Review Article

Mixed effects: a unifying framework for statistical modelling in fisheries biology

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Fisheries biology encompasses a tremendous diversity of research questions, methods, and models. Many sub-fields use observational or experimental data to make inference about biological characteristics that are not directly observed (called "latent states"), such as heritability of phenotypic traits, habitat suitability, and population densities to name a few. Latent states will generally cause model residuals to be correlated, violating the assumption of statistical independence made in many statistical modelling approaches. In this exposition, we argue that mixed-effect modelling (i) is an important and generic solution to non-independence caused by latent states; (ii) provides a unifying framework for disparate statistical methods such as time-series, spatial, and individual-based models; and (iii) is increasingly practical to implement and customize for problem-specific models. We proceed by summarizing the distinctions between *fixed* and *random* effects, reviewing a generic approach for parameter estimation, and distinguishing general categories of non-linear mixed-effect models. We then provide four worked examples, including state-space, spatial, individual-level variability, and quantitative genetics applications (with working code for each), while providing comparison with conventional fixed-effect implementations. We conclude by summarizing directions for future research in this important framework for modelling and statistical analysis in fisheries biology.

Keywords: Gaussian random field, hierarchical, individual-level variability, integration, latent variable, measurement error, mixed-effects model, random effects, spatial variation, state space.

Introduction

> Counting fish is like counting trees - except they are invisible and they keep moving
>
> John Shepherd, quoted in Hilborn (2002)

Role of models in fisheries science

Marine populations are dispersed across varied habitats and are influenced by ecosystem and climatic factors that change over time (Hilborn and Walters, 1992). Population and community dynamics arise from somatic growth, reproduction, maturation, natural and fishing mortality, movement, between-species interactions, and spatial variation in habitat quality (Hilborn and Walters, 1992; Quinn and Deriso, 1999). These processes are generally not possible to measure directly at the spatial scale of the population or community. Predicting the net effect of all these processes simultaneously therefore requires statistical models that are used to reconcile population and community theory with available data. These statistical models must, explicitly or implicitly, make inference from data to biological characteristics that are not directly observed (i.e. statistical models are often used to count invisible moving trees).

The existence of states that are not directly observed (termed "latent states" in the following) causes complications for many statistical models in fisheries biology (see Millar and Anderson, 2004). Spatial variability may cause unexplained residuals in data from multiple sampling units to be statistically correlated ("spatial non-independence"), and interannual changes in population-dynamics

processes may cause temporal correlations in unexplained residuals ("temporal non-independence"). Individuals that are genetically similar may also have unmodelled correlations in life history traits, and shared environmental changes (e.g. trophic effects) may cause synchronous changes in individual behaviours. Unmodelled correlations invalidate the assumption of statistical independence between residuals for different data points, as is commonly assumed by simple regression models (Aitkin *et al.*, 2009). Inference that ignores correlation caused by latent states will provide an imprecise (and potentially biased) estimate of the phenomena of interest, whether it is population status or individual behaviour of fishing vessels (Wagner *et al.*, 2006). Models that neglect latent states may also provide inaccurate estimates of precision, that is, by providing standard errors that are too narrow or wide.

We contend that most fisheries datasets are generated by processes that have variation over space, time, and among individuals, and these dependencies will induce correlations among observations and thus complicate simple regression-based models. Therefore, methodologies that account for latent states and general non-independence are central to inference in fisheries and aquatic research. We therefore seek to make three main points via illustration:

(i) Models using random effects are important for inference when analysing fisheries data that exhibit non-independence.

(ii) Random effects provide a unifying statistical framework for models that might otherwise seem unrelated, for example, time-series models for populations, spatial models, genetics models, and models for variation among individuals;

(iii) Models that include random effects are increasingly easy to build and customize for specific fisheries problems using publicly available modelling tools and software.

Discussions of random effects are available elsewhere (Searle *et al.*, 1992; Gelman and Hill, 2007; Pinheiro and Bates, 2009) so we instead seek to provide an accessible introduction for fisheries biologists using fishery and aquatic examples. The remainder of this paper is devoted to quickly reviewing inference and parameter estimation for models with random effects, followed by four case-study applications that include example code for flexible model development and parameter estimation.

Random effects

In this review, we use *random effects* to broadly refer to parameters that are assumed to arise from a shared stochastic process, where the distribution of likely values can be estimated. *Fixed effects* refers to other model parameters (including the parameters governing the distribution of random effects) where there is not sufficient data to estimate these parameters as arising from a shared distribution of likely values. Finally, a *mixed-effects model* is any model that has a mix of random and fixed effects (see Gelman, 2005 for more discussion). For example, an ecologist might analyse data from a growth experiment involving many individual fish subject to similar environmental conditions (e.g. Shelton *et al.*, 2013). Because individual growth arises from a shared stochastic process (i.e. the conditions of the experiment), parameters representing growth rate for each fish can be treated as if they are randomly drawn from a shared distribution of likely values. By treating growth parameters as if they are drawn from a shared distribution, the ecologist can then estimate characteristics of the distribution of likely growth rates (i.e. its mean and standard deviation). The

parameter representing average growth rate is in this case *fixed*, while individual growth rate parameters are *random* (i.e. the growth rates of individual fish is replicated in the experiment, so the magnitude of variation in growth rate among individuals can be estimated).

Random effects are particularly useful thanks to the phenomenon called *shrinkage*. Shrinkage occurs when random effects are shrunk towards the average value for the distribution of likely values. Shrinkage implies that the estimated value for each random effect includes information from two sources: (i) the data for each sampling unit (e.g. measurements of each individual fish in the experiment), which would be the only source of information if the parameter was treated as a fixed effect, and (ii) the estimated distribution for the random effect, which incorporates information from all other parameters that are also drawn from the same distribution (e.g. measurements from all individuals in the experiment). From a practical perspective, the mixed-effect modelling approach has several useful properties: (i) shrinkage of parameters arising from a shared stochastic process towards an average value, where the degree of shrinkage depends on the uncertainty of the individual-level parameters; (ii) using a smaller number of degrees of freedom than would occur if estimating each parameter independently; and (iii) providing estimates of latent states at various hierarchical levels (e.g. estimates of individual growth rates, in addition to average growth rates among all individuals).

