ECOLOGY AND EVOLUTION OF HEAVILY EXPLOITED FISH POPULATIONS

by

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Abstract

Commercial harvest of fish stocks and their appropriate management requires an understanding of their population dynamics and of their ability to sustain exploitation. Here, some ecological and evolutionary consequences of excessive exploitation are examined.

In Chapter 2 I evaluate the knowledge base and status of commercially exploited marine populations that undergo formal stock assessment. Despite a bias towards industrialised countries and stocks of commercial importance, I show the pervasiveness of overexploitation and, by using reference points of stock status, identify important regional differences in the effectiveness of fisheries management.

In Chapter 3 I develop a data format suitable for ecological analyses to best disseminate the valuable information contained in scientific trawl surveys. This data format is suitable for inclusion into the public Ocean Biogeographic Information System (OBIS) and provides detailed observations that are suitable to the reconstruction of important fisheries-independent stock indices.

In Chapter 4 I examine the spatiotemporal dynamics of groundfish populations. A positive abundance-occupancy relationship was estimated for the majority of groundfish populations examined suggesting that this well-described terrestrial pattern is also pervasive in the marine environment. Spatial hysteresis was exhibited by numerous populations, indicating that the spatial distribution of individuals failed to recover despite recoveries in abundance.

In Chapter 5 I estimate the demographic consequences of changes in growth and maturation characteristics. The ability of a population to sustain harvest, and its ability to recover from previous depletions can be overestimated because of trends towards earlier maturation and slower growth.

In Chapter 6 I conclude the thesis by discussing the implications of my research to fisheries science and management. I argue that trends in the spatial distribution and the overall productivity of populations must be accounted for when determining sustainable fishing levels and when predicting recovery trajectories under various catch abatement scenarios. While successful management measures have been implemented in a number of marine ecosystems, this thesis highlights the importance of improving our capacity to understand the dynamics of exploited populations and to fully use the wealth of available monitoring and assessment data.

List of Abbreviations and Symbols Used

B_{msy}	Biomass at MSY
BRP	Biological reference point
CCGS	Canadian Coast Guard Ship
CPUE	Catch-per-unit-of-effort
DFO	Fisheries and Oceans Canada
DiGIR	Distributed Generic Information Retrieval
EEA	European Environment Agency
EEZ	Exclusive Economic Zone
FAO	Food and Agricultural Organization of the United Nations
F	Fishing mortality
GCMD	Global Change Master Directory
GLM	Generalized linear model
IATTC	Inter-American Tropical Tuna Commission
ICCAT	International Commission for the Conservation of Atlantic Tuna
ICC	Intraclass Correlation Coefficient
ICES	International Council for the Exploration of the Seas
ITIS	Integrated Taxonomic Information System
LME	Large Marine Ecosystem

MTL	Mean Trophic Level
MSY	Maximum Sustainable Yield
NAFO	Northwest Atlantic Fisheries Organization
NEFSC	Northeast Fisheries Science Center
NMFS	The National Marine Fisheries Service of the United States National Oceanic and Atmospheric Administration
NOAA	The United States National Oceanic and Atmospheric Administration
NSERC	Natural Sciences and Engineering Research Council of Canada
OBIS	Ocean Biogeographic Information System
RAM	Ransom Aldrich Myers
RFMO	Regional Fisheries Management Organization
R	Recruits
r	Finite population rate of increase
SQL	Structured Query Language
SSB	Spawning stock biomass
SPRFMO	South Pacific Regional Fisheries Management Organisation
TB	Total biomass
TC	Total catch
TL	Total landings
U_{msy}	Exploitation rate at MSY
VPA	Virtual Population Analysis

WCPFC	Western and Central Pacific Fisheries Commission

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Chapter 1

INTRODUCTION

A population can be defined as a group of individuals with overlapping lifespans that shares a common habitat and whose reproduction is isolated from other populations (Krebs, 2009). Individual species are often composed of a number of geographically separate populations that can differ phenotypically and genetically (Hughes et al., 1997). The study of how populations vary in abundance, biomass and distribution over space and time is the central topic of population ecology.

The factors that regulate variations in population abundance in time and space can either be intrinsic or extrinsic. Intrinsic factors are those associated with the population itself (age structure, mating strategy, etc.) whereas extrinsic factors include environmental variability, exploitation, and habitat loss. Deciphering the underlying mechanisms that control variations in population abundance requires the examination of both the population itself and its ecological reality in terms of habitat productivity, presence of predator and prey species, and other environmental factors that may affect its growth and survival (Krebs, 2009).

At the centre of current ecological theories of population regulation lies the concept of density-dependence (Rose et al., 2001). Without density-dependent mechanisms, exponential growth in abundance over time is expected. In reality there exists an upper abundance and biomass limit that most populations cannot exceed because of finite resources and habitat without external forces acting upon the population. When a population occupies all available habitat, or exists at such an abundance that prey resources are limiting further growth, competition for those limited resources will slow down, stop or reverse population growth (Sibly et al., 2005). At intermediate levels of abundance and biomass the population will be at its most productive and this is used in the theory of fishing to determine the maximum sustainable yield (Hilborn and Walters, 1992).

Extrinsic factors can have a large influence on population abundance as well. Some fish populations have been reduced to historically low abundance by excessive exploitation and provide a test case for how population abundance fluctuates with exploitation, inter- and intra-specific competition, and a dynamic environment. Northwest Atlantic populations of commercially exploited marine fishes are interesting models for studying population dynamics since they have been greatly affected by both extrinsic and intrinsic factors, have withstood a long history of exploitation, experienced large fluctuations in abundance and biomass, and have been monitored by scientific surveys for the last 40 years (e.g Hutchings and Baum, 2005; Shackell et al., 2009).

Despite early beliefs that fish populations were inexhaustible (Huxley, 1884), it has been clear that commercial harvesting can have a significant, measurable, and often catastrophic impact on target populations (Hutchings and Myers, 1994; Walters and Maguire, 1996; Hutchings, 2000; Hutchings and Reynolds, 2004; Pinsky et al., 2011). I use the term "heavily exploited" to describe excessive harvest regimes that exceed sustainable levels. This can reduce population abundance and biomass far below the level associated with maximum sustainable yield (Worm et al., 2009).

Large reductions in population abundance can have further ecological and evolutionary implications. The ecological consequences associated with large declines in abundance can include, for example, changes in the reproductive potential of a population (Birkeland and Dayton, 2005), alterations in its trophic role within a marine ecosystem (Frank et al., 2005; Myers et al., 2007; Baum and Worm, 2009), and changes in its spatial distribution and ecological range (Worm and Tittensor, 2011). Based on some studies in the laboratory (Munch et al., 2004), and in natural systems (e.g. Heino, 1998; Ernande et al., 2004), it has been hypothesized that exploitation can effect evolutionary change such as faster growth and earlier maturation.

The main research goal of this thesis is to examine how intense exploitation can influence fish population dynamics, specifically their abundance and distribution over space and time, as well as their vital life history parameters. I first investigate the pervasiveness of overexploitation and consequential declines of population abundance to levels below those that provide maximum sustainable yield for all available fish stocks that undergo formal stock assessments. I then examine the spatial population dynamics of groundfish species in the Northwest Atlantic. I finally estimate the consequences of exploitation on life-history traits and on population demographics.

I investigate these process by compiling and analysing fisheries-independent research surveys and stock assessment results. The information necessary to properly address the ecological and evolutionary ramifications of heavy exploitation is often difficult to assemble. This is primarily the case because the marine environment is notoriously difficult to sample and provides researchers with numerous logistical challenges. Additionally, the organisms of interest are often migratory, elusive and in many cases increasingly rare. Therefore, a major goal of this thesis was to work towards making standardised stock assessment and trawl survey information widely available, and to demonstrate the usefulness of such compiled data in addressing fundamental questions in fisheries ecology and management.

There exists a trade-off between the quantity and quality of data available to examine spatiotemporal changes in marine ecosystems. Global fisheries catch data collected by the United Nations Food and Agricultural Organization (FAO) provide the widest temporal, geographic and taxonomic breadth of information available, but are also potentially biased by the forces that determine what species are harvested (Branch et al., 2011). Scientific fisheries surveys provide essential fisheries-independent information, but are limited in their spatial and temporal coverage. Proper stock assessments exist for commercially important species and, while they provide the best understanding of the response of populations to harvesting, they are limited to geographic areas where fisheries management institutions exist. Synthetic questions about the nature of exploited fish populations are best addressed by integrating these different data sources (Worm et al., 2009).

The main objective of fisheries management is to minimise the risk of collapse of exploited populations while attempting to maximise their yield (Hilborn and Walters, 1992). The ecology and evolution of harvested species must be considered to determine the level of exploitation that they can sustainably withstand and the most appropriate gear to capture them (Jørgensen et al., 2007; Hutchings, 2009). Therefore, I investigate the ecological and evolutionary effects that intense exploitation can have on fish populations and discuss the implications of my findings on population dynamics and fisheries management.

1.1 Thesis Structure

The thesis examines important factors influencing the population dynamics of marine populations that have experienced substantial declines. A brief description of each chapter follows.

Status Of Exploited Marine Populations

I first provide an overview of what is known about marine species that undergo proper stock assessments. Chapter 2 documents the knowledge-base of available stocks and examines their current biological and exploitation status. Many of the assessed stocks still experience overexploitation and have declined to historically low levels. Other populations experience appropriate levels of exploitation and exist at healthy biological levels. Despite the implementation of stricter catch restrictions, many targeted populations still exist at biological levels that are lower than those that maximise population productivity. This chapter highlights the pervasiveness of populations at low levels of abundance and biomass, and identifies the North Atlantic Ocean as an area with a long, and often excessive, exploitation history.

Population indices from scientific trawl survey

Because of the long exploitation history of populations in the Northwest Atlantic and the availability of scientific trawl surveys for this region, I focused on reconstructing groundfish population abundance indices from the Scotia-Fundy region. In order to foster research in population and community dynamics, researchers need reliable and reproducible data from multiple species. To facilitate the discovery and proper use of scientific trawl survey data, I manipulated catch data from scientific surveys into a format that is compatible for inclusion into a large publicly available biogeographic information system. Chapter 3 examines this theme and documents the reconstruction of stock indices from publicly available groundfish survey data. The population indices derived from the public data are used to examine the relationship between abundance and distribution in Chapter 4.

Population Ranges, Distribution And Abundance

The relationship between population abundance and distribution is another critical component to properly understanding population dynamics. The population indices developed earlier are used in Chapter 4 to examine associations between estimated abundance and biomass of surveyed species and the geographic area that they occupy. This chapter also examines the relationship between local density and abundance in order to help identify critical habitats for a variety of demersal fish species.

Demographic consequences of changes in growth and maturation

The population dynamics of two fish populations with a long history of exploitation are examined further in Chapter 5. Critical components of the study of population dynamics are life-history characteristics, and particularly the processes of growth and maturation (Hutchings, 2005). I use detailed fish observations of length, age and maturity status to estimate temporal changes in life-history characteristics. Decadal changes in growth and maturation are then used in an age-structured population dynamics model to estimate their combined demographic consequences.

Conclusion

The thesis examines critical components of population dynamics and discusses the relationship between how depleted fish populations change ecologically and evolutionarily and how this may affect population abundance and distribution. Chapter 6 summarises the findings and discusses the implications of the findings.

Chapter 2

EXAMINING THE KNOWLEDGE BASE AND STATUS OF COMMERCIALLY EXPLOITED MARINE SPECIES

2.1 Abstract

Meta-analyses of stock assessments can provide novel insight into marine population dynamics and the status of fished species, but the world's main stock assessment database (the Myers Stock-Recruitment Database) is now outdated. To facilitate new analyses, we developed a new database, the RAM Legacy Stock Assessment Database, for commercially exploited marine fishes and invertebrates. Time series of total biomass, spawner biomass, recruits, fishing mortality and catch/landings form the core of the database. Assessments were assembled from 21 national and international management agencies for a total of 331 stocks (295 fish stocks representing 46 families and 36 invertebrate stocks representing 12 families), including nine of the world's 10 largest fisheries. Stock assessments were available from 27 large marine ecosystems, the Caspian Sea and four High Seas regions, and include the Atlantic, Pacific, Indian, Arctic and Antarctic Oceans. Most assessments came from the USA, Europe, Canada, New Zealand and Australia. Assessed marine stocks represent a small proportion of harvested fish taxa (16%), and an even smaller proportion of marine fish biodiversity (1%), but provide high-quality data for intensively studied stocks. The database provides new insight into the status of exploited populations: 58% of stocks with reference points (n = 214) were estimated to be below the biomass resulting in maximum sustainable yield (B_{MSY}) and 30% had exploitation levels above the exploitation rate resulting in maximum sustainable yield (U_{MSY}). We anticipate that the database will facilitate new research in population dynamics and fishery

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2.2 Introduction

Marine wild capture fisheries provide 80 million tons of fisheries products (both food and industrial) annually and wild capture fisheries employ 34 million people around the world (FAO, 2010). At the same time, fishing has been recognised as having one of the most widespread human impacts in the world's oceans (Halpern et al., 2008), and the Food and Agricultural Organization of the United Nations (FAO) estimates that 85% of fish stocks globally are fully exploited or overexploited (FAO, 2010). While some fisheries have reduced exploitation rates to levels that should, in theory, promote recovery, overfishing continues to be a serious global problem (Hilborn et al., 2003; Worm et al., 2009; FAO, 2010). Fisheries managers are asked to address multiple competing objectives, including maximizing yields, ensuring profitability and stability, reducing bycatch, and minimizing the risk of overfishing. Given the large social and economic costs (Rice et al., 2003) and ecosystem consequences (Frank et al., 2005; Myers et al., 2007) of collapsed fisheries, it is imperative that we are able to learn from successful and failed fisheries from around the world.

Global databases of fishery landings, compiled by FAO (FAO, 2009) and extended by the Sea Around Us project (Watson et al., 2004), are valuable resources for understanding the status of, and trends in, global fisheries (e.g. Pauly and Christensen, 1995; Pauly et al., 2002; Worm et al., 2006; Newton et al., 2007; Worm et al., 2009). The trade-off with these comprehensive databases, however, is that they have poor taxonomic resolution for many fisheries in developing countries, and landings data alone can be misleading when used as a proxy for stock size. Most investigations that have used these data to examine changes in fishery status (Worm et al., 2006; Costello et al., 2008) rely (either explicitly or implicitly) on the assumption that catch or landings is a reliable index of stock size. Critics have pointed out that catch can change for a number of reasons unrelated to stock size, including changes in targeting, fishing restrictions, or market preferences (Caddy et al., 1998; Hilborn, 2007; de Mutsert et al., 2008).

Standardizing catch by the amount of fishing effort (catch-per-unit-of-effort, CPUE) and modelling the data to account for spatial, temporal, and operational factors affecting the CPUE is an improvement (Maunder and Punt, 2004), but is only feasible when catch data are collected in fisheries with log book and/or observer programs. Moreover, CPUE can still be an unreliable index of relative abundance since it is difficult to account for all factors that influence catchability (Hutchings and Myers, 1994; Harley et al., 2001; Walters, 2003; Polacheck, 2006).

Other datasets with more limited taxonomic and geographic coverage also exist and have been used in analyses that investigated changes in population biomass and species diversity (Myers and Worm, 2003; Worm et al., 2005). Just like global catch data, the catch and effort components of these datasets can give a biased view of temporal trends in biomass.

Stock assessments, the most data-intensive method of assessing fisheries, consider time series of catch along with other sources of biological information such as growth, maturation, natural mortality rates, changes in size or age composition, stock-recruitment relationships, and CPUE coming from different fisheries and/or from fishery-independent research surveys in order to quantitatively estimate stock abundance (Hilborn and Walters, 1992; Quinn and Deriso, 1999; Cooper, 2006). Because they integrate across multiple sources of information, stock assessment models should provide a more accurate picture of changes in abundance than catch data alone (Sibert et al., 2006), a trade-off being that their complexity renders them difficult for non-experts to evaluate.

Stock assessments are expensive to conduct and hence are usually only done by developed nations for species of commercial importance. For example, in 2009, of the 522 federally managed exploited fish and invertebrate stocks recognised by the National Marine Fisheries Service (NMFS) as exploited in U.S. waters, only 193, or slightly over one-third, were considered fully assessed (National Marine Fisheries Service, 2009). An assessment by the European Environment Agency (EEA) in 2006 indicated that the percentage of commercial landings obtained from assessed stocks (out of all known landings in a region) ranged between 66-97% in northern European waters but only 30-77% in the Mediterranean (European Commission, 2006). The New Zealand Ministry of Fisheries reports the status of only 117 stocks or sub-stocks out of a total of 628 stocks managed under New Zealand's Quota Management System (New Zealand Ministry of Fisheries, 2010). In Australia, 98 federally managed stocks have been assessed (Wilson et al., 2009) out of an unknown total. The extent to which stocks are assessed elsewhere in the world is generally lower (Mora et al., 2009).

Despite these limitations, stock assessment is considered to be an integral component of responsible management in industrialised fisheries (Hilborn and Walters, 1992) where fishing capacity can exceed the productivity of fished stocks. Effective management of these stocks requires an understanding of what the current population abundance and harvest rate are, and where these lie in relation to target or limit abundance and exploitation reference points (e.g., the exploitation rate that maximizes fishery benefits or limits the risk of overfishing).

Comparative analyses of stock assessments can provide insight into the status of fisheries that is complementary to assessments of global landings, as well as providing more fundamental insight into the population dynamics of exploited species. The first database of stock assessment information, the Myers Stock Recruitment Database, was developed by the late Ransom A. Myers and colleagues in the mid-1990s (Myers et al., 1995b). While the database was primarily known for its time series of stock and recruitment, it also contained time series of fishing mortality rates for many stocks; biological reference points (BRPs) were, however, largely absent. The original release version of the Myers database (Myers et al., 1995b) included spawning stock size and recruitment time series for 274 stocks representing 92 species as well as fishing mortality rate time series for 144 stocks. The number of entered stocks grew to approximately 509 stocks (with at least one SR pair) by 2005, of which 290 were anadromous fishes of the family Salmonidae. This database was instrumental in advancing the use of meta-analysis in fisheries science and was used to: 1) decisively show that recruitment is related to spawning stock size (Myers and Barrowman, 1996), 2) investigate potential depensation in stock-recruitment relationships (Myers et al., 1995a; Liermann and Hilborn, 1997; Garvey et al., 2009), 3) discover generalities in the annual reproductive rates of fishes (Myers et al., 1999, 2002b), 4) investigate density-dependence in juvenile mortality (Myers, 2001; Minto et al., 2008), 5) develop informative Bayesian priors on steepness (Myers et al., 1999; Dorn, 2002; Myers et al., 2002a), and 6) examine patterns of collapse and recovery in exploited fish populations (Hilborn, 1997; Hutchings, 2000, 2001a,b).

Interest in fisheries meta-analyses has grown considerably over the past two decades, such that there is a great need for an up-to-date stock assessment database. Yet the publicly available version of the original Myers database (Myers et al., 1995b) is 16 years out of date for most stocks and has not been updated since Dr. Myers' passing in 2007. For stocks that were depleted in 1995, the past 16 years include valuable observations at low stock size or of a recovering population, both of which are critical for estimating population dynamics parameters such as the behaviour of the stock-recruitment relationship near the origin. In addition, there have been numerous improvements in stock assessments (improved knowledge of exploited populations and methodological development that lead to better stock estimates) and assessments have been conducted for the first time for many species.

Meta-analyses of fishery status have also been hampered by the lack of an assessment database containing biological reference points (BRPs, e.g., the total/spawning biomass and exploitation rate that produce Maximum Sustainable Yield (MSY), B_{msy} and U_{msy}). Knowledge of BRPs is important if stocks are to be managed for high yields that can be sustained over time (Mace, 1994). Without information on reference points, previous analyses of stock assessments or catch data have instead relied upon ad hoc thresholds to define fishery status, such as the greatest 15-year decline (Hutchings and Reynolds, 2004) or 10% of maximum catch (Worm et al., 2006). Ad hoc reference points based on some fraction of the maximum of a time series also have undesirable statistical properties and can result in false collapses when applied to inherently variable time series of catch or abundance (Wilberg and Miller, 2007; Branch, 2008; Branch et al., 2011). Complicating comparisons of fishery status is the fact that different BRPs are used in different parts of the world and even the same BRP can be used in a different manner, for example, as a target or as a limit. The biomass reference point is the internationally agreed, legally binding reference point for managed fisheries (UNCLOS, 1982; UNFSA, 1995) and provides a useful basis for comparing stocks.

Here I present an updated version of the stock assessment database and use it to describe the knowledge-base of assessed marine stocks. I use the database to evaluate how much we know about assessed stocks and what we know about their current status. I use the available stock assessment results and biological reference points to estimate current biomass and exploitation status of exploited populations. I discuss how the findings presented here compare to what has emerged from the last 15 years of research on the global status of exploited marine species. I conclude with an overview of ongoing projects that are using the RAM Legacy database and with a roadmap for further database development and usage.

2.3 Methods

2.3.1 Database Of Stock Assessments

The RAM Legacy Stock Assessment Database (hereafter, RAM Legacy database) is a relational database designed to store data from accessible current model-based fisheries stock assessments for marine fish and invertebrate populations. Time series of spawning stock biomass (SSB), total biomass (TB), recruits (R), total catch (TC) or landings (TL), and fishing mortality (F) from individual stock assessments form the core of the database. Apart from catch/landings, these time series are not raw data, but rather the output of population dynamics models; depending on the type of assessment model and the data reported, not all of these time series were available for every stock. The database also contains details about the time series data, including the age and sex of spawners, age of recruits, and the ages used to compute the fishing mortality, as well as BRPs and some life history information (e.g. growth parameters, age and length at 50% maturity, and natural mortality rate). Metadata for each stock assessment consists of taxonomic information about the species and the geographic location of the stock (detailed in "Links to related databases"), the management body that conducted the assessment and the assessment methodology. Some assessments (n=26), particularly those for more recently developed invertebrate fisheries, were based only on CPUE time series rather than population dynamics models. While these are included in the database, the descriptions and analyses presented here include only those stocks assessed using population dynamics models.

A variety of search methods were used in an attempt to obtain as many recent fisheries stock assessments as possible. Publicly available stock assessment reports were the primary data source, and were obtained either from the website of the relevant management agency or directly from stock assessment scientists. Other assessments were obtained from the primary literature and through personal contacts at fisheries management agencies.

2.3.2 Database Structure And Quality Control

The database is implemented in the open source PostgreSQL relational database management system (PostgreSQL Global Development Group, 2010), and includes linked tables for all of the above-mentioned data and metadata. The use of a relational database improves data integrity and facilitates the development of a repeatable analytical framework. Data products that suit a given analyst's need can be automatically created and updated when new information becomes available, either through updates of existing assessments or entry of new assessments results in the database.

Several mechanisms were employed to ensure database quality. During the data recording process, assessment authors were contacted where needed to clarify aspects of the assessment or to obtain more detailed data. Time series data presented only in assessment report figures were, for example, only entered into the database if the exact numbers could be obtained from the assessment author. In cases where multiple models were presented in an assessment without a preferred or best model being denoted, it was attempted to ascertain which model was preferred by the stock assessment scientist, but included all model results whenever this was not possible. Once uploaded into the database all stock assessments underwent an additional Quality Assurance/Quality Control (QA/QC) step to ensure that the entered data replicated that of the original assessment document exactly.

2.3.3 Links To Related Databases

To facilitate integration of the RAM Legacy database with related databases, such as FishBase (Froese and Pauly, 2009) and the Sea Around Us global landings database (Watson et al., 2004), each species present in the RAM Legacy database was assigned a matching FishBase species name and species code, a matching Sea Around Us taxon code, and taxonomic information from the Integrated Taxonomic Information System (ITIS) (http://www.itis.gov). Additionally, each stock was assigned to a primary (and in some cases secondary and tertiary) Large Marine Ecosystem (LME) (Sherman et al., 1993). LMEs encompass the continental shelves of the world's oceans and represent the most productive areas of the oceans. Open ocean areas beyond the continental shelves are, however, not included in the LME classification; nor is the Caspian Sea, for which there is one stock. Large, highly migratory oceanic species such as tuna were therefore assigned to new categories "Atlantic high seas", "Pacific high seas", "Indian high seas", and "Subantarctic high seas".

2.3.4 The Marine Stock Assessment Knowledge-Base

An overview of the temporal and geographic coverage of stock assessments is presented, as well as the types of assessment models used and BRPs estimated for all stock assessments and each management body. To evaluate the taxonomic scope of the database and identify taxonomic biases, I compare the taxonomy of assessed stocks with the diversity of i) all marine fishes (as represented by FishBase), and ii) marine fishes in global fisheries catches (as represented by the species available from the Sea Around Us database). To determine what fraction of world wild-capture fisheries landings come from assessed stocks, I used the Sea Around Us' average global fisheries catches from the most recent ten years of available data (1995-2004); I also discuss limitations to obtaining assessments for some of the world's major fisheries. Direct comparisons between assessments and catch data at a regional level are hampered by the geographic mismatch between stocks and FAO statistical areas or the Sea Around Us' Large Marine Ecosystems.

2.3.5 The Status Of Assessed Marine Stocks

The status of assessed stocks is evaluated overall, by oceanic basin, by management body, by major taxonomic orders included in the database, and by trophic level, using standard reference points so that all stocks are referenced to a comparable benchmark. Following Worm et al. (2009) and Froese and Proelß (2010), I compare the biomass and exploitation rate of stocks for the last available year in the assessment (the "current biomass") relative to their reference points at maximum sustainable yield, B_{msy} and U_{msy}, respectively. MSY-related BRPs are not used by all management agencies, and that their utility as fisheries targets or limits is debated (Larkin, 1977;

Mace, 2001), but they are the most commonly estimated BRPs and hence most easily used to compare multiple stocks.

For those assessments that did not contain MSY reference points, but did include total catch and total biomass time series data, I used a Schaefer surplus production model to estimate total biomass and exploitation rate at MSY (B_{msy} and U_{msy}, respectively).

2.3.6 Temporal Trends In Biomass

The temporal evolution of stock biomass provides a starting point to examine stock status. Estimating the fluctuations in biomass and abundance over time and determining the factors causing them is at the heart of applied ecology.

To examine whether populations that were declining prior to the 1992 ratification of the United Nations Convention on Biological Diversity had fared better since, citeHutchings:etal:2010:cjfas calculate the slope of $log\left(B\right)$ before and after 1992. I use an alternative method that consists in tabulating a transition matrix that describes the biomass and exploitation trajectories of stocks over the timeframe covered by their assessment.

For each year in an assessment, stock status is assigned to one of four categories based on the biomass and exploitationt status compared to their MSY reference points. Starting in the second year of each time series, I keep track of the transition in status compared to the previous year. There are 16 potential transitions between the four quadrants (Fig. A.1). The proportion of transitions in each of the 16 combinations is then tabulated across all available stocks to quantify the probabilities of switching from the different biomass and exploitation states.

2.3.7 Multi-Stock Indices

I use a modified version of the analyses conducted by Hutchings et al. (2010) to compute multi-stock biomass indices for different ocean basins. I combine the ratios of biomass to B_{msy} across stocks using a mixed-effects model. The model uses a fixed-effect mean index per year, an overall random effects deviation for each stock and a first-order autocorrelation structure on the residuals. The multi-stock indices are calculated for the different ocean basins used in Hutchings et al. (2010).

2.4 Results

2.4.1 The Marine Stock Assessment Knowledge-Base

The marine stock assessment knowledge-base In total, 331 recent stock assessments (with population dynamics models) for 295 marine fish stocks and 36 invertebrate stocks are included in the RAM Legacy database (Version 1.0, 2011; Table S1). Together these comprise time series of catch/landings for 313 stocks (95% of all assessments included), SSB estimates for 280 stocks (85%), and recruitment estimates for 274 stocks (83%) (Fig. 2.1). The median lengths of catch/landings, SSB, and recruitment time series were 39, 34, and 33 years, respectively (Fig. 2.1). The time period covered by 50% of assessments is: catch/landings (1983-2004), SSB (1985-2005), recruitment (1984-2003), while that covered by 90% of assessments is: catch/landings (1966-2007), SSB (1972-2007), recruitment (1971-2006) (Fig. 2.1).

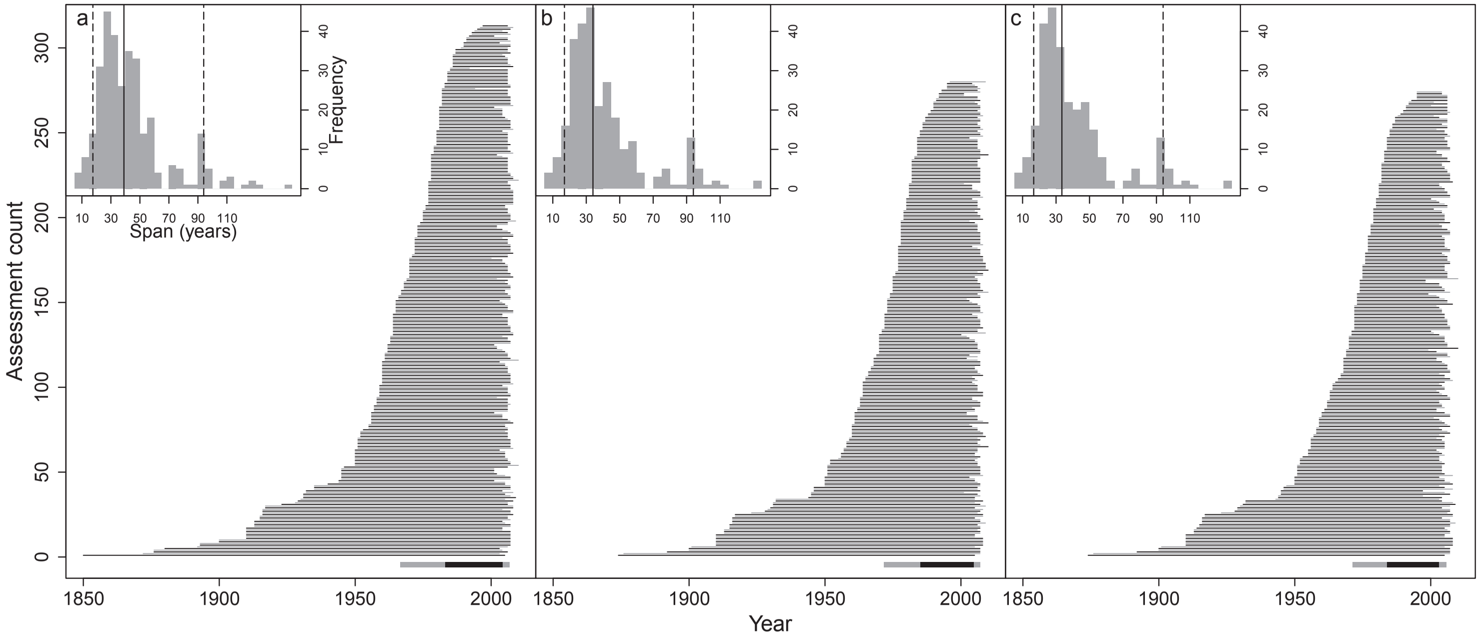

Figure 2.1: Temporal coverage of a) catch/landings, b) spawning stock biomass and c) recruitment. The temporal coverage for individual assessments is represented by thin alternating black and grey horizontal lines in the main panels. Thick horizontal lines at the base of each main panel represent the time periods that are present in 90% (black) and 50% (grey) of all series for that data type. Subfigure histograms contain the frequency of occurrence of the various timespans without reference to time period. Solid and long-dash vertical lines within the subfigures represent the median, 2.5% and 97.5% quantiles, respectively.

2.4.2 Management Bodies And Geography

Stock assessments are derived from fisheries management bodies in Europe, North America, New Zealand, Australia, Russia, South Africa and Argentina, and from eight Regional Fisheries Management Organizations (RFMOs) (Table 1). Assessments from the United States constitute by far the most stocks of any country or region (n=138); assessments from the European Union's management body, the International Council for the Exploration of the Seas (ICES), constitute the second greatest number of stocks (n=63). Whereas nations are responsible for managing all stocks within their EEZs, RFMOs typically focus on a certain type of species (e.g. halibut, tunas) or fisheries (e.g. pelagic high seas) within a given area and hence assess a smaller number of stocks.

Geographically, most assessments are of stocks from North America, Europe, Australia, New Zealand and the high seas (Fig. 2.2). Few assessments were available from regions such as Southeast Asia, South America (except for 6 stocks from Argentina and 2 from the Humboldt Current LME), and the Indian Ocean (outside Australian waters) (Fig. 2). One or more assessments were available from each of 27 LMEs (out of 64 globally), with the greatest number of assessed stocks coming from the Northeast U.S. Continental Shelf (n=59), California Current (n=35), New Zealand Shelf (n=29), Gulf of Alaska (n=27), Celtic-Biscay Shelf (n=26), East Bering Sea (n=21) and Southeast U.S. Continental Shelf (n=20) (Fig. 2.2). Assessments also came from the Caspian Sea and from four High Seas areas (Fig. 2.2).

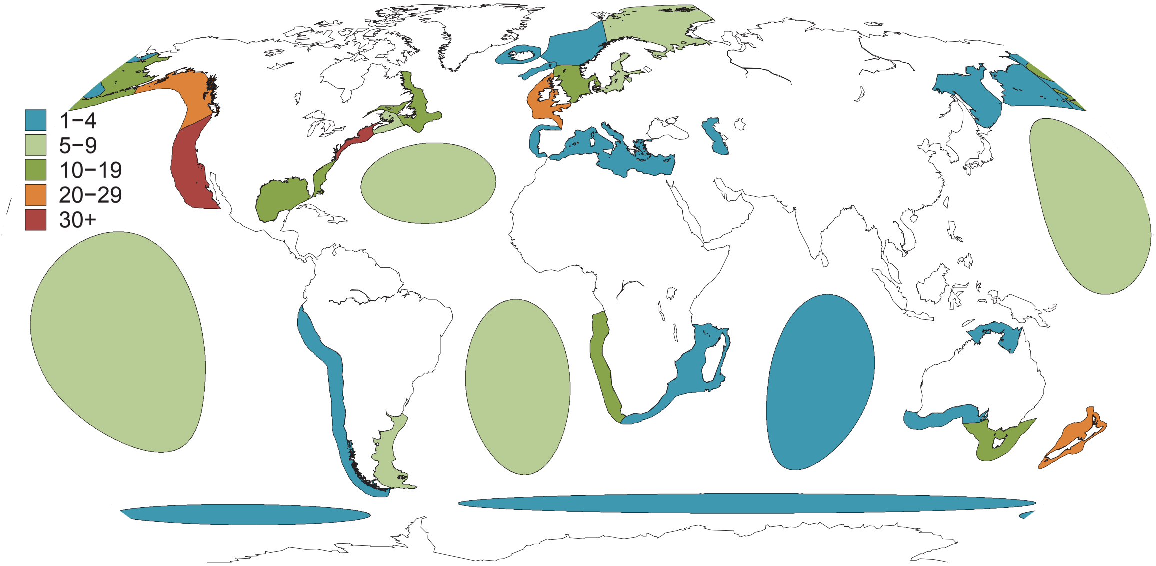

Figure 2.2: Map of Large Marine Ecosystems (LMEs) and high seas areas (ovals) showing the number of stock assessments present in the database per area.

2.4.3 Stock Assessment Methodologies And BRPs

The three most common assessment methods were Statistical catch-at-age/length models (n=169), Virtual Population Analyses (n=92) and Biomass dynamics model (n=45). Regionally, VPA is the most common assessment method in Argentina (83% of 6 assessments), Europe (71% of 63 assessments), and Canada (56% of 26 assessments), whereas statistical catch-at-age and catch-at-length models are more common in Australia (82% of 17 assessments), New Zealand (76% of 29 assessments), and the United States (67% of 138 assessments).

Biomass- or exploitation-based reference points were available for 262 (82%) and 224 (69%) assessments, respectively. The most commonly reported biomass-based BRPs relate to biomass at MSY (B_{msy}), to "limit" biomass (B_{lim}, a biomass level above which stocks should be maintained). Stocks in the United States under the management of NMFS and most of the tuna and billfish stocks assessed by RFMOs are managed using MSY-based reference points (or proxies believed to be equivalent) whereas other fisheries agencies use different BRPs, e.g. ICES have traditionally used SSB-based B_{lim} reference points.

2.4.4 Taxonomy

Stock assessments in the database cover 163 marine fish and invertebrate species from 58 families and 20 orders (Fig. S3). Five taxonomic orders (Gadiformes (n=70), Perciformes (n=65), Pleuronectiformes (n=53), Scorpaeniformes (n=41) and Clupeiformes (n=36)) account for 80% of available stock assessments. Of these, Perciformes, the most speciose order of marine fishes are in fact underrepresented in the database (46% of all marine fish species vs. 19% of all marine fish assessments), while the other four orders are taxonomically overrepresented: Clupeiformes (2.1% of marine fishes vs. 11% in the database), Gadiformes (3.3% of marine fishes vs. 21% in the database), Pleuronectiformes (4.5% of marine fishes vs. 17% in the database), Scorpaeniformes (8.5% of marine fishes vs. 12% in the database) (Fig. S3).

Assessed marine fish stocks constitute a relatively small proportion of harvested fish taxa (16% of fish species from the Sea Around Us database) and an even smaller proportion of marine fish biodiversity (1% of fish species in FishBase; Fig. 2.3). In turn, catches from the Sea Around Us database, which come from 925 species and 36 orders (Fig. 2.3), represent only 5% of the 12339 species and 67% of the 54 different orders present in FishBase (Fig. 2.3). The diversity of harvested marine invertebrates is clearly also underrepresented in the stock assessment database and likely in stock assessments in general.

2.4.5 Global Fisheries

Assessments were available for 9 of the world's 10 largest fisheries for individual fish stocks (Table 2). Looking more broadly, the database contains assessments for 17 of the 30 largest fisheries for individual fish stocks globally, and 18 of the 40 largest fisheries globally (when including those recorded at lower taxonomic resolutions) (Table 2). Many of the fisheries not included in the RAM Legacy database, especially those recorded in the Sea Around Us database as "Marine fishes not identified" (n=7), occur in developing countries and have no known formal stock assessment conducted for them. From a national perspective, assessments are only included for 3 of the top 10 wild-caught marine fisheries producing nations, U.S.A., Russia, and Peru (FAO, 2010), with only two assessments from Russia and one from Peru. We were unable to obtain any assessments from the other top 10 yield-producing countries: China, Indonesia, Japan, India, Chile, Philippines, and Burma (FAO, 2010).

2.4.6 The Status Of Assessed Marine Stocks

MSY related reference points were available from the assessments for 126 stocks (4 invertebrates) and could be estimated using surplus production models for 88 additional stocks (14 invertebrates), for a total of 214 stocks (see Appendix for details). Surplus production models estimated reference points relatively well, and altering the upper bounds of the K parameter in the models did not affect the classification of any of the stocks (Fig. A.2, Table A.1). Overall, 57% of these stocks are estimated to be below B_{msy}, and 31% are estimated to have exploitation rates above U_{msy}, (n=214; Fig. 2.4). Of the stocks for which biomass is currently estimated to be below B_{msy}, 53% have had their exploitation rate reduced below U_{msy}, suggesting potential for recovery. The remaining 47% are still exploited at rates above U_{msy} (Fig. 2.4).

The status of assessed marine stocks, as estimated from biomass- and exploitation-BRPs, varied widely among management bodies (Fig. 2.4). We estimate that about

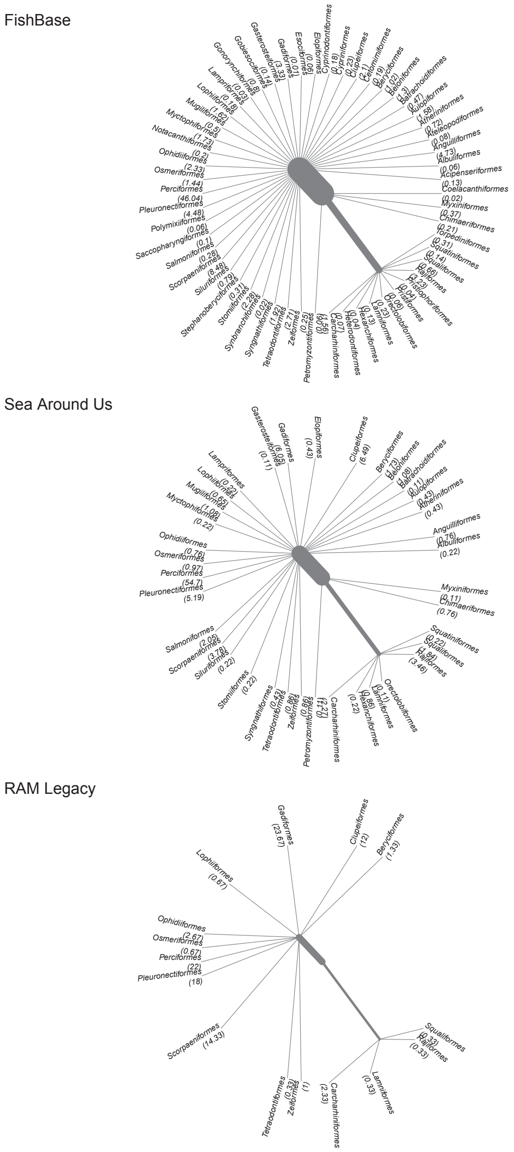

Figure 2.3: Comparison of the taxonomic diversity of marine species as provided by a) FishBase, b) the coverage of catch data as provided by the Sea Around Us Database, and c) the new RAM Legacy database (bottom panel). The circle located near the middle of the circular dendrogram represents kingdom Animalia and each subsequent branching represents a different taxonomic group (Kingdom to Phylum to Class to Order to Family to Genus to Species). The width of each line is proportional to the square root of the number of species in a branch. To facilitate the identification of the taxonomic groups that are not presented in the catch and assessment data, the FishBase branching pattern of the spoked dendrogram is maintained to generate the other two dendrograms. This figure only compares fish and elasmobranch species present in FishBase. Additional species of molluscs and arthropods are present in both the Sea Around Us and RAM Legacy databases but are not presented here.

half (49%) of U.S. stocks (managed by NMFS) are above B_{msy}, and of the 41 stocks that are below B_{msy} almost two thirds (61%) have exploitation rates below (Fig. 2.4). In New Zealand and Australian waters, stocks managed by MFish and AFMA are above B_{msy} in 61% and 36% of cases, respectively (Fig. 2.4). In contrast, we estimate that most European stocks (managed by ICES) have biomasses less than B_{msy} (81%), and over half of these stocks (59%) have exploitation rates exceeding U_{msy} (Fig. 2.4). European stocks are, however, not currently managed based on MSY reference points but rather using limit reference points (B_{lim} , see Discussion). When considered from the perspective of the available limit reference points B_{lim} and F_{lim} , European stocks appear to be in better shape, with 52% of stocks above B_{lim} and 65% below F_{lim} (Fig. S4). Most Canadian stocks (managed by DFO) also had low biomass (69% below B_{msy}), but all of these are estimated to now have exploitation rates below U_{msy} (Fig. 2.4). For the stocks managed by RFMOs in the Atlantic (Fig. 2.4) we found that 6 of the 10 ICCAT stocks and 6 of the 10 NAFO stocks were below B_{msy}. Finally, two thirds (4 of 6) stocks managed by RFMOs in the Pacific had biomasses above B_{msy} (Fig. 2.4).

