

Use of the Kalman filter to reconstruct historical trends in productivity of Bristol Bay sockeye salmon (*Oncorhynchus nerka*)

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Abstract: Fisheries scientists and managers are concerned about potential long-term, persistent changes in productivity of fish stocks that might result from future climatic changes or other alterations in aquatic systems. However, because of large natural variability and measurement error in fisheries data, such changes are usually difficult to detect until long after they occur. Previous research using numerous Monte Carlo simulation trials showed that a Kalman filter performed better than standard estimation techniques in detecting such trends in a timely manner. Therefore, we used historical data along with a Kalman filter that included a time-varying Ricker a parameter to reconstruct changes in productivity (recruits per spawner at a given spawner abundance) of eight Bristol Bay, Alaska, sockeye salmon (*Oncorhynchus nerka*) stocks over the past 40 years. Productivity generally increased for most stocks but varied widely for others and dramatically decreased in another. Such large changes in productivity are important for management. They greatly affected optimal spawner abundances and optimal exploitation rates, suggesting that in the future, scientists should consider using models with time-varying productivity parameters.

Résumé : Les biologistes et les gestionnaires des pêches se préoccupent des changements potentiels permanents et à long terme dans la productivité des stocks de poissons qui peuvent résulter des changements climatiques futurs ou d'autres modifications des systèmes aquatiques. Cependant, à cause de la forte variabilité naturelle et des erreurs de mesure dans les données sur les pêches, de tels changements sont difficiles à déceler et souvent ne le sont que longtemps après leur apparition. Des travaux antérieurs qui ont utilisé de nombreux essais de simulations de Monte Carlo ont montré qu'un filtre de Kalman permettait de reconnaître ces changements plus efficacement et dans un intervalle de temps plus court que les méthodes habituelles d'estimation. Nous utilisons donc des données du passé avec un filtre de Kalman qui comprend un paramètre a de Ricker variable dans le temps pour représenter les changements dans la productivité (nombre de recrues par reproducteur à une abondance donnée de reproducteurs) de huit stocks de saumons rouges (*Oncorhynchus nerka*) de la baie de Bristol, en Alaska, au cours des 40 dernières années. En général, la productivité augmente chez la plupart des stocks, elle est très variable chez d'autres et elle connaît une chute spectaculaire chez l'un d'eux. Des changements d'une telle importance dans la productivité sont d'un grand intérêt pour les gestionnaires. Ils affectent l'abondance optimale des reproducteurs et le taux optimal d'exploitation, ce qui fait croire que, dans l'avenir, les biologistes devraient envisager l'utilisation de modèles où figurent des paramètres de productivité variables dans le temps.

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Introduction

Fisheries scientists and managers are concerned about potential long-term, persistent changes in productivity of fish stocks that might result from future climatic changes or alterations in habitat, food supply, or predators. Such "trends in productivity" — a phrase used in this paper to broadly characterize any systematic changes in recruits produced per spawner or per unit spawning biomass at a given spawner abundance — have been

discussed in the recent fisheries literature using various terms. These include low-frequency variability, regime shifts, decadal-scale variability, autocorrelation, and nonstationarity in productivity. Whatever their form, trends in productivity have important implications for management and industry (Walters 1987). In contrast to the short-term implications of rapid, year-to-year variability, trends in productivity may have profound long-term consequences for sustainable harvest rates and associated economic and social benefits. For example, during periods of low

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productivity, it may be critical that proportional harvest rates are lowered to reduce risks and increase the chance that fish stocks will persist.

Concerns about trends in productivity have been stimulated by observations of large changes in abundance indices of many fish stocks over periods of several years or more. Such changes may reflect the effect of harvesting, as well as changes in oceanographic conditions (Bakun 1996; Kawasaki 1991), food supply, predation, or other factors. For example, multi-decade-long periods of high and low sockeye salmon (*Oncorhynchus nerka*) abundance of the Karluk Lake (Alaska) stock have occurred during the last 2200 years, based on stable isotope analysis of sediment cores (Finney et al. 2000, 2002). As well, other species have shown large changes in abundance indices over the last 2000 years, long before fishing by humans began. The best known cases are for California sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) (Baumgartner et al. 1992; Jacobson and MacCall 1995). In addition, some authors have used catch data to contend that numerous Northeast Pacific salmon (*Oncorhynchus* spp.) stocks experienced multi-decade-long periods of high and low productivity in the 1900s as a result of climatic forcing (Hare et al. 1999).

To account for trends in productivity, which may have contributed to the above changes in abundance, researchers have developed models of population dynamics that assume time-varying productivity parameters (e.g., Walters 1986; Pella 1993; Walters and Parma 1996). However, these models have not been widely used in analyses of Pacific salmon stocks for at least two reasons. The first is pragmatic. Most researchers and managers probably do not recognize that such models are necessary. It is difficult to detect changes over time in the parameters of stock–recruitment curves because of relatively short data sets, large natural variability, and measurement errors. For instance, almost all analyses of Pacific salmon stocks use the Ricker (1975) stock–recruitment model and assume that its a and b parameters are constant over the entire data set. In some situations, researchers go one step further by partitioning their data into different blocks, which are assumed to represent periods of different productivity (e.g., pre- and post-1976 for analyses of sockeye salmon in Bristol Bay, Alaska; Hal Geiger, Alaska Department of Fish and Game, P.O. Box 25526, Juneau, AK 99801, personal communication). However, because of the large variability in typical data sets, such periods are only recognizable well after a change in productivity occurs (Adkison et al. 1996; Peterman et al. 1998). This does not help managers adjust their harvest strategies in a timely manner as productivity changes.

The second reason for the lack of wider use of models with time-varying parameters is that their performance at reflecting real changes in parameters has only recently been examined using comprehensive Monte Carlo simulations (Peterman et al. 2000). That analysis demonstrated that if the Ricker a parameter varies over time, a Kalman filter (state–space) formulation of the Ricker model with a time-varying a parameter performs better at tracking those changes than the standard Ricker model, which assumes that parameters are constant (Peterman et al. 2000). This superior parameter estimation of the Kalman filter approach held across

a wide variety of simulated trends in the Ricker a parameter for a salmon stock (e.g., step function, sine wave, autoregressive process). Consequently, the Kalman filter produced more accurate and precise estimates of the optimal number of spawners as the optimum changed over time than did either the standard linear regression estimation method for the Ricker model or Walters' (1990) bias correction to that method (Peterman et al. 2000).

This superiority of the Kalman filter formulation arises from its explicit partitioning of the observed variation in $\log_e(\text{recruits/spawner})$ into systematic changes over time in productivity (i.e., the “signal”) and random sources of variation that are independent of that trend (see Materials and methods). Thus, in contrast to traditional stock–recruitment models, the Kalman filter approach helps deal with one of the biggest challenges faced by fisheries scientists and managers when trying to detect changes in fish productivity, namely, separating important temporal trends from less important interannual variation. In general, managers need to respond to such trends in productivity by altering harvest or escapement goals, whereas responding to interannual variation would result in chasing “noise” rather than the underlying “signal”.

In this paper, we applied the Kalman filter approach to data for eight Bristol Bay sockeye salmon stocks to reconstruct trends in their productivity over the past 40 years. Previous analyses indicate that these stocks experienced large and persistent increases in productivity beginning in the mid-1970s (Adkison et al. 1996; Peterman et al. 1998). There is currently some debate over whether these stocks might have recently moved back to a less-productive regime. Our purpose was to use trends in productivity estimated by the Kalman filter approach to address the following questions. (1) What are the characteristics of trends in productivity in these Bristol Bay sockeye salmon stocks (e.g., magnitude and rate of changes)? (2) Are these characteristics similar across stocks? (3) What do estimated trends in productivity imply about changes in optimal abundance of spawners and optimal harvest rates? (4) Do these trends correspond with the widely studied “regime shift” in the mid-1970s in the Northeast Pacific Ocean? (5) Is there any evidence of more recent regime shifts? To estimate trends in productivity, we used two different forms of the Ricker model cast in the Kalman filter framework. In addition, we compared results for these two models with results based on the standard Ricker model.

Materials and methods

Data

We used age-specific abundances of spawners and adult recruits (catch plus spawning escapement) for the eight main Bristol Bay sockeye salmon stocks in Alaska (Branch, Egegik, Igushik, Kvichak, Naknek, Togiak, Ugashik, and Wood) from brood years 1956 through 1995, the latest brood year for stocks with complete data on 6-year-old recruits (Lowell Fair, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AL 99518, personal communication). We used the entire data set for each stock except the Kvichak River stock, which has large variations in abundance (over

two orders of magnitude). Although this provided large contrast in the data, there was no evidence of density dependence for the Kvichak stock in any stock–recruitment models that we examined (positive Ricker b parameter in eqs. 1 and 3 below). This created an upward curving stock–recruitment curve with an undefined optimal escapement and optimal harvest rate. For the purpose of this paper, we avoided this problem by omitting 3 years from the Kvichak data set (the 1960, 1965, and 1970 brood years, the last 3 years of the so-called “dominant cycle line” before the mid-1970s shift in productivity). These brood years had extremely large abundances of spawners and recruits relative to the intervening brood years. Given the large natural variability in survival rates, this small sample of three influential brood years masked evidence of density dependence. As noted below, this procedure made little difference to our reconstructed trends in productivity compared with using all data for the Kvichak stock, yet allowed us to compute estimates of optimal escapements.

