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Hierarchical Bayesian modelling of Atlantic Salmon egg to smolt time series from monitored rivers of eastern Canada to define and transport reference points

G. Chaput [1], E. Prévost [2], J.B. Dempson [3], M. Dionne [4], R. Jones [1], A. Levy [5], M. Robertson [3], and G. Veinott [3]

[1] Fisheries and Oceans Canada, P.O. Box 5030, Moncton, NB, E1C 9B6
[2] UMR 1224, Ecobiop, INRA, 64310 St-Pée-sur-Nivelle, France
[3] Fisheries and Oceans Canada, P. O. Box 5667, St. John’s, NL, A1C 5X1
[4] Ministère des Forêts, de la Faune, et des Parcs
880 chemin Sainte-Foy, Québec (Québec), G1S 4X4
[5] Fisheries and Oceans Canada, P.O. Box 1006, Dartmouth, NS, B2Y 4A2

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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TABLE OF CONTENTS

ABSTRACT

This paper presents analyses of the available time series of Atlantic salmon (*Salmo salar*) spawner to smolt data from fourteen monitored rivers in eastern Canada. A freshwater life history model is presented using a hierarchical Bayesian modelling framework to estimate and transfer reference points for Atlantic salmon. The results show that the stock and recruitment dynamic of Atlantic salmon within the freshwater portion of the life cycle is highly variable within and among rivers with consequence that the stock and recruitment parameters are uncertain. These uncertainties propagate into the estimation of reference points for management. Models examined for transport of reference points included three potential covariates; presence of lacustrine habitat, mean age of smolts, and proportion of the egg depositions coming from multi-sea-winter (MSW) salmon. Differences in the freshwater carrying capacity of salmon rivers attributed to the presence of lacustrine habitat which is used by salmon juveniles for rearing is confirmed. Density-independent survival rate is estimated to be higher for rivers with older smolt ages as well as for stocks with increasing proportions of the egg depositions from MSW salmon. The transfer of reference points from data-rich stocks to data-poor stocks, which are the great majority of stocks in eastern Canada, poses the greatest challenge. Analyses using hierarchical Bayesian frameworks are the favored approach for analyzing multiple stock and recruitment data sets and to address data-poor situations.

Modélisation bayésienne hiérarchique de séries chronologiques du stade d'œuf au stade de saumoneau du saumon de l'Atlantique dans les rivières surveillées de l'est du Canada, pour définir et transposer des points de référence

RÉSUMÉ

L'article présente des analyses de séries chronologiques de données du stade de saumoneau au stade de reproducteur chez le saumon de l'Atlantique (*Salmo salar*) dans quatorze rivières surveillées de l'est du Canada. Il propose un modèle de cycle biologique d'eau douce à partir d'un cadre de modélisation bayésienne hiérarchique pour estimer et transposer des points de référence pour le saumon de l'Atlantique. Les résultats montrent que la dynamique des stocks et du recrutement du saumon de l'Atlantique dans la partie de son cycle vital passée en eau douce varie considérablement dans une même rivière et d'une rivière à l'autre. Par conséquent, les paramètres de recrutement et du stock demeurent incertains. Ces incertitudes se reflètent dans l'estimation des points de référence à des fins de gestion. Les modèles examinés aux fins de transposition des points de référence comprenaient trois covariables potentielles : la présence d'un habitat lacustre, l'âge moyen des saumoneaux et la proportion d'œufs pondus par des saumons pluribermarins. L'article confirme que les différences de capacité biotique en eau douce des saumons dans les rivières dépendent de la présence d'un habitat lacustre que les juvéniles utilisent pendant leur croissance. On estime que le taux de survie indépendant de la densité est supérieur dans les rivières où les saumoneaux sont plus âgés ainsi que pour les stocks aux proportions croissantes d'œufs pondus par des saumons pluribermarins. Il reste un défi de taille : la transposition de points de référence établis pour des stocks pour lesquels de nombreuses données sont disponibles à des stocks faiblement documentés, soit la grande majorité des stocks de l'est du Canada. Les analyses reposant sur des cadres bayésiens hiérarchiques sont la méthode privilégiée pour analyser plusieurs ensembles de données de recrutement et de stock, et résoudre les situations où les données sont insuffisantes.

INTRODUCTION

This paper addresses the terms of reference for defining limit reference points and transporting reference points among rivers. The objective of the analyses is to derive transportable reference points for Atlantic salmon derived from a freshwater life history model (DFO 2015).

There are over 1,000 rivers assumed or known to have anadromous runs of Atlantic salmon (*Salmo salar*) in eastern Canada. The species ranges from the southern border of Canada with the USA in New Brunswick to rivers in Ungava Bay in northern Quebec, a latitudinal range of 44ºN to 58.8ºN.

Knowledge of the biological characteristics of these salmon populations and their population dynamics is varied and most complete for populations in the southern areas (Maritime Provinces, Quebec, insular Newfoundland) while poorly studied in the more northern areas such as Labrador and Ungava Bay. Neighbouring populations tend to share biological characteristics which are predictable to some extent (Chaput et al. 2006; O'Connell et al. 2006). For example, the majority of salmon populations on the island of Newfoundland, with exception of the southwest coast of Newfoundland are characterized by salmon which mature almost exclusively after spending one year at sea (1SW salmon or grilse) whereas salmon populations elsewhere have salmon returning at multiple sea ages at maturity (multi-sea-winter salmon; MSW) (Klemetsen et al. 2003; O'Connell et al. 2006). Similarly, the number of years which salmon juveniles spend in freshwater before migrating to the ocean follows a clinal trend, associated with cooler temperatures in more northern areas resulting in older smolts at migration (Metcalfe and Thorpe 1990; Chaput et al. 2006).

Although biological characteristics may be similar among neighbouring populations, and seemingly predictable, it is less clear whether the population dynamics (stock and recruitment dynamics, survival rates) of neighbouring populations are more similar than those of distant populations. Gibson (2006) concluded that there were large differences in early life stage dynamics of salmon juveniles in freshwater, even among geographically neighbouring stocks. Some of the variation noted is attributed to differences in the environment related to productivity of the ecosystem including climate, water chemistry, prey / predator / competing species, and geology (gradient, substrate). It is also clear that the information on population dynamics is quite sparse with only a limited number of populations studied. For example, the status of adult returns and spawners is reported annually for 60 to 70 rivers in terms of estimated adult returns and spawners (ICES 2013). Studies of population dynamics that encompass estimates of spawners, juvenile abundance, smolts, adult returns, age structure, and year class reconstruction have been examined in a limited number of rivers (Chaput et al. 1998; Chaput and Jones 2006; Gibson 2006; Gibson and Bowlby 2013). This limited amount of information on individual salmon populations poses a challenge to the development of reference points to guide management of the fisheries on Atlantic salmon that still take place on a large number of rivers in eastern Canada.

Reference points for Atlantic salmon, defined as conservation requirements, have been set for about half the rivers of eastern Canada (O'Connell et al. 1997; Caron et al. 1999). This conservation definition for managing Atlantic salmon fisheries on the basis of a fixed escapement strategy, is based on five egg deposition rates applied to large regions of eastern Canada(CAFSAC 1991a,b; O'Connell and Dempson 1995; Chaput 2006; Chaput et al. 2012)).

Symons (1979) was the first to consider the question of productivity of Atlantic salmon populations in a species-wide context. He constructed a juvenile life history model for Atlantic salmon and concluded that the freshwater dynamics of salmon populations, expressed as egg depositions for producing optimal smolt production, were exchangeable among rivers conditionally on the average age of smolts produced, i.e. knowing the average river age of the stock, different egg deposition rates could be applied. CAFSAC (1991a) and O'Connell and Dempson (1995) advised on different egg deposition rates based on whether rivers contained lacustrine habitat used by salmon juveniles for rearing. Chaput et al (1998) modelled egg to smolt stock recruitment data from eastern Canada and tested the two hypotheses: 1) that smolt production rates differed based on the mean age of smolts of the populations, and 2) the presence / absence of lacustrine habitat was associated with different production rates of smolts. Chaput et al. (1998) concluded that the presence / absence of lacustrine habitat was a more important covariate than mean smolt age to explain the variation in smolt production adjusted for egg depositions. Caron et al. (1999) and presented in Prévost et al. (2001) considered stock and recruitment dynamics in a hierarchical context, simultaneously estimating the stock and recruitment dynamics for six salmon populations from Quebec and derived an egg deposition rate that could be transferred among Quebec stocks, conditional on a measure of the extent of productive freshwater habitat. Prévost et al. (2003) extended this hierarchical analysis to define reference points to thirteen rivers of the northeast Atlantic and provided reference points that were transferrable among stocks conditional on the habitat area of the river and the latitude of the river.

Since the publication by Chaput et al. (1998), new smolt monitoring programs have been initiated and most of the contemporary data series analysed by them have continued to be collected. In addition, numerous advances in hierarchical Bayesian modelling techniques have been published which could be applied to the larger data set of egg to smolt recruitment series of eastern Canada.

The paper analyses the available time series of spawner to smolt data from fourteen monitored rivers in eastern Canada. The analyses of Chaput et al. (1998) are reconsidered using a hierarchical Bayesian modelling framework. Hierarchical models provide a number of features that facilitate incorporating multiple time series in a coherent and flexible framework, of elucidating assumptions of the model, and that allows for sharing of strengths among data sets. Exchangeability is an important consideration of hierarchical models and covariates that strengthen the exchangeability of data sets can be readily incorporated. The incorporation of covariates potentially strengthens the exchangeability assumption among monitored rivers and facilitates the transfer of reference points among rivers.

Chaput et al. (1998) used a pooled model to analyse the stock and recruitment series but distinguished two stock dynamics based on the presence/absence of lacustrine habitat that would be used by salmon juveniles for rearing. As in the original paper, the covariates corresponding to the mean smolt age, and presence or absence of lacustrine habitat are examined for relevance in the modelling of freshwater life history dynamics. In recent papers, latitude has been used as a covariate of the productivity parameters to model stock and recruitment series from European rivers and Ireland (Prévost et al. 2003; Ó Maoiléidigh et al. 2004). Mean smolt age is used in our analysis as an alternate to latitude. Although there is a latitudinal cline in smolt age, there is also a longitudinal effect on mean smolt age, particularly for salmon in the eastern portion of Newfoundland where the smolts are comparatively older than smolts from the mainland portion of Canada at similar latitude (O'Connell et al. 2006).

A covariate not examined to date in other hierarchical analyses, maternal effects of the parental stock, is also examined in our analyses. Egg survival has been reported to be related to egg size, with egg survival of 1SW salmon (grilse), at least under hatchery conditions being less than that of eggs from MSW salmon (Reid and Chaput 2012). The maternal effect, essentially egg size, is characterized by proxy using the average proportion of the annual egg depositions which are contributed by multi-sea-winter salmon (2SW, 3SW and repeat spawners of these age groups).

The covariates were modelled as explanatory variables for the maximum recruitment rate (carrying capacity) and the density independent mortality rate (maximum survival rate at the origin).

As discussed in Chaput (2015), a limit reference point corresponding to the egg deposition rate that produces half of maximum recruitment is estimated from both Beverton-Holt and Ricker stock and recruitment functions. In consideration of the full uncertainties of the modelled stock and recruitment dynamic, S_{LRP}, the egg deposition that results in 25% probability or less of recruitment being less than half Rmax, is calculated. This latter analysis incorporates the uncertainties in the estimation of the stock and recruitment parameters as well as the uncertainty in the recruitment process.

MATERIALS AND METHODS

DATA

Spawner to smolt time series were provided by regional biologists and research scientists from DFO regions and the province of Quebec (Table 1). The rivers extend from the southern portions of the range in eastern Canada (LaHave River, 44.5ºN) to northern Newfoundland (Western Arm Brook, 51.2ºN) (Fig. 1). Data for some rivers are quite dated, having been collected in the 1950s and the length of individual time series vary from quite short (4 year classes) to very long (37 for Western Arm Brook) (Table 1; Fig. 2). Details on monitoring methods and data analyses are available in various reports and are not repeated here.

Within the rivers examined, the mean smolt age was derived based on production of a cohort. The mean smolt age ranges from 2.12 to 3.75 years and the river with the oldest mean smolt age (Western Arm Brook; Lat. 51.2ºN) is at the highest latitude (Table 1). Five rivers, all in Newfoundland, have lacustrine habitat area which is known to be used by salmon juveniles for rearing. Fluvial habitat areas (wetted areas unadjusted for habitat quality) range from a low of 556 units (100 m^2 per unit) to a high of 53,505 units and the ratio of lacustrine area (m^2) to fluvial area (m^2) for the rivers with lacustrine habitat ranges from a low of 5 to a high of 70 (Table 1; Fig. 2).

The proportions of eggs deposited by MSW salmon were obtained from data provided by the regional specialists, generally presented as eggs from small salmon (1SW salmon, < 63 cm fork length) and from large salmon (MSW salmon, >= 63 cm fork length) (Table 1; Fig. 2). Egg depositions in the southern Gulf and Quebec rivers are predominantly from MSW salmon, egg depositions from Bay of Fundy and Atlantic coast of NS are a mix of 1SW and MSW eggs whereas eggs from Newfoundland rivers are dominated small salmon (Table 1).

There has been a broad range of egg depositions measured in these rivers, from a low of 14 eggs per 100 m^2 to over 3,100 eggs per 100 m^2 (Table 1; Fig. 3, 4). Estimated smolt abundance per 100 m^2 of fluvial habitat has ranged from a low of 0.1 to a high of 10.5 (Table 1; Fig. 3, 4). Only fluvial habitat areas are used to scale egg deposition and smolt production to a common habitat area metric because spawning by anadromous Atlantic salmon is not known to occur in lacustrine habitat.

MODELS

Both Beverton-Holt and Ricker stock and recruitment models were used to model the egg and smolt stock and recruitment time series (Hilborn and Walters 1992).

The Beverton-Holt model formulation used was:

$$R_{i,y} = \frac{\alpha S_{i,y}}{\left(1 + \frac{\alpha_i}{Rmax_i}\frac{S_{i,y}}{Hab_i}\right)} e^{\varepsilon}$$

$R_{i,y} = number\ of\ smolts\ for\ river\ i\ for\ year\ class\ y\ (recruitment)$
$S_{i,y} = number\ of\ eggs\ deposited\ for\ river\ i\ for\ year\ class\ y\ (spawning\ stock)$
$\alpha_i = slope\ at\ the\ origin\ or\ density\ independent\ survival\ rate\ \ for\ river\ i$
$Rmax_i = carrying\ capacity\ or\ asymptotic\ abundance\ for\ river\ i\ in\ units\ of\ fluvial\ habitat$
$Hab_i = fluvial\ habitat\ area\ of\ the\ river\ i\ in\ units\ of\ 100\ m^2$, and
$e^{\varepsilon_i} = process\ error\ with\ \ \varepsilon_i \sim N(0, \sigma_i^2)$

$S_{0.5Rmaxi}$ (S*) is the spawners (in units of eggs per 100 m² of fluvial habitat area) that produce 50% of maximum recruitment for river *i* and is calculated directly as

$$S0.5Rmax_i = \frac{Rmax_i}{\alpha_i}$$

The Ricker model formulation used was:

$$R_{i,y} = \alpha_i S_{i,y} e^{-\beta_i \frac{S_{i,y}}{Hab_i}} e^{\varepsilon_i}$$

with variables and parameters as for the Beverton-Holt model above, except for:

$\beta_i = rate\ of\ decline\ in\ recruits\ per\ spawners\ as\ spawners\ increase\ for\ river\ i$
$Rmax_i = \frac{\alpha_i}{\beta_i} e^{-1}$, and

$S_{0.5Rmaxi}$ (S^*_i) was calculated by solving recursively for S^*_i as

$$0.5\ R_{max,i} = \alpha_i S_i^* \ e^{-\beta_i S_i^*}$$

S_{LRP} defined as egg deposition that results in less than 25% chance that recruitment (*R*) will be less than half of maximum recruitment was calculated for both the Beverton-Holt and Ricker models from the Monte Carlo Markov Chain (MCMC) draws as:

$$P(R_i <= 0.5\ Rmax_i \mid S_i, \sigma_i, \alpha_i, Rmax_i)$$

with $R_i \sim$ Lognormal($\mu.logR_i$, σ^2_i)

$$\mu.LogR_i = \log(\alpha_i) + \log(S_i) - \beta_i S_i; \quad \beta_i = \frac{\alpha_i}{Rmax_i} e^{-1}; \ \ Ricker$$

$$\mu.LogR_i = \log(\alpha_i) + \log(S_i) - \log\left(1 + \frac{\alpha_i}{Rmax_i} S_i\right); \ \ Beverton - Holt$$

and R_i and S_i expressed in units per 100 m².

Hierarchical model

A hierarchical Bayesian framework was used to model the egg to smolt dynamics. The hierarchical structure was placed on the process error (e^{ε}), the slope at the origin ($\alpha = e^{-\delta}$; δ (delta) = instantaneous mortality rate) and the carrying capacity parameter R_{max}. In the initial hierarchical models, no covariates were included, which assumes that the stock and recruitment rates ($Rmax_i$ and δ_i) are exchangeable among rivers (*i*) conditionally on egg deposition and habitat area in river *i*.

Non-informative priors were used for the stock and recruitment parameters (Parent and Rivot 2012).

Parameter	Priors
Instantaneous mortality rate δ_i ($\alpha_i = e^{-\delta i}$)	δ_i ~ Gamma(a, b) $a = 1 / CV_\delta^2$ $b = 1 / (\mu_\delta * CV_\delta^2)$ μ_δ ~ Uniform(0,10) CV_δ ~ Uniform(0,5)
$Rmax_i$	$R_{max\ i}$ ~ Gamma(a, b) $a = 1 / CV_{Rmax}^2$ $b = 1 / (\mu_{Rmax} * CV_{Rmax}^2)$ μ_{Rmax} ~ Uniform(0,6) CV_{Rmax} ~ Uniform(0,5)
Process variance σ^2_i	$1/\sigma_i^2$ ~ Gamma(a,b) $a = \mu * b$ μ ~ Gamma(1, 0.01) b ~ Gamma(0.01, 0.01)

Hierarchical models with covariates

The expected values of $Rmax_i$ or δ_i (μ_{Rmaxi}, $\mu_{\delta i}$) were modelled linearly on the log scale relative to the covariates (θ) of interest as:

- Presence (lac = 1) of lacustrine habitat was treated as a binary covariate of the carrying capacity parameter Rmax
  $$\log(\mu_{Rmaxi}) = \alpha_{lac} + \beta_{lac} * lac_i$$
- The mean age was treated as a continuous variable and modelled as a covariate for δ
  $$\log(\mu_{\delta i}) = \alpha_{m.age} + \beta_{m.age} * (mage_i - mean.mage)$$
- The maternal effect was treated as a continuous variable characterized as the proportion of the egg depositions contributed by multi-sea-winter salmon (pmsw) and modelled as a covariate for δ
  $$\log(\mu_{\delta i}) = \alpha_{p.msw} + \beta_{p.msw} * (pmsw_i - mean.pmsw)$$

Uninformative priors for CV_θ, and the log-linear parameters for the covariates (θ) were used:

- CV_θ ~ Uniform(0,5)
- α_{lac} ~ Uniform(0,4)
- β_{lac} ~ Uniform(-4,4)
- α_{age} ~ Uniform(-5,5)
- β_{age} ~ Uniform(-5,5)
- $\alpha_{p.msw}$ ~ Uniform(-5,5), and
- $\beta_{p.msw}$ ~ Uniform(-5,5)

Note that the prior on α_{lac} (Uniform(0,4)) implies that Rmax must be at least 1 smolt per 100 m^2 ($\exp^{\alpha lac}$) for rivers without lacustrine habitat.

Models were coded and run in Open BUGS with Gibbs sampling (Lunn et al. 2013). The models were run with two chains of initial values. A burnin of 50,000 to 100,000 MCMC draws followed by a second sequence of 50,000 MCMC draws, thinning every 10 MCMC draw, to derived posterior distribution summaries (n = 10,000). Model convergence was assessed visually by examining the mixing of the draws among the chains, by examining for the smoothness of the posterior distribution, and using the BGR diagnostic tool within Open BUGS.

Diagnostics

Residual analyses consisted of estimating the temporal trend of residuals by river and the degree of first-order autocorrelation in the residuals. The first order autocorrelation of the residuals was examined for each data series as per Hilborn and Walters (1992; p. 281) and serial trends were examined by linear regression of the mean of the log residuals from the posterior distribution relative to year-class. Comparisons of model sufficiency were described using the Deviance Information Criterion (DIC), synonymous with the Akaike Information Criterion (Lunn et al. 2013).

RESULTS

The overall pattern of smolt production for all rivers shows the expected compensatory recruitment at increasing spawning stock (Fig. 3), albeit with a large amount of variation of realized smolt production at a given egg deposition, particularly at low egg depositions. The slope of smolt production at low egg depositions appears very steep at the scales shown. There are very few observations at very high egg depositions, i.e. > 1,000 eggs per 100 m^2, for rivers with exclusively fluvial habitat. Maximum estimated smolt production was over 10 smolts per 100 m^2 of fluvial habitat area (Fig. 3). There is a general pattern of higher smolt production at a given egg deposition in rivers where lacustrine habitat is available and used for rearing of salmon juveniles, all these rivers are in Newfoundland (Figs. 3 and 4).

Fitting stock and recruitment functions independently for each of the data sets was not a useful exercise. For many of the data series, it was not possible to estimate R_{max}, the posteriors of the estimates were primarily defined by the prior assumptions (R_{max} ~ Uniform(0,20)). Estimates of δ were also poorly defined in many cases. This was expected given the combination of lack of contrast in many data series, the small number of individual stock observations, and relatively large variation in smolt production even over small contrasts in egg depositions. No results of the independent model fits are provided.

Results of hierarchical model fits for both Ricker and Beverton-Holt dynamics are presented as follows:

- Plots of the log residuals by river
- Smoothed posterior distributions for δ (delta), and Rmax (maximum recruitment) by river
- Box plots of parameters of the model fits by river and for predictions of σ (sigma), delta, α (alpha = $e^{-\delta}$), and Rmax.
- Boxplots of delta and Rmax relative to river type (fluvial only, with lacustrine habitat present), mean smolt age, and proportion of eggs from MSW.

HIERARCHICAL MODEL WITHOUT COVARIATES

The time series of egg to smolt from the fourteen rivers of eastern Canada modelled in a hierarchical structure for Rmax, delta, and sigma are shown in Figure 5. The Beverton-Holt model provides a statistically better fit to the data than the Ricker model; DIC values for Beverton-Holt of 4,533 compared to DIC values of 4,629 for the Ricker model (Tables 2 and 3). A DIC difference of 10 or more has been proposed as sufficient to rule out the model with the higher DIC value (Lunn et al. 2013) however consideration must also be made to the inferences of the models, and as will be seen later, the inferences for the reference points differ between these two models.

The residual plots by yearclass for the Ricker and Beverton-Holt hierarchical model fits are shown in Figures 6 and 7, respectively. There were outlier (the first interquartile value exceeded

+/- 2 std. dev.) predictions (one per river) from the Ricker model in some of the data series (Nashwaak, Pollett, LaHave, Saint-Jean, and Western Arm Brook; Fig. 6). There were fewer outliers from the Beverton-Holt fit but the outliers were from almost the same observations as the Ricker model fit (Pollett, LaHave, Kedgwick, and Saint-Jean; Fig. 7). The LaHave River had a large negative residual for the 2002 year class. There were concerns that the estimated smolt migration in 2004 was very low in the spring following on an exceptionally high discharge event in the winter which may have flushed juveniles out of the system (A. Levy, pers. comm.). The Kedgwick River had a large outlier for the 2007 year class which might be attributable to an underestimate of the spawner abundance for that year class; spawner abundance is based on fall visual spawner counts which can be affected by water conditions whereas the smolt estimates are derived from annual mark and recapture experiments which can correct for some of the variations in monitoring conditions. The Pollett River also had a strong residual for the 1958 year class, for which there is no explanation. There is a suggestion of a systematic change in the dynamic for the St. Jean River for the last four years in the data set; the residuals for those years are all negative and lower than the residuals of all the other years. None of the observations were excluded in subsequent analyses.

The process uncertainty (sigma) varied among rivers with a standard deviation (on the log scale, ~ CV) ranging from 0.27 to 0.47 for the Ricker model (Table 2) and 0.25 to 0.42 for the Beverton-Holt model (Table 3). The predicted sigma was 0.34 for the Ricker model and 0.31 for the Beverton-Holt model.

There were statistically significant ($P<0.01$) auto-correlations in the residuals for 8 and 6 of the 14 stock and recruitment series for the Ricker and Beverton-Holt model fits, respectively (Tables 2, 3). Two rivers, Saint-Jean and de la Trinite, had significantly declining temporal trends in the residuals for both the Ricker and Beverton-Holt models (Tables 2, 3; Figs. 6, 7).

The posterior distributions for delta and Rmax from the Ricker fits are strongly unimodal with the exceptions of the posterior distributions for Rmax for the Nashwaak and Rocky River which are bimodal, particularly Rocky River (Fig. 8). For the Beverton-Holt model, the posterior distributions of delta and Rmax were bimodal for the Nashwaak, LaHave, and to a lesser extent Rocky, with stronger support for high delta and low Rmax than lower delta and higher Rmax (Fig. 9). Nashwaak and LaHave data sets have the lowest estimated egg depositions with limited contrast whereas egg depositions in Rocky reflect a greater range over year classes (Fig. 5).

EXCHANGEABILITY OF RIVERS

Alpha and Rmax

Maximum survival rate estimates (α; median from the posterior distributions) range from 0.7% for Nashwaak to 5.4% for Kedgwick River (Table 2; Fig. 10). The predicted value over all rivers is 1.7% with a 90% Bayesian Credibility Interval (BCI) range of 0.3% to 7.1%. Estimated maximum survival rate at the origin is higher from the Beverton-Holt model, ranging from 0.9% for Nashwaak to 10.7% for Kedgwick (Table 3) and the predicted value over all rivers is 5.3% with a BCI range of 0.5% to 25.3% (Table 3; Fig. 11).

Rmax values from the Ricker model range from 3.8 smolts per 100 m^2 (median from the posterior distributions) to a high of 6.7 smolts per 100 m^2, with a predicted value over all rivers of 4.9 smolts per 100 m^2 (90% BCI range 2.1 to 8.4 smolts per 100 m^2) (Table 2; Fig. 10). Individual river estimates from the Beverton-Holt model are more variable than for the Ricker model, ranging from 1.6 smolts per 100 m^2 for the Nashwaak River to 6.9 smolts per 100 m^2 for the Campbellton River (Table 3; Fig. 11). The predicted maximum smolt production is 4.4 smolts per 100 m^2, with a 90% BCI range of 1.1 to 9.1 smolts per 100 m^2 (Table 3; Fig. 11).

$S_{0.5Rmax}$ was highly variable among rivers and very uncertain within individual rivers (Tables 2, 3). Based on the Ricker model, the medians of the posterior distributions ranged from 46 eggs per 100 m² for Kedgwick River to 866 eggs per 100 m² for Big Salmon River. The predicted $S_{0.5Rmax}$ value over all rivers was 173 eggs per 100 m² with a 90% BCI range of 33 to 1,166 eggs per 100 ² (Table 2). For the Beverton-Holt model, $S_{0.5Rmax}$ values were less variable among rivers, median values ranging from 42 to 234 eggs per 100 m² but highly uncertain within rivers (Table 3). The predicted $S_{0.5Rmax}$ values over all rivers was 78 eggs per 100 ² with a 90% BCI range of 10 to 976 eggs per 100 m² (Table 3).

S_{LRP} values, defined as the eggs which would result in less than 25% probability of recruitment (smolts) being less than 50%Rmax, are higher than the corresponding $S_{0.5Rmax}$ value for all rivers as well as for the predicted values (Tables 2, 3). As with the previous results, the Ricker values are higher than the Beverton-Holt values. Over all rivers, S_{LRP} under the Ricker model is 596 eggs per 100 m² whereas it is 252 eggs per 100 m² under the Beverton Holt model (Tables 2, 3; Figs. 12 and 13).

As a first look, the associations between Rmax and log(delta) relative to presence/absence of lacustrine habitat, to smolt age, and to proportion MSW eggs are shown in Figures 14 and 15 for the Ricker and Beverton-Holt fits, respectively. There is a visually apparent distinction in R_{max} (carrying capacity, smolts per 100 m²) between rivers conditional on the presence or absence of lacustrine habitat (Figs. 14 and 15). All the rivers with lacustrine habitat are in Newfoundland and for 3 of these 5 rivers, R_{max} values are higher than in rivers without lacustrine habitat . Rmax appears to increase with smolt age but the majority of the stocks with older smolt ages are stocks in which there is lacustrine habitat. For both models, log(delta) does not appear to differ between rivers without and with lacustrine habitat but log(delta) declines with increasing smolt age and seemingly less so relative to the proportion MSW eggs (Figs. 14 and 15).

ANALYSES WITH COVARIATES ON RMAX AND DELTA

The analyses are presented for the Ricker and Beverton-Holt stock and recruitment models. Model fit results are summarized for the hierarchical model with lacustrine habitat as a covariate for Rmax (Tables 4 and 5; Figures 16 to 23), with lacustrine habitat as covariate for Rmax and mean age of smolts as a covariate for delta (Tables 6 and 7; Figures 24 to 34), and with lacustrine habitat as covariate for Rmax combined with the proportion MSW eggs as a covariate for δ in Tables 8 and 9 and Figures 35 to 45. Residual plots for these as well as the medians of the posterior distributions of the stock and recruitment curves are shown in Appendices 1 to 3 for each of the covariate model formulations above. Posterior hyperparameter distribution descriptions for the model variants are summarized in Table 10 for the Ricker model and Table 11 for the Beverton-Holt model.

Lacustrine habitat as covariate for Rmax

Ricker model parameter estimates are summarized in Table 4 and posteriors summaries of the model parameters are shown in Figures 16 and 17. Residual plots of the fits are in Appendix 1 Figure 1 and the median from the posterior of the stock and recruitment function in Appendix 1 Figure 2. The Beverton-Holt model fits are similarly summarized in Table 5 and the posterior distributions of delta and Rmax are summarized in Figures 18 and 19. Residual plots of the fits are in Appendix 1 Figure 3 and the median of the posterior stock and recruitment function in Appendix 1 Figure 2.

Based exclusively on the DIC value from the model fits, the Beverton-Holt model provides better short-term predictions than the Ricker model (4,551 versus 4,636, respectively) but the addition of the presence of lacustrine habitat as a covariate for Rmax does not provide better short-term predictions than the models without this covariate for Rmax (DIC = 4,533 for Beverton Holt without the covariate on Rmax).

The posterior distributions of Rmax and delta from the Ricker model are generally unimodal, with exception of Rocky Brook which has a slight bump at low Rmax values (Fig. 17). In contrast, the posterior distributions from the Beverton-Holt model for Rmax are strongly bimodal for four rivers for which there are almost equally probable low or high values of Rmax (Fig. 19).

The posterior predicted Rmax values (smolts per 100 m^2) from the Ricker model for rivers without and with lacustrine habitat are 4.2 (95% BCI 3.1 to 5.8) and 6.3 (95% BCI 4.2 to 8.0), respectively (Table 4). The greater uncertainty in the predicted Rmax values from the Beverton-Holt model are due to the bimodal posterior distributions for four rivers; the posterior distributions of Rmax are 4.0 (95% BCI 1.1 to 8.0) and 5.8 (95% BCI 1.5 to 10.1) for rivers without and with lacustrine habitat, respectively (Table 5).

The delta values from this model are identical to those from the model without lacustrine habitat as a covariate (Tables 10, 11).

The log-linear beta parameter for the presence of lacustrine habitat has the strongest explanatory power for the Ricker model (proportion of MCMC draws with $\beta > 0 = 0.04$) with less important explanatory power for the Beverton-Holt model (proportion of MCMC draws with $\beta > 0 = 0.12$) (Fig. 20).

The estimated S_{LRP} values are generally higher from the Ricker model relative to the Beverton-Holt except for the rivers with bimodal distributions on Rmax (Nashwaak, LaHave, Rocky and NE Trepassey) for which the S_{LRP} values from Beverton-Holt are acutally higher (Figs. 21 and 22). The predicted S_{LRP} value for rivers without lacustrine habitat is about 508 eggs per 100 m^2 for the Ricker and 260 eggs per 100 m^2 for the Beverton-Holt (Fig. 23; Table 10). For rivers with lacustrine habitat, S_{LRP} values are respectively about 760 eggs per 100 m^2 for Ricker and 352 eggs per 100 m^2 for Beverton-Holt (Fig. 23; Table 11).

Lacustrine habitat as covariate for Rmax and mean age of smolts as covariate for delta

The oldest mean ages of smolts are in rivers of Newfoundland with lacustrine habitat (Table 1; Fig. 2) whereas in rivers with fluvial habitat only, the oldest mean age of smolts are in the most northern latitude rivers (de la Trinité, Saint-Jean, and Kedgwick River).

Ricker model parameter estimates are summarized in Table 6 and posteriors summaries of the model parameters are shown in Figures 24 and 25. Residual plots of the fits are in Appendix 2 Figure 1 and the median from the posterior of the stock and recruitment function in Appendix 2 Figure 2. The Beverton-Holt model fits are similarly summarized in Table 7 and the posterior distributions of delta and Rmax are summarized in Figures 26 and 27. Residual plots of the fits are in Appendix 2 Figure 3 and the median of the posterior stock and recruitment function in Appendix 2 Figure 2.

Based exclusively on the DIC value from the model fits, the Beverton-Holt model provides better short-term predictions than the Ricker model (4,550 versus 4,636, respectively) but the addition of the presence of lacustrine habitat as a covariate for Rmax and mean age as covariate for delta does not provide better short-term predictions than the models without these covariates.

The posterior distributions of Rmax and delta from the Ricker model are strongly unimodal (Fig. 25) whereas the posterior distributions from the Beverton-Holt model for Rmax are strongly bimodal for four rivers for which there are almost equally probable low or high values of Rmax (Fig. 27). The posterior predicted Rmax values (smolts per 100 m^2) from the Ricker model for rivers without and with lacustrine habitat are 4.2 (95% BCI 3.0 to 6.0) and 6.3 (95% BCI 3.8 to 8.1), respectively (Table 4). The greater uncertainty in the predicted Rmax values from the

Beverton-Holt model are due to the bimodal posterior distributions for four rivers; the posterior distributions of Rmax are 4.0 (95% BCI 1.2 to 7.4) and 5.7 (95% BCI 1.5 to 9.1) for rivers without and with lacustrine habitat, respectively (Table 5).

The log-linear beta parameter for the presence of lacustrine habitat has strong explanatory power for the Ricker model (proportion of MCMC draws with $\beta_{lac} > 0 = 0.05$) but the explanatory power of mean age of smolts is much less (proportion of MCMC draws with $\beta_{age} > 0 = 0.29$) (Fig. 28). For the Beverton-Holt model, the explanatory power of the lacustrine habitat covariate for Rmax is less than for the Ricker model (proportion of MCMC draws with $\beta_{lac} > 0 = 0.14$) and the explanatory power of mean age of smolts is slightly better than for the Ricker model (proportion of MCMC draws with $\beta_{age} > 0 = 0.19$) (Fig. 29).

The predicted delta values decrease, or conversely survival rates at low egg depositions increase, with increasing smolt age although there is very large uncertainty in the predicted values at age (Figs. 30 and 31; Tables 6 and 7). For the Ricker model, survival rates at low egg depositions increase from 0.014 for age-2 year old smolt populations to 0.024 for age-4 smolt populations whereas for the Beverton-Holt model, survival rates increase from 0.032 for age-2 year old smolts to 0.105 for age-4 year old smolts (Tables 6 and 7).

The estimated S_{LRP} values are higher from the Ricker model relative to the Beverton-Holt except for three of the four rivers with bimodal distributions on Rmax (Nashwaak, LaHave, and Rocky) for which the S_{LRP} values from Beverton-Holt are actually higher (Figs. 32 and 33). Due to the lower survival rates at low egg deposition densities and the greater process uncertainty for the Ricker model, there is always a greater than 25% chance that the predicted smolt production will be less than 50% Rmax over all ages of smolts and regardless of the presence of lacustrine habitat (Fig. 34). For the Beverton-Holt model, predicted S_{LRP} values for rivers without lacustrine habitat decrease from about 570 eggs per 100 m^2 for age-2 year old smolts to 126 eggs per 100 m^2 for age-4 year old smolt populations (Fig. 34; Table 11). For rivers with lacustrine habitat, S_{LRP} values for rivers with age-3 year old smolts are 288 eggs per 100 m^2 and 168 eggs per 100 m^2 for rivers with age-4 smolts (Fig. 34; Table 11).

Lacustrine habitat as covariate for Rmax and proportion MSW eggs as covariate for delta

All the rivers in Newfoundland with lacustrine habitat have salmon populations with the majority of the eggs coming from 1SW salmon (Table 1; Fig. 2). The rivers without lacustrine habitat are characterized by salmon populations with a low proportion of eggs from MSW salmon (Pollett and Big Salmon) to populations in which the eggs come almost exclusively from MSW salmon (Saint-Jean, Kedgwick, Margaree) (Table 1; Fig. 2).

Ricker model parameter estimates are summarized in Table 8 and posteriors summaries of the model parameters are shown in Figures 35 and 36. Residual plots of the fits are in Appendix 3 Figure 1 and the median from the posterior of the stock and recruitment function in Appendix 3 Figure 2. The Beverton-Holt model fits are similarly summarized in Table 9 and the posterior distributions of delta and Rmax are summarized in Figures 37 and 38. Residual plots of the fits are in Appendix 3 Figure 3 and the median of the posterior stock and recruitment function in Appendix 3 Figure 2.

Based exclusively on the DIC value from the model fits, the Beverton-Holt model provides better short-term predictions than the Ricker model (4,566 versus 4,638, respectively) but the presence of lacustrine habitat as a covariate for Rmax and proportion MSW eggs as covariate for delta does not provide better short-term predictions than the models without these covariates.

The posterior distributions of Rmax and delta from the Ricker model are strongly unimodal (Fig. 36) whereas the posterior distributions from the Beverton-Holt model for Rmax are strongly bimodal for four rivers for which there are almost equally probable low or high values of Rmax (Fig. 38). The posterior predicted Rmax values (smolts per 100 m²) from the Ricker model for rivers without and with lacustrine habitat are similar to the other model formulations at 4.1 (95% BCI 3.1 to 5.6) and 6.3 (95% BCI 4.3 to 7.9), respectively (Tables 8 and 10). The greater uncertainty in the predicted Rmax values from the Beverton-Holt model are again due to the bimodal posterior distributions for four rivers; the posterior distributions of Rmax are 3.9 (95% BCI 1.3 to 6.5) and 5.9 (95% BCI 1.9 to 9.5) for rivers without and with lacustrine habitat, respectively (Tables 9, 11).

The log-linear beta parameter for the presence of lacustrine habitat has strong explanatory power for the Ricker model (proportion of MCMC draws with $\beta_{lac} > 0 = 0.03$) as does the proportion of eggs from MSW salmon (proportion of MCMC draws with $\beta_{pmsw} > 0 = 0.06$) (Fig. 39). For the Beverton-Holt model, the explanatory power of the lacustrine habitat covariate for Rmax is also strong (proportion of MCMC draws with $\beta_{lac} > 0 = 0.07$) but the explanatory power of the proportion MSW eggs is much less than for the Ricker model (proportion of MCMC draws with $\beta_{pmsw} > 0 = 0.18$) (Fig. 40).

The predicted delta values decrease, or conversely survival rates at low egg depositions increase, with increasing proportion of eggs from MSW salmon although there is very large uncertainty in the predicted values at proportions of MSW eggs (Figs. 41 and 42; Tables 8 and 9). For the Ricker model, survival rates at low egg depositions increase from 0.013 for populations with 10% of the eggs from MSW salmon to 0.029 for populations with 90% of the eggs from MSW salmon (Tables 8, 10). For the Beverton-Holt model, survival rates increase from 0.045 for populations with 10% of eggs from MSW salmon to 0.088 for populations with 90% of the eggs from MSW salmon (Tables 9 and 11).

