ECOLOGICAL INFERENCE FROM VARIABLE RECRUITMENT DATA

by

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This thesis is dedicated to Corinne, who brings each day anew, and to the memory of Ransom A. Myers

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Abstract

To understand the processes affecting the abundance of wild populations is a fundamental goal of ecology and a prerequisite for the management of living resources. Variable abundance, however, makes the investigation of ecological processes challenging. Recruitment, the process whereby new individuals enter a given stage of a fish population, is a highly variable entity. I have confronted this issue by developing methodologies specifically designed to account for, and ecologically interpret, patterns of variability in recruitment.

To provide the necessary context, Chapter 2 begins with a review of the history of recruitment science. I focus on the major achievements as well as present limitations, particularly regarding environmental drivers. Approaches that include explicit environmental information are contrasted with time-varying parameter techniques.

In Chapter 3, I ask what patterns of variability in pre-recruit survival can tell us about the strength of density-dependent mortality. I provide methods to investigate the presence of density-dependent mortality where this has previously been hindered by highly variable data. Stochastic density-independent variability is found to be attenuated via density dependence.

Sources of recruitment variability are further partitioned in Chapter 4. Using time-varying parameter techniques, significant temporal variation in the annual reproductive rate is found to have occurred in many Atlantic cod populations. Multivariate state space models suggest that populations in close proximity typically have a shared response to environmental change whereas marked differences occur across latitude.

Hypotheses that could result in consistent changes in productivity of cod populations are tested in Chapter 5. I focus on a meta-analytical investigation of potential interactions between Atlantic cod and small pelagic species, testing aspects of the *cultivation-depensation* hypothesis. The findings suggest that predation or competition by herring and mackerel on egg and larval cod could delay recovery of depleted cod populations.

Chapter 6 concludes with a critical reflection on: the suitability of the theories employed, the underlying assumptions of the empirical approaches, and the quality of the data used in my thesis. Application of ecological insights to fisheries management is critically evaluated. I then propose future work on recruitment processes based on methods presented herein.

List of Abbreviations and Symbols Used

This list contains common symbols and their definitions. Some symbols are used more than once to represent different entities. Where this occurs, explicit definitions are provided in the text.

a	Instantaneous linear predation rate per predator
$\tilde{\alpha}$	The maximum lifetime reproductive rate, which is the slope at the origin of the stock-recruit relationship standardized by the spawner per recruit at zero fishing mortality
α	Slope at the origin of the stock-recruit relationship
β	Compensatory density-dependent mortality rate in solved Ricker formulation
e	Mathematical constant, base of the exponential function
f	A function: often used for a probability density function
F	Individual fecundity in number of eggs per female spawner
γ	Predation rate in solved Ricker formulation
I_p	Identity matrix of dimension p
K	Carrying capacity of the total population in numbers or biomass
$\otimes$	Kronecker product of matrices
L	Likelihood
l	Log-likelihood
ln	Logarithm to the base e, referred to as the natural logarithm
μ	Population mean - population in the statistical sense
N	Abundance in numbers
$\mathcal{N}$	Gaussian distribution
p	Instantaneous density-dependent mortality rate
P	Predator abundance in numbers or biomass
q	Instantaneous density-independent mortality rate

r	Intrinsic rate of population growth
R	Recruitment: abundance in numbers or biomass at a given, typically young, age
σ	Population standard deviation - population in the statistical sense
SPR	Spawner per recruit: weight of spawners produced per recruit, typically in kilograms
S	Spawner abundance in numbers or biomass
τ	Age at recruitment in years
θ	A typically unknown set of parameters
$\sim$	The distribution of a random variable, read “is distributed”
t	Time in context-dependent units

Glossary

Allee effects

An effect whereby the per-capita growth rate of a population decreases with decreasing abundance at very low abundances. Hypothesized causes include mate-finding and forms of predation that make individuals more vulnerable to predation at low abundances.

carrying capacity

The maximum biomass of a population that an environmentally constant area can support for an indefinite period of time.

coefficient of variation

The ratio of the standard deviation to the absolute value of the mean. Used as an intuitive measure of dispersion.

cohort

A subset of a population that were spawned or hatched in a given time period - typically a year for temperate species.

compensatory mortality

Mortality that occurs in response to changes in density. The compensatory mortality rate increases with increased abunance.

density dependence

A process affecting individuals within a population that changes in accordance with the density of individuals in space or time.

density independence

A process affecting individuals within a population that behaves independent of the density of individuals in space or time.

depensation

A decrease in the survival of young at low levels of the spawning population.

difference equations

Discrete time recursive relationships of the form: $x_{t+1} = f(x_t)$.

differential equations

An equation that describes how the derivatives of an unknown (variable) change as a function of the unknown and/or other unknowns, e.g. $\frac{dy}{dx} = f(x, y)$

growth overfishing

Fishing a population at a rate above that which allows from maximum productivity e.g. fishing individuals that are too young.

host

An organism that harbors a parasite or parasitoid, typically the organism unwittingly provides shelter and nourishment to its own detriment.

maximum reproductive rate

The maximum number of recruits produced per spawner at low population density; in the absence of density-dependent mortality.

overcompensation

A decline in productivity at high abundance. Typically in Ricker or Schaefer recruitment where density-dependent processes over-compensate density-indendepent processes at high abundances.

parasitoid

Typically a Hymenopteran or Dipetran insect that deposits larvae on or in a host organism on which the developing larvae feeds, typically resulting in the death of the host.

pre-recruit

The life-stage before recruitment, encompassing all stages from egg, larvae, juvenile up to recruit.

recruitment

The process whereby new fish enter the portion of the population vulnerable to fishing from earlier life history stages. Also used for the number of recruits in a given year.

recruitment overfishing

Fishing a population down to a point at which its ability to replace itself via reproduction is impeded.

state

Unobserved latent variable that are assumed to be the true as opposed to observed state of the system at a given time. The states evolve through time according to an assumed dynamic and stochastic forcing.

stock

A management unit of a population. Where the stock consists of more than one population or a given population straddles two or more stocks, the terms ‘population’ and ‘stock’ are not equivalent. They are, however, often used synonymously throughout the thesis.

trophodynamic

The dynamics of metabolism and nutrition.

variability

The state of being variable; a measure of the extent of differences or spread in a set of data points.

year-class

A subset of a population that were spawned or hatched in a given year.

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Chapter 1

INTRODUCTION

1.1 General Introduction

Population renewal via the influx of young individuals is a core focus of population ecology and a primary concern of natural resource management. Despite its central role and a near-century of fruitful investigation, much uncertainty remains in our understanding of sources of mortality resulting in early life history dynamics (Myers, 1998, 2001; Houde, 2008a). Fish species in the marine environment typify this assertion. There, marked variability is often the most striking feature of the data. For example, the *coefficient of variation* of raw recruitment typically occurs around 50% and often at as high as 150% (Myers, 2002). Such variability may hinder the investigation of ecological processes, such as: density-dependent and density-independent mortality, productivity and species interactions. A sole focus on the mean response may ignore patterns present in the variability. Testing the connection between patterns of variability in abundance and the aforementioned ecological processes may provide a rich framework of investigation. As such, it is argued that questions of the mean biological response are inherently related to questions of the variability at multiple levels. Phrased differently, the key question of my thesis was:

What can patterns in the variability of recruitment tell us about the underlying ecological processes involved?

The principal objective of my doctoral research was to investigate the structure of recruitment variability and how that relates to ecological processes in temperate marine fish populations. The approach is to test theory-driven hypotheses with tailored statistical methodologies, which allow us to analyze multiple datasets simultaneously. Methods that I developed and employed include investigations of changes in variance and variance partitioning methods such as state space and hierarchical models. Much emphasis is placed on extended recruitment relationships here defined as stock recruitment relationships derived to include additional environmental variables. By combining the estimation of these extended relationships across multiple populations, optimal use is made of the data, which may be highly variable for any given population. In this regard, global compilations of *stock* assessments such as the original Myers stock-recruitment database (Myers *et al.*, 1995b) and the new RAM Legacy assessment database (Ricard *et al.*, in review) are used extensively throughout. Note that a critique of this approach are presented in the Chapter 6.

A brief introduction to each chapter with their inter-connectivity highlighted follows.

1.1.1 Chapter Structure

An overview of recruitment science

Chapter 2 provides a broad, essay-style overview of *recruitment science* (Cushing, 1996). While other such comprehensive reviews exist (Larkin, 1989; Frank and Leggett, 1994), the purpose of this chapter was to trace the chronological development of the subject, particularly with regard to additional environmental drivers (higher dimensions), and critique accordingly. Studies of recruitment flourished mid-way through the 20th century (Ricker, 1954; Beverton and Holt, 1957; Cushing, 1971, 1975) partly in response to remarkable population collapses, which could not be attributed solely to growth overfishing where fish are removed when they are too small. What followed was a period of intense scientific endeavor and progress where recruitment science became a rich source of development for population ecology as a whole. The science relating spawner biomass to recruits may be considered mature, as indicated by the widespread implementation in applied management. Yet recruits and spawners exist in a dynamic system, where our ability to understand the effect of changing conditions on recruitment is severely limited. The need to extend investigations of hypothesized environmental drivers meta-analytically is therefore stressed. I conclude that time-varying parameter techniques are likely to provide a most useful framework that integrates across many dimensions of tacit change, i.e. there are many possible sources of changes in productivity (physical, biological, and chemical environment, life history etc.) but we don’t explicitly reference them, rather, we allow for a time-varying term that estimates the net effect on productivity across all unmentioned dimensions.

Non-constant recruitment variability

Variable abundance makes the investigation of population regulation challenging. An overlooked aspect in understanding how populations are regulated is the possibility that the pattern of variability - its strength as a function of population size - may be more than 'noise', thus revealing much about the characteristics of population regulation. In chapter 3, I show that patterns in *pre-recruit* survival variability provide consistent evidence of regulation through density. Using a global compilation of stock and recruitment data, the relationship between the variability in survival and population abundance is examined. Observed patterns are consistent with models in which density dependence enters after the larval stage. The findings are compatible with simple forms of density dependence. The model predictions explain why populations with strong regulation may experience large increases in variability at low densities. The inverse relationship between survival variability and the strength of density dependence is discussed in relation to fisheries management and recovery of depleted populations.

Partitioning recruitment variability

While the investigation of any one hypothesized driver of recruitment may yield important insights, the simultaneous omission of others renders such approaches of limited holistic value. The approach used in Chapter 4 partitions the variance in recruitment further. We temporarily move from the question of *why pre-recruit productivity varied?* to *how has pre-recruit productivity varied?* Arguably, such a treatment should preceed more mechanistic investigations. By allowing the parameters of the recruitment function, particularly the annual reproductive rate, to vary (Peterman *et al.*, 2003) across populations and time, we investigate trends that are independent of adult abundance and density-dependent effects. Importantly, we extend previous foundational single-population applications to the multivariate case, where the covariance structure of the trends across geographic regions is of interest. A comprehensive treatment of the formulation, estimation, and interpretation of the covariance of time-varying productivity is presented. The methodology is applied to 16 widely distributed north Atlantic cod (*Gadus morua*) populations, showing that productivity has varied markedly over the time-period investigated with many populations currently at historically low productivity. Trends in productivity were found to be largely conserved across regions, particularly in the western Northeast Atlantic populations of the West of

Scotland, Irish, Celtic, and North Seas, which showed marked contemporaneous coherence.

Higher dimensions as external forces acting on recruitment

Species interactions that play out over large spatial scales are difficult to observe, particularly in the oceans. The lack of empirical evidence for biologically meaningful interaction parameters is likely to delay the application of holistic management procedures. In chapter 5 we address this issue by developing methods to estimate species interactions during the early life history that are comparable and can be combined across regions. We present hierarchical Bayesian models that partition within and between population variability to estimate the direction and strength of interactions between Atlantic cod and small, numerically dominant pelagic fishes across much of their range in the North Atlantic. Specifically we test the hypothesis that small pelagic fish may reduce survival of cod at early life stages, and thereby contribute to the delayed recovery of depleted cod populations. General patterns of negative interaction were found between young cod and the abundance of herring and mackerel across many regions investigated. These patterns are consistently present when the data were investigated hierarchically.

Conclusion: Dimensions of change and the partitioning of variance

Chapter 6 reflects on the developments of the previous chapters and synthesizes the major methodological and empirical advances from this thesis. These include: the elucidation of the strength of density-dependent mortality in attenuating survival variability; temporal patterns in the variance and covariance of time-varying productivity and hierarchical elucidations on the presence of species interactions. The omission of survey data at a higher temporal resolution during the very early life history stages is critiqued. Avenues for further investigation such as an ambitious project to investigate mechanistic density-dependence across multiple systems using extensions of the variance partitioning methods are presented.

Chapter 2

RECRUITMENT SCIENCE: AN OVERVIEW WITH PARTICULAR FOCUS ON HIGHER DIMENSIONS

2.1 Abstract

The development and testing of hypotheses regarding recruitment variability represents a rich cross-over between fisheries and population ecology. Here, a review is provided of the biology, theory and analytical methodologies used to encapsulate the relationships between the number of young fish recruiting to a population and a potentially vast array of biotic and abiotic drivers. An introduction to the biology of the early life history of fish is accompanied by a chronicle of foundational observations and theoretical descriptions. Extensions to the theory are then proposed, with a particular focus on the incorporation of predation during the pre-recruit phase. Previous empirical investigations of pre-recruit predation effects are summarized; potential data analysis pitfalls are highlighted; and the application of statistical methodologies, such as hierarchical mixed effects and time-varying state space methods, are compared. Approaches that include explicit environmental information are contrasted with time-varying latent state parameter techniques. The importance of understanding pre-recruit productivity for the management of fisheries and recovery projections of depleted populations is critically evaluated and presented alongside avenues of further investigation.

2.2 Introduction

In their early life history stages fish are most vulnerable to competition, predation, hydrography, temperature and a multitude of other environmental stressors that result in extraordinarily high levels of natural mortality (Harding and Talbot, 1973; Cushing, 1975). The varying ability to survive and grow through the early stages ultimately determines how many fish will recruit to the adult population. A thorough understanding of this period is therefore critical to understanding fish population dynamics and the management of fisheries (Allen, 1963; Cushing, 1975; Mace and Sissenwine, 1993; Cushing, 1996; Mertz and Myers, 1995; Quinn and Deriso, 1999; Myers, 2001).

The goals of this essay are to: 1) review the major developments of *recruitment* science (Cushing, 1996); 2) propose straightforward and testable extensions to the theory of recruitment in higher dimensions; 3) identify suitable frameworks for analysis; and 4) discuss the potential for applied utility in the management of fisheries resources. Myers (2002) argued that the systematic incorporation of species interactions into recruitment relationships (as a component of the ecosystem approach) represents an essential next step in the maturation of the science. Particular focus is therefore paid to the derivation and analysis of such relationships here.

Note that in an effort to maintain continuity new terms are italicized, with definitions provided in an Appendix glossary.

2.2.1 Early Observations on Fish Recruitment

Consideration of the processes that govern the strength of a *year-class* or *cohort* is a firmly established endeavor of fisheries science. Coastal fishing communities have long observed fluctuations in catches over periods of years, decades and generations (Cushing, 1996). Early explanations as to the cause of these fluctuations involved en masse migration, e.g. that all Atlantic herring (*Clupea harengus*) migrated to and from the refuge of the polar ice. Based upon the detailed work of Heincke (1898), Schmidt (1909), and an early International Council for the Exploration of the Sea committee (ICES Committee A: 1902-1908), the eminent Norwegian fisheries scientist, Johan Hjort, rejected the mass migration hypotheses and put forth the idea that species form discrete populations. Their means of reproductive renewal could thus impart some of the observed *variability* (Hjort, 1914, summarized in Sinclair (1997) and Sinclair and Smith (2002)). Hjort (1914) went further, suggesting two hypotheses to explain recruitment variability: the *critical period* and *aberrant drift* hypotheses.

Hjort's hypotheses

The *critical period* hypothesis suggests that there exists a narrow period during the early larval stage in which the strength of a year-class is determined. The proposed mechanism is *trophodynamic* (Houde, 2008a); that is, the ability of post-yolk larvae to find prey and avoid starvation is critical to surviving the earliest stages in their life history. Where prey is readily available in time and space, high larval survival is to be expected and a strong (in numbers) recruiting year-class would result.

The *aberrant drift* hypothesis drew largely from Hjort's personal observations onboard research vessels. The proposed mechanism of this hypothesis relates to the hydrodynamics of the environment into which the eggs are released. Dynamic conditions could result in retention over suitable post-settlement habitats or dispersal to unsuitable habitats. In this manner, the strength of a recruiting year-class would depend on the physical oceanographic conditions in its early stages (pre-settlement).

Both hypotheses assume that the external environment is the dominant driver. Houde (2008a) argues that many contemporary theories for recruitment variability originate from Hjort's two theories, albeit taking on more sophisticated forms and using new data sources, e.g. the *match-mismatch* (Cushing, 1975; Mertz and Myers, 1994a; Beaugrand *et al.*, 2003; Platt *et al.*, 2003) and *member/vagrant* (Sinclair and Iles, 1989) hypotheses. In addition, later theories on migration such as the migration-triangle arose from considerations of the movement of closed populations first developed by Hjort (Harden Jones, 1968).

Early forecasts

Rather than focusing on these hypotheses and predicting the strength of an incoming year-class via measurements on abiotic drivers (a year-class forecast *per se*), Hjort's approach disregarded his own hypotheses in favor of carefully monitoring the age composition of the catch. Using an early port sampling survey design (Guttorp and Lindgren, 2009) and scale ageing techniques that were discovered independently by Aristotle, van Leeuwenhoek, and Hoffbauer (Radcliffe, 1921, references therein), the relative abundance of age groups within the fishery was established in the present. Hjort's approach of carefully gathering representative statistics was revolutionary in fisheries science and also noteworthy in the broader history of statistical science (Guttorp and Lindgren, 2009). With this data at hand and graphical techniques still in use today (Tufte, 2001), Hjort was able to elegantly show the progression of the exceptionally large 1904 year-class of Norwegian Spring Spawning herring (Hjort, 1914, Figure (2.1) of the present manuscript). An important observation from the data in Figure (2.1) was that the strength of an incoming (earliest age) year-class is exceptionally variable, typically displaying 10-fold, and occasionally 100-fold, inter-annual changes (Houde, 2008a). Explaining such extraordinary variability was, and still is, a key challenge.

At the time Hjort (1914) was somewhat dismissive of the potential to capture the governing processes of the pre-recruit phase with any consistency:

> *A final solution to the problem of fluctuations in the fishery by any permanently valid formula must be regarded as an impossibility and all assertions as to the discovery of such a solution may safely be relegated to the sphere of pure imagination.*

These assertions may have inhibited the development of recruitment science from 1914-1930 (Sinclair, 1997). It is important to note, however, that Hjort based his conclusions on relatively few samples with limited fiscal resources (Hjort, 1926). Furthermore, Hjort (1926) reviewed his stance after having seen the work of Sund (1924) on the coincidence of years of low run-off from the land with strong year-classes of cod. These were the first investigations into the environmental correlates of recruitment variability.

However, Sund's investigations came at a time when the focus of fisheries scientists was directed elsewhere. Hjort's advice on the collection of representative data on age distributions had gathered much momentum. For example, Thompson (1924) gathered extensive data on the age distributions of young haddock in the North Sea. The use of such data in forecasting future fishing opportunities was not lost on Hjort (1926) and the first fishery forecasts, based upon projecting the year-classes present in the fishery forward, were conducted for the East Anglia herring fishery in 1922 (Hodgson, 1957). These forecasts applied to year-classes already available to the fishery with less attention on what was forcing the incoming year-class.

Reproductive failure

The East Anglian forecasts were useful and well received within the economically important herring industry until the forecasts failed in 1951 and 1952 (Sinclair, 2009). The cause of the failures is now attributed to a phenomenon called *recruitment overfishing* (Ricker, 1954; Cushing, 1975). Although overfishing of many coastal stocks had occurred in the past (Lotze *et al.*, 2006) and had been raised as a concern (Garstang, 1900, W. Garstang convenor of ICES Committee B (Rozwadowski, 2002)), these situations were attributed to *growth overfishing*, where a stock is reduced below its productive capacity by the fishing of

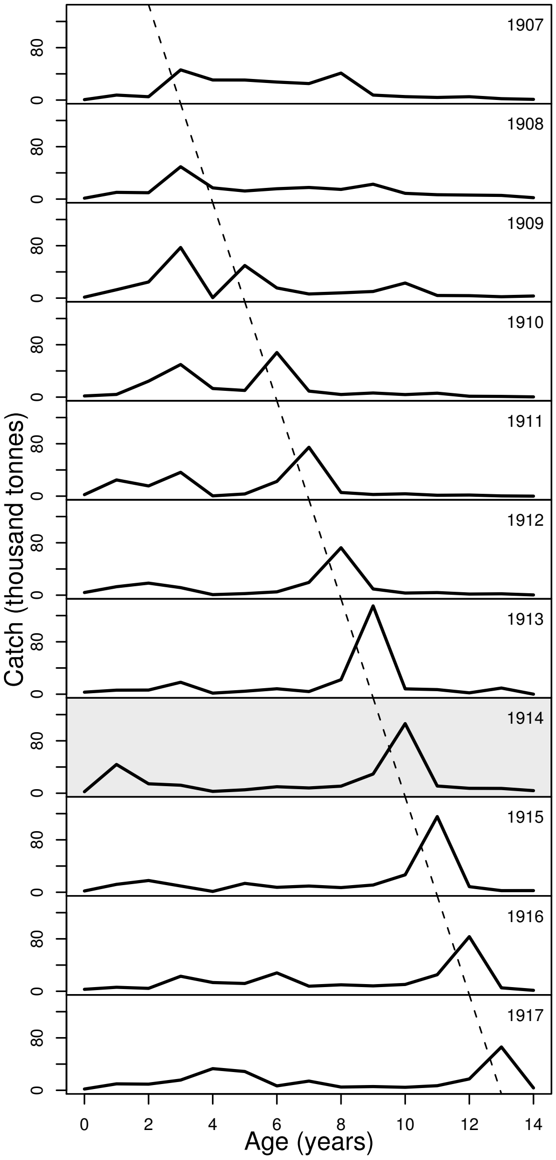


Figure 2.1: Catch at age of Norwegian spring spawning herring, emphasizing the progression of the large 1904 yearclass (dashed line). Shaded panel represents the year of Hjort's synthesis (Hjort, 1914). Data from: Toresen and Østvedt (2000).

small individuals (Cushing, 1975). At the time of the collapse of the East Anglia herring, it was not widely perceived that fishing pressure could deplete the reproductive potential of a stock. Although others had investigated the effect of fishing mortality on adult abundance (Baranov, 1918; Graham, 1935; Thompson, 1937), mathematical models linking adults to young had not yet been conceived. That the strength of a year-class could be related to the size of the parental stock was a costly but important insight of the early 1950s (Sinclair, 2009). The time was therefore right to capture the relationship between the abundance of spawners and recruits into a theory of recruitment.

2.3 Recruitment Theory

Fisheries theory and population ecology

The disciplines of fisheries science and population ecology today borrow and contribute to each other regularly, although the early evolution may have occurred with limited crossover (Getz and Haight, 1989; Quinn, 2003). Fisheries science needed theoretical frameworks distinct from those applied to unexploited populations (Beverton and Holt, 1957; Ricker, 1958; Gulland, 1969, and earlier Russian works of Baranov). These theories revolved around the effects of exploitation on the population and how to extract meaningful information from commercial catch data, which was, and still is, the predominant source of fisheries information (Gudmundsson, 1994). It must be noted, however, that this distinction is now fading with the recognition of fisheries removals as large-scale experiments of value for investigating system dynamics (Frank *et al.*, 2005; Myers *et al.*, 2007). In contrast to later life stages, the processes acting on a pre-recruit from an egg to a given early age, operate when the mortality induced by fishing is typically low due to the mesh size of the nets used (note maternal effects may discredit this line of argument). Theories of recruitment could therefore borrow from, and contribute to, the major concepts of population ecology.

Theoretical precursors

The theoretical treatment of recruitment, like many aspects of population ecology, descended from initial investigations of human demography and subsequent investigations on how species interact. Pearl and Reed (1920) likened human population growth to the chemical process of autocatalysis, where the rate of product formation follows a parabola over time. The resulting single species population model is sigmoidal over time, following a logistic curve (Verhulst, 1838; Pearl and Reed, 1920), with the rate of change given by

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}), \tag{2.1}$$

where N is the population size, r is the intrinsic rate of population growth, and K is the asymptote or *carrying capacity*. When $K \to \infty$ (in an unlimited environment) the population continues to grow exponentially. The logistic model has proven to be an extremely useful heuristic building block for population dynamics models (Turchin, 2001). However, for fish populations, the assumption that the population is homogeneous with respect to age or life history stage structure is unrealistic. This implies that the adult population may undergo *overcompensation* when $N > K$ (Ricker, 1954), a situation that is seldom observed within fish populations where the relative rank of a year-class remains quite constant after recruitment (Cushing, 1975). A diversity of other taxa do exhibit density-dependent mortality during the adult stages, e.g. birds: (McCallum *et al.*, 2001); ungulates: (Owen-Smith *et al.*, 2005, see: Festa-Bianchet *et al.* (2003) for alternative ungulate explanations); and trees (Yoda *et al.*, 1963; He and Duncan, 2000). But for fish it was necessary to explicitly consider stage structure in population regulation.

The inspiration for how stage structure could be included in population dynamics came from early investigations of multispecies dynamics. These pre-date Pearl and Reed's logistic model, e.g. Ross (1911), but it was not until the expositions of Lotka (1925) and Volterra (1926b,a), which built upon the continuous logistic model, that the importance of how species interact was given full consideration. Nicholson (1933) and Nicholson and Bailey (1935) focused on population regulation using the illustrative model system of *parasitoids* and their *hosts*. They derived a system of *difference equations* to describe the population dynamics of the interacting species:

$$\begin{aligned} N(t+1) &= N(t)e^{r_N - aP(t)}, \\ P(t+1) &= cN(t)(1 - e^{-aP(t)}), \end{aligned} \tag{2.2}$$

where $N(t)$ and $P(t)$ are the number of hosts and parasitoids at time t , respectively, r_N is the intrinsic rate of population growth of the host (Turchin, 2003), a is the search rate of the parasitoid, and c is the proportion of attacks leading to parasitoid offspring.

Due to the importance of the Nicholson-Bailey model in: 1) shaping the arguments for early recruitment theories and 2) igniting the debates of population ecology for the decades that followed, the derivation is here explored in depth.

The derivation of the Nicholson-Bailey model, as outlined in Nicholson and Bailey (1935), Hassell (1978), and Ricklefs and Miller (2000), makes use of the Poisson distribution to describe number of eggs laid (encounters) per host:

$$P(N_H) = \frac{\mu^{N_H} e^{-\mu}}{N_H!}, \tag{2.3}$$

where N_H is the number of eggs laid by the parasitoids per host. The probability of no eggs per host is given by $e^{-\mu}$, similarly the probability of at least one egg per host is $1 - e^{-\mu}$. Nicholson and Bailey (1935) assumed that the average number of eggs per host was proportional to the parasitoid density $\mu \propto aP_t$, such that the proportion of hosts with at least one egg laid (attacked) is given by $1 - e^{-aP_t}$, as in Equation (2.2). The proportion of hosts attacked thus increases with increasing abundance of parasitoids but at a decreasing rate. The reason is that as the density of parasitoids increases, the number of non-attacked hosts (limited resource) decreases, resulting in longer search times. The abundance of parasitoids may thus be limited via competition for hosts.

The proposed *balance of nature* of Nicholson (1933) and Nicholson and Bailey (1935) ignited a spirited debate within the discipline of ecology; that of population regulation, *density dependence*, and *density independence* (Smith, 1935; Andrewartha and Birch, 1954; Lack, 1954; Milne, 1958; Solomon, 1958; Andrewartha, 1959; Hairston *et al.*, 1960; Ehrlich and Birch, 1967); see McLaren (1971), Turchin (1995) and Turchin (2003) for extensive summaries, recent additions and reconciliations.

2.3.1 Standard Ricker Derivation

The concept that fish populations could be regulated by virtue of their abundance at an early age was first taken up by Ricker (1954) who extended upon the work of Nicholson and Bailey (1935). Knowing that the potential for *compensatory mortality* was greater for the immature stages as compared to the mature fish, Ricker (1954) focused on the dynamics of the early life history. Ricker (1954) explicitly considered the case of compensatory predation mortality upon the eggs and larvae, i.e. that the rate of predation increases with the density of the prey. One situation where this could occur is when adults cannibalize the young. In this case, one might consider that as the adult density increases, the number of eggs produced also increases but so too does the predation mortality exerted by the adults. In this way cannibalism is a regulatory mechanism inducing compensatory mortality.

The derivation of the original Ricker reproductive curve proceeds with the same arguments of random searching as in the Nicholson-Bailey model, only in the Ricker model parasitoids are replaced by older individuals of the same species (Ricker, 1958). The model was originally derived as a difference equation but for continuity with Beverton and Holt (1957) and to ultimately extend the models into higher dimensions, the original Ricker derivation is here treated with *differential equations* (Hilborn and Walters, 1992). The differential equation describing the rate of change for a cohort under Ricker's assumptions is given by

$$\frac{dN(t)}{dt} = -(q + pS_0)N(t), \tag{2.4}$$

where $N(t)$ is the cohort size, $q + pS_0$ is the instantaneous mortality rate comprised of: the density-independent mortality rate q and the stock-dependent (stock density-dependent) mortality rate pS_0 (Hilborn and Walters, 1992). Note that the density-dependent mortality rate is here a function of the initial spawning stock size S_0. The assumed biological mechanism is the presence of intraspecific compensatory predation mortality i.e. cannibalism (Ricker, 1954). Solving this differential equation with the initial condition $N(0) = N_0$ proceeds as follows:

$$\begin{aligned}
\frac{dN(t)}{dt} &= -(q+pS_0)N(t), \\
\frac{dN(t)}{N(t)} &= -(q+pS_0)dt, \\
\int \frac{1}{N(t)} dN(t) &= \int -(q+pS_0)dt, \\
\ln(N(t)) &= -(q+pS_0)t + C_1, \\
N(t) &= e^{C_1} e^{-(q+pS_0)t}, \\
N(t) &= N_0 e^{-(q+pS_0)t}. \qquad (2.5)
\end{aligned}$$

Note the correspondence between this expression and the dynamics for the prey species in the Nicholson-Bailey model (Equation 2.2). N_0 is the initial number of eggs, which is the product of initial spawner abundance S_0 and fecundity F (number of eggs per spawner), so Equation (2.5) can be written

$$N(t) = S_0 F e^{-(q+pS_0)t}. \qquad (2.6)$$

Setting t at the age of recruitment τ

$$N(\tau) = S_0 F e^{-(q+pS_0)\tau}. \qquad (2.7)$$

Letting $R = N(\tau)$, $\alpha = e^{-q\tau}F$ and $\beta = p\tau$, the familiar Ricker spawner-recruit relationship is obtained:

$$R = \alpha S_0 e^{-\beta S_0}. \qquad (2.8)$$

This is the form regularly statistically fit to stock and recruitment data (assuming lognormally distributed measurement errors) for the purpose of forecasting recruitment in coming years (see discussions in Hilborn and Walters (1992) and Myers (2001).

Parameter interpretation and assumptions

Before extending the relationships to include other factors, it is useful to consider what the parameters mean. The scalar, α, can be interpreted as the number of recruits produced per spawner at low population sizes. It is the slope at the origin where no density-dependent mortality occurs and is often termed the *maximum reproductive rate* (Myers *et al.*, 1999). It is composed of $\alpha = e^{-q\tau}F$, that is, the product of fecundity and density-independent mortality up to the age at recruitment. The term encapsulates sources of mortality that are independent of density. Implicit in this parameter is the assumption that the product of fecundity per unit spawner biomass and density-independent mortality is constant. Where these vary over time, α may be interpreted as the time average of this product (Myers *et al.*, 1999). The legitimacy of the assumption of constant reproductive output per unit spawner biomass has been questioned, primarily based upon maternal effects arguments (Trippel *et al.*, 1997). For example, a truncation of the population age distribution caused by fishing could increase the proportion of first time spawners whose eggs might have less chance of survival. Trippel *et al.* (1997) showed that using older fish as a measure of spawning potential provided a better relationship with recruitment. Changes in the age composition of the stock can also affect the reproductive output (Hutchings and Myers, 1993; Wright and Gibb, 2005). Marshall *et al.* (2006) showed that changes occur in the egg production of cod in the Northeast Arctic related to changes in spawner composition. These considerations will be revisited when time-varying parameters are considered in section (2.4.3) and Chapter 4.

The term β represents the strength of density-dependent mortality, i.e. how fast the recruits produced per spawner decrease with increasing spawner abundance. Again, assumptions of constancy are potential sources for criticism here e.g. if other preferential prey became available to the adults at high density one might not expect compensatory mortality via cannibalism to be a constant function of adult density.

Both inter- and intra-specific compensatory predation mortality assumptions can be used to derive the Ricker model. The assumption that the strength of the density-dependent mortality depends on the initial abundance of the cohort is restrictive and is somewhat of a surprising assumption given that Ricker was, at the time, working on semelparous salmon that spawn once and die without feeding. The opportunity for cannibalism from the parents would be very small but perhaps intercohort cannibalism is important. In addition, limited available habitat and superimposition of eggs on the salmon redds may result in overcompensatory dynamics. It is also useful to consider other forms of compensatory mortality and the dynamics they produce.

2.3.2 Standard Beverton-Holt Derivation

Beverton and Holt (1957) worked in parallel to Ricker and derived a recruitment relationship under alternative assumptions about the nature of density-dependent mortality. The distinction between these two models is often related mechanistically to the assumptions of *scramble* versus *contest* competition (Hassell, 1975; Brännström and Sumpter, 2005). Scramble competition occurs when each competitor obtains a fixed proportion of limited environmental resources whereas in contest competition, competitors receive differential proportions of the resources. Note, however, that the original Ricker was not derived under scramble competition premises. The rate of change for a cohort according to the Beverton-Holt model is given by:

$$\frac{dN(t)}{dt} = -(q + pN(t))N(t). \tag{2.9}$$

where q is a coefficient of density-independent mortality and p is a coefficient of density-dependent mortality. Comparing Equations (2.9) and (2.4) shows that the nature of density dependence is different in both cases. In the Ricker formulation, compensatory mortality occurs via predation or cannibalism in accordance with the initial size of the cohort. In contrast, the Beverton-Holt formulation relates the strength of the density-dependent mortality to the size of the cohort at any given time.

Beverton and Holt (1957) explicitly pointed out that the coefficients of Equation (2.9) vary in time, that is $q = q(t)$ and $p = p(t)$. For the purpose of an illustrative derivation, these coefficients are assumed constant. Solving Equation (2.9) with initial abundance N_0 provides:

$$\begin{aligned} N(t) &= \frac{N_0 q}{-pN_0 + e^{qt}q + e^{qt}pN_0}, \\ &= \frac{1}{\frac{p}{q}\left(e^{qt} - 1\right) + \frac{e^{qt}}{N_0}}. \end{aligned} \tag{2.10}$$

Setting t at the age of recruitment τ

$$N(\tau) = \frac{1}{\frac{p}{q}\left(e^{q\tau} - 1\right) + \frac{e^{q\tau}}{N_0}}, \tag{2.11}$$

and letting $\alpha = \frac{p}{q}\left(e^{q\tau} - 1\right)$, $\beta = e^{q\tau}$, and $N_0 \propto S_0$ provides the familiar Beverton-Holt relationship

$$R = \frac{1}{\alpha + \frac{\beta}{S_0}}. \tag{2.12}$$

Note that Equation (2.12) is more commonly derived to a form similar to $R = \alpha S_0/(1 + \beta S)$, which allows α to be interpreted as a maximum reproductive rate. The original derivation (Beverton and Holt, 1957) is provided above.

Comparative dynamics

The Ricker and Beverton-Holt models display different dynamics (Figure 2.2) by virtue of the assumed nature of density-dependent mortality. The Ricker relationship is typically dome-shaped over adult abundance. The decreasing right limb is termed overcompensation. Overcompensation is a dynamic reserved for *stock-dependent* regulation, where the strength of the compensatory mortality depends upon the initial abundance of the cohort (Harris, 1975). Overcompensation produces a myriad of interesting dynamics in the difference form (Equation 2.8) from stable endogenous cycles (Ricker, 1954; Myers *et al.*, 1998) to non-stable chaotic behaviours (May and Oster, 1976). In contrast, the Beverton-Holt curve is asymptotic, displaying only compensatory mortality and, consequently, a reduced diversity of potential dynamics (deVries *et al.*, 2006). The existence of chaotic dynamics in the basic Ricker model requires very high maximum reproductive rates that are rarely observed outside of the laboratory (Turchin, 2003, note however the case of chaotic dynamics in the Norwegian and brown lemmings) or in any known fish population (Hilborn and Walters, 1992). One might ask what mechanisms could potentially keep the maximum reproductive rate low enough to avoid chaos?

2.3.3 Extended Ricker Derivation

In this section straightforward extensions to the Ricker theory of recruitment are derived to include interspecific predation mortality.

Why focus on predation?

Similar to the intuitions of Hjort (1914) and formalization of Lotka (1925), one could hypothesize that the change in the abundance of a cohort in a multispecies system is a function

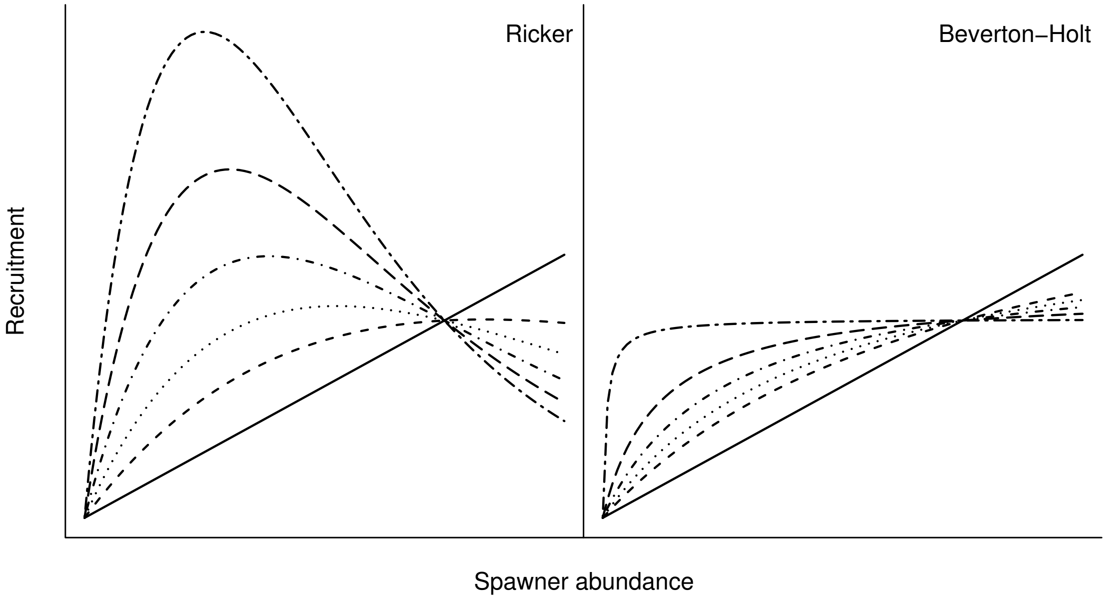


Figure 2.2: Families of Ricker and Beverton-Holt model stock-recruitment relationships to illustrate the 2-dimensional dynamics. Higher and increasingly more dome-shaped Ricker model curves are achieved by increasing the maximum reproductive rate and strength of density-dependence. The different Beverton-Holt curves are distinguished by increasing maximum reproductive rate and strength of density dependence. All curves were forced to converge arbitrarily for illustration. The solid line represents the 1:1 replacement line.

of a bewildering variety of drivers operating at different life stages

$$\frac{dN_1(t)}{dt} = f(N_1, N_2, ..., N_n; X_1, X_2, ..., X_m), \tag{2.13}$$

where N_i are conspecifics and the X_j terms represent the abiotic environment. While the ambitious theoretical investigation of such high dimensional relationships has been fruitful (Andersen and Ursin, 1977), the resulting formulae are exceptionally involved and thus insulated from the rigours of formal testing with available data (Walters and Korman, 1999). To keep the theory testable while addressing a noted missing link of recruitment science (Myers, 2002), I focus on but one section of Equation (2.13); that of the effect of predation.

The effect of predation on pre-recruits in temperate systems has received less synthetic focus than, for example, physical forcing by the abiotic environment (e.g. The Global Ocean Ecosystem Dynamics programme (GLOBEC) program), with important exceptions (e.g. Walters *et al.*, 1986; Basson and Fogarty, 1997; Gjøsæter and Bogstad, 1998; Swain and Sinclair, 2000; Petrie *et al.*, 2009). In an overview of recruitment science, Myers (2002) expounded the importance of extending recruitment functions to include species interactions. Investigations of the contribution of pre-recruit predation to analyses of recruitment variability are hampered by a sparcity of suitable data with sufficient contrast (Bax, 1998; Hilborn and Walters, 1992). Yet, theoretical advances on interactions among species during the early life history stages hypothesize that stage-specific interactions among predators and prey may be key to understanding community dynamics (Walters and Korman, 1999), e.g. the 'cultivation-depensation' hypothesis (Walters and Kitchell, 2001). This hypothesis is related to Ursin's trophic-triangle hypothesis (Ursin, 1982) and involves an adult piscivore population that feeds on a lower trophic level species (such as a planktivore) that is, in turn, a predator of the eggs and larvae of the adult piscivore. Walters and Kitchell (2001) concluded from simulations in EcoSim (Christensen *et al.*, 2005) that the predation effect of large piscivores on predators of their young could reduce mortality in the early life history stages. Conversely, where the adult piscivore population is reduced, e.g. through excessive fishing mortality, the small planktivore increases and induces *depensation* in the adult piscivore population by reducing the survival of its young.

Forms of predation mortality

By assuming Ricker dynamics (Equation 2.4) for the population growth rate in the absence of predators (other than cannibals) P and letting $f(N, P)$ be the predator functional response, the rate of change for the cohort can be generally written

$$\frac{dN}{dt} = -(q + pS)N - f(N, P). \tag{2.14}$$

Potential straightforward functional forms for $f(N, P)$ include linear, hyperbolic and ratio-dependent predation mortality rates (Turchin, 2003).

Linear predation mortality rate

Assuming a linear functional response for the predator-induced mortality rate (Volterra, 1931), provides

$$\begin{aligned} \frac{dN}{dt} &= -(q + pS)N - aNP, \\ &= -(q + pS + aP)N, \end{aligned} \tag{2.15}$$

where a is the instantaneous predation rate per predator. Solving this differential equation with respect to time provides

$$N_t = N_0 e^{-(q+pS+aP)t}. \tag{2.16}$$

With the same assumptions made for the standard Ricker model and letting $\gamma = at$, Equation (2.16) is written

$$R_t = \alpha S e^{-(\beta S + \gamma P)}. \tag{2.17}$$

Note that Equation (2.17) or a re-parameterized variant is also a common form used for general extensions to the Ricker, e.g. including additional sources of mortality such as abiotic forcing (Brander and Mohn, 2004).

Hyperbolic predation mortality rate

The assumption of a linear increase in predation mortality over all predator abundances is restrictive. An asymptotic alternative would be to assume a hyperbolic predation functional response (Rosenzweig and MacArthur, 1963)

$$\begin{aligned}\frac{dN}{dt} &= -(q+pS)N - \frac{cNP}{d+N}, \\ &= -(q+pS+\frac{cP}{d+N})N.\end{aligned} \tag{2.18}$$

Equation (2.18) serves as an example of how relatively simple but biologically plausible forms are difficult to solve (integrate) analytically; although this may be possible via partial fractions. For the purposes of visualizing the dynamics (section (2.3.3)) I used a Runge-Kutta numerical integration routine (Runge, 1895; Kutta, 1901) implemented in the R package 'deSolve' (Soetaert *et al.*, 2010). The approach is discussed further in the conclusions of this essay.

Ratio dependent mortality rate

An interesting option is the possibility that the predation rate depends upon the ratio of the adult populations of both the prey and predator species. This could be a suitable choice for the 'cultivation-depensation' hypothesis where the ratio of the adult populations is key to the dynamics. Note, however, that the theoretical underpinnings of this form have been questioned (Abrams and Ginzburg, 2000). Assuming a ratio-dependent functional response (Turchin, 2003, modified here from original formulation of the ratio of prey to predator to the ratio of predator to spawning adult) for the predator induced mortality rate, provides

$$\begin{aligned}\frac{dN}{dt} &= -(q+pS)N - g\frac{P}{S}N, \\ &= -(q+pS+g\frac{P}{S})N.\end{aligned} \tag{2.19}$$

The differential equation solution is given by

$$N_t = N_0 e^{-(q+pS+g\frac{P}{S})t}. \tag{2.20}$$

Letting $R_t = N_t$, $N_0 = SF$, $\alpha = e^{-qt}F$, $\beta = pt$, and $\psi = gt$, Equation (2.20) is written

$$N_t = \alpha S e^{-\beta S - \psi \frac{P}{S}}. \tag{2.21}$$

Exploring the Dynamics

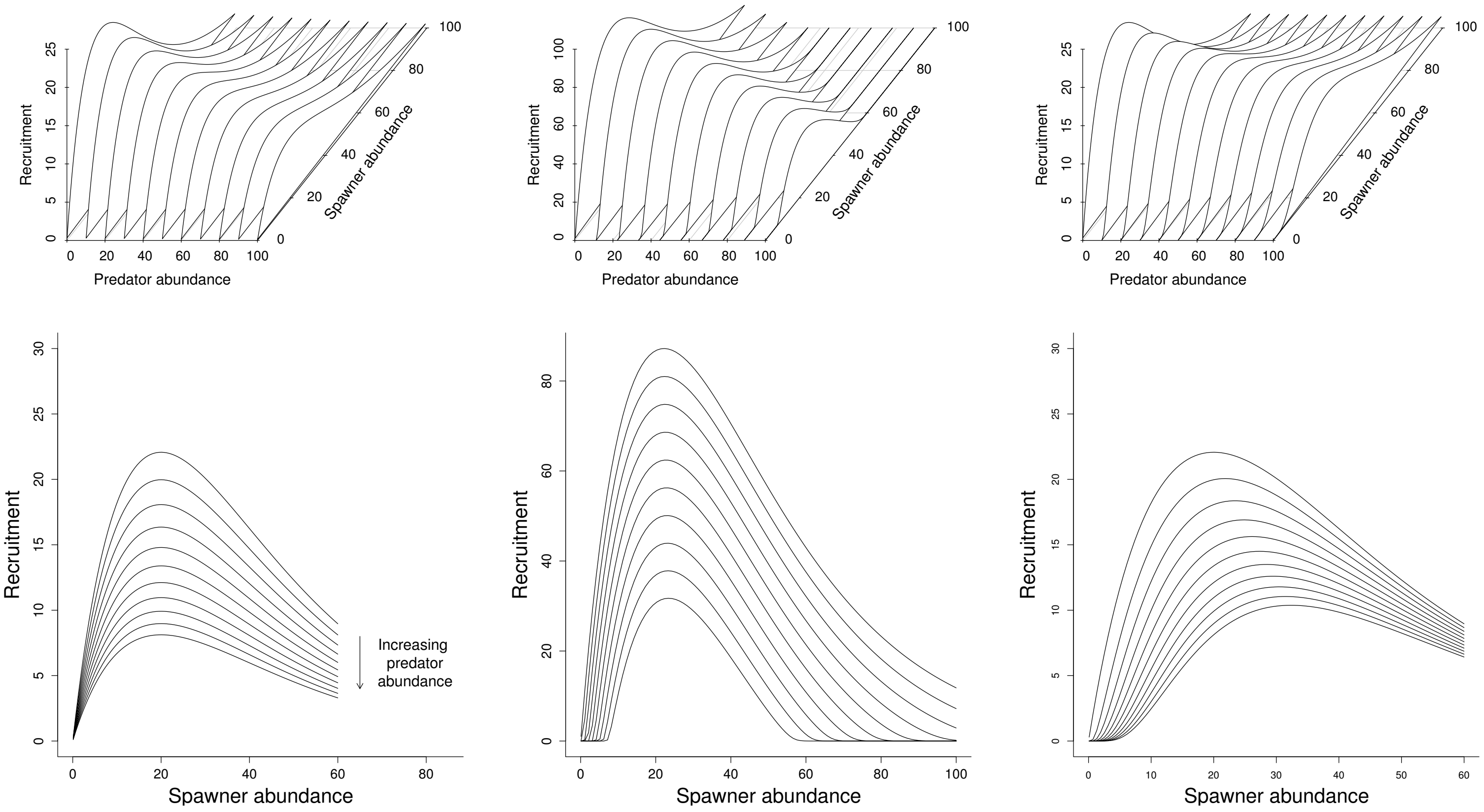
Resultant recruitment dynamics under these three different forms of predation are shown in Figure (2.3). The most important result is that the linear predation mortality rate is the only form that does not give rise to depensatory dynamics. This analytical observation is in agreement with other theoretical and descriptive expositions (Liermann and Hilborn, 2001; Walters and Kitchell, 2001). The strength of depensation increases with increasing predator abundance in both the hyperbolic and ratio-dependent cases. This theoretical insight is of potential importance when considering recovery dynamics for exploited fish populations when potential predators are in high abundance.

Previous empirical investigations on the presence of depensation in SR relationships have yielded conflicting results (Myers *et al.*, 1995a; Liermann and Hilborn, 1997; Walters and Kitchell, 2001). Myers *et al.* (1995a), using a depensatory version of the Beverton-Holt model, reported that evidence for the occurrence of depensation was weak, whereas Walters and Kitchell (2001), using expert opinion on the trajectory of recruitment over spawner abundance, concluded that depensation was more common than Myers *et al.* (1995a) had found. The related topic of *Allee effects*, caused by behavioural or behavioural changes at very low abundance (Frank and Brickman, 2000), was explored in stock-recruitment relationships by Chen *et al.* (2002). One of two populations explored displayed significant Allee dynamics (positive x-axis intercept).

None of these studies empirically included additional dimensions that could give rise to depensatory dynamics, such as those derived here for predation. Analyzing multidimensional data in a 2-dimensional framework can mask such relationships, as illustrated by Frank and Brickman (2000) in the case of ignoring metapopulation structure.

2.4 Data Analysis

Given the propensity to depensatory dynamics in the theoretical explorations above, it is essential that they be tested with data. Data on the number of recruits typically come from an age-structured fisheries assessment such as a Virtual Population Analysis (Gulland, 1965, along with contributions by: Baranov (Ricker, 1975); Fry (1949); and Beverton and Holt (1957)). By recursively tracing the strength of the cohort back through time, an estimate



(d) Linear (e) Hyperbolic (f) Ratio-dependent

Figure 2.3: Resulting recruitment relationships in a higher dimension (top row) and the corresponding family of curves when viewed in 2-D (bottom row). Linear, hyperbolic, and ratio-dependent predation mortality are assumed in columns 1, 2 and 3 respectively.

or tally of the initial abundance is established. The abundance of recruits can thus be related to the size of the spawning proportion of the population in a stock-recruitment (SR) relationship (Myers, 2002). These relationships are often characterized by high variability, which gave rise to debates on whether recruitment was related to the size of the spawning component at all (Myers and Barrowman, 1996a; Gilbert, 1997; Myers, 1997a). Some of this variability may arise from additional dimensions we have previously ignored, such as the effects of biotic (food and predators) and abiotic (physical oceanographic) drivers.

