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ARTICLE

Estimating Spatial and Temporal Components of Variation for Fisheries Count Data Using Negative Binomial Mixed Models

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Abstract

Partitioning total variability into its component temporal and spatial sources is a powerful way to better understand time series and elucidate trends. The data available for such analyses of fish and other populations are usually nonnegative integer counts of the number of organisms, often dominated by many low values with few observations of relatively high abundance. These characteristics are not well approximated by the Gaussian distribution. We present a detailed description of a negative binomial mixed-model framework that can be used to model count data and quantify temporal and spatial variability. We applied these models to data from four fishery-independent surveys of Walleyes *Sander vitreus* across the Great Lakes basin. Specifically, we fitted models to gill-net catches from Wisconsin waters of Lake Superior; Oneida Lake, New York; Saginaw Bay in Lake Huron, Michigan; and Ohio waters of Lake Erie. These long-term monitoring surveys varied in overall sampling intensity, the total catch of Walleyes, and the proportion of zero catches. Parameter estimation included the negative binomial scaling parameter, and we

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quantified the random effects as the variations among gill-net sampling sites, the variations among sampled years, and site \times year interactions. This framework (i.e., the application of a mixed model appropriate for count data in a variance-partitioning context) represents a flexible approach that has implications for monitoring programs (e.g., trend detection) and for examining the potential of individual variance components to serve as response metrics to large-scale anthropogenic perturbations or ecological changes.

Partitioning the total variance of a response variable into its component sources (i.e., variance components; Urquhart et al. 1998; Fletcher and Underwood 2002; Qian and Shen 2007) can inform a variety of research and management questions, particularly those which rely on the detection of regional trends for important indicator variables (Larsen et al. 2001; Lindenmayer and Likens 2009). Accordingly, estimation of variance components has been performed for a variety of aquatic indices, including water chemistry variables, species richness, stream habitat characteristics, fish growth, and catch-per-unit-effort data (Kincaid et al. 2004; Larsen et al. 2004; Wagner et al. 2007, 2009; Anlauf et al. 2011). To date, most variance-components frameworks have been based on linear models that have some fixed effects and assume normally distributed random effects and error structures. These are called mixed-effect models because they include both fixed and random effects, with the variance partitioned among the random effects and observational error. When such normal distribution-based models are applied, the response variable is commonly \log_e transformed to better meet the normality, linearity, and homogeneity-of-variance assumptions. However, assuming a lognormal distribution (or even a normal distribution) for count observations is often not ideal because count observations of organisms are typically recorded as nonnegative integers, which then frequently have a high variance and a low mean (e.g., there are a lot of observations of few fish, few observations of a lot of fish). Further, log transformation of data raises difficult questions such as how to treat zero observations (Power and Moser 1999; Ver Hoef and Boveng 2007; O'Hara and Kotze 2010). Use of the negative binomial distribution represents an alternative to data transformation, allowing the distributions to be modeled as discrete and avoiding the need for zero observations to be manipulated prior to the analysis (Anscombe 1949; White and Bennetts 1996). Although negative binomial models are commonly used to model counts, they have rarely been developed as mixed-effect models (but see Jones et al. 2009 for an application to stuttering rates) or for variance partitioning, which in this context is less straightforward than for general linear mixed models that assume normality.

Throughout the world, fishery-independent surveys provide essential information for understanding, restoring, and managing fish populations (Stobutzki et al. 2006; Allen et al. 2007; Irwin et al. 2008). Data from these surveys are used to assess stock status and population trends (e.g., for monitoring restoration efforts or setting annual harvest levels) and to evaluate the effects of natural and anthropogenic stressors on the spatiotemporal dynamics of populations (Corradin et al. 2008; Jackson et al. 2008;

Irwin et al. 2009). Fishery-independent surveys target a variety of freshwater fish species and their life stages (e.g., Sitar et al. 1999; Tyson and Knight 2001; Rudstam et al. 2011), and thus surveys can be quite variable across studies. Even so, the information produced by these surveys is often in the form of counts occurring over space and time (i.e., indices of relative or absolute abundance). Thus, a variance-component framework for discrete data is needed given the widespread use of such surveys resulting in count data with the characteristics described above. To our knowledge, a framework for variance partitioning using negative binomial mixed models has not been presented previously. The objective of this paper is to present such a framework for estimating the spatial and temporal components of variation for count data using multiple fishery-independent surveys of Walleye *Sander vitreus* from across the Great Lakes basin. We believe that incorporating variance partitioning into the fitting of negative binomial mixed models could have wide application, including in assessing the trend detection capabilities of alternative survey designs and evaluating whether a variance structure is responsive to large-scale ecological changes.

METHODS

Data sources.—We used data from four fishery-independent gill-net surveys targeting Walleyes, with the premise that improved understanding of spatial and temporal variability will allow for a thorough evaluation of current survey designs. Our rationale for focusing on Walleyes was threefold: (1) they are ecologically and economically important (Nepszy 1977; Kinnunen 2003); (2) it is a management priority to maintain or restore this species (Fielder et al. 2007; Wilson et al. 2007); and (3) to allow direct comparison across gill-net surveys for the insights this might provide. We include long-term (16–47-year) data series from Wisconsin waters of Lake Superior; Oneida Lake, New York; Saginaw Bay of Lake Huron, Michigan; and Ohio waters of Lake Erie. All data were collected using multimesh gill nets, with some differences in the use of multi- or monofilament materials. For each survey, we performed the analysis using the catch in a single net set as an observation (i.e., summed across mesh panels). In both the Saginaw Bay and Lake Erie surveys, individual site locations were sometimes sampled multiple times within a year. For each recorded catch (i.e., the number of animals collected in a single net set), we also used the following information: the year sampling occurred, set duration (if variable across net sets; Lake Erie only), and the site (location). For more information on the

TABLE 1. Minimum sampling requirements for estimating different variance components.

Sampling requirement	Site-to-site variability (σ_a^2)	Site-to-site trend variability ($\bar{\sigma}_t^2$)	Coherent temporal variability (σ_b^2)	Ephemeral temporal variability (σ_c^2)
Multiple sites	X	X	X	X
Multiple years	X ^a	X	X	X
Some of the same sites revisited multiple years, with no within-year revisits	X ^b			
Some of the sites revisited within years				X

^aOnly necessary if sites are never revisited within a year.

^bOnly necessary if sites are never sampled over multiple years.

use of gill nets to sample Walleye populations, see Hamley and Regier (1973), Anderson (1998), or Irwin et al. (2008).

