SPATIAL AND TEMPORAL COMPONENTS OF VARIATION IN GREAT LAKE PERCID POPULATIONS: IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

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Project Title: SPATIAL AND TEMPORAL COMPONENTS OF VARIATION IN GREAT LAKE PERCID POPULATIONS: IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

Project Sponsor:

FWS Agreement Number: USFWS 301819G026

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Date Submitted: 30 June 2011

Period Covered: 1 April 2009 – 30 June 2011

Study Objectives:
1. Determine relative magnitudes of spatial and temporal components of variation in percid relative abundance data and how these variance structures may differ among systems in the Great Lakes basin.
2. Determine whether variance structure itself is responsive to large-scale ecological perturbations.
3. Develop recommendations for the design of monitoring programs and analysis of resulting data to support management of important percid fisheries within the Great Lakes region.
Description of Tasks:

In this section, we outline the primary tasks that were completed during this project. Objective 1 was achieved primarily through Tasks I-IV, objective 2 was achieved primarily through task V, and objective 3 was achieved through Tasks VI and VII. We use this outline to provide an overview description of the activities pursued, while many additional details and analyses are provided throughout the supporting appendices.

I. Data collection:

The initial phase of the project consisted of compiling a list of agencies and individuals to contact in order to request percid gillnet and trawl time-series. We contacted several state and provincial agencies as well as academic institutions from around the Great Lakes basin. We focused on fishery-independent surveys for yellow perch and walleye because (1) these species are ecologically important throughout the Great Lakes basin; (2) they are important game fishes in the Great Lakes, and thus they are important to the regional economy; (3) these species have recently or continue to support commercial fisheries (Nepszy 1977; Kinnunen 2003; Wilberg et al. 2005); (4) it is a priority to maintain or restore both species in the Great Lakes basin (Fielder et al. 2007; Wilson et al. 2007; Irwin et al. 2008); and (5) largely because of 1-4 sufficient data exist to accomplish our objectives for these species.

We broadly distributed a letter to solicit participation in this project (Appendix A). We were able to collect fishery-independent time series for one or both of our target species for all of the Great Lakes (Erie, Ontario, Huron, Superior, and Michigan) and Oneida Lake, NY.

II. Data management:

The response to our data request was beyond our initial expectations. We are grateful for such a positive response. However, compiling these data took much longer than anticipated (largely because of differences in data organization across data providers). The provided data sets were transferred into Microsoft Access databases to facilitate later analyses. Ongoing communication with data providers was necessary to understand and account for nuances of the sampling programs and data organization. For example, some of the sampling programs produced time series of yellow perch relative abundance, but the intent of some surveys was to provide a fish community index. As such, some sampling
occurred at depths where perch would not be expected to be found. Thus, these depths were not included in analyses as representative sites for yellow perch. Additionally, the interpretation of what constitutes a gillnet sampling “site” varied among surveys. The data analyses described herein relied on measures of gillnet catch (the response variable), site information, year of sampling, and sampling effort.

Following model development (see next task), we were able to analyze gillnet data from four of the Laurentian Great Lakes (Superior, Huron, Erie, and Ontario) as well as Oneida Lake, NY. We were not able to analyze all of the data that was provided due to differences in data organization and sampling design as well as time constraints. However, we did perform analyses on a large number of gillnet observations from multiple systems for both walleye and yellow perch. These data represented over 11,000 gillnet sets and almost 350,000 collected percids (Tables 1-2).

III. Development of negative binomial mixed models:

A primary component of this work was to develop mixed-models to analyze the various fishery-independent survey data sets. The analytical approach used by Wagner et al. (2007) provided a starting point for model development. Here, we provide an overview of the concepts underlying our analysis and a brief description of the modeling process. A detailed description of the negative binomial mixed models used to estimate spatial and temporal components of variation has been prepared as a complete draft manuscript to be submitted to a peer-reviewed journal. The draft manuscript is included as Appendix B. This draft manuscript details the use of the negative binomial distribution for modeling count data as well as challenges encountered for partitioning variance in this context (i.e., versus generalized linear mixed models that assume normality).

The conceptual basis of our analyses is what is termed a “variance component” framework (Urquhart et al. 1998). As a starting point, it is readily evident to individuals who have analyzed fishery-independent surveys that fish populations are inherently variable over space and time. For example, catch indices vary from repeated samples from a single site, from site-to-site within a lake, from lake-to-lake, and over time. Thus, our framework involved developing a statistical model for total variation in catches (or other population variables) that partitions the total variation into components, which represent different spatial and temporal sources.
As an example, the total variance in catches from a long-term survey could be partitioned into several components including:

1. Site-to-site (spatial) variation, which implies that sites differ in their overall average catch.

2. Coherent (year-to-year) variation affecting all sites (e.g., sample sites within a lake) in a similar manner. The significance of the coherent temporal variation can be interpreted as, that in a given year all sites tend to either have higher or lower than average catch.

3. Ephemeral temporal variation (e.g., site-by-year interaction). Ephemeral temporal variation can be interpreted as, that in addition to coherent variation where all sites respond similarly in a given year, that all sites also deviate independently from one another (e.g., in a given year one site may have higher than average catch, while another may have lower than average catch).

4. Trend variation, where each site has its own trend over time.

5. Residual variation, the remaining unexplained variation that is due to sources such as sampling error (VanLeeuwen et al. 1996; Larsen et al. 2001; Kincaid et al. 2004).

To date, most variance components frameworks have been based on linear models that have some fixed effects and assume both normally distributed random effects and normally distributed residual error structures. These are called mixed-effect models because they include both fixed and random effects, and the variance is partitioned among the random effects and the observational error. Thus the concepts above are treated as random effects in the model (see Appendix B for additional details). As a simple illustration, modeling site-to-site variability as a random effect implies that variation in mean values among sites act as though the means were chosen at random from a larger set of potential sites. Inferences made by the model are then intended to apply to the larger set and not just the sites selected.

Given the differences across systems, we elected to compare variance components on relative scales (i.e., as proportions) rather than as absolute values. Likewise, we moved away from combining data sets across locations given the differences in gear, timing of sampling, and potential selectivity issues. If standardized sampling protocols had been employed across systems, then such a “meta-analysis” would have been more straightforward. Therefore, this final report focuses much more on survey-specific analyses, although we do attempt to make some across-system interpretations.
IV. **Parameter estimation:**

We used AD Model Builder (ADMB), with the random effects module (“ADMB-RE”), to perform maximum likelihood estimation to obtain the model parameters that minimize the negative log-likelihood function (i.e., maximize the likelihood) across all \( n \) observations ([http://admb-project.org](http://admb-project.org); Skaug and Fournier 2011). The resulting parameter estimates are presented in Tables 3 and 4. Additionally, several figures, based on these data sets and the corresponding parameter estimation, are included throughout Appendices C and D. The parameter estimation methodology served as a fundamental basis for all remaining tasks (see Appendices E-G). Some brief footnotes are also included in Appendix H.

V. **Perturbation analysis:**

Understanding drivers of large-scale of ecosystem change (i.e., perturbations) and their effects are relevant from a monitoring perspective because a perturbation may affect the tradeoff between the relative costs of monitoring and the information benefits produced (Gerber et al. 2005). If the dynamics of the system do change over time resulting in a change in the value of information gained through a monitoring program, then this would suggest that an adaptive approach to monitoring might be prudent to consider when monitoring fish populations. This is particularly relevant in the Great Lakes basin because perturbations such as the establishment of invasive species (as well as other perturbations, including human activities and global climate change) have and continue to alter the structure and function of the Great Lakes ecosystem (Ricciardi and Rasmussen 1998; Duggan et al. 2005; Barbiero et al. 2006). For example, if the spatial distribution of a fish species changes over time in response to perturbation, a goal of an adaptive approach to monitoring would be to accommodate this change by shifting sampling effort or modifying the sampling design in an effort to maintain a program with sufficient power to detect change and estimate status. Others have suggested that increased variability of ecosystems may foreshadow impending regime shifts (Brock and Carpenter 2006; Carpenter and Brock 2006), and detection and assessment of regime shifts is a rapidly growing ecological sub-discipline (deYoung et al. 2008; Karunanithi et al. 2008; Gal and Anderson 2010). We used our estimation model (Appendix B) to explore if the structure of variation is responsive to perturbation by evaluating observations from before and after zebra mussel invasion for multiple systems and for both walleye and yellow perch (Appendix E).
VI. **Development of simulation model:**

The estimation model (Appendix B) was modified in order to project simulations forward through time. This simulation model contained routines that allowed different sampling designs to be evaluated with respect to their statistical power to detect temporal trends (Appendix F). The simulation model was constructed to be a very flexible tool, allowing the user to specify multiple control variables (e.g., the number of simulations, effort allocation, and magnitude of desired trend detection). It can accommodate for alternative frequencies for estimation of parameters based on the simulated data (e.g., annually, every 5 years).

VII. **Power analysis:**

The design of fishery-independent surveys and the allocation of sampling effort affect the precision of the estimates resulting from these surveys. Thus, the cost effectiveness of surveys depends on how the target population is structured in time and space (e.g., Appendices B – D), and how well the survey design samples across these sources of variability. Given the importance of fishery-independent surveys and the fiscal resources that are annually devoted to implementing them, surprisingly little work has been directed towards understanding the components that contribute to variation in percid surveys in the Great Lakes basin and how surveys could be improved.

Although data derived from fishery-independent surveys are used to fulfill many objectives, one of the most common uses of these data are to infer changes in indices of relative abundance over time (Pennington and Strømme 1998; Stobutzki et al. 2006; Corradin et al. 2008; DeBruyne et al. 2008). Knowledge of rates of population decline or increase is critical for the sustainable management of exploited species, and for assessing recovery efforts for species of high conservation priority (Zwieten et al. 2002; Maxwell and Jennings 2005). Because of the importance of temporal trend detection for management, we emphasized the evaluation of monitoring programs that have temporal trend detection as a primary goal (Appendix F). As an example of the importance of temporal trend detection capabilities, fisheries management often expects that the effects of management actions can be evaluated and detected within a relatively short time-frame, such as 5 years (Zwieten et al. 2002). For instance, the Walleye Management Plan developed for Lakes Erie establishes fishery sustainability and quality objectives for walleye management (Locke et al. 2008).
2005). Included in this plan is an exploitation policy designed to help meet specific management objectives, and the effects of this exploitation policy are required to be evaluated on a 5-year basis. Our assessments of the spatial and temporal dynamics of walleye help to provide realistic appraisals of what can be detected over such time frames. In addition, our analysis of a variety of sampling scenarios, including varying sample sizes and trend magnitude, brackets a range of potential management scenario possibilities. In addition, the simulation approach that we developed (Task VI) can easily be adapted, as needed, to address specific fishery-independent survey management objectives.

**Major findings and accomplishments:**

**Major findings:**
- We summarize our major finding within categories in the Management Implications Section below.

**Accomplishments:**
- Compiled multiple long-term percid time series – This project relied on multiple agencies providing long-term data series, and we received contributions from several sources across the Great Lakes Basin (e.g., collaborators and contributors from: Michigan State University, Penn State University, Cornell University, Ontario Ministry of Natural Resources, Michigan DNRE, New York DEC, Wisconsin and Ohio DNR, and USGS).
- Developed a negative binomial mixed model (estimation) – Partitioning total variability into component temporal and spatial sources is a powerful approach to better understand ecological time series data and for elucidating population trends. As an alternative to using the Gaussian distribution, we developed new negative binomial mixed models to quantify both spatial and temporal variability.
- Conducted a basin-wide evaluation of variance structure – We applied these newly developed models to several fishery-independent surveys across the Great Lakes basin. The analyzed data represented over 11,000 gillnet sets and almost 350,000 collected percids.
- Developed a simulation tool – We developed a highly flexible simulation tool to evaluate different sampling designs with respect to their statistical power to detect temporal trends.
**Project communication** – We have prepared the first complete manuscript planned for submission to a peer-reviewed journal (others anticipated). This project is the focus of 3 professional conference abstracts. We had several interactions with data providers as well as additional outreach activities over the course of this project and have identified areas for future research.

