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Long-term Changes in Length at Maturity of Pacific Salmon in Auke Creek Alaska

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Abstract

Although decreasing length at maturity has been observed in some Alaska salmon populations, the generality of this trend is poorly understood. This study was undertaken to determine whether this pattern holds for multiple species of salmon from a small watershed in Southeast Alaska (Auke Creek), and, if so, what abiotic and biotic factors are contributing to this phenomenon. We analyzed up to 32 years of data (early 1980s - 2012) for coho salmon (*Oncorhynchus kisutch)*, sockeye salmon (*O. nerka)*, and pink salmon (*O. gorbuscha)*. We observed statistically significant decreases in mean length at maturity for coho salmon adults, as well as increases in mean length of saltwater age-2 sockeye salmon. Non-significant trends in mean length were observed in coho salmon jacks, pink salmon, and saltwater age-3 sockeye salmon. Abiotic and biotic variables that explained interannual variation in length include a combination of climate and resource availability effects. These observed changes should be considered in future management decisions to ensure sustainable harvest for Southeast Alaska's sport, commercial, and subsistence fisheries.

Contents

Introduction

A temporal trend toward decreasing body length at maturity in some Pacific salmon populations was identified over 30 years ago (Ricker 1981). Since that time, this subject has become a growing source of concern and a focus of research due to its implications for commercial, sport, and subsistence fisheries. Understanding how salmon length has responded to past fishing pressures and environmental variation is important for predicting future salmon responses to harvest and climate variability.

In an 18-year period from 1975 to 1993, average length at maturity decreased in 45 of 47 North Pacific salmon populations, despite a near doubling of North Pacific salmon abundance due to improved population management, artificial enhancement, and favorable ocean conditions (Bigler et al. 1996). Coho salmon abundance and size have changed around the Pacific Rim (Shaul et al. 2007). More recent studies have suggested long-term changes in juvenile and adult length may be due to various ecological and environmental processes including sea surface temperature, compensatory growth, size-selective harvest, density-dependence, competitive species biomass, and other large-scale climate shifts (Lewis et al. 2015, Jeffrey et al. 2016, Yasumiishi et al. 2016). The length of sockeye salmon was significantly related to salmon abundance and sea surface temperature in stocks from southern British Columbia to western Alaska (Pyper and Peterman 1999). These size changes will affect commercial, subsistence, and recreational users who harvest Southeast Alaska fish (Beier et al. 2008). Harvest itself can also influence life history variation, including age at maturity, in various fishes including salmon (Ricker 1981, Allendorf and Hard 2009, Quinn et al. 2011, Lewis et al. 2015, Ohlberger et al. 2018). Humans have the unique ability to overexploit resources to an extreme degree and the potential to radically alter both evolutionary and ecological processes on a global scale, unless constrained by proper resource management (Darimont et al. 2015).

We investigated how harvest and environmental variation may affect length at maturity in salmonid populations in Auke Creek, Alaska. Current warming trends in the Pacific Northwest have influenced salmon age structure, length, migration timing, and distributions (Kovach et al. 2013, Lewis et al. 2015, Malick et al. 2015b). We used a time series of salmon length at age from a watershed currently experiencing rapid warming and increased temperature variability to quantify trends in reproductively mature salmon length at age over time (Shanley et al. 2015). We, also identified abiotic and biotic factors that correlated with these observed changes.

Methods

Study Area

The National Oceanic and Atmospheric Administration's (NOAA) Auke Creek Research Station's permanent weir has been in full-time operation since 1980 and is located 16 km northwest of downtown Juneau, Alaska (Fig. 1). This weir structure facilitates complete enumeration of emigrant and immigrant salmonids. This feature makes Auke Creek Weir an ideal location for studying the biological consequences of climate trends observed in Southeast Alaska (Shanley et al. 2015).

Biological Data

Five biological data series were obtained for this project. Adult length of each species was used as a response variable, and the other variables acted as our predictors of change in length.

