Explaining Changes in Fish Community Biomass Using Pressure Indicators: Comparison of Data Analysis Methods and Regional Results

by

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To Nanny Brown

We’re still waiting on the redhead, but at least now there’s a doctor in the family

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ABSTRACT

This thesis focuses on assessing relationships among ecological indicators, including identifying pressures that best explain changes in the fish community of two Northwest Atlantic ecosystems. The Grand Bank experienced complex ecological changes over three decades, including a rapid collapse and partial recovery of fish biomass, and I synthesized fish community, environmental, and human indicators that reflect these changes. I first used this suite to demonstrate that relationships among fish functional groups changed after the collapse, identify a representative subset of pressure indicators, show the response to pressures varies over different time scales, and illustrate that a common conceptual framework can be misleading. Next, I compared multivariate linear regression (MLR) and non-linear neural networks (NN) for modelling the biomasses of six fish functional groups using fishing and environmental pressures, identified the most influential pressures, and assessed the effect of different delay types and lengths. In contrast to MLR, the delays had negligible impact on NN fit, which illustrates the powerful ability of NN to extract patterns from data. However, MLR generally had better fit than simple 1-hidden node NN ensembles. Both approaches showed that top-down and bottom-up pressures are influential, and that the most influential pressures changed after the collapse. A preliminary assessment of NN predictive power showed that future efforts should continue investigating NN forecast ability. Another case study applying these approaches to the Georges Bank fish community supported these main conclusions. Different pressures were influential for each region, highlighting the need for ecosystem-specific indicator sets. My thesis contributes to knowledge of past and present dynamics of these ecosystems and can potentially inform ecosystem based fisheries management approaches. I recommend MLR models over NN for this application because they are easier to construct and interpret, although NN may be able to provide complementary information through forecasts. Finally, I discuss implications of my findings and suggest future work to build on this research.

LIST OF ABBREVIATIONS AND SYMBOLS USED

Adjusted-R^2_{Total}	R^2_{Total} modified to account for the number of predictors
AMO	Atlantic Multidecadal Oscillation
$\mathrm{Area}_{\mathrm{Ice}}$	Total area of sea ice below 55°N
AZMP	Atlantic Zone Monitoring Program
DFO	Fisheries and Oceans Canada
DPSIR	Driver-pressure-state-impact-response
EBFM	Ecosystem based fisheries management
ECI	Environmental composite index
EEZ	Exclusive economic zone
forecast-5	5-year forecast model
forecast-10	10-year forecast model
GLOBEC	GLOBal Ocean ECosystems Dynamics
H	Shannon's diversity index
h	Number of hidden nodes
ICES	International Council for the Exploration of the Seas
ICJ	International Court of Justice
IEA	Integrated Ecosystem Assessment
J	Pielou's index
k	Delay length
L	Mean fish length
$\mathrm{Lat}_{\mathrm{Ice}}$	Minimum latitude of sea ice extent
MLP	Multi-layer perceptron
MLR	Multivariate Linear Regression
MSE	Mean squared error
$\mathrm{MSE}_{\mathrm{All}}$	MSE of all observations
$\mathrm{MSE}_{\mathrm{Test}}$	MSE of the test data
$\mathrm{MSE}_{\mathrm{Train}}$	MSE of the training data
MTI	Mean trophic index
NAFO	Northwest Atlantic Fisheries Organization
NAO	North Atlantic Oscillation

NEFSC	Northeast Fisheries Science Center
NOAA	National Ocean and Atmospheric Administration
n	Sample size, in context
n*	Effective number of observations
nfold-5	Last 5 years of *n*-fold cross validation
nm	nautical mile
NN	Neural network
NOAA	National Ocean and Atmospheric Administration
P50	Proportion of times predictor was included in the top 50 MLR models
p	Number of predictors
PCW	Product of connection weights
J	Pielou's index
PPred	Proportion of predators
r	Number of responses
R_j^2	Coefficient of determination for response j
R_{Total}^2	Average of the R_j^2's
$RI_{i,j}$	Relative importance of predictor *i* for modelling response *j*
RV	Random variable
SSB	Spawning stock biomass
SSE	Sum of squared errors
SSE_{Total}	Total sum of squared errors
SSM_j	Sum of squares of the model for response *j*
SSM_{Total}	Sum of squares of the model summed over all responses
SST_j	Total sum of squares for response *j*
SST_{Total}	Total sum of squares summed over all responses
S0, SSS	Sea surface salinity
S75	Salinity measured at 75 m
S150, Sbottom	Salinity measured at 150 m
T0, SST	Sea surface temperature
T75	Temperature measured at 75 m
T150	Temperature measured at 150 m
TAC	Total allowable catch

Time_{Ice}	Timing of the sea ice melt
TL	Trophic level
TMGC	Transboundary Management Guidance Committee
TRAC	Transboundary Resource Assessment Committee
US	United States
WGNARS	Working Group on the Northwest Atlantic Regional Sea
i, j, k, q	Counters, in context
$\widehat{\boldsymbol{\beta}}$	Matrix of coefficients for multivariate linear regression [p x r]
β_j	Bias associated with node *j*
ρ	Spearman’s correlation coefficient
$w_{i,j}$	Weight from node *i* to node *j*
$\mathbf{X}$	Matrix of predictors [n x p]
x_i	Value *i* of given predictor
$\mathbf{Y}$	Matrix of responses [n x r]
$\widehat{\mathbf{Y}}$	Matrix of modelled responses [n x r]
$\bar{y}_j$	Mean of column *j* of response matrix
$\hat{y}_{i,j}$	i^{th} value of the j^{th} modelled response
$\emptyset_{Hid}$	Activation function in the hidden nodes
$\emptyset_{Out}$	Activation function in the output nodes
$\%Contribution_{i,j}$	Percent contribution of predictor *i* to modelling response *j*

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CHAPTER 1: INTRODUCTION

1.1 Motivation

Many of the world's commercial fish stocks are overexploited (FAO, 2012), and there is a growing understanding that conventional fisheries management is ill-equipped to balance trade-offs between sustainable fishing and socio-economic priorities (Pauly et al. 2002, Pikitch et al. 2004, Jennings 2005, Link 2010, Fogarty 2014). Traditional management aims to maximize the yield of individual stocks without evaluating feedbacks among different fisheries, which can result in conflicting management plans and excess fisheries removals (Pikitch et al. 2004, Fogarty 2014). There are global calls to supplement single species management with more holistic approaches such as ecosystem based fisheries management (EBFM; e.g., Misund and Skjoldal 2005, DFO 2007). EBFM explicitly considers interactions among multiple species in the context of changing environment, human use, and social well-being, while balancing economic, ecologic, and political trade-offs (Larkin 1996, Link 2010, Fogarty 2014). This type of management is supported by policy and legislation worldwide (e.g., Canada's Oceans Act; the United States Magnuson-Stevens Reauthorization Act; the European Marine Strategy Framework Directive), although implementation has been slow because of perceived and real challenges (Link et al. 2011a, Fogarty 2014). This thesis addresses one such challenge, which is identifying subsets of indicators that can inform scientists and managers of relevant changes in the ecosystem – and potentially forecast them.

Implementation of EBFM requires quantitative information on the marine ecosystem, which can be provided in part by indicators. Indicators are measured or derived metrics of the ecosystem, and hundreds have been proposed to describe biological communities, environmental conditions, and human activities and well-being (Cury and Christensen 2005). Biological indicators reflect ecosystem state, which usually refers to the structure and function of the fish community, including fish biomass, trophic level, size, and diversity based metrics (e.g., Bundy et al., 2012; Coll et al., 2016). Indicators of environmental conditions (e.g., temperature, salinity, primary production) and human activities (e.g., fishing, oil and gas exploration, shipping) reflect external pressures that may cause changes in the fish community (e.g., Large et al., 2015b). Unlike conventional management approaches, EBFM considers humans as part of the ecosystem, and indicators have been proposed to monitor the well-being of fishing communities and regions (e.g., income, human development index; Link et al. 2010b, Fogarty et al. 2012). It is generally understood that multiple indicators from each category are required to adequately inform managers on the different dimensions of the ecosystem, and that useful indicator sets will be ecosystem specific (Rice 2003, Jennings 2005, Rice and Rochet 2005, Shin et al. 2010b), although guidelines for selecting indicators are often focused on biological indicators that are sensitive to fishing pressure (Perry et al. 2010, Large et al. 2015b, 2015a, Otto et al. 2018). Criteria for useful indicators have been defined, including measurability, sensitivity to change, ecological meaning, and public awareness (Cury and Christensen 2005, Jennings 2005, Rice and Rochet 2005). Conceptual frameworks that organize indicators into different categories have been suggested as tools that can aid indicator selection, identify causal and redundant relationships among indicators, and facilitate the presentation of results to stakeholders (EEA, 1999; Gari et al., 2015).

Indicators have been used mainly for describing past and current ecosystem status and trends (Dambacher et al. 2009, Coll et al. 2016). Extensive indicator sets spanning several decades exist for some regions, and are updated regularly (e.g., EcoAP, 2009, 2012). Such work provides a baseline of ecosystem conditions, which can be used to monitor the extent of changes, and hints at future changes if trends continue; however, these sets can be difficult for managers to synthesize and turn into actionable objectives (Dambacher et al. 2009). Many regions have few, if any, indicators, because of lack of appropriate data over useful time scales, and/or perhaps a lack of political or scientific impetus to synthesize and publish them. Indicators have also been recently applied to compare the status of exploited marine ecosystems, and to investigate the responses of individual biological indicators to human and environmental pressures (e.g., Bundy et al. 2012, Large et al. 2015b, 2015a, Coll et al. 2016). These and other efforts to apply indicators and contribute to scientific knowledge required for implementing EBFM can be complemented by an improved understanding of multivariate pressure-response relationships, including the ability to model changes in the fish community, and knowledge of which pressures causing these changes are the most influential (Crain et al. 2008, Dambacher et al. 2009, Link et al. 2010b, Perry et al. 2010, Large et al. 2015a).

Identifying the most influential pressure indicators is inherently challenging as a result of the multivariate, non-linear, and dynamic nature of marine ecosystems, and the varied types and ways to measure pressures. Multiple pressures interact and can impact multiple ecosystem components with non-additive results, and fishing, the environment, and other pressures (e.g., predator-prey interactions) can result in non-linear and indirect responses (Daan et al. 2005, Crain et al. 2008, Large et al. 2013, Hunsicker et al. 2016). However, many studies focus on single pressure-response relationships, and often the methods used to study them inherently assume linear relationships (e.g., Blanchard et al. 2005, Fu et al. 2012, Probst et al. 2012, Dempsey et al. 2018). Additionally, the relative importance of pressures may vary over time because of changes in management strategies, the balance of environmental conditions, and biological interactions (Mann and Drinkwater 1994). Another difficulty in teasing out important relationships is that pressures can have both immediate and delayed impacts on the community. For example, fishing has the immediate effect of increased mortality (Beverton and Holt 1957), while changes in size-based indicators have been associated with fishing pressure lagged up to 20 years (Daan et al., 2005; Greenstreet et al., 2011). Finally, there are numerous pressures on marine fish communities, and they can be represented by different metrics. For instance, fishing indicators include metrics of landings (e.g., total or species aggregates), effort (e.g., hours fished), and fishing mortality (e.g., landings/community biomass). Environmental indicators include basin-scale metrics such as the North Atlantic Oscillation (NAO) and regional conditions such as annual mean temperatures (e.g., surface and bottom) and primary production.

This thesis focuses on methods for synthesizing ecological data, with the overall goal of identifying pressures that best explain observed changes in the fish community and providing insight into the dynamics of two important ecosystems in the Northwest Atlantic. Steps taken toward this goal were (i) synthesizing a new set of indicators for an ecologically and economically important ecosystem, (ii) demonstrating novel quantitative methods for selecting pressure indicators that best explain observed changes, (iii) investigating how to best incorporate delayed effects of human and environmental pressures, and (iv) illustrating preliminary forecasts of changes in the fish community on management-relevant timescales. These objectives were met using different statistical models, including simple correlations, a linear modelling approach (multivariate linear regression), and a non-linear modelling approach (neural networks). The Grand Bank (Canadian and international waters) was used as the primary case study, and a secondary case study of Georges Bank (United States and Canada) was included to test the generality of the methods and conclusions.

The Grand Bank and Georges Bank are both traditionally economically and ecologically important, data rich fishing grounds in the Northwest Atlantic Ocean (Fig. 1.1; e.g., Fogarty and Murawski, 1998; Schrank, 2005). They have supported commercial fisheries for centuries, and were among the most productive fishing grounds in the world until the late 20th century, when they each experienced complex ecological changes (Atkinson 1994, Fogarty et al. 1996). Commercially important groundfish species (e.g., cod) collapsed in both regions, resulting in changes in the community structure and related fishing practices. These ecosystems are of significant interest to the scientific community, and there are current efforts to implement EBFM in both regions (Oceans Act 1996, NOAA 2007, Link et al. 2011a, Koen-Alonso et al. 2018). The International Council for the Exploration of the Seas (ICES) Working Group on the Northwest Atlantic Regional Seas (WGNARS) is working on scientific support for Integrated Ecosystem Assessments (IEAs), using the Grand Banks and Georges Bank as case studies (ICES 2017). There is a wealth of data sources for the Grand Bank that can be used to calculate indicators for the past several decades, although no set was published prior to this work. The US Northeast Fisheries Science Center has compiled a suite of biological, fishing, and environmental indicators for Georges Bank that span several decades (EcoAP 2009, 2012), which was provided for this thesis by Robert Gamble and Sean Lucey (personal communication). The high interest in these regions and the available data that captures complex changes over several decades make these ecosystems excellent case studies for this thesis. Additional background is provided on each region in the relevant chapters and in Appendix B.

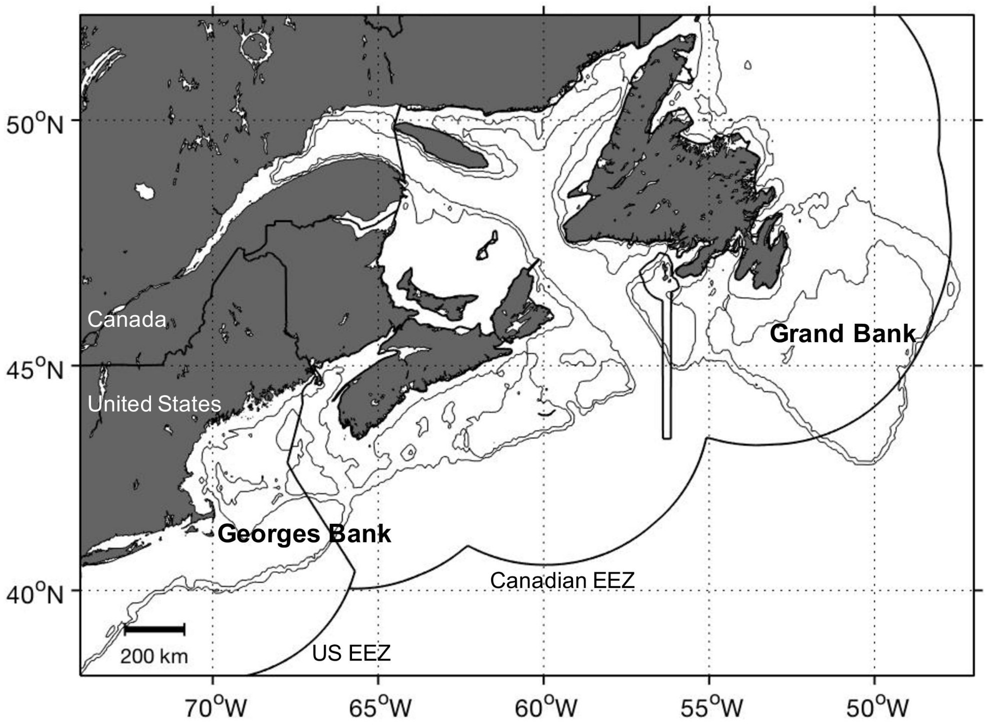

Figure 1.1: The Grand Bank and Georges Bank, the two economically and ecologically important ecosystems used as case studies in this thesis. Map shows the 100-m and 200-m isobaths, and the Canadian and United States (US) exclusive economic zones (EEZs).

1.2 Objectives and Overview of Approach

This thesis has four main objectives, which are each addressed in a dedicated chapter. This section outlines the objectives, and provides a brief overview of the approach used to address each one.

1. Synthesize and analyze indicators for the Grand Bank to draw insights about ecosystem dynamics and investigate the utility of a common management framework (Chapter 2).

There is an abundance of data related to the biological community, environmental conditions, and human activities in the Grand Bank, but to date, this data has not been synthesized as ecological indicators. To remedy this, I compiled a suite of indicators from various data sources, and investigated how these indicators reflect observed changes in the ecosystem. I used simple correlations to determine whether relationships among fish functional groups changed over time, and whether a subset of indicators is sufficient to characterize each indicator category. I also examined lagged relationships to identify when changes in pressures manifest in the fish community structure. Finally, I organized indicators into the DPSIR (driver-pressure-state-impact-response) management framework to explore whether that categorization is straightforward and useful for interpretation.

2. Evaluate the explanatory power of linear models that use fishing and environmental pressures to predict changes in the fish community of the Grand Bank before and after the biomass collapse (Chapter 3).

Ecosystem based fisheries management will benefit from assessment of how various pressures affect the fish community, including delayed responses. The objective of this chapter was to identify which pressures best explain three decades of change in the fish community of the Grand Bank, Northwest Atlantic. I developed assemblages of multivariate linear regression (MLR) models using nine fishing and environmental pressure indicators as predictors of the fish community structure for before and after the collapse, as well as the full data series. Explanatory power of the models was evaluated, and the most influential pressures identified. I repeated the analyses with different delay types (moving average vs. lag) and lengths (0 to 5 years) imposed on the pressures to investigate how considering delays changed the results.

3. Assess the utility of neural networks for explaining observed changes in the Grand Bank fish community using fishing and environmental pressures (Chapter 4).

Disentangling the impacts of multiple pressures on the fish community is challenged by the complex nature of marine ecosystems. The objective of this chapter was to address this challenge using an artificial neural network (NN), which is a non-linear, multivariate statistical model, to identify key pressures on the fish community of the Grand Bank over the past three decades. Nine fishing and environmental pressures were used to simultaneously model the biomass indices of six fish functional groups before and after the collapse of fish biomass in the region, and over the full data series. The analysis was repeated with time delays of different types (moving average vs. lags) and lengths (0–10 years) imposed on the pressures. The fit, predictive power, and most influential pressures were evaluated for each period. I compared the results to the linear model and provided a preliminary assessment of the forecast potential of NN.

4. Assess both linear and non-linear approaches for explaining changes in the Georges Bank fish community and recommend the most useful approach for future analyses (Chapter 5).

The objectives of this chapter were to (i) compare MLR and NN as methods for modelling the Georges Bank fish community and identifying its most influential pressures; (ii) use the results to make inferences about the dynamics of this fish community; (iii) recommend one method for use in future studies. Nine fishing and environmental pressures were used to model the biomass indices of six fish functional groups using both MLR and NN. The most influential pressures were identified using both methods for the Full time series (1985 – 2012), as well as two periods that roughly correspond to important management changes in the region. The analyses were repeated with delays of different lengths (0–8 years) and types (moving average vs. lags) imposed on the predictors, and results from the two approaches were compared.

1.3 Outline

This thesis includes 6 chapters, including this Introduction. Chapters 2 to 5 are intended as standalone manuscripts, and so there is some repetition in content among the chapters. Chapters 2 and 3 have been published (Dempsey et al. 2017, 2018), Chapter 4 is in review, and Chapter 5 is in preparation for submission in Summer 2019. My co-authors are acknowledged at the beginning of each chapter, and I use the first person singular pronoun throughout the thesis.

In **Chapter 2** I synthesized a suite of fish community, environmental, and human indicators that reflect the known changes on the Grand Bank. I used this suite to examine relationships among fish functional groups, to identify potentially redundant human and environmental indicators, and to suggest causal relationships between indicators. I then assessed the utility of categorizing indicators into the DPSIR framework for scientific understanding and provision of management advice. I used a carefully selected subset of this indicator suite throughout the investigations in the remaining chapters.

In **Chapter 3** I used an MLR model to identify subsets of pressure indicators with the most direct influence on the Grand Bank fish community to gain insight into past and present drivers of change. I determined which sets of pressure indicators best model the fish community over the past three decades, and explored whether explanatory power can be increased by incorporating different types and lengths of delays into the predictors.

In **Chapter 4** I conducted a similar analysis to Chapter 3, but used NN, a flexible, non-linear model, and compared the results (e.g., explanatory power, most influential pressures). I made a preliminary assessment of NN forecast potential for fisheries applications, and discussed the advantages and disadvantages of each method in the context of EBFM.

In **Chapter 5** I repeated the MLR and NN analyses for the Georges Bank ecosystem, and recommended one for use in future analyses.

Chapter 6 I synthesized the major findings, pointed out implications of the research, and recommended future work.

Appendix A includes the copyright permissions for Chapters 2 and 3; **Appendix B** provides additional background on the regions of interest; **Appendices C – E** are the supplementary material for Chapters 2, 3, and 4, respectively; **Appendix F** shows additional exploratory analyses of the indicators used throughout the thesis.

CHAPTER 2: COMPILATION AND DISCUSSION OF DRIVER, PRESSURE, AND STATE INDICATORS FOR THE GRAND BANK ECOSYSTEM, NORTHWEST ATLANTIC[1]

2.1 Abstract

There are global calls for new ecosystem based fisheries management (EBFM) approaches. Scientific support for EBFM includes assessing ecosystem indicators of biological communities, environmental conditions, and human activities. As part of a broader research project I synthesized and published a suite of traditional and new indicators for the Grand Bank in the Northwest Atlantic. This is an ideal ecosystem for indicator analysis because it experienced dramatic changes over the past three decades, including a collapse in fish biomass that had profound socio-economic consequences. I exploit the wealth of data for this ecosystem to investigate how individual indicators reflect observed changes in the ecosystem, and then illustrate two applications of this indicator suite. Correlations were used to show that relationships among the fish functional groups changed after the collapse, and that a subset of indicators is sufficient to characterize each ecosystem category. Lagged correlations highlighted how changes in the drivers and pressures are often not immediately manifest in the fish community structure. I also organized indicators into the DPSIR (driver-pressure-state-impact-response) management framework. This exercise illustrated that indicator categorization is contextual and not straightforward, and I advocate for use of simpler categories that clearly show what is actionable. Additional future analyses that can be performed with my newly published suite of indicators are recommended.

2.2 Introduction

There are global calls to supplement traditional single species fisheries management with ecosystem based approaches that account for interactions among multiple factors and commercial and non-target species (e.g., Misund and Skjoldal 2005, DFO 2007). To

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[1] Based on Dempsey, D. P., Koen-Alonso, M., Gentleman, W. C., and Pepin, P. (2017). Compilation and discussion of driver, pressure, and state indicators for the Grand Bank ecosystem, Northwest Atlantic. Ecol. Indic. 75, 331–339. doi:10.1016/j.ecolind.2016.12.011.

support this holistic type of management, decision makers need quantitative information on the state of the marine ecosystem, which can be provided by data-based indicators that describe biological communities, environmental conditions, and human activities (Jennings 2005). Criteria for useful indicators have been defined, including measurability, sensitivity to change, ecological meaning, and public awareness (Cury and Christensen, 2005; Rice and Rochet, 2005). Many indicators have been developed that meet these criteria, and sets of indicators are typically used to capture ecosystem complexity (e.g., Rice 2003, Jennings 2005, Houle et al. 2012). Interpreting these sets can be challenging and subjective, requiring rigorous analysis and historical context (Shin et al. 2010b).

I am engaged in a long term project focused on quantitative analysis that can identify useful sets of indicators for ecosystem based fisheries management (EBFM). As part of that research, I compiled data and calculated a suite of indictors for the Grand Bank, Northwest Atlantic (Fig. 2.1). I subsequently invested thought into how to identify first-order relationships between indicators, and how to categorize them using a management framework. I recognize the value of these efforts for others working in this region, as well as those using indictors for EBFM elsewhere. I made this preliminary work accessible to the broader community, and published the indicator suite in the supplementary material of Dempsey et al. (2017; Appendix C of this thesis).

The Grand Bank is one of the major ecosystem units within the Newfoundland Shelves bioregion (Pepin et al., 2014, NAFO, 2014), and is ideal for indicator analysis because it is a tightly coupled human-ecological system. For centuries it was one of the most productive fishing grounds in the world (Rose, 2007), but prolonged heavy fishing pressure combined with an environmental regime shift led to complex ecological changes, best characterized by the collapse of fish biomass in the early 1990s (Atkinson 1994, NAFO 2010a, Buren et al. 2014). The collapses of major stocks in the bioregion prompted the establishment of fishing moratoria, including several Grand Bank stocks (e.g., Atlantic cod in 1994). Many moratoria remain in place today (Rose 2007), although there are signs of recovery in some stocks (NAFO 2014). These fisheries closures also had socio-economic impacts on Canada's province of Newfoundland and Labrador, where local harvesters adapted by targeting different species (e.g., shrimp and other shellfish), retiring from the fishing industry, or leaving the province to find employment elsewhere (e.g., Hamilton and Butler, 2001; Schrank, 2005).

The bank extends from inside the Canadian exclusive economic zone (EEZ) into international waters. Fisheries management is the responsibility of Fisheries and Oceans Canada (DFO) within the EEZ, and the Northwest Atlantic Fisheries Organization (NAFO; statistical division 3LNO) in international waters (including straddling stocks). Both organizations are currently working towards implementing ecosystem approaches to management (Oceans Act 1996, DFO 2007, Koen-Alonso et al. 2018). While there have been some studies of indicators in the region, most are only available in the grey literature, and have not made their indicators available for other analyses.

I first present my compiled time series of fish community, human, and environmental indicators for the Grand Bank over the past three decades, and relate these trends to *a priori* knowledge of the ecosystem. I then discuss useful applications of these indicators, including correlation analyses to highlight potential redundant and causal relationships, and classification into the common DPSIR (driver-pressure-state-impact-response) management framework.

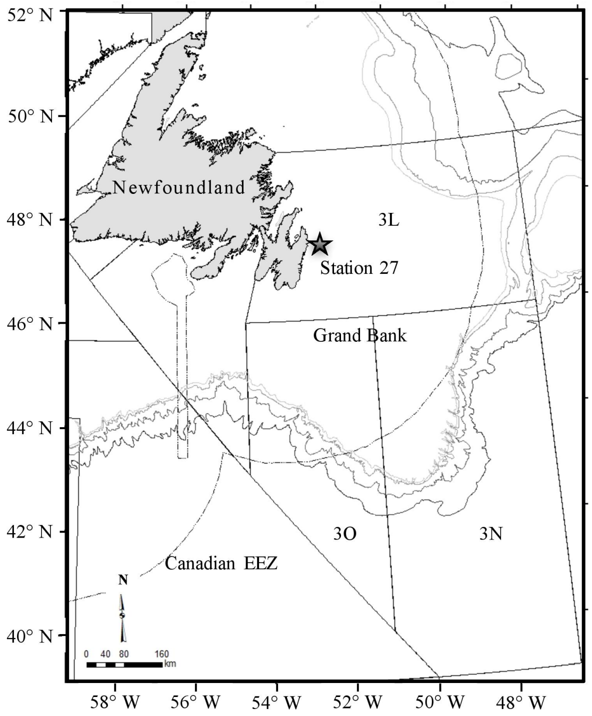

Figure 2.1: Map of the Grand Bank, showing NAFO areas 3L, 3N, and 3O, the Canadian exclusive economic zone (dashed line), and the location of oceanographic monitoring Station 27.

2.3 Methods

A suite of indicators was carefully chosen to describe the complex ecosystem changes that have taken place on the Grand Bank over the past three decades. Choices were constrained by data availability, as well as criteria identified by previous work (e.g., Rice and Rochet, 2005), and were derived from a variety of sources (Appendix C, Table S.1). The fish community indicators are annual mean values from 1985 – 2013, while fishing, socio-economic and environmental indicators extend back to 1975 to provide a broader context. Below I summarize the indicators used and my rationale for their selection.

2.3.1 Fish Community State Indicators

Three types of fish community indicators were included: biomass, trophic level, and biodiversity (Appendix C, Table S.1). These were derived from DFO annual spring bottom trawl surveys, which have been carried out since 1985 for Division 3LNO (Fig. 2.1), and provide biomass and abundance data for nearly 200 fish species. In 1996, there was a change from an Engels to a Campelen trawl, which complicates analyses because the Campelen has improved capture efficiency of shellfish and other smaller species (Koen-Alonso et al. 2010b, Belgrano and Fowler 2011). Recently, biomass scale factors were developed to make Engels biomasses coarsely comparable to Campelen (Koen-Alonso, unpublished work). Here I refer to periods “Before” (1985 – 1995) and “After” (1996 – 2013) the trawl change, which also roughly corresponds to before and after the collapse of fish biomass in the region. Scaling was not possible for invertebrates (e.g., *Pandalus* shrimps and snow crab), because those were not consistently recorded during the Before period. See Koen-Alonso et al. (2010) and McCallum and Walsh (1997) for further details.

I calculated several community biomass indicators to illustrate the ubiquity of the collapse, including total biomass as well as biomasses of benthivores (small, medium, and large), piscivores, planktivores, plank-piscivores, and shellfish (NAFO, 2010a; see Appendix C, Table S.2 for species in each). These functional groups are commonly used in DFO and NAFO analyses of the ecosystem. I also calculated four indicators of community trophic structure: mean trophic level (TL), the marine trophic index (MTI_{Comm}), the proportion of predators (PPred) and the mean length (L_{Comm}; Shannon et al., 2014). I assigned trophic levels to each species collected using established values from DFO, FishBase, and the Sea Around Us databases. I recognize that this approach introduces a degree of uncertainty (Caddy and Garibaldi 2000); however, these indicators are commonly used so I felt it worthwhile to assess their utility for describing changes on the Grand Bank (Shannon et al. 2014). TL is weighted by species biomass, and includes all surveyed species in the fish community (Shannon et al. 2014). MTI_{Comm} is similar, but only considers species with a minimum trophic level of 3.25 to reflect changes in higher trophic level species (Pauly and Watson, 2005). PPred is the biomass of all species with trophic level greater than 3.7 divided by the total community biomass index (Koen-Alonso et al. 2010a). L_{Comm} is the mean length of the fish community weighted by species biomass, which is a size based indicator that has been used as metric of fish community trophic structure (Shin et al., 2005). Note that because mean length is derived from abundance, for which there are no scale factors to approximate Engels data in Campelen units, L_{Comm} cannot be examined across the trawl change. I did not consider any richness indicators of biodiversity, which are based on the number of species recorded in a survey, and therefore prone to bias because rare and dominant species are weighted equally. Instead, I considered two biomass-based diversity indicators that take into account the relative proportions of each species: Shannon's index (H) and Pielou's index (J), where $J = H/H_{Max}$ (Peet 1974), and high values indicate more species diversity. Comparison of these indicators across the trawl change should be made with caution because of the differences in capture efficiency among species.

2.3.2 Human Use Indicators

Eight landings-based indicators were derived from NAFO's online database, STATLANT 21A (Appendix C, Table S.1). These include: landings of commercial species aggregates (groundfish, pelagics, shellfish, and "others"; Appendix C, Table S.3) and their sum (total landings); a fishing index (total landings/total community biomass; Koen-Alonso et al., 2010b); and trophic level indicators (Pauly et al. 1998, Pauly and Watson 2005). The mean trophic level ($\mathrm{TL}_{\mathrm{Land}}$) and marine trophic index ($\mathrm{MTI}_{\mathrm{Land}}$) are the landings version of these same indices calculated using the survey data and described above. Ecosystem indicators are now often expanded to include socio-economic metrics (Levin et al. 2009, McLeod and Leslie 2009). Following the example of Fogarty et al (2012), I included two such metrics (Appendix C, Table S.1): Newfoundland and Labrador's human population size and income (real household disposable income per capita, in 2002 dollars). These were downloaded from CANSIM, a Statistics Canada database.

2.3.3 Environmental Indicators

Environmental indicators included metrics that have been related to growth, species distribution, recruitment, and natural mortality of the Grand Bank fish community (Templeman, 2010). I included two basin-scale indicators for the Northwest Atlantic: the winter North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO). On the Grand Bank positive NAO is related to strong north-westerly winds, colder temperatures and more ice coverage (Mann and Drinkwater, 1994; Colbourne and Anderson, 2003). The AMO is an index of sea surface temperature variability after removing the effect of climate change (Kerr, 2000; Knight, 2005). Positive AMO corresponds to warmer temperatures in the North Atlantic, and negative AMO to cooler temperatures (Knight 2005). Following Large et al. (2015), I used the average of the NAO principal component for December, January, February, and the unsmoothed, detrended AMO, both of which were downloaded from US climate organization websites (Appendix C, Table S.1). The local environment was characterized using temperature and salinity data recorded at DFO monitoring Station 27, which is near St. John's, Newfoundland and considered representative of hydrographic conditions for the Grand Bank (Fig. 2.1). I included temperature and salinity at three depths: surface (0 m), middle (75 m), and near-bottom (150 m), as well as a density-based index of stratification. The DFO spring bottom trawl survey data was used to calculate an additional index, temperature at the depth of fishing, which is often much deeper than 150 m and thereby indicates temperature over the whole region at depths where fish live.

Arctic sea ice flows onto the Newfoundland-Labrador shelf in the winter, and retreats northward in the spring (Tang 1992). The sea ice melt is linked to the spring phytoplankton bloom on the Grand Bank, with earlier ice retreat corresponding to earlier and longer blooms (Wu et al. 2007). I used three sea ice indicators: total area of ice below 55°N ($\mathrm{Area_{Ice}}$), minimum latitude of ice extent ($\mathrm{Lat_{Ice}}$), and timing of ice melt ($\mathrm{Time_{Ice}}$), provided by DFO (Buren et al. 2014). $\mathrm{Time_{Ice}}$ is the only proxy of the spring phytoplankton bloom, as there are no other suitable measures of phytoplankton or primary production for the decades considered here. I also used the environmental composite index (ECI), which combines 26 different indices for the Northwest Atlantic environment, including several described above, as a metric of the overall physical conditions on the Newfoundland Shelf (Colbourne et al., 2014).

2.4 Results

2.4.1 Fish Community State Indicators

Together, the biomass indicators captured the changes in the fish community (Fig. 2.2 and Fig. 2.3; NAFO, 2010). Total biomass decreased rapidly until the mid-1990s, and slowly increased since, with clear changes in community structure (Fig. 2.2). Prior to the collapse, piscivores represented around 40% of total biomass, but since the mid-1990s, they account for only an average of 10%. Even factoring in the limited precision of the gear-related scaling of biomass, it is undeniable that piscivores represent a smaller fraction than they did in past decades. This illustrates the “collapse of the cod”, but examination of the trends at the fish community scale demonstrates that other functional groups also exhibited major declines during this period (Fig. 2.2a).

The trophic level indicators (TL, $TL_{3.25}$, and PPred) summarize the restructuring of the fish community biomass. All three had decreasing overall trends until about 2005, illustrating the loss of higher trophic level biomass (Fig. 2.2). TL_{Comm} (all species) and MTI_{Comm} (high trophic level species) have the same trend, suggesting the additional biomass of lower trophic level species caught by the Campelen trawl had little influence on TL_{Comm}. Shannon’s index is a scaled version of Pielou’s index*,* and thus showed the same pattern of increase through the Before period and slow decrease through the After, with higher values during the After period (Fig. 2.3). These trends are consistent with this ecosystem's historic dominance of few species (e.g., cod), whereas it now has a higher frequency of occurrence of other species. Some indicators were derived from abundance data, and could not be corrected for the gear change because the coarse scaling factors are only available for biomass. Abundance decreased throughout the Before period (1985 – 1995), but initially increased in the After as a result of the decrease of large piscivores and proliferation of smaller shellfish and planktivores (Fig. 2.3a). Length also decreased throughout the Before period, a potential direct effect of high fishing pressure (Jennings et al., 1999; Rochet and Trenkel, 2003), but had no clear trend during the After period (Fig. 2.3b).

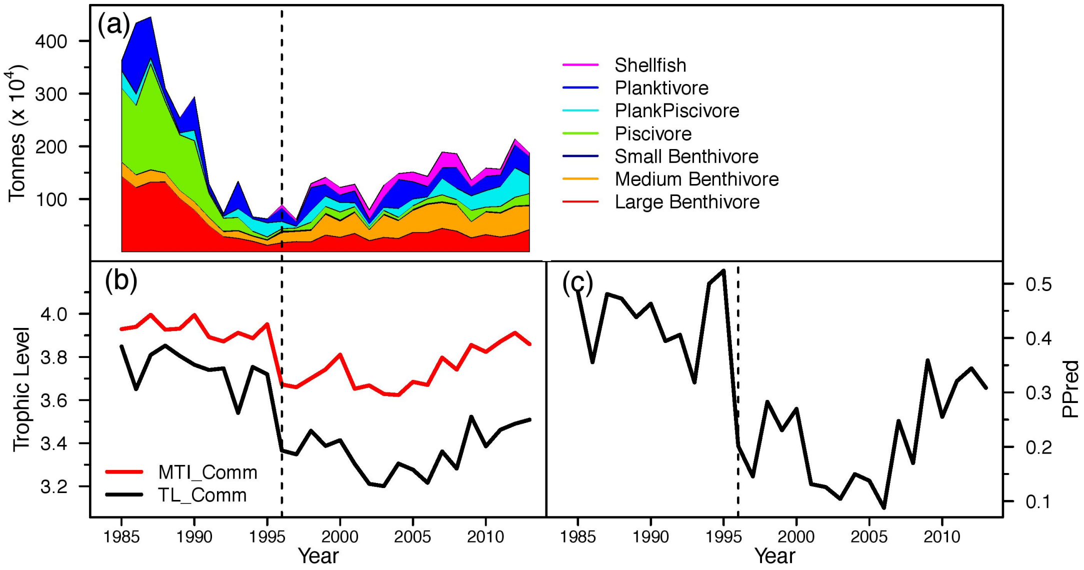

Figure 2.2: Fish community indicators including (a) total biomass index and biomass indices of important functional groups; (b) community trophic level (TL_{Comm}) and community marine trophic index (MTI_{Comm}); (c) percentage of predators in the ecosystem. Note differences in scale. The vertical dashed line indicates when the survey gear switched to a Campelen trawl (i.e., the beginning of the After period).

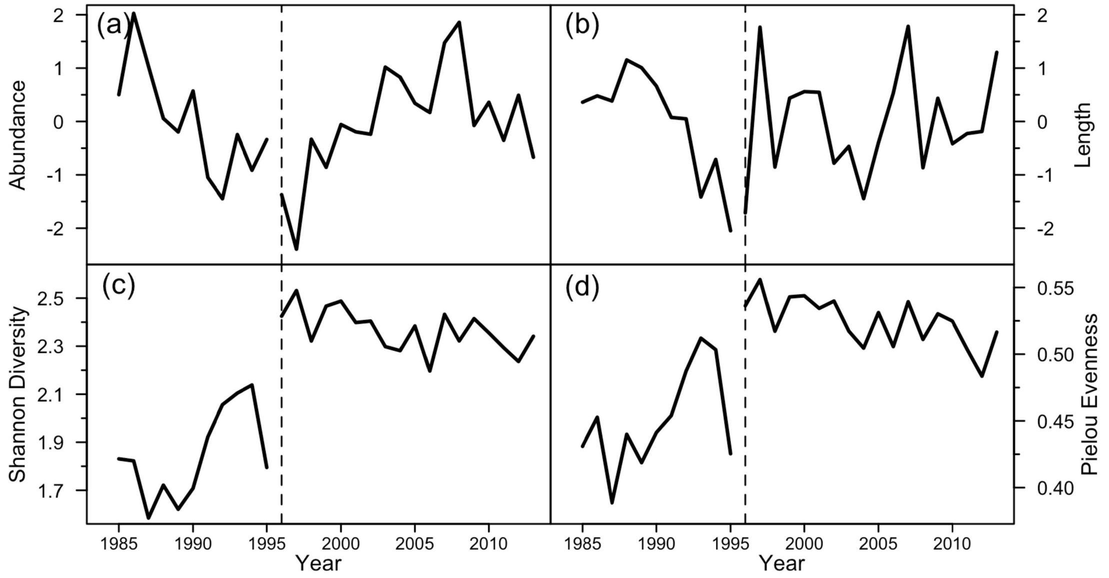

Figure 2.3: Fish community indicators that could not be corrected for the gear change: (a) abundance; (b) mean length of the community; (c) Shannon's diversity index; (d) Pielou's evenness. The vertical dashed line indicates when the survey gear switched to a Campelen trawl (i.e., the beginning of the After period). Indicators were normalized by their respective mean and standard deviations within each gear series.

Consideration of these fish community trends illustrates how *a priori* understanding of the broader ecological context is critical when interpreting indicators. For example, the trophic level indicators (Fig. 2.2) could be misinterpreted as the decline and recovery of one high trophic level group, rather than the collapse of several functional groups and coincidental increase of others. Similarly, the small but significant decreases in diversity metrics throughout the "recovery" period show that post-collapse biomass is becoming less evenly distributed among species (Fig. 2.3). Taken out of context, this could be interpreted as a return towards the historic low diversity of the Newfoundland Shelf (i.e. piscivore dominated). However, this is clearly not the case because piscivores are no longer the dominant functional group (Fig. 2.2a).

2.4.2 Human Use Indicators

After the fishing moratoria were imposed, many Newfoundlanders left to find work in other provinces (Rose 2007), and this is clearly reflected by the human population indicator (Fig. 2.4d). Income had an overall increasing trend, but the *rate* of increase slowed throughout the late 1980s and was essentially zero from 1991- 1997 (Fig. 2.4d), after which oil production began on the Newfoundland and Labrador Shelf (Newfoundland & Labrador Statistics Agency, 2015). The landings indicators capture the major changes in fishing activity, which included harvesters targeting lower trophic level species after the groundfish moratoria (Hamilton and Butler, 2001). Total landings peaked in the mid-1980s, then decreased until 1994 (the year when the Grand Bank cod moratoria was established), and have since increased to about a quarter of their peak (Fig. 2.4a). Proportions of commercial groups that make up the total catch also changed over time (Fig. 2.4a). Notably, groundfish were about 60% of total landings in 1986, but only 15% on average since 1995. Conversely, there were limited shellfish landings prior to 1991, but since 1995 they comprise about 40% of total landings. The fishing index, which evaluates landings as a proportion of the community biomass, declined overall throughout the time period of interest, with the substantial peaks (1992, 2002) revealing years of highest fishing pressure (Fig 2.4c). TL_{Land} was much lower after the collapse than before, reflecting the shift from groundfish to shellfish landings as fishers redirected their efforts. MTI_{Land} remained relatively flat for the entire time series because shellfish are not included in the calculation, so this index does not reflect the decreasing proportion of higher trophic level species that are landed.

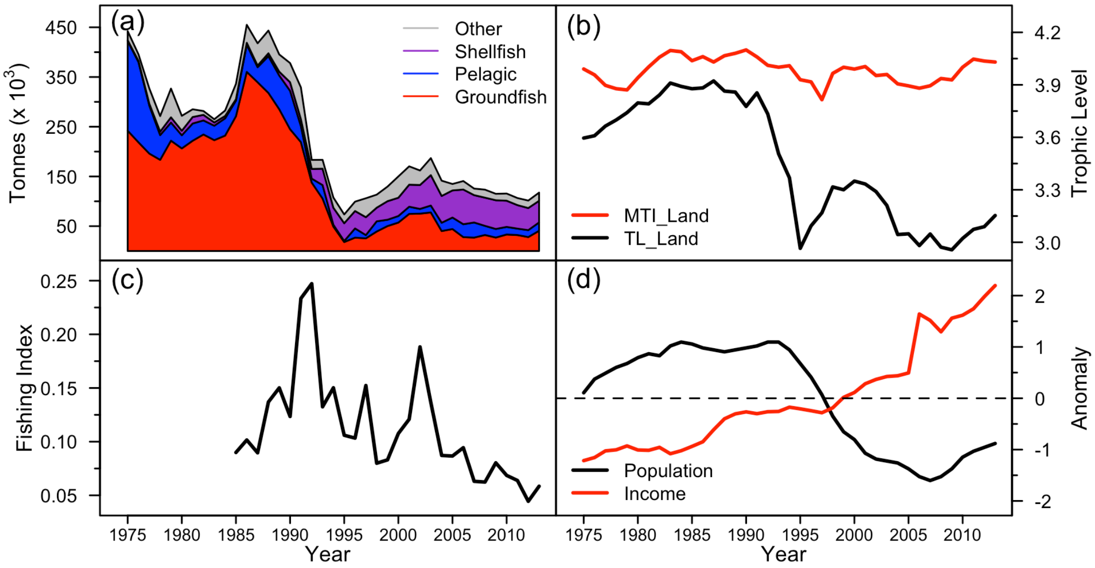

Figure 2.4: Human indicators including (a) total landings and landings of commercially important species aggregates; (b) landings trophic level (TL$_{\text{Land}}$) and landings marine trophic index (MTI$_{\text{Land}}$); (d) fishing index (landings/biomass); and (d) population and income for Newfoundland and Labrador. “Anomaly” represents normalized data, i.e. differences from the mean of the time series, which are scaled by the standard deviation. Note differences in scale.

2.4.3 Environmental Indicators

Environmental changes characterized as a regime shift occurred in the early 1990s (Buren et al. 2014), as reflected in the indicators shown in Fig. 2.5. In the early 1990s, the NAO increased to well above its average, which is associated with the cooler and fresher water during this time. Since then, the NAO exhibited relatively low variance, except in 2010, when it reached an extreme negative value. The ECI anomalies were generally opposite to the NAO – well below zero in the mid-1990s and well above it in 2010. The AMO was negative from the mid-1970s until the mid-1990s, with an overall increasing trend. All four temperature indicators generally increased since reaching minimum values in 1991. Salinity did not have distinct trends, although reduced variance for all three depths was noticeable after the mid-1990s. The early 1990s had the maximum sea ice area and the most southern latitude reached by sea ice in the period of interest (Fig. 2.5e). The past two decades have seen a decrease in the extent of sea ice cover, along with high inter-annual variability and no trend in the timing of sea ice retreat. The stratification index also had high inter-annual variability and no overall trend (Fig. 2.5d).

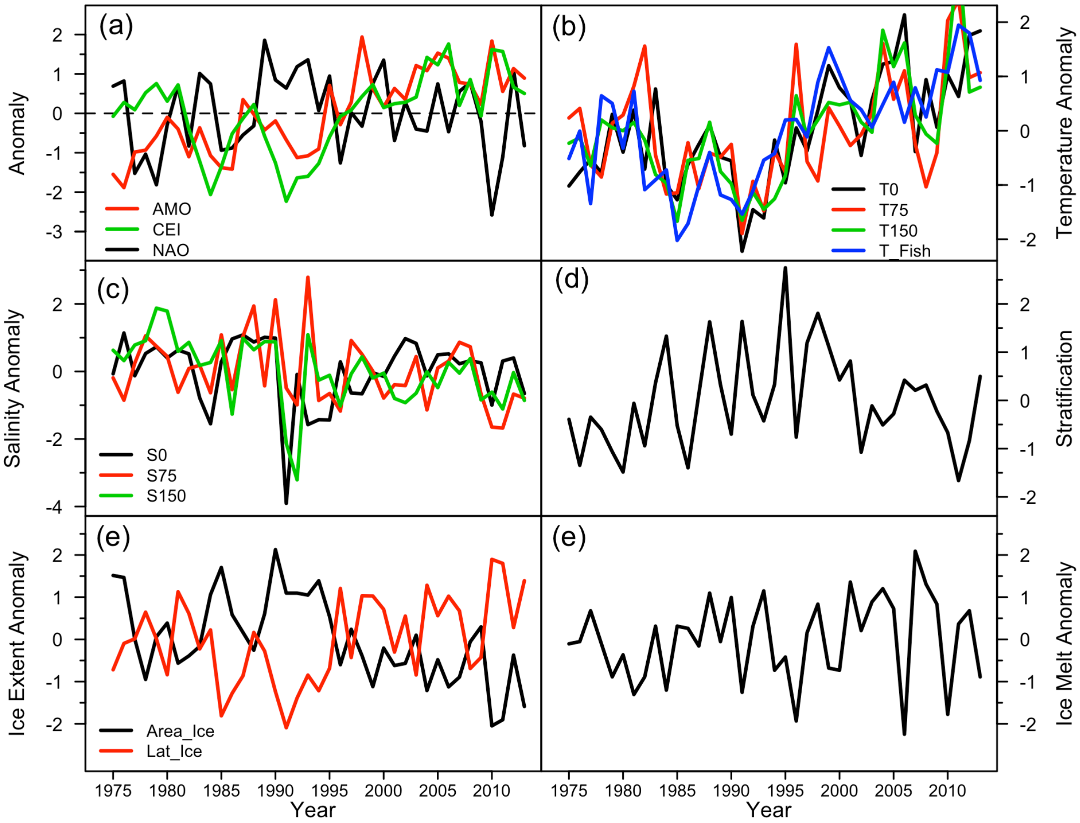

Figure 2.5: Environmental indicators including (a) NAO, AMO, and ECI; (b) temperature measured at Station 27 at 0 m (T0), 75 m (T75) and 150 m (T150) and from DFO bottom trawl surveys (T_{Fish}); (c) salinity measured at Station 27 at 0 m (S0), 75 m (S75), and 150 m (S150); (d) the stratification index; (e) area of sea ice south of 55° N ($Area_{Ice}$) and latitude of southernmost ice edge (Lat_{Ice}); and (e) timing of the sea ice retreat. "Anomaly" represents normalized data, i.e. differences from the mean of the time series, which are scaled by the standard deviation. Note differences in scale.

2.5 Discussion

The indicators can be used for a variety of applications. Here I illustrate a simple correlation analysis and a management categorization exercise, and I discuss the lessons learned from each. The supporting figures and tables are available in Appendix C.

2.5.1 Correlation Analysis

Correlations were used to assess relationships among fish functional groups, identify potentially redundant human and environmental indicators, and to suggest causal relationships. Spearman's rank coefficient (ρ) was used to evaluate the association among indicators instead of the more common Pearson coefficient because I do not expect indicators to be linearly related (e.g., Coll et al., 2016). A strong relationship can be inferred by a high value of ρ (here, $\rho \geq 0.6$), although the significance of this correlation was not assessed because values within individual time series are not independent.

I used such analyses to demonstrate that relationships among the functional groups changed among three periods: Before (i.e., during) the collapse (1985 – 1995), After the collapse (1996 – 2013), and over the Full time series (Appendix C, Table S.2). For example, large and medium benthivores, piscivores, and planktivores were highly correlated Before the collapse, with their biomasses decreasing. Recovery has been less coherent, with functional groups changing such that 20 years later there does not yet appear to be a stable community structure (Fig. 2.2a). Considering only correlations for the Full time period would have obscured these changing relationships. It is clear that this ecosystem is undergoing change, and this exercise illustrates the importance of selecting an ecologically meaningful time frame for indicator analysis.

Strong correlations between pairs of indicators were used to identify potential redundancies within human and environmental indicator groups (Appendix C, Tables S.8 – S.12). Almost half of the correlations between human indicators were high, likely a result of the low inter-annual variability of these indicators. To simplify decision-making, future analyses could exploit such redundancy by considering only a subset of human indicators. For example, the streamlined subset of total landings, pelagic landings, shellfish landings, and MTI_{Land} would reflect the important changes fisheries removals (via total landings) as well changes in fishing practices (via the remaining indicators). The correlations also showed that landings trophic level indicators do not always reflect the community trophic structure (Appendix C, Table S.10), which is contrary to some literature (Pauly and Watson, 2005). I surmise that these findings illustrate the differential pressure fishing exerts on different species, and therefore I do not recommend using trophic level of landings to represent the changes in the fish community.

