Effects of the North Pacific Current on the productivity of 163 Pacific salmon stocks

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ABSTRACT

Horizontal ocean transport can influence the dynamics of higher-trophic-level species in coastal ecosystems by altering either physical oceanographic conditions or the advection of food resources into coastal areas. In this study, we investigated whether variability in two North Pacific Current (NPC) indices was associated with changes in productivity of North American Pacific salmon stocks. Specifically, we used Bayesian hierarchical models to estimate the effects of the north-south location of the NPC bifurcation (BI) and the NPC strength, indexed by the North Pacific Gyre Oscillation (NPGO), on the productivity of 163 pink, chum, and sockeye salmon stocks. Specifically, we used Bayesian hierarchical models to estimate the effects of the north-south location of the NPC bifurcation (BI) and the NPC strength, indexed by the North Pacific Gyre Oscillation (NPGO), on the productivity of 163 pink, chum, and sockeye salmon stocks. We found that for salmon stocks located in Washington (WA) and British Columbia (BC), both the BI and NPGO had significant positive effects on productivity, indicating that a northward-shifted bifurcation and a stronger NPC are associated with increased salmon productivity. For the WA and BC regions, the estimated NPGO effect was over two times larger than the BI effect for pink and chum salmon, and sockeye salmon stocks. We found that for salmon stocks located in Washington (WA) and British Columbia (BC), both the BI and NPGO had significant positive effects on productivity, indicating that a northward-shifted bifurcation and a stronger NPC are associated with increased salmon productivity. For the WA and BC regions, the estimated NPGO effect was over two times larger than the BI effect for pink and chum salmon, whereas for sockeye salmon the BI effect was 2.4 times higher than the NPGO. In contrast to WA and BC stocks, we found weak effects of both horizontal ocean transport processes on the productivity of salmon stocks in Alaska. Our results indicated that horizontal transport pathways might strongly influence population dynamics of Pacific salmon in the southern part of their North American ranges, but not the northern part, suggesting that different environmental pathways may underlie changes in salmon productivity in northern and southern areas for the species under consideration.

Key words: horizontal transport, North Pacific Current, Pacific salmon, productivity

INTRODUCTION

Environmental change can influence demographic rates of marine and anadromous fish populations through multiple environmental pathways (Drinkwater et al., 2010; Ottersen et al., 2010). It is often hypothesized that changes in atmospheric and physical ocean conditions influence higher-trophic-level species via bottom-up forcing that is mediated by vertical ocean transport (Ottersen et al., 2010; Di Lorenzo et al., 2013a; Malick et al., 2015a). For example, upwelling of nutrient-rich water in coastal areas is often assumed to drive primary and secondary production, which in turn provide food for higher-trophic-level species (Rykaczewski and Checkley, 2008). However, recent evidence from the California Current (Bi et al., 2011a; Keister et al., 2011; Sydeman et al., 2011) and Gulf of Alaska (Stabeno et al., 2004; Kline et al., 2008; Combes et al., 2009; Kline, 2010) suggests that bottom-up forcing mediated by horizontal transport (e.g., cross-shore or along-shore transport) may be equally important for higher-trophic-level species (Di Lorenzo et al., 2013a).

Changes in horizontal ocean transport, such as changes in ocean current patterns, could influence higher-trophic-level species production by altering foraging conditions. For Pacific salmon (Oncorhynchus spp.), feeding conditions and growth rates during the early marine life phase can strongly influence stock productivity (i.e., the number of adult recruits produced per spawner) (McGurk, 1996; Farley et al., 2007; Duffy and Beauchamp, 2011; Malick et al., 2011). During this critical period, juvenile salmon diets are largely composed of zooplankton and other weakly-swimming or passive drifters (Beauchamp et al., 2007; Brodeur et al., 2007a; Armstrong et al., 2008). Therefore, changes in ocean currents and
subsequent advection of potential prey into coastal areas may strongly influence juvenile salmon prey availability or prey quality.

Indeed, in the Northern California Current region, a large-bodied lipid-rich zooplankton community is associated with alongshore movement of cooler water from northern areas into the region, whereas a small-bodied lipid-poor zooplankton community is associated with the movement of warmer water from southern and offshore areas into the region (Bi et al., 2011a; Keister et al., 2011). The lipid-rich northern zooplankton community, in particular, is associated with higher coho salmon (Oncorhynchus kisutch) survival in the Northern California Current region (Bi et al., 2011b), suggesting that horizontal transport may be important for salmon productivity in other regions. Also, horizontal transport may be important for other salmon species, especially pink (O. gorbuscha), chum (O. keta) and sockeye (O. nerka) salmon, which tend to feed at a lower trophic level than coho salmon (Brodeur et al., 2007b).

