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Changes in body size of Canadian Pacific salmon over six decades

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Abstract

Body size can sometimes change rapidly as an evolutionary response to selection or as a phenotypic response to changes in environmental conditions. Here, we revisit a classic case of rapid change in body size of five species of Pacific salmon (*Oncorhynchus*) caught in Canadian waters, with a six-decade analysis (1951-2012). Declines in size at maturity of up to 3 kg in Chinook (*O. tshawytscha)* and 1 kg in coho salmon (*O. kisutch*) during the 1950s and 1960s were later reversed to match or exceed earlier sizes. In contrast, there has been little change in sockeye salmon (*O. nerka*) sizes and initial declines in pink (*O. gorbuscha)* and chum salmon (*O. keta*) sizes have halted. Biomass of competing salmon species contributed to changes in size of all five species, and ocean conditions, as reflected by the North Pacific Gyre Oscillation and the Multivariate ENSO indices, explained variation in four of the species. While we have identified a role of climate and density dependence in driving salmon body size, any additional influence of fisheries remains unclear.

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INTRODUCTION

Across biomes and for a variety of reasons, many animals have been becoming smaller (Allendorf and Hard 2009, Gardner et al. 2011). Changes in body size have a myriad of consequences. They affect the physiology (Gardner et al. 2011, Ohlberger 2013) and ecology (Peters 1983, Audzijonyte et al. 2013) of an organism and can affect correlated life-history traits such as fecundity and survival (Blueweiss et al. 1978, Calder 1984). In marine fishes, changes in body size have been linked to oceanic conditions (Satterthwaite et al. 2012, Crozier and Hutchings 2013), competition (Helle et al. 2007), and size-selective fisheries (reviewed in Law 2000, Hard et al. 2008). Whatever the cause, these morphological changes can occur quickly (Law 2000, Conover and Munch 2002), reduce yields to fisheries, and threaten the sustainability of exploited fish stocks (Baker et al. 2011).

Pacific salmon provided early examples of this global trend in declining body size. Between 1951 and 1975, three of these iconic species, Chinook (*Oncorhynchus tshawytscha)*, coho (*O. kisutch*), and pink salmon (*O. gorbuscha)*, caught in British Columbia (BC), Canada, became significantly smaller (Ricker 1981). The decline in body size of these species was muted between 1975 and 1991, especially for northern and central coastal populations (Ricker 1995). In contrast, the body sizes of chum (*O. keta*) and sockeye (*O. nerka*) salmon changed little over those four decades (Ricker 1981, 1995). The BC trend in declining body size was mirrored across North America and Asia where the average body size in 45 of 47 North Pacific salmon populations decreased between 1975 and 1993 (Bigler et al. 1996).

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Oceanic conditions have been hypothesized to affect salmon body size trends through variability in environmental conditions and abrupt changes across ecosystem regime shifts (Helle and Hoffman 1998, Wells et al. 2006, Helle et al. 2007). Environmental variability can be represented by climatic indices. These indices reflect metrics of pelagic productivity, such as net primary productivity, chlorophyll concentrations, and nutrient levels (Di Lorenzo et al. 2008), across the broad geographic scales experienced by salmon during marine migrations (Wells et al. 2006, Di Lorenzo et al. 2008, Satterthwaite et al. 2012). Salmon body size has also been found to vary across more abrupt ecosystem regime shifts (Helle and Hoffman 1998). These regime shifts are characterized by rapid, substantial changes in ecosystem dynamics, including community composition and trophic structure (Polovina 2005). Climate-related shifts in salmon abundance in the North Pacific Ocean have been associated with major ecosystem regime shifts in c. 1947, 1977, and 1989 (Irvine and Fukuwaka 2011).

Body size of Pacific salmon is also influenced by density-dependent interactions such as competition (Kaeriyama 1998, Ruggerone et al. 2012), presumably from the most abundant species, sockeye, chum, and pink salmon (Irvine and Fukuwaka 2011). High biomass of these salmonids can be expected to correspond to smaller body sizes due to food resource limitations (Sebens 1987). Eggers and Irvine (1997) found that average body size for many populations of sockeye salmon was inversely related to aggregate abundance, implying that growth was density-dependent. Pink salmon may be especially influential in density-mediated changes in body size due to their numerical abundance (Irvine and Fukuwaka 2011) and their life history (Ruggerone and Nielsen

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2005). For instance, pink salmon fry enter the ocean early and may reduce prey availability for the salmonids that follow. Their competitive ability is further strengthened by their high consumption rate and their strong diet overlap with sockeye and chum salmon (Healey 1980, Ruggerone and Neilson 2005). Bugaev et al. (2001) estimated that high abundance of pink salmon could reduce the body size of sockeye salmon returning to Ozernaya River, Russia by up to half. Although pink salmon are numerically the most abundant species of Pacific salmon, the second most abundant species, chum salmon, has a greater biomass as they are larger and stay in the ocean longer. Consequently, chum, pink, or a combination of these and other species may be important for inter- and intraspecific density-dependent interactions.

Finally, body size has also been observed to respond quickly to intensive fishing in both natural populations (reviewed in Hard et al. 2008) and in selection experiments (reviewed in Pauli and Heino 2014). Fisheries can act as a source of strong, directional selection on phenotypic traits by causing high levels of mortality and targeting certain size-classes (e.g., through gear selectivity and minimum catch limits) (Law 2000, Hutchings and Fraser 2008). Such changes have been observed across taxa (e.g., Hamon et al. 2000, Haugen and Vøllestad 2001) and regions (e.g., Ricker 1995, Hyer and Schleusner 2005).

Here, we examine trends in body size of Pacific salmon over the past six decades. We extend Ricker's 1981 and 1995 classic analyses on Pacific salmon in two important ways: (1) we lengthen the time series by 21 years such that it now spans the years 1951-2012, and (2) we use generalized additive mixed models (GAMMs), which were unavailable to Ricker, to test the importance of potential correlates of changes in

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body size. The principal advantage of GAMMs is that they allow the data to dictate the structure of the fit while accounting for a temporal correlation structure (Hastie and Tibshirani 1990, Lin and Zhang 1999). This is critical in evaluating the influence of chronic forcing variables, such as climate change, as they are predicted to cause non-linear ecosystem changes (Smith et al. 2009). We include potential effects of oceanic conditions by considering time-series of four climatic indices - the Pacific Decadal Oscillation, the North Pacific Gyre Oscillation, the Northern Oscillation Index, and the Multivariate ENSO Index. We examine the effect of density-dependent interactions by including estimates of the biomass of potentially competing North American sockeye, pink, and chum salmon, as well as chum salmon from Asia. Finally, we test for a latitudinal effect by including the latitude of each fishery's capture location (i.e. statistical area) as a potential factor in our analyses.