**Management implications of your work:**

**Variance-components framework & fishery-independent surveys:**

- In the Laurentian Great Lakes, fishery-independent surveys are used by state, provincial, federal, and tribal fish and wildlife agencies to assess a variety of fish species (see Sitar et al. 1999; Tyson and Knight 2001; Stapanian et al. 2007; Pothoven and Madenjian 2008, among others). Data from fishery-independent surveys are used to assess stock status and population trends (for monitoring restoration efforts or setting annual harvest levels) and to evaluate the effects of natural and anthropogenic stressors on the spatio-temporal dynamics of populations (Corradin et al. 2008; Irwin et al. 2008; Jackson et al. 2009). We applied a variance-component framework for discrete data and provided the opportunity to compare across surveys, species, and time periods considered to be ecologically distinct.

- The proportion of the total variance contained within each of the spatial and temporal components varied among systems and sometimes between time periods. While this is not surprising (i.e., we would predict that variance structures are a function of both the indicator and the system being evaluated), it reinforces the notion that population structure over space and time is variable among systems. From a management perspective, system-specific variance components can have implications for efficiently monitoring population status and trends (see Urquhart et al. 1998).

**Estimation:**

- To date, most variance-components frameworks have been based on linear models that assume normally distributed error structures. When these models are applied to count data, the response variable is commonly transformed (usually using a logarithmic transformation) prior to fitting the model in an attempt to accommodate the normality and homogeneity of variance assumptions. Assuming a normal distribution for observations of fish abundance is often not ideal because these counts are typically non-negative integers.
with high variances and low means, not to mention other issues that arise when log-transforming data such as how to treat zero observations during the analysis.

- The negative binomial distribution represents an alternative to log-transformation (e.g., an alternative assumption about the mean-variance relationship) that can be applied to discrete count data; however, the partitioning of variance in this context is less straightforward than for generalized linear mixed models that assume normality. We developed a method of estimating variance components using negative binomial mixed models. 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 Bennett 1996; Ver Hoef and Boveng 2007). The negative binomial mixed model we have presented here allows for estimating variance components for ecological count data without the need for data transformation (O'Hara and Kotze 2010).

- This model performed well on very complex and unbalanced data sets (i.e., an unbalanced number of observations per site, within years, and across years) that differed in the proportion of zero observations. Although the negative binomial performed well for a variety of data structures, diagnostic plots suggest varying degrees of model suitability across the systems and species considered here. Additional estimation methods should be investigated for analyzing zero-truncated and zero-inflated data sets.

- We partitioned total variance into 5 components. In order to estimate each of these, a survey would need to include within-year site revisits at multiple sites across multiple years. In some systems, additional data collection (e.g., within-year site revisits) would be required in order to estimate certain variance components.

**Perturbation:**

- For the perturbation analyses considered here, total variability was generally lower in the period after zebra mussel invasion. We suggest this is a likely consequence of having fewer high-catch gillnet sets during this time period. This explanation may also explain the reduction in site-to-site variability observed for some systems after ZM invasion. From a monitoring perspective, a decrease in total variance may not translate directly to an increased ability to assess population status and detect temporal trends: it is not only the total variance that is important, but rather how the total variance is partitioned over space and time.
Power:

- The number of years necessary to detect temporal trends with a power of 0.8 ranged from 5 to approximately 15 years for the walleye surveys. However, as expected, power was dependent on trend magnitude, the number of sites sampled each year, and number of years sampled.

- Our results suggest that if management decisions occur over relatively short time-frames (e.g., 5 years) that there can be a relatively high (e.g., between 10% - 40% in our analysis) probability of concluding that the population is trending in the incorrect direction (i.e., the population is actually on a long-term decreasing trend, but short-term monitoring suggests a population increase).

- Monitoring designs should be evaluated within the context of achieving specific management objectives (e.g., high power to make accurate short-term inferences versus sustaining long-term surveys). Allocation of effort (number of sites and years sampled) in monitoring programs affects the ability to partition variance and the power to detect trends.

Additional restoration work needed and/or areas for future research:

Several areas for future research emerged from this research project. We briefly identify some examples below.

a. Comparison of distributional assumptions – The research presented here focused on the negative binomial distribution, but there are alternative approaches for modeling count data (see discussion in Appendix B). Recent research has considered alternative mean-variance relationships (Lindén and Mäntyniemi in press). The sensitivity of variance parameter estimation to these alternatives is yet to be explored.

b. Accounting for autocorrelation – Monitoring data for fish populations are often autocorrelated over time (e.g., repeated captures of a strong cohort across multiple years) or unevenly distributed across space (e.g., depths). Spatial and temporal autocorrelation may also be influenced by large-scale ecological changes. Explicitly accounting for spatial and temporal autocorrelation in an evaluation of alternative survey designs could improve the ability of management to assess population status and detect trends.

c. Analysis of zero inflated or zero-truncated data – Ecological observations are frequently quantified as counts, which may include a high frequency of zero observations (e.g., a trawl haul results in no catch of a target species). Conversely, some processes are only documented based
on occurrences such that the observational data cannot contain zeros. For instance, the
duration of time an organism spends in its inhabited location may be of interest. Zero inflation
and zero truncation are currently receiving attention related to natural resource management
issues (e.g., Vaudor et al. 2011; Webley et al 2011). An extension of the work summarized here
would be to further confront variance-partitioning models with these data types.

d. Alternative monitoring strategies – Simulations/predictions for sampling programs that skip
years (e.g., perform survey only on even years) or reduce the number of sites would likely be of
interest to fishery managers.

In addition, this project relied on MSU’s High Performance Computing Cluster (the HPCC) to
perform many of the simulations. The HPCC would likely be an extremely valuable resource for
making progress on the above areas of research potential.

List of presentations delivered and outreach activities:

This project was the focus of three professional conference abstracts. See Appendices G1-G3
for full abstracts.

temporal variation in Great Lakes percid catch-per-effort data. AFS, Pittsburgh, PA.

components and survey design in detecting trends in recreational fisheries monitoring data.
World Recreational Fishing Conference, Berlin, Germany.

binomial mixed models to partition variance in fishery-independent survey data. AFS, Seattle,
WA.

During 2011, Dr. Irwin provided consultation to Michigan DNR related to the use of offset terms
in Poisson regression analysis, akin to what was developed for effort in the negative binomial
regressions presented here.

During 2011, Dr. Wagner was an invited speaker for a technical session at MSU (jointly hosted
by the Quantitative Fisheries Center and the Quantitative Wildlife Laboratory). The focus of this
meeting was hierarchical and mixed models, which closely relates to this project. It was attended by
both graduate students and faculty from the Department of Fisheries and Wildlife.
The estimation and simulation methods described here are being used collaboratively with the U.S. National Park Service to evaluate their vegetation monitoring protocol for the Eastern Rivers and Mountains Network.

Include relevant pictures or images associated with the project:
Statistical model development and analyses were at the core of this project. As such, we have not included any photographs associated directly with this work. However, we have included numerous figures throughout the report (see incl. appendices).

Geographic region project occurred in or effects:
The locations associated with the analyzed data are identified in Tables 1 and 2. These include Lake Superior, Huron, Erie, Ontario, and Oneida Lake.

List of reports and peer-reviewed papers completed or in-progress:


In addition to the above completed or in-progress reports, we anticipate additional manuscripts. We’ve identified the following topics:

a. Across-lake comparison of variance component estimation from different fishery-independent surveys for percids in the Great Lakes Basin (based on Objective 1)

b. Role of variance components in understanding large-scale perturbation (based on completed tasks related to Objective 2).

c. Evaluation of fishery-independent sampling designs (based on completed tasks related to Objective 3).
References


Table 1. Summary information for walleye gillnet data sets presented in this report.

<table>
<thead>
<tr>
<th>System</th>
<th>Area / Survey</th>
<th>Agency</th>
<th>Contact</th>
<th>Year Range</th>
<th>Years</th>
<th>Sites</th>
<th>Net Sets</th>
<th>% Revisits</th>
<th>Total Catch</th>
<th>% 0 catches</th>
</tr>
</thead>
<tbody>
<tr>
<td>Superior</td>
<td>WI waters</td>
<td>WI DNR</td>
<td>Sieder</td>
<td>1970-2008</td>
<td>37</td>
<td>12</td>
<td>233&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>705</td>
<td>0</td>
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<td>MI DNR</td>
<td>Fielder</td>
<td>1993-2008</td>
<td>16</td>
<td>10</td>
<td>264&lt;sup&gt;b&lt;/sup&gt;</td>
<td>46.9</td>
<td>4,651</td>
<td>4.5</td>
</tr>
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<td>Huron</td>
<td>Les Cheneaux</td>
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<td>188</td>
<td>39.4</td>
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<td>Grand Bend</td>
<td>OMNR</td>
<td>Cotrill</td>
<td>1984-2008</td>
<td>24</td>
<td>13</td>
<td>496&lt;sup&gt;c&lt;/sup&gt;</td>
<td>75.0</td>
<td>479</td>
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<td>Vandergoot</td>
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<td>119</td>
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<td>NY DEC</td>
<td>Einhouse</td>
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<td>11</td>
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<td>Einhouse</td>
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<td>83</td>
<td>543</td>
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<td>Hoyle</td>
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<td>17</td>
<td>24</td>
<td>1,448&lt;sup&gt;e&lt;/sup&gt;</td>
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<td>1,938</td>
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<td>9</td>
<td>715</td>
<td>83.4</td>
<td>6,973</td>
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</table>

<sup>a</sup> data limited to depths < 45 ft
<sup>b</sup> data limited to orgille = 1100 and depth = bottom
<sup>c</sup> data limited to depths < 35 m, effort < 28 hrs, and sites identified with Cotrill
<sup>d</sup> data from Kmulti series
<sup>†</sup> substantial gear change made, resulting in splitting time series into two periods
<sup>e</sup> removed sites that only produced 0 catches (usually deep water)
Table 2. Summary information for yellow perch gillnet data sets presented in this report.

<table>
<thead>
<tr>
<th>System</th>
<th>Area / Survey</th>
<th>Agency</th>
<th>Contact</th>
<th>Year Range</th>
<th>Years</th>
<th>Sites</th>
<th>Net Sets</th>
<th>% Revisits</th>
<th>Total Catch</th>
<th>% 0 catches</th>
</tr>
</thead>
<tbody>
<tr>
<td>Superior</td>
<td>WI waters</td>
<td>WI DNR</td>
<td>Sieder</td>
<td>1970-2008</td>
<td>37</td>
<td>8</td>
<td>155⁹</td>
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<td>1,466</td>
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<td>Oneida</td>
<td>CBFS</td>
<td>Rudstam</td>
<td>1958-2006</td>
<td>47</td>
<td>15</td>
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<td>0.3</td>
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<td>MI DNR</td>
<td>Fielder</td>
<td>1993-2008</td>
<td>16</td>
<td>10</td>
<td>264⁹</td>
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<td>28</td>
<td>8</td>
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<td>10</td>
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⁹ data limited to depths < 45 ft

b data limited to orgille = 1100 and depth = bottom

c data limited to depths < 35 m, effort < 28 hrs, and sites identified with Cotrill

† substantial gear change made, resulting in splitting time series into two periods

d removed sites that only produced 0 catches (usually deep water)
Table 3. Estimated values for model parameters (and 1 SE) and calculated variance components for multiple walleye gillnet time series. NE = not estimated. No SE was reported for the derived quantities $\sigma^2_t$ and $\hat{\sigma}^2_o$.