Alternative models

We used three alternative stock–recruitment models. These were variations on the Ricker (1975) stock–recruitment model, which is almost universally used in studies of Pacific salmon. The first model was the standard Ricker model:

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

where S_t is abundance of spawners in brood year t , R_t is abundance of adult recruits of all ages produced by those spawners (i.e., the brood-year recruits), a is the mean productivity (in units of $\log_e(R/S)$) at low spawner abundance, and b reflects the effects of spawner abundance on productivity (i.e., density dependence). Typically, the residual errors (u_t) are assumed to be independently and normally distributed with mean zero and variance σ_u^2 . However, there was widespread evidence of autocorrelation in these residuals across stocks (e.g., Korman et al. 1995), thus violating the assumption of independence. To account for this autocorrelation, we modeled u_t as a first-order autoregressive (AR(1)) process:

$$(2) \quad u_t = \phi u_{t-1} + \varepsilon_t$$

where ϕ is the autocorrelation coefficient and the errors (ε_t) are independently and normally distributed with mean zero and variance σ_ε^2 . For an AR(1) process, $\sigma_u^2 = \sigma_\varepsilon^2/(1 - \phi^2)$. We refer to eqs. 1 and 2 together as the “standard Ricker” model. For that model, the parameters a and b are assumed to be constant over time.

Second, we formulated a Kalman filter “random-walk” (KF-RW) model to estimate parameters of the Ricker model. Kalman filter models are an example of the broad class of “state–space” models (Chatfield 1989); they consist of two parts. First, in our case, the “observation equation” (Chatfield 1989) describes the relationship between the observed quantities R_t and S_t :

$$(3) \quad \log_e(R_t/S_t) = a_t + bS_t + v_t$$

This equation differs from eq. 1 in one important way: the a parameter is subscripted by brood year to reflect changes over time in productivity, as governed by a second stochastic

process. The second part of the Kalman filter, the “system equation” (Chatfield 1989), describes how the a parameter varies over time; here it is a random walk:

$$(4) \quad a_t = a_{t-1} + w_t$$

The error terms v_t and w_t in eqs. 3 and 4 are assumed to be normally distributed and independent, with variances σ_v^2 and σ_w^2 , respectively. We used a simple, yet flexible, random walk in eq. 4 because no one knows the true temporal pattern of changes that have occurred in a_t . However, as shown by the theoretical analyses in Peterman et al. (2000), a random walk can perform well at tracking a wide variety of true underlying temporal trends in a_t . We formulated the KF-RW model (eqs. 3 and 4) to have a time-varying a parameter because Adkison et al. (1996) found that this parameter changed dramatically from the pre-1976 to the post-1976 period for most Bristol Bay sockeye stocks, whereas the Ricker b parameter did not. Furthermore, the only simulation study done to date evaluating the performance of various parameter-estimation techniques (Peterman et al. 2000) did so in the context of a temporal trend in the a_t parameter, and the KF-RW model performed the best.

The third model was also a Kalman filter model, but with a system equation in which a_t followed an AR(1) process (e.g., Zeng et al. 1998):

$$(5) \quad a_t = \bar{a} + \phi(a_{t-1} - \bar{a}) + w_t$$

where \bar{a} is the long-term mean for a_t . We refer to eqs. 3 and 5 together as the “KF-AR(1)” model. Equations 4 and 5 are equivalent when $\phi = 1$, hence the KF-RW model is a special case of the KF-AR(1) model. The standard Ricker model is also a special case of the KF-AR(1) model. This can be seen by substituting eq. 5 into eq. 3 and eq. 2 into eq. 1; when $\sigma_v^2 = 0$, $\bar{a} \equiv a$, and $w_t \equiv \varepsilon_t$. Thus, although both the standard Ricker model and the Kalman filter model can be formulated to include an AR(1) process, the key distinction is that the Kalman filter model explicitly separates variation in $\log_e(R/S)$ into variation in a_t (e.g., eq. 5) and random variation (v_t ; eq. 3) that is independent of the process governing a_t .

Finally, although the observation-equation error (v_t) can account for both natural sources of random variation in $\log_e(R/S)$ and variation due to measurement error, this formulation does not explicitly model measurement error in spawner abundances (S) in eq. 3. Methods such as Kalman filtering and the “errors-in-variables” approach can be used to incorporate measurement error in S (e.g., Schnute and Kronlund 2002); however, these approaches require specification of the measurement-error variance. Because levels of measurement error in estimates of spawner abundance are not known for the Bristol Bay sockeye stocks examined here, we did not explicitly model this process.

Reconstruction of historical trends in productivity

To derive historical time series of productivity, we fit the three forms of the Ricker model to each of the eight spawner–recruit data sets. For the standard Ricker model, parameters were estimated via maximum likelihood. For this constant-parameter model, the time series of residual errors (u_t in eq. 1) provides estimates of changes in productivity over time (e.g., Peterman et al. 1998).

In contrast to the time series of u_t , which reflects all sources of residual variation (rapid changes, trends, and measurement error) in $\log_e(R_t/S_t)$, the Kalman filter models attempt to isolate systematic changes in productivity through the estimation of a_t . Details of the estimation procedures for the Kalman filter models are provided in Appendix A. In brief, the Kalman filter procedure recursively estimated a_t each year based on the previous year's estimate, a_{t-1} , and the new observation of $\log_e(R_t/S_t)$. In the first year only, we used a diffuse prior distribution for the initial estimate, a_1 , with an arbitrary prior mean of 1.0 and a variance of 1.0. Other model parameters, all of which were assumed to be constant over time, were estimated using maximum likelihood. For the KF-RW model, the other parameters estimated were b , σ_v , and σ_w . For the KF-AR(1) model, we also estimated ϕ and \bar{a} . We formulated this analysis in S-Plus software (Venables and Ripley 1999). For more details on the Kalman filter method, also see Meinhold and Singpurwalla (1983), Harvey (1989), and Zeng et al. (1998).

For each stock, application of the Kalman filter to historical data on recruits and spawners resulted in a complete time series of annual a_t estimates from brood years 1956 through 1995. These are referred to as the "filtered" estimates (Harvey 1989), where each a_t estimate depends only on data up through year t . To derive the best estimates of historical productivity for each stock, we then produced "smoothed" estimates of a_t (Visser and Molenaar 1988). As detailed in Appendix A, the smoothed estimates were based on information provided by the entire time series of filtered a_t estimates. The smoothing approach worked backwards through time starting with the final brood year of the data series. The smoothed values of a_t are the minimum-variance unbiased estimates of a_t , as well as the maximum likelihood estimates (Fraser and Potter 1969). We emphasize that this procedure is *not* the same as simply applying a LOWESS or other common smoother. Instead, the smoothed Kalman filter estimates were derived from a quite different procedure in which the variance of each annual a_t estimate was used in a weighted calculation to obtain a_{t-1} (see Appendix A). Confidence intervals for the smoothed a_t series were derived from the smoothed posterior variance for a_t each year (Visser and Molenaar 1988).

To examine the degree of coherence in trends in productivity among stocks, we calculated Pearson product-moment correlation coefficients for pairwise comparisons between time series of reconstructed a_t values (or, in the case of the standard Ricker model, between time series of u_t). Data series for all comparisons were aligned by brood year.

In addition, we estimated autocorrelation functions for each time series of a_t (or u_t) estimates to examine the persistence of trends in productivity. From a practical management point of view, estimates of a_t should ideally be positively correlated with those in years $t + 6$ or $t + 7$. This is because for these stocks, about 84% of the fish mature by age 5 and 97% by age 6 years. Thus, parameter estimates for brood year t can only be obtained in year $t + 6$ after the 6-year-olds return as adult recruits (or in year $t + 5$ if one is willing to ignore a relatively small group of age-6 recruits). Any resulting change to management actions would then be applied in the following year at the earliest. Thus, for these stocks, manag-

ers can only take action based on revised parameter estimates 6 or 7 years after the brood year that experienced the change in productivity. Such actions will clearly be most appropriate if altered parameter values persist for that long. Autocorrelations of the a_t series estimate this persistence.

