

Historical trends in productivity of 120 Pacific pink, chum, and sockeye salmon stocks reconstructed by using a Kalman filter

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Abstract: Temporal trends in productivity of Pacific salmon (*Oncorhynchus* spp.) stocks are important to detect in a timely and reliable manner to permit appropriate management responses. However, detecting such trends is difficult because observation error and natural variability in survival rates tend to obscure underlying trends. A Kalman filter estimation procedure has previously been shown to be effective in such situations. We used it on a Ricker spawner–recruit model to reconstruct indices of annual productivity (recruits per spawner (R/S) at low spawner abundance) based on historical data for 120 stocks of pink (*Oncorhynchus gorbuscha*), chum (*Oncorhynchus keta*), and sockeye (*Oncorhynchus nerka*) salmon. These stocks were from Washington, British Columbia, and Alaska. The resulting estimated temporal trends in productivity show large changes (on average 60%–70% differences in R/S and average ratios of highest to lowest R/S between 5.4 and 7.9 for the three species). Such changes suggest that salmon stock assessment methods should take into account possible nonstationarity. This step will help provide scientific advice to help managers to meet conservation and management objectives. The Kalman filter results also identified some stocks that did not share temporal trends with other stocks; these exceptions may require special monitoring and management efforts.

Résumé : Il est important de détecter les tendances temporelles de la productivité des stocks de saumons du Pacifique (*Oncorhynchus* spp.) au moment opportun et de façon fiable pour permettre des actions de gestion appropriées. Il est cependant difficile de détecter ces tendances, car les erreurs d'observation et la variation naturelle tendent à masquer les tendances sous-jacentes. On a montré antérieurement qu'une méthode d'estimation à filtre de Kalman peut être efficace dans de tels cas. Nous l'utilisons donc dans un modèle de reproducteurs–recrues de Ricker afin de reconstituer les indices de productivité annuelle (recrues par reproducteur (R/S) dans des conditions de faible abondance des recrues) d'après des données du passé sur 120 stocks de saumons roses (*Oncorhynchus gorbuscha*), kéta (*Oncorhynchus keta*) et rouges (*Oncorhynchus nerka*). Ces stocks proviennent de l'état de Washington, de la Colombie-Britannique et de l'Alaska. Les tendances temporelles estimées de la productivité que nous obtenons montrent d'importants changements (en moyenne, des différences de 60%–70% dans le nombre de R/S et des rapports moyens entre les R/S les plus élevés et les plus bas de 5,4 à 7,9 chez les trois espèces). De tels changements indiquent que les méthodes d'évaluation des stocks de saumons devraient tenir compte de ce que les populations peuvent ne pas être stationnaires. Cette procédure servira à fournir des avis scientifiques aux gestionnaires afin de leur permettre de rencontrer leurs objectifs de conservation et de gestion. Les résultats au filtre de Kalman ont aussi identifié certains stocks qui ne partagent pas les mêmes tendances temporelles que les autres stocks; ces exceptions peuvent requérir des efforts particuliers de surveillance et de gestion.

[Traduit par la Rédaction]

Introduction

Objectives related to the management of Pacific salmon (*Oncorhynchus* spp.) on the west coast of North America often differ among fisheries managers, nongovernmental

organizations, and harvesters. Nevertheless, these groups generally share a common interest in maintaining productive, abundant wild salmon stocks over the long term. There is thus a mutual desire to quickly and correctly detect changes in productivity and abundance over time, including both rapid changes to new persistent levels and gradual long-term trends. Management agencies also need to detect such changes so that appropriate action can be taken to prevent conservation crises when productivity is low or to reduce foregone economic and social benefits from fishing in periods when productivity is high. Furthermore, there is increasing interest in acting to help maintain biological diversity by preserving numerous small or less productive stocks of a given species, in case they might respond differently to environmental changes (e.g., Hilborn et al. 2003; Fisheries and Oceans Canada 2005).

Unfortunately, several factors complicate the task of reliably estimating time trends in salmon abundance (spawners or adult recruits) and productivity (recruits per spawner at

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low spawner abundance). For instance, large natural inter-annual variation tends to mask such trends. Furthermore, salmon data (especially for spawner abundance and in some cases catch as well) often contain unknown, but probably substantial, observation error that arises from several sources (e.g., bias and imprecision in sampling methods and in human perceptions). This combination of observation errors and high-frequency, year-to-year variation in salmon survival rates tends to make it difficult to detect true underlying changes in abundance or productivity.

New opportunities are emerging for dealing effectively with this challenge of reliably estimating temporal trends. In particular, the compilation of salmon and environmental data into large databases covering broad geographical areas has made investigations possible of large-scale patterns of variation in recruitment, catches, indices of survival rates, and also of potential environmental drivers of those changes. Such analyses have been aided by advanced statistical methods such as spatial correlation analysis (Pyper et al. 2001, 2002), principal components analysis (Hare et al. 1999), mixed-effects models (Myers et al. 1997), and hierarchical models that assume some shared components of variability (Mueter et al. 2002; Su et al. 2004). Evidence to date shows a tendency for positive correlations between time series of productivity indices for salmon stocks whose juveniles migrate to the ocean within several hundred kilometres of one another (Peterman et al. 1998; Botsford and Paulsen 2000; Pyper et al. 2005). This effect of distance suggests that these stocks share common physical and biological factors that influence their survival, particularly in the late freshwater and early marine periods. Knowledge of such shared variation among salmon stocks has helped to formulate hierarchical Bayesian models that improve estimates of productivity (Su et al. 2004).

Comparative analyses have also highlighted individual stocks that do not share temporal patterns and trends in productivity that are otherwise common throughout their region (e.g., Pyper et al. 2002). These stocks might be more likely than others to continue to respond differently to future natural and human influences. This type of divergent behavior may arise from differences in life history characteristics or localized habitat conditions, as well as human disturbances. One example of the benefit of maintaining of such biological diversity is the large, commercially valuable fisheries on Bristol Bay, Alaska, where sockeye salmon have maintained a lengthy persistence despite large changes in the stock composition of catch over the last three decades (Hilborn et al. 2003).

Here we use the Kalman filter (Kalman 1960) to provide a broad perspective on temporal patterns in productivity of sockeye (*Oncorhynchus nerka*), pink (*Oncorhynchus gorbuscha*), and chum (*Oncorhynchus keta*) salmon stocks. Unlike the methods of analysis mentioned above, the Kalman filter separately estimates systematic time trends from short-term, nonsystematic variability. Though it has been applied relatively little in ecology so far, the Kalman filter has nonetheless proven useful for a variety of ecological problems

(Visser and Molenaar 1988; Pella 1993; Zeng et al. 1998). Stochastic computer simulations with known, user-defined, “true” underlying trends in productivity have previously shown the potential benefits of using a Kalman filter estimation procedure in conjunction with a Ricker stock-recruitment model (Peterman et al. 2000). Specifically, compared with the standard formulation and maximum-likelihood estimation of the Ricker model, Kalman filter estimation procedure can improve estimates of systematic underlying changes in mean productivity (i.e., the underlying temporal “signal”) amid a large amount of non-systematic, short-term variability (i.e., “noise”, composed of both natural variability and observation error) (Peterman et al. 2000). When used for reconstructing temporal patterns of productivity from historical data for sockeye salmon in Bristol Bay, Alaska, the Kalman filter also revealed clearer underlying trends than indicated by standard Ricker model estimates of productivity (Peterman et al. 2003).

The ability of the Kalman filter to estimate systematic changes in productivity is relevant because some strategic salmon management questions deal with setting long-term goals or modifying harvest policies in the presence of overarching changes in factors such as habitat or climate. Such questions are different from short-term ones faced annually by managers, who need to determine the coming year’s targets and regulations to achieve them. For the former, longer-term strategic questions, managers place higher priority on information about systematic temporal trends in productivity than on the high frequency noise of year-to-year variability. The properties of the Kalman filter noted above make this method well suited to such strategic management needs (Walters 1986; Peterman et al. 2000; Schnute and Kronlund 2002).

More specifically, our purpose was to apply the Kalman filter estimation procedure to examine temporal and spatial trends in productivity of salmon stocks of sockeye, pink, and chum from Washington, British Columbia (BC), and Alaska to address the following questions: (i) What are the spatial and temporal characteristics of historical productivity for salmon stocks in the study area? (ii) How do these patterns compare with those of the residuals from the standard Ricker model that assumes fixed parameters? (iii) Are there specific patterns or trends in productivity for specific stocks or groups of stocks that might indicate existing or potential future management opportunities or conservation concerns?

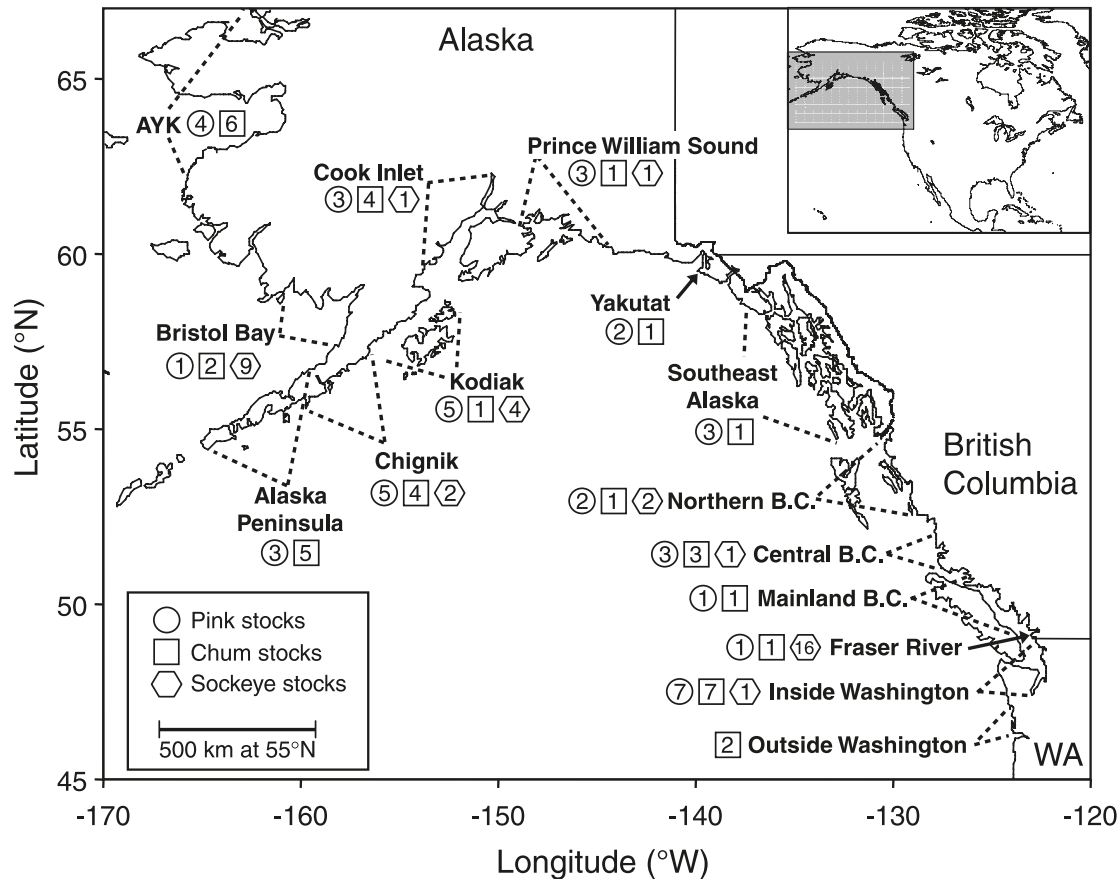
Materials and methods

Data

We used time series of age-specific abundance for spawners and adult recruits (catch plus escapement) for 120 wild stocks of Northeast Pacific salmon (Fig. 1), including pink salmon (Table 1; see also Pyper et al. 2001), chum salmon (Table 2; see also Pyper et al. 2002), and sockeye salmon (Table 3; see also Peterman et al. 1998; Pyper et al. 2005) (for complete data, see the Excel spreadsheet in the online supplementary material⁴). Data series were on average

⁴Supplementary data for this article are available on the journal Web site (cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3793. For more information on obtaining material refer to cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

Fig. 1. Locations of the 120 wild stocks of pink (*Oncorhynchus gorbuscha*), chum (*Oncorhynchus keta*), and sockeye (*Oncorhynchus nerka*) salmon used to calculate indices of productivity from historical time series of spawner and recruitment data. The number of separate stock data sets in a named region is indicated by a number within each species-specific symbol (see legend). AYK is the Arctic–Yukon–Kuskokwim region. Figure is adapted from Pyper et al. (2005).



28 years long for pink salmon stocks (ranging from 15 to 47 years), 27 years for chum salmon stocks (ranging from 15 to 35 years), and 39 years for sockeye salmon stocks (ranging from 15 to 47 years). To explore similarities in productivity trends across space, we organized data on stocks by geographic region (Tables 1–3; Fig. 1). The regions were in most cases the areas used for management decisions. Where necessary, for each stock, we aggregated groups of spawners together to ensure that catch data could be allocated with confidence to that stock (Pyper et al. 2001, 2002, and 2005). For consistency in this paper, we use the term stock to represent such aggregates of fish (e.g., Kvichak River sockeye salmon) and to recognize that stocks are usually composed of multiple spawning populations. “Regions” here contain one or more stocks. Although pink salmon move through the same physical environment every other year, we separated pink salmon data into odd- and even-year runs because, with their fixed 2-year life cycle, they represent separate entities that may encounter different ecological conditions.

Indices of productivity

Throughout this paper, we used the Ricker model (Ricker 1975) as the basic stock–recruitment model:

$$(1) \quad \log_e(R_t/S_t) = a + bS_t + v_t$$

where S_t is abundance of spawners in brood year t , R_t is abundance of adult offspring from those spawners (i.e., adult recruits of all ages), a is the productivity (in units of $\log_e(R/S)$) at low spawner abundance (i.e., in the absence of density dependence), b reflects density-dependent effects, and v_t is a normally distributed error term with a mean of zero and variance σ_v^2 .

From this starting point, we calculated two indices of change in salmon productivity. First, we fit the Ricker model to the entire spawner–recruitment time series for each stock using eq. 1; we then calculated the residuals. The time series of these residuals described year-to-year variability in productivity (in units of $\log_e(R/S)$) that is not explained by density-dependent effects of spawner abundance. These time series of Ricker residuals, scaled to a mean of zero and a standard deviation of one, constituted our first index of productivity.

Our second index was the annual a parameter value of a modified Ricker stock–recruitment model that was fit to the data using a Kalman filter estimation procedure. The strength of the Kalman filter lies in its ability to explicitly partition variation in $\log_e(R/S)$ into systematic trends over

Table 1. Summary of data sets for 43 wild pink salmon (*Oncorhynchus gorbuscha*) stocks used to compute spawner-to-recruit survival rate indices.