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1 effort of 0-CPE net sets assumed = 1; see appendix H.

2 effort of 0-CPE net sets assumed = surrounding values
Table 4. Estimated values for model parameters (and 1 SE) and calculated variance components for multiple yellow perch gillnet time series. NE = not estimated. No SE was reported for the derived quantities $\hat{\sigma}_t^2$ and $\hat{\sigma}_o^2$.

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¹ effort of 0-CPE net sets assumed = 1.0; see appendix H.
² effort of 0-CPE net sets assumed = 0.5
List of Appendices:

Appendix A. Data-request letter sent to solicit participation in this project.

Appendix B. Draft manuscript.

Appendix C. Figures for walleye gillnet surveys.

Appendix D. Figures for yellow perch gillnet surveys.

Appendix E. Perturbation analysis.

Appendix F. Power analysis.

Appendix G. Conference abstracts

Appendix H. Footnotes
15 May 2009

Dear Colleague,

We invite your participation in a Quantitative Fisheries Center project titled “Spatial and Temporal Components of Variation in Great Lake Percid Populations: Implications for Conservation and Management”. This project was recently funded by the Great Lakes Fish and Wildlife Restoration Act, and its overall purpose is to provide monitoring recommendations for fishery-independent surveys of percid populations in the Great Lakes basin. We previously contacted several biologists around the Great Lakes basin with respect to data availability and the responses were encouraging. We are now performing a broader data request to ensure that the information derived from this project benefits biologists and managers throughout the basin. Thus, we are requesting your participation in the form of providing long-term monitoring data (e.g., gillnet and trawl fishery-independent survey data) for yellow perch and walleye for use in statistical analyses and simulations related to this project’s objectives. In addition to providing data, we are also interested in your active participation in publishing papers based on the results. Below, we describe the project’s objectives in more detail, the requested format for supplying electronic data, our data-use policy, and future co-authorship opportunities.

We ask that you respond to this inquiry with an indication of your commitment to participate in this project by 22 May 2009. Further, we ask that all data be provided no later than 30 June 2009 in the requested format. Given the project’s timeline, we cannot ensure that data provided after that date will be incorporated into the analyses.

Project objectives
The specific objectives of the proposed research are to:

4. Determine relative magnitudes of spatial and temporal components of variation in percid relative abundance data and how these variance structures may differ among systems in the Great Lakes basin.
5. Determine whether variance structure itself is responsive to large-scale ecological perturbations (i.e. dreissenid mussel invasion).
6. Develop recommendations for the design of monitoring programs and analysis of resulting data to support management of important percid fisheries within the Great Lakes basin.

Briefly, to meet the project’s objectives, we will analyze data from multiple populations using hierarchical statistical models to estimate the spatial and temporal components of variance (see Figure 1) in relative measures of percid abundance. Once the variance estimates are obtained (objectives 1 and 2), they will be used in
simulation modeling to evaluate how variance structure influences the ability to make inferences from percid survey data (objective 3). That is, the simulation modeling will be used to evaluate the statistical power of different sampling designs, given a particular variance structure (Wagner et al. 2007, Wagner et al. in press).

**Figure 1. Depiction of different variance components.** Panel A illustrates spatial variation, as if this were the only source of variability, so that each of the three sample sites (represented by the dashed and solid lines) has different means but no temporal variability. Panel B illustrates adding coherent temporal variation to the spatial variation, and panel C adds to these sources ephemeral temporal variation where each site deviates independently of other sites in each year. Panel D illustrates slope variation, where each site has its own trend (specifically, slope variation was added to spatial variation to ease interpretation). One could then add all these sources of variation to equal the total variability in an ecosystem response variable.

**Requested format for data**

We are interested in catch-per-effort (CPE) indices for both yellow perch and walleye, namely fishery-independent gillnet and trawl collections of these species. For use in our analyses, data should be summarized for each year, lake, gear, sampling site, and species. That is, we would like to use annual site-specific CPE data generated from long-term fishery-independent sampling programs. Tables 1 and 2 provide examples of a useful organizational format for this project. Please be
Appendix A

sure that all locations are identified consistently or we are likely to treat slight variations in names as different sampling sites.

Table 1. Hypothetical annual site-specific gillnet (GN) catches of yellow perch (YP) and walleye (WE) from two fixed-location sampling sites in Big Lake, Nowhere.

<table>
<thead>
<tr>
<th>Year</th>
<th>Lake</th>
<th>Gear</th>
<th>Site</th>
<th>Effort (hours)</th>
<th>YP</th>
<th>WE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990</td>
<td>BigLake</td>
<td>GN</td>
<td>DeepShoal</td>
<td>12</td>
<td>150</td>
<td>100</td>
</tr>
<tr>
<td>1990</td>
<td>BigLake</td>
<td>GN</td>
<td>ShallowBay</td>
<td>12</td>
<td>500</td>
<td>175</td>
</tr>
<tr>
<td>1991</td>
<td>BigLake</td>
<td>GN</td>
<td>DeepShoal</td>
<td>11</td>
<td>140</td>
<td>75</td>
</tr>
<tr>
<td>1991</td>
<td>BigLake</td>
<td>GN</td>
<td>ShallowBay</td>
<td>11</td>
<td>400</td>
<td>150</td>
</tr>
</tbody>
</table>

Table 2. Hypothetical annual site-specific trawl (TR) catches of yellow perch (YP) and walleye (WE) from two fixed-location sampling sites in Big Lake, Nowhere.

<table>
<thead>
<tr>
<th>Year</th>
<th>Lake</th>
<th>Gear</th>
<th>Site</th>
<th>Effort (# of hauls)</th>
<th>YP</th>
<th>WE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990</td>
<td>BigLake</td>
<td>TR</td>
<td>DeepShoal</td>
<td>2</td>
<td>40</td>
<td>4</td>
</tr>
<tr>
<td>1990</td>
<td>BigLake</td>
<td>TR</td>
<td>ShallowBay</td>
<td>2</td>
<td>20</td>
<td>2</td>
</tr>
<tr>
<td>1991</td>
<td>BigLake</td>
<td>TR</td>
<td>DeepShoal</td>
<td>1</td>
<td>30</td>
<td>3</td>
</tr>
<tr>
<td>1991</td>
<td>BigLake</td>
<td>TR</td>
<td>ShallowBay</td>
<td>2</td>
<td>10</td>
<td>1</td>
</tr>
</tbody>
</table>

In addition to the catch data, please provide a brief summary description of the following information for each survey:

1) Sampling design used (e.g., fixed-site or random over time);
2) Description of gear type (e.g., dimensions of bottom trawl and typical tow duration; gillnet material and mesh size, period of deployment) and if it has changed over time;
3) Identification of timing of notable ecological changes during the survey time period, in particular we would like to be able to separate each time series into periods of before and after zebra mussel establishment, if applicable.

Please also indicate the availability of the following information: annual age-distribution of catches, estimates of gear-selectivity, or water clarity measurements (these may be informative but not likely to play a direct role in the proposed analyses).

Data-use and co-authorship policies

We anticipate two primary uses for any data supplied to this project: 1) achieve the objectives of the proposal, and 2) publish results (we anticipate two or more publications) in a peer-reviewed journal as a multi-authored contribution. Data supplied will not be used or distributed beyond what facilitates achievement of the project’s objectives unless a clear need arises and additional permission is granted by the “owners” of the data. All individuals that provide usable data will be offered the opportunity to be a co-author on any submitted peer-reviewed publication. Being a co-author on papers will entail contributions to the analysis, interpretation, and writing of such publications. We envision these responsibilities to not be overly
onerous, but the provision of data alone will not be sufficient for inclusion as a co-author.

Please feel free to share any suggestions or concerns with us. Likewise, if you are aware of other sources of long-term monitoring data for percids in the Great Lakes basin that we should consider including in this study, then please provide us with appropriate contact information.

**We appreciate your participation in this project – its success depends on it!**

We look forward to hearing from you,

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Appendix B.

**Estimating Spatial and Temporal Components of Variation in Count Data using Negative Binomial Mixed Models**

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Running title: Variance Partitioning in Negative Binomial Models
Summary

1. Count data have a longstanding presence in ecological study, and these data continue to be an important source of information for managing both exploited and unexploited populations. Counts are recorded as discrete non-negative integers, often dominated by many low positive values with few observations of relatively high abundance. These characteristics do not conform well to assumptions of the Gaussian distribution. Ecologists’ interest in count data is frequently connected to how these values vary over time and space.

2. Partitioning total variability into component temporal and spatial sources is a powerful approach to better understand ecological time series data and for elucidating population trends. As an alternative to using the Gaussian distribution, we developed negative binomial mixed models to quantify both spatial and temporal variability, and used data from four fishery-independent surveys across the Great Lakes basin to illustrate the utility of these models.

3. Although these four surveys varied in overall sampling intensity, total catch, and in the proportion of zero catches, negative binomial mixed models produced reasonable approximations to the count data. Estimates of the negative binomial scaling parameter and variance structure varied considerably across systems.

4. We present a method of estimating variance components in a negative binomial regression framework, which has implications for monitoring programs and for examining the potential of individual variance components to serve as indicators of ecological change.
**Introduction**

Partitioning the total variance of a response variable into components (i.e., variance components) representing different spatial, temporal, or treatment factors is often of interest in ecological research (Urquhart et al. 1998; Fletcher and Underwood 2002; Qian and Shen 2007). Estimating variance components can inform a variety of research and management questions such as the design of monitoring and assessment programs (Larsen et al. 2001; Lindenmayer and Likens 2010). The estimation of variance components, for use in evaluating ecological monitoring and assessment designs, has been applied to a wide variety of aquatic indices including water chemistry variables, measurements of 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 both normally distributed random effects and normally distributed error structures. These are called mixed-effect models because they include both fixed and random effects, and the variance is portioned among the random effects and the observational error. When these normal-distribution based models are applied to count data, the response variable is commonly transformed (usually using a logarithmic transformation) prior to fitting the model in an effort to better approximate the normality, linearity, and homogeneity of variance assumptions. Assuming a normal
distribution for count observations is not ideal because counts are typically non-negative integers with high variances and low means. Further, log-transforming count data raises difficult questions such as how to treat zero observations during the analysis (Power and Moser 1999; Ver Hoef and Boveng 2007; O’Hara and Kotze 2010). Use of the negative binomial distribution represents an alternative to log-transformation that explicitly models distributions as discrete and allows for zero counts (Anscombe 1949; White and Bennetts 1996; Jones et al. 2009). Although using the negative binomial distribution has obvious appeal for modeling count data, it has rarely been used in mixed-effect models (but see Jones et al. 2009 for an application of models to stuttering rates). Furthermore, the partitioning of variance in this context is less straightforward than for generalized linear mixed models that assume normality.

Throughout the world, fishery-independent surveys produce count data that are used to provide essential information for understanding, restoring, and managing fish populations (Wilberg et al. 2005; Stobutzki et al. 2006; Allen et al. 2007). Data from these surveys are used to assess stock status and population trends (for monitoring restoration efforts or setting annual harvest levels) and to evaluate the effects of natural and anthropogenic stressors on the spatio-temporal dynamics of populations (Corradin et al. 2008; Irwin et al. 2008; Jackson et al. 2009). In the Laurentian Great Lakes, fishery-independent surveys are used by state, provincial, federal, and tribal fish and wildlife agencies to assess a variety of fish species (see Sitar et al. 1999; Tyson and Knight 2001; Stapanian et al. 2007; Pothoven and Madenjian 2008, among others). 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. Our objective
was to estimate spatial and temporal components of variance for count data, and we illustrate this analysis using multiple fishery-independent surveys from across the Great Lakes basin. Thus, we outline a method of estimating variance components when using negative binomial mixed models to describe count data. We believe that incorporating variance partitioning into fitting negative binomial models to count data could have wide application in ecology, including assessing the trend-detection capabilities of alternative survey designs and evaluating if variance components are sensitive to large-scale ecological changes.

