PERSPECTIVES

Estimating delayed density-dependent mortality in sockeye salmon (*Oncorhynchus nerka*): a meta-analytic approach

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Abstract: Delayed density-dependent mortality can be a cause of the cyclic patterns in abundance observed in many populations of sockeye salmon (*Oncorhynchus nerka*). We used a meta-analytical approach to test for delayed density dependence using 34 time series of sockeye data. We found no consistent evidence for delayed density-dependent mortality using spawner – spring fry or spawner–recruit data. We did find evidence for delayed density-dependent mortality at a 1 year lag for the spawner – fall fry and the spawner–smolt data; however, effects at lags greater than 1 year were weak and not statistically significant. Between-cohort interactions at a 1-year lag are not sufficient to cause the observed cycles in adult abundance, although they will tend to reinforce patterns established by other mechanisms. Our results imply that reductions in fishing mortality in off-peak years should result in an increase in abundance.

Résumé : Un retard dans la mortalité dépendante de la densité pourrait constituer une cause des régimes cycliques d'abondance observés dans de nombreuses populations de saumon rouge (*Oncorhynchus nerka*). Les auteurs ont utilisé une approche méta-analytique pour vérifier cette hypothèse à partir de 34 séries chronologiques de données sur le saumon rouge. Les données sur le rapport géniteurs – alevins du printemps ou géniteurs–recrues n'ont révélé aucune indication solide d'un retard dans la mortalité dépendante de la densité. Les auteurs ont toutefois mis en évidence un retard dans la mortalité avec un écart de 1 an pour le rapport géniteurs – alevins d'automne et géniteurs–smolts. Les effets pour les écarts supérieurs à 1 an étaient faibles et statistiquement non significatifs. Les interactions entre cohortes pour un écart de 1 an sont insuffisantes pour expliquer les cycles observés dans l'abondance des adultes, mais ont plutôt tendance à renforcer les patrons établis par d'autres mécanismes. Les résultats présentés ici révèlent que les réductions dans la mortalité par pêche au cours des années de creux devraient entraîner un accroissement de l'abondance.

[Traduit par la Rédaction]

Introduction

It has been hypothesized that delayed density-dependent mortality is on important contributing factor to population cycles in mammals (Hornfeldt 1994), insects (Turchin 1990; Ginzburg and Taneyhill 1994), and fish (Townsend 1989). Sockeye salmon (*Oncorhynchus nerka*) often fluctuate in abundance by many orders of magnitude in a regular way, and it has been suggested (Ricker 1950; Ward and Larkin 1964; Levy and Wood 1992) that delayed density dependence may play a role in these variations in abundance (such patterns have been termed "cyclic dominance"). Most cyclic populations have a single age-at-maturity (usually 4 but sometimes 5 years), and thus, a population can be thought of as having four or five distinct "lines" or subpopulations. Sockeye cycles result from one or more of the lines being much more abundant than the others; the range in variation can be up to four orders of magnitude (Fig. 1). Thus, cycles in the annual abundance of sockeye salmon caused by differences in the abundance of the four or five lines are somewhat different than most organisms that reproduce continuously, or that have an annual life cycle.

Levy and Wood (1992) recently reviewed mechanisms that could generate cycles in Fraser River, British Columbia, sockeye salmon. Various sources of delayed density-dependent mortality are what Levy and Wood (1992) referred to as "brood interactions," which cause the survival of year-class(es) that follow the most abundant or dominant line to be reduced. Proposed mechanisms for this reduction are competition, i.e., heavy predation on lake zooplankton by dominant year-classes diminishes the food supply of successive broods, or predation, i.e., disease, parasites, or predators are built up by dominant year-classes and inflict higher rates of mortality on the weak years.

Other mechanisms hypothesized to maintain line dominance include biogenic enrichment (Levy and Wood 1992), which is the increased survival of the dominant broods resulting

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Fig. 1. Recruitment time-series for the populations analyzed. Estimates of numbers at age in a year-class are $\log_{10}$ transformed with the mean removed. The mean of each series is separated by 2 units, i.e., a factor of 100, from the one below. Thus, the distance between the horizontal broken lines gives the vertical scale.
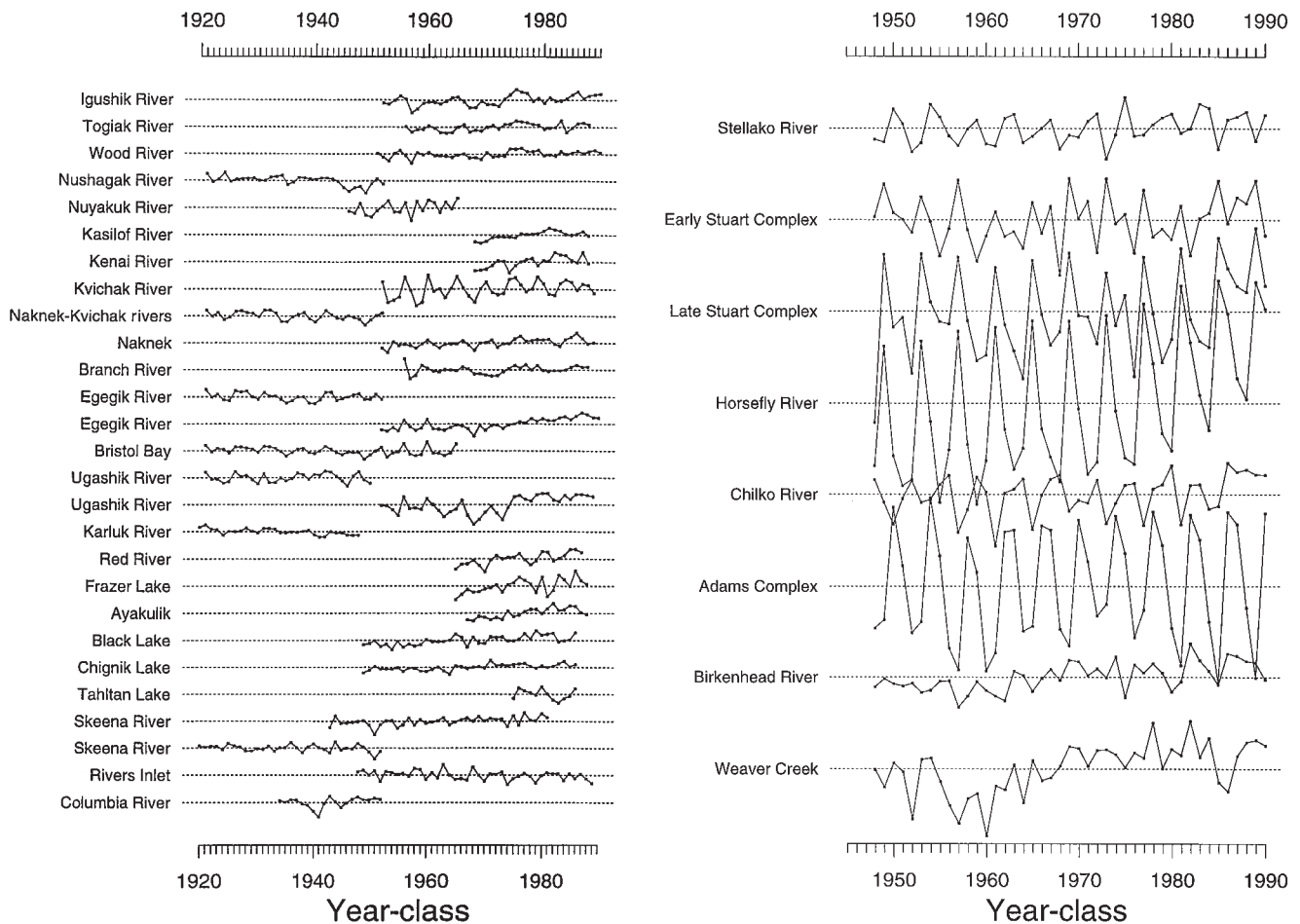
from the inflow of nutrients from decaying salmon carcasses. A genetic mechanism that requires a strongly heritable age-at-maturity has also been proposed (Walters and Woodey 1992). Finally, a simple model of depensatory predation in which predator mortality is negatively related to abundance (without an interaction of other year-classes) may be sufficient to maintain disparities in abundance among lines. Levy and Wood (1992) dismissed the hypothesis that marine environmental factors were driving the cycles because different populations of sockeye that migrate together at sea cycle out of phase with each other.