Applied statisticians increasingly advocate a strategy of "hierarchical modelling" (Berliner, 1996; Royle and Dorazio, 2008; Cressie and Wikle, 2011). In this framework, the data are viewed as forming the bottom of a hierarchy. The data then provide information about latent states that are in the middle of the hierarchy. Latent states are then postulated to have some structure, for example, being replicates of the same stochastic process or having some dynamical structure over time. In population-dynamics models, the latent states might represent population abundance in consecutive periods, and ecological theory might motivate a model representing changes in population abundance over time (Figure 1a). In spatial models, in contrast, latent states might represent densities at different sites where population densities are drawn from a shared distribution (Figure 1b). Our four case studies further illustrate how fishery examples can be decomposed into measurement and process variability. In these and other contexts, research interest may be focused on either the middle level (latent states) or the top level (ecological processes governing latent states). The hierarchical framework allows inference about both levels. These latent states can account for non-independence, including spatial, temporal, and individual-level correlations among sampling units.

Taxonomy of random effects

Random effects underlie many different model types that might otherwise seem unrelated. We broadly distinguish the following four categories. In each case, the model can be conceptualized hierarchically as including fixed-effect parameters (top level), which then govern similarities among latent states (middle level), and where the probability of available data is specified conditional on the value of the latent states.

(i) *State-space models* represent changes in a latent variable over time, for example, population abundance or animal location (Jonsen *et al.*, 2005) given a time-series of measurements of the variable (e.g. a population survey; see Example 1).
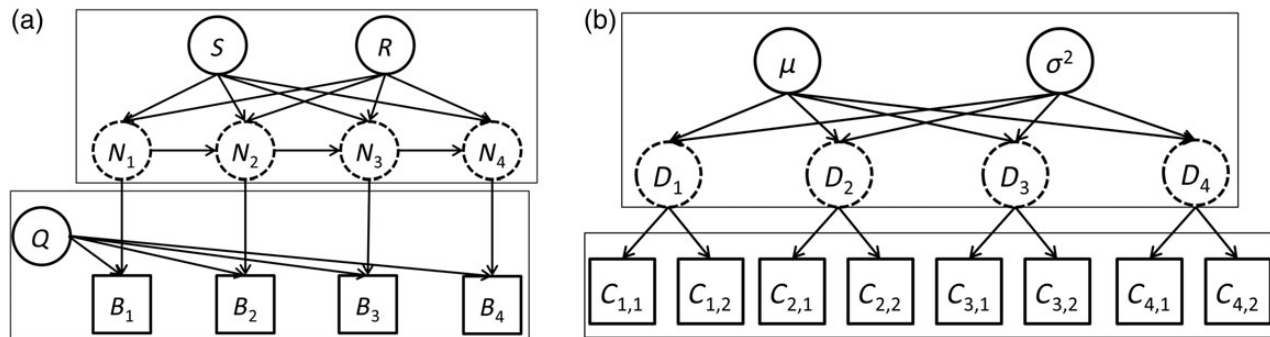
Figure 1. (a) A directed acyclic graph (DAG) representing a simple state-space model, where abundance *N* changes from year 1 through year 4 ($N_1 - N_4$) following survival rate *S* and recruitment rate *R*. Each year has a single survey of abundance B_1 through B_4, where the abundance index is proportional to true abundance with proportionality coefficient *Q*. Abundance in each year is treated as a latent variable, and therefore is estimated as a random effect. Data are represented using squares; fixed effects using solid circles; and random effects using dashed circles. The top box represents the process model, while the bottom box represents the observation model. (b) A directed acyclic graph (DAG) representing a simple multi-level model, where four populations have densities D_1 through D_4, and where they all have a similar density with average μ and between-population variance σ^2. Each population also has two surveys of local density (i.e. count $C_{1,1}$ and $C_{1,2}$ for population 1). Local density at each site is treated as a latent variable, and therefore is estimated as a random effect. Data are represented using squares, fixed effects using solid circles, and random effects using dashed circles. The top box represents the process model, while the bottom box represents the observation model.

(ii) *Spatial models* predict a response variable that is spatially indexed. Given that the response variable is influenced by a latent state (e.g. spatial variation in habitat suitability), the response variable (e.g. local densities) may have residuals that co-vary spatially, for example, residuals for nearby points will often be more correlated than residuals for distant points (see Example 2).

(iii) *Individual- and agent-based models* explain observed patterns in population and community ecology by modelling the dynamics of individual animals (Black and McKane, 2012). Specifically, characteristics of each individual (e.g. size) are treated as a latent state, and changes in individual characteristics are treated as random effects. Agent-based models generally permit estimates of average demographic rates, as well as variation among individuals (Royle and Dorazio, 2008 see Example 3).

(iv) *Multi-level models* treat different units of study (e.g. sites, populations, and species) as replicates of a single, shared ecological process. They are often used in meta-analysis to estimate variability in an ecological process among experimental units (Osenberg *et al.*, 1999; Thorson *et al.*, in press-a), and can also be used to partition variance in observed data among multiple possible causes (e.g. when analysing heritable traits in studies of quantitative genetics; see Example 4).

These four broad categories are not intended as a complete list of all mixed-effect models, and are instead presented to highlight the diversity of applications for random effects.

Parameter estimation for mixed-effects models

The mixed-effect modelling approach requires estimating a parameter representing the variance (scale) of random effects, that is the magnitude of variability of coefficients around their estimated mean (location) value. However, estimating this variance parameter generally requires integrating across all possible values of the random effects. In linear models, this integration can be done using closed-form estimation equations, as reviewed for interested readers in Supplementary Materials A: Linear mixed-effects

models. The integration can also be approximated for other special cases using model-specific methods (i.e. penalized quasi-likelihood, generalized estimation equations, etc., see Breslow and Clayton, 1993 for an example). However, for the general case of non-linear mixed-effect models, this integration takes the following form:

$$\mathrm{L}(\boldsymbol{\theta}, \boldsymbol{\tau}|\boldsymbol{D}) = \int_{\boldsymbol{\varepsilon}} \mathrm{Pr}(\boldsymbol{D}|\boldsymbol{\theta}, \boldsymbol{\varepsilon}) \, \mathrm{Pr}(\boldsymbol{\varepsilon}|\boldsymbol{\tau}) \mathrm{d}\boldsymbol{\varepsilon}, \tag{1}$$

where $\mathrm{L}(\boldsymbol{\theta},\boldsymbol{\tau}|\boldsymbol{D})$ is the marginal likelihood that is maximized to estimate fixed-effects $\boldsymbol{\theta}$ and parameters $\boldsymbol{\tau}$ governing the distribution of random effects given available data $\boldsymbol{D}$, $\mathrm{Pr}(\boldsymbol{D}|\boldsymbol{\theta},\boldsymbol{\varepsilon})$ is the probability of the data conditional on values for fixed and random effects, and $\mathrm{Pr}(\boldsymbol{\varepsilon}|\boldsymbol{\tau})$ is the probability of random effects $\boldsymbol{\varepsilon}$ given the value of parameters $\boldsymbol{\tau}$ governing their distribution. The integral in Equation (1) is essentially taking a weighted average of the probability of data $\mathrm{Pr}(\boldsymbol{D}|\boldsymbol{\theta},\boldsymbol{\varepsilon})$ for all possible values of the random effects, where each possible value of the random effect $\boldsymbol{\varepsilon}$ is weighted by its probability of occurrence $\mathrm{Pr}(\boldsymbol{\varepsilon}|\boldsymbol{\tau})$. $\boldsymbol{\tau}$ includes the variance of random effects, which is estimated along with other fixed-effect parameters. The integral across random effects is the central computational challenge in random effect models (de Valpine, 2009), but there are many efficient computational strategies for implementing this integral. Computational strategies are reviewed in Supplementary Materials B: Computational approaches for mixed-effect estimation.