Adult and Juvenile Auke Creek Salmonids

We used a high-quality time series for immigrant and emigrant coho (1981-2012), sockeye (1982-2012), and pink salmon (1980-2012). Data for each species were composed of paired length and scale samples (for age). For coho salmon, all sexually mature male fish < 400 mm were considered jacks. Coho salmon jacks the Auke Creek are sexually mature males that have returned to reproduce after a summer in saltwater, as opposed to a full year as with adult males.

Southeast Alaska Hatchery Pink Salmon and Chum Salmon Index

An index of total yearly averages of hatchery pink salmon and chum salmon releases was obtained from the Alaska Department of Fish and Game's (ADF&G) hatchery release database (https://mtalab.adfg.alaska.gov/CWT/Reports/hatcheryrelease.aspx). This index can serve as a multi-faceted explanatory variable. Hatchery releases act as an indicator of for food availability, competition, and as a predation buffer across coho, sockeye, and pink salmon. The number of hatchery releases in Southeast Alaska has increased greatly since 1981 (Briscoe et al. 2005). These juvenile salmon have been one of the many food sources for juvenile migrating salmonids in Auke Bay (Parker 1971, Landingham et al. 1998, Mortensen et al. 2000). For coho salmon, hatchery releases serve as a food source. However, pink salmon fry can quickly grow to a size to avoid predation by coho salmon, and instead become a predation buffer (Godin 1981, Fisher and Pearcy 1988, Willette et al. 2001). For pink salmon fry, these releases could serve as a source of competition for food resources. For sockeye salmon, the releases could again be a food source, but also could have a possible competition effect for food resources (Ruggerone and Nielsen 2004).

Northern Southeast Alaska Pink Salmon Harvest

Total pink salmon harvest was obtained from ADF&G (L. Shaul, Alaska Department of Fish and Game, pers. comm.) for the northern Southeast Alaska region. This surrogate for abundance of pink salmon is expected to show a negative relationship with coho, sockeye, and pink salmon length due to competition for resources (Briscoe et al. 2005).

Exploitation Rate

The annual exploitation rate of coho salmon can be estimated precisely because all coho salmon smolts are coded wire tagged at Auke Creek. Sockeye salmon exploitation rates were obtained from annual harvest and escapement on the Stikine River (Pacific Salmon Commission 2015). Exploitation rate has been used to examine effects of size-selective harvest across populations, and we wished to see if exploitation rate contributed to changes in length in coho and sockeye salmon (Lewis et al. 2015). Pink salmon exploitation rate was not used for pink salmon modeling as it is a direct measurement of northern Southeast Alaska pink salmon harvest, which is already included.

Environmental Data

A mix of variables representing large-scale climate patterns and local environmental conditions that encompass all stages of juvenile and adult development were chosen for the modeling process.

Pacific Decadal Oscillation (PDO)

PDO is as measurement of long-term temperature trends that persist for multiple decades over the mid-latitudes in the Pacific basin. PDO was obtained from NOAA's Gulf of Alaska PDO index database (https://www.ncdc.noaa.gov/teleconnections/pdo/). A yearly average of Gulf of Alaska PDO was used. It is expected that a high PDO will result in improved early marine growth upon entry to the ocean (Mantua et al. 1997).

North Pacific Index (NPI)

Yearly NPI was obtained from NOAA Climate Prediction Center database for the East Pacific – North Pacific Index (http://www.cpc.ncep.noaa.gov/data/teledoc/ep.shtml). This index is a measure of the Aleutian low pressure zone and is defined as the area-weighted sea-level pressure. The NPI is expected to have a negative relationship with marine growth because low values indicate low pressure systems in the Gulf of Alaska, which would increase food availability to salmon during early marine life (Malick et al. 2009).

