Spatial covariation in productivity of Pacific herring (*Clupea pallasii*) in the northeast Pacific Ocean

by

Jessica A. Gill

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Examining Committee:	**Chair:** Angus Straight Master of Resource Management Candidate

Sean Cox
Senior Supervisor
Professor

Michael Malick
Supervisor
Researcher
NOAA Fisheries

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Abstract

I examined spatial patterns of covariation in productivity indices estimated for 24 Pacific herring (*Clupea pallasii*) stocks and 5 stock aggregates in the northeast Pacific Ocean. Spatial covariation was weak among stock productivity indices. Correlations existed among stocks at close distances (less than 400 km), but the direction of the correlations were both negative (as low as -0.82) and positive (as high as 0.94), resulting in weak overall correlation (r = 0.16) among nearby stocks, suggesting small-scale oceanic processes are likely driving stock productivity. A small increase in correlation among stocks in distant regions (between 2,000-3,000 km) was seen, which was more evident among the stock aggregates than in the individual stocks analyzed. Developing a better understanding of the underlying productivity among herring stocks in the northeast Pacific offers an approach that can help differentiate competing hypotheses about the drivers of productivity shifts by helping identify the most likely spatial scale of potential drivers of productivity.

Keywords: Pacific herring; spatial covariation; correlation; productivity; process error; Bayesian surplus production model

For my parents,
who never failed to believe in me and support me
through all the stormy seas and sunny skies.

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List of Acronyms

AK	Alaska
BC	British Columbia
CA	California
ENSO	El Niño Southern Oscillation
MCMC	Markov chain Monte Carlo
PDO	Pacific Decadal Oscillation
WA	Washington
PWS	Prince William Sound
PRD	Prince Rupert District
HG	Haida Gwaii
CC	Central Coast
WCVI	West Coast Vancouver Island
SOG	Strait of Georgia
NWA	Northern Puget Sound Washington
SWA	South Central Puget Sound Washington
SFB	San Francisco Bay
AYK	Arctic-Yukon-Kuskokwim
SEAK	Southeast Alaska
PS	Puget Sound

Introduction

Ocean processes drive population dynamics for many marine fish stocks (Hjort 1914; Myers et al. 1997; Hare and Mantua 2009; Vert-pre et al. 2013). However, incorporating ocean processes into stock assessment remains a challenge because fish productivity is influenced at multiple spatial scales affecting recruitment, population structure, and individual growth rates (Williams and Quinn 2000a; Minto et al. 2014; Munch et al. 2018). Understanding the scale of connectivity among fish populations allows managers to gain insights into how environmental processes interact with marine fish populations (Mueter et al. 2002, 2007; Pyper et al. 2005; Bartolino et al. 2014; Minto et al. 2014; Malick et al. 2015b; Keeling et al. 2017; Dorner et al. 2018).

Understanding links between ocean processes and stock dynamics remains a challenge for Pacific herring (*Clupea pallasii*) in the northeast Pacific Ocean. Strong year-classes along the British Columbia (B.C.) coast are correlated with sea level in bays and inlets, suggesting that local retainment in supportive environments promote year-class strength (Ramey and Wickett 1973). In Sitka Sound, Alaska (AK), warmer sea-surface temperatures during the winter prior to spawning is correlated positively with recruitment (Zebdi and Collie 1995); however, in San Francisco Bay (CA), the opposite pattern results, where warmer sea-surface temperatures in the months prior to spawning lead to lower spawning stock biomass (Sydeman et al. 2018). Herring productivity in Prince William Sound, AK, is correlated negatively with the volume of freshwater discharge and density-dependence suggesting at least two mechanisms for changes in herring productivity on small spatial scales (Ward et al. 2017). These studies indicate that small-scale ocean conditions are likely influencing stock productivity.

Large-scale ocean conditions also could be affecting herring dynamics. In the Bering Sea, Prince William Sound, and along the West Coast of Vancouver Island, B.C., modelled herring growth rates shifted at the time of the 1977 and 1998 Pacific Decadal Oscillation regime shifts (Rose et al. 2007). In Puget Sound, Washington (WA), a minor effect of the Pacific Decadal Oscillation was detected on spawning biomass (Siple and Francis 2016) and cumulative coastal upwelling positively influenced recruitment (Reum et al. 2011). Herring recruitment is correlated with air and sea-surface temperatures and the Southern Oscillation Index (Williams and Quinn 2000a); however, the direction of the correlations are different for herring recruitment in British Columbia and Alaska. In British Columbia, herring recruitment is correlated negatively with temperature but correlated positively with the Southern Oscillation Index (Williams and Quinn 2000a). In the Gulf of Alaska, herring recruitment is correlated positively with air and sea-surface temperature but correlated negatively with the Southern Oscillation Index (Williams and Quinn 2000a). Similar trends in year-class strength and recruitment in Prince William Sound and Sitka Sound suggest that population dynamics are influenced by Gulf of Alaska-wide ocean processes (Collie 1990; Zebdi 1991; Pearson et al. 2012), but the specific process has not been identified. Increased primary productivity was associated with a higher carrying capacity for herring stocks in the eastern Bering Sea, Prince William Sound, Sitka Sound, and along the British Columbia coast (Perry and Schweigert 2008), indicating large-scale bottom-up forcings could be affecting population dynamics (e.g., via synchronous timing of larval production and plankton blooms) (Cushing 1975).

Developing a better understanding of the spatial correlation in productivity among herring stocks in the northeast Pacific offers an approach that can help differentiate among competing hypotheses about the drivers of productivity shifts by helping identify the most likely spatial scale of potential productivity drivers. For example, research on spatial covariation patterns among Pacific salmon (*Oncorhynchus* spp.) stocks revealed that regional-scale covariation among stock productivities on the order of a few hundred kilometers, suggesting that ocean processes that operate over similar spatial scales (e.g., temperature) are likely drivers of stock productivity (Mueter et al. 2002; Malick et al. 2015b). Similar research on spatial covariation of Atlantic cod (*Gadus morhua*) in the north Atlantic suggested local environmental effects could be a strong driver of productivity at the early life history stage because covariation among stocks decreased as a function of distance (Minto et al. 2014).

Previous research has indicated that spatial covariation among herring recruitment time series tended to be very strong between neighboring herring stocks and became weaker as the distance between stocks increased (Zheng 1996). In addition, interrelationships among herring populations based on recruitment and weight-at-age time series revealed potential stock clusters (Williams and Quinn 2000b, 2000a) with strong covariation among recruitment deviations for herring stocks that spawn within certain geographic regions (Mueter et al. 2007). Therefore, correlation among stock productivities could decrease to zero with increasing distance among herring stocks along the Pacific coast.

In this study, I examine how productivity among Pacific herring stocks varies across spatial scales. I use a Bayesian state-space Schaefer model to estimate population-specific temporal changes in productivity of 24 Pacific herring stocks and 5 stock aggregates from California to Alaska. I used the resulting process error deviations derived from the Schaefer model to examine the spatial scale and correlation patterns among herring stocks throughout the northeast Pacific Ocean. High correlation among distant stocks could indicate that large-scale ocean processes affect productivity across stocks; whereas, high correlation among nearby stocks could indicate that small-scale environmental processes affect productivity among stocks (Malick and Cox 2016). My research builds off of previous work by increasing the number of stocks included in analysis and the use of process error model as an index of productivity. This method is beneficial because process error models are based on the assumption that observations are made without error and all error occurs as an index of productivity (Polacheck et al. 1993), which allows for variation in stock assessment methods and filters out effects of catch (Schaefer 1954). Using the Schaefer model with process error is valuable because of the limited amount of data needed to produce an estimate of productivity, therefore, stocks that do not have recruitment estimates can be included in this analysis.

Methods

Pacific herring data

I obtained time-series data of spawning stock biomass estimates and commercial catch for 24 Pacific herring stocks along the Northeast Pacific coast (Table 1; Figure 1). The data spanned years 1969-2018 with a minimum time series of 22 years (i.e., 1994-2015 and 1988-2009) and a maximum time series of 50 years (i.e., 1969-2018). Across all stocks, the average time series length was 34 years.

In 11 of the 24 stocks analyzed, management agencies used only spawning ground or aerial survey methods to estimate spawning stock biomass. For 13 of the 24 stocks, data such as catch-at-age, weight-at-age, recruitment, natural mortality, historical information, and age composition were available to managers (Figure 1). For these stocks, management agencies integrate catch and survey data through the use of age-structured assessments, catch-at-age assessments, or hindcasting to produce spawning stock biomass estimates which I used as data for analysis. It would preferable to use raw estimates of spawning biomass to avoid assumptions implicit in stocks assessment outputs (Maunder and Punt 2013; Brooks and Deroba 2015; Free et al. 2019); however, that data was not readily available.

Spawning stock biomass estimates and catch for Washington stocks were infrequent because of small management units (i.e., individual spawning beaches); therefore, I aggregated stocks from 21 small spawning stocks into 3 larger spawning areas (Table 2). The Cherry Point, WA, stock is genetically distinct from other populations (Small et al. 2005; Stick et al. 2014) and was treated as an individual stock in this analysis. Semiahmoo Bay, WA, which is not considered genetically distinct from the Puget Sound population (Small et al. 2005), occupies the same management area (i.e., area 20A) as the Cherry Point stock. Accordingly, I combined the data from the Semiahmoo Bay stock with the data for the Cherry Point stock.

