

Accounting for space-time interactions in index standardization models

James T. Thorson^{*,1}, Eric Ward²

¹ Fisheries Resource Assessment and Monitoring Division

Northwest Fisheries Science Center

National Marine Fisheries Service

National Oceanic and Atmospheric Administration

2725 Montlake Blvd. East

Seattle, WA 98112

² Conservation Biology Division

Northwest Fisheries Science Center

National Marine Fisheries Service

National Oceanic and Atmospheric Administration

2725 Montlake Blvd. East

Seattle, WA 98112

* Corresponding author

James.Thorson@noaa.gov

Phone: 206.302.1772

Fax: 206-860-3217

Abstract

Scientific survey data are used to estimate abundance trends for fish populations worldwide, and are frequently analyzed using delta-generalized linear mixed models (delta-GLMMs). Delta-GLMMs incorporate information about both the probability of catch being non-zero (catch probability) and the expected value for non-zero catches (catch rates). Delta-GLMMs generally incorporate year as a main effect, and frequently account for spatial strata and/or covariates. Many existing delta-GLMMs do not account for random or systematic differences in catch probability or rates in particular combinations of spatial strata and year (i.e. space-time interactions), and do not recognize potential correlation in random space-time interactions between catch probability and catch rates. We therefore develop a novel Bayesian delta-GLMM that estimates correlations between catch probability and rates, and compare it with either (a) ignoring year-strata interactions, (b) modeling year-strata interactions as fixed effects, or (c) estimating year-strata interactions in catch probability or rates as independent random effects. These four models are fitted to bottom trawl survey data for 28 species off the U.S. West Coast. The posterior median of the correlation is positive for the majority (18) of species, including all 5 for which the posterior distribution has little overlap with zero. However, estimating this correlation has little impact on resulting abundance indices or credible intervals. We therefore conclude that the correlated random model will have a little impact on index standardization of the West Coast bottom trawl dataset. However, we propose that the correlated model can quickly identify correlations between occupancy probability and density, and that these identified correlations can generate hypotheses for future research.

Keywords (5 max): index standardization, mixed-effects model, Bayesian model

1. Introduction

Scientific surveys are conducted worldwide and are an important source of information about abundance trends in marine species. Indices of annual stock abundance obtained from survey data are generally incorporated into population dynamics models to estimate stock productivity, current stock status, and allowable catch levels (Quinn and Deriso 1999). These outputs are then used to inform fisheries management policy such as annual catch and/or fishing effort levels.

Scientific survey data usually include catch and effort statistics for each survey occasion, and catch per unit effort (CPUE) is commonly treated as a measure of local densities. CPUE data can be summarized using simple statistics (i.e. mean CPUE in a design-based estimator) or complex standardization models to provide an index of stock abundance. Index standardization models provide several benefits over simple summary statistics when analyzing survey data, including: (1) improving estimates of indices and confidence/credible intervals (Ye and Dennis 2009); (2) estimating the effects of and controlling for variables such as sampling vessel, season, and spatial location; (3) incorporating auxiliary information such as fishing hook depth (Bigelow and Maunder 2007); (4) accounting for stratified and unbalanced sampling designs, i.e. where particular areas and/or years are sampled more or less heavily than others due to intentional sampling design or random chance (Wiedenmann and Essington 2006); and (5) accounting for highly non-normal catch rate distribution, e.g., as caused by fish schooling behaviors (Thorson et al. 2011, 2012).

Delta-generalized linear models (delta-GLMs) have become widely used in fisheries and other fields for index standardization because they allow separation of the model into two biologically meaningful components (Pennington 1983, Stefansson 1996). The first component uses the detection or non-detection of the species at each survey location to estimate changes in

stock range over time. The second component uses the catch rate for survey occasions where the species was detected to estimate population density within its occupied range. Overall stock abundance is then calculated as the product of stock range and densities within the occupied range. Both model components are necessary because marine species will often undergo changes in densities and stock range over time. Delta-GLMs approximate the expected value of each model component as a function of covariates, and have been extended into a mixed-effects modeling framework (delta-GLMMs), allowing model coefficients to also be treated as random effects that differ among grouping variables (e.g., year and strata, Helser et al. 2004). Delta-GLMMs used for index standardization always include a coefficient representing 'Year' for both presence/absence and positive catch model components because the focus of inference during index standardization is on changes in abundance from one year to the next. Standardization models also frequently include 'Area' (a factor representing different sampling regions or strata), for example, to account for consistent differences in stock density between on- and off-shore habitats (Maunder and Punt 2004).

An interaction between year and area (Year×Area) can be included in the delta-GLMM to represent abundance changes that differ among spatial areas in a random or systematic manner. Systematic changes in abundance among areas, e.g., caused by different fishery exploitation rates in different portions of stock range, are treated by including Year×Area as a fixed effect, i.e. by estimating a separate parameter representing stock abundance in each year and area. Random differences, e.g., caused by random annual changes in the distribution of total stock abundance among multiple regions, are treated by including Year×Area as a random effect. Treating Year×Area as a random effect requires estimating an additional coefficient (the variance of random Year×Area deviations), and but is sometimes more parsimonious than treating

Year×Area as a fixed effect because random coefficients are 'shrunk' towards zero (Gelman and Hill 2007). Random effects are appropriate when each random effect coefficient is exchangeable (e.g., believed to arise from a 'random,' independent, and identical distribution) for each year-area combination (Bolker et al. 2009). Treating Year×Area as random will explain some portion of residual variance, likely resulting in tighter estimates of index credible intervals.

Delta-GLMMs generally treat random effects regarding the probability of non-zero catch and the expected catch for non-zero catches in a given year-area combination as statistically independent. This assumption may commonly be violated. As one example, random environmental conditions may cause the target species to be more tightly aggregated in a given year and area, thus causing fewer positive observations but greater expected catches for positive catches. In this case, the random effect for the catch rate component will be negatively correlated with the random effect for presence/absence component, in violation of the common delta-GLMM assumption that all random effects are exchangeable. By contrast, random environmental changes may cause a population to move into different strata than usual. For strata into which they move, the probability of non-zero catch and the expected catch for non-zero catches will both be increasing, causing a positive correlation between Year×Area coefficients. This violation of random effect model assumptions can be rectified by estimating a correlation between random effects within a given year-area combination, although we know of no fisheries studies or models in other fields that have explored this.