We suspect that many ecologists receive their first introduction to mixed-effect estimation using a Bayesian statistical paradigm (Royle and Dorazio, 2008; Kéry and Schaub, 2012). Presumably, this occurs because Bayesian statistics conventionally involves reporting results in terms of the expected value of a posterior distribution for each parameter, and estimating this expected value already requires integration (e.g. via Markov chain Monte Carlo). Given that Bayesians often use integration methods already, switching between fixed- and mixed-effects models is then relatively easy. We follow Cressie and Wikle (2011, p. 15 and elsewhere) in suggesting that the differences between Bayesian and maximum likelihood estimation of mixed-effects models are smaller than sometimes

stated. Specifically, maximum likelihood mixed-effect estimation integrates across random effects only, while Bayesian estimation integrates across both random and fixed effects (with integration weights provided by a prior probability assigned to all fixed effects): see section *Example* 3: *Individual-level models for population and community ecology* for more details on Bayesian estimation. We note that this is the only computational distinction between methods. However, Bayesian and maximum likelihood approaches generally have different implications regarding how uncertainty is propagated and interpreted (Clark and Gelfand, 2006; Stewart *et al.*, 2013). For example, Bayesian estimation allows for easy summary of estimation uncertainty via the estimated posterior probability of parameters given available data, while maximum likelihood has a greater variety of methods for summarizing estimation uncertainty (e.g. likelihood profiles, bootstraping, asymptotic variance; see de Valpine, 2009). These and other contrasts between Bayesian and maximum likelihood approaches are complicated, and depend on both inferential goals and computational limitations, so we refer the reader elsewhere for detailed treatment (e.g. see Cressie *et al.*, 2009; Lele and Dennis, 2009 for contrasting interpretations).

Hot topics in fisheries science

In the following sections, we demonstrate the unified nature of random effects modelling via four disparate applications. First, we illustrate state-space modelling, which includes both single-species population-dynamics models and multispecies ecosystem models. Second, we illustrate spatial modelling, which is increasingly used for management of fish habitat and inference about protected areas. Third, we illustrate individual-level modelling, which includes models for behavioural, spatial, and developmental differences among individuals in a population. Fourth, we illustrate multi-level models via an example from quantitative genetics. In each case, we provide code for implementing simple versions of each model, while emphasizing the increasingly broad range of software tools that are available for mixed-effects modelling.

Example 1: State-space models for populations and ecosystems

State-space models simultaneously estimate variability in ecological dynamics and measurements, and have been used for over 20 years when estimating population dynamics and productivity (Schnute, 1991; Meyer and Millar, 1999). State-space estimation generally outperforms estimation that includes only process errors or measurement errors (Punt, 2003; Ono *et al.*, 2012), but is rarely used in multispecies or whole-ecosystem models. We begin by discussing state-space models for single species because they provide a useful example of separability that can then be used in other modelling contexts.

The conventional state-space surplus production model uses a function that represents population growth to describe average change in biomass as a function of population size:

$$b_{t+1} = (b_t + f(b_t) - c_t) \cdot e^{\tau_t}, \tag{2}$$

where b_t is biomass in year t, $f(b_t)$ is the production function, c_t is known removals, and τ_t is stochastic variability in population dynamics (which is often assumed to follow a normal distribution, i.e. $\Pr(\tau_t) = N(0, \sigma_\tau^2)$, where $N(x,y)$ is the probability density function for a normal distribution with mean x and variance y, and σ_τ^2 is the

estimated variance of random effects τ). This model is estimated using an index that is proportional to population biomass:

$$s_t = q b_t \cdot e^{\varepsilon_t}, \tag{3}$$

where s_t is the survey index in year t, q is the proportionality constant for the index, and ε_t is the measurement error in year t (which is also generally assumed to follow a normal distribution, i.e. $\Pr(\varepsilon_t) = N(0, \sigma_\varepsilon^2)$, where σ_ε^2 is the variance of measurement errors ε). The model can be estimated by integrating across process errors τ, and the dimensionality of this integral scales with the time-series length $N - 1$ (i.e. the number of transitions). However, instead of this high-dimensional integral, we can instead do N two-dimensional integrals by using the state-space parameterization (Gay, 1996; Skaug and Fournier, 2006). This parameterization recognizes that b_{t+1} is statistically independent of b_{t-1} given a fixed value of b_t (and other model parameters representing the production function, catchability, etc.), and hence there is no need to simultaneously integrate over b_{t+1} and b_{t-1}. This statistical independence means that b_{t+1} and b_{t-1} are partially separable. We provide example code (Supplementary data, Appendix A; also available from https://github.com/James-Thorson/mixed-effects/tree/master/State-space_model (last accessed 17 November 2014)) for the separable implementation of the state-space surplus production model (modified from Pedersen *et al.*, 2011; Berg, 2012) using AD Model Builder's random effect module (ADMB-RE; Skaug and Fournier, 2006), and apply it to a publically available dataset (Meyer and Millar, 1999). This separable model incorporates the assumption that process and measurement errors have identical variance, which is a common assumption (Ono *et al.*, 2012) given the difficulty in separately estimating process and measurement variance from a single surplus production dataset (Knape, 2008). We contrast the state-space model with a conventional measurement error implementation (i.e. a model assuming that $\tau = 0$), where both models include a prior on maximum population growth rate r (identical to the prior in Meyer and Millar, 1999). Both models are estimated via maximum likelihood (ADMB-RE automatically approximates the integral across b in Equations (2) and (3) when calculating the marginal likelihood of fixed effects). This comparison (Figure 2) shows that both conventional and state-space implementations can generate the dynamics shown in the index of abundance. However, the state-space model provides estimates of population abundance that have smaller confidence intervals, implying that estimates of the latent state (population abundance) are more precise.

