A Bayesian hierarchical model of size-at-age in ocean-harvested stocks — quantifying effects of climate and temporal variability

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Abstract: Quantifying size-at-age in harvested marine fish populations is a challenge with implications for both conservation and management. We describe a Bayesian hierarchical modeling approach for estimating mean and variation in size-at-age, incorporating environmental covariates. We apply the approach to two runs of Sacramento River Chinook salmon (*Oncorhynchus tshawytscha*): one data-rich (fall) and one data-poor (winter). We combine information on the size of recreationally harvested tagged fish and fishery size limits to reconstruct time-dependent marine size distributions. Our framework allows informed modeling of environmental effects on size-at-age, estimation of annual variability without overfitting, estimating size in years with limited data, and projecting sizes in future years. We found that fall run fish are anomalously small in years following Novembers with low values of the Northern Oscillation Index (NOI). Winter run data did not include anomalously low NOI years, but typical annual variability could be quantified. Importantly, our results suggest that it is possible to predict small size and slow growth during the upcoming fishery season on the basis of an environmental index available months in advance.

Résumé : La quantification de la taille selon l'âge dans les populations de poissons marins capturés est un défi de taille qui a des conséquences tant pour la conservation que pour la gestion. Nous décrivons une approche de modélisation hiérarchique bayésienne pour estimer la moyenne et la variation de la taille selon l'âge, qui intègre des covariables environnementales. L'approche est appliquée à deux migrations de saumons quinnat (*Oncorhynchus tshawytscha*) du fleuve Sacramento: dont une pour laquelle il y a abondance de données (automne) et l'autre pour laquelle les données sont peu nombreuses (hiver). Des données sur la taille de poissons marqués récoltés par pêche sportive et sur les limites de taille pour la pêche commerciale sont combinées afin de reconstituer les distributions des tailles des poissons marins en fonction du temps. Le cadre utilisé permet la modélisation des effets environnementaux sur la taille selon l'âge, l'estimation de la variabilité annuelle sans surapprentissage, l'estimation la taille en fonction de l'âge à partir de données limitées et la projection des tailles pour les années futures. Les poissons de la migration automnale se sont avérés anormalement petits durant les années suivant des mois de novembre présentant de faibles valeurs de l'indice d'oscillation septentrionale (NOI). Les données sur la migration hivernale n'incluaient aucune année de NOI anormalement faible, mais la variabilité annuelle typique pouvait être quantifiée. Fait à noter, nos résultats suggèrent qu'il est possible de prédire de faibles tailles et une croissance lente durant la saison de pêche à venir à la lumière d'un indice environnemental disponible des mois à l'avance.

[Traduit par la Rédaction]

Introduction

Quantifying variation in size-at-age of Pacific salmon (*Oncorhynchus* spp.) in the ocean is of great theoretical and applied interest. Variation in size-at-age has both theoretically (e.g., Mangel 1994; Fujiwara 2008) and empirically been linked to variation in maturation (Healey 1991; Morita et al. 2005; Wells et al. 2007), reproductive success (Healey 1991;

Heath et al. 1999; Quinn et al. 2004), and likely survival (McGurk 1996).

Detailed reconstructions of size-at-age are also important for management models. Pacific salmon fisheries are managed via a combination of quotas, seasonal closures, and minimum size limits. Thus, understanding size-at-age is vital to specifying size limits that will protect life stages or stocks of particular concern and to reconstruct contacts with

sublegal-sized fish from landed harvest. Variation in survival or maturation driven by variation in size-at-age is also relevant. For example, the allowable harvest of Sacramento River fall run Chinook (hereafter SRFC, *Oncorhynchus tshawytscha*) is largely governed by predictions of an adult abundance index based on the escapement of "jacks" (age 2 spawners) observed the previous year (O'Farrell et al. 2009). This formulation might be modified based on predicted variation in maturation or mortality.

Reconstructing size-at-age of ocean fish is challenging, and existing approaches suffer some drawbacks. Most estimates of size-at-age for ocean fish are extrapolated from observed sizes of returning spawners (e.g., California Department of Fish and Game 1989). Variation in the size of returning spawners may then be treated as a proxy for annual variability in growth (e.g., Hobday and Boehlert 2001; Wells et al. 2006), but the size distribution of returning spawners provides a biased estimate of ocean sizes because of size- and growth-dependent maturation (Hankin et al. 1993; Morita and Fukuwaka 2006), with large fish over-represented. Approaches based on increments in scales or otoliths (e.g., Wells et al. 2007, 2008) quantify relative growth rates but may not provide sufficient information on absolute sizes and provide only a filtered (by survival and possibly maturation) description of sizes at a particular time.

The most direct way of reconstructing the size distribution of fish in the ocean at a particular time is to make use of the size distribution of fish harvested from the ocean at that time. However, in addition to potential problems with size-dependent catchability, harvested fish length data reflect a truncated sample of the size distribution of fish in the ocean if minimum size limits are in place for the fishery.

Goldwasser et al. (2001) proposed a basic model for ocean size-at-age applicable to Pacific salmon, in which it was assumed that fish length was a normally distributed random variable with a mean and variance that depended on the age and month in question. Since harvest length data can be truncated, Goldwasser et al. (2001) constructed an appropriate likelihood and used maximum likelihood to estimate mean and standard deviation (SD) in length based on recoveries of coded wire tagged fish (Johnson 1990; Lapi et al. 1990; Nandor et al. 2010). In theory, application of this approach can be restricted to arbitrarily short time periods or specific locations, and estimates can then be compared to evaluate temporal and (or) spatial effects. However, in practice the method breaks down with sample sizes less than about 20 fish per strata (Goldwasser et al. 2001), and the approach provides no formal framework for dealing with missing data, predicting future observations, or correlating observed variability in mean size with potential covariates in a way that fully accounts for uncertainty in the individual estimates at different time points.

While ad hoc solutions to each of these challenges are possible, we propose use of a hierarchical modeling framework (Gelman et al. 2004; Royle and Dorazio 2008) to deal with these challenges in a conceptually unified way. A hierarchical modeling framework is also conducive to exploration of the relationship between environment and size, and when coupled with Bayesian methods (Gelman et al. 2004; Royle and Dorazio 2008), can leverage prior information about relationships between environmental indices and salmon growth (e.g., Wells et al. 2007, 2008).

We first illustrate application of the basic model to a data-rich situation, the SRFC, and to a data-poor situation, the Sacramento River winter run Chinook (hereafter SRWC). We then demonstrate how a hierarchical model allows estimation of the annual variation in SRWC length, while a purely fixed effect maximum likelihood (base) model does not. Finally, we show how combining the hierarchical modeling approach with moderately informative priors allows for estimation of the relationship between an environmental index and variation in size-at-age. This allows partitioning total variation into an environmentally driven component and a remainder that can be quantified and used to make more precise predictions of size-at-age in a year with known environmental conditions but no other auxiliary data.

Materials and methods

Study species and system

We illustrate our methodology with an application to SRFC and SRWC. The Sacramento River supports four runs of Chinook salmon with distinct life histories (Fisher 1994), named based on the timing of their return spawning migrations. Freshwater and estuarine ecosystems of the Sacramento River basin have been substantially altered (Yoshiyama et al. 2000) with deleterious effects on all four runs. SRFC is now numerically dominant (Lindley et al. 2009) and is the primary component of the ocean fishery harvest of Chinook off the coast of California and Oregon (O'Farrell et al. 2009), with hatchery production appearing to dominate natural production (Barnett-Johnson et al. 2007). SRFC, although not listed as threatened or endangered, are considered a "species of concern" (NOAA 2004), and the ocean and river fisheries were closed in 2008–2009 because of their record low abundance. SRWC was listed as threatened in 1989 and as endangered since 1994 under the United States Endangered Species Act (NOAA 2005).

The ocean fishery does not discriminate among stocks of salmon, but the coded wire tagging program (Johnson 1990; Lapi et al. 1990; Nandor et al. 2010) allows identification of marked hatchery fish from distinct stocks when the harvest is sampled. A variable fraction of the hatchery fish produced receive an adipose fin clip and a coded wire tag (CWT) implanted in the nasal cartilage, which allows identification of recovered fish to the individual release group level and hence its age, stock of origin, and other information not directly used in this analysis.