**Methods**

**DATA SOURCES**

We used data collected from four fishery-independent gillnet surveys targeting walleye *Sander vitreus*, with the premise that improved understanding of spatial and temporal variability will subsequently allow for a thorough evaluation of current survey designs. Our rationale for focusing on walleye is: (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; Irwin et al. 2008); and (3) to allow for direct comparison across surveys for insights this might provide. We include long-term (16 – 47 years) data series from Wisconsin waters of Lake Superior; Oneida Lake, NY; Saginaw Bay of Lake Huron; and Ohio waters of Lake Erie. All data were collected using multi-mesh gillnets, with some differences in use of multi- or mono-filament materials. For each survey separately, we performed the analysis at the level of a single net-set (i.e., across mesh panels). In both the Saginaw
Bay and Lake Erie surveys, sites were sometimes sampled multiple times within a year. For each recorded catch (i.e., the number of animals collected in a single sampling event), we also used the following information: the year sampling occurred, set duration (if variable; Lake Erie only), and the site (location) of the net-set. For more information on the use of gillnets to sample walleye populations see Hamley and Regier (1973), Anderson (1998), or Irwin et al. (2008).

VARIANCE COMPONENTS

Several conceptual frameworks have been used for partitioning the total variance of an ecological state variable (e.g., VanLeeuwen et al. 1996; Sims et al. 2006), but for consistency, we will use the framework and terminology set forth by Urquhart et al. (1998) and Wagner et al. (2007). 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 population being sampled do not occur. The basic structure we put forward could be adapted to include fixed season and within-year random effects. The primary components present in fishery-independent survey data include (Table 1; Fig. 1):

6. site-to-site (spatial) variation;
7. coherent (year-to-year) variation;
8. ephemeral temporal variation (i.e., site-by-year interaction);
9. trend variation; and
10. observational variation.
Site-to-site variability represents consistent differences among sites in the magnitude of an attribute of interest. Estimating site-to-site variability requires that multiple sites be sampled multiple times, either by within-year site revisits or by returning to the same site across multiple years (the latter being more common in fishery independent surveys). For catch data, site-to-site variation implies that individual sites differ in their overall average abundance (or catch-per-unit-effort). Coherent 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 that, in a given year, all sites tend to have either higher or lower catches than their respective 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 is some within-year revisits of sites (Table 1; Fig. 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, coherent variation is then the temporal variation common to all sites, above and beyond what
could be explained by the underlying global 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. 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; Fig. 1).
Separating ephemeral variation from observational variation requires multiple visits
within a sampling season for at least some site by 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;

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

\[ Y_{ijk} \sim NB(\mu_{ijk}, \kappa), \quad \text{eqn 1} \]
where $Y_{ijk}$ is the total catch from the $k^{th}$ sample at site $i$ in year $j$, $\mu_{ijk}$ is the expected value for that sample, site and year, and $\kappa$ is the so called scaling parameter of negative binomial distribution. We employ a log link function such that, generally, the $\log_e$ (we represent this by $\ln$ subsequently to make equations more readable) of the expected catch would be a linear function of the predictors:

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

where $\nu$ is the fixed intercept, $\lambda$ is the fixed slope for temporal trends using year as the covariate (i.e., the predictor variable), and $\ln(E_{ijk})$ is an effort offset term. Here we are assuming that the expected catch per effort would be the same for repeat within year samples at a site, but 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 year covariate was centered on the mean year for each data set’s time series separately.

The terms $a_i$ (site-to-site variability), $t_i$ (site-to-site trend variability), $b_j$ (coherent temporal variability) and $c_{ij}$ (ephemeral temporal variability) are all random effects that were assumed to be independent and identically distributed as $N(0, \sigma_i^2)$, where $\sigma_i^2$ 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 (for Saginaw and Erie); in all other cases this source of variation is absorbed into the observational error variance.

It follows that expected catch is estimated by:

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

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

\[ V_{ijk} = \mu_{ijk} + \frac{\mu_{ijk}^2}{\kappa}. \]  

eqn 4

The degree to which variance exceeds the mean is determined by the scaling parameter \( \kappa \).

It follows that from eqn 4, the variance-mean ratio is:

\[ \tau_{ijk} = 1 + \frac{\mu_{ijk}}{\kappa}, \]  

eqn 5

such that \( \tau \) must be \( \geq 1 \). 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). However, the procedures used here included estimation of \( \kappa \). 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 estimation we required software able to integrate multiple random effects out of the likelihood function and perform an efficient numerical search for the best fit parameters which included the scaling parameter.

We used AD Model Builder (ADMB), with the random effects module (“ADMB-RE”), to perform maximum likelihood estimation to obtain the model parameters that minimize the negative log-likelihood function (i.e., maximize the likelihood) across all \( n \) observations (http://admb-project.org; Skaug and Fournier 2011). This software uses the Laplace approximation to integrate out the random effects (Skaug and Fournier 2006; Maunder et al. 2009). For mixed-effect models, the likelihood function that needs to be maximized is the marginal likelihood, obtained by integrating out random effects:
Here \( f_\theta(y | \delta) \) is the likelihood of the data, \( y \), given the vector of random effects \( \delta \), and is subscripted by \( \theta \) to indicate that the likelihood of the data depends on \( \theta \). The probability density function for the vector of random effects, \( \delta \), is \( h_\theta(\delta) \). This too depends on the parameter vector because quantities such as variances for the random effects are part of that vector. It is convenient to rewrite eqn. 6 as:

\[
L(\theta) = \int f_\theta(y | \delta) h_\theta(\delta) d\delta
\]

where,

\[
g(\delta, \theta) = \ln(f_\theta(y | \delta)) + \ln(h_\theta(\delta))
\]

because software such as AD model builder only requires specification of the parameters, the random effects and \(-g()\). 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 (Skaug and Fournier 2006). 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:

\[
-\ln l = \sum_{i}^{n} \left[ -\ln\left(\Gamma(Y_{ijk} + \kappa)\right) + \ln(\Gamma(\kappa)) + \ln(\Gamma(Y_{ijk} + 1)) - \kappa \ln \left( \frac{\kappa}{\mu_{ijk} + \kappa} \right) - Y_{ijk} \ln \left( \frac{\mu_{ijk}}{\mu_{ijk} + \kappa} \right) \right]
\]

(see Hilbe 2007). In ADMB-RE, we used the “-log_negbinomial_density” function on arguments \( Y_{ijk}, \mu_{ijk}, \) and \( \tau_{ijk} \). As previously mentioned, random effects were assumed
Appendix B

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, $-\ln d$. For instance, the component
related to $a_i$ was

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

eqn 10

where $\sigma_a^2$ is an estimated parameter and $m$ 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
parameters $(\sigma^2_a, \sigma^2_t, \sigma^2_b, \sigma^2_c)$ 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 trend),
calculating the total variance is possible by simply summing across the estimated
variance parameters (Urquhart et al. 1998). However, this 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 $\sigma_t^2$.

Although $t_i \sim N(0, \sigma_t^2)$, the influence of $t_i$ on $\hat{\mu}_{ik}$ 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 in this case $X^2$ is the centered year covariate squared. Therefore, we weighted the
slope random effect parameter $\sigma_i^2$ by the centered year covariate and calculated an average value to compare with intercept random effect parameters:

$$\overline{\sigma_i^2} = \frac{\sum (\text{year}^2 \sigma_i^2)}{x},$$

eqn 11

where $x$ is the number of years included in the system’s time series.

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 observational error. For the negative binomial distribution, from eqn. 4 it can be seen that this observational error CV is a function of the mean. Thus, to produce a value comparable to the other variance component terms, and comparable 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 observational error variance in the negative binomial context:

$$\hat{\sigma}_o^2 = \frac{\sum \left( \frac{V_{ijk}}{\hat{\mu}_{ijk}} \right)^2}{n}.$$  

eqn 12

In eqn 12, there is a term in the sum for each observation and $n$ is the total number of observations.

As a visual diagnostic measure, we calculated Anscombe residuals for the negative binomial model (see Anscombe 1953 and Hilbe 2007) as
Appendix B

\[ R_{\hat{\text{ijk}}}' = \frac{\left[ \frac{3}{\alpha}(1 + \alpha Y_{\hat{\text{ijk}}})^{\frac{3}{2}} - \left(1 - \alpha \hat{\mu}_{\text{ijk}} \right)^{\frac{3}{2}} \right] + 3 \left(Y_{\hat{\text{ijk}}}^{\frac{3}{2}} - \hat{\mu}_{\text{ijk}}^{\frac{3}{2}} \right)}{2 \left(\alpha \hat{\mu}_{\text{ijk}}^{\frac{3}{2}} + \hat{\mu}_{\text{ijk}} \right)^{\frac{1}{2}}}, \]

where \( \alpha \) 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; Hardin and Hilbe 2007). For each system separately, these residual values were plotted to 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., years of data collection, number of sites sampled per year), general magnitude of the catch, and in the proportion of 0 catches (range: <1% - 33%; Fig. 2). At the survey level, the total number of net sets employed ranged approximately between 100 and 700 (Table 2); whereas, 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 by far had 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 (Fig. 3). The estimates of the scaling parameter (\( \kappa \)) ranged more broadly across systems (Table 3). For all four systems, the fixed intercepts (\( \nu \)) were estimated to be positive. All of the fixed slope (\( \lambda \)) estimates were near zero, but were positive for Superior and Saginaw Bay and negative for Oneida and Erie. For each system, the plot of Anscombe residuals displayed a fairly consistent
spread across the range of predicted values (Fig. 4). Likewise, the normal probability
plots of the Anscombe residuals suggested approximate normality was achieved in most
cases (Fig. 5).

Estimates of variance structure varied considerably across systems (Table 3; Fig.
6). Lake Superior, which had the highest proportion of zero-catch net sets, had the
proportionally largest site-to-site variation \( \sigma_a^2 \) among all systems considered here. This
was also the only case of a variance component other than observational variability \( \sigma_o^2 \)
exceeding 50%. Site-to-site variability was also the largest variance component for
Saginaw Bay, although variability was partitioned much more equitably among variance
components for Saginaw Bay than for other systems. For all systems, the site-to-site
intercept random effect \( \sigma_y^2 \) exceeded the site-to-site trend variability \( \sigma_t^2 \) (Fig. 6).

Coherent temporal variability \( \sigma_b^2 \) was less than 1% of the total variation for Lake
Superior but ranged from roughly 10-20% for the other systems. For these systems, this
cohort 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 \( \sigma_c^2 \) 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., a large estimated
standard error). The data from Saginaw Bay include more routine site revisits and
ephemeral temporal variability was the second largest variance component for this data
set.
Appendix B

Observational variability was the proportionally largest variance component for both Oneida Lake and Lake Erie, comprising nearly 60% or more of the total variability and exceeded 40% of the variability for Lake Superior (Fig. 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.

Discussion

Count data are pervasive in ecological study and estimating variance components can provide insight into spatial and temporal dynamics. However, the statistical model used to estimate 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 Bennett 1996; Ver Hoef and Boveng 2007). The negative binomial mixed model we have presented here allows for estimating variance components for ecological count data without the need for data transformation. This model performed well on very complex and unbalanced data sets (i.e., an unbalanced number of observations per site, within years, and across years) that differed in the proportion of zero observations.