Finally, the hypothesis that depensatory fishing mortality, i.e., higher fishing mortality at low abundance, was responsible for the cycles has been rejected by Cass and Wood (1994) in a recent analysis of Fraser River data. However, Eggers and Rogers (1987) found evidence for depensatory fishing for Kvichak River, Alaska, sockeye salmon that could be an important mechanism for the maintenance of the cycle in this population.

Delayed density-dependent mortality is of more than a purely academic concern. If there is no delayed density-dependent mortality maintaining "off-cycle" years at low levels, then the economic benefits to rebuilding these runs would be enormous (Walters and Staley 1987; Welch and Noakes

1990). Until the mechanism that causes the cycles is understood, it is difficult to recommend management strategies to maximize catches (Collie and Walters 1987; Levy and Wood 1992; Cass and Wood 1994).

Our approach here is to estimate delayed density-dependent mortality using a meta-analytic approach (Myers 1997). We have attempted to compile all time-series that could be used to estimate delayed density-dependent mortality and have analyzed it in a manner to determine if any reliable conclusions can be drawn.

Data sources

The number of spawners that give rise to cohort t is S_t. These fish migrate upstream to spawn in the spring, summer, or fall and lay eggs that result in F_t fry the following spring which in most cases migrate to nursery lakes. The number of smolts, indicated by M_t, migrate to sea, typically after 1 year of lake rearing in British Columbia populations and after 1 or 2 years in Alaskan stocks. The surviving fish ("recruits" here, R_t) return usually at a total age of 4 years in British Columbia or age 4, 5, or 6 in Alaska to spawn, at which time they enter the fishery.

We use data for spawners and subsequent recruitment after

migration to the sea compiled by Bradford (1995), Myers et al. (1995*a*, 1995*b*), Myers and Barrowman (1996), and unpublished sources. The data are derived from estimates of catch and escapement, the latter being the number of fish in a cohort that are not caught and can potentially spawn. Escapement is estimated using a variety of estimates, e.g., acoustics, visual counts, counting fences, mark–recapture, or counts of redds (spawning nests). There are eight major populations from the Fraser River watershed in British Columbia; the other populations we analyze from British Columbia are the Skeena River, Tahltan Lake, Rivers Inlet, and Smith Inlet populations. The Alaskan populations are from Bristol Bay, with the exception of the Karluk River from Kodiak Island (Eggers and Rogers 1987), and the Black and Chignik lakes from the Alaskan peninsula.

For several rivers, there are two time-series from different sources, e.g., the Skeena and Egegik rivers (Fig. 1); however, there is relatively little overlap between these series. The Naknek and Kvichak rivers in Alaska were originally assessed as one stock, but were later assessed as separate stocks.

We also analyze estimates that do not depend on commercial catch rates. In an attempt to isolate the life stage that density-dependent mortality occurs, we analyzed survival from egg to spring fry estimated during spring migration to lakes, to fall fry lake residence, and to smolt migration to the sea. For these studies, we used data with at least 10 years (thus, we would need at least 12 years of data for our models that include a 2-year lag). We did not use data from spawning channels or rivers where large enhancement programs had been undertaken.

We had access to three studies of survival to spring fry (i.e., fry estimated as they move from spawning gravel into lakes): Chilko River, a tributary of the Fraser River (Roos 1985, updates provided by A.J. Cass, Department of Fisheries and Oceans, Nanimo, B.C.) and Pinkut Creek and Fulton River which drain into Babine Lake (West and Mason 1987, updated and corrected by Wood et al. 1995; we did not use data from the spawning channels). We used data from Fulton River and Pinkut Creek only after 1967, when the flow was controlled. The Pinkut Creek and Fulton River fry were estimated using a counting fence, and the Chilko river data were based on visual estimates, and are probably less reliable.

We had access to two studies of survival of fry to October of the first year of lake rearing from Hume et al. (1996, updated by J. Hume, Cultus Lake Laboratory, Department of Fisheries and Oceans, Cultus Lake, B.C.) for Quesnel and Shuswap lakes of the Fraser River watershed. Fry abundance was estimated in October in the lakes using acoustic and trawl surveys. Fall fry abundance was estimated for dominant brood years since 1977 and for all brood years from 1985 to 1994 in Quesnel Lake and for 7 years from 1974 to 1985 and for all brood years from 1986 to 1992, plus 1994, from Shuswap Lake. These data are contaminated by the presence in the lakes of kokanee (landlocked sockeye salmon) juveniles, which are indistinguishable from sockeye juveniles in the acoustic surveys. Electrophoretic surveys conducted in Shuswap Lake over 3 years indicated that although kokanee comprise a small part of the population in the dominant sockeye years, they can be more numerous than sockeye in off-peak years (Levy and Wood 1992). Unfortunately, there is no way to correct the whole Shuswap time-series, nor are there estimates available for Quesnel Lake.

Smolt data from counting fences or acoustic surveys were available from Lake Dalnee, Kamchatka Peninsula (Foerster 1968), Kvichak River, Alaska (Eggers and Rogers 1987), and Egegik River, Alaska (D.E. Rogers, University of Washington, Seattle, Wash., personal communication). We also use data from Chilko Lake, B.C., for years in which there was no fertilization of the lake.

Our approach in including data in the meta-analysis was to eliminate as few studies as possible before the analysis began, particularly for subjective reasons. This does not imply that all the studies are equally reliable, but only that the results must be carefully examined for biases and consistency. Furthermore, we will investigate the robustness of our results under a variety of conditions, e.g., we eliminated data before 1950 to determine if the results were sensitive to the early, less reliable data.

Model estimation

We examine the hypothesis that survival from eggs produced by generation t spawners that survive to return as recruits, log (R_t / S_t), is a linear function of spawner abundance at lags 0, 1, and 2. This results in the model

$$(1) \qquad R_t = \alpha S_t e^{-\beta S_t - \phi S_{t-1} - \gamma S_{t-2} + \varepsilon_t}$$

where βS_t, ϕS_{t-1}, and γS_{t-2} are the density-dependent mortality due to the number of spawners with lags of 0, 1, and 2. Environmental variability in density-independent survival is given by ε_t, which is assumed to be a zero mean random variable with constant variance σ^2. This model has been studied by Ward and Larkin (1964), Larkin (1971), Collie and Walters (1987), and Welch and Noakes (1990). They considered an additional density-dependent parameter corresponding to a lag term for 3 years. Welch and Noakes (1990) assumed that the interaction at lag 2 was the square of the effect of lag 1, and similar for a lag at year 3; however, there is no empirical justification for this model.

We fit the model after log transformation, i.e.,

$$(2) \qquad \log\!\left(\frac{R_t}{S_t}\right) = \log(\alpha) - \beta S_t - \phi S_{t-1} - \gamma S_{t-2} + \varepsilon_t$$

using least squares multiple regression. The Durbin–Watson statistic was used to test for first-order autocorrelation in survival. In significant cases, the autocorrelation parameters were estimated under the assumption that the errors were described by a first-order autoregressive process using generalized least squares (Judge et al. 1984). For fry or smolt data, R_t in eq. 2 is replaced with F_t or M_t.

Meta-analysis of the results

If several populations share a common pattern of delayed density dependence, then we can apply meta-analytic techniques. We first have to standardize the delayed density-dependent mortality coefficients, ϕ_i and γ_i (i designates the population). We therefore seek a standardization that will render the delayed density-dependent parameters scale independent among populations. From eq. 1, natural scalings are $\phi_i' = \phi_i/\beta_i$, $\gamma_i' =$

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γ_i/β_i and $\phi_i'' = \phi_i \overline{S}_i$, $\gamma_i'' = \gamma_i \overline{S}_i$ (where $\overline{S}_i$ is the mean spawner abundance). We will use both standardizations.

We first test if the standardized density-dependent coefficients are heterogeneous within a region, Alaska or British Columbia, then between regions, and finally overall. If the standardized coefficients appear to be homogeneous, then we will estimate the mean over the region.

Let δ_i be the magnitude parameter, i.e., the "effect size", for the meta-analysis (Hedges and Olkin 1985; Cooper and Hedges 1994). This will be either the ϕ_i' or ϕ_i'', γ_i' or γ_i''. Let **d** be the vector of estimates of effect size for each of the populations. The errors in the estimate are assumed to approximately follow a multivariate normal distribution with mean 0 and variance–covariance Σ. To test heterogeneity of the effect sizes, i.e., all δ_i's are equal, we use the test statistic (Hedges and Olkin 1985, p. 211)

$$Q = \mathbf{d}'\hat{\mathbf{M}}\mathbf{d}$$

where **M** is the matrix

$$\mathbf{M} = \Sigma^{-1} - \Sigma^{-1}\,\mathbf{ee}'\,\Sigma^{-1}/\mathbf{e}'\Sigma^{-1}\mathbf{e}$$

where **e** is a p-dimensional column vector of 1's and $\hat{\mathbf{M}}$ is the estimate of **M**. If the p populations have the same coefficient, then the test statistic Q has an asymptotic chi-squared distribution with $p - 1$ degrees of freedom (Hedges and Olkin 1985, p. 211). If the values of Q are small or statistically nonsignificant, the estimates of the components of **d** may be pooled. We also test if the effect size is heterogeneous among regions.