In this manuscript, we pursue two related study goals. First, we determine whether a correlation between model components is supported by available data for West Coast species and, if so, whether it is generally positive or negative. Second, we explore whether introducing a correlation between model components affects estimated indices of abundance. To accomplish

these goals, we compare four alternative treatments of spatial and temporal interactions ('space-time interactions') in delta-GLMM models: (1) not including any Year×Area interaction; (2) treating Year×Area as fixed effects separately in both the presence/absence and catch rate model; (3) treating Year×Area as independent random effects separately in both the presence/absence and catch rate model; and (4) treating Year×Area as random effects that are correlated between presence/absence and catch rate model components. We first apply all four models to bottom trawl survey data for 28 species obtained from the Northwest Fisheries Science Center (NWFSC) shelf and slope survey conducted annually by the National Oceanic and Atmospheric Administration (NOAA) off the U.S. West Coast (e.g., 2003-2011, Bradburn et al. 2011). We then assess the direction and magnitude of random effect correlations, to identify whether correlations between presence/absence and positive catch components are likely to be positive, negative, or indistinguishable from zero for these 28 species (goal 1). Next, we compare resulting abundance indices and credible interval widths for each model to determine whether including the correlation parameter affects the estimated abundance indices or the width of their credible intervals (goal 2).

2. Methods

2.1 Data availability

As a case study, we use bottom trawl catch and effort data obtained from the NMFS NWFSC shelf and slope survey off the U.S. West Coast (Keller et al. 2008, Bradburn et al. 2011). This survey has operated with similar sampling protocols since 2003, and uses a stratified random sampling design with six sampling strata composed of three depths categories (55-183 m., 184-549 m., and 550-1280 m.) and two latitude categories (32-34.5, and 34.5-50 degrees latitude), wherein sampling intensity is approximately equal to the area in each stratum. For the purposes

of this study, we adopted the default post-stratification used by the NWFSC (A. Hicks, pers. comm. 2012), which uses the three depth categories from the sampling design and five latitudinal categories (32-34.5, 34.5-40.5, 40.5-43, 43-47.5, and 47.5-50 degrees latitude). This results in 15 spatial strata.

We compiled data for 5756 sampling tows from 2003-2011 by the NWFSC shelf/slope survey. We analyze data for 28 finfish species (Table 1) that were chosen because they either (a) are flatfishes, (b) were assessed in 2011, (c) were likely to be assessed in 2013, or (d) had 200-500 positive catches between 2003-2008 ('positive catches' representing occasions when the species was detected on a sampling occasion), where this level was chosen to ensure that species had information for estimating both presence/absence and positive catch rate model components. These species range widely in the probability of occurrence from 84.1% (Dover) to 1.7% (yelloweye), and in the average catch for positive tows from 1.6 kg. (cowcod) to 78.6 kg. (chilipepper). Within each year, sampling for the NWFSC shelf/slope survey occurs in the same time period (May-Oct.) and represents a snapshot of annual biomass that is comparable among years.

2.2 Model overview

We first present the 'correlated model' because it represents the most complicated of the four models. We then present in turn how each other model is derived from the correlated model. We use a Bayesian hierarchical modeling framework, which specifies prior probabilities for model parameters and the conditional probability of the data given parameters to define the posterior distribution of model parameters. We use Bayesian methods to ease computation of the bivariate integral used in the correlated model. This integral, while possible to compute in a

maximum likelihood statistical framework (e.g., Thorson et al. 2011), is computationally easier using Bayesian Markov chain Monte Carlo methods.

2.2.1 Correlated strata×year effects

The probability of catch C (in weight, e.g., kilograms) being non-zero is approximated by a logistic regression model:

$$p(C > 0 | s_i, y_i) = \Phi \left(\sum_{j=1}^{n_{strata}} \omega_j^{(s)} I(s_i = j) + \sum_{k=1}^{n_{year}} \omega_k^{(y)} I(y_i = k) + \sum_{j=1}^{n_{strata}} \sum_{k=1}^{n_{year}} \omega_{j,k}^{(sy)} I(s_i = j) I(y_i = k) \right) \quad (1)$$

where s_i and y_i are strata and year for tow i , $\omega^{(s)}$, $\omega^{(y)}$, and $\omega^{(sy)}$ are parameters representing the effect of strata, year, and the strata×year interaction on the probability that C is non-zero, n_{strata} and n_{year} are the number of strata and years, respectively, j and k are indices representing strata and year, respectively, Φ is the logistic transformation $\Phi(X) = \exp(X)/(1+\exp(X))$, and $I(x=b)$ is an indicator variable that equals one if $x = b$ and zero otherwise.

The probability density for catch C given that catch is non-zero is approximated by a gamma distribution:

$$p(C = c | C > 0, s_i, y_i, a_i) = \text{Gamma}(c | \alpha, \beta_i) \quad (2)$$

where $\alpha = 1 / CV^2$, $\beta_i = 1 / (\mu_i \cdot CV^2)$, CV is the estimated coefficient of variation for C given that $C > 0$, and μ_i is the expected value of catch for non-zero tow i . We parameterize this gamma distribution such that the CV of all non-zero catches is constant (as represented by estimated parameter CV). Other distributions may be appropriate (lognormal, inverse Gaussian, etc) but for skewed distributions that occur in fishery data, the gamma distribution is well behaved (Myers and Pepin 1990). The μ_i is in turn approximated by an exponential-transformed linear model:

$$\mu_i = a_i \cdot \exp \left(\sum_{j=1}^{n_{\text{strata}}} \gamma_j^{(s)} I(s_i = j) + \sum_{k=1}^{n_{\text{year}}} \gamma_k^{(y)} I(y_i = k) + \sum_{j=1}^{n_{\text{strata}}} \sum_{k=1}^{n_{\text{year}}} \gamma_{j,k}^{(sy)} I(s_i = j) I(y_i = k) \right) \quad (3)$$

where a_i is the area swept (in hectares) for tow i , and $\gamma^{(s)}$, $\gamma^{(y)}$ and $\gamma^{(sy)}$ are parameters representing the effect of strata, year and the strata \times year interaction on the expected value of non-zero catch C_i .