Time-varying optimal escapements and harvest rates

As shown below, the reconstructed Ricker a parameter for several stocks showed considerable temporal variation. We therefore estimated how optimal escapement (i.e., spawner abundance) changed over time. We used the entire data set to reconstruct the smoothed a_t values, as described above, and asked, knowing what we know now, what were the optimal escapements each year in the past if productivity changed as estimated? The Alaska Department of Fish and Game estimates optimal escapement as the abundance of spawners that produces maximum sustainable yield (MSY). This optimal escapement is a function of the a and b parameters. For the standard Ricker model, we estimated a constant optimal escapement across all brood years using estimates of a and b . In contrast, for the two Kalman filter models, we computed annual estimates of optimal escapement using the smoothed a_t estimates and the estimate of b . For a given combination of a and b estimates, we iteratively searched for the spawner abundance (S^*) that maximized the difference between total recruits and spawners, where the expected value of total recruits was estimated by exponentiating eq. 3:

$$(6) \quad R = S[\exp(a + bS + \sigma_v^2/2)]$$

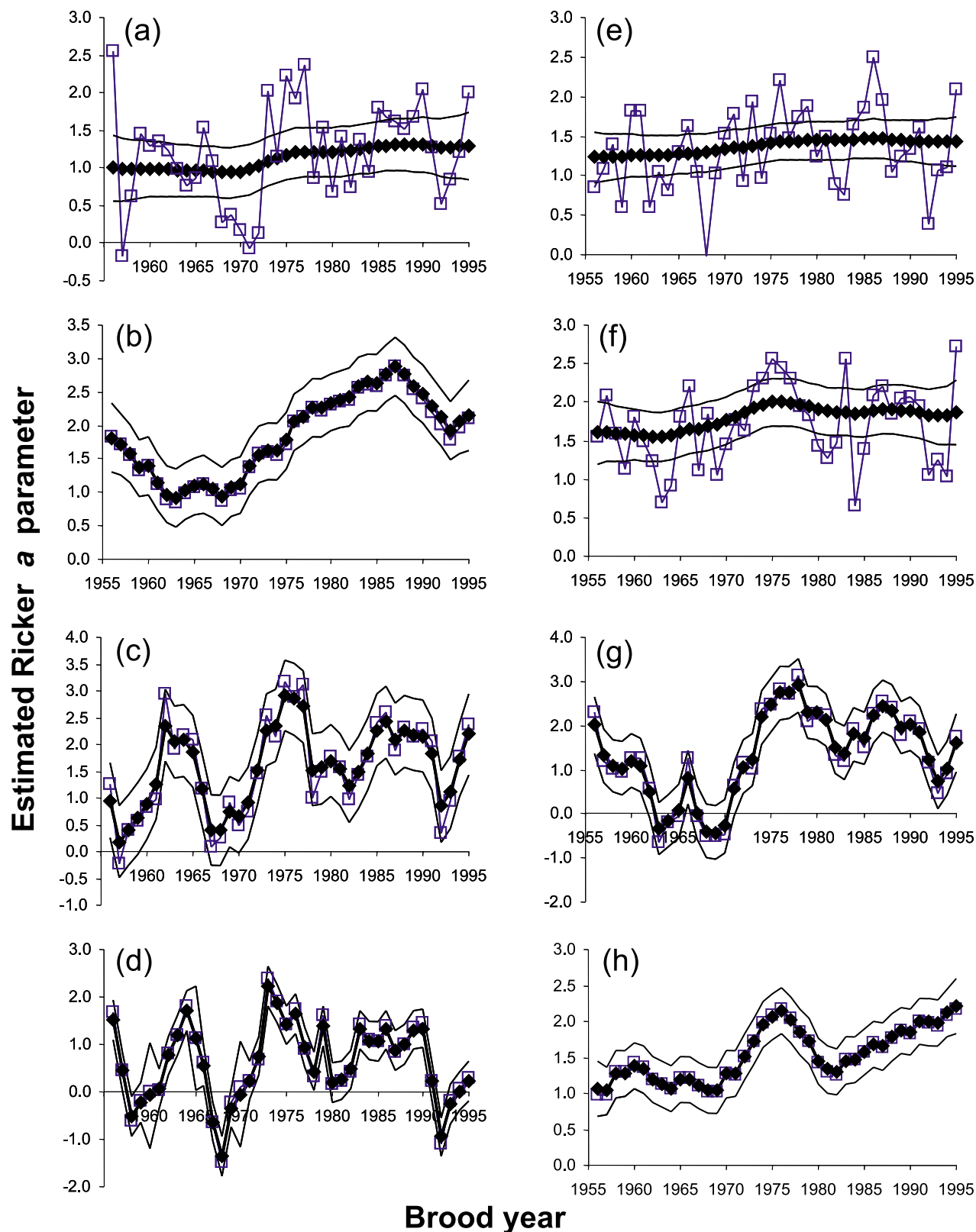
Adding $\sigma_v^2/2$ (or $\sigma_u^2/2$ for the standard Ricker model) to the exponent corrects for the bias incurred when back-transforming from the log-space of eq. 3 to eq. 6 (Hilborn and Walters 1992). The resulting optimal escapements (S^*) from the three models were compared with escapements that occurred historically.

Changes in productivity also affect the optimal proportion of recruits that should be harvested to meet a particular management objective. We estimated this optimal harvest rate as C^*/R^* , where R^* is the expected recruitment calculated from eq. 6 above using the optimal escapement, S^* , and the catch $C^* = R^* - S^*$. Again, we estimated a constant optimal harvest rate for the standard Ricker model, and annual (brood year specific) optimal harvest rates for the Kalman filter models. To compare these brood-year-specific harvest rates to historical harvest data (which are applied to several different brood classes of different ages in a given calendar year), we lined up the brood year optimal harvest rates with the actual harvest rates observed 5 years later. This is because the mean age at maturity of Bristol Bay sockeye salmon stocks is generally between 4.5 and 5 years. For the Kvichak and Ugashik stocks, it was not possible to estimate either S^* or optimal harvest rate for the few years in which smoothed a_t estimates were negative.

Results

All eight Bristol Bay sockeye salmon stocks showed evidence of trends in productivity as reflected by the time series of smoothed a_t estimates from the KF-RW and KF-AR(1) models (Fig. 1). However, most of our discussions will focus

Fig. 1. Smoothed a_t estimates from the Kalman filter AR(1) model (KF-AR(1); \square) and from the Kalman filter random-walk model (KF-RW; \blacklozenge) by brood year. Thin solid lines indicate 95% confidence limits for a_t estimates from the KF-RW model. Results are for the major sockeye salmon (*Oncorhynchus nerka*) stocks in Bristol Bay, Alaska: (a) Branch, (b) Egegik, (c) Igushik, (d) Kvichak, (e) Naknek, (f) Togiak, (g) Ugashik, and (h) Wood.



on results for the KF-RW model because it was deemed the most appropriate model for identifying long-term temporal trends in productivity for the following reasons.

The KF-AR(1) model did not add to our understanding of temporal trends in productivity. Its results were either identical to those from the standard Ricker model or very similar to the results from the KF-RW model. For four stocks — those with the lowest estimates of ϕ (Branch, Kvichak, Naknek, and Togiak) — the KF-AR(1) model gave a maximum likelihood estimate of zero for σ_v , the error in the observation equation (Table 1). This means that the KF-AR(1) model reduced to (i.e., produced the same parameter estimates as) the standard Ricker model (Table 1). Thus, for these four stocks, the KF-AR(1)-smoothed a_t estimates were equivalent to the residual errors from the standard Ricker model (those added to the estimate of the a parameter, i.e., $a + u_t$ from eq. 1). This resulted in highly variable time series of KF-AR(1)-smoothed a_t estimates, in particular for the Branch, Naknek, and Togiak stocks (Figs. 1a, 1e, and 1f). Such rapidly changing time series do not provide an appropriate basis for managers to alter escapement goals or harvest rates because they could end up “chasing noise” rather than an underlying varying signal reflecting changing mean productivity. In contrast, for the four stocks with larger ϕ estimates and nonzero σ_v estimates (Table 1; Egegik, Igushik, Ugashik, and Wood), the KF-AR(1) model produced a_t series almost identical to those of the KF-RW model (Figs. 1b, 1c, 1g, and 1h). The KF-RW model, on the other hand, produced smoothed a_t estimates for all eight stocks that exhibit trends on time scales that may be useful to fisheries managers (Fig. 1), i.e., patterns in productivity that do not vary as widely from year to year as residuals from the standard Ricker model. The remaining sections therefore emphasize results from the KF-RW model and are partly organized as answers to the five questions about trends in productivity that were posed in the Introduction.

What are the characteristics of the trends in productivity?

Some examples of time series of KF-RW smoothed a_t estimates illustrate the characteristics of trends in productivity. Smoothed a_t estimates for the Egegik stock increased from about 0.85 in brood year 1968 to about 2.8 in brood year 1987 (Fig. 1b). Recall that the a parameter is the expected value of the $\log_e(\text{recruits/spawner})$ at low spawner abundance, i.e., when there is little density dependence. Thus, the above change in a_t for the Egegik stock over the 20-year period represents about a sevenfold increase in median productivity at low spawner abundance ($\exp(a_t)$) from about 2.3 to 17 recruits/spawner. Although productivity of the Egegik stock increased, the Kvichak stock, which has historically been the most abundant sockeye salmon stock in the world, suffered about an 87% reduction in productivity from the 1973 to the 1995 brood years as estimated by the decrease in recruits per spawner at low abundance from ~ 9.3 to ~ 1.25 (Fig. 1d). (This series of a_t values for the Kvichak stock was not strongly influenced by the omission of the three data points; the correlation between this series and the a_t series that was reconstructed using all of the data was 0.95.) Some of the other stocks (e.g., Branch) showed a general increasing trend in mean productivity over the 40-year period. These and

other such changes over time in productivity have important implications for sustainable harvest rates and escapement goals, as discussed below.

