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Effects of Climate and Competition for Offshore Prey on Growth, Survival, and Reproductive Potential of Coho Salmon in Southeast Alaska

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Abstract: In the offshore Gulf of Alaska (GOA), coho salmon exhibit strong dependence upon a single prey species, the minimal armhook squid (*Berryteuthis anonychus*). We propose and then test elements of the general hypothesis that coho salmon adult size in Southeast Alaska reflects predator-prey interactions among coho salmon, pink salmon, and squid, where squid are the main prey of coho salmon while pink salmon mediate squid abundance as both competitors and predators of squid. The majority (65%) of variation in size of coho salmon over a 45-year period was explained equally by the catch biomass of pink salmon in the GOA and by the PDO index during squid emergence and development, averaged at lags in 2-year increments (matching the life cycles of pink salmon and squid) of up to four years. We extend the analysis to examine effects on marine survival, sex ratio, and per capita reproductive potential and examine evidence for growth-related late-marine mortality. Our results lend support for an important late-marine period for coho salmon survival and for the role of pink salmon as a keystone predator that controls the trophic structure of salmon forage and the flow of energy in the offshore GOA ecosystem. Our findings also indicate that the capacity of the GOA to produce pink salmon for harvest, while maintaining stable adult coho salmon weight (based on inferred stable squid prey populations), is highly variable and closely linked with atmospheric forcing.

Keywords: coho salmon, *Berryteuthis anonychus*, squid, pink salmon, growth, survival, climate, competition

INTRODUCTION

The relationship among salmon species (*Oncorhynchus* spp.) and their prey in the offshore Gulf of Alaska (GOA) has been described as a “trophic triangle” in which flexible planktivores (pink *O. gorbusha* and sockeye *O. nerka* salmon) function as intra-guild predators that both prey upon minimal armhook squid (*Berryteuthis anonychus*) and compete with them for zooplankton prey (Aydin 2000; Uchikawa et al. 2004; Fig. 1). *Berryteuthis anonychus* is also the predominant prey of obligate nektivores (coho *O. kisutch* and Chinook *O. tshawytscha* salmon, and steelhead *O. mykiss*) that feed primarily on squid and (to a lesser extent) fish in these same waters (Kaeriyama et al. 2004; Atcheson et al. 2012). Here, we examine this relationship through size and survival of coho salmon in Southeast Alaska.

Coho salmon exhibit features that, compared with other salmon species, reduce the range of plausible mechanisms determining their growth at sea, where most spend approximately 16 months. Southeast Alaska coho salmon are limited to the northeast Pacific (Myers et al. 1996) where they are dependent upon a single calorie-rich prey species to fuel an exceptionally rapid growth rate during their second season at sea (Ishida et al. 1998). *Berryteuthis anonychus* has been shown to be the primary offshore prey of maturing coho salmon across varying climate regimes (LeBrasseur 1966; Pearcy et al. 1988; Davis 2003; Kaeriyama et al. 2004). Davis (2003) found that coho salmon in subarctic waters in the central North Pacific consumed almost exclusively large subadult and adult *B. anonychus*, which comprised the majority of the diet of all size classes larger than 500 g, and was highly correlated with stomach fullness. Coho salmon feeding in summertime increased their stomach contents index (SCI) with increasing size, as larger fish were able to catch larger squid, thereby further increasing their capacity for growth. While squid comprised 83% of the prey weight consumed by

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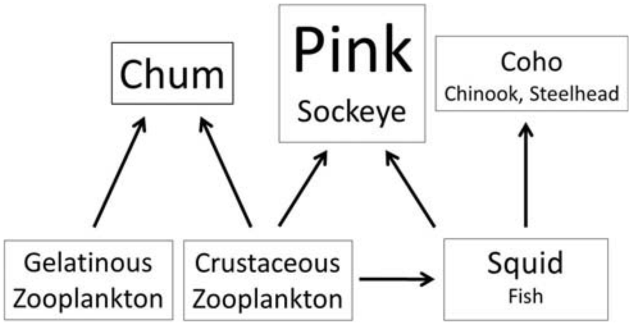

Fig. 1. Primary trophic connections between zooplankton and six species of maturing salmon in offshore waters of the Gulf of Alaska (modified from Aydin 2000).

maturing coho salmon, their contribution to digestible calories was even greater (93%), after accounting for their high caloric density and digestibility (Davis et al. 1998).

Although its rapid early growth rate and small size at maturity have led most investigators to conclude that *B. anonychus* has a 1-year lifespan (Nesis 1997; Katugin et al. 2005; Drobny et al. 2008), Jorgensen (2011) presents compelling evidence for a 2-year lifespan based upon a consistent biennial cycle (over a 19-year period) in abundance of paralarvae in the northwestern GOA that was correlated with abundance of pink salmon. Pink salmon, which also have a 2-year lifespan, have increased in abundance in odd years while even-year returns have remained more stable (Fig. 2A).

Average weight of troll-caught coho salmon in Southeast Alaska shifted from odd-year to even-year dominance in 1982–1983 (Fig. 2B), two cycles after an opposite shift in cyclic dominance in the commercial catch of pink salmon populations in the GOA (Fig. 2A). Coho salmon averaged 5.4% larger in odd years during the first decade of the 45-year series (1970–1979) but 14.1% smaller during 2005–2014. While average weight in odd years declined from a peak of 3.64 kg in 1977 to 2.45–2.60 kg in 2011–2013, even-year weights have remained more stable, increasing from a 1970s average of 3.07 kg to a peak in 1984–1988 (average 3.55 kg) followed by a stable trend (average 3.20 kg) during 1990–2010, before dropping abruptly to 2.69–2.93 kg in 2012–2014.

Climatic variability may also be important for growth of coho salmon, either through temperature mediated effects on growth or food web effects on prey (Aydin et al. 2005; Beauchamp 2009). Studies of covariation between coho salmon length and ocean environmental variables have generally found poor correlation in Alaska populations at time lags considered to be most important (Hobday and Boehlert 2001; Wells et al. 2006). However, Wells et al. (2008) observed a direct positive relationship between growth and the Aleutian Low Pressure Index (ALPI) in a Southeast Alaska population of Chinook salmon, a species with an offshore diet comprised primarily of squid (similar to coho salmon; Kaeriyama et al. 2004). Intensification of the Aleutian Low, and associated positive phase in the related Pacific Decadal Oscillation (PDO) index, has been shown to be potentially important to growth and survival in early stages in GOA fish populations, through increased phytoplankton and zooplankton production (Brodeur and Ware 1992), potentially as a result of shallowing of the mixed layer (Polovina et al. 1995). In addition, the same climatic pattern is also thought to have an important positive effect on transport by currents and subsequent survival of larvae of some marine fish species (Bailey and Picquelle 2002). Although less studied, atmospheric forcing may similarly affect growth and survival of cephalopod larvae.

Review of literature on offshore salmon feeding ecology and climatic effects on salmon growth led us to hypothesize that the observed history of average adult weight (Fig. 2B) was influenced by availability of maturing squid, which we hypothesized was influenced by bottom-up climate-related processes controlling squid recruitment and by direct competition for squid by pink salmon. However, initial exploration

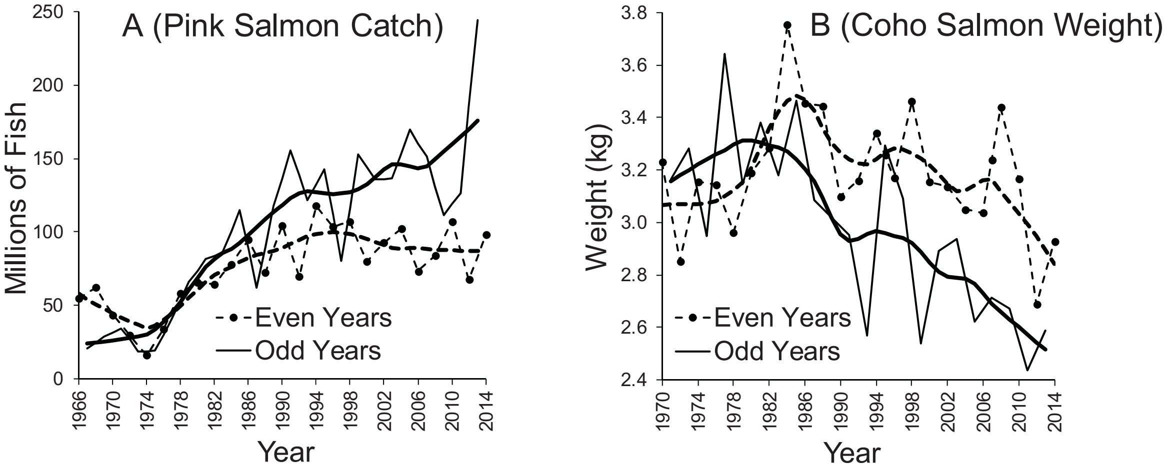

Fig. 2. Commercial catch of pink salmon in North America (A—excluding the Aleutian Islands and Bering Sea) and the average dressed weight of troll-caught coho salmon in Southeast Alaska (B) in even and odd years with 0.3 LOESS trends. Data sources are shown in Table 1.

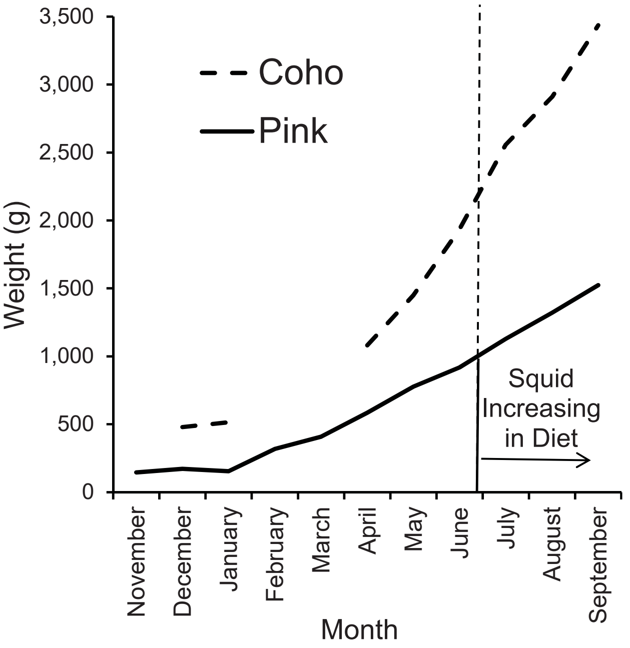

Fig. 3. Monthly average weight of coho and pink salmon during their final months at sea (Ishida et al. 1998) and the approximate threshold weight (1,000 g) for pink salmon to begin preying on maturing *Berryteuthis anonychus* (Aydin 2000; Davis 2003).

of the data produced regression models that were not parsimonious, indicating strongly contradictory relationships between even- and odd-year series. We observed that coho weight was positively correlated with the PDO Index in even years but not in odd years, while coho weight was negatively correlated with the catch of pink salmon in odd years but not in even years (Shaul et al. 2011). The need for a parsimonious explanation for coho weight, based on a consistent relationship with potential causal factors, led us to use multiple regression techniques to explore the hypothesis that pink salmon abundance and atmospheric forcing are both influential, but that the effects on coho growth are lagged. A lagged competitive relationship would be consistent with research findings pointing to an ontogenetic shift in the diet of maturing pink salmon from zooplankton to squid at a weight of about 1,000 g (Aydin 2000; Davis 2003), a size not achieved until late June, on average, after coho salmon have already fed for several months on the same prey cohort and have achieved nearly two-thirds of their final weight (Ishida et al. 1998; Fig. 3). The effect of this late transition in diet by pink salmon likely limits the effect on coho salmon growth of direct competition for the current-year squid cohort by the current-year pink salmon cohort, suggesting that the observed intensifying biennial cycle in coho size may reflect changes in prey populations that have developed over sequential generations.