As any one population may yield uncertain parameter estimates - the uncertainty arising from both natural and sampling processes - statistical methodologies that account for these uncertainties and combine results across multiple populations are required. First, it is informative to explore what has already been done.

2.4.1 Empirical Evidence for Pre-recruit Predation

Prior to discussing previous approaches to empirically investigating predation effects on pre-recruits, there are valuable lessons to be learned from the general topic of including biotic and abiotic correlates. Myers (1998) cautioned that many previously published significant relationships between recruitment and environmental covariates do not hold up when retested. Relationships often last for a number of years and then break down (Cushing, 1996) (see section (2.4.3) here for potential time-varying parameter solutions to these issues). Hutchings and Myers (1994), Myers (1998) and Cardinale and Hjelm (2006) caution against simply regressing recruitment on an environmental correlate without first taking account of the potentially confounding effect of changing spawner abundance, a factor which was found to be generally important (Myers and Barrowman, 1996b), as was density dependence (Cushing, 1996).

Previous investigations on the effect of predation on recruitment can be classified according to the scale and design of the study. Small scale studies of local populations are typically (not always) experimental whereas large scale studies at the stock level are almost always observational in nature. Scale is an important attribute in assessing the effect of a covariate on mortality, as processes operating locally do not always hold true for the stock as a whole (Walters and Korman, 1999). This may be particularly true where an interaction occurs over days or weeks yet data are only available annually. Experimental investigations of coral reef populations have yielded great insights into the nature of recruitment, e.g. the importance of early post-settlement predation in those systems (Carr and Hixon, 1995; Hughes *et al.*, 1992; Hixon and Beets, 2008). Experimentation is more difficult in temperate systems where the scales of nursery grounds are greater than those of individual coral reefs. In temperate systems we typically rely on observational data.

The generation of hypotheses regarding the effects of predation in observational situations relies on diet sampling and correlation analyses of time series data. Large scale stomach sampling protocols (Daan, 1989; Laurinolli *et al.*, 2004) establish what proportion of the diet of species i comes from species j. These studies are usually temporally isolated over large geographic range (e.g., ICES *year of the stomach* in the North Sea (Daan, 1989)), although there are also examples of temporally expansive sampling over large regions (Link and Almeida, 2000, Northeast U.S.). Note that the temporal dimension refers to years as opposed to seasons within a year, which are often poorly covered. These sampling programs are extremely useful to parameterize predation mortality terms of Multispecies Virtual Population Analysis (MSVPA) (Helgason and Gislason, 1979; Pope, 1979; Sparre, 1991), maximum likelihood-based multispecies age-structured assessment models (e.g., MSASA) (Van Kirk *et al.*, 2010) and EcoSim/EcoPath (Christensen and Pauly, 1992; Christensen *et al.*, 2005) mass-balance models. Multispecies models such as these generally focus on the effect of predation mortality among the adults (note pre-recruit age fish are included in Van Kirk *et al.* (2010)), whereas the most important determinant of cohort size occurs much earlier, as discussed previously. It is worth noting, however, that extremely high levels of natural mortality are estimated for adult cod stocks in the Northwest Atlantic (Trzcinski *et al.*, 2006; Swain *et al.*, 2008). Investigations of the diets consisting of young fish are made difficult but not impossible by taxonomic distinction.

For example, Köster and Möllmann (2000) conducted extensive sampling of clupeid fish (herring (*Clupea harengus*) and sprat (*Sprattus sprattus*)) stomachs in the Baltic Sea. They identifyed eggs and larvae from stomachs to the species level and concluded that herring and sprat may contribute significantly toward pre-recruit mortality of Atlantic cod (*Gadus morhua*) (Köster and Möllmann, 2000). Similar observations have also been made for capelin (*Mallotus villosus*) in northeastern Newfoundland (Pepin, 2006) and inferred from spatial overlap of larvae and pelagic species on the southern flank of Georges Bank (Garrison *et al.*, 2002). Predation by herring and Atlantic mackerel (*Scomber scombrus*) upon the early life history stages of cod may also be inhibiting the recovery of cod in the Gulf of St. Lawrence (Swain and Sinclair, 2000). When coupled with a general increase in the abundance of potential egg and larval predators, e.g. small pelagic species (Bundy and Fanning, 2005; Frank *et al.*, 2005; Worm *et al.*, 2009), and a contemporary focus on recovery times and strategies for depleted groundfish (Hutchings and Baum, 2005), these observations necessitate a theoretical and empirical exposition of the contribution of pre-recruit predation by small pelagic species to recruitment variability (Pepin, 2006). In the following two sections I will explore the statistical methodologies available to conduct such a task.

2.4.2 Hierarchical Mixed Effects Modeling

Previous insights

The application of hierarchical mixed models (described below) to recruitment data has greatly increased our understanding of recruitment dynamics by allowing data from multiple populations and regions to be compared in a coherent statistical framework (Gelman and Hill, 2007, for a general introduction) and (Myers, 1997b; Hilborn and Liermann, 1998; Myers and Mertz, 1998b; Myers *et al.*, 1999; Myers, 2001, for recruitment-specific applications). The analysis of individual stocks often fails to elucidate patterns but by collating results across many populations, effectively analysing a natural experiment with varying conditions, consistent patterns emerge, e.g. Worm and Myers (2003). Note that this approach may be thought of as a formalization of the long-pursued comparative approach in biology. Insights gained from the application of hierarchical methods to recruitment studies include: the relationship between spawner abundance and subsequent recruits (Myers and Barrowman, 1996b); relative invariance of the maximum reproductive rate across stocks (Myers *et al.*, 1999); differences in carrying capacity across systems (Myers *et al.*, 2001); presence of ‘top-down’ control (Worm and Myers, 2003); relationship between survival variability and abundance (Myers, 2001; Minto *et al.*, 2008), amongst others.

Implementation

The implementation of a hierarchical mixed effects analysis generally involves the collation of data from a number of systems with similar properties and then analyzing the data through fixed-effects, random effects or hierarchical Bayesian approaches (Normand, 1999; Gelman *et al.*, 2004). Fixed effects analysis, which can be thought of as obtaining an overall weighted average (Normand, 1999), has the advantage of being straightforward to implement but the assumption that there is a fixed average for a given parameter without population-specific variation is restrictive. Random effects analysis circumvents this issue by assuming inter-population variability in the parameter. Random effects analyses are quite straightforward to implement, at least in the linear case, but inference on the resulting predictions for each population (termed Best Linear Unbiased Predictors (BLUPs) or empirical Bayes estimates) requires careful attention, particularly in non-linear cases (Pinheiro and Bates, 2000; Diggle *et al.*, 2003). Bayesian hierarchical mixed model analyses have many of the associated inferential benefits of the Bayesian paradigm (Jaynes and Bretthorst, 2003) and the natural inclusion of data collected at multiple scales (Clark and Gelfand, 2006; Clark, 2007). Choice of what form and information content is chosen for the prior distribution (reflects the prior knowledge of a parameter before data are analyzed) requires careful sensitivity analyses (Calvert *et al.*, 2009).

Proposed hierarchical mixed model extensions

Detailed descriptions of hierarchical mixed models as well as illustrative examples can be found in Efron and Morris (1977); Harley (2002); Gelman and Hill (2007). The example shown below is used in Chapter 5.

An example of a hierarchical approach to parameter estimation in extended recruitment functions, a random effects model of Equation (2.17) is presented. Data are used from all regions j where the hypothesized interacting species coexist and estimates of their abundances exist. The equation is written:

$$R_{t,j} = \alpha_j S_{t-\tau,j} e^{-(\beta_j S_{t-\tau,j} + \gamma_j P_{t-\tau,j})} e^{\varepsilon_{t,j}}, \tag{2.22}$$

where τ is the age at recruitment and the distributions of the parameters is given by

$$\begin{bmatrix} \alpha_j \\ \beta_j \\ \gamma_j \\ \varepsilon_t \end{bmatrix} \sim \mathcal{N}\left(\begin{bmatrix} \mu_\alpha \\ \mu_\beta \\ \mu_\gamma \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma^2_\alpha & & & \\ \sigma_{\alpha,\beta} & \sigma^2_\beta & & \\ \sigma_{\alpha,\gamma} & \sigma_{\beta,\gamma} & \sigma^2_\gamma & \\ \sigma_{\alpha,\varepsilon} & \sigma_{\beta,\varepsilon} & \sigma_{\gamma,\varepsilon} & \sigma^2_\varepsilon \end{bmatrix} \right), \tag{2.23}$$

where the overall means of the distribution of parameter θ ($\theta \in \{\alpha, \beta, \gamma, \varepsilon\}$) are given by μ_θ with variance σ^2_θ and covariance $\sigma_{\theta_1,\theta_2}$. Letting $\Delta\theta_j$ be the deviation from the overall mean of parameter θ by population j and Σ be the variance covariance matrix of the random effects, the joint probability density function can be written:

$$f(\mathbf{R_j}|\mathbf{S_j}, \mathbf{P_j}, \theta, \Delta\theta_j) f(\Delta\theta_j|\Sigma). \tag{2.24}$$

The marginal likelihood of Equation (2.24) may be written (Diggle *et al.*, 2003):

$$L(\theta|) = \prod_{j=1}^{m} \int f(\mathbf{R_j}|\mathbf{S_j}, \mathbf{P_j}, \theta, \Delta\theta_j) f(\Delta\theta_j|\Sigma) d\Delta\theta_j. \tag{2.25}$$

Such a model can be fit non-linearly or a linearized version using a minimization routine such as PROC NLMIXED in SAS (SAS, 2004); nlme in R (R Development Core Team, 2008); or ADMB-RE in AD-Model Builder (ADMB-Project, 2009; Skaug and Fournier, 2006).

This approach provides for overall inference on the significance of an interaction, e.g. μ_γ term while also providing parameter estimates for each population. The BLUPs or empirical Bayes estimates get shrunk toward the overall mean relative to their uncertainty. In this way, the uncertain estimates obtained for each population when estimated in isolation borrow strength from the other populations when analyzed together. To fit the models individually detracts from the fact that the same parameters are being estimated from each population and treating the problem as a whole can yield better estimates (Efron and Morris, 1977). Note that care needs to be taken such that no single population estimate drives the whole relationship. This can be achieved via sensitivity analysis to the presence or absence of a given dataset.

2.4.3 State Space Modeling

State space models may enable an even greater understanding of recruitment dynamics by dealing explicitly with non-independent data and multiple sources of error and also, perhaps most importantly, allowing parameters to vary through time. Data collected over time are typically non-independent (Box *et al.*, 1976), including recruitment data (Walters, 1985). Time series analysis accounts for this non-independence while estimating parameters of interest. Comparatively recent developments in state space modeling provide a suite of methods that allow the contributions of error to be attributed to process variability (actual changes in the system of interest) and measurement error (Harvey, 1991). The application of state space models to questions of ecological interest has yielded significant insights into: patterns and determinants of marine species migration (Jonsen *et al.*, 2003; Mills Flemming *et al.*, 2006); population abundance and regulation (Clark and Bjørnstad, 2004); and population viability analysis for endangered species (Dennis *et al.*, 2008), amongst others.

Extended (Equation 2.17) and non-extended (Equation 2.8) stock-recruit relationships could also be fit in a dynamic framework (Durbin and Koopman, 2001). The time-varying approach can account for the dynamic nature of the physical and biological environment. Using a stochastically evolving parameter equation, the parameters can vary through time in an autoregressive or random walk fashion rather than remaining constant. A simplified version of the non-extended (original Ricker) Equation (2.8) for a single population could be written

$$R_t = \alpha_t S_{t-\tau} e^{-(\beta S_{t-\tau})} e^{\varepsilon_t}. \tag{2.26}$$

Notice that the typically-assumed constant α (Myers *et al.*, 1999) now varies with time according to a stochastic recurrence relationship (Peterman *et al.*, 2003)

$$\alpha_{t+1} = f(\alpha_t) + \eta_t. \tag{2.27}$$

The model can pick up on changes without having the cause of the change explicitly included. Formulations such as this may offer great potential to capture non-constancy of assumptions, e.g., changes in reproductive output per unit spawner biomass (Trippel *et al.*, 1997). A conceptual plot of this model shows that the slope at the origin (maximum reproductive rate α) varies through time (Figure 2.4). Note that the form does not use explicit environmental drivers but allows for the ultimate effect of changes in productivity to be estimated and forecast into coming seasons, a feature not available when the reproductive rate is assumed constant (Peterman *et al.*, 2003).

The likelihood for a linearized version of such a model can be written down directly and optimized using a Kalman filter (Harvey, 1991). Alternatively, non-linear state space models can be fit using Markov Chain Monte Carlo (MCMC) (Spiegelhalter *et al.*, 2004) or particle filtering methods (Doucet *et al.*, 2001).

2.5 Implications for Management

Since its early inception, a goal of recruitment science has been to build a mechanistic understanding of the processes affecting survival in the pre-recruit phase (Cushing, 1995). Cushing (1996) goes so far as to suggest that recruitment relationships are the central problem of fisheries science and management. The relationship between stock and recruitment ultimately determines the productivity of the stock and therefore how much yield the population can sustainably support (Ricker, 1975).

Management agencies, however, typically exercise extreme caution in including other environmental correlates in stock assessment (Myers, 1998), a situation that still persists in the North Atlantic. The status quo in fisheries stock assessments varies from explicit use of an established stock-recruitment relationship to taking the geometric mean of the last five years of recruitment in forecasting coming recruitment (Kell *et al.*, 2005b). So what hope is there that extensions such as those outlined in this essay will have an applied use?

Where extended relationships are found to be significant, the management of the related stocks should not be viewed separately. There are interesting arguments, however, that constant parameters or simple averages of past years may subsume these interactions. This might hold for the short-term but long-term management based upon the time-averaged parameter runs the risk of unsustainable depletion or, conversely, lost yield if the pre-recruit productivity has directionally changed, e.g., due to climate change. Here is where time-varying productivity, as estimated in a state space framework, could have its greatest applied utility. In addition, projections for the recovery of many cod stocks were overly optimistic, as discussed in Myers *et al.* (1997c). Although fishing mortality remained high for some stocks (Kelly *et al.*, 2006a; Rice, 2006) explicit consideration of the dynamic nature of productivity such as that obtained using a state space approach warrants substantial further investigation.

The utility of explicitly including specific extra drivers in recruitment relationships might ultimately depend on the temporal scale these drivers operate on. For example, inter-annual variability in weather patterns might make its inclusion in forecasting as difficult as the predictions of the abiotic environment itself, which are exceedingly difficult. Yet, there also exists low frequency, decadal-scale variation in patterns of recruitment caused by longer term changes in the environment such as the abundance of an interacting species outlined here. It is these that have the greatest potential to be captured and useful in extended higher-dimensional recruitment analyses. But what is first required is a large-scale synthesis using all available populations and data.

2.6 Conclusions

The analytical sections of this essay focus on simple extensions to the theory of recruitment to include the effect of predation during the pre-recruit phase. It is hoped that a combination of: field-driven hypotheses, which are as important today as in Hjort's time; parsimonious theory built upon the strong foundations laid by Ricker and Beverton-Holt; and proven hierarchical and dynamic modeling approaches will assist in broadly answering questions of importance and application.

In concluding, three central issues for further research are proposed:

1) Both hierarchical and state space methods offer considerable promise for the analysis of extended recruitment functions. Measurements on the proposed covariate are required for the hierarchical mixed effects approach, whereas in the state space approach one can let the parameters of an unextended relationship vary over time. Conceivably, a well estimated time-varying maximum reproductive rate could capture unspecified changes in productivity over time. From the resultant time series of the maximum reproductive rate parameter we

could obtain estimates of how productivity has changed. In the hierarchical approach we might discover significant relationships but our focus is admittedly limited to those variables for which we have data. This begs the question: is it enough to know something has changed (e.g. time-varying unextended state space model in Figure 2.4) or do we need to know why it has changed (e.g. extended models of Figure 2.3)? These questions echo earlier mechanistic versus non-mechanistic debates in ecology (Peters, 1986; Lehman, 1986). Time-varying parameters without explicit covariates may prove to be of great utility in management under changing productivity. Understanding the origins of the causes for the changes will be assisted by hierarchical mixed effects analysis but these might ultimately take a backseat in application. Pursuing both may offer a compromise by first discovering if changes have occurred and, subsequently, deciphering the weight of evidence in favour of any particular hypothesis in explaining the observed change.

2) Further theoretical investigation of the extended recruitment relationships using stability analysis (May, 1973) could yield important information on why chaotic dynamics are rarely observed in natural systems.

3) Finally, it is remarkable that many of the models used in fisheries and more generally in population ecology are those that can be neatly solved in time (from their differential formulation) such as the linear and ratio-dependent predation mortality terms used in the extensions in this paper. The space occupied by differential equations that can be thus solved is tiny compared with unsolveable but biologically plausible forms (such as the hyperbolic form used here). For these, numerical methods can be used to solve the equations. There is no reason to believe that biological systems behave in any less complex a fashion than physical systems where numerical solutions are commonplace. The investigation of such relationships could yield deeper insights. It could open a wide range of additional dynamics for theorists and occupy a long-term research objective for quantitative ecologists and biostatisticians in coupling stochastic differential equations within a state space estimation framework. Whether annual data can support such potentially formulations compared to simpler solutions is an open conjecture.

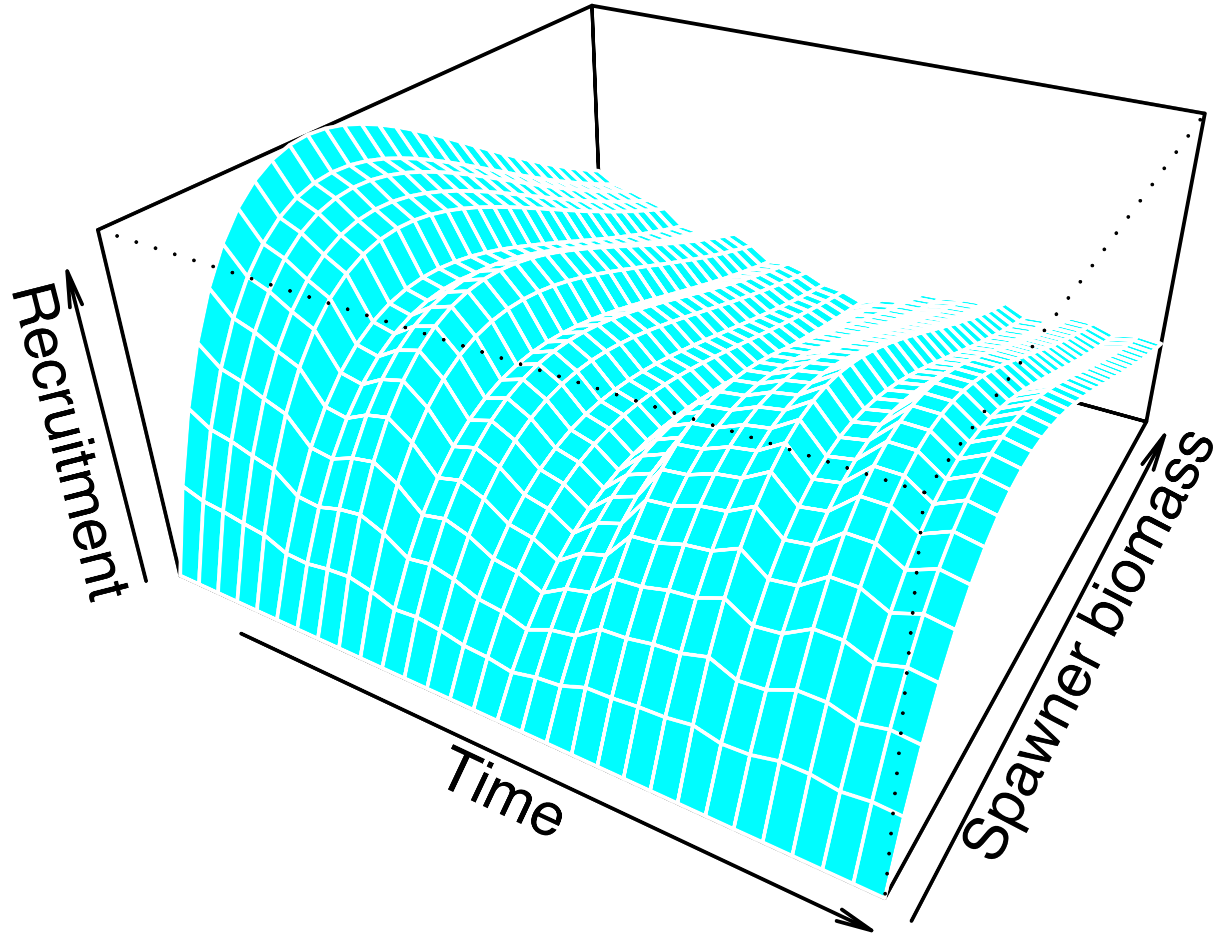


Figure 2.4: Time evolution of the stock recruitment relationship using a state space formulation. The maximum reproductive rate is assumed to vary in time, according to a random walk on the log scale, giving rise to a non-constant surface over time. Note how the surface is depressed at the mid-point of time.

Chapter 3

SURVIVAL VARIABILITY AND POPULATION DENSITY IN FISH POPULATIONS

3.1 Abstract

Understanding the processes that regulate the abundance and persistence of wild populations is a fundamental goal of ecology and a prerequisite for the management of living resources. Variable abundance data, however, make the demonstration of regulation processes challenging (Murdoch, 1994; den Boer and Reddingius, 1996; Shenk *et al.*, 1998). A previously overlooked aspect in understanding how populations are regulated (Murray, 1999; Turchin, 1999; Berryman *et al.*, 2002) is the possibility that the pattern of variability, viz. its strength as a function of population size, may be more than "noise", thus revealing much about the characteristics of population regulation. Here we show that patterns in survival variability provide evidence of regulation through density. Using a large, global compilation of marine, anadromous and freshwater fisheries data, we examine the relationship between the variability of survival and population abundance. The interannual variability in progeny survival increases at low adult abundance in an inversely density-dependent fashion. This pattern is consistent with models in which density dependence enters subsequent to the larval stage. The findings are compatible with very simple forms of density dependence, even a linear increase of juvenile mortality with adult density adequately explains the results. The model predictions explain why populations with strong regulation may experience large increases in variability at low densities (Hsiesh *et al.*, 2006). Furthermore, the inverse relationship between survival variability and the strength of density dependence imparts important consequences for fisheries management and recovery, and population

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Minto, C., Myers, R. A., and Blanchard, W. (2008). Survival variability and population density in fish populations. *Nature*, 452: 344–7.

persistence or extinction (Sæther *et al.*, 1998; Lande *et al.*, 2003; Drake, 2005).

3.2 Introduction

Hitherto, the analysis of population density regulation has focussed on the mean response of the per-capita rate of population change over population density; empirically manifested in tests of return tendency in abundance data (Wolda and Dennis, 1993). This approach has made considerable progress in our understanding of population dynamics (Turchin, 1999) and for many taxa, density-dependent regulation is readily discerned but highly variable populations (chiefly insects) can often defy attempts to detect density regulation of abundance (Godfray and Hassell, 1992). Among highly variable taxa, fish populations have been somewhat neglected in the density regulation literature. In fact, the extreme variability of reproductive success in fish populations (Fig. 3.1) suggests that they provide ideal data for tests of proposed links between variability and the strength of population regulation (Myers, 2001). We develop an alternative approach to understanding population regulation by focussing on the variance in survival. By means of theoretical exposition and a meta-analysis of 147 wild populations, we demonstrate that survival variability in fish populations shows a specific and consistent pattern, increasing with decreasing abundance. Moreover, we show that high variability does not preclude simple density regulation (Sale and Tolimieri, 2000). In the process, we demonstrate the viability of using patterns in the variance rather than the mean response to overcome the general ecological hurdle of markedly variable data.

Fish populations pass through a number of life-history stages, from egg to larval to juvenile, before recruiting to the adult population. In order to analyze the effect of density dependence on the relationship between variability and reproductive adult abundance, we will examine models in which density-dependent mortality arises in the juvenile stage, a treatment which is motivated by the demonstration of the suitability of this choice for many fish populations (Myers and Cadigan, 1993a). Stochastic mortality, independent of density, is assumed to take place during egg, larval, and juvenile stages. Using these assumptions and a suite of commonly applied models for survival ranging from no density dependence (constant productivity) to extreme overcompensation (Myers, 2001) (survival continually declines with increasing abundance), we derive predictions for the relationship between

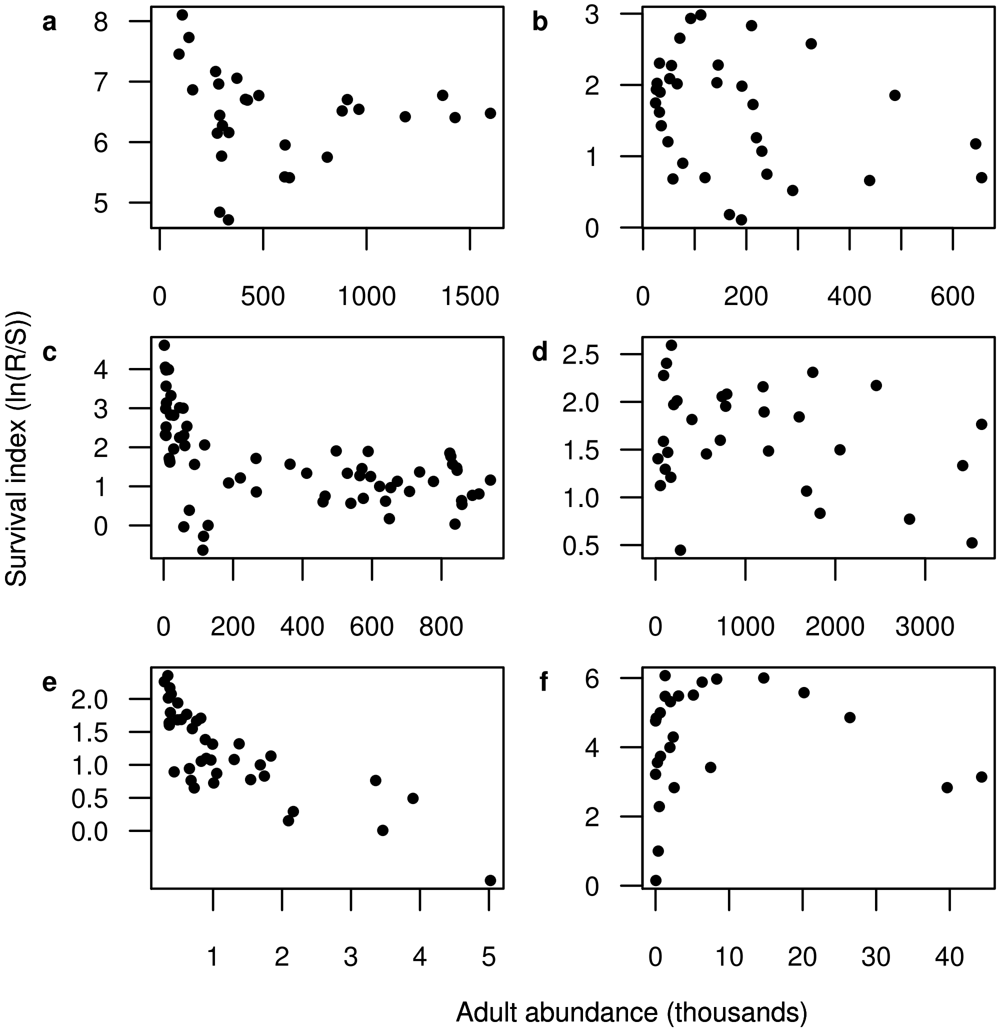


Figure 3.1: Example relationships between the survival index $\ln(R/S)$ and adult abundance (S). Examples of the Gadidae, Clupeidae, and Salmonidae families, chosen to graphically accompany specific points made on the relationship between survival variability and population density. (a) cod, Labrador/N.E. Newfoundland (b) silver hake, Mid-Atlantic Bight (c) herring, Downs stock, North Sea (d) sardine, California (e) atlantic salmon, Margaree River, NS, Canada, and (f) pink salmon, Sashin Creek, Little Port Walter, Alaska. The greatest variability occurs for populations reduced to very low levels (Downs herring) and Icelandic spring spawning herring. Extreme variation is shown in the Sashin Creek pink salmon population, where the highest variation in survival occurs when the number of females spawning was reduced to below 300.

survival variability and population density (see derivations in the Methods and Supplementary Information).

3.3 Methods Summary

Models for the variance in survival. A derivation of the survival variability model is presented in the Methods section and fully expanded upon in the accompanying Supplementary Information.

Data. The data come from a standardized global compilation of stock-recruit data of over 500 species (Myers *et al.*, 1995c). The data are standardized so that recruits and spawners have the same units (Myers, 2001). To avoid the subsequent meta-analytical means being dominated by populations with large ranges of adult abundance and thus small standard errors, the recruits and spawners were further standardized to range between 0 and 1. Only data sets with at least 15 pairs of spawner recruit observations and where the ratio of the maximum observed adult abundance to the minimum was at least 5 were used. This was done in order to eliminate data sets which had little power to address the question (Hassell *et al.*, 1989) and resulted in the analysis of 147 populations of 39 species.

Likelihood. A constant log-likelihood function for a regression of survival $\ln(R/S)$ on spawning stock biomass (S) with normally distributed errors with a fixed mean (Deriso, 1980; Schnute, 1985) $\mu_i = \ln(\alpha) + \ln(1 - \beta\gamma S_i)^{1/\gamma}$ (see Methods section) at a given S_i and variance σ^2 is given by

$$l(\mu, \sigma^2) \propto -\frac{1}{2}\sum_{i=1}^{n} \ln\sigma^2 - \frac{1}{2}\sum_{i=1}^{n} \frac{(\ln(\frac{R_i}{S_i}) - \mu_i)^2}{\sigma^2} \tag{3.1}$$

To investigate the relationship between survival variability and population density, the variance term can be re-parameterized as a functional form of adult abundance (Harvey, 1976; Drake, 2005). The log-likelihood is now written

$$l(\mu, \eta_0, \eta_1) \propto -\frac{1}{2}\sum_{i=1}^{n}(\eta_0 + \eta_1 S_i) - \frac{1}{2}\sum_{i=1}^{n}\frac{(\ln(\frac{R_i}{S_i}) - \mu_i)^2}{e^{\eta_0 + \eta_1 S_i}} \tag{3.2}$$

If the variance is constant over adult abundance, the heteroscedastic coefficient $\eta_1 = 0$ and a constant variance is recovered at $e^{\eta_0} = \sigma^2$.

Meta-analysis. A full description of the fixed and mixed-effects meta-analytical methods, used to estimate the heteroscedastic coefficients, along with sample code is provided in the Supplementary Information.

3.4 Results and Discussion

Fig. 3.2 shows the predicted relationships between survival variability and adult abundance under different survival model formulations. In comparison to the density-independent form, all density-dependent models predict marked changes in the variance in survival over adult density; including a general increase in variance at low abundance where the models exhibit compensatory survival (increasing survival). The degree of compensation increases from the left through the first five panels on the right of Fig. 3.2. The variance in survival declines monotonically for survival models displaying only compensatory survival. For over-compensatory models where survival continually declines with increasing abundance with no asymptote (e.g. Ricker and Schaefer models) the variance in survival is predicted to initially decrease, then increase with adult abundance. Maximum likelihood was used to estimate the parameters of a general Deriso-Schnute (Deriso, 1980; Schnute, 1985) survival model, assuming that the variance is not constant but follows a functional form of the explanatory variable (Harvey, 1976), adult density S as in $\sigma^2 = e^{\eta_0+\eta_1 S}$(Methods). This parameterization enables us to estimate a coefficient of heteroscedasticity (η_1), which indicates how much and in which direction the variance is changing over adult density in a given population. We then combine these estimates within and across species in a formal meta-analysis (Methods).

Fig. 3.3 shows the heteroscedastic coefficient estimates combined across populations by species under three different survival model formulations. There is a consistent trend indicated by both the fixed-effects and overall mixed-effects results for an inverse relationship between the variance in survival and adult abundance (see the individual fits in the Supplementary Information). Species for which there are greater than four populations emphasize this point in that the decline in survival variability is generally conserved across different survival model formulations. We emphasize a general mechanism that can

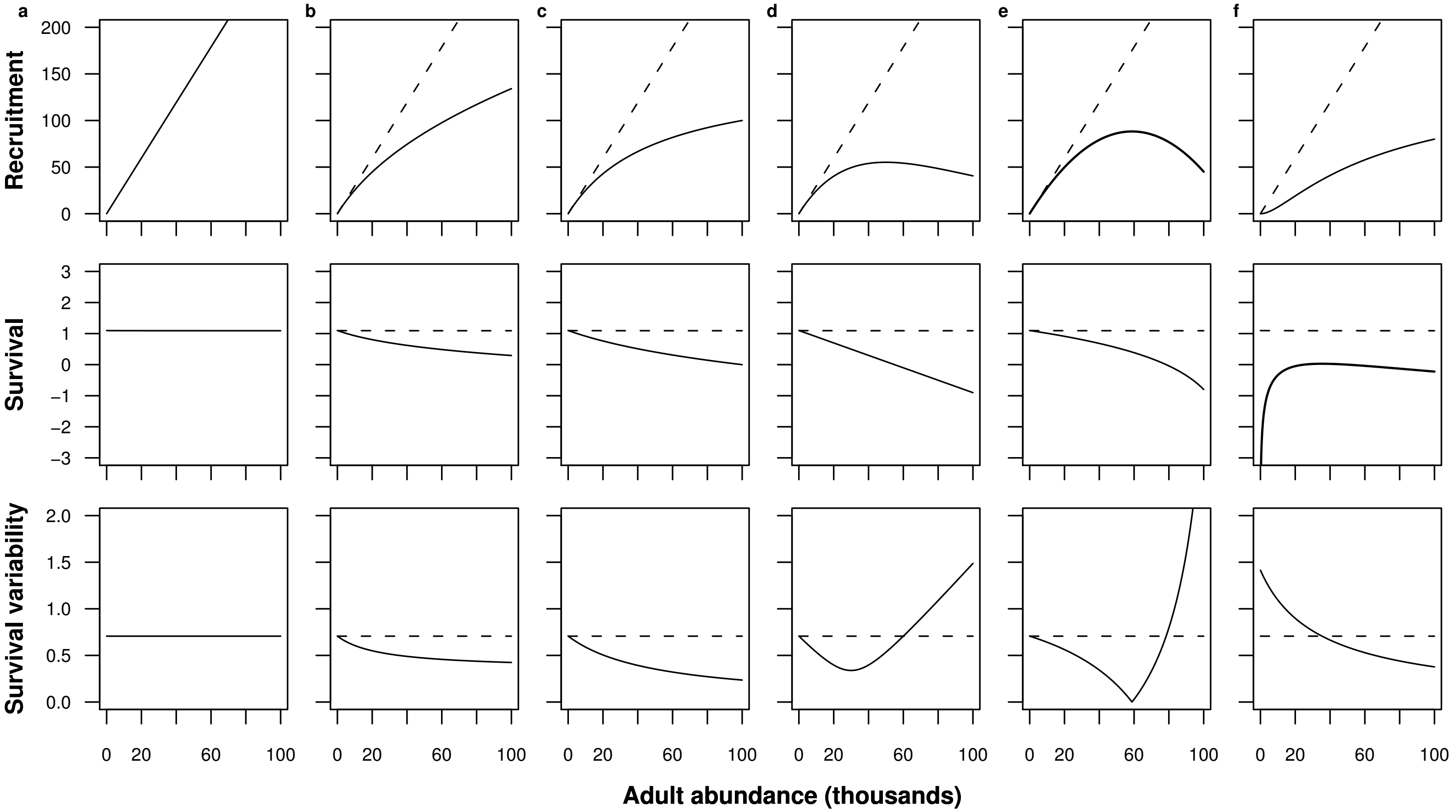


Figure 3.2: The predicted relationships between adult abundance and: recruitment, survival $\ln(R/S)$, and survival variability SD$(ln(R/S))$. The population growth models are realizations of the Deriso-Schnute general stock-recruitment model (Deriso, 1980; Schnute, 1985) at: (**a**) $\gamma = -1000$ (no density dependence), (**b**) $\gamma = -2$ (Cushing-like), (**c**) $\gamma = -1$ (Beverton-Holt), (**d**) $\gamma = 0$ (Ricker), (**e**) $\gamma = 1$ (Schaefer) and (**f**) $\gamma = -1$ for the depensatory Beverton-Holt model (Supplementary Information). The other parameters chosen were $\alpha = 3, \beta = 0.02$ for all models except the Schaefer model for which $\beta = 0.0085$ (Supplementary Information). The dotted lines are realizations in the absence of density dependence.

explain the changing variability in survival over adult abundance, density-dependent mortality in the juvenile phase following stochastic density-independent mortality in the egg and larval stages (Methods). If density-dependent population regulation decreases the variance in survival with increasing density, why then should we witness high variability in strongly regulated populations? We explain this phenomenon by way of example using equation (5) of the Methods section. Assuming that density-dependent mortality is linear in log-abundance, the variance in survival is given by $\mathrm{Var}(\ln(R_t/S_t)) \approx (1-\lambda)^2\sigma_\varepsilon^2 + \sigma_\delta^2$ (Methods), where R_t and S_t are the number of recruits and the number of spawners at time t, λ is density-dependent juvenile mortality and σ_ε^2 and σ_δ^2 are the variance in mortality in the egg and larval stages and the variance in survival during the juvenile phase unrelated to density, respectively. Based on the fitting of a key factor model for cod populations, $\lambda \approx 0.5$ is appropriate (Myers and Cadigan, 1993a). This corresponds to very strong population regulation in that a 100-fold increase in the abundance of cod entering the juvenile stage would yield only a 10-fold increase in the abundance of cod surviving the juvenile stage (Myers and Cadigan, 1993a). Such strong regulation might suggest that recruitment variability of cod should be weak, but such is not the case, since cod populations typically have a standard deviation of log recruitment in the 0.5 to 1.0 range (Mertz and Myers, 1995). That recruitment variability is strong, despite regulation, is a consequence of the extremely large variability in larval abundance (Myers and Cadigan, 1993b; Mertz and Myers, 1994b). If the variance in the juvenile mortality unrelated to density is ignored (see ref. 18) then $\sigma_{\ln(R/S)} = (1-\lambda)\sigma_\epsilon$. Thus, $\sigma_{\ln(R/S)}$ will be reduced to about one-half σ_ϵ; however, despite this attenuation, the large magnitude of σ_ϵ ensures that there will be strong survival variability. The key to understanding population regulation in this taxa is that although the observed survival variability may be high, this is the result of highly variable stochastic mortality in the larval phase but where density-dependent regulation occurs in the juvenile phase we will observe marked patterns of change in survival variability over adult density, as is generally the case (Fig. 3.3).

Our treatment does not amount to previously illuminated demographic stochasticity (May, 1973), where individual fitness variance increases at greatly reduced abundances, accompanying population-level Allee effects. In fact, including depressed survival at very low abundances (depensation) only serves to exacerbate survival variability (Fig. 3.2 panel f: depensatory Beverton-Holt model) atop of underlying changes across the whole range of densities (Fig. 3.2 panel c: usual Beverton-Holt model). In contrast to density-independent random walks, which allow for populations to plummet to irrecoverably low densities, density dependence has long been considered a safeguard from population extinction (Sale and Tolimieri, 2000). From a fisheries perspective, survival should be sufficiently high at low densities so as to mitigate the effects of driving the population down. However, the greatest survival variability occurs for populations reduced to very low levels, e.g., Downs herring in the North Sea and Iceland spring spawning herring, both of which were greatly overexploited (Myers, 2001). Extreme variation is shown in Pink salmon from Sashin Creek, Alaska, where the highest variation in survival occurs when the number of females spawning was reduced to below 300 (Fig. 3.1). The increased variance at lower adult abundance will result in higher extinction risk not accounted for in current projections (Sæther *et al.*, 1998; Lande *et al.*, 2003). An immediately practical implication for recovery is that current biological reference points and recovery projections are based upon the maximum reproductive rate at low population sizes, estimated from the slope of stock-recruitment function at the origin. Under present understanding, recruitment is deemed lognormally distributed by assuming that the survival rates in each life-history stage are an independent random variable and the sum of these on the log scale is normally distributed (Peterman, 1981). This would imply that recruitment variability would increase with the mean recruitment and equivalently that survival should be normally distributed at a given abundance with a constant variance. However, our treatment has shown the variance in survival to be generally non-constant over abundance (Fig. 3.2). If the maximum reproductive rate is estimated from the same data here shown to be naturally heteroscedastic (non-constant variance) erroneous recovery projections could result. Our model results show that survival variability can be inversely density-dependent in that the steepness of the increase in variability of survival as zero density is approached depends on the strength of the density dependence parameter (sensitivity analysis in Supplementary Information). Populations with very strong density dependence may exhibit dramatically increased survival variability during population declines. Incorporating this heteroscedastic component by weighting will affect estimates of the slope at the origin and thus alter recovery projections for severely depleted populations.

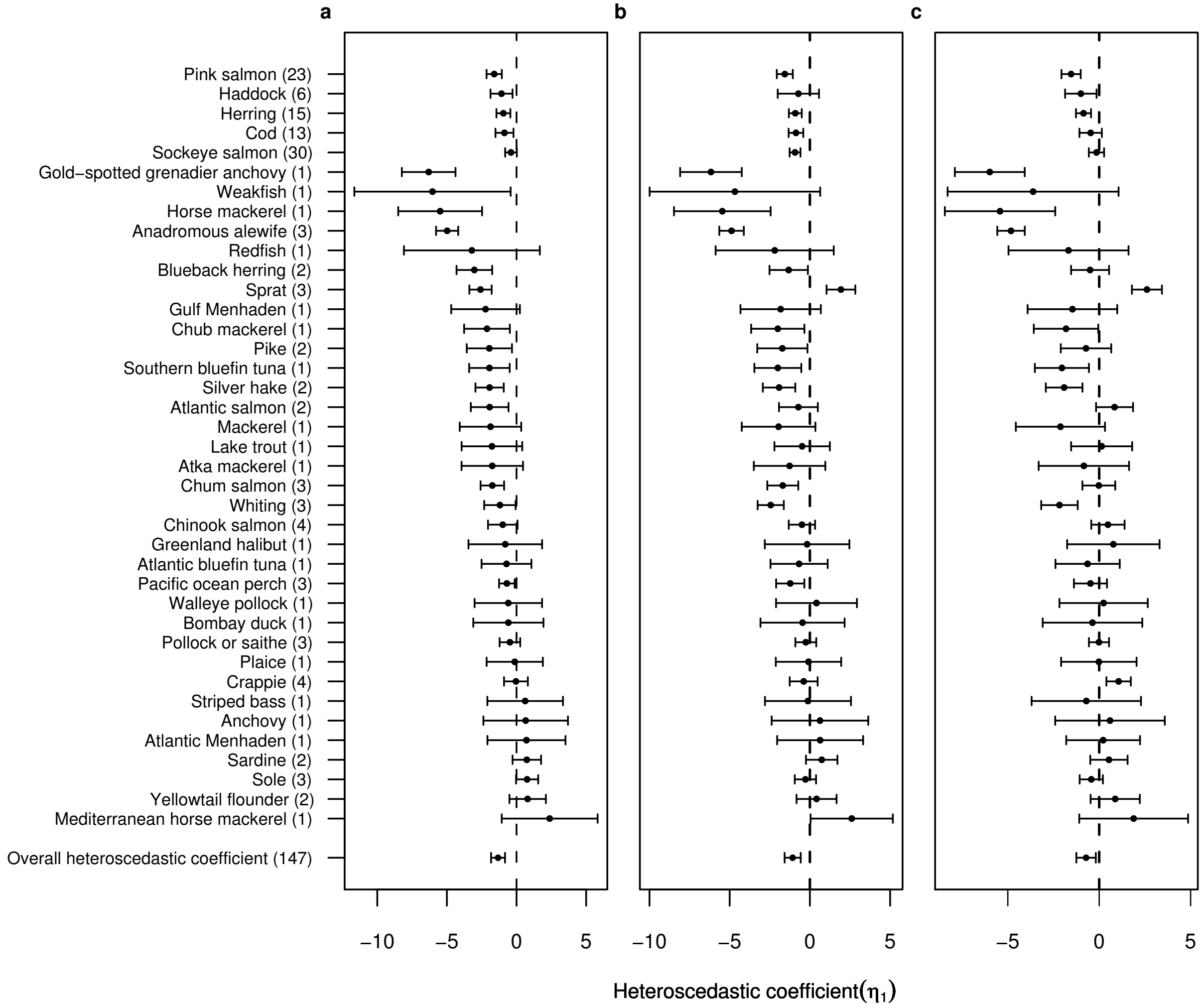


Figure 3.3: Estimates of the heteroscedastic coefficient η_1 in survival across available fish species. The panels corresponding to: (**a**) Schaefer ($\gamma = 1$), (**b**) Ricker ($\gamma = 0$), and (**c**) Beverton-Holt ($\gamma = -1$) survival models. The number of populations per species is given in parentheses and the error bars represent the 95% confidence intervals on the estimate. For species where the number of populations is greater than 4, the estimate represents a fixed-effects estimate using all populations simultaneously. For species with 4 or less populations a weighted average of the individual population estimates is provided. An overall estimate of the heteroscedastic coefficient is provided by a random effects meta-analysis (Supplementary Information).

Chapter 4

TIME-VARYING RECRUITMENT DYNAMICS OF ATLANTIC COD (*GADUS MORHUA*)

4.1 Abstract

The maximum reproductive rate is a parameter of central importance to population ecology and resource management. It determines, amongst others, the intrinsic rate of population growth, productivity, overfishing limits and reference points. Traditional approaches to stock recruitment relationships don't allow for inter-annual variation in the maximum reproductive rate. Allowing for such process variation provides an opportunity to track changes in productivity. Foundational single-stock applications (Peterman *et al.*, 2003) are extended here to the multivariate case, where the covariance structure of the trends in productivity across taxa and geographic regions is also of interest. The formulation, estimation, and interpretation of the covariance of the states, is presented. Univariate and multivariate implementations are applied to 16 widely distributed north Atlantic cod (*Gadus morua*) stocks, showing that productivity has varied markedly over the time-period investigated with many stocks currently at historically low productivity. Trends in productivity were found to be largely conserved across regions, particularly western stocks of the Irish, Celtic, and North Seas in the northeast Atlantic showing notable contemporaneous coherence. Latitudinal differences were evident, showing a differential response to environmental conditions between northern and southern latitude stocks. We conclude that time-varying parameter techniques provide a useful framework that integrates across many dimensions of environmental change affecting recruitment dynamics. Such an approach may be an attractive method for non-explicit incorporation of multiple dimensions of change into stock assessment.

4.2 Introduction

Population renewal by incoming young individuals is a key concern of fisheries ecology and management (Walters and Martell, 2004). Despite its central role and a near-century of fruitful investigation, much uncertainty remains in our understanding of recruitment (Houde, 2008a; Myers, 1998, 2001). In their early life history stages fish are most vulnerable to competition, predation, hydrography, temperature and a multitude of other environmental stressors that result in extraordinarily high levels of natural mortality (Harding and Talbot, 1973; Cushing, 1975). The varying ability to survive and grow through the early stages ultimately determines how many fish will recruit to the adult population. A thorough understanding of this period is therefore critical to understanding fish population dynamics and the management of fisheries (Allen, 1963; Cushing, 1975; Mace and Sissenwine, 1993; Cushing, 1996; Mertz and Myers, 1995; Myers, 2001).

Hypothesized processes affecting the strength of a recruiting year class or cohort are manifold, including: adult abundance and composition (maternal effects) (Trippel *et al.*, 1997; Marshall *et al.*, 2006; Green, 2008), density-dependent and density-independent mortality via predation, competition, and the physical environment, and the many interactions therein (Houde, 2008b; Green, 2008). While investigations of any particular hypothesized agent or indicator of mortality (e.g. temperature anomalies, North Atlantic Oscillation, abundance of predators/competitors) can yield potentially useful insights (Brander and Mohn, 2004; Worm and Myers, 2003; Minto and Worm, in review), other candidate hypotheses are often excluded. An example is that of the contemporary focus on relating recruitment or recruitment deviations to the physical environment (Planque and Fredou, 1999; Brander and Mohn, 2004; Mantzouni *et al.*, 2010; Mantzouni and MacKenzie, 2010, and Global Ocean Ecosystem Dynamics (GLOBEC) reports). While of intrinsic importance, given the rate of change in the physical environment, such investigations often exclude other factors such as maternal effects (Trippel *et al.*, 1997; Marshall *et al.*, 2006; Lambert, 2008) and predation or competition (Minto and Worm, in review). In an extreme case, there can exist more hypotheses than observations to test them with, for example explaining at-sea survival of Atlantic salmon (*Salmo salar*) (Cairns, 2001).

Rather than pose a specific hypothesis as a proximate agent of pre-recruit productivity, we focus here on the question of whether pre-recruit productivity has changed. Our question thus switches from *why pre-recruit productivity has changed?* to *how has pre-recruit productivity changed?* With the plethora of hypotheses available for any given stock, the argument may be made that such an approach is a necessary pre-cursor to tackling multiple and competing hypotheses. Simply asking the question of whether there has been a change and if this change is common across stocks has received remarkably scant attention, with some notable exceptions (Peterman *et al.*, 2003; Rothschild, 2007; Dorner *et al.*, 2008).

Previous investigations on the covariance or coherence (in the spectral domain, which is an alternative method for running time series analyses) of recruitment across stocks serve as a basis to extend the approach. Rothschild (2007) showed that recruitment of cod co-varied across 11 stocks in the northwest Atlantic. It is unclear, however, the degree to which this reflected changes in the adult spawning stock biomass (Cardinale and Hjelm, 2006) and thus common trends in fishing mortality or environmental forcing. Peterman *et al.* (2003) and Dorner *et al.* (2008) presented foundational state space methods to extract filtered and smoothed estimates of trends in productivity for multiple species and stocks of Pacific salmonids. The correlation amongst the various stocks was estimated, but externally to the state space model via correlation of the smoothed states. While this method provides an indication of the inter-stock productivity relationships, it does not provide for a disentanglement of what is environmentally driven and what is a result of direct interactions between the stocks or species (see the Materials and Methods below).

The goals in this paper are both methodological and applied. We develop and apply time-varying parameter estimation techniques to Atlantic cod stocks in order to test: (1) if the maximum reproductive rate has changed over time for individual stocks; (2) elucidate what form of stochastic process best describes changes where they exist; and (3) develop and apply methodologies to investigate how changes compare across regions. The impetus behind developing and applying such methods lies in the need for scientific understanding and management that reflects current productivity conditions. Without time-varying state space methodologies, in both univariate and multivariate implementations, these questions cannot be addressed.

4.3 Materials and Methods

An overview of univariate state space models is presented, followed by a treatment of the multivariate estimation. While excellent expositions of the univariate case are available elsewhere (Harvey, 1991; Durbin and Koopman, 2001; Pella, 1993) this is presented here for both completeness and background to the multivariate implementation. The relationship to recruitment models is presented subsequently along with details of Atlantic cod (hereafter termed 'cod') datasets used.