The estimated S_{LRP} values are higher from the Ricker model relative to the Beverton-Holt except for three of the four rivers with bimodal distributions on Rmax (Nashwaak, LaHave, and Rocky) for which the S_{LRP} values from Beverton-Holt are actually higher (Figs. 43 and 44). Due to the lower survival rates at low egg deposition densities and the greater process uncertainty for the Ricker model, there is generally greater than 25% chance that the predicted smolt production will be less than 50% Rmax for populations with 10% of the egg depositions from MSW salmon (Fig. 45). For populations with 50% of egg depositions from MSW salmon, the S_{LRP} value for rivers without lacustrine habitat is 460 eggs per 100 m² and for rivers with lacustrine habitat, S_{LRP} is in the range of 638 eggs per 100 m² (Fig. 45). For fluvial river populations with >= 90% of egg depositions from MSW salmon, S_{LRP} is less than about 240 eggs per 100 m².

For the Beverton-Holt model, predicted S_{LRP} values for rivers without lacustrine habitat decrease from about 318 eggs per 100 m² for populations with 10% of eggs from MSW salmon to 146 eggs per 100 m² for populations with 90% of eggs from MSW salmon (Fig. 45). For the populations in Newfoundland in which lacustrine habitat is available and for which less than 10% of the eggs are contributed by MSW salmon, the S_{LRP} value is about 474 eggs per 100 m² of fluvial habitat (Fig. 45; Table 11). Current conservation requirements for Conne, Campellton and Western Arm Brook are 330, 490 and 344 eggs per 100 m² of fluvial habitat, respectively.

TRANSFER OF S_{LRP} VALUES

The modelling exercise provides a range of potential S_{LRP} values based on the exclusion or inclusion of covariates which modify the freshwater stock and recruitment dynamics. These covariates could be used to transfer reference points from the monitored rivers data set to rivers without stock and recruitment data. Results are also provided for two of the most common stock and recruitment functions.

Treating all rivers as exchangeable, conditional only on the amount of fluvial habitat, the S_{LRP} value from the Ricker model is 596 eggs per 100 m² and from the Beverton-Holt model S_{LRP} is 252 eggs per 100 m² (Tables 10 and 11).

With the additional exchangeability assumption that includes the presence of lacustrine habitat for rearing of salmon juveniles, S_{LRP} values for rivers with exclusively fluvial habitat are 508 eggs per 100 m² for the Ricker model or 260 eggs per 100 m² for the Beverton-Holt model. (Tables 10 and 11). For rivers with lacustrine habitat, i.e. rivers in insular Newfoundland, S_{LRP} values are 762 eggs per 100 m² for the Ricker model and 352 eggs per 100 m² for the Beverton-Holt model.

Incorporating the covariate mean age for the survival rate near the origin (α) results in decreasing S_{LRP} values with increasing mean smolt age (Fig. 46). Incorporating the covariate proportion of eggs from MSW salmon for the survival rate near the origin (α) results in decreasing S_{LRP} values with increasing proportions of eggs from MSW salmon (Fig. 47) (Tables 10 and 11). The S_{LRP} values are higher for stocks with lacustrine habitat used by juvenile salmon (Figs. 46 and 47).

DISCUSSION

The hierarchical Bayesian analyses of the fourteen egg deposition to smolt recruitment data sets from eastern Canada clearly show that the stock and recruitment dynamic of Atlantic salmon within the freshwater portion of the life cycle is highly variable within and among rivers. A large part of the within river uncertainty is due to the limited number of observations available for individual stocks and in many cases the limited contrast in egg depositions which have been realized for the monitored time series. The large amount of uncertainty associated with the modelled dynamics results in very uncertain stock and recruitment parameters of interest, in this analysis the smolt carrying capacity and the survival rate at low densities of egg depositions. These uncertainties propagate into the estimation of reference points for management.

The analyses confirm the premise of CAFSAC (1991a), O'Connell and Dempson (1995) and Chaput et al. (1998) that differences in the smolt carrying capacity of salmon rivers can be attributed to the presence of lacustrine habitat which is used by salmon juveniles for rearing.

We developed models that could be used to transport reference points based on three potential covariates; lacustrine habitat, mean age of smolts, and proportion of the egg depositions coming from MSW salmon. These three covariates also broadly define regions in eastern Canada. Rivers with lacustrine habitat used by salmon juveniles are all situated in Newfoundland and stocks in Newfoundland tend to have older smolts and a low proportion of eggs from MSW salmon (O'Connell et al. 2006). Outside Newfoundland, there are regional differences in the biological characteristics of the spawning stock and differences in age of smolts with older smolts ages at more northern latitudes (O'Connell et al. 2006). Salmon populations in Quebec (Gaspe region and lower north shore) and in the southern Gulf of St. Lawrence are characterized as multi-sea-winter salmon stocks in which the annual egg depositions are the majority contributed by MSW salmon with minimal amounts by 1SW salmon (Chaput et al. 2006; O'Connell et al. 2006). Salmon stocks in the Atlantic coast of Nova Scotia (excluding the highland areas of Cape Breton) and stocks in the Bay of Fundy are a mixture of 1SW and 2SW female spawners, midway between the values seen in Newfoundland and the Gulf of St. Lawrence (O'Connell et al. 2006).

Density-independent survival rate (at the origin) is estimated to be higher for rivers with older smolt ages as well as for stocks with increasing proportions of the egg depositions from MSW salmon. The predicted increased survival rate at older smolt ages is not immediately obvious.

The expectation would be for the cumulative survival rate to decline as juvenile salmon are exposed to more years of mortality in the river and this is the result modelled by Symons (1979). However, as smolt age is also related to latitudinal clines, lower survival rates for younger smolt age stocks may be associated with increased competition and mortality in southern rivers which have a more diverse fish community. In which case, smolt age may be a proxy for other factors that condition density independent survival rates. There generally remained a probability > 25% that recruitment would be less than 50%Rmax for the Ricker model when age is included as a covariate for density independent survival. This was not the case for the Beverton-Holt model for which there were estimable S_{LRP} values that resulted in less than 25% chance of recruitment being less than 50%Rmax.

Higher survival rates in stocks that have a high proportion of eggs from MSW salmon is consistent with expectations. In fish culture settings, eggs from small salmon (1SW salmon or grilse) survive less well than larger eggs from MSW salmon (Thorpe et al. 1984; Fleming, 1996; Reid and Chaput 2012). Redd characteristics, including depth of excavation, size of substrate, and spawning habitat used, are also related to female size and this could impart a survival advantage to eggs and progeny from large females (Fleming 1996). As with the modelled relationship of survival relative to mean age of smolts, there is a large amount of uncertainty in the predicted survival for both of these covariates, particularly under the Beverton-Holt model. With proportion of eggs from MSW salmon as a covariate for density independent survival, there were estimable values for S_{LRP} under the Ricker model but they were minimally so when the proportion MSW salmon egg contributions were less than 0.1. The Beverton-Holt model provided resolvable solutions to S_{LRp}.

We did not model mean age of smolts or proportion MSW salmon as a covariate for Rmax. Preliminary visualization did not suggest to us that mean age of smolts or proportion MSW eggs could explain variations in Rmax that could not be explained by presence of lacustrine habitat. This was not the case for density independent survival which at first look did not differ on average based on presence/absence of lacustrine habitat. Symons (1979) indicated that carrying capacity would be higher for stocks with younger mean smolt ages but in our analysis, Rmax is higher with older smolt ages which also happen to be rivers with lacustrine habitat. Prévost et al. (2003) reported a positive association between the egg recruitment rate, equivalent to carrying capacity, and latitude and subsequently incorporated this association in the model. Prévost et al. (2003) do not try and explain the ecological basis for this association but higher diversity of competitive species and greater amounts of anthropogenic stress in southern areas are reasonable hypotheses to explain lower productivity in southern areas.

The results from both the Ricker and Beverton-Holt models are described. On the basis of objective model fitting diagnostics reported extensively in literature (Michelsens and McAllister 2004; Gibson 2006; Pulkkinen and Mäntyniemi 2013) and in this analysis, the Beverton-Holt model consistently provides a better fit to the observations than the Ricker model. The process uncertainty is smaller for the Beverton-Holt model compared to the Ricker model but there is very little to distinguish the fits between these models when examining the residuals (Figs. 6 and 7; Appendix Figures). The Ricker model provides lower survival rates at the origin than does the Beverton-Holt model but with generally similar Rmax values for the two models. The slope at the origin is a key stock and recruitment dynamic parameter, which defines the productive capacity of the population, i.e. its capacity to generate surplus production. If the slope at the origin is steeper, as in the Beverton-Holt model, then reference points based on productive capacity will be much lower than those from Ricker model fits. Even under the hierarchical Beverton-Holt model formulation, Rmax values for some rivers are poorly defined and bimodal whereas all the Rmax estimates from Ricker are unimodal. Much of the debate regarding Ricker versus Beverton-Holt models centers around the plausibility of overcompensation as expressed by the Ricker model versus asymptotic recruitment as expressed by the Beverton-Holt model. In fact, if there has been sufficiently large contrast in egg depositions with which to fit the Ricker and the Beverton-Holt models, the asymptotic vs overcompensatory debate is mute as those differences most often will occur at egg depositions beyond the replacement point (equilibrium point) of the population.

The proposed method for calculating the limit reference point (S_{LRP}) consists in estimating the egg deposition that results in less than 25% chance that smolt recruitment would be less than 50%Rmax. There tends to be higher values of S_{LRP} for the rivers in which the posterior distributions of Rmax and survival near the origin were bimodal. The S_{LRP} calculations incorporate the uncertainty in the parameter estimates of the stock and recruitment dynamic, including the process uncertainty. The S_{LRP} values, expressed in terms of eggs per fluvial habitat area, are highest for stocks in Newfoundland which are dominated by 1SW salmon and for which there is lacustrine habitat utilized by juvenile salmon and lowest in the MSW salmon stocks of Quebec and the southern Gulf of St. Lawrence where there is no lacustrine habitat usage and the proportion of eggs from MSW salmon are highest.

The ranges of S_{LRP} values for the Beverton-holt model with different covariates overlap the presently defined conservation requirements of 240 eggs per 100 m² of fluvial habitat for Atlantic salmon rivers in eastern Canada. Based on presence / absence of lacustrine habitat as a covariate for Rmax, S_{LRP} for fluvial habitat only rivers is about 260 eggs per 100 m². With mean age of smolts as an additional covariate on density-independent survival, S_{LRP} for fluvial habitat rivers ranges from a high of 570 eggs for rivers with smolt age of 2 years to 218 eggs for rivers with smolt age of 3 years. Finally, if the proportion of MSW eggs is used as a covariate of density independent survival, then for fluvial habitat only rivers, S_{LRP} values would be 318 eggs per 100 m² for stocks with 10% of the eggs from MSW salmon (for ex. the Pollett River), decreasing to about 200 eggs per 100 m² for stocks with 50% of the eggs from MSW salmon (for ex. LaHave River) to just under 150 eggs per 100 m² for stocks with 90% or greater of the eggs from MSW salmon (for ex. Margaree, Kedgwick, de la Trinite).

For rivers with lacustrine habitat which are exclusively in Newfoundland, the S_{LRP} value based exclusively on the presence of lacustrine habitat as a covariate is 352 eggs per 100 m² of fluvial habitat. With mean age of smolts as an additional covariate on density-independent survival, S_{LRP} for stocks of smolt age 3 years are about 290 eggs per 100 m² of fluvial habitat decreasing to about 170 eggs for stocks of smolt age 4 years. Finally, if the proportion of MSW eggs is used as a covariate of density independent survival, the S_{LRP} values for stocks with 5% of the eggs from MSW salmon (essentially all the stocks in Newfoundland except for Little Codroy River in the data set) is about 500 eggs per 100 m² of fluvial habitat. This compares to the current egg deposition requirements for the five rivers of Newfoundland with lacustrine habitat which range from a low of 252 eggs per 100 m² of fluvial habitat for NE Trepassey, to 314 eggs per 100 m² of fluvial habitat for Western Arm Brook, to a high of 490 eggs per 100 m² of fluvial habitat for Campbellton River. Based on the life history characteristics of salmon stocks in insular Newfoundland, the model in this paper proposes basically a single S_{LRP} value of about 475 eggs per 100 m² of fluvial habitat for most rivers in insular Newfoundland, with the exception of the rivers in the southwest portion of the island where MSW salmon are relatively more abundant and would have a correspondingly lower S_{LRP} reference level.

The use of the presence of lacustrine habitat as an indicator variable for Rmax needs further consideration. O'Connell and Dempson (1995) calculated conservation values for Newfoundland rivers using rates of egg depositions per unit of fluvial habitat (240 eggs per 100 m²) and an additional requirement based on an egg deposition rate 368 eggs per ha of lacustrine habitat or 150 eggs per ha for rivers in the northern peninsula of Newfoundland. In the model presented here, S_{LRP} values are defined as an egg deposition rate for fluvial habitat and considers only whether lacustrine habitat is present, not how much lacustrine habitat may be available. Indeed, the incorporation of the amount of lacustrine habitat in the modelling would need to consider the amount of lacustrine habitat relative to the amount of fluvial habitat and the geographic distribution of the fluvial and lacustrine habitat within the river system. The ratio of lacustrine habitat (m^2) to fluvial habitat (m^2) in the five index rivers of Newfoundland is quite variable (5, 20, 24, 68, 70 for the five rivers), with a lowest value for Northeast Trepassey and the highest values for Campbellton and Western Arm Brook which makes the Northeast Trepassey more similar to a fluvial habitat only river relative to its counterparts in Newfoundland (Table 1). The disposition of the lacustrine habitat is also not evenly distributed within the watershed and juveniles most likely to migrate and use specific lacustrine habitat are likely those located in fluvial habitat in the vicinity of lacustrine habitat.

We have assumed that the 14 data sets are representative of the stock and recruitment dynamics of Atlantic salmon in eastern Canada and have proposed variables to improve the exchangeability assumptions. We are limited in the number of covariates which could be considered in the model given the small sample size of rivers with stock and recruitment data and the lack of contrast among and within the covariates themselves. For example, the contrast within the proportion of eggs from MSW salmon is quite good for the fluvial habitat rivers, ranging from about 10% to over 99%, but for the lacustrine habitat rivers, all five rivers have similar and low proportion of eggs from MSW salmon. This precludes any analyses of the variations in Rmax that would have both presence of lacustrine habitat and proportion of eggs from MSW salmon as potential covariates. The same issue arises with mean age of smolts, the rivers with lacustrine habitat also happen to be the rivers with the oldest smolt ages and all above three years old.

Analyses using hierarchical Bayesian frameworks as developed in Prévost et al. (2003), applied by Brun and Prévost (2013), and as presented in this manuscript are the favored approach for analyzing multiple stock and recruitment data sets and to address data-poor situations. The transfer of reference points from data-rich stocks like Western Arm Brook to data-poor stocks, which are the great majority of stocks in eastern Canada, poses the greatest challenge. Prévost et al. (2003) indicate that the large between-stocks residual variation after accounting for the effects of the readily available covariates impedes precise posterior predictions in data-poor situations. As important is the paucity of stock and recruitment data sets with contrasting population (smolt age, adult stock structure) and ecological characteristics (fluvial and lacustrine habitat abundance and distribution, species distribution). We will never have sufficient data from all the salmon producing rivers of eastern Canada with which to develop river-specific reference points. For all the intensive monitoring efforts that have occurred over the past six decades, we have spawner to smolt data from fourteen rivers in eastern Canada (this manuscript), reconstructed adult to adult data from twelve stocks in Quebec (M. Dionne, Ministère des Forêtes, de la Faune et des Parcs, Province de Québec, unpublished data) and from potentially a dozen or less rivers in Newfoundland and the Maritime provinces (Chaput and Jones 1992, 2006; Gibson and Bowlby 2013; M. Robertson, DFO Newfoundland and Labrador Region, unpublished data). Maintaining the existing monitoring data sets is essential and developing new stock and recruitment series, particularly in areas which are sparsely studied (all areas of eastern Canada) or not studied (northern areas, particularly Labrador) is required. These are not short term actions as the first usable egg to smolt data point takes at least three years of monitoring data in stocks with age 2 year old smolts and this increases to six years or more in northern areas like Labrador where the dominant smolt age is four years and five years old.

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TABLES

Table 1. Egg to smolt data from 14 rivers of eastern Canada.

River	Latitude (ºN)	Habitat: Fluvial (100 m²)	Habitat: Lacustrine (ha)	Mean age	Prop. eggs from MSW	Observa tions	Year-class range	Egg deposition range (X 10^6)	Smolt estimate range	Eggs per 100 m² range	Smolts per 100 m² range
Nashwaak	45.96	53,505	0	2.24	0.61	13	1995 to 2007	0.73 to 6.20	6,949 to 26,857	14 to 116	0.1 to 0.5
Big Salmon	45.42	4,649	0	2.60	0.20	4	1964 to 1967	7.68 to 14.61	11,891 to 26,599	1,652 to 3,142	2.6 to 5.7
Pollett	46.00	3,637	0	2.12	0.12	8	1953 to 1960	0.12 to 3.51	4,098 to 20,674	33 to 964	1.1 to 5.7
LaHave	44.54	26,052	0	2.22	0.51	14	1993 to 2006	0.95 to 1.95	5,802 to 27,220	36 to 75	0.2 to 1.0
Margaree	46.42	28,000	0	2.65	0.95	7	1999 to 2005	12.18 to 26.34	73,576 to 130,875	435 to 941	2.6 to 4.7
Kedgwick	47.65	35,000	0	2.98	0.95	7	1999 to 2007	3.01 to 7.13	75,672 to 275,200	86 to 204	2.2 to 7.9
Saint-Jean	48.77	22,514	0	3.39	0.996	23	1985 to 2007	1.98 to 6.33	35,782 to 174,392	88 to 281	1.6 to 7.7
de la Trinite	49.42	19,161	0	2.99	0.89	28	1980 to 2007	0.90 to 4.17	27,470 to 103,104	47 to 217	1.4 to 5.4
Little Codroy	47.77	3,890	0	2.64	0.55	7	1954 to 1960	0.08 to 1.36	5,354 to 12,490	21 to 350	1.4 to 3.2
Conne River	47.91	13,180	3,187	3.28	0.06	21	1986 to 2006	2.91 to 17.04	47,117 to 98,605	221 to 1,293	3.6 to 7.5
Rocky	47.22	10,823	2,191	3.20	0.05	21	1987 to 2007	0.56 to 2.05	5,416 to 15,589	52 to 189	0.5 to 1.4
NE Trepassey	46.77	556	29	3.61	0.05	24	1984 to 2007	0.15 to 0.53	811 to 2,443	263 to 953	1.5 to 4.4
Campbell-ton	49.27	5,960	4,037	3.45	0.05	14	1993 to 2006	4.04 to 9.57	26,266 to 62,495	678 to 1,605	4.4 to 10.5
Western Arm Brook	51.19	2,900	2,017	3.75	0.04	37	1971 to 2007	0.27 to 5.67	6,153 to 23,319	95 to 1,956	2.1 to 8.0

Table 2. Hierarchical Bayesian fits of Ricker model, with no covariates.

River	Sigma (median)	Serial trend in residuals		Lag 1 autocorrelation		Alpha		R_{max}		$S_{0.5Rmax}$ (eggs per 100 m²)		S_{LRP}
		value	p-value	value	P-value	median	5-95th	median	5-95th	median	5-95th	
Nashwaak	0.469	0.13	> 0.10	0.42	< 0.001	0.007	0.005 to 0.010	4.6	0.6 to 7.8	423	38 to 781	902
Big Salmon	0.333	0.65	0.068	0.41	0.012	0.004	0.002 to 0.010	5.4	4.0 to 8.0	866	354 to 2,212	1,480
Pollett	0.455	0.01	> 0.10	-0.44	0.032	0.023	0.016 to 0.032	5.2	3.8 to 7.5	142	94 to 248	238
LaHave	0.360	-0.01	> 0.10	-0.01	> 0.10	0.011	0.009 to 0.013	4.7	1.5 to 8.1	277	80 to 494	436
Margaree	0.272	0.06	> 0.10	0.02	> 0.10	0.009	0.006 to 0.016	4.9	3.6 to 7.9	356	156 to 733	526
Kedgwick	0.408	0.34	> 0.10	-0.18	> 0.10	0.054	0.026 to 0.128	4.2	3.1 to 6.6	46	21 to 143	92
Saint-Jean	0.391	-0.10	< 0.001	0.64	< 0.001	0.039	0.028 to 0.060	4.7	3.6 to 7.1	76	41 to 150	126
de la Trinite	0.336	-0.05	0.015	0.29	< 0.001	0.033	0.026 to 0.046	4.1	2.9 to 6.6	79	41 to 152	124
Little Codroy	0.332	0.17	> 0.10	-0.19	> 0.10	0.042	0.029 to 0.058	3.9	2.9 to 5.9	57	37 to 117	90
Conne River	0.273	-0.02	> 0.10	0.25	< 0.001	0.025	0.020 to 0.032	5.8	5.2 to 6.5	144	117 to 188	192
Rocky	0.354	0.01	> 0.10	0.43	< 0.001	0.010	0.008 to 0.019	3.8	1.0 to 6.9	247	35 to 494	582
NE Trepassey	0.286	-0.01	> 0.10	0.00	> 0.10	0.008	0.006 to 0.011	3.8	2.8 to 6.2	320	162 to 654	490
Campbellton	0.273	-0.04	> 0.10	0.21	< 0.001	0.013	0.009 to 0.020	6.7	5.9 to 8.0	312	218 to 513	432
Western Arm Brook	0.343	-0.01	> 0.10	0.05	> 0.10	0.021	0.018 to 0.025	6.5	5.9 to 7.1	189	165 to 222	262
Predicted	0.338	na	na	na	na	0.017	0.003 to 0.071	4.9	2.1 to 8.4	173	33 to 1,166	596

Nburnin <- 10000; Niter <- 15000; Thin <- 10; Nchains <- 2; DIC = 4629

Table 3. Hierarchical Bayesian fits of Beverton-Holt model, no covariates.

River	Sigma (median)	Serial trend in residuals		Lag 1 autocorrelation		Alpha		R_{max}		$S_{0.5Rmax}$ (eggs per 100 m²)		S_{LRP}
		value	p-value	value	P-value	median	5-95th	median	5-95th	median	5-95th	
Nashwaak	0.417	0.05	> 0.10	0.34	> 0.10	0.009	0.006 to 0.081	1.6	0.3 to 6.3	183	4 to 945	666
Big Salmon	0.321	0.79	0.082	0.34	> 0.10	0.044	0.005 to 0.245	4.7	3.5 to 6.9	104	18 to 1,266	370
Pollett	0.386	0.11	> 0.10	-0.34	0.052	0.045	0.026 to 0.104	4.2	2.7 to 6.6	93	28 to 227	198
LaHave	0.341	-0.01	> 0.10	-0.06	> 0.10	0.013	0.01 to 0.109	3.0	0.6 to 7.1	234	6 to 652	488
Margaree	0.269	0.16	> 0.10	-0.03	> 0.10	0.033	0.01 to 0.194	4.5	3.4 to 7.8	133	19 to 763	362
Kedgwick	0.377	0.36	> 0.10	-0.20	> 0.10	0.107	0.046 to 0.377	4.6	3.3 to 7.1	42	10 to 140	104
Saint-Jean	0.367	-0.10	< 0.001	0.64	> 0.10	0.086	0.045 to 0.282	5.0	3.8 to 7.6	57	14 to 164	128
de la Trinite	0.322	-0.06	0.003	0.33	<0.001	0.056	0.036 to 0.131	4.6	3.2 to 7.2	81	25 to 194	158
Little Codroy	0.264	0.03	> 0.10	-0.18	> 0.10	0.085	0.049 to 0.191	3.6	2.6 to 5.4	42	14 to 102	74
Conne River	0.251	-0.01	> 0.10	0.42	<0.001	0.102	0.046 to 0.349	5.8	5.1 to 7.0	57	15 to 150	104
Rocky	0.324	0.03	> 0.10	0.47	<0.001	0.018	0.01 to 0.084	1.9	1.0 to 5.5	102	12 to 533	304
NE Trepassey	0.275	-0.03	> 0.10	0.19	> 0.10	0.021	0.009 to 0.124	3.5	2.6 to 5.9	170	22 to 653	388
Campbellton	0.269	-0.05	> 0.10	0.21	<0.001	0.063	0.02 to 0.29	6.9	5.8 to 9.0	108	22 to 444	234
Western Arm Brook	0.297	0.01	> 0.10	0.10	<0.001	0.066	0.041 to 0.146	5.8	5.0 to 6.7	88	36 to 158	148
Predicted	0.314	na	na	na	na	0.053	0.005 to 0.253	4.4	1.1 to 9.1	78	10 to 976	252

Nburnin <- 10000; Niter <- 15000; Thin <- 10; Nchains <- 2; DIC = 4533

Table 4. Hierarchical Bayesian fits of Ricker model, with lacustrine habitat as covariate on Rmax.

River	Sigma (median)	Serial trend in residuals value	Serial trend in residuals p-value	Lag 1 autocorrelation value	Lag 1 autocorrelation P-value	Alpha median	Alpha 5-95th	R_{max} median	R_{max} 5-95th	$S_{0.5Rmax}$ (eggs per 100 m²) median	$S_{0.5Rmax}$ (eggs per 100 m²) 5-95th	S_{LRP}
Nashwaak	0.464	0.14	> 0.10	0.42	< 0.001	0.007	0.006 to 0.009	4.1	2.9 to 5.7	383	243 to 570	630
Big Salmon	0.340	0.67	0.071	0.46	0.001	0.004	0.002 to 0.007	4.4	3.7 to 6.1	714	394 to 1,453	1,106
Pollett	0.449	0.02	> 0.10	-0.56	0.022	0.023	0.016 to 0.031	4.3	3.6 to 6.0	120	85 to 187	200
LaHave	0.361	-0.01	> 0.10	-0.01	> 0.10	0.011	0.009 to 0.013	4.2	3.0 to 5.9	243	164 to 360	356
Margaree	0.284	0.10	> 0.10	0.02	> 0.10	0.010	0.007 to 0.018	4.2	3.6 to 5.7	263	141 to 496	382
Kedgwick	0.391	0.34	> 0.10	-0.22	0.065	0.062	0.029 to 0.127	4.1	3.3 to 5.2	39	21 to 101	72
Saint-Jean	0.387	-0.10	< 0.001	0.63	< 0.001	0.042	0.031 to 0.064	4.2	3.6 to 5.6	62	38 to 108	98
de la Trinite	0.337	-0.05	0.015	0.29	< 0.001	0.034	0.027 to 0.044	4.1	3.2 to 5.3	76	48 to 116	110
Little Codroy	0.333	0.18	> 0.10	-0.19	> 0.10	0.043	0.030 to 0.060	4.0	3.2 to 5.0	58	39 to 96	86
Conne River	0.281	-0.01	> 0.10	0.27	< 0.001	0.026	0.020 to 0.033	6.1	5.4 to 6.7	148	117 to 200	200
Rocky	0.364	-0.01	> 0.10	0.41	< 0.001	0.009	0.008 to 0.011	6.2	2.3 to 7.6	430	138 to 562	634
NE Trepassey	0.298	0.00	> 0.10	-0.05	> 0.10	0.006	0.005 to 0.009	6.1	3.2 to 7.3	621	236 to 813	808
Campbellton	0.280	-0.04	> 0.10	0.21	< 0.001	0.013	0.009 to 0.019	6.6	5.9 to 7.6	304	217 to 468	418
Western Arm Brook	0.345	-0.01	> 0.10	0.05	> 0.10	0.021	0.018 to 0.025	6.4	5.9 to 7.1	189	165 to 221	266
Predicted-fluvial	0.346	na	na	na	na	0.017	0.003 to 0.076	4.2	3.1 to 5.8	153	32 to 1,023	508 [1] (0.27)
Predicted-lacustrine								6.3	4.2 to 8.0	222	47 to 1,497	762 [1] (0.27)

[1] The predicted S_{LRP} values shown are the egg deposition values corresponding to the lowest probability that recruitment would be < 50%Rmax and the values in parentheses are the corresponding probabilities

Nburnin <- 100000; Niter <- 50000; Thin <- 10; Nchains <- 2; DIC = 4638

Table 5. Hierarchical Bayesian fits of Beverton-Holt model, with lacustrine habitat as covariate on Rmax.

River	Sigma (median)	Serial trend in residuals		Lag 1 autocorrelation		Alpha		R_{max}		$S_{0.5Rmax}$ (eggs per 100 m²)		S_{LRP}
		value	p-value	value	P-value	median	5-95th	median	5-95th	median	5-95th	
Nashwaak	0.434	0.09	> 0.10	0.39	> 0.10	0.008	0.006 to 0.068	3.6	0.3 to 5.3	459	4 to 800	824
Big Salmon	0.324	0.79	0.08	0.37	< 0.001	0.054	0.007 to 0.32	4.4	3.5 to 6.1	81	13 to 715	262
Pollett	0.386	0.12	> 0.10	-0.36	0.0488	0.048	0.028 to 0.104	4.0	2.8 to 5.8	85	29 to 187	182
LaHave	0.344	-0.01	> 0.10	-0.05	> 0.10	0.013	0.01 to 0.083	3.7	0.6 to 5.5	295	8 to 504	476
Margaree	0.272	0.18	> 0.10	-0.02	> 0.10	0.047	0.012 to 0.268	4.1	3.4 to 6.5	88	14 to 527	224
Kedgwick	0.373	0.36	> 0.10	-0.22	0.0733	0.129	0.051 to 0.456	4.2	3.3 to 6.5	33	8 to 118	80
Saint-Jean	0.368	-0.10	0.001	0.63	< 0.001	0.111	0.048 to 0.378	4.5	3.6 to 7.1	40	10 to 142	94
de la Trinite	0.322	-0.07	0.003	0.34	< 0.001	0.063	0.039 to 0.139	4.2	3.2 to 6.5	66	23 to 167	128
Little Codroy	0.264	0.04	> 0.10	-0.21	> 0.10	0.084	0.051 to 0.177	3.7	2.7 to 5.0	45	16 to 92	74
Conne River	0.25	-0.01	> 0.10	0.42	< 0.001	0.099	0.046 to 0.345	5.9	5.2 to 7.0	60	15 to 149	108
Rocky	0.336	0.01	> 0.10	0.44	< 0.001	0.012	0.009 to 0.072	4.7	1.1 to 7.0	422	15 to 728	666
NE Trepassey	0.274	-0.02	> 0.10	0.07	> 0.10	0.011	0.008 to 0.094	4.9	2.7 to 6.8	444	29 to 856	716
Campbellton	0.272	-0.05	> 0.10	0.22	< 0.001	0.076	0.021 to 0.362	6.7	5.8 to 8.8	88	17 to 398	192
Western Arm Brook	0.295	0.01	> 0.10	0.10	< 0.001	0.063	0.04 to 0.133	5.9	5.1 to 6.8	94	40 to 163	156
Predicted-fluvial	0.316	na	na	na	na	0.053	0.003 to 0.301	4.0	1.1 to 8.0	73	9 to 1,230	260
Predicted-lacustrine								5.8	1.5 to 10.1	99	12 to 1,711	352

Nburnin <- 100000; Niter <- 50000; Thin <- 10; Nchains <- 2; DIC = 4551

Table 6. Hierarchical Bayesian fits of Ricker model, with lacustrine habitat as covariate on Rmax and age of smolts as covariate on delta.

River	Sigma (median)	Serial trend in residuals value	Serial trend in residuals p-value	Lag 1 autocorrelation value	Lag 1 autocorrelation P-value	Alpha median	Alpha S_{lim}	R_{max} median	R_{max} 5-95th	$S_{0.5Rmax}$ (eggs per 100 m²) median	$S_{0.5Rmax}$ (eggs per 100 m²) 5-95th	S_{LRP}
Nashwaak	0.466	0.13	>0.10	0.42	< 0.001	0.007	0.005 to 0.009	4.1	2.6 to 5.8	383	225 to 579	648
Big Salmon	0.337	0.67	0.070	0.47	>0.10	0.004	0.002 to 0.007	4.4	3.7 to 6.3	734	394 to 1,554	1,154
Pollett	0.450	0.02	>0.10	-0.54	0.027	0.023	0.016 to 0.031	4.3	3.6 to 6.0	122	87 to 192	200
LaHave	0.36	-0.01	>0.10	-0.01	>0.10	0.011	0.009 to 0.013	4.1	2.8 to 5.9	243	154 to 360	360
Margaree	0.282	0.10	>0.10	0.02	>0.10	0.010	0.007 to 0.017	4.2	3.6 to 5.9	270	145 to 510	390
Kedgwick	0.390	0.33	>0.10	-0.23	0.068	0.064	0.030 to 0.131	4.1	3.3 to 5.2	38	21 to 98	68
Saint-Jean	0.387	-0.10	< 0.001	0.63	< 0.001	0.043	0.031 to 0.064	4.2	3.6 to 5.5	60	38 to 105	96
de la Trinite	0.336	-0.05	0.014	0.29	< 0.001	0.034	0.027 to 0.044	4.0	3.1 to 5.3	76	47 to 115	110
Little Codroy	0.332	0.17	>0.10	-0.20	>0.10	0.043	0.030 to 0.061	4.0	3.1 to 4.9	58	38 to 94	86
Conne River	0.278	-0.01	>0.10	0.27	< 0.001	0.026	0.020 to 0.032	6.1	5.4 to 6.8	149	118 to 199	198
Rocky	0.363	-0.00	>0.10	0.41	< 0.001	0.009	0.008 to 0.013	6.2	1.4 to 7.6	429	71 to 565	648
NE Trepassey	0.296	0.00	>0.10	-0.06	>0.10	0.006	0.005 to 0.009	6.1	3.1 to 7.4	619	225 to 815	812
Campbellton	0.278	-0.04	>0.10	0.21	< 0.001	0.013	0.010 to 0.020	6.6	6.0 to 7.6	305	214 to 468	420
Western Arm Brook	0.344	-0.00	>0.10	0.05	>0.10	0.022	0.018 to 0.025	6.5	6.0 to 7.1	189	164 to 222	264
predicted	0.343	-	-	-	-	-	-	-	-	-	-	-
pred-age2	-	-	-	-	-	0.014	0.001 to 0.077	-	-	-	-	-
pred-age3	-	-	-	-	-	0.018	0.002 to 0.082	-	-	-	-	-
pred-age4	-	-	-	-	-	0.024	0.003 to 0.110	-	-	-	-	-
pred-fluv	-	-	-	-	-	-	-	4.2	3.0 to 6.0	-	-	-
pred-lac	-	-	-	-	-	-	-	6.3	3.8 to 8.1	-	-	-
pred-fluv-age2	-	-	-	-	-	-	-	-	-	194	32 to 2,336	610 (0.35) [1]
pred-fluv-age3	-	-	-	-	-	-	-	-	-	147	30 to 1,149	488 (0.29) [1]
pred-fluv-age4	-	-	-	-	-	-	-	-	-	111	22 to 1,086	346 (0.31) [1]
pred-lac-age2	-	-	-	-	-	-	-	-	-	280	45 to 3,460	858 (0.35) [1]
pred-lac-age3	-	-	-	-	-	-	-	-	-	214	43 to 1,661	704 (0.29) [1]
pred-lac-age4	-	-	-	-	-	-	-	-	-	162	31 to 1,595	548 (0.31) [1]

[1] The predicted S_{LRP} values shown are the egg deposition values corresponding to the lowest probability that recruitment would be < 50%Rmax and the values in parentheses are the corresponding probabilities

Nburnin <- 100000; Niter <- 50000; Thin <- 10; Nchains <- 2; DIC = 4636

Table 7. Hierarchical Bayesian fits of Beverton-Holt model, with lacustrine habitat as covariate on Rmax and age of smolts as covariate on delta.

River	Sigma (median)	Serial trend in residuals value	Serial trend in residuals p-value	Lag 1 autocorrelation value	Lag 1 autocorrelation P-value	Alpha median	Alpha 5-95th	R_{max} median	R_{max} 5-95th	$S_{0.5Rmax}$ (eggs per 100 m²) median	$S_{0.5Rmax}$ (eggs per 100 m²) 5-95th	S_{LRP}
Nashwaak	0.432	0.14	> 0.10	0.38	> 0.10	0.008	0.006 to 0.069	3.7	0.3 to 5.4	480	4 to 814	826
Big Salmon	0.322	0.67	0.071	0.37	< 0.001	0.05	0.006 to 0.392	4.4	3.5 to 6.3	88	10 to 953	284
Pollett	0.386	0.02	> 0.10	-0.36	0.045	0.045	0.026 to 0.107	4.1	2.8 to 6.0	91	29 to 206	192
LaHave	0.342	-0.01	> 0.10	-0.05	> 0.10	0.012	0.010 to 0.069	3.8	0.7 to 6.0	310	10 to 545	496
Margaree	0.271	0.10	> 0.10	-0.02	> 0.10	0.044	0.012 to 0.348	4.2	3.4 to 6.5	94	11 to 520	236
Kedgwick	0.371	0.34	> 0.10	-0.23	0.076	0.145	0.054 to 0.550	4.2	3.3 to 6.2	29	7 to 105	74
Saint-Jean	0.368	-0.10	< 0.001	0.63	< 0.001	0.132	0.055 to 0.485	4.3	3.6 to 6.3	33	8 to 112	82
de la Trinite	0.323	-0.05	0.015	0.34	< 0.001	0.065	0.039 to 0.148	4.1	3.1 to 6.3	64	22 to 154	124
Little Codroy	0.265	0.18	> 0.10	-0.21	> 0.10	0.083	0.050 to 0.177	3.7	2.7 to 5.0	45	16 to 93	74
Conne River	0.251	-0.01	> 0.10	0.41	< 0.001	0.115	0.050 to 0.460	5.8	5.1 to 6.8	50	12 to 131	92
Rocky	0.334	-0.01	> 0.10	0.45	< 0.001	0.011	0.009 to 0.096	4.9	1.0 to 6.8	439	11 to 708	620
NE Trepassey	0.276	0.00	> 0.10	0.11	> 0.10	0.011	0.008 to 0.210	4.9	2.6 to 6.8	439	13 to 850	650
Campbellton	0.272	-0.04	> 0.10	0.22	< 0.001	0.104	0.026 to 0.509	6.5	5.6 to 8.2	62	12 to 306	148
Western Arm Brook	0.297	-0.01	> 0.10	0.09	< 0.001	0.071	0.043 to 0.210	5.8	5.0 to 6.6	82	24 to 152	140
predicted	0.316	-	-	-	-	-	-	-	-	-	-	-
pred-age2	-	-	-	-	-	0.032	0.000 to 0.330	-	-	-	-	-
pred-age3	-	-	-	-	-	0.063	0.004 to 0.386	-	-	-	-	-
pred-age4	-	-	-	-	-	0.105	0.006 to 0.530	-	-	-	-	-
pred-fluv	-	-	-	-	-	-	-	4.0	1.2 to 7.4	-	-	-
pred-lac	-	-	-	-	-	-	-	5.7	1.5 to 9.1	-	-	-
pred-fluv-age2	-	-	-	-	-	-	-	-	-	122	9 to 8,527	570
pred-fluv-age3	-	-	-	-	-	-	-	-	-	62	7 to 1,025	218
pred-fluv-age4	-	-	-	-	-	-	-	-	-	37	5 to 674	126
pred-lac-age2	-	-	-	-	-	-	-	-	-	161	12 to 10,564	730
pred-lac-age3	-	-	-	-	-	-	-	-	-	81	10 to 1,367	288
pred-lac-age4	-	-	-	-	-	-	-	-	-	48	7 to 1,060	168

Nburnin <- 100000; Niter <- 50000; Thin <- 10; Nchains <- 2; DIC = 4550

Table 8. Hierarchical Bayesian fits of Ricker model, with lacustrine habitat as covariate on Rmax and proportion MSW eggs as covariate on delta.