We then extended the analysis to examine evidence for growth-related late-marine mortality through effects on marine survival, sex ratio, and per capita reproductive potential. Several studies have pointed to an early marine critical period for survival of coho salmon within the first weeks or months of marine residence (e.g. Holtby et al. 1990; Pearcy 1992; Beamish et al. 2004). However, evidence of such a period has remained elusive in studies of growth and survival of coho salmon in Southeast Alaska, where indirect evidence has instead favored an important late period for growth and survival after juveniles leave coastal waters late in their first summer at sea. Hobday and Boehlert (2001) found that environmental conditions when adults were returning explained more variance in survival of Alaska populations compared with the first season at sea. In northern Southeast Alaska, LaCroix et al. (2009) found no relationship between indices of juvenile coho salmon size, condition, abundance, or biophysical variables and subsequent marine survival and harvest. Although marine survival of adult pink salmon and age-.0 jack coho salmon from Auke Creek was correlated with Southeast Alaska coastal ocean response metrics, adult coho salmon marine survival was not, suggesting that different factors likely influence survival of adults beyond their seaward migration phase (Orsi et al. 2013). The biennial cycle in size of adult coho salmon was not evident in juveniles on 24 July, after approximately 2 months at sea (LaCroix et al. 2009), indicating that the difference in apparent growth likely occurs in offshore waters. Scale growth of Auke Creek adults also indicates that size-at-maturity is determined in the offshore GOA and is not significantly influenced by growth in early-marine or strait habitats (Briscoe 2004).

Findings from these studies led us to extend the analysis from a single growth-related response variable (adult size) to explore relationships with survival-related response variables including marine survival, sex ratio, and the per capita reproductive capacity of a coho salmon population. We tested the set of predictive variables that best explained adult coho weight with growth and survival-related response variables specific to the Berners River in Southeast Alaska. We also examined relationships between growth-related and survival-related variables for evidence of growth-related late-marine mortality to further test the hypothesis that there exists an important growth-related late-marine period for survival.

METHODS

In the first stage of the analysis, multiple regression models were constructed to explore relationships between adult coho salmon weight (1970–2014) and potential explanatory variables at various lags to test our hypothesis that variation in coho weight can be explained by lagged effects of climatic variation and top-down control on squid prey populations. Software used to run the analysis was R (version 3.2.3) (R Core Team 2015).

Data Sources

Response variables used in the analysis were obtained from two sources, (a) commercial catch data showing the av-

Table 1. Description of explanatory and response variables and data sources.

Explanatory variables	Description/Source
Pacific Decadal Oscillation (PDO) index	April-March average of monthly PDO index values ending in the year of maturity for coho salmon. The monthly data series is maintained by Nate Mantua (University of Washington): http://research.jisao.washington.edu/pdo/PDO.latest
Commercial catch of pink and sockeye salmon	Commercial catch by species in North America (excluding NPAFC area W-AK, the Aleutian Islands and Bering Sea) in metric tons; 1964–2011 data are available in Irvine et al. (2012); 2012–2014 catches for Canada, Washington and Oregon were downloaded as a statistical data file from the NPAFC: www.npafc.org/new/science_statistics.html Alaska catches in 2012–2014 (excluding the Aleutian Islands and Bering Sea) were provided by Kurt Iverson, Alaska Department of Fish and Game, Commercial Fisheries Division, Juneau.
Response variables	**Description/Source**
Coho weight	The weekly total weight of head-on, gutted coho salmon landed by the Southeast Alaska troll fishery divided by the number of fish reported in the landings. Weekly average weights were averaged over a period of 11 statistical weeks (weeks 28-38) from early July to mid-September. Data were accessed from the catch data base using the Alaska Department of Fish and Game's ALEX program and are reported by Shaul et al. (in press).
Adult length	Average mid-eye to fork length of male and female age-.1 coho salmon spawners in the Berners River estimated prior to the gillnet fishery. (Shaul et al. in press).
Sex ratio	Number of females-per-male estimated prior to the gillnet fishery. (Shaul et al. in press).
Marine survival	Total return (harvest plus escapement) of age-.1 coho coho salmon returning to the Berners River divided by the number of smolts emigrating in the prior year. (Shaul et al. in press).
Egg biomass per female	Average egg biomass of female Berners River coho salmon (prior to the gillnet fishery) based on an estimated relationship between female length and egg biomass reported by Fleming and Gross (1990) and Shaul et al. (in press).
Per Capita Egg Biomass (PCEB)	Estimated egg biomass per female Berners River coho salmon multiplied by the estimated proportion of females in the population prior to the gillnet fishery. (Shaul et al. in press).

erage weight of troll-caught coho salmon in Southeast Alaska during 1970–2014 and (b) growth and survival-related variables specific to the Berners River population for adult returns in 1990–2014 (Table 1; Shaul et al. in press).

Coho weight was calculated by dividing the weight of head-on, gutted coho salmon landed by the Southeast Alaska troll fishery by the associated number of fish reported on sales slips. There is a seasonal trend of increasing average weight, as well as substantial inter-annual variation in the temporal distribution of the troll catch (Shaul et al. 2011). Therefore, average weight was calculated weekly and averaged across 11 statistical weeks (weeks 28–38), spanning a period from early July through mid-September, in order to obtain a temporally stable measure of average coho salmon weight in coastal waters.

Marine survival and the size and sex composition of age-.1 returning adults were estimated annually for 1990–2014 adult coho salmon returns to the Berners River, located 65 km north of Juneau, Alaska (Shaul et al. in press). A target sample of 600 spawners was captured from upper river pools using a 13.7-m beach seine and sampled for age, sex, and mid-eye to fork (MEF) length. Returns to the Berners River are comprised almost entirely of age-.1 adults that have spent one year at sea, with age-.0 jacks being rare. Marine survival was estimated by dividing the total age-.1 adult return (combined catch and spawning escapement estimates) by the estimated smolt migration in the prior year.

Returning fish are exploited intensively by two major fisheries, including a troll fishery in outer coastal waters and passages, and a gillnet fishery conducted near the river. In order to account for size selection in the latter fishery, we reconstructed the pre-fishery length distribution and computed average length (following Kendall and Quinn 2012), using length measurements from an average of 339 coded-wire tagged Berners River fish sampled annually from the catch. Sex was not determined for the catch, so estimation of the effect of the harvest on the sex ratio required an assumption that fish of the same length were equally vulnerable to the fishery, independent of sex.

Per capita reproductive potential was assumed to be proportionate to the per capita egg biomass (PCEB). We used an average relationship between egg biomass (*EB*) and female length from two British Columbia coastal streams, Mamquam River and Tenderfoot Creek (Fleming and Gross 1990). Letting *MEF* denote the mid-eye to fork length (mm), the following is the conversion relationship applied to females in the Berners River:

$$EB = 2.33 \times 10^{-7}[MEF]^{3.39}.$$

Estimates of egg biomass for individual females were averaged and multiplied by the proportion of females in the adult population to estimate PCEB, which was then converted to a PCEB index by dividing the annual value by the average for all 25 years.

Explanatory variables included the commercial catch of pink and sockeye salmon (in metric tons) as a measure of the biomass of maturing salmon (Table 1) and, by inference, the potential for each species to influence availability of squid prey for coho salmon. Biomass of the catch was selected over numerical abundance as an explanatory variable because biomass includes elements of both abundance and size. Evidence of a strong positive relationship between the individual size of pink and sockeye salmon and the amount of squid in their diet (Aydin 2000; Davis 2003) suggests that total biomass is a more accurate measure of the potential for both species to influence squid prey populations of importance to coho salmon. Salmon biomass variables tested included separate values for pink and sockeye salmon, as well as the combined biomass of both species. We used the combined commercial catch in North America, excluding fishing areas in the Aleutian Islands and Bering Sea, with the objective of indexing the biomass of pink and sockeye salmon maturing primarily within the GOA.

North Pacific climate was represented by a single variable, the 12-month (April–March) average monthly PDO index ending in the coho salmon catch year. This period was targeted to encompass the period of hatching and development for *B. anonychus*, based on the occurrence of new paralarvae in the northern GOA beginning in April and assuming a 2-year lifespan (Jorgensen 2011).

Models

Multiple regression analysis was used to explore relationships between coho salmon weight, as the response variable, and the PDO index and pink and sockeye salmon catches at various lags ranging from 0 to 6 years from the catch year for adult coho salmon. Each predictive series was tested for obvious autocorrelation structure using conventional time-series analysis tools, including calculating the sample autocorrelations and partial autocorrelations out to at least 12 lags. Cross-correlation values were generated between the coho weight series and each of the other variables to see at which lags the variables might be most useful for predicting dependent variables. In cases with correlation at more than one lag, we considered averages across lags to develop new explanatory variables. We tested models that included sockeye salmon catch as a separate variable from pink salmon catch, as well as the pooled catch of both species under the assumption of an equal effect (per unit of weight) on the prey species of interest. Each predictive time series was standardized (the mean of the values actually used in the regression relationship was subtracted and the result was divided by the sample standard deviation). Model residuals were tested for autocorrelation using a Durbin-Watson test and by examining the sample autocorrelations. Models were ranked in order with the change in Akaike Information Criterion differences (ΔAIC; Burnham and Anderson 1992). Models with ΔAIC ≤ 2 were considered to have equivalent support.

