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Stock Status of Fraser River Sockeye

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Abstract

We assess the status of 11 stocks using spawning escapement and adult return data (catch + escapement) compiled by the Pacific Salmon Commission. Together these stocks accounted for 93% of the total sockeye returns in a newly developed database covering spawning years 1948-93 and adult return years 1954-97. Three of the stocks, for which juvenile freshwater biomass data is available, are also assessed to evaluate the utility of these data to measure freshwater capacity. Sockeye spawning escapement increased gradually from an average of 1.5 million/yr in the 1950s to 10.7 million/yr during 1980-97. Increases in escapement mainly occurred in the large actively managed stocks and cycle lines. Returns increased nearly two fold from 6.4 million sockeye/yr to 11.3 million in the same periods. Off-cycle Late Shuswap sockeye abundance has remained at low levels. The abundance of Bowron, Raft and Cultus Lake stocks has declined in the last two decades. We considered two alternative stock-recruitment models in this analysis: 1) a two-parameter Ricker model that assumes no interaction among cycle lines, and 2) a modified Ricker model (Larkin model) that estimates cycle-line interaction terms for escapement at lags 1, 2 and 3 years. Parameter uncertainty is captured by sampling the Bayes posterior distribution. For the Ricker model fit to spawner and adult return data, parameter uncertainty of escapement at MSY is large and most stocks show little evidence of diminished returns within the range of observed spawner abundance. The productivity parameter estimate is comparatively precise. Of the three stocks with juvenile biomass data (Quesnel, Chilko and Shuswap sockeye), only Shuswap Lake sockeye show evidence of diminished returns at high escapements. Negative, cross-cycle interaction is statistically evident in all the large, highly cyclic stocks as revealed by the interaction terms in the Larkin model. High priority should be put on decision analysis that recognizes the risk of strong cross cycle negative interactions.

Résumé

Nous avons évalué la situation de 11 stocks à partir des données sur l'échappée de géniteurs et de la remontée des adultes (captures + échappée) compilées par la Commission du saumon du Pacifique. Ensemble, ces stocks représentaient 93 % des remontées totales de saumon rouge déterminées à l'aide d'une nouvelle base de données couvrant les années de frai de 1948 à 1993 et les années de remontée d'adultes de 1954 à 1997. Trois de ces stocks, pour lesquels des données sur la biomasse de juvéniles en eau douce ont été obtenues, ont aussi été évalués afin de déterminer l'utilité de ces données pour la mesure de la capacité des eaux douces. Les échappées de géniteurs de saumon rouge ont augmenté graduellement pour passer d'une moyenne de 1,5 million de poissons par an au cours des années 1950 à 10,7 millions de poissons par an de 1980 à 1997. L'augmentation de l'échappée s'est surtout produite chez les stocks et cycles importants faisant l'objet d'une gestion active. Les remontées ont presque doublé, pour passer de 6,4 à 11,3 millions de saumon rouge par an cours des mêmes périodes. L'abondance hors cycle tardive du saumon rouge Shuswap est demeurée faible. Celle des stocks des lacs Bowron, Raft et Cultus a diminué au cours des deux dernières décennies. Nous avons examiné deux modèles stock-recrutement pour cette analyse : 1) un modèle de Ricker à

deux paramètres qui suppose l'absence d'interaction entre les cycles et 2) un modèle de Ricker modifié (modèle de Larkin) qui estime des interactions entre cycles pour les échappées, cela à des décalages de 1, 2 ou 3 ans. L'incertitude liée aux paramètres est déterminée par échantillonnage de la distribution à posteriori de Bayes. Dans le cas de l'ajustement du modèle de Ricker aux données sur les remontées de géniteurs et d'adultes, l'incertitude du paramètre des échappées est importante au rendement maximal soutenu (RMS) et la plupart des stocks présentent peu d'indices de remontées réduites au sein de la gamme d'abondance de géniteurs observée. Le paramètre estimé de la productivité est comparativement exact. Des trois stocks pour lesquels nous disposions de données sur la biomasse des juvéniles (Quesnel, Chilko et Shuswap), seul le saumon rouge du lac Shuswap présentait des indices de remontées réduites aux valeurs d'échappées élevées. Comme le montre les termes d'interaction du modèle Larkin, il y a évidence statistique d'une interaction négative entre cycles chez tous les stocks importants très cycliques. La préséance devrait être accordée à l'analyse décisionnelle qui tient compte du risque de fortes interactions négatives entre cycles.

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1.0 Introduction

Fraser River sockeye provide the backbone of the commercial fishing industry off Canada's west coast (Roos 1991). They also have profound social importance to coastal communities and indigenous peoples living in the Fraser River watershed. Over 150 individual stocks can be identified by spawning location and adult migratory timing patterns (Fig 1). Most populations inhabiting the largest lakes in the Fraser River drainage exhibit persistent 4-yr cycles in abundance. The persistence of cycles has contributed to large variability in annual catches and ultimately to considerable economic instability. The propensity to cycle and the collapse of stocks in the early 1900s are the two principal factors to have shaped the present day fishery. In this paper, a cycle line refers to a particular sequence of years in the 4-yr interval that comprises consecutive generations. For example, the 1998 cycle line refers to the sequence of years 1998, 1994, 1990,…, 1950, etc. The term 'dominant-year cycle line' refers to the sequence of years wherein the abundance is persistently larger than the other cycle lines. Abundance is persistently lowest on off-year cycle lines and intermediate on the subdominant cycle line. Differences in abundance among cycle lines in highly cyclic stocks typically vary by an order of magnitude.

Most Fraser sockeye stocks are still recovering from catastrophic mortality inflicted early in this century from river blockages and overfishing. The most notable catastrophe to fisheries in the history of British Columbia occurred during 1913-14 as a result of rock dumping during railway construction along the Fraser River. That event almost completely destroyed the dominant cycle line that had persisted synchronously across all major stocks at that time. Estimates of the number of spawners on the dominant cycle line up to 1913 (1897-1913) ranged from 5 million in 1909 to 13 million in 1901 (Gilhousen 1992). The International Pacific Salmon Fishery Commission (Anon. 1974) reported catches of 31 million in 1913 (Fig. 2). Dominant-year adult abundance prior to 1913 may have been about 100 million sockeye (Ricker 1987). Most sockeye returning to the Fraser River failed to reach the spawning grounds in 1913 and consequently the 1901 (1997) dominant cycle was lost. So too ended the synchrony in the temporal pattern of cycles among the four cycle lines. The build up of stocks in the years that followed eventually resulted in less pronounced differences in sockeye abundance among the four cycle lines as the dominant cycle lines of some major stocks rebuilt in different years. Sustained increases in abundance of all stocks were only achieved following the construction of fishways in the canyon areas of the Fraser River along with a 5-year fishing closure to protect some stocks during 1946-50. Stock rebuilding has continued throughout the later years of this century by increasing spawning escapements. Catches since 1990 have averaged nearly 10 million sockeye/year (Fig. 2). In 1997 the landed value of the commercial catch was $74 million (Canadian dollars).

With ratification of the Pacific Salmon Treaty between Canada and the U.S. in 1985, management of Fraser sockeye fisheries has been regulated by the Fraser River

Panel under auspices of the Pacific Salmon Commission. Fraser sockeye are currently managed to obtain stock-specific target numbers of spawners (spawning escapement) and surplus harvest (Woodey, 1987). Since the Treaty was ratified, spawning escapement goals have been set annually by Canada. In the first section of this report we describe the data and data sources used in this analysis. In the second section we describe DFO rebuilding policies initiated in 1987 and review production trends for 11 stocks. In the third section we present a stock-recruitment analysis of each stock based using a Bayes perspective to capture uncertainty (Schnute et al. 2000).

2.0 Data

We assess 11 stocks using spawning escapement and adult return data (catch + escapement) compiled by the Pacific Salmon Commission (PSC) (Table 1). Each stock is a management unit that consists of one or more spawning population for which estimates of catch by stock are available from catch sampling (Gable and Cox-Rogers, 1993). In 1994, for example, escapements at 148 spawning sites (i.e. streams) were estimated (Schubert 1998, Table 1). The spawning escapement data for these sites are combined with catch estimates and partitioned into 22 stocks. Data for these stocks now reside in an Access database presently being developed by the PSC and DFO. The database is available from the first author upon request. Together the number of returns for the 11 stocks analyzed here account for 93% of the total sockeye returns in the database. Age 4 and age 5 sockeye from naturally spawning stocks with a complete time series of escapement (1948-93) and return data (1954-97) are used in the analysis. Sockeye return data also includes estimates of "missing" fish based on discrepancies between in-season assessments and independent escapement and catch sampling methods. Within the time series assessed here, 1994 and 1997 were years with significant discrepancies.

We also use time series of juvenile abundance data (biomass) available for Quesnel, Chilko and Shuswap sockeye to assess their utility for estimating freshwater capacity. See Hume et al. (1996) for details on juvenile data collection methods. In summary, juvenile data for Quesnel and Shuswap Lake are based on hydro-acoustic sampling of juvenile sockeye in the fall prior to out migration in the spring. Estimates of juvenile abundance for Quesnel and Shuswap Lake are only available since the 1970s and mainly on dominant and subdominant brood years up to 1994 and 1995 respectively. Chilko juveniles are measured during smolt out-migration from Chilko Lake and are available for almost all years up to brood year 1995. Chilko Lake was fertilized for five years starting in 1987 up until brood year 1992 in attempt to enhance juvenile sockeye production. For the present analysis, we have included all available years of data in the Chilko smolt data set.

In addition to the 11 stocks identified in Table 1, data for a sub-stock of Early Stuart sockeye that excludes sockeye from the highly cyclic Driftwood River system is also evaluated based on brood year data from 1959-92. The Driftwood sub-stock is a separate spawning population and has only been important on the 1997 cycle line. Catch estimates by sub-stock are not available directly from catch sampling. Returns to the

non-Driftwood sub-stock were estimated by partitioning the total returns at age according to the proportion at age estimated from spawning escapement age composition data by sub-stock. This procedure assumes each sub-stock was equally vulnerable to fishing and other sources of adult mortality such as in-river mortality.

3.0 Rebuilding policies and stock production trends

In 1987, the Department initiated a management and enhancement plan to increase sockeye salmon production in the Fraser River. The impetus for the plan was the terms of the Pacific Salmon Treaty, signed in 1985, that provided Canada with the benefits from increased production (PST 1985). The potential for increased production was assessed by four methods: historical catch review, stock-recruitment analyses, and spawning and lake rearing habitat capacity estimates. Estimates of production potential varied significantly, due in part to the uncertainty of causal factors that created the cyclic patterns of sockeye returns. A strategy to increase production by increasing spawning escapement was endorsed. The strategy was designed to be conservative because of the production uncertainties, and periodic assessments were recommended, such as provided by this paper.

Interim escapement goals were established as targets to be reached over a period of three to six cycles (12 to 24 years). The escapement goals, reviewed by the Pacific Stock Assessment Review Committee (PSARC) in 1990 (PSARC Working Paper S90-8), were derived by stock and cycle, and reflected the estimated spawning and juvenile rearing habitat capacities. The goals were unequal across cycles to reflect the cyclic pattern of abundance. The goals were interim in status and could be modified on the basis of new information acquired during the course of the plan. To increase escapement, average exploitation rates were reduced from 75-85% to 65-70%. Under this fixed harvest rate strategy, most stocks were expected to reach interim goals within six cycles, assuming average rates of return. The approach was also expected to result in a progressive trend towards the interim goal. Since returns in any year are highly variable, escapement plans each year are based on a three step approach: 1) maintain minimum escapement levels at low stock sizes by reducing harvest rates to zero or slightly above zero, 2) increase escapements at moderate to high stock size to the interim goal by implementing fixed harvest rates of 65-70%, and 3) maintain maximum escapement levels at the interim goal by increasing harvest rates above 70%. The approach taken is schematically shown in Figure 3.

3.1 Escapement trends

Sockeye spawning escapement to the Fraser River gradually increased from an average of 1.5 million fish/yr in the1950s to 10.7 million/yr during 1980-97 (Fig. 2). Much of the increase in the 1980s and 1990s has been on the 1993 and 1994 cycle lines. The 1995 cycle has increased slightly and the 1996 line has persisted at low levels. Increases in escapement mainly have occurred in the large actively managed stocks and cycle lines (Early Stuart, Late Stuart, Quesnel and Late Shuswap) (Fig.4 and Fig. 5). Sockeye escapement in the Stuart and Quesnel Lake systems increased on all cycle lines.

Late Shuswap Lake and Seymour River sockeye escapement increased mainly on the 1994 and 1995 cycle lines and slightly on the 1996 cycle line. For these stocks, declines on the 1994 and 1995 lines occurred since 1993. The second off-cycle line (1993) persisted at low levels showing a decline during the 1980s. Escapement of Birkenhead River sockeye, a non-cyclic stock, also increased, particularly in the mid-1980s and early 1990s but has declined since 1993. Chilko Lake escapement increased on all four cycles in the 1990s. Escapements to less actively managed stocks (Stellako, Raft, Bowron and Cultus) have been highly variable since the 1950s and except for Stellako sockeye have declined on some cycle lines. Escapements to Bowron River were lowest in 1993 at 1,180 sockeye and increased to 4,800 in 1997. Estimates of spawner abundance at Raft River decline to 480 sockeye in 1991 and increased in 1995 to 1,040 fish. The spawner abundance of Cultus Lake sockeye based on fence counts reached a record in 1997 at 82 fish! This is for a stock with a mean of 13,000 spawners since 1948.

3.2 Returns and population growth

Returns of adult sockeye increased nearly two fold from an average of 6.4 million sockeye/yr in the 1950s to 11.3 million fish/yr in 1980-97. Population growth occurred mainly as a result of policies that increased escapements in years of good returns by maintaining harvest rates near historical levels and reducing harvest rates at low returns in some years and stocks. This resulted in a greater allocation of the returns to escapement rather than catch. There were intermittent years of reduced harvest rates since the recent rebuilding policy was initiated (1987-1997) but no clear pattern of reduced harvest rates from the long-term pattern (Fig. 6).

The temporal pattern of returns varies considerably among stocks (Fig. 7 and 8). For Early Stuart and Stellako sockeye, the estimated annual returns have varied without a persistent overall trend since the 1950s but have increased since the mid-1980s. The 1996 Early Stuart off-cycle increased since 1988 as revealed in the log plots (Fig. 8). Late Stuart, Chilko, Quesnel, Seymour, Late Shuswap and Birkenhead sockeye returns have been increasing in recent years. For the highly cyclic Quesnel stock, returns have increased on all four cycles. This has not been the case for the Late Shuswap stock whereby the off-cycle lines have remained at low levels. For the second off-cycle (1993 cycle) in particular, harvest rates of Late Shuswap and Cultus sockeye have remained near or above the long-term mean. The relatively small Bowron, Raft and Cultus stocks show persistent declines in annual returns.

Fraser sockeye have been remarkably productive rarely dropping below the replacement level (R/S=1)[1] (Fig. 9 and Fig. 10). Summing across all stocks and years, each spawner produced a mean of 5.1 recruits. The high average R/S for Late Stuart and Quesnel sockeye (Fig. 10) is attributed to large measurement errors in off-cycle estimates of spawners (typically underestimated in visual surveys) and recruits (overestimated by stock identification methods (Cass and Wood 1994)). The low mean R/S for Raft and Cultus sockeye likely has contributed to the long-term decline of these stocks that are exploited during large mid-summer and late-summer run-timed fisheries. Since the mid-

[1] Recruits per spawner =1

1980s the R/S for some stocks have declined (Early Stuart, Late Stuart, Stellako, Quesnel, Seymour and Birkenhead).

4.0 Bayesian stock-recruitment parameter estimation

We considered two alternative stock-recruitment models in this analysis: 1) a two-parameter Ricker model (Ricker 1954) that assumes no interaction among cycle lines, and 2) a modified Ricker model proposed by Larkin (1971) that estimates cycle-line interaction terms for escapement at lags 1, 2 and 3 years. The two models are referred hereafter respectively as the Ricker model and the Larkin model. In both models we assume log-normal residual error. We chose to use age 4 and age 5 sockeye and multiplying the total spawner abundance by the estimated proportion of 'effective' females. Effective females are estimates of female spawner abundance weighted by estimates of potential egg deposition to account for pre-spawning losses.

For the Ricker model, we apply a dynamics model of the form $R_{t+4} = g(S_t, \theta)$ for each stock, where recruitment R_{t+4} in year $t+4$ is related to spawners S_t in year t with suitable parameters θ. We use a variant of a family of curves proposed by Schnute and Kronlund (1996) and use a Bayes perspective to capture uncertainty. The Ricker model is reformulated so that the productivity and density dependent parameters are represented respectively by the harvest rate h^* and spawner abundance S^* at MSY where

$$g(S,\theta) = \frac{S}{1-h^*}\exp\left[h^*\left(1-\frac{S}{S^*}\right)\right]$$

and $\theta = (h^*, S^*)$.

For the Larkin model $R_{t+4} = g(S_t.S_{t-1}, S_{t-2}, S_{t-3}, \theta)$ where:

$$g(S_0, S_1, S_2, S_3, \theta) = \frac{S_0}{1-h^*}\exp\left[h^*\left(1-\frac{S_0}{S^*}\right) - \beta_1 S_1 - \beta_2 S_2 - \beta_3 S_3\right].$$

Here $\theta = (h^*, S^*, \beta_1, \beta_2, \beta_3)$. The Ricker model is a special case of the Larkin model and the earlier interpretation of (h^*, S^*) applies only if $(\beta_1, \beta_2, \beta_3) = (0,0,0)$. The interaction coefficients $(\beta_1, \beta_2, \beta_3)$ represent the effects of spawning escapements (S_1, S_2, S_3) in years $t-1$, $t-2$, and $t-3$.

We adopt a simple prior distribution, where the prior on each parameter is uniform across an admissible range and 0 elsewhere. The parameter h^* is confined to the interval (0,1). Limits of spawning escapement are confined to the interval $0 \le S^* \le 3 \max S^*$ for each stock. For the Larkin model the interaction terms are confined to $(\beta_1, \beta_2, \beta_3) \ge (0,0,0)$. A Markov chain Monte Carlo (MCMC) sample from the posterior distribution captures uncertainty in the population dynamics (Gelman et al. 1995). For details of the Bayesian estimation methods and MCMC implementation for Fraser sockeye see Schnute et al. (2000).

4.1 The Ricker model

The spawner–adult stock-recruitment relationships for the Ricker model are shown in Figure 11. Residual diagnostics indicate no obvious irregularity in fit over the range of observed escapements (Fig.12) nor is there evidence of serious non-stationarity in residuals over time (Fig. 13). Residual autocorrelation was low ($\bar{r}$=0.16) except for Early Stuart (r=0.38), Birkenhead (r=0.42) and Cultus (r=0.28). Estimates of stock-recruit parameters reveal a high degree of uncertainty in S^* and a relatively precise h^* for most stocks (Fig. 14; Table 2). Estimates of the mean S^* from the Bayes posterior distribution are all larger than modal estimates and more than three times the modal estimate in many cases. Because the stock-recruit parameters are negatively correlated, estimates of the mean h^* from the posterior distribution are all less than the corresponding mode. The high estimates of h^* attests to the high productivity of Fraser sockeye (Table 2). The average h^* for all stocks combined was 0.72 (mean of the posterior distribution) with a range of 0.65 (Raft) to 0.80 (non-Driftwood Early Stuart). For most stocks, a large number of S^* parameter estimates from the posterior distribution are larger than the observed range of spawner abundance (Fig. 14). For the highly cyclic stocks (Early Stuart, Late Stuart, Quesnel and Late Shuswap) the uncertainly in S^* is particularly large. This indicates that despite the increases in escapement that has occurred, the optimal spawning capacity derived from stock-recruit analysis based on the Ricker model is not well known. The posterior distributions for the non-Driftwood River component of the Early Stuart run, Chilko, Bowron and Birkenhead sockeye reveal that S^* for these stocks are less uncertain than for other stocks.