For some stocks, the KF-RW model attributed much more of the observed change in $\log_e(R/S)$ to error in the observation equation (σ_v in eq. 3) than to system-equation error (σ_w in eq. 4). For example, for the Branch, Naknek, and Togiak stocks, σ_v was between 0.5 and 0.63, compared with σ_w between 0.05 and 0.09 (Table 1). The relative magnitude of those sources of error is called the signal-to-noise ratio, i.e., σ_w^2/σ_v^2 (Chatfield 1989), which is very small in these three cases (≤ 0.04). For the other five stocks, the KF-RW model estimated that the observation-equation error was about of the same order as, or smaller than, the system-equation error (Table 1), and the signal-to-noise ratio was at least 11 times greater than for the Branch, Naknek, and Togiak stocks. This is reflected by the greater variation over time in the a_t values reconstructed by the KF-RW model for those five stocks (Figs. 1b, 1c, 1d, 1g, and 1h) compared with the other three stocks.

The stocks differed considerably in the persistence of the changes in a_t values, as reflected by the autocorrelations at various lags. Four stocks (Branch, Egegik, Naknek, and Togiak) had moderately large autocorrelations at lag 6 and 7 years (ranging from 0.48 to 0.63 at 6 years and 0.36 to 0.54 at 7 years). The Ugashik and Wood stocks had small positive autocorrelations at those lags (0 to 0.17), and the Igushik and Kvichak were negatively autocorrelated (-0.19 to -0.43).

The filtered estimates of a_t (Fig. 2, \circ), i.e., those derived annually by the KF-RW model, were quite similar to the smoothed KF-RW estimates of a_t (Fig. 1), which were derived by the Kalman filter working backwards after all annual estimates of a_t were made for the entire data set. Across brood years 1957–1995, the pairwise correlations between these two series for each stock ranged from 0.76 for Branch to 0.99 for Ugashik, with a median r of 0.97 and mean of 0.88.

Are the trends shared among the stocks?

The extent to which the eight stocks of Bristol Bay sockeye salmon encounter similar environmental conditions should be reflected in the correlations among their temporal patterns in productivity. Correlations among the KF-RW smoothed a_t estimates for different stocks indicate that changes in productivity were widely shared among those stocks (Fig. 3b). These smoothed estimates of a_t tended to show greater positive covariation in productivity among the eight stocks than previously (Peterman et al. 1998) indicated by simply examining correlations among residuals in $\log_e(R/S)$ from the standard Ricker model (i.e., u_t from eq. 1). The median of the 28 pairwise correlations among the eight time series of KF-RW smoothed a_t estimates (Fig. 3b) was 0.65 (mean = 0.6), compared with the median of correlations among the u_t residuals of 0.43 (mean = 0.43) for the standard Ricker model (Fig. 3a).

This shared variation among stocks is even more evident when time series of a_t (Fig. 1) or u_t are standardized (mean of zero, standard deviation of 1) and superimposed on one graph (Fig. 4). Standardized estimates from both the standard Ricker model (Fig. 4a) and the KF-RW model (Fig. 4b) indicate a common tendency among all eight stocks to show

Table 1. Optimal parameter values estimated by maximum likelihood for each of the Bristol Bay sockeye salmon stocks for the constant parameters of the two forms of the Kalman filter, a random-walk model (eqs. 2 and 3) and an autoregressive (AR(1)) model (eqs. 2 and 4).

	Branch	Egegik	Igushik	Kvichak	Naknek	Togiak	Ugashik	Wood
Kalman filter random-walk (RW) model								
σ_v	0.63 (0.08)	0.38 (0.06)	0.43 (0.16)	0.22 (0.37)	0.51 (0.06)	0.50 (0.07)	0.38 (0.15)	0.26 (0.05)
σ_w	0.08 (0.09)	0.25 (0.08)	0.62 (0.17)	0.74 (0.20)	0.05 (0.05)	0.09 (0.10)	0.58 (0.15)	0.21 (0.06)
σ_w^2/σ_v^2	0.02	0.42	2.04	11.6	0.01	0.04	2.27	0.64
b	-1.568 (0.51)	-0.305 (0.20)	-1.773 (0.41)	-0.022 (0.03)	-0.320 (0.14)	-4.294 (1.13)	-0.453 (0.16)	-0.617 (0.11)
Log-likelihood	-4.18	5.91	-12.61	-10.87	3.85	3.79	-8.87	17.75
Kalman filter AR(1) model								
σ_v	0.00 (0.43)	0.37 (0.07)	0.17 (0.66)	0.00 (0.21)	0.00 (0.82)	0.00 (0.87)	0.23 (0.32)	0.25 (0.05)
σ_w	0.61 (0.07)	0.27 (0.09)	0.74 (0.22)	0.71 (0.08)	0.52 (0.06)	0.51 (0.06)	0.67 (0.18)	0.22 (0.06)
Mean a	1.155 (0.17)	1.883 (0.58)	1.623 (0.32)	0.568 (0.29)	1.350 (0.19)	1.714 (0.20)	1.265 (0.46)	1.709 (0.30)
b	-1.844 (0.50)	-0.271 (0.20)	-1.746 (0.41)	-0.026 (0.03)	-0.289 (0.13)	-3.752 (0.98)	-0.432 (0.16)	-0.614 (0.11)
ϕ	0.24 (0.15)	0.91(0.09)	0.58 (0.20)	0.56 (0.13)	0.17 (0.16)	0.25 (0.17)	0.76 (0.14)	0.84 (0.12)
Log-likelihood	-0.33	6.67	-8.90	-5.90	6.33	6.44	-6.69	19.39
Standard Ricker model (with an AR(1) error term)								
σ_ε	0.61 (0.07)	0.54 (0.06)	0.76 (0.09)	0.71 (0.08)	0.52 (0.06)	0.51 (0.06)	0.72 (0.08)	0.39 (0.04)
a	1.155 (0.17)	1.684 (0.35)	1.618 (0.31)	0.568 (0.29)	1.350 (0.19)	1.714 (0.20)	1.270 (0.44)	1.605 (0.21)
b	-1.844 (0.50)	-0.146 (0.21)	-1.746 (0.41)	-0.026 (0.03)	-0.289 (0.13)	-3.752 (0.98)	-0.436 (0.16)	-0.625 (0.12)
ϕ	0.24 (0.15)	0.68 (0.12)	0.56 (0.14)	0.56 (0.13)	0.17 (0.16)	0.25 (0.17)	0.72 (0.11)	0.59 (0.14)
Log-likelihood	-0.33	4.57	-8.91	-5.90	6.33	6.44	-6.76	17.19

Note: Standard errors (SE) of these parameter values are in parentheses. Analyses were based on data for abundances of recruits and spawners expressed in millions of fish. Optimal parameter estimates and their standard errors are also given for the standard Ricker model, which assumes an AR(1) error structure. σ_v is the standard deviation of the observation-equation error for eq. 3, σ_w is the standard deviation of the system-equation error for eqs. 4 and 5 for the Kalman filter random-walk and Kalman filter AR(1) models, respectively, and σ_w^2/σ_v^2 is the signal/noise ratio. σ_ε is the standard deviation of the error term for eq. 2 (the standard Ricker model). Other parameter estimates are for b , mean a , and ϕ (autocorrelation coefficient in eq. 5). Log-likelihood values are provided for each model.

Fig. 2. Filtered (○) and smoothed (◆) estimates of a_t derived by the Kalman filter random-walk (KF-RW) model, by brood year, for sockeye salmon (*Oncorhynchus nerka*) stocks in Bristol Bay, Alaska: (a) Branch, (b) Egegik, (c) Igushik, (d) Kvichak, (e) Naknek, (f) Togiak, (g) Ugashik, and (h) Wood.