METHODS

Data sources: Body Size Fishery Data

We calculated average body size from British Columbia (BC) commercial catch statistics for populations of pink, chum, sockeye, coho, and Chinook salmon for each year between 1951 and 2012. The BC commercial catch can include a considerable proportion US-bound fish, especially in the case of Chinook and coho salmon caught in troll fisheries off the west coast of Vancouver Island (Pacific Salmon Commission 2004; Pacific Salmon Commission 2015). However, at least for Chinook salmon, the proportion of US origin fish appears to be relatively stable over time (Pacific Salmon Commission 2015), minimizing any confounding effects on our analyses. The weight of

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the commercial catch and the total number of fish caught are recorded for 29 statistical areas spanning the BC coastline (Area 1- Area 29; http://www.pac.dfo-mpo.gc.ca/fm-gp/maps-cartes/areas-secteurs/index-eng.html). We calculated average body size by dividing the weight of the catch by the number of fish caught. In a series of technical reports, Ricker and colleagues (Ricker et al. 1978, Ricker 1980a, 1980b, 1982, Ricker and Wickett 1980) computed average body sizes as described above for all species of Pacific salmon across BC fisheries from 1951 to 1975. Ricker (1995) extended some of these time series to 1991. We extended all of them to 2012. Round (live) weight is reported in the commercial catch statistics for gillnet- and seine-caught fish. In contrast, dressed weight (completely cleaned but with the head on) is reported for troll-caught fish. Following Ricker and colleagues (Ricker et al. 1978, Ricker 1980a, 1980b, 1982, Ricker and Wickett 1980), we converted dressed weight to round weight by multiplying by 100/85 (Ricker 1995). Ricker et al. also imposed minimum annual catch weights for body size calculations because small catches might produce unreliable average weights. We imposed the same restrictions for the years 1951 – 1975 and set the annual catch minimum to 10,000 lbs (4,536 kg) for the years 1976 – 2012. We were able to accurately replicate the average weights calculated in the technical reports by Ricker and his colleagues and are thus confident that the methods used before and after 1975 are similar.

Data sources: Oceanic Conditions

To represent oceanic conditions, we considered both acknowledged regime shifts and continuous variability. There were three ecosystem regime shifts during our

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148 study period (1976/77, 1988/89, 1998/99) that are generally regarded as being
149 characterized by sudden substantial changes in community composition, including
150 species abundances and trophic structure (Polovina 2005). On the other hand, climatic
151 indices integrate continuous variability in oceanic conditions (e.g., sea surface
152 temperature, sea level pressure) experienced by salmon and other species across
153 broad geographic scales. The climatic indices recognized to have the most generalised
154 effects across salmon populations and species are the Multivariate ENSO Index (MEI;
155 available from www.esrl.noaa.gov/psd/enso/mei/), the Pacific Decadal Oscillation (PDO;
156 available from research.jisao.washington.edu/pdo/), and the Northern Oscillation Index
157 (NOI; available from
158 http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/NOIx/noix.html) (Wertheimer
159 et al. 2004, Wells et al. 2006, Satterthwaite et al. 2012). We also included a fourth
160 index, the North Pacific Gyre Oscillation (NPGO), due to recent evidence indicating that
161 salmon survival since the 1980s is better explained by the NPGO than the PDO (Kilduff
162 et al. 2015; available from www.o3d.org/npgo).

163 The MEI measures the intensity of the El Niño Southern Oscillation (ENSO) by
164 integrating six metrics of environmental variability (sea surface temperature, surface air
165 temperature, sea-level pressure, zonal and meridional surface winds, and cloud cover)
166 (Wolter and Timlin 1998). An increase in MEI (warmer, ENSO-like conditions)
167 corresponds to a decrease in net primary productivity and chlorophyll biomass
168 (Behrenfeld et al. 2006). MEI has been shown to correlate negatively with the average
169 length of age-3 coho salmon returning to rivers from BC south to California. In contrast,
170 the relationship of MEI with average length of age-3 Chinook is variable (positive for

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salmon returning to BC; negative for salmon returning to Washington, Oregon, and California) (Wells et al. 2006). While other indices measure the occurrence of El Niño and La Niña episodes and related ENSO impacts (e.g., Southern Oscillation Index, North Pacific Index, Oceanic Niño Index), we chose the MEI because of its documented influence on salmon body size and because it is based on more information than other ENSO indices (Wolter and Timlin 1998).

The PDO is the dominant pattern of sea surface temperature (SST) variability in the North Pacific Ocean and captures long-term temperature trends that persist for 20-30 years. The PDO is often positive in El Niño years and is associated with climatic regime shifts manifesting in changes in trophic structure and availability of prey fish (Mantua et al. 1997; Mantua & Hare 2002; Wells et al. 2006; Beamish et al. 1999). Negative values of the PDO (cooler conditions) correspond with higher abundance of Pacific salmon in the southern portion of their eastern Pacific range, while the inverse is true in Alaska (Hare et al. 1999; Hare & Mantua 2000). Furthermore, the sizes of coho and Chinook salmon south of Alaska are negatively correlated with the PDO (Wells et al. 2006)

The NOI represents the difference in sea level pressure anomalies from two locations that influence atmospheric circulation – the North Pacific High off the coast of California (high pressure region) and near Darwin, Australia (low pressure region) (Schwing et al. 2002). This index is correlated negatively with ocean temperatures. Positive values of the NOI would be expected to increase salmon body size, as more nutrients are available through stronger trade winds and increased upwelling (Schwing et al. 2002). Mean length of two ocean-winter Chinook and age 3 coho salmon from

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Washington, Oregon and Californian was higher with positive NOI values (Wells et al. 2006, Satterthwaite et al. 2012). However, the influence of NOI may not be consistent across latitudes as positive NOI periods correspond with higher salmon catches in the Pacific Northwest and lower salmon catches in Alaska (Schwing et al. 2002).

Finally, the NPGO represents variability in ocean circulation in the Northeast Pacific Ocean (Di Lorenzo et al. 2008). Strengthening of subpolar and subtropical gyres is reflected in positive values of the NPGO and fluctuations correspond to variability in the horizontal flow of seawater and wind-driven upwelling (Di Lorenzo et al. 2008). The NPGO is positively correlated with salinity, nutrient concentrations, chlorophyll levels, and salmon abundance (Di Lorenzo et al. 2008, Kilduff et al. 2015). Furthermore, the NPGO accounted for substantial variation in survival of juvenile Chinook in the Snake River, Wyoming (Miller et al. 2014).