The spawner-juvenile relationships for Quesnel, Chilko and Shuswap Lake data are shown in Figure 15. Juvenile data for Quesnel and Shuswap sockeye are relatively sparse with 8 years of data for Quesnel Lake and 12 years for Shuswap Lake. Smolt data for Chilko Lake sockeye are available for 47 years. Of the three lakes with juvenile data, only Shuswap Lake sockeye show evidence of diminished returns at high escapements based on the Ricker model with a mean S^* of 2.0 million spawners. This compares to a mean S^* of 4.1 million spawners based on the spawner-adult Ricker model that is outside the maximum observed spawner abundance of 3.6 million fish. The mean S^* for Quesnel Lake based on both adult return and juvenile data is also outside the range of spawner abundance. The mean of S^* for Chilko Lake juvenile data is at the upper range of spawner abundance at 1.0 million spawners compared to 0.6 million based on the

spawner-adult Ricker fit. Estimates of Chilko sockeye returns from the 1991 brood year were low compared to the record spawner abundance of 1 million sockeye. Estimates of ocean survival based on smolt–return data indicate that low ocean survival, not over-seeding of freshwater habitat, resulted in the low return rate. Age 1 smolts from the 1991 brood year entered the ocean in 1993 during an intense El Nino event. The return rates of most stocks from the 1991 brood were also very low (Fig. 9). The spawner-smolt relationship, therefore, does not suggest spawner density in 1991 was limiting freshwater survival but rather that ocean survival was unusually low. The 1991 data point has considerable leverage in estimates of S^* for Chilko sockeye based on the spawner-adult recruitment relationship. If the 1991 data point is removed from the analysis, the mean S^* is 780,000 compared to 613,000 sockeye.

4.2 The Larkin model

The three dimensional representation of the fit of the Larkin model to spawner-adult recruitment data for the highly cyclic Early Stuart (including the highly cyclic Driftwood River), Late Stuart, Quesnel and Late Shuswap stocks are shown in Figure 15. Parameter estimates are presented in Table 3. Figure 16 portrays the value P (θ) for each sample point θ. The posterior profiles (bottom panels of Fig. 16) visually identify the modal estimates in Table 3. Various degrees of interaction among cycle lines are evident depending on the stock. Early Stuart sockeye have the highest mean values of the interaction terms ($\beta_1, \beta_2, \beta_3$) compared to the other cyclic stocks (Table 3). The Late Shuswap stock, the most widely studied cyclic stock (Larkin 1971; Collie and Walters 1987; Welch and Noakes 1990; Myers et al. 1998), has relatively low values of ($\beta_1, \beta_2, \beta_3$). Except for Early Stuart sockeye, the posterior profiles for β_3 are very near the zero constraint indicating that the interaction term for a 3-yr lagged escapement is not as critical as 1 and 2-yr lagged escapements. For Late Shuswap sockeye the mode of β_3 is near zero. Interestingly, the mode of β_1 for Quesnel sockeye is less than higher lagged escapements and near zero. Escapements and returns on all cycle lines of Quesnel sockeye have recently increased significantly compared to other cyclic stocks (Fig. 6a; Fig. 7a), therefore, cycle line interactions perhaps are not so readily detectable.

5.0 Conclusion

Management of Fraser sockeye has focussed on increasing escapements of the large actively managed stocks and cycles. To that end, there has been considerable success in building up the runs. The concurrent build-up of all cycles of Quesnel sockeye is particularly notable, not only because of the economic benefits, but also because it shows that off-cycles can be built up. As reported early in the rebuilding phase of the last decade, very large economic gains are likely if intrinsic differences in productivity among cycle lines do not exist. Walters and Staley (1987) suggested that short-term reductions in harvest rates can increase the long-term economic value of Fraser sockeye by about $150-300 million (Canadian dollars) if fishing pressure on the major stocks is lowered to let the stocks recover. Much of this increase would come from rebuilding off-

cycle lines. Welch and Noakes (1990; 1991) also since concluded that large economic gains are likely if off-cycles can be rebuilt. The persistence of off-cycles at very low levels for some stocks (i.e. Late Shuswap) is disconcerting, as is the recent decline of the small non-managed stocks (Bowron, Raft and Cultus). Spawning escapement for Raft and Cultus recently reached record low levels. For Cultus Lake sockeye, the 82 fish escapement in 1997 is particularly alarming.

For most stocks the uncertainty in S^* based on the Ricker model is very large and we are unable to reliably determine the capacity of the resource. As reported by Collie et al. (1990), estimates of the stock productivity parameter, in this case h^*, are comparatively well determined. Estimates of the mean optimal spawning capacity at MSY reported here (Table 2) are all larger than the estimates of escapement required for maximum juvenile production based on limnological studies of Late Shuswap (1.9 million), Quesnel (0.9 million), and Chilko lake (0.5 million) (Shortreed et al. 2000). It is difficult to reconcile these difference. Both methods to estimate capacity are subject to inherent measurement and process errors. Habitat capacity estimates reported by DFO (Fraser River Action Plan, 1995) based on area measurements of "suitable habitat" and spawning density considerations are difficult to compare. Estimates of S^* reported here are larger in many cases than those derived purely from habitat measures. Uncertainty in habitat-based estimates of capacity are difficult to quantify and, to our knowledge, the estimation methods have not been documented. Results of the Larkin stock-recruitment model indicate cycle line interactions are statistically supportable. Collie and Walters (1987) showed that parameter estimates of the interaction terms in the Larkin model are relatively unbiased for parameters estimated for Shuswap Lake sockeye.

Stakeholders have invested in a billion-dollar experiment designed to determine how large the resource can become. There is little doubt the experiment has had large socio-economic benefits as the build-up of stocks and catches in the last two decades have attested. For the highly cyclic stocks, these increases have come largely from increasing escapements to the dominant and sub-dominant cycle years. The analysis presented here for the four major cyclic stocks and by Collie and Walters (1987) and Welch and Noakes (1990; 1991) for Shuswap Lake sockeye indicate rebuilding should focus on off-cycle lines to avoid potential deleterious effects of reduced productivity as a result of cross-cycle line suppression of productivity.

The decline in catch in the last few years has forced managers and stakeholders alike to question, as in any investment situation, the future investment strategy. The degree to which we should be probing at higher escapements (i.e. risk investment today for future benefits or losses) is clearly a policy issue. The multi-stock Bayesian stock-recruitment analysis presented here is a useful starting point for investigating cross-cycle line linkages in an experimental policy design framework.

6.0 Recommendations

High priority should be put on decisional analyses that recognize risk of strong cycle-line negative interactions and evaluate consequences on policy design that include an

assessment of the trade-off between managing for production from the major stocks and the diversity at risk among numerous smaller populations in mixed-stock fisheries.

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Table 1. Data summary for Fraser sockeye stocks in millions of fish.

Maximum Spawning escapement (1949-97)

	CYCLE			
STOCK	1997	1998	1999	2000
Early Stuart	0.687967	0.097035	0.148194	0.179807
Late Stuart	1.363826	0.189079	0.076860	0.062991
Stellako	0.104720	0.145021	0.290042	0.367702
Bowron	0.022283	0.016146	0.035000	0.018645
Raft	0.007904	0.010214	0.010210	0.046592
Quesnel	2.620454	0.686411	0.214103	0.041187
Chilko	0.985827	0.825837	1.037737	0.974349
Seymour	0.011359	0.272041	0.128253	0.021101
Late Shuswap	0.012510	3.619499	1.255210	0.012816
Birkenhead	0.244954	0.335630	0.293626	0.185908
Cultus	0.020375	0.029928	0.047779	0.027833

Maximum returns (1954-97)

	CYCLE			
STOCK	1997	1998	1999	2000
Early Stuart	1.651872	0.241087	0.520251	0.379290
Late Stuart	5.915320	0.818427	0.386419	0.207234
Stellako	0.285870	1.207988	1.747216	1.011019
Bowron	0.075576	0.074998	0.214288	0.050591
Raft	0.039626	0.050257	0.060515	0.106299
Quesnel	12.489542	3.367742	0.173871	0.028464
Chilko	3.401545	4.750228	4.410079	3.998705
Seymour	0.069911	0.818133	0.442795	0.057264
Late Shuswap	0.093025	15.151080	3.894224	0.038803
Birkenhead	1.071734	1.770420	0.982828	0.884411
Cultus	0.113775	0.275368	0.396151	0.074451

Minimum spawning escapement (1949-97)

	CYCLE			
STOCK	1997	1998	1999	2000
Early Stuart	0.023045	0.004557	0.002159	0.001522
Late Stuart	0.107752	0.005470	0.001535	0.000035
Stellako	0.021826	0.041275	0.039691	0.030368
Bowron	0.001170	0.001305	0.004920	0.001500
Raft	0.000617	0.000630	0.000464	0.005177
Quesnel	0.030664	0.000299	0.000049	0.000081
Chilko	0.034360	0.017308	0.100116	0.238272
Seymour	0.002225	0.011049	0.008971	0.002490
Late Shuswap	0.000563	1.144115	0.063859	0.000604
Birkenhead	0.011905	0.015166	0.014553	0.036838
Cultus	0.000082	0.001860	0.009128	0.000861

Table 1. (cont'd)

Minimum returns (1954-97)

	CYCLE			
STOCK	1997	1998	1999	2000
Early Stuart	0.255212	0.027972	0.020835	0.010412
Late Stuart	0.605871	0.039090	0.006854	0.003041
Quesnel	0.066995	0.232938	0.322895	0.110678
Stellako	0.008564	0.004645	0.020230	0.007112
Bowron	0.003841	0.002917	0.001163	0.016884
Raft	0.463409	0.002014	0.000165	0.000497
Chilko	0.068788	0.203432	0.575443	0.452763
Seymour	0.006040	0.141170	0.068818	0.008786
Late Shuswap	0.008171	2.070075	0.374623	0.002427
Birkenhead	0.064796	0.078416	0.115285	0.099268
Cultus	0.000705	0.010278	0.025000	0.002143

Table 2. Ricker stock-recruitment parameter estimates, standard errors, and MCMC information. The mode and SE_H are the modal value and standard deviation of the posterior Hessian. The mean and SE_M are the mean and standard deviation of the posterior sample obtained from the MCMC algorithm. The mode and mean S^* are in millions of fish.

	h*				S*			
STOCK	**mode**	**mean**	**SE_H**	**SE_M**	**mode**	**mean**	**SE_H**	**SE_M**
Early Stuart	0.649	0.629	0.033	0.035	0.341	0.818	0.141	0.519
Early Stuart[a]	0.820	0.800	0.026	0.030	0.114	0.174	0.030	0.084
Late Stuart	0.733	0.716	0.043	0.044	0.744	2.196	0.610	1.094
Stellako	0.736	0.715	0.029	0.030	0.194	0.374	0.067	0.226
Bowron	0.722	0.695	0.032	0.037	0.018	0.031	0.005	0.020
Raft	0.671	0.651	0.044	0.037	0.017	0.032	0.011	0.014
Quesnel	0.761	0.753	0.027	0.027	2.157	4.230	1.613	1.918
Quesnel[b]	0.988	0.987	0.002	0.002	2.459	3.875	0.925	1.620
Chilko	0.771	0.752	0.028	0.033	0.446	0.613	0.099	0.286
Chilko[b]	0.993	0.993	0.001	0.001	0.781	0.972	0.160	0.302
Seymour	0.663	0.637	0.037	0.040	0.095	0.247	0.034	0.186
Late Shuswap	0.673	0.652	0.036	0.038	1.855	4.081	0.654	2.494
Shuswap[b]	0.993	0.993	0.001	0.001	1.878	2.025	0.224	0.309
Birkenhead	0.783	0.768	0.026	0.031	0.115	0.154	0.022	0.081
Cultus	0.634	0.612	0.052	0.043	0.044	0.080	0.031	0.035

a: excludes the highly cyclic Driftwood R.
b: stock-recruitment based on juvenile biomass estimates. Quesnel and Shuswap are based on fall fry estimates. Chilko is based on smolt estimates.

Table 3. Larkin stock-recruitment parameter estimates and standard errors. The mode and SE_H are the modal parameter values and standard deviation of the posterior Hessian. The mean and SE_M are the mean and standard deviation of the posterior sample obtained from the MCMC algorithm. The mode and mean of S* are in millions of fish.

	STOCK			
	Early Stuart	**Late Stuart**	**Quesnel**	**Late Shuswap**
mode h^*	0.740	0.789	0.739	0.762
mean h^*	0.726	0.779	0.743	0.735
SE_H h^*	0.032	0.049	0.031	0.040
SE_M h^*	0.035	0.046	0.029	0.047
mode S*	0.424	0.603	2.868	1.441
mode S_1	2.695	1.589	0.043	0.262
mode S_2	1.511	1.355	0.555	0.322
mode S_3	1.902	0.348	0.326	0.00001
SE_H S*	0.167	0.331	2.437	0.330
SE_H S_1	0.719	0.756	0.223	0.127
SE_H S_2	0.709	0.756	0.224	0.136
SE_H S_3	1.028	1.233	0.319	0.001
mean S*	0.859	1.908	4.491	2.800
mean S_1	2.589	1.555	0.197	0.254
mean S_2	1.611	1.400	0.529	0.272
mean S_3	1.917	1.089	0.411	0.021
SE_M S*	0.470	1.087	1.847	2.025
SE_M S_1	0.799	0.727	0.147	0.125
SE_M S_2	0.730	0.724	0.218	0.140
SE_M S_3	0.999	0.829	0.241	0.015

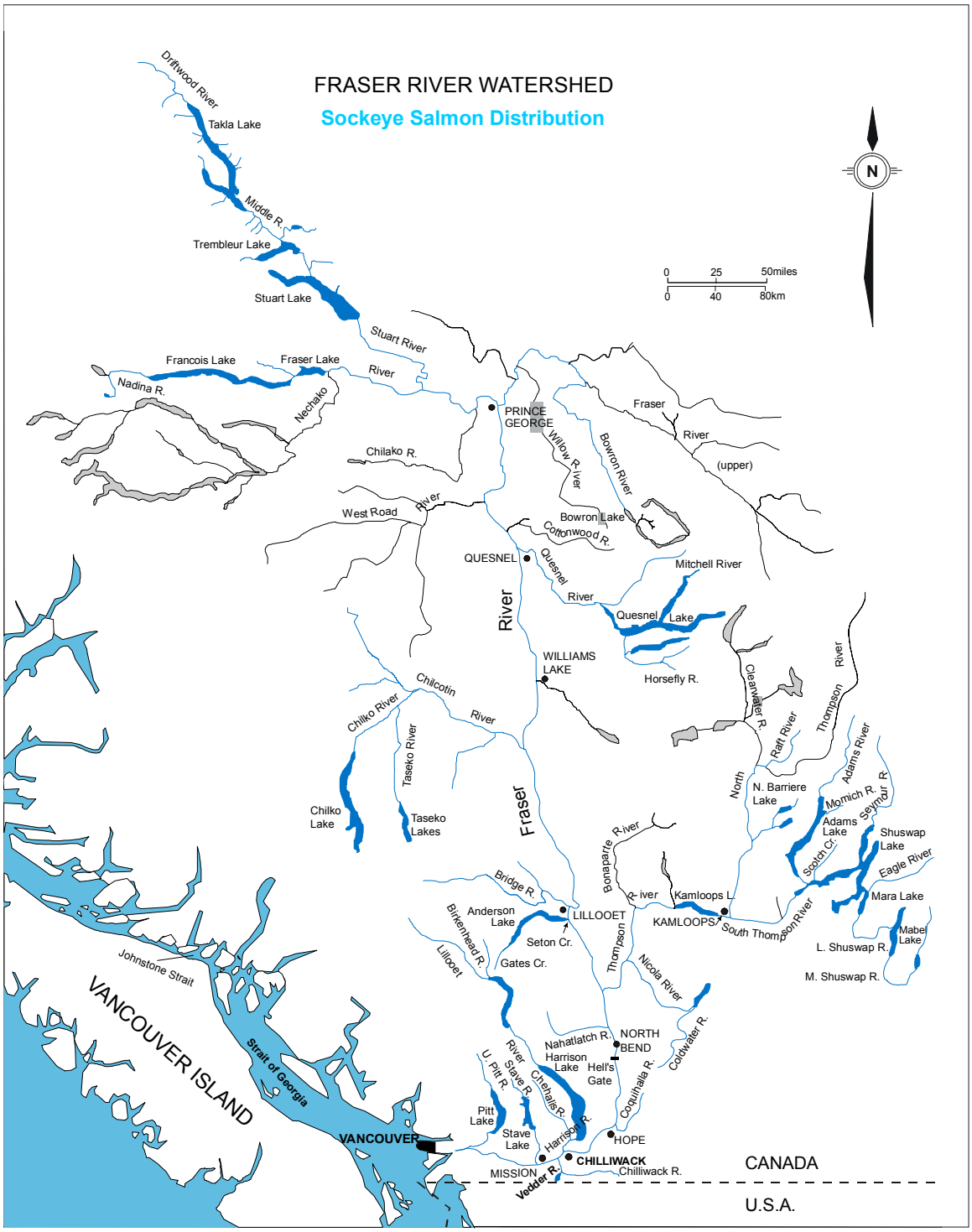

Figure 1. Spawning distribution of Fraser River sockeye.

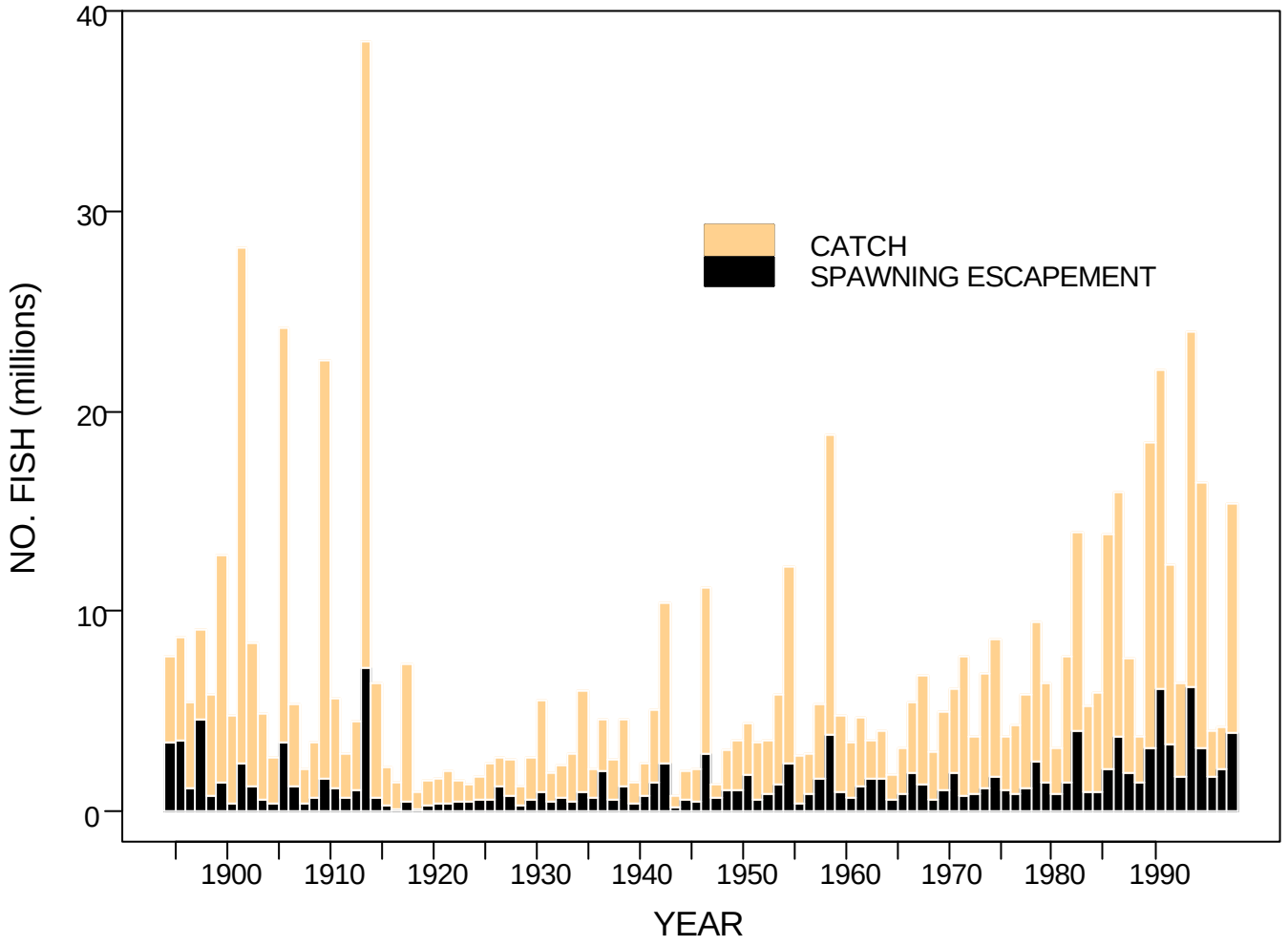

Figure 2. Adult returns (catch + escapement) of Fraser River sockeye (1894-1997).