If the Q statistic indicates homogeneity, then it is appropriate to estimate the common effect size, given by

$$\hat{\delta} = d_1 w_1 + \ldots + d_p w_p = \mathbf{w}'\mathbf{d}$$

with weight vector given by

$$\mathbf{w} = \Sigma^{-1}\mathbf{e}/\mathbf{e}'\Sigma^{-1}\mathbf{e}$$

The weights are obtained by inserting the estimates of Σ^{-1} into the above equation. The estimated asymptotic variance of the estimated mean δ is

$$\hat{\sigma}^2(\hat{\delta}) = 1/\mathbf{e}'\,\hat{\Sigma}^{-1}\mathbf{e}$$

The assumption of multivariate normality was investigated by plotting the model residuals, e.g., Fig. 2. We investigated the effect of relatively small sample size and estimation error in a later section, i.e., we simulated the meta-analysis procedure to help determine its reliability.

If the estimates were uncorrelated, the weights calculated from the above equation would be proportional to the inverse of the estimated variances of the estimates. It is difficult to estimate the covariance matrix because there is variable overlap between the time-series, and that the overlap is often too small to adequately estimate the individual covariances. We approached the problem by estimating the correlation between the residuals of the standard Ricker model among populations as a function of distance between streams (for details, see Myers et al. 1997). We are, in effect, testing the hypothesis that covariation among populations is due to local factors such as weather or hydrological factors or to common errors in the estimates of abundance. We modeled the fall-off of the correlation with separation, $s_{i,j}$, in kilometres, between spawning sites of populations i and j as

$$\rho(s_{i,j}) = \rho_0 e^{-0.5(s_{i,j}/\nu)^2}$$

One difficulty in this, and other analyses, is that the estimated correlations among stocks may be biased towards zero because of estimation error. The model of the decay of correlation was estimated using nonlinear least squares weighted by the number of observations used for the estimate. This function appeared to provide an adequate fit to the data; we estimated $\rho_0 = 0.28$ (SE = 0.03) and $\nu = 220$ km (SE = 25 km) for the spawner recruit data, $\rho_0 = 0.71$ (SE = 0.53) and $\nu = 85$ km (SE = 110 km) for the spawner–fry data, and $\rho_0 = 0.09$ (SE = 0.12) and $\nu = 520$ km (SE = 2100 km) for the spawner–smolt data. The regression parameters for the spawner–recruit data were relatively well determined, while the others were not because of fewer data. This analysis was used for data series that overlapped more than 6 but less than 10 years.

To account for the effect of the variable overlap in the time-series, we multiplied the estimated correlation by the fraction of overlap between the time-series, i.e., the off-diagonal elements of the correlation matrix are estimated as $C_{i,j} = \rho(s_{i,j}) n_o/n$ where n_o is the number of years common to both series and n is the number of years spanned by the two series together. The diagonal elements are equal to 1. The estimated elements of the covariance matrix are then $\hat{\Sigma}_{i,j} = C_{i,j}\,\hat{\sigma}_i\,\hat{\sigma}_j$ where $\hat{\sigma}_i$ is the estimated standard deviation of the individual estimates of the effect size for population i.

That nearby populations are not likely to be independent is usually ignored in statistical analysis of ecological data. The above approach is a reasonable attempt to explicitly deal with the problem. For robustness, we will also carry out the analysis assuming that nearby populations are independent.

Results

We begin with the analysis of delayed density dependence using the spawner–adult recruitment data (eq. 2). If the regression results are viewed on a river by river basis, then only one of the regressions is nominally significant (at a 0.05 level) using a one-sided test at a 1- or 2-year lag for the Alaskan populations (Table 1). For British Columbia data, two of the 1-year lags are significant, as is one of the 2-year lag estimates.

We examine the first standardization, e.g., ϕ' and γ', for all the data before discussing the alternative standardization. We could not reject the hypotheses that the standardized density-dependent coefficients, ϕ' and γ', are homogeneous within Alaska or British Columbia ($p > 0.25$). The hypothesis that the 1-year lag coefficient, ϕ', is homogeneous between the three regions (including Washington) is rejected ($\chi^2 = 6.83$, df = 2, $p < 0.05$), although it cannot be rejected for all individual rivers ($\chi^2 = 36$, df = 34, $p > 0.25$). However, the hypothesis that the 2-year lag coefficient, γ', is homogeneous between regions cannot be rejected ($\chi^2 = 2$, df = 2, $p > 0.25$); indeed, we could not reject the hypotheses that γ' is homogeneous among all populations ($\chi^2 = 30$, df = 34, $p > 0.5$).

The meta-analytic mean standardized density dependence at a 1-year lag for the British Columbia populations is 0.2 (SE = 0.16), while for Alaska, it is –0.069 (SE = 0.075). The meta-analytic mean standardized density dependence at a 2-year lag, over all populations, is 0.11 (SE = 0.066), which is not significant.

We repeated the above analyses for survival to spring fry, fall fry, and smolts (Table 2). Survival to spring fry could be combined over the rivers for both the 1-year lag ($\chi^2 = 1.95$,

Table 1. Estimates of delayed density dependence for the spawner–recruitment data.

Stock	N	β	SE	ϕ'	SE	ϕ''	SE	γ	SE	γ''	SE	$p(\phi)$	$p(\gamma)$
Alaska				−6.9	7.5	−3	5.3	5.7	7.6	8.8	5.3		
Black Lake	36	1.6	0.96	6.7	63	3.7	34	−77	61	−43	35	0.46	0.88
Branch River	31	2.3	0.53	−9.4	20	−5.2	11	21	20	11	11	0.67	0.16
Chignik Lake	36	3.4	0.79	−27	17	−28	19	30	19	32	19	0.93	0.05
Egegik River	30	0.34	0.27	44	96	11	21	55	80	14	20	0.3	0.24
Egegik River	38	0.048	0.22	−460	2 000	−23	25	−530	2 500	−26	25	0.82	0.85
Frazer Lake	24	7.1	1.5	−15	23	−15	24	−23	22	−23	22	0.73	0.84
Igushik River	37	2	0.4	2.1	20	1.4	13	30	20	20	14	0.46	0.073
Karluk River	60	0.65	0.14	−7.6	21	−4.8	13	−12	22	−7.7	13	0.64	0.72
Kasilof River	19	3.9	0.88	−3.1	22	−1.9	14	−39	22	−24	14	0.56	0.95
Kenai River	19	−0.14	0.53	−600	2 100	41	28	830	3 200	−56	43	0.084	0.9
Kvichak River	37	0.033	0.022	87	87	16	12	130	89	23	12	0.099	0.028
Naknek and Kvichak rivers	30	0.16	0.066	−66	41	−33	20	68	44	34	20	0.94	0.054
Naknek	37	0.38	0.15	−110	52	−47	17	−5.7	39	−2.4	17	0.99	0.56
Nushagak River	30	0.5	0.085	8	16	8.3	16	21	15	22	17	0.31	0.095
Nuyakuk River	18	1.2	2.7	22	230	3.6	35	65	250	10	28	0.46	0.36
Red River	23	0.75	0.83	−160	170	−24	17	140	180	22	17	0.92	0.11
Togiak River	31	3.6	1.2	−11	29	−6.6	19	8.4	32	5.3	20	0.63	0.4
Ugashik River	28	1.4	0.48	43	37	33	26	8.1	34	6.2	26	0.11	0.41
Ugashik River	37	0.39	0.2	−67	51	−21	17	−7.5	54	−2.3	17	0.89	0.56
Ayakulik	21	1.5	1.2	22	87	5.3	19	99	120	23	19	0.39	0.12
Wood River	38	0.56	0.13	−12	22	−6.8	13	12	23	7	13	0.7	0.3
Washington				−55	24	−46	26	32	33	27	28		
Columbia River	17	24	6.5	−55	24	−46	26	32	33	27	28	0.95	0.18
British Columbia				20	16	5.2	5.9	27	15	6.2	6.7		
Rivers Inlet	40	1.9	0.58	17	33	13	23	42	29	32	23	0.29	0.084
Skeena River	37	0.76	0.38	−84	72	−44	29	−43	55	−22	28	0.93	0.78
Skeena River	49	0.56	0.26	35	60	12	18	15	47	5	16	0.25	0.38
Smith Inlet	10	5.8	4.1	−21	54	−14	33	30	61	19	35	0.65	0.3
Tahltan Lake	10	52	18	21	33	30	46	52	36	73	60	0.27	0.13
Adams complex	42	0.5	0.51	160	170	24	15	42	100	6.2	17	0.062	0.36
Birkenhead River	41	8.8	2.9	−9.3	33	−3.3	12	7.1	35	2.5	12	0.61	0.42
Chilko River	41	3.3	1	110	41	57	17	22	31	11	17	0.00097	0.26
Weaver Creek	41	11	9	−8.4	78	−1.9	18	−7.3	84	−16	19	0.54	0.81
Early Stuart complex	42	4.6	3.8	110	110	28	18	170	160	43	17	0.066	0.0083
Stellako River	42	3.8	5.3	−40	140	−6.4	22	−290	460	−46	23	0.61	0.98
Horsefly River	41	−0.017	0.81	−250	12 000	0.44	8.1	−1100	52 000.0	1.9	13	0.48	0.44
Late Stuart complex	40	4.8	2.7	110	77	37	19	89	73	30	24	0.027	0.11
Weighted mean								11	6.7	8.2	4.1		

