Multi-scale environmental forcing of Pacific salmon population dynamics

by

Michael J. Malick

M.Sc., University of Alaska Fairbanks, 2008

B.Sc., Mansfield University, 2006

Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

Doctor of Philosophy

in the
School of Resource and Environmental Management
Faculty of Environment

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SIMON FRASER UNIVERSITY
Summer 2017

Approval

Name:	Michael J. Malick
Degree:	Doctor of Philosophy
Title of Thesis:	Multi-scale environmental forcing of Pacific salmon population dynamics

Examining Committee: Dr. Mark Roseland, Professor
Chair

Dr. Sean P. Cox, Senior Supervisor
Associate Professor

Dr. Murray B. Rutherford, Supervisor
Associate Professor

Dr. Franz J. Mueter, Supervisor
Associate Professor, College of Fisheries and Ocean Sciences
University of Alaska Fairbanks

Dr. Jonathan W. Moore, Internal Examiner
Associate Professor, Department of Biological Sciences

Dr. Daniel E. Schindler, External Examiner
Professor, School of Aquatic and Fishery Sciences
University of Washington

Date Approved: May 16, 2017

Abstract

Understanding how environmental forcing governs the productivity of marine and anadromous fish populations is a central, yet elusive, problem in fisheries science. In this thesis, I use a cross-system comparative approach to investigate how environmental forcing pathways could link climatic and ocean processes to dynamics of Pacific salmon (*Oncorhynchus* spp.) populations in the Northeast Pacific Ocean. I begin by showing that phytoplankton phenology and ocean current patterns are both strongly associated with inter-annual changes in salmon productivity, suggesting that two alternative environmental pathways may contribute to changes in salmon productivity: one mediated by vertical ocean transport and subsequent phytoplankton dynamics and the other mediated by horizontal ocean transport and subsequent advection of plankton into coastal areas. The relative importance of these pathways, however, may vary over large spatial scales because the magnitude and direction of the estimated environmental effects on productivity were conditional on the latitude of juvenile salmon ocean entry. I then use a probabilistic network modeling approach to show that changes in climatic and ocean processes can impact salmon productivity via multiple concurrent environmental pathways, including multiple pathways originating from the same climatic process. Finally, I use policy analysis to demonstrate why efforts to integrate highly migratory species, such as Pacific salmon, into ecosystem-based management policies need to explicitly account for mismatches between the scale of ecosystem services provided by these species and the scale at which human activities and natural processes impact those services. Collectively, my thesis provides empirical evidence that accounting for spatial heterogeneity and the relative importance of simultaneously operating environmental pathways may be critical to developing effective management and conservation strategies that are robust to future environmental change.

Keywords: Pacific salmon; population dynamics; productivity; environmental change; spatial non-stationarity; ecosystem-based management

Acknowledgements

that helped support my research.

It is beyond my abilities to thank my family for their encouragement during my education. To my beautiful wife Erin, thank you for providing me a source of joy and happiness every day and your willingness to listen to me discuss the details of my research. To my parents, brother, and extended family, thank you for your unwavering support through all my years of education. Mother and Dad, you have always given me the freedom to pursue my interests and provided me with unconditional encouragement, thank you.

My life has been greatly enriched by these individuals, and for that I am grateful.

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Chapter 1

Introduction

Environmental forcing can have profound impacts on ecosystem services generated by marine and coastal ecosystems. Yet, fundamental uncertainties about the connections among climate patterns, physical and biological oceanographic processes, and productivity[1] of higher-trophic-level species limit our ability to anticipate or quickly detect impacts of changing environmental conditions on commercially valuable species. These uncertainties contribute to risks that have implications for conservation, harvest management, and users of living marine resources. Effectively reducing uncertainties about the links among different ecosystem components requires a quantitative understanding of how perturbations in large-scale climatic and atmospheric conditions propagate to regional and local scale changes in the population dynamics of exploited species. In this thesis, I aim to add to that quantitative understanding by applying a cross-system comparative approach to examine environmental forcing pathways linking climatic and ocean processes to dynamics of Pacific salmon (*Oncorhynchus* spp.) populations in the Northeast Pacific Ocean.

1.1 Large-scale environmental change

Environmental change in marine and coastal ecosystems can arise from anthropogenic sources or natural environmental stochasticity and can manifest as gradual or abrupt changes in mean conditions or changes in the frequency or distribution of extreme events (Jentsch et al. 2007). For example, gradual changes in climate systems over the past five decades due to increased carbon dioxide concentrations in the atmosphere have resulted in warmer mean atmosphere and ocean temperatures, decreased snow and ice pack, rising sea levels, changes in precipitation patterns, increased ocean acidification, and increased frequency of extreme temperature events (IPCC 2013).

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[1]Throughout this thesis, the term productivity refers to the per capita growth rate for a population. For Pacific salmon, productivity is estimated as the number of recruits produced per spawner.

The inter-decadal rate of change for many of these abiotic ecosystem components is unprecedented, with equally rapid changes also being observed for biological processes including shifts in phenology, species distributions, and fish stock productivity (IPCC 2013; Taylor 2008; Pinsky et al. 2013; Peterman and Dorner 2012).

Concurrent with climate and ecosystem changes from anthropogenic forcing are changes resulting from natural climate variability. In the Northeast Pacific, large-scale climate patterns, e.g., the Pacific Decadal Oscillation and North Pacific Gyre Oscillation, at least partially control the dynamics of marine and coastal ecosystems. Fluctuations in these patterns, often referred to as regime shifts, can substantially alter the structure and function of ecosystems that comprise the Northeast Pacific (Chavez et al. 2003). For instance, a rapid ecological shift occurred in the Northeast Pacific in response to a climatic regime shift in 1976/1977 (i.e., the Pacific Decadal Oscillation shifted from a "cool regime" to a "warm regime"), which resulted in a taxonomic reorganization in the Northeast Pacific, where the abundances of wild adult sockeye salmon (*O. nerka*) and pink salmon (*O. gorbuscha*) increased by more than 65% (Ruggerone et al. 2010; Anderson and Piatt 1999; Mueter and Norcross 2000).

For Pacific salmon, effects of environmental change due to perturbations in large-scale climatic conditions are mainly hypothesized to influence survival of pre-recruit life stages. In particular, the first year of marine residency for Pacific salmon is considered a critical period; mortality during this life-stage can have a disproportionately large affect on overall stock productivity compared to other life-stages (Parker 1968; Peterman 1985; Beamish and Mahnken 2001; Wertheimer and Thrower 2007). Although both bottom-up[2] and top-down[3] forcing likely contribute to mortality during this critical period, two pieces of evidence suggest that processes controlling food resource availability are particularly important. First, juvenile salmon mortality during the early marine life-stage is size selective, with larger juveniles tending to survive to adult life-stages in higher proportions than smaller juvenile salmon (Parker 1971; Holtby et al. 1990; McGurk 1996; Moss et al. 2005; Howard et al. 2016). Second, growth rates during the early marine life-stage are strongly and positively associated with overall marine survival rates (Cross et al. 2008; Duffy and Beauchamp 2011; Farley et al. 2007b). Together, this evidence suggests that large-scale climatic perturbations likely have a strong impact on Pacific salmon year class strength through bottom-up forcing pathways (Perry et al. 1996; Armstrong et al. 2005).

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[2]The term 'bottom-up forcing' is used throughout this thesis to describe regulation of ecosystem structure and function through processes that affect the base of the food chain, such as nutrient supply and primary production.

[3]The term 'top-down forcing' is used throughout this thesis to describe regulation of ecosystem structure and function occurring through predation.

1.2 Environmental forcing pathways

A prevailing bottom-up forcing hypothesis in marine ecosystems posits that vertical ocean transport processes mediate the effects of climate variability on phytoplankton dynamics in coastal ecosystems and subsequently, food resource availability for juvenile Pacific salmon (Fig. 1.1; Di Lorenzo et al. 2013b; Rykaczewski and Checkley 2008; Ware and Thomson 1991). In particular, atmospheric and ocean processes controlling water column stability and the near surface nutrient supply are frequently cited as key elements driving phytoplankton dynamics in coastal Northeast Pacific ecosystems (Henson 2007; Gargett 1997). For example, in coastal upwelling areas, winds drive surface waters offshore through Ekman dynamics, causing nutrient rich subsurface water to upwell into the euphotic zone, providing necessary nutrients for primary production (Huyer 1983). In turn, this primary production provides grazing opportunities for copepods and other zooplankton, which are a critical food resource for juvenile Pacific salmon during their early marine residency (Armstrong et al. 2008; Beauchamp et al. 2007; Brodeur et al. 2007a). Over the past two decades, considerable evidence has indicated strong connections between climate variability, vertical ocean transport processes, and phytoplankton dynamics (Chenillat et al. 2012; Polovina et al. 1995; Henson 2007; Henson and Thomas 2007; Stabeno et al. 2004; Weingartner et al. 2002). However, postulated relationships between lower-trophic-level processes (e.g., phytoplankton dynamics in coastal ecosystems) and productivity of Pacific salmon populations largely remain untested assumptions. In chapter 2, I investigate the vertical transport hypothesis by asking whether the phenology or intensity of the spring phytoplankton bloom can explain inter-annual variability in productivity of 27 North American pink salmon stocks.

Recently, evidence for an alternative bottom-up forcing pathway has emerged, suggesting that horizontal ocean transport may be as important as vertical transport in mediating the effects of climate variability on higher-trophic-level species (Di Lorenzo et al. 2013b). This horizontal transport hypothesis proposes that the quantity (or quality) of food resources available to juvenile salmon in coastal ecosystems is driven by climate-induced changes in horizontal transport processes, e.g., ocean currents or eddies, that cause zooplankton or other weakly/passive drifters to be advected into or out of coastal areas (Fig. 1.1). For example, off the central Oregon Coast, research has indicated that the negative phase of the Pacific Decadal Oscillation is associated with increased advection of large-bodied lipid-rich zooplankton into the region from northern areas, which in turn is associated with increased marine survival of coho salmon (*O. kisutch*; Keister et al. 2011; Bi et al. 2011a). Beyond the Northern California Current area, however, the effects of variability in horizontal ocean transport on Pacific salmon productivity are largely untested. In chapter 3, I investigate the horizontal transport hypothesis by examining the effects of two modes
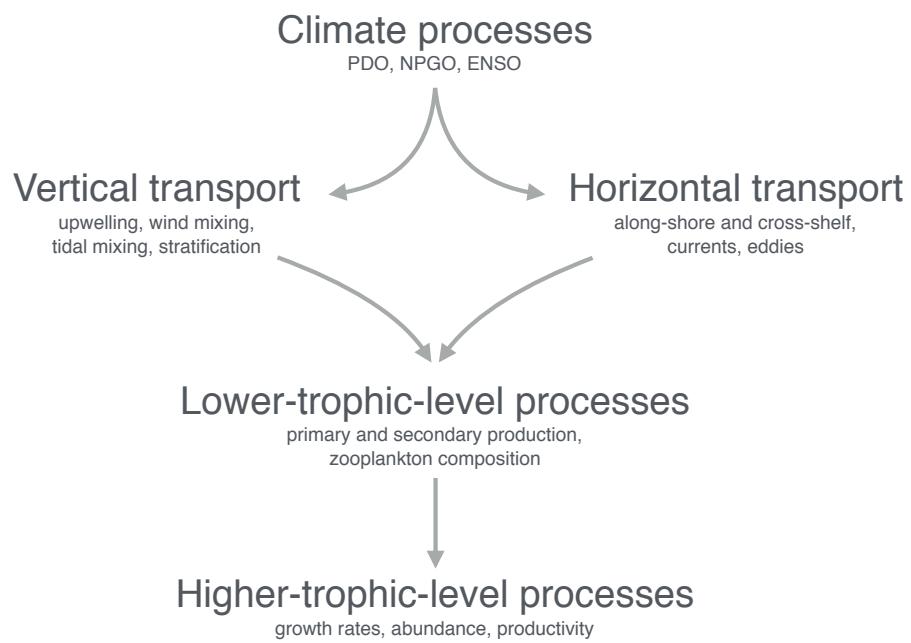
Figure 1.1: Schematic of two environmental forcing pathways linking large-scale climate patterns, ocean processes, and higher-trophic-level species.

of variability in horizontal ocean transport in the Northeast Pacific on productivity of 163 North American pink, chum (*O. keta*), and sockeye salmon stocks.

Although the vertical and horizontal transport hypotheses are individually appealing explanations of how climate forcing may downscale to affect regional and local scale dynamics of higher-trophic-level species, these hypotheses are not mutually exclusive and likely have additive or multiplicative effects on salmon productivity. In particular, regional-scale vertical and horizontal transport processes are both hypothesized to mediate the effects of large-scale climate variability on lower- and higher-trophic-level species. Thus, perturbations to climatic systems from anthropogenic or natural sources may simultaneously influence regional-scale vertical and horizontal transport pathways. Indeed, the Pacific Decadal Oscillation has been shown to influence ocean current patterns in the Northern California Current ecosystem and affect the magnitude of upwelling-favorable winds in the region (Keister et al. 2011; Chhak and Di Lorenzo 2007). Estimating the cumulative effects and relative importance of these simultaneously operating pathways is likely a necessary component of understanding how environmental change impacts higher-trophic-level species. In chapter 4, I use a novel quantitative method, probabilistic networks, to estimate the joint effects and relative strengths of these different pathways on productivity of coho salmon in the Northern California Current.

1.3 Managing for environmental change

A better understanding of how environmental forcing impacts salmon populations is a necessary but not sufficient condition for maintaining viable and productive salmon stocks. We also need to develop a parallel understanding of how these impacts interact with other anthropogenic disturbances, such as commercial harvesting, and how this information can be incorporated into management decisions (Link 2002). Increasingly, management of living marine resources is moving toward ecosystem-based approaches that shift the focus of management from a single species to maintaining critical components of ecosystem structure and function (Grumbine 1994; Murawski 2007; Long et al. 2015). A necessary element of this shift toward ecosystem-based management is defining boundaries that delimit the spatial extent of the system being managed (Engler 2015; Yaffee 1999). However, for highly migratory marine and anadromous fish species, impacts from human or natural sources can occur across a continuum of spatial scales that frequently extend beyond the boundaries of the ecosystem-based management area (Dallimer and Strange 2015). For example, management actions in locations that are geographically distant from the ecosystem-based management area, such as decisions to increase commercial harvests, may strongly impact the supply of ecosystem services provided by a migratory species within the bounds of the

ecosystem-based management area. In chapter 5, I examine challenges associated with integrating highly migratory Pacific salmon into regional and local scale ecosystem-based management policies that arise from mismatches between the scale of management and the biology of Pacific salmon and discuss potential strategies to overcome the identified challenges.

1.4   Statement of interdisciplinarity

The research presented in this thesis includes two levels of interdisciplinarity. First is the incorporation of research ideas, perspectives, and approaches from both oceanography and fisheries. Although both fields are firmly rooted in the natural sciences, the research approaches and the types of questions important to researchers in each field have diverged over time (Platt et al. 2007). In chapters 2–4, I attempt to bring together some of the knowledge and research questions important to both fisheries scientists and oceanographers. The second level of interdisciplinarity involves a bridge between the natural and social sciences. One-quarter of the research presented in this thesis is focused on this bridging by taking a policy perspective to examine potential strategies to more effectively integrate multi-scale information about natural and anthropogenic disturbances into ecosystem-based management programs.

1.5   Contributions

I am the sole author of chapters 1 (Introduction) and 6 (Conclusion) and these chapters are written in the first-person singular. Chapters 2–5 are derived from either published manuscripts or submitted manuscripts with co-authors and these chapters are written in the first-person plural. For each of the chapters deriving from multi-authored manuscripts (chapters 2–5), I am the first author of the work and performed the data analysis and wrote the first draft of the text. These chapters, however, benefited greatly from discussions, editing, and comments from the co-authors. The published versions of these chapters are cited at the beginning of each chapter. The initial ideas for chapter 2 were developed by me, Randall Peterman, Franz Mueter and Sean Cox. Chapter 3 builds on ideas originally presented in an unpublished manuscript by Randall Peterman, Franz Mueter, and Brigitte Dorner. The main idea for chapter 4 came out of discussions between Randall Peterman and me following a presentation on using Bayesian networks for ecological research by Catherine Michielsens. The ideas presented in chapter 5 were developed by me, Murray Rutherford, and Sean Cox.

Chapter 2

Linking phytoplankton phenology to salmon productivity along a north-south gradient in the Northeast Pacific Ocean[1]

2.1 Abstract

We investigated spatial and temporal components of phytoplankton dynamics in the Northeast Pacific Ocean to better understand the mechanisms linking biological oceanographic conditions to productivity of 27 pink salmon (*Oncorhynchus gorbuscha*) stocks. Specifically, we used spatial covariance functions in combination with multi-stock spawner-recruit analyses to model relationships among satellite-derived chlorophyll-a concentrations, initiation date of the spring phytoplankton bloom, and salmon productivity. For all variables, positive spatial covariation was strongest at the regional scale (0–800 km) with no covariation beyond 1500 km. Spring bloom timing was significantly correlated with salmon productivity for both northern (Alaska) and southern (British Columbia) populations, although the correlations were opposite in sign. An early spring bloom was associated with higher productivity for northern populations and lower productivity for southern populations. Furthermore, the spring bloom initiation date was always a better predictor of salmon productivity than mean chlorophyll-a concentration. Our results suggest that changes in spring bloom timing resulting from natural climate variability or anthropogenic climate change could potentially cause latitudinal shifts in salmon productivity.

2.2 Introduction

The dynamics of marine fish populations are often characterized by large inter-annual and inter-decadal variability in abundances. For Pacific salmon (*Oncorhynchus* spp.), the first year of ocean residence is widely viewed as a critical period that can strongly influence stock abundance (Peterman 1985; Parker 1968; Wertheimer and Thrower 2007). During this period, climatic and oceanographic conditions are believed to strongly affect salmon productivity (i.e., the number of adult recruits produced per spawner), yet the ecological pathways connecting environmental variability to upper trophic levels of marine food webs are not well understood (Drinkwater et al. 2010; Ottersen et al. 2010). Evidence suggests that salmon mortality during the early marine life stage is inversely related to body size, indicating that bottom-up forcing mechanisms that affect prey resources may be an important part of these ecological pathways (McGurk 1996; Duffy and Beauchamp 2011; Farley et al. 2007b).

Several bottom-up forcing mechanisms have been proposed to explain productivity variation in marine fish stocks, including salmon (Cushing 1990; Gargett 1997). For example, the "optimal stability window" hypothesis suggests that changes in water column stability may be a critical component linking changes in large-scale climate patterns and salmon productivity (Gargett 1997). However, this hypothesis assumes a strong link between phytoplankton dynamics (e.g., productivity or total biomass) and salmon productivity, which is largely untested beyond a few local-scale studies (Mathews and Ishida 1989; Chittenden et al. 2010). Accounting for both spatial and temporal variability of lower-trophic-level processes is a key challenge to testing the optimal stability window hypothesis on large spatial scales.

In the coastal Northeast Pacific, seasonal biomass of phytoplankton follows a well-known pattern defined primarily by the spring bloom (Henson 2007; Waite and Mueter 2013), which is mainly driven by large-scale climate patterns combined with regional and local-scale physical environmental conditions (Sverdrup 1953; Ware and Thomson 1991; Polovina et al. 1995; Henson 2007). In the coastal Gulf of Alaska, the spring bloom initiation date is strongly correlated with the onset of water column stability, which is at least partially controlled by the strength of the Aleutian Low Pressure system (Henson 2007). In that region, an earlier spring bloom is also associated with a more intense bloom, suggesting that both the phenology of the spring bloom and overall production during the bloom may be important components of bottom-up forcing pathways. Indeed, features of the spring bloom such as initiation date and total phytoplankton biomass are correlated with yield and productivity of certain marine fish populations (Platt et al. 2003; Ware and Thomson 2005; Koeller et al. 2009).

In this paper, we asked whether the spring bloom initiation date and average chlorophyll-

a (chl-a) concentrations (a surrogate for phytoplankton biomass) can explain spatial and inter-annual variability in pink salmon (*O. gorbuscha*) productivity, which we estimated using spawner-recruit data for 27 stocks. Establishing a plausible mechanistic link between the spring phytoplankton bloom and salmon production first requires evidence that the two processes operate at similar spatial scales; that is, spatial covariation of lower-trophic level processes should approximately match the spatial scale of covariation observed in the salmon productivity data that they are being used to explain (Bjørnstad et al. 1999; Koenig 1999). In the Northeast Pacific Ocean, productivity of salmon stocks exhibit spatial synchrony at the scale of 100 to 1000 km (Mueter et al. 2002b) with positive correlations being greatest at distances less than 500 km (Pyper et al. 2005). Therefore, we hypothesized that features of the spring phytoplankton bloom operate at similar regional spatial scales as salmon productivity.

We used spatial covariance analyses to determine the spatial extent of synchrony in the timing of the spring phytoplankton bloom and mean chl-a concentrations along the Northeast Pacific coast, as well as to determine the scale of spatial averaging that should be used on data for these variables. We then used a hierarchical, multi-stock statistical modeling approach to estimate relationships between pink salmon productivity and inter-annual variability in spring bloom initiation date, as well as mean chl-a concentration during spring and late summer. Compared to single-stock analyses, our multi-stock modeling approach can help reduce uncertainty associated with the biological processes that underpin the dynamics of salmon populations and reduce the chance of finding spurious relationships by using different salmon stocks as replicates within the analysis (Myers and Mertz 1998; Myers et al. 1999).

2.3 Methods

2.3.1 Pink salmon data

We estimated annual indices of productivity (in units of adult recruits per spawner) for 27 wild pink salmon stocks from British Columbia (B.C.) and Alaska (AK) using data on spawner abundance and total recruitment (catch plus escapement). The 27 spawner-recruit data sets (Table 2.1) represent aggregations of escapement and catch of adjacent salmon stocks. The aggregation helped ensure that catches were attributed to the correct spawning stocks and was primarily based on jurisdictional management units, although in some cases aggregation occurred at a larger scale because of difficulty allocating catch into individual management units (e.g., Prince William Sound). Hatchery returns were excluded from all estimates of catch and escapement. Estimation methods for spawner abundances varied among stocks, but in general, southern stocks (B.C.) were estimated using expansions of foot surveys, while northern stocks (AK) were estimated using expansions of

aerial surveys (personal communication from data sources listed in footnotes of Table 2.1). Annual recruitment varied widely among stocks with long-term averages ranging from 0.12 million pink salmon for Chignik Bay to 33.31 million for southern southeast Alaska (Table 2.1).

Table 2.1: Summary of pink salmon stock-recruit data sets. Brood years indicate the temporal range of spawning years; N is the number of non-missing years within that range; R is the annual average recruitment (catch plus escapement) in millions across all brood years; S is the average number of spawners in millions across all brood years; α and β are maximum likelihood estimates of the intercept (i.e., stock productivity at low spawner abundances) and slope (i.e., density-dependent effect), respectively, of the single-stock Ricker models (eq. 2.1).

Stock #[a]	Jurisdiction	Stock	Brood years	N	R	S	α	β
1	BC	Southern BC[b]	1953-2008	56	2.02	1.09	0.90	-0.49
2	BC	Statistical Area 9	1980-2008	29	0.46	0.41	0.13	-0.50
3	BC	Statistical Area 8	1980-2008	29	3.28	2.36	0.36	-0.19
4	BC	Statistical Area 7	1980-2008	29	0.53	0.38	0.50	-1.05
5	BC	Statistical Area 6	1980-2008	29	2.76	1.33	0.45	-0.01
6	BC	Statistical Area 5	1982-2008	27	0.45	0.31	0.79	-1.28
7	BC	Statistical Area 4	1982-2008	27	5.93	2.57	1.19	-0.29
8	BC	Statistical Area 3	1982-2008	27	1.50	0.80	1.31	-0.78
9	AK	S SEAK[c]	1960-2008	49	33.31	13.47	1.15	-0.02
10	AK	N SEAK Outside[d]	1960-2008	49	3.98	2.37	1.31	-0.17
11	AK	N SEAK Inside[e]	1960-2008	49	16.48	7.62	1.21	-0.05
12	AK	Prince William Sound	1960-2009	50	10.12	4.40	0.95	-0.06
13	AK	S Cook Inlet[f]	1976-2009	34	0.13	0.09	0.98	-10.67
14	AK	Outer Cook Inlet[g]	1976-2009	34	0.53	0.23	1.36	-2.30
15	AK	Kamishak District[h]	1976-2009	34	0.38	0.32	1.15	-2.82
16	AK	Afognak District	1978-2009	32	1.85	0.75	2.69	-2.38
17	AK	Westside Kodiak	1978-2009	32	10.00	4.13	1.20	-0.06
18	AK	Alitak District	1978-2009	32	3.14	1.58	1.65	-0.61
19	AK	Eastside Kodiak	1978-2009	32	4.47	2.16	0.68	-0.02
20	AK	Mainland Kodiak	1978-2009	32	1.84	1.36	1.16	-0.77
21	AK	Chignik Bay	1962-2009	43	0.12	0.03	1.15	-6.49
22	AK	Central Chignik	1962-2009	48	0.32	0.17	1.12	-1.68
23	AK	Eastern Chignik	1962-2009	48	0.64	0.50	0.73	-0.98
24	AK	Western Chignik	1962-2009	48	0.48	0.16	1.57	-2.97
25	AK	Perryville	1962-2009	48	0.32	0.15	1.37	-8.73
26	AK	AK Peninsula[i]	1962-2009	48	4.94	1.76	1.55	-0.29
27	AK	SW Unimak	1962-2009	48	2.05	0.83	1.37	-0.64

Continued on next page …

Table 2.1 Continued.

[a] Sources of data by stock number: 1: Pieter Van Will, Fisheries and Oceans Canada (DFO), Port Hardy, BC; 2–8: David Peacock, DFO, Prince Rupert, BC; 9–11: Steve Heinl, Alaska Department of Fish and Game (ADFG), Ketchikan, AK and Piston and Heinl (2011); 12: Steve Moffitt, ADFG, Cordova, AK; 13–15: Ted Otis, ADFG, Homer, AK; 16–20: Matt Foster, ADFG, Kodiak, AK; 21–25: Charles Russell, ADFG, Kodiak, AK; 26–27: Matt Foster, ADFG, Kodiak, AK.

[b] Includes statistical areas 11–16; Excludes Fraser River

[c] Includes districts 101–108

[d] Includes districts 109–112, 114, 115

[e] Includes district 113

[f] Sum of Humpy Creek and Seldovia Bay data sets

[g] Sum of Port Chatham, Port Dick, Rocky River, Windy Creek, and South Nuka data sets

[h] Sum of Bruin River, Sunday Creek, and Brown's Peak Creek data sets

[i] Sum of Southeast and Southcentral districts data sets

2.3.2 Chlorophyll-a data

We used satellite-derived chl-a concentration estimates (measured as mg m^{-3}) from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and the Moderate Resolution Imaging Spectroradiometer (MODIS-Aqua) from the Goddard Space Flight Center (http://oceancolor.gsfc.nasa.gov). Level-3 processed data were downloaded for 1998–2010 (but only 2003–2010 had complete MODIS data) in their original 9 km^2, 1-day-resolution. We converted the data to a 1°x1° resolution and subsetted the resulting grid to 46°–61°N and 167°–125°W, including only grid cells adjacent to the coast (Fig. 2.1). We excluded grid cells in the Bering Sea because all salmon stocks in our data set enter the ocean in the Gulf of Alaska.

All analyses were performed using 8-day composite chl-a data because these had less missing data across all years compared to 1-day and 5-day composites (Supporting materials Fig. 2.7). In addition, the SeaWiFS data set had numerous large gaps during the spring and summer for years 2008–2010, which made these years of SeaWiFS data unsuitable for our study (Supporting materials Fig. 2.7). We evaluated the feasibility of concatenating the SeaWiFS and MODIS data sets into a single continuous data set that would provide an additional three years of data (compared to using SeaWiFS data alone) by comparing the two data sets over the first five overlapping years (2003–2007; Supporting materials 2.7.1). We estimated correlations, root mean squared $\log_{10}$ error (RMSE), and $\log_{10}$ bias to quantify differences between the two chl-a data sets. The SeaWiFS and MODIS data sets were highly correlated (average correlation of 0.87 across all grid cells). In addition, over all years and grid cells RMSE (0.16) and log bias (0.012; Supporting materials Fig. 2.8) were consistent with other studies comparing SeaWiFS and MODIS data products over a similar

study region (Waite and Mueter 2013). Based on these minimal differences, we concatenated the SeaWiFS (1998–2002) and MODIS (2003–2010) data sets without further processing.
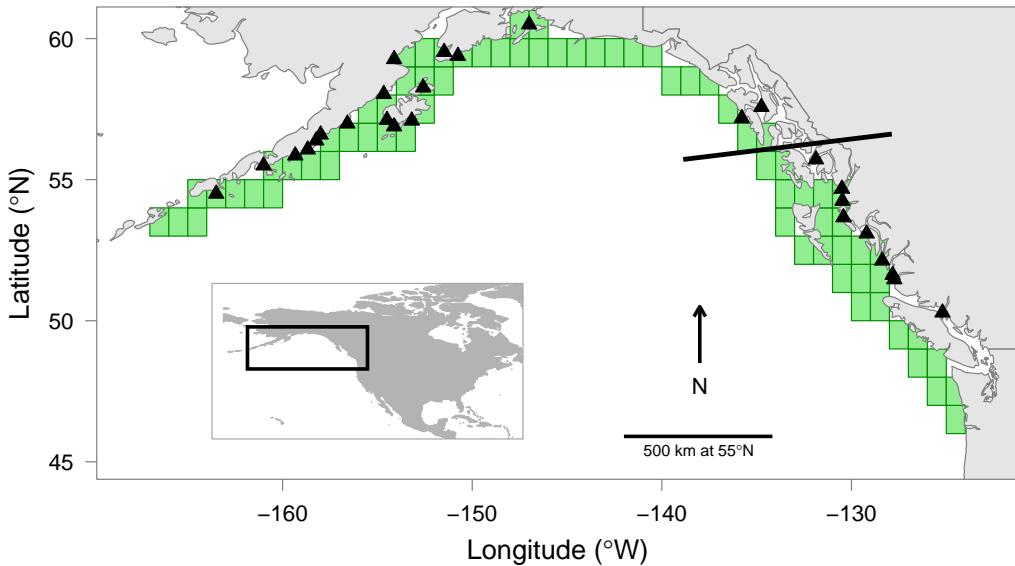
Figure 2.1: Study area indicating the grid cells used to compute the bloom initiation date and mean chl-a concentrations (green squares) and the locations of ocean entry points for the pink salmon stocks (solid black triangles). Solid line indicates break point identified by the intervention model (see text) between northern and southern stock groupings.