4.3.1 State Space Models

Univariate

State space models are a general family of models where the observations result from an underlying (observed or unobserved) *state* process and measurement error (Harvey, 1991). State space implementations were investigated relatively early on in fisheries (Schnute, 1991; Pella, 1993; Gudmundsson, 1994; Freeman and Kirkwood, 1995). A general state space model may be written

$$y_t = h_t(\theta_t, v_t), \tag{4.1}$$

$$\theta_t = g_t(\theta_{t-1}, w_t), \tag{4.2}$$

where θ_t is the state at time t, which is governed by the transition or process relation g_t that maps to the state in the previous time step and a random deviation w_t; the observation y_t is related to the unobserved state via the measurement equation h_t and a random deviation v_t. If g_t and h_t are linear and v_t and g_t are normally distributed and additive, the *dynamic linear model* (Petris *et al.*, 2009) results:

$$y_t = F_t\theta_t + v_t, \qquad v_t \sim \mathcal{N}(0, V_t) \tag{4.3}$$

$$\theta_t = G_t\theta_{t-1} + w_t, \qquad w_t \sim \mathcal{N}(0, W_t). \tag{4.4}$$

The univariate local-level (random walk) model is given by

$$\theta_t = \mu_t, \quad F_t = 1, \quad V_t = \sigma_v^2, \quad G_t = 1, \quad W_t = \sigma_w^2, \tag{4.5}$$

where σ_v^2 is the measurement error variance and σ_w^2 is the variance of the unobserved latent process. It is important to note that the process does not consist of a parameter per year, which would result in an over-parameterized model. The process consists of an unobserved latent state that evolves through time according to an assumed dynamic (Harvey, 1991). The local-level model is useful but restrictive as it assumes an identical relationship between successive states (up to a random deviate). A first-order autoregressive state process is less restrictive and written

$$\theta_t = \mu_t, \quad F_t = 1, \quad V_t = \sigma_v^2, \quad G_t = \phi, \quad W_t = \sigma_w^2, \tag{4.6}$$

where ϕ is the autoregressive coefficient. A first-order autoregressive model can equate with a random walk model when $\phi = 1$, otherwise it shows a quicker decay in the memory of the system. Formulations such as: a local linear trend model (random walk with time-varying drift); moving average; and autoregressive moving average models require that the dimensions of the state, measurement, and variance model matrices be increased. For example, the local linear trend model (Durbin and Koopman, 2001) may be written

$$\theta_t = \begin{pmatrix} \mu_t \\ \nu_t \end{pmatrix}, \quad F_t = \begin{pmatrix} 1 & 0 \end{pmatrix}, \quad G_t = \begin{pmatrix} 1 & 1 \\ 0 & 1 \end{pmatrix}, \quad V_t = \begin{pmatrix} \sigma_v^2 \end{pmatrix}, \quad W_t = \begin{pmatrix} \sigma_\mu^2 & 0 \\ 0 & \sigma_\nu^2 \end{pmatrix}, \tag{4.7}$$

where ν_t is the slope at time t and σ_ν^2 is the variance of the time varying slope. A first-order moving average process model, where the present state is only related to the random deviation at the preceeding time-step may be written

$$\theta_t = \begin{pmatrix} \zeta_{1,t} \\ \zeta_{2,t} \end{pmatrix}, \; F_t = \begin{pmatrix} 1 & 0 \end{pmatrix}, \; G_t = \begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix}, \; V_t = \begin{pmatrix} \sigma_v^2 \end{pmatrix}, \; R_t = \begin{pmatrix} 1 \\ \vartheta \end{pmatrix}, \; W_t = R_t \begin{pmatrix} \sigma_\zeta^2 \end{pmatrix} R_t', \tag{4.8}$$

where ϑ is the moving average coefficient and σ^2_ς is the variance of the moving average process. Equation (4.8) may be converted to a first-order autoregressive moving average ARMA(1,1) model by altering the transition matrix to

$$G_t = \begin{pmatrix} \phi & 1 \\ 0 & 0 \end{pmatrix}. \tag{4.9}$$

Including regressors

Additional regressors may be included in the framework of the dynamic linear model. For example, a linear regression of y on x with a time-varying intercept

$$y_t = \alpha_t + \beta x_t, \tag{4.10}$$

can be written in dynamic linear form as

$$\theta_t = \begin{pmatrix} \alpha_t \\ \beta \end{pmatrix}, \quad F_t = \begin{pmatrix} 1 & x_t \end{pmatrix}, \quad G_t = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}, \quad V_t = \begin{pmatrix} \sigma^2_v \end{pmatrix}, \quad W_t = \begin{pmatrix} \sigma^2_\alpha & 0 \\ 0 & 0 \end{pmatrix}. \tag{4.11}$$

Setting $\sigma^2_\alpha = 0$ would result in a regular linear regression with all error attributed to measurement error. It is important to note that the time-varying parameter states are introduced by a non-zero variance in W_t alone, where these elements are fixed at zero the parameter is constant. The regressors are included here in the measurement equation F_t. They could also be included in the process model in a similar manner to the local linear trend model (Equation 4.7) modified such that the G_t matrix contained x_t.

A time-varying slope β_t is obtained by assigning a variance to the regression slope, i.e.

$$W_t = \begin{pmatrix} \sigma^2_\alpha & 0 \\ 0 & \sigma^2_\beta \end{pmatrix}. \tag{4.12}$$

No covariance structure is assumed between the time-varying intercept and slope here for illustration only. They would likely be highly correlated, as is typical with the intercept and slope of linear regression parameters (Montgomery *et al.*, 2001), although Petris *et al.*

(2009) present dynamic regressions where the dgree of correlation in time-varying intercepts and slopes is not excessive.

Multivariate

A multivariate implementation is required when the observations at time t form a vector Y_t of dimension $p \times 1$, where $(p > 1)$. For example, an independent bivariate $(p = 2)$ $Y_t = (y_{1,t}, y_{2,t})'$ local-level model may be implemented as

$$\theta_t = \begin{pmatrix} \mu_{1,t} \\ \mu_{2,t} \end{pmatrix}, F_t = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}, G_t = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}, V_t = \begin{pmatrix} \sigma^2_{v,1} & 0 \\ 0 & \sigma^2_{v,2} \end{pmatrix}, W_t = \begin{pmatrix} \sigma^2_{\mu,1} & 0 \\ 0 & \sigma^2_{\mu,2} \end{pmatrix}, \tag{4.13}$$

where the off-diagonals of the process and measurement error matrices are zero. Direct interactions between the states can be implemented in the off-diagonals of the G_t transition matrix; covariance in the measurement errors via the V_t matrix; and covariation in the process errors via the W_t off-diagonals. In a species interactions context, Ives *et al.* (2003) interpreted an autocorrelated version of G_t with non-zero off-diagonals as a community matrix representing simple linear relationships between the p species. Ecologically, the W_t matrix governs the yearly fluctuations resulting from undefined stochastic processes of the environment (Ives *et al.*, 2003). This is central to the current analysis (see recruitment section below). A positive off-diagonal in W_t between two species represents a common response to the environment; conversely a negative off-diagonal would imply a differential response to the environment.

Additional regressors may be included in the bivariate local-level model. For example, a bivariate regression with time-varying intercepts would be given by

$$\theta_t = \begin{pmatrix} \alpha_{1,t} \\ \alpha_{2,t} \\ \beta_1 \\ \beta_2 \end{pmatrix}, F_t = \begin{pmatrix} 1 & 0 & x_{1,t} & 0 \\ 0 & 1 & 0 & x_{2,t} \end{pmatrix}, \quad G_t = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}, \tag{4.14}$$

$$V_t = \begin{pmatrix} \sigma^2_{v,1} & 0 \\ 0 & \sigma^2_{v,2} \end{pmatrix}, W_t = \begin{pmatrix} \sigma^2_{\mu,1} & 0 & 0 & 0 \\ 0 & \sigma^2_{\mu,2} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}. \tag{4.15}$$

Again, time-varying slopes ($\beta_{1,t}, \beta_{2,t}$) could be implemented by assigning variances in the bottom right 2×2 block diagonal component. Where the intercepts covary in time, the upper-left 2×2 off-diagonals would be non-zero. Such an implementation is analogous to *seemingly unrelated regressions* (SUR) (Zellner, 1962), commonly applied in econometrics (Greene and Zhang, 2003, §15.4) but differs in that SUR models typically assume measurement errors only.

More generally, a multivariate dynamic linear regression model for p response variables (e.g. p might be the number of stocks in the *Multivariate recruitment formulation* section below) may be written

$$Y_t = (F_t \otimes I_p X_t)(\theta_t) + v_t, \qquad v_t \sim \mathcal{N}(0, V_t) \tag{4.16}$$

$$\theta_t = (G_t \otimes I_p)(\theta_{t-1}) + w_t, \qquad w_t \sim \mathcal{N}(0, W_t), \tag{4.17}$$

where $F_t = \begin{pmatrix} 1 & 1 \end{pmatrix}$, $\otimes$ is the Kronecker product; I_p is the identity matrix of dimension $p \times p$ (Petris *et al.*, 2009); X_t is a diagonal matrix of dimension ($2p \times 2p$) where

$$\text{diag}(X_t) = \begin{cases} 1, & \text{if } j \leq p \\ x_{j-p,t}, & \text{otherwise;} \end{cases} \tag{4.18}$$

$G_t = I_2$ (identity matrix of dimension 2), V_t is of dimensnion ($p \times p$) and W_t is block diagonal of dimension ($2p \times 2p$). The structure of W_t is further elaborated upon when applications to stock-recruitment relationships are discussed below.

Filtering, Smoothing and Estimation

A discussion of the filtering, smoothing and estimation algorithms is provided in Appendix B. This includes a preliminary discussion of computational challenges with high-dimensional state space models. A simulation routine to investigate parameter recovery in a state space model with the time-varying intercept and slope is presented there also.

4.3.2 Application to Recruitment Models

A general deterministic relationship between adult stock S_t and recruitment R_t is given by

$$R_t = \alpha S_{t-\tau} f(S_{t-\tau}) \tag{4.19}$$

where α is the slope at the origin, $S_{t-\tau}$ is the spawner abundance when the recruits of age τ were spawned, and $f(S_{t-\tau})$ is typically a monotonic decreasing function relating survival to spawner abundance. Assumptions for $f(S_{t-\tau})$ include the Ricker $\exp(-\beta S_{t-\tau})$ and Beverton-Holt $1/(1 + S_{t-\tau}/K)$ formulations. For subsequent interpretation it is important to note here that in the derivation of the Ricker model, α is the product of fecundity and density-independent mortality integrated over the time of spawning to recruitment (Ricker, 1954). The slope at the origin has units of recruits per spawner, which for most marine fish is measured in number per weight. This makes interpretations of replacement and comparisons among separate stocks in this parameter cumbersome. Based upon earlier work by Goodyear (1993) and Mace and Sissenwine (1993), Myers *et al.* (1996) introduced a method to convert the units of recruits to that of spawners. The scaling factor used was a stock-specific weight of spawners produced per recruit at zero fishing mortality:

$$\text{SPR}_{F=0} = \sum_{a=\tau}^{A} w_a P_a e^{-\sum_{c=\tau}^{a-1} M_c}, \tag{4.20}$$

where τ is the age at recruitment, A is the maximum age, w_a is the weight at age a, P the proportion mature and M the natural mortality. When a given number of recruits is multiplied by $\text{SPR}_{F=0}$, the biomass produced is the expected weight of spawners produced over the lifetime under natural adult mortality and growth dynamics. Thus scaled, the replacement is along the 1:1 line in spawner and resultant-spawner space and the slope at the origin is now termed the *maximum lifetime reproductive rate* $\tilde{\alpha}$. Hereafter we use the *maximum reproductive rate* for the number of spawners produced per spawner over its lifetime (Myers *et al.*, 1996, 1999); hereafter, where 'productivity' is used it refers to this entity.

Univariate Recruitment Formulation

Myers *et al.* (1999) noted that the maximum annual reproductive rate is a maximum of the annual reproductive rates across the years. Peterman *et al.* (2003) explicitly investigated this for sockeye salmon using the linearized Ricker model

$$\ln(R_t/S_{t-\tau}) = a_t + \beta S_{t-\tau}, \tag{4.21}$$

where $a_t = \ln(\alpha_t)$. which may be included in the dynamic linear modeling framework. For example, assuming a random walk on a_t, as in Equation (4.11), and by writing $y_t = \ln(R_t/S_{t-\tau})$ we obtain:

$$\theta_t = \begin{pmatrix} a_t \\ \beta \end{pmatrix}, \quad F_t = \begin{pmatrix} 1 & S_{t-\tau} \end{pmatrix}, \quad G_t = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}, \quad V_t = \begin{pmatrix} \sigma_v^2 \end{pmatrix}, \quad W_t = \begin{pmatrix} \sigma_a^2 & 0 \\ 0 & 0 \end{pmatrix}. \tag{4.22}$$

Alternative formulations for the dynamics of a_t include the local linear trend and ARMA models outlined above. The ARMA implementation follows

$$\theta_t = \begin{pmatrix} \zeta_{1,t} \\ \zeta_{2,t} \\ \beta \end{pmatrix}, \; F_t = \begin{pmatrix} 1 & 0 & S_{t-\tau} \end{pmatrix}, \; G_t = \begin{pmatrix} \phi & 1 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 1 \end{pmatrix}, \; V_t = \begin{pmatrix} \sigma_v^2 \end{pmatrix}, \tag{4.23}$$

$$R_t = \begin{pmatrix} 1 \\ \vartheta \\ 0 \end{pmatrix}, \; W_t = R_t \begin{pmatrix} \sigma_\zeta^2 \end{pmatrix} R_t'. \tag{4.24}$$

The density-dependent mortality term may also vary through time (Zeng *et al.*, 1998) as β_t. This can be investigated alone, e.g. in a random walk case

$$W_t = \begin{pmatrix} 0 & 0 \\ 0 & \sigma_\beta^2 \end{pmatrix}, \tag{4.25}$$

or in conjunction with a time-varying intercept

$$W_t = \begin{pmatrix} \sigma_a^2 & \rho\sigma_a\sigma_\beta \\ \rho\sigma_a\sigma_\beta & \sigma_\beta^2 \end{pmatrix}, \tag{4.26}$$

where ρ is the correlation of the time-varying intercept and slope. A simulation routine that investigates the recovery of the parameters of Equation (4.26) under various known scenarios is presented in Appendix B.

Model Comparison

Alternative univariate model formulations were compared using Akaike Information Criterion (AIC), defined for dynamic linear models as (Harvey, 1991; Durbin and Koopman, 2001)

$$\text{AIC} = 2\left(-l(\hat{\Theta}) + k + m\right) \tag{4.27}$$

where $l(\hat{\Theta})$ is the log-likelihood evaluated at the maximum (Appendix B), k is the length of the parameter vector Θ and m is the number of diffuse starting parameters (Durbin and Koopman, 2001) (see Appendix B). Seven alternative univariate formulation were thus compared, these were: local-level a_t; local-level β_t; local-level a_t and β_t; local linear trend a_t; AR(1) a_t; MA(1) a_t; and ARMA(1,1) a_t.

An indication of the relative strength of the process variance and measurement error variance may be obtained from the signal-to-noise ratio (SNR) defined for the local-level model with time-varying intercept (Equation 4.22, denoted LL(a_t) for local-level) as

$$\text{SNR}_{\text{LL}(a_t)} = \frac{\sigma_a^2}{\sigma_v^2}. \tag{4.28}$$

Where a and β both vary in time, the SNR is given by

$$\mathrm{SNR}_{\mathrm{LL}(a_t,\beta_t)} = \frac{\sigma_a^2 + \sigma_\beta^2 + 2\rho\sigma_a\sigma_\beta}{\sigma_v^2}, \tag{4.29}$$

where the numerator is the variance of a_t and β_t.

Multivariate Recruitment Formulation

Preliminary univariate fits indicated that the local-level model with time-varying a_t fit best. The multivariate formulation therefore focusses on the multivariate extension of this model (Equations 4.16 and 4.17). In particular, we investigate the covariance matrix of the time-varying intercepts. In a multivariate formulation, W_t is block-diagonal

$$W_t = \left(\begin{array}{c|c} W_a & 0 \\ \hline 0 & W_\beta \end{array}\right), \tag{4.30}$$

with the upper left block (W_a, which is a $p \times p$ matrix), corresponding to the covariance matrix of the time-varying maximum reproductive rates. The off-diagonals of W_a measure the between-stock covariance in the maximum reproductive rates. Where stocks are behaving similarly, positive off-diagonals would be expected in W_a, conversely where they behave differentially negative off-diagonals would be expected. There exists many formulations for the structure of the covariance matrix, such as *exchangeable* (same correlation between all stocks), *exponential* and *half-Gaussian*, amongst others (Diggle *et al.*, 2003). The correlation may also be made a function of the distance (likely geographic distance but also others, if required) between the stocks. An *unstructured* correlation structure, where the correlations between each pair of stocks is free, is chosen here. Although this requires $p(p+1)/2$ parameters to parameterize W_a, it makes the least a priori assumptions on the relationships between the stocks.

Following estimation, the covariance matrix W_a can be converted into the equivalent correlation matrix $\mathcal{W}_a$ for ease of interpretation via

$$\mathcal{W}_a = D_a^{-1} W_a D_a^{-1}, \tag{4.31}$$

where D_a is a diagonal matrix with $\mathrm{diag}(D_a) = \sqrt{\mathrm{diag}(W_a)}$ (Bollen, 1989). Further details regarding the estimation of the covariance matrices, such as the maintenance of positive-definiteness are presented in Appendix B.

In total, allowing for separate measurement error variances per stock and an unstructured covariance matrix for the time-varying intercepts requires $p(p+1)/2 + p$ parameters to be estimated. We therefore analyzed the northeast (10 stocks; 65 parameters) and northwest Atlantic (6 stocks; 27 parameters) separately.

Post-estimation Investigations

Geographic location and distance, ambient temperature

The centroid of each stock, as presented in the original Myers Stock Recruitment Database (Myers *et al.*, 1995b), was used to obtain the mid-latitude of the stock for comparing trends across latitudes. The centroid was also used to calculate the distance in kilometers between the stocks for further investigation of the correlation across geographic distance. The mean spring surface temperature (Mantzouni *et al.*, 2010) was used in addition to latitude to investigate how the time-varying trends compare across stocks.

Depensation

Post-estimation, the a_t series were simply plotted against spawning stock biomass in an exploratory attempt to investigate depensatory dynamics.

Reference points

The implications for management were preliminarily explored using the fitted time-varying recruitment parameters. Where recruits and spawners have the same biomass units, the difference between the stock-recruitment curve and the 1:1 replacement line represents excess recruitment in biomass, termed theoretical yield Y

$$Y = \alpha S e^{-\beta S} - S. \tag{4.32}$$

The rate of change of yield over spawning stock biomass is given by

$$\frac{dY}{dS} = \alpha e^{-\beta S}(1 - \beta S) - 1. \tag{4.33}$$

The spawning stock biomass that results in the maximum equilibrium yield (SSB$_{MSY}$) is found by setting Equation (4.33) equal to zero

$$\alpha e^{-\beta S}(1-\beta S)=1, \tag{4.34}$$

and solving for S (Ricker, 1973). Equation (4.34) is transcendental with the solution (Coby Needle, FRS Marine Laboratory Aberdeen, personal communication) given by:

$$S_{MSY}=\frac{1}{\beta}\left(1-W\left(\frac{e}{\alpha}\right)\right), \tag{4.35}$$

where $W()$ here is the Lambert W function (Lambert, 1758; Euler, 1779). Time varying estimated $\hat{\alpha}_t$ and $\hat{\beta}$ from the univariate local-level model on α_t were substituted into Equation (4.35) and the GNU Scientific Library implementation of Lambert's W (Galassi *et al.*, 2010) within R (R Development Core Team, 2009) was used to solve for S_{MSY}. The corresponding exploitation rate at S_{MSY}, u_{MSY}, was estimated from the ratio of the yield at MSY divided by S_{MSY}, which simplifies to

$$u_{MSY}=\frac{1-e^{\beta \mathrm{S}_{MSY}}}{\alpha}. \tag{4.36}$$

4.3.3 Data

Stock assessments

Estimates of cod spawning stock biomass and recruitment (16 regions) were extracted from a newly developed, quality controlled stock assessment database (Ricard et al., *in review*). Older assessment results, either from the original Myers' stock-recruitment database (Myers *et al.*, 1995c) or the literature, were spliced together with the recent assessments to create the longest possible time series (some dating to the beginning of the 20th century). Assessment methodologies were typically sequential cohort analyses (e.g. VPA, ADAPT) except for the west coast of Scotland cod, which uses a state space model (Fryer *et al.*, 1998). Further details of the assessments used are found in Appendix C of Chapter 5.

Recent assessments for some important regions in the northwest Atlantic (e.g. Northern cod (NAFO subareas 2J3KL), Southern Grand Banks (NAFO subareas 3NO), Southern

Newfoundland (NAFO 3Ps)) were either unavailable or highly uncertain given the lack of recent catch data for these stocks. As a result, these regions are omitted from the present analyses.

The start and the end points of the assessment differ by region with some stretching back close to a century while others beginning within the last 30 years. Technically, this results in ragged start and end points for the analyses. State space models are uniquely capable of dealing with missing values by interpolating over the missing values using the transition equation only during these periods (Durbin and Koopman, 2001; Clark, 2007; Petris *et al.*, 2009). In the multivariate case, this provides an interesting opportunity to speculate on historical trends in productivity for a given stock during a time period in which no data exist for that stock. The method relies on hindcasting (Appendix B: smoothing) using the optimized covariance matrix of the process, which is estimated in the period of overlap.

Data standardization

Differences in growth rates and gear selectivity results in the age at recruitment, when fish first enter the fishery, varying by region. Myers *et al.* (1996) developed a method of comparing the relationships across regions by multiplying the recruits (in numbers) by the predicted spawner biomass per recruit assuming fishing mortality is 0 $\mathrm{SPR}_{F=0}$ (Mace and Sissenwine, 1993, as outlined above). This allows for the estimates of the maximum reproductive rate to be compared across stocks (Myers *et al.*, 1999).

The stock-recruit relationships also include a density-dependent term that limits recruitment and determines the carrying capacity. Comparing such parameters across regions requires that the data are standardized to the area available for the juveniles. Myers *et al.* (2001) and Mantzouni *et al.* (2010) achieved this by dividing cod recruitment by the area occupied by the juveniles between 0-300m and 40-300m, respectively. The 0-300m definition is used here.

4.4 Results

4.4.1 Univariate Fits

As judged by AIC, local-level models typically provided the best fits amongst the candidate univariate models (Table 4.1). Although for some regions, such as: Georges Bank, Gulf of Maine, West of Scotland, and Celtic Sea, a constant model provides equally as good a fit (Table 4.1). Of the local-level models, a time-varying maximum reproductive rate generally provided the lowest AIC, although time-varying maximum reproductive rate and density dependence appeared to fit best for the Eastern Scotian Shelf, Northeast Arctic, and Eastern Baltic (Table 4.1). More complicated structures on a_t (e.g. AR(1), MA(1), and ARMA(1,1)) generally fit poorly in comparison (Table 4.1).

Results of the simulation study of time-varying intercepts and slopes, show the parameters to be typically well-recovered under various assumptions of constancy and strength of the process variability and correlations (Appendix B). The estimates of the correlation in the time-varying intercept and slopes were imprecise, however, when the true correlation was weak (Appendix B).

The signal-to-noise ratios indicated varying degrees of attribution to process and measurement error amongst the stocks and models (Table 4.2). Some regions attributed either all to process (e.g. Northeast Arctic, Norwegian Coastal) or measurement error variance (e.g. Georges Bank, West of Scotland) in the local-level model on a_t (Table 4.2). Regions tended to exhibit either high or low SNR across model formulations with some exceptions, particularly for the moving average fits which tended to pick up on more process variance (Table 4.2).

The observed recruitment dynamics were well captured using the time-varying maximum reproductive rate random walk model (Figure 4.1). Low signal-to-noise ratios and small differences in the AIC values of constant and time-varying parameters (Tables 4.1 and 4.2) are reflected in the dynamic of the estimated states of some regions (Figure 4.1). For example, the Georges Bank maximum reproductive rate appears as a flat line, indicating the suitability of the constant model in this case (Table 4.1). Other regions, such as the Southern Gulf of St. Lawrence, Eastern Scotian Shelf and Eastern Baltic display marked changes in the maximum reproductive rate (Figure 4.1).

Table 4.1: AIC values for the univariate fits by model and region. Lower AIC values exhibit better fits. The lowest AIC values per row are shown in bold. Model names refer to the structure of the parameters a and β and are as follows: Constant refers to time-invariant parameters; LL is a local-level (random walk) model; LLT is a local linear trend model (random walk with time-varying drift); AR(1) is first-order autoregressive; MA(1) is first-order moving average; and ARMA(1,1) is first-order autoregressive, first-order moving average model. Terms that vary in time according to the given model are subscripted t, e.g. a_t.

		Constant	LL			LLT	AR(1)	MA(1)	ARMA(1,1)
Area	ID	a, β	a_t, β	a, β_t	a_t, β_t	a_t, β	a_t, β	a_t, β	a_t, β
Georges Bank	GB	**44.11**	**44.11**	**44.11**	48.11	69.97	45.52	75.40	52.83
Gulf of Maine	GOM	47.83	**47.42**	47.83	50.94	73.02	57.55	71.44	53.67
Southern Scotian Shelf and Bay of Fundy	4X	6.39	**0.46**	6.39	4.58	30.97	2.24	70.71	98.32
Eastern Scotian Shelf	4VsW	111.28	95.33	111.28	**50.96**	122.05	97.24	131.82	100.46
Southern Gulf of St. Lawrence	SGOSL	17.59	**-6.32**	17.59	-2.93	22.67	-4.78	67.63	0.00
Northern Gulf of St. Lawrence	NGOSL	29.16	**22.39**	29.16	22.98	48.43	28.25	53.12	27.78
Northeast Arctic	NEAR	39.02	19.55	39.02	**15.88**	45.90	21.36	156.78	25.76
Norwegian Coastal	NORCOAST	-1.56	**-6.68**	-1.55	-5.68	19.18	-5.09	16.93	-2.55
Iceland	ICE	-16.67	**-17.80**	-16.67	-16.22	16.03	-14.94	151.80	-10.41
West of Scotland	WSCOT	43.16	43.16	43.16	47.24	83.31	**41.27**	79.26	45.84
Irish Sea	IS	53.59	**46.65**	53.59	48.65	76.34	85.44	90.73	50.10
Celtic Sea	CS	**50.19**	**50.19**	**50.19**	54.10	82.03	53.06	71.36	58.60
North Sea	NS	50.53	**49.05**	50.53	52.81	75.20	50.43	144.14	54.87
Kattegat	KAT	41.85	**38.93**	41.85	41.68	63.56	41.86	76.17	44.33
Western Baltic	BA2224	52.26	50.89	52.26	54.63	76.30	**50.80**	78.11	62.85
Eastern Baltic	BA2532	3.91	1.07	3.91	**0.75**	30.59	3.13	54.61	6.31

Table 4.2: Signal-to-noise for the univariate fits by model and region. Values of 0 and 1000 effectively indicate either measurement error or process-error only models. Model details are per the caption of Table 4.1.

		Constant	LL			LLT	AR(1)	MA(1)	ARMA(1,1)
Area	ID	a, β	a_t, β	a, β_t	a_t, β_t	a_t, β	a_t, β	a_t, β	a_t, β
Georges Bank	GB	-	0.00	0.00	0.00	0.00	0.13	3.56	0.09
Gulf of Maine	GOM	-	0.13	0.60	2.36	0.07	1.93	1.16	0.52
Southern Scotian Shelf and Bay of Fundy	4X	-	0.13	0.14	0.09	0.11	0.17	3.59	0.02
Eastern Scotian Shelf	4VsW	-	57.24	0.00	1000	1.21	8.68	15.96	1.14
Southern Gulf of St. Lawrence	SGOSL	-	7.59	0.79	4.14	1000	6.81	33.30	0.58
Northern Gulf of St. Lawrence	NGOSL	-	2.69	0.11	6.76	1.57	0.10	0.00	0.39
Northeast Arctic	NEAR	-	1000	0.23	584.16	99.17	75.54	172.65	3.12
Norwegian Coastal	NORCOAST	-	1000	1000	377.45	2.77	28.73	3.79	6.49
Iceland	ICE	-	0.02	0.00	0.06	0.35	0.05	352.61	0.01
West of Scotland	WSCOT	-	0.00	0.00	0.06	2.49	0.00	6.39	38.15
Irish Sea	IS	-	0.14	0.00	1.05	1.09	1.00	1.37	0.09
Celtic Sea	CS	-	0.11	104.06	27.69	0.35	0.17	9.80	210.66
North Sea	NS	-	0.06	0.67	0.25	0.06	0.08	0.38	0.35
Kattegat	KAT	-	0.08	0.02	0.00	0.06	0.15	1.00	1.79
Western Baltic	BA2224	-	0.35	0.38	0.50	0.49	0.21	2.31	0.52
Eastern Baltic	BA2532	-	1000	1.23	1000	2.63	56.06	230.57	28.33

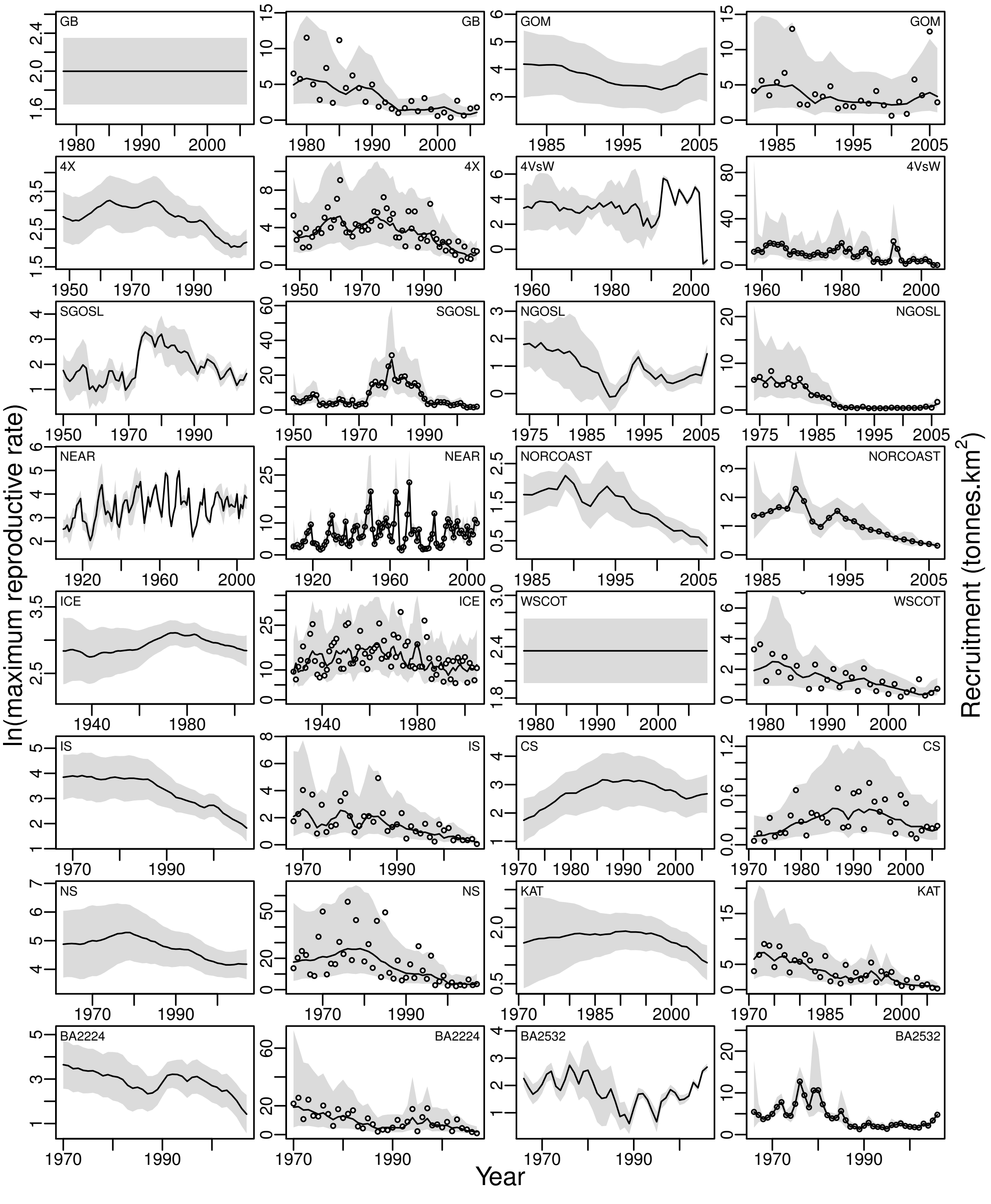


Figure 4.1: Time varying annual reproductive rates and fitted recruitment values of Atlantic cod by region. For each region, the left panel displays the estimated maximum reproductive rates and the right panel the observed and predicted recruitment values. The maximum reproductive rate on the original scale is in numbers. Grey shading represents the 95% confidence intervals. Corresponding area names are provided in Table 4.1.

Many regions display conserved changes in the reproductive rate in recent times, e.g. declines in the Northwest Atlantic: Southern and Eastern Scotian Shelf, Southern Gulf of St. Lawrence, and many of the stocks in the western Northeast Atlantic, e.g. Irish Sea, Celtic Sea, North Sea (Figure 4.1). When standardized to have a mean of zero and standard deviation of one (z-scores) the reproductive rates display a general pattern of productivity decline from approximately 1980 (Figure 4.2). Prior to 1980, the productivity was largely constant or increasing at a slow rate. Approximately post-1980 a decline was observed with an apparent increase in the rate of decline post-1995 for many stocks in the Northeast Atlantic. These patterns appear conserved across latitudes and temperatures (Figures 4.1 & 4.2), although the two northern-most stocks (Northeast Arctic and Icelandic) did not show pronounced recent declines below historic averages as others did. Two series, the Northeast Arctic (NEAR) and Eastern Baltic, showed an increase in the maximum reproductive rate post-2000 (Figures 4.1 & 4.2). The Northeast Arctic also displayed somewhat regular high-frequency (relative to the length of the series) fluctuations over the full time period but without an obvious trend (Figure 4.2).

Approximately half of the regions investigated exhibited decreased maximum reproductive rate at low spawning stock biomasses (Figure 4.3). Although the relationships are highly autocorrelated and no attempt was yet made to adjust the state space model to include this aspect (e.g. explicit depensation model), Figure (4.3) provides preliminary graphical evidence for depensatory dynamics in these stocks (e.g. Southern Scotian Shelf and Inner Bay of Fundy, Irish Sea, Celtic Sea, and North Sea). Although note must be taken that the spawning stock biomass is not at the origin where the maximum reproductive rate is extrapolated to. The Eastern Scotian Shelf stock (4VsW) has an zero recruitment event at the last year in the time series, which appears anomalous in many of the plots. While this point is the latest in the series and likely very uncertain, it is included here until further communication with the assessment scientists.

Reference Points

Time-varying reference points reflected the dynamics observed in the maximum reproductive rates (Figures 4.2 and 4.4). Regions that produced flat reproductive rates in Figure (4.2), such as the Georges Bank and West of Scotland stocks, have constant reference points. Unrealistically high reference points, such as those observed for Georges Bank,

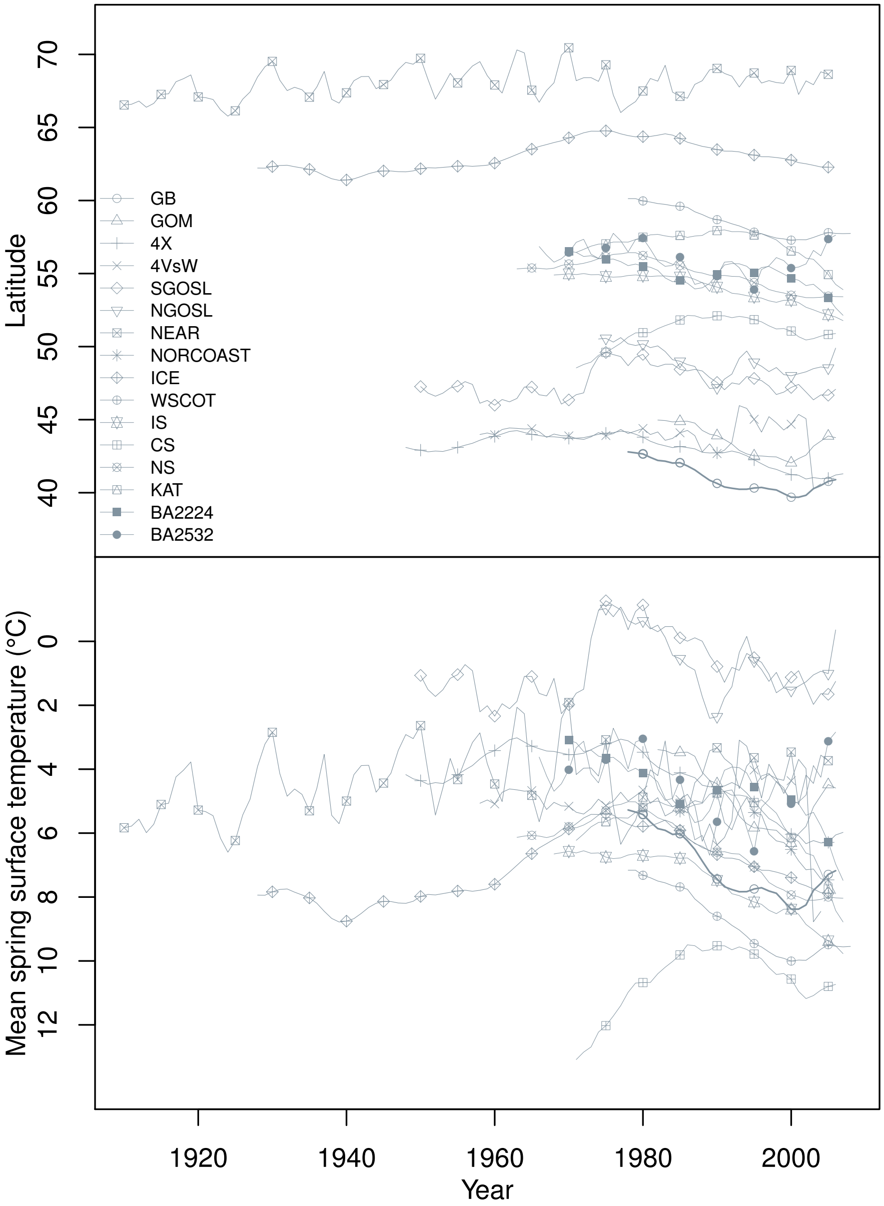


Figure 4.2: Standardized time-varying annual reproductive rates of Atlantic cod across the North Atlantic. Each line represents the individual stock presented in Figure (4.1) normalized to its mean and standard deviation. Each series is then plotted at either its mid-latitude (top panel) or mean spring surface temperature (bottom panel). Points are placed every 5 years for visual clarity.

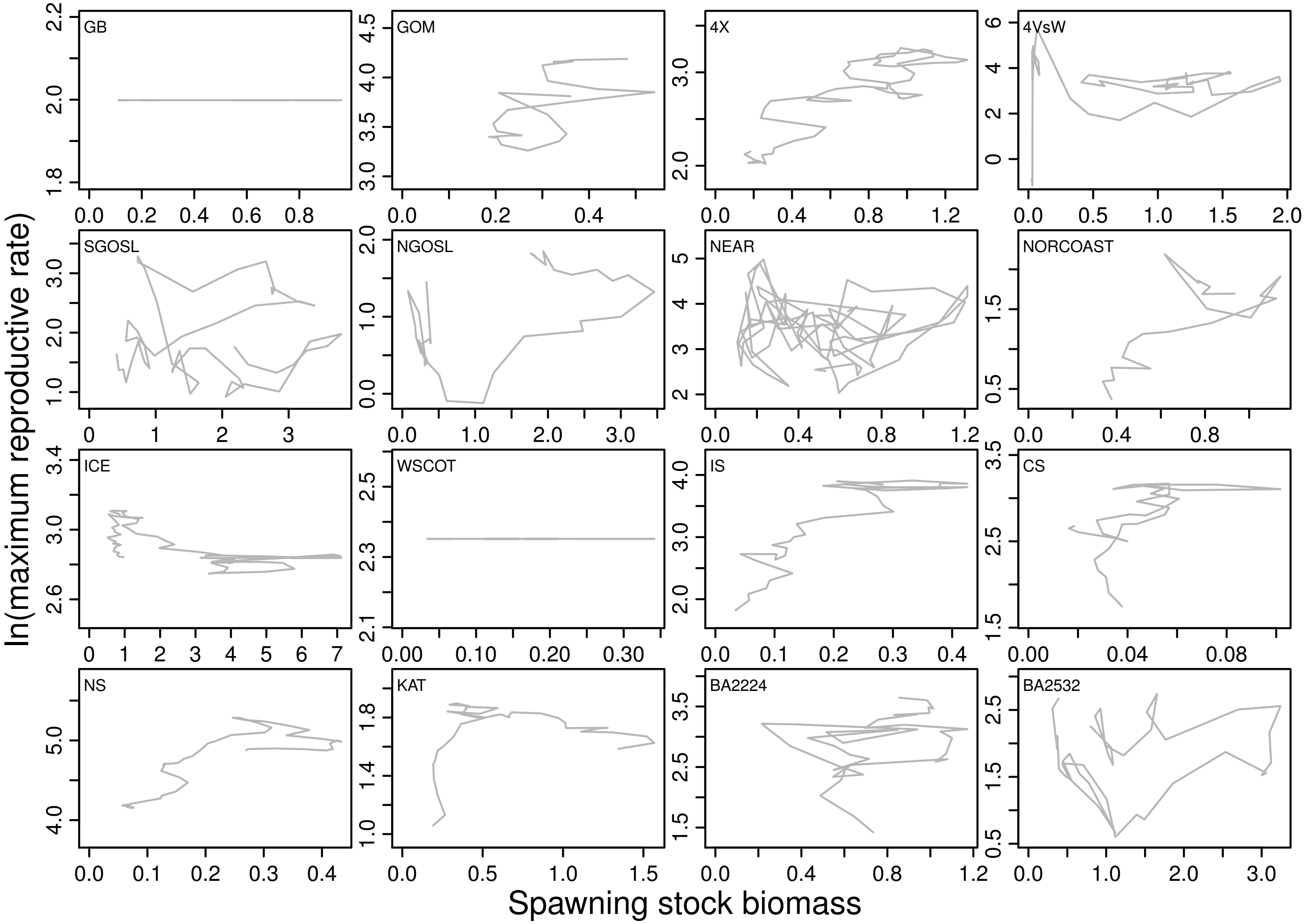


Figure 4.3: Time-varying maximum reproductive rates, as estimated via the local level on α model, plotted against spawning stock biomass. A positive relationship (reproductive rate declines at low SSB) indicates potential depensatory dynamics.

West of Scotland and the Kattegat regions (Figure 4.4) are a result of weak compensatory mortality estimated for these regions (i.e. recruitment linear over spawners with weak density-dependent mortality). This means that yield continually grows with increasing spawner biomass. Many other regions display rational reference point levels that appear relatively stable over time. Exceptions include those regions which exhibited marked jumps (e.g. Gulf of St. Lawrence and Baltic stocks).

4.4.2 Multivariate Fits

The multivariate model was fitted to all stocks on each side of the north Atlantic, simultaneously estimating the time-varying maximum reproductive rate states for each stock and strength of the relationship between stocks. A comparison of the smoothed states from the univariate and multivariate formulations show similar trends for most stocks with overlapping confidence intervals from both methods (Figure 4.5). Although some stocks, such as Georges Bank show dynamics not present in the univariate results (Figure 4.5). The multivariate states typically displayed more variability compared to the smoother univariate states (Figure 4.5). Hindcasts prior to the start of the assessment quickly become uncertain, as demonstrated by the rapidly expanding confidence intervals into the past (where no data exists for that stock). Some stocks, such as the Norwegian Coastal and West of Scotland, however, have relatively narrow confidence bands and dynamically changing hindcasts (Figure 4.5).

The correlation of time-varying maximum reproductive rates across stocks ($\mathcal{W}_a$ in Equation 4.31) shows notable patterns in the northeast and northwest Atlantic (Figure 4.6). In the Northeast Atlantic, clusters of stocks are apparent, e.g. Baltic stocks and the North Sea, and western Northeast Atlantic stocks (West of Scotland, Irish Sea, Celtic Sea, and North Sea) (Figure 4.6). In northern latitudes, the Icelandic and Northeast Arctic stocks positively covary (albeit weakly) but are notable in that they vary inversely in relation to almost all other stocks in the Northeast Atlantic (Figure 4.6(a), left-most and third left-most columns). Strong correlations exist in the Northwest Atlantic, with the Georges Bank, Gulf of Maine and Southern Scotian Shelf and Bay of Fundy stocks behaving similarly but dissimilarly to the Eastern Scotian Shelf and Southern Gulf of St. Lawrence (Figure 4.6).

The correlation between regions decays with distance on both sides of the Atlantic

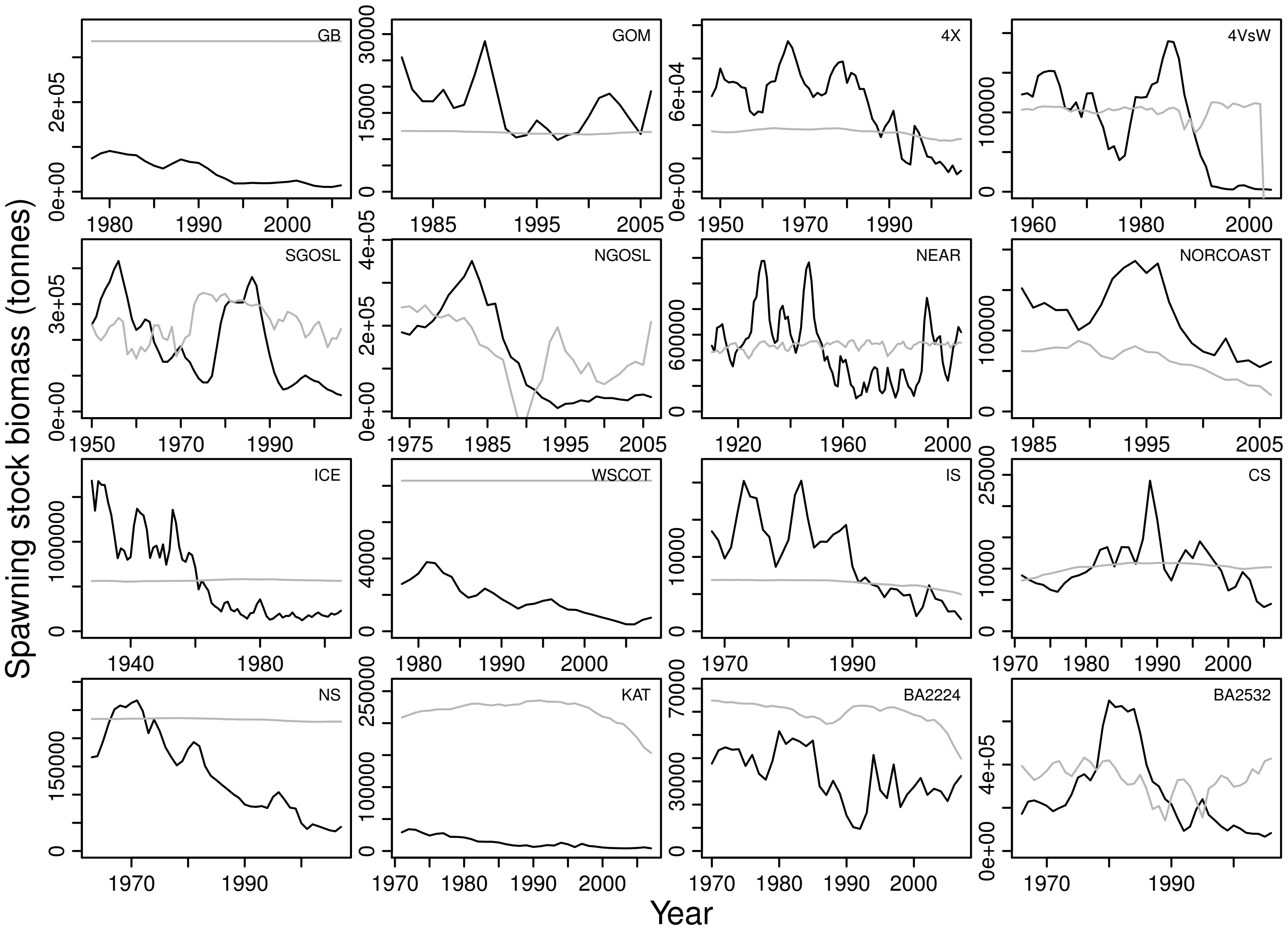


Figure 4.4: Spawning stock biomass (black line) and estimated time-varying reference point S_{MSY} (gray line) by region.