River	Sigma (median)	Serial trend in residuals value	Serial trend in residuals p-value	Lag 1 autocorrelation value	Lag 1 autocorrelation P-value	Alpha median	Alpha HalfRmax	R_{max} median	R_{max} 5-95th	$S_{0.5Rmax}$ (eggs per 100 m²) median	$S_{0.5Rmax}$ (eggs per 100 m²) 5-95th	S_{LRP}
Nashwaak	0.462					0.007	0.006 to 0.009	4.1	2.9 to 5.3	375	244 to 539	620
Big Salmon	0.34					0.004	0.002 to 0.007	4.3	3.6 to 5.8	715	398 to 1,439	1,128
Pollett	0.447					0.022	0.016 to 0.031	4.3	3.6 to 5.7	121	87 to 185	198
LaHave	0.361					0.011	0.009 to 0.013	4.1	3 to 5.5	237	165 to 338	352
Margaree	0.291					0.011	0.007 to 0.021	4.1	3.5 to 5.4	236	122 to 431	348
Kedgwick	0.386					0.071	0.033 to 0.132	4	3.3 to 4.9	34	20 to 85	60
Saint-Jean	0.385					0.045	0.032 to 0.068	4.1	3.6 to 5.2	58	36 to 96	90
de la Trinite	0.337					0.034	0.028 to 0.045	4	3.1 to 5	74	46 to 106	106
Little Codroy	0.331					0.043	0.031 to 0.061	4	3.2 to 4.8	57	38 to 90	84
Conne River	0.28					0.025	0.02 to 0.032	6.1	5.4 to 6.8	151	119 to 206	204
Rocky	0.364					0.009	0.008 to 0.011	6.2	3.1 to 7.6	432	205 to 564	634
NE Trepassey	0.298					0.006	0.005 to 0.008	6.2	3.4 to 7.4	627	269 to 818	828
Campbellton	0.281					0.013	0.009 to 0.019	6.6	5.9 to 7.6	313	222 to 477	428
Western Arm Brook	0.345					0.021	0.018 to 0.025	6.5	5.9 to 7.1	190	165 to 222	264
predicted	0.345	-	-	-	-	-	-	-	-	-	-	-
pMSW-0.1	-	-	-	-	-	0.013	0.002 to 0.057	-	-	-	-	-
pMSW-0.5	-	-	-	-	-	0.019	0.003 to 0.078	-	-	-	-	-
MSW-0.9	-	-	-	-	-	0.029	0.005 to 0.103	-	-	-	-	-
fluv	-	-	-	-	-	-	-	4.1	3.1 to 5.6	-	-	-
lac	-	-	-	-	-	-	-	6.3	4.3 to 7.9	-	-	-
fluv-MSW-0.1	-	-	-	-	-	-	-	-	-	205	43 to 1520	628 (0.30) [1]
fluv- pMSW-0.5	-	-	-	-	-	-	-	-	-	134	32 to 820	460 (0.25) [1]
fluv- pMSW-0.9	-	-	-	-	-	-	-	-	-	91	24 to 505	238
lac- pMSW-0.1	-	-	-	-	-	-	-	-	-	304	64 to 2279	1,038 (0.30) [1]
lac- pMSW-0.5	-	-	-	-	-	-	-	-	-	201	47 to 1170	638 (0.25) [1]
lac- pMSW-0.9	-	-	-	-	-	-	-	-	-	134	35 to 752	350 (0.25) [1]

[1] The predicted S_{LRP} values shown are the egg deposition values corresponding to the lowest probability that recruitment would be < 50%Rmax and the values in parentheses are the corresponding probabilities

Nburnin <- 100000; Niter <- 50000; Thin <- 10; Nchains <- 2; DIC = 4638

Table 9. Hierarchical Bayesian fits of Beverton-Holt model, with lacustrine habitat as covariate on Rmax and proportion MSW eggs as covariate on delta.

River	Sigma (median)	Serial trend in residuals value	Serial trend in residuals p-value	Lag 1 autocorrelation value	Lag 1 autocorrelation P-value	Alpha median	Alpha 5-95[th]	R_{max} median	R_{max} 5-95th	$S_{0.5Rmax}$ (eggs per 100 m²) median	$S_{0.5Rmax}$ (eggs per 100 m²) 5-95th	S_{LRP}
Nashwaak	0.432	0.08	> 0.10	0.38	> 0.10	0.008	0.006 to 0.083	3.6	0.3 to 4.9	476	4 to 752	830
Big Salmon	0.325	0.79	0.084	0.40	< 0.001	0.054	0.007 to 0.364	4.2	3.4 to 5.7	78	11 to 659	252
Pollett	0.386	0.12	> 0.10	-0.36	0.045	0.047	0.028 to 0.105	4.0	2.8 to 5.5	84	30 to 173	176
LaHave	0.344	-0.01	> 0.10	-0.05	> 0.10	0.013	0.01 to 0.092	3.7	0.6 to 5.1	296	7 to 461	476
Margaree	0.276	0.19	> 0.10	-0.01	> 0.10	0.079	0.016 to 0.411	4.0	3.3 to 5.2	49	9 to 313	140
Kedgwick	0.369	0.35	> 0.10	-0.24	0.069	0.171	0.063 to 0.576	4.1	3.2 to 5.7	23	7 to 82	58
Saint-Jean	0.369	-0.10	0.001	0.62	< 0.001	0.152	0.06 to 0.524	4.2	3.5 to 5.9	27	7 to 96	68
de la Trinite	0.324	-0.07	0.002	0.35	< 0.001	0.071	0.043 to 0.175	4.0	3.1 to 5.5	56	18 to 123	106
Little Codroy	0.262	0.02	> 0.10	-0.21	> 0.10	0.087	0.054 to 0.182	3.7	2.7 to 4.7	42	16 to 81	68
Conne River	0.252	-0.00	> 0.10	0.42	< 0.001	0.096	0.043 to 0.383	5.9	5.2 to 7.1	62	14 to 161	112
Rocky	0.336	0.01	> 0.10	0.44	< 0.001	0.011	0.009 to 0.053	5.4	1.1 to 7.1	499	21 to 743	732
NE Trepassey	0.274	-0.02	> 0.10	0.06	> 0.10	0.01	0.008 to 0.068	5.4	2.8 to 7.1	536	42 to 900	782
Campbellton	0.271	-0.05	> 0.10	0.22	< 0.001	0.078	0.022 to 0.431	6.6	5.7 to 8.7	84	14 to 384	198
Western Arm Brook	0.296	0.01	> 0.10	0.11	< 0.001	0.061	0.039 to 0.127	6.0	5.2 to 6.9	98	42 to 169	164
predicted	0.317	-	-	-	-	-	-	-	-	-	-	-
pMSW-0.1	-	-	-	-	-	0.045	0.002 to 0.326	-	-	-	-	-
pMSW-0.5	-	-	-	-	-	0.065	0.004 to 0.376	-	-	-	-	-
MSW-0.9	-	-	-	-	-	0.088	0.006 to 0.434	-	-	-	-	-
fluv	-	-	-	-	-	-	-	3.9	1.3 to 6.5	-	-	-
lac	-	-	-	-	-	-	-	5.9	1.9 to 9.5	-	-	-
fluv-MSW-0.1	-	-	-	-	-	-	-	-	-	84	9 to 2,081	318
fluv- pMSW-0.5	-	-	-	-	-	-	-	-	-	58	8 to 926	204
fluv- pMSW-0.9	-	-	-	-	-	-	-	-	-	43	6 to 703	146
lac- pMSW-0.1	-	-	-	-	-	-	-	-	-	125	13 to 3,203	474
lac- pMSW-0.5	-	-	-	-	-	-	-	-	-	84	11 to 1,393	292
lac- pMSW-0.9	-	-	-	-	-	-	-	-	-	63	10 to 1,008	208

Nburnin <- 100000; Niter <- 50000; Thin <- 10; Nchains <- 2; DIC = 4566

Table 10. Summary statistics of the posterior distributions of the hyper-parameters from the Ricker hierarchical model fits, without and with covariates. Median and 5th to 95th percentile ranges are shown.

Parameters	No covariates	Lacustrine habitat as covariate on R_{max}		Lacustrine habitat as covariate on R_{max} and age of smolts as covariate on δ		Lacustrine habitat as covariate on R_{max} and proportion MSW as covariate on δ	
δ	4.05 (2.64 to 5.89)	4.06 (2.58 to 5.91)		age-2	4.29 (2.56 to 6.76)	p_{msw} = 0.1	4.36 (2.87 to 6.35)
				age-3	4.01 (2.50 to 6.05)	p_{msw} = 0.5	3.94 (2.55 to 5.70)
				age-4	3.75 (2.20 to 5.98)	p_{msw} = 0.9	3.55 (2.27 to 5.24)
alpha	0.017 (0.003 to 0.071)	0.017 (0.003 to 0.076)		age-2	0.014 (0.001 to 0.077)	p_{msw} = 0.1	0.013 (0.002 to 0.057)
				age-3	0.018 (0.002 to 0.082)	p_{msw} = 0.5	0.019 (0.003 to 0.078)
				age-4	0.024 (0.003 to 0.110)	p_{msw} = 0.9	0.029 (0.005 to 0.103)
R_{max}	4.9 (2.1 to 8.4)	Lac = 0	4.2 (3.1 to 5.8)	Lac = 0	4.2 (3.0 to 6.0)	Lac = 0	4.1 (3.1 to 5.6)
		Lac = 1	6.3 (4.2 to 8.0)	Lac = 1	6.3 (3.8 to 8.1)	Lac = 1	6.3 (4.3 to 7.9)
α_{lac}			1.44 (1.29 to 1.70)		1.44 (1.29 to 1.68)		1.42 (1.28 to 1.61)
β_{lac}			0.40 (0.03 to 0.60)		0.40 (0.01 to 0.60)		0.42 (0.12 to 0.61)
α_{age}					1.41 (1.30 to 1.53)		
β_{age}					-0.07 (-0.29 to 0.15)		
α_{pmsw}							1.41 (1.30 to 1.51)
β_{pmsw}							-0.26 (-0.55 to 0.02)
$S_{0.5Rmax}$	173 (33 to 1,166)	Lac = 0	153 (32 to 1,023)	Lac = 0; age = 2	194 (32 to 2,336)	Lac = 0; pmsw = 0.1	205 (43 to 1520)
				Lac = 0; age = 3	147 (30 to 1,149)	Lac = 0; pmsw = 0.5	134 (32 to 820)
				Lac = 0; age = 4	111 (22 to 1,086)	Lac = 0; pmsw = 0.9	91 (24 to 505)
		Lac = 1	222 (47 to 1,497)	Lac = 1; age = 2	280 (45 to 3,460)	Lac = 1; pmsw = 0.1	304 (64 to 2279)
				Lac = 1; age = 3	214 (43 to 1,661)	Lac = 1; pmsw = 0.5	201 (47 to 1170)
				Lac = 1; age = 4	162 (31 to 1,595)	Lac = 1; pmsw = 0.9	134 (35 to 752)
S_{LRP}[1]	596 (0.29)	Lac = 0	508 (0.27)	Lac = 0; age = 2	610 (0.35)	Lac = 0; pmsw = 0.1	628 (0.30)
				Lac = 0; age = 3	488 (0.29)	Lac = 0; pmsw = 0.5	460 (0.25)
				Lac = 0; age = 4	346 (0.31)	Lac = 0; pmsw = 0.9	238
		Lac = 1	762 (0.27)	Lac = 1; age = 2	858 (0.35)	Lac = 1; pmsw = 0.1	1,038 (0.30)
				Lac = 1; age = 3	704 (0.29)	Lac = 1; pmsw = 0.5	638 (0.25)
				Lac = 1; age = 4	548 (0.31)	Lac = 1; pmsw = 0.9	350
DIC	4629	4638		4636		4638	

[1]For S_{LRP}, the values in parentheses are the minimum probabilities of recruitment being less than 50%Rmax.

Table 11. Summary statistics of the posterior distributions of the predicted values of the parameters and the reference values of interest.from the Beverton-Holt hierarchical model fits, without and with covariates. Median and 5th to 95th percentile ranges are shown.

Parameters	No covariates	Lacustrine habitat as covariate on R_{max}		Lacustrine habitat as covariate on R_{max} and Age of smolts as covariate on δ		Lacustrine habitat as covariate on R_{max} and Prop. MSW as covariate on δ	
δ	2.94 (1.37 to 5.29)	2.96 (1.16 to 5.62)		age-2	3.45 (1.11 to 7.62)	p_{msw} = 0.1	3.10 (1.12 to 6.28)
				age-3	2.77 (0.95 to 5.47)	p_{msw} = 0.5	2.73 (0.98 to 5.44)
				age-4	2.25 (0.645 to 5.16)	p_{msw} = 0.9	2.43 (0.84 to 5.14)
alpha	0.053 (0.005 to 0.253)	0.052 (0.004 to 0.312)		age-2	0.032 (0.000 to 0.330)	p_{msw} = 0.1	0.045 (0.002 to 0.326)
				age-3	0.063 (0.004 to 0.386)	p_{msw} = 0.5	0.065 (0.004 to 0.376)
				age-4	0.105 (0.006 to 0.530)	p_{msw} = 0.9	0.088 (0.006 to 0.434)
R_{max}	4.4 (1.1 to 9.1)	Lac = 0	4.0 (1.3 to 6.6)	Lac = 0	4.0 (1.2 to 7.4)	Lac = 0	3.9 (1.3 to 6.5)
		Lac = 1	5.9 (2.1 to 10.2)	Lac = 1	5.7 (1.5 to 9.1)	Lac = 1	5.9 (1.9 to 9.5)
α_{lac}		1.41 (1.06 to 1.73)		1.41 (1.07 to 1.73)		1.37 (1.05 to 1.62)	
β_{lac}		0.35 (-0.21 to 0.78)		0.32 (-0.26 to 0.70)		0.40 (-0.07 to 0.77)	
α_{age}					1.10 (0.79 to 1.34)		
β_{age}					-0.21 (-0.70 to 0.22)		
α_{pmsw}							1.09 (0.81 to 1.32)
β_{pmsw}							-0.32 (-0.86 to 0.31)
$S_{0.5Rmax}$	78 (10 to 976)	Lac = 0	76 (9 to 1,176)	Lac = 0; age = 2	122 (9 to 8,527)	Lac = 0; pmsw = 0.1	84 (9 to 2081)
				Lac = 0; age = 3	62 (7 to 1,025)	Lac = 0; pmsw = 0.5	58 (8 to 926)
				Lac = 0; age = 4	37 (5 to 674)	Lac = 0; pmsw = 0.9	43 (6 to 703)
		Lac = 1	112 (14 to 1,594)	Lac = 1; age = 2	161 (12 to 10,564)	Lac = 1; pmsw = 0.1	125 (13 to 3,203)
				Lac = 1; age = 3	81 (10 to 1,367)	Lac = 1; pmsw = 0.3	84 (11 to 1,393)
				Lac = 1; age = 4	48 (7 to 1,060)	Lac = 1; pmsw = 0.5	63 (10 to 1,008)
S_{LRP}	252	Lac = 0	260	Lac = 0; age = 2	570	Lac = 0; pmsw = 0.1	318
				Lac = 0; age = 3	218	Lac = 0; pmsw = 0.5	204
				Lac = 0; age = 4	126	Lac = 0; pmsw = 0.9	146
		Lac = 1	352	Lac = 1; age = 2	730	Lac = 1; pmsw = 0.1	474
				Lac = 1; age = 3	288	Lac = 1; pmsw = 0.3	292
				Lac = 1; age = 4	168	Lac = 1; pmsw = 0.5	208
DIC	4533	4551		4550		4566	

FIGURES

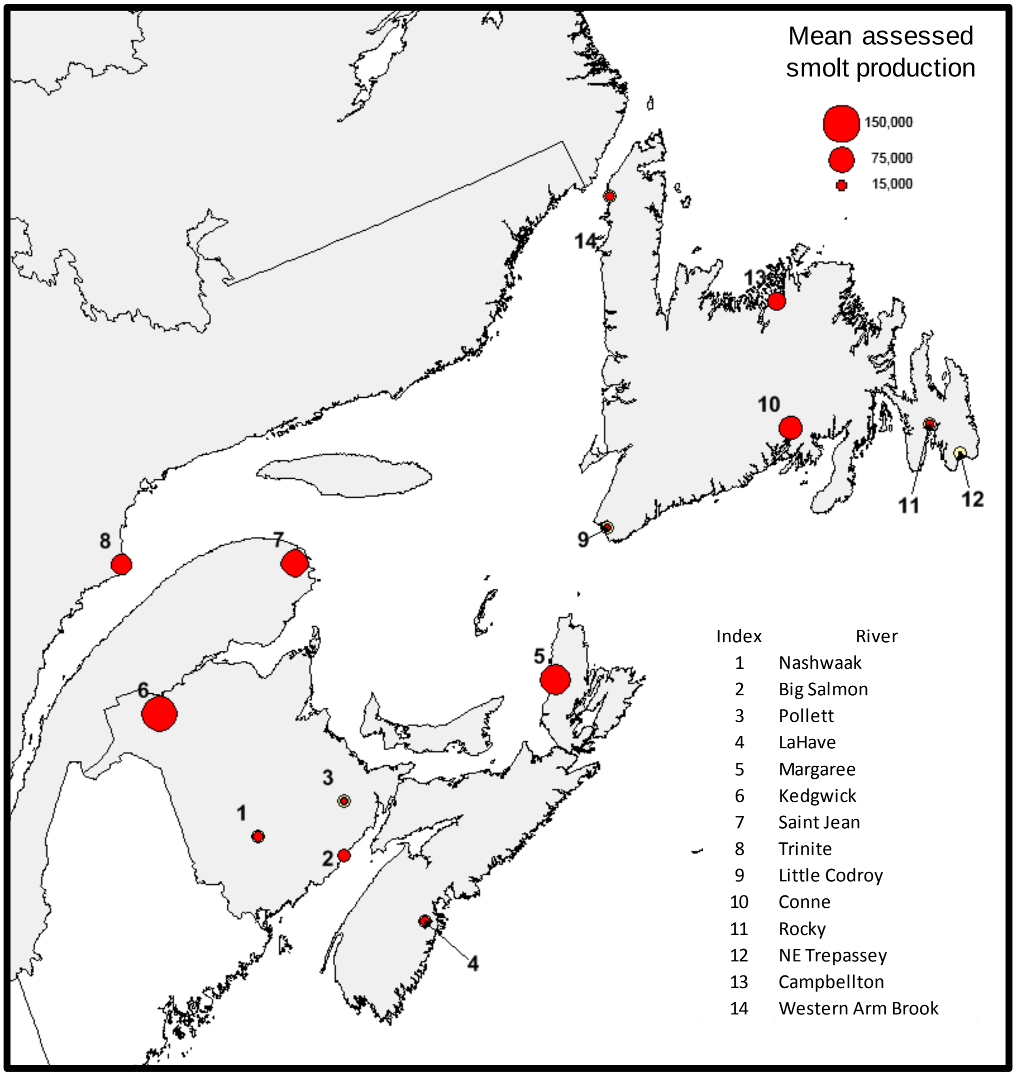


Figure 1. Geographic location and mean smolt production levels of the 14 rivers in the Atlantic salmon stock and recruitment time series analysis.

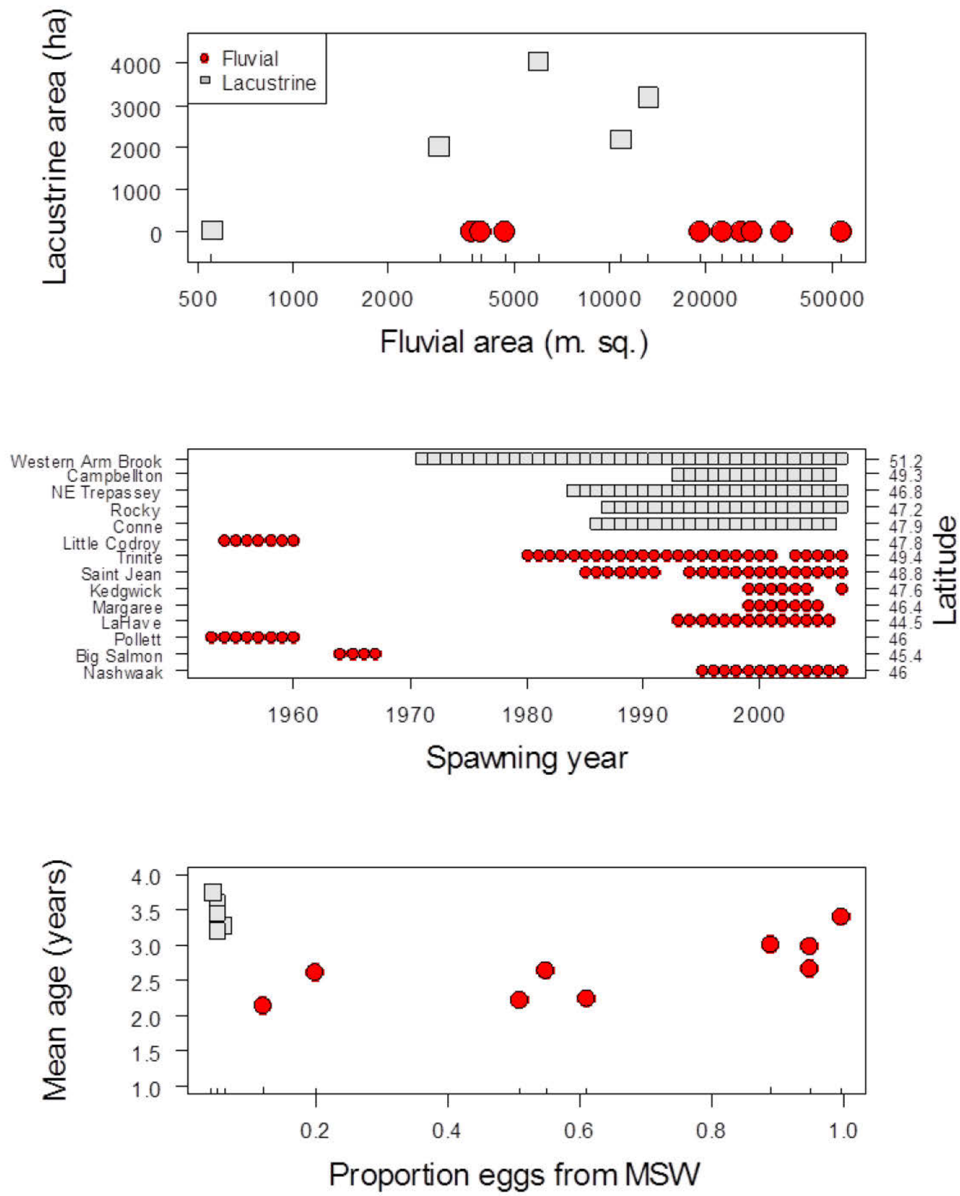


Figure 2 Summaries of the fluvial and lacustrine habitat areas of the rivers (upper panel), time series of available egg and smolt production estimates by year class (middle panel), and biological characteristics (lower panel) of the 14 Atlantic salmon populations in the analysis. Legend reference to fluvial and lacustrine refers to rivers with only fluvial habitat or rivers with both fluvial and lacustrine habitat available for production of Atlantic salmon smolts.

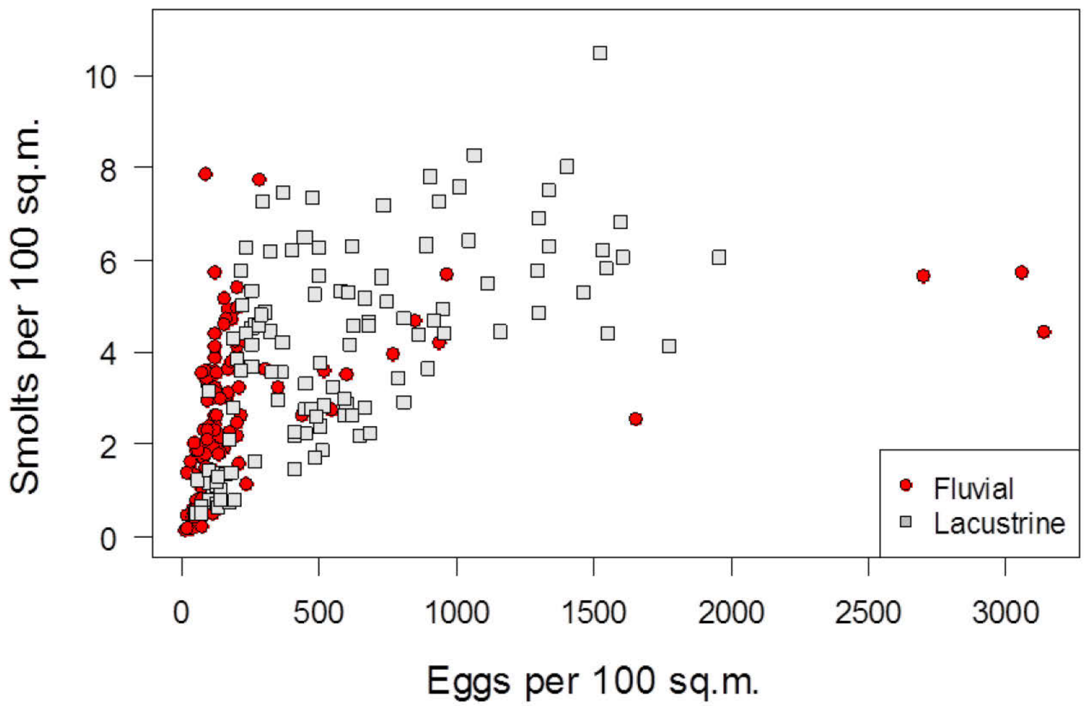


Figure 3. Eggs (per 100 m² of fluvial habitat area) to smolt (per 100 m² of fluvial habitat area) data from fourteen rivers of eastern Canada. Legend reference to fluvial and lacustrine refers to rivers with only fluvial habitat or rivers with both fluvial and lacustrine habitat available for production of Atlantic salmon smolts.

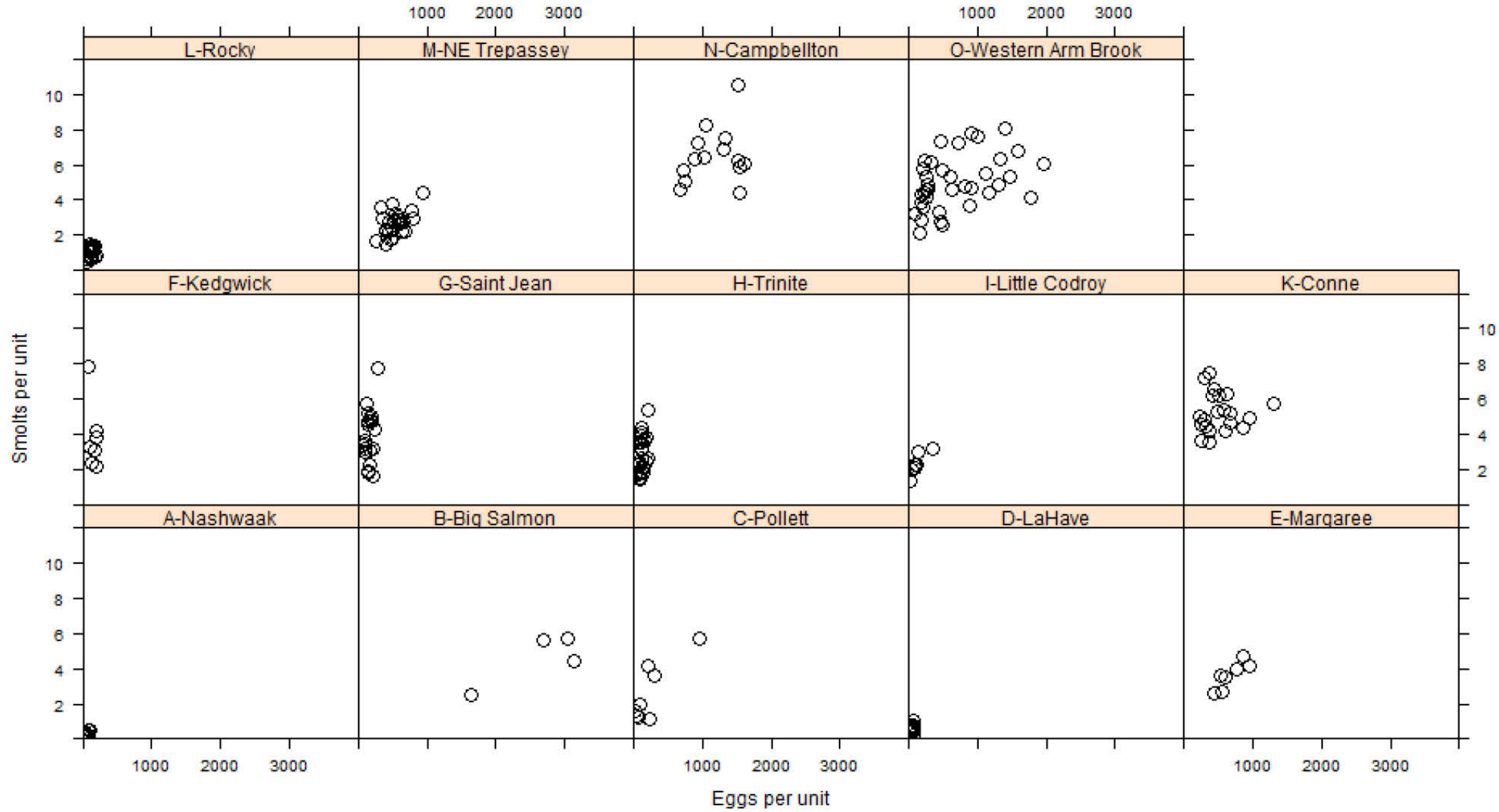


Figure 4. River-specific plots of egg to smolt relationships for 14 rivers of eastern Canada.

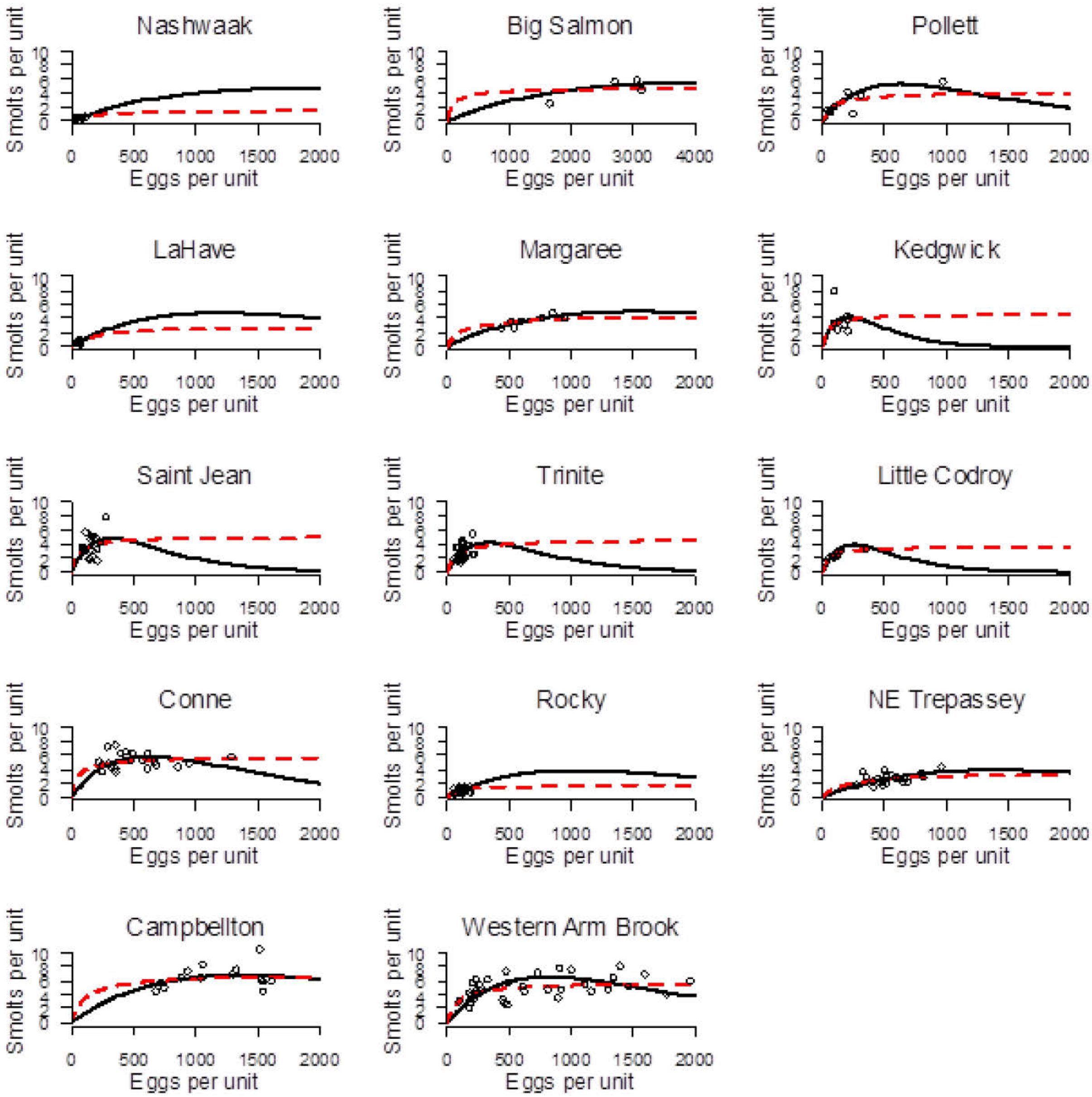


Figure 5. Hierarchical Bayesian fits of Ricker (solid black line) and Beverton-Holt (dashed red line) egg to smolt stock and recruitment relationships without covariates for 14 rivers of eastern Canada. The data are in densities per unit (100 m²) with eggs on the horizontal axis and smolts on the vertical axis. The lines shown are drawn using the median of the posterior distributions of the stock and recruitment parameters (delta, Rmax).

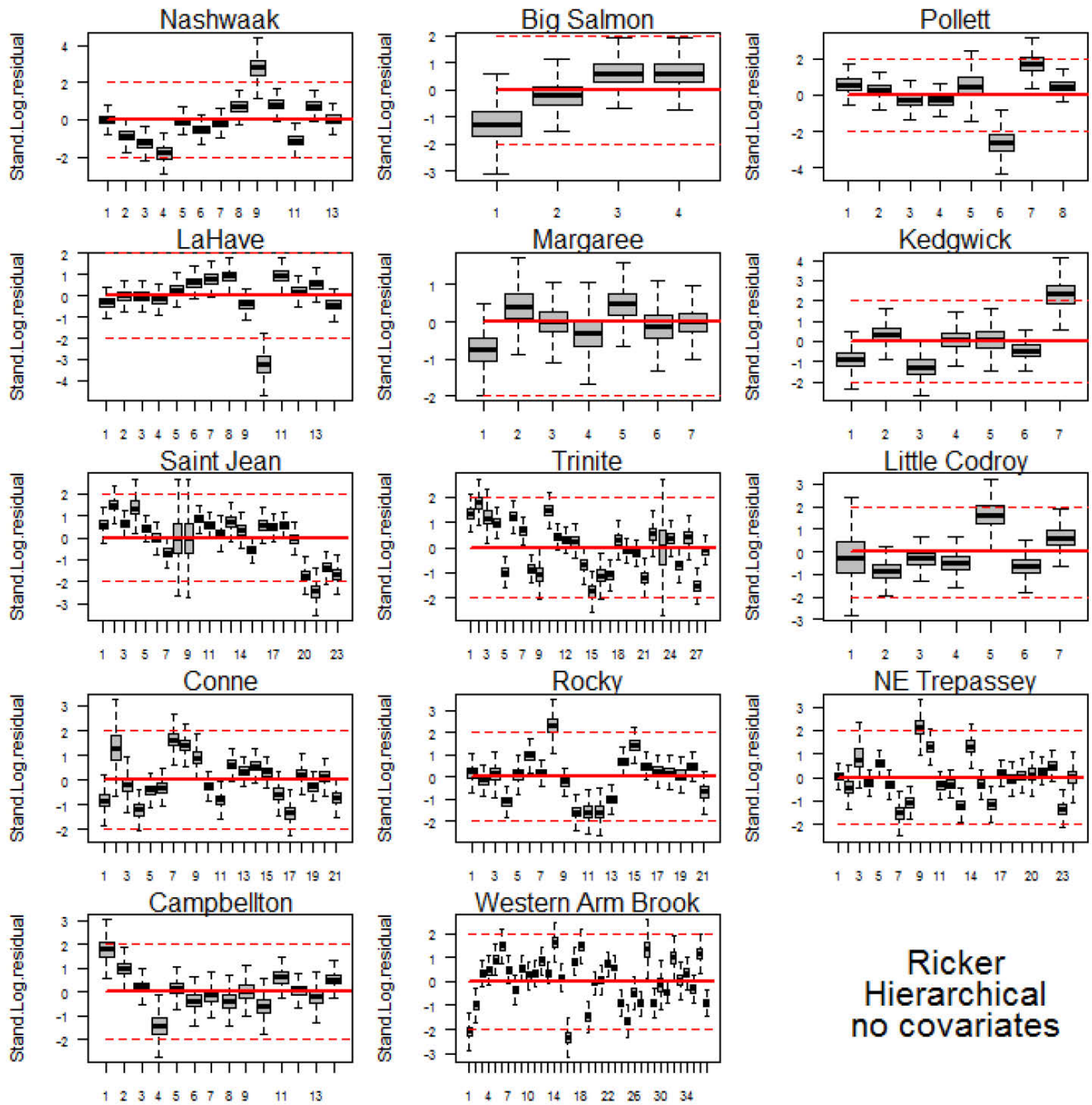


Figure 6. Standardized log residuals of the individual fits from the hierarchical Ricker model without covariates on Rmax and delta. The residuals are standardized by river specific sigma. Residuals that have the interquartile range outside the range of -2 to +2 could be considered outliers and are estimated for Nashwaak, Pollett, LaHave, Saint-Jean, Western Arm Brook rivers.

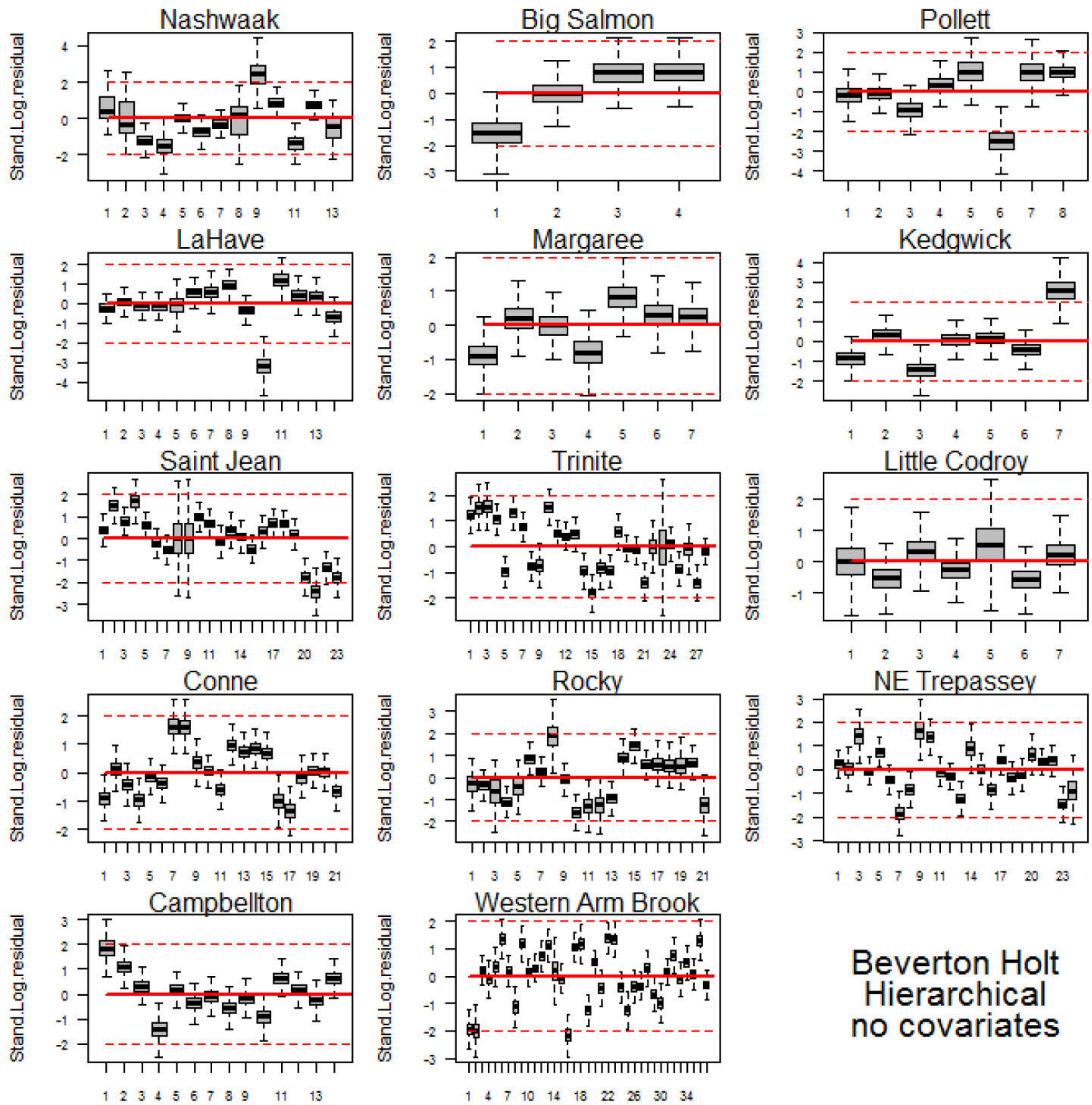


Figure 7. Standardized log residuals of the individual fits from the hierarchical Ricker model without covariates on Rmax and delta. The residuals are standardized by river specific sigma. Residuals that have the interquartile range outside the range of -2 to +2 could be considered outliers and are estimated for Pollett, LaHave, Kedgwick, and Saint-Jean rivers.