Region	Stock or district	Brood year	Run	<i>N</i>	<i>R</i>	<i>a_t</i>				<i>R/S</i>		Source ^a
						Mean	SD	Max.	Min.	Max.	Min.	
Washington	Nooksack ^b	1959–1995	Odd	19	154	1.85	0	1.85	1.85	6.4	6.4	1
	Skagit ^b	1959–1995	Odd	19	889	1.58	0	1.58	1.58	4.8	4.8	1
	Stillaguamish ^b	1959–1995	Odd	19	293	1.08	0	1.08	1.08	3.0	3.0	1
	Snohomish ^b	1959–1995	Odd	19	258	1.28	0	1.28	1.28	3.6	3.6	1
	Puyallup River ^b	1959–1995	Odd	19	46	1.37	0.34	1.70	0.44	5.5	1.6	1
	Hood Canal ^{b,c}	1959–1995	Odd	19	135	0.71	0.30	1.22	0.21	3.4	1.2	1
	Dungeness ^b	1959–1995	Odd	19	88	0.77	0	0.77	0.77	2.2	2.2	1
BC south coast	Fraser River ^b	1957–1995	Odd	20	10 815	1.62	0.08	1.69	1.47	5.4	4.4	2, 3
	South coast without Fraser River (statistical areas 12, 13, 15, 16) ^d	1954–1994	Even	21	2 439	1.51	0	1.51	1.51	4.5	4.5	4, 5
BC central coast	Statistical area 10	1950–1995	Odd	23	32	1.25	0.17	1.39	0.84	4.0	2.3	6, 7
			Even	23	44	2.01	0.47	2.80	1.24	16.4	3.5	6, 7
	Statistical area 9	1950–1996	Odd	23	102	1.42	0.26	1.77	0.95	5.9	2.6	6, 7
			Even	24	409	1.72	0.29	2.12	1.26	8.3	3.5	6, 7
	Statistical area 8	1950–1996	Odd	23	1 299	0.93	0	0.93	0.93	2.5	2.5	6, 7
			Even	24	4 050	1.53	0	1.53	1.53	4.6	4.6	6, 7
BC north coast	Statistical area 6	1950–1995	Odd	23	1 057	1.32	0.37	2.02	0.73	7.5	2.1	6, 7
			Even	23	2 987	1.62	0	1.62	1.62	5.1	5.1	6, 7
	Statistical area 2E	1950–1995	Odd	23	49	0.84	0.57	1.73	−0.07	5.6	0.9	6, 7
			Even	23	838	1.43	0	1.43	1.43	4.2	4.2	6, 7
Southeast Alaska	Southern (districts 101–108)	1960–1996	Odd	18	29 187	2.30	0.88	3.49	0.86	32.9	2.4	8
			Even	19	32 379	1.69	0.30	2.41	1.29	11.1	3.6	8
	Northern inside (districts 109–112, 114, 115)	1960–1996	Odd	18	12 446	1.52	0.37	2.03	0.87	7.6	2.4	8
			Even	19	12 089	1.38	0.35	1.98	0.81	7.2	2.3	8
	Northern outside (district 113)	1960–1996	Odd	18	3 996	0.84	0.06	0.94	0.75	2.6	2.1	8
			Even	19	2 381	0.31	0	0.31	0.31	1.4	1.4	8
Yakutat	Situk River	1962–1990	Odd	13	227	1.57	0.25	1.83	1.12	6.2	3.1	8, 9
			Even	12	179	1.42	0.07	1.51	1.30	4.5	3.7	8, 9
	Humpy Creek	1972–1992	Odd	10	111	1.99	0.47	2.59	1.16	13.4	3.2	8, 9
			Even	11	47	1.43	0	1.43	1.43	4.2	4.2	8, 9
Prince William Sound	Eastern district	1967–1996	Odd	15	3 474	1.65	0	1.65	1.65	5.2	5.2	10
			Even	15	3 477	2.38	0.60	3.03	1.27	20.8	3.5	10
	Montague district	1971–1996	Odd	13	483	1.49	0.31	1.93	1.07	6.9	2.9	10
			Even	13	121	1.28	0.86	3.13	−0.53	22.9	0.6	10
	Southeastern district	1967–1996	Odd	15	1 440	1.79	0.74	2.90	0.58	18.1	1.8	10
			Even	15	518	1.18	0.74	2.48	0.11	12.0	1.1	10

Table 1 (continued).

Region	Stock or district	Brood year	Run	N	R	a_t				R/S		Source ^a
						Mean	SD	Max.	Min.	Max.	Min.	
Cook Inlet	Southern district ^e	1960–1996	Odd	18	246	1.03	0	1.03	1.03	2.8	2.8	11
			Even	19	146	1.17	0.35	1.76	0.62	5.8	1.9	11
	Outer district ^f	1960–1996	Odd	18	478	1.16	0	1.16	1.16	3.2	3.2	11
			Even	19	308	0.72	0	0.72	0.72	2.1	2.1	11
Kodiak	Kamishak district ^g	1960–1996	Odd	16	180	0.98	0	0.98	0.98	2.7	2.7	11
			Even	18	200	0.84	0	0.84	0.84	2.3	2.3	11
	Afognak district	1980–1996	Odd	8	1 440	2.40	0.76	3.62	1.42	37.4	4.1	12
			Even	9	1 245	2.58	0	2.58	2.58	13.2	13.2	12
	Westside district	1980–1996	Odd	8	6 920	2.33	0.61	3.27	1.53	26.3	4.6	12
			Even	9	8 208	2.35	0.18	2.60	2.10	13.5	8.2	12
	Alitak district	1980–1996	Odd	8	3 448	2.38	0.58	3.21	1.60	24.9	5.0	12
			Even	9	1 070	1.32	0.18	1.64	1.16	5.1	3.2	12
	Eastside–northend district	1980–1996	Odd	8	4 430	1.91	0.54	2.64	1.23	14.0	3.4	12
			Even	9	1 457	2.65	0	2.65	2.65	14.2	14.2	12
	Mainland district	1980–1996	Odd	8	1 628	1.05	0	1.05	1.05	2.8	2.8	12
			Even	9	1 178	0.95	0.47	1.81	0.28	6.1	1.3	12
Chignik	Chignik Bay district	1962–1995	Odd	15	88	2.71	1.18	4.78	1.31	118.9	3.7	13, 14
			Even	16	140	2.67	0.38	3.33	2.13	27.9	8.4	13, 14
	Central district	1962–1995	Odd	17	299	0.77	0	0.77	0.77	2.2	2.2	13, 14
			Even	17	191	1.51	0.41	2.05	0.96	7.8	2.6	13, 14
	Eastern district	1962–1995	Odd	17	357	0.72	0.23	1.11	0.39	3.0	1.5	13, 14
			Even	17	792	0.89	0	0.89	0.89	2.4	2.4	13, 14
	Western district	1962–1995	Odd	17	488	1.72	0.15	1.99	1.53	7.3	4.6	13, 14
			Even	17	428	2.64	0.01	2.65	2.62	14.1	13.7	13, 14
	Perryville district	1962–1995	Odd	17	464	1.09	0	1.09	1.09	3.0	3.0	13, 14
			Even	17	264	1.37	0	1.37	1.37	3.9	3.9	13, 14
Alaska Peninsula	Northwestern district	1962–1996	Odd	17	5	0.83	0	0.83	0.83	2.3	2.3	13, 15
			Even	18	112	0.99	0	0.99	0.99	2.7	2.7	13, 15
	Southeast and south-central districts	1962–1996	Odd	17	4 790	1.65	0.44	2.26	1.03	9.6	2.8	13, 16
			Even	18	4 084	2.04	0.55	2.68	1.20	14.6	3.3	13, 16
	Southwest and Unimak districts	1962–1996	Odd	17	1 527	1.31	0.38	1.86	0.80	6.5	2.2	13, 16
			Even	18	2 139	2.29	0.93	3.24	0.67	25.4	2.0	13, 16
Bristol Bay Norton Sound	Nushagak district ^h	1960–1996	Even	17	2 673	1.17	0	1.17	1.17	3.2	3.2	17
	Nome	1978–1995	Odd	8	15	0.89	0	0.89	0.89	2.4	2.4	18, 19
			Even	9	575	1.21	0	1.21	1.21	3.3	3.3	18, 19
	Golovin	1968–1984	Odd	6	40	1.37	0	1.37	1.37	3.9	3.9	18, 19
			Even	9	222	1.35	0	1.35	1.35	3.9	3.9	18, 19
	Moses Point and Norton Bay	1968–1995	Odd	10	66	0.50	0	0.50	0.50	1.6	1.6	18, 19
			Even	12	494	1.47	1.02	2.90	−0.20	18.2	0.8	18, 19

Table 1 (concluded).

Region	Stock or district	Brood year	Run	N	R	a_t		R/S	
						Mean	SD	Max.	Min.
Unalakleet		1970–1995	Odd	10	52	1.81	0	1.81	1.81
			Even	11	251	1.77	0	1.77	1.77

Note: Stocks are arranged from south to north, and data are shown separately for even- and odd-year runs. *N* is the number of brood years available; *R* is the average number of annual recruits (thousands); Mean a_t , SD a_t , Max. a_t , and Min. a_t give the average, standard deviation, maximum, and minimum, respectively, of the Kalman-filtered a_t time series. The maximum and minimum recruits/spawner (Max. and Min. *R/S*) are on the arithmetic scale and are derived from the maximum and minimum a_t values (i.e., $\exp(a_t)$).

^a1. Jeff Haymes, Washington Department of Fish and Wildlife, 1111 Washington Street SE, Olympia, WA 98501, USA (personal communication); 2. Al Cass, Fisheries and Oceans Canada (DFO), 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada (personal communication); 3. Jim Wooley, Pacific Salmon Commission, 600-1155 Robson Street, Vancouver, BC V6E 1B5, Canada (personal communication); 4. Clyde Murray, DFO, 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada (personal communication); 5. Lia Bjesterveld, DFO, 200-401 Burrard Street, Vancouver, BC V6C 3S4, Canada (personal communication); 6. Dennis Rutherford, DFO, 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada (personal communication); 7. Wood et al. (1999); 8. Tim Zadina, Alaska Department of Fish and Game (ADFG), 2030 Sealevel Drive, Suite 205, Ketchikan, AK 99901, USA (personal communication); 9. Clark (1995); 10. Mark Willette, ADFG, P.O. Box 669, Cordova, AK 99574-0669, USA (personal communication); 11. Ted Otis, ADFG, 3298 Douglas Place, Homer, AK 99603-8027, USA (personal communication); 12. Kevin Brennan, ADFG, 211 Mission Road, Kodiak, AK 99615-6399, USA (personal communication); 13. Denby Lloyd, ADFG, 211 Mission Road, Kodiak, AK 99615-6399, USA (personal communication); 14. Owen and Sarafin (1999); 15. Murphy et al. (1999); 16. Campbell et al. (1999); 17. Michael Link, ADFG, 333 Raspberry Road, Anchorage, AK 99518-1599, USA (personal communication); 18. Betsy Brennan, ADFG, 333 Raspberry Road, Anchorage, AK 99518-1599, USA (personal communication); 19. Brennan et al. (1998).

^bData were only available for odd years (e.g., brood years 1959, 1961, ..., 1995), because few if any pink salmon spawn in even years.

^cSum of Dosewallips, Duckabush, and Hamma Hamma data sets.

^dOnly even-year data were used for the Mainland BC data set, because catches in most odd years were confounded by catch of Fraser River pink salmon.

^eSum of Humpy Creek, Port Graham, and Seldovia Bay data sets.

^fSum of Port Chatham, Port Dick, Rocky River, and Windy Creek data sets.

^gSum of Brown's Peak Creek, Bruin River, and Sunday Creek data sets.

^hData were only available for even years, because few if any pink salmon spawn in odd years.

time in productivity and random sources of variation that are independent of those trends. To accomplish this, the Kalman filter requires: (i) an observation equation (Chatfield 1989), which in this case is a description of the underlying biological relationship between spawners and recruits, and (ii) a system or transition equation (Chatfield 1989), in this case, a description of how one of the parameters of that biological model changes over time. More specifically, the observation equation was adapted from the basic Ricker model (eq. 1) by assuming a time-varying a parameter:

$$(2) \quad \log_e(R_t/S_t) = a_t + bS_t + v_t$$

This time-varying a_t was our second index of productivity.

The transition equation for the Kalman filter in our case must describe the expected temporal variation in a_t , but the true underlying pattern of this variation is unknown. However, previous simulation work (Peterman et al. 2000) indicates that a random-walk model can track a wide variety of hypothetical temporal trends in a_t , including a step function, a sine wave, and an autoregressive lag-1 (AR(1)) process. The Kalman filter with a random-walk model for a_t therefore can be expected to effectively attribute appropriate portions of the observed variation in the data to either the systematic time trends in a_t or to short-term variation under a range of natural productivity patterns as well. Other forms of the transition equation (e.g., AR(1), ARIMA: autoregressive integrated moving average) generally do not fit the same data that we used here as well as the random-walk model does (B.J. Pyper, Cramer Fish Sciences, 600 NW Fariss Road, Gresham, Oregon, USA, personal communication). Therefore, we chose that random-walk model for a_t :

$$(3) \quad a_t = a_{t-1} + w_t$$

with error terms v_t and w_t in eqs. 2 and 3 assumed to be normally distributed and independent, with means of zero and variances σ_v^2 and σ_w^2 , respectively.

While it is possible to have either the a or b parameter (or both) vary over time, we limited our analysis to a time-varying a_t for three reasons. First, Adkison et al. (1996) found that for Bristol Bay sockeye stocks, the a parameter tended to change much more over time than the b parameter. Second, assuming that the Ricker b parameter (but not a) was time-varying would imply that substantial changes in $\log_e(R/S)$ would occur only when spawner abundance was large (i.e., a change in the level of density-dependent feedback). However, a changing a_t parameter reflects the more likely situation that environmental processes influence survival rates of a stock to a similar proportional degree regardless of spawner abundance. Third, based on values of the small-sample AIC_c (Akaike information criterion), models with only a time-varying a_t fit data for our 120 salmon stocks better than models either with a time-varying b_t or with both parameters time-varying (B.J. Pyper, Cramer Fish Sciences, 600 NW Fariss Road, Gresham, Oregon, USA, personal communication).

The Kalman filter recursively estimated a_t each year, using a Bayesian approach that weighted the prior expectation for a_t estimated from previous years against the evidence of the data for year t . In the resulting time series of "filtered" (Harvey 1989) annual a_t estimates, each a_t depended only on data up

Table 2. Summary of 40 wild chum salmon (*Oncorhynchus keta*) data sets used to compute spawner-to-recruit indices of survival rate.