Inter-annual variability in phytoplankton standing stock and phytoplankton phenology were quantified using mean monthly chl-a concentration and the spring-bloom initiation date, respectively, which we derived from the 8-day composite chl-a estimates for each grid cell (Fig. 2.1). We linearly interpolated data points in chl-a time series for each grid cell between gaps less than 3 data points (4.1% of all chl-a data points were interpolated). This procedure was done prior to estimating annual spring bloom initiation date and mean chl-a concentrations. We estimated the spring bloom initiation date as the first 8-day period in a given year when the chl-a concentration was more than 5% above the median chl-a concentration of the entire multi-year data set for a particular grid cell (Siegel et al. 2002; Henson 2007). In addition, we $\log_{10}$ transformed the chl-a averages to help normalize the chl-a values.

2.3.3   Spatial covariation analysis

We constructed cross-correlation matrices to quantify spatial covariance patterns for (1) pink salmon stock productivities, (2) spring-bloom initiation dates, and (3) monthly mean chl-a con-

centrations. For salmon stocks, pairwise correlation coefficients were computed between time series of productivity for each of the 27 stocks. For the spring bloom initiation date, correlation coefficients were computed between each pair of grid cells using time series of the estimated annual spring bloom initiation date for years 1998–2010. For chl-a concentration, we calculated correlations across grid cells using time series of the monthly mean chl-a concentration. To account for potential changes in spatial patterns across seasons, we calculated correlations for chl-a concentration for each month (February-October) separately.

We estimated annual salmon productivity using residuals from a Ricker spawner-recruit model, which removed potential within-stock density-dependent effects (Pyper et al. 2001; Mueter et al. 2002a; Ricker 1954). The Ricker model for each stock was of the form,

$$log_e(R_{i,t}/S_{i,t}) = \alpha_i + \beta_i S_{i,t} + \epsilon_{i,t}, \tag{2.1}$$

where $R_{i,t}$ is total pink salmon recruits for the ith stock in brood year t, $S_{i,t}$ is the spawning stock two years earlier, α_i is the maximum log_e recruits-per-spawner, β_i is the coefficient of density-dependence, and $\epsilon_{i,t}$ is the residual.

We fit the Ricker models (eq. 2.1) to two partitions of the data – one including all available brood years and the second including only brood years 1997–2009 (Table 2.1). The latter partition corresponds to the years available for the bloom initiation date and chl-a variables. Because juvenile pink salmon enter the ocean the year following spawning (i.e., brood year + 1), we offset the phytoplankton variables one year to correspond with the ocean entry year for pink salmon (e.g., 2006 brood year was lined up with 2007 phytoplankton variables).

To test whether spatial covariation was present in each of the variables, we first performed Mantel tests using matrices of the cross-correlations and a matrix of great-circle distance (computed using the haversine formula) between all pairs of grid cells or stocks (Legendre and Legendre 1998; Koenig 1999). Statistical significance of Mantel statistics were determined using randomization tests with 1000 permutations. We then determined the spatial scale of covariation for each significant Mantel test by fitting a smooth non-parametric covariance function (Bjørnstad and Falck 2001) between the correlation coefficients for a given variable and the distance separating correlated grid cells or ocean-entry points of salmon stocks. Confidence intervals (CI) for each covariance function were computed by bootstrapping the estimation procedure 1000 times.

Covariance functions were summarized using two distance metrics: (1) the y-intercept of the covariance function, which provides an estimate of the correlation at zero distance (CZD), and (2) 50% correlation scale (D50). The CZD was estimated by extrapolating the fitted covariance function to zero distance to find the y-axis intercept. The D50 was estimated as the distance at which the covariance function falls to 50% of its observed maximum value, which provides a useful

metric of how much the correlation declines with increasing distance between salmon stocks or grid cells (Mueter et al. 2002b).

2.3.4 Salmon productivity models

We used a combination of single-stock linear models and multi-stock linear mixed-effects models to investigate relationships among temporal averages of mean chl-a concentrations (spring and late summer), spring bloom initiation date, and pink salmon productivity. The single-stock model analysis had two purposes. First, we used the values of fitted coefficients for different stocks to inform construction of the multi-stock models and to help evaluate the multi-stock model assumptions. Second, we used the single-stock analysis along with intervention analyses to break up the data sets spatially to provide the best fits of the multi-stock models. For both single-stock and multi-stock models, only pink salmon brood years 1997–2009 were used.

The bloom initiation date and both chl-a covariates included in the models represented spatial and temporal (for chl-a) averages of conditions experienced by juvenile pink salmon during their early marine life phase. The bloom initiation covariate was calculated for each salmon stock as the average of grid cell specific anomalies (i.e., a grid cell's value minus the long term mean for that grid cell) over all grid cells whose centers were within 250 km of the stock's ocean entry point. For chl-a, we calculated April–May averages to capture variability in phytoplankton biomass during the spring bloom and July–September averages to index chl-a variability during the late summer, which is believed to be a critical period for juvenile salmon survival (Beamish and Mahnken 2001; Moss et al. 2005). For both time periods, we first averaged chl-a values over the specified months for each grid cell and then averaged over all grid cells within 250 km of the stock's ocean entry point.

Single-stock models

The single-stock Ricker models took the form (Adkison et al. 1996),

$$log_e(R_{i,t}/S_{i,t}) = \alpha_i + \beta_i S_{i,t} + \gamma_i X_{i,t+1} + \epsilon_{i,t}, \tag{2.2}$$

where $S_{i,t}$ is spawner abundance of pink salmon in brood year t for the ith stock, $R_{i,t}$ is the total recruitment resulting from $S_{i,t}$, α_i indicates stock productivity at low spawner abundances, β_i indicates the magnitude of density-dependence, $X_{i,t+1}$ is a stock-specific measure of either the spring bloom initiation date or mean chl-a concentration (the latter for either the spring or late summer), γ_i is the coefficient for either the stock-specific bloom initiation date or mean chl-a, and $\epsilon_{i,t} \sim N(0, \sigma^2)$ is an independent and identically distributed residual term.

Environmental variables such as sea surface temperature could have opposite effects on northern and southern pink salmon stocks (Mueter et al. 2002a; Su et al. 2004); therefore we used an intervention model with two means (Chatfield 2004; Mueter et al. 2002a) to test for differences in the effect of the bloom initiation date and chl-a concentration between northern and southern stocks (Chatfield 2004; Mueter et al. 2002a). The intervention models were fit to either the estimated chl-a or spring bloom coefficients from the single-stock models (i.e., γ in eq. 2.2) where the coefficients were arranged south to north based on ocean entry locations (i.e., by stock number in Table 2.1).

Multi-stock models

We used hierarchical, multi-stock models to estimate both regional and stock-specific effects of spring and late summer chl-a and the bloom initiation date on pink salmon productivity, while also accounting for heterogeneity in density-dependence among stocks. The multi-stock mixed effects Ricker models took the form (Myers et al. 1999; Mueter et al. 2002a),

$$log_e(R_{i,t}/S_{i,t}) = \alpha + a_i - \beta_i S_{i,t} + X_{i,t+1}(\gamma_X + g_i) + \epsilon_{i,t}, \tag{2.3}$$

where the fixed intercept α is the overall mean productivity common to all stocks and a_i is the stock-specific deviation from that mean, β_i is the fixed stock-specific density-dependent effect, $X_{i,t+1}$ represents either the spring bloom initiation date or mean chl-a concentration (either spring or late summer average), γ_X is the overall mean effect of either the spring bloom initiation date or mean chl-a concentration, g_i is the stock-specific deviation from that overall mean for a particular chl-a variable, and $\epsilon_{i,t}$ is an independent and identically distributed residual term (i.e., $\epsilon_{i,t} \sim N(0, \sigma^2)$). The stock-specific random effects a_i and g_i are assumed to follow a joint normal distribution with means zero, variances σ_a^2 and σ_g^2, and covariance σ_{ag}^2.

Because the chl-a and bloom initiation variables were moderately correlated (average correlations between stock-specific phytoplankton time series ranged from -0.50 to 0.20), the multi-stock models were fit separately for the bloom initiation date and both chl-a metrics. For the bloom initiation date and spring chl-a variables, we also fit multi-stock models separately for a southern stock group (stocks 1–9 in Table 2.1) and a northern stock group (stocks 10–27 in Table 2.1), because the single-stock analysis and intervention models suggested consistent differences in the effects of these variables between northern and southern stock groupings (see Results). For the late summer chl-a variable, we fit a single model using all stocks because the intervention models did not indicate a significant break between northern and southern stock groupings.

In addition to the full models (eq. 2.3) for both chl-a variables and the bloom initiation date,

we investigated two simpler nested models, (1) eq. 2.3 but without the random chl-a or bloom effect (i.e., g_i), and (2) eq. 2.3 but without either the random or fixed chl-a or bloom effect (i.e., g_i and γ_X, which was the null model). Random effect significance was determined using likelihood ratio (L) tests among the nested models, whereas fixed effect significance was tested using F-tests (Pinheiro and Bates 2000). All reported parameters were estimated using restricted maximum likelihood methods; however, for model comparisons, parameters were estimated using maximum likelihood methods to reduce bias (Pinheiro and Bates 2000).

To compare the relative importance of the bloom initiation date and both chl-a variables, we also calculated the small-sample Akaike Information Criterion (AIC$_C$) for all models (Hurvich and Tsai 1989; Burnham and Anderson 2002). For the models that included late summer chl-a, which were fit using all 27 salmon stocks, we calculated a single set of AIC$_C$ values (one for each nested model). For the models that included either the bloom initiation date or spring chl-a variables, we calculated two sets of AIC$_C$ values. First, to compare the relative importance of both variables within the northern and southern areas, we calculated AIC$_C$ values for each model fit to the northern and southern stock groups separately. Second, to compare variable importance with the late summer chl-a variable, we calculated an AIC$_C$ value for the combined northern and southern models. Because northern and southern models for the bloom initiation date and spring chl-a variables were fit using identical salmon data as the late summer chl-a models, we calculated a combined northern and southern AIC$_C$ value for each variable by summing the log-likelihoods and the number of model parameters. To more easily compare models, we also calculated the ΔAIC$_C$, i.e., the difference between each individual model's AIC$_C$ value and the minimum AIC$_C$ value among models. Models within three AIC$_C$ units of the model with the lowest AIC$_C$ value are considered equally plausible (Burnham and Anderson 2002).

2.3.5 Sensitivity analysis

We checked the sensitivity of our results to four assumptions. First, we estimated sensitivity of the spatial analysis results to an alternative Beverton-Holt stock-recruitment model, $log_e(R/S) = log_e(a) - log_e(1 + bS) + \epsilon$ (Beverton and Holt 1957). Second, we checked the sensitivity to the interpolation procedure used on the chl-a time series by re-running each analysis using spring bloom and chl-a values that did not include interpolated data points. Third, we tested our assumption that the error terms of the multi-stock models were temporally independent by refitting the models with first-order autocorrelated errors (i.e., $\epsilon_{i,t} = \phi\epsilon_{i,t-1} + v_t$, where $v_t \sim N(0, \sigma^2)$) and using likelihood ratio tests to determine the significance. Fourth, because our spawner-recruit data sets include variability associated with both freshwater and marine life phases, we checked the sensitivity of our results to the source of pink salmon data by comparing each chl-a metric to pink

salmon marine survival rates for three Alaska hatchery stocks (Armin F. Koernig, Kitoi Bay, and Port Armstrong) using Pearson correlation coefficients (see Supporting materials 2.7.2 for details of the analysis).

2.4 Results

2.4.1 Spatial analysis

Both sets of pink salmon residuals, monthly mean chl-a, and bloom initiation date all showed significant spatial covariation (P < 0.01 for all Mantel tests). For both sets of pink salmon residuals (all brood years and recent, satellite-covered years), the nonparametric covariance functions indicated declining positive covariation with increasing distance between ocean entry points of juvenile salmon, up to approximately 800 to 1000 km where the functions approached zero correlation (Fig. 2.2a and b). The estimated D_{50} was slightly larger for productivity indices fitted using all available brood years (D_{50} = 305 km; 95% CI = 218–488 km) than for indices fitted using only brood years 1997–2009 (D_{50} = 261 km; 95% CI = 148–628 km), although there was considerable overlap in confidence intervals (Figs. 2.2 and 2.3a). Correlations at zero distance (i.e., the y-intercept of the covariance function) for both sets of productivity indices were considerably less than one (CZD = 0.51; 95% CI = 0.41–0.62 and CZD = 0.49; 95% CI = 0.28–0.69 for all brood years and 1997–2009 respectively; Fig. 2.3b). Although the nonparametric covariance function for bloom initiation date had a slightly larger D_{50} (D_{50} = 367 km; 95% CI = 235–776 km) than the two salmon productivity indices, there was considerable overlap in confidence intervals with both productivity indices (Fig. 2.3a). Correlation at zero distance for the bloom initiation date was also considerably less than one (CZD = 0.44; 95% CI = 0.33–0.55; Fig. 2.3b).

For monthly mean chl-a concentrations, covariation decayed steeply with increasing distance over spatial scales of 0–500 km for all months (Fig. 2.4). The D_{50} was highest (~380 to 430 km) during the winter and spring (February–May) and declined to about 250 km during summer and fall (June–October), which was similar to the estimated D_{50} for salmon productivity (Fig. 2.5). In addition, confidence intervals for the chl-a D_{50} for all months overlapped the confidence intervals for salmon productivity D_{50}s (Fig. 2.5). The CZD for chl-a concentrations ranged from 0.56 in June to 0.76 in April, which was slightly higher than the estimated CZD for the bloom initiation date and salmon productivity.
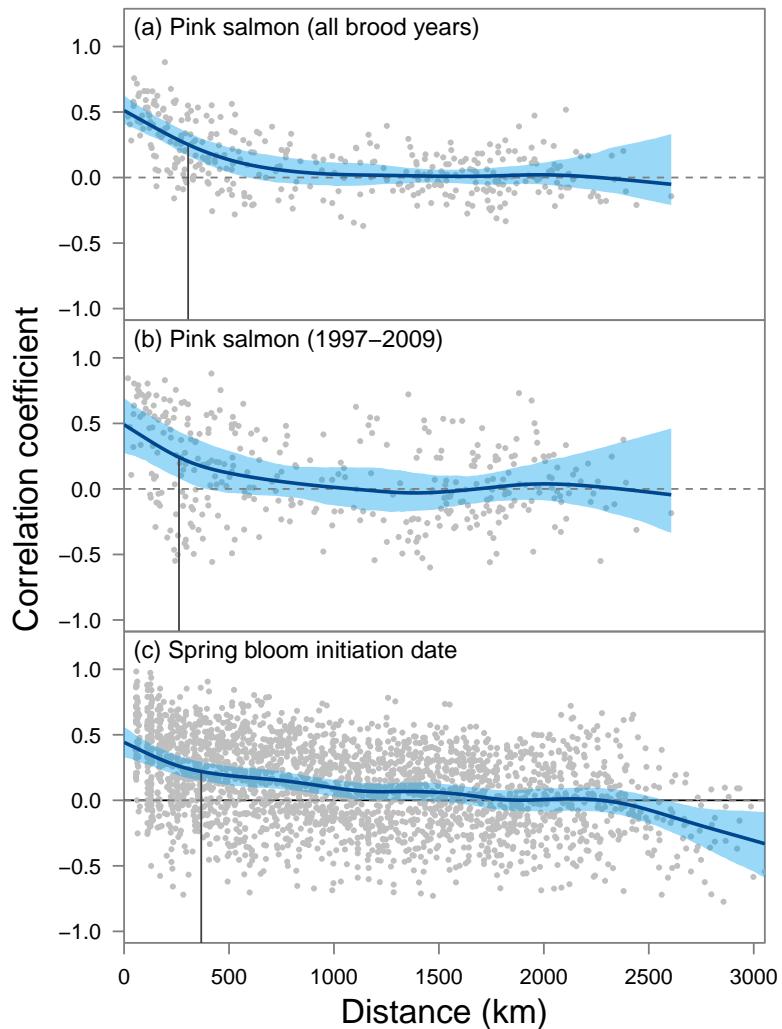
Figure 2.2: Correlograms (pairwise correlations as a function of distance between location of data pairs) of correlations among salmon productivity indices across all brood years (top panel), salmon productivity for brood years 1997–2009 (middle panel), and spring bloom initiation date (bottom panel). Solid curves represent the estimated smooth nonparametric covariance function with 95% confidence band shown as the blue shaded region. Solid vertical lines indicate the 50% correlation scale (D50).
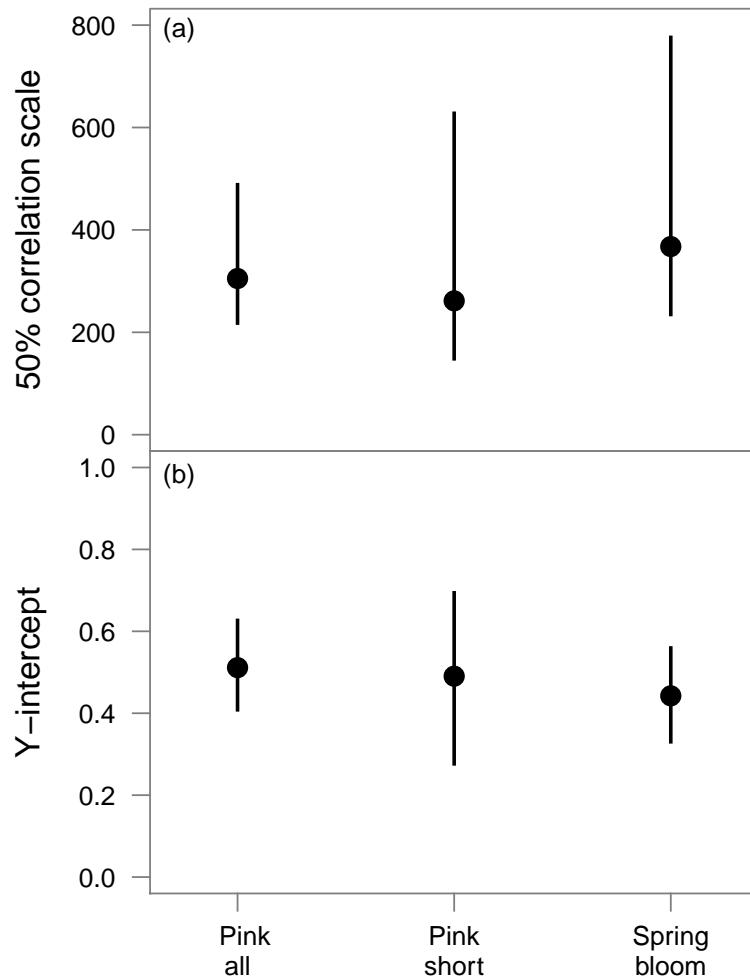
Figure 2.3: Comparison of the estimated 50% correlation scale (D50; top panel) and y-intercept (CZD; bottom panel) for the nonparametric covariance functions fit to pink salmon residuals using all brood years of data ("Pink all" from Fig. 2.2a), pink salmon residuals using only brood years 1997–2009 ("Pink short" from Fig. 2.2b), and initiation date for the spring bloom (from Fig. 2.2c). Dots indicate point estimates for each metric and vertical lines give 95% confidence intervals.
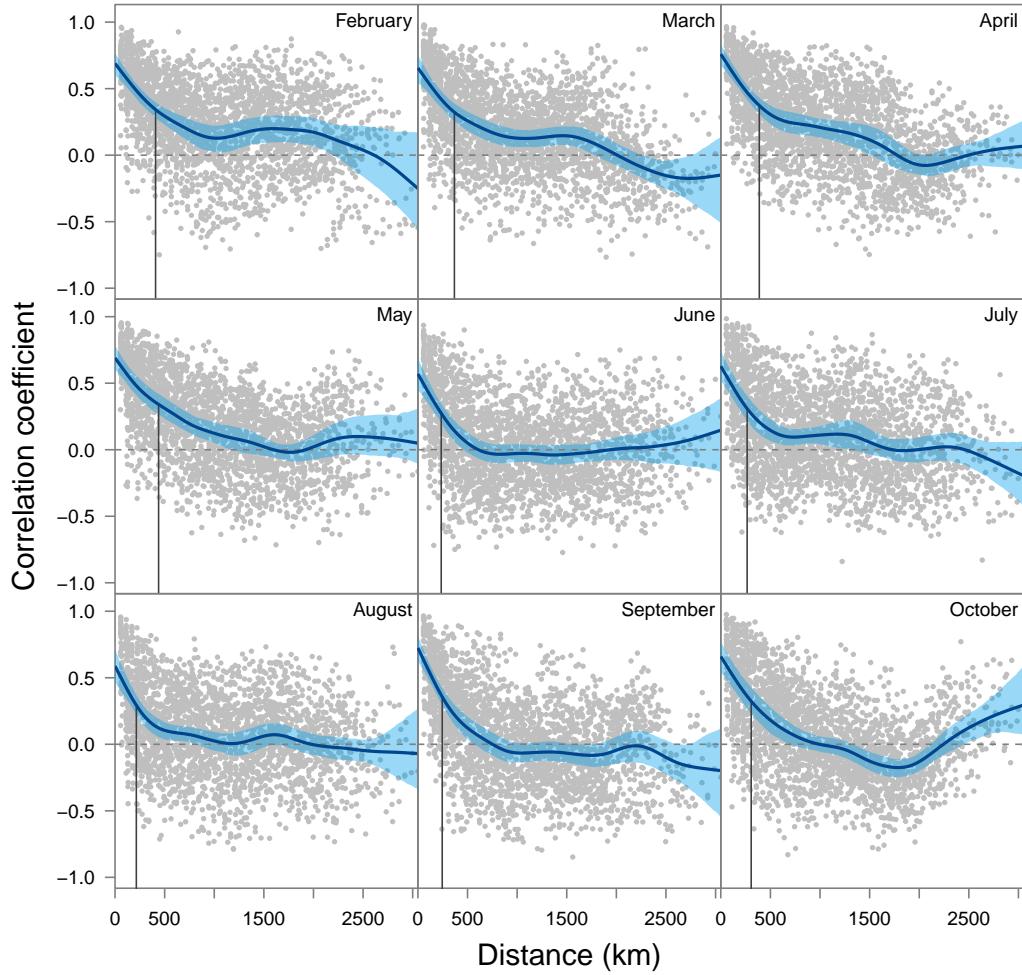
Figure 2.4: Correlograms (pairwise correlations as a function of distance between location of data pairs) of correlations among grid cells for the monthly mean chl-a concentrations. Solid curves represent the estimated smooth nonparametric covariance function with the 95% confidence band shown as the blue shaded region. Solid vertical lines indicate the 50% correlation scale (D50).
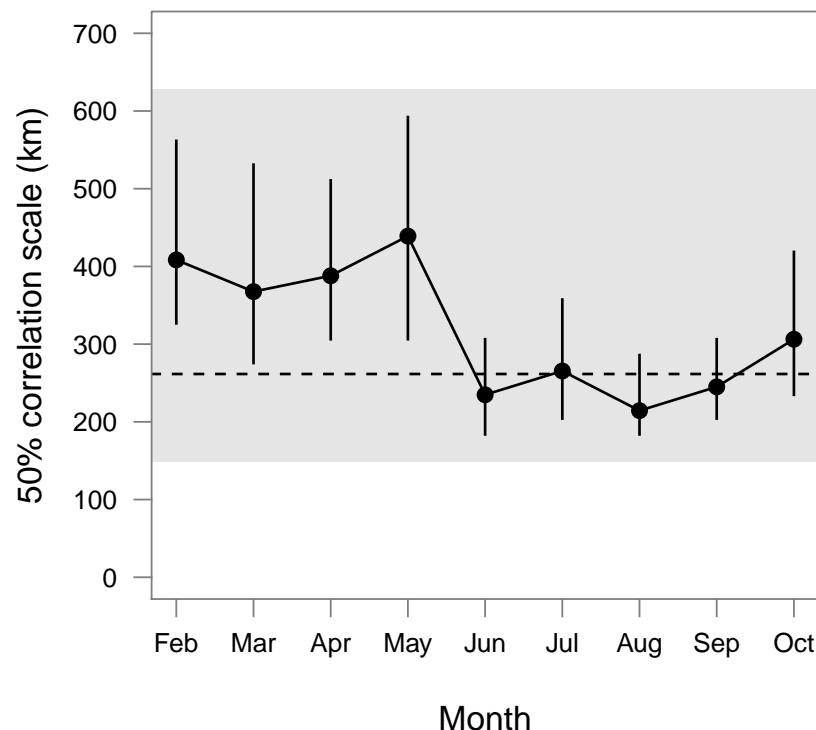
Figure 2.5: The 50% correlation scale (D50) for chl-a concentration by month. Solid vertical lines indicate 95% confidence intervals for each month. Dotted horizontal line indicates the 50% correlation scale for pink salmon using brood years 1997–2009; the grey shaded region indicates the 95% confidence interval for that pink salmon 50% correlation scale.

2.4.2 Single-stock models

The single-stock Ricker models indicated that pink salmon productivity was related to the spring bloom initiation date either positively (15 stocks) or negatively (12 stocks; Fig. 2.6a). The distribution of model coefficients (i.e., γ in eq. 2.2) ranged from -0.55 to 0.25 and was asymmetric about zero with the majority of values between -0.2 and 0.25 (Fig. 2.6d). Productivity of all 9 pink salmon stocks south of northern southeast Alaska (i.e., stocks 1–9 in Table 2.1) was positively related to the spring bloom initiation date, whereas productivity of northern stocks was mostly negatively related (12 of 18 stocks; Fig. 2.6a). The intervention model indicated a significant break ($P < 0.05$) in the sign of these relationships near 55.7°N, which was between the southern southeast Alaska stock (stock 9) and the northern southeast Alaska outside stock (stock 10; Fig. 2.1).

Pink salmon productivity was also both positively (14 stocks) and negatively (13 stocks) related to spring chl-a concentrations (Fig. 2.6b) with the coefficients ranging from -3.4 to 6.0 (Fig. 2.6e). Like the bloom initiation date, the intervention model indicated a significant break ($P < 0.05$) between stocks 9 and 10 for the spring chl-a coefficients (Fig. 2.6b). Productivity for all but two stocks in the southern group had a negative relationship with spring chl-a concentrations, whereas the northern group had a mix of positive and negative relationships.

For the late summer chl-a variable, productivity was consistently negatively related to chl-a, with only 4 of the 27 stocks having a positive relationship (Fig. 2.6c). The coefficients were approximately normally distributed with the magnitudes ranging from -8.6 to 3.2 with a median value of -1.9 (Fig. 2.6f). In contrast to the other two phytoplankton variables, the intervention model did not indicate a significant break in the sign of the coefficients between northern and southern stocks (Fig. 2.6c).

The productivity parameters (α) for the bloom initiation date and both chl-a models were approximately normally distributed (a requirement for the multi-stock models), but the distribution of the density-dependent coefficients (β) had a long left tail (Supporting materials Fig. 2.9).