There is clearly redundancy among the environmental indicators (Fig. 2.5, Appendix C, Table S.12), so a selected subset of these could be used to simplify future analyses. I suggest use of the set: NAO, T0, S0, S150, and Time_{Ice}, as it incorporates indicators that are linked to the fish community through different mechanisms and scales. NAO is an index of basin-scale atmospheric forcing (e.g., Halliday and Pinhorn, 2009), while T0 represents the regional thermal environment because temperature, ice, AMO, and ECI indicators were all highly correlated. Similarly, S0 and S150 together characterize changing salinity and stratification conditions, whereas Time_{Ice} is a proxy for the spring phytoplankton bloom (Wu et al. 2007). Another approach to reduce redundancy would be to generate summary indicators based on ordination analyses that can serve to identify the inter-relationships among variables and separate out the major patterns of variation.

I also examined correlations between each functional group and lagged versions of other functional groups as well as fishing and environmental indicators to determine when maximal direct effects were manifest (Appendix C, Figs S.1 – S.3). For example, I calculated the values of ρ between shellfish biomass during 1985 – 2013 with temperature from 1984 – 2012 (lag 1), 1983 – 2011 (lag 2), etc. through lag 10 and identified that lag 2 had the highest correlation. Between functional groups, correlations generally increased at non-zero lags, with many cases resulting in strong relationships that did not have high ρ at zero lag. Between small and medium benthivores, $\rho = 0.53$ at lag 0 and increased to $\rho = 0.84$ when small benthivores were lagged 8 years. Similarly, the correlation between piscivores and small benthivores increased from $\rho = -0.58$ at lag 0 to $\rho = -0.83$ when piscivores were lagged 2 years. These lagged relationships could indicate a causal relationship between the functional groups (e.g., reduced predation, competitive release), or that both groups elicit response to the same pressure on different time scales.

The functional groups generally had more high correlations with lagged fishing indicators than lagged environmental indicators. This is likely the result of the different timescales over which these two types of pressures affect the community. By removing individuals, fishing reduces the biomass at the time this pressure is exerted. Over longer time scales, fishing can also skew the size spectrum (Shin et al. 2005), or impact future recruitment, both of which can reduce the biomass. Environmental changes generally take longer to percolate through the system because changes in reproductive and growth potential need to be manifest as changes in recruitment before they affect biomass. Furthermore, fishing is regulated so fishing indicators have less inter-annual variability than many environmental indicators. The higher variability of the environmental indicators makes correlations less likely to be high. Use of a high pass filter (e.g., moving average) may help to smooth the environmental variability that masks the relationship.

2.5.2 Management-related categorization

Conceptual indicator frameworks can help clarify causal relationships among indicators, and thereby facilitate decision-making and communication among stakeholders (EEA, 1999; Gari et al., 2015). When I attempted to organize the indicators into a framework (DPSIR, see below) I discovered that such classification was not straightforward, which stimulated debate on the coupled human-environmental ecosystem. I found this debate to be useful for honing my conceptual understanding, and therefore I open the discussion to the broader community.

DPSIR (driver-pressure-state-impact-response) is a common framework that categorizes indicators based on their relationship with the ecosystem state (Fig. 2.6). In the context of EBFM, “state” often refers to the fish community, as characterized by biomass, trophic level, and length indicators. Pressures are forcing factors that can directly affect the state (OECD 2003). The correlation results above suggest that both fishing (e.g., total landings) and the local environment (e.g., temperature) are pressures for the Grand Bank. Drivers have a remote influence on the state, generally through their action on pressures (OECD 2003). Social and political motivations for fishing as well as large-scale environmental metrics, such as the NAO and AMO, are considered as drivers for the Grand Bank. Impacts are the consequences of changes in the state, for example the decrease in Newfoundland’s human population after the collapse of fish biomass, while responses are generally designated as policy or management actions.

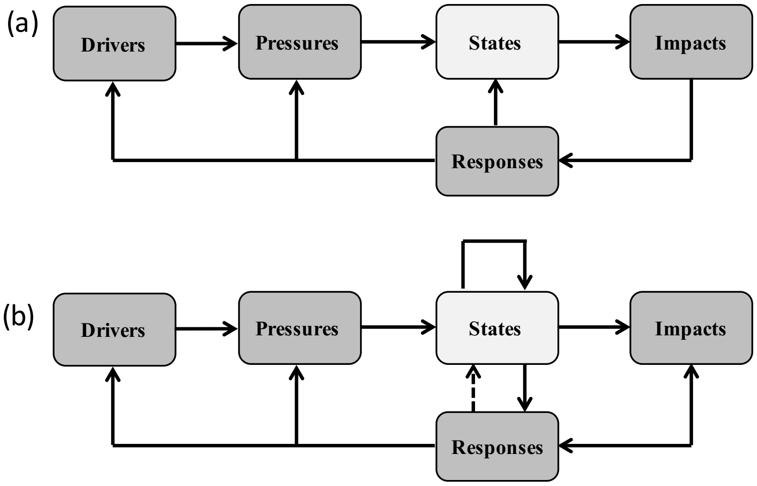

Figure 2.6: (a) Example conceptual model of the DPSIR framework (e.g., Gari et al., 2015); (b) Revised conceptual model that better reflects fisheries management considerations.

Organizing the indicators into the DPSIR categories was not straightforward, as illustrated by several examples. One issue relates to the interactions among the components of the state. Functional groups are related through predator-prey and competitive relationships that are manifest over different time scales, as described above. In this sense, some components of the state are “pressures” and "impacts" for other components. While DPSIR does not explicitly recognize such state-to-state relationships, it could be emphasized by adding a “state to state” arrow (Fig. 2.6b). I also found that it is not sufficient to base categorization on previous DPSIR analyses, because of the profound differences among ecosystems. For example, human population is considered a driver for many ecosystems (e.g., EEA, 1999; Fogarty et al., 2012), which would suggest that the decreasing population of Newfoundland resulted in less fishing pressure and the decreased landings post-1990s on the Grand Bank. However, the reverse is actually true: decreased landings resulted in less economic opportunities in the province, so people left to seek employment elsewhere (Hamilton and Butler, 2001; Rose, 2008), such that human population is better characterized as an impact for this system. Landings are arguably the best representative of the complexity of indicator classification. As discussed above, landings are generally considered pressures because they quantify direct removal of fish biomass from the ecosystem. On the Grand Bank, landings are regulated through management restrictions such as total allowable catches (TACs), which are based on the current and projected status of the stock. Thus, landings can be considered impacts as well as pressures under the DPSIR framework.

Another important lesson highlighted by the DPSIR exercise was that responses differentially affect the other categories. In terms of fisheries management, responses do not generally directly affect the state as indicated in Fig. 2.6a. Instead they influence drivers and pressures, resulting in changes to the state. This can have unintended consequences as illustrated by historical management responses on the Grand Banks. In 1977 Canada extended its exclusive economic zone (EEZ) to 200 nautical miles. A consequence of this expansion of jurisdiction was the displacement of foreign fleets out of some historical fishing grounds (Rose 2007). Landings from 3LNO were initially lower, but increased as Canada expanded its domestic fleet and fish processing capacity (Fig. 2.4a), and as foreign fleets continued to fish just outside the EEZ. The continued fishing pressure is considered one of the main causes of the collapse of biomass (e.g., Hutchings and Myers 1994, Hutchings 1996). This collapse triggered another response, in the form of moratoria on commercially important stocks, which put tens of thousands of Newfoundlanders out of work (Hamilton and Butler 2001). While the total biomass started to recover shortly after the moratoria, the structure of the community shifted towards historically less fished species. A related response is that more harvesters began to target shrimp, especially in area 3L and the northern bank. On the other hand, the state may directly influence responses if decision-makers do not wait for negative impacts to manifest before implementing regulations. Management decisions are often proactive, made based on the current and projected state of the fish stock or community, as illustrated in Fig. 2.6b.

I found it more useful to categorize forcing factors as endogenic (manageable) or exogenic (unmanageable) than as drivers and pressures (Elliott 2011). This distinction is important in a decision-making context because managers can regulate endogenic pressures, but should do so with the understanding of exogenic pressures influences on state (Elliott 2011). The exercise supports this approach, as it was less ambiguous to categorize indicators as manageable or unmanageable than into DPSIR. For example, landings can be managed using TACs, moratoria, closed areas, or other strategies that should take into account the effects of exogenic pressures such as climate change, which cannot be regulated on a fisheries management timescale.

2.6 Conclusions

The suite of indicators for the Grand Bank can have broad applicability for scientists and managers studying the region and EBFM. Here I explored the lessons learned from two simple analyses using these indicators, and have set the stage for a host of future indicator analyses. I showed that drivers and pressures impart different scales of responses at different time lags among state indicators, which reiterates the need to include multiple metrics of ecosystem status in analyses intended to support management decisions (e.g., Jennings, 2005; Rice, 2003). This suggests applying multivariate statistical analysis techniques that can account for simultaneous changes in different variables as well as prioritize monitoring needs by identifying sets of drivers and pressures with comparable explanatory power. Finally, explanation of both time-lags and recognition of early warning signals will need to derive from complementary approaches, such as can be afforded through use of mechanistic or process-based food web models.

CHAPTER 3: EXPLANATORY POWER OF FISHING AND ENVIRONMENTAL PRESSURES ON THE FISH COMMUNITY OF THE GRAND BANK BEFORE AND AFTER THE BIOMASS COLLAPSE[2]

3.1 Abstract

Ecosystem based fisheries management will benefit from assessment of how various pressures affect the fish community, including delayed responses. The objective of this study was to identify which pressures best explain changes in the fish community of the Grand Bank, Northwest Atlantic. These changes are characterized by a collapse and partial recovery of fish biomass and shifting trophic structure over the past three decades. All possible subsets of nine fishing and environmental pressure indicators were evaluated as predictors of the fish community structure (represented by the biomasses of six fish functional-feeding groups), for periods Before (1985 – 1995) and After (1996 – 2013) the collapse, and the Full time series. I modelled these relationships using multivariate linear regression, which simultaneously evaluates the effect of one or more predictors on several response variables. The analysis was repeated with different lengths (0 to 5 years) and types (moving average vs. lags) of time delays imposed on the predictors. Both fishing and environmental indicators were included in the best models, reinforcing that no single type of pressure impacts the fish community in this region. Results show notable differences in the most influential pressures Before and After the collapse, which reflect changes in harvester behaviour. The best models Before the collapse had strikingly high explanatory power when compared to the other periods, which is because of changes in the relationships among and within the pressures and responses. Moving average predictor sets generally had higher explanatory power than lagged sets, implying that trends in pressures are important for predicting changes in the fish community. Assigning a carefully chosen delay to each predictor further improved explanatory power, which is indicative of the complexity of interactions between pressures and responses. Here I add

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[2] Based on Dempsey, D. P., Gentleman, W. C., Pepin, P., and Koen-Alonso, M. (2018). Explanatory Power of Human and Environmental Pressures on the Fish Community of the Grand Bank before and after the Biomass Collapse. Front. Mar. Sci. 5, 1–16. doi:10.3389/fmars.2018.00037.

to the current understanding of this ecosystem while demonstrating a method for selecting pressures that could be useful to scientists and managers in other ecosystems.

3.2 Introduction

Marine fisheries collapses worldwide have important socio-economic and ecological consequences, highlighting the need for ecosystem based fisheries management (EBFM; e.g., DFO, 2007; Misund and Skjoldal, 2005). EBFM supplements conventional single species approaches by explicitly considering interactions among species (target and non-target) in the context of changing human activities and environmental conditions. Implementation of EBFM requires information about the whole ecosystem, which can be provided in part by data-based indicators, i.e. measured or derived proxies of biological status and ecological pressures (Larkin 1996, Jennings 2005). Biological indicators include measures of the fish community structure (e.g., biomass, mean length, and trophic level of the community). Both fishing and the environment are external pressures on the fish community, and can be quantified by a range of indicators (e.g., Link et al., 2010; Shannon et al., 2010). Fishing indicators can refer to metrics of landings (e.g., total or species aggregates), effort (e.g., hours fished), and fishing mortality (e.g., landings/community biomass), while environmental indicators can include large-scale metrics of atmospheric forcing, such as the North Atlantic Oscillation (NAO), and region-specific features such as annual mean temperature and salinity. Managers can regulate (at least partially) fishing pressures, but not environmental pressures (on relevant timescales; Elliott, 2011), and yet their decisions must account for future changes in the environment. It is generally accepted that a suite of indicators from several categories (e.g., biological, fishing, and environmental) is required for successful EBFM (e.g., Jennings, 2005; Link et al., 2010). Considerable effort has focussed on determining which of the hundreds of proposed biological indicators are the most informative (Rice 2003, Jennings 2005, Rice and Rochet 2005, Shin et al. 2010b), but there remains a pressing need to determine which sets of pressures are best predictors of change (Ojaveer and Eero 2011, Large et al. 2015a).

Improving scientific understanding of multivariate pressure-response relationships can contribute to implementation of EBFM. Identifying which pressures are most directly related to changes in the fish community can help focus investigations of thresholds, guide modelling and planning of management scenarios, and direct monitoring efforts. Determining which pressures are the most informative is challenging because of the range ways to quantify them, and because the mechanistic relationships are currently not well defined. For example, there has been fierce debate about whether fishing or poor environmental conditions caused the infamous collapse of cod and other species on the Grand Banks in the 1990s (Myers et al. 1996, Bundy 2001, Halliday and Pinhorn 2009). Furthermore, changes in pressures can have both immediate and delayed effects on fish communities (e.g., Greenstreet et al. 2011, Gröger and Fogarty 2011, Dempsey et al. 2017), adding an additional layer of complexity to the analysis. For example, immediate effects of fishing include the removal of biomass, while delayed effects include changes in the size structure of the community (Daan et al. 2005, Devine et al. 2007). While previous studies have acknowledged such delays (e.g., Chen and Ware, 1999; Large et al., 2015), more investigation into appropriate types and lengths of delays is warranted (Large et al. 2015a).

The objective here was to identify sets of pressures most directly related to three decades of changes in the structure of the fish community of the Grand Bank, Northwest Atlantic (Fig. 3.1). This will add to the current understanding of this ecosystem while demonstrating a method that could be useful to scientists and managers for other areas. This region provides a valuable case study because it experienced complex ecological changes resulting in two distinct periods, which are spanned by the suite of indicators (Dempsey et. al., 2017). I identified pressure indicators from within this suite that can best predict fish community state over the full time series as well as for the two periods, and use the results to examine the past and present dynamics of this ecosystem. I also investigate models with different delay lengths (0 to 5 years) and types (moving average and lags) to determine which delays have the best explanatory power.

3.3 Methods

3.3.1 Study Area

Here I provide historical context for the study area to highlight some of the ecological changes that have occurred in the region over the period of interest. The Grand Bank, within the Northwest Atlantic Fisheries Organization (NAFO) statistical division 3LNO, and the adjacent southern Labrador and northeast Newfoundland shelf (NAFO Division 2J3K) are recognized as major subunits within the Newfoundland-Labrador shelf in the Northwest Atlantic (Fig. 3.1; NAFO, 2014b). The shelf is partly within the Canadian exclusive economic zone (EEZ) established in 1977, but extends into international waters (Fig. 3.1).

For centuries, this region was one of the most productive fishing grounds in the world, with global fisheries for many species including Atlantic cod, flounder, and capelin (Rose, 2007). Fisheries management in the region is the responsibility of Fisheries and Oceans Canada (DFO) within the EEZ, and NAFO in international waters. Throughout the 1980s the primary management strategy for both NAFO and DFO was to set independent quotas for each fish stock; however, these measures were largely ineffective because these limits were ignored by some vessels, and because of error in the calculation of sustainable exploitation rates (e.g., Rose, 2007). In the 1990s, prolonged heavy fishing pressure combined with an environmental regime shift precipitated complex ecological changes, characterized by a collapse of fish biomass. This is commonly referred to as "the collapse of the cod" even though many other species were also impacted (e.g., Atkinson, 1994; NAFO, 2010b). In response to the low biomass of many stocks, groundfish moratoria were enforced for 2J3KL in 1992 and the southern Grand Bank in 1994. Harvesters adapted by targeting different species (e.g., shrimp and crab), retiring from fishing, or leaving the province to find other employment (e.g., Hamilton and Butler, 2001). Over 20 years after imposition of these moratoria, many remain in place (see Annex I.A in NAFO, 2017). The total fish biomass has recovered slowly, although different species are recovering at different rates such that the structure of the ecosystem has shifted from piscivore dominated to include more species at lower trophic levels (Fig. 3.2; Pedersen et al., 2017).

Both DFO and NAFO are working towards ecosystem approaches to management (NAFO, 2010a, 2010b; Oceans Act, 1996; DFO, 2009). Current management strategies include the At-Sea Observer Program (DFO 2014), National Vessel Monitoring System

(DFO 2018a), restrictions on total allowable catches (e.g., for redfish and yellowtail flounder; NAFO 2017) gear restrictions, and restricted entry programs.

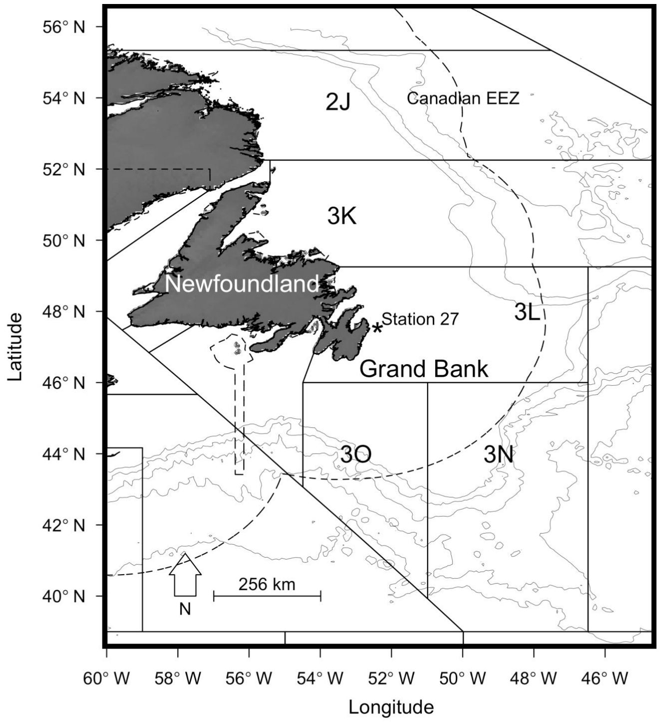


Figure 3.1: Map of the study area, showing the Grand Bank (NAFO division 3LNO), Station 27, and the Canadian exclusive economic zone (dashed lines).

3.3.2 Indicators

The indicator time series used here were synthesized and presented in Chapter 2 (Dempsey et al. 2017). Fish community indicators are annual values for 1985 – 2013, and pressures used to predict them additionally extend to 1980 – 1984 for use with the time delay analysis. Below I present a general overview of these indicators to facilitate the reader's appreciation of the current multivariate analysis, and refer interested readers to Chapter 2 (Dempsey et al. 2017) for more details on indicator trends and data sources.

3.3.2.1 Indicators of fish community status

The structure of the fish community was represented by the mean annual biomass indices of six fish functional feeding groups (aggregated species), which have been analyzed by Dempsey et al. (2017) and others (e.g., NAFO, 2010, 2014; Table 1). Such functional groups are meaningful units to fisheries scientists and managers (NAFO 2014), are compatible with modern ecosystem models (Link et al. 2010a, Heymans et al. 2016), and benefit the present analysis by reducing the number of response variables when compared to the use of individual species (Fogarty 2014). The annual biomass index of each functional group was calculated from DFO spring scientific bottom trawl surveys for NAFO area 3LNO by summing the average catch per tow of the species included in the group. In 1996, the survey gear changed from a commercial Engels to a finer-meshed Campelen trawl, such that the biomass indices cannot be directly compared before and after the gear change due to differing capture efficiencies (Belgrano and Fowler, 2011; McCallum and Walsh, 1997). Scaling factors have been developed to coarsely compare the Engels and Campelen biomasses for most species; however, it was not possible to scale the biomasses of invertebrate species (i.e. shellfish) because they were not sampled consistently by the Engels trawl (Koen-Alonso, unpublished data).

The mid-1990s also correspond to the minimum total fish biomass in the region, marking the end of the rapid collapse of biomass and the beginning of the recovery. These have been characterized as two ecologically different periods (e.g., Buren et al., 2014; Dempsey et al., 2017). Here I analyzed three time periods: the Full period (1985 – 2013; using the scaled Engels data) as well as Before (1985 – 1995) and After (1996 – 2013) the collapse. “Before” and “After” also correspond to the survey gear change to eliminate the reliance on the coarse scaling factors. Note that because there is no appropriate biomass index for shellfish prior to 1996 (NAFO 2010a), this functional group had to be excluded from the Full and Before analyses. I do not expect this exclusion to affect results because even though the build-up of shrimp (the major species by biomass in this group) is believed to have started in the mid 1980s, it only peaked on the Grand Bank in the 2000s (Lilly et al. 2000, NAFO 2014). As discussed later, some After analyses were completed with and without the shellfish index to determine the effect of including this functional group.

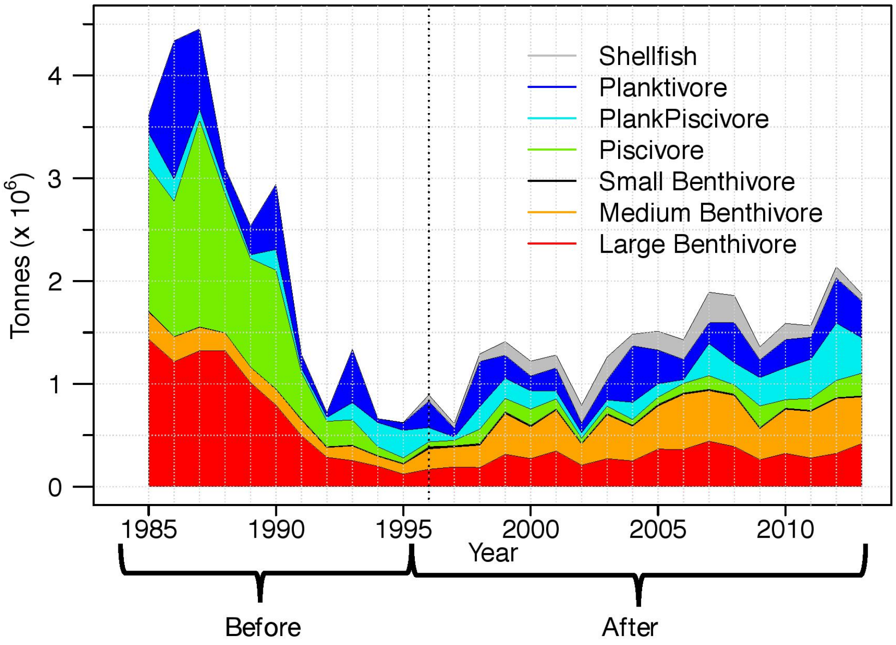


Figure 3.2: Fish functional group biomass in NAFO division 3LNO, illustrating the collapse of total biomass and changing structure of the community. All functional groups except shellfish are included as response variables. The Before period is from 1985 to 1995, the After period is from 1996 to 2013, and the Full period includes 1985 – 2013 (Before + After).

Table 3.1: Functional groups used to represent the fish community structure of the Grand Bank (adapted from NAFO 2010a). See Appendix C, Table S.1 for the species included in each group.

Functional Group	**Number of Species**	**Size Range (cm)**	**Dominant Species (by biomass)**
Large Benthivores	22	max size[1] > 80	American plaice (*Hippoglossoides platessoides*)
Medium Benthivores	33	45 < max size <80	Yellowtail flounder (*Limanda ferruginea*)
Small Benthivores	44	max size < 45	Common grenadier[2] (*Nezumia bairdi*) Mailed sculpins[3] (*Triglops sp.)*
Piscivores	25	All	Atlantic cod (*Gadus morhua*)
Plank-piscivores	9	All	Redfish (*Sebastes mentella*)
Planktivores	14	All	Capelin (*Mallotus villosus*)
Shellfish[4]	3	All	Shrimp (*Panda borealis*)

[1] Max size is the maximum length recorded for a given species.
[2] Before the collapse
[3] After the collapse
[4] Biomass index begins in 1996; not included in most analyses in this paper

3.3.2.2 Indicators of fishing and environmental pressures

The nine pressures chosen as predictors for this analysis were based on the results of Chapter 2 (Dempsey et al. 2017; Fig. 3.3). Note that I do not distinguish “pressures” from “drivers,” as some authors do (e.g., in the DPSIR framework, see Gari et al., 2015 and references therein), because they both ultimately influence the fish community and as such it would be a matter of semantics for this analysis.

Four fishing indicators were included (Fig. 3.3): total, pelagic, and shellfish landings, as well as the marine trophic index (MTI; denoted “MTI_{Land}” in Chapter 2). Total landings are the sum of groundfish, pelagic, shellfish, and “other” species landings, and provide a metric of fishing pressure on the entire community. Pelagic landings are dominated by capelin, which is a key forage species in the system, and shellfish landings are dominated by shrimp and queen crab (also known as snow crab). MTI is the mean trophic level of the landings weighted by the biomass of species landed, including only species with trophic level greater than 3.25 (e.g., Atlantic cod, haddock). MTI reflects evolving fishing practices as fishers target different species to adapt to changes in fishing technologies, the ecosystem, and end markets (Caddy and Garibaldi 2000).

In general, the fishing indicators were highly correlated Before the collapse and for the Full period (Pearson correlation coefficient > 0.60, not shown), but not After the collapse (not shown). Total and pelagic landings both increased in the early 1980s, and then decreased from the late 1980s until the mid-1990s, and to this day remain lower than in the late 1970s and 1980s. MTI also decreased throughout the Before period, but has no trend in the After. Shellfish landings increased over the Full period due to the proliferation of shrimp and crab stocks in the 1980s and a shift in target species after the groundfish moratoria (Dempsey et al. 2017; Schrank 2005), but have been declining since the mid-2000s (Fig. 3.3; Department of Fisheries and Aquaculture 2014; Dempsey et al. 2017).

Five environmental indicators were included as predictors (Fig. 3.3): the North Atlantic Oscillation (NAO), surface salinity (SSS), salinity at 150 m (S150), surface temperature (SST), and the timing of the sea ice melt (Time_{Ice}). The NAO represents basin scale atmospheric circulation patterns that are related to winds, salinity, temperature, and sea ice (Hurrell, 1995; Petrie, 2007). The remaining indicators characterize physical environmental factors local to the Grand Bank, which are thought to have played a critical role in the collapse of fish biomass in the 1990s (e.g., Halliday and Pinhorn, 2009). Time_{Ice} was included as a proxy of the timing of the spring phytoplankton bloom (Wu et al. 2007) because there are no other suitable measures of phytoplankton biomass or productivity over the required historical time frame.

In general, the environmental pressures were not highly correlated with each other or the fishing pressures for any period (not shown). SST was the only environmental pressure with clear trends: it decreased until 1991, and has generally increased since. The remaining indicators were characterized by inter-annual variability. The NAO was well above its average in the early 1990s, which has been related to the cooler and fresher water at this time, which in turn has been characterized as a regime shift (Buren et al. 2014). The salinity indicators had higher variability Before the collapse, with extreme minimum values in the mid-1990s. In contrast, Time_{Ice} had higher variability After the collapse (Fig. 3.3).

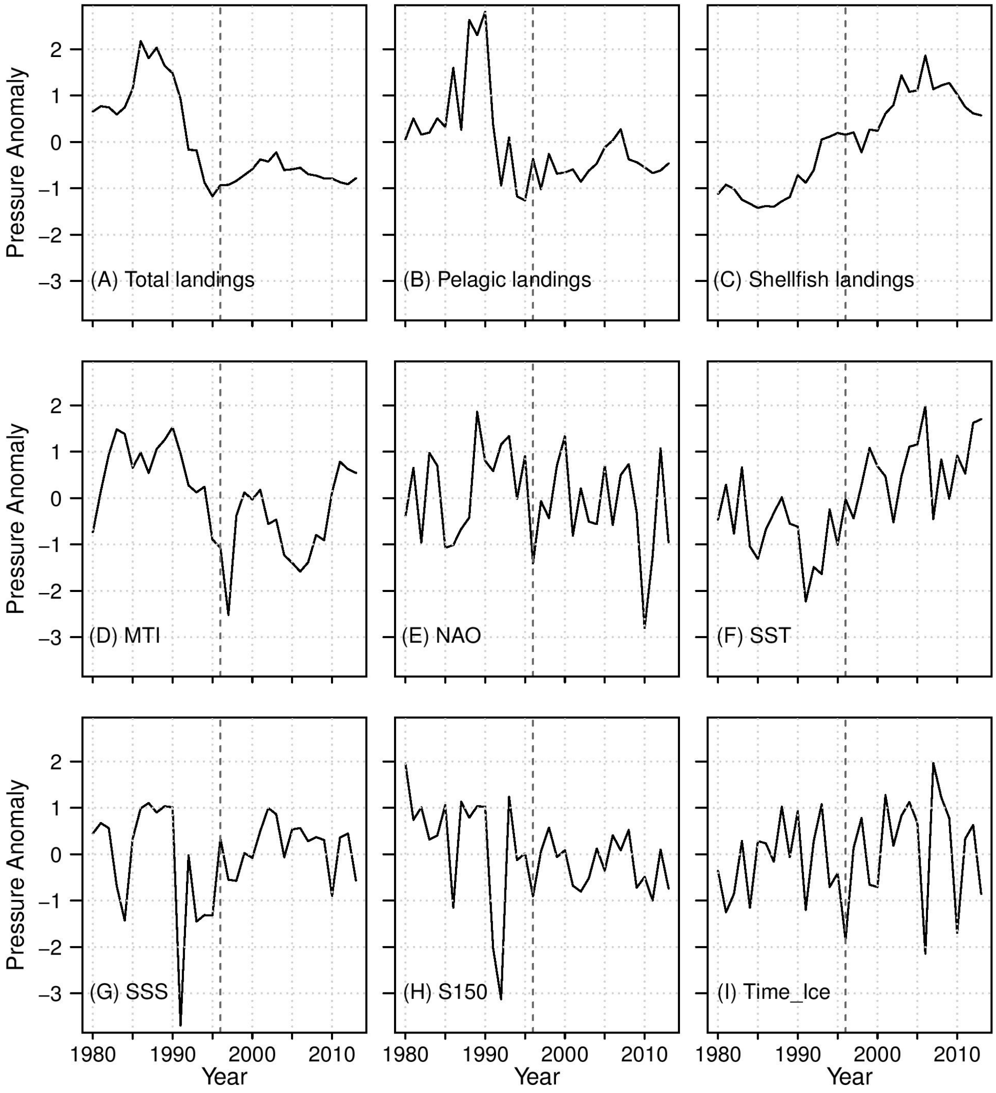


Figure 3.3: Pressure indicators used as predictors in this analysis. Fishing indicators: (A–D); Environmental indicators: (E–I). The thick dashed line indicates the beginning of the After period.

3.3.3 Method of Data Analysis

3.3.3.1 Multivariate Linear Regression

Multivariate linear regression (MLR) was used to assess how well different sets of the pressures modelled the biomasses of all six functional groups over a period of n years. MLR uses p predictors in matrix $\mathbf{X}_{[n \times p]}$ to model r responses in matrix $\mathbf{Y}_{[n \times r]}$. The explanatory power is characterized using goodness of fit metrics related to variances in the responses, the model, and/or the residuals. Commonly used metrics are the coefficient of determination (R^2) and the adjusted-R^2. The R^2 measures the fraction of the total variance in the response(s) that is explained by the variance in predictor matrix $\mathbf{X}$. The adjusted-R^2 is a modification to R^2, which enables comparison among models using different numbers of predictors (see below; Legendre and Legendre, 2012).

The first step in MLR is a multiple linear regression of each response variable (r multiple regressions), which are typically done simultaneously for computational efficiency. The modelled values are stored in the matrix $\widehat{\mathbf{Y}}_{[n \times r]}$, while matrix $\widehat{\boldsymbol{\beta}}_{[p \times r]}$ holds the coefficients for linear combinations of the columns of $\mathbf{X}$ that result in the smallest sum of squares of the residuals for each response:

$$\widehat{\mathbf{Y}} = \mathbf{X}\widehat{\boldsymbol{\beta}} = \mathbf{X}(\mathbf{X}^{\mathbf{T}}\mathbf{X})^{-1}\mathbf{X}^{\mathbf{T}}\mathbf{Y} \tag{3.1}$$

where the superscript symbols “T” and “-1” respectively denote the matrix transpose and inverse. It is assumed that the columns of $\mathbf{X}$ are linearly related to the columns of $\mathbf{Y}$, and so appropriate transformations must be applied if necessary. Commonly, predictors and responses are normalized by centering and scaling them by their respective mean and standard deviation to minimize numerical error in solving for $\widehat{\mathbf{Y}}$ (Legendre and Legendre 2012). Due to the skewed nature of the fish biomass data, in this analysis responses were the log-transformed, normalized biomass indicators, and the predictors were normalized pressure indicators.

A goodness of fit value for each of the *r* multiple regressions can be calculated. R^2 is given by

$$R_j^2 = \frac{SSM_j}{SST_j} = \frac{\sum_{i=1}^{n}(\hat{y}_{i,j}-\bar{y}_j)^2}{\sum_{i=1}^{n}(y_{i,j}-\bar{y}_j)^2} \quad (3.2A)$$

$$R_j^2 = 1 - \frac{SSE_j}{SST_j} = 1 - \frac{\sum_{i=1}^{n}(y_{i,j}-\hat{y}_{i,j})^2}{\sum_{i=1}^{n}(y_{i,j}-\bar{y}_j)^2} \quad (3.2B)$$

where SSM_j is the sum of squares of the model, SST_j is the sum of squares, and SSE_j is the sum of squared errors, all for response *j*. The adjusted-R^2 "penalizes" models with more predictors (for models with the same number of predictors, the relative change in adjusted-R^2 is the same for that of the R^2; Equation 3.3).

$$\text{adjusted-}R^2 = 1 - (1 - R^2)\frac{n-1}{n-p-1} \quad (3.3)$$

Note that in the fraction $\frac{n-1}{n-p-1}$ (Equation 3.3), the numerator is the degrees of freedom of the model for the constant of best fit (i.e., mean), and the denominator is the degrees of freedom of the MLR model error.

The second step of MLR as it is used here is to calculate a single goodness of fit metric that simultaneously evaluates the *r* separate regressions. R_{Total}^2 (also called the “bivariate redundancy statistic”; Legendre and Legendre, 2012) is given by:

$$R_{Total}^2 = \frac{SSM_{Total}}{SST_{Total}} = \frac{\sum_{j=1}^{r}\sum_{i=1}^{n}(\hat{y}_{i,j}-\bar{y}_j)^2}{\sum_{j=1}^{r}\sum_{i=1}^{n}(y_{i,j}-\bar{y}_j)^2} \quad (3.4A)$$

$$R_{Total}^2 = 1 - \frac{SSE_{Total}}{SST_{Total}} = \frac{\sum_{j=1}^{r}\sum_{i=1}^{n}(y_{i,j}-\hat{y}_{i,j})^2}{\sum_{j=1}^{r}\sum_{i=1}^{n}(y_{i,j}-\bar{y}_j)^2} \quad (3.4B)$$

where SSM_{Total} is the total sum of squares of the model, SST_{Total} is the total sum of squares of **Y**, and SSE_{Total} is the total sum of squared errors. This is also equal to the average of the R^2’s for each multiple regression when the responses are normalized

(Legendre et al. 2011; Appendix D). The $\mathrm{R}^2_{\mathrm{Total}}$ can be modified as in Equation 3.3 to give adjusted-$\mathrm{R}^2_{\mathrm{Total}}$. The adjusted-$\mathrm{R}^2$ metrics were used to evaluate models in this analysis because I compared subsets comprised of different numbers of indicators (i.e., different numbers of predictor columns in $\mathbf{X}$). I designated changes in adjusted-R^2 >0.05 as "notable." Note that the significance (e.g., *p*-value) of the model fit was not evaluated because of the presence of autocorrelation in the predictors and responses. This autocorrelation does not affect the value of the R^2, but it could affect the adjusted-R^2 because the reduced independence of the observations changes the effective number of observations (Priestley 1994). As discussed in section 3.5, this is not expected to have a large impact on the results of this analysis.

3.3.3.2 All Possible Models

An MLR model was fit for each possible combination of the nine predictors so that a total of 511 models were evaluated for each period (Full, Before and After). Models were ranked by their adjusted-$\mathrm{R}^2_{\mathrm{Total}}$, with a rank of 1 indicating the predictor set with the highest explanatory power. I chose to evaluate all possible models versus stepwise methods to avoid sensitivity of the results to the selection algorithm (e.g., forward/backward; see Whittingham et al. 2006 and references therein). Additionally, identifying and focussing on a single model ignores the potential that other subsets of predictors may have similar explanatory power (Whittingham et al. 2006). Here, I am not interested in one "best" model; rather, I evaluated a range of models that include different types and numbers of predictors to see if there are multiple sets with similarly high explanatory power.

I repeated the analysis using different lengths and types of time delays in the predictors. I considered two types of delays, lags and moving averages, for delay length from $k = 1$ to $k = 5$ years (Fig. 3.4). For the lag analysis, predictors were shifted forward k years to simulate a delayed response. For an analysis of the Before period, the response time series was from 1985 – 1995, and the predictor time series was from 1984 – 1994 for $k = 1$, 1983 – 1993 for $k = 2$, etc. For the moving average analysis, the predictor value at year i was the average of the current year and the previous k years (resulting in a $k+1$ year moving average). I was therefore able to compare the explanatory power of past predictor values (lags) and low-pass filter values (moving average). All predictors were normalized after the delay was applied, which resulted in minor differences in the values of the lag predictors, and less damping of the moving average predictors as seen in Fig. 3.4. These methods of incorporating time delays did not reduce the length of the time series because the predictors have longer historical data records than the responses. For clarity, "zero delay" (ZD) refers to the original predictors, while Lag*k* and Avg*k* refer to lagged and moving average predictors, respectively, that incorporate *k* years of past data.

I first used a simple approach of incorporating delays by evaluating all combinations of predictors with the same type and length of delay (e.g., all predictors either Avg*k* or Lag*k*; Chen and Ware, 1999). Because pressures may manifest in the fish community biomass on different timescales (i.e., fishing acts immediately, environment generally takes longer), I repeated the analysis using different delay types and lengths for each predictor as presented in the Results section.

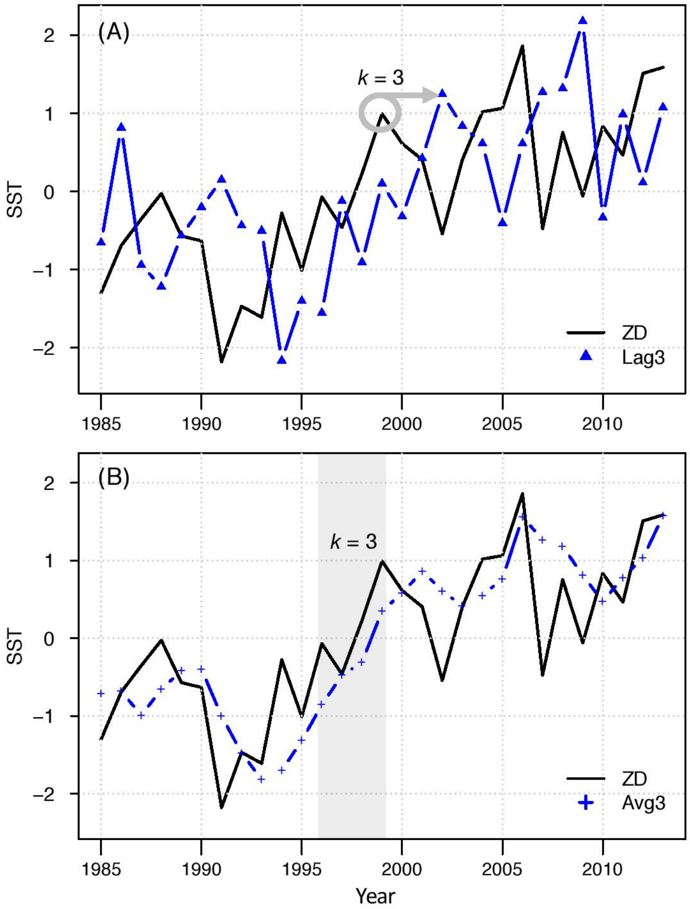


Figure 3.4: Illustration of the different types of time delays for surface temperature (SST) at *k* = 3: (A) forward lag shift; (B) moving average.

3.4 Results

3.4.1 Zero Delay Models

The results for the three time periods using the ZD predictors are illustrated in Fig. 3.5. Appendix D, Tables S.1 – S.3 list which pressures were included in the top 50 models (i.e., top 10%) for each period. Inclusion of shellfish as a response in the After models had minimal effects, increasing the explanatory power only slightly, and highlighting the same number and most frequent predictors.

In general, the Before models had notably higher adjusted-R^2_{Total} than the After models, and the Full models had intermediate values (Fig. 3.5). The best Before models had strikingly high explanatory power when compared to the other periods (adjusted-R^2_{Total}=

0.94 vs. ~0.60); however, lower-ranked (smaller adjusted-R^2_{Total}) Before and Full models had similar explanatory power. The high adjusted-R^2_{Total} of the best Before models highlights the common signal among functional groups and the external pressures during this period. Most of the functional group biomasses decreased (Fig. 3.2), as did total landings and MTI, while shellfish landings increased (Fig. 3.3). The environmental pressures were more variable, but SST had a strong decreasing trend from the late 1980s until the early 1990s (Fig. 3.3).

The adjusted-R^2_{Total} of the top 50 models and the corresponding adjusted-R^2 for each functional group further highlighted differences between the two periods (Fig. 3.6). The high explanatory power for large benthivores and piscivores (average adjusted-R^2 of 0.95 and 0.91, respectively) contributed to the remarkably high overall explanatory power for the Before period. The adjusted-R^2 for medium and small benthivores was also notably higher than the adjusted-R^2_{Total} for this period, while planktivores and plank-piscivores had the lowest average explanatory power. In contrast, plank-piscivores and medium benthivores had the highest explanatory power for the After period. Piscivores and small benthivores, which were among the best predicted in the Before period, had the lowest average adjusted-R^2 for the top 50 After models.

There is a clear plateau in the overall explanatory power of the Full models, with the best set of three predictors (total landings, MTI and SST; Appendix D, Table S.1) having only a marginally different adjusted-R^2_{Total} than sets with more predictors (Fig 3.5b). Six predictors were used in the best model for the Full period, (adjusted-R^2_{Total} = 0.60), although all top 50 sets had adjusted-R^2_{Total} within 0.05 (sets of 3 – 9 predictors). In contrast, the Before models did not plateau, with the best set requiring all 9 predictors (adjusted-R^2_{Total} = 0.94). All of the top 50 Before models had higher explanatory power than the best Full and After models. The best After model used 8 predictors (adjusted-R^2_{Total} = 0.59 including shellfish as a response, and 0.56 excluding shellfish), although there were sets of 6, 7, and 9 predictors with similar explanatory power. The lower adjusted-R^2_{Total} of the After (and Full) models suggests that there is at least one pressure not included here that could improve the explanatory power for these periods. In general, using less predictors in the Before and After models sacrificed more explanatory power than for the Full models. The range of adjusted-R^2_{Total} for a given number of predictors is generally smaller for the Full time series compared to the Before and After models (Fig 3.5b). For example, the range for 6-predictor Before models is over 3 times larger than that of 6-predictor Full time series models. This suggests that for the Full models, the *number* of predictors included is more important than *which* predictors are included. For the other two periods, a specific set of *p* predictors has high explanatory power, while other sets of *p* predictors do not.

Several predictors have much different inclusion frequencies Before and After the collapse, suggesting that different pressures were most influential in these two periods (Fig. 3.5c). These differences are obscured by considering only the Full time series, underscoring the importance of selecting an ecologically coherent time frame for indicator analysis (Dempsey et al. 2017). As expected, the frequency of landings indicators reflects the change in target species after the collapse and subsequent groundfish moratoria. Total landings (which are highly correlated with groundfish landings; Appendix C), are more frequent in the Before models, while pelagic and shellfish landings are more frequent in the After models. The MTI was included in almost all the Full and After models, but less than half of the Before models. This may be explained by the changes in fishing pressures after the collapse and moratoria. Before the collapse, MTI was highly correlated with the other fishing predictors because most of the landings were high trophic level species. After the collapse, MTI was not highly correlated with the other fishing predictors, indicating that it provides different information, which may be why it is included in so many of the best After models. The most notable differences in the environmental predictors were NAO and SST, which were included in all or most of the Before models, respectively, but in only about 60% of the After models. This suggests that environmental conditions were more influential Before the collapse, and/or that relationships between the fish functional groups and these specific environmental pressures were more linear before the collapse.

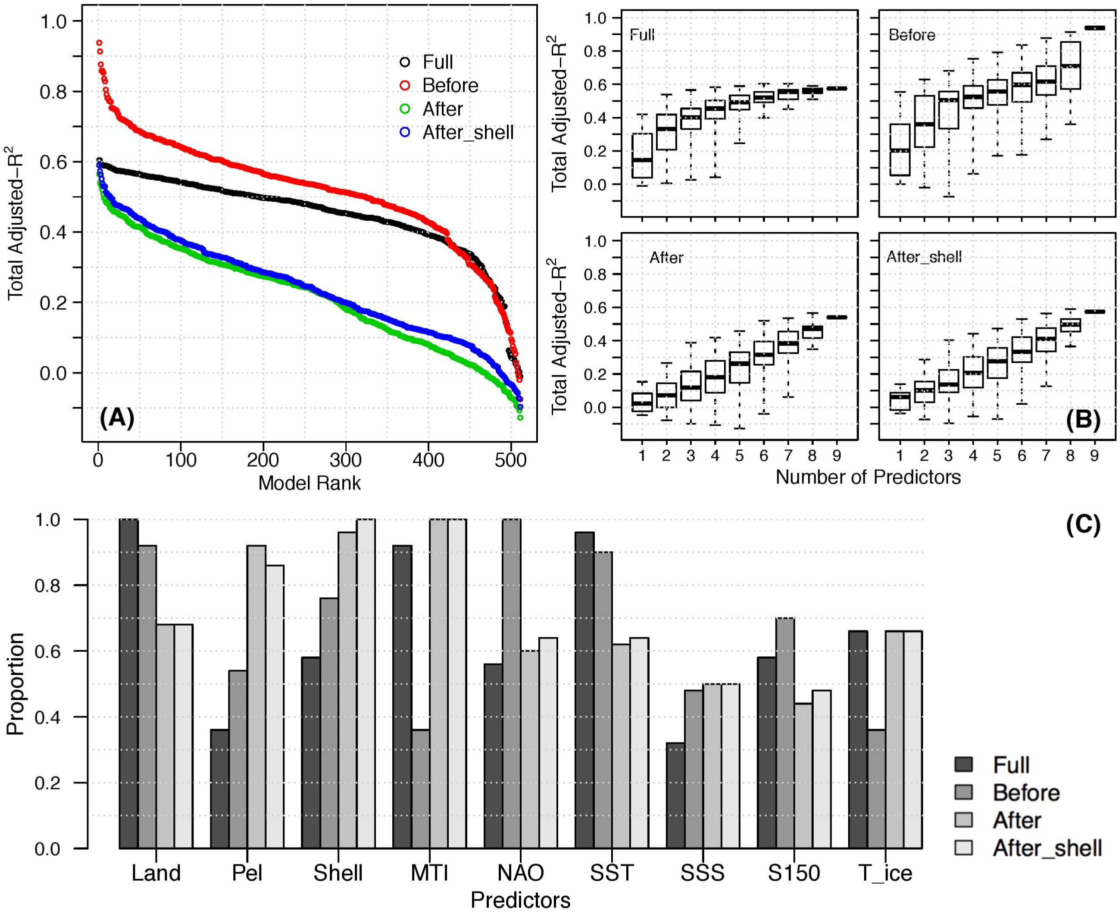


Figure 3.5: (A) $\text{Adjusted} - R^2_{\text{Total}}$ for zero-delay indicators of the three time periods; (B) The range of $\text{adjusted} - R^2_{\text{Total}}$ for a given number of predictors for each time period; (C) Proportion of times each predictor appeared in the top 50 models of each time period. ("After_shell" indicates analysis that included the community shellfish biomass index as a response.)

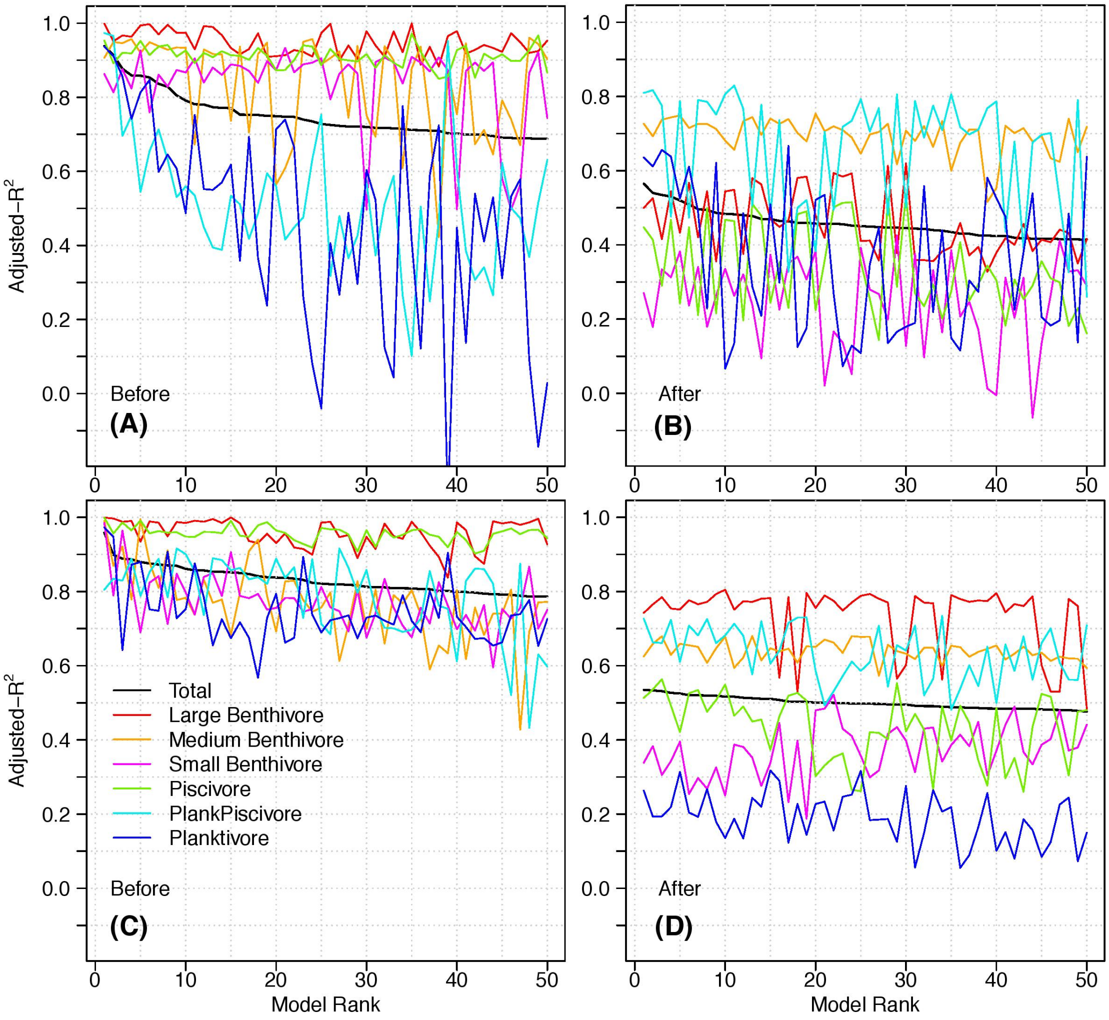


Figure 3.6: The adjusted-$\mathrm{R}^2_{\mathrm{Total}}$ of the top 50 models and corresponding adjusted-R^2 of each functional group for (A) Before models, ZD predictors; (B) After models, ZD predictors; (C) Before models, Avg1 predictors; (D) After models, Avg1 predictors. The legend is the same for each panel.