Although state-space versions of more complicated population and ecosystem models are relatively new to fisheries modelling (Mäntyniemi *et al.*, 2013; Nielsen and Berg, 2014 but see Millar and Meyer, 2000), Gudmundsson and Gunnlaugsson (2012) used a separable implementation of an age-structured population model. Significantly, this model is separable because they admit random variability in survival for each age class in each year, which causes numbers of age 3 fish to be statistically independent of age 1 fish given a fixed value of age 2 fish (note that abundance of ages 1 and 3 fish are not statistically independent when survival of each age class is deterministic). Similarly, an ecosystem model tracking population abundance for each species or guild could exploit separability, wherein abundance of each species in year $t + 1$ is statistically independent of abundance in year $t - 1$ (again, given fixed values for abundance of all species in year t).

Additionally, there is increasing interest in "hierarchical" time-series models, in which different population-specific time-series
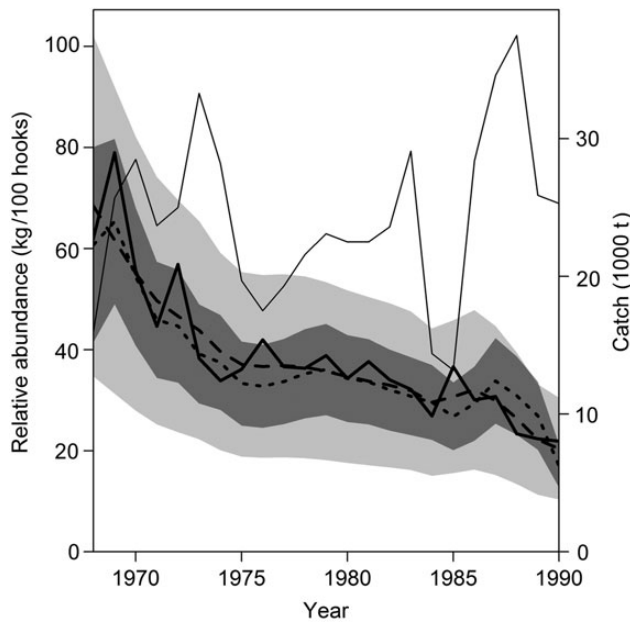
Figure 2. Results from a comparison of state-space (dotted line and dark grey shading) and measurement error (dashed line and light-grey shading) surplus production models (line: maximum likelihood estimate of available abundance qn_t, shaded area: 95% confidence interval) fitted to an abundance index (thick black line) and catch time-series (thin black line), showing that the state-space model provides a more precise (smaller confidence interval) fit to available data.

share a common trajectory. Dynamic factor analysis (Zuur *et al.*, 2003), for example, estimates one or more trajectories, then estimates "loading factors" to relate these to observed time-series. Other models focus more explicitly on "shrinking" individual time-series towards a shared trend, and hence can be used to estimate synchrony of multiple populations, either regionally (Thorson *et al.*, 2014b), as a function of distance (Su *et al.*, 2004), or through the impact of shared environmental effects (Minto *et al.*, 2014). We therefore turn next to spatial models, which ultimately can be combined with state-space time-series methods to generate spatio-temporal models (Royle and Wikle, 2005; Wu *et al.*, 2013).

Example 2: spatial models for understanding and management of habitat

Spatial models are designed to conform to the first law of geography, that is, that "everything is related to everything else, but near things are more related than distant things" (Tobler, 1970). They do this by estimating a statistical correlation in the residuals of nearby points or regions, after accounting for the effect of measured spatial variables (Cressie and Wikle, 2011). We find Gaussian random fields (Haran, 2011; Thorson *et al.*, in press-b) to be the simplest example of spatial modelling:

$$L(x_0, \sigma_m^2, \sigma_s^2|\mathbf{y}) = MVN(\mathbf{y}|x_0, \mathbf{\Sigma}), \qquad (4)$$

where $\mathbf{y}$ is a response variable (e.g. population density) measured at several sites with known locations and $L(x_0, \sigma_m^2, \sigma_s^2|\mathbf{y})$ is the marginal likelihood of parameters where x_0 is the average for the response variable across all locations, σ_m^2 is the variance of measurement errors, and σ_s^2 is the variance of the spatial effect (i.e. the covariance for two different samples at the same location). $MVN(\mathbf{y}|x_0,\mathbf{\Sigma})$ is the

probability density function for a multivariate normal distribution with mean x_0 and covariance matrix $\mathbf{\Sigma}$ estimated given spatial distance between the location of available data $\mathbf{y}$:

$$\mathbf{\Sigma} = \sigma_m^2 \mathbf{I} + \sigma_s^2 \cdot \exp\left[\frac{-\mathbf{D}^2}{2\lambda^2}\right], \qquad (5)$$

where $\mathbf{I}$ is an identity matrix with 1 s on the diagonal and 0 s elsewhere, $\mathbf{D}$ is a distance matrix composed of the distance $d_{i,j}$ between all observations i and j, and λ controls how quickly spatial covariance decreases as a function of distance. Gaussian random fields can be efficiently used to simulate spatial dependencies (i.e. to represent unmodelled spatial effects in a simulation study, e.g. Thorson *et al.*, 2012) or estimate spatial correlations in a statistical model (Shelton *et al.*, 2014). Like all random effect models, the likelihood of fixed effects can be re-formulated as arising from the integral across a latent random effect:

$$L(x_0, \sigma_m^2, \sigma_s^2|\mathbf{y}) = \int_x \Pr(\mathbf{y}|\mathbf{x}, \sigma_m^2)\Pr(\mathbf{x}|\sigma_s^2, \mathbf{D}, \lambda)\mathrm{d}\mathbf{x}, \qquad (6)$$

where the probability of data $\mathbf{y}$ given random effects $\mathbf{x}$, $\Pr(\mathbf{y}|\mathbf{x}, \sigma_m^2) = N(\mathbf{y} - \mathbf{x}, \sigma_1^2)$, is the first term in the integral, and the probability of random effects given the distance between locations, $\Pr(\mathbf{x}|\sigma_s^2, \mathbf{D}, \lambda) = MVN(\mathbf{x}|\sigma_s^2, \exp(-\mathbf{D}^2/2\lambda^2))$, is the second term in the integral.

