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Accounting for multiple pathways in the connections among climate variability, ocean processes, and coho salmon recruitment in the Northern California Current

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Abstract: Pathways linking climate to population dynamics of higher-trophic-level fish species such as Pacific salmon often involve a hierarchy in which regional-scale physical and biological processes mediate the effects of large-scale climate variability. We used probabilistic networks to investigate 17 potential ecological pathways linking climate to Oregon coho salmon (*Oncorhynchus kisutch*) recruitment. We found that pathways originating with the Pacific Decadal Oscillation were the most influential on recruitment, with the net effect being two to four times greater than for pathways originating with the North Pacific Gyre Oscillation or the Oceanic Niño Index. Among all environmental variables, sea surface temperature and an index of juvenile salmon prey biomass had the greatest effects on recruitment, with a 76% chance of recruitment being equal to or below average given that ocean temperatures were above average and a 34% chance of recruitment being below average given that prey biomass was above average. Our results provide evidence that shifts in climate patterns could strongly influence recruitment simultaneously through multiple ecological pathways and highlight the importance of quantifying cumulative effects of these pathways on higher-trophic-level species.

Résumé : Les voies qui relient le climat à la dynamique des populations d'espèces de poissons de niveau trophique élevé comme les saumons du Pacifique définissent une hiérarchie dans laquelle des processus physiques et biologiques à l'échelle régionale modulent les effets de la variabilité à grande échelle du climat. Nous avons utilisé des réseaux probabilistes pour étudier 17 voies écologiques potentielles reliant le climat au recrutement du saumon coho (*Oncorhynchus kisutch*) de l'Oregon. Nous avons constaté que les voies émanant de l'oscillation décennale du Pacifique exercent la plus grande influence sur le recrutement, leur effet net étant de deux à quatre fois supérieur à celui des voies qui émanent de l'oscillation du tourbillon nord-pacifique ou de l'indice Niño océanique. De toutes les variables environnementales, la température de la surface de la mer et un indice de biomasse des proies des saumons juvéniles avaient les plus grands effets sur le recrutement, avec une probabilité de 76 % que le recrutement soit égal ou inférieur à la moyenne étant donné que les températures de l'océan étaient supérieures à la moyenne et une probabilité de 34 % que le recrutement soit inférieur à la moyenne étant donné que la biomasse de proies était supérieure à la moyenne. Nos résultats fournissent des preuves appuyant la thèse voulant que des changements des régimes climatiques puissent exercer simultanément une forte influence sur le recrutement par l'entremise de multiples voies écologiques et ils soulignent l'importance de quantifier les effets cumulatifs de ces voies sur les espèces de niveau trophique élevé. [Traduit par la Rédaction]

Introduction

Pacific salmon (*Oncorhynchus* spp.) populations along the Northeast Pacific coast exhibit large interannual and interdecadal fluctuations in adult abundances. Changes in large-scale climate patterns are often associated with variability in salmon recruitment, although there are many intermediate-scale processes that can link climate and salmon (Mueter et al. 2002; Beamish et al. 2004; Drinkwater et al. 2010; Malick et al. 2015). In particular, several regional-scale oceanographic variables are associated with both large-scale climate patterns and salmon recruitment, including sea surface temperature (SST), upwelling intensity, and ocean transport (Chavez et al. 2003; Keister et al. 2011; King et al. 2011). However, most research on relationships between climate variability and salmon recruitment simplify the ecological system by considering only direct effects of climate on recruitment (Fig. 1*a*).

For instance, multiple studies show correlations between the Pacific Decadal Oscillation (PDO) and indices of salmon survival (Mantua et al. 1997; Malick et al. 2009; Burke et al. 2013) without further investigating possible pathways of bottom-up or top-down processes linking the two.

Pathways linking climate to the dynamics of higher-trophic-level fish species such as salmon often involve a hierarchy in which regional-scale physical and biological processes mediate the effects of large-scale climate variability (Fig. 1*b*) (Dippner 2006; Drinkwater et al. 2010; Ottersen et al. 2010). For example, there are at least two hypothesized pathways connecting the PDO with salmon recruitment in the Northern California Current (Wells et al. 2008; Keister et al. 2011). Under the first hypothesis, regional-scale SST and juvenile salmon prey biomass act as intermediaries between the PDO and recruitment (Cole 2000; Daly et al. 2013), whereas under the second hypothesis, regional-scale ocean trans-

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Fig. 1. Schematic of pathways linking large-scale climate processes and Pacific salmon recruitment: (*a*) climate has a direct effect on recruitment, (*b*) climate effects on recruitment are mediated by a regional-scale oceanographic process (e.g., upwelling), (*c*) climate effects are mediated by multiple regional-scale variables resulting in two pathways connecting climate and recruitment.
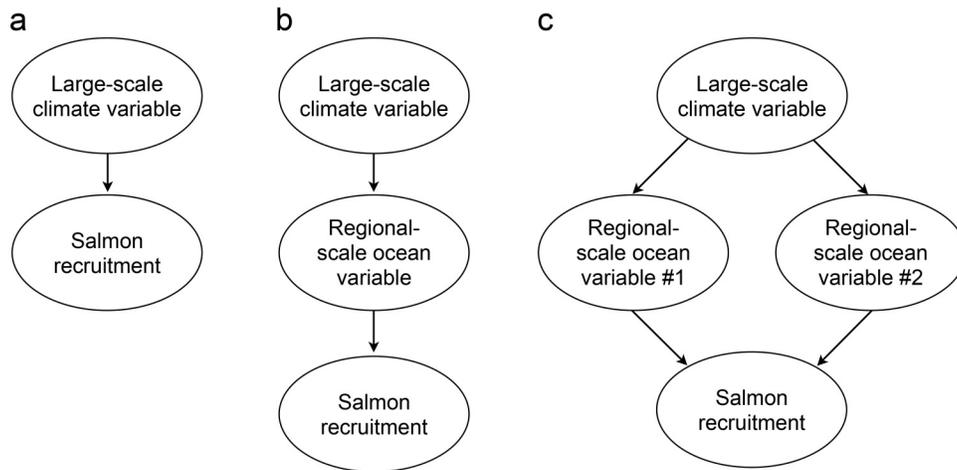
port and copepod community composition act as intermediaries (Bi et al. 2011*b*; Keister et al. 2011). These hypothesized pathways include processes that occur at several temporal, spatial, and functional scales and therefore represent the ecological system more realistically than assuming direct relationships between climate patterns and salmon recruitment (Levin 1992; Bakun 1996; Hunt et al. 2002; Ottersen et al. 2010).

Despite the more intuitive appeal of the hierarchical pathway perspective on relationships between climate and salmon recruitment, it remains incomplete because it assumes a stationary ecosystem structure. Abrupt or persistent changes in climate patterns can substantially alter physical and biological processes in coastal ecosystems, potentially influencing high-trophic-level species through numerous ecological pathways (Fig. 1*c*) (Mantua et al. 1997; Anderson and Piatt 1999). This implies a more complex hierarchy in which the relative strengths of alternative pathways may change over time. However, there has been little research on the relative importance of particular pathways on salmon recruitment or on the joint effect of multiple pathways linking climate to fish recruitment in general.