Region	Stock or district	Brood year	N	R	a_t				R/S		Source ^a
					Mean	SD	Max.	Min.	Max.	Min.	
Washington west coast	Willapa Bay	1968–1993	26	60	1.05	0	1.05	1.05	2.9	2.9	1
	Grays Harbour	1969–1993	21	46	1.03	0.03	1.07	0.97	2.9	2.6	1
Puget Sound	Skagit River	1968–1993	26	125	0.77	0	0.77	0.77	2.2	2.2	2
	Nooksack–Samish rivers	1968–1993	26	65	1.43	0.30	1.80	0.80	6.0	2.2	2
	Stillaguamish–Snohomish rivers	1968–1993	26	124	0.99	0.16	1.19	0.70	3.3	2.0	2
	Hood Canal	1968–1993	26	163	2.27	0.39	2.85	1.69	17.4	5.4	2
	South Sound fall	1968–1993	26	256	2.02	0.11	2.17	1.87	8.8	6.5	2
	South Sound summer	1968–1993	26	40	1.41	0.40	1.95	0.73	7.0	2.1	2
	South Sound winter	1968–1993	26	54	1.59	0	1.59	1.59	4.9	4.9	2
BC south coast	Fraser	1959–1992	34	886	0.99	0	0.99	0.99	2.7	2.7	3
	Inner south coast without Fraser River	1959–1992	34	1188	1.16	0.14	1.33	0.90	3.8	2.5	3
BC central coast	Statistical area 10	1960–1995	36	45	1.60	0.69	3.11	−0.44	22.5	0.6	4
	Statistical area 9	1960–1995	36	60	1.32	0.10	1.45	1.13	4.3	3.1	4
	Statistical area 8	1960–1994	35	488	1.94	0.11	2.12	1.80	8.3	6.0	4
BC north coast	Statistical area 6	1965–1992	28	307	1.32	0	1.32	1.32	3.7	3.7	5
Southeast Alaska	Kadashan River	1969–1984	16	55	1.75	0.61	2.78	1.02	16.2	2.8	6
Yakutat	East Alsek River ^b	1960–1987	21	25	1.60	0	1.60	1.60	4.9	4.9	7
Prince William Sound	Total	1966–1993	28	790	1.88	0.70	2.95	0.63	19.0	1.9	8
Cook Inlet	Outer district ^c	1964–1994	31	40	1.07	0.51	2.16	0.34	8.6	1.4	9
	Southern district ^d	1964–1994	29	20	1.56	0.92	3.68	0.34	39.8	1.4	9
	Kamishak district ^e	1964–1994	25	115	1.41	0.33	1.77	0.95	5.9	2.6	9
	Upper Cook Inlet	1972–1993	22	1505	1.10	0.36	1.59	0.61	4.9	1.8	10
Kodiak	Total	1962–1992	31	1296	2.06	0.34	2.66	1.26	14.3	3.5	11
Chignik	Central district	1962–1992	31	62	1.62	0.74	3.03	0.45	20.6	1.6	12, 13
	Eastern district	1962–1992	31	143	1.44	0.72	3.01	−0.46	20.4	0.6	12, 13
	Western district	1962–1992	31	118	2.04	0	2.04	2.04	7.7	7.7	12, 13
	Perryville district	1962–1992	31	64	1.33	0.52	2.43	0.60	11.3	1.8	12, 13
Alaska Peninsula	Northern district	1962–1994	33	279	1.39	0.65	2.70	−0.35	14.8	0.7	12, 14
	Izembek–Moffet	1962–1994	33	228	0.96	0.34	1.61	0.28	5.0	1.3	12, 14
	Bechevin–Swanson	1962–1994	33	69	1.44	0.69	2.73	0.09	15.4	1.1	12, 14
	Southeast district and south-central districts	1962–1994	33	700	1.76	0.48	2.38	0.74	10.8	2.1	12, 15
	Southwest district and Unimak districts	1962–1994	33	379	2.03	0.71	3.08	0.54	21.7	1.7	12, 15
Bristol Bay	Nushagak River	1974–1993	18	727	1.28	0.44	1.88	0.33	6.6	1.4	16
	Togiak River	1978–1992	15	438	2.13	0.14	2.31	1.91	10.1	6.8	16
AYK ^g and Norton Sound	Yukon River Fall ^f	1974–1995	22	843	0.89	0.46	1.41	−0.36	4.1	0.7	17, 18
	Anvik River	1972–1993	22	1042	1.09	0	1.09	1.09	3.0	3.0	17, 19
	Andreafsky River	1972–1995	24	276	0.81	0.46	1.48	−0.36	4.4	0.7	17, 20
	Kwiniuk and Tubutulik rivers	1965–1995	31	69	1.16	0.36	1.62	0.47	5.1	1.6	17, 21

Table 2 (concluded).

Region	Stock or district	Brood year	N	R	a_t		R/S		Source ^a
					Mean	SD	Max.	Min.	
Norton Sound district 1	Kotzebue Sound	1975–1995	21	55	1.34	0.46	2.19	0.20	17, 22
		1962–1979	18	378	2.48	0.51	3.02	1.55	4, 7, 23

Note: Stocks are arranged from south to north. N is the number of brood years available; R is the average number of annual recruits (thousands); Mean a_t , SD a_t , Max. a_t , and Min. a_t give the average, standard deviation, maximum, and minimum, respectively, of the Kalman-filtered a_t time series. The maximum and minimum recruits/spawner (Max. and Min. R/S) are on the arithmetic scale and are derived from the maximum and minimum a_t values (i.e., $\exp(a_t)$).

^a1. Rick Brix and John Linth, Washington Department of Fish and Wildlife (WDFW), 48 Devonshire Road, Montesano, WA 98563, USA (personal communication); 2. Jeff Haymes, WDFW, 1111 Washington Street SE, Olympia, WA 98563, USA (personal communication); 3. Ryall et al. (1999); 4. Ron Goruk, Fisheries and Oceans Canada (DFO), 417–2nd Avenue West, Prince Rupert, BC V8J 1G8, Canada (personal communication); 5. Les Jantz, DFO, 417–2nd Avenue West, Prince Rupert, BC V8J 1G8, Canada (personal communication); 6. Ben Van Alen, Alaska Department of Fish and Game (ADFG), 802–3rd Street, Douglas, AK 99824-0020, USA (personal communication); 7. Tim Zadina, ADFG, 2030 Sea Level Drive, Ketchikan, AK 99901, USA (personal communication); 8. Mark Willette, ADFG, 43961 Kalifornsky Beh Road, Soldotna, AK 99669-8367, USA (personal communication); 9. Ted Otis, ADFG, 3298 Douglas Place, Homer, AK 99603-8027, USA (personal communication); 10. Ken Tarbox, ADFG, 43961 Kalifornsky Beh Road, Soldotna, AK 99669-8367, USA (personal communication); 11. Kevin Brennan, ADFG, 211 Mission Road, Kodiak, AK 99615-6399, USA (personal communication); 12. Denby Lloyd, ADFG, 211 Mission Road, Kodiak, AK 99615-6399, USA (personal communication); 13. Owen and Sarafin (1999); 14. Murphy et al. (1999); 15. Campbell et al. (1999); 16. Michael Link, ADFG, 333 Raspberry Road, Anchorage, AK 99518-1599, USA (personal communication); 17. Doug Eggers, ADFG, 1255 W. 8th Street, Juneau, AK 99811-5526, USA (personal communication); 18. Eggers (2001); 19. Clark and Sandone (2001); 20. Clark (2001a); 21. Clark (2001b); 22. Clark (2001c); 23. Bigler (1985).

^bSpawner abundances for East Alsek River were used as an index of escapement; catch data were total harvests in districts 181 through 189.

^cSum of Port Graham and Dogfish Lagoon data sets.

^dSum of Port Dick and Rocky River data sets.

^eSum of Bruin, McNeil, and Big and Little Kamishak rivers, Ursus Cove and Lagoon, and Cottonwood Creek – Iniskin River data sets.

^fSum of fall-run chum salmon for Tanana River, Yukon River mainstem, and Yukon River tributary data sets.

^gArtic–Yukon–Kuskokwim.

through year t . We subsequently applied fixed-interval smoothing to the filtered estimates (Visser and Molenaar 1988). This smoothing process begins with the most recent filtered a_t value and works backward through time, computing a weighted average of the filtered estimate for time t and the smoothed estimate for time $t + 1$ at each step (Peterman et al. 2003). The smoothed a_t values thus take into account not only the information provided by the data up to year t , but also the information from year t onward. This smoothing process produces the minimum-variance unbiased estimates of a_t , as well as the maximum likelihood estimates (Fraser and Potter 1969). All results and discussions of a_t estimates below refer to these smoothed a_t values. To facilitate comparisons among the various stocks' a_t estimates that were reconstructed by the Kalman filter and also between those values and standardized Ricker residuals for the same stock, we standardized a_t values for each stock to a mean of zero and standard deviation of one. To examine the level of concordance between estimates of productivity (i.e., a_t) and abundance (i.e., estimates of recruitment and spawner abundance), we also calculated for several key stocks of interest the standardized recruitment and spawner abundance estimates with a mean of zero and a standard deviation of one.

The b parameter and variance terms σ_v and σ_w were assumed constant over time and were estimated using maximum likelihood. The exact procedures for our Kalman filter estimation method are described in Peterman et al. (2003), and its implementation in S-PLUS (Insightful Corporation, Seattle, Washington) code is available in the online supplementary material (NRC Data Depository⁴). Additional details for this general method are found in Meinhold and Singpurwalla (1983), Harvey (1989), and Zeng et al. (1998).

Correlation analysis

We compared correlations across stocks to quantify the extent to which variation in the a_t index of productivity is shared among salmon stocks. Specifically, we examined spatial covariation among productivities of stocks by calculating pairwise Pearson product–moment correlation coefficients between time series of Ricker residuals. We also calculated such correlations for the time series of a_t values reconstructed using the Kalman filter. We excluded from this analysis any pair of stocks for which one or both time series of estimated a_t were constant over time, as was sometimes the case for Kalman filter reconstructions. Such cases arose when the Kalman filter attributed all variance in the data to random sources of error, as opposed to systematic process variation. Pairs of time series were also excluded if they had fewer than 10 brood years in common. We tested correlation coefficients (r) for significance with $H_0: r = 0$ using a modification of the method described by Chelton (1994) to account for the effect of serial autocorrelation (Pyper and Peterman 1998a, 1998b). All tests for statistical significance were two-tailed, using $\alpha = 0.05$. We emphasize, though, that we were most interested in the general patterns of correlations among many salmon stocks, rather than the statistical significance of particular pairwise comparisons.

To provide a concise overview of key results of this analysis and to facilitate comparison with earlier studies, we also computed average correlations among groups of salmon

Table 3. Summary of 37 wild sockeye salmon (*Oncorhynchus nerka*) data sets used to compute spawner-to-recruit indices of survival rate.

Region	Stock or district	Brood year	<i>N</i>	<i>R</i>	<i>a_t</i>				<i>R/S</i>		Source ^a
					Mean	SD	Max.	Min.	Max.	Min.	
Puget Sound	Lake Washington	1967–1993	27	274	0.62	0	0.62	0.62	1.9	1.9	1
Fraser early Stuart	Early Stuart	1950–1996	47	340	1.35	0.48	2.36	0.47	10.6	1.6	1
Fraser early summer run	Bowron	1950–1996	47	45	1.65	0.10	1.76	1.47	5.8	4.3	1
	Gates	1952–1996	45	46	1.38	0	1.38	1.38	4.0	4.0	1
	Nadina	1950–1996	47	68	1.68	0.18	2.01	1.26	7.5	3.5	1
	Pitt	1950–1996	47	72	1.59	0.40	2.28	0.88	9.8	2.4	1
	Raft	1950–1996	47	28	1.31	0.20	1.73	0.95	5.7	2.6	1
	Seymour	1950–1996	47	138	1.51	0.28	1.80	0.91	6.0	2.5	1
	Chilko	1950–1996	47	1 533	2.13	0.12	2.33	1.98	10.3	7.2	1
	Horsefly	1950–1996	47	1 322	1.29	0.36	1.95	0.84	7.1	2.3	1
Fraser summer run	Late Stuart	1950–1996	47	585	1.70	0	1.70	1.70	5.5	5.5	1
	Stellako	1950–1996	47	499	1.95	0	1.95	1.95	7.1	7.1	1
Fraser Birkenhead	Birkenhead	1950–1996	47	424	2.29	0.42	2.95	1.22	19.0	3.4	1
Fraser late run	Adams	1950–1996	47	2 026	1.54	0.09	1.63	1.37	5.1	3.9	1
	Cultus	1950–1996	47	67	1.38	0.09	1.56	1.28	4.7	3.6	1
	Portage	1951–1996	43	45	1.84	0.35	2.26	1.14	9.6	3.1	1
	Weaver	1950–1996	47	289	1.96	0.34	2.27	1.34	9.7	3.8	1
BC central coast	Long Lake	1980–1994	15	350	0.38	1.12	1.73	–2.06	5.6	0.1	2
BC north coast	Skeena	1950–1994	45	2 056	0.82	0.13	0.98	0.55	2.7	1.7	2
	Nass	1967–1991	25	650	1.72	0.34	2.45	1.35	11.6	3.8	3
Prince William Sound	Copper	1961–1993	33	1 435	2.11	0.36	2.81	1.52	16.6	4.6	4
Cook Inlet	Cook	1968–1992	25	4 770	1.64	0.12	1.84	1.46	6.3	4.3	5
Kodiak	Ayakulik	1965–1993	29	574	0.89	0.28	1.30	0.28	3.7	1.3	6
	Frazer	1965–1993	29	409	1.86	0.46	2.53	1.18	12.6	3.3	6
	Early Upper Station	1969–1993	25	104	0.94	0.21	1.16	0.43	3.2	1.5	6
	Late Upper Station	1970–1993	24	539	1.33	0.39	2.18	0.72	8.8	2.1	6
Chignik	Black	1950–1993	44	1 028	1.58	0.27	1.90	1.13	6.7	3.1	6
	Chignik	1950–1993	44	960	1.89	0.30	2.24	1.42	9.4	4.1	6
Bristol Bay	Branch	1956–1995	40	499	1.12	0.14	1.31	0.93	3.7	2.5	7
	Egegik	1956–1995	40	6 424	1.85	0.61	2.88	0.91	17.8	2.5	7
	Igushik	1956–1995	40	965	1.58	0.73	2.92	0.17	18.5	1.2	7
	Kvichak	1956–1995	40	12 450	0.55	0.64	1.77	–0.97	5.9	0.4	7
	Naknek	1956–1995	40	3 487	1.37	0.08	1.47	1.23	4.3	3.4	7
	Nuyakuk	1956–1982	27	932	1.39	0.30	1.81	0.95	6.1	2.6	7
	Togiak	1956–1995	40	518	1.79	0.15	2.02	1.53	7.5	4.6	7

Table 3 (concluded).

Region	Stock or district	Brood year	N	R	a_t		R/S		Source ^a
					Mean	SD	Max.	Min.	
Ugashik Wood		1956–1995	40	2.729	1.35	0.94	2.90	–0.40	7
		1956–1995	40	2.715	1.54	0.36	2.21	1.03	7

Note: Stocks are arranged from south to north. *N* is the number of brood years available; *R* is the average number of annual recruits (thousands); Mean a_t , SD a_t , Max. a_t , and Min. a_t give the average, standard deviation, maximum, and minimum, respectively, of the Kalman-filtered a_t time series. The maximum and minimum recruits/spawner (Max. and Min. *R/S*) are on the arithmetic scale and are derived from the maximum and minimum a_t values (i.e., $\exp(a_t)$).