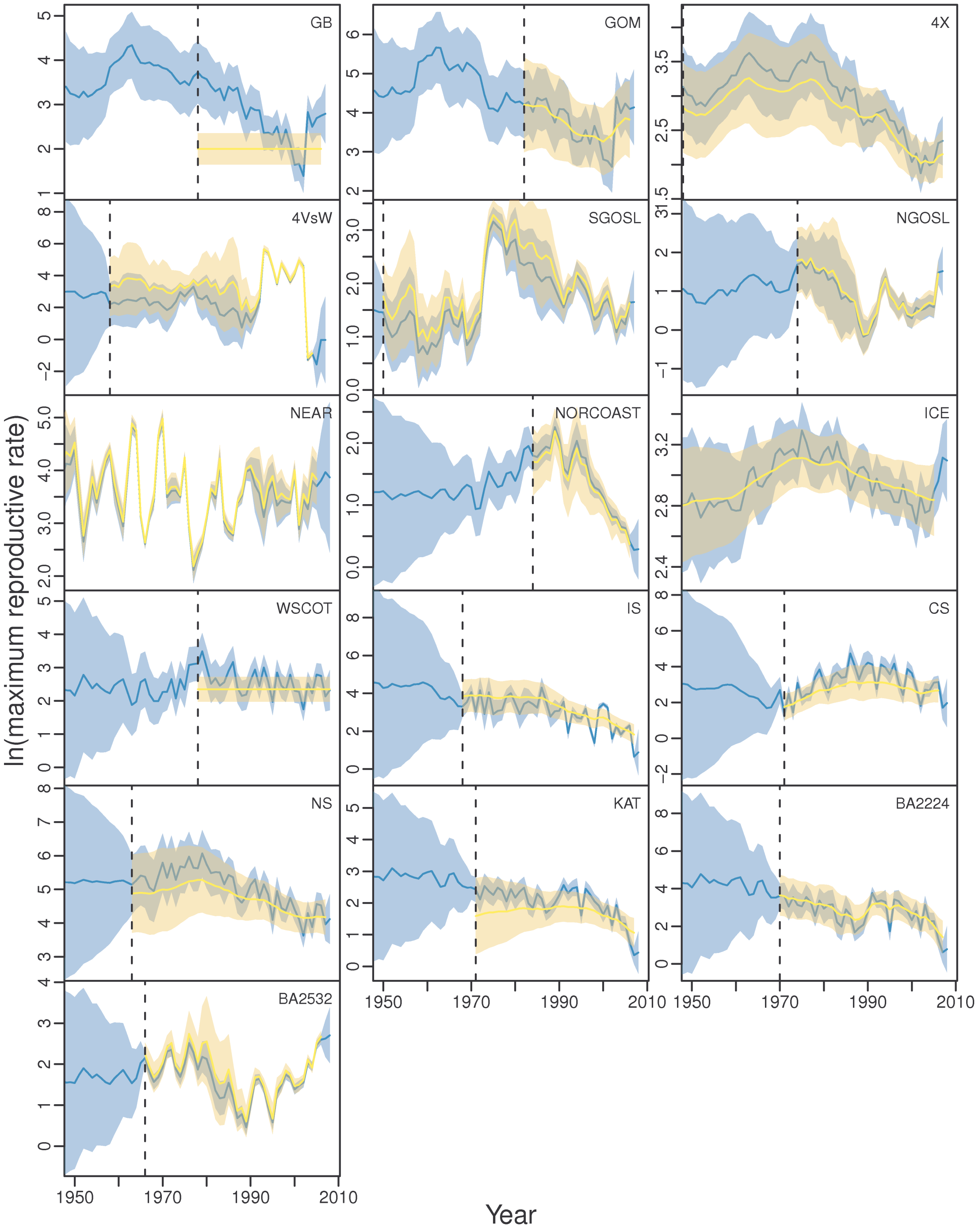
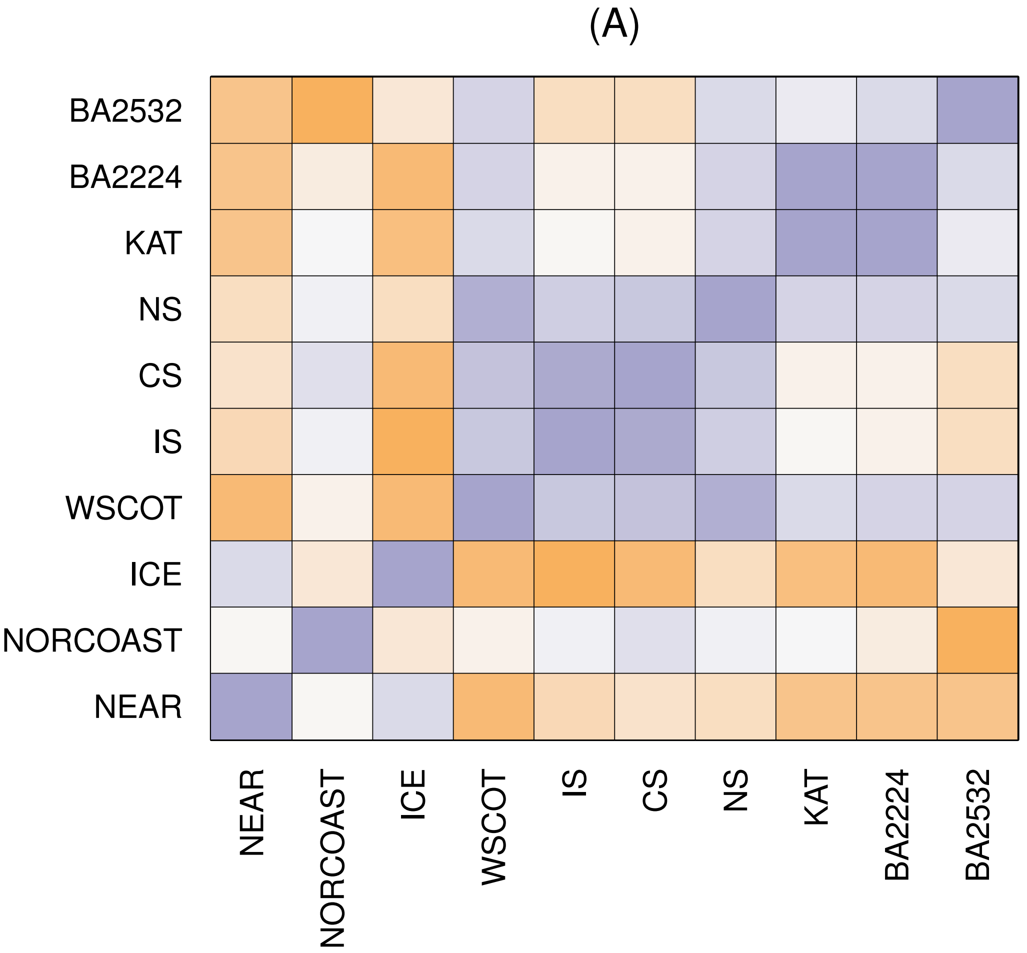


Figure 4.5: Estimated annual reproductive rates and 95% confidence intervals from univariate (yellow) and multivariate (blue) fits. Dashed vertical lines represent the earliest data point for that stock. Pre-dashed line fits are hindcasts from the multivariate Kalman smoother.



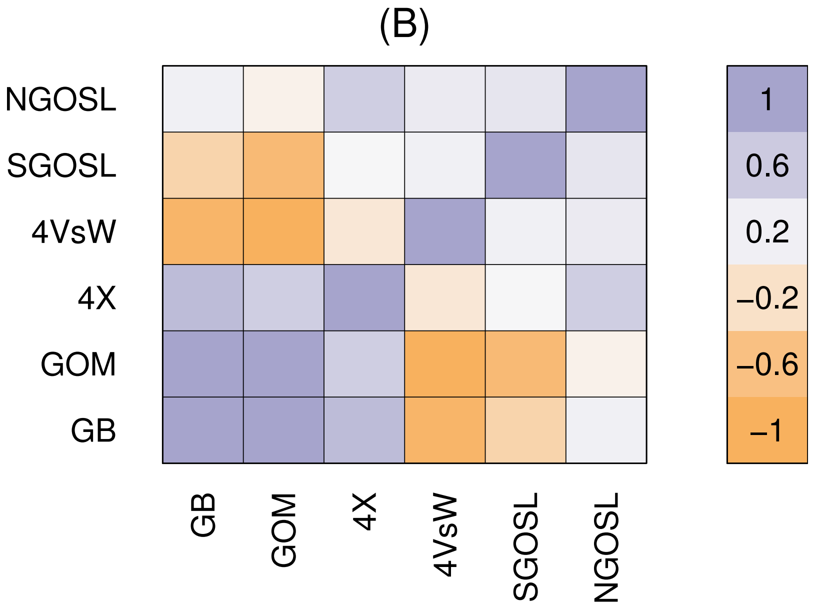


Figure 4.6: Correlations as estimated in the multivariate model for the (A) Northeast and (B) Northwest Atlantic. The strength of the correlation diverges with blue representing positive correlations and orange negative. A legend is provided for reference. Full region names are provided in Table (4.1)

(Figure 4.7). The strength of the correlation appears to decay more quickly with increased geographic distance in the northwest than northeast Atlantic (Figure 4.7). The pattern of decaying productivity with increased distance suggests this form could be parameterized as an exponential or half-Gaussian correlation structure over geographic distance.

4.5 Discussion

The dynamics of the univariate fits are discussed first, followed by the multivariate patterns. The implications are then developed.

4.5.1 Univariate Models

Population dynamics

Using a time-varying implementation of the Ricker stock-recruitment relationship, considerable changes to the population dynamics of Atlantic cod across much of its range were observed. In contrast to the results for Atlantic cod, Peterman *et al.* (2003) found that an autoregressive process best described the time-varying reproductive rate of Bristol Bay sockeye salmon. A random walk may be considered an autoregressive process where the autoregressive coefficient in equal to one. Positive autocorrelation coefficients less than one indicate more variability in the process than a random walk. It is likely that the dynamics of cod have lower frequency variation than that of sockeye, which are typified by regular fluctuations (Myers *et al.*, 1998). The dynamics of the maximum reproductive rate in cod are typified by low frequency trends (Figure 4.1), although some regions, such as the Western Baltic and Northeast Arctic, exhibit higher frequency variation. Higher frequency variation may reflect greater inter-annual variability of the environmental conditions of these regions.

Evidence for thresholds, regime shifts, and depensation?

The Eastern Scotian Shelf and Gulf of St. Lawrence stocks uniquely exhibit large jumps. For example, the Eastern Scotian Shelf stock (4VsW) exhibited relatively stable maximum reproductive rate until 1990, when it rapidly increased to a higher level, which it remained in for approximately 10 years before decreasing rapidly (Figure 4.1). The effect of the distribution of the data, i.e. whether the data in latter years are closer to the origin warrants further investigation for these and all stocks. The Southern Gulf of St. Lawrence (SGOSL) stock experienced a significant increase over a short period of time in the early 1970s from

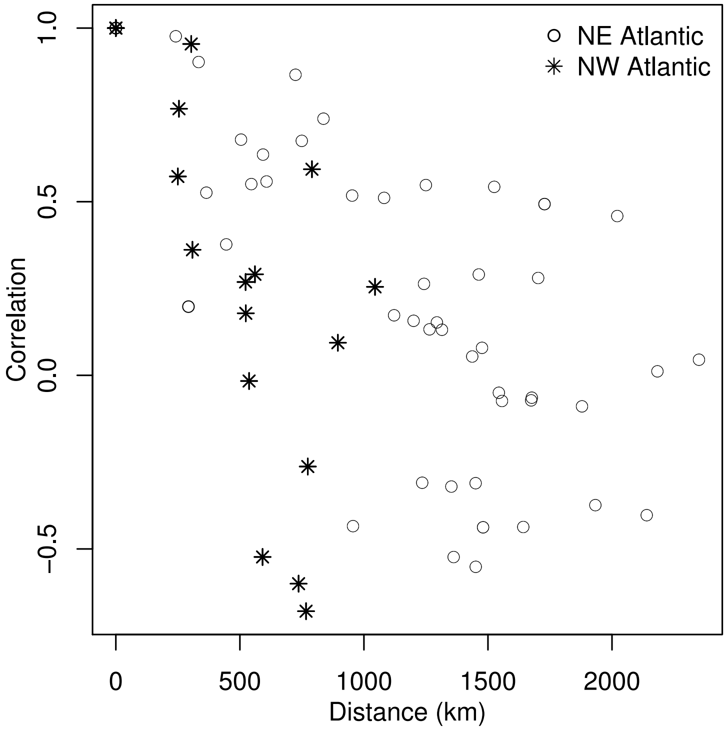


Figure 4.7: The relationship between the correlation of the time-varying productivity between regions separated by a given distance.

which it has declined towards values observed at the beginning of the series (Figure 4.1). The Northern Gulf of St. Lawrence exhibited a marked decline in the maximum reproductive rate up to 1990 when it experienced an equally marked increase over five years. It is notable that although these changes were not contemporaneous (Figure 4.6), those sort of dynamics were only observed in the Atlantic maritimes region of Canada. Potential causes for these rapid changes are elusive, although Swain and Sinclair (2000) observed marked changes in the pelagic species such as Atlantic herring during this period may have resulted in the observed dynamics. Slow, directional change typified the trends in the northeast Atlantic (e.g. Irish Sea, Celtic Sea, North Sea). Although marked changes appear in some regions, hysteretic typical of regime changes are absent, at least in the present analysis. Petraitis and Dudgeon (2004) put forward conditions for the presence of alternative stable states. These included that the system is observed for long enough to ensure the stability of the alternate state. The observed maximum reproductive rates, which reflect environmental conditions have, on occasion and within given systems (e.g. Eastern Scotian Shelf, Gulf of St. Lawrence stocks), experienced large perturbations (Figure 4.1), yet subsequent to these changes, the reproductive rates do not appear to stay in alternate states for long. A possible exception is the Eastern Scotian Shelf, which appeared to undergo a marked increase in productivity in the early 1990s and stay there for ten years before the most recent extremely low recruitment observations. Despite these examples, gradual change typifies much of the observed dynamics.

Depensation is defined as a decrease in the per-capita rate of growth declines at low abundance (Liermann and Hilborn, 2001). Using this definition, it would appear that depensatory dynamics are not as infrequent as previously thought (Myers *et al.*, 1995a). Walters and Kitchell (2001) made a similar argument; however, that study did not isolate the maximum reproductive rate, as we have done here. It must be stressed, however, that no attempt was made to embed depensation in a confirmatory fashion within the state space model. Effectively depensation could be included via the introduction of the adult abundance on the process governing the dynamics of the maximum reproductive rate (transition matrix). The degree to which this would result in an over-parameterized model is unclear and would require substantive simulations before drawing strong conclusions on the presence or absence of depensation.

4.5.2 Multivariate Models

When viewed together, consistent patterns in the maximum reproductive rate across stocks (Figure 4.2) point somewhat toward general environmental conditions forcing productivity change. Yet, when investigated more thoroughly via a multivariate state space formulation, the picture is not as unequivocal as previously thought. Based upon the coherence of spawning stock biomass or recruitment series separately in the Northwest Atlantic, Rothschild (2007) concluded that strong coherence is likely the result of common environmental conditions. Coherence of the spawning stock biomass may reflect factors other than the environment, e.g. coherent fishing mortality patterns. We have focussed on recruitment, specifically on the maximum reproductive rate, which is a combination of fecundity and density-independent (i.e environmental forcing) mortality (Ricker, 1958). Allowing the maximum reproductive rate $\hat{\alpha}$ to vary as $\hat{\alpha}_t$ allows changes in the productivity of the stock unrelated to spawner abundance or the strength of density dependence to be investigated. Environmental effects can therefore be isolated from the effects of density and adult abundance (see comments on maternal effects below), although the potential still exists for fishing mortality to affect the results if pre-recruit discarding is a concern (Kelly *et al.*, 2006a). While considerable correlation appears between some stocks of the Northwest Atlantic with clustering evident (Figure 4.6), the coherence at this life-stage cannot be said to be pan-regional (Figure 4.6). In fact, some stocks within the northwest Atlantic exhibit strongly inverse inter-annual dynamics, even those in close proximity (e.g. the Southern and Eastern Scotian Shelf stocks, Figure 4.6). Kelly *et al.* (2009) investigated temporal degradation in the synchronicity of northwest Atlantic cod recruitment as a result of local level population structure altered via overexploitation.

In the Northeast Atlantic, the northern stocks of Icelandic and Northeast Arctic cod exhibit weakly positive correlation of their time-varying maximum reproductive rates but vary inversely with those of more southern latitudes (Figure 4.6). Given concerns regarding global environmental change, these results suggest that in a very general way, these stocks would respond in an opposite direction to those of southern latitudes. Note however that the same cannot be said of the other northern stock, Norwegian coastal cod, which has weak or no correlation with the Northeast Arctic or Icelandic stocks.

Adopting a multivariate approach allows for information to be shared across stocks, in terms of the covariances amongst stocks. In many regions the similar trends are observed in the univariate and multivariate implementations (Figure 4.5). The multivariate implementation, however enables the strength of the correlation to be estimated within the model, thus accounting for all sources of uncertainty. The variability of the estimated states increases in the multivariate setting with some regions that exhibited constant reproductive rate in the univariate setting showing greatly increased dynamics in the multivariate setting (Figure 4.5). Two regions, Georges Bank and West of Scotland, emphasize this observation. The Georges Bank multivariate implementation exhibits very different dynamics compared to the univariate case. Strong correlations were estimated between the Georges Bank, Gulf of Maine and Southern Scotian Shelf and Inner Bay of Fundy stocks (Figure 4.6). This correlation is influencing the states for the Georges Bank stock. As there were no constraints on the correlation parameters (unstructured), the multivariate implementation may be more reflective of the actual dynamics, in as much as information is shared across stocks. The West of Scotland also displayed strong correlations with adjacent stocks but the multivariate implementation largely follows that of the univariate but with more variability. It is important to note that the multivariate implementation implements the same model across all stocks, whereas the univariate results suggest that while the local level model typically fits best, other formulations may have lower AIC values in specific circumstances (Table 4.1). Using the best-fitting model for each region in a multivariate setting would require the system transition matrices to be adjusted according to whichever model fits best in the univariate case. The covariance of the states could still be investigated in such an analyses.

4.5.3 Hypotheses for Observed Changes

While allowing the maximum reproductive rate to vary in time provides a method to tacitly track population dynamic changes, the approach is without explicit mechanism and may therefore be regarded as scientifically unsatisfactory. Here we discuss potential hypotheses for the observed changes. As the maximum reproductive rate is a combination of the density-independent mortality and fecundity, this could also reflect maternal changes that would affect the total egg production (Marshall *et al.*, 2006).

Density-independent effects

Mantzouni *et al.* (2010) presented a hierarchical model linking the the maximum reproductive rate to changes in temperature for Atlantic cod. Similarly, Brander and Mohn (2004) presented evidence for the effects of large scale climatic indices on recruitment success. Planque and Fredou (1999) showed relationships between temperature and raw recruitment. Drinkwater (2005) used these relationships to predict future scenarios, with with range expansions in the northern areas and contractions and loss in southern areas. The results obtained here are in agreement with these predictions in that differential responses have been observed in southern regions with conserved declines of the maximum reproductive rate in southern stocks, especially in the Northeast Atlantic where the mean spring surface temperature is typically higher than stocks at similar latitudes in the Northwest Atlantic (Mantzouni *et al.*, 2010).

Beaugrand *et al.* (2003) suggested that an interaction between temperature changes and zooplankton dynamics could adversely affect the reproductive success of cod via the match-mismatch hypothesis (Cushing, 1975, 1996). Boyce *et al.* (2010) reported large-scale changes in phytoplankton levels with marked declines being observed in many regions, including the North Atlantic. Changes to the plankton dynamics may reduce the condition of early life history stage larvae and result in increased density-indepenent mortality (Cushing, 1975). Such changes could be reflected in the observed changes to the maximum reproductive rate.

Many small pelagic species such as Atlantic herring and Atlantic mackerel have increased in abundance (Worm *et al.*, 2009). These species are observed to predate on the early life history stages of groundfish, including cod (Köster and Möllmann, 2000; Daan *et al.*, 1985; Segers *et al.*, 2007). Swain and Sinclair (2000) showed a decreased recruitment success of cod in the Southern Gulf of St. Lawrence with increased herring and mackerel abundance. Fauchald (2010) investigated zooplankton, temperature and small pelagic species abundance on cod recruitment and concluded that predation by small pelagics was an important source of pre-recruit mortality.

Maternal effects

Trippel *et al.* (1997) showed that using older fish as a measure of spawning potential provided a better relationship with recruitment. As such, changes in the age composition of the stock can affect the reproductive output (Hutchings and Myers, 1993; Wright and Gibb, 2005). Marshall *et al.* (2006) also showed changes in egg production of cod in the Northeast Arctic via changes in spawner composition. In a meta-analysis of the effect of the diversity of spawner ages on recruitment and recruitment variability, Brunel (2010) observed that such maternal effects can be important for some species (cod included, particularly age diversity) but that the effects are not taxonomically universal. It is also possible that the effects manifest through potentially complex interactions between maternal effects and environmental conditions (Green, 2008).

Ultimately, a multiple hypothesis testing framework (Wolf and Mangel, 2008) may best decipher the most important agents of why changes in productivity occur. The degree to which the observed changes are common across, or specific to, certain stocks and regions will assist in the reduction of plausible hypotheses. Candidate hypotheses must be capable of explaining the scale of the observed changes recorded here (Figures 4.6 and 4.7). Estimated trends in pre-recruit productivity that are independent of adult density and density-dependent effects, such as those proposed here, would also feature in such a testing framework. The current approach may also be amenable to alternative tests of time series forcing such as Granger causality (Hamilton, 1994). In the meantime, management advice is required that reflects the current environmental conditions and the time-varying approach may provide a mechanism for tacitly integrating across the plethora of hypotheses detailed above.

Disentangling density-independent and maternal effects

The penultimate step in the derivation of the Ricker stock recruitment model (Chapter 2) combines the product of fecundity and density-independent mortality into one term -the slope at the origin. Where information is available on the temporal dynamics of fecundity, these may be included directly in the recruitment function (effectively as an offset), this would provide for a cleaner interpretation of changes attributable to density-independent effects. Ricker (1973) makes explicit reference to this approach. Unfortunately the paucity of long-term monitoring of fecundity (Trippel *et al.*, 1997) may preclude such an investigation, although some stocks, such as the Northeast Arctic cod could be amenable to such investigations.

4.5.4 Management Implications

Population viability

Re-scaling the slope at the origin by the spawners per recruit at zero fishing mortality allows the long-term viability of the population to be investigated. A maximum reproductive rate of one would correspond to replacement whereas values below one would indicate population decline with potential extinction risk. Many of the stocks have values much greater than one (exponent of the natural logarithm of the maximum reproductive series in Figure 4.1), as noted by Myers *et al.* (1996), although some stocks such as the Northern Gulf of St Lawrence (around 1990), Eastern Scotian Shelf (recently), Western Baltic (around 1990) had values very close to one. Were they sustained, these values would result in the continued decline and increased extinction risk (Myers and Mertz, 1998a). It is important to note that the calculation of $\text{SPR}_{F=0}$ involves natural mortality of the adult stock. In many cod stocks this is fixed at 0.2, whereas Swain and Chouinard (2008) and Trzcinski *et al.* (2006) have documented marked increases in adult natural mortality that would imply a lower $\text{SPR}_{F=0}$ value than those used here. This would also affect where the replacement line occurs for the interpretation of extinction risk. Other stocks such as the Norwegian Coastal stock, Irish Sea, Kattegat, and the Western Baltic display worrying contemporary trends of decrease (Figure 4.1).

Status relative to reference points

Some stocks display remarkably constant reference points across time (Figure 4.4). For these stocks, there is sufficient evidence that a time-invariant reference point is presently suitable. Yet, other stocks show marked changes in their reference points over time. Management based upon the time-averaged parameter runs the risk of unsustainable depletion or, conversely, lost yield if the pre-recruit productivity has directionally changed. In effect, the reference points become moving targets. Where compensatory mortality exists and is fixed, the maximum sustainable yield increases with increases in the maximum reproductive rate (Equation 4.35). This makes intuitive sense in that a low productivity stock could only sustain a low sustainable yield. When it is known, however, that the stock had a previously higher sustainable yield, managing to a lower level appears counter-intuitive, even if it does reflect conditions. The implications of this merit further explicit investigations of the management implications of time-varying reference points

4.5.5 Methodological Advances and Shortcomings

Myers *et al.* (1999) demonstrated the suitability of the Ricker model in estimating the maximum reproductive rate. This requires an extrapolation but in many of the stocks observed here, very low spawner biomasses have been observed over protracted periods. Atlantic cod may therefore be a suitable model species for these methods. Adopting a linearized version of the Ricker model allows for the use of the Kalman flter in estimating the parameters and predicting the states. Models in which survival is concave over adult abundance such as the Beverton-Holt model cannot be globally linearized but may represent suitable dynamics for some species. Methods for parameter estimation in non-linear state space models will need to be developed for these cases. Options for the estimation in non-linear settings include Markov Chain Monte Carlo Bayesian (Tanizaki and Mariano, 1998; Jonsen *et al.*, 2003); particle filtering methods (Arulampalam *et al.*, 2002) such as sequential importance sampling (Doucet *et al.*, 2000); and additional numerical approximation methods Kitagawa (1987); Skaug and Fournier (2006). Laplace approximations within AD-Model Builder (ADMB) (ADMB Project, 2009) can be used in conjunction with importance sampling. This feature could be particularly useful when the suitability of the Laplace approximation is questioned (Pedersen *et al.*, 2011). Univariate implementations of the random walk models worked well in ADMB, but the multivariate implementations did not converge on relatively powerful processors (Appendix B). It is assumed that high-dimensional integral approximations precludes timely estimation in this case. Assuming linearity allows for the use of the Kalman filter, which greatly increases the speed with which high-dimensional problems can be solved. For multivariate implementations it is an open question whether non-linear approximations via local linearity (e.g. extended or unscented Kalman filters) or specifically designed non-linear methods (outlined above) will prove most practically useful (Grewal and Andrews, 2008).

4.5.6 Further Applications

The methods implemented here could open the way for many further investigations. Time-varying methods were applied only to cod stocks in the North Atlantic in the present analysis. With the development of the RAM Legacy Database (Ricard *et al.*, in review), these could be applied to many species or region combinations to investigate whether relationships are more tightly coupled (positiviely or negatively) between species within a region or within a species across regions. Questions such as these, which empirically inform across a wide gamut of management objectives, have not yet been addressed.

By altering the transition matrix to include direct interactions between species (G matrix) multispecies interactions could be investigated (Ives *et al.*, 2003) and the relative strength of environmental and species interactions within a region could be addressed.

4.5.7 Conclusions

Contrary to the belief that there is little information at low spawning stock biomasses, we have conclusively shown that the dynamics in proximity to the origin can be interpreted for Atlantic cod. Marked variation was observed in the maximum reproductive rate within and across stocks. We presented methods to allow for the simultaneous estimation of time-varying recruitment dynamics across multiple stocks, showing how the relationships change with geographic distance. We thus place the inter-relationships between the various stocks in an inferential framework. Finally, the explicit investigation of the management implications has been provided through traditional fisheries theory, although this requires further investigation.

Chapter 5

INTERACTIONS BETWEEN SMALL PELAGIC FISH AND JUVENILE COD ACROSS THE NORTH ATLANTIC

5.1 Abstract

Species interactions that occur over large spatial scales are difficult to observe, particularly in the oceans. The current lack of empirical evidence for biologically meaningful interaction parameters likely delays the application of holistic management procedures. Here we estimate interactions during the early life history of fish across regions. We present hierarchical Bayesian models that estimate the direction and strength of interactions between Atlantic cod and dominant pelagic fishes across much of their range in the North Atlantic. We test the hypothesis that small pelagic fish may reduce survival of cod at early life stages, and thereby contribute to the delayed recovery of depleted cod populations.

Significant regional variation exists between cod pre-recruit survival and Atlantic herring abundance with eight of fourteen regions displaying a negative relationship, three regions displaying no relationship and a positive relationship observed in two regions. In eight of ten regions where Atlantic mackerel co-occurs there was a negative relationship with cod survival shown, while two regions showed no relationship. Regions with sprat or capelin as dominant pelagics displayed weak or no relationship, although the strength of the negative interaction with sprat increased when autocorrelation was accounted for, similar to other species except capelin. The overall hierarchical interaction estimates with herring and mackerel were found to be negative with high probabilities of between 0.96 – 0.99 for herring and 0.87–0.98 for mackerel, depending on the chosen model. These findings suggest that predation or competition by herring and mackerel on cod could delay recovery

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Minto, C. and Worm, B. (*in review*). Interactions between small pelagic fish and juvenile cod across the North Atlantic. *Ecology*.

of depleted populations. The methods introduced here are applicable in the investigation of species interactions from time series data collected across different study systems.

5.2 Introduction

Fished populations are often depleted past the region of maximum productivity, occasionally to very low biomass levels (Hutchings and Myers, 1994; Myers *et al.*, 1997a, 2001; Rosenberg *et al.*, 2005). Of particular ecological concern is how such large-scale perturbations to the abundance of interacting species may reconfigure the community to an alternative state (Lewontin, 1969; May, 1977; Scheffer *et al.*, 2001; Frank *et al.*, 2005; Casini *et al.*, 2009). An important implication would be that the ability of a fish population to recover from depletion may depend not only on the relaxation of fishing mortality, but also upon the capacity of an altered system to allow for recovery (Scheffer *et al.*, 2001).

Such alternative states have been discussed for the North Atlantic, particularly regarding the slow recovery of depleted Atlantic cod (*Gadus morhua*, in the following simply referred to as 'cod') populations (Walters and Kitchell, 2001; Frank *et al.*, 2005; Shelton *et al.*, 2006; Swain and Chouinard, 2008). While continued directed and discard fishing mortality have been implicated in prolonging recovery (Shelton *et al.*, 2006; Kelly *et al.*, 2006b; Horwood *et al.*, 2006), so too have changes in productivity (Myers *et al.*, 1997a; Shelton *et al.*, 2006). Productivity of a fish population arises from adult survival, somatic growth and the influx of new individuals termed recruits (fish of the youngest age considered in a fishery).

Given that the strength of a cohort, upon which recovery often depends, is typically determined at a young age (Myers and Cadigan, 1993a), attention must focus on processes affecting this vulnerable period (Cushing, 1975). Species interactions, density dependence, and environmental drivers often result in extraordinarily high levels of natural mortality, that may approach 50% loss per day during the egg and larval stages (Harding and Talbot, 1973; Cushing, 1975; Houde, 2008b). This results in a classic type III survivorship curve (Pearl, 1928), where mortality is initially very high and declines as the fish grow. The ability to survive these critical early life stages ultimately determines how many fish recruit into the adult population. It is therefore essential that a thorough understanding of this period be pursued (Cushing, 1975; Mace and Sissenwine, 1993; Mertz and Myers, 1995; Cushing, 1996; Myers, 2001).

Theoretical advances on the dynamics of early life history of fish emphasize the importance of competition and predation (Walters and Korman, 1999). A prominent hypothesis in this regard is the cultivation-depensation hypothesis (Walters and Kitchell, 2001), which predicts that predation and competition by smaller prey fish can limit the survival of larger predatory fish at the egg and larval stages. Hence the larger predator may 'cultivate' the ecosystem for its own young by cropping juvenile predators or competitors to low levels. Conversely, where the large predator population is substantially reduced, small- or medium-sized fish may increase in abundance and begin to inhibit recovery of the large predatory fish at the young stages. This may result in inversely density-dependent (or 'depensatory') dynamics at low population levels (Walters and Kitchell, 2001).

Although the dominant food of many small pelagic fish species is crustacean zooplankton such as copepods and mysids, field studies of predation by Atlantic herring (*Clupea harengus*) and European sprat (*Sprattus sprattus*) in the Baltic Sea indicate that these species can also contribute significantly toward pre-recruit mortality of cod (Köster and Möllmann, 2000). Predation by herring on the eggs of European plaice (*Pleuronectes platessa*) and cod has been observed in the North Sea (Daan *et al.*, 1985; Segers *et al.*, 2007) and by herring and sprat on plaice in the Irish Sea (Ellis and Nash, 1997). Observations of pelagic fish predation on spawning grounds of cod were reported off Norway (Melle, 1985), and capelin (*Mallotus villosus*) predation on cod eggs has been documented in northeastern Newfoundland (Pepin, 2006). Significant spatial overlap between cod larvae and pelagic species has been observed, during specifically designed surveys, on the southern flank of Georges Bank (Garrison *et al.*, 2002) and between the eggs of the gadid Norway Pout (*Trisopterus esmarkii*) and feeding herring in the North Sea (Huse *et al.*, 2008). Predation by herring and Atlantic mackerel (*Scomber scombrus*) upon the early life history stages of cod may also be inhibiting the recovery of cod in the Gulf of St. Lawrence (Swain and Sinclair, 2000).

In turn, cod are important piscivores on clupeid species in most regions, e.g. the Baltic Sea, North Sea, off Norway, the Gulf of St. Lawrence, Scotian Shelf and Bay of Fundy and Georges Bank (Daan, 1973; Harvey *et al.*, 2003; Michalsen *et al.*, 2008; Hanson and

Chouinard, 2002; Link and Garrison, 2002), although in the Celtic Sea clupeids and mackerel were relatively insignificant in the diet of adult cod (Trenkel *et al.*, 2003).

Considering a general increase in the abundance of small pelagic fish (Worm *et al.*, 2009), these observations motivate a more general analysis of the effects of small pelagic fish on young cod survival. Myers (2002) highlighted the importance of extending meta-analytic applications to the study of species interactions affecting fish recruitment. Worm and Myers (2003) first proposed a meta-analytic framework for analyzing species interactions from time series of fisheries stock assessments (in fisheries terminology a *stock* is a management unit of a population; where the stock consists of more than one population or a given population straddles two or more stocks, the terms *population* and *stock* are not equivalent). Here we modify and extend this approach by focusing on interactions during the early life history. We evaluate both the effects of interspecific as well as intraspecific processes on the recruitment of cod across much of their range in the North Atlantic. Our focus is primarily on the effect of dominant planktivorous pelagic species on the survival of cod, while accounting for the effects of changes in adult spawning abundance (Cardinale and Hjelm, 2006) and density-dependence. To answer these questions more generally, we develop hierarchical methods that combine standardized estimates of the strength of the species interaction across multiple regions. Such an approach allows estimates from any given population to maintain their region-specific interpretation while also borrowing strength from other regions (Hilborn and Liermann, 1998).

5.3 Methods

5.3.1 Data

Recent estimates of cod spawning stock biomass, recruitment and total or spawning stock biomass for pelagic species were investigated in 16 regions across the North Atlantic (Table 5.1, Figure 5.1). The pelagic populations comprised of: herring (12 stocks; 14 regions), Atlantic mackerel (2 stocks; 10 regions), capelin (2 stocks, 3 regions), sprat (1 stock, 2 regions) were obtained from a newly developed, quality controlled stock assessment database (Worm *et al.*, 2009, Ricard et al., *in review*). Overlapping species to be included per region were determined from a review of the literature presented in the Appendix and summarized in the Discussion. Where available and corresponding with the latest assessment, older assessment results, either from the original Myers' stock-recruitment database (Myers *et al.*, 1995c) or the literature, were spliced together with the recent assessments (at the earliest time of the most recent assessment) to create the longest possible time series. Most of the assessments use sequential cohort analyses, e.g. Virtual Population Analysis (VPA), with the exception of the west coast of Scotland cod, which is assessed using a state space model. Full details are provided in the Appendix (Table S1), including a description of omitted regions where cod do occur. Note that a single pelagic stock, particularly mackerel, often overlaps with more than one cod stock owing to the wide dispersal of the pelagic species.

Data standardization

The data are standardized in two ways: (1) to convert the recruits into the same units as spawners (Myers *et al.*, 1996, 2001) and (2) to account for differences in the areas occupied by the populations (Myers *et al.*, 2001).

Owing to differences in growth rates and gear selectivity, the age at recruitment, when fish first enter the fishery, varies by region. For example, in the North Sea, cod recruit at age 1, in the Northeast Arctic at age 3. Not standardizing for this difference creates the risk of concluding that the recruitment productivity is lower in the Northeast Arctic whereas the age groups being different would obscure such a conclusion. Myers *et al.* (1996) achieved a method of comparing the relationships across regions by multiplying the recruits (in numbers) by the predicted spawner biomass per recruit assuming zero fishing mortality SPR$_{F=0}$ (Mace and Sissenwine, 1993, Table 5.1 here). This is a region-specific constant metric of the weight of spawners produced per recruit and accounts explicitly for the age at recruitment. It allows for the estimates of the maximum reproductive rate (a parameter of most stock-recruit relationships) to be compared across stocks (Myers *et al.*, 1999).

Stock-recruit relationships also typically include a density-dependent term. Comparing density-dependent parameters across regions requires that the data are standardized to the area available for the juveniles. Myers *et al.* (2001) and Mantzouni *et al.* (2010) achieved this by dividing cod recruitment by the area occupied by the juveniles between 0–300m and

Table 5.1: Details of cod and pelagic populations investigated: $\text{SPR}_{F=0}$ is the weight of cod spawners produced per cod recruit; pelagic species investigated by region comprise: Atlantic herring (H), Atlantic mackerel (M), European sprat (S) and capelin (C). Area is the area of the ocean floor between the contours of 0–300m (used in cod standardization) and 0–200m (used in pelagic species standardization). Note that where a pelagic species covers more than one region, the sum of the areas was used in standardizing.

Region name	Region ID	$\text{SPR}_{F=0}$ kg	Pelagic species	Area km^2 (0–300m)	Area km^2 (0–200m)
Georges Bank	GB	23.8	H,M	94765	85216
Gulf of Maine	GOM	27.9	H,M	53078	34485
Southern Scotian Shelf and Bay of Fundy	4X	14.7	M	68744	56704
Eastern Scotian Shelf	4VsW	11.7	M	97460	90749
Southern Gulf of St. Lawrence	SGOSL	7.0	H,M	110863	100134
Northern Gulf of St. Lawrence	NGOSL	4.1	H,M	101418	70387
Northeast Arctic	NEAR	12.1	H,C	969737	784495
Norwegian Coastal	NORCOAST	6.2	H,C	162857	83759
Iceland	ICE	18.9	H,C	236408	141751
West of Scotland	WSCOT	12.9	H,M	111336	105848
Irish Sea	IS	12.7	H,M	47552	47504
Celtic Sea	CS	19.9	H,M	236522	230764
North Sea	NS	18.2	H,M	616382	579062
Kattegat	KAT	7.8	H	21788	21788
Western Baltic	BA2224	5.3	H,S	44049	44049
Eastern Baltic	BA2532	3.3	H,S	214916	213016

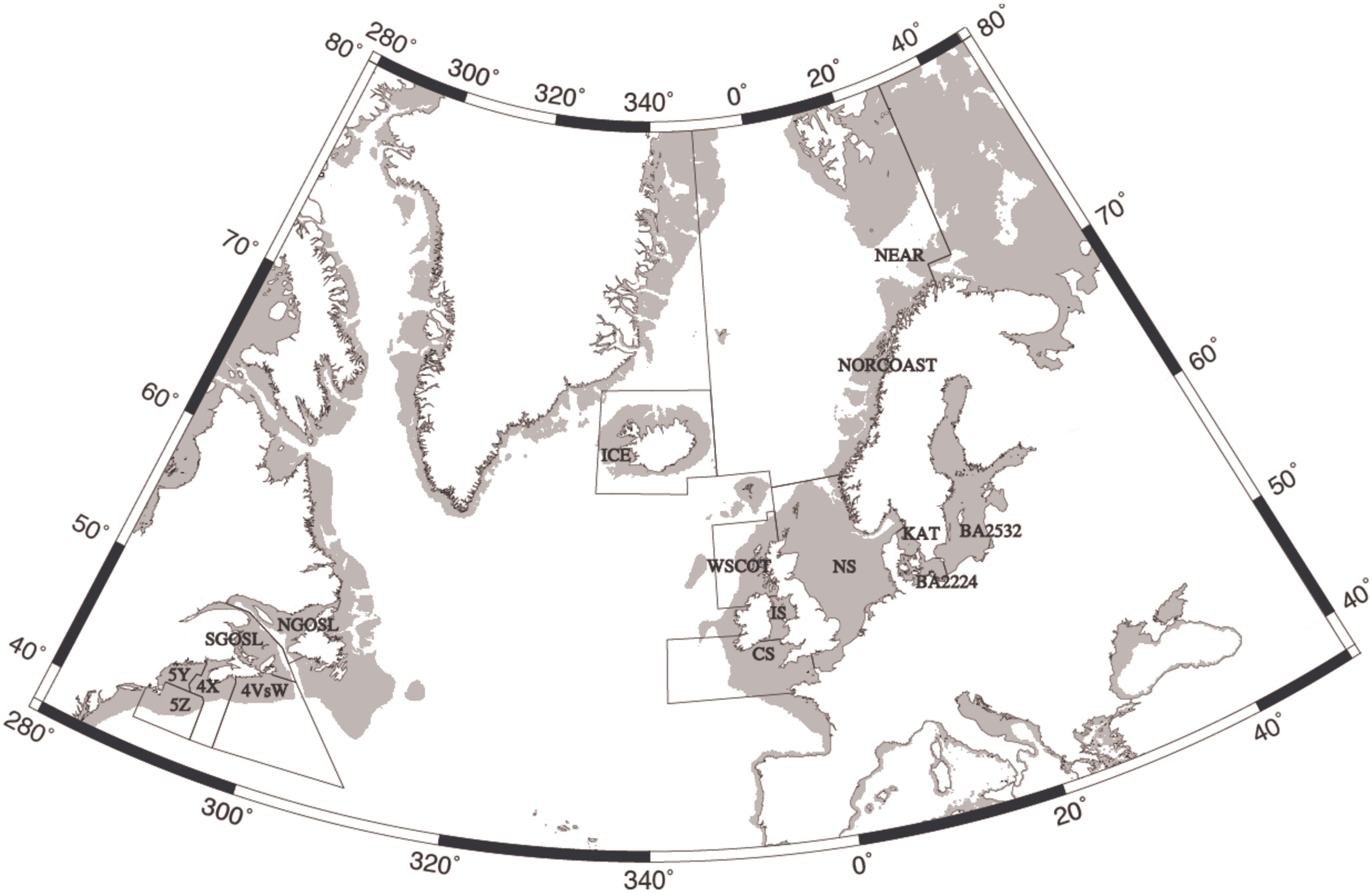

Figure 5.1: Regions of the North Atlantic investigated. Major management areas are represented by solid black polygons. The 0-300m contour line representing the preferred habitat of juvenile cod is shaded in gray. Note that the NEAR stock covers ICES regions I and II - east and west of the 30° meridian.

40–300m, respectively by study. We use the 0–300m definition here (Table 5.1). Similarly, an important issue arises when comparing interaction coefficients across regions, as the area occupied by interacting species is a dynamic region in time and space. This may be exacerbated with most small pelagic species where stock boundaries are difficult to establish. The approach we take is to define bottom depths between 0-200m as suitable small pelagic species habitat. We extracted the bottom-area (Table 5.1) between depth contours within each polygon (management area) using the *GRDVOLUME* function in the Generic Mapping Tools (Wessel and Smith, 1991) and the GEBCO 1 minute bathymetry grid (IOC *et al.*, 2003). The units of pelagic species are thus standardized to tonnes per km^2. Time series of the standardized cod recruitment and pelagic species biomasses are shown in Figure (5.2).

Importantly, these standardizations affect only the scale and not the relative ranking of the data (Myers, 2002).

5.3.2 Theory

Extended Ricker model

Assuming Ricker dynamics for the cohort in the absence of predators P (other than cannibals) and letting $f(N, P)$ be the predation mortality (a function of the abundance of prey and predators), the rate of change for the cohort can then be written (Turchin, 2003)

$$\frac{dN}{dt} = -(q + pS_0)N(t) - f(N(t), P_0). \tag{5.1}$$

where $N(t)$ is the cohort size at time t and q and pS_0 are the density-independent and stock-dependent (stock density-dependent) mortality rates, respectively (Hilborn and Walters, 1992). Note that: (1) the density-dependent mortality rate is here a function of the initial spawning stock size S_0 where the assumed biological mechanism is the presence of intraspecific compensatory predation mortality, e.g. cannibalism (Ricker, 1954); and (2) the predation mortality is a function of the initial predator abundance. Functional forms for $f(N(t), P_0)$ include linear, hyperbolic and ratio-dependent predation mortality rates

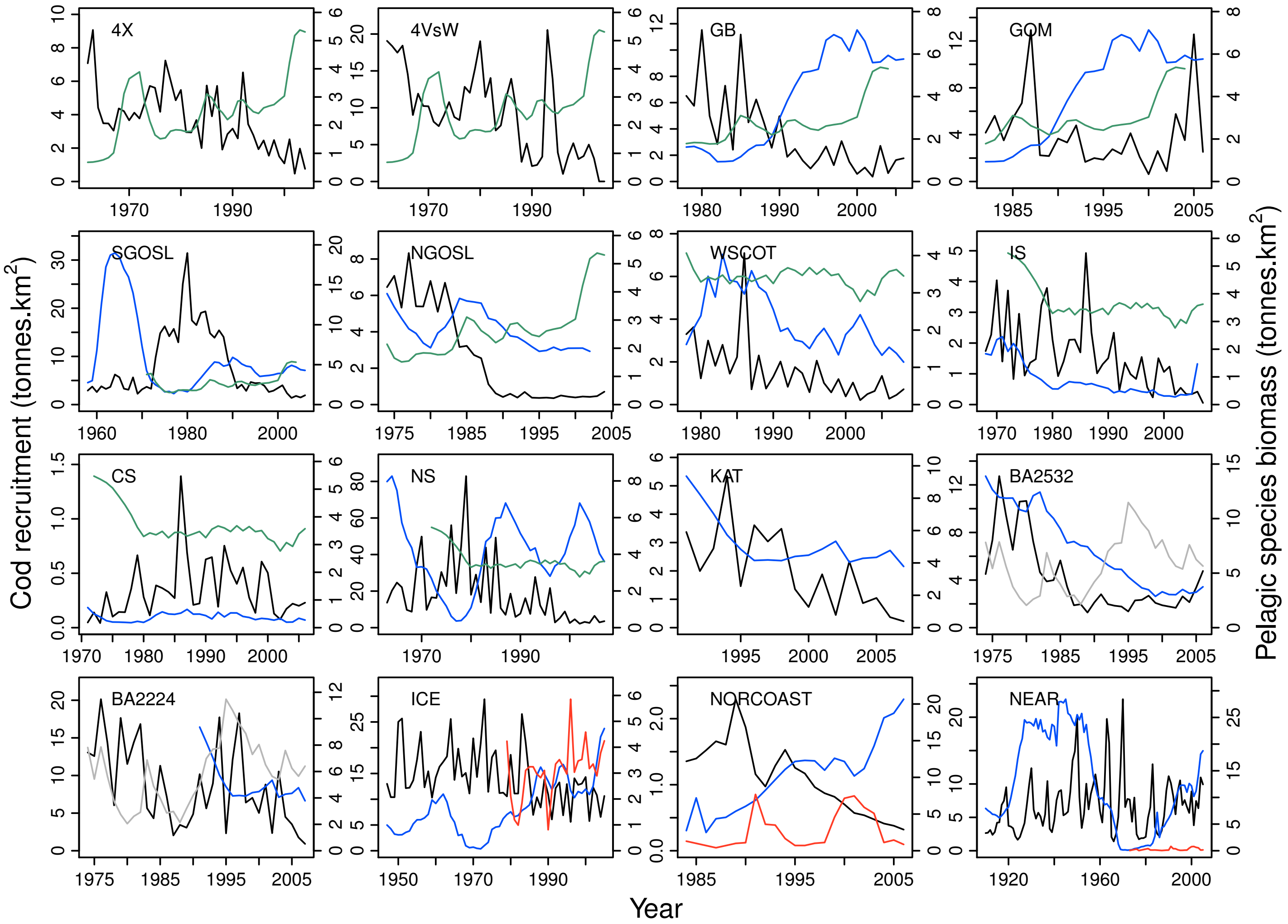

Figure 5.2: Standardized cod recruitment and pelagic species biomasses by region. Cod recruitment is shown by the solid black line, pelagic species line colors are: herring (blue); mackerel (dark green); sprat (gray); and capelin (red). Note that where a pelagic stock covers many regions the biomass per unit area refers to the total pelagic stock area. Full area details are provided in Table 5.1.

(Turchin, 2003). We focus on the linear predation mortality rate (Volterra, 1931), giving

$$\begin{aligned}\frac{dN}{dt} &= -(q + pS_0)N(t) - aN(t)P_0, \\ &= -(q + pS_0 + aP_0)N(t), \end{aligned} \tag{5.2}$$

where a is the instantaneous predation rate per predator. We recognize that the assumption of a linear increase in predation mortality over all predator abundances is restrictive. Hyperbolic and sigmoid predation mortality alternatives for $f(N, P)$ were found to have either complex or non-closed solutions but were also noteworthy in that they readily produced depensatory dynamics. A ratio-dependent predation mortality rate also induced depensatory dynamics.

Solving Equation (5.2) with respect to time provides

$$N_t = N_0 e^{-(q+pS_0+aP_0)t}. \tag{5.3}$$

N_0 is the initial number of eggs, which is the product of initial spawner abundance S_0 and fecundity F (number of eggs per spawner), so Equation (5.3) can be written

$$N(t) = S_0 F e^{-(q+pS_0+aP_0)t}. \tag{5.4}$$

Setting t at the age of recruitment τ,

$$N(\tau) = S_0 F e^{-(q+pS_0+aP_0)\tau}. \tag{5.5}$$

and letting recruitment $R = N(\tau)$, $\alpha = e^{-q\tau}F$, $\beta = p\tau$, and $\gamma = a\tau$, the extended Ricker spawner-recruit relationship is given by

$$R = \alpha S e^{-(\beta S + \gamma P)}. \tag{5.6}$$

Equation (5.6) thus relates recruitment to spawner abundance via two parameters: α the rate at which recruits are produced per spawner at low spawner abundances (slope at the origin); β the density-dependent mortality; and γ the predation rate (hereafter termed the interaction coefficient), all integrated over time τ. Thus a key assumption in the solution is that the the predator abundance is constant over time τ.

Equation (5.6), or a re-parameterized variant, is a common form used for general extensions to the Ricker, e.g. including additional sources of mortality such as abiotic forcing (Brander and Mohn, 2004). The estimation of the parameters of Equation (5.6) will be the focus of the present manuscript.

5.3.3 Statistical Analyses

Analysis of extended recruitment functions for each region can be treated separately or hierarchically. We first present non-hierarchical and then extend to the hierarchical case.

Pooled and unpooled analyses

By assuming a lognormal residual error distribution, the extended Ricker recruitment relationship is written:

$$R_t^* = \alpha S_{t-\tau}^* e^{-(\beta S_{t-\tau}^* + \gamma P_{t-\tau}^*)} e^{\varepsilon_t}, \tag{5.7}$$

where τ is the age at recruitment, $\varepsilon_t \sim \mathrm{N}(0, \sigma_\varepsilon^2)$ and an asterisk denotes the standardized series. The Ricker curve may be linearized by taking logarithms

$$\ln(R_t^*) = \ln(\alpha) + \ln(S_{t-\tau}^*) + \beta^* S_{t-\tau}^* + \gamma^* P_{t-\tau}^* + \varepsilon_t. \tag{5.8}$$

This model is often written with the spawner abundance divided through, i.e. as survival $(\ln(R_t^*/S_{t-\tau}^*))$, we have chosen to write the linearized Ricker with spawner abundance as an offset, as this will assist in an exposition of the treatment of measurement error below. To ease interpretation the signs of the density-dependent and interaction terms have been changed such that $\beta^* = -\beta$ and $\gamma^* = -\gamma$. A statistical fit of the model given in Equation (5.8) to all the data corresponds to a completely pooled analysis (Gelman and Hill, 2007). Although the pooled analysis makes little biological sense, it lies at the extreme of hierarchical data combination and is included here for comparison.

Considering $j = 1, .., M$ regions or stocks, an unpooled version of Equation (5.8) can be written

$$\ln(R_{t,j}^*) = \ln(\alpha_j) + \ln(S_{t-\tau_j,j}^*) + \beta_j^* S_{t-\tau_j,j}^* + \gamma_j^* P_{t-\tau_j,j}^* + \varepsilon_{t,j} \tag{5.9}$$

where the residuals can arise from common ($\varepsilon_{t,j} \sim \mathrm{N}(0, \sigma_{\varepsilon}^2)$) or separate error distributions ($\varepsilon_{t,j} \sim \mathrm{N}(0, \sigma_{\varepsilon,j}^2)$).

Partial regressions were used to visualize the effect of the pelagic species abundance on survival having accounted for the effect of adult cod abundance and density-dependence. The partial regressions per region were between (1) the residuals of a regression between cod pre-recruit survival and cod adult spawner biomass and (2) the residuals of a regression between the scaled abundance of the interacting species and cod adult spawner biomass. The slope of the regression between these residuals estimates γ_j^* in Equation 5.9 (Montgomery *et al.*, 2001). We plot the partial regressions as connected points to graphically investigate time-dependent dynamics.

Hierarchical analysis

A hierarchical implementation of Equation (5.9) can be written

$$\ln(R_{t,j}^*) = \ln(a_j) + \ln(S_{t-\tau_j,j}^*) + b_j S_{t-\tau_j,j}^* + g_j P_{t-\tau_j,j}^* + \varepsilon_{t,j} \tag{5.10}$$

with common or separate (by region) assumptions on the residual error variances and where the region-level parameters are now assumed to be distributed according to a multivariate normal distribution

$$\begin{pmatrix} \ln(a_j) \\ b_j \\ g_j \end{pmatrix} \sim \mathrm{N}\left(\begin{bmatrix} \mu_\alpha \\ \mu_\beta \\ \mu_\gamma \end{bmatrix}, \begin{bmatrix} \sigma_a^2 & \sigma_{a,b} & \sigma_{a,g} \\ \sigma_{a,b} & \sigma_b^2 & \sigma_{b,g} \\ \sigma_{a,g} & \sigma_{b,g} & \sigma_g^2 \end{bmatrix} \right), \tag{5.11}$$

where $\{\mu_\alpha, \mu_\beta, \mu_\gamma\}$ are the overall hierarchical means. Note that a key assumption of Equation (5.11) is that of exchangeability (Gelman *et al.*, 2004), i.e. commensurate with the model being an accurate depiction of the system, the region-specific parameters are randomly distributed around the hierarchical mean. Additional structure such as relationships between the estimated interaction coefficients g_j and mean annual shelf temperature (Myers *et al.*, 2001), mean spring surface temperature (Mantzouni *et al.*, 2010), latitude and longitude were investigated using linear regression post-estimation (Appendix).