3.4.2 Delay Models

The above analysis showed that there are ecologic differences between the Before and After periods, and that the relationships for Full period do not represent either. As such, for the delay analysis I focussed on the two periods separately. In general, the moving average predictors improved the explanatory power more than the lag predictors (Fig. 3.7). The delay with the highest explanatory power for both periods was Avg1, a 2-year moving average including the current year, *i* and year *i* - 1. The Before Avg1 models were marginally better than the top 10 ZD models, and were notably better for most of the remaining models. The other Before moving average models had lower or marginally higher explanatory power than ZD models (until worse ranks). The After Avg1 models were marginally different than the top 25 ZD models, and notably better for the rest of the models.

I investigated how delays affect the explanatory power of individual functional groups using the Avg1 predictors (i.e., the best delay type and length). In general, the adjusted-R^2 for each functional group increased for the Avg1 predictors compared to the ZD predictors (Fig. 3.6). The most notable improvements were for plank-piscivores and planktivores in the Before period, and large benthivores for the After period (adjusted-R^2 increased by ~0.30 for each). The explanatory power for several functional groups decreased with the Avg1 predictors (small and medium benthivores Before; small benthivores, plank-piscivores and planktivores After), but these changes were minor when compared to the improvements of the other groups. Another striking feature of Fig. 3.6 is the reduced variance in the adjusted-R^2 for each functional group (except large benthivores) for the Avg1 predictors. This is most noticeable for the adjusted-R^2 of the planktivores in the Before period, which had a standard deviation of 0.29 with ZD predictors vs. 0.08 with Avg1 predictors.

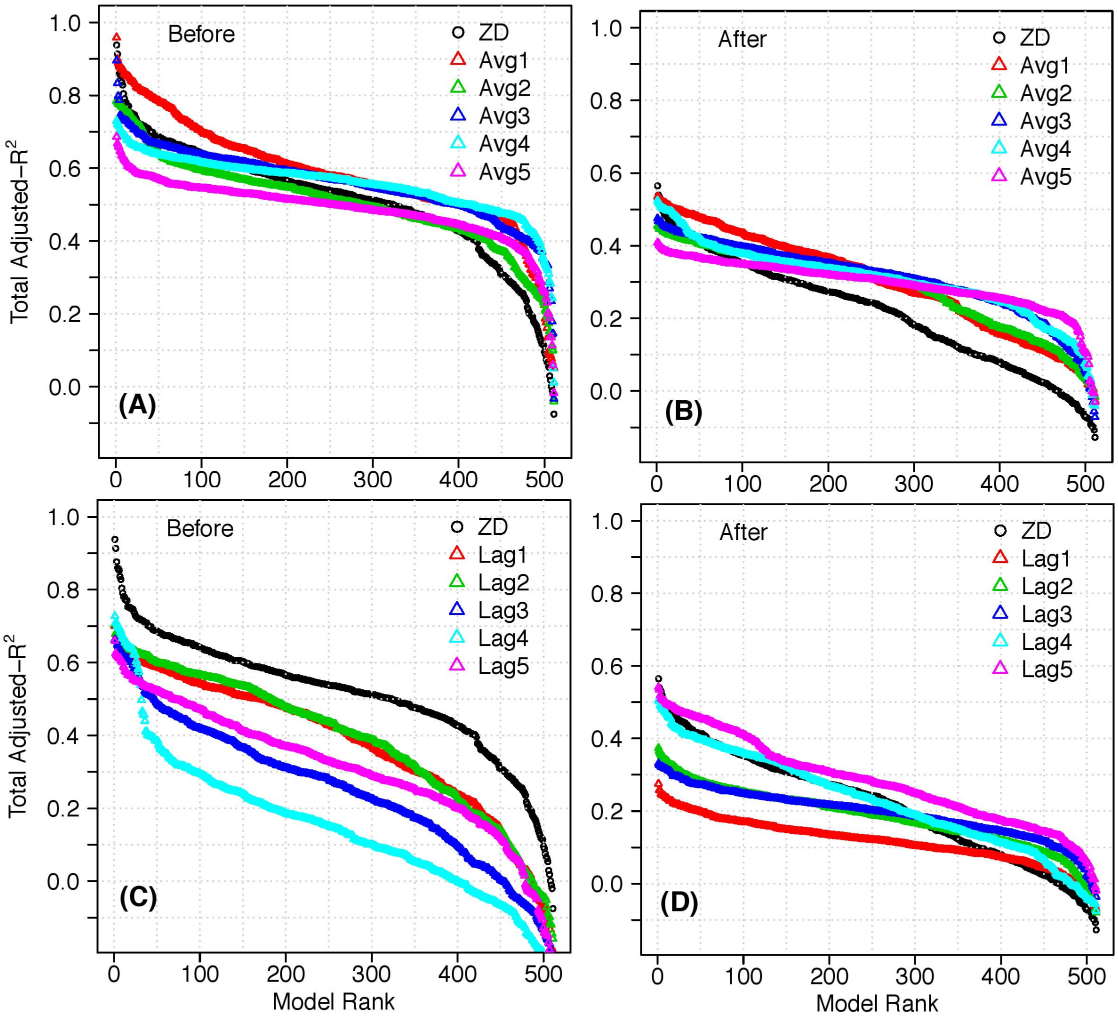


Figure 3.7: Adjusted-R^2_{Total} in decreasing rank for models using predictors with time delays: (A) Before models, moving average predictors; (B) After models, moving average predictors; (C) Before models, lag predictors; (D) After models, lag predictors.

The results of the lag analysis were less consistent between the two periods. All the models with lag predictors for the Before period had notably lower explanatory power than ZD. This could suggest that the major pressures on the fish community during this time were related to fisheries removals, which have immediate primary effects on the ecosystem. In contrast, the After Lag4 models had similar explanatory power as the ZD models, while the Lag5 predictors were similar or marginally better for the top 50 models, and notably better for some models at worse ranks. This suggests that the fish community could be experiencing indirect effects of fishing (e.g., Daan et al. 2005;

Koen-Alonso et al. 2010), or environmental effects that require time to manifest in the system.

For most delays, subsets of the predictors had similar or higher explanatory power than the full suite (Fig. 3.8; Appendix D, Figs. S.1 and S.2). In general, the range of adjusted-R^2_{Total} for a given number of predictors was larger for the Before models than the After, suggesting that which pressures were included in the subset was more important Before, and the number of pressures included was more important After. For all delays (except Before Avg1 and Avg3), the adjusted-R^2_{Total} plateaued or decreased after a certain number of predictors were used.

There are some notable differences in the patterns of most frequent predictors between the two delay types (Fig. 3.9). In the Before models, total landings were most frequent at ZD, which was expected because the ecosystem was heavily exploited during this period, especially for groundfish (represented by total landings). Pelagic and shellfish landings were also expected to be most frequent at ZD, but were more frequent at higher delays, which suggests indirect effects of fishing. Shellfish landings were included in about 80% of the ZD and Avg2 models, and almost all the Lag1, Lag2, and Lag3 models. This was unexpected because shellfish was not included as a functional group response. One possible interpretation is that because shellfish landings were increasing approximately linearly with time (Fig. 3.3), they were highly negatively correlated with the declines in the other functional groups, and therefore contributed to explaining variance in the responses. Both MTI and NAO were included in almost all of the top Lag3 models, but only about 60% of the Avg3 models. In contrast, SST was included in all of the Avg2 and Avg3 models, but less than half of the lag models at these same *k*. S150 and $\mathrm{Time}_{\mathrm{Ice}}$ were also included in more Avg models than Lag models.

In the After models, total landings were more frequent at delays (Avg3 and Lag1; Fig. 3.9), which could indicate delayed effects of fishing on the fish community structure. Pelagic landings were most frequent at ZD (closely followed by Lag2), and shellfish landings were included in almost all the ZD and Lag1 models, which is curious because the community shellfish index was not included as a response for that analysis. MTI was included in most of the ZD, Avg1, and Avg2 models. NAO was included in all the Lag2 models, but only about 80% of the Avg models, while SST was most frequent at delays of 2 and 3 years for both delay types. SSS was not particularly frequent in any of the lag models, but was included in about 70% of of Avg1. S150 and Time$_{\text{Ice}}$ were most frequent at the same *k* for both delay types (*k*=1 and *k* = 3, respectively).

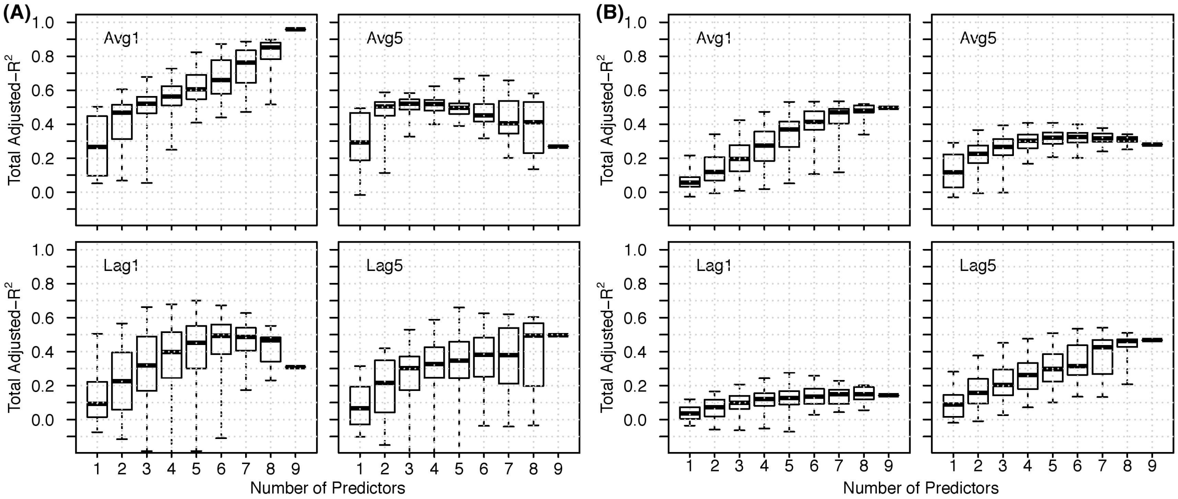


Figure 3.8: The range of Adjusted-R$^2_{\text{Total}}$ for a given number of predictors all delayed by *k* for moving average and lag predictors (A) Before models; (B) After models. Select *k* shown here; see Appendix D, Figures S.1 – S.2 for all k.

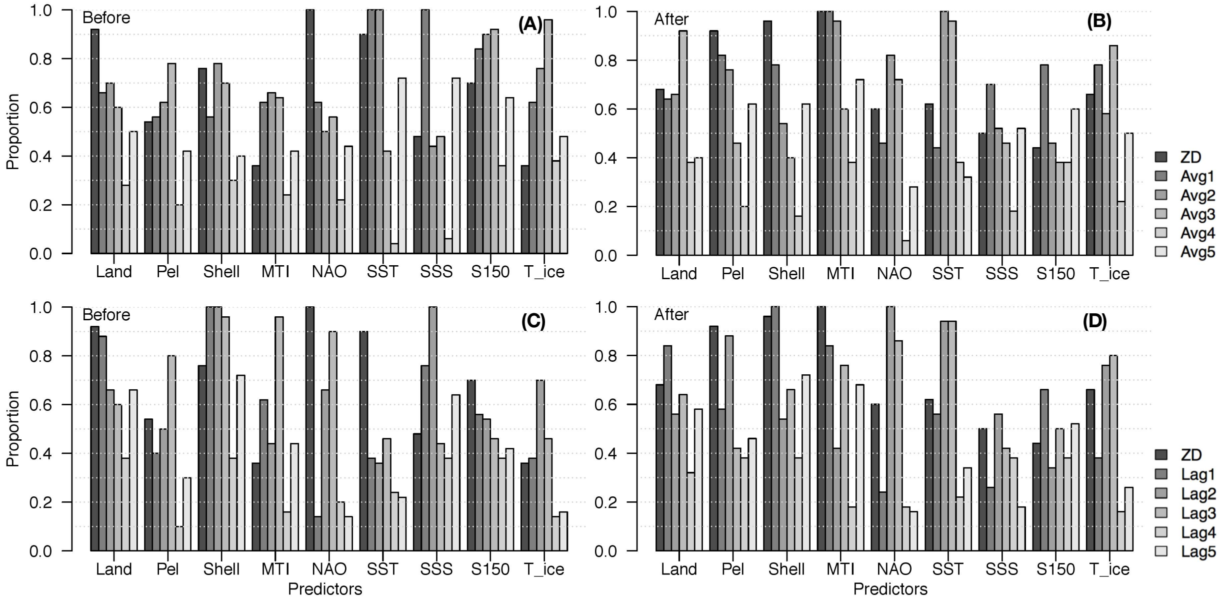
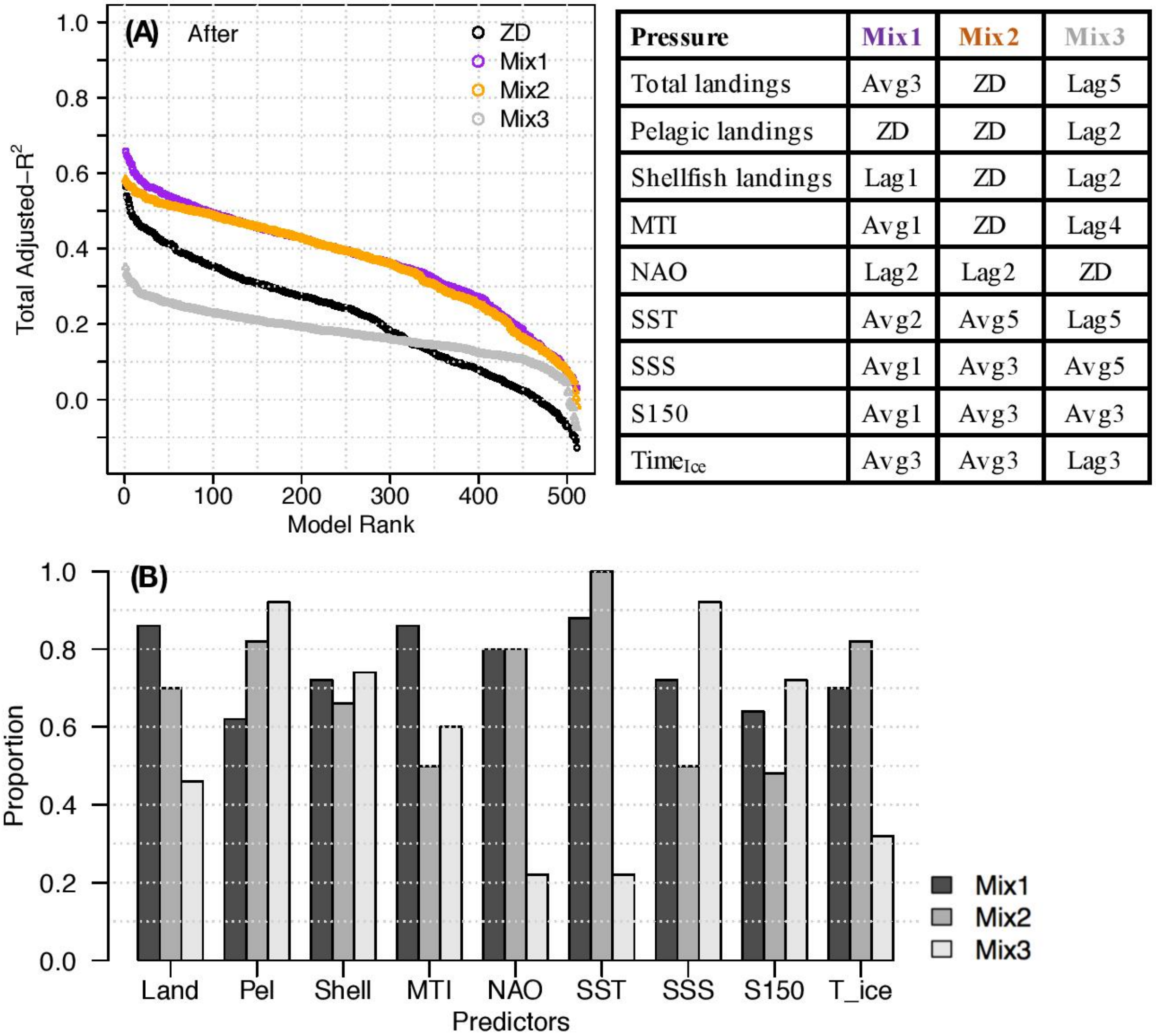


Figure 3.9: Proportion of times each predictor appeared in the top 50 models of the Before and After models for each delay type and length: (A) Before models, moving average predictors; (B) After models, moving average predictors; (C) Before models, lag predictors; (D) After models, lag predictors.

I repeated the analysis using specific delays for each predictor ("Mix" models) based on the idea that fishing pressures have shorter time delays, while environmental pressures generally take longer to manifest in the fish community. None of the combinations of delay types and lengths I tested had notably higher explanatory power than the best ZD and Avg1 Before models (not shown). In contrast, several combinations of mixed delay pressures were notably better than the best After models (e.g., Mix1 and Mix2, Fig. 3.10). Mix1 and Mix2 both had shorter time delays (ZD, $k = 1$) for most of the fishing pressures and longer delays ($k = 2+$) for most of the environmental pressures. The top 50 Mix1 models included sets of 5 – 9 predictors, with total landings, MTI, and SST being the most frequent. The best set used 7 predictors, but there were other sets of 7 – 9 with only marginally different explanatory power. The top 50 Mix2 models included sets of 4 – 9 predictors, with pelagic landings, NAO, SST, and Time_{Ice} the most frequent. The best Mix2 set used 6 predictors, and there were other sets of 5 – 8 with only marginally different explanatory power. The delays for Mix3 were chosen to provide a counter-example where all pressures have longer delays except NAO, which was assigned ZD. As expected, Mix3 was notably worse than the After ZD models, and NAO was not present in most of these “best” models.



Pressure	**Mix1**	**Mix2**	**Mix3**
Total landings	Avg3	ZD	Lag5
Pelagic landings	ZD	ZD	Lag2
Shellfish landings	Lag1	ZD	Lag2
MTI	Avg1	ZD	Lag4
NAO	Lag2	Lag2	ZD
SST	Avg2	Avg5	Lag5
SSS	Avg1	Avg3	Avg5
S150	Avg1	Avg3	Avg3
Time_{Ice}	Avg3	Avg3	Lag3

Figure 3.10: (A) Adjusted-R^2_{Total} in decreasing rank for After models using predictors with mixed time delays; (B) Proportion of times each predictor appeared in the top 50 models for each set of After mix delays. Refer to table legend for type and length of delay used for each predictor.

3.5 Discussion

This analysis adds to the literature demonstrating that there is no single type of pressure driving fish community dynamics on the Newfoundland shelf (e.g., Mann and Drinkwater 1994, Devine et al. 2007, Koen-Alonso et al. 2010b). In this study, both fishing and environmental indicators were included in nearly all the top models for all types and lengths of time delays (exceptions are five After models with adjusted-$R^2_{\mathrm{Total}} \leq 0.40$), which highlights that managers in this area should factor both types of pressures into their decisions. The dominant pressures Before the collapse of fish biomass (i.e., those that caused the collapse) in the Northwest Atlantic have been the subject of debate, especially for commercially important species such as Atlantic cod. Some authors conclude that fishing mortality was the sole major cause of the collapse (e.g., Myers et al., 1996, 1997), even though non-commercial species were also impacted (e.g., Gomes et al. 1995 for Division 2J3KL; NAFO 2010a for Divisions 2K3KL and 3LNO). Others assert the poor environmental conditions were an important driving pressure (e.g., Parsons and Lear 2001, Rothschild 2007, Halliday and Pinhorn 2009), pointing out for example that the community recovered from a similar collapse in the 1970s, when fishing pressure was high, but environmental conditions were more favorable than the early 1990s. My analysis supports a broader argument that the combination of these two drivers (high fishing and poor environment) were necessary for the extensive and widespread changes that occurred (e.g., Rose 2004, Devine et al. 2007, Koen-Alonso et al. 2010b). Specifically, total landings (here also a proxy for groundfish landings), NAO and SST were the most frequent pressures included the best (top 50) Before models. The best 1-predictor model was total landings (adjusted-$R^2_{\mathrm{Total}} = 0.55$), while the best 2-predictor model included total landings and NAO (adjusted-$R^2_{\mathrm{Total}} = 0.63$), and including SST further improved the explanatory power (adjusted-$R^2_{\mathrm{Total}} = 0.67$). The inclusion of both NAO and SST speaks to the importance of both basin-scale and local environmental effects on the ecosystem, further strengthening the need to have regional information to understand and predict changes in the fish community.

The analysis here shows that there was a shift in which fishing and environmental pressures were most directly related to the fish community structure Before and After the collapse. The environment can clearly influence fish community dynamics on the Grand Bank, but the most frequently included pressures in the ZD After models were pelagic and shellfish landings and MTI. This set of three pressures had notably higher overall explanatory power Before the collapse; however, its adjusted-R^2_{Total} represents a higher percentage of the maximum explanatory power for the After period. This suggests that the remaining pressures (e.g., environment) add relatively less predictive information in the After models. This shift reflects the changes in target species after the groundfish moratoria, although it is surprising that shellfish landings were included in all but two top models because the community shellfish biomass was not included as a response. Shellfish landings consist mainly of snow crab and *Pandalus* shrimp, while pelagic landings are mainly capelin. Shrimp and capelin are considered important forage species on the Grand Bank (DFO 2015a, 2015b), and are managed conservatively (for example there is a capelin moratorium in 3NO); however, the analysis suggests landings of these species are impacting the ecosystem. Shellfish landings increased overall in the After period (despite a slight decrease in the last several years), and are negatively correlated with the biomass indices of small benthivores, piscivores, and plank-piscivores, suggesting that they are hindering the recovery of these functional groups. The question remains whether this is indicative of a causal relationship, or is only correlative. One potential mechanistic explanation is given by Koen-Alonso et al. (2010), who speculated that fishing may be reducing food availability for key species on the Grand Banks, and thus hindering their recovery. Another hypothesis is that there are secondary effects on the fish community from shrimp beam trawls. These trawls are considered to have low bycatch rates (for commercial species; NAFO 2014), but they could be negatively impacting the habitat of other species in the community.

Another striking difference between the two periods is the remarkably high explanatory power of the best Before models compared to the best After models (Fig. 3.5) for any time delay (type or length) or number of predictors. I speculate that the reasons for this relate to changes in relationships among and within the pressures and responses. For example, there was a strong common signal in the responses Before the collapse. The biomasses of many functional groups were relatively highly correlated (Dempsey et al. 2017), such that any set of predictors with high explanatory power for one particular group was also high for several of the others (e.g., small, medium, and large benthivores and piscivores; Fig. 3.6). The weaker relationship among the responses After the collapse means prediction of all six functional groups may require a broader spectrum of pressures.

I showed the pressures that were driving changes Before the collapse are no longer as influential After, and the relatively lower adjusted-R^2_{Total} suggests that there may be pressures missing from the After models. Bottom up pressure indicators such as primary production and trophic transfer efficiencies were not included here because there was no suitable data for the required time frame. The models include the timing of the sea ice melt as a proxy for the timing of phytoplankton spring bloom, but other characteristics of the bloom (e.g., magnitude), or lower trophic level energy transfer may prove better predictors for this period through some mechanism not identified here. Other missing pressures are measures of predation by sea birds and marine mammals that could exert a top-down influence on the fish community. For example, harp seals migrate from the Arctic to northern Newfoundland in the Fall, and prey predominantly on capelin, but also eat other species (e.g., Atlantic herring, Arctic cod, shrimp, and Atlantic cod; Stenson 2013). The Northwest Atlantic harp seal population has been increasing rapidly since the 1980s (Hammill et al. 2011), and some authors suggest that seal predation has supressed the recovery of fish species on the Newfoundland-Labrador shelf (e.g., Bundy 2001, Devine et al. 2007). One type of human-related pressure specific to the After period that wasn't considered here is oil production. While oil exploration has occurred on the Grand Banks since the 1960s, active platforms have only been producing oil since 1997. Related pressures could include chemical pollution from regular discharge or accidental spills (Templeman 2010), which can be especially harmful to early life stages, and can disrupt development, growth, and reproductive rates (etc., see JWL 2007 and references therein). These pressures were not included here because I did not expect them to significantly influence the Grand Bank fish community; however, the analyses suggest that future investigations into these pressures are warranted.

Finally, non-linearity in the relationships between pressures and responses may have a stronger influence during the After period, through some unidentified mechanism. Predator-prey relationships, population dynamics, environmental changes, and human impacts can all result in non-linearity in marine ecosystems (Liu et al. 2014). Given the significant changes in the fish community structure and related pressures, I can speculate that the relationships among them could be less linear After the collapse, resulting in lower explanatory power because MLR is a linear model. This could be tested by comparing this analysis to results from a non-linear model such as neural networks or generalized additive models. These flexible models don't require the user to specify the forms of the relationships between predictors and responses, which affords a potential advantage of being able to capture the nonlinearity when the mechanistic forms of these relationships are unknown.

The analysis showed that incorporating delays can improve explanatory power, but that the type and length of delay should be carefully considered. In general, moving average predictors had higher explanatory power than lagged predictors for both periods. Since the moving averages incorporate the trend in the predictors, causing the responses to change gradually over time (see Fig. A1 in Gentleman and Neuheimer 2008), the results suggest that trends in these pressures are influencing the fish community. For the models with the same delay type and length for each predictor, Avg1 was the best, notably improving the explanatory power compared to ZD for both periods. Avg1 also increased the explanatory power and reduced the variability in the adjusted-R^2 for most of the individual functional groups (Fig. 3.6). Other delays, particularly those with lagged predictors, had notably worse explanatory power than ZD. While some of the improved fit of the moving averages may be an artifact of smoothing, the results still strongly suggest that the rates of change are useful for predicting.

There was no one set of pressures that best predicted fish community status for any period or delay type or length, which suggests there are strong indirect effects of many pressures on different trophic levels, such that changes in fish functional group biomass can be directly predicted from different pressures. Examination of Mixed delays illustrated that the explanatory power of the Avg1 After models can be further improved by incorporating pressure-specific delays (Fig. 3.10). This suggests that including the different timescales of influence for the pressures is important for this period, and could improve the ability to forecast changes in the fish community. Even longer time delays could be beneficial because changes in some pressures may take more than five years to manifest in the fish community. For example, Daan et al. (2005) and Greenstreet et al. (2011) found that secondary effects of fishing could impact different size-based metrics of the fish community in the North Sea after lags of 6 - 12 years and 12 – 20 years, respectively. However, while I showed that different mixed delays among the predictor set resulted in similar overall explanatory power, I also showed it could be worse. I therefore recommend that future investigations into suitable delays – and their mechanisms – should come from analysis of mechanistic models, which go beyond statistical relationships by including biologically relevant, measurable parameters.

For all three periods (Full, Before, and After) and delay types and lengths, there was no one set of pressures that "best" predicted fish community status. Rather there was a range of sets, differing in number and type of indicators that had similar explanatory power (Appendix D, Tables S.1 – S.5). For example, there are two sets of 6-pressure Avg1 After models with only marginally different explanatory power; however, one includes two fishing indicators (pelagic landings and MTI) and four environmental indicators (all except S150; adjusted-R^2_{Total} = 0.68), while the other includes all four fishing and two environmental (S150 and $\mathrm{Time}_{\mathrm{Ice}}$; adjusted-$R^2_{\mathrm{Total}}$ = 0.70). In many cases the same base indicators were used in most or all of the top sets (Fig. 3.5c; e.g., for ZD After: pelagic and shellfish landings and MTI), while other pressures improved the explanatory power by adding additional information. This is not to say that any set of nine pressures would have high explanatory power – I curated these pressures because I expected them to have measurable impacts on the Grand Bank fish community. The point here is that pressure sets with similar predictive power may be comprised of different types of strategically selected data. This suggests that effects of many pressures occur for different ecological constituents, such that changes in fish functional group biomass can be directly predicted from different pressures. Therefore, if there was a lack of one type of pressure data, it may be possible to replace it with another type without compromising explanatory power. Furthermore, using a suite of models to predict future changes can provide a measure of uncertainty, much like the model ensembles used by the Intergovernmental Panel on Climate Change to forecast climate changes and associated impacts (Kirtman et al. 2013).

Here I recognize the untreated autocorrelation in the predictors and responses that could affect the results. Calculation of the adjusted-R^2 assumes uncorrelated error, because the number of independent observations is used to adjust the R^2 (Equation 3.3). In the case of autocorrelated errors, the effective number of observations (n^*) is less than the length of the time series, i.e., n* < n (Priestley 1994). Accounting for n* could potentially change the relative ranking of the models in this analysis, and therefore the most influential predictors, because the fraction $\frac{n-1}{n-p-1}$ (in Equation 3.3) will not be the same for models with a different number of predictors (p). However, because larger p is also associated with higher R^2, the changes in the model ranking would likely be small. Problems with autocorrelation can be dealt with by removing it (e.g., by differencing; Thompson and Page 1989); however, it was deemed inappropriate to do so for this study. Removing the autocorrelation would effectively remove trends from the data, which represent true signals that should be included in the model. I recommend that future analyses investigate the effect of autocorrelation on the adjusted-R^2 when comparing models using different subsets of a predictor set. It may also be valuable to revisit the current problem of identifying the most influential pressures for the Grand Bank using time series analysis techniques to account for the autocorrelation (e.g., generalized least squares regression).

Here I provided one case study of how MLR can be applied to learn about the Grand Bank ecosystem. Ultimately the best predictor set(s) for the Grand Bank and other ecosystems would depend on a number of considerations, including the final application of the model. Other considerations may include the responses of interest (i.e., if structure of the fish community were expanded to also consider length and/or biodiversity measures), the explanatory power for the individual responses (Fig. 3.6), data availability (e.g., types of indicators and length of time series), and costs of monitoring (e.g., data collection, database entry, analysis). As well as potentially varying with application-specific criteria, best sets will likely be ecosystem-specific, and depend on the unique combination of exploitation history, oceanographic conditions, and ecological interactions. Finally, because ecosystems are dynamic and the types and intensity of pressures may change over time, the best predictor sets may differ for different time periods of the same ecosystem. Scientists and managers should be aware of this, and watch for declines in the ability of these sets to predict changes in the ecosystem. Here I offer a statistical approach that can be used with various types of data, and is suggestive of being easily calibrated to different systems. This could serve as a useful complementary tool that could help design modelling studies, plan field programs, and direct monitoring efforts. The synergistic use of statistical and mechanistic models to help guide identification of the most informative pressures, their most influential time delays, and their mechanisms are important future research directions that could improve ability to forecast changes in the fish community, and implement appropriate management measures.

CHAPTER 4: APPLICATION OF NEURAL NETWORKS TO MODEL CHANGES IN FISH COMMUNITY BIOMASS IN RELATION TO PRESSURE INDICATORS AND COMPARISON WITH A LINEAR APPROACH[3]

4.1 Abstract

Neural networks (NN) are considered well suited to modelling ecological data, especially non-linear relationships, and were applied here to investigate which pressures best model changes in the fish community of the Grand Bank, Northwest Atlantic. Nine fishing and environmental pressures were used to simultaneously model the biomasses of six fish functional groups before and after the collapse of fish biomass in the region, and over the full data series. The most influential pressures were identified, and both the fit and predictive power were evaluated. The analysis was repeated with time delays of different lengths (0–10 years) and types (moving average vs. lags) imposed on the pressures. Results were compared to those of a similar analysis using a multivariate linear regression model. Both types of models showed different influential pressures before compared to after the collapse, but the MLR models generally resulted in better fit. NN potentially have useful forecast ability, although future work is required to improve the preliminary forecasts shown here before they can be directly used to inform management. I highlight new insights into the ecosystem function and contrast these analytical approaches in the context of ecosystem based fisheries management.

4.2 Introduction

Ecosystem based fisheries management (EBFM) is generally accepted by scientists, managers, and policy makers as necessary for promoting sustainable fishing and preventing future fisheries collapses (DFO 2007, Large et al. 2013, Bundy et al. 2016). EBFM will supplement traditional single species assessments by explicitly accounting for multiple pressures on the fish community (e.g., fishing and environmental conditions), as

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[3] Based on Dempsey, D. P., Pepin, P., and Koen-Alonso, M., and Gentleman, W. C. (In review). Application of neural networks to model changes in fish community biomass in relation to pressure indicators and comparison with a linear approach.

well as interactions among species (target and non-target). This requires a great deal of information on the ecosystem, which can be provided in part by indicators of these pressures and related biological responses. For example, fishing and the environment are both types of external pressures on marine fish communities. Fishing indicators include metrics of landings, effort, and fishing mortality, while environmental indicators include basin-scale metrics (e.g., North Atlantic Oscillation), regional conditions (e.g., bottom and surface temperature and salinity), and ecosystem-specific features (e.g., presence of sea ice). Biological indicators are metrics of the fish community, including biomass, mean trophic level, and size-based indices. Hundreds of such indicators have been proposed and vetted (Rice 2003, Cury and Christensen 2005), and significant effort has focussed on determining which biological ones are the most informative (Rice and Rochet 2005, Shin et al. 2010a). However, efforts to implement EBFM will benefit from further investigations into which sets of pressures can best model changes in the fish community, and ultimately forecast them (Jennings 2005, Ojaveer and Eero 2011, Large et al. 2015b).

Identifying the most informative pressure indicators is inherently challenging because of the dynamic, multivariate nature of marine ecosystems. Although many studies have traditionally focussed on single pressure-response relationships, multiple pressures interact and can impact multiple ecosystem components, with cascading effects across different pathways, and the results are not necessarily additive (Large et al. 2013, Hunsicker et al. 2016). Identifying the most influential pressures is further complicated because their relationships to the changes in these components are often not well understood. Fishing and the environment as well as other pressures (e.g., predator-prey interactions) can result in non-linear responses (Daan et al. 2005, Hunsicker et al. 2016), but the functional form of these relationships is typically unknown. Hunsicker et al. (2016) found that pressure-response relationships should be assumed as non-linear, unless there is strong evidence of linearity. Despite the prevalence of non-linear ecosystem interactions, many methods used to study pressure-response relationships assume linear relationships (Blanchard et al. 2005, Fu et al. 2012, Probst et al. 2012, Dempsey et al. 2018). Additionally, the relative importance of pressures may vary over time because of changes in management strategies, the balance of environmental conditions, and biological interactions (Mann and Drinkwater 1994). A final difficulty in teasing out important relationships is that the fish community can have both immediate and delayed responses to changes in pressures. For example, immediate effects of fishing include increased mortality, while changes in size-based indicators and life history characteristics have been associated with fishing lagged up to 20 years (Daan et al. 2005, Greenstreet et al. 2011, Laugen et al. 2014). The impacts of environmental conditions on the fish community can be mediated through the food web; for example, pressures such as temperature and salinity can influence the timing of plankton production, which can result in a match or mismatch with the food sources of juvenile fish (Cushing 1969). Poor environmental conditions could therefore reduce survivorship of larval fish, which will affect the production rate of the stock when the cohort reaches maturity (Colbourne and Anderson 2003).

To deal with these potential problems, the objective here was to use artificial neural networks (NN), which are non-linear, multivariate statistical models, to identify key pressures on the fish community of the Grand Bank, Northwest Atlantic over the past three decades (Fig. 4.1). NN are a type of machine learning inspired by the numerous connections among brain neurons, which allow humans and animals to solve complex problems (e.g., pattern recognition, classification; Jain et al., 1996). They can be considered a type of non-linear regression, although the parallels are not commonly noted in the literature, likely in part because of the jargon used to explain NN (Table 4.1; Sarle 1994). They have been applied to a variety of problems in different fields (e.g., ecology, economics, epidemiology), including aquatic ecology and fisheries science (e.g., Lek et al. 1995, Chen and Ware 1999, Olden et al. 2006, Krekoukiotis et al. 2016). The main advantage of NN over traditional statistical approaches is that NN can implicitly model non-linear relationships between p predictors and r responses, i.e., the user is not required to specify the form of these relationships. Additionally, many studies have shown that NN have better fit (i.e., smaller error) and predictive power (i.e., ability to model out-of-sample data) than traditional linear models (e.g., Lek et al. 1995, Chen and Ware 1999, Olden et al. 2006).

Table 4.1: Regression vocabulary and related neural network term (adapted from Sarle, 1994).

Regression	**Neural Network**
Independent variables	Inputs
Predicted values	Outputs
Dependent variables	Targets/training values
Residuals	Errors
Estimation	Training/learning
Observations	Training pairs
Parameter estimates	Weights
Regression	Supervised learning
Interpolation and Extrapolation	Generalization

The Grand Bank, within Northwest Atlantic Fisheries Organization (NAFO) statistical division 3LNO, is one of the major subunits of the Newfoundland-Labrador shelf, which extends from the Canadian exclusive economic zone (EEZ) into international waters (Fig. 4.1; NAFO 2014). This region and the adjacent division (2J3K) were among the most productive fishing grounds in the world for centuries, with global fisheries for many species including Atlantic cod and yellowtail flounder (Rose 2007). Fisheries management responsibilities are split between Fisheries and Oceans Canada (DFO; inside the EEZ) and NAFO (outside the EEZ). Quotas were set for each commercial stock through the 1980s, although sustainable exploitation rates were over-estimated, and these limits were ignored by some vessels (Rose 2007). By the 1990s, the heavy fishing pressure combined with poor environmental conditions resulted in extensive ecological changes, including declines in total fish biomass commonly called the "collapse of the cod," although other species were also impacted (e.g., Atkinson 1994; NAFO 2010). In response to these changes, groundfish moratoria were enforced in 3LNO in 1994, and harvesters began targeting different species, for example northern shrimp (*Pandalus borealis*) and snow crab (*Chionoecetes opilio*; also called queen crab). Many of these moratoria remain in place (NAFO 2017), and both DFO and NAFO are currently working towards implementing ecosystem approaches to management (Oceans Act 1996, NAFO 2010a, Koen-Alonso et al. 2018). Despite these efforts, the total fish biomass recovery is slow, and the structure of the ecosystem has shifted from piscivore dominated to include more species at lower trophic levels (Pedersen et al. 2017).

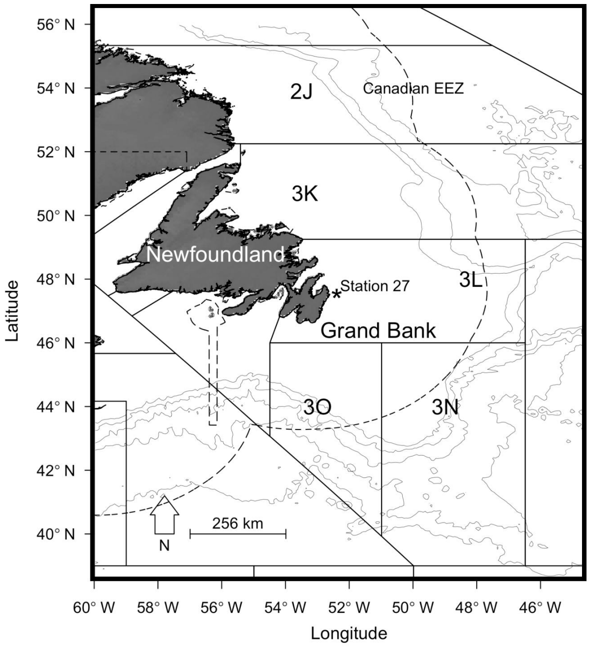


Figure 4.1: Map of the study area, showing the Grand Bank (NAFO Division 3LNO), Station 27, and the Canadian exclusive economic zone (dashed line).

For this analysis, the fish community was represented by the biomass indices of six fish functional-feeding groups, which reflect the collapse and partial recovery of the total fish biomass, and changes in the trophic structure (Dempsey et al. 2017). Key pressures were selected from a suite of four fishing and five environmental indicators considered representative of pressures in the region (Dempsey et al. 2017). The fishing pressures capture the decrease in total landings throughout the 1980s, and the subsequent increase in shellfish landings. The environmental pressures reflect the change in conditions before and after the mid-1990s, which have been referred to as a regime shift (e.g., Buren et al. 2014). A recent analysis of these pressures and fish community responses on the Grand Bank using a multivariate linear regression (MLR) model showed that explanatory power was higher before the collapse, and that the most influential pressures were different before vs. after the collapse (Dempsey et al. 2018). Here I build on this earlier work by applying a more flexible, non-linear model, extending the delay analysis to include more years of historical data, and providing a preliminary assessment of the forecast potential of NN. This analysis will add to the current knowledge of the region, while demonstrating the value of a potentially powerful tool that could be applied by scientists and managers to other regions. Finally, I compare the results of the linear and non-linear models, with the goal of highlighting advantages and disadvantages of the two methods in an EBFM context.

4.3 Methods

4.3.1 Indicators

The indicator time series used in this analysis were synthesized and used to assess linear pressure-response relationships on the Grand Bank in Chapters 2 and 3 (Dempsey et al. 2017, 2018). Below I present a general overview of these indicators, and refer interested readers to Chapter 2 (Dempsey et al. 2017) for more details. Fish community indicators are annual values from 1985 – 2013, and pressure indicators extend back to 1975 for use with the time delay analysis (described below).

4.3.1.1 Fish community indicators

The fish community was represented by the mean annual biomass indices of six fish functional-feeding groups (NAFO 2010a, 2014, Dempsey et al. 2017, 2018). The biomass indices are the sum of the random stratified mean biomass per tow for core strata of all species included in each functional group (Fig. 4.2), as measured by the DFO spring bottom trawl surveys for Division 3LNO (Fig. 4.1). The survey gear changed in 1996 (McCallum and Walsh 1997), so appropriate scaling factors were applied to the biomass indices prior to this year such that the "Full" historical time series of survey data (1985 – 2013) could be analyzed (Koen-Alonso, unpublished work). I also analyzed each period separately, partly to avoid using scaling factors, but more importantly to investigate differences "Before" (1985 – 1995) and "After" (1996 – 2013) the collapse of fish biomass in the region, which occurred approximately coincident with the gear change (Dempsey et al. 2018).

Large benthivores, medium benthivores, and piscivores were highly correlated (Spearman's correlation coefficient > 0.6) Before (i.e., "during") the collapse, when their biomasses decreased rapidly (Fig. 4.2). Planktivore biomass spiked in the mid-1980s, and then decreased for the remainder of this period (highly correlated with medium benthivores and piscivores). In contrast, small benthivore biomass increased, and plank-piscivores had no trend. In the After period, large and medium benthivores were still highly correlated, with recovering biomasses. Piscivores and plank-piscivores were also highly correlated, with increasing biomasses from the mid-2000s. Small benthivore biomass decreased overall, while planktivores had no trend (Fig. 4.2).

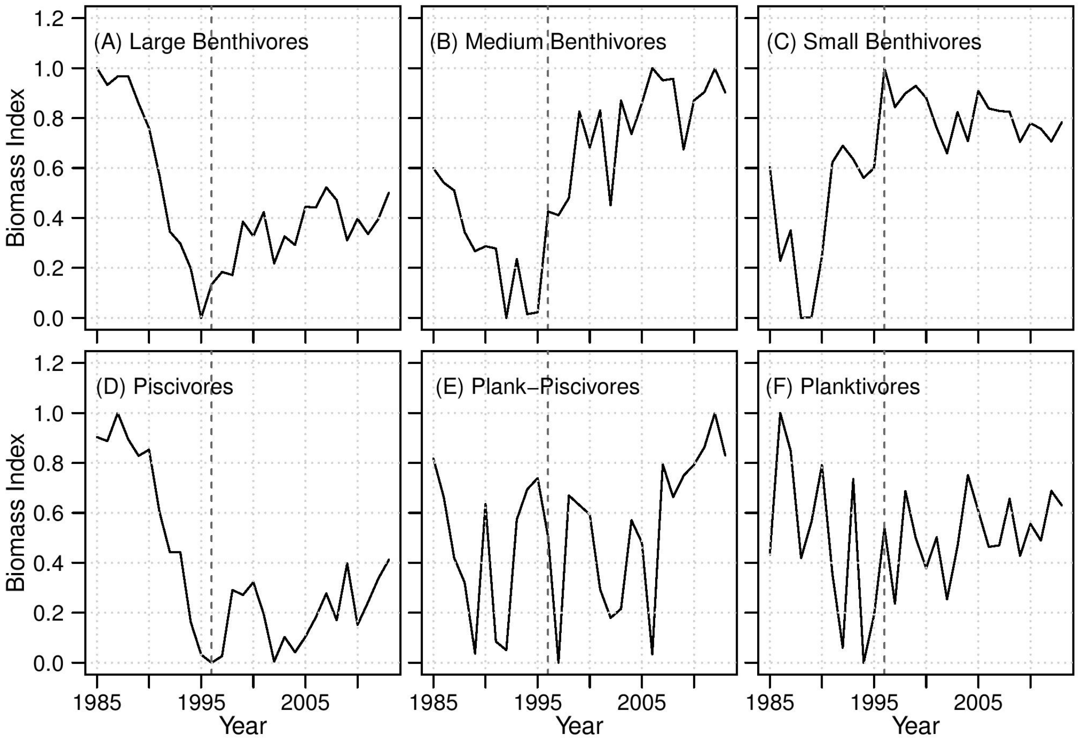


Figure 4.2: Functional group biomass indices (logged and linearly mapped to [0, 1]) used as responses in this analysis. The thick dashed line indicates the beginning of the After period.

4.3.1.2 Fishing and environmental pressures

I used the same four fishing and five environmental pressures investigated in Chapter 3 (Dempsey et al. 2018) so I could compare the most influential pressures identified with the MLR to those highlighted by the NN (Table 4.2; Fig. 4.3). In general, the fishing pressures were highly correlated over the Full and Before periods, while the environmental pressures were not highly correlated with any pressures for any period. Total and pelagic landings decreased overall from the late 1970s until the mid-1990s, but have no trend in the After period. In contrast, shellfish landings increased over the Full period, due in part to the shift in target species after the groundfish moratoria (Schrank 2005, Dempsey et al. 2017), but have been declining since the mid-2000s. The mean trophic index (MTI) increased in the late 1970s until the mid-1980s, and then until the mid-1990s, but has no trend After the collapse. Sea surface temperature (SST) was the only environmental pressure with clear trends, and it has been generally increasing since 1991. Sea surface salinity (SSS) and bottom salinity decreased overall from the mid-1970s until the early 1990s, and showed high inter-annual variability. This variability was smaller After the collapse, but there were no clear trends. The NAO was well above its average in the early 1990s, which has been related to the cooler and fresher water at this time (Fig. 4.3, panels E – H; Buren et al. 2014). The timing of the sea ice melt ($\mathrm{Time}_{\mathrm{Ice}}$) had no trends, but had higher variability After the collapse (Fig. 4.3).

Table 4.2: Pressure indictors used as predictors in this analysis.

Pressure	**Definition**	**Relevance**
Total landings	Sum of reported groundfish, pelagic, shellfish, and "other" species landings	Metric of fishing pressure on the entire community
Pelagic landings	Reported landings of pelagic species	Dominated by capelin, a key forage species
Shellfish Landings	Reported landings of shellfish	Dominated by snow crab; indicative of changing fishing practices after the 1994 moratoria
Mean trophic index (MTI)	Mean trophic level of the landings weighted by the biomass of species landed. Only includes species with trophic level ≥ 3.25	Indicative of changing target species as harvesters adapt to changes in fishing technologies, the ecosystem, and end markets (Caddy and Garibaldi 2000)
North Atlantic Oscillation (NAO)	Index of basin scale atmospheric circulation patterns	Related to wind, salinity, temperature, and sea ice; linked to fish biomass collapse (Halliday and Pinhorn 2009)
Sea surface temperature (SST)	Average annual surface temperature measured at Station 27	Local environmental condition, related to fish growth; linked to fish biomass collapse (Halliday and Pinhorn 2009)
Sea surface salinity (SSS)	Average annual surface salinity measured at Station 27	Local environmental condition; linked to water column stratification and production of lower trophic levels (Greene et al. 2013)
Bottom Salinity	Average annual salinity at a depth of 150 m measured at Station 27	Local environmental condition; linked to productivity (Dutil and Brander 2003)
Timing of sea ice melt (Time_{Ice})	The day the sea ice edge reaches the southernmost most latitude on the Newfoundland-Labrador shelf in a given season	Proxy of the timing of the spring phytoplankton bloom (no other suitable measures of phytoplankton biomass/productivity were available over the required timescales; Wu et al. 2007)

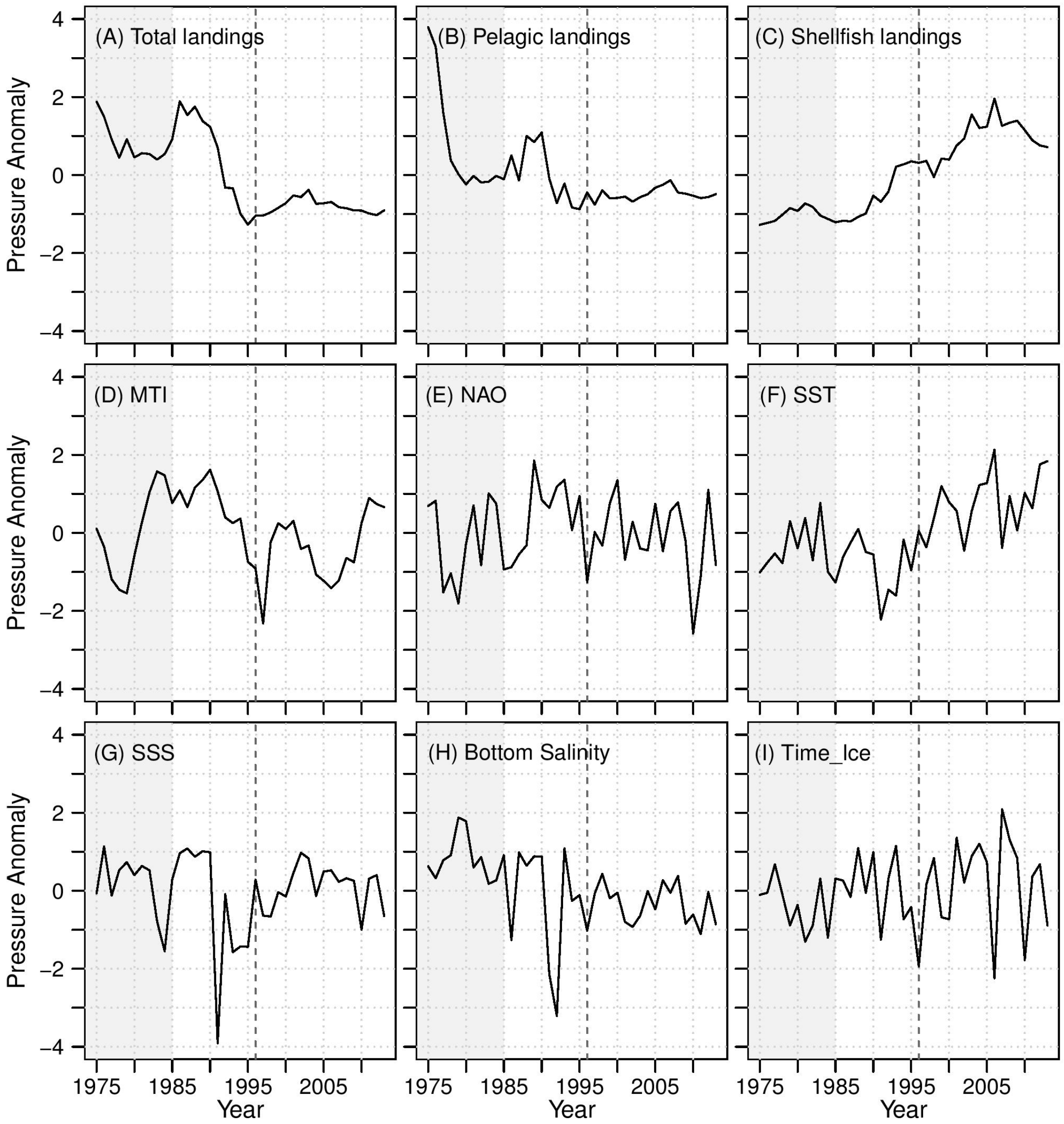


Figure 4.3: Pressure indicators used as predictors in this analysis. Fishing indicators: (A) – (D); Environmental indicators: (E) – (I). The unshaded area represents the zero delay pressures; the shaded area represents the additional data used in the time delay analysis. The thick dashed line indicates the beginning of the After period.

