Application of Regime Change Detection Methods to Productivity Analysis of Skeena Salmon Conservation Units

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Introduction

In this paper we apply a regime-shift detection methodology to uncover changes in the Ricker productivity parameter for salmon conservation units (CUs) in the Skeena watershed. In this paper, the term "regime shift" refers to the statistical concept of an abrupt change or discontinuity in the value of a model parameter, in the present case, the productivity parameter in the Ricker (1954) stockrecruitment model. The productivity parameter can help estimate sustainable harvest levels for individual CUs and inform appropriate management reference points. Therefore it is important to be able to detect, in a timely fashion, significant changes in productivity so that management decisions can be updated as appropriate.

Numerous studies have established that productivity varies with time for salmon stocks. For instance, Adkison et al. (1996) found that productivity for sockeye salmon stocks in Bristol Bay, Alaska increased rapidly in the 1970s. Peterman and Dorner (2012) demonstrated a sharp decrease in the productivity of Skeena sockeye stocks, beginning in the late 1980s and persisting through the 1990s. Using the methodology that we herein propose, Mueter et al. (2007) reported evidence for shifts in productivity for Pacific salmon stocks in 1974, and again in the late 1980s to mid 1990s.

We use the STARS algorithm developed by Rodionov (2004) to test for shifts in productivity. This method has several advantages over other regime-detection methodologies, notably that it can be used reliably toward the endpoints of time series, and has the ability to detect multiple shifts within the same series. The use of a discrete change framework, wherein productivity changes discretely and is constant between these changes, may also be of utility to stock management. For example, other techniques used to model changing productivity, such as the Kalman filter approach advocated by Peterman et al. (2000), require annual updating of productivity and hence of management targets. Alternatively, by modelling productivity as remaining constant between infrequent, discrete changes, management targets need only be updated when evidence of significant changes in productivity arrives.

The remainder of our report is structured as follows: Section 1 describes in detail our method of detecting changes in productivity, Section 2 presents our results, and Section 3 provides a brief discussion on the utility of our method for stock management.

1 Methods

We employ a two-stage method to detect and measure the size of shifts in productivity in Skeena salmon CUs. The first stage of the analysis uses the regime shift detection algorithm called STARS (for sequential *t*-test of analysis of regime shifts) to detect and time the occurrence of changes in productivity for each CU. The second stage uses the productivity shift timing estimated in the first stage to fit a stock-recruitment model in which the value of the productivity parameter is allowed to vary between different periods; the endpoints of these periods are determined by the estimated productivity shift dates. From this model, the resulting differences in the productivity parameter in each period is recovered, which enables us to compute the resulting changes in management statistics that depend on the value of the productivity parameter.

1.1 Detection and Timing of Productivity Changes

We fit the popular stock-recruitment model of Ricker (1954) to the stock-recruitment time series for each CU. The stock-recruitment relationship is given by

$$R_{i,t_{i,j}} = S_{i,t_{i,j}} \exp\left[\alpha_i - \beta_i S_{i,t_{i,j}} + \omega_{i,t_{i,j}}\right] \tag{1}$$

The notation in equation (1) is as follows:

- *i* is an index denoting the CU;
- $j = 1, ..., k_i$ is an index denoting the observation number within the timeseries for CU *i*, with k_i denoting the number of observations available for CU *i*;
- $t_{i,j}$ is a time index denoting the brood year for the *j*th observation within the time-series for CU *i*, with $t_{i,1} < \cdots < t_{i,k_i}$;
- $R_{i,t_{i,j}}$ and $S_{i,t_{i,j}}$ are respectively the recruitment and escapement levels for CU *i* in brood year $t_{i,j}$;
- $\omega_{i,t_{i,j}}$ is an error term, representing random variation around the mean stock-recruitment curve; and
- α_i and β_i are parameters, respectively representing the logarithm of productivity and the density-dependent effect for CU *i*.

In this specification, the parameter β_i is equal to the reciprocal of S_{max} , the stock that maximizes recruitment. Throughout, we assume that β_i is constant through time. Linearizing equation (1) yields the alternate form

$$\log\left(R_{i,t_{i,j}}/S_{i,t_{i,j}}\right) = \alpha_i - \beta_i S_{i,t_{i,j}} + \omega_{i,t_{i,j}},\tag{2}$$

allowing the stock-recruitment relationship to be estimated using standard linear techniques.