Strata \times year interactions are treated as random effects, and specify that the random effect for presence/absence $\omega^{(sy)}$ in strata s and year y is correlated with the random effect for positive catch rates $\gamma^{(sy)}$ in strata s and year y :

$$p(\omega_{j,k}^{(sy)}, \gamma_{j,k}^{(sy)} | \Sigma_{sy}) = \text{MVN}(0, \Sigma_{sy}) \quad (4)$$

where $\text{MVN}(\mu, \Sigma)$ is a multivariate normal density function, and Σ_{sy} is the covariance among strata \times year random effects within a given strata-year combination:

$$\Sigma_{sy} = \begin{bmatrix} \sigma_{\omega}^2 & \rho_{sy} \sigma_{\omega} \sigma_{\gamma} \\ \rho_{sy} \sigma_{\omega} \sigma_{\gamma} & \sigma_{\gamma}^2 \end{bmatrix} \quad (5)$$

where σ_{ω}^2 and σ_{γ}^2 are the variance for positive catch rate and presence/absence random effects, and ρ_{sy} is the estimated correlation between strata \times year random effects for presence/absence and positive catch rates model components. This correlated model therefore has a total of 320 estimated coefficients for each species, although the effective degrees of freedom may be less than this number due to random effect shrinkage (Spiegelhalter et al. 2002).

The Bayesian model specification is completed by including prior distributions for all parameters. We used a weakly-informative gamma prior on α , $p(\alpha) = \text{Gamma}(0.001, 0.001)$, and bounded uniform priors on all fixed-effect parameters $p(X) = 1/40$ if $-20 < X < 20$ and zero otherwise (the value 1/40 ensures that the integral of this prior is one), where X represents $\gamma^{(s)}$,

$\gamma^{(y)}$, $\omega^{(s)}$, and $\omega^{(y)}$. Because the correlated strata-year effects are treated as multivariate normal, we used a standard conjugate inverse-Wishart prior on the covariance matrix (Gelman et al. 2003), which has a prior mean of zero (i.e. represents a prior assumption of no correlation). For the simpler case of uncorrelated random effects, we used weakly-informative bounded uniform priors on the standard deviation of strata \times year random effects $p(X) = 1/20$ if $0 < X < 20$ and zero otherwise, where X represents σ_ω or σ_γ (Gelman 2006). The posterior distribution for the model is then defined as the product of all terms defined previously.

2.2.2 *Uncorrelated Year \times Area effects*

As a second model, we consider allowing Year \times Area effects in the presence/absence and positive catch rate components to be independent ('uncorrelated Year \times Area') by specifying that correlations are zero ($c_{sy} = 0$). This has the result that Σ_{sy} is diagonal, and leaves 319 estimated coefficients for each species.

2.2.3 *Fixed Year \times Area effects*

As a third possible model, we specify that Year \times Area effects are estimated as fixed effects. This model eliminates Eqs. 4-5, and instead specifies bounded uniform priors on Year \times Area effects, $p(X) = 1/40$ if $-20 < X < 20$ and zero otherwise, where X represents $\gamma^{(sy)}$ and $\omega^{(sy)}$. It also requires that all strata and year main effects are set to zero (i.e. $\gamma^{(s)} = \omega^{(s)} = \gamma^{(y)} = \omega^{(y)} = 0$), to prevent confounding of main and interaction effects (where this parameterization additionally minimizes parameter correlations). This leaves 271 estimated coefficients for each species, although the number of effective degrees of freedom is likely higher than for the random Year \times Area models due to an absence of shrinkage of interaction coefficients (Spiegelhalter et al. 2002).

2.2.4 *Absent strata \times year effects*

The fourth model we implement involves no estimation of Year×Area effects, but still retains the fixed area and year effects. The model without Year×Area interactions again eliminates Eqs. 4-5, and specifies that Year×Area effects are zero, $\gamma^{(sy)} = \omega^{(sy)} = 0$, leaving 47 estimated coefficients per species.

2.3 Estimating an index of abundance

All four models (correlated, uncorrelated, fixed, and absent) are then used to estimate an index of abundance for all 28 species. This index is calculated by multiplying the posterior distributions for the probability of non-zero catch and the probability density of catch when non-zero, and taking the sum weighted by strata area A_j for each stratum j :

$$p(B_k | c, s, y, a) = \sum_j^{n_{strata}} A_j \cdot p(C_{j,k} > 0 | c, s, y, a) \cdot p(\mu_{j,k} | C_{j,k} > 0, c, s, y, a) \quad (6)$$

where $p(B_k | c, s, y, a)$ is the probability density for random variable B_k representing abundance (i.e., biomass) in year k given all available data (i.e., catch c , strata s , year y , and area swept a for all tows), $p(C_{j,k} > 0 | c, s, y, a)$ is the probability that catch $C_{j,k}$ in strata j and year k is positive, and $p(\mu_{j,k} | C_{j,k} > 0, c, s, y, a)$ is the probability density of non-zero catches $\mu_{j,k}$ for that year and strata:

$$p(C_{j,k} > 0 | c, s, y, a) = \Phi \left(p(\omega_j^{(s)} | c, s, y, a) + p(\omega_k^{(y)} | c, s, y, a) + p(\omega_{j,k}^{(sy)} | c, s, y, a) \right) \quad (7)$$

$$p(\mu_{j,k} | c, s, y, a) = \exp \left(p(\gamma_j^{(s)} | c, s, y, a) + p(\gamma_k^{(y)} | c, s, y, a) + p(\gamma_{j,k}^{(sy)} | c, s, y, a) \right) \quad (8)$$

where $p(X | c, s, y, a)$ is the posterior distribution for parameter X . We use the median of $p(N_k | c, s, y, a)$ as the index of abundance, and the standard deviation of $p(N_k | c, s, y, a)$ divided by its median as a measure of precision for N_k .