Auke Creek Temperature

A May-June average of Auke Creek temperature was used as a proxy of Auke Bay sea surface temperature due to its high correlation with the bay's temperature (Pearson's $r = 0.94$; Bell et al. 2017). Creek temperature was recorded by an in-stream logger, located approximately 30 m upstream of the average high tide line. Sea surface temperature has a positive relationship with marine survival and growth of salmonids in this region (Briscoe et al. 2005, Malick et al. 2009).

Independent Variable Lags

When biologically relevant, independent variables were lagged to appropriately match environmental conditions with the first year at sea because of the established importance of this time period for Auke Creek stocks (Orsi et al. 2013). Temporal lags were used to predict interannual variation in length at maturity as a function of PDO, NPI, creek temperature, juvenile size, and the hatchery pink salmon and chum salmon index. The variables exploitation rate and pink salmon harvest were not lagged as they have greater influence on the adult life stage. No lags were necessary for coho salmon jacks as they are in saltwater only for a single summer.

Statistical Analysis

We identified ecological and environmental variables related to temporal patterns in length-at-age at maturity for our species of interest. We first established whether there was a trend in length for each dataset using simple linear regression. We then explored the factors affecting each trend using multiple linear regression to model multiple effects on mean length. All analyses were performed using R (R Core Team 2018).

To avoid overfitting, models were chosen *a priori* and limited to three independent variables. Models were fit in the following format: length ~ year + environmental variable (PDO, NPI, and creek temp) + biological variable (juvenile size, hatchery pink salmon and chum salmon index, exploitation rate, and pink salmon harvest rates); length ~ year + environmental variable + environmental variable; and length ~ year + biological variable + biological variable. This gave every possible combination of year, a fisheries effect, and a climate effect. Year was included in every model to provide a time effect and to encompass any variation that was not explained by the other explanatory variables. After the top three models were choosen via AICc (small-sample-size corrected Akaike Information Criterion) they were split in a piecewise fashion into models with three, two, and one independent variables, and the best overall model was choosen via AICc. By using this model selection process, we limited the variables per model, while also not forcing any variable in a model.

Model building and selection then proceeded according to the method described above for coho salmon adults, sockeye salmon adults, and pink salmon. Length at maturity for coho salmon jacks was modeled similarly using the following independent variables: year, creek temperature, juvenile size, and hatchery pink salmon and chum salmon index. Sockeye salmon adults were modeled according to their saltwater age structure. This resulted in two model selection procedures for sockeye salmon, one for saltwater age-2 adults, and another for saltwater age-3 adults. We did not build models to explain interannual variation in length at maturity for sockeye salmon jacks (saltwater age-1) because there were insufficient sample sizes. AICc weights were used to determine relative support for the best model for each time series.

The top models with support for coho, sockeye, and pink salmon that were assessed for violations of the assumptions of linear models. We used box-plots, QQ quartile plots, residual plots, correlation tables, Shapiro-Wilk tests, non-constant error variance tests, and autocorrelation plots to assess possible violations. No violations of normality, variance, or autocorrelation were found. While some violations of multicollinearity were found, there were not between variables in the best-supported models.

Results

Coho Salmon

Adult coho salmon mean length has decreased by 29.32 mm ± 3.04 (standard error) (r^2 = 0.27, P = 0.0025, n = 32; Fig 2.A). The best supported model for adult mean length change over time revealed a positive relationship with PDO and negative relationship with pink salmon harvest (r^2 = 0.56, $P \leq 0.001$, RSE = 11.77; Table 1). In contrast, jack coho salmon mean length varied greatly, but showed no statistically significant changes in mean length over the time series (r^2 = 0.08, P = 0.15, n = 28; Fig 2.B). The top three models have almost equal support (Table 1).

Sockeye Salmon

Saltwater age-2 sockeye salmon mean length increased by 24.86 mm ± 2.52 (r^2 = 0.30, P = 0.0018, n = 30; Fig 2.C). The top model included a positive relationship with year, a negative relationship with temperature, and a negative relationship with the hatchery pink salmon and chum salmon index. However, the top three models have approximately equal support (r^2 = 0.47, P = 0.001, RSE = 10.63; Table 1). Saltwater age-3 sockeye salmon showed no statistically significant changes in mean length over the same period that age-2 individuals increased in length (r^2 = 0.02, P = 0.48, n = 30; Fig 2.D). The top three models have almost equal support (Table 1).