Parameter priors

For the pooled analysis, we chose noninformative normal priors on $\{\ln(\alpha), \beta, \gamma\} \sim \mathrm{N}(0, 1/0.0001)$

and a uniform distribution on the standard error of the residual variance $\sigma_y \sim \mathrm{U}(0, 100)$. The same priors were implemented independently per region in the unpooled analysis, $\{\ln(\alpha_j), \beta_j, \gamma_j\} \sim \mathrm{N}(0, 1/0.0001)$ and $\sigma_y \sim \mathrm{U}(0, 100)$. Separate residual error variances with priors $\sigma_{y,j} \sim \mathrm{U}(0, 100)$ were also investigated. The hierarchical analysis required the specification of prior distributions on the overall means $\{\ln(\mu_\alpha), \mu_\beta, \mu_\gamma\} \sim \mathrm{N}(0, 1/0.0001)$, region-level variances with an inverse Wishart distribution $\{\sigma_\alpha, \sigma_\beta, \sigma_\gamma\} \sim$ Inv-Wishart$_4(I_3)$ where I_3 is an identity matrix of dimension 3 (Gelman and Hill, 2007), and common or separate residual error variances, as above.

Samples were drawn from the posterior distribution of all parameters using Gibbs sampling implemented in WinBUGS (Lunn *et al.*, 2000). Initially, three Markov Chain Monte Carlo (MCMC) chains were run for 25,000 iterations from dispersed starting values for all models. All model were then compared using deviance information criterion DIC (Spiegelhalter *et al.*, 2002) with the effective number of parameters estimated by half the variance of the deviance (Gelman *et al.*, 2004). Following model selection, final runs consisted of 100,000 MCMC iterations. The first half of each chain was conservatively discarded (Gelman *et al.*, 2004) and the second half sampled every 50 iterations to provide approximately 3,000 posterior samples per parameter. Chain convergence was assessed by assessing autocorrelation and the Raftery and Lewis diagnostic within each chain, and the Gelman and Rubin diagnostic between chains (Gelman *et al.*, 2004).

Time series and measurement error biases

The data used form time series and thus violate the assumption of independence. We examined the effect of temporal autocorrelation by investigating the fits under the assumptions of independent and autocorrelated AR(1) errors.

In addition, the data used in the analysis are not raw data but estimates of absolute abundances from complex population dynamics models. These results are not typically presented with estimates of the measurement error. It is known, however, that the presence of measurement errors can bias the coefficients of the Ricker model, contingent on the range of spawner values observed (Walters and Ludwig, 1981; Kehler *et al.*, 2002). The extent of the measurement error likely decreases further back in the time series where cohorts have completely passed through the fishery but recent estimates are likely to contain higher levels of measurement error. We investigated the sensitivity of the results to varying degrees of measurement error (Appendix).

5.4 Results

Time series trends

Time series of cod recruitment typically displayed high inter-annual variability with overall declining trends observed in many regions (Figure 5.2). Pelagic total biomass series are generally smoother, as would be expected from a summed biomass across many age groups. Importantly, periods of relatively high and low pelagic species biomass occur in most regions with some (e.g. North Sea herring) exhibiting multiple peaks and troughs. Many pelagic species display increasing trends over time, although the Baltic stocks of herring are decreasing (Figure 5.2). In some regions, periods of high pelagic abundance coincide with decreased recruitment of cod, e.g. Southern Gulf of St. Lawrence, Georges Bank; in others, this varies over the course of the series, e.g. early and late periods in the North Sea. The degree to which these observations are attributable to interactions or changing adult cod abundance is presented below.

Model comparisons and diagnostics

All MCMC chains mixed well and appeared to converge relatively quickly, as indicated by low within-chain autocorrelation (≤ 0.07, typically lower or negative), Gelman and Rubin diagnostics of 1 or at most 1.01 and Raftery and Lewis diagnostics of approximately 1 also.

For all pelagic species, except capelin, models including density dependence and the pelagic species biomass with autocorrelated region-specific error variance structures had the lowest DIC values in both the un-pooled and hierarchical models (Table 5.2). Although the autocorrelated residual variance structure typically fit best we also draw inference on the non-autocorrelated implementations, as Myers *et al.* (1999) noted that autocorrelated residual errors in a hierarchical analysis can overly shrink the region-specific values toward the overall mean. The pooled analysis fit poorly compared to the separate and hierarchical equivalents (Table 5.2).

Effect of herring

Visually inspecting the partial regression plots of the marginal relationship between herring abundance and juvenile cod survival shows a negative relationship in 8 regions, no relationship in 2 regions, and a positive relationship in 4 regions (Figure 5.3). Regions with a positive relationship in the separate analysis generally became flat or weakly negative in the hierarchical analyses (Table 5.3, Figure 5.3). The overall mean interaction coefficient from the best fitting model (hierarchical with separate autocorrelated errors by region: model *h8* in Table 5.2) was -0.037 with a 99% probability of being negative. The non-autocorrelated version (model *h5* in Table 5.2) had a mean interaction of -0.042 with a 97% probability of being negative. A comparison of the posterior densities by region and model assumptions (unpooled, hierarchical, autocorrelated) is shown in Figure 5.5.

There was evidence of shrinkage of both strongly positive and negative separate estimates toward the overall mean in the hierarchical independent error analysis (Figure 5.5). The hierarchical autocorrelated error analysis showed strong shrinkage. The inner Baltic regions displayed either a flat or positive relationship between herring abundance and juvenile cod survival in the separate analysis (Table 5.3, Figure 5.5). These became either flat or weakly negative in the hierarchical and hierarchical autocorrelated models (Figure 5.5).

Effect of other pelagics.

Negative trends were observed between mackerel abundance and juvenile cod survival in 8 of 10 regions examined (Figure 5.4). The mackerel-cod interaction in both the West Coast of Scotland and Irish Sea became weakly negative in the hierarchical analysis (Figures 5.4 and 5.5, Table 5.3). The overall mean interaction coefficient from the best fitting model (hierarchical with separate autocorrelated errors by region: model *h8* in Table 5.2) was -0.1 with a 96% probability of being negative. The non-autocorrelated version (model *h5* in Table 5.2) had a mean interaction of -0.16 with a 98% probability of being negative. Estimates for the Eastern Scotian shelf (NAFO are 4VsW) cod recruitment in 2004 and 2005 were exceptionally low and outlying on the partial regression plots (Figure 5.4). A sensitivity analysis to the hierachical analysis for mackerel with region 4VsW omitted resulted in the overall probability of being negative in model *mh8* declining from 96% to 87%.

The three regions with capelin showed no or weakly negative relationships with juvenile cod survival (Figure 5.4–5.5, Table 5.3). Sprat in the Baltic regions had low probabilities of being negative when analyzed with independent residual error structures (Western Baltic:

0.29; Eastern Baltic: 0.61) although the evidence for negative impacts was greater when autcorrelation was accounted for (Western Baltic: 0.8; Eastern Baltic: 0.82) (Figures 5.4–5.5, Table 5.3).

Post-estimation relationships

No relationships were found between the strength of the interaction terms and temperature or latitude in the herring or mackerel analyses (Figure C.1–C.2). The relationship with longitude showed that the interaction terms for herring were typically stronger in the Northwest Atlantic regions (Figure C.1).

5.5 Discussion

Our meta-analysis of species interactions documented an overall negative relationship between Atlantic herring or mackerel abundance and pre-recruit cod survival across the North Atlantic (Figures 5.3–5.5). This illustrates the importance of considering predation as a driving factor in recruitment relationships. Our findings consolidate results from a number of investigations at the regional level and suggest a general ecological link between pelagic and demersal communities via interactions occurring during the early life stages. The Bayesian approach allowed for probabilistic assertions on the direction, strength and uncertainty associated with these interactions at mutiple levels.

Regional variation and interpretation

The six Northwest Atlantic regions displayed negative relationships with herring (Eastern and Western Scotian Shelf excluded) and mackerel (Table 5.3, Figures 5.3-5.5). Many of the Northeast Atlantic populations exhibited negative relationships with both herring and mackerel. The finding that the strength of the effect of herring becomes increasingly more negative further west (Appendix) could reflect the historical differences in exploitation between the Northwest and Northeast Atlantic, with intense fisheries for both species in the Northeast Atlantic preventing the dominance of herring.

In the Baltic and Kattegat regions, however, flat or positive relationships with both herring and sprat were observed, although these became weakly negative when autocorrelation was accounted for (Table 5.3). Paradoxically, the Baltic region is where predation by herring on cod eggs was directly observed (Köster and Möllmann, 2000) and a negative

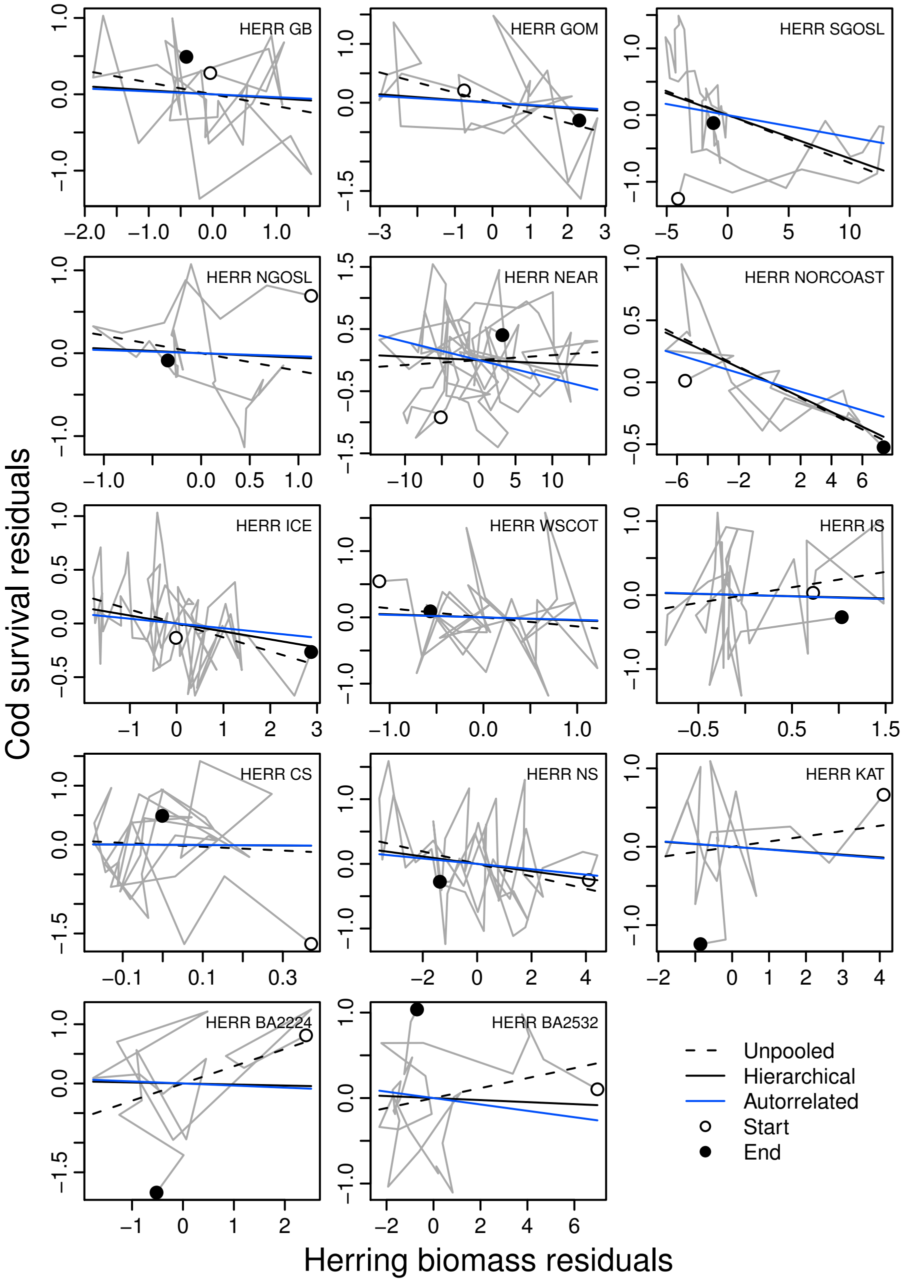

Figure 5.3: Partial regression plots of the relationship between standardized cod pre-recruit survival and herring total biomass by region. The effect of cod spawning stock biomass is removed prior to plotting, making the slope of the relationship interpretable as the interaction coefficient. Observations are displayed as grey lines with the first and last time point indicated by a white and black point, respectively. The dashed, solid black and solid blue lines are from the: separate (unpooled), hierarchical and autocorrelated best fitting models (Table 5.2), respectively.

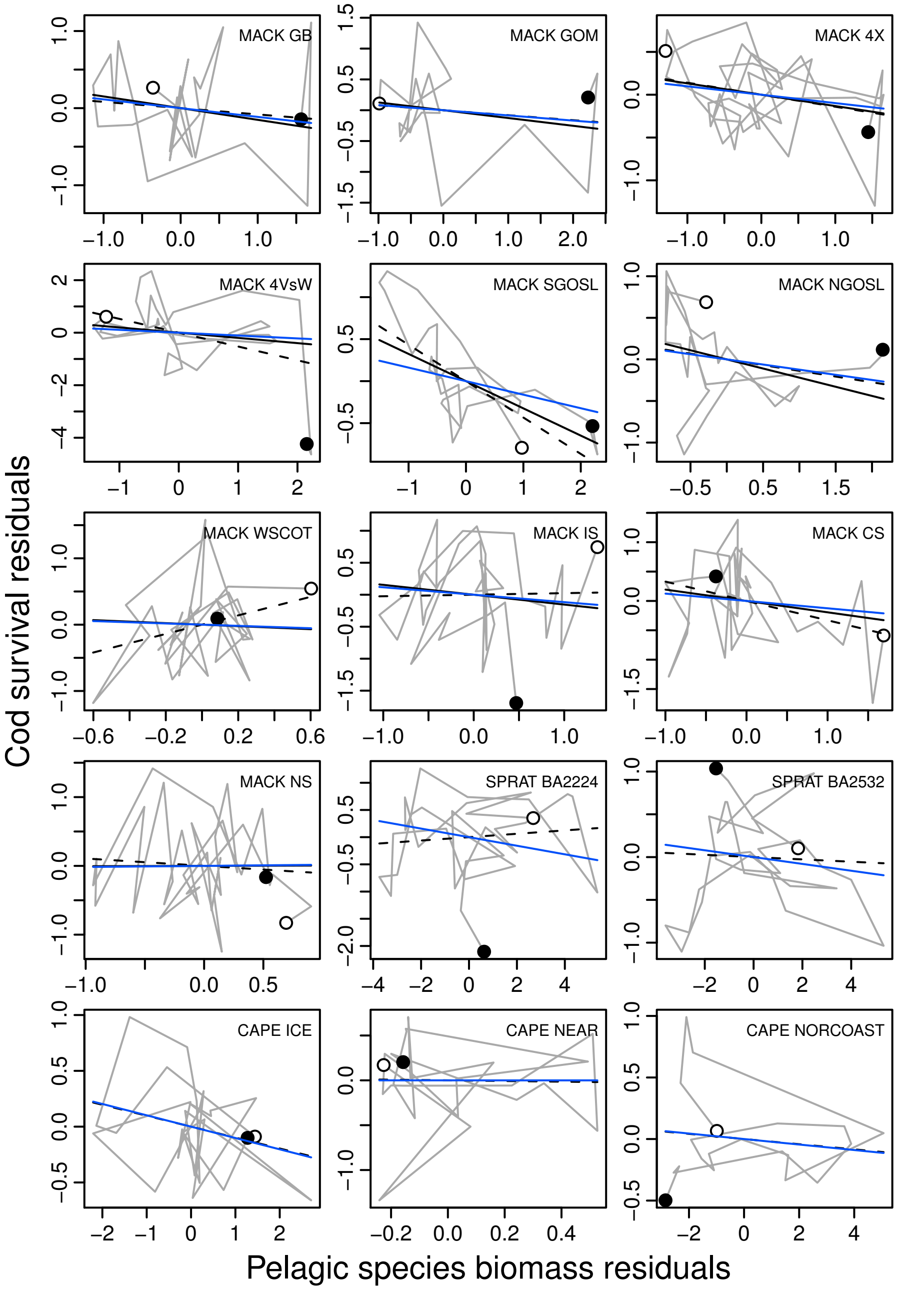

Figure 5.4: Partial regression plots of the relationship between standardized cod pre-recruit survival and other pelagic species total biomass by region. Details as in Figure 5.3.

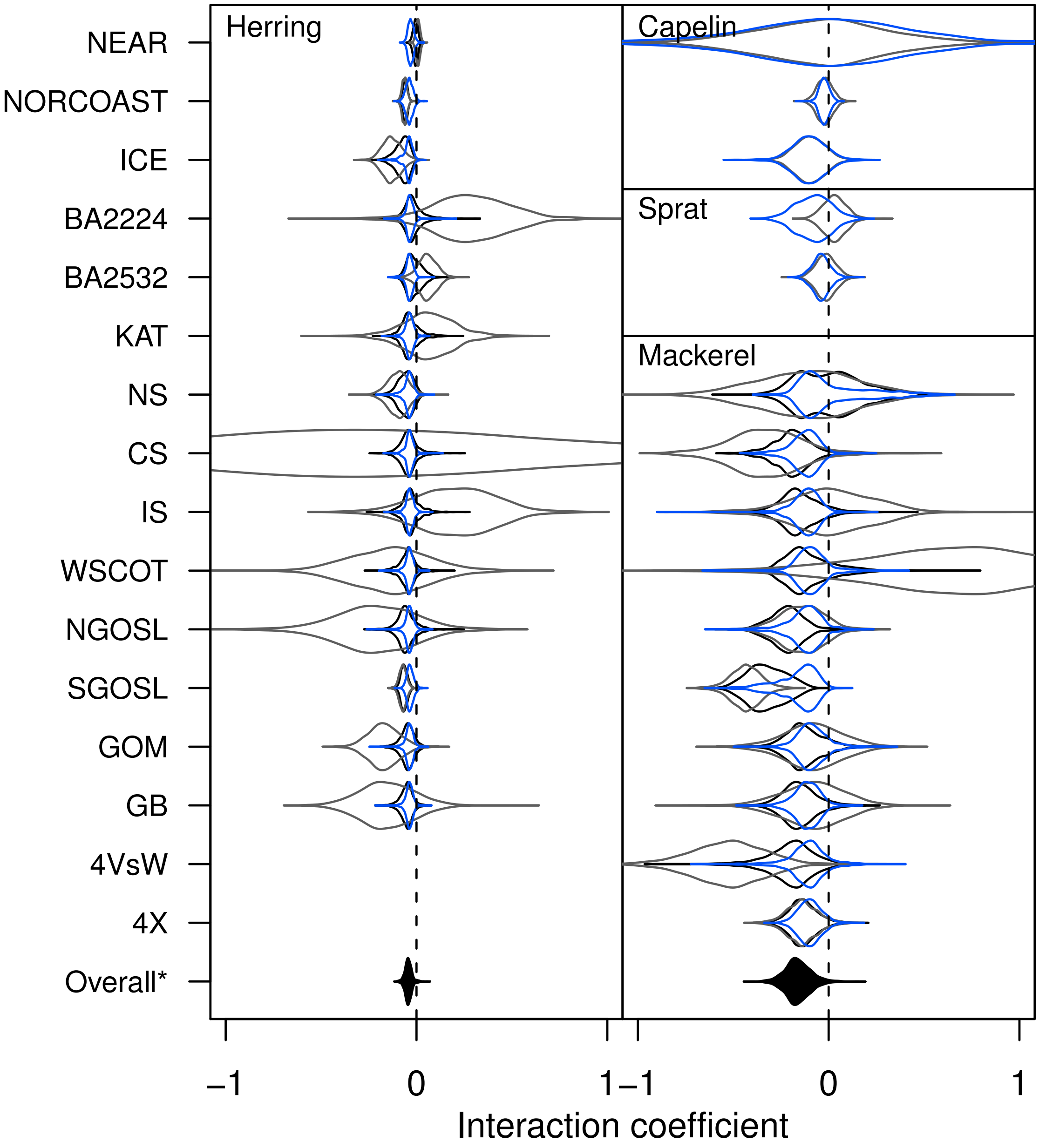

Figure 5.5: Posterior densities of the interaction coefficient between standardized juvenile cod survival and pelagic biomass by region. Best fitting separate, hierarchical and autocorrelated posterior densities are in grey and black, and blue respectively (Table 5.3). Each density arises from 3000 MCMC thinned samples from the posterior density. Overall refers to the overall effect in the best fitting herring and mackerel hierarchical analysis.

Table 5.2: Cod and pelagic model comparison table. Each model has an ID referred to in the text. Terms for each model also includes an offset ($\ln(S)$). Complete pooling refers to fits in which all the data were combined without reference to region; unpooled refers to separate parameter estimates per region; and hierarchical refers to the partial pooling model. The residual variance structure is either independent or autocorrelated with combined or separate parameters by region. The effective number of parameters is given by p_V, DIC is the sum of the mean deviance and p_V, and ΔDIC is the difference in the DIC values between the model in that row and the best model of those investigated per interacting species. Boxed cells refer to best fitting models with alternative error variance structures in unpooled and hierarchical independent and autocorrelated settings. These are further discussed within the text.

			Herring			Mackerel			Sprat			Capelin		
ID	Terms	Residual Variance	$\bar{D}$	pV	ΔDIC	$\bar{D}$	pV	ΔDIC	$\bar{D}$	pV	ΔDIC	$\bar{D}$	pV	ΔDIC
			Complete pooling											
p1	α	$\mathrm{N}(0,\sigma_\varepsilon^2)$	1624.59	1.84	763.07	1069.46	2.16	385.58	179.15	2.26	62.46	228.74	2.05	145.65
p2	$\alpha+\beta S$	$\mathrm{N}(0,\sigma_\varepsilon^2)$	1552.27	3.13	692.03	1035.88	3.25	353.1	161.19	3.19	45.45	224.79	3.14	142.79
p3	$\alpha+\gamma H$	$\mathrm{N}(0,\sigma_\varepsilon^2)$	1621.01	3.12	760.76	1068.51	2.87	385.34	178.92	3.42	63.4	222.93	3.31	141.10
p4	$\alpha+\beta S+\gamma H$	$\mathrm{N}(0,\sigma_\varepsilon^2)$	1550.56	3.97	691.16	1034.4	4.43	352.8	162.03	5.2	48.3	221.08	4.04	139.98
p5	$\alpha+\beta S+\gamma H$	$\mathrm{N}(\phi\epsilon_{j,t-1},\sigma_\varepsilon^2)$	1090.45	5.52	232.6	807.21	5.49	126.67	119.22	5.43	5.71	113.66	5	33.53
			Unpooled											
u1	α_j	$\mathrm{N}(0,\sigma_\varepsilon^2)$	1119.36	15.16	271.15	781.23	11.6	106.8	144.14	3.24	28.44	91.74	4.41	11.01
u2	$\alpha_j+\beta_j S$	$\mathrm{N}(0,\sigma_\varepsilon^2)$	1005.48	30.64	172.75	755.98	22.61	92.56	138.62	5.61	25.3	77.65	7.49	0
u3	$\alpha_j+\gamma_j H$	$\mathrm{N}(0,\sigma_\varepsilon^2)$	1079.83	31.39	247.86	773.24	22.7	109.91	144.01	5.55	30.62	93.75	8.09	16.70
u4	$\alpha_j+\beta_j S+\gamma_j H$	$\mathrm{N}(0,\sigma_\varepsilon^2)$	972.25	44.78	153.67	720.26	34.02	68.24	140.2	7.86	29.13	79.03	11.7	5.59
u5	$\alpha_j+\beta_j S+\gamma_j H$	$\mathrm{N}(0,\sigma_{\varepsilon,j}^2)$	928.72	67.51	132.86	657.95	47.91	19.83	138.6	9.25	28.92	81.07	17.28	13.21
u6	$\alpha_j+\beta_j S+\gamma_j H$	$\mathrm{N}(\phi\epsilon_{j,t-1},\sigma_\varepsilon^2)$	938.05	61.58	136.26	715.83	45.71	75.51	119.35	10.76	11.17	82.38	16.5	13.73
u7	$\alpha_j+\beta_j S+\gamma_j H$	$\mathrm{N}(\phi\epsilon_{j,t-1},\sigma_{\varepsilon,j}^2)$	881.81	106.94	125.39	658.59	70.02	42.58	107.26	12.12	0.45	84.66	26.03	25.56
u8	$\alpha_j+\beta_j S+\gamma_j H$	$\mathrm{N}(\phi_j\epsilon_{j,t-1},\sigma_{\varepsilon,j}^2)$	802.44	98.76	37.84	627.88	73.36	15.21	106.52	12.42	0	67.60	21.57	4.03
			Hierarchical											
h1	a_j	$\mathrm{N}(0,\sigma_\varepsilon^2)$	1119.36	14.88	270.87	781.38	11.69	107.03	–	–	–	–	–	–
h2	$a_j+b_j S$	$\mathrm{N}(0,\sigma_\varepsilon^2)$	1008.51	28.1	173.24	756.94	20.38	91.28	–	–	–	–	–	–
h3	$a_j+g_j H$	$\mathrm{N}(0,\sigma_\varepsilon^2)$	1087.52	18.05	242.2	774.94	13.97	102.88	–	–	–	–	–	–
h4	$a_j+b_j S+g_j H$	$\mathrm{N}(0,\sigma_\varepsilon^2)$	988.75	78.25	203.63	727.06	38	79.02	–	–	–	–	–	–
h5	$a_j+b_j S+g_j H$	$\mathrm{N}(0,\sigma_{\varepsilon,j}^2)$	938.04	74.82	149.50	668.04	52.4	34.41	–	–	–	–	–	–
h6	$a_j+b_j S+g_j H$	$\mathrm{N}(\phi\epsilon_{j,t-1},\sigma_\varepsilon^2)$	953.21	47.61	137.46	723.17	40.5	77.64	–	–	–	–	–	–
h7	$a_j+b_j S+g_j H$	$\mathrm{N}(\phi\epsilon_{j,t-1},\sigma_{\varepsilon,j}^2)$	888.15	75.04	99.82	662.3	55.13	31.39	–	–	–	–	–	–
h8	$a_j+b_j S+g_j H$	$\mathrm{N}(\phi_j\epsilon_{j,t-1},\sigma_{\varepsilon,j}^2)$	809.01	54.35	0	629.88	56.16	0	–	–	–	–	–	–

Table 5.3: Posterior means of the interaction coefficients by region. Herring and mackerel estimates derive from models: *u5* unpooled; *h5* hierarchical with independent errors; and *h8* hierarchical with autocorrelated errors in Table 5.2. Sprat unpooled independent and autocorrelated estimates derive from models *u5* and *u8*, respectively. Capelin independent error estimates derive from model *u4*. Probability of the interaction coefficient being negative is given in parentheses.

	Herring			Other species			
Region	Unpooled	Hierarchical	Autocorrelated	Species	Unpooled	Hierarchical	Autocorrelated
GB	-0.155 (0.864)	-0.053 (0.954)	-0.038 (0.979)	Mackerel	-0.082 (0.697)	-0.152 (0.94)	-0.114 (0.969)
GOM	-0.172 (0.986)	-0.047 (0.926)	-0.038 (0.971)	Mackerel	-0.081 (0.707)	-0.126 (0.892)	-0.084 (0.884)
4X	–	–	–	Mackerel	-0.14 (0.954)	-0.132 (0.957)	-0.098 (0.949)
4VsW	–	–	–	Mackerel	-0.526 (0.998)	-0.199 (0.962)	-0.109 (0.91)
SGOSL	-0.072 (1)	-0.065 (1)	-0.033 (0.954)	Mackerel	-0.433 (1)	-0.324 (1)	-0.161 (0.994)
NGOSL	-0.214 (0.86)	-0.055 (0.891)	-0.037 (0.96)	Mackerel	-0.138 (0.891)	-0.22 (0.987)	-0.124 (0.951)
NEAR	0.008 (0.227)	-0.006 (0.662)	-0.03 (0.97)	Capelin	-0.036 (0.526)	–	-0.001 (0.505)
NORCOAST	-0.063 (1)	-0.06 (1)	-0.038 (0.974)	Capelin	-0.021 (0.704)	–	-0.022 (0.815)
ICE	-0.13 (0.996)	-0.074 (0.996)	-0.044 (0.985)	Capelin	-0.098 (0.903)	–	-0.102 (0.887)
WSCOT	-0.137 (0.754)	-0.046 (0.894)	-0.038 (0.968)	Mackerel	0.699 (0.076)	-0.114 (0.824)	-0.09 (0.906)
IS	0.209 (0.152)	-0.03 (0.803)	-0.036 (0.96)	Mackerel	0.024 (0.463)	-0.154 (0.924)	-0.116 (0.97)
CS	-0.325 (0.616)	-0.042 (0.868)	-0.036 (0.952)	Mackerel	-0.33 (0.96)	-0.194 (0.976)	-0.125 (0.978)
NS	-0.096 (0.966)	-0.057 (0.942)	-0.042 (0.973)	Mackerel	-0.107 (0.653)	0.005 (0.498)	0.016 (0.627)
KAT	0.067 (0.296)	-0.034 (0.805)	-0.037 (0.962)	-	–	–	–
BA2224	0.291 (0.063)	-0.017 (0.731)	-0.035 (0.953)	Sprat	0.031 (0.289)	–	-0.079 (0.796)
BA2532	0.058 (0.096)	-0.012 (0.645)	-0.037 (0.977)	Sprat	-0.014 (0.614)	–	-0.04 (0.819)

recruitment relationship with sprat has been previously published (Sparholt, 1996). Potential reasons for this disparity include confounding environmental variables, particularly changes in salinity and oxygen levels. These may override or mask the effects of species interactions on cod recruitment. The time period used to investigate the sprat relation also differed from previous investigations (Sparholt, 1996). The series used for herring for the western Baltic and Kattegat is the shortest series used with comparatively little contrast over the 17 years of abundance data (Figure S14). Similarly, no relationship existed between herring abundance and juvenile cod survival in the longest time series available, the Northeast Arctic. Hjermann *et al.* (2007) concluded that the effect of herring on the recruitment of cod in that region is likely an indirect effect mediated via exclusion of capelin and increased cannibalism in cod, which is in turn dependent on the stock size. So in the case of the Northeast Arctic cod, it is unlikely that a direct effect of herring would be detected in our models.

Caveats

While the present study attempted to use all the available information to investigate the hypothesis, ultimately our approach remains correlative. Yet, the analysis goes beyond other observational studies, in that it is essentially replicated across regions with differing historical trajectories, particularly for herring. As potentially confounding factors remain uncontrolled for, however, our conclusions must be treated with caution (Montgomery *et al.*, 2001).

The rationale behind the hierarchical approach is that we effectively treat each population as a realization of a natural experiment (Myers and Mertz, 1998b). An underlying assumption is that the same processes operate in all populations. The validity of this assumption may be critically questioned for investigating species interactions where assemblages of prey, predators, and competitors vary in their composition between regions. Yet, in adherence with the ecosystem-based management approach (Larkin, 1996), there remains a requirement to understand pertinent interactions over the large scales at which these populations are managed. This requirement is all the more important when considering the roles of trophic cascades (Pace *et al.*, 1999; Frank *et al.*, 2005; Myers *et al.*, 2007) and alternative stable states (Scheffer *et al.*, 2001; Beisner *et al.*, 2003) in determining population persistence and recovery at low population levels.

By assembling the longest available time series and visualizing the partial regressions, the time-dynamic of the relationship between pelagic fish abundance and cod survival can be inspected. Ideally multiple historical peaks and troughs in the abundance of the interacting pelagic species would ensure that the hypothesized effect on survival does not appear unidirectional in Figures 5.3 and 5.4.

It is also important to note that the dominant small pelagic species within a region are treated separately whereas their combined effect as a functional group may be more relevant (Petrie *et al.*, 2009). Given that some small pelagic species such as mackerel are highly ranging, we did not attempt to combine their abundance with that of more localized stocks. Index combination methods may be of useful in this regard.

Spatial overlap in spawning and feeding areas

Given the relatively small gape size of small pelagic species, the inferred predation or competition for the same food source (early stage copepods) must concern eggs and small larvae, either prior to or shortly after settling. Cod spend up to 10 weeks in the planktonic phase before metamorphosis. The overlap between feeding pelagic fish and the larvae during this stage is critical in determining the strength of this source of potential mortality (Huse *et al.*, 2008). Inter-annual variability in temporal and spatial dynamics make it difficult to obtain accurate estimates of spatial overlap. The approach used here was to review of literature on the general spawning areas for cod and feeding areas of pelagic species (Appendix). Broadly, there appears to be sufficient evidence for the potential overlap of feeding herring and cod eggs and larvae. The picture is less clear for mackerel stocks, which are typically highly migratory. An a-priori decision was made to analyse only those regions presented in the stock assessment report but it is noteworthy that mackerel are increasingly caught in other regions, e.g., off the Faroe Islands and Iceland. However, these did not appear in the dominant migratory patterns and were thus excluded. It is also questionable how much mackerel foray into the North Sea, especially since this historic component was virtually extirpated and has not recovered. The results from the North Sea were in agreement in that no relationship was observed between cod survival and mackerel abundance there (Table 5.3).

Other potential covariates

Much attention has focused on the important effects of temperature anomalies and climatic trends (O'Brien *et al.*, 2000; Brander and Mohn, 2004; Planque and Fredou, 1999; Mantzouni *et al.*, 2010) on cod recruitment. With the effect of temperature varying according to the geographical position, for example, higher temperatures favouring strong recruitment in more northern areas but lower temperatures favouring recruitment in more southern stocks. There have also been studies into the effects of larval prey availability and subsequent recruitment, e.g. match-mismatch between young cod and zooplankton in the North Sea cod (Beaugrand *et al.*, 2003). Recently, a detailed study of the North Sea by Fauchald (2010) investigated the effect of sea surface temperature, copepod (*Calanus finmarchicus*) abundance, adult herring abundance and a competitive effect of herring predation on *C. finmarchicus*. The effect of herring on cod survival remained significant after having accounted for the effects of a non-linear function of adult cod abundance and the abundance of *C. finmarchicus* in the best fitting model. Although the present study ignored possible covariates detailed above, it is the first to investigate this potential ecological interaction across the north Atlantic region. Ultimately a multiple-hypothesis testing framework or hierarchical implementation of the approach adopted in Fauchald (2010), including the methods developed in Mantzouni *et al.* (2010), may best determine the proximal relationships. Deriso *et al.* (2008) present promising generalized methods at the stock assessment stage that allow for the investigation of multiple factors through a combination of multiple factor and randomization tests. Such an approach is beyond the scope of the present analysis.

Modelling assumptions

The key modeling assumptions are that the strength of density dependence is a function of the initial stock density and that the predation mortality term is linear in predator abundance; hence the extended Ricker formulation. Cannibalism has been observed for many cod stocks so the first choice appears appropriate. Given that eggs are likely only a small proportion of the pelagic species diet, satiation is unlikely to occur so that the linear functional form may also be a suitable choice (Sparholt, 1996). From a purely practical perspective, the extended Ricker model also lends itself to relatively straightforward visualization, including marginal effects such as the partial regression plots we present.

Using a standard definition for depensation: ".. the per-capita rate of growth decreases as the density or abundance decreases to low levels" (Liermann and Hilborn, 2001), the linear predation mortality term we have used does not give rise to a depensatory model. The per-capita rate of growth is monotonic decreasing over adult abundance at a given predator abundance. Rather, what we have addressed here is a simpler question of whether the per-capita growth rate is depressed with increasing predator abundance.

Implications

Our extension of the Ricker model is basic and provides a surface with no discontinuities, thresholds or inherent depensatory dynamics. Therefore, we cannot say conclusively whether the systems under investigation have entered new regimes or stable states. Petraitis and Dudgeon (2004) set out conditions for the detection of alternative stable states in the marine environment, including: that the alternate states occur in the same habitat; the perturbation must occur quickly; and the system observed for long enough to ensure the stability of the alternate state. In comparison, our observational data are gathered over dynamic environmental conditions where fishing has been relatively protracted over modest time periods. So the ability to detect true alternate states may be limited. From the time-dynamic of Figures 5.3 and 5.4, the relationships are noisy but do not display any sharp transitions to indicate alternate states.

Given the finding that the survival of pre-recruit cod generally co-varies inversely with pelagic fish abundances, a direct applied utility is in adjusting the recovery time for populations at severely reduced abundances. Myers *et al.* (1997b) estimated recovery times from maximum population growth rates based on past data. The inherent assumption that the environment remains constant may not be realistic, given the large changes in prey abundance, and the potential feedback on predator recruitment discussed here. Incorporating changes in the abundance of potential egg and larval predators will modify the realized population growth rates. Time series alternatives that don't include specific drivers but allow the population growth rates to evolve in time (Peterman *et al.*, 2003) should also merit further investigation in predicting recovery times given contemporaneous environmental conditions.

From a management perspective, the question must ultimately be posed whether the negatively interacting species should be fished down or cropped. Given the correlative nature of the present study, to advocate such an action without taking into account secondary interactions of importance (Bax, 1998) would be ill-advised. For example, were the small pelagics in a region to be fished down, predators of those species and cod, e.g. grey seals (*Halichoerus grypus*), could increase the per-capita predation rate on cod. We anticipate that further investigation of these secondary interactions will provide important insights into the lilkely indirect effects of intervening management options. Such an approach generalizes to holistic ecosystem models. These models are far more general than those presented here but they also carry many assumptions and ignore uncertainties (Whipple *et al.*, 2000). The hierarchical posterior distributions we have estimated could contribute in this regard.

Chapter 6

DISCUSSION

In this thesis, I have sought to contribute further understanding of important ecological processes that influence highly variable fish recruitment. Questions on the effects of fish density, environmental forcing, and predation were addressed using methods specifically designed to accommodate and interpret patterns of variability. In this general discussion, I first consider the main findings holistically; the general approach and details are then critiqued retrospectively; and finally, I discuss potential avenues for future work.

6.0.1 Ecological Inference from Variable Recruitment Data: Thesis Summary

Advances in the investigation of population renewal for any one fish population may be hampered by highly variable abundance data (Myers and Mertz, 1998b; Myers, 2001). In Chapter 2, I reviewed the history of recruitment science from early observations on the variability in yearclass strength (Hjort, 1914), through the foundational contributions, to a discussion on the contemporary challenges of incorporating multiple dimensions of change. Much progress has been made, as also reviewed in Frank and Leggett (1994), but I showed that we are still confronted with: highly variable data, multiple hypotheses and inconclusive inference. What is required is a synthetic approach to investigating these outstanding issues. Such a procedure should incorporate information across multiple populations to address stated hypotheses on the structure of the mean and variance of fish recruitment. The development of this approach and the inference based thereon was the central goal of my thesis.

Studies of fish and insect populations are shown to have contributed significantly toward the development of population dynamics theory (Allison, 1999). Commercial interests in both groups spurred research into questions of population regulation. Questions regarding the relative importance of density-dependent and density-independent mortality fueled over half a century of research and debate (McLaren, 1971; Turchin, 1999, for summaries). I argued in Chapter 2 that highly variable abundance data contributed toward the many divergent theories of regulation; a topic which was examined in detail in Chapter 3.

Myers (1998) contended that the incorporation of environmental data into population-specific recruitment studies often results in ephemeral relationships that don't survive subsequent re-testing and, as a result, often have little relevance in resource management. The argument was made for the extension of meta-analytical techniques to investigate such relationships. The latter half of Chapter 2 considers these extensions theoretically and empirically. Specifically, I focused on extensions to include predation during the early life history stages. From a theoretical perspective, functional forms other than a linear predation mortality rate were found to readily induce depensatory dynamics. If common, such dynamics could generally interfere with the recovery of populations that were depleted to low levels. The ubiquity of depensatory dynamics in marine fish is, however, debated with hierarchical analyses describing it as rare (Myers *et al.*, 1995a; Liermann and Hilborn, 2001) whereas expert visual inspection found it to be a more prevalent phenomenon (Walters and Kitchell, 2001). The question of depensation is examined in greater detail in Chapter 4. Returning to the investigation of environmental relationships, the need for methods to standardize interaction coefficients while making maximal use of available datasets across many populations is stressed. An application of these methods was presented later, in Chapter 5.

Chapter 2 concludes with a critique of the hypothesis-specific framework. While specific hypotheses are central to any scientific endeavor, the sheer number of potential hypotheses (e.g. concerning physical, chemical, and biological environments, life-history, and maternal effects) means that there will likely always be alternative explanatory relationships touted. By combining datasets the meta-analytical approach may safeguard against such ephemeral relationships, yet it remains essentially correlative. As a result of these considerations, I emphasize the importance of time-varying parameter techniques (Zeng *et al.*, 1998). These allow for stochastic variation in parameters of interest and, as such, have the potential to integrate across many sources of environmental change. The state space modeling framework (Harvey, 1991; Durbin and Koopman, 2001) is central in this regard and forms the subject matter of Chapter 4. From an applied fisheries perspective, this approach may ultimately be a more attractive prospect for incorporating dynamic change into stock assessments than explicit environmental hypotheses.

Chapter 3 began to address the challenges of ecological inference in the presence of highly variable recruitment data outlined in Chapter 2. A theoretical and empirical treatment of the relationship between survival variability and population density in marine, freshwater and anadromous fishes was presented. It was shown that where density dependence occurs, changes in the mean survival will also be accompanied by changes in the variance in survival. The theory presented in Chapter 3 suggests that the pattern of variability relates to the functional form of density dependence. A general increase in variability at low densities was predicted from most commonly applied functional forms of density dependence. We employed meta-analytical techniques to test for changes in variability, where the parameters governing the change were estimated and combined hierarchically. The results of this meta-analysis, applied to 147 populations comprising 39 species, showed a general increase in variability of survival at low adult abundance in agreement with the theoretical expectations. We conclude that density dependence can explain such changes and, moreover, that variable abundance data need not preclude its investigation. In fact, the highly variable nature of fish recruitment may represent more than just ‘noise’ and may actually reflect ecological processes that can be studied and quantified using the meta-analytical techniques that underlie this thesis.

Recruitment variation was further partitioned in Chapter 4, where state space models were employed to investigate changes in the maximum reproductive rates of Atlantic cod. There, recruitment variation was partitioned into that arising from measurement error and that owing to variability in the maximum annual reproductive rate. Specifically, I tested and rejected the null hypothesis that pre-recruit productivity in Atlantic cod has remained constant through time. The univariate (single population) application largely followed that of Peterman *et al.* (2003). Results of univariate analyses showed that the local-level (random walk) model typically provided the best fit. When applied to 16 datasets of cod recruitment, substantial temporal changes in productivity were estimated with an underlying tendency of declining reproductive rates observed across many regions. The methodology was then extended to the multivariate case where the covariance structure of the trends in productivity across geographic regions is also of interest. The multivariate treatment showed the between-population coherence to decay with increasing geographic distance. Northern populations showed a differential response to those at southern latitudes in the response to environmental conditions, i.e. populations at southern latitudes showed a positive correlation in their annual reproductive rates but a negative correlation with those in the north. Some regions such as, in the northeast Atlantic: the North Sea, West of Scotland, Irish and Celtic Seas; and in the northwest Atlantic: Georges Bank, Gulf of Maine, and Southern Scotian Shelf and Bay of Fundy showed an apparent clustering of positive correlation. In the northwest Atlantic, the correlations were found to be weaker and in some cases inverse to that presented in Rothschild (2007). I conclude that distinct changes in productivity have occurred in these populations over time and that time-varying parameters are likely to play a central role in the incorporation of such change into stock assessment. Further avenues for the application of the multivariate methodology to a multispecies setting are presented below (see: *Future work*).

A potential hypothesis capable of explaining the conserved trend in productivity decline observed in Chapter 4 was the subject of Chapter 5. I asked whether predation by small pelagic species has the potential to depress survival of early life history stage cod thereby reducing its pre-recruit productivity. In particular, I investigated the effect of the abundance of Atlantic herring, Atlantic mackerel, European sprat, and capelin on cod recruitment across 16 regions in the Northwest and Northeast Atlantic. Methods to standardize interaction coefficients across regions (via the area occupied) were developed, as well as a treatment of time series and measurement error variances. I partitioned the variance using a hierarchical Bayesian mixed effects model, which incorporates the effects of adult abundance and density dependence as well as interactions between the species. Negative effects of herring and mackerel were observed across many regions, whereas the relationship with other small pelagics was more ambiguous. The extended hierarchical models consistently fit the data better than analyzing the populations separately. It is concluded that hypotheses of negative interactions between herring and mackerel and cod pre-recruit survival are largely borne out in the hierarchical analyses and may be capable of explaining declines in the productivity of Atlantic cod populations investigated. The critique section below expands on this surmise.

6.0.2 A Critique on the Methods Applied

The work presented in my thesis centered on the separation of variation into different components explained by ecological processes, measurement error and between-population variation. This section proceeds with a critique on the strengths and weaknesses of the theory, methods and data employed.

Suitability of the Theories

As with all observational studies, the need for theory to inform the design and contextualize the results of meta-analytic stock recruitment relationships is great. When investigating large datasets, there is the potential to *mine* the data for information without explicitly alluding to theory. I think this exploratory approach may be of use where no theory exists or perhaps when first approaching a very large dataset. In contrast, population ecology has, as its base, laws and postulates very similar to those of the physical sciences (Turchin, 2001; Murray, 2000; Quinn, 2003), although see Lawton (1999) for an alternative view on the difficulty or establishing laws at the community level; secondly, individual abundance datasets are typically short, auto-correlated and highly variable. As a result, I stress the need for theories derived from first principles, which can subsequently be tested on multiple datasets.

The theory of changing patterns in variability derived in Chapter 3 attempts to derive the expected relationships between the variability in survival and adult density. The functional forms of density dependence considered included a range of models from density independence to compensatory and over-compensatory density-dependent mortality. While this encompasses the gamut of most commonly applied functional forms, higher order or delayed density-dependent relationships (Turchin, 1990) were ignored. Also, expectations on the patterns of variability between stages from egg to juvenile were derived but not further investigated, as the data available were only spawner and recruit abundances. This issue is further elaborated upon in the *Future work* section below.

The derivations of Chapter 2 contain a suite of functional forms for the predation mortality. These were found to readily induce depensatory dynamics in correspondence with the *cultivation-depensation* hypothesis (Walters and Kitchell, 2001). Yet in Chapter 5, I only apply the straightforward linear predation mortality rate put forth by Lotka (1925) and Volterra (1926a). Although the suitability of this form for filter feeding predators such as herring was suggested in Swain and Sinclair (2000), other forms of predation mortality might also be interesting to investigate. The hyperbolic and sigmoidal forms were found to be analytically intractable. Although a large portion of mathematical analysis is dedicated towards the numerical solution of such problems, I opted for the tractability of the simpler relationship. Numerical solvers such as the Runge Kutta method (Runge, 1895; Kutta, 1901) can be applied using the *lsoda* package in *R* (Soetaert *et al.*, 2010). The numerical solver could also be embedded in a maximum likelihood framework to optimize over unknown parameters for a given dataset. This would provide a method to investigate alternative model formulations of increased biological realism.

Chapter 4 also contains a narrow range of theoretical models. Here, linear, normal models were used such that the Kalman filter could be employed. The Ricker model is central in this regard. Where the models are non-linear or non-Gaussian, more complicated filtering algorithms must be applied such as extended Kalman filters, Bayesian filtering or integral approximation methods such as the Laplace approximation (Pedersen *et al.*, 2011). Initial investigations undertook using the Laplace method in AD-Model Builder's random effects package (Skaug and Fournier, 2006), showed it to perform well in the univariate case. For the multivariate case, however, the dimension of the integral required a prohibitively large amount of time to compute and converge so as to render it impractical for testing and simulation purposes. Nevertheless, methods that accomodate non-linear and non-Gaussian dynamics merit further investigation given the propensity of ecological systems to behave in more complex, non-linear ways (Turchin, 2003).

Meta-analytical Assumptions

While the generality and utility of the meta-analytical approach have been highlighted elsewhere (Myers and Mertz, 1998b; Hilborn and Liermann, 1998; Harley, 2002; Peterman, 2004), it is important to briefly discuss its main strengths and weaknesses here. Meta-analysis can be applied to collated results from separate studies on the same question (Normand, 1999) or to all sets of original 'raw' data using a hierarchical model (Gelman and Hill, 2007). The latter approach is typically favored as it doesn't rely on point metrics and standard errors alone to carry the information content of the whole dataset. Implementing a hierarchical analysis on a stated question requires that decisions be made on: the methods employed to collate component datasets, how representative these are and if any other biases exist that might restrict the generality of the conclusions (Cooper and Hedges, 1994). Of particular concern in studies of stock recruitment relations is *selection bias* (Hilborn and Liermann, 1998). Collated databases of stock assessment output can hardly be considered random samples of fish populations, as they mostly concern commercially exploited populations of sufficient economic value that are relatively persistent in the face of fishing pressure (Hilborn and Liermann, 1998; Harley, 2002). As such, fish populations in regions where assessments are not feasible, for a variety of ecological and economic regions, will be omitted. I think this issue is closely related to that of extrapolation in regression analysis (Montgomery *et al.*, 2001). In both regression and meta-analysis we may be tasked with predicting the expected outcome of an, as yet, unobserved set of conditions. Directives for drawing cautious inference only within the domain of the collated data are well founded in both settings. That is, if we have collated and meta-analytically analyzed abundance data on commercially exploited temperate marine fish populations, we draw our inference and discussion on the same. In the case of Chapter 5, it is not be necessary to generalize to all cod stocks, as we were predominantly interested in the interactions estimated only in those regions presented.

By addressing questions of population dynamics across taxonomic and geographic distances with straightforward normally-distributed random effects analyses, we implicitly assume random deviations around the fixed effect. Where gradients other than those explicitly included in our analyses might cause non-random deviations these could alter the inference drawn. For example, were the interaction coefficients of Chapter 5 found to deviate around a relationship with latitude, we might conclude that the between-study variability in the effect is greater than it actually is. Such effects may be particularly important on the boundaries of significance. As the potential number of environmental gradients along which these deviations may lie is great, the need for guiding theory is stressed once again. Incidentally, we tested such gradients in Chapter 5.

Inferential Framework

Debate on the appropriateness of frequentist or Bayesian inference in Statistics has a long and often polemical history (Hald, 2007; Stigler, 2007). I have adopted a pragmatic approach to model implementation. Where circumstances required, such as in Chapter 5 where assumptions regarding the effect of measurement error in the data were explored, the flexibility of Markov Chain Monte Carlo methods in Bayesian inference was utilized. Sensitivity to the prior assumptions was also investigated. Elsewhere, I have mostly adopted maximum-likelihood-based inference, although a Bayesian interpretation may be assigned to the Kalman filter of Chapter 4 when initiated at a diffuse starting density (Petris *et al.*, 2009). In fact, Bolker (2008) notes that the difference between frequentist and Bayesian approaches becomes increasingly subtle in relatively advanced approaches such as hierarchical and state space models. While I adopted a pragmatic approach to inference, I recognize that this could be seen as inconsistent by ardent followers of either school.

Data Used

Throughout my thesis, extensive use was made of large databases that collate abundance time series and metadata from many populations (Myers *et al.*, 1995b; Ricard *et al.*, in review). As with all meta-analyses the issue of knowing the data is centrally important. For Chapters 4 and 5, I extracted directly from assessments, which I read thoroughly. Chapter 3 used the original database, where I did not read all of the assessments, although these were quality controlled for consistency previously (Myers *et al.*, 1995b).

