UNDERSTANDING THE ROLE OF VARIABILITY IN FISH POPULATION AND COMMUNITY RESPONSE TO CHANGING ENVIRONMENTAL CONDITIONS

by

TIFFANY VIDAL

(Under the Direction of Brian Irwin)

ABSTRACT

Understanding how populations, and the ecosystems of which they are a part, respond to fluctuations in the environment is paramount for conservation, sustainable management of natural resources, and perpetuation of ecosystem function. In this dissertation, I evaluated the role of source components of variability as statistical indicators of large-scale ecological shifts, assessed the impact of age truncation on frequency signals in catches of a prey population over time, and investigated how a fish community has responded to a suite of environmental drivers. An analysis of variability in standardized fish catch data showed that spatial and temporal components of variability can be responsive major perturbation, offering finer-scale information about ecological reorganization than a mean response or total variability alone. This analytical framework is flexible and could be broadly applicable to questions about population responses to a changing climate, physiographic differences, or monitoring program efficacy, for example. In the next chapter, I evaluated demographic changes to test the hypothesis that predation can induce similar effects as fishing. Age truncation of an important prey fish was associated with increased variability in recruitment and biomass, and greater correlation between these population metrics and temperature indices. These results suggest that the relative abundance of a fish population could be tracking the environment more closely due to the loss of a buffering capacity otherwise associated with a broader reproducing age structure. Lastly, I went beyond single-species assessment by evaluating data for a fish community in relation to environmental fluctuations. Using gradient forest methods, I was able to quantify the influence of different environmental signals on community indicators and identify thresholds along gradients of those environmental signals. Collectively, this research highlights tools and approaches to disentangle variability in standardized fish catch data. The findings illustrate the complexity of patterns and correlative relationships that may exist between populations and their environment, which may change over time, and which are likely consequential for effectively managing dynamic ecological systems.

INDEX WORDS: Climate change, Fish, Great Lakes, Perturbation, Population dynamics, Statistical modeling, Variance partitioning

UNDERSTANDING THE ROLE OF VARIABILITY IN FISH POPULATION AND COMMUNITY RESPONSE TO CHANGING ENVIRONMENTAL CONDITIONS

by

TIFFANY VIDAL

B.S., University of Vermont, 2002

M.S., University of Massachusetts, School for Marine Sciences and Technology, 2010

A Dissertation Submitted to the Graduate Faculty
of The University of Georgia in Partial Fulfillment
of the
Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2017

UNDERSTANDING THE ROLE OF VARIABILITY IN FISH POPULATION AND COMMUNITY RESPONSE TO CHANGING ENVIRONMENTAL CONDITIONS

by

TIFFANY VIDAL

Approved:

Major Professor:	Brian Irwin
Committee:	Richard Chandler Nicole Lazar Seth Wenger

Electronic Version Approved:

Suzanne Barbour
Dean of the Graduate School
The University of Georgia
August 2017

ACKNOWLEDGMENTS

I would like to express my sincere gratitude to my advisor, Brian Irwin, for his guidance, mentoring, support, and patience. Working with Brian has been a privilege and a delight. I am grateful for his dedication to my professional development, valuable editing of my work throughout the process, thoughtful discussions and different perspectives, and for the respect to maintain a healthy balance between school and my personal life. In addition, Brian has been instrumental in helping me network with some of the most amazing collaborators and coauthors I could ask for.

I would also like to thank my dissertation committee, Dr.'s Seth Wenger, Nicole Lazar, and Richard Chandler, for their expertise and unique perspectives that have helped shape my dissertation research. Thank you for your dedication to this project and mentoring to help me become a better scientist.

This project has largely been a collaborative one, working with many talented and supportive scientists throughout the Great Lakes region. It has been a pleasure working with Lars Rudstam and Randy Jackson at the Cornell Biological Field Station; Jim Bence at Michigan State University's Quantitative Fisheries Center; Chuck Madenjian with the USGS Great Lakes Science Center; Ty Wagner at Penn State; and Jeremy Holden, Mike Yuille, and Jim Hoyle with the Canadian Ministry of Natural Resources. Their contributions have been invaluable in elevating this research.

I thank the Northeast Climate Science Center for their financial support of this project allowing my to investigate the potential role of environmental drivers in influencing shifts in fish populations in the Great Lakes Basin. The consequences of a changing climate are largely unknown; funding research to continue to address questions and enhance our understanding of the connections between biogeophysical processes is imperative. I thank the University of Georgia and the USGS Cooperative Fish and Wildlife Research Unit for providing a positive work environment and opportunities to foster my professional development. I am grateful to the Warnell alumni for their generous scholarships, specifically the family of Archie E. Patterson.

I would like to thank my friends, colleagues, and community at Warnell, UGA, and in Athens, for helping to make my experience enjoyable and transformative. I couldn't have done it without your support. Specifically, I'd like to thank Abby Sterling, because ice cream, baked goods, and puppies can always brighten the day; Tara Gancos Crawford for your unending and inspiring ambition; Cassie Jansch, my sole labmate and traveling companion; in addition to so many others including: Jace Nelson, Bryan Nuse, Elizabeth Hunter, Joanna Hatt, Mason Cline, Tom Prebyl, Ellen Cheng, and Shannon Curry. I am most thankful to my climbing partners while in Georgia, as rock climbing nourishes my soul and keeps me grounded. Shadrock and Megan, I can't thank you enough for solid belays, long days, and the beautiful friendships that flourished from days on the rock.

Finally, I'd like to thank my family, especially my husband Matthew, for your love and support. I am forever grateful.

TABLE OF CONTENTS

List of Figures

List of Tables

Chapter 1

Introduction

The Laurentian Great Lakes are the largest group of freshwater lakes in the world, comprising 25% of the Earth's freshwater by surface volume. The ecosystems of the Great Lakes have undergone major changes throughout history due to overexploitation, pollution and nutrient loading, habitat degradation and loss, the introduction of non-native species, and shifts in climatic patterns (Christie, 1974; Chapra and Robertson, 1977; Bunnell et al., 2013). It is estimated that the region has been affected by more than 180 invasive and non-native species (Mills et al., 1993; Ricciardi, 2006; Sturtevant et al., 2014).

The Great Lakes Water Quality Agreement (1972), a joint commitment between the United States and Canada to promote science and governance to improve the water quality and ecosystem health of the Great Lakes, was instrumental in improving water quality through reductions in phosphorous inputs (Millard et al., 1996; Binding et al., 2015). In 2012 the agreement was updated with annexes that identified areas of concern and addressed non-native species, habitat and species protection, and climate change, with a focus on ecosystem services. Great strides have been made to improve water quality, manage fishing effort, and control non-native species; however, the ecosystems of today are markedly different from those of decades and centuries prior.

In moving forward, it is important to determine clear objectives for management of fisheries resources, identify important drivers of change, understand how populations are responding to those drivers, and to evaluate how different management actions can be used to affect desired outcomes. In this dissertation, I sought to use information contained within the variability in fish catch data to better understand how fish populations are responding to changing environments. Specifically, I used data from three different systems to address the following questions:

1. Can spatial and temporal components of variability in fish catch data be used as an indicator of response to perturbation?;
2. Have changes to the age-structure of a prey fish population in Lake Michigan changed the population's response to environmental signals?; and
3. Are environmental drivers influencing the fish community of the Bay of Quinte, and if so, are there thresholds along gradients of the environmental variables that are important in structuring the community?

A common theme that threads the following chapters together is one of characterizing variability associated with fish population response to changing environments. Variability can be defined as displacement or deviation from the mean. Ecological systems are inherently variable due to natural variation as well as our imperfect ability to observe natural processes. Sources contributing to variability are many, yet these deviations are often treated as noise that is separate from the true processes of interest. We are learning that understanding variability can have great value (e.g., Kratz et al., 1995; Brock and Carpenter, 2006; Vasseur et al., 2014), be it variability in time, space, the environment, or biological responses. In each chapter of this dissertation, I focused specifically on variability and examined ways to extract, decompose, and interpret the information contained within it.

Population-level variability

In Chapter 2, I focused on a population-level response to major ecological perturbations associated with the invasion of non-native mussels and an increase in abundance of a top predator. I hypothesized that the spatial and temporal source components of variability would be responsive to these large-scale ecological shifts. The motivation for this analysis was rooted in the regime shift literature, and the development of generalizable statistical indicators of systems in flux. Ecological systems do not exist in perfect equilibria; however, resilient systems tend to remain in relatively stable states, or 'basins of attraction', for extended periods of time (Scheffer et al., 2001; Folke et al., 2004; Walker et al., 2004). Basins of attraction can be defined by the structure, function, identity, and feedbacks of a system (Walker et al., 2004). It is possible for a system to switch from one stable state into another, often resulting in major ecological shifts or bifurcations. Such shifts can manifest from gradual changes over time that reduce the capacity of the system to reorganize to the present state, or from more abrupt perturbations. Both gradual and abrupt perturbations can propel a system beyond a threshold (Carpenter, 2003; Guttal and Jayaprakash, 2008), resulting in the transition to a new state with different characteristics and feedbacks from the previous state. Identification of reliable indicators of ecosystem dynamics as it relates to the state space (Walker et al., 2004) is an important area of research because although some systems may exhibit stochastic switching between basins of attraction (Drake, 2013), in other systems, the transition into a new basin of attraction may represent a unidirectional shift into an alternate, long-term stable state. These shifts matter because alternate stable states may represent undesirable conditions relative to conservations goals, management objectives, and socio-economic dynamics (Biggs et al., 2012).

In other systems, statistical indicators of ecological shifts, other than a mean response (e.g., increased total variability, autocorrelation, and skewness) have shown promise as early-warning signals (Brock and Carpenter, 2006; Carpenter and Brock, 2006; Van Nes and Scheffer, 2007). Even so, the ability to reliably forecast large-scale ecological shifts remains limited. I was interested in investigating whether variance, partitioned into its spatial and temporal source components, could offer a new indicator associated with large-scale ecological shifts and finer-scale information about the nature of ecological reorganization.

I evaluated the Walleye *Sander vitreus* population in Oneida Lake, New York, using an index of relative abundance from a long-term, standardized, fixed-site gillnet survey.

Variability in Walleye catches was partitioned into temporal and spatial source components to determine if these quantities were responsive to major perturbations associated with the invasion of non-native dreissenid mussels and an increase in the abundance of a piscivorous bird species. The results suggested that variance components shifted at a time consistent with large-scale perturbations observed in Oneida Lake, and that by decomposing variability we were able to gain finer-scale insights into the spatial reorganization of the system following the perturbations, than would be possible from evaluating a mean response alone. We conducted a retrospective analysis with known timing of major perturbations to evaluate if source components of variability could be used as quantitative metrics of system shifts. Extending this approach more broadly to address uncertainty surrounding areas such as climate induced shifts in communities and species distributions, effects of invasive species, sustainability of exploitation, pollution, and habitat degradation, would be a valuable next step.

Population-environment interactions

In Chapter 2, the putative drivers of the major ecosystem shifts and their timing were largely known. For Chapter 3, I examined long-term data for alewife to test the hypothesis that age-truncation increases correlation between population dynamics and environmental drivers. alewife, a non-native prey fish, are of interest because they serve as the primary forage base for Chinook salmon *Oncorhynchus tshawytscha*, a non-native but recreationally important fish species, in Lake Michigan. In recent years the alewife population has been alarmingly low, and evidence of age-truncation has been documented (Madenjian et al., 2014). Predation by Chinook has largely been credited with the alewife decline (He et al., 2014; Tsehaye et al., 2014), but despite efforts to reduce the Chinook population, the alewife have failed to rebound (Madenjian et al., 2014). Additionally, several of the largest recruitment events of the past 40 years were in the mid to late 1990s, a time when the population had declined dramatically. I was interested in evaluating if there was evidence of increased correlation between environmental signals and endogenous oscillations of the alewife population when those large recruitment events occurred.

Selective mortality (e.g., through fishing) can alter the demographic structure of fish populations, changing the way a population responds to environmental signals (Hsieh et al., 2010). The underlying theory comes from signal processing and the concept of resonance (Bjørnstad et al., 1999; Bjørnstad and Grenfell, 2001). Resonance is a phenomenon that causes the amplification of a signal due to interaction with another signal at a similar frequency. This behavior has been shown to influence population dynamics (Cazelles et al., 2008; Hidalgo et al., 2011; Botsford et al., 2014). I used wavelet analysis to decompose the variability in time series data into oscillatory components that can vary through time. The wavelet analysis illustrated that with truncation of the age structure, the frequency of spawning stock biomass (SSB) dynamics began to approximate the mean spawner age. Although we saw only weak correlation between SSB and the environmental time series, we expect this signal to increase, as age truncation has become very pronounced and biomass remains critically low.

I supplemented the wavelet analysis with more traditional stock-recruit modeling to quantify the relationship between recruitment, SSB, and the temperature indices. The top models included an index of summer temperatures, and indicated that the effect of temperature on recruitment increased through time. These results support observations from the wavelet analysis, that the sensitivity of the population to environmental signals has increased as the overall population size has declined and the number of reproducing age classes has been reduced.

Community-level analysis

The analyses from the first two research research chapters offer novel ways to analyze long-term survey data to better understand population dynamics, but both remain rooted in single species assessments. The limitations of single species assessments are many, but a major one is that inter-specific interactions are neglected. For example, it would not be possible to simultaneously achieve maximum sustainable yield (MSY) for all species in a system (Link, 2002); the ecosystem MSY would be lower because of the interactions and dependencies. For these reasons, I was interested in the effects of climate-related changes on an entire fish community in the Bay of Quinte for chapter 4. The fish community data were aggregated into indicator metrics representative of the overall community (e.g., mean trophic level, proportion of native species, mean fish length; Jennings, 2005). This analysis enabled monitoring of transitions in the community indicators as a suite of environmental signals evolved through time. I hypothesized that the emerging ecosystem would reflect a shift towards non-native, warmer water species due to warming water temperatures. I used gradient forest, an extension of random forest, to partition the variability in a suite of community indicator variables using multivariate climate and environmental predictor variables. Random forests are the foundation for gradient forests and represent powerful, computationally efficient algorithms with high prediction accuracy.

The results indicated that the mean trophic level was most responsive to observed environmental changes, increasing positively with Secchi depth. Secchi depth was most important in predicting the fish community, followed by cumulative spring and mean summer temperatures. A negative trend in water clarity was observed throughout the time series, while water temperatures indicated a general warming trend, but with substantial inter-annual variability. An analysis of beta diversity, the spatial or temporal variability among species assemblages, was used to evaluate which species were driving the community changes. I found that three individual species were most influential in driving fluctuations in the indicator variables. Two of the three species have increased over time, both of which are non-native species with a warm thermal preference. The third influential species was a native, cool-water species, which has precipitously declined through time. These results suggested that although the overall predictive power of the gradient forest model was low, water clarity and warming temperatures are correlated with changes in the structure of the fish community in the Bay of Quinte. With predicted warming trends, the transition away from cold-water species towards species with a warmer thermal preference may continue to alter the composition, structure, and function of aquatic ecosystems. It will be imperative to understand how ecosystems respond to climate change in order to inform management decisions aimed at conserving ecosystem function and services.

References

Biggs, R., Blenckner, T., Folke, C., Gordon, L., Norström, A., Nyström, M., and Peterson, G. (2012). Regime shifts. *Encyclopedia of theoretical ecology*, pages 609–617.

Binding, C. E., Greenberg, T. A., Watson, S. B., Rastin, S., and Gould, J. (2015). Long term water clarity changes in North America's Great Lakes from multi-sensor satellite observations. *Limnology and Oceanography*, 60(6):1976–1995.

Bjørnstad, O. N., Fromentin, J.-M., Stenseth, N. C., and Gjøsæter, J. (1999). Cycles and trends in cod populations. *Proceedings of the National Academy of Sciences*, 96(9):5066–5071.

Bjørnstad, O. N. and Grenfell, B. T. (2001). Noisy clockwork: time series analysis of population fluctuations in animals. *Science*, 293(5530):638–643.

Botsford, L. W., Holland, M. D., Field, J. C., and Hastings, A. (2014). Cohort resonance: a significant component of fluctuations in recruitment, egg production, and catch of fished populations. *ICES Journal of Marine Science: Journal du Conseil*, 71(8):2158–2170.

Brock, W. A. and Carpenter, S. R. (2006). Variance as a leading indicator of regime shift in ecosystem services. *Ecology and Society*, 11(2):9.

Bunnell, D. B., Barbiero, R. P., Ludsin, S. A., Madenjian, C. P., Warren, G. J., Dolan, D. M., Brenden, T. O., Briland, R., Gorman, O. T., He, J. X., et al. (2013). Changing ecosystem dynamics in the laurentian great lakes: bottom-up and top-down regulation. *BioScience*, page bit001.

Carpenter, S. and Brock, W. (2006). Rising variance: a leading indicator of ecological transition. *Ecology letters*, 9(3):311–318.

Carpenter, S. R. (2003). *Regime shifts in lake ecosystems: pattern and variation.* Excellence in Ecology Series 15. Ecology Institute, Oldendorf/Luhe, Germany.

Cazelles, B., Chavez, M., Berteaux, D., Ménard, F., Vik, J. O., Jenouvrier, S., and Stenseth, N. C. (2008). Wavelet analysis of ecological time series. *Oecologia*, 156(2):287–304.

Chapra, S. C. and Robertson, A. (1977). Great Lakes eutrophication: the effect of point source control of total phosphorus. *Science*, 196(4297):1448–1450.

Christie, W. (1974). Changes in the fish species composition of the Great Lakes. *Journal of the Fisheries Board of Canada*, 31(5):827–854.

Drake, J. M. (2013). Early warning signals of stochastic switching. *Proceedings of the Royal Society of London B: Biological Sciences*, 280(1766):20130686.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., and Holling, C. (2004). Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics*, pages 557–581.

Guttal, V. and Jayaprakash, C. (2008). Changing skewness: an early warning signal of regime shifts in ecosystems. *Ecology Letters*, 11(5):450–460.

He, J. X., Bence, J. R., Madenjian, C. P., Pothoven, S. A., Dobiesz, N. E., Fielder, D. G., Johnson, J. E., Ebener, M. P., Cottrill, R. A., Mohr, L. C., et al. (2014). Coupling age-structured stock assessment and fish bioenergetics models: a system of time-varying models for quantifying piscivory patterns during the rapid trophic shift in the main basin of Lake Huron. *Canadian Journal of Fisheries and Aquatic Sciences*, 72(1):7–23.

Hidalgo, M., Rouyer, T., Molinero, J. C., Massutí, E., Moranta, J., Guijarro, B., and Stenseth, N. C. (2011). Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. *Marine Ecology Progress Series*, 426:1–12.

Hsieh, C.-H., Yamauchi, A., Nakazawa, T., and Wang, W.-F. (2010). Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences*, 72(2):165–178.

Jennings, S. (2005). Indicators to support an ecosystem approach to fisheries. *Fish and Fisheries*, 6(3):212–232.

Kratz, T. K., Magnuson, J. J., Bayley, P., Benson, B. J., Berish, C. W., Bledsoe, C. S., Blood, E. R., Bowser, C. J., Carpenter, S. R., Cunningham, G. L., et al. (1995). Temporal and spatial variability as neglected ecosystem properties: Lessons learned from 12 North American ecosystems. In *Evaluating and monitoring the health of large-scale ecosystems*, pages 359–383. Springer.

Link, J. S. (2002). What does ecosystem-based fisheries management mean? *Fisheries*, 27(4):18–21.

Madenjian, C. P., Bunnell, D. B., Desorcie, T. J., Ksotich, M. J., Armenio, P. M., and Adams, J. V. (2014). Status and trends of prey fish populations in Lake Michigan, 2013. Report, A report to the Great Lakes Fishery Commission, Lake Michigan Committee.

Millard, E., Myles, D., Johannsson, O., and Ralph, K. (1996). Phytoplankton photosynthesis at two index stations in Lake Ontario 1987-1992: assessment of the long-term response to phosphorus control. *Canadian Journal of Fisheries and Aquatic Sciences*, 53(5):1092–1111.

Mills, E. L., Leach, J. H., Carlton, J. T., and Secor, C. L. (1993). Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research*, 19(1):1–54.

Ricciardi, A. (2006). Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. *Diversity and Distributions*, 12(4):425–433.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., and Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413(6856):591–596.

Sturtevant, R., Larson, J., Berent, L., McCarthy, M., Bogdanoff, A., Fusaro, A., and Rutherford, E. (2014). An impact assessment of the Great Lakes aquatic nonindigenous species.

Technical Report NOAA Technical Memorandum GLERL-161, Great Lakes Environmental Research Laboratory.

Tsehaye, I., Jones, M. L., Brenden, T. O., Bence, J. R., and Claramunt, R. M. (2014). Changes in the salmonine community of Lake Michigan and their implications for predator–prey balance. *Transactions of the American Fisheries Society*, 143(2):420–437.

Van Nes, E. H. and Scheffer, M. (2007). Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. *The American Naturalist*, 169(6):738–747.

Vasseur, D. A., DeLong, J. P., Gilbert, B., Greig, H. S., Harley, C. D., McCann, K. S., Savage, V., Tunney, T. D., and O'Connor, M. I. (2014). Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society of London B: Biological Sciences*, 281(1779):20132612.

Walker, B., Holling, C. S., Carpenter, S. R., and Kinzig, A. (2004). Resilience, adaptability and transformability in social–ecological systems. *Ecology and Society*, 9(2):5.

Chapter 2

Using variance structure to quantify responses to perturbation in fish catches

---

Vidal, T.E., Irwin, B.J., Wagner, T., Rudstam, L.G., Bence, J.R., and Jackson, J.R. (2017). Using variance structure to quantify responses to perturbation in fish catches. Transactions of the American Fisheries Society 146(4):584:593.

Reprinted here with permission from the journal.

Abstract

We present a case-study evaluation of gill-net catches of Walleye *Sander vitreus* to assess potential effects of large-scale changes in Oneida Lake, New York, including disruption of trophic interactions by double-crested cormorants *Phalacrocorax auritus* and invasive dreissenid mussels. We used the empirical long-term gill-net time series and a negative binomial linear mixed model to partition variability into spatial and coherent temporal variance components, hypothesizing that variance partitioning can help quantify spatiotemporal variability and determine whether variance structure differs before and after large-scale perturbation. We found that the mean catch and the total variability of catches decreased following perturbation, but that not all sampling locations responded in a consistent manner. There was evidence of some spatial homogenization concurrent with a restructuring of the relative productivity of individual sites. Specifically, offshore sites generally became more productive following the estimated break point in the gill-net time series. These results provide support for the idea that variance structure is responsive to large-scale perturbations; therefore, variance components have potential utility as statistical indicators of response to a changing environment more broadly. The modeling approach described herein is flexible and would be transferable to other systems and metrics. For example, variance partitioning could be used to examine responses to alternative management regimes, compare variability across physiographic regions, and to describe differences among climate zones. Understanding how individual variance components respond to perturbation may yield finer-scale insights into ecological shifts than focusing on patterns in mean responses or total variability alone.

Introduction

Perturbation, due to anthropogenic or natural forces can disrupt stable ecosystem conditions. Understanding how ecological systems respond to large-scale perturbations, both gradual and abrupt, has important implications for management and monitoring of natural resources. Ecological systems include dynamic networks of complex interactions, within which organisms vary over space and time, but in far more complex ways than independent deviations from a constant mean. Although variability has often been viewed as something to minimize through adequate sampling, it may also provide valuable information about ecological processes (Kratz et al., 1995). Ecosystems are influenced by many drivers (Scheffer et al., 2001), which can induce changes in an ecosystem state rapidly (e.g., invasive species) or more gradually over a longer period of time (e.g., climate change). The ways in which a system responds to perturbations depend upon complex interactions between physical (e.g., climate and hydrology) and biological processes (e.g., demographic and trophic). In resilient systems, there is a high capacity to reorganize after a disturbance such that the state-space remains essentially unchanged; whereas, in less resilient systems, the organization following disturbance can substantially differ from the predisturbance ecological state. State-space can be defined as the function, structure, identity, and feedbacks that characterize an ecosystem state (Walker et al. 2004). Reorganizations are important phenomena to understand because they may be undesirable relative to conservation goals, management objectives, and socioeconomic dynamics.

The idea that perturbation elicits a response in the variability of a state variable was set forth by Odum et al. (1979), who defined an ecosystem perturbation as “any deviation, or displacement, from the ‘nominal state’ in structure or function at any level of organization. The nominal state is the normal operating range, including expected variance.” In recent decades, attention has been dedicated to the identification of generalizable indicators (e.g., changes in mean, variance, and skewness in variables including: pollutants, climatic moisture, greenhouse gases, and chlorophyll) to detect and even predict major ecological shifts (Brock and Carpenter, 2006; Scheffer et al., 2009; Carpenter et al., 2011).

We propose that shifting variance structure can be used as an indicator of perturbation-induced ecological reorganization. Partitioning total variability into dominant source components (e.g., spatial and temporal) may provide quantifiable indicators of population-level responses associated with major ecosystem shifts, and on time-scales relevant to monitoring and management of fishery resources. Changes in variance structure may even indicate cascading effects of perturbations attenuating through a food web (e.g., via species interactions). Similarly, Underwood (1991, 1994) proposed using temporal change in variance as an indicator of perturbation-induced change, although his proposed approach was flawed because the "variance" estimates in his tests combine systematic and chance temporal variation, sampling error, and autocorrelation (Stewart-Oaten and Bence, 2001). Variance partitioning allows variability to be partitioned into component sources, such as spatial (site-to-site), coherent temporal (year-to-year), ephemeral temporal (site x year), trend, and observational error (VanLeeuwen et al., 1996; Urquhart et al., 1998; Wagner et al., 2013). Irwin et al. (2013) applied such a variance-partitioning framework to fish count data, and they quantified the contribution of each component by using a negative binomial mixed modeling approach. If it can be shown that source components of variability are sensitive to how populations respond to ecological shifts, then this approach may prove valuable by identifying or improving measurable attributes of responses to large-scale perturbation.

Our objective was to examine whether indirect effects of a large-scale ecological perturbation could be quantified as a response, retrospectively, in the structure of variation (e.g., spatial and temporal variation) in a target population monitored using standardized sampling. We present a case study analysis of long-term monitoring data to explore the idea that an ecological perturbation may induce a shift in a populations underlying variance structure. Specifically, we analyzed count data from a fishery-independent gill-net survey targeting Walleye *Sander vitreus* in Oneida Lake, NY. Sustained monitoring of Oneida Lake provides one of the most complete data sets on freshwater fish populations in the world, and data from this system have been used to advance understanding of food webs, fish populations, and fisheries (Forney, 1980; Nate et al., 2011; Rudstam et al., 2016). We chose to use Oneida Lake because it is a well-studied system that underwent a major ecological shift during the early 1990s, when an increase in the double-crested cormorant Phalacrocorax auritus (hereafter, cormorant) population (Coleman et al., 2016) and an invasion of dreissenid mussels (i.e., zebra *Dreissena polymorpha* and, later, quagga mussels *Dreissena bugensis*) occurred. We predicted that these disturbances would be a strong enough perturbation to the ecosystem that their effects would be detectable in the variance structure of time series data produced by fishery-independent surveys. Specifically, we were interested in three questions: (1) Can we detect a statistical signal to support the timing of perceived transitions related to these perturbations? (2) Do the magnitudes and relative contributions of the variance components change in response to perturbation? (3) Is there evidence of spatial reorganization as a result of the perturbations? We used a model-based evaluation with time-period-specific parameters to address these questions.

Methods

Study site.— Oneida Lake has the largest surface area (206.7 km^2) of any lake entirely inside the borders of New York State, and it supports important recreational fisheries, including for Walleyes. Major changes to this ecosystem occurred during the early 1990s, including increased cormorant abundance (Rudstam et al., 2004; Irwin et al., 2008a), and the establishment of nonnative dreissenid mussels. The cormorant population increase is largely attributed to reductions in environmental organochlorines (e.g., DDT) and release from human persecution (Weseloh et al., 1995; Rudstam et al., 2004). Acting as a top-predator in Oneida Lake, cormorants have exerted strong predation pressure on the fish populations, in some cases a pressure comparable to angler harvest for adult fish, and exceeding angler impact on subadult fish (VanDeValk et al., 2002; Rudstam et al., 2004; DeBruyne et al., 2013). At the same time, dreissenid mussels altered the ecosystem through increased water clarity (Secchi depth increased from approximately 2.6 m prior to the invasion to 3.5 m after), disruptions to trophic dynamics, and significant habitat modifications (Mayer et al., 2002; Zhu et al., 2006).

The Oneida Lake ecosystem in recent decades has been thought to be fairly ecologically distinct from that in the years prior to major perturbations (Zhu et al., 2006; Irwin et al., 2016). The early 1990s have previously been identified as the approximate break point in the time series associated with the major changes in the lake (Mayer et al., 2000; Irwin et al., 2008b). It should be noted that other ecological changes have likely also had influence on Oneida Lake during the past several decades. For instance, nutrient loadings were reduced following the signing of the Great Lakes Water Quality agreement in 1972, and invasive White Perch *Morone americana* and Gizzard Shad *Dorosoma cepedianum* periodically contribute high-production of young (Fitzgerald et al., 2006) which can alter Walleye forage behavior and potentially their catchability. Angler harvest is also likely to vary over time. Even so, cormorant predation and dreissenid mussels have been thought to be major drivers of change, including contributing to the decline of some fish populations (Coleman et al., 2016; Irwin et al., 2016). For example, the average densities of Walleyes remained below historical averages for a number of years following the establishment of dreissenid mussels and increased cormorant abundance during the early 1990s (Rudstam et al., 2004; Irwin et al., 2008a).

Data sources.— We used data from a long-term (1958-2014; [except 1974, as data were unavailable]) fishery-independent survey of Oneida Lake by researchers at Cornell University (Rudstam and Jackson 2015). This is a fixed-site, annual survey conducted with standardized, variable mesh, multifilament gill nets. The sampling gear is comprised of four gangs (i.e., a string of nets) of six 7.6 m panels sewn together, for a total net length of 183 m long by 1.83 m deep. The mesh sizes within a gang consist of one panel at each of the following stretched mesh sizes: 38, 51, 64, 76, 89, and 102 mm. The gill nets were set around sunset and hauled around 0730. The survey spans from June through mid-September, with one site sampled per week in a standardized sequence, for a total of 15 sites sampled annually. All fish captured in the nets were identified to species and enumerated, resulting in 15 spatially explicit observations of Walleye catch per survey year.

Statistical analyses.—We used a negative binomial linear mixed model to evaluate hypotheses as to how variance structure responds to perturbation. The negative binomial distribution was assumed for the response variable because the variability in predicted Walleye catches was greater than the mean (i.e., the data were overdispersed), thereby violating the assumptions of the Poisson distribution. (The negative binomial is an extension of the Poisson distribution with a shape parameter that makes it suitable for overdispersed count data, which are characteristic of ecological survey data.) Parameter estimation was based on the 1958-2014 time series; however, an indicator variable (p) was used to identify years associated with the pre- and postperturbation periods and allow for period-specific parameter estimates. All analyses were performed using AD Model Builder (Fournier et al., 2012) and R (R Development Core Team, 2015).

We used a log link function to determine expected Walleye catch, such that the natural logarithm of the expected catch (η_{tj}) in year t at site j would be a linear function of the predictors:

$$\eta_{tj} = \nu_p + \lambda \cdot t + a_{tp} + b_{jp}$$

where ν_p was the period-specific intercept and λ was the fixed slope for the temporal trend using year (t) as the covariate, and a_{tp} and b_{jp} are period-specific estimates of random effects (VanLeeuwen et al., 1996) associated with year and site, respectively. The year covariate was centered on the mean year to improve convergence and increase the interpretability of the intercept parameter. The global trend (λ) was assumed to be influenced by longer-term processes and therefore was estimated as a single parameter applied to the full time series. Random effects provide a way to quantify the effect of a grouping level (year or site) in relation to the mean effect of all groups combined. All random effects were assumed to be independent and identically distributed according to a Gaussian distribution with a mean of

0 and a variance of σ_x^2, where x represents the distinct random effects (spatial or temporal). Specific parameters were allowed to vary by time period based on our prediction that variance structure would be responsive to perturbation, such that the mean and variance components were time-period specific.

