 Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences (SLU) Umeå, Uppsala, Sweden, 750 07

Keywords: body mass, differential migration, *Oncorhynchus tshawytscha,* Pacific salmon, recreational fishing, trends

This draft manuscript is distributed solely for purposes of scientific peer review. Its content is deliberative and predecisional, so it must not be disclosed or released by reviewers. Because the manuscript has not yet been approved for publication by the U.S. Geological Survey (USGS), it does not represent any official USGS finding or policy.

Abstract

In Pacific salmon, downward trends in size and abundance have been reported for species and stocks for over 40 years, but the patterns are inconsistent among regions and species. Interpretation of these trends is complicated by the many possible contributing factors, including short time series, data comprising a mix of stocks, and varying gear types. Here, we present data on the mass of individual Chinook Salmon, *Oncorhynchus tshawytscha*, caught in the winter from 1946 to 2019 in central Puget Sound, Washington by participants in what may be the longest running salmon derby in North America, the Tengu Derby. In this annual recreational fishing competition, established by Japanese-Americans immediately after release from internment camps at the end of World War II, participants follow strict gear, area, and methods regulations, and catch almost exclusively salmon originating from and remaining in Puget Sound. Records revealed an overall decline in fish mass over the decades with a high degree of variability throughout the time series. Specifically, resident Chinook Salmon exhibited several shifts, including an increase in size from a high in the 1950s to a low around 1980, followed by an increase to another high around 1990, and then a decline over the most recent 30 years. These salmon, displaying a form of differential migration by remaining in Puget Sound rather than migrating to the ocean coast, showed dissimilar trajectories compared with size trends of Puget Sound Chinook Salmon as a whole reported previously. These distinct patterns in size for Chinook Salmon from common origins associated with different migration patterns exemplify yet another important factor to be considered in the analysis and interpretation of such trends.

Introduction

Long-term trends in size and age at maturity of fishes have been the subject of interest for many decades, as they may reflect natural changes in environmental conditions ([Cox and Hinch 1997](#_ENREF_7); [Rogers et al. 2011](#_ENREF_35)), density dependence ([Millner and Whiting 1996](#_ENREF_19); [Pyper and Peterman 1999](#_ENREF_25)), fishery management ([Richards and Rago 1999](#_ENREF_30)), fishery induced evolution ([Sharpe and Hendry 2009](#_ENREF_39); [Swain et al. 2007](#_ENREF_43)), and other processes or combinations of processes ([Edeline et al. 2007](#_ENREF_8)). For example, scientists have investigated long-term trends (typically declines) in body size and age at maturity in Atlantic Salmon, *Salmo salar* ([Gardner 1976](#_ENREF_10); [Summers 1995](#_ENREF_42)), using data from commercial fisheries ([Shearer 1990](#_ENREF_40)) and recreational fisheries, recorded by governmental bodies ([Bal et al. 2017](#_ENREF_2)), angling clubs ([Bielak and Power 1986](#_ENREF_3)), privately held fisheries ([Quinn et al. 2006](#_ENREF_29)), or newspapers ([Valiente et al. 2011](#_ENREF_44)).

As with Atlantic Salmon, there is also a long history of interest in trends in Pacific salmon (*Oncorhynchus* spp.) body size, with reports of decreases in many species, regions, and periods of record ([Bigler et al. 1996](#_ENREF_4); [Lewis et al. 2015](#_ENREF_17); [Oke et al. 2020](#_ENREF_23); [Ricker 1981](#_ENREF_32); [Ricker 1995](#_ENREF_33)). As outlined by Ricker (1980) and echoed in subsequent reviews of size trends, many factors may cause genuine or apparent changes over decades. Catch data may include shifting proportions of immature and maturing fish of multiple ages, hence different sizes; or fishing may occur at different times of the year, affecting average size because fish caught early in the season had less time to grow. In addition, smolts produced in hatcheries tend to be larger than wild smolts and this reduces the number of years spent at sea, and hatchery production has become an increasing proportion of the runs in some areas. Salmon growth is also affected by oceanographic conditions and salmon density, both of which have changed. Impassable hydroelectric dams extirpated some runs, and if they were especially large then the average size of the salmon might decline. Fisheries themselves can be size selective, shifting the observed size distribution depending on where and when sampling occurs, and causing evolutionary shifts in age and size at maturity. There is extensive scientific literature on these and other factors; they are not mutually exclusive, making it especially difficult to explain the many declines (and some increases) in size and age in Pacific salmon (see Quinn (2018) for a discussion and review of these factors).

