

POPULATION STATUS OF EXPLOITED MARINE FISH
POPULATIONS

by

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For Harrison.

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Abstract

Estimating the population status and trajectory of marine fishes is hampered by limited data and the assumptions needed to augment these data gaps can have broad implications. Poor management decisions based on poor inference can have far reaching socio-economic and ecosystem consequences. Here, I examine critical assumptions commonly employed in fisheries models and how they affect our beliefs on the population status of exploited marine fisheries. The assumption that catch rates are proportional to abundance is a critical assumption that can influence estimates of stock status. In chapter 3, this assumption is evaluated via a state-space modelling framework to obtain better estimates of the stock status of cusk (*Brosme brosme*) by incorporating multiple population time series in the estimation of population biomass. By relaxing the assumption that catch rates were directly proportional to population biomass, I found that the research trawl survey was likely hyperdepleted, thus exaggerating estimates of population decline. Indeed, previous estimates of population decline based solely on the the research trawl survey were 93% compared to my estimate of 64% once non-proportionality was incorporated in the modelling structure. In chapter 4, I model the spatial distribution and population trajectory of different size classes of thorny skate (*Amblyraja radiata*) to test for density dependent habitat selection (DDHS). I found large declines in both abundance and distribution for all size classes with the greatest declines observed in large juvenile and adult size classes. I found strong evidence for DDHS for the large juvenile and adult size classes, however, small juveniles exhibited limited changes in distribution associated with changes in abundance. In chapter 5, I examine how biological reference points used by fisheries to monitor harvest sustainability compare to those developed by conservation organizations, such as the IUCN Red List, to estimate extinction risk. I show that the two approaches frequently arrive at similar categorizations of stock status and differences are primarily a result of decline thresholds used to trigger conservation action. Conservation and fisheries metrics aligned well (70.5% to 80.7% for riskier and more conservative reference points respectively) despite their mathematical disconnect in decline thresholds. My analyses suggest conservation and fisheries scientists will agree on the status of exploited marine fishes in most cases, leaving only the question of appropriate management responses for populations of mutual concern still unresolved.

List of Abbreviations and Symbols Used

NAFO	Northwest Atlantic Fisheries Organization
AIC	Akaike information criterion
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
CPUE	Catch per unit effort
CR	Critically endangered
DDHS	Density dependent habitat selection
DFO	Fisheries and Oceans Canada
DIC	Deviance information criterion
EN	Endangered
ESA	Endangered Species Act
GAM	Generalized additive model
GLMM	Generalized linear mixed-effects model
GLM	Generalized linear model
GPS	Global positioning satellite system
IFD	Ideal free distribution
IUCN	International Union for Conservation of Nature
LME	Large marine ecosystem
LOESS	Local Polynomial Regression
MCMC	Markov Chain Monte Carlo
MSP	Maximum surplus production
MSY	Maximum sustainable yield
NSERC	Natural Sciences and Engineering and Research Council of Canada
RAM	Ransom Aldrich Myers
REML	Restricted maximum likelihood
SARA	Species at Risk Act
VU	Vulnerable

ZINB	Zero-inflated negative binomial
B_{lim}	Limit reference point below which recruitment will be impaired
B_{msy}	The biomass at MSY
B_{pa}	Precautionary biomass reference point
cdf	cumulative distribution function
statHBS	Statistical habitat-based standardization

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Ardeant in ignibus inferni.

Chapter 1

Introduction

Wild marine capture fisheries currently have an annual global production of approximately 80 – 90 million tons and it is generally accepted that this is close to, or at, the maximum global production limit (Frid and Paramor, 2012). Indeed, as of 2011, 28.8% of the world’s managed fisheries were fished at biologically unsustainable levels, 61.3% of stocks were fully exploited and 9.9% were under utilized (FAO, 2014). Fisheries management is tasked to balance multiple and often conflicting objectives: maximizing biological or economic goals, reducing bycatch, meeting conservation goals, and ensuring that exploited stocks are maintained above threshold levels in order to minimize the risk of overfishing (Harwood and Stokes, 2003). To complicate matters, limited data require that management frequently operates in a cloud of uncertainty to meet these conflicting objectives (Wade, 2001). One of the main sources of uncertainty lies in the challenges inherent in estimating the abundance of marine fishes both precisely and accurately (Harwood and Stokes, 2003).

Estimating the status or abundance trajectory of marine fishes can be challenging due to poor resolution of the current and historical range and distribution of many marine fishes, generally low and potentially changing catchability due to gear changes and increased fishing efficiency, and frequent high stochasticity in recruitment caused by a myriad of biotic and abiotic forces (Millar and Methot, 2002; Fraser et al., 2007). Precise and accurate abundance estimation is further hampered by sampling events that are often limited in frequency and spatial breadth. Indeed, the conclusions that are desired from fitting population models to estimate abundance frequently outstrips the information contained in the available data (Schnute and Richards, 2001). As a consequence, simplifying assumptions are required about model structure and data relationships. Unfortunately, many of these assumptions are not directly testable and their use has the potential to result in incorrect estimates of stock status (Schnute

and Richards, 2001). These assumptions need to be critically examined and not be haphazardly employed (Schnute and Richards, 2001).

The use of assumptions in fisheries models, particularly the assumption that catch rates are proportional to population abundance, has led to some spectacular failures in fisheries management (Harley et al., 2001; Walters and Martell, 2004). Indeed, one of the critical assumptions that contributed to the collapse of the 400 year Atlantic cod (*Gadus morhua*) fishery of the northwest Atlantic was that the catch rate series calculated from the commercial cod fishery better reflected changes in the population abundance compared to the Fisheries and Oceans Canada (DFO) fishery-independent research survey (Walters and Martell, 2004). This assumption was incorrect and its use resulted in management decisions that contributed to the collapse of the commercial cod fishery in 1992. Cod populations in the northwest Atlantic are still at historically low levels of abundance despite near removal of all sources of fishing mortality (Bundy and Fanning, 2005; Shelton and Morgan, 2014). This demonstrates not only the consequences of using poor assumptions but also that the consequences of their use may not be easily reversible.

Changes in the trophic structure of marine ecosystems, and the abundance of the species present in them, can arise from direct and indirect sources and may not be reversible within expected time scales (Bundy and Fanning, 2005; Bundy et al., 2009). The abundance and distribution of marine fish populations are a function of a myriad of top-down and bottom-up controls (Baum and Worm, 2009) such as temperature, depth, environmental variability, climate change (Rijnsdorp et al., 2009), fishery exploitation and predator and prey dynamics and distribution (Swain and Benoît, 2006). Disentangling the causal mechanisms responsible for changes in population distribution and abundance is rarely trivial and becomes increasingly complex when indirect effects via cascading trophic interactions are considered (Fung et al., 2013). This can have wide-ranging consequence on ecosystem structure and stability (Myers et al., 2007; Petrie et al., 2009) and presents challenges and potentially difficult choices, such as favouring one fishery over another, for fisheries and ecosystem management (Hutchings and Reynolds, 2004).

Substantial declines in population abundance as a consequence of exploitation is frequently considered to be an unwanted side effect of fishing. Large declines in

abundance, however, are frequently a management objective to increase the population growth rate from compensatory density-dependent process in the population dynamics (Rose et al., 2001). This fundamental concept of population dynamics is exploited to increase fishery yields and is the basis for the concept of maximum sustainable yield (MSY), the largest catch that can be removed sustainably from a population indefinitely. Many fisheries management agencies, including those in the U.S. and Canada, use reference points related to the concept of MSY: B_{msy} , the population biomass that should provide the MSY and has historically been considered to be a fisheries management target (Caddy and Mahon, 1995). Increasingly, however, it is recognized both from economic (Grafton et al., 2007; Froese et al., 2010) and ecosystem (Walters et al., 2005; Smith et al., 2011) perspectives that it is beneficial to maintain populations above B_{msy} , and thus it is better regarded as a limit that should not be exceeded. Alternate reference points, such as those used by the International Union for Conservation of Nature (IUCN), that are used to estimate extinction risk can give potentially conflicting evaluation regarding the status of exploited fish communities. Therefore, not only does management need to function in the cloud of uncertainty due to data limitations and necessary assumptions required to support evaluations of population status but also consider potentially conflicting advice regarding conservation and population sustainability.

1.1 Rationale & Goals of Research

To that end, the goals of this thesis can be divided in four main points:

- 1) Conduct a broad literature review to understand the consequences that seemingly small assumptions can have on the inference of the population status of marine fish populations.
- 2) Estimate the population status of cusk (*Brosme brosme*) using a Bayesian state-space model and evaluate the assumption of proportionality of multiple catch rate indices to population biomass.
- 3) Estimate changes in relative abundance and spatial structure of different size classes of thorny skate (*Amblyraja radiata*) and test the assumption of homogeneous distribution on the Scotian shelf.

- 4) Understand how abundance based biological reference points used by fisheries compare to rate based reference points used by conservation organizations to evaluate extinction risk and determine whether there is common ground between the two approaches as they pertain to sustainability of exploited marine fish populations.

1.2 Thesis Overview

In this thesis, I include four chapters which address the questions and goals listed above. I begin with a critique of the common assumptions that are frequently used to estimate the abundance and population status of marine fishes and discuss some of the consequences that making wrong assumptions about models or data can have on the inference on population status (Chapter 2). I particularly focus on the assumption of proportionality of catch rates to population abundance through time and space. Although the problem of nonproportionality is well known for commercial catch rates it can also be an issue with fishery-independent data and lead to erroneous designations of stock status particularly for species that are not the primary targets of fisheries-independent surveys.

In Chapter 3, I employ a Bayesian state-space biomass production model to estimate population trends for cusk. This chapter demonstrates how multiple time series can be incorporated in a single model and model both process and observation error simultaneously to estimate population biomass trends and test for non-proportionality in multiple time series that alone may be biasing estimates of population status. I also use a simulation approach to demonstrate the consequences to inference about population status by not accounting for non-proportionality of each time series.

In Chapter 4, I examine changes in the abundance and distribution of different size classes of thorny skate (*Amblyraja radiata*) and employ various statistical methods to test for density dependent habitat selection for the different size classes.

Finally, Chapter 5 focuses on the how biological reference points used to monitor harvest sustainability by fisheries compare to those developed by conservation organizations, such as the IUCN, that are used estimate extinction risk. I show that the two approaches frequently arrive at similar categorizations of stock status and the main differences lie in the decline thresholds used by each to trigger conservation action.

I explicitly identify how abundance based fisheries reference points and rate based conservation reference points largely share common ground in the goal of population persistence and much of the disagreement between fisheries and marine conservation fields is based on relatively subtle differences in the assumption in the approaches employed.

1.3 Publications Arising From This Thesis

At this time two publications have arisen from this thesis, and another is being considered.

Davies, T. D. and I. Jonsen 2011. Identifying Nonproportionality of Fishery-Independent Survey Data to Estimate Population Trends and Assess Recovery Potential for Cusk (*Brosme brosme*). Canadian Journal of Fisheries and Aquatic Sciences 68(3): 413 – 425. doi:10.1139/F10-165.

Davies T.D. and J.K. Baum (2012) Extinction Risk and Overfishing: Reconciling Conservation and Fisheries Perspectives on the Status of Marine Fishes. Scientific Reports 2 doi: 10.1038/srep00561

Chapter 2

Estimating the Abundance Trajectory of Marine Fishes: Common Pitfalls

2.1 Introduction

Over exploitation has been responsible for the collapse of large marine fisheries (Hutchings and Festa-Bianchet, 2009); however, exploitation levels, and the effects that the loss of many incidentally captured non-target species may have on ecosystems are difficult to estimate and are poorly understood (Dulvy et al., 2004). In 2007, approximately 28% of the world’s managed fisheries were either overexploited (19%), depleted (8%) or recovering from depletion (1%), 52% of stocks were fully exploited and 20% were underutilized (FAO, 2008). What is absent from these statistics are incidentally captured (bycatch) species of little or no commercial importance that are generally not actively monitored. Indeed, detailed population dynamics models (i.e. fisheries stock assessments) are generally data intensive endeavors and thus generally limited to target species of large-scale commercial fisheries (Davis, 2002; Kelly and Codling, 2006). On the east coast of Canada, for example, population assessments have been conducted for fewer than 5% of all marine fish species (Dulvy et al., 2004; Hutchings and Baum, 2005) leaving the population status of many species, particularly bycatch species, unknown. These species, or geographically restricted populations, may be considered to be “data-poor”, where there is insufficient data to infer the trajectory or exploitation history of the population with a precision that is useful in guiding management decisions (Kruse et al., 2005).

Whether a population should be considered “data-poor” is really dependent on what one wants to do with the data and the precision desired in the conclusions. Because so many assumptions are required in the population assessment process of most fish stocks, one could easily consider almost any marine population to be data-poor (Walters and Martell, 2004). Global fisheries have continued to expand in range

and exploit more trophic levels without a concurrent increase in monitoring. As a result, the number of fished species with little or no data for their assessment is increasing (Essington et al., 2006). Although the number of these fisheries is relatively low in comparison to the majority of the world's fisheries, their contribution has increased from 20 to 30% of the world's landings over the last 50 years (Vasconcellos and Cochrane, 2005; Costello et al., 2012).

The monitoring and conservation of marine species can entail significant cost and therefore a reasonable question to ask is: "why should we bother?" There are both biocentric, and anthropocentric motivations for conserving marine fishes that are not directly commercially exploited. The biocentric viewpoint assigns value to species, species assemblages, and ecosystem services even if no economic benefit is derived from these features themselves (Schug, 2008). Economic costs are inevitable due to the expenses associated with the monitoring and management of these species. In contrast, the anthropocentric viewpoint that pervades the fisheries literature (Farber et al., 2002) generally uses biomass production as proxies for economic benefits such as "maximum sustainable yield" (MSY) which is frequently used as a reference point for the maximum amount of biomass that can sustainably be removed from a fish stock. This concept generally has limited practical relevance to many bycatch marine species or from the perspective that fisheries frequently have competing economic, social and political objectives (Hilborn, 2007b). Anthropocentric motivations to conserve commercially unimportant species may be found in the potential consequences that the removal of non-target species may have on the organization of complex oceanic food webs and trophic linkages with commercially important fisheries (Pope et al., 2000; Kaiser and Jennings, 2001). For example, Myers et al. (2007) showed how the removal of apex predator shark guilds had devastating economic consequences through a trophic cascade causing the collapse of a commercially important scallop fishery in North Carolina, U.S. Awareness that non-target species may also play important roles in stabilizing ecosystem functions and resilience has begun to move traditional fisheries management towards an ecosystem-based approach to management that includes the interactions between fish predators and their prey species (Fraser et al., 2007). Ultimately, legislation such as the Species at Risk Act (SARA; 2003) in Canada, or the Endangered Species Act (ESA; 1973) in the United States

are designed with a mixture of biocentric and anthropocentric motivations (Farber et al., 2002). If maintaining commercially unimportant populations at specified levels of abundance is a goal of ecosystem management, data allowing the estimation and tracking of the abundance of these populations are needed. When the data available are not adequate to adequately describe the population of interest, assumptions need to be employed to fill in these information gaps.

Numerous statistical models exist that can be used to estimate and/or track abundance with the general rule (omitting model misspecification) that the more complex the model, the greater the ecological realism and data requirements. Uncertainties about the current and historical abundance, spatio-temporal distribution, movement rates, and life-history parameters of many species are frequently poorly defined and consequently many assumptions are needed to estimate the abundance trajectory of many marine species (McAllister et al., 2001; Hall and Mainprize, 2005). Because of the potential for indirect ecosystem consequences to occur from the removal of non-target species that can suffer significant incidental mortality as bycatch (Crowder and Murawski, 1998; Baum et al., 2003), it is essential that quantitative and unbiased methods are used to assess the impact that indirect exploitation may be having on these populations. Due to the lack of data, it is important that the assumptions used to fill in data gaps are critically examined to ensure that proper assessments are done and limited funds and efforts are directed where conservation concerns truly exist. Unfortunately, the validity of many assumptions are frequently untestable due to the lack of data, yet the consequences of making incorrect assumptions can have broad implications. Indeed, careless interpretation of fisheries statistics increases confusion and can undermine legitimate conservation efforts (Walters, 2003), potentially close fisheries when it is not warranted, or conversely, result in the collapse of populations leading to fishery closures and have other socioeconomic and ecosystem wide implications. It is therefore critical that the consequences of the assumptions used in place of data be fully understood in the estimation of population abundance in data-poor situations.

2.2 Data

Estimating a reliable indicator of population abundance is necessary to answer many ecological questions, effectively manage exploited populations, and evaluate the effectiveness of recovery programs for species that have been impacted by human disturbances. Monitoring the abundance of populations, or its rate of change, can be challenging for many species as a complete census of the population is usually impractical due to prohibitive financial, logistical and time constraints. Consequently, the data available to estimate abundance are frequently limited to a relatively small number of sampling events when put in the context of the vast geographical range of many marine fish species. The frequently high levels of uncertainty in population level parameter estimates derived from populations with few individuals and/or have large or unknown spatial distributions can make the monitoring and study of many marine populations difficult.

Fishery-dependent and fishery-independent data are the two general sources available for the assessment of marine fishes. Fishery-dependent data are derived from commercial fishing activities and originate directly from the fisheries vessels via log books, from independent scientific observers stationed on commercial vessels, or a combination of the two via port sampling when catches are offloaded at ports. Species misidentification and misreporting can occur in logbook data and numbers caught are frequently only visually estimated and aggregated into species groups, some species may be absent from logbook statistics, and consequently estimates of the number caught can suffer from poor precision and accuracy. Data collected from scientific observers onboard commercial vessels can provide more reliable estimates of catch composition, however, these estimates are usually extrapolated from small samples (e.g. a 300 kg random sample can be extrapolated to an entire bottom trawl set that can be greater than 100 tonnes). Onboard observers occasionally collect size and/or age structure data but these data are usually limited to the target species of the fishery being monitored. Port sampling can collect similar age and size structure information as onboard observers but without the advantage of having a presence on the fishing vessels to ensure all catches are reported.

For some fish populations, commercial data can provide a wealth of information as fishing fleets generally have far greater spatial and temporal coverage and can have

higher catch rates than government operated research surveys. The exclusive use of these data, however, can result in biased population estimates due to the influence that the non-random fishing behaviour of commercial fleets can have on commercial catch rates. Specifically, many assessment methods rely on the assumption that catch rates are proportional to population abundance which is difficult to prove for many target species (Hilborn and Walters, 1992; Harley et al., 2001), and especially so for bycatch species (Heales et al., 2007). Standardization approaches exist that aid in reducing the influence that fishing practices can have on commercial catch rates and are discussed later.

Fishery-independent data are derived from activities that do not involve the commercial harvest of fish and is usually collected by research surveys conducted by federal or state/provincial governments or by academic institutions. For example, on the east coast of Canada, a fishery-independent groundfish trawl survey of the Scotian Shelf and Bay of Fundy has been conducted annually in July since 1970 by the Canadian Department of Fisheries and Oceans (DFO). The survey was designed to monitor commercially important groundfish stocks such as Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefin*; Fisher and Frank, 2004). The survey follows a stratified random design with stratification based on depth and geographic area with the number of tows proportional to stratum area (Shackell and Frank, 2003). In the calculation of a geographically aggregated CPUE index, separate abundance estimates are produced for each stratum which are proportionally weighted to stratum size to calculate an overall weighted mean abundance (Blanchard et al., 2008). The basis for a stratified design is that depth and location can have a large influence on species distribution and abundance (Maunder and Punt, 2004); consequently the variance of abundance estimates is less with a stratified, rather than a simple random design (Stamatopoulos, 2002). Catch statistics are frequently reported as the number (or mass) of fish caught per unit of effort (for example, per hook, or per tow). Fishery-independent data is frequently favoured over fishery-dependent data due to their randomized designs and strict sampling protocols that are used to reduce bias that can be introduced from changes in gear and fishing behaviour.

Various species specific behaviours, habitat preferences, demographic characteristics, and gear types can greatly affect the catchability of individuals within a population and need to be considered when interpreting both fishery-independent and fishery-dependent catch rate data. This can be important for fishery-independent trawl surveys that restrict fishing to areas with low habitat complexity to avoid gear damage thus potentially missing species or age-classes that favour more complex habitat. Consequently, trawl surveys give a picture of a fish community that is restricted in time and space and filtered by the selectivity of the survey gear that can be biased towards different species and size classes (Fraser et al., 2007). Tagging and mark-and-recapture data also fall under the category of fishery-independent data. Such studies can be used to estimate the movement rates within and between stocks, the natural mortality rate and reproductive output, growth rates, maturity schedules (the percent of individuals mature at each age), and hooking or discard mortality rates. These data can provide invaluable information to assess a population. Unfortunately these data are rarely available for species that are not of high commercial importance and can also contain bias if recaptures are derived from commercial fishing activities (Pollock et al., 2004).

2.2.1 Missing the Context of Catch Data

Catch data is the minimum, and sometimes the only, data available to assess marine fish populations impacted from commercial fishing and understand its exploitation history (Vasconcellos and Cochrane, 2005). Although not directly targeted, bycatch species are frequently retained and sold, or are at least recorded in logbooks or by onboard observers. Unfortunately, commercial catch data alone are generally poor indicators of fish abundance (Hilborn and Walters, 1992; Longhurst, 2007; Murawski et al., 2007; Branch, 2008). Indeed, catch is influenced by numerous factors including market demand, phase of fishery development (Vasconcellos and Cochrane, 2005), operating costs, changing fishing regulations, processing capacity, the environment, local abundance of predators and competitors (Longhurst, 2007), misreporting (Watson and Pauly, 2001), and potential errors in catch databases. It is therefore rarely utilized alone to assess the status of fish populations (Hilborn, 2007c; Murawski et al., 2007; Branch, 2008).

One noteworthy example of how using commercial catch data as an index of abundance can lead to incorrect conclusions of stock status is found in a criticism of Worm et al. (2006) which predicted that at present trends of over-exploitation, all of the worlds commercial fisheries would be collapsed by 2048 (Figure 2.1). The foundation of this claim was based on commercial catch data and defined a fishery to be collapsed if its current catches were less than 10% of the largest historical catch. This analysis has been broadly criticized on data use, statistical methodology, and interpretation (Hilborn, 2007a,c; Jaenike, 2007; Longhurst, 2007; Murawski et al., 2007; Wilberg and Miller, 2007; Branch, 2008; Kleiber and Maunder, 2008). The criticism by Hilborn (2007a) focused on how the use of catch data alone can lead to faulty interpretations about the condition of fishery ecosystems. In his review, Hilborn (2007a) used catch data from American fisheries in the Bering Sea to illustrate the problems associated with inferring the population status on the exclusive use of these data. Indeed, using the methodology of Worm et al. (2006), the majority of the American fisheries in the Bering Sea would be defined as collapsed, however, more complex abundance-based analyses and assessments that used a combination of fishery-independent and fishery-dependent data for this region have shown that only two species should be classified as overfished (defined as less than one-half the biomass needed to produce MSY). A broader analysis was conducted by de Mutsert et al. (2008) who examined 72 commercial fisheries in the Gulf of Mexico. Using the methodology of Worm et al. (2006), $\approx 80\%$ of these fisheries were identified as collapsed. In contrast, detailed assessments that considered changes in regulations, market forces, and fishing effort found that only 15 stocks ($\approx 21\%$) should be considered to be collapsed (indicating 43 stocks incorrectly categorized as collapsed).

It is well established that the use of commercial catch data alone can lead to erroneous designation of stock status and are unreliable indicators of the abundance trajectory of many species due to the corrupting influence that management and markets forces can have on catch statistics. Many fisheries in less developed countries are lacking in the most basic fisheries statistics and therefore catch data may be the only data available to assess a population. In these cases, where catches may be less influenced by socioeconomic factors and management actions, catch data may provide

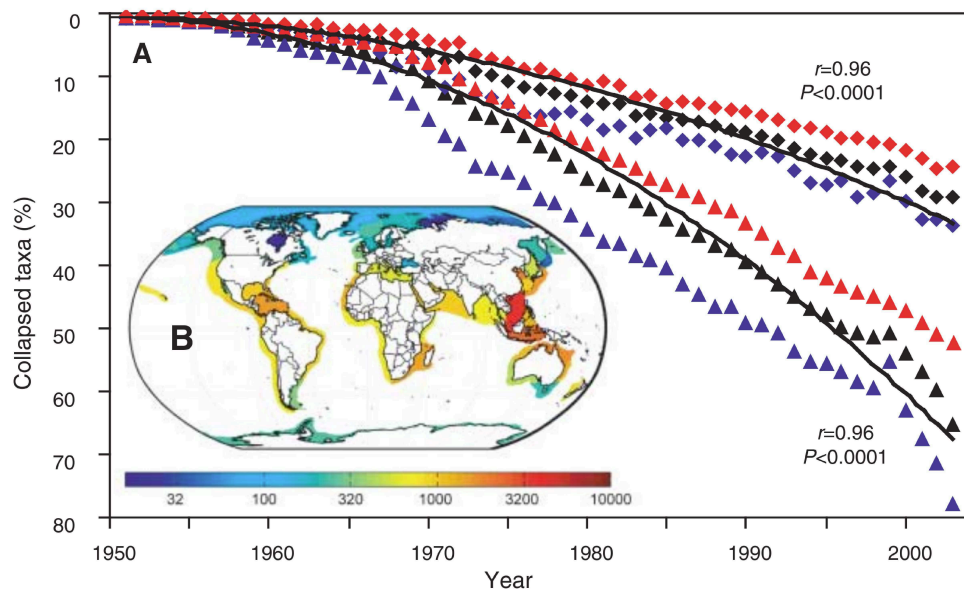


Figure 2.1: Global loss of species from Large Marine Ecosystems (LMEs). (A) Trajectories of collapsed fish and invertebrate taxa over the past 50 years (diamonds, collapses by year; triangles, cumulative collapses). Data are shown for all (black), species-poor (< 500 species, blue), and species-rich (> 500 species, red) LMEs. Regression lines are best-fit power models corrected for temporal autocorrelation. (B) Map of all 64 LMEs, color-coded according to their total fish species richness. Figure from Worm et al. (2006).

reasonable estimates of population trends and result in fewer erroneous designations of stock status (Kleisner et al., 2013).

2.2.2 Catch Standardization & Consequences of Data Aggregation

Standardizing catch data by the amount of fishing effort that was used to produce that catch increases its value to identify population trends because it removes the potential bias caused by changes in fishing effort. Dividing catches by effort creates a ratio estimate of CPUE which is frequently used as an index of relative abundance. Common standardization measures are number per hook (longline fisheries), tons per tow (trawl fisheries), or tons per trip (any fishery with poor resolution of fishing effort). This metric is a valuable tool to identify instances where catches are high or increasing due to a concurrent increase in fishing effort rather than increases in population abundance. Unfortunately, CPUE as a relative measure of population abundance also has limitations and standardization approaches (e.g. Gavaris, 1980) are frequently needed to remove factors other than population abundance that can influence catch rates.

The non-random distribution of fish and fishing effort can result in biased estimates of relative abundance if catches are simply summed over a region and divided by the total fishing effort without regard to the interaction between the exploitation history of the fishery, spatial distribution of the population (Walters, 2003), and/or spatial restriction of a fishery or fishery-independent survey. Critical and difficult to test assumptions that are frequently employed when using CPUE data are that the catch rate index is proportional to abundance and the catchability of fish does not change over time or as population size changes (Heales et al., 2007). When a catch rate index declines more quickly than population abundance it is known as hyperdepletion and can result, for example, from fishing effort being concentrated on a vulnerable subset of a population that is depleted while a significant part of the population remains unaccounted for in the catch rate index or survey design (Quinn and Deriso, 1999). For example, the fixed area design of fishery-independent surveys can result in a hyperdepleted catch rate index if the core density of a species is outside the survey area and species specific processes such as density dependent habitat selection results in incomplete mixing of the population within its full range

(Blanchard et al., 2008). How a fishery-independent fixed-area survey can result in a hyperdepleted catch rate index is illustrated in Figure 2.2. In this example, panels a-c show the geographic range of a species at years 0, 5, and 10 (grey shading) with degree of shading being proportional to fish density. Gridding represents the area covered by the fishery-independent survey. Panels d-f show how the catch rate index (solid lines) decreases much more quickly than the total abundance of the population (dashed-lines) due to the most favoured habitat of the species of interest being outside the survey area. In this example, assuming the catch rate index to be proportional to population abundance would result in overestimates of population decline and exploitation rate. If however, there is little habitat selectivity and there is good mixing between the surveyed and non-surveyed areas, hyperdepletion would not be expected to occur in the catch rate index (Hilborn, 2001). Hyperdepletion has also been shown to occur in multispecies aggregated catch rate indices (Kleiber and Maunder, 2008) as a result of model assumptions rather than ecological processes such as density dependent habitat selection.

It is well established that the non-random fishing behaviour of commercial fishing vessels and species specific behaviours of many fish species such as shoaling and range contraction in response to decreased abundance can lead to a situation known as hyperstability where a catch rate index declines more slowly than population abundance (Quinn and Deriso, 1999; Harley et al., 2001). This can be particularly severe in fisheries that exploit spawning aggregations at known location at predictable times of year. Indeed, when this occurs, catch rates can remain high even as the stock declines because fish density at catch locations remains high and/or the processing capacity of fishing vessels can become saturated. Assuming a hyperstable catch rate index is proportional to abundance can result in underestimates of exploitation rate and population decline (Hilborn and Walters, 1992). It is therefore important to account for changes in fishing behaviour and gear improvements by applying statistical approaches to commercial catch rate indices.

To improve the link between catch rates and population abundance, it is beneficial to remove the influence that other factors besides population abundance may be having on a catch rate index (Maunder and Punt, 2004). Technological and gear improvements, increased catch efficiency of fishers, latitude, gear depth, and time of

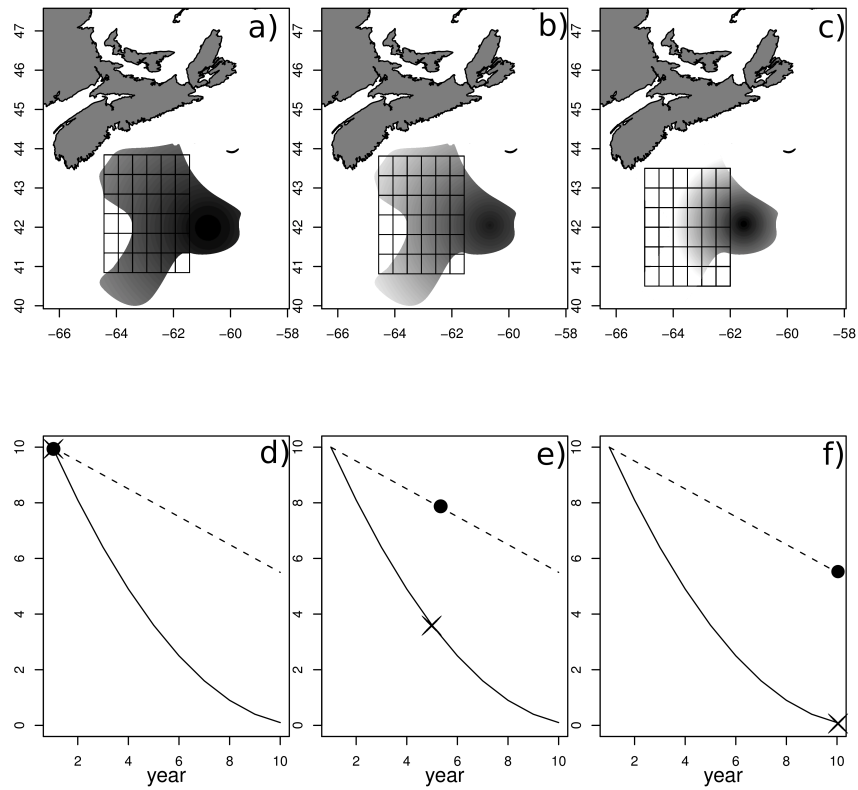


Figure 2.2: Hypothetical scenario of a fishery-independent survey showing hyperdepletion in a catch rate index. Panels a-c show the geographic range of a species (grey shading) with degree of shading being proportional to fish density at years 0, 5, and 10. Gridding represents the area covered by the fishery-independent survey. Panels d-f show how the catch rate index (solid lines) drop much more quickly than the total abundance of the population (dashed-lines) due to the most favoured habitat of the species of interest being outside the survey area.

year can all influence catch rates, and consequently influence trends in a catch rate index. For example, Maunder and Punt (2004) describe an example where two fishing vessels are exploiting the same stock which does not change in abundance over a ten year period. In this scenario, one highly effective vessel with high catch rates is initially responsible for 80% of the combined catches and reduces its contribution to the fishery to 20% of all catches over the ten year period (Figure 2.3). In this example, the combined CPUE catch rate shows a substantial decline even though the abundance of the stock has stayed constant over the ten year period. If one were to use the raw combined catch indices as an index of relative stock abundance, the conclusion would be that the stock had decline by almost 50% over the time period even though abundance of the stock had remained unchanged. Generalized linear models (GLMs) were first applied by Gavaris (1980) to remove bias caused by factors other than population abundance that can influence trends in a catch rate index and has received wide adoption in fisheries science. The general approach is to use some linear combination of a set of explanatory variables (e.g. vessel, latitude, hook depth etc.) and relate them to the catch rate index. This approach removes the influence of the explanatory variables from the catch rate index making it a better reflection of abundance trends. Generalized additive models (GAMs) and generalized linear mixed-effects models (GLMMs) can also be used but have not received as wide an application (Maunder and Punt, 2004). These standardization approaches are generally applied to fishery-dependent data rather than fishery-independent research survey data due to the commonly held belief that survey design is adequate to make fishery-independent data valid indices of relative abundance. However, there is increased awareness that survey design alone may be insufficient for rare and incidentally captured species and therefore standardization approaches will likely be more broadly applied to fishery-independent data in the future (Maunder and Punt, 2004).

The assumption that the *a priori* standardization of fishery-independent data through the survey design make them reliable measures of relative abundance needs further examination for non-target species that have patchy distributions and/or are poorly sampled by survey gear (Blanchard et al., 2008). Changing ocean temperatures have been shown to modify the distribution of demersal fish species (Perry et al., 2005)

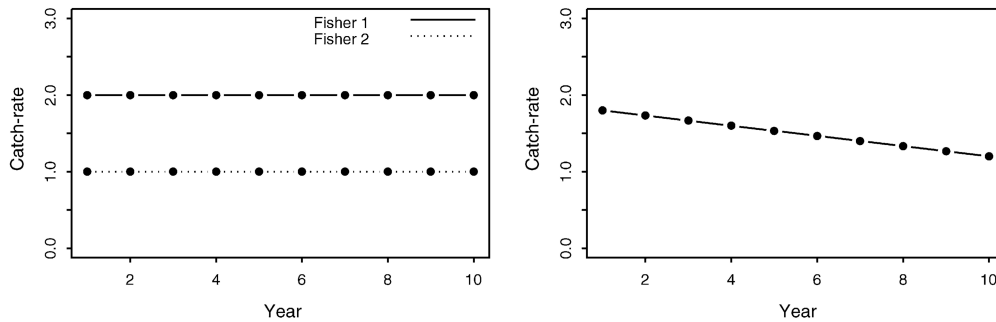


Figure 2.3: Catch rate time series of two hypothetical fishers (left panel) and the trend in raw combined catch rate (total catch divided by total effort of both fishers; right panel) with fish abundance held constant. Fisher 1 (solid line) has a higher catch rate compared to fisher 2 but reduces his contribution to the fishery from 80% to 20% over years 1 to 10. A declining combined raw catch rate trend is observed even though fish abundance is held constant. Figure from Maunder and Punt (2004).

and these changes in distribution will likely influence catch rates of fixed area fishery-independent surveys thus potentially biasing the catch rate index. Similar to the GLM methods of standardizing catch rates described above, a promising approach is statistical habitat-based standardization (statHBS) that allows for catch rate indices to be adjusted by habitat type (substrate type, temperature, depth) and can also be extended to include species associations (Maunder et al., 2006a). Detailed benthic habitat data is becoming increasingly available and can be used within a statHBS framework to predict species distribution and density outside fixed-area surveys and potentially test fishery-independent survey data for nonproportionality.