The remaining two equations in the model are

$$\begin{aligned} &\mu_{tj} = exp(\eta_{t,j}) \\ &Y_{tj} \sim NegBinom(\mu_{tj}, \kappa_p) \end{aligned}$$

where μ_{tj} was the expected Walleye catch in year t at site j on the original (nonlogarithmic) scale, Y_{tj} is the observed Walleye catch in year t at site j, and κ_p is the period-specific shape parameter of the negative binomial distribution. In each year, κ determines how much extra (above-Poisson) variation there is among sites through its relationship with μ. The variance of the negative binomial distribution is assumed to be a quadratic function of the mean, with the quadratic term dependent on the shape parameter, that is,

$$var_{tj} = \mu_{tj} + \frac{\mu_{tj}^2}{\kappa_p}.$$

Thus, the relationship of the variation to the mean is allowed to differ between periods. Model fit was evaluated using Anscombe residuals (Anscombe, 1953; Hilbe, 2011).

Likelihood profiling was used to determine the year in which the change from the pre- to the postperturbation period occurred. We evaluated the above model at every possible change-point year for the available data (i.e., all years except the first and last in the time series) using the log-likelihood. All models were equally parsimonious, so that the change point associated with the model with the largest log-likelihood was deemed most appropriate. Subsequent results are based on the single, optimal change point.

We then used the linear mixed model with the optimal change-point year to evaluate the magnitude and structure of variability in gill-net catches prior to and following the dreissenid invasion and cormorant population increase. We compared the relative proportions of coherent temporal and spatial variability between periods to evaluate whether the structure of variability changed after perturbation.

In mixed models, random effects are often used to account for clustering in the data, but they can also offer additional information about the behavior of the individual grouping variables (e.g., sites and years). In this case study, we were specifically interested in understanding whether all sites have proportionately declined from historical catch levels, or whether there has been a disproportionate shift among sites. A large positive site random effect would indicate that a site contributed more than average for a particular time period, and a large negative random effect would indicate a that a site contributed less than average. If there were no changes in the relative contributions of sites following the perturbations, we would not expect a shift in the site random effect rankings even if a decline in the mean response was observed due to lower overall catch rates.

Results

The likelihood profiling indicated that 1989 was the optimal change-point year for separating the gill-net time series into pre- and postperturbation periods. There was a distinct peak in the log-likelihood surrounding the perceived timing (1988-1991) of the ecological shifts in Oneida Lake (Figure 2.1). The minimum, mean, and maximum annual catches of Walleyes were lower during the latter time period. The mean catch was reduced by about 50%, and the maximum catch was about 40% of the preperturbation period (Figure 2.2, Table 2.1).

Importantly, we also observed a reduction in variability in catch rates over time, as high catches at individual sites became less frequent (Figure 2.2). The shape parameter of the negative binomial was slightly higher during the postperturbation period (Table 2.1), indicating a small reduction in the rate that variance in gill-net catches changed with the mean. Thus, in addition to the reduction in the total variability, the structure of the variability also changed following 1989, particularly spatial variability (Figure 2.3, Table 2.1). The predicted catches from the negative binomial mixed model were in general agreement with the observed data, for both the pre- and postperturbation periods (Figure 2.4). The Anscombe residuals that were used to further evaluate model fit appeared to be approximately normally distributed across the range of the predicted values; there was no indication of extreme outliers (Figure 2.5).

In the model, the maximum likelihood estimate for spatial variability (σ_b^2) was 0.35 for the years prior to the break point, declining to 0.10 in the postperturbation period (Figure 3) a 72% reduction in estimated among-site variability (Table 2.1). By contrast, the temporal variability remained relatively stable between the two time periods (pre σ_a^2=0.10; post σ_a^2=0.12). Additionally, the decline in spatial variability reflected proportionally different relative changes at different sites, as indicated by the shifting rank order of site-specific random effects (Figure 2.6A). The difference between the post- and preperturbation random effects provided a relative measure of the contributions of individual sites that might help us understand these patterns by pinpointing the relevant site-specific attributes. This analysis, however, was not designed to investigate specific causal mechanisms operating within this system but to investigate the potential for variance structure to serve as a statistical indicator of some complex responses to large-scale perturbation. Purely for illustrative purposes, we performed post hoc analyses to evaluate the site characteristics (i.e., substrate type, depth, and distance from shore) of the survey locations vis-à-vis the difference in spatial random effect values between the pre- and postperturbation time periods. This exploratory analysis indicated that Walleye catches at the inshore sites have generally declined more severely than the offshore sites (Figure 2.6B). The mean catches at the inshore sites (n=9) all declined following the perturbations, while one third of the offshore sites (n=6) improved slightly. Even so, some of the highest overall catches continue to come from the inshore sites. Coherent temporal variability (σ_a^2) was relatively unchanged between time periods (Figure 2.3) and represented a relatively small component of total variability during the preperturbation period (about 23%). Due to the decline in spatial variability, however, the estimates of coherent temporal and spatial variability were about the same in the postperturbation period (Table 2.1).

Discussion

We were able to objectively detect a change point in the time series of Walleye catches that is consistent with the timing of perceived ecological shifts in Oneida Lake (e.g., Mayer et al., 2000; Irwin et al., 2008b; Coleman et al., 2016; Irwin et al., 2016) and quantify shifts in the variance structure using a mixed modeling approach. In this lake, there has been a marked decline in gill-net catches of Walleyes over time. Concurrent with a decline in the average catch of Walleyes, a reduction in the site-to-site variability was observed, suggesting homogenization across sites in terms of relative catches. Additionally, we have shown that variance structure was time sensitive; therefore, variance partitioning appears useful for providing additional, finer-scale information about responses to ecological shifts—information that provided by the changes in means or total variability.

Disentangling the spatial and temporal components of variability provides information about how a system is changing across space and through time, a property that could be useful for adaptation of management and monitoring to dynamic ecosystems. For example, random effects could be used to evaluate differential growth rates due to geographic location or gradual shifts over time. Increasing variance has been proposed as a signal associated with the transition between stable states (Brock and Carpenter, 2006; Scheffer et al., 2009; Carpenter et al., 2011), but the responsiveness of variance components to large-scale ecological change appears to be a relatively new development (however, see Guttal and Jayaprakash, 2009). By decomposing variability into time-varying component sources, we were able to identify spatially-explicit changes (e.g., a disproportionate diminishing of high-catch events) beyond those that could have been inferred from a mean response alone. In this study, we were interested in the general behavior of variance structure in response to perturbation; however, this analytical approach could be extended to investigate other questions, such as examining responses to alternative management regimes, comparing variability across physiographic regions, or describing differences among climate zones.

Our mixed modeling approach provided evidence that the sources of variability associated with a response variable can change in relative importance over time and in response to perturbation. In our study, temporal variability remained relatively unchanged, whereas, the spatial variance component was reduced by 72%. In addition to the fact that the overall spatial variance parameter was reduced in the latter part of the time series, the individual sampling sites did not respond in a consistent manner. Generally, there was a homogenization across sites towards lower Walleye catches, with a reduction in spatial patchiness of catch rates and a reorganization of the rankings of site-level random effects.

The estimated timing of the change point as determined through likelihood profiling (1989) was generally consistent with the observed timing of important changes in Oneida Lake. Expansion of the cormorant colony throughout the 1980s and 1990s led to increased consumption of percids (Coleman et al., 2016), while the dreissenid invasion increased water clarity, thereby altering the food web structure (Mayer et al., 2002) and perhaps altering predator-prey and species-gear interactions. Following the establishment of dreissenid mussels, the mortality of larval Walleyes increased, possibly as a result of higher predation due to increased water clarity (Jackson et al., 2016; Rudstam et al., 2016). Additionally, competition with littoral predators (Fetzer et al., 2016; Jackson et al., 2016) has increased, likely due to a loss of the Walleyes' competitive advantage in more turbid waters. Cormorants and dreissenid mussels are considered the putative drivers of change in Oneida Lake, but other factors are likely to have contributed changes in Walleye abundance (e.g., abundance of White Perch, a predator of larval percids). The optimal change-point year was fairly robust to the length of the time series; when we re-profiled the likelihood with truncated time series the change-point was estimated to be between 1988 and 1991 for each analysis (Figure 1). The long-term trend was estimated to be approximately 0 and therefore was not likely to influence the timing of the change point. However, modeling multiple change points and trends would be possible with this framework (assuming sufficient data to avoid overparameterization).

The shift in site rank order suggests that Walleyes have transitioned away from the littoral zone into more offshore habitats. The mechanisms driving this shift are unknown, but the changes to water clarity and cormorant predation may have made the littoral zone less suitable as Walleye habitat. The observed shifts also could be partly a consequence of changes in gill-net catchability in the different habitats. For example, the sampling gear may have been more visible to Walleyes in the clear, inshore waters, enhancing their avoidance strategies. If catchability has changed, this bifurcation in the time series is important with respect to possible inferences about population trends. There is some evidence of a rebounding of the Walleye population and increasing spatial variability toward the latter portion of the time series, which may be a response to a cormorant control program that intensified in 2004, combined with a reduced creel limit in 2001 (Coleman et al., 2016).

Understanding major ecological shifts is important to the management of natural resources (Folke et al., 2004; Brock and Carpenter, 2006; Scheffer et al., 2009). Continued development of quantifiable signals of such shifts was the motivation for this study. Our model provides some evidence that variance components can be responsive to perturbations and thus they may serve as indicators of large-scale ecological reorganization. This approach could also help reveal patterns that may not otherwise be obvious, prompting investigation into the mechanisms driving population-level responses or even ecological shifts. Likewise, the variance-partitioning approach may help managers more fully consider what types of changes would be desirable or acceptable. For instance, the loss of rare top-performers (e.g., abundant species; high-catch locations) might be undesirable, even if a decline, on average, is not significant.

Additional research on shifting variance structures for different systems and dynamics will help confirm whether reliable, general behavior of variance components will emerge as an improved technique for quantifying responses to large-scale perturbation and detecting shifting dynamics in a changing environment. Understanding how ecosystem dynamics are shifting through time, and in response to environmental conditions will require a commitment to spatially and temporally consistent data collection over the long term. Even at Oneida Lake, which is a well-studied system with rich biological data from long-term monitoring programs, there are important data limitations. For instance, the basic data structure (one observation per site per year) prevented us from assessing ephemeral-temporal variability (Kratz et al., 1995; Irwin et al., 2013). Proper sampling design is therefore paramount to addressing specific research questions.

The approach described in this article could be extended to address the uncertainties surrounding other important issues, such as climate-induced shifts in communities' and species distributions, the effects of invasive species, the sustainability of exploitation, pollution, and habitat degradation. For example, climate models have predicted that extreme events (e.g., drought, above average temperatures, high precipitation events) will increase in prevalence and intensity (Rahmstorf and Coumou, 2011; Rummukainen, 2012), thereby potentially altering the variance and variance structure of natural phenomena irrespective of changes to the mean response. Additionally, as species' distributions change other consequences will manifest themselves through changes in food web dynamics and competition for habitat resources as well as through potential shifts in vital rates for species that approach their range limits, either geographic or thermal. Any of the aforementioned disturbances can create instability in the state-space of a system— instability that could eventually lead into a new nominal state, perhaps necessitating new monitoring and management measures.

Acknowledgments

We thank John Forney, Tony VanDeValk, Tom Brooking for their insights into a changing ecosystem, as well as the staff and students at the Cornell Biological Field Station for collecting the gillnet data over the last 60 years. This research was funded by the Department of Interior Northeast Climate Science Center to BJI, TW, and JRB, and by New

York State Department of Environmental Conservation through Federal Aid in Sport Fish Restoration project F-48-R to JRJ and LGR. The Georgia Cooperative Fish and Wildlife Research Unit is sponsored jointly by the U.S. Geological Survey, the Georgia Department of Natural Resources, the U.S. Fish and Wildlife Service, the University of Georgia, and the Wildlife Management Institute. This is publication number 2017-10 of the Quantitative Fisheries Center at Michigan State University. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Anscombe, F. (1953). Contribution to the discussion of H. Hotelling's paper. *Journal of the Royal Statistical Society*, 15(2):229–230.

Brock, W. A. and Carpenter, S. R. (2006). Variance as a leading indicator of regime shift in ecosystem services. *Ecology and Society*, 11(2):9.

Carpenter, S. R., Cole, J. J., Pace, M. L., Batt, R., Brock, W., Cline, T., Coloso, J., Hodgson, J. R., Kitchell, J. F., Seekell, D. A., et al. (2011). Early warnings of regime shifts: a whole-ecosystem experiment. *Science*, 332(6033):1079–1082.

Coleman, J. T. H., DeBruyne, L., Rudstam, L. G., Jackson, J. R., VanDeValk, A. J., Brooking, T. E., Adams, C. M., and Richmond, M. E. (2016). Evaluating the influence of Double-crested Cormorants on Walleye and Yellow Perch Populations. In Rudstam, L., Mills, E., Jackson, J., and Stewart, D., editors, *Oneida Lake: Long-term Dynamics of a Managed Ecosystem and its Fisheries.* American Fisheries Society.

DeBruyne, R. L., Coleman, J. T., Jackson, J. R., Rudstam, L. G., and VanDeValk, A. J. (2013). Analysis of prey selection by double-crested cormorants: a 15-year diet study in Oneida Lake, New York. *Transactions of the American Fisheries Society*, 142(2):430–446.

Fetzer, W. W., Farrell, C. J., Jackson, J. R., and Rudstam, L. G. (2016). Year-class variation drives interactions between warm-water predators and yellow perch. *Canadian Journal of Fisheries and Aquatic Sciences*, 73(9):1330–1341.

Fitzgerald, D. G., Forney, J. L., Rudstam, L. G., Irwin, B. J., and VanDeValk, A. J. (2006). Gizzard shad put a freeze on winter mortality of age-0 yellow perch but not white perch. *Ecological Applications*, 16(4):1487–1501.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., and Holling,

C. (2004). Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics*, pages 557–581.

Forney, J. L. (1980). Evolution of a management strategy for the walleye in Oneida Lake, New-York. *New York Fish and Game Journal*, 27(2):105–141.

Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M. N., Nielsen, A., and Sibert, J. (2012). AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, 27(2):233–249.

Guttal, V. and Jayaprakash, C. (2009). Spatial variance and spatial skewness: leading indicators of regime shifts in spatial ecological systems. *Theoretical Ecology*, 2(1):3–12.

Hilbe, J. M. (2011). *Negative binomial regression.* Cambridge University Press.

Irwin, B., Rudstam, L., Jackson, J., VanDeValk, A., and Forney, J. (2016). Long-term trends in the fish community of Oneida Lake: analysis of the zebra mussel invasion. In Rudstam, L., Mills, E., Jackson, J., and Stewart, D., editors, *Oneida Lake: Long-term Dynamics of a Managed Ecosystem and its Fisheries.* American Fisheries Society.

Irwin, B. J., Treska, T. J., Rudstam, L. G., Sullivan, P. J., Jackson, J. R., VanDeValk, A. J., and Forney, J. L. (2008a). Estimating walleye (*Sander vitreus*) density, gear catchability, and mortality using three fishery-independent data sets for Oneida Lake, New York. *Canadian Journal of Fisheries and Aquatic Sciences*, 65(7):1366–1378.

Irwin, B. J., Wagner, T., Bence, J. R., Kepler, M. V., Liu, W., and Hayes, D. B. (2013). Estimating spatial and temporal components of variation for fisheries count data using negative binomial mixed models. *Transactions of the American Fisheries Society*, 142(1):171–183.

Irwin, B. J., Wilberg, M. J., Bence, J. R., and Jones, M. L. (2008b). Evaluating alternative harvest policies for yellow perch in southern Lake Michigan. *Fisheries Research*, 94(3):267–281.

Jackson, J., Rudstam, L., Brooking, T., VanDeValk, A., Holeck, K., Hotaling, C., and Forney, J. (2016). The Fisheries and Limnology of Oneida Lake 2015. Report, Cornell Biological Field Station, Department of Natural Resources, Cornell University.

Kratz, T. K., Magnuson, J. J., Bayley, P., Benson, B. J., Berish, C. W., Bledsoe, C. S., Blood, E. R., Bowser, C. J., Carpenter, S. R., Cunningham, G. L., et al. (1995). Temporal and spatial variability as neglected ecosystem properties: Lessons learned from 12 North American ecosystems. In *Evaluating and monitoring the health of large-scale ecosystems*, pages 359–383. Springer.

Mayer, C., Keats, R., Rudstam, L., and Mills, E. (2002). Scale-dependent effects of zebra mussels on benthic invertebrates in a large eutrophic lake. *Journal of the North American Benthological Society*, 21(4):616–633.

Mayer, C., VanDeValk, A., Forney, J., Rudstam, L., and Mills, E. (2000). Response of yellow perch (Perca flavescens) in Oneida Lake, New York, to the establishment of zebra mussels (Dreissena polymorpha). *Canadian Journal of Fisheries and Aquatic Sciences*, 57(4):742–754.

Nate, N. A., Hansen, M. J., Rudstam, L. G., Knight, R. L., and Newman, S. P. (2011). Population and community dynamics of walleye. *Biology, management, and culture of Walleye and Sauger*, pages 321–374.

Odum, E. P., Finn, J. T., and Franz, E. H. (1979). Perturbation theory and the subsidy-stress gradient. *BioScience*, 29(6):349–352.

R Development Core Team (2015). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

Rahmstorf, S. and Coumou, D. (2011). Increase of extreme events in a warming world. *Proceedings of the National Academy of Sciences*, 108(44):17905–17909.

Rudstam, L. G., Mills, E. L., Jackson, J. R., and Stewart, D. J. (2016). *Oneida Lake: Long-term Dynamics of a Managed Ecosystem and its Fisheries.* American Fisheries Society, Bethesda, Maryland.

Rudstam, L. G., VanDeValk, A. J., Adams, C. M., Coleman, J. T., Forney, J. L., and Richmond, M. E. (2004). Cormorant predation and the population dynamics of walleye and yellow perch in Oneida Lake. *Ecological Applications*, 14(1):149–163.

Rummukainen, M. (2012). Changes in climate and weather extremes in the 21st century. *Wiley Interdisciplinary Reviews: Climate Change*, 3(2):115–129.

Scheffer, M., Bascompte, J., Brock, W. A., Brovkin, V., Carpenter, S. R., Dakos, V., Held, H., Van Nes, E. H., Rietkerk, M., and Sugihara, G. (2009). Early-warning signals for critical transitions. *Nature*, 461(7260):53–59.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., and Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413(6856):591–596.

Stewart-Oaten, A. and Bence, J. R. (2001). Temporal and spatial variation in environmental impact assessment. *Ecological Monographs*, 71(2):305–339.

Underwood, A. (1991). Beyond baci: experimental designs for detecting human environmental impacts on temporal variations in natural populations. *Marine and Freshwater Research*, 42(5):569–587.

Underwood, A. (1994). On beyond BACI: sampling designs that might reliably detect environmental disturbances. *Ecological applications*, 4(1):3–15.

Urquhart, N. S., Paulsen, S. G., and Larsen, D. P. (1998). Monitoring for policy-relevant regional trends over time. *Ecological Applications*, 8(2):246–257.

VanDeValk, A. J., Adams, C. M., Rudstam, L. G., Forney, J. L., Brooking, T. E., Gerken, M. A., Young, B. P., and Hooper, J. T. (2002). Comparison of angler and cormorant harvest of walleye and yellow perch in Oneida Lake, New York. *Transactions of the American Fisheries Society*, 131(1):27–39.

VanLeeuwen, D. M., Murray, L. W., and Urquhart, N. S. (1996). A mixed model with both fixed and random trend components across time. *Journal of Agricultural, Biological, and Environmental Statistics*, pages 435–453.

Wagner, T., Irwin, B. J., Bence, J. R., and Hayes, D. B. (2013). Detecting temporal trends in freshwater fisheries surveys: statistical power and the important linkages between management questions and monitoring objectives. *Fisheries*, 38(7):309–319.

Weseloh, D., Ewins, P., Struger, J., Mineau, P., Bishop, C., Postupalsky, S., and Ludwig, J. (1995). Double-crested cormorants of the Great Lakes: changes in population size, breeding distribution and reproductive output between 1913 and 1991. *Colonial Waterbirds*, pages 48–59.

Zhu, B., Fitzgerald, D., Mayer, C., Rudstam, L., and Mills, E. (2006). Alteration of ecosystem function by zebra mussels in Oneida Lake: impacts on submerged macrophytes. *Ecosystems*, 9(6):1017–1028.

Tables

Table 2.1: Summary statistics (sample sizes, minimum, mean, and maximum Walleye gill-net catches) aggregated across all sites and parameter estimates (SDs in parentheses) from the linear mixed model for the pre- (1958-1988, except 1974) and postperturbation (1989-2014) periods in Oneida Lake, New York. Slope was not modeled as time-period specific.

Observed catches	**Pre**	**Post**
Sample size	450	390
Minimum	1	0
Mean	32	17
Maximum	220	90

Parameter estimates	**Pre**	**Post**
Fixed effects		
Intercept (μ)	3.267 (0.186)	2.709 (0.148)
Slope (λ)	0.002 (0.006)	0.002 (0.006)
Shape parameter (κ)	2.091 (0.155)	2.346 (0.203)
Random Effects		
Coherent temporal (σ_a^2)	0.102 (0.039)	0.117 (0.045)
Spatial (σ_b^2)	0.345 (0.133)	0.096 (0.043)

Figures

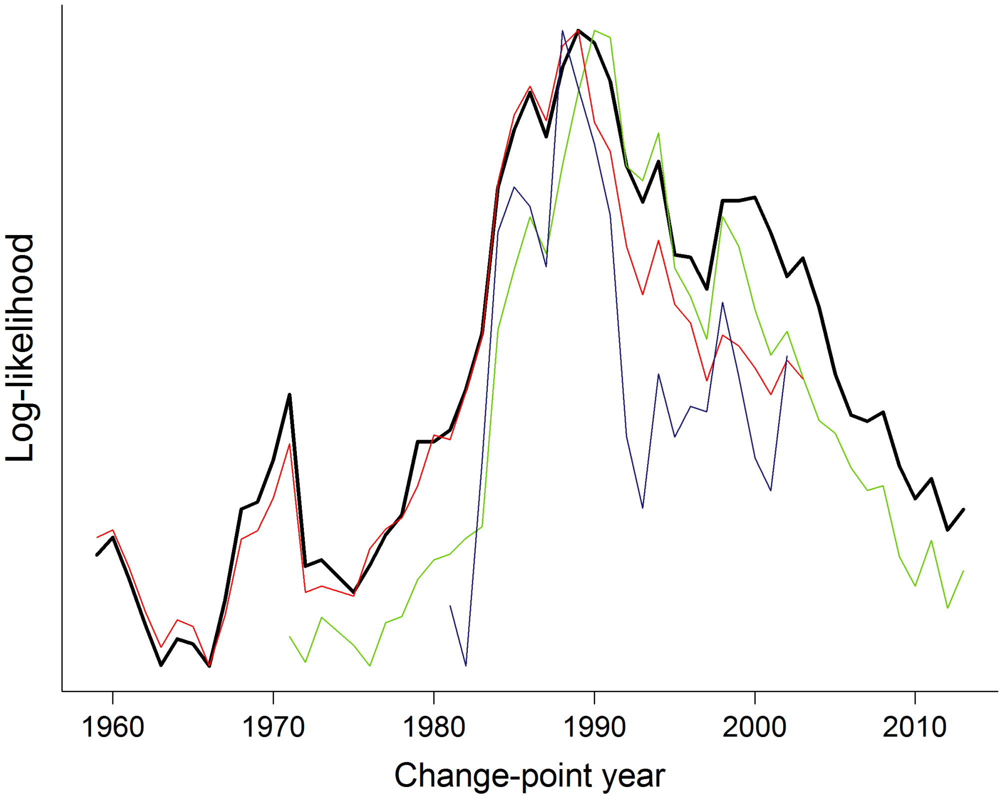

Figure 2.1: Log-likelihood values of Walleye catch plotted across possible change-point years. The solid black line represents the full time series; the colored lines represent likelihood profiles from truncated time series (i.e., with the removal of early and/or latter years in the time series). The change-point was robust to time series length. The log-likelihood values are not shown on the y-axis owing to scaling differences among the four time series; the peak around 1989 indicates the optimal change point.

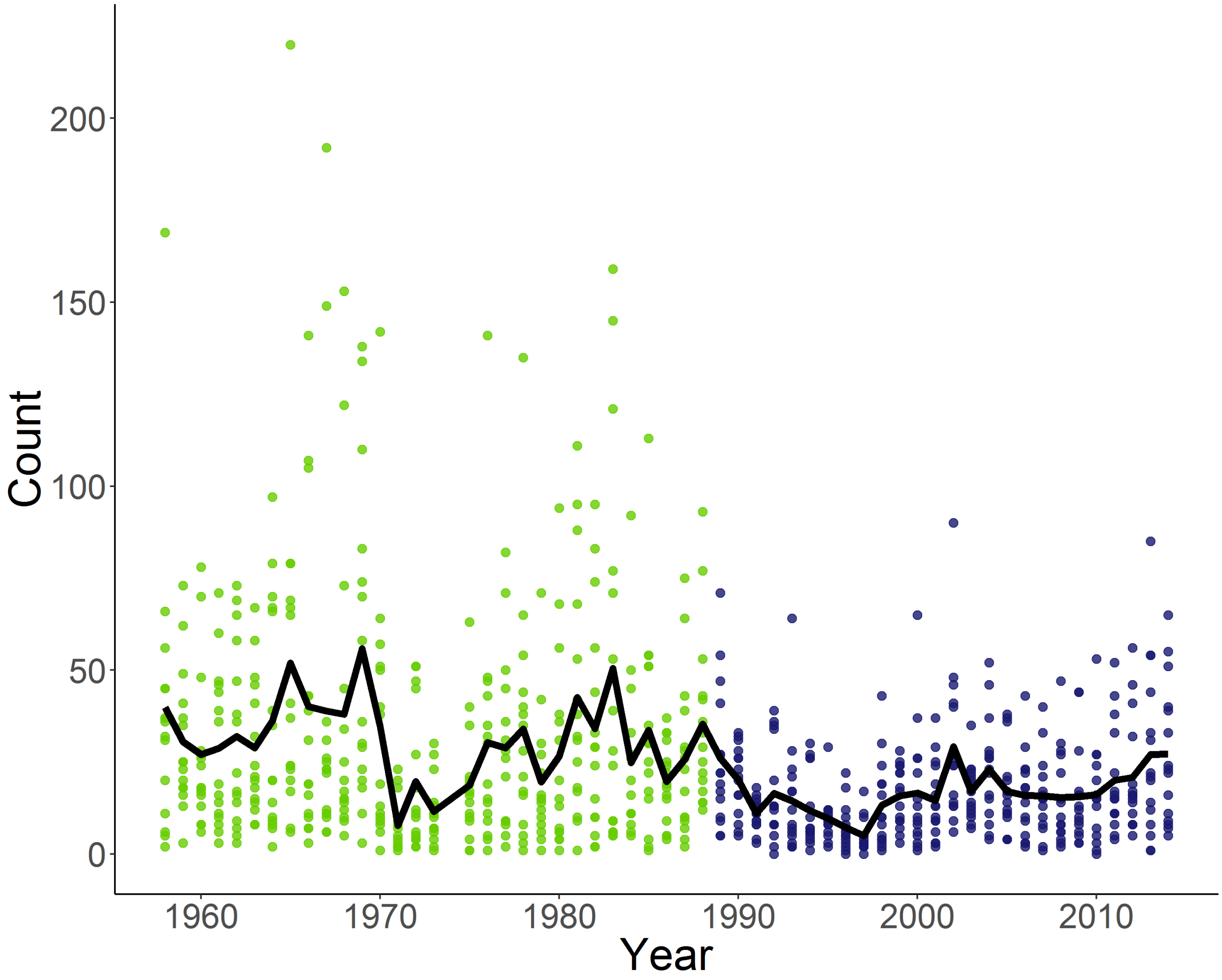

Figure 2.2: Observed Walleye catch by site and year for fifteen fixed sites in Oneida Lake, NY from 1958 to 2014 (data were not available for 1974). The black solid line represents the mean catch over time, the green dots represent the catches ay individual sites in the preperturbation period, and the blue dots represent the catches at individual sites in the postperturbation period.

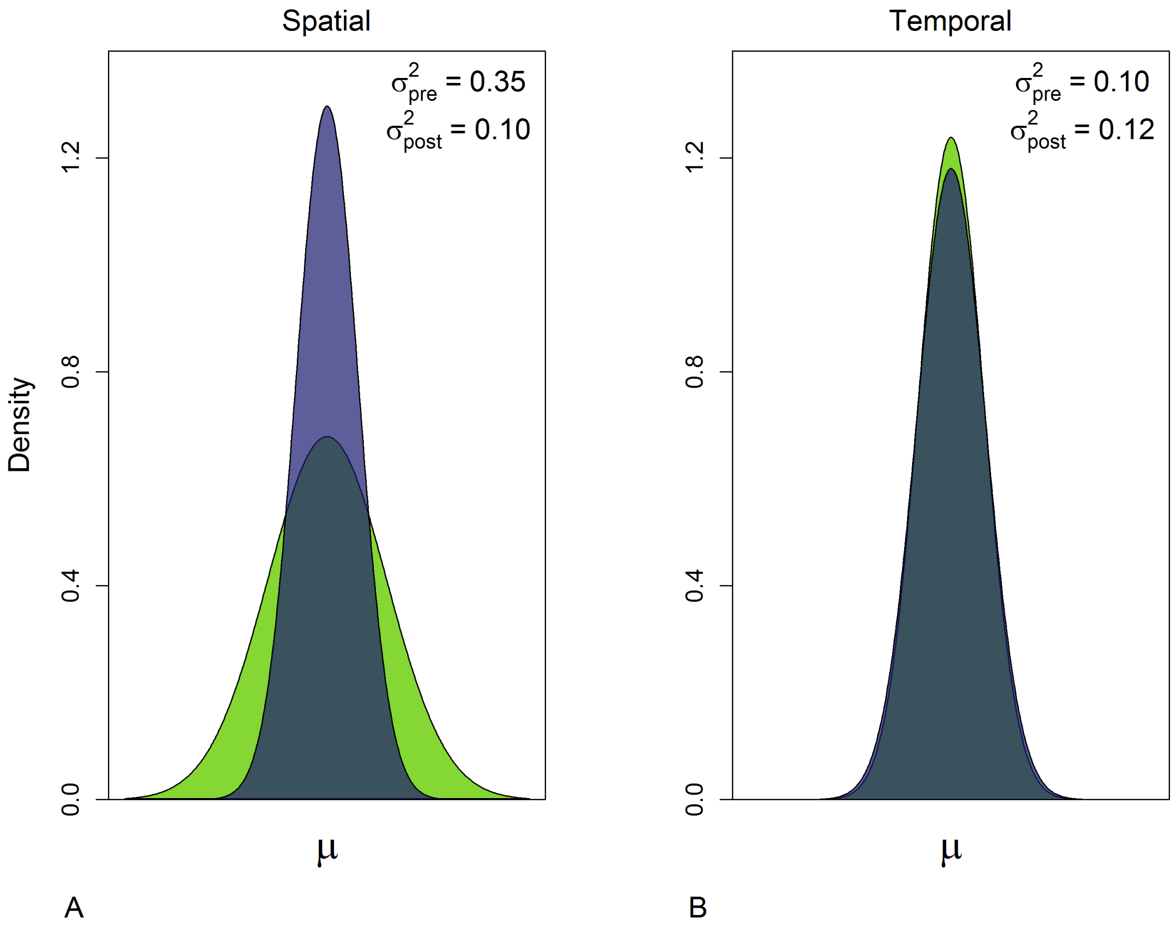

Figure 2.3: Normal density plots showing the shifts in **(A)** spatial and **(B)** temporal variability relative to the period-specific mean catch, during the pre- and postperturbation time periods (represented by the green and blue areas, respectively).