^a1. Jim Woodey and Mike Lapointe, Pacific Salmon Commission, 600–1155 Robson Street, Vancouver, BC V6E 1B5, Canada (personal communication); 2. Chris Wood, Fisheries and Oceans Canada (DFO), 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada (personal communication); 3. Les Jantz, DFO, 417-2nd Avenue West, Prince Rupert, BC V8J 1G8, Canada (personal communication); 4. Mark Willette, Alaska Department of Fish and Game (ADFG), 43961 Kalifornsky Beh Road, Soldotna, AK 99669-8367, USA (personal communication); 5. Ken Tarbox, ADFG, 43961 Kalifornsky Beh Road, Soldotna, AK 99669-8367, USA (personal communication); 6. Patricia Nelson, ADFG, 211 Mission Road, Kodiak, AK 99615-6399, USA (personal communication); 7. Michael Link, ADFG, 333 Raspberry Road, Anchorage, AK 99518-1599, USA (personal communication).

stocks for larger geographic regions. These regions correspond to those used in Pyper et al. (2001, 2002, 2005) and reflect a mixture of natural geographic boundaries and management jurisdictions.

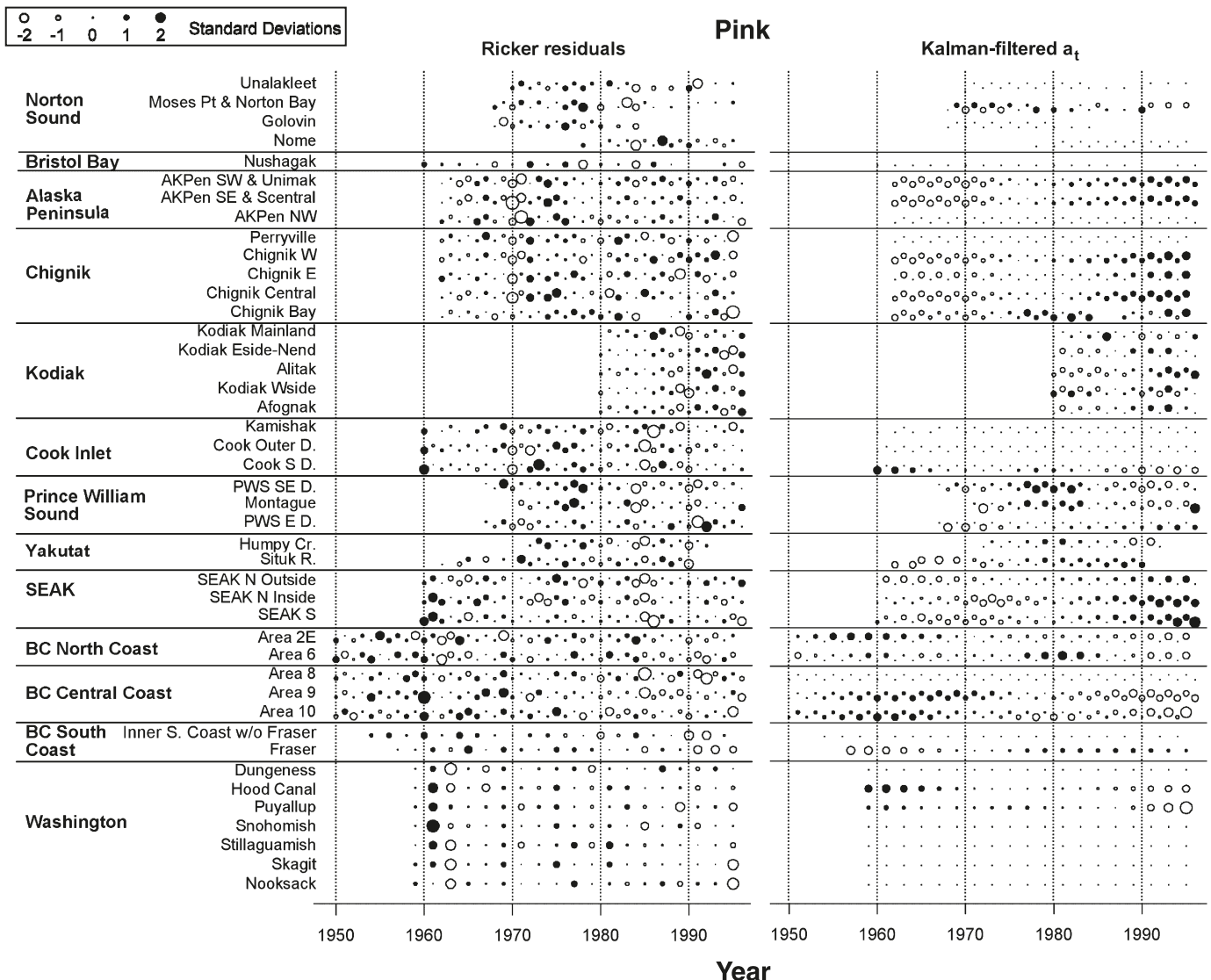
In addition to formal correlation analysis, we show time series plots of reconstructed a_t because simple correlation values between complete time series do not fully describe particular trends during certain time periods, reversals of direction of trends, or other features relevant to conservation and management. Because our main focus in this paper is on changes in productivity across time within salmon stocks and on comparisons among stocks, we primarily refer in the Results section to the compact dot plots of standardized productivity index values shown in Figs. 2–4. For readers interested in actual rather than standardized values of productivity indices, we provide graphs of original, unscaled, smoothed Kalman filter a_t time series as online supplementary material (Supplementary Figs. S1–S4, available from the NRC Data Depository⁴).

Results

Kalman filter reconstructions of a_t identified many clear underlying temporal trends in productivity of all three salmon species (right-hand columns of Figs. 2–4 in standard deviation units). For instance, the pink salmon stocks of the Alaska Peninsula and Chignik show increasing trends in a_t from about 1970 through the 1990s (Fig. 2). This right-hand column shows large open circles (values between 1 and 2 standard deviations below the respective stock-specific means) during the 1960s and early 1970s, shrinking in size over time until they become small solid dots (near-mean values), and then becoming increasingly large solid dots (between 1 and 2 standard deviations above the respective stock-specific means during the 1980s and 1990s). The Kalman filter extracted such long-term temporal trends that were obscured by large short-term variability in the noisier index of productivity based on Ricker residuals (compare left and right columns of Figs. 2–4). These Kalman filter time series are considerably smoother than the Ricker residuals, because the Kalman filter suppresses much of the random (i.e., nonsystematic), short-term variability and emphasizes the underlying time trends in mean productivity, whereas the Ricker residuals reflect all variation in the stock–recruitment data, both random, short-term variability as well as long-term trends. Many changes in productivity estimated by the Kalman filter were monotonic (e.g., Alaska Peninsula and most Chignik pink salmon; Fig. 2), whereas others were nonmonotonic trends (e.g., Bristol Bay and Fraser River sockeye salmon; Fig. 4). Some of those changes occurred over only a few years, but others occurred across decades. It is notable that periods of unusually high or low a_t values often persisted for at least 5 years. In some cases, all variability in the time series of stock–recruitment data was interpreted by the Kalman filter as high-frequency variation not related to systematic trends, resulting in constant smoothed a_t values without any time trend (e.g., the series of equally small dots in Fig. 2 for most Washington pink salmon stocks).

On average, the variance due to the temporal trend (σ_w^2) was smaller than the remaining variation not related to that

Fig. 2. Pink salmon (*Oncorhynchus gorbuscha*) time series of Ricker residuals (left) and a_t values produced by Kalman filter estimation (right) by brood year (year when the group of fish was spawned). Even-year runs and odd-year runs were analyzed separately. For ease of comparison, results for even-year runs are shown vertically offset slightly below results for odd-year runs. Stocks are arranged from south (bottom of figure) to north (top of figure). Time series are in standard deviation units (i.e., scaled to a mean of zero and a standard deviation of one); scale is at top left. Solid circles represent above-average values; open circles represent below-average values. The radius of circles represents the magnitude (absolute value) of indices (i.e., large solid circles represent years with very high values, whereas large open circles represent years with very low values). Zero (or near-zero) values are shown as small dots to distinguish them from years with missing values.

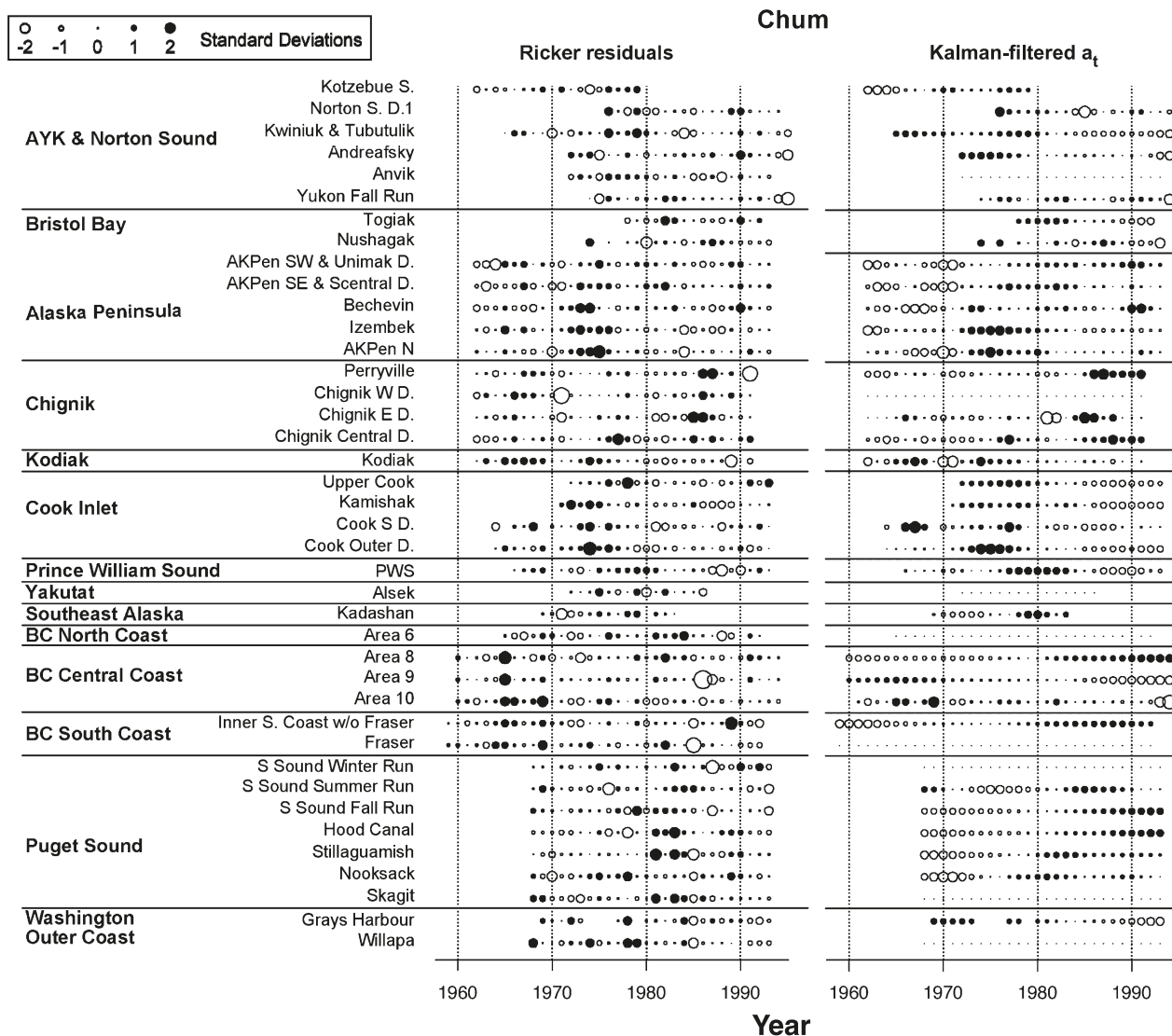


trend (σ_v^2); the ratio of (average σ_w^2 / average σ_v^2) was 0.26 for pink salmon, 0.34 for sockeye salmon, and 0.61 for chum salmon. Thus, the slowly changing trend was an important part of the total variation. This relative magnitude of the variances differed widely among stocks; those stocks that had a large range in productivity over time had a ratio of between 0.4 and 0.7. This ratio provided no new information beyond what is shown in Figs. 2–4, because it tended to be similar within species and within regions, just like similarities in productivity trends shown in those figures.

From the standpoint of conservation and management, many of the changes in a_t were extremely large and important. Recall that the a_t parameter is equivalent to the average logarithm of recruits per spawner at extremely low spawner

abundance (eq. 2). Thus, to put the changes in a_t into perspective, we converted each a_t value to the equivalent recruits per spawner (R/S , using e^{a_t}) (Tables 1–3, second- and third-to-last columns). Then, for each stock, we calculated the difference between the highest and lowest R/S in the time series as a percentage of the highest R/S . Across the stocks that showed a time-varying a_t , the average of these percentages for each species was unexpectedly large and was also surprisingly consistent across species: 66% for even-year pink salmon, 60% for odd-year pink salmon, 70% for chum salmon, and 60% for sockeye salmon. These large changes in productivity were also reflected by the average of stock-specific ratios of the highest to the lowest R/S over the course of a given time series. The average ratios were

Fig. 3. Chum salmon (*Oncorhynchus keta*) time series of Ricker residuals (left) and a_t values produced by Kalman filter estimation (right) by brood year (year when the group of fish was spawned). Stocks are arranged from south (bottom of figure) to north (top of figure). Time series are in standard deviation units (i.e., scaled to a mean of zero and a standard deviation of one); scale is at top left. Solid circles represent above-average values; open circles represent below-average values. The radius of circles represents the magnitude (absolute value) of indices (i.e., large solid circles represent years with very high values, whereas large open circles represent years with very low values). Zero (or near-zero) values are shown as small dots to distinguish them from years with missing values.