When calculating a spatially aggregated commercial catch rate index, careful consideration needs to be given to the exploitation history of a fish stock. When spatially stratifying a catch rate index, catches should be partitioned into small enough spatial units or time periods to effectively have random sampling within each unit. The consequences of not stratifying a spatially aggregated CPUE index is that areas that are more heavily fished gain more “weight” in the CPUE calculation which can bias the index towards highly fished areas that have high catch rates. An additional problem is how to treat catch rate data from the early developmental phases of the fishery that usually have a much more restricted spatial distribution compared to the fully developed fishery. Fishers do not fish at locations randomly, rather, they attempt to

fish in areas that produce the greatest profit by maximizing catches and minimizing expenses (such as fuel and travel time, Sampson, 1991). Consequently, when a fishery first starts to develop, fishers will tend to focus their efforts at locations close to ports that have high catch rates and gradually move effort farther away as catch rates near home ports decline. If inference on the population trajectory is going to be made on the current fishing distribution of the fleet, careful consideration of how to treat historically unfished areas is needed. There are three general approaches (Walters, 2003):

Assumption 1: Restrict analysis to the fished areas contained in the dataset by omitting a substantial (likely a majority) portion of the data and therefore be unable to estimate the trend of overall stock abundance. Tracking abundance for the relatively small areas that were exploited early in the fishery is of little value as it would provide little indication of the status of the entire stock which is likely the ultimate goal of the analysis.

Assumption 2: Assume catch rates in historically unfished areas would have been the same as those that were fished early in the development of the fishery (I.e. population exhibited complete mixing).

Assumption 3: Assume fish density of unfished areas to be some function of later catches (such as assigning a mean of the first few years of fishing to unfished areas earlier in the time series; I.e population had a heterogenous spatial structure through time).

Difficulties lie with all of these assumptions; however, one needs to be chosen if the analysis is to proceed. We can discard applying the methods in assumption 1 because our goal is to estimate the population trajectory of total population and not simply in the restricted regions that were exploited early in the development of the fishery. Assumption 2, although conceivable, is mathematically equivalent to the unlikely assumptions that fishers employed simple random sampling when choosing fishing locations early in the development of the fishery or that fish densities were randomly distributed throughout the fishing areas within the spatial confines of what is currently exploited. In contrast, assumption 3 seems to be the most reasonable because we know

that fishers do not fish at random but rather fish at areas that maximize economic returns. Assumption 3, however, does make broad assumptions about the historical distribution of the population. Indeed, this assumption also implies that population density in unfished areas did not change in response to reduced abundance caused by fishing in neighbouring areas. More complex approaches such as temporal linear interpolation could be employed; however, using the assumption that catch rates in unfished cells are equal to the mean of the first three years of fishing is sufficient to illustrate the consequences of using this assumption in place of assumption 2 which assumes unfished cells have the same catch rate as fished cells throughout the time series.

The consequences of choosing assumption 2 over assumption 3 is illustrated by Walters (2003) that reanalyzed the data described in Myers and Worm (2003) who concluded large tuna and billfish in the Pacific had declined by over 90% since 1950. This conclusion is controversial and many aspects of the analysis and assumptions about the data have been criticized (Maunder et al., 2006b; Polacheck, 2006; Sibert et al., 2006; Kleiber and Maunder, 2008). The consequences of choosing either assumption 2 or 3 are summarized in Figure 2.4 that shows that population declines are more severe using the unlikely assumption that catch rates in the unfished cells were equal to that of fished cells at the beginning of the time-series (assumption 2). Although both assumptions result in population declines, one would infer using assumption 2 that populations have collapsed in contrast to what is inferred when one uses assumption 3, which results in the populations being close to the “ideal” biomass that produces MSY. Indeed, a common fisheries management strategy is to substantially reduce population abundance in order to reduce density dependent growth factors to increase population growth rates. Regardless, whether the population is too low or at the desired level of abundance is a socioeconomic consideration and is a different question from what is the current exploitation status of the stock. Assumption 3 is more reasonable from the context of how the behaviour of commercial fishers likely changed over time and how these changes in behaviour would influence the catch rate statistics.

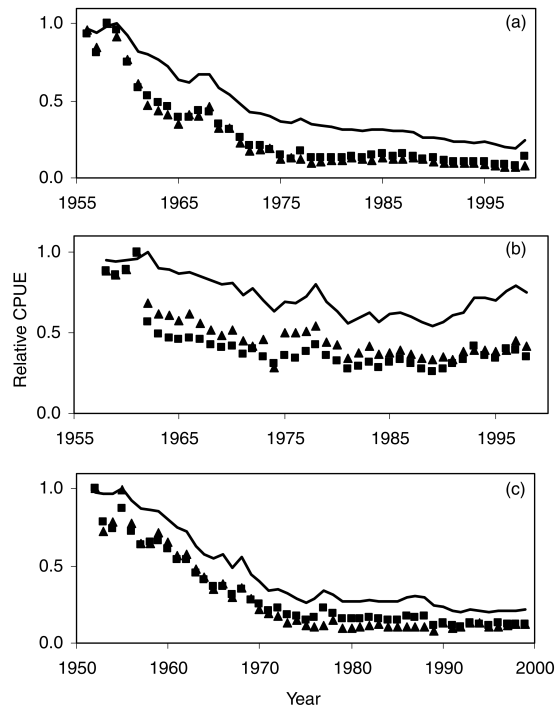


Figure 2.4: Catch per unit effort (CPUE) trends for large tuna and billfish (total number of fish per hook) from the 5 x 5 degree cell Japanese long-line database (Myers and Worm 2003), estimated by three alternative methods for (a) Atlantic, (b) Pacific, and (c) Indian oceans. Full spatial (solid line) assigns mean of first three observed catch rates to each cell for years before it was first fished and the last observed catch rate for years after it was last fished. Restricted spatial (\blacktriangle) is the mean catch rate over only those cells that were actually fished each year. Ratio (\blacksquare) is simply total catch summed over all cells divided by total effort. Figure from Walters (2003).

2.3 Modelling Issues

The use of mathematical models helps to formalizes hypothesis testing and gives a more transparent mechanism for addressing the assumptions used in an analysis. As described above, assumptions about the data can have a large influence on the inference on the status and trends of populations. An additional layer of uncertainty is the result of the large natural variability in abundance of many marine populations and frequently even larger observation error caused by limited sampling and few individuals captured during sampling. Incorporating the stochastic forces affecting populations and/or the observation processes requires that the mathematical model be extended to a statistical model (Dennis et al., 2006). The majority of statistical marine population assessment models have two implicit components: at least one observation model that links the unknown quantity of interest (e.g. abundance) to the observations (e.g. CPUE index), and at least one process model that represents the unobservable processes governing the population dynamics. The observation model is of particular importance in monitoring marine populations as fish are generally not observed directly but inferred from a limited number of observations (e.g. spawners, larval surveys, specific age-classes, indices of relative abundance) using a function to link the parameter of interest, such as numbers or biomass, to the observations.

2.3.1 Data Mismatch

Production models are frequently used to assess stocks in data-poor situations where only total landings and CPUE data are available. The CPUE data can be derived from fishery-independent surveys, commercial catch rate indices, or both may be included in the model, however, the latter approach requires some form of weighting factor to inform the model which time series better tracks the abundance of the population. Because it is unlikely that catch rate indices exploit the entire range and all demographic components of a population, using multiple series can fill in these data gaps.

The Schaefer form of a production model is frequently employed and can give fairly accurate estimates of stock productivity and carrying capacity when there is adequate contrast in the exploitation history of the stock (Hilborn and Walters, 1992).

The Schaefer model is:

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{K}\right) - C_t \quad (2.1)$$

where B_t and C_t denote biomass and total fishery removals (ideally all catches and total bycatch mortality from other fisheries) respectively for year t . Carrying capacity, K , is the equilibrium unfished biomass of the population prior to commencement of the fishery, and r is the intrinsic population growth rate.

An observation equation is used to link the unobserved states of the population biomass to the process model as follows:

$$I_t = \frac{C_t}{E_t} = qB_t \quad (2.2)$$

where I_t is the catch rate index at time t , C_t is the catch for the vessels used to calculate the catch rate index, E_t is the amount of effort required to produce that catch, and q is the fraction of the abundance that is captured by one unit of effort (often referred to as the catchability coefficient) and in this example is assumed to be constant throughout the index time-series (Maunder and Punt, 2004).

Numerous criticisms of the Schaefer model exist that focus on the symmetric dome-shaped production function implied by the model (Maunder, 2003), static model parameters (Hilborn and Walters, 1992), and whether the observation model component that assumes the catch rate index is proportional to biomass is realistic (Harley et al., 2001). Data mismatch, however, is rarely addressed and can occur when the catch rate index is temporally and/or spatially restricted and/or tracks a smaller demographic component of the population due to gear selectivity issues in comparison to the total fishery removal data used in the model. Fishery removals are an aggregation of all direct and indirect (bycatch) mortality incurred by a population from all gear types and fishing behaviours that impact the species of interest. Therefore, there can be spatial and demographic components of the population contained in the fishery removal data that are not present in the CPUE index. The implicit assumption when using these two data sources within the same model is that the non-overlapping components of the catch rate index and fishery removal data must have the same proportional rates of change in order for the index to be remain being

proportional to abundance. This is a similar issue presented by Kleiber and Maun-der (2008) that examined the consequences of using a multispecies aggregated CPUE and fishery removal data to track the abundance of individual stocks in multispecies fisheries. Their finding indicated that the multispecies aggregated CPUE index was hyper-responsive (i.e. would display either hyperdepletion or hyperstabilty) depend- ing on the catchability and productivity of the individual species contained within the index and fishery removal data; with hyperdepletion being more common. Once the index being used is no longer a reliable index of abundance (or biomass), infer- ence on the population trajectory and parameter estimates (r and K in the case of the Schaefer model) become difficult to interpret and likely biased. Age, or stage structured models that separate demographic components are able to more easily accommodate different proportional rates of change in the various age components of the population. Unfortunately, age-disaggregated data is frequently only available for target high-value species and not for species of low commercial importance.

2.3.2 Conflicting Data

Trends contained in commercial and fishery-independent CPUE time-series are a re- sult of many embedded processes such as environmental forcing, fishing behaviour (or survey design), gear selectivity, and different levels of observation error in addition to the population and demographic dynamics of the population being tracked (Rouyer et al., 2008). It is therefore common when multiple time-series exist that they display different and sometimes conflicting population trends due to differences in spatial or temporal coverage and other embedded process. In this situation, the assessment biologist needs to decide whether to use both indices in some way, or to choose the catch rate index that is thought to better track the demographic component of the stock of interest (e.g. spawning stock).

Incorporating multiple indices to estimate population trends can be advantageous if the two indices have important non-overlapping spatial or temporal components. For example, cusk (*Brosme brosme*) was designated as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2003 due to a 93% decline from 1970 to 2001 in the Scotian Shelf DFO summer bottom trawl survey in- dex (COSEWIC, 2003). This estimate of decline has been contested due to concerns

that because the trawl survey samples outside the preferred habitat and depth range of cusk, it is unlikely that the trawl index is proportional to biomass (DFO, 2004). In support of this concern, a commercial longline catch rate index, that is thought to better track cusk biomass because it targets preferred cusk habitat, shows a much less severe decline over the overlapping time period (Figure. 2.5). An ecological explanation for the different trends is that the trawl index suffers from hyperdepletion because it targets poor cusk habitat while the longline fishery targets deeper water rocky habitats where substantial cusk densities remain. We used both indices in a Bayesian state-space model and accommodated index non-proportionality and found evidence that the trawl index suffered from hyperdepletion, thus exaggerating estimates of biomass decline. Our median estimates were that cusk biomass declined 64% since 1970, rather than 93% as estimated in the COSEWIC assessment. By using both indices and allowing for index non-proportionality, we were able to obtain biomass estimates back to 1970 rather than being limited to 1986, the beginning of the longline index. Furthermore, if we had utilized the longline index exclusively, we would have estimated cusk decline to be 62% from 1986 to 2007 (Davies and Jonsen, 2008) rather than 52% for this time period when both indices were included. By utilizing both data sources and critically examining (and rejecting) the assumption that the indices were proportional to biomass, we were able to obtain better estimates of recent and historical biomass trends.

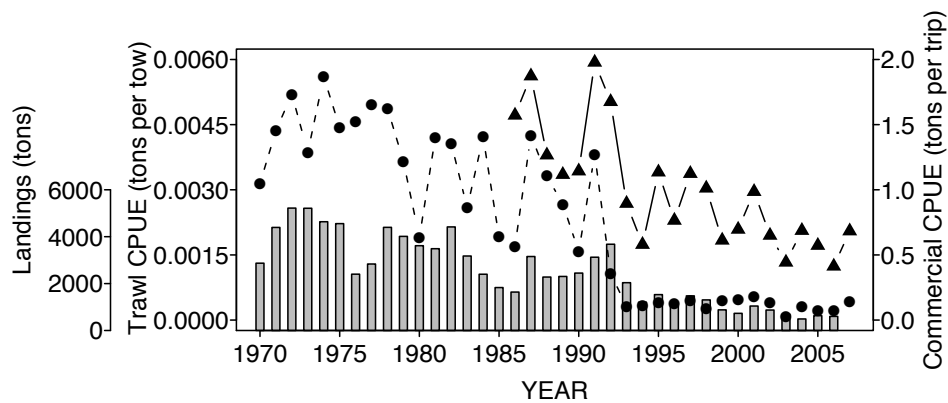


Figure 2.5: Time-series of fishery independent bottom trawl (●), and commercial longline catch-per-unit-effort (▲) indices for cusk (*Brosme brosme*) from the 4Xnopq NAFO subdivisions. Recorded landings (bars) are from the 4X NAFO division.

One of the most notorious examples of using poor assumptions when multiple catch rate indices give conflicting signals on population trends is illustrated by the the collapse of one of largest and historically relevant fisheries in the world: the Newfoundland northern cod fishery. Data available were catch-at-age data, a fishery-independent survey index, and a commercial catch rate index. The two catch rate indices gave divergent signals from 1978 to 1986, with the commercial catch rate index suggesting the stock had increased three-fold while the fishery-independent index suggested that the stock had been relatively stable over the time period (Figure 2.6). Although both indices were used in the assessment, the commercial index was weighted more heavily in setting harvest levels, even though there was little scientific justification to do so (Pennington and Strømme, 1998). The heavily weighted commercial CPUE index was later found to suffer from fairly severe hyperstability issues and the fishery-independent index that showed much lower population abundance more closely tracked stock abundance. The consequence of assuming the commercial index more closely tracked abundance was that unsustainable harvest levels were consistently set and the 400 year cod fishery collapsed. Over 20 000 people lost their livelihoods (Hilborn and Walters, 1992). This is an example to the very real human costs that can occur in fisheries when poor assumptions are made.

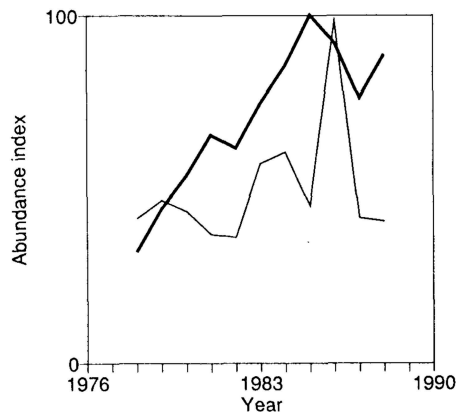


Figure 2.6: Catch per tow and commercial catch rate index for Newfoundland northern cod. Thick line is commercial CPUE, thin line is the fishery-independent survey. Figure from Hilborn and Walters (1992).

2.3.3 Power to Detect Trends

Fishery-independent surveys are increasingly being used to monitor non-commercial species because they have known survey designs, document gear changes that may change catchability, collect biological data that are frequently absent from commercial catch statistics, and may be the only source of time-series distribution and abundance data for rarer fish species and species of low commercial importance (Maxwell and Jennings, 2005). The majority of research surveys were established to monitor abundant target species that have relatively high catchability to the survey gear (Shackell and Frank, 2003). The trend towards taking an ecosystem approach to fisheries monitoring and management and increased conservation concern about non-target species has broadened the use of these surveys beyond their original focus. The distribution and range of many species is poorly understood and low catchability coupled with unknown demographic gear selectivity makes it problematic to assess many non-target species with these data (Maxwell and Jennings, 2005; Fraser et al., 2007). Increased understanding of the value and limitations of current and historical survey data is needed (Blanchard et al., 2008).

Whether a species is detected in a fish survey is a function of the sampling design, the number of samples, the efficacy of the sampling methods to detect a species within a sample unit, the abundance of the species, its habitat specificity, and its geographical range relative to survey coverage (Cunningham and Lindenmayer, 2005). Power analysis is used to estimate the probability that a test will detect a statistically significant result under different experimental design and sampling intensities (Zar, 2007) and is a useful tool for determining whether benchmarks of recovery plans of depleted species can be identified under various management scenarios and sampling designs. Trends in abundance can be obscured by high levels of observation error and year-to-year natural variation in abundance (process error). The power to detect trends can be further reduced by low population sizes, habitat patchiness, density dependent changes in distribution, and whether spatial distribution changes over time due to changes in the environment (Blanchard et al., 2008).

A simulation approach offers a method to estimate the power of different survey designs to detect changes and trends in abundance of various species by using different assumptions about their current and predicted distribution and life history

parameters. Blanchard et al. (2008) used ideal free distribution theory to model the density dependent habitat selection which is widely observed in fish populations, different levels of habitat patchiness, potential impacts of climate change, and various survey designs to estimate the power of the English North Sea Groundfish Survey to detect changes in abundance of non-target species. Their findings indicated that a single survey that only covers part of the range of a species generally has little power to detect trends in depletion and recovery or disentangle the relative impacts that fishing and the environment may be having on population abundance. For example, using a fixed stratified monitoring design, 25 years was needed to detect changes in abundance of a population with 90% certainty that was defined to be increasing at 2% per year if the species had a patchy distribution and whose range was not fully within the survey area. Under climate change scenarios where fish distribution changed over time, >30 years was needed to detect trends in abundance for patchy distributed species. This suggests that fishery-independent surveys may be of little use in tracking the recovery of depleted bycatch species whose range are only partially covered by the research surveys and have patchy distributions and whether inference about population trajectories derived from these data are valid. Unfortunately, due to limited information on the spatial distribution of many bycatch species, the true statistical power to detect abundance trends for many non-target species remains unknown (Blanchard et al., 2008).

2.4 Ways Forward

The ability to obtain precise and unbiased estimates of the population size and trajectory of marine populations is constrained by the number of assumptions required for most assessments due to the limited amounts of data available. Indeed, the number of unknowns in most assessment models typically exceeds the number of observations, and therefore numerous simplifying, and frequently untestable, assumptions are needed in the assessment process (Schnute and Richards, 2001). Many of these assumptions are easy to apply without fully realizing the consequences that they may have on the conclusions of the analysis. Applying incorrect assumptions can have large socioeconomic impacts and/or result in the depletion of vulnerable fish populations. The prohibitive monitoring cost required to monitor marine species

limits the certainty that is realistically achievable in marine population monitoring. For instance, sampling intensity needs to be increased fourfold in order to double the precision of an estimate because precision is inversely proportional to the square root of the sample size (Pennington and Strømme, 1998). The costs required to assess all marine species within levels of certainty needed to provide detailed management advice for each species would be prohibitive and logistically impractical. Consequently, the monitoring of many species or taking an ecosystem approach to fisheries management will always be within a large cloud of uncertainty and robust assessment and monitoring strategies are needed to effectively manage these populations.

The most critical assumptions used when tracking the abundance of marine populations lie in the observation component of most population models (Walters and Martell, 2004). In particular, the assumptions about the spatial and temporal distribution and movement within the range of the population of interest can have broad ramifications for population estimates. Both fisheries-dependent and fishery-independent data have the potential for introducing bias. The non-random search behaviour of commercial fishing activities can lead to over estimates of population abundance which can result in unsustainable harvest levels. Conversely, patchy distribution and lack of mixing within the range of the population of interest can cause hyperdepletion of a catch rate index and result in exaggerated estimates of population decline and result in unnecessary socioeconomic hardship and/ the loss of limited conservation funding that could have been applied elsewhere.

Collecting additional information about the spatial distribution of species can reduce the need to make as broad assumptions about the range, movement and patchiness of marine populations and be relatively low cost. Improved information on changes in distribution, which would improve estimates of abundance, could be obtained by linking presence-absence data from existing surveys and fisheries dependent data in contiguous areas (Blanchard et al., 2008). Delineating changes in range and distribution will become increasingly important as climate change has already changed the distribution of groundfish, for example, in the North Sea (Perry et al., 2005). This approach could identify changes in distribution and help to evaluate whether the proportionality assumption of catch rates derived from surveys with restricted spatial

designs is justified and whether changes in catch rates are due to changes in population abundance or simply movement of the population to outside of the survey area.

Fishery-independent data is an important source of information for the assessment of non-target marine fishes. Indeed, on the east coast of Canada, the summer bottom trawl survey that began in 1970 is the longest contiguous time-series for many commercially unimportant species on the Scotian Shelf. It is, however, important to understand the limitations of these data, both in terms of statistical power to detect trends and whether the assumption that the survey index is proportional to abundance is justified. The statistical power of analyses using these data are limited, particularly when the species under study has a range that extends outside the survey area, is patchily distributed, and has low catchability to the survey gear (Blanchard et al., 2008). The extreme costs associated with marine monitoring limits the quantity of additional effort that can be allocated to monitoring commercially unimportant species. Other data sources, such as habitat mapping and remotely sensed environmental data, can play a role in standardizing catch rate indices, identify habitat associations that cause distribution patchiness, and estimate densities outside surveyed areas in both time and space. Using habitat data to identify areas of patchiness would help delineate species specific stratification sampling designs that could reduce the variance in catch rate indices. Indeed, stratified sampling designs exist to accommodate patchiness in distributions and if these patches can be identified, statistical power to detect trends will increase.

The use of demographic methods (Dulvy and Reynolds, 2002), meta-analysis (Myers and Mertz, 1998), and Bayesian methods (Etienne and Olf, 2005), or a combination thereof (McAllister et al., 2001), are additional approaches that can be used to reduce the uncertainty in population studies of extinction risk, estimating population trajectory, and inference using the distributional assumptions of poorly sampled marine populations. Demographic approaches use theoretical life-history correlates and data from better studied species to indirectly estimate extinction risk, growth, and natural mortality rates (Dulvy and Reynolds, 2002). Basically, one infers that a population that has similar life-history characteristics will be susceptible to similar levels of exploitation and population decline. Similarly, meta-analysis can reduce

uncertainty in parameters of interest by combining data across multiple studies of different populations much the same way that replicates are used in more traditional hypothesis testing approaches (Myers and Mertz, 1998). Similarly, the Bayesian approach has commonalities to the demographic and meta-analytical approaches but also provides an opportunity to objectively address uncertainty in assumptions that can be appropriately modified through the use of priors based on quantitative data or derived from more abstract expert opinion. For example, studies that examine catchability of various species can be easily incorporated into a population assessment by specifying a prior on the catchability parameter of the population model. A Bayesian approach to population assessment allows one to admit the full range of uncertainty and use the collective experience of multiple stake holders and information obtained from demographic or meta-analytic approaches (Punt and Hilborn, 1997).

2.5 Conclusions

The ability to effectively monitor the abundance of many marine populations, and their rates of change, is limited due to generally unknown proportionality relationships of both commercial and fishery-independent catch data, relatively few sampling events when put in the geographical range of most species, low catchability to survey gear, and frequent non-static and patchy spatial and temporal distribution of many species. Many assumptions need to be employed in the estimation process that cannot be explicitly tested with data on-hand. Therefore, careful consideration of the consequences of the assumptions used, and whether they are justified by data and/or ecological theory, is critical to avoid unnecessary economic hardship, diverting limited conservation dollars away from where they are needed, and avoid population depletions contrary to desired benchmarks.

Chapter 3

Identifying Nonproportionality of Fishery Independent Survey Data to Estimate Population Trends and Assess Recovery Potential for Cusk (*Brosme brosme*)

3.1 Introduction

Fisheries stock assessments are frequently based on data intensive population dynamics models and thus generally limited to the target species of large-scale commercial fisheries Davis (2002); Kelly and Codling (2006). On the east coast of Canada, for example, stock assessments have been conducted for fewer than 5% of all marine fish species (Hutchings and Baum, 2005). Detailed life-history information and appropriate long-term catch and monitoring data required for such assessments are typically lacking for incidentally caught species (McAllister et al., 2001; Hall and Mainprize, 2005). These species may, however, experience significant incidental mortality as bycatch (Crowder and Murawski, 1998; Baum et al., 2003), and it is therefore essential that quantitative estimates of the impacts of exploitation on them are developed.

Cusk is a data-poor benthic teleost (Family Gadidae) of the north Atlantic, that is commonly caught as bycatch in benthic longline and lobster fisheries (DFO, 2004). Little is known about its life history and ecology; however, catch rates in eastern Canada's groundfish longline fishery suggest cusk prefer rocky complex habitat in relatively deep water (400 - 600 m, Oldham, 1966; DFO, 2002). Life history parameters including growth rate, natural mortality and maximum age are unknown. Cusk is principally a bycatch species in Canada and the U.S., but is frequently retained prior to landing limits being reached. In Canada, landings were unregulated until 1999, after which a limit of 1 000 t was imposed for the majority of the Scotian Shelf

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(4VWX Northwest Atlantic Fisheries Organization (NAFO) divisions). Due to increased conservation concerns, this limit was reduced to 750 t in 2003 and extended to include the Canadian portion of Georges Bank (5Zc; DFO, 2008).

Cusk was designated as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2003 based on an estimated 93% decline between 1970 and 2001 in the Fisheries and Oceans Canada (DFO) Scotian Shelf summer bottom-trawl survey index (COSEWIC, 2003). This estimate has been contested by DFO scientists because the trawl survey samples outside the preferred habitat and depth range of cusk and therefore the survey index may not be proportional to cusk population abundance (DFO, 2004). The assumption that catch rate indices are proportional to abundance is commonly made in population models, and was used in the COSEWIC assessment, despite the fact that it rarely holds (Richards and Schnute, 1986; Harley et al., 2001; Maunder et al., 2006b). Non-proportionality has been recognized to occur in commercial catch-rate data (Harley et al., 2001), however, fishery-independent data can also suffer from non-proportionality if a large component of the stock is found outside the survey area (Blanchard et al., 2008). Failure to account for non-proportionality when present, in either commercial catch rate or fishery-independent data can result in biased estimates of stock decline.

The objectives of our research were to estimate historical population trends, current status, and recovery potential of western Scotian Shelf cusk (NAFO division 4X; Figure 3.1) by using two indices of relative biomass and evaluating each of them for non-proportionality. We incorporated a fishery independent bottom-trawl survey index and a fishery dependent catch-per-unit-effort (CPUE) benthic longline index within a Bayesian state-space surplus production model and used a power curve function in the observation model to test for non-proportionality of the indices. We then used the model-derived biomass and parameter estimates in stochastic simulations to project biomass forward and assess recovery potential based on three different landing limits. Finally, we used a simulation approach to evaluate consequences of model misspecification and the advantages of using both indices to obtain unbiased parameter estimates.

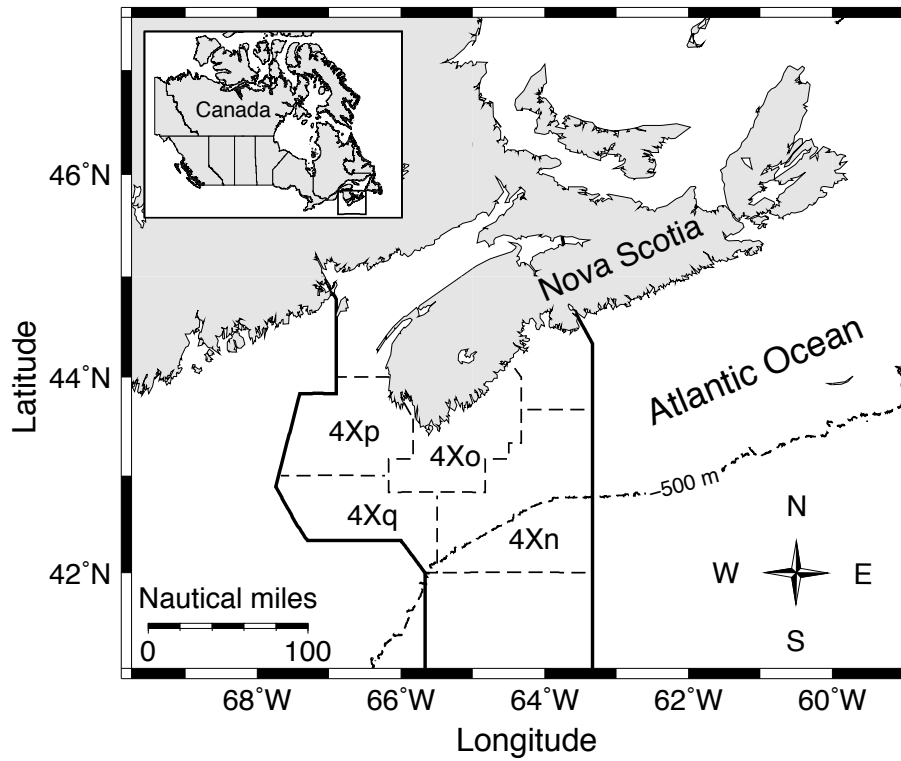


Figure 3.1: Location of study. Thick solid line is the 4X major Northwest Atlantic Fisheries Organization management unit area. Dashed lines are the minor management units from which the commercial longline index is derived. Ragged dashed line is the 500 m isobath.

3.2 Materials and Methods

3.2.1 Data

Time-series data for cusk on the western Scotian Shelf include annual reported landings and two catch rate indices of relative biomass (Figure 3.2). One index is a fishery-independent index based on the DFO summer bottom-trawl survey, and the second is a fishery-dependent index derived from the commercial groundfish longline fishery, in which cusk is bycatch. Due to insufficient data on unreported and incidental mortality, we make the assumption that reported landings are synonymous with fishery removals and are known without error.

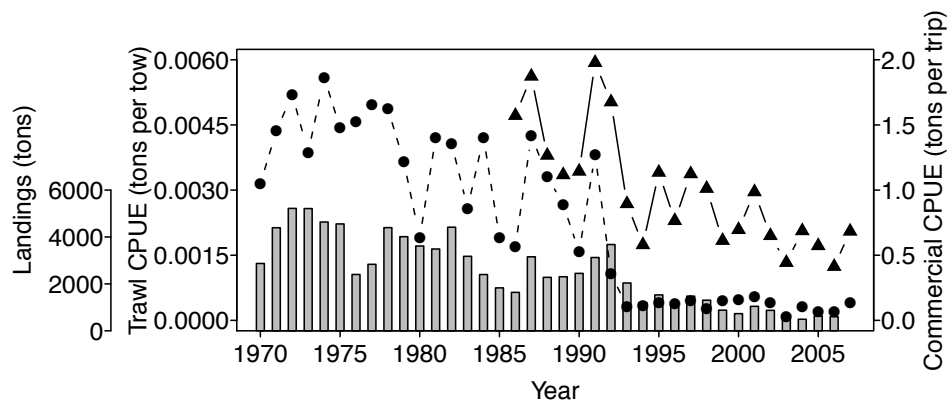


Figure 3.2: Time-series of fishery independent bottom trawl (\bullet), and commercial longline catch-per-unit-effort (\blacktriangle) indices for cusk from the 4Xnopq NAFO subdivisions. Recorded landings (bars) are from the 4X NAFO division.

The DFO summer bottom-trawl survey covers most of the Scotian Shelf and has been conducted each July since 1970. The survey follows a stratified random design with stratification based on depth and geographic area (Shackell and Frank, 2003). The stratified mean catch per standard 1.75-nmi tow is used as an index of relative biomass. We restricted the index to only include the western Scotian Shelf (4X NAFO division) so that it would cover the same region as the commercial catch rate index. Cusk catch rates in the survey have always been low because the rocky complex habitat preferred by cusk (Oldham, 1966) is poorly sampled by the survey trawl gear.

The CPUE index from the commercial groundfish longline fishery covers most of the western Scotian Shelf (4Xnopq NAFO subdivisions) and spans from 1986 to

2007. We focused on this fishery because it has the highest cusk catches in Atlantic Canada (> 95% of all cusk landings on the Scotian Shelf and Georges Bank since 1990). Catches from areas of marginal cusk habitat, such as the Bay of Fundy and shallow inshore regions were not included. The index was restricted to vessels of 25 to 149.9 gross registered tons since no effort information was available for smaller longliners in early parts of the time-series. To avoid introducing bias from landing limits being reached, we restricted the commercial catch rate index to the first three months of each year's fishing season (July to September).

Reported landings and the commercial index may be biased high in the time series. The lack of a landings limit for cusk prior to 1999 could, for example, have resulted in target-species such as cod (*Gadus morhua*) being reported as cusk when cod quotas were exceeded, thus potentially inflating the cusk landings and commercial catch rates. Because the level of misreporting could not be quantified we did not apply corrections to either time series. However, the level of misreporting, if present, in the longline fishery index prior to 1999 appears minor as the index follows the yearly catch rate dynamics in the fishery-independent trawl index over the same period (Figure 3.2).

The lack of age and/or length disaggregated data for both indices limited our choice of population models and our ability to track year class variability and population age-structure. Although age and length disaggregated information exists for the trawl survey time-series, commercial data was limited to yearly biomass and effort, and landings simply as biomass. If catch-at-age/length data were available for all the data series we could have compared the catch rates of each size class over time to better understand the relationship of each time-series to population abundance.

Population Model

Recognition of the importance of both observation error and process variability has increased the application of state-space models in the assessment of fish and endangered species in the last decade (Harwood and Stokes, 2003; Clark and Bjørnstad, 2004). State-space models differ from traditional deterministic population models in that they consist of two components: a process model, which represents the unobservable stochastic processes governing the population dynamics, and an observation model,

which describes the error structure inherent in the observations (Meyer and Millar, 1999a; Harwood and Stokes, 2003). By coupling these components in a state-space framework, the errors in the observations can be separated from natural variability in the population processes. We employed a Schaefer surplus production model (Schaefer, 1954) as our process model because there was insufficient age-disaggregated and life history data to use more complex age-structured models. Surplus production models are commonly employed when indices of relative biomass and landings are the only data available for population assessment (Hilborn and Walters, 1992). Implicit assumptions of the Schaefer model are a symmetrical surplus production curve where maximum surplus production (MSP) occurs at 50% of unfished biomass, and a population at equilibrium (Schaefer, 1954; Hilborn and Walters, 1992). The Schaefer surplus production model is:

$$B_t = \left(B_{t-1} + rB_{t-1} \left(1 - \frac{B_{t-1}}{K} \right) - C_{t-1} \right) \eta_t \quad (3.1)$$

where B_{t-1} and C_{t-1} denote biomass and catch (landings), respectively for year $t-1$. Carrying capacity, K , is the biomass of the population at equilibrium prior to commencement of the fishery; r is the intrinsic population growth rate; and η_t is a log-normal random variable with a mean of zero and variance σ^2 to account for stochasticity in the population dynamics, $\eta_t \sim LN(0, \sigma^2)$. Recruitment, growth, and natural and unreported fishing mortality are combined in the time-invariant parameter, r . All parameters are held constant over time (i.e. changes in the biotic and abiotic environment are not included) and catchability is the same for all individuals in the population.

The observation model relates the unobserved states, B_t , to the indices of relative biomass, $I_{i,t}$, that are observed with error. We incorporate both the trawl survey index and longline index in a single model by specifying a separate observation equation for each. A commonly used observation model is:

$$I_{i,t} = q_i B_t \epsilon_{i,t} \quad (3.2)$$

where $I_{i,t}$ is the relative abundance of index i at time t ; q_i is the catchability coefficient for index i which describes the effectiveness of each unit of fishing effort; and $\epsilon_{i,t}$ is a

log-normal random variable with a mean of zero and variance τ_i^2 to account for error in the observations of index i , $\epsilon_{i,t} \sim LN(0, \tau_i^2)$.