Most of the data sets examined for patterns of body size in Pacific salmon come from commercial fisheries targeting the most numerous species: sockeye (*O. nerka*), chum (*O. keta*), and pink (*O. gorbuscha*) salmon. However, Chinook (*O. tshawytscha*) and Coho Salmon (*O. kisutch*) are also commonly caught by anglers in coastal marine waters and rivers. Recreational fisheries can complicate analysis of size trends because they may differ in places and times of the year from commercial fisheries, and the lack of centralized processing means that often no data on size are recorded. However, when used with appropriate caution, recreational fisheries can also be a source of data to augment and complement data from commercial fisheries and recoveries at spawning grounds and hatcheries. For example, [Fagen (1988](#_ENREF_9)) examined data from recreational fishing derbies for Chinook Salmon in four areas of southeastern Alaska going back as much as four decades, and reported significant declines in the largest fish in two of the four, but no clear trend in the other two. Interpretation of these data was complicated by the factors noted by Ricker (1980), especially because southeastern Alaska is a feeding area for wild and hatchery Chinook Salmon originating from a range of locations ([Healey and Groot 1987](#_ENREF_12); [Weitkamp 2012](#_ENREF_45); [Weitkamp 2009](#_ENREF_46)). Indeed, [Ricker (1980](#_ENREF_31)) concluded that analysis of size trend data and attribution to causal agents is especially complicated for Chinook Salmon owing to their variation in age at maturity, marine distribution patterns, and timing of return to fresh water ([Quinn 2018](#_ENREF_26); [Riddell et al. 2018](#_ENREF_34)). One other issue noted by Ricker is the problem that fisheries catch data may include multiple salmon stocks differing in average size. Here we consider this issue, with special reference to the size differences resulting from differential migration.

Recent analysis of trends in survival, abundance, and body size of Chinook Salmon in Puget Sound, Washington, based on commercial purse seine fishery data, revealed a decline in average body mass from 1970 through 2015 ([Losee et al. 2019](#_ENREF_18)). However, these salmon would have differed in feeding locations at sea. Specifically, some might have migrated to the coastal ocean whereas others remained in Puget Sound as so-called “residents.” Such resident Chinook and coho Salmon are smaller than those that migrate to the coast ([Jensen 1948](#_ENREF_14); [Milne 1950](#_ENREF_20); [Pressey 1953](#_ENREF_24)), complicating interpretation of catch data if the proportion of residents is not constant or if their trends differ from those of the conspecifics feeding along the coast. Here we present data on the size of resident Chinook Salmon (see details below on this migratory variant), caught in the winter in central Puget Sound in a culturally unique recreational fishery with consistent methods held annually since 1946. Trends in these data, specific to resident Chinook Salmon originating in Puget Sound, were examined and compared with those of the species caught in Puget Sound as a whole using non-size-selective commercial purse seines ([Losee et al. 2019](#_ENREF_18)).

Methods

Resident Chinook Salmon

It has long been known that Chinook and coho Salmon occur in Puget Sound and other inland marine waters at all months of the year ([Jordan and Evermann 1896](#_ENREF_15)), in addition to the fraction of the populations feeding along the coast that pass through Puget Sound on their homeward migration ([Haw et al. 1967](#_ENREF_11); [Pressey 1953](#_ENREF_24)). The resident salmon are fully anadromous but exhibit differential migration ([Quinn 2021](#_ENREF_27)), remaining in the general vicinity of their natal rivers for much of their period of marine life ([Arostegui et al. 2017](#_ENREF_1); [Chamberlin et al. 2011](#_ENREF_5); [Chamberlin and Quinn 2014](#_ENREF_6); [Kagley et al. 2017](#_ENREF_16)). In the winter and spring, these resident Chinook are subject to capture before they mature and spawn the following fall, or thereafter. Analysis of coded wire tagging (CWT) data indicated that Chinook Salmon caught in Marine Area 10 (central Puget Sound, including the location where the derby occurs that produced the data examined here) were almost exclusively from Puget Sound. Specifically, 90.2% of CWT recovered from Chinook Salmon from October through April (the resident period) in central Puget Sound between 1973 and 2018 originated from Puget Sound (WDFW data, average of annual values). Consistent with this analysis, [Shelton et al. (2019](#_ENREF_41)) examined CWT data from the west coast of North America and concluded, “Virtually all fish estimated to be present in the Salish Sea (Puget Sound, Strait of Georgia) originated there, indicating few Chinook Salmon from the outer coast migrate into the Salish Sea.” Consequently, it is appropriate to consider the fish caught in the winter as having originated from Puget Sound rivers and hatcheries.