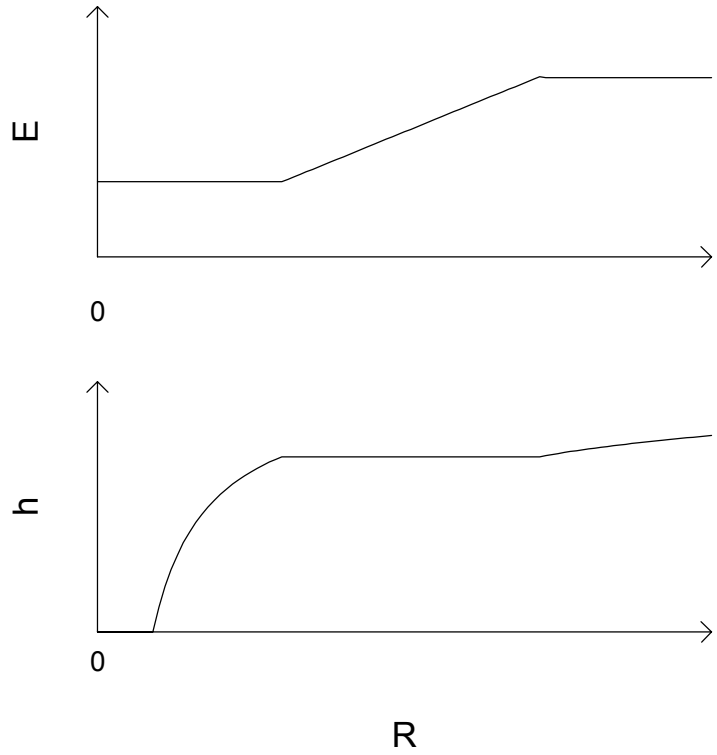

Figure 3. Schematic plot of escapement target (E) and harvest rate (h) goals versus sockeye returns based on 1987-98 stock rebuilding policies for Fraser sockeye.

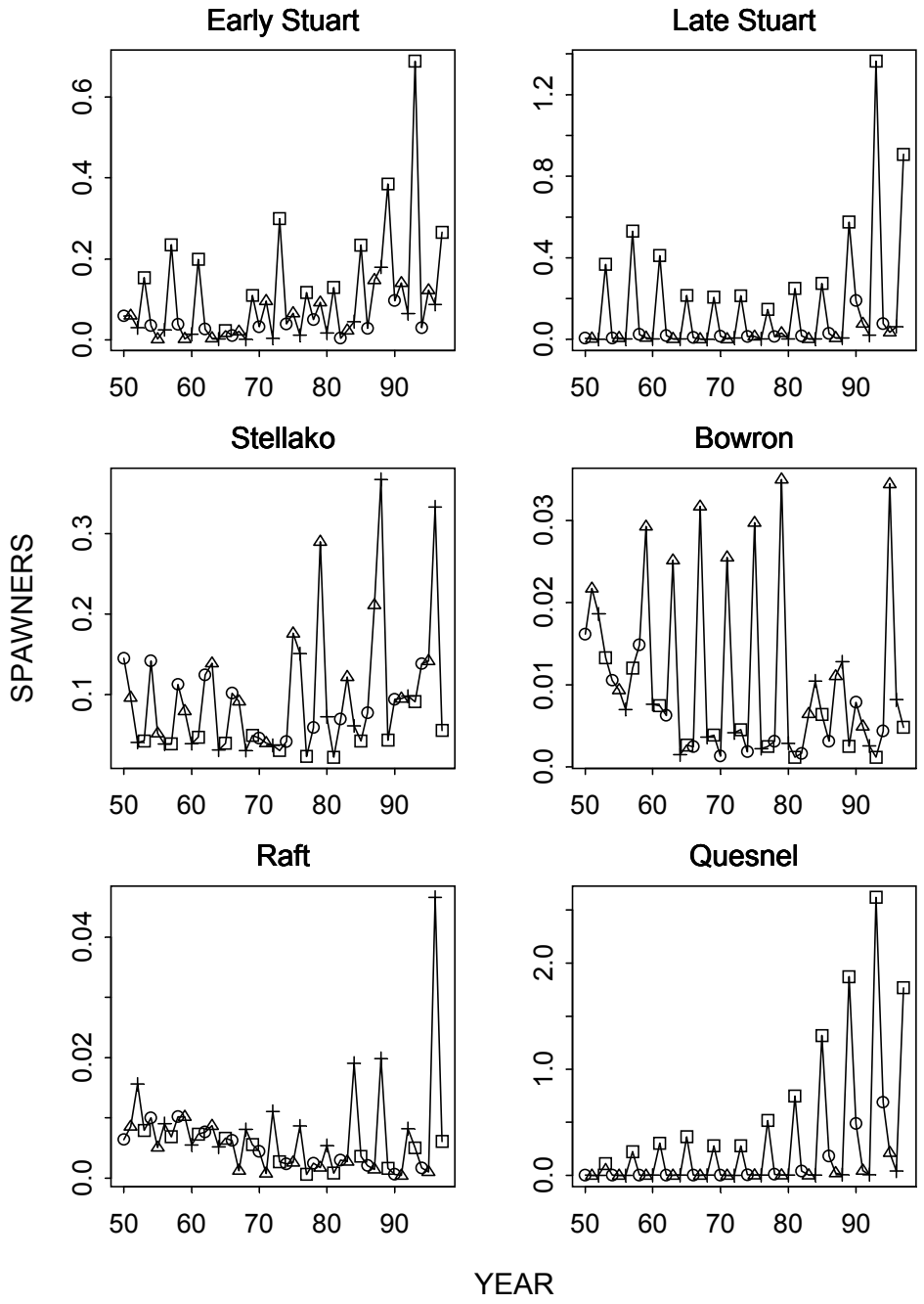

Figure 4a. Spawning escapement (millions) of Fraser sockeye (Early Stuart, Late Stuart, Stellako, Raft, Bowron, Quesnel). Symbols (□,△,O, +) denote cycle lines (1993, 1994, 1995, 1996).

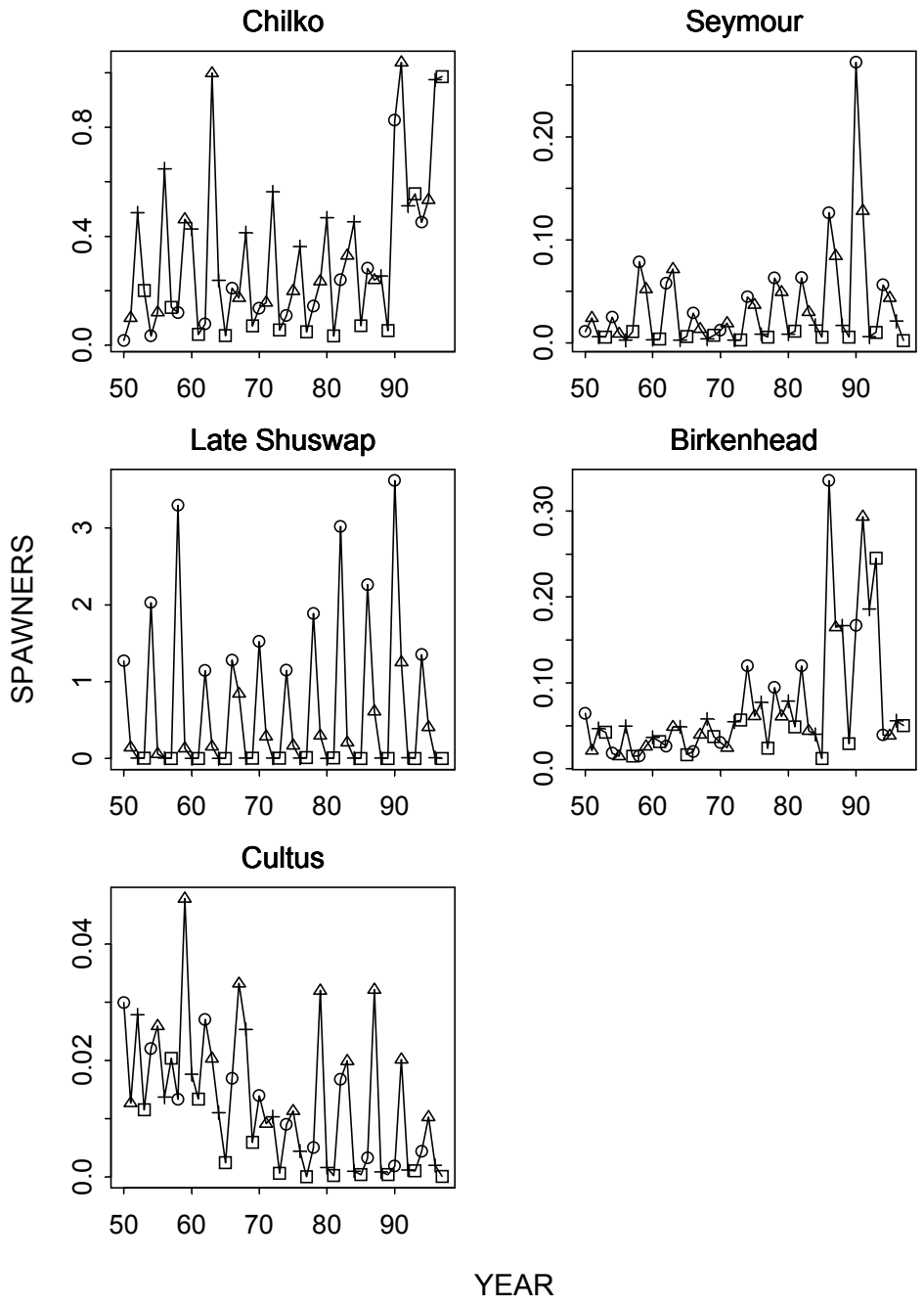

Figure 4b. Spawning escapement (millions) of Fraser sockeye (Chilko, Seymour, Late Shuswap, Birkenhead, Cultus). Symbols (□,△,O, +) denote cycle lines (1993, 1994,1995,1996).

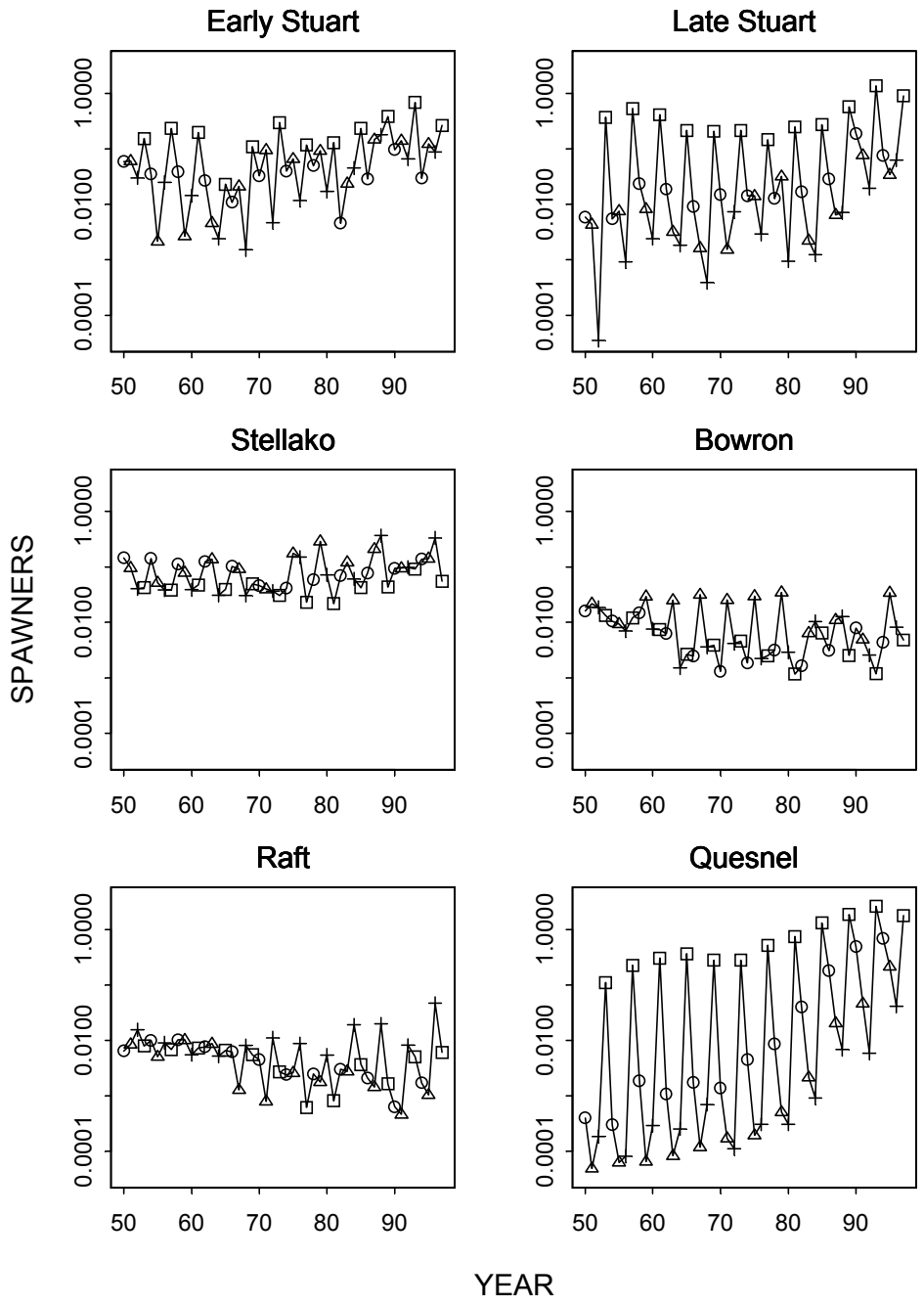

Figure 5a. Spawning escapement (millions) (log10 scale) of Fraser sockeye (Early Stuart, Late Stuart, Stellako, Raft, Bowron, Quesnel). Symbols (□,△,O, +) denote cycle lines (1993, 1994,1995,1996).

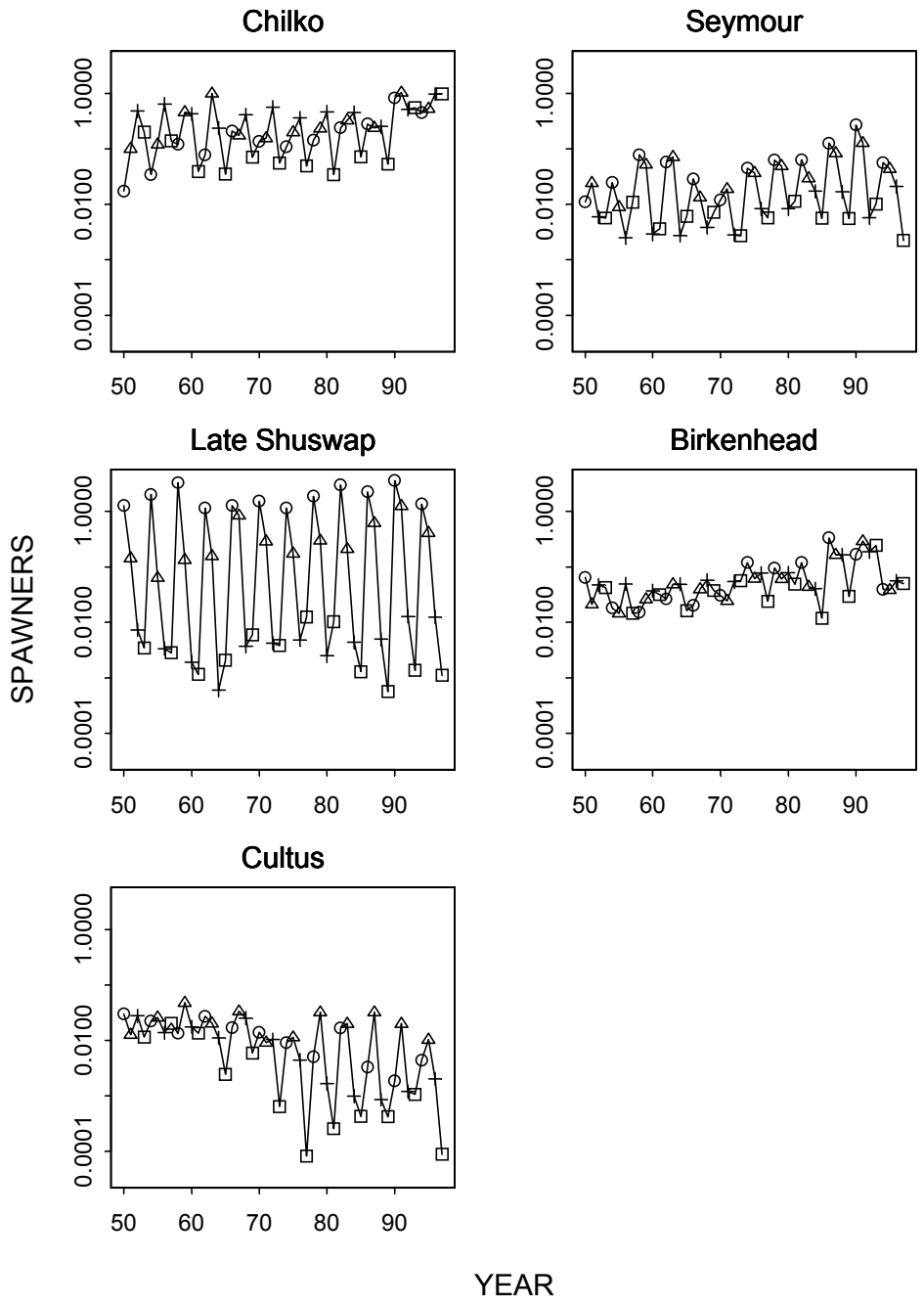

Figure 5b. Spawning escapement (millions) (log10 scale) of Fraser sockeye (Chilko, Seymour, Late Shuswap, Birkenhead, Cultus). Symbols (□,△,O, +) denote cycle lines (1993, 1994,1995,1996).