A critical assumption of Eq. 3.2 is that the catch rate indices are assumed to be proportional to biomass regardless of population size (ie. constant q). Because our data are spatially aggregated and have no age-disaggregation, the catchability parameter is a conglomeration of the three different processes governing the effectiveness of the fishing gear: availability, catchability, and selectivity. Density dependent habitat selection exhibited as range contraction to optimal habitat areas as abundance declines is observed in many exploited fish stocks (Blanchard et al., 2008). We hypothesize that as cusk biomass declined, remaining individuals retreated to optimal habitat areas where they remained available to the longline fleet but were less available to trawl gear, which is restricted to non-complex substrate that is considered to be poor cusk habitat. Unfortunately, spatially disaggregated catch rate data for the commercial fleet was unavailable to directly test this hypothesis. Rather, to account for this potential change in cusk availability to the trawl gear, we relaxed the assumption of constant catchability by adding a shape parameter to the observation model. This power curve relationship between the catch rate indices and population biomass allows catchability to change as population biomass changes. Catchability then becomes a function of q and β , (catchability = $qB^{\beta-1}$ (Harley et al., 2001)). Our observation model becomes:

$$I_{i,t} = q_i B_t^{\beta_i} \epsilon_{i,t} \quad (3.3)$$

where β_i is a shape parameter for index i .

Equation 3.3 reduces to Eq. 3.2 when $\beta = 1$. In the context of population declines, $\beta < 1$ implies the catch rate index declines more slowly than population biomass, a condition known as hyperstability (Figure 3.3). Hyperstability occurs in many commercial catch rate indices (Harley et al., 2001) and can be the result of the non-random search behaviour of fishers and/or schooling behaviour or range contraction of target species (Rose and Kulka, 2000). Assuming proportionality of a hyperstable index can result in underestimates of exploitation rate and total population decline (Hilborn and Walters, 1992). Conversely, hyperdepletion occurs when $\beta > 1$ and describes the situation where the catch rate declines faster than population biomass (Figure 3.3).

This can occur when fishing effort is concentrated on a subset of the population that may be depleted, while a significant subset of the population remains unaccounted for in the catch rate index (Quinn and Deriso, 1999). For example, the fixed area design of fishery-independent surveys can potentially result in a hyperdepleted catch rate index if the core density of a species is outside the survey area and species specific processes such as density dependent habitat selection results in incomplete mixing of the population within its full range (Blanchard et al., 2008). Assuming a hyperdepleted index is proportional to biomass can result in overestimates of population decline and exploitation rate (e.g., Myers and Worm (2003) as pointed out by Walters (2003), Maunder et al. (2006b) and Sibert et al. (2006)).

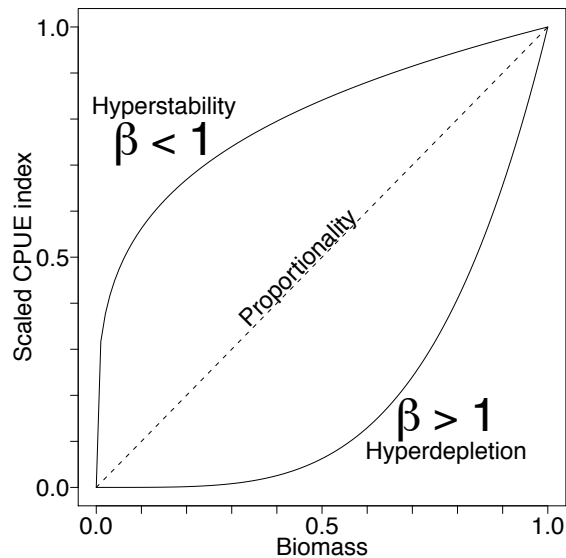


Figure 3.3: Three possible power curve relationships of catch-per-unit-effort and biomass. Figure adapted from (Hilborn and Walters, 1992).

Four variants of the observation component of the surplus production model were compared: (1) both indices fixed to be proportional to biomass (ie. $\beta = 1$); (2) shape parameters estimated for both indices; (3) the longline index fixed to be proportional to biomass and a shape parameter estimated for the trawl index; and (4) the trawl index fixed to be proportional to biomass and a shape parameter estimated for the longline index.

We implemented the state-space models in WinBUGS (version 1.4.3, Lunn et al., 2000) via the R2WinBUGS package (Sturtz et al., 2005) in the statistical programming environment R (R Development Core Team, 2008). WinBUGS uses a Markov Chain Monte Carlo (MCMC) approach to estimate the joint posterior distribution of the model parameters. Marginal posterior distributions of model parameters and unobserved states were based on 300 000 iterations of two chains after discarding the first 260 000 iterations (burn-in). These 40 000 iterations were reduced to 2 000 by sampling every 20th value to reduce sample autocorrelation. Models were considered to have converged when the potential scale reduction factor \hat{R} was < 1.2 for all parameters (Brooks and Gelman, 1998). See Appendix A for WinBUGS code.

3.2.2 Priors

A potential advantage of the Bayesian approach is that other sources of information can be incorporated into the analysis in the form of priors (Gelman et al., 2004). Unfortunately, since little is known about cusk ecology or its catchability on trawl or longline gear, we were limited to relatively broad flat priors (Table 3.1). We specified a vague prior for carrying capacity, K , using a uniform distribution with a lower boundary of the maximum reported landings of 5 219 t and an upper boundary of 500 000 t. Although the upper boundary is greater than reasonable predictions for K , it was used to ensure that some probability density would be present in unlikely, although possible estimates of K . The purpose of this prior was to restrict the parameter search away from mathematically possible yet biologically implausible parameter combinations (e.g. a high estimate for r coupled with an extremely low estimate for K). We made the assumption that the cusk population at the beginning of the trawl index (1970) was equal to K with an error distribution equal to the estimated process error because the trawl catch rate was relatively stable from 1970 to 1980, and estimating, rather than specifying B_0 , increases confounding in the model parameters (Hilborn and Walters, 1992). Furthermore, the low contrast and “one-way-trip” trends exhibited by both the survey and commercial data make estimating B_0 as a free parameter difficult. Estimates of absolute decline therefore need to be viewed in the context of this assumption.

Parameter	Prior
r (intrinsic growth rate)	uniform(0,4)
K (carrying capacity; tons)	uniform(5219, 500000)
σ^2 (Process error variance)	uniform(0, 100)
τ^2 (Observation error variance)	uniform(0, 100)
q (Catchability coefficient)	uniform(0,1)
β (Shape parameters)	uniform(0.01,10)

Table 3.1: Summary of specified priors for Bayesian state-space model

We considered including an informative prior for the shape parameter, β . Harley et al. (2001) obtained maximum-likelihood estimates of shape parameters for commercial catch rate indices of flatfish, cod and other gadiformes and found strong evidence of hyperstability in many indices. This property likely arose because of the searching and targeting behaviour of fishers for these target species (Hilborn and Walters, 1992). We did not incorporate their findings into our analyses because cusk is taken primarily as bycatch, and there was weak a priori reason to expect hyperstability in the commercial catch rate index.

3.2.3 Model Selection & Sensitivity

We used two methods for model selection and to evaluate model fit. First, we utilized the estimated deviance information criterion (DIC) which penalizes model complexity and a lower score identifies a better model fit. Second, we conducted a retrospective analysis by omitting the last seven years of the biomass indices (but retained the landings data) and checked the model’s ability to predict the missing data by projecting the model forward seven years (e.g. (Gelman et al., 2004; Snover, 2008b)). The decision to omit seven years was largely arbitrary, however, we felt that seven years was a good balance between retaining enough data for representative model fits and evaluating the predictive ability of the model. We used this approach to determine how well each model could predict future states and to assess the robustness of the parameter estimates. This approach also had the added benefit of evaluating the robustness of the recovery scenarios under different future catch rates. Lastly, we evaluated the sensitivity of parameter estimates to alternative specifications of the r and error variance priors for the model that received the most support according to

the two criteria described above to ensure that the Bayesian analysis was not driven by the priors (McAllister et al., 2001). Therefore, we re-fit Model 3 with either log-normal priors with a mean of 0.25 or 1.0 and a variance of 1.0 for r and normal priors with a mean and variance of 1.0 for the process and observation error variances (σ^2 , τ_L^2 , and τ_T^2).

3.2.4 Biomass Projections

Biomass was projected into the future to evaluate if the current landing limit of 750 t is sufficient to allow for population recovery. Because the error associated with the observation process has no effect on the true population biomass, the state-space approach can be particularly useful when generating biomass projections using model derived population parameters. Indeed, if observation error is significant, and simply combined with process error, the uncertainty of population projections can be overestimated and potentially biased (Dennis et al., 2006).

Three catch landings levels were evaluated: 0, 750, and 1 500 t per year. Projections were done in R using a stochastic simulation approach with the retained MCMC parameter realizations (B_{2007} , r , K , σ) from the joint posterior probability distribution of the model that assumed the longline index was proportional to biomass but estimated a shape parameter for the trawl index (Model 3 because this model received the most support according to the criterion described above). We changed modeling platforms for the projections due to the lack of programming flexibility in WinBUGS and because the lognormal distributional assumption of the population in the retrospective model can become invalid at unsustainable specified catch levels. We generated five process error deviated biomass realizations per year using the retained associated parameter realizations (n=4 000 after burn-in and thinning; for a total of 20 000 biomass estimates per year). Population realizations were fixed to zero once they became extinct.

The equilibrium assumption of the Schaefer model means that a change in exploitation rate will result in an immediate change in the population growth rate, thus potentially omitting important ecological processes such as recruitment time-lags and changes in population growth rate resulting from an altered age structure.

Consequently, projections will likely overestimate biomass increases in response to reductions in fishing mortality.

3.2.5 Simulations

We used a simulation approach to investigate the consequences of model misspecification on the parameter and biomass estimates, and to quantify the advantage of including both indices of relative biomass, rather than just one (Table 3.2). To retain features of our best estimates of the true biomass trajectory, the landings data, and index histories for this particular stock, we employed a method akin to a parametric bootstrap by taking the median biomass estimates obtained from Model 3 as the true biomass trajectory for our simulations. We created our simulated indices of relative biomass (spanning 1970 to 2007 and 1986 to 2007 for the simulated trawl and long-line indices, respectively) by multiplying the median yearly biomass estimates by the estimated catchability coefficients for each index. We generated two indices for the trawl index, one that was proportional to biomass, and a hyperdepleted index that had a power curve relationship with a defined shape parameter of $\beta = 2.5$. Small amounts of observation error ($\tau = 0.1$) were added to each index for efficient MCMC sampling. We kept the observation error low as we wanted to observe the effects of model misspecification on the parameter estimates and not have the results obscured by noise in the observation process. To aid in comparison between models, the same random seed was used to generate observation noise for the proportional and non-proportional trawl indices.

3.3 Results

3.3.1 Model Summaries & Trends

In all four models, posterior distributions for r and K were correlated and had a strong positive skew. Both of these features were expected as r and K are frequently confounded in a Shaefer model (Haddon, 2001) and the positive skew arises from the defined log-normal distribution of the biomass parameter. Regardless, all models passed convergence diagnostics. Model 1, in which both indices were defined to be proportional to biomass, did not fit the data well. This is evident by the lack of fit

Scenario		Data			
ID	Model assumptions	P_{longline}	P_{trawl}	S_{trawl}	Landings
Model 3	Parameter estimates from Model 3	-	-	-	-
A	Trawl survey assumed proportional		✓		✓
B	Trawl survey assumed proportional			✓	✓
C	Longline index assumed proportional	✓			✓
D	Both indices assumed proportional	✓	✓		✓
E	Both indices assumed proportional	✓		✓	✓
F	Both indices assumed non-proportional	✓		✓	✓
G	Trawl survey assumed non-proportional & longline index assumed proportional	✓		✓	✓

Table 3.2: Summary of data and scenarios used for simulation evaluation. Two simulated trawl indices were created, one that is proportional to biomass (P_{trawl}), and another that is hyperdepleted and follows a power curve ($\beta=2.5$; S_{trawl}). Both span from 1970 to 2007. The simulated longline series is proportional to biomass and spans 1986 to 2007 (P_{longline}).

to the trawl index early in the time series and the underfitting during the transition period of high to low biomass in the early 1990s (DIC: -436; Figure 3.4a & Figure 3.5a). The model accounted for the lack of fit by estimating a large observation error variance (τ_T^2) for the trawl index (Table 3.3). Posterior density plots indicated that there was sufficient information to estimate the r and K parameters (Figure 3.6a & b).

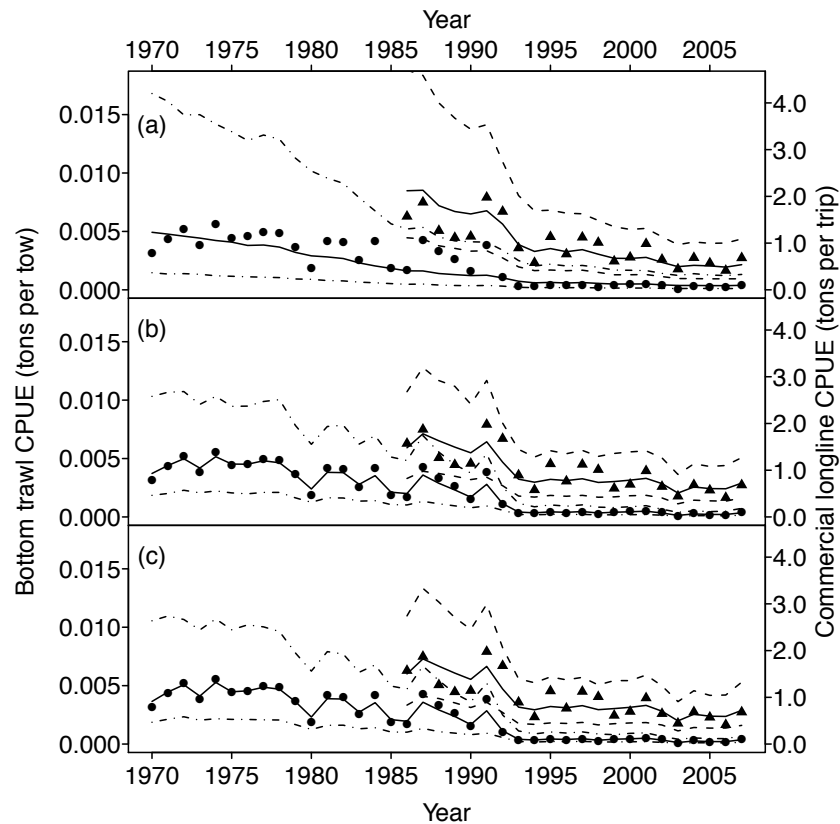


Figure 3.4: Surplus production model fits to commercial longline catch-per-unit-effort (\blacktriangle) and fishery-independent bottom trawl (\bullet) indices. Panel (a) assumes both indices are proportional to biomass (Model 1); Panel (b) Estimated shape parameters (β_i) in the observation equation for both indices (Model 2); Panel (c) is fit of model assuming commercial longline index is proportional to biomass and estimates a shape parameter for the bottom trawl survey (Model 3). Solid and dashed lines are median and 95% credible limits, respectively.

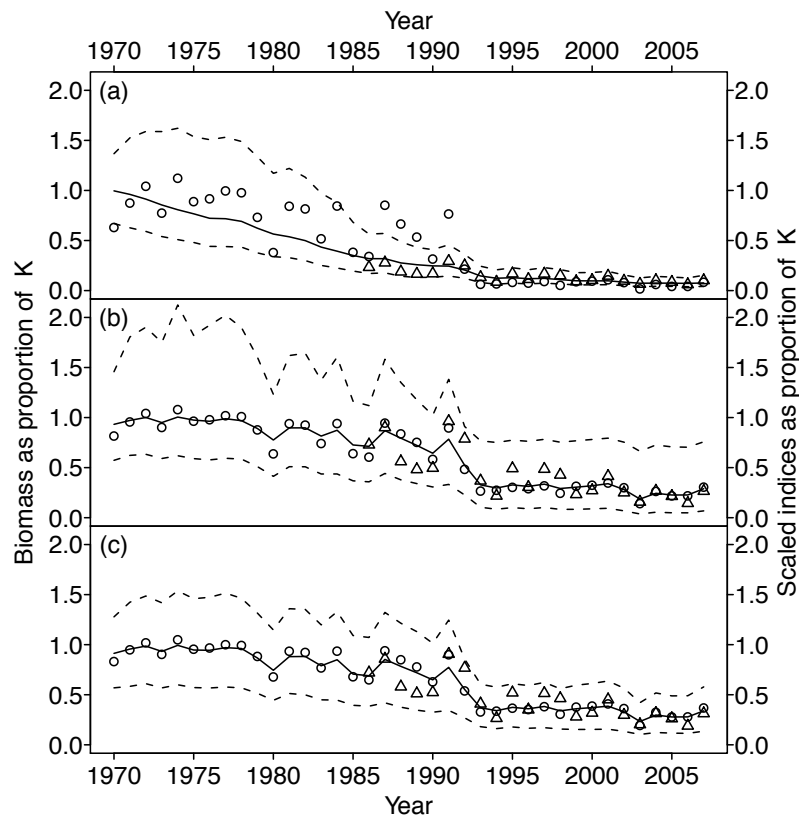


Figure 3.5: Biomass as proportion of carrying capacity (B_t/K) estimates from surplus production model fit to commercial longline catch-per-unit-effort (Δ) and fishery independent (\circ) bottom trawl indices. Panel (a) assumes both indices are proportional to biomass (Model 1); Panel (b) Estimated shape parameters (β_i) in the observation equation for both indices (Model 2); Panel (c) is fit of model assuming commercial longline index is proportional to biomass and estimates a shape parameter for the bottom trawl survey (Model 3). Observations have been scaled, where appropriate, by the estimated catchability coefficient ($q_{\text{longline}}; q_{\text{trawl}}$) and shape parameter(s) ($\beta_{\text{longline}}; \beta_{\text{trawl}}$) for each index. Solid and dashed lines are median and 95% credible limits, respectively.

Parameter	Model 1			Model 2			Model 3		
	2.5%	median	97.5%	2.5%	median	97.5%	2.5%	median	97.5%
Intrinsic rate of pop. growth (r)	0.015	0.149	0.505	0.007	0.126	0.555	0.007	0.115	0.362
Carrying capacity (K ; tons)	24750	53270	126708	20480	57225	232605	24399	51580	192013
Biomass in 1970 (B_{1970} ; tons)	22477	53670	124902	14810	53900	235223	18470	47430	190718
Biomass in 2007 (B_{2007} ; tons)	1721	4204	10440	2248	15565	137713	5371	16900	85271
B_{1970}/K	0.67	1.00	1.37	0.57	0.93	1.46	0.57	0.91	1.28
B_{2007}/K	0.04	0.08	0.15	0.07	0.29	0.76	0.14	0.34	0.58
Longline catchability (q_L)	5.1×10^{-5}	1.3×10^{-4}	3.1×10^{-4}	8.0×10^{-6}	3.6×10^{-5}	1.2×10^{-4}	8.9×10^{-6}	4.2×10^{-5}	1.3×10^{-4}
Trawl catchability (q_T)	3.8×10^{-8}	9.4×10^{-8}	2.3×10^{-7}	1.5×10^{-8}	8.4×10^{-8}	3.6×10^{-7}	1.6×10^{-8}	9.6×10^{-8}	4.0×10^{-7}
Process error variance (σ^2)	0.00	0.02	0.14	0.00	0.04	0.25	0.01	0.03	0.09
Longline Obs. error variance (τ_L^2)	0.02	0.09	0.27	0.03	0.06	0.14	0.03	0.06	0.14
Trawl Obs. error variance (τ_T^2)	0.18	0.32	0.57	0.00	0.09	0.26	0.00	0.08	0.27
Shape parameter for longline	-	-	-	0.35	0.83	3.49	-	-	-
Shape parameter for trawl	-	-	-	1.00	2.06	8.61	1.62	2.48	3.60
Max. surplus prod. (MSP; tons)	340	2005	4012	153	1846	6486	142	1538	5281
Biomass giving MSP (B_{MSP} ; tons)	12380	26635	63373	10240	28615	116302	12200	25790	96025
B_{2007}/B_{mSP}	0.08	0.15	0.31	0.14	0.58	1.52	0.27	0.68	1.16
DIC		-436			-522			-577	

Table 3.3: Summary of posterior quantiles of parameters for Models 1, 2 and 3.

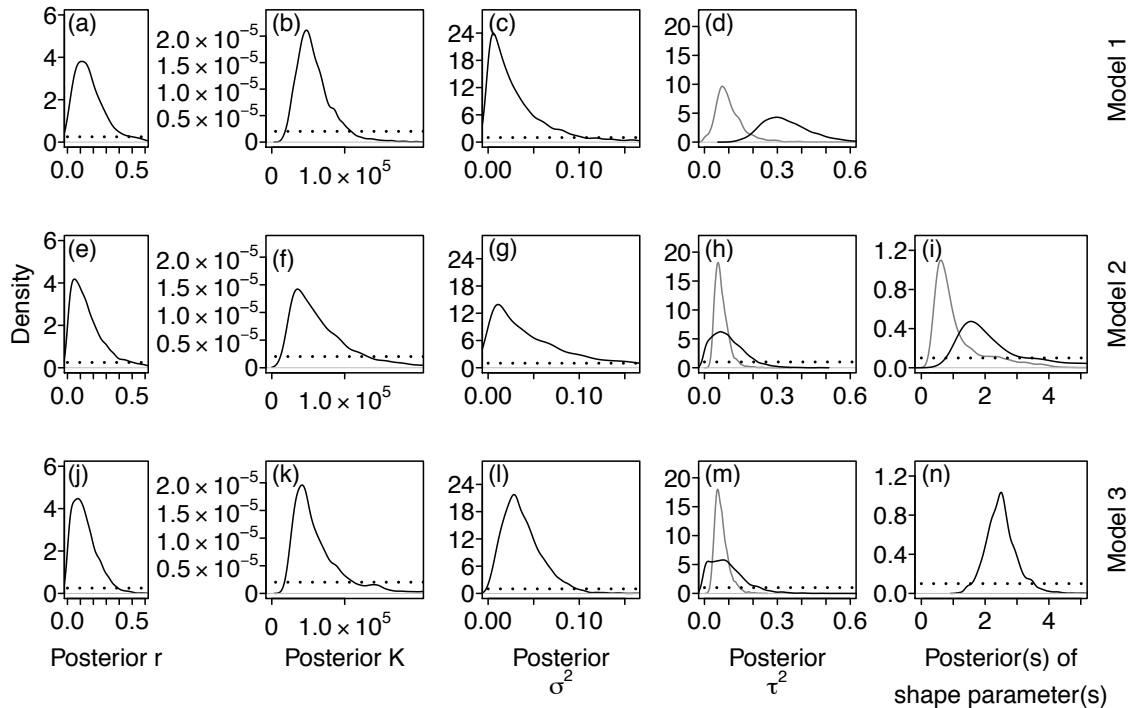


Figure 3.6: Posterior density plots of select model parameters (solid lines) for: (a) Model 1 which assumed both indices were proportional to biomass, (b) Model 2 which estimated a shape parameter for both indices where the dashed and solid line are the posteriors for the shape parameters for the commercial longline catch-per-unit-effort and fishery-independent trawl indices respectively; and (c) Model 3 that estimated a shape parameter for the trawl survey only. Priors are identified as dashed lines.

Estimating shape parameters for both indices (Model 2) improved the model fit (Fig.3.4b; DIC: -522). The credible limits of the biomass estimates contained all of the scaled index values. The credible limits were also substantially wider than in Model 1 due to the increased uncertainty in K (Figure 3.5b). The median of the posterior for r , although slightly smaller, was similar to Model 1 and credible limits were slightly larger. Conversely, the median of the posterior for K was slightly larger but the upper 95% credible limit was almost double that estimated by Model 1 (Table 3.3). Observation error for both indices was smaller than Model 1, and the estimated observation error for the trawl index was larger than the longline index. Although there was overlap in the posterior densities of the shape parameters, both were identifiable and the modes of the posterior densities were well separated (Figure 3.6i). The median estimate for the longline index shape parameter was 0.83, however,

about 62% of the probability density of the posterior was less than 1.0 which suggests weak evidence that the index is hyperstable. Conversely, the median estimate for the trawl index shape parameter was 2.06 and 97.5% of the probability density was greater than 1.0 suggesting substantial hyperdepletion in the trawl index. The results from Model 2 suggested that a more parsimonious model, in which a shape parameter is estimated for the trawl index only, would result in a comparable model fit, and indeed Model 3, with one less parameter, had the most support (DIC: -577). Model fit to the observations was similar to Model 2 (Figure 3.4c); however, yearly biomass estimates had tighter credible limits and still contained all scaled trawl and longline index values (Figure 3.5c). Estimates of observation error for both indices were virtually identical to Model 2. The range of uncertainty in K was greater compared to Model 1 but less so than Model 2. In contrast, the credible limits of r were much more narrow, yet the median estimate was similar to both Model 1 and 2. The model estimated greater hyperdepletion in the trawl index compared to Model 2 and the posterior of the estimated shape parameter was well defined and had less skew (Figure 3.6n). We estimate a 59% decline in cusk biomass between 1970 and 2001, a 64% decline from 1970 to 2007 and estimate stock biomass to be at 68% of maximum surplus production under Schaefer model assumptions (MSP, Table 3.3) in 2007.

Model 4, in which a shape parameter was estimated for the longline index only, had the least support of all shape parameter models (DIC: -497). Severe hyperstability was estimated in the longline index (median: 0.41) and process error was substantially larger than all other shape models (plots not shown).

3.3.2 Model Sensitivity

We evaluated the robustness of the model fits and parameter estimates for Models 1 to 3, and further tested Model 3 against alternate forms of the r prior. Omitting the last seven years of data had little effect on the estimated parameters; however, the predicted observations for both indices were all greater than the omitted data for all models (Figure 3.7). Alternate forms of the r prior for Model 3 had relatively little effect on either the model fit or parameter estimates. Indeed, the more informative of the alternate log-normal priors, which had a mean and variance of 1.0, only changed the median posterior estimate of r from 0.115 to 0.122 (95% credible limits of 0.03 -

0.35), which is very similar to the original Model 3 that had a flat r prior (Table 3.3). Similar minor changes to the parameter estimates were observed when we replaced the flat priors with informative normal priors with a mean and variance of 1.0 for σ^2 , τ_L^2 , and τ_T^2 . The median estimates for Model 3 became r : 0.124, K : 48 075, σ^2 : 0.036, τ_L^2 : 0.064, and τ_T^2 : 0.085 which are very close to those estimated when flat priors were used (Table 3.3).

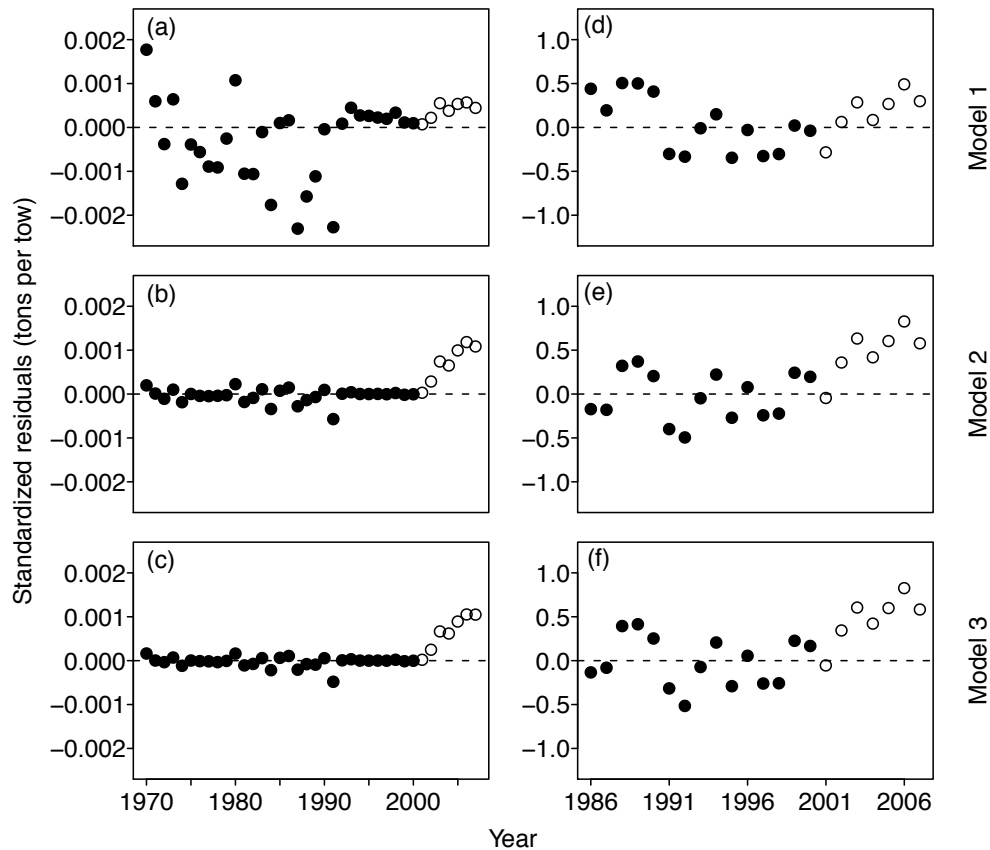


Figure 3.7: Standardized residuals of predicted catch rates with the last seven years of observation data removed. Solid circles (\bullet) are for years where observation data are present (1970 to 2000) and open circles (\circ) are where no observation data other than fishery removals are included (2000 to 2007). Panels a to c are for the fishery independent trawl index, and d to f are for the commercial longline catch rate index.

3.3.3 Biomass Projections

Population projections using the derived parameter estimates from Model 3 suggest that the current landing limit of 750 t is sustainable and should result in a biomass

increase (Figure 3.8), however, robustness test indicate a bias in predicted recovery rates and the biomass predictions are likely overly optimistic (Figure 3.7). The projection predicts a median biomass increase to 50% of K by the end of the 15-year projection period, which equates to the biomass level that would give MSP under Shaefer model assumptions. In terms of risk, 4% of projected populations went extinct after 15 years at this landings limit. Terminal biomass estimates had wide credible limits due to the large uncertainty in the parameter values and stochastic nature of the projections. Indeed, some realizations of the joint posterior distribution for the r parameter were close to zero (3.7% were < 0.01) resulting in very little biomass production during the projection period. A landings limit of 1 500 t was clearly unsustainable with 30% of the simulated populations going extinct after 15 years. Reducing landings to zero resulted in predicted biomass increases to 70% of K after 15 years. An obvious limitation of the projections is that they are based on equilibrium conditions, which do not account for the age-structure of the population or recruitment time-lags. Furthermore, the robustness tests suggest that the models have poor predictive ability and tend to over predict biomass increases.

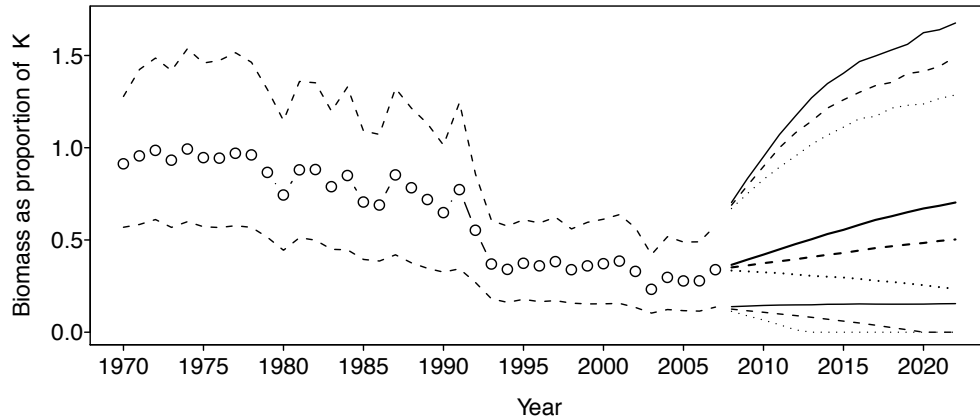


Figure 3.8: Stochastic projections using parameter realizations from the surplus production model that estimated a shape parameter for the trawl survey and assumed the longline index was proportional to biomass (Model 3). Solid and dashed lines are median and 95% credible limits, respectively of biomass estimates corresponding from high to low to catch levels of 0, 750, and 1500 tons per year.

3.3.4 Simulations

Simulations provided a clearer picture of the benefits of including both indices and the consequences of model misspecification on parameter estimates. Beanplots comparing posteriors of the parameter estimates between Model 3 and the simulated data reveal that model misspecification can cause large biases in initial and terminal biomass estimates and including both indices improved the precision of parameter estimates. As with the models in the primary analysis, all models using simulated data had negative mean deviance, pD , and DIC.

The biomass trajectory derived from Model 3 is the basis for all the simulated data scenarios and is the baseline for comparison to all simulations (Table 3.2). Both posteriors in the Model 3 column are identical, and hence, the beanplots are symmetrical. The parameter estimates for Scenario A show that even when the model assumptions are consistent with the data, a single proportional index spanning the entire time-period (38 years) had insufficient power to fully recapture the parameters of interest (Figure 3.9). Scenario B describes the model fit that assumed proportionality to a single 38-year hyperdepleted index and had similarly diffuse posteriors for r , K , and B_0 as scenario A, however, the biomass estimate for 2007 was lower compared to both Model 3 and scenario B (Figure 3.9).

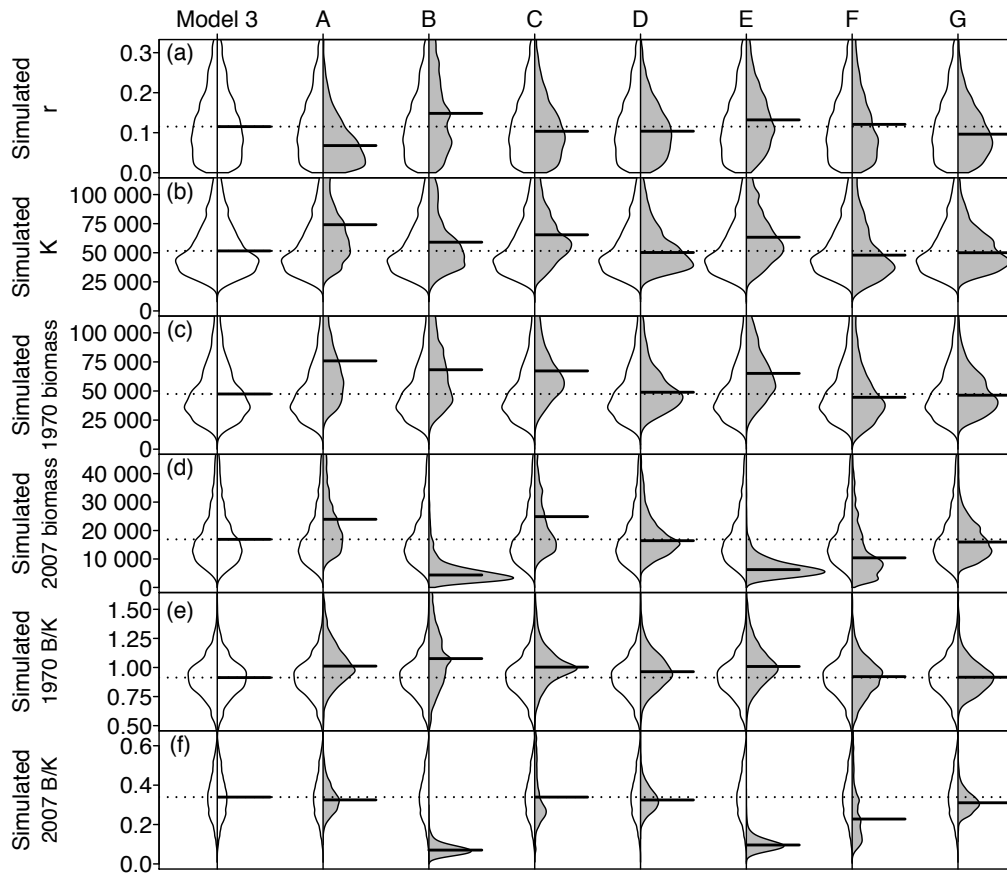


Figure 3.9: Select model parameters from simulation models. Beanplots (Kampstra, 2008) compare the posteriors of select model parameters from Model 3 (white) to the posteriors from alternate model scenarios (grey posteriors in columns B to G) which use simulated indices of relative biomass derived from the median biomass trajectory estimated from Model 3. The horizontal dotted line is the median of posteriors of select model parameters from Model 3. The thick solid horizontal lines are the medians of the posteriors of the alternative model and data scenarios. Rows are estimates of: the intrinsic rate of population increase, r , carrying capacity, K , biomass in 1970 and 2007, and the ratio of biomass divided by K . Model assumptions and data used are summarized in Table 3.2.