We tested the combination of predictive variables for coho weight with the lowest ΔAIC score in models explaining adult length, sex ratio, PCEB index, and marine survival for the Berners River population. Multiple regression models were developed for length of adults of each sex and the mean-average of both sexes prior to exposure to the gillnet fishery. Additional models were developed for marine survival, ratio of females-to-males, and the PCEB index. Single-variable regression models were also used to explore relationships between the catch of pink salmon and variables representing adult length, sex ratio, PCEB index, and marine survival for the Berners River population, as well as relationships among growth and survival-related variables. Additionally, these variables were also differenced so as to show the relationship between pink salmon biomass and the year-to-year change in adult length, sex ratio, PCEB index, and marine survival for the Berners River population. Relationships among response variables were plotted and examined separately for the second half of the series (2002–2014), which occurred after a shift to a cooler North Pacific climate (Peterson and Schwing 2003).

We rearranged the top-ranked predictive model for coho weight to examine the effects of salmon biomass separately from climate, and to estimate a climate-based

Table 2. Model selection statistics for analyses of hypotheses for average weight of troll-caught coho salmon, 1970–2014. Terms in the hypotheses are the commercial catch of pink salmon or pink and sockeye salmon combined (in millions of fish) and the April–March average monthly Pacific Decadal Oscillation (PDO) index ending in the coho salmon return year. The independent variables are lagged from 0 to 4 years (denoted 0, -2 or -4). Models are ranked by the Akiaike Information Criterion differences (ΔAIC). Models with ΔAIC ≤ 4 are listed, with the best model shown at the top.

Hypothesis	Coefficient weights		R^2	Adjusted R^2	ΔAIC
	Salmon	PDO			
Pink (average -2, -4) + PDO (average 0, -2, -4)	0.508	0.492	0.646	0.629	0.00
Pink & Sockeye (average -2, -4) + PDO (average 0, -2, -4)	0.483	0.517	0.644	0.627	0.29
Pink (-2) + Pink (-4) + PDO (average 0, -2, -4)	0.522[a]	0.478	0.651	0.625	1.72
Pink & Sockeye (-2) + Pink & Sockeye (-4) + PDO (average 0, -2, -4)	0.497[a]	0.503	0.648	0.623	2.00
Pink & Sockeye (average 0, -2, -4) + PDO (average 0, -2, -4)	0.504	0.496	0.625	0.608	2.53
Pink (-2) + PDO (average 0, -2, -4)	0.494	0.506	0.618	0.600	3.38
Pink & Sockeye (-2) + PDO (average 0, -2, -4)	0.474	0.526	0.615	0.597	3.75
Pink (average 0, -2, -4) + PDO (average 0, -2, -4)	0.504	0.496	0.615	0.597	3.76

[a] Coefficient weights at specific lags are: Pink (-2): 0.329, Pink (-4): 0.193, Pink & Sockeye (-2): 0.312, Pink & Sockeye (-4): 0.185.

carrying capacity for the GOA to produce pink salmon for harvest, given an objective of maintaining a constant average coho salmon size. The regression model describing coho weight (*W*) as a function of the pink salmon catch biomass (*Pink*), the PDO index (*PDO*), and a random (uncorrelated) normally distributed error (ε), where b_1 and b_2 are respective variable coefficients and *c* is a constant, is shown as follows:

$$W = (b_1)\ Pink + (b_2)\ PDO + c + \varepsilon.$$

By ignoring the error and fixing coho weight (*W*) at a constant value (in this case the 45-year average of 3.09 kg), we can rearrange the model to estimate the capacity (*K*) of the GOA to produce pink salmon for harvest while achieving the coho weight target under observed climatic conditions (PDO index) associated with the same coho return year:

$$\hat{K} = \frac{3.09 - (b_2)\ PDO - c}{b_1}.$$

RESULTS

Coho Weight Model

Positive autocorrelation was detected in the data series at lags of 1, 2, 3, 4, and 6 years for pink salmon biomass, 1–5 years for sockeye salmon biomass, and 1–7 years for combined biomass of the two species, while the PDO index had significant positive autocorrelation only at lag 1. The best models explaining troll coho weight included salmon abundance and climate variables only in the current year and at lags in 2-year increments up to 4 years (Table 2). Diagnostics for the best models were generally acceptable, with no detected autocorrelation in the residuals (diagnostic checks included calculating the autocorrelation in the residuals out 12 lags, plotting the fitted variables against the residuals, examining Q-Q plots, looking for large leverage in the residuals, and calculating the Durbin-Watson statistics). Models that included salmon biomass or climate variables for the alternate biennial cycle (at lags of 1 or 3 years) ranked poorly, consistent with a 2-year life cycle in *B. anonychus* (Fig. 4). Models that included sockeye salmon as a variable separate from pink salmon did not rank high. Among the four top-ranked models considered to have equivalent support ($\Delta AIC \leq 2$), two that included the combined biomass of pink and sockeye salmon as a single variable ranked slightly below similar models that included only pink salmon. Highest ranked models consistently indicate a nearly even split in influence (regression coefficients) between salmon abundance and the PDO (Table 2). All highly-ranked models ($\Delta AIC \leq 4$) included the average PDO lagged at 0, 2, and 4 years. Salmon biomass was most influential at a lag of 2 years, followed by 4 years, while biomass at lag 0 was substantially less influential. The third highest ranked model included pink salmon biomass at separate lags of 2 and 4 years, with the lag 2 coefficient weight (0.329) comprising 63% of the total coefficient weight assigned to salmon (0.522) while the lag 4 coefficient weight (0.193) accounted for 37%. The top ranked model (hereafter this predictor set will be referred to as the Pink-PDO predictors) included the pink salmon catch biomass averaged over the two prior cycles (lag 2 and 4 years; Fig. 5). No significant autocorrelation was detected in the residuals for this model at lags of 1–15 years and the Durbin-Watson statistic was not significant ($p = 0.474$). Partial residual plots indicate a strong negative relationship with pink salmon biomass (Fig. 5C) and a strong positive relationship with the PDO index (Fig. 5D), with 1995 and 1999 appearing as principal outliers.

Climate-Based Capacity

PDO-based estimates of the climate-based capacity of the GOA to produce pink salmon biomass for harvest while maintaining a constant average target coho salmon weight (3.09 kg) are highly variable, ranging over an order of magnitude from a low of 24.1 thousand metric tons in 1976 to 245.7 thousand metric tons in 1998 (Fig. 6). The relationship between the estimated climate-based capacity ($\hat{K}$) for pink salmon harvest (in metric tons) at the 3.09 kg

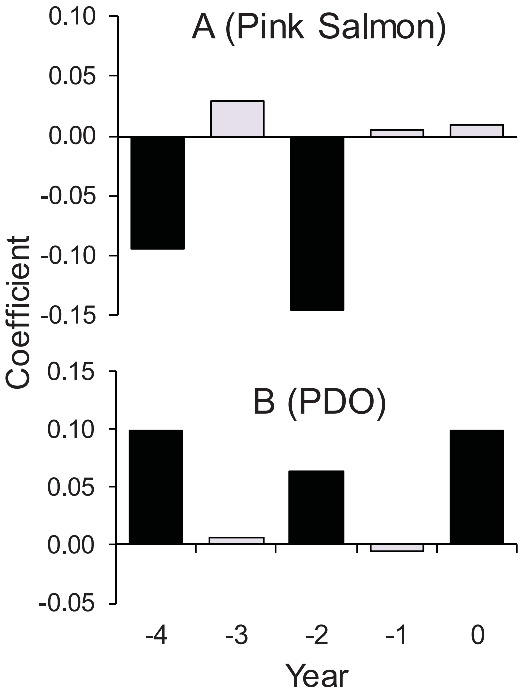

Fig. 4. Annual predictive variable coefficients for coho weight, including (A) pink salmon catch biomass and (B) PDO fitted at lags from 0 to 4 years in a regression model with 10 variables (5 lags each for pink salmon and PDO). Years that were averaged for the respective predictive variables in the top-ranked model (Table 2) are shaded black.

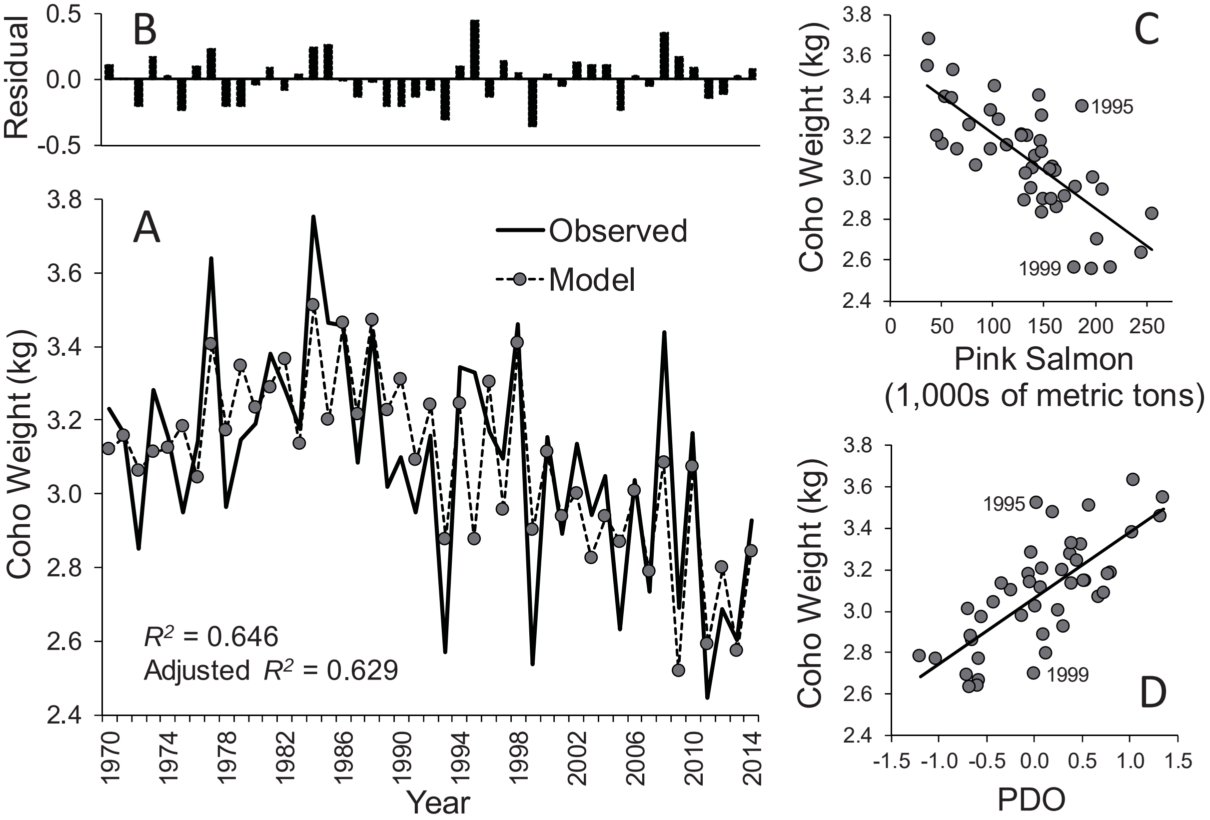

Fig. 5. Southeast Alaska troll-caught coho salmon average dressed weight compared with modeled weight (A) based on a multiple regression model with two variables: the standardized April–March PDO Index (average for lag 0, 2, and 4 years; 0.492 weighting based on the regression coefficient) and the standardized average commercial catch of pink salmon in North America (excluding the Bering Sea and Aleutian Islands) lagged by 2 and 4 years (0.508 weighting). The model residual is shown (B), as well as partial residual plots for pink salmon (C) and the PDO index (D).

target coho weight is shown by the following relationship with the PDO index:

$$\hat{K} = 86.928(PDO) + 128{,}066,$$

where K at a neutral (0) PDO index value is estimated at 128,066 metric tons, an amount that has been consistently equaled or exceeded by the lagging pink salmon catch biomass variable since 1987.