California Department of Fish and Game (CDFG) and Oregon Department of Fish and Wildlife attempt to sample approximately 20% of the landed ocean catch. Sampled fish with an adipose fin clip have their fork length (FL) measured and their head taken for later CWT extraction and decoding. Once the CWTs are decoded, the origin, harvest location, time, fishery sector (commercial, recreational), and length of the individual recovered fish are uploaded to the Regional Mark Processing Center hosted by the Pacific States Marine Fisheries Commission (Nandor et al. 2010). The length of the fishing season varies from year to year, but for most years there is at least some harvest during the period from March through October. Fishery management measures often include a minimum size limit for legal retention, which can vary by month, location, and fishery sector. Our analysis fo-

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Table 1. Symbols used and their definition.

Symbol	Definition
l	Total length of fish
$l*$	Size limit in effect when fish harvested
i	Subscript denoting individual fish out of total I in a class
y	Year of capture, with index running from $y = 1$ to $y = Y$
μ	Mean length of fish
σ	Standard deviation in length of fish
x	Long-term mean of annual mean length of fish (for low-NOI environment in model with environmental covariate)
s	Long-term mean of annual standard deviation in fish length
υ	Standard deviation in yearly mean lengths (after accounting for environmental covariate if appropriate)
τ	Standard deviation in yearly standard deviations in length
g_1	Critical value of NOI above which g_2 is added to mean length
g_2	Amount added to mean length if NOI is above g_1
E	Environmental state (NOI)
ϕ	Probability density function for normal (Gaussian) distribution
Φ	Cumulative distribution function for normal (Gaussian) distribution

cuses on the recreational fishery data, which has lower size than the commercial fishery, allowing for larger sample sizes for SRWC (which are smaller than SRFC and often below commercial minimum size limits). Data collection for the recreational fishery began in 1978, although initially SRWC were not tagged in great numbers, and all but two SRWC CWT recoveries have occurred since 1993. Our analysis included all fish captured through the end of the 2007 fishing season, prior to the 2008–2009 closure.

Data

Our analyses were based on records of recovered CWT fish obtained from the online Regional Mark Information System databases maintained by the Regional Mark Processing Center (http://www.rmpc.org; RMIS 1977). To estimate the size distribution of ocean fish, we queried "Standard Reporting, All Recoveries" for all CWT Chinook salmon originating from hatcheries in the Sacramento River basin of California recovered in the ocean recreational fishery off the coasts of California and Oregon. (Very few tagged Sacramento River origin Chinook are recovered north of Oregon: 1760/81 696 reported from 1976–2009 for SRFC and 3/511 for reported from 1980–2007 for SRWC; all fisheries combined.)

We calculated the age of SRWC, with an assumed birthday of 1 March, as recovery year – brood year + 1 (O'Farrell et al. 2011). In theory we would have to adjust the ages of fish caught in January or February, but the fishery was not open during those months in any of the years covered by this study. For SRFC, with an assumed birthday of 1 September, we calculated age as recovery year – brood year for fish recovered through the end of August and as recovery year – brood year + 1 for fish recovered in September or later (O'Farrell et al. 2009). We obtained information on the size limit in effect at the time and the port of each fish's landing using a database maintained by CDFG (M. Palmer-Zwahlen, CDFG, Santa Rosa, California, personal communication, 2010). Because fishery minimum size limits are based on total length (TL), we converted the reported FL (mm) of each recovered fish to TL (cm) using CDFG's established formula (M. Palmer-Zwahlen, CDFG, Santa Rosa, California, personal communication, 2010):

$$(1) \qquad \mathrm{TL_{cm}} = [1.0403(\mathrm{FL_{mm}}) + 26.504]/10$$

We thereby obtained for each CWT recovery individual its estimated total length (l), the size limit in effect ($l*$), its age, and the year (y) and month of recovery. For the purposes of this paper, we limited our evaluation of these data to age 3 fish recovered in the months of March, May, July, and September (every other month).

For each recovery, we then compared l to $l*$. A small fraction (64/7805 SFRC caught in March, May, July (age 3), or September (age 4) and 1/126 SRWC caught in July at age 3) of the recovered fish were shorter than the minimum size limit in effect when they were harvested. Either these fish had been retained illegally or their length was measured incorrectly upon sampling. Since we do not know what fraction of sublegal size fish are retained or how often measurement error misclassifies a legally retained fish as illegal, we excluded all fish shorter than the minimum legal size limit from our analysis. Additional analyses, not reported here, showed that the alternate assumption that all sublegal fish were at the minimum legal size for retention did not substantially affect our results.

Basic model (BM)

The basic model assumes that fish length in the ocean for a given run–age–month–year combination is distributed as a normal random variable (Goldwasser et al. 2001):

$$(2) \qquad p(l|\mu, \sigma) = \phi(l|\mu, \sigma^2)$$

where $p(l|\mu,\sigma)$ denotes the conditional probability density of l given its mean μ and standard deviation σ, and $\phi(l|\bullet)$ is the normal (Gaussian) probability density function evaluated at l. (In Table 1, we define all of the symbols used in this paper.)

For each run–age–month combination, we used the method of maximum likelihood to estimate the BM year-specific parameters, μ_y and σ_y ($y = 1,2, …, Y$), as follows. Because of the minimum size limit, the distribution of recovered fish lengths must be truncated to values greater than or equal to this limit. Therefore, the probability density of l for the ith observation in year y ($i = 1,2, …, I_y$) depends on the size limit $l*$ in effect (Goldwasser et al. 2001):

$$(3) \qquad p(l_{yi}|\mu_y, \sigma_y, l_{yi}^*) = \frac{\phi(l_{yi}|\mu_y, \sigma_y^2)}{1 - \Phi(l_{yi}^*|\mu_y, \sigma_y^2)}$$

where $\Phi(l^*|\bullet)$ is the normal (Gaussian) cumulative probability density function evaluated at l^*, thus renormalizing $\phi(\bullet)$ to integrate to 1 over the observable size range. The probability density for the length data set of year y (likelihood) assuming statistical independence of the observations is thus

$$(4) \qquad p(\widetilde{l}_y|\mu_y, \sigma_y, \widetilde{l}_y^*) = \prod_{i=1}^{I_y} p(l_{yi}|\mu_y, \sigma_y, l_{yi}^*)$$

where
$\widetilde{l}_y = \{l_{yi}; \; i = 1, 2, \dots, I_y\}$ and $\widetilde{l}_y^* = \{l_{yi}^*; \; i = 1, 2, \dots, I_y\}$.

To determine the maximum likelihood estimates of μ_y and σ_y (those values that together make the observed length data as likely as possible), we used the R statistical software (R Development Core Team 2010) package "bbmle" (Bolker and R Development Core Team 2011) function "mle2", with 95% confidence intervals extracted using function "confint", method "uniroot". The likelihood itself was calculated using the intrinsic functions "dnorm" and "pnorm" to compute $\phi(\bullet)$ and $\Phi(\bullet)$, respectively.

We limited this portion of the analysis to age 3 recoveries in the month of July. For SRWC, sample sizes for individual years were small (Table A1 of Appendix A), and we did not obtain convergent estimates for most years. Following the recommendations of Goldwasser et al. (2001), we required a minimum sample size of 20 fish for each age 3–month–year combination estimated. This precluded estimation of the size distribution of SRFC fish in 1979 and 2007 and of SRWC fish in all years except 2004.

Hierarchical model (HM)

The BM application above assumes no structural association among the model parameters for the various run–age–month–year combinations. Treating each run–age–month combination independently has the advantage that it allows for complex shapes of the size-at-age relationship because of the multiple effects on mean size that could vary both seasonally and with fish size, including growth, natural mortality, harvest, and maturation. For this reason, we continue to treat each run–age–month combination independently in our proposed HM. However, it is reasonable to assume that size-at-age in a particular month should be similar across years. Treating year as a random effect in the BM directly is one option for accounting for this structure; however, we pursued a HM approach because it provides a framework for dealing directly with missing data and predictions and can be extended to include environmental covariates (next section) in a manner that makes use of existing information concerning relationships between environment and growth.