A single proportional index spanning only the last 22 years (Figure 3.9; scenario C), akin to only using the longline index and landings data, leads to similarly diffuse parameter estimates as those obtained by only using a single longer time series (scenario A). However, the B/K ratios were less biased compared to scenario A although median estimates for K and biomass estimates were still biased high compared to Model 3 (Figure 3.9). This is likely a symptom of both the lack of CPUE data prior to 1986 and possible limitations of the Schaefer process model to fully capture the population dynamics. According to Schaefer model dynamics, the substantial landings prior to 1990 should have resulted in a decline in biomass during this period if the population was starting at carrying capacity. This was not observed in the simulated trawl survey data (which closely resembles the true trawl data; Figure 3.2). Indeed, although some biomass decline was observed, the trawl survey declines only slightly, far less than should have been observed if the population was following Schaefer dynamics. The lack of observation data in the earlier years allows the model to fully follow Schaefer dynamics earlier in the time series thus making K and initial biomass larger than what is estimated by the model that used both datasets. Using two indices which were proportional to biomass and modeled as such, allowed us to recapture the parameters of interest (Figure 3.9; scenario D); both the posteriors and medians were almost identical to that of Model 3. The median of the posterior for r was slightly lower than the reference model (0.104 compared to 0.115) which is likely due to MCMC noise and/or the observation error introduced to the simulated indices. In contrast, when the simulated trawl index is hyperdepleted and the shorter index is proportional to biomass, yet we do not account for non-proportionality in the model (scenario E), the posteriors of K and 1970 biomass were almost identical to those of Scenario B, which only used a simulated hyperdepleted trawl index, indicating that the trawl index is driving the estimates of these two parameters (Figure 3.9E).

Scenario F had the same data characteristics as scenario E but estimated a shape parameter for both indices. The model was able to obtain better parameters estimates in comparison to scenario E with the exception of the 2007 biomass estimate which was approximately 70% of the true value (Figure 3.9F). The medians of the shape parameters were 0.81 (95% credible limits of 0.45 - 3.65) for the simulated proportional longline index and 1.99 (95% credible limits of 1.13 - 8.93) for the simulated

hyperdepleted trawl index both of which are very similar to those estimated by Model 2 in our primary analysis (Table 3.3). Finally, we were able to recapture the parameters of interest when the longer time-series was non-proportional and we included non-proportionality in the model (Figure 3.9G). Similar to Scenario D, which correctly matched the model assumptions to the proportionality of the simulated data, the median of the posterior of r was slightly lower than the reference model. The model was able to estimate the non-proportional shape parameter close to its defined value of 2.5 (median $\beta = 2.44$).

3.4 Discussion

By using a Bayesian state-space modeling approach in WinBUGS, we were able to combine multiple indices in a single population model and identify and accommodate index non-proportionality, thereby improving estimates of cusk population trends and current status. There was weak evidence for non-proportionality of the commercial longline index, however, model fits substantially improved when a shape parameter was estimated in the observation equation of the trawl index, suggesting hyperdepletion of the trawl survey index for cusk. Using Model 3 as a baseline for the “true” biomass trajectory we determined that including both indices in the model resulted in more precise and unbiased parameter estimates, and yielded better biomass estimates in the terminal and beginning years of the indices. COSEWIC’s estimate of decline was primarily based on decline observed in the trawl survey index and assumed it was proportional to biomass. Our median estimates of decline of 59% between 1970 and 2001, and a 64% decline from 1970 to 2007, while still substantial, are much less severe than the 93% decline from 1970 to 2001 estimated in the COSEWIC assessment that used the raw index data (COSEWIC, 2003). However, because our biomass estimates are smoothed by the model and determining percent declines from raw index data can be unreliable, to make the estimates of decline of the two analyses more comparable we ran the model using only the survey data and estimated a median 89% decline from 1970 to 2001 assuming the index was proportional to biomass. Use of the longline index alone, also leads to overestimates of cusk decline: a decline of 81% from 1970 to 2007, and 63% from 1986 to 2007 compared to 52% for this time period when both indices are used and non-proportionality of

the survey index is included in the model (i.e. Model 3). Our lower estimate of decline will likely not have an impact on the COSEWIC designated status for cusk. Although the estimated decline is less severe, the new aging analyses, although preliminary, suggest that generation time is approximately 15 years, rather than 9, as cited in the COSEWIC report (COSEWIC, 2003). A decline of 64% in 2.5 generations is sufficient to warrant Threatened status under the COSEWIC guidelines (COSEWIC 2009). Accounting for non-proportionality can substantially improve estimates of population trends, however, our simulations highlight that caution needs to be applied when using estimates of index non-proportionality from other analyses. For example, in Scenario F of our simulations, 70% of the probability density of the estimated shape parameter for the simulated longline index was less than 1.0 (median 0.81), even though the index was simulated to be directly proportional to biomass. This is an indication that there is confounding in the estimation of multiple shape parameters and thus using shape parameter estimates as informative priors in other analyses could lead to biased biomass trajectories. Furthermore, in our primary analysis, Model 4 had a median shape parameter estimate 0.41 and had more DIC support compared to Model 1 that assumed both indices were proportional to biomass. This estimate of hyperstability is far more severe than those estimated for directed commercial fisheries (Harley et al., 2001) and is therefore unlikely for a bycatch species such as cusk. Therefore, when specifying a model with shape parameter(s), it is important to consider whether there is an a priori reason to expect non-proportionality in the indices.

Our simulation models also show that including multiple indices substantially increases power to recapture parameter estimates when non-proportionality is accounted for in the model when, and if, present in the data. We also discovered that DIC alone may not be a reliable metric for some Bayesian state-space model applications. An additional model we preliminarily tested, but is not described in the manuscript, was to test for a knife edge change in catchability in the trawl survey in 1992 when the survey trawl index rapidly declined. According to DIC, this model had the most support using both the real and the simulated data even though in the latter case we specified that a change in catchability was not responsible for the declines.

This underscores the importance of using simulated data to investigate further the plausibility of the models.

We have shown that simply assuming the trawl survey index to be proportional to biomass can result in incorrect estimates of population change. This is of concern because this trawl survey is being used increasingly for population assessments of by-catch species because it is frequently the only source of long-term fishery-independent time-series data on the east coast of Canada. Non-proportionality may be an issue for any species whose distribution is not well represented in the trawl survey design. While it maybe tempting to discard indices that have questionable proportionality relationships in favor of other time-series data with known relationships to population biomass, this approach is unsatisfactory for a number of reasons. First, the index to biomass relationship is poorly known for most bycatch species and choosing one index over another will likely be ad hoc. Second, the potentially non-proportional index may be the longest time-series available and other indices may have little contrast and only begin after population declines have already occurred. Discarding long time-series has the potential to create shifting baselines (Pauly, 1995) where current estimates of population status are viewed from a recent perspective. This can lead to underestimates of population decline (Rosenberg et al., 2005). Even with the inclusion of these relatively long time-series data, a lack of baseline data will still be a challenge because they began on the east coast of Canada in 1970, which is well after large scale industrial fishing began.

Although we were limited to using broad flat priors in this analysis, the Bayesian approach allows for ancillary information to be incorporated through the priors to reduce uncertainty in the parameter and biomass estimates and hence is particularly useful for data-poor species (Chaloupka and Balazs, 2007; Swain et al., 2009). For example, demographic methods can be used to construct a prior for r (McAllister et al., 2001). We abandoned efforts to develop an informative r prior as the dearth of life history data and current uncertainty in aging would have resulted in a highly diffuse and bi-modal prior that would have added little to the analysis. Indeed, preliminary radio-carbon bomb calibration of cusk otoliths suggest that 95% of cusk are mature by 15 years and maximum age may be over 40 (P. Comeau personal communication, 2008; Marine Fish Division, Bedford Institute of Oceanography, Fisheries and

Oceans Canada, Box 1006, 1 Challenger Drive Dartmouth, NS B2Y 4A2 Canada), which is twice that of earlier estimates (COSEWIC, 2003). Developing a credible prior for carrying capacity is also problematic as the true historical biomass of cusk before the onset of fishing will never be known with much precision. However, a joint posterior probability plot (not shown) of the r and K parameters indicate substantial confounding between the two. Although this can cause problems for parameter estimation, it also means an informative prior on r also provides information for the K parameter as well (McAllister et al., 2001).

The stochastic projections suggest that the current landing limit of 750 t should be sufficient to increase population biomass. However, the retrospective analysis we conducted by removing the last seven years of data indicate that biomass should have increased over the last seven years but this has not been observed. This suggests that our projections have limited value for determining if biomass increases should be expected at the current landing limit and calls into question the utility of our parameter estimates for predicting population recovery. The lack of recovery may be due to a number of factors. First, landing limits may be ineffective because of high bycatch mortality. Although landing limits were designed to reduce fishery induced mortality, they may be ineffective because, as a relatively deep water species, cusk may suffer substantial barotrauma when captured. There are no estimates of bycatch mortality in the longline fishery, but estimates in the lobster fishery, which operates at similar depths, are >50% (DFO, 2008). In our analyses, we equated landings with fishery removals and therefore we almost certainly underestimated true fishing mortality after 1999 when the first landings limit was implemented. Second, the Schaefer model does not include age-structure or recruitment time lags, and therefore our projections may exaggerate the predicted recovery rate. Evidence that time lags may be important can be seen in Figure 3.2 where substantial biomass was removed in the early 1970s without a concurrent decline in the trawl survey index. Also, the symmetrical biomass production relationship of the Schaefer model may be unrealistic if age structure has a strong influence on the population production rate (Maunder, 2003). Third, abnormally poor recruitment between 2000 and 2007 could also explain the lack of recovery. Alternatively, a regime change of reduced productivity or increased natural mortality in the latter period of the time series

would result in a decrease population growth rate and be consistent with our poor model predictions. We attempted to model this by estimating separate r parameters before and after, the mid-90's, but model fits did not improve, nor did the predictive ability of the model. Unfortunately, there are limited data to test these hypotheses.

In conclusion, our analysis suggests that the cusk fishery-independent trawl survey index suffers from hyperdepletion, which, if not accounted for results in exaggerated estimates of population decline. The high levels of uncertainty in our parameter estimates are a result of the limited data available as well as the low contrast and “one-way trip” trends in both catch rate indices. High levels of uncertainty in population parameters and historical biomass levels are characteristic of many bycatch species and management strategies that include these levels of uncertainty need to be employed. Managers also may seek to increase monitoring to achieve greater certainty in parameter estimates, and hence greater management control of this species. The effectiveness of the current landings limit to aid population recovery is uncertain as our robustness tests suggest that the population should be recovering, but monitoring data suggest that it is not. Further research is needed to estimate bycatch rates in the longline fishery to determine whether a landings limit is an effective management strategy for cusk recovery. In addition, further aging and age validation research is needed so that more realistic models, for example, that include time lags in recruitment can be used (e.g. (Meyer and Millar, 1999b; Millar and Meyer, 2000)). Although we were unable to include life-history information through the use of informative priors, the Bayesian approach is promising for the assessment of poorly monitored species where data is limited and time series have little information on population parameters.

Chapter 4

Changes in the Distribution and Abundance of Different Size Classes of Thorny Skate (*Amblyraja radiata*) on the Scotian Shelf

4.1 Introduction

Large scale changes in marine ecosystems resulting from environmental change and/or exploitation by fisheries arise from both direct and indirect mechanisms and may not be reversible within expected time scales (Bundy et al., 2009; Petrie et al., 2009; Bundy and Fanning, 2005). The abundance and distribution of marine fish populations are a function of a myriad of top-down and bottom-up controls (Baum and Worm, 2009) such as temperature, depth, environmental variability, climate change (Rijnsdorp et al., 2009), fishery exploitation and predator and prey dynamics and distribution (Swain and Benoît, 2006). Disentangling the causal mechanisms responsible for changes in population distribution and abundance is rarely trivial and becomes increasingly complex when indirect effects via cascading trophic interactions are considered (Fung et al., 2013). This can have wide-ranging consequence on ecosystem structure and stability (Petrie et al., 2009; Myers et al., 2007) and presents challenges and potentially difficult choices for fisheries and ecosystem management (Hutchings and Reynolds, 2004).

The relative abundance and distribution of thorny skate (*Amblyraja radiata*) has changed dramatically over the past forty years in the northwest Atlantic (Swain and Benoît, 2006; Shackell et al., 2005). Thorny skate has consequently been designated as a species of special concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2012). Population declines in the 1970s to the early 1990s may be a result of high levels of fishing mortality from thorny skate being incidentally captured in the large commercial groundfish fisheries (Swain et al., 2013) which were largely closed in the early 1990s due to the collapse of many groundfish populations

in Atlantic Canada. Limited fishery mortality on thorny skates occurred from 1994 to 2006 during a directed fishery for winter skate (*Leucoraja ocellata*) on the eastern Scotian Shelf from 1994 to 2006 where larger thorny skate made up approximately 5% of retained landings (Swain et al., 2013; DFO, 2006). Despite the near elimination of all major sources of direct and indirect fishing mortality thorny skate populations have continued to decline. Like many elamobranchs, skates may be at greater risk of extinction because of a relatively low resilience to heavy exploitation due to its relatively slow growth rate, late maturation, and low fecundity compared to teleosts (Dulvy and Reynolds, 2002).

Changes in distribution are frequently concurrent with large changes in abundance (Borregaard and Rahbek, 2010; Holt et al., 2002; Swain and Sinclair, 1994). An ideal free distribution (IFD) model can be used to explain these changes and predicts range contraction at reduced levels of abundance (Shackell et al., 2005; Shepherd and Litvak, 2004). A central assumption of this model is that animals have complete information about all available environments and choose to occupy habitats that maximize their reproductive success. Habitat suitability is a function of the availability of biotic and abiotic resources and the demand on these resources from intraspecies competition (Borregaard and Rahbek, 2010; Shepherd and Litvak, 2004). At elevated levels of abundance, competition for resources (e.g. food, predation avoidance, access to reproductive sites etc) reduce the habitat quality as more animals attempt to exploit a common limiting resource (Shackell et al., 2005). As this occurs, other habitats that are less suitable in the absence of competition become relatively more attractive. This resultant pattern in distribution due to habitat choice exhibits itself as density dependant habitat selection (DDHS; (Shepherd and Litvak, 2004)). Habitat choice and resource needs are not static throughout the life history of most marine fishes and partitioning a population into important life stages can help to understand the causal mechanisms that govern its distribution patterns (Gerber et al., 2005).

It can be important to account for the demographic structure and spatial distribution of a population to understand how populations have been affected by fishing, predation, or habitat loss to develop effective recovery strategies for populations reduced to low levels of abundance (Miller and Rudolf, 2011; Gerber et al., 2005). Indeed, for many fish species, reproductive potential is strongly linked to maturity

schedules and to the age and size of the reproductive component of the population (Trippel et al., 1997). Further, ontogenetic habitat shifts are common in mobile marine organisms and distribution can be differentially influenced by predators that target prey at different life stages (Snover, 2008a). Habitat and diet preferences can also have an ontogenetic basis and interactions between these factors is important to identify critical habitat and important trophic linkages that may be limiting recovery and changes in distribution (Scharf et al., 2000).

The continued decline and changes in distribution of thorny skate on the Scotian Shelf despite removal of fishing mortality point to a need to identify potential mechanisms that may be driving these patterns. Here, I compare and contrast the demographic components of the thorny skate population on the Scotian Shelf and how each exhibit different patterns in changes in abundance, range and distribution over the past 44 years.

4.2 Materials and Methods

4.2.1 Fisheries & Abiotic Data

Time-series data for thorny skate are from the summer bottom-trawl survey that has been conducted each July since 1970 by Fisheries and Ocean Canada (DFO). The survey covers the majority of the Scotian Shelf (Figure 4.1) and follows a stratified random design with stratification based on depth and geographic area and sampling intensity proportional to stratum size. Number of tows per year has been inconsistent with more tows recently compared to the beginning of the survey (mean of 139 tows per year in the 1970's compared to 203 tows per year from 2003 to 2013). My area of interest are the 48 strata that comprise the 4VWX Northwest Atlantic Fisheries Organization (NAFO) area. All strata were sampled at least once per year with the exception of one stratum that was not surveyed in 1984 (stratum 474). The stratified mean catch per standard 1.75 nautical mile tow (1 international nautical mile = 1.852 km) is used as the basis for an index of relative abundance. More detailed description about sampling design is summarized in Shackell et al. (2005). All statistical analyses were done in the statistical programming environment R (R Core Team, 2013).

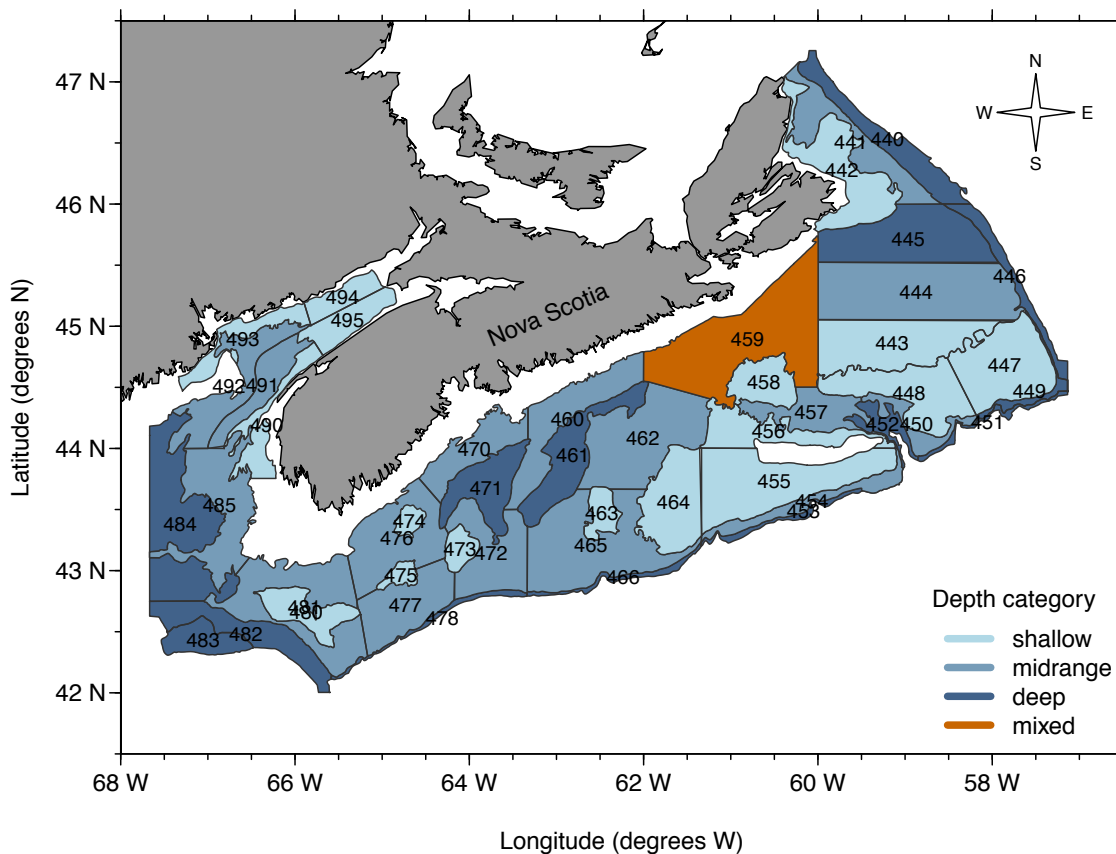


Figure 4.1: Survey area of the Fisheries and Oceans Canada annual bottom trawl survey on the Scotian Shelf. The area covered by strata 443–445 is a bathymetrically complex area of mixed depths, with depths ≤ 50 fathoms comprising stratum 443, 51–100 fathoms stratum 444, and >100 fathoms 445. The depiction of these strata in the figures do not show their actual geographic locations, which are discontinuous within the 443–445 area.

4.2.2 Trends in Population Abundance and Geographical Range

I partitioned catches of thorny skate into the ecologically relevant size classes identified in Swain et al. (2013) which corresponded to small and large juveniles ($\leq 32\text{cm}$; >32 and $\leq 53\text{cm}$, respectively), and adults ($>53\text{cm}$). I describe yearly variation in the relative abundance of partitioned size classes and sexes by calculating the stratified mean catch per standard tow in the summer survey for the NAFO division 4VWX as follows:

$$\bar{N}_t = \sum_{h=1}^L \frac{A_h}{A_T} \bar{y}_{ht} \quad (4.1)$$

where \bar{N}_t is the mean standardized catch rate for year t , A_h is the area of stratum h , A_T is the total area surveyed, L is the number of strata, and \bar{y}_{ht} is the mean catch rate of each size class and sex in each stratum h in year t . A third category for sexes combined was also calculated. A_T was 50032 nm^2 in all years, except 1984 where one stratum was not sampled reducing the total area sampled to 49871 nm^2 for that year. I used Local Polynomial Regression Fitting (LOESS) to smooth yearly catch rate variation and to estimate total declines in relative abundance.

I calculated the minimum area over which 95% of skates were distributed as a measure of geographic range for each sex and size class by first generating a cumulative distribution function (cdf) using the following equation for each sex and size class (Swain and Morin, 1996).

$$F_t(c) = 100 \frac{\sum_{h=1}^L \sum_{i=1}^{n_{ht}} \frac{A_h}{n_{ht}} X_{hit} I}{\sum_{h=1}^L \sum_{i=1}^{n_{ht}} \frac{A_h}{n_{ht}} X_{hit}} \quad \text{where } I = \begin{cases} 1 & \text{if } X_{hi} \leq c \\ 0 & \text{otherwise} \end{cases} \quad (4.2)$$

$F_t(c)$ provides an estimate of the percentage of skate (of a given size class and sex for each year) that occur at a local density of c or less. X_{hit} is the number of skate captured in stratum h , in tow i , in year t and n_{ht} is the number of tows in stratum h in year t . Because the equation calculates estimates of $F_t(c)$ at observed catch levels, I used linear interpolation to approximate $F_t(c)$ at desired discrete values when needed. I then used the following equation to calculate the area over which the most sparsely distributed 5% of skate are estimated to occur for each size group and sex:

$$G_t(c) = 100 \sum_{h=1}^L \sum_{i=1}^{n_{ht}} \frac{A_h}{n_{ht}} X_{hit} I \quad \text{where } I = \begin{cases} 1 & \text{if } X_{hi} \leq c \\ 0 & \text{otherwise} \end{cases} \quad (4.3)$$

where $G_t(c_{5\%})$ is the estimated area containing the most sparsely distributed 5% of thorny skate for each year. Finally, I calculated the minimum area containing 95% of skate (D_{t95}) by:

$$D_{t95} = A_T - G_t(c_{5\%}) \quad (4.4)$$

I calculated estimates of D_{t50} in a similar manner. Differences greater than a factor of two between estimates of D_{t95} and D_{t50} can give a signal of non-homogenous distribution throughout a species range and is indicative that density dependent habitat selection may exist. An IFD model predicts that declines in abundance are expected to be greater in suboptimal compared to preferred habitats which would manifest itself in large differences between estimates of D_{t95} and D_{t50} . Estimates of D_{t95} and D_{t50} were standardized to the proportion of total area sampled (i.e bounded by 0 and 1.0) to accommodate 1984 when one stratum was not sampled. I used Pearson product-moment correlations of the natural log of abundance and the arcsine square-root transformed distribution index for each sex and size group (Shackell et al., 2005) to test the relationship between relative abundance and area occupied. Next, I used estimates of stock area that contained 95% of thorny skates in a linear model to test whether size class, sex or logged yearly abundance were significant in predicting total area occupied. The arcsine transformed proportion of the total area area occupied that contained at least 95% of thorny skate was the dependent variable and was regressed against the natural logarithm of relative abundance and the categorical variables size class and sex.

4.2.3 Regional Variation in Rates of Local Density Change

Under IFD theory, catch rates in marginal habitats change more quickly relative to shelf wide estimates of relative abundance, and conversely, core habitat areas should either decline more slowly or not decline at all. To test whether stratum level catch rates have changed linearly with stock abundance, I use a power curve relationship between stratum level catch rates to the shelf wide stratified mean catch rate per tow using the following equation:

$$y_{hit} = \alpha_h \bar{N}_t^{\beta_h} \quad (4.5)$$

where y_{hit} is the skate catch (for a particular length and sex) in tow i of stratum h in year t and \bar{N}_t is the shelf wide relative abundance estimates calculated in equation (4.1) in year t (i.e the yearly stratified mean catch per tow of each age and sex). Estimates of β_h are used as a signal to identify core habitat areas. When stratum level catch rates decline more quickly than \bar{N}_t , a relationship known as hyperdepletion occurs (resulting in estimates of $\beta > 1$) and is used as a signal to identify marginal habitat areas. Conversely, core habitat areas would be expected to exhibit a hyperstable relationship where stratum level catch rates remain high despite declines in shelf wide abundance and is identified when $\beta < 1$. I evaluated Poisson and negative binomial (Venables and Ripley, 2002) distributions both with a log-link function. I was concerned that the low catchability of skates to the trawl gear may result in over dispersion that could not be fully accommodated by the negative binomial and therefore I also fit a zero-inflated negative binomial model (ZINB). I used a likelihood ratio test for model selection to choose between the Poisson model and negative binomial model and the Vuong's test to compare the negative binomial to the ZINB model (Zeileis et al., 2008)

I tested for evidence of DDHS by using weighted correlation of my estimates of β (weighted by the inverse of the standard errors (Pasek et al., 2012)) with an index of habitat quality which I defined to be the natural logarithm of the stratum level mean catch rate of the years with relative abundance between the 25 – 50% quantiles of LOESS smoothed estimates of relative abundance. Although these bounds are somewhat arbitrary, I wanted to restrict ranges of abundance to periods where habitat choice was not restricted by high population density (Gillis and Kramer, 1987) or a complete loss of signal due to stratum level extirpation caused by low population size. I also tested for correlation between estimates of β and categorical assignments of habitat quality based on the mean depth of each stratum. Categories of mean stratum depth were assign as shallow, midrange, deep or mixed based on depths of ≤ 50 , 51 - 100, > 100 fathoms, and mixed depths respectively (Simon and Comeau, 1994).

4.2.4 Distribution in Periods of Low Versus High Abundance

I test for shifts in distribution between periods of low and high abundance by comparing catch rates from the years that had catches in the lowest 20th, to the those in the upper 80th, quantiles obtained from the LOESS smoothed estimates of regional stratified mean catch rates calculated using equation 4.1. This corresponded to nine years for each category and size class. I used a negative binomial generalized linear model with a log link function and regressed tow catches with strata, abundance period (either high or low) and their interaction, and year nested in abundance period.

4.3 Results

4.3.1 Population Trends and Geographical Range

All size classes of thorny skate have shown steep declines in relative abundance in the DFO summer trawl over the last 44 years (Figure 4.2). There was little difference in overall rates of decline between sexes within each size class. The greatest decline was observed in the adult size class, a reduction of 95% in relative abundance by 2013 from its peak at the beginning of the time series (sexes combined). For the first time, no adult female thorny skates were captured in the summer survey in 2013. Large juveniles also showed a substantial reduction (86%) in relative abundance (sexes combined) by 2013 after a peak biomass in 1980. Small juveniles showed the smallest, yet still substantial, decline of 67% after peaking in 1979. The minimum area over which 95% of skates were distributed (D_{95} ; sexes aggregated) was either at, or near, its maximum for all size classes at the beginning of time series (Figure 4.3). Similar to changes in relative abundance, adults and large juveniles had the largest reductions in estimates of area occupied compared to more modest reductions in range observed for small juveniles. Based on LOESS smoothed estimates, adults and large juveniles started with the widest distribution, being found across 45.6 and 39.2% of 4VWX at their maximum but declined to 3.6 and 9.3% respectively by 2013. Small juveniles were distributed less broadly at 26% of 4VWX, however, they showed lesser but still substantial reductions by 2013 (down to 10%). Maximum estimates of D_{50} for adult, large and small juvenile thorny skates were 10.1, 7.9 and 4.3% and declined to 1.1, 2.3 and 2.2 % by 2013, respectively.

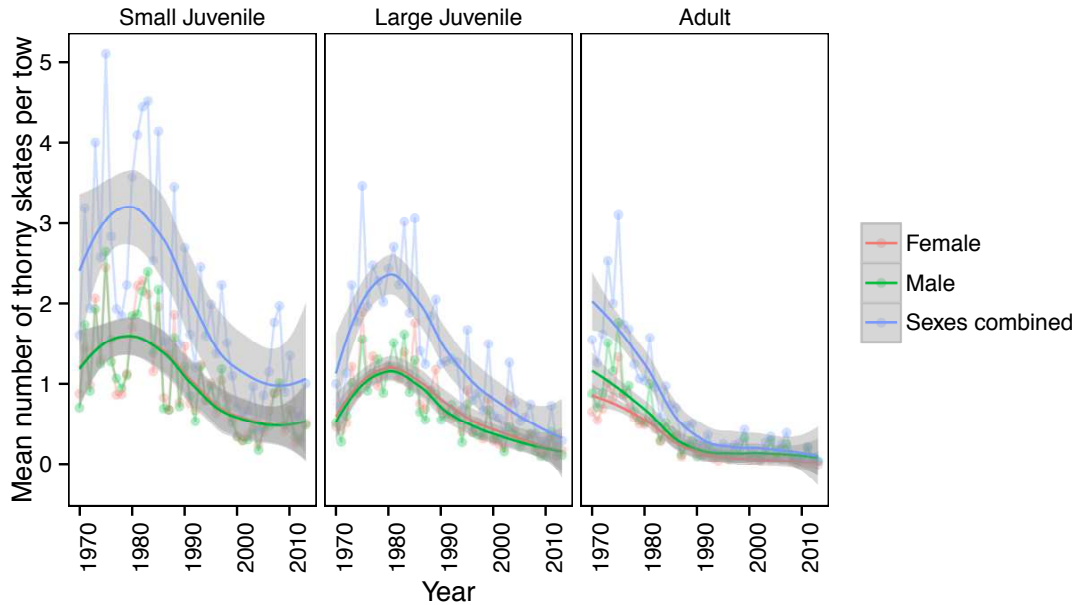


Figure 4.2: Stratified mean catch per tow of thorny skate in 4VWX for juvenile, large juveniles, and adult size classes from 1970 – 2013. Trend line is based on local polynomial regression fitting (LOESS) and shaded region is the 95% confidence region of the LOESS smooth.

Pearson product-moment correlations between the arcsine square-root transformed D_{95} distribution index and the natural logarithm of relative abundance were highly significant for adults and large juveniles of both sexes but were either marginally or not significant for small juveniles (Table 4.1 & Figure 4.4). The level of correlation was substantially less for the D_{50} index such that there was no significant correlation for area occupied and relative abundance for small juveniles. These results are further supported by the generalized linear model that identified size-class and abundance, but not sex, as significant factors in area occupied and explained 64% of the variation in D_{95} and 46% of the variation in D_{50} (Table 4.2). Effects of size-class and relative abundance were highly significant, and those terms and their interaction accounted for the majority of explained variation in stock area. Because sex was not a significant predictor of stock area, all further analyses aggregate sexes within each size-class.

Sex	Size class	Correlation	p-value	2.5%	97.5%
Female	Small juvenile	0.32	0.03	0.0288	0.57
Male	Small juvenile	0.21	0.16	-0.0880	0.48
Sexes combined	Small juvenile	0.31	0.04	0.0190	0.56
Female	Large juvenile	0.82	0.00	0.6915	0.90
Male	Large juvenile	0.78	0.00	0.6281	0.87
Sexes combined	Large juvenile	0.75	0.00	0.5850	0.86
Female	Adult	0.95	0.00	0.9150	0.97
Male	Adult	0.90	0.00	0.8255	0.95
Sexes combined	Adult	0.92	0.00	0.8617	0.96
Female	Stages combined	0.83	0.00	0.7024	0.90
Male	Stages combined	0.70	0.00	0.5126	0.83
Sexes combined	Stages combined	0.78	0.00	0.6228	0.87

Table 4.1: Pearson Product correlations between annual indices of stock area (D_{95} ; arcsine square-root-transformed) and the natural log of relative abundance

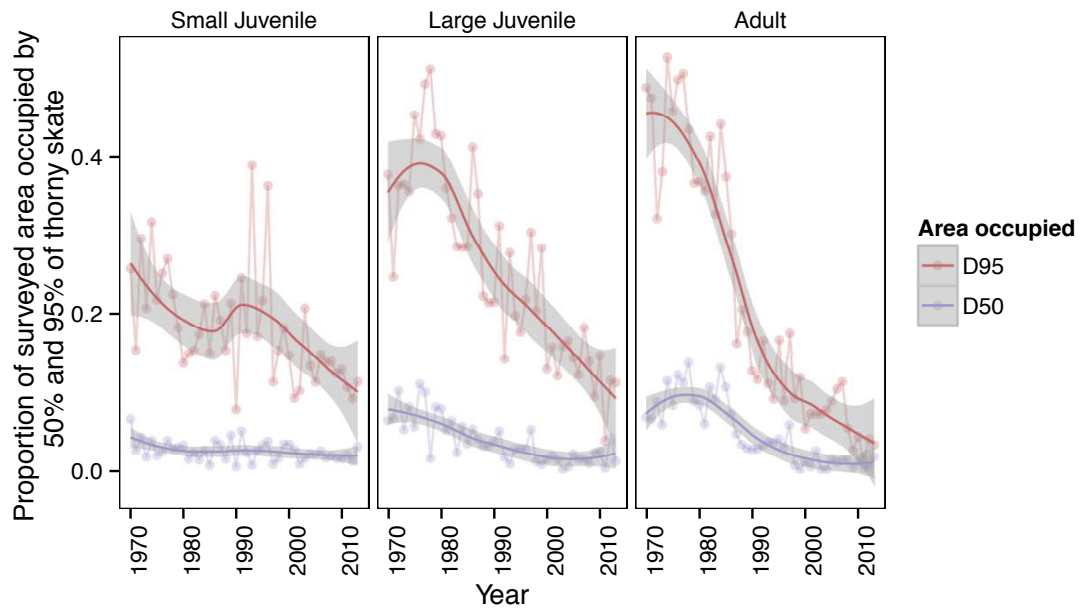


Figure 4.3: Minimum area containing 50 and 95% of thorny skate (sexes combined) in 4VWX from 1970 – 2013. Trend line is based on local polynomial regression fitting (LOESS) and shaded region is the 95% confidence region of the LOESS smooth.

Variable	$R^2 D_{95}$	D_{95} as proportion R^2	$R^2 D_{50}$	D_{50} as proportion R^2
Sex	64%	0.0	46%	0.5
Size class		7.4		12.4
Abundance		45.3		24.9
Sex \times size class		0.1		1.1
Sex \times abundance		0.2		1.0
Size class \times abundance		45.1		54
Sex \times size class \times abundance		1.8		6

Table 4.2: Effects of sex, size class, and relative abundance on area occupied (D_{95} or D_{50}) for thorny skate in the 4VWX area. Values are the percentage of explained variation as a proportion of R^2 of the model of each term. Asterisks indicate the significance level (P =0.01; P =0.001; P<0.0001).

Measures of D_{95} likely include a larger proportion of less ideal habitats compared to estimates of D_{50} . For example, at the beginning of the time series 95% of adults were found over 45.6% of the shelf compared to 50% of the adults being found on 10.1% of the shelf. Correlations between stock area and relative abundance were highly significant for large juveniles and adults for both levels of stock area (D_{95} or D_{50}) giving a strong signal for DDHS, however, correlations were only marginally or not significant for small juveniles (Figure 4.4). Small juveniles showed only a small correlation between D_{95} and relative abundance but correlation was absent between the relative abundance and the measure that effectively focused on core habitats (D_{50}) suggesting that strong DDHS does not occur in many areas where small juveniles are found (Figure 4.4).