2.4.3 Multi-stock models

Over all pink salmon stocks we considered, productivity was significantly related to spring bloom initiation date (northern and southern models), spring chl-a concentrations (southern model only), and late summer chl-a (γ in Table 2.2), although stock-specific differences were not significant in any models. For the bloom initiation date, regional effects were opposite in sign for the northern and southern stock groups (γ in rows 2 and 5 in Table 2.2; Fig. 2.6a), suggesting that salmon productivity for the southern stock group is higher than average when the bloom is later (positive coefficient), whereas productivity is higher than average for the northern stock group when the
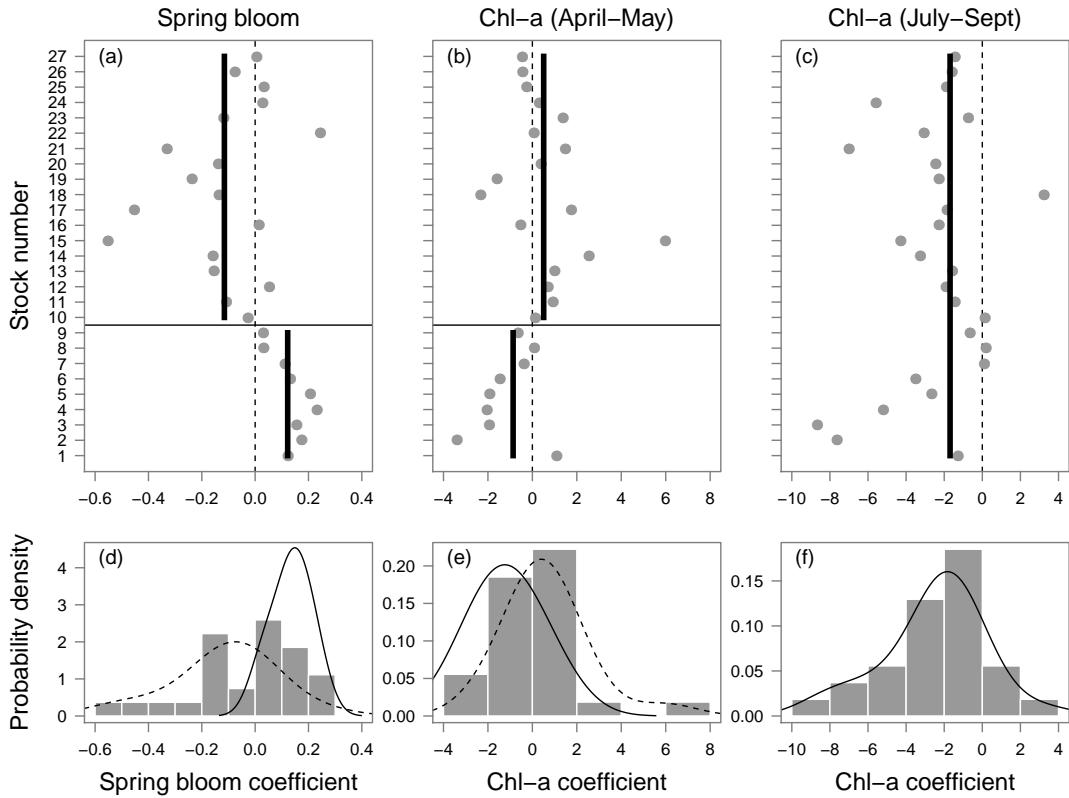
Figure 2.6: Estimates of the effects on pink salmon productivity of spring bloom initiation date (left panels), mean April–May chl-a concentration (middle panels), and mean July–September chl-a concentration (right panels) from the single-stock and best-fit multi-stock models. In panels *a–c* the ordinate gives the stock number, as defined in Table 2.1, solid circles represent the estimated effect for either chl-a or the bloom initiation from the single stock models (i.e., γ in eq. 2.2), and the solid vertical line gives the estimated region-wide effect for either the bloom initiation or chl-a from a multi-stock model (i.e., γ in eq. 2.3). Based on results from the single-stock analyses, separate multi-stock models were fit to northern and southern stocks for the spring bloom and April–May chl-a covariates, which are separated by a solid horizontal line. Bottom panels *d–f* show histograms of the spring bloom and chl-a effects based on single-stock models (eq. 2.2) and estimated probability density functions (smooth curves) of the single-stock model coefficients for northern and southern stocks.

bloom is early (negative coefficient). This result contrasts with those for spring (southern model only) and late summer chl-a, where the regional effect was negative, implying reduced salmon productivity when chl-a concentrations are higher (γ in rows 6 and 10 in Table 2.2). Furthermore, the spring bloom initiation date was a better predictor of salmon productivity than mean chl-a concentration for all subsets of data (i.e., northern stock group, southern stock group, and all stocks; AIC_C values in Table 2.2).

Table 2.2: Summary of the best-fit multi-stock Ricker model coefficients (eq. 2.3). The Subset column identifies the stocks included in the hierarchical model (North = stocks 1–9, South = stocks 10–27, and All = stocks 1–27). The Stocks column indicates the number of stocks used to fit the model; N is the total number of data points across all stocks used to fit the model; α is the intercept representing average productivity of pink salmon at low spawner abundance (fixed effect; see eq. 2.3); γ is the fixed effect corresponding to either the bloom initiation or mean chl-a concentration (see eq. 2.3); and SE is the standard error for the fixed-effect coefficients. AIC_C is the Akaike Information Criterion, corrected for small sample size.

Subset	Covariate	Stocks	N	α	SE_α	γ	SE_γ	AIC_C	ΔAIC_C
North	Null	18	232	1.25**	0.11			566.0	5.6
	Bloom Initiation	18	232	1.25**	0.11	-0.12**	0.04	560.3	0.0
	Mean Chl-a (Apr–May)	18	232	1.07**	0.16	0.51	0.32	565.7	5.4
South	Null	9	108	0.71**	0.15			266.6	13.8
	Bloom Initiation	9	108	0.69**	0.15	0.12**	0.03	252.8	0.0
	Mean Chl-a (Apr–May)	9	108	1.16**	0.28	-0.87*	0.45	265.4	12.5
All	Null	27	340	1.05**	0.10			834.8	22.1
	Bloom Initiation	27	340					812.7	0.0
	Mean Chl-a (Apr–May)	27	340					830.7	17.9
	Mean Chl-a (July–Sept)	27	340	1.65**	0.18	-1.69**	0.43	820.3	7.5

* Significantly different from zero at $P < 0.05$
** Significantly different from zero at $P < 0.01$

Estimates of the regional effect of the spring bloom initiation date on salmon productivity were significantly different than zero for both northern and southern multi-stock models (γ in rows 2 and 5 in Table 2.2), but the models were not significantly different than the full model (eq. 2.3), which included both the regional and stock-specific effects ($L = 0.03$, $P > 0.1$). The estimated region-wide effect of spring chl-a concentrations on salmon productivity of southern stocks and late summer chl-a on productivity of all stocks were significantly different from zero (γ in rows 6 and 10 in Table 2.2). However, for both models and chl-a variables, there was no evidence of stock-specific effects based on likelihood ratio tests comparing the full models to a model without the random chl-a effects ($L = 0.001$, $P > 0.1$ for both spring and late summer chl-a). In addition, for the northern stock group there was no support for either a regional or stock-specific effect of

spring chl-a (row 3 in Table 2.2; $L = 0.001$, $P > 0.1$).

In both the northern and southern areas, the bloom initiation date had a stronger effect on pink salmon productivity than spring chl-a concentrations as shown by the ΔAIC_C of 5.4 between the best fit models for chl-a and the bloom initiation for the northern stock group and 12.5 for the southern stock group (Table 2.2). The bloom initiation date also had the highest relative importance ($\Delta AIC_C = 0$) when the northern and southern models were combined with an AIC_C value considerable less than late summer chl-a, spring chl-a, and the null model (rows 7–10 in Table 2.2). Between the two chl-a variables, the late summer chl-a average had a higher relative importance (i.e., lower AIC_C value) than the average spring chl-a concentration as indicated by the 10 unit difference between AIC_C values (rows 9 and 10 in Table 2.2).

2.4.4 Sensitivity analysis

Our estimates of the spatial covariation in pink salmon productivity were not sensitive to the form of stock-recruit model because residuals from the Ricker and Beverton-Holt models were highly correlated (average correlation across stocks = 0.97). The D50 and CZD values were nearly identical between models fit using the Ricker and Beverton-Holt residuals. Similarly, the spatial analyses were not sensitive to the interpolation of data points in the chl-a time series. Difference between D50 values for the interpolated and non-interpolated spring bloom series was 10 km, with almost complete overlap of the confidence intervals. In addition, changes in D50 for monthly chl-a without interpolation values ranged from 0 km to 10 km across months with almost complete overlap of the confidence intervals. Coefficients of the multi-stock Ricker model were also insensitive to the interpolation of missing data.

The results from the multi-stock models were not sensitive to our initial assumption of uncorrelated errors. Specifically, the single-stock models did not indicate strongly autocorrelated errors, and adding an autocorrelated error term to the best-fit multi-stock models did not significantly improve the fits for any of the models, which is consistent with other research on pink salmon productivity (Pyper et al. 2001). In addition, comparisons between the three chl-a metrics and hatchery marine survival rates broadly agreed with the results of the multi-stock models (Supporting materials 2.7.2 and Fig. 2.10).

2.5 Discussion

We investigated two indices of phytoplankton dynamics, spring bloom initiation date and mean chl-a concentration, to better understand the potential mechanisms linking biological oceanographic conditions to Pacific salmon productivity. Our results indicated that (1) spatial covariation

patterns for the spring bloom initiation date, average chl-a concentration, and pink salmon productivity were similar, with strongest positive covariation at the regional scale (0–800 km), (2) there were opposing effects of the spring bloom initiation date on northern and southern pink salmon stock productivity with an early bloom initiation date being associated with higher northern stock productivity and a late bloom being associated with higher southern stock productivity, (3) phytoplankton biomass during the late summer (July–September) was more strongly associated with salmon productivity than phytoplankton biomass during the spring (April–May), and (4) the spring bloom initiation date was a better predictor of salmon productivity than mean chl-a concentration for both southern and northern stocks.

Spatial synchrony for all three variables was strongest at regional spatial scales and declined rapidly with increasing distance. For the bloom initiation date and chl-a concentration, this suggests that physical processes operating on relatively small spatial scales (e.g., summer sea surface temperature and sea surface salinity) drives the spatial variability, rather than larger-scale atmospheric processes such as the Pacific Decadal Oscillation (Mueter et al. 2002b). For pink salmon productivity, our results suggest that both phytoplankton biomass and the bloom initiation date could be factors driving the regional-scale covariation. Furthermore, the match in spatial synchrony between both phytoplankton variables and salmon productivity supports the inclusion of these variables in the single-stock and multi-stock models and also lends support for the observed correlations between pink salmon productivity and both phytoplankton variables.

Spatial correlation of all three variables was less than one at zero distance, indicating the presence of a "nugget effect", which represents variability due to sampling error or spatial dependence at smaller scales than those sampled (Cressie 1993). For pink salmon productivity, this could be caused by errors enumerating spawner abundances. For chl-a and the bloom initiation date, the nugget effect may be caused by measurement errors in the chl-a estimates and spatial averaging, or from the presence of small-scale oceanographic features such as tidal mixing or river plumes that can lead to large changes in the bloom initiation date and chl-a concentrations over short distances (< 100 km; Henson 2007). The latter process could reduce the explanatory power of both phytoplankton variables for salmon productivity because the phytoplankton variables may not index conditions that salmon actually experience at small spatial scales.

There was a marked reduction in the D50 for monthly chl-a concentrations between May and June. The winter and spring period (February–May) included months with both the highest annual chl-a concentrations (April and May) and the lowest (February and March), whereas the chl-a concentrations during June–October were relatively constant (Supporting materials Fig. 2.11). These periods correspond to times before the spring bloom (February and March), during it (April and May), and after it (June–October). Our results also showed that coherence in chl-a

concentrations following the spring bloom is smaller than prior to and during the bloom, which may result from different mechanisms underlying the spatial synchrony at different periods. For example, spatial synchrony before and during the bloom may be primarily driven by regional-scale physical oceanographic conditions such as sea surface temperature or sea surface salinity (Henson 2007). In contrast, the period after the bloom also tends to correspond to the period of peak zooplankton abundances in the Northeast Pacific, indicating that chl-a concentrations after the bloom may be more influenced by top-down grazing pressure, as suggested by others (Chittenden et al. 2010; Bornhold 2000; Mackas et al. 2012).

A plausible explanation for the opposite effects of the bloom initiation date on productivity of northern and southern stocks is that the spring bloom initiation date is a surrogate for other processes that have direct effects on salmon productivity such as predator abundances or zooplankton distributions. The dividing line between the northern and southern stocks occurred in southern southeast Alaska, which falls in the transition zone between the northern downwelling domain and southern upwelling domain (Ware and McFarlane 1989). In the northern region, the spring bloom initiation date has been shown to be closely linked to the timing of water column stability, which is primarily determined by freshwater runoff in the spring (Weingartner et al. 2005; Henson 2007). Moreover, both stability and the bloom initiation date in the northern domain tend to occur earlier in warmer, wetter years that are associated with a more intense Aleutian Low, higher zooplankton biomass, and increased salmon productivity (Brodeur and Ware 1992; Mueter et al. 2002a). In the southern domain, an earlier spring bloom is also associated with increased water column stability, however, stability in this region is primarily driven by increased thermal warming and reduced upwelling-favorable winds, both of which are also associated with a stronger Aleutian Low (Polovina et al. 1995; Henson 2007). In contrast to the northern domain, these conditions in the south for an early bloom initiation have been shown to be associated with increased predator abundances, reduced zooplankton biomass, and decreased salmon productivity (Ware and McFarlane 1995; Mackas et al. 2001; Mueter et al. 2002a).

The optimal stability window hypothesis (Cury and Roy 1989; Gargett 1997) provides another possible explanation for the opposite effects of the bloom initiation date on productivity of northern and southern stocks. This bottom-up forcing mechanism posits that synchronous changes in water column stability in northern and southern areas, which are driven by strength of cyclonic circulation in the Gulf of Alaska (Gargett 1997), can lead to out-of-phase salmon survival rates between the two areas. However, the degree to which our results support the optimal stability window hypothesis depends on the extent to which (1) water column stability and the spring bloom initiation date are linked, (2) water column stability has opposite effects on primary production in northern and southern regions, and (3) there is a strong positive relationship between

phytoplankton biomass and salmon productivity. Although the first two relationships are beyond the scope of this research, our results indicate that there is only a weak relationship between phytoplankton biomass during the spring and salmon productivity and a stronger but negative relationship between phytoplankton biomass during the late summer and salmon productivity.

The latitudinal shift in the effect of the spring bloom initiation date on northern and southern stock productivity corresponds with previous studies that showed opposite effects of sea surface temperature on the productivity of northern and southern pink salmon, chum salmon (*O. keta*), and sockeye salmon (*O. nerka*) stocks (Mueter et al. 2002a; Su et al. 2004). In particular, Mueter et al. (2002a) and Su et al. (2004) indicated that warm sea surface temperatures were associated with higher pink salmon productivity for northern stocks and lower productivity for southern stocks with the north/south break occurring near the southern end of Southeast Alaska (~54°N), which closely matches the break point we identified for the spring bloom initiation date (~56°N). This consistency in the latitude of the north/south break point across studies of different environmental variables further supports the idea that the opposite effects are driven by differences in ocean conditions between the northern and southern domains.

It is not clear why a lower late summer chl-a concentration would be associated with greater salmon productivity, but a possible explanation relates to top-down grazing pressure. Our chl-a variable represents variability in the phytoplankton standing stock, which can be influenced by both phytoplankton productivity and top-down grazing pressure. Zooplankton grazers in the Northeast Pacific at least partially control the standing stock of phytoplankton (Strom et al. 2001; Frost 1987) and, in turn, are an important food source for juvenile pink salmon (Boldt and Haldorson 2003; Armstrong et al. 2005; Beauchamp et al. 2007). If pink salmon do not significantly control zooplankton abundance, then lower phytoplankton biomass could represent higher zooplankton abundances available to support higher growth and survival of pink salmon. This hypothesis is supported by observations in the Strait of Georgia, British Columbia indicating that peak zooplankton biomass (in particular *Neocalanus* spp.) often coincides with phytoplankton biomass minima (Bornhold 2000). Furthermore, grazing by zooplankton may also partially explain the weak positive effect of spring chl-a on northern stock productivity and the negative effect on southern stock productivity if the seasonal timing of peak zooplankton biomass follows a north-south gradient with later peaks in more northern areas. For example, in the north the spring chl-a variable may index phytoplankton biomass prior to increases in zooplankton biomass, while in the south zooplankton biomass may have already started to increase by the end of May (Mackas et al. 2012).

Mortality of pink salmon in the marine life phase is thought to primarily occur in coastal environments during the first summer in the ocean (Farley et al. 2007a; Parker 1968; Wertheimer and Thrower 2007). In particular, research on pink salmon in Southeast Alaska and Prince William

Sound, AK has indicated that a considerable portion of marine mortality occurs in inside waters prior to salmon migrating to the Gulf of Alaska (Orsi et al. 2013; Farley et al. 2007a). While the majority of these coastal environments were indexed by our satellite-derived estimates for the spring bloom initiation date and chl-a averages (Fig. 2.1), there were a few areas that were poorly covered (e.g., inside Southeast Alaska and the inner coast of Vancouver Island) due to missing satellite data. For stocks in these areas, we assumed that oceanographic conditions on the outer coast were representative of conditions experienced by juvenile salmon during their first few months in the ocean. This assumption is supported by the correspondence of our estimates of the spring bloom initiation date and several studies that estimated the spring bloom start date using *in situ* observations. For example, the average estimate for the spring bloom initiation date for the inner SEAK pink salmon stock group over the years 1998–2009 was the first week in April, which matches *in situ* observations for the bloom start date in Auke Bay, AK (Ziemann et al. 1991). Likewise, the average bloom start date for the southern BC stock was the second to third week in March, which matches *in situ* observations from the inner coast of Vancouver Island (Chittenden et al. 2010). Because of this coherence between the satellite estimates and *in situ* observations, we believe our assumption about outside waters being representative of coastal environments is valid for our study region.

Although we focused on pink salmon productivity, phenology and biomass of phytoplankton in coastal ecosystems may also be important factors controlling covariation in other salmon species. For instance, productivity indices of sockeye salmon, chum salmon, and coho salmon (*O. kisutch*) also tend to covary at a regional spatial scale with sockeye and coho salmon having the most similar spatial scales of covariation to that of pink salmon (Mueter et al. 2002b; Teo et al. 2009; Peterman and Dorner 2012). In particular, our results may be most applicable to sockeye salmon, which tend to feed at a similar trophic level as pink salmon (Johnson and Schindler 2009).

Our results suggest a link between the spring bloom initiation date and pink salmon productivity; however, further research is needed to understand the mechanisms underlying this relationship. For example, comparing the potential match/mismatch between salmon out-migration timing and initiation of phytoplankton and zooplankton blooms could help clarify how phenologies are coupled across trophic levels. Similarly, research into the relationships between primary productivity and salmon productivity, as opposed to phytoplankton biomass, would help in understanding the importance of the optimal stability window. Our spatial correlation results indicate that such research should focus on regional-scale processes and avoid correlating large-scale climate indices with salmon productivity (Mueter et al. 2002a; Peterman and Dorner 2012).

In conclusion, our results suggest that the phenology of bottom-up biological oceanographic processes are more important for higher trophic level species such as pink salmon than the standing stock of phytoplankton. This conclusion has important implications as the climate warms. It

is generally recognized that a warming climate will lead to an earlier onset of spring conditions, including earlier timing of peak zooplankton biomass and outmigration of pink salmon (Parmesan and Yohe 2003; Taylor 2008; Mackas et al. 2012). Phenological mismatches could occur across trophic levels if separate processes do not change in synchrony (Edwards and Richardson 2004), potentially leading to northward latitudinal shifts in peak pink salmon productivity.

2.6 Acknowledgments

2.7 Supporting materials

2.7.1 Comparison of SeaWiFS and MODIS chlorophyll-a data products

Lengthy periods of missing data in 2008–2010 for the SeaWiFS chl-a data set made these years of data unsuitable for calculating an initiation date of the spring bloom (Fig. 2.7). Therefore, we investigated the feasibility of combining the SeaWiFS and MODIS chl-a data products. We used Pearson correlation coefficients between the two time series of $\log_{10}$ transformed data, root mean squared $\log_{10}$ error (RMSE), and $\log_{10}$ bias (mean of the absolute value of $\log_{10}$ transformed MODIS chl-a values minus SeaWiFS values) to quantify the covariation and differences between the SeaWiFS and MODIS data sets for the first five complete years of overlap, 2003–2007 (Gregg and Casey 2004; O'Reilly et al. 2000; Zhang et al. 2006) . We performed two primary comparisons. First, to assess the similarities between the data sets across the entire study region and time period, we calculated the average of each of the three metrics (i.e., correlation coefficients, RMSE, and $\log_{10}$ bias) for all grid cells and years. Second, to assess differences among years, we calculated the averages of the RMSE, as well as $\log_{10}$ bias metrics for all grid cells by year.

The average correlation between the MODIS and SeaWiFS chl-a data sets across grid cells was 0.87, with correlations for individual grid cells ranging from 0.69 to 0.95. The RMSE of the differences between the SeaWiFS and MODIS chl-a data sets over all years and grid cells was 0.16 and annually it ranged from 0.09 in 2007 to 0.22 in 2006 (Fig. 2.8). These RMSE values are slightly smaller than RMSE values of the differences between satellite chl-a estimates and field sampled

chl-a data (RMSE of 0.22; O'Reilly et al. 2000), indicating our RMSE values are within the range of background noise of the algorithm used to produced the chl-a estimates. The $\log_{10}$ bias of MODIS data compared to SeaWiFS data over all grid cells and years was 0.012 and annually ranged from 0.04 in 2004 to -0.01 in 2007 (Supporting materials Fig. 2.7) with 79% of absolute differences being less than 0.1 and 90% of differences being less than 0.2. These $\log_{10}$ bias values are generally small differences given the estimated chl-a values (Supporting materials Fig. 2.11). In addition, the $\log_{10}$ bias values indicate that the MODIS values are slightly higher than the SeaWiFS values at this temporal composite and spatial resolution for most years.

Our comparison of the SeaWiFS and MODIS chl-a data products concurs with values reported by other researchers over the same time and a similar region (Waite and Mueter 2013). Given the strong covariation, low RMSE, and small $\log_{10}$ bias between chl-a data products, we deemed it appropriate to concatenate the SeaWiFS and MODIS data products for our study region without further data processing.

2.7.2 Hatchery pink salmon marine survival

To further test the effects of the spring bloom initiation date and chl-a concentrations on pink salmon dynamics, we compared the three chl-a metrics to pink salmon marine survival rates for three hatchery stocks located around the Gulf of Alaska (Armin F. Koernig, Kitoi Bay, and Port Armstrong). Marine survival rates for each hatchery stock were estimated for release years 1998–2010 by dividing the total adult pink salmon returns resulting from juveniles released in year *t* by the total number of juvenile pink salmon released into marine waters in year *t*. To estimate the association between each of the three chl-a metrics and marine survival, we calculated Pearson correlation coefficients between marine survival rates and the spring bloom initiation date, average April–May chl-a concentration, and average July–September chl-a concentration. Like the analysis in the main text, each chl-a metric and the spring bloom initiation date were averaged over all grid cells within 250 km of the ocean release location for each hatchery.

Marine survival rates for all three hatcheries were negatively correlated with the spring bloom initiation date (Supporting materials Fig. 2.10), which corresponds with our hierarchical model results that indicated a negative region-wide effect of the spring bloom initiation on salmon productivity for northern stocks. The correlations between marine survival rates and spring chl-a concentration were mostly positive with two positive correlations and a negative correlation (Supporting materials Fig. 2.10), which corresponds with the results from our single-stock and multi-stock models for northern stocks that indicated a weak positive region-wide effect. The correlations for the late summer chl-a concentration diverged from our single-stock and multi-stock model results with two positive correlations and a negative correlation (Supporting materials Fig.

2.10), however, the correlations were weak for all three hatcheries (less than 0.35 for all hatcheries). On average, the absolute values of correlations between marine survival and the spring bloom were higher (average correlation = 0.34) than for the spring chl-a concentration (average correlation = 0.27) and the late summer chl-a concentration (average correlation = 0.23).

Results of the hatchery marine survival analysis broadly agreed with the results from the single-stock and multi-stock models in the main text. In particular, the hatchery results support our conclusions that (1) an early spring bloom timing is associated with increased productivity for northern pink salmon stocks, and (2) the spring bloom initiation date is more strongly associated with pink salmon productivity than phytoplankton biomass.

2.7.3 Supporting figures
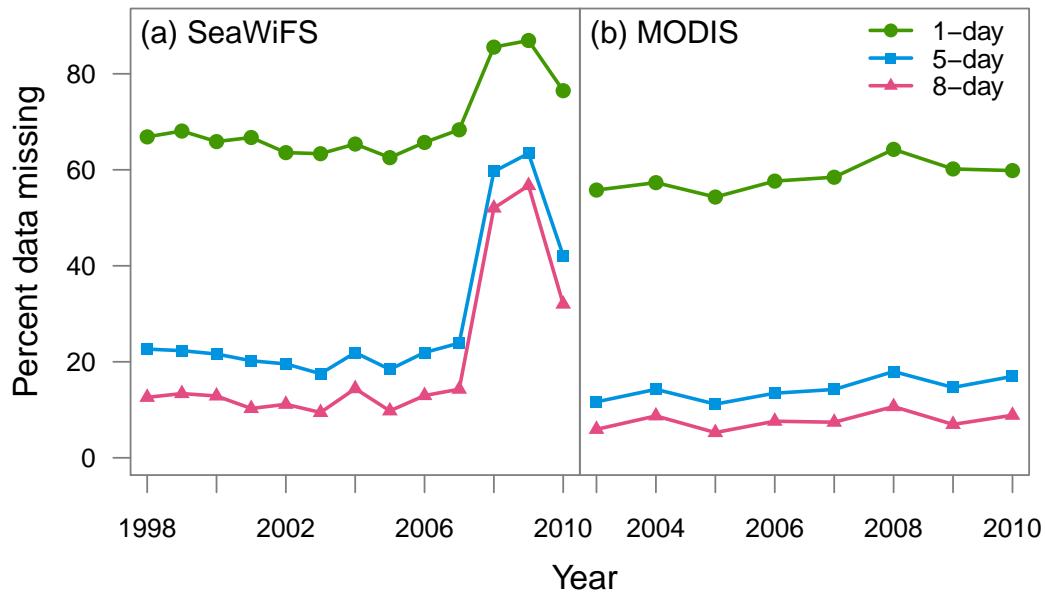
Figure 2.7: Percent of all grid cells with missing chl-a data by year (see Fig. 2.1 of the main text) for SeaWiFS (left panel) and MODIS (right panel) chl-a data. Green line with closed circles indicates 1-day composites, blue line with filled squares indicates 5-day composites, and red line with filled triangles indicates 8-day composites.
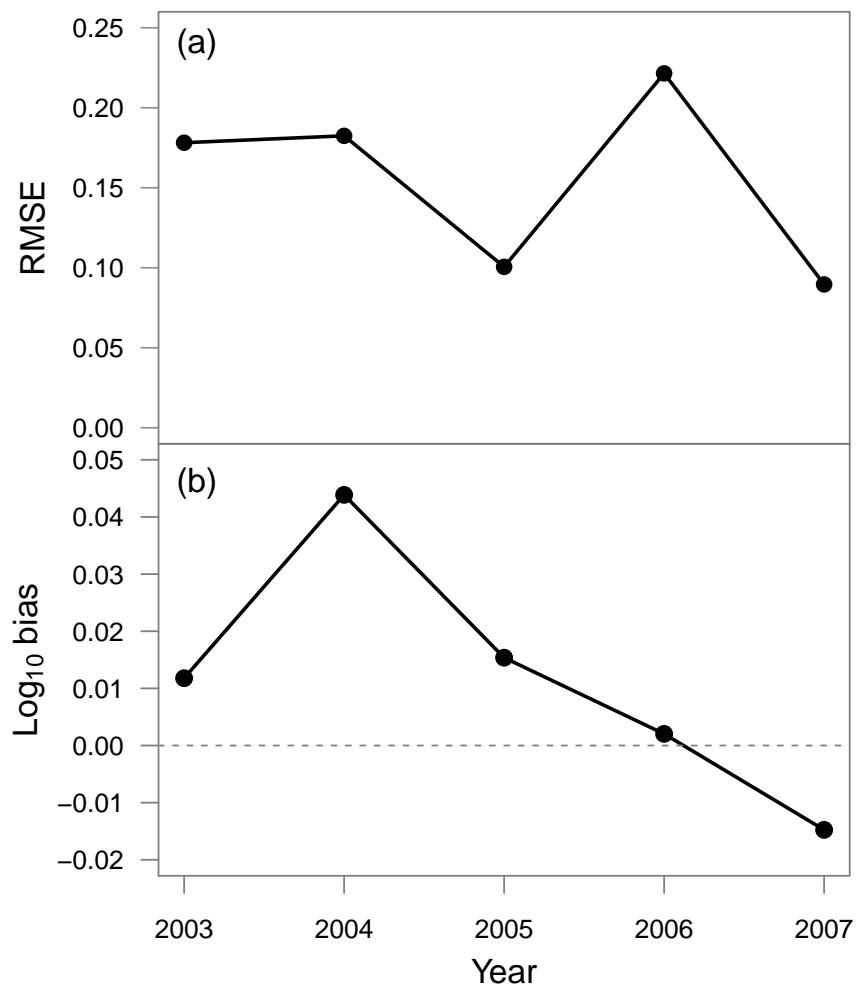
Figure 2.8: Annual values for the root mean squared $\log_{10}$ error (RMSE; top panel) and $\log_{10}$ bias (bottom panel) calculated as MODIS minus corresponding SeaWiFS chl-a value.
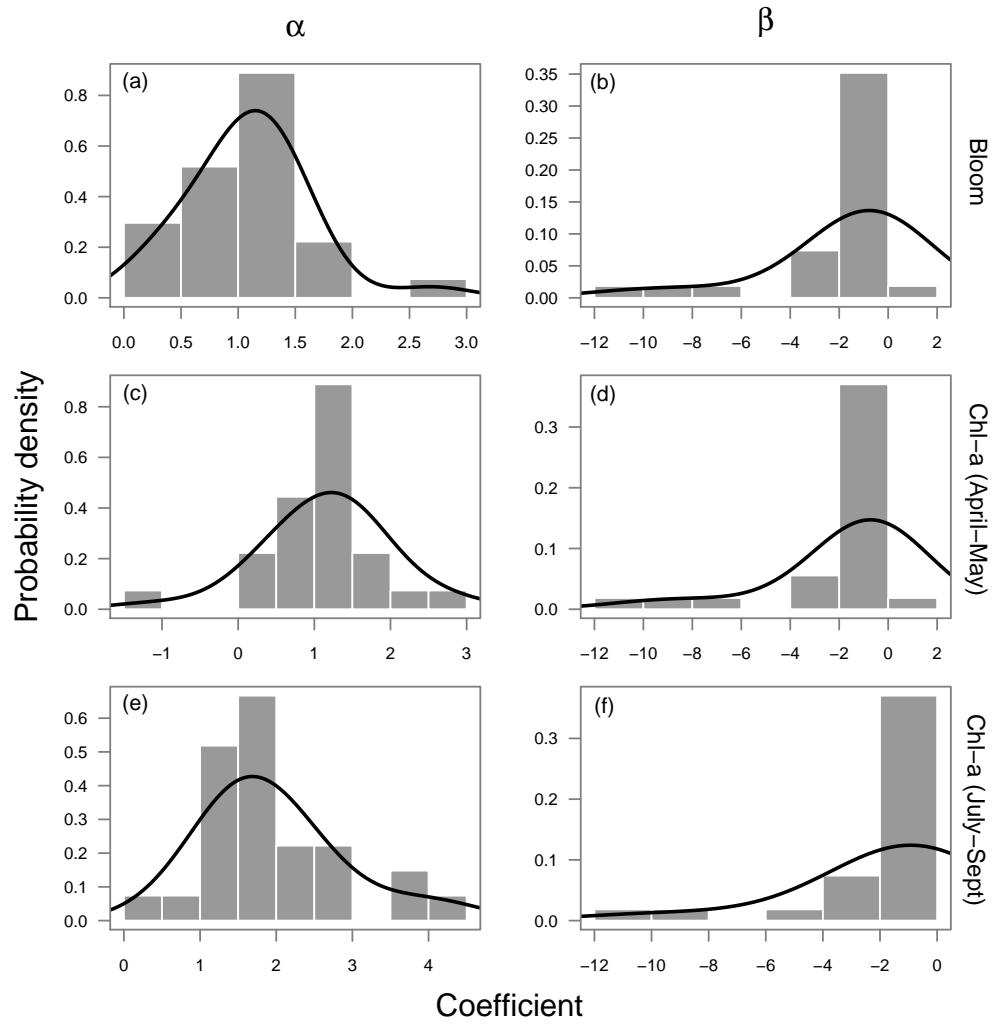
Figure 2.9: Histograms of the estimated α and β coefficients for the single stock models (eq. 2.2) and estimated probability density functions (smooth solid black lines) for bloom initiation date (top row), average spring chl-a concentrations (middle row), and average late summer chl-a concentrations (bottom row).
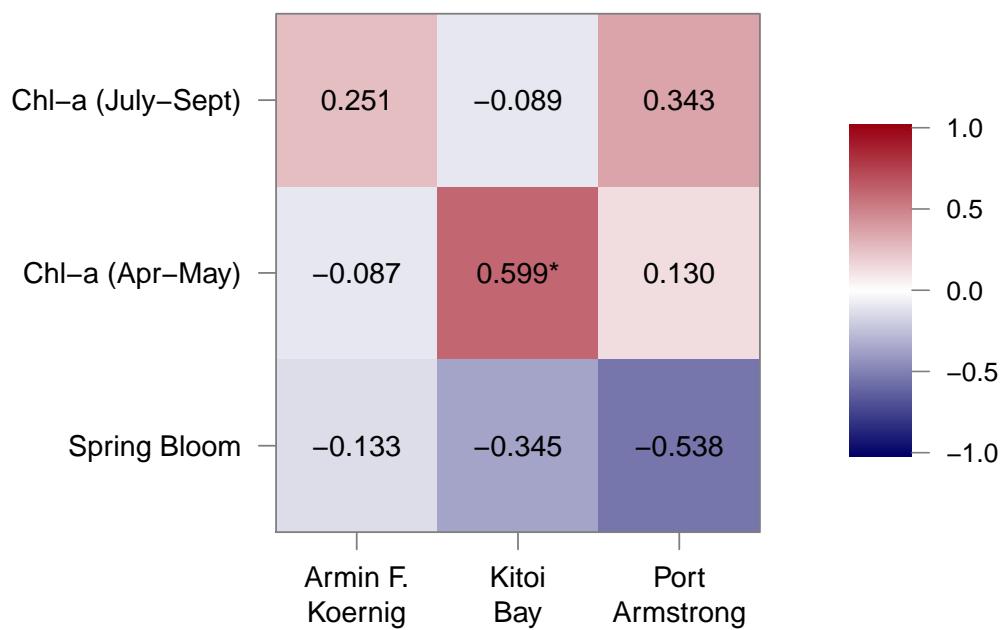
Figure 2.10: Correlation matrix showing the Pearson correlation coefficients between each of the hatchery marine survival time series and the three chl-a metrics (* indicates significantly different from zero at $P < 0.05$).
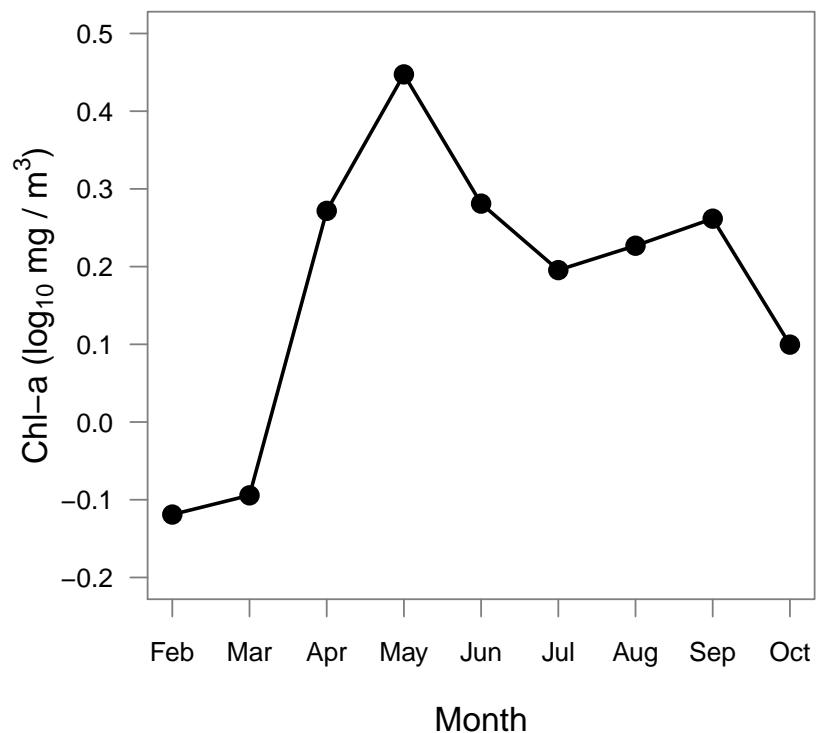
Figure 2.11: Average monthly $\log_{10}$ transformed chlorophyll-a values across all grid cells and years.