In the Northeast Pacific Ocean, circulation is at least partially controlled by the North Pacific Current (NPC) (Ware and McFarlane, 1989; Cummins and Freeland, 2007), which flows approximately along 50°N from west to east, bifurcating at the west coast of North America into the northward flowing Alaska Current and the southward-flowing California Current (Fig. 1a) (Chelton and Davis, 1982; Ware and McFarlane, 1989). On average, the NPC bifurcates near the latitude of Vancouver, BC, but the latitudinal position varies annually from southern Southeast Alaska to southern Washington (Cummins and Freeland, 2007; Sydeman et al., 2011). In addition to variability in the positioning of the bifurcation, there is interannual variability in the strength of the NPC, measured as volume of water transported per unit time (Freeland, 2006; Cummins and Freeland, 2007). This volume is likely driven by large-scale atmospheric and oceanographic patterns such as the North Pacific Oscillation and the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo et al., 2008).

In this study, we asked whether variability in the NPC can explain inter-annual changes in productivity of 163 North American pink, chum, and sockeye salmon stocks. Specifically, we evaluated the relationships between two indices of variability in the NPC and productivity of those salmon stocks. One NPC index represented inter-annual variability in the north-south positioning of the bifurcation and the other represented inter-annual variability in strength. Because the oceanography of coastal ecosystems in the Northeast Pacific differs among geographic locations, we evaluated the relationships between salmon productivity and the NPC indices separately for three large marine ecosystems in the Northeast Pacific: the west coast of Washington and British Columbia, Gulf of Alaska, and Bering Sea (Longhurst, 1995; Sherman and Duda, 1999). We used a Bayesian hierarchical modeling approach to estimate both stock-specific and ecosystem-level effects of the NPC on salmon productivity, which allowed us to leverage the large number of available salmon data sets by using the stocks as replicates within the analysis, reducing the chances of finding spurious relationships between salmon productivity and the NPC indices (Myers and Mertz, 1998; Mueter et al., 2002; Thorson and Minto, 2015).

**METHODS**

**Salmon data**

We used spawner (escapement) and total recruitment data (catch plus escapement) for 163 wild sockeye (64 stocks), pink (46 stocks), and chum (53 stocks) salmon stocks throughout their North American ranges (Fig. 1). The duration of stock-specific data sets ranged from 12 to 56 brood years (i.e., years of spawning) 1950–2009, with mean time series lengths of 34 yr for pink salmon, 33 yr for chum salmon, and 38 yr for sockeye salmon. For pink and chum salmon, data sets generally represented aggregations of adjacent salmon populations, which helped ensure that catch records were properly attributed to the correct spawning population. Details of the data sets can be found in Peterman and Dorner (2012) and Malick and Cox (2016).

We organized the salmon data sets into three large marine ecosystems based on the ocean entry locations of each stock. All stocks that enter the ocean along the west coast of Washington and British Columbia were grouped into the West Coast ecosystem (WC). Stocks entering the ocean in Southeast Alaska and South Central Alaska were grouped into the Gulf of Alaska ecosystem (GOA), and Western Alaska stocks were grouped into the Bering Sea ecosystem (BS; Fig. 1). Organization of the salmon data sets into three large marine ecosystems was based on two pieces of information. First, the underlying oceanographic processes tend to be substantially different across these regions with the WC ecosystem being primarily an upwelling domain and the GOA ecosystem being primarily a downwelling domain (Ware and McFarlane, 1989). Second, several previous studies, e.g., Malick et al. (2015b) and Mueter et al. (2002), have indicated that regional-scale ocean conditions can have opposite effects on salmon productivity in northern and southern regions with the dividing line occurring...
approximately at the border between Southeast Alaska and British Columbia.

**North Pacific Current indices**

We used the Ocean Surface Current Simulations (OSCURS) model to compute inter-annual variability in the north-south location of the NPC bifurcation (Ingraham, 1997) and the NPGO to index broad-scale variability in the strength of the NPC (Di Lorenzo et al., 2008).

The OSCURS model simulates trajectories of surface currents in the North Pacific by adding wind velocity fields (derived from daily atmospheric sea-level-pressure data) to the long-term mean geostrophic current fields. The resulting simulated surface current trajectories have been shown to closely match satellite-tracked drifters in the North Pacific (Ingraham, 1997). We developed an index for the north-south location of the NPC bifurcation by generating annual trajectories for 215 simulated drifters for all years between 1967 and 2010, inclusive, using a procedure analogous to that of Watters and Bessey (2008). In our case, drifters were seeded on a 1-degree grid in the area bounded by –140°W longitude eastward to the coast of North America and from 40°N to 55°N latitude (Fig. S1). Simulated drifters were released annually on 1 February and the daily trajectory was tracked until 30 June to reflect ocean conditions relevant to seaward-migrating juvenile salmon (Di Lorenzo et al., 2013b). We indexed the location of the bifurcation based on differences between the starting and ending latitude of each drifter within a year. The

annual bifurcation index (BI) was calculated as the proportion of the 215 simulated drifters that ended south of their starting latitude in a particular year (Fig. S2). Positive values of the index indicate a northward-shifted bifurcation (the majority of drifters ending south of their starting latitude), whereas negative values of the index indicate a southward-shifted bifurcation (the majority of drifters ending north of their starting latitude).