Note: The populations are separated into geographical areas. For each population, the number of years for which recruits and spawners (including lags 1 and 2) are estimated (N), the standard Ricker density-dependent parameter, β, coefficient multiplied by 10^6 and its standard error, the standardized 1-year lag delayed density-dependent parameters, $\phi' = \phi/\beta$ and $\phi'' = \phi\overline{S}$, and their standard errors (all multiplied by 100), and the one-sided p-value for ϕ are given. Similar estimates are given for the 2-year lag, γ. For each geographical area, an estimate is given of the meta-analytic combined estimate, i.e., a weighted mean that uses a correlation based on the distance between two populations to weight the combined parameter estimates. If no combined estimate is given, then our statistical tests showed that the groups were not homogeneous.

df = 2, $p > 0.25$) and the 2-year lag ($\chi^2 = 0.17$, df = 2, $p > 0.9$). The meta-analytic 1-year lag parameter was significantly negative ($\hat{\gamma} = -0.24$, SE = 0.1) and the 2-year lag parameter was almost significant ($\hat{\gamma} = -0.19$, SE = 0.096).

Survival to fall fry was not significantly heterogeneous at a 1- or 2-year lag. Delayed density dependence at a 1-year lag was statistically significant for both Quesnel and Shuswap lakes individually (Table 2; Fig. 2); the meta-analytic combined estimate of $\hat{\phi}'$ was 0.53 (SE = 0.14). The relationship for Quesnel Lake is driven by the three year-classes that occur the year after the dominant line in this lake (1968, 1990, and 1994;

Fig. 2). At a 2-year lag, the meta-analytic delayed density-dependent mortality was not different from zero ($\hat{\gamma} = -0.18$, SE = 0.19).

No statistically significant heterogeneity among rivers was detected for survival to the smolt stage at the 1-year lag for Alaska ($\chi^2 = 0.003$, df = 1, $p > 0.95$) or for all rivers combined ($\chi^2 = 0.58$, df = 2, $p > 0.75$). The meta-analytic standardized delayed density dependence at a 1-year lag was of a similar magnitude to survival at the fall fry stage, 0.41 (SE = 0.28). The 2-year lag delayed density dependence was not different among Alaskan rivers ($\chi^2 = 0.003$, df = 1, $p > 0.95$) or for all

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Table 2. Estimates of delayed density dependence for fry and smolt data (see note to Table 1).

Stock	N	β	SE	ϕ'	SE	ϕ''	SE	γ	SE	γ'	SE	$p(\phi)$	$p(\gamma)$
Spawners to fry in spring													
British Columbia													
Chilko Lake	32	2.4	0.92	–2.8	36	–1.1	14	–33	48	–13	15	0.53	0.79
Fulton River	28	6.7	0.69	–26	11	–23	8.9	–19	9.7	–17	9	0.99	0.96
Pinkut Creek	26	21	4.6	–0.59	22	–0.55	20	–25	21	–23	20	0.51	0.87
Weighted mean				–24	10	–17	7.8	–19	9.6	–16	8		
Egg to fry in fall													
British Columbia													
Quesnel Lake	10	1.7	0.46	82	27	29	8.2	–63	48	–22	13	0.0051	0.93
Shuswap Lake	14	1.9	0.34	44	16	31	12	–10	20	–7.3	14	0.018	0.7
Weighted mean				53	14	39	7.9	–18	15	–16	8.4		
Egg to smolt													
Alaska				120	120	25	13	110	78	23	15		
Kvichak River	21	0.036	0.029	120	120	25	13	110	78	23	13	0.042	0.08
Egegik River	12	0.079	1.1	580	9000	62	150	710	11 000	75	220	0.35	0.37
British Columbia				32	30	8.6	8.4	9	31	2.4	9		
Chilko Lake	43	1.9	0.68	32	30	8.6	8.4	9	31	2.4	9	0.16	0.39
Russia				130	330	–99	100	65	130	–49	82		
Lake Dalnee	10	–0.0095	0.017	130	330	–99	100	65	130	–49	82	0.82	0.71
Weighted mean				38	29	13	7.1	25	28	7	7.7		

rivers combined ($\chi^2 = 1.5$, df = 2, $p > 0.5$) and was estimated to be 0.27; however, this was not statistically different from zero (SE = 0.23).

We repeated the above analysis for the alternative standardization (i.e., parameters were standardized by mean spawner abundance). The results were the same for the smolt and for the 2-year lag parameter in all cases. However, for the spawner to recruit data, the 1-year lag parameter was not homogeneous for British Columbia ($\chi^2 = 22$, df = 12, $p < 0.05$) or over all individual rivers ($\chi^2 = 52$, df = 34, $p < 0.05$). Thus the density-dependent effects for the two standardizations were similar.

We display the results for the delayed density-dependent mortality by plotting the residuals for the standard Ricker model versus spawner abundance from the previous brood year for the fry and smolt data (Fig. 2). Delayed density-dependent mortality should result in a negative slope for the residuals; in cases where we could not detect density-dependent mortality (Table 2), there should be no trend in residuals with abundance. The spring fry data show no negative slopes, supporting the statistical result that delayed density-dependent mortality was not detectable at this stage. Evidence for delayed density-dependent mortality (negative slopes) is seen for Quesnel Lake, Shuswap Lake, and Kvichak River (and nominally for Chilko Lake) for lag 1. No evidence for delayed density dependence is seen for Lake Dalnee or Egegik River. These represent two of the shorter series, with the smallest range of observed spawner biomasses. Note also that Lake Dalnee has the largest variance in survival, which may represent large estimation error. The plots of survival residuals for a 2- or 3-year lag show almost no evidence for delayed density dependence (Fig. 2).

Statistical bias and power

We investigated the statistical bias and power of our estimates by simulation studies. There are at least two types of statistical biases that could affect our results. Errors in the estimation of spawner abundance will negatively bias the estimates of β in eq. 2 because spawner abundance appears in the denominator of the left-hand side of the equation (Hilborn and Walters 1992). However, errors in estimation of spawners will bias the estimate of ϕ and γ towards zero because S_{t-1} and S_{t-2} only appear on the right-hand side of eq. 2. Thus, errors in estimation will bias our estimates of ϕ and γ towards zero and will make our tests conservative. Time-series bias (Walters 1985; Dennis and Taper 1994) is caused by the nonindependence of recruitment and subsequent spawners. This type of bias is enhanced by autocorrelation in density-independent survival (Williams and Liebhold 1995).