4.3.2 Neural Networks: Overview

4.3.2.1 Structure

The most common type of NN for regression problems is the feed-forward multi-layer perceptron (MLP) with one hidden layer, which is considered sufficient to approximate any continuous function (Hornik et al. 1989, Olden and Jackson 2001). I refer readers interested in other types of NN to the text of Ripley, 1996. The basic units of a NN are nodes (also called neurons), which are arranged into three layers: an input layer with p nodes (one for each predictor), a hidden layer with h nodes (user-specified), and an output layer with r nodes (one for each response; Fig. 4.4). The number of nodes in each layer describes the architecture (also called the structure) of the NN. Each node connects to all of those in the adjacent layer, and the strength of the connections is given by weights. Each node in the hidden layer sums the weighted predictor values and a bias weight (similar to the intercept term in linear regression), and then transforms the data through a continuous, differential activation function (also called a transfer function), usually a logistic function (Jain et al. 1996, Basheer and Hajmeer 2000; Appendix E.1). The results from each hidden node are treated similarly (i.e. multiplied by their associated weights, summed with a bias, and transformed through an activation function) in each output node (Equation 4.1; Olden and Jackson, 2001):

$$\hat{y}_k = \emptyset_{Out}\left\{\beta_k + \sum_{j=1}^{h} w_{jk} * \emptyset_{Hid}\left(\beta_j + \sum_{i=1}^{p} w_{ij} * x_i\right)\right\} \tag{4.1}$$

Here, $\hat{y}_k$ are the modelled output (i.e., response) values, x_i are the predictor values, w_{ij} are the weights from input node i to hidden node j, β_j is the bias associated with hidden node j, and $\emptyset_{Hid}$ is the activation function in the hidden nodes. Similarly, w_{jk} are the weights from hidden node j to the output node k, β_k is the bias associated with output node k, and $\emptyset_{Out}$ is the activation function in the output nodes.

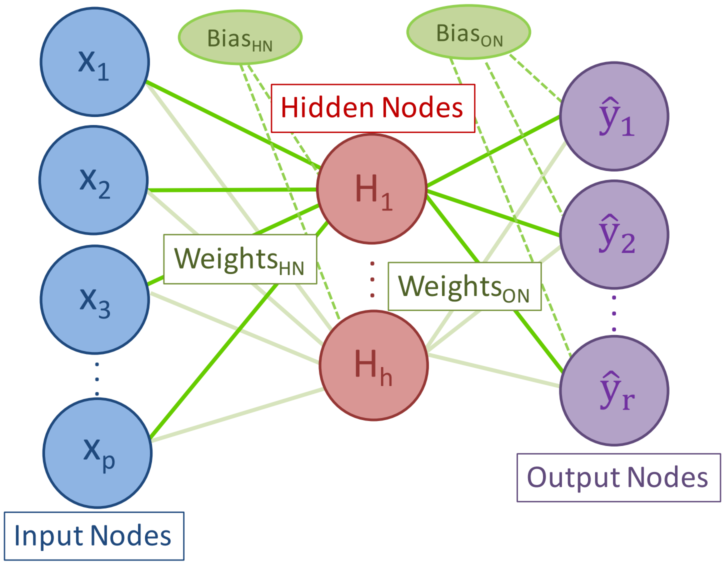


Figure 4.4: Illustration of neural network structure, with one input node for each predictor, x_i, one output node for each modelled response, $\hat{y}_j$, and h hidden nodes. Each node is connected to all of the nodes in the next layer by weights; biases are associated with each hidden and output node (similar to regression y-intercept). Subscripts "HN" and "ON" refer to weights/biases from the input nodes to hidden nodes, and the hidden nodes to output node, respectively.

4.3.2.2 Training

The fitting procedure is called "training," and the NN is often described as learning patterns in the data (Jain et al. 1996). The most common training algorithm is backpropagation, which minimizes an error function by iteratively adjusting the initial weights based on the gradient of the error function (i.e., gradient descent; Rumelhart et al. 1986). Initial weights are assigned randomly with small values to improve the probability and speed of convergence (Bishop 1995). As with other non-linear regression algorithms, backpropagation is sensitive to the initial conditions (weights), and may converge on a local minimum. An ensemble model approach is recommended to address these problems, where the NN is trained multiple times with different initial weights (but the same architecture), and the average results are reported (e.g., Zhou 2003, de Ona and Garrido 2014). Other training parameters include the learning rate and momentum, which increase the rate of convergence while avoiding local minima (Bishop 1995, Günther and Fritsch 2010). There are several options for stopping criteria, including defining a minimum error threshold.

The magnitude and sign of the final weights describe the connections between the predictors and responses. In this sense, they are similar to regression coefficients, although their interpretation is complicated by the need to consider the input-hidden *and* hidden-output connections, as well as the backpropagation algorithm's sensitivity to the initial weights. Several methods for using the final weights to rank the importance of the predictor variables have been proposed and applied in different disciplines (Garson 1991, Goh 1995, Olden and Jackson 2002). Other techniques, including sensitivity analyses (e.g., Lek et al. 1996) and partial derivatives (e.g., Dimopoulos et al. 1999), have also been used for this purpose. There is no consensus on which way is the best for ranking variable importance; however, de Oña and Garrido (2014) examined four different methods and showed they give similar results when an ensemble approach is used.

The number of nodes in the hidden layer is specified by the user, and can affect the fit, out-of-sample predictions, training duration, and predictor importance (e.g., Basheer and Hajmeer 2000). The hidden layer gives the NN its flexibility by introducing non-linearity through the activation functions (Sarle 1997). Increasing the number of hidden nodes will improve the fit to the data used for training; however, too many hidden nodes will allow the NN to model the noise rather than the signal. This is called over-fitting the data, and generally results in poor predictions on out-of-sample data. Too few hidden nodes will under-fit the data, which also results in poor predictive performance (Appendix E.2). Despite the importance of this modelling decision, there are no stringent rules for choosing the number of hidden nodes, and many authors use a trial and error approach (e.g., Ozesmi and Ozesmi 1999, Heiat 2002; Appendix E.1). The model is generally trained on a subset of data and tested on the remaining observations, and a separate goodness of fit metric is calculated for the training and test data. The model should perform suitably well on the test data for the NN to be considered "general enough," with the threshold determined by the user. *n*-fold cross validation (as described below) is commonly used to evaluate the predictive performance because it has been shown to provide unbiased estimates, unlike other data splitting methods (Olden and Jackson 2000). In general, a small number of hidden nodes should be used to improve generalization and reduce training time (Ozesmi and Ozesmi 1999).

Finally, the scaling of predictors and responses prior to use in the NN can impact the training, results, and interpretation of the model (Bishop 1995, Sarle 1997). While not strictly necessary from a theoretical perspective, the predictors should be standardized to a similar measurement scale (e.g., z-score: subtract mean and divide by standard deviation). Such scaling can speed up convergence of the gradient descent in the backpropagation algorithm (Sarle 1997), reduce numerical errors due to computation with finite precision, and facilitate interpretation of the final weights for predictor contribution analyses (similar to analysis of regression coefficients; Olden and Jackson 2001; Ozesmi and Ozesmi 1999). The response variables should be scaled to reflect their relative importance. If they are all equally important, the outputs should be scaled to the same range (often [0,1], see Appendix E.1) or standard deviation so that the NN does not spend effort learning the one with the highest values to the exclusion of the others (Basheer and Hajmeer 2000). Table E.1 in Appendix E.1 lists the modelling decisions (e.g., number of hidden nodes, training/testing procedures, scaling) and rationale (where discussed) for applications of NN, with a focus on regression-type problems in marine ecology.

4.3.3 Neural Networks: Application

4.3.3.1 Zero Delay Analysis

I used a one hidden layer feedforward MLP trained by resilient backpropagation with weight backtracking (Joy and Death 2004, Fritsch and Guenther 2012). The predictors were the nine pressures (Table 2; Fig. 4.3), centered and scaled by their respective mean and standard deviation. The responses were the biomass indices of the six fish functional groups, logged to account for the skewed nature of trawl biomass, and then linearly mapped to the interval [0,1] (Fig. 4.2). I chose a sigmoidal logistic function for the hidden nodes (Fig. 4.5; Equation 4.2), one of the most common choices of activation function (Appendix E.1). The output nodes had a linear activation function, which is recommended for regression problems where the response is unbounded (Sarle 1997, Palacz et al. 2013).

$$f(x) = \frac{1}{1+e^{-x}} \tag{4.2}$$

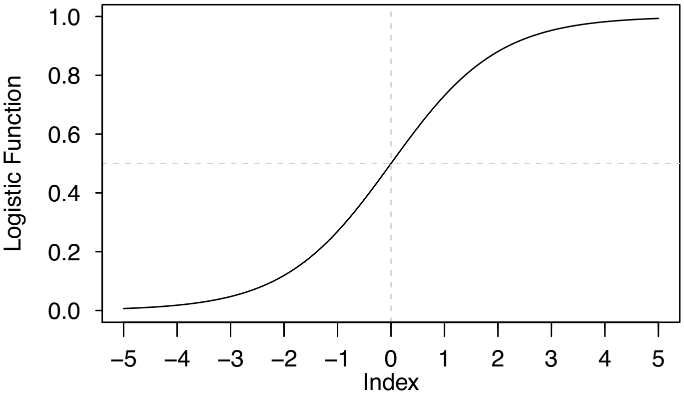


Figure 4.5: The sigmoidal logistic function, a common choice of activation function. Applied in the present analysis as the activation function in the hidden nodes.

I used the sum of squared errors (SSE; Equation 4.3) as the error function (another common choice; Appendix E.1), where *n* is the number of observations, the y_j are the observed values, and the $\hat{y}_j$ are the modelled values. Finally, the maximum number of iterations was set to 10^4, and all models converged. All NN were trained and tested using the neuralnet package in R (Günther and Fritsch 2010, Fritsch and Guenther 2012, R Core Team 2015).

$$SSE = \sum_{j=1}^{n} \left(y_j - \hat{y}_j\right)^2 \tag{4.3}$$

An *n*-fold cross validation procedure was used to inform the decision of the number of hidden nodes to include for each time period, and to assess the predictive power (i.e., ability to model out-of-sample data) of each model (Zhou 2003). I chose *n*-fold cross validation over other procedures based on the recommendation in Olden 2000, and because preliminary attempts at block validation showed the results were highly sensitive to the number of observations in each block. First, the network was trained on *n* – 1 observations, and tested on the remaining one. This was repeated *n* times, such that each observation was used as test data, and an average goodness of fit for both the training and test data was recorded. To address the potential variability caused by choosing different initial weights, I used a model ensemble approach (e.g., Zhou 2003, de Ona and Garrido 2014, Krekoukiotis et al. 2016). The training procedure was repeated with 35 different sets of initial weights (following Krekoukiotis et al. 2016), assigned randomly from a uniform distribution on the range of [-0.3, 0.3] (Lek et al. 1995, Aoki and Komatsu 1997). The range and average mean squared error (MSE; Equation 4.4) of the 35 trials for both the training data ($\overline{\text{MSE}}_{\text{Train}}$) and the test data ($\overline{\text{MSE}}_{\text{Test}}$) were recorded. This procedure was performed with 1 to 10 hidden nodes, and I chose the number that minimized $\overline{\text{MSE}}_{\text{Test}}$ for each period. Differences in MSE > 0.050 were considered "notable."

$$MSE = \frac{1}{n} * SSE \tag{4.4}$$

To assess the relative importance of each predictor, I trained an ensemble using the optimal number of hidden nodes and all of the observations, where each ensemble consisted of 35 models trained with different initial weights (Krekoukiotis et al. 2016). The percent contribution of each predictor to each response was evaluated for each ensemble using the product of connection weights method (PCW; Olden and Jackson 2002, Olden et al. 2004), modified for multivariate responses and an ensemble method. PCW performed the best in a previous comparison of different methods for quantifying variable importance in NN (Olden et al. 2004), and preserves the sign of the relationship between variables (i.e., signifies the nature of the relationship like the correlation coefficient in linear regression; Olden and Jackson 2002, Olden et al. 2004). The PCW assigns a relative importance (RI) for a given predictor-response pair by summing together the product of the input-hidden and hidden-output weights for all hidden nodes. Because this method assigns a *relative* importance to the input variables, the raw RI values should not be compared between models (Beck 2016). To use this method with the ensemble approach, I converted the RIs to percent contributions, and then reported the average value over the ensemble (Olden et al. 2006). To calculate the percent contribution of predictor *i* to response *j*, I divided $\text{RI}_{i,j}$ (RI of predictor *i* to response *j*) by the total contribution to response *j* (sum of the absolute values of the RI of each predictor to response *j*; Equation 4.5):

$$\%Contribution_{i,j} = \frac{\sum_{k=1}^{h} w_{i,k} * w_{k,j}}{\sum_{q=1}^{p} abs\left(\sum_{k=1}^{h} w_{q,k} * w_{k,j}\right)} * 100\% = \frac{RI_{i,j}}{\sum_{q=1}^{p} abs\left(RI_{q,j}\right)} * 100\% \tag{4.5}$$

where h is the number of hidden nodes and p is the number of predictors. I considered a predictor to be “influential” if it had an average percent contribution >10.0% for at least three of the functional groups. The raw RI values were calculated using the NeuralNetTools package in R (Beck 2016); %Contributions were calculated using original script written in R Version 3.2.0 (R Core Team 2015).

For a NN with only 1 hidden node, a given predictor will have the same magnitude contribution to each response (although the sign can differ). This is because $w_{1,o}$ (the weight from the single hidden node to the given output) can be factored out of the numerator and denominator of Equation 4.5, leaving only:

$$\%Contribution_{i,j} = \frac{w_{i,1}}{\sum_{q=1}^{p} abs(w_{q,1})} * 100\% \tag{4.6}$$

which does not depend on the output of interest. However, because the sign of the contribution can be different, there may be some discrepancy in the contributions to each response over the entire ensemble.

4.3.3.2 Delay Analysis

I repeated the analysis using two different methods of incorporating delays in the predictors: moving averages and lags (Dempsey et al. 2018), and considered delay lengths from $k = 1$ to $k = 10$ years (Appendix E.2), based on the recommendation in Chapter 3 (Dempsey et al. 2018). The delay type and length for which each pressure has maximum impacts on the fish community is unknown, and so I chose to impose the same delay on each pressure in a given model (Chen and Ware 1999). Avg*k* refers to the set of moving average predictors at delay length k (values calculated as the average of the current year and the previous k years), while Lag*k* refers to the set of lag predictors at delay length k (values shifted forward k years). These methods did not reduce the length of the time series because the predictors have longer historical data records than the responses (Fig. 4.3). “Zero delay” (ZD) refers to the original ($k = 0$) predictors.

4.3.3.3 Forecast Ability

The predictive power of the *n*-fold cross validation provides an estimate of how well the model will perform on out-of-sample data and can be roughly interpreted as a metric of the model's ability to forecast. To further investigate the forecast ability, I separated the observations into training data (first 24 years) and test data (remaining 5 years). The NN ensemble was fit using the training observations (with the predictors standardized and responses linearly mapped to the interval [0,1] as above), and then used to predict the test data response matrix. Each column of the test data predictor matrix was standardized (i.e., "centered" and scaled) using the mean and standard deviation of the corresponding column of the training predictor matrix. Similarly, the mapping of the test data response matrix was based on the maximum and minimum values of the corresponding column from the training matrix. Note that this can result in response test values outside of the range [0,1] if the maximum or minimum observation occurs in the test data.

To compare the *n*-fold and forecast models, I calculated the $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ for each functional group from the observed values and the average predicted values from the ensemble for: (i) all values of the *n*-fold procedure, (ii) the last 5 years of the *n*-fold procedure (nfold-5), and (iii) the 5 test values of the forecast model (forecast-5).

4.4 Results

4.4.1 Zero delay

4.4.1.1 n-fold cross validation

As expected, the $\overline{\mathrm{MSE}}_{\mathrm{Train}}$ decreased as the number of hidden nodes increased for each period, reaching nearly zero ($\overline{\mathrm{MSE}}_{\mathrm{Train}} < 0.01$) with 9 nodes for Full, 5 for Before, and 7 for After (Fig. 4.6). The range of $\overline{\mathrm{MSE}}_{\mathrm{Train}}$ over the ensemble was negligible in all cases (range < 0.05). The $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ were more variable, and were all higher than the corresponding $\overline{\mathrm{MSE}}_{\mathrm{Train}}$ (Fig. 4.6). The $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ for the Full period were lower than most of those for the other periods, suggesting that models constructed for the Full period have better predictive power. The Full $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ was minimized with 2 hidden nodes, although 1 hidden node was not notably worse. The $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ for both the Before and After periods was minimized with only 1 hidden node.

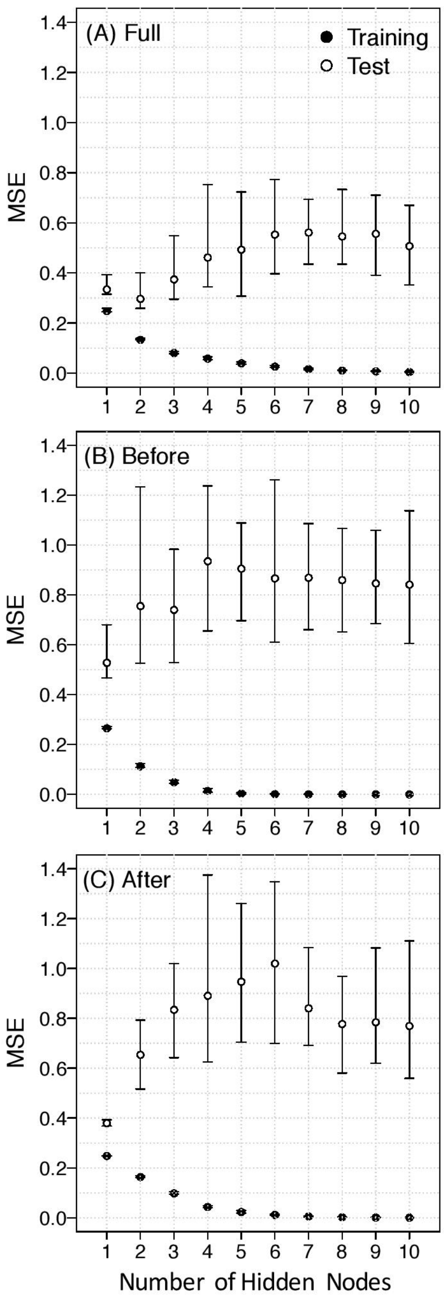


Figure 4.6: *n*-fold cross validation results for each period using zero delay predictors: mean (points) and range (lines) of the $\overline{\text{MSE}}_{\text{Train}}$ and $\overline{\text{MSE}}_{\text{Test}}$ for a given number of hidden nodes. (A) Full period, (B) Before and (C) After the collapse. Note that the range of $\overline{\text{MSE}}_{\text{Train}}$ is so small that is not visible at this scale.

4.4.1.2 Predictor Contributions

For the Full period predictor contribution analysis, I first trained an ensemble with 2 hidden nodes, and then repeated the analysis with 1 hidden node to test the sensitivity of the results (Figs. 4.6A and 4.6B). The 2-hidden node ensemble highlighted four influential variables: total, pelagic, and shellfish landings, and bottom salinity (Fig. 4.7A). Total landings had positive relationships with large and small benthivores and negative relationships with the other functional groups, while the remaining influential pressures had positive relationships with all of the functional groups except small benthivores. The 1-hidden node ensemble also highlighted three fishing pressures, although pelagic landings was replaced by MTI. Two different environmental pressures were included: NAO and Time_{Ice} (Fig. 4.7B). These results suggest that the most influential pressures are sensitive to the number of hidden nodes.

The Before period had similar influential pressures as the Full period trained with 2 hidden nodes: total landings, shellfish landings, SST, and bottom salinity (Fig. 4.7C). Total landings and bottom salinity had negative relationships with small benthivores and plank-piscivores, and positive relationships with the other functional groups; shellfish landings and SST had the opposite relationships. Shellfish landings was the only pressure also highlighted for the After period, and it had opposite relationships to most functional groups in the two periods. Four other pressures were considered influential for the After period: pelagic landings, MTI, NAO, and SSS (Fig. 4.7D). SSS had a positive relationship with small benthivores, and negative relationships with the other functional groups. In contrast, the other influential predictors had positive relationships with all of the functional groups except small benthivores.

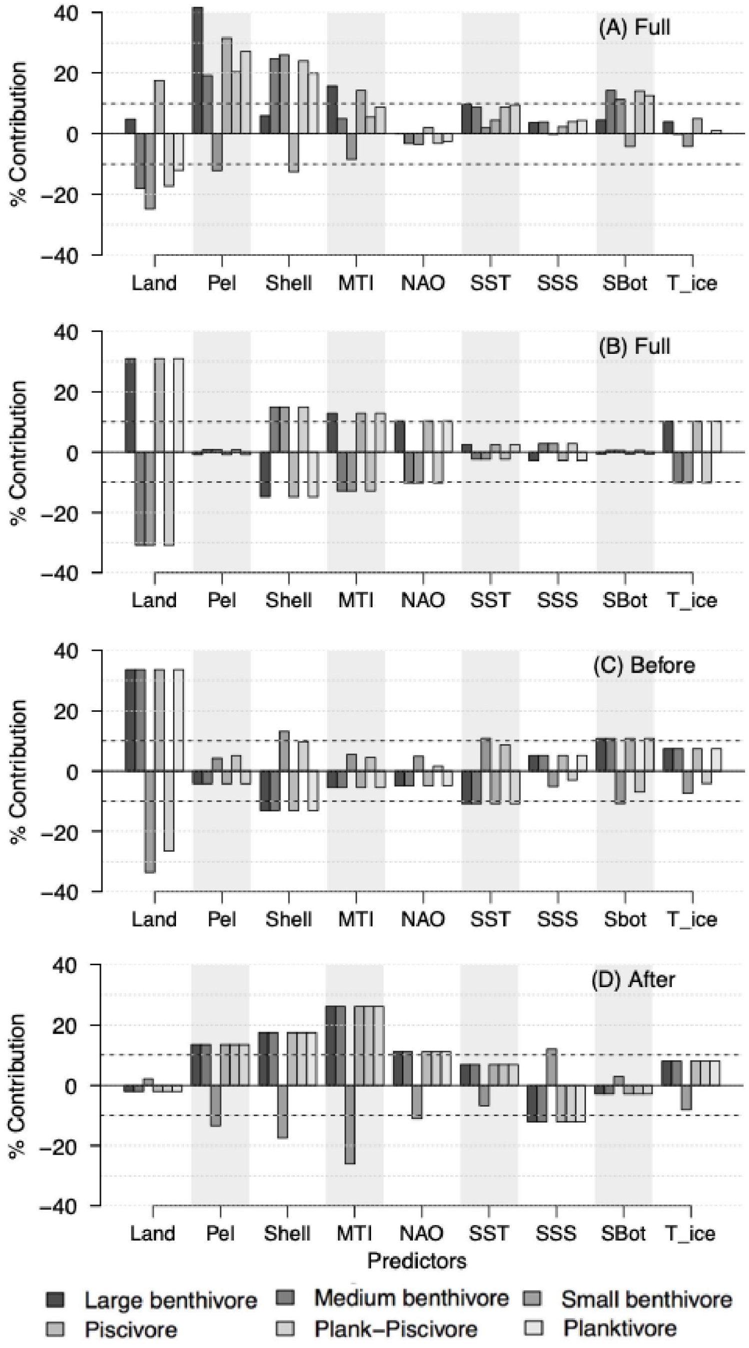


Figure 4.7: Average percent contributions of each ZD predictor to each functional group. The thick dashed line indicates average contribution of 10%. (A) Full period, 2 hidden nodes; (B) Full period, 1 hidden node; (C) Before period, 1 hidden node; (D) After period, 1 hidden node.

4.4.2 Delay Analysis

4.4.2.1 n-fold cross validation

Models with 1 hidden node resulted in the minimum $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ (or an $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ not notably different from the minimum) in most cases of the *n*-fold cross validation procedure with delayed predictors (not shown). For consistency, the delay models analyzed here are 1-hidden node ensembles (Zhou 2003).

There were no notable differences in $\overline{\mathrm{MSE}}_{\mathrm{Train}}$ within a given period for any type or length of delay, and very few between the periods (Fig. 4.8A). The similarity of the $\overline{\mathrm{MSE}}_{\mathrm{Train}}$ across types and lengths of time delays illustrates the ability of small NN to extract patterns from differing inputs to fit the same responses. Differences in $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ were more prevalent, and the Avg models generally had better $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ than the Lag models for a given period and delay length.

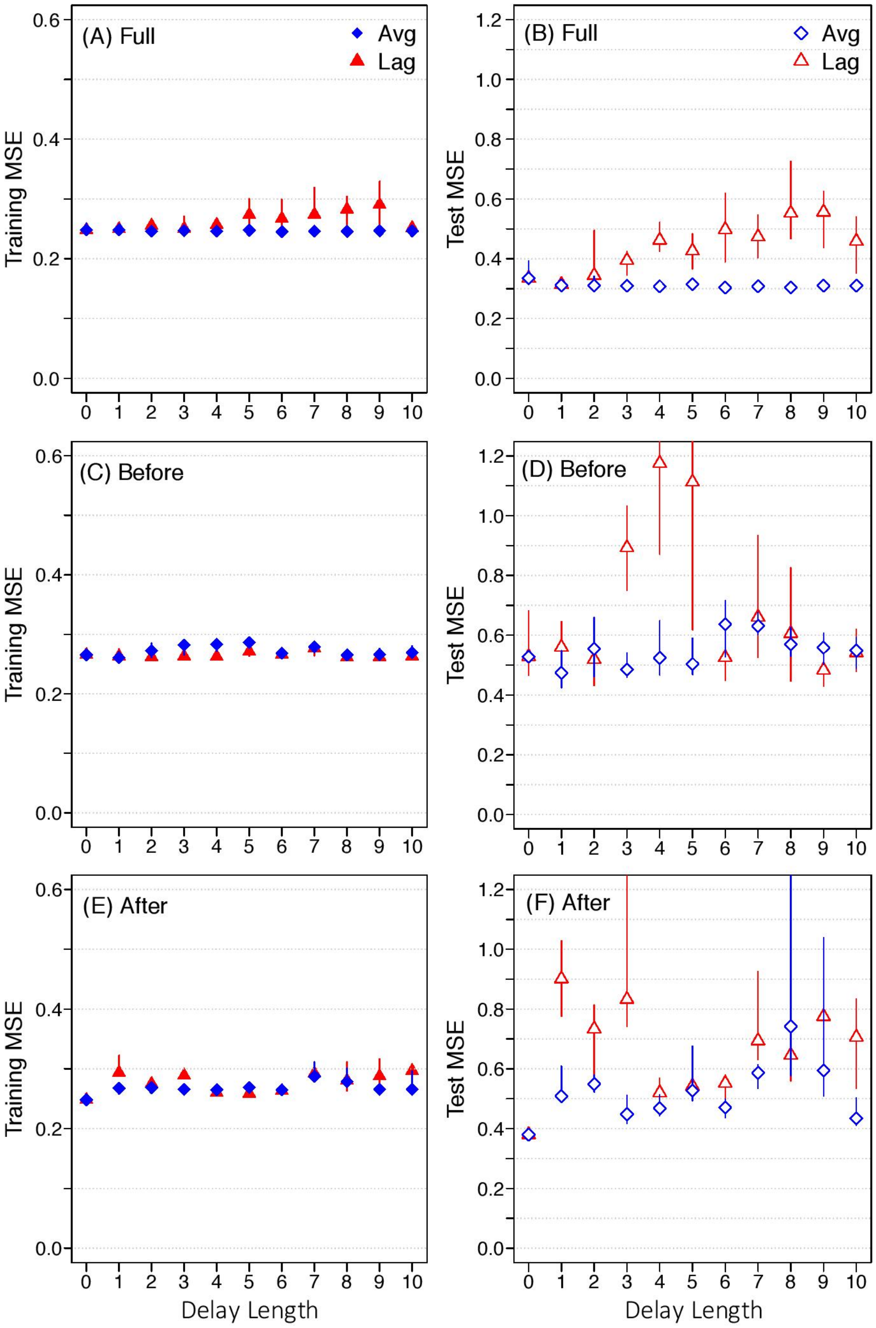
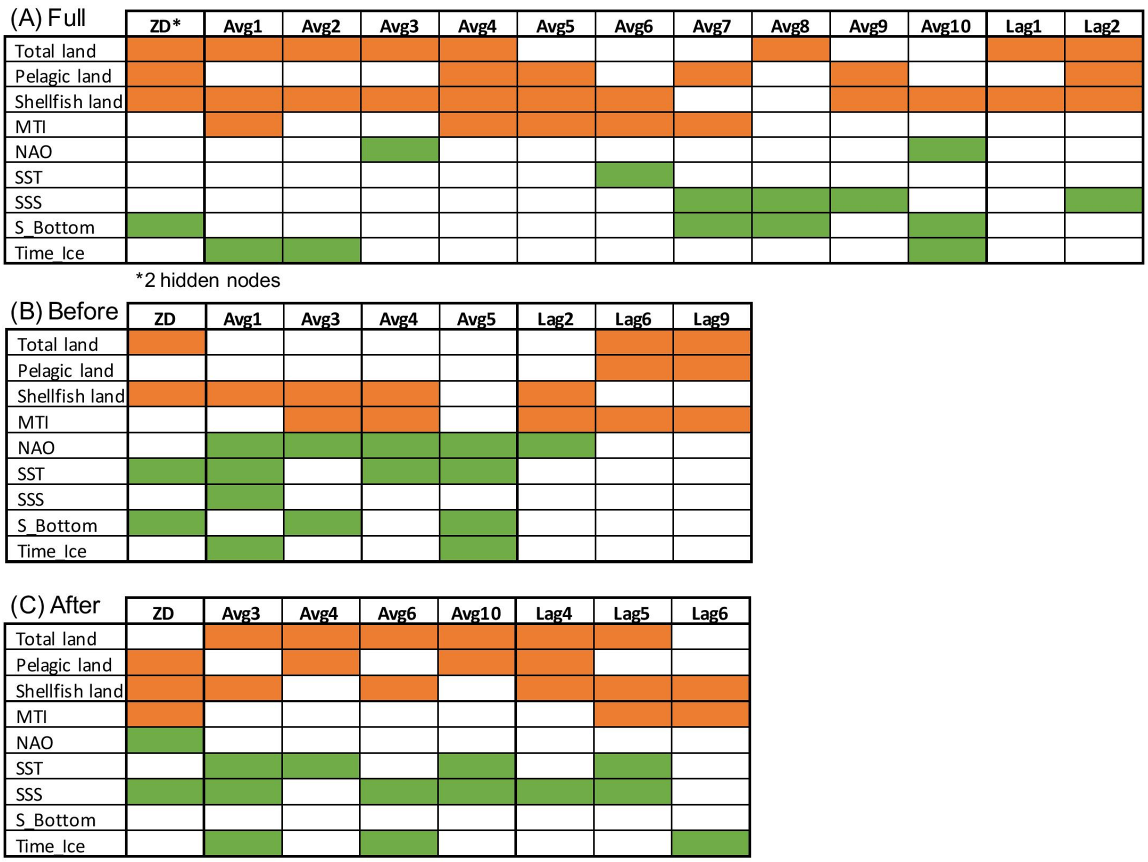


Figure 4.8: (A) – (C) $\overline{\mathrm{MSE}}_{\mathrm{Train}}$ and (D) – (F) $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ from the cross validation procedure of models with delayed predictors (1 hidden node). Note the difference in scale between the left and right columns.

4.4.2.2 Predictor Contributions

Here I describe the predictor contribution results from the “best” models, which I consider as the delay lengths resulting in $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ that were not notably different than the lowest $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ within each period and delay type. I summarized the results for each period in a single figure (Fig. 4.9).

For the Full period, none of the moving average models were notably different than the best model (Fig. 4.8A), although different influential pressure sets were highlighted for each delay length (Fig. 4.9A). Overall, more fishing than environmental pressures were included, with shellfish landings being the most frequent, followed by total landings and the MTI. Only fishing pressures were highlighted at two delay lengths (Avg4 and Avg5). Salinity (surface and bottom) and $\mathrm{Time}_{\mathrm{Ice}}$ were the most frequent environmental pressures. The best Lag models for the Full period were Lag1, which highlighted two fishing pressures, and Lag2, which highlighted one additional fishing and environmental pressure (Fig. 4.9A). The best Before Avg models were Avg1, Avg3, Avg4, and Avg5 (Fig. 4.7B), and more environmental pressures were influential (Fig. 4.9B). NAO was included in all four models, and SST included in three. Avg5 included only environmental pressures. In contrast, fishing pressures were more frequent in the best Lag models for this period (Lag2, Lag6, and Lag9). Lag6 and Lag9 included only fishing pressures, while Lag2 included two fishing pressures, and one environmental. For the After period, the ZD models had the lowest $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ (Fig. 4.8C), which was notably better than all delay types and lengths. Disregarding ZD, the best Avg models included a broad range of delay lengths (Avg3, Avg4, Avg6, Avg10). These models all highlight both fishing and environmental pressures, with total landings included in all four (Fig. 4.9C). The best Lag models were Lag4, Lag5, and Lag6 (Fig. 4.8C), which also highlighted both fishing and environmental pressures, with shellfish landings included in all three (Fig. 4.9C). The inclusion of both fishing and environmental pressures for most of the best delay models over the Full period and each period separately suggests that both top-down and bottom-up pressures are measurably impacting the fish community in this region. Additionally, the results suggest that pressures can be manifest in the fish community on short (i.e., “immediate”) and longer time scales (up to 10 years based on this analysis).



(A) Full

	ZD*	Avg1	Avg2	Avg3	Avg4	Avg5	Avg6	Avg7	Avg8	Avg9	Avg10	Lag1	Lag2
Total land	🟧	🟧	🟧	🟧	🟧				🟧			🟧	🟧
Pelagic land	🟧				🟧	🟧		🟧		🟧			🟧
Shellfish land	🟧	🟧	🟧	🟧	🟧	🟧	🟧			🟧	🟧	🟧	🟧
MTI		🟧			🟧	🟧	🟧	🟧					
NAO				🟩							🟩		
SST							🟩						
SSS								🟩	🟩	🟩			🟩
S_Bottom	🟩							🟩	🟩		🟩		
Time_Ice		🟩	🟩								🟩		

*2 hidden nodes

(B) Before

	ZD	Avg1	Avg3	Avg4	Avg5	Lag2	Lag6	Lag9
Total land	🟧						🟧	🟧
Pelagic land							🟧	🟧
Shellfish land	🟧	🟧	🟧	🟧		🟧		
MTI			🟧	🟧		🟧	🟧	🟧
NAO		🟩	🟩	🟩	🟩	🟩		
SST	🟩	🟩		🟩	🟩			
SSS		🟩						
S_Bottom	🟩		🟩		🟩			
Time_Ice		🟩			🟩			

(C) After

	ZD	Avg3	Avg4	Avg6	Avg10	Lag4	Lag5	Lag6
Total land		🟧	🟧	🟧	🟧	🟧	🟧	
Pelagic land	🟧		🟧		🟧	🟧		
Shellfish land	🟧	🟧		🟧		🟧	🟧	🟧
MTI	🟧						🟧	🟧
NAO	🟩							
SST		🟩	🟩		🟩		🟩	
SSS	🟩	🟩		🟩	🟩	🟩	🟩	
S_Bottom								
Time_Ice		🟩		🟩				🟩

Figure 4.9: Most influential pressures for the ZD and best delay models for each period. Orange shading indicates influential fishing pressures; green shading indicates influential environmental pressures. (A) Full period; (B) Before period; (C) After period. Note that "land" and "S_bottom" stand for "landings" and "bottom salinity," respectively.

4.4.3 Reduced Models

I compared $\overline{\text{MSE}}_{\text{Train}}$ and $\overline{\text{MSE}}_{\text{Test}}$ of models using all predictors (9-predictor models) to those using only the most influential predictors (reduced models; Fig. 4.10) for the ZD and best delay models. For all three periods and delay types, the difference between $\overline{\text{MSE}}_{\text{Train}}$ of the 9-predictor and the reduced models was negligible (Appendix E.2). The same was true for the $\overline{\text{MSE}}_{\text{Test}}$ for the Full period, and most Before models (Fig. 4.10). In contrast, for the After period the reduced models were either notably better or not notably different than the corresponding 9-predictor models.

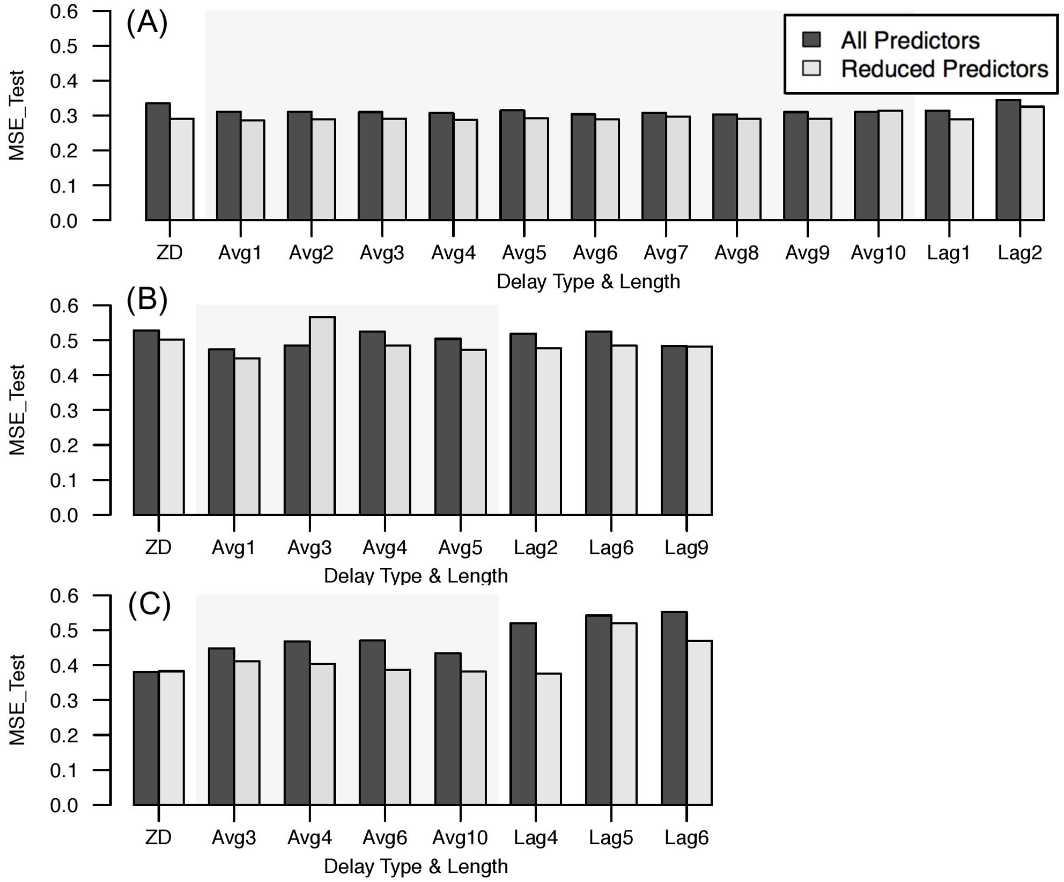


Figure 4.10: $\overline{\text{MSE}}_{\text{Test}}$ of the best delays for each period. Dark grey represents the models trained with all predictors; light grey represents the models trained with the reduced predictor set (i.e., only the most influential pressures for the given delay). (A) Full period; (B) Before period; (C) After period. Faint shaded box indicators the moving average models (to differentiated from ZD and lag).

4.4.4 Forecast Potential

To include the maximum number of observations for training, I assessed the forecast potential using the Full period (ZD, 2 hidden nodes, all pressures). The *n*-fold cross validation showed that the model was able to capture the general trends in each functional group, although there were some obvious discrepancies (e.g., in the early 1990s for large benthivores and piscivores; Fig. 4.11A). The main exception was plank-piscivores, for which the model had difficulty predicting the inter-annual variability. The 5-year forecast model also performed poorly for the plank-piscivores, underestimating the biomass by about 50% for each year, perhaps because the test observations were near or above the maximum value included in the training data. The forecasts were variable for the other functional groups, under-estimating piscivore biomass for several years, over-estimating small benthivore biomass, and predicting planktivore biomass noticeably well.

In general, the $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ of the *n*-fold cross validation was not notably different than the $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ of the nfold-5 or forecast-5 for a given functional group (Fig. 4.12). The sole exception was plank-piscivores, for which the *n*-fold $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ was notably worse than that of the nfold-5, but notably better than that of the forecast-5. Note that $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ comparisons among functional groups should be made with caution because the error represents a different fraction of total sum of squares for each functional group. Here, some general observations can be made that are supported by visual observations from Fig. 4.11. For example, plank-piscivores were modelled relatively poorly, while large benthivores were modelled relatively well.

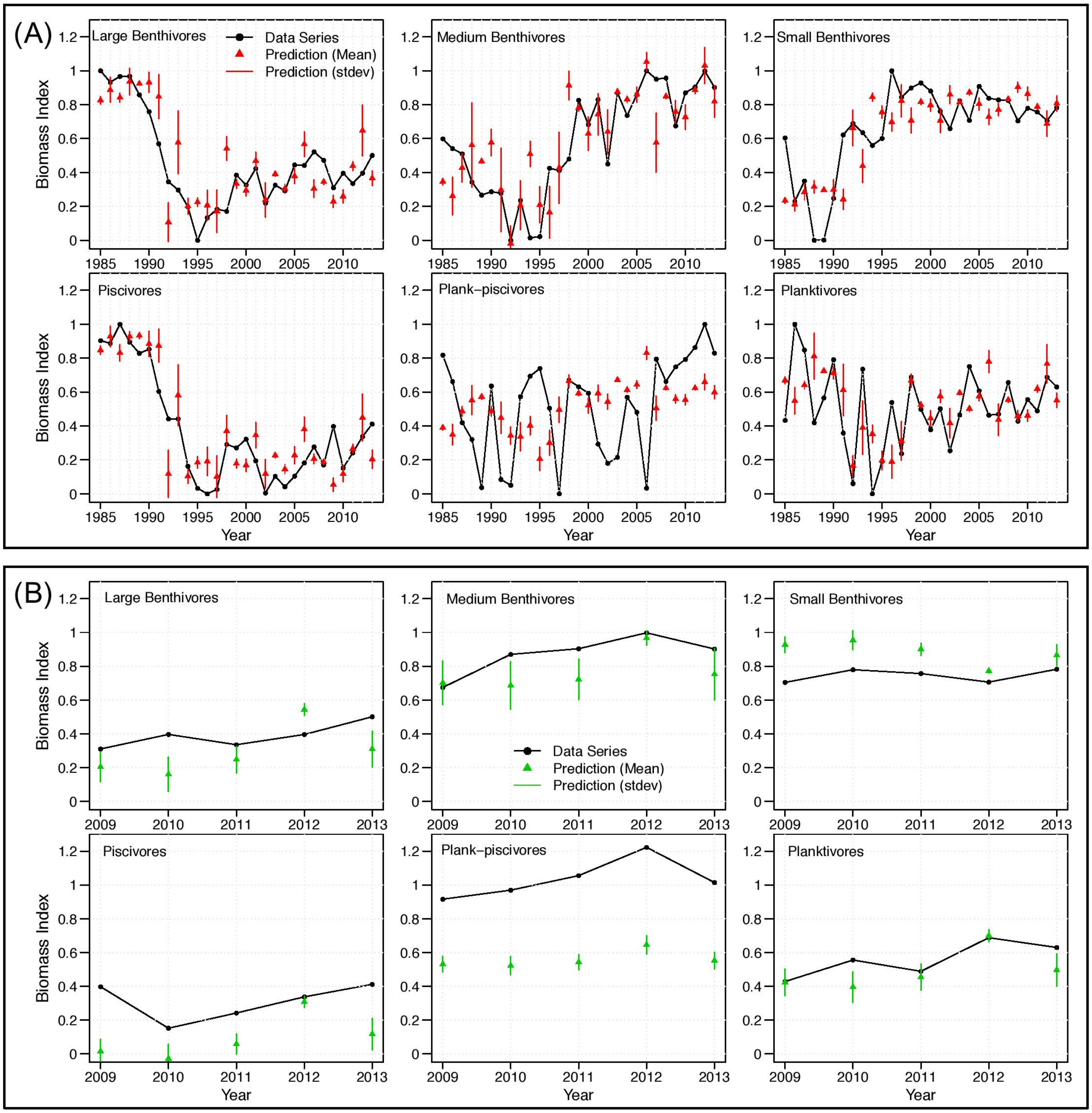


Figure 4.11: (A) Average and standard deviation of the test values of the n-fold cross validation predictions for each functional group over the Full period using ZD predictors (2 hidden nodes). (B) Average and standard deviation of predictions for the last five years of data for each functional group using ZD predictors (2 hidden nodes).

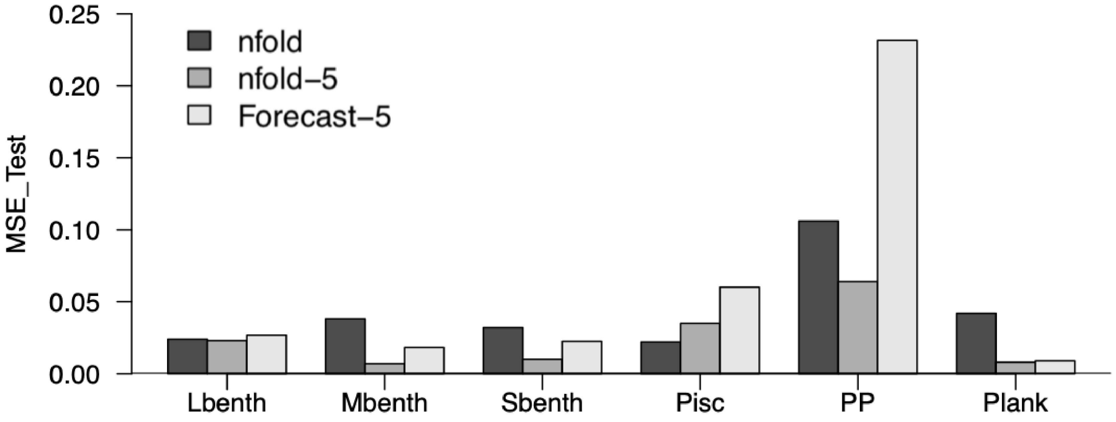


Figure 4.12: Mean squared error of the predictions for each functional group over the Full period using ZD predictors for the three prediction cases. (Lbenth = large benthivores; Mbenth = medium benthivores; Sbenth = small benthivores; Pisc = piscivores; PP = plank-piscivores; Plank = planktivores.)

4.5 Discussion

The cause of the collapse of groundfish biomass on the Newfoundland-Labrador shelf has been highly debated, particularly for commercially important species such as cod. Some authors conclude that fishing pressure was the main cause of the collapse (Myers et al. 1996, 1997), while others argue that the poor environmental conditions played a larger role (e.g., Parsons and Lear 2001, Rothschild 2007, Halliday and Pinhorn 2009). Still others have shown that the combination of heavy fishing and harsh environmental conditions were necessary for the pervasive changes that occurred in the region (e.g., Mann and Drinkwater 1994, Koen-Alonso et al. 2010b, Dempsey et al. 2018). The findings here support the latter theory by highlighting both fishing metrics and environmental conditions as influential pressures Before (i.e., during) the collapse (Fig. 4.9B). The functional groups have been recovering at different rates After the collapse, such that the community biomass is now more evenly spread over several groups, rather than being piscivore-dominated (e.g., Dempsey et al. 2017). This has been described as an ecologically different period than Before the collapse (Buren et al. 2014, Dempsey et al. 2017, 2018). The analysis supports this description by highlighting different influential pressures for each period (Fig. 4.9).

For the Before and Full periods, models with delayed pressures were the best overall, although the ZD models were not notably different. In apparent contrast, the ZD model had the best predictive power for the After period, and was notably better than all of the other delays (for the 9-predictor models; Fig 4.7C). This suggests that post-collapse, the primary impacts of the pressures were manifest in the community on very short timescales (<1 year), for example through fishing activity, which has an immediate effect by directly removing biomass. Pelagic and shellfish landings and MTI were all considered influential at this time, pointing to continued fishing in the region as a significant immediate pressure on the community. However, the reduced models for this period suggest that there are also significant delayed impacts on the community. Most of the After reduced models improved the predictive power significantly (compared to models with all pressures), such that their $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ was not notably different from the ZD model (Fig. 4.10C). This is a non-intuitive result and implies that pressures included in the full suite misdirected the model. MTI, NAO, and bottom salinity were not included in most of the After period reduced models, suggesting they represent signals that weaken the predictive power of the NN for this period. This is an interesting result, particularly for NAO, which was considered an influential pressure for the ZD After ensemble and for most of the best Before delay ensembles. It suggests that the fish community was less dependent on basin-scale processes in the After period, and highlights the differences between the two periods. Together, the results for all three periods suggest that a combination of current and past pressures influence the fish community on the Grand Bank, and illustrate the complexity of teasing them apart. Future analyses could explore incorporating both ZD and delayed pressures into the same model, which could potentially improve the fit and predictive power (Mann and Drinkwater 1994).