Although not significantly correlated over the full time series ($r = 0.264$; $p = 0.079$), pink salmon catch biomass and estimated climate-based capacity (i.e., scaled PDO index variable) showed strong positive correlation during 1970–1990 ($r = 0.809$; $p < 0.001$), with capacity exceeding catch biomass in all but 2 years. However, pink salmon biomass and estimated capacity were essentially uncorrelated in the subsequent period from 1991–2014 ($r = -0.148$; $p = 0.490$), as biomass remained high while the PDO index trended lower. This change was associated with a substantial (43%) increase in variation in annual coho weight (Fig. 5A). However, the model fit was consistent between the periods (Fig. 5B), with no meaningful change in the average residual between 1970–1990 (-0.014) and 1991–2014 (0.012), or in coefficients of variation (*CV*) in the residuals (0.164 and 0.188, respectively).

Climate-based capacity estimates based on the target coho weight were exceeded only a few times in even years and by modest percentages prior to 2012, when a series of low trailing PDO index values and substantial even-year pink salmon returns were associated with biomasses that exceeded capacity estimates by 102% in 2012 and 83% in 2014 (Fig. 6). Coho weight was the lowest on record for an even year in 2012, and third lowest in 2014 (Fig. 2). Since the early 1990s, differences between pink salmon biomass and estimated capacity have been greater in odd years as odd-year biomass transitioned from being consistently below estimated capacity during 1971–1991 (by an average of 26%) to consistently above capacity by an increasing margin since 1993 (158% in 2009, 205% in 2011, 364% in 2013; Fig. 6).

Adult Length

During 1982–2014, Berners River spawners of both sexes declined in length by an average of 1.6 mm/year for males and 1.1 mm/year for females (Fig. 7). Variation in length among spawners returning in the same year increased for both sexes. Males showed substantially greater intra-annual variation in length among individual spawners (average $CV = 0.109$) compared with females (average $CV = 0.059$) as well as greater in-

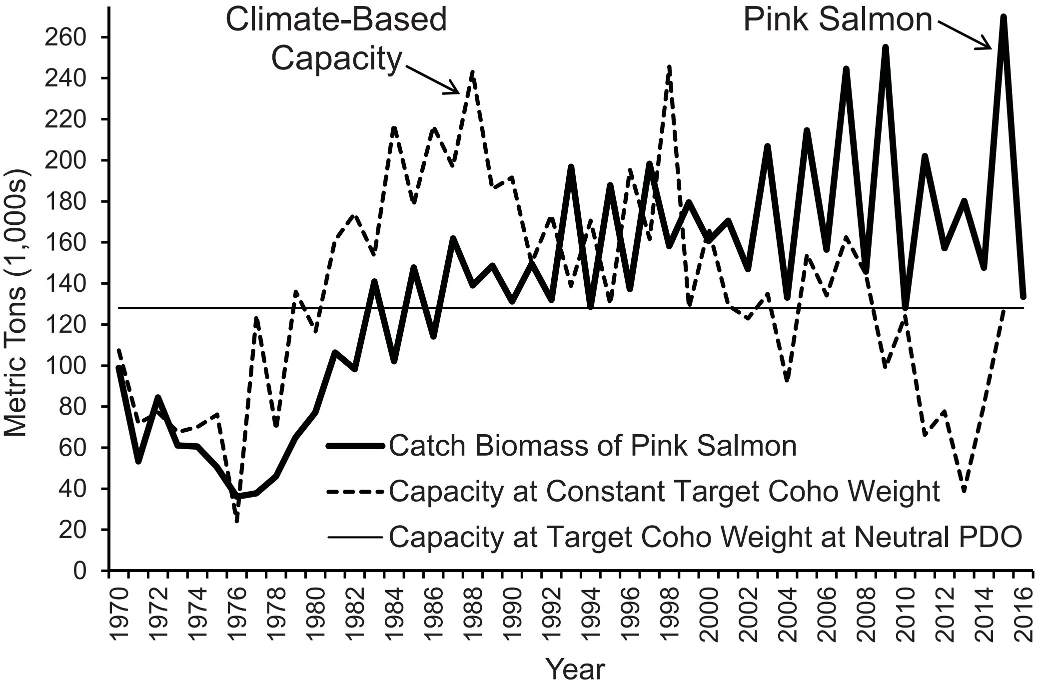

Fig. 6. Average Gulf of Alaska pink salmon catch in the preceding two cycles (lag 2, 4) compared with the estimated catch at a constant target coho salmon weight of 3.09 kg (45-year average) at both the trailing 3-cycle average PDO index (lag 0, 2, 4) and at a constant neutral PDO index. The PDO variable is converted to an estimate of the climate-based capacity of the Gulf of Alaska to produce pink salmon for harvest while also achieving a target coho salmon weight.

ter-annual variation in average length (*CV* = 0.044) compared with females (*CV* = 0.028). During 1998–2010, average length of both sexes became increasingly cyclical, declining in odd years while remaining relatively stable in even years until 2012, when even-year length decreased sharply.

The linear selection differential (LSD), the difference in average length before and after the gillnet fishery, averaged -12.3 mm for males and -3.7 mm for females during 1990–2014 (Shaul et al. in press). On average, the estimated effect of the gillnet fishery on the ratio of females-to-males was not meaningful, with the average ratio before and after the fishery decreasing from 0.80 to 0.75.

Relationships Between Population Variables

There was a moderate correlation between marine survival and adult length (Spearman's rho = 0.669, $p < 0.001$; Fig. 8A). The correlation between adult length and the ratio of females-to-males was lower, with greater variability in the female-to-male ratio at larger adult length (Fig. 8B). The correlation between marine survival and the female-to-male ratio was considerably lower, and did not reach statistical significance (Fig. 8C). The PCEB index, which has as factors both female length and the proportion of the adult population comprised of females, had a small to moderate correlation with marine survival (Fig. 8D).

The regression slope for the 2002–2014 length-survival relationship did not differ from the slope for the entire series (Fig. 8A), but recent relationships between length and sex ratio and between marine survival and PCEB index exhibit greater slope. Variation in the length-survival relationship decreased at smaller adult sizes, suggesting a more limited range of survivals for cohorts with slower growth, as a potential consequence of size-selective mortality (Fig. 8A).

During 1990–2014, there were important differences between even and odd years in the length of age-.1 adults, the female-to-male ratio, and the PCEB index (Fig. 9). Average marine survival estimates in odd years (14.6%) were not significantly different from even years (17.9%; $p = 0.157$). However, the relative survival of females (female-to-male ratio) was lower in odd years ($p = 0.012$) with a pre-gillnet female-to-male ratio of 0.71 compared with 0.88 in even years (assuming a 1:1 sex ratio in smolts; Spidle et al. 1998). The PCEB index was also significantly different, averaging 18% lower in odd years prior to the gillnet fishery ($p = 0.002$) and 23% lower in the spawning escapement ($p < 0.001$).

Pink Salmon and PDO Predictors

The Pink-PDO predictors consistently explained at least a moderate amount of the variation in average size of returning coho salmon of both sexes in 1990–2014 (Table 3; Fig. 9A). Results were consistent with troll weight (1970–2014) in indicating an approximately equal split between pink salmon biomass and climate (PDO) as factors influencing

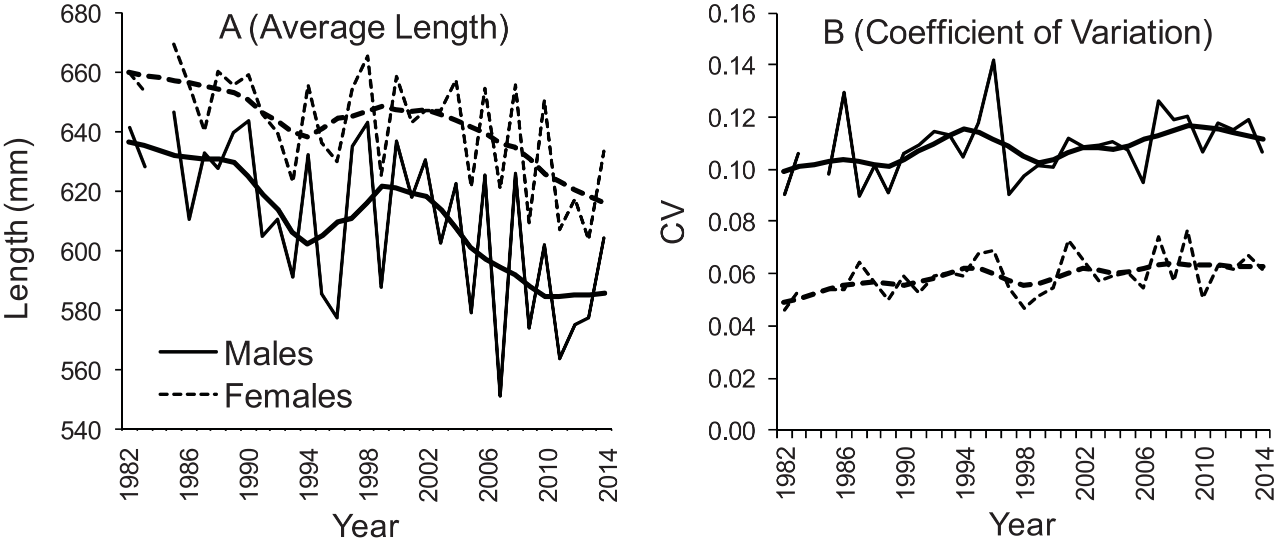

Fig. 7. Average mid-eye to fork length (A) and coefficient of variation of length (B) of age-.1 male and female coho salmon spawners in the Berners River with 0.3 LOESS trends (data are from Shaul et al. in press).

coho salmon size-at-maturity. The proportion of variation in size explained by the Pink-PDO predictors was lower for Berners River adults (0.508 for males and 0.610 for females) compared with troll weight (0.646).