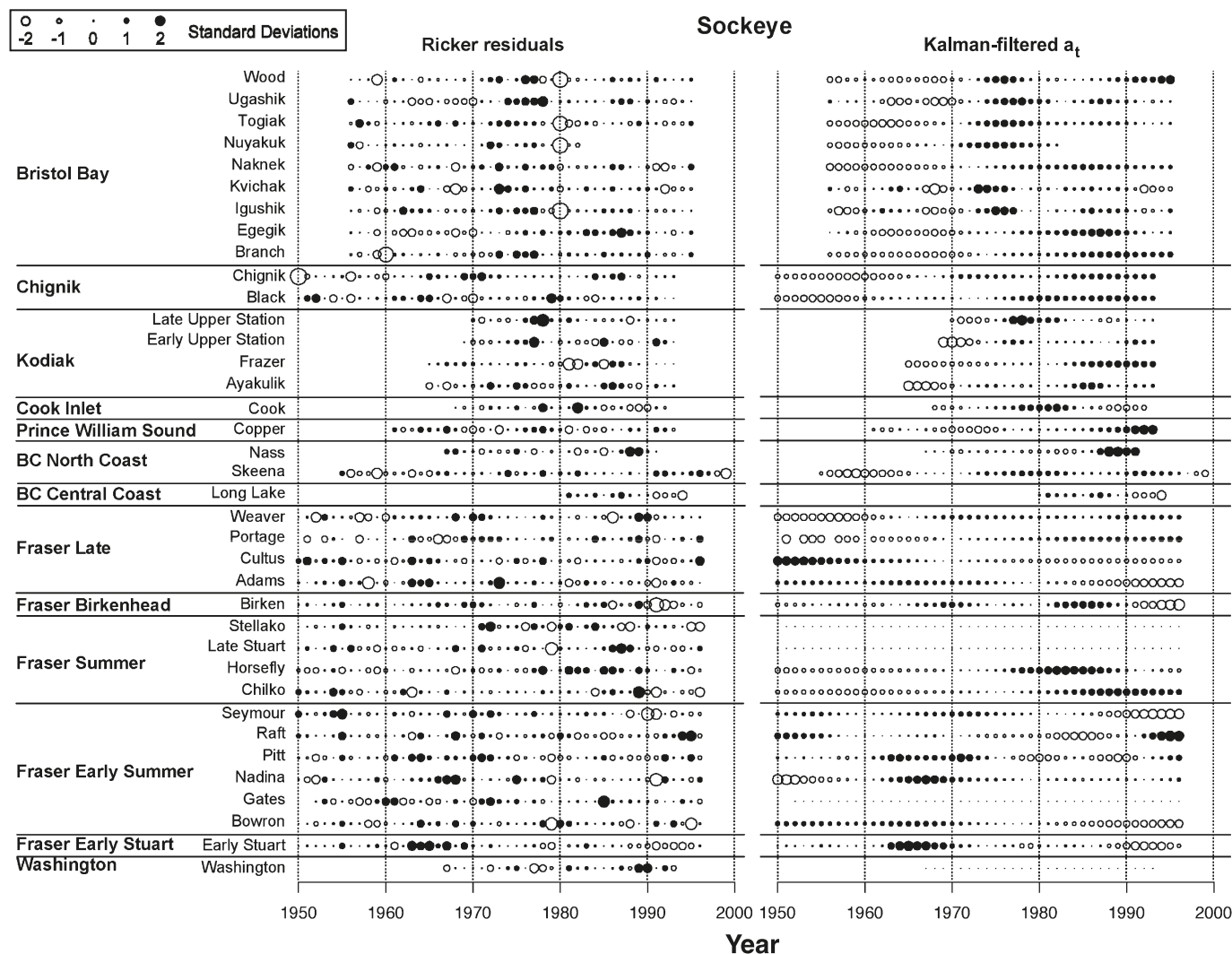
7.1 for even-year pink salmon, 5.4 for odd-year pink salmon, 7.9 for chum salmon, and 5.6 for sockeye salmon. Some of these ratios of the maximum to minimum R/S were particularly large, as exemplified by ratios of 35 for chum salmon in statistical area 10, 39 for even-year pink salmon in the Montague district, and 44 for sockeye salmon from Long Lake. Such large values for changes in R/S have important implications for management and conservation (see Discussion section). We found no consistent patterns in these percentage differences or ratios of R/S between and within regions or between and within species. This lack of patterns was due to the wide range of values commonly found among stocks within each species and within each region (Tables 1–3).

The Kalman filter results also illustrate three other important points. First, the a_t series were typically positively cor-

related for stocks of a given species within the same geographic region (Table 4 and diagonal cells of Figs. 5a–5d). Second, in most cases, we found that within-region correlations for a_t series were stronger than correlations for Ricker residuals (Table 4). In some cases, such as within Alaska Peninsula pink salmon and Chignik sockeye salmon, virtually identical patterns in smoothed a_t for stocks in each area resulted in within-region correlations close to 1.0. Third, comparisons of a_t series among regions within species showed mostly positive correlations within Alaska (“northern area”: top-right block of cells bordered by broken lines in Figs. 5a–5d) and within BC–Washington (“southern area”: lower-left block of cells), but predominantly negative correlations between these areas (Fig. 5, lower-right block).

Despite the general coherence of temporal patterns of a_t

Fig. 4. Sockeye salmon (*Oncorhynchus nerka*) time series of Ricker residuals (left) and a_t values produced by Kalman filter estimation (right) by brood year (year when the group of fish was spawned). Stocks are arranged from south (bottom of figure) to north (top of figure). Time series are in standard deviation units (i.e., scaled to a mean of zero and a standard deviation of one); scale is at top left. Solid circles represent above-average values; open circles represent below-average values. The radius of circles represents the magnitude (absolute value) of indices (i.e., large solid circles represent years with very high values, whereas large open circles represent years with very low values). Zero (or near-zero) values are shown as small dots to distinguish them from years with missing values.



within species and regions (Table 4), high and low productivities often occurred at different times for different stocks within a region (Figs. 2–4). For example, temporal trends were out of phase to various degrees among chum salmon stocks in Puget Sound and also in the Alaska Peninsula regions (Fig. 3), as well as among Kodiak sockeye stocks (Fig. 4).

While the Kalman filter analysis thus identified shared, positively correlated long-term trends in productivity among salmon stocks, not all short-term variability quantified in the process of Kalman filtering was necessarily due to observation error or purely local factors. Examples of short-term fluctuations that affected stocks across large geographical areas include (i) the rapid change from high to low productivity between 1961 and 1963 brood year Washington pink salmon (left side of Fig. 2), (ii) extremely low productivity during the mid-1980s for pink salmon stocks from the BC

central coast up through Cook Inlet, (iii) the episode of unusually high productivity experienced by 1965 brood year chum salmon throughout BC (left side of Fig. 3), and (iv) the very low productivity experienced by several stocks of 1980 brood year Bristol Bay sockeye salmon (left side of Fig. 4). None of these short-term variations in Ricker residuals appears clearly in the a_t signals. This lack of sensitivity of the Kalman filter to such spatially-correlated short-term variation is also apparent in the analysis of within-region correlations (Table 4). In the case of the BC central coast chum salmon and Fraser late-run sockeye salmon, for example, the stocks in each of those regions shared similar patterns of short-term variation, but differed with respect to longer-term patterns (Figs. 3 and 4), which resulted in a positive correlation for Ricker residuals, but negative correlation for Kalman a_t series (Table 4). The opposite was the case for the Chignik sockeye salmon (Fig. 4), where diver-

Table 4. Average within-region correlations for pairs of stock-specific time series of Ricker residuals and also for Kalman filter reconstructions of Ricker a_t time series.

Region	Ricker residuals	Kalman-filtered a_t
Even-year pink salmon		
BC central coast	0.41	0.75
BC north coast	0.56	—
Southeast Alaska	0.23	0.84
Yakutat	0.30	—
Prince William Sound	0.61	0.53
Cook Inlet	0.57	—
Chignik	0.53	0.79
Alaska Peninsula	0.59	0.99
Norton Sound	0.47	—
Odd-year pink salmon		
Puget Sound	0.49	—
Washington	0.81	—
BC central coast	0.20	0.89
BC north coast	0.02	0.14
Southeast Alaska	0.58	0.82
Prince William Sound	0.50	0.95
Cook Inlet	0.36	—
Chignik	0.42	0.78
Alaska Peninsula	0.75	1.00
Chum salmon		
Washington west coast	0.81	—
Puget Sound	0.31	0.60
BC south coast	0.51	—
BC central coast	0.41	-0.25
Cook Inlet	0.36	0.68
Chignik	0.47	0.60
Alaska Peninsula	0.49	0.54
Bristol Bay	0.09	0.22
Norton Sound and Kotzebue	0.33	0.45
Sockeye salmon		
Fraser early summer	0.20	0.26
Fraser summer	0.18	0.72
Fraser late	0.19	-0.27
BC north coast	0.45	—
Kodiak	-0.04	0.34
Chignik	-0.12	0.88
Bristol Bay	0.35	0.62

Note: We only show regions that had two or more series with at least 10 valid data years. Because series with constant a_t values had to be excluded from correlation analyses, within-region correlations for Kalman a_t could not be calculated for some regions.

gent short-term patterns in the Ricker residuals (correlation of -0.12) masked the strong positive correlation (0.88) between long-term trends identified by the a_t series.

In the remainder of this section, we describe the a_t time trends in more detail. The purpose is not to convey fine points of individual stocks' timing and direction of changes in productivity, but rather to illustrate general points about similarities among stocks, regions, and species, as well as differences among them. Unless stated otherwise, "productivity" henceforth refers only to a_t values.

Pink salmon a_t time series

Pink salmon show a range of patterns. For the majority of northern (i.e., Alaskan) pink stocks, Kalman filter a_t values were low during the 1960s, followed in most cases by a steady increasing trend that continued through to the 1990s (Fig. 2). In contrast, productivities for southern (i.e., Washington and BC) stocks were generally moderate or high during the 1960s but then declined during the 1970s, a trend that continued into the 1990s for the majority of these stocks. For many pink stocks in the northern and a few in the southern regions, an increase in a_t values in the 1970s was the only other distinct change in long-term dynamics. Some pink stocks experienced another major reversal, declining from above-average to below-average values through the 1980s. As might be expected, patterns for odd- and even-year runs of the same stock were mostly similar (Fig. 2). However, there were some exceptions, the most notable being odd- and even-year runs of Kodiak, Prince William Sound eastern district, Cook Inlet southern district, and BC north coast stocks.

Similarities in a_t time series of pink salmon stocks produced strong positive correlations within certain regions that contained more than one stock (thick-lined diagonal cells in Figs. 5a, 5b). Pairwise correlations were also predominantly positive among Alaskan pink stocks. In contrast, correlations between Alaskan and BC-Washington pink stocks (both even- and odd-year runs) were predominantly negative, although mixed in sign for odd-year pink salmon (Figs. 5a, 5b). For example, a_t series for odd-year pink salmon from Washington and the central and north coast of BC were mostly negatively correlated with a_t series for southeast Alaskan odd-year pink salmon (average correlation -0.69, ranging from -0.06 to -0.97; Fig. 5b).

Chum salmon a_t time series

Like a_t patterns for pink salmon, patterns for chum salmon were generally consistent within regions (Fig. 3); correlations within regions were mostly positive (diagonal in Fig. 5c). However, patterns across larger geographical areas were more variable than those for pink salmon, especially for the southern part of the study area. Although negative correlations predominate, there is considerable variability in the magnitudes and signs of correlations among southern chum stocks and among correlations between southern and northern chum stocks (Fig. 5c).

As with the pink salmon stocks, the late 1960s and early 1970s covered a period of very low productivity for about half the chum salmon stocks, followed by increases during the mid- to late 1970s (Fig. 3). Most southern chum stocks continued to increase in productivity into the 1990s, a trend shared by Alaskan, but not BC-Washington, pink stocks.

There were some positive between-species correlations in a_t patterns for Alaskan pink and chum salmon within regions (diagonal cells of Figs. 6a, 6b) and between nearby regions such as Chignik and the Alaska Peninsula (top right of Figs. 6a, 6b). For other Alaskan regions though, most correlations between pink and chum stocks were negative because Alaskan pink productivity was mostly stable or increasing after the mid-1970s, whereas productivity for Alaskan chum stocks in the Arctic-Yukon-Kuskokwim (AYK), Bristol Bay, Kodiak, and Cook Inlet regions

Fig. 5. Matrix of pairwise correlations between stock-specific, Kalman-filtered a_t time series for (a) even-year pink (*Oncorhynchus gorbuscha*), (b) odd-year pink, (c) chum (*Oncorhynchus keta*), and (d) sockeye (*Oncorhynchus nerka*) salmon. Within a given region, a row (or a column) of circles represents results for a given salmon stock. Thick solid lines delineate within-region correlations along the diagonal. Broken lines separate Alaskan stocks from those in Washington and British Columbia. Positive correlation coefficients are shown as solid circles; negative coefficients are shown as open circles. The radius of circles represents the strength of the correlation. Correlation coefficients that are not significantly different from zero at the $\alpha = 0.05$ level are shown in gray rather than black shading. Some columns or rows are empty (indicating that data exist, but fewer than 10 data points exist for the correlation analysis) or missing (indicating that there are no such stocks in the region; e.g., even-year Washington pink salmon).