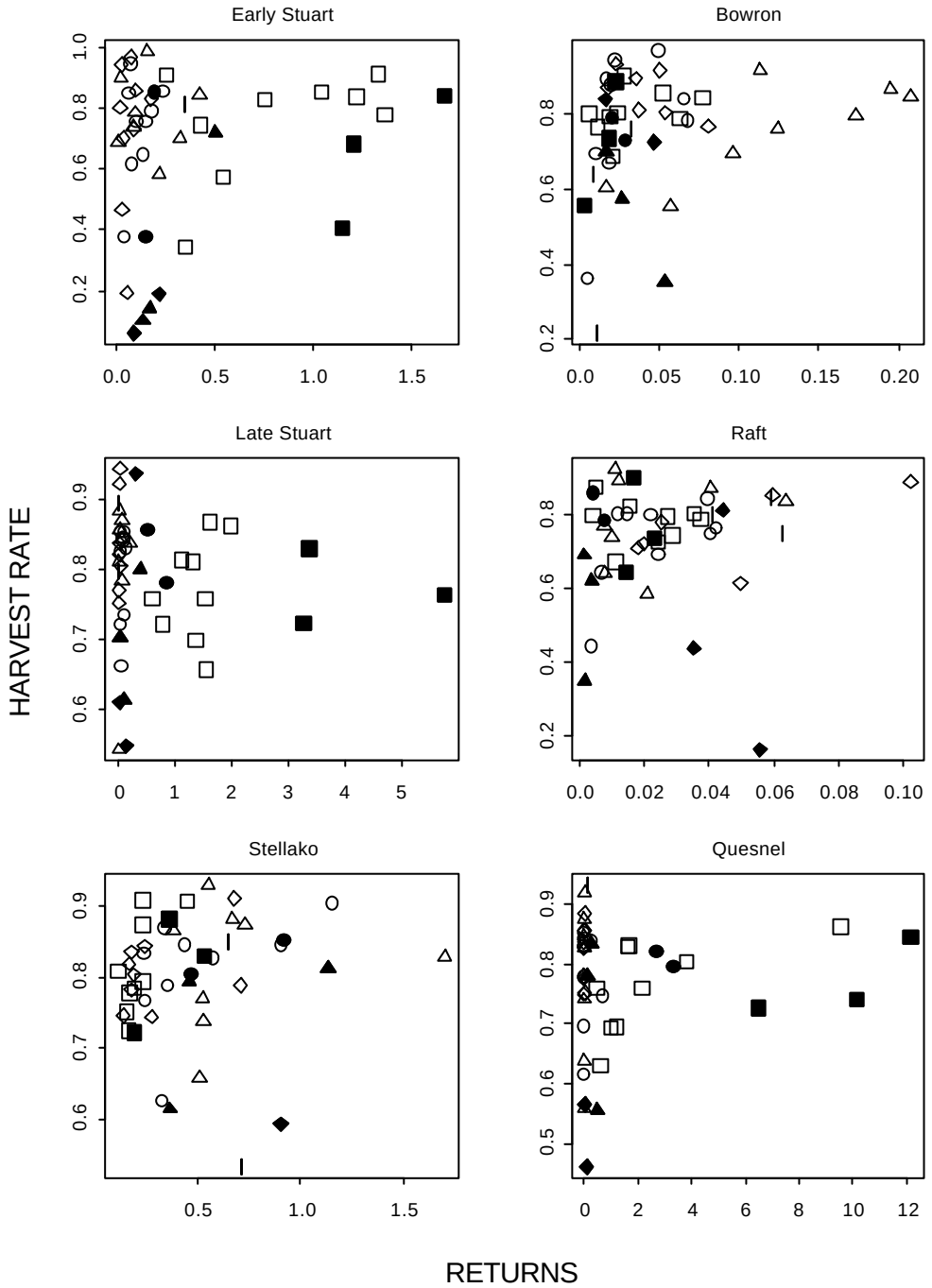

Figure 6a. Relationship between harvest rate and returns (millions) for Fraser sockeye (Early Stuart, Late Stuart, Stellako, Raft, Bowron, Quesnel). Symbols (□,O,△, ◇) denote cycle lines (1993, 1994,1995,1996). Filled symbols denote 1987-97 rebuilding years.

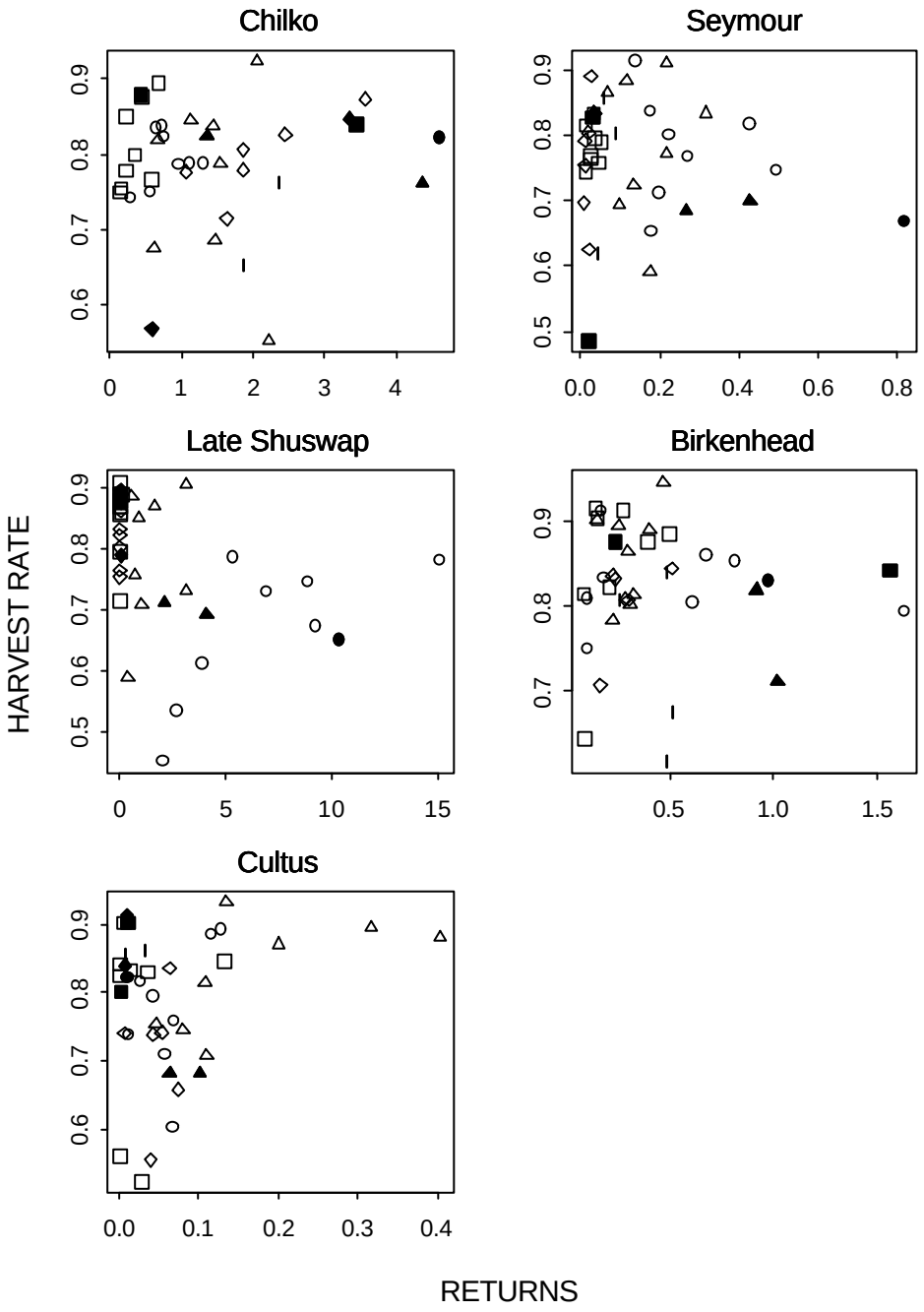

Figure 6b. Relationship between harvest rate and returns (millions) for Fraser sockeye (Chilko, Seymour, Late Shuswap, Birkenhead and Cultus). Symbols (□,O,△, ◇) denote cycle lines (1993, 1994,1995,1996). Filled symbols denote 1987-97 rebuilding years.

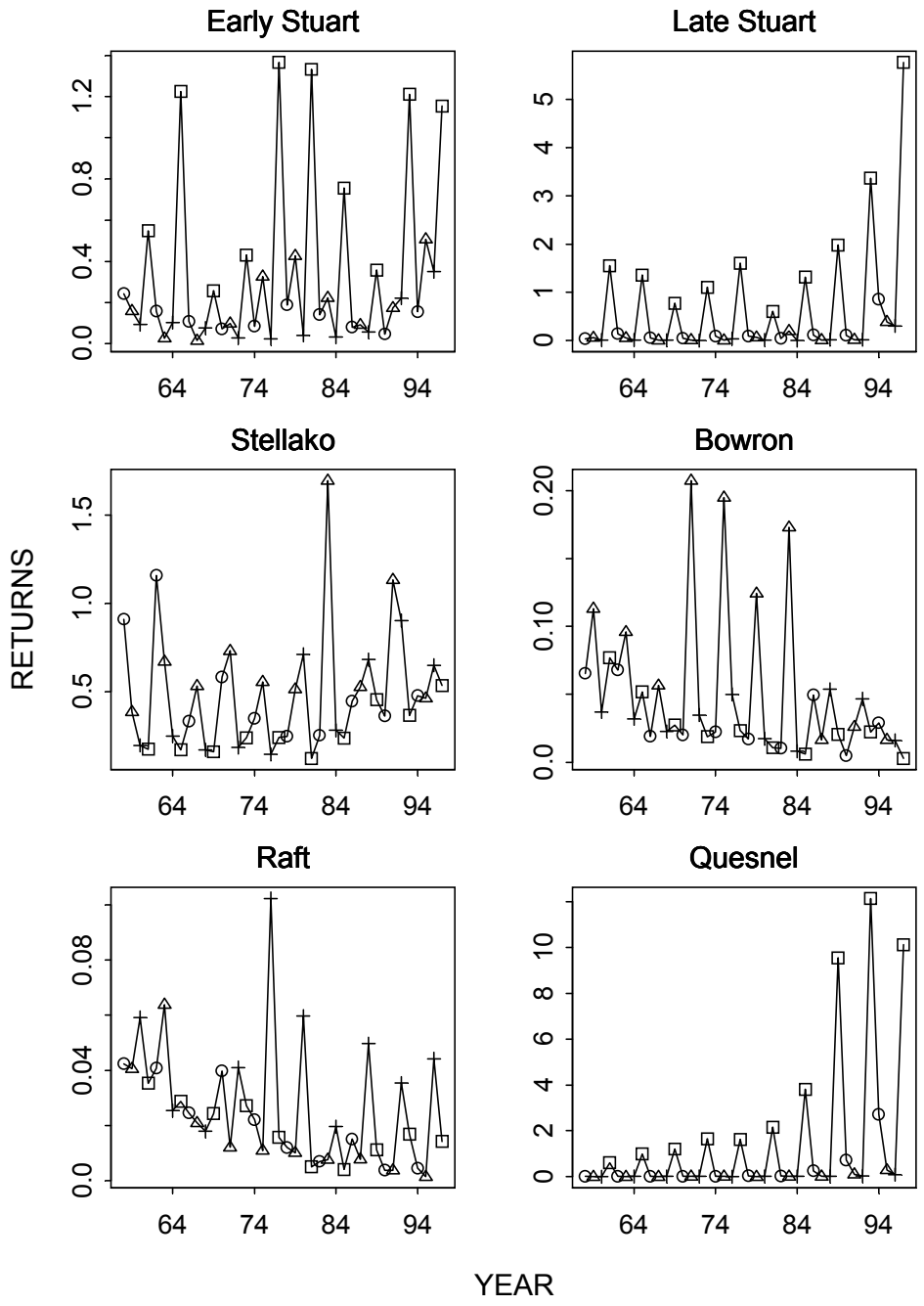

Figure 7a. Returns (millions) of Fraser sockeye (Early Stuart, Late Stuart, Stellako, Raft, Bowron, Quesnel). Symbols (□,△,O, +) denote cycle lines (1993, 1994,1995,1996).

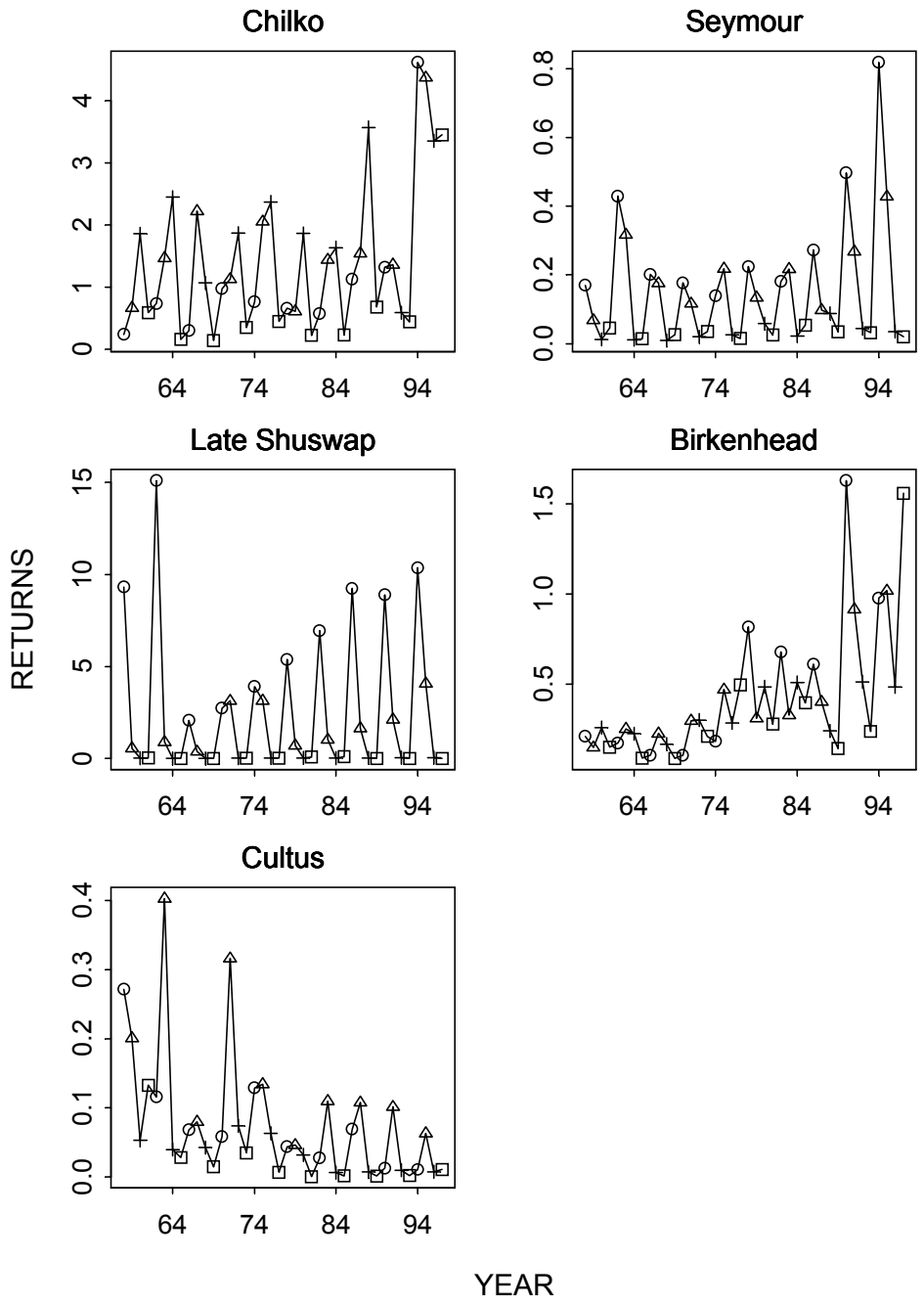

Figure 7b. Returns (millions) of Fraser sockeye (Chilko, Seymour, Late Shuswap, Birkenhead, Cultus). Symbols (□,△,O, +) denote cycle lines (1993, 1994,1995,1996).

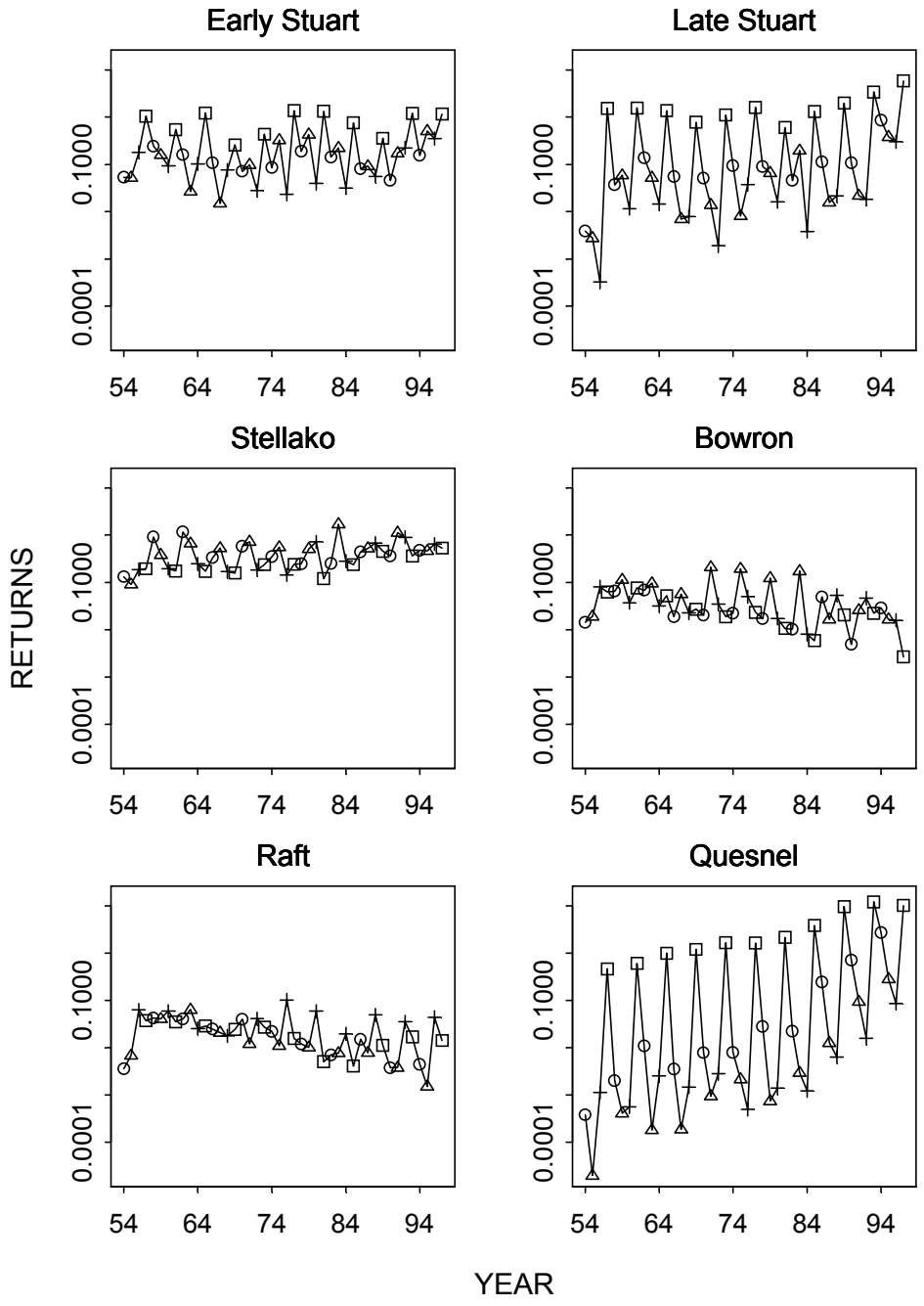

Figure 8a. Returns (millions) (log10 scale) of Fraser sockeye (Early Stuart, Late Stuart, Stellako, Raft, Bowron, Quesnel). Symbols (□,△,O, +) denote cycle lines (1993, 1994, 1995, 1996).