Because past values of recruitment affect stock abundance, the error series in equation (2) are likely not to be statistically independent. In order to use the STARS algorithm, it is essential that the series of residuals resulting from estimating equation (2) be statistically independent. Therefore, we model the error term as an AR(1) process:

$$\omega_{i,t} = \rho_i \omega_{i,t-1} + \varepsilon_{i,t}, \qquad |\rho_i| < 1, \qquad \varepsilon_{i,t} \sim \mathcal{N}\left(0, \sigma_i^2\right), \tag{3}$$

where ρ_i is the autocorrelation between consecutive values of the error term, and $\varepsilon_{i,t}$ is the white noise component of the error, and is uncorrelated between observations. Note that in equation (3), the lagged error term appearing on the right-hand side is from the previous brood year, which is not necessarily the previous observation in the time series for a given CU. That is, when the available time series for a particular CU contains a missing observation (such that for some observation j, $t_{i,j} - t_{i,j-1} > 1$), the autocorrelation between the jth error term and the (j-1)th error term is no longer equal to ρ_i . Instead, the autocorrelation decays exponentially according to the length of time between observations:

$$\operatorname{Corr}(\omega_{i,t_{i,j}},\omega_{i,t_{i,j-1}}) = \rho_i^{\Delta t_{i,j}},\tag{4}$$

where $\Delta t_{i,j} = t_{i,t_{i,j}} - t_{i,j-1}$ is the number of brood years between observations. When there is no gap between observations, $\Delta t_{i,j} = 1$ and so the autocorrelation reduces to ρ_i .

We use the correlation structure in equation (4) to estimate equation (2) by generalized least squares (GLS). The residuals obtained from this GLS fit, denoted by $w_{i,t_{i,j}}$, are then differenced and scaled to obtain an independent and identically-distributed series that is used as input into the STARS algorithm. The input series $\{e_{i,j}\}$ is constructed as

$$e_{i,j} = \frac{w_{i,t_{i,j}} - \hat{\rho}_i^{\Delta t_{i,j}} w_{t_{i,j-1}}}{\sqrt{\hat{\sigma}_i^2 \sum_{\nu=0}^{\Delta t_{i,j}-1} \hat{\rho}_i^{2\nu}}}, \qquad e_{i,1} = \sqrt{\frac{1 - \hat{\rho}_i^2}{\hat{\sigma}_i^2}} w_{i,t_{i,1}}; \tag{5}$$

in equation (5), $\hat{\rho}_i$ and $\hat{\sigma}_i^2$ denote the GLS estimates of ρ_i and σ_i^2 , respectively.

If the value of the productivity parameter α_i is constant throughout the period of observation for CU *i*, then model (1) is well-specified, and the resulting series of normalized residuals will have a constant mean throughout the sample. Alternatively, if there is a shift in productivity at some point during the series, then equation (1) is misspecified and the error term will no longer have a constant mean throughout the time series. This is why we use the standardized residuals series as an indicator of changes in productivity: abrupt changes in the value of α_i , the productivity parameter, will manifest as abrupt changes in the mean value of the series of standardized residuals.

We use the STARS algorithm developed by Rodionov (2004), which conducts running *t*-tests at each observation of the following hypothesis: the current mean value for the series differs from its value in previous periods. A given observation is flagged as potentially being the beginning of a productivity shift in the mean when that observation differs from the current mean at a significance threshold p. As further observations are added, these observations are used to test the hypothesis that the mean value of the series has changed in the direction indicated by the flagged observation. If, after a predetermined number (M) of observations past the flagged observation, the hypothesis that the mean has changed has not been rejected, a productivity change is declared at the flagged observation and testing continues with the new estimated value of the mean. Use of the STARS algorithm thus requires the choice of two parameters, the significance level p and the assumed period length M (in years). Following Mueter et al. (2007), we use the values p = 0.10, M = 10. Choosing p = 0.10makes the algorithm more sensitive to potential changes in productivity than a smaller value of p; however, practically all of the changes in productivity that we detected using p = 0.10 were large enough to be significant at p = 0.05, so our choice of the threshold p would not introduce a significant amount of error. In reporting our results below, we exclude shifts that are detected with fewer than three observations remaining in the time series, to avoid the possibility of declaring a productivity change on the basis of a single outlier near the end of a series.