An important issue arises with modern-day stock assessments that will affect their use in meta-analyses. Stock assessment techniques such as statistical catch-at-age and separable models can often tie the estimation of recruitment to a survey index that covers only part of the catch time series. The resultant recruitment series will be largely deterministic (in accordance with the assumed stock recruitment relationship) in the period of no survey. Such series should, in general, not be used within meta-analyses of the stock recruitment relationship. Generally, the level at which assumptions are made on the form of the stock recruit relationship within an assessment is extremely important. More traditional assessment methods such as VPA (which made up the majority of assessment in the original database) make no assumption on the relationship between spawner abundance and recruitment. Others assume a stock-recruit relationship but allow the parameters of which to be estimated within the assessment. Still others use the output from other meta-analyses as priors for the parameters of the assumed relationship. In this regard, subsequent meta-analysis could be unduly influenced by the assumptions in the stock assessment process itself, including the potential for double use of meta-analytical results (Minte-Vera *et al.*, 2005). This situation can only be avoided by thoroughly knowing the assessments and communicating with the ultimate authority of the assessment scientists.

A coefficient of variation of sampling/measurement error of 30% or higher may be common for recruitment estimates (Kehler *et al.*, 2002). The treatment of this source of variance is therefore of primary concern. The effects of measurement error on the estimated parameters of stock recruitment relationships, particularly in the linearized Ricker model have been investigated by Walters and Ludwig (1981) and Kehler *et al.* (2002). Both studies found the magnitude of the bias in the estimated parameters to depend on the range of spawning stock biomasses recorded with the bias typically decreasing at greater ranges. Traditional stock assessment outputs are not usually accompanied by estimates of their uncertainty unless bootstrap methods have been applied. Newer methods such as state space approaches do include estimates of uncertainty on annual estimates (Pella, 1993; Gudmundsson, 1994; Fryer *et al.*, 1998; Meyer and Millar, 1999). Yet these methods are not implemented widely enough such that estimates of the measurement error could be applied directly in my analyses for all populations, e.g. only the west coast of Scotland cod population has these estimates presented currently. The approach I adopted in Chapter 5 was to investigate the effects of a range of CVs of measurement error on the overall- and region-level parameter estimates. This was implemented in a hierarchical Bayesian framework that can readily incorporate additional sources of variability. Such an approach was not performed in the earlier Chapter 2.

The resolution of the data used here is also important to discuss. I have used annual estimates from fisheries stock assessments. Admittedly, this is a coarse tool for investigating processes which occur at a finer spatial and temporal resolution. Much of the interesting dynamics happens at distinct stages within this period (Myers and Cadigan, 1993c,a; Houde, 2008a). Better temporal resolution could be achieved using survey data where the abundance at various ages/stages would be available. Long-term survey data covering the egg to larval to juvenile phases are rare but do exist. These have the potential to address further foundational questions on critical stages in population regulation (Harley, 2002) and species interactions. The use of variance partitioning methods will likely be central to those investigations (see: *Future work* below).

6.0.3 Application to Fisheries and Oceans Management

A major goal of recruitment science is to inform and guide the rational exploitation of natural resources, as part of successful fisheries and oceans management. I think the greatest potential for application of my thesis results lies in the results of Chapters 4 and 5. Chapter 4 shows that, as we manage to the long-term average of pre-recruit productivity, we may severely over or under-estimate contemporary productivity of the population. Time-varying parameter techniques allow for more adaptive management based on present conditions. Forecasts in most assessments are typically based on an average small number of recruitment values in the preceding years. The implicit assumption is that the process is stationary. It would be an interesting exercise to retrospectively compare predictions from both approaches with subsequent observations for a number of populations.

Another, arguably more pressing, application might be in the recognition that management reference points are dynamic entities. This will bring chagrin to fisheries managers, where long-term strategies rely on stable conditions. Yet, as the ecosystem approach to fisheries management (Larkin, 1996) is adopted, it is essential that the dynamic nature of the environment is resolved with the need for consistent and long-term management goals. Time-varying parameter techniques may have a lot to contribute in this regard by providing near real-time estimates of the productivity of the population.

Walters and Collie (1988) made the convincing argument that sanctioning research into environment- recruitment relationships under the pretense of management application is questionable. They contend that the identification of reliable pre-recruit survey indices is likely more effective. While I agree that there is an important role for good survey indices, there is no reason why continued investigation of environmental relationships cannot exist in parallel. Environmental data are relatively easily obtained, particularly with developments in remote sensing. I contend that this situation is exactly what state space models were developed for. As an aside, much of the origins of state space methodology lie in aerospace research (Shumway and Stoffer, 2000); no control engineer tracking a spacecraft would rely solely on the equations governing the motion without measurements on the position. State space models were designed to couple the scientific model with observations. Analogously, the underlying relationship between spawners, recruits and the environment (containing unknown parameters) would, in turn, be updated using the survey index measurements. In this way, maximal use is made of theory and data in addressing uncertainties regarding the strength of an incoming yearclass.

Much ecosystem modeling has necessarily focused on deterministic parameterization of process-oriented whole ecosytem models (Whipple *et al.*, 2000). Much of this work has focused on interaction within the adult stages. The hierarchical parameter estimates and their uncertainties of Chapter 5 could be used to parameterize whole ecosystem models to better reflect understanding of interactions during the early life stages. I have preliminarily implemented this approach for Georges Bank cod with colleagues from the University of Rhode Island using the LeMANS ecosystem model (Hall *et al.*, 2006). Using this approach, the interactions can be placed in a more holistic framework and the effect of fishing on the interacting species can be investigated via simulation.

The biological and economic relevance of the parameters estimated within my thesis might best be explored via management strategy evaluation (MSE) (Kell *et al.*, 2005a). MSE is a simulation routine designed to develop harvest and management strategies robust to uncertainties. By including the results of Chapters 3-5 and simulating under various harvest regimes, the results could be attributed biological and economic significance within the system of interest.

6.0.4 Future Work

Moving forward, it is essential that a thorough examination of the potential effects on subsequent meta-analyses made by assumptions on the stock-recruit relationship within an assessment is conducted. It would be of great instruction to re-run the assessments for multiple populations (e.g. all cod populations) under a variety of realistic assumptions on the recruitment relationship. The output could then be used as input to a benchmark meta-analysis, and the differences in inference highlighted along with potential avenues to either avoid such a situation or incorporate the assumptions directly within the meta-analysis. A similar analysis on simulated data with known parameters would also be instructive. It is possible that the recruitment estimates are still useful although the absence of the investigative analysis outlined here precludes this conclusion.

Multispecies modelling has, to date, largely focused on interactions occurring during the adult phase, although exceptions do exist, e.g. Hall *et al.* (2006). Yet, the strength of the cohort is typically determined during the young phases. As such there is a great need to parameterize species interactions during this stage within holistic models. The results of Chapter 5 could be used in such parameterizations, as outlined above. In addition, Chapter 4 considered the multivariate case where environmental forcing was evaluated via the covariance structure in the unobserved states. No directed interactions were formulated between these disparate Atlantic cod populations. If we were interested in direct interactions between species within a community we could formulate the transition equation of the multivariate state space models presented in Chapter 4 to include the estimation of such interactions. Such an approach has previously been applied to estimate community interactions in plankton (Ives *et al.*, 2003) and may have much potential to bridge the ever-present gap present between process-orientated (Whipple *et al.*, 2000) and empirical approaches to ecosystem modeling.

With regards to the inter-relationships of the chapters, although all concern recruitment variability, the species interactions of Chapter 5 should be further combined with the approaches in Chapter 4, both in the univariate and multivariate settings. Considerations would need to be made on whether the hypothesized species interactions affect the process or the measurement equations (Shumway and Stoffer, 2000). The class of models termed autoregressive moving average with exogenous inputs (ARMAX) could be very useful in formulating the process variant. Consideration would also need to be made on the dynamics of the interacting species, which could also be modeled in state space, as the exogenous driver would no longer be considered deterministic. How the inclusion of the explicit driver affects the stochastic behaviour of the productivity term would be of considerable interest.

The relative strength of density-dependent and density-independent mortality is of critical importance in determining at what life stages abundance is regulated. Central to estimating these effects are abundance data at different stages and an explicit treatment of the sources of variability. Previously, Myers and Cadigan (1993a) analyzed the relative strength of density-dependent and density-independent mortality at different life history stages assuming a density-dependent functional form that was linear in log abundance (Varley and Gradwell, 1960). Harley (2002) extended this approach to include non-linear functional forms in a state space framework. Yet data-deficiencies, in the Georges Bank and North Sea cod survey data used, precluded the investigation of Hjort's critical period hypothesis, which states that the strength of a cohort is determined very early and is thereafter fixed relative to other cohorts (Hjort, 1914). I would like to couple the theory of Chapters 2 and 3 with these analytical approaches to investigate hypotheses on critical periods. The parameters could also be allowed to vary through time (Zeng *et al.*, 1998) thus providing a dynamic setting for the continued investigation of Hjort's hypotheses. In contrast to Houde (2008a), I think there is still much to be learned in Hjort's shadow, particularly when variable data are investigated using extended meta-analytical methods such as those presented in this thesis.

Appendix A

APPENDIX FOR CHAPTER 3: SURVIVAL VARIABILITY AND POPULATION DENSITY IN FISH POPULATIONS

A.1 Supplementary Methods

A.1.1 Analytical Models for Survival Variability

The full theoretical treatment of survival variability and population density proceeds as follows. Note that the salient features are presented in the Methods section of the manuscript but are repeated here for continuity.

Recruitment can be written(Mertz and Myers, 1996) as

$$R_t = E_t \exp(-(C_{1,t} + C_{2,t} + C_{3,t})) \tag{A.1}$$

Where E_t is the number of eggs produced in year t and $C_{i,t}$ is the cumulative mortality in stage i; $i = 1$ for the egg stage, $i = 2$ for the late larval stage, and $i = 3$ for the juvenile phase. Population size in the egg, late-larval, and late juvenile phase (when they recruit to the older population) are given by E_t, N_t, and R_t, respectively. In order to analyze the effect of density dependence on the relationship between variability and reproductive adult abundance we will examine a model in which density dependence arises in the juvenile stage, a treatment which is motivated by the demonstration of the suitability of this choice for many fish populations(Myers and Cadigan, 1993a,b). Stochastic mortality, independent of density, is assumed to take place during both the larval and juvenile stages. The number of late-stage larval fish, is $N_t = E_t \exp(-(C_{1,t} + C_{2,t}))$. The number of fish surviving from the late-larval stage through to the end of the juvenile phase is given by

$$R_t = N_t \exp(-C_{3,t}) \tag{A.2}$$

It is useful to formulate the above equations in terms of deviations from their means. Letting $C_{3,t} = \overline{C_3} + \Delta C_{3,t}$ and $\ln N_t = \overline{\ln N} + \Delta \ln N_t$ gives

$$\ln R_t = \overline{\ln R} + \Delta \ln N_t - \Delta C_{3,t} \tag{A.3}$$

where

$$\overline{\ln R} = \overline{\ln N} - \overline{C_3} = \ln(N_* \exp(-\overline{C_3})) \tag{A.4}$$

and N_* is the geometric mean abundance of the late-larval stage(Mertz and Myers, 1996). Rearranging (A.3)

$$\begin{aligned}
\ln R_t - \overline{\ln R} &= \Delta \ln N_t - \Delta C_{3,t} && \text{(A.5)}\\
\exp(\ln R_t - \overline{\ln R}) &= \exp(\Delta \ln N_t - \Delta C_{3,t}) && \text{(A.6)}\\
\frac{R_t}{R_*} &= \exp(\Delta \ln N_t - \Delta C_{3,t}) && \text{(A.7)}\\
R_t &= R_* \exp(\Delta \ln N_t - \Delta C_{3,t}) && \text{(A.8)}
\end{aligned}$$

where R_* is the geometric mean recruitment. The effect of density dependence can be incorporated by writing

$$\Delta C_{3,t} = f(\Delta \ln N_t) + \delta_t - \bar{f} \ , \tag{A.9}$$

where f is an as yet unspecified function representing density dependence, δ_t represents mortality in the juvenile stage unrelated to density and $\bar{f}$ is the time average of $f(\Delta \ln N_t)$. Letting $\varepsilon_t = \sum_{i=1}^{2} \Delta C_{i,t}$ be the sum of the demeaned mortalities in the egg and larval stages, it has been shown(Mertz and Myers, 1995) that

$$\Delta \ln N_t = \Delta \ln E_t - \varepsilon_t \approx \Delta \ln S_t - \varepsilon_t = \ln S_t - \ln S_* - \varepsilon_t = \ln(S_t/S_*) - \varepsilon_t \tag{A.10}$$

where E_t is egg production, S_* is geometric mean adult abundance, and we have used $\Delta \ln S_t \approx \Delta \ln E_t$, valid when egg production is linearly related to adult abundance. Substituting (A.10) and (A.9) into (A.8), we can now write

$$\begin{aligned} R_t &= R_* \exp(\ln(S_t/S_*) - (\varepsilon_t + f(\Delta \ln S_t - \varepsilon_t) + \delta_t - \bar{f})) && \text{(A.11)} \\ &= \frac{R_* \exp(\ln(S_t/S_*))}{\exp(\varepsilon_t + f(\Delta \ln S_t - \varepsilon_t) + \delta_t - \bar{f})} && \text{(A.12)} \\ &= R_* \frac{S_t}{S_*} \exp(-(\varepsilon_t + f(\Delta \ln S_t - \varepsilon_t) + \delta_t - \bar{f})) && \text{(A.13)} \end{aligned}$$

At a given adult abundance, $S_t = S_0$, log survival is $\ln(R_t/S_0)$, therefore, from (A.13), we have

$$\ln(R_t/S_0) = \ln(R_*/S_*) - \varepsilon_t - f[\ln(S_0/S_*) - \varepsilon_t] - \delta_t + \bar{f} \qquad \text{(A.14)}$$

One conclusion is immediately apparent from (A.14): the variability of survival, Var$[\ln(R_t/S_0)]$, will be independent of adult abundance only if $f[\ln(S_0/S_*) - \varepsilon_t]$ is linear. Specifically, write $f[\ln(S_0/S_*) - \varepsilon_t] = \lambda[\ln(S_0/S_*) - \varepsilon_t]$. Prescribing a density-dependent mortality which is linear in log-abundance is the core of key factor analysis(Varley and Gradwell, 1960; Manly, 1990) and is essential to the analytic tractability of key factor analysis. The variability of survival is derived as follows, substituting $\lambda[\ln(S_0/S_*) - \varepsilon_t]$ into (A.14)

$$\begin{aligned} \ln(R_t/S_0) &= \ln(R_*/S_*) - \varepsilon_t - \lambda[\ln(S_0/S_*) - \varepsilon_t] - \delta_t + \bar{f} && \text{(A.15)} \\ &= \ln(R_*/S_*) - \varepsilon_t(1-\lambda) - \lambda \ln(S_0/S_*) - \delta_t + \bar{f} && \text{(A.16)} \\ \text{Var}(\ln(R_t/S_0)) &\approx (1-\lambda)^2 \sigma_\varepsilon^2 + \sigma_\delta^2 && \text{(A.17)} \end{aligned}$$

where σ_ε and σ_δ are the standard deviations of ε and δ, respectively. The survival variability is independent of S_0 and the effect of density dependent juvenile mortality (λ) is clearly to reduce survival variability. A similar expression was previously obtained for the Gompertz form of density dependence(Lande *et al.*, 2003). Note that for small ε_t an expression analogous to (A.17) may be derived, using the delta method(Stuart and Ord, 1987), which is a Taylor series expansion, valid for any smooth f

$$\text{Var}[\ln(R_t/S_0)] \approx [1 - f'(\ln(S_0/S_*) - \varepsilon_t)]^2 \sigma_\varepsilon^2 + \sigma_\delta^2 \qquad \text{(A.18)}$$

Here, $f'(\ln(S_0/S_*) - \varepsilon_t)$ is the first derivative of f with respect to ε_t, evaluated at its mean. It is evident that the variance of survival will be a minimum for the adult abundance at which $f'(\ln(S_0/S_*) - \varepsilon_t)$ is maximum. However, this result is not valid for large σ_ε and thus it is necessary to consider a case where the variance of survival can be derived without demanding that σ_ε be small.

It is useful to consider common models and how the variability in recruitment and survival is a function of egg abundance. For the commonly applied Ricker spawner-recruit function, where survival is a linear function of adult abundance

$$f[\ln(S_0/S_*) - \varepsilon_t] = \exp[\ln(S_0/S_*) - \varepsilon_t + \gamma] = \beta S_0 \exp(-\varepsilon_t) \tag{A.19}$$

where $\beta = e^\gamma/S_*$. From (A.19) and (A.13), one has

$$R_t = \alpha S_0 \exp(-\beta S_0 e^{-\varepsilon_t} - \varepsilon_t - \delta_t) \tag{A.20}$$

where several constants have been combined into the parameter α. In the limit of zero noise one obtains from (A.20) the Ricker form, $R_t = \alpha S_0 \exp(-\beta S_0)$.

From (A.20), the variability of survival is

$$\text{Var}[\ln(R_t/S_0)] = \sigma_\varepsilon^2 + \beta^2 S_0^2 \text{Var}(\exp(-\varepsilon_t)) + 2\beta S_0 \text{Cov}(\varepsilon_t, \exp(-\varepsilon_t)) + \sigma_\delta^2 \tag{A.21}$$

The variance term on the right side of (A.21) may be obtained from the variance of a lognormal distribution, $\text{Var}(\exp(-\varepsilon_t)) = \exp(\sigma_\varepsilon)(\exp(\sigma_\varepsilon) - 1)$, and the covariance term may be computed as follows

$$\begin{aligned}
\text{Cov}(\varepsilon_t, \exp(-\varepsilon_t)) &= E[\varepsilon_t \exp(-\varepsilon_t)] - E[\varepsilon_t]E[\exp(-\varepsilon_t)] && \text{(A.22)}\\
E[\varepsilon_t] &= 0 && \text{(A.23)}\\
\therefore \text{Cov}(\varepsilon_t, \exp(-\varepsilon_t)) &= E[\varepsilon_t \exp(-\varepsilon_t)] && \text{(A.24)}\\
\text{Cov}(\varepsilon_t, \exp(-\varepsilon_t)) &= \int_{-\infty}^{\infty} \varepsilon_t \exp(-\varepsilon_t) \frac{1}{\sqrt{2\pi}\sigma_\varepsilon} \exp(-\frac{\varepsilon_t^2}{2\sigma_\varepsilon^2})\, dx && \text{(A.25)}\\
&= -\exp(\frac{\sigma_\varepsilon^2}{2})\sigma_\varepsilon^2 && \text{(A.26)}
\end{aligned}$$

where $E[\cdot]$ is the expectation operator and we have used $E[g(x)] = \int g(x) f(x)\, dx$, where $f(x)$ is the density function of x. Equation (A.21) may now be reduced to

$$\text{Var}[\ln(R_t/S_0)] = \sigma_\varepsilon^2 + \beta^2 S_0^2 \exp(\sigma_\varepsilon^2)[\exp(\sigma_\varepsilon^2) - 1] - 2\beta S_0 \sigma_\varepsilon^2 \exp(\sigma_\varepsilon^2/2) + \sigma_\delta^2 \tag{A.27}$$

For small σ_ε

$$\text{Var}[\ln(R_t/S_0)] \approx \sigma_\varepsilon^2 (1 - \beta S_0)^2 + \sigma_\delta^2 \tag{A.28}$$

which can also be obtained from (A.18). In general, it is apparent from (A.28) that for large $\beta S_0 > 1$, the term containing $\beta^2 S_0^2$ will dominate and the variability of survival will increase with S_0. For $\beta S_0 \ll 1$, the term in $2\beta S_0$ will dominate that containing $\beta^2 S_0^2$ and thus the variability of survival will decrease as S_0 increases. Therefore, the variability of survival will have a bowl-shaped dependence on S_0. As σ_ε increases the bottom of the bowl will be pushed closer to the $S_0 = 0$ axis. These aspects of the function's behaviour and a comparison with the delta method approximation are illustrated in Fig. SA.1.

A.1.2 Delta Method Approximations to Survival Variability

Direct analytic calculation of the variance terms for population growth models that do not exhibit linearity between survival and adult abundance are not available in closed form, here we use a delta method approximation to the variance of a function(Stuart and Ord, 1987). In order to generalize the results across commonly applied models, the three-parameter Deriso-Schnute(Deriso, 1980; Schnute, 1985) stock-recruitment model is used

$$\begin{aligned} R_t &= \alpha S (1 - \beta\gamma S_0)^{\frac{1}{\gamma}} && \text{(A.29)} \\ \ln(R_t/S_0) &= \ln(\alpha) + \frac{1}{\gamma} \ln(1 - \beta\gamma S_0) && \text{(A.30)} \end{aligned}$$

The delta method approximation follows from equation (A.18) where

$$\begin{aligned} f[\ln(S_0/S_*) - \varepsilon_t] &= \frac{1}{\gamma} \ln(1 - \beta\gamma S_0 \exp(-\varepsilon_t)) && \text{(A.31)} \\ f'[\ln(S_0/S_*) - \varepsilon_t] &= \beta S_0/(1 - \gamma\beta S_0) && \text{(A.32)} \\ \text{Var}(\ln(R_t/S_0)) &\approx (1 - \beta S_0/(1 - \gamma\beta S_0))^2 \sigma_\varepsilon^2 && \text{(A.33)} \end{aligned}$$

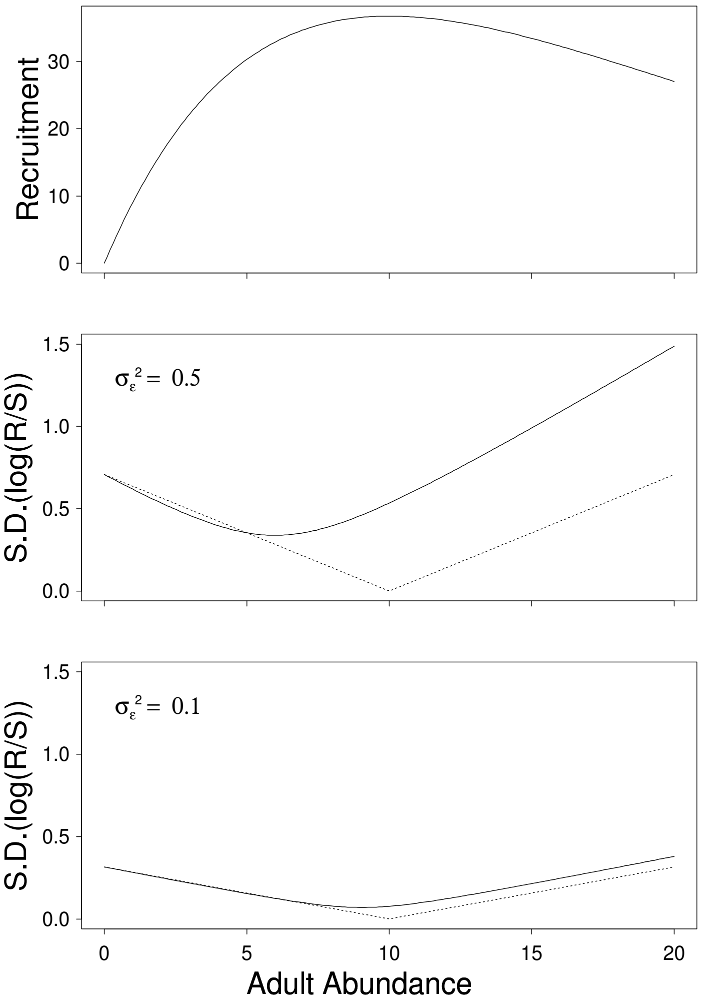

Figure A.1: The relationship between recruitment (top panel) and the standard deviation of survival at median ($\sigma_\varepsilon^2 = 0.5$, middle panel) and low ($\sigma_\varepsilon^2 = 0.1$, lower panel) pre-density-dependent variable mortality levels. The solid line is the exact solution and the dotted line in the delta approximation. The recruitment is from the equation $R = 3Se^{-\frac{1}{10}S}$.

Possible models of survival range over a degree of compensation continuum between constant productivity (no density dependence) when $\gamma << -1$ and high degrees of over-compensation when $\gamma \geq 0$ (e.g. Ricker and Schaefer model). We fix $\gamma \in \{-1000, -2, -1, 0, 1\}$ for cases of no density dependence, Cushing-like density dependence (non-asymptotic recruitment), Beverton-Holt compensation, and Ricker and Schaefer over-compensation models, respectively. $\sigma_\epsilon^2 = 0.5$ and $\beta = 0.02$ for all models except the Schaefer model for which $\beta = 0.0085$. The delta method at $\beta = 0.02$ gives well behaved approximate variances for all models except the Schaefer. The Schaefer model is problematic at this value due to the behaviour of the term $(1 - \beta S_0)$ as it approaches 0. For this reason we chose to use a smaller value of β which avoids this situation but still retains the properties of this model. The depensatory Beverton-Holt survival model used was $\ln(R_t/S_0) = \ln(\alpha) + \frac{1}{\gamma}\ln(1 - \beta\gamma S_0) + \ln(S_0) - \ln(S_0 + d)$, where d is the strength of depensation at low S.

A.1.3 Sensitivity Analysis

The purpose of the sensitivity analysis is to determine what effect parameter values have on the model outcome of survival variability. We perform sensitivity analyses on the Beverton-Holt and Ricker model cases of the Deriso-Schnute model to illustrate the general concepts. We perform the sensitivity analysis over a reasonable set of parameter ranges as estimated from the individual fits. To estimate the effect of a given parameter, we hold the other parameters fixed at the median estimate for that parameter and estimate a target function. The two target functions were: for the Beverton-Holt, an estimate of the change in the variance in survival $\Delta\sigma^2_{ln\frac{R}{S}}$ from the lowest parameter value to the highest (estimate of the slope); for the Ricker: because of the quadratic nature of the function of survival variability over adult density, the difference between the first and last values tells us little, therefore we estimate the sum of the absolute value of the first order difference $(\sum_{i=1}^{n}|\sigma^2_{ln\frac{R_i}{S_i}} - \sigma^2_{ln\frac{R_{i-1}}{S_{i-1}}}|)$ over all densities to provide a metric for how much change occurs in the variance in survival over the parameter space. The results of the sensitivity analysis are illustrated in Fig. SA.2.

The effect of increasing the variance in survival in the egg and larval stages is to increase the rate of change of survival variability. Consequently, a large value for σ_ϵ^2 will

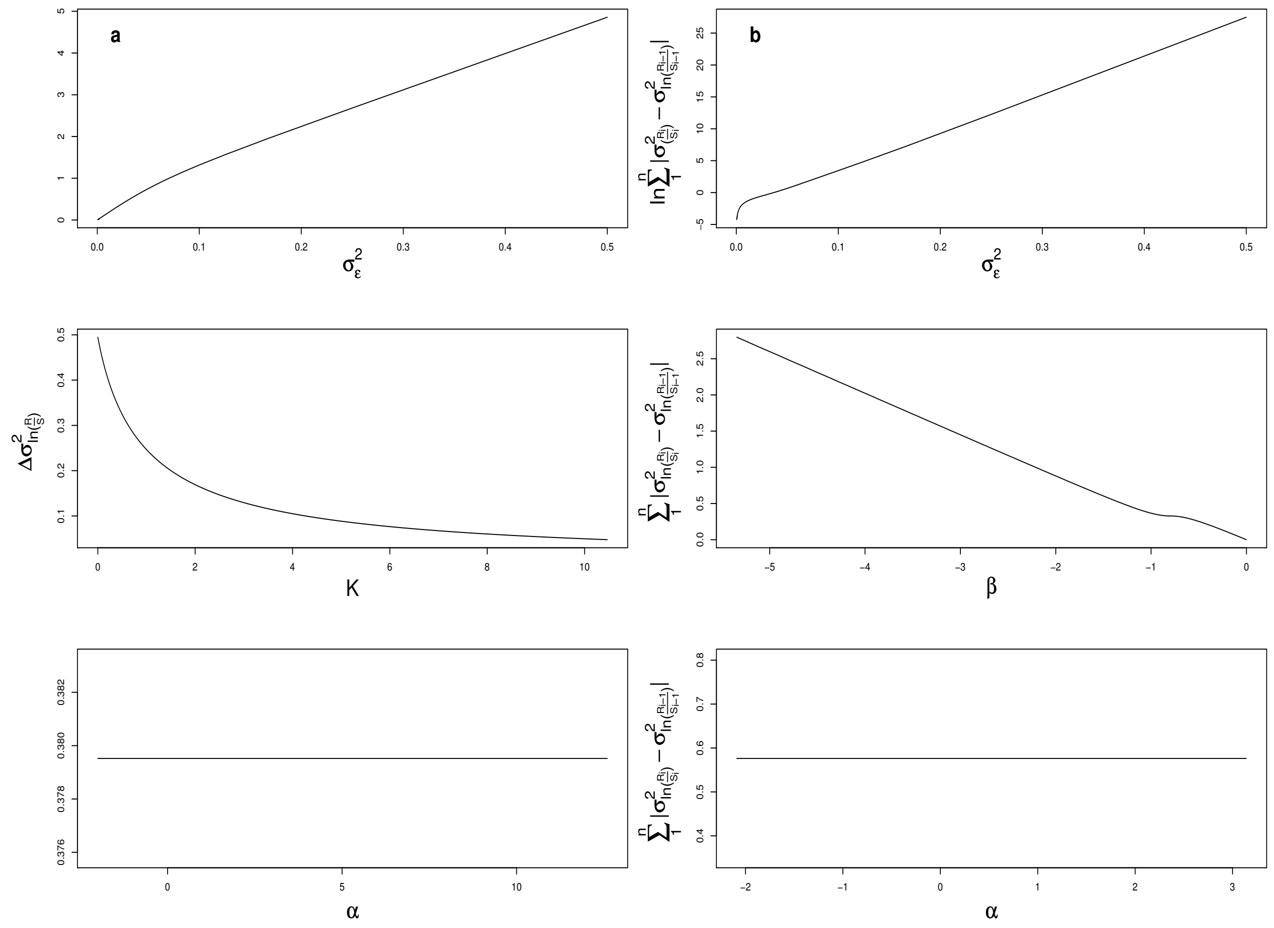

Figure A.2: Sensitivity analysis results for the Beverton-Holt (**a**) and Ricker (**b**) survival models. The re-scaled adult abundance ranges between 0 and 1. The range of values chosen were Beverton-Holt: $\alpha \in [-2.0, 12.6]$, $K = 1/\beta \in [1e - 09, 10.46]$) and (Ricker: $\alpha \in [-2.0, 3.1]$, $\beta \in [-5.34, -1e - 09]$). For the variance of mortality in the egg and larval stages we chose $\sigma^2_\epsilon \in [0, 0.5]$. The target function for the Beverton-Holt was change in the variance in survival forom the lowest parameter value to the highest $\Delta\sigma^2_{ln\frac{R}{S}}$ and for the Ricker: the sum of the absolute value of the first order difference ($\sum_{i=1}^{n} |\sigma^2_{ln\frac{R_i}{S_i}} - \sigma^2_{ln\frac{R_{i-1}}{S_{i-1}}}|$).

ensure strong survival variability. Note that the positive values of $\Delta\sigma^2_{ln\frac{R}{S}}$, indicate that the variability will decrease over adult abundance where this form of density dependence arises in the juvenile phase. The density-dependent parameters also behave in an intuitive manner. The stronger the regulation (low carrying capacity $K = 1/\beta$ in the Beverton-Holt), the greater the change of survival variability over adult density. If we consider a weakly regulated population to have a high K value, survival variability over adult density will be relatively flat, thus the value of $\Delta\sigma^2_{ln\frac{R}{S}}$ will be low. In contrast, strongly regulated populations (low K) will experience marked changes in survival variability (strongly negative slope approximated by $\Delta\sigma^2_{ln\frac{R}{S}}$) over adult density. For the Ricker β, stronger regulation results in more change in the variance in survival over adult density. Weakly regulated populations are characterised by small changes in survival variability over adult density. No change is observed in the survival variability over the ranges for α in both the Beverton-Holt and Ricker models. This is because α is independent of density.

A.1.4 Meta-analytical Methods

Data were analyzed taxonomically by population within a species. To investigate whether the results are robust to different survival model formulations, we fit survival models with fixed $\gamma \in \{1, 0, -1\}$ in

$$\ln(R_t/S_t) = \ln(\alpha) + \frac{1}{\gamma}\ln(1 - \beta\gamma S_t) \tag{A.34}$$

corresponding to the commonly applied Schaefer, Ricker ($\lim_{\gamma\to 0}\alpha S_t(1-\beta\gamma S_t)^{1/\gamma} = \alpha S e^{-\beta S_t}$), and Beverton-Holt models, respectively.

The fixed-effects estimates are estimated by species in two seperate ways.

1. For species with greater than 4 populations a mixed-effects meta-analysis combining all the populations was used. The model fit to each species was

$$\ln(\frac{R_{t,i}}{S_{t,i}}) = \ln(\alpha + \mu_{i1}) + \frac{1}{\gamma}\ln(1 - (\beta + \mu_{i2})\gamma S_i) + e^{(\eta_0 + \mu_{i3}) + \eta_1 S_i} \tag{A.35}$$

Where $\alpha, \beta, \eta_0, \eta_1$ are the fixed-effects parameters for a given species and the μ_{ij} are the random effects parameters distributed $N(0, \sigma^2_{\mu_j})$. There are random effects on all parameters except the slope of the variance because we want maximum flexibility for the model form for each population within a species but want to obtain an overall estimate of the change in the variance over abundance.

2. For species with less than 5 populations, there aren't enough degrees of freedom to estimate all parameters (the degrees of freedom in a mixed-effects analysis in SAS PROC NLMIXED is the number of populations minus the number of random effects). Here, estimates of the slope of the variance were combined within a species using a weighted average of the individual population estimates, weighted by their respective sampling variances

$$\hat{\eta} = \frac{\sum_{i=1}^{k} W_i \eta_i}{\sum_{i=1}^{k} W_i} \tag{A.36}$$

   where $W_i = 1/s_i^2$, s_i being the standard deviation associated with the estimated heteroscedastic coefficient η_i in population i.

Ideally all species-level estimates would come from the fixed-effects parameters from a mixed-effects fit, which makes the best use of all the data.

We are primarily interested in the general trend of the change in variance over adult abundance per species but provide an overall estimate of η_1 by combining the estimates of the fixed-effects estimated from 1 and 2 above using a random effects meta-analysis (Normand, 1999). The fixed-effects results per species were combined to provide an overall heteroscedastic coefficient result according to

$$\hat{\eta_{me}} = \frac{\sum_{i=1}^{k} w_i(\hat{\tau}) \eta_i}{\sum_{i=1}^{k} w_i(\hat{\tau})} \tag{A.37}$$

where $\hat{\tau}$ is the inter-population variation estimated by restricted maximum likelihood (Normand, 1999) and

$$w_i(\hat{\tau}) = \frac{1}{s_i^2 + \hat{\tau}^2} \tag{A.38}$$

A.2 Supplementary Figures

Presented in Fig. SA.3-SA.8 are the individual population-level fits to the survival data from each available population under the Schaefer, Ricker, and Beverton-Holt survival model assumptions. Provided in the top-right of each plot is the population ID and estimate of the heteroscedastic coefficient.

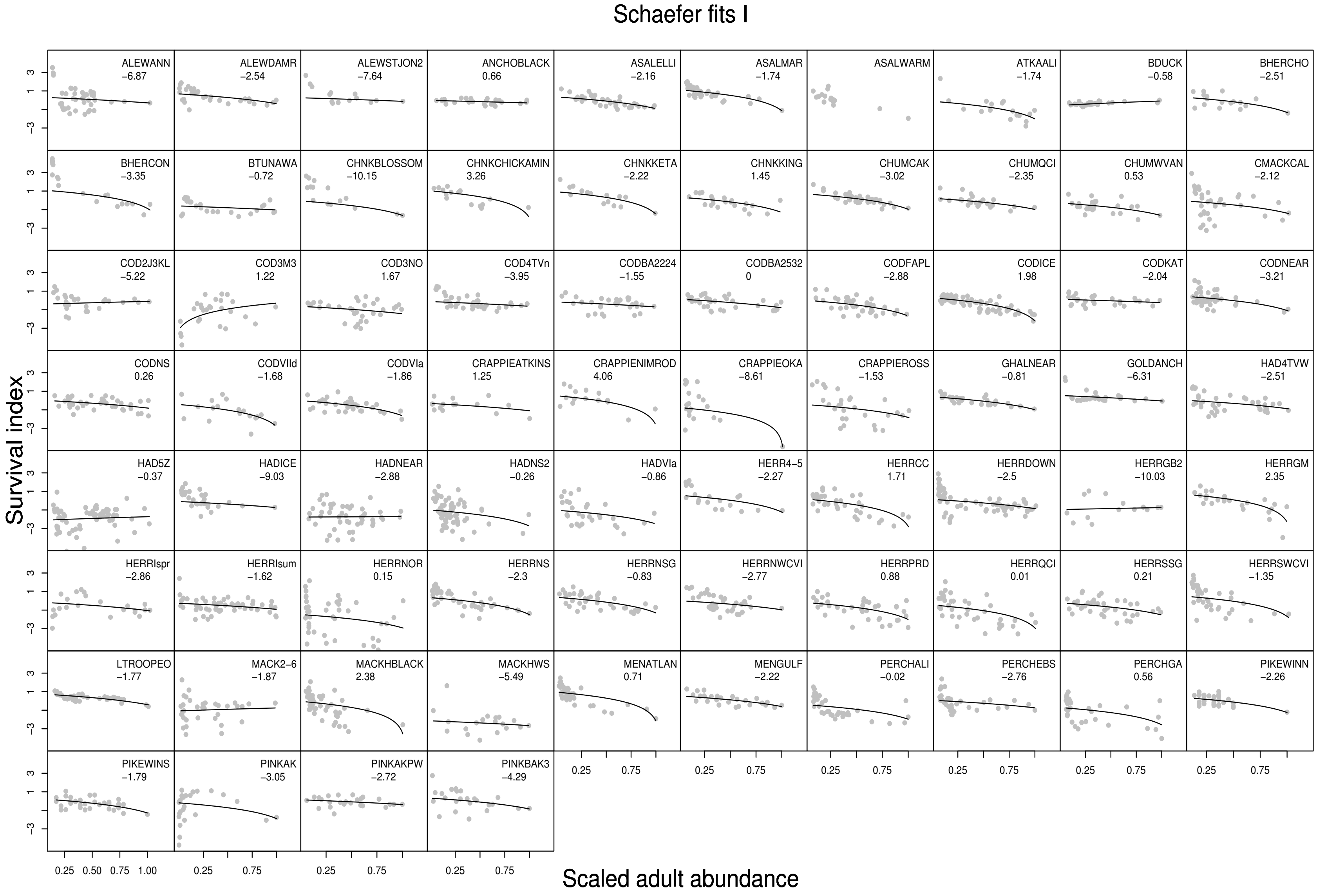

Figure A.3: Individual population-level fits of the heteroscedastic Schaefer survival model. The legend in each plot represents the population ID and the estimate of the slope of the variance for that population.

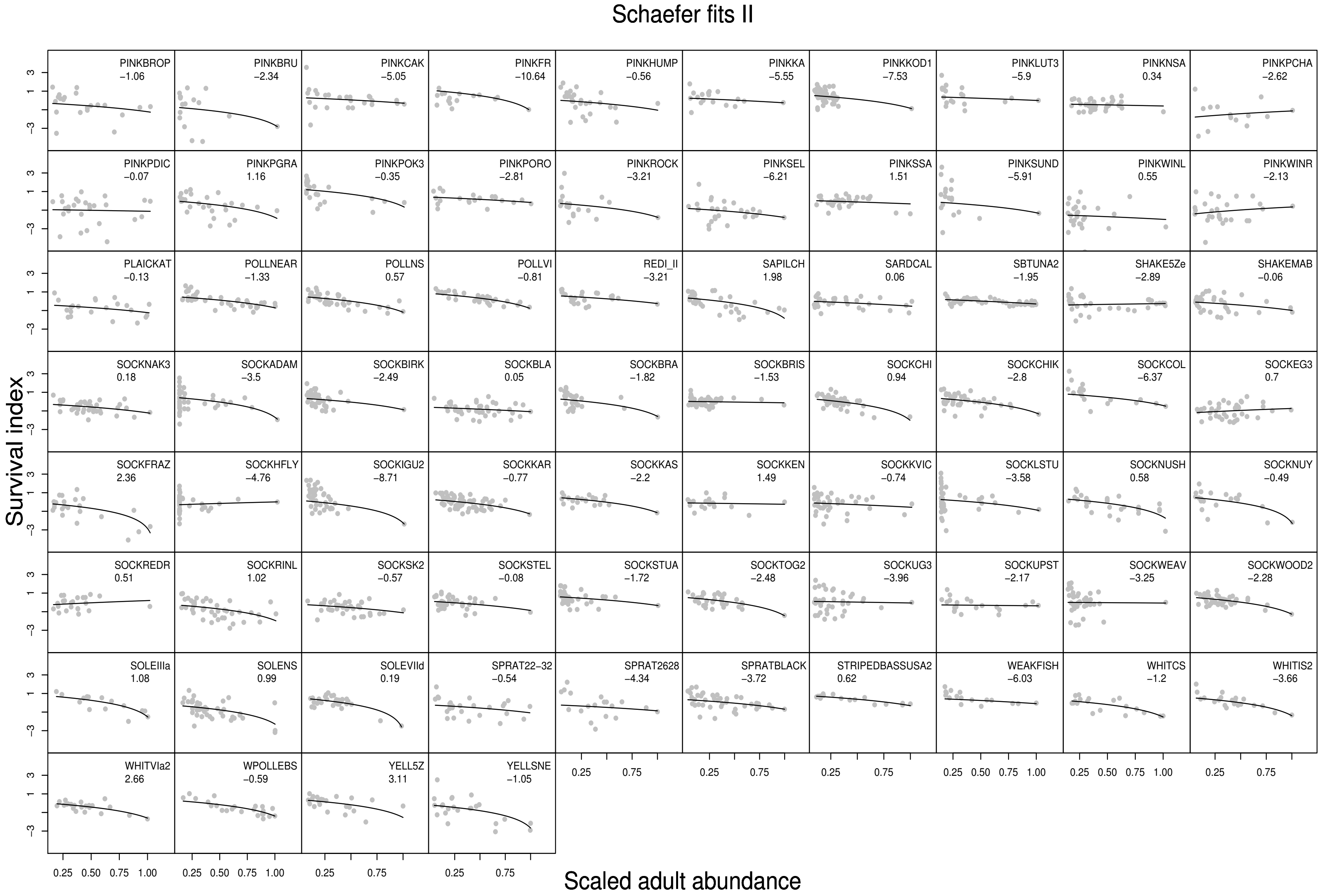

Figure A.4: Individual population-level fits of the heteroscedastic Schaefer survival model continued. The legend in each plot represents the population ID and the estimate of the slope of the variance for that population.

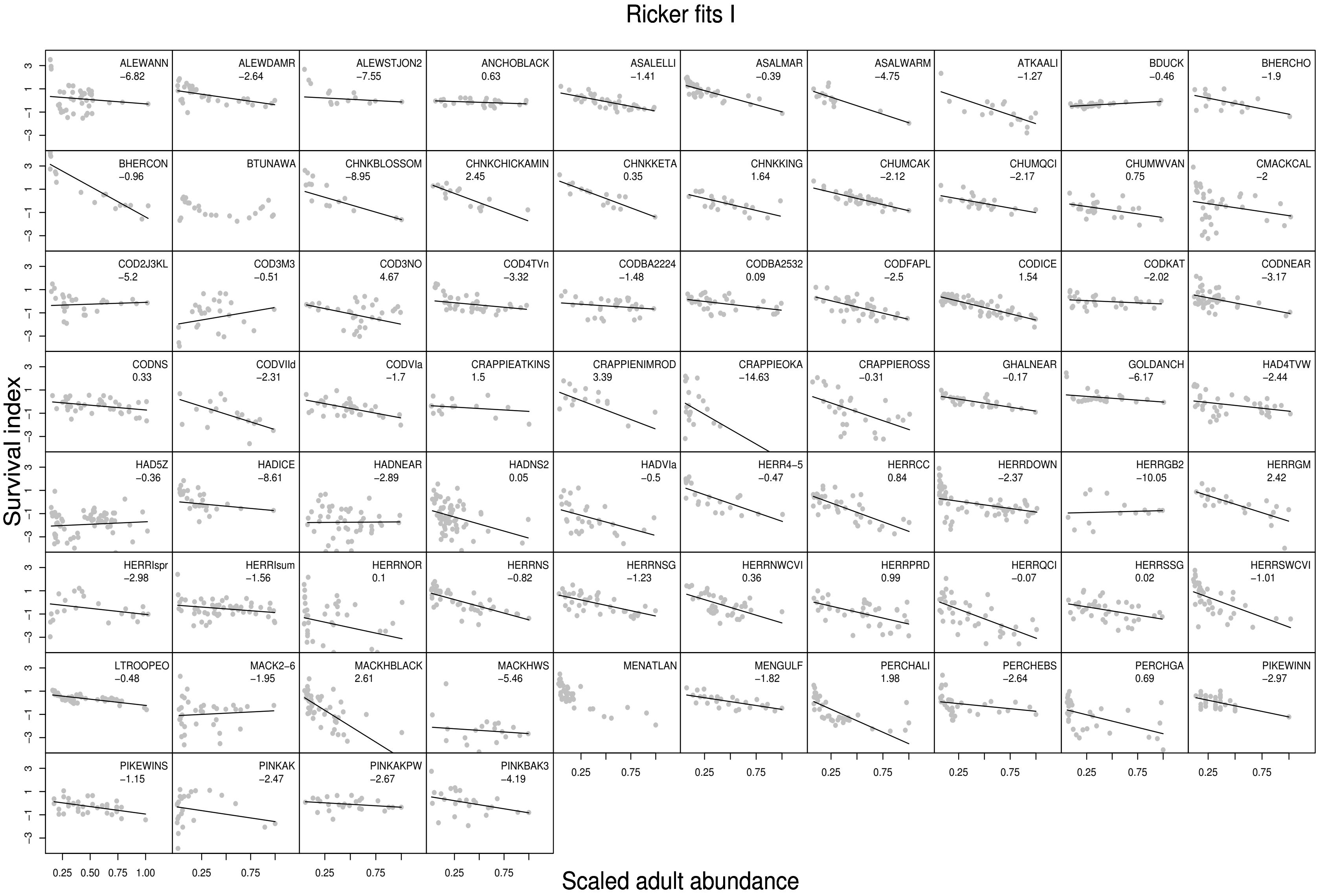

Figure A.5: Individual population-level fits of the heteroscedastic Ricker survival model. The legend in each plot represents the population ID and the estimate of the slope of the variance for that population.

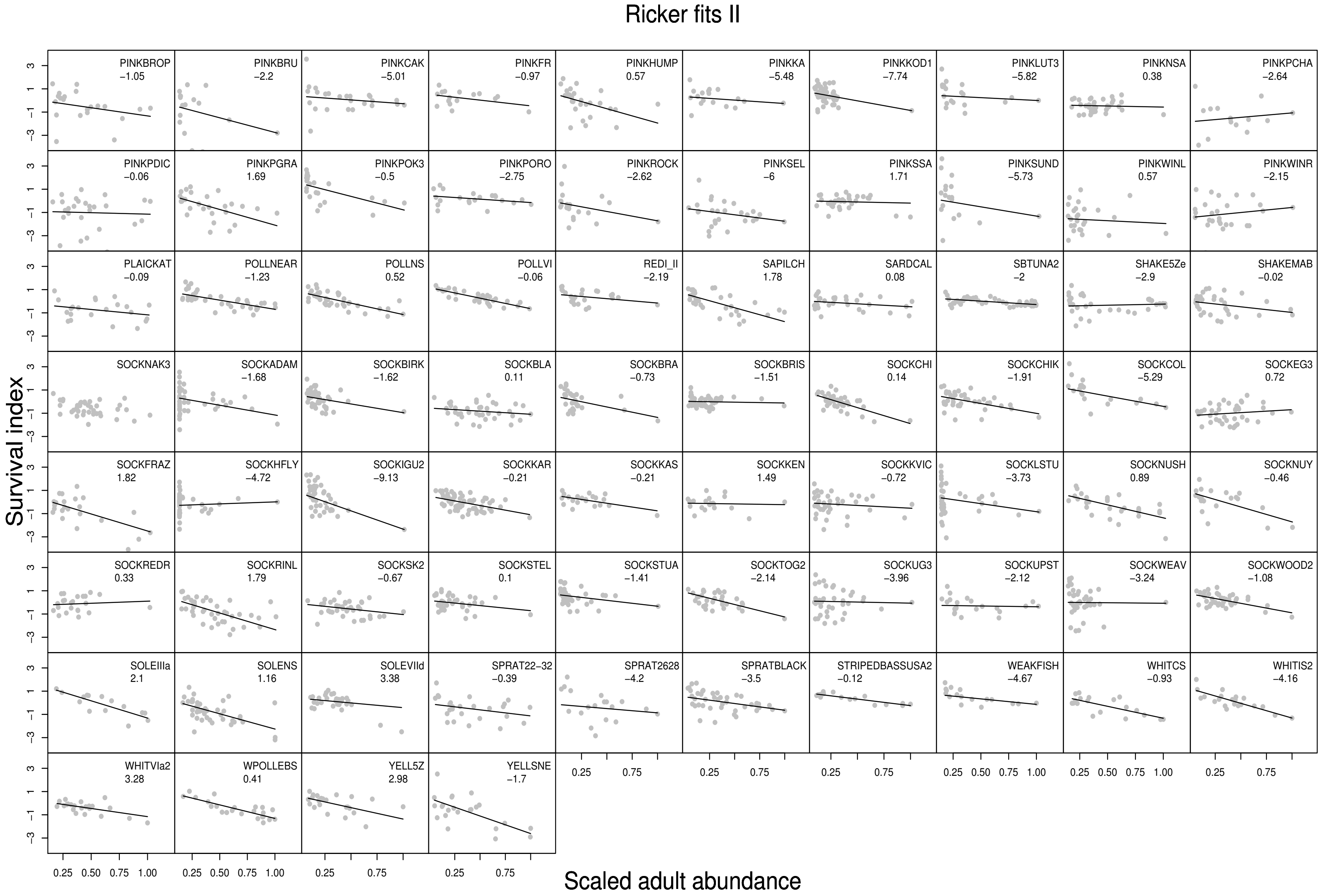

Figure A.6: Individual population-level fits of the heteroscedastic Ricker survival model continued. The legend in each plot represents the population ID and the estimate of the slope of the variance for that population.