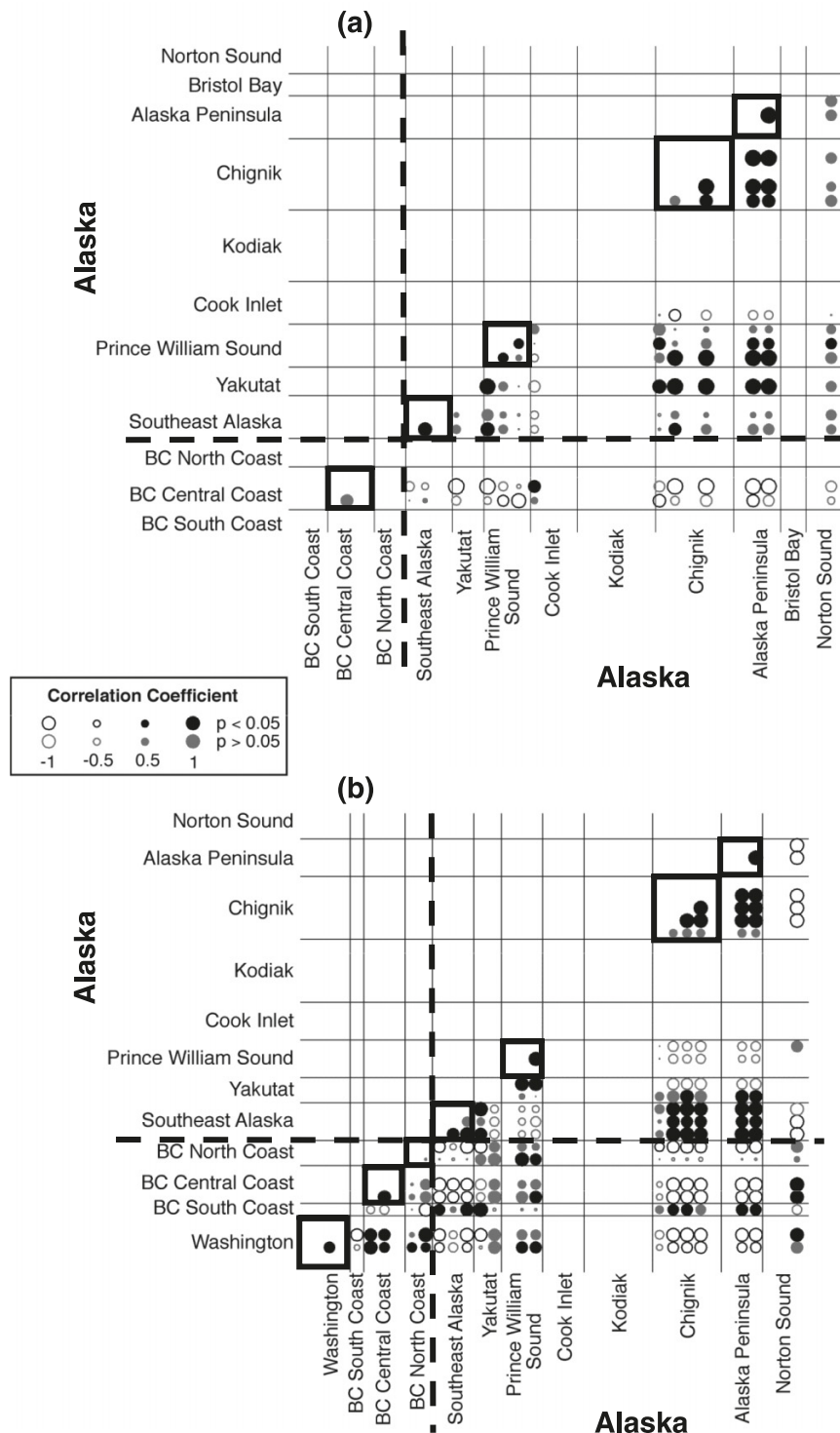
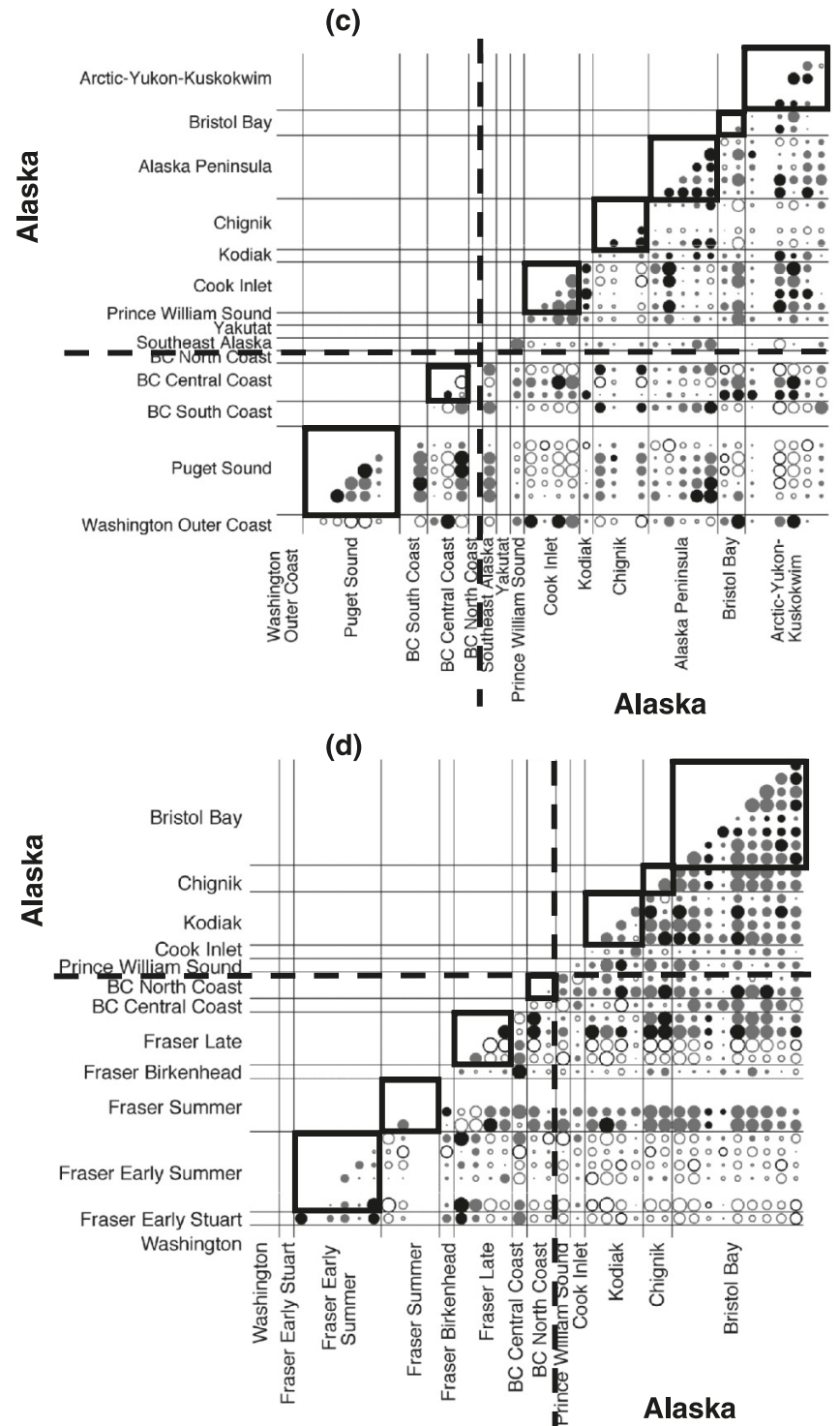


Fig. 5. (concluded).



decreased during that period (Figs. 2, 3). One notable exception to such negative between-region correlations is the strong positive correlation between Puget Sound chum salmon and Alaskan pink salmon, mainly due to increased productivity in both groups after the mid-1970s (top left block of Figs. 6a, 6b).

Sockeye salmon a_t time series

Time trends in a_t for sockeye salmon were also similar within regions and among certain regions (Figs. 4 and 5d). Correlations in productivities between pairs of northern (i.e., Alaskan) sockeye stocks were typically strong and almost universally positive (upper right of Fig. 5d), whereas

Fig. 6. Cross-species correlations between (a) chum salmon (*Oncorhynchus keta*) and even-year pink salmon (*Oncorhynchus gorbuscha*) stocks, (b) chum salmon and odd-year pink salmon stocks, (c) sockeye salmon (*Oncorhynchus nerka*) and even-year pink salmon stocks, (d) sockeye salmon and odd-year pink salmon stocks, and (e) chum salmon and sockeye salmon stocks. Thick-lined rectangles outline results for between-species comparisons within the same region. Positive correlation coefficients are shown as solid circles; negative coefficients are shown as open circles. The radius of circles represents the strength of the correlation. Correlation coefficients that are not significantly different from zero at the $\alpha = 0.05$ level are shown in gray rather than black shading. Some columns or rows are empty (indicating that data exist, but fewer than 10 data points exist for the correlation analysis) or missing (indicating that there are no such stocks in the region).

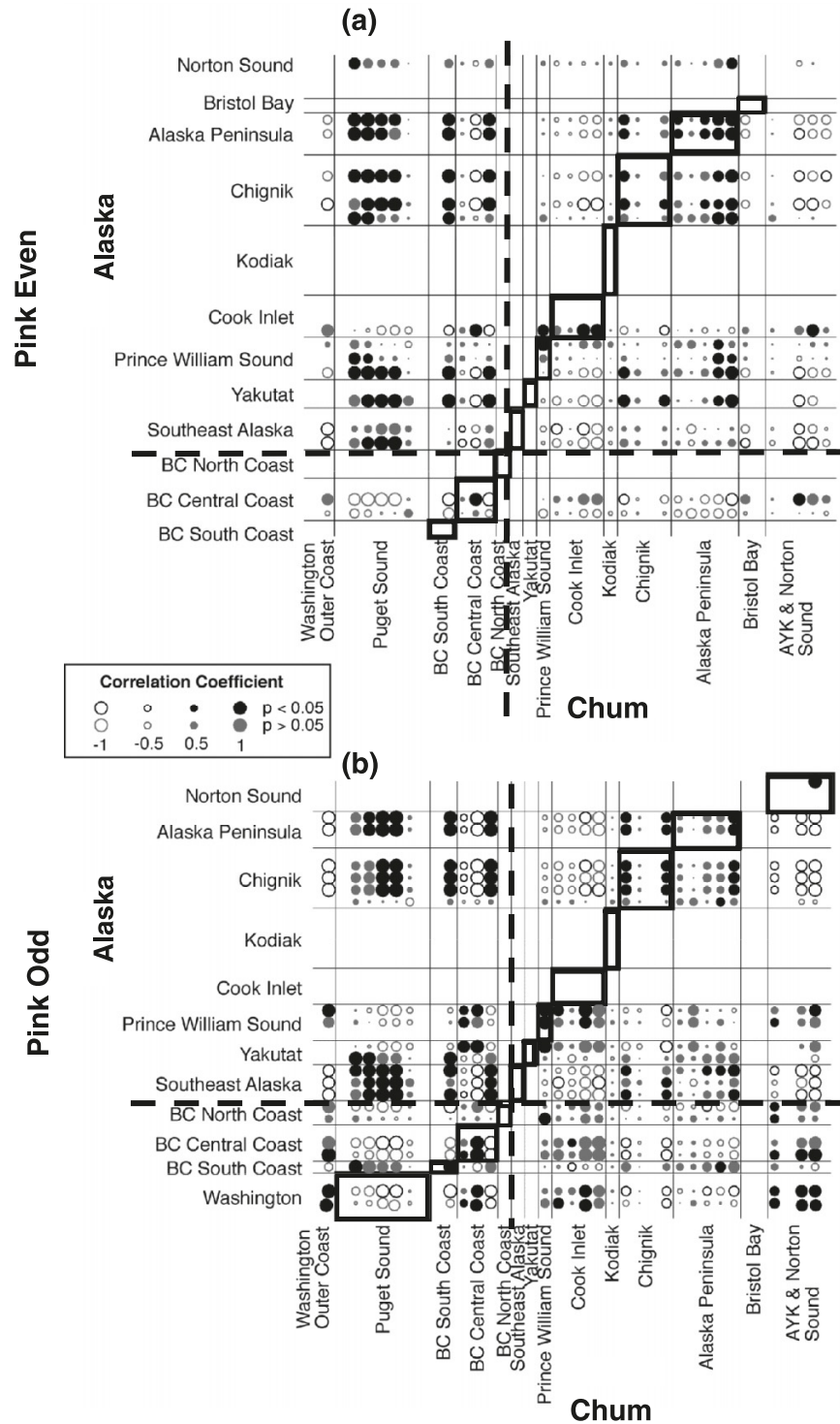
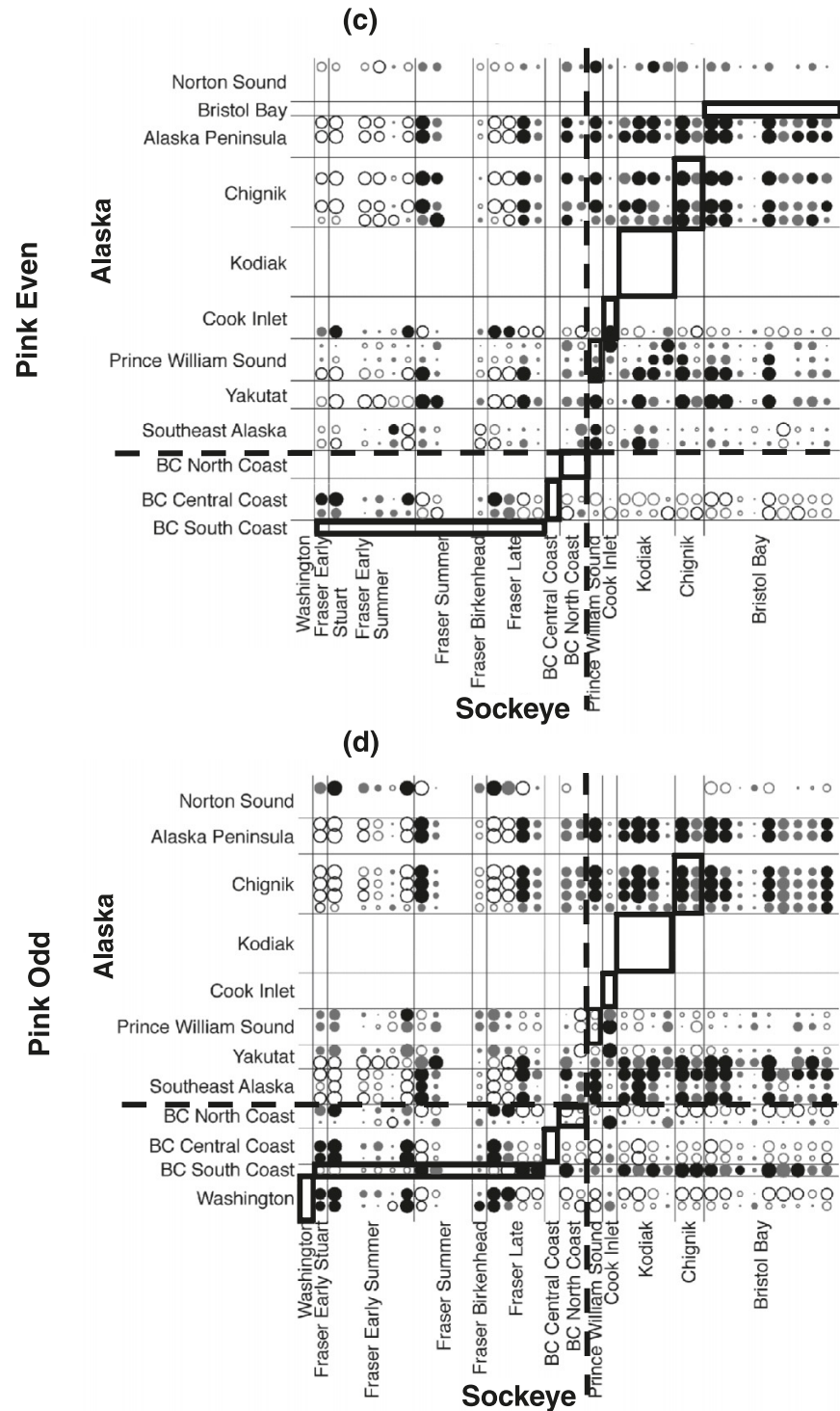


Fig. 6. (continued).



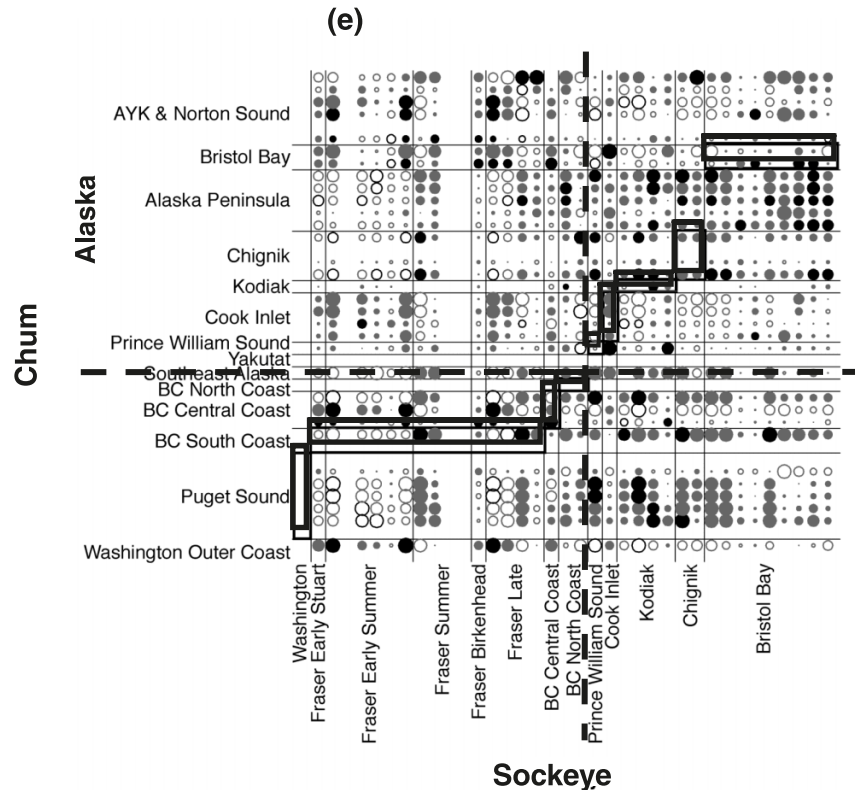
correlations between northern and southern sockeye stocks were quite variable but negative correlations predominated (lower right of Fig. 5d).