The HM components include the likelihood of the observed lengths across years and a process model for the interannual joint distribution of μ_y and σ_y, itself dependent on hyperparameters. The likelihood is given by

$$(5) \qquad p(\widetilde{l}|\widetilde{\mu}, \widetilde{\sigma}, \widetilde{l}^*) = \prod_{y=1}^{Y} p(\widetilde{l}_y|\mu_y, \sigma_y, \widetilde{l}_y^*)$$

where

$$\widetilde{l} = \{\widetilde{l}_y; \; y = 1, 2, \dots, Y\},$$
$$\widetilde{l}^* = \{\widetilde{l}_y^*; \; y = 1, 2, \dots, Y\},$$
$$\widetilde{\mu} = \{\mu_y; \; y = 1, 2, \dots, Y\}, \; \text{and}$$
$$\widetilde{\sigma} = \{\sigma_y; \; y = 1, 2, \dots, Y\}$$

For the process model component, we assumed that μ_y and σ_y were statistically independent and that each was distributed as a normal random variable across years:

$$(6) \qquad p(\mu_y|x, \upsilon) = \phi(\mu_y|x, \upsilon^2)$$

and

$$(7) \qquad p(\sigma_y|s, \tau) = \phi(\sigma_y|s, \tau^2)$$

While a gamma distribution bounded at zero is typically recommended for modeling standard deviations, for our data set the fitted gamma distributions were well-approximated by normal distributions, so we used the normal distribution for ease of interpretation.

We used Bayesian inference methods to estimate the HM size-at-age parameters, including the yearly means $\widetilde{\mu}$ and standard deviations $\widetilde{\sigma}$, the long-term (across years) average mean x and standard deviation s, and the variability in the yearly means υ and standard deviations τ. Bayesian inference focuses on the posterior distribution (joint density) of the parameters given the observed length data, which is easy to specify within a constant of proportionality given the hierarchical structure of the HM (Gelman et al. 2004; Royle and Dorazio 2008). If $p(x,s,\upsilon,\tau)$ is the prior distribution for the hyperparameters, which we assumed to be statistically independent so that $p(x,s,\upsilon,\tau) = p(x)p(s)p(\upsilon)p(\tau)$, then the posterior distribution is

$$(8) \qquad p(\widetilde{\mu}, \widetilde{\sigma}, x, s, \upsilon, \tau|\widetilde{l}, \widetilde{l}^*)$$
$$\propto p(\widetilde{l}|\widetilde{\mu}, \widetilde{\sigma}, \widetilde{l}^*)p(\widetilde{\mu}|x, \upsilon)p(\widetilde{\sigma}|s, \tau)p(s, x, \upsilon, \tau)$$

Rather than estimating the joint posterior distribution directly, we randomly sampled from it enough times to determine its properties indirectly using the Metropolis algorithm, a Markov chain Monte Carlo (MCMC) simulation method (Gelman et al. 2004). Our implementation used the Metropolis algorithm to sample sequentially from a set of conditional univariate posterior distributions, one for each parameter, each conditioned on the full set of the remaining parameters and data. The set of univariate posterior distributions were as follows (inconsequential conditioning parameters are suppressed below):

$$(9) \qquad p(x|\widetilde{\mu}, \upsilon) \propto p(x)p(\widetilde{\mu}|x, \upsilon)$$

$$(10) \qquad p(\upsilon|\widetilde{\mu}, x) \propto p(\upsilon)p(\widetilde{\mu}|x, \upsilon)$$

$$(11) \qquad p(\widetilde{\mu}|x, \upsilon, \widetilde{\sigma}, \widetilde{l}, \widetilde{l}^*) \propto p(\widetilde{\mu}|x, \upsilon)p(\widetilde{l}|\widetilde{\mu}, \widetilde{\sigma}, \widetilde{l}^*)$$

$$(12) \qquad p(s|\widetilde{\sigma}, \tau) \propto p(s)p(\widetilde{\sigma}|s, \tau)$$

$$(13) \qquad p(\tau|\widetilde{\sigma}, s) \propto p(\tau)p(\widetilde{\sigma}|s, \tau)$$

$$(14) \qquad p(\widetilde{\sigma}|s, \tau, \widetilde{\mu}, \widetilde{l}, \widetilde{l}^*) \propto p(\widetilde{\sigma}|s, \tau)p(\widetilde{l}|\widetilde{\mu}, \widetilde{\sigma}, \widetilde{l}^*)$$

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The MCMC algorithm steps sequentially through each of these distributions, taking a random sample conditioned on the most recently accepted values of the remaining parameters. The prior distributions used, along with further details describing our MCMC implementation and diagnostics, are provided in the online Supplementary Materials[1]. We generally used diffuse priors. We used uniform priors on the standard deviations of random effects (υ, τ), as suggested by Gelman (2006).

Exploration of environmental covariates

In this paper, we do not provide a detailed treatment of environmental drivers; however, we illustrate an application of using an environmental covariate with some ability to predict growth. We examined the correlation between a variety of potentially useful environmental metrics at different lags in predicting mean length (as estimated by the BM) of age 3 SRFC fish in July from 1978 to 2006. We restricted our analysis to values of indices in the latter half of the previous year so that we would be working with indices available when setting fishery management measures for the coming season, a process which begins in February, choosing several candidate indices based on the findings of Wells et al. (2006): the Northern Oscillation Index (NOI) values in each month July–December of the previous year (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/NOIx/noix_download.html); the Multivariate El Niño – Southern Oscillation (ENSO) Index (MEI) in each month July–December of the previous year (ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/soi, via http://www.esrl.noaa.gov/psd/enso/mei/); the integrated summer Pacific Decadal Oscillation (PDOs) averaged over June through August of the previous year (http://www.beringclimate.noaa.gov/data/index.php); the Aleutian Low Pressure Index (ALPI) for the previous year (http://www.pac.dfo-mpo.gc.ca/science/species-especes/climatology-ie/cori-irco/indices/alpi.txt).

Generally, positive MEI values indicate ENSO-like conditions, positive NOI values indicate stronger North Pacific High conditions, positive PDO values indicate warm-water conditions along the entire northeast Pacific coast, and positive ALPI conditions indicate a stronger Aleutian low-pressure system, warmer conditions, and stronger Alaskan gyre.

For this portion of our work, we only considered SRFC because their associated data spanned more years and covered a broader range of environmental conditions than did the SRWC data (Appendix A, Table A1). We corrected significance tests of correlations for the effects of temporal autocorrelation using the methods of Pyper and Peterman (1998), although our primary interest is not hypothesis testing per se but simply picking an index with potential predictive power, and we note that this approach may be overly conservative (Fujiwara and Mohr 2009). We thus selected a single significant, highly correlated metric (NOI the previous November) for inclusion in the hierarchical model with environmental covariate.

NOI represents the difference between the sea level pressure of the January climatological mean position of the North Pacific High and the sea level pressure near Darwin, Australia (Schwing et al. 2002). Functionally, it relates positively to the strength of the California Current, northerly winds, and upwelling. The conditions in November, as considered here, may represent a degree of preconditioning occurring along the California Current that has been related to aspects of production in the system in the coming spring (Schroeder et al. 2009).

Hierarchical model with environmental covariate (HME)

Based on the exploration of environmental covariates described above and the apparent bimodality of the distribution of mean sizes (see Results, Fig. 1), we modeled a step-function response of the mean size-at-age to values of NOI above or below a fitted threshold. We evaluated both the location of the threshold and the size of the step by substituting the following distribution for that specified in eq. 6:

$$(15) \qquad p(\mu_y | x, \upsilon, \widetilde{g}) = \phi\left[\mu_y | x + g_2 I(E_y > g_1), \upsilon^2\right]$$

where E_y is the value of environmental variable E for year y (in this case, NOI the previous November), $\widetilde{g} = \{g_1, g_2\}$ is the environmental threshold (g_1) and response step size (g_2) for the month–age under consideration, and $I(\bullet)$ is an indicator function equal to 1 if $\bullet$ is true and equal to 0 otherwise. The standard deviation in length varied among years as in eq. 7 (and was independent of E).