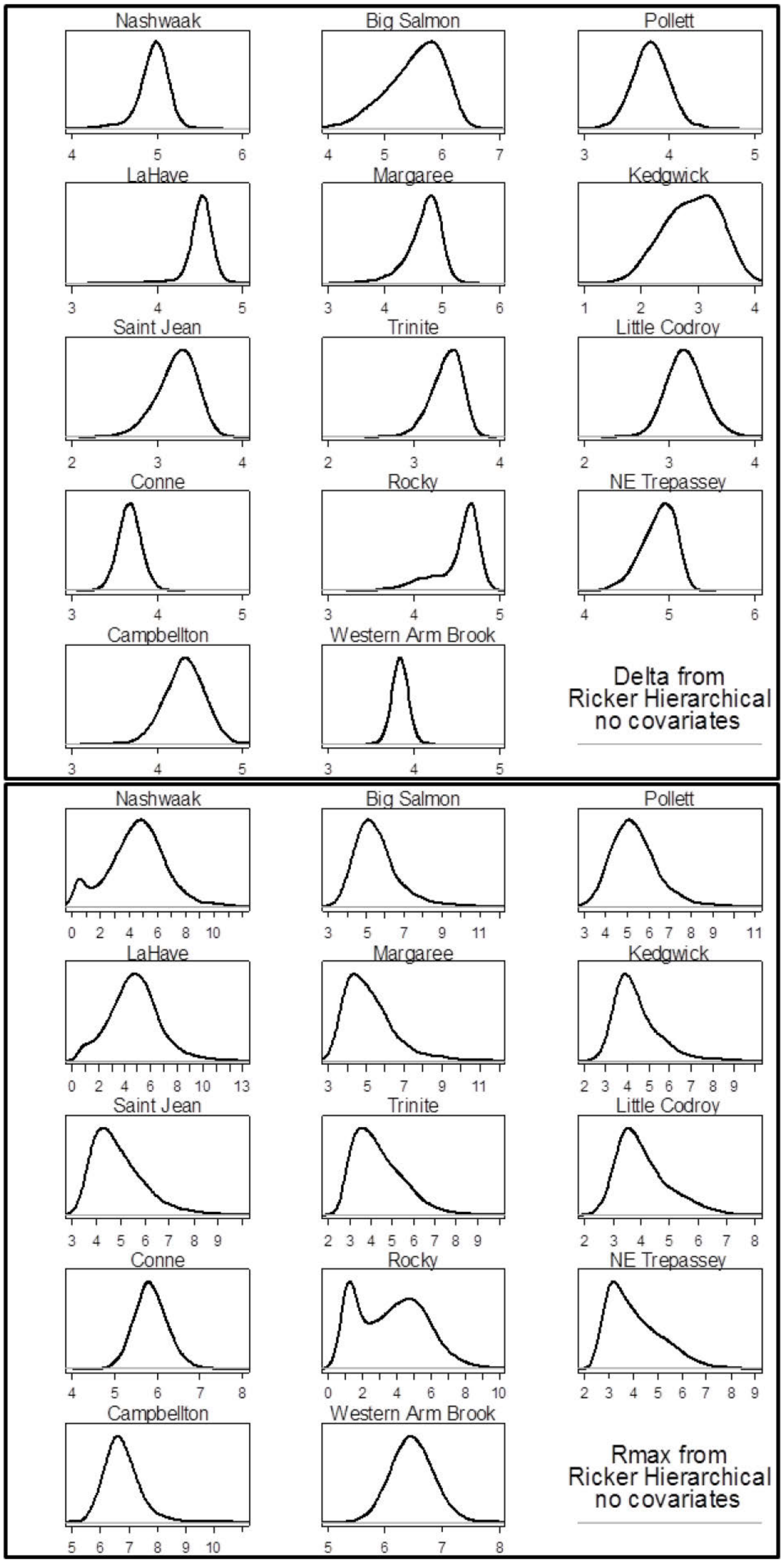


Figure 8. Posterior distributions of delta (upper panel) and Rmax (lower panel) from the Ricker hierarchical model without modifiying covariates.

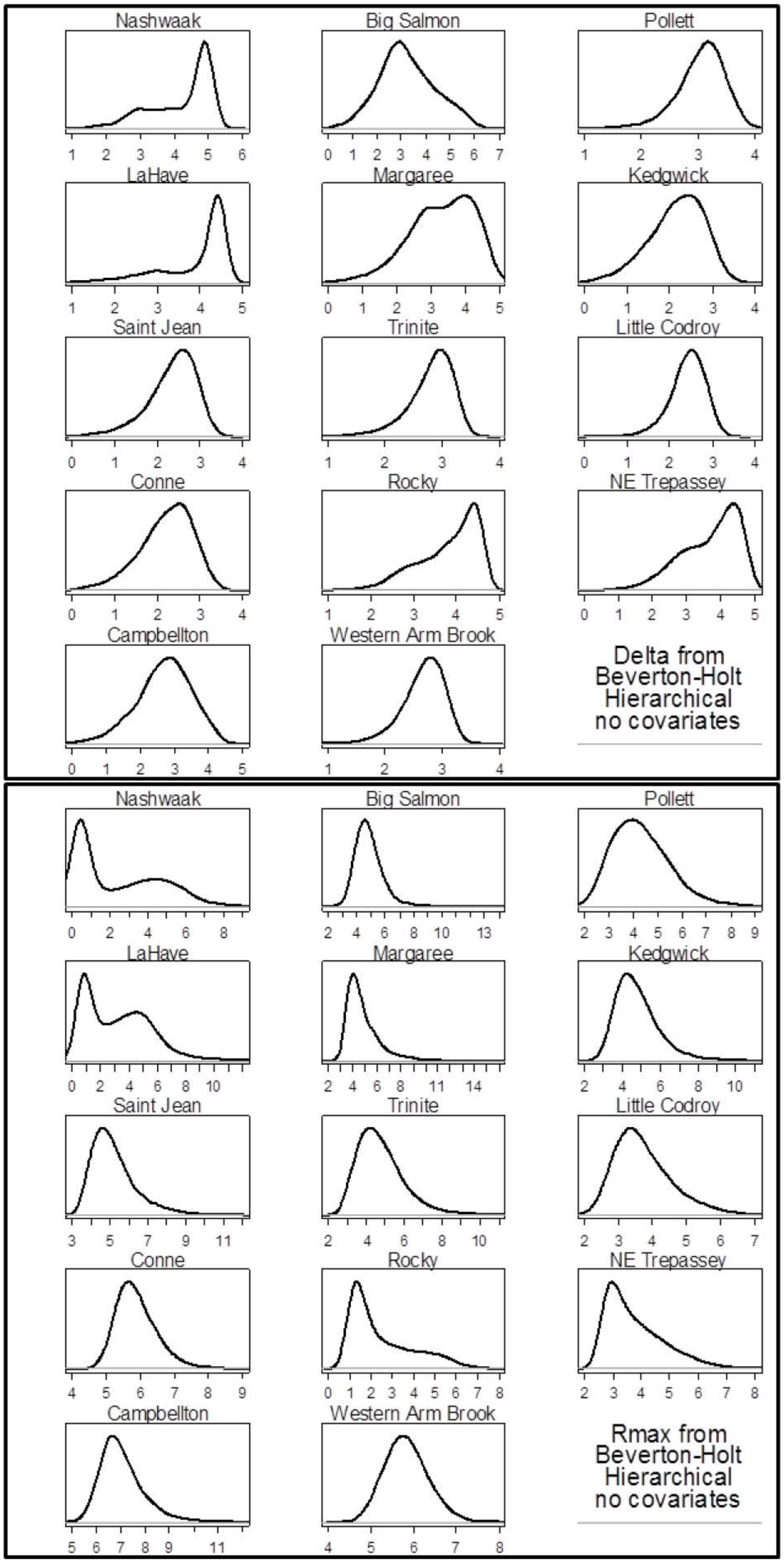


Figure 9. Posterior distributions of delta (upper panel) and Rmax (lower panel) from the Beverton-Holt hierarchical model without modifying covariates.

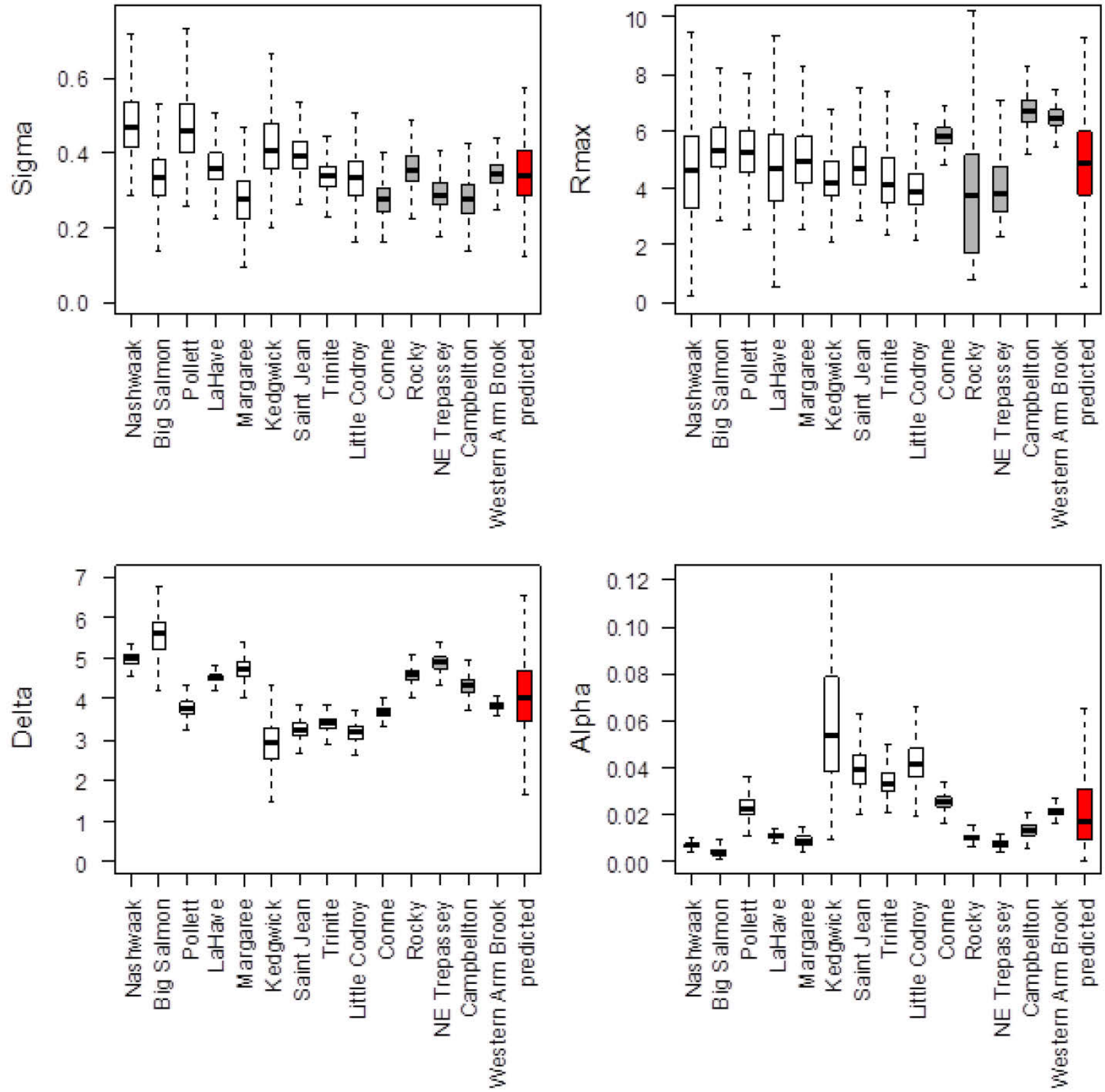


Figure 10. Boxplots of posterior distributions of the stock and recruitment parameters (sigma, Rmax, delta) from the hierarchical Ricker model without covariates. Rmax expressed as smolts per 100 m² of fluvial habitat and delta as the instantaneous mortality rate. Rivers with fluvial habitat only are in white shading and rivers with lacustrine habitat are in grey shading. The predicted values are in red shading. Alpha is the survival rate at the origin (maximum density independent survival rate) = exp(-delta).

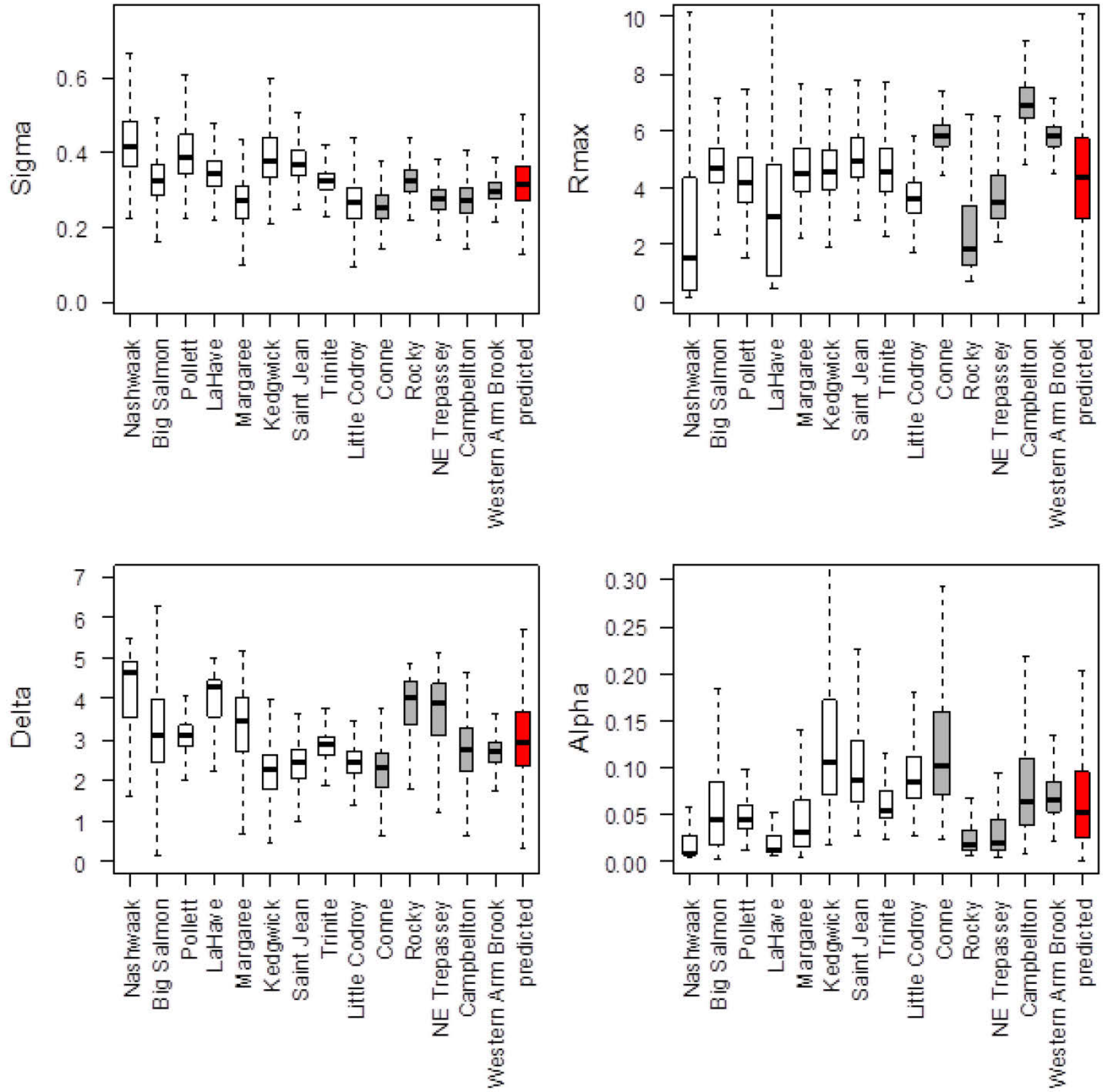


Figure 11. Boxplots of posterior distributions of the stock and recruitment parameters from the hierarchical Beverton-Holt model without covariates. Rmax expressed as smolts per 100 m² of fluvial habitat and delta as the instantaneous mortality rate. Rivers with fluvial habitat only are in white shading and rivers with lacustrine habitat are in grey shading. The predicted values are in red shading. Alpha is the survival rate at the origin (maximum density independent survival rate) = exp(-delta).

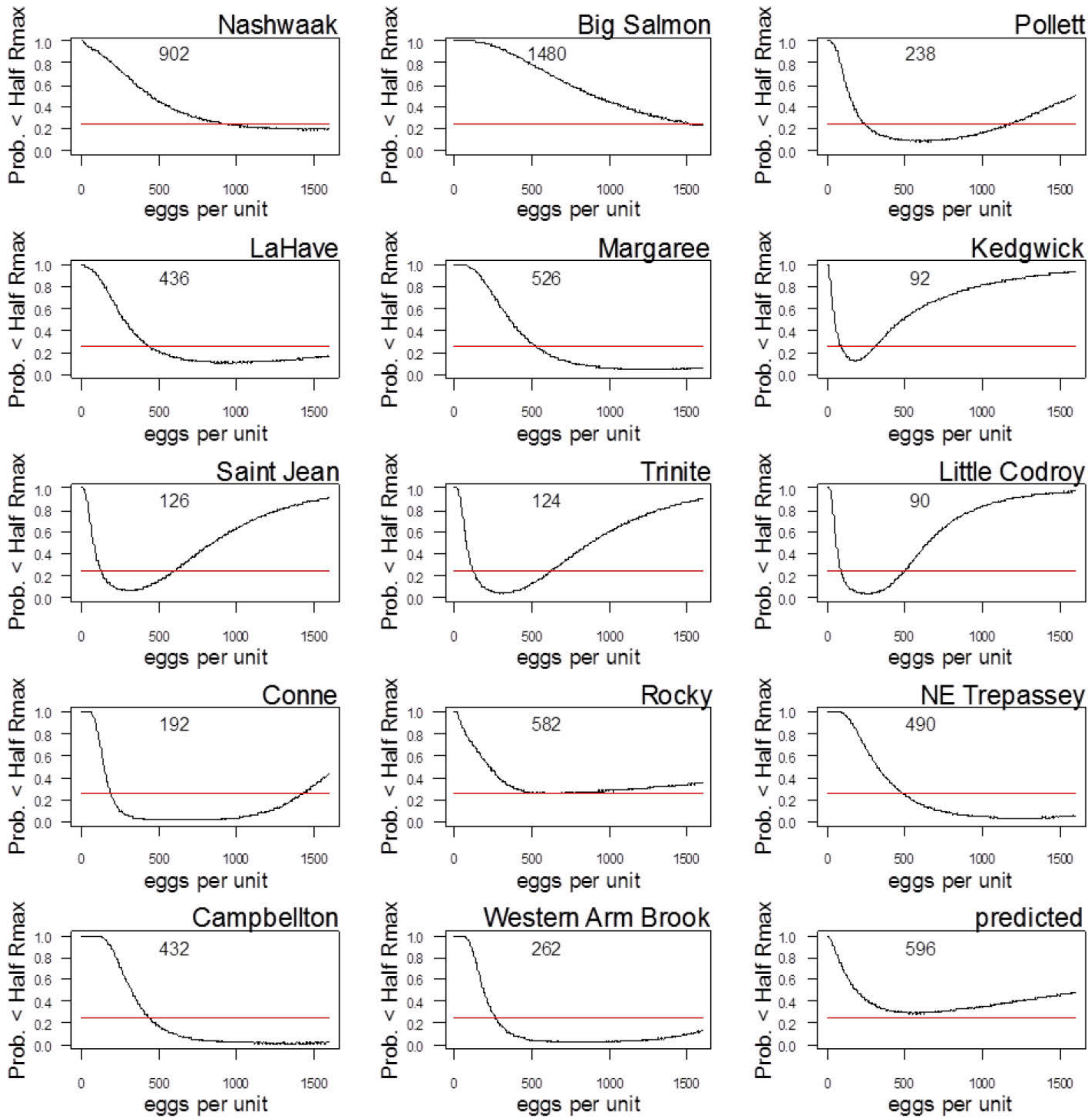
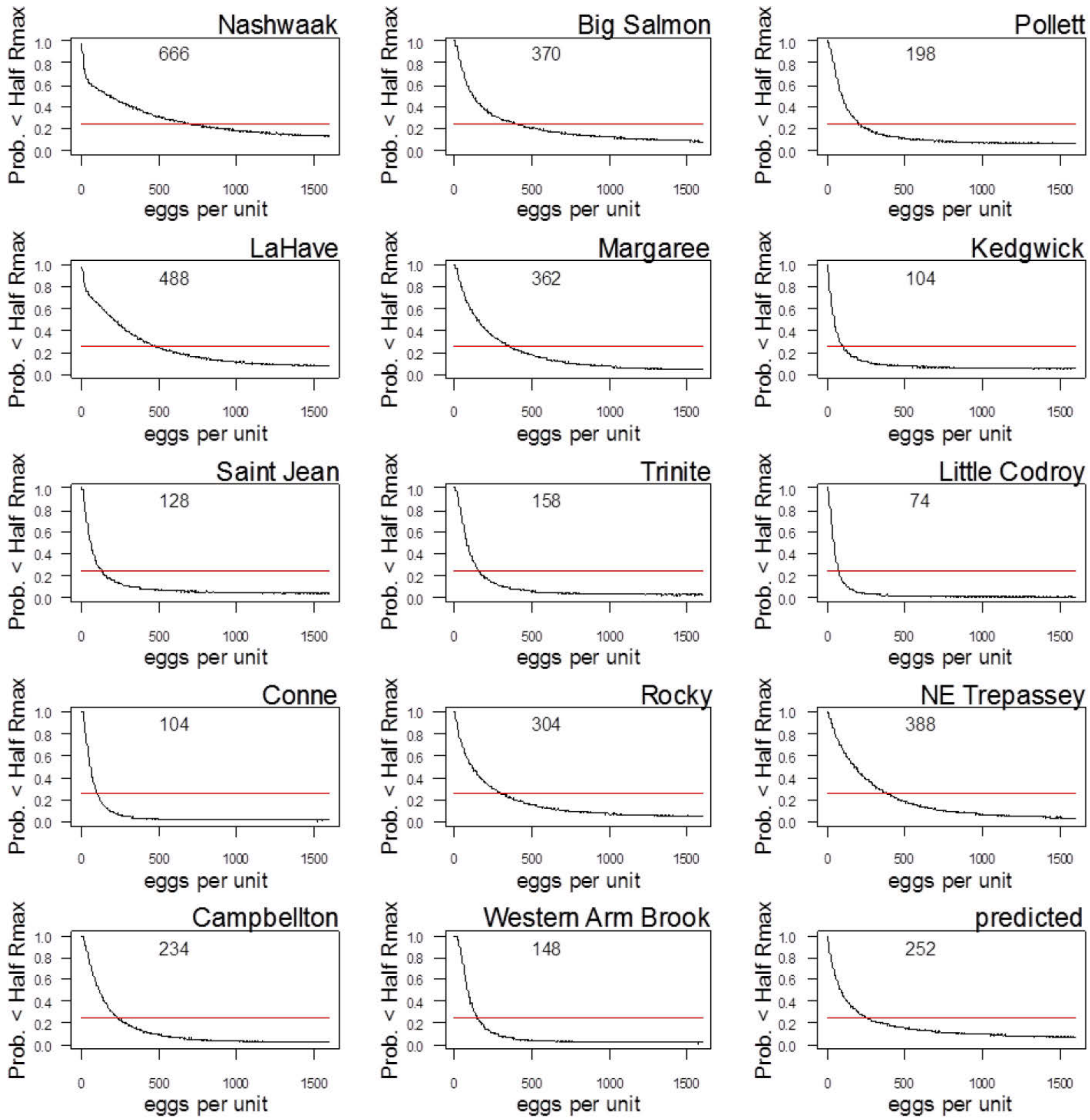


Figure 12. Ricker: egg depositions (eggs per unit, unit = 100 m²) versus probability that smolts produced will be < Half Rmax, taking into account the uncertainty of the stock and recruitment relationships and the estimated process error (sigma). Values on each panel are the eggs corresponding to a probability of ~ 0.25 of recruitment being below Half Rmax (S_{LRP}). The probability of recruitment being less than Half Rmax for the predicted panel is 0.286 for eggs per unit of 596.



Figue 13. Beverton-Holt: egg depositions (eggs per unit, unit = 100 m²) versus probability that smolts produced will be < Half Rmax, taking into account the uncertainty of the stock and recruitment relationships and the estimated process error (sigma). Values on each panel are the eggs corresponding to a probability of ~ 0.25 of recruitment being below Half Rmax (S_{LRP}).

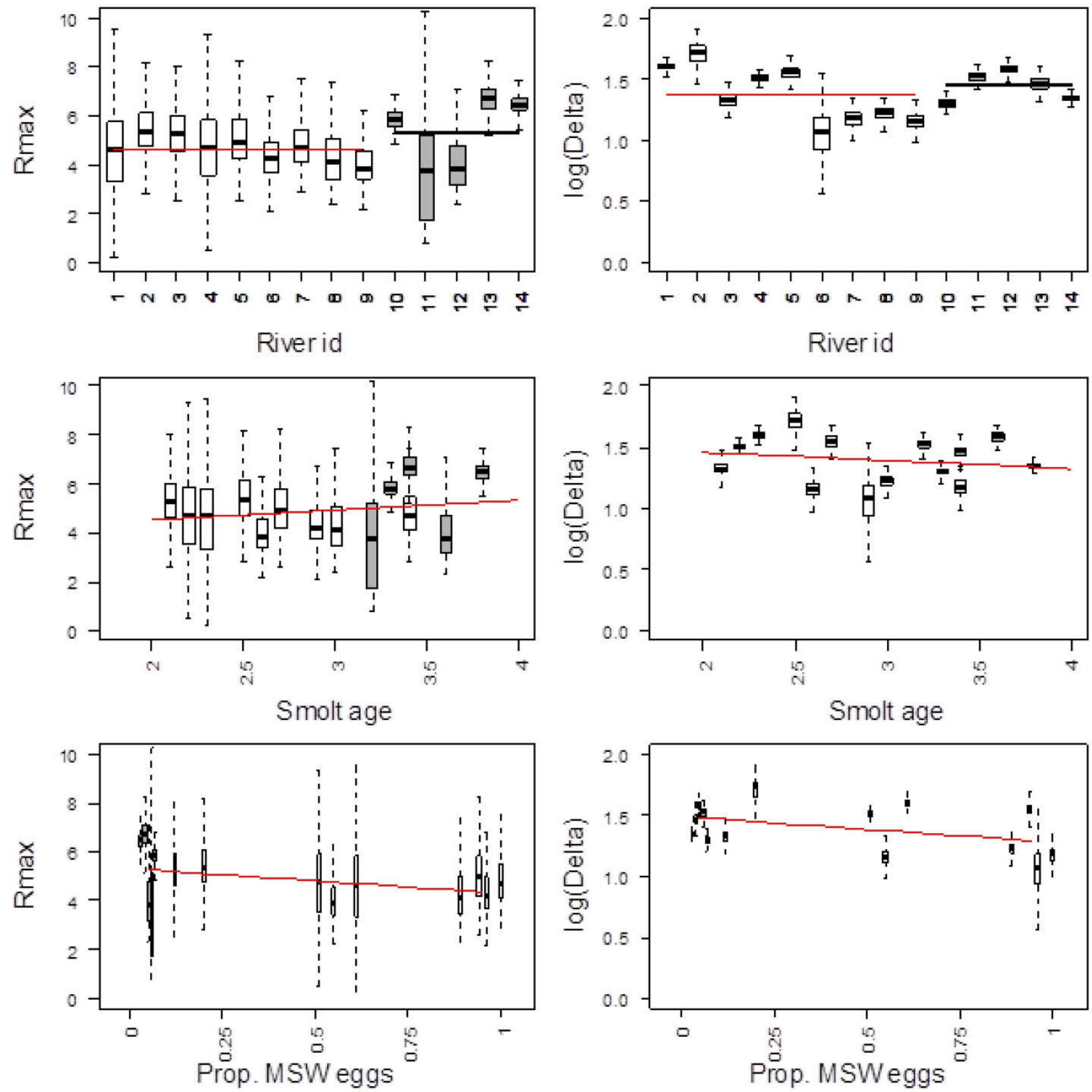


Figure 14. Ricker model hierarchical fits with no covariates showing relationships of Rmax and log(delta) to potential covariates as: presence/absence of lacustrine (upper row), mean age of smolts (middle row), and proportion MSW eggs (bottom row). The horizontal lines in the top row represent the mean of the posterior medians for Rmax and log(delta) for the groups of rivers within the fluvial only category (red line) and the rivers with lacustrine habitat (thick black line). The red lines in the middle and bottom rows are the linear regressions of the median values of Rmax or log(delta) from the posterior distributions versus mean age or proportion MSW eggs.

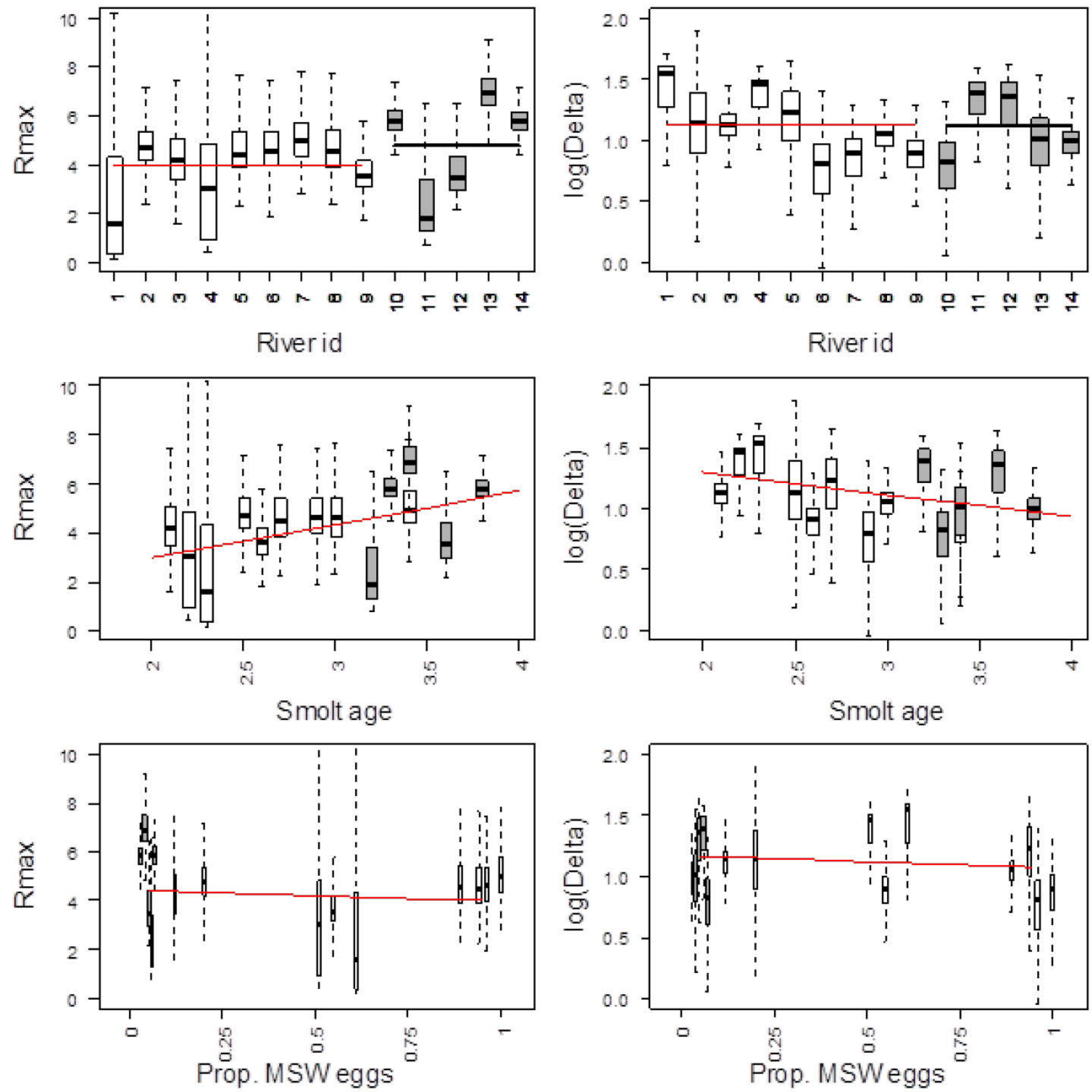


Figure 15. Beverton-Holt model hierarchical fits with no covariates showing relationships of Rmax and log(delta) to potential covariates as: presence/absence of lacustrine (upper row), mean age of smolts (middle row), and proportion MSW eggs (bottom row). The horizontal lines in the top row represent the mean of the posterior medians for Rmax and log(delta) for the groups of rivers within the fluvial only category (red line) and the rivers with lacustrine habitat (thick black line). The red lines in the middle and bottom rows are the linear regressions of the median values of Rmax or log(delta) from the posterior distributions versus mean age or proportion MSW eggs.

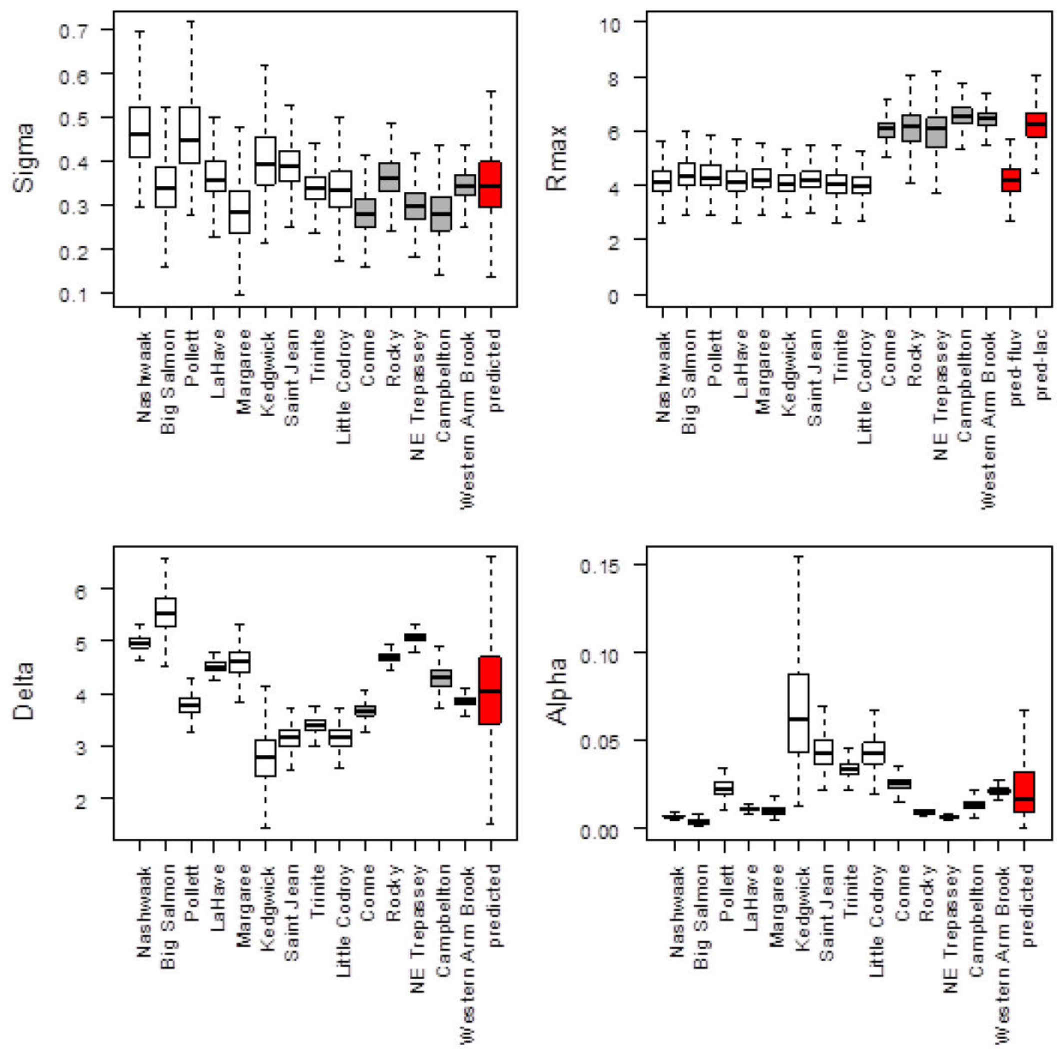


Figure 16. Ricker model: boxplots of posterior distributions of the stock and recruitment parameters (sigma, Rmax, delta, alpha) from the hierarchical model with presence of lacustrine habitat as covariate on Rmax. Rivers with fluvial habitat only are in white shading, with lacustrine habitat in grey shading and the predicted values are in red shading.