2.4 Estimation and convergence

Samples from the posterior distribution are calculated using Markov chain Monte Carlo (MCMC) methods as implemented in JAGS (Plummer 2003) and called from the R statistical

platform (R Development Core Team 2011) using the R2jags package (Su and Yajima 2012). We used 3 chains, each obtaining 70,000 samples, the first 50,000 of which are used to adapt the sampling algorithm and hence are discarded. The remaining 20,000 samples were then thinned to obtain 4,000 samples per chain that were approximately independent.

All results that we present are made after checking for evidence of non-convergence. Convergence checks include visual inspection of sampling chains for estimated parameters. We additionally estimate the Gelman-Rubin R statistic, representing the ratio of variance within and between chains, and the first-order autocorrelation for all derived parameters, i.e. the probability of occurrence, density, and resulting abundance for each strata and year. For the total abundance indices across all strata and years, for example, the median Gelman-Rubin R statistic was below 1.1 for nearly all species and models. For two species (cowcod, halfbanded), the median Gelman-Rubin R statistic was less than 1.1 for the fixed effects model, but was in the range 1.2-1.3 for all other models. Similarly, the median absolute autocorrelation across strata and years was < 1.03 for all species and the first 3 models (no strata-year effects, fixed effects, uncorrelated random effects). For the correlated model, which had slower mixing, approximately half of the species had median lag-1 autocorrelations between 0.1-0.2.

3. Results

3.1 The direction and importance of correlated random interactions

We first address study goal #1, i.e. whether a correlation between model components is common for West Coast species and, if so, whether it is generally positive or negative. Specifically, we use the posterior distribution for the random-effect correlation c_{sy} to interpret whether the correlation is likely to be non-zero. The posterior for c_{sy} is greater than 95% positive for Dover sole, English sole, hake, rosethorn rockfish, and shortbelly rockfish. Inspection of the posterior

distribution for c_{sy} for each species individually (Fig. 1) suggests that other species (e.g. widow) might be positive, although the length of the current dataset is not sufficient to be confident. This positive correlation of Year×Area random effects between presence/absence and positive catches could arise from random changes in spatial distribution among years which causes increased (decreased) abundance in particular strata and years, in turn causing increased (decreased) probability of detection and catches when detected.

3.2 Comparing abundance index estimates and precision

Next, we address study goal #2, i.e., whether introducing a correlation between model components affects estimated indices of abundance. Comparison of the abundance indices for the random and correlated models for those species where $\Pr[c_{sy} > 0] > 0.9$ (Fig. 2) shows that there is little difference in the estimated indices or credible intervals. However, minor exceptions do occur, such as the 10% lower log-standard deviation for the “correlated” model than the “random” model for shortbelly rockfish. Indices for all stocks and models (Supp. Fig. 1) similarly show little difference among index standardization methods. In general, the greatest difference is seen for the model without any Year×Area interactions. This difference arises because the “zero” model is unable to account for any space-time interaction, and is hence the difference between the “zero” model and other models most pronounced for species such as canary rockfish that have previously been shown to be susceptible to extraordinarily large catches (Thorson et al. 2011).

4. Discussion

Simple survey analysis models for count data imply a linkage between the probability of detection and the expected catch. For example, sampling locations with a greater expected value for non-zero catches will also have a greater probability of non-zero catch when using a Poisson-

distributed GLM. This correlation between probability of detection and expected catch for count data is also maintained for more-complex models, e.g., zero-inflated negative binomial GLMMs. However, survey analysis models for continuous-valued data (e.g. catch weight per hectare as often used in fisheries stock assessment) have not previously been developed that incorporate a correlation between the probability of positive catch and the expected catch. We rectified this absence by developing a novel delta-GLMM that estimates a correlation between random effects affecting the positive and presence/absence model components. This model allows for greater comparability with count-data models, and is also intended as a method to evaluate the strength of evidence for such a correlation.

Overall, we find mixed support for a correlation between the probability of positive catch and the expected value of non-zero catch. This correlation has a posterior distribution with little (<10%) overlap with zero for only 5 of 28 species, but is positive for all five of these. A noteworthy caveat is that the strength and magnitude of this correlation is likely affected by the spatial strata stratification chosen *a priori* in any assessment, and the correlation might change if strata were chosen at a more fine or coarse spatial scale. A positive correlation can arise when environmental or anthropogenic factors cause random interannual changes in distribution among spatial strata. Potential environmental factors include transient oceanographic effects, which could cause a relocation of migratory species (e.g., Pacific hake) to suitable habitats (Methot and Dorn 1994). Potential anthropogenic factors resulting in a correlation include changes over time in the fishing intensity in different strata, which by decreasing total abundance in particular strata will cause a synchronized decrease in the probability of detection and expected catch size when detected in those strata.

For the NWFSC dataset analyzed here, the exact mechanism responsible for observed correlations in Year×Area terms remains unclear, because the species for which it is supported differ greatly in their distribution (e.g., Pacific hake are encountered throughout the bottom trawl sampling strata while shortbelly rockfish is primarily encountered in S. California), degree of fishing pressure (shortbelly has close-to-zero fishing mortality, the relative exploitation rate of English sole is close to 2%, and the relative exploitation rate of hake is 10% in recent years; Field et al. 2007, Stewart 2007, Stewart et al. 2011), migration (rockfish are sedentary, English sole and Pacific hake are migratory) and age at maturity (English sole and Pacific hake have lower age at maturity than most rockfish). As exploratory analysis, we plotted trends in the CPUE-weighted center-of-mass of depth and latitude for each of the 28 species as a proxy for spatial shifts in stock range. While no substantial trends in latitude were apparent, changes in depth were apparent for Dover sole, hake, sablefish, and some rockfish species (rosethorn, widow, and halfbanded). Thus, shifts in abundance among depths may explain the positive correlation between the probability of non-zero catch and catch rates for Dover and rosethorn, although this shift in depth distribution could itself be attributed to either environmental or anthropogenic factors.