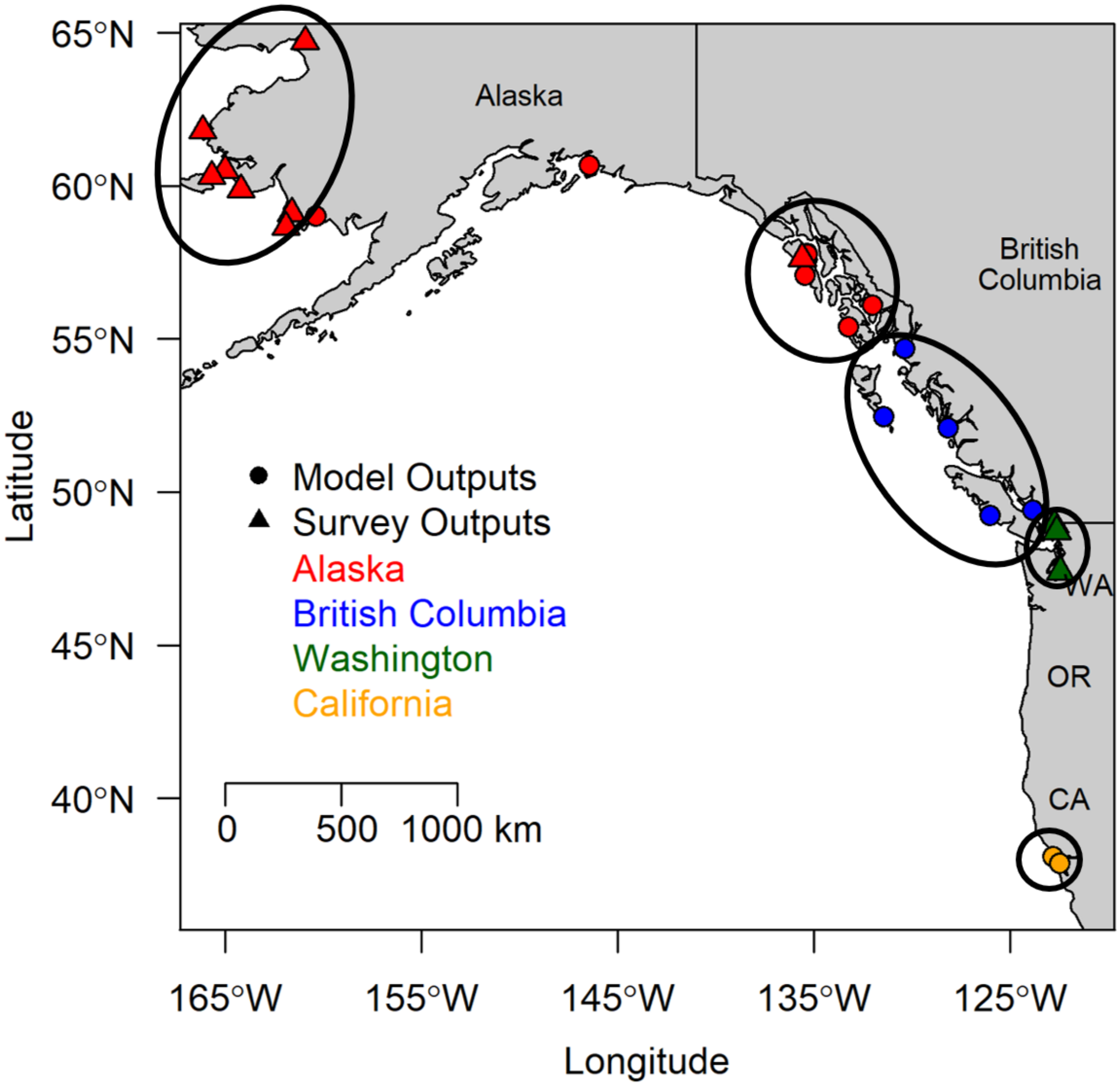

Figure 1. **Locations of Pacific herring stocks used in analysis. Triangles indicate survey outputs and circles indicate model outputs. Black ovals identify stocks consolidated for stock aggregates.**

Commercial landings came from the sac-roe fishery (i.e., seine and gillnet), the food and bait fishery (i.e., seine, gillnet, and lampara), and the converted estimates from the spawn-on-kelp fishery (i.e., pound structures). Catch time series from British Columbia included estimates from the herring-reduction fishery prior to 1970, which include juvenile herring resulting in catch estimates that often were larger than the biomass estimates; therefore, the years prior to the reduction fishery (i.e., 1951-1969) for B.C. were not included in the analysis. Further, the B.C. data were truncated to begin in 1988 to account for the change in spawning ground surveys from a surface survey to a dive survey that occurred in 1987 (Schweigert 1993; Benson 2012).

Additionally, I treated 22 of the individual stocks as 5 aggregates to account for varying spatial scales of management and stock dynamics. In particular, I aggregated 7 stocks in the Bering Sea: Norton Sound, Cape Romanzof, Nelson Island, Nunivak Island, Cape Avinof, Goodnews Bay, and Security Cove. I aggregated the 5 stocks in Southeast Alaska, the 5 stocks in British Columbia, and the 3 Puget Sound stocks. The 2 stocks in California, Tomales Bay and San Francisco Bay, were aggregated into one stock aggregate (Table 2; Figure 1).

Productivity indices

I used the Schaefer surplus production model with process error to estimate the intrinsic rate of growth, r, and the equilibrium unfished biomass, B_0, (Schaefer 1954; Hilborn and Walters 1992; Polacheck et al. 1993) for each stock i. In the surplus production model, the equation for total biomass took the form,

$$B_{i,t} = \left(B_{i,t-1} + r_i B_{i,t-1}\left(1 - {B_{i,t-1}}/{B_{i,0}}\right) - C_{i,t-1}\right) e^{w_{i,t}} \qquad \text{(Equation 1)}$$

where $B_{i,t}$ is the biomass of stock i in year t, $C_{i,t}$ is the catch of stock i in year t, and $w_{i,t}$ is a log-normally distributed process error term for stock i in year t where $w_{i,t} \sim \log N(0, \sigma_{i,proc})$. The Schaefer model approximates the overall change in biomass due to somatic growth, recruitment, natural mortality, and catch (Hilborn and Walters 1992; Millar and Meyer 2000; Punt 2003). The use of the Schaefer model with process error enabled me to process all stocks with the same criteria. The process error term w accounts for variation that is not explained by the Schaefer model (Hilborn and Walters 1992) and can be used as an index of productivity that is useful for comparing stocks (Polacheck et al. 1993).

Table 1. **Summary of biomass and catch data sets used in analysis, arranged North to South.**

STOCK CODE	STOCK	MANAGEMENT AREA	REGION	YEARS USED IN MODEL	SOURCES
NORT	Norton Sound	Arctic-Yukon-Kuskokwim	Alaska	1990-2015	1
ROMAN	Cape Romanzof	Arctic-Yukon-Kuskokwim	Alaska	1994-2015	2
NELS	Nelson Island	Arctic-Yukon-Kuskokwim	Alaska	1985-2015	3
NUNI	Nunivak Island	Arctic-Yukon-Kuskokwim	Alaska	1985-2015	3
AVI	Cape Avinof	Arctic-Yukon-Kuskokwim	Alaska	1988-2015	3
GOOD	Goodnews Bay	Arctic-Yukon-Kuskokwim	Alaska	1982-2015	3
SEC	Security Cove	Arctic-Yukon-Kuskokwim	Alaska	1982-2015	3
TOG	Togiak Bay	Togiak Bay	Alaska	1980-2016	4, 5, 6, 7, 8
PWS	Prince William Sound	Prince William Sound	Alaska	1977-2015	9, 10, 11
TEN	Tenakee Inlet	Southeast	Alaska	1979-2010	12
HOON	Hoonah Sound	Southeast	Alaska	1990-2015	12
SIT	Sitka Sound	Sitka	Alaska	1979-2018	13, 14, 15,
ERN	Ernest Sound	Southeast	Alaska	1976-2016	12
CRG	Craig/Klawock	Southeast	Alaska	1988-2016	12
PRD	Prince Rupert District	Prince Rupert District	British Columbia	1988-2017	12
HG	Haida Gwaii	Haida Gwaii	British Columbia	1988-2017	16
CC	Central Coast	Central Coast	British Columbia	1988-2017	16
WCVI	West Coast Vancouver Island	West Coast Vancouver Island	British Columbia	1990-2017	16
SOG	Strait of Georgia	Strait of Georgia	British Columbia	1988-2017	16
CHERRY	Cherry Point/Semiahmoo Bay	Area 20A	Washington	1973-2016	17, 18
NWA	Northern Puget Sound	Northern Puget Sound	Washington	1975-2016	17, 18
SWA	South Central Puget Sound	South-Central Puget Sound	Washington	1976-2016	17, 18
TOM	Tomales Bay	Tomales Bay	California	1974-2006	19
SFB	San Francisco Bay	San Francisco Bay	California	1980-2016	20

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Table 2. Stock aggregate groupings used in analysis.

Stock Code	Stock	Smaller spawning aggregates included:	Years used in model
AYK	Arctic-Yukon-Kuskokwim	Norton Sound, Cape Romanzof, Nelson Island, Nunivak Island, Cape Avinof, Goodnews Bay, Security Cove	1982-2015
SEAK	Southeast Alaska	Tenakee Inlet, Hoonah Sound, Sitka Sound, Ernest Sound, Craig/Klawock	1969-2018
BC	British Columbia	Prince Rupert District, Haida Gwaii, Central Coast, West Coast Vancouver Island, Strait of Georgia	1988-2017
PS	Puget Sound	Cherry Point, Northern Puget Sound, South Central Puget Sound	1977-2016
CA	California Coast	Tomales Bay, San Francisco Bay	1980-2016
NWA	Northern Puget Sound	Northwest San Juan Islands, Interior San Juan Islands, Fidalgo Island, Samish/Portage Bay, Semiahmoo Bay, Cherry Point	
SJDF[1]	Strait of Juan de Fuca	Discovery Bay, Sequim Bay, Dungeness Bay	
SWA	South Central Puget Sound	Port Susan, Skagit Bay, Holmes Harbor, South Hood Canal, Quilcene Bay, Port Gamble, Port Orchard/Port Madison, Elliot Bay, Quartermaster Harbor, Purdy, Wollochet Bay, Squaxin Pass	

[1] Strait of Juan de Fuca was not included in analysis.