The status of marine stocks also varies substantially amongst the major assessed taxonomic orders (Fig. 2.5). Gadiformes and Decapoda have the highest proportions of stocks below B_{msy} (75% and 75% respectively), but most Gadiformes have now had their fishing mortality rate reduced below U_{msy} (65%), while most invertebrate stocks in the order Decapoda still have excessively high fishing mortality rates ($U > U_{msy}$ in 50%; Fig. 2.5). In contrast, biomasses of the majority of Scorpaeniformes are above B_{msy}, and fishing mortalities are below U_{msy} for 92% of stocks in this order (Fig. 2.5). Perciformes display overall status around B_{msy}, while Pleuronectiformes display an interesting bimodality with one mode above B_{msy} and below U_{msy} and another mode below B_{msy} and above U_{msy} (Fig. 2.5). Clupeiformes display an overall mode below B_{msy} but with exploitation rates reduced below U_{msy} (Fig. 2.5).

When stock status is considered from a trophic level perspective, it appears (at least for those assessed stocks with BRPs) that high trophic level stocks are no worse off than lower trophic level stocks (Fig. 2.6): 18 of 26 stocks (69%) with mean trophic level (MTL) between 2.0 and 3.0 had biomasses depleted below B_{msy} (Fig. 2.6), whereas just over half of higher trophic level stocks did (56% of stocks with MTL

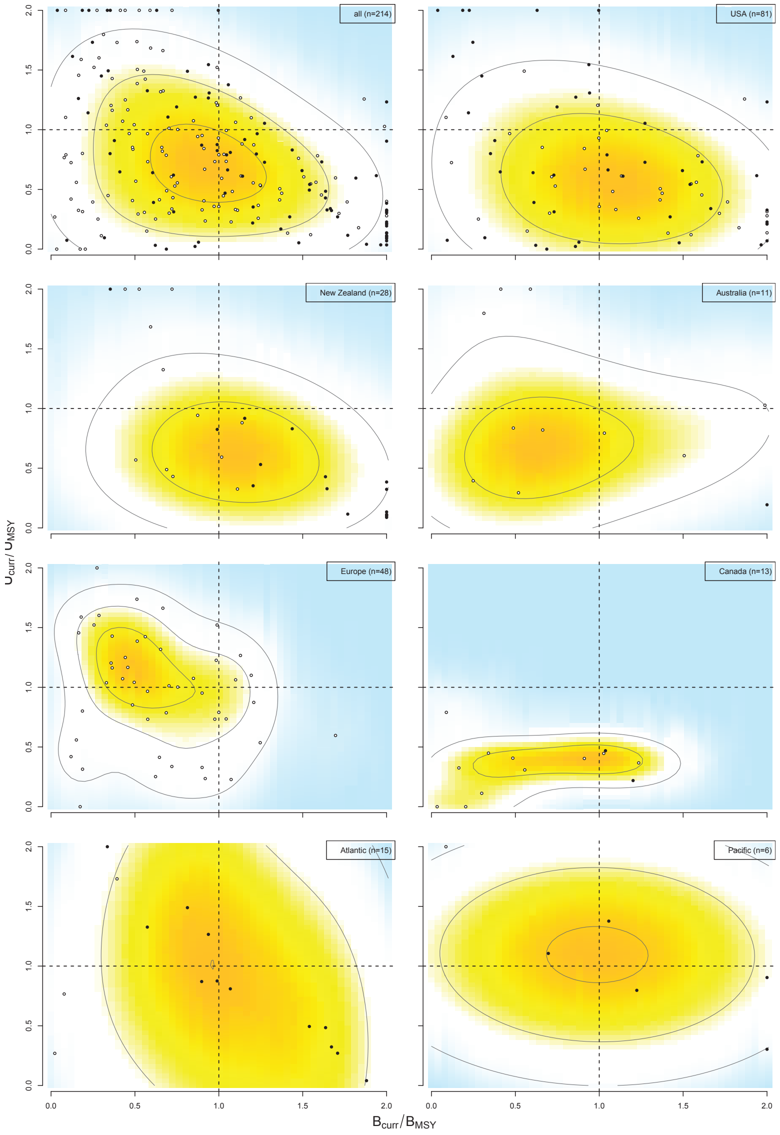

Figure 2.4: Current exploitation rate versus current biomass for individual stocks from a) all management units combined (updated from Worm et al. (2009)) and for b-h) individual management units b) U.S., c) New Zealand, d) Australia, e) Europe, f) Canada, g) Atlantic (multinational stocks managed by ICCAT and NAFO) and h) Pacific (including multinational stocks managed by IATTC, WCPFC and SPRFMO). In each panel, exploitation rate is scaled relative to the exploitation rate expected to result in maximum sustainable yield (U_{msy}); biomass is scaled relative to B_{msy}. Shading indicates the probability of occurrence as revealed by a kernel density smoothing func- tion. Solid circles indicate and estimates that were obtained directly from assessments; open circles indicate estimates from surplus production models.

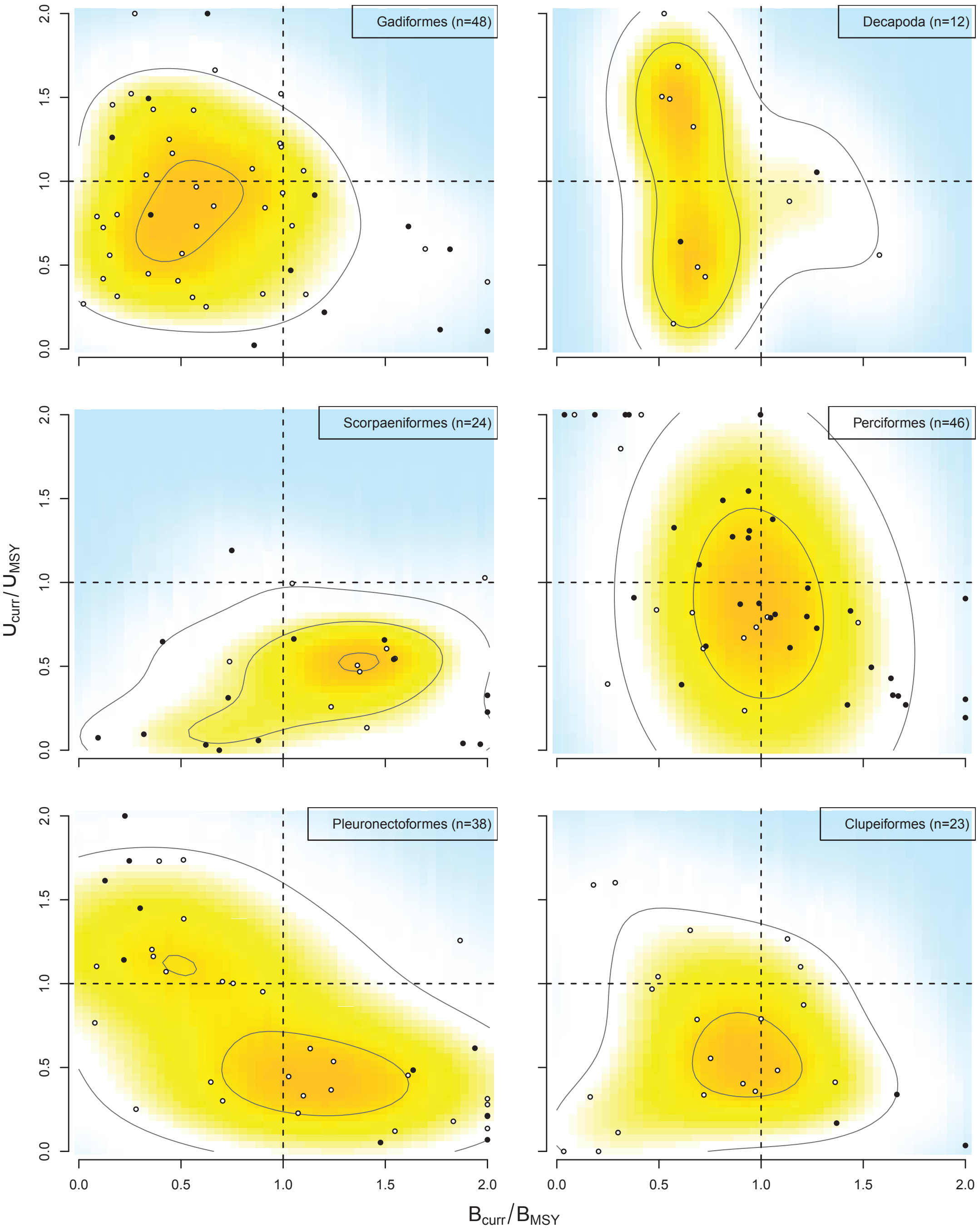

Figure 2.5: Current exploitation rate versus current biomass for individual stocks from the major orders of marine fishes a) Gadiformes, b) Decapoda, c) Scorpaeniformes, d) Perciformes, e) Pleuronectiformes and f) Clupeiformes, in the RAM Legacy database. Plot details as in Figure 2.4.

between 3.0 and 4.0, 55% of stocks with $MTL > 4.0$; Fig. 2.6). Similarly, while almost half of the low trophic level stocks had fishing mortalities exceeding U_{msy} (42%; Fig. 2.6), only 23% of stocks with MTL between 3.0 and 4.0 and 35% of stocks with $MTL > 4.0$ did (Fig. 2.6).

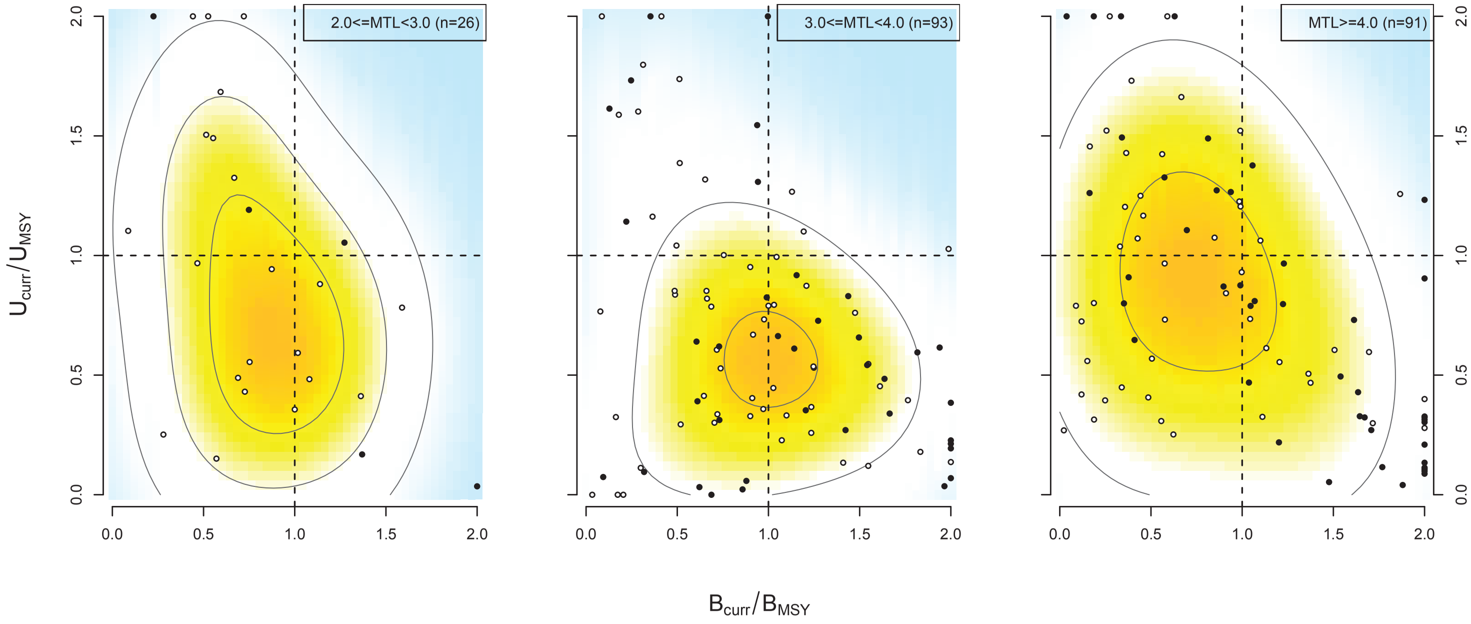

Figure 2.6: Current exploitation rate versus current biomass for individual stocks from a) low (>= 2.0 - < 3.0), b) medium (>= 3.0 - < 4.0) and c) high (>= 4.0) trophic levels. Plot details as in Figure 2.4.

2.4.7 Temporal Trends In Biomass

A total of 214 stocks can be used to estimate the transition probabilities between the four status-exploitation quadrants. Fig. 2.7 reports the percentage of occurence of each of the 16 possible transitions (Fig. A.1). The four most common transitions are "self-transitions" where a stock stays within a quadrant.

Quadrant 1 represents a stock below B_{msy} and above U_{msy}. The second most probable transition from quadrant 1 is to quadrant 4, indicating a reduction in U to a level below U_{msy}. Some stocks stays within quadrant 1 for the entire time series (100% of years) while others never reach quadrant 1 (0% of years).

Quadrant 2 represents a stock above B_{msy} and above U_{msy}, i.e. a stock experiencing overfishing but not considered overfished. The second most probable transition from quadrant 2 is to quadrant 1, indicating a reduction in B to a level below B_{msy}.

Quadrant 3 represents a stock above B_{msy} and below U_{msy}, which should represent a situation of sustainable harvest. The second most probable transition from quadrant 3 is to quadrant 2 indicating an increase in U to a level above U_{msy}, i.e. overfishing. Some stocks stays within quadrant 3 for the entire time series (100% of years) while others never reach quadrant 3 (0% of years).

Quadrant 4 represents a stock below B_{msy} and below U_{msy}. The second most probable transition from quadrant 4 is to quadrant 1 indicating an increase in U to a level above U_{msy}, overfishing an already overfished stock.

2.4.8 Multi-Stock Indicess

Mean values of the multi-stock indices for the different oceanic basins used in Hutchings et al. (2010) (Fig. 2.8) are presented in Table 2.1. Mean values for the periods 1971-1975 and 2001-2005 are reported and so is the percentage change between the early 1970s and early 2000s.

The multi-stock index for North Atlantic basins were reduced by 40-50% over between the 1970s and the 2000s, and all reached a level below B_{msy}. For the Northwest and Northeast Atlantic, the multi-stock index was already below B_{msy} in the 1970s. In contrast, the multi-stock index from the Northeast Pacific remained mostly unchanged (4% reduction) and is still above B_{msy}. Stocks from Australia and New Zealand experienced the largest redution in the multi-stock index (59%) but are still

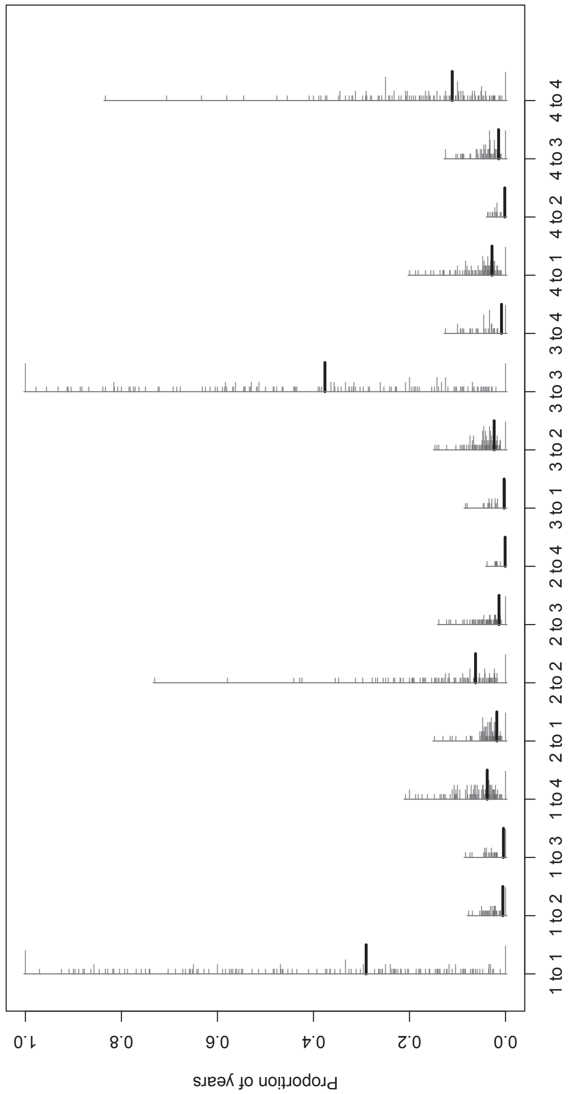

Figure 2.7: Proportion of years in each assessment time-series where each status-exploitation quadrant transition was observed. The x-axis contains the sixteen potential transitions between the four status-exploitation quadrants. The y-axis presents the proportion of years where a given transition was observed for the different stocks present in the RAM Legacy database.

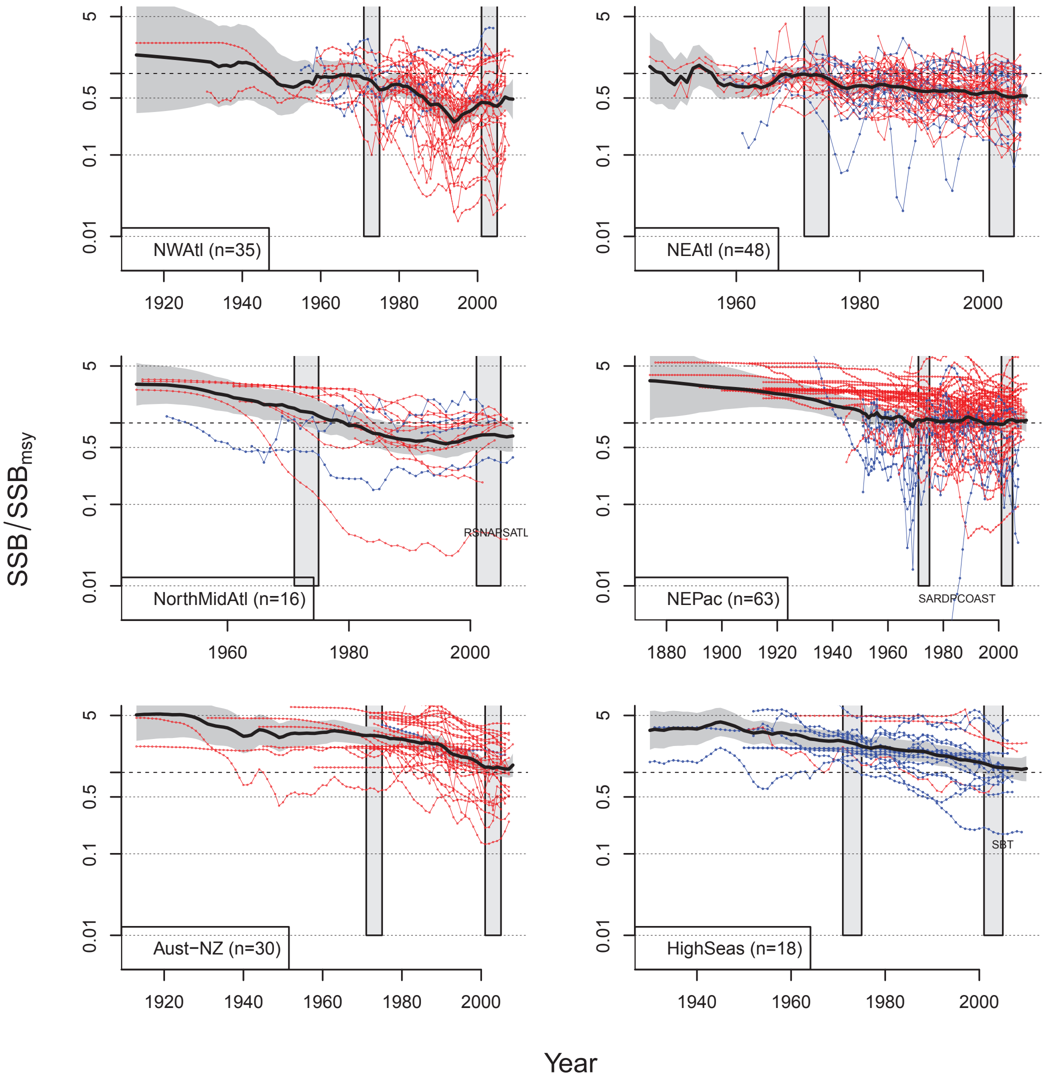

Figure 2.8: Temporal trends in biomass (B) relative to the estimated biomass at which the maximum sustainable yield should be obtained (B/B_{msy}) for the different oceanic regions used in Hutchings et al. (2010). Thin solid blue lines represent individual pelagic stocks and thin solid red lines represent individual demersal stocks. The solid black lines represent the fixed-effect mean yearly estimates, based on a mixed-effects model with population as a random effect. The shaded regions represent the 95% confidence intervals on the fixed-effect mean. Shaded boxes show the periods 1971-1975 and 2001-2005 for which indices values are reported in the text.

Table 2.1: Multi-stock indices for the different oceanic basins under consideration.

Region	Value 1970s	Value 2000s	change
NWAtl	0.775	0.423	-45
NEAtl	0.937	0.549	-41
NorthMidAtl	1.364	0.706	-48
NEPac	1.094	1.034	-5
Aust-NZ	2.813	1.147	-59
High Seas	2.349	1.237	-47

above B_{msy}. High Seas stocks were reduced by 47% but on average are still above B_{msy}.

2.5 Discussion

2.5.1 The Marine Stock Assessment Knowledge-Base

The RAM Legacy database provides detailed time series data and reference points from available stock assessments for the world's most intensively studied, industrially fished marine stocks, thus providing a basis for evaluating the existing knowledge-base of assessed stocks and the current status of these fisheries. In comparison to its predecessor, the Myers Stock- Recruit database, the RAM Legacy database contains 112 more stock assessments for marine species (when only those with at least one pair of stock-recruitment time series data are considered), but as of yet no assessments for anadromous species. Other researchers have compiled authoritative datasets on Pacific salmon species and interested readers should consult the rich literature on these species (e.g. Dorner et al., 2008).

2.5.2 Temporal, Geographic, And Taxonomic Patterns In Stock Assessment Data

While stock assessments provide high quality and detailed information about stock abundance, the trade-off to producing these complex and data-rich assessments is that they are conducted for only a small subset of fished stocks. Thus, just as global fisheries analyses based on catch databases must be clear about the limitations of the data, meta-analyses of stock assessments must acknowledge the temporal, geographic, and taxonomic biases that exist in these data, and hence in the RAM Legacy database.

Most marine stock assessments contain time series from only the past few decades (Fig. 2.1), whereas many industrial fisheries began long before this. Dominant age-structured assessment methodologies rely on catch-at-age data, which are often available for considerably shorter periods of time than total catch unless significant reconstruction efforts are made. Such historical reconstructions of catch-at-age data are highly uncertain (Quinn and Deriso, 1999) and in many cases the "base case" models used for management are based only on more reliable recent catch data. For assessments used in a tactical sense and for short-term projection (e.g., to understand whether a particular quota level will result in an increase or decrease in stock size), using only reliable recent catch data may be preferable. This is particularly true for backward projection methods (e.g., VPA), which may converge on parameter estimates within the more reliable recent period and potentially benefit little from reaching further back in time. Nevertheless, a focus on only the recent history of a fishery can be seriously misleading for strategic decisions about goals and BRPs. Put simply, if we do not know what's historically possible (in terms of stock size and variability), it's hard to know where we should set our goals, and more likely that degraded ecosystem states will be perceived as natural. This "shifting baseline" problem has been widely recognized (Pauly, 1995; Sáenz-Arroyo et al., 2005).

Geographically, accessible stock assessments are predominantly from developed nations in north-temperate regions, a limited region relative to that of all fisheries globally. Indeed, since the majority of assessed stocks are from the United States, our analysis (Fig. 2.4) is highly influenced by U.S. stock status and therefore may suggest an overly optimistic view of the state of assessed stocks globally. Inclusion of new stocks from other management bodies and of stocks with longer exploitation histories will provide an interesting opportunity to see how it modifies our view on the status of world fisheries. Assessments of stocks from regions experiencing intense exploitation but with limited management institutions would provide an informative contrast to assess the state of world fisheries.

The geographic pattern of assessed stocks arises for several reasons (each of which varies geographically in its prevalence): 1) an assessment is not conducted on a stock; 2) it is not possible to access the assessment; or 3) the non-exhaustive collation we undertook overlooked the assessment. In general, conducting stock assessments is a costly endeavour that is restricted to developed fishing nations. Whether an assessment is conducted for a given stock depends upon many factors, including the economic value of the stock, the availability of resources to collect the data required for an assessment (which frequently includes conducting fisheries-independent research surveys) and the quantitative expertise to conduct assessments. The legal context where fisheries are prosecuted can also strongly influence the requirement for conducting stock assessments. In the United States, the Magnuson-Stevens Act defines which stocks are to be monitored and managed, hence a large number of the assessments in the RAM Legacy database are under the jurisdiction of the US National Marine Fisheries Services. The accessibility of assessments depends upon the transparency and access policies of the relevant management agencies, which also varies geographically. Our search for assessments could also give rise to geographic biases, as concerted collation efforts have only been conducted in those known assessment-rich regions. It is hoped that readers of this article can assist in correcting these biases by participating in future updates of the RAM Legacy database, in particular, by helping to expand our coverage of stocks in developing countries and for species of limited commercial interest.

Marine stock assessments also are available for a very limited subset of the accepted taxonomic coverage of marine species worldwide, and of globally exploited species (Fig. 2.3). Stock assessments also are heavily biased (relative to existing species) toward species within the orders Gadiformes and Clupeiformes (Fig. A.3). The over-representation of the Gadiformes and, to a lesser degree, the Clupeiformes, continues when caught and assessed taxa are compared (Fig. 2.3). Overrepresentation of these taxa might partially reflect behavioural tendencies of these fishes to form large aggregated populations in temperate regions, which are accessible to industrial fisheries and in areas where fisheries management exists. Historical economic importance as well as the geographic distribution of the taxa in relation to areas where assessments are mandated may play important roles in determining what fished taxa are assessed. Of note is the absence of assessments for tropical species (with the exception of tunas) from the database. Inshore (e.g. estuarine species) and anadromous stocks are also are absent as a result of our focus on federally or internationally managed marine species.

2.5.3 The Status Of Assessed Marine Stocks

Overall, we estimate that 58% of assessed stocks (with reference points; n=214) are below the biomass reference point that maximises their yield (B_{msy}). Almost half of stocks below B_{msy} still experience exploitation rates above those that would maximise yield. This analysis presents a slightly more optimistic outlook on assessed stocks globally than that of (Worm et al., 2009), which used an earlier version of the database, and estimated 63% of assessed stocks were below B_{msy} (n=166 stocks). In comparison, in the latest State of the World Fisheries and Aquaculture (FAO, 2010), the FAO reports that of the 445 stocks with available status reports 15% are under-exploited or moderately exploited, 53% are fully exploited, 28% are overexploited, 3% are depleted and 1% are recovering. Direct comparison with these categories is difficult since our status is either above or below B_{msy}, whereas the categories used by the FAO are based on stock levels compared to their unfished state.

2.5.4 Regional-Level Status Of Assessed Marine Stocks

Examining the overall status of stocks under one's jurisdiction, and comparing the status of stocks amongst jurisdictions, may be useful for identifying management priorities and informing various stakeholders. Most stocks under European management seem caught in a situation of long-term unsustainability ($B_{current} < B_{msy}$; Fig. 2.4 and their potential to recover is hampered by excessive exploitation rates, $U_{current} > U_{msy}$. Our findings are in line with those of (Froese and Proelß, 2010), although our results are slightly more optimistic about the status of European stocks. The International Council for the Exploration of the Seas (ICES) has not historically used MSY-based reference points and all the European stocks presented in Fig. 2.4 are based on Schaefer-derived values. ICES is currently transitioning to the use of MSY-based reference points, which should be fully implemented by 2015 (European Commission, 2006). When looking at ICES traditional B_{lim} reference points instead (Fig. A.4) the situation for European stocks appears slightly more positive since the reference points used correspond to lower biomass levels and higher levels of exploitation, but overexploitation of depleted stocks is still common in European waters.

The situation is quite different for North American stocks and suggests that Canadian stocks are at historically low biomass levels but are also under reduced exploitation that should promote recovery (Fig. 2.4). Note that some of those stocks (most notably, cod stocks) were drastically depleted and have thus far failed to recover to the productive levels experienced in past decades. U.S. stocks are the most numerous in our database and suggest that appropriate management measures and regulations have brought many stocks to sustainable harvest levels (Fig. 2.4). Some stocks under US jurisdiction are still experiencing excessive exploitation rates and may reflect regional differences in management within the NMFS. In New Zealand, a large proportion of stocks are at relatively high biomass and low exploitation rate relative to their MSY reference points (Fig. 2.4). Worm et al. (2009) found that the New Zealand shelf was one of only two LMEs (the other was the California Current) in which overall multi-species exploitation rates are low enough that fewer than 10% of stocks are expected to be collapsed. Management through catch-shares is widespread in New Zealand and is thought to have contributed to the relatively low exploitation rates (Worm et al., 2009). Nevertheless, there are a number of stocks below B_{msy} in New Zealand that are still experiencing high exploitation rates, most notably New Zealand snapper in Area 8. In Australia, the picture is similar to the global aggregate, with 7 out of 11 stocks thought to be below B_{msy} and the same fraction also being exploited at levels below U_{msy} (Fig. 2.4). However, most of the stocks in Australia have MSY reference points estimated from the (relatively more uncertain) surplus production models. Stocks managed by RFMOs in the Pacific appear to be better off - both in terms of biomass and exploitation rates - than those in the Atlantic. Relatively low sample sizes in other parts of the world make it difficult to draw firm conclusions about assessed stock status.

2.5.5 Temporal Trends In Biomass

The approach used here to tabulate the biomass and exploitation status of stocks shows the high dgree of autocorrelation present in the time series since the "self-transitions" are the most common.

The biomass and exploitation time series arise from 2 very different processes. While the biomass time series is biologically driven, the exploitation regime is dictated by a variety of economic and management decisions. While it is impossible for the stock to grow faster than its maximum natural intrinsic growth rate, the exploitation rate experienced by a stock can rapidly and significantly increase or decrease over short periods of time.

A typical exploitation scenario would be for a stock to start in quadrant 3 where its biomass level is above B_{msy} and the exploitation rate is still under U_{msy}. As exploitation increases, the biomass decreases. If overfishing is taking place, we expect the stock to move to quadrant 2 and to eventually reach quadrant 1 since the excessive exploitation rate will reduce the stock to below B_{msy}. In this hypothetical scenario, the exploitation rate is curbed back to a level below U_{msy} which should promote stock recovery. So the transition from quadrant 1 to quadrant 4 indicates an economic and/or management decision, whereas the transtion from quadrant 4 to quadrant 3 follows a biological process.

The transition probabilites obtained from stocks in the RAM Legacy database provide some insight into the evolution of biomass and exploitation of harvested marine populations. First, many stocks seem under appropriate management and sustain exploitation rates below U_{msy} while maintaining their biomass above B_{msy}. These conditions correspond to quadrant 3 and are highlighted by the high probability of self-transition in quadrant 3. This self-transition has the highest mean probability of all 16 possible transitions. However, many stocks never experience this transition since they are never in quadrant 3 over the time frame covered by their assessment.

2.5.6 Multi-Stock Indices

The interpretability of the multi-stock indices suffers from the limited taxonomic coverage of assessed stocks. Each index properly represents the overall state of stocks in a given oceanic basin but must be carefully interpreted since assessed stocks may or may not reflect the ecological reality of each ocean basin. Marine populations that do not undergo proper stock assessments are important components of marine ecosystems and are not accounted for in the interpretation of the multi-stock indices reported here. As such, it is best to interpret the indices as the fisheries portfolio of each basin.

The inclusion of more stocks in the database would improve the usefulness of the multi-stock indices to evaluate status of fisheries. I believe that the plots of Fig. 2.8 could be used by fisheries managers that want an overview of the state of the fisheries in a given spatial unit. For example, this figure could be generated for different management bodies instead of oceanic basins.

Unlike Hutchings et al. (2010), I decided not to model the pelagic and demersal species separately. Because of the limited number of stocks with reference points, the distinction between pelagic and demersal stocks and any inference they may suggest about their covariation is not possible. Here again, adding more stocks to the database so that a larger proportion of species are represented would alleviate this shortcoming.

2.5.7 Applications And Caveats Of The RAM Legacy Database

Applications

Over the past two years, while still in development, the RAM Legacy database has been used to conduct comparative analyses of fisheries status (Worm et al., 2009; Hutchings et al., 2010; Melnychuk et al., 2011), the utility of mean trophic level as a biodiversity indicator (Branch et al., 2010), the relationship between catch and stock assessment data (Branch et al., 2011), and the relationship between life history characteristics and the propensity for stocks to collapse (Pinsky et al., 2011). Hopefully, the RAM Legacy database will continue to be of utility for fisheries scientists, ecologists, and marine conservation biologists, and that its public release with this publication will enable and foster further comparative analyses of marine fisheries on a variety of topics including collapse and recovery patterns, fisheries productivity, and marine population dynamics.

Caveats

Stock assessment outputs (e.g. biomass time series), which constitute the majority of the new RAM Legacy database are model estimates, not raw data. Ideally, the uncertainty associated with these estimates should be carried forth in subsequent analyses. Although the database structure allows for inclusion of estimates of uncertainty (standard errors, 95% credible/confidence intervals), uncertainty estimates for time series data were typically missing from assessments and hence are not included in the current version of the database. As with any analysis, clearer inference on the strength of a signal is available when all uncertainty in the data is carried forth. Sensitivity tests to various levels of measurement error on the time series may be necessary in many investigations.

The original database developed by Ransom A. Myers was used to address a variety of ecological questions derived from stock-recruit relationships. This synthesis was possible because the VPA-type assessment models that constituted most of that database generated time series of stock and recruitment with relatively few a priori assumptions. In contrast, the forward projection methods that are common in the RAM Legacy database generally specify the form of the stock-recruit relationship, and in many cases even fix parameters such as steepness. Stock-recruitment "data" from such models, are clearly inappropriate for straightforward meta-analysis. In general, as more assessments incorporate some type of prior information from other stocks or species (Hilborn and Liermann, 1998), there is less stockspecific information available for future meta-analysis (Minte-Vera et al., 2005). One solution is for stock assessments to report not only best estimates of parameters based on all available data, but also stock-specific parameter estimates that do not incorporate prior information from other stocks or species.

Reference points which we have derived from surplus production models are to be interpreted with great care. For stocks with both assessment-derived and Schaefer-derived BRPs, we found that B_{msy} estimates from surplus production models were generally lower than those obtained from assessments, particularly at high B_{msy} values; the converse was observed for U_{msy} (see details in Supporting Information Fig. S2). This discrepancy stems from the fact that in the Schaefer surplus production model, MSY occurs at 50% of the carrying capacity whereas in most age-based assessment models, yield is maximised at a lower fraction of the carrying capacity. All exploitation rate reference points, whether estimated within the assessment model or by a surplus production model, must be interpreted with caution as changes through time in size/age selectivity of the fishery also alter the exploitation rate reference points.

2.6 Concluding Remarks

Despite its limited taxonomic and geographic coverage, the RAM Legacy database can be used to conduct many interesting analyses about various aspects of fisheries ecology. The use of a relational database and source control software provides the necessary framework to reproducible analyses. The database provides information that can be used in conjunction with other data sources to establish the status of fisheries and the progress being made in establishing a sustainable regimes of marine harvest.

Chapter 3

DERIVING STOCK INDICES FROM SCIENTIFIC TRAWL SURVEYS

3.1 Abstract

Scientific trawl surveys have been conducted in different regions of the world and by a variety of countries and agencies since the mid- 1900s. Although the data are collected in a scientifically and statistically appropriate context and represent an important source of fishery-independent information for agency-specific stock assessments, their use and dissemination has often been limited to the agencies conducting the surveys. In recent years, Internet data portals such as the Ocean Biogeographic Information System have provided an arena for the wider distribution and use of marine fish data. Despite the increased accessibility of such data, their scientific acceptability has been limited by a lack of reproducibility in data analyses. We present a methodology for the computation of timeseries of groundfish stock indices using publicly available trawl survey data derived from the Canadian Department of Fisheries and Oceans Maritimes region. Potential pitfalls associated with the computation of time-series are discussed and proper stratified random estimates of temporal abundance trends are compared with other methods for a selected subset of species. Also, the broader applicability of the methods for datasets collected under similar sampling designs is discussed, along with the reproducibility of the analyses and results.

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3.2 Introduction

In the Northwest Atlantic, routine scientific trawl surveys have been conducted since the mid-1900s to provide fisheries-independent information about fish populations (Doubleday, 1981; Doubleday and Rivard, 1981). In the Scotian Shelf and Bay of Fundy region of Canada, the surveys have been conducted since 1970. Sampling activities started later off Newfoundland and in the Gulf of St Lawrence. In the United States, survey activities on Georges Bank and in the Gulf of Maine and parts of the Scotian Shelf date back to 1963. Although these surveys concentrate on commercially exploited species, they also record catch information for all species taken and provide an invaluable source of information about marine organisms.

Surveys are a major source of information for fisheries management in Canada and around the world. Agencies conduct sampling activities using a variety of gear types, vessels, and protocols. Here we concentrate on surveys conducted on the Scotian Shelf and in the Bay of Fundy region of Canada [57-68W 43-47N; Northwest Atlantic Fisheries Organization (NAFO) divisions 4X, 4V, and 4W; Figure 3.1). The sampling design was originally based on the distribution of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). Survey samples use a bottom trawl and consist of 30-min tows at a speed of 3.5 knots, giving a towed distance of 1.75 nautical miles. Beginning in 1970, tow-level data on the numbers and weights caught, and the size compositions, were recorded for all fish and some invertebrate species. Since 2000, data have been recorded for all marine species caught in the survey trawl (Tremblay et al., 2007). The surveys are manned by trained scientists whose responsibilities include gathering the data within a planned sampling design and using consistent fishing gear and methods. The sampling protocol also ensures correct species identification and appropriate digital storage of the data.

For researchers outside government agencies, obtaining data from marine ecosystems often follows an ad hoc process: data are made available under certain conditions and analyses are run using the version received. Controversies about data interpretation often arise when analyses are not reviewed by the data custodians. In contrast, data that are made publicly available through Internet-based systems need to follow metadata standards, ensuring that data sources can be correctly referenced/cited and that analyses can be replicated.

Figure 3.1: The Scotia-Fundy region of the Northwest Atlantic showing NAFO divisions 4X, 4W, and 4V. The solid black polygon shows the extent of DFO Maritimes' SUMMER and SUMMER_TELEOST surveys. Fishing tow locations are plotted as tiny grey crosses, and the 200m isobath is also shown.

The metadata consist of all the information necessary to understand a dataset. This includes, but is not limited to, the appropriate citation of the data, and their spatial and temporal coverage. Good metadata give credibility to publicly available datasets and foster proper interpretation of biogeographic data. Several digital standards exist to capture metadata, and being tasked with authoring them can be daunting; discussion of the merits and pitfalls of the different metadata standards, however, is beyond the scope of this paper.

The Internet has changed the way that data are shared and obtained by researchers, though in fields of marine science such as physical oceanography, datasets have historically been shared among scientists. Examples of such datasets include bathymetric grids, conductivity-temperature-depth (CTD) profiles of the water column, infrared imagery (sea surface temperature products), and ocean colour imagery (chlorophyll a products). As such, the computational tools and standards required to store, query, extract, and analyse the data are mature and available. In contrast, marine biogeographic datasets such as those derived from scientific surveys are often held in disparate formats by various agencies. The standards and tools required to share biogeographic information were only recently formulated, and are now beginning to gain acceptance within the biogeographic research community.