Variance components common to fishery-independent surveys.—Partitioning the total variance of an ecological state variable into its component sources using linear mixed models premised on underlying normal probability distributions has been described elsewhere (see VanLeeuwen et al. 1996; Sims et al. 2006). For consistency, we will use the terminology set forth by Urquhart et al. (1998) and Wagner et al. (2007), although the analyses presented here apply to negative binomial mixed models. Our presentation is written in the context of sampling that is done by annual surveys. We assume that within-year sampling occurs in a short sampling season within which substantial systematic or random changes in the fish population being sampled do not occur. The basic structure we put forward could be adapted to include fixed seasonal and within-year random effects. The primary components of variation present in fishery-independent survey data include (Table 1; Figure 1):

1. site-to-site (spatial) variation;
2. coherent temporal (year-to-year) variation;
3. ephemeral temporal variation (i.e., site \times year interaction);
4. trend variation; and
5. observational variation.

Site-to-site variation represents consistent differences among sites in the magnitude of an attribute of interest. Estimating site-to-site variation requires that multiple sites be sampled multiple times, either by within-year site revisits or by returning to the same site across multiple years. For catch data, site-to-site variation implies that individual sites differ in their overall average abundance, or catch per unit effort). Coherent temporal variation is annual variation that affects all sites (e.g., sampling sites within a system) in a similar manner within a year. That is, strong coherent temporal variation would reflect the fact that, in a given year, all sites tend to have either higher or lower catches than the overall average (i.e., synchronous year-to-year variation is expressed by all of the sites together). Ephemeral temporal variation can be interpreted as independent year-to-year variation among sites. For instance, one site may produce

higher than average catch while another may produce lower than average catch in a given year (given the overall effect of the year stemming from coherent variation and the overall effect of the site stemming from site-to-site variation). Ephemeral variation would have the same influence on all samples from a site taken during a given year. Estimating ephemeral temporal variation requires that multiple sites be sampled each year over multiple years *and* that there be some within-year revisits of sites (Table 1; Figure 1).

A more complex situation occurs when trends are overlaid on the sources of temporal variation identified above. “Trend variation” may encompass both a systematic overall trend over time and a site-specific trend that allows each site’s trend in catch to vary from this overall mean trend over time. When an overall trend is present, the coherent variation is then the temporal variation common to all sites, above and beyond what could be explained by the underlying overall trend. With both overall and site-specific trends present, ephemeral variation is the temporal variation at a site that is not part of the trends (overall or site specific) or coherent variation but which would apply to all samples from a site and sampling year. It can be viewed as real but local variation in abundance (assuming constant catchability). In many sampling designs, ephemeral variation remains lumped in with observational variation (see below). Estimating site-specific trend variability requires sampling multiple sites over multiple years but not within-year revisits (Table 1; Figure 1). Separating ephemeral variation from observational variation requires multiple visits within a sampling season for at least some site \times year combinations. Lastly, observational variation is the remaining unexplained variation in catch that is not captured by the other estimated effects. If ephemeral variation is estimated separately, then observational variation is the random variation that occurs at the same site when it is sampled repeatedly within a single year (i.e., within a short sampling season; VanLeeuwen et al. 1996; Larsen et al. 2001; Kincaid et al. 2004).

Model specification: negative binomial mixed-effects models.—Many commonly used statistical analyses (e.g., simple linear regression) assume an underlying normal probability distribution, which implies symmetry and continuous data. Here, we apply regression models that use the negative binomial

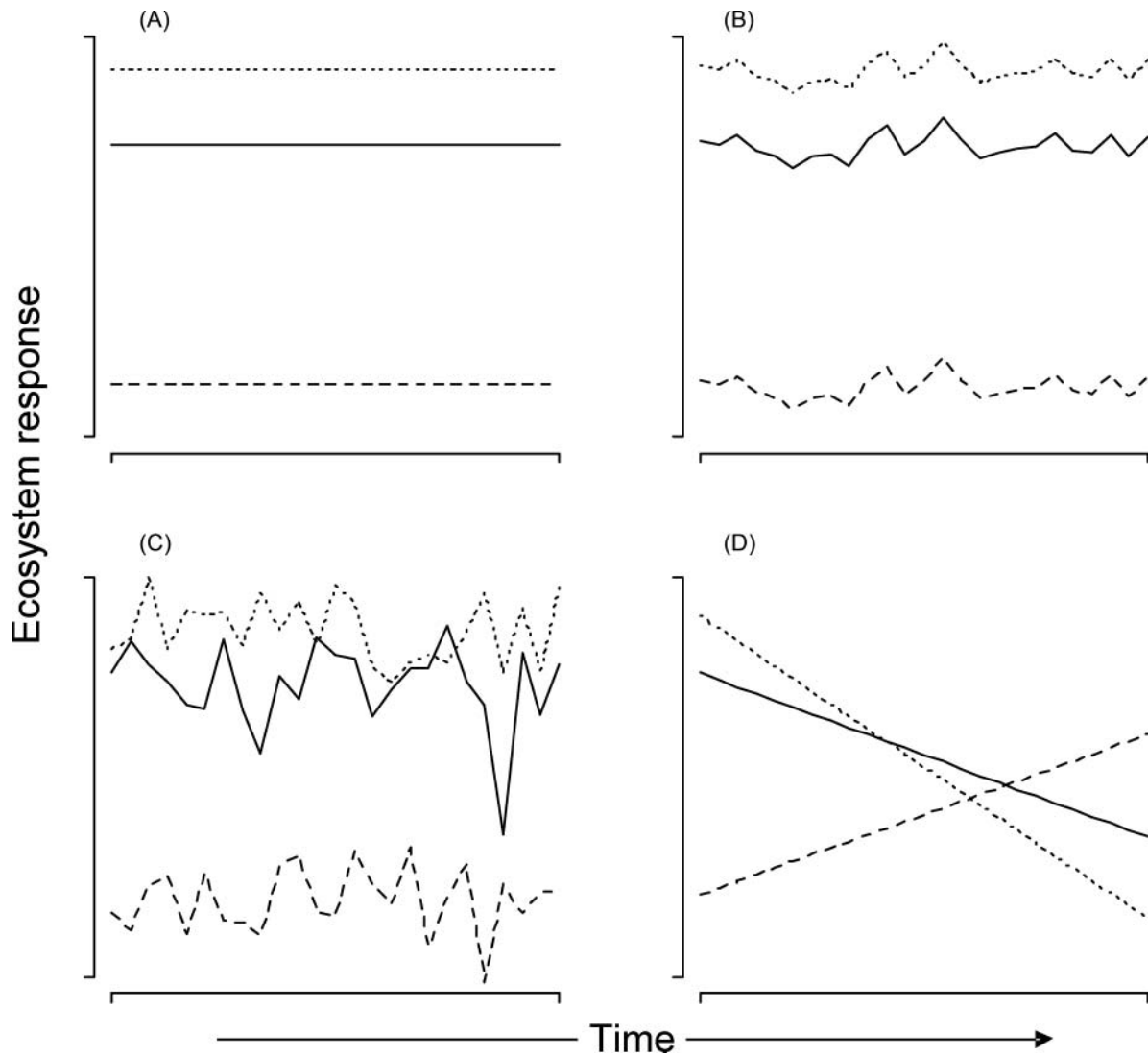


FIGURE 1. Depiction of different variance components in the context of a count time series. Panel (A) illustrates spatial variation as the only source of variability, so that each of the three sample sites (represented by the dashed and solid lines) has a different mean but no temporal variability. Panel (B) illustrates the addition of coherent temporal variation to the spatial variation and panel (C) the further addition of ephemeral temporal variation, so that in (C) each site varies independently of the other sites in each year. Panel (D) illustrates the addition of slope variation to spatial variation, so that each site has its own trend over time. One could also add coherent and ephemeral variation in panel (D) (not shown).