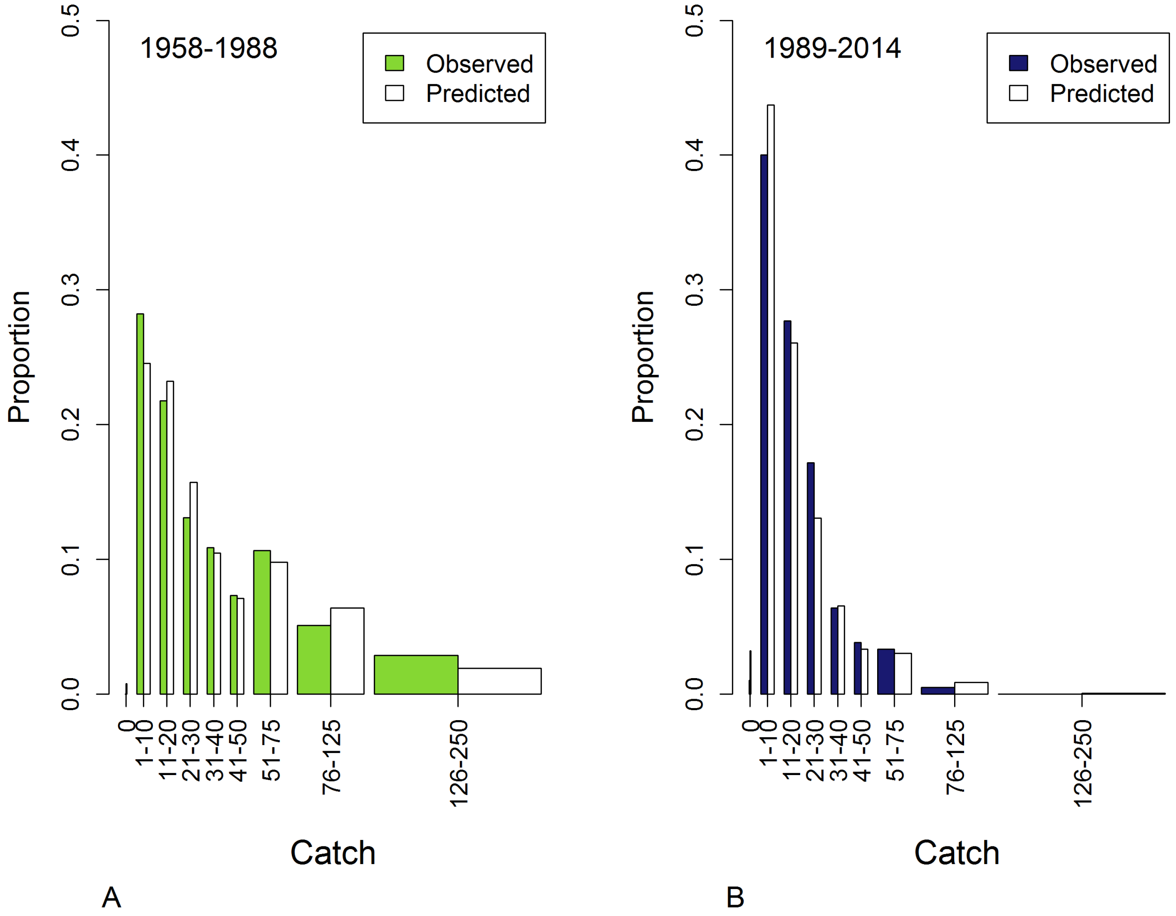

Figure 2.4: Observed (green and blue areas) versus predicted (white areas) Walleye catch during **(A)** the preperturbation period and **(B)** the postperturbation period. Catches are aggregated across sites and years for display.

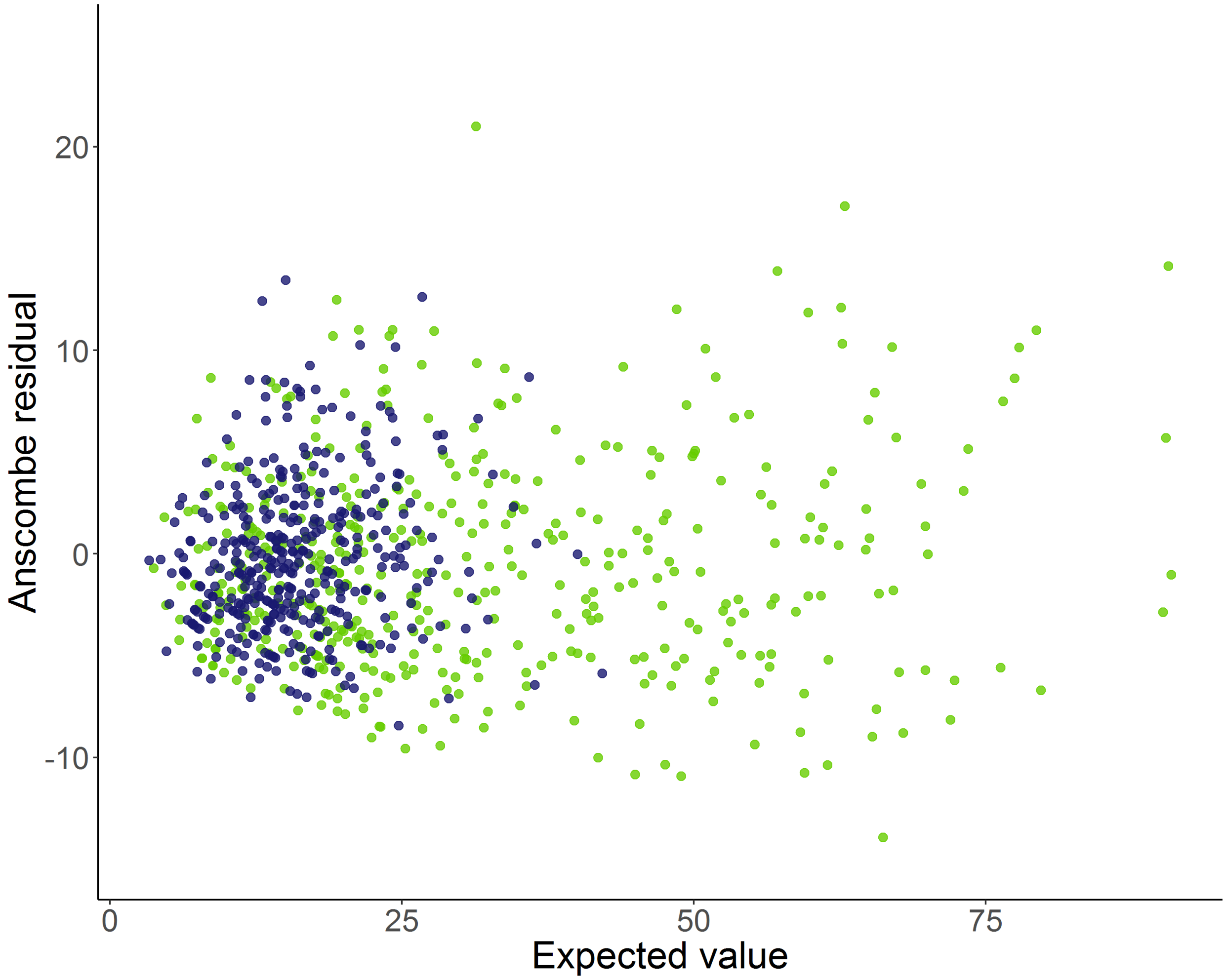

Figure 2.5: Plot of Anscombe residuals based on fitting a negative binomial mixed model to the catches of Walleyes. Green dots depict values from the preperturbation period, blue dots values from the postperturbation period.

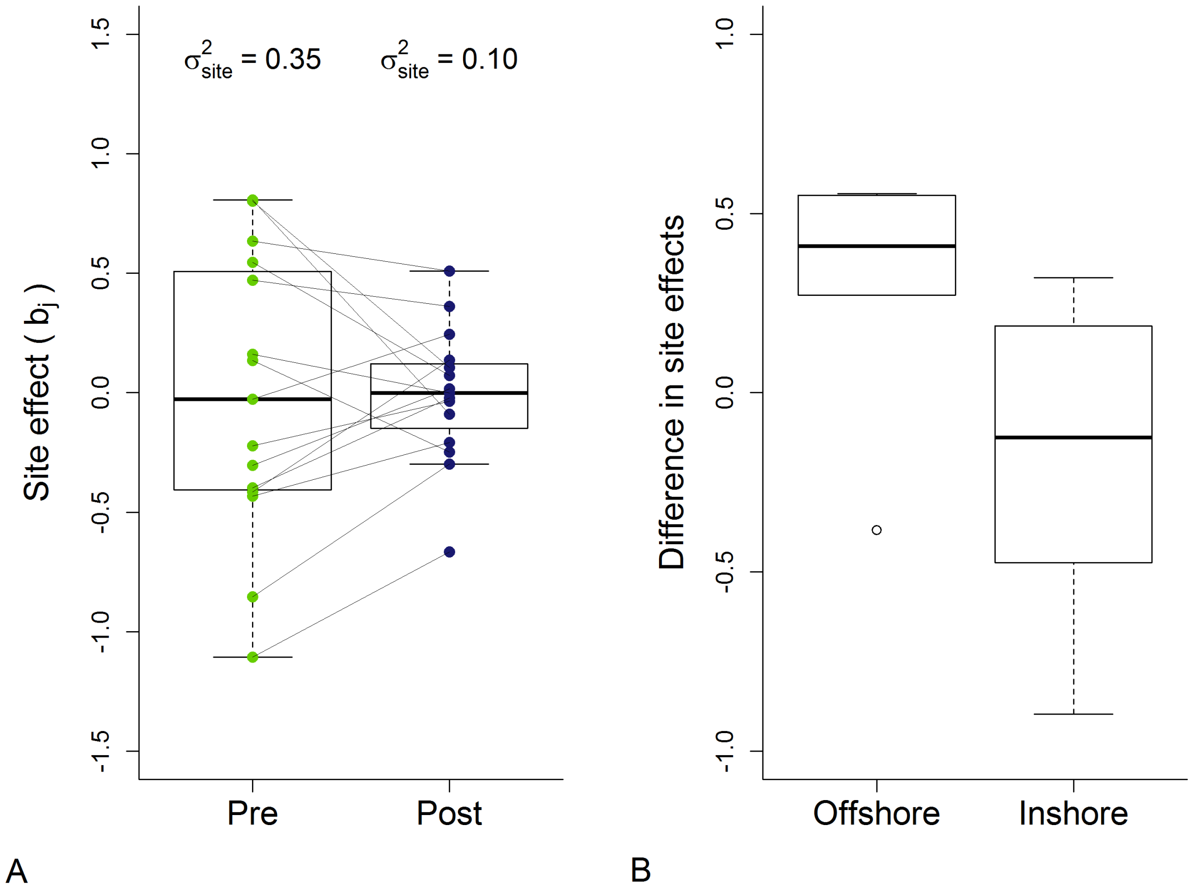

Figure 2.6: Boxplots showing **(A)** the spread of the individual-site random effects in the pre- and postperturbation periods and **(B)** the change in site random effects (i.e. postperturbation less preperturbation) for inshore and offshore sites. The circles in panel **(A)** represent individual sites; the lines connect the individual site random effects between the two time periods to show how a site's rank changed relative to the other sites in terms of catch magnitude.

Chapter 3

Demographic structure influences oscillations of the alewife population in Lake Michigan

---

Vidal, T.E., Irwin, B.J., Wagner, S.J, and Madenjian, C.P. To be submitted to *Journal of Great Lakes Research*

Introduction

The importance of interactions between age structure and environmental signals in fish populations has been elevated in recent decades as evidence mounts that selective harvest can change the way in which populations respond to external drivers (Berkeley et al., 2004; Hsieh et al., 2010). Fisheries often harvest in a size selective manner, which can lead to a truncated age structure in the targeted population when larger, often older, individuals are disproportionately removed. In populations with several reproducing age classes, there exists a sort of storage capacity that helps to buffer against transient adverse environmental conditions (Hsieh et al., 2010; Planque et al., 2010; Hidalgo et al., 2011), but when the age structure becomes truncated, the population becomes increasingly reliant on younger age classes to produce offspring. In addition, both over-exploitation and strong predation pressure have the ability to reduce the genetic and spatial structure of a population, which can further reduce a population's resilience to environmental perturbations. In both cases the net result can be a strengthening of the linkage among population dynamics, recruitment and environmental variability (Anderson et al., 2008; Hidalgo et al., 2011). Previous effort has focused on understanding how fishing may alter a population's response to environmental drivers in marine systems (Bjørnstad et al., 2004; Hidalgo et al., 2011; Botsford et al., 2014), but less attention has been given to freshwater fishes.

In fish species with iteroparous reproduction, populations can exhibit cycles due to inter-cohort interactions resulting from multiple age-classes contributing to the offspring in a given year (Bjørnstad et al., 2004). These cycles can arise from age-structured interactions 'echoing' stochastic recruitment. This inter-cohort interaction is one facet to a phenomenon identified as 'cohort resonance' (Bjørnstad and Grenfell, 2001; Bjørnstad et al., 2004; Worden et al., 2010; Botsford et al., 2014). Resonance, in general, is the concept that any signal exposed to noise containing a similar frequency component will be amplified at that common frequency, regardless of the coupling strength. For example, the Bay of Fundy experiences the most extreme tides in the world because of the coupling between the resonant frequency in the bay, or the amount of time it takes for water to move up and back down out of the bay, and the frequency of the principal lunar semi-diurnal gravitational tidal constituent (i.e., the M2 tide). Both the bay resonance and the M2 tide have a frequency of approximately 1/12 hours (frequency is equal to 1/periodicity), thereby amplifying the overall signal (Silvert, 1997). The concept of resonance may also be informative for understanding dynamic fish populations.

In this analysis, I focus specifically on one type of inter-cohort interaction: the association between recruitment and the multiple age classes that comprise the spawning stock. Alewife *Alosa pseudoharengus*, an anadromous Clupeid native to the Atlantic coast of the United States, has established in Lake Michigan as an important prey fish. Chinook salmon *Oncorhynchus tshawytscha* are the dominant predator and an important recreational fish species that brings valuable revenue to the region. The viability of the alewife population has been threatened, largely due to strong predation pressure (He et al., 2014; Tsehaye et al., 2014). Fishery managers are interested in better understanding the drivers of alewife recruitment to encourage sustainable predator-prey dynamics. I hypothesized that alewife recruitment success in Lake Michigan is influenced by both endogenous (i.e., internal population oscillations) and exogenous drivers (e.g., predation and environmental variability). Recruitment is notoriously variable and difficult to predict in fish populations; however, the ability of a population to produce strong year classes while on the brink of collapse, deserves attention. Empirical evidence has shown increased recruitment variability in exploited fish populations (Brander, 2005; Ottersen et al., 2006; Hsieh et al., 2010), and although exploitation has been shown to contribute to these recruitment dynamics, recent studies have illustrated that in some cases it is the interaction between external drivers that are influencing population trends (Bjørnstad et al., 2004; Hidalgo et al., 2011; Botsford et al., 2014). I investigated whether the endogenous oscillations of the alewife population have been altered due to the truncation of the age structure, and if, as a result, population fluctuations are tracking environmental signals more closely. Water temperature was chosen to represent environmental variability because it is an important driver of many ecosystem and population level processes. I explored the idea that coherence, or correlation, between the alewife population and an environment signal could shift through time following changes to the alewife age structure.

Study site

Our analysis is focused on Lake Michigan because understanding recruitment variability is important to fishery managers striving to maintain a viable alewife population to provide forage for ecologically and recreationally important fish species. During recent decades of low alewife abundance, recruitment has been characterized by high variability. Poor recruitment has been the norm, yet relatively large year classes have occasionally been observed (Figure 3.1), despite relatively low total abundance.

The Laurentian Great Lakes comprise unique ecosystems which have been highly altered through time. Many native fish populations have been reduced or extirpated due to overfishing, habitat destruction, nutrient loadings, and competition with non-native species. As native species have declined non-natives have filled in niche gaps becoming important components of the ecosystem function and predator-prey dynamics (Eshenroder and Burnham-Curtis, 1999). Alewife, an anadromous fish native to the Atlantic coast of the United States, ranging from Newfoundland to the Carolinas, were introduced into the Great Lakes as early as 1873 (Lake Ontario; Miller, 1957) and represent one of the many perturbations to these ecosystems. After establishing in Lake Ontario, alewife subsequently spread into each of the remaining lakes throughout the mid-1900s. When alewife arrived in Lake Michigan in the 1940s the abundance of top piscivores (namely lake trout *Salvelinus namaycush*) was severely depressed, due to overexploitation and sea lamprey *Petromyzon marinus* induced mortality. In the absence of predators and with an abundance of food, the alewife population exploded, composing more than half of the total fish biomass by 1968 (Ludwig, 2013). Alewife were affecting native fish species through competition and predation on eggs and larvae, and they were also affecting the human population as mass die-off events were occurring with dead alewife washing up on the shores of Lake Michigan (Brown Jr, 1968). Fishery managers, in response to the alewife situation, developed a piscivore stocking program aimed at simultaneously controlling the non-native populations, rehabilitating native piscivorous fish species, and creating recreational fishing opportunities (Claramunt et al., 2012). Chinook salmon emerged as the preferred species to stock given their fast growth, low production costs, value as a recreational fishery, and high predation rate on alewife (Hansen et al., 2002).

Chinook salmon have established successfully in Lake Michigan, and are now supported through natural reproduction and continued, yet reduced, stocking efforts (FWS/GLFC, 2010). Alewives serve as the preferred and dominant prey species for the salmonids in the lake, with the majority of alewife mortality thought to be from Chinook predation (Madenjian et al., 2002). Throughout the history of the stocking program, reaching an appropriate predator-prey balance has been a management concern. Overstocking in the 1980s led to a crash of the alewife, and a subsequent decline of Chinook (Hansen et al., 2002; Benjamin and Bence, 2003). The release from predation pressure allowed the alewife to rebound, and to this day, managers are working to maintain viable populations of both predator and prey, native and non-native. The interest in maintaining the Chinook population is largely due to the economic and recreational benefits it supports. In recent years, the alewife population in Lake Michigan has declined substantially, accompanied by signs of a truncated age structure. Predation has been identified as the dominant force driving the decline (He et al., 2014; Tsehaye et al., 2014), with evidence of preference for larger alewife by adult Chinook (Rybicki and Clapp, 1996). Historically, eight year old fish were observed in the age composition of survey catches with some fish reaching nine years of age; since 2012, age five has been the maximum observed age (Madenjian et al., 2014). Stocking of Chinook has been reduced to promote alewife growth and survival, yet the population has failed to rebound.

Methods

Data and preliminary calculations

Using survey indices of abundance-at-age obtained from standardized annual bottom trawl surveys conducted by the U.S. Geologic Survey Great Lakes Science Center (USGS GLSC), I analyzed alewife recruitment dynamics through time with respect to spawning stock size, age structure of the population, and environmental indices. Wavelet analysis was used as a descriptive tool to decompose the variability in the index of alewife biomass into oscillatory components with the potential to vary across time in both frequency and amplitude, revealing dominant signals or oscillations in the time series. To evaluate correlation between alewife population fluctuations and environmental signals at common frequencies, I used wavelet coherence analysis. A strong correlation between two signals indicates a common frequency at which signals could be amplified due to resonant behavior. I then performed more traditional stock-recruit analyses to predict recruitment based on spawning stock biomass and temperature indices for comparison with the exploration of shifting resonance.

Environmental variability

Climate has been identified as one of the most important drivers of change in a wide range of systems, including freshwater ecosystems, primarily due to associated temperature changes (Rosenzweig et al., 2007). It was assumed that the time-series of water temperatures was representative of large-scale environmental variation able to affect alewife populations. Water temperature profiles, obtained from NOAA's Great Lakes Environmental Research Laboratory (GLERL), are the predicted temperatures at depth based on a model of evaporation and thermal fluxes (Croley, 1989, 1995). The model incorporates measurements of air temperature, humidity, wind speed, and cloud cover to generate estimates of mean water temperature at depth in 1 meter increments. These data include daily profiles from 1973-2011, averaged to obtain a monthly mean temperature, and were used to characterize environmental variability and long-term temperature trends in the Lake Michigan.

Summer temperatures were hypothesized to have a positive effect on alewife recruitment due to optimal growing conditions for spring hatches, while colder winter temperatures were predicted to have a negative effect on recruitment due to overwinter mortality (Madenjian et al., 2005; Collingsworth et al., 2014). I evaluated the effects of summer and winter temperatures individually, as well as the combination of the two in predicting recruitment. For each year, a value for the summer index was calculated as the mean water temperature between May 1 and August 31. The winter index was calculated as the mean temperature (°C) between December 1 and April 30.

Alewife catch data

Alewife abundance-at-age indices were derived from the annual USGS GLSC bottom trawl surveys (1973-2014). Each fall, the bottom trawl survey samples sites along seven transects throughout Lake Michigan, with nine transects in some years. The sampling protocol is to tow the trawl net along depth contours at 9-m depth increments for 10 minutes per site (Madenjian et al., 2014). The survey gear has low detection of age one and two fish; therefore, when assessing trends I evaluated data for those ages thought to be fully recruited to the sampling gear: fish aged three and older (Madenjian et al., 2005). Throughout this paper, when I refer to 'recruits' I am referring an index of recruitment based on age-3 abundance, lagged three years to align with the year in which that cohort of fish would have been age-0. For example, the abundance of age-3 alewife in the year 1983 is used as an index of recruitment for the 1980 year-class. Spawning stock biomass is the aggregate biomass of all fish aged three and older in a given year. Catches from the seven transects were combined and used as the catch-at-age index.

Analyses

Time series analysis

I used wavelet analyses to identify patterns in the recruitment and spawning stock biomass time series. Wavelet analysis decomposes variability in time series into oscillatory components localized in the time and frequency domains (Cazelles et al., 2008). I was interested in how the dominant frequency spectra of the signal (i.e., time series of alewife recruitment or biomass) were changing over time, and how those signals behaved in relation to temperature fluctuations. For this analysis, I chose the Morlet mother wavelet because of my interest in quantitatively assessing the phase interactions between different time series (Cazelles et al., 2008). Wavelet coherency analysis was then used to evaluate the evolution of the correlation between the alewife time series (biomass) and the seasonal temperature indices; coherence (R_w^2) is constrained between 0 and 1 (Cazelles et al., 2008). Phase arrows in the coherence plots are used to indicate whether the two signals being compared are in phase or out of phase when strong correlation exists (Gouhier and Grinsted, 2012). Arrows pointing to the right indicate the signals are in phase with one another, whereas arrows pointing to the left suggest that the signals are in anti-phase. Arrows pointing upward suggest that alewife recruitment or biomass is lagging the temperature signal, and downward arrows indicate the alewife signal is leading the respective time series. Readers are referred to Torrence and Compo (1998) and Cazelles et al. (2008) for a detailed description of the wavelet analysis. These analyses were conducted with the R package biwavelet (Gouhier and Grinsted, 2012).

Stock-recruit modeling

The spawning stock of a population, comprised of reproductively mature individuals, is often estimated as the biomass of those individuals as opposed to abundance, especially when considering stock-recruit relationships. The consideration of maternal effects is one of the main reasons for considering a metric that extends beyond abundance alone. Older females tend to be larger and more fecund, with the potential for higher quality eggs (Hilborn and Walters, 1992). Alewife in Lake Michigan mature at about age 3; however, reproductive potential doesn't peak until about age 7 (Lake and Schmidt, 1997). To account for the disproportionate egg production by age class, and potential effects of age-truncation on recruitment, I modeled spawning stock biomass (SSB) as the abundance at age N_a multiplied by the average weight-at-age W_a. Catch-at-age data were converted to catch-at-length and then used an allometric growth equation with parameters from Madenjian et al. (2003) to generate biomass estimates. Because I do not have data for the most recent years, I assumed the length-weight relationship from the terminal year in their study has remained constant throughout the most recent years.

$$W_a = \alpha L_a^{\beta}$$

Because SSB is an aggregate of age classes, it provides only a very coarse picture of population structure.

$$SSB_y = \sum_{a=3}^{a\max_y} N_{a,y} W_{a,y}$$

For fish populations, stock-recruit models are used to predict recruitment strength based on the size of the spawning stock. The Ricker stock-recruit model (Ricker, 1954) is one of several commonly used models to estimate the relationship between spawning stock size and recruits in fish populations, and was chosen for this analysis because alewife recruitment in Lake Michigan has been shown to decline at high spawner biomass (O'Gorman et al., 2004; Madenjian et al., 2005). The general Ricker model

$$\mathrm{R}_y = \alpha \mathrm{SSB}_y e^{(-\beta \mathrm{SSB}_y + \epsilon_y)}$$

predicts recruitment (R), in each year (y), as a function of spawning stock biomass (SSB) where α is the density-independent parameter, and β is a measure of density-dependence. This equation can be linearized by taking the natural logarithm of both sides, assuming lognormal error structure.

$$ln(\mathrm{R}_y/\mathrm{SSB}_y) = a - b\mathrm{SSB}_y + \epsilon_y$$

$$\epsilon_y \sim N(0, \sigma^2)$$

I evaluated the standard Ricker model as well as multiple modified models to evaluate the predictions that recruitment varies in response to temperature, and that the relationship between recruitment and temperature is not constant over time. To address the prediction that recruitment is influenced by temperature, I included a linear effect of temperature (both summer SUM and winter WIN indices).

$$ln(R_y/SSB_y) = a + b\mathrm{SSB}_y + cSUM_y + \epsilon_y$$

$$ln(R_y/SSB_y) = a + b\mathrm{SSB}_y + cWIN_y + \epsilon_y$$

$$ln(R_y/SSB_y) = a + b\mathrm{SSB}_y + cSUM_y + dWIN_y + \epsilon_y$$

The effects of the environment on population dynamics rarely conform to assumptions of linearity; I therefore evaluated the possibility of nonlinear temperature effects on recruitment by using generalized additive models. The smoothing function f applied to temperature is a penalized regression spline; the R package mgcv (Wood, 2006) was used to fit these models.

$$ln(R_y/SSB_y) = a + b\mathrm{SSB}_y + f(SUM_y) + \epsilon_y$$

$$ln(R_y/SSB_y) = a + b\mathrm{SSB}_y + f(WIN_y) + \epsilon_y$$

To evaluate whether the relationship between recruitment and temperature varied through time, I considered a model with a linear effect of temperature and a linear trend (i.e., effect of year), following Ottersen et al. (2013).

$$ln(R_y/SSB_y) = a + b\text{SSB}_y + c(SUM_y) + d(YEAR_y) + \epsilon_y$$

$$ln(R_y/SSB_y) = a + b\text{SSB}_y + c(WIN_y) + d(YEAR_y) + \epsilon_y$$

A separate model was used to further evaluate the interaction effect between year and temperature.

$$ln(R_y/SSB_y) = a + b\text{SSB}_y + c(SUM_y) + d(YEAR_y) + e(SUM_yYEAR_y) + \epsilon_y$$

$$ln(R_y/SSB_y) = a + b\text{SSB}_y + c(WIN_y) + d(YEAR_y) + e(WIN_yYEAR_y) + \epsilon_y$$

In total, I evaluated a set of 10 candidate models that represented our hypotheses about how the potential factors influenced recruitment. Akaike's information criterion, corrected for small sample size (AIC$_c$),

$$AIC_c = 2k - 2logLik + \frac{2k(k+1)}{n-k-1}$$

was used as the model evaluation criterion, where k is the number of estimated parameters, n is the number of observations, and $logLik$ is the log-likelihood from the fitted model (Akaike, 1973; Burnham and Anderson, 2002). All covariates were standardized for the stock-recruit modeling, to improve convergence and interpretability of the parameters.

To address parameter uncertainty, a nonparametric bootstrap technique was employed, resampling the data 500 times, to generate distributions of parameters estimates from each model iteration. The basic idea for this bootstrapping approach is to fit a model to observed data and obtain the predictions (or fitted values). The residuals from the model are then sampled (with replacement) and added to each fitted value from the original model. The model is refit to the new data, and parameter estimates obtained. This is repeated many times, yielding a distribution of parameter values that can be used to evaluate parameter uncertainty. This was done for each of our top models.

Results

From the early-2000s on, the age structure of the alewife population became noticeably truncated with most of the fish aged five and younger (Figure 3.2). However, individuals from the strong 1998 year class persisted to the older age classes. The recent alewife population dynamics are characterized by greater variability, boom and bust recruitment years, than has been observed historically (Figure 3.3). The summer and winter temperature indices both displayed a step change towards warmer conditions during the late 1990s which persisted through the end of the time series (Figure 3.3).

Alewife recruitment lacked a strong oscillatory signal until about the early 1990s at which point a strong 3-4 year periodicity developed and persisted through the mid-2000s (Figure 3.4 A). Additionally, a weak low frequency (∼11 year) oscillation was observed. In the wavelet plots, the color gradients indicate the power of different frequencies through time (dark red indicating a strong signal and dark blue indicating virtually no signal); the right-hand plots depict the global wavelet spectrum which shows the frequencies that dominate throughout the entire time series (Figure 3.4). A periodic signal in the alewife spawner biomass time series wasn't detected until the mid-1990s when a 4-6 year periodicity emerged and persisted through the cone of influence (Figure 3.4 B). The cone of influence is the white shaded area along the bottom and outer portions of the wavelet plots; the accuracy of this region is reduced due to the estimation procedure, length of the time series, and periodicity of signal (Torrence and Compo, 1998). For that reason, I have described results from the wavelet plots only for the region inside the cone of influence. The summer index showed a consistent signal at a 4-year cycle as well as low frequency 11-12 year signal (Figure 3.4 C). Transient signals were also apparent at approximately 2 and 7-year cycles. The winter index, on the other hand, showed several, more ephemeral peaks: 2, 4, and 7-year periodicities which developed during the 1990s and persisted for about a decade (Figure 3.4 D). Prior to the 1990s, strong periodic oscillations in the winter signal were lacking.

Wavelet coherence analysis revealed strong in-phase coherence ($R^2_w \approx$ 0.8-1) between alewife recruitment and the summer index throughout the 1990s and 2000s at periodicities ranging from 2-5 years (Fig. 3.5 A), and moderate coherence at the leading edge of the cone of influence from about 8-12 years, with little coherence prior. There was strong coherence ($R^2_w \approx$ 0.7-0.9) between alewife recruitment and winter temperatures at high frequencies during the mid-1990s, as well as lagged coherence ($R^2_w \approx$ 0.6-0.8) around a 4 year oscillation throughout the 1990s (Figure 3.5 B). The coherence between recruitment and the temperature indices, over the past decade, appears to be most prominent at a frequency that approximates the mean age of the spawning stock (Figure 3.3), however there is considerable uncertainty in that signal. There was less coherence between spawner biomass and the temperature indices (Fig. 3.5 C, D); however correlation begins to develop during the mid-2000s, but remains weak within the region of inference.

Out of the candidate set of stock-recruit models, four models emerged as superior based on our model selection criterion (lowest AIC$_c$; Table 3.1). The top model included spawning stock biomass, an additive effect of the summer temperature index, and a linear temporal trend in the intercept, explaining 34% of the variability in the recruitment (Table 3.2). Warmer summer temperatures had a positive effect on recruitment ($\delta_{SUM} = 0.56$) while mean recruitment declined over time ($\delta_{YEAR} = -0.44$). The second best model was similar to the top model, with the addition of an interaction term between summer temperatures and year, suggesting a positive trend in the effect of temperature through the time series ($\delta_{YEAR*SUM} = 0.33$). The remaining models indicated similar parameter estimates in their shared regression coefficients. The winter temperature index was included in one model and showed a negative effect, suggesting that warmer winter temperatures were less favorable for alewife recruitment ($\delta_{WIN} = -0.37$). Nonlinear temperature effects did not appear in any of the top models. The bootstrapped parameter estimates indicated that the estimates from the top stock-recruit models were reasonably robust (Appendix A).