The majority of Pacific herring stocks were fished prior to the beginning of their respective biomass estimates; therefore, I initialized the model at the first observed biomass estimate rather than B_0. Based on the properties of the Schaefer model, if a stock was missing catch data, the model could not run to completion; therefore, I analyzed years that had catch data with the corresponding biomass observations (Table 1). I initialized the process error time series at the second time step (i.e., $t = 2$) (Millar and Meyer 2000).

Prior Specification

For estimated model parameters for stock i, r_i, $B_{i,0}$, and $\vec{w_i}$, the negative log-likelihood function is

$$\ell\left(Y_{i,1}, Y_{i,2} \ldots, Y_{i,n} \middle| r_i, B_{i,0}, w_{i,2}, w_{i,3} \ldots, w_{i,n-1}\right) \propto \sum_{t=1}^{i,n} \frac{1}{2\sigma^2}\left(\log Y_{i,t} - \log B_{i,t}\right)^2 \qquad \text{(Equation 2)}$$

where Y_i is the observed biomass of stock i at time t, i, n is the length of the time series of stock i, and $B_{i,t}$ is the modeled biomass estimate for stock i at time t, where B_t is a function of Equation 1. I estimated model parameters using Markov chain Monte

Carlo (MCMC) Bayesian methods, which typically stabilizes model fitting via prior distributions of parameters (Pedersen and Berg 2017). Informative priors for the intrinsic rate of growth for stock i, r_i , were log-normally distributed as $r \sim \log N\ (\mu_r, \sigma_r)$ for all stocks and stock groups and assigned as $r \sim \log N\ (0.5, 0.5)$. For each stock and stock group i, equilibrium unfished biomass, B_0, was assigned as a weakly informative prior derived from existing information on estimated carrying capacity for stocks in the northeast Pacific (Perry and Schweigert 2008) and expected unfished biomass estimates for herring and other forage fish stocks (Pikitch et al. 2012) (Table 3). To test sensitivity to the prior, I used alternative starting values of the B_0 mean and tightened standard deviations and to test sensitivity to the r parameter values of $r \sim \log N\ (0.7, 0.7)$ and $r \sim \log N\ (0.3, 0.3)$ were tested. The process error standard deviation was initially set for each stock i at $\sigma_{i,proc} = 0.1$ then adjusted as needed, from $\sigma_{i,proc} = 0.05$ to $\sigma_{i,proc} = 0.4$ to achieve better model convergence (Knape 2008; Anderson et al. 2017) (Table 3).

I used the Metropolis-Hastings algorithm for MCMC simulations implemented in the MCMCpack package in R (Martin et al. 2011; R Core Team 2018) to sample posterior distributions. Prior distributions were multiplied by the likelihood function to obtain posterior probability distribution estimates for model parameters (Gelman et al. 1995; Millar and Meyer 2000; Pedersen and Berg 2017). The full negative log posterior can be expressed as the following function

$$\begin{aligned}-\log P\left(Y_{i,1}, Y_{i,2} \ldots, Y_{i,n} \middle| r_i, B_{i,0}, \vec{w}_i\right) \propto\ & \sum_{t=1}^{i,n} \frac{1}{2\sigma^2}\left(\log Y_{i,t} - \log B_{i,t}\right)^2 \\ & + \frac{1}{2\sigma_{r_i}^2}(\log r_i - \log \mu_{r_i}) \\ & + \frac{1}{2\sigma_{B_{i,0}}^2}(\log B_{i,0} - \log \mu_{B_{i,0}})^2 \\ & + \frac{1}{2\sigma_{i,proc}^2}\sum_{t=2}^{n} w_{i,t}^2 \qquad \text{(Equation 3)}\end{aligned}$$

The initial MCMC runs used three chains of 50,000 iterations keeping every 10th sample with the first 1,000 discarded as burn-in. I used disparate starting values for each chain to achieve representative convergence. The first chain was initialized at the logged mean of the priors (i.e., the maximum-likelihood parameter estimates), the second chain was the log-transformed mean of the priors multiplied by 1.5 for r and multiplied by 0.66 for B_0, and the third chain was the log-transformed mean of the priors multiplied by 0.66 for r and multiplied by 1.5 for B_0. I did this to account for the correlation between r and B_0 (Hilborn and Walters 1992; Forrest et al. 2010). Based on the MCMC results, to improve effective sample size I extended the number of sampling iterations up to 5,000,000. I tested convergence and effective sample size using posterior predictive checks from the coda package in R and the Gelman-Rubin statistic ($\hat{R}$) (Gelman et al. 1995; Plummer et al. 2006; R Core 2018).

Table 3. Priors used for MCMC simulations, process error standard deviation, and resulting r and B_0 parameters. * Indicates that the MCMC simulations did not converge.

Stock Code	r Prior	r Mean	r SD	B_0 Prior	B_0 Mean	B_0 SD	σ_{proc}
Nort	0.5 ± 0.5	0.193	0.121	80 ± 80	84.125	44.522	0.05
Roman*	0.5 ± 0.5	0.069	0.082	9 ± 2	8.352	2.051	0.2
Nels*	0.5 ± 0.5	0.279	0.215	80 ± 40	26.936	32.796	0.05
Nuni*	0.5 ± 0.5	0.014	0.043	45 ± 10	41.899	10.911	0.4
Avi*	0.5 ± 0.5	0.103	0.102	15 ± 5	13.809	4.753	0.05
Good	0.5 ± 0.5	0.213	0.015	50 ± 5	48.158	5.171	0.05
Sec	0.5 ± 0.5	0.254	0.055	7 ± 7	12.267	2.831	0.1
Tog	0.5 ± 0.5	1.224	0.323	190 ± 190	140.284	13.099	0.05
PWS	0.3 ± 0.3	0.852	0.188	29 ± 29	45.243	8.458	0.05
Ten	0.5 ± 0.5	0.395	0.142	8 ± 8	7.885	3.002	0.2
Hoon*	0.3 ± 0.3	0.001	0.014	10 ± 10	0.656	2.841	0.05
Sit*	0.5 ± 0.5	0.335	0.094	80 ± 80	147.771	33.750	0.1
Ern*	0.3 ± 0.3	0.327	0.265	5 ± 5	1.707	1.401	0.1
Crg	0.5 ± 0.5	0.156	0.019	47 ± 47	81.500	29.067	0.05
PRD*	0.5 ± 0.5	0.189	0.019	52 ± 52	97.851	25.898	0.05
HG*	0.5 ± 0.5	0.012	0.026	60 ± 60	5.381	8.429	0.1
CC*	0.5 ± 0.5	0.192	0.020	61 ± 61	151.136	35.345	0.05
WCVI	0.5 ± 0.5	0.118	0.015	150 ± 150	221.691	96.105	0.05
SOG*	0.5 ± 0.5	0.307	0.077	200 ± 200	283.903	146.296	0.05
Cherry*	0.3 ± 0.3	0.001	0.005	15 ± 15	0.859	4.861	0.1
NWA	0.5 ± 0.5	1.190	0.254	10 ± 10	8.994	0.464	0.1
SWA	0.5 ± 0.5	0.672	0.176	6 ± 6	8.695	0.882	0.1
Tom*	0.5 ± 0.5	0.170	0.081	30 ± 30	13.530	16.011	0.05
SFB*	0.5 ± 0.5	0.279	0.097	193 ± 193	105.183	58.021	0.05
AYK	0.5 ± 0.5	0.442	0.036	215 ± 215	87.296	7.022	0.05
SEAK	0.5 ± 0.5	0.267	0.027	200 ± 200	237.706	49.582	0.05
BC*	0.5 ± 0.5	0.246	0.027	200 ± 200	443.328	75.887	0.05
PS*	0.3 ± 0.3	0.075	0.050	25 ± 25	34.095	14.585	0.1
CA*	0.5 ± 0.5	0.204	0.081	250 ± 250	238.919	168.571	0.05

Spatial covariation

I expect productivity among Pacific herring stocks to be correlated positively at short distances and decrease to zero as a function of distance apart from stocks. To determine the degree of correlation, I calculated the Pearson correlation coefficient for each unique pair of process error time-series derived from the Schaefer surplus production model. I made a total of 406 (i.e., $(N^2 - N)/2$) (Peterman et al. 1998) comparisons. I removed the first value of the process deviations for all of the 24 stocks and 5 stock aggregates and fit a nonparametric covariance function (Bjornstad and Falck 2001; Pyper et al. 2005; Malick et al. 2015a) to the pairwise correlation coefficients as a function of great-circle distance between the spawning grounds for each pair of stocks. I calculated confidence intervals for each covariance function by bootstrapping the estimate procedure 2000 times.

I used two metrics to summarize the covariance functions: (1) the *y*-axis intercept, which provides an estimate of the correlation at zero distance (CZD), and (2) the 50% correlation scale, which provides a metric of the degree of correlation decline with increasing distance between herring stocks (Mueter et al. 2002; Malick et al. 2015a).