The Tengu Salmon Derby

The history and origins of the derby that provided the data for our analyses are described on a monument plaque at the current weigh-in station in West Seattle:

“The Tengu Club of Seattle, formed in the 1930s by Japanese Americans, held its first Tengu Blackmouth Salmon Fun Derby in 1946. Arguably the longest continually running salmon derby in North America, it continues to be held each winter in Elliott Bay. Club members, returning from wartime internment camps, were denied entry into local salmon derbies so they organized the first Tengu Derby in December of 1946. More than 170 people, including about a dozen non-Japanese, fished in the first four Sundays-long competitions. The technique of ‘mooching’ was invented in Elliott Bay by these fishers, who perfected a way to entice salmon by working bait in an up-and-down motion while drifting. This method proved to be so effective that non-Japanese would “mooch” herring from them. The Tengu Club recognized the historical significance of mooching and adheres to this ‘purist’ way of salmon fishing to this day. The name ‘Tengu’ is from Japanese folklore that describes mythical creatures that were mischievous braggarts. Their long noses are symbolic of exaggerating the truth, which is typical of fish stories.”

In the decades that followed, participants in the Tengu Derby continued to use the same technique (e.g., no artificial lures, no use of a motor while fishing, no downriggers) and in precisely the same small, well-defined area east of a line between Alki Point and Fourmile Rock (Fig. 1). Each year the club’s Board of Directors determines the specific dates but fishing typically occurs on Sundays in November and December. Dates and other details are posted annually and registration provides a record of the number of participants, though there is no record of how many days each registrant fished that season. Fish are brought to a central weighing station rather than being self-reported, and thus the data on fish mass (recorded in pounds but converted to kg) can be considered to be very accurate.

Each year the mass of the largest five fish was recorded, and these data were the focus of our analysis, but the numbers of Chinook salmon over 10 pounds and over 5 pounds were also recorded, and we present these in graphical form for comparison. The total number of Chinook Salmon caught was also recorded each year. However, changes in the size limits over the decades complicate analyses of the count data because fish were retained and counted in early decades that would now have to be released and so not counted. For the present analysis we used the average mass of the top five fish from 1946 - 2017, omitting two years (2010 and 2013) when fewer than five Chinook Salmon were recorded, and 2015 when fishing was closed. In 2018 and 2019, fewer than five salmon were caught so the averages were not included. The trends were compared to annual mean body mass of Chinook Salmon caught in Puget Sound commercial purse seine fisheries (chosen because of their lack of size-selectivity) from 1970 – 2014 ([Losee et al. 2019](#_ENREF_18))and updated through 2019 (WDFW, unpublished data). Consistent with Losee et al. (2019), we divided the total number landed in Washington State and Treaty Indian Tribal commercial catches by the total landed weight annually.

Statistical models

We modeled the sizes of fish caught in the Tengu Derby and WDFW surveys using simple forms of multivariate state-space models. These models consist of two parts: 1) a state model that describes the changes in the true but unknown size of fish; and 2) an observation model that relates the observed time series of fish sizes to the true state. Each of the component models varied subtly, depending on the underlying hypothesis about how the two sources of data were related. Here we wanted to evaluate 1) if there was any evidence for a systematic change in fish size over time; and 2) whether or not changes in the size of salmon caught in the derby over time were similar to those fish caught by purse seines.

Beginning with the state model, we modeled changes in fish size using a random walk, for which the change in size over time was assumed to be either biased or unbiased, indicating whether the changes in fish size over time were random or generally trending upward/downward. Specifically, the model takes the form

(1)

where *xi,t* is the natural logarithm of fish size from source *i* in year *t*, *ui* is the bias term for source *i*, and *wi,t* is a residual process error for source *i* in year *t*, such that *wi,t* ~ N(0, *q*). We compared the data support for models with and without a bias term using AICc, in combination with different forms of observation models (see below).