However, including the correlation between presence/absence and positive catch rate components had very little effect on either the estimated indices or standard errors for any of these species in our study. These species represent a diversity of data qualities (ranging from easy to hard to detect) and life histories (migratory to sedentary). We therefore suspect the correlated model will have little impact on index estimates for other species and study systems with comparable data quantity and quality. The correlated model may still affect abundance index estimates in study systems with less data within particular strata or years, e.g., surveys

before and after establishing no-take areas. In the latter case, continued collection of presence/absence data may be feasible even when the total weight of catch cannot be measured (i.e. because it is not brought onto a sampling vessel).

Despite the lack of difference in estimated indices between random and correlated models, we believe that the correlated model provides one possible way additional to introduce 'biological realism' (Kuparinen et al. 2012) into conventional delta-GLMM index standardization models. By biological realism, we mean that this correlation represents a fish behavior (i.e. synchronized changes in local densities and the probability of occurrence) that is biologically plausible for a wide variety of fishes. This definition applies to a general research trajectory in fisheries (Bigelow and Maunder 2007, Zhou and Griffiths 2007, Thorson et al. 2011) and ecological modeling (MacKenzie et al. 2005, Dail and Madsen 2011) that attempts to incorporate biological processes and behaviors into survey analysis models using biologically interpretable parameters and equations. Although the correlation explored in this study may or may not be parsimonious for any given dataset or affect estimated indices of abundance, it allows researchers to estimate and account for spatial processes such as localized depletion and/or migration when analyzing survey data.

5. Acknowledgements

This work was improved by discussions with J. Cope, E.J. Dick, O. Hamel, A. Hicks, O. Shelton, I. Stewart, I. Taylor, and J. Wallace. We are grateful to the NMFS NWFSC survey team that collects the shelf/slope survey data, including (among others) J. Buchanan, K. Bosley, and D. Kamikawa. Data was provided by B. Horness and J. Wallace, sample code was provided by E.J. Dick and J. Wallace, and editorial help was provided by L. Brooks, J. Hastie, A. Punt, I. Taylor, and an anonymous reviewer.

6. Bibliography

- Bigelow, K.A., and Maunder, M.N. 2007. Does habitat or depth influence catch rates of pelagic species? *Canadian Journal of Fisheries and Aquatic Sciences* **64**: 1581–1594.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H., and White, J.S.. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* **24**: 127–135.
- Bradburn, M.J., Keller, A.A., and Horness, B.H. 2011. The 2003 to 2008 U.S. West Coast bottom trawl surveys of groundfish resources off Washington, Oregon, and California: Estimates of distribution, abundance, length, and age composition. Northwest Fisheries Science Center, Seattle, WA.
- Celeux, G., Forbes, F., Robert, C.P., and Titterton, D.M. 2006. Deviance information criteria for missing data models. *Bayesian Analysis* **1**: 651–673. [accessed 21 November 2012].
- Cope, J.M., and Punt, A.E. 2011. Reconciling stock assessment and management scales under conditions of spatially varying catch histories. *Fisheries Research* **107**: 22–38. doi: 10.1016/j.fishres.2010.10.002.
- Dail, D., and Madsen, L. 2011. Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics* **67**: 577–587.
- Field, J.C., Dick, E.J., and MacCall, A.D. (n.d.). Stock assessment model for the shortbelly rockfish, *Sebastes jordani*, in the California Current. U.S. Department of Commerce, Santa Cruz, CA.
- Gelman, A. 2006. Prior distributions for variance parameters in hierarchical models. *Bayesian analysis* **1**: 515–533.
- Gelman, A., Carlin, J.B., Stern, H.S., and Rubin, D.B. 2003. *Bayesian Data Analysis*, Second Edition. Chapman & Hall, Boca Raton, FL.
- Gelman, A., and Hill, J. 2007. *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, Cambridge, UK.
- Gneiting, T., Balabdaoui, F., and Raftery, A.E. 2007. Probabilistic forecasts, calibration and sharpness. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* **69**: 243–268. [accessed 27 August 2012].
- Helser, T.E., Punt, A.E., and Methot, R.D. 2004. A generalized linear mixed model analysis of a multi-vessel fishery resource survey. *Fisheries Research* **70**: 251–264. doi: 10.1016/j.fishres.2004.08.007.
- Keller, A.A., Horness, B.H., Fruh, E.L., Simon, V.H., Tuttle, V.J., Bosley, K.L., Buchanan, J.C., Kamikawa, D.J., and Wallace, J.R. 2008. The 2005 U.S. West Coast bottom trawl survey of groundfish resources off Washington, Oregon, and California: Estimates of distribution, abundance, and length composition. U.S. Dept. of Commerce, NOAA Tech. Memo., NMFS-NWFSC-93.
- Kuparinen, A., Mantyniemi, S., Hutchings, J.A., and Kuikka, S. 2012. Increasing biological realism of fisheries stock assessment: towards hierarchical Bayesian methods. *Environmental Reviews* **20**: 135–151.
- Lennert-Cody, C.E., Maunder, M.N., Aires-da-Silva, A., and Minami, M. In press. Defining population spatial units: Simultaneous analysis of frequency distributions and time series. *Fisheries Research*. doi: 10.1016/j.fishres.2012.10.001.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., and Hines, J.E. 2005. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Academic Press.
- Maunder, M.N., and Punt, A.E. 2004. Standardizing catch and effort data: a review of recent approaches. *Fisheries Research* **70**: 141–159. doi: 10.1016/j.fishres.2004.08.002.
- Methot, R.D., and Dorn, M.W. 1994. Biology and fisheries of North Pacific hake (*M. productus*). In *Hake biology, fisheries and markets*. Edited by J. Alheit and T.J. Pitcher. Chapman & Hall, London. pp.