Chapter 3

Effects of the North Pacific Current on productivity of 163 Pacific salmon stocks[1]

3.1 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 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, 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 productivity of salmon stocks in Alaska. Our results indicated that horizontal transport pathways may 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

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[1]A version of this chapter appears as Malick, M.J., S.P. Cox, F.J. Mueter, B. Dorner, R.M. Peterman. Effects of the North Pacific Current on productivity of 163 Pacific salmon stocks. Fisheries Oceanography. http://doi.org/10.1111/fog.12190.

species under consideration.

3.2 Introduction

Environmental change can influence demographic rates of marine and anadromous fish populations through multiple environmental pathways (Ottersen et al. 2010; Drinkwater 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 (Malick et al. 2015b; Di Lorenzo et al. 2013b; Ottersen et al. 2010). 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. 2011b; Keister et al. 2011; Sydeman et al. 2011) and Gulf of Alaska (Stabeno et al. 2004; Combes et al. 2009; Kline 2010; Kline et al. 2008) 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. 2013b).

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. 2007b; 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 (Armstrong et al. 2008; Beauchamp et al. 2007; Brodeur et al. 2007a). 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. 2011b; Keister et al. 2011). The lipid-rich northern zooplankton community, in particular, is associated with higher coho salmon (*O. kisutch*) survival in the Northern California Current region (Bi et al. 2011a), suggesting that horizontal transport may be important for salmon productivity in other regions. In addition, horizontal transport may also 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 Pa-

cific 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. 3.1a; Ware and McFarlane 1989; Chelton and Davis 1982). 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 also inter-annual 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 (Sherman and Duda 1999; Longhurst 1995). 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; Thorson and Minto 2015; Mueter et al. 2002a).

3.3 Methods

3.3.1 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. 3.1). 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 years for pink salmon, 33 years for chum salmon, and 38 years for sockeye salmon. For pink and chum salmon, data sets generally represented aggregations of adjacent salmon populations, which helped ensure that
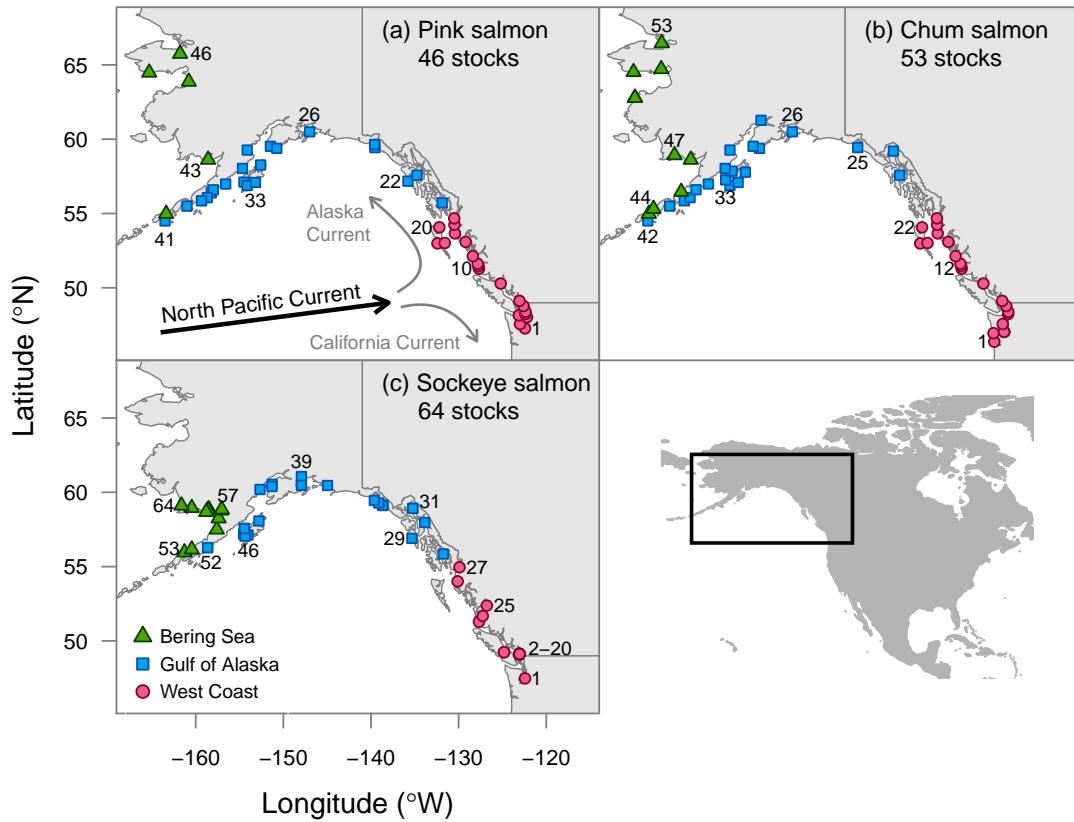
Figure 3.1: Study area indicating the ocean entry locations for (a) pink salmon stocks, (b) chum salmon stocks, and (c) sockeye salmon stocks. Solid circles (red) indicate stocks located in the West Coast ecosystem; solid squares (blue) indicate stocks located in the Gulf of Alaska ecosystem; solid triangles (green) indicate stocks in the Bering Sea ecosystem. Stocks are numbered consecutively from south to north for each species. In panel (a), the thick black arrow shows the North Pacific Current, which flows from west-southwest to east-northeast, and the grey arrows show the bifurcation of the North Pacific Current into the northward flowing Alaska Current and southward flowing California Current.

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. 3.1). 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. (2015a) and Mueter et al. (2002a), 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.

3.3.2 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 Jr. 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 Jr. 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 (Supporting materials Fig. 3.6). Simulated drifters were released annually on February 1 and the daily trajectory was tracked until June 30 to reflect ocean conditions relevant to seaward-migrating juvenile salmon (Di Lorenzo et al. 2013a). 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 (Supporting materials Fig. 3.7). Positive values of the index indicate a northward-shifted bifurcation (majority of drifters ending

south of their starting latitude), whereas negative values of the index indicate a southward-shifted bifurcation (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 (Chhak et al. 2009; Di Lorenzo et al. 2009; 2008). Positive values of the NPGO are also associated with higher nutrient concentrations (e.g., NO_3), 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 prior to ocean entry of salmon smolts.

For pink and chum salmon, which enter the ocean the first spring following spawning, the BI and NPGO indices were offset by 1 year (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 one or two years before entering the ocean, we used a weighted average of index values offset by 2 years and 3 years, 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. 2002a).

3.3.3 Modeling the data

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

$$y_{i,t} = \alpha_i + \beta_i S_{i,t} + \epsilon_{i,t}, \tag{3.1}$$

where $y_{i,t}$ is the log_e of recruits per spawner, $log_e(R_{i,t}/S_{i,t})$, for stock i in year t, α_i is the density-independent stock productivity at low spawning stock sizes, β_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 σ_ϵ^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.,

$$y_{i,t} = \alpha_i + \beta_i S_{i,t} + \gamma_{BI,i} BI_t + \gamma_{NPGO,i} NPGO_t + \epsilon_{i,t}, \tag{3.2}$$

where $\gamma_{BI,i}$ is the stock-specific coefficient for the BI and $\gamma_{NPGO,i}$ 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 prior to 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., $\epsilon_{i,t} = \phi_i \epsilon_{i,t-1} + \delta_{i,t}$, where $\delta_{i,t} \sim N(0, \sigma_i^2)$ and ϕ_i is the first-order autocorrelation coefficient for stock i (Mueter et al. 2002a; Chatfield 2004). For both the standard and generalized forms of the Ricker model, the autoregressive process was modeled as,

$$y_{i,t} = \begin{cases} \hat{y}_{i,t} + \phi_i \epsilon_{i,t-1} + \delta_{i,t} & \text{for } t > 1 \\ \hat{y}_{i,t} + \delta_{i,t} & \text{for } t = 1 \end{cases} \tag{3.3}$$

where $\hat{y}_{i,t}$ is the predicted stock productivity from either the standard Ricker model (eq. 3.1) or the generalized Ricker model (eq. 3.2).

3.3.4 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., α_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 2006). In this study, we fit species-specific Bayesian hierarchical models that used hierarchical prior distributions for α_i, $\gamma_{BI,i}$, and $\gamma_{NPGO,i}$ 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 α_i were exchangeable across all stocks within a species and we used a normal prior distribution, i.e., $\alpha_i \sim N(\mu_\alpha, \tau_\alpha^2)$ with hyperparameters μ_α and τ_α^2 representing the overall mean and variance, respectively. We used a diffuse normal distribution, $\mu_\alpha \sim N(0, 10^3)$, for the hypermean μ_α and an improper uniform prior for the hypervariance, $\tau_\alpha^2 \sim U(0, 25)$ (Gelman 2006).

We assumed that the $\gamma_{BI,i}$, and $\gamma_{NPGO,i}$ parameters were only exchangeable among stocks within the same ecosystem (WC, GOA, BS) for each of the BI and NPGO because ocean conditions can influence salmon stocks in different ecosystems in opposite ways (Mueter et al. 2002a; Malick et al. 2015a). 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., $\gamma_{i,WC} \sim N(\mu_{\gamma_{WC}}, \tau_{\gamma_{WC}}^2)$), whereas all pink salmon stocks in the GOA ecosystem were assumed exchangeable and were assigned a separate prior distribution (i.e., $\gamma_{i,GOA} \sim N(\mu_{\gamma_{GOA}}, \tau_{\gamma_{GOA}}^2)$). For a particular ecosystem and oceanographic variable, the hypermean μ_γ represents the mean ecosystem-level effect and the hypervariance τ_γ^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 α and γ parameters, which we assumed were exchangeable across salmon stocks within a species or ecosystem, we treated the remaining parameters, i.e., β_i, σ_i, and ϕ_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 (Mueter et al. 2002a; Malick et al. 2015a; Su et al. 2004). We assigned diffuse independent priors for the density-dependence parameters, $\beta_i \sim N(0, 10^3)$, and assigned the variances, σ_i^2, and autocorrelation coefficients, ϕ_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 σ_i^2 and ϕ_i parameters across stocks within a species, we also fit several simpler models in which σ_i^2 and ϕ_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 σ_i^2 and ϕ_i (Table 3.1).

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., μ_γ) 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).

Table 3.1: 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.

#	Type	α	β	σ^2	ϕ	γ_{BI}	γ_{NPGO}
1	standard	exchange	different	same			
2	standard	exchange	different	different			
3	standard	exchange	different	same	same		
4	standard	exchange	different	different	same		
5	standard	exchange	different	different	different		
6	generalized	exchange	different	same		ecosystem	ecosystem
7	generalized	exchange	different	different		ecosystem	ecosystem
8	generalized	exchange	different	same	same	ecosystem	ecosystem
9	generalized	exchange	different	different	same	ecosystem	ecosystem
10	generalized	exchange	different	different	different	ecosystem	ecosystem

3.3.5   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 5 000 iterations per chain. Gibbs chain convergence was assessed graphically (e.g., traceplots, 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).

3.3.6   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-pointwise 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 WAIC $= -2*(lppd - pD)$. 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.

3.3.7 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 (Supporting materials Fig. 3.6). Second, we checked the sensitivity of our results to the manner in which the BI was calculated. Specifically, we re-calculated the BI following 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 February 1 and the median ending latitude on June 30. 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 prior to calculating the BI index. We assessed the sensitivity of our analysis to specifics of BI calculation by determining 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.

We also conducted an additional sensitivity analysis to test if our grouping of salmon stocks into three large marine ecosystems adequately captured the spatial distribution of the effects of the BI and NPGO. In particular, we fit single-stock generalized Ricker models (i.e., eq. 3.2) to each of the 163 salmon stocks separately using maximum likelihood to identify potential differences among stocks within our three ecosystem groupings. Unlike the Bayesian hierarchical models where the γ_i coefficients are centered around a common mean, in the single-stock models each stock is independent of the other stocks, which allowed us to better determine if smaller spatial-scale patterns were evident in the $\gamma_{BI,i}$ and $\gamma_{NPGO,i}$ coefficients.

3.4 Results

3.4.1 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. 3.2; Supporting materials Fig. 3.7). 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.
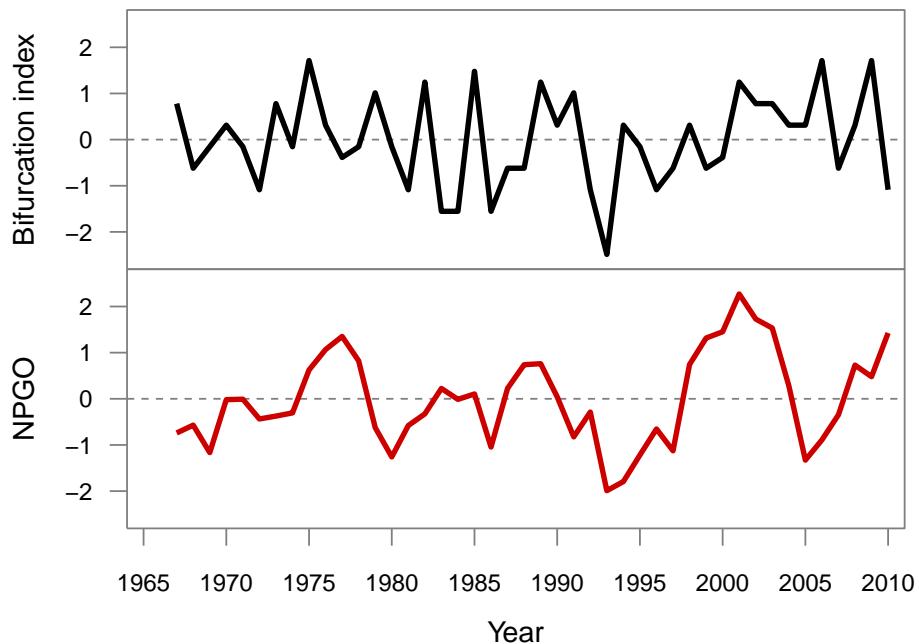
Figure 3.2: Time series for the bifurcation index (BI; upper panel) and North Pacific Gyre Oscillation (NPGO; bottom panel). Both time series are standardized to a mean of 0 and a standard deviation of 1 (i.e., standard deviation units, SDUs). Positive values of the BI reflect a northward-shifted bifurcation in the NPC, whereas negative BI values indicate a southward-shifted bifurcation. Positive values of the NPGO indicate a stronger NPC, whereas negative NPGO values indicate a weaker NPC.

3.4.2 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 3.2). 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 increased productivity of pink, chum, and sockeye salmon, i.e., positive $\gamma_{BI,i}$ and $\gamma_{NPGO,i}$ values (Figs. 3.3 and 3.4). 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 (Figs. 3.3 and 3.4).

Table 3.2: Model selection quantities for each fitted model. # gives the model number as defined in Table 3.1; Np gives the nominal number of parameters in a model; 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.

	Pink			Chum			Sockeye		
#	Np	pD	ΔWAIC	Np	pD	ΔWAIC	Np	pD	ΔWAIC
1	95	71	260.0	109	89	292.1	131	104	589.0
2	140	115	51.7	161	133	180.2	194	164	287.8
3	96	71	254.1	110	85	156.8	132	102	328.0
4	141	113	42.6	162	134	48.0	195	164	6.0
5	186	152	101.0	214	175	22.6	258	218	16.1
6	199	98	224.4	227	119	266.4	271	148	556.8
7	244	135	10.8	279	155	156.1	334	204	248.7
8	200	97	214.4	228	115	148.7	272	138	322.7
9	245	134	**0.0**	280	156	29.7	335	189	**0.0**
10	290	174	57.2	332	198	**0.0**	398	250	3.2

For pink and chum salmon stocks in the WC ecosystem, the estimated median ecosystem-level effect (i.e., μ_γ) for the NPGO was 2.4 times higher than the BI for pink salmon and 2.5 times higher for chum salmon (Table 3.3; Fig. 3.4). Similarly, the estimated median stock-specific effects (i.e., γ_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. 3.3; pink salmon: γ_{NPGO} range = 0.22–0.29 vs. γ_{BI} range = 0.06–0.13; chum salmon: γ_{NPGO} range = 0.12–0.15 vs. γ_{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. 3.5).

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 3.3; Fig. 3.4). Furthermore, the median stock-specific effects of the BI on sockeye salmon productivity (i.e., γ_{BI} range = 0.09–0.13) were consistently higher than stock-
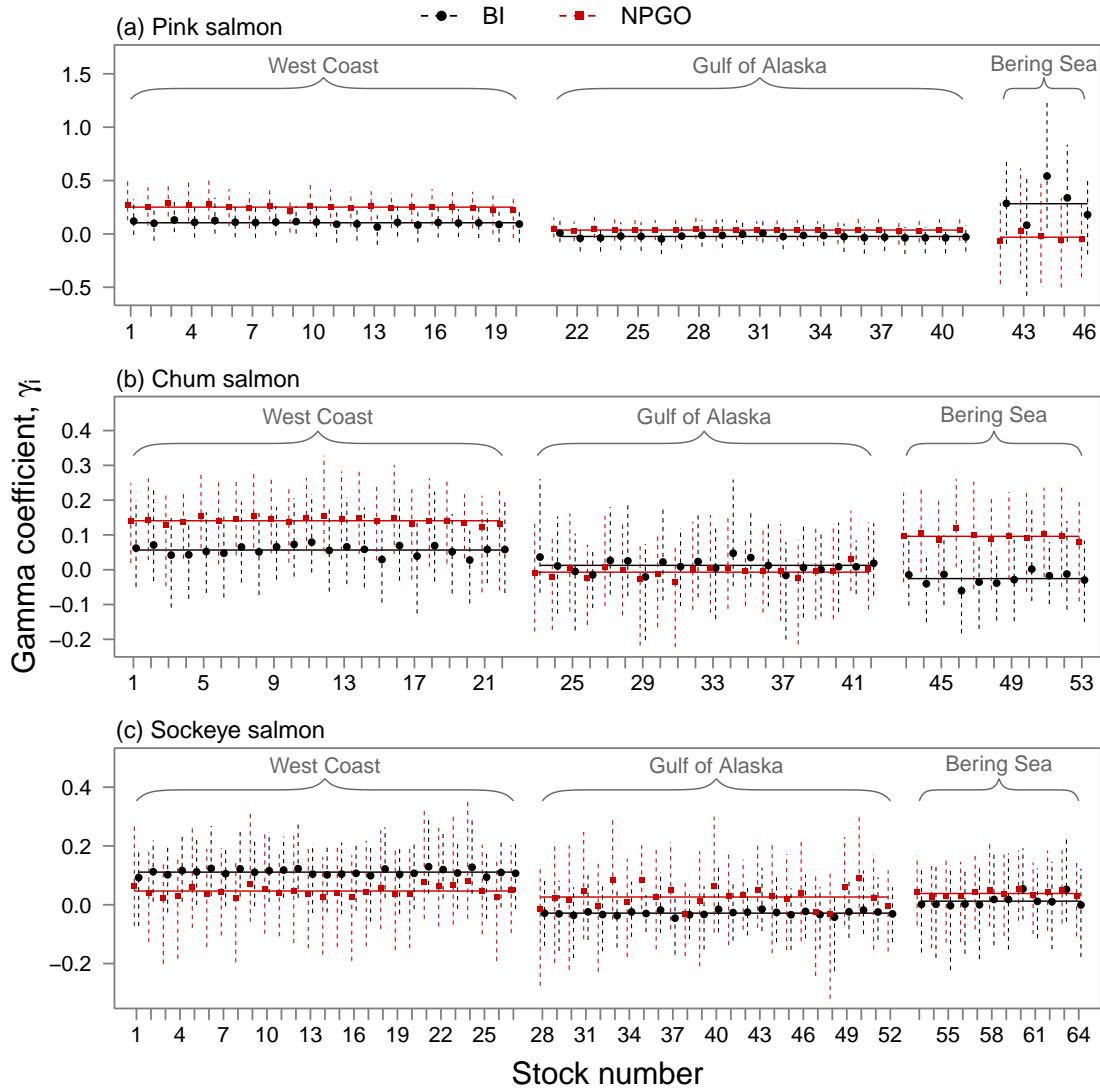
Figure 3.3: Posterior medians and 95% credible intervals for the stock-specific bifurcation index (BI) and North Pacific Gyre Oscillation (NPGO) effects, $\gamma_{BI,i}$ and $\gamma_{NPGO,i}$, respectively, as derived from the best-fit models (9 and 10 in Table 3.1). Coefficients (in standard deviation 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. 3.1. Solid circles (black) indicate $\gamma_{BI,i}$ median values and dashed black lines indicate the 95% credible intervals for the BI effect. Solid squares (red) indicate $\gamma_{NPGO,i}$ 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_γ.
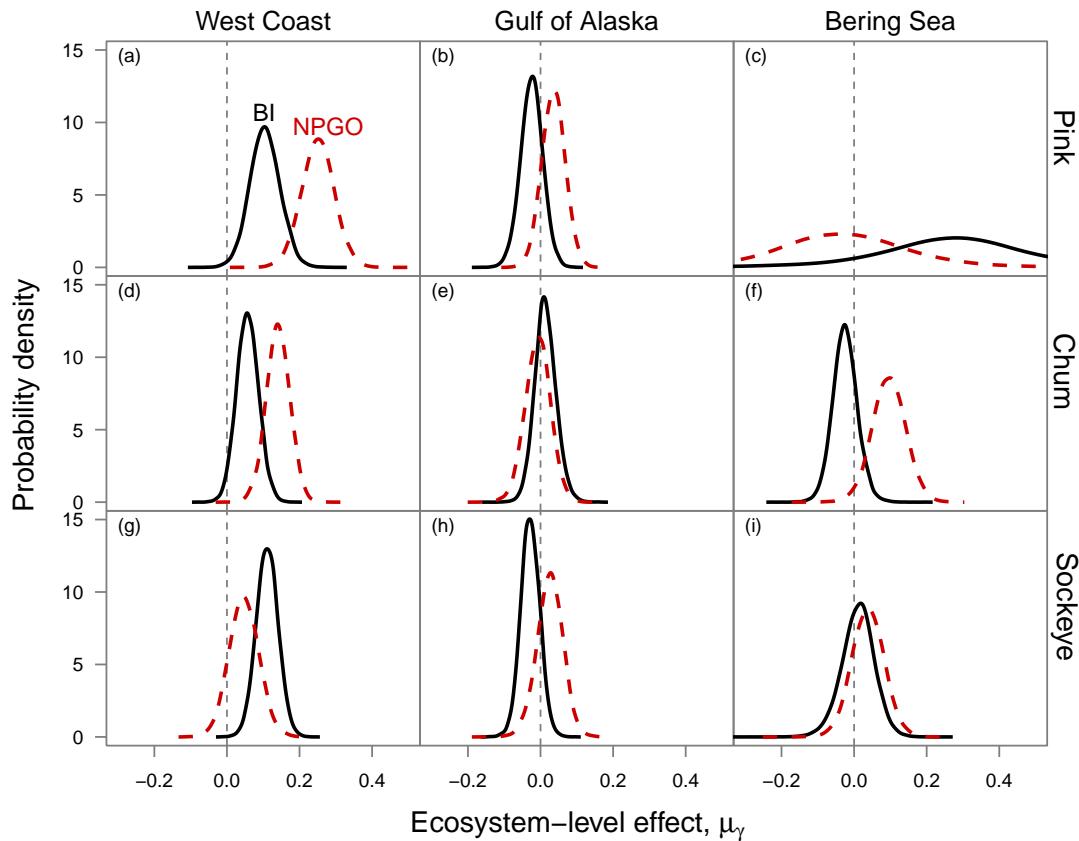
Figure 3.4: Posterior distributions for the ecosystem-level effects, μ_γ, of the bifurcation index (BI) and North Pacific Gyre Oscillation (NPGO) in standard deviation units. Distributions are shown for pink salmon (top row), chum salmon (middle row), and sockeye salmon (bottom row), as well as for the 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.

specific effects of the NPGO (γ_{NPGO} range = 0.02–0.08; Fig. 3.3c). 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 productivity given a one SD-unit increase in the NPGO index (Fig. 3.5).