We modified methods described in Myers and Barrowman (1995); 1000 simulated time-series of length 30 (the median length of the number of years with recruitment estimates and spawner estimates from the previous two cohorts was 31.5) were generated using estimates of α, ϕ, γ, and H (the harvest rate) within the range of observed values (Fig. 3) using eq. 1. The random, environmental component of survival. i.e., ϵ_t in eq. 1, was assumed to be be either a i.i.d. normal random variable with standard deviation 0.65 (the approximate median of the observed) or a first-order autoregressive process with standard deviation 0.65 with autocorrelation of 0.45 (75% of the residuals from the model fit had estimated autocorrelation less than this). We used this relatively high estimate of autocorrelation because the sample estimates may be negatively biased (Walters 1985). The effect of α and H are confounded in the simulations; therefore, the number of spawners is calculated using a harvest rate of 0.5, i.e., $S_{t+2} = 0.5 R_t$ and α is varied. An α equal to 3 in the simulations is equivalent to a high exploitation rate, and an α equal to 5 is equivalent to a low exploitation rate. Estimation was carried out as described for the observed time-series. It was not

Fig. 2. Residuals from Ricker model or modified Ricker model versus spawner abundance at lags of 1, 2, and 3 years. A negative slope in the residuals indicates delayed density-dependent mortality. The spawners for Chilko, Quesnel, and Shuswap lakes are measured as the numbers of effective females, for Lake Dalnee as females, and for Fulton River, Pinkut Creek, Kvichak River, and Egegik River as number of males and females. Residuals for lag 1 are from a standard Ricker model ($\log(R_t/S_t) = \log(\alpha) - \beta S_t$) versus spawner abundance in the previous brood year. Residuals for lag 2 are from a Ricker model that includes the effect of the spawner abundance in the previous brood year ($\log(R_t/S_t) = \log(\alpha) - \beta S_t - \phi S_{t-1}$) versus spawner abundance with a 2-year lag. Residuals for lag 3 are from $\log(R_t/S_t) = \log(\alpha) - \beta S_t - \gamma S_{t-1} - \gamma S_{t-2}$ versus spawner abundance with a 3-year lag. Influential points are identified by the brood year. The scale for the residuals is consistent for all rivers to allow the variability to be compared among populations.
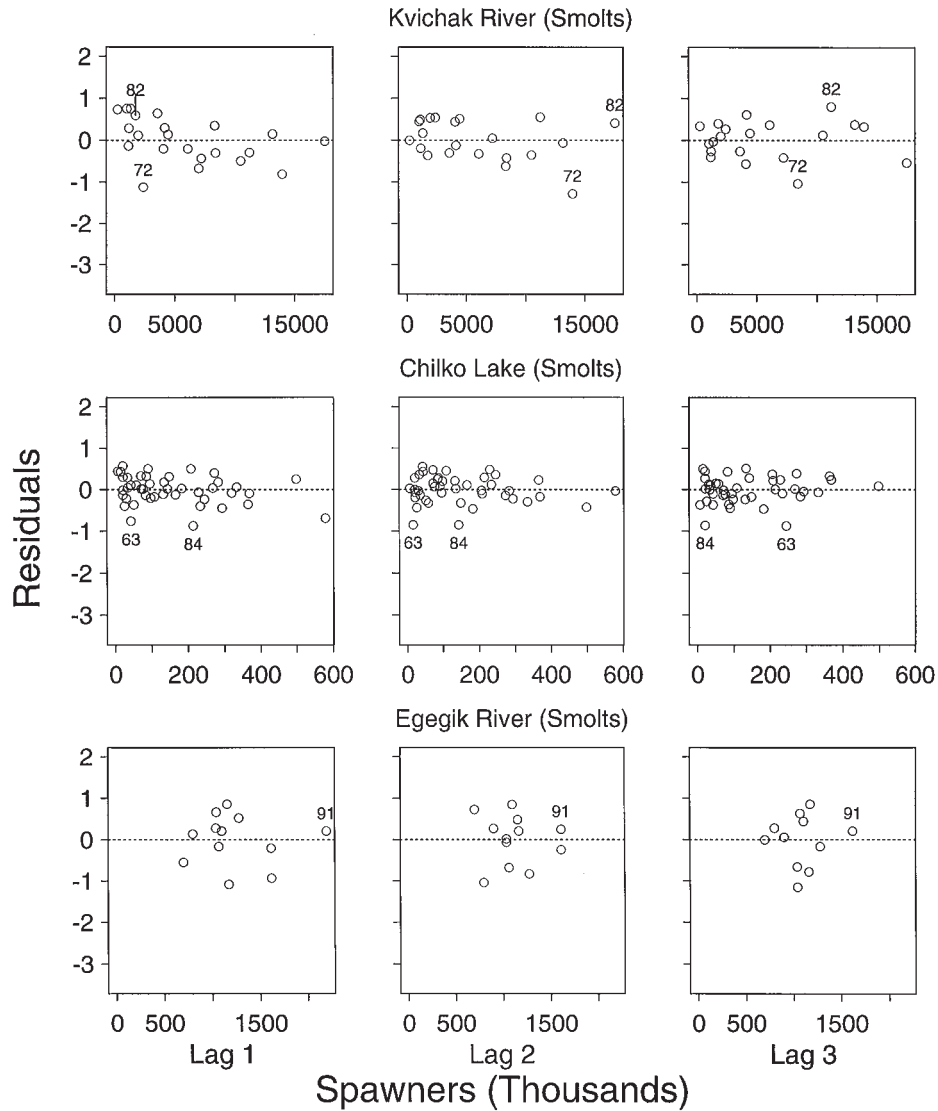

possible to incorporate all known errors in the simulations of the spawner recruit data, e.g., the errors in estimation at low spawner abundance identified by Cass and Wood (1994); therefore, we believe that the fishery-independent data are more reliable.

We also simulated the types of errors associated with the research estimates of egg to fry or smolt survival using eq. 1 except that F_t or M_t replaces S_t on the left-hand side of the equation. The stochastic component of mortality is simulated as before except that a lower standard deviation, 0.45, is assumed because Bradford (1995) found that approximately half the interannual variance in survival occurs in the freshwater stage (i.e., $(0.45)^2 = (0.65)^2/2$).

Estimation errors in the simulations are assumed to be log-normal in the simulation. The estimated spawner abundance will be Se^{ε_s}, recruit estimates will be $Re^{(\varepsilon_s + \varepsilon_c)}$, and for the fry and smolt estimates, they will be Fe^{ε_f} where ε_s, ε_c, and ε_f are estimation errors in spawner abundance, catch, and fry or smolt abundance, respectively. They are assumed to be zero mean Gaussian white noise with a standard deviation of 0.25 for ε_s, 0.15 for ε_c, and 0.15 for ε_f (based on estimates by Peterman 1982).

The results of the simulations (Table 3) show that for longer time-series, e.g., $n = 30$ years, the bias in the estimates of the standardized delayed density-dependent mortality parameters, when no delayed density dependence was assumed, was

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Fig. 2. (*continued*).
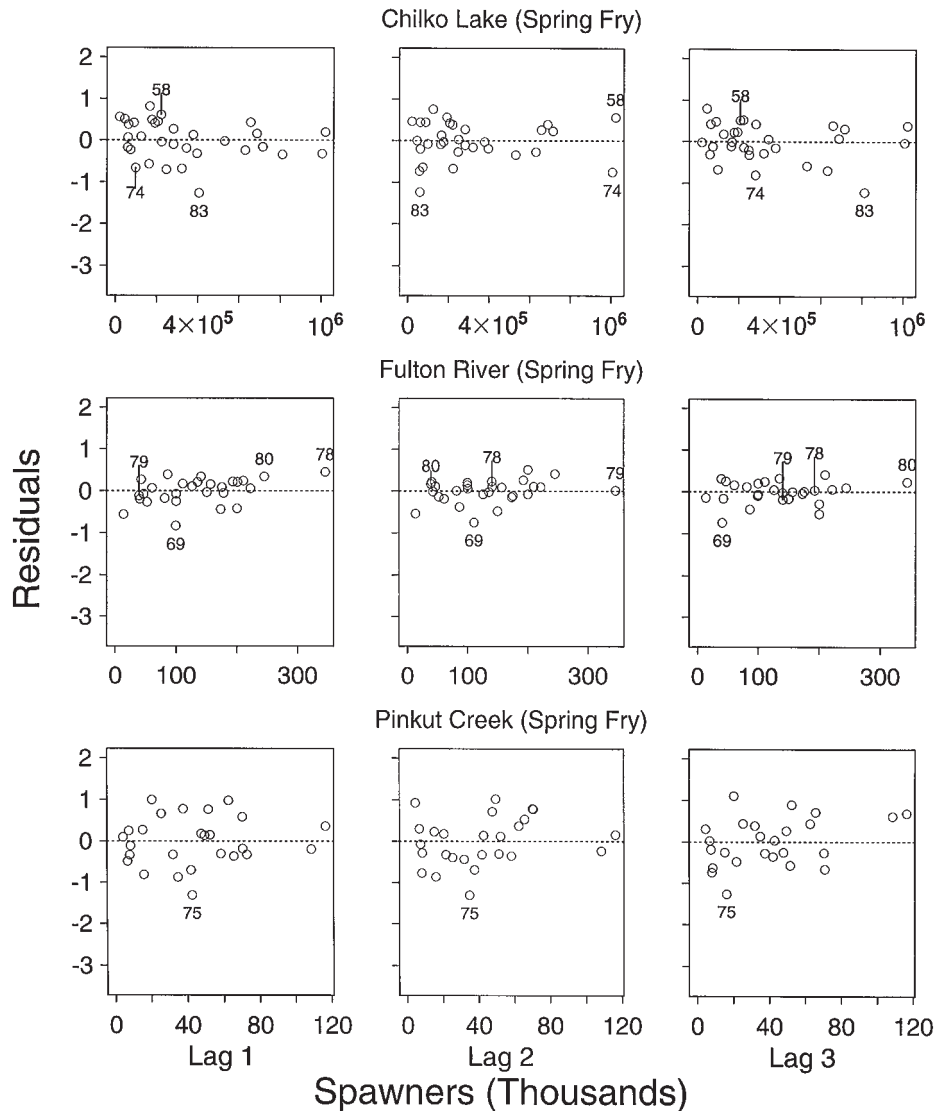
between 0.02 and 0.11 for the spawner–recruit simulation. For shorter time-series, 20 years, the bias increased to as high as 0.17. For survival to the fry or smolt stage, the bias was much less if the time-series had 30 overlapping years, on the order of 0.02, and between 0.02 and 0.21 if there were only 10 overlapping years. We repeated the analysis with large estimation error in the estimates of catch ($\varepsilon_c = 0.25$) and found the only minor changes in the results.