- 389–414. Available from <http://www.springerlink.com/index/R0R482282K11L01T.pdf> [accessed 27 August 2012].
- Myers, R.A., and Pepin, P. 1990. The robustness of lognormal-based estimators of abundance. *Biometrics* **46**: 1185–1192.
- Pennington, M. 1983. Efficient Estimators of Abundance, for Fish and Plankton Surveys. *Biometrics* **39**: 281–286.
- Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *In* Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003). March. pp. 20–22. Available from <http://www.ci.tuwien.ac.at/Conferences/DSC-2003/Drafts/Plummer.pdf> [accessed 17 July 2012].
- Quinn, T.J., and Deriso, R.B. 1999. *Quantitative Fish Dynamics*. Oxford University Press, Oxford, UK.
- R Development Core Team. 2011. *R: A Language and Environment for Statistical Computing*. Vienna, Austria. Available from <http://www.R-project.org/>.
- Shelton, A.O., Dick, E.J., Pearson, D.E., Ralston, S., Mangel, M., and Walters, C. 2012. Estimating species composition and quantifying uncertainty in multispecies fisheries: hierarchical Bayesian models for stratified sampling protocols with missing data. *Canadian Journal of Fisheries and Aquatic Sciences* **69**: 231–246.
- Spiegelhalter, D.J., Best, N.G., Carlin, B.P., and Linde, A. van der. 2002. Bayesian Measures of Model Complexity and Fit. *Journal of the Royal Statistical Society. Series B (Statistical Methodology)* **64**: 583–639.
- Stefansson, G. 1996. Analysis of groundfish survey abundance data: combining the GLM and delta approaches. *ICES J. Mar. Sci.* **53**: 577–588.
- Stewart, I.J. 2007. Updated US English sole stock assessment: Status of the resource in 2007. Seattle, WA: National Marine Fisheries Service. Available from http://www.pcouncil.org/wp-content/uploads/2007_English_sole_update_council.pdf [accessed 27 August 2012].
- Stewart, I.J., Forrest, R.E., Grandin, C., Hamel, O.S., Hicks, A.C., Martell, S.J.D., and Taylor, I.G. 2011. Status of the Pacific hake (whiting) stock in US and Canadian waters in 2011. Status of the Pacific Coast Groundfish Fishery through 2011, Stock Assessment and Fishery Evaluation: Stock Assessments, STAR Panel Reports, and Rebuilding Analyses: 217.
- Sturtz, S., Ligges, U., and Gelman, A. 2005. R2WinBUGS: A Package for Running WinBUGS from R. *Journal of Statistical Software* **12**: 1–16.
- Su, Y.-S., and Yajima, M. 2012. R2jags: A Package for Running jags from R. Available from <http://CRAN.R-project.org/package=R2jags>.
- Thorson, J.T., Stewart, I., and Punt, A. 2011. Accounting for fish shoals in single- and multi-species survey data using mixture distribution models. *Canadian Journal of Fisheries and Aquatic Sciences* **68**: 1681–1693.
- Thorson, J.T., Stewart, I.J., and Punt, A.E. 2012. Development and application of an agent-based model to evaluate methods for estimating relative abundance indices for shoaling fish such as Pacific rockfish (*Sebastes* spp.). *ICES Journal of Marine Science* **69**: 635–647.
- Walters, C. 2003. Folly and fantasy in the analysis of spatial catch rate data. *Canadian Journal of Fisheries and Aquatic Sciences* **60**: 1433–1436.
- Wiedenmann, J., and Essington, T. 2006. Density-dependent overwinter survival in young-of-year bluefish (*Pomatomus saltatrix*)? A new approach for assessing stage-structured survival. *Canadian Journal of Fisheries and Aquatic Sciences* **63**: 1934–1943. doi: 10.1139/F06-094.
- Ye, Y., and Dennis, D. 2009. How reliable are the abundance indices derived from commercial catch-effort standardization? *Canadian Journal of Fisheries and Aquatic Sciences* **66**: 1169–1178.
- Zhou, S., and Griffiths, S.P. 2007. Estimating abundance from detection–nondetection data for randomly distributed or aggregated elusive populations. *Ecography* **30**: 537–549.

461 Table 1 – List of species

Common name	Scientific name	Proportion with positive catch	Average positive catch (kg.)
Arrowtooth	<i>Atheresthes stomias</i>	0.315	24.306
Aurora	<i>Sebastes aurora</i>	0.145	5.411
Bocaccio	<i>Sebastes paucispinis</i>	0.044	10.398
Canary	<i>Sebastes pinniger</i>	0.054	39.471
Chilipepper	<i>Sebastes goodie</i>	0.114	78.603
Cowcod	<i>Sebastes veils</i>	0.021	1.613
Darkblotched	<i>Sebastes crameri</i>	0.167	12.403
Dover	<i>Microstomus pacificus</i>	0.841	55.004
English	<i>Parophrys vetulus</i>	0.326	10.780
Greenspotted	<i>Sebastes chlorostictus</i>	0.050	5.956
Greenstriped	<i>Sebastes elongates</i>	0.214	11.159
Halfbanded	<i>Sebastes semicintus</i>	0.058	22.722
Hake	<i>Merluccius productus</i>	0.530	33.669
Longspine thornyhead	<i>Sebastolobus alascanus</i>	0.429	46.886
Petrale	<i>Eopsetta jordani</i>	0.333	8.395
Pacific Ocean perch	<i>Sebastes alutus</i>	0.069	29.355
Redbanded	<i>Sebastes babcocki</i>	0.084	1.828
Rosethorn	<i>Sebastes helvomaculatus</i>	0.076	6.738
Rougheyeye	<i>Sebastes aleutianus</i>	0.047	5.272