All four of the top models were able to predict the mean recruitment fairly well (Figure 3.6). Even so, no model was able to capture the rare high recruitment events with much success. The residuals from the stock-recruit model were reasonably normally distributed (on the log scale). When back-transformed to the original scale a few large residuals associated with the 1995, 1998, and 2010 year classes stood out. Analysis of the residuals against the age structure metrics (MA and H) failed to explain remaining variation in the recruitment time-series. There was very little correlation between the residuals and both MA and H (corr $< |0.15|$).

Discussion

In Lake Michigan, alewife biomass has generally been declining over time, although infrequent strong year classes have been observed, substantially boosting biomass. In recent decades, the age composition reflects fewer old fish. Predation pressure in a freshwater ecosystem has been an important driving force in inducing similar changes to the population structure of a prey species, as fishing has been shown to do to harvested populations in the marine environment (Anderson et al., 2008; Hsieh et al., 2010), through reduced abundance and a truncation of the age structure. The wavelet analysis conformed largely to the hypothesis, that with a truncated age structure the endogenous population oscillations can strengthen, and tend to approximate the mean spawner age.

Cohort resonance is a phenomenon where the population begins to echo the stochasticity in recruitment due to a reduction in the ability to smooth that variability on account of several reproducing age classes. Multiple reproducing age classes can help to stabilize or buffer the population against variability in the environment, thereby dampening the effects of individual cohort contributions on subsequent recruitment. When a source of mortality has a disproportionate effect on older ages in a targeted population, the life cycle is accelerated due to reduced longevity. In the wavelet analysis, a strengthening of a periodic signal at approximately the mean spawner age develops during the latter years of the time series, first in the recruitment series then spawner biomass. As these signals develop, greater coherence with temperature at a similar frequency is observed. During the mid-1990s two very strong year classes were observed during the time period of strong coherence with temperature. In the latter years, the development of a signal in the spawner biomass begins to develop at approximately the mean spawner age, a potentially important observation that could have influence on the population in the years following. Although I have observed patterns supportive of my hypothesis, the most severe age truncation doesn't begin until about 2012, years that extend beyond the cone of influence. As a result, the ability to make inference from about the population is inhibited by the length of the time series, and the proximity of major shifts to the terminal years in the data.

These results offer some support for the theoretical behavior of an age truncated population, which pose important questions about the vulnerability of this population to environmental fluctuations in the most recent years. From 2012 on no fish older than age five has been observed in the trawl survey (Figure 3.2). If the linkage between the alewife population and the environment strengthens, the alewife population could become more vulnerable to adverse conditions. The interest in resonant behavior in fish populations is typically associated with concerns of decline and even extinction risk, and less so, potential positive effects of the synchrony; however, despite continued low abundance and loss of older ages, another strong recruitment pulse was observed in 2010. A retrospective analysis in a few years, with additional data, could shed light on this prediction.

Hidalgo et al. (2011) showed that in European hake exploitation of the stock shifted the index of biomass from an internally generated 12-year oscillation, postulated to arise from density-dependent mechanisms, to a higher frequency signal. The higher frequency oscillations indicate greater reliance on recruitment strength. They also found through simulation, that with a truncated age structure, biomass began to track the environmental signal (i.e., white and red noise) more closely. Running the simulations for 200 years allowed for the evolution of hypothesized changes to be observed, while the patterns in the empirical data support their findings. The alewife time series is barely long enough to detect lower frequency signals, but there is evidence of a small region with increased strength at about a 7-8 year period, a signal that would correspond to a 2T signal that has been attributed to overcompensation (Botsford and Wickham, 1978).

Temperature can be influenced by large-scale climate processes as well as local weather conditions (Stenseth et al., 2003). Identification of variability at different time scales, revealed through wavelet analysis, does not provide insight into the mechanisms driving variability, but this information can be used to uncover linkages between physical and biological processes (Ménard et al., 2007). The indices of temperature used in this analysis were considered important exogenous drivers influencing the alewife population; however, I recognize that temperature is but one exogenous driver of population dynamics, yet can influence recruitment success through many pathways (e.g., survival and growth, phenology and abundance of prey resources, availability of alternate prey items for alewife predators).

The stock-recruit modeling suggested that temperature was an important factor in predicting recruitment, and that the influence of summer temperatures in particular has become stronger over time. The increase in the effect of temperature could be due to a step change to warmer, more favorable conditions as well as an amplification of the favorable conditions due to moderate synchrony between biomass and the summer temperature oscillations in the most recent years. The stock-recruit model indicated that warmer summer temperatures had a positive effect on recruitment, corroborating the results from Madenjian et al. (2005) and Collingsworth et al. (2014) and explaining a similar amount of recruitment variability (Collingsworth et al., 2014); however, I found no evidence of a clear temperature signal associated with the large recruitment events. Because I used age three as an index of recruitment, temperature could be influencing growth and survival at multiple earlier life stages, from hatch to age three. Warmer summer temperatures and colder winters both being favorable for recruitment seem at odds with one another, and in other studies the positive correlation between recruitment and winter temperatures has been described as spurious (Madenjian et al., 2005; Collingsworth et al., 2014). Underlying mechanisms of population dynamics are often elusive and difficult to identify; however, distinguishing patterns in empirical data can serve as a tool to develop more informed hypotheses.

The presence of cohort resonance effects from this analysis does not appear strong. Our ability to make inferences about cohort resonance was somewhat limited because age truncation appears more pronounced towards the end of the time series. Although the time series represents decades of monitoring effort, it remains relatively short for detecting periodic signals developing in the most recent years. Evaluating additional covariates, as temperature is unlikely to be the only environmental signal influencing population dynamics, could prove valuable in disentangling the drivers of alewife dynamics. For management to make use of these patterns additional work will be required to elucidate the mechanisms driving recruitment success. For example, are these banner years driven by spawning success, initial growth due to food abundance and phenology, reduced competition or reduced predation rates because of the availability of other fish species? These are important questions that remain unanswered.

Incorporating age structure into analyses developed to predict recruitment and population dynamics may sometimes lead to finer-scale insights than aggregate measures. It will be interesting to evaluate the changes over the next few years to determine if the intrinsic cycle at the generational time perpetuates as total abundance remained low, and if synchrony with environmental variables is correlated with strong recruitment pulses. A report from Lake Ontario has documented that despite regional warming trends in recent years (13 of the last 20 years have been above average), the winters of 2014 and 2015 were both colder than the long-term average, and the summer temperatures were below average (Ontario Ministry of Natural Resources and Forestry, 2016). Observations of the fully recruited age-3 alewife in the years 2017 and 2018 may help to further elucidate the effects of temperature on this population. A similar analysis with Lake Huron data could also provide insight into the effects of age-truncation and environmental response to evaluate if synchrony with the environment played a role in the collapse of that population.

Acknowledgments

I sincerely thank Chuck Madenjian for his insightful comments and ideas regarding alewife dynamics in Lake Michigan. I also thank Tarik Gouhier for his support regarding the technical aspects of the biwavelet package along with Paris Collingsworth and Tim Hunter for sharing the temperature data.

References

Akaike, H. (1973). Maximum likelihood identification of Gaussian autoregressive moving average models. *Biometrika*, 60(2):255–265.

Anderson, C. N., Hsieh, C.-h., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., May, R. M., and Sugihara, G. (2008). Why fishing magnifies fluctuations in fish abundance. *Nature*, 452(7189):835–839.

Benjamin, D. M. and Bence, J. R. (2003). *Statistical catch-at-age framework for Chinook salmon in Lake Michigan, 1985-1996.* Michigan Department of Natural Resources, Fisheries Division Ann Arbor.

Berkeley, S. A., Hixon, M. A., Larson, R. J., and Love, M. S. (2004). Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, 29(8):23–32.

Bjørnstad, O. N. and Grenfell, B. T. (2001). Noisy clockwork: time series analysis of population fluctuations in animals. *Science*, 293(5530):638–643.

Bjørnstad, O. N., Nisbet, R. M., and Fromentin, J. (2004). Trends and cohort resonant effects in age-structured populations. *Journal of animal ecology*, 73(6):1157–1167.

Botsford, L. W., Holland, M. D., Field, J. C., and Hastings, A. (2014). Cohort resonance: a significant component of fluctuations in recruitment, egg production, and catch of fished populations. *ICES Journal of Marine Science: Journal du Conseil*, 71(8):2158–2170.

Botsford, L. W. and Wickham, D. E. (1978). Behavior of age-specific, density-dependent models and the northern California Dungeness crab (Cancer magister) fishery. *Journal of the Fisheries Board of Canada*, 35(6):833–843.

Brander, K. M. (2005). Cod recruitment is strongly affected by climate when stock biomass is low. *ICES Journal of Marine Science: Journal du Conseil*, 62(3):339–343.

Brown Jr, E. H. (1968). Population characteristics and physical condition of alewives, *Alosa pseudoharengus*, in a massive die-off in Lake Michigan, 1967. Technical report, Great Lakes Fishery Commission.

Burnham, K. and Anderson, D. (2002). Information and likelihood theory: a basis for model selection and inference. *Model selection and multimodel inference: a practical information-theoretic approach*, pages 49–97.

Cazelles, B., Chavez, M., Berteaux, D., Ménard, F., Vik, J. O., Jenouvrier, S., and Stenseth, N. C. (2008). Wavelet analysis of ecological time series. *Oecologia*, 156(2):287–304.

Claramunt, R. M., Madenjian, C. P., and Clapp, D. (2012). Pacific salmonines in the Great Lakes basin.

Collingsworth, P. D., Bunnell, D. B., Madenjian, C. P., and Riley, S. C. (2014). Comparative recruitment dynamics of alewife and bloater in Lakes Michigan and Huron. *Transactions of the American Fisheries Society*, 143(1):294–309.

Croley, T. E. (1989). *Lumped modeling of Laurentian Great Lakes evaporation, heat storage, and energy fluxes for forecasting and simulation*, volume 70. US Department of Commerce, National Oceanic and Atmospheric Administration, Environmental Research Laboratories, Great Lakes Environmental Research Laboratory.

Croley, T. E. (1995). Laurentian Great Lakes dynamics, climate, and response to change. In *The role of water and the hydrological cycle in global change*, pages 253–296. Springer.

Eshenroder, R. L. and Burnham-Curtis, M. K. (1999). Species succession and sustainability of the Great Lakes fish community. In Taylor, W. W. and Ferreri, C. P., editors, *Great Lakes fisheries policy and management: a binational perspective*, pages 141–180. University Press, East Lansing, Mich.

FWS/GLFC (2010). Great Lakes Fish Stocking database. U. S. Fish and Wildlife Service, Region 3 Fisheries Program, and Great Lakes Fishery Commission.

Gouhier, T. and Grinsted, A. (2012). biwavelet: Conduct univariate and bivariate wavelet analyses. *R package version 0.13*.

Hansen, M. J., Holey, M. E., Lynch, K., Jones, M., and Taylor, W. (2002). Ecological factors affecting the sustainability of Chinook and coho salmon populations in the Great Lakes, especially Lake Michigan. *Sustaining North American salmon: perspectives across regions and disciplines. American Fisheries Society, Bethesda, Maryland*, pages 155–179.

He, J. X., Bence, J. R., Madenjian, C. P., Pothoven, S. A., Dobiesz, N. E., Fielder, D. G., Johnson, J. E., Ebener, M. P., Cottrill, R. A., Mohr, L. C., et al. (2014). Coupling age-structured stock assessment and fish bioenergetics models: a system of time-varying models for quantifying piscivory patterns during the rapid trophic shift in the main basin of Lake Huron. *Canadian Journal of Fisheries and Aquatic Sciences*, 72(1):7–23.

Hidalgo, M., Rouyer, T., Molinero, J. C., Massutí, E., Moranta, J., Guijarro, B., and Stenseth, N. C. (2011). Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. *Marine Ecology Progress Series*, 426:1–12.

Hilborn, R. and Walters, C. J. (1992). Quantitative fisheries stock assessment: choice, dynamics and uncertainty. *Reviews in Fish Biology and Fisheries*, 2(2):177–178.

Hsieh, C.-H., Yamauchi, A., Nakazawa, T., and Wang, W.-F. (2010). Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences*, 72(2):165–178.

Lake, T. R. and Schmidt, R. E. (1997). The relationship between fecundity of an alewife (*Alosa pseudoharengus*) spawning population and egg productivity in Quassaic Creek, a Hudson River tributary (HRM 60) in Orange County, New York. *Final Reports of the Tibor T. Polgar Fellowship Program*, pages 1–26.

Ludwig, J. P. (2013). *The Dismal State of the Great Lakes.* Xlibris Corporation.

Madenjian, C. P., Bunnell, D. B., Desorcie, T. J., Ksotich, M. J., Armenio, P. M., and Adams, J. V. (2014). Status and trends of prey fish populations in Lake Michigan, 2013. Report, A report to the Great Lakes Fishery Commission, Lake Michigan Committee.

Madenjian, C. P., Fahnenstiel, G. L., Johengen, T. H., Nalepa, T. F., Vanderploeg, H. A., Fleischer, G. W., Schneeberger, P. J., Benjamin, D. M., Smith, E. B., Bence, J. R., et al. (2002). Dynamics of the Lake Michigan food web, 1970–2000. *Canadian Journal of Fisheries and Aquatic Sciences*, 59(4):736–753.

Madenjian, C. P., Holuszko, J. D., and Desorcie, T. J. (2003). Growth and condition of alewives in Lake Michigan, 1984–2001. *Transactions of the American Fisheries Society*, 132(6):1104–1116.

Madenjian, C. P., Höök, T. O., Rutherford, E. S., Mason, D. M., Croley, T. E., Szalai, E. B., and Bence, J. R. (2005). Recruitment variability of alewives in Lake Michigan. *Transactions of the American Fisheries Society*, 134(1):218–230.

Ménard, F., Marsac, F., Bellier, E., and Cazelles, B. (2007). Climatic oscillations and tuna catch rates in the Indian Ocean: a wavelet approach to time series analysis. *Fisheries Oceanography*, 16(1):95–104.

Miller, R. R. (1957). Origin and dispersal of the alewife, *Alosa pseudoharengus*, and the gizzard shad, *Dorosoma cepedianum*, in the Great Lakes. *Transactions of the American Fisheries Society*, 86(1):97–111.

O'Gorman, R., Lantry, B. F., and Schneider, C. P. (2004). Effect of stock size, climate, predation, and trophic status on recruitment of alewives in Lake Ontario, 1978–2000. *Transactions of the American Fisheries Society*, 133(4):855–867.

Ontario Ministry of Natural Resources and Forestry (2016). Lake Ontario Fish Communities and Fisheries: 2015 Annual Report of the Lake Ontario Management Unit. Ontario Ministry of Natural Resources and Forestry, Picton, Ontario, Canada.

Ottersen, G., Hjermann, D. Ø., and Stenseth, N. C. (2006). Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fisheries Oceanography*, 15(3):230–243.

Ottersen, G., Stige, L. C., Durant, J. M., Chan, K.-S., Rouyer, T. A., Drinkwater, K. F., and Stenseth, N. C. (2013). Temporal shifts in recruitment dynamics of North Atlantic fish stocks: effects of spawning stock and temperature. *Marine Ecology Progress Series*, 480:205–225.

Planque, B., Fromentin, J.-M., Cury, P., Drinkwater, K. F., Jennings, S., Perry, R. I., and Kifani, S. (2010). How does fishing alter marine populations and ecosystems sensitivity to climate? *Journal of Marine Systems*, 79(3):403–417.

Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fisheries Board of Canada*, 11(5):559–623.

Rosenzweig, C., Casassa, G., Karoly, D. J., Imeson, A., Liu, C., Menzel, A., Rawlins, S., Root, T. L., Seguin, B., Tryjanowski, P., et al. (2007). Assessment of observed changes and responses in natural and managed systems. *Climate Change*, pages 79–131.

Rybicki, R. W. and Clapp, D. F. (1996). *Diet of Chinook Salmon in Eastern Lake Michigan, 1991-93*. Michigan Department of Natural Resources, Fisheries Division.

Silvert, W. (1997). The role of interactions in long-term population cycles. *Environmental Modeling & Assessment*, 2(1-2):49–54.

Stenseth, N. C., Ottersen, G., Hurrell, J. W., Mysterud, A., Lima, M., Chan, K.-S., Yoccoz, N. G., and Ådlandsvik, B. (2003). Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society of London B: Biological Sciences*, 270(1529):2087–2096.

Torrence, C. and Compo, G. P. (1998). A practical guide to wavelet analysis. *Bulletin of the American Meteorological Society*, 79(1):61–78.

Tsehaye, I., Jones, M. L., Bence, J. R., Brenden, T. O., Madenjian, C. P., Warner, D. M., and Kraft, C. (2014). A multispecies statistical age-structured model to assess predator–prey balance: application to an intensively managed Lake Michigan pelagic fish community. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(4):627–644.

Wood, S. (2006). mgcv 1.3. R package.

Worden, L., Botsford, L. W., Hastings, A., and Holland, M. D. (2010). Frequency responses of age-structured populations: Pacific salmon as an example. *Theoretical Population Biology*, 78(4):239–249.

Tables

Table 3.1: Summary of the top Ricker stock-recruit models, the recruitment variability explained (R^2), and model selection criteria. Models within two AIC_c units from the top model were considered indistinguishable. SSB = spawning stock biomass; SUM and WIN, the seasonal temperature indices; YEAR is the year covariate used detect a linear trend; and YEAR*SUM, the interaction between year and summer temperatures.

Model Rank	Model	R^2	AIC_c	ΔAIC_c
1	SSB + SUM + YEAR	0.33	125.93	0.00
2	SSB + SUM + YEAR + YEAR*SUM	0.37	126.27	0.34
3	SSB + SUM + WIN	0.32	126.77	0.84
4	SSB + SUM	0.26	127.02	1.09

Table 3.2: Model parameter estimates from the top four Ricker stock-recruit models (in rank order). α and β are the standard parameters of the Ricker model. δ_x indicates regression coefficients associated with the additional covariates. x = not included in the model

Parameter	Model 1	Model 2	Model 3	Model 4
α	-4.22 (0.28)	-4.38 (0.30)	-4.42 (0.26)	-4.43 (0.27)
β	9.56e-5 (2.73e-5)	9.56e-5 (2.68e-5)	7.12e-5 (2.37e-5)	6.95e-5 (2.43e-5)
δ_{SUM}	0.57 (0.20)	0.53 (0.20)	0.55 (0.21)	0.38 (0.19)
δ_{WIN}	x	x	-0.35 (0.21)	x
δ_{YEAR}	-0.44 (0.23)	-0.50 (0.23)	x	x
$\delta_{YEAR*SUM}$	x	0.34 (0.23)	x	x

Figures

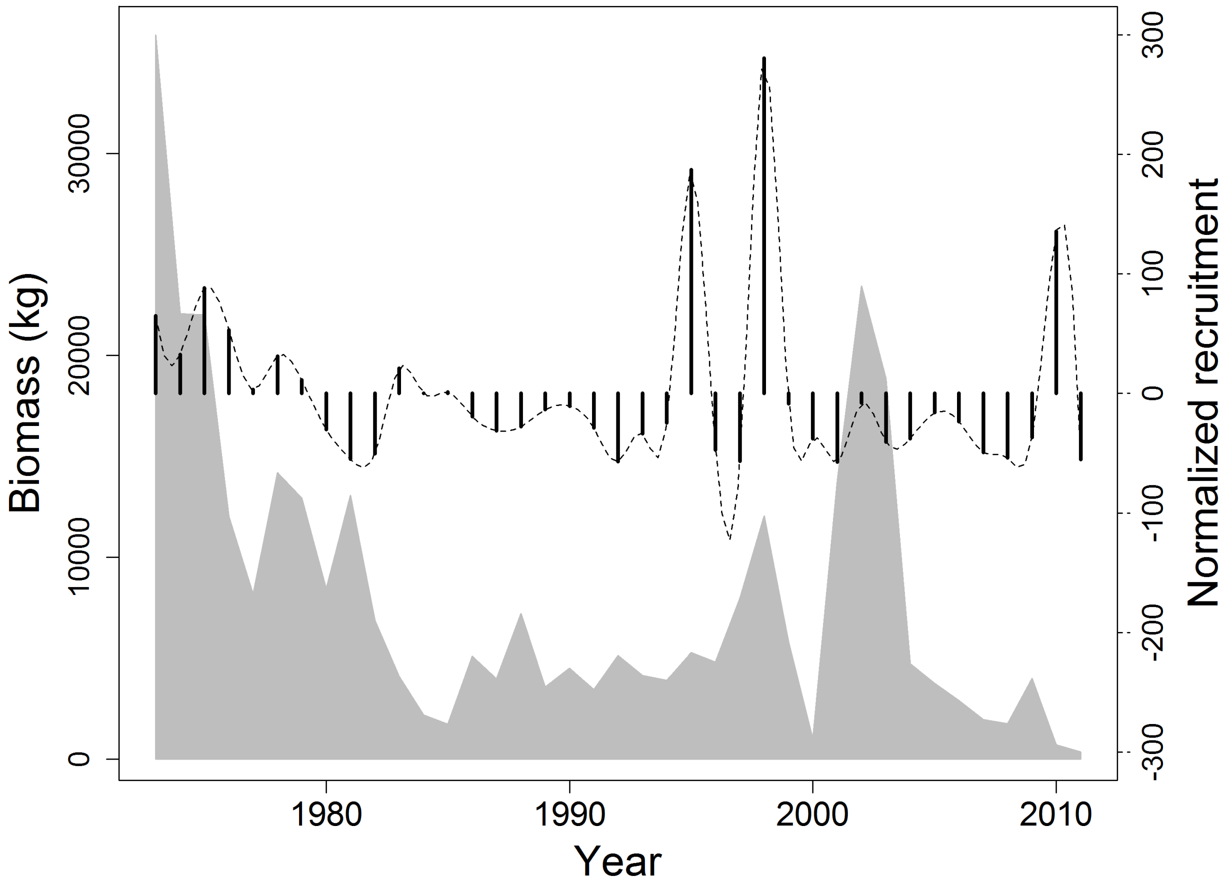

Figure 3.1: Alewife biomass (gray shaded area) is plotted alongside normalized recruitment (age-3 alewife) to show relationship across the time series.

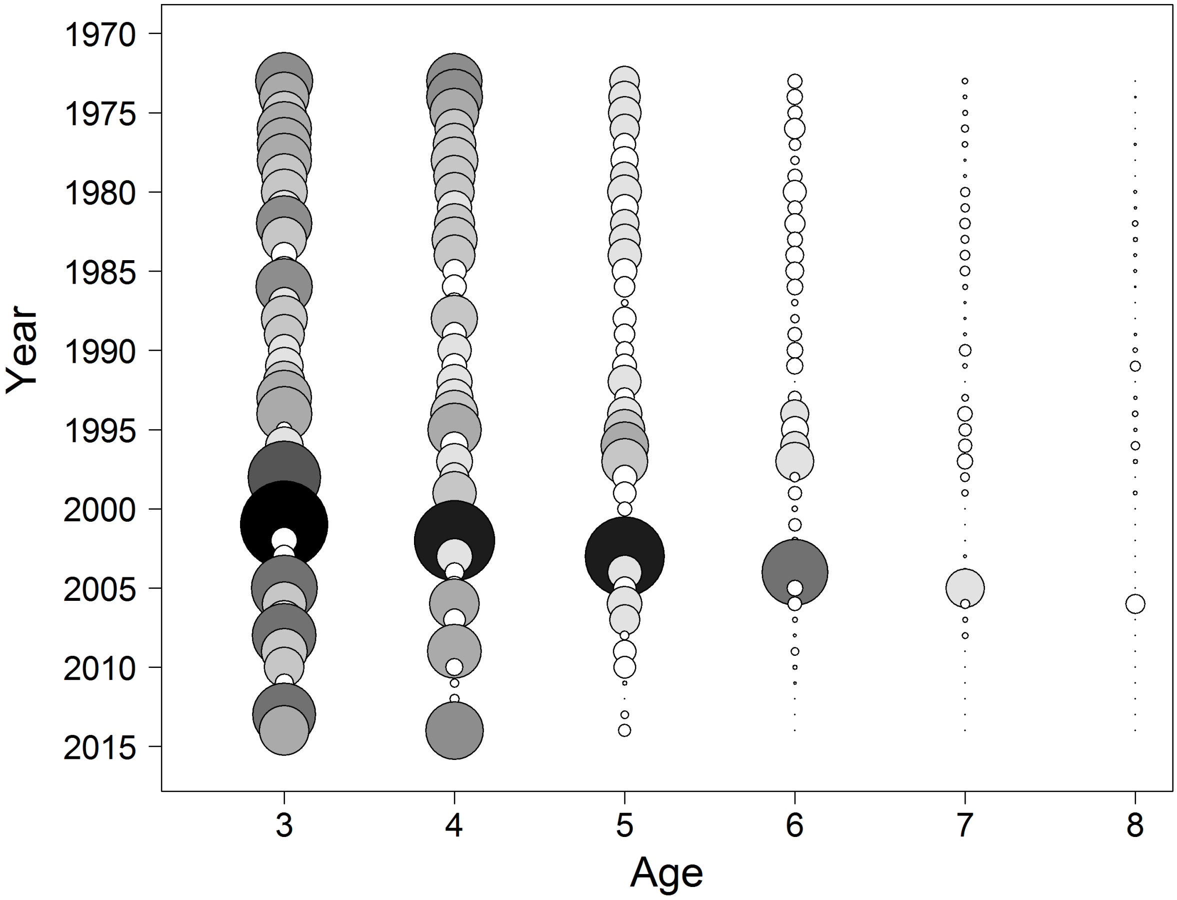

Figure 3.2: Bubble plot showing the relative proportion of each age class through time. The size and color of the circles represent the relative proportion of each age class. Larger darker circles represent a larger proportions while smaller, light circles represent smaller proportions.

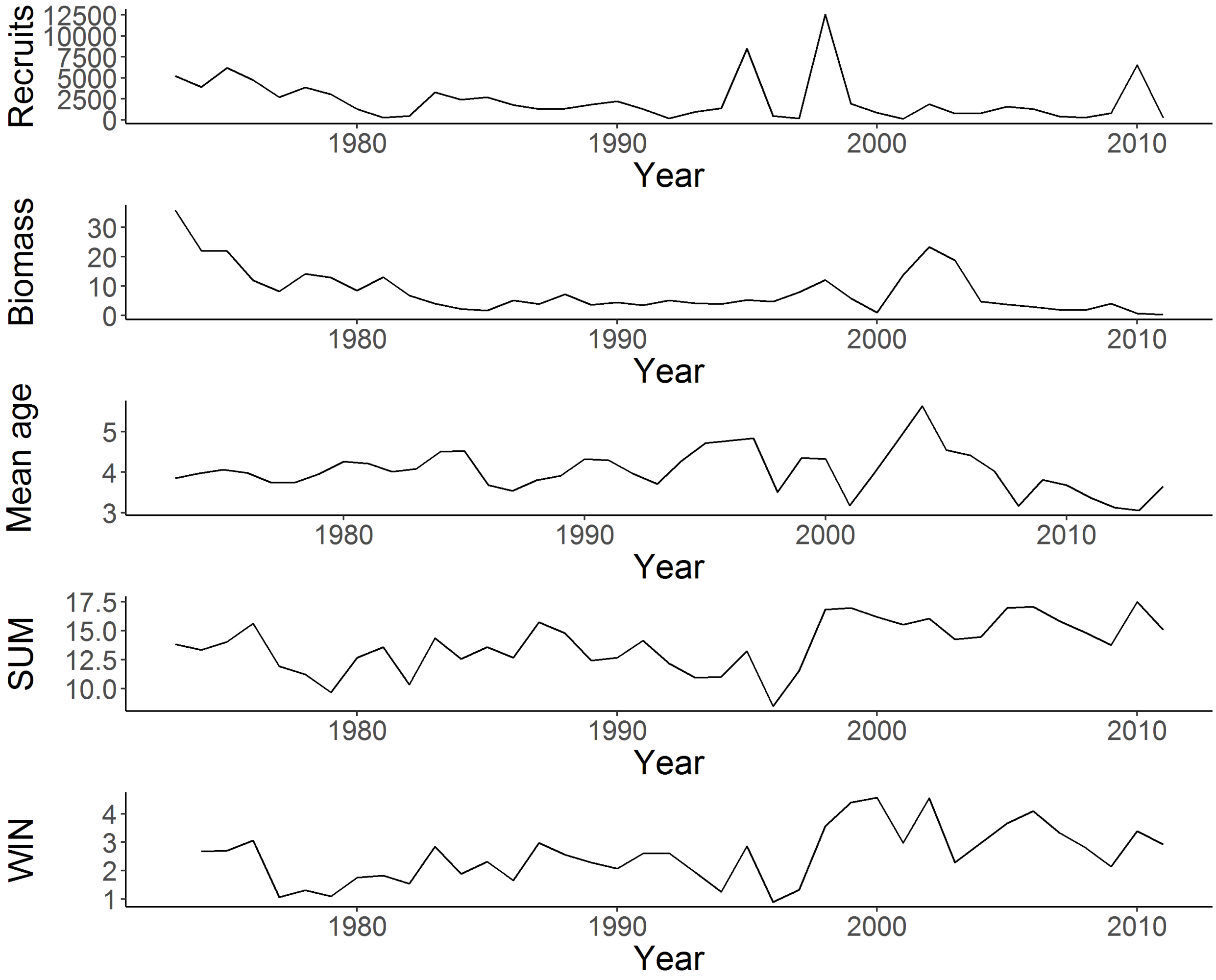

Figure 3.3: Time series of the observed recruitment index (number of age 3 fish), index of alewife biomass (thousands of kg), mean spanwer age, summer temperature and the winter temperature indices (°C; SUM and WIN, respectively).