distribution rather than the more commonly assumed normal or lognormal distributions. Thus, we assume that

$$Y_{ijk} \sim NB(\mu_{ijk}, \kappa), \quad (1)$$

where Y_{ijk} is the total catch from the k th sample at site i in year j , μ_{ijk} is the expected value for that sample, site, and year, and κ is the so-called scaling parameter of the negative binomial distribution. We employ a log-link function such that, generally, the \log_e (hereafter, “ln”) transformed value of the expected catch (η_{ijk}) would be a linear function of the predictors, i.e.,

$$\eta_{ijk} = v + a_i + (\lambda + t_i) \text{year}_j + b_j + c_{ij} + \ln(E_{ijk}), \quad (2)$$

where v is the fixed intercept, λ is the fixed slope (i.e., the underlying overall temporal trend) using year as the covariate (i.e., the predictor variable), and $\ln(E_{ijk})$ is an effort offset term. The year covariate was centered on the mean year for each data set’s time series separately to improve the robustness of converging on best-fitting solutions. Thus, year is a centered value of j . In this model, we are assuming that the expected catch per unit effort would be the same for repeated within-year samples at a site but that if one sample represents more effort than another its expected catch would be proportionally higher. The effort offset was only applied to Lake Erie data, as the other sampling programs were designed to have constant effort among net sets. The terms a_i (site-to-site effects), t_i (site-to-site trend effects), b_j

(coherent temporal effects) and c_{ij} (ephemeral temporal effects) are all random effects (i.e., the best linear unbiased predictors) that were assumed to be independent and identically distributed as $N(0, \sigma_x^2)$, where σ_x^2 is the unique variance parameter for each random effect. The c_{ij} values were only estimated for data sets that had repeat sampling of a site within a year (Saginaw Bay and Lake Erie); in all other cases this source of variation is absorbed into the observational error variance.

It should be noted that data transformation is not required in order to apply a log-link function within a negative binomial mixed model. With the above log-link function, the expected value is log transformed (rather than the observed data itself), so zero observations (i.e., net sets that do not catch any of the target fish species) do not require special adjustments prior to performing the regression (O’Hara and Kotze 2010). There is no “residual” error term in equation (2) like those seen in many standard presentations of regression models because this equation and the assumed link function connects expected rather than actual catch to the estimated model parameters. Although the above equation allows for standardizing catches based on effort, it assumes that gear catchability remains constant over the observed time series.

It follows that expected catch in the negative binomial mixed model is estimated by

$$\hat{\mu}_{ijk} = e^{(\hat{\eta}_{ijk})}, \tag{3}$$

where $\hat{\eta}$ is from equation (2), with all random and fixed effects replaced by their estimates. The variance of a negative binomial distribution can be parameterized as a quadratic function of the mean (see Ver Hoef and Boveng 2007), i.e.,

$$V_{ijk} = \mu_{ijk} + \frac{\mu_{ijk}^2}{\kappa}. \tag{4}$$

The degree to which variance exceeds the mean is determined by the scaling parameter κ . It follows from equation (4) that the variance–mean ratio is

$$\tau_{ijk} = 1 + \frac{\mu_{ijk}}{\kappa}, \tag{5}$$

such that τ must be ≥ 1 . Our estimation model includes both fixed and random effects so that it is akin to generalized linear mixed models (GLMM; e.g., Venables and Dichmont 2004; Bolker et al. 2009). However, the procedures used here included estimation of κ . Thus, in this case, the negative binomial is not a member of the exponential family and the associated analyses are not GLMMs, strictly speaking (Power and Moser 1999). Because the model is not truly a GLMM, in order to obtain maximum likelihood estimates we required software capable of integrating multiple random effects out of the likelihood function and performing an efficient numerical search for the best-fit parameters, which included the scaling parameter.

Model specification: parameter estimation.—We developed the models presented here using the flexible software environment AD Model Builder (ADMB) with the random effects module (ADMB-RE) to perform maximum likelihood estimation to obtain the model parameters that minimized the negative log-likelihood function (i.e., maximized the likelihood) across all n observations (<http://admb-project.org>; Fournier et al. 2012). This software uses the Laplace approximation to integrate out the random effects. For mixed-effect models, the likelihood function that needs to be maximized is the marginal likelihood, which is obtained by integrating out random effects, i.e.,

$$L(\theta) = \int_{\delta} f_{\theta}(y | \delta) h_{\theta}(\delta) d\delta. \tag{6}$$

Here, $f_{\theta}(y | \delta)$ is the likelihood of the data y given the vector of random effects δ ; it is subscripted by θ to indicate that the likelihood of the data depends on θ (i.e., the parameters). The probability density function for the vector of random effects is $h_{\theta}(\delta)$. This too depends on the parameter vector because quantities such as the variances for the random effects are part of that vector. It is convenient to rewrite equation (6) as

$$L(\theta) = \int_{\delta} \exp[g(\delta, \theta)] d\delta, \tag{7}$$

where

$$g(\delta, \theta) = \ln[f_{\theta}(y | \delta)] + \ln[h_{\theta}(\delta)] \tag{8}$$

because software such as ADMB-RE only requires specification of the parameters, the random effects, and $-g(\cdot)$. The software then automatically integrates out the random effects using the Laplace approximation at each stage as it uses a quasi-Newton search for the parameters that maximize the likelihood (Fournier et al. 2012). We will refer to $\ln[f_{\theta}(y | \delta)] = \ln l$ as the log-likelihood for the data conditioned on the random effects and to $\ln[h_{\theta}(\delta)] = \ln d$ as the log-density for the random effects. The negative log-likelihood function for the negative binomial distribution is

$$-\ln l = \sum_1^n \left[-\ln(\Gamma(Y_{ijk} + \kappa)) + \ln(\Gamma(\kappa)) + \ln(\Gamma(Y_{ijk} + 1)) - \kappa \ln\left(\frac{\kappa}{\mu_{ijk} + \kappa}\right) - Y_{ijk} \ln\left(\frac{\mu_{ijk}}{\mu_{ijk} + \kappa}\right) \right] \tag{9}$$

(also see Bolker 2008; Hilbe 2008). In ADMB-RE, we used the “-log_negbinomial.density” function on arguments Y_{ijk} , μ_{ijk} , and τ_{ijk} .