Data portals exist that provide access to a wide variety of data that can be used for scientific analyses of fish population dynamics and fish diversity. It is hoped that the increasing quantity of publicly available biogeographic data will foster novel research initiatives that will utilize the data in a context broader than that for which they were collected. For example, the Census of Marine Lifes Ocean Biogeographic Information System (OBIS) provides access to more than 20 million records from almost 700 different data sources (OBIS, 2009a). The OBIS data portal provides a centralized location to access data from a multitude of sources. It also provides visualization tools and the possibility of downloading data in OBIS schema format. The OBIS schema format (OBIS, 2009b) is derived from the Darwin Core 2 specification for exchange of information on the geographic occurrence of living organisms (Taxonomic Diversity Working Group, 2009). Although the number of records on the OBIS portal is staggering and making maps of the data is encouraged, it is important for such systems to go beyond map production. To gain acceptance in the wider ecological community, data portals need to provide information that can be used in a broader context, such as the analysis of temporal and spatial dynamics of marine populations (Myers, 2000).

Here we describe the steps and methods involved in making the Department of Fisheries and Oceans (DFO) Maritimes survey data available on OBIS. This includes creating effective metadata and generating a properly formatted version of the dataset. We also demonstrate how the data can be used and misused by comparing computation methods that generate abundance time-series with various degrees of knowledge on the sampling design of the trawl surveys. We also discuss the temporal changes observed in the survey-derived abundance estimates of eight fish species caught commercially. We show that a nave interpretation of the publicly available data yields improper time-series of species abundance, but that appropriate temporal trends can be computed using additional information about the sampling design.

The steps detailed here can be applied to other datasets generated in scientific surveys conducted by other fisheries agencies, and we hope therefore that the methods described to document and encode survey data collections can and will be repeated. This will ensure that erroneous interpretations of trawl survey data are minimized while still promoting wider dissemination of data through portals such as OBIS.

3.3 Methods

The metadata record for the OBIS version of the DFO Maritimes Research Vessel Trawl Surveys Fish Observations data was created in Directory Interchange Format (DIF NASA (National Aeronautics and Space Administration), 2008) and made available and discoverable on NASA's Global Change Master Directory (GCMD, http://gcmd.nasa.gov/) metadata portal. The metadata records contained in the GCMD also appear on Canada's equivalent metadata discovery site named Geodiscover (http://geodiscover.cgdi.ca/). These metadata records provide information about the surveys' spatio-temporal coverage, and their citation details, and also provide links to the data available on the OBIS portal. Additionally, the OBIS portal provides an extended metadata record containing additional information about the dataset. The url to both the GCMD and the OBIS metadata records is listed in the References (Clark and Branton, 2007a,b).

To be made accessible to the OBIS portal, the data need to be formatted to follow the OBIS schema. The groundfish survey data from DFO Maritimes are stored in a relational database management system at the Bedford Institute of Oceanography in Dartmouth, NS, Canada. The database contains all information recorded during the surveys and in subsequent post-survey analyses, such as the age records of fish determined from otoliths. Using the Structured Query Language (SQL), the data are formatted to follow the OBIS format and made available to the data portal through a Distributed Generic Information Retrieval (DiGIR) server, also located at the Bedford Institute of Oceanography.

For the DFO Maritimes Research Vessel Trawl Surveys Fish Observations data (Clark and Branton, 2007a), only "valid" tows are included in the OBIS version. This means that fishing tows that did not meet the requirements for acceptance (accurate duration and functioning of the gear, not crossing a stratum boundary, etc.) are removed. Additionally, the catch data are normalized for the distance towed and can be used directly as an indicator of abundance and biomass. An example OBIS record from the survey data is provided in Table 3.1.

The OBIS version of the data used in this paper was obtained in ASCII format from the OBIS data portal. We used the Advanced Search facility of the portal to obtain the data from the DFO Maritimes Research Vessel Trawl Surveys Fish Observations dataset. The data available from OBIS contain many different survey series conducted throughout the year with different vessels and gears. For the current analysis, we concentrated on the SUMMER and SUMMER_TELEOST survey series, which consist of data collected during July and August in the Bay of Fundy and on the Scotian Shelf from 1970 to present. Over the time frame of available data, the SUMMER and SUMMER_TELEOST series follow a consistent sampling design. Additionally, we only include data from stratum 440 to stratum 495, because they are the most consistently sampled over the duration of the survey series.

Before 1982, fishing was carried out with a Yankee 36 otter trawl, but is now conducted with a Western IIa trawl. There were also vessel changes during the survey series, CCGS "A.T. Cameron" being the main survey platform from 1970 to 1981, CCGS "Lady Hammond" from 1982 to 1991, and CCGS "Alfred Needler" from 1983 to today. However, for technical reasons, the CCGS "Alfred Needler" was substituted

Table 3.1: Example of a single OBIS record from the SUMMER survey of the DFO Maritimes Research Vessel Trawl Surveys Fish Observations dataset.

Field name	Value
res_name	DFOgfsDBfish
scientificname	Gadus morhua
institutioncode	BIO
catalognumber	TEM2008830-178-10-1
latitude	44.34
longitude	261.9
collectioncode	SUMMER
datelastmodified	2007-07-13T18:24:50Z
yearcollected	2008
monthcollected	7
daycollected	31
minimumdepth	163
maximumdepth	164
slatitude	44.35767
slongitude	261.90883
elatitude	44.33
elongitude	261.89983
Class	Actinopterygii
kingdom	Animalia
ordername	Gadiformes
phylum	Chordata
family	Gadidae
genus	Gadus
species	morhua
scientificnameauthor	Linnaeus, 1758
collector	TEM
fieldnumber	TEM2008830-178
locality	462
observedindividualcount	1
observedweight	0.345
samplesize	1.71 nautical miles x 41.0 ft

Table 3.2: Species used in the analysis and the number of records from the SUMMER and SUMMER_TELEOST survey data (for stratum 440 to stratum 495) available in the OBIS dataset.

Common name	Scientific name	Number of records in OBIS
American plaice	*Hippoglossoides platessoides*	5049
Atlantic cod	*Gadus morhua*	4613
Haddock	*Melanogrammus aeglefinus*	4373
Silver hake	*Merluccius bilinearis*	3470
Redfish species	*Sebastes* spp.	3108
White hake	*Urophycis tenuis*	2790
Herring	*Clupea harengus*	2262
Pollock	*Pollachius virens*	2143

by its sister ship CCGS “Wilfred Templeman” in 2008 and by CCGS “Teleost” in 2004 and 2007. For purposes of illustration, abundance time-series were generated for eight species caught commercially that have .2000 records in the SUMMER and SUMMER_TELEOST series of the OBIS dataset (Table3.2). These species cover a wide range of taxa, abundance, and exploitation history, and provide a base case to evaluate the methods presented here.

Following recommendations made by Branton and Ricard (2007), individual tows i in the OBIS version of the DFO dataset can be identified by the value in the “fieldnumber” field of the OBIS schema. Similarly, stratum s is identified by the “locality” field, the swept-area of the trawlnet by the “samplesize” field, and the vessel by the “collector” field. The OBIS version of the dataset consists of observations only, and all sampling locations (including those where a species is not caught) need to be used to determine observations of zero catch. We assigned values of zero catch to tows where a species was not observed. For each combination of year y, stratum s, and tow i, we used the OBIS data to create observations of fish abundance for the eight species of interest. Each abundance observation is either the value observed in the “observedindividualcount” field of the OBIS data record, or zero if a tow did not have a catch record for a given species. In other words, for each species we generated observations $a^0_{y,s,i}$. For illustration purposes, we also created catch records $a_{y,s,i}$ that included only the observations and that did not account for records of zero catch.

Using the two types of record generated from the OBIS data ($a^0_{y,s,i}$ and $a_{y,s,i}$), we used four computation methods to generate annual time-series that corresponded to varying degrees of understanding about the dataset. The methods rely on the assumptions made about the data and how they were collected. The different computations presented below range from naïve interpretations of the data to appropriate estimation of catch rates with knowledge of the sampling design.

The first method does not take into account the stratification scheme of the survey and also does not take the zeroes into account. The annual estimate of population abundance for each species is calculated as the mean abundance for that year, excluding the zero observations. We refer to this time-series as OBIS raw:

$$\hat{a_y} = \frac{\sum_{s=1}^{S} \sum_{i=1}^{n_{y,s}} a_{y,s,i}}{n_y} \tag{3.1}$$

where $n_{y,s}$ is the number of catch records from the OBIS dataset in year y and stratum s, n_y the total number of catch records in year y ($n_y = \sum_{s=1}^{S} n_{y,s}$), and S the number of strata sampled in year y.

This method can result in overestimation of abundance, because samples with zero catch are not included in the calculations. The annual estimates for the second method take the zeroes into account. We refer to this time-series as OBIS with zeroes:

$$\hat{a_y^0} = \frac{\sum_{s=1}^{S} \sum_{i=1}^{n_{y,s}^0} a_{y,s,i}^0}{n_y^0} \tag{3.2}$$

where n_y^0 is the number of catch records from the OBIS dataset in year y and stratum s, including catches with zero individuals, and n_y^0 the total number of catch records, including catches with zero individuals, in year y ($n_y^0 = \sum_{s=1}^{S} n_{y,s}^0$). Note that, while accounting for observations of zero catch, the time-series generated from Equation 3.3 still does not account appropriately for the sampling design, because it assumes that each sample was independent.

To attempt to account for the stratum and year effects, a third time-series was generated using a generalized linear model (GLM) with negative binomial error and a log link using strata (s) and year (y) as factors. In other words, population abundance $a_{y,s}^0 = \sum_{i=1}^{n_{y,s}^0} a_{y,s,i}^0$ is assumed to follow a negative binomial distribution of mean μ, and the linear predictor (LP) of μ is

$$log(\mu_{y,s}) = LP_{y,s} = \alpha + \beta_y + \gamma_s \tag{3.3}$$

where α is the overall mean, β_y the year effect, subject to $\sum_{y=1}^{Y} \beta_y = 0$, and γ_s is the strata effect, subject to $\sum_{s=1}^{S} \gamma_s = 0$. The fitted model was then used to predict an annual time-series that we refer to here as OBIS GLM.

Finally, the fourth time-series was generated by computing the annual stratified random estimates of species abundance using strata statistics obtained from the OBIS Canada site (OBIS Canada, 2009). These statistics are required for computation of stratified random estimates of abundance. The additional information required consisted of the surface area of each stratum s, which was divided by the swept-area of the gear to obtain the number of towable units in each stratum (N_s). The data from OBIS were used to compute annual estimates of fish abundance for the different species of interest. Following the methods documented in Smith (1996) and Lohr (1999), we computed the stratified mean for each year and refer to the time-series as OBIS stratified:

$$\bar{a_y} = \sum_{s=1}^{S} \frac{N_s}{N} \bar{a_{y,s}} \tag{3.4}$$

where $s = 1, 2, 3, \ldots, S$ are the different strata, $\bar{a_{y,s}}$ the catch sample mean for stratum s in year y ($\bar{a_{y,s}} = \sum_{i=1}^{n^0_{y,s}} a^0_{y,s,i}$), N_s the number of towable units in stratum s, and $N = \sum_{s=1}^{S} N_s$ the total number of towable units in the area surveyed.

Although useful, time-series of population abundance need to be interpreted carefully, and the uncertainty associated with the estimates needs to be provided. This can be done readily using the OBIS data. Following from Equation 3.3, the estimated stratified variance for each year can be calculated from

$$\hat{V}(\bar{a_y}) = \sum_{s=1}^{S} \left(1 - \frac{n_s}{N_s}\right) \left(\frac{N_s}{N}\right)^2 \left(\frac{\nu_s}{n_s}\right) \tag{3.5}$$

where n_s is the number of tows in stratum s, and ν_s the catch sample variance for stratum s.

It is common to report the standard error of an estimator, which is the square root of the estimated variance. In our case, the standard error (s.e.) is

$$s.e.(\bar{a_y}) = \sqrt{V(\hat{\bar{a}}_y)} \tag{3.6}$$

The four time-series generated from the publicly available data (OBIS raw, OBIS with zeroes, OBIS GLM, and OBIS stratified) were compared with each other to identify differences in interpretation associated with each methodology. The stratified random estimate of abundance was used as the reference case because it accurately accounted for the survey design (Smith, 1996). We were interested in seeing how well the different methods estimated the abundance trends of the eight species of interest.

For comparing the different methodologies used to derive the time-series, we reported Spearman's and Pearson's correlation coefficients between the reference case (OBIS stratified) and OBIS raw, OBIS with zeroes, and OBIS GLM. These measures of standard correlation provide an indication of the association between a computation method and the reference case, but they do not account for systematic differences. If two methods are identical in their measurement properties, we would expect them to follow a linear relationship of unit slope and zero intercept. The intraclass correlation coefficient, ICC(1,1), as defined in Shrout and Fleiss (1979), measures deviations from the unit slope and zero intercept (an ICC value of near 1 would indicate values that fall close to this ideal).

All data handling was carried out using a PostgreSQL relational database management system (PostgreSQL Global Development Group, 2009). Statistical analyses and generation of plots were conducted with the R Environment for Statistics and Graphics (R Development Core Team, 2011) using the packages beanplot (Kampstra, 2008), irr (Gamer et al., 2007), MASS (Venables and Ripley, 2002), and RODBC (Ripley et al., 2009). The map in Figure 1 was generated using the Generic Mapping Tools (Wessel and Smith, 1991).

3.4 Results

The four abundance time-series generated using the OBIS data plotted for the eight species of interest are presented in Figure 3.2. The stratified random estimate of the number of fish per tow in a given year ranged from a maximum of 571.07 per tow for redfish species (Sebastes spp.; Figure 3.2) in 2009 to a minimum of 0.13 fish per tow for herring (Clupea harengus; Figure 3.2) in 1978. Species such as pollock (Pollachius virens; Figure 3.2) showed a high variability in annual estimates. Other species, such as haddock (M. aeglefinus; Figure 3.2) and redfish, showed an increasing trend in abundance over the time-series.

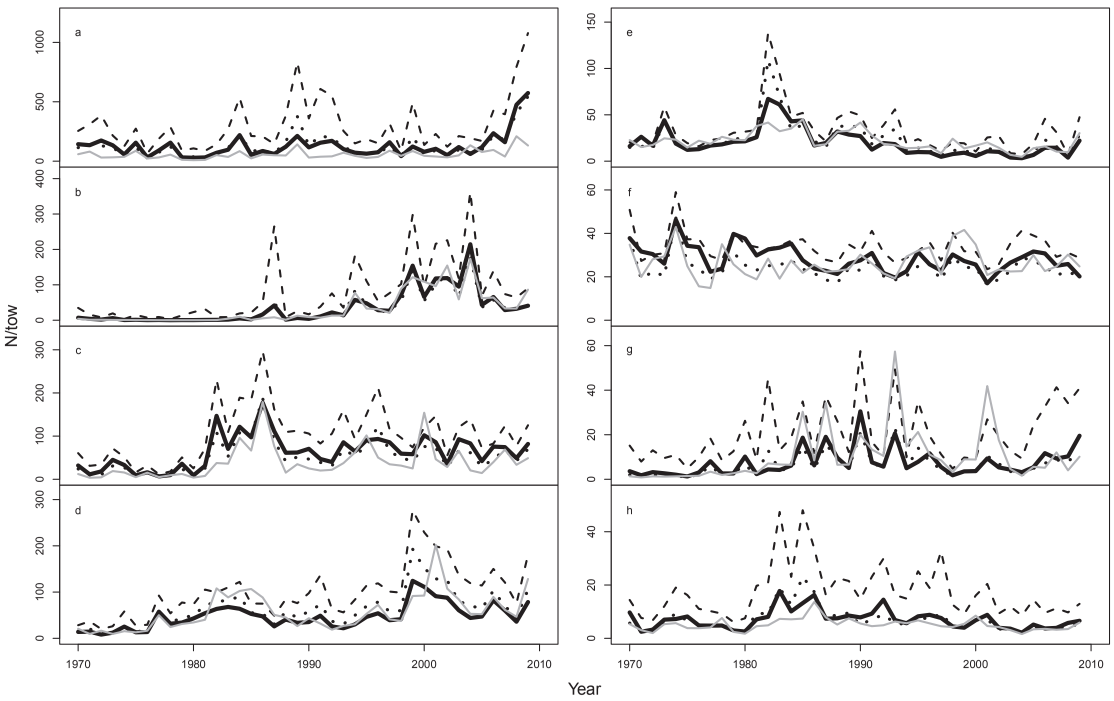

Figure 3.2: Abundance time-series for (a) redfish (*Sebastes* spp.), (b) Atlantic herring (*C. harengus*), (c) silver hake (*Merluccius bilinearis*), (d) haddock (*M. aeglefinus*), (e) Atlantic cod (*G. morhua*), (f) American plaice (*H. platessoides*), (g) pollock (*P. virens*), and (h) white hake (*Urophycis tenuis*) obtained using the OBIS version of the DFO's SUMMER and SUMMER_TELEOST survey data from 1970 to 2009 in the Scotia-Fundy region of the Northwest Atlantic (NAFO divisions 4X and 4VsW). The heavy black line is the OBIS stratified reference time-series, the dashed line the OBIS raw time-series, the dotted line the OBIS with zeroes time-series, and the grey line the OBIS GLM time-series.

For the eight species of interest, the Spearman's correlation coefficients, Pearson's correlation coefficients, and intraclass correlation coefficients, ICC(1,1), between the three methods used with the OBIS data and the reference methodology (OBIS stratified) are listed in Table 3.3. In general, the ICC value was lower than that of either the Spearman's or Pearson's coefficients, indicating that although the time-series were highly correlated, there were discrepancies between the reference case and the other methods.

An example of the standard error being added to the timeseries, to provide an estimate of the uncertainty associated with the stratified random mean for Atlantic cod (*G. morhua*), is given in Figure 3.3.

3.5 Discussion

The GCMD and Geodiscover websites provide access to the metadata record for the DFO Maritimes Research Vessel Trawl Surveys Fish Observations. The clear documentation of the dataset through a proper metadata record provides authority and citability to the data. However, the DIF format used by GCMD is limited in its ability to describe the details associated with the data collection in full. An alternative metadata standard that can be used is the Ecological Metadata Language (EML EML Project, 2008)), and we hope to provide the DFO Maritimes Research Vessel Trawl Surveys Fish Observations as an EML record in future.

Each computation method includes a different degree of understanding of the data collection, which is reflected in how well the results compare with the reference method. In general, the OBIS raw method yielded the least agreement with the reference case. ICC values were lower than either Spearman's or Pearson's correlation coefficients, indicating that methods that seem to do a good job at estimating annual abundance are in reality rather poor. Because it takes the sampling design into account, the stratified random methodology is the most appropriate estimator of yearly abundance.

The OBIS raw time-series tended to overestimate the average number of fish caught per tow for most years and most species, likely because the computed annual average does not include observations of zero catch. As a large proportion of the tows have zero catch (Figure 3.4), it is important to account for zeroes in the

Table 3.3: Value of correlation coefficients between the reference time-series and the other OBIS-derived time-series.

Species	Correlation measure	OBIS raw	OBIS with zeroes	OBIS GLM
Hippoglossoides platessoides	Spearman	0.768	0.823	0.583
	Pearson	0.808	0.841	0.624
	ICC(1,1)	0.531	0.627	0.089
Gadus morhua	Spearman	0.866	0.942	0.910
	Pearson	0.899	0.922	0.930
	ICC(1,1)	0.618	0.877	0.885
Melanogrammus aeglefinus	Spearman	0.908	0.957	0.872
	Pearson	0.956	0.979	0.708
	ICC(1,1)	0.290	0.815	0.644
Merluccius bilinearis	Spearman	0.957	0.979	0.908
	Pearson	0.954	0.954	0.859
	ICC(1,1)	0.617	0.917	0.777
Sebastes spp.	Spearman	0.917	0.931	0.520
	Pearson	0.890	0.934	0.587
	ICC(1,1)	0.369	0.935	0.453
Urophycis tenuis	Spearman	0.899	0.881	0.671
	Pearson	0.886	0.863	0.705
	ICC(1,1)	0.062	0.847	0.628
Clupea harengus	Spearman	0.936	0.991	0.971
	Pearson	0.921	0.982	0.955
	ICC(1,1)	0.636	0.976	0.814
Pollachius virens	Spearman	0.853	0.917	0.745
	Pearson	0.842	0.888	0.616
	ICC(1,1)	0.197	0.867	0.457

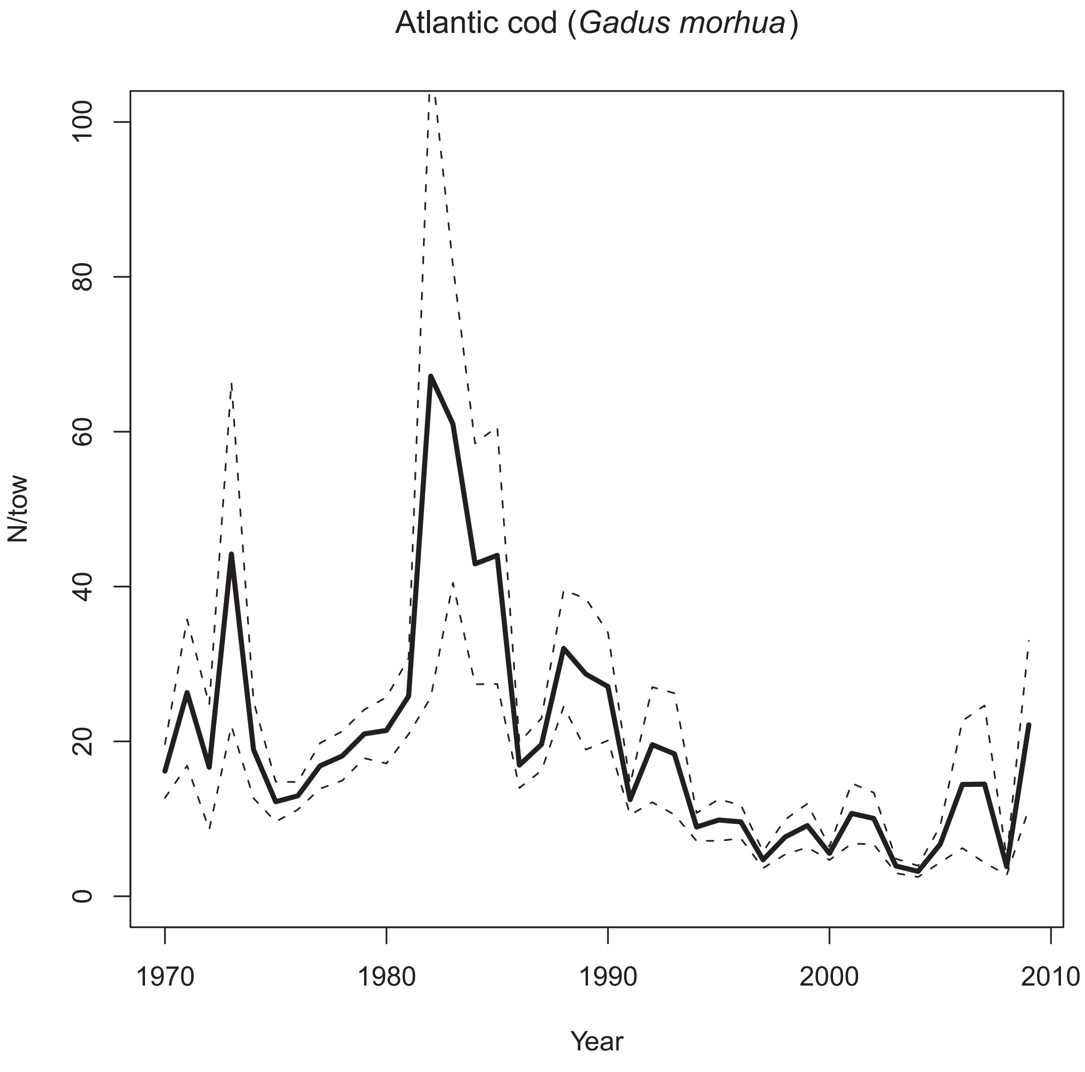

Figure 3.3: Abundance time-series for Atlantic cod obtained using the OBIS version of the DFO's SUMMER and SUMMER_TELEOST survey data from 1970 to 2009 in the Scotia-Fundy region of the Northwest Atlantic (NAFO divisions 4X and 4VsW), including an estimate of the uncertainty of the annual estimate of stratified random mean abundance. The mean annual estimate is plotted as a solid line along with ±1 s.e. (dotted lines).

computation of the time-series. Note, however, that the OBIS raw time-series sometimes provided annual estimates less than the stratified random estimates (e.g. 1971, 1972, and 1980 for American plaice, Hippoglossoides platessoides; Figure 3.2). Using raw annual averages from the OBIS data is, however, wrong, so the time-series derived should not be used for analysing trends in population abundance, especially when combining data from different sources (as was unfortunately done by NOAA (2005b)).

The OBIS with zeroes time-series more closely matched the reference time-series than the OBIS raw time-series but still did not account for the sampling design. For species with a large proportion of tows of zero catch (Figure 3.4), accounting for the zeroes provided time-series estimates that more closely matched the reference time-series but still did not account for the sampling design.

The OBIS GLM time-series was generated from a fitted model that aimed to account for stratum and year effects, estimating a parameter for each year and each stratum. However, the model assumes that the strata effects are the same over the whole timeseries and that the year effects are the same over all strata. As the GLM uses a log link and a negative binomial error distribution it treats catches of zero differently from the other methods and also reduces the effects that large catches have on the overall annual estimate.

The number of records in the OBIS datasets is a reflection of how common a species is in the survey samples. Although a species may be taken frequently, its real abundance in the samples may be less than that of species that are taken less often. This is the case for American plaice, the species with the most records in the OBIS record but with values of annual abundance far less than those of other species (Figure 3.2).

Agencies conducting similar surveys to those conducted by DFO Maritimes should consider making their data available on OBIS. An essential step in making data available on OBIS is to provide authoritative metadata. Additionally, using interpretations of OBIS fields similar to those used here will facilitate the wider use of groundfish survey datasets by researchers. Trawl survey scientific data from the US Northeast Fisheries Science Center were recently made available on OBIS (NOAA, 2005a), and they use similar encodings to DFO Maritimes data.

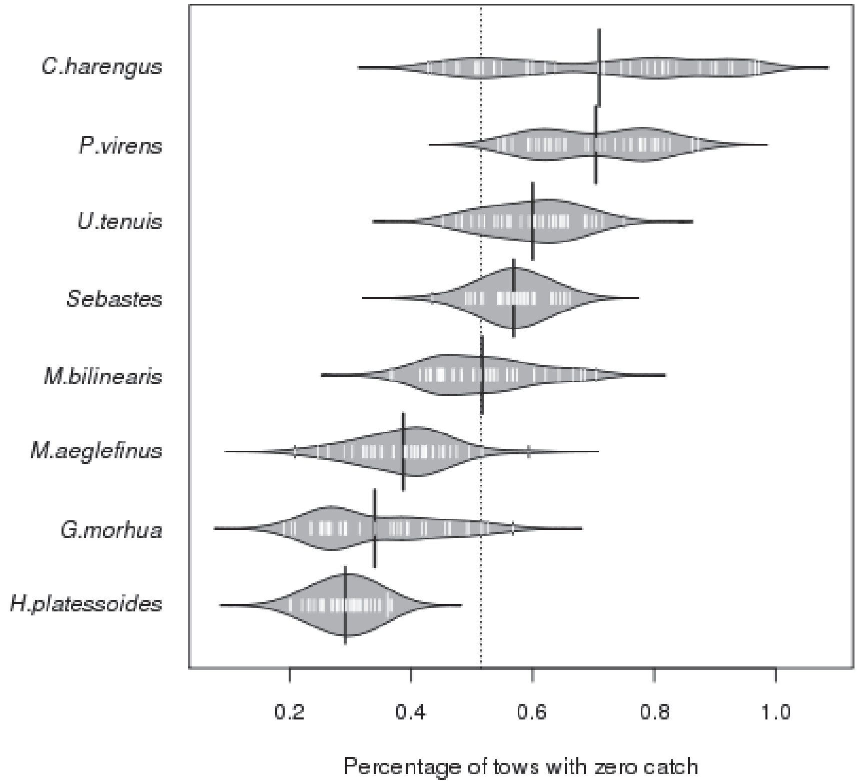

Figure 3.4: Proportion of tows with zero catch for the eight species of interest. The proportion of tows with zero catch is computed for each species and each year in the survey data (n = 40 for each species) and presented as a beanplot, showing the proportion of tows with zero catch for each year (thin vertical white lines) and the mean proportion of tows with zero catch (thick vertical black line). The dotted vertical line represents 50% of tows with zero catch.

Although they provide crucial baseline information about a particular area, trawl surveys still have limited spatio-temporal coverage. Although combining survey time-series poses many challenges, doing so can augment knowledge of the spatiotemporal dynamics at scales that exceed those of individual surveys. As the different time-series computed from the OBIS data show, it is important to incorporate the sampling design into computations of abundance time-series.

To interpret correctly how trawl survey data relate to fish population dynamics, it is also important to consider seasonal migrations and other spatial shifts in the distribution of species during the time-series available. As such, the estimates derived from the survey data are just a starting point for further analysis of fish population dynamics. A stock assessment will also use data on landings and other sources of information about the species. The range of a species may also be limited to a subset of the strata, and assessment scientists need to use this knowledge to generate realistic time-series of abundance and biomass over the survey area. The methodology presented here can be used also to compute stratified random estimates over a subset of strata in the surveyed area.

We are aware that the time-series we computed provide only a measure of the number of fish caught per tow and not an estimate of total abundance over the area surveyed. Knowledge of the catchability of the fish species to the gear is also necessary in computing a value of total abundance. We only considered species abundance, but the OBIS data also contain biomass data for the surveys (stored in the "observedindividualweight" field of each OBIS record). As such, estimates of population biomass can also be computed using publicly available data.

The methods used to generate the OBIS version of the DFO Maritimes Research Vessel Trawl Surveys Fish Observations also mean that once the results of a survey have been uploaded into the production database, new data can be quickly updated in the public domain. In other words, additional catch records added to the OBIS version of a dataset are soon available for use. The data available on OBIS can also be used to conduct analyses of the diversity of fish species. The sampling protocols for fish species are consistent for the duration of the surveys, but care is necessary in accounting for the catchability of different fish species. Nevertheless, a dataset similar to that provided on OBIS has been used successfully to examine changes in fish diversity in the surveyed area (Shackell and Frank, 2003).

One of the many limitations of the OBIS data format is that it is not well suited for life-history analyses. For example, analyses of growth rate, maturation schedules, and age-specific fecundity cannot be performed using the data available on OBIS. However, such data are usually easily available from the data custodians identified in the OBIS metadata record, making the data discoverable and authoritative and providing a vehicle for wider dissemination of scientific trawl survey data.

Chapter 4

EXAMINING THE SPATIAL POPULATION DYNAMICS OF GROUNDFISH IN THE NORTHWEST ATLANTIC

4.1 Abstract

The range-abundance relationship is one of the most well-documented macroecological pattern, but has received little attention in the fisheries literature, where stock abundance is often assessed over a whole stock area with little consideration for finer distribution trends. Here I examine the spatial distributions of 46 groundfish populations in the Northwest Atlantic from trawl survey data collected by management agencies in Canada and the United States. Positive correlations between the stratified random estimate of abundance and area occupied were observed for most species examined and suggest a tight spatial response to fluctuations in abundance. Yet, the magnitude of distribution changes was smaller than that of abundance. I also documented some spatial hysteresis in that populations that experienced large abundance declines failed to expand their distribution after recovering to a higher level of abundance; this might be explained by changes in population structure. The relationship between local density an overall abundance was also examined to determine whether density-dependent mechanisms were important in regulating population abundance in different habitats of the survey area. Areas of positive and negative relationships were observed for each population, but when examined across different populations, there is little evidence for the existence of "core habitats" that are important to all species. These findings are relevant to the spatial management of demersal fisheries and suggest that the protection of particular core habitats will benefit only a subset of species and that conservation of ecosystem-wide processes can only be achieved through a variety of measures designed to limit the scale of abundance and distribution changes caused by exploitation.

4.2 Introduction

Studying the spatiotemporal fluctuations in abundance and biomass of living organisms is a central theme of ecology. The estimation of how populations vary over time and space provides a basis for studying their intra-specific and inter-specific relationships. Changes in abundance of terrestrial species are often accompanied by changes in distribution (Gaston, 1996). Such "abundance-distribution" relationships are expected to be positive, can arise from a variety of mechanisms and have important ecological consequences for the management and conservation of species (Gaston et al., 2000). The relationship has been clearly documented for terrestrial species (e.g. Zuckerberg et al., 2009) but its existence in the marine environment, although documented (Crecco and Overholtz, 1990; Swain and Sinclair, 1994), has been the focus of less scrutiny.

The abundance of many groundfish populations in the Northwest Atlantic fluctuated markedly over their documented history. The purpose of this chapter is to examine how the distribution of groundfish populations changes as their abundance varies, to examine how local density relates to abundance, and to establish the suitability of local habitats to the fish community as a whole. Fisher and Frank (2004) examined the relationship between abundance and distribution for several stocks sampled by scientific trawl surveys in the Scotia-Fundy region and from Fisheries and Oceans Canada. I build upon and extend the analyses of Fisher and Frank (2004) by using an analytical framework that properly accounts for the stratified random sampling design of the survey, by including observations from the National Marine Fisheries Services (NMFS) surveys conducted on the Northeast continental shelf of the United States, and by expanding the analyses to investigate the relationship between local density and abundance for populations inhabiting the Northwest Atlantic continental shelf.

The way that a population changes in density when its abundance fluctuates provides insight into the importance of local habitats to overall range. Density-dependent habitat selection is a mechanism that can explain how local density will relate to abundance. Relating local density to overall abundance has been used to study individual populations (e.g. Marshall and Frank, 1995; Swain and Morin, 1996; Brodie et al., 1998) but has not been applied to a suite of species that form a community. The increasing reliance on spatial ocean management and planning, and the identification of “core habitats” as areas of special interest for conservation initiatives requires a detailed understanding of the relationship between local density and abundance. Under density-dependent habitat selection, local density in marginal habitats is expected to increase more than in preferred habitats as the overall abundance increases (MacCall, 1990; Marshall and Frank, 1995). It may therefore be possible to identify habitat suitability through the relationship between local density and overall abundance.

This chapter examines the spatial population dynamics of groundfish species in the Northwest Atlantic to determine which species exhibit positive occupancy-abundance relationships, to document how temporal changes in abundance and distribution covary and to identify habitats that are of importance for the whole fish community.

4.3 Methods

The number of individuals caught during a standardised trawl tow provided an estimate of local density in each stratum sampled. This density estimate was transformed into a stratum abundance estimate because both the area of the stratum and the area swept by the trawl can be estimated. The number of towable units in each stratum was typically used to generate the stratified random estimate of abundance from the trawl survey. Pooled density estimates from individual tows were used to create an index of relative density.

Distributional and abundance changes, and their relationship to overall abundance were examined for marine species that were reliably sampled by trawl gear used by scientific surveys in the Northwest Atlantic. I used the scientific trawl survey data from the Fisheries and Oceans Canada (DFO) and from the United States’ National Marine Fisheries Services of the National Oceanic and Atmospheric Administration (NMFS/NOAA), as publicly available from the Ocean Biogeographic Information System (OBIS) to estimate species-level temporal trend in abundance and distribution. The Canadian surveys started in 1970 and those from the United States in 1963. The species included here were those that were consistently and reliably sampled by the trawl survey gear (Tables 4.1 and 4.2) and that were caught in more than 500 tows over the time period covered by each survey. The most commonly observed species of taxonomic order Gadiformes (Atlantic cod, haddock, pollock, silver hake, white hake and red hake) and Pleuronectiformes (American plaice, yellowtail flounder, winter flounder, witch flounder and Atlantic halibut) were used in this analysis. I also included four species of skates (thorny skate, smooth skate, winter skate and little skate), spiny dogfish, four species of order Scorpaeniformes (redfish species, longhorn sculpin, moustache sculpin and sea raven) as well as Atlantic herring, monkfish, ocean pout and northern shortfin squid. Two species, little skate and moustache sculpin, appeared in sufficient numbers only in the DFO data and were absent from NMFS data for a total of 24 species for DFO (Table 4.1) and 22 species for NMFS (Table 4.2).

For each combination of survey k, species n, year y, stratum s and tow i, I used the OBIS data to create observations of abundance for each species of interest. In other words, I generated observations $y^0_{k,n,y,s,i}$ which included catches of zero individuals. The catch data and the survey strata boundaries were used to generate maps and time series of distribution and abundance. I focused on strata that were consistently sampled for the duration of the survey and excluded tows from exploratory deep strata. Additionally, each stratum must have had a minimum of 5 tows with catch of a given species over the duration of the survey to be included in the analyses. These procedures removed strata of marginal importance and improved the fitting of models that used strata as class variables.

4.3.1 Estimating Species Abundance And Distribution

Because of the sampling design of the survey, the appropriate estimator of yearly abundance used for each species was the stratified random estimate. To minimise the effects of the year-to-year variability introduced by the small number of tows in some stratum-year combinations I computed the stratified estimates for 5-year periods (pentad, hereafter). The stratified random estimate of abundance per tow for each pentad p ($p = \lfloor y/5 \rfloor$) was calculated as:

$$\overline{Y}_{k,n,p} = \sum_{s=1}^{S} \frac{N_s}{N} \overline{y}_{k,n,p,s} \tag{4.1}$$

where,

$\overline{y}_{k,n,p,s}$ is the mean abundance per tow computed using the t tows conducted during pentad p in stratum s (i.e. $\overline{y}_{k,n,p,s} = (\sum_{i=1}^{t} y^0_{k,n,p,s,i})/t$)

N_s is the number of sampling units in stratum s

N is the total number of sampling units in the surveyed area (i.e. $N = \sum_{s=1}^{S} N_s$)

The pentadal stratified estimates was used to derive fisheries-independent trends of species-level abundance over the area surveyed. An alternative was to define “stock areas” within the survey region to separate the observed individuals to sub-areas. I decided against that for this chapter and chose to compute the temporal indices of distribution and abundance over the whole survey area. Variation in local components of a population was investigated through mapping and visual analysis.

The surveys followed a stratified random protocol where tow locations were randomly assigned within each stratum. However, the overall distribution of tows over the survey area was not randomly distributed in space since samples are allocated to different strata based on a stratum’s area and other considerations such as reducing sample variance in certain strata. Therefore, applying a grid to the dataset to define spatial units for comparison (e.g. as done by Fisher and Frank (2004)) was not an appropriate approach since each grid cell is not necessarily independent of each other. The independence of the survey data was within a stratum, and there were often few tows in each stratum-year combinations. The use of pentad estimates that include catch information for 5-year periods helped to increase sample size.

I used three measures of distribution for each survey-species combination. The first measure was the area of occupancy which I defined as the sum over all strata of the proportions of tows with catch in each stratum multiplied by the surface area of each stratum:

$$O_{k,n,p} = \sum_{s=1}^{S_k} \frac{t^c_{k,n,p,s}}{t_{k,n,p,s}} A_{k,s} \tag{4.2}$$

where,

$t^c_{k,n,p,s}$ is the number of tows with catch in pentad p and stratum s (i.e. where $a^0_{k,n,y,s,i} > 0$)

$t_{k,n,p,s}$ is the total number of tows in pentad p and stratum s (i.e. where $a^0_{k,n,y,s,i} \geq 0$)

S_k is the number of strata in survey k

$A_{k,s}$ is the surface area of stratum s from survey k

Several alternatives methods exist to quantify distribution (see Rindorf and Lewy, 2012, for a good overview), and I used two measures based on the Lorenz curve of abundance and distribution. The Lorenz curve (see Swain and Sinclair, 1994) is generated for each pentad by ordering the stratum-level estimates of abundance and computing the associated cumulative surface area of strata. The first measure was the minimum area required to account for a certain percentage of the total population abundance. Strata abundance estimates were ordered by decreasing values and the minimum number of strata required to obtain $x\%$ of the total population abundance is identified. The total area of these strata was then defined as $D^{x\%}$.

The second method using the Lorenz curve was the Gini index (as used by Swain and Sinclair, 1994; Myers et al., 1995c; Brodie et al., 1998) which was computed for each pentad to examine changes in the area over which the abundance was distributed. Strata abundance estimates were ordered by increasing values and the cumulative area was computed. The Gini index was computed as twice the difference between the area under the Lorenz curve and the area under the identity function. An increase in the value of the Gini index indicated that the abundance was distributed over a smaller area.

For each survey k and species n, the correlation between the abundance (as estimated by the stratified random estimate) and distribution (as estimated by area occupied, the Gini index and $D^{75\%}$) were computed. I used the Pearson correlation coefficient to quantify this correlation and report whether the relationship was statistically significant.