The NPGO, defined as the second principal component of monthly sea surface height anomalies in the North Pacific over the region 25°N–62°N, 180°–110°W (Di Lorenzo et al., 2008), is thought to represent variability in sub-polar and sub-tropical gyre strengths in the North Pacific, where higher NPGO values indicate a strengthening of the gyres and increased NPC transport (Di Lorenzo et al., 2008, 2009; Chhak et al., 2009). Positive values of the NPGO are also associated with higher nutrient concentrations (e.g., NO3), higher salinity, and higher survival of both coho and chinook salmon (Di Lorenzo et al., 2008, 2009; Kilduff et al., 2015). Salmon survival during the early marine life phase is believed to be the dominant driver of overall stock productivity, and ocean conditions prior to salmon ocean entry may strongly influence conditions experienced by salmon during this period (Parker, 1968; Wertheimer and Thrower, 2007; Yeh et al., 2011; Di Lorenzo et al., 2013a). Therefore, we averaged the NPGO over the months of December–March, which represents the winter period just before ocean entry of salmon smolts.

For pink and chum salmon, which enter the ocean the first spring after spawning, the BI and NPGO indices were offset by 1 yr (e.g., salmon spawning in 2000 were lined up with the BI for 2001 and the NPGO for the December 2000 to March 2001 period). For sockeye salmon, which rear in lakes for 1 or 2 yr before entering the ocean, we used a weighted average of index values offset by 2 and 3 yr, respectively, with the weights equal to the stock-specific average proportion of juveniles entering the ocean at either age two or three (Mueter et al., 2002).

Modeling the data

We modeled salmon stock productivity as a function of spawner abundance using the standard Ricker model (Ricker, 1954),

\[ y_{i,t} = x_i + \beta_i S_{i,t} + \epsilon_{i,t}, \]  

where \( y_{i,t} \) is the loge of recruits per spawner, \( \log_e(R_{i,t}/S_{i,t}) \), for stock \( i \) in year \( t \), \( x_i \) is the density-independent stock productivity at low spawning stock sizes, \( \beta_i \) is the coefficient representing the strength of density-dependence, and \( \epsilon_{i,t} \) is the residual error term assumed to be normally distributed with mean 0 and variance \( \sigma_e^2 \).

We estimated BI and NPGO effects on salmon productivity using a generalized Ricker model in which the oceanographic variables were included as additional predictor variables (Quinn and Deriso, 1999), i.e.,

\[ y_{i,t} = x_i + \beta_i S_{i,t} + \gamma_{BI} BI_i + \gamma_{NPGO} NPGO_i + \epsilon_{i,t}, \]  

where \( \gamma_{BI} \) is the stock-specific coefficient for the BI and \( \gamma_{NPGO} \) is the stock-specific coefficient for the NPGO index. The annual value of the BI index was the same for all pink and chum salmon stocks, as was the value of the NPGO index, but index values for sockeye salmon stocks were stock-specific, as explained above. In addition, both the BI and NPGO indices were standardized to a mean of 0 and a standard deviation (SD) of 1.

We included both the standard and generalized Ricker models in the analysis for model comparison purposes, which allowed us to compare models with and without the NPC indices to determine the relative importance of these terms in the model (see model comparison section for details). Because data were not available to calculate the BI before 1967, we fit both the standard and generalized Ricker models using data from brood years 1966 and after.

We included a first-order autocorrelation model for residuals, i.e., \( \epsilon_{i,t} = \phi \epsilon_{i,t-1} + \delta_{i,t} \), where \( \delta_{i,t} \sim N(0, \sigma_e^2) \) and \( \phi \) is the first-order autocorrelation coefficient for stock \( i \) (Mueter et al., 2002; Chatfield, 2004). For both the standard and generalized forms of the Ricker model, the autoregressive process was modeled as,

\[ y_{i,t} = \begin{cases} \hat{y}_{i,t} + \phi \epsilon_{i,t-1} + \delta_{i,t} & \text{for } t > 1 \\ \hat{y}_{i,t} + \delta_{i,t} & \text{for } t = 1 \end{cases} \]  

where \( \hat{y}_{i,t} \) is the predicted stock productivity from either the standard Ricker model (Eqn 1) or the generalized Ricker model (Eqn 2).

Modeling the parameters

The Bayesian hierarchical modeling approach is increasingly common in multi-stock population dynamics research, in part because allowing dependence among stock-specific parameters can improve parameter estimates (Gelman et al., 2004; Thorson and Minto, 2015). In particular, modeling stock-specific parameters (e.g., \( x_i \) or \( \gamma_{BI,i} \)) as arising from a common prior distribution (i.e., assuming stocks are exchangeable units) improves the mean of parameter estimates where hyperparameters for the common distribution are informed by data from all stocks (Gauch,
In this study, we fit species-specific Bayesian hierarchical models that used hierarchical prior distributions for \( x_i, \gamma_{\text{BLI}}, \) and \( \gamma_{\text{NPGO}} \) parameters, where the hierarchical priors were further defined by a set of hyperprior distributions (Gelman et al., 2004).