Model specification: partitioning variance.—As previously mentioned, the random effects were assumed to follow normal distributions. For example, the random effect allowing for site-to-site variability assumed $a_i \sim N(0, \sigma_a^2)$. For each random

effect, an additional normal density component was added to the negative log-density function. For instance, the component related to a_i was

$$-\ln d_a = \frac{m}{2} \ln(\sigma_a^2) + \frac{1}{2\sigma_a^2} \sum_{i=1}^m (a_i^2), \quad (10)$$

where σ_a^2 is an estimated parameter and m , in this case, is the number of unique sites sampled. Thus, $-\ln d$ will consist of up to four such terms in our analyses, and up to four additional variance parameters (σ_a^2 , σ_t^2 , σ_b^2 , σ_c^2) associated with the random effects will be estimated.

We wished to compare variance components within and across systems, which required the calculation of the total variability across all sources of variation. For models including only normally distributed random intercept terms (i.e., without random slope effects), the total variance can be calculated by simply summing across the estimated variance parameters (Urquhart et al. 1998). However, this calculation is less straightforward when applying random slope effects or the negative binomial distribution. Random effects that apply to the slope term are more challenging to interpret in a variance partitioning context. For example, we included site-to-site trend perturbations (t_i) by estimating σ_t^2 . Although $t_i \sim N(0, \sigma_t^2)$, the influence of t_i on $\hat{\mu}_{ijk}$ is also affected by the value of the year covariate (specifically, the variance is a function of the covariate squared [$\sigma_t^2 X^2$], where X^2 is the centered year covariate squared). Therefore, we weighted the slope random effect parameter σ_t^2 by the centered year covariate and calculated an average value (across all j years) to compare with intercept random effect parameters, that is,

$$\bar{\sigma}_t^2 = \frac{\sum_j (\text{year}_j^2 \sigma_t^2)}{x}, \quad (11)$$

where x is the number of years included in the system's time series. Thus, the average weighted quantity $\bar{\sigma}_t^2$ rather than the direct parameter estimate for σ_t^2 was included in the calculation of total variance across the specified components.

Given the differences across systems, we elected to compare variance components on relative scales (i.e., as proportions) rather than as absolute values. Had we assumed that the count data followed a lognormal distribution, the remaining variance would have simply been the constant variance associated with the additive residual error term for the log-transformed data. That variance term approximately equals the squared coefficient of variation associated with the observational error. For the negative binomial distribution (from equation 4), it can be seen that this observational error CV is a function of the mean. Thus, to produce a value comparable to the scale of the other variance component terms and to what is estimated when lognormal error is assumed in simple linear regression, we calculated a quantity to represent the average of the squared CV for the observational

error variance in the negative binomial context, namely,

$$\hat{\sigma}_o^2 = \frac{\sum (\frac{\sqrt{\hat{V}_{ijk}}}{\hat{\mu}_{ijk}})^2}{n}. \quad (12)$$

In equation (12), there are terms in the sum for each observation and n is the total number of observations. For each data set, we then interpret this derived quantity as the remaining observational variation not accounted for by the other estimated spatial and temporal variance components described above.

As a visual diagnostic measure, we calculated Anscombe residuals for the negative binomial model (see Anscombe 1953 and Hilbe 2008) as

$$R_{ijk}^A = \frac{[3/\alpha((1+\alpha Y_{ijk})^{2/3} - (1 - \alpha \hat{\mu}_{ijk})^{2/3}) + 3(Y_{ijk}^{2/3} - \hat{\mu}_{ijk}^{2/3})]}{2(\alpha \hat{\mu}_{ijk}^2 + \hat{\mu}_{ijk})^{1/6}}, \quad (13)$$

where α is equal to $1/\kappa$. This Anscombe transformation is expected to help achieve approximate normality for the residuals (Pierce and Schafer 1986; Jiao and Chen 2004). These residual values were plotted for each system separately so that we could visually inspect for heterogeneity or possible severe outliers, although we ultimately did not eliminate any observations based on residual values. We also examined normal probability plots for the Anscombe residuals for each data set.

RESULTS

Across the four locations, the fishery-independent surveys varied in overall sampling intensity (i.e., the number of years of data collection and sites sampled per year), the general magnitude of the catches of Walleyes, and the proportion of zero catches (range, <1–33%; Figure 2). At the survey level, the total number of net sets employed ranged approximately between 100 and 700 (Table 2), whereas the total catch over time and space ranged approximately between 3,000 and 45,000. While the catches for all of the surveys shared a lower bound of zero, Lake Erie had by far more observations of large catches (e.g., >75 fish/net) by individual net sets. Even with these differences, negative binomial models produced reasonable approximations to the count data (Figure 3). For all four systems, the fixed intercepts (ν) were estimated to be positive (Table 3). All of the fixed slope (λ) estimates were near zero, but they were positive for Lake Superior and Saginaw Bay and negative for Oneida Lake and Lake Erie. The estimates of the scaling parameter (κ) ranged more broadly across systems. For each system, the plot of Anscombe residuals displayed a fairly consistent spread across the range of predicted values (Figure 4). Likewise, the normal probability plots of the Anscombe residuals suggested that approximate normality was achieved in most cases (Figure 5).

TABLE 2. Summary information for Walleye gill-net data sets.

System	Year range	Total no. of years of data	Total no. of net sets	Total no. of sites visited	Total no. of zero catches	Maximum observed catch
Lake Superior	1970–2008	37	233	12	79	197
Oneida Lake	1958–2006	47	705	15	3	220
Saginaw Bay	1993–2008	16	264	10	12	86
Lake Erie	1978–2008	27	451	119	1	493

Estimates of variance structure varied considerably across systems (Table 3; Figure 6). Lake Superior, which had the highest proportion of zero-catch net sets, had the proportionally largest site-to-site variation (σ_a^2) among all systems considered here. This was also the only case of a variance component other than observational variability ($\hat{\sigma}_o^2$) exceeding 50% of the total variance. Variability was partitioned much more equitably among the variance components for Saginaw Bay than for the other systems. For all systems, the site-to-site intercept variability (σ_a^2) exceeded the site-to-site trend variability ($\bar{\sigma}_t^2$). Coherent

temporal variability (σ_b^2) was less than 1% of the total variation for Lake Superior but ranged from roughly 10% to 20% for the other systems. For these systems, this coherent temporal variability suggests that sites tended to have either higher than average or lower than average catches in a given year.