Salmon body size is likely to respond to wintertime oceanic indices summarizing atmospheric circulation as this period has been credited for the physical changes seen in the North Pacific Ocean (Mantua et al. 1997, Yeh et al. 2011). As with Litzow et al. (2014), we included only winter values of the PDO and the NPGO by averaging monthly values from November to March (as per convention for each index) and assigning the winter values to the fish growth year that included March. We included only December to May values of the NOI as they have the greatest and most lasting effect in the Northeast Pacific Ocean. We lagged annual mean values of the MEI by one year to align oceanic conditions experienced by salmon with the propagation of the ENSO signal into our study region (Litzow et al. 2014).

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Data sources: Density effects

To evaluate the effect of competition and density-dependent interactions, we included three estimates of salmon biomass as covariates in our model: (1) the total biomass of chum salmon, (2) the total biomass of pink salmon, and (3) the combined total biomass of sockeye, chum, and pink salmon (in millions of kg, from BC, WA, and from Alaskan rivers entering the Gulf of Alaska, GOA). No model was allowed to include more than one biomass index. Since the marine distribution of BC salmon also overlaps with Asian salmon, in particular chum salmon (Myers et al. 2007, Urawa et al. 2009), we also included the total biomass of potentially competing Asian chum salmon to test if it improved model support for BC chum salmon size.

Total biomass included the biomass of younger salmon in the ocean as well as older returning mature salmon. The biomass of mature salmon only was estimated by Irvine and Ruggerone (2016) by multiplying numerical run size (i.e. catch + escapement) estimates for groups of sockeye, pink, and chum salmon from Ruggerone and Irvine (2015) by individual fish weights, which were computed by dividing catches in numbers by catches in weights (data from http://www.npafc.org/new/science_statistics.html). Irvine and Ruggerone (2016) applied species-specific ratios of total biomass to the biomass of mature salmon only from Eggers (2009) to yield the total biomass estimates of young and mature salmon that we used in our analyses.

Biological Considerations

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Because our fish size data were from fish caught in fisheries, we assumed that fish were mature, fully grown individuals returning to fresh water to spawn. However, this may not be accurate for troll-caught Chinook and coho salmon as they can be caught prior to their return migration when they are still growing (Ricker 1981). For these species, a temporal shift in fishing effort could alter the mean weight of fish caught that year, as the catch may be composed of fish at different stages of growth. For the purposes of this analysis, we assumed that the monthly distribution of catches was similar among years to allow a comparison of annual mean weights in these species. We also included latitude as a factor in the analysis, which should help account for any such shifts if they occurred and if their effects were strong for those two species. Furthermore, time series were fairly evenly distributed among regions (Fig. S2b). In contrast, pink, chum, and sockeye salmon are generally caught after the completion of most of their growth (Ricker 1981). In the case of pink salmon, which has a two-year lifecycle, odd- and even-year fish were treated as separate populations as they are genetically distinct (Irvine et al. 2014).

Analyses

We ran all analyses on salmon caught by the least selective gear (i.e., troll for Chinook and coho salmon and seine for chum, pink, and sockeye salmon) to minimize the potential for gear size-selectivity to dictate observed changes in body size. We are confident that the body size trends observed in the British Columbia catch statistics are not artifacts of the fishery as temporal trends were similar across all gear types (Fig. S1). We only included time series from a statistical area if there were more than 20 years of

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body size data (10 years for odd- and even-year pink salmon). Missing data were mainly due to years with no fishery in the region or with annual catches that were less than the required minimum weight for inclusion. Time series for each species were, in general, evenly distributed among gear types (Fig. S2a) and regions (Fig. S2b). To examine overall trends in body size, we used local polynomial regression smoothing (loess) to plot a smoothed mean and 95% confidence interval of the mean through average weight data for each species caught in all statistical areas across BC.

We used generalized additive mixed models (GAMMs) to evaluate the importance of climatic indices and biomass estimates on body size. We controlled for spatial effects by including latitude as a covariate in the model. Generalized additive models are an extension of generalized linear models that allow for both semi-parametric (smoothed) and parametric linear terms as predictor variables (Hastie and Tibshirani 1990). Generalized additive models permit departure from the common statistical assumption of linearity by allowing the data to dictate a non-linear structure of the fit. Generalized additive mixed models are an extension of generalized additive models that allow for the inclusion of correlation structures (Lin and Zhang 1999).

We centered time series from each statistical area and each species by the mean to allow compilation across areas. We averaged each climatic index (NPGO, PDO, MEI and NOI) and biomass estimate (pink only, chum only, total pink, chum, and sockeye) over the average number of ocean winters of each species (i.e., coho and pink salmon: one year, sockeye salmon: two years, chum and Chinook salmon: three years). We also calculated the latitudinal midpoint of each statistical area to test for a latitudinal gradient in changes in body size.

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To evaluate the effect of competition and density-dependent interactions, we included an estimate of the combined biomass of competing sockeye, chum, and pink salmon (in millions of kg) from BC, WA and from Alaskan rivers entering the GOA as a potential covariate of salmon body size. We also included an estimate of only pink salmon biomass and only chum salmon biomass. Only one biomass estimate – biomass of competing pink, chum, or the combined total of pink, chum, and sockeye salmon biomass – was included in any given model due to non-independence. We included the biomass of chum salmon from Asia in the top model for chum salmon by adding it to the GOA, BC, and WA biomass estimate to determine if Asian chum have an additional effect on BC chum body size. Collinear variables, as defined by variance inflation factors > 5 and Pearson's R correlation coefficients > 0.8, were not permitted in the same model (Table S1; Zurr et al. 2007). No climatic indices exceeded our thresholds for collinearity (Table S1).

We fit a separate GAMM to each species of the form:

$$Y = \beta_0 + \sum_{k=1}^{n} S_k(x_k)$$

where Y is the mean weight of salmon in kilograms, β_0 is the intercept term and $\sum_{k=1}^{n} S_k(x_k)$ is the sum of each smoothed explanatory variable, where S_k is a one-dimensional smoothing function of the x_k explanatory variable. The degrees of freedom associated with each term dictate the degree of smoothing. We set the maximum degrees of freedom for each parameter to four to prevent overfitting and spurious results (Guntenspergen 2014). Under this constraint, the effective degrees of freedom were determined using cross-validation. A parameter with one effective degree of

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307 freedom is essentially reduced to a linear term. A thin-plate regression spline function
308 was used to smooth each variable x_k.