In this study, we investigate how multiple ecological pathways potentially link climate and oceanographic processes to wild Oregon coho salmon (*Oncorhynchus kisutch*) recruitment. Specifically, we developed two probabilistic network models, similar to Fig. 1*c*, to determine the joint effect of multiple ecological pathways on coho salmon recruitment as well as the relative strength of specific pathways. In addition, we investigated two time periods to determine whether the dominant pathways changed over time. Our use of probabilistic networks allowed us to (*i*) clearly and intuitively model recruitment as a function of multiple ecological pathways, (*ii*) quantify the effects of both direct and indirect effects of environmental variables on salmon recruitment, and (*iii*) account for uncertainty in the relationships among variables by describing the relationships probabilistically rather than deterministically (Varis 1995). We also identify important environmental variables that could be used as indicators of salmon recruitment and contribute to the understanding of the mechanisms that control recruitment of Pacific salmon in the Northern California Current region.

Methods

Overview

We used data for nine environmental variables to estimate the relative strength and net effects of 17 ecological pathways on recruitment of wild Oregon coho salmon. The pathways were orga-

nized into two independent probabilistic networks (e.g., Fig. 1*c*), a physical network and a biophysical network, which we used to perform two analyses. First, to determine the relative strength of each of the 17 pathways within the networks, we used partial correlation coefficients to estimate the strength of each link in the networks. Second, to quantify the joint effect of multiple pathways on coho salmon recruitment, we used fitted probabilistic networks along with Monte Carlo sampling to estimate conditional posterior probability distributions for various levels of coho salmon recruitment, given several scenarios (i.e., sets of conditions) for the environmental variables.
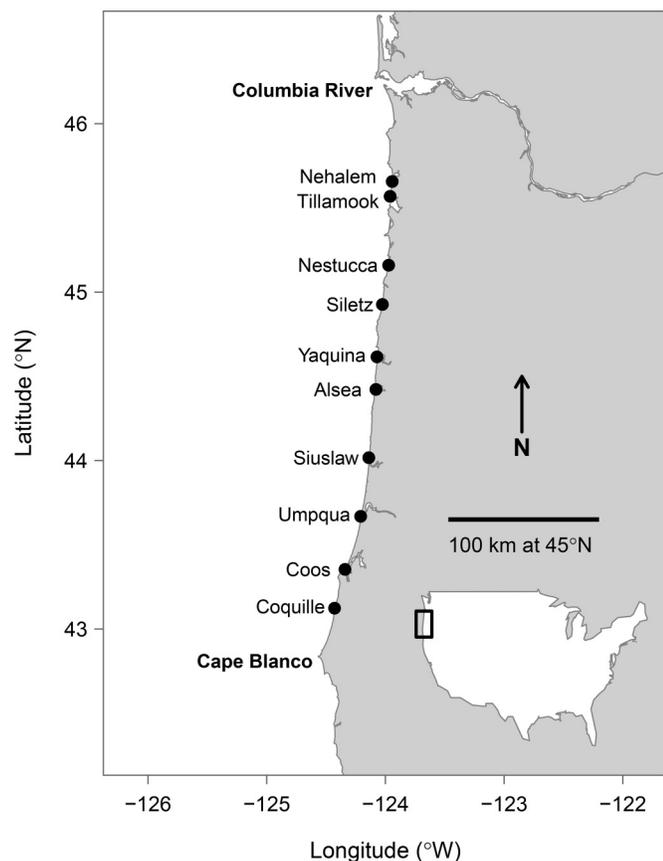
Data sources

Coho salmon recruitment

Oregon's wild coho salmon populations are divided into three discrete evolutionarily significant units (ESU) (Weitkamp et al. 1995; Lawson et al. 2007). The focus of our study is on the Oregon Coast ESU, the largest one, which extends from the mouth of the Columbia River south to Cape Blanco (Fig. 2). It contains 21 independent coho salmon populations (i.e., populations that were historically self-supporting) located in several different river basins (Lawson et al. 2007). Oregon Coast coho salmon rear mainly in coastal streams and rivers, but some populations rear primarily in coastal lakes and have a distinct life history and different population dynamics than the river populations (Lawson et al. 2004; PFMC 2013). Because of this, we restricted our analysis to the river populations only. In the past, there was also substantial production of hatchery coho salmon on the Oregon Coast — we have excluded this production from our analysis and concentrate on just the wild production.

Annual aggregate adult recruitment and escapement estimates for the wild river coho salmon populations within the Oregon Coast ESU were available for brood years 1968–2009 from the Pacific Fisheries Management Council (Rupp et al. 2012; PFMC 2013). Recruitment estimates were generated from adult escapement and harvest rate estimates, where escapement was estimated through statistical expansion of survey counts in a subset of stream reaches within the Oregon Coast ESU (Lewis et al. 2010). For return years 1971 through 1990, adult escapements were monitored using spawner surveys on standard index areas along the Oregon Coast. Since 1990 a stratified random sampling design has been implemented, which covers all spawning habitats within the Oregon Coast ESU (Jacobs and Nickelson 1998; Lewis et al. 2010). Because spawner survey methods prior to 1990 did not allow reliable reconstruction of population-specific abundance, we used

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Fig. 2. Study area showing the ocean-entry locations of the ten largest river basins located within the Oregon Coast coho salmon evolutionarily significant unit (ESU).
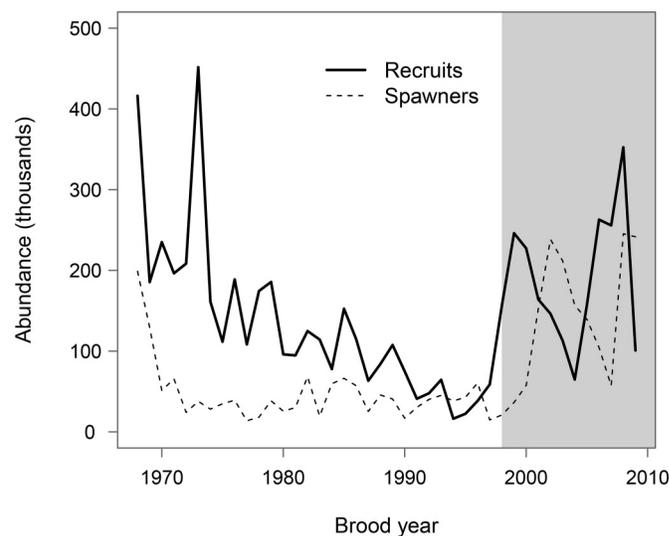

Fig. 3. Time series of spawning stock size (dashed line) and the resulting total recruitment (solid line) for Oregon Coast coho salmon. Grey shaded region indicates the period used for the biophysical network.

after accounting for density-dependent effects of spawner abundance (see online supplemental Fig. S1[1]).

Environmental variables

Nine environmental variables were included in the probabilistic networks (Table 1; footnotes in that table indicate the data sources). Three of the variables represent large-scale climate patterns, which reflect variability over thousands of kilometres (King et al. 2011). The first, PDO, is defined as the leading principle component of monthly SST anomalies in the North Pacific poleward of 20°N (Mantua et al. 1997). Second, the North Pacific Gyre Oscillation (NPGO) is defined as the second principle component of monthly sea-surface-height anomalies in the North Pacific and represents variability that is orthogonal to the PDO over the period 1950–2010 (Di Lorenzo et al. 2008). Third, we used the Oceanic Niño Index (ONI) to index variability associated with El Niño and La Niña events; it is defined as the 3-month running average of SST anomalies in the Niño 3.4 region (120°W–170°W and 5°S–5°N; Trenberth 1997). Unlike the PDO and NPGO, which have most of their variance at decadal and interdecadal periods, the ONI has most of its variance at interannual time scales (Sarachik and Cane 2010). Because large-scale climate variables are believed to set the stage for regional-scale physical and biological processes, each of the three large-scale variables was averaged over the months of December–March in the winter prior to smolt out-migration (Mantua et al. 1997; Yeh et al. 2011; Di Lorenzo et al. 2013).