The STARS algorithm has at least two important advantages over other methods of change detection. Firstly, it allows for the detection of multiple changes, where certain other methods assume only one change. Because some of the stock-recruitment series that we consider span more than fifty years, it seems plausible that productivity might shift more than once over the span of the series. Secondly, it allows changes in productivity to be detected up to the end of the time series, while other change detection methods deteriorate toward the end of the sample (Rodionov, 2004).

1.2 Quantification of Changes in Productivity

Once we obtain timings of productivity changes from the STARS method, for each CU in which we detect a change, we estimate a modified version of equation (2), which allows for different levels of productivity in between each change:

$$\log \left(R_{i,t_{i,j}} / S_{i,t_{i,j}} \right) = \alpha_i + \sum_{r=2}^{T_i} \delta_{i,r} \tau_{r,i,t_{i,j}} - \beta_i S_{i,t_{i,j}} + \omega_{i,t_{i,j}}, \tag{6}$$

where the parameters $\delta_{i,2}, \ldots, \delta_{i,T_i}$ are contrasts in productivity between the *r*th period and the first period for CU *i*; T_i is the number of productivity changes detected for CU *i*, plus one. The endpoints of the periods are determined by the estimated dates of the changes in productivity for the CU. The variables τ_r are indicators of the current period; $\tau_{r,i,t_{i,j}}$ is set to 1 if brood year $t_{i,j}$ lies within the *r*th period for CU *i*, and is set to 0 otherwise. Hence, productivity during the first period for CU *i* is α_i , and in subsequent periods $r \geq 2$ is equal to $\alpha_i + \delta_{i,r}$; positive values of $\delta_{i,r}$ indicate increases in productivity, relative to the first period, and negative values indicate decreases in productivity.

Having estimated the timing, size and direction of productivity changes for each CU, we proceed to translate these changes into their effects on two management indicators, the optimal harvest rate $(U_{\rm opt})$ and the maximum sustainable yield $(S_{\rm msy})$. Both of these indicators are increasing in the productivity parameter α_i , and are easily computed from estimates of productivity.

2 Results

2.1 Presence and Timing of Shifts in Productivity

Several CUs had insufficient data to be analyzed (Table 1). For those CUs that we were able to analyze, the presence of structural breaks in productivity differs significantly between species (Table 2; Figures 1–6). For instance, only one third of Chinook and chum CUs showed significant shifts in productivity (Chinook: Lower Skeena and Upper Bulkley; chum: Lower Skeena), while all but one of the coho and pink CUs (Middle Upper Skeena Odd pink) failed to exhibit a shift in productivity. Alternatively, the sockeye CUs were more evenly split between those in which a shift in productivity was detected (all four of the Babine runs, plus Kitsumkalum and Stephens) and those in which no shift was detected (Alastair, Azuklotz, Bear, Lakelse, Mcdonell, Morice and Swan). Note also that six sockeye CUs (Asitika, Damshilgwit, Johnston, Kitwancool, Motase, and Skeena River High) had insufficient data to be analyzed.

The sockeye CUs were both the largest in number in the analysis and the most varied in terms of data quality and the presence of productivity changes. Several of the sockeye CUs had long stock-recruitment series with few gaps, while the stock-recruitment series for other sockeye CUs covered short time intervals or were very sparse (Figures 5 and 6). In particular, the Babine CUs, Alastair, and Kitsumkalum all had time series covering a period in excess of fifty years, with only a very small number of gaps in the series or no gaps at all. Of these data-rich CUs, all except for Alastair showed significant evidence of a change in productivity. Of the remaining sockeye CUs analyzed (Azuklotz, Bear, Lakelse, Mcdonell, Morice, Stephens, and Swan), only Stephens showed evidence of a productivity change.

In terms of the timing of detected productivity changes, most changes were found in the mid- to late-1990s or early 2000s, although there were a few exceptions. A productivity change was found in 1966 for the Lower Skeena coho CUs, and two sockeye CUs, Babine Enhanced and Kitsumkalum, experienced productivity changes in the 1970s (1977 and 1978, respectively).