Sablefish	<i>Anoplopoma fimbria</i>	0.712	20.426
Sanddab	<i>Citharichthys sordidus</i>	0.245	34.733
Sharpchin	<i>Sebastes zacentrus</i>	0.059	70.163
Shortbelly	<i>Sebastes jordani</i>	0.070	53.779
Dogfish	<i>Squalus acanthias</i>	0.289	42.247
Shortspine thornyhead	<i>Sebastolobus alascanus</i>	0.599	11.999
Widow	<i>Sebastes entomelas</i>	0.034	11.395
Yelloweye	<i>Sebastes ruberrimus</i>	0.017	7.070
Yellowtail	<i>Sebastes flavidus</i>	0.050	63.554

462

463

464

465 Table 2 – Comparisons among four candidate models for all 28 species, showing the posterior
 466 distribution for the random effect correlation parameter including the median estimate and the
 467 posterior probability that the correlation is positive.

Species	Median	5%	95%	$\Pr(c_{sy}>0)$
Arrowtooth	-0.016	-0.403	0.373	0.471
Aurora	0.094	-0.381	0.518	0.653
Bocaccio	0.326	-0.343	0.758	0.840
Canary	0.255	-0.317	0.663	0.810
Chilipepper	0.059	-0.452	0.521	0.587
Cowcod	-0.044	-0.700	0.638	0.462
Darkblotched	-0.070	-0.471	0.334	0.374
Dover	0.421	0.154	0.641	0.999
English	0.480	0.129	0.726	0.995
Greenspotted	0.093	-0.441	0.556	0.626
Greenstriped	-0.043	-0.430	0.354	0.414
Halfbanded	0.001	-0.613	0.662	0.501
Hake	0.307	0.016	0.557	0.981
Longspine thornyhead (LST)	-0.075	-0.423	0.293	0.352
Petrale	0.041	-0.350	0.411	0.581
Pacific Ocean perch (POP)	-0.255	-0.682	0.338	0.193
Redbanded	-0.253	-0.684	0.345	0.210
Rosethorn	0.451	-0.068	0.756	0.960
Rougheye	-0.089	-0.601	0.526	0.387

Sablefish	0.145	-0.135	0.410	0.842
Sanddab	-0.218	-0.597	0.243	0.177
Sharpchin	0.241	-0.386	0.698	0.772
Shortbelly	0.532	-0.038	0.823	0.967
Dogfish	0.079	-0.238	0.376	0.682
Shortspine thornyhead (SST)	0.050	-0.297	0.386	0.611
Widow	0.336	-0.327	0.739	0.851
Yelloweye	0.020	-0.593	0.664	0.522
Yellowtail	-0.008	-0.571	0.558	0.491