Neither predictive variable was significant in models with the sex ratio of returning adults as the response variable (Table 3; Fig. 9B). The Pink-PDO predictors accounted for about a third of variation in the PCEB index for adults prior to the gillnet fishery ($R^2 = 0.356$) but the PDO variable missed statistical significance (Table 3; Fig. 9C). These predictors also explained over a third of the variation in marine survival ($R^2 = 0.378$; Fig. 9D) but the coefficient of the PDO again failed to reach statistical significance.

Although the pink salmon variable that best predicted adult size (average lags 2 and 4) did not explain a significant amount of the variation in the sex ratio (Fig. 10A), there was a small-to-moderate negative correlation with the PCEB index (Fig. 10C). However, pink salmon biomass showed a moderate-to-strong negative correlation with year-over-year change in both the sex ratio (Figs. 10B, 11A) and the PCEB index (Figs. 10D, 11B).

While pink salmon biomass alone was negatively correlated with marine survival, explaining about a third of variation ($R^2 = 0.332$; Fig. 10E), significant autocorrelation was detected in the residuals at lag 1 and the Durbin-Watson statistic was significant ($p = 0.029$). In other words, although there is an obvious negative correlation between marine survival and pink salmon biomass, we are not able to produce a good predictive model for marine survival. However, a proportion of the difference, or year-to-year change, in the marine survival rate was explained by pink salmon biomass with acceptable model diagnostics ($R^2 = 0.376$; Figs. 10F, 11C).

Results of studies conducted at Auke Creek and in nearby waters have led to the hypothesis that abundant wild pink salmon and hatchery chum and pink salmon juveniles have a positive effect on coho survival by providing food or a "predation shelter" (Briscoe 2004; LaCroix et al. 2009), indicating a potential countervailing positive effect at lag 0 that, combined with biennially autocorrelated pink salmon returns, might offset a negative influence on late-marine growth at lags 2 and 4. We examined similar early marine predictor variables for Berners River coho salmon survival, including (a) the number of fish harvested in four local commercial fishing districts (111, 112, 114 and 115) where pink salmon are likely to intermingle as juveniles with Berners River coho salmon, and (b) combined releases of pink and chum fry by the local DIPAC (Douglas Island Pink and Chum) hatchery. However, regression results did not support a positive interaction, either with predominantly wild pink salmon ($r = -0.072$; $p = 0.733$) or with combined releases of pink and chum salmon in the common sea-entry year ($r = -0.078$; $p = 0.713$). In contrast with the lagged GOA pink salmon catch (pink-PDO predictors), the un-lagged pink salmon catch in local districts did not explain much variation in the year-to-year change in marine survival ($R^2 = 0.033$). The same was true for the un-lagged GOA pink salmon catch.

DISCUSSION

Coho Weight Model

The Pink-PDO predictors explain a substantial amount (65%) of the variation in Southeast Alaska coho salmon weight over a 45-year period spanning both warm and cold North Pacific regimes. Because the predictors were standardized, the estimated regression parameters are compara-

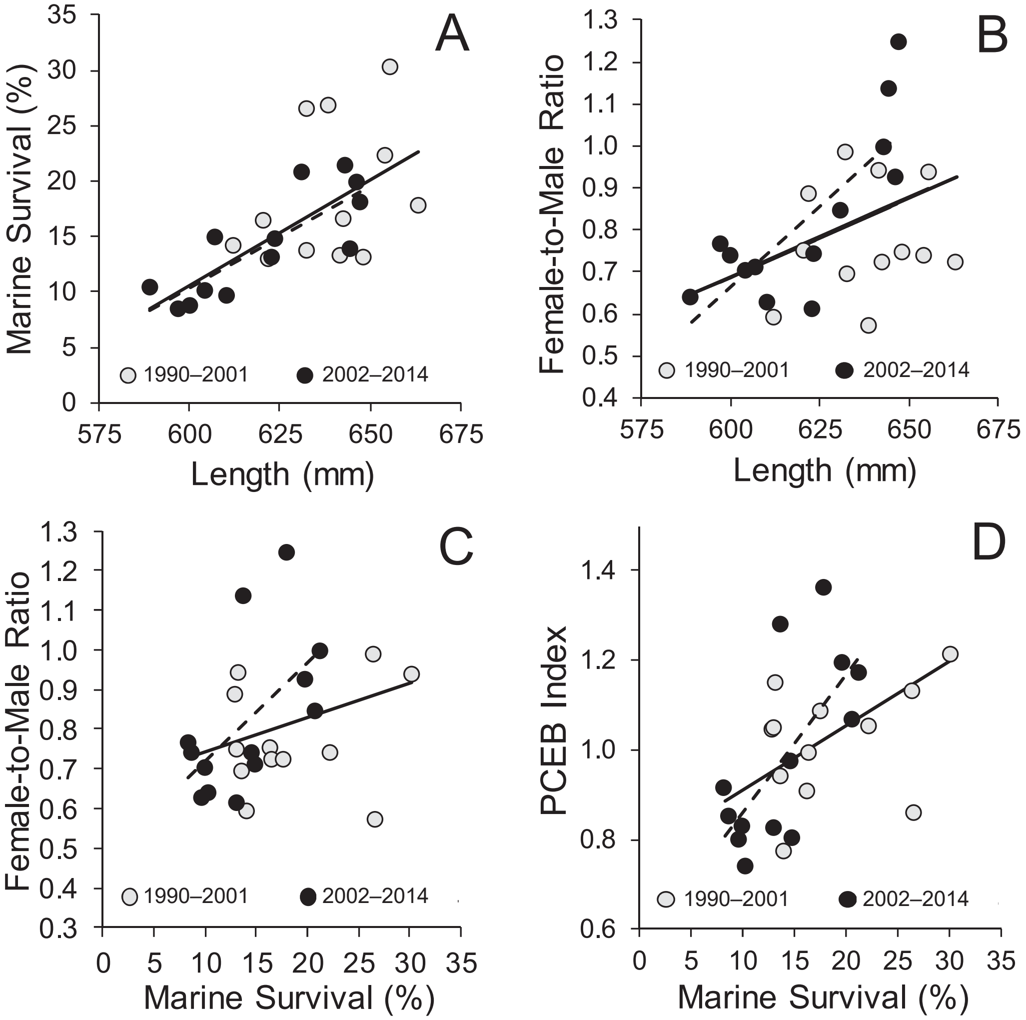

Fig. 8. Regression relationships for age-.1 Berners River coho salmon: marine survival *vs.* length (A), sex ratio *vs.* length (B), sex ratio *vs.* marine survival (C), and PCEB index *vs.* marine survival (D). Earlier years (1990-2001) are shown with gray dots and later years (2002–2014) with black dots. Linear relationships for the entire data series are shown with solid lines while relationships for 2002-2014 only are indicated with dashed lines. Length, sex ratio and PCEB index values are estimated prior to the gillnet fishery and length values are the mean-average for both sexes. Spearman's rho correlations are significant ($p \leq 0.05$) for all relationships except for sex ratio *vs.* survival for the full data series (1990–2014). Note: sex ratio (C) and the PCEB index (D) include elements of survival and are, therefore, not entirely independent from marine survival.

ble, with approximately equal weighting indicated for top-down control (0.508) and climate (0.492) variables targeted at squid recruitment and survival. Our results are in strong agreement with Jorgensen's (2011) hypothesized 2-year lifespan for *B. anonychus*, as well as our hypothesis that coho salmon size reflects a lagged response by reproductively isolated even- and odd-year populations of *B. anonychus* to variable intensity of top-down control by pink salmon. The most likely explanation for the lagged response (Fig. 4) is a related delay in predation on maturing squid by maturing pink salmon that limits the effect on coho salmon growth of direct competition for the current prey cohort. Pink salmon appear to influence coho salmon growth primarily through predation on the parents and grandparents of the current squid cohort, with the parent generation being most important (accounting for 63% of the combined pink salmon coefficients).

One obvious criticism of our approach is that both the predictive and response variables contain autocorrelation. The important effect of this is to potentially produce misleading error rates in statistical hypothesis tests of zero correlation (e.g., Pyper and Peterman 1998). However, our intent was never to simply test the hypothesis that there was zero correlation between any two variables. Rather, we were looking for consistent relationships between coho salmon size and environmental and competition metrics—consistent over a period of improving environment (from 1970 to the early 1990s) and a period of declining environment (mid-1990s to the present, Fig. 6). We did not attempt to adjust error rates or *p*-values, but rather we were guided by the notion that we were especially skeptical of any hypothesis tests that were not highly significant using conventional *p*-value calculations. In the end, we found essentially the same Pink-PDO predictor signal in different measures of coho size, and coho size consistently trended upwards with increases the PDO metric and downwards with increases in the pink salmon metric, in a way that was consistent along both even- and odd-year lines.

The two predominant outlying years when coho salmon weighed substantially more (1995) and less (1999) than indicated by the model (Fig. 5) occurred during a period when salmon were sampled in July in the offshore GOA from the research vessel *Oshoro maru*. Neither outlier is evident in average coho salmon length reported by Kaeriyama et al. (2004) which was more closely correlated with modeled Southeast Alaska coho weight ($r = 0.844$) than with observed weight ($r = 0.444$; Fig. 12), suggesting that growth of mature adults may have been heavily influenced by food availability in geographic areas not sampled during the cruises, likely including the coastal forage fish community which continues to support growth of maturing coho salmon after they arrive in coastal fishing areas. The strong correlation with offshore size provides further support for the hypothesis that the Pink-PDO predictive variables in the Southeast Alaska coho weight model represent the principal climatic and top-down factors affecting *B. anonychus*, the dominant prey species in the diet of fish in the offshore sample (Kaeriyama et al. 2004).