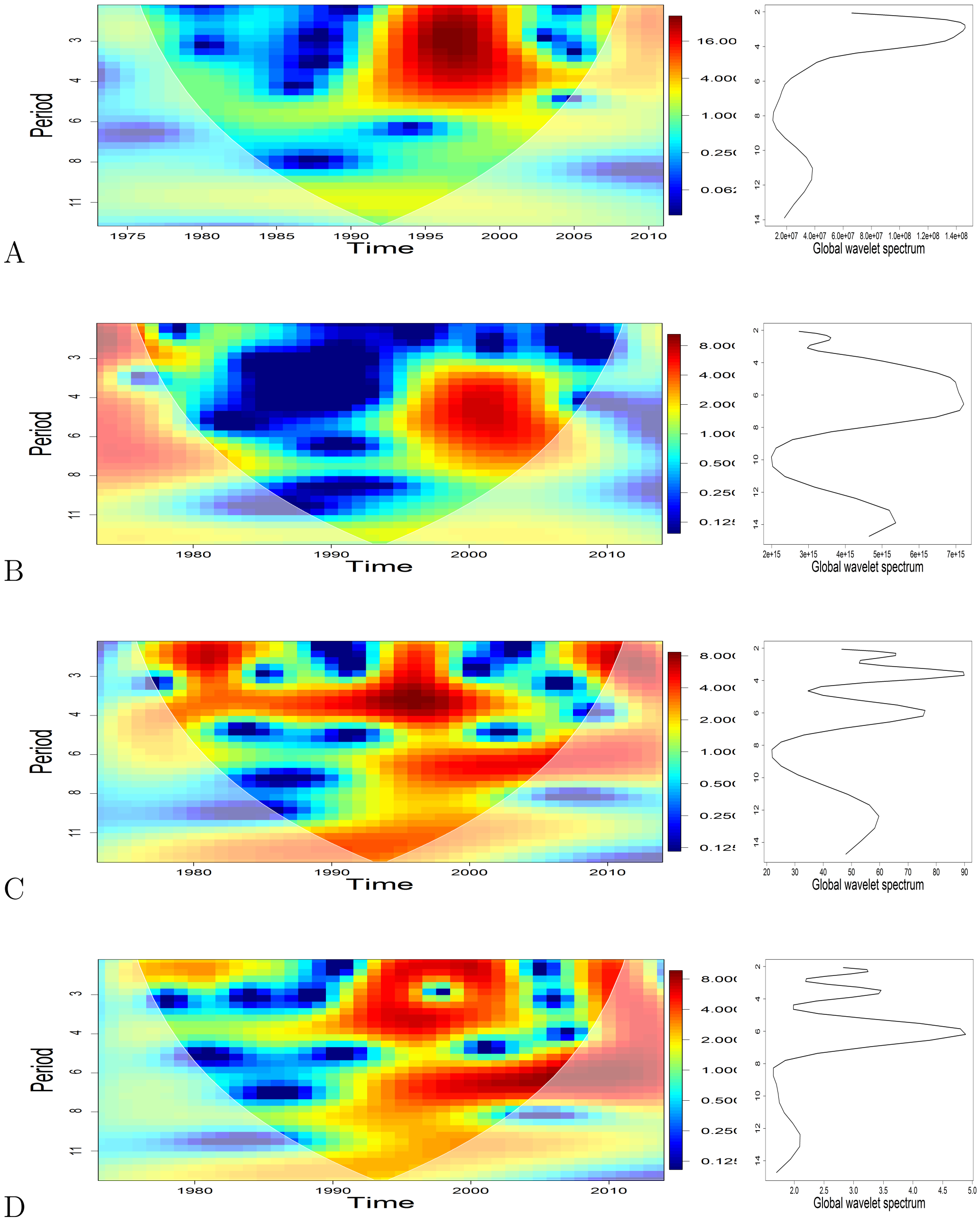

Figure 3.4: Graphically representation of the univariate wavelet analysis for (A) alewife recruitment, (B) alewife biomass, (C) summer temperature index, and (D) the winter temperature index for 1973-2011. The plots on the left-hand side show the strength of different periodic signals throughout the time series, ranging from a weak or non-exist signal (dark blue) to a strong signal (dark red). The plots on the right-hand side depict the global wavelet spectrum, or the dominant periodicities present throughout the aggregated time series.

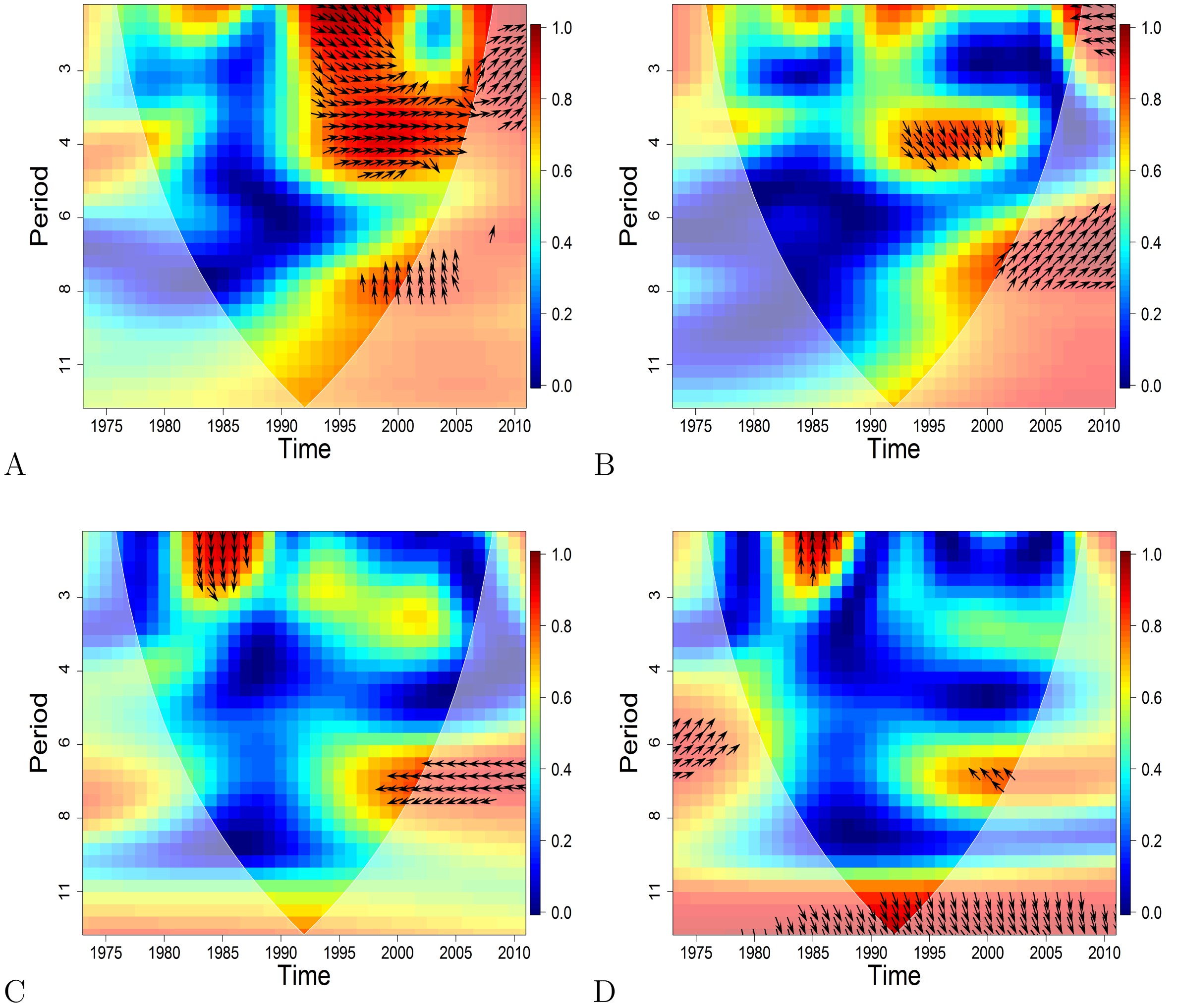

Figure 3.5: Wavelet coherence plots illustrate the strength of the correlation between two univariate time series: alewife recruitment and the summer and winter indices (A and B, respectively); and alewife biomass and the summer and winter indices (C and D, respectively). The colors indicate the strength of the correlation with dark blue representing no to very low correlation and dark red representing a strong correlation.

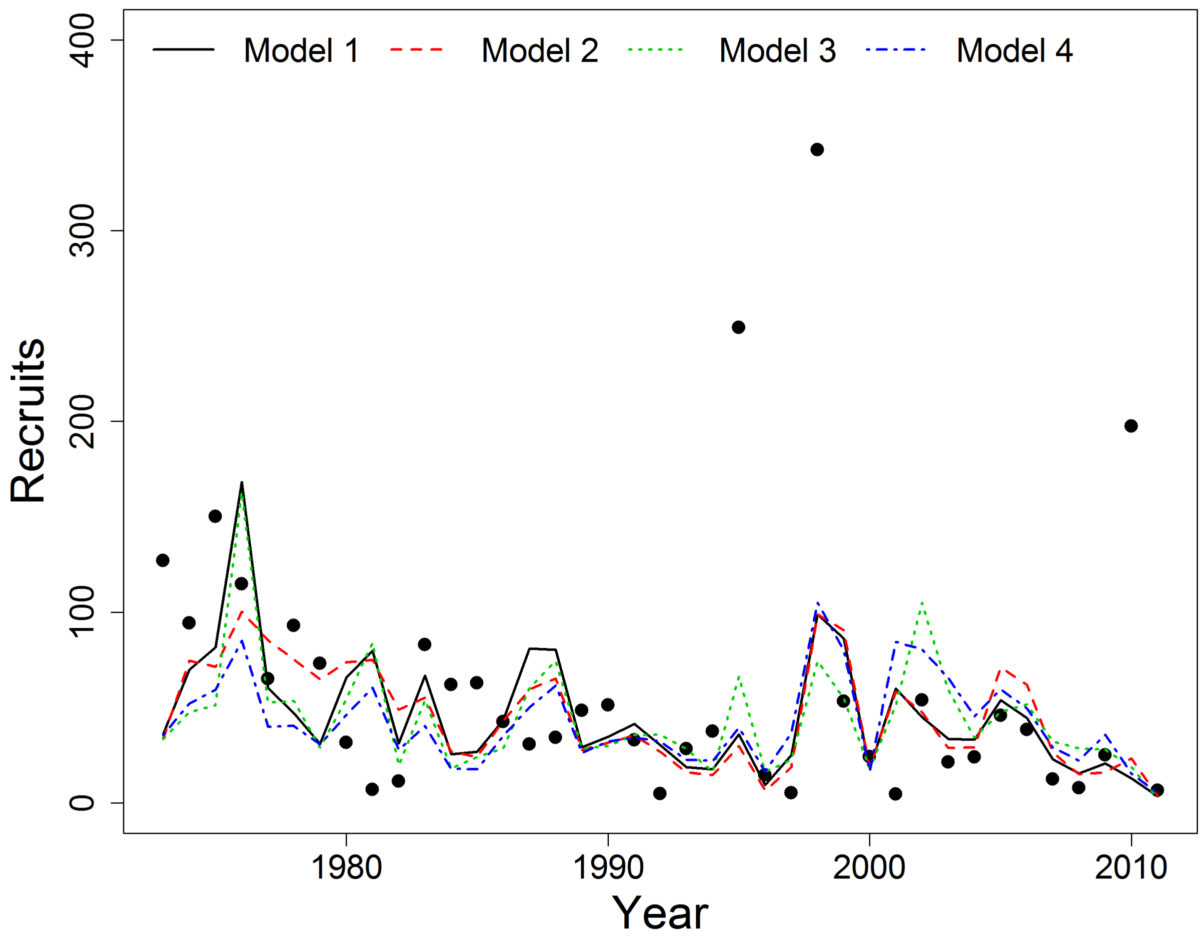

Figure 3.6: Observed recruitment over time, plotted with predicted recruitment from the top four models.

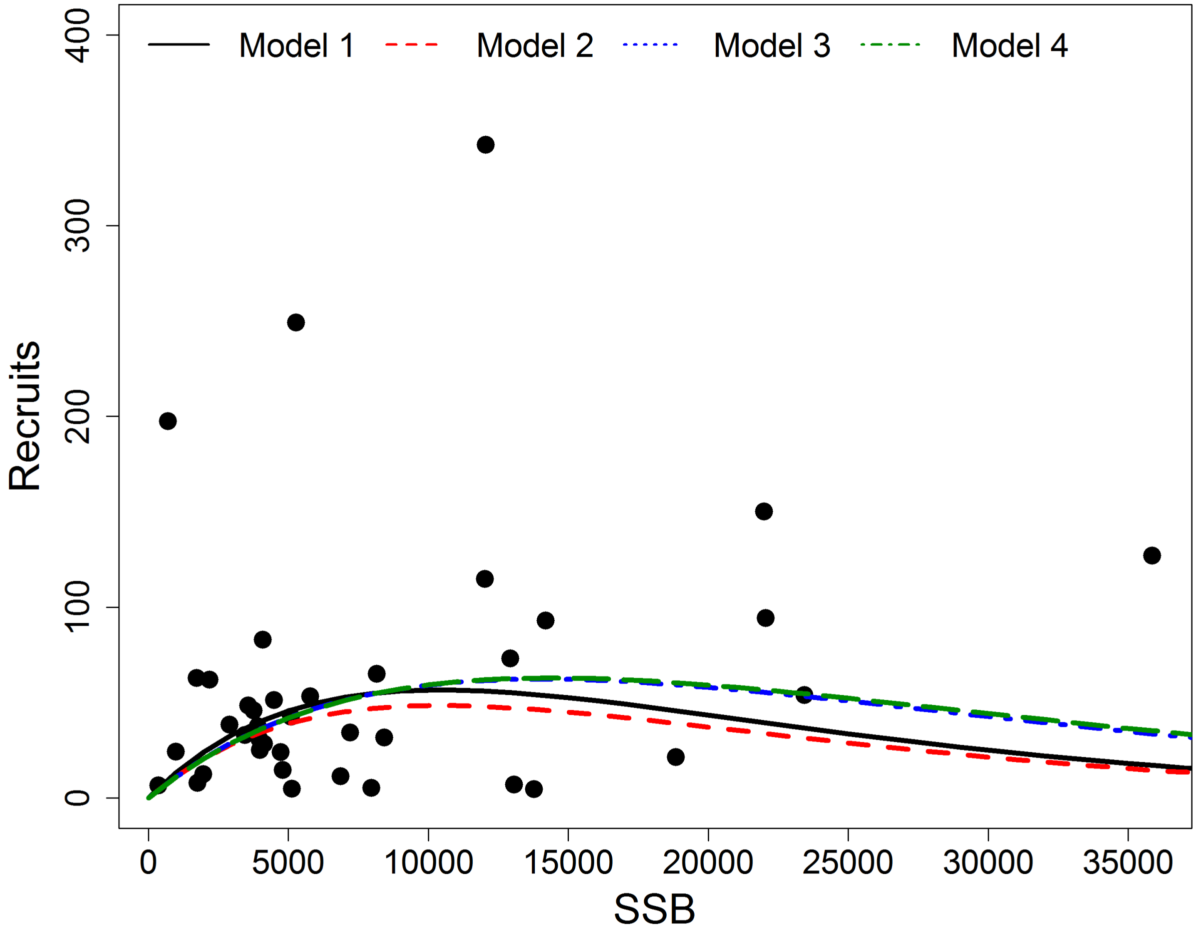

Figure 3.7: Mean stock-recruit relationships predicted by each of the top models. The points represent observed data.

Appendix 3.A

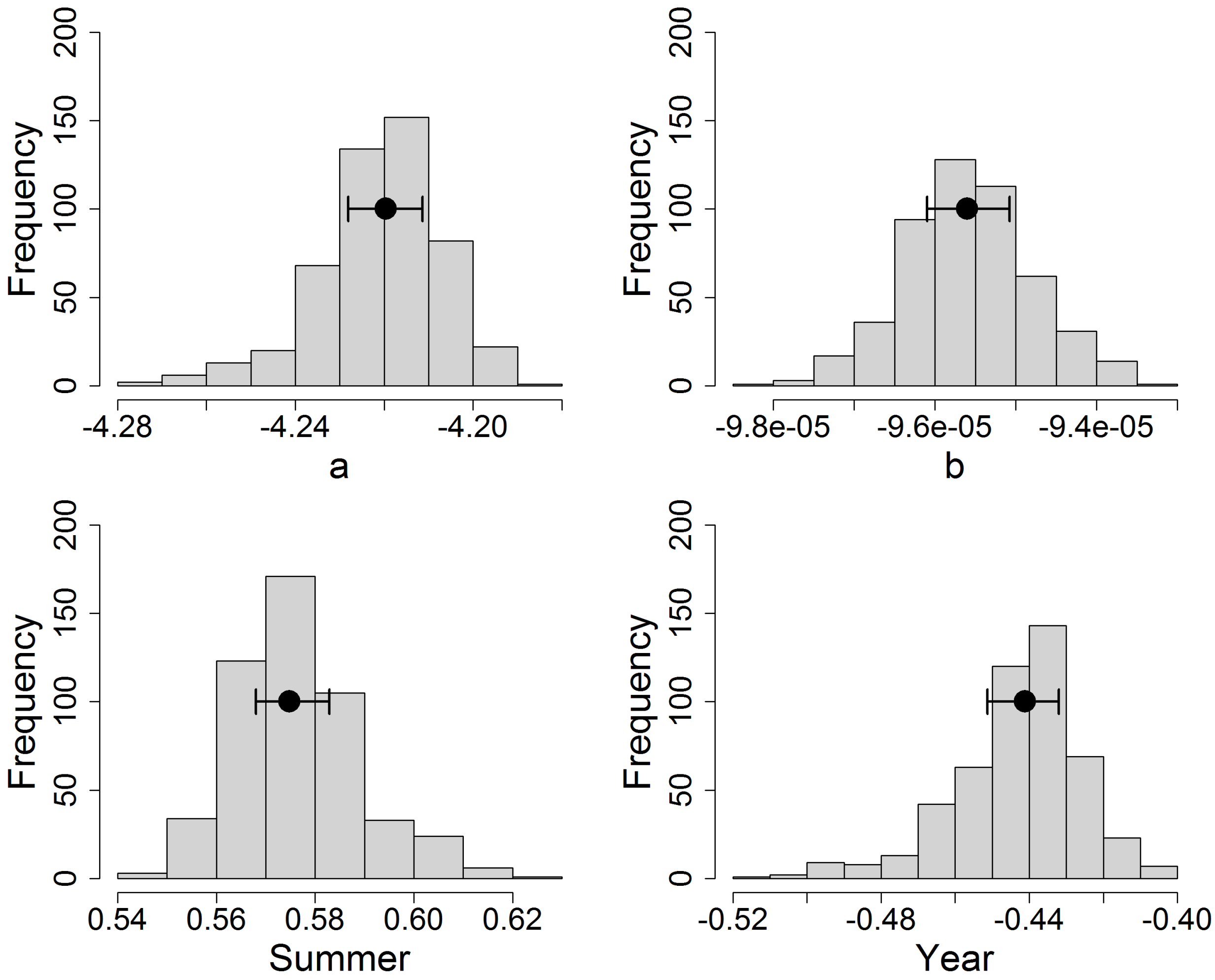

Figure 3.A1: Bootstrapped parameter estimates from Model 1. The solid dot represents the median and the bars represent the first and third quartiles.

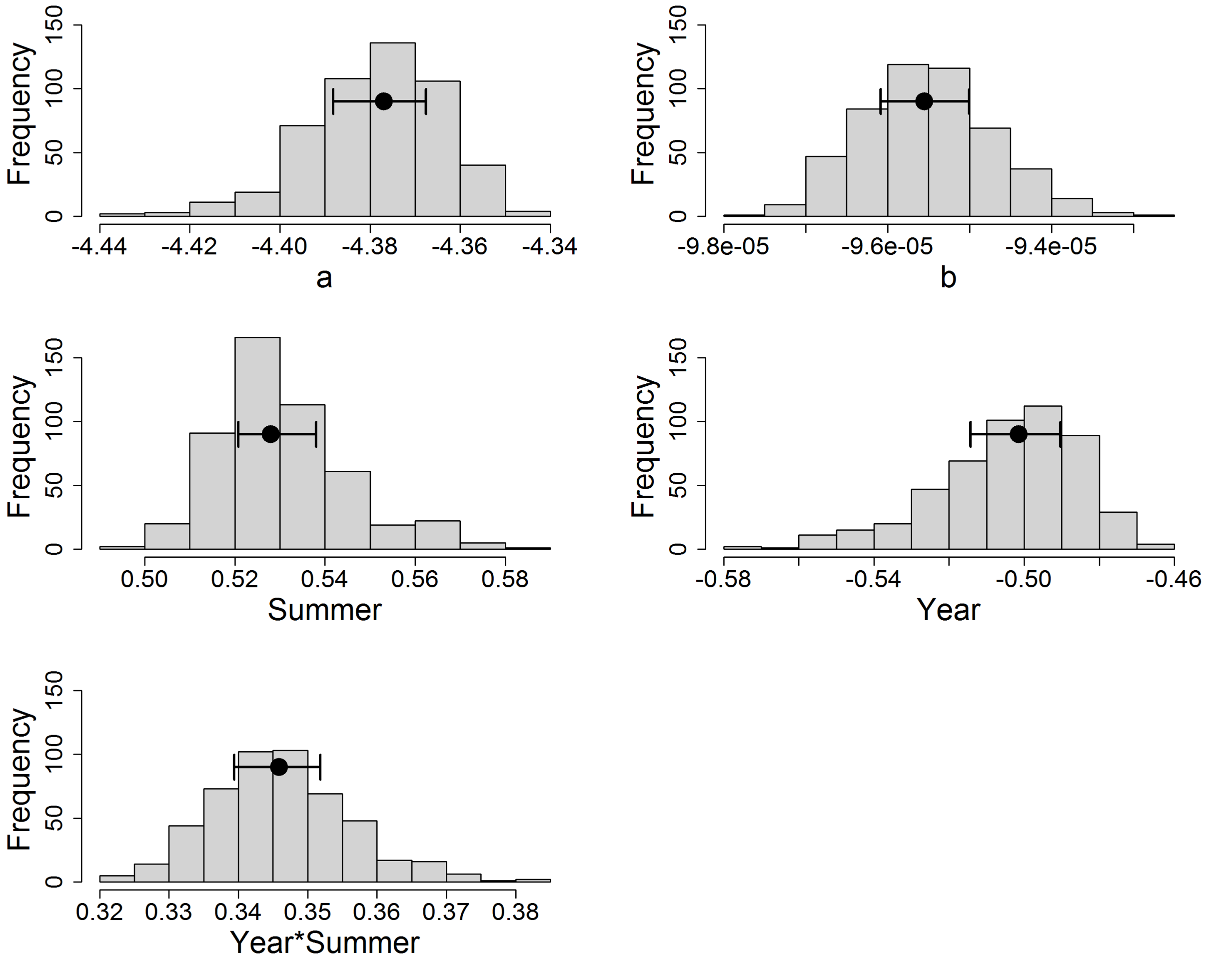

Figure 3.A2: Bootstrapped parameter estimates from Model 2. The solid dot represents the median and the bars represent the first and third quartiles.

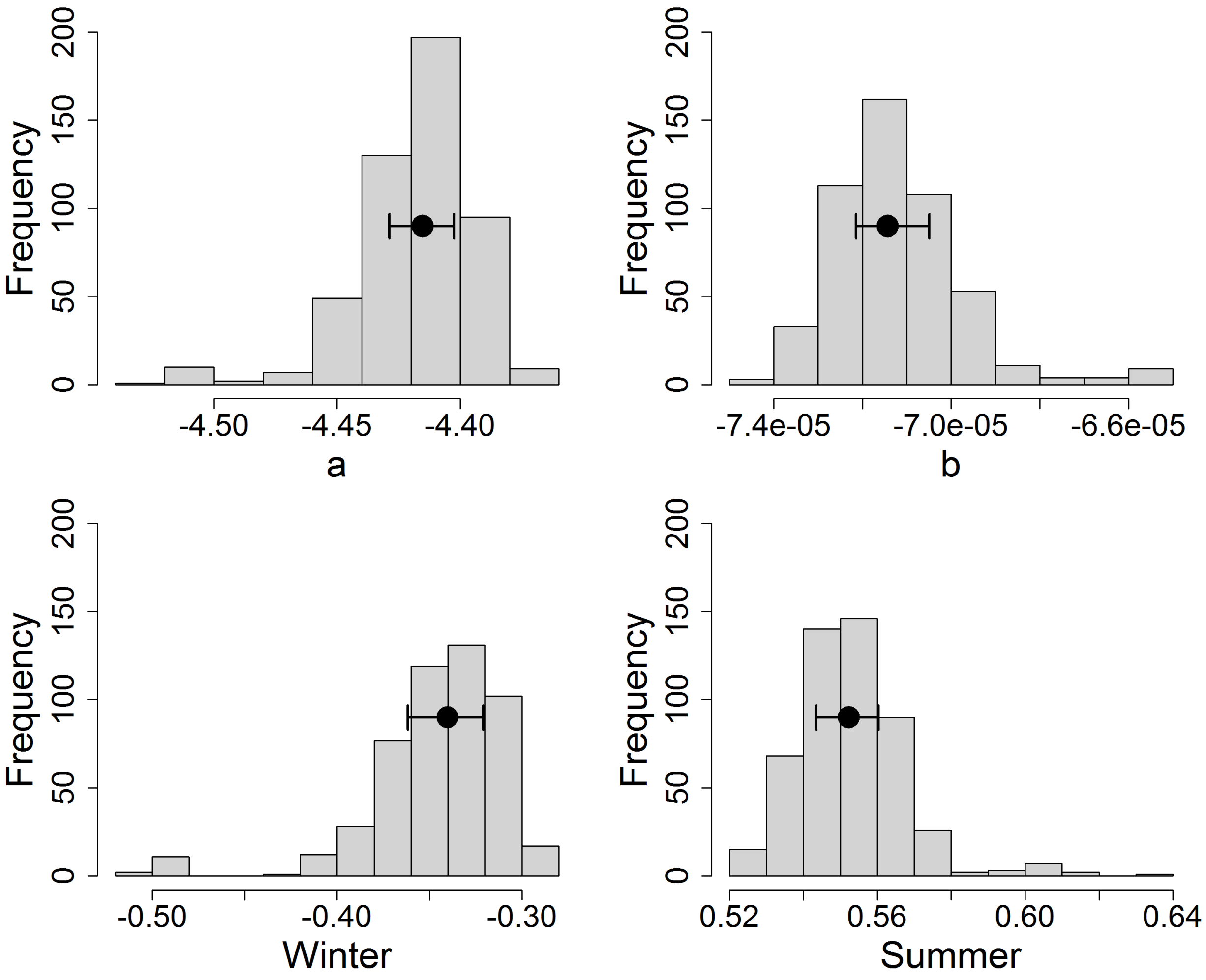

Figure 3.A3: Bootstrapped parameter estimates from Model 3. The solid dot represents the median and the bars represent the first and third quartiles.

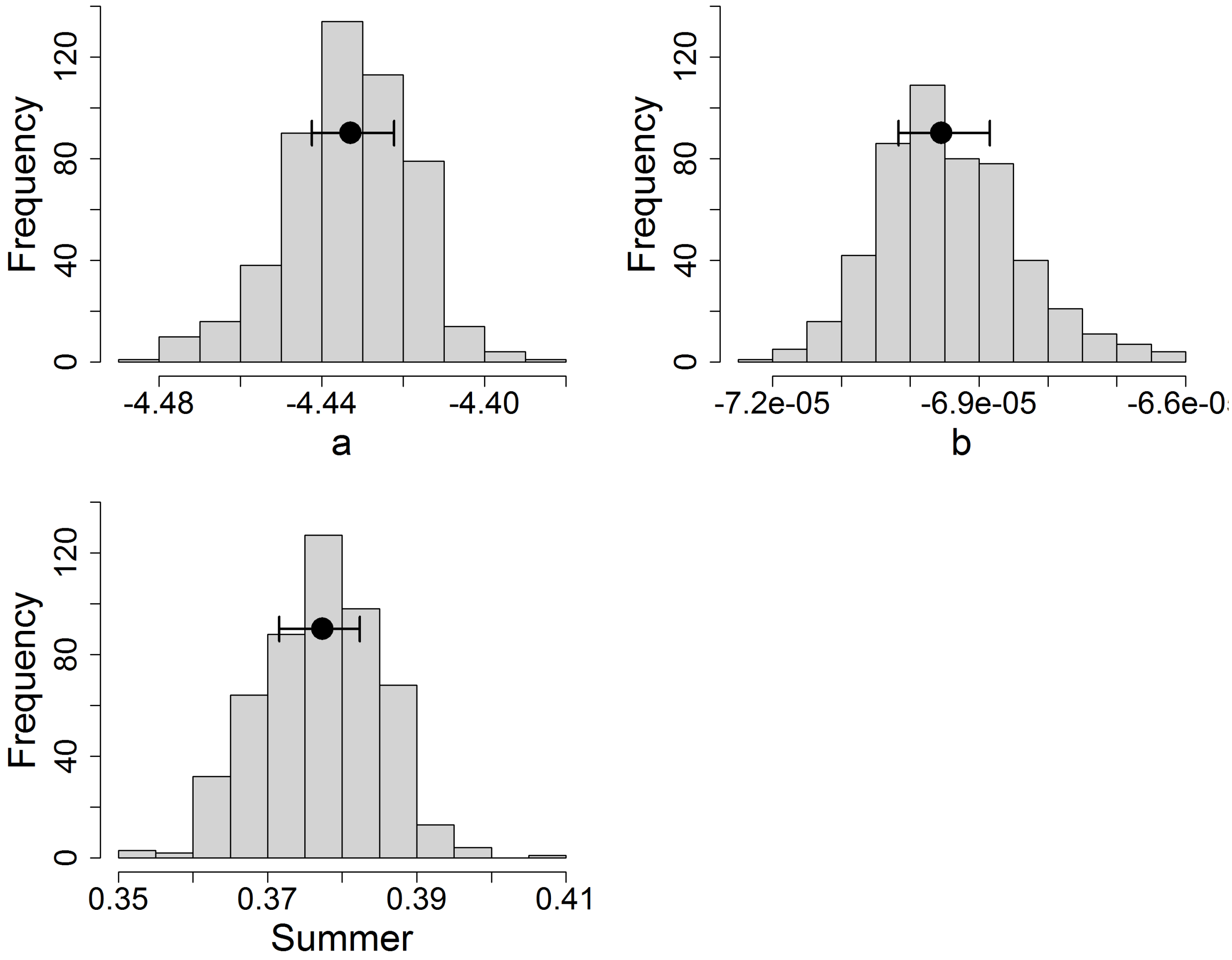

Figure 3.A4: Bootstrapped parameter estimates from Model 4. The solid dot represents the median and the bars represent the first and third quartiles.

Appendix 3.B

Wavelet analysis example

Ecological processes observed through time (e.g., biomass or abundance) can be composed of different oscillatory signals, some transient and short-lived, as well as trends and random noise. This variability can be driven by various processes, both known and unknown. Below is an example illustrating the creation of a synthetic time series by combining different oscillatory components and random noise. I then use the wavelet analysis to decompose the variability, demonstrating how signals known to be present can be detected using this approach.

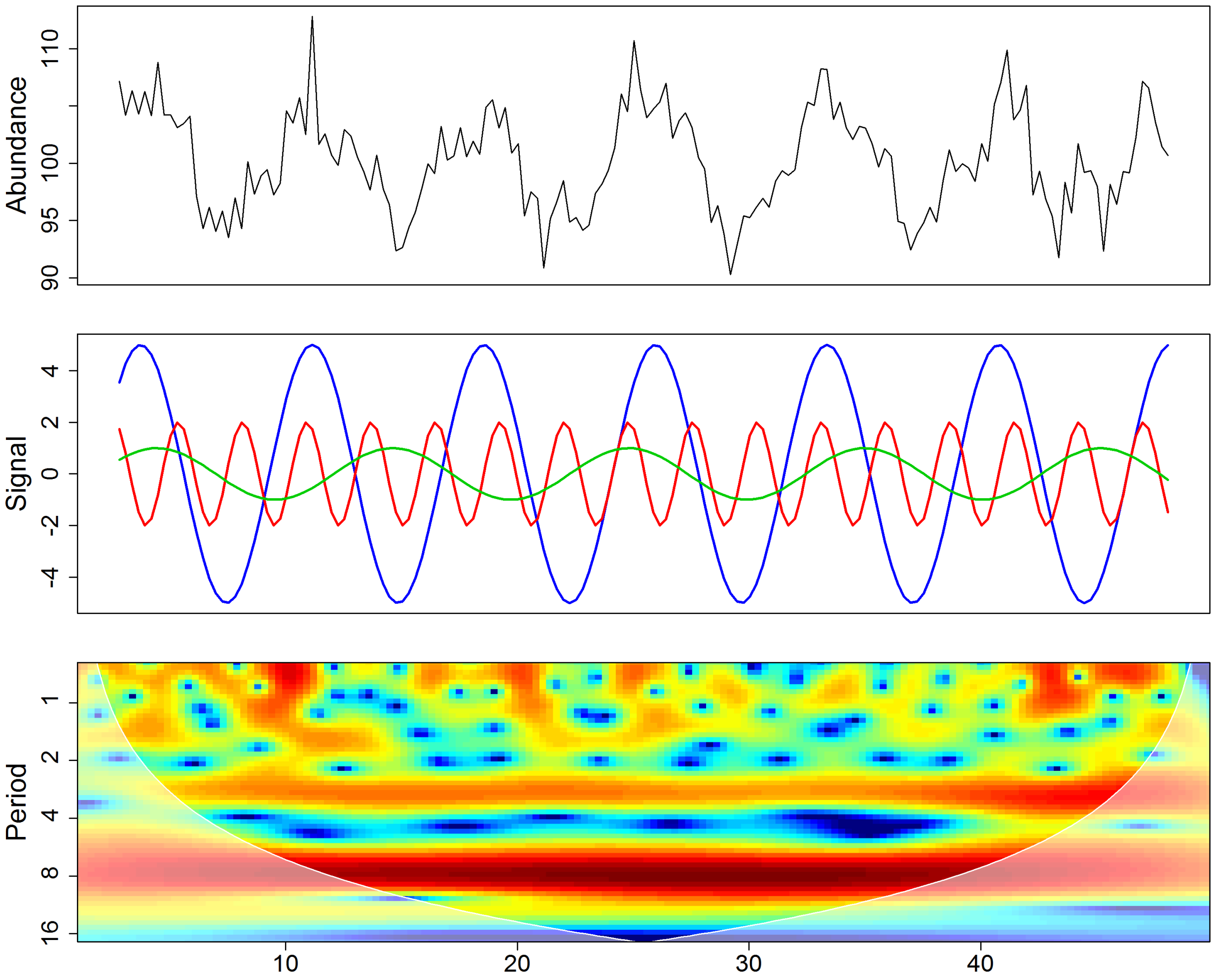

Figure 3.B1: Illustration of a synthetic time-invariant time series of abundance (top), a decomposition of the oscillatory signals used to create variability in the time series (center), and the wavelet decomposition of the time series highlighting the dominant signals in darker shades of red. There are three different cyclic signals: a 3 year (red), 8 year (blue), and an 11 year (green). The 8 year cycle has the largest amplitude and is the dominant, while the other two are weaker. In the wavelet heat map the dark orange at the 8 year cycle is constant throughout the time series, while the three year is present, but not always obvious. The 11 year signal is barely detectable given the relatively short length of the time series relative to the periodicity of that signal. Additionally, very high frequencies are detected (dark red); these regions are likely indicative of random noise.