Shellfish landings was the only common influential ZD pressure for the Before and After periods, and it was included in most of the best delay models for all three periods. This supports and adds to the findings of the MLR, which also identified shellfish landings as an important predictor for the After ZD and several Before and After delay models. This is a curious result because the community shellfish biomass index – which one would expect to be the primary correlate – was not included as a response for any of these analyses. To investigate, I review some historical changes in shellfish landings that are not explicitly reflected by the pressure indicator. There are three main types of shellfish landed on the Grand Bank (Fig. 4.12): snow crab and *Pandalus* shrimp, which are mainly caught in the more northern region of the study area, and clams (plus other molluscs), which are mainly harvested in the more southern region. Throughout the 1970s and 1980s, most of the fishing effort in the region targeted groundfish. Shellfish landings were limited, and consisted mainly of snow crab caught in baited traps (DFO 2010). Snow crab landings increased until the late 1990s, and it continues to be the most landed shellfish species by biomass. Hydraulic dredging of clams began in the late 1980s, and there have been two main peaks in these landings: one from 1990 – 1996, and a smaller one from 2001 – 2006 (Fig. 4.12). After the groundfish moratoria in 1994, many harvesters began targeting shrimp using bottom trawls, and total shellfish landings continued to increase, as reflected by the indicator (Fig. 4.3). Shrimp landings increased rapidly throughout the 2000s, but have declined since 2010, and the fishery was closed in 2015. The precise mechanism(s) through which these landings impact the functional groups is unknown, but based on the changes in the main shellfish species landed over time (Fig. 4.12), there could be different mechanisms Before and After the collapse. Shrimp are considered an important forage species in the region for cod and other groundfish (i.e., piscivores and benthivores; DFO 2018), so one simple explanation is that fishing reduces the food available to key species within the functional groups (Koen-Alonso et al. 2010b, Dempsey et al. 2018). Another explanation is that fishing for shellfish has a negative physical impact on the habitat of other species. A panel of 97 stakeholders (fishermen, scientists, conservation professionals, and managers) ranked bottom trawls and dredging in the top three “most destructive” fishing gears (out of 11 gears; Fuller et al. 2008). It is also possible that shellfish landings act as a proxy for another pressure not identified here. For example, groundfish landings are highly negatively correlated (Pearson correlation coefficient < -0.80) with shellfish landings over the Full and Before periods, so the shellfish pressure could be reflecting groundfish landings. The same does not hold true for the After period, for which these pressures are essentially uncorrelated (correlation = -0.02). For more insight into the mechanism(s) relating shellfish landings to the fish functional groups included here, it may be useful to consult additional fishing indicators that account for changes in effort, gear type, and/or spatial considerations. The findings suggest that more research should be done to identify the effects of shellfish exploitation on the broader fish community.

The results clearly indicate that the Grand Bank fish community has been impacted by fishing over the Full study period. All of the ZD and best delay models included at least one fishing pressure, and three included only fishing pressures (Fig. 4.9A). As discussed above, shellfish landings were an important fishing pressure indicator over this period, as were total landings. Here I note that landings in the region are regulated in part through total allowable catches (TACs), which in turn are based on the stock assessments of the target species (i.e., includes consideration of the stock biomass). While this cyclic relationship could potentially confound some analyses, the pressures and responses are suitably decoupled such that the interpretation and conclusions here are not erroneous. First, TACs are based on the status of individual stocks rather than the community or functional group level. Second, some functional groups are not targeted by fisheries (e.g., small benthivores). Conversely, shellfish landings are included as a pressure, but the shellfish functional group was not included as a response. Finally, total landings aggregates catches from several functional groups that change their correlation structures over time.

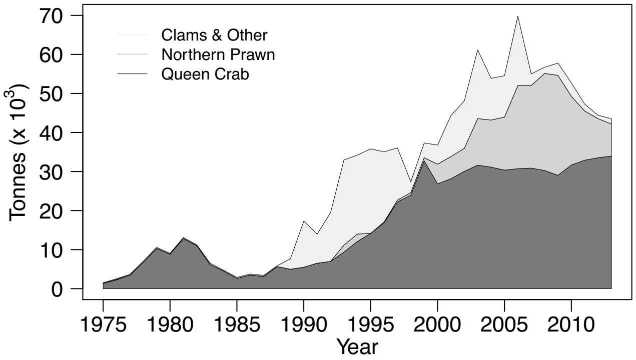


Figure 4.13: Shellfish landings from NAFO Division 3LNO (data from the NAFO Statlant 21A database).

Surface and bottom salinity were among the most frequently included environmental pressures over the Full period, each occurring in three moving average models at long delays, and one lag model for short delays. Changes in salinity could be related to changes in the freshwater content exported from the Arctic (Greene and Pershing 2007) that can impact primary and/or secondary production. In this analysis, salinity could be acting as a proxy for lower-trophic level dynamics. In other Northwest Atlantic ecosystems, changes in salinity have been linked to changes in the abundance and size structure of zooplankton communities (Pershing et al. 2005, Kane 2007), which in turn has been related to fish community dynamics, including recruitment regimes (Perretti et al. 2017), record high levels of planktivore biomass (Kane 2007), and recovery (or lack thereof) of commercially important species (Mountain and Kane 2010). On the Newfoundland shelf, changes in zooplankton community structure have been linked to water mass properties (e.g., Pepin et al. 2011, 2015), but the relationship with salinity is less well defined and thought to vary seasonally (Pepin et al. 2015). $\mathrm{Time}_{\mathrm{Ice}}$, which is linked to the timing and duration of the spring phytoplankton bloom, was also included in several models for this period. Together, the results suggest that both top-down and bottom-up forcing have influenced the fish community over the past several decades.

There were very few notable differences in fit within a given period for any type or length of delay imposed on the predictors (Fig. 4.8). The differences in fit between the periods were also negligible, although this should be interpreted with caution and is not discussed further because the error represents a different fraction of total sum of squares for each period. The MLR showed that moving average predictors generally had better explanatory power than lagged predictors, so it was surprising to find here that the delay type had negligible differences on the fit. This result perhaps speaks more to the ability of "simple" NNs (i.e., one hidden node) to extract patterns from data than to the dynamics of the fish community.

It is not trivial to choose a metric to compare the fits of the NN and MLR models. The adjusted-R^2 was used to evaluate the MLR models (Chapter 3; Dempsey et al. 2018), but this metric is based on the R^2 and is therefore not suitable for evaluating non-linear models (Appendix E.3; Kvalseth 1985, Spiess and Neumeyer 2010). The MSE, applied here to evaluate the NN model fit, is only useful if the responses are scaled the same for both approaches, *which may not be the case* for NN and MLR. As is common practice, in this thesis NN outputs were linearly mapped to the interval [0,1] to increase the speed of convergence of the backpropagation (gradient descent) algorithm, while MLR outputs were normalized to have zero mean and unit variance to reduce numerical errors. To compare with the NN fits, I re-ran the MLR all-possible-combinations analyses (Chapter 3; Dempsey et al. 2018) with the responses linearly mapped to [0,1]. I calculated the MSEs for the top 50 ZD models for each period and reported the average and best MSE of the assemblage (Fig. 4.14). I compared these to the average and best MSE of the NN ensemble trained on all observations. The average MSE of the MLR models was better than that of the NN ensemble for all three periods (although not notably so for the After period), and the best MLR model was notably better than that of the 1-hidden node NN ensemble for all three periods. The difference is particularly striking for the Before period, for which the best MLR model is about 60 times better than the best NN model. In Chapter 3 (Dempsey et al. 2018), I suggested that the exceptionally small error of the best MLR model for the Before period was caused by the high coherency among the pressures and responses during the collapse. I expected the NN to also take advantage of this coherency, but that does not appear to be the case.

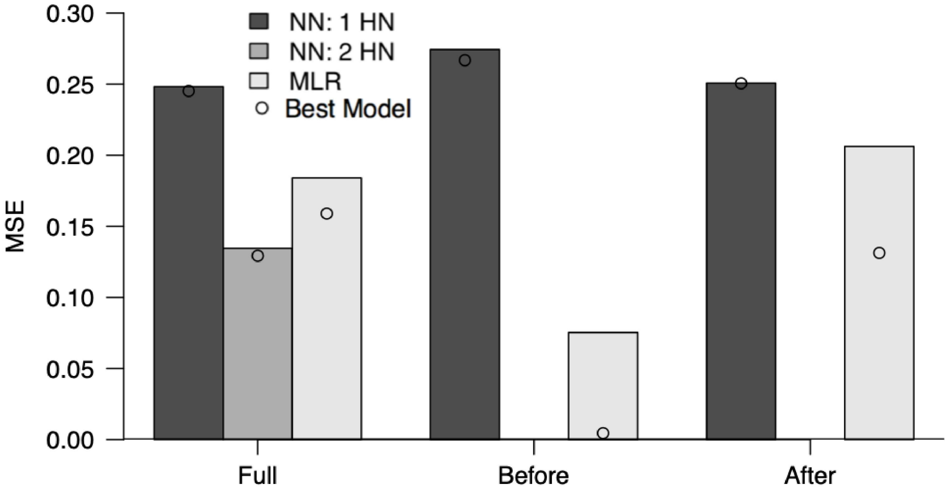


Figure 4.14: Average fit of the NN ensembles and top 50 MLR models for ZD pressures. Open circles indicate the overall best fit of each approach.

Considering the significant array of literature showing that NN outperform MLR for a variety of metrics and applications (Appendix E.1), the fact that the MLR resulted in better fit than NN was surprising. However, in the literature reviewed, it is more common to compare MLR and NN models with a single output rather than multiple outputs

(Appendix E.1). The current analysis illustrates that including multiple outputs can be more challenging for NN, which minimize the total error of all responses simultaneously (i.e., with one set of weights). In contrast, MLR minimizes the error for each response separately (i.e., each response has a unique set of coefficients) and reports the average goodness of fit. Future investigations could consider fitting a separate NN for each functional group and comparing the average of these MSEs to the MLR. However, the ability of the NN to fit multiple outputs with a single set of weights may be considered an advantage in an EBFM context because it implicitly accounts for the relationships among functional groups. Of course, increasing the number of hidden nodes in the NN can improve the fit to the data. Here, the average fit and best model for the 2-hidden node ensemble for the Full period were about the same as those of the MLR model for this period (Fig. 4.14). The NN fits for the Before and After periods could also be improved by including more hidden nodes. For example, for the After period, a 3-hidden node NN ensemble has an average fit that is notably better than the average MLR fit and about the same as the best MLR model. However, increasing the number of hidden nodes for these periods would sacrifice predictive power (Fig. 4.6), and potentially result in overfitting the data (i.e., modelling the noise as well as the signal). Additionally, the most influential pressures can be highly sensitive to the number of hidden nodes (Fig. 4.7A and B). Clearer guidelines on how to choose the number of hidden nodes for given application would be valuable for this type of situation, and may make this type of modelling more appealing to more ecologists. In the meantime, I recommend a careful consideration of the tradeoff between fit and predictive power (also called the “bias-variance dilemma”; Geman et al., 1992) for any NN application.

Because the differences in the fit of the NN ensembles were so slight, I used the *n*-fold cross validation predictive power ($\overline{\mathrm{MSE}}_{\mathrm{Test}}$) as the main metric for comparing the models within a given period. In general, the moving average predictors performed better at a given delay length than the lag predictors, although the best models for each delay type were often similar for a given period (Fig. 4.8). Comparisons of predictive power between periods should be made with caution for the same reason noted above. Overall, the Before period had the worst predictive power, which is likely due to the challenge of predicting the collapse from a short time series (only 10 observations for training). The

Full period performed notably better than both periods separately, even considering the improved $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ of the After reduced models. This suggests that forecasts of changes in the fish community should be made using a NN trained on the whole time series and not only observations from the After period.

In general, the $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ of the *n*-fold cross validation provided an accurate assessment of the predictive power of the model (Fig. 4.12), despite concerns about autocorrelation in the predictors and responses (e.g., the model knows the conditions before and after the observation omitted during the training). The preliminary analyses showed that the quality of the forecast differs among functional groups (Figs. 4.11, 4.12). The forecasts were particularly poor for the plank-piscivore functional group, which is dominated by deepwater redfish (*Sebastes mentella*; >95% by biomass on average over the Full period), a species that is notoriously difficult to sample (COSEWIC, 2010). This highlights a challenge of using survey-based indices: the index is assumed to be an accurate representation of reality, but there is inherent uncertainty associated with the sampling that these models are not considering. I suggest further rigorous investigations into the forecast abilities of such models for fisheries applications. Even if forecast ability remains variable, such analyses could inspire new investigations that provide additional scientific insight into the dynamics of the fish community. For example: What additional pressures improve forecasts for piscivores and plank-piscivores? Why were forecasts for medium benthivores so much better than for the other groups? Is it necessary to sacrifice forecast ability for one group to improve that of another? Forecasts using the NN method proposed here would require future projections of the pressures for the ZD and moving average predictors, because they incorporate information on the current year in the prediction. To reduce the reliance on such projections, it would be worth exploring whether the predictive power of lagged pressures can be improved by applying a low-pass filter to extract the trends prior to forecasting. Additionally, the forecast ability may be improved using pressure-specific delays, including the same pressure at different delay lengths to account for primary and secondary impacts, and/or building separate models for each functional group. I recommend further investigation into suitable delays and pressures for forecasting using additional statistical analyses and/or mechanistic models.

Both types of models discussed here were built with the same relatively small dataset of pressures and responses. Based on the current understanding of the Grand Bank ecosystem, these methods identified reasonable influential pressure sets for the three periods. The two approaches have the potential to inform EBFM in similar ways, for example in the "indicator development" step of an Integrated Ecosystem Assessment (Levin, 2009) or other indicator scoping exercises to highlight pressures that should be monitored throughout the management process. Results could also help focus studies of ecological thresholds and those characterizing pressure-response relationships (e.g., Large et al. 2015b, Hunsicker et al. 2016) by prioritizing which pressures should be included. Finally, they could help account for changes in the ecosystem over time by highlighting different influential pressures for ecologically disparate periods (Francis et al. 2007, Dempsey et al. 2018).

Each approach has advantages and disadvantages that should be considered prior to such applications. The main advantage of the MLR approach is that linear regression has been an accepted ecological tool for decades. It is readily understood by ecologists and relatively easy to explain results to decision makers. Its main disadvantage is the assumption that predictors and responses are linearly related, which is rarely the case for ecological interactions (Hunsicker et al. 2016). Linear models can represent non-linear relationships if transformations are applied to the predictors and/or responses, but the appropriate form of these relationships is generally unknown. In contrast, NN implicitly model non-linear relationships between predictors and responses, which is also an advantage over non-linear regression methods that require the user to specify the forms of the relationships. Another potential advantage in an EBFM context is that the NN algorithm finds one set of parameters that minimizes the total error of the responses, which may provide a more holistic representation of the interactions between functional groups. Finally, as demonstrated here, smaller predictor sets can have the same or better predictive power and fit than the full suite of predictors, which may prove advantageous in data-poor regions. However, NN are considered relatively complicated, and have been criticized as "black boxes," especially before methods for analyzing their weights were developed (e.g., Garson 1991, Olden and Jackson 2002). Perhaps the main disadvantage of NN is the absence of best practices for building and interpreting the model. Results can be sensitive to these modelling decisions, as illustrated by the influential pressures identified by the 1- and 2-hidden node ensembles for the Full period (Fig. 4.7). There is no universally accepted method of quantifying predictor contributions, and there has been recent criticism of the PCW method (Fischer 2015, Giam and Olden 2015). There is a wealth of literature on these subjects (Bishop 1995, Hagan et al. 2014), but these publications are often conflicting (e.g., Fischer 2015, Giam and Olden 2015), vague, and full of technical jargon. This may be prohibitive to some fisheries scientists and managers, who are not traditionally trained to use and interpret NN, and may partly explain why NN are not as common in ecology as some other fields (Olden 2008).

My results suggest that the MLR approach is better than the NN approach for this application. The MLR models had similar or better fit than the NN ensembles and were also easier to build and interpret. However, I recognize that NN have been shown to be powerful tools in other applications, and believe it is worth continuing to investigate how NN can be applied to fisheries management problems. For example, rather than focusing on the model fit, it may be useful to exploit the NN ability to generalize and continue investigating their forecast potential on management timescales. If NN can be shown to produce accurate forecasts using landings and environmental pressure data, they could be used as low-cost (in terms of data, and time to build, run, and analyze) strategic models to complement existing mechanistic modeling approaches. While I do not suggest that NN models can replace current mechanistic models, they may provide a viable alternative in data-poor regions, or in data-rich areas where such models are not yet operationalized (Link et al. 2010a, Olsen et al. 2016). The potential of NN suggests that at least a basic understanding should be in the modelling toolbox of ecologists, and their ability to inform the implementation of EBFM should be further explored.

CHAPTER 5: COMPARISON OF A LINEAR AND A NON-LINEAR APPROACH FOR EXPLAINING CHANGES IN THE GEORGES BANK FISH COMMUNITY

5.1 Abstract

Disentangling the impacts of multiple pressures on a fish community is inherently challenged by the dynamic, non-linear, multivariate nature of marine ecosystems. Here I compare multivariate linear regression (MLR) and non-linear neural networks (NN) for modelling the Georges Bank (US and Canada) fish community and identifying its most influential pressures. Nine fishing and environmental pressures were used to model the biomass indices of six fish functional groups using first MLR, and then NN. The most influential pressures were identified for the Full time series (1985 – 2012) and two periods that roughly correspond to important management changes in the region (1985 – 1995 and 1996 – 2012). The analyses were repeated with delays of different lengths (0 – 8 years) and types (moving average vs. lags) imposed on the predictors. MLR models were more straightforward to fit and interpret than the NN models, and also resulted in better fit, which suggests that the MLR approach is more suitable for this application. However, NN are considered skillful at out-of-sample predictions and may be able to provide complementary information through forecasts. Here, preliminary investigations of NN forecast ability suggest that *n*-fold cross validation provides a useful estimation of predictive power, particularly for short term forecasts, although future efforts are needed to improve these forecasts.

5.2 Introduction

Ecosystem based fisheries management (EBFM) is meant to supplement traditional single species assessments by explicitly considering interactions among fish species, multiple pressures on the community, and socio-ecological trade-offs (Link 2010). EBFM is generally accepted as necessary to prevent future fisheries collapses, and although implementation has been slow (Link et al. 2011a), it is supported by policy and legislation worldwide (e.g., Canada's Oceans Act; the United States Magnuson-Stevens Act; the European Marine Strategy Framework Directive). This holistic management approach requires substantial and diverse information on the ecosystem, which can be provided in part by data-based indicators of the fish community status and the pressures impacting it. Fish community indicators include metrics of biomass, trophic level, length and diversity, while pressure indicators include measures of fishing (e.g., landings, mortality, effort) and the environment (e.g., North Atlantic Oscillation, temperature). Hundreds of indicators have been proposed and vetted (Rice 2003, Cury and Christensen 2005), and significant effort has focussed on determining which fish community indicators are the most informative. Efforts to implement EBFM will benefit from improved understanding of multivariate pressure-response relationships, and in particular, methods to identify the most influential pressures on a fish community.

Disentangling the impacts and ranking the influences of different pressures acting on a fish community is challenged by the dynamic, multivariate nature of the ecosystem. To reduce this complexity, previous studies often focused on linear pressure-response relationships and/or univariate responses (e.g., Blanchard et al. 2005, Fu et al. 2012, Probst et al. 2012, Dempsey et al. 2018). However, individual pressures can impact multiple ecosystem components through cascading effects or different pathways, and multiple pressures can interact with each other with non-additive results (Large et al. 2013, Hunsicker et al. 2016). Identifying the most influential pressures is further complicated because both fishing and the environment as well as other pressures (e.g., predator-prey interactions) can result in non-linear responses (Daan et al. 2005, Hunsicker et al. 2016), and the functional form of these relationships is not generally known. Additionally, the relative importance of pressures may vary over time because of changes in management strategies, environmental conditions, and biological interactions (Mann and Drinkwater 1994). A further difficulty in teasing out important relationships is that changes in pressures can be manifest in the fish community over different timescales. For example, fishing has the immediate impact of increasing the mortality of the target and bycatch species, but can also impact the size distribution of the community over longer periods (Daan et al. 2005, Greenstreet et al. 2011).

The objective of this chapter was to asses a linear and a non-linear approach for explaining changes in the Georges Bank fish community and recommend the most useful approach for future analyses. I first compared multivariate linear regression (MLR) and neural networks (NN) as methods for modelling the Georges Bank fish community and identifying its most influential pressures. I used the results to make inferences about the dynamics of this fish community, evaluate forecast potential, and make recommendations as to which method should be used in future studies. Georges Bank is a highly productive ecosystem in the Northwest Atlantic, with commercial fisheries for scallops, haddock and other species. Complex ecological changes and management responses have occurred in the region over the past few decades (as discussed below). It has long garnered interest from the scientific community, and there exist relatively long time series of many ecological indicators. For example, Georges Bank was a focus of the U.S. GLOBEC (GLOBal Ocean ECosystems Dynamics) program, which was implemented in the 1990s with the aim of understanding how climate change will influence the structure and function of marine ecosystems and fisheries. The International Council for the Exploration of the Seas (ICES) Working Group on the Northwest Atlantic Regional Sea (WGNARS) is currently using Georges Bank as a case study in their work on providing scientific support for Integrated Ecosystem Assessments (one component of EBFM; ICES 2017). Additionally, there has been significant progress in developing and applying an end-to-end ecosystem model for Georges Bank and the surrounding region (the Atlantis model; Link et al. 2010; Olsen et al. 2016). Identifying which pressures are most directly related to changes in the fish community could benefit such efforts by directing monitoring, focussing indicator investigations, and guiding modelling scenarios.

Here, I first identified the most influential pressures from a predefined suite using both an MLR approach (Dempsey et al. 2018), and a NN approach (Dempsey et al. in review). Both methods can use multiple pressure indicators to model multiple metrics of the fish community, represented here by the biomass indices of six fish functional groups. The main difference between these approaches is that MLR is confined to modelling linear or user-defined non-linear relationships, while NN can implicitly model non-linear relationships. Within each approach, I also investigated the effects of incorporating different delay types (moving average vs. lag) and lengths (from $k = 0$ to $k = 8$ years) on the most influential pressures and model fit. Influential pressures for each delay were identified from a predefined suite of four fishing and five environmental pressures in the region. The four fishing pressures capture the overall decrease and high inter-annual variability of total and mollusk landings, and the rapid increase of pelagic (e.g., herring, mackerel) and elasmobranch (e.g., dogfish and skates) landings in the region over the time period of interest. Environmental pressures capture changes in basin-scale and local metrics, including freshening in the 1990s that may have led to changes in the zooplankton community and higher trophic level predators (Kane 2007, Mountain and Kane 2010, Perretti et al. 2017).

I synthesized the results of all analyses to make general observations about the efficacy of the analytic methods and what the results imply about the dynamics of the Georges Bank ecosystem. This analysis provides a complementary case study to recent work that compares the results and ease of use of these methods for the Grand Bank (Chapters 3 and 4; Dempsey et al. 2018, in review), another historically rich ecosystem in the Northwest Atlantic.

5.3 Methods

5.3.1 Study Area

Georges Bank is a shallow plateau in the Gulf of Maine (Fig. 5.1), bordered by three American states (New Hampshire, Massachusetts, and Maine), and two Canadian provinces (New Brunswick and Nova Scotia; Herbert 1995). It is considered one of the four ecological productivity units (i.e., EBFM management unit) of the Northeast Continental Shelf Large Marine Ecosystem (Lucey and Fogarty 2013), and is considered particularly vulnerable to climate change because it is at the southern edge of an ecotone separating cold and warm fish species (GLOBEC 1991). This region is characterized by high productivity and is a historically rich fishing ground for a variety of species including scallops, cod, haddock, and flounder (Bubier and Rieser 1986, Fogarty and Murawski 1998). Like other regions in the Northwest Atlantic (e.g., Scotian Shelf, Grand Banks), the Georges Bank fish community experienced complex ecological changes over the past several decades. Commercially important gadid and flatfish species (e.g, cod, haddock) collapsed throughout the 1960s, followed by small pelagic species (e.g., Atlantic herring, Atlantic mackerel) in the 1970s. In contrast, the biomass of species with relatively low economic value such as elasmobranches (e.g., dogfish and skates) increased rapidly (Fogarty and Murawski 1998). These species remained dominant throughout the 1980s and 1990s, although their biomass has been generally decreasing since 1990 (particularly dogfish). More recently, there has been significant recovery of Atlantic herring, which are now at historically high levels (NMFS 2009).

Fisheries management in the Georges Bank region is also complex, and has evolved throughout the decades since restrictions were first advised in the 1950s. In 1977, Canada and the US extended their exclusive economic zones (EEZs), creating a disputed area where the claims overlapped (Fig. 5.1; Herbert 1995). After failed attempts at a bilateral agreement, the dispute was brought to the International Court of Justice (ICJ). With little regard to the fisheries or related management and socio-economic considerations, the ICJ decided on a boundary between the original Canadian and US claims (Herbert 1995). This resulted in several transboundary stocks, and differing management philosophies on either side of the boundary (Bubier and Rieser 1986, Herbert 1995, Pudden and Vanderzwaag 2010). Canadian management focussed on fishing mortality limits, and management regulations primarily relied on effort control, including limited entry programs and vessel licensing, as well as output control such as total allowable catches (TACs) and quotas. US management aimed to conserve the spawning stock biomass (SSB), and management regulations included minimum mesh sizes and closed areas (Herbert 1995).

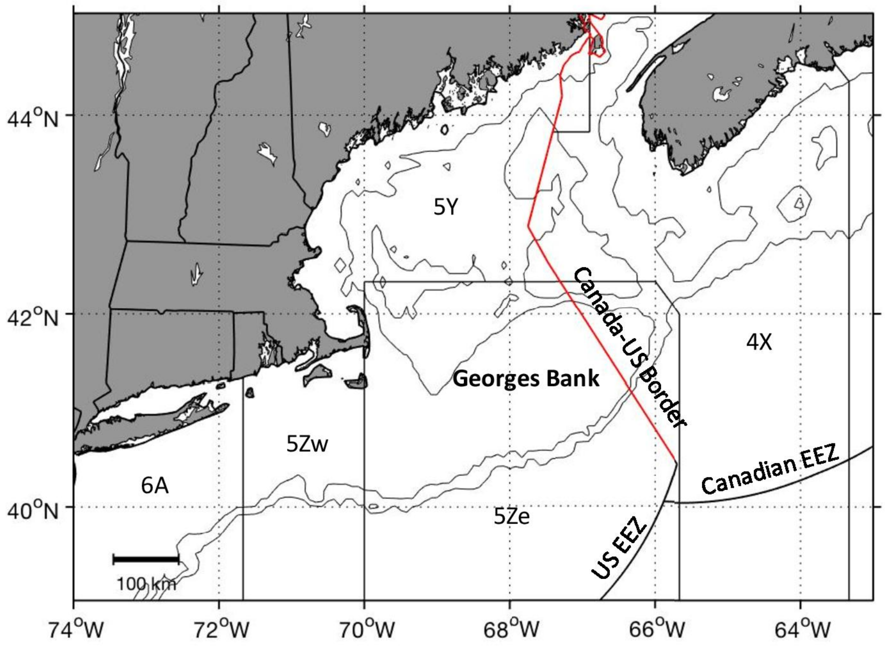


Figure 5.1: Map of the study area, showing Georges Bank (NAFO division 5Ze), the 100 and 200-m isobaths, the Canada-US border, and the Canadian an US exclusive economic zones.

Today, transboundary management in the region is coordinated by the Canada-US Steering Committee, which was formed in 1995 and oversees three sub-committees. The Transboundary Management Guidance Committee (TMGC) provides non-binding management advice in an annual Guidance Document for cod, haddock, and yellowtail flounder. The Transboundary Resource Assessment Committee (TRAC) conducts joint Canada-US assessments for these stocks, providing the results to the TMGC. The Canada–USA Integration Committee, the newest of the cooperative initiatives, is meant to facilitate the Ecosystem Approach to Management by coordinating relevant working groups (Pudden and Vanderzwaag 2007). More generally, significant scientific and management efforts are underway to implement EFBM in the Georges Bank-Gulf of Maine region (e.g., EcoAP 2012, NEFMC 2016, WGNARS 2018).

5.3.2 Indicators

The suite of indicator time series used here were provided by the US National Ocean and Atmospheric Administration’s (NOAA) Northeast Fisheries Science Center (NEFSC). Fish community indicators are annual values for 1985 – 2012 (the “Full” period), and pressure indicators extend from 1977 – 2012 for use with the delay analysis. Significant changes in the Georges Bank ecosystem occurred in the 1990s (Pershing et al. 2005, Liu et al. 2014, Perretti et al. 2017), so to determine how pressures on the fish community have changed over time, and for comparison with analyses of the Grand Bank, I also split the Full data series into Time1 (1985 – 1995) and Time2 (1996 – 2012). Below I present a general overview of these indicators to give context for the current analysis.

5.3.2.1 Indicators of Fish Community Status

The fish community was represented by the biomass indices of six fish functional groups (i.e., groups of species with similar feeding behaviors; Table 5.1). Functional groups are expected to be more stable than individual species because of within-group compensatory dynamics (Fogarty 2014), and are considered meaningful units to fisheries scientists and managers (NAFO 2014, NEFMC 2016). Additionally, they benefit the present analysis and other modelling studies by reducing the number of response variables when compared to using individual species (Fogarty 2014). Fisheries-independent bottom trawl surveys are conducted on Georges Bank in the spring and fall by the NEFSC. Fish species found in the region have been assigned to a functional group (NEFMC 2016; called “feeding guilds” in that document). The annual spring biomass index for each functional group was calculated by summing the expanded, swept-area biomass (corrected for catchability) of each species assigned that group in a given year (Fig. 5.2). Here, the “biomass” and “biomass index” of a functional group refers to the logged index (to account for the skewed nature of the trawl data), and the logged indices were additionally scaled appropriately for each approach (see section 2.3).

Table 5.1: Functional groups used to represent the fish community structure of Georges Bank.

Functional Group	**Number of Species**	**Dominant Species (by biomass)**
Benthos	2	Sea scallops (*Placopecten magellanicus*)
Benthivores	21	Haddock (*Melanogrammus aeglefinus*)
Mesoplanktivores	6	Atlantic herring (*Clupea harengus*)
Macroplanktivores	6	Longhorn sculpin (*Myoxocephalus octodecemspinosus*)
Macrozoo-piscivores	11	Little skate (*Leucoraja erinacea*)
Piscivores	11	Spiny dogfish (*Squalus acanthias*)

Benthos and mesoplanktivore biomass had no trend over Time1, but increased marginally over Time2 and the Full period (Fig. 5.2A, 5.2C). Mesoplanktivore biomass had two main dips (in the late 1980s and the early 2000s) that were each followed by a dip in benthos biomass (early 1990s and mid-2000s). Benthivores also had high variability in Time1, but had the most obvious increasing trend over the Full period and Time2 (Fig. 5.2B). Macroplanktivore biomass generally increased over Time1, with a spike in the early 1990s, followed by an overall decreasing trend from 2000 – 2012 (Fig 5.2D). Macrozoo-piscivores exhibited high inter-annual variability throughout Time1 and over the Full period, but had an overall increasing trend throughout Time2 (Fig. 5.2E). In contrast, piscivore biomass generally decreased over all three periods, with a small peak in 2003 (Fig. 5.2F). Pearson and Spearman correlation coefficients were used to assess pairwise correlation between the functional groups. None of the functional group biomass indices were highly correlated (defined as correlation coefficient ≥ 0.60) over any of the time periods using either metric.

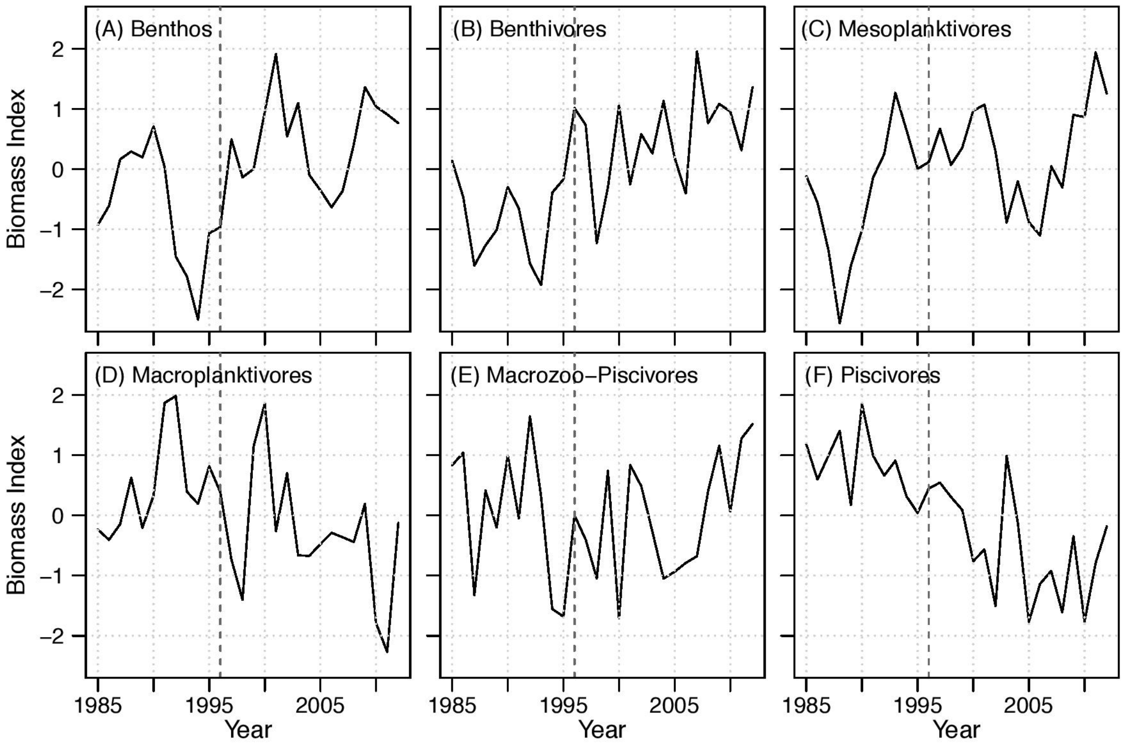


Figure 5.2: Functional group biomass indices (logged, centered and scaled over the Full period) used as responses in this analysis. The thick dashed line indicates the beginning of Time2.

5.3.2.2 Indicators of Fishing and Environmental Pressures

The NEFSC's Ecosystem Assessment Group has calculated an annual suite of 41 fishing and environmental indicators spanning 1977 – 2012 (EcoAP 2012). This suite was provided for the current analysis, and I selected four fishing and four environmental indicators to include as predictors (along with one additional environmental indicator; Fig. 5.3). When possible, I chose indicators to mirror those used in recent analyses of the Grand Bank (Chapters 3 and 4; Dempsey et al. 2018; Dempsey et al. in review) to facilitate comparison of the most influential pressures in each region. However, there are some discrepancies because of data constraints and differences between the two ecosystems.

The four fishing indicators include: total, pelagic, mollusk, and elasmobranch landings (Fig. 5.3). Total landings decreased overall from 1977 – 1995, although there was a slight increase from 1985 – 1991. Since 1995, total landings have fluctuated with high inter-annual variability. Mollusks (mainly sea scallops) are one of the most lucrative fisheries in the region (NOAA 2018). They contribute about 35% of the total landed biomass (on average over the Full period), and were highly correlated with total landings for all three periods. No other landings indicator pairs were highly correlated for any period. Commercial fishing for elasmobranchs (mainly dogfish and skates) began in the early 1990s, after the collapse of the valuable groundfish stocks (MAFMC and NEFMC 1999, NEFMC 2003). Elasmobranch landings increased rapidly throughout Time1, but there has been no discernable trend throughout Time2. There was little directed fishing on pelagic species in Time1 because of the collapse of the Atlantic herring stock in the late 1970s, but the stock has since recovered and pelagic landings have generally increased since the mid-1990s (Melvin and Stephenson 2007).

Total and pelagic landings were included in the prior Grand Bank analysis. For that analysis, mollusk and crustacean landings were combined in the "shellfish landings" pressure. Here I kept mollusks separate, because they are one of the main landings in the Georges Bank region (in terms of biomass and value; NOAA 2018). I did not want to confound the influence of mollusks landings with that of crustaceans, which are generally a minor component of total landings (3% on average over the whole time period, but up to 12% in 2005). The fourth fishing-related pressure used in the Grand Bank analysis was the mean trophic index of the landings (MTI). This could not be calculated using the data provided by NEFSC, because the data only included the total biomass landed within each commercial group, rather than the biomass of each species in the group. Instead, I included elasmobranch landings, which have increased along with pelagic landings as groundfish and total landings decrease. This may be a more useful pressure to include than MTI, because it is more directly linked to management action. It can be difficult to parse out what is causing changes in the MTI, and how that relates to changes in the fish community. In contrast, elasmobranch landings has the direct effects of removing biomass from the community and disrupting habitat (plus other related impacts such as bycatch).

The five environmental indicators include: the winter North Atlantic Oscillation (NAO); as calculated and applied in previous chapters (Dempsey et. al 2017, 2018, in review), sea surface temperature (SST), surface salinity (SSS), bottom salinity (Sbottom), and total copepod abundance (all provided by NEFSC). The NAO is a metric of basin-scale atmospheric forcing that is related to local environmental conditions in the Northwest Atlantic. On Georges Bank, positive NAO is related to warmer temperatures, increased precipitation, and stronger westerly winds; the converse is true for negative NAO values. A 2-year lag between changes in the NAO index and subsequent changes in the local Georges Bank environmental conditions has been observed (Greene and Pershing 2007). Temperature is one of the most influential pressures on marine organisms, and increasing temperature is generally correlated with increased growth, metabolism, and maturity rates of many fish species (Jones 1976, Gillooly et al. 2001, Colbourne and Anderson 2003). Temperature also influences species distribution, and there has been a poleward shift in the distribution of several species on the US continental shelf in response to warming waters over the past several decades (Nye et al. 2009). Changes in temperature could be particularly important for the Georges Bank ecosystem in the coming decades, because the Gulf of Maine region has been shown to be warming faster than 99% of the world's oceans (Pershing et al. 2015). Many organisms are also sensitive to changes in salinity, which is influenced by the interactions of Gulf Stream and Scotian Shelf Water in the region (Lentz 2003). Specifically, salinity can impact the abundance and community composition of lower trophic level species such as zooplankton (Pershing et al. 2005, Kane 2007, MERCINA 2012). Calanoid copepods are the dominant group of zooplankton on Georges Bank, and form an important link in the marine food web. They feed on phytoplankton and smaller zooplankton, and are the primary food source for forage fishes (e.g., herring and mackerel), the larvae of several fish species (e.g., cod and haddock), and baleen whales (e.g., the endangered North Atlantic right whale; EcoAP 2012). Copepod abundance and size regime shifts have been linked to regimes of fish recruitment on the Northeast continental shelf, with periods of lower zooplankton abundance dominated by larger zooplankton species and corresponding to lower fish recruitment across 18 fish species (and vice versa; Perretti et al. 2017).

The NAO was characterized by inter-annual variability (Fig. 5.3). It had several years of sustained positive values from the late 1980s until the mid-1990s, and a notable anomalously low value in 2010. SSS and bottom salinity both decreased over the Full period, although the trend is harder to discern in each period separately because of high inter-annual variability (Fig. 5.3). The salinity metrics were very highly correlated with one another for all three periods. They were both kept for this analysis to be parallel with the Grand Bank analysis (where they were not highly correlated). Similar to the salinity metrics, SST increased over the Full period, but had no notable trend within each time period (Fig. 5.3). SST was highly correlated with both SSS and bottom salinity for Time1. Copepod abundance was relatively low from the late 1970s until the mid 1980s, at which point it increased rapidly until the early 2000s, when it decreased again (Fig. 5.3).

Local values of SST, SSS, and bottom salinity, as well as the basin-scale NAO were calculated and used in the prior Grand Bank analyses and these Georges Bank analyses. The main difference in these two environmental pressure sets is the metric representing lower trophic levels (e.g., primary and secondary production). There was no consistent, direct measure of these on the Grand Bank over the period of interest, so the timing of the sea ice melt was included as a proxy of the timing and duration of the spring phytoplankton bloom. However, sea ice is not expected to have a significant impact on Georges Bank, and a more direct measure of secondary producers was available over the Full period for this region, so I used total copepod abundance instead of the timing of the sea ice melt.

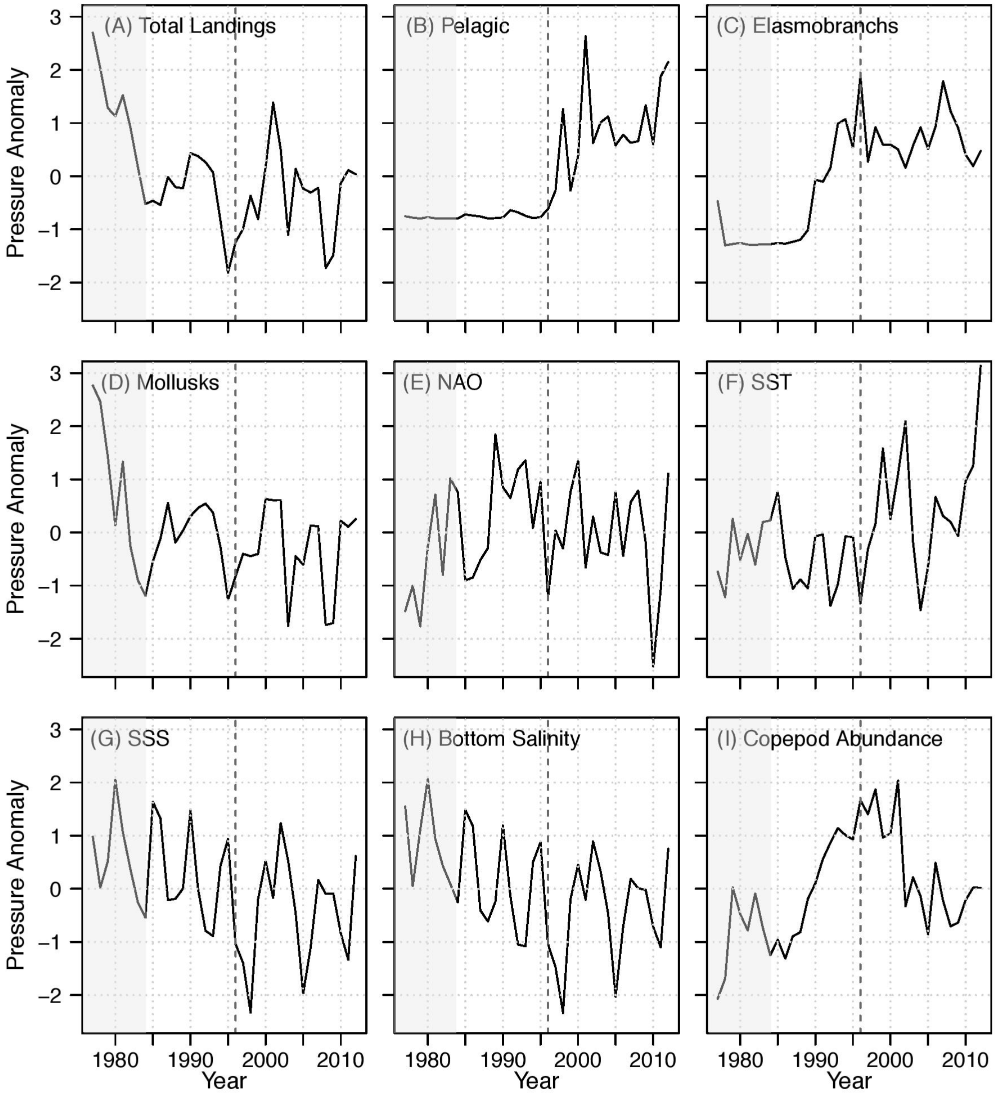


Figure 5.3: Pressure indicators used as predictors in this analysis (centered and scaled over Full period). Fishing indicators: (A) – (D); Environmental indicators: (E) – (I). The unshaded area represents the zero delay pressures; the shaded area represents the additional data used in the time delay analysis. The thick dashed line marks the beginning of Time2.

5.3.3 Data Analysis

This analysis followed the methods of Chapters 3 and 4 (Dempsey et al. 2018, in review), identifying the most influential pressures first using MLR, and then NN. Significant similarities and discrepancies in the results are examined in the discussion. The methods are outlined briefly here, but readers are referred to the Chapters referenced above for more detailed explanations.

5.3.3.1 Delay Analysis

For both methods, the pressure indicators were used as predictors to model the six functional group biomass indices (responses) for the Full period, Time1, and Time2. The "zero delay" (ZD) analysis used predictors and responses over the same time period (e.g., for the Full period, all predictors and responses span 1985 – 2012). The analysis was then repeated using different types and lengths of time delay in the predictors. I considered two delay types: moving averages and lags, for delay lengths from $k = 1$ to $k = 8$ years. The predictor value at year i for moving average predictors was the average of the current year and the previous k years (resulting in a $k + 1$ year backwards moving average). For the lag analyses, predictors were shifted forward k years to simulate a delayed response. Incorporating delays did not reduce the number of observations used to fit the model because the predictor data series are longer than the responses. Within a given model, all predictors had the same type and length of delay. I refer to moving average and lag predictors that incorporate k years of past data as Avg*k* and Lag*k* models, respectively. To streamline presentation and discussion of results, the most influential pressures for each period will be determined for only the best delay lengths within each delay type (ZD, Avg, and Lag). The criteria for best models and most influential pressures depend on the method, as described below.

5.3.3.2 Multivariate Linear Regression

For each period, an MLR model was fit for all of the possible combinations of the nine predictors (resulting in a total of 511 models), first with ZD predictors, and then again for each delay length and type. I call the set of models for a given period and delay an "assemblage." Within an assemblage, the models were ranked on their explanatory power, with the model with the highest adjusted-R^2_{Total} (i.e., the average of the adjusted-R^2 of each functional group; see Appendix D) given a rank of 1. For linear models, the R^2 will always increase with an additional predictor (that is not perfectly correlated with previous predictors). The adjusted-R^2 applies a penalty to the R^2 for every predictor included, which makes it a better metric for comparing linear models with different numbers of predictors. I considered any difference in adjusted-$R^2_{\text{Total}} > 0.050$ to be "notable." Predictors and responses were centered and scaled by their respective standard deviations within each period and delay.

I focussed the analysis of the results on the top 50 models (i.e., top 10%) of each assemblage. For a given period and delay type, the best delay lengths were those with average adjusted-R^2_{Total} (of the top 50 models) that was not notably different than the best average adjusted-R^2_{Total}. I additionally calculated the average and best MSE for comparison with the NN. The most influential pressures were determined for the best assemblages of each period. To do this, I calculated the proportion of times each predictor was included in the top 50 models (P50; e.g., maximum = 50/50 = 1; minimum = 0/50 = 0). Within a given assemblage, a predictor was considered influential if it had P50 within 0.10 of the most frequent predictor. For example, if one predictor was included in all of the top 50 models, the other predictors must have P50 ≥ 0.90 to be considered influential.

5.3.3.3 Neural network analysis

For the NN analysis, the optimal number of hidden nodes for each period was determined using *n*-fold cross validation. A model ensemble approach (N = 35 models in each ensemble) was applied to account for sensitivity to the starting weights. I trained and tested networks with 1 to 5 hidden nodes, and evaluated the average mean squared error (MSE) of the fit (based on the training data; $\overline{\text{MSE}}_{\text{Train}}$) and predictive power (based on the test data; $\overline{\text{MSE}}_{\text{Test}}$). I chose the number of hidden nodes resulting in the best predictive power (i.e., smallest $\overline{\text{MSE}}_{\text{Test}}$). 1 hidden node was considered optimal for each period using the ZD predictors, and so I chose to also use 1 hidden node for each of the delay analyses to facilitate comparison among models. Other NN parameters (e.g., activation function, threshold) were the same as those used in Chapter 4 (Dempsey et al. in review). Predictors were centered and scaled by their respective standard deviations, while responses were linearly mapped to the interval [0,1] within each period and delay.

Next, a NN ensemble with the optimal number of hidden nodes (one) was fit to all of the data observations using all of the predictors. This was repeated for all types and lengths of time delay, and I identified the most influential pressures for the best delay lengths within each type. The best delay lengths were those that resulted in ensembles with predictive power ($\overline{\mathrm{MSE}}_{\mathrm{Test}}$) that was not notably different than the overall lowest $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ for the given period and delay type (differences in MSE > 0.050 were considered "notable"). I identified the most influential predictors using the product of connection weights (PCW) algorithm, modified for multivariate output and the ensemble approach (Dempsey et al. in review, Olden and Jackson 2002, Olden et al. 2004). This method sums together the product of the input-hidden and hidden-output weights for a given predictor and response, and uses this to calculate the percent contribution of each predictor for modelling each response. Because only one hidden node was used, each predictor contributed the same to modelling a given functional group (i.e., percent contribution is based entirely on the input-hidden weights; see Chapter 4). Predictors were considered influential if they contributed ≥10.0% to modeling at least three functional groups.

n-fold cross validation was also used as a rough metric of the NN forecast ability. To further investigate how well the model performed on out-of-sample data, I built two "forecast" models. One was trained on the first 23 years of data and tested on the last 5 (forecast-5), while the other was trained on the first 18 years of data and tested on the last 10 (forecast-10; see Chapter 4 for more detail on the training/testing procedure). To compare the *n*-fold and forecast models, I calculated the $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ for each functional group from the observed values and the average predicted values from the ensemble for all values of the *n*-fold procedure, the last 5 and 10 years of the *n*-fold procedure (nfold-5 and nfold-10, respectively), and the test values of the forecast models. The nfold-5 and nfold-10 provide a metric that is more directly comparable to the forecast-5 and forecast-10 models, because their MSEs are calculated for the same subset of data. If *n*-fold cross validation provides a useful estimation of the predictive power of the NN for a given functional group, I would expect the $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ of the *n*-fold to be about the same as that of the forecast models.

5.3.3.4 Comparison of modelling approaches

There are some obvious and subtle differences between the model approaches that could influence interpretation and discussion of the results. The most obvious difference is that MLR is restricted to modelling linear relationships between predictors and responses, while NN implicitly model non-linear relationships. This leads to a subtler point, which is reflected in the goodness of fit metrics used to evaluate each type of model. The fit of a linear model will improve with the addition of a predictor that is independent of the ones already included, and metrics that account for this should be used to compare models with different numbers of predictors. Hence, the adjusted-$\mathrm{R}^2_{\mathrm{Total}}$was used for the MLR analysis, which evaluated models with one to nine predictors. In contrast, the fit of a non-linear model is not guaranteed to improve with an extra predictor, and the mean squared error of the training data ($\overline{\mathrm{MSE}}_{\mathrm{Train}}$) was used to evaluate the fit of NN models. For comparisons among NN models, the $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ was used (because there were no notable differences in fit for any delay length within a given delay type and period; see Results section, Fig. 5.9). It was not trivial to choose a metric to compare the fits of these different models. Based on the rationale in Appendix E.3, I chose the MSE, although there were still some differences in its calculation for the two approaches. For the MLR approach, the MSE was calculated for the top 50 MLR models (ranked by adjusted-$\mathrm{R}^2_{\mathrm{Total}}$), and the average and best MSE were reported. Note that each of these MLR models was built from a different subset of the nine predictors. For the NN approach, I reported the average and best MSE of the ensemble, i.e., the 35 NN iterations trained with different starting weights, using all observations and all nine pressures. Because the MSE is scale dependent, care should be taken when comparing MSEs for models of different responses (e.g., for different periods and functional groups). A final relevant difference between the approaches is that the MLR fits each response separately, while the NN optimizes the fit for all responses simultaneously.

5.4 Results

5.4.1 Multivariate Regression

Here I describe the results of the MLR analysis for each period, focussing on the top 50 models for each assemblage. In general, Time1 had the highest explanatory power, and Time2 had the lowest (Fig. 5.4). Within a given period, the Avg assemblages generally had better explanatory power than the Lag assemblages. The most influential pressures were different for each period, and varied within periods depending on the delay type and length (Fig. 5.5).