4.3.2 Examining The Relationship Between Local Density And Abundance

The relationship between abundance and distribution is likely to vary in different parts of the survey area because of the relative habitat quality of each stratum. Examining how stratum-level density relates to abundance can yield insight into the local response of populations and can help identify areas of particular importance to a given population. Such an analysis can also help determine whether density-dependent mechanisms are observable for the populations under study. A model used by many others (Myers and Stokes, 1989) to investigate this relationship is:

$$y^{0}_{k,n,p,s,i} = \alpha_{k,n,s} Y^{\beta_{k,n,s}}_{k,n,p} \tag{4.3}$$

The model defined by equation (4.3) is best fitted to data through a logarithmic transformation. However, this introduces serious shortcomings because catch values of zeroes ($y^{0}_{k,n,y,s,i} = 0$) can not be log transformed. Other studies have resolved this problem by adding a small constant to catch (e.g. 0.5 in Myers and Stokes (1989)) to make the model appropriate for parameter estimation:

$$log\left(y^{0}_{k,n,p,s,i} + 0.5\right) = log\left(\alpha_{k,n,s}\right) + \beta_{k,n,s} log\left(Y_{k,n,p}\right) \tag{4.4}$$

Adding a small value to catch may or may not introduce biases in the parameter estimates. A better alternative to evaluate how local density relates to overall abundance is to use another model that can account for catch values of zero:

$$E\left[y^{0}_{k,n,p,s,i}\right] = \mu = exp\left(\alpha_{k,n,s} + \beta_{k,n,s} Y_{k,n,p}\right) \tag{4.5}$$

This model is best formulated as a generalized linear model using an error distribution that can accommodate zeroes (Poisson or negative binomial) and a log link function to linearise the response variable. The value of parameter estimates can be interpreted for evidence of density-dependent habitat selection. Slope estimates of zero mean that the local density stays the same as the overall abundance changes. A positive value means that there is a positive relationship between local density and overall abundance so that changes in overall abundance are met with changes of similar direction in local density. Negative slope values indicate that changes in overall abundance and changes in local density are in opposite direction.

Under an ideal free distribution, individuals of a population are distributed through their habitat in a manner that reflects the resources available (Fretwell and Lucas, 1970). Habitats that provide more resources will sustain more individuals. Different habitats will react differently to changes in overall abundance and the changes in local density are expected to be greater for marginal habitats than for core habitats (Marshall and Frank, 1995). Core habitats should have slope value of zero and marginal habitat should have positive slope. Negative slope estimates are interpretable differently based on whether the overall abundance is increasing or decreasing.

The estimated parameter values can also be related to the stratum-level density to examine whether high and low density habitats behave similarly to changes in overall population abundance. Mean and median density estimates for each survey strata can be calculated to better interpret the slope estimates.

4.3.3 Summarisation Of Results

The analyses described above yield a large amount of results that are best presented in a summarised format. The trends in abundance and distribution for each population examined were used to generate ratios of area occupied versus ratios of minimum abundance over maximum abundance. I call these "vulnerability plots" because they show the maximum changes in abundance and the associated changes in distribution over the time series. The ratios of abundance and area occupied were also computed for time periods of 10, 20, 30 and 40 years since the beginning of the time series (as per Worm and Tittensor, 2011). This allowed the identification of the relationship between temporal changes in abundance and distribution.

The slope estimates ($\beta_{k,n,s}$ values from equation 4.5) were summarised across species for both the DFO and NMFS surveys. The average slope value across all species for which a proper model fit could be obtained was computed and mapped for each stratum. The average values of slope estimates provided a community-wide index of the response of stratum density to changes in abundance.

An additional summarisation of results was generated by computing and mapping the average normalised abundance across species for each stratum. For each pentad, the stratum with the highest abundance per tow was identified and used to normalise all strata catch abundance from 0 to 1. The average value of normalised catch abundance over the whole time series was then computed and mapped for each stratum.

These summaries provided a spatial overview of the habitat quality of each stratum across species and allow the identification of “core habitats” that are important to numerous species. All the above analyses were conducted using the publicly available trawl survey data from OBIS (Clark and Branton, 2007b; NOAA, 2005a). DFO strata statistics were obtained from the OBIS Canada website (OBIS Canada, 2009) and the NMFS strata statistics were obtained from authoritative scientific personnel familiar with the survey methodologies (Chad Keith, Northeast Fisheries Science Center, pers. comm.). Data processing, statistical analyses, plots and maps were done using the R software environment (R Development Core Team, 2011) using packages “PBSmapping” (Schnute et al., 2010), “MASS” (Venables and Ripley, 2002) and “xtable” (Dahl, 2009). All modelling results were subjected to visual analysis of residuals to ensure the appropriateness of the fits.

Table 4.1: DFO survey data summary. Scientific name, common name, number of records, mean catch per tow and range of catch per tow for the 24 species used in the analyses. The species are ordered in decreasing order of their mean stratified random estimate of abundance over the time period covered by the survey.

Common name	*Scientific name*	Num. records	Mean stratified	Range stratified
Redfish	*Sebastes* species	3452	122.18	80.6 to 273.83
Silver hake	*Merluccius bilinearis*	3781	62.77	15.32 to 100.94
Haddock	*Melanogrammus aeglefinus*	4691	46.59	14.62 to 80.35
Shortfin squid	*Illex illecebrosus*	3978	39.32	12.67 to 87.59
Herring	*Clupea harengus*	2542	33.53	0.59 to 115.68
American plaice	*Hippoglossoides platessoides*	5378	28.61	24.03 to 35.62
Spiny dogfish	*Squalus acanthias*	1615	21.60	3.77 to 35.52
Atlantic cod	*Gadus morhua*	4899	19.27	6.62 to 43.29
Yellowtail flounder	*Limanda ferruginea*	2776	17.41	13.07 to 23.78
Pollock	*Pollachius virens*	2301	7.18	2.6 to 13.42
White hake	*Urophycis tenuis*	3010	7.04	5.03 to 10.51
Longhorn sculpin	*Myoxocephalus octodecemspinosus*	2811	5.68	2.89 to 9.42
Witch flounder	*Glyptocephalus cynoglossus*	3594	4.91	2.56 to 8.36
Thorny skate	*Amblyraja radiata*	3741	4.24	1.56 to 6.98
Winter flounder	*Pseudopleuronectes americanus*	1292	2.63	0.63 to 4.45
Red hake	*Urophycis chuss*	1563	2.30	0.13 to 4.21
Moustache sculpin	*Triglops murrayi*	1093	1.09	0.11 to 2.29
Sea raven	*Hemitripterus americanus*	1832	0.66	0.49 to 1.24
Winter skate	*Leucoraja ocellata*	1075	0.61	0.4 to 0.93
Monkfish	*Lophius americanus*	1725	0.55	0.4 to 0.85
Smooth skate	*Malacoraja senta*	1568	0.54	0.3 to 0.96
Ocean pout	*Zoarces americanus*	1361	0.53	0.28 to 0.81
Little skate	*Leucoraja erinacea*	551	0.33	0.13 to 0.6
Halibut	*Hippoglossus hippoglossus*	1247	0.22	0.14 to 0.35

Table 4.2: NMFS survey data summary. Scientific name, common name, number of records, mean catch per tow and range of catch per tow for the 22 species used in the analyses. The species are ordered in decreasing order of their mean stratified random estimate of abundance over the time period covered by the survey.

Common name	*Scientific name*	Num. records	Mean stratified	Range stratified
Silver hake	*Merluccius bilinearis*	15392	48.29	28.66 to 68.67
Redfish	*Sebastes fasciatus*	5256	43.95	10.44 to 94.92
Spiny dogfish	*Squalus acanthias*	16081	29.29	18.28 to 44.16
Herring	*Clupea harengus*	5927	19.09	2.22 to 48.34
Haddock	*Melanogrammus aeglefinus*	6905	12.48	4.01 to 31
Red hake	*Urophycis chuss*	10093	9.95	6.32 to 11.92
Yellowtail flounder	*Limanda ferruginea*	6070	7.87	2.14 to 26.08
Longhorn sculpin	*Myoxocephalus octodecemspinosus*	6993	7.72	5.46 to 11.21
American plaice	*Hippoglossoides platessoides*	7000	7.70	4.94 to 10.75
Shortfin squid	*Illex illecebrosus*	7159	5.66	1.08 to 10.72
White hake	*Urophycis tenuis*	7004	3.75	2.31 to 5.81
Winter skate	*Leucoraja ocellata*	4650	2.80	1.34 to 5.63
Winter flounder	*Pseudopleuronectes americanus*	4794	2.79	1.95 to 3.89
Atlantic cod	*Gadus morhua*	7408	2.42	1.41 to 3.55
Ocean pout	*Zoarces americanus*	4594	1.86	0.72 to 4.09
Witch flounder	*Glyptocephalus cynoglossus*	5275	1.65	0.87 to 2.19
Pollock	*Pollachius virens*	3741	1.42	0.86 to 2.31
Thorny skate	*Amblyraja radiata*	5070	1.29	0.34 to 2.54
Sea raven	*Hemitripterus americanus*	5322	0.83	0.51 to 1.07
Monkfish	*Lophius americanus*	6176	0.61	0.39 to 0.86
Smooth skate	*Malacoraja senta*	2244	0.59	0.38 to 0.82
Halibut	*Hippoglossus hippoglossus*	651	0.06	0.04 to 0.17

4.4 Results

Statistically significant positive correlations between abundance and area occupied were estimated for 17 of the 24 species in the DFO survey and for 11 of the 22 species in the NMFS survey, indicating the existence of an occupancy-abundance relationship (Tables 4.3 and 4.4 and Figures 4.1 and 4.2). The correlation between abundance and the distribution measures derived from the Lorenz curve were only statistically significant for 3 species from the DFO and NMFS surveys.

Table 4.3: Correlation coefficients between abundance and three measures of distribution obtained from DFO survey data.

Species	area occupied	Gini	$D^{75\%}$
Sebastes species	0.913 **	-0.132	-0.307
Merluccius bilinearis	0.642	-0.629	0.36
Melanogrammus aeglefinus	0.528	-0.101	0.1
Illex illecebrosus	0.745 *	-0.378	0.495
Clupea harengus	0.866 **	-0.817 *	0.818 *
Hippoglossoides platessoides	0.755 *	0.486	-0.574
Squalus acanthias	0.625	-0.618	0.658
Gadus morhua	0.734 *	0.138	-0.194
Limanda ferruginea	0.36	0.53	-0.495
Pollachius virens	0.664	-0.284	0.354
Urophycis tenuis	0.351	0.35	-0.257
Myoxocephalus octodecemspinosus	0.723 *	0.486	-0.374
Glyptocephalus cynoglossus	0.887 **	0.745 *	-0.7
Amblyraja radiata	0.975 **	-0.644	0.559
Pseudopleuronectes americanus	0.927 **	-0.654	0.4
Urophycis chuss	0.894 **	-0.741 *	0.781 *
Triglops murrayi	0.903 **	-0.388	0.347
Hemitripterus americanus	0.755 *	0.068	0.128
Leucoraja ocellata	0.485	0.034	0.018
Lophius americanus	0.872 **	0.028	0.003
Malacoraja senta	0.918 **	-0.575	0.542
Zoarces americanus	0.935 **	0.554	-0.538
Leucoraja erinacea	0.936 **	-0.126	0.162
Hippoglossus hippoglossus	0.986 **	-0.395	0.249

The Electronic Supplement of this thesis contains additional figures, maps and tabular parameter estimates.

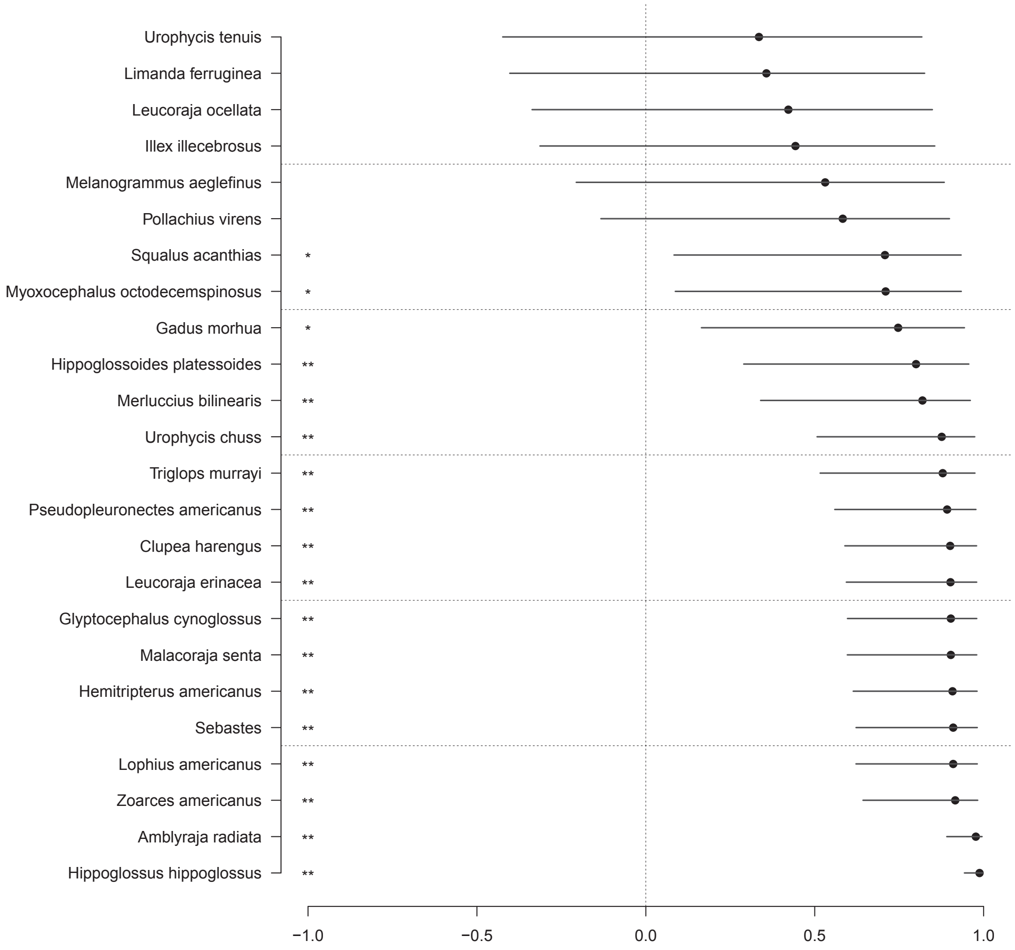

Figure 4.1: Correlations between area occupied and abundance for DFO groundfish populations. Pearson correlation coefficient values are reported for area occupied only. Species with statistically significant correlation coefficients are marked by a single ($p \leq 0.05$) or double ($p \leq 0.01$) asterisk. The species are ordered by decreasing value of the correlation coefficients.

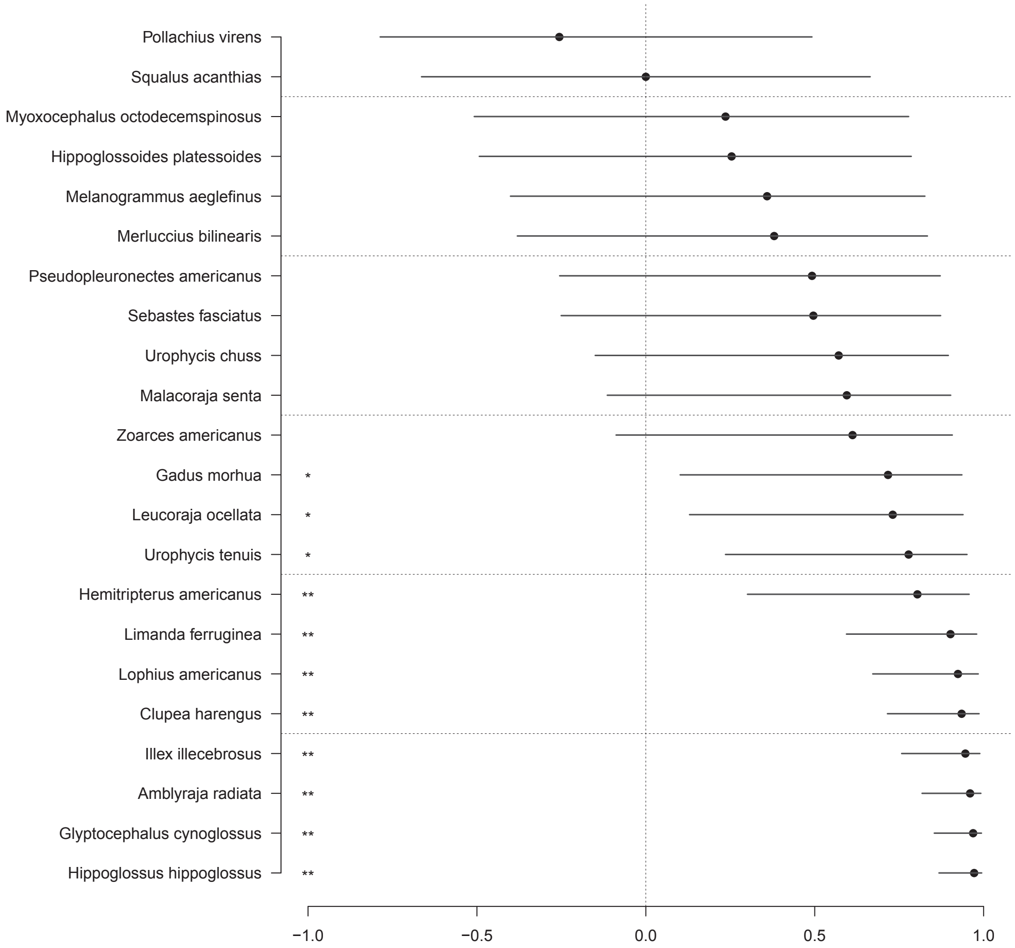

Figure 4.2: Correlations between area occupied and abundance for NMFS groundfish populations. Pearson correlation coefficient values are reported for area occupied only. Species with statistically significant correlation coefficients are marked by a single ($p \leq 0.05$) or double ($p \leq 0.01$) asterisk. The species are ordered by decreasing value of the correlation coefficients.

Table 4.4: Correlation coefficients between abundance and three measures of distribution obtained from NMFS survey data.

Species	area occupied	Gini	$D^{75\%}$
Merluccius bilinearis	0.38	0.192	-0.303
Sebastes fasciatus	0.496	0.255	-0.534
Squalus acanthias	0	-0.342	0.412
Clupea harengus	0.935 **	-0.85 **	0.832 **
Melanogrammus aeglefinus	0.359	-0.128	-0.005
Urophycis chuss	0.571	-0.313	0.417
Limanda ferruginea	0.902 **	0.023	0.069
Myoxocephalus octodecemspinosus	0.236	0.469	-0.522
Hippoglossoides platessoides	0.254	-0.233	0.243
Illex illecebrosus	0.946 **	-0.688 *	0.544
Urophycis tenuis	0.778 *	-0.471	0.645
Leucoraja ocellata	0.731 *	-0.044	0.127
Pseudopleuronectes americanus	0.492	0.484	-0.528
Gadus morhua	0.717 *	0.069	-0.069
Zoarces americanus	0.612	0.62	-0.68 *
Glyptocephalus cynoglossus	0.969 **	-0.172	0.045
Pollachius virens	-0.256	0.608	-0.583
Amblyraja radiata	0.96 **	-0.815 **	0.001
Hemitripterus americanus	0.804 **	0.191	-0.394
Lophius americanus	0.924 **	0.013	0.165
Malacoraja senta	0.595	0.546	-0.503
Hippoglossus hippoglossus	0.972 **	0.32	-0.523

All computed ratios, except one (DFO little skate), fall on the left side of the 1:1 line, indicating that declines in abundance were of greater magnitude than concomitant changes in distribution (Figure 4.3). The temporal evolution of both the abundance and distribution identifies cases of spatial hysteresis where abundance recoveries were not matched by increases in area occupied (Figure 4.4). For example, the 40 years changes for NMFS that appear below the horizontal line indicate that the abundance has increased over the time period but the area occupied has decreased over the same period. This is the case for haddock which, despite a 230% increase after 40 years saw its area occupied decrease by 30%.

Average slope values ($\beta_{k,n,s}$ values from equation 4.5) across species in the survey area appear on Figures 4.5 and 4.6. Averaging over all species yields weak spatial

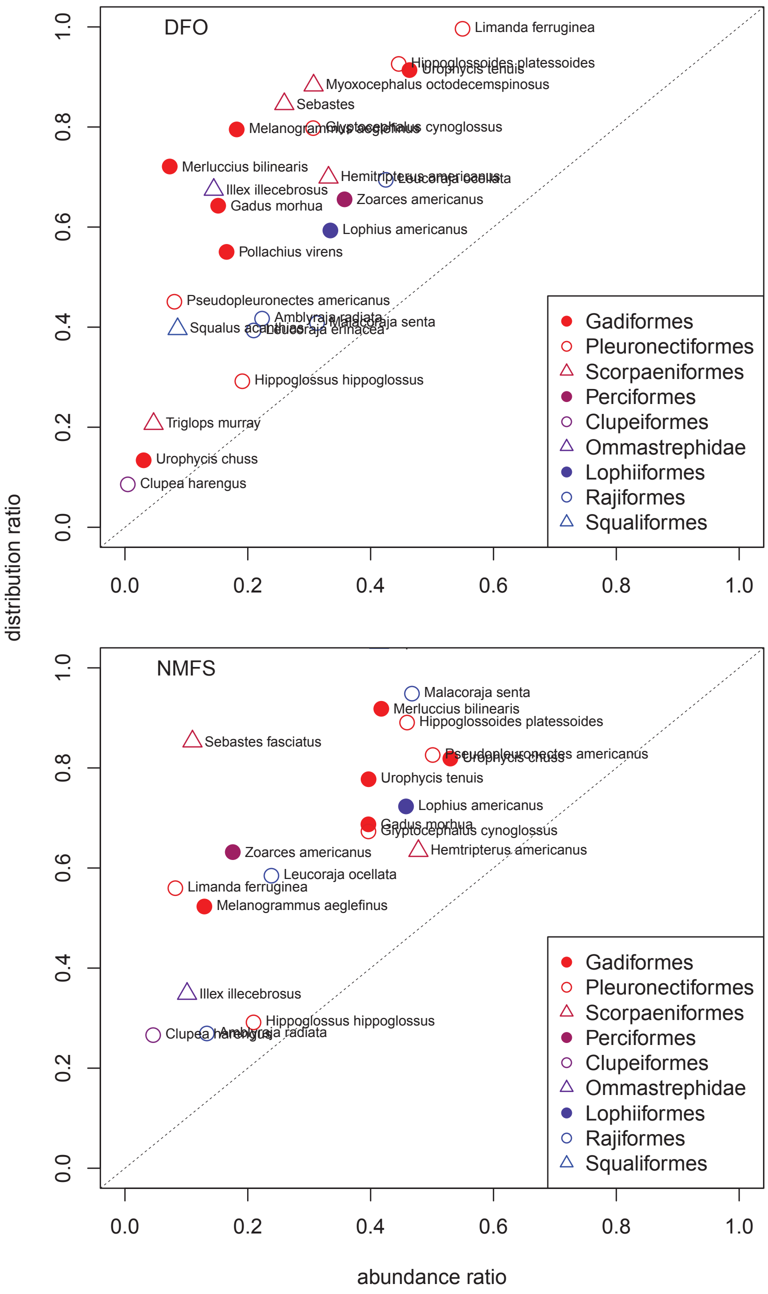

Figure 4.3: Plot of the ratios of minimum distribution over maximum distribution versus ratios of minimum abundance over maximum abundance. The ratios are computed using the minimum and maximum values of area occupied and abundance over the available time-series from the DFO (top panel) and NMFS (bottom panel) surveys. Each point represents a population and is colour- and symbol-coded for different taxonomic families.

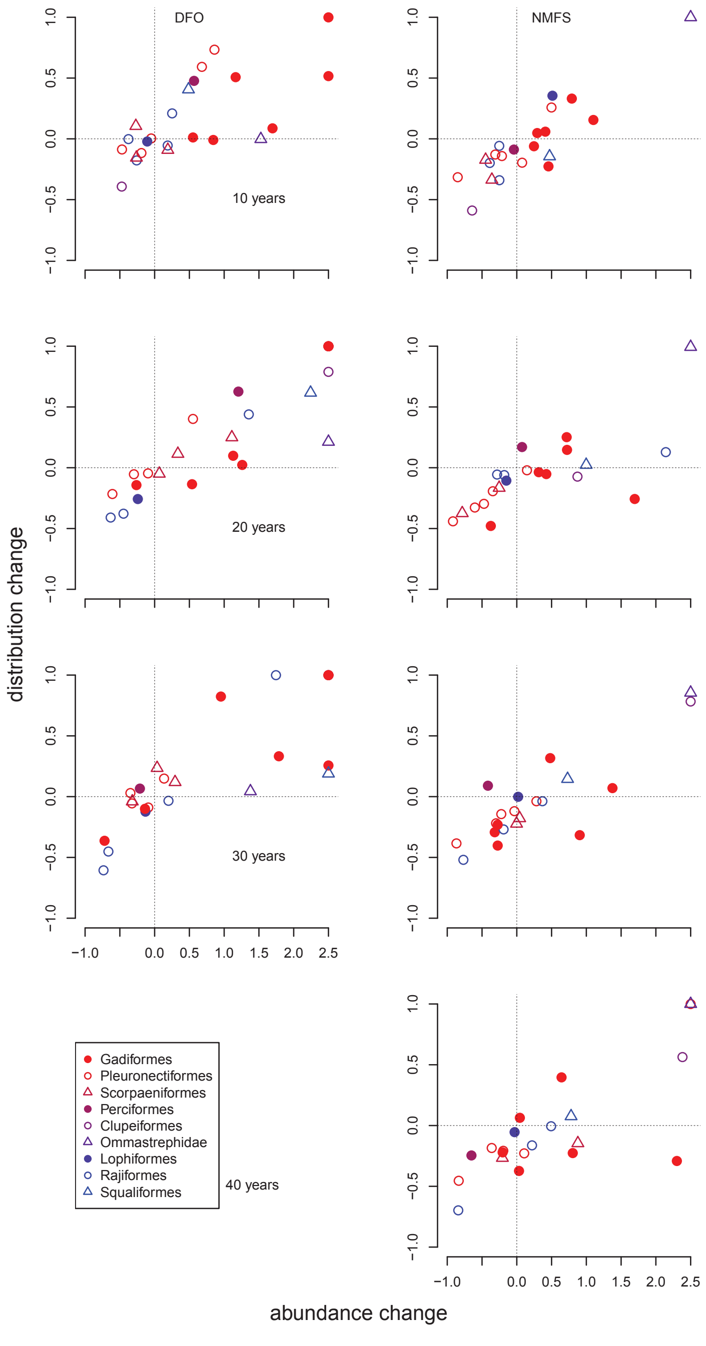

Figure 4.4: Distribution versus abundance changes for DFO and NMFS populations. The distribution and abundance changes are computed for periods of 10, 20, 30 and 40 years after the beginning of surveys and are colour- and symbol-coded for different taxonomic families. Positive values on the y-axis indicate range expansions and negative values indicate range contractions. Positive values on the x-axis indicate increases in abundance and negative values indicate decreases in abundance. Distribution changes greater than 1.0 are plotted at 1.0 on the y axis and abundance changes greater than 2.5 are plotted at 2.5 on the x axis.

patterns in the slope values and suggests that the habitat suitability of strata is not shared across all species.

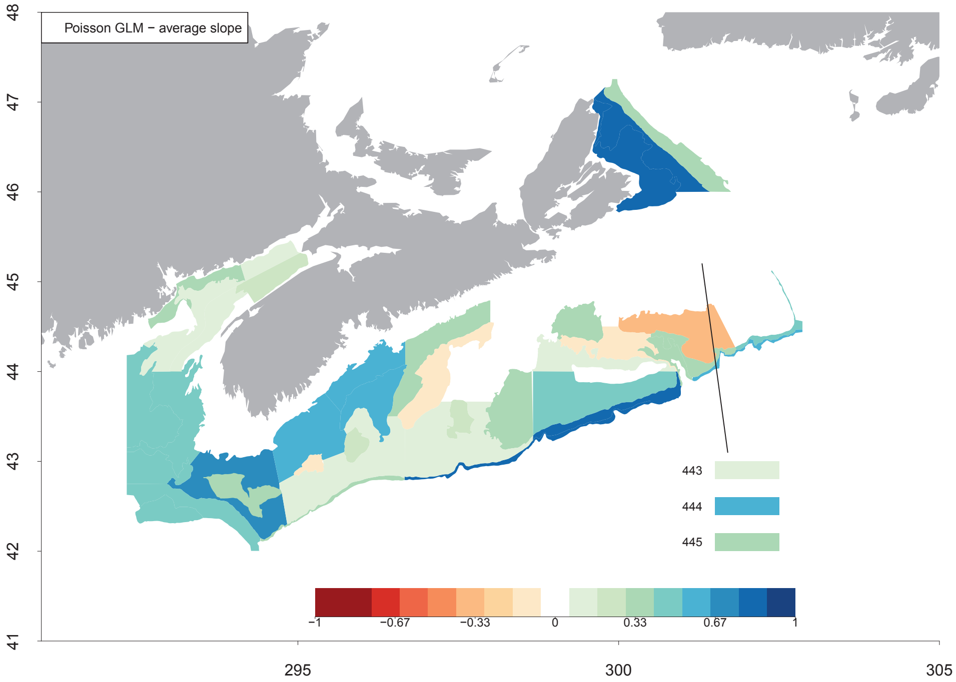

Figure 4.5: Average slope values ($\beta_{DFO,n,s}$ values from equation 4.5) across all populations from the DFO survey.

There is no striking spatial pattern in the normalised abundance (Figures 4.7 and 4.8), suggesting that different strata are of varying importance to different species. One signal that is apparent in the NMFS survey region is the higher normalised abundance along the coast of the Gulf of Maine, along the northern edge of Georges Bank and along the shelf edge at the southern end of the region.

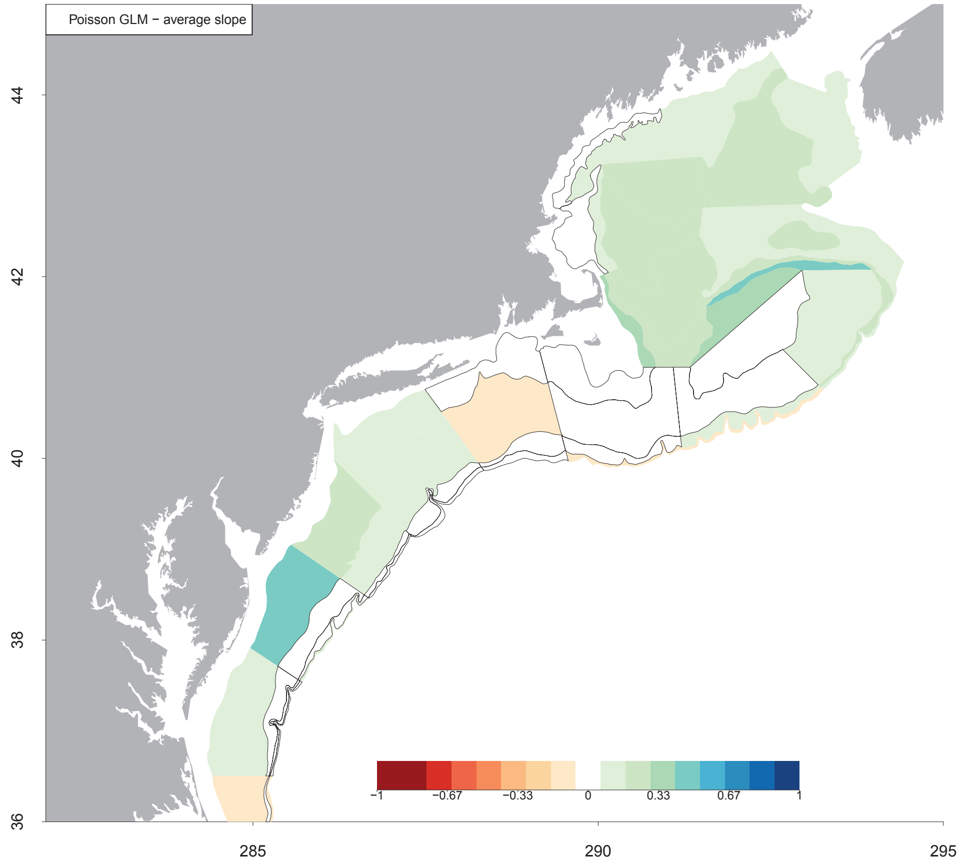

Figure 4.6: Average slope values ($\beta_{NMFS,n,s}$ values from equation 4.5) across all populations from the NMFS survey.

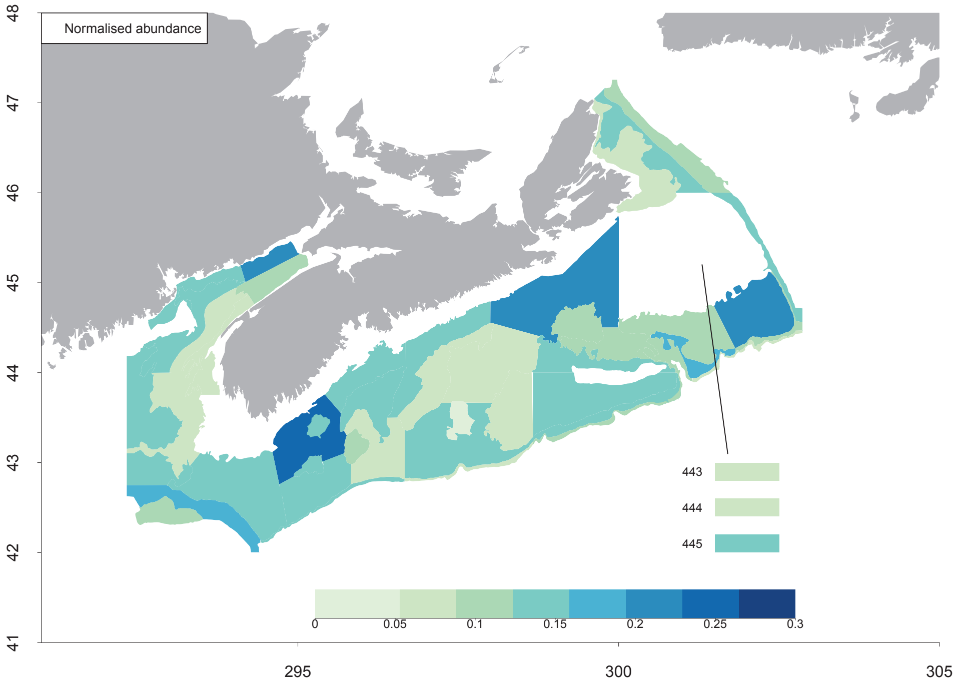

Figure 4.7: Normalised abundance across all populations from the DFO survey.

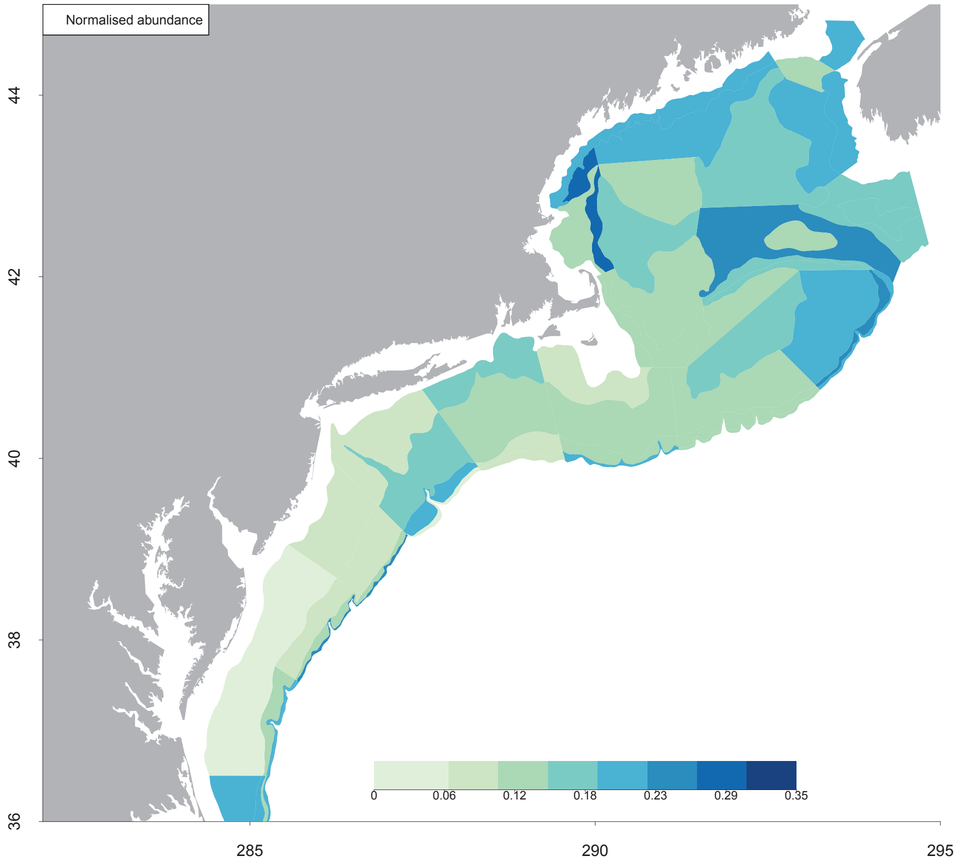

Figure 4.8: Normalised abundance across all populations from the NMFS survey.

Some species-specific results are of interest because they exemplify patterns that are masked by the integration of estimates across species in a community-wide manner. I concentrated on three species which displayed interesting temporal patterns in abundance and distribution.

The first population presented is Atlantic cod (*Gadus morhua*, Figures 4.4 and 4.4), because of its important historical and commercial importance and also because of its well-documented reductions in abundance and the subsequent closures of many of its fisheries. The abundance of Atlantic cod declined significantly in both the DFO and NMFS survey regions. There is evidence for a recent recovery of the population in the Eastern Scotian Shelf but also a clear disappearance of the population from the southern regions of the NMFS survey.

I also report the results for herring (*Clupea harengus*, Figures 4.4 and 4.4) because it had such strong and significant positive correlations between abundance and distribution and also increased greatly in abundance in the trawl surveys. There were increases in abundance during the mid-1990s and early-2000s on the Scotian Shelf and on the northeast continental shelf of the United States. This species was only marginally present in the early parts of the surveys but has now become an abundant and ubiquitous part of the catch.

Finally, I present the results for thorny skate (*Amblyraja radiata*, Figures 4.4 and 4.4) which sustained clear declines in both abundance and distribution. In the 1970s, a large proportion of tows had catch on the Scotian Shelf, the Bay of Fundy and the Gulf of Maine. The populations then show clear declines in abundance and, starting in the late 1980s, complete disappearance from a number of survey strata.

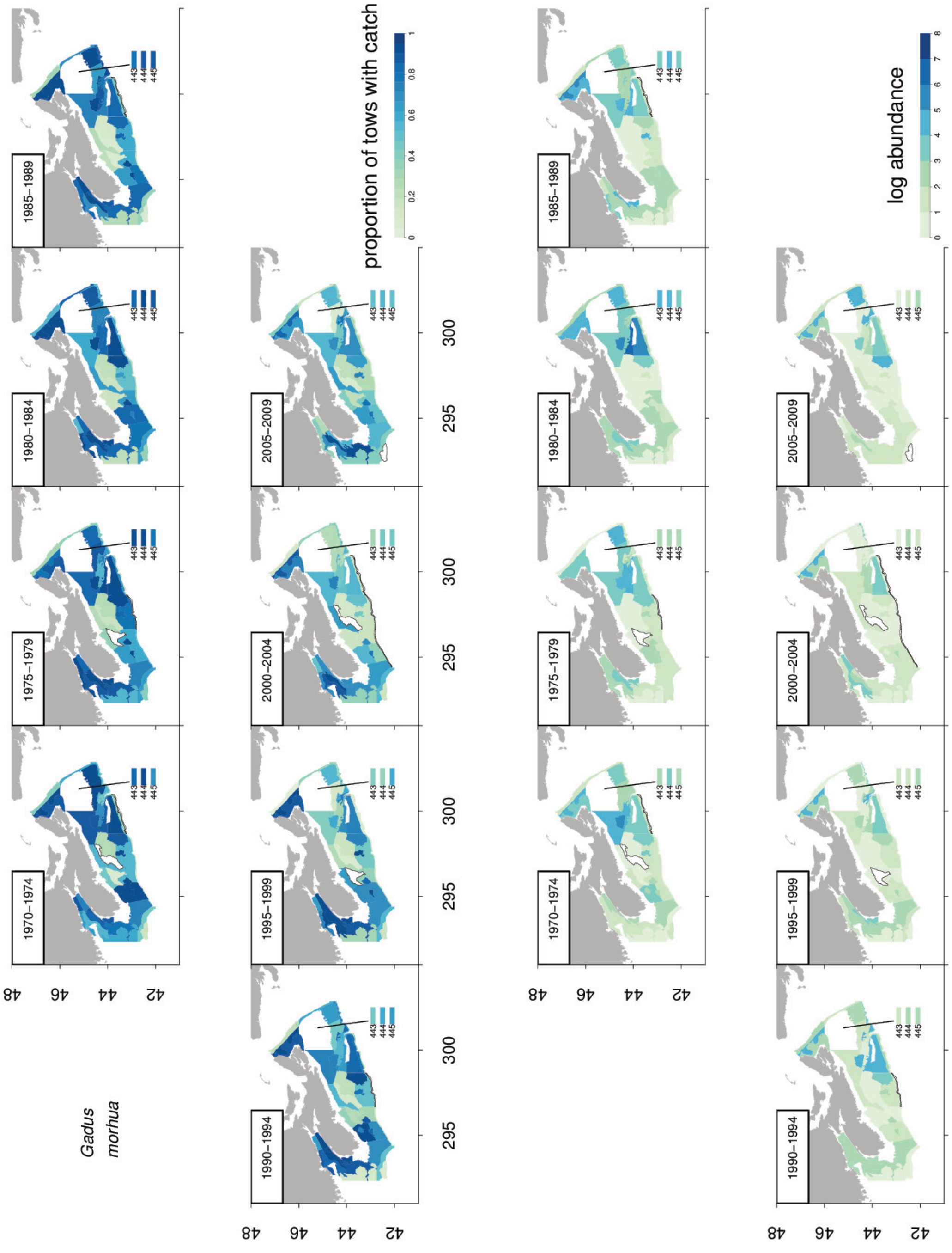

Figure 4.9: Proportion of tows with catch and stratified random estimates of abundance for DFO Atlantic cod (*Gadus morhua*).