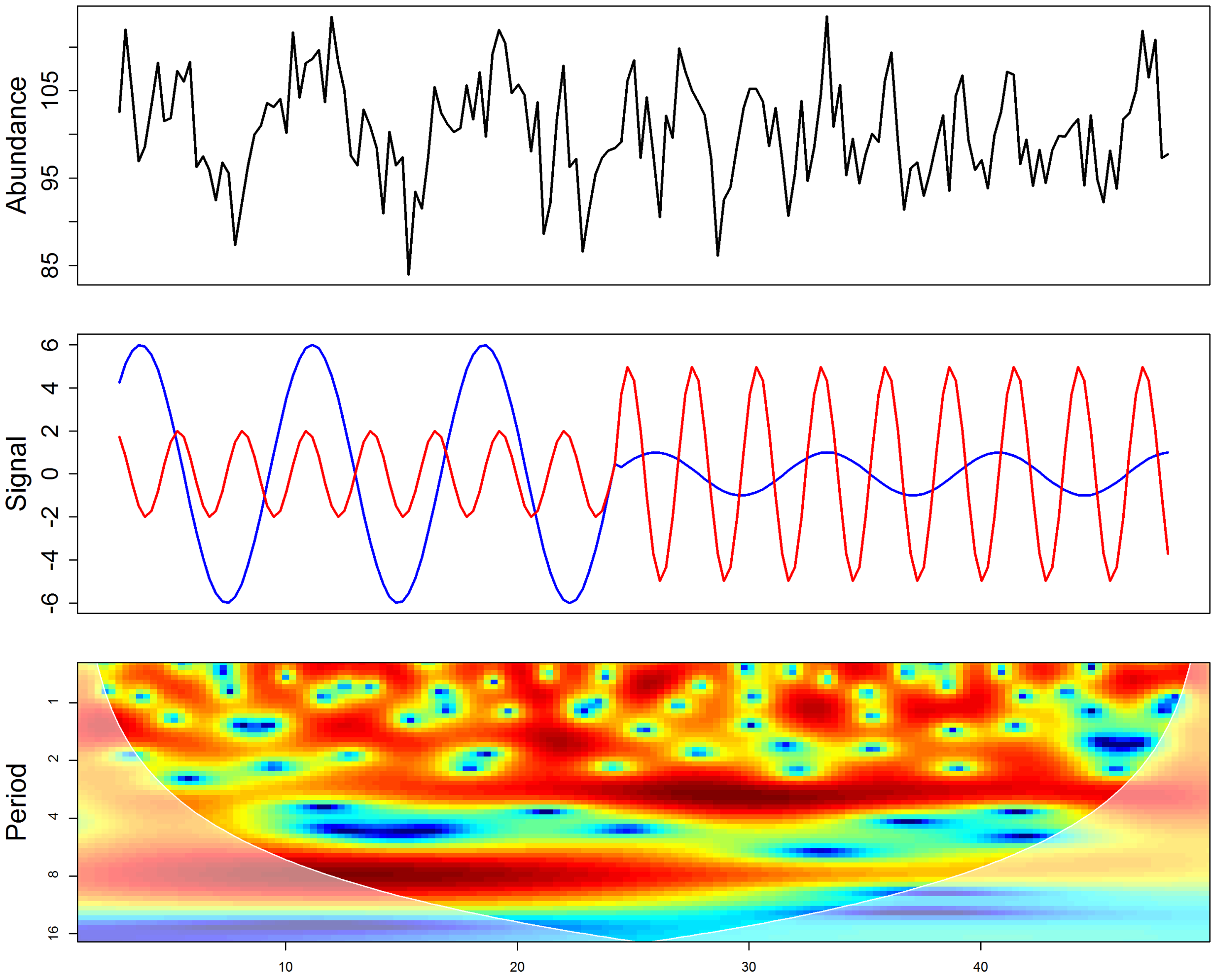

Figure 3.B2: In this example, the oscillatory signals creating variability in the abundance time series are allowed to vary between two time periods. For the first 25 years (for example) there is a dominant 8 year cycle (blue) with a weaker 3 year cycle (red). At year 26, the 8 year cycle all but fades away while the 3 year cycle increases in amplitude and becomes the dominant periodicity. This shift is seen in the wavelet analysis as the dark red shading at the 8 year periodicity fades around the time series' mid-point, giving way to a strong high-frequency signal at the 3 year periodicity.

R code:

```
# Load biwavelet package

library(biwavelet)


# TIME-INVARIANT SIGNALS


# Create a time sequence (years, perhaps)

t=seq(1,50,.3)

# Define desired periodicities


p1 = 3  # periodicity of 3 (units depends on time scale)

p2 = 8  # a second periodicity of 8

p3 = 11 # a third periodicity of 11


# Setting a mean value for the univariate time series

mu = 100


# Adding white noise to the mean

p.eps = rnorm(t,0,2)


# Create wave signals

w1 = mu + sin((2*pi*t)/p1)

w2 = mu + sin((2*pi*t)/p2)

w3 = mu + sin((2*pi*t)/p3)


# Plot the signals individually (with different amplitudes)

  # y = amp*sin((2*pi*t)/period)
```

```
  # 8 year cycle; amp=5
plot( w2 $<$- mu + 5*(sin((2*pi*t)/p2)), type="l" , ylab="", col="blue")
  # 3 years cycle; amp=2
lines( w1 $<$- mu + 2*(sin((2*pi*t)/p1) ), type="l", col="red")
  # 11 yr cycle; amp=1
lines( w3 $<$- mu + sin((2*pi*t)/p3), type="l", col="green")

# Now, imagine a time series is comprised of the 3 signals plus noise
  # this is something we might observe
plot( y $<$- mu + 5*sin((2*pi*t)/p2) + 2*sin((2*pi*t)/p1) +
sin((2*pi*t)/p3) + p.eps, type="l", ylab="")

# Plot results from wavelet analysis
plot.biwavelet( wt (cbind(t,y), mother="morlet"), type="power.corr.norm")
```

```
# TIME-VARYING SIGNALS


y $<$- w1 $<$- w2 $<$- w3 $<$- c()

# Alter the strength of the signals by time period (t1 \& t2)

t1=seq(1,24.1,.3)

p.eps = rnorm(t1,0,4)


for(i in 1:length(t1)){

  y[i] $<$- mu + 2*sin((2*pi*t1[i])/p1) + 6*sin((2*pi*t1[i])/p2) + p.eps[i]

  w1[i] $<$- mu + 2*sin((2*pi*t1[i])/p1)

  w2[i] $<$- mu + 6*sin((2*pi*t1[i])/p2)

 }

t2 = seq(24.4,50,.3)

p.eps = rnorm(t2,0,4)


for(i in (length(t1)+1):(length(t1)+length(t2)) ) {

  y[i] $<$- mu + 5*sin((2*pi*t2[i-length(t1)])/p1) +

  sin((2*pi*t2[i-length(t1)])/p2) + p.eps[i-length(t1)]

  w1[i] $<$- mu + 5*sin((2*pi*t2[i-length(t1)])/p1)

  w2[i] $<$- mu + sin((2*pi*t2[i-length(t1)])/p2)

 }
```

CHAPTER 4

FISH COMMUNITY FLUCTUATIONS IN RESPONSE TO ENVIRONMENTAL VARIABILITY IN THE BAY OF QUINTE

Vidal, T.E., Irwin, B.J., Holden, J.P, and Wenger, S.J. To be submitted to *Canadian Journal of Fisheries and Aquatic Sciences*

Introduction

In the Laurentian Great Lakes region, changing climatic conditions represent near and long-term uncertainties including how freshwater ecosystems may respond to those changes. The Great Lakes are the largest group of freshwater lakes in the world, and they provide important ecosystem services. Regional observations suggest that changes to climate regimes are already having effects through increased air and water temperatures, changing precipitation patterns, decreased ice cover, and reduced water levels. Climate models predict a continuation of the warming trend observed over the past century (Smith et al., 2005; Kirtman et al., 2013), with an expected global increase in mean surface air temperatures of between 0.3 and 0.7° C by year 2035 (Kirtman et al., 2013). The northern latitudes, however, are expected to experience the most significant warming of air temperatures due to melting of sea and winter ice formations. In the Great Lakes, surface temperatures are expected to increase by between 0.6 and roughly 4.6° C by 2039 (Ruosteenoja et al., 2003), and in Lake Superior there has been an observed increase of 2.5° C between 1979 and 2006 (Austin and Colman, 2007). Temperature increases likely mean shorter winters. Declining winter ice results in an earlier stratification of the water column, which contributes to a longer warming period, decreased dissolved oxygen in the deep water habitats (Kling et al., 2003), and more dramatic water temperature changes than would be expected from rising air temperatures alone. These warming trends are expected to impact the composition and distribution of fish species, potentially altering overall ecosystem function.

Ecosystems are stochastic, yet most have some capacity to reorganize following disturbance. This reorganization is reliant on the interconnected biotic and abiotic processes, as well as diversity in functional roles. Warming trends and increased hydrologic variability may prove deleterious to the native fish populations, especially cold-water species approaching thermal thresholds. Non-natives unable to invade due to environmental constraints may be released from limitations, posing further challenges to native fish communities and desired ecosystem structure (Britton et al., 2010). In many parts of the world, biodiversity is declining, causing changes to the structure, function, and resilience of ecosystems (Butchart et al., 2010; Oliver et al., 2015).

Aquatic resources have largely been exploited and managed to maximize economic gains through selective harvesting. In response to these selective harvest strategies, fisheries management has traditionally been rooted in single-species approaches (Hilborn and Walters, 1992). Managing single species, as isolated entities within a system neglects the interconnectedness and fails to manage for the benefit and integrity of the system as a whole. Effectively sampling whole ecosystems to evaluate change is generally unrealistic, but ecological indicators can be used as proxies to assess ecosystem condition and to evaluate how the system is responding to changes in the environment (Jennings, 2005; Rochet and Trenkel, 2009). Ecosystem or community based assessments go beyond single-species approaches to evaluate changes to species composition and community function in response to changing environmental conditions; approaches that are imperative for crafting effective management strategies.

To bridge this gap between single-species assessments and full ecosystem-based analyses, I used ecological indicators to represent the structure, function, and composition of the fish community. I then evaluated how these indicators responded along gradients of multiple environmental drivers. Just as species don't exist in isolation, nor do environmental variables, so simultaneously evaluating multiple environmental pressure variables was important. This analysis was focused on the Bay of Quinte (BOQ), located on the northeastern shore of Lake Ontario in the Laurentian Great Lakes. The BOQ is representative of the lower Great Lakes, yet is small enough to allow for intensive sampling which has produced rich, long-term data sets. In 1987, the Canadian government identified the BOQ as one of the areas of concern (AOC; http://www.ec.gc.ca/raps-pas/) because of severely degraded water quality and environmental health. Research showed that agricultural runoff, wastewater discharge, and shoreline development were large factors influencing the state of the system. In addition, large-scale shifts in the BOQ were detected following the dreissenid mussel invasion, resulting in a reorganization of the four main biological communities: phytoplankton, zooplankton, benthos, and fish (Nicholls et al., 2011). The new regime had negative effects on some native species, yet species diversity and native fish abundance and biomass all increased during the recent time period (Hoyle et al., 2012). In 2016, an evaluation of the BOQ fish community was performed using an index of biotic integrity (IBI), the results of which showed that remediation efforts in the bay have improved the IBI score, suggesting improved ecosystem health and diversity (Hoyle and Yuille, 2016). In this chapter, I explored whether environmental drivers have influenced the structure and composition of the BOQ fish community over recent decades. I hypothesized that there would be a shift towards higher abundance of species tolerant of warmer water and indications of non-natives expanding while cold water natives declined. I report on a random forest analysis applied to the long-term fish community data from the BOQ. Improving our understanding of how environmental variability has contributed to changes in the fish community may enhance managers' ability to manage for ecosystem integrity under changing environmental conditions.

Methods

I evaluated how the fish community in the BOQ has responded along environmental gradients over the past couple decades using gradient forest methods, an extension to random forests (Breiman, 2001; Ellis et al., 2012). Random forests, the foundation for gradient forest, is an ensemble learning algorithm that uses a collection of regression trees (i.e., the forest), with modified *bagging* (bootstrap aggregation) to improve prediction accuracy. In a regression tree, quantitative response variables are recursively partitioned based on a set of explanatory variables. Regression trees are able to capture complex structure in the data, including nonlinearities and interactions between predictor variables. These gradient forest approach is useful to explore patterns in the shape and magnitude of a community response along gradients of environmental drivers. Once broad community-level patterns are detected, one can further identify the individual species within the indicator groups that had the greatest contribution to the observed changes in species composition. I assessed individual species contributions using an analysis of temporal beta diversity. Together these analyses were used to investigate whether changes in the species composition of the BOQ could be explained by environmental drivers and to identify threshold values along the environmental gradients, associated with community response.

Fish community indicators

Indicators of the BOQ fish community were selected and developed based on observations and predictions about how the fish community has changed over time as well published literature using community indicators (e.g., Link, 2005; Large et al., 2015). The data on the species present in the bay, their relative abundance, and biomass, were obtained from the annual, fixed-site gillnet survey from 1995-2015. The gillnet gear is made from monofilament and is set along bottom contours at fixed sampling location. Mesh sizes varied by net panel, ranging from 38-152 mm stretched in 13 mm increments, for a total of ten panels in a single gillnet gang (Hoyle et al., 2012). I used samples from July and August (the months of greatest sampling effort) for a total of 698 net sets throughout the time series. These gillnets sample larger-bodied fish and are used to sample the offshore areas (>5 m; Hoyle et al., 2012). A total of 41 species from 17 families were included in this analysis. Catches from the gillnet survey were aggregated by year for an annual index fish abundance and biomass.

I used species characteristics from Hoyle and Yuille (2016) to develop indicator variables representative of the fish community structure and function to include: 1) habitat preference (benthic, benthopelagic, pelagic), 2) trophic niche (invertivore, piscivore, planktivore), 3) origin (native or exotic), and 4) thermal preference (cold, cool, warm). Specifically, I calculated the proportion, abundance, and biomass of native, piscivorous, benthic, and warm water species. I chose the aforementioned reference levels for the four community categories described above as the response indicator variables based on hypotheses about how the system has changed. I hypothesized that benthic species increased over time due to increased water clarity caused by expansion of dreissenid mussels. I predicted that consequences of these changes would mean a shift towards more benthic species due to the reallocation of energy from the water column to the benthos. I hypothesized an increase in warm-water species due to increased water temperature; warm-water species also tend to be non-native. In addition, I evaluated mean trophic level and mean fish length. The trophic level for each species was obtained from FishBase (www.fishbage.org), weighted by each species' annual biomass, and then averaged across species to obtain an annual estimate of the mean trophic level. Trophic level was included as a measure of energy flow and functional composition of the fish community. To estimate proportion, biomass, and abundance of warm water species, we assigned a categorical preferred thermal regime (i.e., cold < 15 ° C; cool $\approx$ 15-25 °C; and warm $>$ 25 °C; Casselman et al., 2011) to each species collected. Indicator variables for the fish community were developed as annual metrics weighted by species biomass (excepting abundance based indicators), and aggregated to an annual level to align with resolution of the environmental indicators. It should be noted that each species is included in several indicator groups. For example, an exotic warm water species could also be grouped as pelagic and piscivorous, thus included in multiple indicator variables. For a complete description of the indicator variables used in this analysis see Table 4.1.

Environmental variables

A set of environmental indicators, thought to influence the composition of the fish community through time, were developed as the predictor variables. These indicators were selected to be representative of large-scale patterns in precipitation, water levels, primary production and turbity, and thermal fluctuations that could influence vertical mixing and present physiological thresholds. Specifically, the environmental variables were cumulative spring temperature (March - June), mean summer (May - August) and winter (December - March) temperatures (°C), Secchi depth (m) in BOQ, precipitation (mm), and water level (meters above sea level). The environmental data available for the region were of a coarser spatial scale than the fish community data; therefore, all indicator variables were aggregated to the annual level, all sampling locations combined. Table 4.2 provides additional descriptions of the six environmental variables and the associated data sources.

Statistical analyses

Gradient forest (Ellis et al., 2012), an extension of random forest, was used to evaluate the importance of the suite of environmental predictors in explaining the structure and function of the fish community in the BOQ. Random forest approaches are a type of machine learning algorithm, the foundation of which is a regression tree. In regression trees, the response variables are partitioned on split values for the predictor variables, minimizing the sum of the squared deviations from the group mean. Splits are dichotomous partitions of the response variable observations. The subgroups created by the splits are then recursively partitioned until additional partitions do not improve fit or there are a minimum number of observations in the resulting groups; these groups are referred to as terminal nodes. Random forests are an ensemble of many regression trees (i.e., the forest; 5000 trees were used in this analysis), where each tree is fit to a bootstrapped sample of the full data set (Breiman, 2001). Observations not included in the bootstrapped samples for an individual tree are referred to as the out-of-bag (OOB) sample. Predictions for each observation are calculated as the average prediction from all trees in which the observation was omitted; these observations provide a measure of the expected variance of the residuals for new observations (i.e., cross-validated estimate of the generalized error; Ellis et al., 2012). The tree partitions at each node are determined using a random subset of the predictor variables, ensuring that the trees in the 'forest' are independent from one another (i.e., decorrelated). Additionally, potential correlation among predictor variables is controlled for by using conditional permutation (Strobl et al., 2008; Ellis et al., 2012). The resulting regression forest predictions are made by averaging the predictions from each tree in the forest. Gradient forest approaches allow for an assessment of how response variables behave along predictor gradients, and where thresholds occur, if they exist. Thresholds, or change points, can emerge due to directional changes in environmental variables leading to biological shifts. For example, an increase in water temperature may exceed an individual species' thermal tolerance, resulting in reduced growth and increased mortality. This threshold would likely show up in the gradient forest as a bifurcation in the abundance of that species around that thermal threshold, assuming abundance was used as a response variable. The R package *gradientForest* (Ellis et al., 2012) was used to perform these analyses.

A random forest yields several measures to interpret the importance of the environmental variables in predicting the fish community response: the goodness of fit R_f^2 for fish community indicator f, the importance I_{fp} of environmental indicator (i.e., predictor variable) p in predicting indicator f, and the raw importance values I_{fpts} at every split s from each tree t in the forest (Ellis et al., 2012; Large et al., 2015). The goodness of fit for each indicator f is calculated as

$$R_f^2 = 1 - \sum_i \frac{(Y_{fi} - \hat{Y}_{fi})^2}{(Y_{fi} - \bar{Y}_f)^2}$$

where Y_{fi} is the *ith* observation of the *fth* indicator, $\hat{Y}_{fi}$ is the OOB prediction, and $\bar{Y}_f$ is the mean value for indicator f.

Importance I_{fp} of each environmental variable is a measure of improved model fit with the inclusion of the predictor, evaluated by a comparison of prediction error between the full and reduced model (Ellis et al., 2012). R_f^2 can be partitioned across all environmental predictor R_{fp}^2 proportional to the conditional predictor importance I_{fp} (Strobl et al., 2008).

$$R_{fp}^2 = \frac{R_f^2 I_{fp}}{\sum\limits_p I_{fp}}$$

Therefore, the sum of the R_{fp}^2 will equal the R_f^2 for a community indicator f. To evaluate splits s associated with each predictor p, the raw importances I_{fpts} from every tree t in the forest are standardized by the density of predictor values and normalized to sum to R^2_{fp} (Ellis et al., 2012). Peaks in the split densities along predictor gradients provide support for thresholds. Values of the environmental predictors repeatedly chosen to partition the community data may represent ecological thresholds the fish community is responsive to.

Gradient forest methods were used to integrate the results of the random forest models across multiple response variables, to determine a community level response curve based on partitions from all explanatory variables, free from parametric assumptions. The overall importance of a predictor R^2_p is calculated by averaging the predictor importance across the community indicators, where N^{ind} is the number of community indicator variables (i.e., 14).

$$R^2_p = \frac{1}{N^{ind}} \sum_f R^2_{fp}$$

The importances for each predictor are aggregated across community indicators to yield a combined importance density I_{ps} for each value of the predictor, at different splits. The combined importance provides insight into community response threshold values along predictor gradients.

Beta diversity

The gradient forest analysis of community indicators reveals which indicators are most responsive to environmental drivers. Beta diversity was used as a complementary tool, to decompose the evolution of the species assemblage over time to evaluate the relative contribution of individual species to total assemblage diversity. Indicators are useful because they integrate information about an entire community or ecosystem, but one of the caveats is that they can be overwhelmed by abundance or biomass of individual species. Beta diversity is typically defined as differentiation of species composition across space (Whittaker, 1960). Space was replaced with time to evaluate changes in the BOQ species composition across years in the BOQ long-term fish community data.

The analysis of beta diversity was used to complement our results from the gradient forest and provide inferential context. Beta diversity is a measure that has been conceptually and computationally defined in many different ways (Anderson et al., 2013). I am using the definition from Legendre and De Cáceres (2013), in which beta diversity is defined as the total variance in an i x j species matrix where each element s_{ij} is the squared deviation from the mean for each of the j species in year i. Raw biomass values y_{ij} were transformed using the hellinger transformation prior to calculating beta diversity metrics (Legendre and Gallagher, 2001).

$$y'_{ij} = \sqrt{\frac{y_{ij}}{\sum\limits_{j=1}^{p} y_i}}$$

$$s_{ij} = (y'_{ij} - \bar{y'_j})^2$$

$$SS_{Total} = \sum_{i=1}^{I} \sum_{j=1}^{J} s_{ij}$$

$$BD = Var(\mathbf{Y}) = SS_{Total}/(n-1)$$

Temporal beta diversity, calculated in this way, is a measure of the difference in species assemblages through time. I partitioned total beta diversity, by dividing the sum of squares for the j species by SS_{Total}, to evaluate the relative contribution of individual species to overall beta diversity.

$$SS_j = \sum_{i=1}^{n} s_{ij}$$

Results

Indicator time series

There was little contrast in the fish community indicators over the time period analyzed (Figure 4.1). A decline in mean fish length was observed through time, from a mean total length of 150 mm to mean fish length of 118 mm, as well as a reduction in the proportion of cold and cool water species from the gillnet catches (Figure 4.2). The proportion of native, piscivorous, and benthic species remained relatively unchanged although there was a slight increase in the proportional biomass of native and piscivorous fish towards the end of the time series, concurrent with an increase in abundance of warm water species.

Both summer and winter temperature indices showed a warming trend throughout the time series, excepting the winters of 2014 and 2015, which were below average (Figure 4.3). Cumulative spring temperatures also showed a slight warming trend, but with substantial interannual variability. Secchi depth increased during the 1990s, but generally declined following the peak around 1998. Precipitation and water levels were highly variable from year to year, with no discernible trend.

Random and gradient forest

The mean importance of the environmental predictors (R_p^2) in explaining community response, ranged between <0.001 and 0.062. Secchi depth stood out as the most important predictor followed by cumulative spring and mean summer temperatures. Water level and mean winter temperatures had an $R_p^2 < 0.001$ (Figure 4.4), explaining very little of the community variability. Individual predictor importance ranged between <0.001 and 0.099, with Secchi depth having the greatest individual importance for predicting community response.

Mean prediction performance (R_f^2) from the random forest model was highest for mean trophic level, followed by proportion of biomass attributed to piscivores, and abundance of warm water species (R_f^2 = 0.031, 0.017 and 0.011, respectively). The remainder of the community variables were not predicted by the model ($R_f^2 = 0$). Thresholds in the fish community response were identified as peaks in the cumulative importance distributions of model improvement based on split location along environmental gradients, scaled by R^2 weighted importance and standardized by the density of the observations (Figure 4.5), where the ratio is greater than one (Large et al., 2015). The peaks indicate values along the environmental gradients that were selected repeatedly in the random forest analyses as a break point for the response variables. Secchi depth and mean summer temperatures had well defined threshold values, whereas cumulative spring temperatures and the weaker predictor variables had multiple peaks in the density ratios, indicating a lack of clear thresholds (Figure 4.5). Mean trophic level and proportion biomass associated with piscivores indicated a similar threshold response to cumulative Secchi depth (∼2.5 m) and mean summer temperatures (∼21°C; Figure 4.6), whereas abundance of warm water species indicated multiple thresholds associated with cumulative spring temperatures (∼1400 and 1700°C), but to no other predictor. The cumulative importance is the cumulative sum of split importance values along the observed range of environmental predictors. When the cumulative importance jumps dramatically (as in the Secchi depth plot) there is an indication that a split at that level of the predictor is important in predicting the response variables. Figures 4.5 and 4.6 are essentially illustrating the same information, but in different ways. It is important to note, that although the Secchi depth threshold is pronounced, there are only three years with observed Secchi depths greater than 2.5 m.

Beta diversity

Temporal beta diversity from 1995-2015 was estimated to be 0.12; the differences in species composition were overwhelmingly attributed to three species: alewife *Alosa pseudoharengus*, yellow perch *Perca flavescens*, and white perch *Morone americana*. Alewife explained 40% of total beta diversity, while yellow perch and white perch explained 21% and 13%, respectively. Alewife and white perch abundance has increased through the time series; whereas yellow perch has declined dramatically (Figure 4.7). This restructuring of the species assemblages represents a shift away from a dominant native, cool-water species (yellow perch) towards increased presence of non-native, warm water species (alewife and white perch) that operate at a lower trophic level (Figure 4.8).

Discussion

The results from these analyses suggest that measures of water clarity, followed by indices of water temperature, were most influential in the structuring of the fish community in the BOQ. Environmental fluctuations over recent decades didn't appear overly influential in structuring species composition, and observed changes were likely due to fluctuations in a few key species as opposed to systemic shifts driven by changing conditions. Although prediction performance was low, the model was able to detect a shift in the community indicator variables along environmental gradients.

Evaluating the influence of climate drivers and environmental variables is of broad interest (e.g., Stenseth et al., 2002; Walther et al., 2002; Lehodey et al., 2006). This analysis, focused on evaluating how climate drivers and environmental variability were influencing this post-regime shift community (Nicholls et al., 2011). I hypothesized that warming water temperatures, and short winters would stand out as important predictors shaping the species composition during the post-dreissenid era. The results, however, indicate that fluctuations in water clarity remain a primary driver of species composition in the gillnet catches from the BOQ, and although temperature was a important predictor, the effect of Secchi depth was of greater magnitude. Threshold response in the indicator of trophic structure existed towards the upper end of observed Secchi depth values, suggesting a shift in the species composition and functional characteristics of the community at Secchi depths greater than about 2.7 m. Empirical data showed a slight decline in Secchi depth during this time period. So, although water clarity remains an important driver, the direction of change during this recent time period has reversed from the 1990s when dreissenid mussels (i.e., zebra *Dreissena ploymorpha* and quagga mussels *Dreissena bugensis*) were rapidly increasing water clarity.

A gradual decline in water clarity could in part be attributed to the goby invasion. Round gobies (*Neogobius melanostomus*) are voracious benthic predators, that feed largely on zebra mussels. Their foraging may have important implications for water clarity due to a reduction in the abundance of zebra mussels, and thus, filtering capacity (Nicholls et al., 2011). Warming water temperatures are also predicted to increase intensity and duration of precipitation events, the result of which could be increased runoff, including phosphorous inputs, into the bay (Kunkel et al., 1999).

Shifts in the species assemblages from the 1995 on has trended towards a greater presence of non-native, smaller-bodied species with a warmer thermal preference, and higher tolerance of eutrophic conditions (e.g., alewife and white perch). The invasion of non-native species combined with changes in habitat and environmental conditions can result in novel restructuring of inter-specific interactions. For example, alewife have been shown to negatively impact recruitment of yellow perch by preying on newly hatched larval fish (Brandt et al., 1987). Alewives typically live in the open waters of the Great Lakes, but they migrate to the littoral areas and embayments to spawn in the spring. The spawning migration can overlap with the spring hatching of yellow perch; typically occurring within two weeks of the hatch (Brandt et al., 1987). White perch have been shown to negatively impact walleye recruitment through predation on the larval stages (Hurley and Christie, 1977), and has a diet that overlaps significantly with the yellow perch diet, especially in the summer (Parrish and Margraf, 1990).

Globally, environmental and climate-related changes are forecasted to be one of the greatest threats facing ecosystems (Pimm, 2009), with many ecosystems already showing signs of response to climate changes through poleward species range expansions (Chen et al., 2011; Sunday et al., 2012), phenological shifts (Parmesan, 2006), and reduced body size, in aquatic systems (Daufresne et al., 2009). In the Great Lakes region there is considerable uncertainty about how changing climatic conditions will affect aquatic ecosystems. This community-level analysis revealed that the functional characteristics of the community, as described by the community indicator variables, have tended to oscillate through time in response to increases and decreases in water clarity. However, there are important directional changes detected, associated with warming conditions, changes that may be setting the groundwork for larger fish community shifts if temperatures continue to rise, as expected (Kirtman et al., 2013).

In this analysis, the evidence for a clear persistent association between fish community indicators and environmental indicators is lacking; however, even if environmental shifts have small direct or indirect effects on a few species, a restructuring of species interactions may promote cascading effects. The gillnet survey data used for this analysis provide useful, long-term, and detailed biological data; however, the resolution of associated environmental observations is at a much coarser level, which is why indicator metrics were aggregated annually. This loss of spatial and temporal resolution has likely hampered our ability to detect finer scale relationships, and has likely reduced predictive power.

As assessment of aquatic systems moves towards greater incorporation of environmental variability and ecosystem-based approaches, efficient and powerful tools such as those presented in this chapter will be important. Gradient forest can not only identify relationships between environmental drivers and community response variables, but can also identify critical values along gradients of the predictor variables. Identification of such critical values could provide useful reference points for management. Further investigation into the mechanisms driving these shifts, as well as into the utility of additional environmental drivers in predicting biological community response, is warranted. Combining approaches, such as those presented here, with improved monitoring of environmental variables at similar spatial and temporal scales of biological monitoring, will help to inform decisions about resource management, evaluate potential consequences, and identify sources of uncertainty under changing environmental conditions.