Four of the environmental variables represent physical oceanographic variability on a smaller, regional scale. First, we used monthly National Oceanic and Atmospheric Administration extended reconstructed SST version 3b data to index regional-scale variability in SST off the coast of Oregon (Smith et al. 2008). Monthly SST values were averaged over January–June for a 2° × 2° grid cell centered on 44°N, 126°W. The January–June period was chosen because research has suggested that coastal SST can strongly influence salmon survival at time periods just prior to and during smolt out-migration (Mueter et al. 2005).

Second, we used the Bakun upwelling index to represent interannual variability in upwelling intensity, where intensity was quantified as the volume of surface water transported offshore

aggregate recruitment data across all coho salmon populations in the Oregon Coast ESU (Fig. 3), which is consistent with the current preseason forecasting methods used by the Pacific Fisheries Management Council (PFMC 2013).

We chose to focus on wild coho salmon production instead of hatchery production because of a potential mismatch between the biological data used in this study and the geographic location of coho salmon hatcheries. The most widely used and reliable source of hatchery data in the Northern California Current region is the Oregon Production Index (Cole 2000; Koslow et al. 2002; Logerwell et al. 2003), which is largely composed of data for Columbia River hatcheries (90% Columbia River fish since 1991; PFMC 2013). Because the Columbia River is approximately 425 km north of the sampling locations used to produce the biological data set, the biological variables may not be representative of early ocean conditions of coho salmon entering the ocean from the Columbia River. In addition, Columbia River fish enter the ocean in the Columbia River plume, which can have different dynamics than other coastal areas owing to the large freshwater influence (Hickey et al. 1998).

While our main focus was on total recruitment, we also investigated an index of coho salmon productivity. To create the productivity index, we fit a Beverton–Holt model ($\log_e(R/S) = \log_e(a) - \log_e(1 + bS)$; Beverton and Holt 1957) to the spawner–recruitment time series and then calculated the residuals. We used this residual series as our productivity index, which describes interannual variability in productivity (in units of $\log_e(R/S)$)

Table 1. Summary of environmental variables used to construct the probabilistic networks.

Variable	Seasonal average	Extent	Years	Source[a]
ONI	December–March	5°N–5°S	1970–2011	1
PDO	December–March	20°N–65°N	1970–2011	2
NPGO	December–March	25°N–62°N	1970–2011	3
SST	January–June	43°N–45°N	1970–2011	4
Upwelling	March–April	43.5°N–46.5°N	1970–2011	5
Spring transition	—	43.5°N–46.5°N	1970–2011	5
Deep temperature	May–September	44.6°N	1998–2011	6
Ichthyoplankton	January–March	44.6°N	1998–2011	6
Copepod biomass	May–September	44.6°N	1998–2011	6
Coho recruitment	—	43°N–46°N	1970–2011	7

Note: Seasonal average indicates the period over which each variable was averaged. Extent refers to the north–south spatial area that the variable covers (degrees latitude). ONI, Oceanic Niño Index; PDO, Pacific Decadal Oscillation; NPGO, North Pacific Gyre Oscillation; SST, sea surface temperature.

[a]1: http://www.cpc.ncep.noaa.gov; 2: http://jisao.washington.edu/pdo/PDO.latest; 3: http://www.o3d.org/npgo/npgo.php; 4: http://www.ncdc.noaa.gov/ersst/; 5: http://www.pfel.noaa.gov; 6: Peterson et al. 2012; 7: PFMC 2013.

caused by geostrophic wind fields (Bakun 1973; Schwing et al. 1996). Daily values for the upwelling index were available for 1970–2011 for the 45°N, 125°W station. We averaged the upwelling index over March–April to represent ocean conditions just prior to the spring transition and smolt out-migration (Lawson 1997; Logerwell et al. 2003). Third, to index interannual variability in the start date of the upwelling season, we used the Bakun upwelling index to calculate the spring transition date as the day of the year corresponding to the minimum value of the cumulative upwelling index (Bakun 1973; Bograd et al. 2009), where the cumulative upwelling index was calculated by taking the daily cumulative sum of the Bakun upwelling index starting on 1 January of each year. Fourth, we used deepwater temperature (i.e., temperature at 50 m depth) at a station 8 km off the coast of Newport, Oregon, to index interannual variability of the source of waters that upwell along the Oregon Coast. This source water is thought to be primarily influenced by wind intensity and large-scale climate patterns such as the PDO and NPGO (Chhak and Lorenzo 2007; Jacox et al. 2014). In particular, when northerly winds are strong, water from a deeper (and thus colder) offshore source upwells onto the shelf; when winds are weak, waters upwell from a shallower (thus warmer) source.

The two remaining environmental variables represent interannual variability in regional-scale biological (rather than physical) processes. First, to index prey availability of juvenile fish available to coho salmon during their first summer at sea, we used the mean biomass (mg carbon·1000 m⁻³) of those ichthyoplankton species that in January–March will develop into the individuals that the coho salmon will eat in summer (primarily sand lance (*Ammodytes hexapterus*) and osmerids). Sampling of ichthyoplankton occurred from 1998 to 2011 (Table 1). All fish larvae were identified to the species level, and a subset of lengths were taken for each species. Length-to-biomass conversions were made using published values, and total biomass at each station was estimated (Peterson et al. 2012). Details of the ichthyoplankton sampling procedures can be found in Daly et al. (2013). Although our ichthyoplankton biomass variable indexes prey resource availability prior to smolt out-migration (i.e., January–March), previous research has indicated that ichthyoplankton biomass during this period is correlated with coho salmon survival (Daly et al. 2013).

Second, to index the quality of food (rather than the quantity) available to coho salmon during their early marine residency, we used the mean May–September log₁₀ biomass (mg carbon·m⁻³) of three primary copepod species, *Pseudocalanus mimus*, *Acartia longiremis*, and *Calanus marshallae*. These copepod species are associated with northern water sources and generally have a higher lipid content than copepod species characteristic of other water

sources off the coast of Oregon (Hooff and Peterson 2006; Lee et al. 2006). Copepods were sampled biweekly from 1998 to 2011 during May–September at the NH05 station along the Newport Hydrographic Line. Details of the copepod sampling procedures can be found in Lamb and Peterson (2005), Peterson and Keister (2003), and Bi et al. (2011a). We used a May–September mean to represent conditions experienced by coho salmon during and just after smolt out-migration (Bi et al. 2011b).

In general, all environmental variables were averaged over a temporal period corresponding to either the winter prior to ocean entry or the first summer the coho salmon were in the ocean to represent conditions coho salmon experience during the first ocean summer (Table 1). Unless stated otherwise, all reported years correspond to the ocean entry year for the coho salmon cohort.

Probabilistic networks

Probabilistic networks are a class of graphical models that permit the explicit and intuitive modeling of ecological networks while also taking uncertainties into account explicitly (Pearl 1988; Varis 1995). A complete probabilistic network is composed of three parts: (*i*) a set of variables, (*ii*) a network structure in the form of a directed acyclic graph, and (*iii*) a set of local probability distributions associated with each variable (Heckerman 1996). These three components of a probabilistic network produce a joint probability distribution over all variables in a network (also known as the global distribution for the network).