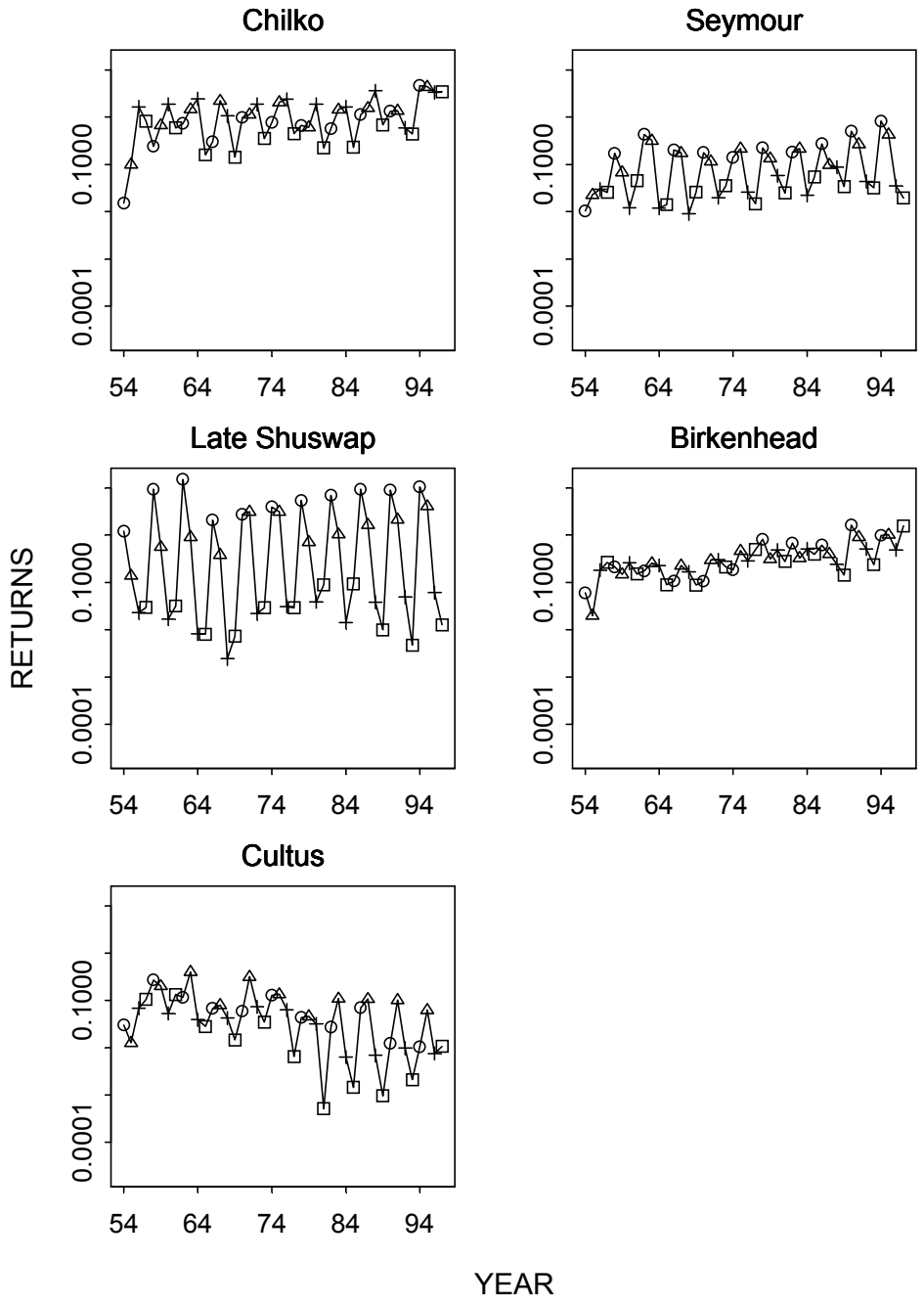

Figure 8b. Returns (millions) (log10 scale) of Fraser sockeye (Chilko, Seymour, Late Shuswap, Birkenhead, Cultus). Symbols (□,△,O, +) denote cycle lines (1993, 1994 1995, 1996).

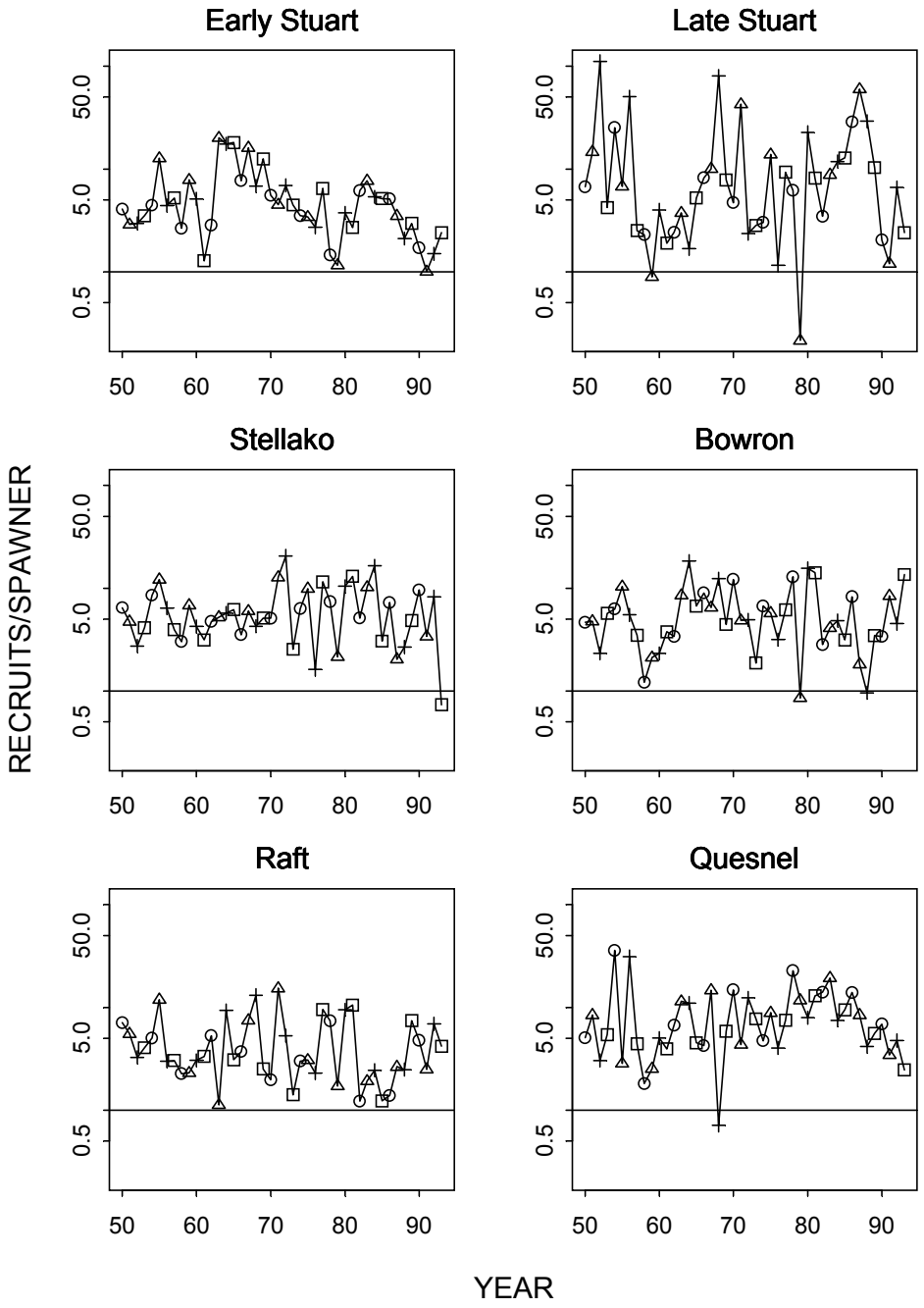

Figure 9a. Recruits/spawner (log10 scale) of Fraser sockeye (Early Stuart, Late Stuart, Stellako, Raft, Bowron, Quesnel). Symbols (□,△,O, +) denote cycle lines (1993, 1994 1995, 1996).

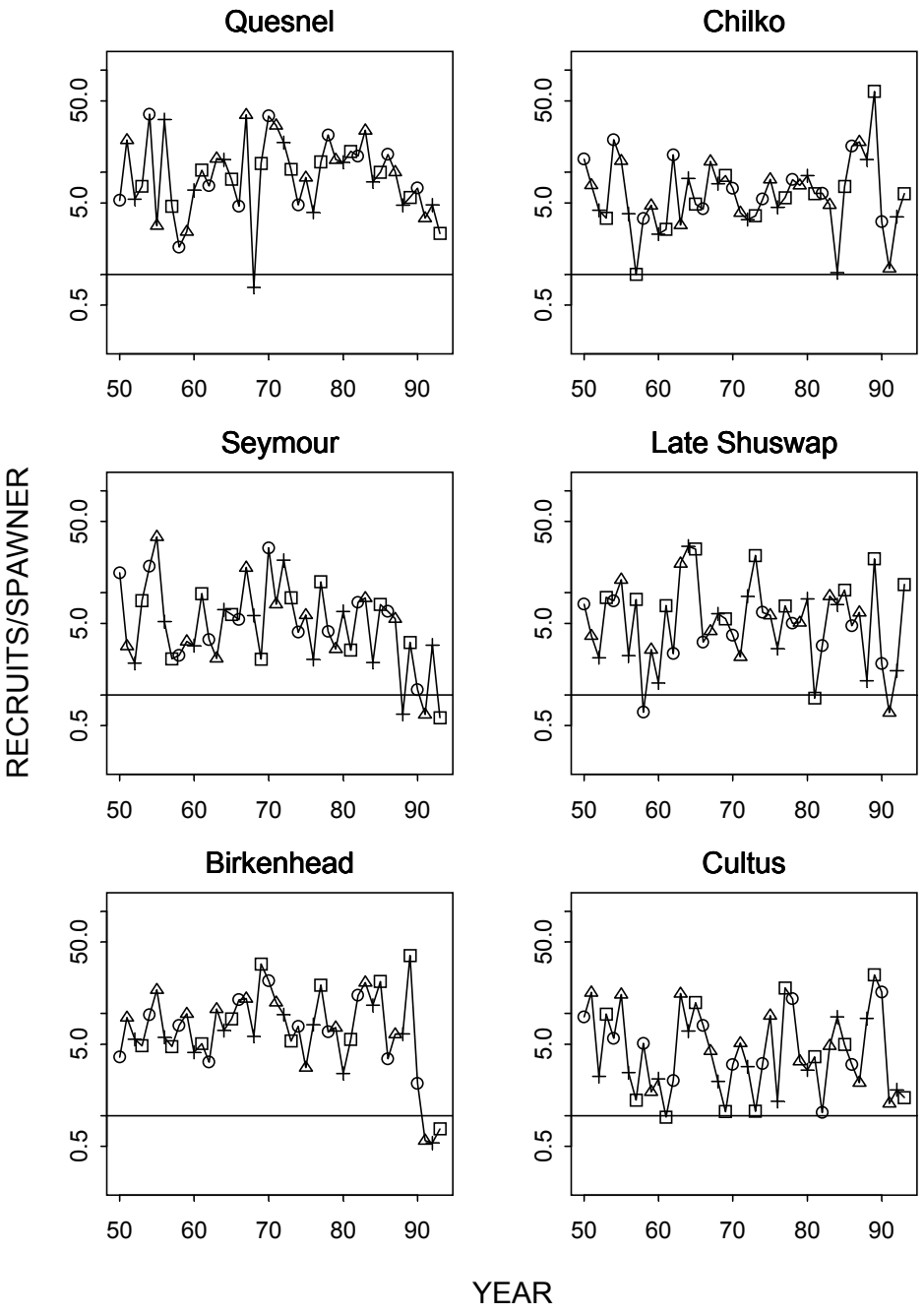

Figure 9b. Recruits/spawner (log10 scale) of Fraser sockeye (Chilko, Seymour, Late Shuswap, Birkenhead, Cultus). Symbols (□,△,O, +) denote cycle lines (1993, 1994, 1995 1996).

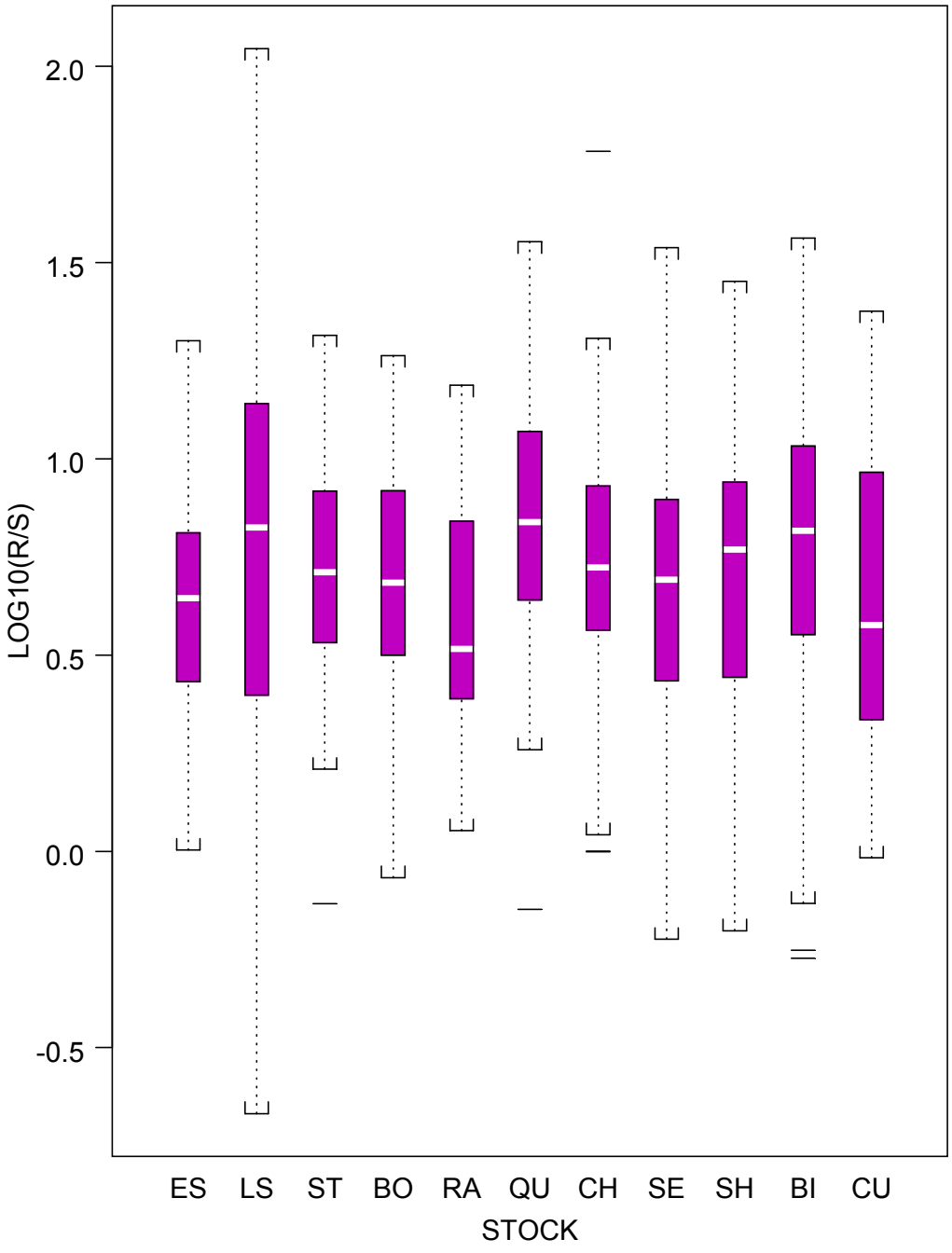

Figure 10. Boxplot of log10 recruits-per-spawner (ES=Early Stuart, LS=Late Stuart, ST=Stellako, BO=Bowron, RA=Raft, QU=Quesnel, CH=Chilko, SE=Seymour, SH=Late Shuswap, BI=Birkenhead, CU=Cultus).

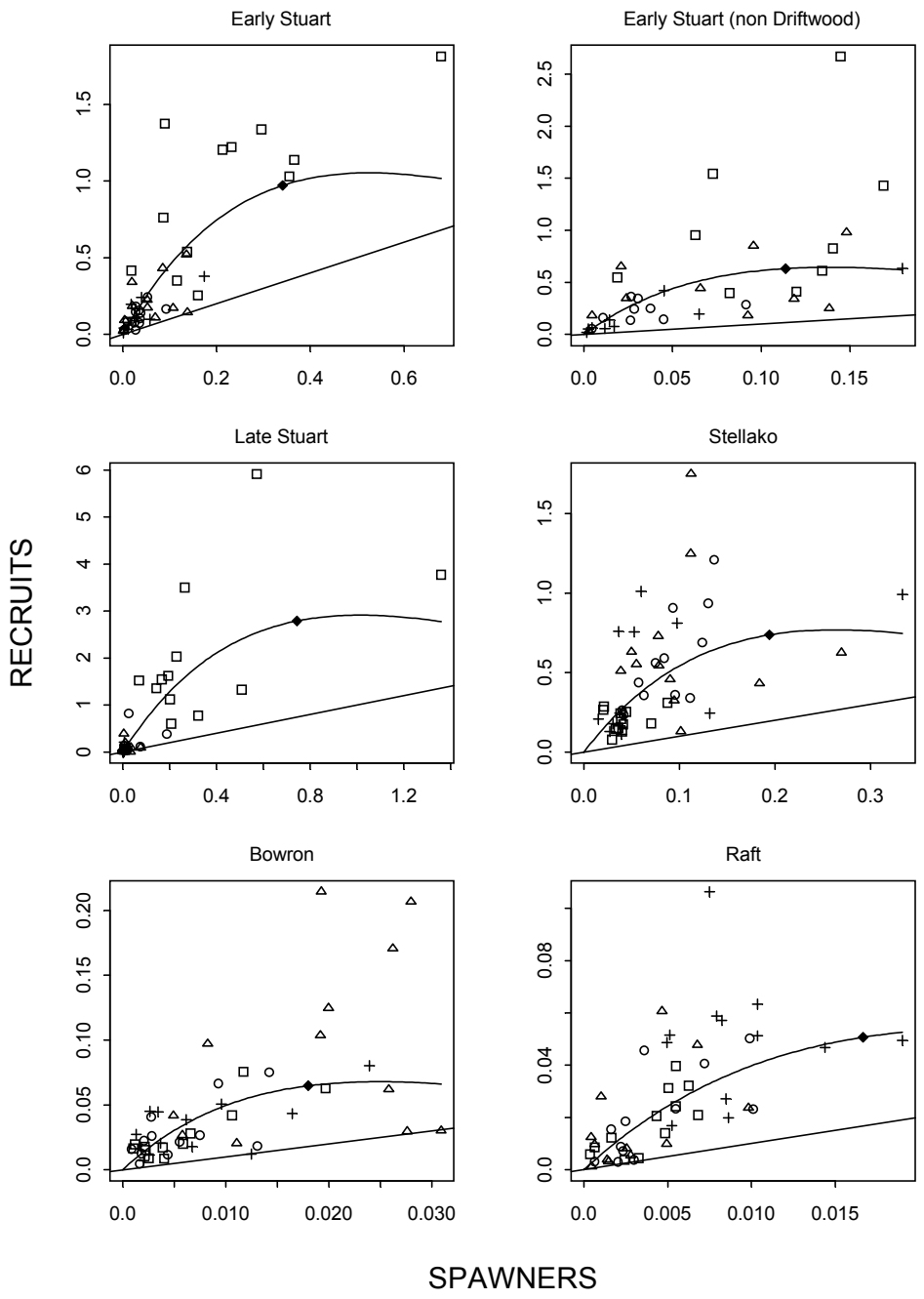

Figure 11a. Stock-recruit relationships (millions). Curves are based on modal Ricker parameter estimates (see Table 2). Symbols (□,△,O, +) denote cycle lines (1993, 1994, 1995, 1996). The symbol ♦ is the MSY point where spawners equal S^*. It is excluded if the estimate is beyond the data range.