309 An autoregressive moving average (ARMA) correlation structure was fitted to
310 each GAMM to account for temporal autocorrelation. The autoregressive order (p) and
311 the moving average order (q) of the ARMA structure were selected by minimizing the
312 Akaike information criterion. We report the best models that can be constructed from the
313 climatic indices, biomass estimates, and latitudinal gradient as determined by
314 minimizing the second-order Akaike information criterion (AICc). The AICc imposes a
315 larger penalty for additional model terms than the AIC with a correction for finite sample
316 sizes. We report the best supported models as those with an AICc deviation from the
317 top model (ΔAICc) less than two (Burnham and Anderson 2002).

318 Partial plots of each explanatory variable included in the top model are presented
319 (with 95% confidence intervals) to visualize the relationship between the smoothed
320 explanatory variable and residualized and mean-centered body size (i.e., mean-
321 centered body size after removing the effect of all other explanatory variables).
322 Consequently, the plots represent how body size changes relative to its mean for a
323 given explanatory variable.

324

325 **RESULTS**

326 The mean weight of all species of Pacific salmon caught in the BC commercial
327 catch changed over time (Figs. 1 and 2). The mean weight of Chinook salmon declined
328 markedly, by approximately 3 kg, from 1951 to the early 1970s, but this decline was
329 then mirrored by an increase of weight back to its former mean through the 1980s and

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330 1990s (Fig. 2a). The body size of coho salmon followed a similar pattern; however, the
331 minimum body size of coho salmon was not reached until the 1990s before rebounding
332 (Fig. 2b). Chum, odd- and even-year pink salmon initially declined in body size with little
333 change over the past two decades (Fig. 2c, e, f). There was relatively little change in the
334 body size of sockeye salmon (Fig. 2d).

335 Visual examination of unsmoothed trends indicated no obvious, consistent effect
336 of abrupt climate-related regime shifts on salmon body size (Fig. 1). However,
337 continuous climatic indices, combined with an estimate of salmon biomass as a proxy
338 for competition, were more informative. The best statistical models of salmon body size
339 variability invoked at least two climatic indices for each species. The top models
340 explained substantial variation in even- and odd-year pink salmon body size (R^2 = 0.40
341 and 0.70, respectively), and moderate variation in chum, and Chinook salmon body size
342 (R^2 = 0.23 and 0.21, respectively; Table 1). The best model explained minimal variation
343 in sockeye and coho salmon body size (R^2 = 0.10 and 0.16, respectively; Table 1).
344 There was little evidence of a latitudinal effect, as latitude was not present in any of the
345 top models (Table 1) and trends in body size were not drastically different among
346 regions (Fig. S3).

347 The NPGO index was in the top model of Chinook, coho, sockeye, even- and
348 odd-year pink salmon (Table 1, Fig. 3). High values of the NPGO (> ~1) were
349 associated with increases in body size in Chinook coho, and sockeye salmon whereas
350 values near zero were related to reductions in body size in all species. NPGO values <
351 -1 had variable effects on body size (Fig. 3). The MEI was in the top model of Chinook,
352 chum, sockeye, even-, and odd-year pink salmon (Table 1, Fig. 3). However, there was

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353 no consistent relationship between MEI and body size. MEI values close to -0.5 were
354 associated with the greatest reduction of size in Chinook and chum salmon, and
355 positive values, with increases in size (Fig. 3). In contrast, sockeye, even- and odd-year
356 pink salmon were smaller at higher values of MEI (Fig. 3).

357 The biomass of pink salmon from BC, WA, and Alaskan rivers entering the GOA
358 was important in explaining variation in body size of BC even- and odd-year pink
359 salmon. In contrast, Chinook, coho, and chum salmon body sizes were most influenced
360 by the combined biomass of pink, chum, and sockeye salmon (Table 1, Fig. 3). The
361 body size of sockeye salmon was most influenced by the biomass of chum salmon.
362 Including the biomass of chum salmon from Asia in the biomass estimate used in the
363 top model for chum salmon did not improve the model's AICc (ΔAICc = 41.33). The
364 relationship between biomass of competing salmon and body size was variable. High
365 biomass of GOA, BC, and WA salmonids was associated with a reduction in body size
366 in chum and even- and odd-year pink salmon (Fig. 3). In contrast, body size of Chinook,
367 coho, and sockeye salmon increased with high biomass of all GOA, BC, and WA
368 species (Fig. 3).
369

370 **DISCUSSION**

371 Body size of Pacific salmon caught in Canadian waters has varied considerably
372 over the past 60 years. The declines in size of most species observed through the
373 1950s and 1960s have either halted or reversed since then. Although abrupt climatic
374 regime shifts do not appear to have had any consistent or substantial effect on salmon
375 body size, continuous indicators of oceanic conditions contribute to explaining size

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variation in each species. Density-dependent interactions also appear to be important for all species of Pacific salmon. Latitude did not appear to be important in explaining size variation. However, there might have been evidence for spatial effects if we had considered the full extent of the species ranges, beyond the catch data available to us.

It is important to ask whether the changes in body size documented here, which are based on fish caught by commercial fisheries, accurately reflect shifts in body size. We may have underestimated rates of decline if there has been an increasing bias toward capture of larger fish over time, for example due to changes in gear characteristics or regulations. If so, then decreases in body size may have been stronger than shown here, and more recent apparent increases might be less marked than we have shown. The changes in body size of Chinook salmon may be the most likely to be fishery artifacts because there have been significant changes in minimum size regulations in the commercial troll fishery for this species (Supplemental Material). However, we have analyzed data from the least selective gear for each species, which reduces the likelihood of size-based catch biases. Moreover, it is reassuring that fish caught by different commercial fishing gear types exhibited similar trends through time (Fig. S1). In addition, our findings from the earlier part of our time series are generally consistent with trends in body size found in previous studies (Bigler et al. 1996, Eggers and Irvine 2007, Shaul et al. 2007). Consequently, we are confident that our findings indicate true changes in body size.