Pink Salmon

Pink salmon showed no statistically significant changes in mean length over time (r^2 = 0.03, P = 0.42, n = 27; Fig 2.E). The best supported model for their change in mean length included non-significant, relationship with pink salmon harvest ($r^2 = 0.11$, $P = 0.1$, $RSE = 10.92$; Table 1).

Discussion

We observed decreases in length of coho salmon and pink salmon, and increases in length of sockeye salmon over the last three decades, but only the decreases in coho salmon length and increases in age-2 sockeye salmon were statistically significant. Our results indicate the varying changes in length amongst Pacific salmon that were noticed in the early 1980s are still present today in Auke Creek salmon (Ricker 1981).

Coho salmon adults are decreasing in mean length and affected by PDO and pink salmon harvest. There is a positive relationship of length with PDO, indicating that in warmer ocean conditions, coho salmon are able to grow to a length greater than that in colder years. This pattern has been reported elsewhere and attributed to the bottom-up increase of overall ocean productivity in years with warmer conditions (Mantua et al. 1997, Malick et al. 2015a). Additionally, abundance has fluctuated over interdecadal timescales in a pattern that mirrors the PDO (Hare 1996). The negative relationship between coho salmon length and pink salmon harvest suggests negative impacts of competition for food resources at high pink salmon harvest. Pink salmon harvest has increased over time ($r^2 = 0.16$, $P = 0.040$). There was little evidence of large-scale climate effects on coho salmon jacks. This could be expected as they only spend 4 months in the marine environment and tend to remain nearshore. There was no significant trend in jack length nor much evidence for a driving factor in jack length variation from our modelling efforts.

Auke Creek, age-2 sockeye salmon are increasing in length. A negative correlation with Auke Creek temperature was found, and temperature was used as a proxy for Auke Bay sea surface temperature. Additionally, a negative relationship was found with hatchery releases, which have increased over the last three decades ($r^2 = 0.51$, $P \leq 0.001$). The negative relationship with increasing hatchery production suggests a possible competition between sockeye juveniles and pink and chum hatchery releases. As these hatchery releases increase, so may competition, leading to a decrease in food availability and thus size at age of sockeye. There was no clear trend in length of age-3 sockeye salmon, nor did a top model emerge. In comparison to other age classes, age-3 sockeye salmon spend the most time in the ocean and the top models reflect the influence of large-scale climate indices.

The decrease in pink salmon length over time is not statistically significant, but it could become significant if the observed trend continues. There were no top models that distinguished themselves in the model selection process.

Human harvest has been shown to affect phenotypic traits and age structure of other fish species (Bromaghin et al. 2011, Uusi-Heikkilä et al. 2015). While we may not be fully able to attribute these changes to human-induced selection, it would be imprudent to assume that there is no effect (Allendorf and Hard 2009). The successful management of the harvest of our wild populations should take into account and monitor the selective effects of harvest, before it has serious, lasting impacts that will take disproportionally more time to reverse (Kuparinen and Merilä 2007, Hard et al. 2008, Allendorf and Hard 2009).

Management Implications

Within sport, commercial, and subsistence fisheries, larger fish are preferred. Thus, there are clear negative economic, social, and cultural consequences for fisheries of species that are decreasing in length. If this trend in decreasing length at age continues, it will lead to a decrease in size at harvest and total weight for a given number of fish, which will impact price. As salmon are a subsistence resource of cultural importance in Southeast Alaska, changes in size could lead to reduced numbers of fish available for subsistence catch. In addition to economic impacts, there are direct ecological impacts. As female fecundity is directly related to size, variations in length could cause changes that will make maintaining population productivity difficult (Quinn et al. 2011). Additionally, changes in male length may influence mate choice and spawning success (Hanson and Smith 1967).