Our probabilistic network analysis consisted of four steps. First, we constructed two directed acyclic graphs, which represented alternative network structures, using the nine environmental variables. Second, we estimated the strength of each link and pathway in the networks using partial correlation coefficients. Third, we fit the probabilistic networks by estimating the parameters of the local probability distributions for each network. Fourth, we used the fitted networks to estimate conditional posterior probability distributions for recruitment given various scenarios for the environmental variables.

Network structures

We used the nine environmental variables to construct two probabilistic network structures (Figs. 4 and 5) that represented the hypothesized structure of the ecological system. Both network structures took the form of directed acyclic graphs, meaning neither network contained feedback loops. Within the networks, ovals represent variables and arrows connecting variables indicate dependencies among the variables. The networks in this study contain three types of variables: (*i*) variables with no incoming arrows
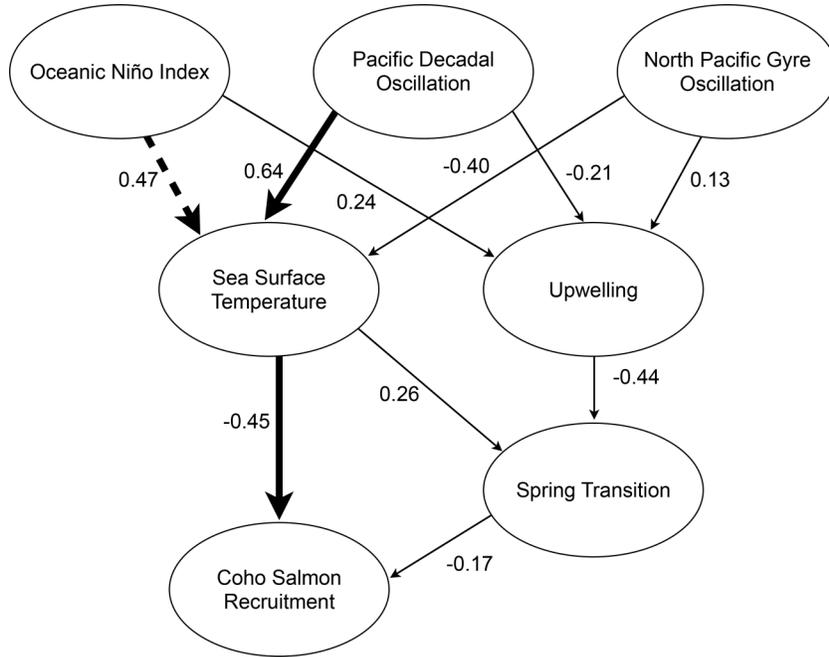
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Fig. 4. Directed acyclic graph for the probabilistic network fit using only physical environmental variables (called the physical network here). Ovals represent variables and arrows indicate dependencies among variables within the network. Numbers next to each arrow are the partial correlation coefficients. Thick solid arrows indicate the pathway with the highest mean partial correlations ("link strength"; i.e., PDO to SST to coho recruitment), whereas the thick dashed arrow indicates the first link in the pathway with the second-highest mean link strength.

Fig. 5. Directed acyclic graph for the probabilistic network fit using both physical and biological environmental variables (called the biophysical network here). Ovals represent variables and arrows indicate dependencies among variables within the network. Numbers next to each arrow are the partial correlation coefficients. Thick solid arrows indicate the pathway with the highest mean partial correlations (i.e., link strength), whereas thick dashed arrows indicate the pathway with the second highest mean link strength.
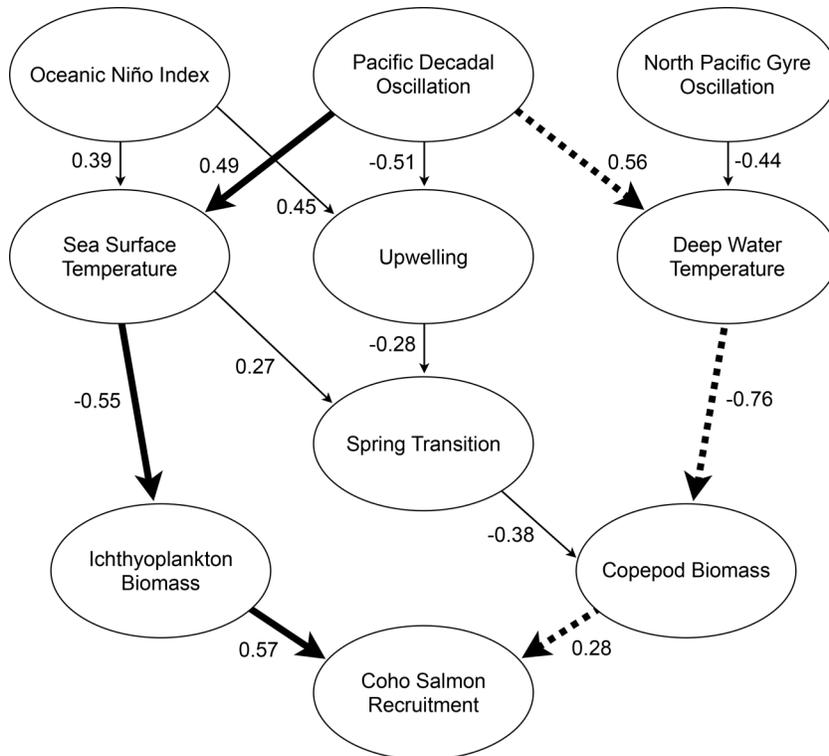
(root variables), (*ii*) variables with incoming and outgoing arrows (intermediate variables), and (*iii*) variables with only incoming arrows (in our networks, recruitment was the only variable with no outgoing arrows). Because intermediate variables can be both dependent and independent variables within the network, we refer to variables at the base of an arrow as parent variables and variables at the tip of an arrow head as child variables, as is the convention for such analyses of probabilistic network models (Korb and Nicholson 2004; Koller and Friedman 2009).

The first network structure was a physical network based on only physical environmental variables for coho salmon ocean entry years 1970–2011. The physical network structure included 7 variables, 10 links among the variables, and 9 pathways connecting large-scale climate variables with recruitment (Fig. 4). The second network structure was a biophysical network that combined physical and biological environmental variables for ocean entry years 1998–2011. The biophysical network structure had 10 variables, 13 links, and 8 pathways connecting climate variables and recruitment (Fig. 5).

Both the physical and biophysical network structures were organized in a spatial, temporal, and functional manner to represent bottom-up forcing on coho salmon recruitment. For example, large-scale climate and oceanographic patterns of variability were designated as root variables and were averaged over the winter months prior to smolt outmigration (Table 1). These large-scale variables were independent of each other in the networks (as indicated by the absence of arrows connecting these variables in the networks) and directly influenced a set of regional-scale physical oceanographic variables such as SST that represented variability in the late winter and spring (Table 1). In the physical network, SST was directly linked to coho salmon recruitment (Fig. 4), whereas in the biophysical network the regional-scale physical variables directly influenced a set of regional-scale biological variables (e.g., copepod biomass), which were then directly connected to coho salmon recruitment (Fig. 5).