Results

Bayesian model convergence was achieved for 10 of 24 stocks and 2 of 5 stock groups based on criteria of $\hat{R} < 1.1$ with an effective sample size greater than 1,000 for both r and B_0. The effective sample size for the r parameter was the disqualifying criterion for the majority of stocks that did not converge (55%). I excluded stocks that failed to converge on r and B_0 in analysis of those parameters because the simulations could not produce reliable estimates of the two parameters (Table 3). All stocks analyzed, except Ernest Sound (Ern), had convergence by both criteria for the process error, $\vec{w}$, estimates. Ernest Sound failed convergence on 26% (11 out of 41) of the process error estimates but was included in further analysis. Twenty-two stocks analyzed had acceptable qualitative model fits using the maximum posterior density estimate and 15 stocks had acceptable qualitative model fits using the median posterior density (MPD) estimate estimated via MCMC (Figure 2). One stock (i.e., NWA) had an unreliable maximum posterior density estimate and I did not include this individual stock in analysis of covariation, resulting in a total of 23 stocks and 5 stock groupings analyzed for covariation (Figure 2).

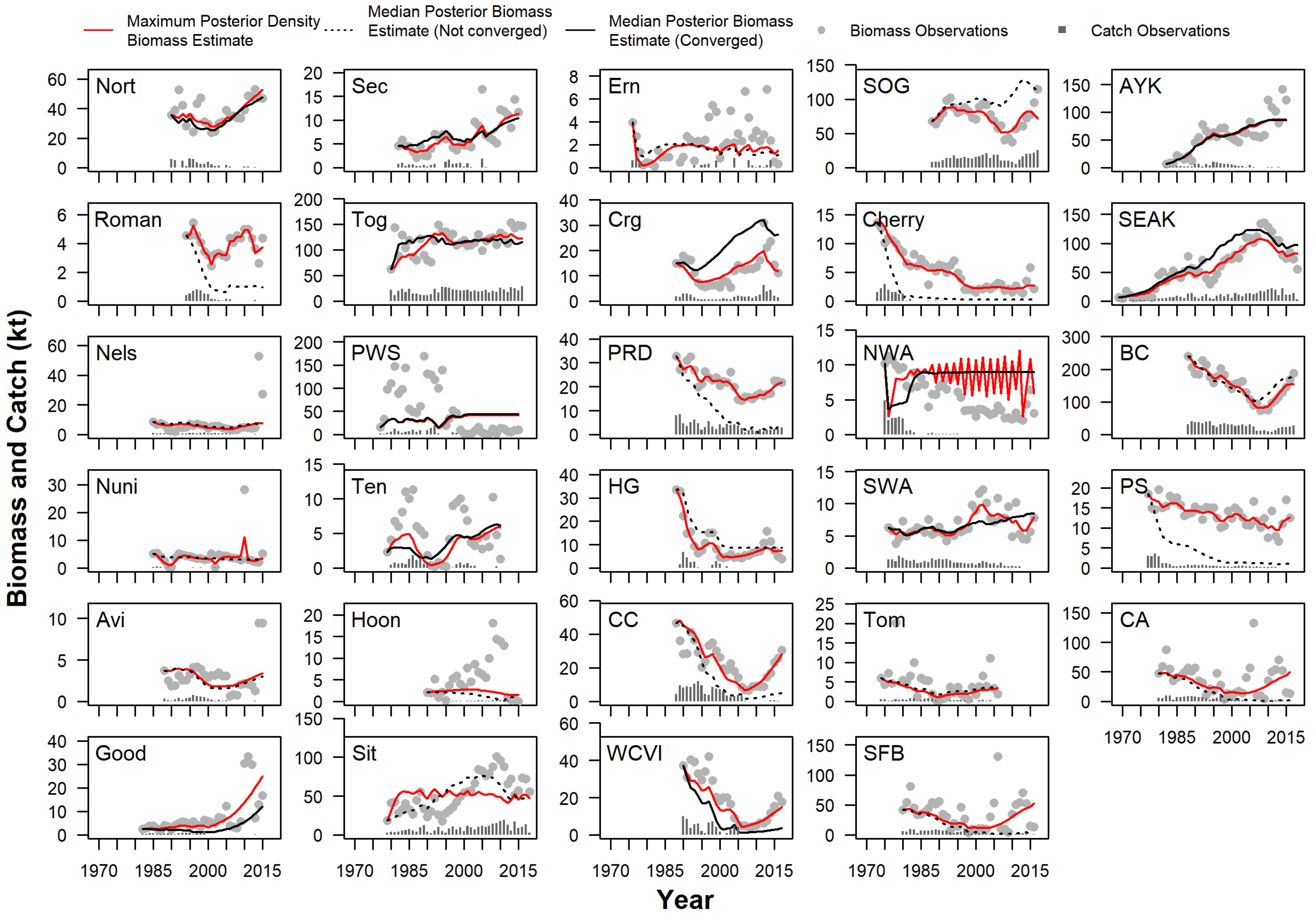


Figure 2. **Time series of Schaefer surplus production model fits incorporating log-normally distributed process errors.**

Stock productivity trends

Time series of estimated process deviations, $\vec{w}$, (Figure 3) served as a productivity index and demonstrated high variability among stocks. Across the 28 process deviation time series, I observed three qualitative trends. The first, exemplified by Cape Avinof (Figure 3, Avi), was characterized by a peak in productivity early in the series followed by a gradual decline with a small but abrupt increase in productivity toward the end of the series. The second trend was high variability in productivity with no obvious increase or decrease in productivity throughout the time series. This was most evident in the South Central Puget Sound stock (Figure 3, SWA) and the Prince Rupert District stock (Figure 3, PRD). The third trend was gradual changes in production, typically increasing or decreasing over many years, as exemplified by the Hoonah Sound stock (Figure 3, Hoon).

Prince William Sound (PWS) exhibited increasing productivity in the years prior to the 1989 *Exxon Valdez* oil spill, peaking in 1992. Since the peak, productivity has been declining and has remained negative since 1995, consistent with other studies of PWS productivity (Figure 3) (Shelton et al. 2012; Ward et al. 2017). Four stocks in British Columbia, Prince Rupert District, Central Coast (CC), West Coast Vancouver Island (WCVI), and Strait of Georgia (SOG), had the lowest productivity between 2003 and 2005 and have been steadily increasing since (Figure 3). Twelve stocks had increasing trends in the last five years and 11 stocks have decreasing trends in the same time period.

Reliable estimates for 10 individual stocks and 2 stock groups from MCMC simulation convergence were analyzed for posterior r and B_0 estimates (Table 3; Figure 4). Point estimates of r and B_0 were highly variable across stocks. The majority of stocks (88%) have r estimates less than 0.5 indicating low growth rates for most of the populations in the northeast Pacific (Table 3; Figure 4). Only Northern Puget Sound (NWA) (1.19 ± 0.25), South Central Puget Sound (0.67 ± 0.18), Togiak Bay (Tog; 1.22 ± 0.32), and Prince William Sound (0.85 ± 0.19) had estimates greater than 0.5. For stocks with B_0 estimates over 50,000 tons, all had r estimates less than 0.35 with the exception of Togiak Bay (140,284 ± 13,099 tons) and Arctic-Yukon-Kuskokwim stock group (AYK) (87,296 ± 7,022 tons) (Table 3; Figure 4).

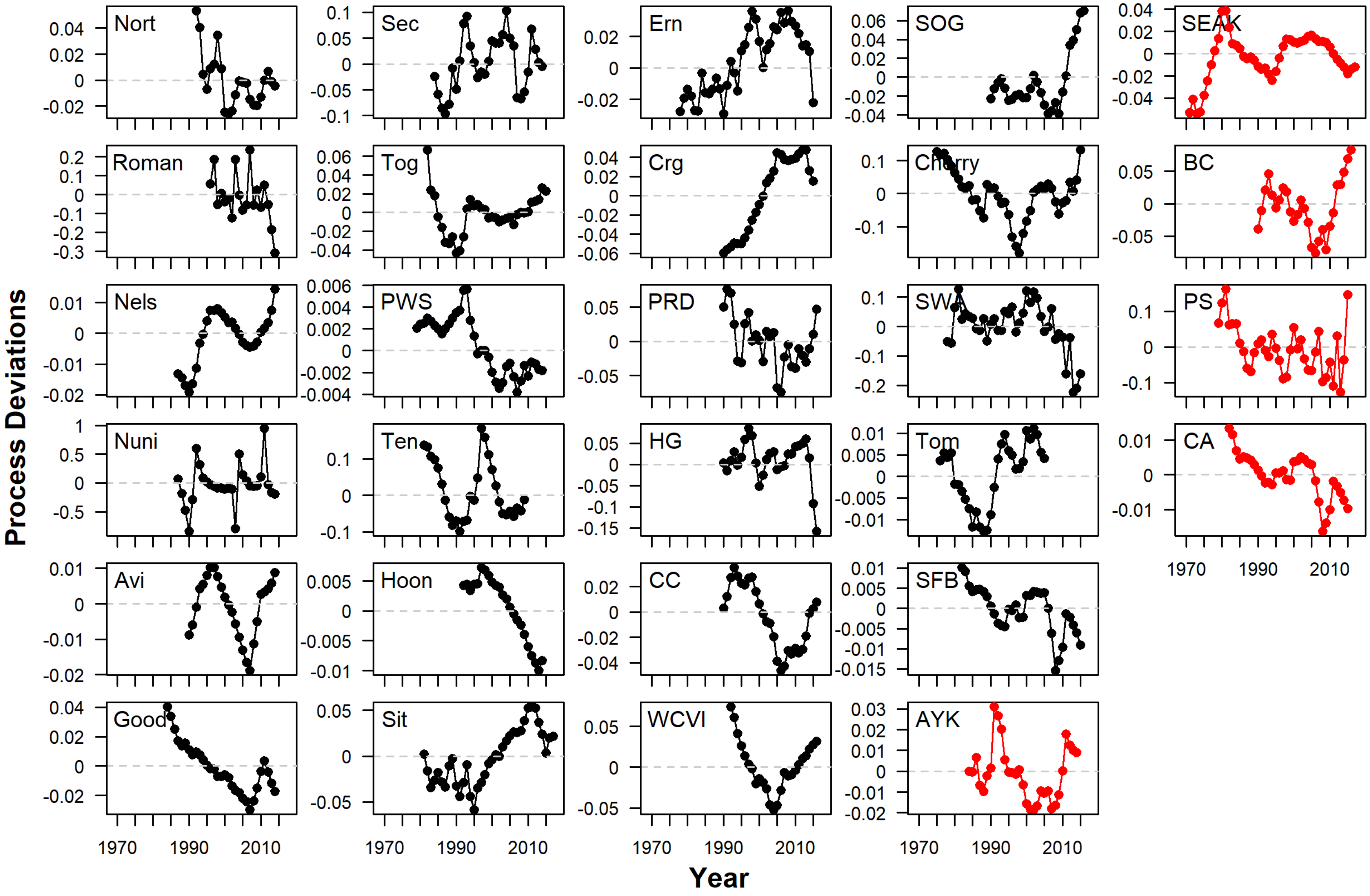


Figure 3. **Time series of process errors, $\vec{w}$, from a Schaefer model for 27 Pacific herring stocks. Red lines indicate stock aggregates.**