In summary, our findings indicate considerable variation in the length of Auke Creek salmon that are related to environmental variations corresponding with climate variability, as well as more direct human-induced effects. These physical changes should be considered in future management decisions to ensure the successful management of Southeast Alaska's sport, commercial, and subsistence fisheries, resulting in sustainable harvests for future generations.

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Table 1. -- The top three models explaining change in length of coho, sockeye, and pink salmon. Results include: number of parameters (K), Akaike Information Criterion corrected (AIC_c), delta AIC_c (Δ AIC_c), AIC_c weights (AIC_c Wt.), and cumulative weights (Cum.Wt.).

Model	AIC_c	ΔAIC_c	AIC_c Wt.	Cum. Wt.
Coho Salmon Adults				
PDO + Pink Harvest	254.9363	0	0.6078	0.6078
PDO + Temperature	257.7248	2.7885	0.1507	0.7585
Year + PDO + Pink Harvest	257.7556	2.8194	0.1484	0.9070
Coho Salmon Jacks				
Year	223.0380	0	0.2120	0.2120
Year + Temperature	223.1925	0.1544	0.1962	0.4082
Temperature	223.6952	0.6572	0.1526	0.5608
Sockeye Salmon SW Age 2				
Year + Temperature + Hatchery Pink Chum Index	235.1448	0	0.2130	0.2130
Year + Hatchery Pink Chum Index	235.2269	0.0821	0.2045	0.4175
Year + North Pacific Index	235.5100	0.3652	0.1775	0.5950
Sockeye Salmon SW Age 3				
Year + PDO + North Pacific Index	233.2322	0	0.1293	0.1293
North Pacific Index	233.4667	0.2345	0.1150	0.2443
PDO + North Pacific Index	233.6947	0.4625	0.1026	0.3469
Pink Salmon				
Pink Harvest	210.6964	0	0.2463	0.2463
Temperature	212.5378	1.8414	0.0981	0.3443
PDO	212.6146	1.9182	0.0944	0.4387

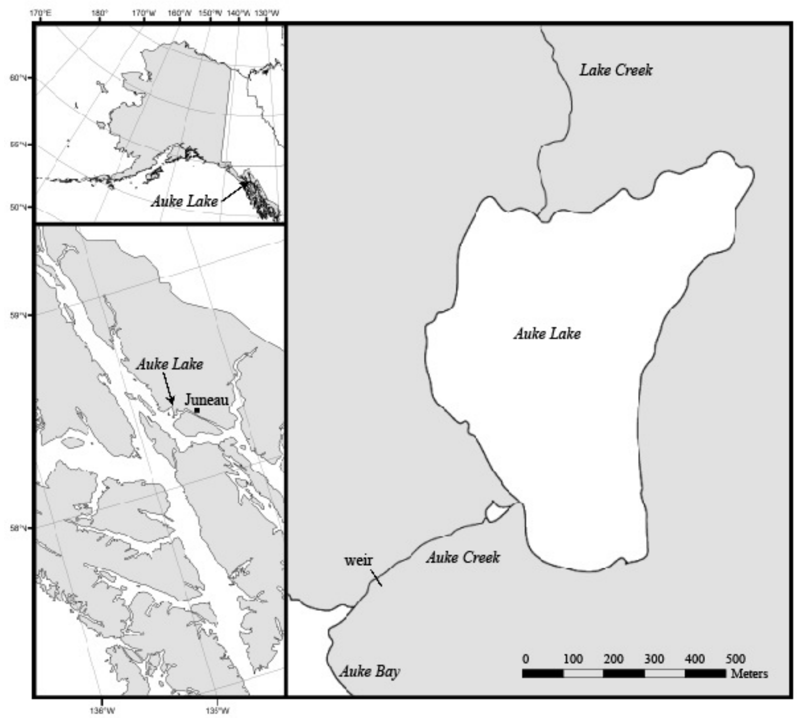

Figure 1. -- Map of the Auke Creek watershed in Southeast Alaska. Weir location indicates the position of the Auke Creek Research Station.