The bias of the unstandardized parameters was generally greater; for a true value of 0.5 the estimates were between 0.4 and 0.54. The extent of the positive bias means that we probably should not believe small positive estimates of the delayed density-dependent parameters.

We also carried out a power analysis (Table 3). A standardized delayed density-dependent mortality of 0.50 was detected to be statistically significant at the 0.05% level about 14–44% of the time for spawner–recruit data that were 30 years long. The power was larger for the spawner to fry data; delayed density-dependent mortality was detected in 24–65% of the simulations. These results demonstrate the importance of a meta-analytic approach to this problem. One should not expect all the results to be statistically significant, and the fact that they are not all significant does not necessarily imply that there are biological differences among the stocks.

Robustness

We investigated the robustness of our results by investigating alternative data analysis methods and data sets.

We investigated the robustness of our results if we excluded studies from our analysis that were questionable. The estimate for the density-dependent parameter with no lag, β, was negative for the Horsefly River, which makes the interpretation of the standardized parameters questionable. The Bristol Bay series is a compilation of many populations, and thus may give misleading results. We also eliminated the Babine Lake data because this population could have been affected by an enhancement program (Macdonald and Hume 1987). We reran the above analyses without these populations; the results did not change because the standard errors of ϕ' and γ' were large in these cases.

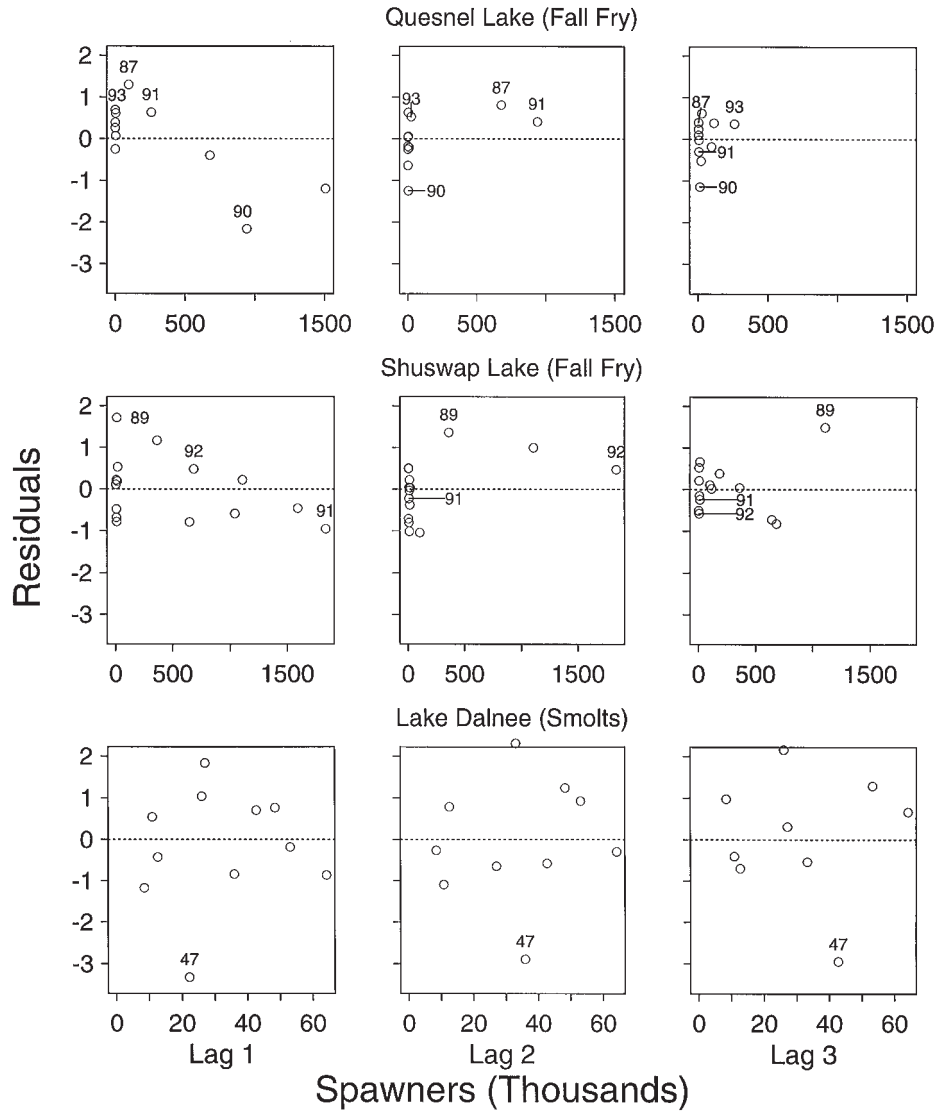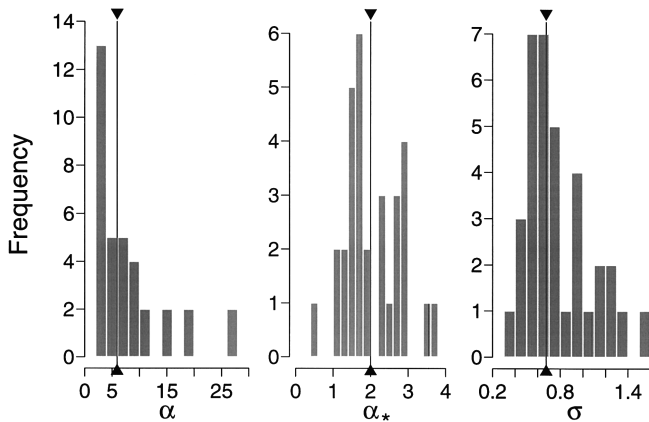**Fig. 2.** (*concluded*).

Fig. 3. Histograms of estimates for population parameters in Table 1 using eq. 1: α (reproduction rate at low population sizes), α_* (reproductive rate with harvest), and σ (standard deviation of survival). The median is represented by a vertical line with solid triangles.

We tested if some of the earlier, and perhaps less reliable, data were affecting our results. We reran our analysis leaving out the earlier series when there were two available for the same population. We also removed all data before 1948. Our results were not substantially different in either case.

We estimated a model with a 3-year, as well as a 1- and 2-year, lag for density dependence; this is the model considered by Ward and Larkin (1964) and Collie and Walters (1987). For the Alaskan spawner–recruit data, there was no change and no significant relationship for the region. For British Columbia, the 1- and 2-year lag parameter estimates were approximately 0.4 and became significant. The 3-year lag parameter was estimated to be 0.26 (SE = 0.16), which is not significant. The estimates of ϕ' and ϕ'' were not significant for the spring fry analysis. The 2-year lag parameters became positive but were greatly changed. For the fall fry and smolt analysis, the 1-year lag was similar, but ϕ' increased to approximately 0.55. However, the results for lags 2 and 3 were generally not comparable among populations. These estimates were usually positive for some populations and negative for

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Table 3. Simulation results with estimation error described in the text.