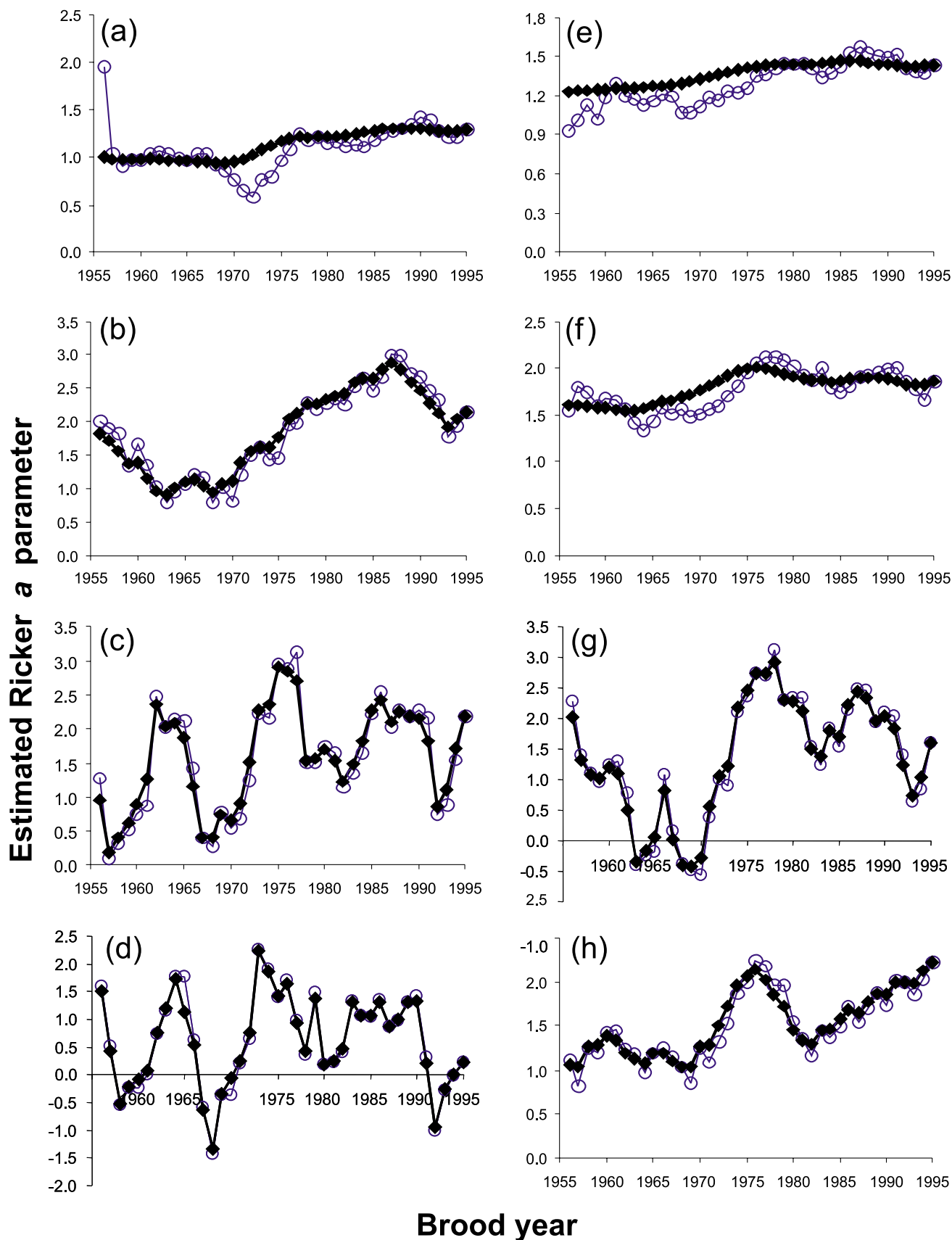
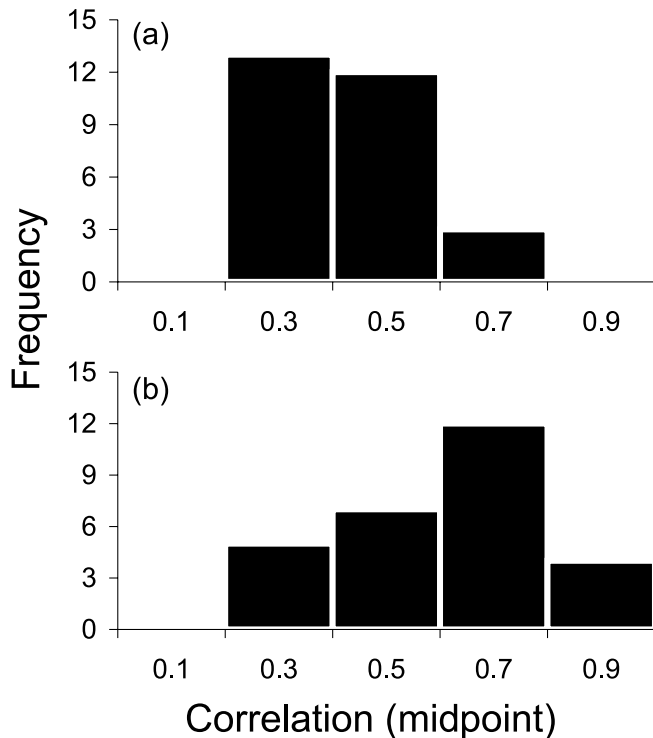


Fig. 3. Frequency distributions of the 28 correlations (a) among residuals from the standard Ricker model (u_t in eq. 1) in units of $\log_e(\text{recruits/spawner})$ and (b) among smoothed a_t estimates from the Kalman filter random-walk (KF-RW) model.



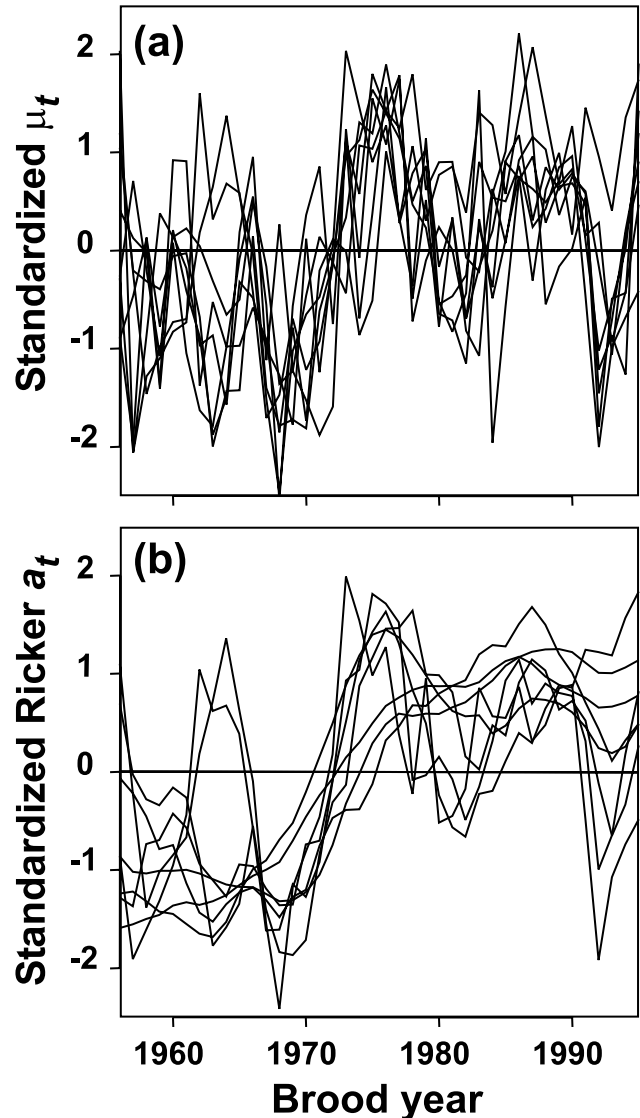
a rapid increase in productivity beginning in the late-1960s brood years. This tendency is particularly clear in the KF-RW results (Fig. 4b) because the Kalman filter attributed some of the high-frequency variation in the data to the variance in the observation equation (“noise”, which likely includes random process error and measurement error), thus isolating more of the underlying trend (“signal”) in mean productivity.

Some important differences among stocks also emerge from the standardized a_t values in Fig. 4b. Two stocks, the Igushik and Kvichak, were unusual in having relatively high a values in the 1960s brood years. More interestingly, starting with brood year 1990, the coherence among stocks observed since the late 1960s broke down to some extent as the trends in a_t diverged for different stocks (Fig. 4b). In this post-1990 period, the Kvichak stock had the largest negative deviations in a values from the long-term mean, whereas the Wood stock had the largest positive deviations.

What are the implications of trends in productivity for optimal escapements and harvest rates?

The changes in a_t exhibited by the Bristol Bay sockeye salmon stocks, especially the relatively rapid changes within 10-year periods in the Igushik, Kvichak, and Ugashik stocks (Figs. 1c, 1d, and 1g), are important to management. The a_t values for the Igushik and Ugashik stocks, for instance, both increased over a range of about three over an 8-year period starting with brood year 1969 and decreased by about one-third to one-half of that over the next 7 years. Because optimal management regulations are a function of the parameter values of the Ricker model (Ricker 1975), such strong time

Fig. 4. Standardized time series for all eight Bristol Bay sockeye salmon (*Oncorhynchus nerka*) stocks of (a) residuals from the standard Ricker model (u_t in eq. 1) and (b) smoothed a_t estimates from the Kalman filter random-walk (KF-RW) model. Time series were standardized to have a mean of zero and a standard deviation of 1.



trends in productivity suggest that in such situations, appropriate harvest rates and escapement goals should be revised appreciably and in a timely manner, more so than would be the case when management advice is based on a standard (i.e., constant-parameter) Ricker model.