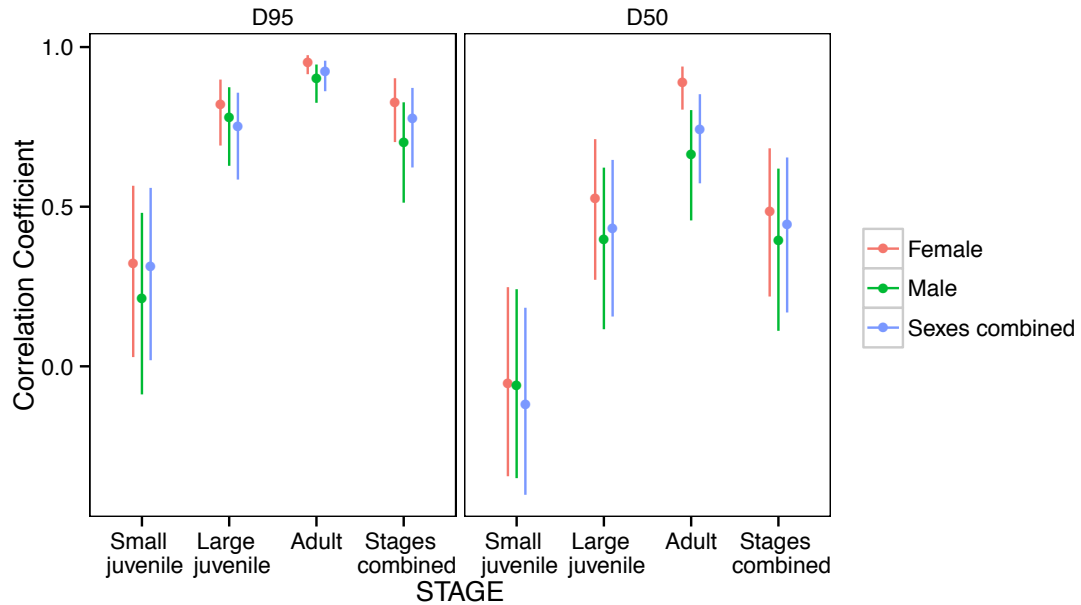


Figure 4.4: Pearson product correlation between the arcsine square-root-transformed minimum area containing 50% and 95% of thorny skate and the natural logarithm of the mean stratified catch per tow in 4VWX from 1970 – 2013. See Tables 4.1 & 4.3 for numerical estimates.

Sex	Size class	Correlation	p-value	2.5%	97.5%
Female	Small juvenile	-0.05	0.73	-0.3444	0.25
Male	Small juvenile	-0.06	0.70	-0.3503	0.24
Sexes combined	Small juvenile	-0.12	0.44	-0.4025	0.18
Female	Large juvenile	0.53	0.00	0.2710	0.71
Male	Large juvenile	0.40	0.01	0.1161	0.62
Sexes combined	Large juvenile	0.43	0.00	0.1559	0.65
Female	Adult	0.89	0.00	0.8040	0.94
Male	Adult	0.66	0.00	0.4570	0.80
Sexes combined	Adult	0.74	0.00	0.5732	0.85
Female	Stages combined	0.48	0.00	0.2186	0.68
Male	Stages combined	0.40	0.01	0.1112	0.62
Sexes combined	Stages combined	0.44	0.00	0.1686	0.65

Table 4.3: Pearson Product correlations between annual indices of stock area (D_{50} ; arcsine square-root-transformed) and the natural log of relative abundance

4.3.2 Regional Variation in Rates of Local Density Change

I found the negative binomial model was selected over the Poisson model for more than 90% of strata for all size classes and 65% of the ZINB models. Therefore, I used the negative binomial distribution for all model comparisons. The majority of models converged, however, 2, 1, and 2 stratum did not converge for small and large juveniles and adults, respectively and thus were omitted from further analysis.

Small juveniles had the largest number of strata where estimates of β were not significantly different from zero (Table 4.4) and no trend between regional and local catch rates was identified. Not surprisingly because of the non-significance of the Pearson Product Correlation tests for small juveniles, the majority of strata were either proportional (n=17) or not significant (n=23) to regional trends in abundance and only one small stratum (stratum 451) located in the most south easterly edge of the shelf was hyperstable (Figure 4.5). Stratum level catch rates of large juveniles were mostly proportional (n=19) or not significant (n=10), however, almost one-third of the strata were hyperdepleted (n=15) and only three strata were hyperstable (Figure 4.6). Adults had the same number of hyperdepleted strata and were generally the same strata that exhibited hyperdepletion for large juveniles. Adults also had the most proportional (n=25) and hyperstable (n=4) strata and only two were not significant (Figure 4.7).

	Combined size classes	Small juveniles	Large juveniles	Adult	Total
Hyperdepleted	21	5	15	15	56
Hyperstable	4	1	3	4	12
Not significant	8	23	10	2	43
Proportional	15	17	19	25	76
Total	48	46	47	46	187

Table 4.4: Negative binomial model fit results of relationship between stratum level catch rates to yearly stratified mean catch rates for thorny skate in 4VWX. See Figures 4.5 to 4.7.

Generally, very few strata were identified as being hyperstable. Not surprisingly, most strata were identified as being proportional to regional catch rates with the exception of small juveniles that were dominated by strata where no relationship

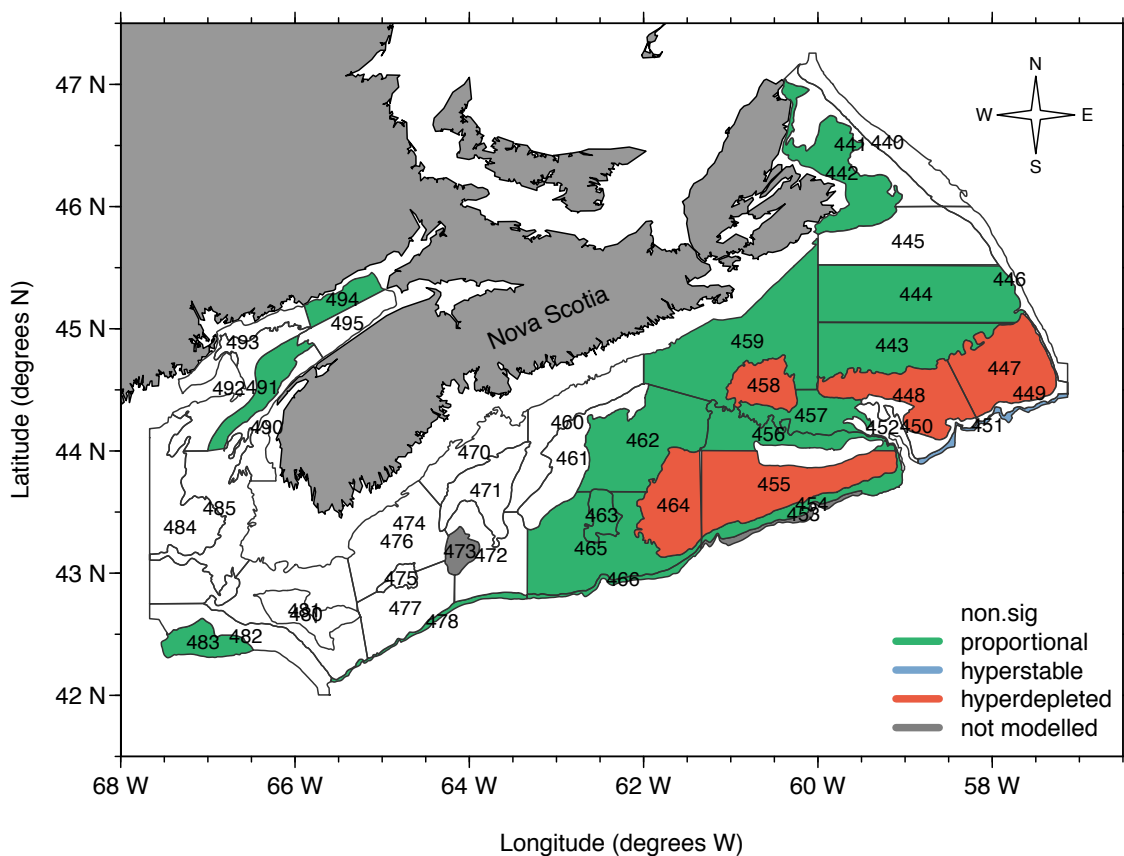


Figure 4.5: Proportionality of stratum catch rates for small juvenile thorny skates relative to the yearly stratified mean catch rate (skates per tow) in 4VWX from 1970 – 2013. Note that strata 443, 444, and 445 are within the same area but are depth stratified.

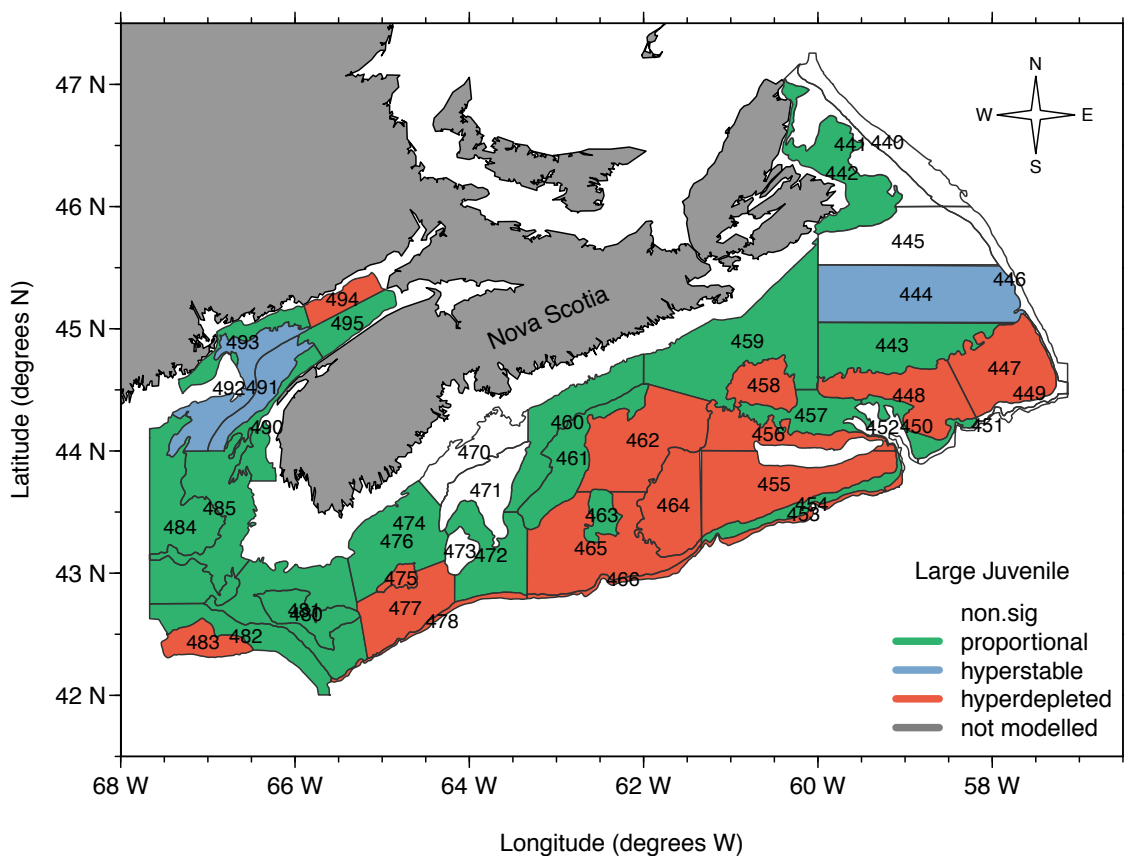


Figure 4.6: Proportionality of stratum catch rates for large juvenile thorny skates relative to the yearly stratified mean catch rate (skates per tow) in 4VWX from 1970 – 2013. Note that strata 443, 444, and 445 are within the same area but are depth stratified.

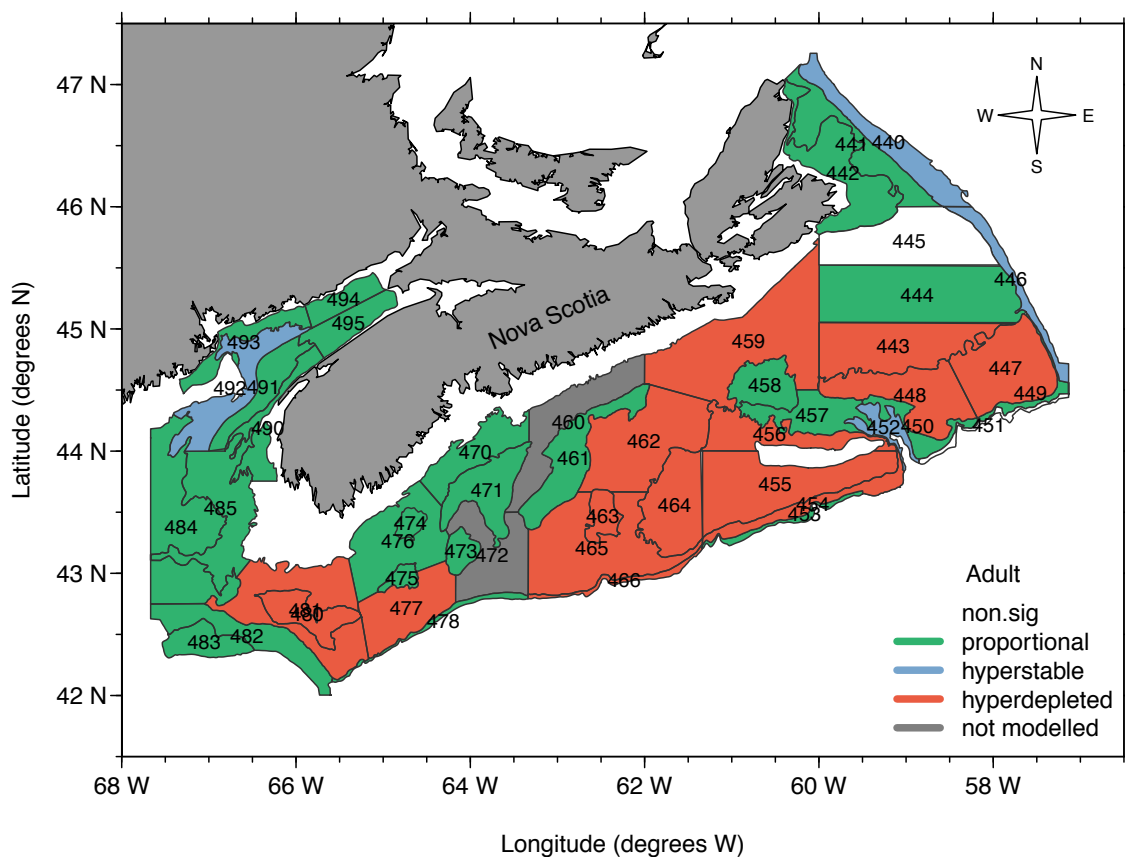


Figure 4.7: Proportionality of stratum catch rates for adult thorny skates relative to the yearly stratified mean catch rate (skates per tow) in 4VWX from 1970 – 2013. Note that strata 443, 444, and 445 are within the same area but are depth stratified.

was identified (i.e. non-significant). Hyperdepletion was found to occur more than four times as often as hyperstability. The large difference between D_{t95} and D_{t50} for large juveniles and adults (Figure 4.3) is an indication that thorny skates have been extirpated from many strata after the large declines in relative abundance. Indeed, a large number of strata that were identified to have local catch rates that were hyperdepleted had extremely low or no catches by 2013. Stratum 451 that is a deep stratum on the SE slope of Banquereau Bank in the south eastern corner of the shelf (Figure 4.1) had significant and negative estimates for (β : -1.59 (-2.58 – -0.61)) for small juveniles indicating that catches increased in this stratum while population declined. Large juveniles and adults also had negative estimates for β for stratum 451, however, upper confidence limits spanned zero and thus were considered to be non-significant.

The weighted correlation tests between estimates of β and my index of habitat quality were significant for large juvenile and adults providing further evidence for DDHS for these size classes (Figure 4.8). Tabulation of the categories of β to mean stratum depth (Tables 4.5 – 4.7) indicated that all hyperstable strata were either of midrange or deep depth and the majority of hyperdepleted strata were shallow (Figure 4.9).

	proportional	hyper depleted	hyper stable	not significant	not modelled	Total
Shallow	7	5	0	4	1	17
Midrange	6	0	0	10	0	16
Deep	3	0	1	9	1	14
Mixed	1	0	0	0	0	1
Total	17	5	1	23	2	48

Table 4.5: Strata depth and proportionality relationship for small juvenile thorny skate.

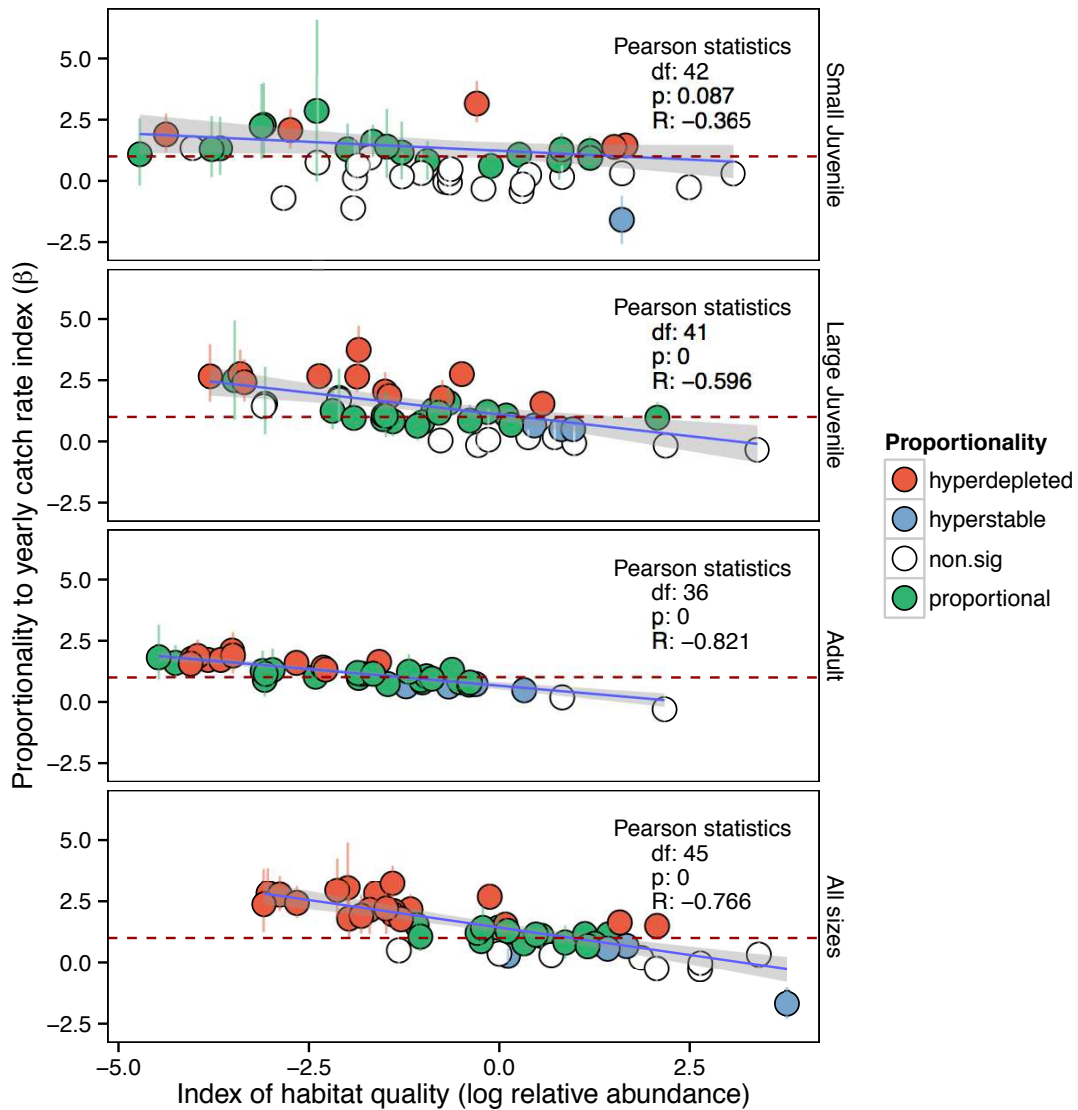


Figure 4.8: Relationship between habitat quality and proportionality of strata level catches to survey area relative abundance. Index of habitat quality is the log of the strata level mean of the years with relative abundance within the 25 to 50% quantiles maximum stratified mean catch per tow for each stage estimated from a LOESS smoothing algorithm. β is the estimated proportionality relationship parameter of the strata level catch rates and the area wide yearly stratified mean abundance described earlier where $\beta > 1$, equal to 1, and < 1 indicate the strata is either hyperdepleted, proportional, or hyperstable respectively, relative to the stratified mean catch rate index. Only strata with significant estimates of β and strata with mean catches > 0 are modelled. Error bars are the 95% confidence limits of the estimates of β . Regression is weighted by the inverse of the standard error for estimates of β and non-significant estimates of β had a weight of zero.

	proportional	hyper depleted	hyper stable	not significant	not modelled	Total
Shallow	7	8	0	1	1	17
Midrange	8	3	3	2	0	16
Deep	3	4	0	7	0	14
Mixed	1	0	0	0	0	1
Total	19	15	3	10	1	48

Table 4.6: Strata depth and proportionality relationship for large juvenile thorny skate.

	proportional	hyper depleted	hyper stable	not significant	not modelled	Total
Shallow	9	8	0	0	0	17
Midrange	8	5	1	0	2	16
Deep	8	1	3	2	0	14
Mixed	0	1	0	0	0	1
Total	25	15	4	2	2	48

Table 4.7: Strata depth and proportionality relationship for adult thorny skate.

4.3.3 Distribution in Periods of Low Versus High Abundance

Large shifts in distribution were apparent for both large juveniles and adults but were much less pronounced for small juveniles. Comparison of the catch rates of the different size classes showed a hollowing-out of the species range for all size classes but was most extreme for adults (see Figures B.1 – B.3).

Indeed, abundant catches of adults in 1970 have been reduced to less than 10 individuals in 2013 and were restricted to the most eastern part of the Scotian Shelf. Once I adjusted catch rates to a common mean abundance to focus on changes in distribution during the nine years of highest and lowest abundance, range shifts were similarly substantial and showed strong shifts from a shelf-wide distribution to being centred on the most north and south eastern parts of the shelf and the upper Bay of Fundy (Figures 4.10 – 4.12). Direct comparisons of adjusted catch rates showed a similar pattern for all size classes. Strata 440–452 which are found on the eastern portion of the shelf exhibited similar adjusted catch rates in the high abundance period compared to remaining strata (453–495) that showed lower adjusted catch

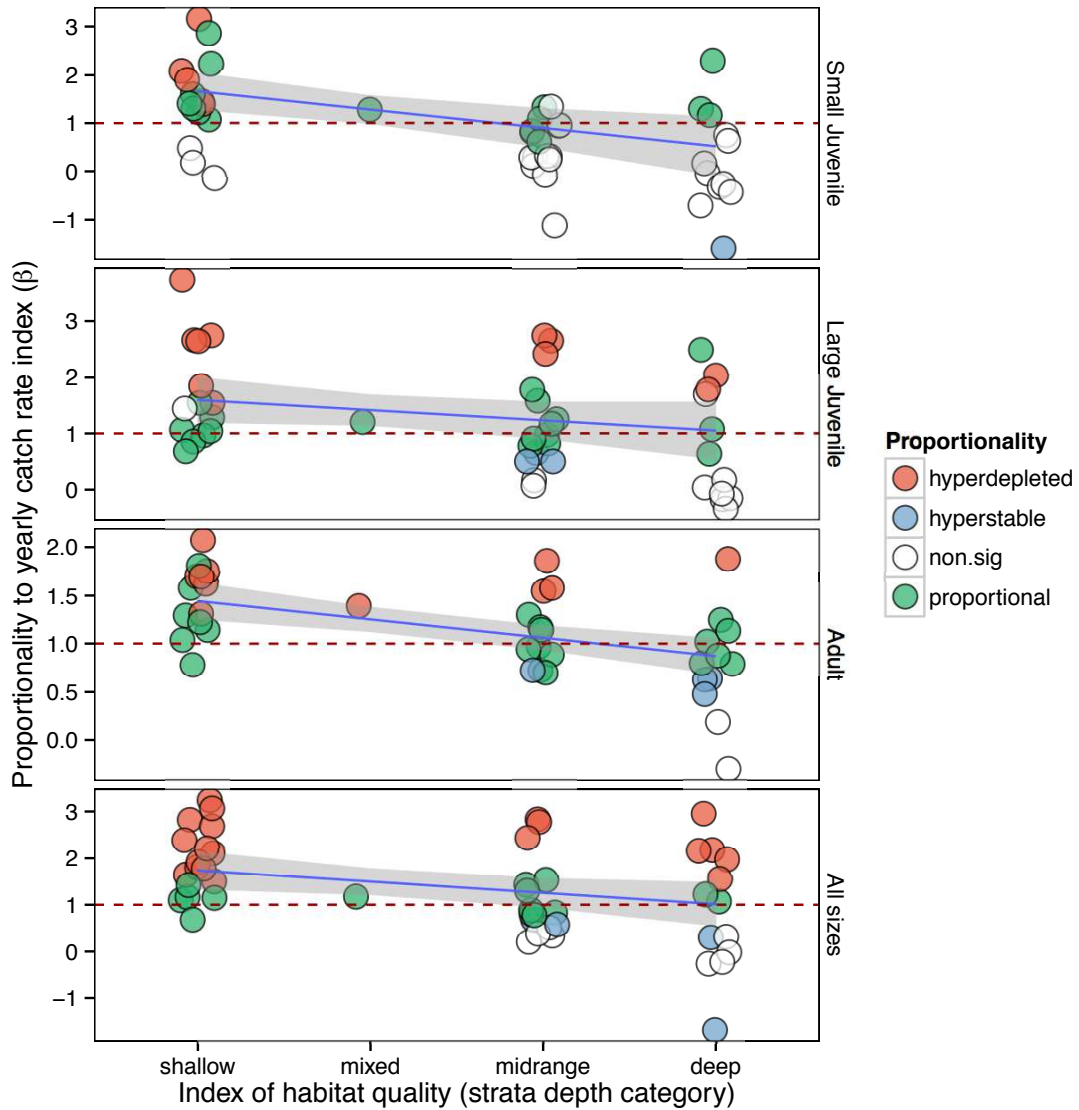


Figure 4.9: Relationship between habitat type (based on depth) and proportionality of strata level catches to survey area relative abundance. β is the estimated proportionality relationship parameter of the strata level catch rates and the area wide yearly stratified mean abundance described earlier where $\beta > 1$, equal to 1, and < 1 indicate the strata is either hyperdepleted, proportional, or hyperstable respectively, relative to the stratified mean catch rate index. Only strata with significant estimates of β and strata with mean catches > 0 are modelled. Regression is weighted by the inverse of the standard error for estimates of β and non-significant estimates of β had a weight of zero..

rates during the low abundance period (Figure 4.13). The most striking change was observed in the adult size-class where catches were zero in many strata during the nine-year period of low abundance.

Models with terms for strata, abundance period, their interaction, and year nested in abundance period showed that both small and large juveniles had more significant differences in the interaction term (both 21 out of the 48 strata) compared to adults that only had six. During periods of high abundance, however, adults were found in all strata but were absent from 22 strata during the period of low abundance. Juveniles were absent from fewer strata with small and large juveniles being absent from 2 and 1 strata during periods of high abundance and absent from 13 and 12 during the low abundance period, respectively.

4.4 Discussion

The large declines in abundance of all size classes of thorny skates brings into question the long-term viability of the population on the Scotian Shelf. Indeed, no adult females were captured in 2013 which is a first for the 44 year long research survey. Similarly large declines in area occupied, particularly for the large juvenile and adult size classes, resulted in a distribution restricted primarily to the most easterly and western areas of the Scotian Shelf. Associated declines in relative abundance and area occupied gave strong evidence for DDHS for large juveniles and adults but was relatively weak for small juveniles.

Adults had the largest distribution over the shelf at the beginning of the time-series compared to both juvenile size classes and also showed the greatest proportional decline in both relative abundance and stock area. The initial broader geographic range of adults could reflect a wider habitat and/or dietary breadth as there are ontogenetic shifts in the diet of thorny skate. The diet of small juveniles is primarily made up of invertebrates and increasingly focuses on fishes as they get older. For example, fish in the family Gadidae and offal historically made up more than 50% of the diet of large thorny skates compared to juveniles where fish were almost absent from their diet (Templeman, 1982). The differences in the strength of correlation between relative abundance and stock area for the different size classes of thorny skate may have a basis in the diet preferences as many Gadoid prey species have also exhibited large

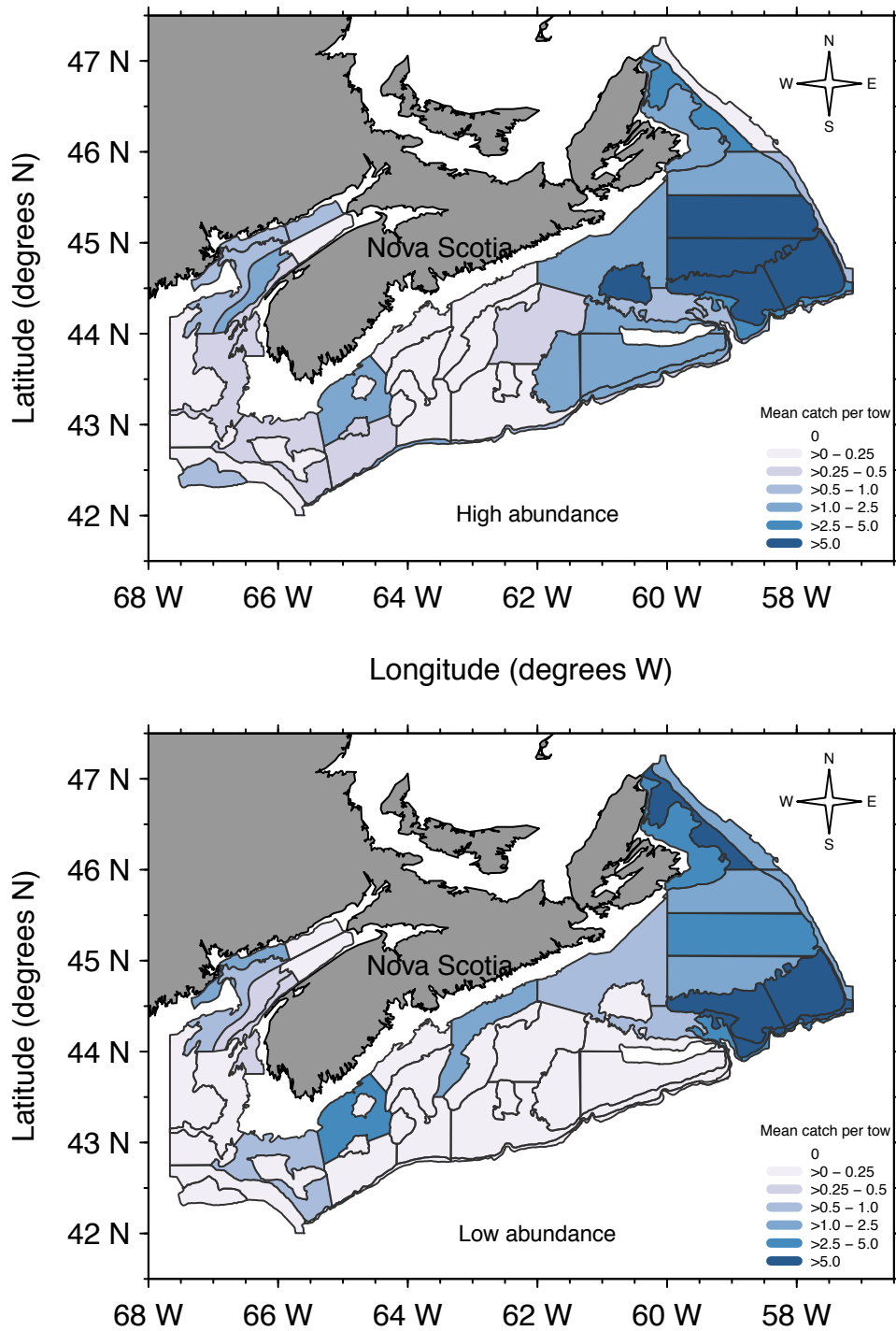


Figure 4.10: Relative abundance of small juvenile thorny skates years of highest and lowest (90 and 10% quantiles) mean catch per tow.

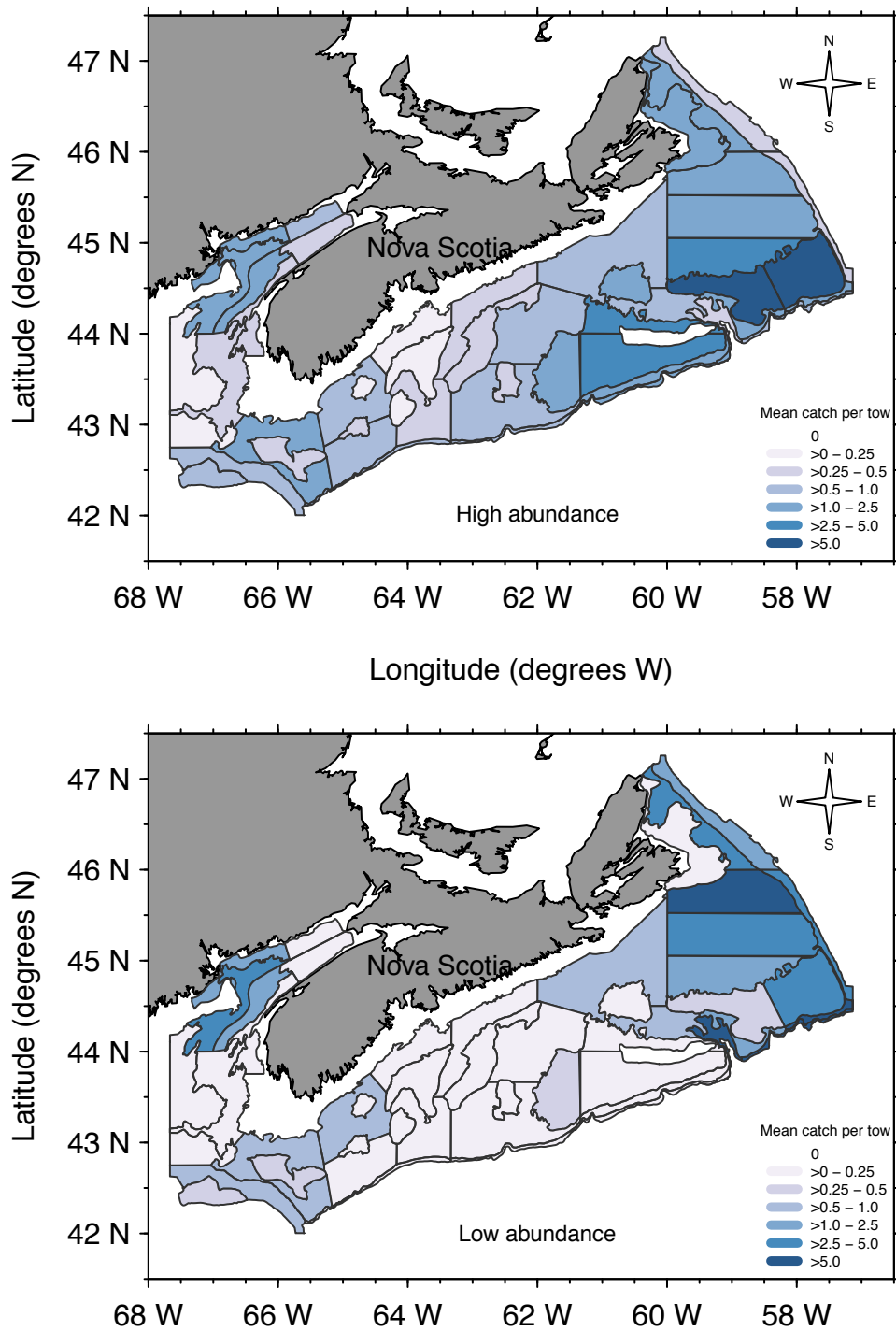


Figure 4.11: Distribution of large juveniles thorny skates during six years of highest and lowest (90 and 10% quantiles) mean catch per tow.