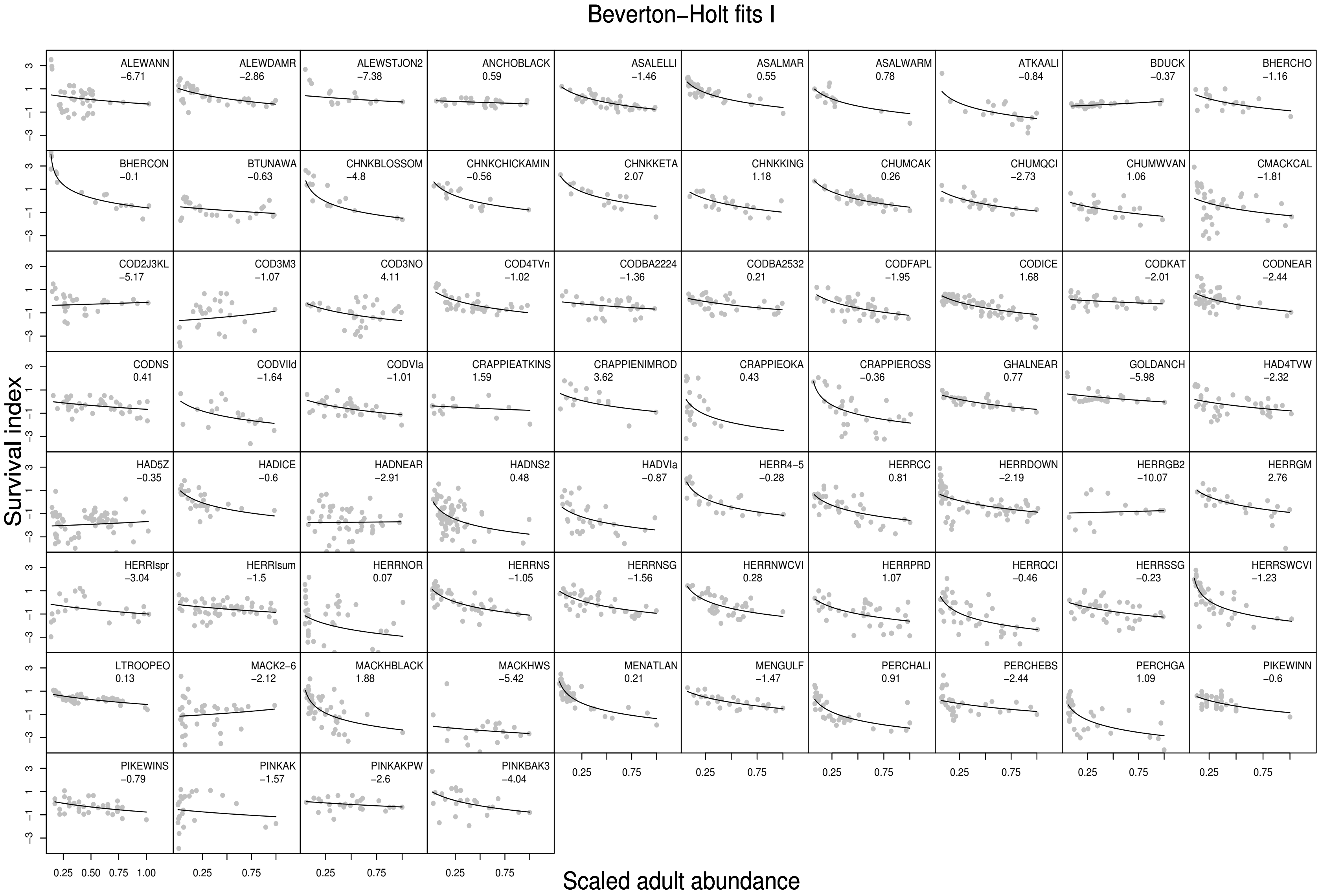

Figure A.7: Individual population-level fits of the heteroscedastic Beverton-Holt survival model. The legend in each plot represents the population ID and the estimate of the slope of the variance for that population.

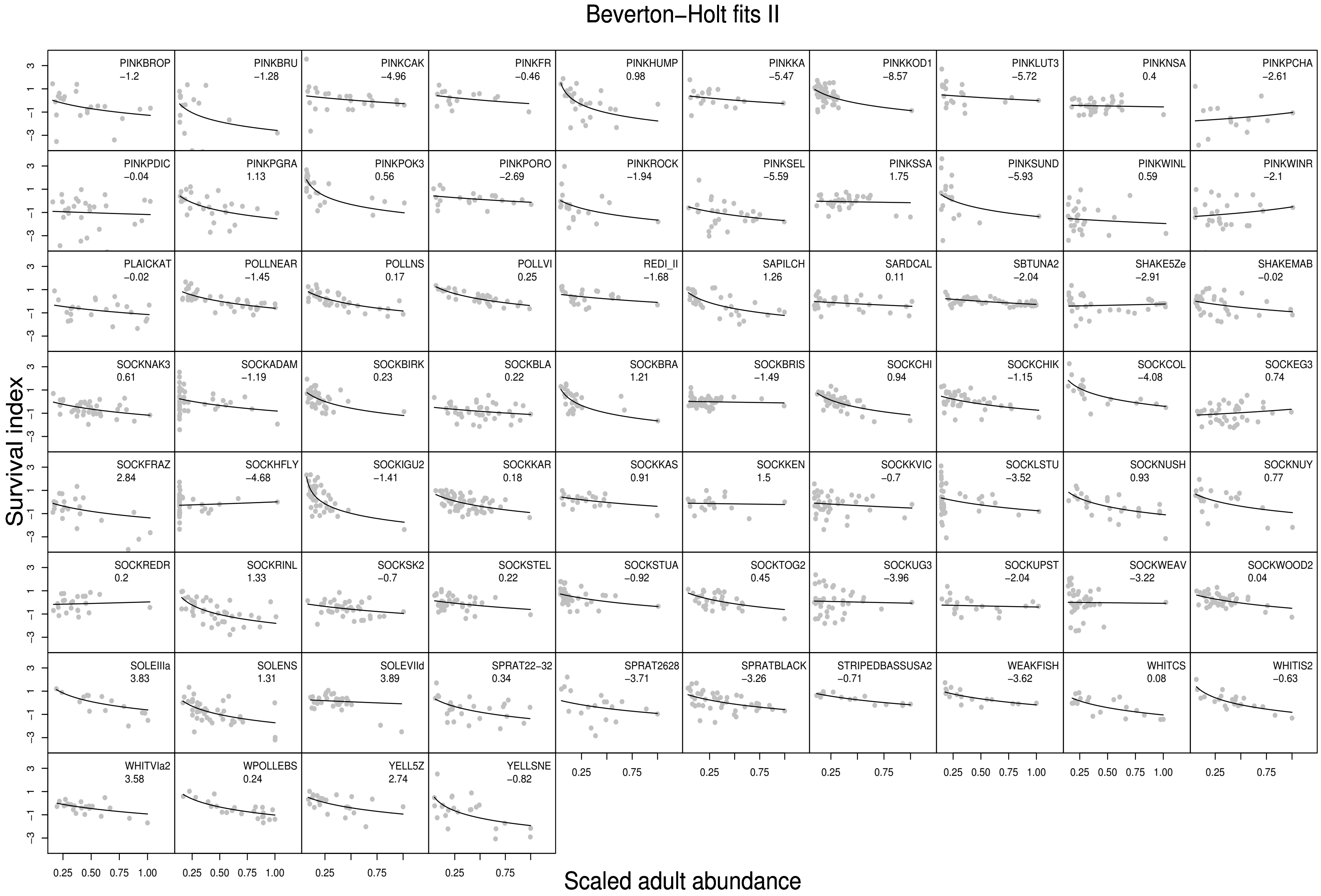

Figure A.8: Individual population-level fits of the heteroscedastic Beverton-Holt survival model continued. The legend in each plot represents the population ID and the estimate of the slope of the variance for that population.

A.3 Supplementary Tables

The details of each population ID analysed are presented in Table SA.1.

Table A.1: Stock details for each population analysed

ID	Order	Family	Latin name	Common name	Area
ALEWANN	Clupeiformes	Clupeidae	*Alosa pseudoharengus*	Anadromous alewife	Annaquatucket River, USA
ALEWDAMR	Clupeiformes	Clupeidae	*Alosa pseudoharengus*	Anadromous alewife	Damariscotta River
ALEWSTJON2	Clupeiformes	Clupeidae	*Alosa pseudoharengus*	Anadromous alewife	Saint John River
ANCHOBLACK	Clupeiformes	Engraulidae	*Engraulis encrasicolus*	Anchovy	Black Sea
ASALELLI	Salmoniformes	Salmonidae	*Salmo salar*	Atlantic salmon	Ellidaar River, Iceland
ASALMAR	Salmoniformes	Salmonidae	*Salmo salar*	Atlantic salmon	Margaree River, NS , Canada
ASALWARM	Salmoniformes	Salmonidae	*Salmo salar*	Atlantic salmon	Western Arm Brook, Canada
ATKAALI	Scorpaeniformes	Hexagrammidae	*Pleurogrammus monopterygius*	Atka mackerel	Eastern Bering Sea and Aleutian Islands
BDUCK	Aulopiformes	Synodontidae	*Harpodon nehereus*	Bombay duck	Northwest coast of India
BHERCHO	Clupeiformes	Clupeidae	*Alosa aestivalis*	Blueback herring	Chowan River, USA
BHERCON	Clupeiformes	Clupeidae	*Alosa aestivalis*	Blueback herring	Connecticut River, USA
BTUNAWA	Perciformes	Scombridae	*Thunnus thynnus*	Atlantic bluefin tuna	West Atlantic
CHNKBLOSSOM	Salmoniformes	Salmonidae	*Oncorhynchus tshawytscha*	Chinook salmon	Blossom River, Alaska-B.C
CHNKCHICKAMIN	Salmoniformes	Salmonidae	*Oncorhynchus tshawytscha*	Chinook salmon	Chickamin River, Alaska-B.C
CHNKKETA	Salmoniformes	Salmonidae	*Oncorhynchus tshawytscha*	Chinook salmon	Keta River, Alaska-B.C
CHNKKING	Salmoniformes	Salmonidae	*Oncorhynchus tshawytscha*	Chinook salmon	King Salmon River, Alaska
CHUMCAK	Salmoniformes	Salmonidae	*Oncorhynchus keta*	Chum salmon	Central Alaska
CHUMQCI	Salmoniformes	Salmonidae	*Oncorhynchus keta*	Chum salmon	Queen Charlotte Islands, B.C
CHUMWVAN	Salmoniformes	Salmonidae	*Oncorhynchus keta*	Chum salmon	West Coast Vancouver Island, B.C
CMACKCAL	Perciformes	Scombridae	*Scomber japonicus*	Chub mackerel	Southern California
COD2J3KL	Gadiformes	Gadidae	*Gadus morhua*	Cod	NAFO 2J3KL
COD3M3	Gadiformes	Gadidae	*Gadus morhua*	Cod	Flemish Cap (NAFO Div 3M)
COD3NO	Gadiformes	Gadidae	*Gadus morhua*	Cod	NAFO 3NO

Table A.1 – continued on next page

Table A.1 – continued from previous page

ID	Order	Family	Latin name	Common name	Area
COD4TVn	Gadiformes	Gadidae	*Gadus morhua*	Cod	NAFO 4TVn
CODBA2224	Gadiformes	Gadidae	*Gadus morhua*	Cod	Baltic Areas 22 and 24
CODBA2532	Gadiformes	Gadidae	*Gadus morhua*	Cod	Baltic Areas 25-32
CODFAPL	Gadiformes	Gadidae	*Gadus morhua*	Cod	Faroe Plateau
CODICE	Gadiformes	Gadidae	*Gadus morhua*	Cod	Iceland
CODKAT	Gadiformes	Gadidae	*Gadus morhua*	Cod	Kattegat
CODNEAR	Gadiformes	Gadidae	*Gadus morhua*	Cod	North East Arctic
CODNS	Gadiformes	Gadidae	*Gadus morhua*	Cod	North Sea
CODVIId	Gadiformes	Gadidae	*Gadus morhua*	Cod	ICES VIId
CODVIa	Gadiformes	Gadidae	*Gadus morhua*	Cod	ICES VIa
CRAPPIEATKINS	Perciformes	Centrarchidae	*Promoxis annularis* and *nigromaculatus*	Crappie	Atkins Reservoir, Arkansas
CRAPPIENIMROD	Perciformes	Centrarchidae	*Promoxis annularis* and *nigromaculatus*	Crappie	Nimrod Reservoir, Arkansas
CRAPPIEOKA	Perciformes	Centrarchidae	*Promoxis annularis* and *nigromaculatus*	Crappie	Okatibbee Reservoir, Mississippi
CRAPPIEROSS	Perciformes	Centrarchidae	*Promoxis annularis* and *nigromaculatus*	Crappie	Ross Barnett Reservoir, Mississippi
GHALNEAR	Pleuronectiformes	Pleuronectidae	*Reinhardtius hippoglossoides*	Greenland halibut	North East Arctic
GOLDANCH	Clupeiformes	Engraulidae	*Coilia dussumieri*	Gold-spotted grenadier anchovy	Northwest coast of India
HAD4TVW	Gadiformes	Gadidae	*Melanogrammus aeglefinus*	Haddock	NAFO 4TVW
HAD5Z	Gadiformes	Gadidae	*Melanogrammus aeglefinus*	Haddock	NAFO 5Z
HADICE	Gadiformes	Gadidae	*Melanogrammus aeglefinus*	Haddock	Iceland
HADNEAR	Gadiformes	Gadidae	*Melanogrammus aeglefinus*	Haddock	North East Arctic

Table A.1 – continued on next page

Table A.1 – continued from previous page

ID	Order	Family	Latin name	Common name	Area
HADNS2	Gadiformes	Gadidae	*Melanogrammus aeglefinus*	Haddock	North Sea
HADVIa	Gadiformes	Gadidae	*Melanogrammus aeglefinus*	Haddock	ICES VIa
HERR4-5	Clupeiformes	Clupeidae	*Clupea harengus*	Herring	NAFO 4-5
HERRCC	Clupeiformes	Clupeidae	*Clupea harengus*	Herring	Central Coast B.C
HERRDOWN	Clupeiformes	Clupeidae	*Clupea harengus*	Herring	Downs stock
HERRGB2	Clupeiformes	Clupeidae	*Clupea harengus*	Herring	Georges Bank
HERRGM	Clupeiformes	Clupeidae	*Clupea harengus*	Herring	Gulf of Maine
HERRIspr	Clupeiformes	Clupeidae	*Clupea harengus*	Herring	Iceland (Spring spawners)
HERRIsum	Clupeiformes	Clupeidae	*Clupea harengus*	Herring	Iceland (Summer spawners)
HERRNOR	Clupeiformes	Clupeidae	*Clupea harengus*	Herring	Norway (Spring spawners)
HERRNS	Clupeiformes	Clupeidae	*Clupea harengus*	Herring	North Sea
HERRNSG	Clupeiformes	Clupeidae	*Clupea harengus*	Herring	North Strait of Georgia
HERRNWCVI	Clupeiformes	Clupeidae	*Clupea harengus*	Herring	North West Coast Vancouver Island
HERRPRD	Clupeiformes	Clupeidae	*Clupea harengus*	Herring	Prince Rupert District
HERRQCI	Clupeiformes	Clupeidae	*Clupea harengus*	Herring	Queen Charlotte Islands
HERRSSG	Clupeiformes	Clupeidae	*Clupea harengus*	Herring	Southern Strait of Georgia
HERRSWCVI	Clupeiformes	Clupeidae	*Clupea harengus*	Herring	South West Coast Vancouver Island
LTROOPEO	Salmoniformes	Salmonidae	*Salvelinus namaycush*	Lake trout	Lake Opeongo, Ontario
MACK2-6	Perciformes	Scombridae	*Scomber scombrus*	Mackerel	NAFO 2 to 6
MACKHBLACK	Perciformes	Carangidae	*Trachurus mediterraneus*	Mediterranean horse mackerel	Black Sea
MACKHWS	Perciformes	Carangidae	*Trachurus trachurus*	Horse mackerel	Western ICES
MENATLAN	Clupeiformes	Clupeidae	*Brevoortia tyrannus*	Atlantic Menhaden	U S Atlantic
MENGULF	Clupeiformes	Clupeidae	*Brevoortia patronus*	Gulf Menhaden	Gulf of Mexico
PERCHALI	Scorpaeniformes	Scorpaenidae	*Sebastes alutus*	Pacific ocean perch	Aleutian Is
PERCHEBS	Scorpaeniformes	Scorpaenidae	*Sebastes alutus*	Pacific ocean perch	Eastern Berring Sea

Table A.1 – continued on next page

Table A.1 – continued from previous page

ID	Order	Family	Latin name	Common name	Area
PERCHGA	Scorpaeniformes	Scorpaenidae	*Sebastes alutus*	Pacific ocean perch	Gulf of Alaska
PIKEWINN	Salmoniformes	Esocidae	*Esox lucius*	Pike	North Basin, Windermere Lake
PIKEWINS	Salmoniformes	Esocidae	*Esox lucius*	Pike	South Basin, Windermere Lake
PINKAKPW	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Prince William Sound, Alaska
PINKBAK3	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Bakhura River, Sakhalin Is
PINKBROP	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Brown’s Peak Creek, Cook Inlet, Alaska
PINKBRU	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Bruin Bay, Cook Inlet, Alaska
PINKCAK	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Central Alaska
PINKFR	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Fraser River, B.C
PINKHUMP	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Humpy Creek, Cook Inlet, Alaska
PINKKA	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Kodiak Area, Alaska
PINKKOD1	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Kodiak Archipelago, Alaska
PINKLUT3	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Lutoga River, Sakhalin Is
PINKNSA	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Northern Panhandle, Alaska
PINKPCHA	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Port Chatham, Cook Inlet, Alaska
PINKPDIC	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Port Dick, Cook Inlet, Alaska
PINKPGRA	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Port Graham, Cook Inlet, Alaska
PINKPOK3	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Pokosnaya River, Sakhalin Is
PINKPORO	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Poronal River, Sakhalin Is
PINKROCK	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Rocky River, Cook Inlet, Alaska
PINKSEL	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Seldovia, Cook Inlet, Alaska
PINKSSA	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Southern Panhandle, Alaska
PINKSUND	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Sunday Creek, Cook Inlet, Alaska
PINKWINL	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Windy Left, Cook Inlet, Alaska

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ID	Order	Family	Latin name	Common name	Area
PINKWINR	Salmoniformes	Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Windy Right, Cook Inlet, Alaska
PLAICKAT	Pleuronectiformes	Pleuronectidae	*Pleuronectes platessa*	Plaice	Kattegat
POLLNEAR	Gadiformes	Gadidae	*Pollachius virens*	Pollock or saithe	North East Arctic
POLLNS	Gadiformes	Gadidae	*Pollachius virens*	Pollock or saithe	North Sea
POLLVI	Gadiformes	Gadidae	*Pollachius virens*	Pollock or saithe	ICES VI
REDI_II	Scorpaeniformes	Scorpaenidae	*Sebastes mentella*	Redfish	North East Arctic
SAPILCH	Clupeiformes	Clupeidae	*Sardinops sagax*	Sardine	South Africa
SARDCAL	Clupeiformes	Clupeidae	*Sardinops sagax*	Sardine	California
SBTUNA2	Perciformes	Scombridae	*Thunnus maccoyii*	Southern bluefin tuna	Southern Pacific
SHAKE5Ze	Gadiformes	Gadidae	*Merluccius bilinearis*	Silver hake	NAFO 5Ze
SHAKEMAB	Gadiformes	Gadidae	*Merluccius bilinearis*	Silver hake	Mid Atlantic Bight
SOCKADAM	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Adams Complex, B.C
SOCKBIRK	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Birkenhead River, B.C
SOCKBLA	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Black Lake, Alaska
SOCKBRA	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Branch River, Alaska
SOCKBRIS	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Bristol Bay, Alaska
SOCKCHI	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Chignik Lake, Alaska
SOCKCHIK	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Chilko River, B.C
SOCKCOL	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Columbia River
SOCKEG3	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Egegik River, Alaska
SOCKFRAZ	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Frazer Lake, Alaska
SOCKHFLY	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Horsefly River, B.C
SOCKIGU2	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Igushik River, Alaska
SOCKKAR	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Karluk River, Alaska
SOCKKAS	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Kasilof River, Alaska
SOCKKEN	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Kenai River, Alaska
SOCKKVIC	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Kvichak River, Alaska
SOCKLSTU	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Late Stuart Complex, B.C
SOCKNAK3	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Naknek, Alaska

Table A.1 – continued on next page

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ID	Order	Family	Latin name	Common name	Area
SOCKNUSH	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Nushagak River, Alaska
SOCKNUY	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Nuyakuk River, Alaska
SOCKREDR	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Red River, Alaska
SOCKRINL	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Rivers Inlet, B.C
SOCKSK2	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Skeena River, B.C
SOCKSTEL	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Stellako River, B.C
SOCKSTUA	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Early Stuart Complex, B.C
SOCKTOG2	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Togiak River, Alaska
SOCKUG3	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Ugashik River, Alaska
SOCKUPST	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Ayakulik, Kodiak Island, Alaska
SOCKWEAV	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Weaver Creek, B.C
SOCKWOOD2	Salmoniformes	Salmonidae	*Oncorhynchus nerka*	Sockeye salmon	Wood River, Alaska
SOLEIIIa	Pleuronectiformes	Soleidae	*Solea vulgaris*	Sole	ICES IIIa
SOLENS	Pleuronectiformes	Soleidae	*Solea vulgaris*	Sole	North Sea
SOLEVIId	Pleuronectiformes	Soleidae	*Solea vulgaris*	Sole	ICES VIId
SPRAT22-32	Clupeiformes	Clupeidae	*Sprattus sprattus*	Sprat	Baltic Areas 22-32
SPRAT2628	Clupeiformes	Clupeidae	*Sprattus sprattus*	Sprat	Baltic Areas 26 and 28
SPRATBLACK	Clupeiformes	Clupeidae	*Sprattus sprattus*	Sprat	Black Sea
STRIPEDBASSUSA2	Perciformes	Moronidae	*Morone saxatilis*	Striped bass	East Coast, USA
WEAKFISH	Perciformes	Sciaenidae	*Cynoscion guatucupa*	Weakfish	East Coast, USA
WHITCS	Gadiformes	Gadidae	*Merlangius merlangus*	Whiting	Celtic Sea
WHITIS2	Gadiformes	Gadidae	*Merlangius merlangus*	Whiting	Irish Sea
WHITVIa2	Gadiformes	Gadidae	*Merlangius merlangus*	Whiting	ICES VIa
WPOLLEBS	Gadiformes	Gadidae	*Theragra chalcogramma*	Walleye pollock	E Bering Sea
YELL5Z	Pleuronectiformes	Pleuronectidae	*Pleuronectes ferrugineus*	Yellowtail flounder	NAFO 5Z
YELLSNE	Pleuronectiformes	Pleuronectidae	*Pleuronectes ferrugineus*	Yellowtail flounder	Southern New England

Appendix B

APPENDIX FOR CHAPTER 4: TIME-VARYING RECRUITMENT DYNAMICS OF ATLANTIC COD (*GADUS MORHUA*)

B.1 Filtering, Smoothing and Estimation

Note that the following description largely follows that presented in Petris *et al.* (2009). It is given here for completeness.

Where all the parameters of the state space model are known a priori, the main task is usually to draw inference on the unobserved states. Where some or all of the parameters of the state space model are unknown, they must also be estimated. Both the estimation of unknown parameters and states involves filtering recursions. In a general state space model, the unobserved states are represented by the conditional density of the states given the data $f(\theta_s|y_{1:t})$, where $s = t$ or $s < t$ we refer to filtered or smoothed densities, respectively. The difference is that filtered states use all information up to the present to estimate the current state, whereas smoothing uses all past and future information to estimate the state. In filtering, the task is to update the filtered density between successive timesteps, i.e. to obtain $f(\theta_{t+1}|y_{1:t+1})$ from $f(\theta_t|y_{1:t})$ (Durbin and Koopman, 2001; Petris *et al.*, 2009).

B.1.1 Filtering

Assuming we are at time $t - 1$, filtering proceeds by predicting the density of the state in the next time period $f(\theta_t|y_{1:t-1})$ (termed the one-step-ahead predictive density) given the filtered density of the state currently $f(\theta_{t-1}|y_{1:t-1})$ and the transition relation. The one step ahead prediction density is then updated with the observation density $f(y_t|\theta_t)$ via Bayes rule. This produces the filtered state in the next time period $f(\theta_t|y_{1:t})$, which is then recursively updated once more. The integrals involved in these densities and updating relations are generally not analytically tractable, except where the densities are Gaussian and the transition and measurement equations are linear. This special case is solved by the Kalman filter (Kalman, 1960) (independently discovered earlier by Swerling (1958); see Simon (2006) Appendix A for a discussion on the naming of this important algorithm). Where the functional forms of the process and measurement equations are linear and both sets of errors assumed Gaussian, the Kalman filter is found to be an optimal filter (Harvey, 1991, §3.2).

The Kalman filter relies on a result of the multivariate Gaussian distribution, which states that where a set of variables is multivariate Gaussian, linear transformation of those variables are also multivariate Gaussian (Grewal and Andrews, 2008). As such, the joint and marginal distributions of the filtering recursions are Gaussian and the complete distribution is characterized by the mean and the variance. The task is then to obtain the expected means and variances of the filtered, predicted state and predicted observation densities. These are provided below without derivation.
Given that the current filtered has a Gaussian distribution

$$f(\theta_{t-1}|y_{1:t-1}) \sim \mathcal{N}(m_{t-1}, C_{t-1}) \tag{B.1}$$

where m_{t-1} and C_{t-1} are the mean and variance of the filtered density at time $t-1$. The expected mean (denoted a_t) and the variance (denoted P_t) of the one step ahead predicted state density are given by

$$a_t = \mathrm{E}\left(\theta_t|y_{1:t-1}\right) = G_t m_{t-1}, \tag{B.2}$$

$$P_t = \mathrm{Var}\left(\theta_t|y_{1:t-1}\right) = G_t C_{t-1} G_t'. \tag{B.3}$$

The expected mean (denoted a_t) and the variance (denoted Q_t) of the predicted observation density are given by

$$u_t = \mathrm{E}\left(y_t|y_{1:t-1}\right) = F_t a_t, \tag{B.4}$$

$$Q_t = \mathrm{Var}\left(y_t|y_{1:t-1}\right) = F_t P_t F_t' + V_t. \tag{B.5}$$

Finally, defining the predicted error as $\varepsilon_t = y_t - u_t$ and the Kalman gain as $K_t = P_t F_t' Q_t^{-1}$ (this is a measure of the ratio of the variance of the predicted state to the variance of the predicted observations) the expected value and variance of the filtered density at the next time step are given by

$$m_t = \mathrm{E}\,(\theta_t|y_{1:t}) = a_t + K_t\varepsilon_t, \tag{B.6}$$

$$C_t = \mathrm{Var}\,(\theta_t|y_{1:t}) = P_t - K_tF_tP_t. \tag{B.7}$$

It remains to initialize the filter. The approach adopted here is to give the initial density a diffuse prior

$$f(\theta_0) \sim \mathcal{N}(m_0, C_0) \tag{B.8}$$

where m_0 is often chosen at 0 and C_0 very large, e.g. 1e+7 (Harvey, 1991; Petris *et al.*, 2009).

B.1.2 Smoothing

Starting with the filtered density at the end time point T

$$f(\theta_T|y_{1:T}) \sim \mathcal{N}(m_T, C_T), \tag{B.9}$$

smoothing proceeds by hindcasting the smoothed density given the filtered density the preceding time. The filtering recursions for the mean (denoted s_t) and variance (denoted S_t) of are given written in terms of expectation as

$$s_t = \mathrm{E}\,(\mathrm{E}\,(\theta_t|\theta_{t+1}, y_{1:t})|y_{1:T}), \tag{B.10}$$

$$S_t = \mathrm{Var}\,(\mathrm{E}\,(\theta_t|\theta_{t+1}, y_{1:t})|y_{1:T}) + \mathrm{E}\,(\mathrm{Var}\,(\theta_t|\theta_{t+1}, y_{1:t})|y_{1:T})). \tag{B.11}$$

Which, in terms of the model matrices, is given by

$$s_t = m_t + C_tG'_{t+1}R^{-1}_{t+1}(s_{t+1} - a_{t+1}), \tag{B.12}$$

$$S_t = C_t - C_tG'_{t+1}R^{-1}_{t+1}(R_{t+1} - S_{t+1})R^{-1}_{t+1}G_{t+1}C_t. \tag{B.13}$$

B.1.3 Estimation

The preceeding sections on Kalman filtering and smoothing were based on the assumption that the parameters of the system matrices are known. Where the parameter vector Θ is unknown, they must be estimated from the data. Schweppe (1965) was first to show how the parameters of the system matrices could be estimated using the predicted errors ε_t and their variance Q_t. The log-likelihood is given by

$$\ln L(\Theta) = -\frac{T}{2}\ln(2\pi) - \frac{1}{2}\sum_{t=1}^{T}\ln|Q_t| - \frac{1}{2}\varepsilon_t Q_t^{-1}\varepsilon_t' \tag{B.14}$$

which is maximized (or more typically its negative minimized) with respect to Θ using an optimizer. Note that Θ contains the variances of the intercept and slope processes so the likelihood given by Equation (B.14) is general to time-varying or time-invariant estimation in the Kalman filter. For the simulation routine, a Nelder-Mead optimization algorithm was implemented in the *optim* function in R (R Development Core Team, 2009), which facilitated the large number of runs. Simulated annealing was used for the real data analysis. This global optimization algorithm may potentially avoid local structures in the likelihood surface, observed by Zeng *et al.* (1998). Similar results were, however, obtained using Nelder-Mead and quasi-Newton algorithms. Estimation was also attempted using the AD-Model Builder, which can work with non-linear and non-Gaussian models via a Laplace approximation to the marginal likelihood (Skaug and Fournier, 2006; Pedersen *et al.*, 2011). Preliminary results were comparable in the univariate case but the multivariate case did not converge after a number of trials lasting up to three hours on a 32GB Dell PowerEdge processor. The same model estimated via a Kalman filter converged within 5 minutes on the same machine. While the Laplace approximation and importance sampling extensions are more general, where the model is linear, the Kalman filter is optimal (Harvey, 1991) and in this case, practically necessary for tackling the problem.

B.1.4 Covariance Matrices

The Cholesky decomposition was used to maintain positive-definiteness of the covariance matrices in optimization. The Cholesky decomposition of the covariance matrix of the process is given by

$$W_t = L_t L_t' \tag{B.15}$$

where L_t is a lower triangular matrix. Other decomposition parameterizations may have more direct interpretations (Pinheiro and Bates, 1996) but the Cholesky decomposition is relatively stable and straightforward to implement.

B.2 Simulation

B.2.1 Setup

A simulation routine was conducted to investigate the recovery of known parameters using the Kalman filter. A time-varying slope at the origin has previously been shown to be recovered well by the Kalman filter (Peterman *et al.*, 2003). Zeng *et al.* (1998) showed the recovery of the density-dependent term, however, neither study investigated the recovery of both terms simultaneously and it is unclear whether a time-varying intercept and slope are so strongly correlated as to be confounded. The goal of this simulation was to investigate this.

There are many possible combinations of simulations, we chose to fix the length of the spawner recruit series to 50 observations. For each run, spawner values were chosen at random over a Uniform(0,30) distribution, the starting values: $a_0 = \ln(\alpha_0) = \ln(3)$ and $\beta_0 = 0.1$. One hundred runs were then simulated with random walks on a_t and β_t for each combination of coefficients of variation of $\{0, 0.1, 0.3, 0.6\}$ on σ_a and σ_β and correlations of $\{-1, 0.5, 0, 0.5, 1\}$ between σ_a^2 and σ_β^2. Measurement error was fixed at $\sigma_{\ln(R)} = 0.3$. This resulted in 8000 simulated stock-recruitment series, covering plausible levels of variation and covariation in the time-varying slope at the origin and density-dependent terms.

B.2.2 Parameter Recovery

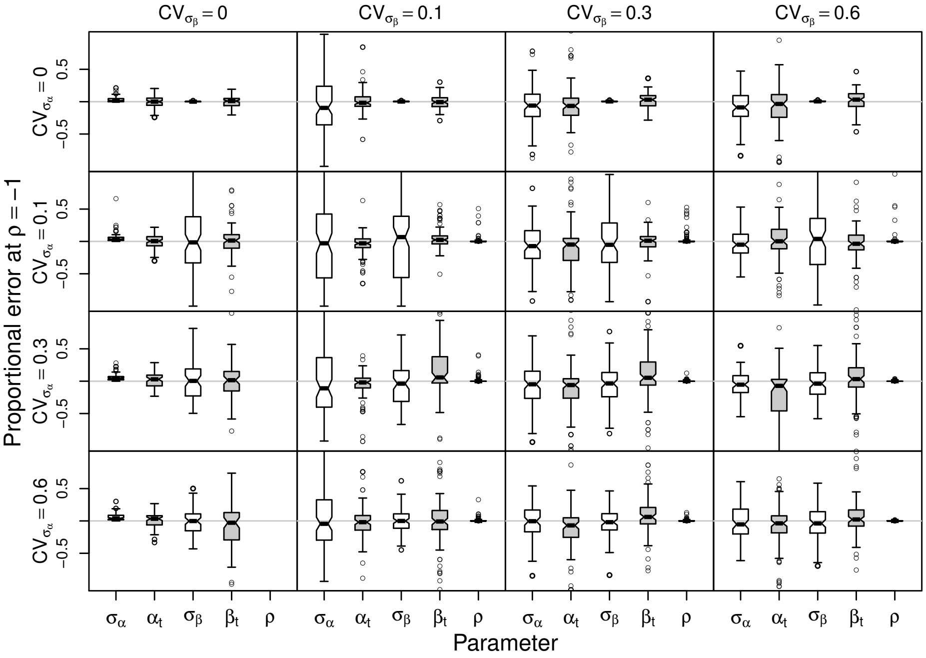
A local-level model with time-varying slope at the origin and density-dependent terms was used to recover parameters. The proportional error was used to investigate estimated parameter bias (Kehler *et al.*, 2002; Cope and Punt, 2007, termed *relative bias* in Kehler *et al.* (2002)). The proportional error is defined as

$$\mathrm{PE}(\hat{\theta}) = \frac{\hat{\theta} - \theta_{\text{true}}}{|\theta_{\text{true}}|} \tag{B.16}$$

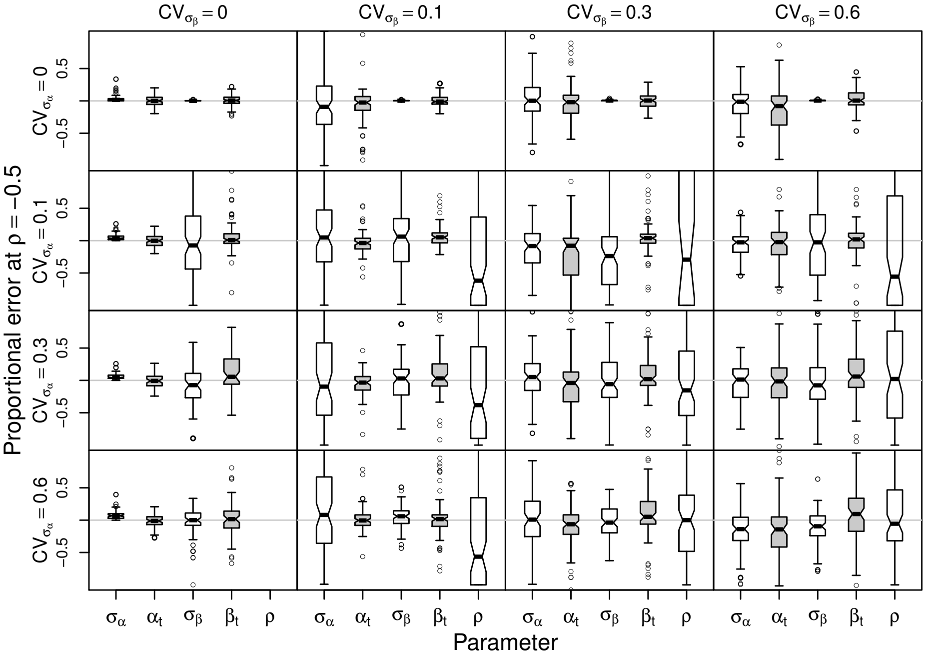
where θ_{true} and $\hat{\theta}$ are the true and estimated parameter values, respectively. When $\theta_{\text{true}} = 0$, as in the zero process variance (i.e. constant parameter) runs, the right-hand side of Equation (B.16) is not defined; in this case the error alone (numerator of Equation B.16) was used to measure bias. Note that in the case of either $\sigma_{a,\text{true}}$ or $\sigma_{\beta,\text{true}}$ equal to zero, the correlation between them is undefined and therefore the proportional error is also undefined. To investigate the recovery of the simulated states (actual series as opposed to parameters that govern the series), the average proportional error over the series was used.

B.2.3 Results

Plots of the proportional error of the recovered parameters over the various combinations of variance and correlation are provided in Figures B.1–B.3. Overall, estimates of σ_a and σ_β and accompanying series were typically well-recovered. Although where the $\sigma_\beta = 0$, the estimate for σ_a is marginally biased upward (Left-most column of Figures B.1–B.3). Simulated parameters were typically well-recovered at strong negative or positive or absent correlation between the processes. However, medium-strength correlations between the parameters resulted in highly uncertain estimates of the correlation between the processes (Figures B.1(a) and B.2(b)).

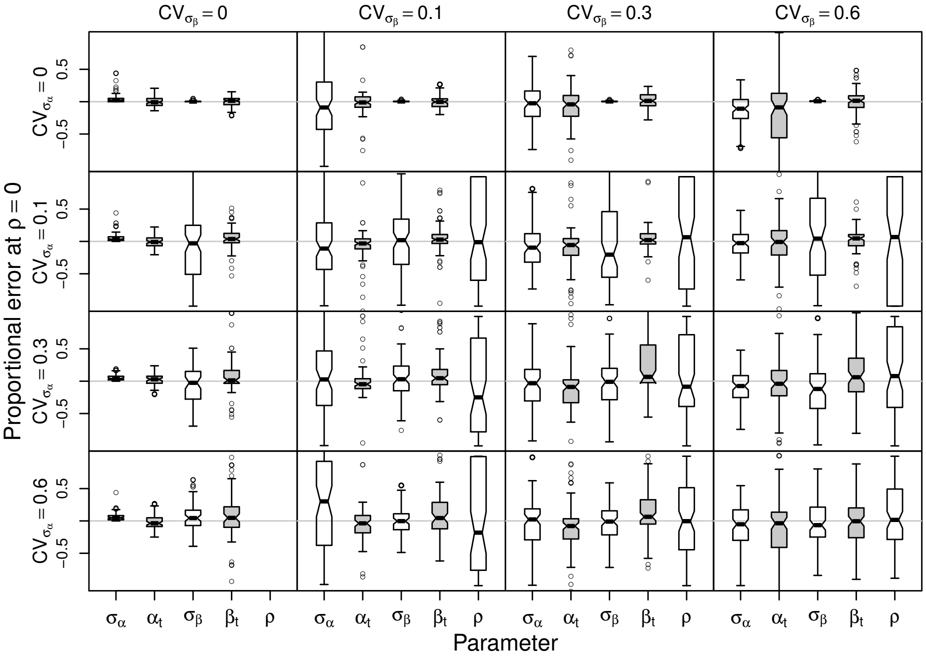


(a) Proportional error at perfect negative correlation ($\rho = -1$)

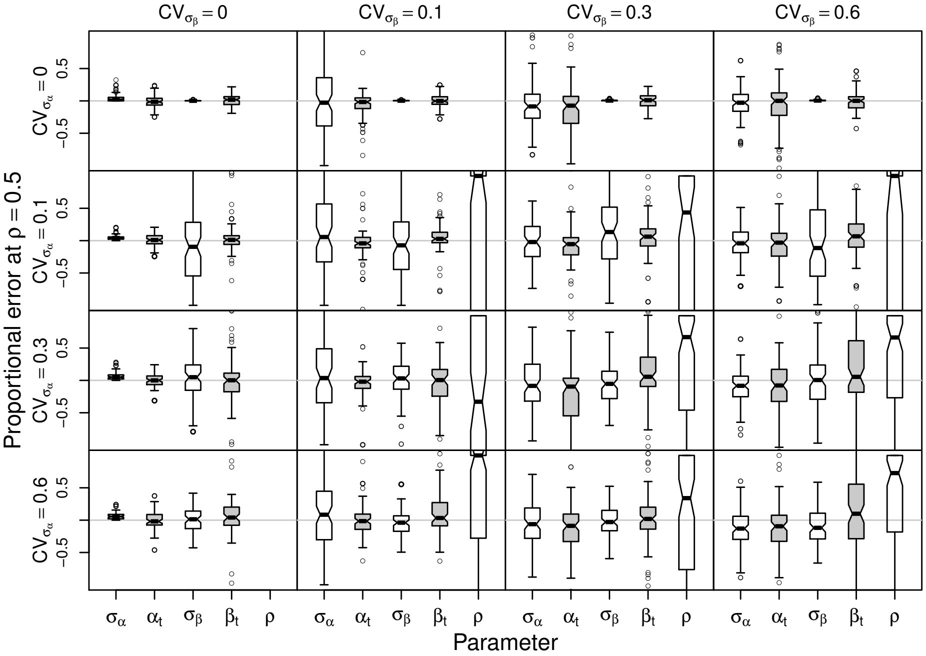


(b) Proportional error at medium negative correlation ($\rho = -0.5$)

Figure B.1: Results of parameter recovery at various levels of variation and negative correlation in the simulated time-varying parameters. Boxes for σ_a, σ_β and ρ show the distribution of the proportional error over 100 simulations in that combination. Boxes for α_t and β_t show the distribution of the average proportional error over the simulated and estimated states. No proportional error is reported when the true variance term is zero, as it is undefined. In these cases, boxes of α_t and β_t show parameter recovery for constant parameters.



(a) Proportional error at zero correlation ($\rho = 0$)



(b) Proportional error at medium positive correlation ($\rho = 0.5$)

Figure B.2: Results of parameter recovery at various levels of variation and no or medium-strength positive correlation in the simulated time-varying parameters. Details as per Figure B.1.

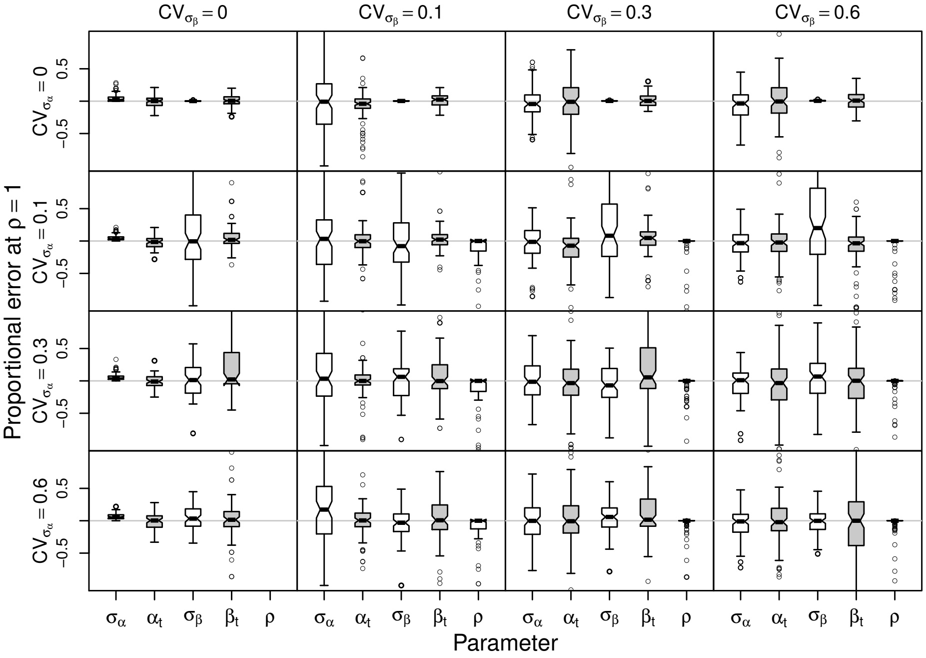


Figure B.3: Results of parameter recovery at various levels of variation and strong positive correlation in the simulated time-varying parameters. Details as per Figure B.1.

Appendix C

APPENDIX FOR CHAPTER 5: INTERACTIONS BETWEEN SMALL PELAGIC FISH AND JUVENILE COD ACROSS THE NORTH ATLANTIC

C.1 Spawning and Feeding Region Overlap Review

In the northwest Atlantic, spawning of Georges Bank cod occurs over a protracted period of time between November and May, with peak spawning activity during February and March (ICES, 2005, and references therin). Spawning occurs on the eastern (particularly the Northeast Peak) and western parts of the bank; spawning is also noted from the Nantucket Shoals (ICES, 2005). Spring bottom trawl surveys show the presence of non-spawning (outside mid-September to mid-October) Gulf of Maine-Georges Bank (GMGB) herring in overlapping areas from 1968-1998 (Overholtz and Friedland, 2002). Using specifically designed research surveys, Garrison *et al.* (2002) established that a significant overlap occurs between pelagic fish such as Atlantic herring and mackerel and larval fish, including cod, on the southern flank of Georges Bank. Gulf of Maine cod spawn during the winter and early spring with a north-south gradient in timing - later spawning occurring in the north (ICES, 2005). Spawning predominantly occurs on the western side, particularly in Massachusetts Bay and north of Cape Ann; although spawning also occurs off the coast of Maine (ICES, 2005). GMGB herring are found in overlapping areas (Overholtz and Friedland, 2002) during the same time of year as cod are spawning. Unusually, Western and Eastern Scotian Shelf cod have traditionally had spring (February-March) and fall (October-November) spawning components (ICES, 2005). Spawning locations are broadly distributed over the region with high activity occurring on Brown's Bank and the mouth of the Bay of Fundy in Spring and inshore along the Nova Scotian coastline from Yarmouth to Halifax Harbour (ICES, 2005).

The northwest Atlantic mackerel stock over-winters off Cape Hatteras and then splits into a Northern and Southern component in the Spring. Mackerel show a strong temporal variability in distribution but are broadly distributed within the northwest Atlantic. The potential for spatial overlap of cod spawning and herring and mackerel feeding areas have previously been established in the Northern and Southern Gulf of St. Lawrence (Swain and Sinclair, 2000; Duplisea and Robert, 2008, and references therein).

In the northeast Atlantic, northeast Arctic and Norwegian coastal cod spawn from mid-February to early May with peak spawning at the end of March and start of April (ICES, 2005). Spawning locations for both stocks are mostly near-shore and widely distributed from mid- to northern-Norway. Prominent spawning locations occur near Lofoten and off-shore from Vesterålen (ICES, 2005). Norwegian spring spawning (NSS) migration patterns have changed in the past 60 years (Dragesund *et al.*, 1997; Kvamme *et al.*, 2003). Currently, adult herring over-winter (October-January) close to Lofoten before spreading out to spawn along the Norwegian coast in February and March (Devold, 1963). Juvenile fish spend the early part of their life in the Barents Sea (Dragesund *et al.*, 1997) and feeding along the Norwegian coast. Post-spawning adult herring undertake extensive feeding migrations far out into the Norwegian Sea (Dragesund *et al.*, 1997; Kvamme *et al.*, 2003). The overlap between young cod and feeding herring might therefore be restricted to the early part of the herring life history in the Barents Sea.

Icelandic cod spawn off the south and southwest coast from mid-March to early May (Marteinsdóttir *et al.*, 2000). Eggs and larvae drift around the coast in a clockwise direction to where they settle off the north coast (Marteinsdóttir *et al.*, 2000). Icelandic summer spawning herring migrate in late February from the over-wintering grounds off Snæfellsnes and the south coast to feed off the west and east coasts (Óskarsson *et al.*, 2009). The potential for overlap with cod eggs and larvae exists.

Capelin have a circumpolar boreal water distribution (Rose, 2005). In the North Atlantic, major concentrations occur around Newfoundland and Labrador, north of Iceland and the Barents Sea (Rose, 2005). The distribution of feeding in Iceland and the Barents Sea potentially overlap with the presence of early stage cod.

Peak spawning activity occurs in March for West of Scotland cod (ICES, 2005). Based on egg survey, trawl, and tagging data, Wright *et al.* (2006) showed that, during the 1950s, cod eggs were distributed widely in area VIa with particularly high densities in the Minch and north of the Isle of Lewis. These observations were corroborated with recent trawl surveys of ripe fish, which also indicated the importance of the Clyde region Wright *et al.* (2006). West of Scotland herring aggregations are distributed widely. There is evidence that juvenile herring from this stock migrate into the North Sea (ICES, 2009c) but relatively little is known about general migration patterns in this stock. Irish sea cod predominantly spawn in the western Irish Sea between Dublin and Carlingford Lough (ICES, 2008a), although spawning also occurs in the north and east of the Isle of Man (Brander, 1994; Wright *et al.*, 2006; Fox *et al.*, 2000). Spawning occurs between January and May with the peak spawning activity in March (Brander, 1994). Herring in the Northern part of the Irish Sea are typically distributed around the Isle of Man (ICES, 2009c). A Mourne fishery in closer proximity to the Irish coast (where cod spawn) does exist but the overlap with cod is potentially minimal. Celtic Sea cod spawn in February-March close inshore off the Southwest of Ireland (ICES, 2008b). Spawning also occurs in the Bristol channel in mid- to late-March (Brander, 1994). Celtic Sea herring spawn inshore off the south and southwest coast of Ireland in the Autumn and Winter and migrate offshore to summer feeding regions (ICES, 2009c). It is possible that the overlap in this region is also minimal.

Fox *et al.* (2008) consolidated historical and contemporary records of cod spawning locations in the North Sea. Spawning predominantly occurs on the southern and eastern Dogger Bank, the German Bight and to the north in the Moray Firth and east of the Shetland Islands. The timing of spawning is earlier in the southern regions (late January) compared to northern regions (March) (Brander, 1994). Based upon the dominant spawning locations, North Sea herring comprise four major sub-components: Shetland, Buchan, Banks and Downs (Bierman *et al.*, 2010). The sub-components mix to feed between April and June in the northern part of the North Sea (Cushing and Bridger, 1966). Given that the spawning of cod is predominantly in the south of the North Sea (Fox *et al.*, 2008) the overlap with feeding herring is potentially small. Although Daan *et al.* (1985) showed that herring do eat cod and plaice eggs in the early part of the season in the North Sea.

Northeast Atlantic mackerel comprise three components: North Sea, Western, and Southern. Western mackerel spawn from March-July along western Europe, particularly on the Porcupine and Great Sole Banks (Lockwood, 1988; Uriarte and Lucio, 2001). Following spawning, the stock moves up along the Irish coast and west of Scotland to feed in the Norwegian Sea and northern North Sea (Uriarte and Lucio, 2001). It is difficult to establish whether significant overlap will occur with eggs and larval cod. Although the western component has been used for all regions here because the North Sea component has never recovered from severe depletion. The western component does dip into the northern part of the north sea.

Kattegat cod spawn between January and March, predominantly in the southeast in the vicinity of Skälderviken, Laholmsbukten, and Falkenburg (Vitale *et al.*, 2008). Herring in this region are grouped under the Western Baltic Spring Spawning herring that migrate out of the Baltic to the Kattegat, Skagerrak and the North Sea to feed. There is a potential for overlap during this time. The Western Baltic cod stock spawn from the January to May with peak spawning in February-April (Bagge *et al.*, 1994). Spawning occurs predominantly in the south of subdivision 22 (ICES, 2005). The overlap between WBSS herring and cod eggs has been studied intensely (Köster and Möllmann, 2000) with the conclusion that there is a potential for overlap but this is strongly time-varying. Eastern (also known as central) Baltic cod spawn at a different time to the western Baltic stock, now preferring summer to spring (Wieland *et al.*, 2000). The spawning locations are in deep waters to the south (Bornholm Basin and Slupsk Furrow) with sufficient salinity for fertilization and buoyancy (ICES, 2009b). The overlap with herring in this region has been investigated by (Köster and Möllmann, 2000).

Baltic sprat is a very large stock with a wide distribution in both coastal and offshore areas of ICES subdivisions 22-32 (ICES, 2009b). The overlap between cod eggs and sprat populations has previously been established by (Köster and Möllmann, 2000).