For instance, optimal escapements (defined as those producing MSY) based on the a_t values reconstructed by the KF-RW model changed annually and in some years differed considerably from the optimal values estimated by the standard Ricker model (Fig. 5). Brood years in which KF-RW estimates of a_t increased (Fig. 1) were associated with increases in estimates of optimal escapement (Fig. 5). For some stocks, the KF-RW estimates of optimal escapement were greater than the actual escapements in most years (e.g., Branch, Egegik, and Naknek), whereas in other stocks, the

Fig. 5. Actual spawner abundances (solid line) and optimal spawner abundances (◆ for the Kalman filter random-walk (KF-RW) model; broken line for the standard Ricker model) by brood year for 1956–1995. Four data points were off-scale for actual spawner abundances, three for Branch in 1956 (0.78 million fish), 1959 (0.83), and 1960 (1.24), and one for Igushik in 1980 (1.99). The broken line for the Egegik is off-scale at 4.4 million fish. Results are for sockeye salmon (*Oncorhynchus nerka*) stocks in Bristol Bay, Alaska: (a) Branch, (b) Egegik, (c) Igushik, (d) Kvichak, (e) Naknek, (f) Togiak, (g) Ugashik, and (h) Wood.

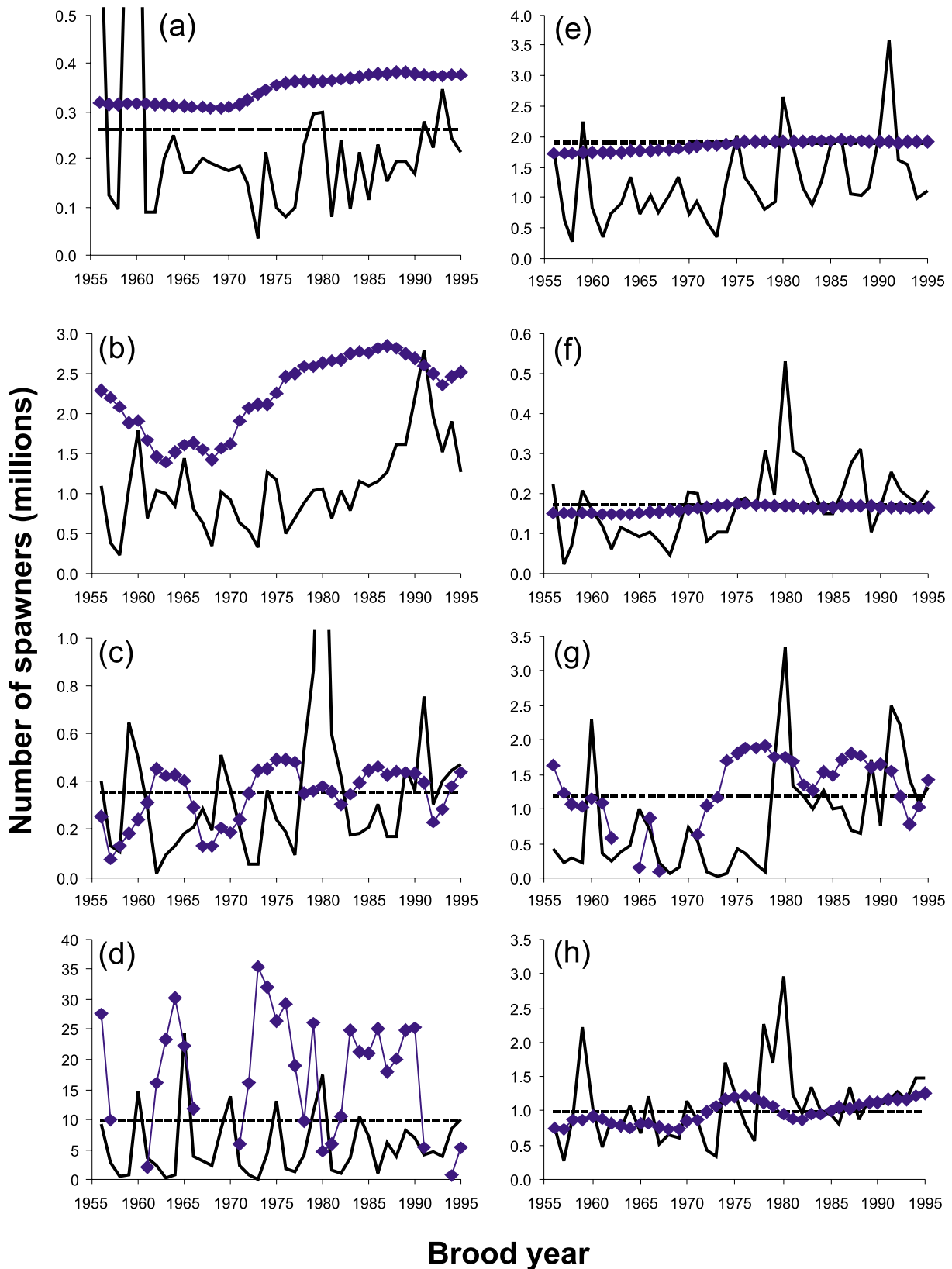
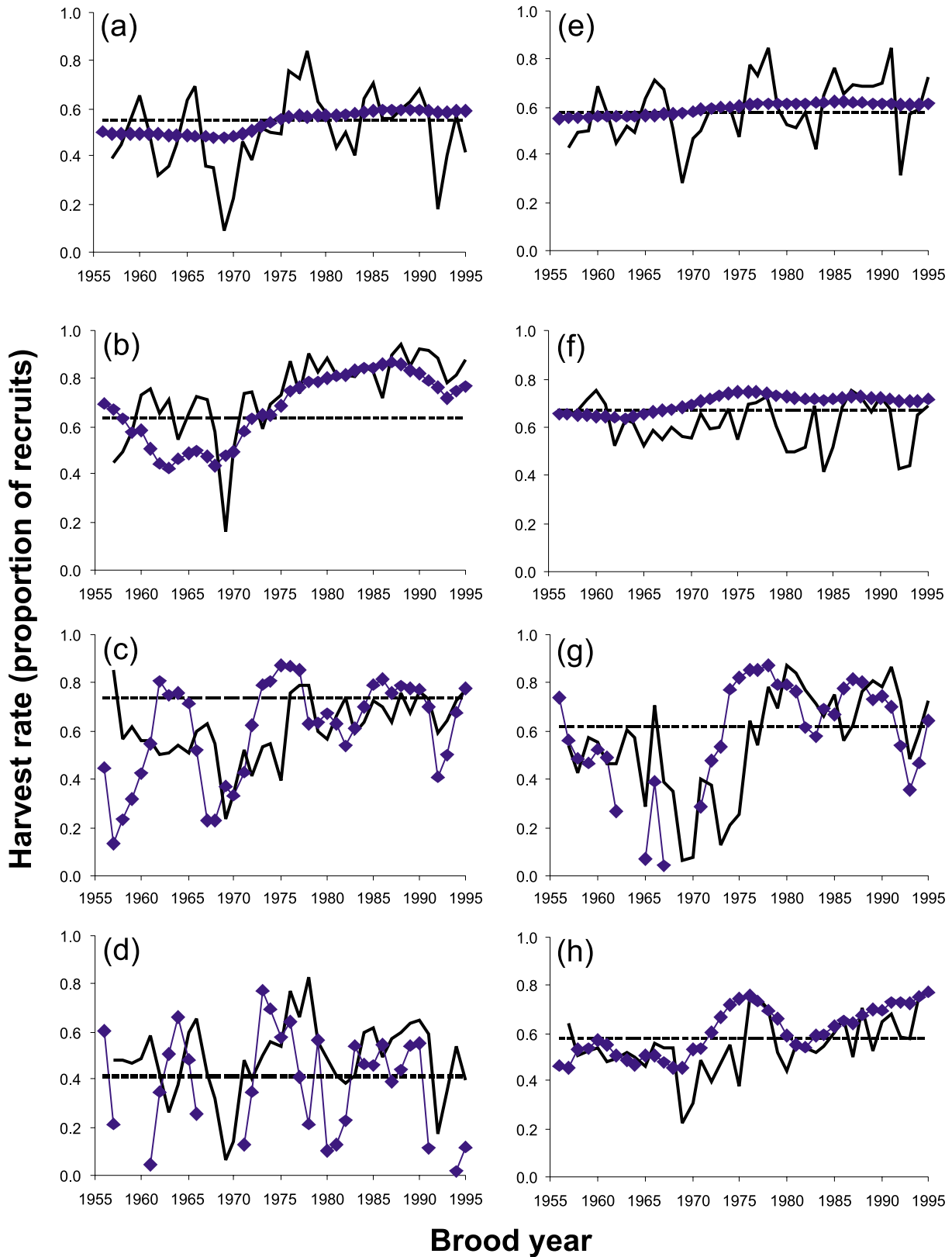


Fig. 6. Optimal harvest rates (proportion of recruits) for the standard Ricker model (broken line) and the Kalman filter random-walk (KF-RW) model (◆), by brood year t . Estimates for the Ricker model were based on single a , b , and σ_u^2 parameter values for each stock, whereas optimal harvest rate estimates for the KF-RW model were based on the reconstructed time-varying a_t values and the fixed b and σ_v^2 estimates. Actual proportional harvest rates (solid line) that occurred in calendar year $t + 5$ are plotted at brood year t , reflecting a 5-year age-at-maturity. Results are for sockeye salmon (*Oncorhynchus nerka*) stocks in Bristol Bay, Alaska: (a) Branch, (b) Egegik, (c) Igushik, (d) Kvichak, (e) Naknek, (f) Togiak, (g) Ugashik, and (h) Wood.



estimated and actual escapements were in a similar range (Fig. 5).