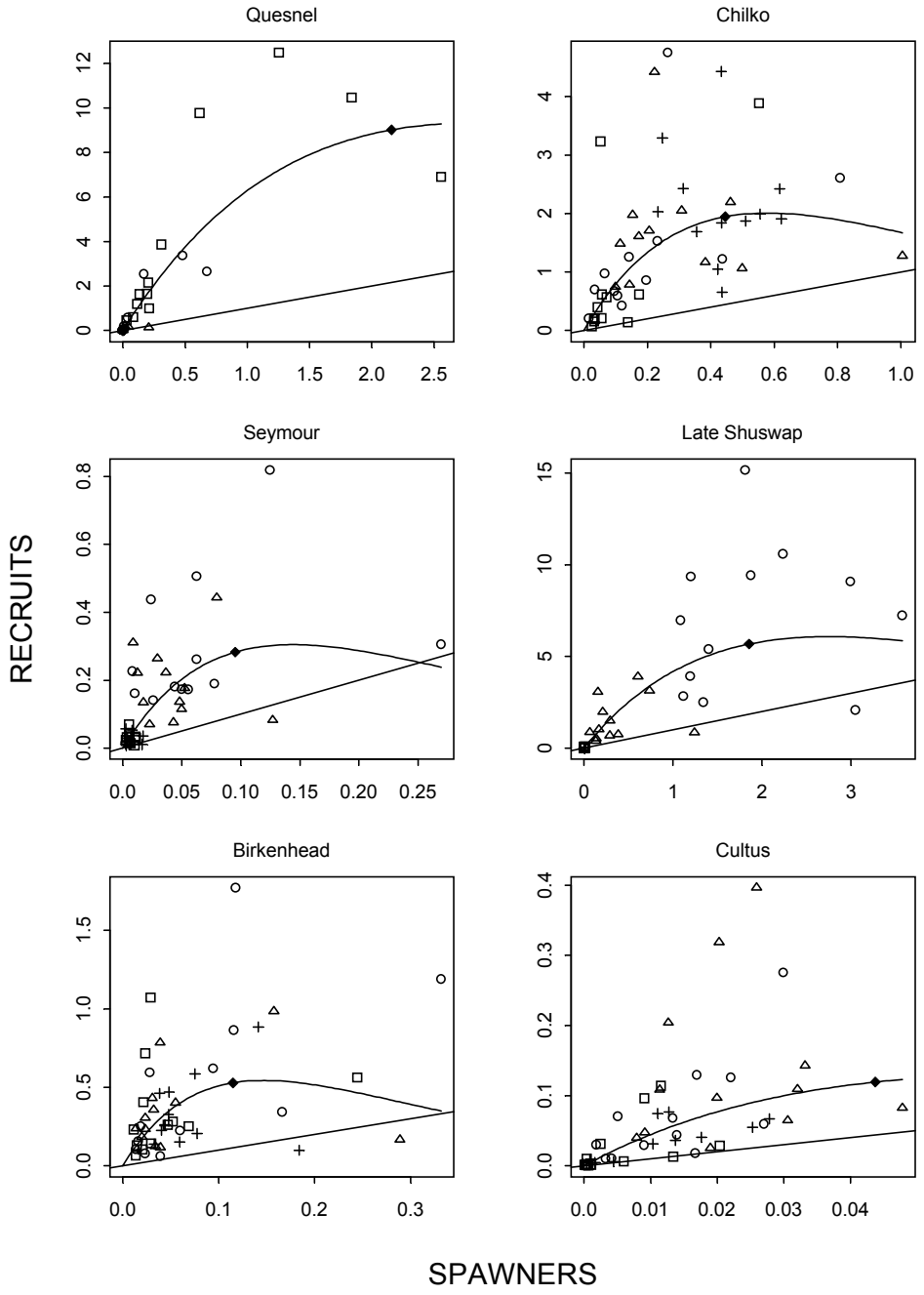

Figure 11b. Stock-recruit relationships (millions). Curves are based on modal Ricker parameter estimates (see Table 2). Symbols (□,△,O, +) denote cycle lines (1993, 1994, 1995, 1996). The symbol ♦ is the MSY point where spawners equal S^*. It is excluded if the estimate is beyond the data range.

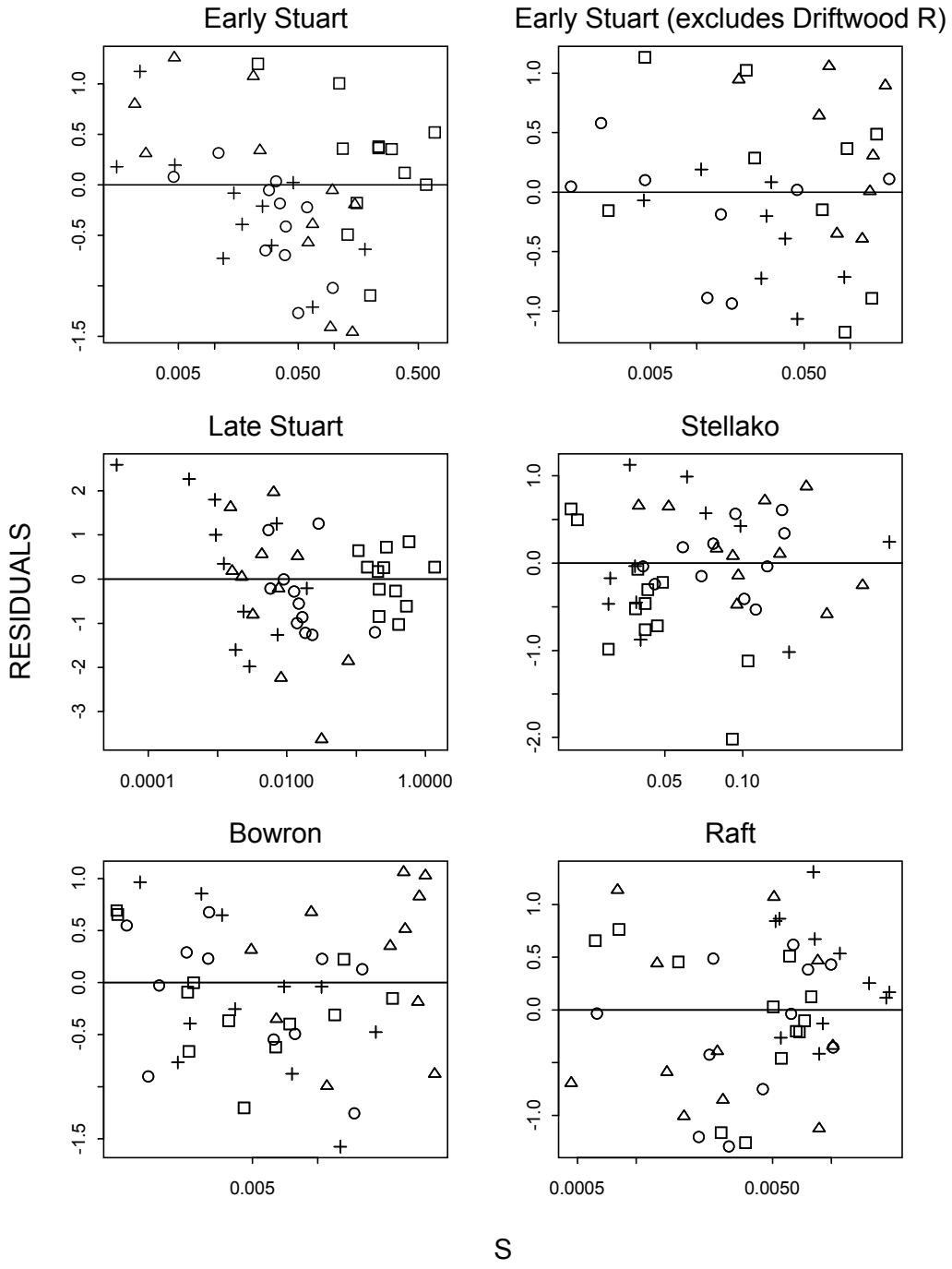

Figure 12a. Log_e Residuals from stock-recruit curve versus spawning escapement (S) (log10 scale). Symbols (□,△,O, +) denote cycle lines (1993, 1994, 1995, 1996).

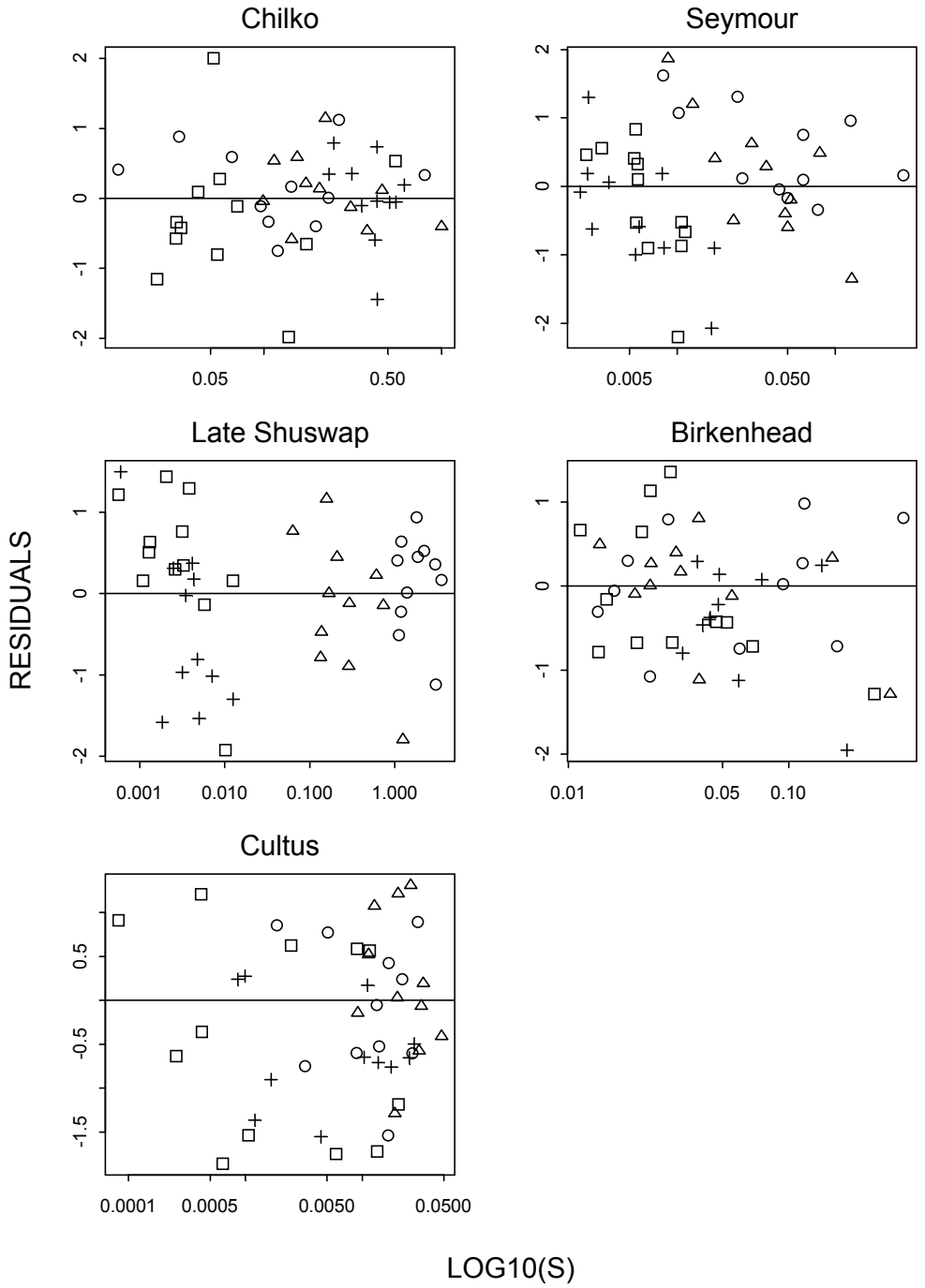

Figure 12b. Log_e Residuals from stock-recruit curve versus log10 spawning escapement (S) log10 scale. Symbols (□,△,O, +) denote cycle lines (1993, 1994, 1995, 1996).

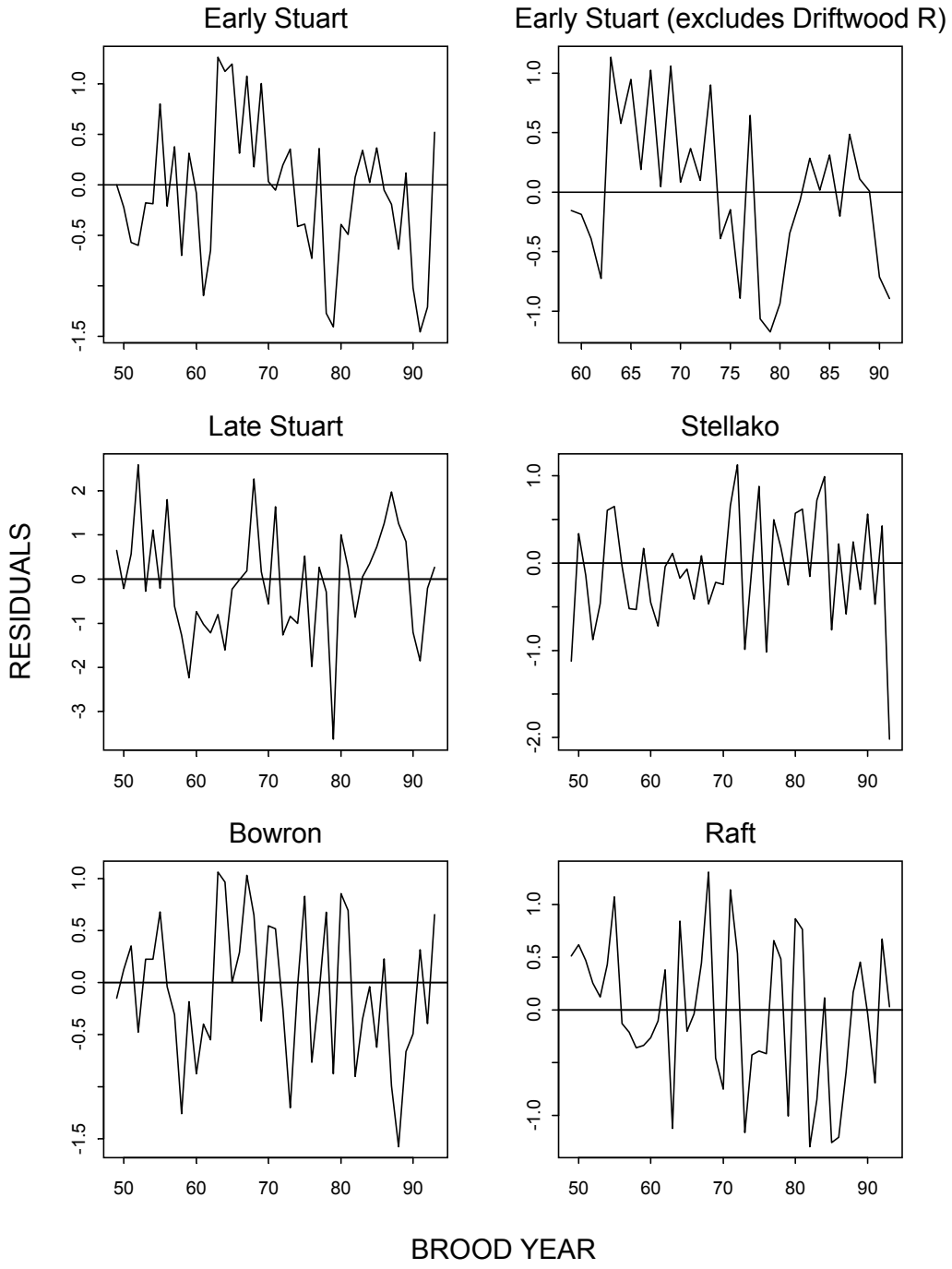

Figure 13a. Log_e Residuals from Ricker stock-recruit curve versus year.

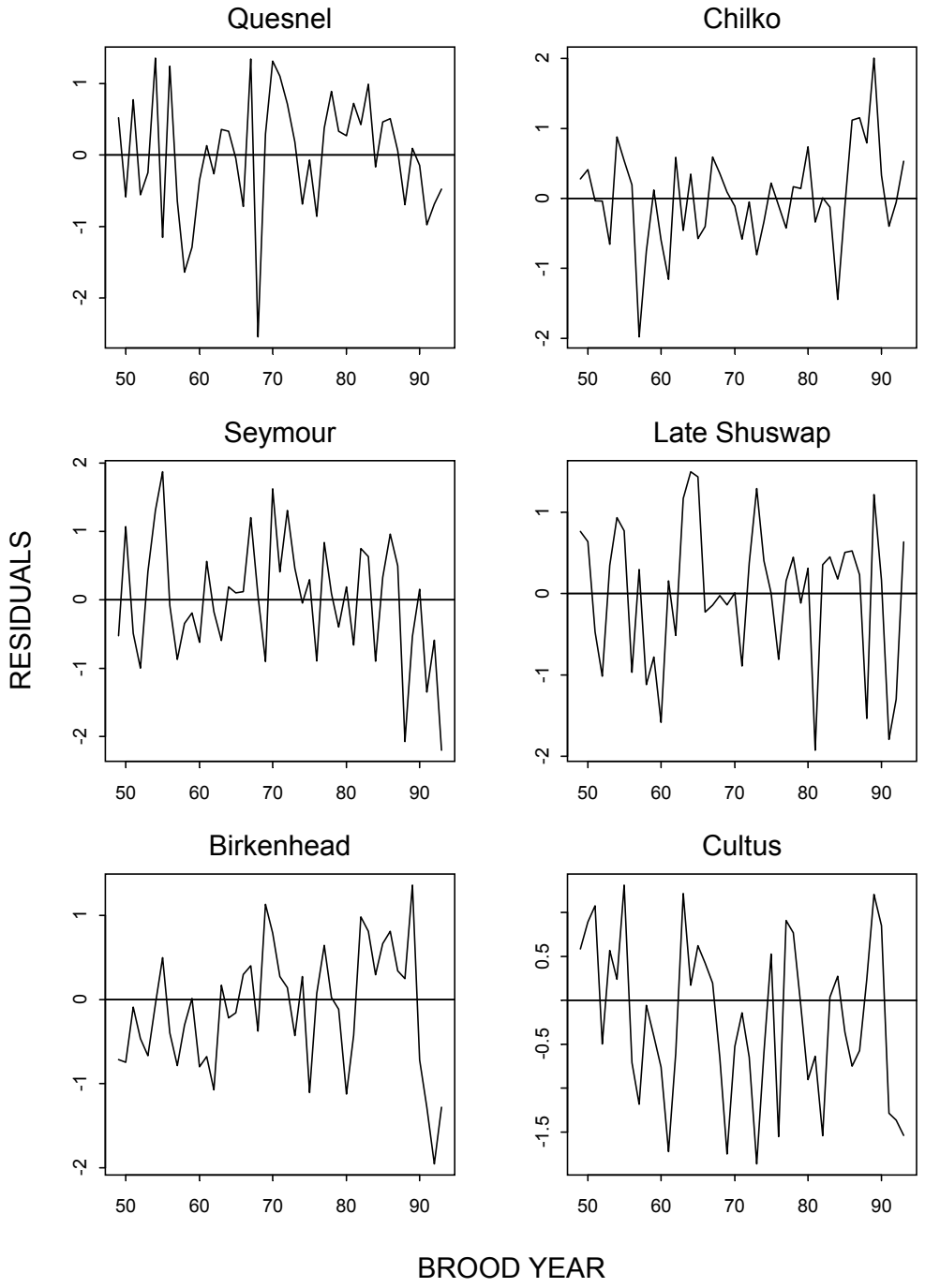

Figure 13b. Log_e Residuals from Ricker stock-recruit curve versus year.