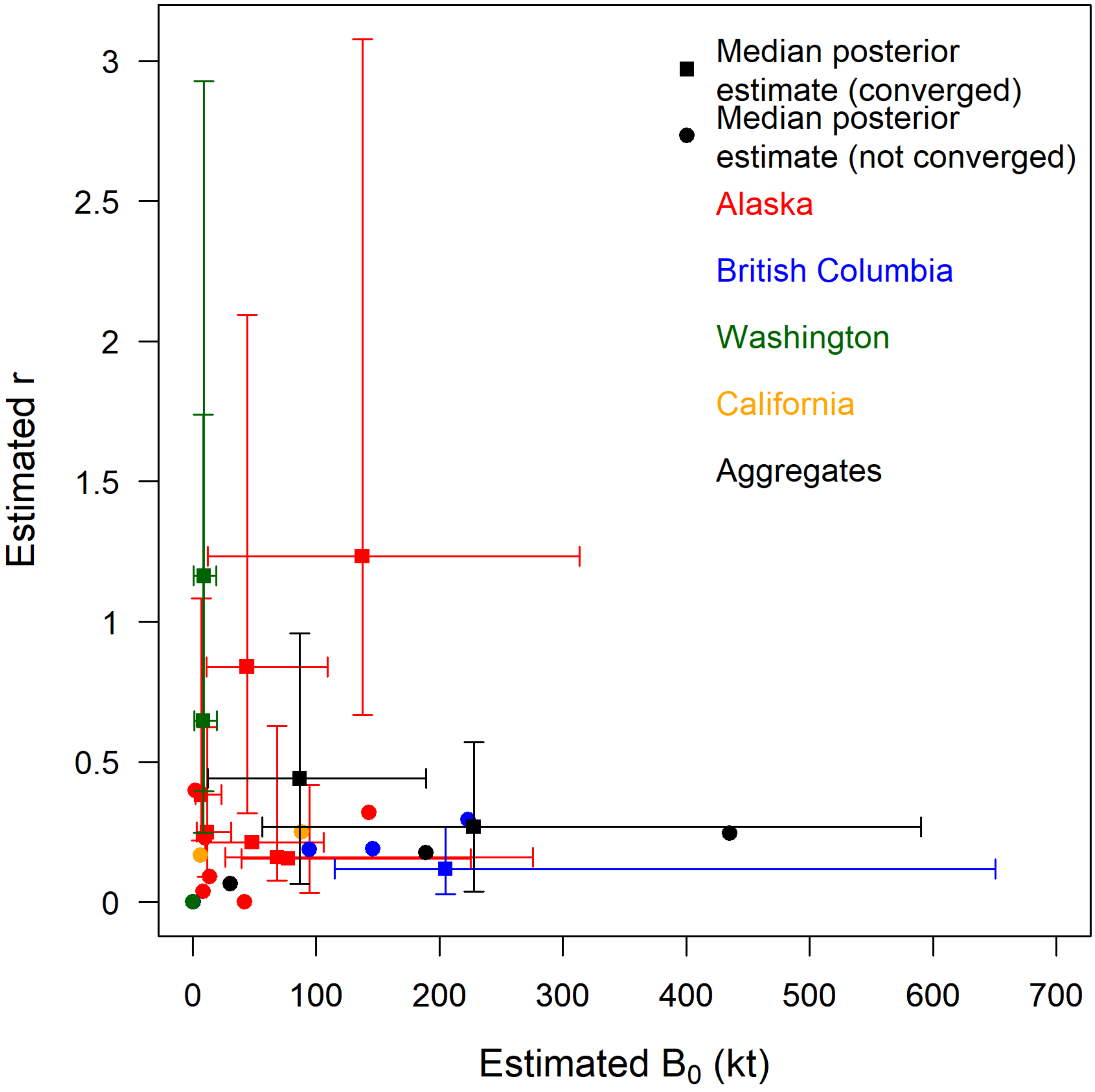


Figure 4. **Posterior r and B_0 estimates for 24 Pacific herring stocks and 5 stock aggregates. Squares indicate converged median posterior density estimates with error bars. Circles indicate non-converged median poster density estimates. Color designates location of stocks.**

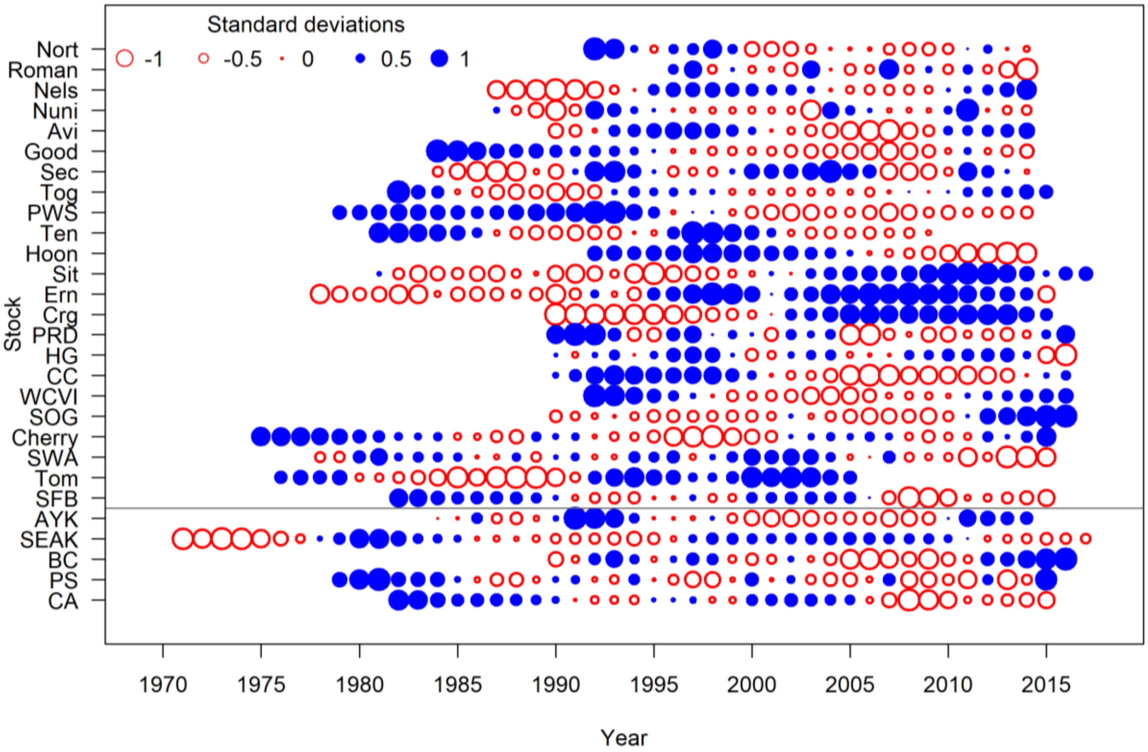


Figure 5. **Pacific herring time series from the Schaefer surplus production model process errors. Open circles (red) represent negative values and filled circles (blue) indicate positive values. Horizontal line indicates break for stock aggregates.**

Common stock productivity trends

Large-scale spatial synchrony was not evident based on the correlations among $\vec{w}$ time series (Figure 5), but stocks in proximity have similar trends over particular periods in their time series. In particular, trends between nearby stocks were prevalent during positive production periods (Figure 5). There was a period of positive production during the early part of the time series for all B.C stocks; however, the synchrony did not exist throughout the entire time series for all stocks (Figure 5). Prince Rupert District, Central Coast, West Coast Vancouver Island and Strait of Georgia had some degree of synchrony during the later part of the time series. These trends were opposite of three stocks in Southeast Alaska. Sitka Sound (Sit), Ernest Sound (Ern), and Craig/Klawock (Crg) had synchrony throughout the time series, which did not extend to the other Southeast Alaska stocks in Tenakee Inlet (Ten) and Hoonah Sound. Prince William Sound and Goodnews Bay (Good) had similar trends throughout the time series. The