For each species-specific model, we assumed that the \( x_i \) were exchangeable across all stocks within a species and we used a normal prior distribution, i.e., \( x_i \sim N(\mu_x, \tau_x^2) \) with hyperparameters \( \mu_x \) and \( \tau_x^2 \) representing the overall mean and variance, respectively. We used a diffuse normal distribution, \( \mu_x \sim N(0, 10^3) \), for the hypermean \( \mu_x \) and an improper uniform prior for the hypervariance, \( \tau_x^2 \sim U(0, 25) \) (Gelman, 2006).

We assumed that the \( \gamma_{\text{BLI}} \) and \( \gamma_{\text{NPGO}} \) parameters were only exchangeable among stocks within the same ecosystem (WC, GOA, and BS) for each of the BI and NPGO because ocean conditions can influence salmon stocks in different ecosystems in opposite ways (Muter et al., 2002; Malick et al., 2015b). As examples of our exchangeability assumption, parameters for all pink salmon stocks in the WC ecosystem were assumed exchangeable and were assigned one prior distribution (i.e., \( \gamma_{\text{WC}} \sim N(\mu_{\gamma_{\text{WC}}}, \tau_{\gamma_{\text{WC}}}^2) \)), whereas all pink salmon stocks in the GOA ecosystem were assumed exchangeable and were assigned a separate prior distribution (i.e., \( \gamma_{\text{GOA}} \sim N(\mu_{\gamma_{\text{GOA}}}, \tau_{\gamma_{\text{GOA}}}^2) \)). For a particular ecosystem and oceanographic variable, the hypermean \( \mu_{\gamma} \) represents the mean ecosystem-level effect and the hypervariance \( \tau_{\gamma}^2 \) represents the ecosystem-level variance. Diffuse normal prior distributions, \( \mu_{\gamma} \sim N(0, 10^3) \), and uniform prior distributions, \( \tau_{\gamma}^2 \sim U(0, 25) \), were used for the ecosystem-level hypermeans and hypervariances, respectively (Gelman, 2006).

In contrast to the \( x \) and \( \gamma \) parameters, which we assumed were exchangeable across salmon stocks within a species or ecosystem, we treated the remaining parameters, i.e., \( \beta_i, \sigma_i, \) and \( \phi_i \), as non-exchangeable (i.e., stock-specific) because the magnitudes of these parameters can vary greatly among salmon stocks within a species and ecosystem (Muter et al., 2002; Su et al., 2004; Malick et al., 2015b). We assigned diffuse independent priors for the density-dependence parameters, \( \beta_i \sim N(0, 10^3) \), and assigned the variances, \( \sigma_i^2 \), and autocorrelation coefficients, \( \phi_i \), to be uniform priors, \( \sigma_i^2 \sim U(0, 25) \) and \( \phi_i \sim U(-1,1) \), respectively.

Because we were uncertain about the similarity of the \( \sigma_i^2 \) and \( \phi_i \) parameters across stocks within a species, we also fit several simpler models in which \( \sigma_i^2 \) and \( \phi_i \) were shared across stocks, i.e., they were not stock specific. In total, for each species we fit five standard Ricker models and five generalized Ricker models that differed in their assumptions about \( \sigma_i^2 \) and \( \phi_i \) (Table 1).

To better demonstrate the effects of the NPGO and BI on salmon productivity, we also calculated the percent change in productivity given a one unit change in the NPGO or BI. More specifically, we used the estimated ecosystem-level effects of the NPGO and BI (i.e., \( \mu_x \)) to calculate the estimated percent change in productivity that would result from an increase in the BI or NPGO corresponding to one SD above their respective long-term means (1967–2010).

**Model fitting and diagnostics**

We estimated all model parameters using the Gibbs sampling algorithm implemented in JAGS version 3.4.0 (Plummer, 2003). For each model, we ran five chains with dispersed starting values. Each chain had a burn-in period of 10,000 iterations followed by 75,000 iterations that were monitored with a thinning interval of 15, where the thinning interval was determined by monitoring within-chain autocorrelation. We based posterior inference on a total of 25,000 posterior samples per parameter obtained by sampling 5000 iterations per chain. Gibbs chain convergence was assessed graphically (e.g., traceplots and histograms) and via the Gelman-Rubin statistic (Gelman and Rubin, 1992; Brooks and Gelman, 1998). We assessed model fits using posterior predictive checks, including fitted values, realized residuals, and posterior predictive distributions (Gelman et al., 2004).