In addition to coherent temporal variability, we attempted to estimate ephemeral temporal variability (σ_c^2) separately

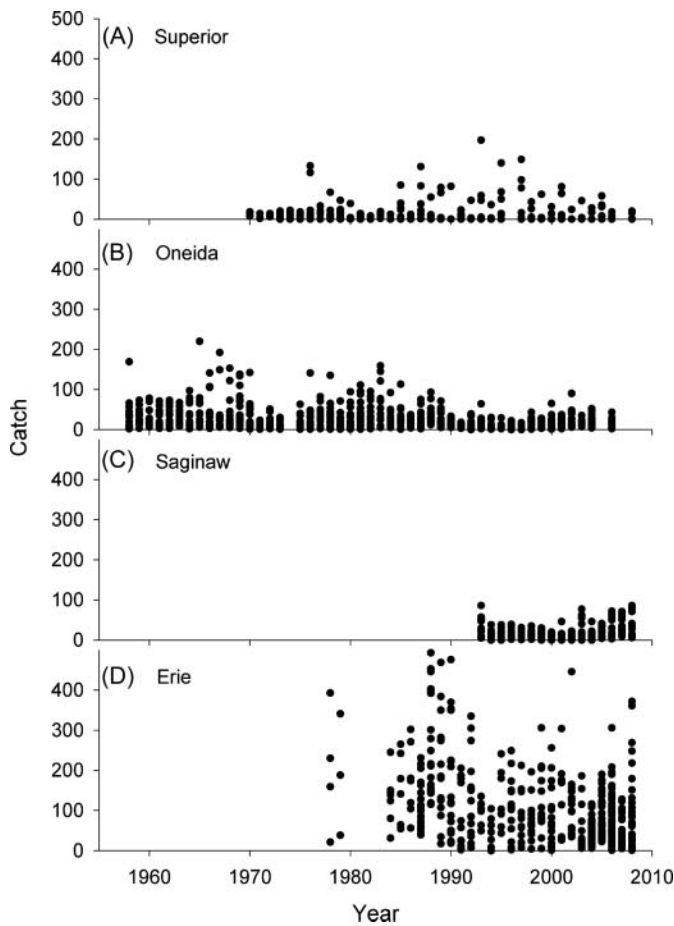


FIGURE 2. Site-specific catch data (not catch per unit effort) over time for four fishery-independent surveys.

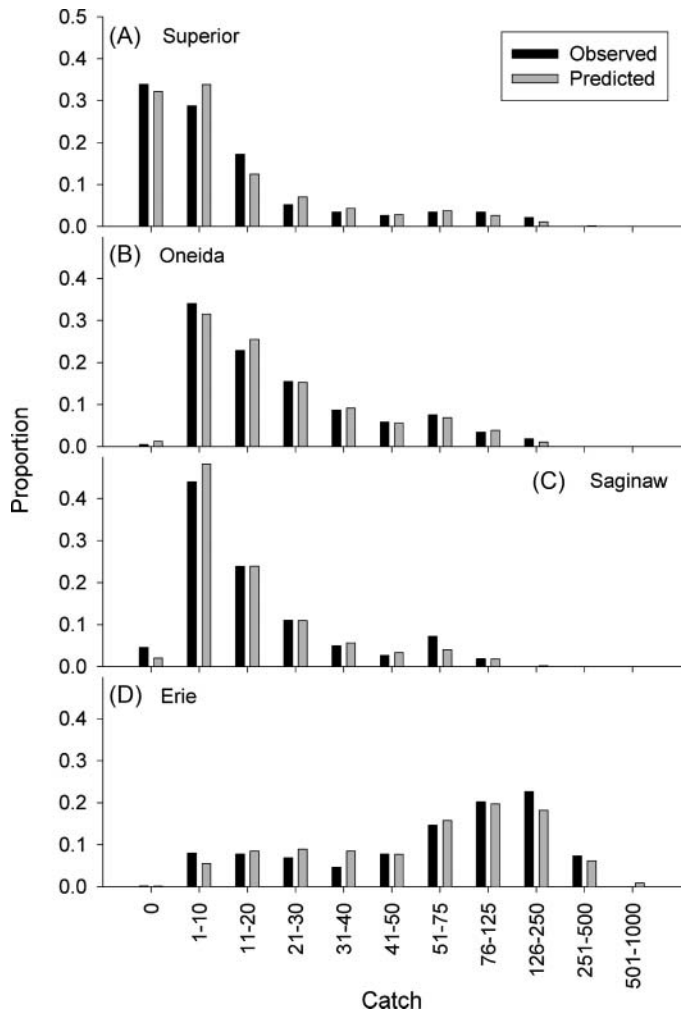


FIGURE 3. Observed versus predicted probabilities of gill-net catches of Walleyes for four systems.

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TABLE 3. Estimated model parameters (SEs in parentheses) and calculated variance components for four lake systems; NE = not estimated. No SE is reported for the derived quantities $\bar{\sigma}_t^2$ and $\hat{\delta}_o^2$. The quantity $\bar{\sigma}_t^2$ is an average weighted value based on the estimated parameter σ_t^2 (see Methods for details). Total variance is defined as the sum of σ_a^2 , σ_b^2 , σ_c^2 , $\bar{\sigma}_t^2$, and $\hat{\delta}_o^2$.

System	Area of survey	κ (scaling parameter)	ν (fixed intercept)	λ (fixed slope)	σ_a^2 (site-to-site variance)	σ_t^2	σ_b^2 (coherent temporal variance)	σ_c^2 (ephemeral temporal variance)	$\bar{\sigma}_t^2$ (site-to-site trend variance)	$\hat{\delta}_o^2$ (observational variance)	Total variance
Lake Superior	Wisconsin waters	0.875 (0.114)	1.125 (0.747)	0.017 (0.010)	6.326 (2.938)	9.51×10^{-10} (8.21×10^{-7})	0.079 (0.080)	NE	1.17×10^{-7}	4.880	11.285
Oneida Lake	Oneida Lake	2.100 (0.127)	3.033 (0.131)	-0.018 (0.005)	0.202 (0.078)	1.25×10^{-4} (6.95×10^{-5})	0.143 (0.039)	NE	0.024	0.535	0.904
Lake Huron	Saginaw Bay	4.925 (0.974)	2.464 (0.206)	0.049 (0.037)	0.233 (0.119)	4.53×10^{-3} (2.98×10^{-3})	0.232 (0.104)	0.266 (0.066)	0.096	0.327	1.154
Lake Erie	Ohio waters	1.789 (0.142)	1.844 (0.107)	-0.045 (0.011)	0.143 (0.080)	6.74×10^{-4} (5.18×10^{-4})	0.078 (0.034)	1.40×10^{-7} (8.07×10^{-5})	0.049	0.573	0.843

from observation variability for Saginaw Bay and Lake Erie. Estimating this source of variability required that sites be revisited within a sampling year. Site revisits were extremely rare in Lake Erie, and thus little information existed to estimate this variance component, which was essentially zero and highly

uncertain (i.e., it had a large estimated standard error relative to the estimated parameter value). The data from Saginaw Bay included more routine site revisits, and ephemeral temporal variability was the second largest variance component for this data set. Our estimates of observational variability included ephemeral variability for Oneida Lake and Lake Superior, where gill-net sites were not revisited within years. Likewise, given the relatively few site revisits within a year for Lake Erie, ephemeral variability may have been incorporated into our estimate of observational variability for that lake. Nominally, observational variability was the proportionally largest variance component for both Oneida Lake and Lake Erie, comprising nearly 60% or more of the total variability; it also exceeded 40% of the variability for Lake Superior (Figure 6). Although the percentage of variability in the observation component was substantially lower for Saginaw Bay than for the other systems, the sum of ephemeral and observational variability for this system is similar to that seen in the three other systems.