The variation, albeit minimal in some cases, that is explained by oceanic and density-dependent correlates should be highlighted, given the expected noise in our data (see Table 1 for R^2 values). Commercial catch statistics are subject to changes in

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399 regulations, gear selectivity, and collection rigour throughout time. Furthermore,
400 changes in body size of Pacific salmon, with the exception of pink salmon, can be
401 confounded by changes in the age at which salmon mature and by the complexity of the
402 system. Our models demonstrate the importance of oceanic and density-dependent
403 influences on salmon body size, which emerges clearly despite the many sources of
404 unaccounted variability in our data.
405
406 **Oceanic Conditions**
407 In general, salmon body size did not exhibit any consistent or substantial change
408 following abrupt ecosystem regime shifts in either the raw data or smoothed trends (Fig.
409 1 and 2, respectively). There is some evidence of an abrupt increase in Chinook size
410 immediately following the 1976/77 regime shift. However, this increase in size occurs
411 prior to the regime shift adjusted for ocean-entry and is not sustained the following year
412 (Fig. 1). This result is perhaps surprising, given previous demonstrations of changes in
413 salmon abundance across regime shifts (Beamish et al. 1999, Hare et al. 1999, Irvine
414 and Fukuwaka 2011), as well as some evidence for associated changes in body size
415 (Helle and Hoffman 1998). However, Litzow and Mueter (2014) argued that the primary
416 axis of biological variability in the North Pacific Ocean changed gradually rather than
417 abruptly following regime shifts. In the case of Pacific salmon and many other fish
418 species, the effects of regime shifts can be spread across multiple years due, in part, to
419 the multi-year lifespan of most species. If regime shifts have a gradual effect on salmon
420 body size then it is better to use climate indices as continuous variables to understand
421 environmental impacts on salmon body size.

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422 The best-supported model for each species contained at least two climatic
423 indices (Table 1). These indices capture variation in environmental parameters, such as
424 sea surface temperature, across the geographic scale of salmon marine distributions.
425 The North Pacific Gyre Oscillation (NPGO) emerged in the top model for every species
426 of Pacific salmon except chum salmon (Table 1). The NPGO made a positive
427 contribution to body size of Chinook, chum, and sockeye salmon as it approached and
428 exceeded +1 (Fig. 3). Positive NPGO values correspond to increased net primary
429 productivity (Di Lorenzo et al. 2008) and salmon survival (Kilduff et al. 2015). In contrast,
430 the NPGO made a negative contribution to body size at values close to zero and a
431 variable contribution at values approaching and lower than -1 (Fig. 3). The importance
432 of allowing for non-linear relationships is highlighted here because persistent climate
433 forcing is expected to create non-linear changes in ecosystem dynamics (Smith et al.
434 2009). To the best of our knowledge, the NPGO has never been incorporated into
435 discussions of salmon body size, perhaps due to its recent inception (Di Lorenzo et al.
436 2008). However, our results, combined with the increasing support of the NPGO's
437 influence in the North Pacific Ocean (Di Lorenzo et al. 2008), suggest that it is an
438 important driver of variation in salmon body size.
439 The Multivariate ENSO Index (MEI) was included in the top model for every
440 species of Pacific salmon except coho salmon. While positive values of the MEI
441 correspond to warmer, ENSO-like conditions and a reduction in net primary productivity
442 (Behrenfeld et al. 2006), the MEI does not have a consistent effect on body size across
443 species (Fig. 3; see also Wells et al. 2006, Satterthwaite et al. 2012). For example,
444 Wells et al. (2006) found that the average length of age-3 BC-Puget Sound Chinook

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salmon was positively correlated with the MEI. Similarly, we found that MEI values close to -0.5 corresponded to the greatest reduction in Chinook salmon body size and positive values were associated with an increase in body size (Fig. 3). The association was similar for chum salmon body size while even-year pink salmon showed a more linear positive correlation with the MEI (Fig. 3). In contrast, Wells et al. (2006) found that the body size of coho salmon returning to BC was negatively correlated with the MEI. Although the MEI was not in our top model for coho salmon (Table 1), we found a similar negative relationship in sockeye and odd-year pink salmon (Fig. 3).

Density-dependent Interactions

Density-dependent interactions are important in explaining variation in body size of all species of Pacific salmon. Body size of Chinook, coho, and chum salmon was most influenced by the total biomass of the three most abundant salmon species in the Gulf of Alaska - sockeye, chum, and pink salmon (Table 1, Fig. 3), many of which are of hatchery origin. There is some debate regarding the competitive influence of chum salmon from Asia on salmon from North America (Ruggerone et al. 2012, Irvine and Akenhead 2013). However, our results suggest that competition from Asian chum salmon does not have an additional effect on body size of BC chum salmon, as including them in the biomass estimate of competing salmon did not improve the model's AICc. Intraspecific density-dependent interactions appeared to be more important among pink salmon as pink-only biomass emerged in the top models for body size of both lines of pink salmon (Table 1, Fig. 3). This may be due, in part, to young

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pink salmon migrating into marine waters prior to most other species and consequently minimizing interspecific competition during this life stage.

Surprisingly, the direction of the effect of density-dependent interactions, as estimated by salmon biomass, was variable across species. One might expect that when biomass of competing salmonids is high, the ocean may be near its 'salmon carrying capacity' and density-dependent interactions would limit how large a salmon can grow. This expected negative relationship was found in even- and odd-year pink salmon and chum salmon (Table 1, Fig. 3). However, the relationship is more clearly defined for odd-year than even-year pink salmon, possibly because the higher and increasing abundance of odd-year compared to even-year pink salmon strengthens intraspecific competition within odd-year runs (Irvine et al. 2014). On the other hand, body size of Chinook and coho salmon increased with increasing salmon biomass, suggesting little competitive interactions. Indeed, there is little diet overlap between Chinook or coho salmon and the three other, more abundant species (Welch and Parsons 1993). Instead, this positive relationship may be driven by favourable environmental conditions, which allows for greater total biomass of salmon species and larger size in Chinook and coho salmon.

Fishing pressure

There is a growing body of evidence suggesting that fisheries may be responsible for evolutionary changes (e.g., Law 2000, Quinn et al. 2007) and/or plastic changes in fish body size (Price et al. 2003). Fisheries can also alter the age structure of the species that have multiple age classes (Chinook, sockeye and chum salmon). In BC,

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overall fishing intensity on salmon has decreased in recent years due to conservation concerns. For instance, commercial coho salmon fisheries have been closed in southern BC since 1997 (Irvine et al. 2013). In addition, fisheries for sockeye salmon, especially from the Fraser River watershed, and pink salmon fisheries (odd and even years) have been substantially reduced in recent years (Irvine et al. 2014). Furthermore, Chinook and coho salmon fishing effort throughout BC has been shifting away from the commercial fleet to the recreational fishery (DFO 1999). This decrease in selection pressure from the various fisheries could have led to some increase in salmon body size. However, we would expect this rebound to still fall short of 1950s values because such recoveries can take much longer than that. Kuparinen and Hutchings (2012), for example, demonstrated that size at maturity of a simulated Atlantic cod (*Gadus morhua*) population would still be 11% lower than pre-fishing sizes 200 years after fishing ceased. Admittedly, cod has a longer generation time than salmon, so relaxation of fishing pressure might still have played a role in the recovery of salmon body size, but it is perhaps less important than the ecological and climatic effects that we have shown here.