In the GOA ecosystem, there was no evidence for consistent stock-specific or ecosystem-level effects of either the BI or NPGO on productivity of all three species (Figs. 3.3 and 3.4; Table 3.3). The 95% credibility intervals for stock-specific effects included zero for all species, stocks, and both the BI and NPGO indices (Fig. 3.3). Similarly, the posterior distributions for the GOA ecosystem-level effects of the BI and NPGO on salmon productivity were close to zero for all species (Fig. 3.4; Table 3.3).

In the BS ecosystem, the effects of the BI and NPGO on salmon productivity were quite variable across species. For BS pink salmon, the effects of the NPGO were close to zero, and the effects of the BI were consistently positive (γ_{BI} range = 0.08–0.54), although there was considerable uncertainty associated with the pink salmon γ_i parameter estimates (Figs. 3.3 and 3.4; Table 3.3). In contrast, for BS chum salmon the estimated effects of the NPGO were consistently positive (γ_{NPGO} range = 0.08–0.12), but the BI effects were close to zero (γ_{BI} range = -0.06–0.002). For sockeye salmon in the BS ecosystem, the posterior distributions for the stock-specific and ecosystem-level effects of the BI and NPGO were both near zero (Figs. 3.3 and 3.4; Table 3.3), indicating neither index has strong effects on productivity of sockeye salmon in the Bering Sea.

Table 3.3: Ecosystem-wide effects (i.e., μ_γ) for the BI and NPGO indices from the best-fit models (9 and 10 in Table 3.1). Values are in standard deviation units and show the median for μ_γ with 95% credible intervals given in parentheses.

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

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 3.2). In addition, 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 3.2).
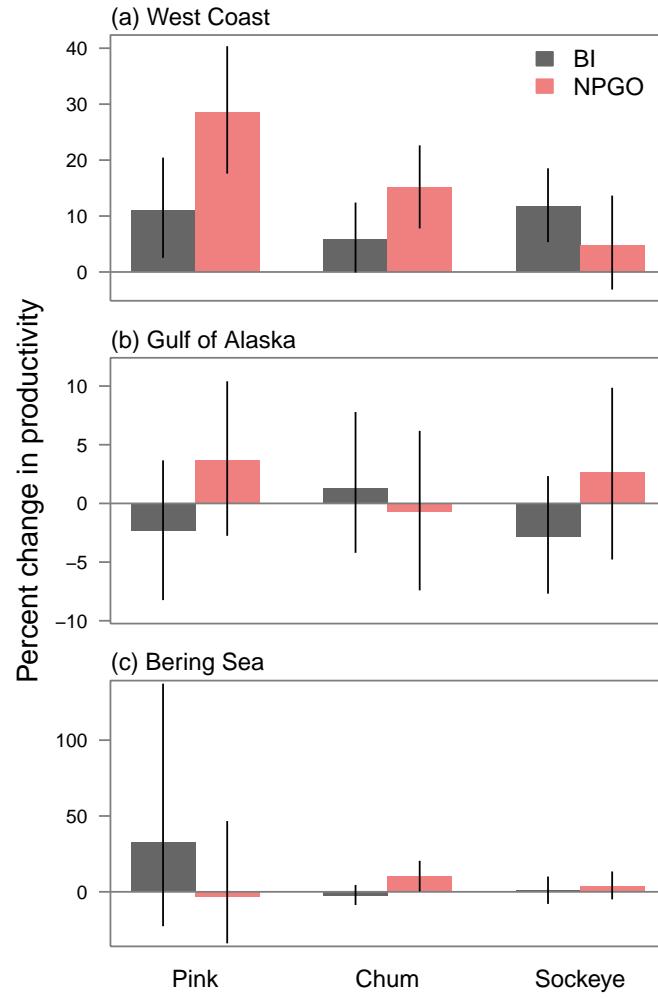
Figure 3.5: Percent change in productivity given a one unit increase in either the bifurcation index (BI; grey) or North Pacific Gyre Oscillation (NPGO; red) for stocks in the (a) West Coast ecosystem, (b) Gulf of Alaska ecosystem, and (c) Bering Sea ecosystem. Vertical bars indicate the 95% credible interval for the estimated percent change.

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 3.2). For all three species, there was also greater support for models that included a stock-specific variance term compared to models that only included a shared variance term (Table 3.2). 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 3.2).

3.4.3 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 (Supporting materials Table 3.4). 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 (Supporting materials Table 3.5). 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; Supporting materials Table 3.5). 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 (Supporting materials Fig. 3.8).

3.5 Discussion

In this study, we estimated the effects of two modes of variability in the NPC on 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, a northward-shifted bifurcation and increased NPC strength was 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 (Kilduff et al. 2015; Sydeman et al. 2011; Batten and Freeland 2007). 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 (Armstrong et al. 2008; Beauchamp et al. 2007; Brodeur et al. 2007a). For example, Keister et al. (2011) and Bi et al. (2011b) indicated that changes in along-shore transport can 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; Sydeman et al. 2011; Keister 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 to 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 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 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. (2002a) showed opposite effects of sea surface temperature on pink, chum, and sockeye salmon in northern and southern areas, with the dividing line occurring around southern Southeast Alaska. Similarly, Malick et al. (2015a) 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. (2002a) and Malick et al. (2015a) 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 (1) neither index had a strong effect on sockeye salmon productivity, (2) the NPGO was positively related to chum salmon productivity, and (3) 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. 2013a).

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; Malick et al. 2015b; Di Lorenzo et al. 2013b). 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 production of higher-trophic-level species.

3.6 Acknowledgments

3.7 Supporting materials

3.7.1 Supporting figures and tables

Table 3.4: 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 3.1 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.

#	Pink			Chum			Sockeye		
	Np	pD	ΔWAIC	Np	pD	ΔWAIC	Np	pD	ΔWAIC
1	95	71	263.4	109	89	298.0	131	104	592.8
2	140	115	55.1	161	133	186.0	194	164	291.5
3	96	71	257.6	110	85	162.6	132	102	331.7
4	141	113	46.1	162	134	53.9	195	164	9.7
5	186	152	104.5	214	175	28.4	258	218	19.8
6	199	98	233.0	227	123	268.1	271	149	553.2
7	244	136	11.9	279	159	157.6	334	206	249.0
8	200	98	222.0	228	118	149.4	272	137	319.8
9	245	133	**0.0**	280	159	30.8	335	189	**0.0**
10	290	175	58.5	332	202	**0.0**	398	251	3.7

Table 3.5: 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 3.1 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.

#	Pink			Chum			Sockeye		
	Np	pD	ΔWAIC	Np	pD	ΔWAIC	Np	pD	ΔWAIC
1	95	71	252.3	109	89	292.4	131	104	583.1
2	140	115	44.0	161	133	180.5	194	164	281.8
3	96	71	246.4	110	85	157.1	132	102	322.0
4	141	113	34.9	162	134	48.3	195	164	**0.0**
5	186	152	93.3	214	175	22.9	258	218	10.1
6	199	96	236.2	227	119	268.6	271	147	555.7
7	244	135	10.2	279	154	156.8	334	205	246.3
8	200	97	228.1	228	114	150.1	272	137	328.7
9	245	133	**0.0**	280	154	29.7	335	190	2.5
10	290	174	56.0	332	197	**0.0**	398	251	4.4
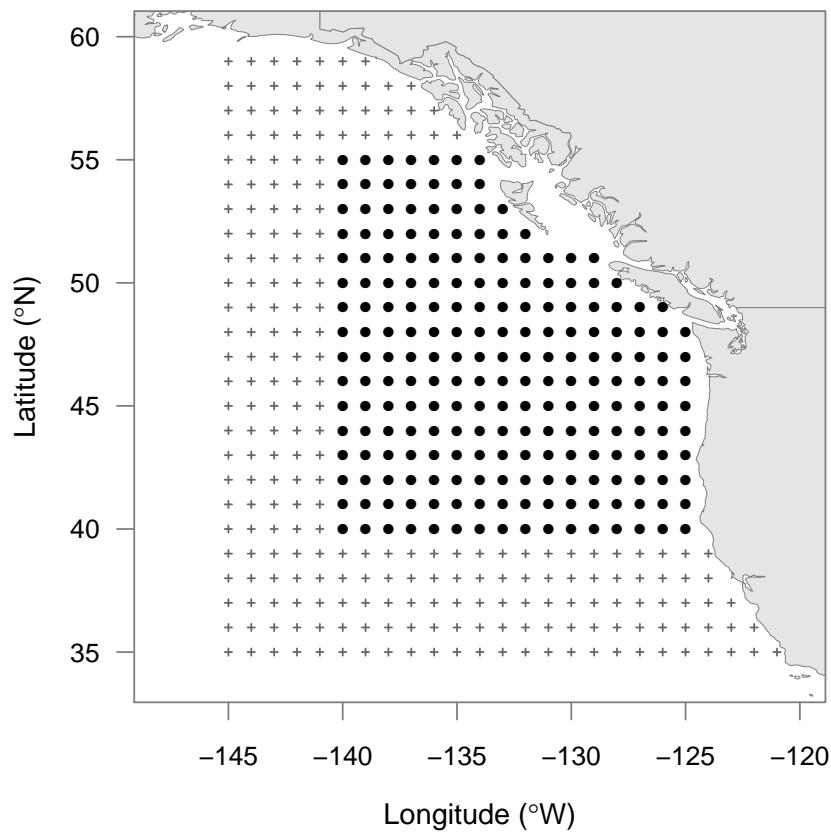
Figure 3.6: Starting location for the OSCURS model drifters used to calculate the bifurcation index. Black dots show the locations where the drifters were seeded for the main bifurcation index and grey plus signs indicate the additional drifter starting locations for the bifurcation index calculated using the expanded grid of drifters, which was part of a sensitivity analysis examining changes in assumptions underlying the bifurcation index.
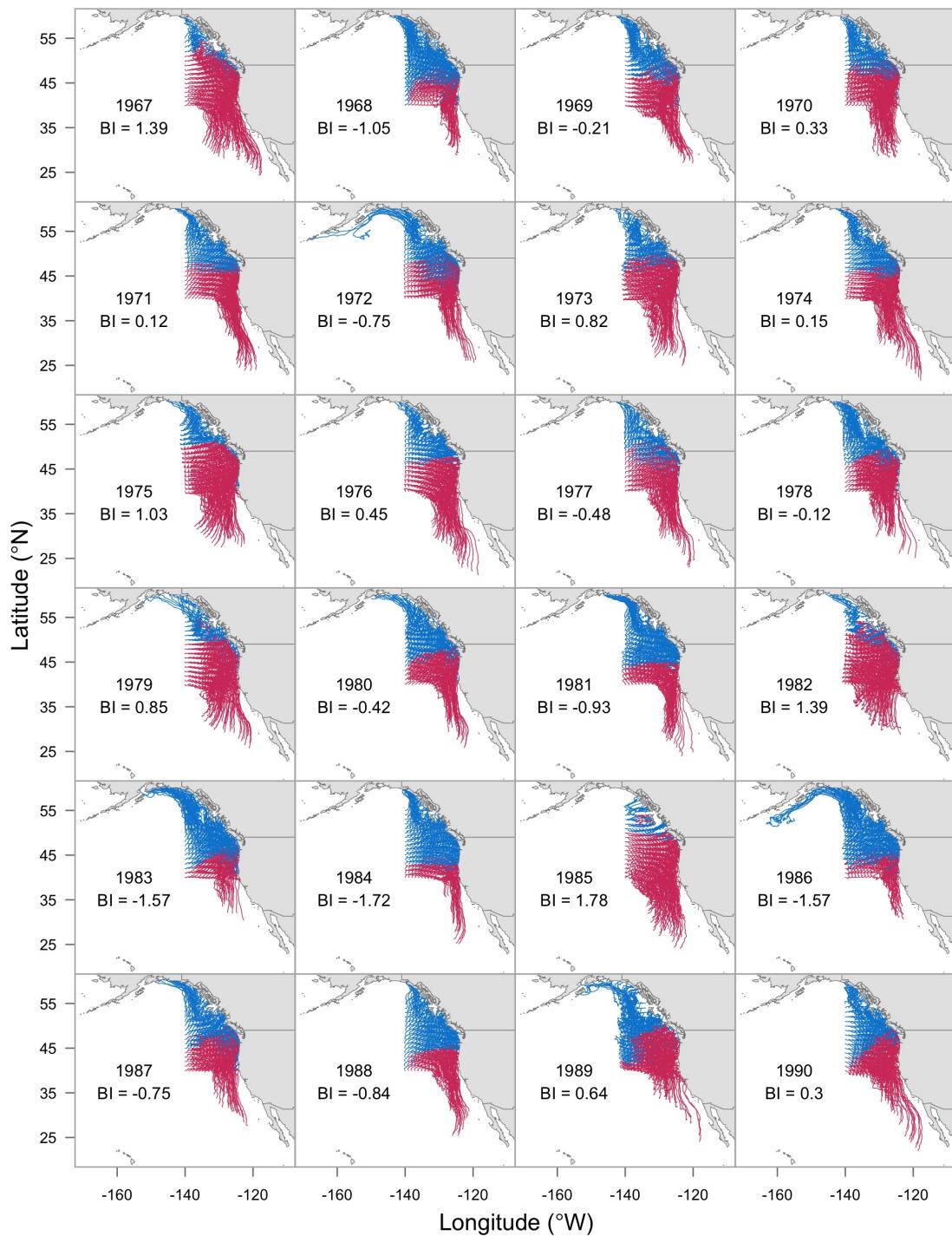
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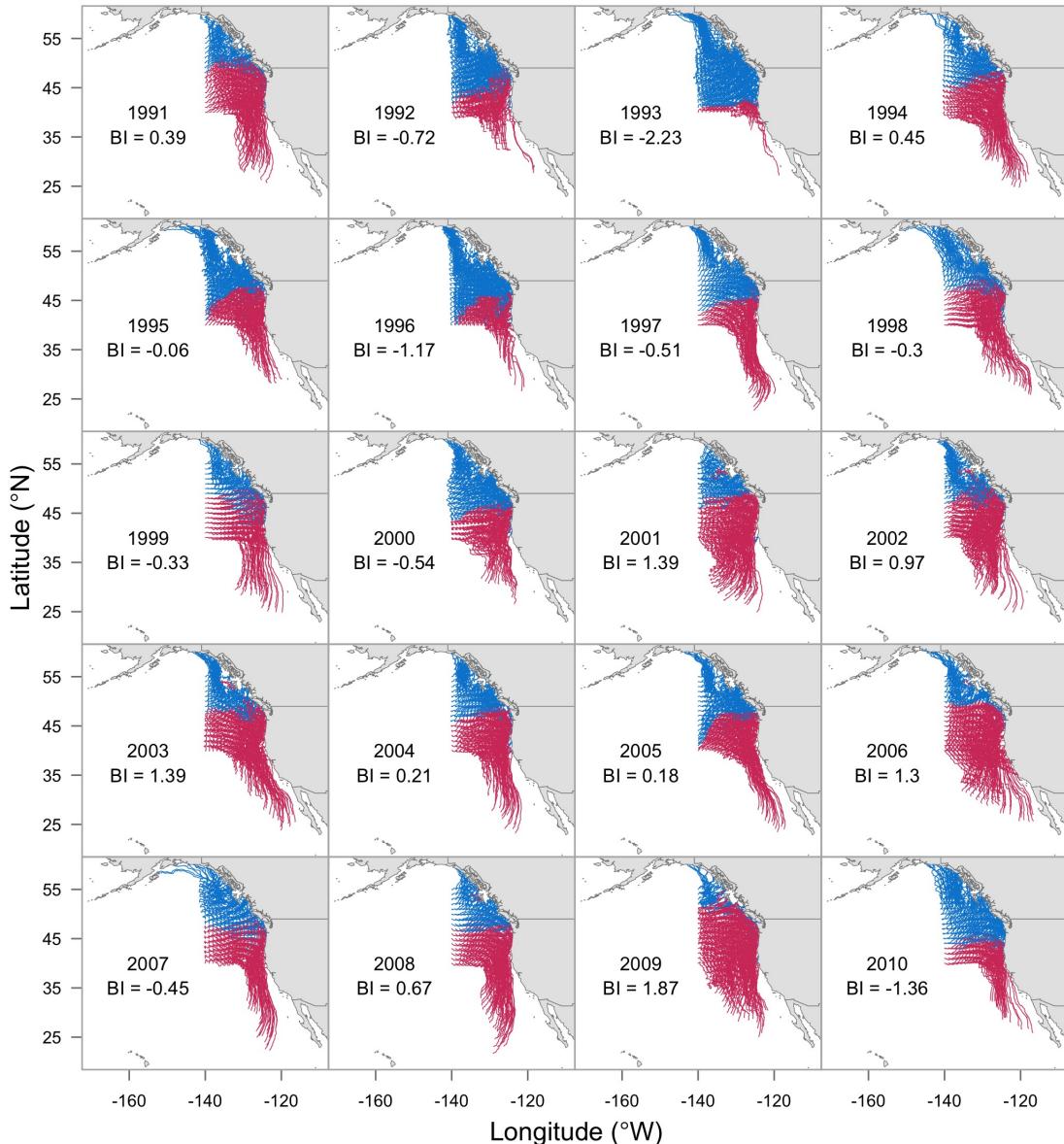
Figure 3.7: OSCURS model drifter trajectories for years 1967–2010. Each panel shows the drifter tracks for a single year where the drifters were simulated from February 1 to June 30. Red tracks indicate drifters that ended south of their starting location and blue tracks indicate drifters that ended north of their starting location. The lower left corner in each panel 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).
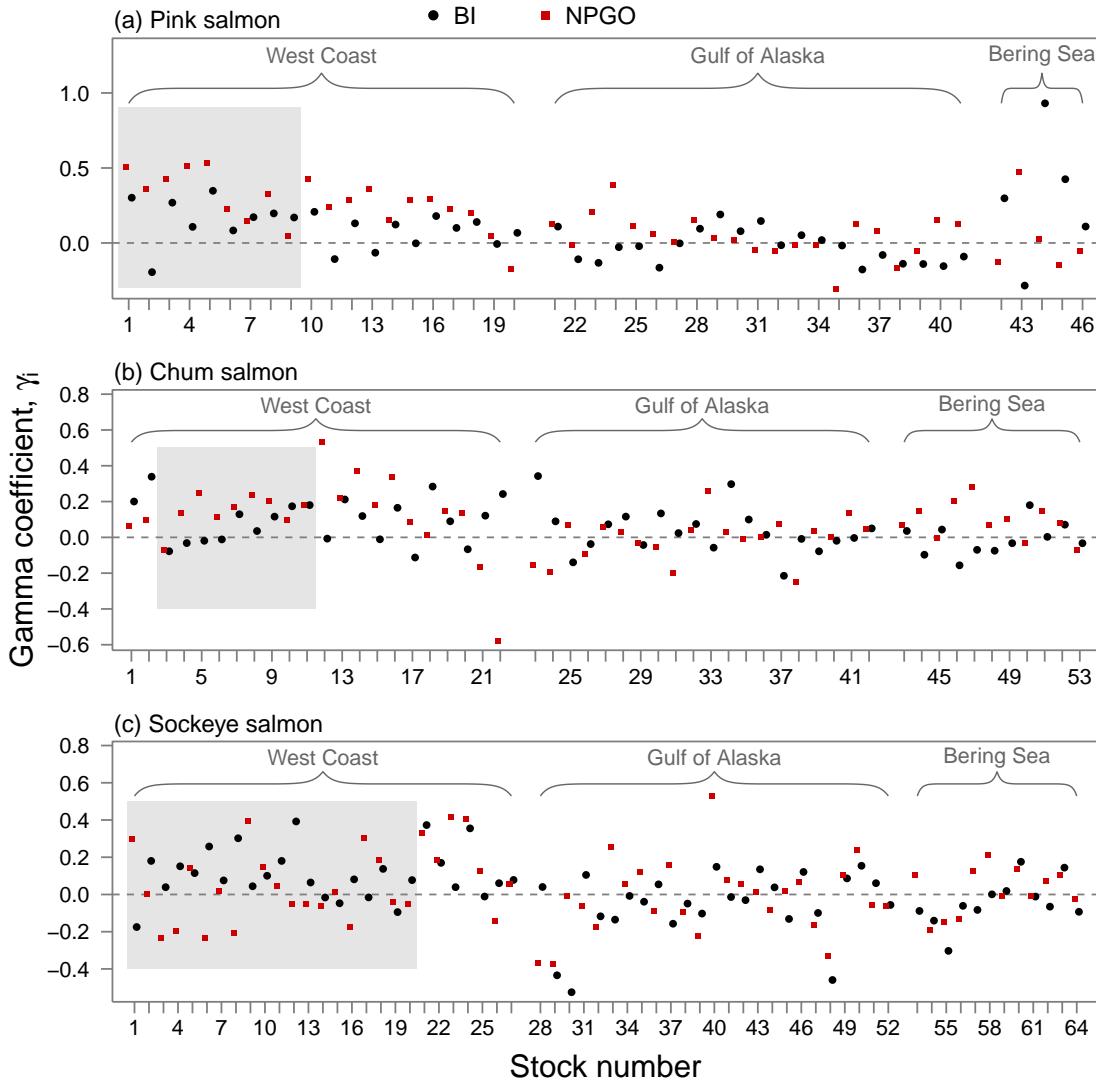
Figure 3.8: Single-stock model coefficients for the BI and NPGO (i.e., γ_i). Gamma coefficients were estimated by fitting generalized Ricker models (i.e., eq. 3.2) to each of the 163 salmon stocks separately using maximum likelihood. Coefficients (in standard deviation units) are shown for pink salmon (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 Fig. 3.1 of the main text. Solid circles (black) indicate the maximum likelihood estimate for the BI effect, $\gamma_{BI,i}$, and solid squares (red) indicate the NPGO effect, $\gamma_{NPGO,i}$. Points inside the grey boxes indicate salmon stocks that enter the ocean in the Salish Sea.

Chapter 4

Accounting for multiple pathways in the connections among climate variability, ocean processes, and coho salmon recruitment in the Northern California Current[1]

4.1 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 recruitment. We found that pathways originating with the Pacific Decadal Oscillation were the most influential on recruitment with the net effect being 2 to 4 times greater than for pathways originating with the North Pacific Gyre Oscillation or 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.

4.2 Introduction

Pacific salmon (*Oncorhynchus* spp.) populations along the Northeast Pacific coast exhibit large inter-annual and inter-decadal 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. 2002a; Beamish et al. 2004; Drinkwater et al. 2010; Malick et al. 2015a). 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 (King et al. 2011; Chavez et al. 2003; Keister 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. 4.1a). For instance, multiple studies show correlations between the Pacific Decadal Oscillation (PDO) and indices of salmon survival (Mantua et al. 1997; Burke et al. 2013; Malick et al. 2009) 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. 4.1b; Drinkwater et al. 2010; Ottersen et al. 2010; Dippner 2006). 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 (Daly et al. 2013; Cole 2000), whereas under the second hypothesis, regional-scale ocean transport and copepod community composition act as intermediaries (Bi et al. 2011a; 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; Ottersen et al. 2010; Bakun 1996; Hunt et al. 2002).

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. 4.1c; Anderson and Piatt 1999; Mantua et al. 1997). 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.
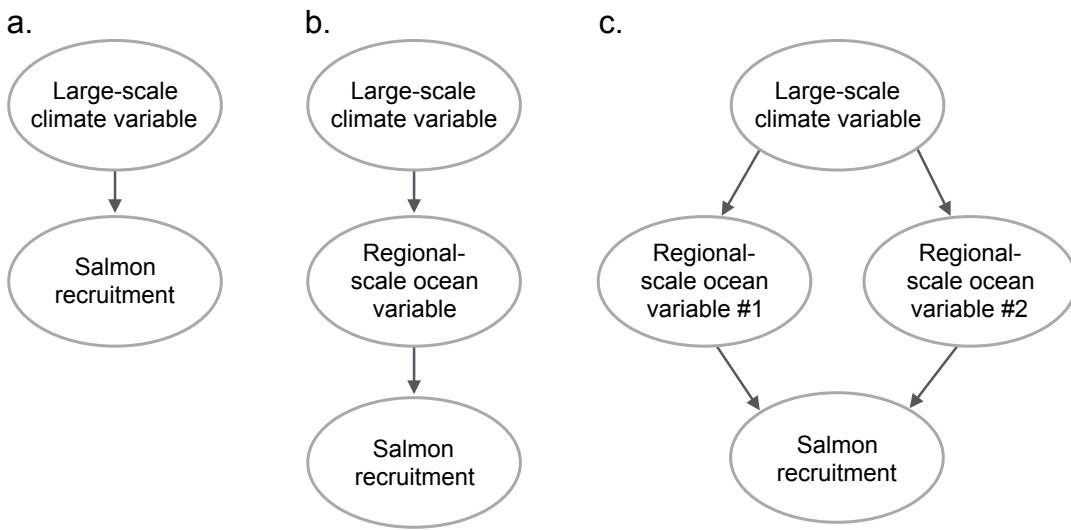
Figure 4.1: Schematic of pathways linking large-scale climate processes and Pacific salmon recruitment; (a) pathway where climate has a direct effect on recruitment, (b) pathway where climate effects on recruitment are mediated by a regional-scale oceanographic process (e.g., upwelling), (c) climate effects are mediated by multiple regional-scale variables resulting in two pathways connecting climate and recruitment.

In this study, we investigate how multiple ecological pathways potentially link climate and oceanographic processes to wild Oregon coho salmon (*O. kisutch*) recruitment. Specifically, we developed two probabilistic network models, similar to Fig. 4.1c, 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 (1) clearly and intuitively model recruitment as a function of multiple ecological pathways, (2) quantify the effects of both direct and indirect effects of environmental variables on salmon recruitment, and (3) 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.

4.3 Methods

4.3.1 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 organized into two independent probabilistic networks (e.g., Fig. 4.1c), 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.

4.3.2 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. 4.2). 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 (PFMC 2013; Rupp et al. 2012). 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
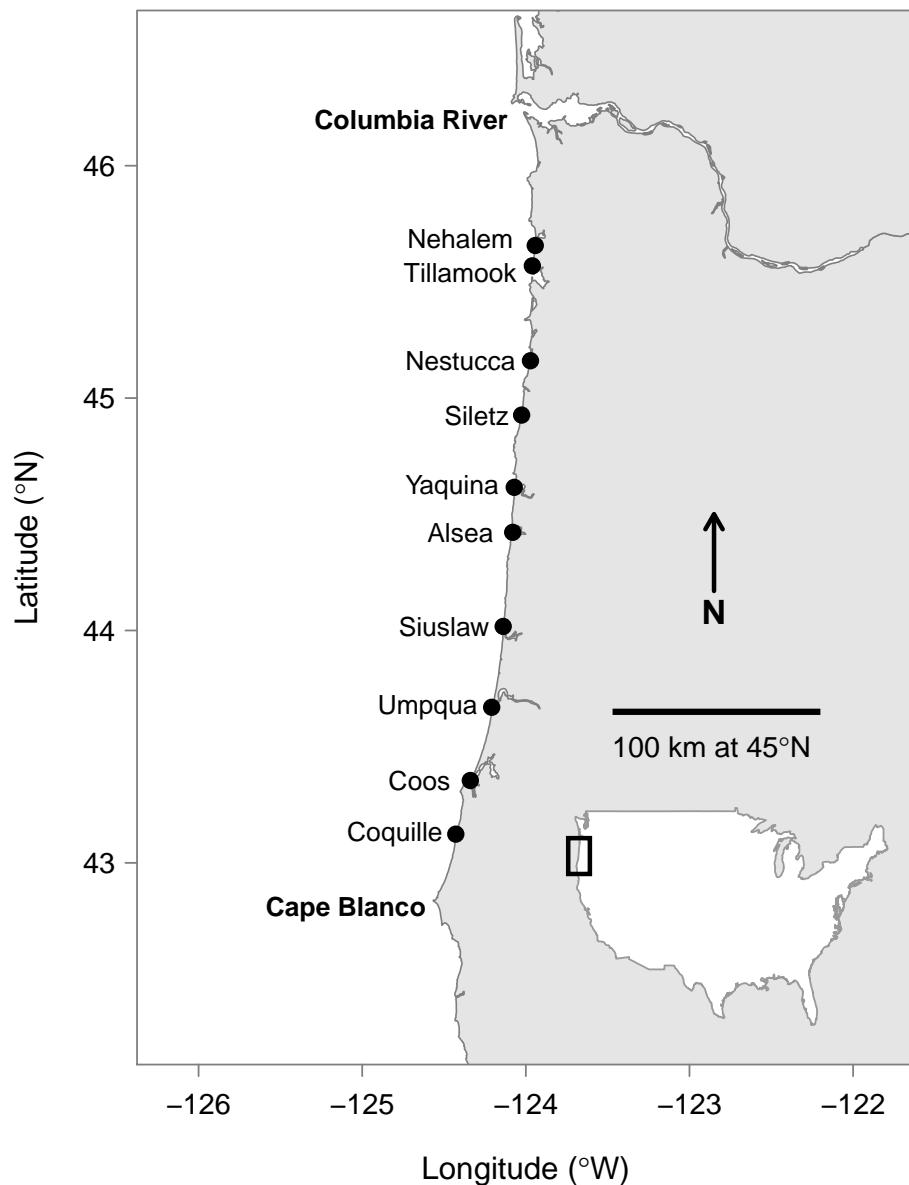
Figure 4.2: Study area showing the ocean-entry locations of the ten largest river basins located within the Oregon Coast coho salmon evolutionarily significant unit (ESU).