Late Marine Effects

Studies in northern Southeast Alaska have generally failed to support an early-marine critical period for growth and survival of coho salmon in that region and have instead pointed toward an important late-marine period after juveniles leave coastal waters late in their first summer at sea (Briscoe 2004; LaCroix et al. 2009; Orsi et al. 2013). Our results are consistent with these studies in a number of ways. Our predictive model explains the majority of variation in adult size with variables targeted at recruitment of the predominant prey species found in the offshore diet of coho salmon. This finding is consistent with research on coho

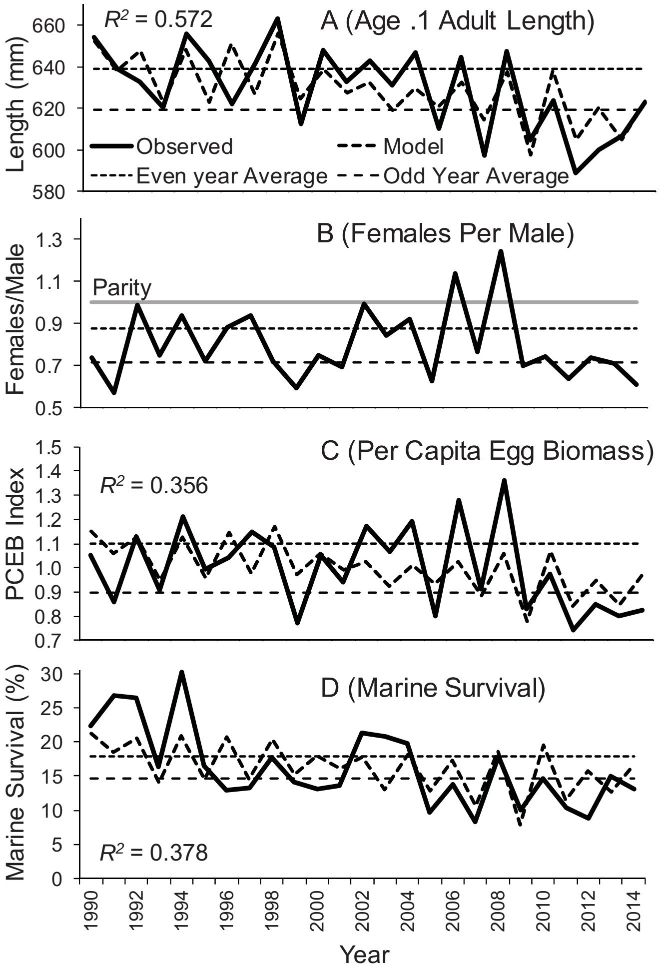

Fig. 9. Average adult length (males and females averaged), females per male, per capita egg biomass (PCEB) index, and marine survival rate of age-.1 Berners River coho salmon. All response variables are prior to exposure to the drift gillnet fishery. Also shown are even- and odd-year averages and significant fits ($p \leq 0.05$) for combined Pink-PDO predictors. Differences between even- and odd-year averages were significant ($p \leq 0.05$) for length, sex ratio, and PCEB index but not for marine survival.

Table 3. Coefficient weights (with 95% confidence intervals), R^2 and adjusted R^2 values, and variable p values for multiple regression models correlating adult size, sex ratio, marine survival, and predicted egg biomass per adult (PCEB index) with the catch of pink salmon in North America (excluding Bering Sea-Aleutian Islands areas) averaged for lags of 2 and 4 years, and the Pacific Decadal Oscillation (average for lags of 0, 2, and 4 years). Variables that are not significant ($p > 0.05$) are marked with an asterisk.

Response variable	Pink salmon			PDO			R^2	Adjusted R^2
	p	Coefficient Weight (C.I.)		*p*	Coefficient Weight (C.I.)			
Troll weight (1970–2014)	<0.001	0.508	(0.363–0.653)	<0.001	0.492	(0.347–0.637)	0.646	0.629
Berners River (1990–2014):								
Length (Males)	0.004	0.536	(0.192–0.880)	0.010	0.464	(0.120–0.808)	0.508	0.463
Length (Females)	0.003	0.454	(0.174–0.734)	0.001	0.546	(0.266–0.826)	0.610	0.574
Length (Average)	0.002	0.501	(0.199–0.803)	0.002	0.499	(0.197–0.801)	0.572	0.533
Females per male	0.151*	0.691	(-0.272–1.654)	0.513*	0.309	(-0.654–1.272)	0.126	0.047
PCEB index	0.027	0.539	(0.069–1.009)	0.054*	0.461	(-0.009–0.931)	0.356	0.298
Marine survival	0.005	0.709	(0.235–1.182)	0.215*	0.291	(-0.182–0.765)	0.378	0.321

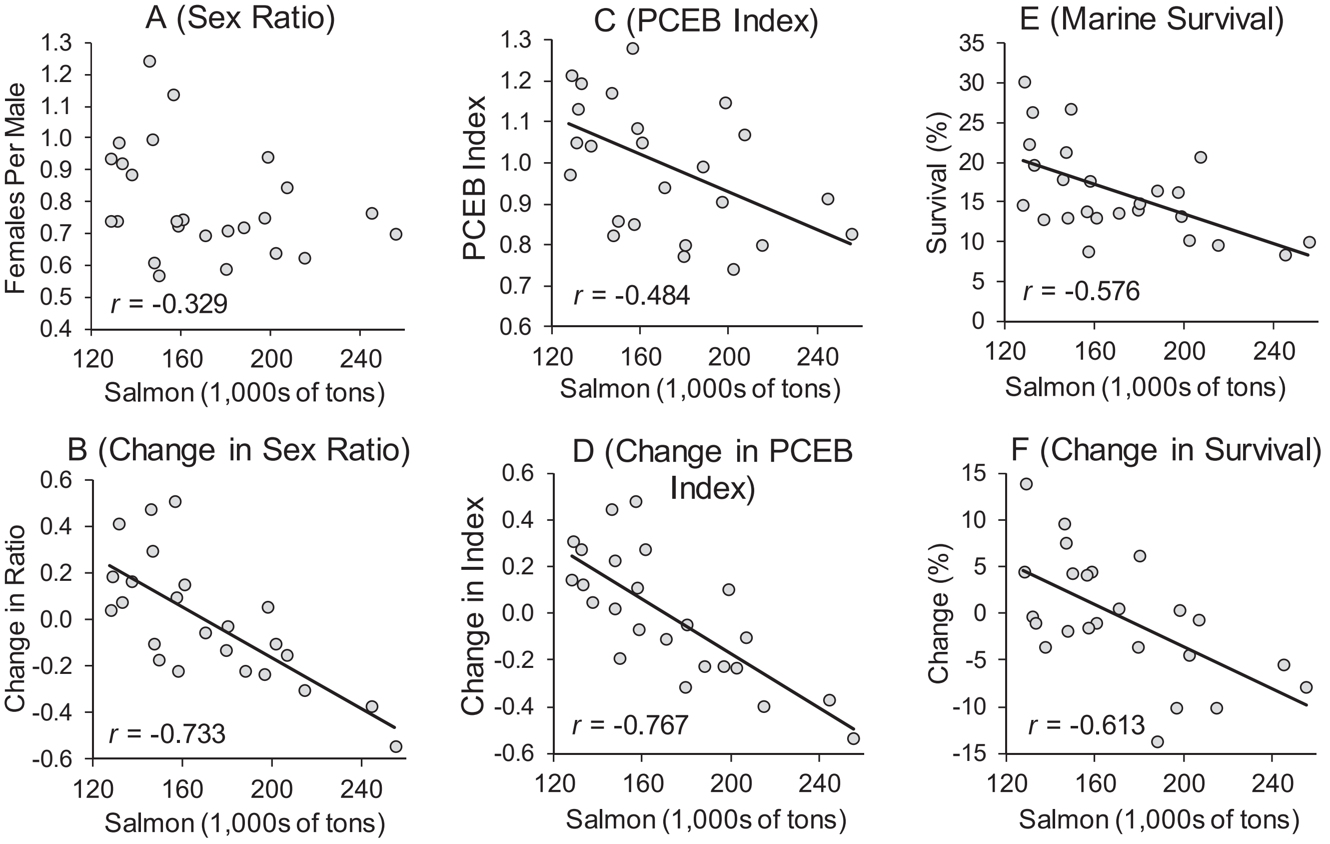

Fig. 10. Relationship between the average pink salmon harvest (lag 2 and 4 years) and the sex ratio (females per male; A), the year-over-year change in sex ratio (B), the PCEB index (C), the change in the PCEB index (D), the marine survival rate (E), and the change in marine survival (F) for coho salmon returning to the Berners River, 1990–2014. Sex ratio and PCEB index values are prior to exposure to the drift gillnet fishery.

scale growth (Briscoe 2004) in indicating that adult size is influenced primarily by conditions encountered in offshore waters of the GOA.

The moderately strong positive correlation between marine survival and size of Berners River adults is, therefore, consistent with the hypothesis that overall survival in the ocean is related to late-marine growth. The evident decrease in variation in survival at smaller adult sizes (Fig. 8A) suggests that slower late-marine growth may reduce both average survival and the potential range of survival rates. This suggests that as the rate of growth slows in the offshore environment, growth-related late-marine mortality may become a proportionately more important influence on marine survival compared with other factors.

Our model indicates about half of the nearly two-thirds of variation in adult size explained by the coho weight model is attributed to the biomass of pink salmon in the GOA while the other half is attributed to climatic factors related to atmospheric forcing (measured by the PDO index). However, when the same Pink-PDO predictors from models explaining adult size were applied to survival-related response variables, only the pink salmon biomass variable showed a consistent statistically significant influence. For example, marine survival for the Berners River population was poorly explained by the Pink-PDO predictors that explain much of the variation in adult size. The model containing these variables together accounted for over a third of variation in marine survival ($R^2 = 0.378$) but the PDO coefficient was not significant. Although the pink salmon predictor alone was significant ($r = -0.576$; Fig. 10E), model diagnostics were poor with the variance of the residuals decreasing with increases in the predictor and with significant autocorrelation in the residuals. In contrast, a direct relationship with adult length explained somewhat more of the variation in marine survival and the model diagnostics were better. This may mean that variation related to late-ocean growth accounted for some of the variation in marine survival for the Berners River population, but that the link to the PDO and pink salmon is less direct. Potential countervailing effects (perhaps less growth-related) by the predictive variables on survival should be considered, however, we found no evidence of a positive relationship with indicators of abundance of pink salmon (or hatchery chum salmon) in near-shore environments.

The pink salmon catch (average for lags of 2 and 4 years) included in the pink-PDO predictors explained much of the year-to-year change in marine survival, sex ratio and PCEB index (with acceptable model diagnostics) suggesting that while trends in marine survival may be influenced by other factors, the biomass of pink salmon has an important effect on year-to-year variation in survival of coho salmon. We infer that the probable underlying mechanism is control of squid prey populations by pink salmon.

More recently (2002–2014), variables associated with growth were more strongly correlated with marine survival (Fig. 8). This suggests that growth-related late marine mortality may have increased in importance as a component of overall marine mortality and has become more sex-specific as adult size has continued to trend lower with increased inter-annual variation (Fig. 7A, 8B). Climate may also have been a factor in this change, as the earlier part of the series (1990–2001) occurred primarily during a warm North Pacific regime that appears to have ended in 1998 (Peterson and Schwing 2003). The return to a colder regime may have influenced both growth and survival of maturing coho salmon in a number of potential ways, including through changes in prey and predator abundance and distribution, and through temperature-related physiological processes.