468

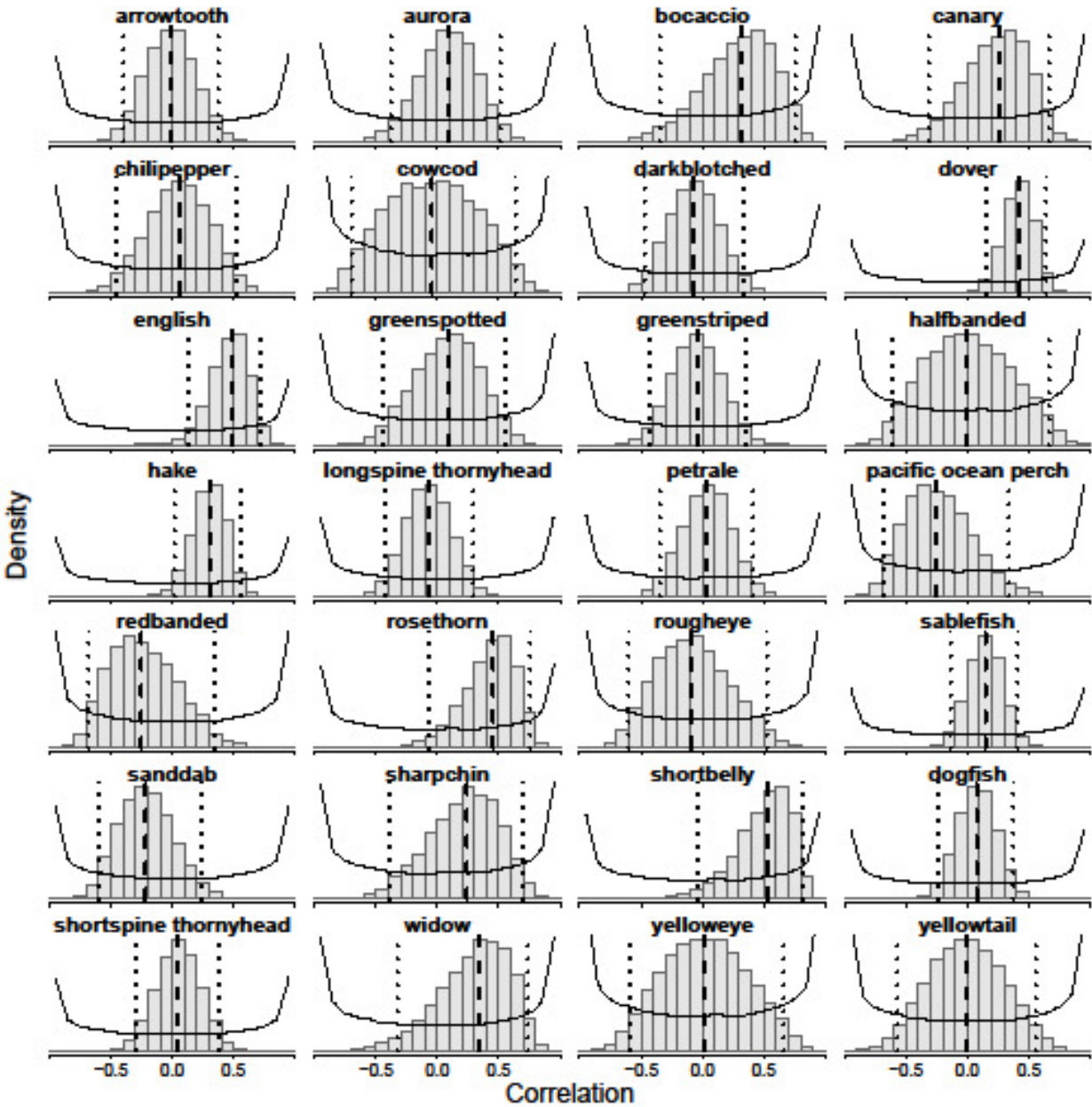
469

470

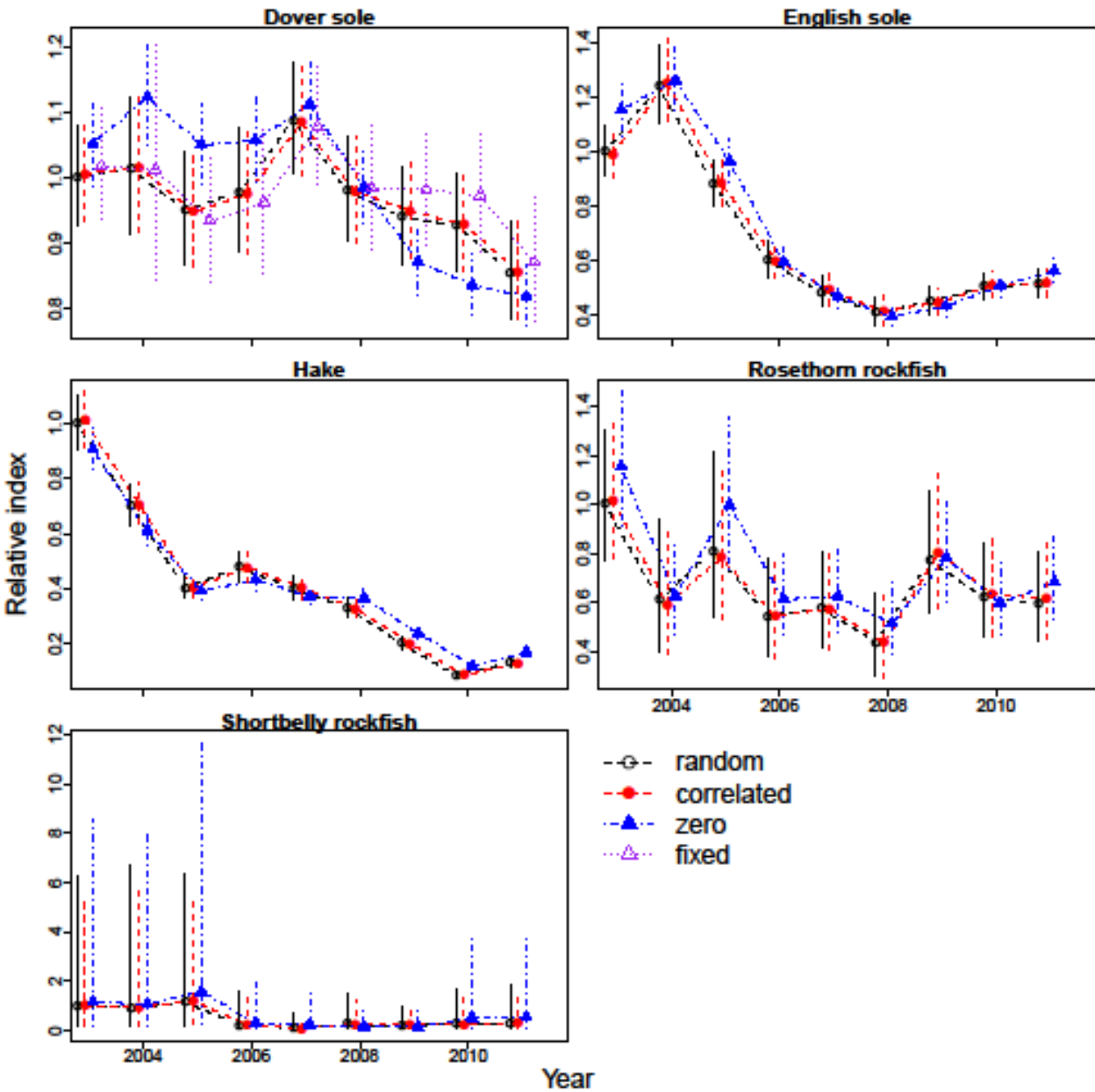
Figure Captions

Fig. 1 -- Posterior distribution for correlation c_{sy} between Strata×Year random effects for positive catch $\gamma^{(sy)}$ and for presence/absence $\omega^{(sy)}$ model components, with median (dashed line) and 95% credible interval (dotted lines) as well as the Wishart prior distribution (solid line).

Fig. 2 – Indices of abundance (lines, standardized) and +/- one posterior standard deviation for those five species where the posterior distribution for correlations was significant ($\Pr[c_{sy} > 0] > 0.9$). Lines for are offset along the x-axis to improve legibility, and the fixed-effect Strata×Year model is only included for those species that have at least one encounter in every strata-year combination (e.g., Dover sole).



484 Fig. 2



485

486

487

Supplementary figure captions

Suppl. Fig. 1 – Panel figure showing the estimated indices (lines, standardized) and +/- one posterior standard deviation for indices estimated without Strata×Year interactions (blue filled triangle), with Strata×Year interactions as a fixed effect (purple hollow triangle), and with Strata×Year interactions as independent (black hollow circle) or correlated random effects (red filled circle), for each stock. Lines for are offset along the x-axis to improve legibility, and the fixed-effect Strata×Year model is only included for those species that have at least one encounter in every strata-year combination (e.g., Dover sole).