When sample sizes are low, $\mathbf{\Sigma}$ can be calculated to estimate parameters in Equations (4)–(6) directly. However, these equations (i.e. calculating $\Pr(\mathbf{x}|\sigma_s^2, \mathbf{D}, \lambda)$) require inverting $\mathbf{\Sigma}$, which becomes computationally infeasible for a large number of points. In this case, there are several approaches that are computationally efficient. One is to use Equation (6), and use a limited number of points for spatial variable $\mathbf{x}$ (so that the number of random effects in $\mathbf{x}$ is much smaller than the number of observations in $\mathbf{y}$). Equation (6) must then be modified to account for the projection of $\mathbf{x}$ to the location of each $\mathbf{y}$, but this can be done in a computationally efficient manner (Shelton *et al.*, 2014). Alternatively, the inverse–covariance matrix of the Gaussian random field can be approximated using three sparse matrices as calculated using a stochastic partial differential equation approach (Lindgren *et al.*, 2011; Illian *et al.*, 2012). This latter approximation is extremely fast, can be generalized to include many other spatio-temporal and random-effect models (Rue *et al.*, 2009; Thorson *et al.*, in press-b), and is easily implemented using the *R-INLA* (integrated nested Laplace approximation) package (Lindgren, 2012; Rue *et al.*, 2013) in the *R* statistical platform (R Core Development Team, 2012).

Given the ease, efficiency, and generality of the *R-INLA* package, we demonstrate its use in a simple spatial model using simulated data (code is included as Supplementary data, Appendix B; https://github.com/James-Thorson/mixed-effects/tree/master/Spatial_model (last accessed 17 November 2014)). Specifically, we simulate 1000 data points from a Poisson distribution within a square sampling domain, where the logarithm of the expected value increases from West to East and has a residual pattern along the diagonal. These parameters for a spatial model are estimated using *R-INLA*, using a Poisson distribution for measurement errors, including eastings as a covariate, and assuming spatial residuals follow a Gaussian random field (using an exponential covariance function). We compare the *R-INLA* parameter estimates with a conventional, Poisson-distributed generalized linear model, which uses the Akaike
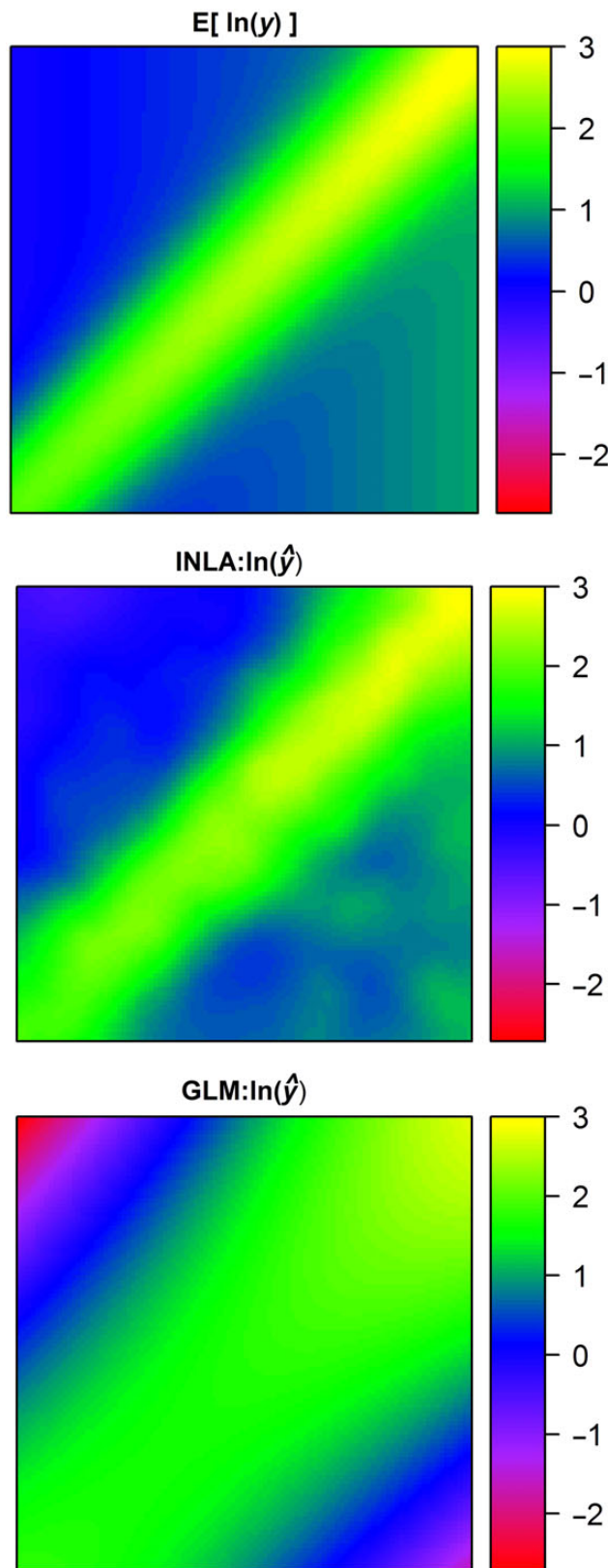
Figure 3. Depiction of results from using R-INLA to implement a spatial random-effect model. The top panel shows the true value of a spatial field (e.g. the log of population densities). The middle panel shows spatial estimate of log-population densities. The bottom panel, in contrast, shows estimates of the spatial field arising from a

information criterion (AIC; Akaike (1974)) to select among all linear and quadratic combinations of eastings and northings as covariates. *R-INLA* estimates all parameters in 58 s, and the estimated slope of the east–west covariate is accurate, although imprecise (true value: 1.0; estimated value: 1.09 with standard error 1.48). Inspection of the predicted surface (Figure 3) shows that the INLA model is also able to recover the residual surface without it being explicitly specified, while the conventional GLM provides poor estimates of the surface, particularly in northwest and southeastern corners of the spatial domain.

Example 3: individual-level models for population and community ecology

Variation among individuals, whether due to genetic, phenotypic, spatial, and/or behavioural differences, is increasingly recognized as central to predictions about populations, communities, and ecosystems (Black and McKane, 2012; Smallegange and Coulson, 2012). Although conventional dynamical models (e.g. the surplus production model in Example 1) assume that all individuals have an equal probability of interacting with each other, variability among individuals will arise most obviously from spatial limitations, and simple spatial limitations (e.g. limited dispersal range) can have surprising and non-intuitive impacts on population and community stability (Levin and Pacala, 1997; Leibold et al., 2005).