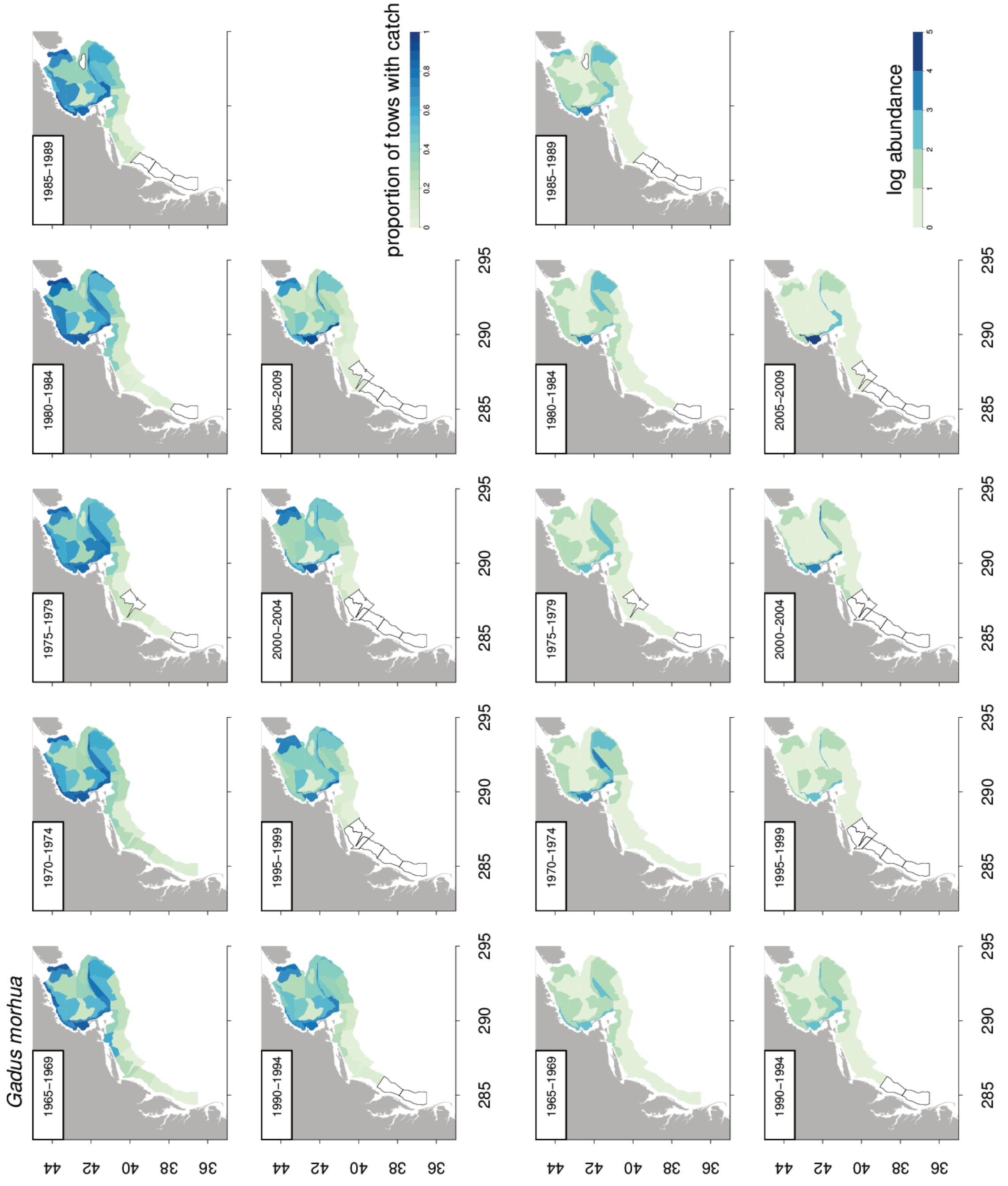

Figure 4.10: Proportion of tows with catch and stratified random estimates of abundance for NMFS Atlantic cod (*Gadus morhua*).

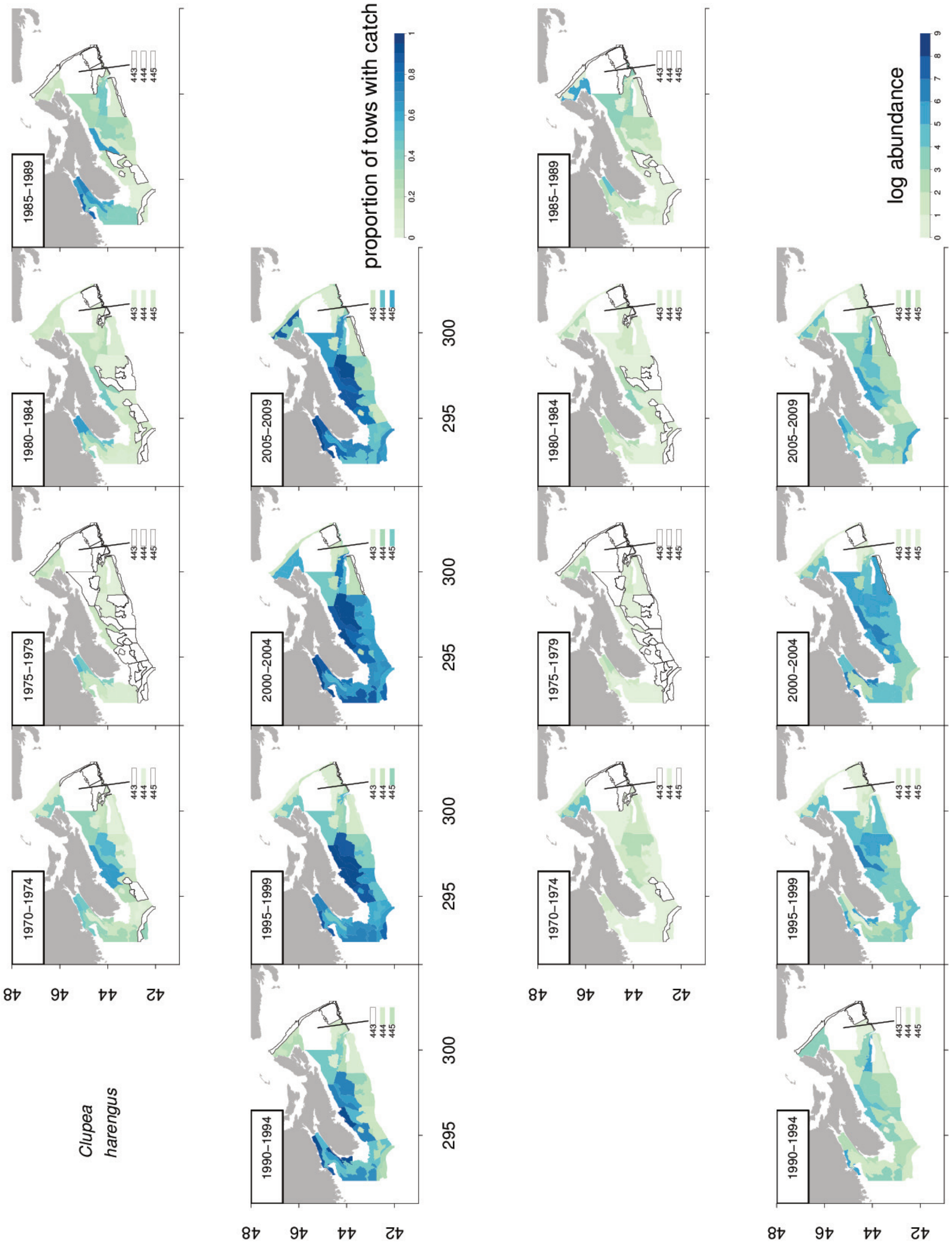

Figure 4.11: Proportion of tows with catch and stratified random estimates of abundance for DFO herring (*Clupea harengus*).

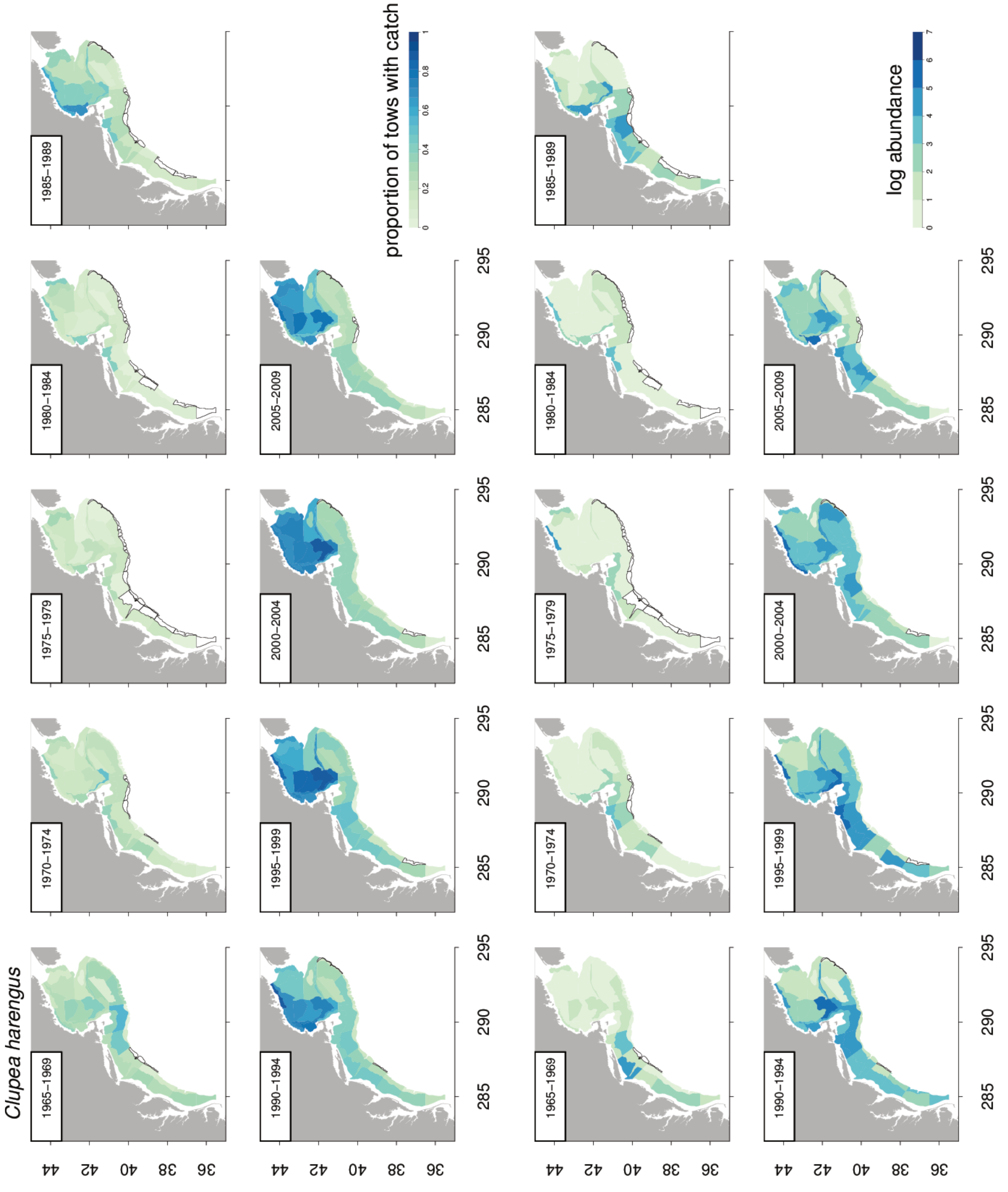

Figure 4.12: Proportion of tows with catch and stratified random estimates of abundance for NMFS herring (*Clupea harengus*).

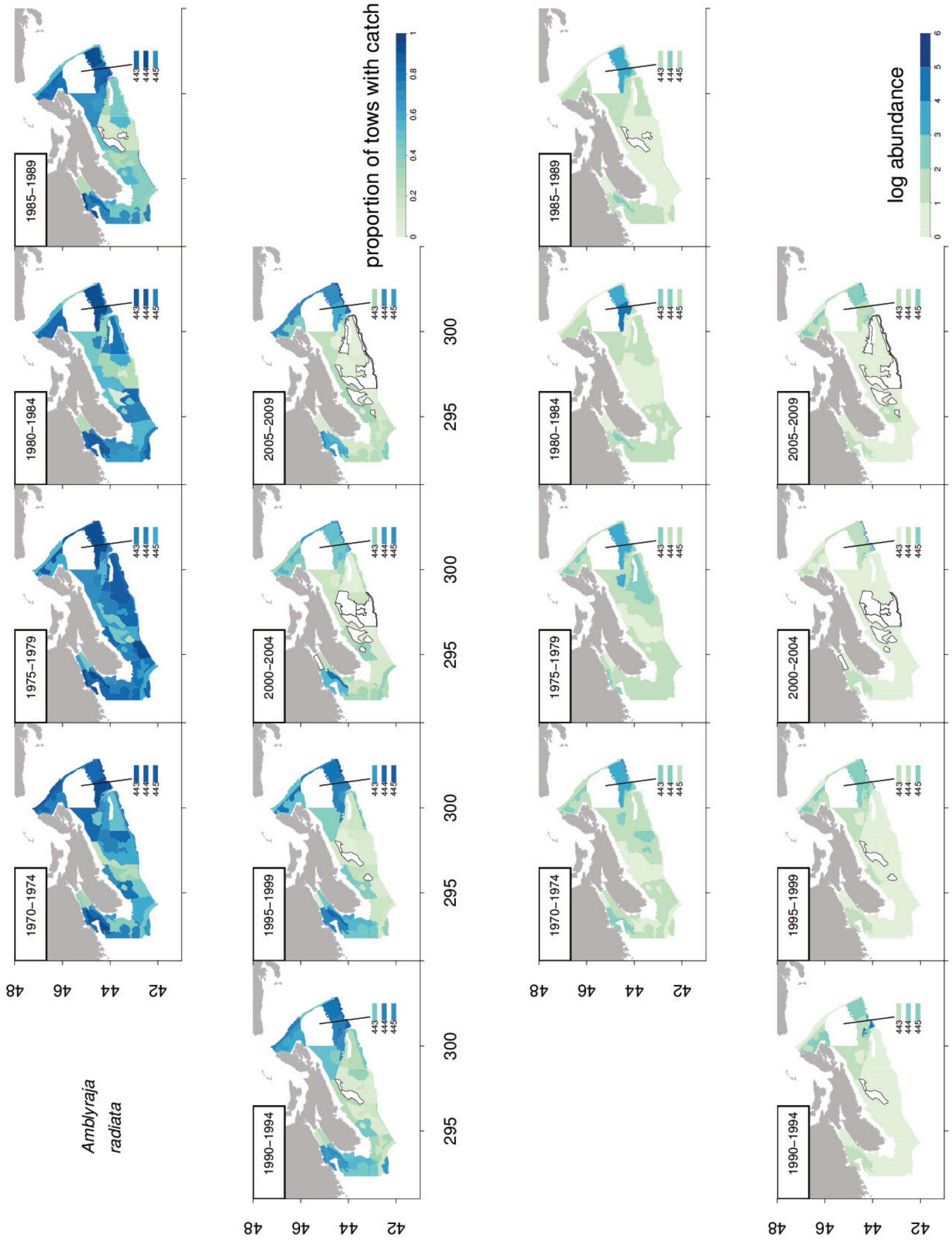

Figure 4.13: Proportion of tows with catch and stratified random estimates of abundance for DFO thorny skate (*Amblyraja radiata*).

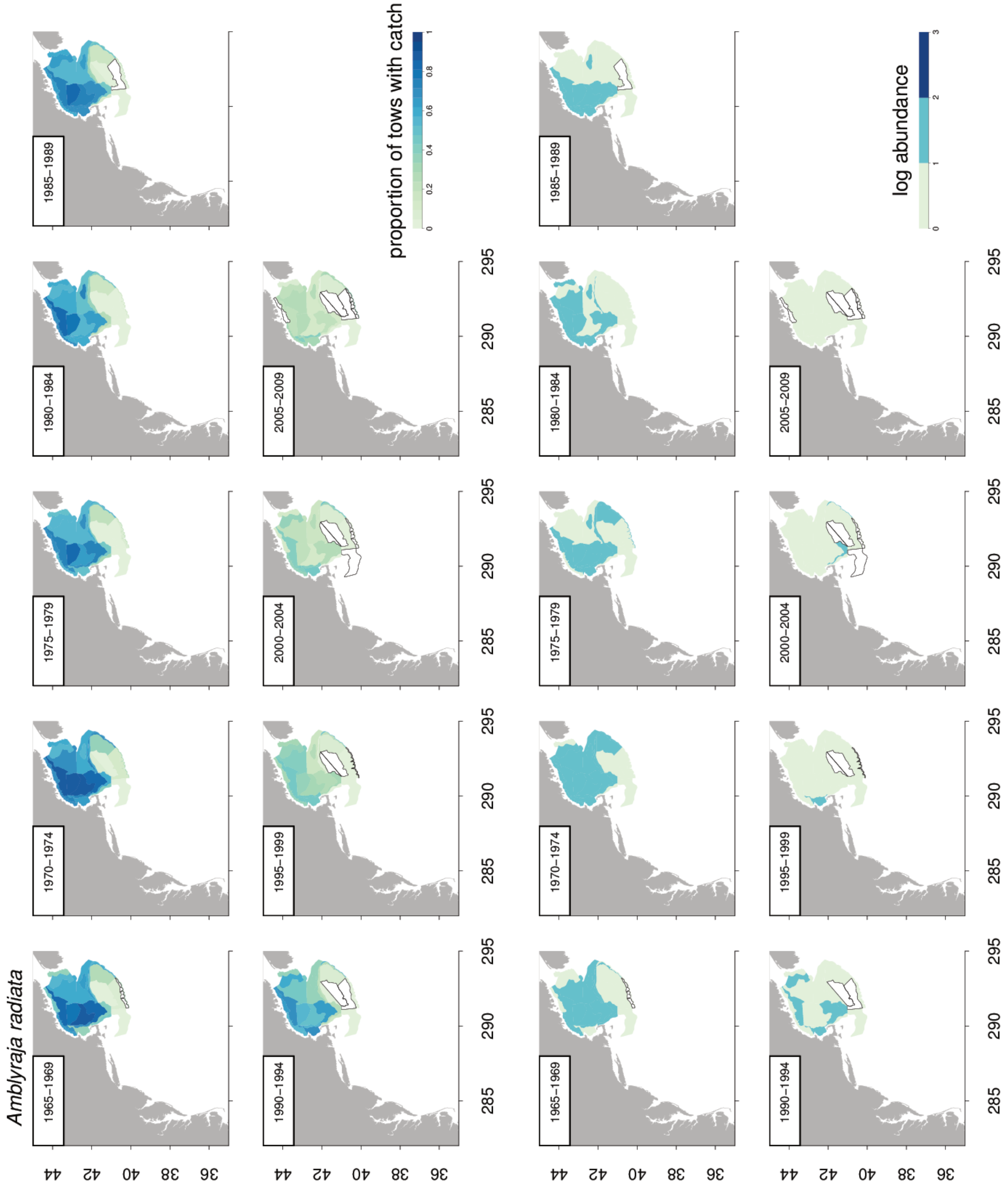

Figure 4.14: Proportion of tows with catch and stratified random estimates of abundance for NMFS thorny skate (*Amblyraja radiata*).

4.5 Discussion

Statistically significant positive correlations between abundance and area occupied were estimated for many of the DFO and NMFS populations under scrutiny, suggesting that, as is the case for terrestrial systems, the abundance-distribution relationship is a recognisable pattern of marine populations.

Swain and Morin (1996) examined distribution and abundance changes of American plaice in the Southern Gulf of St Lawrence and concluded that there was little evidence for distribution expansion associated with increases in abundance. In contrast, Brodie et al. (1998) found an important range contraction associated with declines in abundance of yellowtail flounder on the Grand Banks of Newfoundland.

The Gini index and $D^{75\%}$ are derived from the same Lorenz curve are highly negatively correlated. This is expected since the two indices describe opposite processes. A situation in which the minimum area required to find 75% of the population is decreasing would see an increase in the value of the Gini index, because the same abundance would be found over a smaller area.

The important and recognisable increases in herring abundance and distribution have been hypothesised to be a result of predatory release (Bundy, 2005; Frank et al., 2005), but these findings have been contested (McQuinn, 2009). The strong positive correlations between abundance and area occupied are likely associated with the pelagic nature of herring and the fact that, when present, they occur at densities that "saturate" the available habitat. Increases in abundance therefore require similar increases in area occupied.

The time-series of abundance and distribution used in the analyses were not completely independent since they are derived from the same survey information. Some other analyses have related local densities to trends in abundance from population models (e.g. from Virtual Population Analysis in Myers and Stokes, 1989), while other have, as is the case here, used the stratified random estimates obtained from the same survey as that used to estimate local densities (e.g. Swain and Morin, 1996). In the case of model-derived abundance estimates, the stratified random estimate of abundance is used as an important fisheries-independent index to fit the stock assessment model. While the population estimates use other sources of information to calculate time-series (fisheries catch-at-age, natural mortality, etc.) they are still not completely independent of the survey index. The analyses presented here include species that do not undergo formal stock assessment (longhorn sculpin, moustache sculpin, ocean pout, sea raven and skates species), so I decided to use the stratified random estimates as the index of abundance.

In a management context, species are often are treated as single units over the entire survey area, whereas they can in fact occur as separate populations within these regions. Other studies have used stock-level estimates of abundance to evaluate the survey data (Fisher and Frank, 2004). To reduce the number of units studied, I decided to look at populations over the whole survey area instead of separating them into finer units.

The subset of species used here only covers a fraction of the biological diversity encountered in the marine environment covered by the surveys. Other species are present in the ocean and do not reliably appear in the sampling gear used in fisheries surveys. The focus, and bias, of the analyses conducted here are towards large, bottom-associated fauna. Nonetheless, the analyses conducted here are representative of an important part of the fish community and provide a defensible methodology to evaluate the spatial population dynamics of groundfish and their analyse ecological mechanisms.

The ability of distribution indices to properly establish abundance-distribution relationships has recently been investigated and established the potential bias of certain indicators, especially at low population abundance (Rindorf and Lewy, 2012). This study undermines many previous studies that have suggested that abundance-distribution relationships are ubiquitous features of ecological systems (e.g. Blanchard et al., 2005; Zuckerberg et al., 2009). It also casts a shadow over the findings presented here since the positive correlations estimated could arise spuriously.

Averaging across all species provide a synoptic view of the different models used but also masks some more interesting species-specific patterns in how distribution and abundance are related and how local density relates to overall abundance. The additional maps presented in the electronic appendix of the thesis provide additional information about each species, but their interpretation is beyond the scope of the present chapter.

Relating the slope values to the stratum-level density was done by Myers and Stokes (1989) to test whether density-dependent or site-neutral habitat selection was governing the dynamics of groundfish populations. They concluded that none of the groundfish populations they examined showed evidence for habitat saturation, where the local density in marginal habitats should increase more with overall abundance than the local density in optimal habitats.

An increased reliance on marine spatial planning means that spatially-explicit analyses are necessary to inform decision-making. Human activities in the ocean are associated with the location of fisheries resources, fossil fuels, shipping lanes that link major ports, and with other geographical realities that determine the location of infrastructure such as undersea communication and power transmission cables. To minimise the environmental impact of such activities require the formulation, implementation and enforcement of management measures that ensure that the ecological integrity of marine ecosystems is maintained. Focusing on a subset of commercially important fish species is unlikely to capture the true scope of impacts and can mislead decision-makers into thinking that appropriate measures are in place.

The ocean environment is dynamic and the populations that inhabit it are mobile and often migratory. Some important assumptions must be made to properly evaluate the results obtained from trawl survey data. We assume that the surveyed region is a closed system and that immigration and emigration are not important and do not contribute to the estimated temporal trends. Presentation of results in a spatially-explicit matter such as the maps presented here assumes that each stratum is a consistent sampling unit over time.

The preservation of ecosystem-wide structure and functions will require more than concentrating on preserving a certain percentage of the marine environment. Measures to limit fisheries catch and to exclude some areas from commercial activities will still require proper monitoring programs.

Chapter 5

DEMOGRAPHIC CONSEQUENCES OF CHANGES IN LIFE-HISTORY PARAMETERS OF COD AND HADDOCK IN THE NORTHWEST ATLANTIC

5.1 Abstract

The life-history characteristics of a species determine the intrinsic ability of its populations to numerically increase. Here, the population demographic consequences associated with observed changes in growth and maturation are estimated for populations of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). Decadal changes in growth and maturation are modelled using detailed age, length and maturity observations of cohorts of individuals born in decades ranging from the 1950s to the 2000s and collected from two scientific trawl surveys conducted in the northeast continental shelf of the United States and the Scotia-Fundy region of Canada. The spatial relatedness in growth conditions is estimated to have a clear latitudinal component for Atlantic cod and a more variable one for haddock. Decadal estimates of changes in growth of mature and immature individuals indicate non-monotonic trends where growth rates of mature and immature individuals vary over time. Growth was fastest during the middle decades and slowest during the early and late decades. Temporal trends in maturation are more monotonic and unidirectional, indicating earlier maturation over the timespan over the available surveys. When combined into an age-based population dynamics model that allows the calculation of the maximum rate of increase of the populations under study, the estimated changes in growth and maturation yield decreased population growth rates for the past four decades. The estimated reductions in population growth rates can have an important influence in determining the recovery rate of depleted populations and the level of harvesting that they can sustainably withstand. Solely using estimates of population

growth rate obtained during the middle decades of the surveys will provide an overly optimistic view of the recovery potential of depleted populations.

5.2 Introduction

Studying the dynamics of populations of organisms, or specific groups occurring in specified habitats, can be very useful in understanding and predicting factors affecting change in these groups. Over their lifespan, the individuals that make up populations go through a life cycle that includes birth, growth, maturation, reproduction and eventual death. The components of this cycle are called life-history characteristics (Roff, 1984, 1992) and are important factors that help determine the dynamics of a population (Hutchings, 2011). Much variability exists in these traits among individuals of a population, among populations of the same species and among different species. Comparisons of life-history variations across species yield insight into evolutionary histories, the vulnerabilities to negative impacts and population dynamics of species. On the other hand, studying how life-history traits vary within a population provides the ability to identify spatial and temporal changes and to investigate their potential drivers.

A key population demographic parameter is the potential intrinsic growth rate, which is itself determined by the growth, fecundity and survival of individuals over their lifespan. A commonly used metric is the finite population rate of increase often symbolised as r (Cole, 1954; Roff, 1992). The value of r ultimately determines how a population can recover from declines and how much harvesting it can sustain (Myers et al., 1999). Despite the biological realities of a dynamic environment and temporal changes in species interactions, the estimation of r for a population often assumes a time-independent relationship where growth, maturation and survival levels are constant over the period covered by observations.

The changes expected to be observed when an animal population is harvested for the first time include a reduction in its abundance and biomass and a modification of the age structure of the population (Hilborn and Walters, 1992). Under intense exploitation, the magnitude of reduction in abundance and biomass will reflect the amount of removals through harvest. Changes in population age structure arises from the selective nature of harvesting methods which often preferentially remove larger and older individuals (Hutchings, 2009), resulting in an age distribution skewed towards younger ages. If harvesting stops, the population is expected to increase in abundance and biomass to pre-harvest levels and the original stable age structure of the population is expected to be restored. However, in many instances where excessive exploitation was followed by reductions in harvesting populations, recovery has been slower than expected (e.g. for Southern and Northern Gulf of St. Lawrence Atlantic cod (Swain and Chouinard, 2008; Lambert, 2011), Grand Banks Atlantic cod (Hutchings and Rangeley, 2011) and Eastern Scotian Shelf Atlantic cod (Bundy and Fanning, 2005)). The reasons to explain the lack of recovery are numerous and include changes in environmental conditions and primary productivity, changes in multi-species dynamics such as predator-prey relationships, elevated natural mortality and evolutionary changes in growth and maturation.

Because of its selective nature, fishing may have evolutionary consequences on targeted populations (Heino, 1998; Ernande et al., 2004). The fitness of an individual can be quantified by estimating the number of offspring that it can produce over its lifetime (Stearns, 1992). Individuals that grow faster will become susceptible to harvest earlier than those that grow slower. Similarly, individuals that mature early will have a better chance of producing offspring before they are captured by fisheries. Therefore, an expectation from evolutionary theory is that populations that are subject to harvesting will have fitness advantages to growing slower and maturing earlier. The demographic consequences of these changes have not been clearly examined because of the complex trade-offs that exist between allocating energy towards somatic and reproductive tissues. Earlier maturation should increase a population's ability to renew itself (Cole, 1954), but the costs of early reproduction on future growth of an individual, on its fecundity and on the viability and survival of its offspring can negate the positive demographic effects of early maturation (Hutchings, 2005; Kuparinen et al., 2012).

Determining the temporal evolution of a harvested population requires some means to estimate its abundance and biomass.This is always a difficult task because of the wide distribution of a population in its environment and the reliance on sampling methods, and it is a particularly challenging endeavour for marine populations. The sampling methods used for marine populations such as fish are often indirect observations obtained through fishing. The sampling protocols used for monitoring marine populations have sound statistical basis but suffer from the vast expanse of the ocean, the movement of animals through their environment and the fact that sampling gear preferentially targets certain ages. Nonetheless, there exist a variety of ways to estimate temporal trends in biomass and abundance and the preferred methods rely on fisheries-independent scientific surveys.

The Northwest Atlantic has a long history of commercial exploitation and is host to a number of fish populations whose abundance and biomass have been reduced to historically low levels because of excessive harvesting. Despite significant reductions in fishing mortality, some of these populations have failed to recover to productive levels. This may suggest that important demographic changes occured in these populations and that their ability to renew themselves has been modified.

In this chapter I use length, age and maturity information collected on scientific trawl surveys in the Northwest Atlantic to examine evidence for decadal changes in growth and maturation of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) populations. The estimated changes in growth are used in a population dynamics model to determine their demographic consequences. Changes in maturation are used in the interpretations of the demographic consequences. Implications for the sustainable management of these and similar populations are discussed.

5.3 Methods

5.3.1 Data Sources

Fisheries And Oceans Canada Maritimes Region

Fisheries and Oceans Canada (DFO) data from the Maritimes Region consists of 1) pre-1970 opportunistic data, and 2) post-1970 data collected in scientific trawl surveys. Pre-1970 data was collected in an opportunistic fashion through a variety of research cruises that did not share the underlying sampling design of most of the surveys conducted after 1970. The pre-1970 surveys were conducted at various times of the year between 1958 and 1969 throughout the Southern Gulf of Saint Lawrence, Scotian Shelf, Bay of Fundy and Georges Bank. Since 1970, yearly summer surveys have followed stratified random protocols and have utilised standardised fishing gear.

Spring surveys in NAFO divisions 4VWX have been conducted between 1979 and 1984 and then in NAFO divisons 4VW since 1986 using similar sampling protocol. The basic sampling unit of surveys is a 30-minute tow at a speed of 3.5 knots, resulting in a distance towed of 1.75 nautical miles (Doubleday, 1981). The catch of each tow was sorted by species, weighed and counted, and additional length, maturity and ageing sub-sampling is performed.

To make pre-1970 data comparable to those collected at later periods under standardised protocols, I assigned each tow location from the pre-1970 data to its corresponding stratum under the stratification scheme used in the summer survey implemented in 1970. DFO changed the stratification scheme of its spring survey in 1986 to improve the precision of abundance estimates for Atlantic cod (Smith and Gavaris, 1993). Since I am interested in analysing the available data as a whole, tows conducted in the spring survey since 1986 were also assigned to their equivalent summer survey strata. To ensure that the different strata used have sufficient sampling and to exclude exploratory deep-water strata I restricted my analyses of Canadian data to strata 440 to 495 on the Scotian Shelf and Bay of Fundy (Figures 5.1 and B.1).

United States National Marine Fisheries Services Northeast Fisheries Science Center

Surveys conducted by the National Marine Fisheries Services (NMFS) are available from 1963 to the present and cover an area from Cape Hatteras to the Scotia-Fundy region (Figure 5.1). These surveys followed a similar stratified random protocol as those conducted by DFO and also gather data on length, weight and maturity status (Doubleday and Rivard, 1981). I used data from spring and fall surveys conducted on NMFS offshore strata 1010 to 1990 (Figure B.2) since these data reflect the most consistent sampling over the duration of survey activities.

To account for the relatedness of individuals born within a certain time window all subsequent analyses were conducted using the "cohort year" of each individual fish. The age of each fish (as determined by ageing of otoliths) is used in conjunction with the year of capture to back-calculate its year of birth. Individuals born during a given decade are grouped together for analysing the decadal changes in growth and maturation ($D_k = (d_i)$ for $i \in (1950s, 1960s, 1970s, 1980s, 1990s, 2000s)$ for DFO and for $i \in (1960s, 1970s, 1980s, 1990s, 2000s)$ for NMFS). All following analyses are conducted for both Atlantic cod and haddock and using both the DFO and NMFS surveys. Parameter estimates for each decade were obtained by defining decades as factors in the different analyses used below. Under this framework, the first decade available was the reference case and deviations for this reference are estimated for the other decades. Maturity status was treated as a binomial variable describing whether and individual is mature or not.

5.3.2 Spatial Patterns In Growth

Earlier studies of Scotia-Fundy fish populations surveyed by DFO show evidence of a clear spatial gradient in growth characteristics associated with water temperature (Shackell et al., 1997). Populations along the Northwest Atlantic coast experienced different thermal regimes and environmental conditions that influence their growth. Colder areas and areas with lower productivity tend to be associated with slower growth. The geographic variation in growth must be accounted for to properly estimate temporal changes in growth. A similar influence of temperature and environmental conditions on growth is also present in US waters where the survey area extends to the edge of the range of the species considered.

I used length instead of weight as the response variable for modelling growth. This decision was taken because the variability in length measurements is smaller and simpler than that of weight measurements. There have been a number of changes in the instrumentation used to measure weight and the changes in precision and accuracy of available measurements are complex since they are influenced by the scales used, the vessels used and the sea conditions encountered during the sampling. Additionally, weight measurements are highly influenced by whether a fish has recently ingested prey and it is common to find a whole fish inside a larger fish during survey activities. Length measurements are simpler to measure and have also been more consistently observed over the surveys used in this analysis.

To identify spatial differences in growth, I partitioned the surveyed strata from each survey dataset into four separate stratum-based groupings that share similar growth conditions. I used a non-linear mixed-effects implementation of a Brody-Bertalanffy growth model parameterised to estimate an x-axis intercept. Survey strata were used as random effects on the log growth rate parameter. For both

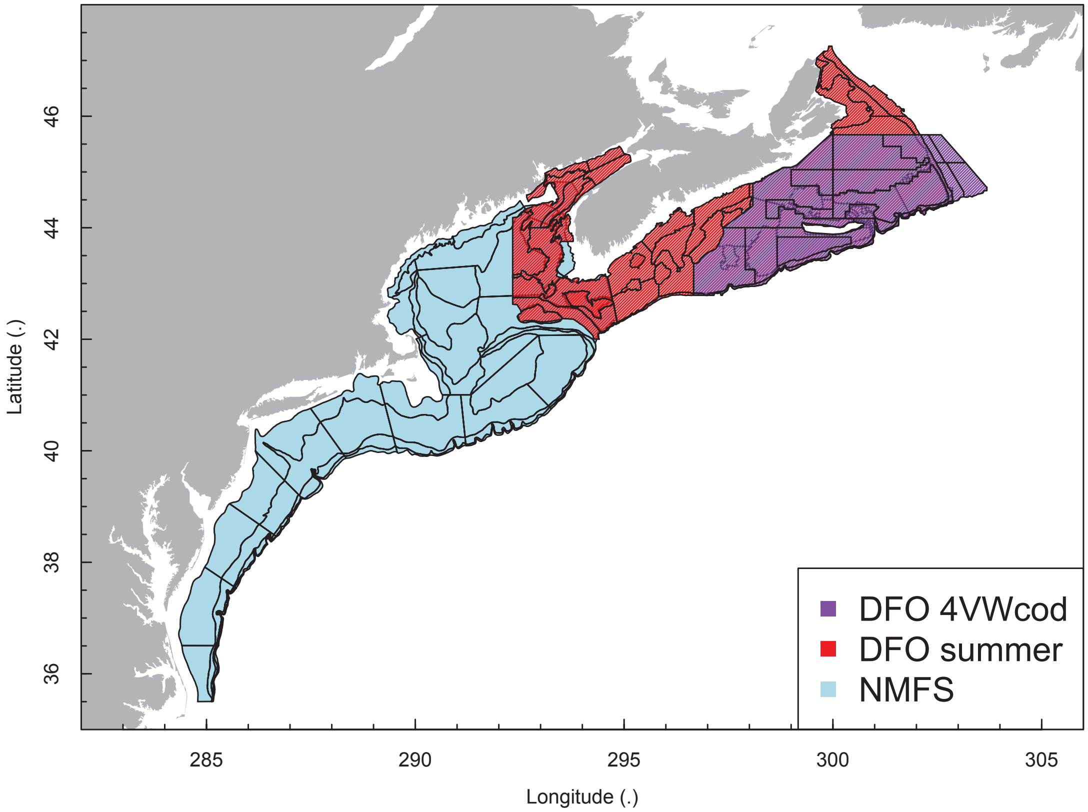

Figure 5.1: Study region. Geographic coverage of scientific trawl surveys conducted by the National Marine Fisheries Service (NMFS) of the United States (southern blue polygons indicating the location of offshore strata units) and Fisheries and Oceans Canada (DFO) (northern red and purple polygons indicating the survey area and strata locations).

surveys and for both species of interest, the basic unit of observation is the length of individual fish i of age a caught in stratum s ($L_{a,s,i}$). This data is used to estimated the following model:

$$L_{a,s,i} = L_\infty + ((L_0 - L_\infty)\, exp\, (-exp\, (R + \rho_s)\, a)) \tag{5.1}$$

where,

$L_{a,s,i}$ is the length of fish i and age a caught in stratum s

L_∞ is the asymptotic length

L_0 is the length at age 0

R is the log of the growth rate

ρ_s is the deviation in growth rate in each stratum s

For each survey and species, the estimated stratum-level random effects (ρ_s) were partitioned to their respective quartiles to define four growth rate regions ($\rho^1, \rho^2, \rho^3, \rho^4$) used in subsequent analyses. This step allowed me to estimate the spatial relatedness in growth that exists over the survey area. Regions with similar growth regimes are subsequently used when estimating temporal changes in growth and maturation. Because the strata were grouped into four categories, the number of model parameters required to account for spatial relatedness can be reduced in subsequent analyses.

5.3.3 Decadal Model Of Changes In Growth

The surveys used here are conducted annually. The observed temporal changes in growth are best looked at for longer time periods since the number of fishing tows conducted each year in each stratum can be as low as one. Additionally using yearly estimates requires a large number of parameters since the surveys used here span numerous decades. For this reason I used ten-year periods to estimate temporal changes. This strikes a trade-off between the number of parameters required and the temporal resolution of the estimates. Separating the data into decades imposes arbitrary and subjective temporal groupings but provides a method, albeit imperfect, to estimate temporal trends.

Growth in length was modelled as a linear function of age with a reduction in growth rate after maturity. I included an additional decadal component to the model to evaluate temporal changes in growth. To implement the model, I used a linear mixed effects model with the four spatial units used as random effects on the slope and intercept of the linear growth function. The following model is estimated using individual observations from the available trawl survey data:

$$\begin{aligned} L\left(d, r, a\right) = {} & (\alpha + \zeta_\rho) + \alpha^d + \alpha^m + \alpha^{dm} \\ & + a\left((\beta - b_\rho) + \beta^d + \beta^m + \beta^{dm}\right) \end{aligned} \tag{5.2}$$

where,

$L\left(d, r, a\right)$ is the length at age a in region r during decade d

$(\alpha + \zeta_\rho)$ is the intercept from region r (α is the overall intercept)

α^d is the decadal effect on the intercept

α^m is the maturity effect on the intercept

α^{dm} is the decadal effect on the intercept for mature individuals

$(\beta - b_\rho)$ is the slope from region r (β is the overall slope)

β^d is the decadal effect on the slope

β^m is the maturity effect on the slope

β^{dm} is the decadal effect on the slope for mature individuals

The model accounted for some of the strong spatial gradients observed in growth regimes by the inclusion of random effects on the slope and intercept parameters (ζ_ρ and b_ρ). The fitted model was used to predict length-at-age of both mature and immature individuals for each decade. The decade-specific estimates of change in growth rate for mature individuals (β^d, β^{dm}) were used to predict the decadal lengths-at-age associated with different ages-at-maturity (see equation (5.5) in section 5.3.5 below).