Different populations of squid may be affected differently by top-down control and climate. Those migrating toward the shelf during summer months (Bower et al. 2002) face an increasing density of increasingly effective predators as growing and maturing salmon concentrate in the northern gulf during their return to coastal streams and hatcheries. A highly regular biennial cycle in *B. anonychus* in the northwestern GOA, with odd-year peaks in paralarvae density averaging over 20 times off-peak density in 1991–2009 (Jorgensen 2011), is consistent with an even-year dominant pattern in the stomach contents index (SCI) of coho salmon in the Alaska Gyre in 1994–2000, but inconsistent with an opposite odd-year dominant pattern in the SCI index to the south in the Subarctic Current (Kaeriyama et al. 2004). Increased variation in size among maturing coho salmon and evidence of a proportionately greater decline in adult size in less migratory fish (Shaul et al. 2011) is consistent with a change in the spatial distribution of squid prey in favor of the more distant Subarctic Current over more northern areas. We hypothesize that the typically high abundance of *B. anonychus* reported in salmon diets in the Subarctic Current, including in odd-numbered years, includes distinct populations that are less exposed to the gauntlet of maturing salmon compared with populations that spawn near the shelf.

A higher female-to-male ratio among coho salmon returning in even years and a moderate positive correlation between this ratio and average length at maturity (Fig. 8B) are consistent with the hypothesis of increased risk-taking by female coho salmon nearing maturity and in poor feeding conditions (Holtby and Healey 1990) and with an apparent strong even-year dominant cycle in mature *B. anonychus* in the northern gulf (Jorgensen 2011). Aydin et al. (2005) observed that, while pink and sockeye salmon switch diets from squid to zooplankton as they move northward from the Subarctic Current, coho salmon appear to consume little during this migration before reaching abundant forage fish populations near the coast. In odd years, females that may have benefited from abundant forage in the relatively squid-rich Subarctic Current must still cross an increasingly prey-barren expanse of water during their northward migration, potentially inducing them to take increased risk through energy expenditure and exposure to predators in pursuit of food. An increase in correlation between the sex ratio and length and marine survival after 2001 (Fig. 8) suggests that the spatial and temporal distribution of coho salmon mortality, and potentially the underlying mechanisms, may have changed during the study period.

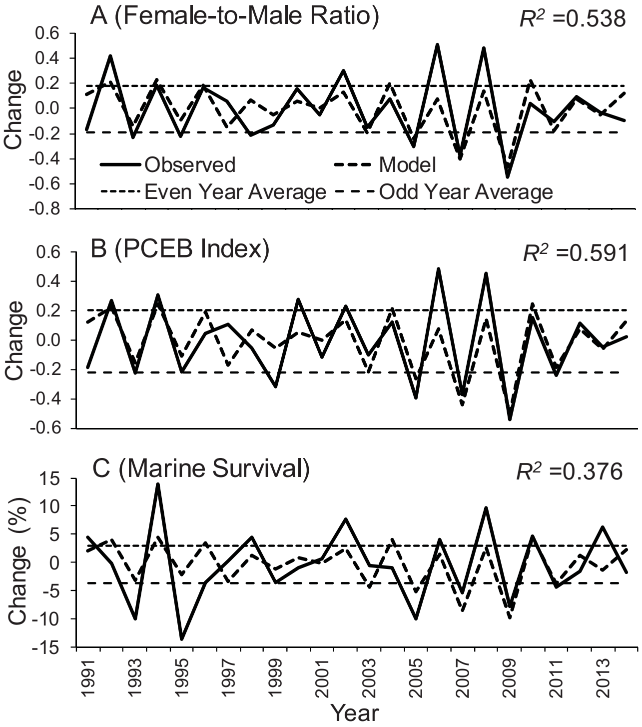

Fig. 11. Year-over-year change in the sex ratio, PCEB index, and marine survival rate for Berners River coho salmon compared with the modeled change based on the average pink salmon catch (lag 2 and 4 years).

Fishery managers should note that variation in factors affecting late-ocean growth and survival tends to magnify variation in effective spawning escapement. That is, our results show that the usual assumption of stable per capita reproductive capacity is simply wrong. Variation in the PCEB index of the Berners River spawning escapement was substantial (range 0.74–1.39). That means that a typical measured or nominal escapement of 12,000 spawners could represent a potential effective escapement ranging from 8,900–16,700 spawners. Spawner-recruit analysis used to establish escapement goals may be improved by accounting for such variation and the associated variation in marine survival (Fig. 8D). That is, low adult returns lead to potentially low nominal escapement, and this condition will likely coincide with even lower effective spawning escapement, and *vice versa*.

Other studies have pointed to increased growth-related late-marine mortality related to competition for prey with

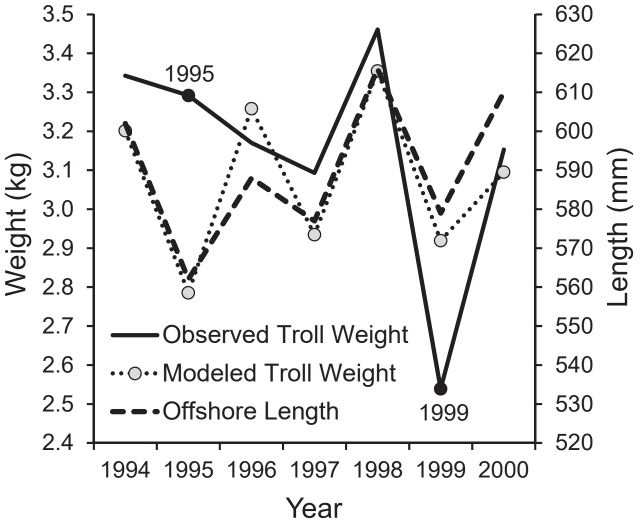

Fig. 12. Observed and modeled average weight of troll-caught coho salmon (with 1995 and 1999 outliers indicated; see Fig. 5) compared with average fork length of fish sampled at offshore stations along longitude 145°W (Kaeriyama et al. 2004).

pink salmon. Ruggerone et al. (2003, 2005) and Ruggerone and Connors (2015) presented evidence indicating that growth and survival of sockeye salmon returning to Bristol Bay and the Fraser River, respectively, was reduced by a competitive interaction with pink salmon occurring primarily in the second year at sea. The reduction in apparent growth in odd years for Bristol Bay sockeye salmon occurred in summer after highly abundant Russian pink salmon populations had migrated to coastal areas, an effect that may have been reinforced by a biennial cycle in prey, including squid (Ruggerone et al. 2005; Ruggerone and Connors 2015).

Wide-spread declines in abundance of Chinook salmon populations have occurred throughout Alaska since 2007 (ADF&G 2013) concurrent with consistent over-prediction by sibling-based forecast models for stocks contributing to Southeast Alaska fisheries (CTC 2014). Broad declines since the early 1980s have been documented in size-at-age and age-at-maturity of Alaska Chinook salmon populations (Kendall and Quinn 2011; Lewis et al. 2015). The steepest declines in size-at-age have occurred in older fish, primarily those that have spent four years at sea, while age-.2 fish have shown little change. A combination of decreasing size-at-age and decreasing age-at-maturity is unexpected, as Chinook salmon have been shown to delay maturity when growth is poor (Healy 1991; Wells et al. 2007).

As in coho salmon, the decrease in apparent growth and survival of Chinook salmon is potentially related to a decline in gonatid squids, which are typically the dominant prey of older Chinook salmon in offshore waters of the northeast and north-central Pacific and the Bering Sea (Davis 2003; Kaeriyama et al. 2004; Davis et al. 2009). Evidence pointing to an increase in late-ocean mortality as a factor in declines in Chinook salmon abundance since the mid-2000s is consistent with an increase since 2002 in the correlation between marine survival and size-at-maturity for Berners River coho salmon.

The timing and mechanisms underlying late-marine mortality remain unclear. While maturing squid (*B. anonychus*) have been found to comprise the majority of the summer diet of coho salmon above a weight of 500 g (Davis 2003), a size that is reached on average in January (Ishida et al. 1998), *B. anonychus* may also be important in the diet of coho salmon during winter months when growing squid are also smaller (Aydin 2000). If so, variation in growth-related mortality linked to squid abundance may begin during winter from a physiologically based process (Beamish and Mahnken 2001). Unfortunately, this hypothesis is difficult to assess because of a scarcity of information on the winter diet and condition of coho salmon in offshore waters.

Predation appears to be the most likely cause of mortality of maturing fish during summer. While females may take greater risks with predators when food is scarce because of their greater energy and growth requirement for successful reproduction (Holtby and Healey 1990), a substantial proportion of males may be motivated by similar pressures. The large amount of variation in size of age-.1 males appears to stem from disruptive selection associated with the option of two viable breeding strategies: stealth (satellite) or dominance (alpha; Healey and Prince 1998). The largest (as well as smallest) individuals returning to the Berners River are invariably males, suggesting that larger males have also expressed a willingness to trade survival for growth in order to be competitive as dominant spawners, even as a substantial proportion of males may pursue an opposite strategy in years of poor growth when a reduced female-to-male ratio likely enhances the advantage to middle-sized males of trading growth for survival, thereby accepting a stealth role over dominance in a more competitive breeding environment.

Specific mechanisms behind risk-taking as a cause of late-marine mortality are poorly understood but may include some combination of increased metabolic cost relative to reward and increased exposure to salmon predators while undertaking searching movements or while pursuing prey in the vicinity of "patches" of food that may concentrate biota at multiple trophic levels (Benoit-Bird and Au 2003). Spatial variation in food and risk factors may occur across different geographic scales, from intensive patches of mesozooplankton (Russell et al. 1992) to the scale of oceanographic domains. Salmon dietary studies indicate that *B. anonychus* typically appears in higher density in the Subarctic Current compared with other North Pacific domains (Davis 2003; Kaeriyama et al. 2004), while on a smaller scale, the species has been found concentrated above seamounts (Nesis 1997). Depending upon their persistence, such aggregations may attract not only higher trophic level salmon species, but species such as salmon sharks, which are abundant and effective predators on maturing salmon (Nagasawa 1998) and also feed extensively on *B. anonychus* and other squids (Kubodera et al. 2007).

Climatic Effects

The occurrence of biennial lags in both of the Pink-PDO predictors (Fig. 4) leads us to infer that the connection between the PDO and coho weight likely occurs through a climatic link to recruitment of squid. The positive association between coho weight and the PDO index across multi-generational lags, with no evidence of influence during off-cycle years, suggests that *B. anonychus* survival is closely coupled with atmospheric forcing in the North Pacific. Potential mechanisms include improved early survival in response to more abundant food associated with a shallower mixed layer (Polovina et al. 1995) and improved transport of larvae by currents to locations favorable for survival (Bailey and Picquelle 2002) during conditions associated with a strong Aleutian Low and high PDO index values. The distribution of squid within the Alaska Gyre, as well as their abundance, may be linked to physical oceanographic variables (Aydin et al. 2000).