Individual-level models can be interpreted to include a broad range of ecological research, ranging from dynamic programming approaches to foraging behaviours (Clark and Mangel, 2000) to Ornstein–Uhlenbeck models for representing spatial movement of individual animals (Johnson et al., 2008). However, we here focus attention on the estimation and population-level implications of variation in demographic rates among individuals (e.g. growth, fecundity, survival, and detection probabilities). In particular, a tremendous body of research is devoted to inferring ecological processes from the allometric (non-linear) scaling relationships among life history parameters such as individual growth rates, natural mortality, and age at maturity (Andersen and Beyer, 2006; Pauly, 2010; Charnov et al., 2013). By and large, estimation of life history relationships does not extend to estimating the magnitude of variation among individuals within a given population in each of these rates. Variation among rates such as growth has an important effect on the distribution of traits in surviving individuals whenever human-induced mortality is size selective (Taylor and Methot, 2013).

Variation among individuals can also be easily included by treating each individual's demographic parameters as a random effect that arises from a population-level distribution, where this random effect approximates a shared stochastic process (i.e. environmental influences). As an example, we show how data regarding the size of individual fish over time can be used to estimate the magnitude of variation in individual growth rates. We start with the specialized von Bertalanffy growth rate function:

$$\frac{dl}{dt} = q_i - k_i l, \tag{7}$$

where dl/dt is change in length l as a function of time t, q_i represents the energy acquisition rate for individual i, and k_i represents

fixed-effect model using eastings and northings as linear and quadratic terms, as well as their interaction, and selecting among these possible variables using stepwise-AIC model selection.

metabolic upkeep costs for individual i. However, individuals that are more highly active may obtain more food (increased q_i) and simultaneously have greater upkeep costs (increased k_i). Following Shelton *et al.* (2013), we include this association between energy acquisition and metabolic rates via the power equation:

$$q_i = \gamma k_i^{\psi}, \qquad (8)$$

where γ and ψ approximate the allometric scaling of energy costs and acquisition. We estimate average and individual-specific growth rates using data where a sequence of lengths are available for each individual fish. Consequently, we solve Equation (8) for length at specified times. Integration then yields:

$$l(t + \Delta_t) = l(t)e^{-k_i \Delta_t} + \frac{\gamma k_i^{\psi}}{k_i}(1 - e^{-k_i \Delta_t}), \qquad (9)$$

where Δ_t is the number of periods elapsed between length intervals. Equation (9) also requires estimation of $l_{0,i}$, that is, the length upon first observation for each individual i, and we treat this as a normally distributed random effect, with estimated mean and variance parameters. Readers are referred to Shelton *et al.* (2013) for an expanded model that incorporates variability in γ over time, although we retain the assumption that k_i varies among individuals (and hence has subscript i), where it follows a lognormal distribution with estimated log-mean and log-*SD* parameters. We also assume that $\psi = 0.2$ as estimated by Shelton *et al.* (2013) using profiling optimization methods.

Following previous notation, parameters are estimated by integrating across all random effects k and l_0. We implement this as a Bayesian model, and hence must specify a prior distribution $\Pr(\theta, \tau)$ for all fixed effects θ and τ, in addition to the probability of the data and the probability of random effects:

$$\Pr(\theta, \tau | D) = \int_{k, l_0} \frac{\Pr(D|\theta, k, l_0) \Pr(k|\tau) \Pr(l_0|\tau) \Pr(\theta, \tau)}{C} dk \, dl_0, \qquad (10)$$

where the probability of data conditional on fixed and random effects, $\Pr(D|\theta, k, l_0)$, is derived from Equation (9), $\Pr(k|\tau)\Pr(l_0|\tau)$ is the probability of random effects k and l_0, and C is the constant of integration necessary for the Bayesian implementation. We implement this model using the *Just Another Gibbs Sampler* (Plummer, 2003) software called from *R* using the *R2jags* package (Su and Yajima, 2012) and provide the code as an example of how to call *JAGS* from *R* (Supplementary data, Appendix C; https://github.com/James-Thorson/mixed-effects/tree/master/Individual_variability (last accessed 17 November 2014)). We fit it to data collected during a growth experiment using steelhead trout (*Oncorhynchus mykiss*) wherein each individual is uniquely tagged and repeatedly measured (details in Shelton *et al.*, 2013), and restricted analysis to the low-feeding periods of the fourth treatment of the Coleman National Fish Hatchery broodstock. Comparison of mixed-effect and conventional estimation of the model (Figure 4) shows that the conventional model cannot explain the variation in growth trajectories among individuals, where most individuals remain either above or below the predicted interval for the entire duration of the experiment. The mixed-effect model, by contrast, estimates a predictive interval for an unobserved individual that
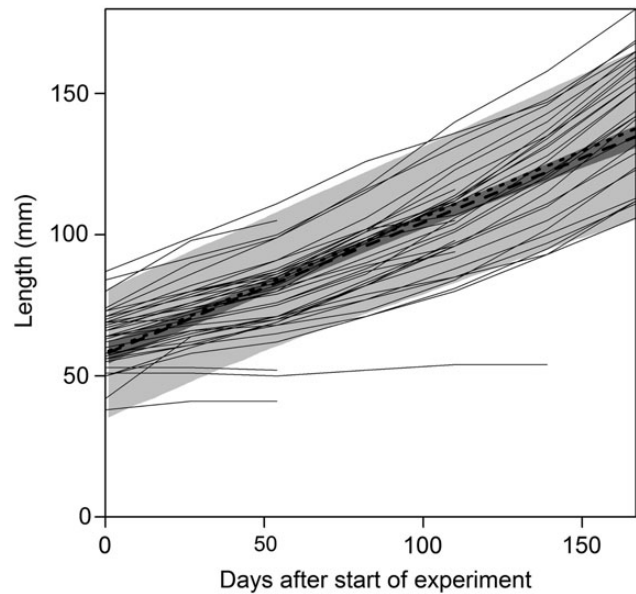
Figure 4. Growth trajectories (black lines) for 40 marked individuals (*x*-axis: time in days after the beginning of an experiment; see Shelton *et al.*, 2013 for details), showing the predicted growth trajectory for an unobserved individual using as estimated using a fixed-effect (dashed line and dark grey shading) or mixed-effect (dotted line and light grey shading) model, where the solid line in each case is the mean of the predictive distribution, and the shaded area is the 95% predictive interval from the mixed-effects model.

includes most individual growth trajectories (although three individuals still grow less than expected under the model).