In conclusion, this study updated changes in body size of Pacific salmon caught in Canadian waters and provided evidence of climatic and density-dependent explanations for these trends. Rapid reductions in body size of some species of Pacific salmon from the 1950s through the 1970s or 1980s have either halted or, in the case of Chinook and coho salmon, completely reversed. While the role of fisheries-induced selection in driving these patterns is unclear, the changes in salmon body size are correlated with variation in ocean conditions and density-dependent competition with other salmon.

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768 Table 1. Second-order Akaike information criterion (AICc) model selection results for the top GAMMs constructed for
769 each Pacific salmon species. The full model includes four climatic indices (NPGO, PDO, MEI, NOI), estimates of the
770 biomass of salmon from rivers entering the GOA, BC, and WA (combined sockeye, chum and pink salmon, pink salmon
771 only, or chum salmon only; only one per model) and latitude. + indicates the variables included in each model. Only the
772 models with ΔAICc < 2 are shown. ΔAICc is the difference in AICc values between each model and the best-supported
773 models. Weight is a measure of the relative likelihood of each model given the set of candidate models. The adjusted R^2
774 indicates the explanatory power of the model adjusted for the number of predictors in the model.
775

	Model No	NPGO	PDO	NOI	MEI	Biomass	Biomass Metric	Latitude	df	AICc	ΔAICc	Weight	Adjusted R^2
Chinook	1	+	+	+	+	+	pink + sock + chum		14	2148.69	0.00	0.38	0.21
	2	+	+		+	+	pink + sock + chum		12	2148.94	0.26	0.34	0.22
Coho	1	+		+		+	pink + sock + chum		13	976.62	0.00	0.38	0.16
	2	+		+	+	+	pink + sock + chum		15	978.45	1.83	0.15	0.18
Chum	1			+	+	+	pink + sock + chum		10	1158.78	0.00	0.45	0.23
	2	+		+	+	+	pink + sock + chum		12	1160.03	1.24	0.24	0.23

Sockeye	1	+	+		+	+	chum	14	20.94	0.00	0.35	0.10
	2	+			+	+	chum	12	21.64	0.71	0.25	0.08
Pink	1	+	+	+	+	+	pink	16	-129.51	0.00	0.47	0.40
even year	2	+	+		+	+	pink	14	-129.31	0.20	0.43	0.37
Pink	1	+	+	+	+	+	pink	14	-136.00	0.00	0.75	0.70
odd year												

776

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777 **Figure Captions**

778 Figure 1. Mean weight (kg) of Pacific salmon from 1950 to 2012 by statistical area (grey
779 lines) caught with the least selective gear type for each species (pink, chum, sockeye =
780 seine; Chinook and coho = troll). Vertical lines indicate the calendar year (solid) and the
781 year adjusted for ocean entry (dashed) of three well-studied ecosystem regime shifts
782 characterized by abrupt changes in marine community composition.
783
784
785 Figure 2. Locally weighted polynomial regressions of mean weight (kg) of Pacific
786 salmon caught by the least selective gear for each species (pink, chum, sockeye =
787 seine; Chinook and coho = troll) across all statistical areas. Grey areas are 95%
788 confidence intervals of the mean across all statistical areas. Vertical lines indicate the
789 calendar year (solid) and the year adjusted for ocean entry (dashed) of three well-
790 studied ecosystem regime shifts characterized by abrupt changes in marine community
791 composition.
792
793 Figure 3. Partial plots illustrating the nature of the relationship between the smoothed
794 predictor (i.e., the explanatory variable) and the residualized dependent variable (i.e.,
795 body size after removing the effect of all other predictor variables) for each variable
796 included in the top model constructed for each salmon species. The Y-axis is mean
797 centered and thus the plots represent how body size changes relative to its mean for a
798 given explanatory variable. Grey bands represent 95% confidence intervals. Tick marks
799 along the bottom of each plot indicate the number of data points for each value of X.