References

Anderson, M. J., Tolimieri, N., and Millar, R. B. (2013). Beta diversity of demersal fish assemblages in the North-Eastern Pacific: interactions of latitude and depth. *PLoS One*, 8(3):e57918.

Austin, J. A. and Colman, S. M. (2007). Lake Superior summer water temperatures are increasing more rapidly than regional air temperatures: A positive ice-albedo feedback. *Geophysical Research Letters*, 34(6).

Brandt, S. B., Mason, D. M., Macneill, D. B., Coates, T., and Gannon, J. E. (1987). Predation by alewives on larvae of yellow perch in Lake Ontario. *Transactions of the American Fisheries Society*, 116(4):641–645.

Breiman, L. (2001). Random forests. *Machine learning*, 45(1):5–32.

Britton, J., Cucherousset, J., Davies, G., Godard, M., and Copp, G. (2010). Non-native fishes and climate change: predicting species responses to warming temperatures in a temperate region. *Freshwater Biology*, 55(5):1130–1141.

Butchart, S. H., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J. P., Almond, R. E., Baillie, J. E., Bomhard, B., Brown, C., Bruno, J., et al. (2010). Global biodiversity: indicators of recent declines. *Science*, 328(5982):1164–1168.

Casselman, J., Kunjikutty, S., Lehman, P., Marcogliese, L., and Oblak, J. (2011). Fish, Fisheries, and Water Resources: Adapting to Ontario's Changing Climate. Report, Natural Resources Canada, Climate Change Impacts and Adaptation Directorate, Study A1367, Ottawa, Canada, in conjunction with Queen's University and Mississippi Valley Conservation.

Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., and Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333(6045):1024–1026.

Daufresne, M., Lengfellner, K., and Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences*, 106(31):12788–12793.

Ellis, N., Smith, S. J., and Pitcher, C. R. (2012). Gradient forests: calculating importance gradients on physical predictors. *Ecology*, 93(1):156–168.

Hilborn, R. and Walters, C. J. (1992). Quantitative fisheries stock assessment: choice, dynamics and uncertainty. *Reviews in Fish Biology and Fisheries*, 2(2):177–178.

Hoyle, J., Bowlby, J., Brousseau, C., Johnson, T., Morrison, B., and Randall, R. (2012). Fish community structure in the Bay of Quinte, Lake Ontario: The influence of nutrient levels and invasive species. *Aquatic Ecosystem Health & Management*, 15(4):370–384.

Hoyle, J. A. and Yuille, M. J. (2016). Nearshore fish community assessment on Lake Ontario and the St. Lawrence River: A trap net-based index of biotic integrity. *Journal of Great Lakes Research*, 42(3):687–694.

Hurley, D. and Christie, W. (1977). Depreciation of the warmwater fish community in the Bay of Quinte, Lake Ontario. *Journal of the Fisheries Board of Canada*, 34(10):1849–1860.

Jennings, S. (2005). Indicators to support an ecosystem approach to fisheries. *Fish and Fisheries*, 6(3):212–232.

Kirtman, B., Power, S., Adedoyin, J., Boer, G., Bojariu, R., Camilloni, I., Doblas-Reyes, F., Fiore, A., Kimoto, M., Meehl, G., et al. (2013). Near-term climate change: projections and predictability. *Climate change*, pages 953–1028.

Kling, G., Hayhoe, K., Johnson, L., Magnuson, J., Polasky, S., Robinson, S., Shuter, B., Wander, M., Wuebbles, D., and Zak, D. (2003). Confronting climate change in the Great Lakes region. *Union of Concerned Scientists, Ecological Society of America*.

Kunkel, K. E., Andsager, K., and Easterling, D. R. (1999). Long-term trends in extreme precipitation events over the conterminous United States and Canada. *Journal of climate*, 12(8):2515–2527.

Large, S. I., Fay, G., Friedland, K. D., and Link, J. S. (2015). Quantifying patterns of change in marine ecosystem response to multiple pressures. *PLoS One*, 10(3):e0119922.

Legendre, P. and De Cáceres, M. (2013). Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecology Letters*, 16(8):951–963.

Legendre, P. and Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129(2):271–280.

Lehodey, P., Alheit, J., Barange, M., Baumgartner, T., Beaugrand, G., Drinkwater, K., Fromentin, J.-M., Hare, S., Ottersen, G., Perry, R., et al. (2006). Climate variability, fish, and fisheries. *Journal of Climate*, 19(20):5009–5030.

Link, J. S. (2005). Translating ecosystem indicators into decision criteria. *ICES Journal of Marine Science: Journal du Conseil*, 62(3):569–576.

Nicholls, K., Hoyle, J., Johannsson, O., and Dermott, R. (2011). A biological regime shift in the Bay of Quinte ecosystem (Lake Ontario) associated with the establishment of invasive dreissenid mussels. *Journal of Great Lakes Research*, 37(2):310–317.

Oliver, T. H., Heard, M. S., Isaac, N. J., Roy, D. B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C. D. L., Petchey, O. L., et al. (2015). Biodiversity and resilience of ecosystem functions. *Trends in ecology & evolution*, 30(11):673–684.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, pages 637–669.

Parrish, D. L. and Margraf, F. J. (1990). Interactions between White Perch (Morone americ´ana) and Yellow Perch (Perca flavescens) in Lake Erie as determined from feeding and growth. *Canadian Journal of Fisheries and Aquatic Sciences*, 47(9):1779–1787.

Pimm, S. L. (2009). Climate disruption and biodiversity. *Current Biology*, 19(14):R595–R601.

Rochet, M.-J. and Trenkel, V. M. (2009). Why and how could indicators be used in an ecosystem approach to fisheries management? In *The Future of Fisheries Science in North America*, pages 209–226. Springer.

Ruosteenoja, K., Carter, T. R., Jylhä, K., and Tuomenvirta, H. (2003). Future climate in world regions: an intercomparison of model-based projections for the new IPCC emissions scenarios. *The Finnish Environment*, 644:83.

Smith, T. M., Peterson, T. C., Lawrimore, J. H., and Reynolds, R. W. (2005). New surface temperature analyses for climate monitoring. *Geophysical Research Letters*, 32(14).

Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K.-S., and Lima, M. (2002). Ecological effects of climate fluctuations. *Science*, 297(5585):1292–1296.

Strobl, C., Boulesteix, A.-L., Kneib, T., Augustin, T., and Zeileis, A. (2008). Conditional variable importance for random forests. *BMC bioinformatics*, 9(1):1.

Sunday, J. M., Bates, A. E., and Dulvy, N. K. (2012). Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, 2(9):686–690.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., Fromentin, J.-M., Hoegh-Guldberg, O., and Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416(6879):389–395.

Whittaker, R. H. (1960). Vegetation of the Siskiyou mountains, Oregon and California. *Ecological monographs*, 30(3):279–338.

Table 4.1: Descriptions of the fish community indicator variables used as the response variables in the gradient forest analysis, and the data sources.

Indicator	Description	Data source
Fish length (mean)	Average fish length (mm) from all fish measured in a given year	Quinte fish survey data
Trophic level (mean)	Mean trophic level, weighted by biomass	FishBase www.fishbage.org
Abundance of benthic species	Combined abundance of all species that primarily utilize the benthic habitat to all fish species observed	Hoyle et al. (2012)
Abundance of native	Combined abundance of all native species to all fish species in the community	Hoyle et al. (2012)
Abundance of piscivorous	Combined abundance of all piscivorous fish species to all fish species in the community	Hoyle et al. (2012)
Abundance of warm water species	Combined abundance of all species with a warm thermal preference to all fish species in the community (thermal regimes: warm > 25 °C; cool ≈ 15-25 °C; and cold < 15 ° C; Casselman et al., 2011)	Hoyle et al. (2012)
Biomass of benthic species	Combined biomass of all species that primarily utilize the benthic habitat to all fish species observed	Hoyle et al. (2012)
Biomass of native	Combined biomass of all native species to all fish species in the community	Hoyle et al. (2012)
Biomass of piscivorous	Combined biomass of all piscivorous fish species to all fish species in the community	Hoyle et al. (2012)
Biomass of warm water species	Combined biomass of all species with a warm thermal preference to all fish species in the community (thermal regimes: warm > 25 °C; cool ≈ 15-25 °C; and cold < 15 ° C; Casselman et al., 2011)	Hoyle et al. (2012)
Proportion benthic species	Ratio of species that primarily utilize the benthic habitat to all fish species observed	Hoyle et al. (2012)
Proportion native	Ratio of native species to all fish species in the community	Hoyle et al. (2012)
Proportion piscivorous	Ratio of piscivorous fish species to all fish species in the community	Hoyle et al. (2012)
Proportion warm water species	Ratio of species with a warm thermal preference to all fish species in the community (thermal regimes: warm > 25 °C; cool ≈ 15-25 °C; and cold < 15 ° C; Casselman et al., 2011)	Hoyle et al. (2012)

Table 4.2: Descriptions of the environmental indicator variables used to predict the fish community indicators, and the respective data sources.

Indicator	Description	Rationale	Data source
Cumulative spring temperature	Cumulative sum of daily water temperature °C between March and June	The timing and duration of spring warming can influence phenology of food resources, critical to spring hatched fish	Temperature gauge at the intake pipe for the Bellville water treatment facility
Precipitation	Amount of annual precipitation in mm	Precipitation was predicted to influence water levels in addition to altering runoff and nutrient loadings	https://www.glerl.noaa.gov//data/dashboard/data/hydroIO/precip/
Secchi depth	Measure of water clarity	Secchi depth can be used as a proxy for primary production	BOQ survey data from July and August net sets
Summer water temperatures	Mean water temperature between May and September, based on daily temperature observations	Summer temperatures can influence phenology of food resources, growth rates and metabolic demand	Temperature gauge at intake pipe for the Bellville water treatment facility
Water level	Bay water level in meters above sea level	Water levels can affect spawning habitat and success in nearshore waters	Stationary water level gauge at Cobourg, Lake Ontario
Winter water temperature	Mean water temperature between December and March, based on daily temperature observations	Winter water temperatures can influence many processes including overwinter mortality, reproductive success, and thermal stratification	Temperature gauge at the intake pipe for the Bellville water treatment facility

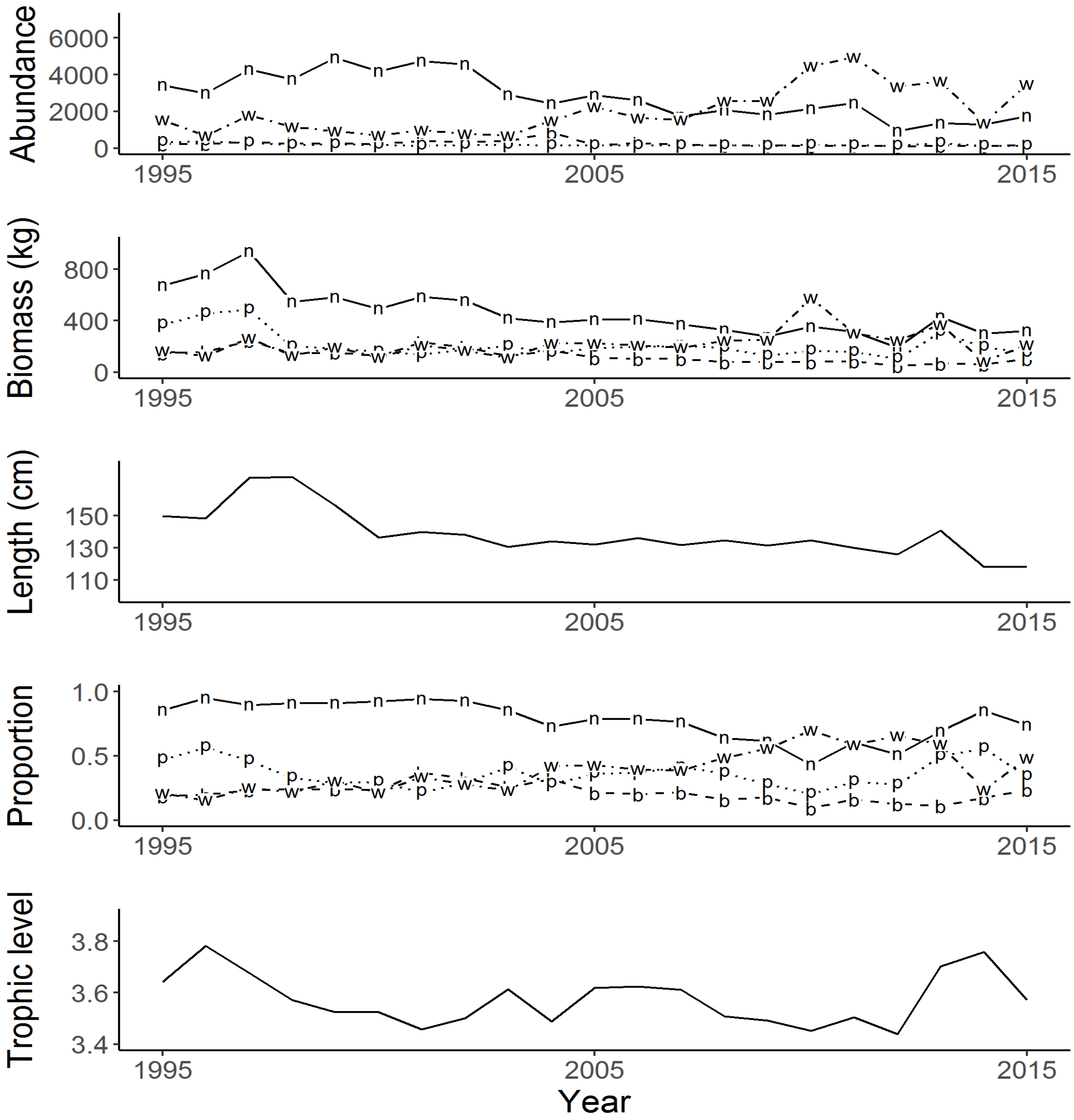

Figure 4.1: The five panels illustrate the time series of the fish community indicator variables generated from the gillnet survey data. The top panel illustrates the abundance of benthic 'b', native 'n', piscivorous 'p', and warm water species 'w'; the second panel from the top shows biomass (kg) of those same indicator groups. These four indicator groups represent habitat preference, trophic niche, orgin, and thermal preference. The third panel shows mean fish length (cm), all species combined, through time. The fourth panel shows the proportion of the biomass associated with the benthic, native, piscivorous, and warm water species groups. The last panel indicates mean trophic level of all species combined, weighted by biomass, in a given year. Note: in some of the figures it is difficult to see the benthic 'b' group due to overlap with the other indicator groups.

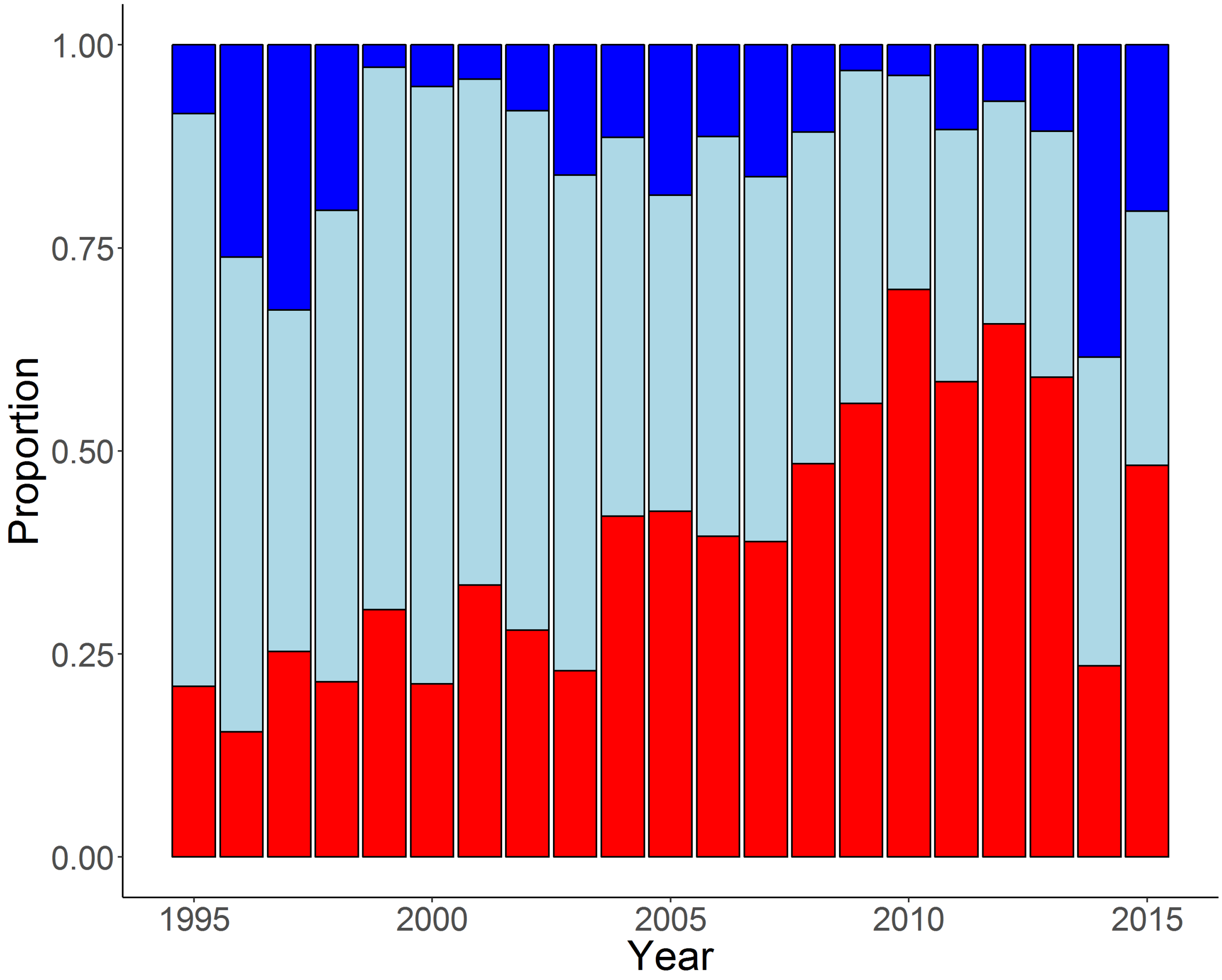

Figure 4.2: The stacked barchart shows the proportion of survey catch biomass, aggregated by thermal preference. The red bars indicate species with warm thermal preference, the light blue is a preference for cool water, and the darker blue, cold water.

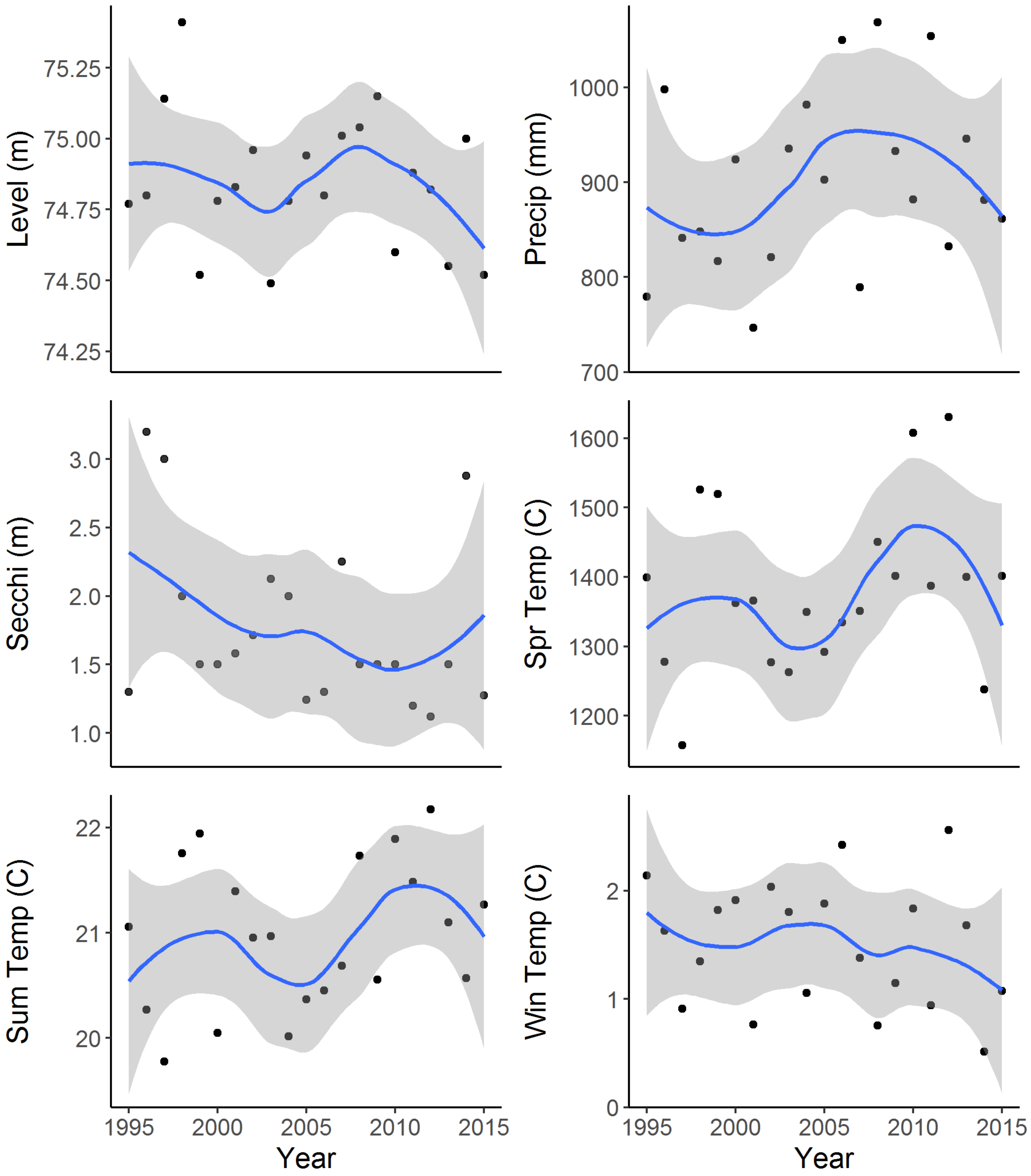

Figure 4.3: The panel plot illustrates the time series for the aggregate environmental indicator variables, in each year. The observed data are represented by the black points. The blue line is a loess polynomial regression line through the points, while the gray represents the standard error around the predicted relationship.

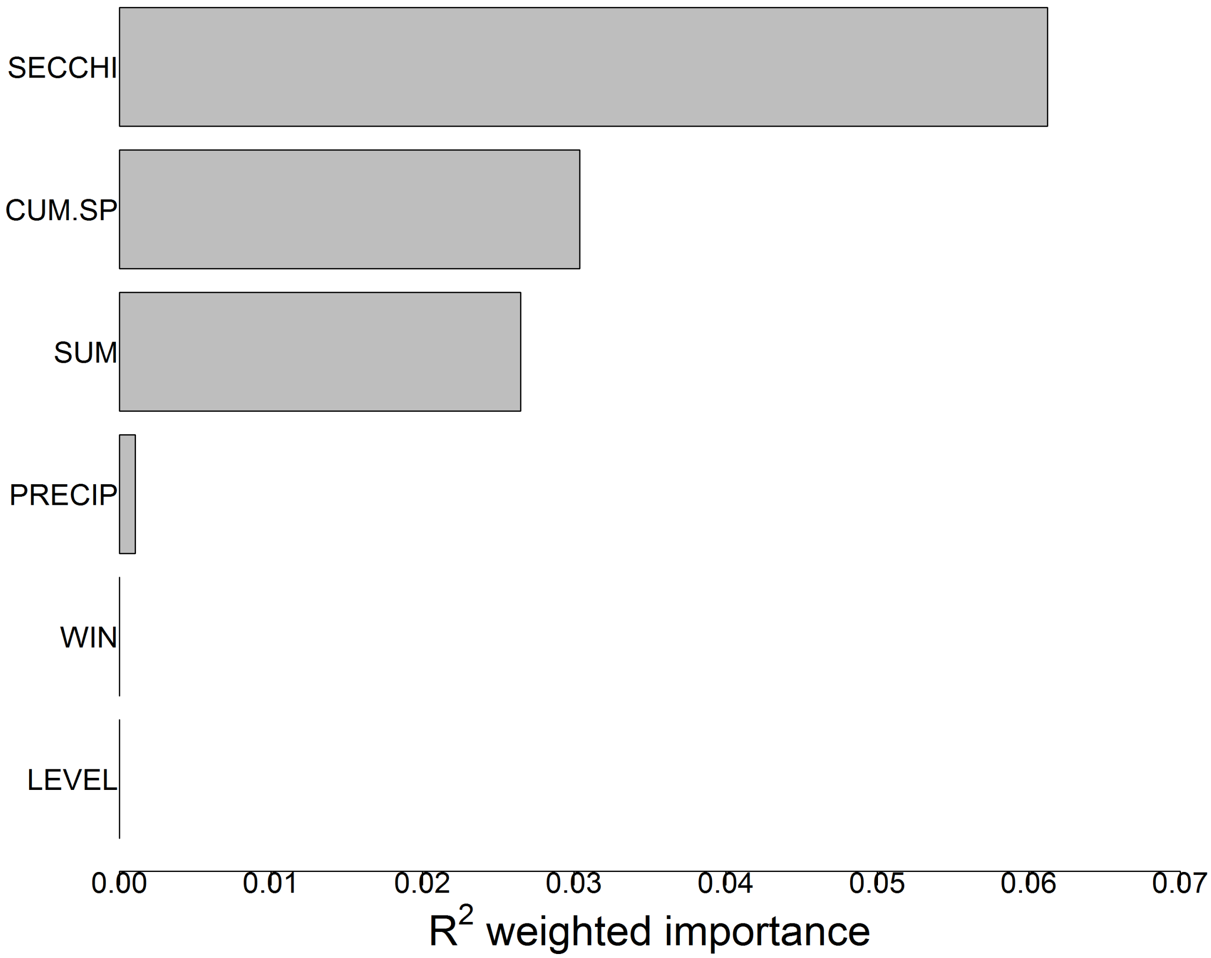

Figure 4.4: Weighted predictor importance R_p^2 of the environmental variables in predicting the community response variables from the gillnet data.

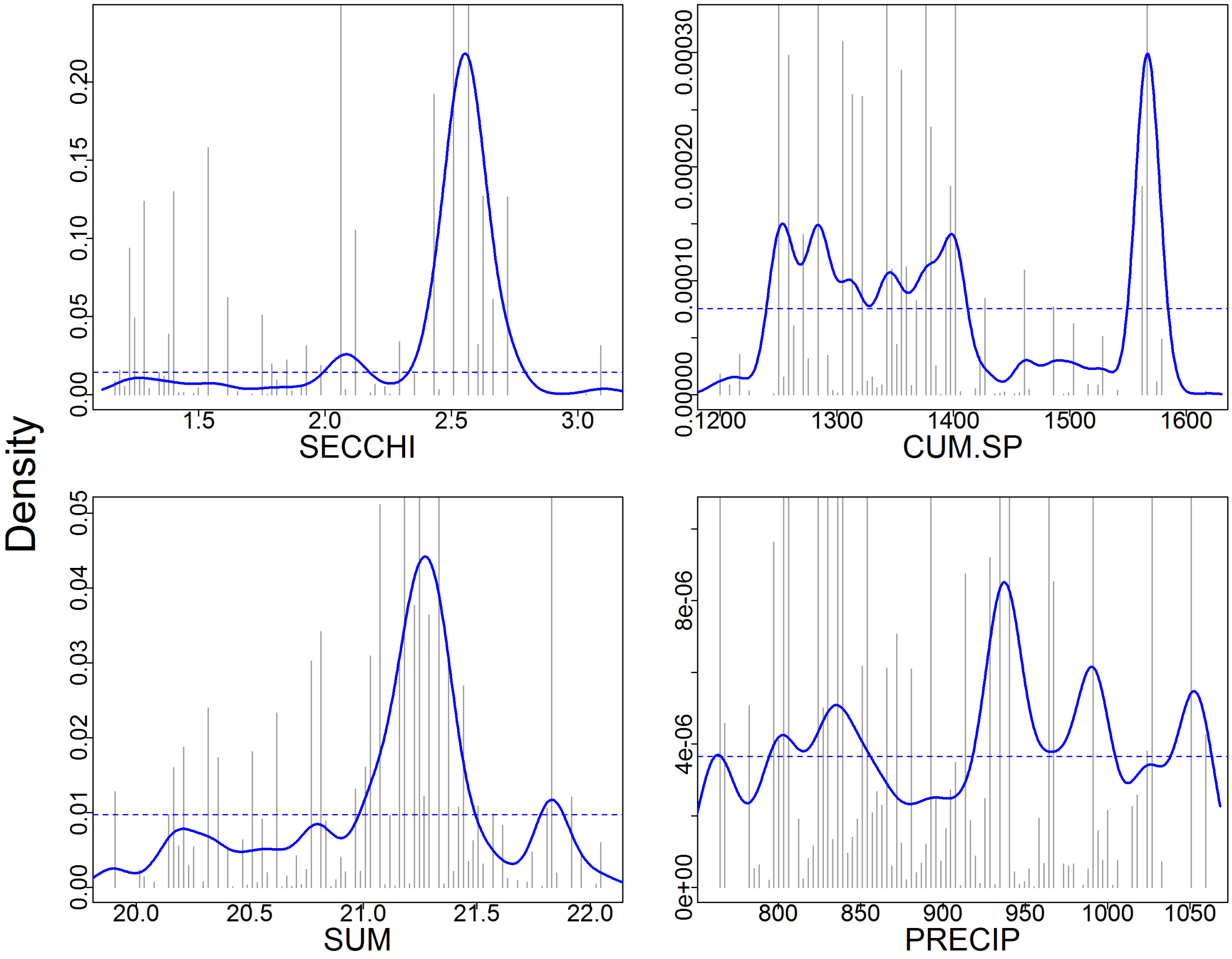

Figure 4.5: Split importance along predictor gradients, where the solid lines are the estimated density of split importance at each value of the predictor variables, standardized to the density of observations. The dashed line represents a ratio of unity, above which are locations along the predictor gradients associated with change in the community response. The peaks represent predictor threshold values where a community shift is expected.