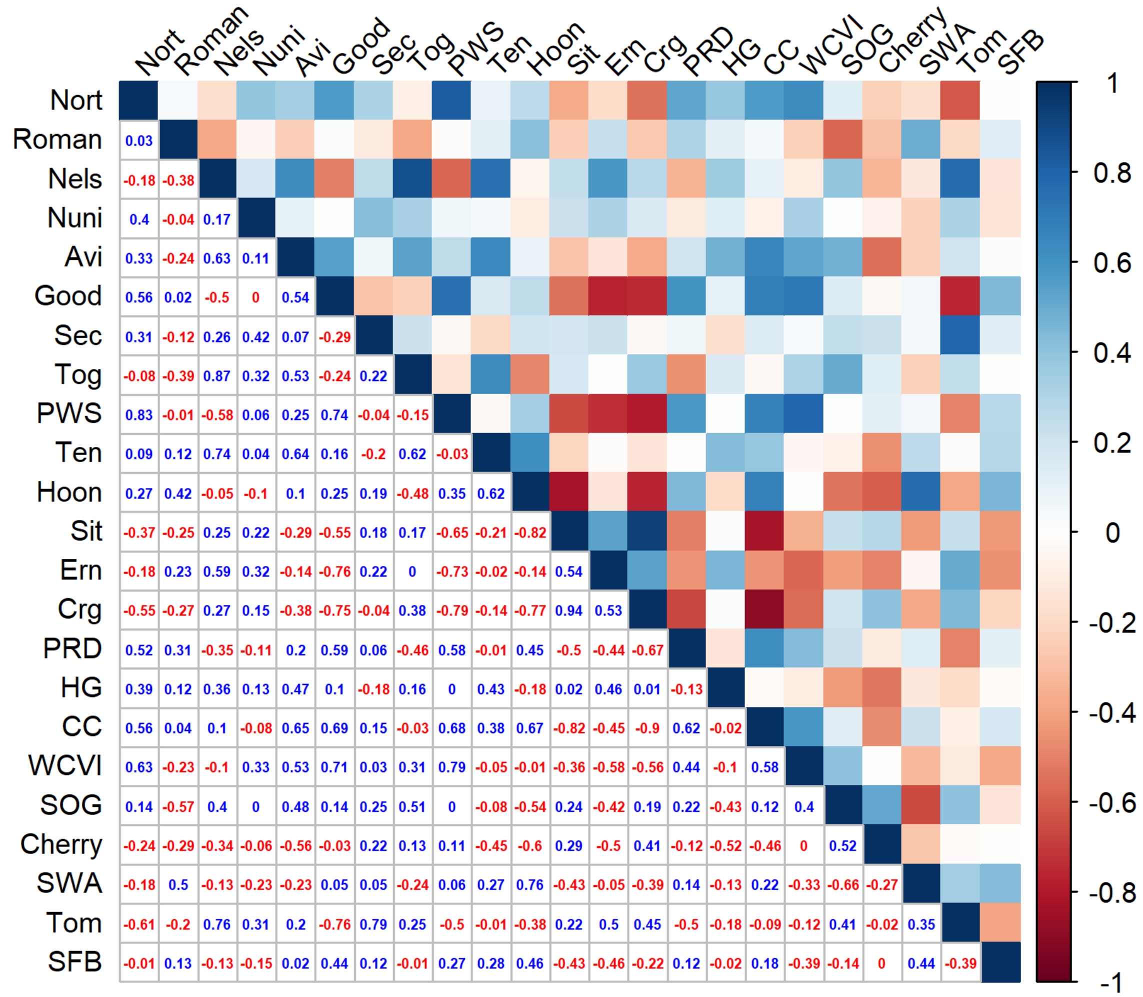
Arctic-Yukon-Kuskokwim and Southeast Alaska (SEAK) stock groups had opposite patterns of production (Figure 5).

Spatial covariation

Productivity indices for herring stocks in the northeast Pacific were, on average, not correlated (mean correlation across all comparisons $\bar{r}$ = 0.030; Figure 6). However, the larger stock aggregates showed evidence of correlation. Arctic-Yukon-Kuskokwim was strongly negatively correlated (r = -0.716) with the Southeast Alaska stock group and had a strong positive correlation (r = 0.554) with the British Columbia (BC) stock group (Figure 7). Southeast Alaska and British Columbia had a strong negative correlation (r = -0.642) (Figure 7). Puget Sound (PS) and California (CA) stock grouping had only weak correlations with all stock groups (Figure 7).

In Southeast Alaska, Hoonah Sound and Tenakee Inlet, which are 20 km apart, were highly correlated (r = 0.62), but both stocks were negatively correlated with Sitka Sound (61 km and 76 km, respectively; r = -0.82 and -0.21, respectively). However, Sitka Sound was highly positively correlated with Ernest Sound, 237 km away, and Craig/Klawock, 232 km away (r = 0.54 and 0.94, respectively; Figure 6).

The British Columbia stock aggregate showed a significant positive correlation between four of the five individual stocks when compared to the aggregate and to each individual population. The only British Columbia stock that did not show a significant or positive correlation with the stock aggregate was Haida Gwaii (HG) (r = -0.22), which, instead, showed a weak positive correlation with the Southeast Alaska stock group (r = 0.24).



	Nort	Roman	Nels	Nuni	Avi	Good	Sec	Tog	PWS	Ten	Hoon	Sit	Ern	Crg	PRD	HG	CC	WCVI	SOG	Cherry	SWA	Tom	SFB
Nort																							
Roman	0.03																						
Nels	-0.18	-0.38																					
Nuni	0.4	-0.04	0.17																				
Avi	0.33	-0.24	0.63	0.11																			
Good	0.56	0.02	-0.5	0	0.54																		
Sec	0.31	-0.12	0.26	0.42	0.07	-0.29																	
Tog	-0.08	-0.39	0.87	0.32	0.53	-0.24	0.22																
PWS	0.83	-0.01	-0.58	0.06	0.25	0.74	-0.04	-0.15															
Ten	0.09	0.12	0.74	0.04	0.64	0.16	-0.2	0.62	-0.03														
Hoon	0.27	0.42	-0.05	-0.1	0.1	0.25	0.19	-0.48	0.35	0.62													
Sit	-0.37	-0.25	0.25	0.22	-0.29	-0.55	0.18	0.17	-0.65	-0.21	-0.82												
Ern	-0.18	0.23	0.59	0.32	-0.14	-0.76	0.22	0	-0.73	-0.02	-0.14	0.54											
Crg	-0.55	-0.27	0.27	0.15	-0.38	-0.75	-0.04	0.38	-0.79	-0.14	-0.77	0.94	0.53										
PRD	0.52	0.31	-0.35	-0.11	0.2	0.59	0.06	-0.46	0.58	-0.01	0.45	-0.5	-0.44	-0.67									
HG	0.39	0.12	0.36	0.13	0.47	0.1	-0.18	0.16	0	0.43	-0.18	0.02	0.46	0.01	-0.13								
CC	0.56	0.04	0.1	-0.08	0.65	0.69	0.15	-0.03	0.68	0.38	0.67	-0.82	-0.45	-0.9	0.62	-0.02							
WCVI	0.63	-0.23	-0.1	0.33	0.53	0.71	0.03	0.31	0.79	-0.05	-0.01	-0.36	-0.58	-0.56	0.44	-0.1	0.58						
SOG	0.14	-0.57	0.4	0	0.48	0.14	0.25	0.51	0	-0.08	-0.54	0.24	-0.42	0.19	0.22	-0.43	0.12	0.4					
Cherry	-0.24	-0.29	-0.34	-0.06	-0.56	-0.03	0.22	0.13	0.11	-0.45	-0.6	0.29	-0.5	0.41	-0.12	-0.52	-0.46	0	0.52				
SWA	-0.18	0.5	-0.13	-0.23	-0.23	0.05	0.05	-0.24	0.06	0.27	0.76	-0.43	-0.05	-0.39	0.14	-0.13	0.22	-0.33	-0.66	-0.27			
Tom	-0.61	-0.2	0.76	0.31	0.2	-0.76	0.79	0.25	-0.5	-0.01	-0.38	0.22	0.5	0.45	-0.5	-0.18	-0.09	-0.12	0.41	-0.02	0.35		
SFB	-0.01	0.13	-0.13	-0.15	0.02	0.44	0.12	-0.01	0.27	0.28	0.46	-0.43	-0.46	-0.22	0.12	-0.02	0.18	-0.39	-0.14	0	0.44	-0.39	

Figure 6. **Pairwise correlation coefficients between Pacific herring process error deviation time series. Negative correlations between stocks are shown in shades of red and positive correlations are shown in shades of blue. Stocks are arranged north (top, left) to south (bottom, right).**