One key exception to the general within-area coherence was the group of Fraser River sockeye salmon stocks, which showed quite diverse temporal patterns (Fig. 4). Correlations among productivities of pairs of Fraser River stocks tended to be weak and were often negative (lower left of Fig. 5d). There was little consistency in either long- or short-term

patterns for Fraser River sockeye as a whole or within the run-timing groups (e.g., early summer, summer, or late runs).

Like northern pink salmon and chum salmon stocks, northern sockeye salmon stocks generally experienced a period of below-average a_t during the 1960s, followed by sharp increases in a_t over the next decade or so (Fig. 4). These similarities resulted in predominantly positive between-species correlations between northern sockeye and

Fig. 6. (concluded).



northern pink and chum stocks, although the correlations with chum salmon were weaker (upper right of Figs. 6c, 6d, 6e). Patterns for sockeye were not as well synchronized as those for pink salmon though, and for Alaskan stocks, productivity typically began to increase for sockeye and chum a few years earlier than for pink salmon (Figs. 2–4). Correlations between BC and Alaska pink and sockeye salmon, though, were primarily negative.

A closer look at the relationship among recent productivity trends, abundance of recruits, and spawning escapement (Fig. 7) illustrates the implications of nonstationary productivity patterns and also highlights management opportunities and challenges arising from these patterns. For example, several stocks in the study area experienced a substantial increase in productivity through the early 1990s, yet not all cases showed similar increases in recruitment (Fig. 7). Conditional upon sufficient recruitment and low harvest rates, such increases in productivity can quickly restore abundance of spawners after low periods, as has been the case, for example, for Pitt and Raft sockeye after 1990. High productivity also creates potential for increased harvest levels, although the substantial increase in spawner abundance for the majority of stocks in Fig. 7 indicates that harvesting did not take full advantage of the increase in productivity, possibly because higher priority was placed on rebuilding spawning stocks. Because the evidence from the Kalman filter analysis suggests that temporal trends in productivity often persist for at least half a decade, such reconstructions of recent productivity trends may help to guide harvesting capacity away from stocks that are in a low-productivity phase.

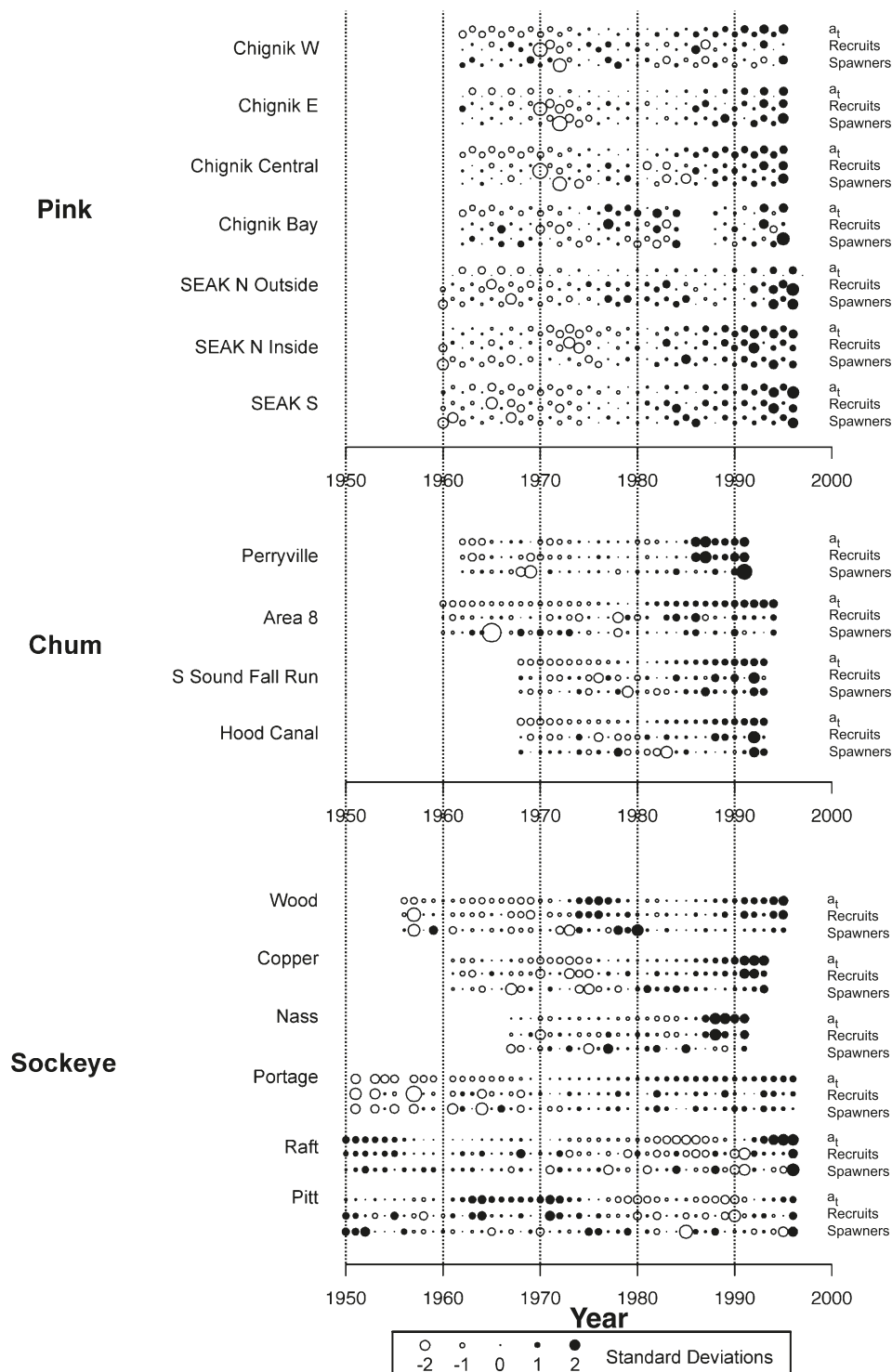
At the other extreme, stocks that have experienced a

strong decline in productivity in recent years pose a major management concern (Fig. 8). Such a decline in productivity in the 1990s was most evident for several pink salmon stocks from Washington and BC, chum salmon stocks from the BC central coast and the AYK region, and sockeye salmon stocks from the Fraser River and BC central coast (Fig. 8). In all these cases, the continued decline in productivity eventually resulted in declining recruitment, in spite of mostly average escapement (or, in the case of Andreafsky, Kwiniuk and Tubutulik chum, above-average escapement; Fig. 8). It thus appears that for the stocks shown in Fig. 8, management actions were often adequate to constrain the fishery and maintain spawning escapement at or near historical levels, but it is also clear that those escapement levels were not high enough to reduce the impact of declining productivity sufficiently to maintain abundance of recruits. Kalman filter analysis might help detect such persistent downward trends in productivity early enough to implement a proactive management regime and perhaps prevent a substantial decline in adult recruits.

Discussion

The Kalman filter results document considerable temporal variation in productivity of pink, chum, and sockeye salmon stocks on the west coast of North America. We re-emphasize that in this paper, we are mainly concerned with productivity (reflecting recruits per spawner), not simply abundance. Some variation in productivity was shared among stocks, whereas other stocks showed distinctive patterns. In most cases, the systematic changes in productivity reflected by Kalman filter a_t values were substantial, resulting in large

Fig. 7. Kalman-filtered a_t time series, recruitment, and spawner abundance for some stocks with high and (or) increasing productivity in the 1990s. Like the Kalman-filtered a_t time series, spawner and recruit time series are scaled to a mean of zero and a standard deviation of one to highlight common patterns.



average differences between the highest and lowest recruits per spawner during the time series. Those changes occurred at various rates, from slow in some stocks to rapid in others and highly variable in still others. Recall that the variation indicated by the Kalman-filter-estimated a_t values describes systematic trends or changes to persistent new

levels of productivity, as opposed to short-term, year-to-year variation in recruits per spawner. This distinction is important because the systematic trends mainly affect long-term policies and planning, estimation of conservation concerns, and evaluation of success of past management actions. In contrast, short-term variation is obviously also

a sockeye salmon stock's a_t parameter decreases rapidly, then the standard Ricker model method for estimating target escapement (which depends in part on that a parameter) will put too much weight on older data (even when refit each year) and will not reflect the reduced mean productivity as promptly as a Kalman filter analysis, as demonstrated by Monte Carlo simulations comparing performances of the standard Ricker and Kalman filter methods (Peterman et al. 2000). The standard Ricker estimation method will thus be more likely to suggest an exploitation rate that is too high compared with a stock assessment method based on the Kalman filter that tracks such changes better. This difference in performance of the two methods results from their differing assumptions. The Ricker method (eq. 1) assumes that the productivity parameter was constant over the entire data set up through the latest data point. Thus, updating estimates annually with this model produces the average a value for the previous n years and repeats this process each year. In contrast, the Kalman filter method (eqs. 2, 3) is more flexible because it assumes that the productivity parameter a_t can differ each year of the data set, rather than being constant over some given period. An empirical analysis (Peterman et al. 2003) showed situations in which productivity of Bristol Bay, Alaska, sockeye salmon stocks decreased, but to meet management objectives, target escapements should have changed more than estimated by the standard Ricker analysis. That paper also showed analogous examples of the opposite situation, in which productivity increased, implying more improved prospects for sustainable harvest than a standard Ricker analysis.

Biologists have been well aware of such implications of temporal changes in salmon productivity for many years, but methods for dealing with them have been relatively ad hoc. For instance, Alaskan scientists have often split their sockeye salmon data sets into before and after 1976, the year that ocean productivity apparently increased dramatically and rapidly (H. Geiger, Alaska Department of Fish and Game, 1255 West 8th St., Juneau, Alaska, USA, personal communication). However, although that was an unusually large-magnitude event, it took about a decade for enough data to accumulate before that change became well-recognized by salmon scientists. Kalman filter analysis might have been able to highlight that change earlier and thus provide managers with more timely information on which to base their decisions.

To reduce the frequency of situations in which over-exploitation leads to conservation concerns, salmon biologists may therefore want to consider using the Kalman filter version of the Ricker stock–recruitment model. The same can also be said for reducing the frequency of situations in which less harvest is taken than could be sustainable; fewer such situations will increase social and economic benefits from catching salmon. In both cases, the Kalman filter is a comparatively useful method for tracking changes in productivity relatively quickly (Peterman et al. 2000). The Kalman filter could also be beneficial in the context of future climatic change, about which there is large uncertainty concerning its effects on the direction and rate of change in productivity of Pacific salmon stocks in different locations (Beamish 1995).

However, analysis of Kalman-filtered a_t time series com-

plements, rather than replaces, analysis of Ricker residuals. As noted above, at least some of the short-term variability apparent in the Ricker residuals, but not in the a_t time series, is highly correlated among stocks and likely reflects the influence of short-term variation in shared regional environmental forcing factors that is not well captured in the long-term signal estimated by the Kalman filter a_t time series. Because in this paper we are primarily interested in longer-term trends that are of special concern to management, our focus has been on smoothed Kalman filter a_t time series, but both indices reveal important aspects of temporal patterns in productivity. The juxtaposition of these indices in future research may help to differentiate between hypotheses about factors driving productivity within and across regions at different time scales.

Other methods for estimating temporal trends in salmon productivity could be compared with the Kalman filter in the future. For instance, some preseason forecasting models of salmon abundance use time-varying environmental covariates (e.g., Cass et al. 2006; Haeseker et al. 2008), and they could be applied retrospectively rather than just in a forecasting mode. If such mechanistically based models explain past variability well, then the nonmechanistic Kalman filter will be unnecessary for identifying shifts in underlying productivity. However, such mechanistically based models usually tend to not be very successful (Walters and Collie 1988; Myers 1998), so until reliable ones are found, a Kalman filter is probably the best option for describing past (not forecasting future) changes in underlying productivity. It works with spawner–recruit data and does not require environmental data. Furthermore, because a Kalman filter does not rely on covariates, it is not susceptible to climatic change altering parameters of existing relationships between environmental variables and productivity.

Mechanisms of change

There are at least three possible causes of the temporal changes in stock-specific a_t shown here. First, the population structure of a stock might have changed because of non-selective harvesting of co-migrating groups of fish, thereby causing less productive populations to gradually decrease in abundance and leaving mainly more productive populations. This could contribute to a gradual increase in a stock's productivity over time. Second, selective and heavy harvesting of the most productive populations composing a stock might have had the opposite effect, resulting in a gradual decrease in productivity of the aggregate stock. These two mechanisms related to harvesting pressure are unlikely, however, to explain the large and commonly observed reversal of time trends in productivity that we showed occurred during the study period. Thus, changing environmental conditions are another explanation that should be considered. For example, environmental changes may alter abundance and distribution of prey, predators, or competitors, or these changes may favor some age structure, life history types, or populations over others (Hilborn et al. 2003).

The importance of environmental factors in changing salmon productivity is supported by the correlations among our Kalman filter time series, which reveal positive covariation in productivity within and among certain regions that is consistent with shared environmental forcing factors at the re-

gional scale. There was also a surprising number of high correlations between quite distant stocks, not necessarily because of sharing similar physical and biological conditions, but possibly because they had monotonic, smoothed a_t series, which would tend to lead to high correlations (either positive or negative). However, even if some of these high correlations between separate stocks were due to chance arising from similar but unrelated time trends, the large number of positive correlations suggests that at least some of these cases result from shared environmental effects at very large spatial scales.

Similar to Pyper et al. (2005), we found that changes in productivity for stocks within the same geographic region or within nearby regions tend to be positively correlated both within species and to some extent also between species. Although smoothing could create spurious correlations where none existed before, if real underlying patterns did not exist, we would not expect the correlations to be so systematic and similar across nearby regions. Compared with analyses of Ricker and Beverton–Holt residuals for most of the same stocks examined here (Peterman et al. 1998; Pyper et al. 2001, 2002), our analyses of Kalman-filtered a_t time series produced higher correlations and also more cases of high correlations between more distant regions. As mentioned above, the higher correlations may result because common environmental or biological drivers are more clearly expressed in the Kalman filter series than in the noisier Ricker and Beverton–Holt residuals, but the correlations could also be at least partially an artifact of the relative smoothness of the Kalman filter series. Time series were predominantly positively correlated for all three species among Alaskan stocks, whereas negative correlations predominated between Alaskan stocks and stocks from BC and Washington, especially for pink salmon and sockeye salmon (though not necessarily for chum salmon). These negative correlations are consistent with the findings of Hare et al. (1999) and Mueter et al. (2002), who found that indices of productivity for northern stocks have been dominated by historical trends that were opposite to those in southern stocks, suggesting that the stocks in these areas are subject to different environmental forcing factors or that they are affected in opposite ways by shared environmental conditions (Mueter et al. 2002).