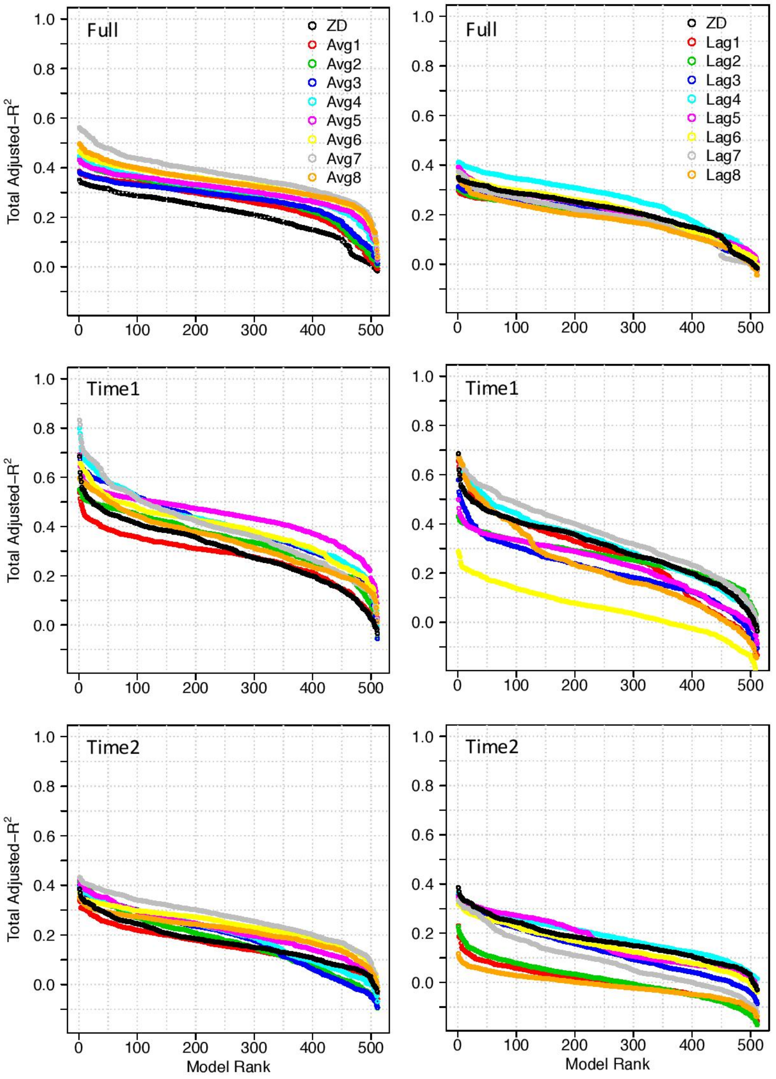


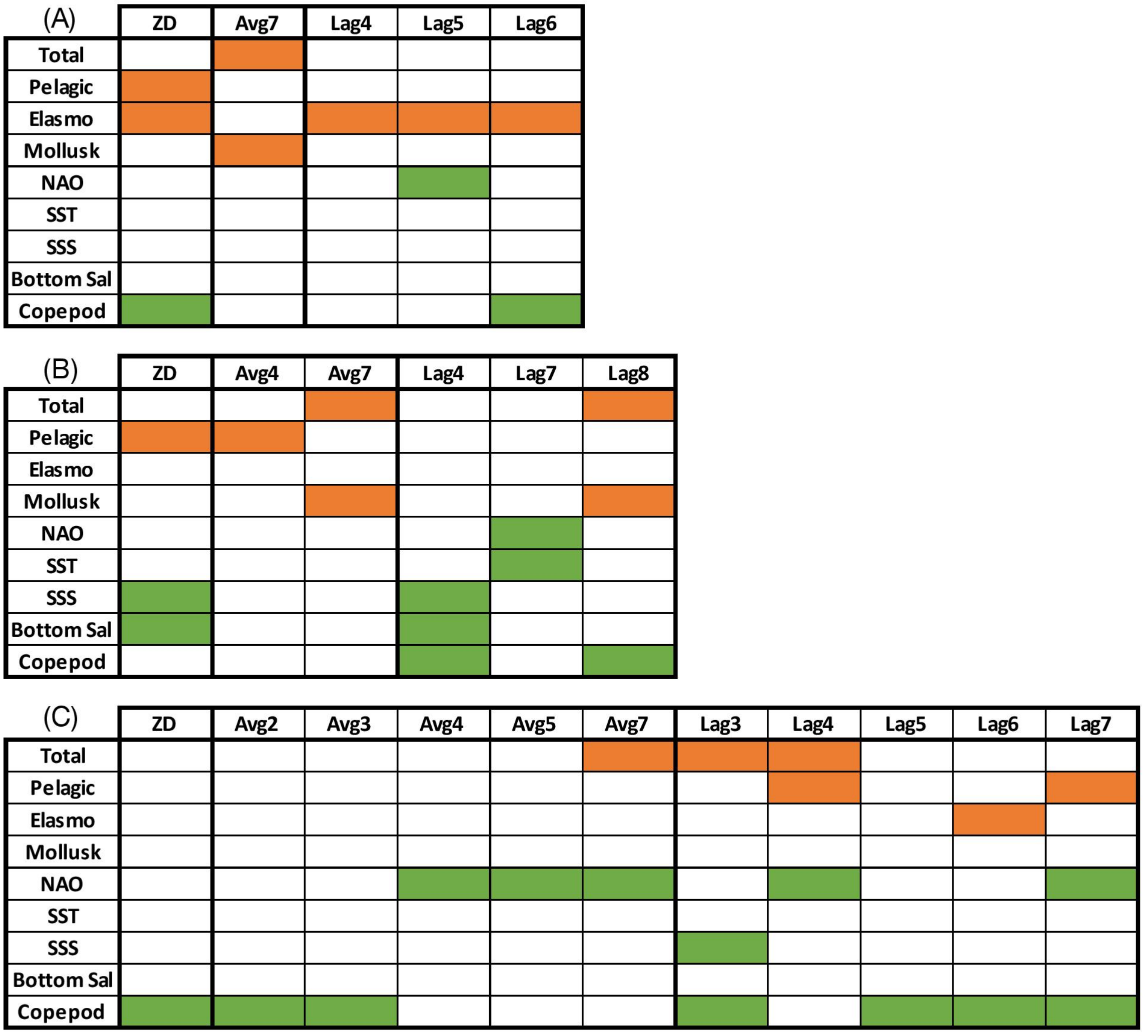
Figure 5.4: Adjusted-R^2_{Total} in decreasing rank for moving average predictors (left) and lag predictors (right) for the three periods. Top: Full; middle: Time1; bottom: Time2. Panels in each column have the same legend.

For the Full period, the ZD assemblage had moderate adjusted-R^2_{Total}, ranging from about 0.32 to 0.35 (Fig. 5.4). The most influential ZD predictors were pelagic and elasmobranch landings and copepod abundance (Fig. 5.5). All of the models in the Avg assemblages had higher explanatory power than the correspondingly ranked ZD model, and most were notably higher (Fig. 5.4). The best Avg assemblage for the Full period was Avg7, which was notably better than all of the other delay types and lengths for most of the top 50 models (adjusted-R^2_{Total} about 0.48 to 0.56; Fig. 5.4). The most frequent Avg7 predictors were two fishing pressures: total and mollusk landings (Fig. 5.5). The best Lag models were Lag4, Lag5, and Lag6 (adjusted-R^2_{Total} about 0.31 to 0.41). All three of these models highlighted elasmobranch landings, while Lag5 also highlighted NAO, and Lag6 highlighted copepod abundance (Fig. 5.5). The overall best Avg and Lag models each had 8 predictors (all except elasmobranch landings for Avg7; all except mollusk landings for Lag4), while the best for the ZD assemblage included only 6 predictors (all except total and mollusk landings and bottom salinity; not shown).

Time1 had the highest explanatory power of the three periods, with the top three models overall (Avg4 and Avg7) having adjusted-$R^2_{\text{Total}} \geq 0.80$ (Fig. 5.4). The ZD assemblage had adjusted-R^2_{Total} ranging from about 0.45 to 0.69. The most frequent ZD predictors were pelagic landings and the two salinity metrics (Fig. 5.5). The best Avg assemblages were Avg4 and Avg7. Similar delay lengths were highlighted for the Lag models: Lag4, Lag7, and Lag8; however, the most influential pressures differed between the delay types (Fig. 5.5). Avg4 and Avg7 both highlighted only fishing pressures (pelagic landings for Avg4; total and mollusk landings for Avg7). In stark contrast, Lag4 and Lag7 highlighted only environmental pressures (SSS, Sbottom, and copepod abundance for Lag4; NAO and SST for Lag7). The most frequent Lag8 predictors included both fishing and environmental pressures: total and mollusk landings and copepod abundance. The best overall Avg model used 8 predictors (Avg7; all except pelagic landings), while the best Lag model used 7 (Lag8; all except pelagic landings and SSS).

The Time2 ZD assemblage had about the same explanatory power as the Full ZD assemblage; however, the Time2 delay assemblages were generally worse than those for the Full period (Fig. 5.4). The only ZD predictor highlighted for this period was copepod abundance. Most of the Avg assemblages had similar explanatory power, such that all delay lengths except Avg1 and Avg8 were considered in the predictor contribution analysis. A single environmental pressure was influential for four Avg assemblages (Fig. 5.5; copepod abundance for Avg2 and Avg3; NAO for Avg4 and Avg5). Total landings and NAO were both influential for Avg7. Most of the Lag models also had similar explanatory power, and Lag3 – Lag7 were included in the predictor analysis (Fig 5.4).

Most of these delay lengths highlighted both fishing and environmental pressures, although copepod abundance was the only influential predictor highlighted for Lag5. Copepod abundance was also highlighted for three of the other Lag assemblages (Fig. 5.5).



(A)

	ZD	Avg7	Lag4	Lag5	Lag6
Total		🟧			
Pelagic	🟧				
Elasmo	🟧		🟧	🟧	🟧
Mollusk		🟧			
NAO				🟩	
SST					
SSS					
Bottom Sal					
Copepod	🟩				🟩

(B)

	ZD	Avg4	Avg7	Lag4	Lag7	Lag8
Total			🟧			🟧
Pelagic	🟧	🟧				
Elasmo						
Mollusk			🟧			🟧
NAO					🟩	
SST					🟩	
SSS	🟩			🟩		
Bottom Sal	🟩			🟩		
Copepod				🟩		🟩

(C)

	ZD	Avg2	Avg3	Avg4	Avg5	Avg7	Lag3	Lag4	Lag5	Lag6	Lag7
Total						🟧	🟧	🟧			
Pelagic								🟧			🟧
Elasmo										🟧	
Mollusk											
NAO				🟩	🟩	🟩		🟩			🟩
SST											
SSS							🟩				
Bottom Sal											
Copepod	🟩	🟩	🟩				🟩		🟩	🟩	🟩

Figure 5.5: Most influential pressures from the multivariate regression analysis for the ZD and best models for each delay type and period. Orange shading indicates influential fishing pressures; green shading indicates influential environmental pressures. (A) Full period; (B) Time1; (C) Time2.

I evaluated the explanatory power of the best assemblages for each period and delay type using only their respective influential pressures as predictors ("reduced predictor sets"; Fig. 5.6). In most cases, the reduced sets consist of only one or two predictors (Fig. 5.5), and the explanatory power of the resulting model is far worse than the best model of the assemblage (difference in adjusted-R^2_{Total} >> 0.05; Fig. 5.6). For two delay lengths (ZD for the Full period and Lag7 for Time2), there is no notable difference between the explanatory power of the reduced model and the best model of the assemblage (although these "best" models had only moderate explanatory power to begin with). On average, the reduced models explained about 44% of the variance explained by the best model in the assemblage.

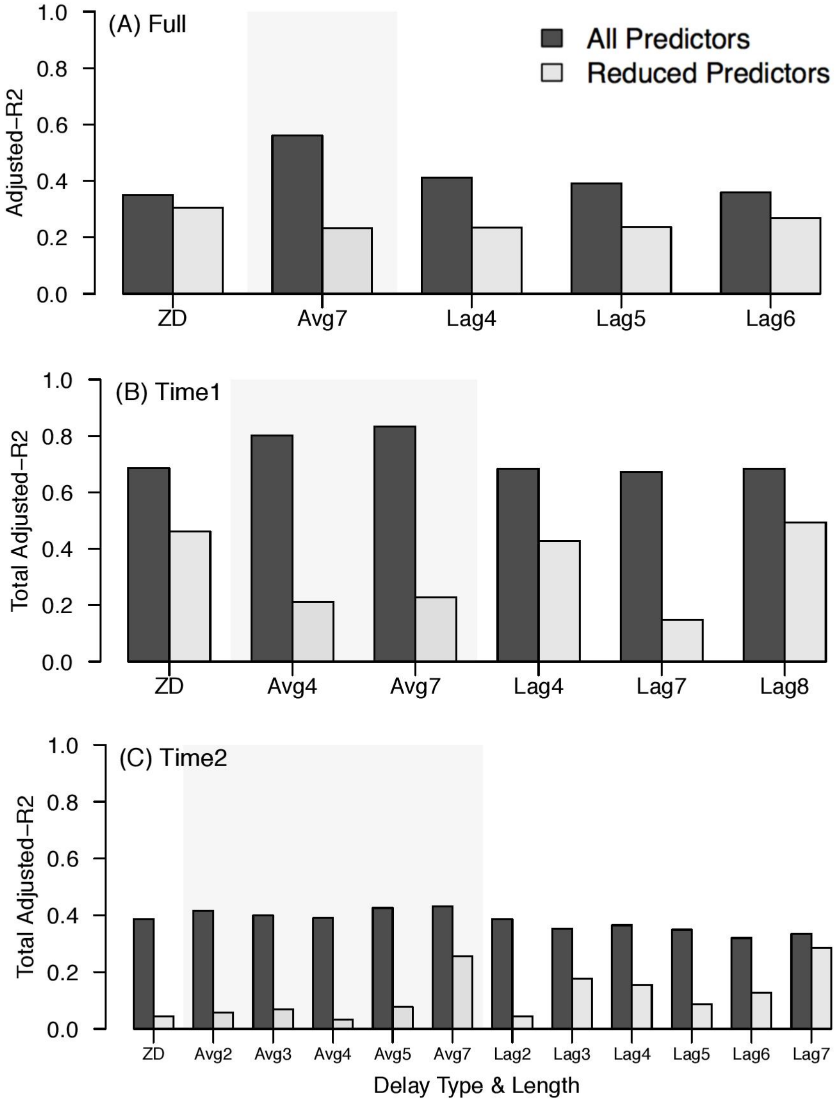


Figure 5.6: Adjusted-R^2_{Total} of the best MLR assemblages for each delay type and period. Dark grey bars show the best overall explanatory power; light grey bars show the explanatory power of the reduced predictor set (i.e., only the most influential pressures for the given delay). (A) Full period; (B) Time1; (C) Time2. The faint shaded boxes indicate the moving average models (to differentiate from ZD and lag).

5.4.2 Neural Network Analysis

As expected, $\overline{\text{MSE}}_{\text{Train}}$ decreased as the number of hidden nodes increased for each period, and its range over the 35 repetitions of the *n*-fold cross validation procedure was negligible in all cases (range < 0.05; Fig. 5.7). In contrast, $\overline{\text{MSE}}_{\text{Test}}$ was more variable and generally increased with additional hidden nodes, such that 1 hidden node minimized $\overline{\text{MSE}}_{\text{Test}}$ for all periods with the ZD predictors. One hidden node was used in all remaining ZD and delay analyses to facilitate comparison among models. These analyses showed there were no notable differences in $\overline{\text{MSE}}_{\text{Train}}$ within a given period for any delay type or length (Fig. 5.8A).

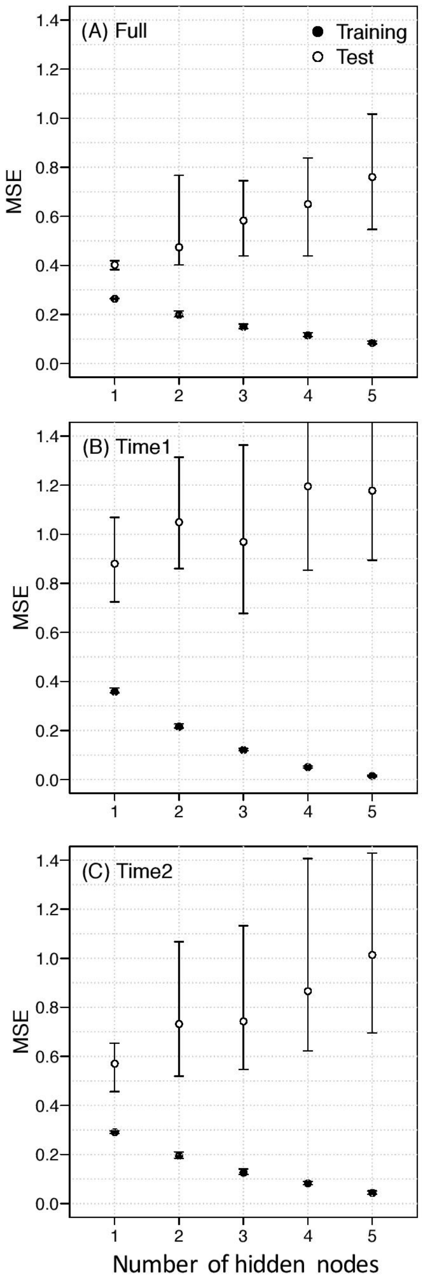


Figure 5.7: *n*-fold cross validation results for each period using zero delay predictors: mean (points) and range (lines) of the $\overline{\text{MSE}}_{\text{Train}}$ and $\overline{\text{MSE}}_{\text{Test}}$ for a given number of hidden nodes. (A) Full period, (B) Time1 and (C) Time2. Note that the range $\overline{\text{MSE}}_{\text{Train}}$ is so small that is not visible at this scale.

All of the Full period delay ensembles had similar predictive power (Fig. 5.8B), which was notably better than all of the corresponding Time1 ensembles, and most of Time2. Only the ZD ensemble was notably worse than the best Avg ensemble (Avg4), and only

ZD and Lag5 were notably worse than the best Lag ensembles (Lag2 and Lag4; Fig. 5.8B). The most influential ZD predictors were the four fishing pressures and copepod abundance (Fig. 5.9). The most influential pressure sets depended on the delay length and type, although some general observations can be made. All of the Avg influential sets included at least one fishing pressure, and all of the Lag sets included at least two. Elasmobranch landings were influential for all except one delay (Avg2), and pelagic landings were influential for several Avg and all of the Lag ensembles. Avg5 only included the four fishing pressures, while Lag4 included only three fishing pressures (total, pelagic, and elasmobranch landings). Both salinity metrics were included in five of the Avg influential pressure sets, and three of the Lag (Fig. 5.9).

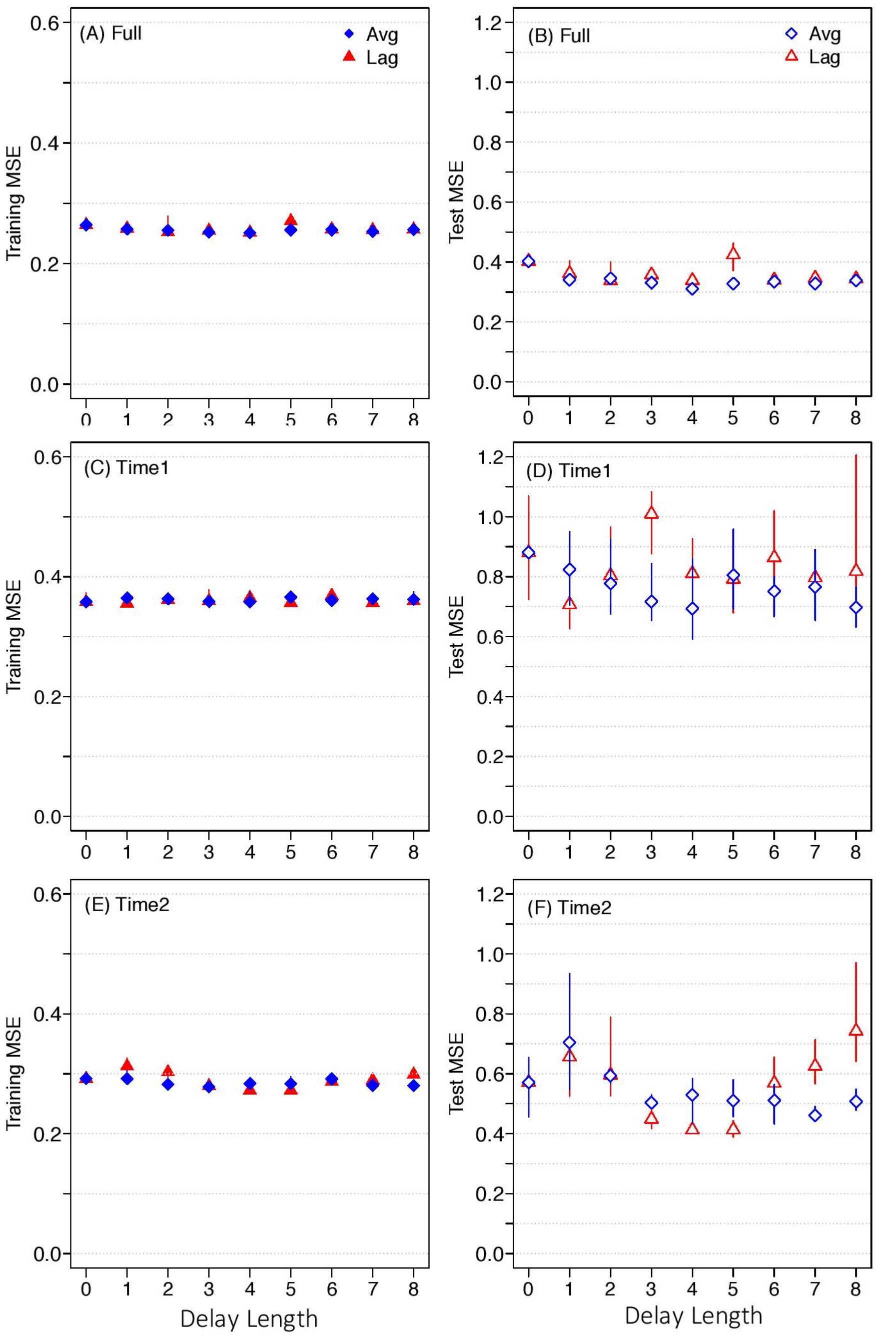
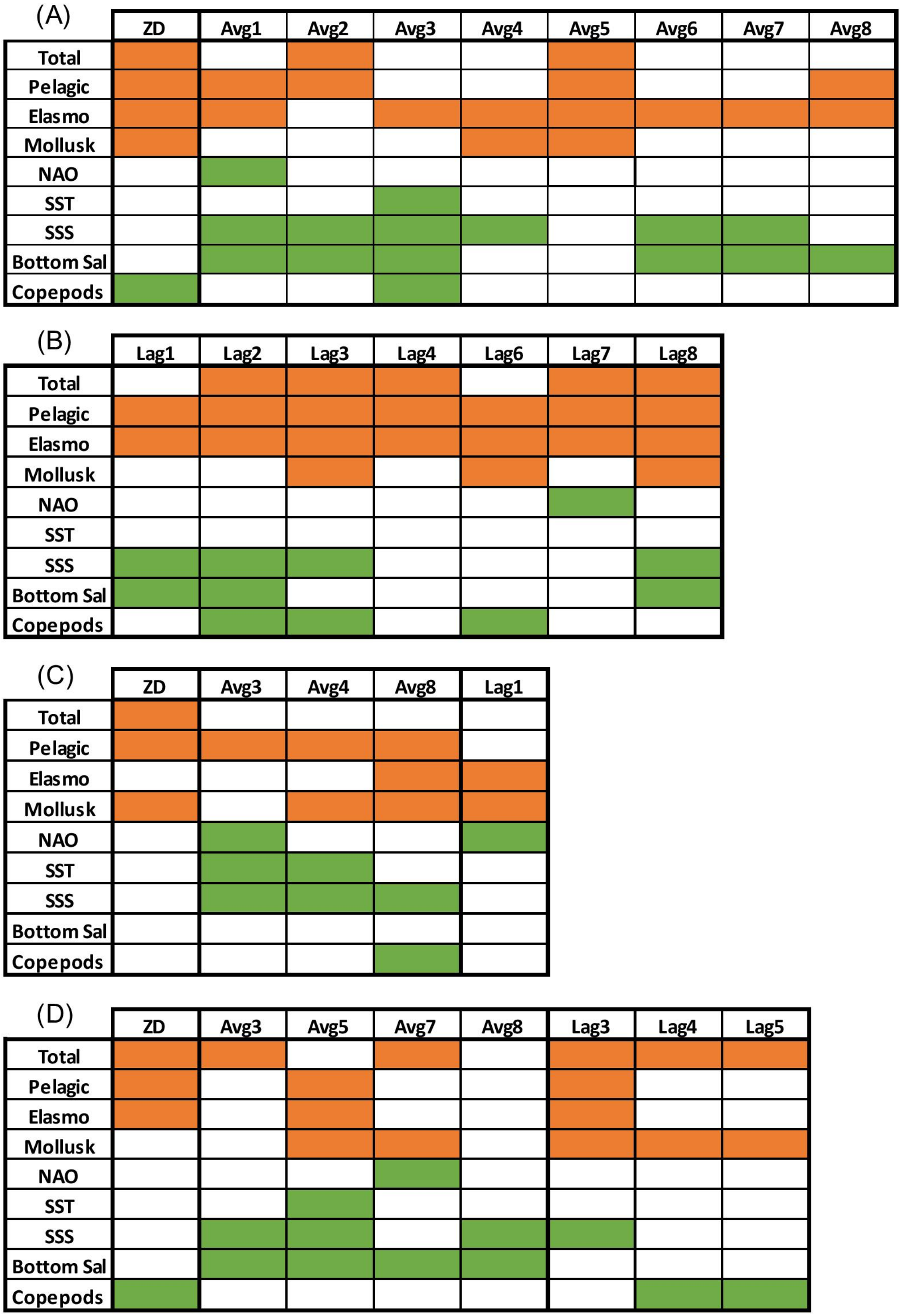


Figure 5.8: (A) – (C) $\overline{\text{MSE}}_{\text{Train}}$ and (D) – (F) $\overline{\text{MSE}}_{\text{Test}}$ from the cross validation procedure of models with delayed predictors (1 hidden node). Note the difference in scale between left and right columns.

The best Avg ensembles for Time1 were Avg3, Avg4, and Avg8, all of which had notably better predictive power than the ZD. Lag1 was notably better than all of the other Lag ensembles and the ZD ensemble for this period. The most influential ZD predictors were fishing pressures: total, pelagic, and mollusk landings (Fig. 5.9). Pelagic landings and SSS were considered influential for all three Avg ensembles. Lag1 influential pressures were elasmobranch and mollusk landings and NAO.

For Time2, the best Avg (Avg3, Avg5, Avg7, and Avg8) and Lag (Lag3, Lag4, and Lag5) ensembles all had notably better predictive power than the ZD ensemble. This was the only period that had a Lag ensemble with the best overall predictive power (Lag4). The most influential ZD predictors were total, pelagic, and elasmobranch landings and copepod abundance (Fig. 5.9). The two salinity metrics were influential for three of the Avg ensembles, and were the only pressures included in Avg8. Total and mollusk landings were influential for the three lag ensembles, with Lag4 and Lag5 including those and copepod abundance (Fig. 5.9).



(A)

	ZD	Avg1	Avg2	Avg3	Avg4	Avg5	Avg6	Avg7	Avg8
Total	🟧		🟧			🟧			
Pelagic	🟧	🟧	🟧			🟧			🟧
Elasmo	🟧	🟧		🟧	🟧	🟧	🟧	🟧	🟧
Mollusk	🟧				🟧	🟧			
NAO		🟩							
SST				🟩					
SSS		🟩	🟩	🟩	🟩		🟩	🟩	
Bottom Sal		🟩	🟩	🟩			🟩	🟩	🟩
Copepods	🟩			🟩					

(B)

	Lag1	Lag2	Lag3	Lag4	Lag6	Lag7	Lag8
Total		🟧	🟧	🟧		🟧	🟧
Pelagic	🟧	🟧	🟧	🟧	🟧	🟧	🟧
Elasmo	🟧	🟧	🟧	🟧	🟧	🟧	🟧
Mollusk			🟧		🟧		🟧
NAO						🟩	
SST							
SSS	🟩	🟩	🟩				🟩
Bottom Sal	🟩	🟩					🟩
Copepods		🟩	🟩		🟩		

(C)

	ZD	Avg3	Avg4	Avg8	Lag1
Total	🟧				
Pelagic	🟧	🟧	🟧	🟧	
Elasmo				🟧	🟧
Mollusk	🟧		🟧	🟧	🟧
NAO		🟩			🟩
SST		🟩	🟩		
SSS		🟩	🟩	🟩	
Bottom Sal					
Copepods				🟩	

(D)

	ZD	Avg3	Avg5	Avg7	Avg8	Lag3	Lag4	Lag5
Total	🟧	🟧		🟧		🟧	🟧	🟧
Pelagic	🟧		🟧			🟧		
Elasmo	🟧		🟧			🟧		
Mollusk			🟧	🟧		🟧	🟧	🟧
NAO				🟩				
SST			🟩					
SSS		🟩	🟩		🟩	🟩		
Bottom Sal		🟩	🟩	🟩	🟩			
Copepods	🟩						🟩	🟩

Figure 5.9: Most influential pressures from the NN analysis for the ZD and best models for each delay type and period. Orange shading indicates influential fishing pressures; green shading indicates influential environmental pressures. (A) Full period, moving average predictors; (B) Full period, lag predictors; (C) Time1; (D) Time2.

I evaluated the fit and predictive power of the best ensembles for each period using only their respective influential pressures as predictors (“reduced predictor sets”). There were no notable changes in fit for the Full period or Time1, although there were several Time2 models (Avg3, Lag4, Lag5) for which the reduced predictor set had notably worse $\overline{\mathrm{MSE}}_{\mathrm{Train}}$ than the whole set (not shown). Results for predictive power were mixed. The $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ of the ZD ensemble was notably improved with the reduced predictor set for all three periods. The smaller set also improved the predictive power of Avg3 and Avg4 for Time1 and Avg5 and Avg8 for Time2, suggesting that the training is being misdirected by extraneous information in at least one of the pressures in the full suite. In contrast, Lag4 and Lag5 for Time2 were notably worse with the reduced set (Fig. 5.10).

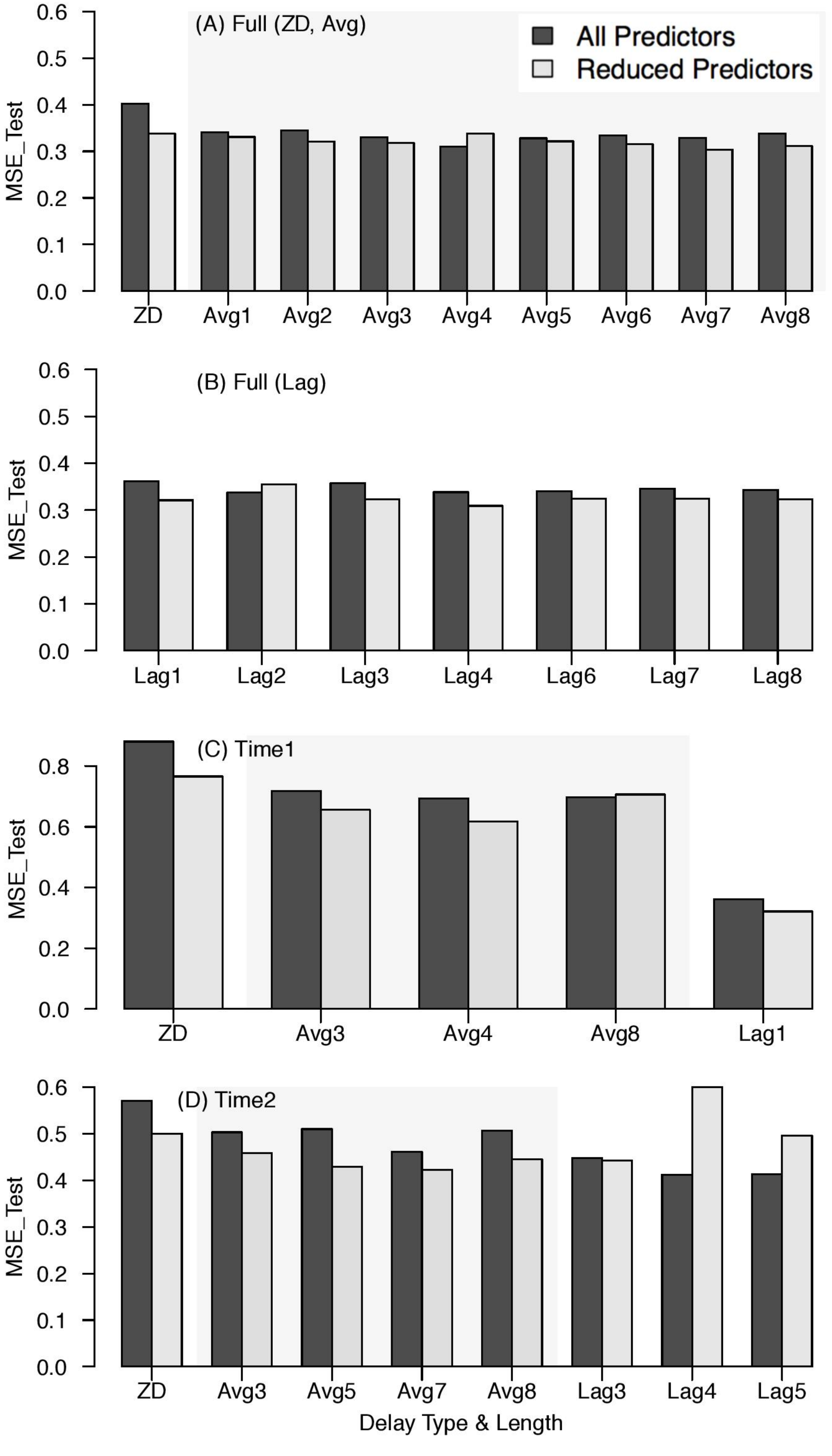


Figure 5.10: $\overline{\text{MSE}}_{\text{Test}}$ of the best delay lengths for each delay type and period. Dark grey bars represent the models trained with all predictors; light grey bars represent the models trained with the reduced predictor set (i.e., only the most influential pressures for the given delay. (A) Full period, moving average predictors; (B) Full period, lag predictors;

(C) Time1; (D) Time2. The faint shaded boxes indicate the moving average models (to differentiate from ZD and Lag). Note difference in scale for Time1.

I assessed the forecast potential using the Full period to include the maximum number of observations for training. The Avg4 pressures had the best predictive power for this period and were therefore used to build the forecast models. The *n*-fold cross validation results showed that the model captured the general trends in the functional groups, but little of the variability around the trends (Fig. 5.11A). For example, the benthivore and piscivore biomass indices exhibited obvious linear trends over the Full period, which were well represented by the model. In contrast, the macrozoo-piscivore index had high inter-annual variability with no overall trend, and the model essentially fit the mean of the index (Fig. 5.11A). This is likely a consequence of the simple NN structure (e.g., 1 hidden node), which constrains the flexibility of the model.

The forecast-5 model generally reflected the results of the n-fold cross validation. The accuracy of the forecast-5 predictions varied for the different functional groups, and generally did not reflect inter-annual variability. Based on Fig. 5.11B and 5.12, this model performed the best for benthivores and piscivores, and tended to underestimate the biomass of the other functional groups (particularly macrozoo-piscivores). The only notable difference in $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ between the forecast-5 and *n*-fold cross validation results was for macrozoo-piscivores, for which the forecast-5 $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ was notably worse than that of the *n*-fold and nfold-5 (by a factor of about 2.5; Fig. 5.12). In contrast, the forecast-10 model performed notably worse than the *n*-fold cross validation for three functional groups: benthivores, macroplanktivores, and piscivores (by a factor ranging from about 2.5 to 6; Fig. 5.12). This model generally underestimated the biomass of benthivores and overestimated that of macroplanktivores and piscivores (Fig. 5.11C). There was more uncertainty in the ensemble predictions of most functional groups for the forecast-10 models compared to the *n*-fold and forecast-5 models (Fig. 5.11).

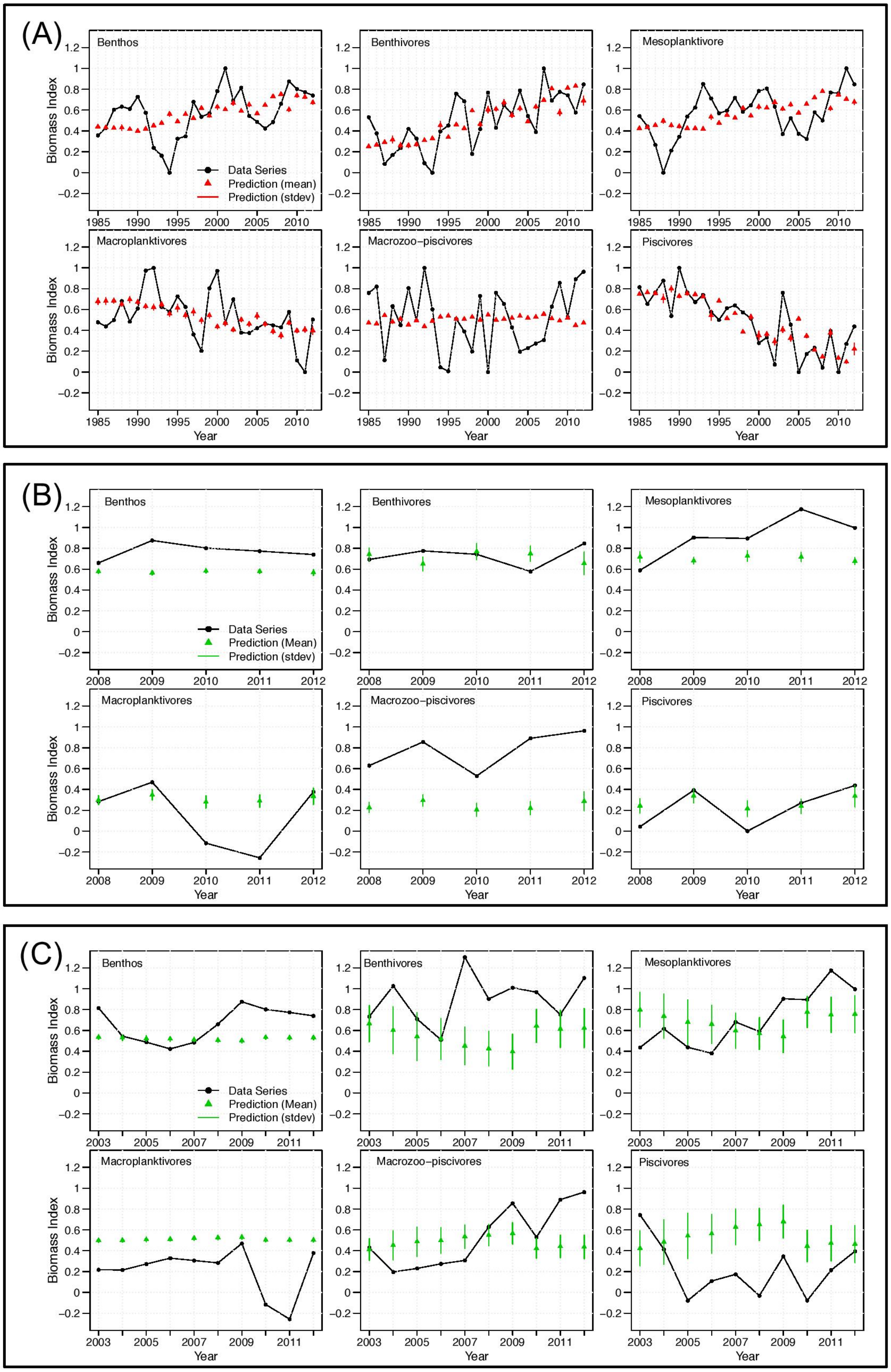


Figure 5.11: Average and standard deviation of the predictions for each functional group over the Full period using Avg4 predictors: (A) n-fold cross validation; (B) 5-year forecast; (C) 10-year forecast.

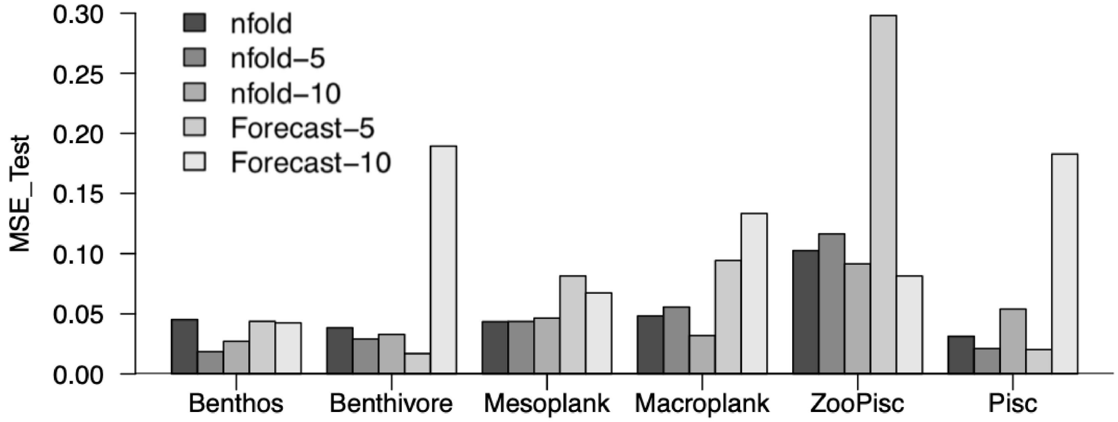


Figure 5.12: Mean squared error of the predictions for each functional group over the Full period using Avg4 predictors for the three prediction cases. (mesoplank = mesplanktivore; macroplank = macroplanktivore; zoopisc = macrozoo-piscivore.)

5.4.3 Results comparison

The best delay lengths and most influential pressures varied depending on the model type, delay type, and period. The NN models generally highlighted more influential pressures than the MLR models. Avg predictors generally performed the best for both approaches, with most delay lengths similar to or notably better than the corresponding ZD predictors. Most of the NN Lag ensembles were also similar to or notably better than the ZD predictors, although three delay lengths for Time2 were notably worse (Fig. 5.8). In contrast, the MLR Lag assemblages were similar to or notably *worse* than the corresponding ZD predictors. Considering the best NN models, a higher proportion of environmental pressures were considered influential in the Avg ensembles compared to the Lag ensembles for each period. In contrast, a higher proportion of environmental pressures were considered influential for the best MLR Lag assemblages – in fact, no environmental pressures were influential for the Full or Time1 Avg assemblages. There were no such patterns for the fishing pressures.

There was some overlap in the best delay lengths for each period across the model types (where best delay lengths were identified with the adjusted-R^2 for the MLR assemblages and $\overline{\mathrm{MSE}}_{\mathrm{Test}}$ for the NN ensembles; see sections 5.3.3.2 and 5.3.3.3). Here I highlight these common delay lengths (including ZD) to provide a more direct comparison of the goodness of fit and influential pressures resulting from each method. In all cases, the

MLR assemblages had notably better fit than the corresponding NN ensembles. The difference in MSE between the two approaches was smallest for the Full period, which had three overlapping best delay types and lengths: Avg7, Lag4, and Lag6. No single pressure was influential in all of these models, although elasmobranch landings was influential for all except one (MLR Avg7). For all delay lengths except Avg7, the NN highlighted the same pressures as the MLR analysis, plus two additional fishing pressures. This provides strong evidence for considering these common pressures as influential for the associated delay length and type, and is consistent with the observation that the NN criteria generally highlighted more pressures than the MLR criteria. The common pressures included pelagic and elasmobranch landings and copepod abundance for ZD; elasmobranch landings for Avg4; and elasmobranch landings and copepod abundance for Lag6. Both Lag4 models and the MLR Avg7 model highlighted only fishing pressures. Influential environmental pressures were copepod abundance (in both ZD and Lag6 models), SSS, and bottom salinity (in NN Avg7).

Time1 had the largest difference in fit between the NN and MLR models (Fig. 5.13). The only overlapping delays were ZD and Avg4, so I also compared the fits of the best overall Lag results from each approach (Lag1 for NN; Lag7 for MLR). The average MLR MSE was about 3.5 times better than the corresponding average NN MSE, while the *best* MLR model was about 15 times better than the best NN model for ZD and Avg4. The ZD and Avg4 models for both NN and MLR included pelagic landings and SSS. The NN Avg4 ensemble additionally highlighted mollusk landings, SST, and SSS. The NN ZD ensemble highlighted two additional fishing pressures (total and mollusk landings), while the MLR ZD assemblage highlighted bottom salinity.

Time2 had the most overlapping delay lengths, with three Avg delays (Avg3, Avg5, Avg7), and three Lag delays (Lag3, Lag4, Lag5). The average MLR MSE ranged from 1.5 to 2 times better than the average NN MSE. Most of these delays had common pressures between the two approaches: copepod abundance for ZD; total landings and NAO for Avg7; total landings and SSS for Lag3; total landings for Lag4; copepod abundance for Lag5. Copepod abundance was the only influential pressure for several MLR models (ZD, Avg3, and Lag5).

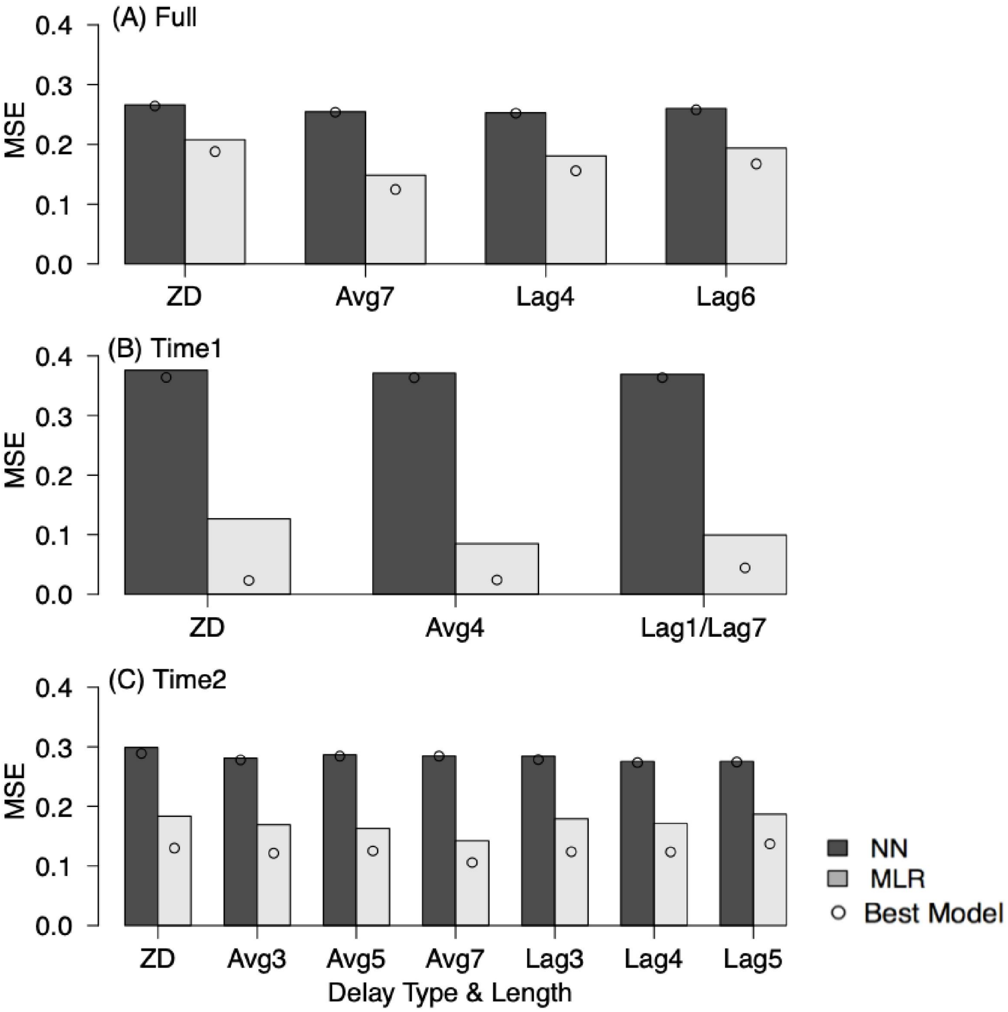


Figure 5.13: Average fit of the NN ensemble (dark bars) and MLR assemblage (light bars) for the common best delay lengths. Open circles indicate the overall best fit of the ensemble or assemblage. Note that for Time1 there was no common delay length for the lag models, so I compared the best delay length for each approach (Lag1 for NN; Lag7 for MLR).

The MLR approach generally highlighted one to three influential pressures for each assemblage (Fig. 5.5). On average, these reduced models explained less than half (~44%) of the variance explained by the best model in the assemblage (Fig. 5.6). In contrast, the NN approach generally highlighted three to five influential pressures for each ensemble, and these reduced sets typically had marginally different fit and predictive power as compared to the whole predictor set (Figs. 5.9 and 5.10), although there were a few exceptions.

5.5 Discussion

Here I synthesized the results to gain new insight into the methods used and the dynamics of the Georges Bank fish community. The average fit of the MLR assemblages was notably better than that of the corresponding NN ensembles (Fig. 5.13). This is likely because MLR finds the best fit for each functional group, and then averages the MSEs. In contrast, NN fits all of the responses simultaneously, which may result in compromises among the different functional groups (i.e., for a given functional group the fit could be worse than if it was the only response). Increasing the number of hidden nodes does improve the NN fit. For example, for Time1 ZD pressures, a 3-hidden node ensemble has about the same average fit as the corresponding MLR assemblage, and the best model of a 4-hidden node ensemble has about the same fit as the best MLR model. However, increasing the number of hidden nodes may be at the cost of losing predictive power (Fig. 5.8), and care should be taken when applying this strategy to avoid over-fitting the data.

For a broad perspective on the pressures in the region, I reviewed the most influential pressures from the best NN ensembles and MLR assemblages. The salinity metrics stand out as the most common influential environmental pressures overall for the NN models (Fig. 5.9). Both SSS and bottom salinity were influential in most of the best NN ensembles for the Full period, and several of the best Time2 ensembles, while SSS was included in most of the best ensembles for Time1. Salinity has been related to zooplankton community size structure on Georges Bank and adjacent regions (Pershing et al. 2005, Kane 2007), which in turn has been related to fish community dynamics, including recruitment regimes (Perretti et al. 2017), record high levels of planktivore biomass (Kane 2007), and recovery (or lack thereof) of commercially important species (Mountain and Kane 2010). It is reasonable to suggest that in the analysis, changes in salinity were a proxy for changes in the structure of the zooplankton community. A more direct measure of copepod abundance was also included as a pressure; however, it was considered influential less often than salinity for the best NN models of all three periods. This suggests that zooplankton community structure is a more important non-linear driver of the fish community than total abundance. Shifts in zooplankton community structure may favour certain fish species over others, thus impacting the structure of the fish community. For example, Mountain and Kane (2010) suggest that a shift to smaller zooplankton on Georges Bank in the 1990s contributed to the recovery of haddock and lack of recovery of cod because of the different feeding characteristics of the two fish species. In contrast to the NN results, total copepod abundance was the most common influential environmental pressure for the MLR models. It was considered influential more often than either salinity metric for the best MLR assemblages, and is the only influential pressure highlighted for several of the Time2 models (Fig. 5.5). This suggests a direct, linear relationship between total copepod abundance and the fish community biomass, but that it can be eclipsed by the strength of the non-linear relationships extracted by the NN. It is encouraging that both types of model highlight environmental pressures related to secondary production, and this provides strong evidence that it is an important driver.