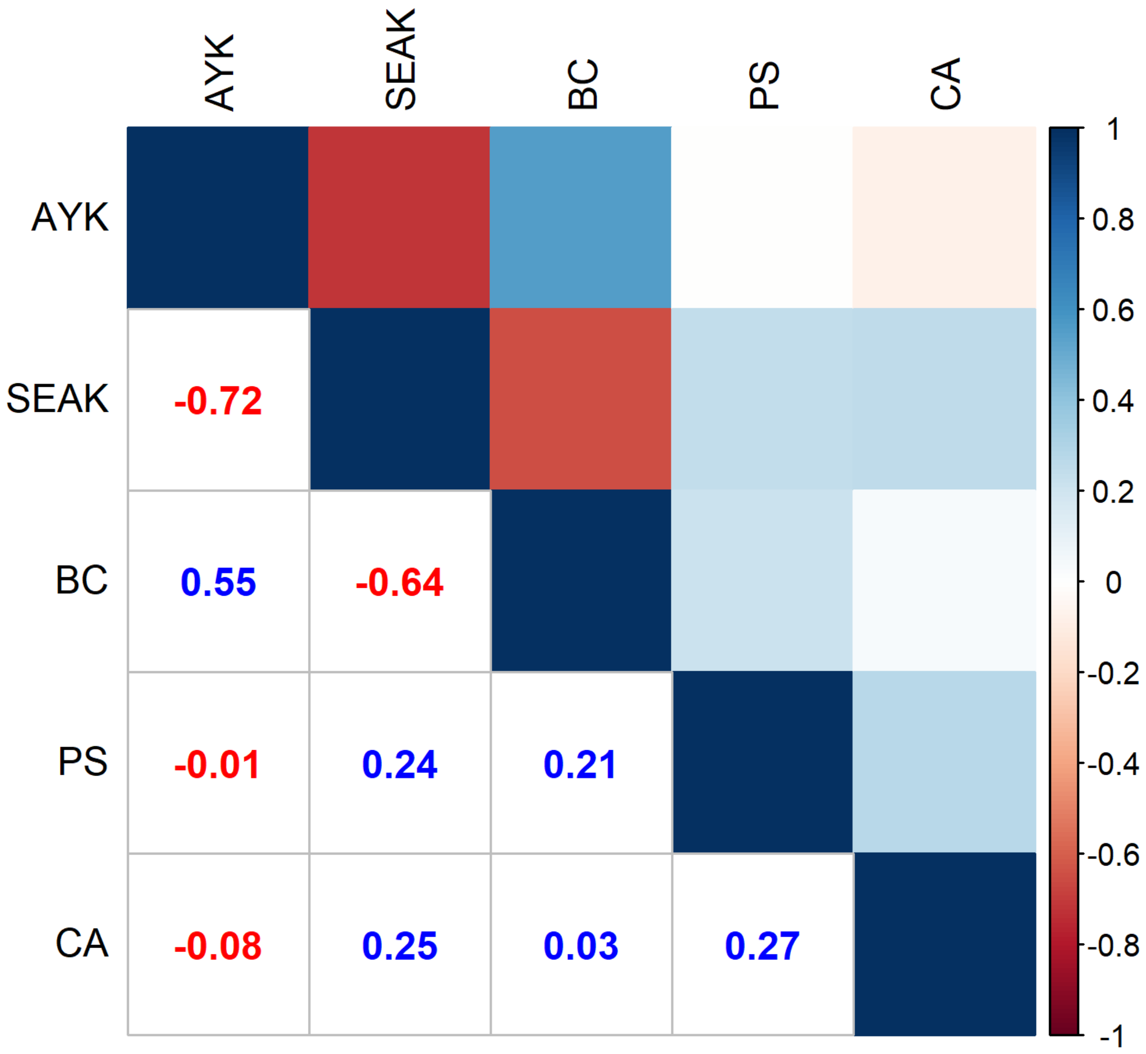


Figure 7. **Pairwise correlation coefficients between Pacific herring stock aggregates process error deviation time series. Negative correlations between stocks are shown in shades of red and positive correlations are shown in shades of blue. Stocks are arranged north (top, left) to south (bottom, right).**

There was weak positive correlation for productivity indices of herring stocks in the northeast Pacific (Figure 8). The fitted covariance function indicated weak covariation across all distances among stocks, hovering around zero as distance between stock increased. Correlation at zero distance (i.e., the y intercept of the covariance function) was weakly positive (CZD = 0.19, 97.5% CI = -0.01-0.40).

There was a small increase in correlation between 2,000-3,000 km distance between spawning grounds (Figure 8). These positive correlations existed between the Arctic-Yukon-Kuskokwim stock grouping and the British Columbia stock grouping (i.e., 2,377 km apart; Figure 7). These two stock groupings had a strong positive correlation (r = 0.55). When examined at the individual stock level, correlations existed between the two regions, though were not as strong at the individual stock level.

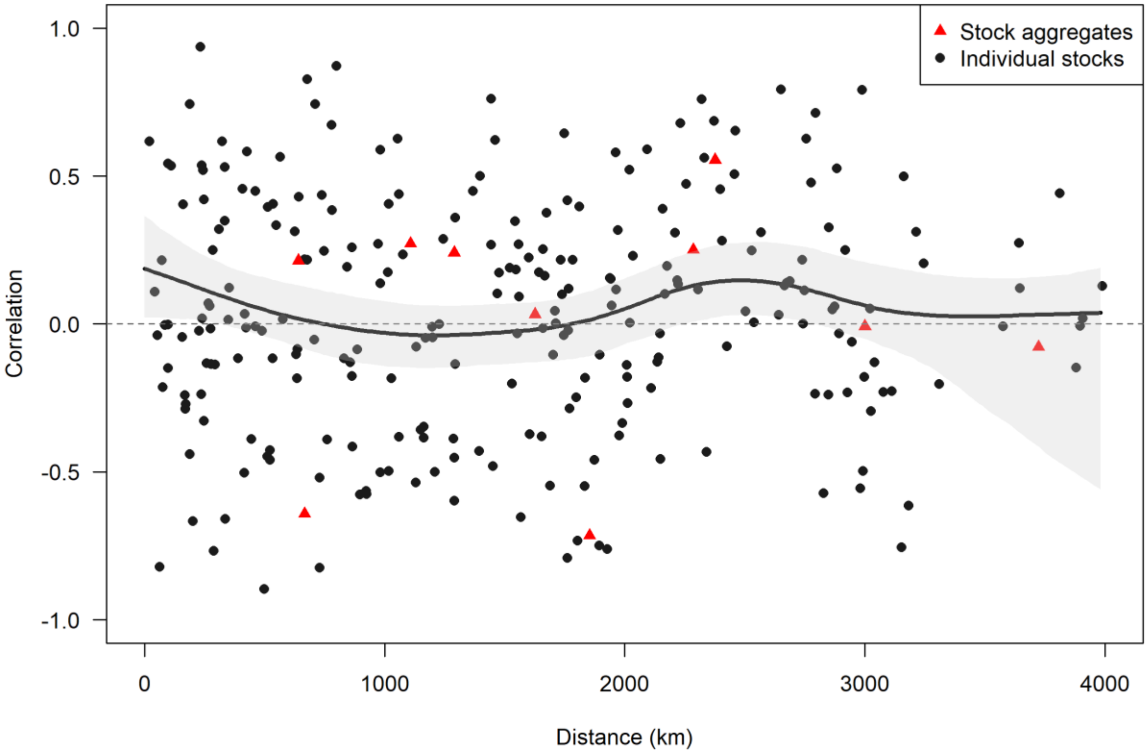


Figure 8. **Pairwise correlation as a function of distance between locations of data pairs among Pacific herring process errors time-series. Solid curve represents the estimated smooth nonparametric covariance function, with 95% confidence band shown with the grey polygon. Red triangles indicate stock aggregates.**

Discussion

Marine fish population dynamics are influenced at multiple spatial scales by oceanic conditions, yet linking ocean processes to fish productivity, especially for forage fish species such as Pacific herring, can be challenging without understanding the scale of connectivity among stocks (Mueter et al. 2002, 2007). A useful precursor to analyzing environmental effects on stock dynamics is to determine spatial and temporal variation in processes among stocks in nearby areas using correlation and covariation analysis (Peterman et al. 1998). Understanding the spatial scale of covariation among fish stocks can assist in providing more robust assessment models linking oceanic variation to stock productivity (Mueter et al. 2002).

I examined the spatial extent of covariation in productivity among Pacific herring stocks in the northeast Pacific Ocean to help identify the spatial scale at which oceanic processes are influencing herring population dynamics. The index of productivity provided by the process error term used in the Schaefer model accounts for density-independent effects on abundance, provides an estimate of variation not accounted for in the best-fit abundance models for each stock, and filters out effects of fishing on populations (Schaefer 1954; Hilborn and Walters 1992; Polacheck et al. 1993). Assumptions implicit in the assessment models, such as time-varying natural mortality and weight-at-age (DFO 2019), and quality of data used by management agencies might affect the results of the analysis; however, it is useful to look at stock productivity for Pacific herring using process errors because stocks are monitored and assessed in different ways and estimates of recruitment are not available for roughly half of the stocks analyzed.

My results suggest that oceanic processes influencing year-to-year variability in productivity of Pacific herring operate at small spatial scales. Spatial covariation at zero distance was only slightly greater than zero, indicating that productivity is more likely independent among stocks. This was evident both positive and negative correlations among stocks within the same regions. However, the low correlation at zero distance could represent variability caused by sampling error or spatial dependence at scales different than the available data (Cressie 1993; Malick et al. 2015a).Habitat features, contributing to oceanographic mixing, could explain the variation in regional correlation patterns, providing a useful next step in investigation. In the 5 Southeast Alaska populations spawning occurs within differing habitats, impacted by oceanographic mixing. The Hoonah Sound and Tenakee Inlet stocks spawn primarily in fjords (Thornton et al. 2010; Hebert 2017) where there is high water column stratification (Farmer and Freeland 1983; Cottier et al. 2010); whereas, the other three stocks in Southeast Alaska spawn in larger bays or sounds (Thornton et al. 2010; Hebert 2017) which have more overturning circulation (Sundberg 1981; Weingartner et al. 2009) and are more connected to the open ocean.

Spatial correlations at greater distance (e.g., 2,000-3,000 km) increased slightly. Puget Sound stock aggregate and the California stock aggregate were not strongly correlated with any stock groups, which could be due to their spatial isolation. The Arctic-Yukon-Kuskokwim stock aggregate was strongly negatively correlated with the Southeast Alaska stock aggregate suggesting differing responses to oceanic processes are driving stock productivity. The British Columbia stock aggregate was also negatively correlated with the Southeast Alaska stock aggregate, but moderately positively correlated with the Arctic-Yukon-Kuskokwim stock. Numerous mechanisms account for the correlations among the Arctic-Yukon-Kuskokwim stock, the B.C. coast, and Southeast Alaska stock aggregates. Localized adaptation to sea surface temperatures, ocean currents, strength of localized upwelling (Thomson 1981; Danielson et al. 2014) are possible hypotheses, but the correlation among stock aggregates is likely a combination of interacting mechanisms, such as sea-surface temperature and current strength.