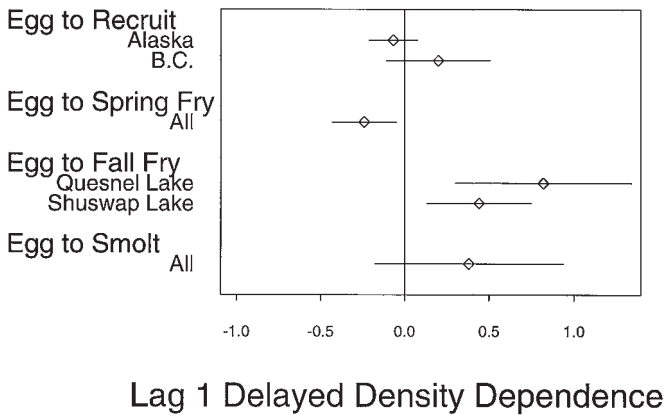| n	Assumed				Estimated						
	α	ϕ	γ	ρ	$\hat{\beta}$	$\hat{\phi}$	$\hat{\gamma}$	% (ϕ)	% (γ)	$\hat{\phi}'$	$\hat{\gamma}'$
					Spawners to recruits						
30	3	0	0	0	124	9	10	5	3	6	7
	3	0	0	45	143	11	19	4	4	8	11
	3	0	50	0	140	10	55	3	19	7	44
	3	0	50	45	156	16	64	5	22	7	40
	3	50	0	0	144	53	13	18	4	42	8
	3	50	0	45	171	62	25	20	7	41	14
	3	50	50	0	154	54	61	14	15	54	38
	3	50	50	45	179	61	76	15	20	37	49
	5	0	0	0	99	2	2	4	4	2	2
	5	0	0	45	100	4	5	5	5	5	5
	5	0	50	0	107	3	43	4	39	2	43
	5	0	50	45	110	6	46	4	44	5	44
	5	50	0	0	108	43	3	37	5	44	5
	5	50	0	45	112	43	8	36	5	41	7
	5	50	50	0	113	45	45	31	29	43	42
	5	50	50	45	119	46	49	32	33	43	44
20	3	0	0	0	139	13	12	4	3	11	6
	3	0	0	45	161	15	26	5	5	17	14
	5	0	0	0	101	3	3	3	4	3	2
	5	0	0	45	105	5	9	5	5	5	8
					Spawners to fry						
30	3	0	0	0	116	4	5	4	6	2	3
	3	0	0	45	127	5	10	4	8	0	0
	3	0	50	0	125	6	51	6	31	4	45
	3	0	50	45	137	4	59	4	33	3	42
	3	50	0	0	124	50	5	39	4	45	4
	3	50	0	45	141	50	14	24	7	40	7
	3	50	50	0	132	49	53	24	26	45	47
	3	50	50	45	146	53	63	27	28	41	47
	5	0	0	0	96	2	1	5	5	2	1
	5	0	0	45	97	2	1	4	5	2	1
	5	0	50	0	102	2	43	4	65	2	43
	5	0	50	45	104	3	44	6	64	3	43
	5	50	0	0	102	44	1	65	4	44	1
	5	50	0	45	107	43	4	58	6	41	3
	5	50	50	0	107	46	46	55	52	44	44
	5	50	50	45	111	44	47	53	56	42	44
10	3	0	0	0	129	9	10	5	4	21	18
	3	0	0	45	149	10	12	7	5	10	9
	5	0	0	0	105	3	1	6	6	2	0
	5	0	0	45	108	4	6	6	7	10	10

Note: n is the length of time-series, the assumed parameters in the simulation are as follows: α, the slope at the origin, β (set to 1 in all the simulations), ϕ and γ, the coefficients of the 1- and 2-year lag delayed density dependences, and ρ, the autocorrelation coefficient of the error term. $\hat{\beta}$, $\hat{\phi}$, and $\hat{\gamma}$ are the mean estimated values of these variables. $\hat{\phi}'$ is the average of the estimate of the ratio of $\hat{\phi}/\hat{\beta}$, while $\hat{\gamma}'$ is the average of the estimate of the ratio of $\hat{\gamma}/\hat{\beta}$. % (ϕ) is the percentage of $\hat{\phi}$ that are significant (i.e., the percentage of cases for which the null hypothesis $\phi = 0$ is rejected), and similarly for % (γ), i.e., these columns show the statistical power under different assumptions. All columns except for n and α have been multiplied by 100.

others, often significantly so, e.g., the standardized 3-year delay parameter for Quesnel Lake was estimated to be 0.63 (SE = 0.26) but –2.3 (SE = 1.1) for Shuswap Lake. This suggests that the estimates of the lag 3 parameter are not reliable. An examination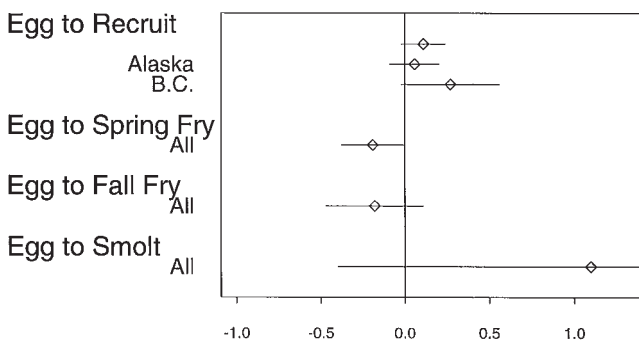 of the residuals from the lag 2 model for the fry and smolt data does not indicate any evidence of delayed density-dependent mortality at a lag of 3 years (Fig. 2).

We reran the meta-analysis under an alternative assumption for the correlation in the errors among populations, i.e., we assumed that there were no correlations among rivers. In all

Fig. 4. Estimates with confidence limits of ϕ', standardized 1-year lag delayed density-dependent mortality, for egg to recruit (adult homeward migrants), egg to spring fry, egg to fall fry, and egg to smolt. All estimates are from the meta-analysis. Means for regions are given if they are not homogeneous among regions. The lower panel shows the 2-year lag standardized delayed density-dependent mortality (γ').

Egg to Recruit
Alaska
B.C.
Egg to Spring Fry
All
Egg to Fall Fry
Quesnel Lake
Shuswap Lake
Egg to Smolt
All

-1.0   -0.5   0.0   0.5   1.0

Lag 1 Delayed Density Dependence

Egg to Recruit
Alaska
B.C.
Egg to Spring Fry
All
Egg to Fall Fry
All
Egg to Smolt
All

-1.0   -0.5   0.0   0.5   1.0

Lag 2 Delayed Density Dependence

cases, the results were similar. We had access to five shorter time-series, less than 10 years, of survival from egg to fry and egg to smolt that were not used in the analysis. Including these had no substantial effect on the results because the standard errors were large for the estimates.

Discussion

We begin with a discussion of the interpretation of meta-analytic results and then discuss each type of data in turn. We have summarized the meta-analysis in Fig. 4.

Interpretation of meta-analytic results

The interpretation of contradictory evidence is always difficult; however, we can use meta-analysis to at least determine if different pieces of data are consistent (i.e., the estimates appear to measure the same phenomenon) and combine them in a reasonable manner if they are. However, meta-analysis cannot cope with fundamental inadequacies and biases in the data or the primary analysis. As with any analysis the data must be carefully examined for violations of assumptions and influential outliers.

If estimates appear to be homogeneous, then the meta-analytic approach we have used combines them by averaging the estimates weighted by the inverse of the estimation error variance (we have also applied a correction to account for the fact that the estimates of nearby populations may not be independent). By choosing this approach, we attempt to take into consideration that all estimates may not be equally reliable, i.e., reliability of estimates of regression parameters depends on the range of the independent variable, the measurement error variance, and the environmental variability.

Spawner recruit data

For both Alaskan and British Columbia populations, we found no overall statistically significant delayed density dependence for the spawner–recruit analysis. Our test of homogeneity showed that the mean 1-year lag parameter estimated from the Alaskan data was significantly smaller (and in fact was negative) than the value estimated from the British Columbia data. For the Kvichak River, the most cyclic of the Alaskan populations, the 1-year lag parameter was positive, as Eggers and Rogers (1987) found, although in neither case is the effect statistically significant. We believe that the simplest explanation for the difference between the British Columbia and Alaskan estimates is existence of a vastly more complex age structure in Alaskan sockeye populations. Many Alaskan populations have a number of smolt and ocean ages, and there are considerable overlaps between year-classes in lacustrine and marine rearing environments (Burgner 1991). These temporal overlaps likely contribute to the observed positive autocorrelations in recruitment in Alaskan sockeye (Korman et al. 1995), which will in turn lead to negative estimates of the delayed density-dependent parameter in eq. 1 (Williams and Liebhold 1995). Ageing errors will also create positive autocorrelations in recruitment where none existed and obscure any density-dependent mortality (Bradford 1991). Thus, delayed density dependence may be very difficult to detect in the Alaskan stock and recruit data, unless it is very strong.