The proportion of the total variance contained within each of the spatial and temporal components varied among systems. This is not unexpected as we would predict that variance structures are 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. 1996; Larsen et al. 2004). The partitioning of variance in walleye catch data among the four Great Lakes basin systems examined here illustrates that population structure over space and time is variable among systems. Much of this variability among systems is likely due to system-specific abiotic and biotic characteristics. For freshwater fishes, we would expect that system-specific characteristics (e.g., lake morphometry, food web structure, and fishing pressure) would be important factors governing spatial and temporal population dynamics. System-specific variance components can have implications for efficiently monitoring population status and trends (see Urquhart et al. 1998). The need to efficiently monitor the status and trends of populations is critical because many wild populations continue to be exploited at high levels and changing ecological conditions, such as effects from the establishment of non-native species and climate change, continue to affect both aquatic and terrestrial ecosystems.

There are alternative approaches for modeling count data. Our approach involved estimation of a single negative binomial scale parameter for each data set we analyzed, implying 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 (in press) 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 started 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 in press). Likewise, the negative binomial parameter estimates,
generated as described here, could be subsequently input into standard generalized linear
model software, which would treat the scaling parameter as a known constant, to take
advantage of pre-existing software’s capabilities to produce various diagnostics for
evaluating model fit (Hilbe 2007).

We have provided a flexible framework for achieving the goal of partitioning
variance for 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 was most flexible in terms of model
parameterizations and most stable in terms of convergence. The program R (R
Development Core Team 2009) has libraries that contain functions that will estimate
negative binomial mixed models, a notable one being “glmmADMB” (https://r-forge.r-
project.org/projects/glmmadmb/). The glmmADMB function, as its name implies,
interacts with ADMB and uses ADMB-RE for estimating parameters. However,
programming directly within ADMB provides much more flexibility, including allowing for more control over model parameterization, the specification of derived quantities (e.g., \( \bar{\sigma}_t^2 \)), and the ability to include multiple random effects (in some R functions the number of random effects allowed when assuming the negative binomial distribution is 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 (the year covariate in our model) can help improve the model’s ability to converge. In addition, providing reasonable starting values, 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.
Detection and assessment of regime shifts is a rapidly growing ecological sub-
discipline (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”; Scheffer 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 in lakes. 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 variation (i.e., variance components
themselves), not just the total variance, will be responsive to severe large-scale
perturbation, 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 ecological studies.

Acknowledgements

We thank the U.S. Fish and Wildlife Service Great Lakes Restoration Act for
funding this work. Likewise, we acknowledge several individuals who have generously
provided long-term data, including Mike Seider, Dave Fielder, Lars Rudstam, and Chris
Vandergoot for providing the walleye gillnet data used here. We also thank Josh Schmidt
and Joe Witt for helpful suggestions on the presentation of this work. This paper is
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1 contribution number 201X-XX of the Quantitative Fisheries Center at Michigan State University. Use of trade names does not imply endorsement by the federal government.
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Appendix B


Appendix B

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Appendix B


Table 1. Minimum data requirements for estimating different variance components.

<table>
<thead>
<tr>
<th>Sampling requirements</th>
<th>Site-to-site variability ($\sigma_a^2$)</th>
<th>Site-to-site trend variability ($\sigma_t^2$)</th>
<th>Coherent temporal variability ($\sigma_b^2$)</th>
<th>Ephemeral temporal variability ($\sigma_c^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Multiple sites</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Multiple years</td>
<td>X¹</td>
<td>X¹</td>
<td>X¹</td>
<td>X¹</td>
</tr>
<tr>
<td>Some of the same sites revisited multiple years, with no within-year revisits</td>
<td>X²</td>
<td>X²</td>
<td>X²</td>
<td>X²</td>
</tr>
<tr>
<td>Some of the sites revisited within a year</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>

¹ only necessary if sites are never revisited within a year

² only necessary if sites are never sampled multiple years
Table 2. Summary information for walleye gillnet data sets.

<table>
<thead>
<tr>
<th>System</th>
<th>Year range</th>
<th>Total # of years of data</th>
<th>Total # of net sets</th>
<th>Total # of sites visited</th>
<th>Total # of zero catches</th>
<th>Maximum observed catch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Superior</td>
<td>1970-2008</td>
<td>37</td>
<td>233</td>
<td>12</td>
<td>79</td>
<td>197</td>
</tr>
<tr>
<td>Oneida</td>
<td>1958-2006</td>
<td>47</td>
<td>705</td>
<td>15</td>
<td>3</td>
<td>220</td>
</tr>
<tr>
<td>Saginaw Bay</td>
<td>1993-2008</td>
<td>16</td>
<td>264</td>
<td>10</td>
<td>12</td>
<td>86</td>
</tr>
<tr>
<td>Erie</td>
<td>1978-2008</td>
<td>27</td>
<td>451</td>
<td>119</td>
<td>1</td>
<td>493</td>
</tr>
</tbody>
</table>
Table 3. Estimated values for model parameters (and 1 SE) and calculated variance components for four systems. NE = not estimated.

No SE was reported for the derived quantities $\hat{\sigma}_t^2$ and $\hat{\sigma}_o^2$ (see Methods for details).

<table>
<thead>
<tr>
<th>System</th>
<th>Area / Survey</th>
<th>$\kappa$ (scaling param.)</th>
<th>$\nu$ (fixed int.)</th>
<th>$\lambda$ (fixed slope)</th>
<th>$\sigma_u^2$</th>
<th>$\sigma_t^2$</th>
<th>$\sigma_b^2$</th>
<th>$\sigma_c^2$</th>
<th>$\hat{\sigma}_t^2$</th>
<th>$\hat{\sigma}_o^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Superior</td>
<td>WI waters</td>
<td>0.875</td>
<td>1.125</td>
<td>0.017</td>
<td>6.326</td>
<td>8.13E-10</td>
<td>0.079</td>
<td>NE</td>
<td>1.00E-7</td>
<td>4.880</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.114)</td>
<td>(0.747)</td>
<td>(0.010)</td>
<td>(2.938)</td>
<td>(7.96E-7)</td>
<td>(0.080)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oneida</td>
<td>Oneida</td>
<td>2.100</td>
<td>3.033</td>
<td>-0.018</td>
<td>0.202</td>
<td>1.25E-4</td>
<td>0.143</td>
<td>NE</td>
<td>0.024</td>
<td>0.535</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.127)</td>
<td>(0.131)</td>
<td>(0.005)</td>
<td>(0.078)</td>
<td>(6.96E-5)</td>
<td>(0.038)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Huron</td>
<td>Saginaw</td>
<td>4.925</td>
<td>2.464</td>
<td>0.049</td>
<td>0.233</td>
<td>4.53E-3</td>
<td>0.232</td>
<td>0.265</td>
<td>0.096</td>
<td>0.327</td>
</tr>
<tr>
<td></td>
<td>Bay</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.974)</td>
<td>(0.206)</td>
<td>(0.037)</td>
<td>(0.119)</td>
<td>(2.98E-3)</td>
<td>(0.104)</td>
<td>(0.066)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Erie</td>
<td>OH waters</td>
<td>1.789</td>
<td>1.844</td>
<td>-0.045</td>
<td>0.143</td>
<td>6.74E-4</td>
<td>0.078</td>
<td>9.08E-9</td>
<td>0.049</td>
<td>0.573</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.142)</td>
<td>(0.107)</td>
<td>(0.011)</td>
<td>(0.080)</td>
<td>(5.18E-4)</td>
<td>(0.034)</td>
<td>(2.08E-5)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 1. Depiction of different variance components in the context of a count time series. Panel A illustrates spatial variation, as if this were the only source of variability, so that each of the three sample sites (represented by the dashed and solid lines) has different means but no temporal variability. Panel B illustrates adding coherent temporal variation to the spatial variation, and panel C adds to these sources ephemeral temporal variation where each site deviates independently of other sites in each year. Panel D illustrates adding slope variation, where each site has its own trend over time, to spatial variation. One could then add coherent and ephemeral variation in panel D (not shown).
Figure 2. Site-specific catch data (not catch per effort) over time for four fishery-independent surveys.
Figure 3. Observed vs. predicted frequencies of gillnet catches of walleye for four systems.
Figure 4. Anscombe residuals plots ($R_{ijk}^A$ vs. $\hat{\mu}_{ijk}$) based on fitting a negative binomial mixed model to gillnet catches of walleye for four systems.
Figure 5. Anscombe residuals normality diagnostic based on fitting a negative binomial mixed model to gillnet catches of walleye for four systems.
Figure 6. Estimated variance components for four fishery-independent surveys. $\sigma^2_a =$ site-to-site variability; $\sigma^2_t =$ site-to-site trend variability; $\sigma^2_b =$ coherent temporal variability; $\sigma^2_c =$ ephemeral temporal variability; $\hat{\sigma}^2_o =$ observational variability; NE = not estimated.
Appendix C

a. Superior

b. Observed vs. predicted frequencies of gillnet catches;

c. Anscombe residuals plots;

d. Normality diagnostic; and

e. Estimated variance components. NE = not estimable.
Appendix C

Appendix C2. a) Site-specific gillnet catch for walleye in Oneida Lake, NY; b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components. NE = not estimable.
Appendix C

a. Saginaw

Year


Observed Catch

0 20 40 60 80 100

b. Observed vs. Predicted frequencies of gillnet catches;

Catch

0 1-10 11-25 26-50 51-100 101-200 201-500 501-1000 1001-2500

Proportion

0.0 0.1 0.2 0.3 0.4 0.5 0.6

c. Anscombe residuals plots;

Residual

0 10 20

Predicted Catch

0 2 04 06 08 0

Residual

0.00 0.25 0.50 0.75 1.00

d. Normality diagnostic;

e. Estimated variance components.

Appendix C3. a) Site-specific gillnet catch for walleye in Saginaw Bay, Lake Huron; b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix C

Appendix C4. a) Site-specific gillnet catch for walleye in Les Cheneaux Islands, Lake Huron; b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix C

Appendix C5. a) Site-specific gillnet catch for walleye in Lake Huron (Grand Bend); b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix C

Appendix C6. a) Site-specific gillnet catch for walleye in Ohio waters of Lake Erie; b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix C. a) Site-specific gillnet catch for walleye in NY waters of Lake Erie (1981-1992); b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix C

Appendix C. a) Site-specific gillnet catch for walleye in NY waters of Lake Erie (1993-2009); b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix C

Appendix C9. a) Site-specific gillnet catch for walleye in the eastern basin of Lake Ontario; b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix C

Appendix C10. a) Site-specific gillnet catch for walleye in the Bay of Quinte, Lake Ontario; b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components. 0-CPE values assumed to have effort = 1.
Appendix C

a. Bay of Quinte

b. Observed vs. predicted frequencies of gillnet catches;
c. Anscombe residuals plots;
d. Normality diagnostic; and e) estimated variance components. 0-CPE values assumed to have effort approximately = surrounding values.