The most influential fishing pressure was less coherent across the periods. Over the Full period, the most influential fishing pressure was elasmobranch landings for both types of model (Fig. 5.5 and Fig. 5.9). This suggests that unlike copepod abundance, elasmobranch landings have a first-order linear impact not dwarfed by non-linearity in the other pressures. Historically, elasmobranches were considered low-value, "under-utilized" species on Georges Bank and the surrounding regions (MAFMC and NEFMC 1999, NEFMC 2003). Landings were low (Fig. 5.3), and often the result of bycatch in other fisheries (Burgess et al. 2005). Throughout the 1980s, the more lucrative fishery for groundfish (e.g., cod, haddock) collapsed, and directed fishing on alternative species such as dogfish and skates was encouraged (NEFMC 2003, Burgess et al. 2005). Spiny dogfish (*Squalus acanthias*) is the dominant species by biomass in the piscivore functional group, and is thought to be the major predator in the region (i.e., can out-compete other piscivores for food resources; Link and Garrison 2002). The dogfish fishery was unregulated and expanded rapidly in the early 1990s, as total piscivore biomass decreased (Fig. 5.2; MAFMC and NEFMC, 1999). Landings peaked in 1996, at about five times higher than the average of the 1980s (NEFSC 2003). Landings subsequently declined, and stringent management quotas were implemented in the early 2000s (NEFSC 2003). By the late 2000s, dogfish spawning stock biomass had recovered (NMFS 2009). Skates are targeted with trawls as bait for lobster traps, and are also sometimes landed as food for humans when caught as bycatch in other fisheries (e.g., monkfish, scallops; NEFMC

2003, Burgess et al. 2005). The three main landed species are: little skates (*Leucoraja erinacea*), which is the dominant species in the macro-zoopiscivore functional group, and winter skates (*Leucoraja ocellata*) and thorny skates (*Amblyraja radiata*), which are both piscivores (Burgess et al. 2005). Elasmobranch landings are likely considered influential over the Full period because they reflect major changes that occurred in the ecosystem, including the collapse of groundfish species, and the decline and recovery of dogfish, the major piscivore. Additionally, these landings directly impacted two functional groups by removing biomass, and likely indirectly impacted others through removal of predators and competition.

Pelagic and mollusk landings were the most influential fishing pressures for Time1, particularly for the NN ensembles. Pelagic fisheries target several species, including Atlantic herring, which dominates the meso-planktivore functional group, and Atlantic mackerel, another meso-planktivore (Tyrrell et al. 2008). These small pelagic fish are considered key forage species in the region, providing a trophic link between secondary producers and higher trophic level consumers (e.g., cod, sharks, seabirds, and whales). Like elasmobranches, pelagic landings were low throughout the 1980s, albeit for different reasons. While harvesters attempted to avoid elasmobranch species, the principal pelagic species were heavily exploited through the 1960s and 1970s. This contributed to a collapse of herring stocks, and subsequently limited pelagic landings (Melvin and Stephenson 2007). However, the results here suggest that the pelagic fishery continued to have immediate and delayed impacts on the fish community. Even small landings at this time would have represented a relatively large proportion of the forage fish available to predators, and may have kept the food supply sufficiently low to limit growth of higher trophic level species. In fact, the biomass indices of most functional groups in this analysis had small, negative slopes over this period (Fig. 5.2; slope values not shown), indicating there was a decrease in abundance and/or decrease in mean size of individuals. The mollusk fishery targets and mainly lands Atlantic sea scallops (dominant species in the “benthos” functional group), which is one of the most lucrative fisheries in the region (NEFSC 2014). There was no distinct trend in mollusk landings for this period. Landings were high in the late 1970s, but there was a rapid decline from 1977 – 1985, prior to a small increase in the late 1980s and subsequent decrease in the early 1990s (Fig. 5.3).

Medium to long delays were among the best models for this period (Avg4, Avg8 for NN; Avg7, Lag8 for MLR), which suggests that delayed effects of the previously high landings were still affecting the fish community during Time1. Shorter delays from the NN analysis (ZD, Lag1) also suggest more immediate impacts on the community, such as direct removals of benthos biomass. Indirect impacts could be removal of prey, and destruction of habitat from scallop dredges (Hall-Spencer and Moore 2000, Fuller et al. 2008).

Few fishing pressures were considered influential for Time2 in the MLR analysis, particularly for the ZD and Avg assemblages (Fig. 5.5). This may be related to management measures, including the three year-round Closed Areas (two on Georges Bank proper and one in southern New England) that were implemented to support the recovery of groundfish. These regions (comprising nearly 25% of the bank; Link et al. 2005) were closed to commercial bottom trawling gear in late 1994, and have yet to be fully re-opened (i.e., have been closed for the duration of Time2). Closed areas have been shown to improve size, density, biomass, and diversity of organisms inside compared to outside the area (Halpern 2003, Davies et al. 2015). Increases in mean individual size of several species (e.g., haddock, skates, scallops) and dramatic increases in scallop density (~25-fold) have been reported inside the Georges Bank Closed Areas (Link et al. 2005, Fogarty and Botsford 2007, Davies et al. 2015). The reduced fishing pressure in these regions may have made environmental pressures such as NAO and copepod abundance relatively more influential on the whole community. In contrast to the MLR results, total landings were included in most of the best NN models for Time2, along with mollusk landings (Fig. 5.9). This suggests that impacts of fishing are still occurring in the region, but through non-linear or indirect mechanisms.

Alternatively, the differences in the NN and MLR results for Time2 could be an indication that the criteria for selecting influential pressures from the MLR analysis was too stringent. This may also explain why the MLR analysis generally highlighted fewer pressures than the NN. To investigate, I ran a brief sensitivity analysis on the thresholds used for identifying influential pressures. First, I increased the threshold for the MLR analysis such that a pressure was considered influential if it had P50 within 0.20 of the most frequent pressure (from the original threshold of 0.10). This did not change the conclusions for the Full and Time1 periods, although additional pressures were highlighted for several assemblages. For Time2, additional environmental as well as fishing pressures were highlighted, including for assemblages that only had influential environmental pressures at the lower threshold (e.g., pelagic and mollusk landings for ZD; pelagic landings for Avg2; total landings for Avg4; not shown). This shows that fishing pressures, while not technically “influential” based on the original criteria, are still important during this period. I also experimented with the threshold used for the NN analysis. First, I doubled it such that pressures with *%Contribution* ≥0.20 were considered influential, but this highlighted very few pressures for any period or delay (i.e., no pressures were considered influential for most ensembles). Next, I halved the threshold, which was also not informative because it highlighted most pressures for most ensembles. This supports the use of the original, moderate threshold. I recommend that future applications of these methods apply such sensitivity analyses to provide a measure of confidence in the results.

The most influential pressures were sensitive to modelling decisions, including choice of model, delay type and length, and the number of observations. Some of this may reflect real ecosystem dynamics. For example, the NN can reflect non-linear pressure-response relationships. The delay types incorporate different information into the predictors: the Avg predictors smooth the data, and reflect the trend in the pressure, while the Lag predictors emphasize the inter-annual variability. Additionally, it is not unreasonable to expect the relative influence of pressures to change over delay length and time period studied (Mann and Drinkwater 1994). For example, I argued that total landings were less influential for the MLR models in Time2 because large portions of the bank were closed to fishing.

Although the fit was generally improved with the MLR models, there remains unexplained variance in the model. It is unreasonable to expect the model to explain all of the variance in such a dynamic system, particularly because there is inherent uncertainty in the data used to calculate the response and pressure indicators; however, the fit could possibly be improved by including pressures not considered here. Based on the results, alternative indicators of secondary production may be useful. For example, direct metrics of the size structure of the zooplankton community (e.g., small-large copepod anomaly, as recorded by the NEFSC) may be more ecologically meaningful than total copepod abundance, because they better reflect the availability of food for size-selective predators (Mountain and Kane 2010, Suca et al. 2018). Different metrics of fishing pressure may also prove to be informative (e.g., fishing mortality rate or fishing effort). Other metrics of mortality not represented in the models include recreational landings and predation by sea birds and mammals. I also recommend monitoring and eventually including new pressures on the ecosystem, for example noise and chemical pollution from future oil and gas activities (Templeman 2010, DOI 2018), and ocean acidification (Preziosi and Runge 2014, Di Santo 2015, Lesser 2016).

The accuracy of the forecasts was variable among the functional groups (Fig. 5.11), but in general there was significant room for improvement in all of the forecast models analyzed here. It appears that the 1-hidden node NN ensembles were only able to model the trends in the data and did not have the flexibility required to capture inter-annual variability. Increasing the number of hidden nodes is a tempting option to increase the complexity of the model. I re-ran the forecast analyses (n-fold, forecast-5, and forecast-10) using 2 hidden nodes, but the only notable difference was worse predictive power for mesoplanktivores in the forecast-5 model (by a factor of about 3). This, along with the results in Fig. 5.7, demonstrates that the added complexity can over-fit the data, resulting in worse forecast ability. I recommend exercising caution when increasing the number of hidden nodes. Results of the forecast analysis suggest that the predictive power of the *n*-fold cross validation provides a good estimation of the model's performance on short-term forecasts (e.g., 5 years), but not for longer term forecasts (e.g., 10 years). However, it is possible that the forecast-10 results were relatively poor because reserving 10 years of data for testing left a small number of observations for training. I recommend continued monitoring and analysis of traditional and novel pressure indicators to create long time series for such applications. Although the forecasts in their current incarnation would not be precise enough to directly inform management, the exercise highlights additional questions for scientific inquiry (e.g., Which additional pressure(s) could improve forecast ability and why? Would including pressure-specific delays improve the predictive power? Is forecast ability improved when a separate model is built for each functional group?).

Linear regression has been an accepted ecological tool for decades, but its assumption that predictors and responses are linearly related is rarely appropriate for ecological interactions, and the form of these relationships is generally unknown (Hunsicker et al., 2016). It may therefore seem intuitive that NN, which can implicitly model non-linear relationships, would be a more appropriate tool for ecological investigations. However, MLR had a better fit and was easier to build and interpret than NN for the current application. It is possible that the approaches could provide complementary information in a management context, because NN are often considered skillful at out-of-sample predictions (e.g., forecasts). NN forecasts in this analysis were variable and could possibly be improved by including longer time series and pressure-specific delays. I recommend that future analyses compare the forecast ability of these two approaches and apply the results to EBFM initiatives.

CHAPTER 6: CONCLUSIONS

Marine fisheries collapses worldwide – including in Canada and the US – have led to global calls to supplement traditional single species management with EBFM approaches, which explicitly consider interactions among species in the context of changing environment, human use, and social well-being (e.g., Misund and Skjoldal 2005, DFO 2007). EBFM requires a vast array of information about the coupled human-ecological system. This can be provided in part by data-based indicators, including metrics of the fish community, pressures on this community, and socio-economic conditions. Implementation of EBFM will benefit from a better understanding of the relationships among these indicators, and analytic methods for choosing which to include in scientific and management exercises.

Throughout this thesis, I developed methods for assessing relationships among ecological indicators, including identifying pressures that best explain changes in the fish community. I first synthesized a suite of indicators for the Grand Bank, and used simple correlations to examine relationships among fish functional groups, to identify potentially redundant human and environmental indicators, and to suggest causal relationships between indicators. Efforts to categorize them into a commonly used conceptual framework were used to critique the ability of such qualitative approaches to interpret indicators. Next, I applied a multivariate linear regression approach to model the biomass indices of six fish functional groups using nine fishing and environmental pressures, and identified the most influential pressures. I conducted a similar analysis using a neural network approach, assessing the fit, predictive power, and most influential pressures, and then compared the results to the linear approach where appropriate. Finally, I applied both approaches to the Georges Bank ecosystem to test the generality of the results and conclusions.

6.1 Major Findings

The major findings of this thesis correspond to the objectives listed in Chapter 1, as summarized below.

1. Synthesize and analyze indicators for the Grand Bank to draw insights about ecosystem dynamics and investigate the utility of a common management framework.

I synthesized and published a suite of 39 biological, human activity, and environmental indicators spanning 29 – 39 years for the Grand Bank ecosystem. These indicators can be used in a variety of applications, which I illustrated in this chapter with correlation analyses and a management categorization exercise. I demonstrated that relationships between the fish functional groups changed among the three periods of interest, and that correlations between these functional groups generally increased at non-zero lags. I identified a subset of indicators that were representative of the human activities and environmental categories, and showed that the fish community responds to changes in drivers and pressures over different time scales. These findings reiterated the need to include multiple indicators in analyses intended to support management decision-making, and illustrated the importance of selecting an ecologically meaningful time frame for indicator analysis. The attempt to organize the indicators into the DPSIR framework showed that this classification is not straightforward, and could have resulted in erroneous conclusions about the ecosystem dynamics. I proposed a revised DPSIR framework that better reflects fisheries management considerations, including interactions among components of the state and management responses differentially affecting the other categories. I found it was more useful to categorize forcing factors as endogenic (manageable) or exogenic (unmanageable) than as drivers and pressures.

2. Evaluate the explanatory power of linear models that use fishing and environmental pressures to predict changes in the fish community of the Grand Bank before and after the biomass collapse (Chapter 3).

A linear approach was used to evaluate the explanatory power of all possible subsets of nine pressures for predicting changes in six fish functional group biomass indices. I identified the most influential predictors, and showed that there is no single type of pressure driving fish community dynamics on the Grand Bank. The Before period had remarkably high explanatory power compared to the other periods, due to changes in the relationships among and within the pressures and responses. Results showed a shift in the most influential pressures After the collapse, which reflects the change in environmental conditions and harvester behavior in response to the groundfish moratoria in the mid-

1990s. There was no one set of pressures that best predicted fish community status for any period or delay type length, which suggests there are strong indirect effects of many pressures on different ecosystem constituents, such that changes in fish functional group biomass can be directly predicted from different combinations of pressures. In general, moving average predictors had higher explanatory power than lagged predictors for both periods, which suggests that trends in pressures are important for predicting changes in the fish community. My analysis of pressure-specific delays showed that assigning a carefully chosen delay to each predictor can further improve the explanatory power; however, many of the mixed delay models did not, which highlighted the need for mechanistic models to investigate suitable delays. Here I added to the current understanding of this ecosystem, while demonstrating a method for selecting pressures that could be useful to scientists and managers in other ecosystems.

3. Assess the utility of neural networks for explaining observed changes in the Grand Bank fish community using fishing and environmental pressures (Chapter 4).

Neural networks (NN), a non-linear approach, was used to model the six fish functional group biomass indices using nine fishing and environmental pressures. I evaluated the fit and predictive power, and identified the most influential pressures for each period for different delay types (moving average and lag) and lengths (0 – 10 years). Unlike for the multivariate linear regression (MLR) approach, the delay type and length had negligible impacts on the NN fit; however, the MLR fit was notably better than that of the corresponding NN models. The NN predictive power was impacted by the delay choices, and I showed that a combination of current and past pressures is needed to best predict the fish community on the Grand Bank. The results of both approaches suggested that both top-down and bottom-up forcing have influenced the fish community over the past several decades, and that the most influential pressures shifted after the collapse. A preliminary investigation of NN forecast ability showed that the accuracy of the forecast differs among functional groups, and that *n*-fold cross validation provides a useful estimation of the model's predictive power. Finally, I summarized advantages and disadvantages of the linear and non-linear approaches, and concluded that MLR may prove more useful for this application, although NN may be able to provide complementary information from other applications.

4. Assess both linear and non-linear approaches for explaining changes in the Georges Bank fish community, and recommend the most useful approach for future analyses (Chapter 5).

I compared the linear (MLR) and non-linear (NN) approaches developed in the previous chapters for modelling the Georges Bank fish community, and for identifying the most influential pressures over different time periods comprising three decades. MLR models were more straightforward to build and interpret than the NN models, and also resulted in better fit, which suggests that the MLR approach is more suitable for this application. Total copepod abundance was the most influential environmental pressure for the MLR models, suggesting a direct, linear relationship between total copepod abundance and the fish community biomass. Elasmobranch landings were the most influential fishing pressure over the Full period, likely because they reflect major changes that occurred in the region, directly impact two functional groups, and indirectly impact others by removing predators and competition. Preliminary investigations of NN forecast ability suggest that *n*-fold cross validation provides a useful estimation of predictive power, particularly for short term forecasts, although future efforts are needed to improve these forecasts. I recommended MLR as the most useful approach for the current application, but suggested that future analyses into NN forecast ability are warranted.

6.2 Implications

The MLR approach is superior to the NN approach for this application

There are advantages and disadvantages associated with both modelling approaches. The results of this thesis show that the MLR approach is superior to the NN approach for the application explored here. The MLR models consistently fit the data better than the corresponding 1-hidden node NN in both regions, which implies that we can give more credence to the influential pressures identified from the MLR approach. Additionally, the MLR models were easier to build and interpret, which suggests that it would be more straightforward disseminate results among non-experts (e.g., managers and other stakeholders).

Fishing and environmental pressures are influential

With few exceptions, all of the best models (particularly NN) highlighted both fishing and environmental pressures as influential for the two ecosystems. This implies that other analyses attempting to model (mechanistically or statistically) the fish community in these regions should consider both types of pressures. Additionally, this implies that environmental conditions should be considered in management decisions, e.g., managers should adjust the pressures they can control to account for the ones they cannot.

Influential pressures are sensitive to modelling decisions

For a given region and period of interest, the most influential pressures were sensitive to modelling decisions, including choice of model, and delay type and length. This highlights that the two approaches model different types of relationships, demonstrates that the delay types provide different information to the model, and illustrates that the delay length impacts the relative importance of pressures. While these differences may have ecological meaning, the range of best sets can be difficult to parse. To refine the results, I recommend only applying only MLR for the reasons discussed above. Depending on the objective of the analysis, it may also be appropriate to choose a delay type and length of interest *a priori* (e.g., 3 – 5 year delay lengths for medium-term management forecasts). Otherwise, it is reasonable to identify the most influential pressures as those that influence the fish community consistently over different delays, as done here.

Influential pressures sets should be updated after pronounced ecosystem change

I showed that the most influential pressures changed in the mid-1990s for both ecosystems, illustrating the dynamic nature of marine ecosystems. This implies that the most influential pressures should be re-evaluated after pronounced change (e.g., regime shift, significant management changes), and provides motivation for incorporating principles of adaptive management (i.e., adjusting strategies based on new scientific insights; DFO 2018c) into EBFM approaches.

Pressure sets should be ecosystem specific

There were differences in the pressure sets highlighted for each region, even though most of the candidate pressure indicators were the same. This implies there are true differences between these ecosystems, and provide evidence for development of ecosystem-specific pressure sets for scientific and management purposes.

Collect and analyze lower trophic level data

I found that the structure of the zooplankton community may be an important pressure on the Georges Bank fish community, which implies that programs to continue collecting and monitoring these data should be supported.

6.3 Future Work

Address autocorrelation

Throughout this thesis I chose to mainly ignore the issue of autocorrelation. In terms of the MLR approach, it is possible that autocorrelation could affect the goodness of fit (adjusted-R^2) and therefore the influential pressures. It may be useful to run a simulation exercise to investigate this issue. For example, one could simulate a dataset such that:

$$\mathbf{Y} = \mathbf{X}\boldsymbol{\beta} + \boldsymbol{\epsilon} \tag{6.1}$$

where $\mathbf{Y}$ is an n x r matrix of response variables; $\mathbf{X}$ is an n x p matrix of predictor variables, $\boldsymbol{\beta}$ is a p x r matrix of regression coefficients, and $\boldsymbol{\epsilon}$ is an n x r error matrix, where each column of $\boldsymbol{\epsilon}$ is drawn from an autoregressive model (i.e., errors are correlated). Next, calculate the adjusted-R^2 (Equation 3.3). The level and/or type of autocorrelation in $\boldsymbol{\epsilon}$ can then be modified to evaluate how this impacts the adjusted-R^2. Similar methods could be used to explore how the number of predictors and the number of observations affect these results.

It is unclear if or how autocorrelation may have impacted the fit and influential pressures of the NN approach. Based on the literature review for this thesis (e.g., Appendix E.1), it appears that autocorrelation is rarely discussed in the context of NN models. Some NN users claim that interpretation of NN does not rely on assumptions about the underlying error distribution of the data (e.g., Olden and Jackson 2001); however, this has been refuted (Sarle 1997). In terms of forecast potential, autocorrelated variables could over-estimate the predictive power of the models, particularly when it is assessed using *n*-fold cross validation (i.e., the model knows the values of the pressures and responses before and after the observation omitted during the training, and because of the trends in the indicators, the model can essentially interpolate the omitted value). This was addressed to some extent with the forecast models, which showed that the *n*-fold cross validation provided a useful estimate of predictive power for most functional groups, particularly for short-term forecasts (e.g., 5 years). Another method to address the autocorrelation in this application would be to used block validation (e.g., train on all except k observations, $k > 1$, and then test on the omitted values).

Finally, future work could apply methods of time series analysis to model the autocorrelation (e.g., generalized least squares regression; Shannon et al. 2009, Bundy et al. 2012) and identify the most influential pressures, and compare the results to those presented here.

Capitalize on forecast potential

This thesis mainly focussed on interpreting model fit and most influential pressures from the two approaches, but did a preliminary assessment of the forecast potential of the NN models. I recommend assessments of the predictive power of the MLR models for comparison with the NN. Further investigations into the approach that performs the best should include additional rigorous test procedures, for example using more recent data (e.g., 2014 – 2018) to validate models trained on the data available for this thesis. Interpretation should consider the overall model as well as the results for each functional group separately, which could highlight groups that respond differently to the pressures, suggest the need to include additional pressures, and expose issues with data. Ultimately, these models could be used as low-cost (in terms of data, and time to build, run, and analyze) strategic models to complement existing approaches, and could provide warning signs of change in the fish community, allowing for early management action.

Identify pressure-specific delays

Most of the models in this thesis were fit using the same delay type and length imposed on all of the pressures; however, it is reasonable to expect different pressures to manifest over different time scales. A brief analysis in Chapter 3 showed that the MLR fit can be improved using pressure-specific delays, but it was beyond the scope of this work to identify the most useful delay type and length for each pressure. I do not expect pressure-specific delays to improve the NN fit, which was not notably impacted by the delay type and length; however, imposing meaningful delays on the pressures may improve NN predictive power and/or MLR fit. Additionally, a single pressure may manifest over different times scales (e.g., fishing has immediate and long-term impacts; Beverton and Holt 1957, Daan et al. 2005, Greenstreet et al. 2011), and so including the same pressure at different delays may also improve NN predictive power and/or MLR fit. I recommend further investigation into suitable pressure-specific delays for modelling and forecasting using additional statistical analyses or mechanistic models.

Develop an idealized model

In this thesis, two statistical approaches for modelling and identifying the most influential pressures on the fish community were applied to empirical data from two regions. These analyses would be complemented by development of an idealized model of a generic ecosystem, with pressure and response indicators simulated such that the responses have varying degrees of dependence on the pressures (e.g., from highly linear or non-linear to no relationship). Such a model would be particularly useful for verifying how well each approach ranks the most influential predictors. It could help refine details of the approach, including the optimal number of candidate pressure indicators to include as predictors (for fitting efficiency and ranking importance). For the NN approach, it could also help to determine the most efficient number of ensembles and the most effective number of hidden nodes for identifying the influential pressures.

Additionally, a random variable (RV) could be included as a pressure in the empirical models used here to see how often the approach identified such erroneous information as an influential pressure. If the RV is rarely considered influential, this would improve confidence that the model highlighted truly influential pressures. In contrast, if the RV is highlighted as influential, this could indicate that none of the candidate pressures have strong relationships with the responses, or that the model is over-fitting the data.

Assess impacts of harvesting shellfish on the finfish community

The linear and non-linear approaches both highlighted shellfish landings as an influential pressure on the Grand Bank fish community, even though no metric of community shellfish biomass was included as a response. The mechanism(s) through which these landings impact the fish community could include the reduction of available food and alteration of habitat. Alternatively, shellfish landings could be acting as a proxy for another pressure not included here. I recommend further studies on the community impacts of shellfish harvesting. For example, statistical analyses of stomach content of key fish species could reveal how satiation levels and proportion of shellfish in their diet have changed over the period of interest. Underwater video assessments of the seafloor (e.g., using a "HabCam") inside and outside of shrimp fishing areas would provide insight into whether habitat destruction is slowing the recovery of benthic species. Additionally, mechanistic modelling of the ecosystem could simulate removal of shellfish biomass and habitat destruction to help resolve their impacts on the community. Finally, further research could assess whether shellfish landings were considered influential in these analyses because they are a proxy for a co-occurring or highly correlated pressure (e.g., groundfish landings) through additional literature review and modelling exercises.

Continue and expand monitoring of marine ecosystems

Here I calculated indicators from a variety of data sources for the Grand Bank. I recommend continued efforts to collect and process these data so the indicators can be updated regularly to build long indicator time series (e.g., similar to the Ecosystem Assessment Program updates to the Georges Bank indicator set; EcoAP 2012). Long time series provide a baseline of ecosystem conditions and allow scientists and managers to monitor changes over time, and may also result in more robust statistical analyses (Hardison et al., *in press*). I also recommend expanding monitoring and/or data processing to calculate additional indicators, including metrics of lower trophic level dynamics (see below) and pressures that could become more influential in the future (e.g., acidification). Additionally, the spatial and/or temporal extent of data collection and processing could be expanded. For example, the local environmental indicators for the Grand Bank are based on point observations from Station 27; separate indicators for disparate locations may provide additional useful information. Similarly, indicators presented here were annual values (generally averages), while seasonal signals may prove more informative. Ideally, these indicators will be stored in a single database and easily accessed by scientists at various government and academic institutions.

Investigate alternative lower trophic level pressure indicators

Different metrics of lower trophic level dynamics were included for the two regions. $\mathrm{Time}_{\mathrm{Ice}}$ was included as a metric for the timing of the spring phytoplankton bloom for the Grand Bank, and total copepod abundance was included for Georges Bank. Copepod abundance was considered an influential pressure for Georges Bank far more often than $\mathrm{Time}_{\mathrm{Ice}}$ was for the Grand Bank (when considering MLR and NN results). This could imply that lower-trophic level dynamics are more important for Georges Bank; however, it is possible that $\mathrm{Time}_{\mathrm{Ice}}$ as a proxy for the timing of the spring phytoplankton bloom is too far removed from higher trophic level dynamics to be a useful predictor of the fish community. To investigate the influence of secondary production on the Grand Bank, future analyses could incorporate zooplankton data from the Atlantic Zone Monitoring Program (AZMP), which has collected biological, chemical, and physical data from the Newfoundland shelf since the late 1990s (e.g., Pepin et al. 2005). I suggest repeating key analyses for the new time period using the pressures in this thesis along with zooplankton abundance to see how much it improves the fit and whether it is considered influential. Additionally, based on results in Chapter 5, future analyses should assess the utility of metrics of the zooplankton community structure (e.g., small−large copepod anomaly; Perretti et al., 2017) rather than total abundance.

Expand consideration of ecosystem state

Throughout this thesis the biomass indices of fish functional groups were considered the main metrics of ecosystem state; however, other ecosystem characteristics such as biodiversity are also of interest for EBFM (e.g., CBD, 2010; Fogarty, 2014). The approaches outlined in this thesis could potentially be applied to model, forecast, and identify the most influential pressures on these characteristics, given appropriate indicator time series. I recommend assessing the utility of these models, because the results could complement those discussed in this thesis, and provide a broader picture of the pressures impacting the ecosystem.

Apply methods to other ecosystems

The approaches used in this thesis can also be applied to other ecosystems. Scientists at DFO and NOAA have expressed interest in using these methods to explore dynamics of the Scotian Shelf (off the Southwest coast of Nova Scotia) and the Mid-Atlantic Bight (along the US East coast from southern New England to North Carolina). These analyses would complement the Northwest Atlantic case studies included in this thesis, and could add to the understanding of how the Atlantic region will respond to climate change. It would also be worthwhile to explore more disparate ecosystems to contribute to (or begin) efforts to learn about pressure-response relationships in those regions. I suggest partnering with the IndiSeas project to help inform which ecosystems to focus on and for access to data. As shown in this thesis, such analyses and their interpretation should be assessed by a local expert, e.g., someone familiar with the history of the ecosystem, including significant regime shifts, exploitation, and management decisions.

Improve understanding of neural networks

NN are considered relatively complicated, have been criticized as “black boxes,” and have limited accessible best practices for building and interpreting the model. I recommend a comprehensive review that expands on my table in Appendix E.1 by also suggesting best practices, including how to choose the number of hidden nodes and quantify predictor contributions. Additionally, I recommend that ecologists include at least a basic understanding of NN in their modelling toolbox.

Apply results to EBFM initiatives

These approaches for identifying the most influential pressure sets could be applied in an EBFM context in the “indicator development” step of an Integrated Ecosystem Assessment (Levin et al. 2009) or other indicator scoping exercises to highlight pressures that should be monitored throughout the management process. Results could also help focus studies of ecological thresholds and those characterizing pressure-response relationships (Large et al. 2015b, Hunsicker et al. 2016) by prioritizing which pressures should be included. Finally, these approaches could be used for management strategy evaluations in data-poor regions, or in data-rich areas as where mechanistic models are not yet operationalized.

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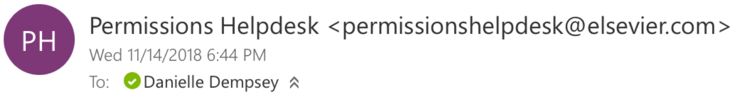
A.1: Permission form for Chapter 2



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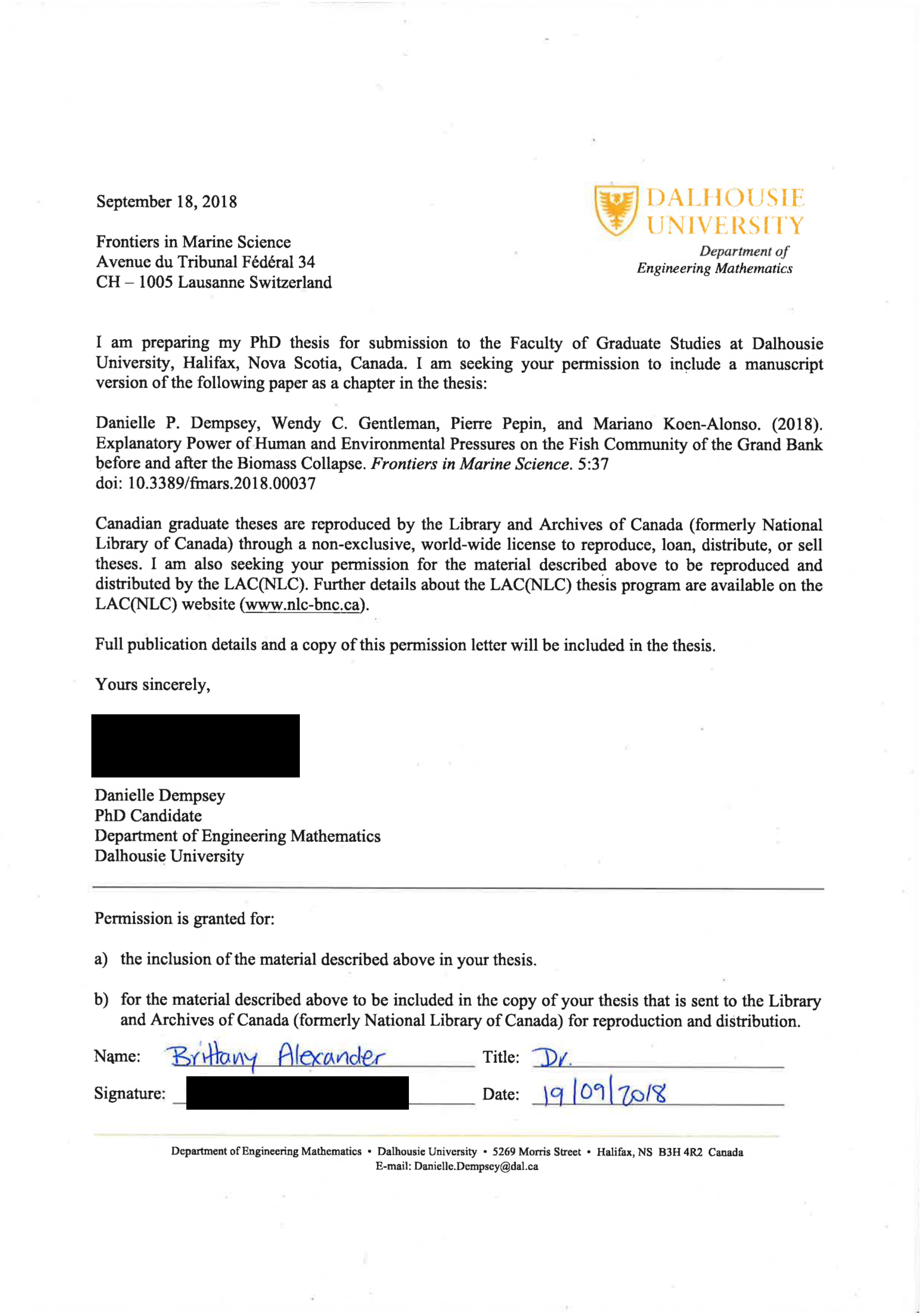

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APPENDIX B: Additional Background on Regions of Interest

B.1 Common History

The Grand Bank, (of Canadian and international waters), and Georges Bank (United States and Canada) are both economically and ecologically important, data rich fishing grounds in the Northwest Atlantic (e.g., Fogarty and Murawski 1998, Schrank 2005). These regions share common history, beginning in the Middle Ages when Vikings and Basques discovered and began to exploit their abundant fish stocks (Kurlansky 1997). Other European nations joined the fishing throughout the 1500s, and these distant water fisheries transitioned into temporary settlements, which eventually became permanent. These regions were still considered among the most productive fishing grounds in the world throughout the 20th century (Herbert 1995, Rose 2007).

In the 1930s and 1940s it was recognized that fish stocks in the Northwest Atlantic were declining (Bubier and Rieser 1986). In response, an international convention was signed by countries with fishing interests in the region (e.g., Canada, United States, Portugal, Spain, United Kingdom) to create the International Commission for the Northwest Atlantic Fisheries (ICNAF) in 1949. ICNAF was responsible for coordinating the management of stocks fished by more than one country. They organized scientific studies and set regulations meant to conserve the resources (Bubier and Rieser 1986); however, members were free to file formal objections to any regulations, and then ignore them. ICNAF had no real enforcement power, and stocks continued to decline (Rose 2007).

In 1977, Canada and the United States (US) each extended their exclusive economic zone (EEZ) from 12 nautical miles (nm) to 200 nm. The EEZ delimits an area where the state has sole exploitation rights over natural resources (including fish), and the responsibility for managing and conserving living marine resources (UNCLOS 1982). The number of stocks fished by more than one country decreased dramatically, so several countries withdrew from ICNAF, which disbanded (Rose 2007). In its stead, a treaty was signed to form the Northwest Atlantic Fisheries Organization (NAFO) in 1979. NAFO adopted some of the responsibilities of ICNAF, including scientific research for species outside of the 200 nm zones (essentially only Grand Banks stocks). All of the former ICNAF nations signed the treaty, except for the US, whose main resources fell within its new EEZ (Rose, 2007).

B.2 The Grand Bank

The Grand Bank (NAFO Division 3LNO) and the adjacent southern Labrador and northeast Newfoundland shelf (NAFO Division 2J3KL) are the major subunits of the Newfoundland-Labrador Shelf in the Northwest Atlantic (NAFO 2010a). The banks are a series of shallow plateaus where the cold Labrador current meets the warm Gulf stream, creating a nutrient rich environment that is an ideal spawning and feeding ground for many fish species. For centuries, this region was one of the most productive fishing grounds in the world, with global fisheries for Atlantic cod, flatfishes, and other species (Rose 2007).

In the late 1970s there was a decline Canadian landings from the Grand Banks (NAFO divisions 2J3KLNO), which was blamed on foreign trawlers (Rose 2008). In response, Canada extended its EEZ to 200 nm (the maximum allowed under international law), excluding foreign vessels from most of the area. Fisheries management in the region became the responsibility of Fisheries and Oceans Canada (DFO) within the EEZ, and NAFO in international waters (including straddling stocks, which cross between the EEZ and the high seas; Rose 2007). Canadian landings initially increased, but declined again as foreign fleets continued to fish on the edge of the EEZ, and Canada expanded its offshore fleet (Rose 2007, 2008). Throughout the 1980s the main management strategy for both NAFO and DFO was to set independent quotas for each fish stock; however, these measures were largely ineffective due to the disregard of these limits by some vessels and scientific challenges in calculating sustainable quotas (e.g., Rose 2007). In the 1990s prolonged heavy fishing pressure combined with an environmental regime shift caused complex ecological changes characterized by a collapse of fish biomass. This is known worldwide as “the collapse of the cod” even though many other species were also impacted (e.g., Atkinson 1994; NAFO 2010b).

In response to the low biomass of many stocks, groundfish moratoria were enforced for 2J3KL in 1992, and two years later for the Grand Bank. The moratoria were meant to reduce fishing pressure so that the fish community could rebuild (Rose 2007). At the time, government officials estimated the fisheries would be closed for two years, but many of the moratoria still remain in place over 20 years later (Rose 2007). These fisheries closures are likely part of the reason there has been some degree of recovery in the community biomass, but they also had socio-economic impacts on Newfoundland and Labrador, requiring fishers to adapt by targeting different species (e.g., shrimp and other shellfish), retiring from the fishing industry, or leaving the province to find employment elsewhere (e.g., Hamilton and Butler 2001, Schrank 2005).

Both DFO and NAFO are currently working towards implementing ecosystem approaches to management (NAFO, 2010a, 2010b; Oceans Act, 1996; DFO, 2009). Current management strategies include the At-Sea Observer Program (DFO 2014), National Vessel Monitoring System (DFO 2018a), restrictions on total allowable catches (e.g., for redfish and yellowtail flounder; NAFO 2017) gear restrictions, and restricted entry programs.

There is a wealth of data sources for Newfoundland and the Grand Bank that can be used to calculate indicators, although no set was previously published for use by scientists and managers. For example, fisheries-independent bottom trawl surveys have been carried out by DFO consistently since 1985, and provide annual biomass and abundance indices for nearly 200 fish species (McCallum and Walsh 1997). Local environmental indicators can be derived from data recorded at DFO monitoring Station 27, which is located near St. John’s, Newfoundland, and is considered representative of hydrographic conditions for the Grand Bank. Basin scale environmental indicators can be downloaded from US climate organization websites. NAFO has a database of commercial landings in the region, which can be used to calculate several fishing-related indicators, including landings of aggregate species, trophic level of landings, and fishing pressure. Finally, socioeconomic indicators data can be downloaded from the Statistics Canada database CANSIM.

B.3 Georges Bank

Georges Bank is a shallow plateau in the Gulf of Maine, bordered by three American states (New Hampshire, Massachusetts, and Maine), and two Canadian provinces (New Brunswick and Nova Scotia; Herbert 1995) in NAFO Division 5Ze. It is considered one of the four ecological productivity units (i.e., management unit) of the US Northeast Continental Shelf Large Marine Ecosystem (Lucey and Fogarty 2013), and is considered particularly vulnerable to climate change because it is at the southern edge of an ecotone separating cold and warm fish species (GLOBEC 1991). Like the Grand Bank, this region is characterized by high productivity and is a historically lucrative fishing ground for scallops, cod, haddock, and other species (Bubier and Rieser 1986).

The 200 nm limit imposed by Canada and the US created a 30,000 km^2 disputed area where the EEZs overlapped (Herbert, 1995). Canada claimed the boundary should be equidistant from each country, which would place the north-eastern half of Georges Bank under Canadian jurisdiction. The US argued that the Northeast Channel created a natural ecological boundary, which would place the entire Bank under US jurisdiction (Herbert 1995). Several attempts at bilateral agreements ultimately failed, and the boundary dispute was brought to the International Court of Justice (ICJ) in The Hague, Netherlands (Herbert 1995). The final decision was a 260 nm (480 km) long boundary between the original Canadian and US claims. Little to no regard was given to the fisheries or the related management and socio-economic considerations (Herbert 1995), and the boundary resulted in several transboundary stocks (those that cross between the EEZs of more than one country). The need for cooperative management of these stocks was recognized almost immediately; however, different management philosophies evolved on either side of the boundary (e.g., Bubier and Rieser 1986, Herbert 1995, Pudden and Vanderzwaag 2010). As on the Grand Banks, Canadian management focussed on fishing mortality limits, and management regulations primarily relied on effort control, including limited entry programs and vessel licensing, as well as output control such as TACs and quotas. US management aimed to conserve the spawning stock biomass (SSB), and management regulations included minimum mesh sizes and closed areas (Herbert 1995). Informal discussions for more cooperative management of groundfish began in 1994, and resulted in coordinated efforts on both sides of the boundary (Pudden and Vanderzwaag 2010).

Like the Grand Bank, Georges Bank experienced complex ecological changes over the past several decades. The biomass of commercially valuable groundfish species collapsed, and in response three important spawning areas in the US were closed to fishing year round, beginning in 1994 (Murawski et al. 2000). An increase in the biomasses of other species lead to a shift in the community structure and fishing effort towards species of relatively low economic value such dogfish and skates (MAFMC and NEFMC 1999, NEFMC 2003)

Today management in the region is coordinated by the Canada-US Steering Committee (SC), which was formed in 1995 and oversees three sub-committees. The Transboundary Management Guidance Committee (TMGC) provides non-binding management advice in an annual Guidance Document for cod, haddock, and yellowtail flounder. The Transboundary Resource Assessment Committee (TRAC) conducts joint Canada-US assessments for these stocks, providing the results to the TMGC. The Canada–USA Integration Committee (IC), the newest of the cooperative initiatives, is meant to facilitate the Ecosystem Approach to Management by coordinating relevant working groups (Pudden and Vanderzwaag 2007). There are also other significant efforts to implement ecosystem management approaches in the region (e.g., Link et al. 2011b, EcoAP 2012, WGNARS 2018). The Georges Bank ecosystem has long been of interest to scientists, and long data series exist. The NEFSC's Ecosystem Assessment Group has calculated a suite of biological, fishing, and environmental indicators (EcoAP, 2012), which was used in this thesis.

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APPENDICES C, D, E.1 and E.2 are attached in separate files

APPENDIX E.3: Discussion of fit metrics for comparing NN and MLR

It is not trivial to choose a goodness of fit metric to compare the neural network (NN) and multivariate linear regression (MLR) results. Here I first describe three tempting yet naïve metrics, and then discuss the metric used in this thesis. The first "naïve" metric is the R^2, which is among the most extensively used metrics for evaluating regression models (Kvalseth 1985); however, R^2 is not suitable for non-linear models, e.g., NN (Kvalseth 1985, Spiess and Neumeyer 2010). For linear models:

$$\mathrm{SS_{Total}} = \mathrm{SS_{Model}} + \mathrm{SS_{Error}} \tag{1}$$

where $\mathrm{SS_{Total}}$ is the total sum of squares of the response, $\mathrm{SS_{Model}}$ is the sum of squares of the model, and $\mathrm{SS_{Error}}$ is the sum of squares of error (residuals).

$$\mathrm{SS_{Total}} = \sum_{\mathrm{i}=1}^{\mathrm{n}} (\mathrm{y_i} - \bar{\mathrm{y}})^2 \tag{2}$$

$$\mathrm{SS_{Model}} = \sum_{\mathrm{i}=1}^{\mathrm{n}} \left(\mathrm{y_i} - \bar{\hat{\mathrm{y}}}\right)^2 = \sum_{\mathrm{i}=1}^{\mathrm{n}} (\mathrm{y_i} - \bar{\mathrm{y}})^2 \tag{3}$$

$$\mathrm{SS_{Error}} = \sum_{\mathrm{i}=1}^{\mathrm{n}} (\mathrm{y_i} - \hat{\mathrm{y}}_\mathrm{i})^2 \tag{4}$$

Where n is the number of observations, $\mathrm{y_i}$ are the observed values, $\hat{\mathrm{y}}_\mathrm{i}$ are modelled values, $\bar{\mathrm{y}}$ is the mean of the observed values, and $\bar{\hat{\mathrm{y}}}$ is the mean of the modelled values. For linear models, $\bar{\mathrm{y}} = \bar{\hat{\mathrm{y}}}$, leading to the two equations for $\mathrm{SS_{Model}}$ (equation 3). Note that equations 2, 3, and 4 are for models with a single response variable. For multivariate models, these metrics are summed across each response prior to inclusion in equation 1.

Equation 1 holds true because the vector of errors is perpendicular to the vector subspace containing the predicted values of the responses, and leads to the common R^2 equations:

$$\mathrm{R}^2 = \frac{\mathrm{SS_{Model}}}{\mathrm{SS_{Total}}} \tag{5A}$$

$$\mathrm{R}^2 = 1 - \frac{\mathrm{SS_{Error}}}{\mathrm{SS_{Total}}} \tag{5B}$$

For non-linear models, equation 1 may not hold true because the error vector is no longer guaranteed to be perpendicular to the vector of predicted responses. This leads to problems calculating R^2, e.g., equations 5A and 5B (and other R^2 formulations) may not be equivalent (Kvalseth 1985), and R^2 may be less than 0 or greater than 1 (Spiess and Neumeyer 2010). Spiess and Neumeyer (2010) used a simulation model to demonstrate that R^2 can lead to erroneous conclusions, and recommend other metrics be used when investigating non-liner models. Note that the adjusted-R^2 (which was used to evaluate the MLR models in Chapter 3 and Chapter 5) is based on the R^2, and so the above discussion also applies to why I did not compare the approaches using adjusted-R^2. Additionally, adjusted-R^2 recognizes that the degrees of freedom of the error vector decreases as more predictors are added, which is not necessarily true for non-linear models.

A second "naïve" metric that is often applied in the NN literature is the squared correlation between the modelled and observed values (Appendix E.1), here designated with the lower-case r^2 to distinguish it from the R^2 of the multiple regression shown in equation 5. Intuitively, it may seem that a high r^2 suggests a good model; however, this only holds true when the modelled vs. observed values fall on the 1-to-1 slope line. A relationship with a higher or lower slope could also have a high r^2 but would suggest a bias in the model (i.e., over- or under-estimating the observations; Fig. 1). While it may be possible to identify and correct the bias, this does not appear to be common in the literature.

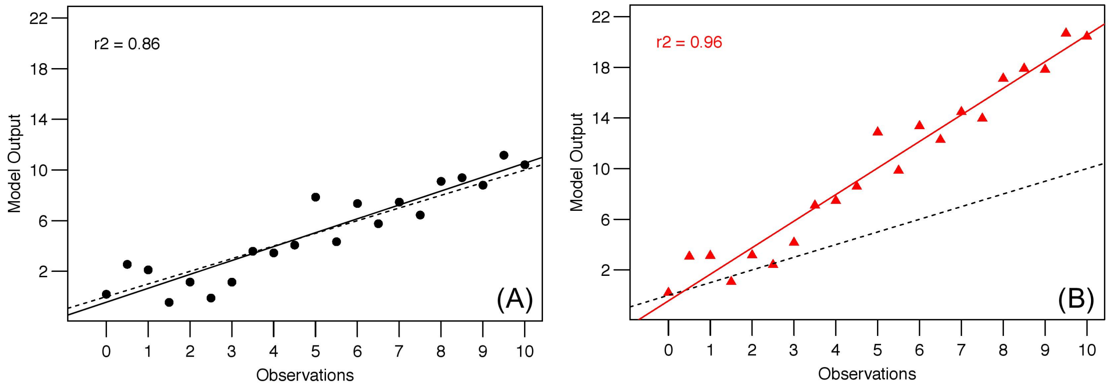

Figure 1: Illustration of why the r^2 of the modelled vs. observed values is not a useful goodness of fit metric. The r^2 is high for both models, but the model in panel B over-estimates the observations.

Finally, it may seem reasonable to compare the approaches using a metric based only on the errors between the observed and modelled values, for example the mean squared error (MSE).

$$\mathrm{MSE} = \frac{1}{n}\sum_{i=1}^{n}(y_i - \hat{y}_i)^2 \qquad (6)$$

Where (as above) n is the number of observations, y_i are the observed values, and $\hat{y}_i$ are the corresponding modelled values. This metric is valid only if the responses are scaled the same for both approaches, *which may not be the case* for NN and MLR. NN outputs are generally linearly mapped to the interval [0,1] to increase the speed of convergence of the backpropagation (gradient descent) algorithm, while MLR outputs are generally normalized to have zero mean and unit variance to reduce numerical errors. Figure 2 shows two models that at first glance appear to have the same fit, but inspection of the scale of the ordinate axes shows that the errors in B are larger than those in A, i.e., they have different units. For a proper comparison of the fits, the outputs must be on the same scale. Additionally, because MSE depends on scale, it should not be used to compare models for data sets that have different ranges of values.

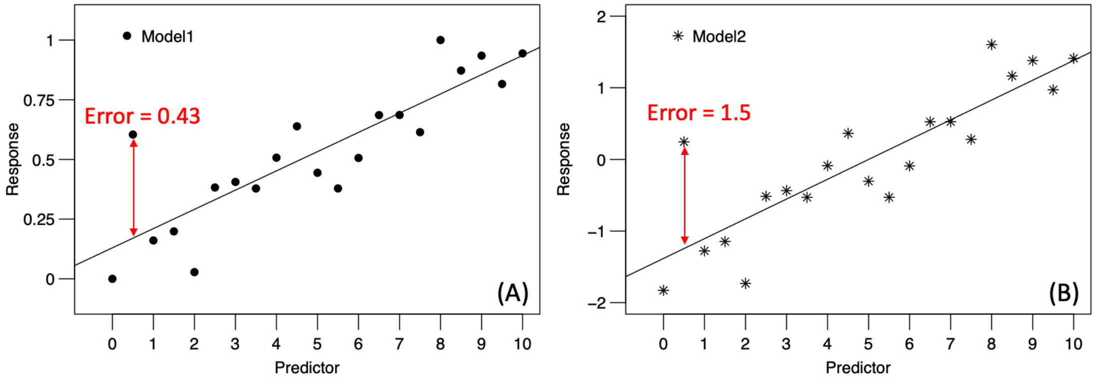

Figure 2: Illustration of how different scaling of the output can influence the value of the errors. Note that because $\mathrm{SS_{Total}}$ is also on a different scale in the two figures, the ratio $\mathrm{SS_{Error}}/\mathrm{SS_{Total}}$ is the same, and hence they have the same R^2.

To compare the fits of the two approaches, I re-ran the MLR all-possible-combinations analyses with the responses linearly mapped to [0,1] to be consistent with the scaling of the NN responses.

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APPENDIX F: Principal Component Analysis and Redundancy Analysis: Methods and Results

This section briefly describes the methods and results of (i) principal component analyses on the functional group biomass indices and the pressure indicators for the three periods of interest, and (ii) redundancy analysis using the functional group indices as responses and the pressures and predictors.

F.1 Methods

F.1.1 Principal component analysis

Principal component analysis (PCA) is a data reduction technique that partitions the variability of a dataset $\mathbf{Y}_{\mathrm{nxr}}$ into *r* linear combinations of the original variables. It is often used to identify and explore common trends in the variables comprising the columns of $\mathbf{Y}$. The linear combinations are called principal components (PC), and are defined such that the "first" PC accounts for as much of the variance in $\mathbf{Y}$ as possible. The "second" PC accounts for as much of the remaining variance as possible, under the constraint that it is orthogonal to the first. Successive PCs continue to explain the remaining variance, subject to the constraint of being orthogonal to all of the preceding components. All *r* PCs are required to reproduce the total variability of $\mathbf{Y}$, but in general most of this variability can be accounted for by the first *k* PCs.