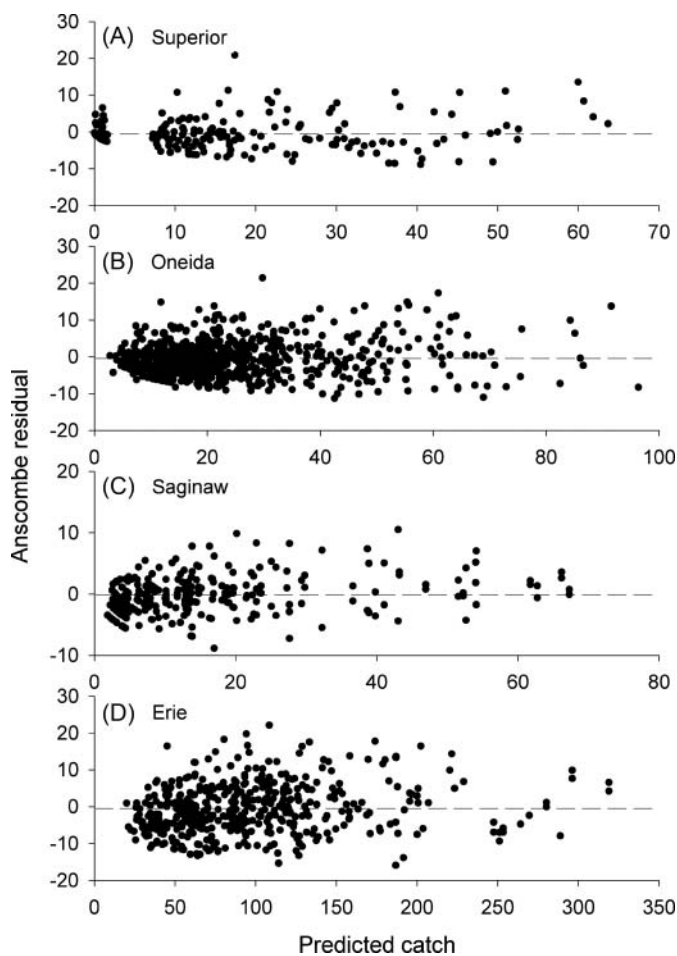


FIGURE 4. Anscombe residuals plots (R_{ijk}^A versus $\hat{\mu}_{ijk}$) based on fitting a negative binomial mixed model to gill-net catches of Walleyes for four systems.

DISCUSSION

Count data are pervasive in ecological studies (Elphick 2008), and estimating variance components can provide insight into spatial and temporal dynamics. However, the statistical model used to estimate the variance components must be appropriate for the discrete and often zero-inflated nature of these data. The negative binomial distribution is worthy of consideration for modeling biological count data, particularly when the variance is expected to exceed the mean (Anscombe 1949; White and Bennetts 1996; Ver Hoef and Boveng 2007). The variance partitioning framework using negative binomial mixed models presented here allows for estimating variance components without the need for data transformation (fish catches are often log transformed in an attempt to better approximate the assumptions of normality and constant variance). We were able to partition the variance for all four fishery-independent data sets, which differed in the proportion of zero observations and often in the number of observations per site, within and across