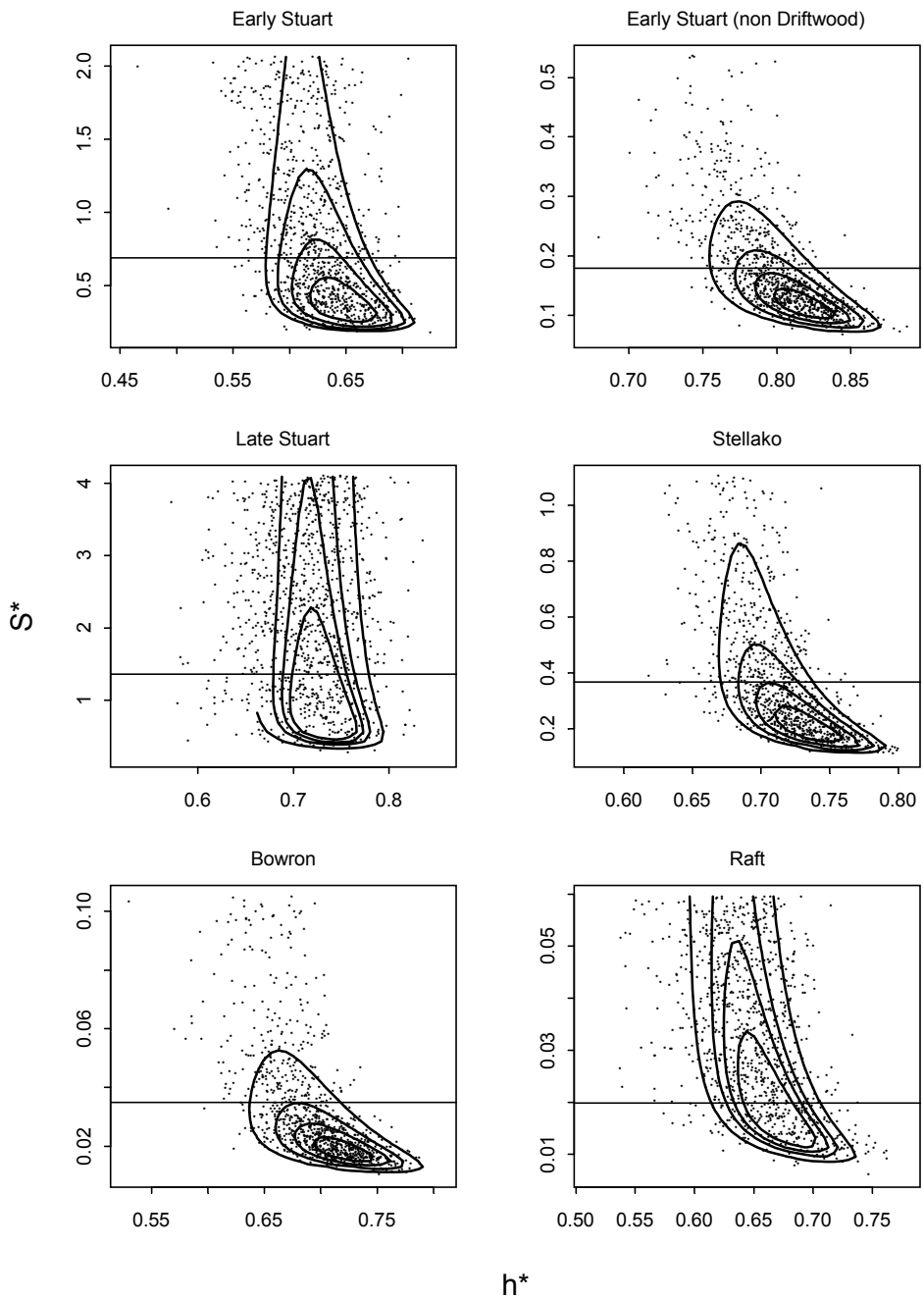

Figure 14a. Scatter plot of 1,000 estimates (h^*, S^*) taken from an MCMC sample of length 20,000 by stock. S^* is in millions of fish. Contour lines correspond to 20%, 40%, 60% and 80% posterior confidence regions. The solid horizontal line denotes the maximum observed spawners (1948-97).

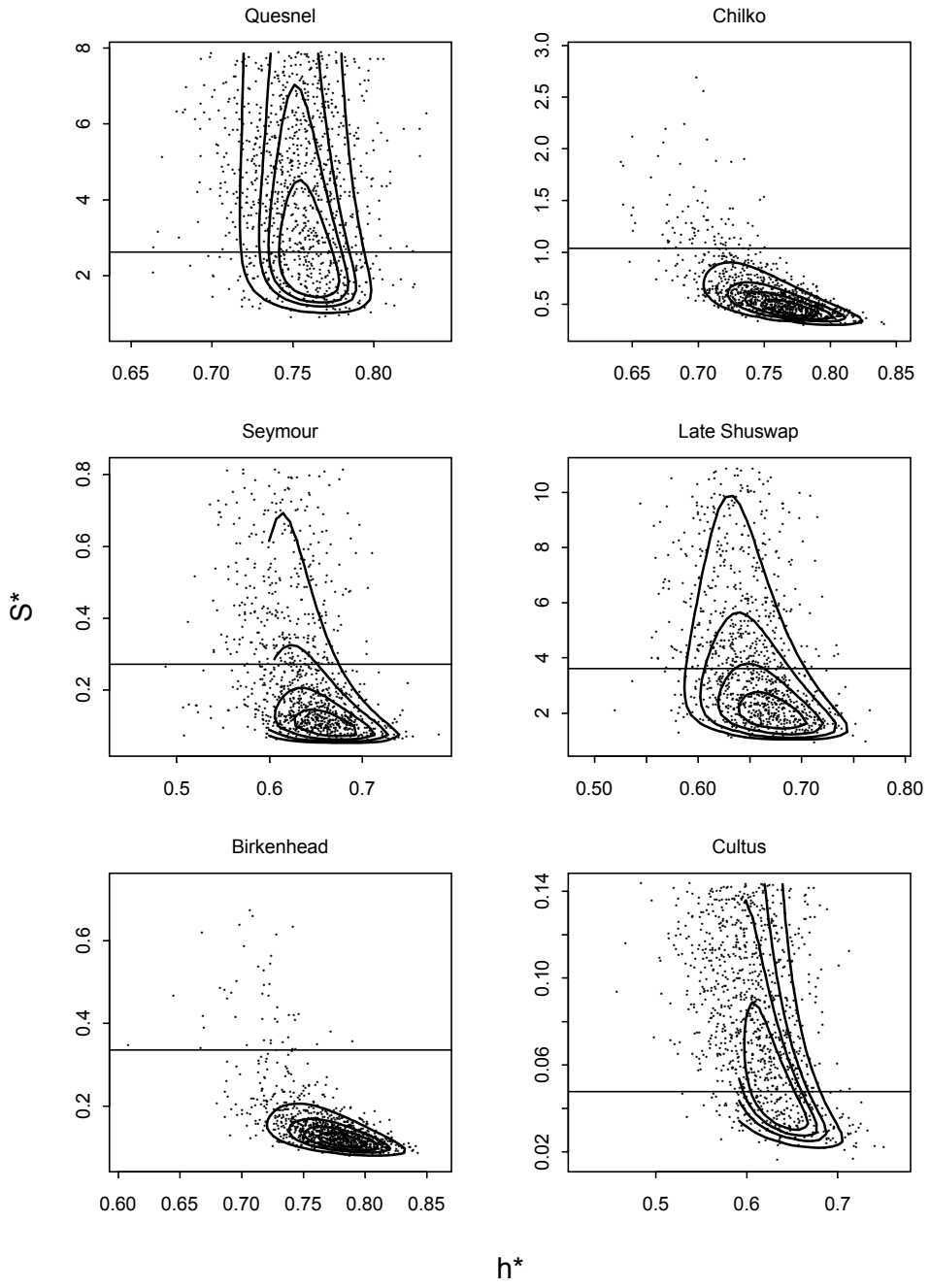

Figure 14b. Scatter plot of 1,000 estimates (h^*, S^*) taken from an MCMC sample of length 20,000 by stock. S^* is in millions of fish. Contour lines correspond to 20%, 40%, 60% and 80% posterior confidence regions. The solid horizontal line denotes the maximum observed spawners (1948-97).

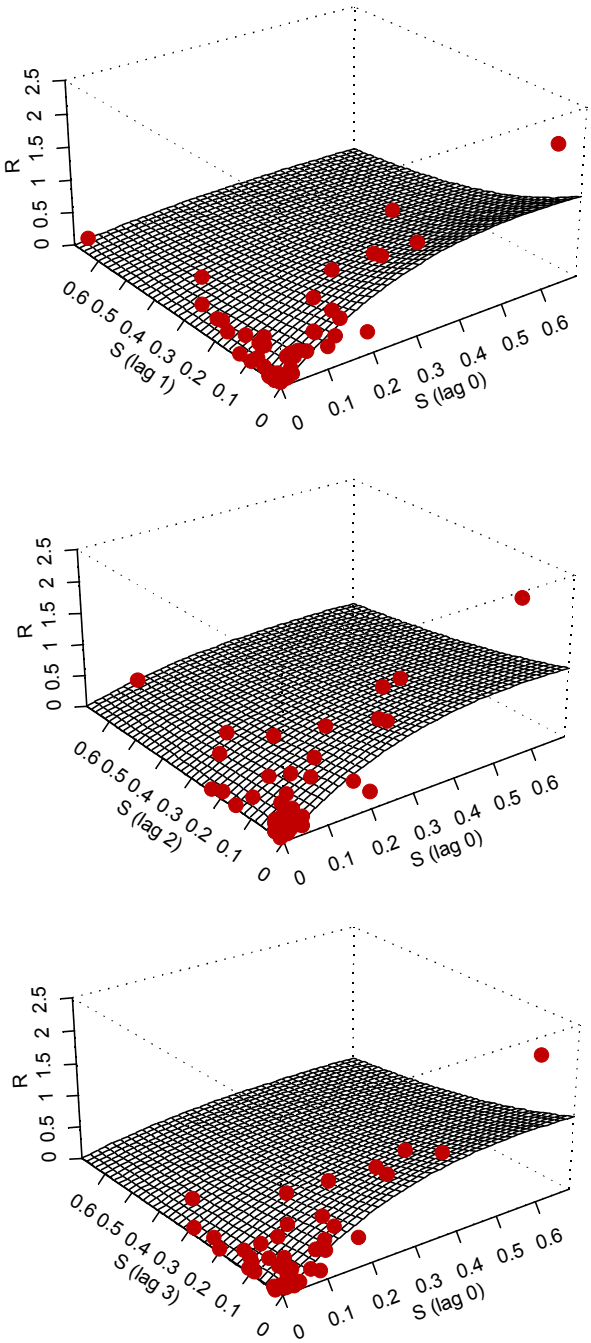

Figure 15a. Larkin stock-recruitment relationship for Early Stuart sockeye. Recruitment is plotted as a function of spawning escapement S at 1, 2 and 3 year lags. The additional spawning escapement is fixed at the mean S.

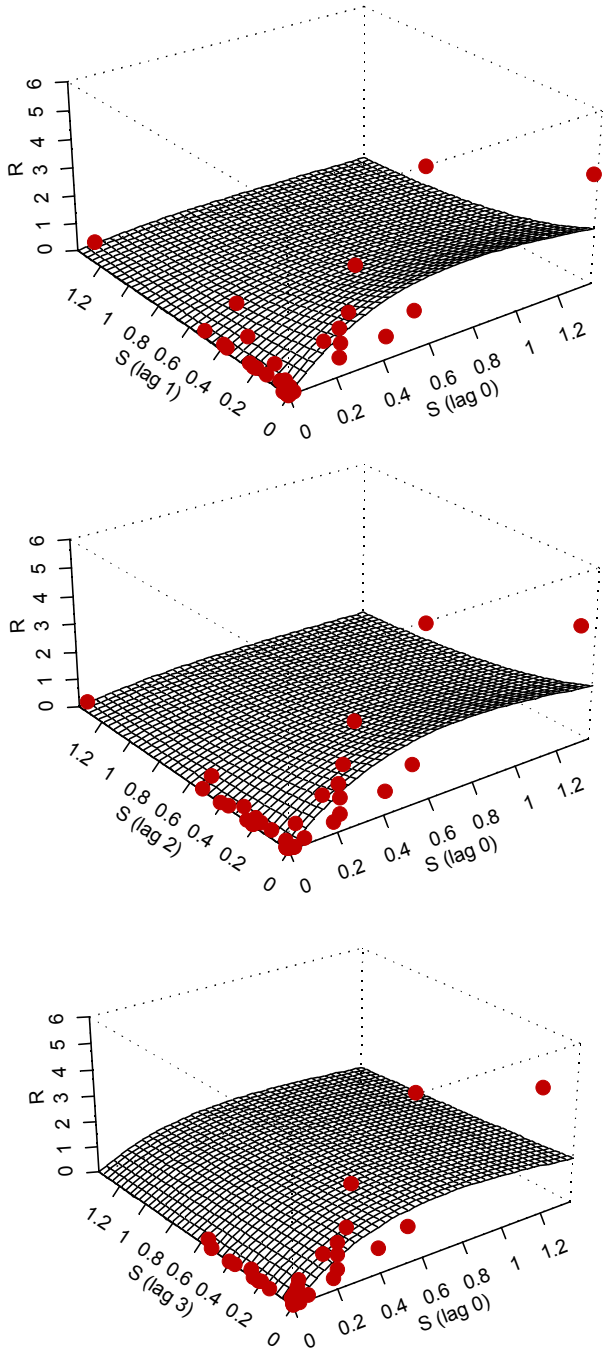

Figure 15b. Larkin stock-recruitment relationship for Late Stuart sockeye. Recruitment is plotted as a function of spawning escapement S at 1, 2 and 3 year lags. The additional spawning escapement is fixed at the mean S.

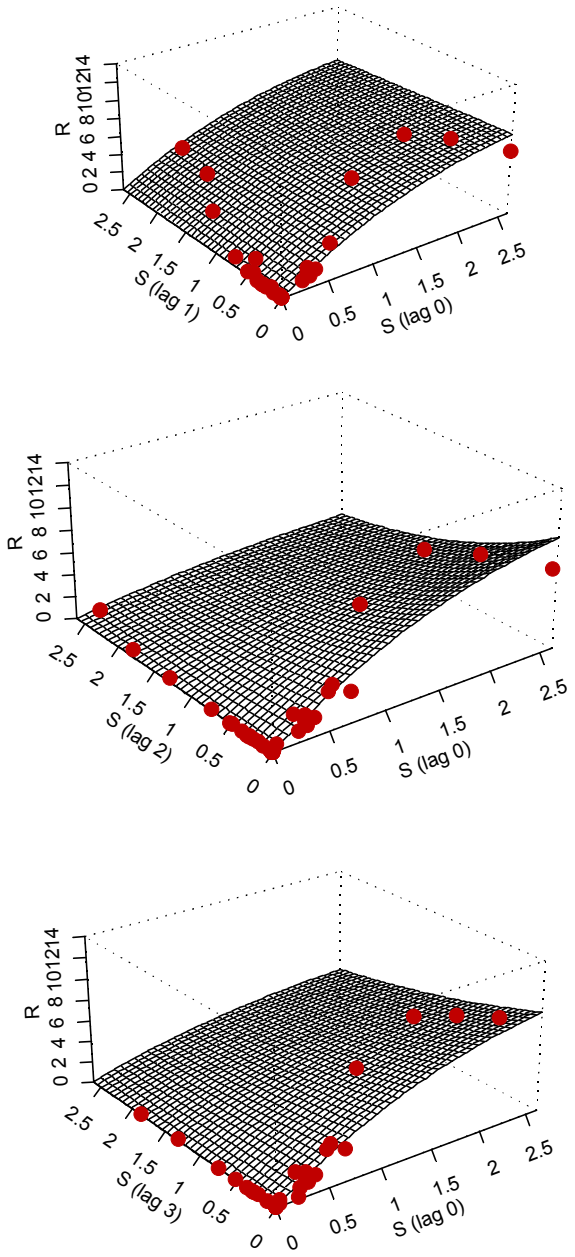

Figure 15c. Larkin stock-recruitment relationship for Quesnel sockeye. Recruitment is plotted as a function of spawning escapement S at 1, 2 and 3 year lags. The additional spawning escapement is fixed at the mean S.

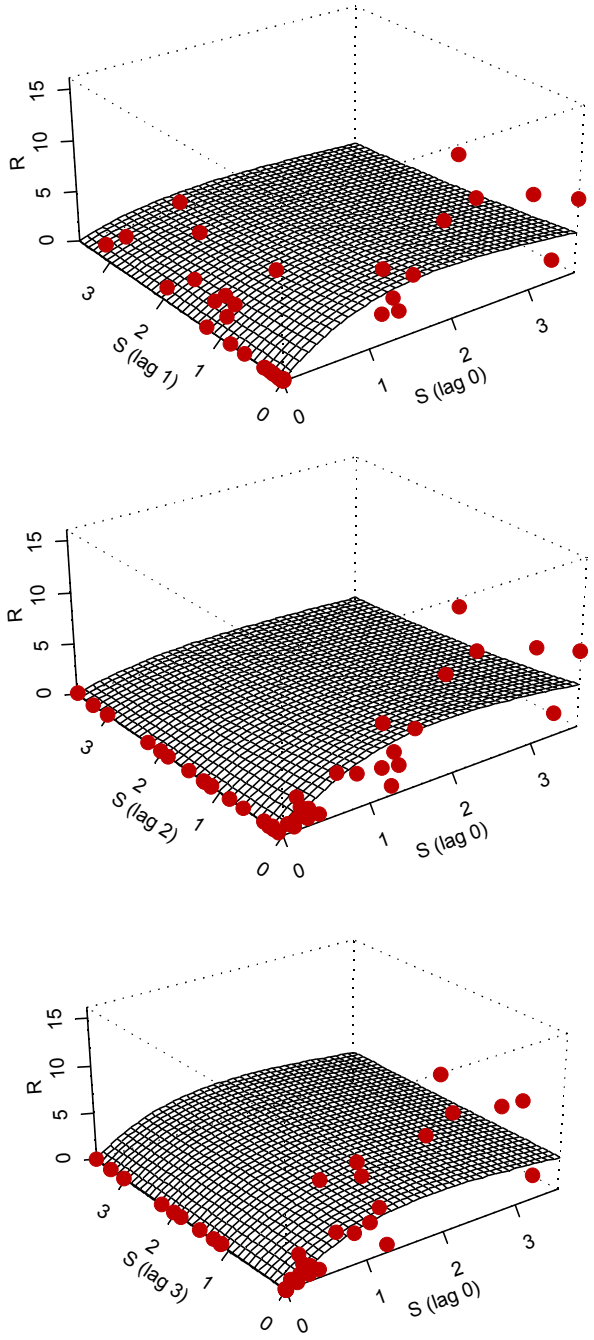

Figure 15d. Larkin stock-recruitment relationship for Late Shuswap sockeye. Recruitment is plotted as a function of spawning escapement S at 1, 2 and 3 year lags. The additional spawning escapement is fixed at the mean S.