For the British Columbia populations the meta-analytic combined estimates of delayed density-dependent parameters were positive, as hypothesized, although none were large relative to their standard errors. Among individual populations, there were a number of negative parameter estimates, but because there were large standard errors associated with many of them the weighted mean reflected the more precise positive estimates. Our results are consistent with previous analyses of the Fraser River populations that have found statistically significant delayed density dependence in some populations but not others (Walters and Staley 1987).

In both the Alaska and British Columbia data, there are likely problems with recruit estimates from the commercial catch when more than one stock is fished simultaneously because allocation errors will bias the estimates for very small runs upwards. This problem can lead to large biases when the different stock components are of very different sizes (Cass and Wood 1994), and subsequent fitting of the Ricker curve will tend to overestimate both α and β, which will affect the estimates of delayed density-dependent effects. The problem of accurately estimating abundances in recruitment when different runs vary by many orders of magnitude, coupled with the various sources of bias we identified, may place fundamental limits on the inferences that can be made from these data. Since

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delayed density dependence is likely to occur in the freshwater stages (Levy and Wood 1992), the greatest success in detecting it will occur through the analysis of fry and smolt data that are independent of the fishery, and not contaminated by highly variable marine survival rates.

Spring fry data

The data on survival from egg to spring fry do not show evidence of delayed density-dependent mortality of the hypothesized form; in fact, there is evidence of negative delayed density-dependent mortality for one population (Fulton River). This would imply that survival increases the year after a large return of spawners. The Fulton River and Pinkut Creek data come from a period when the river was regulated for the purposes of providing an optimal incubation environment (West and Mason 1987), and it is conceivable that in the absence of large floods that mobilize the streambed, the cleaning effect of a large spawning may carry over into the following year, to give rise to a better than average survival. In contrast, Myers et al. (1998) found significant positive delayed density-dependent mortality for pink salmon (*Oncorhynchus gorbuscha*) at a 1-year lag that occurred during the fry stage; however, most of these data were from unregulated rivers and coastal streams where the positive effects of heavy spawning are probably eliminated by large rain-induced winter floods. Chilko River, the source of the other egg–fry data series, is unregulated; however, these data were estimated by a semiquantitative (and undocumented) visual method and may not be very reliable.

Fall fry and smolt data

The survival data to fall fry and the smolt stage are potentially the most useful for addressing the problem of delayed density-dependent mortality because the juvenile estimates were made after density-dependent mortality is hypothesized to occur (Ward and Larkin 1964; Levy and Wood 1992).

Although the statistical evidence for the delayed density-dependent mortality at lag 1 is stronger for the fall fry data than the smolt series, the estimated parameters are similar and suggest that the effect strength is about one half that of the direct density-dependent survival (Fig. 4). The lower precision of the smolt estimate is due to the highly variable Lake Dalnee data and to the relatively small variation in the range of the spawner abundance for the Egigik data (Fig. 2).

The fall fry and smolt data did not not support the hypothesis of a 2-year lag; the estimated relationship was positive for the smolt data and negative for the fall fry data; both estimates had large standard errors.

Our analysis of the freshwater stages cannot identify whether delayed density-dependent mortality may be occurring in the stream (incubation) or lake (rearing) environments. Based on the egg – spring fry data we used, we might be tempted to rule out the incubation environment; however, as we detail above, the series we had available may not be particularly representative of typical spawning streams. The other interpretation is that our analysis supports the food limitation or predation hypotheses (Levy and Wood 1992); these are thought to take place in the nursery lakes.

The data from Quesnel Lake are particularly compelling. In recent years, very large escapements in the dominant year, up to triple those estimated to be optimum based on the

productivity of the lake (Hume et al. 1996), have resulted in fry populations that have depleted zooplankton populations in the lake. Strong direct density-dependent survival was also observed over the summer and fall for these large broods, presumably resulting from a combination of poor feeding conditions and high rates of predation. Fry of the subsequent (subdominant) brood have experienced poorer than average survival, resulting in a significant model fit for delayed density dependence at a 1-year lag. Sufficient data are not available to determine whether the reduced survival of the subdominant brood is the result of an increase in the abundance or a numerical response of predators or decreased food resources. The strength of this case rests partially on the fact that the subdominant brood is relatively abundant, and the data should be relatively free of estimation problems associated with small population sizes and the unknown abundances of juvenile kokanee in the lake.

The evidence for delayed density dependence in Shuswap Lake is consistent with Quesnel Lake; however, the results must be viewed with caution because significant kokanee populations will bias the fry/sockeye spawner ratio upwards in the small years, which may change the outcome of the fit of eq. 2. Also, the higher productivity and different lake physics of Shuswap Lake would seem to make the food availability hypothesis less likely than in Quesnel Lake (Hume et al. 1996). For Chilko Lake, nearly all spawning populations were well below the optimum based on productivity considerations, which could limit the likelihood of detecting delayed density dependence in the smolt data.

Evidence from changes of the dominant line

Finally, we return to the question of whether the type of density dependence we have detected in the sockeye is sufficient to generate population cycles observed in many populations. Clearly, a 1-year lag effect that we found in some of the freshwater data will generate, in the absence of other factors, a 2-year cycle of abundance rather than the 4- or 5-year pattern observed and therefore could not be considered a causal mechanism. Some evidence of 2-year cycling is seen in some of the populations shown in Fig. 1 and very strongly in some of the smaller Fraser populations, e.g., Late Nadina (Walters and Woodey 1991), which were judged not to have sufficiently reliable recruitment data to be included in this analysis. But the 1-year lag effect will tend to reinforce cyclic patterns that were established by another mechanism by supressing the line that follows the dominant year. The empirical evidence suggests that this supression is weak, as a number of Fraser River populations have changed their dominance pattern. Examples include the Adams run to Shuswap Lake, in which in 1963 the "subdominant" run exceeded the dominant cycle in abundance (Levy and Wood 1992). Heavy fishing was imposed on the subdominant line to prevent the dominance pattern from changing. Recently, the dominant cycle for the Scotch Creek (Shuswap Lake) population has shifted by 1 year; the spawning population of the new dominant year grew from seven fish in 1966 to over 73 000 in 1994. Interestingly, in both examples the increasing line has been the one that followed the dominant line and should have been the line most supressed by delayed density-dependent effects. Levy and Wood (1992) used the Scotch Creek population as evidence that delayed density dependence was not acting in Shuswap Lake because that

population was asynchronous to the others that reared in the lake, and lake processes should affect all runs in a similar fashion. Whether the subsequent shift in the dominance pattern in Scotch Creek sockeye has anything to do with the effects that the other much larger runs (totaling over 3 million spawners in peak years) have on food or predators in Shuswap Lake is open to debate.

We suggest that the role of random environmental effects in creating and maintaining sockeye cycles needs to be revisited. The research to date, including this study, has failed to identify a single factor that has had a strong enough effect to generate and maintain the observed cycles, at least for the Fraser River populations. It would be useful to evaluate the relative contributions of chance events, the occasional deliberate management action that results in depensatory fishing, and mild delayed density dependence in creating and reinforcing population cycles. We do not, of course, rule out the possibility of a yet undiscovered mechanism for generating cycles in sockeye populations.

Conclusions

Our analysis of many of the data available for sockeye salmon suggests that there is some evidence for weak delayed density dependence with a 1-year lag, most likely occurring in the lake-rearing phase. Since our analysis of additional stock and recruit data beyond those available to Walters and Staley (1987) has yielded little new information on Fraser sockeye, apart from the meta-analysis, it seems that further investigations in freshwater (e.g., Hume et al. 1996) will lead to more biological insights.

The major management implication of our analysis for sockeye salmon is that nondominant lines should be allowed to rebuild, since earlier analysis including between-year interactions of similar magnitude to those we estimated suggests that building up escapements on the off years was still the optimal policy (Walters and Staley 1987; Welch and Noakes 1990). For the Fraser sockeye stocks, this may require a reduced fishing mortality on all stock components (Walters and Staley 1987).

Note added in proof

In Ricker's (1997) excellent review, he concludes that the maintenance of sockeye cycles in the Fraser River is caused by some type of interaction among lines. While we have identified the presence of weak line interactions in Fraser populations, we cannot verify whether these interactions are sufficient to maintain the observed patterns. We will deal with this conundrum in a subsequent paper.

Acknowledgements

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