The HME posterior distribution within a constant of proportionality is therefore

$$(16) \qquad p(\widetilde{\mu}, \widetilde{\sigma}, x, s, \upsilon, \tau, \widetilde{g} | \widetilde{l}, \widetilde{l}^*, \widetilde{E})$$
$$\propto p(\widetilde{l} | \widetilde{\mu}, \widetilde{\sigma}, \widetilde{l}^*) p(\widetilde{\mu} | x, \upsilon, \widetilde{g}, \widetilde{E}) p(\widetilde{\sigma} | s, \tau) p(x, s, \upsilon, \tau, \widetilde{g})$$

As before, we assume statistical independence of the hyperparameters. As in the HM, we used the Metropolis algorithm MCMC to sample the univariate full conditional posterior distributions of each parameter sequentially, rather than sampling directly from the joint posterior specified in eq. 16 (see Supplementary Material[1] for details). Our priors for the critical level of the environment g_1 reflected the assumption that it lay somewhere in the observed 1978–2007 range of observed values, with the most likely value close to that distinguishing El Nino type conditions from other years. The response g_2 was essentially unconstrained, reflecting the assumption that El Nino type conditions are likely important, but not assuming any sign or magnitude of response.

Ages and months analyzed

For illustrative purposes, we present results for age 3 fish, the most abundant age-class among fish caught in the California ocean recreational Chinook fishery. For SRFC, we present estimates of size-at-age in March, May, July, and September (at which time fish transition to age 4 based on an assumed 1 September birthday) to illustrate changes in mean length through time (which reflects growth, but also size-selective mortality, fishing, and potentially loss of maturing fish from the system as they begin to return to fresh water). March is typically the first month of the year open to fishing. For SRWC, we present results only for July, the month with the greatest sample size. Because we have no SRWC data from years following low NOI, we present the environmental covariate model only for SRFC.

Assessment of predictive ability

One advantage of the HM approach is the natural frame-

Fig. 1. Annual mean length of age 3 fish in July predicted for (*a*) Sacramento River fall run Chinook salmon (SRFC) and (*b*) Sacramento River winter run Chinook salmon (SRWC) populations. Note different *y*-axis scales in the two panels. Filled circles are basic model (BM) estimates with 95% confidence intervals, and open circles are hierarchical model (HM) estimates with 95% credible intervals. The solid horizontal line indicates the interannual mean size estimated under the HM (posterior mean), with the dashed horizontal lines denoting ±1 standard deviation and the dotted horizontal lines denoting ±2 standard deviations in annual mean length. Note that use of the HM allows estimation of means for years with sample sizes too small to fit the BM. (*c*) Histogram of BM annual mean length estimates; open bars are SRFC in typical Northern Oscillation Index (NOI) years, grey bars are SRFC in low NOI years, and the black bar is SRWC in the single year with sufficient SRWC data (2004).
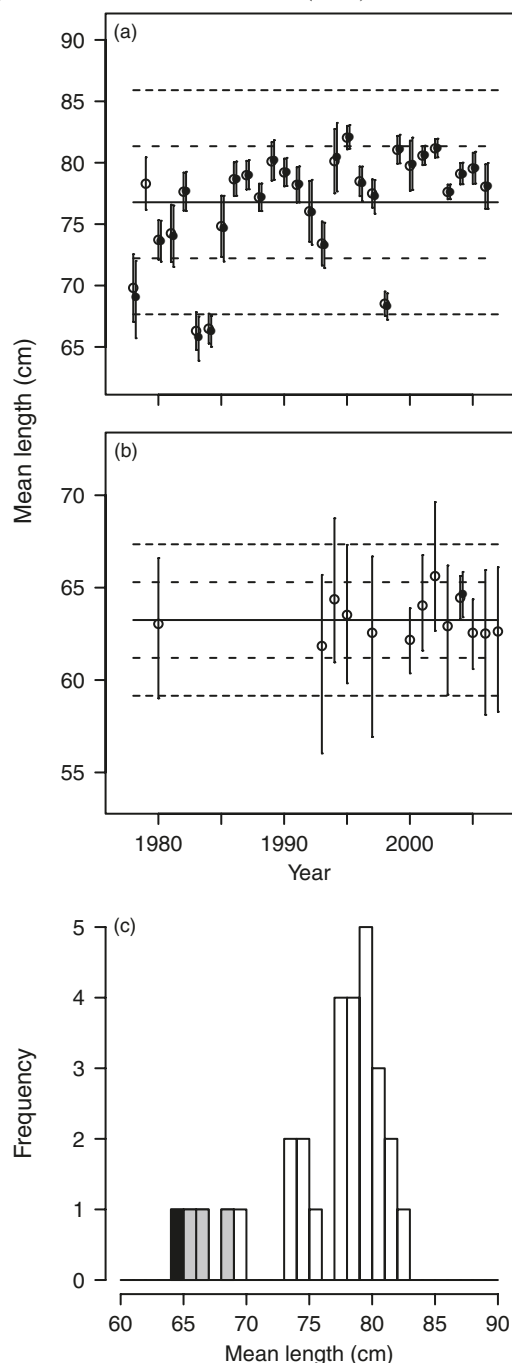
work it provides for predicting a distribution of expected sizes in future years. To assess this predictive ability, we fit both the HM and HME to only the first half of the data set (1978–1992) or the first 20 years (1978–1997) and compared the predictive distributions (mean and standard deviation of annual mean sizes) estimated from these partial datasets with the distribution of BM estimates of sizes in the remaining years. For simplicity, we compared the distribution of BM estimates for unfitted years with the posterior mean values of annual mean and standard deviation in annual mean sizes predicted by the HM or HME fitted to the early part of the data set, while also comparing the posterior credible intervals of the mean and standard deviation to the observed distribution of BM estimates for the remaining years.
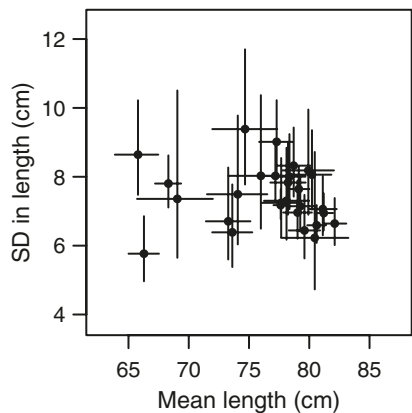
Results

BM vs. HM

The BM and HM gave broadly similar results when estimating the July mean sizes for SRFC (Fig. 1*a*), and the HM was able to provide estimates for one year (1979) with too few data to fit the BM. For the HM, the estimated mean of annual mean lengths (*x*, hereafter interannual mean) was 76.8 cm TL (95% credible interval (CI): 75.1–78.5 cm), with standard deviation in annual mean lengths of 7.4 cm (95% CI: 7.2–7.6 cm). The HM estimates for years far from the interannual mean were generally closer to the interannual mean than the BM estimates, especially for years with small sample sizes (compare the shift in 1978 vs. 1998). The only exceptions to this pattern were 1996 and 1997, for which the HM identified a very slightly higher mean. This results from the large standard deviation in fish lengths these 2 years. The BM is free to fit an unusually large standard deviation for both of these years, while the standard deviation estimated for the HM is drawn down toward the long-term mean standard deviation. Because of the truncated observed size distributions, the lower tail of a broad distribution is masked, meaning that the upper tail brings up the estimated mean of the distribution if it is fit, while the standard deviation is constrained to be inappropriately small.

The estimated distribution of annual mean lengths was not normal, with more outliers far below the mean than above (Figs. 1*a*, 1*c*). Estimated annual standard deviations of SRFC fish lengths within a year (*v*; Fig. 2) ranged from approximately 4.8 to 9.3 cm under either model formulation, with slightly smaller range in the HM formulation as described above. For most years the standard deviation was near 7 cm, and there was no apparent relationship between mean length in a given year and the corresponding standard deviation in lengths (Fig. 2).

Both models estimated shorter mean lengths for SRWC (Fig. 1*b*). For 2004, the only year with sufficient data to fit the BM, the estimated annual mean lengths were similar for both models. The HM was also able to provide estimates (with broader credible intervals) for years where too few data were available for reliable BM estimates. The HM estimated an interannual mean length of 63 cm (95% CI: 61–65 cm) total length, with a standard deviation in annual mean length of 4.6 cm (95% CI: 3.8–5.5 cm). Posterior means for estimated standard deviations of fish lengths within a year (not shown in figure) ranged from 4.4 to

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Fig. 2. Annual BM estimates of standard deviation versus mean length of age 3 SRFC fish in July. Vertical and horizontal bars on annual estimates are 95% confidence intervals.