The observation model treats the observed lengths of adult salmon in a given year as a sample from the distribution of true lengths in the population. Specifically, the model is

(2)

where *yj,t* is the natural logarithm of observed fish size from source *j* in year *t*, *aj* is on offset term for source *j*, and *vj,t* is a residual sampling error for source *j* in year *t*, such that *vj,t* ~ N(0, *r*). When *i = j*, each of the two methods (i.e., derby and WDFW) are assumed to be sampling their own unique populations.

We can write equations (1) and (2) in a more compact form using matrix notation. The first case, where each set of fish lengths are assumed to come from two different groups of fish, becomes

(3a)

. (3b)

The second model, where each set of lengths is assumed to be a sample from one large population, is

. (4a)

(4b)

In equations (3a), (3b), and (4b), the errors are distributed as a multivariate normal. In all of those cases, we assumed that the errors were independent, but not identically distributed, such that the covariance matrices had a different variance term in each of the elements of the diagonal, and 0’s in the off-diagonals.

Results

The Tengu Derby data indicated that body size was initially high in the late 1940s and 1950s, declined to a low in about 1980, rose to another peak about as high as the first peak around 1990, and then declined steadily to a current size below the earlier low. These patterns were evident in our primary metric, the average mass of the five largest salmon (Fig. 2), and also in the maximum size each year, and the numbers caught exceeding 5 and 10 pounds (Fig. 3), with peaks occurring in the middle of the time series in the early 1990’s. Given these large shifts in fish mass over time, it was perhaps expected that we did not find any data support for a model that included a single systematic trend in size over the entire time period; the AICc for the unbiased random walk was ~0.6 units lower than that for the biased random walk.

During the period from 1970 to 2014, observed changes in the mass of fish from the Tengu Derby were not similarly reflected in the mean size of fish caught in the purse seine fisheries, despite some similarities in fish mass from the late 1980s to the late 1990s (Fig. 4). Models with only one underlying state had AICc values that were about 35 units greater than models with two unique states. Furthermore, although the mean fish mass from commercial fisheries appeared to generally decrease over the period of record, we found minimal data support for a model with a consistent downward bias in either time series (i.e., the model with biases had an AICc value that was 1 unit less than the model without bias terms).

Discussion

The data from the Tengu Derby showed a decline in average mass of the five largest fish (also evident in the maximum mass, and the numbers caught per angler over 5 and 10 pounds each year), from the first records in the mid-late 1940s to a low about 1980. This initial decline mirrored that reported by [Ricker (1981](#_ENREF_32)) for several regions along the British Columbia coast. Subsequent investigations in British Columbia reported an increase in Chinook salmon average mass from that low period to a high around 1990-2000 ([Bigler et al. 1996](#_ENREF_4)), followed by another decline ([Jeffrey et al. 2017](#_ENREF_13)). These patterns approximated those seen in the Tengu Derby data, but they may not reflect underlying common causes. Importantly, we found a lack of alignment between the Puget Sound data from commercial purse seine fisheries targeting migratory adults and those from the derby.

Changes in average size may result from differences in growth rate and shifts in the population’s age composition ([Bigler et al. 1996](#_ENREF_4); [Lewis et al. 2015](#_ENREF_17); [Ohlberger et al. 2018](#_ENREF_22)). Indeed, declines in overall size recently reported for Alaskan Chinook, Coho, Chum, and Sockeye salmon were attributed primarily to reductions in age at maturity rather than size at age ([Oke et al. 2020](#_ENREF_23)). The specific causal mechanisms and factors controlling these changes in age and size remain uncertain, in part because 1) growth and age at maturity are complex inter-related traits, 2) the data typically include varying proportions of populations that differ in size and age, and 3) there are many environmental influences ([Oke et al. 2020](#_ENREF_23); [Ricker 1980](#_ENREF_31)). As with other salmon species, the number of years Chinook Salmon spend at sea is typically inversely related to smolt size ([Quinn 2018](#_ENREF_26); [Scheuerell 2005](#_ENREF_37); [Whitman 1987](#_ENREF_47)). Salmon produced in hatcheries are commonly larger at release than wild conspecifics, and thus younger at maturity ([Norris et al. 2000](#_ENREF_21)). The proportion of hatchery origin Chinook Salmon caught in Puget Sound has increased considerably over the past decades, from < 40% in 1968 and 1969 to an average of 64% in the 1970s, 74% in the 1980s, 79% in the 1990, 82% in the 2000s, and 87% from 2010 – 2015 ([Losee et al. 2019](#_ENREF_18)), complicating interpretation of size trends.