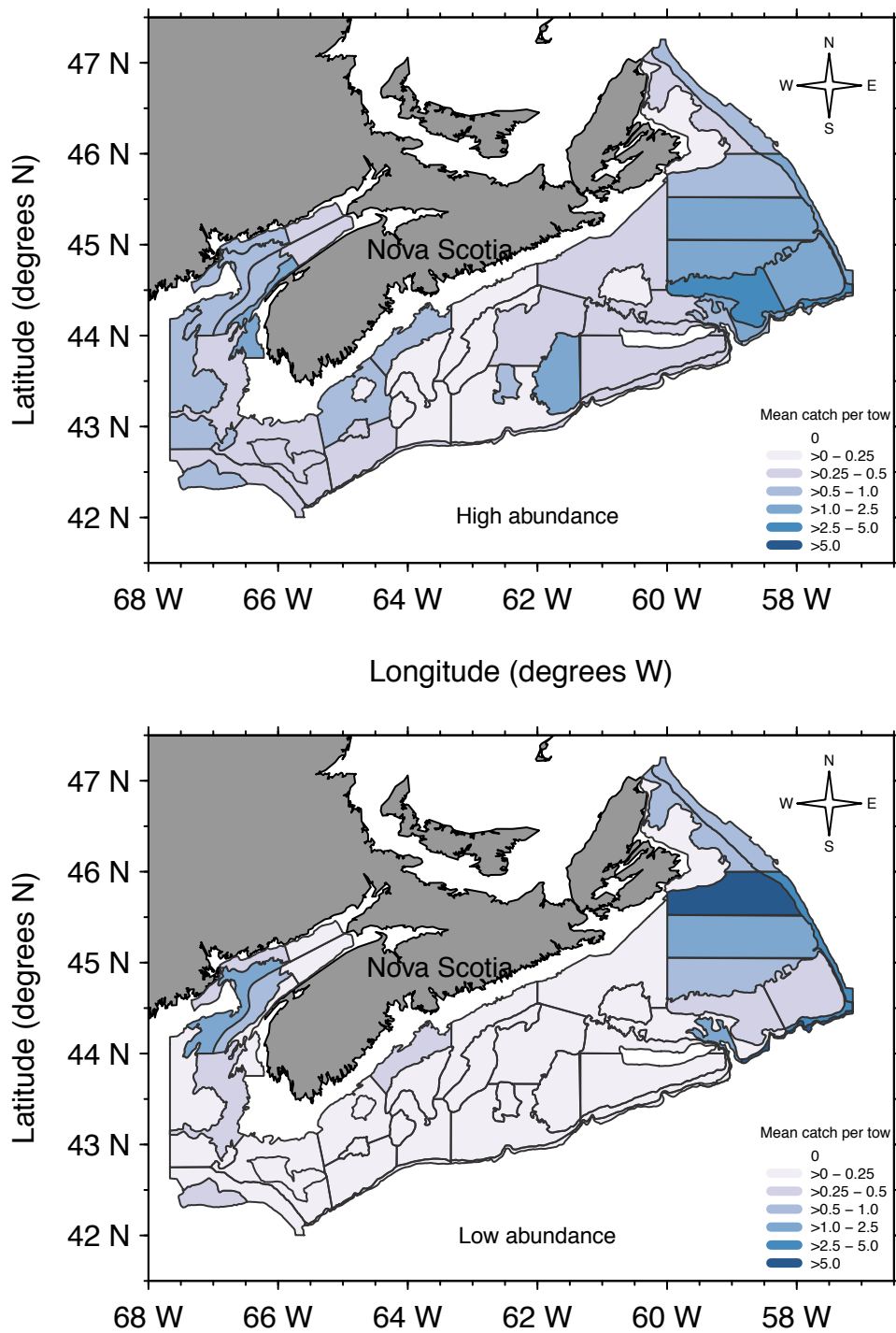


Figure 4.12: Distribution of adult thorny skates during six years of highest and lowest (90 and 10% quantiles) mean catch per tow.

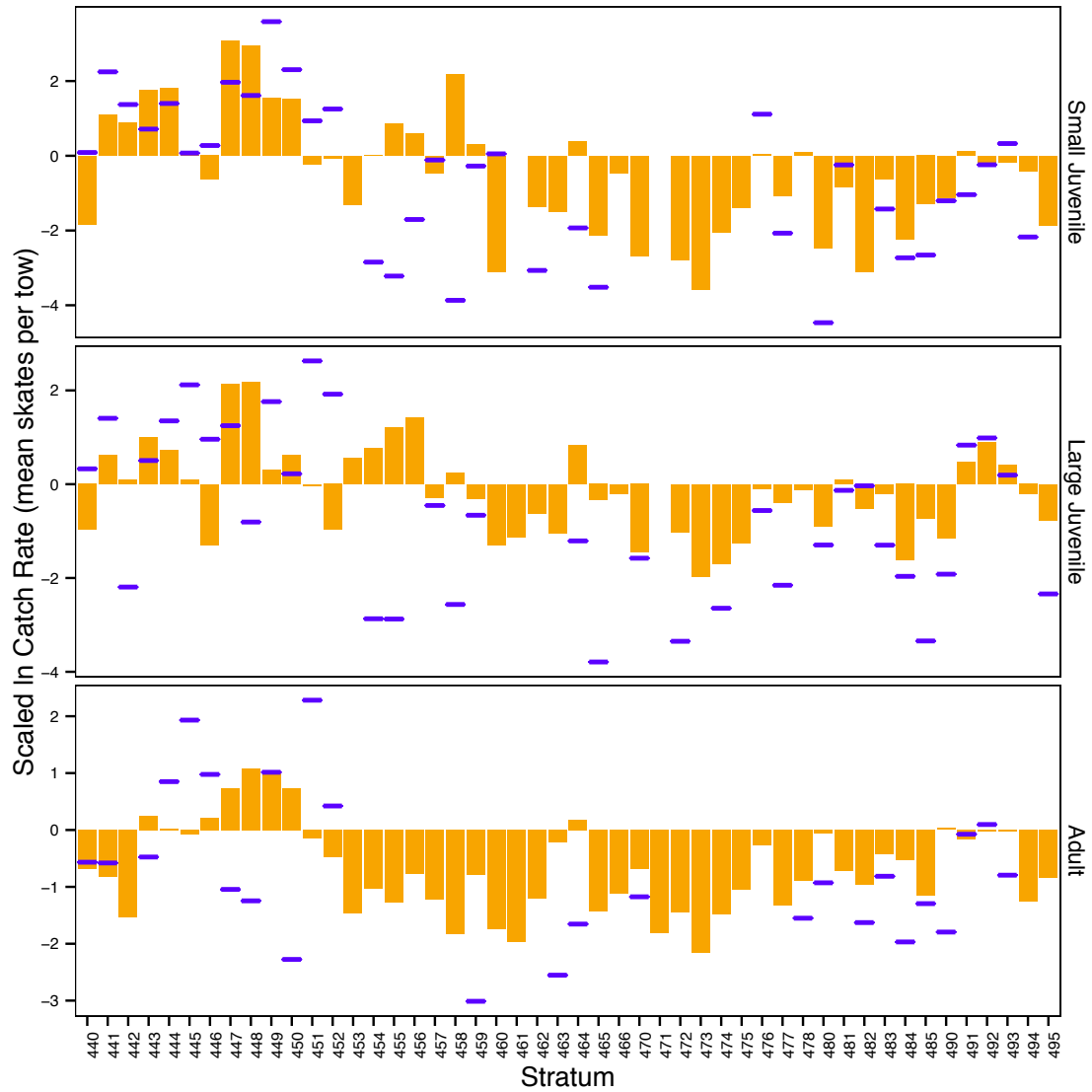


Figure 4.13: Mean ln catch rate of thorny skates in each stratum scaled by maximum average catch during each period of low (blue bars) or high abundance (orange columns). Stratum where bars or columns are absent indicate no thorny skate were caught.

declines in abundance and distribution (Shackell et al., 2005). Alternatively, predator avoidance, from both fishing and/or potentially grey seals (*Halichoerus grypus*), may also be a contributing driver for these changes. For example, there was a directed fishery on the eastern Scotian Shelf from 1994 to 2006 for winter skate that also captured large thorny skate although no obvious changes in the rate of population decline can be seen in the catch rate index over this time period. Alternatively, grey seals have exhibited a near exponential increase in abundance on the eastern Scotian Shelf since the 1970s due to recovery from hunting (Fu et al., 2012; DFO, 2011b). The seal population on the Scotian Shelf is now at the highest population observed in the past hundred years (DFO, 2011a) and the majority of their diet is fish (Bowen and Harrison, 1994).

The analysis that correlated strata proportionality to the index of habitat quality found strong evidence for DDHS for large juveniles and adults but not so for small juveniles (Figure 4.8). These results were not driven by the number of core habitat areas identified but rather by the number of hyperdepleted strata identified for each size class. Indeed, there were generally four times more hyperdepleted than hyperstable strata for all size classes (Table 4.4) and no shallow strata were identified as being hyperstable. The negative estimate of β for small juveniles in the deep strata along the edge of Banquereau Bank (stratum 451) indicates that abundance within this stratum increased while population abundance decreased. This stratum also maintained comparatively higher densities of large juveniles and adults, however, estimates of β spanned zero and were thus deemed to not be significant. Skate redistributing themselves to deeper areas is consistent with the observation that seals most commonly forage in shallower water (Breed et al., 2009) and this observed shift in habitat usage towards deeper depths may be a response to increased predation risk from seals. Further research is needed to investigate these patterns.

Large changes in range observed during the contrast between periods of low and high abundance were strongest in adults compared to the two juvenile size-classes. Catches, however, of adults have always been low giving the tests comparing periods of low and high abundance low statistical power. For example, far fewer strata showed significant differences in the adult size-class even though all other test suggest a very strong DDHS effect and even extirpation from many local habitats during periods

of low abundance. As mentioned previously, low statistical power is frequently a problem when estimating patterns and trends of species with low catchability and low abundance (Blanchard et al., 2008) and this is an example of how a variety of approaches are needed.

The present study demonstrates how different size-classes of thorny skate are differentially changing in both abundance and distribution on the Scotian Shelf. The extremely large declines in the reproductively mature size-class of thorny skate and its extirpation from a large portion of the shelf suggests that the populations viability may be in danger. The large declines of large bodied thorny skates in terms of both abundance and restricted distribution to the eastern portion of the Scotian Shelf and the upper Bay of Fundy has implications for delineating protected areas to encourage population recovery or stop further declines.

Chapter 5

Extinction Risk and Overfishing: Reconciling Conservation and Fisheries Perspectives on the Status of Marine Fishes

5.1 Introduction

Human impacts on natural ecosystems are diverse and accelerating (MEA (Millennium Ecosystem Assessment), 2005; Halpern et al., 2008). On land, where the primary threat to wildlife is habitat loss, recent comprehensive assessments of birds, mammals, and amphibians have revealed 13%, 21%, and 30% of these species to be threatened with a heightened risk of extinction, respectively (Hoffmann et al., 2010). But whereas there is a general consensus in the scientific community about the status of terrestrial species (Butchart et al., 2010; Hoffmann et al., 2010), the state of marine species, and in particular marine fishes, remains deeply controversial (Worm et al., 2006; Hilborn, 2007b; Longhurst, 2007; Branch, 2008; Pauly, 2009; Branch et al., 2011).

Much of the controversy over the status of marine fishes can be traced to divergent beliefs about how these species should be regarded - as commodities to be managed for maximum productivity, or as wildlife, and integral components of diverse ecosystems (Reynolds et al., 2005; Salomon et al., 2011). Within fisheries contexts, the most valuable populations are evaluated using complex population dynamics models, termed stock assessments, that estimate biomass trajectories as well as reference points against which to benchmark population status (Hilborn and Stokes, 2010). In contrast, conservation evaluations typically focus on extinction risk; for exploited marine species this is most commonly evaluated against the rate of change in abundance (Mace et al., 2008). Under the most widely used conservation framework, the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species,

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species that have declined $\geq 50\%$ within the most recent ten year or three generation period (whichever is longer) are considered to be threatened with extinction (IUCN Standards and Petitions Subcommittee, 2011).

A longstanding and unresolved aspect of this debate is the relevance of Red List evaluations to marine fishes. Critics have argued that these conservation evaluations exaggerate threat status for marine fishes, positing these species have low extinction risk relative to other vertebrates, may still number in the millions of individuals when listed as threatened, and that declines in abundance are usually the result of managed exploitation (Matsuda et al., 1998; Musick, 1999; Powles et al., 2000; Punt, 2000; FAO, 2002; Mace et al., 2002; Mace, 2004). Embedded in these criticisms is the question of whether the Red List and fisheries assessments disagree as to which populations are in trouble, which is our focus herein, or whether they agree but still differ as to what the appropriate management response should be for populations deemed to be in trouble. Disagreement about the latter stems from the fact that there are significant biological differences between falling below a fishery reference point, which might signal impaired productivity or recruitment, and being threatened with extinction. While populations threatened with extinction require bold management action, such as mandatory prohibitions on all forms of human-induced mortality, overfished ones may require only a moderate management response, such as catch restrictions to stop or reverse their declines. Critics argue that, in the worst cases, threat listings could lead to unnecessary fisheries closures with high associated socioeconomic costs (Rice and Legacè, 2007). Despite these concerns, momentum for marine fish conservation listings is growing (Figure 5.1; IUCN (2011); GMSA (2012)). In light of this trend, and because the relevance of extinction risk criteria to marine fishes and the state of marine fisheries are both still hotly debated (COSEWIC, 2005; Worm et al., 2006; Longhurst, 2007; Branch, 2008; Cooke, 2011; Hilborn, 14 Apr 2011; Sala et al., Apr 21 2011), there is an urgent need to understand why fisheries scientists' and conservation biologists' perceptions about the status of marine fishes differ.

Here, we take a critical step toward resolving this debate by systematically evaluating two of its central questions: 1) What is the status of marine fishes according to fisheries (above or below reference points) and conservation (Red List threatened or not) metrics? and 2) How well do these metrics align? We hypothesize that if the Red

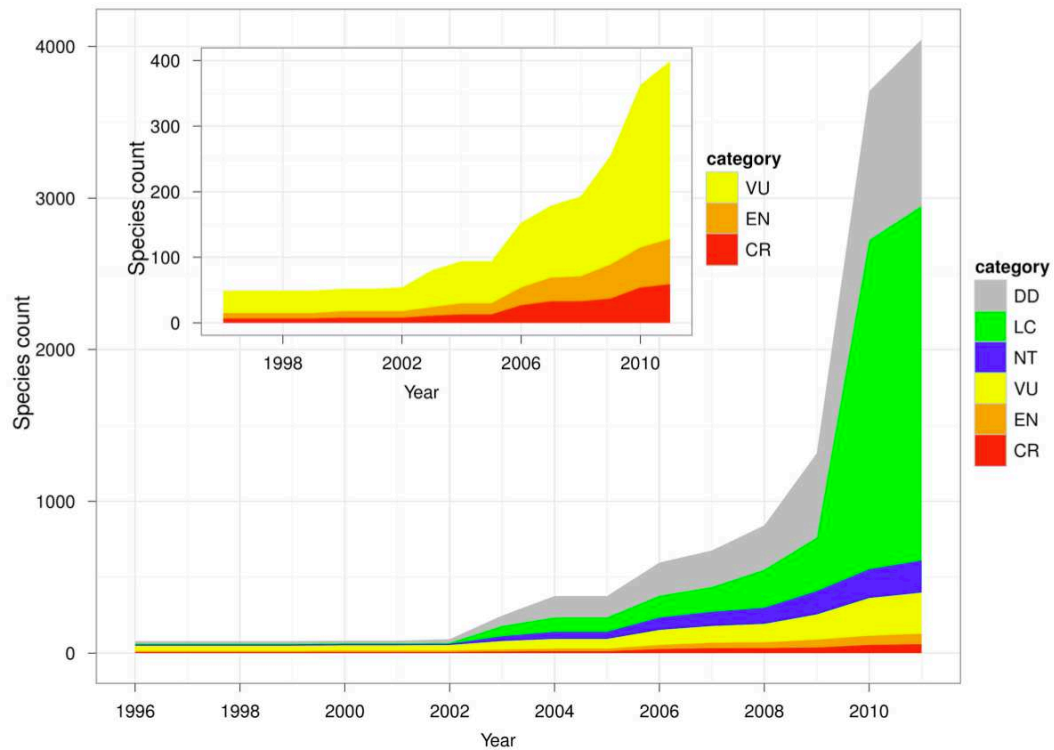


Figure 5.1: Total number of marine fish species on the IUCN Red List each year by category. Red List categories are Data Deficient (DD), Least Concern (LC), Near Threatened (NT), or one of the three threatened categories, Vulnerable (VU), Endangered (EN), Critically Endangered (CR). Inset is expanded view of the species listed in threatened categories: VU, EN, or CR.

List is an accurate measure of extinction risk then comparing a population's Red List status with its fishery status should result in poor alignment, since falling below a fishery reference point is not generally considered equivalent to heightened extinction risk. In contrast, if alignment between these metrics is high, it suggests that the Red List exaggerates extinction risk but shows that the two metrics do provide consistent measures of when a population is considered to be in trouble and requiring improved management measures. We used the IUCN Red List (Version 2011.2 (IUCN, 2011)) and a new compilation of fisheries stock assessments from around the world (updated from Ricard et al. (2012)), to first summarize the extinction risk categorizations of the 4048 marine fish species on the Red List, and the fisheries statuses of 166 assessed marine fish populations relative to their reference points. Direct comparison of conservation and fishery statuses are challenging because Red List evaluations typically are conducted at the species, not population, level and because few populations with stock assessments also have recent Red Listings ($n=31$) (IUCN Standards and Petitions Subcommittee, 2011; Ricard et al., 2012). To facilitate such a comparison, we assigned each assessed marine fish population to a Red List Category using the most common IUCN Criteria (A1), which measures the proportional change in the mature component of populations over the longer of ten years or three generations (IUCN Standards and Petitions Subcommittee, 2011). We then quantified the alignment of these two metrics using a hits, misses, false alarms framework (Rice, 2003) (Table 5.1), and diagnosed why discrepancies occur.

5.2 Materials and Methods

5.2.1 Data.

To assess the fishery status of marine populations, we used all available recent stock assessments with estimates of adult (spawning stock) biomass and biological reference points (referred to herein as assessed populations). All assessments, except those from Europe ($n=42$), are from Version 1.0 of the RAM Legacy Stock Assessment Database, a new global database of stock assessments for commercially exploited marine populations (Ricard et al., 2012). For European populations, we obtained the 2011 assessments from the International Council for the Exploration of the Sea (ICES)

(ICES, 2012). Overall, populations in our analysis came from Argentina, Australia, Canada, Europe, New Zealand, South Africa, and the U.S., and their adult biomass time series averaged 46 years (range 15 - 132 years). We benchmarked the biomass of populations against the upper and lower biological reference points from their stock assessments (Hilborn and Stokes, 2010), rather than estimating a common set of reference points (as in Worm et al. (2009); Ricard et al. (2012)). Assessments from the RAM Legacy Database used B_{msy} and $0.5B_{msy}$; European ones used B_{pa} and B_{lim} . Six of the European populations had only B_{pa} calculated, and four had only B_{lim} . For these we used the relationship:

$$B_{lim} = B_{pa}e^{(-1.645\sigma)} \quad (5.1)$$

from (Marshall et al., 2003) with $\sigma = 0.3$ to estimate these few missing reference points.

To assess the conservation status of marine fish populations, we first summarized the status of all marine fishes listed on the Red List (Version 2011.2 (IUCN, 2011)). However, the limited number of marine fish populations with both a recent stock assessment and a recent IUCN Red List evaluation ($n=31$, with Red List evaluations coming from only twenty-four different fish species) precluded a broad direct comparison of these two metrics. Instead, we estimated the Red List status of all assessed marine fish populations according to Criterion A1, which requires an estimate of generation length. Generation length is defined as the average age of mature individuals in a population and thus reflects the turnover rate of breeding individuals (IUCN Standards and Petitions Subcommittee, 2011). We estimated generation length for all assessed marine fish populations as:

$$\text{Generation length} = A_{50} + 0.25 \times (\text{longevity} - A_{50}) \quad (5.2)$$

modified from the IUCN guidelines (IUCN Standards and Petitions Subcommittee, 2011), using population specific estimates for A_{50} (the age at 50% maturity), and longevity, the theoretical maximum age of each population prior to the commencement of exploitation, wherever possible. We extracted these estimates (A_{50} $n=93$, longevity $n=74$) from the RAM Legacy Database, and when absent, sought them

from the populations' respective assessments and/or the primary literature. Where population-specific longevity estimates were not available, we used species-level estimates, seeking these first from the primary literature and secondarily from FishBase (Froese and Pauly, 2011) ($n=63$). In the six cases where these also were not available, we used the maximum age from the stock assessment model (typically a "plus group" in which all individuals greater than that age are combined, as in Dulvy et al. (2005)). The mean age at A_{50} of assessed populations was 5.7 years (range 0.3 - 38 years), and the mean generation length was 12.7 years (range 1.6 - 69 years) (Table S1). Thus, while some previous analyses have used 15 years as a coarse approximation for three generations in marine fishes (Hutchings and Reynolds, 2004; Rice and Legacè, 2007), our analysis - in which three generations averages 38.1 years - reveals this to be a significant underestimate.

5.2.2 Analysis

We assigned each population to Red List Categories by calculating its proportional change in adult biomass over the longer of ten years or three generations (Criterion A1 (IUCN Standards and Petitions Subcommittee, 2011)), in each of two time periods: 1) the current Red List status by calculating the proportional change in biomass back from the most recently available biomass estimate, 2) the theoretical "worst case" Red Listing by identifying the time period of greatest proportional decline in biomass. According to the Red List Guidelines, Criterion A1 applies when declines are reversible, understood, and have ceased; when these conditions are not met, one of Criterion A2 – A4, which have lower decline thresholds for threatened status (30%, as opposed to 50% for A1), is to be used (IUCN Standards and Petitions Subcommittee, 2011). We used Criterion A1 for each of our main analyses because all of the populations included have stock assessments and are managed to some degree, suggesting declines are potentially reversible, and the cause is understood to be primarily fishing in each case. Criterion A1 also has been most commonly applied to marine fishes (Dulvy et al., 2005). An additional analysis, based upon the A2 – A4 decline threshold is presented in Table S3. In all of our Red List assignments, we calculated the proportional change in biomass between the mean of the last three years and the mean of the first three years of the time period under consideration, so

as to reduce the influence of single year fluctuations in population biomass on threat designation. Although we initially considered estimating the proportional change in biomass by fitting generalized linear models, we found they occasionally fit the data poorly. Where three generations was longer than a population’s time series ($n=45$), the entire time series was used.

We then quantified the alignment between populations’ estimated current Red List status and their current fisheries status using a hits, misses and false alarms framework (Table 5.1 Rice (2003); Piet and Rice (2004); Dulvy et al. (2005)). We assigned the fisheries status of each population first by benchmarking it against its upper biomass reference point, and second against its lower biomass reference point (described in Data), in each case designating the population as being above or below the reference point by comparing its mean biomass in the most recent three years to the reference point. There are four possible outcomes under the hits, misses, false alarms framework: i) a positive hit occurs when a population is below its reference point and the Red List criterion for a threatened listing is met; ii) a negative hit occurs when a population is above its reference point and the threat criterion is not met; iii) a miss occurs when a population is below its reference point but did not meet the criterion for a threatened listing; and iv) a false alarm occurs when a population is above its reference point but the threat criterion is (erroneously) met. Thus, positive and negative hits are indicative of alignment between the conservation and fisheries metrics, while misses and false alarms indicate inconsistent signals.

Fishery Status	IUCN Red List status (%)	
	Threatened	Not threatened
OK	False Alarm	Hit (True negative)
In trouble	Hit (True positive)	Miss

Table 5.1: Framework for assessing the performance of the IUCN Red List (Criterion A1) in relation to fisheries reference points. The fishery status categories of “Okay” or “In trouble” correspond to whether the biomass of the population was above or below its fishery reference point (e.g. B_{msy} or B_{lim}), respectively. The IUCN Red List status of threatened includes populations fitting the Red List Critically Endangered, Endangered, and Vulnerable categories.

We examined the extent of the alignment or misalignment by comparing individual Red List threat categories (CR, EN, VU) with the upper and lower reference points, and two additional ones, $1.5B_{\text{msy}}$ and $0.2B_{\text{msy}}$. $1.5B_{\text{msy}}$ is an arbitrary level used to identify populations well above their upper reference points, while $0.2B_{\text{msy}}$ has been used as a metric of “collapsed” populations (Pinsky et al., 2011; Worm et al., 2009). Listing a population as Critically Endangered when its biomass is well above its upper reference point (e.g. $>1.5B_{\text{msy}}$) would be indicative of an egregious false alarm, whereas a Vulnerable listing when biomass is just slightly above the upper reference point would be a minor one. At the other extreme, listing a population as not threatened when its biomass is well below its lower reference point (e.g. $<0.2B_{\text{msy}}$) would be an egregious miss, whereas listing such a population as Critically Endangered would be a strong positive hit.

Finally, we repeated the application of the hits, misses, false alarms framework twice more, to gauge the alignment between the theoretical “worst case” Red Listing for each population and its fishery status at the end of this decline period, when benchmarked against i) its upper fisheries biomass reference point or ii) its lower one.

5.3 Results

5.3.1 Status of Marine Fishes

We first evaluated the fishery status of each assessed population by comparing its current adult biomass to the upper and lower reference points from its stock assessment. Because there is no consensus amongst fisheries scientists as to which reference point is most robust, different management agencies use different types of reference points. Many fisheries management agencies, including the U.S. and Canada, use reference points related to the concept of maximum sustainable yield (MSY): B_{msy} , the population biomass that should provide the MSY is often considered by jurisdictions as a fisheries target. Increasingly, however, it is recognized both from economic (Grafton et al., 2007; Froese et al., 2010) and ecosystem (Smith et al., 2011; Walters et al., 2005) perspectives that it is beneficial to maintain populations above B_{msy} , and thus it would be better regarded as a limit. Still, in at least the U.S. and Australia, $0.5B_{\text{msy}}$ is used as the lower limit (Campbell, 2010; Rayns, 2007). Thus we also used

$0.5B_{\text{msy}}$ as a lower reference point in our analyses of populations with MSY based reference points. Populations in Europe are benchmarked against a lower reference point B_{limit} (B_{lim}), the biomass below which recruitment is likely to be impaired, and an upper one $B_{\text{precautionary}}$ (B_{pa}), meant to provide a buffer above B_{lim} (Murawski, 2010). We note that because MSY is a measure of population productivity, there is no fixed proportion of B_{msy} for all populations below which recruitment is impaired, nor is there a direct translation between B_{msy} and B_{lim} . We included both types of reference points in our analyses because they are the benchmarks used by the fisheries management agencies themselves to flag populations they consider to be in trouble.

Forty percent ($n=67$) of assessed marine fish populations currently are below their upper (more conservative) reference point (B_{pa} or B_{msy}), and over half of these populations ($n=35$, 21% of total) also are below their lower (riskier) reference point (B_{lim} or $0.5B_{\text{msy}}$; Figure 5.2A and B). Of these overfished populations, five U.S. ones (Georges Bank Atlantic cod (*Gadus morhua*, Figure 5.3A), southern New England-Mid Atlantic winter flounder (*Pseudopleuronectes americanus*) and yellowtail flounder (*Limanda ferruginea*, Figure 5.3G), southern Atlantic coast red snapper (*Lutjanus campechanus*), and southern California cowcod (*Sebastes levis*) appear to be in the worst shape, having each declined to less than 10% of their upper reference points (Table S2).

In comparison, 29.5% ($n=49$) of assessed populations currently would be classified as threatened on the Red List (Criterion A1; Figure 5.2C), almost midway between the numbers considered to be in trouble from conservative and risky fisheries perspectives. Of these threatened populations, eight (4.8% of total) have declined by a sufficient amount ($\geq 90\%$) to be classified as Critically Endangered (CR) : U.S. populations of snowy grouper (*Epinephelus niveatus*), southern California cowcod (*S. levis*), and red snapper (*L. campechanus*) on the southern Atlantic coast and Gulf of Mexico; blue warehou (*Seriolella brama*) and orange roughy (*Hoplostethus atlanticus*) in Australia; southern bluefin tuna (*Thunnus maccoyii*); and Irish Sea cod (Figure 5.3C, Table S2). Nineteen populations (11.4% of total), including Georges Bank Atlantic cod (*G. morhua*, Figure 5.3A) and Atlantic bluefin tuna (*Thunnus thynnus*, Figure 5.3B), would qualify as Endangered (EN), declines $\geq 70\%$ but $< 90\%$), and the remaining twenty-two threatened populations (13.3% of total), including two rockfish

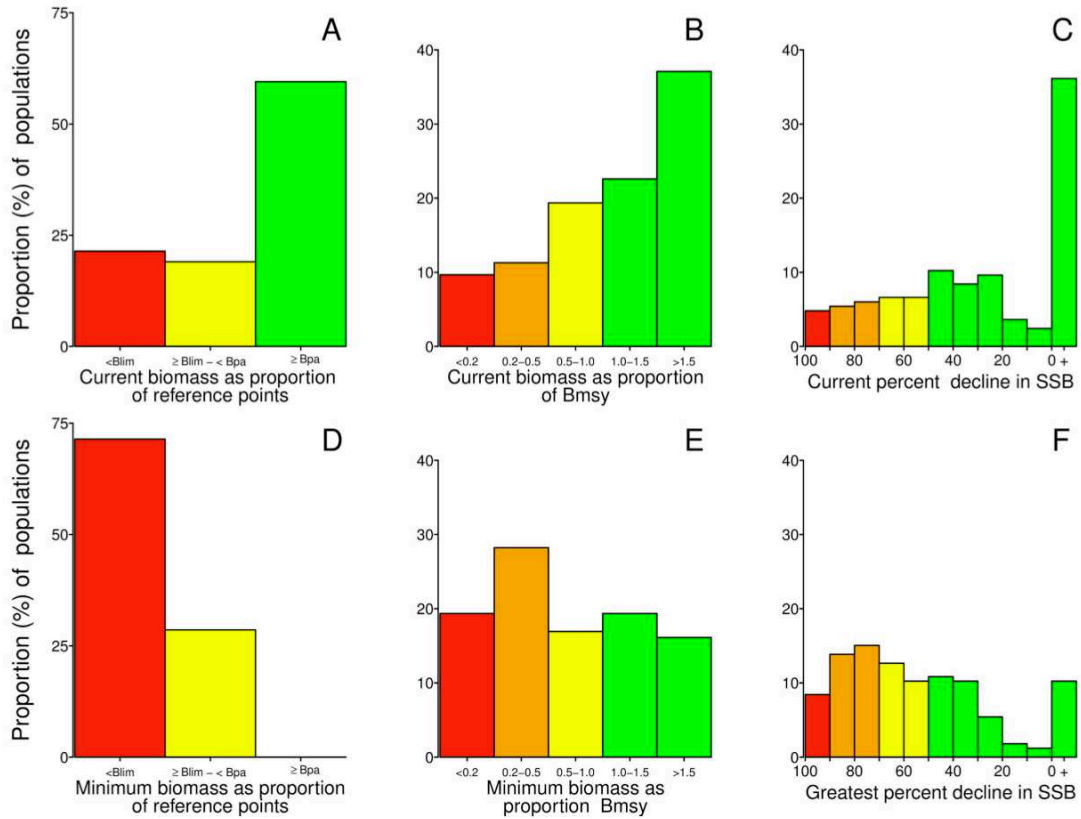


Figure 5.2: Proportion (%) of marine fish populations that currently meet (A-C), or have ever met (D-F), fisheries or conservation criteria for concern. (A) Current adult biomass of European populations ($n=42$) as proportion of their B_{pa} and B_{lim} reference points, and (D) the minimum adult biomass ever experienced by those same populations as proportion of their reference points. Colors correspond to fisheries threat level: above upper ICES reference point B_{pa} (green), between upper and lower ICES reference points (yellow), and below B_{lim} (red); (B) Current adult biomass of all other assessed populations ($n=124$) as proportion of their B_{msy} reference point, and (E) the minimum adult biomass ever experienced by those same populations as proportion of their B_{msy} reference point. Colors correspond to increasing threat, from not overfished (green) through to overfished (orange and red). (C) Estimated percent change in adult biomass for each population ($n=166$), from the most recent year back over the longer of ten years or three generations, and the corresponding IUCN Red List category: CR (red), EN (orange); VU (yellow); or not threatened (green), under Criterion A1. (F) Estimated greatest percent decline in adult biomass for the same populations ($n=166$) over the longer of ten years or three generations, and the corresponding IUCN Red List category, as above.

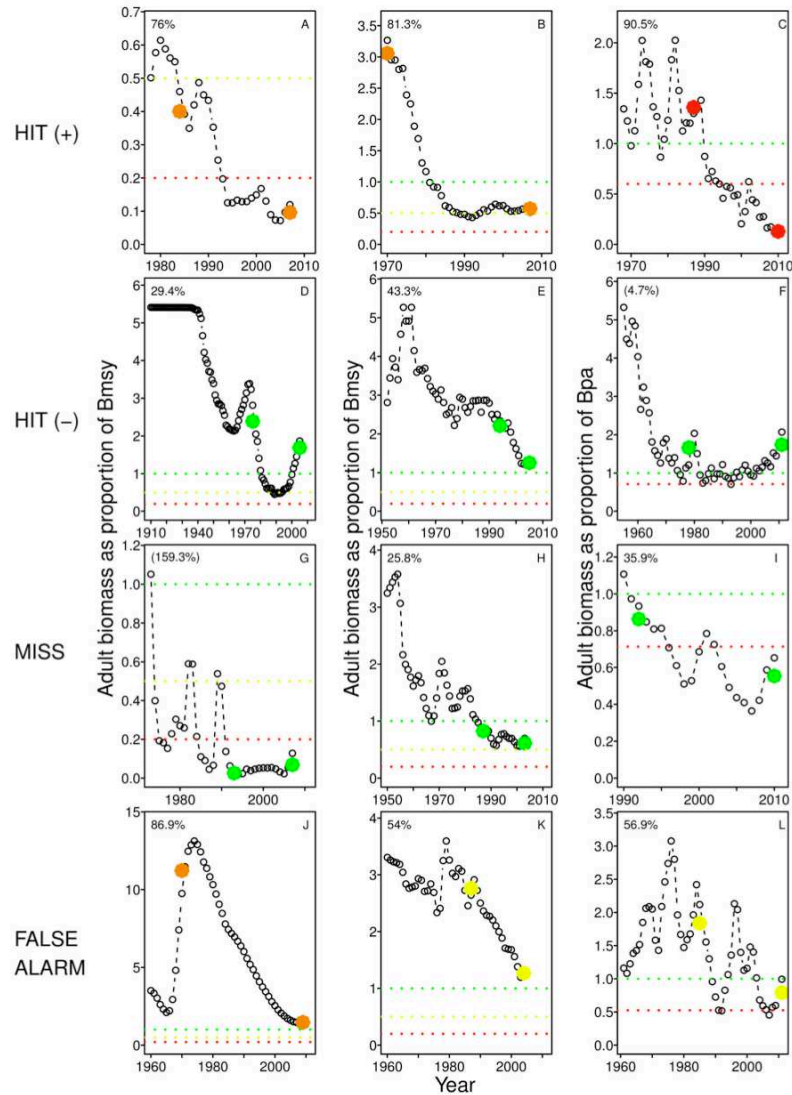


Figure 5.3: Time series of adult biomass illustrating cases of alignment and misalignment. Populations are organized by management region: US (left column), non-US (middle column), or Europe (right column), and illustrate cases where the current fisheries reference points and estimated IUCN Red List status (Criterion A1) align (positive hits (top row) or negative hits (2nd row)), where the Red List would miss listing a population that is overfished as threatened (3rd row), or would list a population that is not considered overfished as threatened, producing a false alarm (bottom row): (A) Georges Bank Atlantic cod (*Gadus morhua*), (B) Atlantic bluefin tuna (*Thunnus thynnus*), (C) Irish Sea Atlantic cod (*G. morhua*), (D) U.S. northern Pacific Coast petrale sole (*Eopsetta jordani*), (E) Central western Pacific yellowfin tuna (*Thunnus albacares*), (F) Iceland cod (*G. morhua*), (G) Southern New England-Mid Atlantic yellowtail flounder (*Limanda ferruginea*), (H) Western Pacific Ocean striped marlin (*Kajikia audax*), (I) North Sea and eastern Channel whiting (*Merlangius merlangus*), (J) Bering Sea and Aleutian Islands Greenland turbot (*Reinhardtius hippoglossoides*), (K) Indian Ocean bigeye tuna (*T. obesus*), and (L) Faroe Plateau Atlantic cod (*G. morhua*). Note (L) is only a false alarm from the perspective of its lower fisheries reference point. Colored circles correspond to IUCN Red List categories: Critically Endangered (red), Endangered (orange), Vulnerable (yellow), or not threatened (green); associated estimated decline is located in the upper left of each plot. Colored dotted lines correspond to fisheries reference points: B_{msy} or B_{pa} (green), $0.5B_{msy}$ (yellow), $0.2B_{msy}$ or B_{lim} (red).