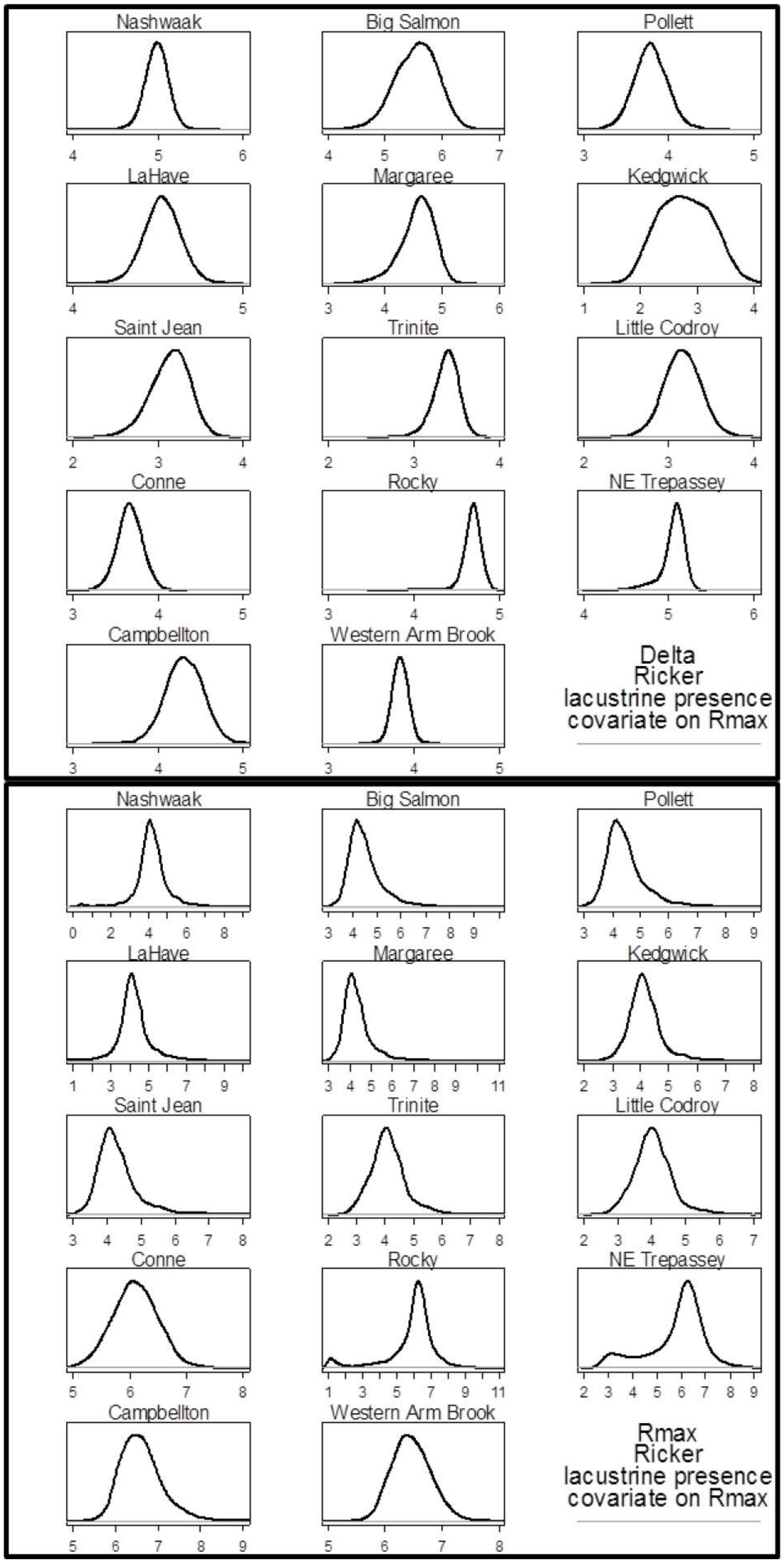


Figure 17. Posterior distributions of delta (upper panel) and Rmax (lower panel) from the Ricker hierarchical model on sigma, delta, and presence of lacustrine habitat as covariate on Rmax.

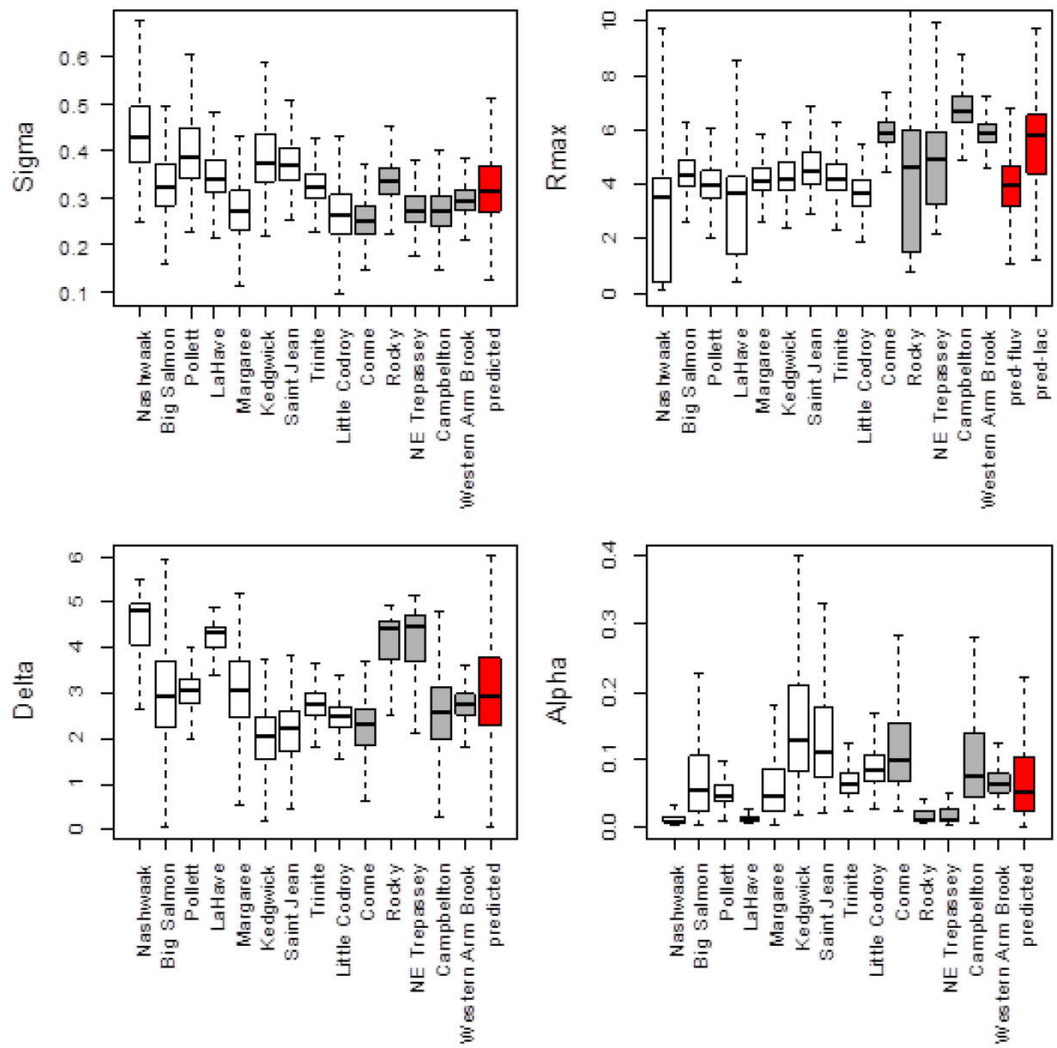


Figure 18. Beverton-Holt: boxplots of posterior distributions of the stock and recruitment parameters (sigma, Rmax, delta, alpha) from the hierarchical model with presence of lacustrine habitat as covariate on Rmax. Rivers with fluvial habitat only are in white shading, with lacustrine habitat in grey shading and the predicted values are in red shading.

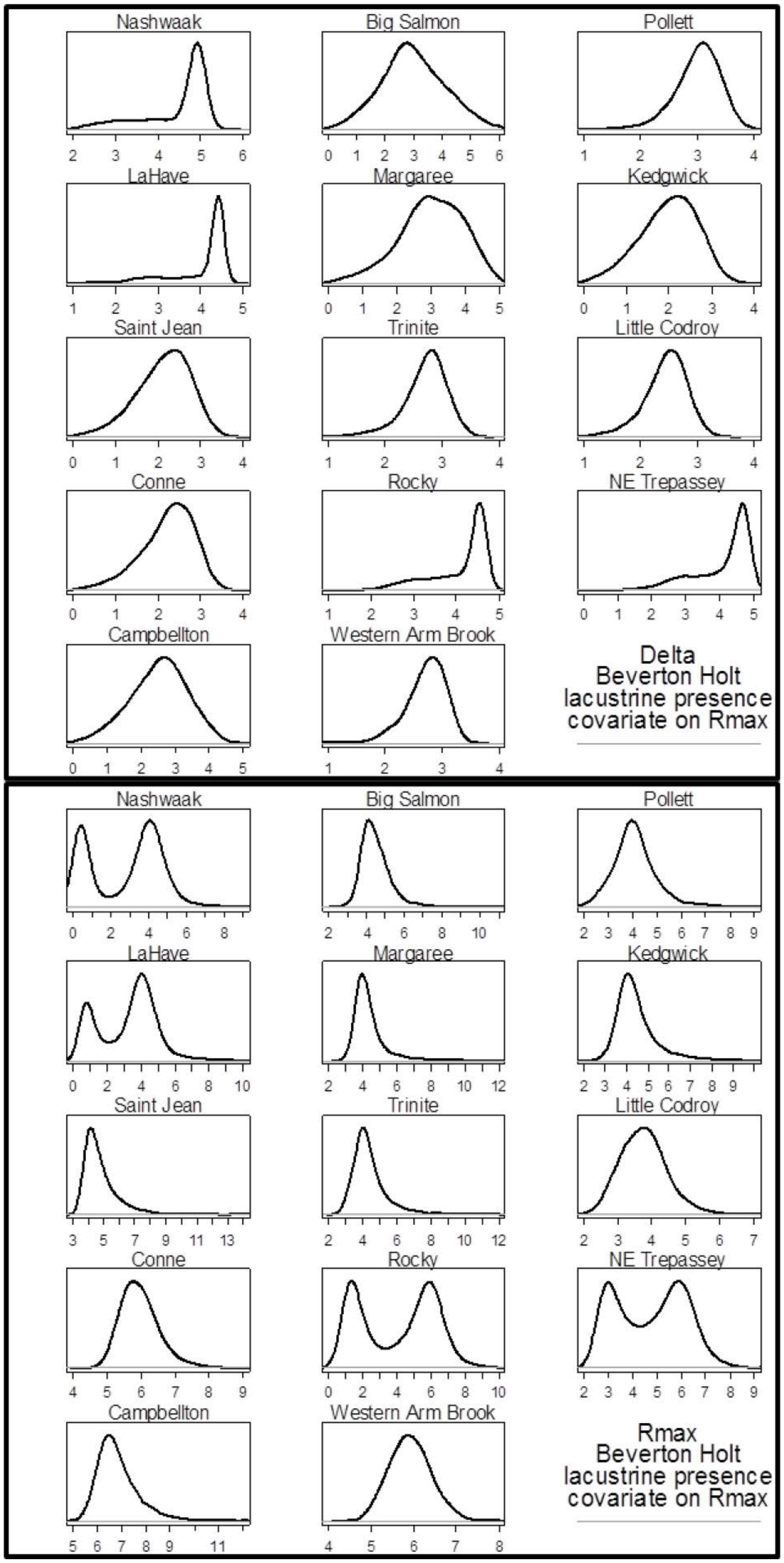
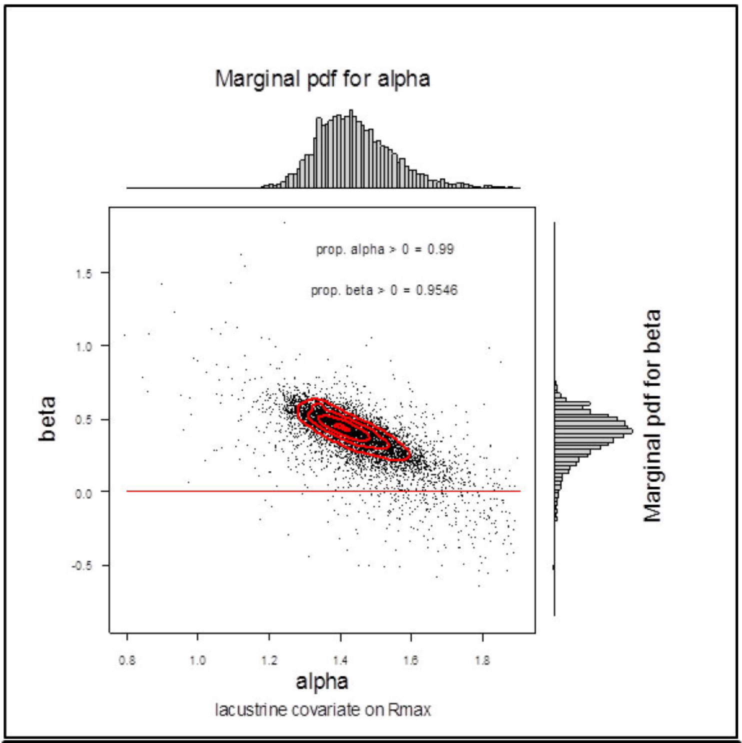


Figure 19. Posterior distributions of delta (upper) and Rmax (lower) from the Beverton-Holt hierarchical model on sigma, delta, and presence of lacustrine habitat as covariate on Rmax.



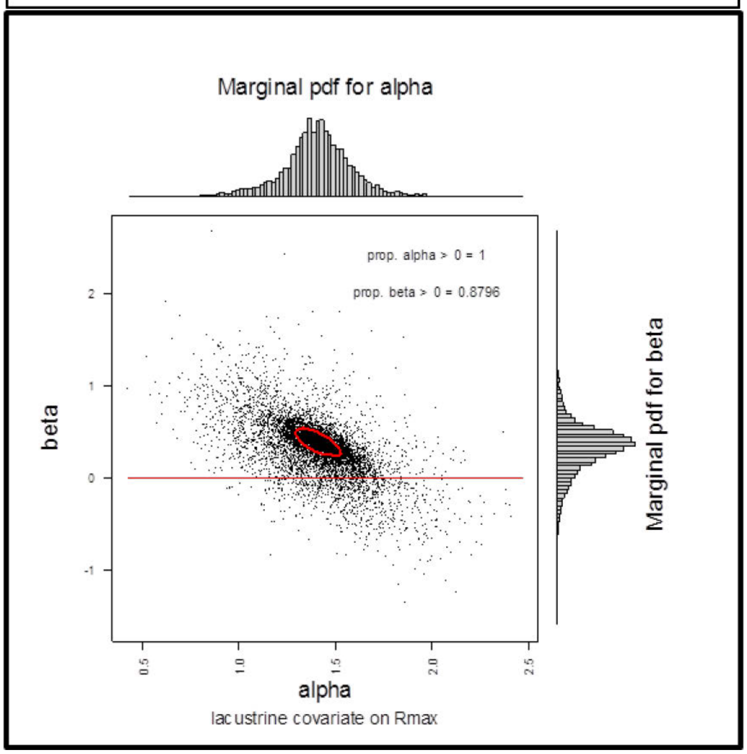


*Figure 20. Bivariate and marginal distributions of the coefficients (alpha, beta) of the presence of lacustrine habitat as a covariate for Rmax for the Ricker model (upper panel) and the Beverton-Holt (lower panel). For Rmax, the function is: E(log.Rmax) = alpha + beta * Lac with Lac = 0 for fluvial rivers and Lac = 1 for lacustrine rivers. The one-tail significance of the beta coefficient for the Ricker model is 0.04 and for the Beverton-Holt model is 0.12.*

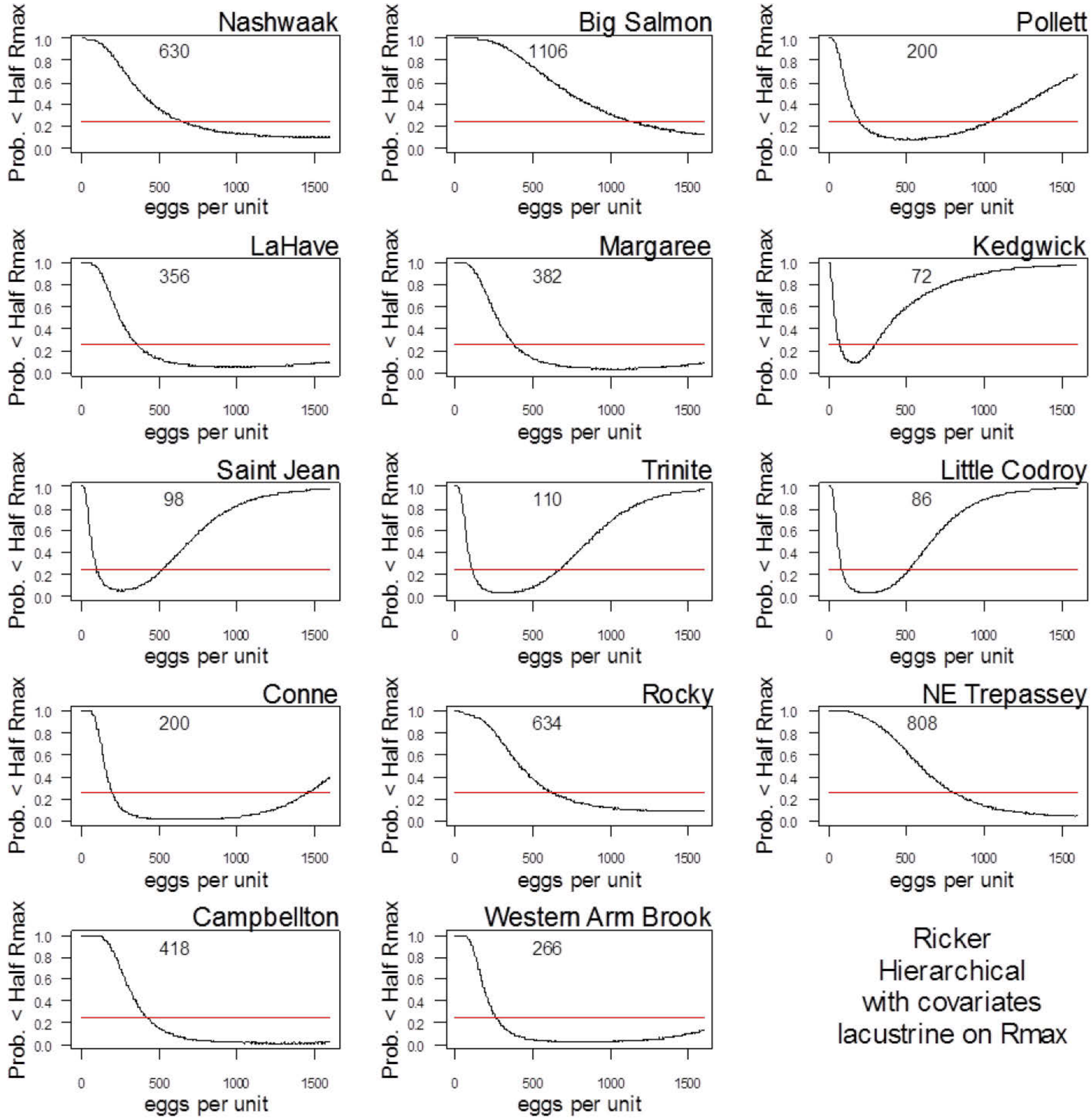


Figure 21. Results of the hierarchical Ricker model with presence of lacustrine habitat as a covariate on Rmax for the estimated egg depositions versus probability that smolts produced will be < Half Rmax, taking into account the uncertainty of the stock and recruitment relationships and the estimated process error (sigma). Values on each panel are the eggs corresponding to a probability of ~ 0.25 of recruitment being below Half Rmax (S_{LRP}).

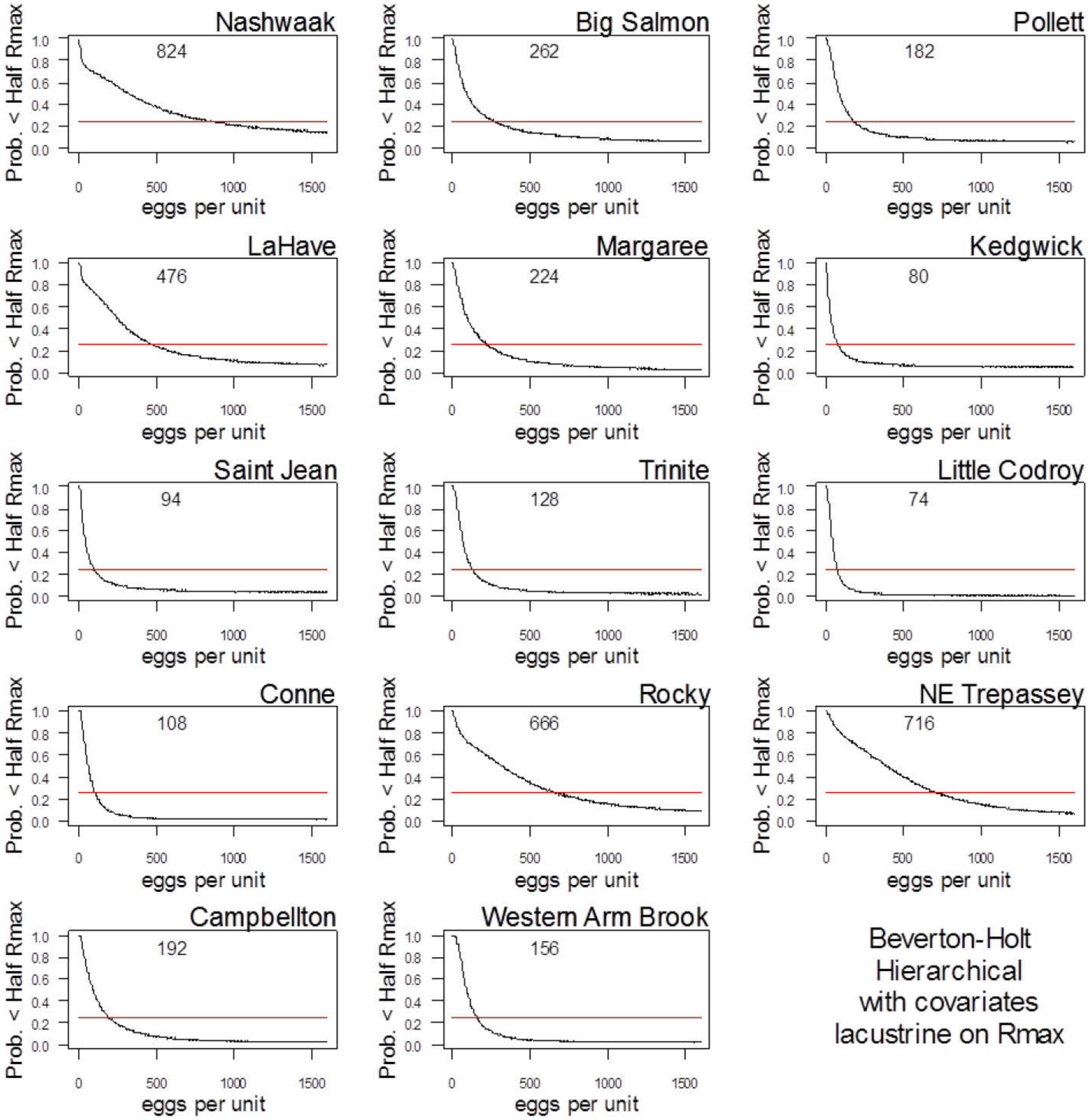


Figure 22. Results of the hierarchical Beverton-Holt model with presence of lacustrine habitat as a covariate on Rmax for the estimated egg depositions versus probability that smolts produced will be < Half Rmax, taking into account the uncertainty of the stock and recruitment relationships and the estimated process error (sigma). Values on each panel are the eggs corresponding to a probability of ~ 0.25 of recruitment being below Half Rmax (S_{LRP}).

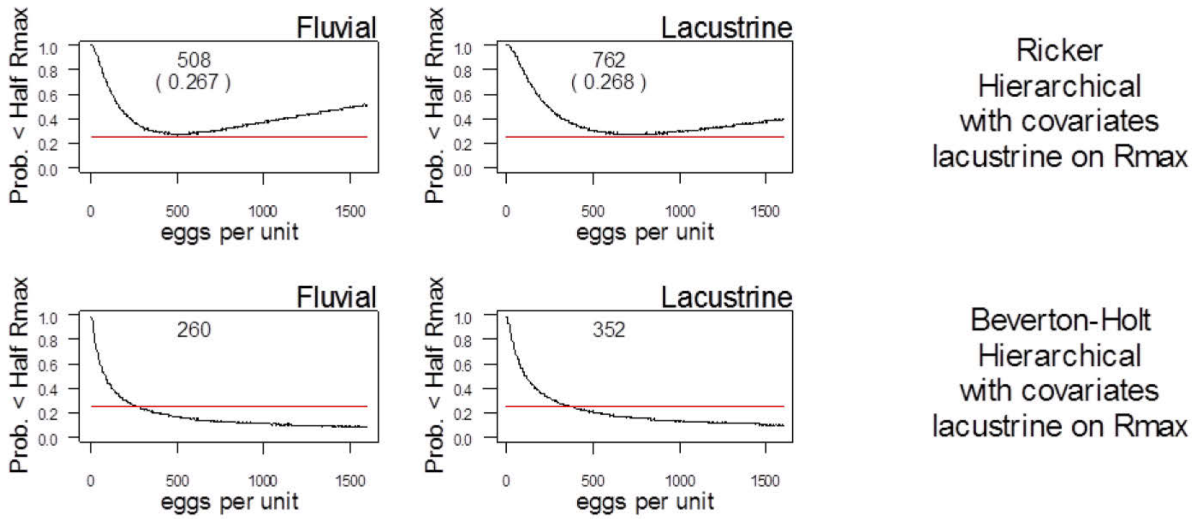


Figure 23. Results of the hierarchical model with presence of lacustrine habitat as a covariate on Rmax for the estimated egg depositions versus probability that smolts produced will be < Half Rmax, taking into account the uncertainty of the stock and recruitment relationships and the estimated process error (sigma). The upper row show the results for the Ricker model and the lower row the results of the Beverton-Holt model. Values on each panel are the eggs corresponding to a probability of ~ 0.25 of recruitment being below Half Rmax (S_{LRP}) and the values in parentheses are the corresponding minimum probabilities when this exceeds 0.25.

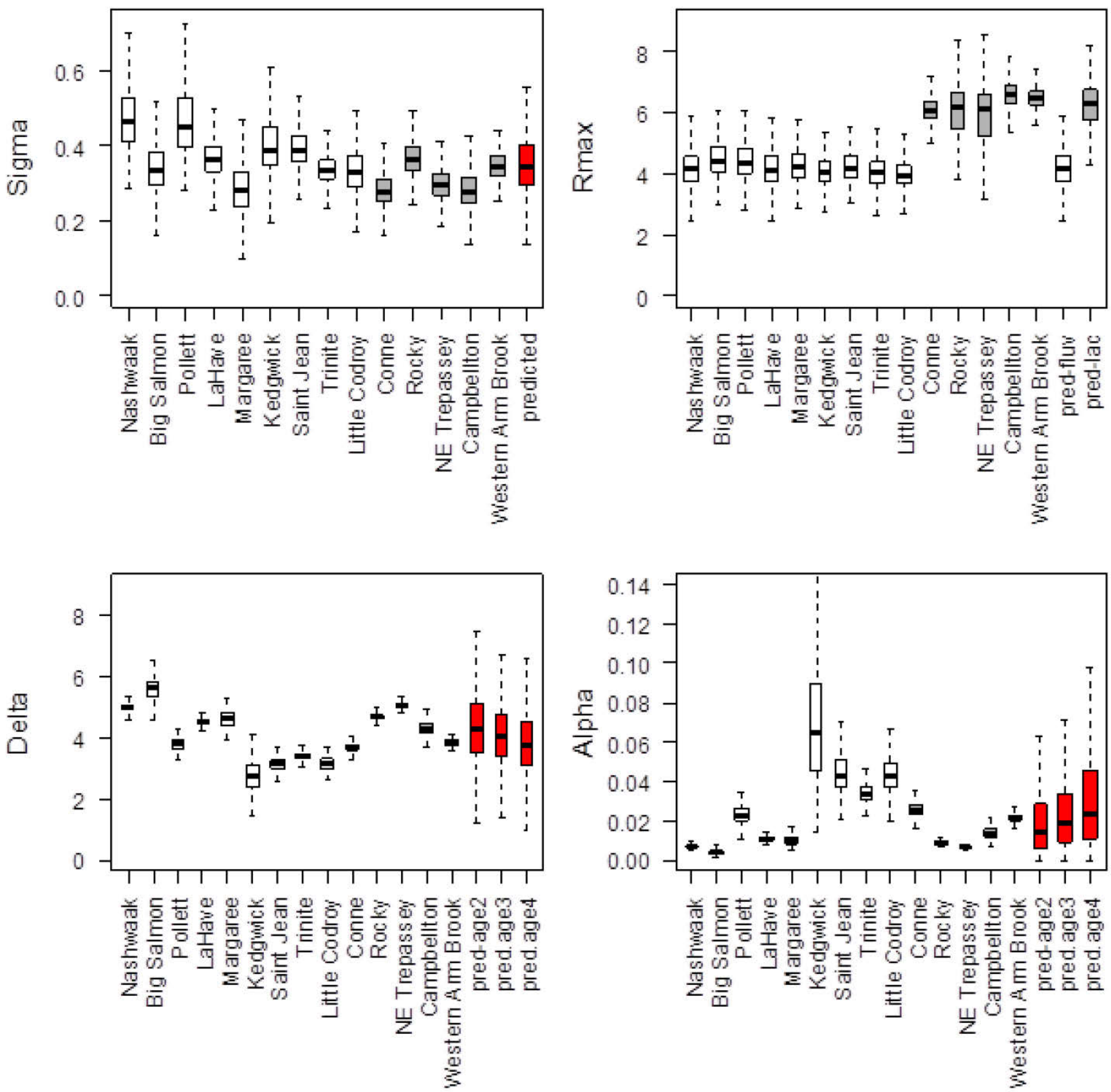


Figure 24. Ricker with covariate of lacustrine habitat for Rmax and mean age of smolts for Delta. White shading of boxplots are rivers with only fluvial habitat, grey shading of boxplots are rivers with lacustrine habitat. Red shading of boxplots are posterior distributions of the predicted values for fixed covariate values (fluvial or lacustrine for Rmax, mean smolt ages 2, 3 and 4 for delta).

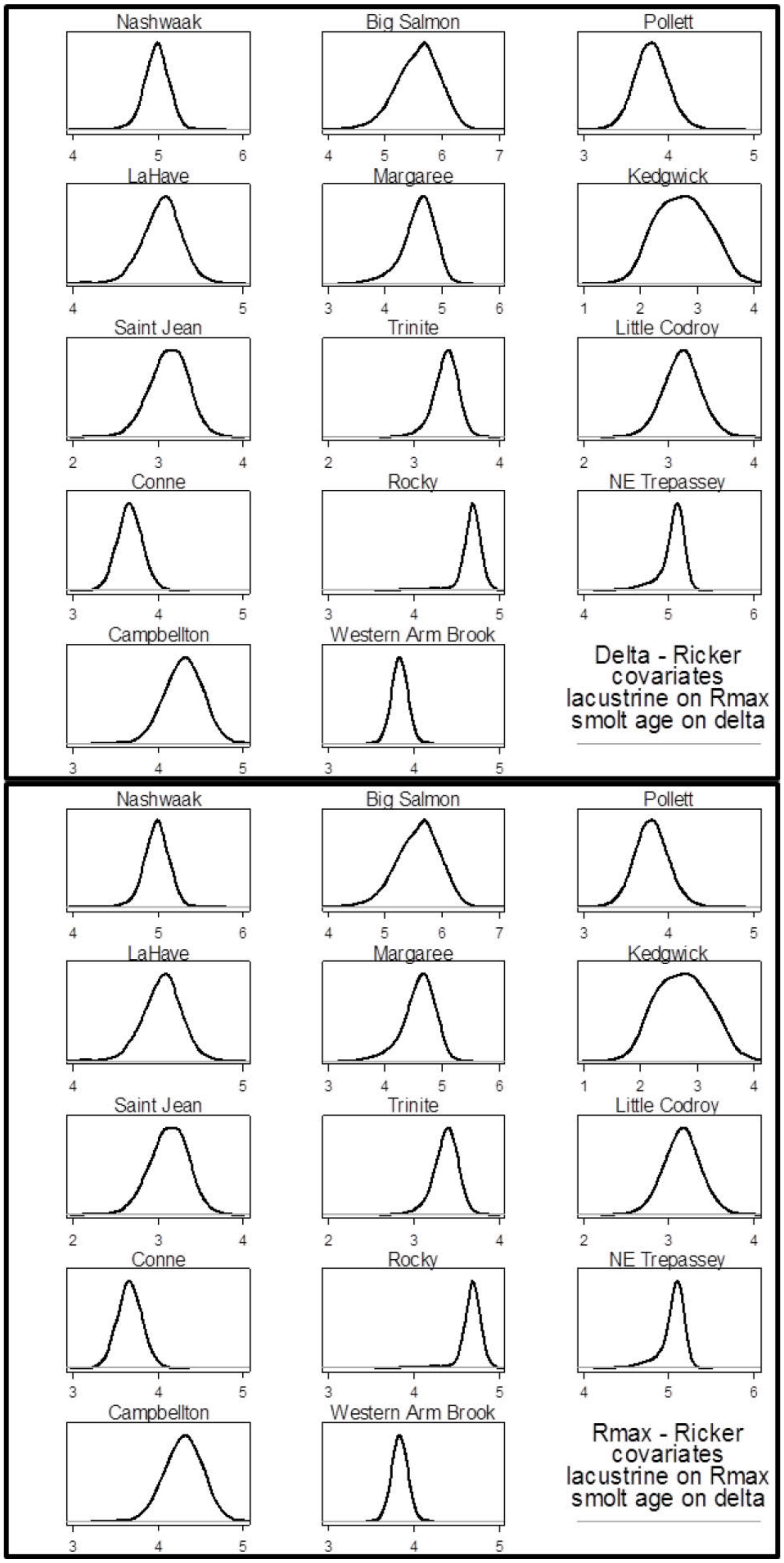


Figure 25. Posterior distributions of delta (upper) and Rmax (lower) from the Ricker hierarchical model on sigma, with lacustrine presence as covariate on Rmax and mean age of smolts as covariate on delta.

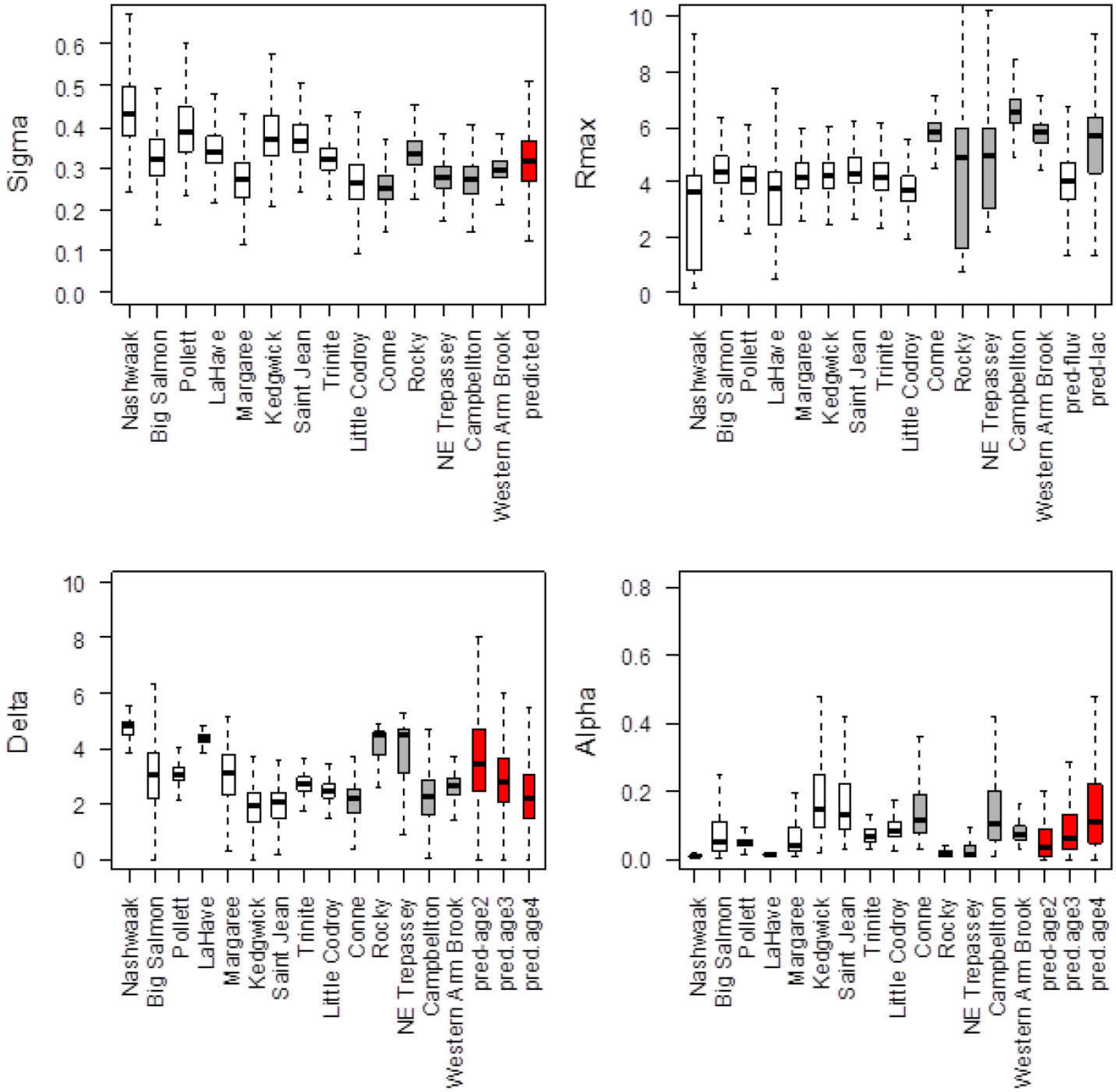


Figure 26. Beverton-Holt with covariate of lacustrine habitat for Rmax and mean age of smolts for Delta. White shading of boxplots are rivers with only fluvial habitat, grey shading of boxplots are rivers with lacustrine habitat. Red shading of boxplots are posterior distributions of the predicted values for fixed covariate values (fluvial or lacustrine for Rmax, mean smolt ages 2, 3 and 4 for delta).

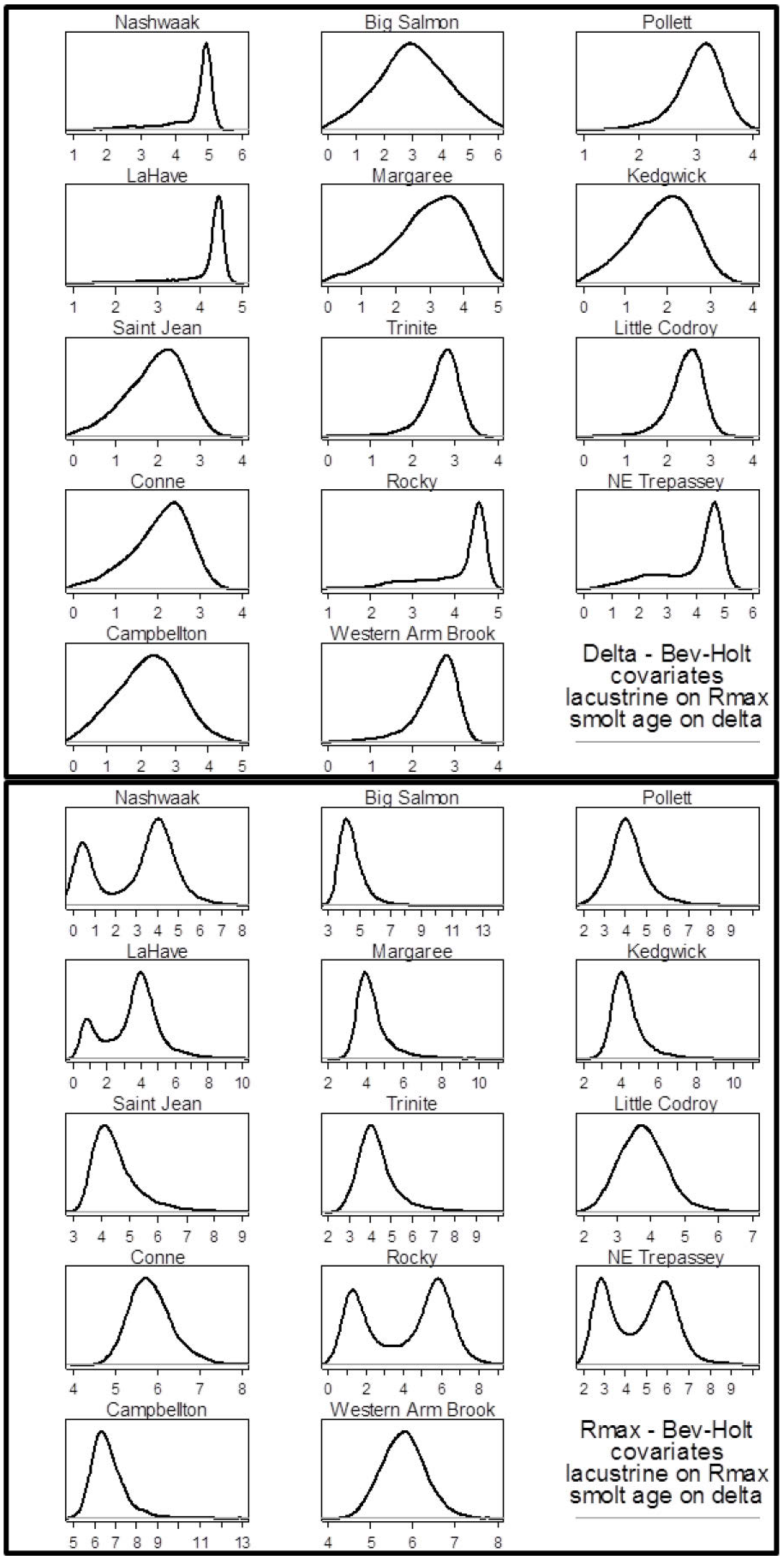


Figure 27. Posterior distributions of delta (upper panel) and Rmax (lower panel) from the Beverton-Holt hierarchical model on sigma, with lacustrine presence as covariate on Rmax and mean age of smolts as covariate on delta.