Puget Sound and the entire Salish Sea have undergone many changes over the past decades in physical and ecological attributes, preventing us from ascribing the observed changes in Chinook Salmon mass to specific causes. However, data such as these on the resident component, over such a long period, are unique and especially valuable. Salish Sea resident salmon are smaller than those feeding along the Pacific Ocean coast ([Milne 1950](#_ENREF_20); [Pressey 1953](#_ENREF_24); [Rohde et al. 2014](#_ENREF_36)), thus changes in the proportions of residents and migrants could strongly affect mean body size, depending on where and when the sampling took place. Indeed, the proportion of Chinook salmon remaining as residents in Puget Sound has decreased over the period covered by the Tengu Derby data ([Quinn and Losee in review](#_ENREF_28)). The lack of correspondence between the Tengu Derby and purse seining data presented here spanning more than four decades, and the decreasing resident component in the populations, illustrates yet another important complexity in the analysis of temporal trends in salmon size. That is, the differential migration patterns observed in several salmon species, and especially Chinook and Coho salmon ([Quinn 2021](#_ENREF_27); [Quinn and Losee in review](#_ENREF_28)), can cause differences in vulnerability to fisheries of contingents that migrate to different areas ([Sharma and Quinn 2012](#_ENREF_38)). If those migratory contingents also differ in size, then the resulting data can be biased, depending on where and when the fish were sampled.

Acknowledgments

First and foremost, we thank Doug Hanada of the Tengu Blackmouth Club for generously sharing the data with us, giving us permission to report them, and providing information needed to interpret the data, and the many hundreds of anglers over the decades whose catches revealed the patterns we describe here. We also acknowledge the discrimination and internment that Japanese-Americans endured, and recognize the dedication to salmon fishing evident in the derby’s persistence over more than seven decades, the inclusion of participants of all races, and the reputations of club members for their skill as anglers. Many helpful comments were provided by retired Washington Department of Fisheries – Fish and Wildlife staff, notably Frank Haw, Ray Buckley, and Steve Mathews, and by Eli Holmes (NOAA-Fisheries).

Figure 1. Map of Puget Sound, Washington, with an insert showing the location of the Tengu Blackmouth Derby that provided data on mass of Chinook Salmon.

Map

Description automatically generated

Figure 2. Time series of the mean mass of the five largest Chinook Salmon caught in the Tengu Derby (connected blue dots), with the model fitted values (black line) and approximate 95% confidence intervals (gray line). Missing points reflect years when < 5 were caught.

Chart

Description automatically generated

Figure 3. Time series of the mass of the largest Chinook Salmon caught in the Tengu Derby (top), and the number of fish ≥ 5 pounds in light blue and ≥ 10 pounds in dark blue divided by the number of participating anglers each year (bottom).

Chart, histogram

Description automatically generated

Figure 4. Time series of observed Chinook Salmon mass from purse seine fisheries (red) from 1970-2014 and the Tengu derby (blue), including fits from the multivariate random walk model for both time series (dashed lines). Note the shorter period of record compared to Fig. 2.

Chart, line chart

Description automatically generated

References Cited

Arostegui, M. C., and coauthors. 2017. Spatially clustered movement patterns and segregation of sub-adult Chinook Salmon within the Salish Sea. Marine and Coastal Fisheries 9:1-12.

Bal, G., and coauthors. 2017. Evidence for long-term change in length, mass and migration phenology of anadromous spawners in French Atlantic salmon *Salmo salar*. Journal of Fish Biology 90:2375-2393.

Bielak, A. T., and G. Power. 1986. Changes in mean weight, sea-age composition, and catch-per-unit-effort of Atlantic salmon (*Salmo salar*) angled in the Godbout River, Quebec, 1859-1983. Canadian Journal of Fisheries and Aquatic Sciences 43:281-287.

Bigler, B. S., D. W. Welch, and J. H. Helle. 1996. A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). Canadian Journal of Fisheries and Aquatic Sciences 53:455-465.