**Model comparison**

We used the Watanabe–Akaike information criterion (WAIC) for model comparison and model selection within species (Watanabe, 2010; Gelman et al., 2013). The WAIC measures the fit of a model to the data while also accounting for model complexity. Both the ‘fit’ and ‘complexity’ terms of the WAIC were readily computed from posterior samples of the parameters. The model fit was assessed using the log-point-wise predictive density (lppd), whereas model complexity was estimated as the effective number of model parameters (pD) (Watanabe, 2010; Gelman et al., 2013). The WAIC was then calculated as

\[ \text{WAIC} = -2 \times (\text{lppd} - \text{pD}) \]

The model with the lowest WAIC value was considered the most parsimonious and models within 3 WAIC units of the minimum were considered equally plausible. Models with WAIC values greater than 10 more than the minimum were rejected.
Sensitivity analysis

We tested the sensitivity of our results to two assumptions underlying the oceanographic variables. First, to check whether our grid of simulated OSCURS model drifters captured broad-scale surface current patterns in the North Pacific, we re-calculated the BI using an expanded 1-degree grid that extended from 145°W longitude eastward to the west coast of North America and from 35°N to 59°N latitude (Fig. S1). Second, we checked the sensitivity of our results to the manner in which the BI was calculated. Specifically, we re-calculated the BI according to the method of Watters and Bessey (2008), where the annual index values were calculated as the sum of the differences in the longitude of the drifter ensemble (i.e., all drifters released at the same longitude) between the median starting latitude on 1 February and the median ending latitude on 30 June. This contrasts with our original BI index, which was calculated as the proportion of drifters that ended south of their starting latitude, by summarizing the start and end latitudes of the drifters before calculating the BI index. We assessed the sensitivity of our analysis to specifics of BI calculation by determining the strength of correlation between our original BI time series and the alternate BI series, as well as by comparing model coefficients and rankings for models fit using the alternate BI time series.

RESULTS

BI and NPGO indices

The BI time series indicated substantial inter-annual variability in the latitude of the NPC bifurcation ranging from 11% of all drifters ending south of their starting latitude in 1993 (i.e., the bifurcation was shifted southward) to 74% of all drifters ending south of their starting latitude in 2009 (i.e., the bifurcation was shifted northward; Fig. 2; Fig. S2). The BI index tended to have more inter-annual variability than the NPGO with fewer series of consecutive positive or negative values. For example, years with a northward-shifted bifurcation were often followed by years with a southward shifted bifurcation, such as 1982–83, 1985–86, and 2009–10. The BI and NPGO indices were only weakly correlated ($r = 0.24$), suggesting that they capture different modes of NPC variability.

BI and NPGO effects

Hierarchical models that included the BI and NPGO indices fit the data substantially better than models without these terms for all species, as indicated by the WAIC (Table 2). The best models (i.e., models with the lowest WAIC) showed that the strongest effects of the BI and NPGO were on stocks in the WC ecosystem, where a northward-shifted bifurcation (i.e., positive BI values) and a stronger NPC (i.e., positive NPGO values) were consistently associated with

Table 1. Summary of Bayesian hierarchical models fit for each species. # gives the model number; type indicates whether the model is a standard or generalized Ricker model; ‘exchange’ indicates the parameters were exchangeable across all stocks; ‘ecosystem’ indicates the parameters were exchangeable across stocks within an ecosystem; ‘same’ indicates the parameter was shared (i.e., the same) across stocks and ecosystems; ‘different’ indicates the parameter was stock-specific.

<table>
<thead>
<tr>
<th>#</th>
<th>Type</th>
<th>$\alpha$</th>
<th>$\beta$</th>
<th>$\sigma^2$</th>
<th>$\varphi$</th>
<th>$\gamma_{BI}$</th>
<th>$\gamma_{NPGO}$</th>
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<tr>
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<td>Different</td>
<td>Same</td>
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<td>Same</td>
<td>Same</td>
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<td>Different</td>
<td>Same</td>
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<td>Ecosystem</td>
</tr>
<tr>
<td>5</td>
<td>Standard</td>
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<tr>
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<td>Same</td>
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<td>Same</td>
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</table>
increased productivity of pink, chum, and sockeye salmon, i.e., positive \( c_{BI} \) and \( c_{NPGO} \) values (Figures 3 and 4). In contrast, the BI and NPGO effects on salmon productivity tended to be weaker for stocks in the GOA ecosystem and less consistent across species in the BS ecosystem than in the WC ecosystem (Figures 3 and 4).

For pink and chum salmon stocks in the WC ecosystem, the estimated median ecosystem-level effect (i.e., \( \mu_e \)) for the NPGO was 2.4 times higher than the BI for pink salmon and 2.5 times higher for chum salmon (Table 3; Fig. 4). Similarly, the estimated median stock-specific effects (i.e., \( \gamma_i \)) for the NPGO (which are centered around the mean ecosystem-level effect) were consistently higher than for the median stock-specific effects of the BI (Fig. 3; pink salmon: \( \gamma_{NPGO} \) range = 0.22–0.29 versus. \( \gamma_{BI} \) range = 0.06–0.13; chum salmon: \( \gamma_{NPGO} \) range = 0.12–0.15 versus. \( \gamma_{BI} \) range = 0.03–0.08). An increase in the NPGO by one SD above the long-term mean (1967–2010) in any given year would be expected to result in 28.5 and 15.1% higher recruits-per-spawner for pink and chum salmon, respectively (Fig. 5).
In contrast to pink and chum salmon, sockeye salmon productivity in the WC ecosystem was more strongly related to changes in the BI than the NPGO, indicating that the location of the bifurcation has a stronger effect on sockeye salmon productivity than NPC strength. The estimated median ecosystem-level effect of the BI on WC sockeye salmon productivity was 2.4 times higher than for the NPGO (Table 3; Fig. 4). Furthermore, the median stock-specific effects of the BI on sockeye salmon productivity (i.e., $γ_{BI,i}$) are shown in Figure 3. Coefficients (in standard deviation units) are shown for pink salmon (panel a), chum salmon (panel b), and sockeye salmon (panel c). Within each panel, stock-specific estimates are grouped by ecosystem and stocks are ordered south (left) to north (right) where the stock number (x-axis) corresponds to the numbers in Fig. 1. Solid circles (black) indicate $γ_{BI,i}$ median values and dashed black lines indicate the 95% credible intervals for the BI effect. Solid squares (red) indicate $γ_{NPGO,i}$ median values and dashed red lines indicate the 95% credible intervals for the NPGO effect. Solid horizontal lines indicate posterior medians for the ecosystem-level effects, $μ_{c}$.