2.2 Size and Direction of Detected Productivity Changes

Both the magnitude and direction of the changes in productivity showed considerable variation (Table 3). Of the fifteen CUs in which changes in productivity were detected, nine experienced significant (p < 0.05) declines in productivity. In many cases the changes in productivity were quite large; for instance, decreases in the productivity parameter α_i were larger in magnitude than 2.0 for the Babine Late Wild and Babine Mid Wild CUs. Babine Enhanced, the only CU to experience multiple productivity shifts, experienced both increases and decreases in productivity. In this CU productivity was at its highest following a positive shift estimated to occur in 1977; towards the end of the series, in 2005, an additional shift resulted in productivity decreasing below its level at the beginning of the series.

In general, there were two clusters of changes in productivity (Figure 7). The earlier cluster occurred in the late 1960s to late 1970s, and involved increases in productivity (the exception was the Lower Skeena chum CU, where a decrease in productivity was detected in 1966). The later cluster, occurring in the mid 1990s to mid 2000s, generally saw decreases in productivity; of the 12 CUs experiencing productivity changes in this period, 9 significantly decreased in productivity, compared to 2 that significantly increased in productivity.

2.3 Effect of Productivity Changes on Management Indicators

As management statistics like the optimal harvest rate (U_{opt}) and the stock that maximizes yield (S_{msy}) depend on the value of the productivity parameter α , the shifts in productivity that we detected imply corresponding shifts in these statistics (Tables 4 and 5). In general, CUs that experienced smaller changes in productivity tended to experience smaller changes in U_{opt} than CUs that experienced larger changes in productivity. For example, the Lower Skeena Chinook CU experienced relatively small changes in both the productivity parameter α_i and in $U_{\rm opt}$ (-0.32 and -0.09, respectively) compared to the changes that were detected in the Babine Late Wild sockeye CU (changes of -2.05 in the productivity parameter and -0.65 in $U_{\rm opt}$). However, this trend was not universal; this is because U_{opt} is a nonlinear function of α and hence the change in U_{opt} depends not only on the size of the change in α , but also on its value before the change. Because $S_{\rm msy}$ depends on the density-dependent effect β as well as on productivity, changes in S_{msy} did not correspond in any consistent way to changes in productivity. In general, the pink salmon CUs experienced the largest changes in maximum sustainable yield, while experiencing moderate changes in the level of the productivity parameter α . This is indicative of the size of these CUs relative to the CUs of other species. By and large, of the CUs where productivity changes were detected, the largest ones experienced negative shifts in productivity, so that on aggregate the result was a negative shift in maximum sustainable yield.

3 Discussion

Several past studies have used a variety of techniques to study changes in productivity in salmon stocks. For instance, a recent study by Peterman and Dorner (2012) used Kalman filtering techniques to uncover evidence for large declines in productivity of sockeye salmon stocks in the Skeena watershed, beginning in the late 1980s and continuing throughout the 1990s. Our results for the Babine CUs are consistent with this finding. We detected decreases in productivity for each of the Babine CUs between 1993 and 2005; note that two such decreases were detected for Babine Enhanced, one in 1993 and another in 2005. We also detected an increase in productivity for the Stephens sockeye CU. Because this CU is quite small when compared to the Babine CUs, on the whole it would seem that the positive change in the productivity of this one CU was overshadowed by decreases in productivity for the larger Babine CUs.

The use of a discrete change approach to modelling productivity offers a possibly attractive method of measuring productivity changes for fisheries managers. Models where changes in productivity occur consistently require constant updating of models, such as through a Kalman filter, in order to produce upto-date productivity (and hence benchmark) estimates. Furthermore, it may not be practical to change escapement goals or harvest rates on a yearly basis. Modelling productivity as changing discontinuously and remaining constant between those changes allows a constant target to be set, and when significant evidence is received to indicate a shift in productivity, appropriate management action can be taken to adjust targets in response. Methods for productivity change detection, such as the STARS algorithm, can be tuned by choice of the algorithm parameters (in this case, the significance level p and period length M), in order to achieve an appropriate level of sensitivity to changes in the productivity parameter.

References

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Table 1: List of CUs included in (top half) and excluded from (bottom half) the STARS analysis. Column "Gaps" indicates the number of contiguous sets of observations in the time series that are incomplete due to missing stock or recruitment data.