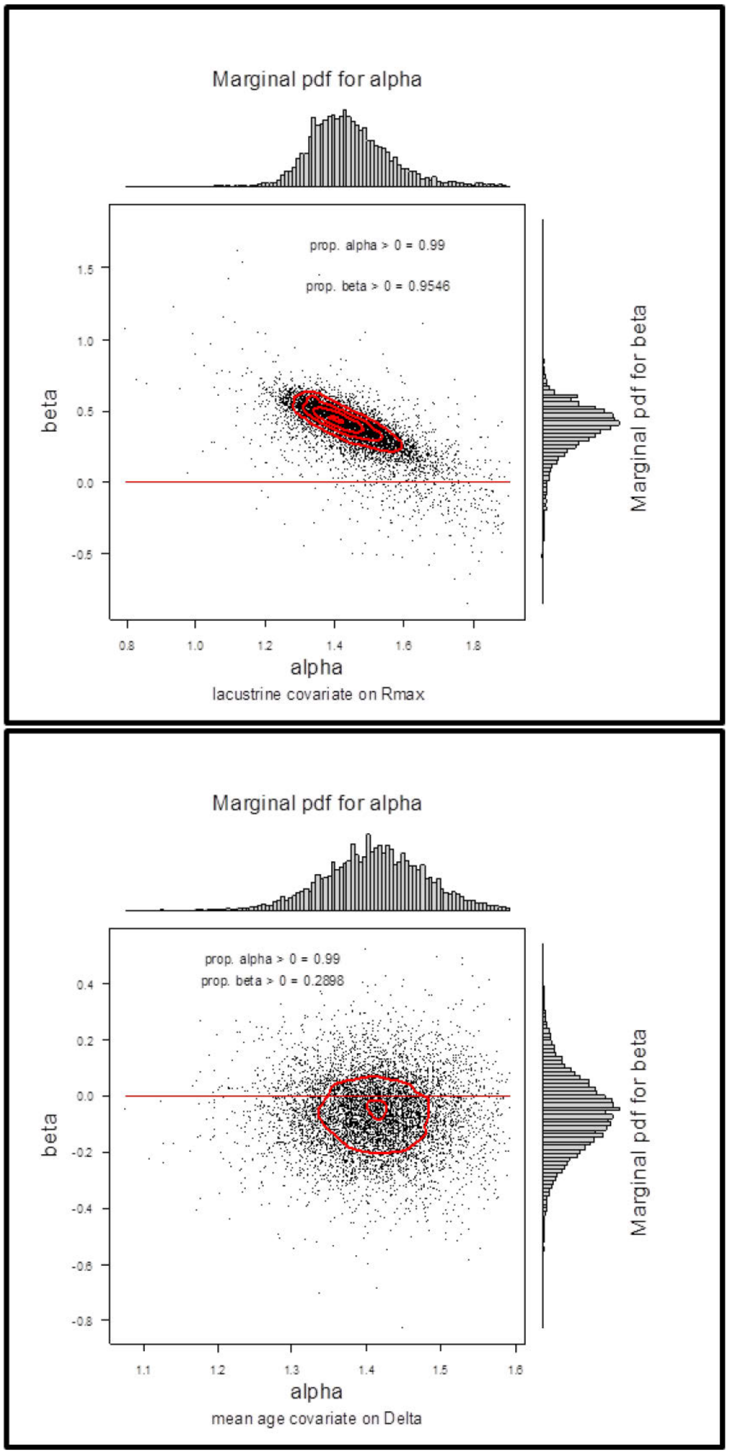


*Figure 28. Ricker: bivariate and marginal distributions of the coefficients (alpha, beta) of the covariate variables associated with Rmax (upper panel) and delta (lower panel). For Rmax, the function is: E(log.Rmax) = alpha + beta * Lac with Lac = 0 for fluvial rivers and Lac = 1 for lacustrine rivers. For delta, the function is : E(log.delta) = alpha + beta * (age – uage) where age is the mean age of smolts for the stock and uage is the mean of the mean ages over the 14 rivers. The one-tail significance of the- beta coefficient for Rmax is 0.05 and for the beta coefficient for delta is 0.29.*

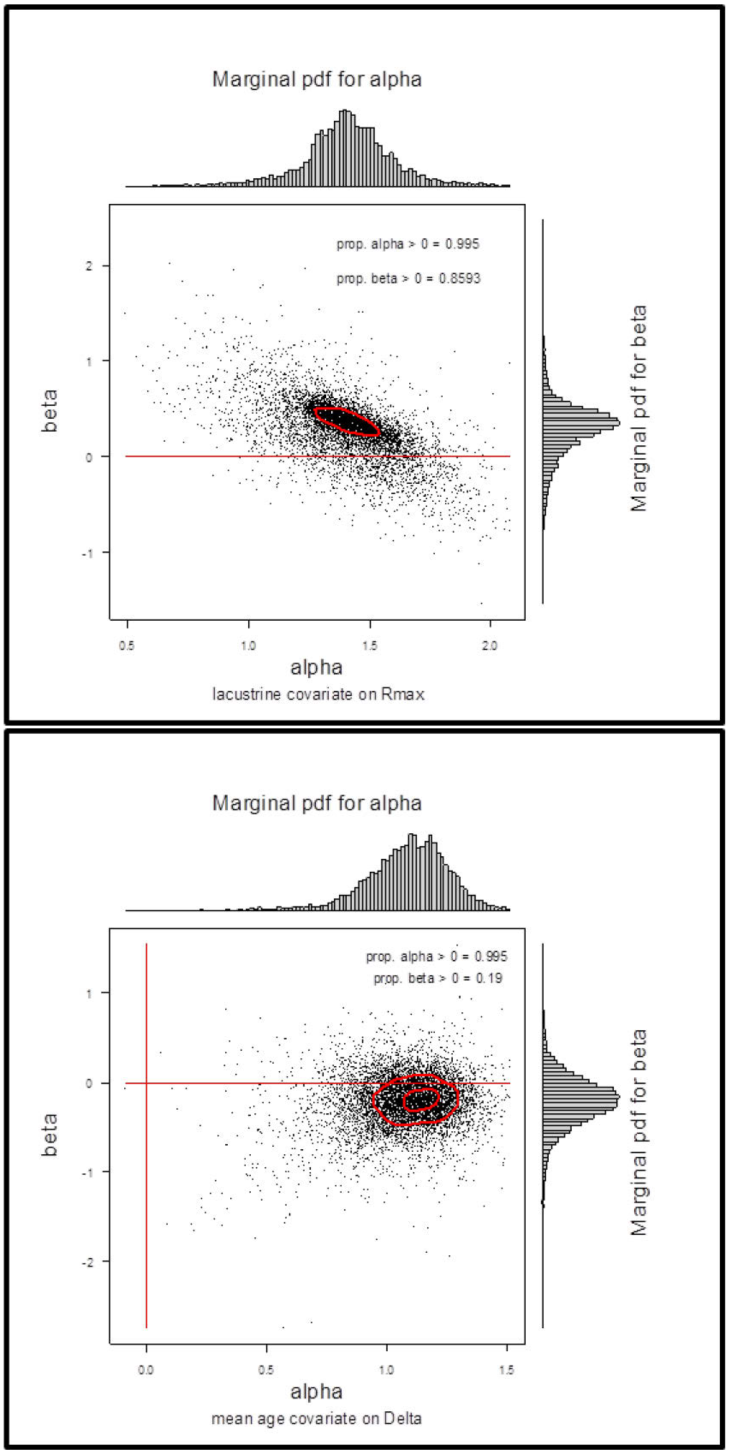


*Figure 29. Beverton-Holt: bivariate and marginal distributions of the coefficients (alpha, beta) of the covariate variables associated with Rmax (upper panel) and delta (lower panel). For Rmax, the function is: log(uRmax) = alpha + beta * Lac with Lac = 0 for fluvial rivers and Lac = 1 for lacustrine rivers. For delta, the function is : log(udelta) = alpha + beta * (age – uage) where age is the mean age of smolts for the stock and uage is the mean of the mean ages over the 14 rivers. The one-tail significance of the beta coefficient for Rmax is 0.14 and for the beta coefficient for delta is 0.19.*

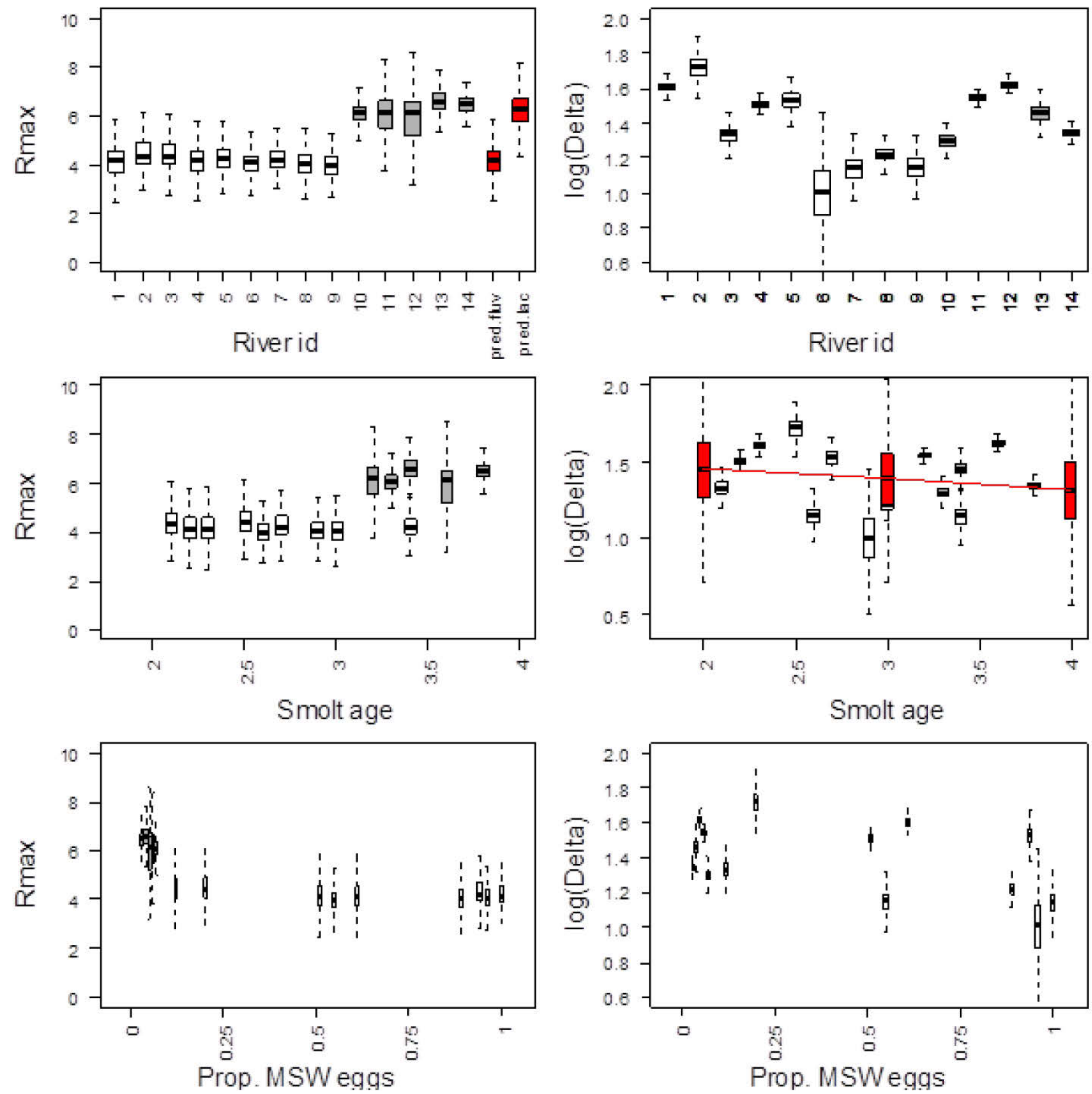


Figure 30. Ricker model hierarchical fits with covariates Rmax (presene/absence of lacustrine habitat) and delta (mean age of smolts) and relationships between Rmax and delta to: presence/absence of lacustrine, mean age of smolts, prop MSWeggs. White shading of boxplots are rivers with only fluvial habitat, grey shading of boxplots are rivers with lacustrine habitat. Red shading of boxplots are posterior distributions of the predicted values for fixed covariate values (fluvial or lacustrine for Rmax, mean smolt ages 2, 3 and 4 for delta).

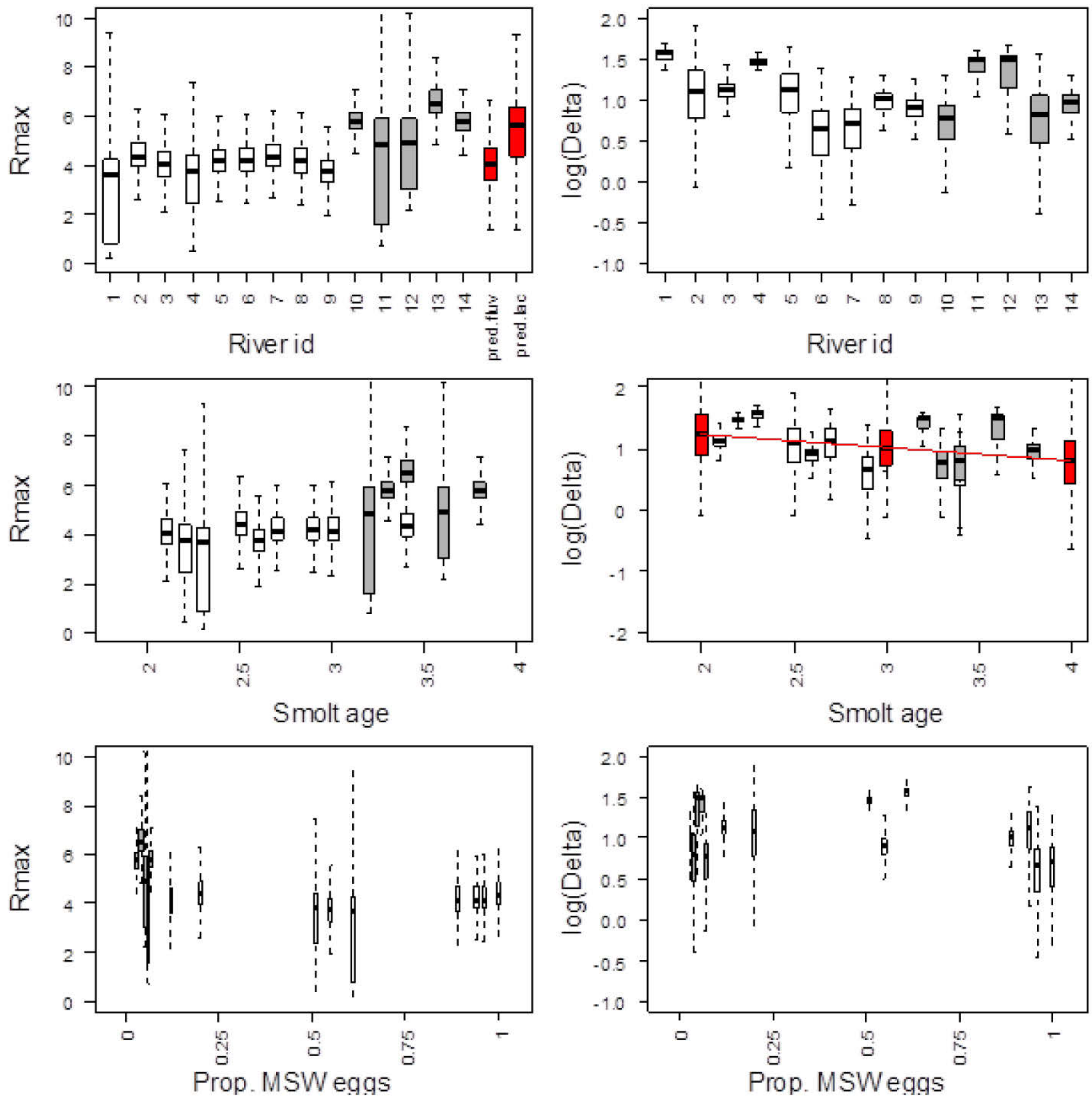


Figure 31. Beverton-Holt model hierarchical fits with covariates Rmax (presene/absence of lacustrine habitat) and delta (mean age of smolts) and relationships between Rmax and delta to: presence/absence of lacustrine, mean age of smolts, prop MSWeggs. White shading of boxplots are rivers with only fluvial habitat, grey shading of boxplots are rivers with lacustrine habitat. Red shading of boxplots are posterior distributions of the predicted values for fixed covariate values (fluvial or lacustrine for Rmax, mean smolt ages 2, 3 and 4 for delta).

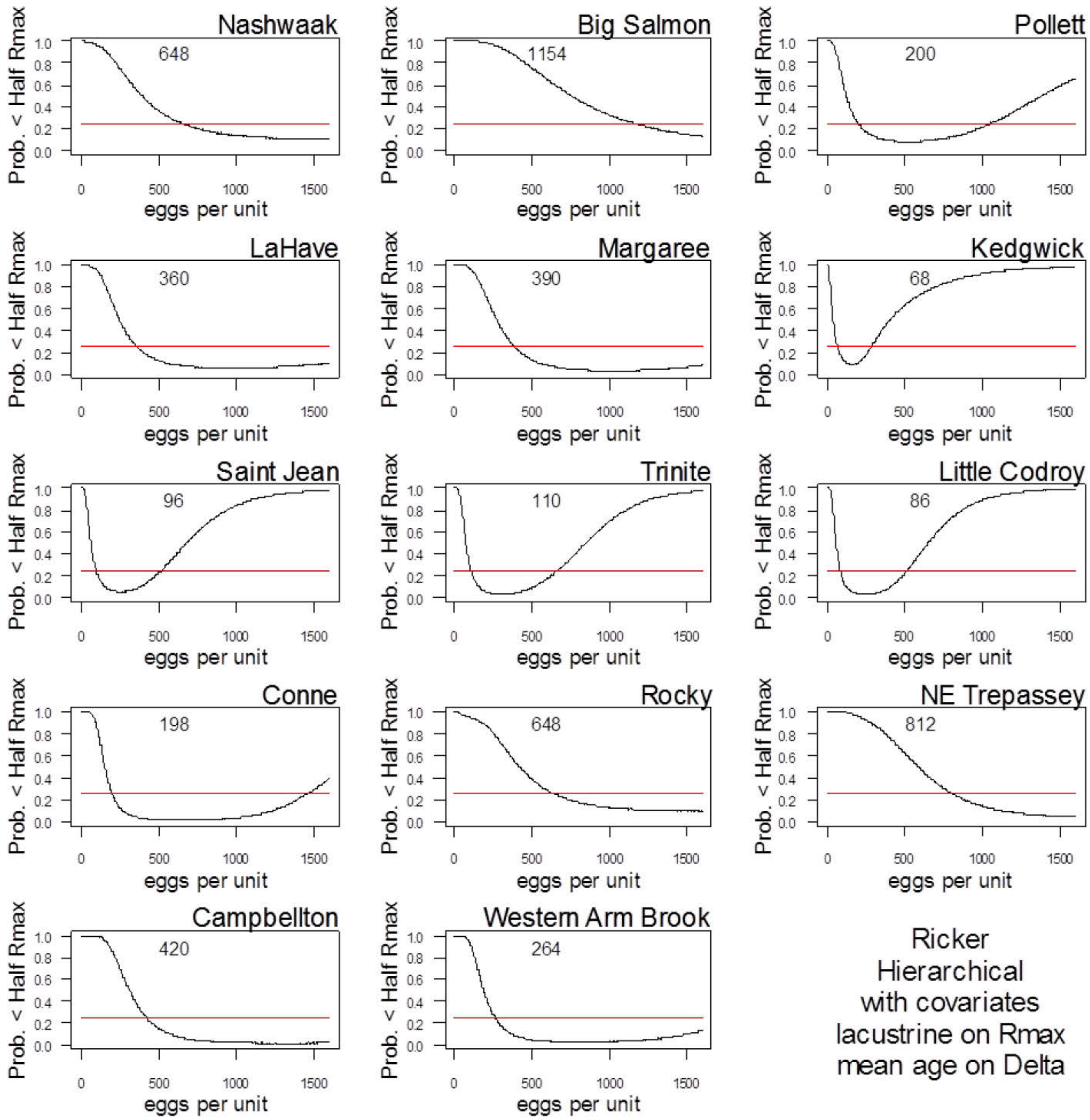


Figure 32. Eggs depositions versus probability that smolts produced will be < Half Rmax, taking into account the uncertainty of the stock and recruitment relationships and the estimated process error (sigma). Values on each panel are the eggs corresponding to a probability of ~ 0.25 of recruitment being below Half Rmax (S_{LRP}).

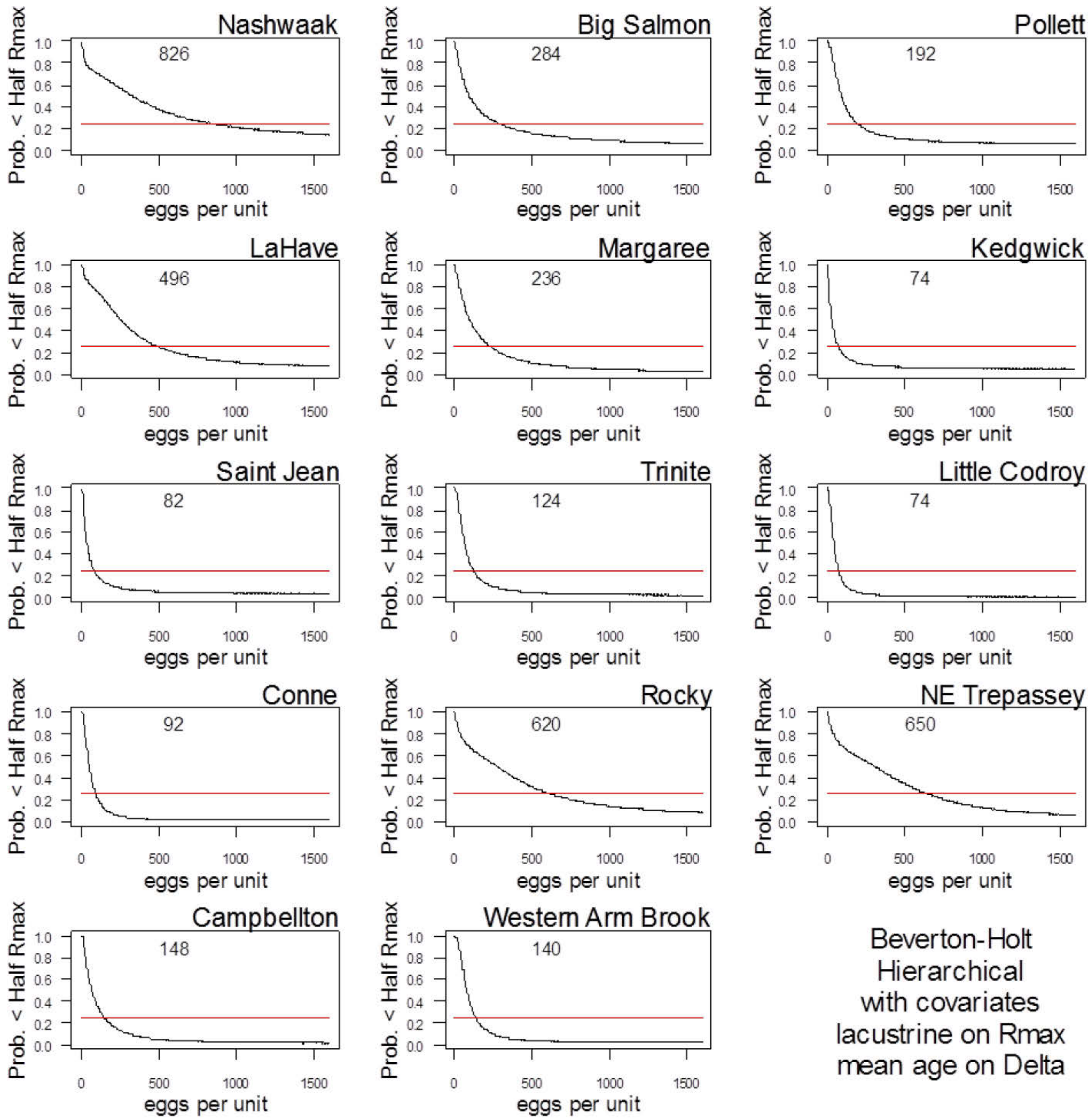


Figure 33. Eggs depositions versus probability that smolts produced will be < Half Rmax, taking into account the uncertainty of the stock and recruitment relationships and the estimated process error (sigma). Values on each panel are the eggs corresponding to a probability of ~ 0.25 of recruitment being below Half Rmax (S_{LRP}).

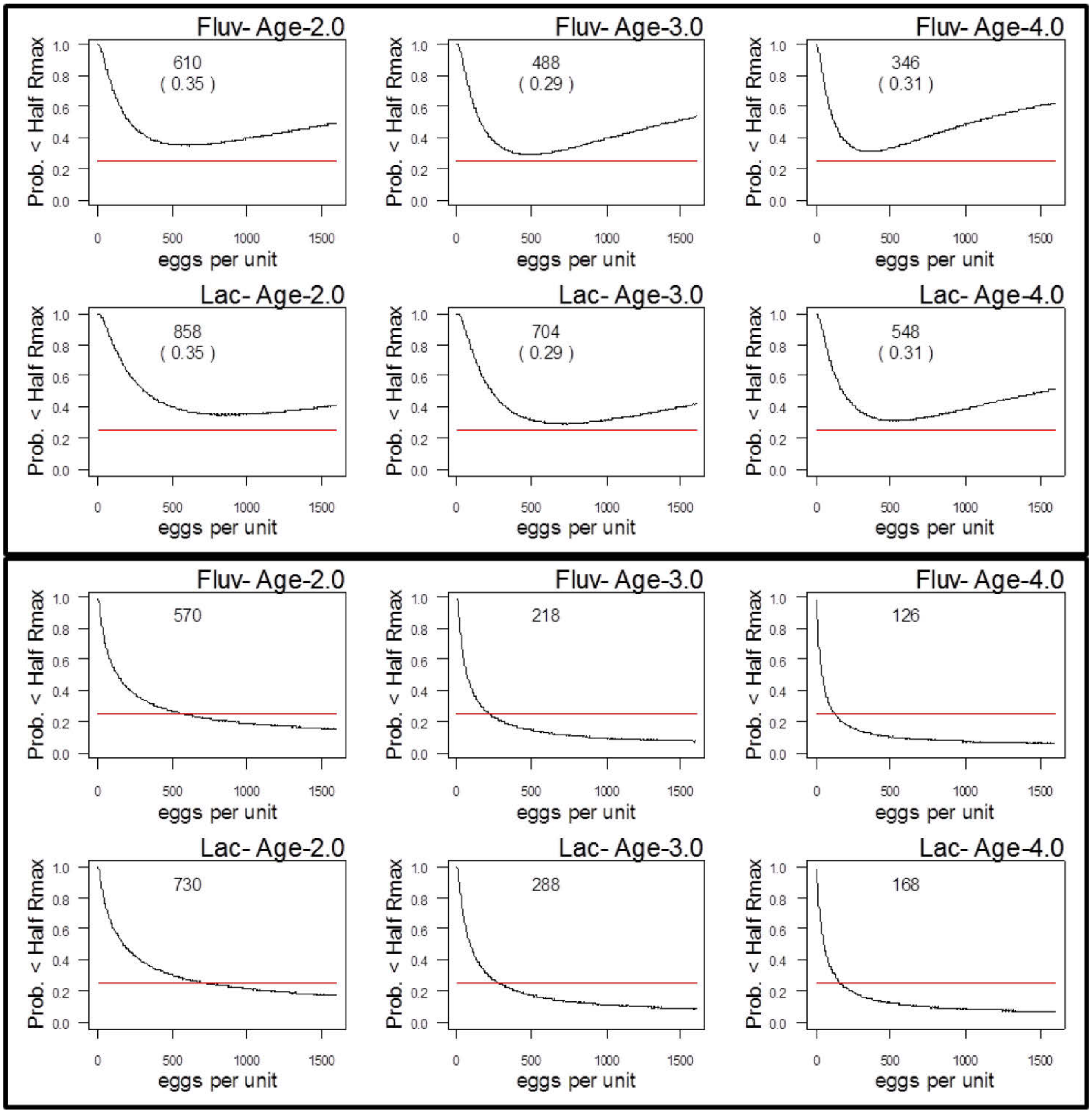


Figure 34. Eggs depositions versus probability that smolts produced will be < Half Rmax, for the Ricker (upper panel) and the Beverton-Holt (lower panel) models with presence of lacustrine habitat as covariate for Rmax and mean age of smolts as covariate for delta. Predicted values shown are for rivers without lacustine habitat (Fluv) and with lacustrine habitat (Lac) for mean ages of smolts of 2 (age2), 3 (age3) and 4 (age4) years. Values on each panel are the eggs corresponding to a probability of ~ 0.25 of recruitment being below Half Rmax (S_{LRP}) and the values in parentheses are the corresponding minimum probabilities when this exceeds 0.25.

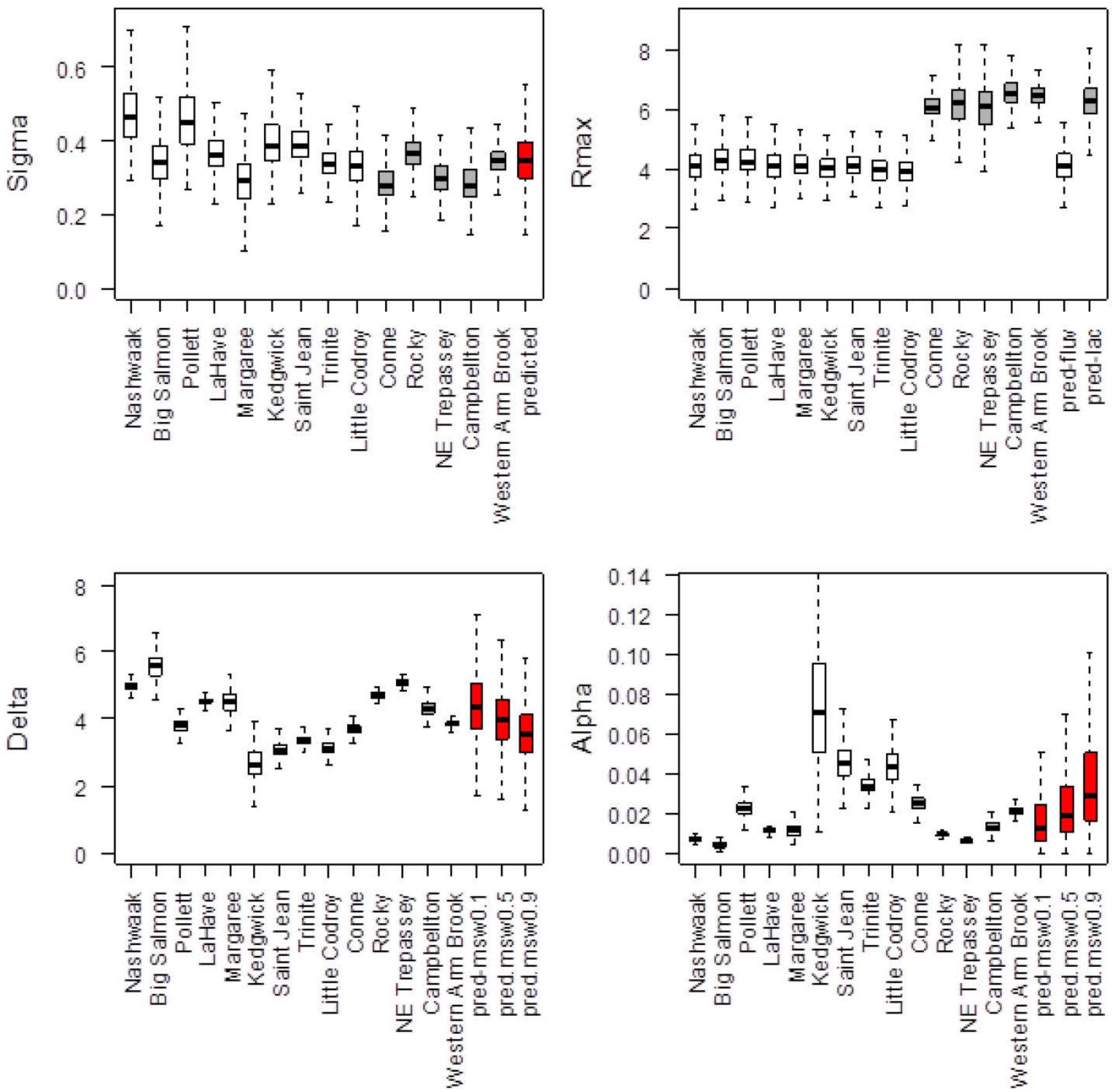


Figure 35. Ricker with covariate lacustrine habitat for Rmax and proportion MSW eggs for Delta. White shading of boxplots are rivers with only fluvial habitat, grey shading of boxplots are rivers with lacustrine habitat. Red shading of boxplots are posterior distributions of the predicted values for fixed covariate values (fluvial or lacustrine for Rmax, proportion MSW of 0.1, 0.5, and 0.9 for delta).

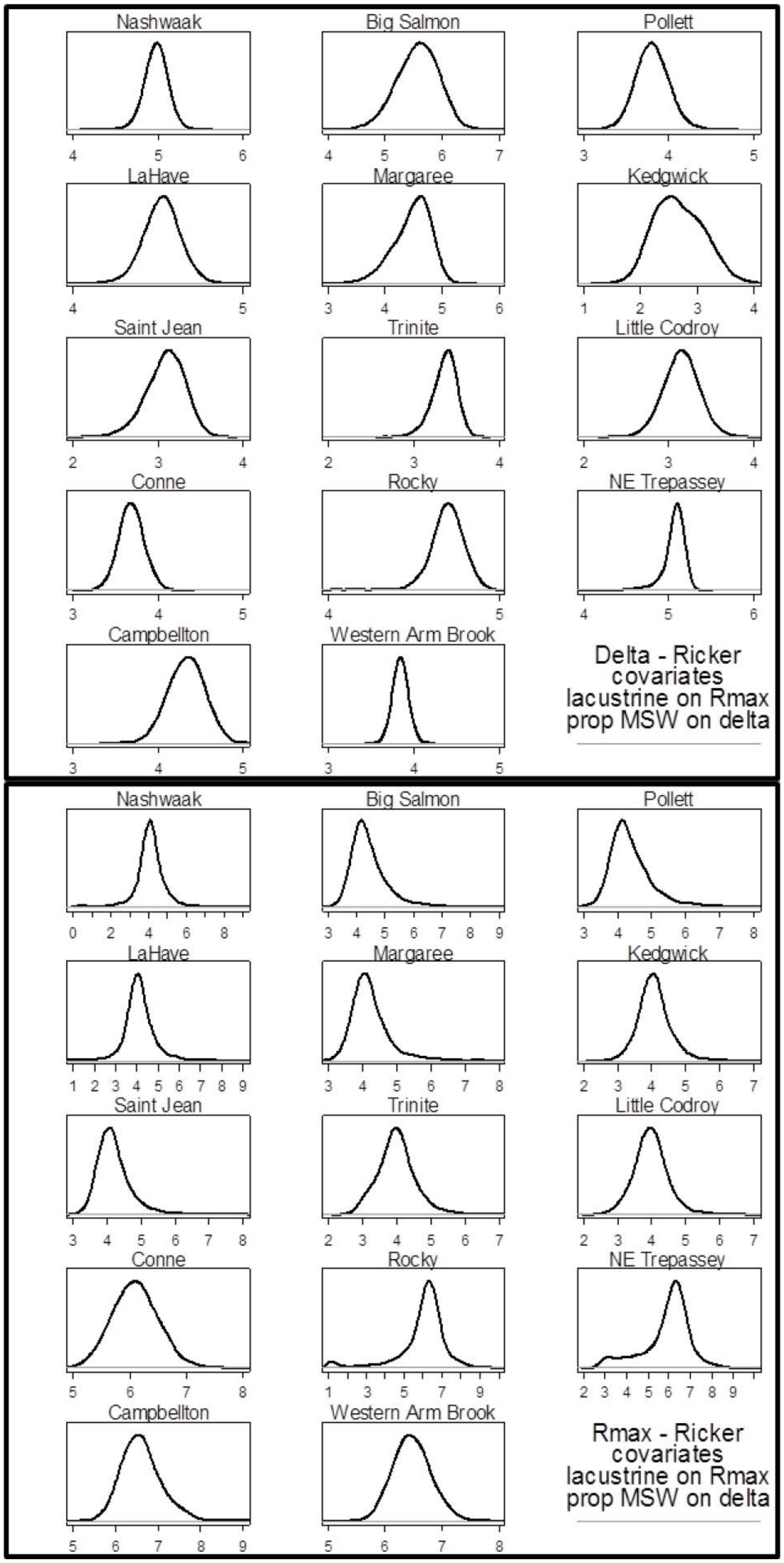


Figure 36. Posterior distributions of delta and Rmax from the Ricker hierarchical model on sigma, with lacustrine presence as covariate on Rmax and proportion MSW eggs as covariate on delta.

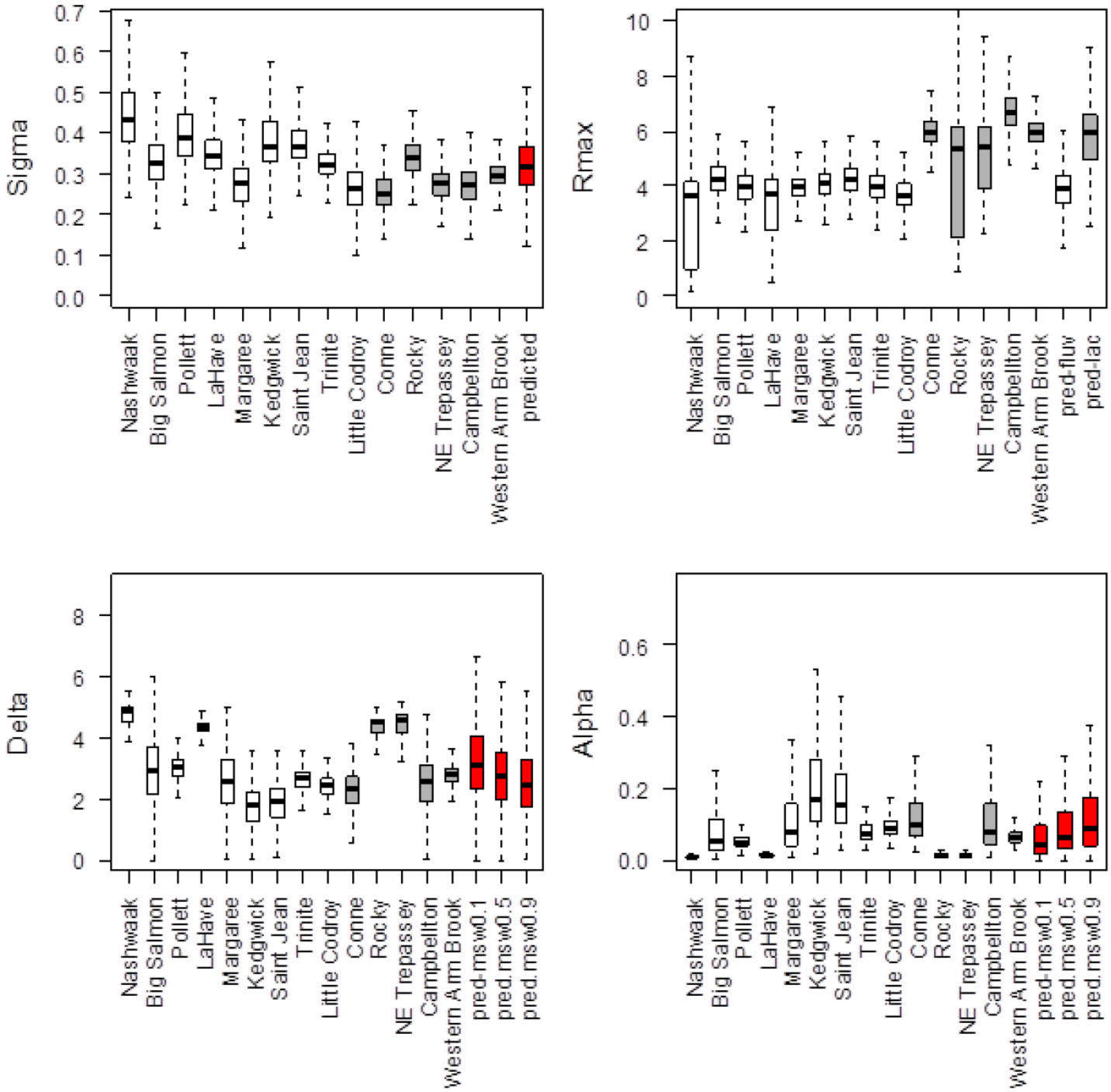


Figure 37. Beverton-Holt with covariate of lacustrine habitat for Rmax and proportion MSW eggs for Delta. White shading of boxplots are rivers with only fluvial habitat, grey shading of boxplots are rivers with lacustrine habitat. Red shading of boxplots are posterior distributions of the predicted values for fixed covariate values (fluvial or lacustrine for Rmax, proportion MSW of 0.1, 0.5, and 0.9 for delta).