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 aggregate recruitment data across all coho salmon populations in the Oregon Coast ESU (Fig. 4.3), which is consistent with the current pre-season forecasting methods used by the Pacific Fisheries Management Council (PFMC 2013).
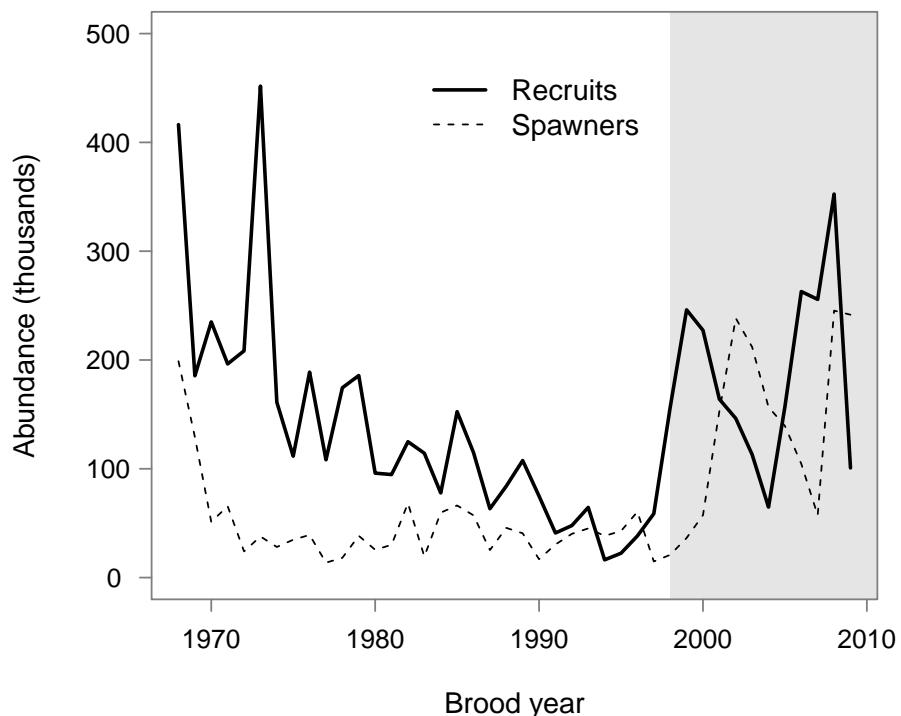
Figure 4.3: Time series of spawning stock size (dashed line) and the resulting total recruitment (solid line) for Oregon Coast coho salmon. Grey shaded region indicates the period used for the biophysical network.

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 (Logerwell et al. 2003; Koslow et al. 2002; Cole 2000), 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 due 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 inter-annual variability in productivity (in units of $\log_e(R/S)$) after accounting for density-dependent effects of spawner abundance (Supporting materials Fig. 4.9).

Environmental variables

Nine environmental variables were included in the probabilistic networks (Table 4.1; footnotes in that table indicate the data sources). Three of the variables represent large-scale climate patterns, which reflect variability over thousands of kilometers (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 inter-decadal periods, the ONI has most of its variance at inter-annual 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. 2013a).

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°x2° grid cell centered on 44°N 126°W. The January–June period was chosen because research has suggested

Table 4.1: Summary of environmental variables used to construct the probabilistic networks. 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).

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

[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).

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 inter-annual variability in upwelling intensity, where intensity was quantified as the volume of surface water transported offshore 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 (Logerwell et al. 2003; Lawson 1997). Third, to index inter-annual 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 January 1 of each year. Fourth, we used deep water temperature (i.e., temperature at 50m depth) at a station five miles off the coast of Newport, Oregon to index inter-annual variability of the source of waters which 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 (Jacox et al. 2014; Chhak and Di Lorenzo 2007). 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 inter-annual 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 average 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 and osmerids). Sampling of ichthyoplankton occurred from 1998–2011 (Table 4.1). 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 average May–September $\log_{10}$ 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 (Lee et al. 2006; Hooff and Peterson 2006). Copepods were sampled biweekly from 1998–2011 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. (2011b). We used a May–September average to represent conditions experienced by coho salmon during and just after smolt out-migration (Bi et al. 2011a).

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 4.1). Unless stated otherwise, all reported years correspond to the ocean entry year for the coho salmon cohort.

4.3.3 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: (1) a set of variables, (2) a network structure in the form of a directed acyclic graph, and (3) 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. 4.4 and 4.5) 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 (1) variables with no incoming arrows (root variables), (2) variables with incoming and outgoing arrows (intermediate variables), and (3) 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 (Koller and Friedman 2009; Korb and Nicholson 2004).

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. 4.4). 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. 4.5).

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 4.1). 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
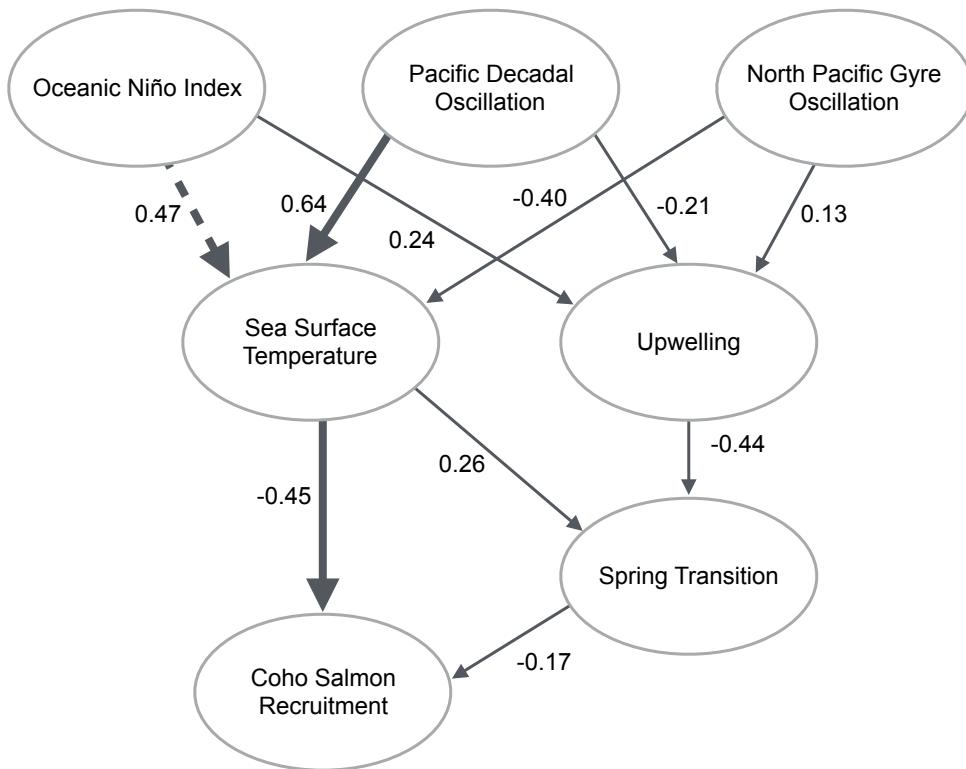
Figure 4.4: Directed acyclic graph for the probabilistic network fit using only physical environmental variables (called the physical network here). Ovals represent variables and arrows indicate dependencies among variables within the network. Numbers next to each arrow are the partial correlation coefficients. Thick solid arrows indicate the pathway with the highest average 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 average link strength.
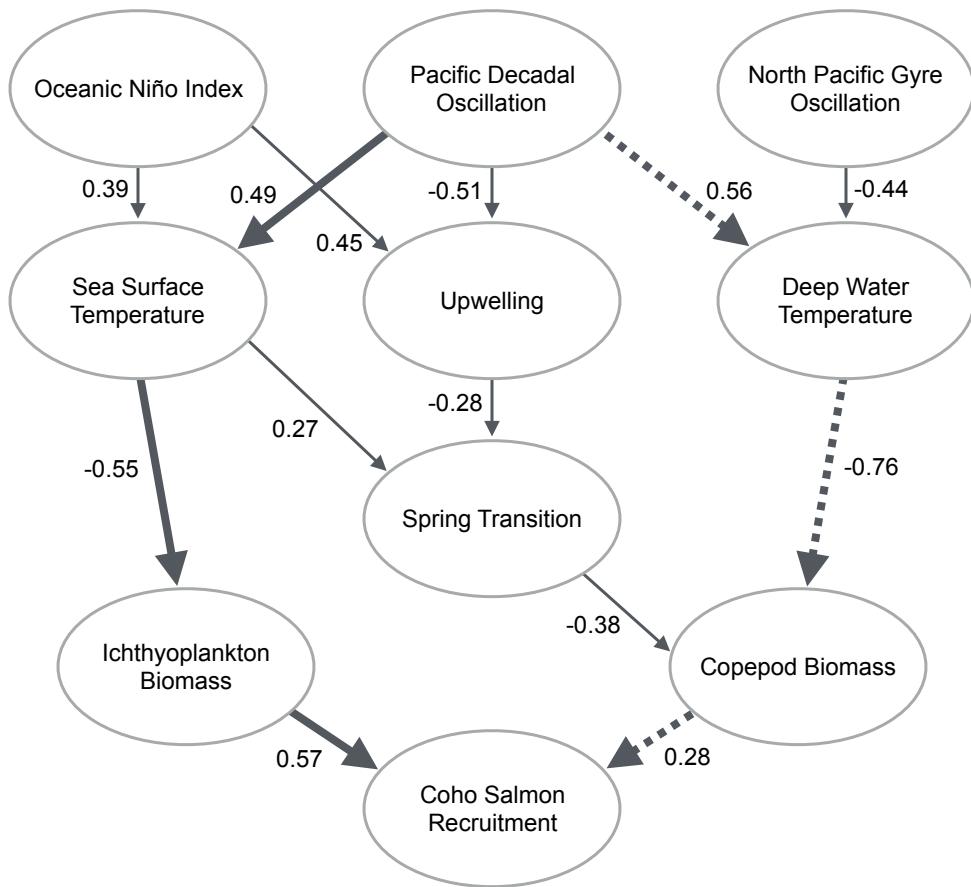
Figure 4.5: Directed acyclic graph for the probabilistic network fit using both physical and biological environmental variables (called the biophysical network here). Ovals represent variables and arrows indicate dependencies among variables within the network. Numbers next to each arrow are the partial correlation coefficients. Thick solid arrows indicate the pathway with the highest average partial correlations (i.e., link strength), whereas thick dashed arrows indicate the pathway with the second highest average link strength.

(Table 4.1). In the physical network, SST was directly linked to coho salmon recruitment (Fig. 4.4), 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. 4.5).

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. 4.5), 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 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 of 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 average 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 in order to ensure that events with low probabilities were sufficiently sampled (Koller and Friedman 2009).

4.4   Results

4.4.1   Pathway and link strength

In both networks, the pathway with the highest relative strength originated with the PDO (Table 4.2). In the physical network, the pathway with the highest average link strength included the PDO, SST, and recruitment (average of the absolute values of the two relevant correlations = 0.54; Fig. 4.4 and Table 4.2) and the pathway with the second highest relative strength included the ONI, SST, and recruitment (average 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 (average correlation = 0.54; Fig. 4.5 and Table 4.2), while the pathway with the second highest relative strength went from the PDO through deep temperature and copepod biomass to recruitment (average correlation = 0.53).

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. 4.4). 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. 4.4). 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. 4.5).

4.4.2   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. 4.6 and 4.7). In the physical network, SST had the strongest effect on recruitment with Δp =

Table 4.2: Relative pathway strength for each pathway connecting large-scale climate variables and coho salmon recruitment in the physical and biophysical networks; $\bar{r}$ gives the average of the absolute value of the partial correlation coefficients for each link in a pathway.

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

0.29 (Fig. 4.6d), which was moderately larger than the next most influential variable, the PDO (Δp = 0.18; Fig. 4.6b). For the biophysical network, ichthyoplankton biomass had the strongest effect on recruitment with Δp = 0.40, which was considerably stronger than all other variables in the network (Fig. 4.7). 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. 4.6d). 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. 4.7g).

Among the three large-scale climate variables, the PDO had the strongest overall effect on recruitment in both networks with a Δp between 2 and 4 times greater than for the ONI and NPGO (Figs. 4.6 and 4.7). In particular, a warm PDO (i.e., when the PDO was above average) was associated with lower recruitment. For example, 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. 4.6b and 4.7b). 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,
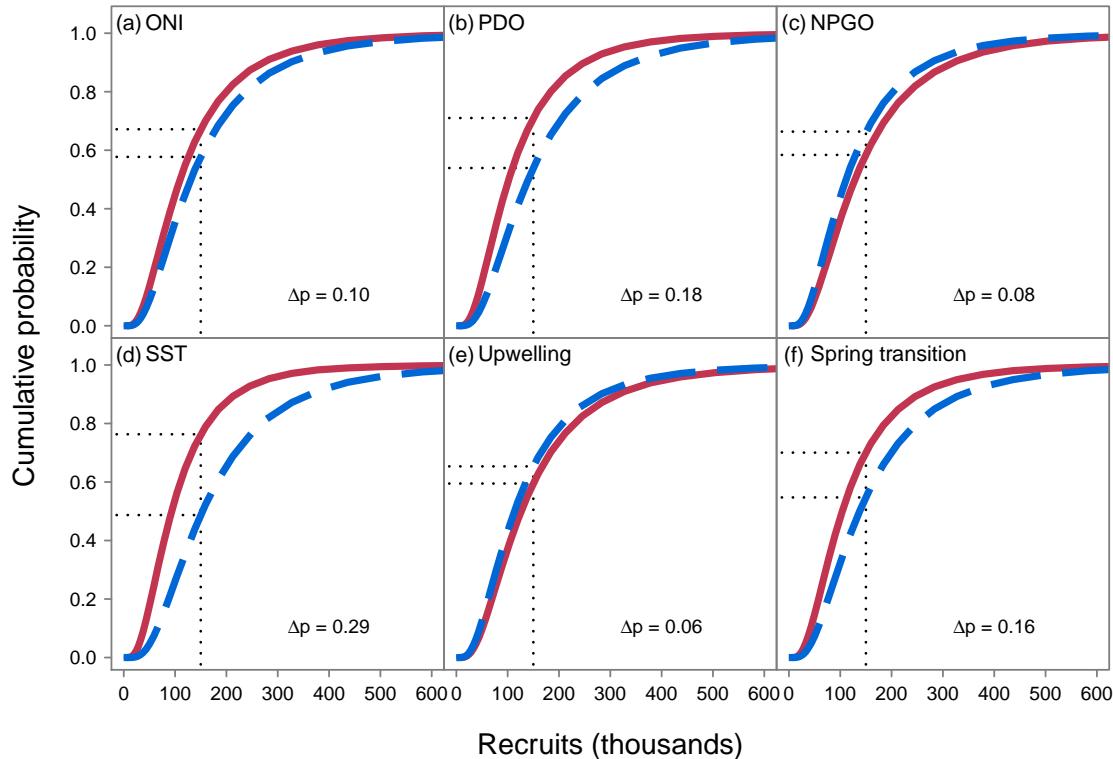
Figure 4.6: Cumulative probability distributions of coho salmon recruitment for the physical network conditioned on each variable in the network. Solid red curves indicate the cumulative probability for recruitment given that the environmental variable is greater than average, whereas dashed blue curves 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.

Figure 4.7: Cumulative probability distributions of coho salmon recruitment for the biophysical network conditioned on each variable in the network. Solid red curves indicate the cumulative probability for recruitment given that the environmental variable is greater than average, whereas dashed blue 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.

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 (solid red curve in Fig. 4.8a) was considerably steeper compared to when SST was cool and the spring transition occurred early (solid blue curve in Fig. 4.8a). 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. 4.8a). 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 (solid red curve in Fig. 4.8b) than when the prey resource indices were below average (solid blue curve in Fig. 4.8b). 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 a 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. 4.8). For instance, the cumulative probability distribution when ichthyoplankton biomass was below average and copepod biomass was above average (blue dashed curve in Fig. 4.8b) was moderately steeper compared to when ichthyoplankton biomass was above average and copepod biomass was below average (red dashed curve in Fig. 4.8b).

4.4.3 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 average partial correlation coefficients was identical for both the physical and biophysical networks (Supporting materials Table 4.3). 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 (Supporting materials Figs. 4.10, 4.11, and 4.12).
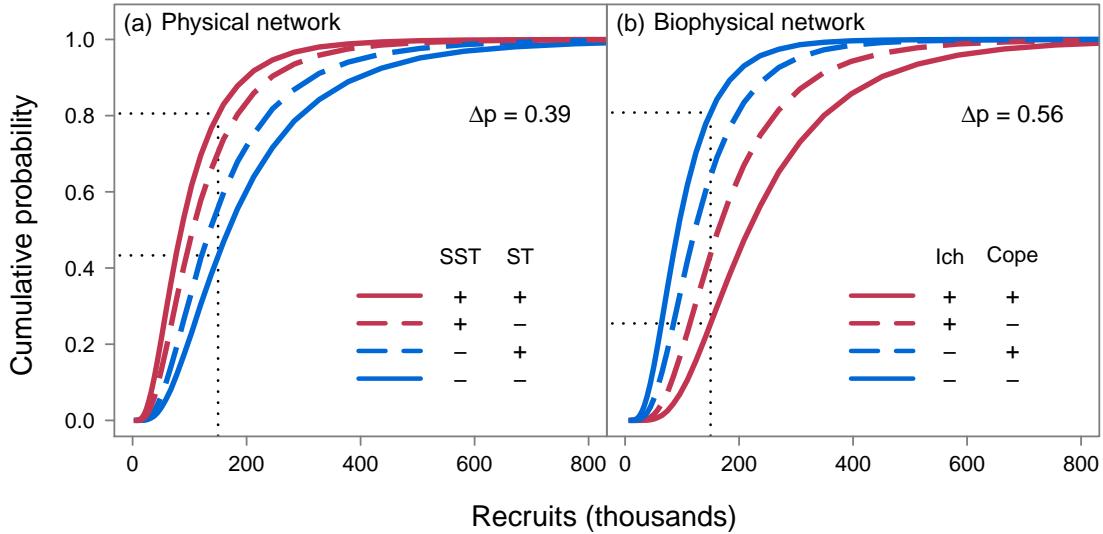
Figure 4.8: Cumulative conditional posterior probability distributions for coho salmon recruitment conditioned on the parent variables of recruitment for (a) the physical network (conditioned on sea surface temperature (SST) and spring transition (ST) date) and (b) the biophysical network (conditioned on ichthyoplankton biomass (Ich) and copepod biomass (Cope)). Solid red curves indicate the cumulative probability for recruitment given that both conditioning variables are greater than average (+). Solid blue curves show cumulative probabilities when both variables are less than their long-term averages (−). Dashed curves indicate scenarios when the conditioning variables are mixed. For the physical network, the red dashed curve indicates cumulative probabilities when SST is above average and the spring transition is below average, whereas the dashed blue curve shows the cumulative probabilities for the opposite conditions. For the biophysical network, the red dashed curve indicates cumulative probabilities when ichthyoplankton biomass is above average and copepod biomass is below average, whereas the dashed blue curve shows the cumulative probabilities for the opposite conditions. Thin dotted lines indicate the cumulative probabilities for 150 000 salmon. The Δp gives the maximum vertical difference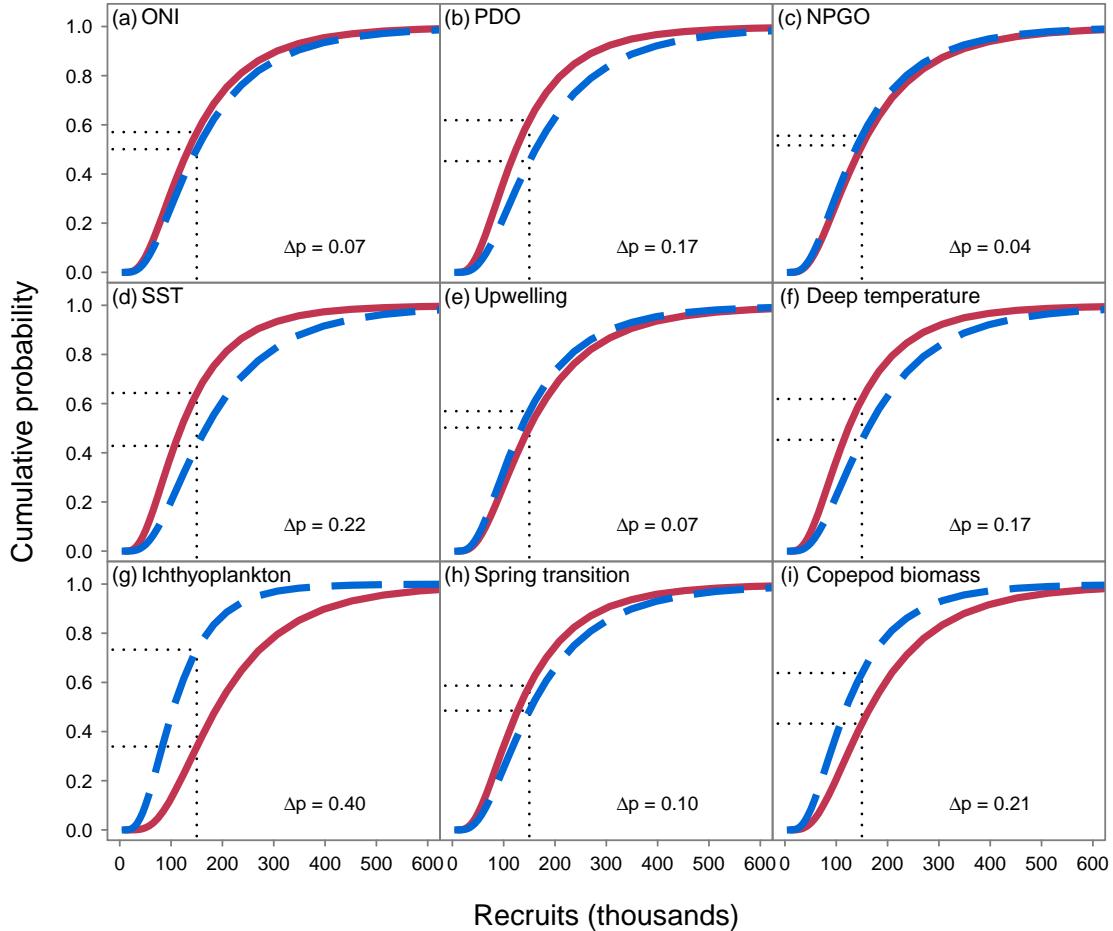 in probability between the two cumulative distributions where both conditioning variables are either above or below average within a panel.

4.5 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 mechanisms linking climate variability and salmon recruitment. We found (1) pathways originating with the PDO were the most influential on recruitment with a joint effect considerably larger than for the ONI or NPGO, (2) 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 to cool years, and (3) 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 (Martins et al. 2012; Planque and Frédou 1999; Hunt et al. 2011). Although temperature can influence salmon directly, for example, by influencing metabolic or growth rates (Mortensen et al. 2000; Farley et al. 2007b), 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, (1) a northern community that has low species diversity and large copepod species that are rich in lipids, or (2) a southern community that has high species diversity and small copepod species that are poor in lipids (Hooff and Peterson 2006). The observed negative relationship between deep water temperature and copepod biomass

supports the findings of previous studies that indicated the lipid-rich zooplankton community is associated with the transport of cooler water from northern areas into the Northern California Current (Keister et al. 2011). Furthermore, the positive relationship between copepod biomass and recruitment suggests increased lipid-rich copepod prey resources are associated with higher salmon recruitment (Bi et al. 2011a).

In both networks, cool PDO conditions (i.e., when the PDO was below the long-term average) were associated with increased recruitment compared to warm conditions. Furthermore, cool periods were also associated with cooler deep water temperatures (indicative of increased equator-ward transport), increased upwelling, increased ichthyoplankton biomass, and a more northern copepod community composition off the coast of Oregon. Although numerous previous studies have indicated similar associations among these environmental variables during cool PDO regimes (King et al. 2011; Peterson and Schwing 2003; Keister et al. 2011; Mantua et al. 1997), our results extend those findings by explicitly quantifying the uncertainty in these relationships in the form of posterior probabilities. For example, the results for the biophysical network indicated that under warm PDO conditions, there was a 62% chance that recruitment would be below the long-term average. In contrast, under cool PDO conditions, there was only a 45% chance recruitment would be below average. Although this suggests that cool ocean conditions are beneficial for coho salmon, it also indicates there is considerable uncertainty about recruitment levels even when the PDO is below average. This uncertainty may partly arise due to our focus on recruitment, which also includes variability from the freshwater life phase, although our sensitivity analysis using productivity showed almost the same results as using total recruitment.

We found that ichthyoplankton biomass tended to be more influential than copepod biomass on recruitment with an effect twice as strong. The importance of ichthyoplankton biomass over copepod biomass was surprising because several previous studies have reported strong positive relationships between the biomass of northern copepod species and coho salmon survival (Bi et al. 2011a; Ruzicka et al. 2011; Peterson and Schwing 2003). However, the finding is consistent with evidence indicating that coho salmon diets during the first ocean summer are primarily composed of small fish species (by percent weight) such as Pacific sand lance and osmerids (Brodeur et al. 2007a; Weitkamp and Sturdevant 2008). The importance of ichthyoplankton biomass likely reflects a bottom-up forcing mechanism where increased ichthyoplankton biomass results in increased growth rates, body size, and marine survival of coho salmon. However, because ichthyoplankton are also prey for numerous other species (Gladics et al. 2014; Miller et al. 2010; Miller and Brodeur 2007) and because ocean conditions that influence ichthyoplankton biomass may also influence other marine species, this variable may act as a surrogate for other biological processes that directly influence survival such as predator distributions, abundances, or diets.

The result that upwelling did not have a strong effect on recruitment deviates from earlier findings that increased upwelling intensity is associated with increased marine survival of Oregon coho salmon (Fisher and Pearcy 1988; Logerwell et al. 2003). This difference in results may be due to at least three factors. First, in this study we used total recruitment from wild coho salmon stocks, which includes variability associated with the freshwater life phase, whereas the previous studies used marine survival of hatchery reared coho salmon as the response variable. Second, there is some evidence that the relationship between upwelling 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 due to transport of nutrients and phytoplankton out of the system (Botsford et al. 2006; 2003). 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. 4.3 and Supporting materials Fig. 4.9) may reflect non-stationarity in the recruitment time series. Detecting non-stationarity and its causes is often problematic in fisheries abundance time series due to 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 non-stationarity, 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 influence coho salmon, the networks could also be used as a tool to help managers of salmon fisheries by providing pre-season 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).

4.6 Acknowledgments

4.7 Supporting materials

4.7.1 Supporting figures and tables

Table 4.3: Relative pathway strength for each pathway connecting large-scale climate variables and the *coho salmon productivity index* in the physical and biophysical networks; $\bar{r}$ gives the average of the absolute value of the partial correlation coefficients for each link in a pathway.