range = 0.09–0.13) were consistently higher than stock-specific effects of the NPGO (\( \gamma_{NPGO} \) range = 0.02–0.08; Fig. 3c). This stronger effect of the BI on sockeye salmon productivity corresponded to an 11.7% increase in productivity given a one SD-unit increase in the BI compared to a 4.8% increase in

Table 3. Ecosystem-wide effects (i.e., \( \mu_e \)) for the BI and NPGO indices from the best-fit models (9 and 10 in Table 1). Values are in standard deviation units and show the median for \( \mu_e \) with 95% credible intervals given in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>Ecosystem</th>
<th>( \mu_e,BI )</th>
<th>( \mu_e,NPGO )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pink</td>
<td>WC</td>
<td>0.104 (0.025, 0.186)</td>
<td>0.251 (0.162, 0.339)</td>
</tr>
<tr>
<td></td>
<td>GOA</td>
<td>-0.024 (-0.086, 0.036)</td>
<td>0.036 (-0.028, 0.099)</td>
</tr>
<tr>
<td></td>
<td>BS</td>
<td>0.283 (-0.257, 0.864)</td>
<td>-0.031 (-0.415, 0.383)</td>
</tr>
<tr>
<td>Chum</td>
<td>WC</td>
<td>0.057 (-0.001, 0.117)</td>
<td>0.141 (0.075, 0.204)</td>
</tr>
<tr>
<td></td>
<td>GOA</td>
<td>0.013 (-0.043, 0.075)</td>
<td>-0.007 (-0.077, 0.060)</td>
</tr>
<tr>
<td></td>
<td>BS</td>
<td>-0.025 (-0.091, 0.044)</td>
<td>0.096 (0.003, 0.186)</td>
</tr>
<tr>
<td>Sockeye</td>
<td>WC</td>
<td>0.111 (0.052, 0.170)</td>
<td>0.047 (-0.032, 0.128)</td>
</tr>
<tr>
<td></td>
<td>GOA</td>
<td>-0.029 (-0.080, 0.023)</td>
<td>0.026 (-0.049, 0.094)</td>
</tr>
<tr>
<td></td>
<td>BS</td>
<td>0.012 (-0.083, 0.096)</td>
<td>0.038 (-0.051, 0.126)</td>
</tr>
</tbody>
</table>

Figure 4. Posterior distributions for the ecosystem-level effects, \( \mu_e \), of the bifurcation index (BI) and North Pacific Gyre Oscillation (NPGO) in standard deviation units. Distributions are shown for pink salmon (top row), chum salmon (middle row), and sockeye salmon (bottom row), as well as for the West Coast ecosystem (left column), Gulf of Alaska ecosystem (middle column) and Bering Sea ecosystem (right column). Solid lines (black) indicate distributions for the ecosystem-level BI effect and dashed lines (red) indicate distributions for the NPGO ecosystem-level effect. [Colour figure can be viewed at wileyonlinelibrary.com].
productivity given a one SD-unit increase in the NPGO index (Fig. 5).

In the GOA ecosystem, there was no evidence for consistent stock-specific or ecosystem-level effects of either the BI or NPGO on the productivity of all three species (Figures 3 and 4; Table 3). The 95% credibility intervals for stock-specific effects included zero for all species, stocks, and both the BI and NPGO indices (Fig. 3). Similarly, the posterior distributions for the GOA ecosystem-level effects of the BI and NPGO were close to zero for all species (Fig. 4; Table 3), indicating neither index has strong effects on productivity of sockeye salmon in the Bering Sea.

Model selection results indicated that for all three species there were no alternative models with a WAIC within three units of the minimum WAIC (Table 2). Also, for pink and chum salmon, no models had a WAIC within 10 units of the minimum WAIC, whereas sockeye salmon had two models that had WAIC values within 10 units of the minimum (models 4 and 10; Table 2). Models that included a stock-specific autocorrelation term tended to fit the data better for chum salmon, whereas for pink and sockeye salmon there was more support for an autocorrelation term shared across stocks (Table 2). Furthermore, all models showed a lower number of effective parameters compared to the nominal number of parameters, suggesting considerable borrowing of information across stocks within the models (Table 2).