Appendix C11.
Appendix D

Appendix D1. a) Site-specific gillnet catch for yellow perch in Wisconsin waters of Lake Superior; b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix D2. a) Site-specific gillnet catch for yellow perch in Oneida Lake; b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix D

Appendix D3. a) Site-specific gillnet catch for yellow perch in Saginaw Bay, Lake Huron; b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix D

Appendix D4. a) Site-specific gillnet catch for yellow perch in Les Cheneaux Islands, Lake Huron; b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix D

Appendix D5. a) Site-specific gillnet catch for yellow perch in Lake Huron (Southampton); b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix D

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Appendix D6. a) Site-specific gillnet catch for yellow perch in Lake Huron (Grand Bend); b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix D

Appendix D7. a) Site-specific gillnet catch for yellow perch in Lake Huron (Clapperton); b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix D

Appendix D8. a) Site-specific gillnet catch for yellow perch in NY waters of Lake Erie (1981-1992); b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix D

Appendix D9. a) Site-specific gillnet catch for yellow perch in NY waters of Lake Erie (1993-2009); b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix D10. a) Site-specific gillnet catch for yellow perch in the eastern basin of Lake Ontario; b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components. 0-CPE values assumed to have effort = 1.
Appendix D11. a) Site-specific gillnet catch for yellow perch in the eastern basin of Lake Ontario; b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components. 0-CPE values assumed to have effort = 0.5.
Appendix D

Appendix D12. a) Site-specific gillnet catch for yellow perch in the Bay of Quinte, Lake Ontario; b) observed vs. predicted frequencies of gillnet catches; c) Anscombe residuals plots; d) normality diagnostic; and e) estimated variance components.
Appendix E1. Perturbation Analysis.

Objective 2: Determine whether variance structure itself is responsive to large-scale ecological perturbations.

Methods

Datasets. – We focused our perturbation analysis on Oneida Lake (walleye and yellow perch); the Bay of Quinte, Lake Ontario (walleye and yellow perch); and Ohio waters of Lake Erie (walleye only) in an effort to evaluate whether the variance structure from percid fishery-independent surveys were responsive to large-scale perturbations. We focused on these three systems for two primary reasons (1) they support regionally important percid fisheries and (2) we were able to identify time periods that were classified as ‘before’ zebra mussel (ZM) *Dreissena polymorpha* invasion and ‘after’ zebra mussel invasion (Koops et al. 2006; Irwin et al. accepted; Wagner et al. 2009).

Before – after zebra mussel analysis. – To assess whether or not the structure of variability changed between the time period before ZM invasion compared to after ZM invasion, each time series was split into a ‘before’ and ‘after’ ZM invasion periods. The before – after time periods for Oneida Lake were 1958 – 1991 and 1991 – 2006; for the Bay of Quinte before – after time periods were 1972 – 1994 and 1995 – 2008; and for Lake Erie the before – after time periods were 1978 – 1995 and 1996 – 2008. Variance components were then estimated for each time period separately using the negative binomial mixed model regression framework (Appendix B). The difference in the proportion of variability before and after for each system were then visually assessed for patterns.

In addition to examining whether or not variance structures differed between time periods, we plotted coherent temporal best linear unbiased predictors (BLUPs) over time for the entire time series for each system (i.e., in this case, we did not break the time series into before and after invasion periods prior to parameter estimation). Because we were interested in assessing the effects of a system-wide disturbance, we examined whether or not the coherent temporal BLUP could be useful as an indicator, which integrated across all sites within a given year, to detect temporal, system-wide, patterns in percid dynamics. A loess curve was fitted to each time series to aid visualization of patterns and interpretation.
Appendix E

Results

For walleye, there typically were fewer net sets that contained large numbers of fish in the period after ZM invasion compared to before the invasion, although the actual magnitude varied among systems. In addition, there were shifts in the structure of variability between the period before and after ZM invasion. For yellow perch, a reduction in large catches was less apparent, however, there were variance structure changes between the two periods (Figures E1 -E6). To assist visualizing the differences in variance structures before compared to after ZM invasion, we plotted the differences (as After – Before) for each variance component. Interestingly, in three out of the four analyses the proportion of the total variance attributed to site-to-site variability and coherent temporal variability decreased in the time period after ZM invasion, and in all analyses the proportion of variability due to observational error increased (Figure E7). Variance estimates for all analyses are found in Tables E1 – E3. Plots of the coherent temporal BLUPs over time tended to track system – level changes in perch dynamics (Figures E8 and E9). For example, the decline in average walleye catch observed in the mid-1990s in Oneida Lake is apparent when examining the coherent temporal BLUPs.

Discussion

For 4 out of 5 analyses, total variability in catch per effort (CPE) was lower in the period after zebra mussel invasion (Oneida Lake walleye, 22% lower; Oneida Lake yellow perch, 2% lower; Bay of Quinte walleye, 32% lower; Bay of Quinte yellow perch, 38% lower; Lake Erie walleye, 4% higher). Although total variability declined in most of the analyses, the proportion of total variance shifted between time periods (the interpretation of the before-after comparisons in variance component proportions (Figure E7) should be done with caution for trend variation and ephemeral temporal variation because these variances were often poorly estimated, being estimated near zero and highly uncertain. Even so, difference in variance structures suggests that the spatial and temporal dynamics of these populations has changed. Also, from a monitoring perspective, a decrease in total variance may not translate directly to an increased ability to assess population status and detect temporal trends: it is not only the total variance that is important, but rather how the total variance is partitioned over space and time. Because site-to-site variability in perch populations is important to understand the ecological processes governing their spatial distributions and is important from a monitoring perspective, we further
investigated the site-to-site variability in Oneida Lake. We focused on Oneida Lake because the same 15 sites were sampled throughout the time series. In Oneida Lake, the site-to-site variance for walleye and yellow perch declined (both in magnitude and proportion of the total) after ZM invasion. To investigate how specific sites behaved between the two ZM periods, we plotted the site BLUPs for each period and species (Figure E10). The lower site-to-site variability is readily apparent in these plots. In addition, it appears that some sites that caught higher than average fish in the period before ZM invasion were sites with lower than average catch in the period after ZM invasion, and the opposite was also true. We hypothesize that this ‘shifting’ of some sites in average catch may be due to the abiotic conditions at each site, possible influenced by site depth. Future research could focus on distributional shifts of percids along depth gradients in response to ZM invasions.

Plotting coherent temporal variance BLUPs provided a simple approach to examine among-year dynamics in CPE data. The BLUP plots provide a visual assessment of what years were below or above average CPE for the time series, in addition to identify temporal patterns. These annual BLUPs could be modeled as a function of annual covariates (e.g., climate variables) to provide additional insight into system-wide dynamics.

References


Table E1. Estimated values for model parameters (and 1 SE) and calculated variance components for before (1958-1991) and after (1992-2006) zebra mussel establishment for both walleye and yellow perch gillnet time series from Oneida Lake, NY. NE = not estimated. No SE was reported for the derived quantities \( \hat{\sigma}_i^2 \) and \( \hat{\sigma}_o^2 \).

<table>
<thead>
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<th>( \nu )</th>
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<th>( \sigma_c^2 )</th>
<th>( \sigma_{	ext{site-to-site var.}}^2 )</th>
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<tr>
<td>Before</td>
<td>Walleye</td>
<td>2.092 (0.150)</td>
<td>3.221 (0.154)</td>
<td>-0.009 (0.007)</td>
<td>0.291 (0.112)</td>
<td>9.92E-5 (9.68E-5)</td>
<td>0.101 (0.036)</td>
<td>NE (0.10)</td>
<td>0.527 (0.10)</td>
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<tr>
<td>After</td>
<td>Walleye</td>
<td>2.454 (0.318)</td>
<td>2.603 (0.126)</td>
<td>0.052 (0.027)</td>
<td>0.089 (0.047)</td>
<td>2.20E-3 (1.61E-3)</td>
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<tr>
<td>Before</td>
<td>Yellow perch</td>
<td>2.146 (0.146)</td>
<td>4.285 (0.205)</td>
<td>-0.010 (0.007)</td>
<td>0.573 (0.215)</td>
<td>1.15E-4 (1.09E-4)</td>
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<td>After</td>
<td>Yellow perch</td>
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<td>2.06E-3 (1.88E-3)</td>
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<td>NE (0.036)</td>
<td>0.586 (0.048)</td>
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Table E2. Estimated values for model parameters (and 1 SE) and calculated variance components for before (1972-1994) and after (1995-2008) zebra mussel establishment for both walleye and yellow perch gillnet time series from the Bay of Quinte, Lake Ontario. No SE was reported for the derived quantities $\hat{\sigma}_r^2$ and $\hat{\sigma}_o^2$.

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<th>$\lambda$</th>
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<td>(fixed slope)</td>
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<td>(ephemeral temporal var.)</td>
<td>(site-to-site trend var.)</td>
<td>(obs. var.)</td>
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<tr>
<td>Before</td>
<td>Walleye</td>
<td>1.731 (0.170)</td>
<td>1.152 (0.326)</td>
<td>0.178 (0.051)</td>
<td>0.149 (0.169)</td>
<td>1.25E-2 (9.79E-3)</td>
<td>0.714 (0.298)</td>
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<td>Walleye</td>
<td>1.262 (0.156)</td>
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<td>0.762 (0.653)</td>
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<td>0.038 (0.060)</td>
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<td>1.40E-9</td>
<td>1.159</td>
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<tr>
<td>Before</td>
<td>Yellow perch</td>
<td>1.717 (0.119)</td>
<td>4.156 (0.149)</td>
<td>0.026 (0.021)</td>
<td>0.053 (0.054)</td>
<td>1.41E-3 (1.22E-3)</td>
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<td>0.094</td>
<td>0.062</td>
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<tr>
<td>After</td>
<td>Yellow perch</td>
<td>2.047 (0.188)</td>
<td>4.770 (0.068)</td>
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<td>0.002 (0.062)</td>
<td>0.088</td>
<td>0.009</td>
<td>0.497</td>
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Table E3. Estimated values for model parameters (and 1 SE) and calculated variance components for before (1978-1995) and after (1996-2008) zebra mussel establishment for both walleye and yellow perch gillnet time series from the Ohio waters of Lake Erie. No SE was reported for the derived quantities $\hat{\sigma}_i^2$ and $\hat{\sigma}_o^2$.

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<th>$\lambda$ (fixed slope)</th>
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<th>$\sigma_i^2$</th>
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<th>$\sigma_t^2$ (coherent temporal var.)</th>
<th>$\sigma_o^2$ (site-to-site trend var.)</th>
<th>$\hat{\sigma}_i^2$ (obs. var.)</th>
<th>$\hat{\sigma}_o^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Before</td>
<td>Walleye</td>
<td>2.303 (0.443)</td>
<td>2.080 (0.194)</td>
<td>-0.042 (0.025)</td>
<td>0.296 (0.251)</td>
<td>2.61E-11</td>
<td>0.107 (0.061)</td>
<td>3.32E-7 (2.75E-4)</td>
<td>7.07E-10 (8.50E-7)</td>
<td>0.0443</td>
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<tr>
<td>After</td>
<td>Walleye</td>
<td>1.639 (0.160)</td>
<td>1.463 (0.105)</td>
<td>-0.047 (0.027)</td>
<td>0.142 (0.073)</td>
<td>3.84E-3</td>
<td>0.058 (0.037)</td>
<td>2.51E-11 (8.50E-7)</td>
<td>0.054 (8.50E-7)</td>
<td>0.626</td>
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</table>
Figure E1. Observed and predicted total catch for Oneida Lake before (1958 – 1991) and after (1992 – 2006) zebra mussel invasion.
**Figure E2.** Proportion of total variance attributed to different spatial and temporal components for Oneida Lake before (1958 – 1991) and after (1992 – 2006) zebra mussel invasion (see Table 1 for definition of variance symbols).
Figure E3. Observed and predicted total catch for The Bay of Quinte before (1972 – 1994) and after (1995 – 2008) zebra mussel invasion.
Figure E4. Proportion of total variance attributed to different spatial and temporal components for The Bay of Quinte before (1972 – 1994) and after (1995 – 2008) zebra mussel invasion (see Table 1 for definition of variance symbols).
Figure E5. Observed and predicted total catch for the Ohio waters of Lake Erie before (1978 – 1995) and after (1996 – 2008) zebra mussel invasion.
Figure E6. Proportion of total variance attributed to different spatial and temporal components for the Ohio waters of Lake Erie before (1978 – 1995) and after (1996 – 2008) zebra mussel invasion (see Table 1 for definition of variance symbols).
Appendix E

Figure E7. Change in the proportion of total variance attributed to spatial and temporal components between time periods before and after zebra mussel invasion (see Table 1 for definition of variance symbols).
Figure E8. Coherent temporal best linear unbiased predictors (BLUPs) for walleye versus year.
Figure E9. Coherent temporal best linear unbiased predictors (BLUPs) for yellow perch versus year.
Figure E10. Site best linear unbiased predictors (BLUPs) for Oneida Lake percid catch during the periods before (1958 – 1991) and after (1992 – 2006) zebra mussel establishment. Error bars are ± one standard error. Lines connect sites from Before to After time periods.
Appendix F. Power analysis.