However, other plausible mechanisms may contribute to the observed positive relationship between adult coho weight and the PDO. Exceptionally warm climatic conditions in the northeast Pacific in 1997 and 2015 were associated with peaks in average size of juvenile coho salmon sampled during late-July in trawl surveys in northern Southeast Alaska (J. Orsi, joe.orsi@noaa.gov, pers. comm.), suggesting that warm conditions associated with high PDO index values are favorable for early-marine growth of coho salmon prior to when they move offshore and begin feeding on *B. anonychus*. In addition, results of bioenergetics simulation indicate that optimal temperatures for growth are positively related to daily rations (Beauchamp 2009), indicating that warmer temperatures associated with high PDO index values may reinforce the effect of an increase in prey availability by also increasing the growth response in coho salmon. Aydin (2000) estimated that a systemic 10% increase in sea surface temperature in the vicinity of the squid-rich Subarctic Current would favor squid-feeders like coho salmon, as they currently find enough food to benefit from increased metabolic activity associated with warmer water.

Although specific mechanisms behind the inferred connection between the PDO and recruitment of *B. anonychus* await further study, it seems likely that other subarctic cephalopods with similar life histories may be similarly influenced by climate, a factor that should be considered when investigating causes of variation in growth of other higher trophic level species known to consume cephalopods. For example, Wells et al. (2008) found a direct positive relationship between apparent growth of Chinook salmon from the Taku River in Southeast Alaska and the Aleutian low pressure index (closely related to the PDO index used in this study) during their 3rd and 4th ocean years, when Chinook salmon are known to feed heavily upon squid (Davis 2003; Davis et al. 2009).

Our findings do not appear applicable to more southern coho salmon populations that do not feed extensively in offshore subarctic waters. In contrast with our results, size variation of coho salmon stocks south of Alaska has been shown to be negatively correlated with warm conditions (positive PDO; Wells et al. 2006), while recruitment of natural coho salmon from Oregon coastal rivers showed a strong negative correlation with the spring/summer PDO averaged over a period of four years prior to the return year (Rupp et al. 2012).

Interactions with Pink Salmon

An important feature of the relationship between pink salmon biomass and estimates of climate-based capacity (i.e., scaled PDO index variable) is their transition from being strongly correlated with each other during 1970–1990 to being uncorrelated afterward (Fig. 6). The marked change in the relationship between atmospheric forcing and pink salmon returns in the northeast Pacific was associated with a substantial increase in variation in annual coho weight. We infer from these results that a decrease in synchrony between variables representing bottom-up (positive) and top-down (negative) influences has increased vulnerability of epipelagic squid populations to steep declines during periods when both factors are unfavorable for survival. Our model for estimating the climate-based capacity of the GOA ecosystem to produce pink salmon for harvest while maintaining coho salmon at a historical average weight provides a potential template for evaluating some of the ecosystem trade-offs associated with ocean ranching.

Other investigators have found evidence of control of squid populations by pink salmon, based on opposing biennial cycles in the western North Pacific and Bering Sea (Ito 1964; Davis 2003). Ogura et al. (1991) observed an even-year dominant pattern in length of coho salmon in the western North Pacific that developed during the second summer at sea when diet overlap with pink salmon increases. Our results indicate that a similar interaction exists and has been intensifying in the northeast Pacific.

Wild pink salmon populations appear to have benefited from recent climatic patterns and effective fishery management practices. These salmon have remained at high abundance, particularly in odd years, despite a recent turn in the North Pacific climate cycle to cold conditions that have historically been associated with poor returns (Beamish and Bouillon 1993). Interest in further increasing utilization of offshore salmon forage through ocean ranching of pink salmon (Stopha 2013) underscores the importance of understanding the trade-offs at higher trophic levels. Chum salmon, which have the most distinctive diet among species of Pacific salmon (Welch and Parsons 1993) and consume few maturing squid (Kaeriyama et al. 2004), offer an alternative to pink salmon for aquaculture that may substantially reduce the negative effects on higher trophic level species indicated by this study.

We hope that our findings help clarify which species (pink salmon or *B. anonychus*) holds the commanding position in the offshore trophic triangle (Fig. 1). Aydin (2000)

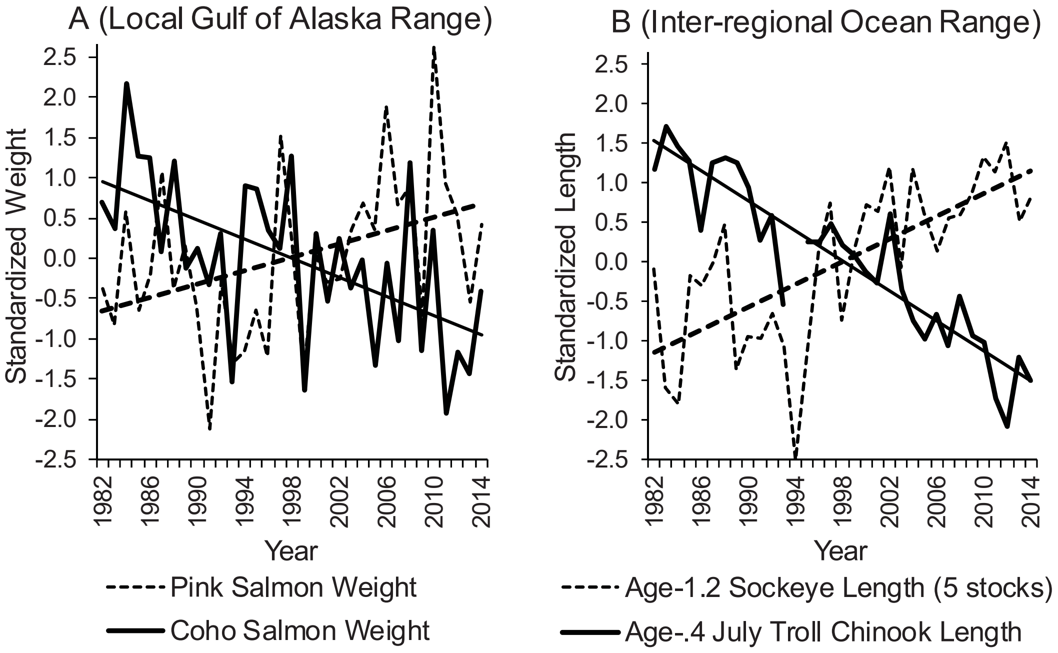

Fig. 13. Standardized size of salmon in harvests and escapements in Southeast Alaska including (A) weight of commercially-caught pink salmon and troll-caught coho salmon, and (B) length of age-1.2 sockeye salmon spawners (male and female average for Chilkoot River, Situk River, Ford Arm Creek, McDonald Lake, and Hugh Smith Lake) and troll-caught age-.4 Chinook salmon (mean-average for ages 0.4 and 1.4). All slopes are significant ($p \leq 0.05$).

has suggested that the trophic position and presumed high productivity of *B. anonychus* may give it a controlling position in the ecosystem. However, our findings suggest that *B. anonychus* is less productive and more vulnerable to intensive predation by salmon than had been presumed. We infer from our results that the pink salmon is a keystone predator that exerts top-down control (over squid) and thereby directs energy flow in the ecosystem.

Aydin (2000) produced from his extensive investigation of trophic dynamics and bioenergetics relationships a conceptual model of salmon carrying capacity in the GOA that predicts that adding more small salmon to the ecosystem through ocean ranching may be self-defeating. He hypothesized that introducing increasing numbers of small salmon may, through density-dependent effects, reduce their early growth rate, thereby delaying their ontongenetic shift to squid prey while placing further pressure on zooplankton. Release of squid from top-down control by their intra-guild predator (pink salmon) may lead to an increase in squid abundance, placing further demand on zooplankton and leading to further decline in salmon growth in a self-defeating cycle.

Our findings, supported by trends in size-at-age for various salmon species in Southeast Alaska (Fig. 13), are consistent with the feed-back loop proposed by Aydin (2000) but suggest that the mechanism has been operating in direct reverse of his hypothesized self-defeating response. Flexible planktivores (age-.1 pink salmon and age-.2 sockeye salmon) have increased in size during 1982–2014 while obligate nektivores (age-.1 coho salmon and age-.4 Chinook salmon) have decreased, suggesting that increased top-down control by salmon (combined with recent unfavorable climatic conditions for squid) may be reducing the mean trophic level of prey in the forage base in a way similar to the phenomenon of “fishing down marine food webs” (Pauly et al. 1998). A shortened food chain, with squid reduced as an intermediate trophic component, may have instead increased energy transfer efficiency between primary production and salmon. Thus, increased top-down pressure by pink salmon on micro-nektonic squid occupying an intermediate trophic level may actually increase the capacity of the GOA to produce salmon biomass, in direct reversal of the self-defeating hypothesis. A key element determining the direction of the feed-back response to increasing pink salmon abundance lies in squid populations, which appear substantially less resilient and more vulnerable to top-down control by salmon than has been assumed.

An important area for future investigation is to explain how flexible planktivores have been able to increase in adult size in the face of indications of decreased squid abundance, and in apparent contradiction with bioenergetics results reported by Aydin et al. (2005) indicating that the zooplankton found in the diet of maturing pink salmon do not have the caloric density needed to support the apparent growth trajectory of pink salmon as they approach maturity. Although untested, one mechanism that could potentially explain an increase in average size of salmon in the face of a decline in squid is a temporal advance in the growth curve resulting from an increase in abundance or nutritional quality of available zooplankton prey beginning earlier in marine life that may allow pink salmon and age-.2 sockeye salmon to achieve larger adult size even while experiencing a smaller boost near maturity from an ontogenetic shift to calorie-rich squid. Under this hypothesis, pink salmon may have become less dependent upon squid for growth while at the same time increasing their per capita impact on squid populations during a longer window of time when they are of sufficient size to be effective predators on maturing squid.

Although a simplified forage base may benefit overall salmon biomass production in the GOA, it is important to emphasize that the inferred transition in the trophic structure of the salmon forage community can be expected to entail offsetting losses among a wide range of higher trophic level species that utilize epipelagic squid (Nesis 1997), including coho, steelhead, and Chinook salmon that occur in far lower abundance than benefiting planktivores but have high per capita value to fisheries. Our results indicate that for Berners River coho salmon, the trade-offs entail not only a reduction in size of maturing fish, but a decrease in their rate of survival and therefore their total number.

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