Example 4: Multi-level models for partitioning phenotypic trait variation

Analysis of variance in phenotypic traits contributed significantly to the development of random-effects modelling (Henderson *et al.*, 1959; Searle *et al.*, 1992). Understanding phenotypic trait variation explicitly or implicitly underlies many studies on fish populations (e.g. Swain and Foote, 1999) and changes in traits such as growth and maturation in response to selective fishing (Law, 1991) is an important contemporary topic in fisheries science (Jorgensen *et al.*, 2007). Experiments conducted on fish in a shared environment have an important role in determining genetic components of such changes (Conover and Munch, 2002; van Wijk *et al.*, 2013). Total variance in the phenotypic trait is decomposed into variance from multiple different sources, and each estimated variance component has a specific interpretation. This approach is similar to the recently proposed paradigm of Bayesian analysis of variance (Gelman, 2005) where, instead of treating variance as a nuisance in a given analysis, the magnitude of variance is interpreted as evidence of the magnitude of different hypothesized processes.

In quantitative genetics, phenotypic variation of a trait can be decomposed into variation arising from genetic and environmental effects (Falconer *et al.*, 1996). Genetic effects comprise additive, dominant, and epistatic effects. Often additive genetic variance is the main focus (Falconer *et al.*, 1996) and the ratio of additive genetic to total phenotypic variation is termed "narrow-sense" heritability. Quantifying the heritability of a given phenotypic trait is central to understanding the potential for anthropogenic or natural selection to alter genotypes (Law, 1991). Multi-level

models, which partition variance among multiple factors, are key to this understanding.

In this case study, we illustrate the use of a particular type of multi-level model, termed an *animal model* (reviewed in Wilson *et al.*, 2010), by investigating data on phenotypic trait variation of alevin weight in Atlantic salmon (*Salmo salar*). Phenotypic observations are non-independent among related individuals because they may have alleles in common. For a single trait, an animal model assumes that the random effects covariance matrix $\mathbf{G} = \mathbf{A}s_a^2$, where $\mathbf{A}$ is an additive genetic relationship matrix with a correlation value of 0.5 for parentoffspring or full-siblings, 0.25 for half siblings and 0.125 for first cousins (Wilson *et al.*, 2010). We fit an example animal model similar to Debes *et al.* (2013a) for alevin weight using data stored at Debes *et al.* (2013b). The first 100 entries of the alevin relatedness matrix (Figure 5a) illustrate the genetic dependence in the dataset, which ultimately allows for components of genetic and environmental variation to be estimated.

The final model used here is:

$$y_i = a_{j[i]} + bd_i + u_{a[i]} + u_{m[i]} + u_{t[i]} + u_{f[i]} + e_i, \qquad (11)$$
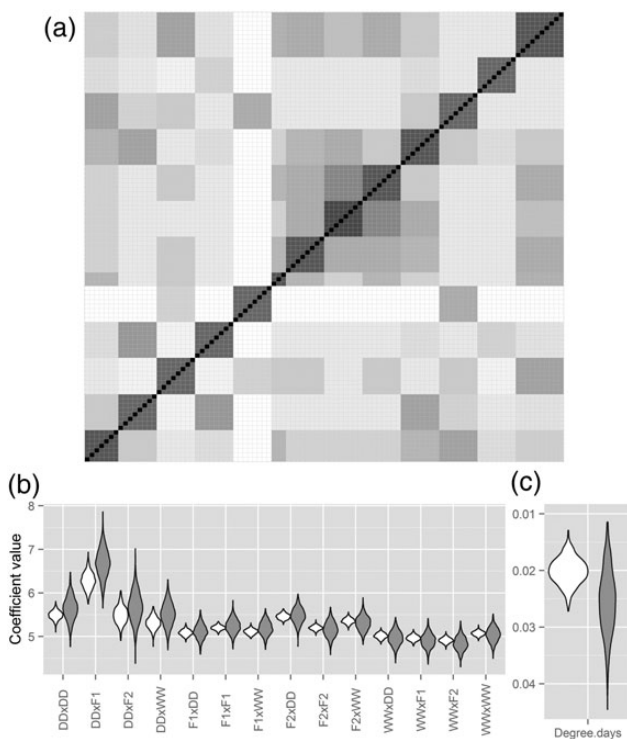
Figure 5. (a) Genetic relatedness matrix for the first 100 alevins in Debes *et al.* (2013b). Relatedness goes from zero (white), implying independence, to one (black) implying complete dependence (same individuals along the diagonal from bottom left to top right). (b) Cross and (c) degree day posterior distributions from the mixed-effects model including an additive genetic component (grey) and a fixed effects only model (white). Labels in (b) refer to: DDxDD (domesticated); DDxF1, F1xDD (first-generation domesticated backcross); DDxF2, F2xDD (second-generation domesticated backcross); WWxDD, DDxWW (first-generation hybrid); F1xF1 (second-generation hybrid); WWxF1, F1xWW (first-generation wild backcross); WWxF2, F2xWW (second-generation wild backcross); F2xF2 (third-generation hybrid); WWxWW (wild); Degree.days in (c) is centered accumulative growing degree days (°C).

where y_i is the body dry weight of individual alevin i; a_j is fixed effects of cross (F1, F2, back-cross, etc.); b is a fixed effect of the continuous variable representing opportunity for growth, that is, growing-degree day d; u designates random effects including additive genetic effects $\Pr(u_a) = N(0, \mathbf{A}s_a^2)$, maternal effects $\Pr(u_m) = N(0, s_m^2)$, tank effects $\Pr(u_t) = N(0, s_t^2)$, and family effects $\Pr(u_f) = N(0, s_f^2)$. Finally, $\Pr(e_j) = N(0, s_e^2)$ is the residual errors. Random effects are assumed to be independent across factors and residuals. We implement this as a Bayesian model using the MCMCglmm package in R (Hadfield, 2010) (code provided in Supplementary data, Appendix D; https://github.com/James-Thorson/mixed-effects/tree/master/quantitative_genetics (last accessed 17 November 2014)) by specifying diffuse normal priors on fixed effects and inverse Wishart ($V = 0.1$, $n = 1$) priors on variance components. The MCMC chains were run for 1 million iterations with the first half discarded and the second half thinned at a thinning interval of 500. The wide thinning interval was necessary to reduce very high autocorrelation in the chains for the posterior additive and residual variance components. For comparison, we fit a linear model excluding all random effects and compare estimated fixed-effect coefficients for cross and growing-degree day.