Objective 3: Develop recommendations for the design of monitoring programs and analysis of resulting data to support management of important percid fisheries within the Great Lakes region.

Methods

Datasets. – We used variance estimates from the Ohio waters of Lake Erie and Oneida Lake walleye fishery-independent gillnet surveys to evaluate the statistical power to detect temporal trends under different scenarios (see Power analysis scenarios). Lake Erie and Oneida Lake were chosen because they represent important walleye fisheries in the Great Lakes basin. Although our power analysis focuses on these two systems, the methods we have developed can be used on any of the fishery-independent survey presented in this report, assuming variance components were estimable.

Variance estimation. – Estimation of variance components for the Ohio waters of Lake Erie and Oneida Lake was performed using the negative binomial mixed model regression framework (Appendix B).

Power analysis. – We used a simulation approach to evaluate the statistical power to detect temporal trends across several different scenarios (see Power analysis scenarios). For each scenario, 250 simulations were performed. For each simulation, a 30-year times series of catch data were simulated for 1,000 sites (an assumed total population of sites from which to sample from) using the estimated spatial and temporal components of variation. A population-average temporal trend \( \lambda \) was then specified; however, each individual site could deviate from this population-average trend. The magnitude of the deviation was dependent on the magnitude of trend variation \( \sigma^2 \) used in the simulation. Each year, catch data were “sampled” from the population of sites under different user-specified scenarios (see Power analysis scenarios). During each simulation, every 5 years of the sampling process a negative binomial mixed model (see Appendix B) was used to test the null hypothesis that \( \hat{\lambda} = 0 \), and the test statistic was calculated and compared to a critical value \( (\alpha = 0.05) \). Because the data generated depict a
situation where we know the null hypothesis is false (i.e., $\hat{\lambda} \neq 0$), power was estimated as the percentage of simulations (out of 250) that rejected the null hypothesis (Figure F1). Thus, there were three possible outcomes: (1) rejecting the null hypotheses because a trend was detected in the correct direction (i.e., statistical power); (2) failure to reject the null hypothesis when a trend was in fact present; and (3) rejecting the null hypothesis because a trend was detected in the incorrect direction, which we term $\gamma$-error (Forney et al. 1991). Thus, a $\gamma$-error would occur if, for example, there was a negative trend imposed in the simulated abundance over time, but estimates from monitoring observations suggested a significant positive trend in abundance.

**Power analysis scenarios.** – We investigated the extent to which the following factors affected the ability to detect a temporal trend: trend magnitude (3% or 10% per year decrease), the number of sites within a lake sampled each year (5, 10, or 30 sites), variance structure, and survey design. The three survey designs we investigated were as follows (also see Figure F2). Design 1 was a fixed site design where sites were randomly chosen the first year and then the same sites were sampled each year thereafter (resulting in a single panel). Design 2 consisted of new sites randomly sampled each year (i.e., there was a new panel each year and therefore the number of panels equals the number of years). Design 3 was an augmented serially alternating design, which consisted of both rotating panels and a common panel across years. Rotating panels consisted of multiple sites that were sampled on a rotating basis (i.e., if there were 2 rotating panels called panels A and B, sites within panel A were sampled on year one and sites within panel B sampled on year 2; sites within panel A were then revisited and sampled on year 3, and so on). In addition to the sites contained in the rotating panels, each year a common panel was also sampled. The sites contained in the common panel were sampled each year (Figure F2). The complete set of scenarios investigated is summarized in Table F1. In addition, because of the difficulty in estimating the ephemeral temporal variances for most datasets, we performed simulations using the Lake Erie variance estimates but increased the proportion of the total variance contributed by ephemeral temporal variation. Specifically, we investigated the effects of increasing ephemeral temporal variance to 20% and 60% of the total variation on the power to detect trends. This also increased the contrast among the variance structures imposed on the simulations.
Appendix F

Results

We investigated the effects of variance structures, trend magnitude, sampling effort (i.e., number of sites samples per year and the number of years sampled), and monitoring design on the statistical power to detect temporal trends in fishery-independent catch per effort data for walleye. Combinations of variance structure, trend magnitude, and number of sites sampled per year resulted in 48 potential scenarios (see Table F1). Of these, four were not evaluated (30 sites, design 2) due to time constraints and two failed to run to completion (Table F1). As expected, however, the power to detect trends increased with increasing trend magnitude, sampling duration, and the number of sites sampled each year. These patterns were consistent across the Lake Erie and Oneida Lake analyses (Figures F3 – F14). The number of years required to sample in order to detect a 3% per year decline with 80% power ranged from approximately 10 to 17 years. The number of years required to sample in order to detect a 10% per year decline with 80% power ranged from approximately 5 to 8 years. The variability in the number of years taken to detect a given trend was primarily dependent on the number of sites sampled each year (Figures F3 – F14).

Effect of monitoring design. – In most cases, the effect of a monitoring design was less important in terms of increasing statistical power compared to the effects of trend magnitude, the number of sites sampled each year, or sampling duration. A notable exception was for Oneida Lake when sampling only 5 sites per year. Under this scenario, it took approximately 4 years longer to detect a 3% per year decrease using Design 2 compared to Designs 1 and 3. However, the difference between designs diminished as the number of sites sampled per year increased and as the number of years sampled increased (Figures F9 – F11). The general pattern was also apparent for Oneida Lake under the 10% per year decline scenario; however, the pattern was less pronounced (Figures F12 – F14).

γ-errors. – In all of the simulations, a negative trend was added to the simulated time series. As a result, a γ-error was committed if a significant positive trend was detected. The probability of committing a γ-error was greatest over relatively short sampling durations (e.g., 5 – 10 years), decreased over time, and was dependent on trend magnitude (Figures F3 – F14). For a 3% per year decrease, statistical power to detect trends over 5 – 10 years was usually < 0.8, however γ-errors ranged from approximately 20% to nearly 40%. Interestingly, under a 3% trend scenario,
as power increased with increasing number of sites sampled each year, so did the probability of committing a γ-error (Figures F3 – F5 and F9 – F11). Under a scenario with a 10% trend, the probability of committing a γ-error was low after 5 years of sampling (approximately 10 – 18%) and was reduced to near zero after 10 years.

_Ephemeral temporal variation._ – Because of difficulties estimating the ephemeral temporal variance component, largely due to a lack of within-year site revisits, some of the simulations did not fully contain this source of variation. To investigate the influence of ephemeral temporal variation on trend detection, we re-ran simulations using the variance structure for Lake Erie, under a -3% per year trend magnitude and 5 or 10 sites samples per year scenarios, with ephemeral temporal variation increased and set to either 20% or 60% of the total variance (Table F1). Results from these simulations demonstrated negligible effects on the statistical power to detect trends or on γ-error rates (Figures F15 – F18).

**Discussion**

The number of years necessary to detect temporal trends with a power of 0.8 ranged from 5 to approximately 15 years. However, as expected, power was dependent on trend magnitude, the number of sites sampled each year, and number of years sampled. Previous analyses have shown similar response curves for a variety of indicators (Urquhart et al. 1998; Wagner et al. 2007; Wagner et al. 2009; Dauwalter et al. 2010). Overall, there were not large differences in the statistical power to detect temporal trends for Lake Erie compared to Oneida Lake, for a given sampling scenario. Although we focused our analyses on these two lakes because of the importance of their walleye fisheries, both lakes had relatively similar variance structures, and thus we would predict that statistical power would be similar, for similar monitoring scenarios, in these two systems.

Although statistical power was similar between lakes, the monitoring design used did influence power; however, the effect of the design was most apparent when few (i.e., five) sites were sampled each year. Specifically, Design 2 (a new panel each year) was consistently outperformed by Designs 1 (a single fixed panel) and 3 (an augmented serially alternating design), which performed similarly. The poorer performance of Design 2 compared to Designs 1 and 3 was apparent for both a 3% and 10% trend magnitude, but was most pronounced when attempting to detect relatively small trends (i.e., 3% per year decline). These results are
consistent with Urquhart et al. (1998), who also found Designs 1 and 3 performed similarly for trend detection, whereas, Design 2 had comparatively lower power.

From a management perspective it may be important to know not only if a population is changing monotonically over time, but if a trend in the correct direction can be detected. If this is the case, then quantifying the probability of committing a γ-error will be important. Our results suggest that if management decisions occur over relatively short time-frames (e.g., 5 years) that there can be a relatively high (e.g., between 10% - 40% in our analysis) probability of committing a γ-error (i.e., the population is actually on a long-term decreasing trend, but the short term monitoring suggested that the population was increasing). The importance of the probability of committing a γ-error will be case specific, and should be evaluated relative to management objectives and other risks to the fishery. However, it is also important to note that specific aspects of a monitoring design can affect the probability of accepting a false alternative hypothesis.

The estimated variance structures of Lake Erie and Oneida Lake appear to not differ sufficiently to result in dramatic differences in the power to detect trends between the trend magnitudes considered here. However, other research (e.g., Urquhart et al. 1998; Wagner et al. 2007) has demonstrated that the influence of specific variance components on trend detection can be minimized by changing aspects of the monitoring design and others cannot. For example, the effect of coherent temporal variation on trend detection cannot be reduced by changing aspects of the sampling design; only increasing sampling duration will increase power (Urquhart et al. 1998). To further examine the potential effect of ephemeral temporal variation on trend detection, we set this source to 20% or 60% of the total variation, using all other variance sources at their estimated values. We did not find a noticeable effect of increasing ephemeral temporal variability on trend detection, although there was some evidence that increasing this source of variation led to a slight increase in the number of years required to detect a trend with 80% power. Additional simulations should be performed to further evaluate the effect of different sources of variation on trend detection for Great Lakes fisheries and what, if any, sampling designs provide the greatest power to detect trends under those scenarios. This is important because changes to lake ecosystems could alter the spatial and temporal variances of fish populations (see Appendix E) and monitoring programs may need to be adaptive in order to maintain sufficient statistical power to achieve management objectives.
A larger number of alternative scenarios could be constructed using different combinations of various sampling designs, the numbers of sites and years sampled (i.e., allocation of sampling effort), levels of trend magnitude, and different variance structures. The simulations reported here are highly computationally expensive (i.e., they sometimes take a very long time to run). Preliminary estimates suggested that some possible scenarios would take on the order of months for the simulations to complete. Thus practical considerations must be made when performing this type of power analysis. However, during this project, we began conducting simulations on Michigan State University’s High Performance Computing Cluster (HPCC). While this did not readily reduce the amount of time that was required to complete an individual simulation, it did allow for a much larger number of simulations to be run (across multiple computing processors). Future evaluations of the sensitivity of alternative sampling designs to variance structures would benefit from a priori identification of possible implementable sampling designs that are directly linked to important management objectives.
Appendix F

References


Table F1. Summary of power analysis scenarios evaluated using variance structures estimated from Oneida Lake (O) and Lake Erie (E). A letter representing each lake (O or E) designates that a simulation was performed for a given scenario. Trend magnitudes were a 3 or a 10% year decline, the number of sites sampled per year were 5, 10, or 30. Design 1 was a fixed site design (i.e., a single panel with the same sites sampled each year). Design 2 had new sites randomly sampled each year (i.e., a new panel each year) with no designed repeat visits to any sites. Design 3 was an augmented serially alternating design. When 5 sites were sampled per year, 3 were in a rotating panel each year and 2 were in the common panel; for 10 sites sampled per year, 5 sites were in a rotating panel each year and 5 sites were in the common panel; for 30 sites sampled each year, 25 sites were in a rotating panel each year and 5 sites were in a common panel.