Table 2. Correlations (and significance after accounting for autocorrelation) between mean size of age 3 SRFC fish in July (estimated via BM) and various environmental indices.

| Index	Correlation	p
MEI previous June	0.371	0.052
MEI previous July	0.392	0.040
MEI previous Aug.	0.348	0.070
MEI previous Sept.	0.304	0.116
MEI previous Oct.	0.472	0.020
MEI previous Nov.	0.599	0.002
MEI previous Dec.	0.424	0.025
NOI previous June	0.228	0.243
NOI previous July	0.165	0.402
NOI previous Aug.	0.311	0.107
NOI previous Sept.	0.303	0.123
NOI previous Oct.	0.373	0.077
NOI previous Nov.	0.578	0.002
NOI previous Dec.	0.535	0.007
PDOs previous year (June–Aug.)	–0.042	0.839
ALPI previous year	–0.066	0.740

Note: Considering these 16 tests as multiple comparisons, the Bonferroni correction would suggest a threshold p value of 0.003125 for $\alpha = 0.05$. MEI, Multivariate El Niño – Southern Oscillation (ENSO) Index; NOI, Northern Oscillation Index; PDOs, integrated summer Pacific Decadal Oscillation; ALPI, Aleutian Low Pressure Index.

4.9 cm, with typical widths of the 95% CI ranging from 1.6 to 3.2 cm. SRWC annual mean lengths did not obviously deviate from normality to the same extent as SRFC, but there were fewer years of data available, and in particular there were no data from years where SRFC mean sizes were especially small.

Correlations of annual mean length with environmental covariates

Several environmental indices measured during the previous year were significantly correlated with the estimated mean length of age 3 SRFC fish in July (Table 2), although only MEI the previous November and NOI the previous November were significant after applying a Bonferroni correction for 16 comparisons. Based on mechanistic hypotheses (described in the Discussion) and its high correlation with mean size (0.578, $p = 0.002$, corrected for autocorrelation), we chose NOI the previous November for incorporation in the HME. MEI in the previous November had an almost identically high correlation (0.599), but the correlation for MEI the previous December fell to 0.424, while NOI the previous December had a higher correlation of 0.535. Wells et al. (2006) demonstrated covariation between NOI and MEI during September–November ($r = -0.73$). In addition, visual inspection of the relationships between MEI or NOI and fish size suggested that NOI was more successful (over the observed range of years) in classifying distinct year types (Fig. 3).

HME

SRFC were smaller in years with low values of NOI the previous November (Fig. 4). The difference in mean size between low NOI years and typical years increased from March ($g_2 = 6.82$ cm with 95% CI –3.7 to 15.8 cm) to May ($g_2 = 11.4$ cm, 95% CI: 6.5–16.1 cm), with the mean size in low NOI years remaining very nearly constant. The difference in mean sizes between low and high NOI years remained similar in July ($g_2 = 11.1$ cm, 95% CI: 7.7–14.5 cm), while means of both year types increased similarly between months. In typical NOI years, the mean size of age 3 fish did not appear to increase between July and September (at which point nonmaturing fish remain in the ocean and transition to age 4), while mean size continued to increase during

this period in low NOI years, resulting in a smaller difference between mean size in typical versus low NOI years ($g_2 = 8.7$ cm, 95% CI: 3.4–13.2 cm).

Predictive ability

Fitting the HM with no environmental covariates to the first half of the data set, we predicted mean sizes for the remaining years would follow a normal distribution with mean 75.2 cm (95% CI: 74.4–78.0 cm) and standard deviation 5.1 cm (95% CI: 4.3–7.8 cm), as shown by the dotted line in Fig. 5a. BM estimates for mean lengths in the remaining years had an observed mean of 78.4 cm with standard deviation 1.4 cm. The log-likelihood of the observed BM estimates, given the best-fit HM predictive distribution, was –43.93. Fitting the HME with NOI as a covariate, we predicted a mean of 76.7 cm (95% CI: 76.1–78.5 cm) in typical years (solid line in Fig. 5a) and a mean of 67.3 cm (95% CI: 64.8–76.4 cm) in low NOI years, both with standard deviation 3.1 cm (95% CI: 2.6–4.7 cm). BM estimates for mean length in typical years had mean 79.1 cm with standard deviation 0.9 cm, and there was a single observation of a 68.3 cm mean length in 1998 for low NOI years. The log-likelihood of the observed BM estimates, given the best-fit HME predictive distribution, was –36.08. The HM and HME are nested models differing by one extra parameter, with a likelihood ratio test suggesting the HME is much more consistent with the data ($D = 15.7$, df = 1, $p = 0.00007$). Results for fitting the first 20 years and predicting the remaining years were qualitatively similar, with narrower CIs but little change in estimated means (Fig. 5b). Thus, both the HM and HME underpredicted mean length for the latter part of the data set when fit to the first part, and both overestimated the standard deviation in annual mean lengths. However, the HME came closer in predicting both mean and standard deviation.

Fig. 3. Annual BM estimates of mean length of age 3 SRFC fish in July plotted against (*a*) NOI or (*b*) MEI the previous November. Vertical bars on annual estimates are 95% confidence intervals.
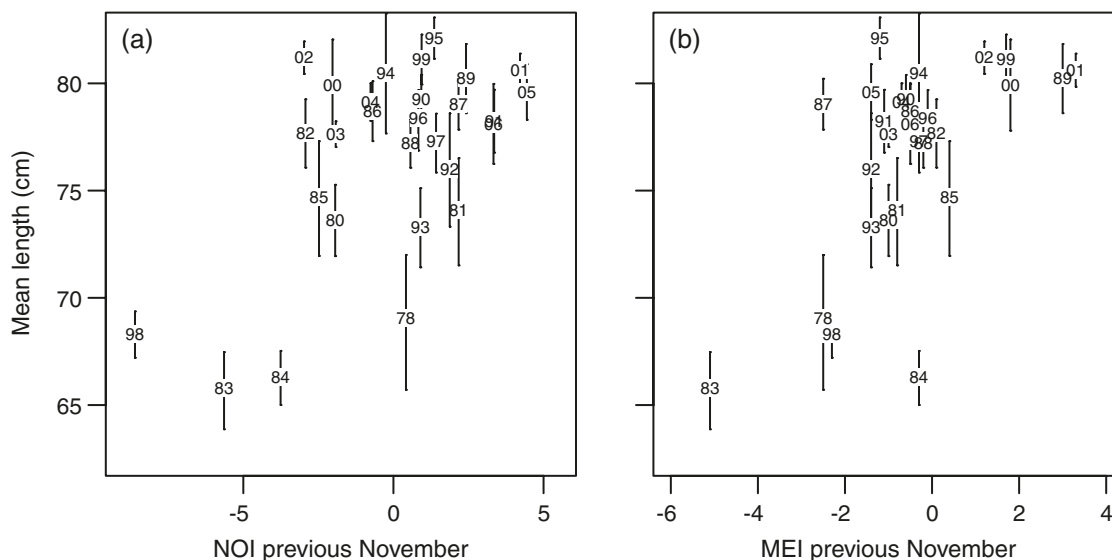
Discussion

HM vs. BM formulations

In a data-rich situation like SRFC, the HM provides similar results to the well-established BM method of estimating size distributions of ocean fish from size-truncated harvest data (Goldwasser et al. 2001). This concordance with established methodology is reassuring. However, the HM formulation offers numerous benefits. First, the HM provides an inherent, internally consistent framework for making predictions about size distributions in unobserved or future years. For example, one could generate a posterior predictive distribution for mean size in an upcoming year by taking numerous draws of x and s from the HM posterior distribution and then drawing sets of predicted μ values from each drawn set of hyperparameters. Accounting for environmental covariates would follow a similar process, but performing the draws for both high and low NOI years and then creating a summed posterior that weights the draws from the two environments by their expected probability of occurring in a given year.

Second, the HM allows for estimating interannual variation in mean size even when data in some years are inadequate for independent BM estimates. The credible intervals for such years are necessarily broader than those for data-rich years, but this is entirely appropriate. Year-specific estimates of size distributions are of direct management relevance, as discussed later.