Pathway and link strength

We used partial correlation coefficients to quantify the strength of each link in the network graphs (Zar 1999; Scutari 2010; Yang et al. 2011). Coefficients were computed for each link in a network by correlating two variables connected by an arrow while accounting for the effects of other variables that had incoming arrows to the child variable of the arrow of interest. For example, the partial correlation coefficient for the link connecting ichthyoplankton biomass and coho salmon recruitment in the biophysical network was computed by correlating these two variables, after removing the effect of copepod biomass on ichthyoplankton biomass and recruitment. To help identify the pathways with the strongest associations between pairs of variables (i.e., relative pathway strength), we averaged the absolute value of the partial correlation coefficients for each link in a particular pathway connecting large-scale climate variables with coho salmon recruitment. For example, to estimate the relative strength of the pathway including the PDO, SST, and coho salmon recruitment in the physical network, we averaged the partial correlation coefficients for the link between the PDO and SST and between SST and recruitment.

Network parameter estimation

Both the physical and biophysical probabilistic networks took the form of linear Gaussian probabilistic networks where the local probability distributions associated with each variable were assumed to be Gaussian and the joint distribution of all variables in the network was assumed to be multivariate normal (Shachter and Kenley 1989; Koller and Friedman 2009). Parameters of local distributions were estimated using linear regression models fit by maximum likelihood. For variables with incoming arrows, the regression models were fit with the child variable as the response variable and the parent variables as the predictor variables. For

example, in the biophysical network (Fig. 5), parameters for the local distribution for SST were estimated using a linear regression model where SST was the dependent variable and the ONI and PDO were the independent variables. For root variables, models were fit with only an intercept term. For coho salmon recruitment, models were fit using natural log-transformed coho salmon recruitment data. Model fitting was performed using R and the Bayesian network package bnlearn (Scutari 2010; R Core Team 2015).

Unlike conventional path analysis (Wright 1934), the parameters of the regression models (i.e., the parameters of the local distributions) were not of direct interest in our probabilistic network analysis (Korb and Nicholson 2004; Koller and Friedman 2009). Instead, the fitted regression parameters were used along with a Monte Carlo sampling algorithm to query the joint probability distribution of the probabilistic network, which allowed us to estimate conditional posterior probability distributions for recruitment given various scenarios for the environmental variables, as explained in the following two sections (Henrion 1988).

Posterior distributions

Using the fitted probabilistic networks, we estimated two sets of conditional posterior probability distributions for coho salmon recruitment to quantify the effect of the environmental variables on recruitment. For both sets of posterior distributions, we first discretized the predictor environmental variables into two categories, above or below the arithmetic mean value. The choice of using two categories for the predictor variables was partly due to the low sample sizes available for the environmental variables and to simplify presentation of the results (Koller and Friedman 2009). We then estimated conditional posterior probabilities for a range of recruitment values that corresponded to the observed recruitment data, which allowed us to summarize the posterior probabilities using cumulative probability distributions.

For the first set of posterior distributions, we estimated the probability of recruitment being less than a range of abundance values given values of a single environmental variable in the network (i.e., we only specified conditions for a single environmental variable at a time). For instance, we estimated the conditional probability that recruitment would be less than or equal to 150 000 salmon given that SST was above average. For environmental variables not directly connected to recruitment (e.g., the PDO), this set of posterior distributions accounts for all pathways connecting that variable and recruitment by propagating through the network uncertainty about the relationships among pairs of variables (see the Posterior sampling section below for details). That is, this set of posterior distributions quantifies the joint effect of all pathways specified in the network connecting the environmental variable and recruitment. We evaluated two scenarios for each environmental variable corresponding to the variable either being above or below average.

For the second set of posterior distributions, we estimated the probability of recruitment being less than a range of abundance levels, given that all parent variables of recruitment were either above or below their mean value. For the physical network, this corresponded to estimating the conditional probability of various levels of recruitment, given values for both SST and the spring transition, whereas the conditioning variables on recruitment for the biophysical network were ichthyoplankton biomass and copepod biomass. We estimated probabilities for four scenarios of environmental variables. Because both networks had two variables directly linked to recruitment, scenarios included cases in which both environmental variables were either above or below average and the two cases in which one of the environmental variables was above average and the other was below average.

Each set of posterior distributions included a single probability distribution for each discrete case of an environmental variable (i.e., above and below average). To facilitate the interpretation of

results, we calculated the maximum difference between cumulative probability distributions (Δp) for each discrete case of an environmental variable. For instance, Δp for the two cumulative probability distributions showing the effects of SST on recruitment was calculated by finding the maximum vertical difference (i.e., probability) between the cumulative probability distributions for recruitment given above- and below-average SST conditions. To more easily compare results from the physical and biophysical networks, we also estimated the posterior probability that coho salmon recruitment would be less than or equal to 150 000 salmon, which is approximately equal to mean recruitment for 1970–2011 (149 152 salmon).

Posterior sampling

We estimated the conditional posterior probability distributions for recruitment using logic sampling (also known as forward sampling), which is a type of rejection sampling (Henrion 1988; Korb and Nicholson 2004). As an example, to estimate the conditional probability of recruitment being below 150 000 salmon given that the PDO was above average in the physical network, we first sampled values for the three large-scale variables independently of each other, weighting by the prior distribution for each variable. We then sampled values for SST and upwelling weighting by the known values of the large-scale variables. The spring transition was then sampled, weighting by the known values of SST and upwelling. Finally, recruitment values were sampled, weighting by the known values of both parent variables. The probability of recruitment being below 150 000 given an above average PDO value was then estimated by dividing the number of samples where recruitment was less than 150 000 and the PDO was above average by the number of samples where the PDO was above average.

More generally, the estimation algorithm consisted of sampling from the joint posterior distribution, where the samples were weighted either by the prior distribution for variables with no parents or the value of the parent variables. The prior distributions for the root variables corresponded to the observed distribution over the period included in the model and were sampled independently for each root variable. Samples were only retained if the value of the sampled evidence variable of interest (e.g., PDO is above average) was the same as the value specified in the analysis. The conditional probability for coho salmon recruitment given the evidence was then computed as the number of samples where both the evidence and recruitment values matched the specified value divided by the total number of samples where the sampled evidence values match the specified value (Henrion 1988). For each analysis, we generated 1 000 000 samples from the posterior distribution to ensure that events with low probabilities were sufficiently sampled (Koller and Friedman 2009).

Results

Pathway and link strength

In both networks, the pathway with the highest relative strength originated with the PDO (Table 2). In the physical network, the pathway with the highest average link strength included the PDO, SST, and recruitment (mean of the absolute values of the two relevant correlations = 0.54; Fig. 4 and Table 2), and the pathway with the second highest relative strength included the ONI, SST, and recruitment (mean correlation = 0.46). The pathway with the strongest association among variables in the biophysical network was nearly identical to the strongest pathway in the physical network, but also included ichthyoplankton biomass (mean correlation = 0.54; Fig. 5 and Table 2), while the pathway with the second highest relative strength went from the PDO through deep temperature and copepod biomass to recruitment (mean correlation = 0.53).

Table 2. Relative pathway strength for each pathway connecting large-scale climate variables and coho salmon recruitment in the physical and biophysical networks.