The orthogonal transformation of the original data into the matrix of PCs ($\widetilde{\mathbf{Y}}_{\mathrm{nxr}}$) is given by the eigenvectors of the covariance matrix of $\mathbf{Y}$, $\mathbf{S}_{\mathbf{YY}}$ (Equation F.1):

$$\widetilde{\mathbf{Y}} = \mathbf{Y} * \mathbf{E}_{\mathrm{rxr}} \tag{F.1}$$

where each column of $\mathbf{E}_{\mathrm{rxr}}$ is one eigenvector. Thus, the coefficients for the *i*th PC are the elements of the *i*th eigenvector of $\mathbf{S}_{\mathbf{YY}}$, denoted $\boldsymbol{e_i}$ (Equation F.2). The variance of the resulting PC_i is given by the corresponding eigenvalue, λ_i, such that $\lambda_1 > \lambda_2 > \ldots \lambda_r$. The eigenvalues guide selection of *k*, i.e., the number of principal components that together represent an acceptable amount of the variability in $\mathbf{Y}$ (as defined by the user).

The elements of eigenvector *i* provide insight into the relationships highlighted by PC_i (Equation F.3).

$$PC_{\mathrm{i}} = \mathbf{Y} * \mathbf{e_i} \tag{F.2}$$

$$\mathrm{PC_i} = \begin{bmatrix} y_{11} & y_{21} & \cdots & y_{r1} \\ y_{12} & y_{22} & \cdots & y_{r2} \\ \vdots & \vdots & \cdots & \vdots \\ y_{1n} & y_{2n} & \cdots & y_{rn} \end{bmatrix} * [\mathrm{e_1} \quad \mathrm{e_2} \quad \cdots \quad \mathrm{e_r}]_{\mathrm{i}}^{\mathrm{T}} \tag{F.3}$$

Here, PCA was used to identify the dominant trends in the functional groups and pressures for the three periods of interest.

F.1.2 Multivariate Regression

Multivariate regression is an extension of simple linear regression that uses *n* observations on *p* predictors in $\mathbf{X}_{\mathrm{nxp}}$ to fit a multiple regression model for each of the *r* responses in $\mathbf{Y}_{\mathrm{nxr}}$ (Equation F.4). The fitted (also called "modelled" or "predicted") values are stored in the matrix $\widehat{\mathbf{Y}}_{\mathrm{nxr}}$, and matrix $\widehat{\boldsymbol{\beta}}_{\mathrm{nxr}}$ holds the coefficients for linear combinations of the predictors. The values of $\widehat{\boldsymbol{\beta}}_{\mathrm{nxr}}$ that minimize the squared error between the modelled values and observations are calculated using the normal equations:

$$\widehat{\boldsymbol{\beta}} = (\mathbf{X^TX})^{-1}\mathbf{X^TY} \tag{F.4}$$

where the superscript symbols "T" and "-1" respectively denote the matrix transpose and inverse. It is assumed that the columns of **X** are linearly related to the columns of **Y**, and so appropriate transformations must be applied if necessary. Commonly, predictors and responses are normalized by centering and scaling them by their respective mean and standard deviation to minimize numerical error in solving for $\widehat{\mathbf{Y}}$ (Legendre and Legendre 2012). When the predictors are scaled, the $\widehat{\boldsymbol{\beta}}$ values can be interpreted to help to identify the most influential predictors. For example, if $|\widehat{\boldsymbol{\beta}}_{1,1}| \gg |\widehat{\boldsymbol{\beta}}_{2,1}|$, then predictor 1 is more influential for modelling response 1 than predictor 2.

F.1.3 Redundancy Analysis

Redundancy analysis (RDA) is a combination of multivariate regression and PCA that can be used to identify the most influential predictors of a multivariate analysis. As applied here, RDA has three main steps:

1. Multivariate regression: $\widehat{\mathbf{Y}} = \mathbf{X} * \widehat{\boldsymbol{\beta}}$

Compute $\widehat{\mathbf{Y}}$, i.e., the "predictable part" of $\mathbf{Y}$.

2. PCA: $\widetilde{\mathbf{Y}}_{\mathbf{k}} = \text{first } k \text{ columns of } \widetilde{\mathbf{Y}} = \widehat{\mathbf{Y}} * \mathbf{E}_{\mathrm{rxr}}$

Perform PCA on $\widehat{\mathbf{Y}}$ to determine the *k* dominant modes.

3. Multivariate regression: $\widehat{\boldsymbol{\beta}} = (\mathbf{X}^{\mathbf{T}}\mathbf{X})^{-\mathbf{1}}\mathbf{X}^{\mathbf{T}}\widetilde{\mathbf{Y}}_{\mathbf{k}}$

Model $\widetilde{\mathbf{Y}}_{\mathbf{k}}$, the *k* dominant modes of $\widehat{\mathbf{Y}}$. Compute $\widehat{\boldsymbol{\beta}}$ and analyze coefficients to determine the most influential predictors.

RDA was applied here to see which pressures had the most influence on the predictable part of the functional groups biomass matrix.

F.2 Results for the Grand Bank

F.2.1 Principal Component Analysis

F.2.1.1 Full Period

Functional Groups

The dominant mode of the Full period functional group biomass indices ($\mathrm{PC1}_{\mathrm{Full,Fgroups}}$) accounts for nearly half of their variance (47%; Fig. F.1). It approximately represents the sum of large benthivores and piscivores contrasted with small benthivores (and to a lesser extent planktivores contrasted with medium benthivores; Fig. F.2A). This PC shows a rapid decline from the late 1980s to the mid-1990s, and a slow increase over the remainder of the period, reflecting the collapse and slow recovery of fish biomass on the Grand Bank over the past three decades (Fig. F.2A). The second mode ($\mathrm{PC2}_{\mathrm{Full,Fgroups}}$) accounts for 30% of the variance, such that together the first two PCs account for 77% of the functional group biomass variability over the Full period (Fig. F.1). $\mathrm{PC2}_{\mathrm{Full,Fgroups}}$ is a weighted average of the six functional groups (Fig. F.2A), with highest weights for medium benthivores, planktivores, and plank-piscivores; mid-range weights for large and small benthivores; piscivores have an insignificant role. $PC2_{Full,Fgroups}$ reflects a similar overall trend as $PC1_{Full,Fgroups}$, but incorporates more inter-annual variability from the planktivores and plank-piscivores, begins to increase earlier (~1992 vs. 1996), and increases at a faster rate.

Pressures

The dominant mode of the Full period pressure indicators ($PC1_{Full,Press}$) accounts for 38% of the variance (Fig. 3). It mainly reflects the fishing pressures, and represents the sum of total and pelagic landings contrasted with shellfish landings (and to a lesser extent, temperature; Fig. 4A). It declines until the late 1990s, and then has no trend for the remainder of the period (Fig. 4A). The second mode ($PC2_{Full,Press}$) accounts for 20% of the variance, such that together the first two PCs account for over half (58%) of the variation in the pressures of the Full period (Fig. F.3). $PC2_{Full,Press}$ mainly reflects the environmental pressures, and is an average of SST, SSS, bottom salinity, and Time_Ice (and to a lesser extent, pelagic and shellfish landings; Fig. F.4A). The sharp reduction in salinity in the the early 1990s is reconstructed with this index (Fig. F.4A).

F.2.1.2 Before Period

Functional Groups

The dominant mode of the Before period functional group biomass indices ($PC1_{Before,Fgroups}$) accounts for 63% of their variance, more than for any other period (Fig. F.1). It approximately represents the sum of large and medium benthivores, piscivores, and planktivores contrasted with small benthivores (Fig. F.2B). It has an overall decreasing trend with little inter-annual variability, reflecting the collapse of fish biomass in the region during this period (Fig F.2B). The second mode ($PC2_{Before,Fgroups}$) accounts for 21% of the variance, such that together the first two PCs account for 84% of the variance (Fig. F.1). $PC2_{Before,Fgroups}$ is a weighted sum of the functional groups, with the highest weight on plank-piscivores, mid-range weights for medium and small benthivores and planktivores, and small negative weights for large benthivores and piscivores (Fig. F.2B). $PC2_{Before,Fgroups}$ mainly captures the changes in plank-piscivore biomass, which is highlighted by the high correlation between the two indices (Pearson correlation coefficient = ~0.91; not shown).

Pressures

The dominant mode for the Before period pressure indicators ($PC1_{Before,Press}$) accounts for 50% of their variance, more than for any other period (Fig. F.3). It had no trend for the first five years, but decreased rapidly for the last five years (Fig. F.4B). This index is a weighted average of the nine predictors, with the highest weights for total and pelagic landings, shellfish landings (negative), MTI, and SSS, and moderate weights for NAO (negative), SST, Sbottom, and Time_Ice (Fig. F.4B). The moderate differences in the weights for each pressure shows they all contributed to this dominant decreasing trend. The second mode ($PC2_{Before,Press}$) accounts for 18% of the variance, such that together these two modes account for 68% of the variance in the pressure over the Before period (Fig. F.3). Shellfish landings, SST, bottom salinity, and TimeIce have the highest weights, while total landings (negative), MTI (negative), NAO, and SSS have moderate weights (Fig. F.4B). This PC has a slight overall increase over the period, with a sharp decrease in the early 1990s reflecting the salinity anomaly at that time (Fig. F.4B).

F.2.2.3 After

Functional Groups

The dominant mode of the After period functional group biomass indices ($PC1_{After,Fgroups}$) represents nearly half of their variance (~48%; Fig. F.1). This mode increases over the period, and approximately represents the average of all the functional groups except small benthivores (Fig. F.2C). The second mode ($PC2_{After,Fgroups}$) accounts for 19% of the variance, so together the first two PCs account for 67% of the variance (Fig. F.1). $PC2_{After,Fgroups}$ is a weighted average of small benthivores, plank-piscivores, and planktivores contrasted with large and medium benthivores (Fig. F.2C). It has a slight decreasing trend over the period, but little to no trend in the later years of the period, reflecting the slow recovery of fish biomass in the region (Fig. F.2C).

Pressures

The dominant mode of the After period pressures accounted for 26% of the variance, notably less than the other periods (about half of that explained for the Before period; Fig. F.3). It increased from the beginning of the period until about 2006, and then decreased (Fig. F.4C). Total and shellfish landings had the highest weights, with moderate weights assigned to pelagic landings, MTI (negative), bottom salinity, and Time_Ice (Fig. F.4C). The second mode ($PC2_{After,Press}$) accounted for 19% of the variance, such that the first two modes accounted for 45% of the variance (Fig. F.3). $PC2_{After,Press}$ had no distinct trend over this period. It was dominated by bottom salinity, but the remaining pressures (except for SST and Time_Ice) had moderate weights (Fig. F.4C).

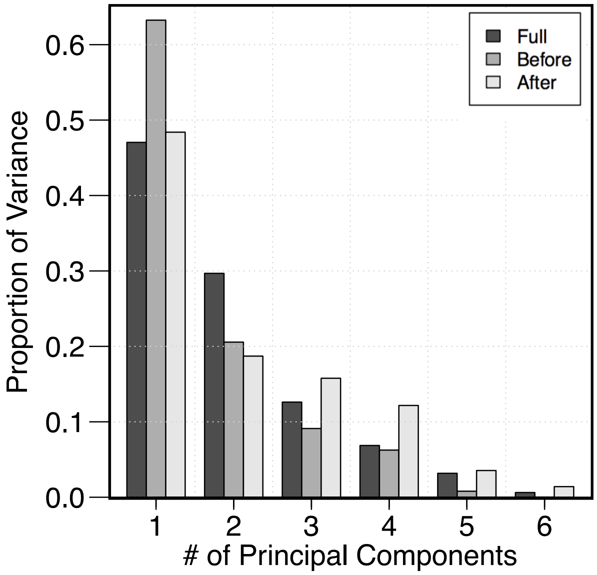

Figure F.1: Scree plot for the PCA of the Grand Bank fish functional group biomasses for each period.

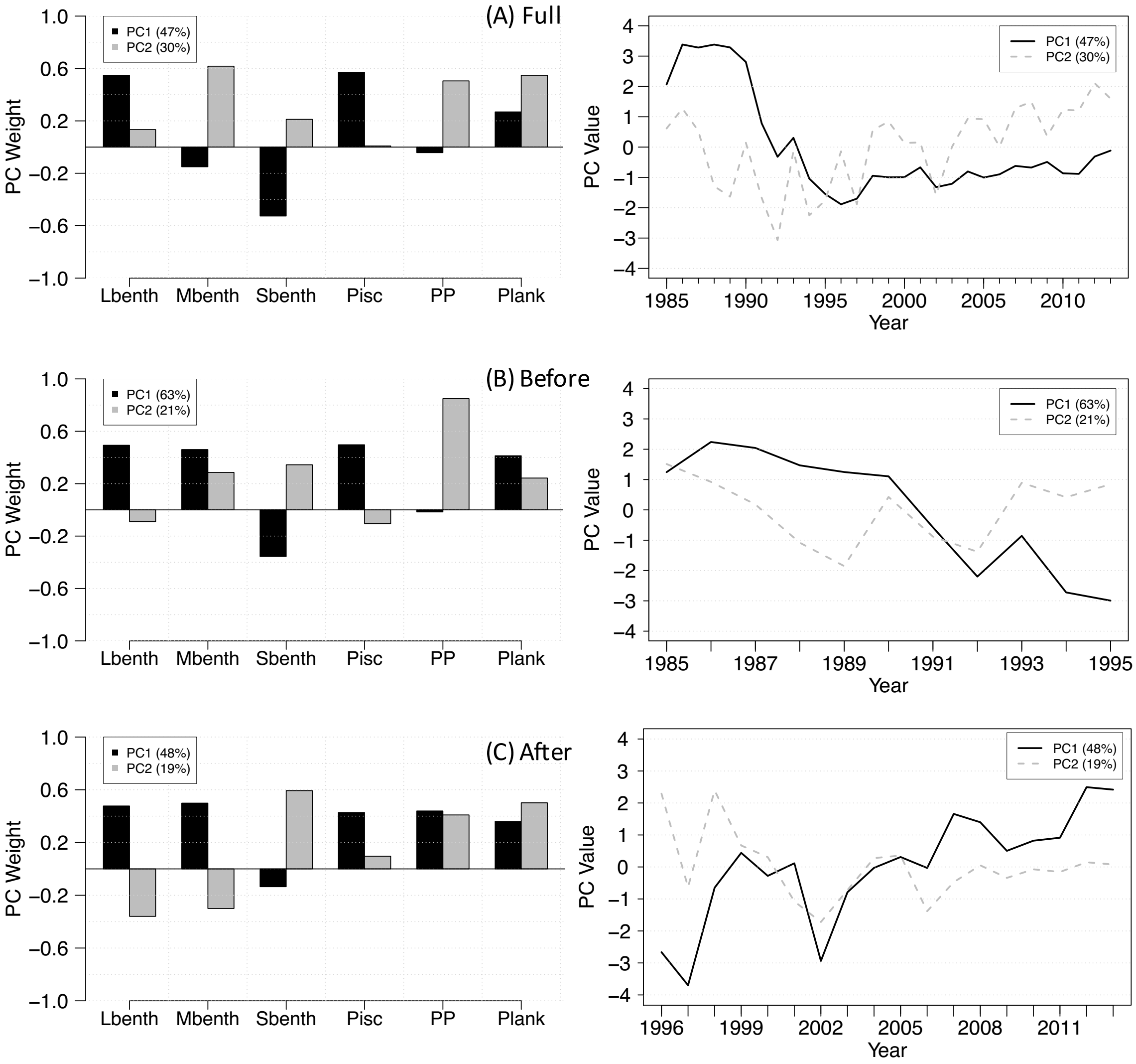

Figure F.2: Weights (left column) and values (right column) for the principal components of the Grand Bank fish functional groups for the (A) Full, (B) Before, and (C) After periods.

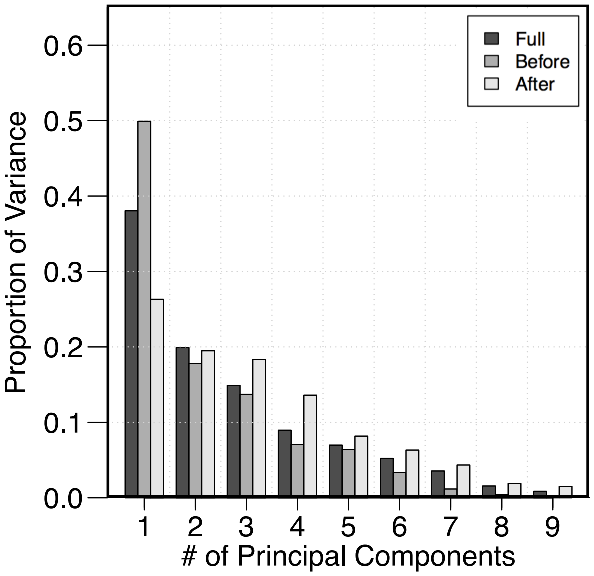

Figure F.3: Scree plot for the PCA of the Grand Bank pressure indicators for each period.

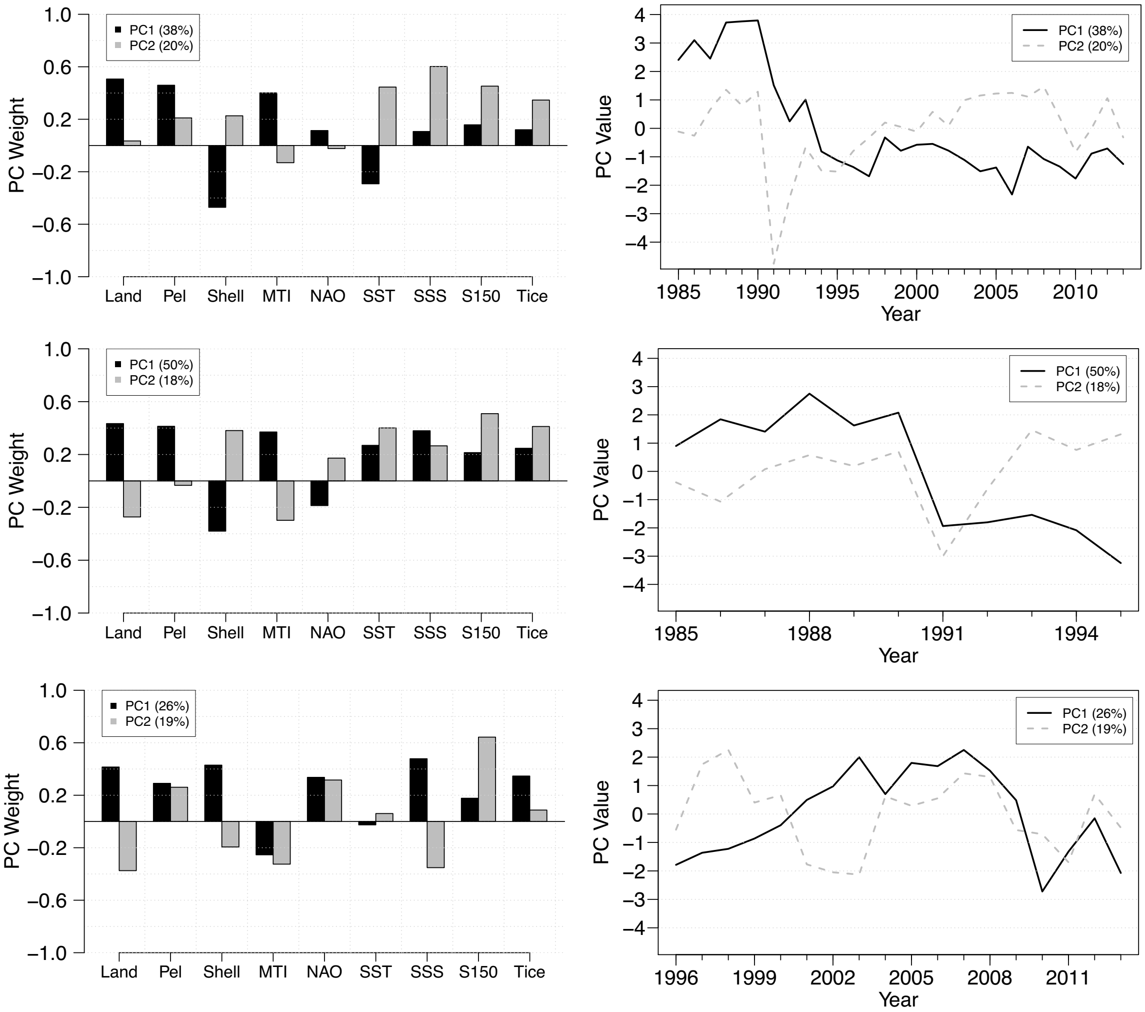

Figure F.4: Weights (left column) and values (right column) for the principal components of the Grand Bank pressure indicators for the (A) Full, (B) Before, and (C) After periods.

F.2.2 Redundancy Analysis

The first principal component of the fitted values of the functional groups ($\hat{\mathbf{Y}}$, the “predictable part of Y”) accounted for >=60% of the variance for each period, and the second principal component accounted for an additional 15 – 25 % (Fig. F.5). The weights and values of the dominant models were almost identical to their counterparts for the PCA performed on the Y matrix (Figs. F.2 and F.6). This shows that the regressions were able to model the dominant trends in the fish community data.

Total landings were the most important predictor for the Full and Before periods, with a regression coefficient 6 and 4 times larger, respectively, than the next biggest coefficient

(Fig. F.7). In contrast, there was no obvious single most important predictor for the After period. Two fishing related pressures (MTI and shellfish landings) had the highest coefficients. The smallest magnitude coefficient was for S150, and the remaining pressures had mid-range coefficient values (Fig. F.7).

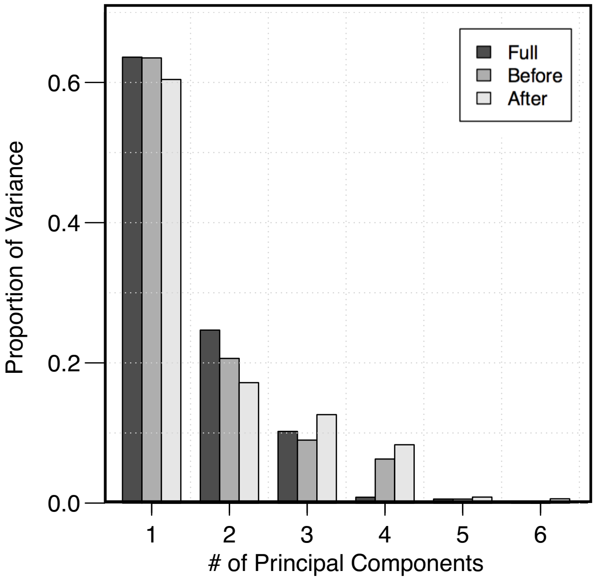

Figure F.5: Scree plot for the PCA of fitted values of the Grand Bank fish functional group biomasses ($\widehat{\mathbf{Y}}$) for each period.

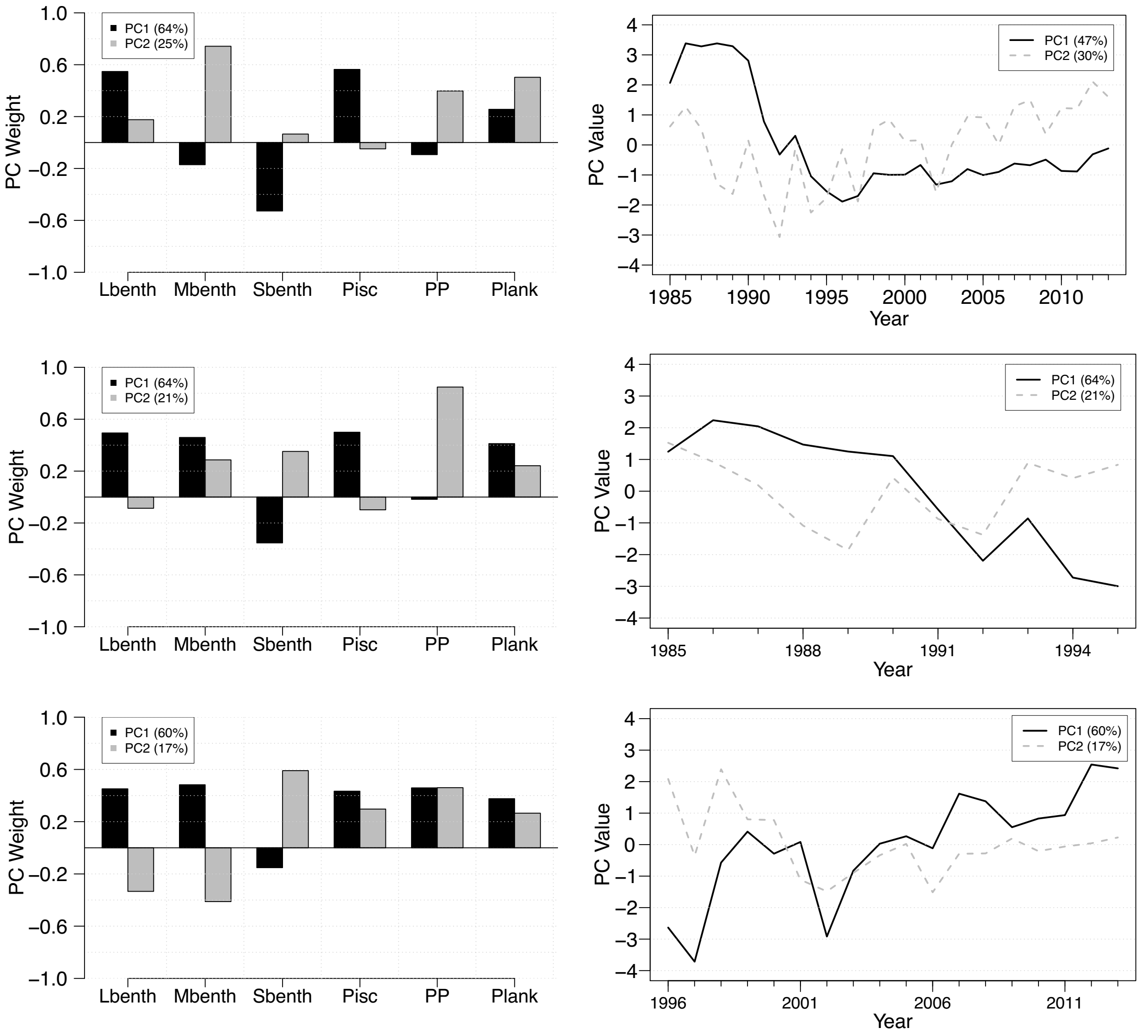

Figure F.6: Weights (left column) and values (right column) for the principal components of the fitted values of the Grand Bank fish functional groups for the (A) Full, (B) Before, and (C) After periods.

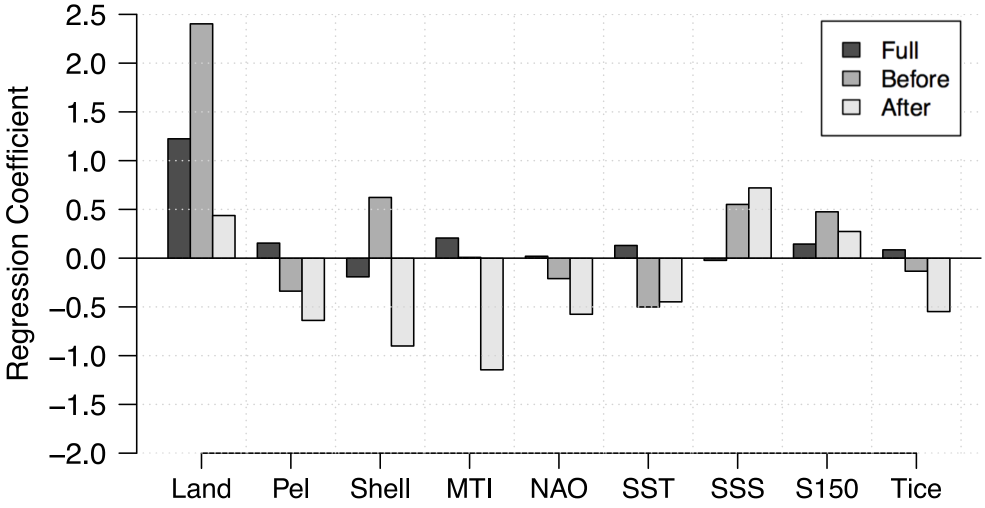

Figure F.7: Regression coefficients for PC1 projected onto the pressure indicators for each period (Grand Bank).

F.3 Results for Georges Bank

F.3.1 Principal Component Analysis

F.3.1.1 Full Period

Functional Groups

The dominant mode of the Full period functional group biomass indices ($PC1_{Full,Fgroups}$) accounts for about 36% of their variance (Fig. F.8). It approximately represents the sum of macroplanktivores and piscivores contrasted with the sum of benthos, benthivores, and mesoplanktivores (Fig. F.9A). This PC had a decreasing trend (Fig. F.9A), which reflects the decrease in piscivore and macroplanktivore biomass and overall increase in benthos, benthivores, and mesoplanktivores over the Full period. The second mode ($PC2_{Full,Fgroups}$) accounts for 20% of the variance, such that together the first two PCs account for 56% of the functional group biomass variability for this period (Fig. F.8). $PC2_{Full,Fgroups}$ has the highest weight for macrozoo-piscivores, and its values reflect the changes in the macrozoo-piscivore biomass index (Fig. F.9A).

Pressures

The dominant mode of the Full period pressure indicators ($PC1_{Full,Press}$) accounts for 29% of the variance (Fig. F.10). It approximates the sum of the two salinity metrics contrasted with the sum of elasmobranch landings and copepod abundance. Its trend reflects the changes in salinity, with a decreasing trend from 1985 – 1998 and no distinct trend for the rest of the period (Fig. F.11A). The second mode ($PC2_{Full,Press}$) accounts for 23% of the variance, such that together the first two PCs account for over half (52%) of the variance in the pressures of the Full period (Fig. F.10). $PC2_{Full,Press}$ mainly reflects the sum of total landings and mollusk landings, with moderate weights for pelagic landings, SST, and copepod abundance (Fig. F.11A). This PC is characterized by inter-annual variability, and has no distinct trend over the Full period (Fig. F.11A).

F.3.1.2 Time1

Functional Groups

The dominant mode of the Time1 functional group biomass indices ($PC1_{Time1,Fgroups}$) accounts for 38% of their variance (Fig. F.8). It approximately represents the sum of benthos, macrozoo-piscivores, and piscivores contrasted with mesoplanktivores, and has an overall decreasing trend (Fig. F.9B). The second mode ($PC2_{Time1,Fgroups}$) accounts for 24% of the variance, such that together the first two PCs account for 62% of the variance (Fig. F.8). $PC2_{Time1,Fgroups}$ is the sum of macroplanktivores and macrozoo-piscivores (and to a lesser extent mesoplanktivores and piscivores) contrasted with benthivores. This index has very little variability until 1989, at which point it increases until 1992, and then decreases for the remaining three years.

Pressures

The dominant mode for the Time1pressure indicators ($PC1_{Time1,Press}$) accounts for 45% of their variance, more than for any other period (Fig. F.10). It is approximately the sum of SST, SSS, and bottom salinity contrasted with total landings, mollusk landings, NAO, and copepod abundance. It decreased until 1992, and then increased for the remaining three years (Fig. F.11B). The second mode ($PC2_{Time1,Press}$) accounts for 26% of the variance, such that together these two modes account for 71% of the variance in the pressure over the Before period (Fig. F.10). $PC2_{Time1,Press}$ is approximately the sum of elasmobranch landings, NAO, and copepod abundance contrasted with the sum of total landings and mollusk landings. This PC has an overall increasing trend throughout this period (Fig. F.11B).

F.3.2.3 Time2

Functional Groups

The dominant mode of the Time2 functional group biomass indices ($PC1_{Time2,Fgroups}$) represents 35% of their variance (Fig. F.8). This mode is approximately the sum of benthos, mesoplanktivores, and macrozoo-piscivores. It has a slight increasing trend over the period, but a notable decrease from 2001 – 2006 (Fig. F.9C), which reflects a similar decrease in the biomass indices of these functional groups. The second mode ($PC2_{Time2,Fgroups}$) accounts for 20% of the variance, so together the first two PCs account for 55% of the variance (Fig. F.8). $PC2_{Time2,Fgroups}$ is approximately the sum of benthivores and macroplanktivores, and has no distinct trend over the period (Fig. F.9C).

Pressures

The dominant mode of the Time2 pressures ($PC1_{Time2,Press}$) accounted for 35% of the variance (Fig. F.10). It was approximately a weighted average of six pressures (total landings, pelagic landings, mollusk landings, SST, SSS, and bottom salinity) contrasted with elasmobranch landings. It increased from the beginning of the period until about 2002, and then decreased and had no trend for the rest of the period (Fig. F.11C). The second mode ($PC2_{Time2,Press}$) accounted for 24% of the variance, such that the first two modes accounted for 59% of the variance (Fig. F.10). This mode also had similar weights for several pressures, and was approximately the sum of total landings mollusk landings, and copepod abundance contrasted with NAO, SSS, and bottom salinity. It had a slight decreasing trend over the whole period, but was mainly characterized by inter-annual variability.

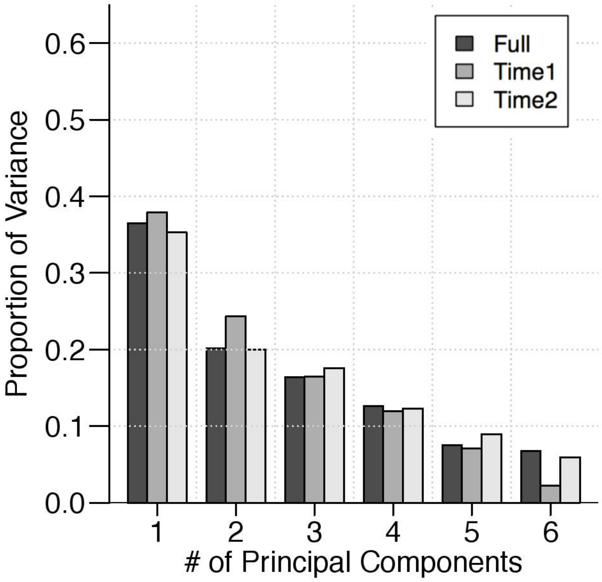

Figure F.8: Scree plot for the PCA of the Georges Bank fish functional group biomasses for each period.

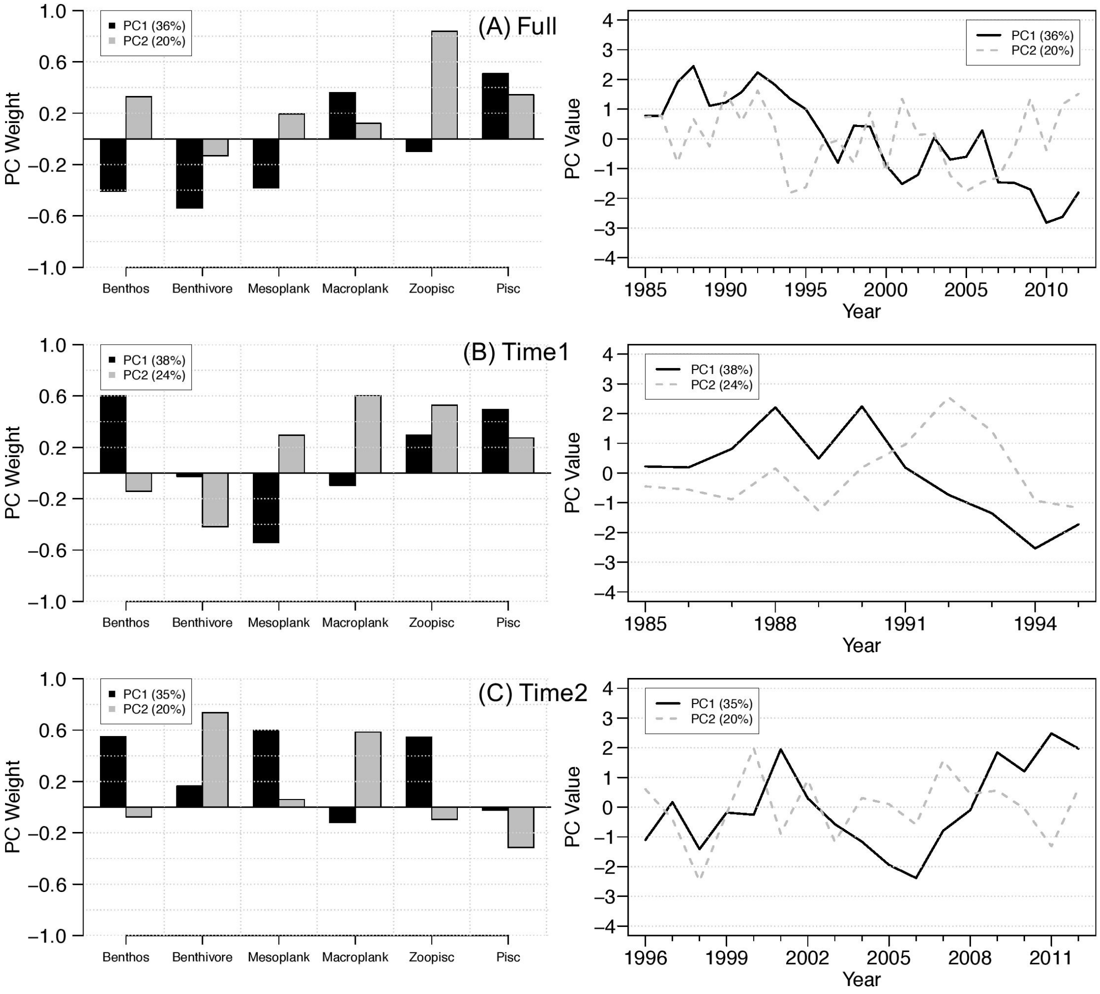

Figure F.9: Weights (left column) and values (right column) for the principal components of the Georges Bank fish functional groups for the (A) Full period, (B) Time1, and (C) Time2.

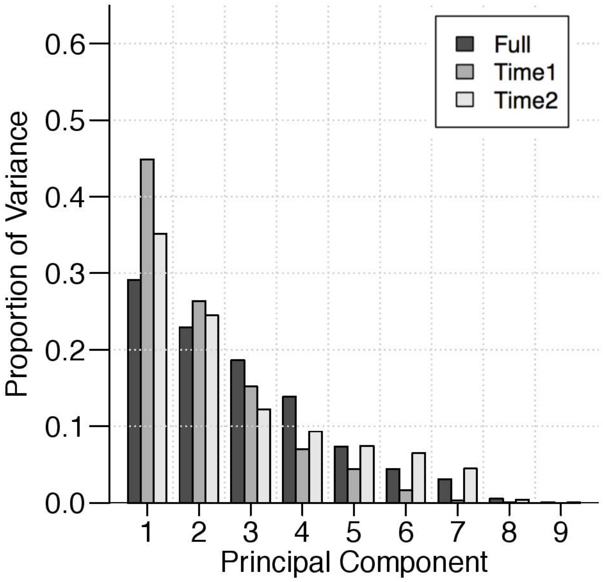

Figure F.10: Scree plot for the PCA of the Georges Bank pressure indicators for each period.

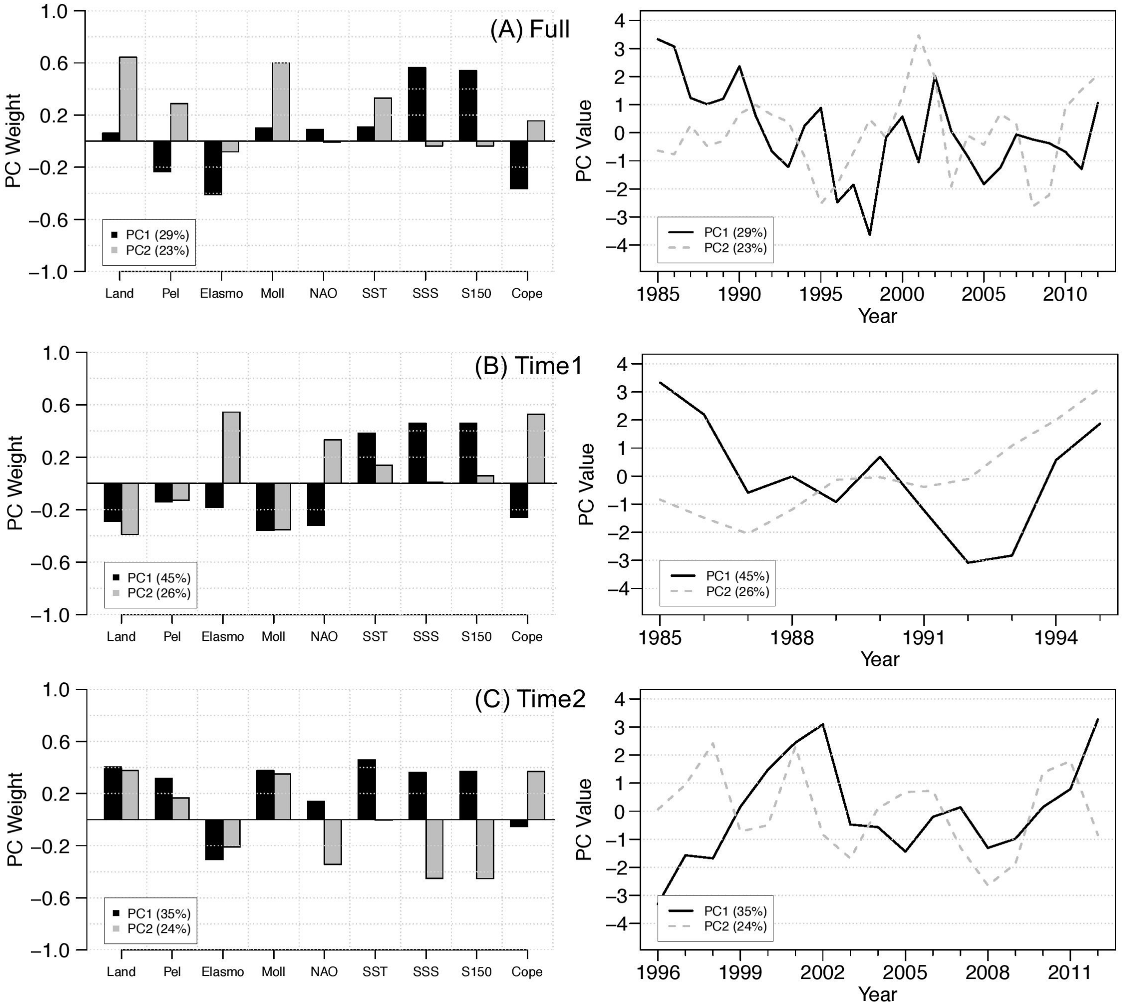

Figure F.11: Weights (left column) and values (right column) for the principal components of the Georges Bank pressure indicators for the (A) Full, (B) Time1, and (C) Time2.

F.3.2 Redundancy Analysis

The first principal component of the fitted values for the Full period accounted for more variance than that of the other periods (53% for the Full compared to 39% for Time1 and 36% for Time2; Fig. F.12). In general, the weights and values of the dominant modes were similar to their counterparts for the PCA performed on the Y matrix (Figs. 9 and 13), which shows that the regressions were able to model the dominant trends in the fish community data reasonably well.

The salinity metrics were very clearly the most important predictors for Time1, with regression coefficients ~4.5 times larger than the next largest coefficient (Fig. F.14A). The most important predictors for Time2 were total landings, pelagic landings, and the salinity metrics. For the Full period, pelagic landings had the largest coefficient, closely followed by total landings, mollusk landings, and the two salinity metrics (Fig. F.14B).

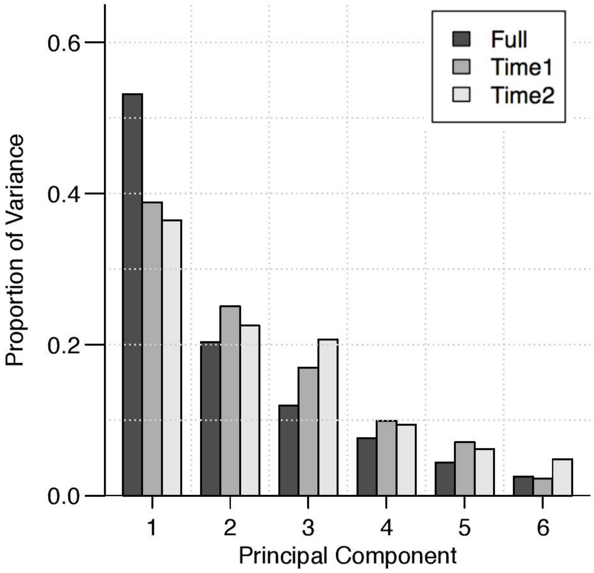

Figure F.12: Scree plot for the PCA of fitted values of the Georges Bank fish functional group biomasses ($\hat{\mathbf{Y}}$) for each period.

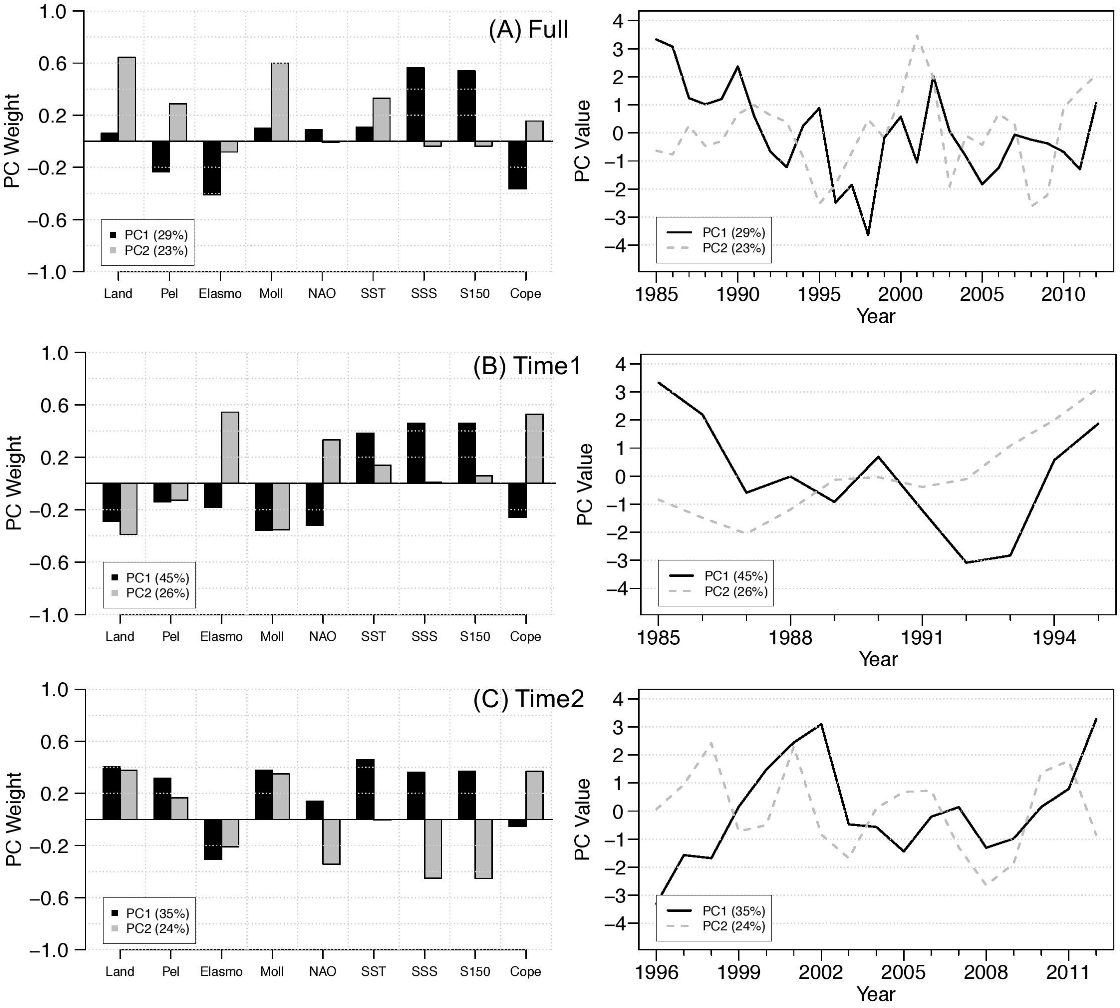

Figure F.13: Weights (left column) and values (right column) for the principal components of the fitted values of the Georges Bank fish functional groups for the (A) Full period, (B) Time1, and (C) Time2.

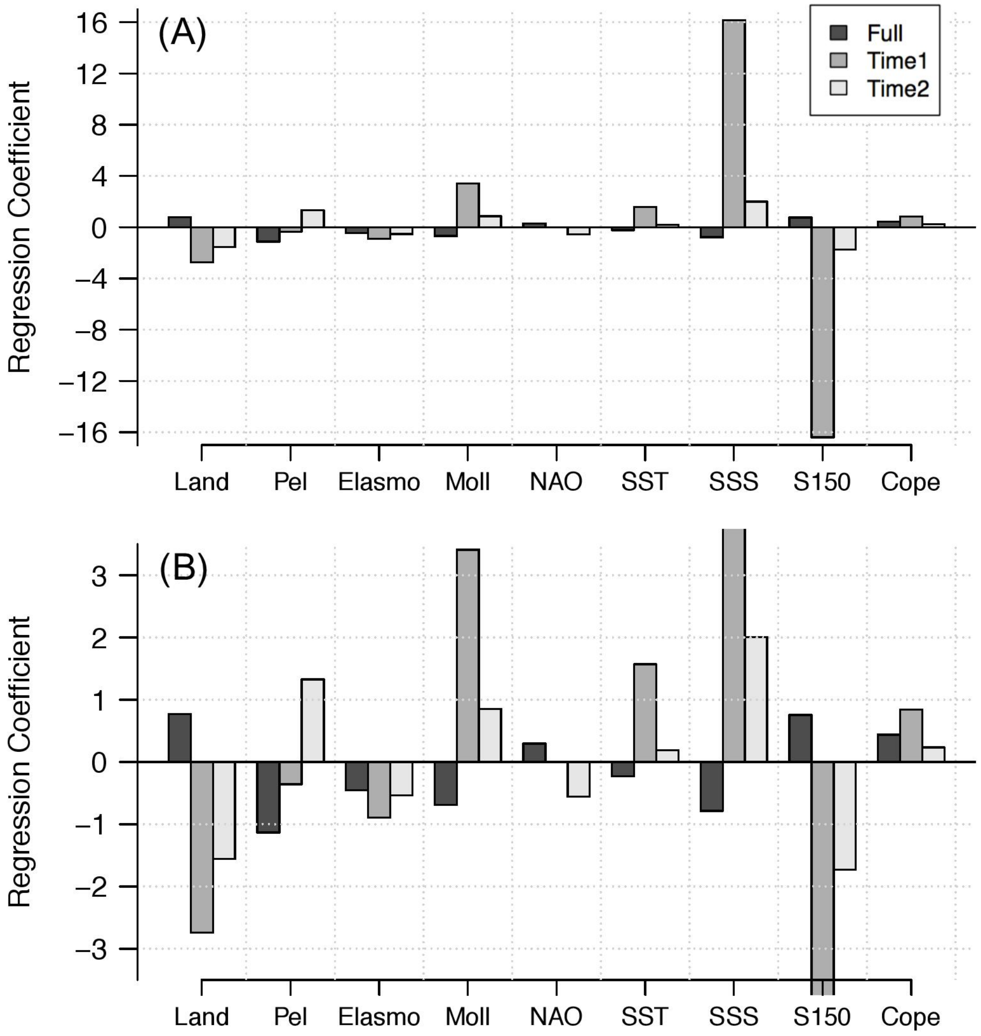

Figure F.14: Regression coefficients for $PC1_{Fgroups}$ projected onto the pressure indicators for each period (Georges Bank). (A) shows the coefficients for the salinity metrics for Time1; (B) zooms in on the y-axis to more clearly show the coefficients for the other periods.