Species	Included CUs	Total Observations	Gaps
Chinook	Kalum early	24	0
	Kalum late	25	0
	Lower Skeena	22	0
	Mid Skeena Large Lakes	25	0
	Mid Skeena Main Tributaries	24	1
	Upper Bulkley	18	0
Chum	Lower Skeena	45	2
	Middle Skeena	35	5
	Skeena Estuary	17	6
Coho	Lower Skeena	53	0
	Middle Skeena	53	0
Pink	Lower Skeena Odd	27	0
	Middle Upper Skeena Even	28	0
	Middle Upper Skeena Odd	27	0
	Nass Skeena Estuary Even	28	0
	Nass Skeena Estuary Odd	27	0
Sockeye	Alastair	47	1
	Azuklotz	20	4
	Babine Early Wild	48	0
	Babine Enhanced	48	0
	Babine Late Wild	48	0
	Babine Mid Wild	48	0
	Bear	16	6
	Kitsumkalum	45	2
	Lakelse	39	2
	Mcdonell	28	4
	Morice	42	5
	Stephens	35	6
	Swan	22	7
Species	Excluded CUs	Total Observations	Gaps
Chinook	Ecstall	6	0
Chum	—		
Coho	Upper Skeena	14	1
Pink	—		
Sockeye	Asitika	2	0
	Damshilgwit	5	0
	Johnston	12	3
	Kitwancool	6	1
	Motase	12	2
	Skeena River High	2	0

ID	CU	Productivity Shifts		
	Chinook			
CN01	Kalum early	_		
CN02	Kalum late	—		
CN03	Lower Skeena	1999		
CN04	Mid Skeena Large Lakes	—		
CN05	Mid Skeena Main Tributaries			
CN06	Upper Bulkley	1995		
	Chum			
CM01	Lower Skeena	2003		
CM02	Middle Skeena	—		
CM03	Skeena Estuary	—		
Coho				
CO01	Lower Skeena	1966		
CO02	Middle Skeena	1995		
	Pink			
PK01	Lower Skeena Odd	1995		
PK02	Middle Upper Skeena Even	1996		
PK03	Middle Upper Skeena Odd	—		
PK04	Nass Skeena Estuary Even	2004		
PK05	Nass Skeena Estuary Odd	1979		
	Sockeye			
SX01	Alastair	_		
SX02	Azuklotz	—		
SX03	Babine Early Wild	2003		
SX04	Babine Enhanced	1977, 1993, 2005		
SX05	Babine Late Wild	2003		
SX06	Babine Mid Wild	2005		
SX07	Bear			
SX08	Kitsumkalum	1978		
SX09	Lakelse	—		
SX10	Mcdonell	—		
SX11	Morice	—		
SX12	Stephens	1999		
SX13	Swan			

Table 2: Date of productivity changes detected by the STARS algorithm for each CU. A dash indicates that no productivity change was found for the indicated CU. Column "ID" indicates the code used to identify the CU in Figure 7.

Table 3: Contrasts in the productivity parameter α_i relative to the first period for each CU in which a productivity change was detected. Endpoints for periods are determined by the dates of the detected changes in productivity, given in Table 2, with "Period 1" referring to the time period from the beginning of the stock-recruitment series for the CU up to the first productivity change that was detected for the CU. *: Significant at the 10% level. **: Significant at the 5% level. ***: Significant at the 1% level. Column "ID" indicates the code used to identify the CU in Figure 7.

		Productivity relative to Period 1 in		
ID	CU	Period 2	Period 3	Period 4
	Chi	nook		
CN03	Lower Skeena	-0.32 **		
		(0.14)		
CN06	Upper Bulkley	+0.61		
		(0.41)		
	Ch	um		
CM01	Lower Skeena	-1.70 **		
		(0.75)		
	Co	oho		
CO01	Lower Skeena	-1.23 ***		
		(0.35)		
CO02	Middle Skeena	$+1.16^{***}$		
		(0.28)		
	Pa	ink		
PK01	Lower Skeena Odd	-0.69 **		
		(0.32)		
PK02	Middle Upper Skeena Even	-1.08 ***		
		(0.38)		
PK04	Nass Skeena Estuary Even	-0.99 **		
		(0.46)		
PK05	Nass Skeena Estuary Odd	+1.04 ***		
	·	(0.34)		
Sockeye				
SX03	Babine Early Wild	-1.91 ***		
		(0.38)		
SX04	Babine Enhanced	+1.16 ***	+0.32	-1.05 *
		(0.32)	(0.37)	(0.56)
SX05	Babine Late Wild	-2.05 ***		
		(0.43)		
SX06	Babine Mid Wild	-2.43 ***		
		(0.49)		
SX08	Kitsumkalum	$+1.11^{***}$		
		(0.41)		
SX12	Stephens	+1.09*		
	-	(0.62)		

Table 4: Contrasts in the optimal harvest rate U_{opt} implied by the contrasts in the productivity parameter α_i presented in Table 3. Endpoints for periods are determined by the dates of the detected changes in productivity, given in Table 2, with "Period 1" referring to the time period from the beginning of the stock-recruitment series for the CU up to the first productivity change that was detected for the CU.