Network	Pathway	$\bar{r}$
Physical	PDO, SST	0.54
	ONI, SST	0.46
	NPGO, SST	0.43
	PDO, SST, spring transition	0.35
	ONI, SST, spring transition	0.30
	ONI, upwelling, spring transition	0.28
	NPGO, SST, spring transition	0.28
	PDO, upwelling, spring transition	0.27
	NPGO, upwelling, spring transition	0.24
Biophysical	PDO, SST, ichthyoplankton	0.54
	PDO, deep temperature, copepod biomass	0.53
	ONI, SST, ichthyoplankton	0.50
	NPGO, deep temperature, copepod biomass	0.49
	PDO, upwelling, spring transition, copepod biomass	0.36
	PDO, SST, spring transition, copepod biomass	0.35
	ONI, upwelling, spring transition, copepod biomass	0.35
	ONI, SST, spring transition, copepod biomass	0.33

Note: $\bar{r}$ gives the mean of the absolute value of the partial correlation coefficients for each link in a pathway. ONI, Oceanic Niño Index; PDO, Pacific Decadal Oscillation; NPGO, North Pacific Gyre Oscillation; SST, sea surface temperature.

In the physical network, the two environmental variables with a direct effect on recruitment (SST and spring transition) had a negative relationship with recruitment, indicating that cooler surface temperatures and an earlier spring transition date are associated with higher recruitment (Fig. 4). Between these two variables, SST had a considerably stronger relationship with recruitment than the spring transition, with a partial correlation coefficient more than twice as strong (Fig. 4). In the biophysical network, both variables with a direct effect on recruitment (ichthyoplankton and copepod biomass) had a positive relationship with recruitment, suggesting higher prey biomass is associated with increased recruitment, although the relationship between ichthyoplankton biomass and recruitment was twice as strong as the relationship between copepod biomass and recruitment (Fig. 5).

Posterior distributions

In the probabilistic analysis, the variables with the strongest overall effect (i.e., the joint effect of all pathways connecting a single environmental variable and recruitment) on the probability of recruitment were regional-scale physical and biological variables with a direct effect on recruitment (Figs. 6, 7). In the physical network, SST had the strongest effect on recruitment with $\Delta p = 0.29$ (Fig. 6d), which was moderately larger than the next most influential variable, the PDO ($\Delta p = 0.18$; Fig. 6b). For the biophysical network, ichthyoplankton biomass had the strongest effect on recruitment with $\Delta p = 0.40$, which was considerably stronger than all other variables in the network (Fig. 7). Differences in steepness of the two conditional probability distributions for the physical network meant that there was a 76% chance that recruitment would be 150 000 or less when SST was above average and a 49% chance of recruitment being equal to or below that level when SST was below average (Fig. 6d). Likewise, for the biophysical network, there was a 34% chance that recruitment would be 150 000 or less when ichthyoplankton biomass was greater than average and a 73% chance when ichthyoplankton biomass was less than average (Fig. 7g).

Among the three large-scale climate variables, the PDO had the strongest overall effect on recruitment in both networks, with a Δp between two and four times greater than for the ONI and NPGO (Figs. 6, 7). In particular, a warm PDO (i.e., when the PDO was above average) was associated with lower recruitment. For exam-

Fig. 6. Cumulative probability distributions of coho salmon recruitment for the physical network conditioned on each variable in the network. Thick grey curves indicate the cumulative probability for recruitment given that the environmental variable is greater than average, whereas thick black dashed curves show cumulative probability when the environmental variable is less than average. Thin dotted lines indicate the cumulative probabilities for 150 000 salmon. The Δp gives the maximum vertical difference in probability between the two cumulative distributions within a panel.
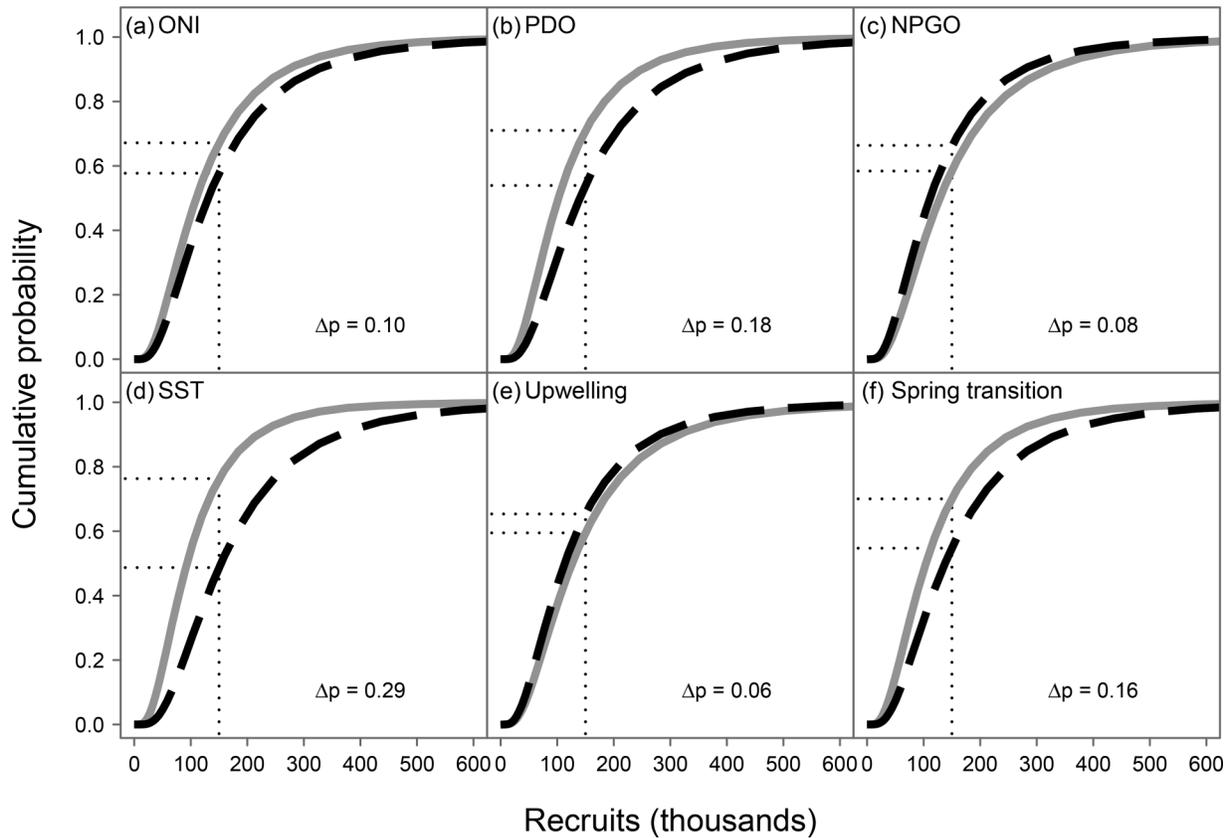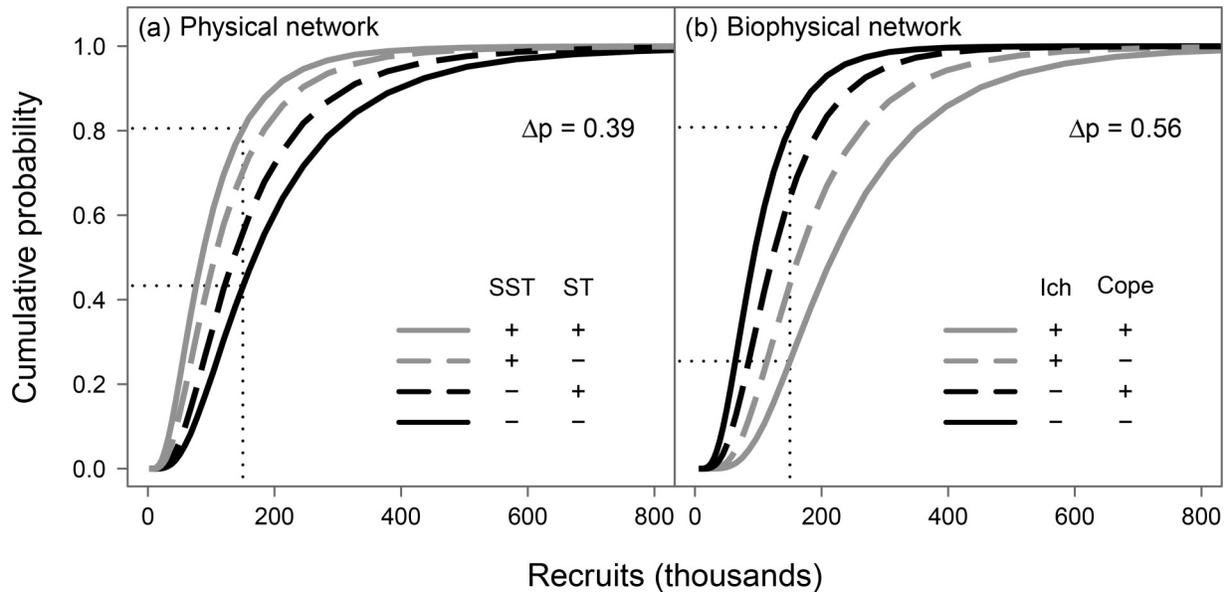
ple, there was a 71% chance that recruitment would be 150 000 salmon or less when the PDO was in a warm phase for the physical network and a 62% chance for the biophysical network (Figs. 6b, 7b). When the PDO was cool, the probability of recruitment being equal to or below 150 000 was considerably less, with a 54% chance in the physical network and a 45% chance in the biophysical network. In contrast, for the NPGO and ONI, the probability of recruitment being 150 000 or less was nearly identical, regardless of whether these variables were above or below average.