(*Sebastes spp.*), Bering Sea and Aleutian Islands Greenland turbot (*Reinhardtius hippoglossoides*, Figure 5.3J), Indian Ocean bigeye tuna (*Thunnus obesus*, Figure 5.3K), and four Atlantic cod populations (*G. morhua*, including the Faroe Plateau population, Figure 5.3L) would qualify as Vulnerable (VU), declines $\geq 50\%$ but $< 70\%$ (Table S2).

In contrast, only 13.5% ($n=399$) of the 2952 marine fish species listed on the IUCN Red List (in categories other than Data Deficient) are considered to be threatened, and very few of these are considered to be at a high risk of extinction ($n=59$ CR, 2.0% of total and $n=69$ EN, 2.3% of total; Figure 5.1). The vast majority are classified as Least Concern ($n=2350$; 79.6%). When only those marine fishes subject to large scale intentional use (Threat 5.4.2 (IUCN, 2011); total $n=282$) were considered, however, the proportion of threatened ones more than doubled, to 29.1% ($n=82$), almost exactly the same as in our estimated Red List.

To set the current status of marine fishes in context, we asked what proportion of assessed populations would ever have been considered to be in trouble from fisheries and conservation perspectives? Almost three-quarters (73%) of populations have fallen below their upper fisheries benchmark at some point in the past, and just over half (54%) have ever fallen below their lower one. The extent of overexploitation varied significantly by region: whereas all populations under European management ($n=42$) have been below their upper benchmark (B_{pa}) and 71% have been below their lower one (B_{lim}) (Figure 5.2D), only 77% and 58% of U.S populations ($n=77$), and 45% and 30% of non-U.S. populations ($n=47$) have been below their upper (B_{msy}) or lower ($0.5B_{msy}$) benchmarks, respectively (Figure 5.2E). From a conservation perspective, 60% ($n=100$) of assessed marine fish populations could have been classified as threatened at some point in their past, according to Criterion A1, which is almost midway between the number of populations that have ever been considered to be in trouble from conservative or risky fisheries perspectives, and over twice as many as would be listed currently (Figure 5.2F). Under this “worst case” scenario, 14 populations would have been classified as Critically Endangered, 48 as Endangered, and 38 as Vulnerable.

5.3.2 Alignment of Conservation and Fisheries Metrics

Overall, the current fishery and conservation statuses of individual marine fish populations are well-aligned: 75.9% alignment (sum of positive and negative hits) when estimated Red Listings were compared to the populations benchmarked against their upper (more conservative) fisheries reference points, and 80.7% when populations were compared to their lower (riskier) ones (Table C.4). In both cases, negative hits, where populations were not considered to be in trouble from either a fishery or conservation standpoint, made up the majority of alignments (Figure 5.3D-F). Misalignments were dominated by misses, where the Red List criterion failed to classify a population below its fishery reference point as threatened, when Red Listings were compared to the upper fisheries reference points (17.5%, Figure 5.3G-I). False alarms, where the Red List classified a population as threatened but the population was above its fishery reference point, dominated when Red Listings were compared to the lower reference points (13.9%; Figure 5.3J-L; Table C.4). Different outcomes can occur only for populations whose biomass is between its two reference points. Western Pacific striped marlin (*Kajikia audax*), for example, is categorized as a miss when compared to its upper reference point (B_{msy}) but a negative hit when compared to its lower one ($0.5B_{\text{msy}}$; Figure 5.3H). Alignment was greater for European populations, benchmarked against B_{pa} (81.0%) and B_{lim} (90.5%), than for U.S. and other populations, benchmarked against B_{msy} (74.2%) and $0.5B_{\text{msy}}$ (77.4%). Relative to those other populations, European ones had a greater proportion of negative hits, and almost no false alarms (none for B_{pa} and two (4.8%) for B_{lim}). A related analysis based upon Red List Criterion A4, which identifies populations as threatened for declines $\geq 30\%$, showed a much higher proportion of false alarms and lower overall alignment than analyses using Criterion A1 (Table S3).

To gain further insight into the extent of the alignment, and severity of misalignments, we compared the alignment of each population's individual estimated Red List category (Criterion A1: CR, EN, VU or not threatened) with its upper and lower fisheries reference points, as well as two additional MSY-based ones ($1.5B_{\text{msy}}$ and $0.2B_{\text{msy}}$). Five populations were considered to be of greatest concern from both conservation and fisheries perspectives, being classified as Critically Endangered and below their lowest fisheries reference point (B_{lim} or $0.2B_{\text{msy}}$): Irish Sea cod (*G.*

	Ref. point	Hit(+ve)	Hit (-ve)	Miss	False Alarm	Number of populations
A) Current Status	Upper	22.9	53.0	17.5	6.6	166
	Lower	15.7	65.1	5.4	13.9	166
B) Greatest Decline	Upper	47.0	33.1	6.6	13.3	166
	Lower	32.5	38.0	1.8	27.7	166

Table 5.2: The proportion (%) of populations meeting each of four possible alignment outcomes (positive hit, negative hit, miss or false alarm) under four different scenarios. A) Current estimated Red List status or B) Estimated Red List status following the population’s greatest decline, each compared to upper (more conservative; B_{msy} or B_{pa}) or lower (riskier; $0.5B_{msy}$ or B_{lim}) reference points.

morhua, Figure 5.3C), southern Atlantic coast red snapper (*L. campechanus*) and snowy grouper (*E. niveatus*), southern California cowcod (*S. levis*), and southern bluefin tuna (*T. maccoyii*). We found few egregious errors, where populations were categorized at opposite extremes of the fisheries and conservation metrics: only nine populations (4.8% of European, Table 5.3; and 3.2% of other populations, Table 5.4) that were below their lowest fisheries reference point were classified as not threatened, and only eleven populations (all B_{msy} -based ones) that were above their upper fisheries reference point were classified as threatened (0.8% EN and 4.0% VU; Table 5.4). Encouragingly, there were no cases where a population above its upper reference point was classified as Critically Endangered. In fact, most misalignments occurred when populations either were near the threshold of where they would be classified as threatened or near their fisheries reference points (e.g. Figure 5.3K-L).

Finally, the overall level of alignment between populations’ theoretical “worst case” conservation status, according to Criterion A1, and their fishery status at the corresponding point in time was similar to that of the current statuses: 80.1% for the upper fisheries reference points, and 70.5% for the lower ones (Table C.4). The relative proportion of positive and negative hits, however, was substantially different, with over twice as many positive hits under this worst case scenario than currently. Moreover, the number of false alarms doubled, occurring in 13.3% and 27.7% of populations when compared to upper and lower reference points respectively, while misses became rare (Table C.4).

5.4 Discussion

Extinction risk criteria and fisheries reference points provided consistent signals for most assessed marine fishes. Total alignment was high both for populations' current statuses (75.9% and 80.7% for upper and lower reference points, respectively) and their "worst case" scenarios (80.1% and 70.5%), although the composition of hits differed markedly (Table C.4). Negative hits dominated the alignment of populations' current statuses, indicating populations that are considered to be both well-managed and at a low risk of extinction. Still, almost 23% of populations currently are considered to be in trouble from both conservation and fisheries perspectives, and a further 24.1% are considered to be in trouble from either conservation (6.6%) or (the more conservative) fisheries perspectives (17.5%). In contrast, the "worst case" analysis was dominated by positive hits, revealing that almost half of populations would have been considered both threatened and overfished (by more conservative standards) at some point in their past (Table C.4). Although we focus our discussion solely on the analyses involving Criterion A1, we note that our general discussion points relating to the causes and consequences of misalignment between conservation and fisheries reference points, also holds for Criterion A4 (Table S3).

Despite high overall alignment, the concern that the Red List exaggerates the threat status of marine fishes (Matsuda et al., 1998; Punt, 2000) is warranted under some circumstances. We found the proportion of false alarms varied substantially depending on the time period and reference points, with the greatest proportion (27.7%) occurring when "worst case" Red Listings were compared to lower reference points (Table C.4). False alarms arise under this scenario because the reference points are so low that despite substantial declines, the populations remain above them. Notably, fewer than half of these same Red List evaluations were flagged as false alarms when the populations were benchmarked against upper reference points (13.3%, Table C.4).

False alarms reflect conflicting signals between conservation and fisheries metrics, and a concern is that threat listings in these cases may undermine successful fishery management, giving the impression that populations are not being properly managed even when, according to fishery metrics, they are. Additionally, legislation in Australia (Environmental Protection and Biodiversity Conservation Act), Canada

(Species at Risk Act), and the U.S. (Endangered Species Act) requires mandatory conservation measures be implemented if a population is deemed threatened with extinction (Rice and Legacè, 2007; Powles, 2011), potentially resulting in catch restrictions and lost income to communities depending on the resource. Critics of the Red List argue such conservation measures can be overly aggressive because rapid declines in managed fish populations typically result from the “fishing-down” phase of developing fisheries, in which biomass is reduced to a target level (e.g. B_{msy}) after which the exploitation rate is set to maintain the population at that level (Punt, 2000). Our analysis partially supports this contention: ten of eleven populations classified as false alarms in our “worst case” scenario analysis (whose decline ended at least ten years prior to the end of its time series, to allow investigation of subsequent population changes), subsequently stabilized above their upper fishery reference points, such that their current statuses aligned as negative hits. Recognizing this may occur, the IUCN guidelines provide flexibility in extinction risk evaluation for populations whose declines are being actively managed (IUCN Standards and Petitions Subcommittee, 2011). In fisheries lacking effective management controls, however, it seems unlikely that population declines would be curtailed in this manner. For these populations, false alarms may in fact be useful warning signals of impending overfishing. Indeed, even in our analysis of the most data-rich, and presumably best managed marine fishes effective curtailment of declining populations was not the norm: the majority of populations meeting the Red List A1 criterion for threatened also had fallen below their fisheries reference points and thus were positive hits, not false alarms (Table C.4).

Encouragingly, false alarms were rare when the current statuses of marine fishes were compared, especially when populations were benchmarked against their upper reference points ($n=14$, 6.6%, Table C.4; Figures 5.3J-L and S1). Few of these false alarms were egregious: none of the populations was listed as Critically Endangered, which would have indicated an enormous mismatch between the two metrics, and only three were listed as Endangered (Figure 5.3J, Tables 5.3 and 5.4). What’s more, two of the false alarms, smooth oreo (*Pseudocyttus maculatus*) on the west end of New Zealand’s Chatham Rise and orange roughy (*H. atlanticus*) along the mid-east coast of New Zealand, were very close to their fishery reference point thresholds (the latter

had recently been below it) and thus were on the verge of being classified as positive hits (Figure S1). Legitimate concern remains, however, for the other nine false alarms. Threat status was exaggerated for many of these populations because they started at very high biomass (mean = $4.9 B_{\text{msy}}$, range = 2.8 to $11.2 B_{\text{msy}}$; Figure S1). For populations exhibiting high long-term variability, such as these, establishing relevant population baselines is a challenge (Hilborn and Sibert, 1988). Greenland turbot (*R. hippoglossoides*) in the Bering Sea and Aleutian Islands, for example, plummeted only after peaking at an estimated 13 times B_{msy} during the 1970s North Pacific regime shift, and thus we evaluated it as Endangered when it was still at $1.5B_{\text{msy}}$ (Figure 5.3J). Notably, where extreme fluctuations or repeated natural population cycles are shown to be the drivers of declines, they are not to invoke threatened listings (Red List Guidelines Section 4.7: Extreme fluctuations) to avoid triggering false alarms.

Although false alarms are a real concern, the perception that the Red List is systematically biased towards exaggerating threat status in marine fishes is unfounded - misses also occur, and were in fact the main source of misalignment in our analysis of current status and upper reference points (17.5%; Table C.4, Figures 5.3G-I and S1). Four of these cases were egregious misalignments: Southern New England winter flounder (*P. americanus*) and three of yellowtail flounder (*L. ferruginea*) populations on the U.S. east coast were each below $0.2B_{\text{msy}}$ yet evaluated as not threatened (Tables 5.3 and 5.4). Yet, we caution that such misses should not necessarily be regarded as a failure of the Red List criterion. Exploited populations may stabilize at low biomass following substantial declines (as occurs in their initial fishing down phase), and if they persist in that state for multiple generations it suggests they do not face imminent extinction and the Red List criterion is working appropriately. Such populations would still require increased management and conservation attention to maintain current biomass levels or restore them to former levels. Misses are, however, of concern for those populations below their fishery reference points that have not stabilized, but instead continue to decline at a rate insufficient to trigger an IUCN threat listing and subsequent conservation action. In such cases, the Red List would only be effective if a population declined to the extent that it triggered one of the other threat criteria (IUCN Standards and Petitions Subcommittee, 2011). This could have serious implications for data-poor populations in which the fishery status is unknown

and the Red List is the only means of assessing population status, as it implies that populations requiring conservation attention will be overlooked.

The propensity for misses to occur appears greater for populations with shorter generation times and those for which artificially short generation times are used in Red List calculations (Dulvy et al., 2005; Rice and Legacè, 2007). Such populations must decline at a faster annual rate to trigger a threatened designation (Mace et al., 2008) and the three-generation period can be too short to capture the full extent of their declines, as illustrated by striped marlin (Figures 5.3H). Indeed, 39.1% of populations in our analysis for which the three generation period was ≤ 20 years were misses (when benchmarked against upper reference points), compared to only 9.2% for those with longer generation times. Similarly, when we fixed the three generation period for all populations to be 15 years (as in (Hutchings and Reynolds, 2004; Rice and Legacè, 2007)), the number of populations classified as Endangered or Critically Endangered dropped from twenty-seven to six, while the number of misses increased substantially (69% when benchmarked against upper reference points, 135% against lower ones; Tables C.4 and S4). This may explain why an earlier comparison of fishery statuses and Red List statuses estimated using shorter generation times had a much higher proportion of misses (48% overall; Dulvy et al. (2005)) than our analysis. Longer exploitation times also may increase the likelihood of misses because these populations are more likely to have already undergone their most substantial declines (during their initial fishing down phase) and have stabilized (e.g. Figure 5.3H).

Misalignment between Red Listings (A1) and fisheries reference points is heavily influenced by the fundamental difference in how these two metrics evaluate if populations are in trouble. The former is a rate based approach, while the latter is based upon relative biomass levels without reference to the time period over which the changes occurred. Perfect alignment would occur if, for example, all populations started at unfished biomass, B_0 , their maximum sustainable yields occurred at 50% of this level (i.e. the simplistic assumption of the Schaefer model (Schaefer, 1954)), and they declined by at least this amount. In reality, the proportion of B_0 at which B_{msy} occurs is strongly linked to compensatory population dynamics, and often occurs at much lower levels (Myers et al., 1999). Species with high maximum population growth rates, such as herring (*Clupea harengus*), can have $B_{\text{msy}}:B_0$ ratios between 0.20 and

0.30 (Hilborn and Stokes, 2010). Reference points also may be set at a fixed ratio of B_0 when data to estimate B_{msy} are lacking (e.g. Australia uses a default B_{msy} of $0.4 B_0$ in such cases (Hilborn and Stokes, 2010)). This mathematical disconnect is a major source of misalignment between these conservation and fishery metrics: whereas a $\geq 50\%$ decline would trigger a threatened listing under the Red List, a 70% or 85% decline would be needed for a productive population (assuming a $B_{\text{msy}}:B_0$ ratio of 0.3) to fall below its upper or lower fishery reference points, respectively (e.g. Figure 5.3J-L). These populations are prone to false alarms early in the development of their fisheries if their populations started at high biomass.

Several caveats must be borne in mind when interpreting our findings. First, although the Red List is primarily a species level assessment tool, we conducted our evaluations at the population level. Apart from the pragmatic reason that this facilitated direct comparisons fisheries assessments for widely distributed species, such as many marine fishes, the population is the most relevant level when considering ecological roles and contributions to individual ecosystems. Populations can be highly adapted to local conditions, such that specific morphological and behavioral adaptations may limit the potential for recolonization by populations from other regions (Hutchings, 2001). Moreover, loss of individual populations typically precedes species level extinctions (Musick et al., 2000; Gärdenfors et al., 2001). As such, regional Red List assessments have been conducted for many marine fish species (IUCN Standards and Petitions Subcommittee, 2011; IUCN, 2011). Second, only the most data rich populations, which have stock assessments and reference points, could be included in our analysis. These populations all are actively managed, which could limit the transferability of our findings to fisheries lacking the management control necessary to effectively curtail exploitation rates. For relatively data-poor fisheries (i.e. those without a stock assessment or reference points, but with some index of abundance), however, our results suggest threat listings could serve as accurate flags for ones that are in trouble.

Additionally, we assumed fishery reference points are true measures of marine fish population status. Clearly, however, there is great variation in the types of reference points used which can strongly influence alignment of fishery and conservation metrics (Tables C.4 - 5.4). Reference points used in Europe are, for example, set at a much

lower proportion of B_0 than MSY-based ones (Froese et al., 2010; Murawski, 2010), and we therefore had expected to find low levels of alignment for these populations. Instead, European populations had very high alignment (90.5%) compared to B_{msy} managed ones (77.4%), and alignments comprised mainly of negative hits (Table 5.3) despite these populations generally being in poor shape (Froese et al., 2010). This seemingly contradictory finding arises from the extremely low reference points and the long exploitation history of European populations, such that for these populations the majority of declines occurred prior to the most recent three-generation period and did not trigger the Red List threat criteria. If European fisheries management moves to more conservative B_{msy} -based reference points, as is proposed for 2015 (Froese and Proelß, 2010), many of these depleted but stable populations would likely become misses. A general move by fisheries management agencies around the world towards B_{msy} based reference points (Grafton et al., 2007; Hilborn, 2010), would help alleviate the problem of a lack of consistent reference points that has hindered recent global fisheries analyses (Worm et al., 2009; Hutchings et al., 2010; Ricard et al., 2012)

Reference point	IUCN Red List status (%)				Total populations
	CR	EN	VU	not threatened	
$\geq B_{\text{pa}}$	0.0	0.0	0.0	59.5	25
$< B_{\text{pa}} - \geq B_{\text{lim}}$	0.0	0.0	4.8	14.3	8
$< B_{\text{lim}}$	2.4	9.5	4.8	4.8	9
Total	2.4	9.5	9.5	78.6	42

Table 5.3: The proportion (%) alignment between the estimated IUCN Red List Status and the actual (upper (B_{pa}) and lower (B_{lim})) fishery reference points of European marine fish populations (managed by ICES). IUCN threatened categories are Critically Endangered (CR), Endangered (EN), Vulnerable (VU).

Perhaps the most critical assumption of our analysis is that we equated falling below a fishery reference point with a Red List threatened status, and hence an increased extinction risk. This assumption embodies a central component of the debate about the relevance of the Red List to marine fishes: few fisheries scientists would consider overfished populations to be at risk of extinction. Thus, while the mix of false alarms and misses in our results provides empirical support that the Red List is not systematically biased towards exaggerating when populations

Reference point	IUCN Red List status				Total populations
	CR	EN	VU	NT	
$> 1.5 B_{\text{msy}}$	0.0	0.8	4.0	32.3	46
1.0-1.5 B_{msy}	0.0	1.6	2.4	18.5	28
0.5-1.0 B_{msy}	0.0	3.2	4.8	11.3	24
0.2-0.5 B_{msy}	2.4	4.8	1.6	2.4	14
$< 0.2 B_{\text{msy}}$	3.2	1.6	1.6	3.2	12
Total	5.6	12.1	14.5	67.7	124

Table 5.4: The proportion (%) alignment between the estimated IUCN Red List Status and the actual B_{msy} fishery reference points of US and other non-European marine fish populations. IUCN threatened categories are Critically Endangered (CR), Endangered (EN), Vulnerable (VU).

are in trouble, the overall high degree of alignment suggests that the Red List does exaggerate actual extinction risk, since populations just below their reference points are unlikely to face a heightened risk of extinction. This conclusion is supported by simulation models that suggest marine fishes with threatened listings have low probabilities of going extinct in the near future (Matsuda et al., 1998; Punt, 2000), and by the discrepancy between the number of marine fishes listed on the Red List as being threatened with extinction ($n=399$, Fig. 1) and the number listed as having gone extinct ($n=1$, New Zealand Grayling (*Prototroctes oxyrinchus*) (IUCN, 2011)). Still, we acknowledge that the process of extinction is poorly understood (Mace et al., 2008; Reynolds et al., 2005; Hutchings, 2001), and that while global extinctions of marine fishes appear to be exceedingly rare, local extirpations are not (Dulvy et al., 2003). Thus, while it appears marine fishes listed as threatened are not necessarily imminently at risk of biological extinction, substantial declines in their abundance still are likely to have significant consequences for biodiversity, ecosystem functioning, and human welfare (Holmlund and Hammer, 1999), especially if such depletions are not easily reversed. Others have therefore suggested the Red List categories should be renamed as conservation priorities I-IV (Hutchings, 2001) to better reflect its intent of serving as a method of conservation prioritization. We believe such a renaming is unlikely, but would advocate consideration of the Red List threat categories in this

manner as a useful heuristic solution for helping to move the debate between the fisheries and conservation communities forward.

Despite fundamental differences in methodology, Red List and fisheries assessments for marine fishes align well. Thus, while debate about the relevance of the Red List to marine fishes continues (COSEWIC, 2005; Cooke, 2011), the empirical evidence indicates conservation and fisheries scientists will, in most cases, agree on which exploited marine fishes are in trouble and require improved management measures. We hope this research will encourage similar scrutiny of other conservation evaluation frameworks, which have been developed for marine fishes to “improve upon” the Red List (Musick, 1999; FAO, 2002; Powles, 2011). Those who argue that the Red List exaggerates threat status for marine fishes also may be surprised to learn the proportion of marine fishes listed as threatened on the Red List is very low (13.5%; Figure 5.1 IUCN (2011)). Although this contention was borne out for some of the marine fish populations in our analysis (typically those assessed against riskier reference points or in the “fishing down” phase of fishery development (Punt, 2000)), more populations were considered to be in trouble from both perspectives (positive hits) than by the Red List alone (false alarms). Moreover, for fisheries lacking stock assessments and management controls to curtail fishing mortality, such threat listings might serve as useful warnings signals of (impending) overfishing. Indeed, while stock assessments are a financial impossibility in most fisheries ($n \cong 350$ assessments globally (Ricard et al., 2012)), the Red List provides a relatively easy and transparent means of flagging populations in trouble ($n=2952$ marine fish assessments to date (IUCN, 2011)). Our results suggest it also is an accurate means of doing so. Thus, with momentum for conservation evaluations of marine fishes growing, we urge fisheries scientists to recognize the Red List as a useful, complementary approach to evaluating the global impacts of marine fisheries, and for the fisheries and conservation communities to work together to determine mutually acceptable management responses for population which they both deem to be of concern.

Chapter 6

Discussion

My thesis has yielded a number of important findings relevant to the estimation of population status and trajectory of exploited marine fishes and how conservation and fisheries reference points align.

6.1 Summary of Findings

In Chapter 2, I discuss some common assumptions that are used when estimating population abundance and trajectory of marine fishes. I critique a number of published studies that have used assumptions that later proved to be incorrect. For this chapter, I focus on a critical relationship in fish population models: how catch rates relate to population abundance both in time and space. I provide examples for how critical this assumption is and how the intersection of the spatial distribution of a fish population and the sampling method (i.e. fishery independent or fishery dependent collection methods) has the potential to result in biased estimates of population trends. Using biased estimates of population status in the management of fish populations without adequate precaution can lead to poor management outcomes and potentially catastrophic fishery collapses.

In Chapter 3, I examined the population status of cusk, a species that was categorized as “threatened” by COSEWIC in 2003, based on an estimated 93% decline between 1970 to 2001 in the DFO Scotian Shelf summer bottom trawl survey index. I demonstrate how fishery-independent data can also suffer from issues of nonproportionality and result in biased estimates of population status if the potential for nonproportionality is not accounted for in the model structure. The analysis used two indices of relative biomass, one fishery-dependent and the other fishery independent, in a Bayesian state-space model where I relaxed the assumption of strict proportionality of catch rates to population biomass by using a power curve relationship. I found that the research survey was strongly hyperdepleted, likely due to the differences in

habitat preferences of cusk and research survey site selection, and when used alone led to highly biased estimates of population decline. By incorporating multiple data sources and allowing for nonproportionality of the catch rates indices my estimates of decline over the same time period were 64% compared to 93% when only the research survey data was used. I also demonstrated that a metric used for Bayesian model selection, Deviance Information Criterion (DIC), was not a reliable metric for model selection for this particular modelling approach by conducting an extensive simulation evaluation. Further, I also demonstrated via simulation the consequences of assuming proportionality of the two non proportional catch rates indices would have on the inference of population trends.

In Chapter 4, I demonstrated how the abundance and distribution of different size classes of thorny skate have changed on the Scotian Shelf over the last 44 years. The analysis showed profound differences in changes in distribution and abundance of the different size classes with the most extreme changes occurring in adults. By assuming an ideal free distribution model I was able to show there was weak evidence for density dependent habitat selection for small juveniles but was likely for large juveniles and adults.

In Chapter 5 I examine how perceptions of population status are influenced by the method in which they are estimated. I compared the alignment of abundance based biological reference points that are used for the management of marine fisheries to those used to evaluate extinction risk by conservation organization. I found that the two approaches had a high degree of alignment (70.5% to 80.7% for riskier and more conservative reference points respectively) despite the differences in mathematical thresholds used by each approach. Further, the data necessary to estimate an extinction risk categorization is far less than most biological reference points and can therefore be employed in data limited situations. Indeed, both approaches should be considered to be complementary to evaluating the status marine fisheries and this research shows the common ground that both approaches share in the shared interest of population sustainability.

6.2 Future Research

My research has shed light on the consequences that poor assumptions, particularly about the spatial structure of a population, can have on the estimation of stock status. A number of lines of future research exist that would further the understanding about the research topics that I have examined here.

In Chapter 3, my explanation for the hyperdepletion in the research survey catch rate series was that cusk prefer rocky complex habitat that was not sufficiently sampled by the trawl gear and thus biased estimates of population decline. The critical assumption of my analysis was that the differences in the spatial coverage of the research survey and the spatial distribution of cusk is adequately approximated by the power curve that I employed in the observation equation of my population model. An alternate and more direct approach would be to standardize both the commercial fishery dependent and fishery independent catch rate series as they pertain to habitat characteristics at specific catch locations. At a minimum, this would provide an objective test to my conjecture that differences in the trends in relative abundance of the two series arose from the different habitats sampled by the two gear types.

In Chapter 4, I investigated changes in distribution of different size classes of thorny skate on the Scotian Shelf. What is lacking from these analyses is a causal link, i.e. what is responsible for these changes in distribution and abundance? All major sources of fishing mortality have been removed yet declines in abundance and changes in distribution are still being observed. Grey seals are a potential mechanism to explain these patterns, however, data are currently limited to test this hypothesis.

In my last research chapter, I compare fishery-based biological reference points to estimates of extinction derived using IUCN extinction risk criteria for 166 marine fish populations. There were, however, features of the data that were used for this analysis that may have exaggerated alignment between the two approaches. For my method of estimating extinction risk, I assigned each population to Red List Categories by calculating its proportional change in adult biomass over the longer of ten years or three generations. Many of the marine fishes examined have long generation times and the estimates of three generations (mean 38.1) exceeded the length of the time series that was used in analysis. Therefore, my estimates of extinction risk included the developmental phase of the fishery when a rapid “fishing down” of the population

is frequently a management objective to increase the population growth rate from compensatory density-dependent processes in the population dynamics. Once this decline phase is outside the three generation window, I expect comparisons of the rate based approach to calculate extinction risk to have much less alignment in population designations.

This research taken together increases our understanding of the population trends, and factors that may be affecting these observed trends for cusk and thorny skate. The high level of alignment I identified between extinction risk and fishery based reference points show that the methods used by fisheries and conservation scientists largely agree upon similar designations of stock status during the developmental phases of a fishery.

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Appendix A

Supplemental Information for Identifying Nonproportionality of Fishery Independent Survey Data to Estimate Population Trends and Assess Recovery Potential for Cusk (*Brosme brosme*) (Chapter 3)

Here I provide the WinBUGS code and data for the state-space surplus production model that also estimated a shape parameter in the observation equation for the fishery-independent trawl survey (I2). The code was modified from that published in Meyer and Millar (1999).

```
model; {
# Prior for intrinsic rate of increase; r
r ~ dunif(0, 4)
# Prior for carrying capacity K (t)
logK ~ dunif(8.56,13.12) # 8.56 is log(max(landing))
K <- exp(logK)
# Priors for catchabilities; q
for (i in 1:2) { q[i] ~ dunif(0,1) }
# Prior for process noise; sigma
sigma ~ dunif(0, 10)
isigma2 <- pow(sigma, -2)
# Prior for observation errors; tau
for(i in 1:2){ tau[i] ~ dunif(0, 10)
                itau2[i] <- pow(tau[i], -2) }
# Prior for shape parameter
shapeRV ~ dunif(0.01,10)
# Prior for initial population size as proportion of K; P[1]
Pmed[1]<-log(1) # proportion of carrying capacity
```

```

P[1] ~ dlnorm(Pmed[1], isigma2)I(0.01, 10)

# State equation
for(t in 2:T2) {
  Pmed[t] <- log(max(P[t-1] + r*P[t-1]*(1-P[t-1])-C[t-1]/K,0.0001))
  P[t] ~ dlnorm(Pmed[t], isigma2)I(0.0001, 10) }
# Observation equations
# Commerical Index
for (t in 1:T1) {
  Imed1[t] <- log(q[1] * K * P[t+16])
  I1[t] ~ dlnorm(Imed1[t], itau2[1])
  Pred1[t] ~ dlnorm(Imed1[t], itau2[1]) }
# Fishery independent survey with shape equation
for (t in 1:T2) {
  Imed2[t] <- log(q[2] * K * pow(P[t],shapeRV))
  I2[t] ~ dlnorm(Imed2[t], itau2[2])
  Pred2[t] ~ dlnorm(Imed2[t], itau2[2]) }
# Biomass estimation
for(t in 1:T2) {
  B[t] <- P[t] * K }
# Management Parameters
  MSY <- r * K / 4
  Bmsy <- K / 2 } }
# Data Section
list(I1=c(1.571590, 1.872840, 1.266000, 1.116690, 1.143340, 1.977970,
1.675930, 0.894639, 0.579649, 1.135370, 0.764688, 1.124050, 1.011710,
0.612211, 0.695887, 0.985724,0.649635, 0.443307, 0.686838, 0.572330,
0.412810, 0.683190),I2=c(0.00314667, 0.00436356, 0.00519993,
0.00386293, 0.00559915, 0.00443471, 0.00457475, 0.00496960, 0.00487649,
0.00365140, 0.00189693, 0.00420523, 0.00407129, 0.00258319, 0.00421571,

```

```
0.00190961, 0.00170143, 0.00425573, 0.00331920, 0.00266711, 0.00157374,  
0.00381933, 0.00107107, 0.00031410, 0.00033406, 0.00041117, 0.00037375,  
0.00045440, 0.00026304, 0.00044221, 0.00047269, 0.00054054, 0.00040099,  
0.00008497, 0.00030616, 0.00020843, 0.00020934, 0.00041708), T1=22,  
T2=38, C=c(2870, 4395, 5219, 5212,4638, 4557, 2402,2835, 4398, 4013,  
3616, 3488, 4417, 3176, 2399, 1831, 1639, 3154, 2279, 2304, 2448, 3125,  
3678, 2039, 1207, 1530, 1044, 1476, 1304, 880,732, 1043, 872 ,688, 492,  
632, 601))  
#init section (single chain)  
list(q=c(0.001, 0.001), r=0.1, sigma =0.5, tau=c(0.75 ,0.5), P=c(0.562,  
0.779, 0.929, 0.690, 1.00, 0.792, 0.817, 0.888, 0.871, 0.652, 0.339,  
0.751, 0.727, 0.461, 0.753, 0.341, 0.304, 0.760, 0.593, 0.476, 0.281,  
0.682, 0.191, 0.0561, 0.060, 0.073, 0.067, 0.0812, 0.0470, 0.079,  
0.084, 0.097, 0.072 ,0.015, 0.055, 0.037, 0.037, 0.074), logK=11,  
shapeRV=0.5)
```

Appendix B

Supplemental Information For Changes in the Distribution and Abundance of Different Size Classes of Thorny Skate (*Amblyraja radiata*) on the Scotian Shelf (Chapter 4)

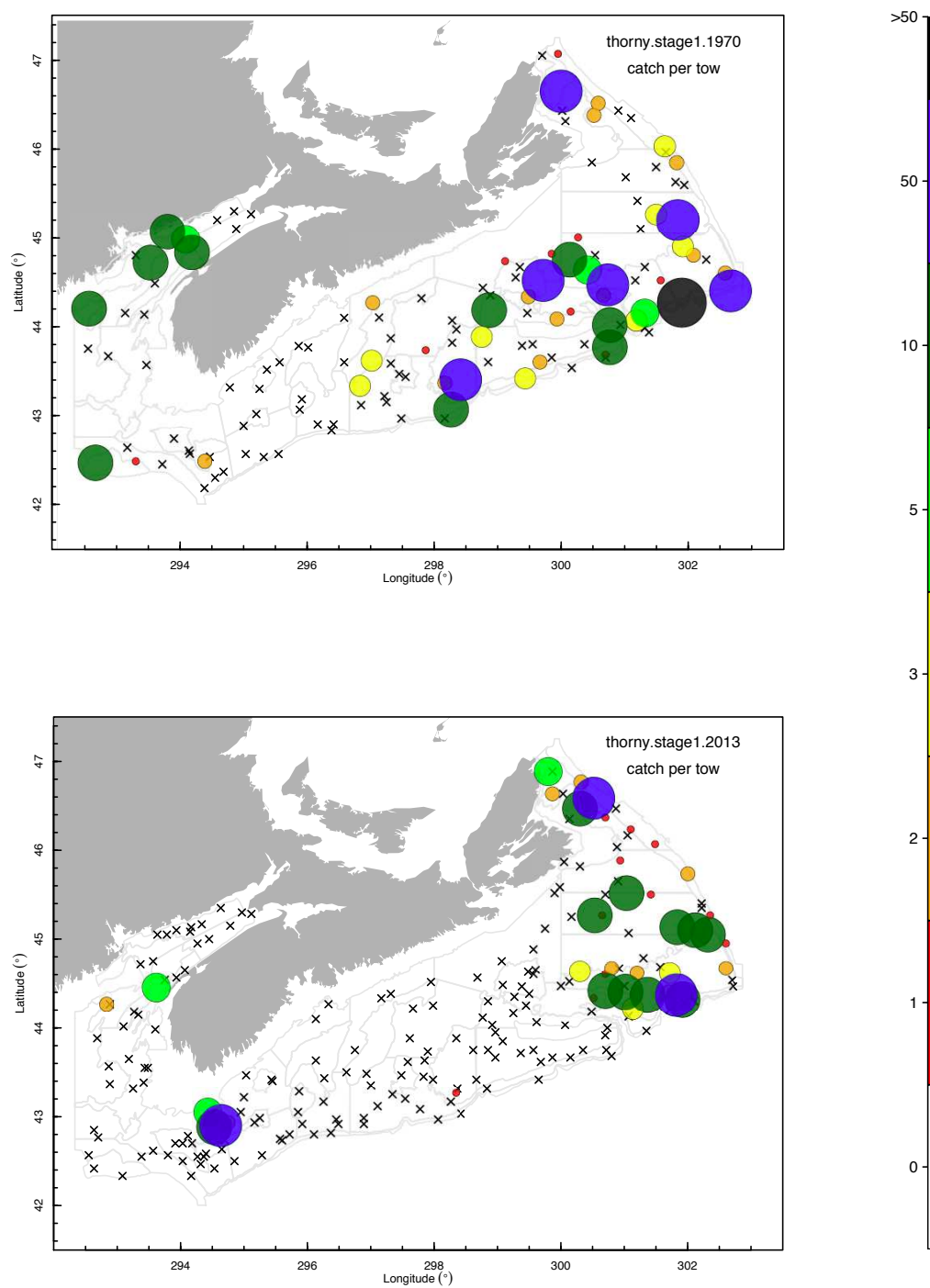


Figure B.1: Changes in small juvenile thorny skate catches from DFO summer survey from 1970 to 2013