Third, by providing a framework for accounting for annual effects, the HM allows comparison between groups of fish that have variation in their temporal patterns of data availability. For example, because of periods without marking and low catch rates of tagged SRWC, we have data from many fewer years than for SRFC. This could potentially confound comparisons of mean lengths between runs. In this particular case, it is fairly obvious that SRWC fish are substantially smaller than SRFC fish that have spent the same number of winters in the ocean (as might be expected, since SRFC fish have spent longer in the ocean; cf. Healey 1991), but strictly speaking a direct comparison of mean lengths for the two

runs, each calculated using data pooled across years with differential representation of the two runs, could be confounded and inappropriate. Our approach allows year-by-year comparisons of credible intervals, and in cases with very limited temporal overlap at least allows quantification of annual variability and its likely impacts on unpaired comparisons. In addition, the approach with environmental covariates allows the identification of particular year types that would introduce biases if included in only one of the groups being compared.

HME

Even without environmental covariates, the HM approach shows that there is variation from year to year in mean sizes, and this variation is not symmetrically distributed, with some outlier years of anomalously small size but almost no correspondingly anomalously large outliers (with the exception of March 2002). We might expect such a pattern due to state-dependent life history theory (Mangel and Satterthwaite 2008) and the observation that maturation rates are correlated with size and (or) growth (e.g., Hankin et al. 1993; Morita and Fukuwaka 2006). Anomalously rapid growth may simply lead to increased early maturation with large fish leaving the ocean and thus little change in mean size of remaining fish. By contrast, anomalously slow growth and delayed maturation can decrease the mean size of fish remaining in the ocean. Alternately, however, this skewed distribution in annual mean sizes might simply reflect physiological constraints on maximum growth.

By explicitly exploring environmental covariates with the HME formulation, we have shown an association between low NOI the previous year and reduced size-at-age. This is not an entirely new or unexpected result (e.g., Johnson 1988; MacFarlane et al. 2005; Wells et al. 2006), but this is the first time to our knowledge that this relationship has been demonstrated for size-at-age of fish in the ocean. In addition, by applying the method to multiple time points within a single year, we can demonstrate differences in not just size-at-age, but also growth rates between year types. Note that the difference between low NOI and "normal" years in mean length

Fig. 4. Annual HME estimates of mean length of age 3 SRFC fish in (*a*) March, (*b*) May, (*c*) July, and (*d*) September (at which point they become age 4) plotted against NOI the previous November. The solid horizontal lines indicate the interannual mean annual sizes predicted for low or high NOI, with dashed horizontal lines representing ±1 and ±2 standard deviations in annual mean size. Vertical bars on annual estimates are 95% credible intervals. Note that mature SRFC fish start to return to their natal rivers by or even slightly before September.
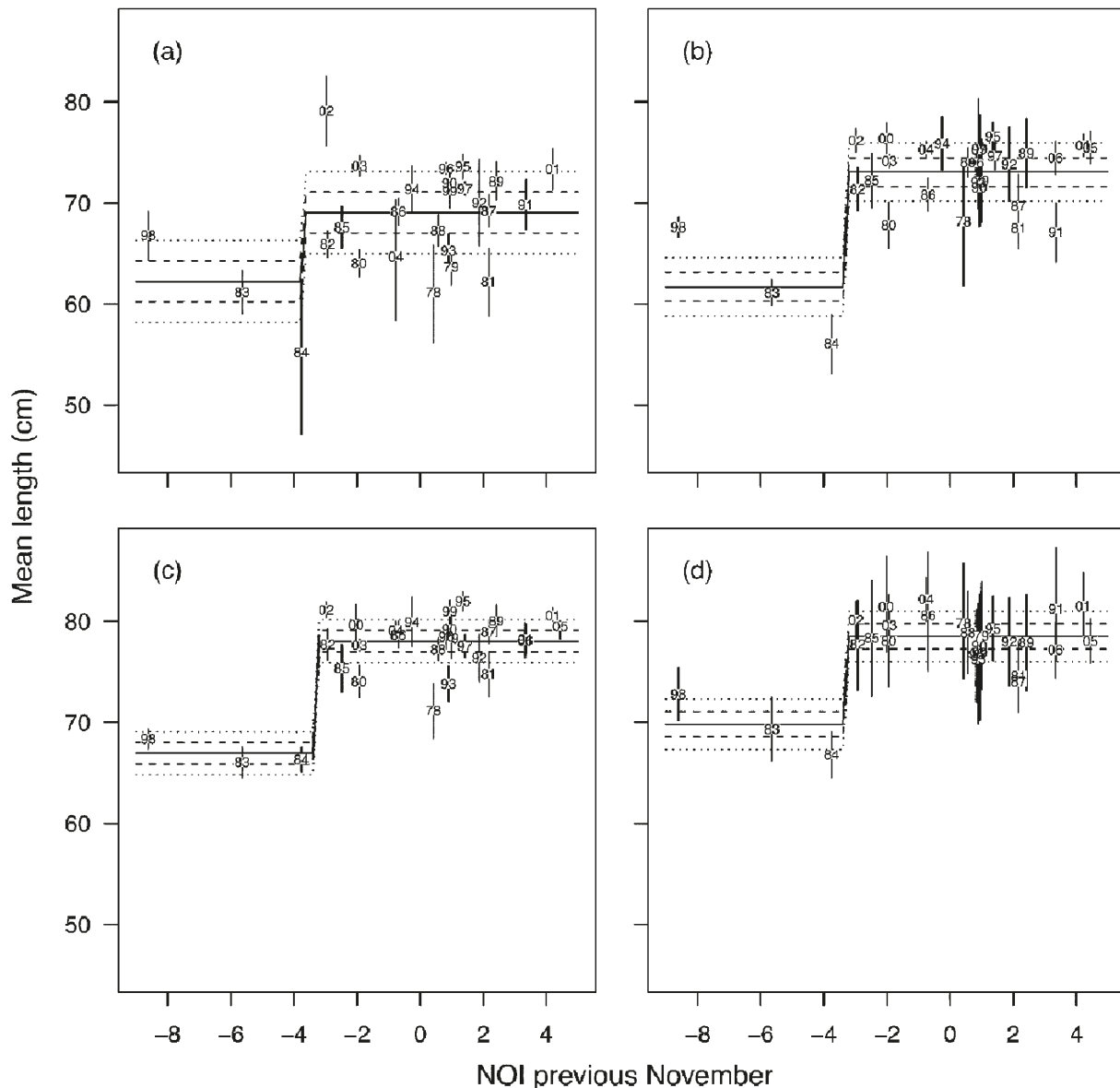
increases greatly between March and May, suggesting that fish grow slower during March through May in years characterized by low NOI the previous November. However, caution is needed in interpreting changes in mean length as growth rates, since fisheries, maturation, and size-dependent natural mortality also influence changes in mean size. Still, there is low fisheries impact and no maturation of fall run fish during this period.

Clearly correlation is not causation, and we have data for a limited number of low NOI years. Nevertheless, we hypothesize that low NOI in November predicts small sizes the following year. The lower values of NOI in November represent a weaker North Pacific High as winter approaches, which can lead to reduced upwelling and nutrient introduction along the coast (Schroeder et al. 2009; Black et al. 2011). This limited nutrient introduction could lead to repro-

ductive failure of zooplankton and numerous prey fish during the winter, which could substantially reduce the standing stock of prey in the upcoming spring (Wells et al., in press). In addition, very weak northerly winds in fall and winter associated with a stronger northward transport along the coast may act to disperse or transport nutrients and prey away from typical hot spots along the coast (Dorman et al. 2011; Santora et al. 2011). That the relationships between NOI and growth appear nonlinear suggests a threshold response of production to the fall and winter conditions. Such years appear to occur rarely based on our existing data set (on the order of once or twice per decade). Thus, the environmental effect, while evident, may not be apparent in most years, with remaining variation in size traceable to other sources.