Network	Pathway	$\bar{r}$
Physical	PDO, SST	0.56
	ONI, SST	0.48
	NPGO, SST	0.44
	PDO, SST, Spring Transition	0.36
	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	0.25
Biophysical	PDO, SST, Ichthyoplankton	0.58
	PDO, Deep Temperature, Copepod Biomass	0.55
	ONI, SST, Ichthyoplankton	0.54
	NPGO, Deep Temperature, Copepod Biomass	0.51
	PDO, Upwelling, Spring Transition, Copepod Biomass	0.37
	PDO, SST, Spring Transition, Copepod Biomass	0.36
	ONI, Upwelling, Spring Transition, Copepod Biomass	0.36
	ONI, SST, Spring Transition, Copepod Biomass	0.34
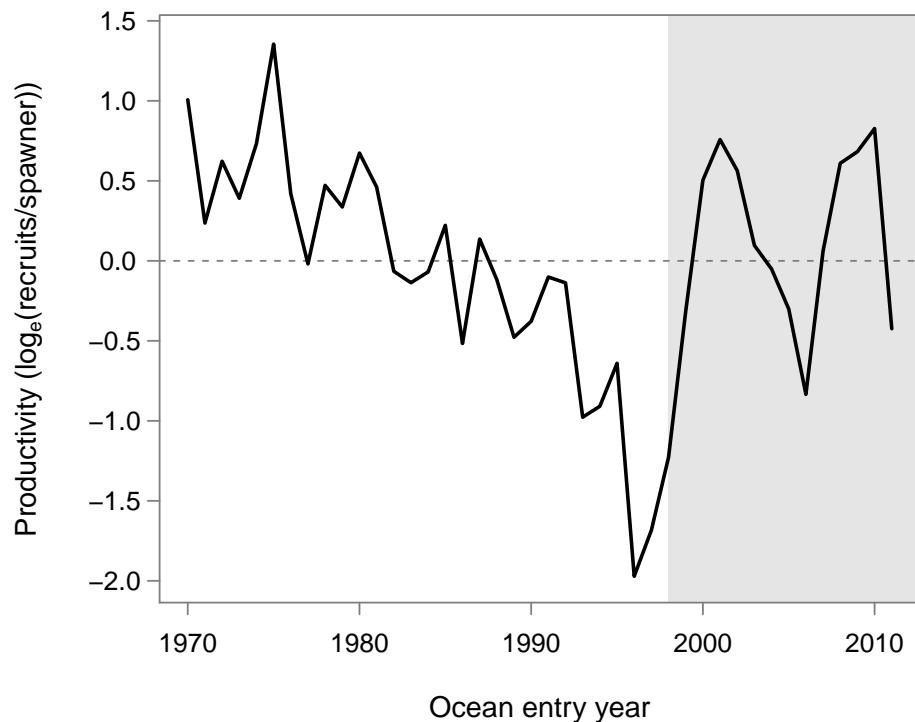
Figure 4.9: Time series of the coho salmon productivity index. The productivity index was calculated as the residuals from a Beverton-Holt spawner-recruit model. Grey shaded region indicates the period used for the biophysical network.
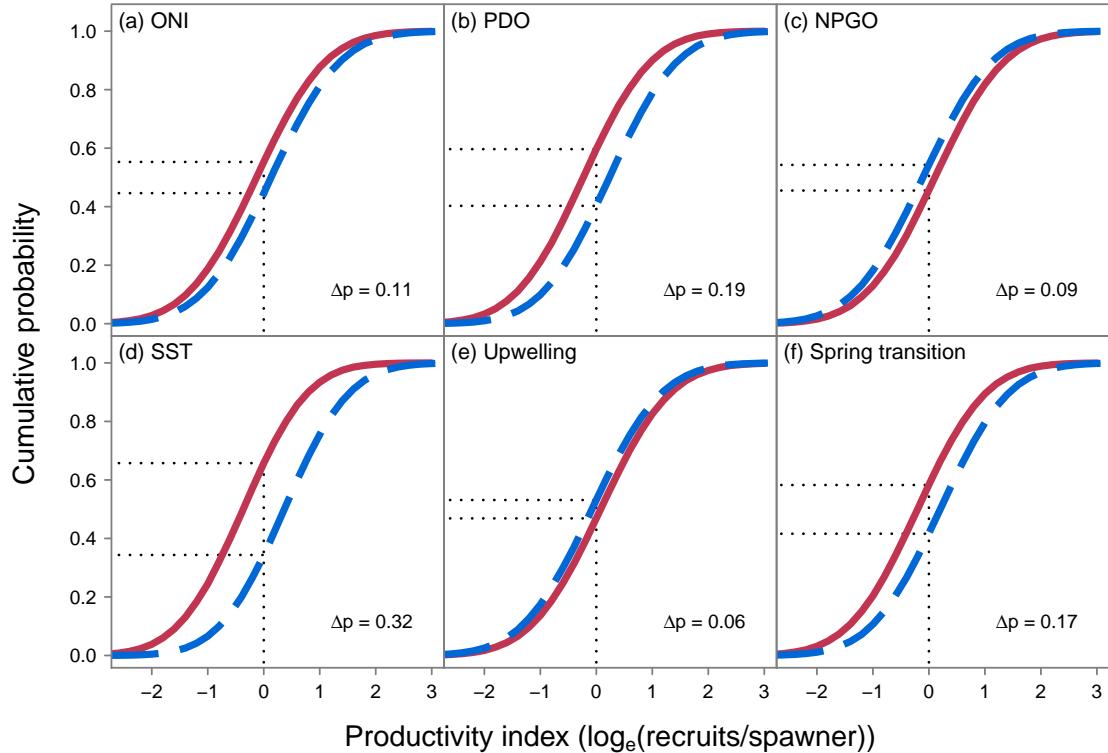
Figure 4.10: Cumulative probability distributions of the *coho salmon productivity index* for the physical network conditioned on each variable in the network. Solid red curves indicate the cumulative probability for the productivity index given that the environmental variable is greater than average, whereas dashed blue curves show cumulative probability when the environmental variable is less than average. Thin dotted lines indicate the cumulative probabilities for average productivity. The Δp gives the maximum vertical difference in probability between the two cumulative distributions within a panel.
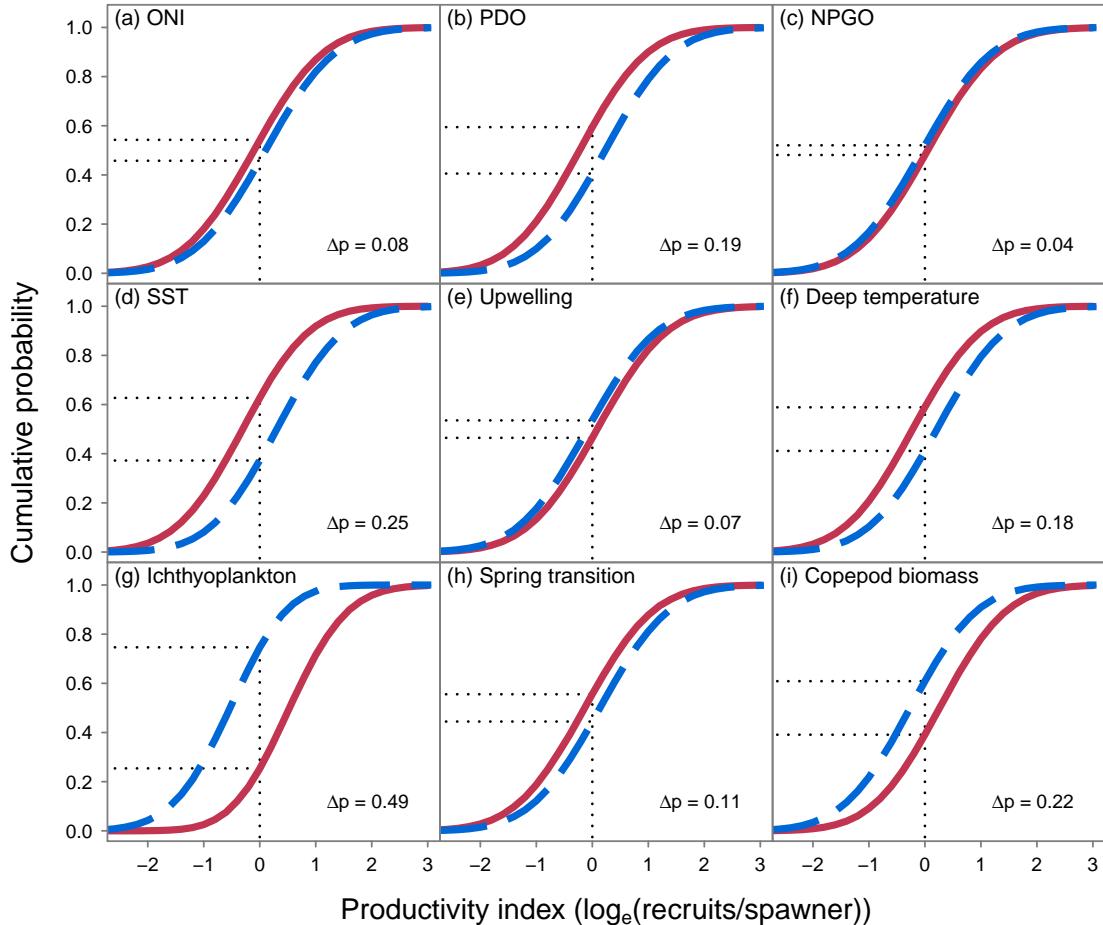
Figure 4.11: Cumulative probability distributions of the *coho salmon productivity index* for the biophysical network conditioned on each variable in the network. Solid red curves indicate the cumulative probability for the productivity index given that the environmental variable is greater than average, whereas blue dashed curves show cumulative probability when the environmental variable is less than average. Thin dotted lines indicate the cumulative probabilities for average productivity. The Δp gives the maximum vertical difference in probability between the two cumulative distributions within a panel.
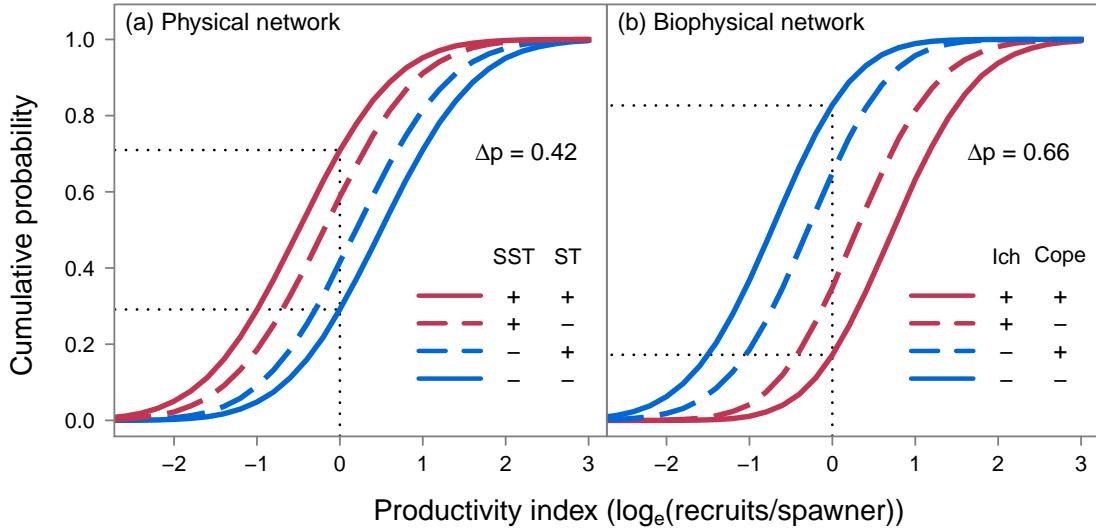
Figure 4.12: Cumulative conditional posterior probability distributions for the *coho salmon productivity index* conditioned on the parent variables of productivity for (a) the physical network (conditioned on sea surface temperature (SST) and spring transition (ST) date) and (b) the biophysical network (conditioned on ichthyoplankton biomass (Ich) and copepod biomass (Cope)). Solid red curves indicate the cumulative probability for the productivity index given that both conditioning variables are greater than average (+). Solid blue curves show cumulative probabilities when both variables are less than their long-term averages (−). Dashed curves indicate scenarios when the conditioning variables are mixed. For the physical network, the red dashed curve indicates cumulative probabilities when SST is above average and the spring transition is below average, whereas the dashed blue curve shows the cumulative probabilities for the opposite conditions. For the biophysical network, the red dashed curve indicates cumulative probabilities when ichthyoplankton biomass is above average and copepod biomass is below average, whereas the dashed blue curve shows the cumulative probabilities for the opposite conditions. Thin dotted lines indicate the cumulative probabilities for average productivity. The Δp gives the maximum vertical difference in probability between the two cumulative distributions where both conditioning variables are either above or below average within a panel.

Chapter 5

Confronting challenges to integrating Pacific salmon into ecosystem-based management policies[1]

5.1 Abstract

Ecosystem-based management is an increasingly prominent paradigm for the management of living marine resources with a focus on maintaining ecosystem level properties and processes in the presence of anthropogenic and natural disturbances. Although highly migratory marine and anadromous fish species often disproportionately contribute to the structure and function of ecosystems, incorporating these species into ecosystem-based management policies remains challenging because they spend a considerable portion of time outside the boundaries that define a particular management area. In this paper, we use two case studies to examine how challenges arising from ecosystem openness, imperfect information, and ecosystem complexity can impede efforts to integrate highly migratory Pacific salmon (*Oncorhynchus* spp.) into ecosystem-based management policies. Our analysis highlights three main factors that hinder more effective integration: (1) uncertainties about the impacts of human activities and ecological processes that occur in geographically distant jurisdictional areas or at spatial scales larger than the ecosystem-based management area, (2) spatial asymmetries in the distribution of costs and benefits associated with management decisions (i.e., positive or negative externalities), and (3) static management policies that prevent updating management decisions in a timely manner when ecosystem conditions change or new information becomes available. Given these factors, we suggest two potential

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[1]S.P. Cox and M.B. Rutherford are co-authors on this chapter, which is in preparation for submission to a journal.

strategies to address migratory challenges. First, we recommend the creation of an international ecosystem synthesis group to facilitate the collection, analysis, and dissemination of ecological, social, and policy information across national and other jurisdictional boundaries. Second, we recommend the expanded use of dynamic in-season management policies that allow rapid updating of management decisions based on evolving information about ecosystem conditions. Our findings further suggest that ecosystem-based management policies need to explicitly account for mismatches in the scale at which ecosystem services are provided by highly migratory species and the scale at which human activities and natural processes impact those services.

5.2   Introduction

Over the past few decades, ecosystem-based management (EBM) has emerged as a leading paradigm for the management of living marine resources in many parts of the world, with a focus on maintaining ecosystem level properties and processes (e.g., nutrient cycles and trophic interactions) in the presence of anthropogenic and natural disturbances (Engler 2015; Skjoldal and Misund 2008; Fletcher 2008; Constable 2011; Olsson et al. 2008). A key principle underlying EBM is that distinct boundaries demarcate the management area, with the boundaries ideally being chosen based on the ecological properties of the system rather than existing socio-political boundaries (Long et al. 2015; Engler 2015). However, in addition to the difficulties of managing across existing jurisdictional boundaries, most marine ecosystems cannot be easily discretized into manageable units because ecosystem boundaries remain open, i.e., organisms, energy, or matter can move across specified ecosystem boundaries (O'Neill 2001).

Ecosystem openness presents a key challenge to integrating highly migratory species into EBM policies because these species frequently move across ecosystem and jurisdictional boundaries. Indeed, highly migratory marine and anadromous fish species provide critical connectivity between geographically distant ecosystems and these species often play a disproportionately large role in the structure and function of ecosystems by translocating organic material, nutrients, and energy (Lundberg and Moberg 2003; Heupel et al. 2015). However, factors external to the management area may strongly affect the status and contributions of species that spend a considerable portion of their life cycle outside the human defined boundaries of an ecosystem. In particular, this movement across management and jurisdictional boundaries may lead to mismatches between the scale of management and the biology of a migratory fish stock (Cash et al. 2006; Epstein et al. 2015). To overcome these potential mismatches, some EBM initiatives are using very large spatial boundaries (e.g., large marine ecosystems) in an attempt to capture full ecosystems; however, even these larger EBM initiatives are often not successful at including the full life cycle of many highly mi-

gratory species, such as Pacific salmon (*Oncorhynchus* spp.; Field and Francis 2006; Sherman and Duda 1999; Wang 2004). Jurisdictional challenges make it unrealistic to expect that management will be able to scale up to the necessary level to capture the full spatial range of highly migratory species (Cowan et al. 2012; Lascelles et al. 2014). Therefore, in this study, we focus on the challenges associated with accounting for and incorporating highly migratory species into existing local and regional scale EBM initiatives.

A second major source of challenges to integrating highly migratory marine species into EBM is the quality of the available information. In order to practice EBM, we must identify and estimate cumulative impacts from a diverse suite of physical, biological, and human influences on marine ecosystems across multiple spatio-temporal scales (Lascelles et al. 2014; Halpern et al. 2008). However, our ability to study and manage these cumulative impacts is limited because we often have imperfect information (e.g., non-existent data or data with potentially large observation error) about the status of particular ecosystem components or the drivers of ecosystem dynamics. For instance, information is usually lacking to separate particular cause and effect relationships because we tend to study only the most economically dominant components and drivers of ecosystems. A third source of challenges is that even when good information is available, ecosystem complexity (i.e., numerous ecological processes interacting in multiple, and often non-linear ways) can limit our ability to recognize the drivers of patterns and processes in natural systems because underlying cause-effect relationships may be spontaneous and non-stationary over space and time (Hsieh et al. 2005; Burkett et al. 2005; Scheffer et al. 2001). In other words, new cause-effect relationships may emerge while others disappear by the time we accumulate enough information to understand any particular one (Myers 1998).

These three features—ecosystem openness, imperfect information, and ecosystem complexity—are clearly evident in coupled marine-terrestrial ecosystems along the west coast of North America, where policy-makers are struggling to integrate highly migratory Pacific salmon into EBM policies. In this paper, we first examine how challenges arising from openness, imperfect information, and ecosystem complexity can impede efforts to integrate highly migratory Pacific salmon into EBM policies and then we explore potential strategies that could be implemented to overcome these challenges. Although we focus on two case studies involving Pacific salmon, the challenges and strategies discussed appear to be widely applicable to other highly migratory marine or anadromous fish species that move among jurisdictions and ecosystems.

5.3 Salmon and ecosystem-based management

Pacific salmon typically require a continuum of ecosystems spanning hundreds or thousands of kilometers to complete their anadromous life cycle. The combined extent of these ecosystems ranges from diverse headwaters of large river systems to the pelagic ocean environment of the North Pacific Ocean, Gulf of Alaska, and Bering Sea. Within these varied ecosystems, Pacific salmon provide numerous ecosystem services, including contributing to critical ecosystem functions (e.g., nutrient cycles in freshwater ecosystems), providing economic and food provisioning services to commercial, subsistence, and recreational fishing sectors, and contributing to social and cultural dimensions of coastal North Pacific communities.

Declines in Pacific salmon abundance over the past few decades highlight their importance in numerous regions along the west coast of North America. For example, the Yukon and Kuskokwim River regions in western Alaska were declared economic disaster areas following declining returns of adult chinook salmon (*O. tshawytscha*) and chum salmon (*O. keta*) throughout the 1990s and 2000s. Conflicts continue in these regions as government managers and stakeholders struggle to allocate the diminished adult salmon returns among fishery sectors (Ebbin 2002; 2003). Similarly, in southern British Columbia (BC), declining adult abundances of Fraser River sockeye salmon (*O. nerka*) throughout the 2000s resulted in limited opportunities for commercial, subsistence, and recreational harvest and prompted a federal judicial inquiry (the Cohen Commission) involving government officials, scientists, and other stakeholders to determine the causes of the declines (Cohen 2012). Along the west coast of the United States, many salmon populations have been extirpated and several others are listed as threatened or endangered under the United States Endangered Species Act, severely reducing the ecosystem services provided by Pacific salmon in this region (Nehlsen et al. 1991; NMFS 2015; Williams et al. 2011).

Declining adult salmon abundances have widespread effects on ecosystem structure and function that can detrimentally affect other valued components of ecosystems, including economically important species. For example, migration of adult salmon into freshwater provides a large influx of marine derived nutrients to aquatic and terrestrial ecosystems (Claeson et al. 2006; Johnston et al. 2004; Chaloner and Wipfli 2002). This large subsidy of nutrients (e.g., nitrogen and phosphorous) and organic matter (e.g., organic carbon) gets incorporated into multiple levels of the food chain, providing critical connectivity between marine and terrestrial ecosystems (Claeson et al. 2006; Johnston et al. 2004). Migrating and spawning salmon, as well as post-spawning carcasses, are also a key food resource for numerous predators and scavengers in marine, freshwater, and terrestrial systems including birds, bears, whales, seals, and sea lions (Ford et al. 2016; Olesiuk 1993; Trites et al. 2007; Hilderbrand et al. 1999). In some cases, such as orca whales (*Orcinus orca*)

in the Salish Sea, adult chinook salmon are the primary diet item for most of the year (Ford et al. 2016).

Maintaining ecosystem level properties such as nutrient cycles and trophic linkages requires a holistic, ecosystem-based approach to management of living marine resources because of the complex and non-linear connections among ecosystem components (Engler 2015). Indeed, several state and federal agencies responsible for managing marine resources along the west coast of North America have either started to implement EBM policies or are in the process of developing EBM policies. For example, in 2007 the state of Washington (WA) created the Puget Sound Partnership, a public-private partnership made up of government agencies, scientists, and private groups, with the goal of implementing an ecosystem-based management approach to resource use in Puget Sound, WA (Ruckelshaus et al. 2009; Samhouri et al. 2011). Similarly, in BC, the Marine Plan Partnership for the North Pacific Coast (MaPP)—a co-led partnership between the provincial government and First Nations—was created in 2011 to facilitate EBM efforts along the BC North Coast. At the federal level, the United States National Marine Fisheries Service recently released a policy directive that establishes "a framework of guiding principles to enhance and accelerate the implementation of EBFM [ecosystem-based fisheries management]" (NMFS 2016).

A common element of these EBM initiatives is that they are largely confined within existing socio-political boundaries. For instance, Ruckelshaus et al. (2009) notes that the "Puget Sound Partnership is focusing on ecosystem-based management of the marine waters and lands within Washington State, while recognizing that the entire ecosystem spans Washington State and British Columbia." For highly migratory species, such arbitrarily defined ecosystem boundaries can result in a mismatch between the scale of the management or jurisdictional area and the biology of the fish stock. For example, an adult salmon returning to WA State from the Gulf of Alaska may pass through as many as five jurisdictional areas in the marine environment, including international waters, federally managed waters in Canada and the United States, and state managed waters in Alaska and WA.

Spatial mismatches, arising from the limited spatial extent of the EBM area, the openness of the ecosystems, and the large migratory range of Pacific salmon, create challenges for integrating salmon into EBM policies. In particular, natural processes and human activities occurring either at locations that are geographically distant from the EBM area (e.g., targeted fisheries and bycatch in non-targeted fisheries; Fig. 5.1a) or at spatial scales larger than the EBM area (e.g., environmental change and interactions between hatchery and wild salmon; Fig. 5.1b) may strongly impact salmon populations and the effectiveness of local EBM policies. In the following section, we detail two of these broad scale impacts, including fisheries that intercept salmon at geographically distant locations and competition between wild and hatchery salmon for limited food resources throughout

the North Pacific. In doing so, we highlight how imperfect information and ecosystem complexity contribute further to the difficulties in overcoming these challenges.
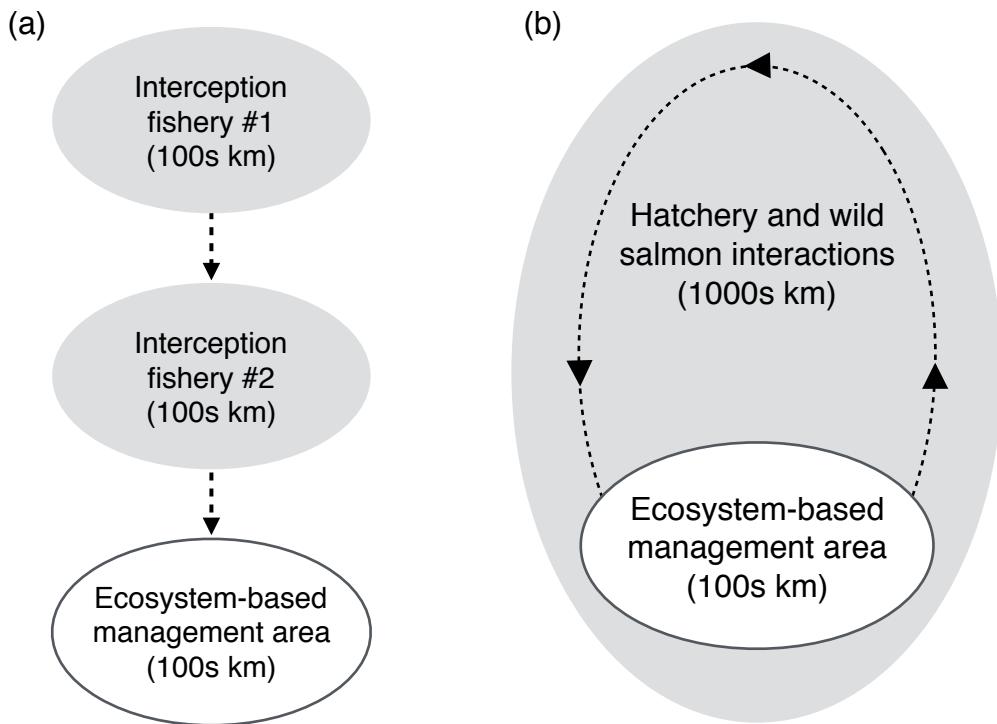
Figure 5.1: Schematic of two spatial mismatches between ecosystem-based management areas and the migratory range of Pacific salmon. The left panel (a) indicates a mismatch due to geographic distance between two interception fisheries and the ecosystem-based management area. Black dashed arrows in panel (a) indicate the migratory direction of adult salmon. The right panel (b) indicates a mismatch due to interactions between wild and hatchery salmon occurring at a larger spatial scale than the ecosystem-based management area. The black dashed arrows in panel (b) indicate the marine migratory route of wild salmon that originate within the ecosystem-based management area.

5.4 Migratory challenges

5.4.1 Interception harvest of highly migratory salmon

A common policy problem for migratory species occurs when commercial fisheries intercept a species (or population) at multiple points along its migration route (Lascelles et al. 2014). These

interception fisheries pose a particularly difficult challenge for local or regional scale EBM policies because the harvesting is often outside the boundaries of the EBM decision-making area and may be spread across numerous management jurisdictions. Further, interception fisheries frequently result in externalities (both positive and negative) where an asymmetric distribution of costs and benefits occurs from management decisions made in up-migration or down-migration areas (Scherer 1990). For instance, users of the resource in down-migration areas often bear costs or benefits of management decisions made in up-migration areas (e.g., decisions to increase or decrease harvest rates) because the migratory species passes through the up-migration area prior to entering the down-migration area. For Pacific salmon, the down-migration area often represents the source location for a population, i.e., the natal spawning locations, and harvest in up-migration areas can reduce both the number of salmon available for harvest in the down-migration area and the number of eggs deposited by spawning adults.

Adult and sub-adult Pacific salmon are harvested in coastal waters throughout their migratory range by both targeted fisheries and as bycatch in fisheries targeting other species. Targeted harvesting frequently occurs in mixed-stock fisheries where salmon stocks with distant origins co-mingle with local stocks and are harvested jointly. For example, the Southeast Alaska (SEAK) chinook salmon troll fishery, the largest commercial chinook salmon fishery in SEAK, harvests salmon originating from SEAK, BC, WA, and Oregon, with more than 80% of the chinook salmon catch originating outside SEAK (Templin and Seeb 2004).

The challenges posed by interception fisheries for Pacific salmon have been recognized for over a century and the bi-lateral Pacific Salmon Treaty between the United States and Canada specifically deals with interception of salmon from distant origins (Knight 2000; Noakes et al. 2005). In particular, the 'State of Origin' principle within the treaty states that the primary harvest rights and burden of conservation of Pacific salmon stocks are assigned to the jurisdictional area where the stock originates. However, such policies developed to achieve equity in salmon harvesting across the migratory range of adult salmon can be unsuccessful for numerous reasons including (1) inability to selectively harvest certain salmon stocks within mixed stock fisheries because information is lacking about which salmon stocks are currently migrating through a particular harvest area, and (2) over harvest (or under harvest) of salmon in up-migration areas because of an incomplete understanding of the complex ecosystem dynamics that drive variability in adult salmon returns.

This latter reason is exemplified by chinook salmon fisheries management along the west coast of North America. Under the Pacific Salmon Treaty the SEAK chinook salmon troll fishery is regulated using aggregate abundance-based management where the total allowable catch in a given year is set based on pre-season abundance forecasts estimated by the Chinook Techni-

cal Committee (PST 2014, Annex IV, Chapter 3, Section 6). The pre-season abundance forecasts, however, are often not accurate representations of actual total run size due to difficulties in forecasting salmon productivity. In other words, salmon productivity is often linked to natural and anthropogenic drivers in complex and nonlinear ways and we often lack information to identify and predict particular cause and effect relationships in a timely manner (Peterman and Dorner 2012; Malick and Cox 2016; Myers 1998). For instance, from 2009 to 2013, the pre-season chinook salmon abundance index for SEAK overestimated abundance in all but one year (i.e., 2013), resulting in disproportionately large chinook harvests in SEAK (Fig. 5.2; CTC 2015a). In these years, stakeholders in down-migration areas, e.g., Puget Sound, bear the cost of uncertainty associated with the pre-season forecasts in the form of reduced adult salmon returns and the ecosystem services they provide. Moreover, the management of chinook salmon under the Pacific Salmon Treaty is largely implemented using static reference points that are estimated to produce the maximum sustained yield for a stock (or group of stocks) without consideration of other ecosystem services provided by salmon (CTC 2015b). By focusing on a single ecosystem service, in this case providing food and associated economic benefits for humans, the other ecosystem roles of salmon in local or distant areas are discounted or ignored, such as providing prey for orca whales and other marine mammals and providing connectivity between marine and freshwater ecosystems in the form of marine derived nutrients.

At the same time, the costs of management decisions made within down-migration areas may disproportionately be borne by stakeholders in down-migration areas compared to stakeholders in up-migration areas. For example, the 'State of Origin' principle puts the responsibility for salmon conservation on the jurisdictional area where the stock originates. However, efforts to restore ecosystems or rebuild salmon abundances in down-migration areas may result in positive externalities, in that the stakeholders in the down-migration area bear the full costs of the rebuilding or restoration efforts, but users throughout the migratory range of the salmon population gain the potential benefits of increased salmon abundances.

5.4.2 Salmon hatcheries

Releasing hatchery-reared juvenile Pacific salmon into freshwater and marine ecosystems is a common management practice throughout the North Pacific Rim. The primary objective of these hatcheries is to augment wild salmon production for either conservation purposes or to supplement commercial and other harvests. Despite widespread debate about the effectiveness of hatchery releases to increase adult salmon returns (Hilborn and Eggers 2000; Wertheimer et al. 2001; Hilborn and Eggers 2001), releases of juvenile Pacific salmon from hatcheries located around the North Pacific Rim have increased ten fold over the past five decades, exceeding seven billion salmon
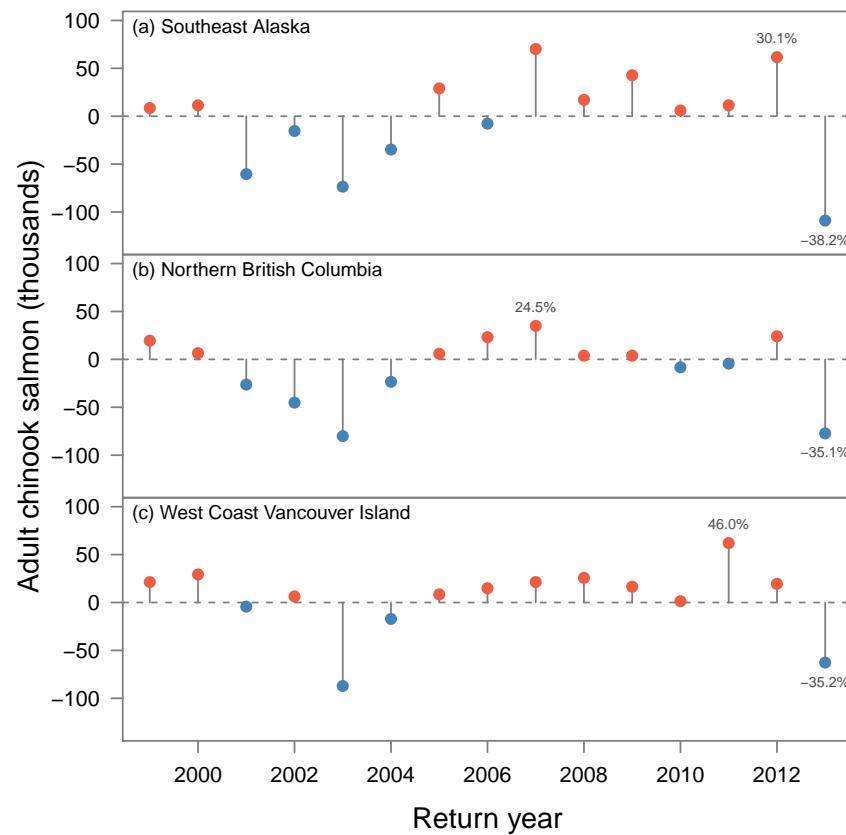
Figure 5.2: Difference between pre-season and post-season allowable catch estimates for three North American chinook salmon fisheries managed using aggregate abundance-based management outlined in the Pacific Salmon Treaty. Positive values (red) indicate the pre-season estimate overestimated the allowable catch in a given year and fishery, whereas negative values (blue) indicate the pre-season estimate underestimated the allowable catch. All values are in thousands of adult chinook salmon. Values within each panel give the maximum and minimum relative error of the preseason estimate compared to the post-season estimate.

released in 2015 (Fig. 5.3). These hatchery salmon co-mingle with wild salmon throughout their marine migratory range and compete with wild salmon and other species that feed at similar trophic levels for a limited common-pool of prey resources throughout the North Pacific Ocean.