Chamberlin, J. W., T. E. Essington, J. W. Ferguson, and T. P. Quinn. 2011. The influence of hatchery rearing practices on salmon migratory behavior: Is the tendency of Chinook salmon to remain within Puget Sound affected by size and date of release? . Transactions of the American Fisheries Society 140:1398-1408.

Chamberlin, J. W., and T. P. Quinn. 2014. Effects of natal origin on localized distributions of Chinook salmon, *Oncorhynchus tshawytscha*, in the marine waters of Puget Sound, Washington. Fisheries Research 153:113-122.

Cox, S. P., and S. G. Hinch. 1997. Changes in size at maturity of Fraser River sockeye salmon (*Oncorhynchus nerka*) (1952-1993) and associations with temperature. Canadian Journal of Fisheries and Aquatic Sciences 54:1159-1165.

Edeline, E., and coauthors. 2007. Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. Proceedings of the National Academy of Science 104:15799–15804.

Fagen, R. 1988. Long-term trends in maximum size of sport-caught Chinook salmon (*Oncorhynchus tshawytscha*): a data-analytic approach to weights of first-prize fish in four southeastern Alaska salmon derbies. Fisheries Research 6:125-134.

Gardner, M. L. G. 1976. A review of factors which may influence the sea-age and maturation of Atlantic salmon *Salmo salar* L. Journal of Fish Biology 9:289-327.

Haw, F., H. O. Wendler, and G. Deschamps. 1967. Development of Washington State salmon sport fishery through 1964. Washington Department of Fisheries, Research Bulletin 7.

Healey, M. C., and C. Groot. 1987. Marine migration and orientation of ocean-type chinook and sockeye salmon. American Fisheries Society Symposium 1:298-312.

Jeffrey, K. M., I. M. Côté, J. R. Irvine, and J. D. Reynolds. 2017. Changes in body size of Canadian Pacific salmon over six decades. Canadian Journal of Fisheries and Aquatic Sciences 74:191-201.

Jensen, H. M. 1948. Puget Sound salmon investigation. Washington Department of Fisheries.

Jordan, D. S., and B. W. Evermann. 1896. The Fishes of North and Middle America. Smithsonian Institution, Washington, D. C.

Kagley, A. N., J. M. Smith, K. L. Fresh, K. E. Frick, and T. P. Quinn. 2017. Residency, partial migration, and late egress of sub-adult Chinook salmon (*Oncorhynchus tshawytscha*) and comparisons with coho salmon (*O. kisutch*) in Puget Sound, Washington. Fishery Bulletin 115:544-555.

Lewis, B., W. S. Grant, R. E. Brenner, and T. Hamazaki. 2015. Changes in size and age of Chinook salmon *Oncorhynchus tshawytscha* returning to Alaska. PLoS ONE 10(6):e0130184.

Losee, J. P., N. W. Kendall, and A. Dufault. 2019. Changing salmon: an analysis of body mass, abundance, survival, and productivity trends across 45 years in Puget Sound. Fish and Fisheries 20:934-951.

Millner, R. S., and C. L. Whiting. 1996. Long-term changes in growth and population abundance of sole in the North Sea from 1940 to the present. ICES Journal of Marine Science 53:1185–1195.

Milne, D. J. 1950. The difference in the growth rate of coho salmon on the east and west coasts of Vancouver Island in 1950. Fisheries Research Board of Canada, Progress Report of the Pacific Coast Stations 85:80-82.

Norris, J. G., S.-Y. Hyun, and J. J. Anderson. 2000. Ocean distribution of Columbia River upriver bright fall chinook salmon stocks. North Pacific Anadromous Fish Commission Bulletin 2:221-232.

Ohlberger, J., E. J. Ward, D. E. Schindler, and B. Lewis. 2018. Demographic changes in Chinook salmon across the Northeast Pacific Ocean. Fish and Fisheries 19:533-546.

Oke, K. B., and coauthors. 2020. Recent declines in salmon body size impact ecosystems and fisheries. Nature Communications.

Pressey, R. T. 1953. The sport fishery for salmon on Puget Sound. Fisheries Research Papers, Washington Department of Fisheries 1(1):33-48.

Pyper, B. J., and R. M. Peterman. 1999. Relationship among adult body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*), 1967-1997. Canadian Journal of Fisheries and Aquatic Sciences 56:1716-1720.