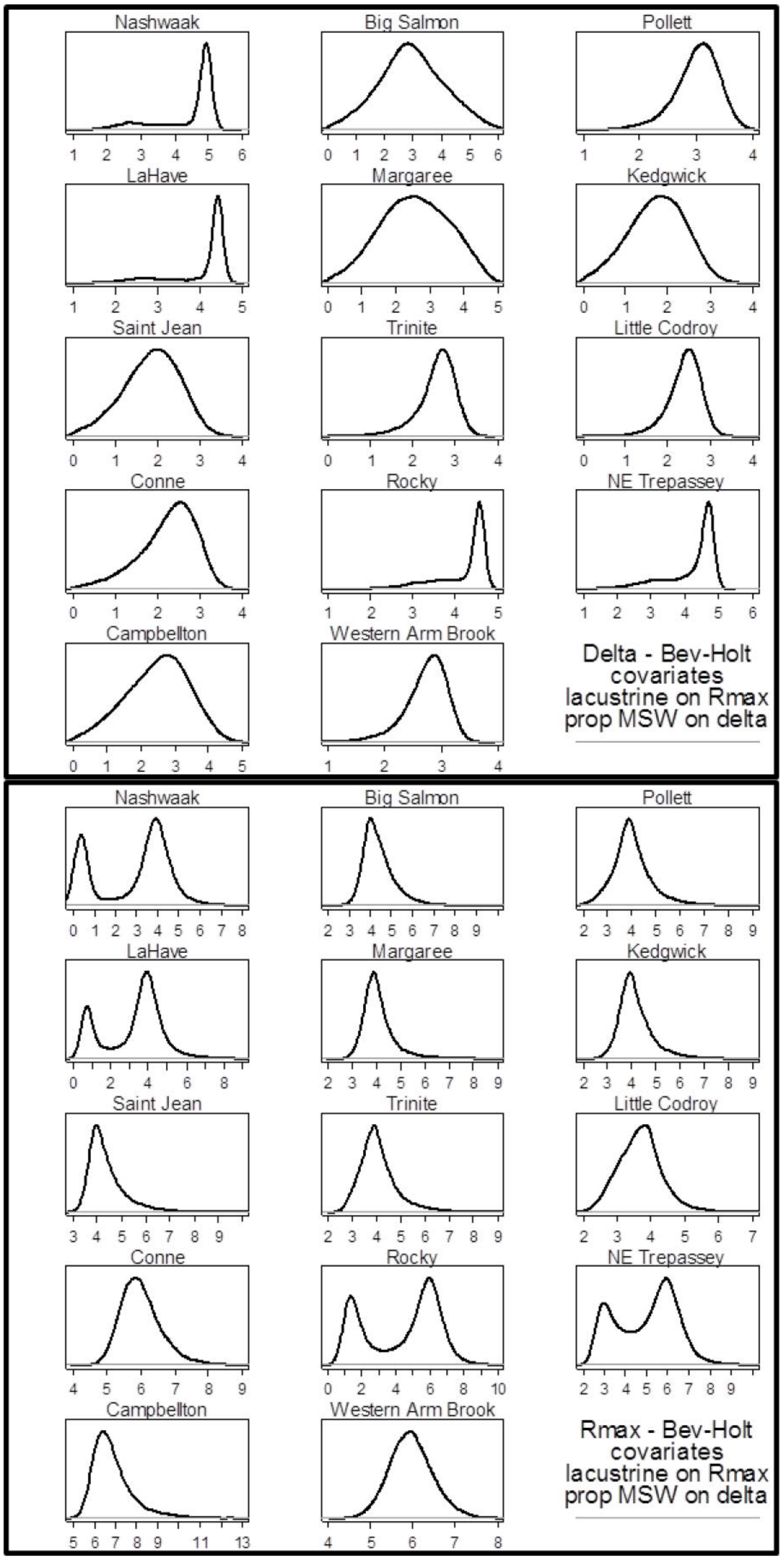


Figure 38. Posterior distributions of delta and Rmax from the Beverton-Holt hierarchical model on sigma, with lacustrine presence as covariate on Rmax and proportion MSW eggs as covariate on delta.

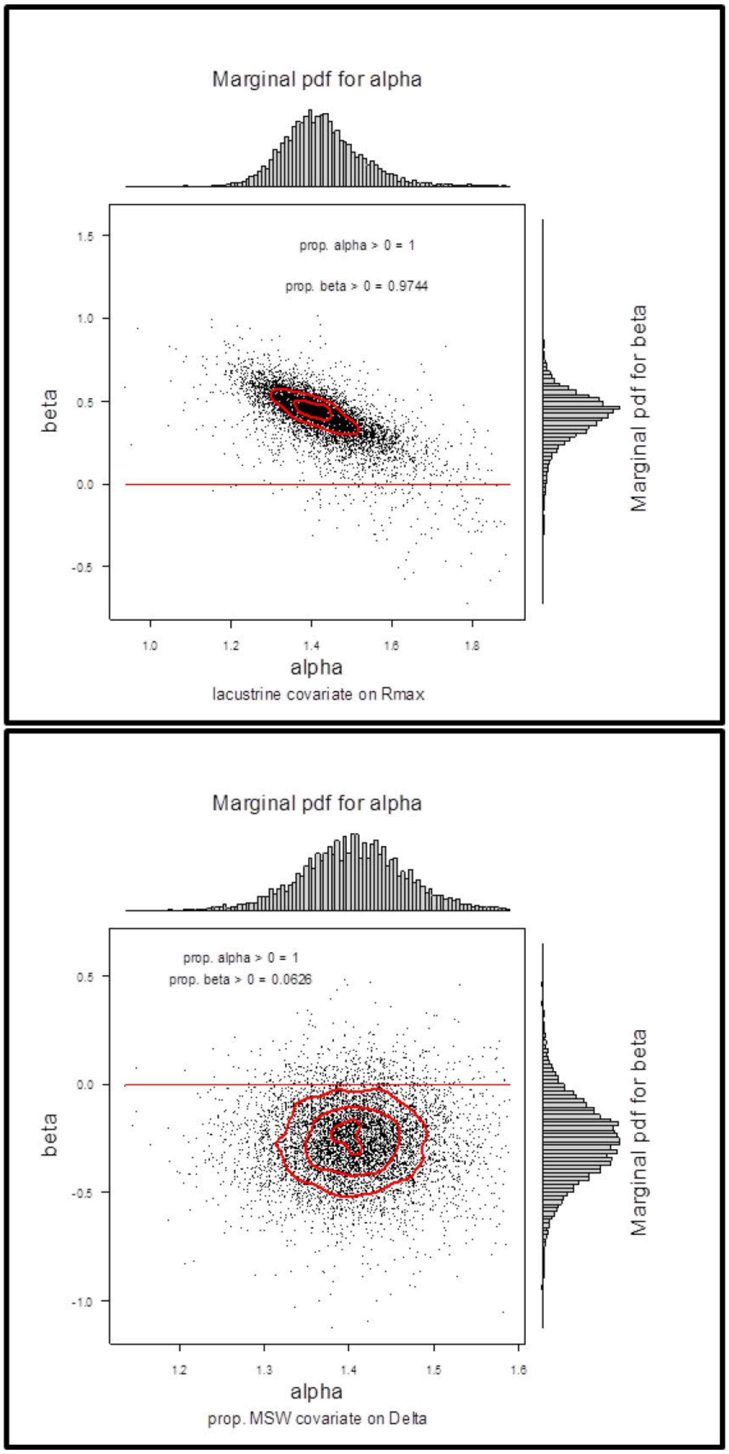


*Figure 39. Ricker: bivariate and marginal distributions of the coefficients (alpha, beta) of the covariate variables associated with Rmax (upper panel) and delta (lower panel). For Rmax, the function is: log(uRmax) = alpha + beta * Lac with Lac = 0 for fluvial rivers and Lac = 1 for lacustrine rivers. For delta, the function is : log(udelta) = alpha + beta * (pmsw – upmsw) where pmsw is the proportion of eggs from MSW salmon for the stock and upmsw is the mean of the proportions MSW over the 14 rivers. The one-tail significance of the beta coefficient for Rmax is 0.03 and for the beta coefficient for delta is 0.06.*

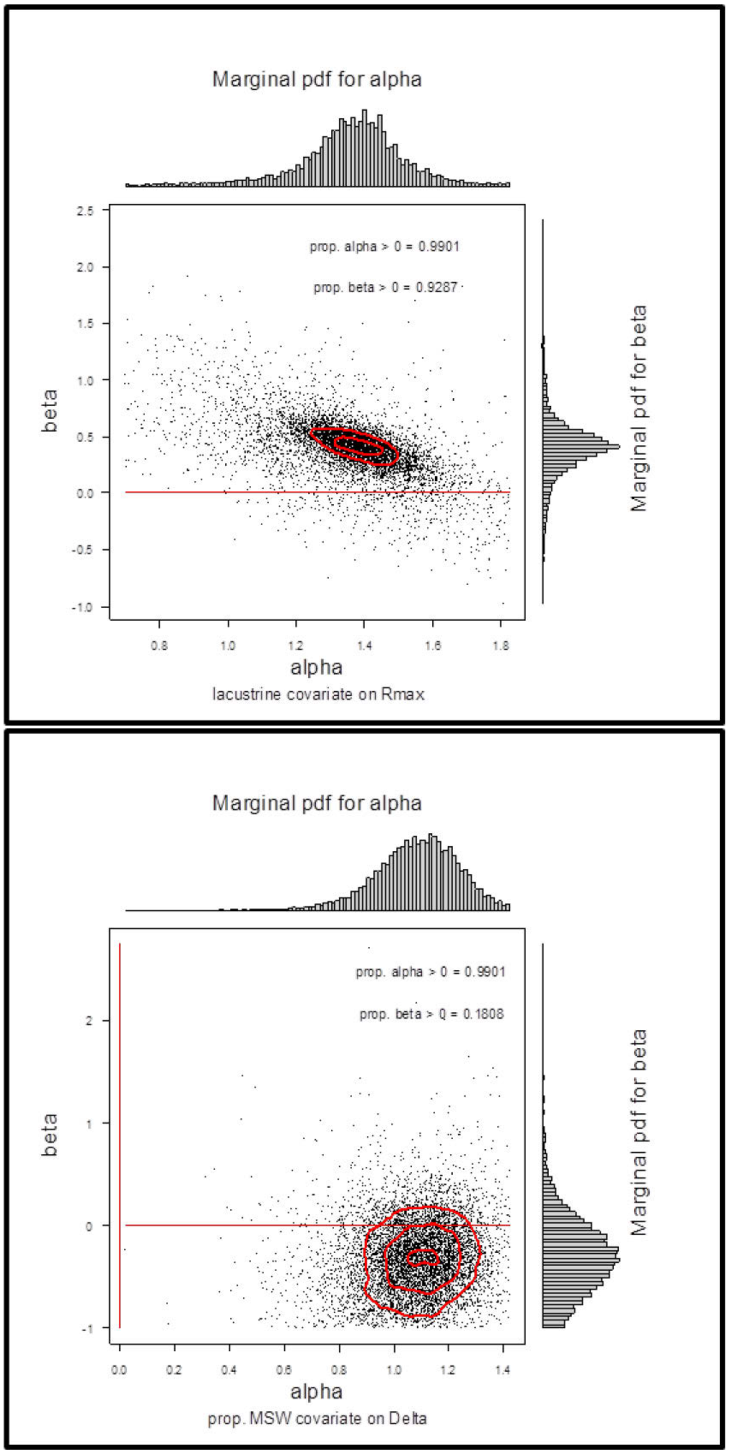


*Figure 40. Beverton-Holt: Bivariate and marginal distributions of the coefficients (alpha, beta) of the covariate variables associated with Rmax (upper panel) and delta (lower panel). For Rmax, the function is: log(uRmax) = alpha + beta * Lac with Lac = 0 for fluvial rivers and Lac = 1 for lacustrine rivers. For delta, the function is : log(udelta) = alpha + beta * (pmsw – upmsw) where pmsw is the proportion of eggs from MSW salmon for the stock and upmsw is the mean of the proportions MSW over the 14 rivers. The one-tail significance of the beta coefficient for Rmax is 0.07 and for the beta coefficient for delta is 0.18.*

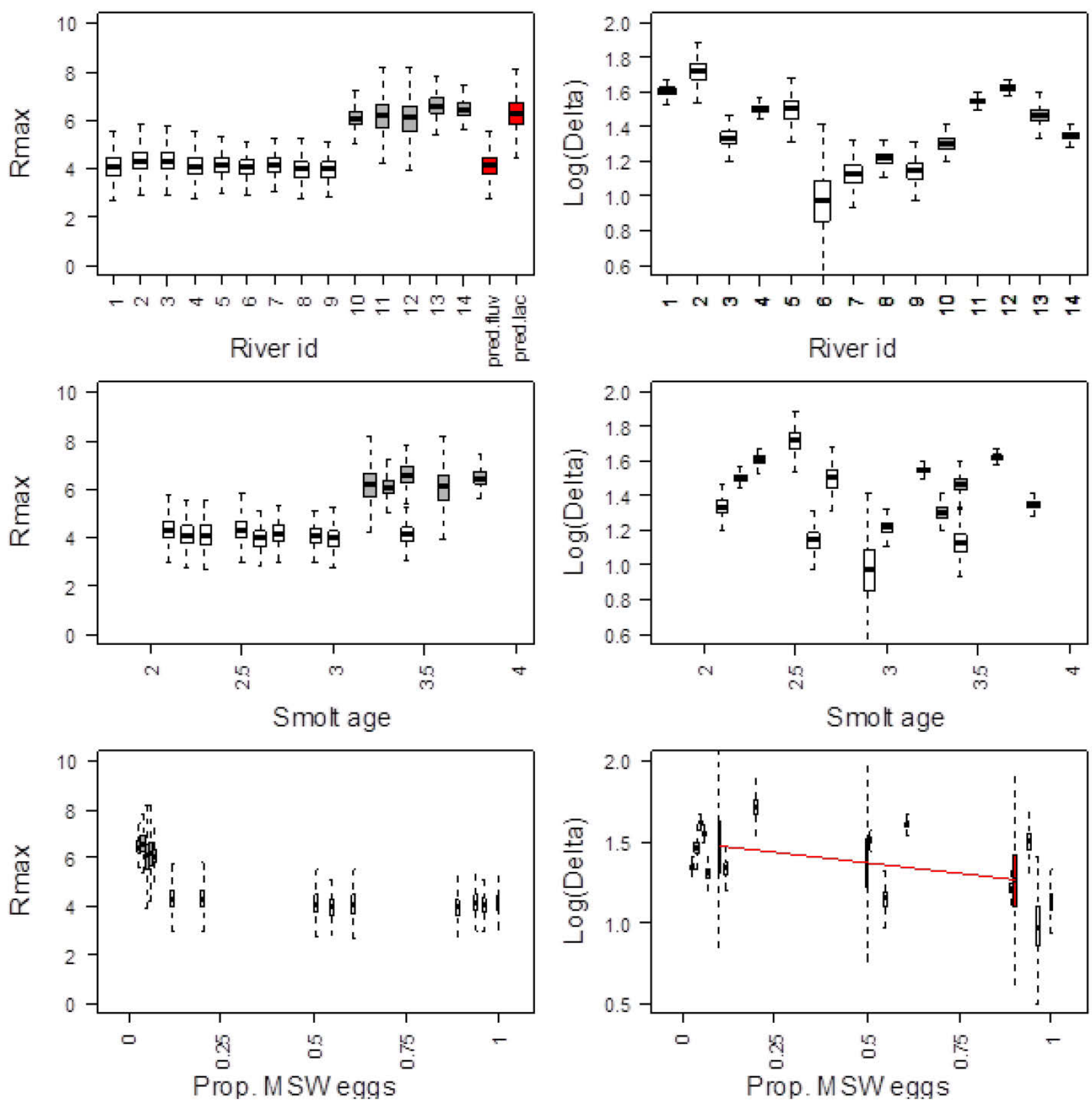


Figure 41. Ricker model hierarchical fits with covariates Rmax (presene/absence of lacustrine habitat) and delta (proportion MSW eggs) and relationships between Rmax and delta to: presence/absence of lacustrine, mean age of smolts, prop MSWeggs. White shading of boxplots are rivers with only fluvial habitat, grey shading of boxplots are rivers with lacustrine habitat. Red shading of boxplots are posterior distributions of the predicted values for fixed covariate values (fluvial or lacustrine for Rmax, proportion MSW eggs of 0.1, 0.5, and 0.9 for delta).

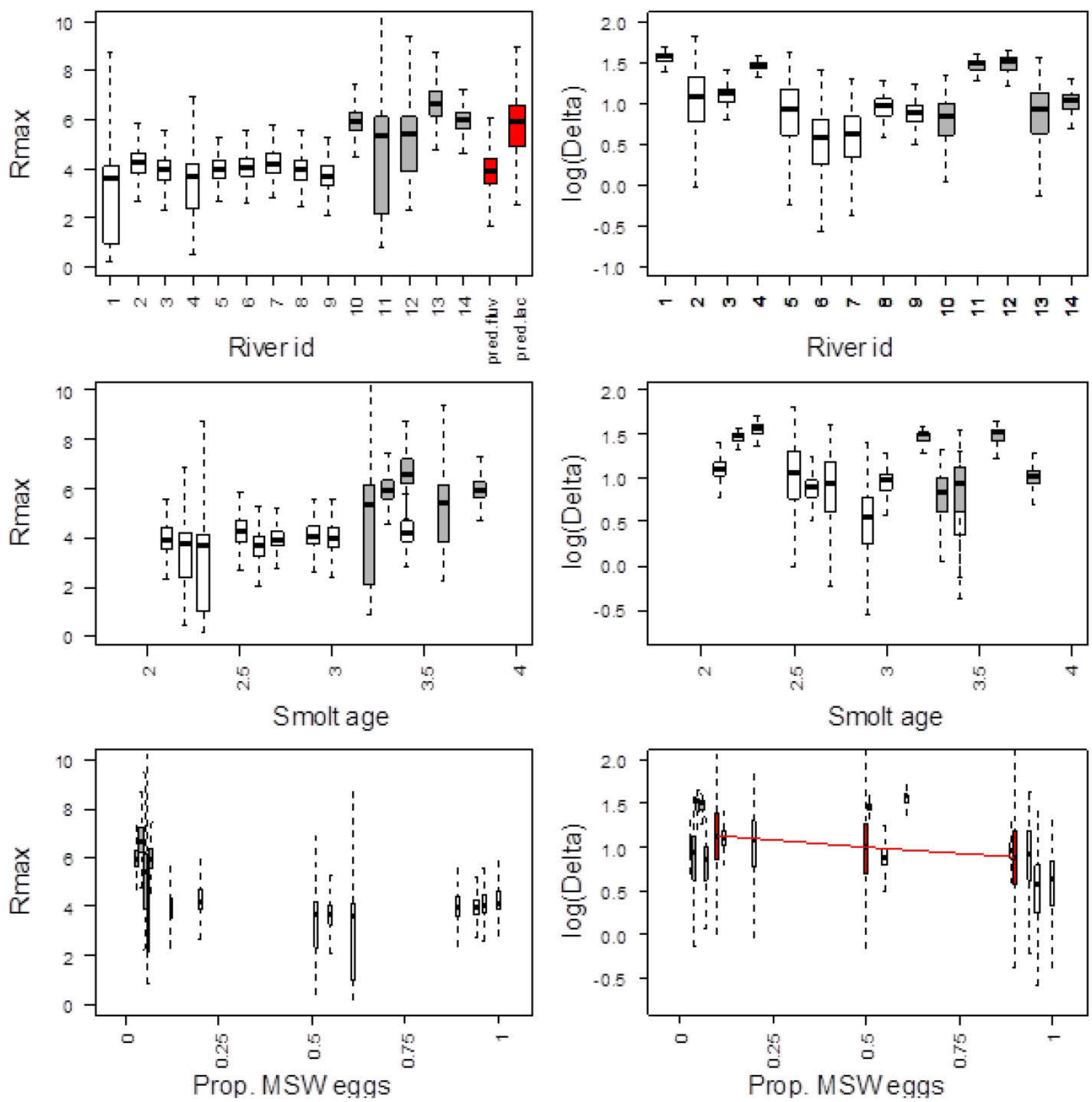


Figure 42. Beverton-Holt model hierarchical fits with covariates Rmax (presene/absence of lacustrine habitat) and delta (proportion MSW eggs) and relationships between Rmax and delta to: presence/absence of lacustrine, mean age of smolts, prop MSWeggs. White shading of boxplots are rivers with only fluvial habitat, grey shading of boxplots are rivers with lacustrine habitat. Red shading of boxplots are posterior distributions of the predicted values for fixed covariate values (fluvial or lacustrine for Rmax, proportion MSW eggs of 0.1, 0.5, and 0.9 for delta).

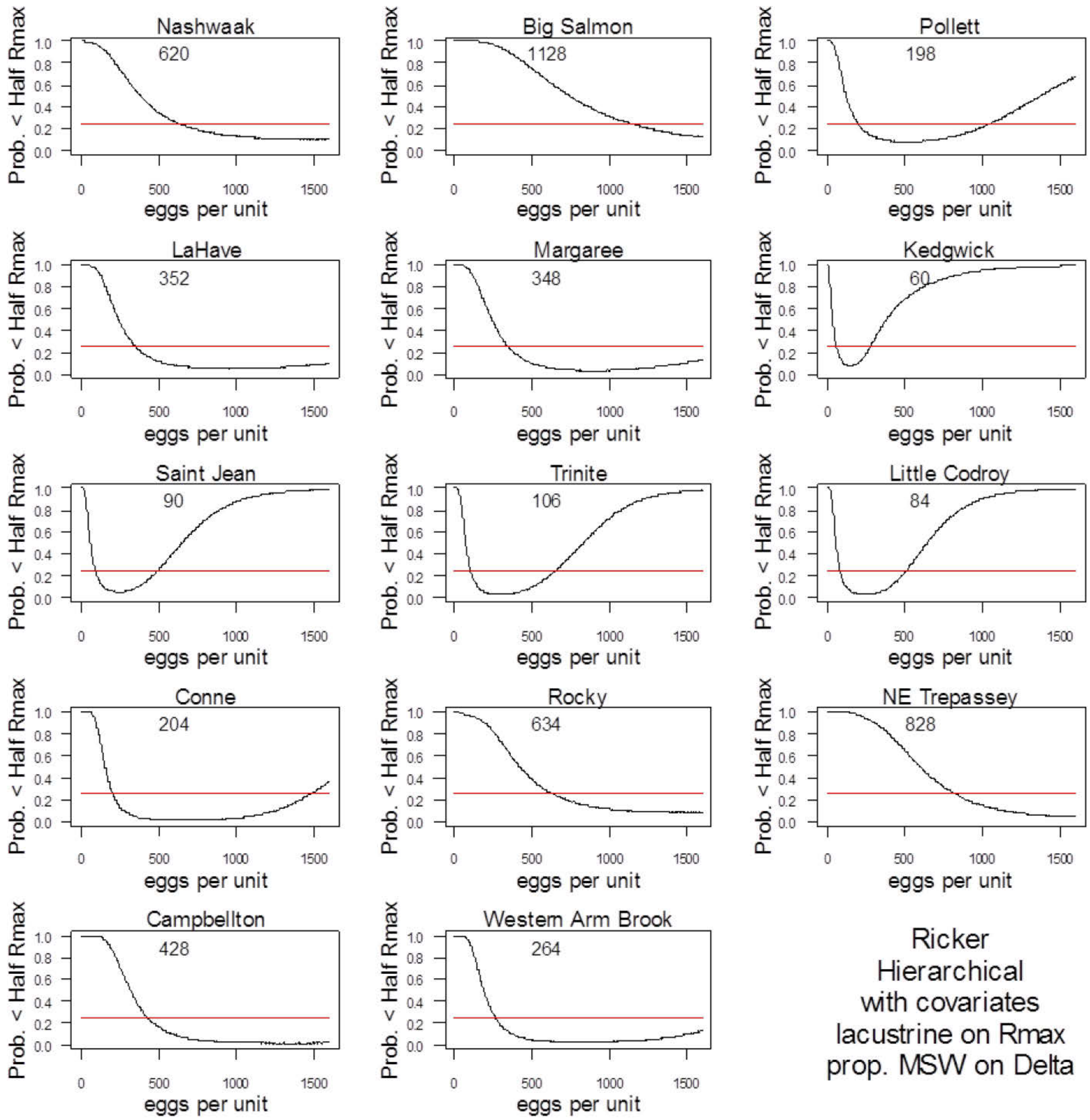


Figure 43. Eggs depositions versus probability that smolts produced will be < Half Rmax, taking into account the uncertainty of the Ricker stock and recruitment relationships and the estimated process error (sigma). Values on each panel are the eggs corresponding to a probability of ~ 0.25 of recruitment being below Half Rmax (S_{LRP}).

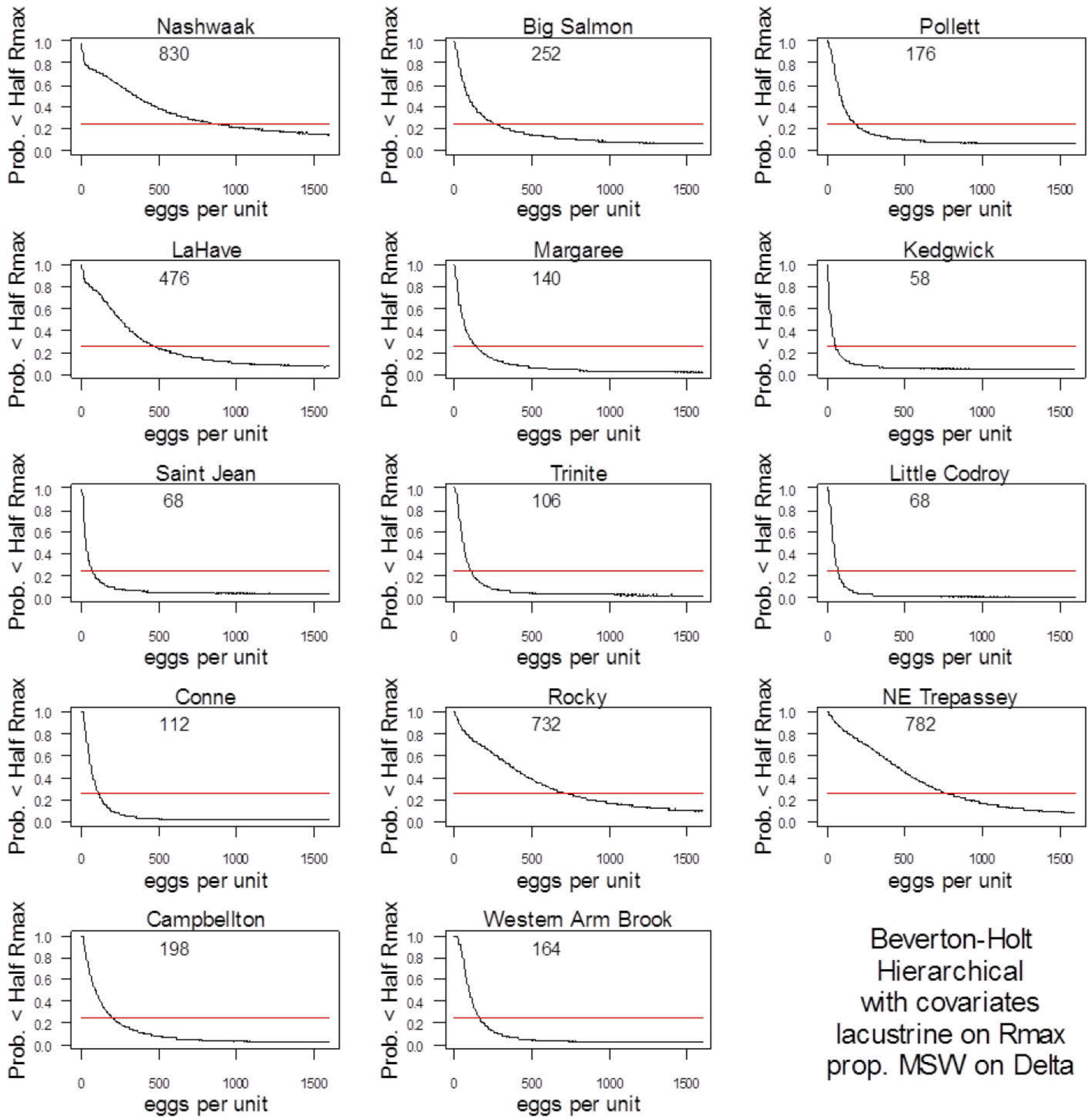


Figure 44. Eggs depositions versus probability that smolts produced will be < Half Rmax, taking into account the uncertainty of the Beverton-Holt stock and recruitment relationships and the estimated process error (sigma). Values on each panel are the eggs corresponding to a probability of ~ 0.25 of recruitment being below Half Rmax (S_{LRP}).

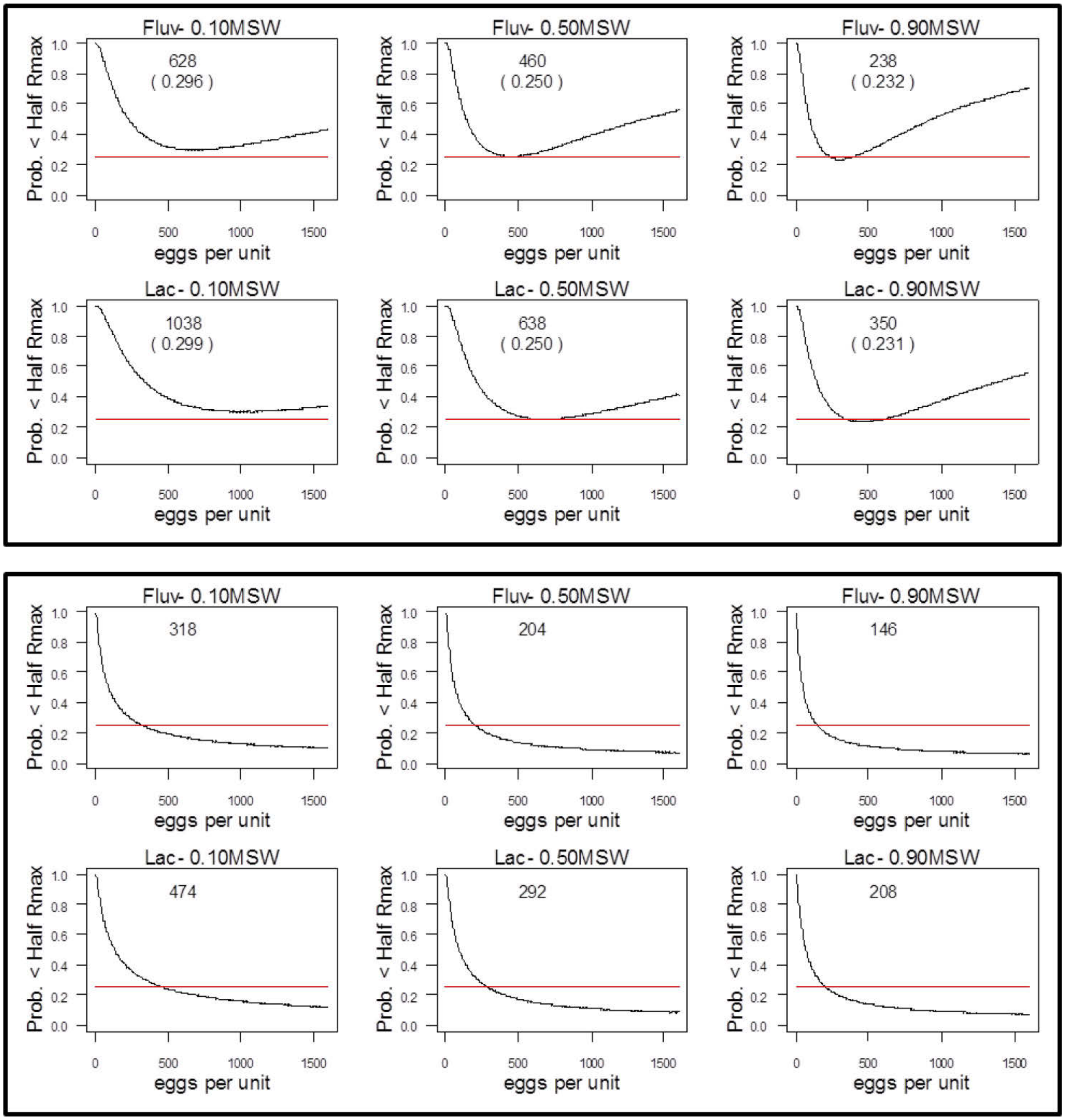


Figure 45. Eggs depositions versus probability that smolts produced will be < Half Rmax, for the Ricker (upper panel) and the Beverton-Holt (lower panel) models with presence of lacustrine habitat as covariate for Rmax and proportion of eggs from MSW salmon as covariate for delta. Predicted values shown are for rivers without lacustine habitat (Fluv) and with lacustrine habitat (Lac) for proportion of eggs from MSW as 0.1,(0.10MSW), 0.5 (p.50MSW), and 0.9 (0.90MSW). Values on each panel are the eggs corresponding to a probability of ~ 0.25 of recruitment being below Half Rmax (S_{LRP}) and the values in parentheses are the corresponding minimum probabilities when this exceeds 0.25.

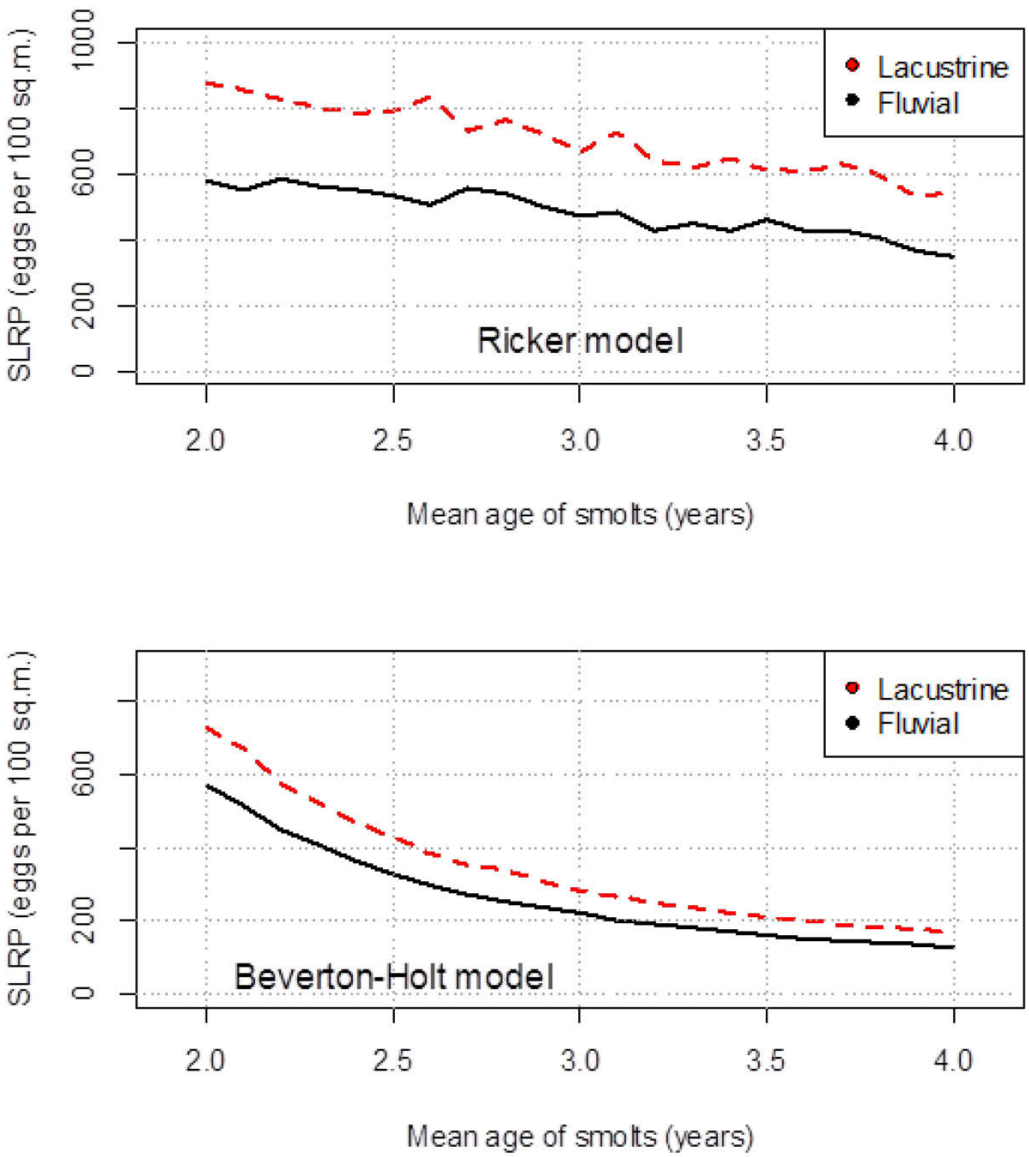


Figure 46. S_{LRP} (eggs per 100 m²) versus mean age of smolts for lacustrine rivers and rivers without lacustrine (fluvial) habitat for the Ricker model (upper panel) and the Beverton-Holt model (lower panel).