Optimal proportional harvest rates estimated by the KF-RW model were generally in similar ranges to both the actual historical harvest rates and the optimal rates derived from the standard Ricker model (Fig. 6). However, as with optimal escapements, there were periods when these rates differed considerably. For instance, in the late-1960s brood years when a_t values tended to be relatively low (Fig. 1), the KF-RW estimates of optimal harvest rate were much lower than the standard Ricker model estimates (e.g., Figs. 6b, 6c, 6g, Egegik, Igushik, and Ugashik, respectively). When a_t values were high in the 1970s brood years for most stocks, optimal exploitation rates from the KF-RW model tended to be higher (by between 0.01 and 0.36) than suggested by the standard Ricker model and higher (by between 0.08 and 0.4) than actual harvest rates (e.g., Togiak, Igushik, Ugashik, and Wood) (Fig. 6). In other stocks, all three harvest rates were quite comparable during that period of increasing productivity.

Discussion

The reconstructions from the Kalman filter random-walk (KF-RW) model showed strong evidence of temporal changes in productivity of the eight Bristol Bay sockeye salmon stocks. Many stocks showed a general tendency for increasing Ricker a parameters over time during the 40-year period, reflecting increased recruits produced per spawner at low abundance. Some stocks showed 5- to 28-fold increases in recruits per spawner at low spawner abundance over this period, but even stocks without such dramatic changes showed increased recruits per spawner (e.g., Naknek, 27% increase; Branch, 45%).

However, the nature of these trends varied qualitatively among certain groups of stocks. Specifically, the Igushik, Kvichak, and Ugashik stocks showed wide-ranging increasing and decreasing trends over a decade or less, whereas the Egegik and Wood stocks showed fairly steady but less-rapid large changes over two or more decades. The latter decadal-scale changes are consistent with Finney et al.'s (2000) conclusion that Karluk Lake sockeye salmon vary over multi-decadal scales (Karluk Lake is on the south side of the Alaskan peninsula from Bristol Bay), if those variations were due to changes in productivity. Our time trends in productivity also show examples that are qualitatively consistent with Ware's (1995) three dominant periodic components of physical oceanographic and atmospheric variables (5–7, 25, and 50 years).

Although it is clear that the point estimates of a_t from the Kalman filter random-walk model show important changes through time for most stocks, the confidence intervals on those estimates are too small. This is because the confidence limits are conditional on the maximum likelihood estimates of the constant parameters in Table 1. If full uncertainty in those parameters were accounted for, the confidence intervals would be wider.

Management implications

Some stocks showed large changes over time in optimal escapement as estimated by the KF-RW model, and these estimates often differed considerably from optimal escapements

estimated by the normal approach, i.e., a standard Ricker model. These differences have important management implications. They suggest that using a Kalman filter approach that assumes some form of time-varying parameter may lead to different escapement goals and perhaps greater long-term benefits, as demonstrated by the simulation results of Peterman et al. (2000).

A comparison of actual escapements with optimal escapements derived from the Kalman filter model shows that in some stocks such as the Wood stock, actual escapements were near the optimal values and had similar temporal trends. However, in other cases, actual escapements were consistently lower than optimal values (Branch, Egegik, and Naknek). Note that actual escapements reflect not only the escapement goals of the management agency, but also differences between desired and target escapements caused by inherent difficulties of in-season estimation of run sizes and management of fishing effort.

From the viewpoints of conservation and economic benefits, the proportion of recruits harvested should go down when stocks become less productive and increase when they become more productive. The KF-RW optimal harvest rate estimates do this because of the constant b parameter and time-varying a values. Actual historical harvest rates also tended to change in the correct direction as a_t values changed, although often with a several-year lag behind the optimal ones estimated by the KF-RW model (Igushik, Kvichak, Ugashik, and Wood stocks). In addition, actual proportional harvest rates tended to vary more widely than the KF-RW optimal values (lower than needed or higher than advisable). Thus, costs were incurred through foregone present or future catches. These results suggest that there are advantages to using models with time-varying parameters, which can help reduce risks when populations become relatively unproductive and take advantage of increased productivity.

Generally, the actual and estimated optimal harvest rates were in closer agreement than were the actual and estimated optimal spawner abundances. This difference largely reflects the fact that the optimal proportional harvest rate for a goal of MSY is only a function of the Ricker a parameter, whereas the optimal spawner abundance is a function of both Ricker a and Ricker b parameters. The b parameter for a given stock is often imprecisely estimated because of a lack of good contrast in the data, few data points at high abundance, and large variability. Our results indicate that despite the constant escapement policy used by the Alaska Department of Fish and Game, actual proportional harvest rates were historically closer to the optimal harvest rates estimated by the KF-RW than actual escapements were to optimal escapements. This suggests that proportional harvest-rate targets might be more reliably estimated and easier to achieve.

The difficulty of recognizing changes in underlying mean productivity of salmon in a timely manner amid highly variable data suggests that salmon scientists and managers need more sophisticated models, such as the Kalman filter. This need is particularly acute in the presence of climatic change. Although climate is likely to alter salmon productivity, there is considerable uncertainty about the direction and rate of change in productivity on the west coast of North America (Beamish 1995). Models with time-varying parameters should

also improve estimates of temporally trended but uncertain effects of human activities and natural processes on freshwater habitat for salmon (e.g., destruction of spawning or rearing habitat through erosion or sedimentation).

Although we have shown that the KF-RW model has advantages over standard methods for several Bristol Bay sockeye salmon stocks, this advantage will likely be smaller for the four stocks that exhibit little positive temporal autocorrelation in productivity (e.g., Igushik, Kvichak, Ugashik, and Naknek). For example, such low autocorrelation at a lag of 6 or 7 years will reduce the benefits of the KF-RW model as a tool for setting escapement goals because the productivity estimated in a given year may no longer be applicable a generation later. As well, British Columbia sockeye salmon south of the Skeena River and most Northeast Pacific pink salmon (*Oncorhynchus gorbuscha*) stocks show low autocorrelation in the past (Korman et al. 1995; Peterman et al. 1998; Pyper et al. 2001). However, future temporal trends in productivity may be different if climatic changes continue. In that event, it is worth considering the use of models that assume time-varying parameters to detect such changes in a timely manner.

Biological interpretation

The causes of the changes in productivity of a given Bristol Bay sockeye stock are not clear. Previous analyses of spawner-to-recruit survival rate indices for these stocks suggest that they vary as a result of changes in both marine and freshwater survival rates, with marine conditions generally being the larger contributor to changes (Peterman et al. 1998), but other possibilities exist. For example, the eight Bristol Bay stocks examined here are composed of large numbers of relatively independent spawning groups (substocks; e.g., there are 93 known unique spawning areas thought to represent substocks in one of the two lakes in the Kvichak system (Iliamna); Michael Link, LGL Ltd., 9768 Second Street, Sidney, BC V8L 3Y8, personal communication). It is possible that the magnitude and rate of change in the Ricker a parameter reported here for the Bristol Bay sockeye stocks is due to a change in the substock composition of the stock group in which the relative contribution of the more productive substock(s) either increased or decreased (Michael Bradford, Canada Department of Fisheries and Oceans and the Cooperative Resource Management Institute at Simon Fraser University, Burnaby, BC V5A 1S6, personal communication). For instance, differential harvesting of these substocks based on their different timing of adult returns is one mechanism that could cause such a change. However, this mechanism seems unlikely because the change in smoothed a_t values was both rapid and reversed direction several times in many of the stocks. It is also unlikely that the observed changes were due to alteration in the quality of spawning and rearing habitat, either for specific substocks or overall; habitat in the region is relatively undisturbed by human activities. It is likely that some of the estimated variability in a_t values from year to year is due to different levels of interception of a given stock in other fishing districts. However, such measurement error is not likely the source of temporal trends (slowly changing a_t values) unless there was a systematic change over time in bias of sampling, aging, stock identification, etc. Such trends in bias seem unlikely.

Do trends in productivity correspond with the mid-1970s regime shift?

In general, the reconstructed estimates of a_t demonstrate rapid increases in productivity across stocks about the time of the so-called "regime shift" in the mid-1970s. For a given brood year t , most Bristol Bay sockeye salmon juveniles migrate to the ocean in either year $t + 2$ or $t + 3$. Thus, the reconstructed estimates of a_t are generally consistent with the best-fit models of Adkison et al. (1996) and Peterman et al. (1998), which suggested that higher survival rates occurred starting with the 1973 brood year (i.e., 1975 ocean-entry year at the earliest).

However, our results also suggest that trends in productivity of Bristol Bay sockeye salmon showed greater complexity over time and diversity among stocks than indicated by the simple step functions used in previous analyses to describe the mid-1970s regime shift (e.g., Hare and Francis 1995; Adkison et al. 1996). For instance, as noted above, the Igushik, Kvichak, and Ugashik stocks experienced several coherent and wide-ranging fluctuations in productivity both before and after the mid-1970s, whereas the Egegik and Wood stocks showed fairly steady but less-rapid large changes over the 40-year period. Such diversity likely reflects the complexity of mechanisms and processes by which physical and biological conditions influence the productivity of individual stocks — a complexity far greater than reflected by the simplistic concept of decadal-scale regime shifts.