Sensitivity analysis
Estimated BI effects on salmon productivity were mostly insensitive to the methods we used to calculate the index. For instance, our original BI index was highly correlated with the alternative index calculated using a larger grid of drifters ($r = 0.94$) and with the index calculated using the methods outlined in Watters and Bessey (2008) ($r = 0.94$). For the index calculated using a larger grid of drifters, the rank order of the fitted models did not change compared to the models fitted using the original BI index for all three species (Table S1). For the index based on Watters and Bessey (2008), the rank order of models did not change for pink and chum salmon, but were moderately sensitive for sockeye salmon (Table S2). In particular, the top three models were the same for sockeye salmon for both indices, although the order was different, with a model without the BI or NPGO having the lowest WAIC when the alternate Watters and Bessey (2008) BI index was used (model 4; Table S2). In addition, the single-stock model analysis did not indicate substantial differences in the effects of the BI and

NPGO across stocks at smaller spatial scales than those of the three large marine ecosystems (Fig. S3).

DISCUSSION

In this study, we estimated the effects of two modes of variability in the NPC on the productivity of 163 pink, chum, and sockeye salmon stocks to better understand how horizontal ocean transport pathways could influence population dynamics of Pacific salmon. We found that indices of north-south positioning of the NPC bifurcation and the NPC strength both had strong estimated effects on pink, chum, and sockeye salmon productivity and were included in the best-fit hierarchical models for each species. We also found that the most consistent effects of the BI and NPGO were on salmon stocks in the WC ecosystem. There was a northward-shifted bifurcation and increased NPC strength associated with increased salmon productivity. Finally, we found that neither index was correlated with salmon productivity for stocks in the Gulf of Alaska, and there were less consistent effects for salmon stocks in the Bering Sea than in the West Coast ecosystem.

Our result that variability associated with the NPC is an important driver of changes in Pacific salmon productivity, particularly for stocks in the WC ecosystem, is consistent with the results of several previous studies that have indicated that horizontal transport pathways can strongly influence coastal marine ecosystems in the Northeast Pacific (Batten and Freeland, 2007; Sydeman et al., 2011; Kilduff et al., 2015). In particular, our finding that a stronger NPC (i.e., a positive NPGO) is associated with increased salmon productivity in the WC ecosystem corresponds with the result of Kilduff et al. (2015), which showed that the dominant modes of variability for hatchery coho and chinook salmon survival rates along the west coast of North America are significantly and positively related to the NPGO index. Although the mechanisms linking variability in the NPGO and salmon productivity are not clear, several studies have indicated that broad-scale variability in the strength of the sub-polar and sub-tropical gyres, as indexed by the NPGO, is linked with changes in salinity, nutrients, and chl-a concentrations in coastal ecosystems in the Northeast Pacific (Di Lorenzo et al., 2008; Chenillat et al., 2012). This suggests that the effects of the NPGO on salmon productivity may be mediated by changes in physical and biological oceanographic conditions that affect prey availability in those ecosystems.

Our results further suggested that a northward-shifted positioning of the NPC was associated with increased salmon productivity in the WC ecosystem. This is consistent with previous research that indicated that the majority (~64%) of variability in biological productivity in the Northern California Current is related to the north-south location of the NPC bifurcation, with higher productivity being associated with a northward-shifted positioning of the NPC (Sydeman et al., 2011). One possible explanation for this result is that shifts in the location of the NPC may influence the advection of zooplankton communities into coastal ecosystems, which are a key food resource for juvenile salmon (Beauchamp et al., 2007; Brodeur et al., 2007a; Armstrong et al., 2008). For example, Keister et al. (2011) and Bi et al. (2011a) indicated that changes in along-shore transport could strongly influence zooplankton communities in the Northern California Current with the transport of cooler water from northern areas into the Northern California Current being associated with a more lipid-rich copepod community.

Alternatively, the location of the bifurcation may also have indirect effects on high-trophic-level species by altering physical or biological oceanographic conditions such as inorganic nutrient concentrations, water column stability, or thermal regimes (Di Lorenzo et al., 2009; Keister et al., 2011; Sydeman et al., 2011). These indirect effects may be particularly important for salmon stocks that enter the ocean in areas sheltered from coastal currents. For example, within the WC ecosystem, the Salish Sea (which includes the Strait of Georgia East of Vancouver Island, B.C., and Puget Sound, Washington) is largely isolated from coastal ocean currents and the oceanography of this region is strongly influenced by freshwater discharge from the Fraser River, which brings land-derived nutrients into coastal waters and can influence water column stability (Hickey and Banas, 2008). Despite this difference in oceanographic conditions in the Salish Sea compared with other parts of the West Coast ecosystem, we found that the single-stock effects of the BI and NPGO did not differ substantially between stocks that first enter the salt water in the Salish Sea and stocks that enter the ocean elsewhere within the West Coast ecosystem. Thus, the effects of conditions encountered by Salish Sea stocks outside of the Salish Sea appear to dominate the effects of oceanographic conditions that are unique to the Salish Sea.