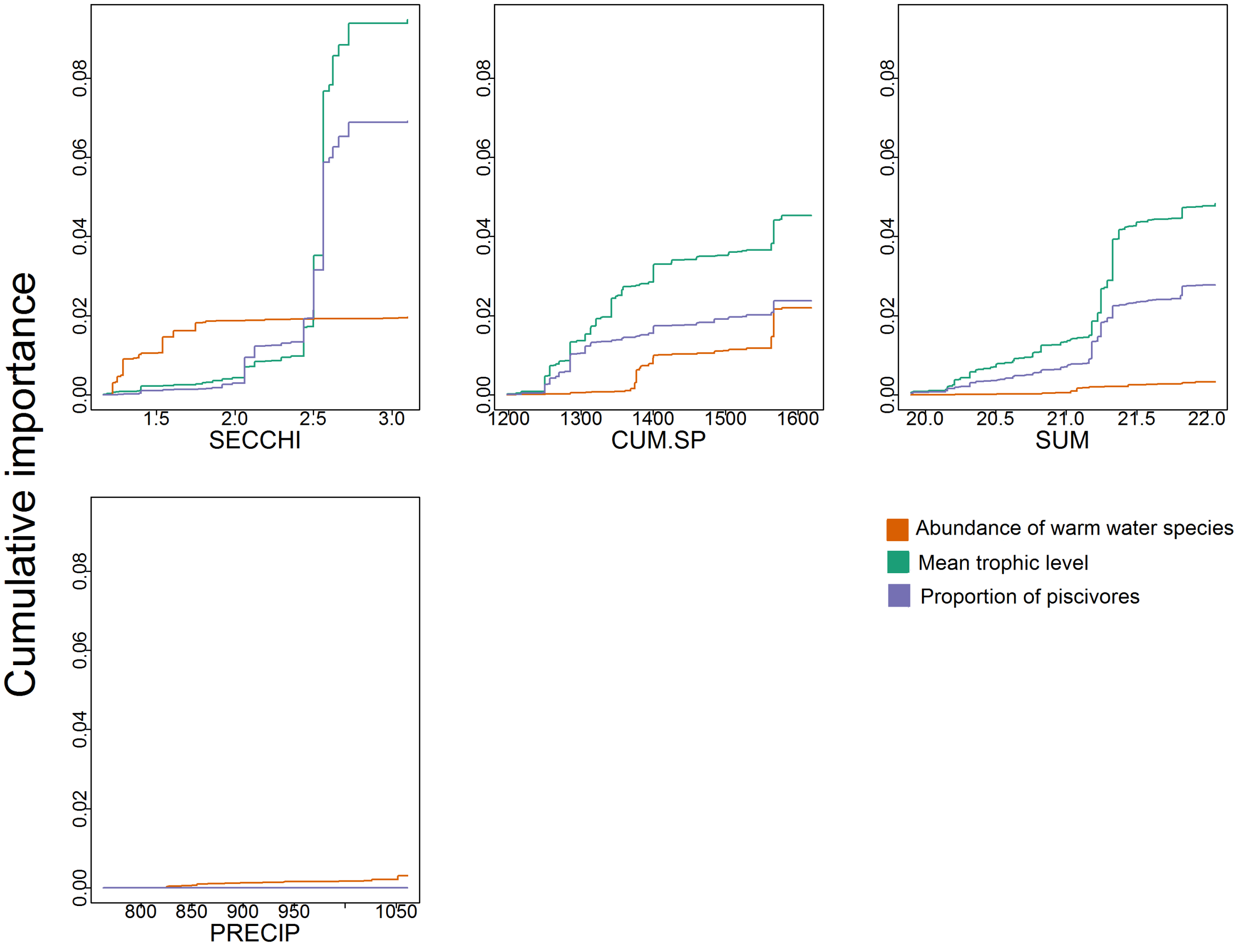

Figure 4.6: Cumulative importance of four environmental indicators in predicting a suite of fish community indicators. Separate lines are shown for the abundance of warm water fishes (orange), mean trophic level (green), and the proportion piscivorous (purple). The three colors represent the community indicator variables that were predicted by the environmental variables (fish community indicators not predicted by the environmental variables are not displayed). A steep slope in the indicator line is an indication of the presence of a threshold along the associated environmental gradient. All panels are scaled to have the same y-axis, illustrating the relative strength of cumulative spring temperatures over all other environmental signals.

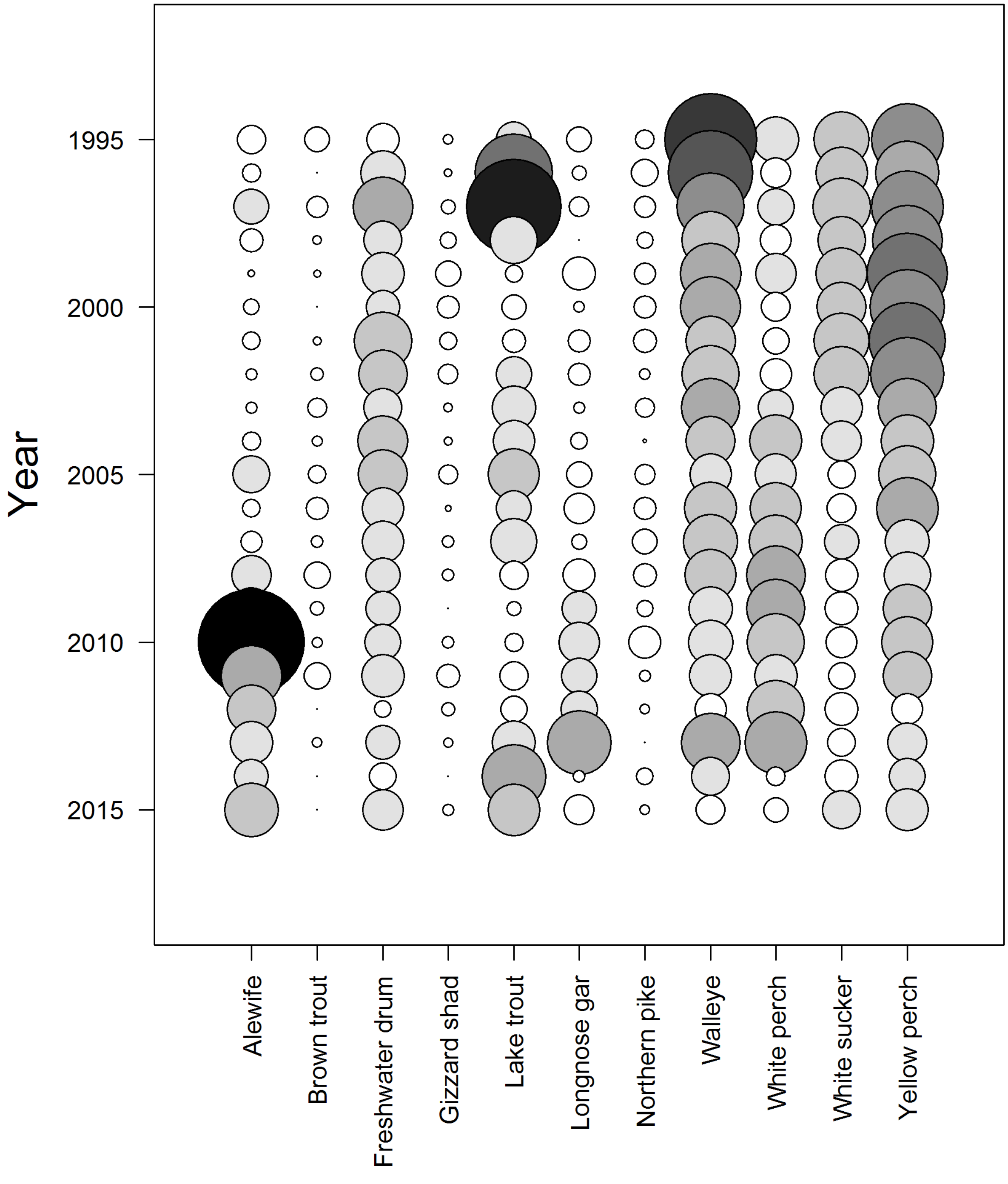

Figure 4.7: Bubble plot showing relative gillnet catch (biomass) by species through the time series (1995-2015). The larger and darker bubbles indicate larger biomass values. Species that made up less than 5% of the total gillnet biomass through time were excluded, for aesthetics.

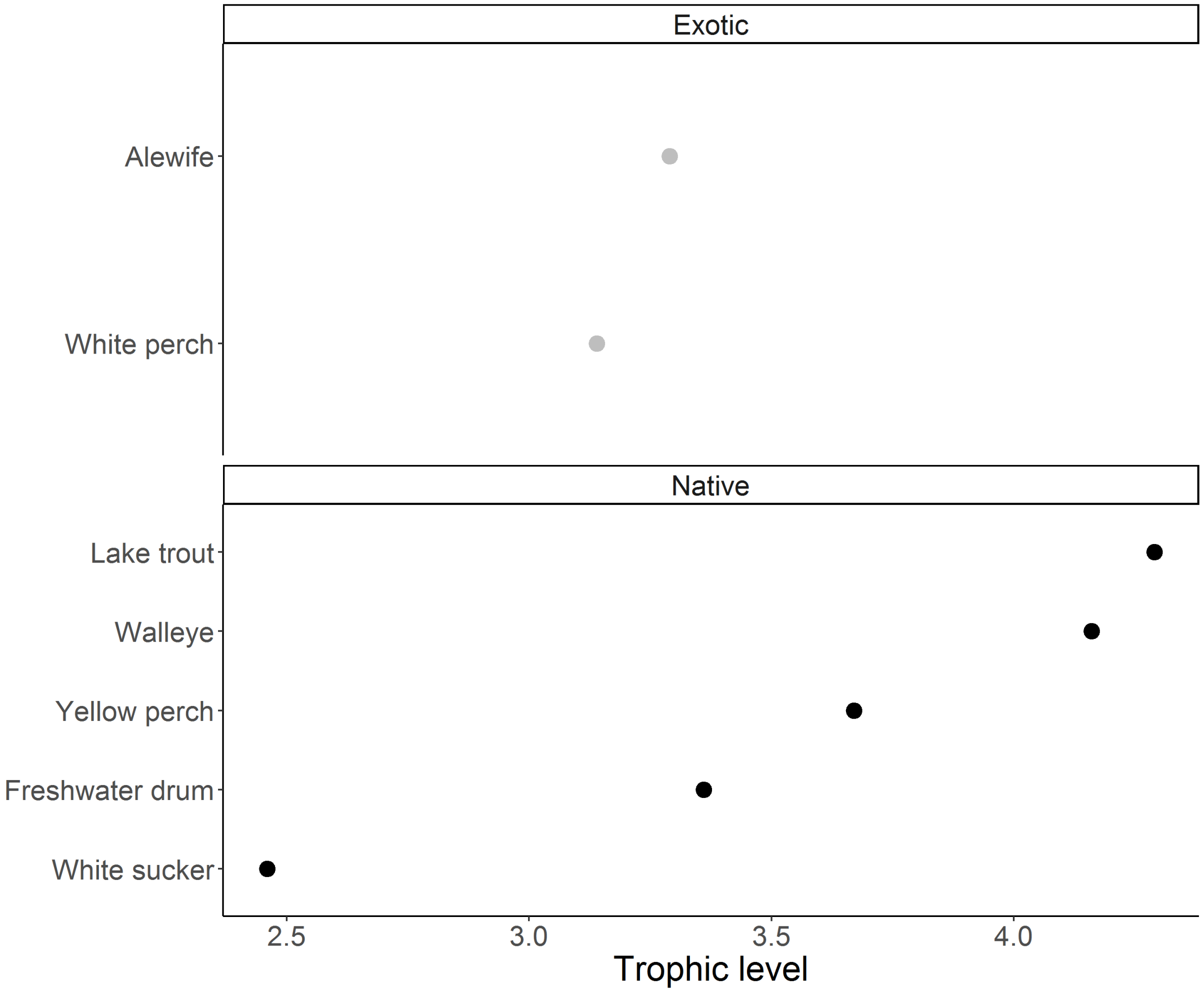

Figure 4.8: Dotchart showing the approximate trophic level of the seven species that were the main contributers to beta diversity through the time series. The x-axis show the approximate trophic level and the species are grouped by their origin.

Appendix 4.A

Table 4.A1: List of species encountered in the gillnet surveys, their origin (E= exotic, N=native), thermal preference, trophic niche and level, as well as habitat association.

Species	Origin	Thermal pref	Trophic niche	Trophic level	Habitat
Alewife *Alosa pseudoharengus*	E	warm	planktivore	3.29	pelagic
Atlantic salmon *Salmo salar*	N	cold	piscivore	4.5	benthopelagic
Black crappie *Pomoxis nigromaculatus*	N	cool	invertivore	3.81	benthopelagic
Bluegill *Lepomis macrochirus*	N	warm	invertivore	3.53	benthopelagic
Bowfin *Amia calva*	N	warm	piscivore	3.81	benthopelagic
Brook trout *Salvelinus fontinalis*	N	cold	piscivore	3.31	benthopelagic
Brown bullhead *Ameiurus nebulosus*	N	warm	invertivore	3.28	benthic
Brown trout *Salmo trutta*	E	cold	piscivore	3.36	benthopelagic
Burbot *Lota lota*	N	cold	piscivore	3.84	benthic
Channel catfish *Ictalurus punctatus*	N	warm	invertivore/piscivore	3.4	benthic
Chinook salmon *Oncorhynchus tshawytscha*	E	cold	piscivore	4.4	pelagic
Common carp *Cyprinus carpio*	E	warm	invertivore/detritivore	3.06	benthopelagic
Freshwater drum *Aplodinotus grunniens*	N	warm	invertivore	3.36	benthic
Gizzard shad *Dorosoma cepedianum*	N	warm	herbivore	2.4	pelagic
Golden shiner *Notemigonus crysoleucas*	N	cool	invertivore/herbivore	2.65	benthopelagic
Greater redhorse *Moxostoma valenciennesi*	N	warm	invertivore	3.32	benthic
Lake herring *Coregonus artedi*	N	cold	planktivore/invertivore	3.35	pelagic
Lake trout *Salvelinus namaycush*	N	cold	piscivore	4.29	benthopelagic
Lake whitefish *Coregonus clupeaformis*	N	cold	invertivore	3.23	benthic
Largemouth bass *Micropterus salmoides*	N	warm	piscivore	4.42	benthopelagic
Longnose gar *Lepisosteus osseus*	N	warm	piscivore	4.19	benthopelagic
Mooneye *Hiodon tergisus*	N	warm	invertivore	3.72	pelagic
Northern pike *Esox lucius*	N	cool	piscivore	4.07	benthopelagic
Pumpkinseed *Lepomis gibbosus*	N	warm	invertivore	3.27	benthopelagic
Rainbow smelt *Osmerus mordax*	E	cold	invertivore	3.44	pelagic
Rainbow trout *Oncorhynchus mykiss*	E	cold	piscivore	4.08	benthopelagic
Rock bass *Ambloplites rupestris*	N	warm	invertivore	3.33	benthopelagic
Sea lamprey *Petromyzon marinus*	E	cold	parasite	4.37	benthopelagic
Shorthead redhorse *Moxostoma macrolepidotum*	N	warm	invertivore	3.13	benthic
Silver redhorse *Moxostoma anisurum*	N	cool	invertivore	3.01	benthic
Smallmouth bass *Micropterus dolomieu*	N	warm	invertivore/piscivore	3.56	benthopelagic
Trout-perch *Percopsis omiscomaycus*	N	cool	invertivore	3.38	benthopelagic
Walleye *Sander vitreus*	N	cool	piscivore	4.16	benthopelagic
White bass *Morone chrysops*	N	warm	invertivore/piscivore	4.04	benthopelagic
White perch *Morone americana*	E	warm	invertivore	3.14	benthopelagic
White sucker *Catostomus commersonii*	N	cool	invertivore/detritivore	2.46	benthic
Yellow perch *Perca flavescens*	N	cool	invertivore	3.67	benthopelagic

Chapter 5

Synthesis and Conclusions

This dissertation has focused on approaches to quantify variability in standardized fish catch data to 1) evaluate if variance components are responsive to large-scale perturbation, and therefore have potential as statistical indicators of ecological shifts; 2) decompose the variability in age-structured time series data using wavelet analysis to evaluate if age truncation could alter the endogenous population oscillation, and as a result sensitivity to environmental signals; and 3) partition the variability in multivariate community data to evaluate response to multiple environmental drivers thought to be representative of changing climatic conditions. All three chapters relied on fish survey data from the Great Lakes Basin. Variability represents departures from the mean, and is often treated as a quantity to control or minimize through carefully designed sampling programs (Kratz et al., 1995), but we are learning that deviations from the norm may represent important behaviors or phenomena associated with ecological processes. It is not global averages that organisms respond to, but regional and local conditions, which are spatially and temporally heterogeneous (Walther et al., 2002). This work has tested theoretical behavior with empirical data to approach long standing questions about population dynamics from different perspectives. Our results have highlighted different modeling tools that have promise for questions more broadly, yet have uncertainty and limitations as well. Advancing a field such as fisheries science requires exploration of new techniques and applications to enhance the toolbox of approaches required to address these very complex problems. This work is a contribution to that endeavor.

Variance components as statistical indicators

There is a growing body of literature dedicated to the detection and prediction of regime shifts. Ecosystem regime shifts are unidirectional shifts that result in a new stable state with different characteristics and feedbacks from the previous stable state (Walker et al., 2004). Shifts of this nature may represent undesirable conditions relative to conservations goals, management objectives, and socio-economic dynamics (Biggs et al., 2012), and therefore identification of reliable signals to detect and ideally predict when a system is approaching a critical transition point is an important area of research (May, 1977; Lluch-Belda et al., 1989; Scheffer et al., 2001; Kuehn, 2011; Drake, 2013). From this literature several indicators have been developed as generalizable signals, one such indicator is variability. It has been shown through simulation and experimentation that variability in a response variable tends to increase as a system is approaching a critical transition (Brock and Carpenter, 2006; Scheffer et al., 2009; Carpenter et al., 2011). This increased variability is a chaotic state when the system is oscillating between responding to the current state and the conditions of the new, potential, steady state.

The idea that variance could indicate major ecological shifts led to the conjecture that source components of variability may also be indicative of systems in transition. We sought out a system with long-term biological data and a history of major ecological shift, potentially a regime shift. The fish community of Oneida Lake presented itself as a viable option. The perceived shift observed in Oneida Lake was rather abrupt, due in large part to the invasion of a non-native species. To address the abrupt nature of the ecologcal shift, a pre- and post-perturbation analysis with an estimated change point to delineate the time periods was adopted. With this approach, we evaluated the hypothesis that the structure of variability would be responsive to the observed changes; our results supported that hypothesis. A point of interest that arose while contemplating variability, and the components of variability, as indicators of major shifts in a fish population, related back to the general behavior of increased variability when approaching a major transition. With fish count data, all observations were positive integers, and therefore there is a lower limit of possible observation values, i.e., zero. In Oneida Lake, the response to the ecological perturbations was an overall reduction in catches and the variability among catches from different sampling locations. For variability to have increased, the transition time period would have produced some exceptionally high catches and many low catches during the transition to overall lower catches. Observing this behavior seems unlikely, which raises questions about the type of response variables that could exhibit these general signals of regime shifts, and if different signals could arise in those that may deviate from the predicted response.

The approach we have laid forth can offer insight into ecological patterns that may be obscured through modeling of fixed effects alone. For example, in our study, total variability declined following the perturbations as did the mean Walleye catch. Modeling this time series with a linear regression, with a fixed year effect would have suggested that the population has declined and the rate at which catches were reduced. Using a mixed model, as we have shown, illustrated that although overall catches declined, that reduction was not uniform, and it was the inshore sites that were reduced most severely. The model is not a mechanistic one, but the detection of fine-scale spatial and temporal patterns can inform the development of new hypotheses. This analysis has spawned many new questions regarding this inshore/offshore restructuring that we observed. For instance, is this shift the result of water clarity (e.g., the nets are easier for Walleye to see and avoid), evasion of predation in deeper waters, or an alternate explanation? This approach is simple enough to implement, yet flexible enough to adapt to many different research questions, and for those reasons it is anticipated to be a useful tool.

Adapting this approach to monitor the behavior of variance components in response to gradual perturbation could provide additional insights. For example, if there was interest in shifting spatial distribution due to warming temperatures, one could use a similar approach but allow the spatial variance term to vary through time as an autoregressive process. This would allow the among-site variability to vary in each time step, and the sites would be random draws from that distribution in each year. This approach could shed light on the gradual behavior of variance components, and may offer potential early warning signals similar to the indicators developed for regime shift detection, assuming sufficient data collected at appropriate scales are available.

Another potential application for this variance partitioning framework is to make logistical decisions about monitoring efforts. Imagine, that the funding for an annual survey has been reduced by half. As a scientist or manager, a decision about how to continue the most representative survey, yet with half the funds, becomes an important decision. Possible options might include to continue the survey on an annual basis, but only sample half the sites, whereas an alternate option could be to survey every other year and sample all the sites. Based on the results from this analysis, the latter might be the more reasonable option because we observed very little interannual variability, and much greater variability among sites. This example is an oversimplification of such decisions, but is used for illustrative purposes. For example, the gillnet gear used for this survey is capable of capturing the same cohort over multiple seasons, potentially reducing temporal variability. These considerations are important to note of course, but will vary by project, system, and sampling gear.

Wavelet analysis

In marine systems, selective harvest through fishing has been shown to alter age and size structure of fish populations, and as a result has increased variability and sensitivity to environmental signals (Berkeley et al., 2004; Hsieh et al., 2010). Predation, when preference for larger individuals is detected, can act in a similar way, especially when supplemental stocking of the predator is taking place. As discussed in chapter 2, the result can be a truncation of the age structure and tightening of the link between population dynamics and environmental variability. Our results were consistent with expected behavior of an age-structured population experiencing severe age truncation. Analyzing population dynamics with signal processing methodologies is not new (Bjørnstad et al., 1999; Bjørnstad and

Grenfell, 2001; Bjørnstad et al., 2004; Worden et al., 2010), but is gaining traction in the ecological literature (Cazelles et al., 2008; Hidalgo et al., 2011; Botsford et al., 2014).

Wavelet analysis is a powerful tool to detect patterns at scales that are not as obvious using standard analytical tools; tools that assume stationarity and linearity. However, pattern detection does not indicate mechanistic drivers. Lack of mechanistic inference is an issue that extends to many commonly used models in fisheries, and discussions around which models are better, mechanistic or phenomenological, and how to distinguish between the two continue to this day (Hilborn and Mangel, 1997; Bolker, 2008). Wavelet analysis is a descriptive tool, and although not a model it offers insights in more of a phenomenological way than a mechanistic one. As mentioned in chapter 3, the development of the mean spawner age oscillation is important, and it suggests that alewife could be more sensitive to environmental signals at that frequency. That is not to say that signal has to be temperature, and in fact it may not be. There are many exogenous drivers that have potential to influence fish populations. It is also challenging to predict how the alewife population will respond if another signal at a similar frequency does interact. Those questions will require additional research, but even so, the alewife behavior over the next few years may improve the understanding of the role of age structure in determining the response to environmental forcing.

The results from the stock-recruit modeling in chapter 3 suggested that temperature is an important factor in influencing recruitment success in the alewife population in Lake Michigan. Our results also suggested that the effect of temperature has increased through the time series. At the time of the development of this signal, there was only weak correlation with the frequency of the temperature indices. As a result, although some echoing of stochastic recruitment was observed in the empirical data during the latter years of the time series, an amplification of that signal wasn't observed. These observations highlight concern about the future of the population. Specifically, it has been shown that truncation of the age structure has continued and even worsened in recent years (Madenjian et al., 2014); what remains unknown is whether the anomalous recruitment events in recent years (both high and low) were influenced by an interaction with oscillatory environmental signals.

The extremely large recruitment events of the 1990s, did not appear to arise from correlation with temperature indices at a similar frequency, but was likely the result of amenable conditions during a brief period of relatively broad age structure. Specifically, during the high recruitment in the mid-1990s, there were fish as old as 8 and 9 in the population, and only a weak oscillatory signal in the alewife spawner biomass. As a result, it is unlikely that cohort resonance was influential in those recruitment events. It was not until the mid-2000s that the dominant frequency of the alewife population approximated the mean spawner age. The shift to a strong signal at the mean spawner age, concurrent with truncation of the age structure, is compelling, and potentially important for managers to incorporate demography into management decisions as opposed to biomass or abundance alone.

Community analysis

In the Bay of Quinte (BOQ), a recent study synthesizing changes in the aquatic community showed high biotic integrity and a rebounding of native fishes (Hoyle and Yuille, 2016). In that analysis, the influence of large-scale environmental signals were not included, and with a rapid pace of climate induced changes, evaluating the community response to environmental sifts stood out as an important research priority. The gradient forest approach combined with the estimate of species contribution to beta diversity suggested that the community as a whole was most sensitive to changes in Secchi depth, yet only a small portion of the variability in the community was predicted by the environmental signals. Overall there haven't been tremendous fluctuations in the community indicators we evaluated, over the relatively short time scale extending back to the mid-1990s. However, our analysis did reveal some important shifts consistent with predictions about aquatic community response to climate change.

Native cold-water species declined throughout the time series, while non-native warm water species abundance are on the rise. In addition, the mean trophic level declined with reductions in water clarity. Many piscivores rely on visual cure for predation, cues that are likely obscured when the water clarity declines. Water clarity itself could be influenced by various procesess. Wind and turbulence can stir up sediment and cause reductions in water clarity, but in the Great Lakes, much of this shift is due to phytoplankton production. In the BOQ, the phytoplanoton biovolume has been relatively stable, but the composition is changing, shifting towards greater abundance of eutrophic diatoms and cyanobacteria, many of which are inedible (Estepp and Reavie, 2015). Despite a relatively robust and diverse fish community, the base of the trophic structure has changed and continues to be representative of eutrophic conditions (Munawar et al., 2012). In addition, reduced light penetration can impact submerged aquatic vegetation, which can impact habitat and refugia for larvae and juvenile fish. The interconnectedness of ecosystems poses many challenges to whole system level assessments; modeling tools that can synthesize complex information, such as gradient forest, are important to progress ecosystem-based approaches. Future research could apply a similar methodology but move beyond the assessment of the fish community, and include phytoplankton, zooplankton, and benthos, and include more direct anthropogenic drivers such as phosphorous levels, human population density, and exploitation.

Limitations and data needs

With interest in understanding how climate-related shifts may impact fish communities in the Great Lakes, we have sought out established, long-term data sets for use in our analyses. Even so, observations of coupled biological and physical variables, at similar resolution, were often lacking. Some analyses we have presented would not have been possible with more limited data sets. We are aware that many constraints contribute to a gap between ideal data collection and feasible data collection, but careful thought should be given to expand monitoring programs with climate change in mind. It is extremely challenging to identify correlative or causal links between environmental signals and changing fish distributions due to the scarcity of sufficient and long-term data sets, especially those that include relevant covariate measures (Booth et al., 2011). The Oneida Lake data we presented, spanned back to 1958, yet some would argue that this is still a relatively short time scale (Izzo et al., 2016), as some researchers have found fish populations to cycle between collapse and recovery at 60-100 year cycles (Baumgartner et al., 1992). A commitment to consistent collection of spatial and temporal biological and physical data, alongside the development of novel and innovative modeling approaches is imperative to confronting these challenging questions regarding how ecological systems will respond to different climate scenarios.

References

Baumgartner, T., Soutar, A., and Ferreira-Bartrina, V. (1992). Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara basin, california. *CalCOFI Rep*, 33:24–40.

Berkeley, S. A., Hixon, M. A., Larson, R. J., and Love, M. S. (2004). Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, 29(8):23–32.

Biggs, R., Blenckner, T., Folke, C., Gordon, L., Norström, A., Nyström, M., and Peterson, G. (2012). Regime shifts. *Encyclopedia of theoretical ecology*, pages 609–617.

Bjørnstad, O. N., Fromentin, J.-M., Stenseth, N. C., and Gjøsæter, J. (1999). Cycles and trends in cod populations. *Proceedings of the National Academy of Sciences*, 96(9):5066–5071.

Bjørnstad, O. N. and Grenfell, B. T. (2001). Noisy clockwork: time series analysis of population fluctuations in animals. *Science*, 293(5530):638–643.

Bjørnstad, O. N., Nisbet, R. M., and Fromentin, J. (2004). Trends and cohort resonant effects in age-structured populations. *Journal of animal ecology*, 73(6):1157–1167.

Bolker, B. M. (2008). *Ecological models and data in R.* Princeton University Press.

Booth, D. J., Bond, N., and Macreadie, P. (2011). Detecting range shifts among Australian fishes in response to climate change. *Marine and Freshwater Research*, 62(9):1027–1042.

Botsford, L. W., Holland, M. D., Field, J. C., and Hastings, A. (2014). Cohort resonance: a significant component of fluctuations in recruitment, egg production, and catch of fished populations. *ICES Journal of Marine Science: Journal du Conseil*, 71(8):2158–2170.

Brock, W. A. and Carpenter, S. R. (2006). Variance as a leading indicator of regime shift in ecosystem services. *Ecology and Society*, 11(2):9.

Carpenter, S. R., Cole, J. J., Pace, M. L., Batt, R., Brock, W., Cline, T., Coloso, J., Hodgson, J. R., Kitchell, J. F., Seekell, D. A., et al. (2011). Early warnings of regime shifts: a whole-ecosystem experiment. *Science*, 332(6033):1079–1082.

Cazelles, B., Chavez, M., Berteaux, D., Ménard, F., Vik, J. O., Jenouvrier, S., and Stenseth, N. C. (2008). Wavelet analysis of ecological time series. *Oecologia*, 156(2):287–304.

Drake, J. M. (2013). Early warning signals of stochastic switching. *Proceedings of the Royal Society of London B: Biological Sciences*, 280(1766):20130686.

Estepp, L. R. and Reavie, E. D. (2015). The ecological history of Lake Ontario according to phytoplankton. *Journal of Great Lakes Research*, 41(3):669–687.

Hidalgo, M., Rouyer, T., Molinero, J. C., Massutí, E., Moranta, J., Guijarro, B., and Stenseth, N. C. (2011). Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. *Marine Ecology Progress Series*, 426:1–12.

Hilborn, R. and Mangel, M. (1997). *The ecological detective: confronting models with data*, volume 28. Princeton University Press.

Hoyle, J. A. and Yuille, M. J. (2016). Nearshore fish community assessment on Lake Ontario and the St. Lawrence River: A trap net-based index of biotic integrity. *Journal of Great Lakes Research*, 42(3):687–694.

Hsieh, C.-H., Yamauchi, A., Nakazawa, T., and Wang, W.-F. (2010). Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences*, 72(2):165–178.

Izzo, C., Doubleday, Z. A., Grammer, G. L., Gilmore, K. L., Alleway, H. K., Barnes, T. C., Disspain, M. C., Giraldo, A. J., Mazloumi, N., and Gillanders, B. M. (2016). Fish as proxies of ecological and environmental change. *Reviews in Fish Biology and Fisheries*, 26(3):265–286.

Kratz, T. K., Magnuson, J. J., Bayley, P., Benson, B. J., Berish, C. W., Bledsoe, C. S., Blood, E. R., Bowser, C. J., Carpenter, S. R., Cunningham, G. L., et al. (1995). Temporal and spatial variability as neglected ecosystem properties: Lessons learned from 12 North American ecosystems. In *Evaluating and monitoring the health of large-scale ecosystems*, pages 359–383. Springer.

Kuehn, C. (2011). A mathematical framework for critical transitions: Bifurcations, fast–slow systems and stochastic dynamics. *Physica D: Nonlinear Phenomena*, 240(12):1020–1035.

Lluch-Belda, D., Crawford, R., Kawasaki, T., MacCall, A., Parrish, R., Schwartzlose, R., and Smith, P. (1989). World-wide fluctuations of sardine and anchovy stocks: the regime problem. *South African Journal of Marine Science*, 8(1):195–205.

Madenjian, C. P., Bunnell, D. B., Desorcie, T. J., Ksotich, M. J., Armenio, P. M., and Adams, J. V. (2014). Status and trends of prey fish populations in Lake Michigan, 2013. Report, A report to the Great Lakes Fishery Commission, Lake Michigan Committee.

May, R. M. (1977). Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature*, 269(5628):471–477.

Munawar, M., Fitzpatrick, M., Munawar, I., Niblock, H., and Kane, D. (2012). Assessing ecosystem health impairments using a battery of ecological indicators: Bay of Quinte, Lake Ontario example. *Aquatic Ecosystem Health & Management*, 15(4):430–441.

Scheffer, M., Bascompte, J., Brock, W. A., Brovkin, V., Carpenter, S. R., Dakos, V., Held, H., Van Nes, E. H., Rietkerk, M., and Sugihara, G. (2009). Early-warning signals for critical transitions. *Nature*, 461(7260):53–59.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., and Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413(6856):591–596.

Walker, B., Holling, C. S., Carpenter, S. R., and Kinzig, A. (2004). Resilience, adaptability and transformability in social–ecological systems. *Ecology and Society*, 9(2):5.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., Fromentin, J.-M., Hoegh-Guldberg, O., and Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416(6879):389–395.

Worden, L., Botsford, L. W., Hastings, A., and Holland, M. D. (2010). Frequency responses of age-structured populations: Pacific salmon as an example. *Theoretical Population Biology*, 78(4):239–249.