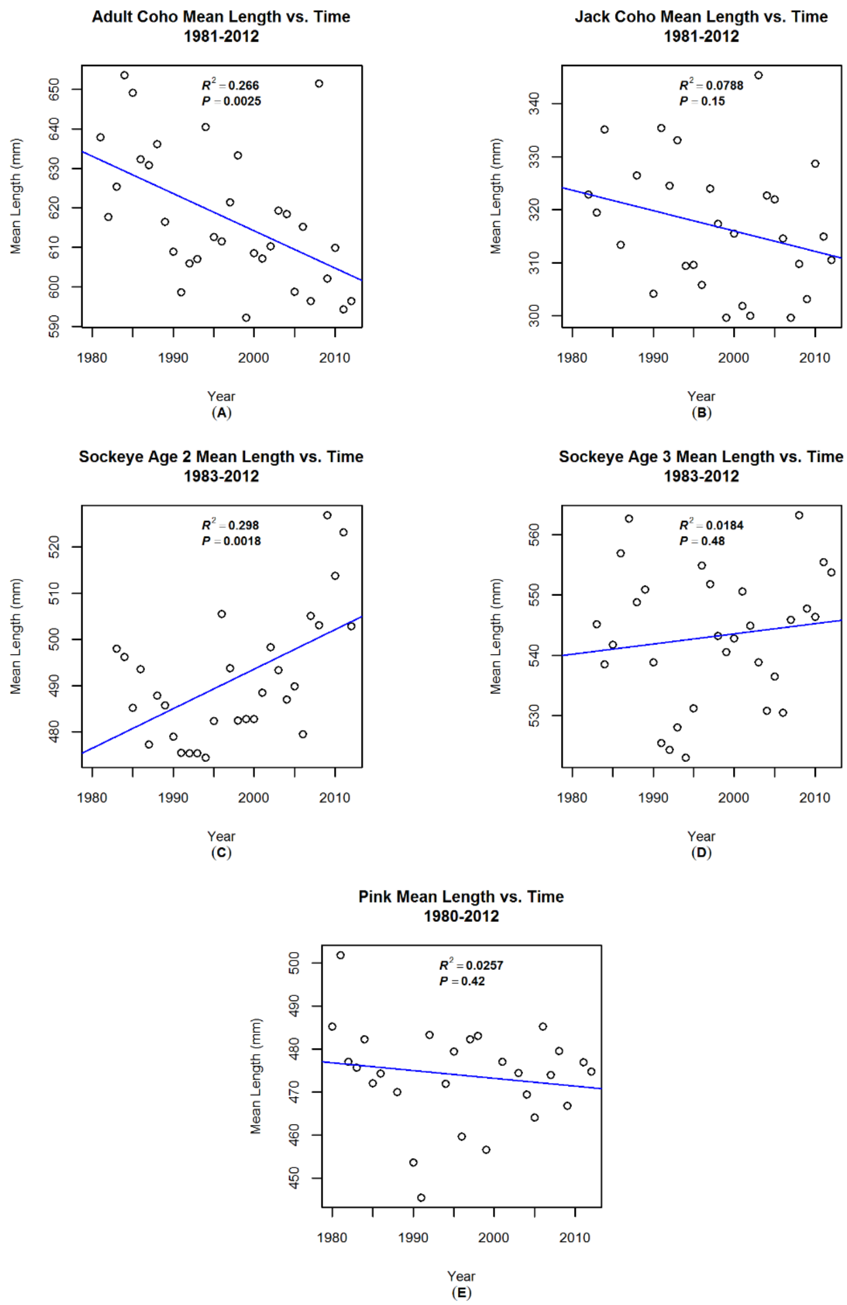

Figure 2. -- Mean length of adult coho salmon has decreased 29.32 mm ± 3.04 (± SE) over the 32-year time period [Panel A]. Mean length of saltwater age-2 sockeye salmon has increased by 24.86 mm ± 2.52 over a 30-year time period [Panel C]. Non-significant trends were observed for jack coho salmon [Panel B], saltwater age-3 sockeye salmon [Panel D], and pink salmon [Panel E].