	$U_{\rm opt}$ relative to Period 1 in			
CU	Period 2	Period 3	Period 4	
C_{ℓ}	hinook			
Lower Skeena	-0.09			
Upper Bulkley	+0.18			
(Chum			
Lower Skeena	-0.48			
Coho				
Lower Skeena	-0.25			
Middle Skeena	+0.24			
	Pink			
Lower Skeena Odd	-0.21			
Middle Upper Skeena Even	-0.34			
Nass Skeena Estuary Even	-0.34			
Nass Skeena Estuary Odd	+0.35			
Sockeye				
Babine Early Wild	-0.61			
Babine Enhanced	+0.20	+0.07	-0.34	
Babine Late Wild	-0.65			
Babine Mid Wild	-0.62			
Kitsumkalum	+0.36			
Stephens	+0.07			

Table 5: Contrasts in S_{msy} , the maximum sustainable yield, implied by the contrasts in the productivity parameter α_i presented in Table 3. Endpoints for periods are determined by the dates of the detected changes in productivity, given in Table 2, with "Period 1" referring to the time period from the beginning of the stock-recruitment series for the CU up to the first productivity change that was detected for the CU.

	$S_{\rm msy}$ relative to Period 1 in			
CU	Period 2	Period 3	Period 4	
(Chinook			
Lower Skeena	- 200			
Upper Bulkley	+ 230			
	Chum			
Lower Skeena	-22,542			
Coho				
Lower Skeena	-36,482			
Middle Skeena	+ 25,591			
	Pink			
Lower Skeena Odd	-399,042			
Middle Upper Skeena Even	$-332,\!240$			
Nass Skeena Estuary Even	$-595,\!361$			
Nass Skeena Estuary Odd	$+130,\!976$			
Sockeye				
Babine Early Wild	-38,267			
Babine Enhanced	+ 69,160	+25,767	$-119,\!552$	
Babine Late Wild	$-189,\!473$			
Babine Mid Wild	-15,066			
Kitsumkalum	+ 5,780			
Stephens	+ 271			

Figure 1: Standardized residuals from the stock-recruitment model 2 (solid line), along with mean values for the periods in between the productivity changes detected by the STARS method (dashed line), with M = 10, p = 0.1, for Chinook CUs.



Brood Year

Brood Year

Figure 2: Standardized residuals from the stock-recruitment model 2 (solid line), along with mean values for the periods in between the productivity changes detected by the STARS method (dashed line), with M = 10, p = 0.1, for chum CUs.





Brood Year

Figure 3: Standardized residuals from the stock-recruitment model 2 (solid line), along with mean values for the periods in between the productivity changes detected the STARS method (dashed line), with M = 10, p = 0.1, for coho CUs.



Figure 4: Standardized residuals from the stock-recruitment model 2 (solid line), along with mean values for the periods in between the productivity changes detected by the STARS method (dashed line), with M = 10, p = 0.1, for pink CUs.



Middle Upper Skeena Odd

Nass Skeena Estuary Even







Figure 5: Standardized residuals from the stock-recruitment model 2 (solid line), along with mean values for the periods in between the productivity changes detected by the STARS method (dashed line), with M = 10, p = 0.1, for sockeye CUs. (Continued in Figure 6.)







Brood Year



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Figure 6: Standardized residuals from the stock-recruitment model 2 (solid line), along with mean values for the periods in between the productivity changes detected by the STARS method (dashed line), with M = 10, p = 0.1, for sockeye CUs. (Continued from Figure 5.)













Figure 7: Timing and magnitude of shifts in productivity parameter α for CUs in which productivity shifts were detected. Contrasts in α are presented relative to the first value for each CU, so that values above the horizontal line indicate changes to productivity levels above their initial value, and values below the vertical line indicate changes to productivity levels below their initial value. Identifiers correspond to CUs appearing in Tables 2 and Tables 3.



Brood Year