5.3.4 Decadal Model Of Changes In Maturation

The maturation process is the increase in the proportion of individuals that are sexually mature at increasing ages. I modeled the maturation process as a logistic regression of the proportion of individuals from region r in decade d that are mature at each age a ($p^{mat}_{d,r,a}$). I included additional parameters that evaluate a decadal effect on maturation. The growth regime regions regions identified are used again as random effects for the slope and intercept parameters of the logistic regression model. I implemented this model using a generalized linear mixed effects model with a logit link ($\text{logit}\left(p\right) = log\left(\frac{p}{1-p}\right)$) and binomial error structure. The linear predictor of the proportion of individuals that are mature is then:

$$\text{logit}\left(p^{mat}_{d,r,a}\right) = \left(\alpha + \zeta_\rho\right) + \alpha^d + a\left(\left(\beta + b_\rho\right) + \beta^d\right) \tag{5.3}$$

where,

$p^{mat}_{d,r,a}$ is the proportion of individuals from region r in decade d that are mature at age a

$\left(\alpha + \zeta_\rho\right)$ is the intercept from region r (α is the overall intercept)

α^d is the decadal effect on the intercept

$\left(\beta + b_\rho\right)$ is the slope from region r (β is the overall slope)

β^d is the decadal effect on the slope

The estimated model parameters provided decadal estimates of changes in maturation. The random effects on the intercept and slope parameters (ζ_ρ and b_ρ) preserve the groupings of strata into areas of similar growth regime and ensures that spatial relatedness is accounted for when estimating temporal trends in maturation. The fitted models were used to predict the maturity-at-age for each decade and are used in the interpretation of the demographic parameters obtained from the population dynamics model (below).

5.3.5 Population Dynamics Model

To determine the demographic consequences of the estimated decadal changes in growth and maturation I used an age-based population dynamics model to calculate decadal intrinsic rates of population increase r_{d,a^m}. For each survey and species, population projection matrices (a.k.a. Leslie matrices) for each decade d and age-at-maturity a^m were generated:

$$\omega_{d,a^m} = \begin{matrix} f^1_{d,a^m} & f^2_{d,a^m} & f^3_{d,a^m} & ... & f^\tau_{d,a^m} \\ s^{1,2}_{d,a^m} & 0 & 0 & ... & 0 \\ 0 & s^{2,3}_{d,a^m} & 0 & ... & 0 \\ 0 & 0 & \ddots & ... & 0 \\ 0 & 0 & ... & s^{\tau-1,\tau}_{d,a^m} & 0 \end{matrix} \tag{5.4}$$

where,

ω_{d,a^m} is the Leslie matrix for decade d and age-at-maturity a^m

τ is the terminal age used in the population dynamics model

f^i_{d,a^m} is the number of recruits produced by individuals of age i (often referred to as "fecundity")

$s^{i,i+1}_{d,a^m}$ is the survivorship between age i and age $i+1$

Each projection matrix ω_{d,a^m} is associated with a given age-at-maturity a^m, so I can define a vector of matrices corresponding to the decadal estimates of projection matrices ($\Omega_d = (\omega_{d,1}, ..., \omega_{d,\tau})$). The predicted temporal changes in the decadal rates of population increase r_{d,a^m} are examined along with the estimated decadal changes in maturation to determine potential demographic consequences.

There are two parts to this projection matrix, 1) the age-specific fecundity (f_{d,a^m}) and 2) the survivorship over age (s_{d,a^m}). The estimated decadal changes in growth influence the age-specific fecundity since fecundity is related to body size. The survivorship over age will likely be influenced by maturation since there is a survival cost associated with maturating.

The different population projection matrices generated (ω_{d,a^m}) are useful because their dominant Eigen values are the population finite rate of increase λ^1_{d,a^m}, whose logarithm is the intrinsic rate of population increase r_{d,a^m}. So an estimate of r_{d,a^m} can be calculated for each decade for both species and both surveys and provides a demographic parameter that translates the changes in individual growth into changes in population growth.

I used the estimates from the decadal growth model of equation (5.2) to predict the fecundity associated with each age-at-maturity a^m. The decadal changes in growth rate used are the estimates of β^d and β^{dm} from equation (5.2). For each decade I calculate length-at-age for different ages-at-maturity a^m as:

$$l_{d,a^m} = \begin{cases} \alpha + \alpha^d + a\left(\beta + \beta^d\right) & \text{if } m = 0 \\ \\ \alpha + \alpha^d + a\left(\beta + \beta^d\right) + \\ (a - a^m)\left(\beta + \beta^d + \beta^m + \beta^{dm}\right) & \text{if } m = 1 \end{cases} \tag{5.5}$$

The length-at-age predicted by equation (5.5) is a hinged model with decadal changes in growth rate for both mature and immature individuals. Each age-at-maturity follows a growth trajectory predicted for immature individuals until age a^m is reached, at which point the maturation effect on the growth rate is applied and the growth trajectory follows the rate associated with mature individuals. The predicted length-at-age was then used to derive the number of eggs produced and the number of eggs surviving to age 1 under a variety of scenarios based in literature-derived parameters. The number of eggs surviving to age 1 ("recruits" hereafter) is computed by imposing a survival rate on the eggs produced.

The survival of eggs into recruits was modelled to allow for higher survivorship of eggs produced by larger, later-maturing individuals (Trippel et al., 1997). This can be captured by making the survival rate of eggs into recruits a function of the length-at-age. I used a two-parameter sigmoidal model to calculate the egg survivorship for different ages-at-maturity a^m. The model uses $l^{50\%}$ as the length where individuals reach 50% of the maximum egg survivorship γ^{max}:

$$\gamma_{d,a^m} = \frac{1}{\left(1 + exp\left(-\left(l_{d,a^m} - l^{50\%}\right)\right)\right)} * \gamma^{max} \tag{5.6}$$

I finally used the following model to predict the number of recruits produced based on age-at-maturity a^m and predicted length-at-age for each decade d:

$$f_{d,a^m} = \left(\alpha^f \left(l_{d,a^m}\right)^{\beta^f}\right) \gamma_{d,a^m} \tag{5.7}$$

Finally, the second part of the population projection matrix, the survivorship, is determined for each matrix ω_{d,a^m}. The survivorship of immature individuals was set to S_{imm} and was multiplied by $\delta_{S,mat}$ after maturation. The survivorship of individuals from one year to the next was computed using the following survivorship function:

$$s_{d,a^m}^{a,a+1} = \begin{cases} = S_{imm} & \text{if } a < a^m \\ = \delta_{S,mat} S_{imm} & \text{if } a >= a^m \end{cases} \tag{5.8}$$

Using the above models for fecundity-at-age (equation 5.7) and survival-at-age (equation 5.8), I used literature-derived parameter values for the length-fecundity relationship, egg survivorship relationship and adult survivorship relationship (Table 5.1) to generate population projection matrices ω_{d,a^m}. There was a large amount of uncertainty associated with the different parameters required to build the population projection matrices, so instead of using a single set of values, I used a variety of scenarios that represent different costs of reproduction.

The magnitude of the cost of reproduction was accounted for by varying the values of the length at which egg survival is 50% of the maximum egg survival (parameter $l^{50\%}$ from equation (5.6)) and the change in adult survivorship associated with maturity (parameter $\delta_{S,mat}$ from equation (5.8)). The other parameter values used presented in Table 5.1 were chosen so that the resulting population projection matrices yield values of population growth rate that are within the range estimated by other studies (Myers et al., 1999). In other words, the parameter values used were biologically sensible but are also subjective, and are chosen to provide a basis for interpreting estimated changes in growth and maturation.

All analyses were conducted using the R software environment for statistics and graphics (R Development Core Team, 2011) using packages “nlme” and “lme4” for mixed-effects models (Pinheiro et al., 2011; Bates et al., 2011), “popbio” for Eigen analysis of population dynamics models (Stubben and Milligan, 2007), “RODBC” for database connectivity (Ripley and Lasley, 2010) and “PBSmapping” for mapping (Schnute et al., 2010). Data extractions were performed in December 2011 from the Oracle groundfish survey databases of DFO Maritimes and the Northeast Fisheries

Science Center of the NMFS available from the Bedford Institute of Oceanography in Dartmouth, Nova Scotia. All modelling results were subjected to visual analysis of residuals to ensure the appropriateness of the fits.

Table 5.1: Parameters used in the population dynamics model

Survey	Species	Scenario	Length-fecundity		Egg survival		Survivorship		Ref
			α^f	β^f	s^{max}	$l^{50\%}$	S_{imm}	$\delta_{S,mat}$	
DFO	*G. morhua*	(1)	0.5	3.4	1E-05	70	0.9	1.0	McIntyre and Hutchings (2003)
		(2)				70		0.75	
		(3)				70		0.5	
		(4)				35		1.0	
		(5)				35		0.75	
		(6)				35		0.5	
		(7)				0		1.0	
		(8)				0		0.75	
		(9)				0		0.5	
DFO	*M. aeglefinus*	(1)	1	3.35	1.5E-05	50	0.9	1.0	Blanchard et al. (2003)
		(2)				50		0.75	
		(3)				50		0.5	
		(4)				25		1.0	
		(5)				25		0.75	
		(6)				25		0.5	
		(7)				0		1.0	

Table 5.1: (continued)

Survey	Species	Scenario	Length-fecundity		Egg survival		Survivorship		Ref
			α^f	β^f	s^{max}	$l^{50\%}$	S_{imm}	$\delta_{S,mat}$	
		(8)				0		0.75	
		(9)				0		0.5	

Table 5.1: (continued)

Survey	Species	Scenario	Length-fecundity		Egg survival		Survivorship		Ref
			α^f	β^f	s^{max}	$l^{50\%}$	S_{imm}	$\delta_{S,mat}$	
NMFS	*G. morhua*	(1)	0.5	3.2	1E-05	70	0.9	1.0	Alonso-Fernández et al. (2009)
		(2)				70		0.75	
		(3)				70		0.5	
		(4)				35		1.0	
		(5)				35		0.75	
		(6)				35		0.5	
		(7)				0		1.0	
		(8)				0		0.75	
		(9)				0		0.5	
NMFS	*M. aeglefinus*	(1)	0.5	3.3	1E-05	70	0.9	1.0	Alonso-Fernández et al. (2009)
		(2)				70		0.75	
		(3)				70		0.5	
		(4)				30		1.0	
		(5)				30		0.75	
		(6)				30		0.5	
		(7)				0		1.0	
		(8)				0		0.75	

Table 5.1: (continued)

Survey	Species	Scenario	Length-fecundity		Egg survival		Survivorship		Ref
			α^f	β^f	s^{max}	$l^{50\%}$	S_{imm}	$\delta_{S,mat}$	
		(9)				0		0.5	

5.4 Results

5.4.1 Survey Strata With Similar Growth Conditions

Figure 5.2 shows the stratum-level random effects estimates for the growth parameter R (ρ_s from equation (5.1)) for Atlantic cod and haddock from the DFO and NMFS surveys. The survey strata are partitioned into four quantiles of similar growth regimes based on the value of random effect estimates. The four growth regimes are identified by different colours for each survey in Figure 5.2.

The observed gradient in growth for Atlantic cod follows a spatial trend as one moves from the Eastern Scotian Shelf towards the Bay of Fundy (Figure 5.2). Growth rates are smaller in the Eastern Scotian shelf and increase towards the Western Scotian shelf and the Bay of Fundy. A similar gradient is evident in the region surveyed by the United States. Atlantic cod growth rates are highest in southern waters towards Cape Hatteras and lowest in the northern waters of Georges Bank and the Gulf of Maine as well as in deeper strata.

Results for haddock do not show as clear a spatial trend and the strata supporting fastest growth in the DFO survey region occur both in the Bay of Fundy and in the Eastern Scotian Shelf (top right panel of Figure 5.2). In the US surveys, the fastest growth is observed in strata located in Georges Bank as well as in strata at the southern edge of the species range (bottom right panel of Figure 5.2).

5.4.2 Changes In Growth

The model I use estimates the effects of maturity and a decadal component on both the slope and the intercept of a linear growth model. The fixed effects parameter estimates and standard errors obtained from model fitting can be found in Tables C.1 to C.4. To facilitate the interpretation of the estimates I use them to calculate the absolute decadal estimate values of slope and intercept for mature and immature individuals (under “Growth” in Table 5.2). I also generate plots of predicted decadal growth of mature and immature individuals (Figures C.5 to C.8 in section C.2).

For all species-survey combinations evaluated, the growth of mature individuals in a given decade is slower than that of immature individuals as indicated by negative values of parameter β^m for equation (5.2). The decadal trends in growth for mature

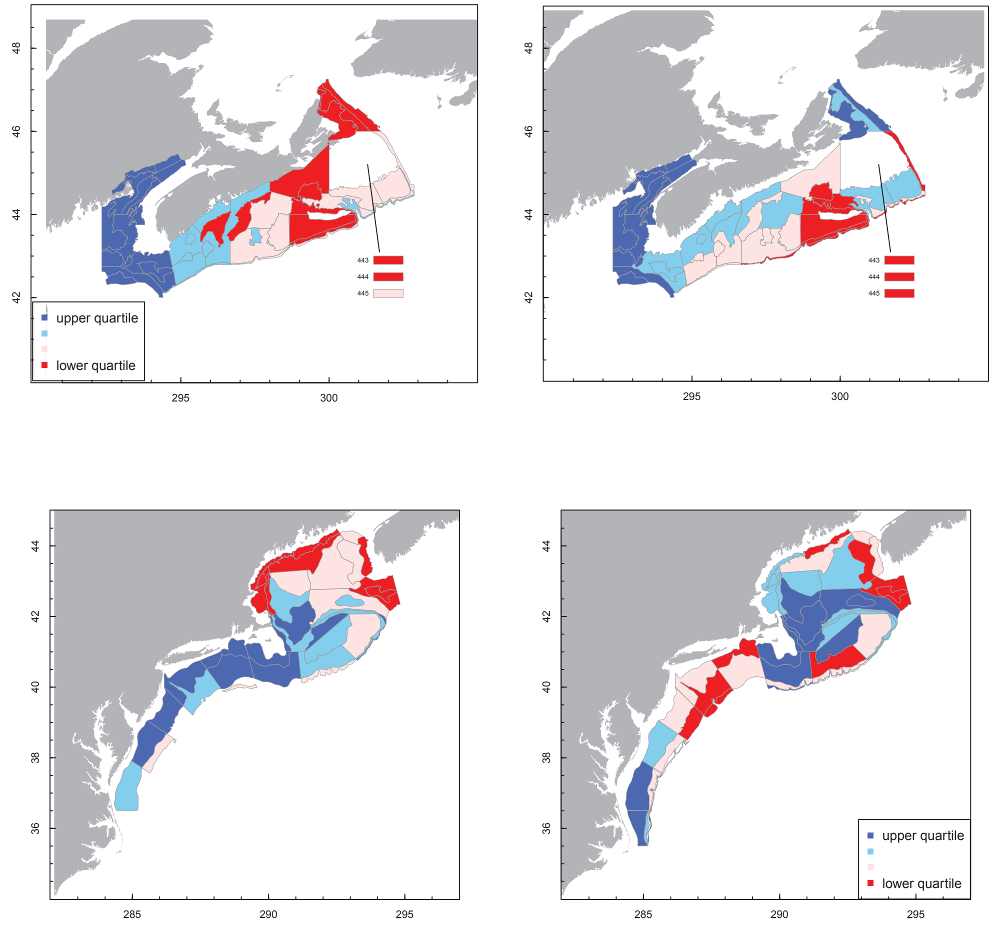

Figure 5.2: Spatial variability in Atlantic cod and haddock growth rates. Stratum-level deviations in the growth rate parameter R (ρ_s from equation 5.1) for Atlantic cod (left column) and haddock (right column) estimated from DFO (top row) and NMFS (bottom row) detailed fish observations collected on scientific trawl surveys. Each quartile is colour-coded to show the partition of the survey area into four separate regions of similar growth regime.

and immature individuals are not monotonically increasing or decreasing over the time period covered by the data.

I concentrate on discussing the parameter estimates associated with the slope of the growth model since the intercept estimates are negatively correlated with the slopes. This correlation makes the interpretability of the intercept estimates less clear in terms of identifying decadal changes in growth rate.

Decadal estimates are available from the 1950s to the 2000s for DFO Atlantic cod (Table 5.2). The slope estimates are compared to the 1950s and the results suggest that the growth rate of immature individuals increased in the 1960s, 1970s and 1980s and was reduced in the 1990s and 2000s. The reduction in growth rate of immature individuals between the 1970s and the 1990s was such that the resulting slope estimate for the 1990s is comparable to the slope estimate of mature individuals in the 1970s. In other words, the reduction in growth rate of immature individuals in the 1990s was comparable to the reduction in growth rate associated with maturation. The growth rate of mature individuals is highest in the 1970s and the estimates from the earliest three decades are larger than those from the latest three decades. Estimates for DFO haddock (Table 5.2) suggest the highest growth rate of immature individuals in the 1970s and the lowest in the 2000s. The estimates for mature individuals show drastic declines in growth rate in the last three decades.

Because NMFS surveys start at a later date, the first decade presented is the 1960s and parameter estimates are compared to this reference decade. The parameter estimates for NMFS Atlantic cod (Table 5.2) suggest an increase in the growth rate of immature individuals, especially in the 1980s and 1990s. In contrast, the growth rate of mature individuals was slowest in the 1960s and the 2000s and highest in the 1980s. The parameter estimates for NMFS haddock (Table 5.2) suggest that the slowest growth of immature individuals was during the 1960s and the fastest growth occurred in the 1970s and 1980s. Growth of mature individuals followed a similar trend with the fastest growth rates also occurring in the 1970s and 1980s.

Table 5.2: Parameter estimates of the decadal growth and maturation models.

Survey	Species	Trait	Parameter	Maturity	Decadal estimates					
					1950s	1960s	1970s	1980s	1990s	2000s
DFO	*G. morhua*	growth	α	0	11.55	11.61	14.57	11.95	14.79	11.66
				1	27.32	28.18	23.80	29.70	25.59	22.54
			β	0	8.27	8.81	8.58	8.35	6.72	7.74
				1	6.53	6.55	7.49	5.32	5.55	5.74
		maturity	α	n/a	-4.83	-5.56	-5.42	-5.81	-5.16	-5.25
			β	n/a	1.05	1.65	1.93	1.83	1.77	1.98
	M. aeglefinus	growth	α	0	15.57	15.47	14.84	13.04	14.65	14.60
				1	29.57	33.14	31.07	34.66	27.12	24.68
			β	0	6.20	6.56	7.91	6.97	6.24	5.20
				1	3.85	3.43	4.16	1.96	2.60	2.69
		maturity	α	n/a	-6.21	-5.37	-6.45	-6.28	-3.24	-4.28
			β	n/a	1.47	1.50	2.27	1.98	1.43	1.85

Table 5.2: (continued)

Survey	Species	Trait	Parameter	Maturity	Decadal estimates					
					1950s	1960s	1970s	1980s	1990s	2000s
NMFS	*G. morhua*	growth	α	0		26.62	20.53	15.02	14.56	15.38
				1		43.39	33.10	28.78	31.00	30.87
			β	0		8.32	10.14	12.35	11.94	10.78
				1		6.36	8.59	9.46	8.46	7.74
		maturity	α	n/a		-3.70	-3.45	-3.27	-4.00	-3.67
			β	n/a		1.39	1.31	1.61	1.98	1.62
	M. aeglefinus	growth	α	0		27.67	36.14	33.88	39.38	31.95
				1		45.21	36.14	33.88	39.38	31.95
			β	0		5.31	8.62	8.23	7.67	6.86
				1		2.48	5.05	5.19	2.84	3.57
		maturity	α	n/a		-3.83	-3.12	-3.20	-3.24	-3.21
			β	n/a		1.51	1.60	2.00	1.82	1.65

5.4.3 Changes In Maturation

The parameter estimates from the maturation model of equation (5.3) can be interpreted based on the changes in both the slope and intercept parameters for each decade. For a fixed age at 50% maturity, reducing the range of ages over which the maturation process takes place will decrease the value of the intercept and increase the value of the slope. The slope and intercept parameters are negatively correlated which complicates the interpretation of the model estimates. Trends toward earlier maturation can be identified by either an increase in the intercept or the slope. The parameter estimates are best used to make predictions of the age at 25%, 50% and 75% maturity (Figure 5.3). The decadal estimates derived from the fitted model are available in Table 5.2 and the tabular parameter estimates and standard errors can be found in Tables C.5 to C.8.

Parameter estimates for Atlantic cod from the DFO survey area suggest that age-at-maturity is in overall decline. Slope estimates of the logistic regression model are highest in the 2000s and have been steadily increasing over the time frame of the data. In addition, the range of ages at 25% and 75% maturity is shrinking. Haddock in the region surveyed by DFO also witnessed an overall decrease in their age-at-maturity. Strongly driving this downward trend are the earliest estimates from the 1950s and 1960s cohorts.

There is less evidence for monotonic temporal changes in maturation of Atlantic cod and haddock sampled in the NMFS surveys. There is evidence for a decrease in the age at 25%, 50% and 75% maturity in the first three decades but there is also an increase in those values in the last two decades.

5.4.4 Demographic Consequences

For each species-survey combination decadal intrinsic population growth rates associated with different ages at maturity a^m are presented for nine scenarios of varying levels of cost of maturation. The scenarios for all surveys and species are ordered such that the cost of reproduction increases as we move towards the right (larger reductions in survivorship due to maturation) or towards the top of the multi-panel plot (larger values of the length at which the egg survivorship is 50% of the maximum). The timeseries plots on the bottom row of each figure use $l^{50\%}$ values of zero and

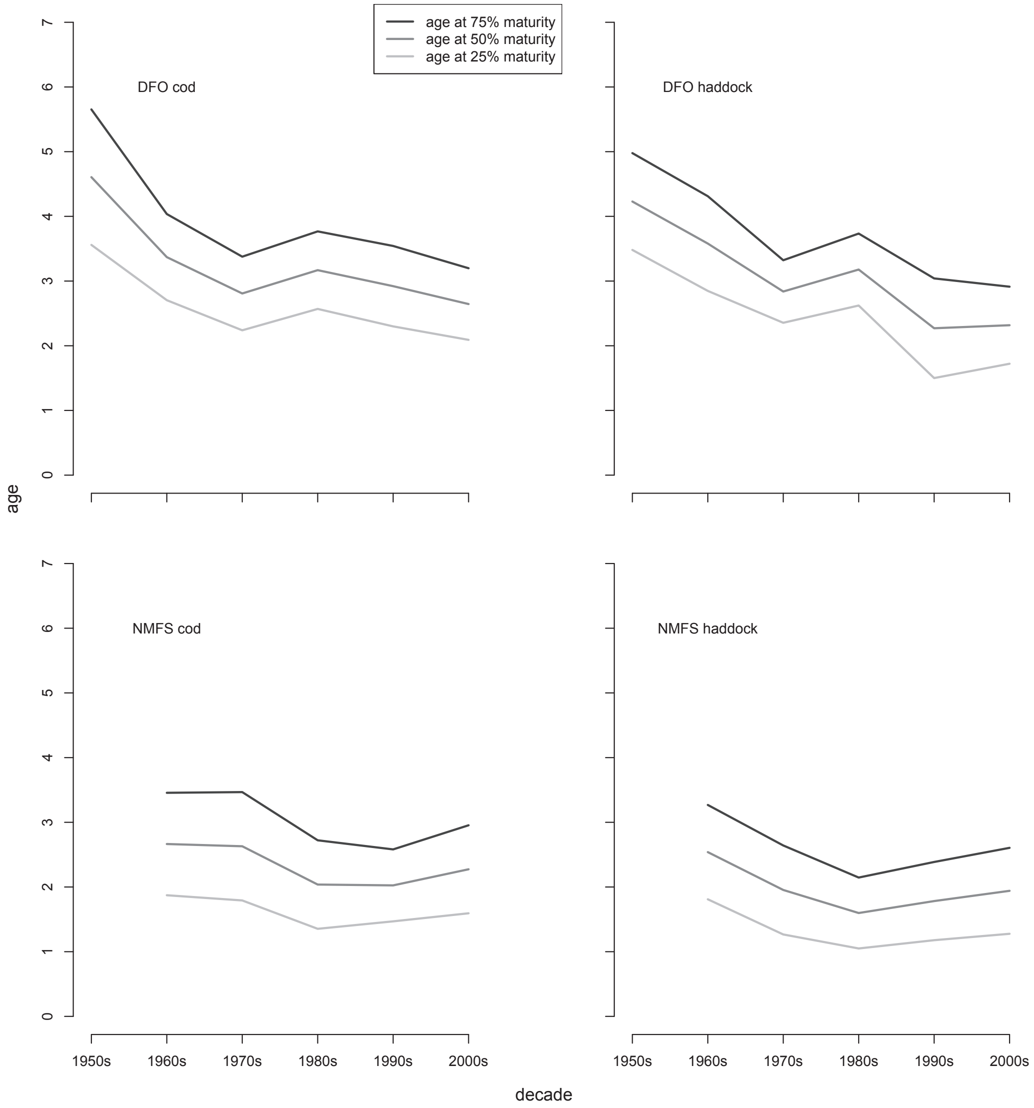

Figure 5.3: Temporal trends in maturity. Decadal estimates of age at 25%, 50% and 75% maturity for Atlantic cod and haddock from the DFO and NMFS surveys.

represent a situation where the survivorship of eggs is the same for all a^m. Under this situation, the length of an individual does not affect the survivorship of its eggs. Similarly, timeseries plots in the left column use $\delta_{S,mat}$ values of 1.0, which means that the survivorship of individuals is the same before and after maturation.

Estimated values of r_{d,a^m} that are above zero mean positive population rates of increase and negative values mean negative population rates of increase (Figures 5.4 to 5.7 and Figures C.1 to C.4). The decadal trends in r_{d,a^m} for the different scenarios are determined only by the decadal estimates of growth. The decadal estimates of maturation do not come into play in the population projection matrices since the fecundity and survivorship are calculated from the predicted lengths of individuals over their lifetime under different values of a^m.

Values r_{d,a^m} for DFO Atlantic cod, DFO haddock and NMFS haddock are highest in the 1970s, suggesting a decline thereafter. Population growth rate was highest in the 1980s for NMFS Atlantic cod and has been decreasing for the last two decades.

To synthesize how both the decadal growth and maturation changes influence population demographics, I used scenario (5) of each species and survey to calculate the value of r_{d,a^m} for ages at 25%, 50% and 75% maturity (Figure 5.8). The ages-at-maturity used in the population projection matrices are integer values whereas estimated values of r_{d,a^m} are rational numbers with decimals. This step essentially combines the decadal maturity estimates of the ages at 25%, 50% and 75% maturity with the decadal estimates of population growth rate. I simply interpolated the values of r_{d,a^m} for the integers above and below the estimated ages at 25%, 50% and 75% maturity to determine their estimated population growth rate. Incorporating the estimated decadal changes in maturation to the time-series of r_{d,a^m} suggests that population growth rates of both species from both surveys have been steadily declining since the 1970s.

5.5 Discussion

The available scientific trawl survey observations of length, maturity and age for the Northwest Atlantic cod and haddock populations studied here suggest that temporal changes in growth and maturation exist. The observed changes in growth and

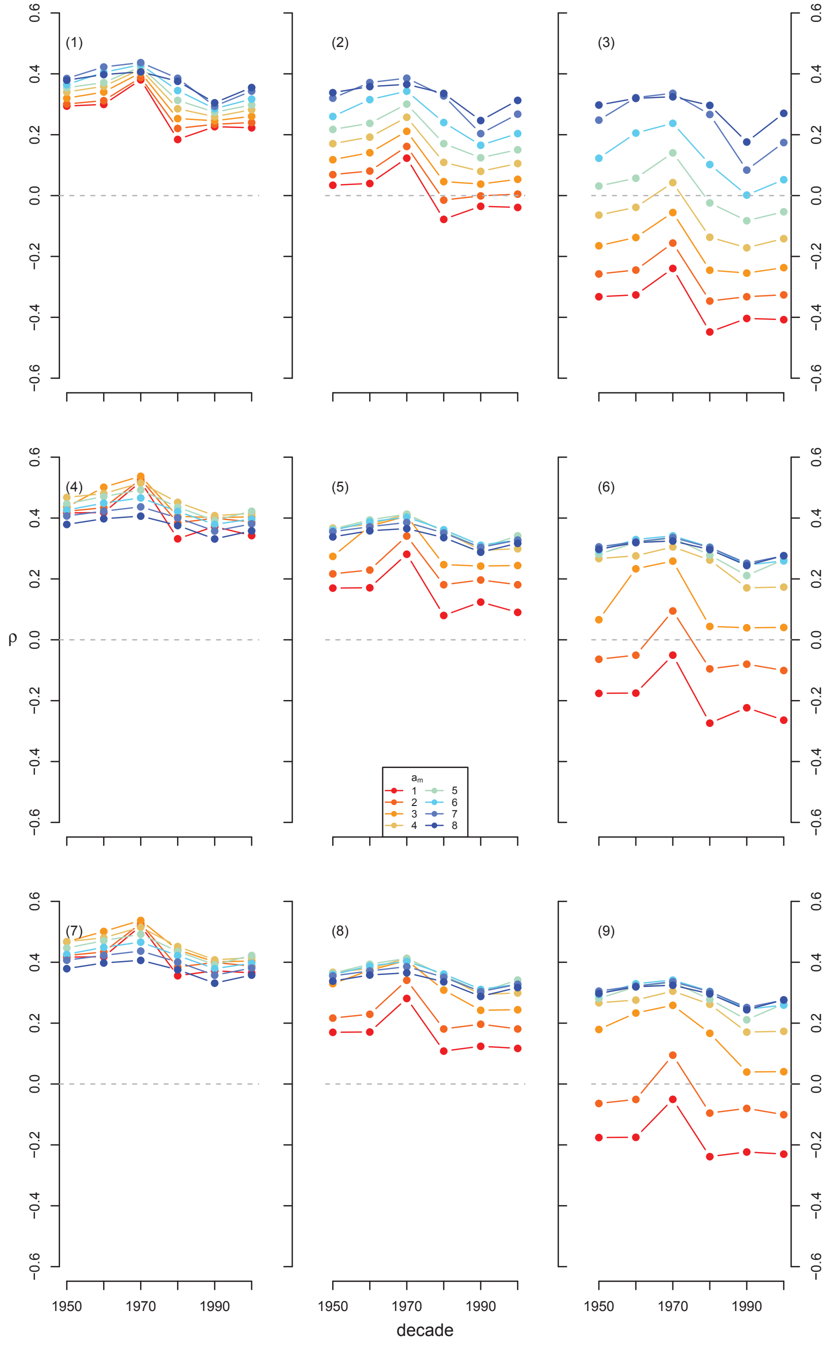

Figure 5.4: Temporal trends in population growth rate. Decadal demographic changes for Atlantic cod in DFO survey under nine different scenarios of the cost of reproduction on egg and adult survivorship. For each decade, the population rate of increase (r) is plotted for ages-at-maturity 1 to 8.

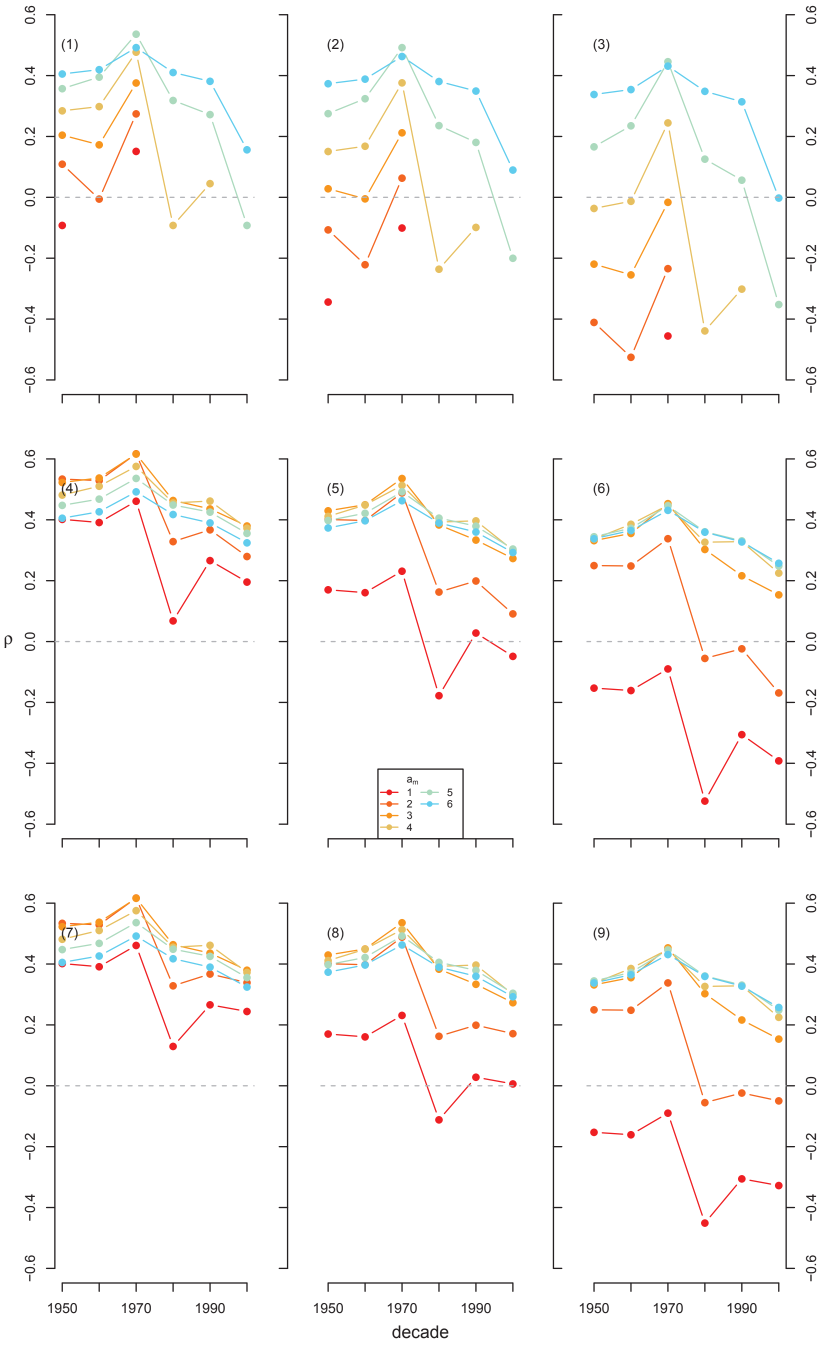

Figure 5.5: Temporal trends in population growth rate. Decadal demographic changes for haddock in DFO survey under nine different scenarios. For each decade, the population finite rate of increase (r) is plotted for ages-at-maturity 1 to 6.

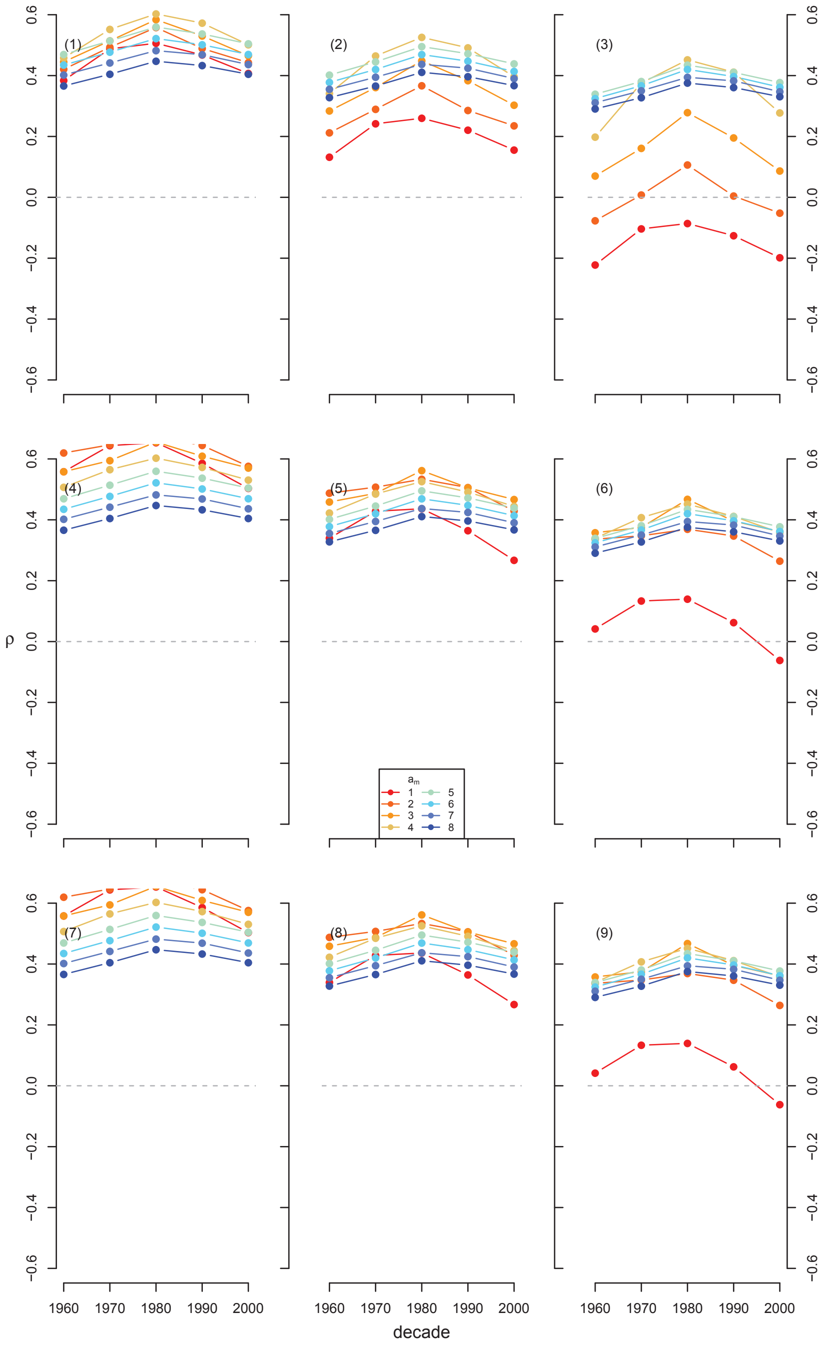

Figure 5.6: Temporal trends in population growth rate. Decadal demographic changes for Atlantic cod in NMFS survey under nine different scenarios. For each decade, the population finite rate of increase (r) is plotted for ages-at-maturity 1 to 8.

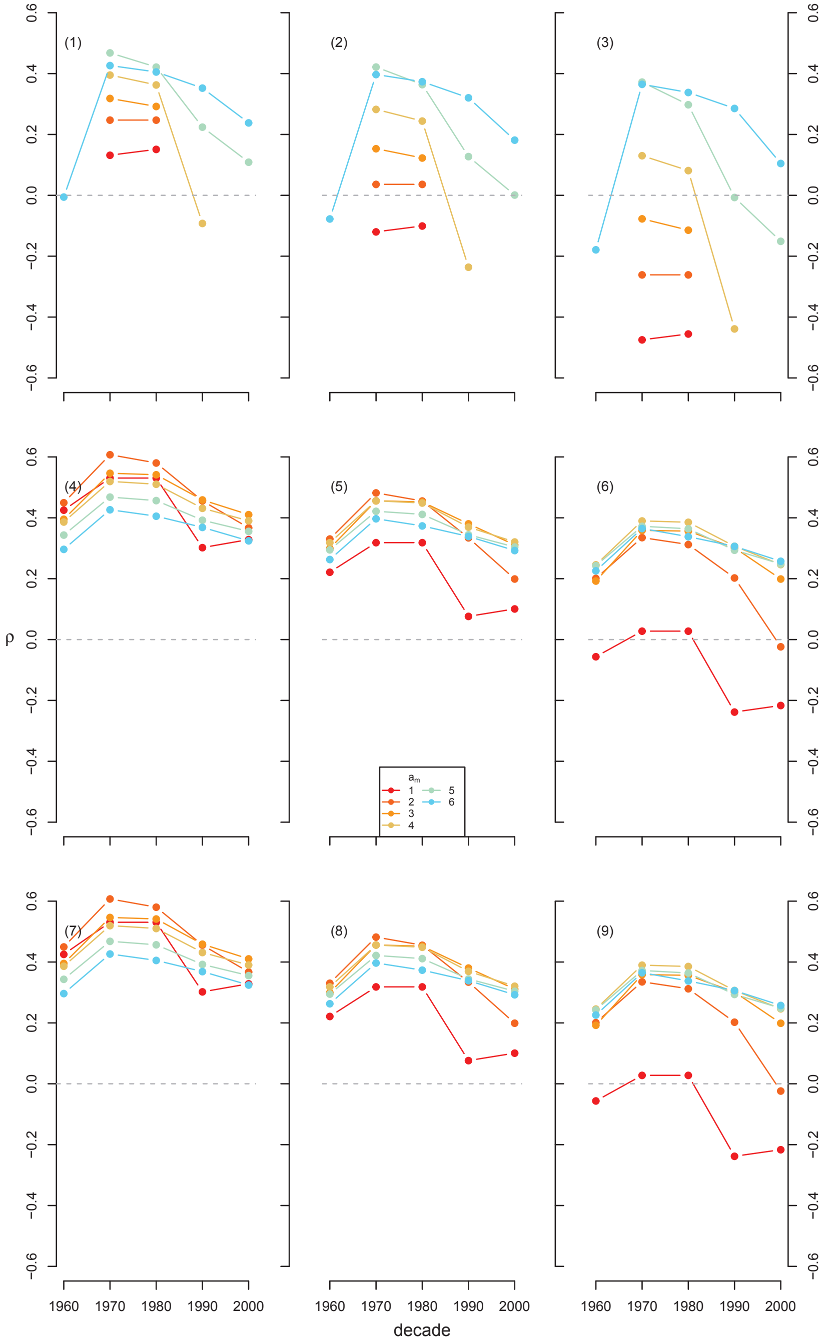

Figure 5.7: Temporal trends in population growth rate. Decadal demographic changes for haddock in NMFS survey under nine different scenarios. For each decade, the population finite rate of increase (r) is plotted for ages-at-maturity 1 to 6.