Supplementary Tables

Supplementary Table S1. -- Mean length (mm) ± 95% confidence interval by year for each species model.

Year	Coho Adult	Coho Jack	Sockeye SW Age 2	Sockeye SW Age 3	Pink
1980	-[a]	-	-	-	485 ± 4
1981	638 ± 6	-	-	-	502 ± 3
1982	618 ± 8	323 ± 9	-	-	477 ± 2
1983	625 ± 4	319 ± 8	498 ± 22	545 ± 6	476 ± 2
1984	654 ± 4	335 ± 5	496 ± 36	539 ± 3	482 ± 2
1985	649 ± 6	-	485 ± 14	542 ± 10	472 ± 2
1986	632 ± 7	313 ± 7	494 ± 4	557 ± 6	474 ± 3
1987	631 ± 11	-	477 ± 25	563 ± 5	-
1988	636 ± 5	326 ± 7	488 ± 5	549 ± 3	470 ± 2
1989	617 ± 4	-	486 ± 10	551 ± 4	-
1990	609 ± 7	304 ± 10	479 ± 7	539 ± 3	454 ± 1
1991	599 ± 6	335 ± 8	476 ± 5	525 ± 3	446 ± 2
1992	606 ± 8	325 ± 5	475 ± 5	524 ± 4	483 ± 2
1993	607 ± 5	333 ± 3	475 ± 6	528 ± 3	-
1994	641 ± 6	309 ± 6	474 ± 18	523 ± 4	472 ± 2
1995	613 ± 5	310 ± 6	482 ± 5	531 ± 3	479 ± 2
1996	612 ± 6	306 ± 7	506 ± 4	555 ± 3	460 ± 3
1997	621 ± 6	324 ± 4	494 ± 5	552 ± 4	482 ± 3
1998	633 ± 6	317 ± 8	482 ± 10	543 ± 4	483 ± 4
1999	592 ± 6	300 ± 8	483 ± 6	541 ± 6	457 ± 2
2000	609 ± 6	316 ± 10	483 ± 7	543 ± 4	-
2001	607 ± 7	302 ± 11	489 ± 9	551 ± 2	477 ± 3
2002	610 ± 7	300 ± 10	498 ± 4	545 ± 6	-
2003	619 ± 4	345 ± 9	493 ± 9	539 ± 4	474 ± 3
2004	618 ± 6	323 ± 7	487 ± 7	531 ± 6	469 ± 4
2005	599 ± 8	322 ± 5	490 ± 7	537 ± 3	464 ± 3
2006	615 ± 5	315 ± 9	480 ± 5	530 ± 3	485 ± 5
2007	596 ± 8	300 ± 10	505 ± 9	546 ± 3	474 ± 4
2008	651 ± 5	310 ± 8	503 ± 7	563 ± 10	480 ± 4
2009	602 ± 8	303 ± 5	527 ± 5	548 ± 5	467 ± 4
2010	610 ± 9	329 ± 4	514 ± 5	546 ± 4	-
2011	594 ± 8	315 ± 4	523 ± 8	555 ± 3	477 ± 3
2012	596 ± 6	311 ± 9	503 ± 4	554 ± 4	475 ± 3
Total Sample Size	6930	1618	2456	5155	10945

[a] "-" Indicates data not available for indicated year. When not available at beginning of time series, analysis was truncated to first year with available data.

Supplementary Table S2. -- Explanatory variable correlation tables.