The timing of major changes in productivity trends apparent in the a_t series also suggests a connection to atmospheric and (or) oceanographic forcing factors. We found that most stocks of the three species in Alaska experienced a period of very low productivity in the 1960s followed by a sharp increase throughout the 1970s, consistent with the major regime shift in physical conditions around 1976–1977 that has been well documented for the eastern North Pacific (e.g., Trenberth and Hurrell 1994; Mantua et al. 1997; Hare et al. 1999). Beamish et al. (1999) describes various indices of climatic drivers that also indicate major regime shifts in conditions during that same period and that are associated with substantial changes in aggregate salmon catches.

While our results are thus consistent with the hypothesis that in some cases longer-term changes in productivity are at least partially associated with corresponding changes in oceanographic conditions, we found some exceptions that indicate more complex responses to factors than previously

thought. For example, major shifts in productivity trends, such as the one during the 1970s, did not always commence in the same year for all stocks affected, and both sockeye salmon and chum salmon stocks were often out of phase with their nearby conspecific stocks by several years. The explanation of these latter differences is unclear, but may be due to the interplay among environmental conditions and human-induced changes in habitats and amount of selective harvesting.

Differences among stocks

In addition to the productivity of stocks being slightly out of phase for some areas, large deviations from common regional patterns were also shown by individual component stocks, which again suggests complex responses to environmental drivers, human activities, or both. For instance, we identified several distinct “divergent” stocks that did not match the predominant regional pattern, including, among others, the Kodiak mainland and westside even-year pink salmon, Cook Inlet southern district even-year pink salmon, and sockeye salmon from Kodiak early and late Upper Station. Divergent stocks that do not conform to common regional productivity patterns might reflect real differences in biological or habitat conditions or might simply reflect factors such as relatively poor quality data on spawner abundance or an inappropriate level of aggregation of component populations (aggregation is expected to affect the quality of recruitment data through the extent of misallocation of catch to spawning stocks). However, poor data quality and aggregation appear unlikely as an explanation for most divergent stocks. For instance, Fraser River sockeye spawner and recruit data are considered some of the highest-quality data available, yet we showed above that the 16 stocks diverge considerably in their temporal patterns in a_t . Such differences among stocks also occur, but to a lesser extent, for Bristol Bay sockeye data, which are again considered high quality. In contrast, southeast Alaska pink spawner abundance data are viewed as much more uncertain, yet we showed a strong positive correlation among those a_t series. We believe that our results represent a conservative, one-sided interpretation of actual within-region coherence of productivity patterns. That is, cases in which we found an apparently highly correlated group of stocks may in fact include some stocks that are divergent, but the reverse is less likely to be true (i.e., a group of apparently uncorrelated or weakly correlated stocks is unlikely to be highly correlated in reality).

To the extent that the divergent series of Kalman filter a_t represent real diversity in life history traits or environmental conditions within a region, these a_t series and cases of low or negative correlations between these data series help identify components important for monitoring or conservation. For example, certain stocks within an area might be particularly sensitive (or insensitive) to climate-driven disturbances such as low water levels, flooding, or high water temperatures because of their run timing or the nature of their habitat. Consequently, large-scale climatic shifts may affect some stocks differently than others and may represent potential compensatory responses to environmental changes. Thus, special attention should be paid to monitoring stocks that deviate from the dominant productivity patterns in the

area. Conversely, groups of stocks with highly synchronous productivity trends, such as the Chignik and Alaska Peninsula pink salmon, may have limited ability to buffer the effects of environmental changes, at least with respect to the drivers that have historically been most important. It is especially important in such groups of stocks to recognize declining trends in productivity early and implement precautionary measures to reduce potential ecological and socio-economical impacts of low recruitment.

Though the extent of aggregation represented by our Pacific salmon stocks is too large to provide advice on efficient designs of monitoring programs, our data provide some pertinent information. In particular, our results underscore the importance of maintaining extensive, high-quality monitoring programs for spawners and catches by stock because of the large changes in productivity documented here. This is particularly important given the potential for future climatic and human-induced changes in marine and freshwater habitats. Without such monitoring programs, it might be difficult to detect and respond to reductions in productivity in an appropriate and timely manner. That monitoring, combined with the Kalman filter estimation procedure, can help to identify conservation and management issues related to productivity.

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References

- Adkison, M.D., Peterman, R.M., Lapointe, M.F., Gillis, D.M., and Korman, J. 1996. Alternative models of climatic effects on sockeye salmon, *Oncorhynchus nerka*, productivity in Bristol Bay, Alaska, and the Fraser River, British Columbia. *Fish. Oceanogr.* **5**: 137–152. doi:10.1111/j.1365-2419.1996.tb00113.x.
- Beamish, R.J. (Editor). 1995. Climate change and northern fish populations. *Can. Spec. Publ. Fish. Aquat. Sci.* 121.
- Beamish, R.J., Noakes, D.J., McFarlane, G.A., Klyashtorin, L., Ivanov, V.V., and Kurashov, V. 1999. The regime concept and natural trends in the production of Pacific salmon. *Can. J. Fish. Aquat. Sci.* **56**: 516–526. doi:10.1139/cjfas-56-3-516.
- Bigler, B. 1985. Kotzebue Sound chum salmon (*Oncorhynchus keta*) escapement and return data. Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development, Kotzebue, Alaska. Tech. Data Rep. 149.
- Botsford, L.W., and Paulsen, C.M. 2000. Assessing covariability among populations in the presence of intraseries correlation: Columbia River spring–summer chinook salmon (*Oncorhynchus tshawytscha*) stocks. *Can. J. Fish. Aquat. Sci.* **57**: 616–627. doi:10.1139/cjfas-57-3-616.
- Brennan, E.L., Bue, F.J., Lean, C.F., and Lingnua, T.L. 1998. Annual management report 1997: Norton Sound, Port Clarence, Kotzebue. Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development, Anchorage, Alaska. Reg. Info. Rep. No. 3A98-28.
- Campbell, R.D., Shaul, A.R., Witteveen, M.R., and Dinnocenzo, J.J. 1999. South Peninsula annual management report, 1998. Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development, Kodiak, Alaska. Reg. Info. Rep. No. 4K99-29.
- Clark, J.H. 1995. Biological escapement goals for even- and odd-year pink salmon returning to the Situk River and to Humpy Creek near Yakutat, Alaska. Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development, Douglas, Alaska. Reg. Info. Rep. No. 1J95-08.
- Clark, J.H. 2001a. Biological escapement goal for Andreafsky River chum salmon. Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development, Anchorage, Alaska. Reg. Info. Rep. No. 3A01-07.
- Clark, J.H. 2001b. Biological escapement goals for Kwiniuk and Tubutulik chum salmon. Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development, Anchorage, Alaska. Reg. Info. Rep. No. 3A01-08.
- Clark, J.H. 2001c. Biological escapement goal for chum salmon in district one of Norton Sound. Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development, Anchorage. Reg. Info. Rep. No. 3A01-09.
- Clark, J.H., and Sandone, G.H. 2001. Biological escapement goal for Anvik River chum salmon. Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development, Anchorage, Alaska. Reg. Info. Rep. No. 3A01-06.
- Cass, A., Folkes, M., Parken, C., and Wood, C.C. 2006. Pre-season run size forecasts for Fraser River sockeye for 2006. DFO Canadian Science Advisory Secretariat, Ottawa, Ont. Res. Doc. 2006/060.
- Chatfield, C. 1989. The analysis of time series: an introduction. Chapman and Hall, London, UK.
- Chelton, D.B. 1994. Commentary: short-term climatic variability in the Northeast Pacific Ocean. In *The influence of ocean conditions on the production of salmonids in the North Pacific*. Edited by W. Percy. Oregon State University Press, Corvallis, Ore. pp. 87–99.
- Eggers, D.M. 2001. Biological escapement goals for Yukon River fall chum salmon. Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development, Anchorage, Alaska. Reg. Info. Rep. No. 3A01-10.
- Fisheries and Oceans Canada. 2005. Canada's policy for conservation of wild Pacific salmon. Queen's Printer, Vancouver, B.C.
- Fraser, D.C., and Potter, J.E. 1969. The optimum linear smoother as a combination of two optimum linear filters. *IEEE Trans. Automat. Contr.* **14**: 387–390. doi:10.1109/TAC.1969.1099196.
- Haeseker, S.L., Peterman, R.M., Su, Z., and Wood, C.C. 2008. Retrospective evaluation of pre-season forecasting models for sockeye and chum salmon. *N. Am. J. Fish. Manag.* **28**: 12–29 [plus Appendixes 1 and 2 available online (A1-1–A2-7)]. doi:10.1577/M06-287.1.
- Hare, S.R., Mantua, N.J., and Francis, R.C. 1999. Inverse production regimes: Alaska and west coast Pacific salmon. *Fisheries*, **24**: 6–14. doi:10.1577/1548-8446(1999)024<0006:IPR>2.0.CO;2.
- Harvey, A.C. 1989. Forecasting, structural time series models, and the Kalman filter. Cambridge University Press, Cambridge, UK.
- Hilborn, R., Quinn, T.P., Schindler, D.E., and Rogers, D.E. 2003. Biocomplexity and fisheries sustainability. *Proc. Natl. Acad. Sci. U.S.A.* **100**: 6564–6568. doi:10.1073/pnas.1037274100.
- Kalman, R.E. 1960. A new approach to linear filtering and prediction problems. *J. Basic Eng.* **82**: 34–45.
- Mantua, N., Hare, S., Zhang, Y., Wallace, J., and Francis, R. 1997.

- A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* **78**: 1069–1080. doi:10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2.
- Meinhold, R.J., and Singpurwalla, N.D. 1983. Understanding the Kalman filter. *Am. Stat.* **37**: 123–127. doi:10.2307/2685871.
- Mueter, F.J., Peterman, R.M., and Pyper, B.J. 2002. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. *Can. J. Fish. Aquat. Sci.* **59**: 456–463. doi:10.1139/f02-020.
- Murphy, R.L., Shaul, A.R., and Dinnocenzo, J.J. 1999. North Alaska Peninsula commercial salmon annual management report, 1998. Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development, Kodiak, Alaska. Reg. Info. Rep. No. 4K99-34.
- Myers, R.A. 1998. When do environment–recruitment correlations work? *Rev. Fish Biol. Fish.* **8**: 285–305. doi:10.1023/A:1008828730759.
- Myers, R.A., Mertz, G., and Bridson, J. 1997. Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. *Can. J. Fish. Aquat. Sci.* **54**: 1400–1407. doi:10.1139/cjfas-54-6-1400.
- Owen, D.L., and Sarafin, D.R. 1999. Chignik management area annual finfish management report, 1996. Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development, Kodiak, Alaska. Reg. Info. Rep. No. 4K99-33.
- Pella, J.J. 1993. Utility of structural time series models and the Kalman filter for predicting consequences of fishery actions. In *Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations*, Anchorage, Alaska, 21–24 October 1992. Edited by G. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn. Alaska Sea Grant College Program, University of Alaska, Fairbanks, Alaska. AK-SG-93-02. pp. 571–593.
- Peterman, R.M., Pyper, B.J., Lapointe, M.F., Adkison, M.D., and Walters, C.J. 1998. Patterns of covariation in survival rates of British Columbian and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. *Can. J. Fish. Aquat. Sci.* **55**: 2503–2517. doi:10.1139/cjfas-55-11-2503.
- Peterman, R.M., Pyper, B.J., and Grout, J.A. 2000. Comparison of parameter estimation methods for detecting climate-induced changes in productivity of Pacific salmon (*Oncorhynchus* spp.). *Can. J. Fish. Aquat. Sci.* **57**: 181–191. doi:10.1139/cjfas-57-1-181.
- Peterman, R.M., Pyper, B.J., and MacGregor, B.W. 2003. Use of the Kalman filter to reconstruct historical trends in productivity of Bristol Bay sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* **60**: 809–824. doi:10.1139/f03-069.
- Pyper, B.J., and Peterman, R.M. 1998a. Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Can. J. Fish. Aquat. Sci.* **55**: 2127–2140. doi:10.1139/cjfas-55-9-2127.
- Pyper, B.J., and Peterman, R.M. 1998b. Erratum: Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Can. J. Fish. Aquat. Sci.* **55**: 2710. doi:10.1139/cjfas-55-12-2710.
- Pyper, B.J., Mueter, F.J., Peterman, R.M., Blackburn, D.J., and Wood, C.C. 2001. Spatial covariation in survival rates of Northeast Pacific pink salmon (*Oncorhynchus gorbuscha*). *Can. J. Fish. Aquat. Sci.* **58**: 1501–1515. doi:10.1139/cjfas-58-8-1501.
- Pyper, B.J., Mueter, F., Peterman, R.M., Blackburn, D.J., and Wood, C.C. 2002. Spatial covariation in survival rates of Northeast Pacific chum salmon. *Trans. Am. Fish. Soc.* **131**: 343–363. doi:10.1577/1548-8659(2002)131<0343:SCISRO>2.0.CO;2.
- Pyper, B.J., Mueter, F.J., and Peterman, R.M. 2005. Across-species comparisons of spatial scales of environmental effects on survival rates of Northeast Pacific salmon. *Trans. Am. Fish. Soc.* **134**: 86–104. doi:10.1577/T04-034.1.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Fish. Res. Board. Can. Bull.* 191.
- Ryall, P., Murray, C., Palermo, V., Bailey, D., and Chen, D. 1999. Status of Clockwork chum salmon stock and review of the Clockwork management strategy. Fisheries and Oceans Canada, Canadian Stock Assessment Secretariat, Ottawa, Ont., Canada. Res. Doc. 99/169.
- Schnute, J.T., and Kronlund, A.R. 2002. Estimating salmon stock–recruitment relationships from catch and escapement data. *Can. J. Fish. Aquat. Sci.* **59**: 433–449. doi:10.1139/f02-016.
- Su, Z., Peterman, R.M., and Haeseker, S.L. 2004. Spatial hierarchical Bayesian models for stock–recruitment analysis of pink salmon (*Oncorhynchus gorbuscha*). *Can. J. Fish. Aquat. Sci.* **61**: 2471–2486. doi:10.1139/f04-168.
- Trenberth, K.E., and Hurrell, J.W. 1994. Decadal atmosphere–ocean variations in the Pacific. *Clim. Dyn.* **9**: 303–319. doi:10.1007/BF00204745.
- Visser, H., and Molenaar, J. 1988. Kalman filter analysis in dendroclimatology. *Biometrics*, **44**: 929–940. doi:10.2307/2531724.
- Walters, C.J. 1986. Adaptive management of renewable resources. MacMillan, New York.
- Walters, C.J., and Collie, J.S. 1988. Is research on environmental factors useful to fisheries management? *Can. J. Fish. Aquat. Sci.* **45**: 1848–1854. doi:10.1139/f88-217.
- Wood, C.C., Rutherford, D.T., and Janz, L. 1999. Trends in abundance and pre-season 1999 stock size forecasts for major sockeye, pink, and chum salmon stocks in northern British Columbia. Fisheries and Oceans Canada, Canadian Stock Assessment Secretariat, Ottawa, Ont., Canada. Res. Doc. 99/126.
- Zeng, Z., Nowierski, R.M., Taper, M.L., Dennis, B., and Kemp, W.P. 1998. Complex population dynamics in the real world: modeling the influence of time-varying parameters and time lags. *Ecology*, **79**: 2193–2209.