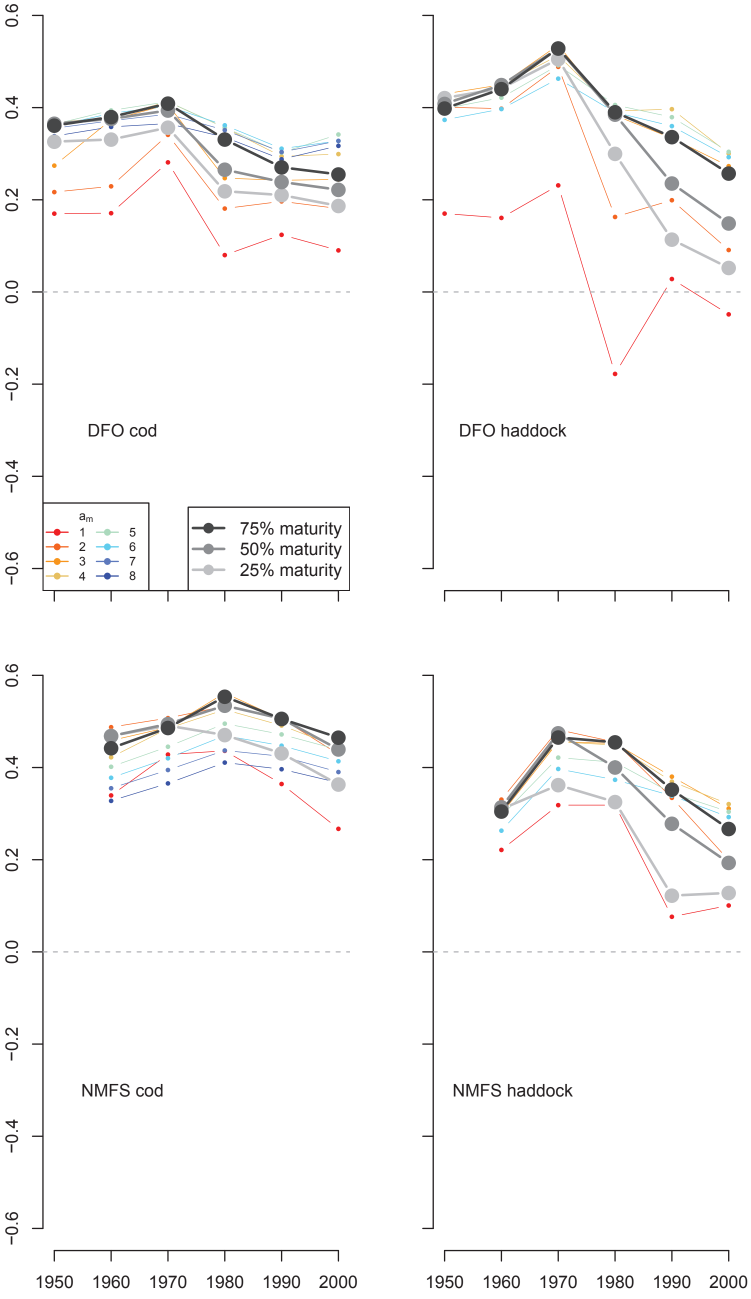

Figure 5.8: Temporal trends in population growth rate r for Atlantic and haddock from the DFO and NMFS surveys, including the estimated changes in age-at-maturity.

maturation have measurable demographic consequences on the populations, including slower recovery rates and sustainable harvest levels, as these factors impact the fecundity of individuals, their survivorship and the survivorship of their eggs.

The populations examined here have been the subject of extensive scientific scrutiny and the changes in age-at-maturity and growth have been documented by others. A number of studies have used probabilistic reaction norms of growth and maturation to determine whether these changes are caused by environmental conditions or by evolutionary forces (e.g. Barot et al., 2004). Other studies have documented changes in life-history characteristics of commercially exploited fish populations (Hutchings and Baum, 2005; Darimont et al., 2009; Sharpe and Hendry, 2009). Determining the demographic consequences of these changes (e.g. Hutchings, 2005) adds another level of complexity since many trade-offs exist in life-history traits. For example, earlier maturation will allow an individual to start producing offspring early but will also have consequences on future growth and survival. The analysis presented here links the estimated decadal changes in growth and maturation to population demographics. A similar study of the northern Gulf of St. Lawrence Atlantic cod population (Lambert, 2011) found that changes in growth and potential fecundity were sufficient to explain reduced rates of population increase.

Under the modelling framework used here, the resulting values of r_{d,a^m} for different ages-at-maturity a^m result from the interplay between growth of individuals before and after maturation, the survivorship of eggs into recruits and the survivorship of individuals over their lifetime. The fact that a later age-at-maturity can yield higher values of r_{d,a^m} is counter-intuitive since the age at first reproduction is the dominant life-history trait that determines intrinsic population growth rate (Cole, 1954). The "best" age-at-maturity, resulting in the highest population growth rate at an intermediate age, is determined by the trade-off between maturing earlier but smaller and maturing later but bigger. When there is no decrease in egg and adult survivorship associated with maturing earlier, the length-based fecundity of individuals determines the age-at-maturity that has the highest population growth rate. This tends to be at early ages; however when reproductive costs are included in the population dynamics model the age-at-maturity with the highest population growth rate shifts to later ages.

A major statistical difficulty arises from the fact that the processes that I am interested in modelling (temporal changes in growth and maturation) are longitudinal in nature whereas the available data (length, age and maturity status of individual fish) are cross-sectional. Ideally, one would follow individuals over the course of their life and record their length, age and maturity status over that time period. While this is not possible to do, analysis of incremental otolith structures can be used to determine the lifetime growth of an individual. However, this procedure requires a much larger amount of data processing than the more common ageing protocols used on scientific trawl survey data. The wider availability of cross-sectional observations where we only know the age and length of an individual, not a history of its growth, motivated the development of the methods used here to estimate the decadal changes that are themselves longitudinal.

Decadal changes in growth were estimated using a hinged linear model instead of a more common asymptotic model like the von Bertalanffy model. The main reason behind this is that the parameters of asymptotic non-linear models are highly correlated and confound the estimation of temporal changes in growth. The linear model used here captures the decrease in growth rate associated with maturation and is simple enough to allow for the estimation of decadal changes in growth. The more commonly used von Bertalanffy growth model (von Bertalanffy, 1938) is non-linear, has three highly correlated parameters and does not include a change in growth rate associated with maturation. The flexibility of the simpler linear model used and the biologically plausible fitted parameter estimates it returns indicate its appropriateness for the examination of temporal changes in growth.

Other studies divide the species studied here into separate populations over the surveyed area. This basically means that strata subsets are assigned to each component of the population. I decided to use the entire survey area to obtain a regional overview of the demographics consequences of changes in growth and maturation.

Based on the population projection matrices used here, trends towards earlier maturation decrease the value of r_{d,a^m} and also increase the possibility of negative population growth. This is of consequence since the estimated trends in maturation indicate earlier maturation for the populations under scrutiny. A worrying picture emerges when both the decadal changes in maturation and the decadal changes in population growth rate are merged into a single decadal demographic estimate for age at 25%, 50% and 75% maturity (Figure 5.8). The demographic consequences of the estimated decreases in r_{d,a^m} in recent decades are exacerbated by the decreases in age-at-maturity over the same time period. In addition to an overall decrease in r_{d,a^m} associated with each a^m there is an overall decrease in age-at-maturity over time. The combined effects of growth and maturation on population demographics cause an overall decrease of r_{d,a^m} and a higher probability that the populations will experience negative growth. These decreases in r_{d,a^m} mean that the populations are not able to recover as quickly as they could previously and also suggest that the harvest rates that can be sustainably withstood have also decreased.

The estimated changes in growth seem to be environmentally driven whereas the changes in maturity seem genetically driven. Changes in growth are more variable over time and are also not monotonic. Increases and decreases in growth of mature and immature individuals are observed over the period covered by the surveys. Changes in maturation, on the other hand, seem more directional and less reversible. This suggests that changes in growth may be associated with stochastic variations in primary productivity whereas trends towards earlier maturation may be a result of changes in heritable traits.

The Leslie projection matrix has a single conformation that yields stable population abundance over time. All other potential projection matrices either yield exponential growth (as indicated by a positive value of r_{d,a^m}) or exponential decline (as indicated by a negative value of r_{d,a^m}). Care must be taken in interpreting the demographic parameters since the biological realism of the population dynamics model used is limited. The value of r is best thought of as the theoretical maximum rate at which the population will be able to increase. The absolute changes in the magnitude of r_{d,a^m} are sensitive to a variety of factors that are difficult to capture in a single population dynamics model. The different scenarios used here attempt to capture some of the variability associated with the cost of reproduction but ultimately the values of population growth obtained come from defensible yet subjective assumptions about the length-fecundity relationship used and the survival of eggs into recruits.

It is possible to include the effects of fishing in the Leslie matrix through an additional age-specific term on the survivorship function. Values of r_{d,a^m} will decrease when fishing is included because there is increased mortality. In contrast, population productivity is expected to increase under a surplus production model when an intermediate level of exploitation is applied to a virgin population (Hilborn and Walters, 1992). The difference between the Leslie matrix and surplus production models is that no density-dependent mechanisms are included when an additional mortality component is added to a population projection matrix.

The inclusion of temporal changes in life-history characteristics into assessment methodologies can better ensure that catch quotas are sustainable and that population projections for recovery account for the potential demographic consequences of changes in growth and maturation. The sustainable management of fish stocks requires their careful monitoring because of the stochastic nature of population dynamics and the strong possibility that there are temporal changes in both the environmental conditions that control primary productivity and in the underlying determinants of population demographics.

Changes in natural mortality is another key component determining the rate of recovery of collapsed populations. For example the Atlantic cod in the Southern Gulf of St. Lawrence that has failed to recover despite the near elimination of fishing mortality on the population, an outcome caused by an increase in natural mortality (Swain and Chouinard, 2008; Swain, 2011). I chose not to include time-varying values for natural mortality for simplicity and to isolate the demographic effects of changes in growth and maturation.

The Canadian data of DFO Maritimes comes from two survey eras with no overlap and the results derived from early observations greatly impact the estimates of growth and maturation of population cohorts from the 1950s and 1960s. The quality and validity of the earlier data is not in question since the opportunistic surveys were also conducted by trained scientists. The earliest observations available suggest later maturation over a wider range of ages and faster growth than in later stages of the survey. An explanation of this possibly spurious result is that the ageing methodology used in earlier observations was biased and overestimated the age of individuals. This would make the length-at-age of individuals from earlier surveys consistently smaller than individuals from later surveys. Biased ageing would also skew the maturation model estimates towards later maturation ages. However, there is no indication that such a bias exists in the earliest ageing materials and that the estimated temporal trends result from different ageing methodologies and protocols.

A seasonal effect is present in the observations because surveys are conducted at different times of the year. In the case of the NMFS surveys I am using both the spring and fall surveys. One method to account for the seasonal effect is to recode ages into their decimal value prior to model fitting. For example if an individual of age 8 was caught in the month of March, his age would be 8.25 $(8 + (3/12))$ and an individual caught in September would be 8.75 $(8 + (9/12))$. Model results are not noticeably improved by using such a correction since the variability in the lengths observed at a given age is largely responsible for the model fitting results. Of more serious concern is the effect of seasonal movement within the survey area and the fact that each stratum's independence within a single survey may not be maintained when using multiple surveys.

A significant statistical improvement of the analyses conducted here would be to carry forth the uncertainty of the decadal growth and maturation models into the population dynamics model. Propagating the uncertainty associated with the estimated decadal changes in growth remains a challenge and I decided against it to simplify the evaluation of demographic consequences.

To sustainably manage exploited fish populations requires proper monitoring programs such as scientific trawl surveys. A source of fisheries-independent data will always be an important part of stock assessments and of recovery potential analyses. The social and economic forces behind commercial fisheries have shown their ability to over-harvest populations and that tendency must be counter-balanced by scientific assessments and the rigorous application of appropriate management measures.

I conclude that the changes in growth and maturation observed over the last five decades have decreased the natural intrinsic growth rate of Atlantic cod and haddock populations of the Scotia-Fundy and United States northeast continental shelf. Analyses of growth and maturation conducted in the 1970s and 1980s would provide overly optimistic recovery scenarios and would also over-estimate the sustainable level that these populations can withstand.

Chapter 6

DISCUSSION

6.1 Thesis Summary

This thesis examines aspects of the ecology and evolution of highly exploited fish populations. In this general discussion I summarise my findings, placing them in a broader ecological and evolutionary context. Further, I critique the methodologies used, I highlight the implications of my research for fisheries management, and conclude with some directions for future work.

Determining the knowledge base and status of commercially exploited fish stocks was the focus of Chapter 2. This analysis demonstrated that overexploitation of commercial fish stocks is pervasive, that many stocks continue to be exploited at unsustainable levels, and that large regional differences in stock status exist. There is also evidence that appropriate fisheries management can ensure the ecological sustainability of harvested populations. However, the institutional requirements for proper management are unlikely to exist in developing countries. Having an established management regime does not equate to immunity from overexploitation either, as evidenced for example by the mismanagement of many stocks in Europe (Froese and Proelß, 2010) and Canada (Hutchings et al., 2012).

The database of stock assessment that was assembled as part of the undertaking of this thesis has generated much novel work among fisheries ecologists and has led to a number of recent publications (Worm et al., 2009; Hutchings et al., 2010; Branch et al., 2010, 2011; Pinsky et al., 2011; Melnychuk et al., 2011; Ricard et al., 2011; Hilborn et al., 2012; Jensen et al., 2012; Thorson et al., 2012; Anderson et al., 2012), which continues to generate scientific debate and new research projects. One of the most important improvement over the original database compiled by Myers et al. (1995b) is the inclusion of reference points that allow the explicit determination of fisheries status instead of relying on relative trends in biomass and catch.

Creating a scientifically useful data format of trawl survey information for inclusion into OBIS and documenting how to reconstruct appropriate population indices from such data was accomplished in Chapter 3 (Ricard et al., 2010). Making such valuable fisheries-independent data more widely available will likely stimulate novel analyses and will also move ecological research a step closer to achieving reproducible science, where analyses can be replicated by others through the sharing of data and computer code (Ince et al., 2012). Prior to being publicly available from OBIS, the scientific trawl survey data analysed here could only be accessed internally at Fisheries and Oceans Canada which required a data transaction each time a researcher was interested in using the information for conducting analyses. The public version of the trawl survey data does not carry such constraints, however it misses the detailed observations about length frequencies, ageing materials and maturity stages contained in the original dataset. Nevertheless it provides a useful format to conduct analyses of abundance, distribution and biodiversity.

The spatial population dynamics of groundfish populations were the focus of Chapter 4. Positive correlations between abundance and distribution were documented for a number of groundfish populations. Further it was shown that the spatial distribution of stocks does not contract as quickly as stock abundance, but also recovers more slowly from previous losses.

The demographic consequences associated with changes in life-history characteristics were estimated in Chapter 5. I concluded that changes in individual growth were non-monotonic over the time period covered by the surveys and seemed to be associated with environmental conditions whereas changes in age at maturity were more directional and likely driven by size-selective fishing. The estimated demographic changes are predicted to reduce the sustainable harvest level that fish populations can withstand and impact their recovery potential. A novel aspect of the work presented in this chapter was the development of an analytical framework to establish the population-level consequences of changes in individual growth and maturation characteristics.

6.2 Ecology And Evolution Of Heavily Exploited Fish Populations

The effects of fishing on targeted and non-targeted populations will depend on a variety of ecological, environmental, social and economic factors. The ecology of a population will set the limits of the sustainable level of exploitation that it can support. The impacts of environmental variability on productivity, habitat quality and natural mortality will affect the dynamics of fish populations and can exacerbate the negative effects of harvesting. While unrelated to ecology, social and economic factors can have dramatic consequences on harvested populations since they directly influence the intensity of fishing that takes place. Over-harvesting can occur when a fishing fleet is allowed to develop an excessive harvest potential and also when the economic incentives of resource extraction exceed the biological limits of the targeted populations. All these factors have led to numerous situations where fish stocks have collapsed to historically low levels of abundance and biomass (Hutchings, 2000).

To allow a population to recover in abundance and biomass requires the implementation of a variety of fisheries management measures such as harvest quotas, gear restrictions and the establishment of no-take zones (Worm et al., 2009). Just as the effects of fishing on targeted populations are linked to their ecology, the recovery potential of collapsed populations will depend on the magnitude of reduction in fishing mortality and on biological and ecological factors determining the potential rate of population increase (Hutchings, 2001b; Hutchings and Reynolds, 2004). While some populations have successfully rebounded from collapses, many populations have failed to recover despite significant reductions in fishing.

The relationships between different populations of a marine ecosystem are often dynamic and non-linear and it is very difficult to predict how the different components of an ecosystem will react when fisheries are focused on a subset of species. Alteration of trophic dynamics in heavily exploited marine ecosystems have been documented (Frank et al., 2005; Myers et al., 2007; Baum and Worm, 2009). The unintended consequences of reductions in population abundance and biomass mean that great precautions must be taken in managing exploited stocks and that it is imperative to look at the ecosystem as a whole instead of just targeted populations of commercial interest.

An increasing body of evidence points to the potential evolutionary and genetic effects that fishing can have on targeted populations. This stems from the size-selective nature of modern fishing gear such as bottom trawls (Hutchings, 2009). Because of its genotypic basis, the reversibility of fisheries-induced evolution may be slow to reverse if fishing pressure is reduced (Jørgensen et al., 2007). However, selection reversal has been demonstrated under experimental settings (Conover et al., 2009) and in simulation studies (Kuparinen and Hutchings, 2012).

The perception of what constitutes a "healthy" population abundance is dependent on whether one wants to maximise yield or ensure the maintenance of ecological integrity in marine ecosystems. There exists a trade-off between exploitation and conservation which means that the harvest rate that maximises the yield of a single stock will have negative consequences on conservation objectives such as the maintenance of biodiversity and the minimisation of extinction risks. While the ecological role of a population might be maintained at abundance levels that maximise yield, non-target species will likely be affected as well because of the inability of most fishing gear to target a single species. Using ecosystem models to evaluate multi-species scenarios, Worm et al. (2009) show that a slight reduction in harvest rate can have significant positive impacts on conservation objectives. While there is a loss in yield, the structure and resilience of marine ecosystems and the provision of ecosystem services are better maintained at lower harvest rates.

6.3 Reproducible Science

The evolution of scientific thoughts is iterative and the process that leads to novel discoveries often involves the critique of earlier studies and the eventual acceptance of new hypotheses in light of updated observations and analyses (Kuhn, 1962). Only through the availability of data used in scientific analyses can other researchers be expected to reproduce published results and to offer alternative analytical approaches. This process can not take place when the data used only exists in "vaults" that are only accessible to a subset of the research community. All the analyses behind Chapters 2, 3 and 4 use publicly available data and can be reproduced and improved by other researchers.

6.4 Novelty Of Research

Building on the seminal work of Myers et al. (1995b), Chapter 2 extended the geographical and taxonomic coverage of stock assessment results, utilised a proper relational database management system that allow secure access from multiple users, and included biological reference points that can be used to estimate biomass and exploitation status.

The data format developed in Chapter 3 is the first attempt to disseminate scientific trawl survey data to a wide ecological audience and allows practitioners to conduct sophisticated analyses on valuable fisheries-independent datasets. Earlier attempts at synthesising available trawl surveys from the Northwest Atlantic, the East Coast North America Strategic Assessment Groundfish Atlas (ECNASAP of Fisheries et al., 1996), focused on pictorial products whose underlying data were not widely available. This atlas also restricted the number of species included in the dataset and failed to provide the observational details required for conducting meaningful ecological investigations. In contrast, the OBIS version of the trawl survey that was created in Chapter 3 is publicly accessible on the internet, and provides the sufficient level of detail required to conduct spatiotemporal studies of the dynamics of marine populations.

The analyses conducted in Chapter 4 expanded the geographical coverage of previous analyses (Fisher and Frank, 2004), improved previously used analytical methods by incorporating the sampling design into the modelling framework, and used methods that properly deal with the catch records where no individuals were observed. Using the publicly available data source developed in Chapter 3, the methods used in Chapter 4 and their results can be subjected to the scrutiny of other researchers.

Linking life-history characteristics to their demographic consequences requires an innovative analytical framework such as that developed in Chapter 5. As such, this work allows to translate observed changes in life-history evolution to estimates of productivity and recovery potential in exploited fish populations.

An important aspect of the study of marine populations that was identified in this thesis is the issue of data richness associated with different species. While some species have vast amounts of high-quality detailed information available, the majority of marine populations are poorly sampled, under-studied, and suffer from a general lack of ecological knowledge. Moreover, many populations that inhabit international waters and areas with limited data gathering and scientific expertise remain virtually undocumented in terms of understanding their ecology and the effects that human activities have on them.

6.5 Critique Of Methods

The sample provided by the RAM Legacy database is a biased representative of the state of the world fisheries because the assessments that it contains come mostly from highly industrialised countries with strong governmental institutions that are able to implement and enforce fisheries management measures. However, when used in conjunction with other data sources from similar areas it is possible to examine the relationship between stock biomass, fisheries catch and survey information (Worm et al., 2009; Branch et al., 2010, 2011).

Using a Schaefer surplus production model to estimate biomass and exploitation reference points assumes that the biomass level level associated with maximum sustainable yield occurs at 50% of the unexploited biomass. Since the maximum yield of many stocks can occur at lower biomass levels (Hilborn and Stokes, 2010), the biomass reference point estimated by the Schaefer model will be higher, and the associated ratio of current biomass to B_{msy} will be underestimated. In other words, using Schaefer-derived reference points can provide overly pessimistic estimates of stock status and potentially skew the ratios used in the "fried egg" plots. To address this potential shortcoming, I compared Schaefer-derived and assessment-derived BRPs for stocks where both could be obtained and showed that, while the Schaefer-derived estimates do show some bias (Figure A.2), the majority of Schaefer-derived BRPs correctly classified stocks as being either below or above B_{msy} (Table A.1).

The "fried egg" figures presented in Chapter 2 are static in nature and do not portray the historical trajectory of each assessed stock. Seeing the temporal evolution of exploitation and biomass provides more meaningful information to inform decision-making. Moreover, reference points will also vary over time as fisheries objectives and assessment methods evolve and populations react to harvest.

While the benefits of wider data dissemination through internet-based information systems such as the one used in Chapter 3 (OBIS) is undeniable, there remains a risk that such systems and the interlinkages between different initiatives will not be maintained in the future. This is clearly problematic, since it can lead to end-users accessing dysfunctional internet links, and limits their ability to access the authoritative data sources that information systems aim to provide. An enthusiastic approach to further improve such systems, and an active user-base that can provide timely and meaningful feedback is essential to the proper development of accessible, useful, and scientifically rigorous data sources.

The time frame of the survey data used in Chapters 4 and 5 is much shorter than that of the history of exploitation and it remains essential to establish historical baselines for marine populations (Lotze and Worm, 2009). A true understanding of the estimated fluctuations in population abundance and biomass requires a historical understanding of what marine ecosystems were like, prior to being impacted by human activities.

The analyses of spatial population dynamics of Chapter 4 attempt to elucidate the relationship between abundance and distribution and to estimate how local density varies as a function of overall abundance.

The decadal estimates of changes in growth and maturation presented in Chapter 5 do not implicitly include fisheries removals into the modelling framework. This is a potential topic for further development of the approach.

Finally, the focus of the thesis was the analysis of trawl survey and stock assessment data to examine some important aspects of fish population dynamics. Other important sources of information exist for the populations examined here, namely catch data, and stock indices derived for example from historical studies, recreational fisheries, or other sources. Ideally, these data should be analysed in concert with the data presented in this thesis.

6.6 Application To Fisheries Management

The methods developed in this thesis, and the results of my analyses have some important implications for the management of exploited fish stocks. First, the fisheries management agencies that perform stock assessments are welcome to make their results available through the RAM Legacy database. The “fried egg” plots that appear in Chapter 2 (and originally in Worm et al. (2009)) have gained in popularity and are now used by many agencies as a useful way to document the status of fish stock biomass and exploitation. This information is essential for fisheries managers.

The mandate of many fisheries management agencies has been influenced by international instruments such as the United Nations Convention on the Law of the Sea (UNCLOS, 1982) and the United Nations Fish Stock Agreement (UNFSA, 1995). These international agreements provide a shared set of guidelines towards the elaboration of national policies. Of particular recent interest is the use of target and limit reference points that can guide decision-making.

Scientific trawl survey data similar to those used in Chapters 3, 4, and 5 of this thesis exist in many agencies worldwide. The OBIS format developed in Chapter 3 can be replicated to make survey data publicly available. It is encouraging that the United States NOAA has also decided to make their trawl survey available on OBIS. These surveys are conducted using public funds and it is the mandate of fisheries agencies to make them more widely available. The potential for misuse of these data still exists but it is only through proper documentation (in the form of authoritative metadata) that practitioners can understand the usefulness and limitations of the available information.

The availability of scientific trawl survey data is determined by the internal policies of the fisheries-related agencies that conduct the surveys. Accessing such data to support research on marine populations usually involves communicating with data managers and obtaining a data product suitable for the proposed analyses. Unlike physical and environmental information from the oceans which is often publicly available and is supported by a variety of mature and tested software tools for access, biogeographic data such as that from trawl surveys are usually more private. To increase the availability of trawl survey data, an appropriate format must be devised.

Temporal changes in biological traits can lower the ability of a population to renew itself and can change the level of exploitation that it can withstand over time. Fishing mortality targets should account for the observed range of finite rate of increase documented in Chapter 5. The adaptability of management measures can only be achieved through proper monitoring and the continued availability of fisheries-independent information.

More generally, marine populations have the ability to provide a bountiful harvest if they are kept at productive abundance and biomass levels. It is imperative for fisheries management agencies to properly limit extractive activities to sustainable levels, and to ensure that decision making is based on ecological as well as social and economic factors.

6.7 Directions For Future Research

The RAM Legacy database presented in Chapter continues to be updated and expanded to include stocks from other regions and will be an important source of information for researchers interested in the status of fisheries, the effects of fishing of marine ecosystems, and the elucidation of the fundamental mechanisms of population dynamics. The work that led to Chapter 2 and the release of version 1.0 of the database will hopefully lay the foundations of an important source of information about marine populations that are monitored.

Putting together a comprehensive database of available scientific trawl survey from around the world and making it widely available would be an invaluable resource to fisheries ecologists. The compilation of available trawl surveys performed by Worm et al. (2009) was a good starting point for such an endeavour, but was limited to yearly estimates of abundance and biomass for a subset of species caught. The ability to access tow-level information from different surveys, and the creation of a single, authoritative, citable, and accessible repository containing information from numerous surveys conducted worldwide would represent a great step forward towards the utilisation of these invaluable fisheries-independent sources of information about marine ecosystems.

Further research in the spatial dynamics of groundfish populations should concentrate on examining how environmental conditions such as water temperature influence distribution and abundance. This topic is of interest since predicted changes in thermal regimes associated with global climate change will likely influence the distribution of marine species, and there is a need to untangle the effects of fishing and those of environmental parameters on groundfish spatial dynamics.

Monitoring how individuals grow and mature in exploited populations requires detailed observations that are only available for a very small subset of species present in a marine ecosystem. These detailed observations will also only be available from regions with sufficient sampling resources and scientific expertise, which means that many of the world's marine ecosystems will not be closely monitored. This further highlights the importance of applying the precautionary approach to fisheries management so that the risk of overexploitation is minimised, and to ensure that ecosystem-wide integrity is maintained.

Recent reductions in exploitation rates associated with restrictions on fishing effort, implementation of no-take zones and gear restrictions provide an opportunity to study the response of marine populations and their recovery to more productive abundance and biomass levels. The expected stock recoveries associated with more stringent conservation measures will hopefully guide future fisheries management initiatives, and lead to an improved provision of marine ecosystem services to an ever-increasing human population.

Appendix A

Supporting Information For Chapter 2

A.1 Technical database details

The database is implemented in the Open Source PostgreSQL relational database management system (RDBMS)(PostgreSQL Global Development Group, 2010). RDBMSs form the server back-end to many applications of interest to ecologists, including web-clients and GIS software, and have a number of advantages over spreadsheet or flat text file data compilations. First, housing stock assessments in an RDBMS allows multiple users to concurrently access and extract subsets of data in an efficient and reproducible manner. Second, with the development of Application Programming Interfaces (APIs) that allow analytical software to directly communicate and extract data from the database, a common data environment is established, independent of one's choice of analytical software (e.g., SAS:SAS ACCESS, Matlab: Matlab/Database, R:RDBI/RODBC, Perl:DBI, etc.). Users familiar with Structured Query Language (SQL) can also query the database directly from their analytical software of choice and the same SQL query will extract the same data through each of these applications. Third, data products tailored to specific projects can be generated and stored as dynamic (i.e., continually updated)"views" within the database. These are typically rectangular, spreadsheet-like results of an expansive query of the relevant tables that can be readily read into all commonly-used analytical software. The use of views is advantageous over manipulating spreadsheets or flat text files for importing into a specific analytic software, which runs the risk of losing data integrity (e.g. multiple copies) and becomes impractical with large, non-tabular datasets and multiple users. The static version of the database used for this manuscript (RAM Legacy v1.0 2011) can be obtained from the RAM Legacy website at http://fish.dal.ca.in Microsoft Access and Microsoft Excel formats. The database uses Open DataBase

Connectivity (ODBC) and can be accessed from a variety of ODBC-capable software including MS Access, MS Excel and R.

A.2 QAQC process

This process consisted of creating a QA/QC summary document for each assessment, containing summary details of the stock, a selection of biometrics and ratios for comparison (e.g. current status relative to BRP), and time series plots of the biomass, recruitment, and exploitation trajectories. QA/QC documents were then returned to assessment recorders and an electronic trail of subsequent correspondence was captured using a bug tracking system. Recorders were responsible for checking and, where necessary, correcting their QA/QC documents, after which all corrections were transmitted back to the operational database and a quality controlled flag was inserted to signify the assessment had passed the check. The database contents required further modifications when various analyses identified unforeseen errors.

A.3 Schaefer surplus production model

For those assessments that did not contain MSY reference points, but did include total catch ($TC_{i,s}\ i \in 1, ..., n_s$) and total biomass ($TB_{i,s}\ i \in 1, ..., n_s$) time series data, I used a Schaefer surplus production model to estimate total biomass and exploitation rate at MSY (TB_{msy_s} and U_{msy_s}, respectively). Surplus production of stock s in year t, $P_{s,t}$, is a commonly used measure of stock productivity, representing the amount of catch that can be taken while maintaining the biomass at a constant size, and can be calculated as:

$$P_{s,t} = TB_{s,t+1} - TB_{s,t} + TC_{s,t} \tag{A.1}$$

where,

$TB_{s,t}$ is the total biomass of stock s in year t

$TC_{s,t}$ is the total catch of stock s in year t

I fit a Schaefer surplus-production model, which is based on a logistic model of population growth to the catch and total biomass time series data. The predicted surplus production in each year in the Schaefer model is given by:

$$\hat{P_{s,t}} = \frac{4mTB_{s,t}}{K} - 4m\left(\frac{TB_{s,t}}{K}\right)^2 \tag{A.2}$$

where,

m is the maximum sustainable yield, equal to $rK/4$ (r is the maximum intrinsic population growth rate)

K is the carrying capacity or equilibrium total biomass in the absence of fishing (Hilborn and Walters, 1992)

I estimated the model parameters (m and K) using maximum likelihood in AD Model Builder (ADMB Project, 2009) assuming that the residuals $\epsilon_{s,t} = P_{s,t} - \hat{P_{s,t}}$ were normally distributed. For the Schaefer model, B_{msy} is simply $0.5K$, and the harvest rate that results in maximum sustainable yield, U_{msy} , is m/B_{msy}. For model fitting, the carrying capacity parameter K was constrained to be less than twice the maximum observed total biomass.Sensitivity to this assumption was conducted using an upper bound on K of five times the maximum observed total biomass. Note that the exploitation rate defined here (U) is related to the more widely used fishing mortality (F) through .

I also tested the more flexible Pella-Tomlinson surplus production model (Pella and Tomlinson, 1968) which allows for an asymmetric production function where MSY can occur at a wider range of relative biomass. Pella-Tomlinson models provided a better fit to data from individual stocks, which is to be expected given their greater flexibility and the inclusion of an additional parameter, however they performed no better in cross-validation than did the Schaefer model.

Surplus production model fits to individual stocks were assessed visually by the authors to ensure that no biologically implausible estimates were included in the analyses. The acceptance or rejection of a given fit relied on a variety of criteria including convergence diagnostics, presence of appropriate contrast in the available data and appropriate distribution of the model residuals.

The influence of setting different upper bounds on the K parameter of the Schaefer model were investigated by using two different constraints when fitting to available time-series. I evaluated the changes brought about by allowing the upper bound for K to be five times the maximum observed total biomass.

A.4 Reference points

To evaluate stock status, I single out stocks for which both a biomass BRP and an exploitation BRP are available. Of the 214 stocks presented in Fig. 2.4, 110 and 104 of the biomass reference points and 82 and 132 of the exploitation reference points come from assessments and from surplus production model fits, respectively. To identify potential biases arising from using BRPs derived from surplus production models I computed a contingency table of status classification for stocks that have both assessment- and Schaefer-derived BRPs (Table A.1). Surplus production models correctly classified ratios of current biomass to BRPs in 76% of cases (for 58 of 76 assessments) and 64% of cases for exploitation BRPs (for 28 of 44 assessments). The BRP estimates obtained from the Schaefer model were also biased (Fig. A.2).

Table A.1 and Fig. A.2 present their information for both of the upper bound settings for the Schaefer K parameter.

A.5 Tables

Table A.1: Contingency tables of stock status classification for biomass and exploitation reference points obtained from assessments and those derived from surplus production models.

	Schaefer $\frac{B}{B_{msy}} < 1$	Schaefer $\frac{B}{B_{msy}} >= 1$
$\frac{B}{B_{msy}} < 1$	29	6
$\frac{B}{B_{msy}} >= 1$	12	31

	Schaefer $\frac{U}{U_{msy}} < 1$	Schaefer $\frac{U}{U_{msy}} >= 1$
$\frac{U}{U_{msy}} < 1$	20	14
$\frac{U}{U_{msy}} >= 1$	2	8

A.6 Figures

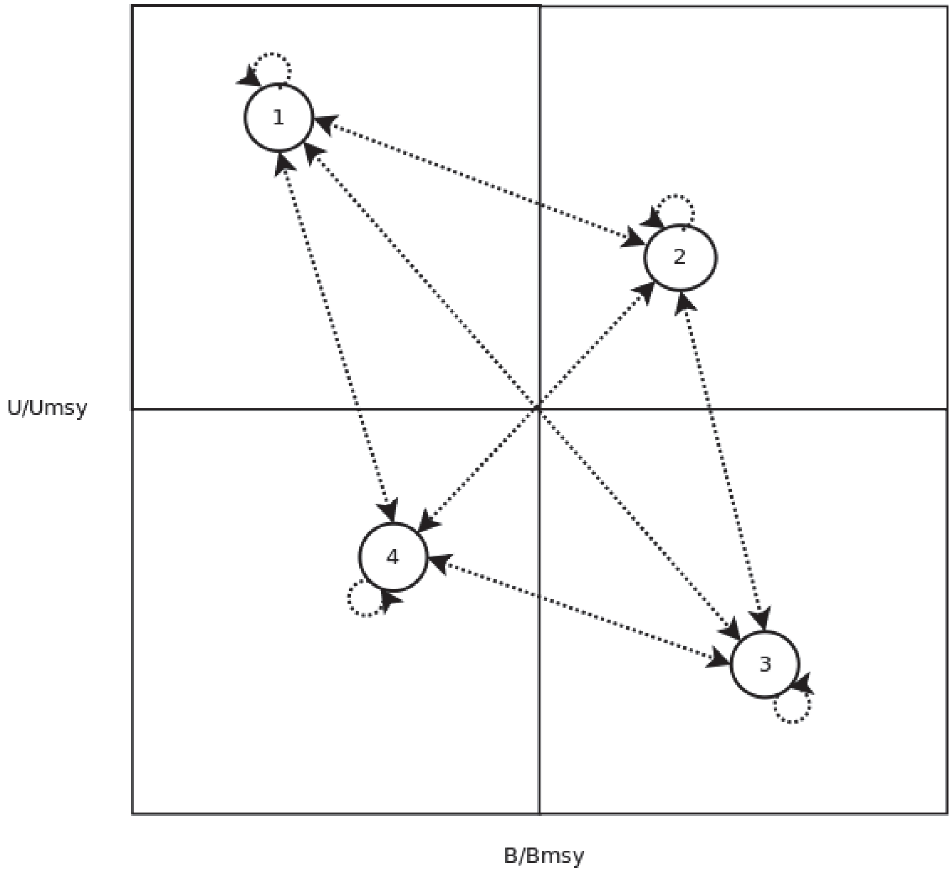

Figure A.1: The four quadrants (numbered 1 to 4) and 16 possible state transitions (arrows linking the states) in the U/U_{msy} vs. B/B_{msy} space.

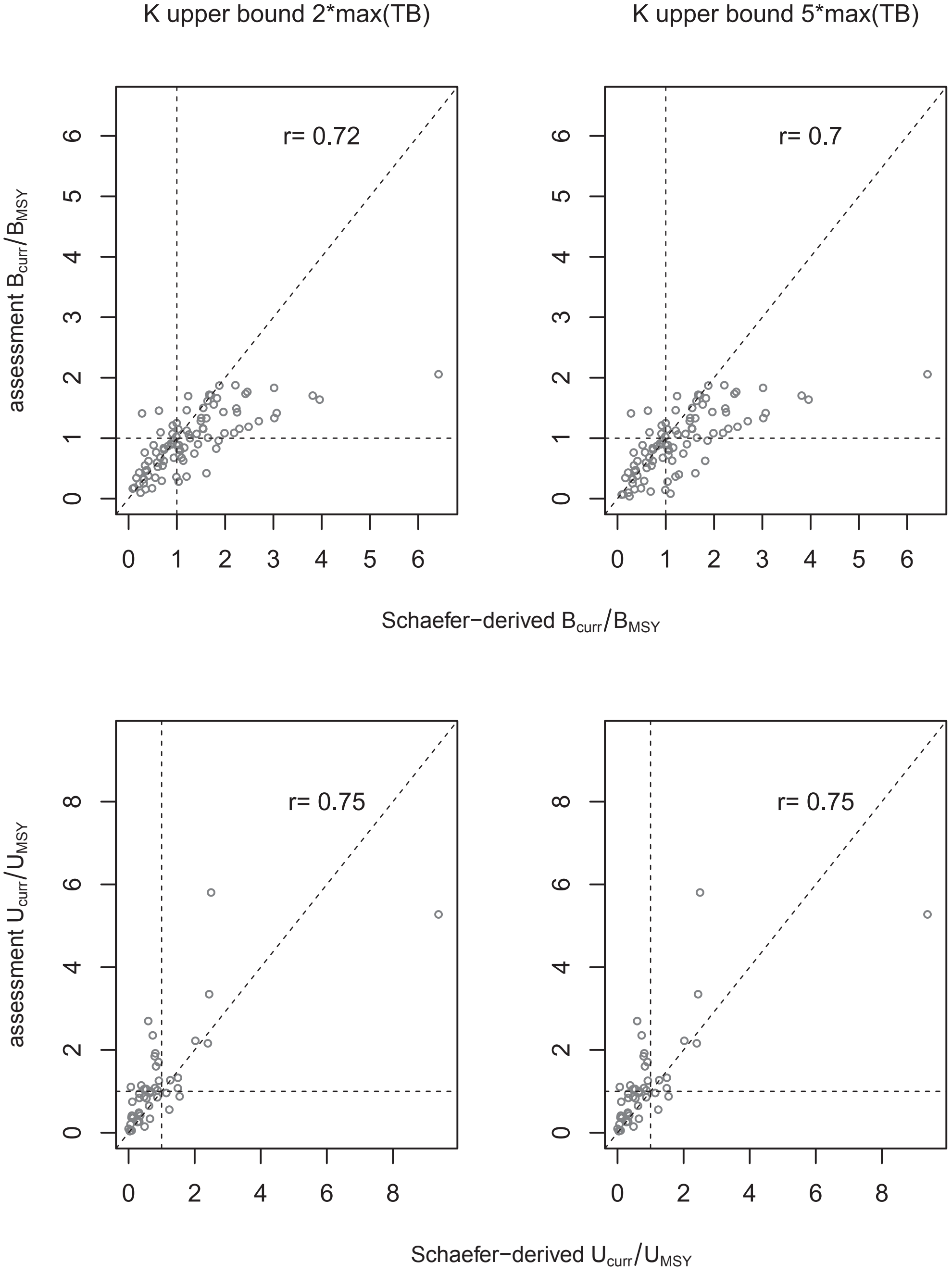

Figure A.2: B_{msy} and U_{msy} vs. B_{msy} and U_{msy} obtained from Schaefer model under two different constraints for the upper bound of the Schaefer K parameter.