Is there evidence of a recent regime shift?

Some researchers have found evidence for another regime shift in 1989 in various biological components of the Northeast Pacific ecosystem (Hare and Mantua 2000). We see little consistent evidence of this for Bristol Bay sockeye salmon. Although several stocks (e.g., Egegik, Igushik, Kvichak, and Ugashik) showed decreased smoothed a values beginning in the late 1980s, that decrease appears to have been short-lived rather than persistent. Our conclusions on this point may be weak because of the lack of complete brood years beyond 1995 (6-year-old fish just returned in 2001). Nevertheless, at present it appears too early to conclude that any regime shift in productivity of Bristol Bay sockeye salmon occurred in 1989 or later, despite evidence for such a shift across other biological components of the ecosystem.

In conclusion, the strong positive covariation among smoothed KF-RW estimates of a for the eight Bristol Bay sockeye stocks indicates that their productivities respond more similarly to environmental conditions than previously indicated by studies involving residuals of $\log_e(\text{recruits/spawner})$ (e.g., Peterman et al. 1998). The latter study was based on fitting the standard Ricker model under the assumption that its parameters are constant over time. In contrast, the Kalman filter attributed some of the observed variation in recruits/spawner to observation-equation error (random process error and measurement error), thus revealing a time series of reconstructed a values that reflect more of the systematic medium- to long-term trends in underlying ecological or process variation than has been possible previously. In this way, a Kalman filter is better able to estimate slowly changing underlying trends in productivity amid large interannual variation and measurement error than is a model with con-

stant parameters. Stronger correlations among the eight Bristol Bay stocks thus emerged from the reconstructed estimates from the KF-RW model.

Not only do such reconstructed estimates of stock productivity provide insight into past changes in the ecological system, but they also may provide better dependent variables than previously available for studying the influence of environmental variables on fish productivity (Mueter et al. 2002). Future studies of potential relationships between salmon survival rates and environmental conditions should consider using smoothed Kalman filter estimates of productivity as shown here.

Finally, our reconstructed trends in past productivity of sockeye salmon stocks resulted from the random-walk version of a Kalman filter estimation procedure. For tracking simulated trends in productivity, this was the best method of the ones examined by Peterman et al. (2000). However, there are other methods for estimating trends in parameters, but to our knowledge, the performance of those methods has not yet been examined via simulations. For instance, models that assume both time-varying Ricker a and Ricker b parameters are possible, as are other forms of Box–Jenkins type time series models. It is conceivable that these other methods might estimate different temporal patterns in productivity.

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Appendix A. Kalman filter procedures

Overview

The Kalman filter is a recursive procedure for making inferences about the state of nature, in this case, a_t , based on observed data, $\log_e(R_t/S_t)$. To reconstruct values of a_t through time, the first step in applying the Kalman filter to the Ricker model (eqs. 3 through 5 above) is to determine the prior probability distribution for a_t . In the first year, we used a broad distribution (standard deviation (SD) = 1 with a mean of 1), whereas in subsequent years, equations determined the prior distribution for a_t . This prior distribution was used to predict $\log_e(R_t/S_t)$ one year into the future. Second, estimates for the mean and variance of a_t were updated based on how well the model predicted the next observation (Meinhold and Singpurwalla 1983). This procedure was applied iteratively, working through the data set one year at a time. We then applied a smoothing algorithm to these filtered estimates to obtain smoothed estimates of a_t , which take into account information from the entire data set (Harvey 1989). The procedures below are drawn from Meinhold and Singpurwalla (1983), Visser and Molenaar (1988), Chatfield (1989), and Peterman et al. (2000).

Prior distribution

The prior value (denoted by the subscript $t|t-1$ because it is the value at time t , given the information up to $t-1$) for the mean of a_t is a function of the posterior value from the previous year (denoted by the subscript $t-1|t-1$). The prior means for the random walk and AR(1) Kalman filter (KF-RW and KF-AR(1), respectively) models are given respectively by the system equations:

$$(A1) \quad a_{t|t-1} = a_{t-1|t-1}$$

$$(A2) \quad a_{t|t-1} = \bar{a} + \phi(a_{t-1|t-1} - \bar{a})$$

Similarly, the prior variance of a_t ($P_{t|t-1}$) depends on the posterior variance from the previous year ($P_{t-1|t-1}$). Prior variances for the random walk and AR(1) models, respectively, are given by

$$(A3) \quad P_{t|t-1} = P_{t-1|t-1} + \sigma_w^2$$

$$(A4) \quad P_{t|t-1} = \phi^2 P_{t-1|t-1} + \sigma_w^2$$

For the first year of data, no posterior estimates from the previous year were available, so initial guesses were used. We assumed an initial value of 1.0 for both the prior mean and prior variance of a_t for the first year (i.e., $a_{1|0} = P_{1|0} = 1$). These values were arbitrary, but it has been shown that estimates are updated quickly by the Kalman filter starting with these initial values so that subsequent estimates are soon dominated by the data (Chatfield 1989), especially with longer time series such as ours (Zeng et al. 1998).

Posterior distribution

The first stage for updating prior estimates of the mean and variance of a_t is the prediction stage (Chatfield 1989). The one-step-ahead prediction error (e_t) was calculated by predicting $\log_e(R_t/S_t)$ using the prior mean for a_t and subtracting this prediction from the observed value:

$$(A5) \quad e_t = \log_e(R_t/S_t) - (a_{t|t-1} + bS_t)$$

The variance (f_t) of this prediction error is given by:

$$(A6) \quad f_t = P_{t|t-1} + \sigma_v^2$$

These values were then used in the updating equations to derive the filtered (i.e., posterior) estimates of the mean ($a_{t|t}$) and variance ($P_{t|t}$) of a_t :

$$(A7) \quad a_{t|t} = a_{t|t-1} + \frac{P_{t|t-1}e_t}{f_t}$$

$$(A8) \quad P_{t|t} = P_{t|t-1} - \frac{P_{t|t-1}^2}{f_t}$$

For the 3 years of omitted data for the Kvichak stock, the posterior values for the mean and variance of a_t were set to equal the prior values (i.e., $a_{t|t} = a_{t|t-1}$ and $P_{t|t} = P_{t|t-1}$) and the updating eqs. A5–A8 were omitted (e.g., Zeng et al. 1998). This is essentially equivalent to assuming that the omitted data points have infinite observation–equation variances (σ_v^2).

Maximum likelihood estimates of constant parameters

Iteratively applying eqs. A1 through A8 produced a time series of filtered estimates ($a_{t|t}$) that was conditional on estimates of the other constant parameters. Estimates of these constant parameters (b , σ_v , and σ_w in the KF-RW model or b , ϕ , \bar{a} , σ_v , and σ_w in the KF-AR(1) model) were obtained by maximizing the following “concentrated” likelihood function over the entire data set (Harvey 1989):

$$(A9) \quad \log_e(L_c) = -\frac{1}{2} \left[\sum_{t=2}^N \log_e(f_t) + \sum_{t=2}^N \frac{e_t^2}{f_t} \right]$$

where N is the total number of years of data. As in Zeng et al. (1998), we conditioned our estimates on the first year of data to limit the influence of the initial, arbitrary prior distribution. Standard errors of these constant parameters were estimated via the information matrix, i.e., the second partial derivatives of the log-likelihood function (Pella 1993).

Smoothed estimates

The filtered estimates provide the expected value of a_t conditional on all information through time t , but they do not take account of information after time t . The object of Kalman filter smoothing is to produce better estimates of the a parameter (denoted with the subscript $t|N$) that are conditional on information from the entire data set (Harvey 1989). The smoothed estimates have a mean-squared error less than (or equal to) that of the filtered estimates. Note that in the final year ($t = N$), the smoothed estimates of the mean and variance of a_t are equal to the filtered estimates for that year. For the remaining years, the smoothing procedure works backwards from $t = N - 1$ to $t = 1$. This is known as “fixed-interval smoothing”, and the resulting smoothed estimate at a given time t is a weighted average of the smoothed estimate at time $t + 1$ and the filtered estimate at time t (Harvey 1989). The smoothed estimates of the mean and variance of a_t , respectively, are given by

$$(A10) \quad a_{t|N} = a_{t|t} + P_t^*(a_{t+1|N} - a_{t+1|t})$$

$$(A11) \quad P_{t|N} = P_{t|t} + (P_t^*)^2(P_{t+1|N} - P_{t+1|t})$$

where values of P_t^* for the KF-RW and KF-AR(1) models, respectively, are given by

$$(A12) \quad P_t^* = \frac{P_{t|t}}{P_{t+1|t}}$$

$$(A13) \quad P_t^* = \phi \frac{P_{t|t}}{P_{t+1|t}}$$

Unlike the filtered estimates, smoothing greatly reduces the influence of starting values for the prior distribution of a_t used to initialize the Kalman filter (Visser and Molenaar 1988).