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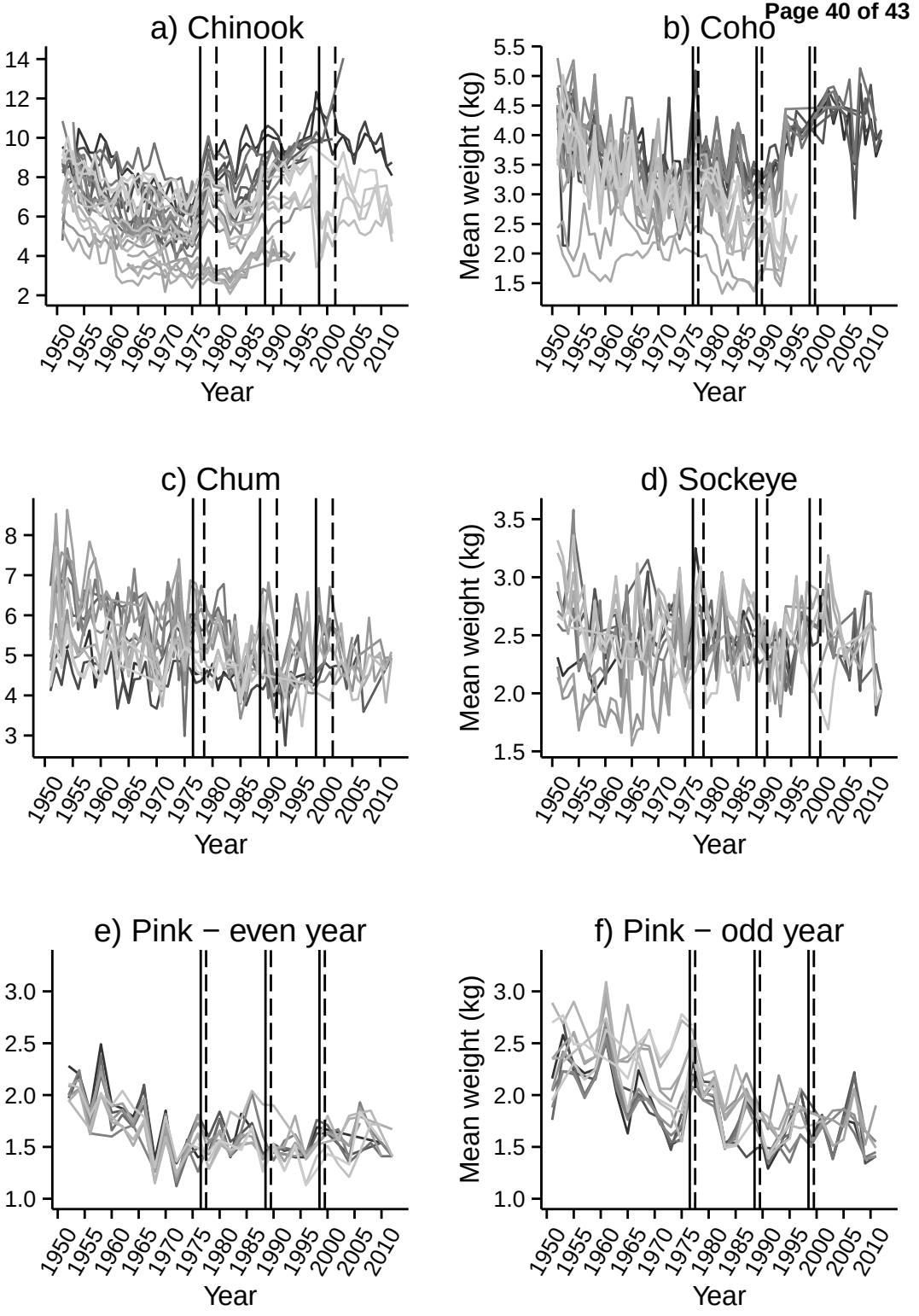
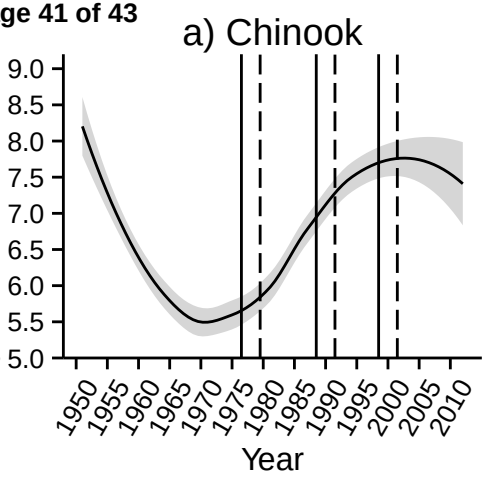
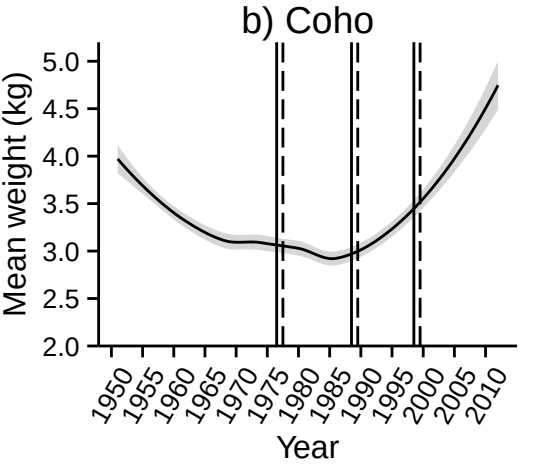
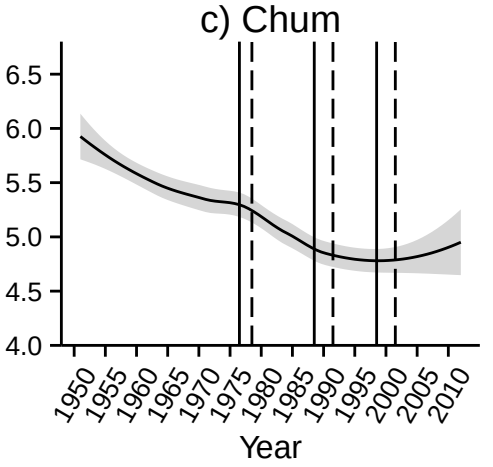
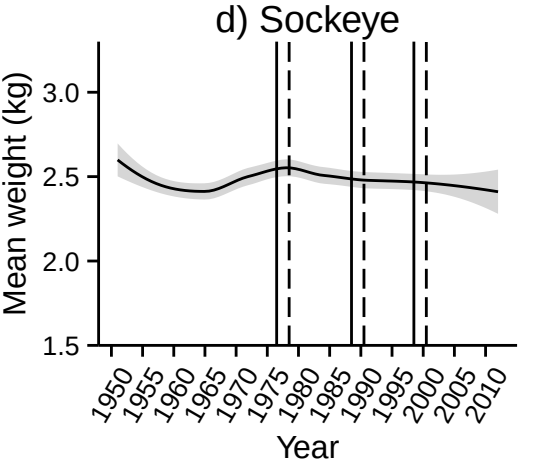


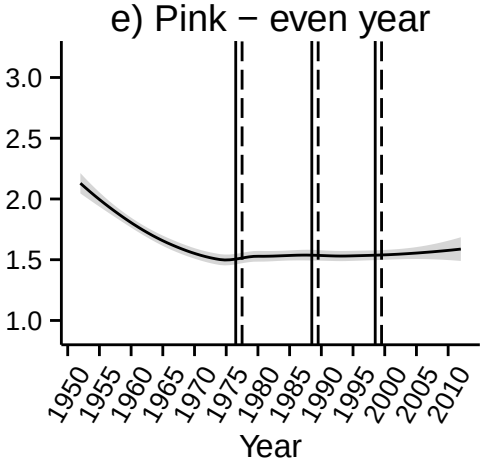
Mean annual weight (kg)