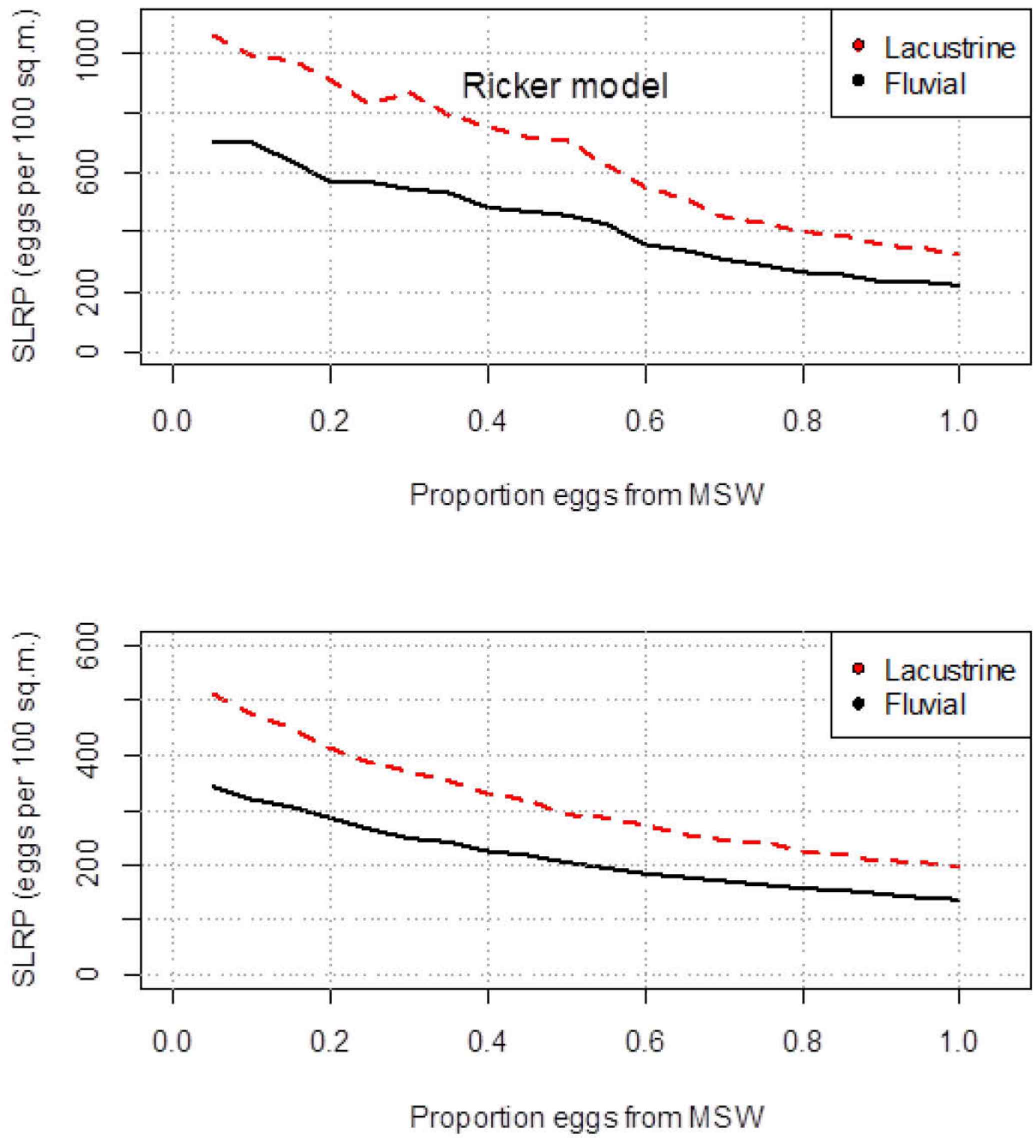
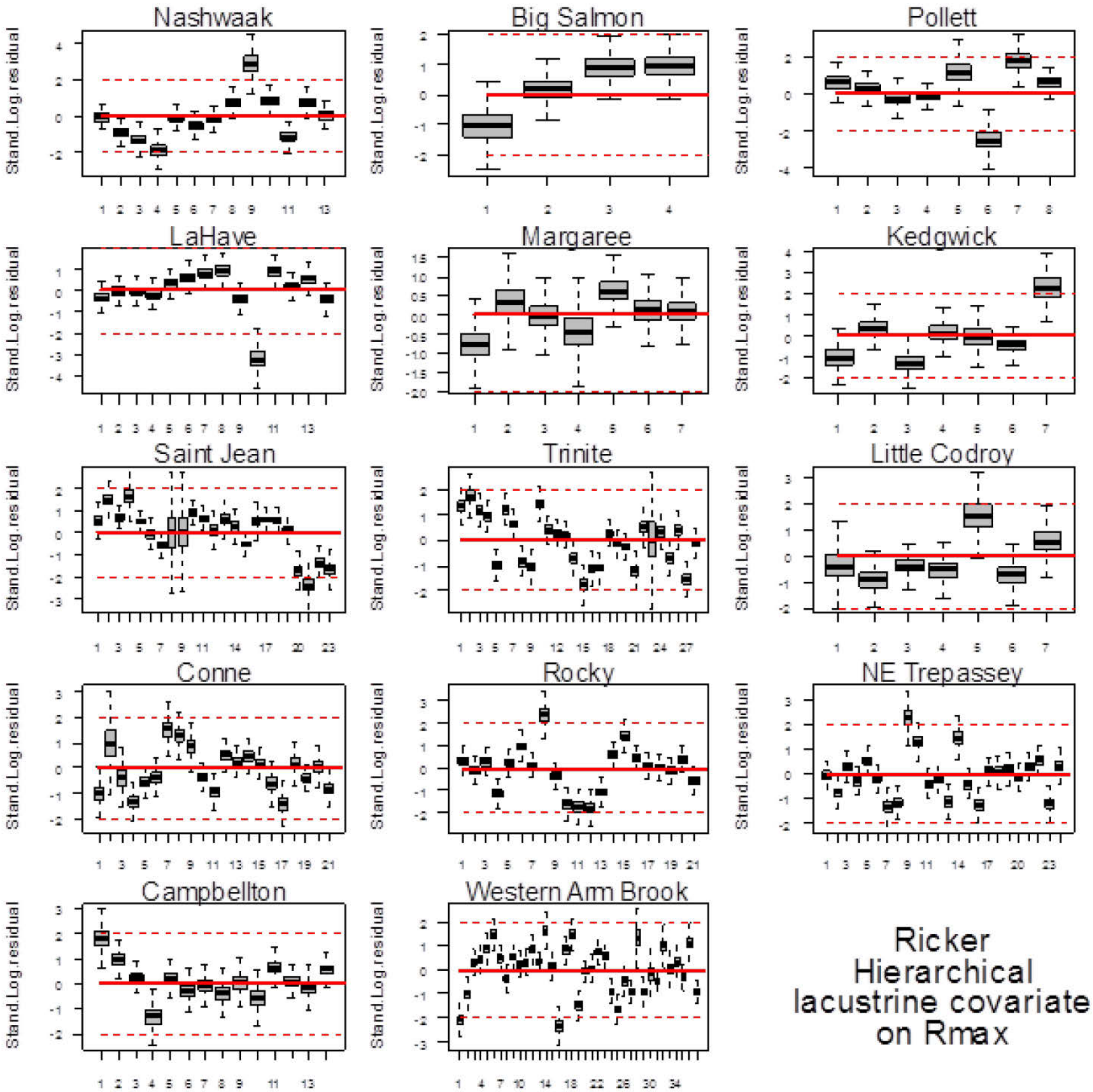
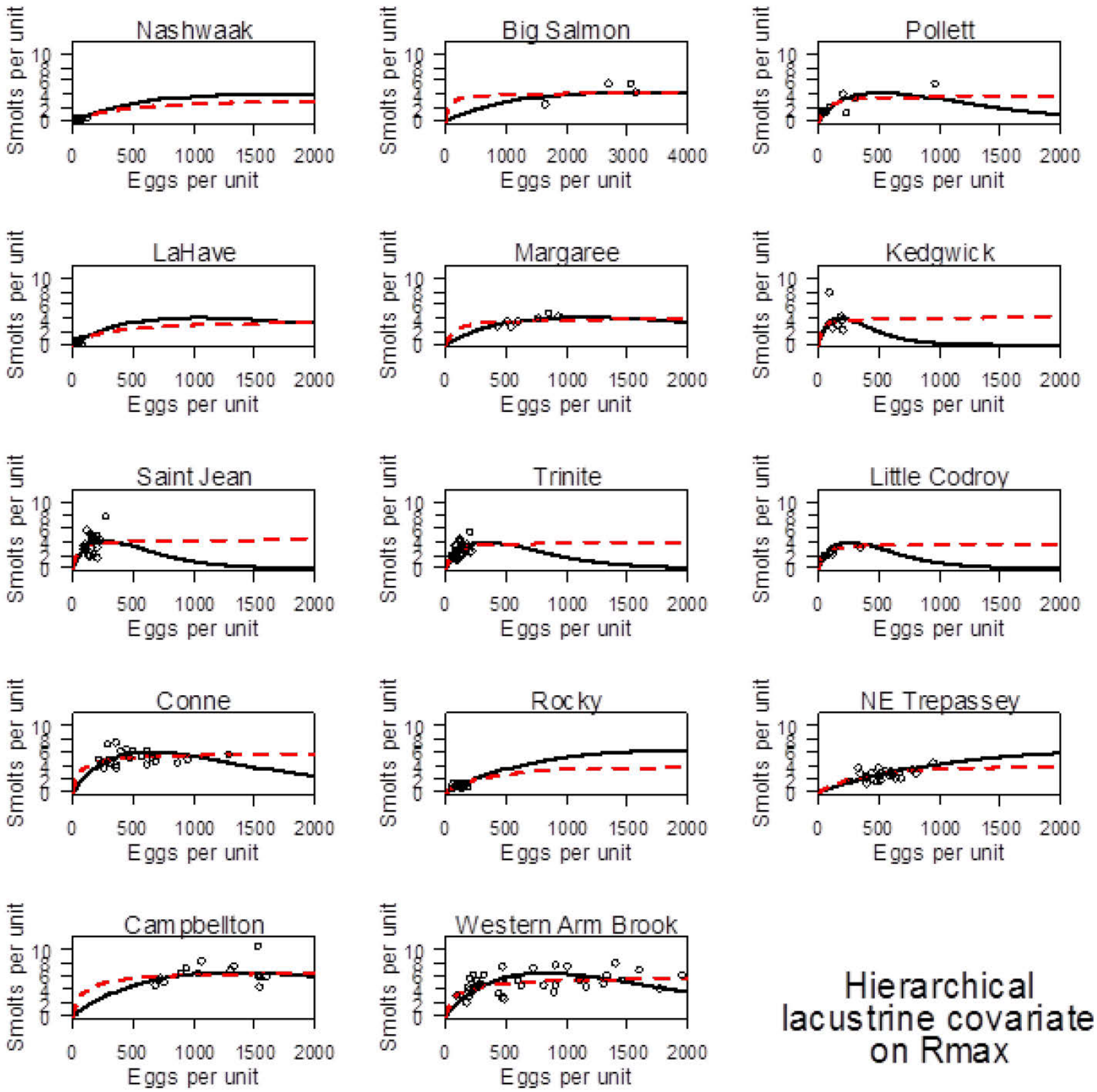


Figure 47. S_{LRP} (eggs per 100 m²) versus proportion of eggs from MSW salmon for lacustrine rivers and rivers without lacustrine (fluvial) habitat for the Ricker model (upper panel) and the Beverton-Holt model (lower panel).

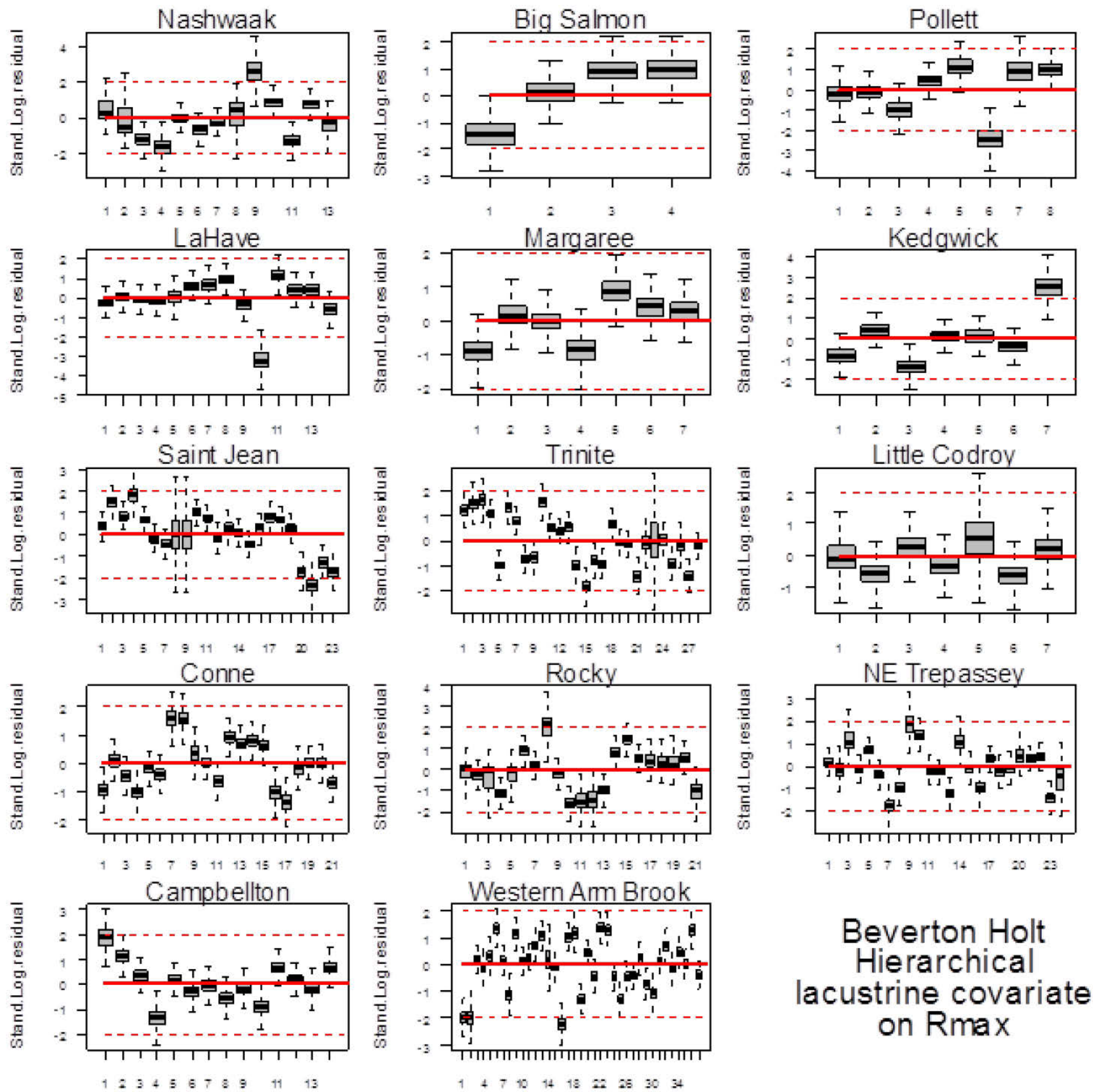
APPENDICES



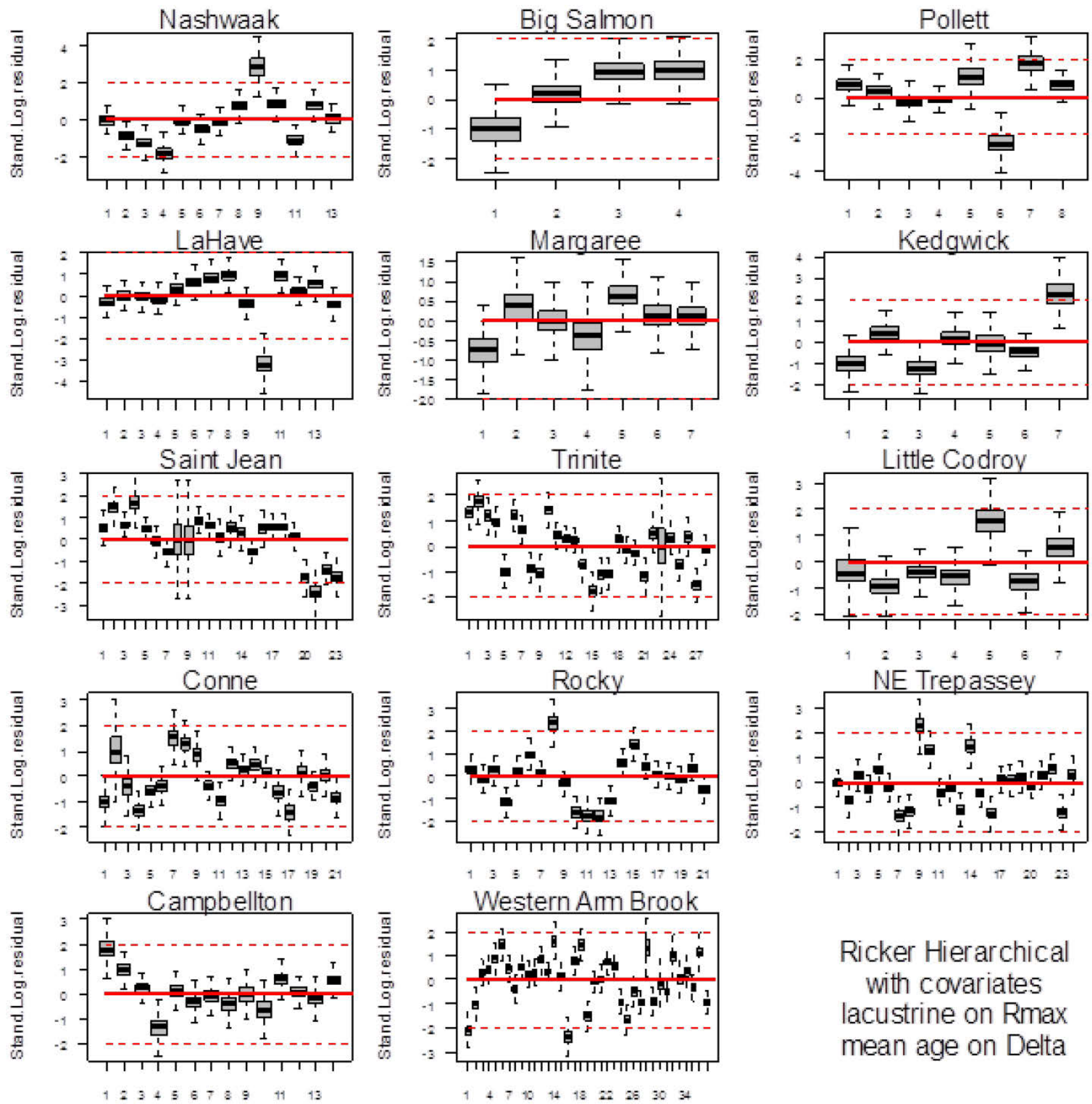
Appendix 1 Figure 1. Standardized log residuals of the individual fits from the hierarchical Ricker model with presence of lacustrine habitat as a covariate on Rmax. The residuals are standardized by river specific sigma. Residuals that have the interquartile range outside the range of -2 to +2 could be considered outliers and are estimated for Nashwaak, Pollett, LaHave, Saint-Jean, Rocky and Western Arm Brook.



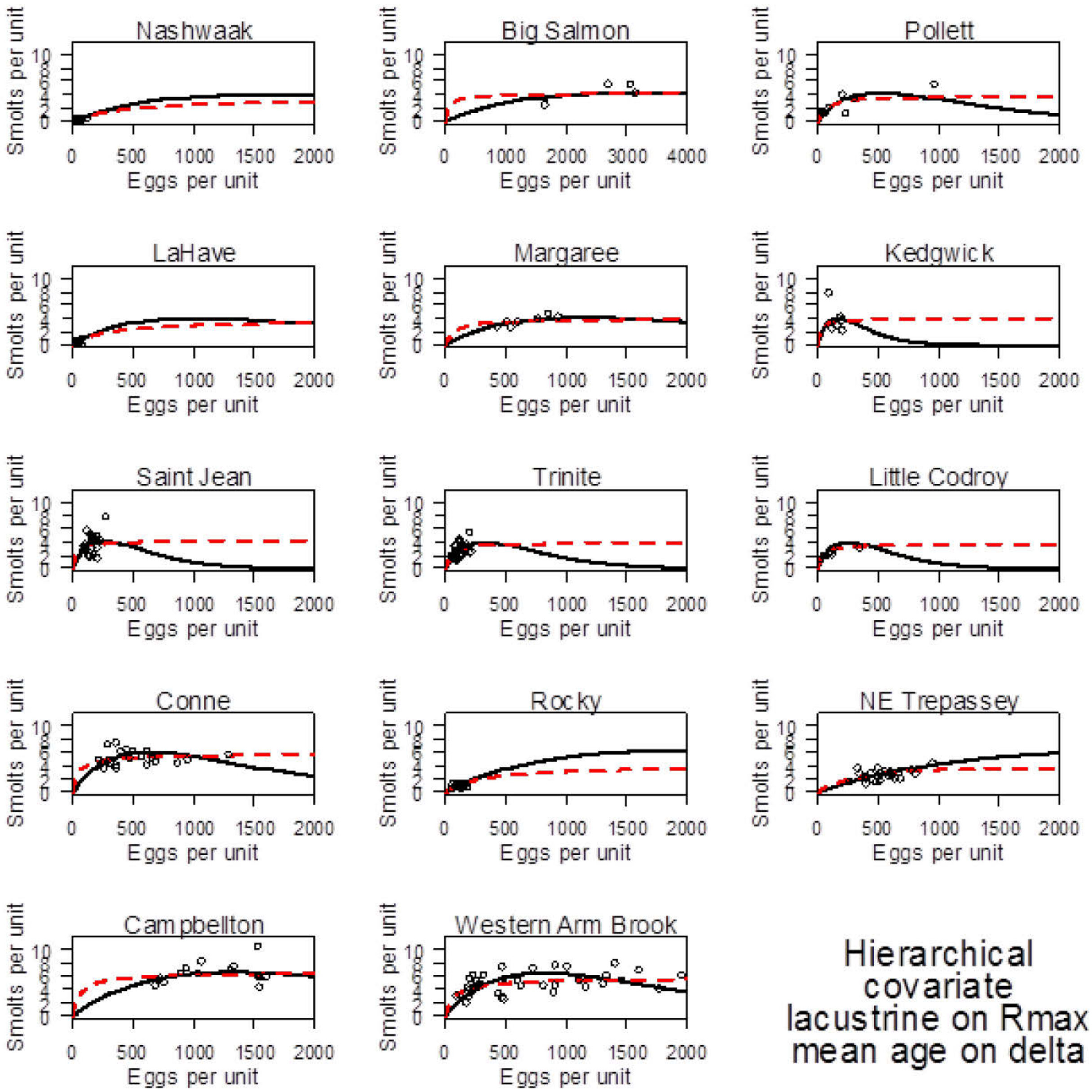
Appendix 1 Figure 2. Hierarchical Bayesian fits of Ricker (black line) and Beverton-Holt (dashed red line) egg to smolt hierarchical stock and recruitment relationships with presence of lacustrine habitat as covariate for Rmax for 14 rivers of eastern Canada,. The data are in densities per 100 m² with eggs on the horizontal axis and smolts on the vertical axis.



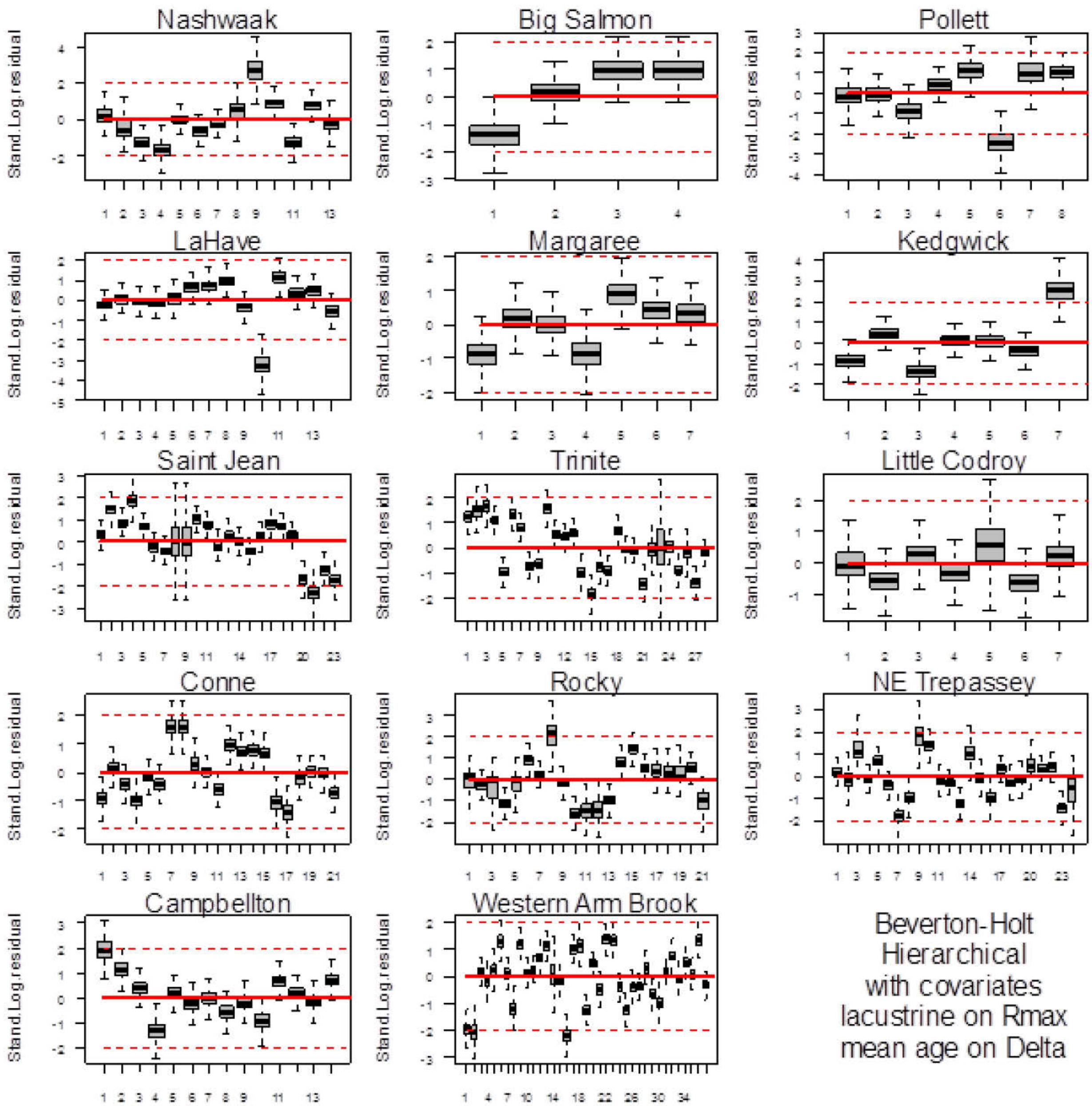
Appendix 1 Figure 3. Standardized log residuals of the individual fits from the hierarchical Beverton-Holt model with presence of lacustrine habitat as a covariates on Rmax. The residuals are standardized by river specific sigma. Residuals that have the interquartile range outside the range of -2 to +2 could be considered outliers and are estimated for Nashwaak, Pollett, LaHave, Kedgwick, Saint-Jean, and Western Arm Brook.



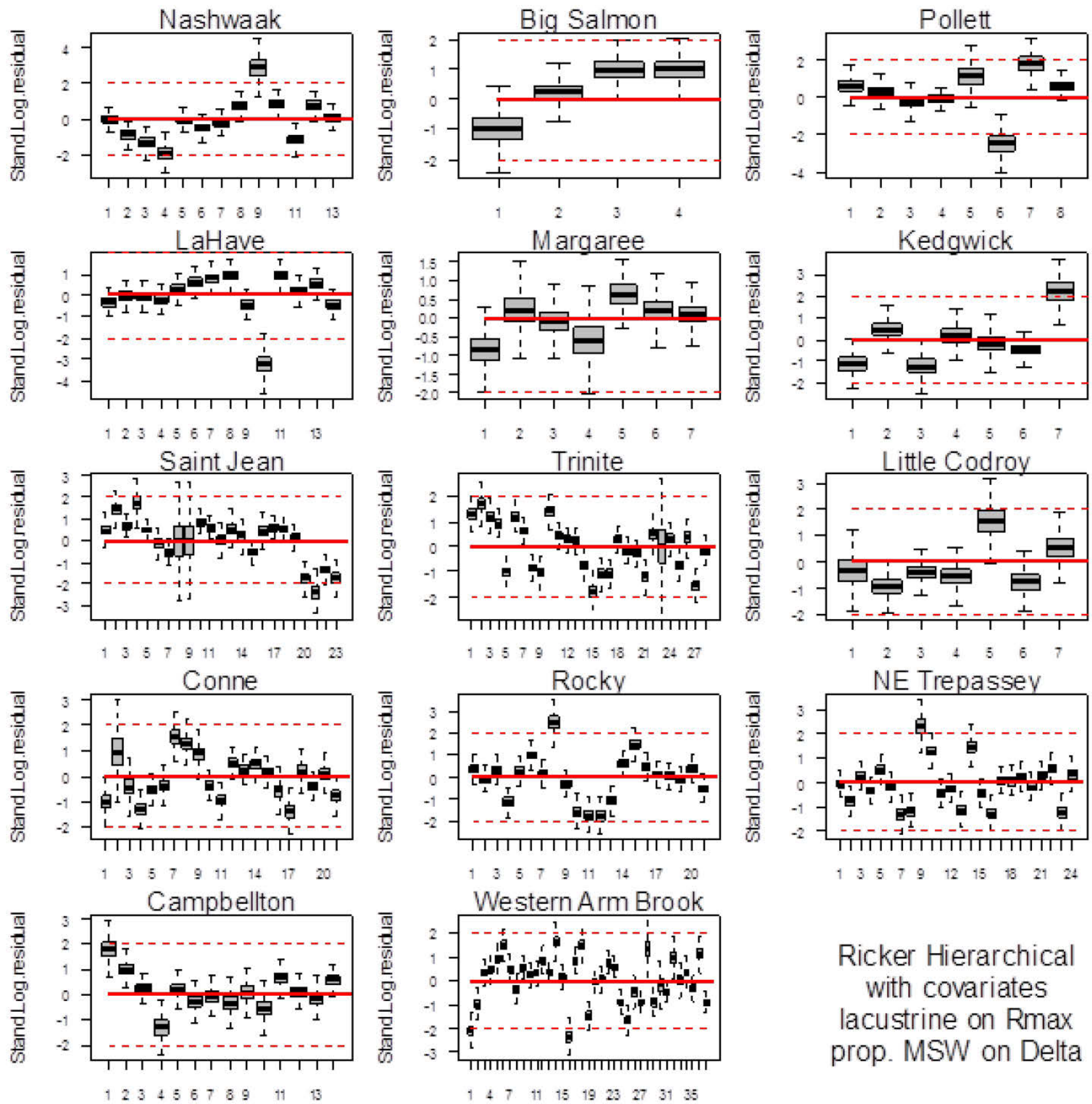
Appendix 2 Figure 1. Standardized log residuals of the individual fits from the hierarchical Ricker model with presence of lacustrine habitat as a covariates on Rmax and mean age of smolts as covariate for delta. The residuals are standardized by river specific sigma. Residuals that have the interquartile range outside the range of -2 to +2 could be considered outliers and are estimated for Nashwaak, Pollett, LaHave, Saint-Jean, Rocky, NE Trepassey, and Western Arm Brook.



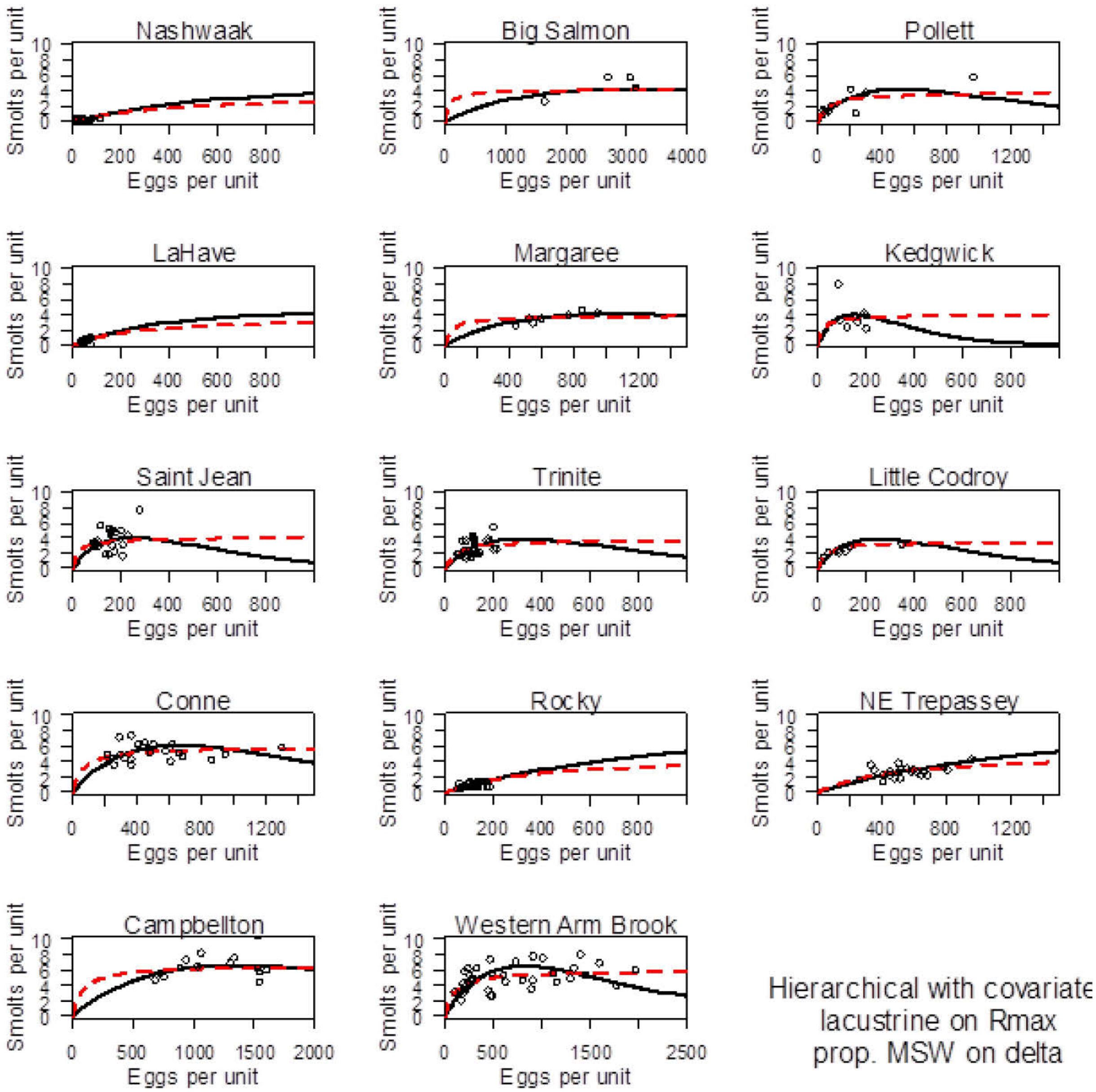
Appendix 2 Figure 2. Hierarchical Bayesian fits of Ricker (black line) and Beverton-Holt (dashed red line) egg to smolt hierarchical stock and recruitment relationships with presence of lacustrine habitat as covariate for Rmax and mean age of smolts as covariate for delta, for 14 rivers of eastern Canada,. The data are in densities per 100 m² with eggs on the horizontal axis and smolts on the vertical axis.



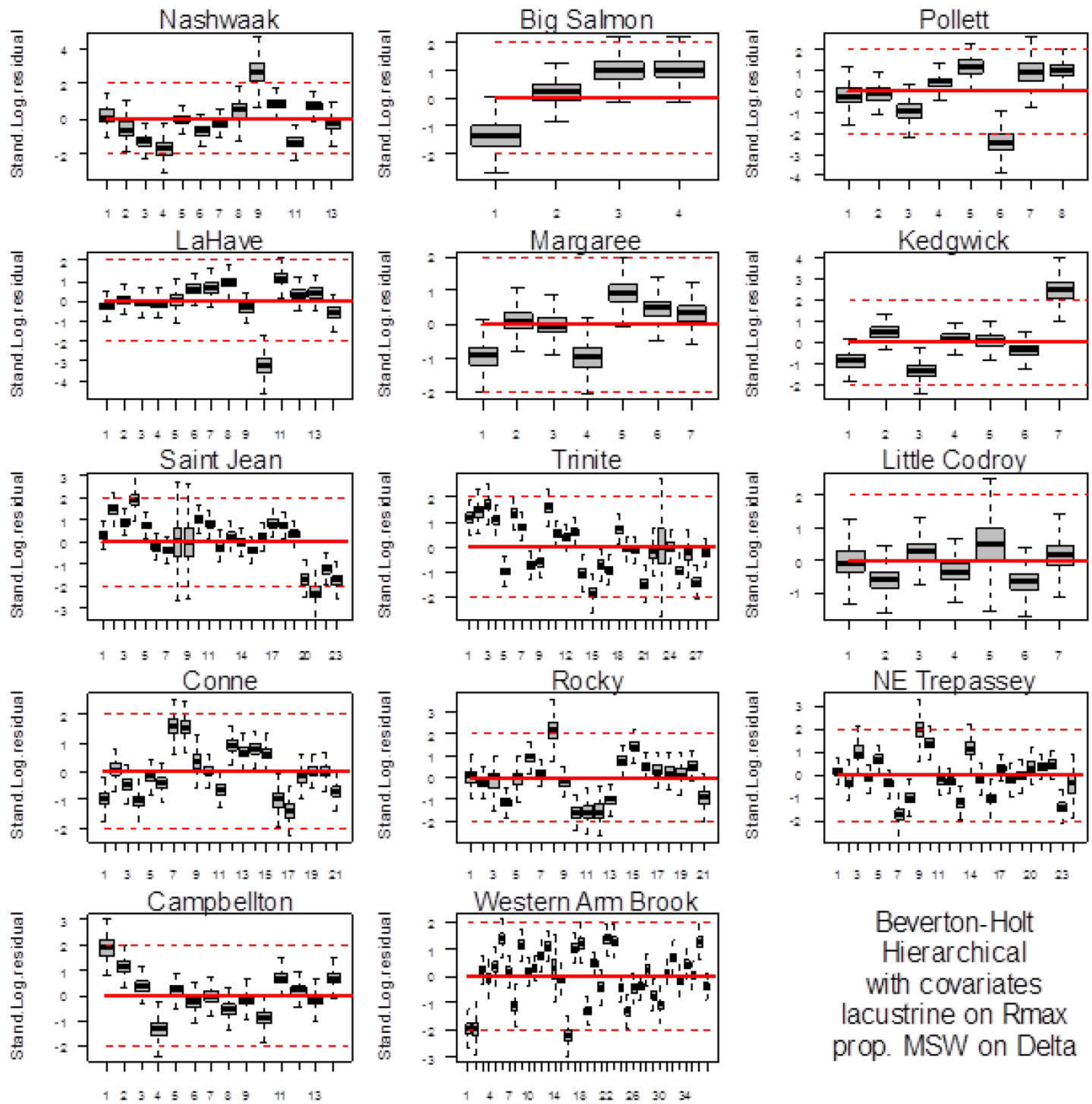
Appendix 2 Figure 3. Standardized log residuals of the individual fits from the hierarchical Beverton-Holt model with presence of lacustrine habitat as a covariates on Rmax and mean age of smolts as covariate for delta. The residuals are standardized by river specific sigma. Residuals that have the interquartile range outside the range of -2 to +2 could be considered outliers and are estimated for Nashwaak, LaHave, Kedgwick, Saint-Jean, and Western Arm Brook.



Appendix 3 Figure 1. Standardized log residuals of the individual fits from the hierarchical Ricker model with presence of lacustrine habitat as a covariates on Rmax and proportion MSW eggs as covariate for delta. The residuals are standardized by river specific sigma. Residuals that have the interquartile range outside the range of -2 to +2 could be considered outliers and are clearly shown for Nashwaak, LaHave, Saint-Jean, Rocky, and Western Arm Brook.



Appendix 3 Figure 2. Hierarchical Bayesian fits of Ricker (black line) and Beverton-Holt (dashed red line) egg to smolt hierarchical stock and recruitment relationships with presence of lacustrine habitat as covariate for Rmax and proportion MSW eggs as covariate for delta, for 14 rivers of eastern Canada,. The data are in densities per 100 m² with eggs on the horizontal axis and smolts on the vertical axis.



Appendix 3 Figure 3. Standardized log residuals of the individual fits from the hierarchical Beverton-Holt model with presence of lacustrine habitat as a covariates on Rmax and proportion MSW eggs as covariate for delta. The residuals are standardized by river specific sigma. Residuals that have the interquartile range outside the range of -2 to +2 could be considered outliers and is clearly shown for LaHave.