Posterior estimates of the variance components from the mixed-effects model (% in parentheses) were: additive genetic effects: $\hat{s}_a^2 = 0.0878$ (18.1), maternal effects: $\hat{s}_m^2 = 0.144$ (29.7), tank effects: $\hat{s}_t^2 = 0.0267$ (5.5), family effects: $\hat{s}_f^2 = 0.038$ (7.9), and residual effects: $\hat{s}_e^2 = 0.187$ (38.8). The posterior mean heritability (the ratio of additive variance and total variance) was $h^2 = 0.18$ with wide 95% credible intervals ($0.024-0.387$), caused by an uncertain additive component at the sampling level implemented. The fixed-effects model ignores the genetic and environmental correlations among observations, resulting in narrower posterior distributions for cross-bred individuals and the effect of degree days on growth compared with the model accounting for genetic and environmental correlations using random effects (Figure 5b and c). We conclude by noting the multiple traits (e.g. size and maturity at age) may be analysed in such a manner and that the covariance of the additive genetic traits may contribute to understanding how fisheries selection may influence both growth and maturation simultaneously, both of which are central to understanding fisheries-induced evolution.

Future prospects

We have used four worked examples to show that random-effects modelling provides a unifying framework for many sub-fields in fisheries biology that might otherwise seem unrelated. We support the emerging view (Royle and Dorazio, 2008; Kéry and Schaub, 2012) that the explicit separation of ecological and observation processes within a "hierarchical model" represents a unifying strategy for statistical modelling in fisheries biology across all sub-fields. In this paradigm, random and uncontrolled differences among experimental units (e.g. individual differences in genetics or growth rates) or transitions among ecological states (e.g. changes in abundance over time) are treated as random effects, while parameters governing ecological dynamics may be either random or fixed. Fisheries science adopted the distinction between process and observation models early on, e.g. in using structural equation modelling to elucidate density-dependent phases in the life history (Myers and Cadigan, 1993) or using state-space models to estimate population dynamics over time (Pella, 1993). Yet fisheries science has lagged in the realization of how pervasive these methods are across what

might otherwise be seen as disparate areas of application (molecular, individual, population, communities in time and space). Clarifying these connections across diverse sub-fields has been a focus of this review. Additional details regarding Bayesian implementations (Clark and Gelfand, 2006) or comparing software options and listing best practices (Bolker *et al.*, 2013) can be found elsewhere. However, we now turn to the future and make a few predictions about the next decade of statistical modelling in fisheries science.

We predict that the application of random effects methods will continue to grow in population dynamics and stock assessment modelling, given that stock assessment scientists must often understand population dynamics that vary spatially, over time, among individuals, and between species. As we have shown, mixed-effects models provide an important tool for estimating the relative contribution of different hierarchical sources of variation, and these models are already widely used when synthesizing information across multiple study systems, species, and scales (Hilborn and Liermann, 1998; Thorson *et al.*, in press-a). In particular, mixed-effects models can be used to characterize the plausible scenarios or "states of nature" (Carpenter, 2002) that are used in simulation modelling to evaluate the performance of proposed assessment methods and management procedures (Punt, 2008). However, future research will need to explore whether mixed-effects estimation is likely to improve management outcomes when applied in assessment models that are used for tactical fisheries management (i.e. setting annual harvest quotas).

One recurring theme in fisheries science is quantifying the productivity of juveniles and adults in space and time, arising from basic demographic processes including growth and reproduction (Schaefer, 1954; Beverton and Holt, 1959). An apparent dichotomy appears between treating productivity either (i) as a latent characteristic of a population that is approximately constant over time or (ii) or as a result of the physical and biological environment that may cause changes over time. In marine systems, many correlations between-population productivity and environmental conditions prove ephemeral over time (Myers, 1998), and this favours models that treat productivity as approximately constant over time (although perhaps including autocorrelated residuals; Thorson *et al.*, 2014a). On the other hand, the assumption of time-invariant demographic rates risks focusing on average conditions that may mask fluctuations and directional changes in productivity over time (Peterman *et al.*, 2000; Minto *et al.*, 2014). Time-varying estimates of population productivity circumvent these issues but may be criticized for a lack of explicit mechanism. Here, we envisage fruitful work combining mixed-effect models with causal inference methods (Sugihara *et al.*, 2012). Indeed, the relationship between environmental drivers and ecological processes may be allowed to vary with time (Petris *et al.*, 2009). Alternatively, variation in productivity may be well-explained by additional information and modelling for fish fecundity and density dependence (Morgan *et al.*, 2011; Shelton *et al.*, 2012). We predict that this will provide a useful avenue for research regarding population productivity over the coming decade.

Applications of non-normal random effects can also improve estimation in populations that lack tagging programmes but where individuals can be repeatedly counted (Royle, 2004; Dail and Madsen, 2011). We envisage that these "occupancy and abundance" methods (MacKenzie *et al.*, 2005) could contribute greatly to areas such as the estimation of swept-area abundance in fisheries. In particular, these models allow researchers to model spatial dependencies while estimating detection probabilities (Thorson *et al.*, 2013). Count data are ubiquitous in sampling designs that estimate species densities, age and length composition, and trophic interactions (e.g. diet samples). Therefore, continued improvement in random effect models for count data will likely be important in the coming decade, and situations where a latent state follows a discrete distribution (e.g. local densities at a small site) will require continued development of methods for non-normal random effects.

Finally, genetic effects (e.g. heritable changes over time and trade-offs in adaption to environmental conditions) are as important (and as complicated) as ecological dynamics and interactions. We therefore view it as telling that a great deal of inference in genetics has been achieved from decomposition of observed phenotypic variation into multiple hypotheses represented by estimated variance contributions (Falconer *et al.*, 1996). Indeed, time-series signal-to-noise ratios, intraclass correlation coefficients and heredity are all variance ratios depicting useful properties of complex underlying systems. Developing analogous methods to partition variance in ecosystems may enable the bewildering complexity of ecosystems to be reduced to manageable variance components, which could at least be used to limit the plausible hypotheses for a given phenomenon. We therefore conclude by reiterating Gelman's (2005) call for Bayesian analysis-of-variance modelling: when an ecological system is complicated and influenced by many different processes, then the analyst can start their investigation by including all factors and their interactions, and partition the observed variance among these various factors and interactions. In this way, available data can be used to update expectations regarding the relative importance of multiple possible processes. This updated expectation can then be used to formulate or refine more mechanistic models involving explicit species interactions and abiotic effects.

In conclusion, these and other research goals require inference about latent characteristics of the natural environment, whether local densities, genetic traits, or spatial and temporal variability. Latent states will violate the assumption that model residuals are statistically independent, as made by simple regression and non-linear models, and controlling for this effect requires integrating (i.e. taking a weighted average) across the value of latent states when estimating model parameters. Mixed-effect modelling provides a unified framework for doing this, and hence eases inference in a variety of statistical models in fisheries biology. We therefore believe that every fisheries biologist requires some basic understanding of these models to participate in current research and modelling.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

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