Coho Salmon Adults	Year	PDO	NPI	Temperature	Juvenile Size	Hatchery Releases	Exploitation Rate	Pink Harvest
Year	1.00	-0.64	-0.31	0.21	0.12	0.71	-0.28	0.30
PDO	-0.64	1.00	0.56	0.19	0.05	-0.33	0.07	-0.06
NPI	-0.31	0.56	1.00	0.13	0.05	0.12	0.03	0.07
Temperature	0.21	0.19	0.13	1.00	0.34	0.25	-0.27	0.50
Juvenile Size	0.12	0.05	0.05	0.34	1.00	0.25	-0.16	0.53
Hatchery Releases	0.71	-0.33	0.12	0.25	0.25	1.00	-0.01	0.30
Exploitation Rate	-0.28	0.07	0.03	-0.27	-0.16	-0.01	1.00	-0.18
Pink Harvest	0.30	-0.06	0.07	0.50	0.53	0.30	-0.18	1.00

Coho Salmon Jacks	Year	Juvenile Size	Hatchery Releases	Temperature
Year	1.00	0.17	0.68	0.18
Juvenile Size	0.17	1.00	0.28	0.20
Hatchery Releases	0.68	0.28	1.00	0.27
Temperature	0.18	0.20	0.27	1.00

Sockeye Salmon SW Age 2	Year	PDO	NPI	Temperature	Juvenile Size	Hatchery Releases	Exploitation Rate	Pink Harvest
Year	1.00	-0.60	-0.21	0.26	0.65	0.69	0.53	0.28
PDO	-0.60	1.00	0.50	0.15	-0.34	-0.31	-0.10	0.01
NPI	-0.21	0.50	1.00	0.16	-0.02	0.21	0.34	0.15
Temperature	0.26	0.15	0.16	1.00	0.23	0.28	0.33	0.10
Juvenile Size	0.65	-0.34	-0.02	0.23	1.00	0.50	0.39	0.10
Hatchery Releases	0.69	-0.31	0.21	0.28	0.50	1.00	0.66	0.30
Exploitation Rate	0.53	-0.10	0.34	0.33	0.39	0.66	1.00	0.42
Pink Harvest	0.28	0.01	0.15	0.10	0.10	0.30	0.42	1.00

Sockeye Salmon Age 3	Year	PDO	NPI	Temperature	Juvenile Size	Hatchery Releases	Exploitation Rate	Pink Harvest
Year	1.00	-0.58	-0.18	0.22	0.65	0.74	0.53	0.28
PDO	-0.58	1.00	0.49	0.18	-0.31	-0.32	-0.17	-0.43
NPI	-0.18	0.49	1.00	0.19	0.01	0.17	0.42	-0.02
Temperature	0.22	0.18	0.19	1.00	0.20	0.27	0.28	-0.25
Juvenile Size	0.65	-0.31	0.01	0.20	1.00	0.56	0.52	0.44
Hatchery Releases	0.74	-0.32	0.17	0.27	0.56	1.00	0.69	0.25
Exploitation Rate	0.53	-0.17	0.42	0.28	0.52	0.69	1.00	0.42
Pink Harvest	0.28	-0.43	-0.02	-0.25	0.44	0.25	0.42	1.00

Pink Salmon	Year	PDO	NPI	Temperature	Juvenile Size	Hatchery Releases	Pink Harvest
Year	1.00	-0.61	-0.32	0.36	-0.03	0.77	0.41
PDO	-0.61	1.00	0.43	0.00	0.05	-0.33	-0.16
NPI	-0.32	0.43	1.00	0.02	-0.17	0.07	-0.02
Temperature	0.36	0.00	0.02	1.00	-0.12	0.33	0.48
Juvenile Size	-0.03	0.05	-0.17	-0.12	1.00	0.12	-0.38
Hatchery Releases	0.77	-0.33	0.07	0.33	0.12	1.00	0.36
Pink Harvest	0.41	-0.16	-0.02	0.48	-0.38	0.36	1.00

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