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<tr>
<td></td>
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<td>10</td>
<td>30</td>
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<tr>
<td>Design 2</td>
<td>O, E</td>
<td>O, E</td>
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* Simulation failed to run.

** Simulations not performed.

† Simulations performed with ephemeral temporal variation set at 20% and 60% of the total variation

‡ design 1, site/year = 5 and ephemeral temporal set to 60%, simulation failed to run.
Figure F1. Schematic detailing the simulation approach used to evaluate the statistical power to detect temporal trends in catch per effort data under different sampling scenarios (see Methods for additional details).
### Appendix F

#### Figure F2.

Schematic of fishery independent survey designs evaluated for monitoring percids in the Great Lakes basin. Schematic adapted from Urquhart et al. (1998).

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<th>Design 2</th>
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<td>Design 3</td>
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</table>

Figure F2. Schematic of fishery independent survey designs evaluated for monitoring percids in the Great Lakes basin. Schematic adapted from Urquhart et al. (1998).
**Figure F3.** Power and $\gamma$-error curves for detecting temporal trends in catch per effort of walleye caught in annual gillnet surveys in Lake Erie. Power and $\gamma$-error were evaluated for three sample designs (see Table F1 and Figure F2 for details), with a trend magnitude set at a 3% per year decline and 5 sites sampled each year.
Figure F4. Power and $\gamma$-error curves for detecting temporal trends in catch per effort of walleye caught in annual gillnet surveys in Lake Erie. Power and $\gamma$-error were evaluated for three sample designs (see Table F1 and Figure F2 for details), with a trend magnitude set at a 3% per year decline and 10 sites sampled each year.
**Figure F5.** Power and γ-error curves for detecting temporal trends in catch per effort of walleye caught in annual gillnet surveys in Lake Erie. Power and γ-error were evaluated for two sample designs (see Table F1 and Figure F2 for details), with a trend magnitude set at a 3% per year decline and 30 sites sampled each year.
Figure F6. Power and γ-error curves for detecting temporal trends in catch per effort of walleye caught in annual gillnet surveys in Lake Erie. Power and γ-error were evaluated for three sample designs (see Table F1 and Figure F2 for details), with a trend magnitude set at a 10% per year decline and 5 sites sampled each year.
Figure F7. Power and γ-error curves for detecting temporal trends in catch per effort of walleye caught in annual gillnet surveys in Lake Erie. Power and γ-error were evaluated for three sample designs (see Table F1 and Figure F2 for details), with a trend magnitude set at a 10% per year decline and 10 sites sampled each year.
Figure F8. Power and γ-error curves for detecting temporal trends in catch per effort of walleye caught in annual gillnet surveys in Lake Erie. Power and γ-error were evaluated for two sample designs (see Table F1 and Figure F2 for details), with a trend magnitude set at a 10% per year decline and 30 sites sampled each year.
Figure F9. Power and γ-error curves for detecting temporal trends in catch per effort of walleye caught in annual gillnet surveys in Oneida Lake. Power and γ-error were evaluated for three sample designs (see Table F1 and Figure F2 for details), with a trend magnitude set at a 3% per year decline and 5 sites sampled each year.
Figure F10. Power and γ-error curves for detecting temporal trends in catch per effort of walleye caught in annual gillnet surveys in Oneida Lake. Power and γ-error were evaluated for three sample designs (see Table F1 and Figure F2 for details), with a trend magnitude set at a 3% per year decline and 10 sites sampled each year.
**Figure F11.** Power and γ-error curves for detecting temporal trends in catch per effort of walleye caught in annual gillnet surveys in Oneida Lake. Power and γ-error were evaluated for two sample designs (see Table F1 and Figure F2 for details), with a trend magnitude set at a 3% per year decline and 30 sites sampled each year.
Figure F12. Power and γ-error curves for detecting temporal trends in catch per effort of walleye caught in annual gillnet surveys in Oneida Lake. Power and γ-error were evaluated for three sample designs (see Table F1 and Figure F2 for details), with a trend magnitude set at a 10% per year decline and 5 sites sampled each year.
Figure F13. Power and $\gamma$-error curves for detecting temporal trends in catch per effort of walleye caught in annual gillnet surveys in Oneida Lake. Power and $\gamma$-error were evaluated for three sample designs (see Table F1 and Figure F2 for details), with a trend magnitude set at a 10% per year decline and 10 sites sampled each year.
Figure F14. Power and γ-error curves for detecting temporal trends in catch per effort of walleye caught in annual gillnet surveys in Oneida Lake. Power and γ-error were evaluated for two sample designs (see Table F1 and Figure F2 for details), with a trend magnitude set at a 10% per year decline and 30 sites sampled each year.
**Figure F15.** Power and y-error curves for detecting temporal trends in catch per effort of walleye caught in annual gillnet surveys in Lake Erie. Power and y-error were evaluated for two sample designs (see Table F1 and Figure F2 for details), with a trend magnitude set at a 3% per year decline, 5 sites sampled each year, and ephemeral temporal variation set to 20% of the total.
Figure F16. Power and \( \gamma \)‐error curves for detecting temporal trends in catch per effort of walleye caught in annual gillnet surveys in Lake Erie. Power and \( \gamma \)‐error were evaluated for one sample designs (see Table F1 and Figure F2 for details), with a trend magnitude set at a 3\% per year decline, 5 sites sampled each year, and ephemeral temporal variation set to 60\% of the total.
Figure F17. Power and y-error curves for detecting temporal trends in catch per effort of walleye caught in annual gillnet surveys in Lake Erie. Power and y-error were evaluated for two sample designs (see Table F1 and Figure F2 for details), with a trend magnitude set at a 3% per year decline, 10 sites sampled each year, and ephemeral temporal variation set to 20% of the total.
Figure F18. Power and γ-error curves for detecting temporal trends in catch per effort of walleye caught in annual gillnet surveys in Lake Erie. Power and γ-error were evaluated for two sample designs (see Table F1 and Figure F2 for details), with a trend magnitude set at a 3% per year decline, 10 sites sampled each year, and ephemeral temporal variation set to 60% of the total.

Title: Spatial and Temporal Variation in Great Lakes Percid Catch-Per-Effort Data

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Abstract:

Fishery-independent surveys are widely used to collect data on yellow perch and walleye across the Great Lakes basin. Although used to fulfill many objectives, one of the most common uses of survey data is to infer changes in relative abundance over time, based on indices such as catch per effort (CPE). However, our ability to detect changes in CPE is reduced by the large variability inherent in percid CPE time series. Partitioning total variability into multiple spatial and temporal sources (i.e., variance components) is a powerful approach to accommodate variable time series data and for elucidating population trends and refining monitoring and assessment programs. Furthermore, variability itself may be a useful indicator of large-scale ecological perturbations. We are analyzing CPE time series from multiple percid populations using hierarchical statistical models to quantify the spatial and temporal variability across the Great Lakes basin. We will discuss the results from these models in terms of (1) similarities and differences in variance components across Great Lakes, (2) the implications for monitoring programs, and (3) the usefulness of individual variance components as indicators of ecological change.
Appendix G2. Abstract for 2011 World Recreational Fishing Conference, Berlin, Germany

The Role of Variance Components and Survey Design in Detecting Trends in Recreational Fisheries Monitoring Data

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High levels of resource exploitation and changing ecological conditions, such as effects from the establishment of non-native species and climate change, emphasize a need to efficiently monitor the status and trends of fish populations. Fishery-independent surveys are one source of this critical information. In the Laurentian Great Lakes basin such surveys are used to monitor percid stocks, which support some of the words largest recreational fisheries. These surveys commonly sample a network of sites within or across lakes over time. Thus, statistical power of surveys depends both on how variation in the target population is structured and how well the survey samples across sources of variability. We developed negative binomial mixed models to decompose the total variation in percid fishery-independent surveys in the Laurentian Great Lakes basin into spatial and temporal components, and used the resulting variance estimates to evaluate potential survey designs. The structure of variation in percid populations varied across the Great Lakes basin, with some among-lake differences consistent with existing hypotheses of how local and regional abiotic factors structure fish populations. We will present results from simulations of different sampling designs employed on populations with different variance structures. These results show how statistical power to detect trends relates to both variance structure and survey design.
Appendix G3. Abstract for 2011 American Fisheries Society Meeting, Seattle, WA.

Developing Negative Binomial Mixed Models to Partition Variance in Fishery-Independent Survey Data
Irwin, B. J., T. Wagner, W. Liu, J. R. Bence, and D. B. Hayes

Partitioning total variability into multiple temporal and spatial sources (i.e., variance components) is a powerful approach to accommodate complex data structures. For example, an environmental state variable may vary among repeated samples from a single site, from site-to-site within a lake, from lake-to-lake, and over time. Models for estimating variance components have been applied to a wide variety of aquatic indices including water chemistry variables, measurements of species richness, stream habitat characteristics, metrics of fish growth, and catch-per-unit effort data. To date, most variance-components frameworks have been based on linear models that assume normally distributed error structures. When these models are applied to count data, the response variable is commonly transformed (usually using a logarithmic transformation) prior to fitting the model in an attempt to accommodate the normality and homogeneity of variance assumptions. Assuming a normal distribution for observations of fish abundance is often not ideal because these counts are typically non-negative integers with high variances and low means, not to mention other issues that arise when log-transforming data such as how to treat zero observations during the analysis. The negative binomial distribution represents an alternative to log-transformation (e.g., an alternative assumption about the mean-variance relationship) that can be applied to discrete count data; however, the partitioning of variance in this context is less straightforward than for generalized linear mixed models that assume normality. We developed a method of estimating variance components using negative binomial mixed models. We applied these models to count data generated by multiple fishery-independent surveys of percids from across the Great Lakes basin. These surveys varied in overall sampling intensity, general magnitude of the catch, and in the proportion of zero catches. Even so, negative binomial models produced reasonable approximation to the count data. Results show that spatial and temporal partitioning of variability in survey catch, adjusted for effort, differed among the lakes, and this has an influence on what survey design will best achieve different objectives.
Appendix H. Footnotes.

1. We had to make some assumptions because effort information was not retained in the summary data used for Lake Ontario (four data series). However, we did have access to both catch and catch-per-effort (CPE) indices. We were able to extrapolate effort from these two sources of information so long as CPE was greater than zero. In the cases where CPE equaled zero, we made assumptions to assign values to the otherwise missing effort. For the walleye data from the eastern basin of Lake Ontario, we assumed missing effort values were equal to 1 (approximately the average unit for all non-zero values). We made the same assumption for yellow perch in this system but, in this case, the average value used was 0.5. For walleye in the Bay of Quinte, we assigned effort value based on other observations from around that sampling year. For yellow perch in the bay of Quinte, we used effort equal to 1 for the single missing value. For this data set, the effort assumption is likely of no consequence because zero-CPE observations were rare (1 occurrence in the entire data series). However, parameter estimates for the other Ontario data should be treated with more caution because of the higher frequency of missing effort values. Based on preliminary sensitivity analyses, the assumed effort value (e.g. 0.5 or 1) did not have a large effect on the model’s ability to approximate the number of zero observations in the data set (Appendices C10-C11, D10-D11).