The link between environment and size-at-age is a complicated topic worthy of a more detailed investigation than we

Fig. 5. Predicted distribution (lines) and observed BM estimates (bars) of annual mean length of age 3 SRFC in July for the later part of the data set as predicted by fitting only data from (*a*) the first half of the data set or (*b*) the first 20 years of data. The dashed line is the predictive distribution for the HM without environmental covariates, the solid black line is the predictive distribution from the HME for typical years, and the solid grey line is the predictive distribution from the HME for low NOI years. The shaded grey bar is 1998 (low NOI year). BM estimates span through 2006, as there were no SRFC CWT sample recoveries in July 2007.
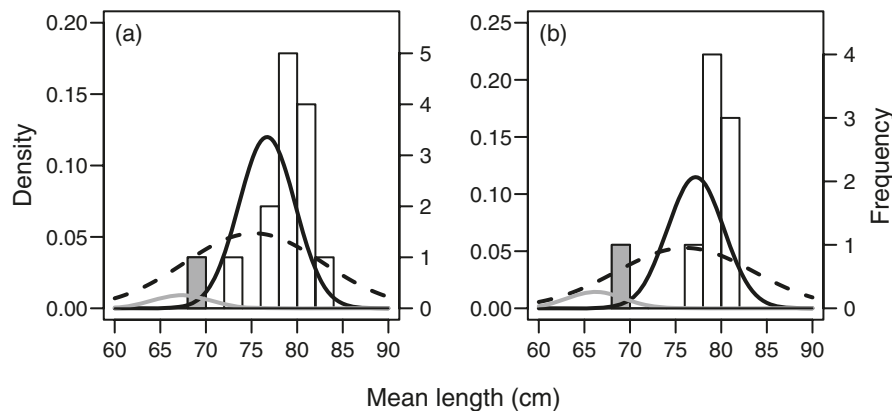
are able to undertake here. Ideally, such investigation would involve exploring a wider range of environmental indices, prey base, variation in fishing intensity, and multiple functional forms in addition to the simple step function assumed here. However, it would be imperative that the investigation account for time-dependent sizes of all fish in the ocean, which are directly estimable via the HME but not by the methods used in many previous studies of correlation between size and environment in salmonids.

Our chosen environmental covariate did not identify every year in which fish were smaller than usual. In particular, 1978 appears to be a year of anomalously small sizes, at least in July. Sample sizes were small in 1978, but there is indirect evidence for poor ocean conditions off California in 1978 from multiple sources, such as poor performance of numerous bird species (Sydeman et al. 2009). However the different timing of its divergence from the remaining years could suggest alternate mechanisms (i.e., poor conditions may have developed later in the year than those that typically follow a low NOI in November). Ultimately, it is unreasonable to expect any single index to capture all of the observed variation, but an approach such as this one that can predict some anomalies may be useful both in developing ecological understanding and in fishery management.

Predictive ability

The HM as fit to the first 14–20 years of the data set provided imperfect predictions of the remaining years' mean lengths. It underestimated the observed mean (which lay outside the credible intervals of the predicted mean) and substantially overestimated the observed variation in annual mean sizes. Adding an environmental covariate allowed the HME to perform significantly better, meaning that predicted lengths were usefully improved by incorporating environmental data. The HME not only came closer to predicting the observed means in low NOI and typical NOI years, but also had an upper bound on the predictive interval more in line with the largest observed sizes. Still, observed sizes in the later part of the data set had both a higher mean and lower standard deviation than the HME (as applied to the early data) predicted. This may reflect a trend of increasing size

through time and suggests that application of this method in the presence of possible trends warrants caution. The causes of the potential increase through time in mean size of SRFC are unclear, but reduced exploitation rates since 1990 (Pacific Fishery Management Council 2011*a*) may be a factor. One approach might be to fit a temporal trend as well, but extrapolating this trend into the future is likely ill-advised. Alternately, if the trend is deemed unlikely to continue, one might make future predictions based on only the latter part of the existing data set.

Possible extensions to the HM and HME

We have proposed a flexible model structure that can be applied to any system where group-specific (e.g., stock, but could be expanded to broader categories like species or restricted to narrower categories like specific hatchery release groups) and age-specific size data are available, and the method can be applied in fisheries with or without size limits. Equations 6–7 provide a template for adding the effects of additional discrete covariates. For example, we might model an effect of location of tag recovery on mean size to attempt to separate out larger maturing from smaller, immature fish across space or for purposes of reconstructing underlying fish density in different areas based on catch-per-unit-effort (CPUE) data that counts only fish large enough to harvest. We might also examine differences among individual release groups in their size-at-age to see if they are consistent with observed correlations of release timing and maturation schedule (Hankin 1990). This could be done comparing discrete groups or using continuous covariates such as release date or mean size at release using eq. 15.

Management relevance

Our results and statistical approach are relevant to fishery management in multiple ways. First, understanding the size distribution of fish actually in the ocean, rather than a potentially biased reconstruction of such sizes obtained from spawners, is important in prospectively predicting the proportion of a cohort that will be vulnerable to harvest under alternative size limits. It is also required when retrospectively estimating nonlanded mortalities from historical catches in

fisheries with size limits. Because this approach allows for quantifying and predicting annual variability in size distributions, it will also allow quantifying the expected variability through time and uncertainty in the proportion of a cohort vulnerable to harvest under alternative size limits.

In addition, when combined with consideration of state-dependent life history, improved knowledge of size-at-age and its variation may improve demographic projections and models used in management. For example, a major aspect of setting harvest regulations for the upcoming season in California's ocean salmon fishery is the predicted value of the Sacramento Index (SI; O'Farrell et al. 2009), the total estimated adult SRFC abundance (escapement plus harvest, dominated typically by age 3 fish). Currently, a regression model (O'Farrell et al. 2009) is used to predict the SI for an upcoming year based on the previous year's jack escapement. Fishing season structures are then set such that the expected escapement meets or exceeds the goals set for SRFC. For jack escapement to unbiasedly predict adult abundance the next year, there would need to be a consistent age structure (with no fish older than age 3) across cohorts and thus a consistent maturation and survival schedule. While this statistical model performs fairly well because of the dominance of age 3 fish, life history theory (e.g., Mangel 1994; Fujiwara 2008) and empirical data (Morita and Fukuwaka 2006) suggest that fish are more likely to delay maturation if they are small or growing slowly, so we might expect a lower ratio to occur in years when fish are small or growing poorly. Thus, if growth between age 2 and age 3 is poor, we may see fewer age 3 spawners than expected from the cohort strength estimated on the basis of jacks the previous year. Indeed, smaller than normal age 3 fish in 1983, 1984, and 1998 all corresponded to outliers below the typical jack–SI relationship, with realized SI values lower than would have been predicted by the regression model (as demonstrated in Fig. 6). Fish were also small in 1978, but SI value reconstructions only extend back to 1983, so we cannot directly test whether 1977 jack returns would also have underpredicted 1978 adult abundance. Small sizes and poor growth may not explain every occurrence of smaller than expected returns (e.g., despite large age 3 fish, returns in 2005 were lower than expected, which may reflect the importance of age 4 fish and earlier cohorts not captured by the previous year's jacks; Pacific Fishery Management Council 2011b), but these results do suggest a situation that would merit extra caution in applying the regression model or similar approaches in other systems.

Thus, it is possible to explain deviations from model predictions in a post hoc manner. While useful for increased understanding, such retrospective explanations are not a direct aid to management. In a prospective approach, environmental indices available at the time of fishery preseason planning (such as NOI the previous November) that correlate with smaller than expected size might trigger extra caution in the development of management measures for the upcoming year. That is, developing a more detailed and mechanistic understanding of climate variables that predict later size and growth is of applied as well as theoretical interest.

Other explanations besides reduced maturation are consistent with the observed low SI relative to jacks the previous year when age 3 fish are small. The small size and poor growth may reflect conditions that also reduce sur-

Fig. 6. Sacramento Index (SI) plotted against jack escapement the previous year. A regression model fit to a subset of these data serves as a predictor of the current SI for use in managing ocean fisheries to achieve SRFC spawning escapement goals. Note that 1983, 1984, and 1998 (circled) were all preceded by a November with low NOI and all had anomalously small mean lengths of age 3 fish based on our assessment using the HME. Data are from Pacific Fishery Management Council (2011a) for SI and Pacific Fishery Management Council (2011b) for jack escapement.
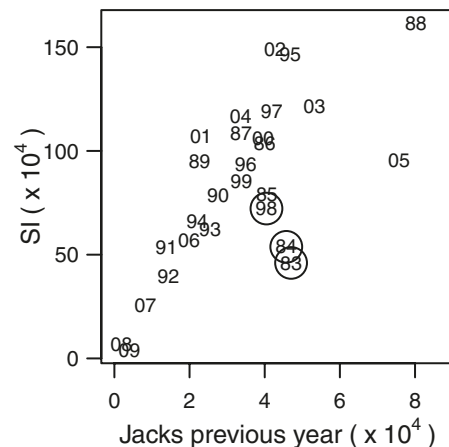
vival between age 2 and age 3, such that cohort strength has been reduced compared with that estimated from jacks the previous year. In addition, SI is a composite of harvest and escapement. If age 3 fish (the bulk of the harvest) are unusually small, a larger fraction will be too small to retain and will not count fully toward the harvest component of SI. Sublegal size fish are partially accounted for in the current harvest estimates, but not in a way that accounts for the potential of greater nonlanded mortalities when fish are unusually small.