Figure A.3: Taxonomic dendrogram of the RAM Legacy Stock Assessment Database.

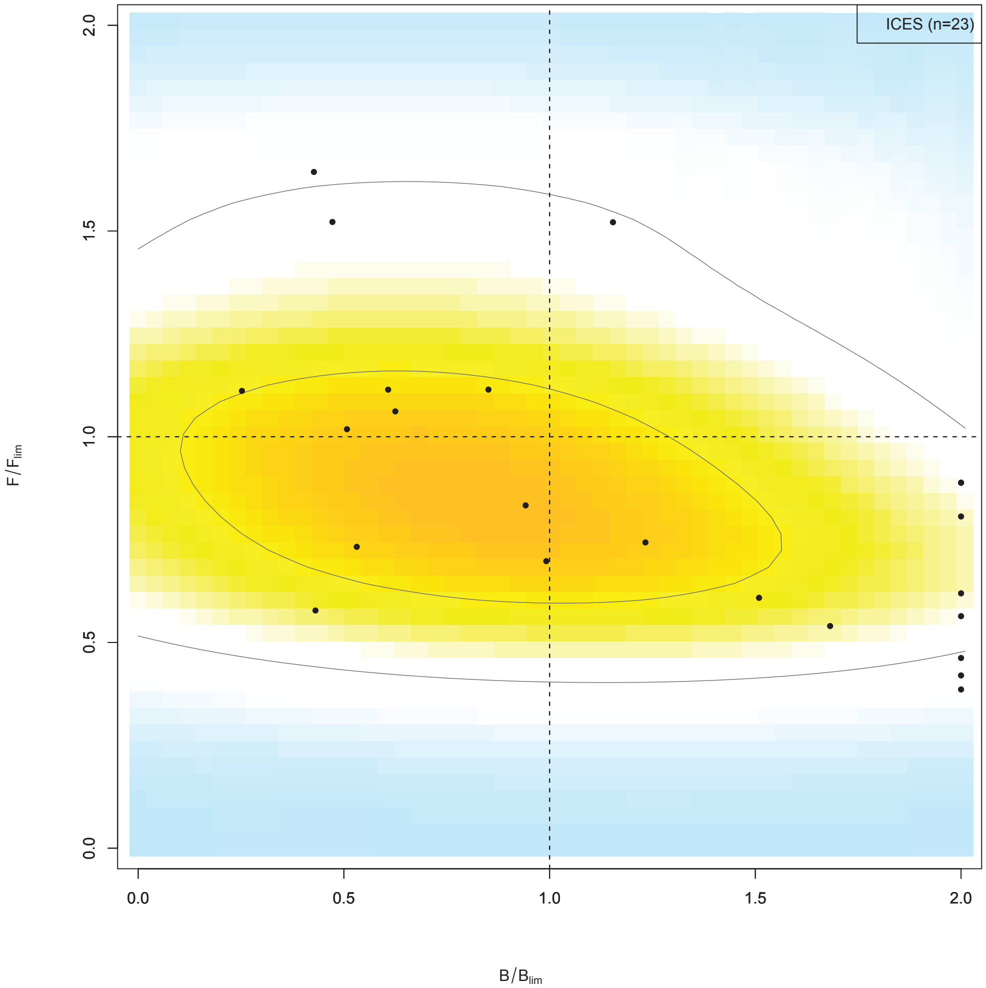

Figure A.4: Ratio of current biomass and fishing mortality to limit biomass and fishing mortality reference points (B_{lim} and F_{lim}) for European stocks managed by ICES.

Appendix B

Supporting Information For Chapter 4

B.1 Figures

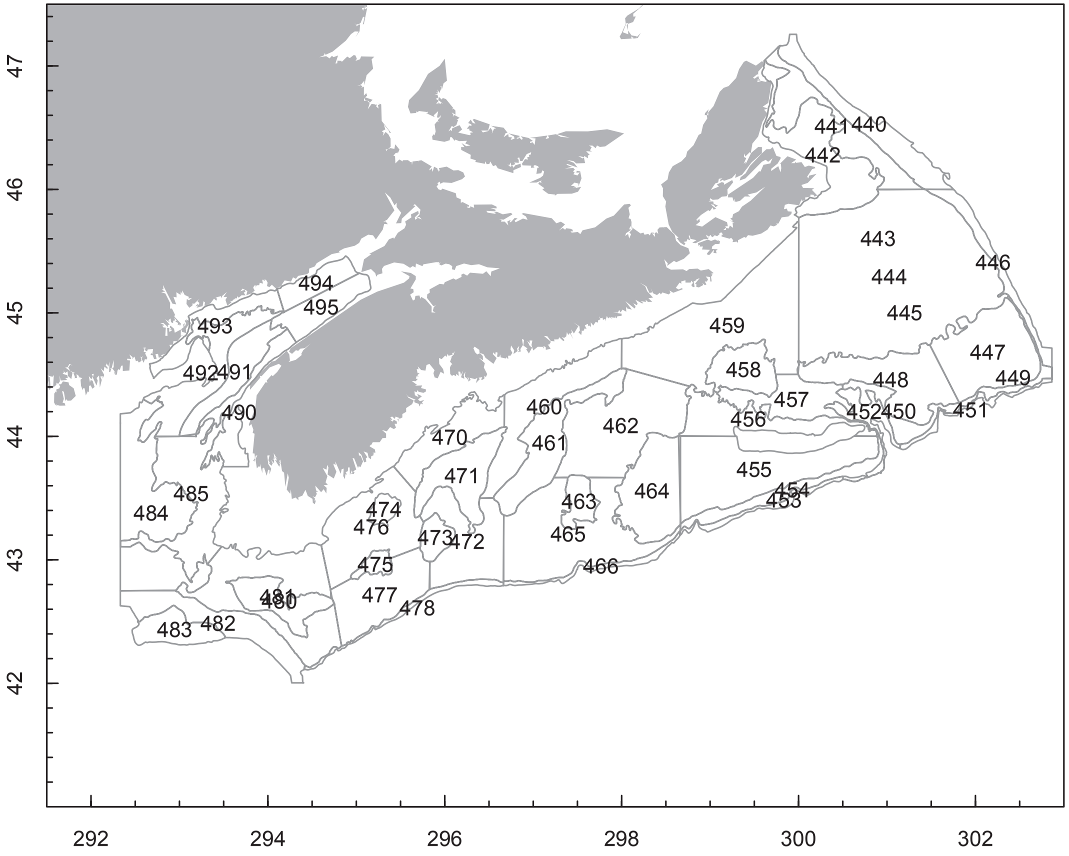

Figure B.1: Map of DFO summer strata.

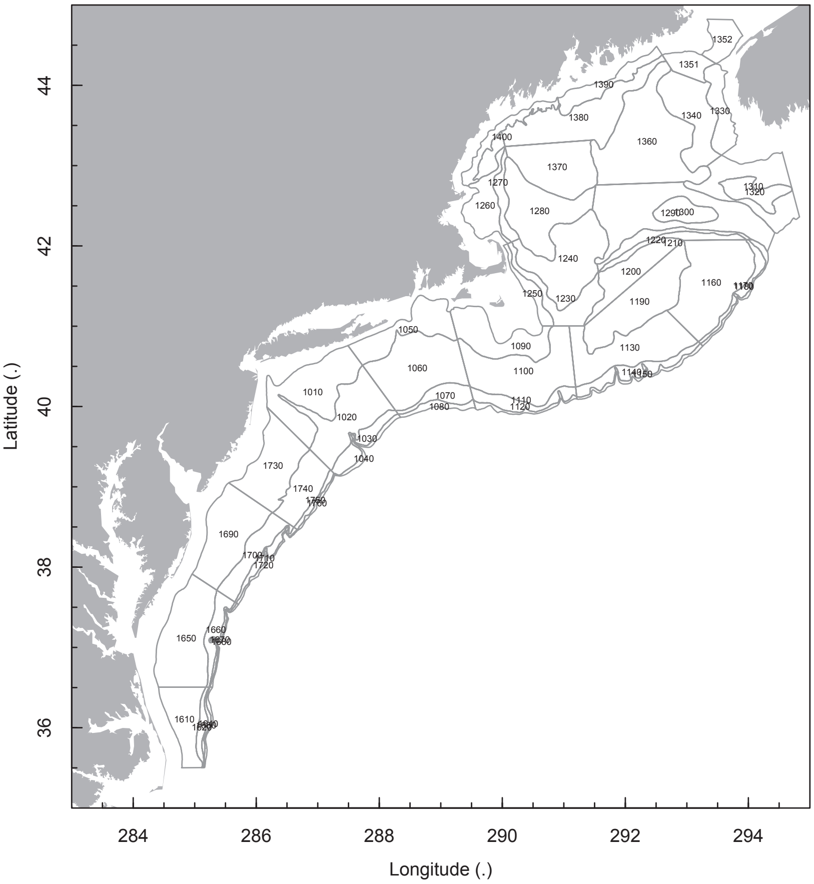

Figure B.2: Map of NMFS offshore strata.

Appendix C

Supporting Information For Chapter 5

C.1 Tables

Table C.1: Parameter estimates of decadal growth model for DFO cod.

survey	species	parameter name	estimate	std. err.
DFO	Atlantic cod	α	11.55	1.47
		β	8.27	3.31
		α^{1960s}	0.06	0.50
		α^{1970s}	3.02	0.40
		α^{1980s}	0.40	0.40
		α^{1990s}	3.24	0.55
		α^{2000s}	0.11	0.97
		α^{m}	15.77	0.51
		β^{1960s}	0.54	0.15
		β^{1970s}	0.31	0.11
		β^{1980s}	0.07	0.12
		β^{1990s}	-1.55	0.18
		β^{2000s}	-0.53	0.41
		β^{m}	-1.75	0.09
		$\alpha^{1960s,m}$	0.80	0.69
		$\alpha^{1970s,m}$	-6.54	0.58
		$\alpha^{1980s,m}$	1.98	0.63
		$\alpha^{1990s,m}$	-4.98	0.85
		$\alpha^{2000s,m}$	-4.89	1.59
		$\beta^{1960s,m}$	-0.51	0.16
		$\beta^{1970s,m}$	0.65	0.13
		$\beta^{1980s,m}$	-1.28	0.14
		$\beta^{1990s,m}$	0.57	0.22
		$\beta^{2000s,m}$	-0.25	0.51

Table C.2: Parameter estimates of decadal growth model for DFO haddock.

survey	species	parameter name	estimate	std. err.
DFO	Haddock	α	15.57	1.08
		β	6.20	0.13
		α^{1960s}	-0.10	0.25
		α^{1970s}	-0.73	0.24
		α^{1980s}	-2.53	0.23
		α^{1990s}	-0.93	0.29
		α^{2000s}	-0.97	0.45
		α^{m}	14.00	0.33
		β^{1960s}	0.37	0.08
		β^{1970s}	1.71	0.08
		β^{1980s}	0.77	0.08
		β^{1990s}	0.05	0.12
		β^{2000s}	-0.99	0.22
		β^{m}	-2.34	0.08
		$\alpha^{1960s,m}$	3.67	0.40
		$\alpha^{1970s,m}$	2.22	0.36
		$\alpha^{1980s,m}$	7.62	0.38
		$\alpha^{1990s,m}$	-1.53	0.42
		$\alpha^{2000s,m}$	-3.92	0.63
		$\beta^{1960s,m}$	-0.79	0.10
		$\beta^{1970s,m}$	-1.40	0.09
		$\beta^{1980s,m}$	-2.66	0.09
		$\beta^{1990s,m}$	-1.30	0.13
		$\beta^{2000s,m}$	-0.17	0.23

Table C.3: Parameter estimates of decadal growth model for NMFS cod.

survey	species	parameter name	estimate	std. err.
NMFS	Atlantic cod	α	26.62	2.27
		β	8.32	0.26
		α^{1970s}	-6.09	0.57
		α^{1980s}	-11.60	0.61
		α^{1990s}	-12.05	0.73
		α^{2000s}	-11.23	0.66
		α^{m}	16.78	0.63
		β^{1970s}	1.82	0.21
		β^{1980s}	4.03	0.25
		β^{1990s}	3.63	0.32
		β^{2000s}	2.46	0.28
		β^{m}	-1.96	0.20
		$\alpha^{1970s,m}$	-4.21	0.66
		$\alpha^{1980s,m}$	-3.02	0.74
		$\alpha^{1990s,m}$	-0.34	0.87
		$\alpha^{2000s,m}$	-1.29	0.86
		$\beta^{1970s,m}$	0.41	0.21
		$\beta^{1980s,m}$	-0.93	0.27
		$\beta^{1990s,m}$	-1.52	0.34
		$\beta^{2000s,m}$	-1.07	0.31

Table C.4: Parameter estimates of decadal growth model for NMFS haddock.

survey	species	parameter name	estimate	std. err.
NMFS	Haddock	α	27.67	1.83
		β	5.31	0.16
		α^{1970s}	-6.79	0.28
		α^{1980s}	-6.88	0.32
		α^{1990s}	-8.30	0.31
		α^{2000s}	-7.92	0.30
		α^{m}	17.54	0.31
		β^{1970s}	3.31	0.12
		β^{1980s}	2.92	0.17
		β^{1990s}	2.36	0.15
		β^{2000s}	1.56	0.14
		β^{m}	-2.83	0.11
		$\alpha^{1970s,m}$	-2.28	0.33
		$\alpha^{1980s,m}$	-4.45	0.41
		$\alpha^{1990s,m}$	2.47	0.39
		$\alpha^{2000s,m}$	-5.34	0.39
		$\beta^{1970s,m}$	-0.73	0.12
		$\beta^{1980s,m}$	-0.20	0.18
		$\beta^{1990s,m}$	-2.00	0.16
		$\beta^{2000s,m}$	-0.46	0.15

Table C.5: Parameter estimates of decadal maturity model for DFO cod.

survey	species	parameter name	estimate
DFO	Atlantic cod	α	-4.83
		β	1.05
		α^{1960s}	-0.73
		α^{1970s}	-0.59
		α^{1980s}	-0.98
		α^{1990s}	-0.33
		α^{2000s}	-0.42
		β^{1960s}	0.60
		β^{1970s}	0.88
		β^{1980s}	0.78
		β^{1990s}	0.72
		β^{2000s}	0.94

Table C.6: Parameter estimates of decadal maturity model for DFO haddock.

survey	species	parameter name	estimate
DFO	Haddock	α	-6.21
		β	1.47
		α^{1960s}	0.84
		α^{1970s}	-0.24
		α^{1980s}	-0.07
		α^{1990s}	2.97
		α^{2000s}	1.93
		β^{1960s}	0.03
		β^{1970s}	0.80
		β^{1980s}	0.51
		β^{1990s}	-0.04
		β^{2000s}	0.38

Table C.7: Parameter estimates of decadal maturity model for NMFS cod.

survey	species	parameter name	estimate
NMFS	Atlantic cod	α	-3.70
		β	1.39
		α^{1970s}	0.25
		α^{1980s}	0.42
		α^{1990s}	-0.30
		α^{2000s}	0.02
		β^{1970s}	-0.08
		β^{1980s}	0.22
		β^{1990s}	0.59
		β^{2000s}	0.23

Table C.8: Parameter estimates of decadal maturity model for NMFS haddock.

survey	species	parameter name	estimate
NMFS	Haddock	α	-3.83
		β	1.51
		α^{1970s}	0.70
		α^{1980s}	0.62
		α^{1990s}	0.59
		α^{2000s}	0.62
		β^{1970s}	0.09
		β^{1980s}	0.50
		β^{1990s}	0.31
		β^{2000s}	0.15

C.2 Figures

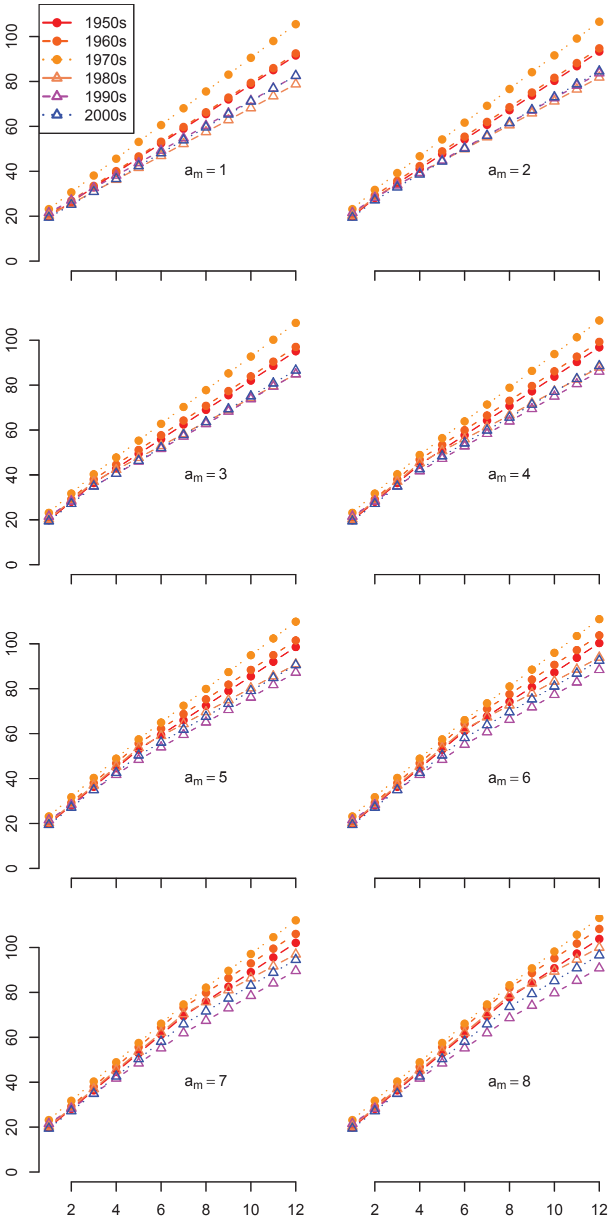

Figure C.1: Predicted lengths of Atlantic cod from the DFO survey for each decade and for different ages-at-maturity.

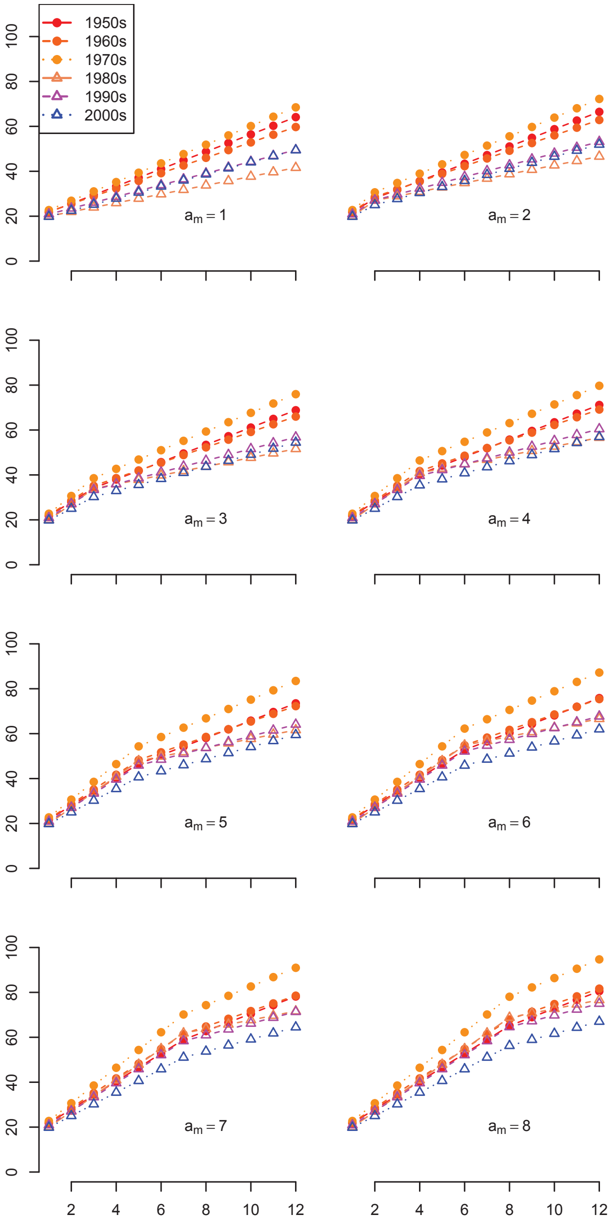

Figure C.2: Predicted lengths of haddock from the DFO survey for each decade and for different ages-at-maturity.

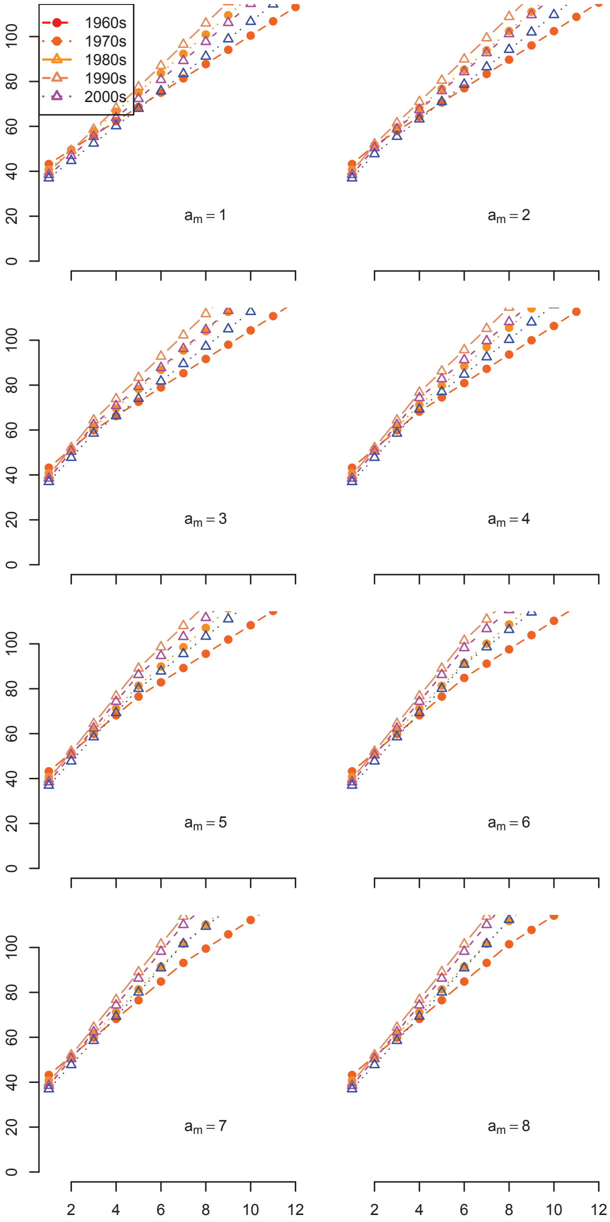

Figure C.3: Predicted lengths of Atlantic cod from the NMFS survey for each decade and for different ages-at-maturity.

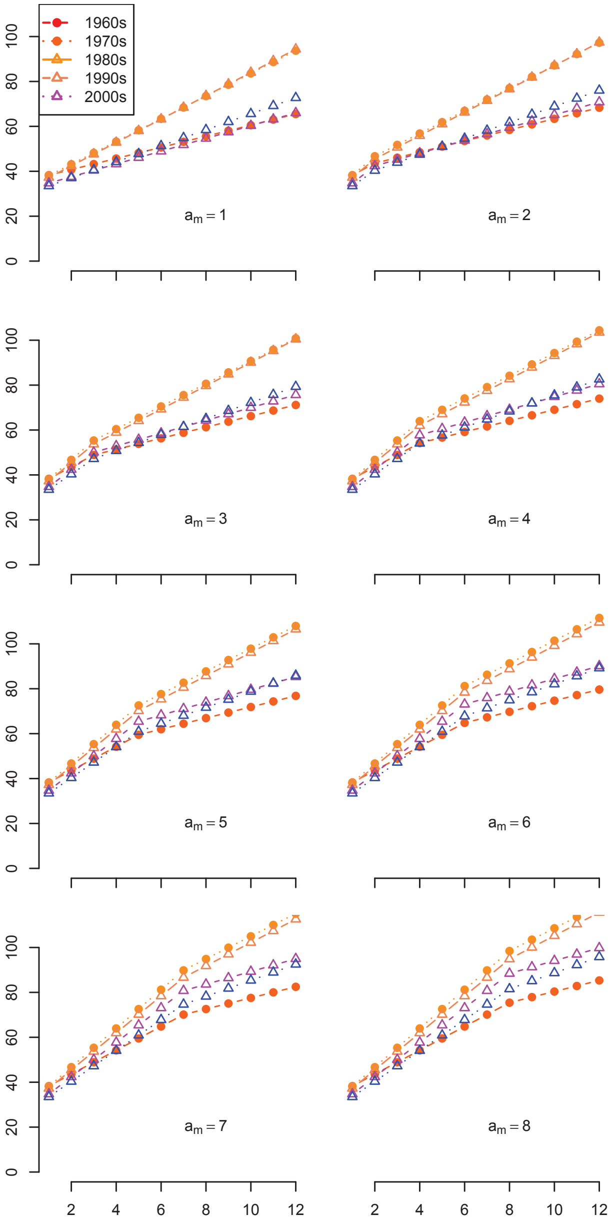

Figure C.4: Predicted lengths of haddock from the NMFS survey for each decade and for different ages-at-maturity.

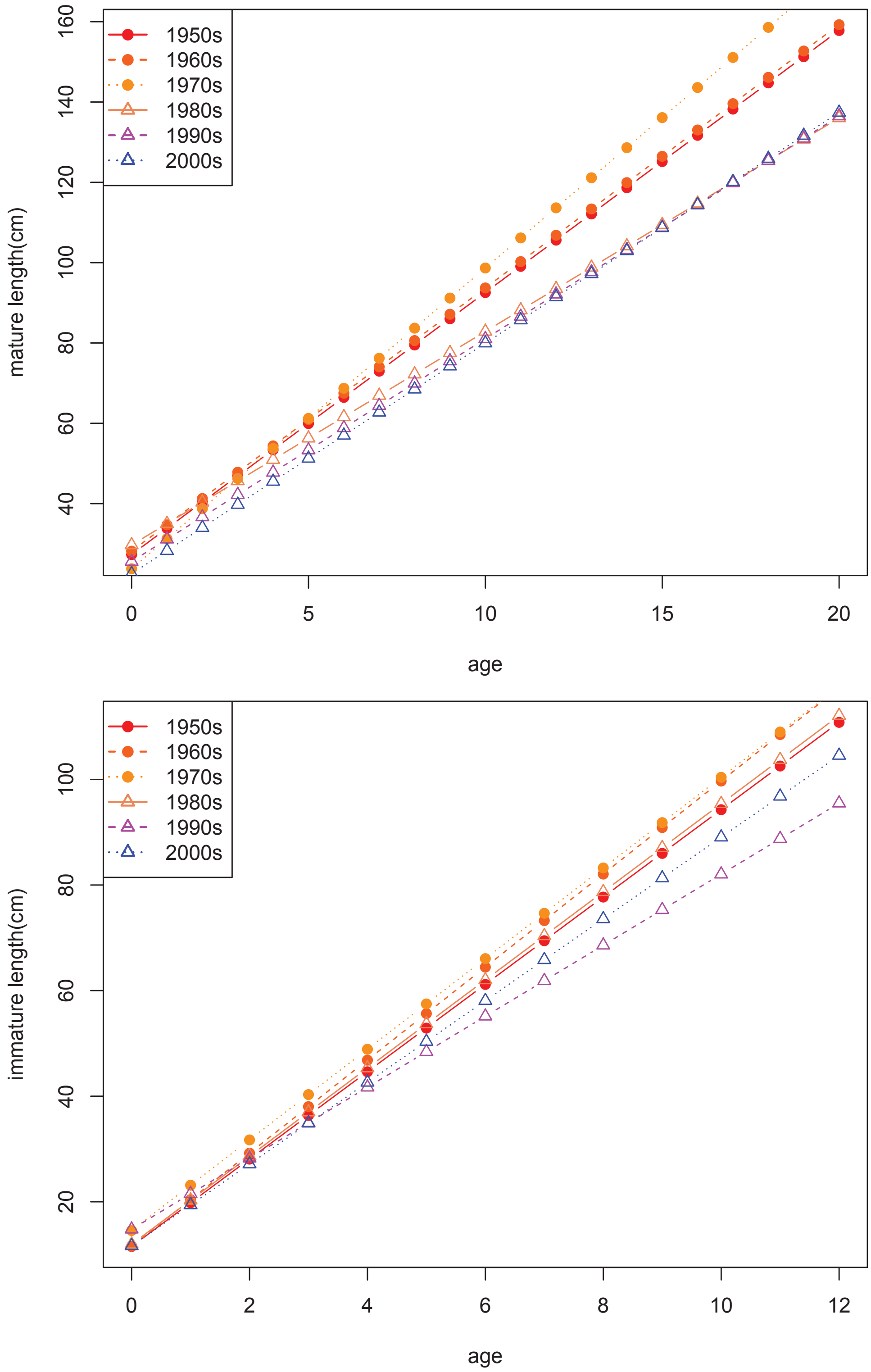

Figure C.5: Decadal changes in growth of Atlantic cod from the DFO survey.

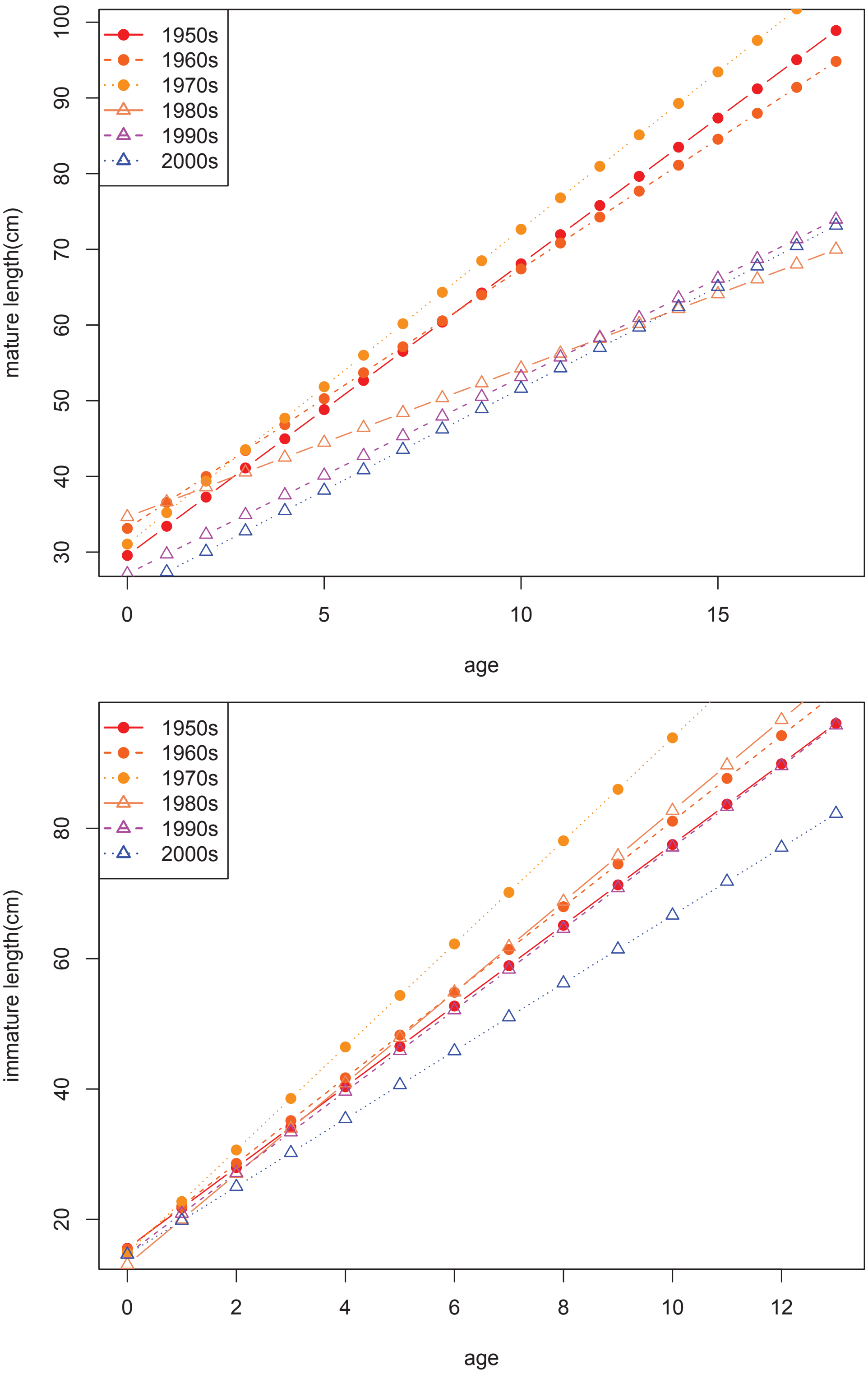

Figure C.6: Decadal changes in growth of haddock from the DFO survey.

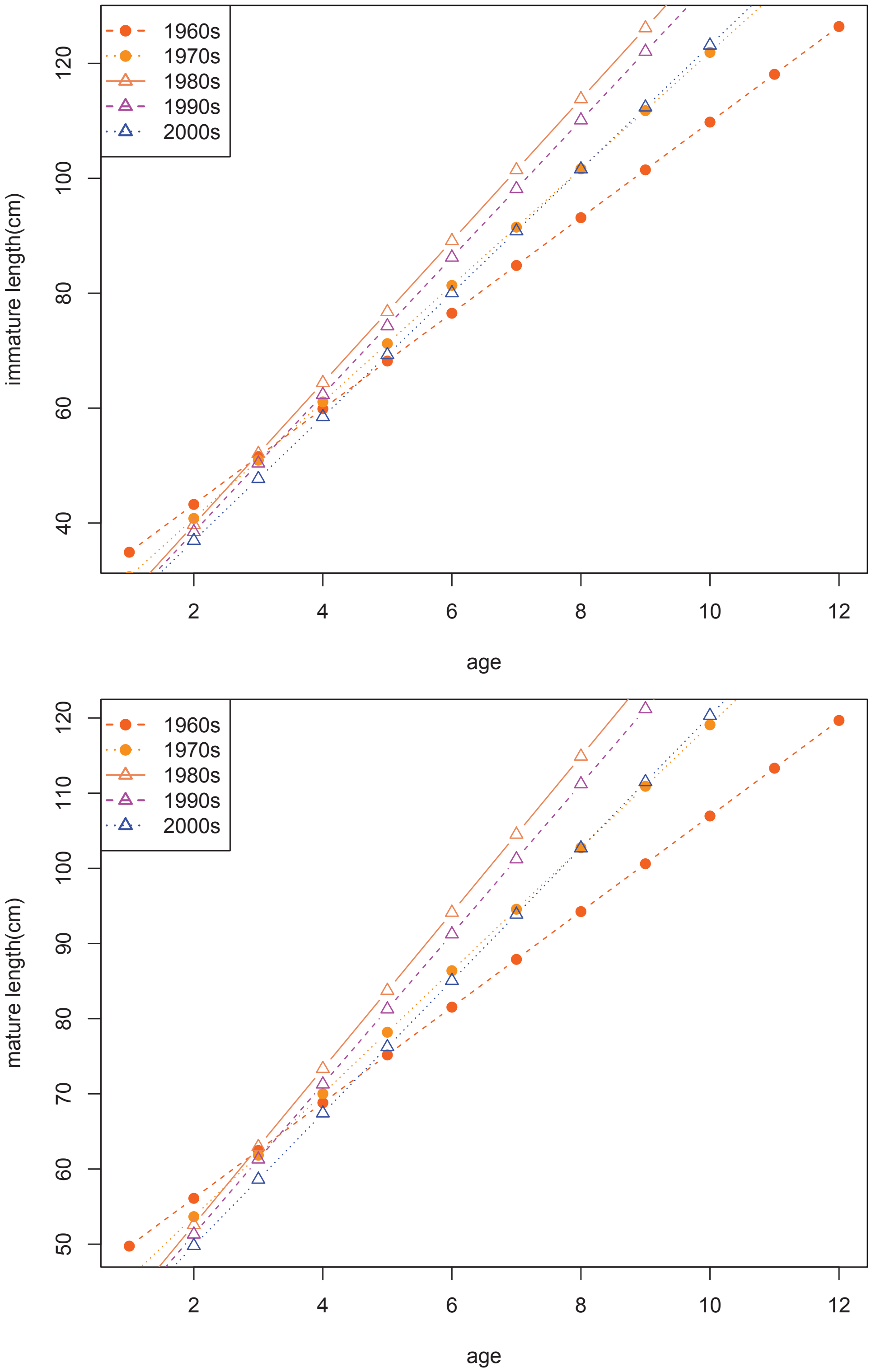

Figure C.7: Decadal changes in growth of Atlantic cod from the NMFS survey.

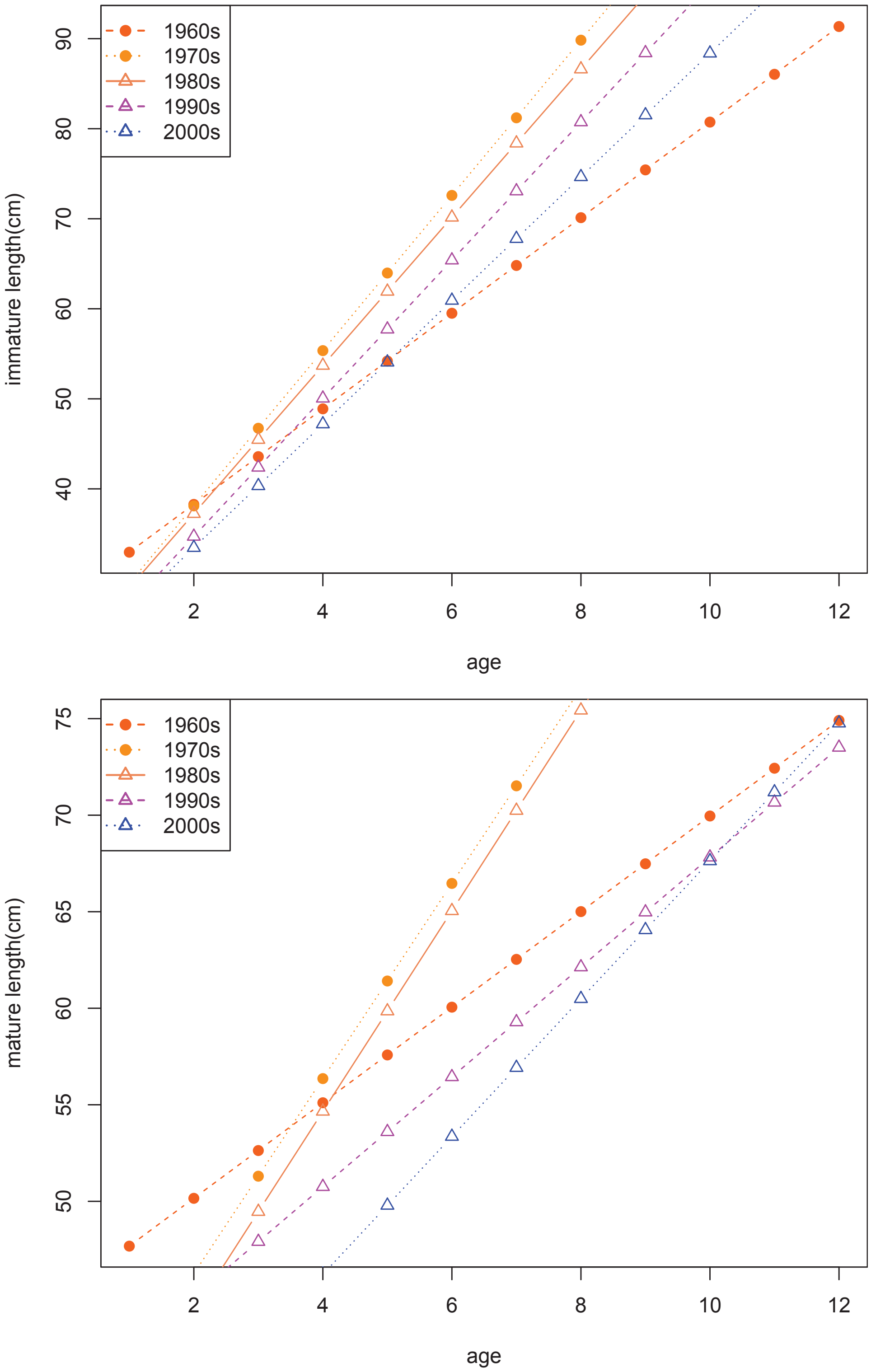

Figure C.8: Decadal changes in growth of haddock from the NMFS survey.

Appendix D

Description Of Electronic Supplement

The Electronic Supplement associated with this thesis contains Tables and Figures associated with the analyses conducted in Chapter 4. It consists of a total of 31 Tables and 118 Figures. The tables contain parameter estimate values for the different models introduced in the Chapter. In addition, maps of distribution, abundance and stratum-based parameter estimates are provided for 24 species from Fisheries and Oceans Canada (DFO) surveys and 22 species from the National Marine Fisheries Service (NMFS) surveys.

The Electronic Supplement is available from DalSpace (`http://dalspace.library.dal.ca`).

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