When both parent variables of recruitment in the physical network were above average, that is, when SST was warm and the spring transition occurred late, the cumulative probability distribution for recruitment (thick grey curve in Fig. 8a) was considerably steeper compared with when SST was cool and the spring transition occurred early (thick black curve in Fig. 8a). This difference in steepness corresponded to an 81% chance recruitment would be equal to or below 150 000 salmon when both conditioning variables were above average but only a 43% when both variables were below average (Fig. 8a). For the biophysical network, when both variables that index coho salmon prey resources (i.e., ichthyoplankton and copepod biomass) were above average, the cumulative probability distribution for recruitment was considerably less steep (thick grey curve in Fig. 8b) than when the prey resource indices were below average (thick black curve in Fig. 8b). This difference in the cumulative probability distributions equated to a 25% chance that recruitment would be 150 000 salmon or less when both prey indices were above average and an 81% chance recruitment would be equal to or below that level when both prey indices were below average.

When oceanographic conditions were mixed, that is, when one parent variable of recruitment was above average and the other was below average, the probability that recruitment would be 150 000 salmon or less tended to be more influenced by SST than the spring transition date in the physical network and by ichthyoplankton biomass than copepod biomass in the biophysical network (Fig. 8). For instance, the cumulative probability distribution when ichthyoplankton biomass was below average and copepod biomass was above average (black dashed curve in Fig. 8b) was moderately steeper compared with when ichthyoplankton biomass was above average and copepod biomass was below average (grey dashed curve in Fig. 8b).

Productivity index

The results from the networks fitted using an index of coho salmon productivity were qualitatively the same as the results shown above for the networks fitted using total coho salmon recruitment. The rank order of the pathways with the highest mean partial correlation coefficients was identical for both the physical and biophysical networks (see online supplemental Table S1[1]). Similarly, the rank order of the influence of each environmental variable on coho salmon (as indicated by Δp) was identical for both the physical and biophysical networks (supplemental Figs. S2–S4[1]).

Discussion

In this study, we estimated the joint effect and relative strength of multiple ecological pathways on coho salmon recruitment in the Northern California Current to better understand the mecha-

Fig. 7. Cumulative probability distributions of coho salmon recruitment for the biophysical network conditioned on each variable in the network. Thick grey curves indicate the cumulative probability for recruitment given that the environmental variable is greater than average, whereas thick black dashed curves show cumulative probability when the environmental variable is less than average. Thin dotted lines indicate the cumulative probabilities for 150 000 salmon. The Δp gives the maximum vertical difference in probability between the two cumulative distributions within a panel.
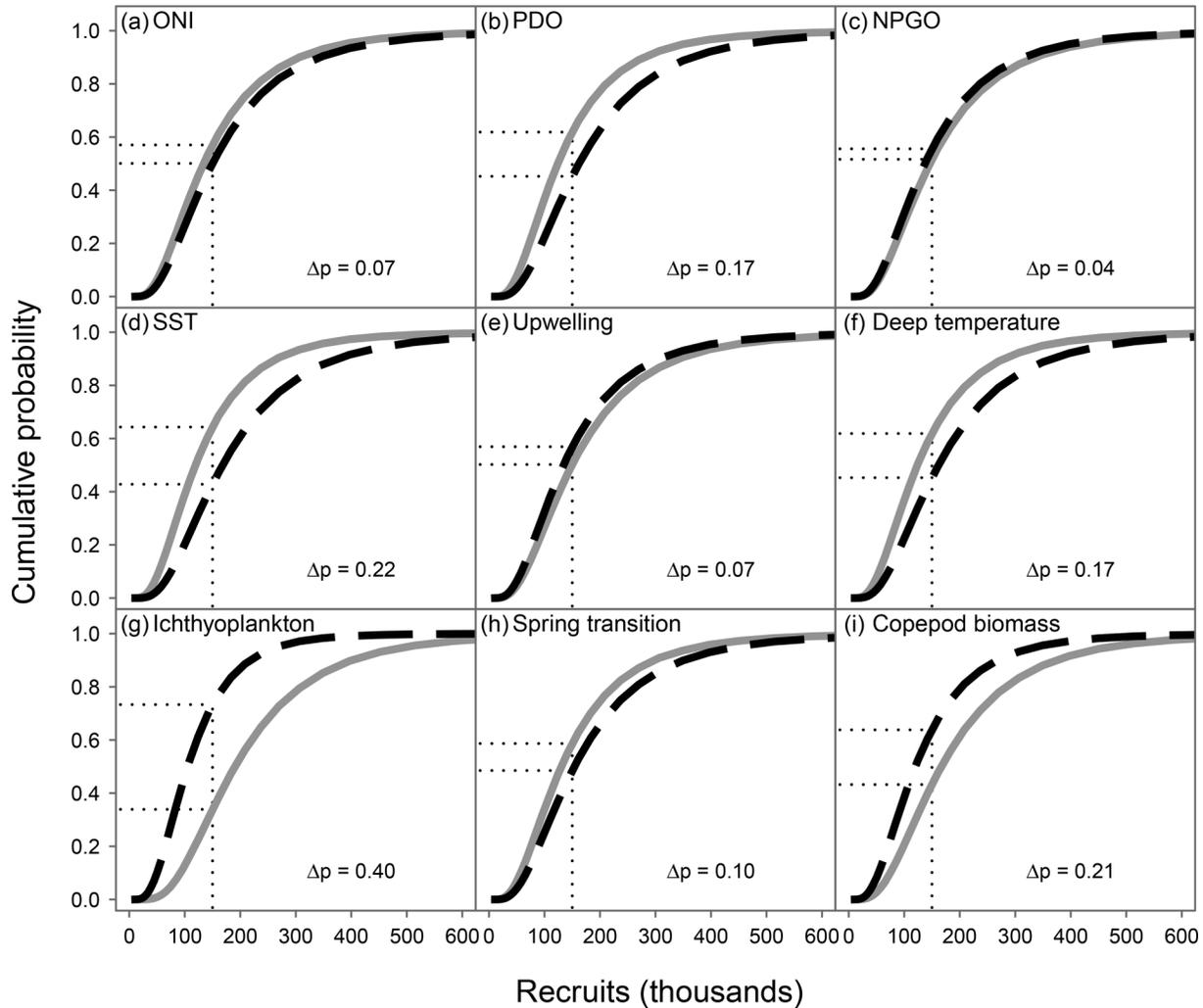
nisms linking climate variability and salmon recruitment. We found (*i*) pathways originating with the PDO were the most influential on recruitment with a joint effect considerably larger than for the ONI or NPGO, (*ii*) warm ocean years (i.e., when surface temperatures were above average) were associated with reduced salmon prey biomass as well as lower recruitment levels compared with cool years, and (*iii*) the probability of coho salmon recruitment being below average was most strongly influenced by regional-scale SST and ichthyoplankton biomass. These results suggest that shifts in climate and ocean conditions resulting from natural variability or anthropogenic climate change could influence salmon recruitment through multiple mechanisms.