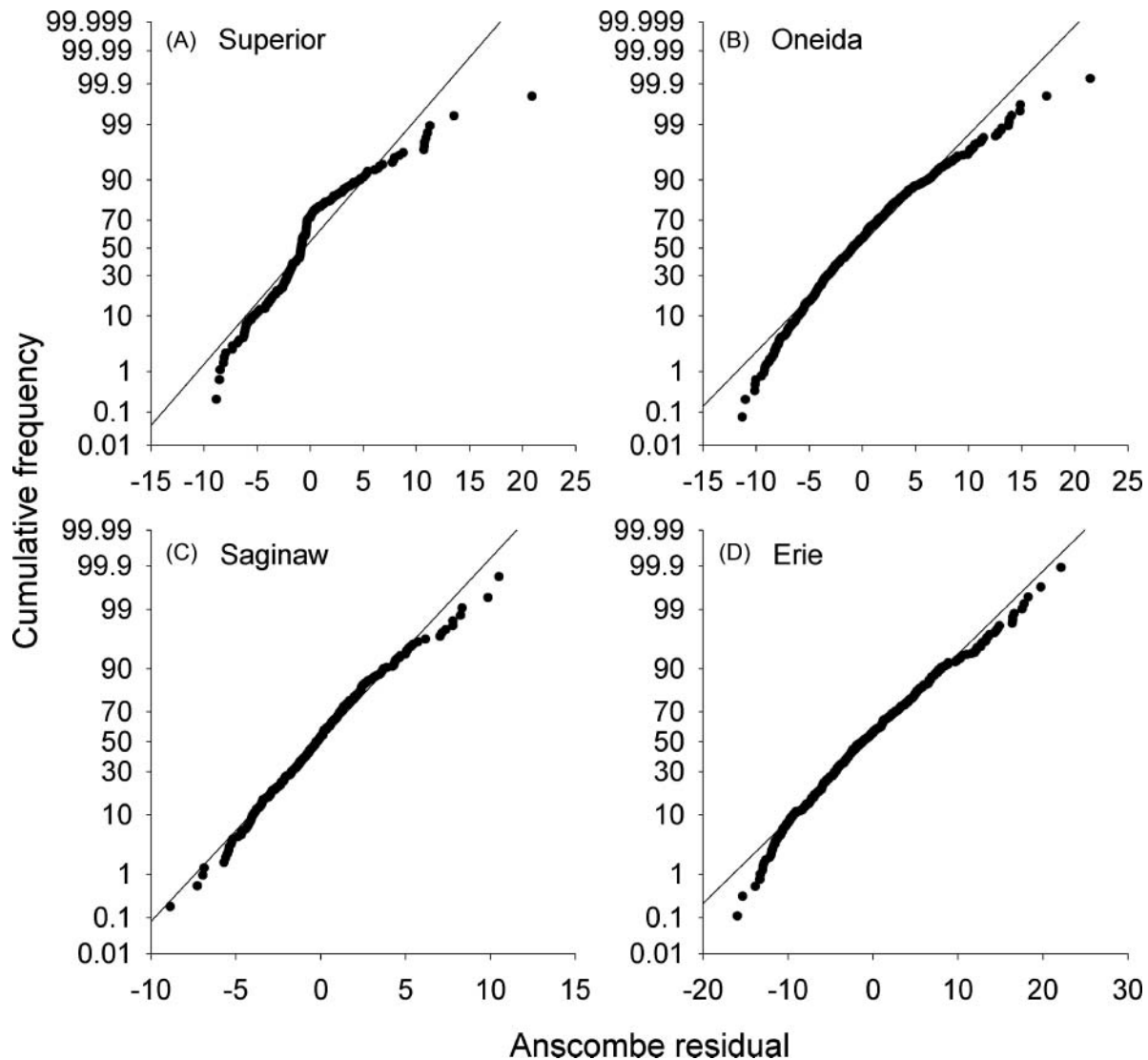


FIGURE 5. Anscombe residuals normality diagnostic based on fitting a negative binomial mixed model to gill-net catches of Walleyes for four systems.

years. For each of these Great Lakes basin surveys, the proportion of the total variance contained within each of the spatial and temporal components also varied. This is not unexpected, as we would predict that variance structure is a function of both the indicator and the system being evaluated. Previous studies have shown that variance structure varies considerably among indicators (e.g., Urquhart et al. 1998; Larsen et al. 2004).

Our variance-partitioning estimates for Walleye catch data illustrate the variability in population structure over space and time among systems, assuming constant catchability within each data series. Much of this variability among systems is likely due to system-specific abiotic and biotic characteristics. In freshwater ecosystems, we would expect that system-specific characteristics (e.g., lake morphometry, food web structure, and fishing pressure) would be important factors governing the spatial and temporal dynamics of fish populations. However, count indices

may not accurately depict underlying population dynamics due to changes in gear catchability (Pennington and Godo 1995; Wilberg et al. 2010). For instance, time-varying catchability can result from both density-dependent factors (e.g., range contraction) and the effects of environmental changes on either fish behavior or gear efficiency (e.g., responses to increased water clarity). Although we did not attempt to model the variation in population state as separate from the observational process, there are emerging modeling frameworks that focus on variation in observed counts and attempt to separate the often confounded variation in abundance from the variation in catchability (see Royle and Dorazio 2008 and Kéry and Schaub 2012). Measurement error can also affect fishery stock assessments that rely on survey or catch data as a model input (Krause et al. 2002). When catch time series are used to inform stock assessments, it is typical to assume that interannual variability in the data reflects

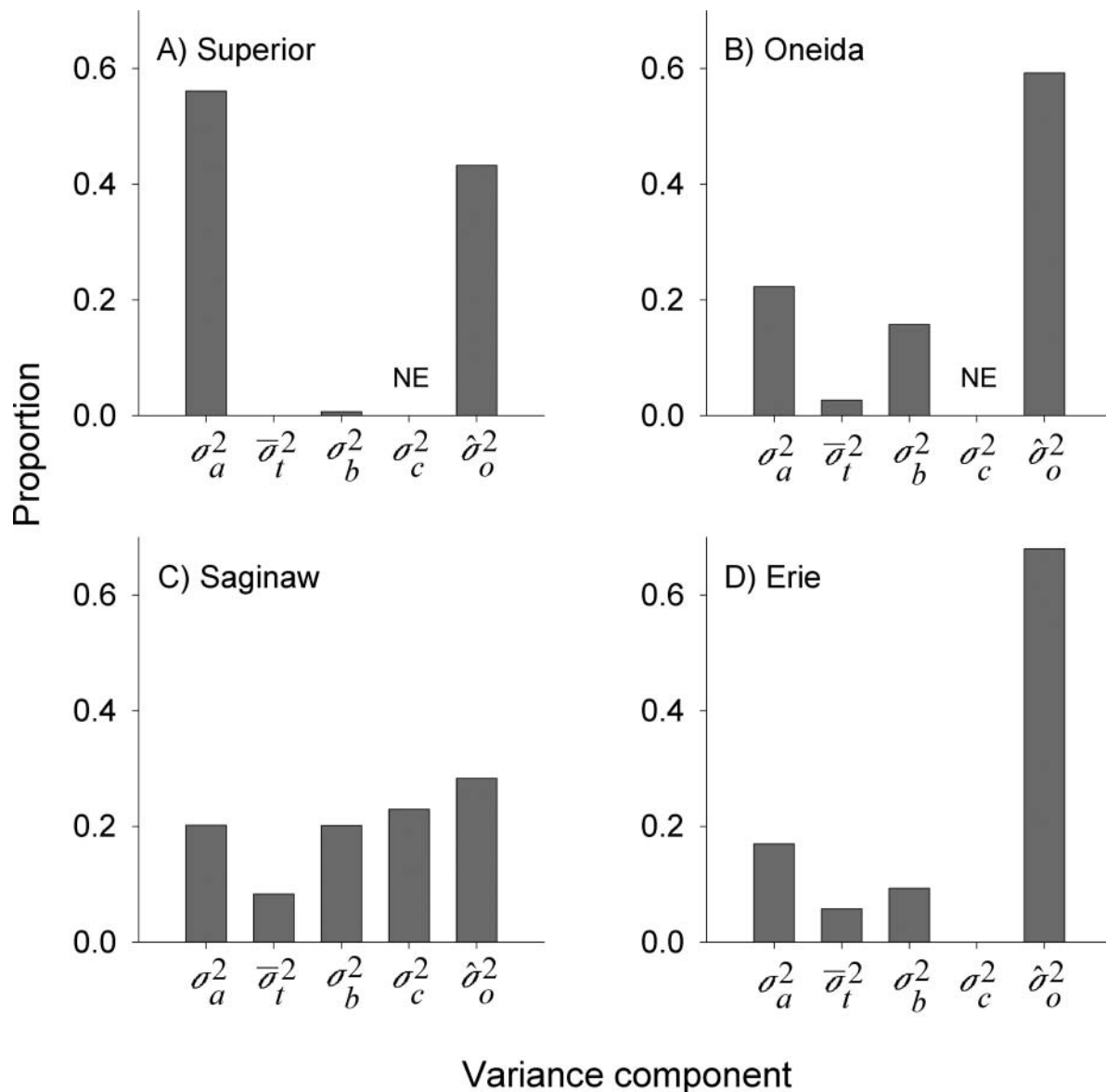


FIGURE 6. Estimated variance components for four fishery-independent surveys. The components are as follows: σ_a^2 = site-to-site variability; σ_t^2 = site-to-site trend variability; σ_b^2 = coherent temporal variability; σ_c^2 = ephemeral temporal variability; and σ_o^2 = observational variability; NE = not estimated.

temporal variation in relative abundance. Similar in concept to the variance-partitioning approach outlined here, methods exist for removing the effects of other factors contributing to interannual variability of catch data (Maunder 2001; Maunder and Punt 2004). For example, Deroba and Bence (2009) adjusted commercial fishery catch-per-unit-effort information for effects like boat size, season, and license holder to develop a model-based index of fish abundance. They applied general linear mixed models to account for the variation that was not attributable to abundance and then used the resulting estimates of annual least-squares means as a temporal abundance index. Estimation of fixed year effects would be an alternative to incorporating coherent variability as a random effect.