Acknowledgements

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Appendix A. Sample sizes

Table A1. Number of legal-sized fish of target age sampled: by run, month, and year.

Year	SRWC July	SRFC March	May	July	September
1978	0	7	3	26	2
1979	0	32	9	17	3
1980	2	77	30	59	6
1981	0	15	32	38	13
1982	0	73	36	82	7
1983	0	17	104	118	23
1984	0	4	17	86	14
1985	0	30	28	51	2
1986	0	82	63	139	2
1987	0	37	22	134	19
1988	0	40	81	199	9
1989	0	37	12	98	5
1990	0	60	13	152	9
1991	0	22	11	112	3
1992	0	7	12	38	7
1993	1	34	25	53	2
1994	2	18	26	21	0
1995	2	53	75	184	19
1996	0	325	125	161	7
1997	1	195	140	221	0
1998	0	29	147	241	21
1999	0	23	15	147	1
2000	13	0	59	59	6
2001	8	14	139	280	15
2002	5	16	122	325	47
2003	3	66	289	554	81
2004	64	6	220	294	39
2005	19	0	48	97	24
2006	2	0	69	61	12
2007	2	0	5	0	0

Supplementary Materials for Satterthwaite et al. CJFAS

Markov Chain Monte Carlo (MCMC) details

Prior distributions

For prior distributions we used:

$p(x) = \phi(x|82.5 \text{ cm}, (250 \text{ cm})^2)$ for Sacramento River fall run Chinook (SRFC) and

$p(x) = \phi(x|66.8 \text{ cm}, (250 \text{ cm})^2)$ for Sacramento River winter run Chinook (SRWC). These

are diffuse priors with means taken from CDFG (1989) estimates for the mean length of age

3 fish in July from each run.

$p(s) = U(1.25 \text{ cm}, 15 \text{ cm})$; a uniform distribution with minimum 1.25 cm and

maximum 15 cm. Having a nonzero minimum helped to avoid numerical difficulties

experienced in month-year combinations with very few fish all of the same length, while

the maximum was well above the standard deviation estimated by CDFG (1989).

$p(\upsilon) = U(0.25 \text{ cm}, 12.5 \text{ cm})$. This allowed the inter-annual standard deviation in

mean length to be as large as 12.5 cm, which allowed the bulk of years to vary over a range

of 50 cm in mean length, far greater than that observed.

$p(\tau) = U(0.25 \text{ cm}, 5 \text{ cm})$. This allowed the inter-annual standard deviation (SD) of

within-year standard deviations of length to be up to two thirds of CDFG (1989's)

estimated SD of fish lengths for SRFC.

For the hierarchical model with environmental covariate (HME), we assumed

$p(\tilde{g}) = p(g_1)p(g_2)$ and specified these prior distributions as $p(g_1) = \phi(g_1|3.6 \text{ cm}, (2 \text{ cm})^2)$ and

$p(g_2) = \phi(g_2|0 \text{ cm}, (2500 \text{ cm})^2)$. This specification states that the environmental threshold is

likely in the observed range of -7.6 to 0.4 for values of the Northern Oscillation Index (NOI),

while the size (and sign) of the response to changing environmental conditions is essentially unconstrained. The prior is centered on the value corresponding to the switch between years characterize by El Niño type conditions and other years. This corresponds to an *a priori* assumption that El Niño like conditions are important but does not assume anything about how size-at-age responds (and in fact there can be no response). Similar results are obtained with an unconstrained prior on g_1 but constraining $0 \leq g_2 \leq 20$ cm, which implies that El Niño like conditions are a priori assumed to have a negative (but bounded) effect or no effect on size-at-age, but not a positive effect. Without either of these constraints, the MCMC can accept values of g_1 that classify all years as above the threshold, at which point g_2 and x are no longer separately estimable. Alternately, the MCMC can accept values of g_1 classifying all years below the threshold, at which point g_2 becomes independent of the data. If the chain spends much time in this region of the parameter space, it can lead to accepted values of g_2 that make it essentially impossible to later accept a proposed value for the environmental threshold g_1 that would disentangle g_2 and x (in the first case) or add g_2 onto x (in the second case).

Conditional posteriors for HME

The conditional posterior distributions of s, τ, and σ are provided by Equations 12, 13, and 14, respectively, as they are unaffected by the hyper-parameters related to mean length. For those hyper-parameters related to length, the conditional posterior distributions now depend on the environmental covariate and are given by

(S1) $\quad p\left(x \mid \tilde{\mu}, \upsilon, \tilde{g}, \tilde{E}\right) \propto p(x) p\left(\tilde{\mu} \mid x, \upsilon, \tilde{g}, \tilde{E}\right)$

(S2) $\quad p\left(\upsilon \mid \tilde{\mu}, x, \tilde{g}, \tilde{E}\right) \propto p(\upsilon) p\left(\tilde{\mu} \mid x, \upsilon, \tilde{g}, \tilde{E}\right)$

(S3) $\quad p\left(\tilde{g} \mid \tilde{\mu}, x, \upsilon, \tilde{E}\right) \propto p(\tilde{g}) p\left(\tilde{\mu} \mid x, \upsilon, \tilde{g}, \tilde{E}\right)$

(S4) $\quad p\left(\tilde{\mu} \mid x, \upsilon, \tilde{g}, \tilde{\sigma}, \tilde{l}, \tilde{l}^{*}, \tilde{E}\right) \propto p\left(\tilde{\mu} \mid x, \upsilon, \tilde{g}, \tilde{E}\right) p\left(\tilde{l}, \mid \tilde{\mu}, \tilde{\sigma}, \tilde{l}^{*}\right)$.

Implementation details

We ensured that the sampled chains did not closely approach either the upper or lower bounds of any of the uniform priors used so as to not inappropriately constrain the posterior distribution.

For years with two or fewer fish sampled (multiple cases for SRWC, and September of 1999 for SRFC), we did not attempt to estimate σ_y, and instead drew a random value using equation 7 given the current value of the hyperparameters.

For the Metropolis-algorithm MCMC sampling, we used normal (and hence symmetric) distributions to propose jump sizes (multivariate normals for $\tilde{\mu}$ and $\tilde{\sigma}$), with the standard deviation in the jump size distribution for each parameter tuned during an adaptive phase. After 2000 iterations of burn-in, we ran 200 sets of 100 iteration tuning runs after each of which we adjusted the jump size for each parameter with the goal of an acceptance rate of 0.23 for vector parameters and 0.44 for scalars (Gelman et al. 2004). This resulted in a total burn in of 22 000 iterations. We then held the jump sizes constant for 100 000 iterations of the retained chain. To assess convergence, we compared hierarchical model (HM) outputs to basic model (BM) estimates, visually inspected traces started from different initial estimates, and used Geweke's (1992) convergence diagnostic as implemented in the "geweke.diag" function contained in R package "coda" (Plummer et

al, 2010) to compare the mean in the first 10% of the retained chain to the last 50% of the chain. If |z|-scores for all parameters were < 2, we considered the chains to have converged and burn-in adequate. If not, we increased burn-in until all parameters had |z|<2, with some situations requiring burn-in of up to 50 000 iterations. To assess adequacy of chain length relative to autocorrelation, we used the Raftery and Lewis (1995) run length control diagnostic as implemented in the function "raftery.diag" contained in R package "coda" (Plummer et al. 2010) to calculate the recommended post burn-in length of the posterior chain for each parameter required to estimate the .025 quantile with accuracy of 0.005 with 95% probability. We ran additional iterations as necessary, from a minimum of 200 000 for SRWC to a maximum 1 100 000 for SRFC in July with environmental covariates. We then used quantiles of the full retained chains to estimate the credible intervals of the posterior distributions.

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