Quinn, T. P. 2018. The Behavior and Ecology of Pacific Salmon and Trout, second edition. University of Washington Press, Seattle.

Quinn, T. P. 2021. Differential migration in Pacific salmon and trout: Patterns and hypotheses. Animal Migration 8:1-18.

Quinn, T. P., and J. P. Losee. in review. Diverse and changing use of the Salish Sea by Pacific salmon, trout, and char. Canadian Journal of Fisheries and Aquatic Sciences.

Quinn, T. P., P. McGinnity, and T. F. Cross. 2006. Long-term declines in body size and shifts in run timing of Atlantic salmon in Ireland. Journal of Fish Biology 68:1713-1730.

Richards, R. A., and P. J. Rago. 1999. A case history of effective fishery management: Chesapeake Bay striped bass. North American Journal of Fisheries Management 19:356-375.

Ricker, W. E. 1980. Causes of the decrease in age and size of chinook salmon (*Oncorhynchus tshawytscha*). Canadian Technical Report of Fisheries and Aquatic Sciences 944:1-25.

Ricker, W. E. 1981. Changes in the average size and average age of Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 38:1636-1656.

Ricker, W. E. 1995. Trends in the average size of Pacific salmon in Canadian catches. Canadian Special Publication of Fisheries and Aquatic Sciences 121:593-602.

Riddell, B. R., and coauthors. 2018. Ocean ecology of Chinook Salmon. Pages 555-696 *in* R. J. Beamish, editor. The Ocean Ecology of Pacific Salmon and Trout. American Fisheries Society, Bethesda.

Rogers, L. A., and coauthors. 2011. Climate and population density drive changes in cod body size throughout a century on the Norwegian coast. Proceedings of the National Academy of Sciences 108:1961–1966.

Rohde, J., K. L. Fresh, and T. P. Quinn. 2014. Factors affecting partial migration in Puget Sound Coho Salmon (*Oncorhynchus kisutch*). North American Journal of Fisheries Management 34:559-570.

Scheuerell, M. D. 2005. Influence of juvenile size on the age at maturity of individually marked wild Chinook salmon. Transactions of the American Fisheries Society 134:999-1004.

Sharma, R., and T. P. Quinn. 2012. Linkages between life history type and migration pathways in freshwater and marine environments for Chinook salmon, *Oncorhynchus tshawytscha*. Acta Oecologica 41:1-13.

Sharpe, D. M. T., and A. P. Hendry. 2009. Life history changes in commercially exploited fish stocks: an analysis of trends across studies. Evolutionary Applications 2:260-275.

Shearer, W. M. 1990. The Atlantic salmon (*Salmo salar* L.) of the North Esk with particular reference to the relationship between river and sea age and time of return to home waters. Fisheries Research 10:93-123.

Shelton, A. O. S., W H, E. J. Ward, B. E. Feist, and B. Burke. 2019. Using hierarchical models to estimate stock-specific and seasonal variation in ocean distribution, survivorship, and aggregate abundance of fall run Chinook salmon. Canadian Journal of Fisheries and Aquatic Sciences 76:95-108.

Summers, D. W. 1995. Long-term changes in the sea-age at maturity and seasonal time of return of salmon, *Salmo salar* L., to Scottish rivers. Fisheries Management and Ecology 2:147-155.

Swain, D. P., A. F. Sinclair, and J. M. Hanson. 2007. Evolutionary response to size-selective mortality in an exploited fish population. Proceedings of the Royal Society B 274:1015-1022.

Valiente, A. G., F. Juanes, and E. Garcia-Vazquez. 2011. Increasing regional temperatures associated with delays in Atlantic salmon sea-run timing at the southern edge of the European distribution. Transactions of the American Fisheries Society 140:367–373.

Weitkamp, L. 2012. Marine distributions of coho and Chinook salmon inferred from coded wire tag recoveries. American Fisheries Society Symposium 76:191-214.

Weitkamp, L. A. 2009. Marine distributions of Chinook salmon from the west coast of North America determined by coded wire tag recoveries. Transactions of the American Fisheries Society 139:147-170.

Whitman, R. P. 1987. An analysis of smoltification indices in fall chinook salmon (*Oncorhynchus tshawytscha*). University of Washington, Seattle.