Monitoring the status and trends of fish populations is critical because many populations continue to be exploited at high levels and changing ecological conditions, such as the establishment of nonnative species and climate change, continue to affect aquatic ecosystems. Because system-specific variance components can have implications for efficiently monitoring fish population status and trends, models that partition variability can play a critical role in designing monitoring programs (e.g., fishery-independent surveys) and developing research and management objectives. For example, coherent temporal variation has been shown to have a disproportionately large effect on the power to detect trends in monitoring data (Wagner et al. 2007), with trend detection capabilities decreasing with increases in

temporal coherent variation. Coherent temporal variation may be of particular interest for fisheries monitoring programs because of its substantial influence on the ability to detect trends over short, management-relevant time periods (e.g., 5–10 years) and because the influence of this variance component on trend detection cannot be directly reduced through alteration of the survey's sampling design (Urquhart et al. 1998; Wagner et al. 2007). The ability to estimate ephemeral temporal variation, which can be interpreted as independent year-to-year variation among sites, is dependent on the sampling design used. In the analysis of Walleye catch data from the four long-term data series considered here, within-year site revisits were routine only in the Saginaw Bay survey. Thus, the separation of ephemeral temporal variation from observational variation was only possible for the Saginaw Bay survey data, where we saw a relatively large ephemeral–temporal variance component. For this reason, modifications to many ongoing fishery-independent survey designs (i.e., revisiting some sites within a year) may be required if estimating this source of variation is important to answering management questions or obtaining better understanding of site \times year interactions (Wagner et al. 2009).

There are alternative approaches to modeling count data. Our approach involved estimation of a single negative binomial scale parameter for each data set we analyzed, implying that there was a particular quadratic relationship between the variance and the mean. An overdispersed Poisson distribution is an extension of the generalized linear (mixed) model that assumes direct proportionality (rather than equality, as is the case with a standard Poisson distribution) between the variance and the mean. Sometimes results can be robust to the assumed variance-to-mean relationship, but this is not always the case (Ver Hoef and Boveng 2007; O'Hara and Kotze 2010). If the negative binomial model with a constant scale parameter does not produce a good fit, the scale parameter could be modeled as a function of the mean at the cost of estimating one or a few additional parameters. For example, Lindén and Mäntyniemi (2011) suggested using a two-parameter function allowing a more general quadratic relationship between the variance and the mean, for which the negative binomial distribution we used and the overdispersed Poisson distribution would be special cases. An advantage of modeling count data using an overdispersed Poisson distribution is that standard generalized linear model software can be used. A disadvantage is that if the assumed variance-to-mean relationship is called into question, there is no easy solution within that modeling framework. Adapting code that starts with a negative binomial distribution with a constant scale parameter, to allow for other variance-to-mean relationships, on the other hand, is more straightforward (Lindén and Mäntyniemi 2011). Likewise, the negative binomial parameter estimates generated as described here could be subsequently input into standard generalized linear model software that would treat the scaling parameter as a known constant to take advantage of the capabilities of preexisting software to produce various diagnostics for evaluating model fit (Hilbe 2008).

We have provided a flexible framework for achieving the goal of partitioning variance for fisheries count data using freely available software. Although a variety of programs are available (e.g., SAS and R) for estimating variance components (i.e., models with random effects), we found that ADMB-RE was the most flexible in terms of model parameterizations and the most stable in terms of convergence. The program R (R Development Core Team 2009) has libraries containing functions that will estimate negative binomial mixed models, a notable one being `glmmADMB` (<https://r-forge.r-project.org/projects/glmmadmb/>). As its name implies, the `glmmADMB` function interacts with ADMB and uses ADMB-RE for estimating parameters. However, programming directly within ADMB provides much more flexibility, including more control over model parameterization and the specification of derived quantities (e.g., $\bar{\sigma}_i^2$) and greater ability to include multiple random effects (in some R functions, the number of random effects allowed when assuming the negative binomial distribution is currently limited to one or two). The GLIMMIX procedure in SAS (SAS 2008) is also capable of fitting negative binomial mixed models; however, we found that convergence was often difficult to obtain for models with more than a few random effects. Model convergence can be a problem regardless of the software used to fit the negative binomial variance component model. In this regard, we have found that centering (e.g., grand mean centering) or standardizing covariates (such as the year covariate in our model) can help improve the model's ability to converge. In addition, providing reasonable starting values for parameters to the estimation software, especially for variance component parameters, is sometimes necessary to achieve convergence.

The modeling framework we present is flexible and could be readily expanded. For instance, it would be possible to explicitly model the longitudinal nature of many count data sets by including an autoregressive (i.e., AR[1]) structure on, for example, the coherent temporal random effect. In addition, although sampling gear differences precluded us from modeling these multiple data sets concurrently, the negative binomial variance components modeling framework could also be extended to fit other count data sets simultaneously. Fitting a model to multiple data sets together may allow for parameter estimation that would not be possible for the data sets individually (i.e., allowing less informative data sets to “borrow information”). Likewise, we believe that analysis of the response of variance structure to large-scale ecological changes is a logical extension of the methods described here.

The detection and assessment of regime shifts is a rapidly growing ecological subdiscipline (Mantua 2004; deYoung et al. 2008; Karunanithi et al. 2008; Gal and Anderson 2010). One area being emphasized is identifying early-warning signals for critical thresholds (i.e., “tipping points”; Scheffér et al. 2009). Others have suggested that increased variability of ecosystems may foreshadow impending regime shifts (Brock and Carpenter 2006; Carpenter and Brock 2006). For example, Carpenter and

Brock (2006) demonstrated that variability in lake water phosphorus concentrations during the summer stratification period increased prior to a shift from a clear, macrophyte-dominated state to a eutrophic, phytoplankton-dominated state. Anderson et al. (2008) document that perturbation (in the form of exploitation) resulted in increased variability in fish stocks over time. We expect that the structure of the variation (i.e., the variance components themselves) and not just the total variance will be responsive to severe large-scale perturbations and that this change in variance structure will have implications for how we conduct ecological monitoring. This emphasizes the need to continue to extend and evaluate existing approaches for estimating variance components to deal with count data of the type frequently seen in fisheries studies.

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