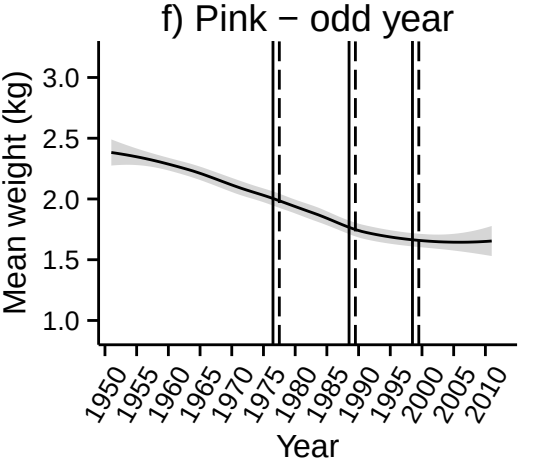












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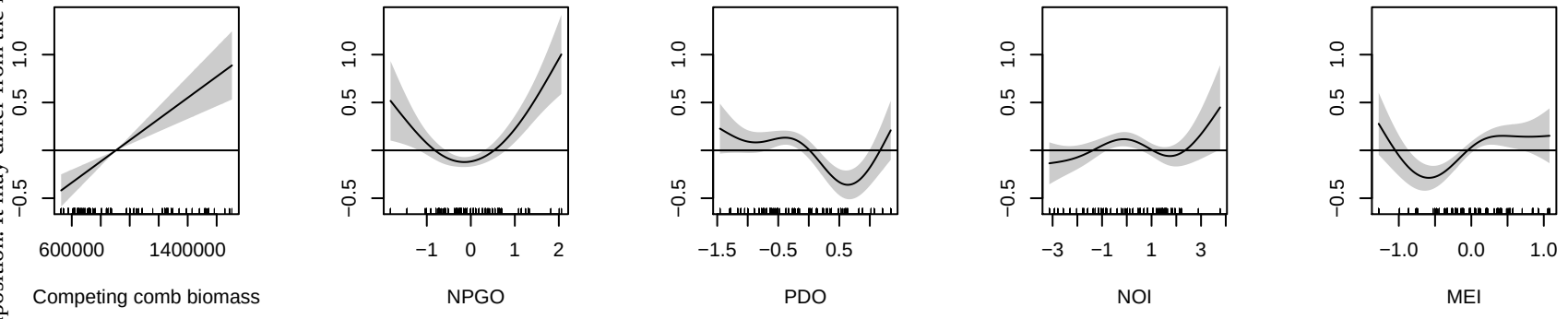
Chinook



Coho

Chum

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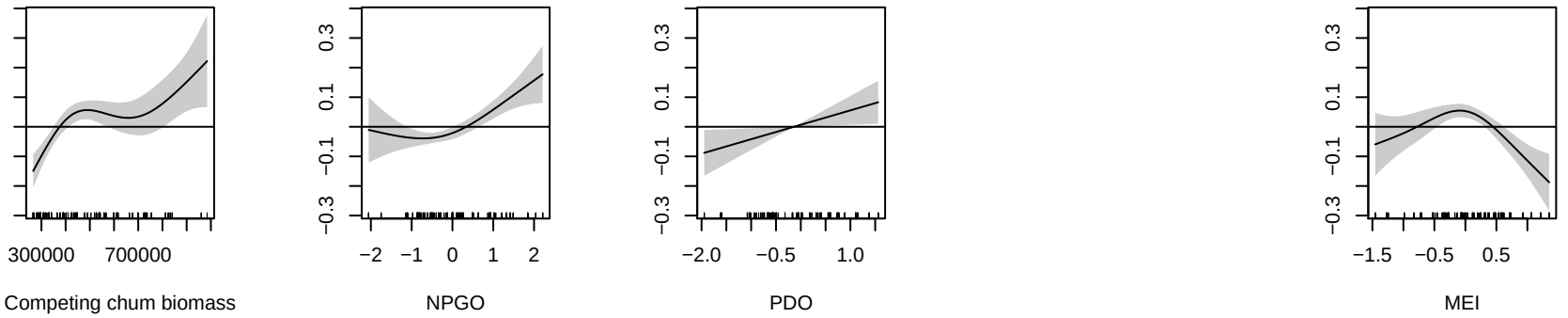
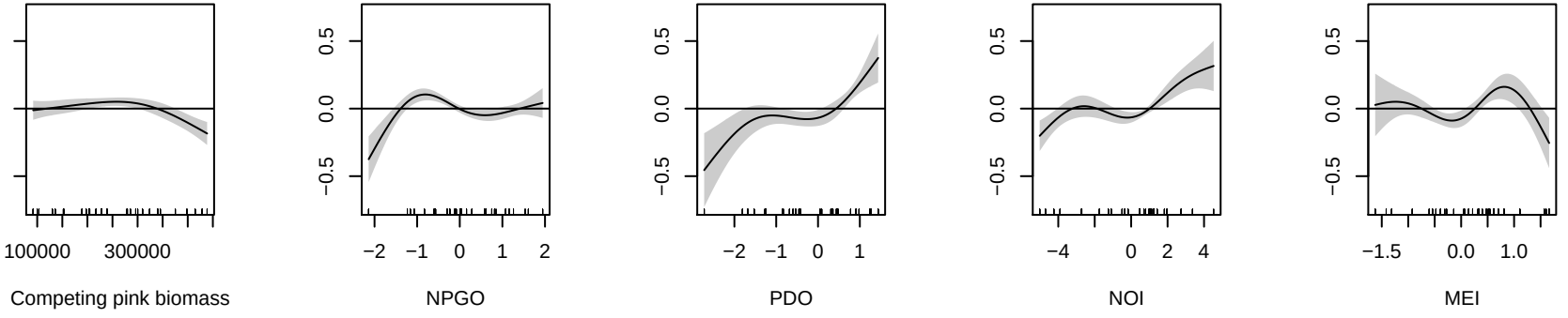
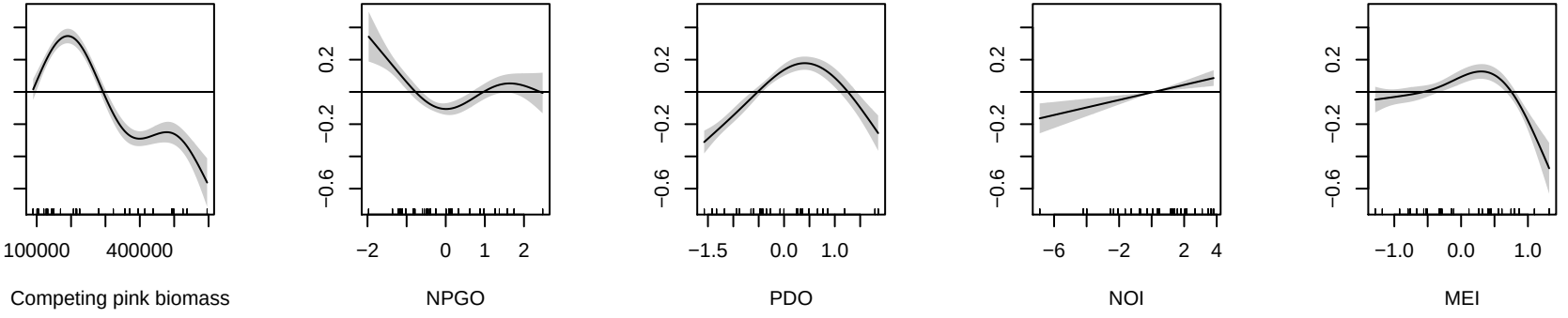
Sockeye



Pink − even year



Pink − odd year