C.2 Post-estimation Interaction Coefficient Relationships

The relationships between the interaction coefficients and temperature, latitude and longitude are shown in Figures (SC.1-SC.2). Linear regressions were fit separately to each relationship.

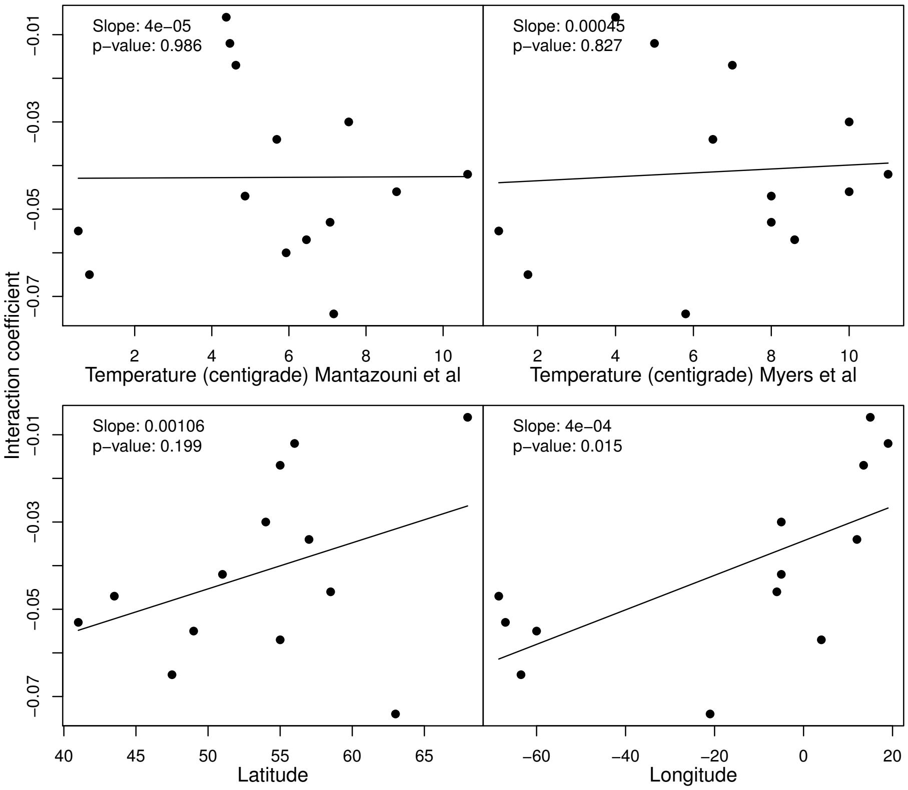


Figure C.1: Relationships between the estimated interaction coefficients for Atlantic herring and mean spring surface temperature (Mantzouni *et al.*, 2010) and mean annual shelf temperature (Myers *et al.*, 2001), latitude and longitude. The slope and associated p-value from a linear regression are presented in the legend for each.

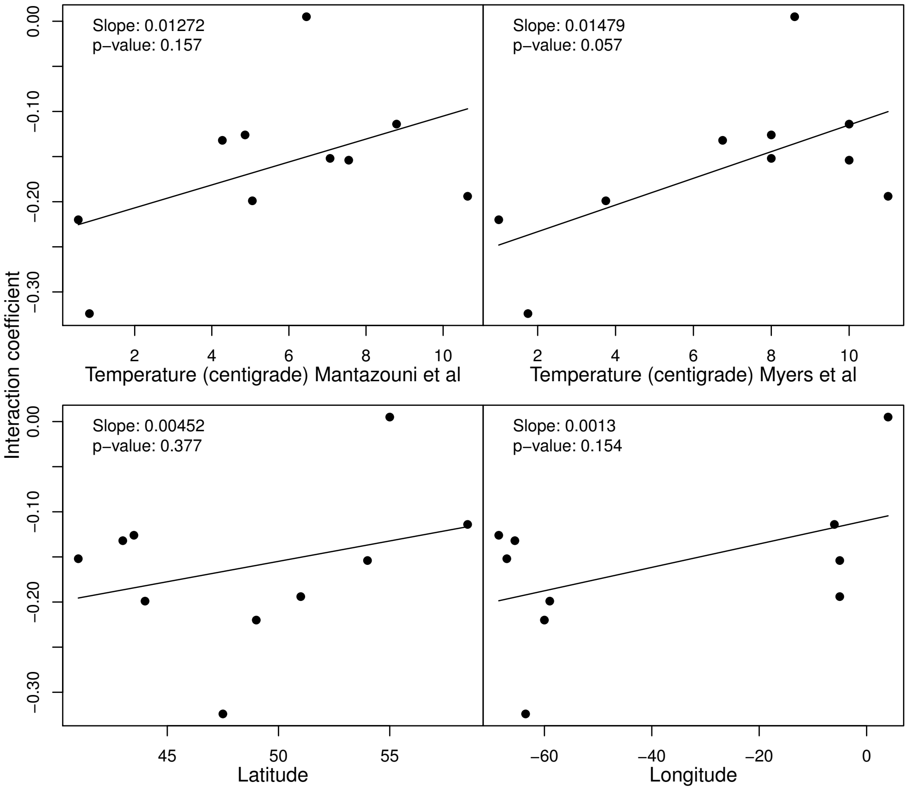


Figure C.2: Relationships between the estimated interaction coefficients for Atlantic mackerel and mean spring surface temperature and mean annual shelf temperature, latitude and longitude. The slope and associated p-value from a linear regression are presented in the legend for each.

C.3 Measurement Error

We assume that the measurement errors are lognormally distributed, such that an observation s of the true spawner abundance S is distributed as $\ln(s) \sim \mathrm{N}(\ln(S), \sigma^2_{\text{obs}})$. The coefficient of variation of the lognormal is given by $CV(s) = \sqrt{e^{\sigma_{\text{obs}}} - 1}$, such that $\sigma^2_{obs} = \log(CV(s) + 1)$. A Bayesian implementation allows for previously deterministic measurements to be assigned stochastic distributions. The parameters of these are non-identifiable, as formulated, but we can assess the sensitivity to a range of assumed values. We investigated the sensitivity of the posterior parameter distributions for the unpooled and hierarchical models (with independent errors) to four levels of measurement error variation: $CV(s) \in \{0, 0.1, 0.3, 0.6\}$, corresponding to absent, low, medium and high levels (Kehler *et al.*, 2002) on all variables. We only investigated the effect of measurement error using herring as the interacting species and model *h4*.

The effect of four levels of assumed measurement error on the posterior distributions of the overall means and region-level variances is shown in Figure (C.3). The hierarchical means are relatively insensitive to the inclusion of low to medium levels of measurement error (CV: 0-0.3). At high levels (CV: 0.6), however, the overall mean of the interaction coefficient γ becomes less negative and the region-level variance becomes more peaked and less negative. The residual error variance decreases with increasing measurement error because the measurement error variance is added to the total residual variance, which is constant.

At the region level, the estimates from the unpooled analysis are more sensitive to measurement error compared to their hierarchical counterparts. The unpooled estimates for α typically increase, β becomes more negative and γ does not show a directional change (Figure C.4). Results from the hierarchical analysis show the α and β parameters to be less affected but that the interaction coefficients display a greater spread.

C.4 Data Sources

Details of the data coverage and sources are provided in Table C.1 and plotted in Figures C.5-C.12.

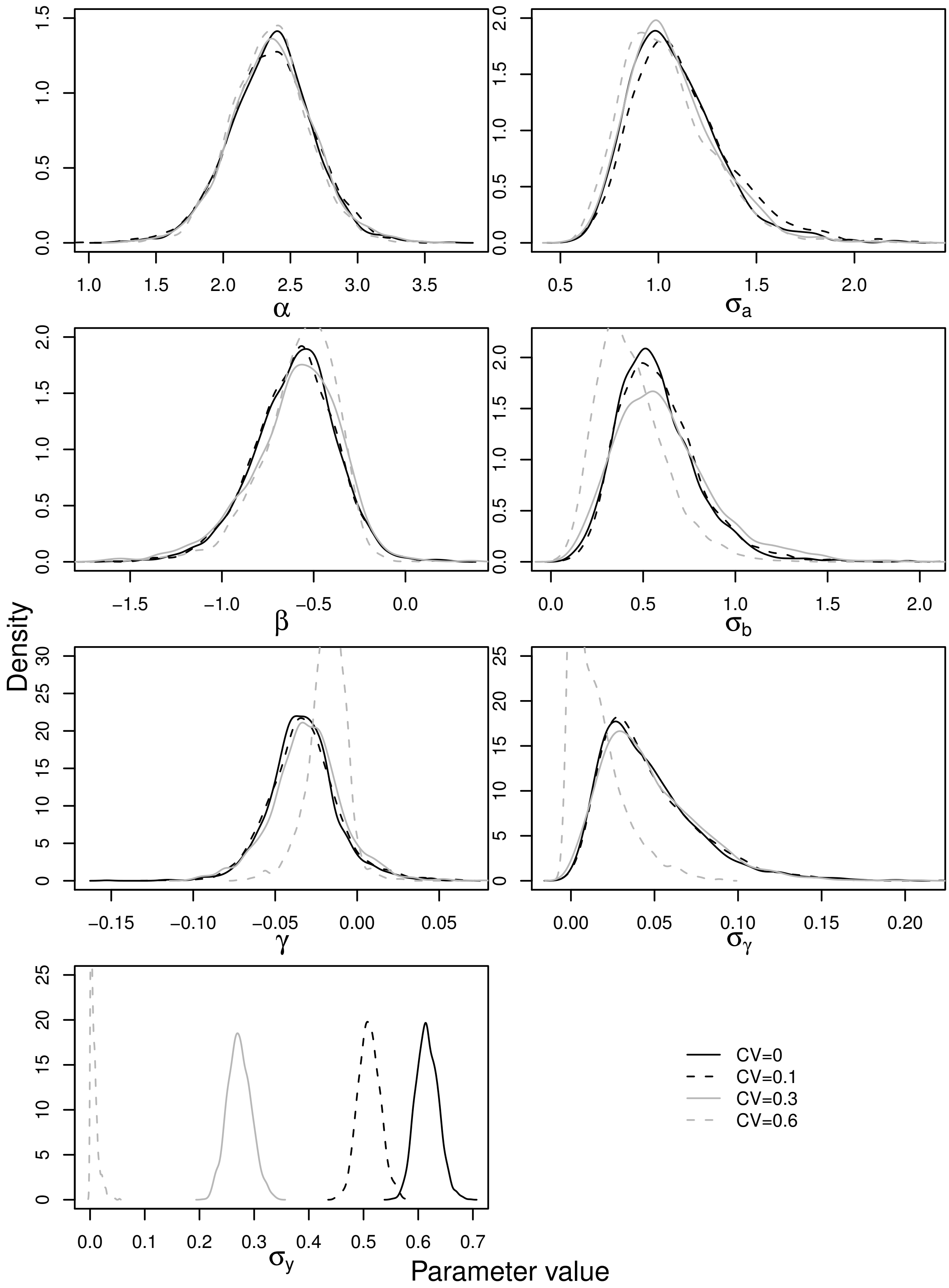


Figure C.3: Posterior overall mean parameter distributions and region-level variances under four levels of assumed measurement error all series.

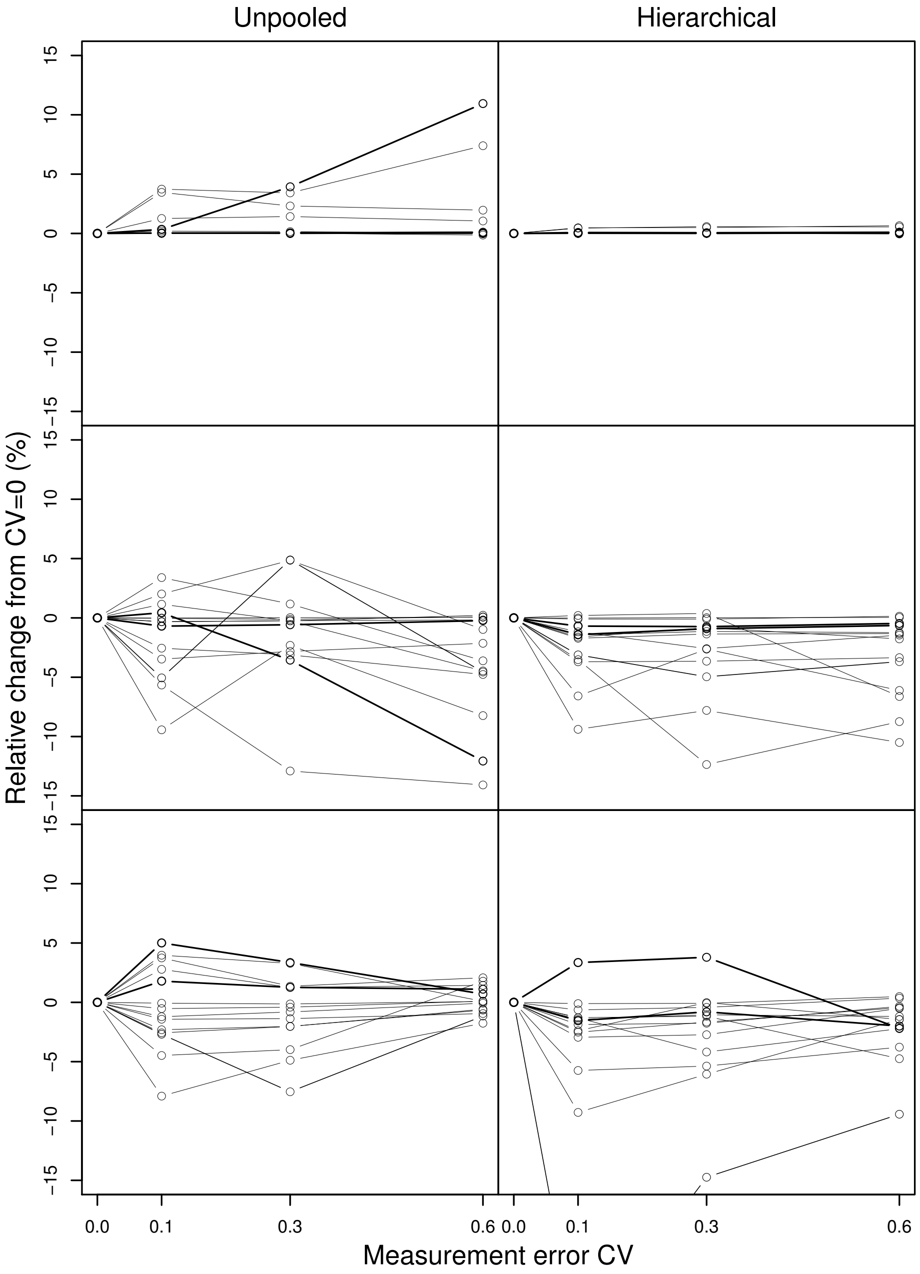


Figure C.4: Percentage change in the region-level parameter estimates under 4 levels of measurement error. The parameters $\{\alpha, \beta, \gamma\}$ are presented in the top, middle, and bottom rows respectively. The effect on the unpooled analysis is presented on the left while the effect on the hierarchical analysis is shown on the right. Each line representes a region.

Table C.1: Details of cod and pelagic assessments used. NAFO/ICES refers to the primary region of the stock. NWAMC and NEAMC refer to the large northwest and northeast Atlantic mackerel complexes, respectively.

Region	Species	NAFO/ICES	#	Years	Notes	Source
Georges Bank	Cod	5Z	1	1978-2007	VPA split model results	NEFSC (2008)
	Herring	5Z,5Y	1	1967-2008	TRAC preferred model results	Shepherd *et al.* (2009)
	Mackerel	NWAMC	1	1962-2004	SSB used.	NEFSC (2006)
Gulf of Maine	Cod	5Y	1	1982-2007	VPA results	NEFSC (2008)
	Herring	5Z,5Y	1	1967-2008	TRAC preferred model results	Shepherd *et al.* (2009)
	Mackerel	NWAMC	1	1962-2004	SSB used.	NEFSC (2006)
Southern Scotian Shelf and Bay of Fundy	Cod	4X	2	1948-1993		(Gavaris *et al.*, 1994)
				1980-2008		(Clark and Emberley, 2009)
	Mackerel	NWAMC	1	1962-2004	SSB used.	NEFSC (2006)
Eastern Scotian Shelf	Cod	4VsW	1	1958-2005	M changing in blocks 0.2 to 0.4 to 0.8 presently	Bob Mohn, DFO
	Mackerel	NWAMC	1	1962-2004	SSB used.	NEFSC (2006)
Southern Gulf of St. Lawrence	Cod	4TVn	1	1971-2009	SPA Model 1	Swain *et al.* (2008)
	Herring (Spring)	4T	1	1978-2008	ADAPT with gillnet CPUE and acoustic survey indices	LeBlanc *et al.* (2008)

Continued overleaf

Region	Species	NAFO/ICES	#	Years	Notes	Source
	Herring (Fall)	4T	1	1978-2008	ADAPT with gillnet CPUE2 tuning index	LeBlanc *et al.* (2008)
	Mackerel	NWAMC	1	1962-2004	SSB used.	NEFSC (2006)
Northern Gulf of St. Lawrence	Cod	3Pn4RS	1	1974-2008		Fréchet *et al.* (2009)
	Herring (Spring)	4R	1	1965-2002	West coast of Newfoundland stock	Grégoire *et al.* (2004)
	Herring (Fall)	4R	1	1973-2002	West coast of Newfoundland stock	Grégoire *et al.* (2004)
	Mackerel	NWAMC	1	1962-2004	SSB used.	NEFSC (2006)
Northeast Arctic	Cod	I, II	2	1900-1999	Data digitized from figures	Hylen (2002)
				1946-2008		ICES (2009a)
	Herring	I, II	3	1907-1998	Norwegian spring spawning	Toresen and Østvedt (2000)
				1950-2007		ICES (2007a)
				1988-2009		ICES (2009f)
	Capelin	I, II	1	1973-2009	SSB in April used. Eight missing years.	ICES (2009a)
Norwegian Coastal	Cod	I,II	1	1984-2008	Output from trial XSA	ICES (2009a)
	Herring	I, II	3	1907-1998	Norwegian spring spawning	Toresen and Østvedt (2000)
				1950-2007		ICES (2007a)
				1988-2009		ICES (2009f)
	Capelin	I, II	1	1973-2009	SSB in April used. Eight missing years.	ICES (2009a)
Iceland	Cod	Va	2	1928-1992	Data digitized from figures	Schopka (1994)

Continued overleaf

Region	Species	NAFO/ICES	#	Years	Notes	Source
				1955-2008		ICES (2009d)
	Herring	Va	2	1947-1995	Icelandic summer spawning herring. SSB used.	ICES (1995)
				1986-2008		ICES (2009d)
	Capelin		1	1979-2009	SSB used. 1978/1979 fishing season included as 1979 etc.	ICES (2009d)
West of Scotland	Cod	VIa	1	1978-2009		ICES (2008a)
	Herring	VIa (North)	1	1957-2008	North of 56°N component	ICES (2009c)
	Mackerel	NEAMC	1	1972-2008		ICES (2009f)
Irish Sea	Cod	VIIa	1	1968-2007		ICES (2008a)
	Herring	VIIa (North)	1	1961-2006	Covers northerly part of the Irish Sea only. Consider using Celtic Sea herring also.	ICES (2007b)
	Mackerel	NEAMC	1	1972-2008		ICES (2009f)
Celtic Sea	Cod	VIIe-k	1	1971-2007	No analytical assessment was conducted on the Celtic Sea cod stock in 2009 owing to concerns regarding catch values.	ICES (2008b)
	Herring	VIIg,h,j,k, VIIa(South)	1	1958-2008		ICES (2009c)
	Mackerel	NEAMC	1	1972-2008		ICES (2009f)
North Sea	Cod	IV, IIIa (N), VIId	1	1963-2008		ICES (2009e)
	Herring	IV, VIId	1	1960-2008		ICES (2009c)
	Mackerel	NEAMC	1	1972-2008		ICES (2009f)

Continued overleaf

Region	Species	NAFO/ICES	#	Years	Notes	Source
Kattegat	Cod	IIIa (S)	1	1971-2008	Run with unallocated removals estimated used.	ICES (2009b)
	Herring	IIIa, 22-24	1	1991-2008	Western Baltic Spring Spawners (WBSS). Short herring series. Retrospective differences in older assessments.	ICES (2009c)
Western Baltic	Cod	22-24	1	1970-2008		ICES (2009b)
	Herring	IIIa, 22-24	1	1991-2008	WBSS. Short herring series. Retrospective differences in older assessments.	ICES (2009c)
	Sprat	22-32	1	1974-2008		ICES (2009b)
Eastern Baltic	Cod	25-29, 32	1	1966-2008	Run with misreported catches estimated used.	ICES (2009b)
	Herring	25-27, 28.2, 29, 32	1	1974-2008	Natural mortality estimated from MSVPA.	ICES (2009b)
	Sprat	22-32	1	1974-2008		ICES (2009b)

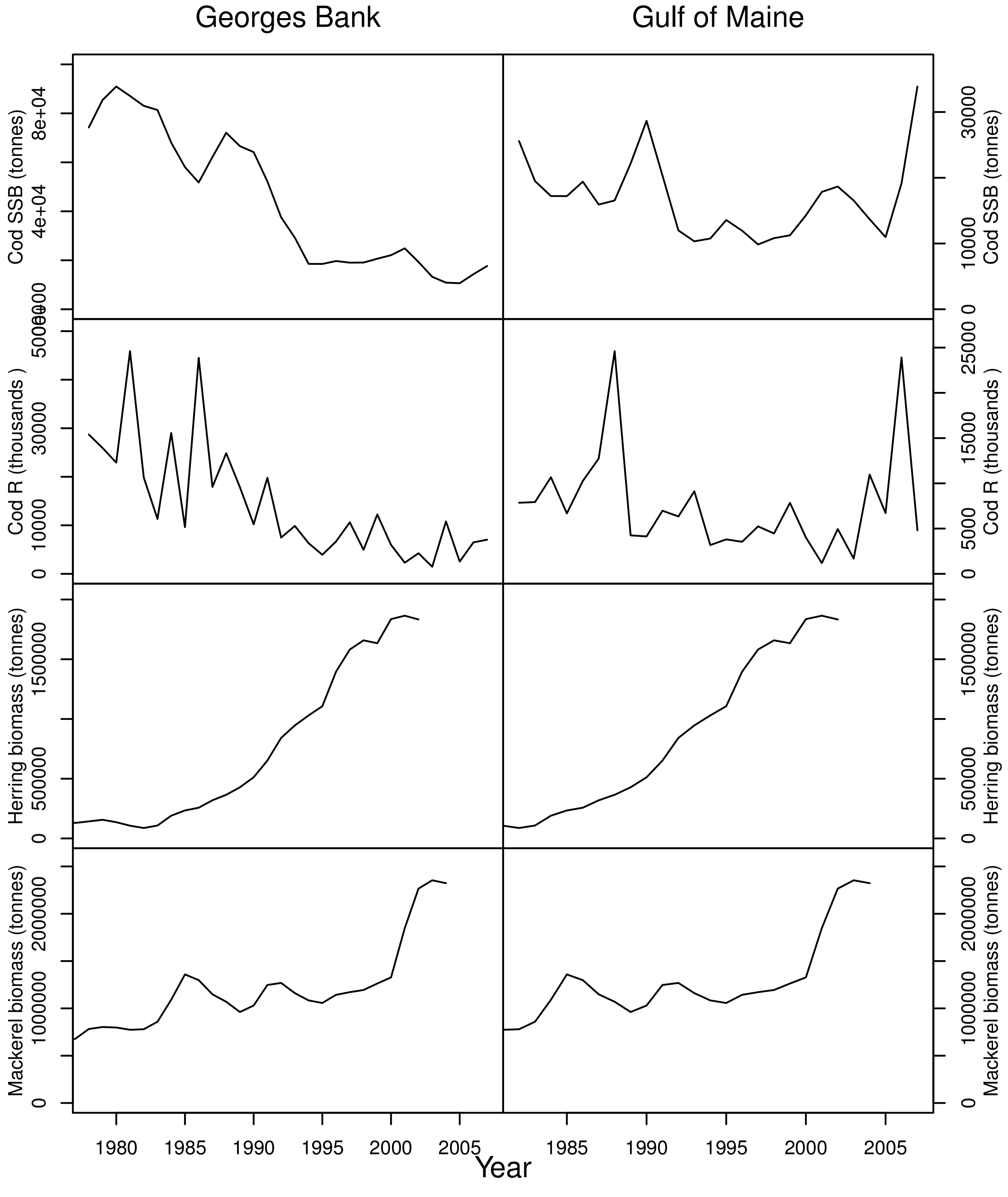


Figure C.5: Cod-pelagic data used per region. Solid and dashed lines represent recent and older assessments, respectively. Data sources are provided in Table C.1.

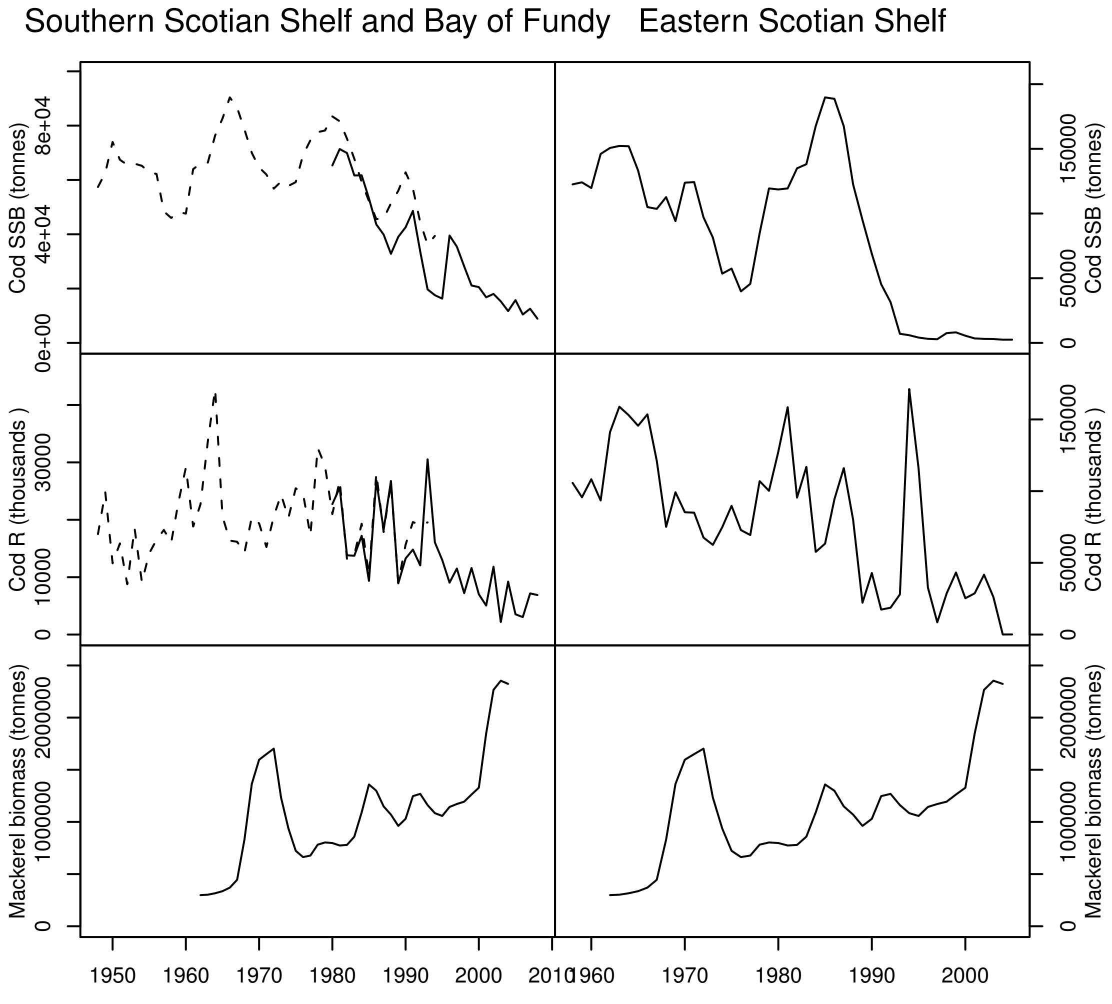


Figure C.6: Cod-pelagic data used per region. Solid and dashed lines represent recent and older assessments, respectively. Data sources are provided in Table C.1.

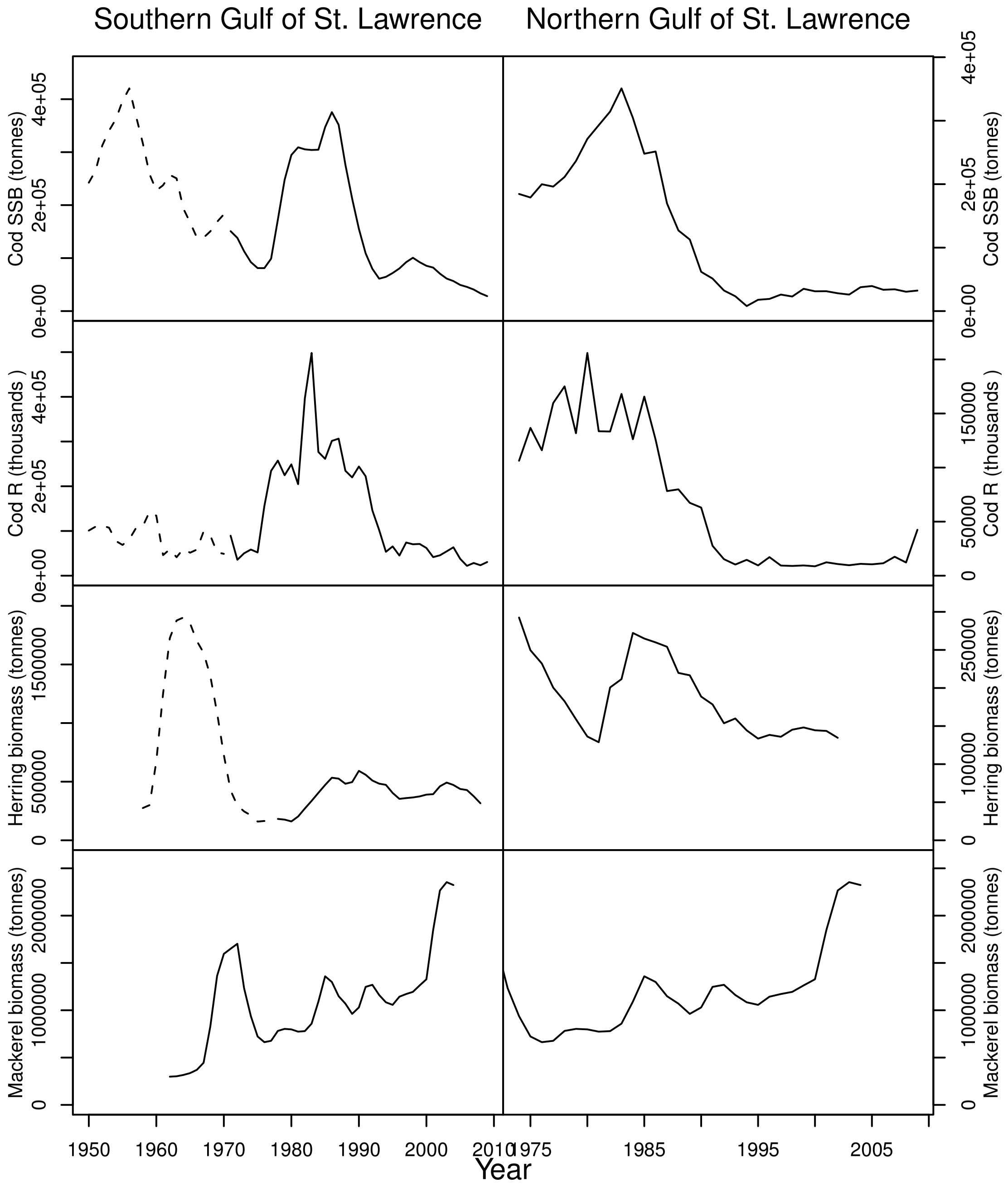


Figure C.7: Cod-pelagic data used per region. Solid and dashed lines represent recent and older assessments, respectively. Data sources are provided in Table C.1.

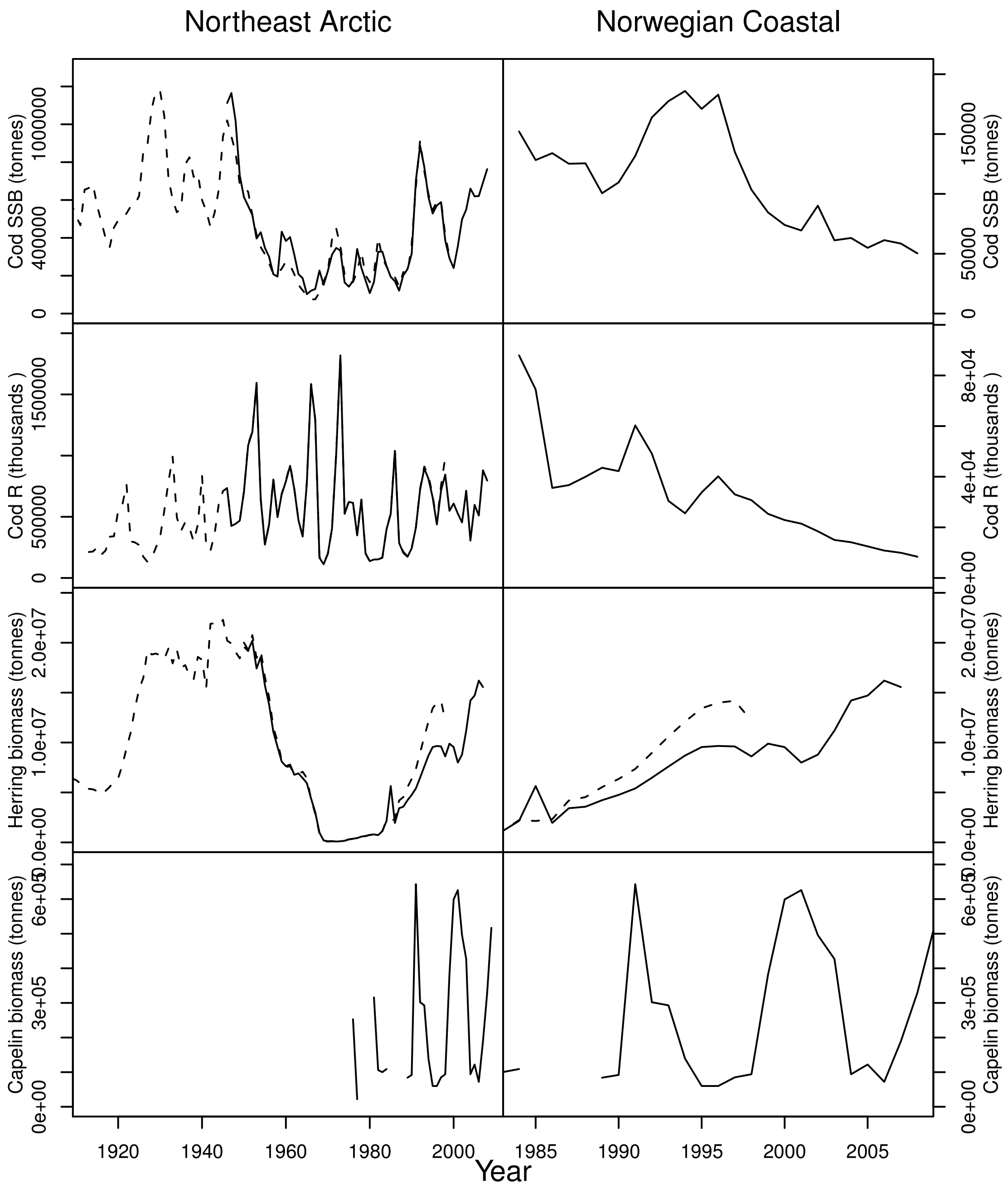


Figure C.8: Cod-pelagic data used per region. Solid and dashed lines represent recent and older assessments, respectively. Data sources are provided in Table C.1.

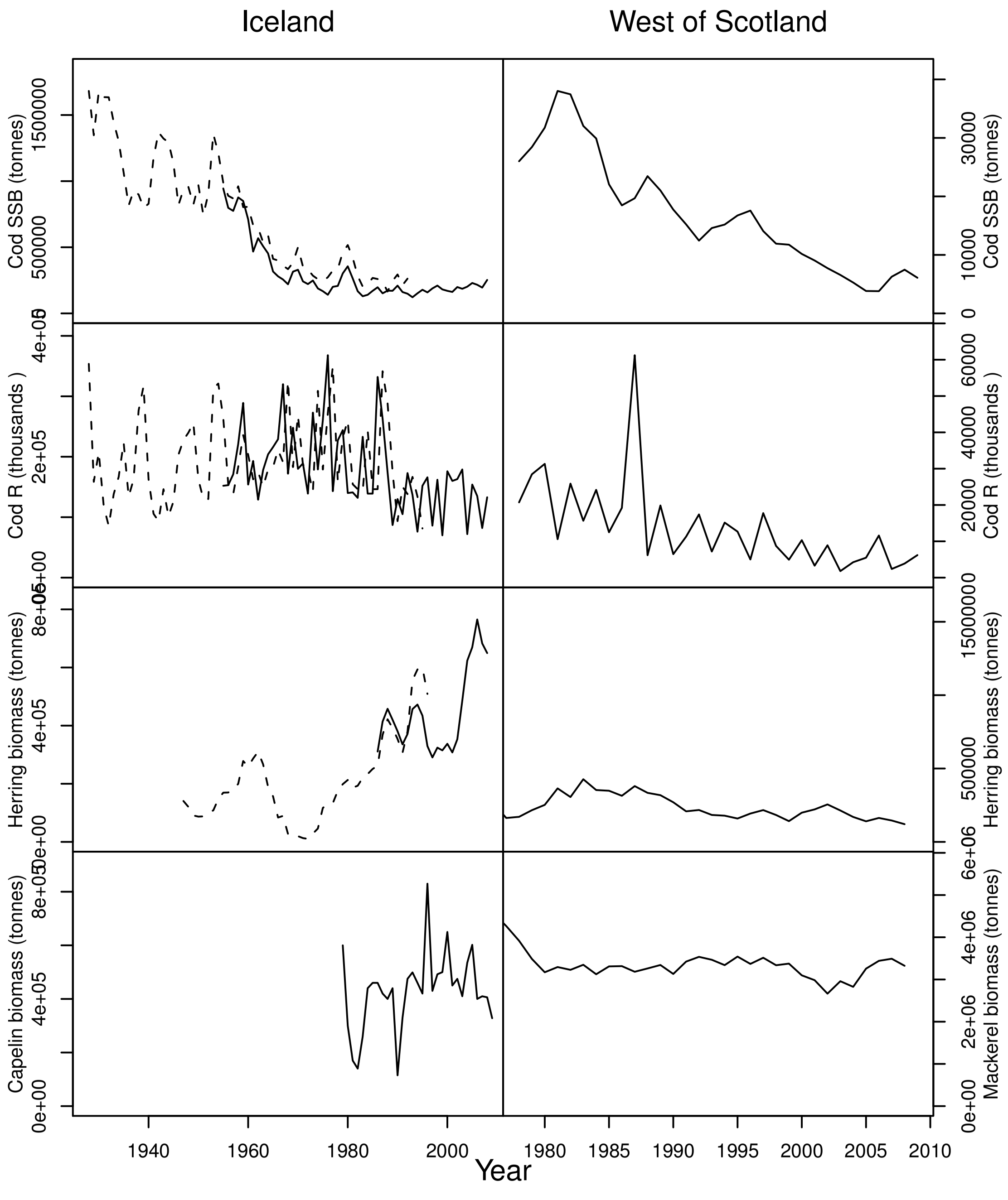


Figure C.9: Cod-pelagic data used per region. Solid and dashed lines represent recent and older assessments, respectively. Data sources are provided in Table C.1.

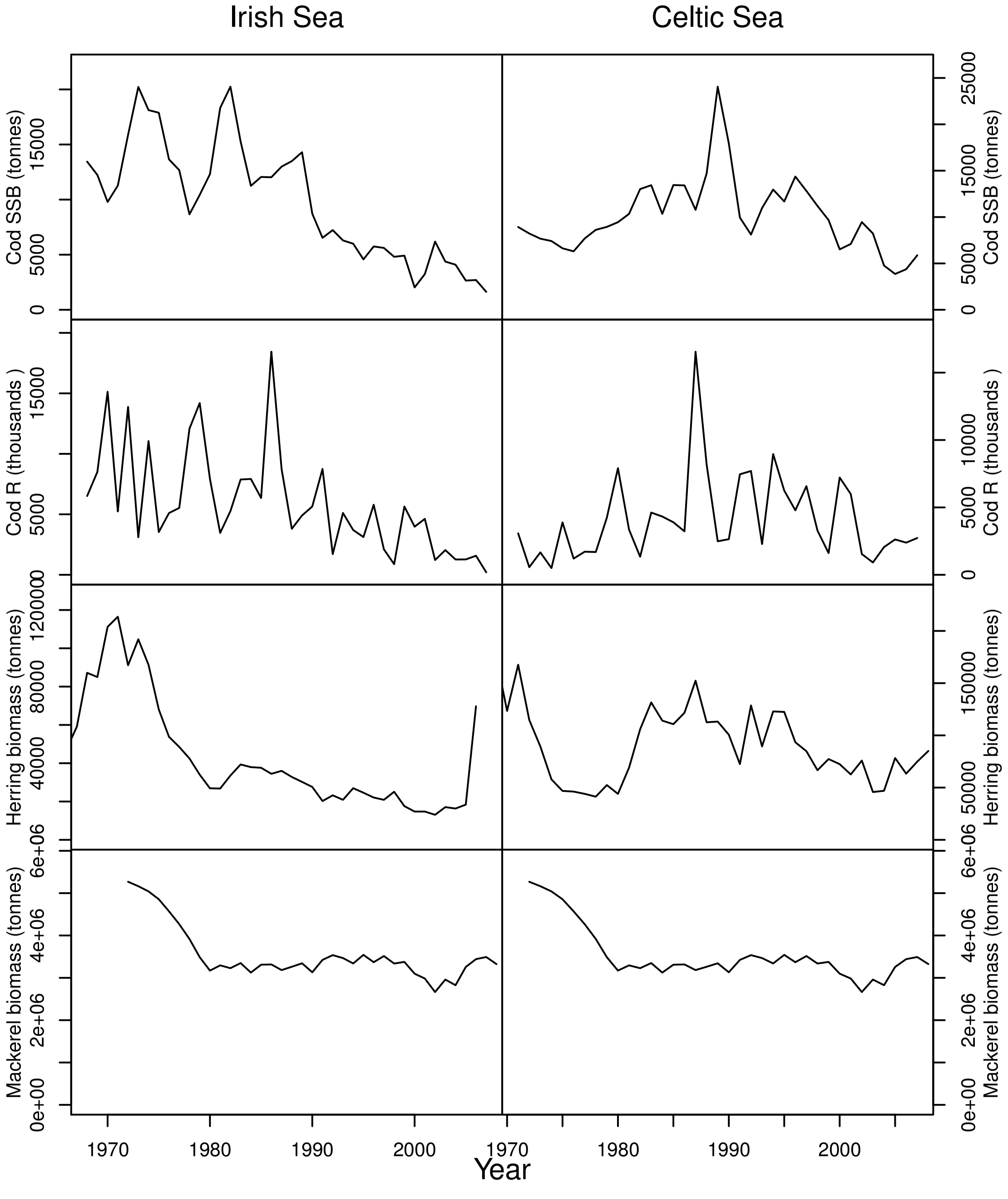


Figure C.10: Cod-pelagic data used per region. Solid and dashed lines represent recent and older assessments, respectively. Data sources are provided in Table C.1.

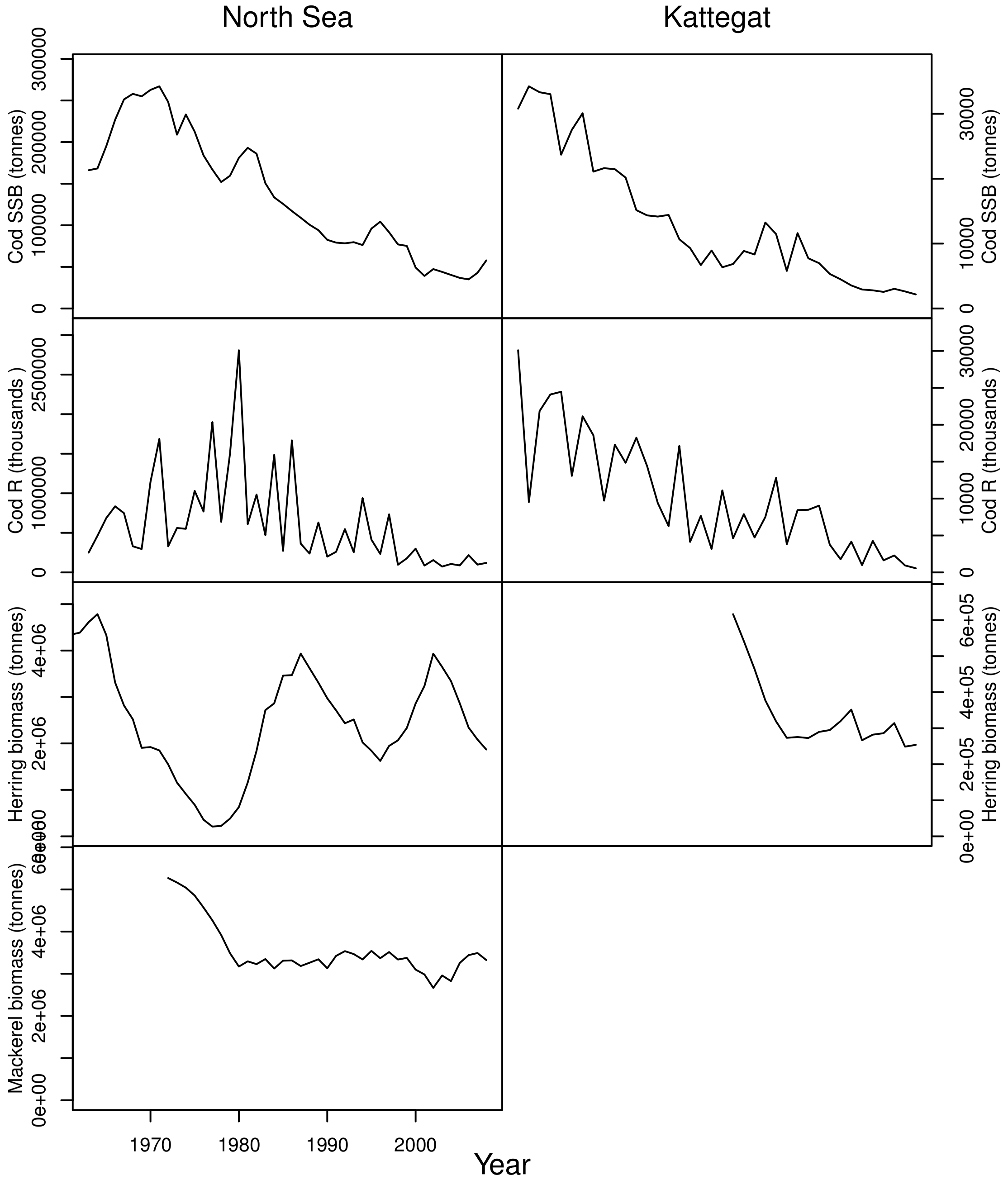


Figure C.11: Cod-pelagic data used per region. Solid and dashed lines represent recent and older assessments, respectively. Data sources are provided in Table C.1.

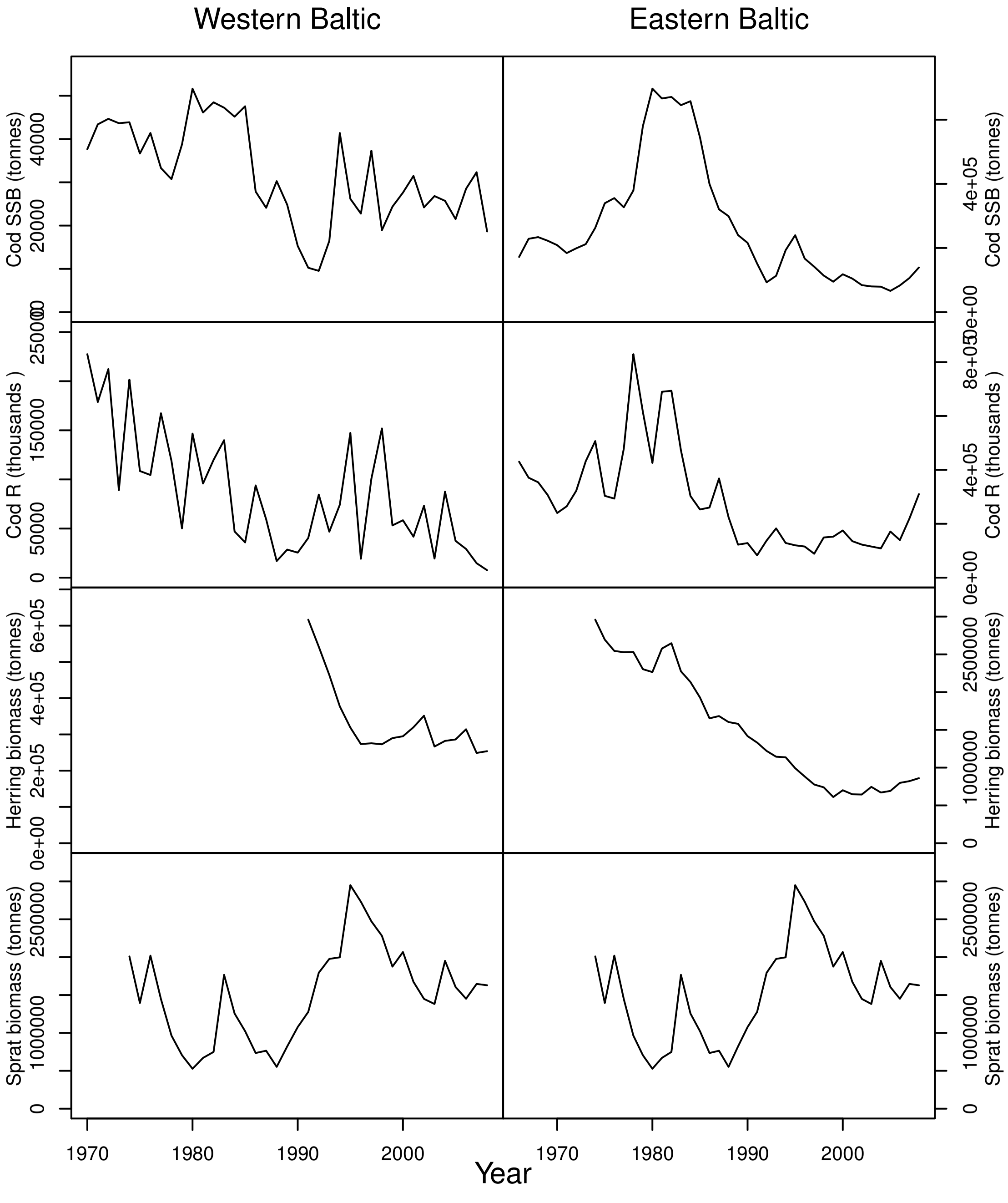


Figure C.12: Cod-pelagic data used per region. Solid and dashed lines represent recent and older assessments, respectively. Data sources are provided in Table C.1.

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