The British Columbia stock aggregate showed a significant positive correlation between four of the five individual stocks. This suggests connection among stocks, which could indicate an oceanic process linking these 4 populations or population links as identified through genetic analysis (Haegele and Schweigert 1985; Beacham et al. 2008). The only British Columbian stock that did not show a significant or positive correlation with the stock aggregate was Haida Gwaii, which showed a weak positive correlation with the Southeast Alaska aggregate stock group. Decreasing productivity trends exist for 4 of 5 Southeast Alaska stocks, which could point to similar oceanographic processes or habitat features driving similar production between the two regions, but would require further investigation.

When examined at the individual stock level, correlations were not as strong as the aggregates for most individual stocks, suggesting small-scale mechanisms driving dynamics at the local level. The discrepancy between stock aggregates and individual stocks could be explained through portfolio effects (Figge 2004), where a diversity of stocks is more stable across the aggregate of stocks (Schindler et al. 2010). In fact, biomass observations were considerably less stable as individual stocks for BC than as the stock aggregate (Table A1). Evidence of portfolio effects existed for all stock aggregates (Table A1) and has been previously identified for Pacific herring Puget Sound (Siple and Francis 2016). Maintaining diversity and variability in spawning stock is critical for maintaining stability among populations (Siple and Francis 2016). The small difference in variability between the Southeast Alaska stock aggregate and individual stocks (Table A1) could be due to the number of stocks included in the analysis. There are more individual stocks in Southeast Alaska than analyzed here (Hebert 2017), but data was unavailable from all stocks to perform the analysis.

The local and regional correlation among stocks could be considered in management decisions and the delineation of management areas particularly if managers believe that sub-stocks exist (Siple and Francis 2016; Punt et al. 2018). Developing spatially structured population dynamics models at the scale at which stock correlations are present could help the local-scale management of harvest efforts (Figge 2004; Schindler et al. 2010; Benson et al. 2015) and buffer populations from collapse or loss of stock structure, especially if portfolio effects might exist (Beverton 1990; Essington et al. 2015; Siple and Francis 2016).

A challenge to understanding the correlation patterns among nearby stocks is that commercial fisheries could mask or exacerbate the effects of ocean conditions (Essington et al. 2015). Forage fish such as herring are particularly vulnerable to fishing-induced collapses because of their school behavior and spatial distributions (Beverton 1990). Collapses of Pacific herring were evident during the reduction fishery (i.e., 1880-1969) where many stocks were at their lowest recorded biomass (Thornton et al. 2010), though stocks have recovered since that time. Commercial fisheries have existed on all of the stocks analyzed and many stocks are currently experiencing fishing pressure. Using the productivity or process error term, $\vec{w}$, in population dynamics models could help avoid overfishing and population collapses in years with low or decreasing productivity by identifying when fishing pressure should be reduced (Essington et al. 2015).

Limitations

Achieving reliable estimates of parameters r and B_0 from MCMC simulations or maximum posterior density estimates can be challenging based on the available data for a stock. MCMC simulations can be unreliable due to non-representative sampling from the posterior distribution, e.g., lack of chain convergence indicates the MCMC simulation did not fully explore the posterior distribution (Gelman et al. 1995). Poor or lacking MCMC convergence could arise if the Schaefer model is an inappropriate structure for biomass dynamics of herring. For instance, the Schaefer model assumes that herring stocks follow a symmetric population growth function of biomass (Hilborn and Walters 1992). This simple form is intended to capture the main effect of fishing on spawning biomass and production. Changes in biomass independent of the underlying Schaefer growth model would then be attributable to external forcing of population growth (Schaefer 1954). If fishing is, indeed, the dominant effect driving interannual variability or trends in herring biomass, then the process error estimates would be small and probably weakly estimated, resulting in poor MCMC convergence. For many stocks, reduced fishing pressure was followed by increasing biomass in subsequent years, as predicted by the Schaefer model (see WCVI and CC in Figure 2); however, in some stocks, such as Cherry Point and Haida Gwaii (see Cherry and HG in Figure 2), stock biomass did not recover, or recovered far more slowly than predicted, which could indicate that forces external to the Schaefer model structure are affecting recovery for those stocks. In these cases, poor MCMC convergence is likely to occur on Schaefer model parameters r and B_0 because of weak association of the model predictions to the actual biomass data.

Additionally, convergence could be affected by the input data used. Spawning biomass estimates used were a combination of stock assessment model outputs and surveyed biomass estimates. These biomass accounting methods have differing degrees of observation error associated with them, which could in influencing MCMC simulation convergence and the variability in process errors. Of the 11 stocks that used survey methods to estimate spawning stock biomass, 6 did not converge on estimates of r and B_0, and 6 had high or moderate interannual variability in process errors. Whereas, for the 13 stocks where the biomass accounting method included modelling efforts, only two stocks (PRD and Ern) had high interannual variability. The differences in process error variability could be attributed to the biomass accounting model is filter out process error, resulting in a smoothing effect from year to year.

Alternative population dynamics, as well as model structures may improve parameter estimation across herring stocks in the northeast Pacific. For example, a delay-difference population dynamics model could bridge the gap between age-structured models and simple surplus-production models by retaining stock-specific parameters for recruitment, growth, and natural mortality (Hilborn and Walters 1992; Meyer and Millar 1999; Millar and Meyer 2000), as well as accounting for latitudinal differences in age-at-maturity. A hierarchical statistical modelling approach for the r and B_0 parameters (or stock-recruit parameters of a delay-difference model) would enable information sharing across stocks such that stocks with more precise parameter estimates provide information about parameters for stocks with poor data (Gelman 2006; Jiao et al. 2011; Punt et al. 2011). Hierarchical models can also be developed for process error parameters (Johnson and Cox 2019), which could provide a way to also incorporate shared oceanographic predictors.

Several factors can create spurious correlations among process errors of stocks and stock aggregates, masking the real correlation patterns. For example, the largest contributing stock typically drives the time-series trend of an aggregate stock, as seen in the Southeast Alaska and California Coast stock aggregates. In these cases, the main correlations among the stock aggregates would mimic the largest stocks, not the actual correlations among the smaller individual stocks. Simulation studies examining the power of process error correlation analyses under different assumptions of stock groupings and aggregations would provide a way to determine how aggregating biomass data across stocks affects estimation correlation patterns and inferences about spatial scales of correlation (Pyper et al. 2002).

Conclusions

My results show weak spatial correlation existed among Pacific herring stock productivity indices, suggesting small-scale oceanic processes are driving stock dynamics. Geographic features that are similar among spawning sites may help explain local correlation variation. Oceanic processes can only explain covariation in herring productivity to the extent that the scale of oceanographic variables is similar to that of herring productivity (Mueter et al. 2002).

My results offer a first step in identifying spatial scales of productivity for Pacific herring stocks that can inform future work on understanding mechanisms driving herring productivity in the northeast Pacific Ocean. For some stocks, such as West Coast Vancouver Island, fishing pressure has a direct influence on stock productivity, whereas for others, such as Cherry Point, fishing pressure can not accurately describe the patterns in productivity, which suggests an oceanic process or geographic feature is driving production. Future studies of Pacific herring population dynamics should focus on small-scale processes, such as local habitat and oceanographic features.

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Appendix

Methods

Portfolio effects can be calculated simply by comparing the coefficient of variation (CV) for aggregate populations and each subpopulation (Schindler et al. 2010), though a more robust method to analyze portfolio effects is account for the variation in size of the subpopulations (Siple and Francis 2016). Interannual variability for spawning stock biomass was calculated as the coefficient of variation for each individual stock and each of the 5 stock aggregates.

Results

Spawning stock biomass within stock aggregates was considerably less variable (average coefficient of variation, CV = 49%) than the individual stocks (average CV = 62%; Table A1). The largest interannual variability was seen in the Puget Sound stock aggregate (aggregate CV = 22%, individual average CV = 48%; Table A1). For the British Columbia stock aggregate, the stock aggregate was 17% less variable than the individual stocks (aggregate CV = 31%, individual average CV = 48%; Table A1). In the Arctic-Yukon-Kuskokwim stock aggregate, the CV was 58%, 15% less variable than the individual stocks (average CV = 72%; Table A1).

In Southeast Alaska and California, not all individual stocks that are monitored by agencies were included in the analysis for portfolio effects, reducing the variability difference between individual stocks and the stock aggregate. For the California coast stock aggregate, the difference between the stock aggregate (CV = 70%) was smaller than other groups (average individual CV = 82%; Table A1). In Southeast Alaska, the aggregate was only 1% less variable (CV = 63%) than the average of the individual stocks (CV = 64%; Table A1).

Table A1. Coefficient of variation in observed biomass estimates for all stocks and stock aggregates.

Stock Code	Mean Biomass (kt)	SD (kt)	CV	Average CV
Nort	37.543	8.778	23%	72%
Roman	3.971	0.805	20%	
Nels	7.306	9.483	130%	
Nuni	4.285	4.651	109%	
Avi	3.083	2.044	66%	
Good	7.647	8.087	106%	
Sec	6.654	3.498	53%	
AYK	58.688	33.802		58%
Tog	116.570	22.366	19%	
PWS	51.360	52.515	102%	
Ten	5.172	3.470	67%	64%
Hoon	5.579	4.884	88%	
Sit	52.635	22.852	43%	
Ern	2.353	1.764	75%	
Crg	12.585	6.018	48%	
SEAK	59.347	37.561		63%
PRD	21.722	5.327	25%	48%
HG	10.341	7.725	75%	
CC	22.494	10.943	49%	
WCVI	19.082	12.691	67%	
SOG	74.855	18.185	24%	
BC	150.715	46.911		31%
Cherry	5.158	3.305	64%	48%
NWA	5.600	2.712	48%	
SWA	6.776	2.115	31%	
PS	13.606	2.936		22%
Tom	4.397	3.907	89%	82%
SFB	34.878	26.058	75%	
CA	37.542	26.332		70%