Horizontal transport pathways that are controlled by changes in the NPC do not appear to substantially contribute to variability in salmon productivity for stocks in what we called the GOA ecosystem. For instance, we found no support for consistent effects of either NPC index on the productivity of salmon stocks in this region. This finding is in contrast to the strong
and consistent positive effects of the NPC indices on productivity in the WC ecosystem, which further suggests that different environmental pathways may control productivity of higher-trophic-level species in these two ecosystems. This hypothesis that different mechanisms may control salmon productivity in different ecosystems is supported by several previous studies that have also indicated differences in the effects of environmental variables on salmon productivity between the WC and GOA ecosystems. For example, Mueter et al. (2002) showed opposite effects of SST on pink, chum, and sockeye salmon in northern and southern areas, with the dividing line occurring around southern Southeast Alaska. Similarly, Malick et al. (2015b) indicated that the phenology of the spring bloom of phytoplankton has effects of opposite sign on pink salmon stocks in Alaska compared to stocks in British Columbia. Both Mueter et al. (2002) and Malick et al. (2015b) suggested that the different effects may be driven by differences in oceanography between the WC and GOA ecosystems, which is further supported by our results. Differences in the effects of the NPC between northern and southern areas further suggests that prey availability for salmon in the GOA may either not be affected by variability in horizontal transport or prey availability may not be limiting.

In the Bering Sea, we found less consistent effects of the BI and NPGO on salmon productivity than in the West Coast ecosystem. For example, we found that (i) neither index had a strong effect on sockeye salmon productivity, (ii) the NPGO was positively related to chum salmon productivity, and (iii) the estimated effects of both indices on pink salmon productivity were highly uncertain. Because the BS ecosystem is geographically isolated from the NPC, it is unlikely that variability associated with the NPC has a direct effect on salmon productivity in this region. Instead, the BI and NPGO likely represent indirect indicators of broad atmospheric or oceanographic patterns, such as changes in the North Pacific Oscillation, that link conditions in the Bering Sea to the mid-latitude conditions driving variability in the NPC (Di Lorenzo et al., 2013b).

Finally, our results demonstrate that ocean current patterns and horizontal transport pathways can strongly influence Pacific salmon stocks, with the strongest effects being observed for stocks in Washington and British Columbia. This conclusion, combined with previous research, indicates that in some areas multiple environmental pathways may underlie changes in salmon productivity, where one set of pathways is mediated by vertical ocean transport (e.g., upwelling) and another set is mediated by horizontal ocean transport (Ottersen et al., 2010; Di Lorenzo et al., 2013a; Malick et al., 2015a). Furthermore, our results provide some evidence that the relative importance of horizontal transport pathways may differ between northern and southern areas for the species we considered. Taken together, this suggests that quantifying the relative importance and cumulative effects of multiple environmental pathways is important for understanding how future environmental change will influence the production of higher-trophic-level species.

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REFERENCES


**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Model selection quantities from the sensitivity analysis that used the bifurcation index calculated using an expanded grid of drifters. # gives the model number as defined in Table 1 of the main text; Np gives the nominal number of parameters; pd gives the effective number of parameters; and ΔWAIC gives the WAIC value for each model relative to the model with the minimum WAIC value.

**Table S2.** Model selection quantities from the sensitivity analysis that used the bifurcation index calculated using the methods outlined in Watters and Bessey (2008). # gives the model number as defined in Table 1 of the main text; Np gives the nominal number of parameters; pd gives the effective number of parameters; and ΔWAIC gives the WAIC value for each model relative to the model with the minimum WAIC value.

Figure S1. Starting location for the OSCURS model drifters used to calculate the bifurcation index. Black dots show the locations where the drifters were seeded for the main bifurcation index and grey plus signs indicate the additional drifter starting locations for the bifurcation index calculated using the expanded grid of drifters, which was part of a sensitivity analysis examining changes in assumptions underlying the bifurcation index.

Figure S2. Video of OSCURS model drifter trajectories for years 1967–2010. Each frame of the video shows the drifter tracks for a single year where the drifters were simulated from February 1 to June 30. Red tracks indicate drifters that ended south of their starting location and blue tracks indicate drifters that ended north of their starting location. The upper right hand corner in each frame gives the year and the bifurcation index (BI) for that year. The BI values are standardized to a mean of 0 and a standard deviation of 1 (i.e., standard deviation units, SDUs).

Figure S3. Single-stock model coefficients for the BI and NPGO (i.e., γ). Gamma coefficients were estimated by fitting generalized Ricker models (i.e., Eqn 2) to each of the 163 salmon stocks separately using maximum likelihood. Coefficients (in standard deviation units) are shown for pink salmon (panel a), chum salmon (panel b), and sockeye salmon (panel c). Within each panel, stock-specific estimates are grouped by ecosystem and stocks are ordered south (left) to north (right) where the stock number (x-axis) corresponds to the numbers in Figure 1 of the main text. Solid circles (black) indicate the maximum likelihood estimate for the BI effect, γBI,i and solid squares (red) indicate the NPGO effect, γNPGO,i. Points inside the grey boxes indicate salmon stocks that enter the ocean in the Salish Sea.