Our findings indicate there were multiple pathways with high average link strength connecting the PDO and recruitment of Oregon coho salmon, suggesting that a single large-scale climate event can influence salmon recruitment simultaneously through multiple mechanisms. In the pathway with the strongest associations among variables, SST and ichthyoplankton biomass mediated the effects of the PDO on recruitment. This result broadly agrees with those of several previous studies that suggest thermal environments are important for the recruitment processes of higher-trophic-level species (Planque and Frédou 1999; Hunt et al.

2011; Martins et al. 2012). Although temperature can influence salmon directly, for example, by influencing metabolic or growth rates (Mortensen et al. 2000; Farley et al. 2007), the occurrence of ichthyoplankton biomass as an intermediary between SST and recruitment in the biophysical network suggests that the indirect effect of temperature through bottom-up forcing can also strongly influence recruitment. In particular, it appears that cooler ocean temperatures are associated with increased prey resources for juvenile salmon. This is consistent with the findings of Daly et al. (2013) and also supports the idea of a combined influence of ocean temperature and prey resources on juvenile salmon (Pearcy 1992).

The pathway with the second strongest association among variables included deep water temperature and copepod biomass as intermediaries between the PDO and recruitment, indicating changes in ocean current patterns and the subsequent advection of zooplankton into the Northern California Current region may also influence recruitment. Off the Oregon Coast, zooplankton are generally associated with one of two community structures: (*i*) a northern community that has low species diversity and large copepod species that are rich in lipids or (*ii*) a southern community that has high species diversity and small copepod species that are poor in lipids (Hooff and Peterson 2006). The observed nega-

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and salmon survival may not be stationary. In particular, Botsford and Lawrence (2002) and Pearcy (1997) indicated that the previous strong correlation between upwelling and coho salmon survival in the Northern California Current has broken down since the early 1990s. Third, the weak relationship may also be due to how upwelling was indexed. To index upwelling intensity, we averaged the daily Bakun upwelling index over the months of March and April. However, this index does not differentiate between magnitude and duration of upwelling events within this period. In particular, sustained wind speeds over a certain threshold may reduce ecosystem productivity because of transport of nutrients and phytoplankton out of the system (Botsford et al. 2003, 2006). Therefore, it is possible that shorter-term upwelling "events" on the scale of days or weeks may be more important for determining productivity in the coastal ecosystem than the seasonal upwelling average.

Some results from the physical and biophysical networks were similar, including showing the importance of the PDO and SST in the strongest pathways and the minimal influence of the NPGO and upwelling on recruitment. These similarities between the networks, which were fit using different but overlapping years, suggests that the major pathways and the most important climate and physical variables for determining recruitment did not differ greatly between the 1970–2011 and 1998–2011 time periods. In addition, this similarity indicates that our results are not sensitive to the different network structures that we used to connect large-scale climate and regional-scale physical variables.

The parameters of the local distributions in our probabilistic networks were estimated using linear regression models; therefore, we implicitly assumed these relationships were stationary (i.e., the parameters were constant over time; Walters 1987). However, sharp changes in the abundance and productivity index for Oregon Coast coho salmon over the past 40 years (Fig. 3 and online supplemental Fig. S1[1]) may reflect nonstationarity in the recruitment time series. Detecting nonstationarity and its causes is often problematic in fisheries abundance time series because of small sample sizes, the lack of contrast in the data, and confounding with environmental conditions and changes in harvest management (Walters 1987; Peterman 2009). In the case of Oregon Coast coho salmon, the short time series make it difficult to detect nonstationarity, as opposed to large variations, even though there is moderately good contrast in the recruitment estimates. In addition, potential changes in the underlying relationships between recruitment and the environmental variables may be confounded with other factors including changes in harvest management strategies or changes in freshwater habitat. Because the results of the physical and biophysical networks were similar (suggesting there was little change in relationships between the entire study period and the most recent 14 years), we believe our stationarity assumption is valid for the time periods investigated, although we caution against extrapolating the reported relationships outside the temporal bounds used to fit the probabilistic networks.

Our network modeling approach explicitly depicted the hypothesized ecological network; however, relationships within the network are correlative rather than causative. Therefore, our results could be confounded with variables or pathways not included in the networks. For example, the networks presented in this study only included pathways representing bottom-up forcing. It is likely, though, that shifts in large-scale climate patterns also influence top-down forcing pathways, for instance, by influencing the distribution of predators of juvenile coho salmon (Pearcy 2002; Perry et al. 2005). Therefore, our findings merely represent an initial step in understanding how salmon recruitment is influenced by the ecological network; further research is needed into other ecological pathways to more clearly identify the ecological mechanisms.

While our research focused on using the fitted probabilistic networks to better understand how environmental conditions in-

fluence coho salmon, the networks could also be used as a tool to help managers of salmon fisheries by providing preseason forecasts of recruitment given different scenarios of environmental conditions (Nyberg et al. 2006; Araujo et al. 2013). The probabilistic network approach has several advantages over more traditional modeling and forecasting methods (e.g., stock–recruitment models with environmental effects), including explicitly depicting the underlying ecological network, accounting for multiple pathways and indirect effects, and presenting results in a probabilistic form. In particular, such explicit representation of uncertainty is an important aspect of using ecological models to guide decision-making (Clark et al. 2001).

In conclusion, our results demonstrate that large-scale climate patterns can strongly influence coho salmon recruitment simultaneously through multiple ecological pathways. This suggests that multiple ecological mechanisms may underlie the large fluctuations observed in adult returns of Pacific salmon. In particular, it appears that both thermal regimes and prey resources are important processes in the mechanisms connecting climate variability and salmon recruitment. Taken together, these conclusions highlight the importance of quantifying the cumulative effects of these pathways to better understand how future changes in climate patterns will influence higher-trophic-level species (Ainsworth et al. 2011; Fulton 2011).

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