Because Pacific salmon migrate and feed across broad regions of the North Pacific Ocean and Bering Sea, competition occurs between wild and hatchery salmon originating in different jurisdictions, nations, and continents. For example, wild sockeye salmon originating in Bristol Bay, Alaska compete with abundant hatchery pink salmon released from hatcheries in Russia and Japan during their second and third years of ocean residency (Ruggerone et al. 2003). A major consequence of competition between hatchery and wild salmon across their marine migratory range is density dependent growth, which can result in (1) reduced age-specific body sizes of wild adult salmon, and (2) declines in wild salmon population productivity (Ruggerone and Connors 2015; Ruggerone et al. 2003). For instance, widespread declines in age-specific adult body sizes observed in many salmon populations since the 1980s have been attributed to density dependent growth in the marine environment (Ricker 1981; Ishida et al. 1993; Pyper and Peterman 1999). Indeed, the large increases in hatchery releases, combined with the strong evidence for reductions in adult body sizes and stock productivities, have led to concerns about carrying capacity limitations of the North Pacific Ocean for Pacific salmon (Pearcy et al. 1999; Nielsen and Ruggerone 2009).

These ocean-basin scale effects of hatchery salmon on wild salmon present a challenge for EBM policies because they indicate that management actions implemented for salmon originating in one jurisdictional area or nation can affect salmon populations originating in distant jurisdictions or nations. In other words, declines in wild stock productivity or age-specific adult body sizes due to competition with hatchery salmon released from multiple nations can strongly influence the provisioning of ecosystem services provided by Pacific salmon within an EBM area. In particular, the ecological effects of hatchery salmon on wild salmon populations can (1) reduce harvest opportunities for stakeholders of affected stocks, (2) influence ecosystem structure and function within an EBM area by affecting trophic interactions and connectivity between marine and terrestrial ecosystems, and (3) inhibit conservation efforts within an EBM area to recover threatened or endangered salmon populations (Ruggerone et al. 2003; Nielsen and Ruggerone 2009).

Addressing the challenges posed by the ocean-basin scale effects of hatchery salmon on wild salmon populations would likely require the creation of a new international agreement, organization, or other institution to either regulate hatchery releases or alter the incentives associated with releasing juvenile hatchery salmon (Holt et al. 2008). The common-pool prey resources that hatchery and wild salmon compete for are both rivalrous and non-exclusive, i.e., the consumption of prey by hatchery salmon reduces food availability for wild salmon and it is difficult to exclude nations or agencies from releasing juvenile hatchery salmon. As with many common-pool re-
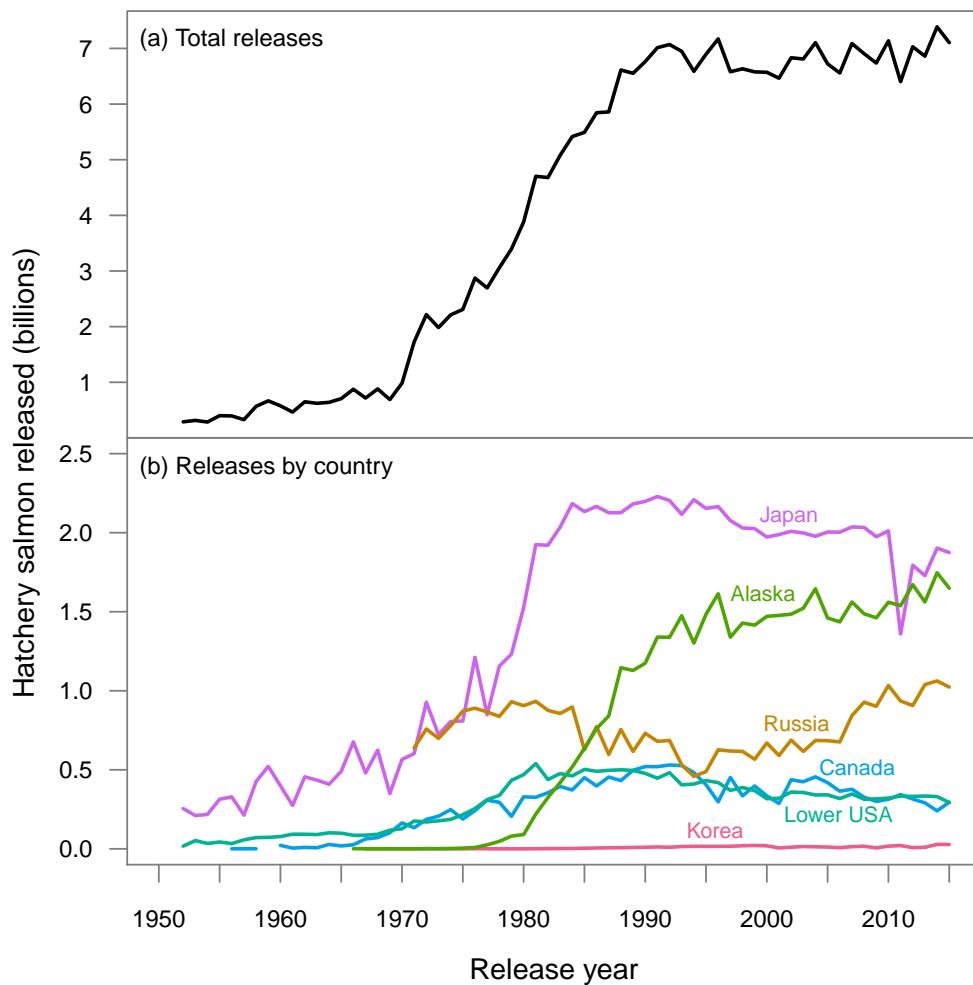
Figure 5.3: Hatchery releases of juvenile Pacific salmon for (a) all North Pacific Rim nations combined and (b) each North Pacific Rim nation individually. For the United States, releases from Alaska are shown separate from those in the lower mainland because of the order-of-magnitude differences in total releases between the two.

source problems, this creates a disincentive for a particular agency or nation to reduce hatchery releases because that agency or nation receives most of the benefits from the releases, in terms of harvest of returning adult hatchery salmon, but only bears a fraction of the costs of deterioration of the prey resources, which are spread across multiple nations (Holt et al. 2008).

Even if such an international institution were created to manage hatchery releases, determining an ecologically acceptable level of total hatchery releases each year would be challenging because the productivity levels of the ecosystems that comprise the North Pacific are non-stationary, varying on inter-annual and inter-decadal scales corresponding to large-scale shifts in the climate (Hare et al. 1999; Chavez et al. 2003). For example, an abrupt and unanticipated reversal of the Pacific Decadal Oscillation in 1976/77 precipitated an ecological regime shift that resulted in the species composition of the North Pacific shifting from a crustacean-dominated system to a gadid- and flatfish-dominated system (Mantua et al. 1997; Anderson and Piatt 1999; Mueter and Norcross 2000). Similarly, as the climate warms, the frequency of extreme events in marine ecosystems (e.g., marine heat waves) is expected to increase, which can influence hatchery-wild interaction by altering food resource availability (Jentsch et al. 2007; Di Lorenzo and Mantua 2016). For instance, between the winters of 2013–2014 and 2014–2015 offshore ocean temperatures in the Northeast Pacific Ocean were anomalously warm (nearly 2.5°C above the long term average) resulting in widespread changes in ecosystem dynamics including reductions in large lipid-rich prey resources for juvenile salmon (Bond et al. 2015; Di Lorenzo and Mantua 2016).

5.5 Potential strategies to address migratory challenges

A common element of the challenges discussed here is a mismatch between the scale of management and the migratory life history of Pacific salmon, with the challenges being exacerbated by imperfect information about cause and effect relationships and complex non-stationary ecosystem dynamics. The two case studies highlight three main factors that hinder more effective integration of highly migratory species into EBM policies, including (1) uncertainties about the impacts of human activities and ecological processes that occur at distant locations or at scales larger than the EBM area, (2) spatial asymmetries in the distribution of costs and benefits associated with management decisions, and (3) static management policies that prevent updating management decisions in a timely manner when ecosystem conditions change. In this section, we present two strategies that could help overcome these problems: increased cross-scale synthesis of information; and expanded near real-time data analysis of ecosystem dynamics.

5.5.1 Cross-scale synthesis of information

Our first proposed strategy is the collection and synthesis of ecological, economic, and policy information across jurisdictional areas along with the dissemination of strategic management advice that is informed from this broad-scale synthesis. Such advice could at least partially address two of the factors hindering integration of highly migratory species into EBM policies: uncertainty about impacts of processes outside the EBM area and asymmetrical distribution of costs and benefits. Currently, there are numerous organizations and programs that conduct ecological, economic, and policy research on Pacific salmon at the local and regional scales. For example, the Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative, the National Oceanic and Atmospheric Administration's Southeast Alaska Coastal Monitoring Program, and the Salish Sea Pacific Salmon Marine Survival Project all collect empirical data on Pacific salmon and other ecosystem components to increase knowledge about how ecosystem dynamics and human activities influence Pacific salmon populations. These research efforts are largely used to provide scientific and management advice at the local and regional spatial scales. However, the limited spatial extent of these research efforts omits social and ecological forces that occur at distant locations or at scales larger than the management area, which can influence the ecosystem services generated by Pacific salmon within the local or regional management area, and therefore, should be taken into account in EBM.

The need to collect and synthesize information at larger scales and across jurisdictional boundaries is not unique to Pacific salmon, and ecosystem working groups have become increasingly common elements of international management organizations because of their effectiveness at synthesizing information across multiple jurisdictional areas (Engler 2015; Lascelles et al. 2014). For example, the International Commission for the Conservation of Atlantic Tunas, the Inter-American Tropical Tuna Commission, and the Northwest Atlantic Fisheries Organization have all created ecosystem working groups as a key part of their research efforts. These working groups conduct cross-scale ecological and social research that is used to provide strategic management advice to multiple smaller-scale jurisdictional areas. For instance, the Northwest Atlantic Fisheries Organization collects and synthesizes data from member states and, in turn, disseminates strategic management advice (e.g., identifying vulnerable marine ecosystems).

Following these examples, we recommend the creation of an international ecosystem synthesis group to facilitate the collection and analysis of ecological, economic, and policy information across jurisdictional areas in the North Pacific and to disseminate strategic management advice to local and regional scale EBM programs (Fig. 5.4). The creation of an international synthesis group would not necessarily require a new international organization, but instead could be implemented through the modification of an existing organization. In particular, the North Pacific Anadromous Fish Commission (NPAFC), the organization charged with implementing the multi-lateral Con-

vention for the Conservation of Anadromous Stocks, would be an obvious starting point for two reasons. First, the NPAFC has an existing mandate to conduct scientific research "for the purpose of the conservation of anadromous stocks including, as appropriate, scientific research on other ecologically related species" (CCAS 1992). Second, the NPAFC already has an established structure for international cooperation among North Pacific Rim nations along with established political relationships that would enable the dissemination of strategic management advice.
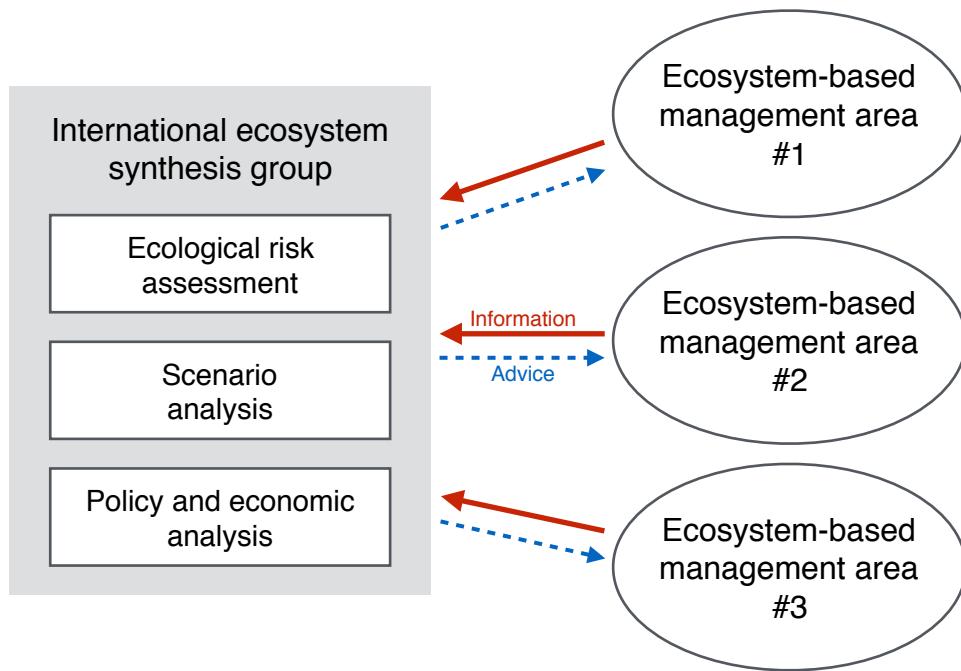
Figure 5.4: Schematic of hypothesized interactions between local and regional scale ecosystem-based management areas and an international ecosystem synthesis group. Solid arrows (red) represent the flow of data and information from ecosystem-based management programs to the international synthesis group, whereas dashed arrows (blue) represent the flow of strategic management advice from the international synthesis group to specific ecosystem-based management programs.

Based on the case studies provided here, we further suggest that a key focal point of this synthesis group should be identifying critical uncertainties and risks to ecosystem services provided by Pacific salmon from an array of human activities and natural processes across their migratory range including current and proposed management actions. Uncertainties arise in social and ecological systems for numerous reasons including natural variability, imperfect information about complex social and ecological processes, vague management objectives, and limited control

over fisheries and other human activities (Peterman 2004). For EBM policies, these widespread uncertainties are important to identify and quantify because they create risks for management agencies, ecosystems, and communities that rely on salmon for economic and cultural prosperity. Further, understanding how these uncertainties may affect the outcomes of current and proposed management actions across multiple spatio-temporal scales is a necessary component of implementing policies that are robust to a wide range of potential future changes in the dynamics of social-ecological systems.

Ecological risk assessment represents one well established framework for identifying critical uncertainties and quantifying risks within social-ecological systems. The primary goal of risk assessment is to estimate "the magnitudes of adverse consequences that will arise from events that are uncertain, and the chances (i.e. probabilities) of those events and their consequences occurring" (Peterman 2004). Numerous risk assessment techniques might be used successfully to assess uncertainties and risks to ecosystem services provided by highly migratory species. For example, Smith et al. (2007) and Hobday et al. (2011) outline a technique, referred to as Ecological Risk Assessment for the Effects of Fishing (ERAEF), that is based on a hierarchy of assessments in which each level in the hierarchy acts as a screening process. Low risk threats are screened out at lower levels in the hierarchy and higher risk threats are moved up the hierarchy for more detailed evaluation. For EBM policies that need to integrate highly migratory species, the ERAEF technique is appealing for at least two reasons. First, the ERAEF method can be used to assess a wide range of threats or impacts and, because the first level of the assessment hierarchy is primarily based on expert opinion, threats or impacts with limited empirical information can be included in the assessment. Second, the ERAEF method explicitly incorporates a precautionary approach by assuming that a threat or impact is high risk unless data or information are available that indicate otherwise.

In addition to risk assessment, scenario analysis is an increasingly popular method for analyzing risks associated with current and proposed management actions. Using scenario analysis and simulation modeling, researchers can analyze multiple potential ecosystem or management outcomes given a set of alternative management actions. These analyses can be used to inform managers and decision-makers about the potential of different management actions to impact social-ecological systems. Within fisheries science, the most widely used framework for scenario analysis is management strategy evaluation where "models are used to simulate the behavior of ecosystems and provide the ability to forecast changes in ecosystem state as a consequence of management scenarios and decision rules" (Levin et al. 2009). Scenario analysis in general, and management strategy evaluation in particular, can thus be used to help identify policies and management actions that have the greatest potential to achieve stated management objectives, such

as maintaining connectivity between marine and terrestrial ecosystems. Further, with simulation modeling, a broad range of potential management actions that span multiple spatial scales and jurisdictional areas can be considered within a scenario analysis. For example, Dorner et al. (2009) and Dorner et al. (2013) used management strategy evaluation to assess how alternative Pacific salmon stock assessment models and management actions across several spatial scales perform under a wide variety of climate change scenarios.

Although synthesis of ecological information, such as how climate change may affect salmon food availability and hatchery-wild salmon competition in coastal and pelagic ecosystem, would be a key function of the proposed synthesis group, synthesis of economic and policy information would also be important. In particular, the group could provide advice on how best to address the positive and negative externalities arising from the migratory life histories of salmon (i.e., the asymmetric spatial distribution of costs and benefits). The synthesis group should seek to better understand how different policy instruments and management actions could alter the incentives and behavior of stakeholders across the migratory range of Pacific salmon. As discussed earlier, ecological restoration efforts within a localized EBM area can result in positive externalities if the benefits of the restoration accrue to stakeholders outside the EBM area. This is a frequent occurrence for Pacific salmon stocks that are harvested in interception fisheries. Policy instruments that could be implemented to overcome this positive externality include side-payments from stakeholders in distant locations that benefit from the restoration efforts, a tax on the harvest of salmon originating in a particular area, or assigning property rights to the resource (e.g., individual transferable quotas). Determining the potential of these alternative policy instruments to achieve stated policy objectives and how they may influence incentives of stakeholders across broad geographic regions is a necessary component of overcoming the challenges of effectively integrating Pacific salmon into EBM policies.

5.5.2 Near real-time analysis of ecosystem dynamics

Our second proposed strategy relies on the increased availability of near real-time data analysis on ecosystem conditions and migration timing, which can be used to inform in-season management decisions. Despite the complex dynamics of ecosystems, several of the management prescriptions outlined in the Pacific Salmon Treaty are static within a given year. For instance, in the aggregate abundance-based management policy used to manage SEAK chinook fisheries, the quota is set before the fishing season and is not updated regardless of the actual timing or strength of the salmon runs. Similarly, since about 1990 the magnitude of releases of juvenile salmon from hatcheries around the North Pacific Rim has remained nearly constant, despite annual and decadal changes in the productivity of pelagic and coastal ecosystems. In many cases, however, information on

current ecosystem conditions and migration timing can be collected, analyzed, and disseminated in near-real time to help align management decisions with current ecosystem conditions. Indeed, dynamic in-season management, a management strategy that uses near real-time information to better match management decisions with the state of currently observed ecosystem conditions, is becoming increasingly popular for management and conservation of highly migratory species (Maxwell et al. 2015; Lewison et al. 2015).

At the local scale (i.e., the scale of individual salmon fisheries), Pacific salmon fisheries management has pioneered several methods for implementing intensive in-season management policies. In Alaska, management of most marine fisheries for Pacific salmon are adapted in-season using time and area closures that are informed by near real-time data collected on the number of adult salmon that escape the fisheries and move into freshwater to spawn. For instance, in 2013, the Alaska Department of Fish and Game issued 48 in-season management decisions (i.e., emergency orders) regarding salmon fisheries around Kodiak Island, Alaska, which allowed managers to use near real-time data to update decisions based on pre-season forecasts and better match fisheries harvest with the strength of salmon runs (Jackson and Keyse 2013). Using in-season information on the number of adult spawners for management of salmon fisheries in this way, however, requires that salmon harvesting occur concurrently with salmon entering their natal rivers. For those chinook salmon in the SEAK fishery that originate from natal rivers in BC, WA, or Oregon, information on salmon escapements to those rivers may not be available until after harvest in Alaska has taken place, so it would not be feasible to adaptively change quotas in-season based on escapement.

It may be possible, however, to use in-season data about migration routes and timing to increase the selective harvest of local origin and highly productive stocks within mixed-stock salmon fisheries such as the SEAK chinook fisheries. For example, management of several high value salmon fisheries (e.g., Bristol Bay and Fraser River sockeye salmon fisheries) employ test fisheries and genetic sampling to determine the population composition of the salmon currently migrating through a particular location, which allows managers to close a fishery if large proportions of threatened or low productivity populations are currently migrating through the commercial fishing area (Dann et al. 2013). Similar test fisheries and the subsequent near-real time analysis of genetic sampling could be expanded to SEAK (as well as other areas that intercept salmon bound for distant natal rivers) to determine which populations are migrating through the commercial fishing area and potentially reduce the interception of distance origin or low productivity stocks by informing in-season management decisions about time or area closures.

In addition to expanding dynamic in-season management for salmon fisheries, dynamic management could also be applied to management of juvenile salmon releases from hatcheries.

Historically, there has been minimal effort to modify the magnitude of salmon releases in response to changing ocean conditions, which results in either salmon hatcheries gradually increasing total salmon releases or releasing approximately the same number of salmon each year regardless of whether ocean conditions are favorable for salmon survival or not (Pearsons 2010). While a consistent release strategy may allow hatcheries to plan operations more efficiently, this could be detrimental to marine ecosystems in general and wild Pacific salmon specifically. For example, releasing a large number of hatchery-reared juvenile salmon into coastal ecosystems when food availability is low may lead to high levels of competition between hatchery and wild salmon for limited food resources. Instead, release strategies could be updated on an annual basis in response to new information about ecosystem conditions (Pearsons 2010; Peterman and Routledge 1983). For instance, the previously proposed ecosystem synthesis group could use an ecosystem model of the North Pacific within a management strategy evaluation framework to estimate how different hatchery release levels could impact wild salmon populations given current ecosystem conditions.

5.6 Conclusions

We used two case studies from the Pacific salmon literature to examine how three features of social-ecological systems—ecosystem openness, imperfect information, and ecosystem complexity—present challenges to integrating highly migratory Pacific salmon into EBM policies. The first example, chinook salmon interception fisheries in SEAK, showed that human activities (in this case, commercial fishing) in one location can influence the supply of ecosystem services and incentives to conserve salmon populations in distant locations. Stakeholders and managers in EBM areas located in down-migration areas from the interception fisheries bear the costs of uncertainty (imperfect information about ecosystem dynamics) associated with management decisions made in up-migration areas. The second example, competition between hatchery and wild salmon for a limited common-pool of prey resources, showed that processes that occur over larger spatial scales than an EBM area can influence the provisioning of ecosystem services within the EBM area. In this case, the aggregate releases of juvenile salmon from North Pacific Rim nations resulted in reductions in ecosystem services provided by salmon within a localized EBM area due to reduced age-specific body sizes and productivity of wild salmon stocks. This example further indicated that overcoming this collective action problem would likely require estimating an acceptable level of aggregate hatchery releases for current ecosystem conditions, which is impeded by large uncertainties about the complex non-stationary dynamics of the ecosystems that comprise the North Pacific Ocean.

Confronting the challenges arising from ecosystem openness, imperfect information, and

ecosystem complexity will require cooperation across socio-political borders; unilateral management actions are unlikely to resolve the challenges because many impacts occur outside the bounds of a given EBM area. Our examination of the case studies suggested two potential strategies to address these challenges. First, we recommend the creation of an international ecosystem synthesis group that is charged with aggregating and analyzing ecological, economic, and policy information from local and regional scale research and management areas, along with disseminating strategic management advice based on this synthesis. Second, we recommend the expansion of dynamic in-season management practices to better match management actions to current ecosystem conditions, which would require increased near real-time data collection and analysis. Our findings further indicate that no single solution is likely to overcome the challenges associated with integrating highly migratory species into local or regional scale EBM policies; instead a variety of strategies will likely need to be implemented to maintain key ecosystem properties in the presence of human and natural disturbances. Finally, our results suggest that ecosystem-based management policies should explicitly account for mismatches in the scale at which ecosystem services are generated by highly migratory species and the scale at which human activities and natural processes impact those services.

Chapter 6

Conclusion

In this thesis, I contribute to our broader understanding of how environmental forcing pathways link climatic and ocean processes to dynamics of Pacific salmon populations in the Northeast Pacific Ocean. My second and third chapters apply a cross-system comparative approach to rigorously assess the evidence for population responses to inter-annual changes in two meso-scale ocean processes. In chapter 2, I investigate the hypothesis that vertical ocean transport and subsequent coastal phytoplankton dynamics are associated with changes in Pacific salmon productivity. In chapter 3, I examine an alternative hypothesis that suggests ocean processes driven by horizontal ocean transport, such as the advection of zooplankton, are also important drivers of salmon productivity. My fourth chapter builds on the previous chapters, which each focused on a single meso-scale ocean process, by estimating the joint effects and relative strength of multiple environmental forcing pathways on Pacific salmon dynamics. My fifth chapter applies an interdisciplinary approach to examine challenges to integrating highly-migratory anadromous fish species into local and regional scale ecosystem-based management policies and provides practical recommendations for overcoming the identified challenges. In total, this thesis further develops our quantitative understanding about how climatic and ocean processes influence the population dynamics of Pacific salmon and in doing so contributes to reducing uncertainties about how environmental change impacts living marine resources.

My thesis makes two main substantive contributions to our understanding of how large-scale climate processes downscale to affect regional and local scale dynamics of higher-trophic-level species. First, my thesis provides empirical evidence that the dynamics of higher-trophic-level species respond to forcing from multiple concurrent environmental forcing pathways. In chapters 2 and 3, I show that environmental pathways mediated by either vertical or horizontal ocean transport processes can impact the dynamics of higher-trophic-level species. Although I investigate

effects of phytoplankton dynamics and ocean currents on salmon productivity individually, these meso-scale ocean processes likely influence higher-trophic-level species simultaneously. Indeed, my fourth chapter indicates that large-scale climate processes can impact Pacific salmon year-class strength via multiple simultaneously operating environmental pathways. For instance, large-scale climate variability indexed by the Pacific Decadal Oscillation can propagate to affect regional and local scale dynamics of Pacific salmon through concurrent pathways that are mediated by different ocean processes. This implies that only considering a single mechanism may be insufficient to understand how environmental forcing impacts living marine resources.

Second, my thesis provides empirical evidence that the effects of environmental forcing on higher-trophic-level species can be non-stationary across space. My second and third chapters indicated that effects of the spring bloom initiation date and horizontal ocean transport on salmon productivity were dependent on the latitude of juvenile salmon ocean entry. For example, in chapter 2, I show that effects of the spring bloom initiation date on pink salmon productivity were opposite in sign for stocks that enter the ocean south and north of $55.7°N$. Similarly, in chapter three, my results indicate that ocean current patterns are strongly associated with changes in salmon productivity for stocks that enter the ocean in the southern Northeast Pacific upwelling domain, but not for stocks that enter the ocean in the northern downwelling domain, suggesting that different environmental forcing pathways may drive salmon productivity in northern and southern areas. A practical implication of this spatial non-stationarity is that relationships inferred from data in one location may not be applicable to another location.

Collectively, my thesis highlights the need to pursue evidence for multiple competing hypotheses to explain observed spatial and temporal changes in demographic rates of exploited species. Over a century ago, T.C. Chamberlin warned that

> We [scientists] are so prone to attribute a phenomenon to a single cause, that, when we find an agency present, we are liable to rest satisfied therewith, and fail to recognize that it is but one factor, and perchance a minor factor, in the accomplishment of the total result. (Chamberlin 1890, p. 94)

Yet, broadening our focus beyond a single hypothesis or set of hypotheses focused around a single mechanism remains challenging (Hare 2014). As I show in this thesis, competing environmental forcing hypotheses are not necessarily mutually exclusive and future research efforts should strive to understand the cumulative effects and relative importance of a broad range of environmental forcing hypotheses. In particular, increasing our understanding of how the relative importance of different environmental pathways changes through space and time may be an important component to estimating the current and future impacts of climatic change on coastal ecosystems and the fish populations they support.

Environmental variability is an intrinsic element of coastal ecosystems and can have profound impacts on ecosystem structure and function. As climatic processes and ecosystem dynamics change at unprecedented rates, finding effective strategies to integrate empirical information about natural and anthropogenic forcing into management decisions may be critical to maintaining viable and productive living marine resources. My fifth chapter highlights two potential strategies that may prove effective, including dynamic in-season management of commercial fisheries and scenario analysis. Ultimately, uncertainties about the impacts of changing environmental conditions on living marine resources are always likely to be present. Effective decision-making in the face of this uncertainty is vital to preserving the ecological, social, and economic benefits generated by marine ecosystems.

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