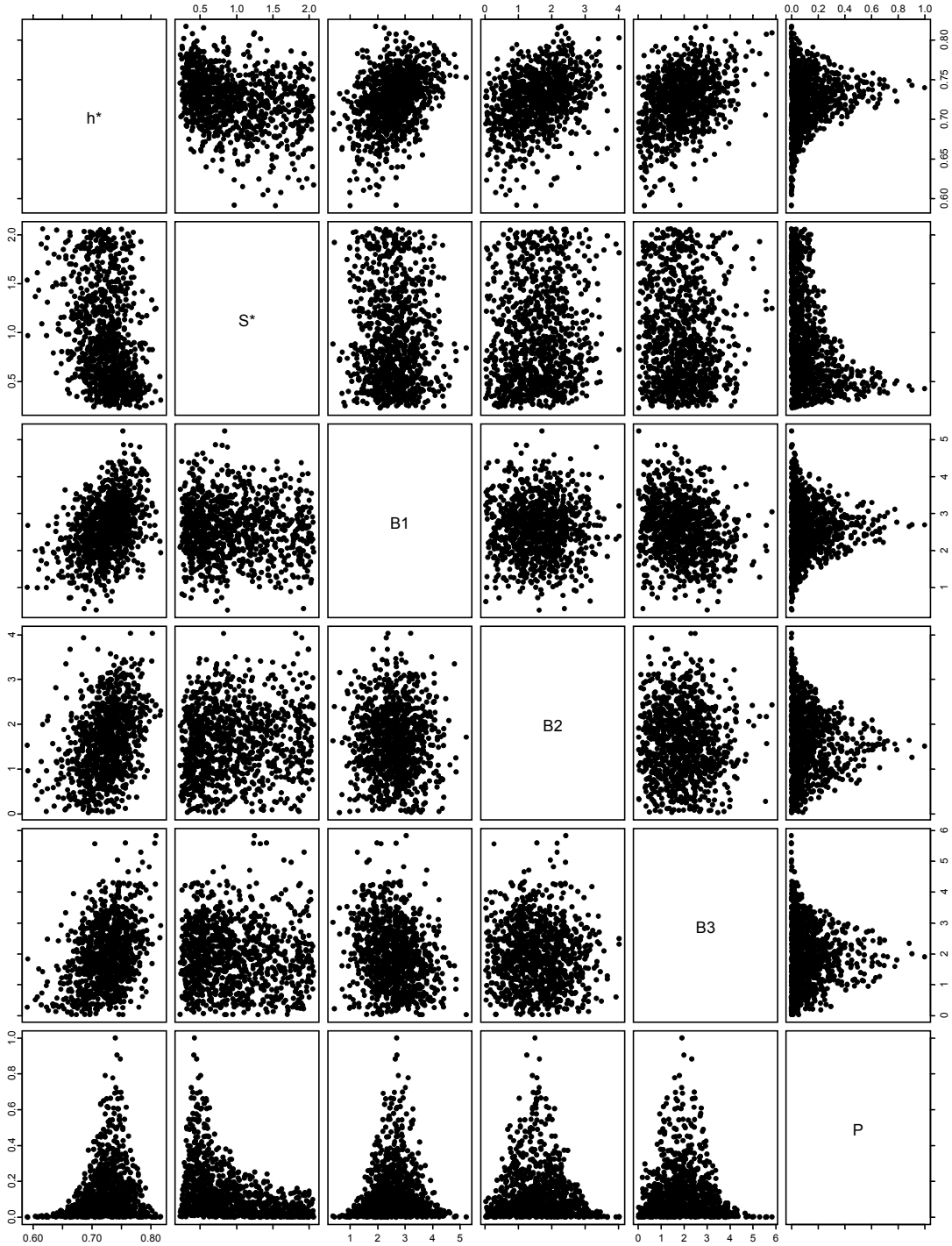

Figure 16a. Scatter plot of 1,000 estimates ($h^*, S^*, \beta_1, \beta_2, \beta_3$) for the Larkin model taken from an MCMC sample of length 20,000 for Early Stuart sockeye.

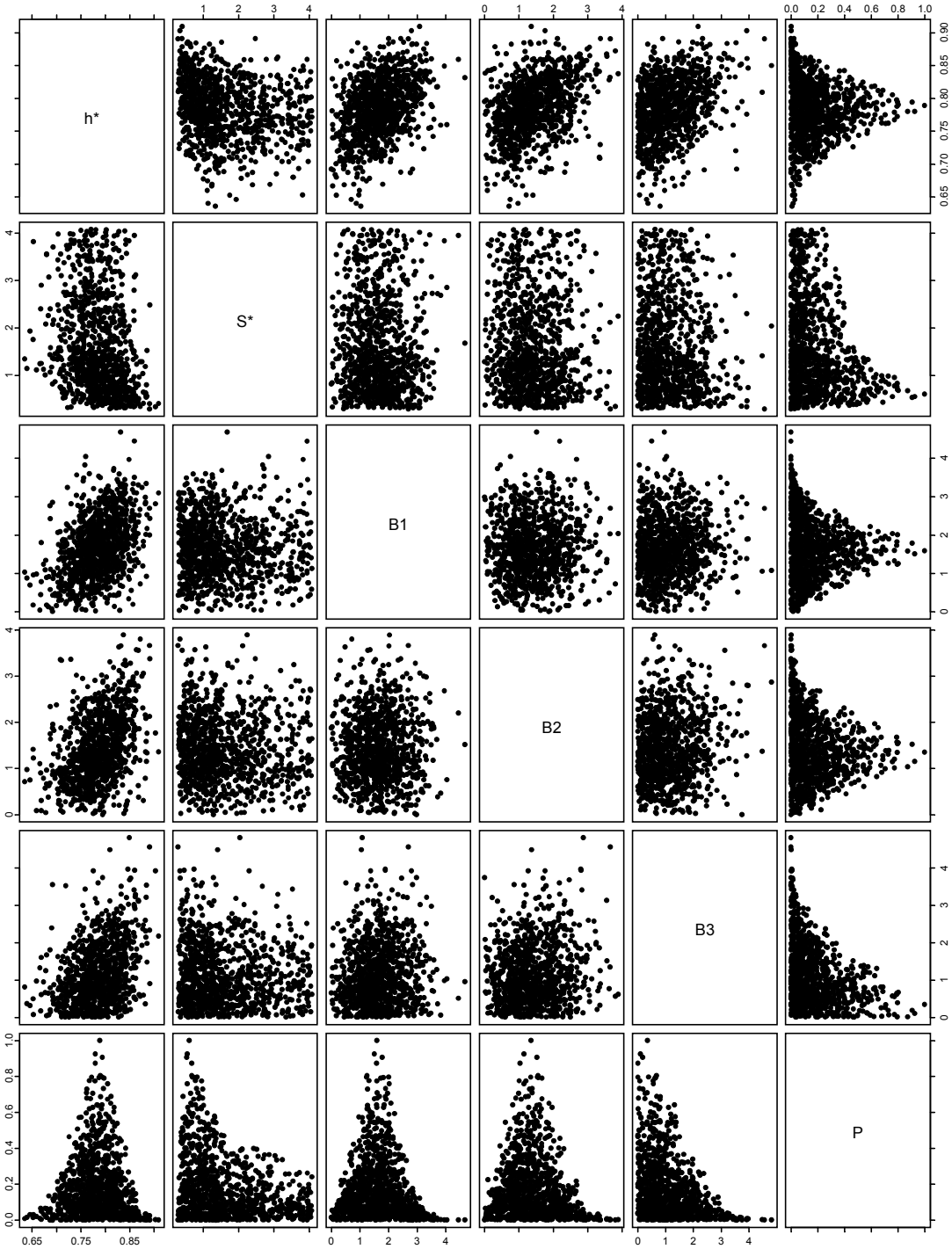

Figure 16b. Scatter plot of 1,000 estimates ($h^*, S^*, \beta_1, \beta_2, \beta_3$) for the Larkin model taken from an MCMC sample of length 20,000 for Late Stuart sockeye.

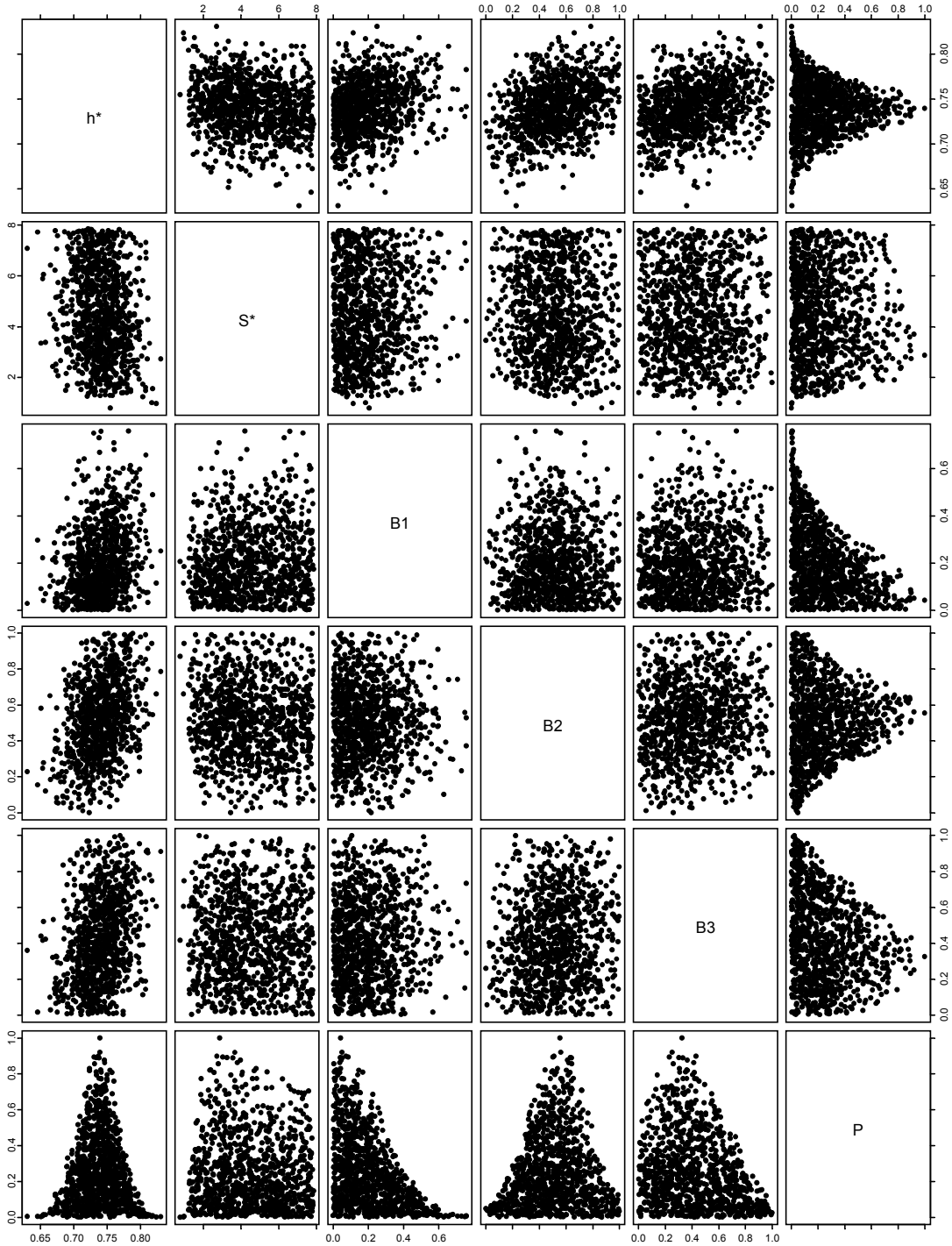

Figure 16c. Scatter plot of 1,000 estimates ($h^*, S^*, \beta_1, \beta_2, \beta_3$) for the Larkin model taken from an MCMC sample of length 20,000 for Quesnel sockeye.

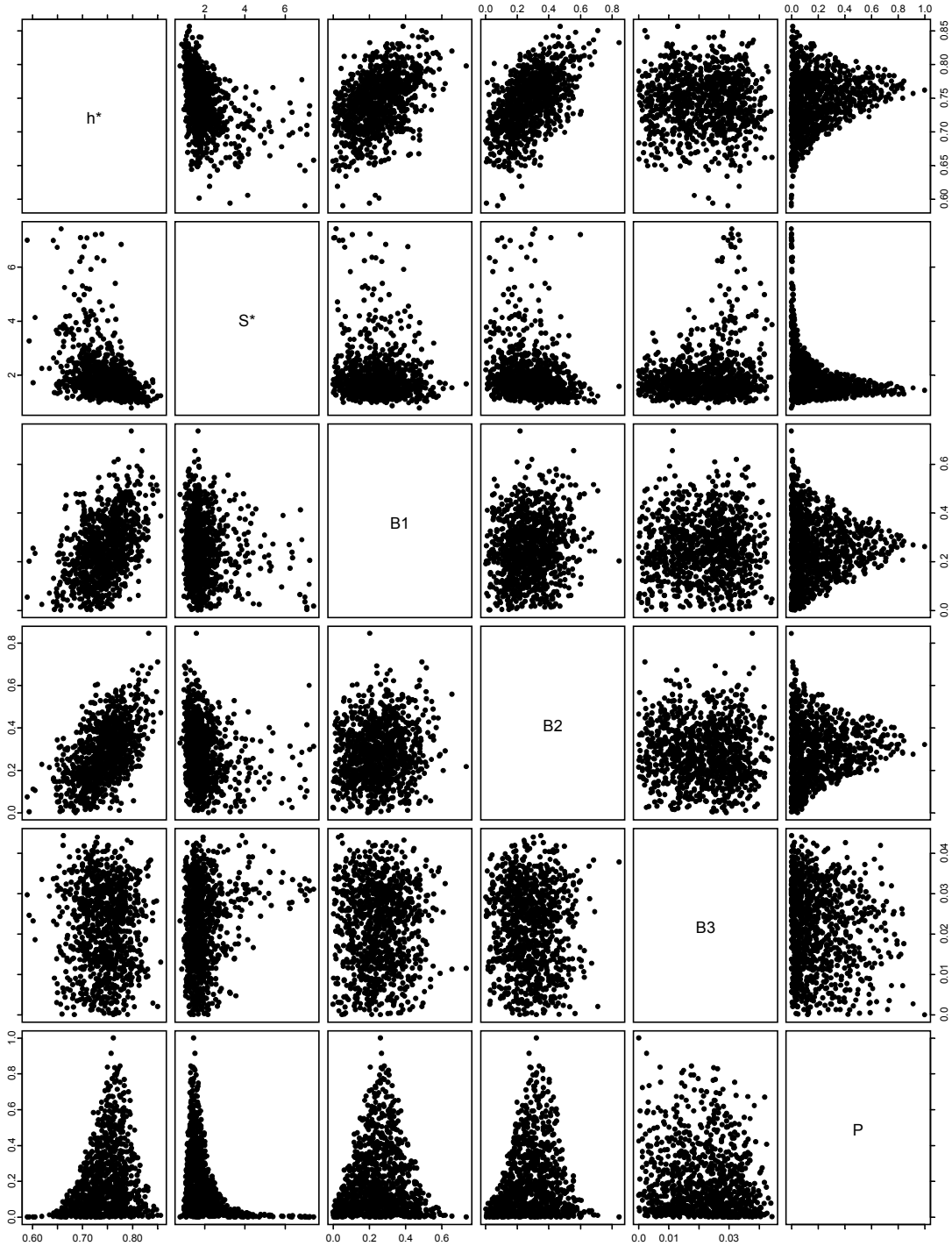

Figure 16d. Scatter plot of 1,000 estimates ($h^*, S^*, \beta_1, \beta_2, \beta_3$) for the Larkin model taken from an MCMC sample of length 20,000 for Late Shuswap sockeye.

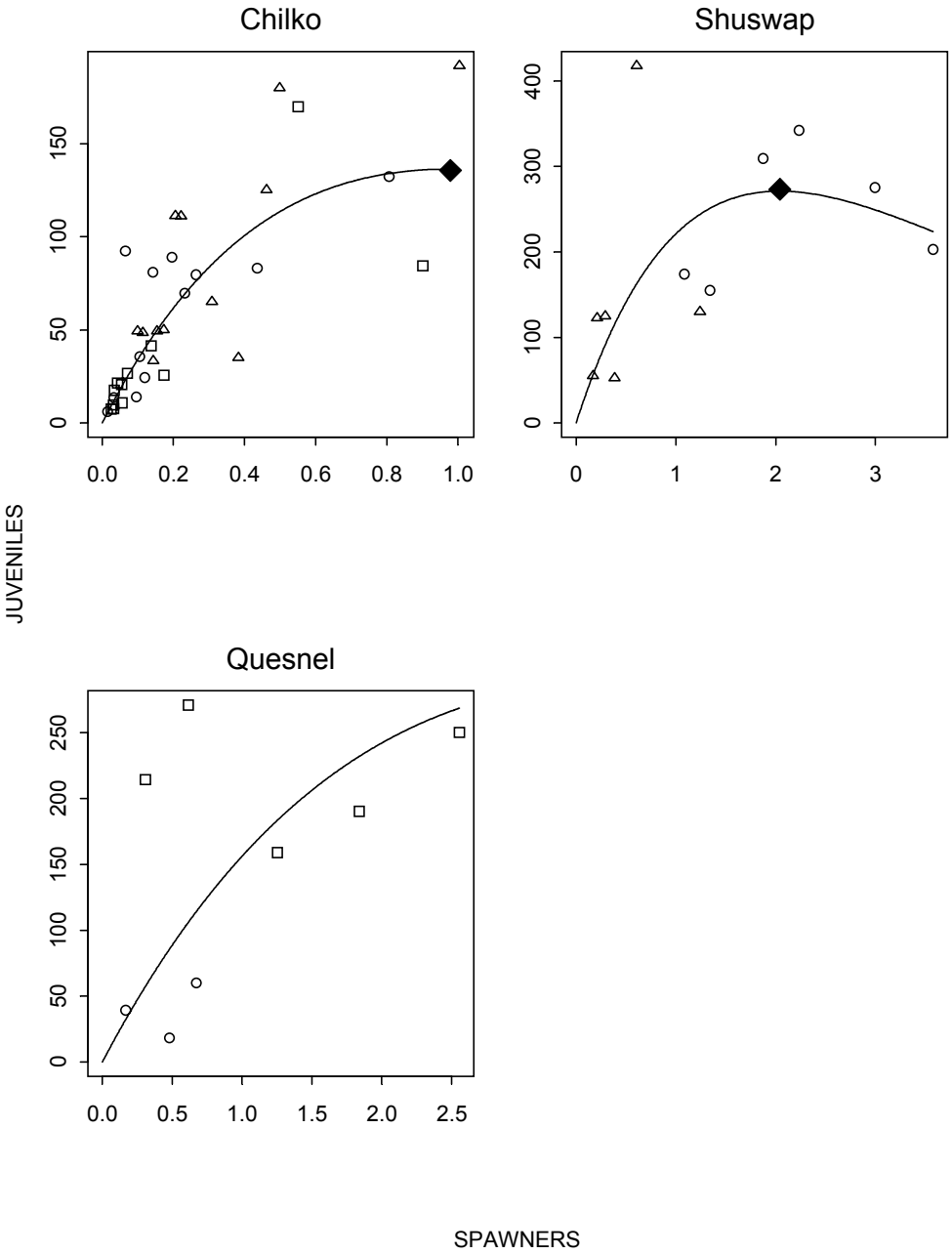

Figure 15. Ricker Spawner-juvenile relationship for Quesnel. Chilko and Shuswap Lake. Spawners are in millions of fish. Juveniles are in metric tons. Symbols (□,△,O, +) denote cycle lines (1993, 1994, 1995, 1996). The symbol ♦ is the MSY point where spawners equal S^*. It is excluded if the estimate is beyond the data range.