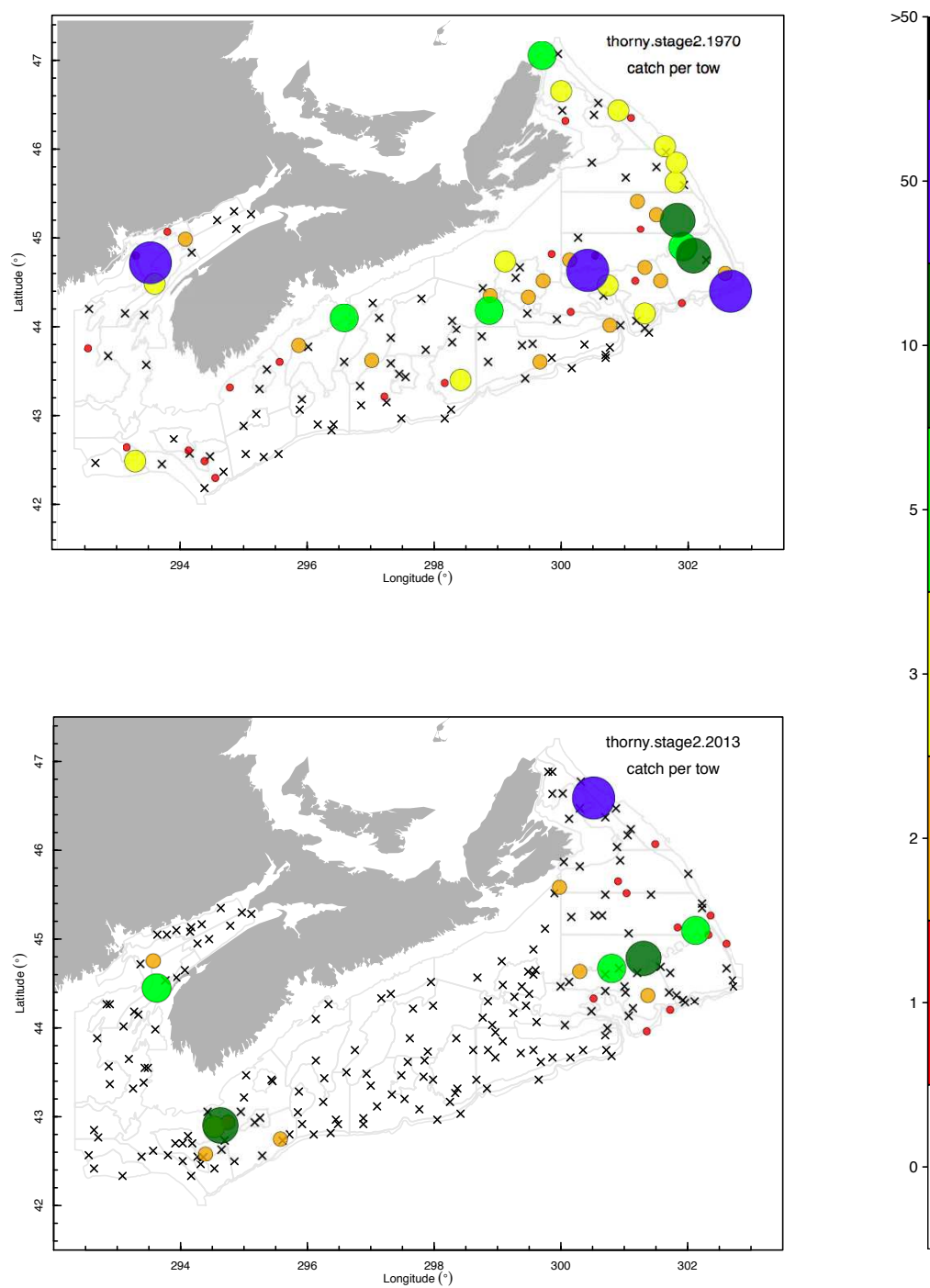


Figure B.2: Changes in large juvenile thorny skate catches from DFO summer survey from 1970 to 2013

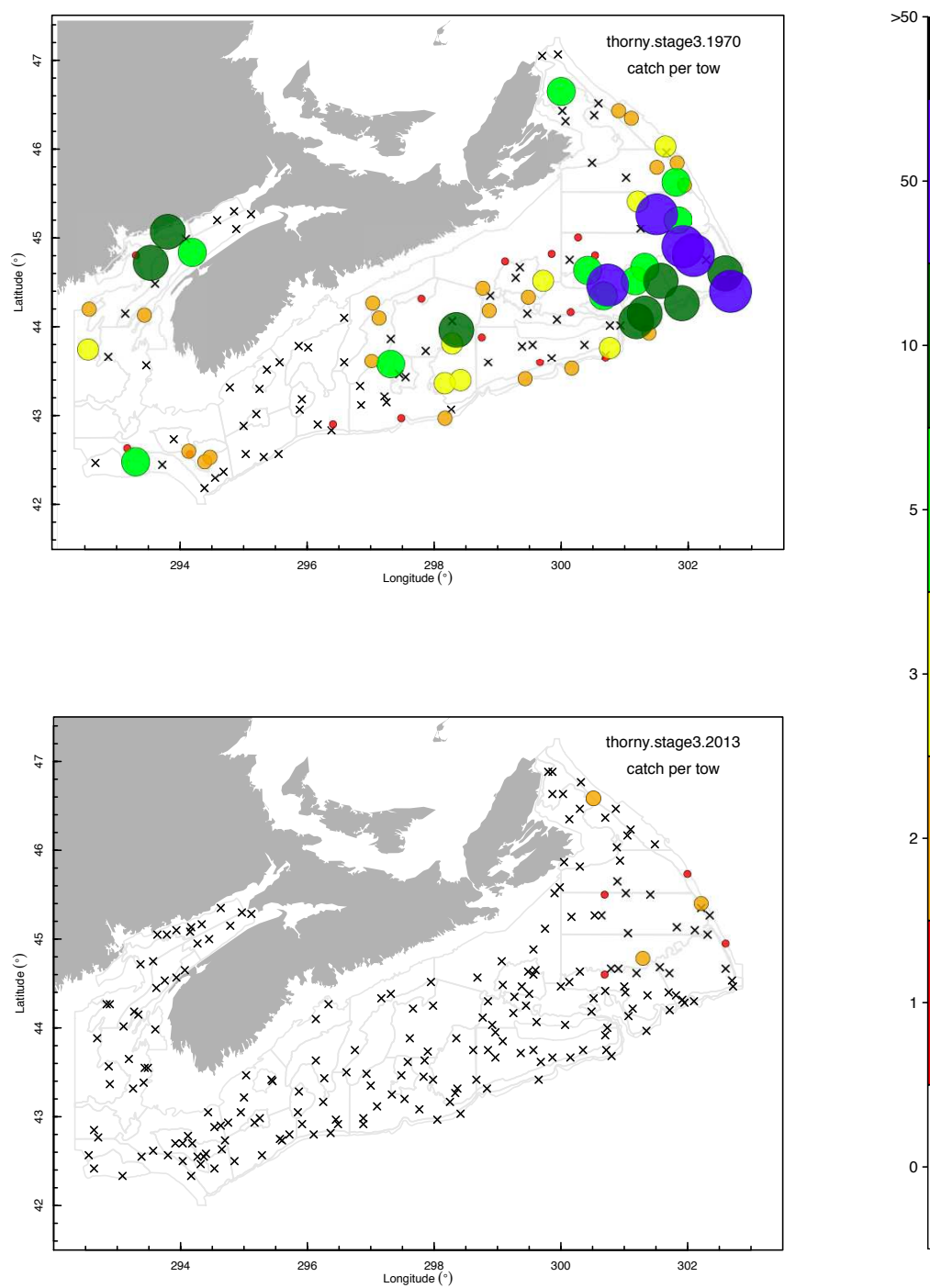


Figure B.3: Changes in adult thorny skate catches from DFO summer survey from 1970 to 2013

Appendix C

Supplemental Information For Extinction Risk and Overfishing: Reconciling Conservation and Fisheries Perspectives on the Status of Marine Fishes (Chapter 5)

Table C1. Description of the 166 assessed marine fish populations. Population ordering by stock identification code (from the RAM Legacy Database), description includes common and scientific name, management country, estimated generation time, and fishery reference point type.

Stockid	Common name	Scientific name	Management country	Generation length	Reference type
ACADREDGOMGB	Acadian redfish Gulf of Maine / Georges Bank	<i>Sebastes fasciatus</i>	USA	16.7	BMSY
ALBASPAC	Albacore tuna South Pacific Ocean	<i>Thunnus alalunga</i>	Multinational	6.4	BMSY
ALPLAICBSAI	Alaska plaice Bering Sea and Aleutian Islands	<i>Pleuronectes quadrituberculatus</i>	USA	12.7	BMSY
AMPL5YZ	American Plaice NAFO-5YZ	<i>Hippoglossoides platessoides</i>	USA	13.8	BMSY
ARFLOUNDBSAI	Arrowtooth flounder Bering Sea and Aleutian Islands	<i>Reinhardtius stomias</i>	USA	8.4	BMSY
ARFLOUNDGA	Arrowtooth flounder Gulf of Alaska	<i>Atheresthes stomias</i>	USA	8.4	BMSY
ARFLOUNDPCOAST	Arrowtooth flounder Pacific Coast	<i>Reinhardtius stomias</i>	USA	10.1	BMSY
ARGANCHONARG	Argentine anchoita Northern Argentina	<i>Engraulis anchoita</i>	Argentina	2.5	BMSY
ARGANCHOSARG	Argentine anchoita Southern Argentina	<i>Engraulis anchoita</i>	Argentina	2.5	BMSY
ARGHAKENARG	Argentine hake Northern Argentina	<i>Merluccius hubbsi</i>	Argentina	5.5	BMSY
ARGHAKESARG	Argentine hake Southern Argentina	<i>Merluccius hubbsi</i>	Argentina	5.5	BMSY
ATBTUNAWATL	Bluefin tuna Western Atlantic	<i>Thunnus thynnus</i>	Multinational	14.0	BMSY
ATKABSAI	Atka mackerel Bering Sea and Aleutian Islands	<i>Pleurogrammus monopterygius</i>	USA	6.2	BMSY
ATLCROAKMATLC	Atlantic croaker Mid-Atlantic Coast	<i>Micropogonias undulatus</i>	USA	1.6	BMSY
AUSSALMONNZ	Australian salmon New Zealand	<i>Arripis trutta</i>	New Zealand	9.5	BMSY
BGROCKPCOAST	Blackgill rockfish Pacific Coast	<i>Sebastes melanostomus</i>	USA	37.5	BMSY
BIGEYEIO	Bigeye tuna Indian Ocean	<i>Thunnus obesus</i>	Multinational	5.6	BMSY
BIGEYEWPO	Bigeye tuna Western Pacific Ocean	<i>Thunnus obesus</i>	Multinational	5.5	BMSY
BLACKOREOWECR	Black oreo West end of Chatham Rise	<i>Allocyttus niger</i>	New Zealand	53.5	BMSY
BLACKROCKNPCOAST	Black rockfish Northern Pacific Coast	<i>Sebastes melanops</i>	USA	20.2	BMSY
BLACKROCKSPCOAST	Black rockfish Southern Pacific Coast	<i>Sebastes melanops</i>	USA	17.8	BMSY
BLUEROCKCAL	Blue rockfish California	<i>Sebastes mystinus</i>	USA	15.5	BMSY
BSBASSMATLC	Black sea bass Mid-Atlantic Coast	<i>Centropristis striata</i>	USA	5.3	BMSY
CABEZNCAL	Cabezon Northern California	<i>Scorpaenichthys marmoratus</i>	USA	5.5	BMSY
CABEZSCAL	Cabezon Southern California	<i>Scorpaenichthys marmoratus</i>	USA	5.5	BMSY
CHAKESA	Shallow-water cape hake South Africa	<i>Merluccius capensis</i>	South Africa	4.0	BMSY
CMACKPCOAST	Pacific chub mackerel Pacific Coast	<i>Scomber japonicus</i>	USA	6.7	BMSY
CODBA2224	Atlantic cod Baltic Areas 22 and 24	<i>Gadus morhua</i>	Multinational	8.4	Bpa
CODCOASTNOR	Atlantic cod coastal Norway	<i>Gadus morhua</i>	Multinational	10.0	Bpa
CODFAPL	Atlantic cod Faroe Plateau	<i>Gadus morhua</i>	Multinational	8.5	Bpa
CODGB	Atlantic cod Georges Bank	<i>Gadus morhua</i>	USA	7.8	BMSY
CODICE	Atlantic cod Iceland	<i>Gadus morhua</i>	Multinational	11.1	Bpa
CODIS	Atlantic cod Irish Sea	<i>Gadus morhua</i>	Multinational	7.7	Bpa
CODKAT	Atlantic cod Kattegat	<i>Gadus morhua</i>	Multinational	7.7	Bpa
CODNEAR	Atlantic cod Northeast Arctic	<i>Gadus morhua</i>	Multinational	11.1	Bpa
CODNS	Atlantic cod North Sea	<i>Gadus morhua</i>	Multinational	9.0	Bpa
CODVIa	Atlantic cod West of Scotland	<i>Gadus morhua</i>	Multinational	7.7	Bpa
COWCODSCAL	Cowcod Southern California	<i>Sebastes levis</i>	USA	22.0	BMSY
CROCKPCOAST	Canary rockfish Pacific Coast	<i>Sebastes pinniger</i>	USA	30.7	BMSY
DEEPCHAKESA	Deep-water cape hake South Africa	<i>Merluccius paradoxus</i>	South Africa	3.5	BMSY

DEEPFLATHEADSE	Deepwater flathead Southeast Australia	<i>Platycephalus conatus</i>	Australia	11.3	BMSY
DSOLEPCOAST	Dover sole Pacific Coast	<i>Microstomus pacificus</i>	USA	16.3	BMSY
DUSROCKGA	Dusky rockfish Gulf of Alaska	<i>Sebastes variabilis</i>	USA	27.5	BMSY
ESOLEPCOAST	English sole Pacific Coast	<i>Parophrys vetulus</i>	USA	10.0	BMSY
FLSOLEBSAI	Flathead sole Bering Sea and Aleutian Islands	<i>Hippoglossoides elassodon</i>	USA	12.5	BMSY
FLSOLEGA	Flathead sole Gulf of Alaska	<i>Hippoglossoides elassodon</i>	USA	11.8	BMSY
GAGGM	Gag Gulf of Mexico	<i>Mycteroperca microlepis</i>	USA	10.5	BMSY
GAGSATLC	Gag Southern Atlantic coast	<i>Mycteroperca microlepis</i>	USA	10.1	BMSY
GEMFISHNZ	common gemfish New Zealand	<i>Rexea solandri</i>	New Zealand	10.0	BMSY
GEMFISHSE	common gemfish Southeast Australia	<i>Rexea solandri</i>	Australia	6.3	BMSY
GHALBSAI	Greenland turbot Bering Sea and Aleutian Islands	<i>Reinhardtius hippoglossoides</i>	USA	13.1	BMSY
GOPHERSPCOAST	Gopher rockfish Southern Pacific Coast	<i>Sebastes carnatus</i>	USA	10.1	BMSY
GRAMBERSATLC	Greater amberjack Southern Atlantic coast	<i>Seriola dumerili</i>	USA	5.2	BMSY
HAD5Y	Haddock NAFO-5Y	<i>Melanogrammus aeglefinus</i>	USA	6.8	BMSY
HADFAPL	Haddock Faroe Plateau	<i>Melanogrammus aeglefinus</i>	Multinational	7.3	Bpa
HADGB	Haddock Georges Bank	<i>Melanogrammus aeglefinus</i>	USA	6.5	BMSY
HADICE	Haddock Iceland	<i>Melanogrammus aeglefinus</i>	Multinational	8.0	Bpa
HADNEAR	Haddock Northeast Arctic	<i>Melanogrammus aeglefinus</i>	Multinational	9.5	Bpa
HADNS-IIIa	Haddock ICES IIIa and North Sea	<i>Melanogrammus aeglefinus</i>	Multinational	6.9	Bpa
HADV1a	Haddock West of Scotland	<i>Melanogrammus aeglefinus</i>	Multinational	6.5	Bpa
HERR30	Herring ICES 30	<i>Clupea harengus</i>	Multinational	7.2	Bpa
HERRIsum	Herring Iceland (Summer spawners)	<i>Clupea harengus</i>	Multinational	8.0	Bpa
HERRNIRS	Herring Northern Irish Sea	<i>Clupea harengus</i>	Multinational	6.7	Bpa
HERRNS	Herring North Sea	<i>Clupea harengus</i>	Multinational	7.0	Bpa
HERRNWATLC	Atlantic herring Northwestern Atlantic Coast	<i>Clupea harengus</i>	USA	7.7	BMSY
HERRV1a	Herring ICES VIa	<i>Clupea harengus</i>	Multinational	6.9	Bpa
HERRV1aVIIbc	Herring ICES VIa-VIIb-VIIc	<i>Clupea harengus</i>	Multinational	6.9	Bpa
KELPGREENLINGORECOAST	Kelp greenling Oregon Coast	<i>Hexagrammos decagrammus</i>	USA	6.3	BMSY
KINGKLIPSA	Kingklip South Africa	<i>Genypterus capensis</i>	South Africa	11.3	BMSY
LNOSEKAPCOAST	Longnose skate Pacific Coast	<i>Raja rhina</i>	USA	16.6	BMSY
LSTHORNHPCOAST	Longspine thornyhead Pacific Coast	<i>Sebastolobus altivelis</i>	USA	21.4	BMSY
MACKGOMCHATT	Atlantic mackerel Gulf of Maine / Cape Hatteras	<i>Scomber scombrus</i>	USA	6.2	BMSY
MORWONGSE	Jackass morwong Southeast Australia	<i>Nemadactylus macropterus</i>	Australia	14.7	BMSY
MUTSNAPSATLCGM	Mutton snapper Southern Atlantic coast and Gulf of Mexico	<i>Lutjanus analis</i>	USA	12.8	BMSY
NPOUTNS	Norway pout North Sea	<i>Trisopterus esmarkii</i>	Multinational	2.2	Bpa
NROCKBSAI	Northern rockfish Bering Sea and Aleutian Islands	<i>Sebastes polyspinis</i>	USA	18.4	BMSY
NROCKGA	Northern rockfish Gulf of Alaska	<i>Sebastes polyspinis</i>	USA	26.5	BMSY
NRSOLEEBSAI	Northern rock sole Eastern Bering Sea and Aleutian Islands	<i>Lepidopsetta polyzostra</i>	USA	11.6	BMSY
NZLINGESE	New Zealand ling Eastern half of Southeast Australia	<i>Genypterus blacodes</i>	Australia	9.7	BMSY
NZLINGLIN3-4	New Zealand ling New Zealand Areas LIN 3 and 4	<i>Genypterus blacodes</i>	New Zealand	14.3	BMSY
NZLINGLIN5-6	New Zealand ling New Zealand Areas LIN 5 and 6	<i>Genypterus blacodes</i>	New Zealand	13.5	BMSY
NZLINGLIN6b	New Zealand ling New Zealand Area LIN 6b	<i>Genypterus blacodes</i>	New Zealand	14.3	BMSY
NZLINGLIN72	New Zealand ling New Zealand Area LIN 72	<i>Genypterus blacodes</i>	New Zealand	14.1	BMSY
NZLINGLIN7WC	New Zealand ling New Zealand Area LIN 7WC - WCSI	<i>Genypterus blacodes</i>	New Zealand	13.7	BMSY

NZLINGWSE	New Zealand ling Western half of Southeast Australia	<i>Genypterus blacodes</i>	Australia	9.7	BMSY
NZSNAPNZS	New Zealand snapper New Zealand Area 8	<i>Chrysophrys auratus</i>	New Zealand	11.0	BMSY
OROUGHYNZMEC	Orange roughy New Zealand Mid East Coast	<i>Hoplostethus atlanticus</i>	New Zealand	60.7	BMSY
OROUGHYSE	Orange roughy Southeast Australia	<i>Hoplostethus atlanticus</i>	Australia	69.0	BMSY
PATGRENADIERSARG	Patagonian grenadier Southern Argentina	<i>Macruronus magellanicus</i>	Argentina	8.9	BMSY
PCODBSAI	Pacific cod Bering Sea and Aleutian Islands	<i>Gadus macrocephalus</i>	USA	8.2	BMSY
PCODGA	Pacific cod Gulf of Alaska	<i>Gadus macrocephalus</i>	USA	7.7	BMSY
PERCHEBSAI	Pacific Ocean perch Eastern Bering Sea and Aleutian Islands	<i>Sebastes alutus</i>	USA	32.9	BMSY
PHAKEPCOAST	Pacific hake Pacific Coast	<i>Merluccius productus</i>	USA	6.0	BMSY
PLAICECHW	European Plaice ICES VIIe	<i>Pleuronectes platessa</i>	Multinational	14.7	Bpa
POLLFAPL	Pollock Faroe Plateau	<i>Pollachius virens</i>	Multinational	10.0	Bpa
POLLNEAR	Pollock Northeast Arctic	<i>Pollachius virens</i>	Multinational	10.0	Bpa
POLLNS-VI-IIIa	Pollock ICES IIIa, VI and North Sea	<i>Pollachius virens</i>	Multinational	9.6	Bpa
POPERCHGA	Pacific ocean perch Gulf of Alaska	<i>Sebastes alutus</i>	USA	32.9	BMSY
POPERCHPCOAST	Pacific ocean perch Pacific Coast	<i>Sebastes alutus</i>	USA	31.0	BMSY
PSOLENPCOAST	Petrale sole Northern Pacific Coast	<i>Eopsetta jordani</i>	USA	10.0	BMSY
PSOLESPCOAST	Petrale sole Southern Pacific Coast	<i>Eopsetta jordani</i>	USA	10.0	BMSY
PTOOTHFISHMI	Patagonian toothfish Macquarie Island	<i>Dissostichus eleginoides</i>	Australia	23.0	BMSY
PTOOTHFISHPEI	Patagonian toothfish South Africa Subantarctic Prince Edward Islands	<i>Dissostichus eleginoides</i>	South Africa	23.0	BMSY
REXSOLEGA	Rex sole Gulf of Alaska	<i>Glyptocephalus zachirus</i>	USA	10.9	BMSY
REYEROCKBSAI	Rougheye rockfish Bering Sea and Aleutian Islands	<i>Sebastes aleutianus</i>	USA	49.3	BMSY
REYEROCKGA	Rougheye rockfish Gulf of Alaska	<i>Sebastes aleutianus</i>	USA	49.3	BMSY
RPORGYSATLC	Red porgy Southern Atlantic coast	<i>Pagrus pagrus</i>	USA	6.0	BMSY
RSNAPEGM	Red snapper Eastern Gulf of Mexico	<i>Lutjanus campechanus</i>	USA	15.7	BMSY
RSNAPSATLC	Red snapper Southern Atlantic coast	<i>Lutjanus campechanus</i>	USA	15.5	BMSY
RSNAPWGM	Red snapper Western Gulf of Mexico	<i>Lutjanus campechanus</i>	USA	15.7	BMSY
SABLEFEBSAIGA	Sablefish Eastern Bering Sea / Aleutian Islands / Gulf of Alaska	<i>Anoplopoma fimbria</i>	USA	33.4	BMSY
SABLEFPCAN	Sablefish Pacific Coast of Canada	<i>Anoplopoma fimbria</i>	Canada	32.8	BMSY
SBT	Southern bluefin tuna Southern Oceans	<i>Thunnus maccoyii</i>	Multinational	18.0	BMSY
SBWHITACIR	Southern blue whiting Campbell Island Rise	<i>Micromesistius australis</i>	New Zealand	8.0	BMSY
SFLOUNMATLC	Summer flounder Mid-Atlantic Coast	<i>Paralichthys dentatus</i>	USA	3.2	BMSY
SILVERFISHSE	Silverfish Southeast Australia	<i>Seriolella punctata</i>	Australia	8.0	BMSY
SKJCWPAC	Skipjack tuna Central Western Pacific	<i>Katsuwonus pelamis</i>	Multinational	3.2	BMSY
SMOOTHOREOCR	Smooth oreo Chatham Rise	<i>Pseudocyttus maculatus</i>	New Zealand	47.9	BMSY
SMOOTHOREOWECR	Smooth oreo West end of Chatham Rise	<i>Pseudocyttus maculatus</i>	New Zealand	44.1	BMSY
SNOWGROUPSATLC	Snowy grouper Southern Atlantic coast	<i>Epinephelus niveatus</i>	USA	9.7	BMSY
SOLECS	common European sole Celtic Sea	<i>Solea vulgaris</i>	Multinational	8.8	Bpa
SOLEIS	common European sole Irish Sea	<i>Solea vulgaris</i>	Multinational	8.3	Bpa
SOLEVIII	common European sole Bay of Biscay	<i>Solea vulgaris</i>	Multinational	8.3	Bpa
SOUTHHAKECR	Southern hake Chatham Rise	<i>Merluccius australis</i>	New Zealand	12.7	BMSY
SOUTHHAKESA	Southern hake Sub-Antarctic	<i>Merluccius australis</i>	New Zealand	12.9	BMSY
SPANMACKSATLC	Spanish mackerel Southern Atlantic Coast	<i>Scomberomorus maculatus</i>	USA	1.7	BMSY
SSTHORNHPCOAST	Shortspine thornyhead Pacific Coast	<i>Sebastolobus alacanus</i>	USA	35.5	BMSY
STFLOUNNPCOAST	Starry flounder Northern Pacific Coast	<i>Platichthys stellatus</i>	USA	8.3	BMSY

STFLOUNSPCOAST	Starry flounder Southern Pacific Coast	<i>Platichthys stellatus</i>	USA	8.3	BMSY
STMARLINSWPO	Striped marlin Southwestern Pacific Ocean	<i>Kajikia audax</i>	Multinational	5.3	BMSY
SWHITSE	School whiting Southeast Australia	<i>Sillago findersi</i>	Australia	6.0	BMSY
TIGERFLATSE	Tiger flathead Southeast Australia	<i>Neoplatycephalus richardsoni</i>	Australia	9.3	BMSY
TILESATLC	Tilefish Southern Atlantic coast	<i>Lopholatilus chamaeleonticeps</i>	USA	14.6	BMSY
TREVALLYTRE7	Trevally New Zealand Areas TRE 7	<i>Pseudocaranx dentex</i>	New Zealand	16.0	BMSY
WAREHOUSEE	Blue Warehou Eastern half of Southeast Australia	<i>Seriola lalandi</i>	Australia	6.0	BMSY
WAREHOUSEW	Blue Warehou Western half of Southeast Australia	<i>Seriola lalandi</i>	Australia	6.0	BMSY
WEAKFISHATLC	Weakfish Atlantic Coast	<i>Cynoscion regalis</i>	USA	5.3	BMSY
WHAKEGBGOM	White hake Georges Bank / Gulf of Maine	<i>Urophycis tenuis</i>	USA	7.7	BMSY
WHITNS-VIIId-IIIa	Whiting ICES IIIa, VIId and North Sea	<i>Merlangius merlangus</i>	Multinational	6.1	Bpa
WHITVIIek	Whiting ICES VIIe-k	<i>Merlangius merlangus</i>	Multinational	5.9	Bpa
WINFLOUN5Z	Winter Flounder NAFO-5Z	<i>Pseudopleuronectes americanus</i>	USA	4.9	BMSY
WINFLOUNSNEMATL	Winter Flounder Southern New England-Mid Atlantic	<i>Pseudopleuronectes americanus</i>	USA	5.7	BMSY
WITFLOUN5Y	Witch Flounder NAFO-5Y	<i>Glyptocephalus cynoglossus</i>	USA	10.7	BMSY
WPOLLAI	Walleye pollock Aleutian Islands	<i>Theragra chalcogramma</i>	USA	7.1	BMSY
WPOLLEBS	Walleye pollock Eastern Bering Sea	<i>Theragra chalcogramma</i>	USA	6.4	BMSY
WPOLLGA	Walleye pollock Gulf of Alaska	<i>Theragra chalcogramma</i>	USA	9.2	BMSY
YELLCCODGOM	Yellowtail flounder Cape Cod / Gulf of Maine	<i>Limanda ferruginea</i>	USA	4.5	BMSY
YELLGB	Yellowtail flounder Georges Bank	<i>Limanda ferruginea</i>	USA	4.5	BMSY
YELLSNEMATL	Yellowtail Flounder Southern New England-Mid Atlantic	<i>Limanda ferruginea</i>	USA	4.5	BMSY
YEYEROCKPCOAST	Yelloweye rockfish Pacific Coast	<i>Sebastes ruberrimus</i>	USA	42.1	BMSY
YFINATL	Yellowfin tuna Atlantic	<i>Thunnus albacares</i>	Multinational	3.7	BMSY
YFINCWPAC	Yellowfin tuna Central Western Pacific	<i>Thunnus albacares</i>	Multinational	3.7	BMSY
YSOLEBSAI	Yellowfin sole Bering Sea and Aleutian Islands	<i>Limanda aspera</i>	USA	14.4	BMSY
YTROCKNPNCOAST	Yellowtail rockfish Northern Pacific Coast	<i>Sebastes flavidus</i>	USA	21.3	BMSY
ANCHOBAYB	Anchovy ICES VIII	<i>Engraulis encrasicolus</i>	Multinational	2.0	Bpa
CODVIIek	Celtic Sea cod	<i>Gadus morhua</i>	Multinational	7.7	Bpa
HADROCK	Haddock Rockall Bank	<i>Melanogrammus aeglefinus</i>	Multinational	6.9	Bpa
HERRSIRS	Celtic Sea and South of Ireland Herring	<i>Ammodytes marinus</i>	Multinational	6.7	Bpa
PLAICNS	European Plaice North Sea	<i>Pleuronectes platessa</i>	Multinational	14.4	Bpa
POLLIEG	Iceland and East Greenland pollock in Division Va (Icelandic saithe)	<i>Ammodytes marinus</i>	Multinational	9.6	Bpa
SEELNSSA1	North Sea Sandeel in the Dogger Bank area (SA 1)	<i>Ammodytes marinus</i>	Multinational	3.6	Bpa
SEELNSSA2	North Sea Sandeel in the South Eastern North Sea (SA 2)	<i>Clupea harengus</i>	Multinational	3.6	Bpa
SEELNSSA3	North Sea Sandeel in the Central Eastern North Sea (SA 3)	<i>Pollachius virens</i>	Multinational	3.6	Bpa
SOLENS	common European sole North Sea	<i>Solea vulgaris</i>	Multinational	8.4	Bpa
SOLEVIId	common European sole ICES VIId	<i>Solea vulgaris</i>	Multinational	8.7	Bpa
WHITVIa	Whiting ICES VIa	<i>Merlangius merlangus</i>	Multinational	6.1	Bpa

Table C.1:

Table C2. Threat status and alignment for the 166 assessed marine fish populations. Population ordering by stock identification code. Included are the estimated percent decline (numbers in parentheses indicate an increase in population biomass), estimated Red List threat status, biomass relative to reference point at end of decline, alignment between threat status and the upper and lower fisheries references points, and final year of the population decline. IUCN threatened categories are Critically Endangered (CR), Endangered (EN), Vulnerable (VU) and not threatened. Refer to Table S1 for further population descriptions.

Stockid	Percent decline	Estimated IUCN threat category	Biomass relative to upper reference point	Alignment relative to upper reference point	Alignment relative to lower reference point	Final Year
ACADREDGOMGB	(59.9)	not threatened	0.7	miss	-ve hit	2007
ALBASPAC	42.6	not threatened	2.7	-ve hit	-ve hit	2006
ALPLAICBSAI	(38.5)	not threatened	2.2	-ve hit	-ve hit	2008
AMPL5YZ	59.1	VU	0.6	+ve hit	false	2007
ARFLOUNDBSAI	(274.4)	not threatened	2.5	-ve hit	-ve hit	2008
ARFLOUNDGA	(104.9)	not threatened	3.0	-ve hit	-ve hit	2010
ARFLOUNDP Coast	(56.6)	not threatened	3.6	-ve hit	-ve hit	2007
ARGANCHONARG	24	not threatened	1.8	-ve hit	-ve hit	2007
ARGANCHOSARG	16.4	not threatened	2.6	-ve hit	-ve hit	2007
ARGHAKENARG	66.6	VU	0.2	+ve hit	+ve hit	2007
ARGHAKESARG	25.8	not threatened	0.4	miss	miss	2008
ATBTUNAWATL	81.3	EN	0.6	+ve hit	false	2007
ATKABSAI	8.2	not threatened	1.7	-ve hit	-ve hit	2009
ATLCROAKMATLC	(5.7)	not threatened	1.5	-ve hit	-ve hit	2002
AUSSALMONNZ	50.3	VU	1.7	false	false	2006
BGROCKPCoast	47.6	not threatened	1.3	-ve hit	-ve hit	2005
BIGEYEIO	54	VU	1.3	false	false	2004
BIGEYEWPO	35.9	not threatened	1.2	-ve hit	-ve hit	2006
BLACKKOREOWECR	69	VU	1.0	+ve hit	false	2007
BLACKROCKNPCoast	47.1	not threatened	1.7	-ve hit	-ve hit	2006
BLACKROCKSPCoast	26.5	not threatened	2.1	-ve hit	-ve hit	2007
BLUEROCKCAL	65.2	VU	0.7	+ve hit	false	2007
BSBASSMATLC	(65.2)	not threatened	0.9	miss	-ve hit	2007
CABEZNCAL	(32)	not threatened	1.1	-ve hit	-ve hit	2005
CABEZSCAL	(35.5)	not threatened	0.6	miss	-ve hit	2005
CHAKESA	30	not threatened	2.2	-ve hit	-ve hit	2008
CMACKPCoast	75.9	EN	0.5	+ve hit	+ve hit	2008
CODBA2224	2.3	not threatened	1.2	-ve hit	hit.n	2011
CODCOASTNOR	46.3	not threatened	0.5	miss	miss	2010
CODFAPL	56.9	VU	0.8	+ve hit	false	2011
CODGB	76	EN	0.1	+ve hit	+ve hit	2007
CODICE	(4.7)	not threatened	1.7	-ve hit	hit.n	2011
CODIS	90.5	CR	0.1	+ve hit	hit.p	2010
CODKAT	80	EN	0.2	+ve hit	hit.p	2010
CODNEAR	(287.6)	not threatened	2.1	-ve hit	hit.n	2010
CODNS	58.3	VU	0.4	+ve hit	hit.p	2011
CODVIa	67.3	VU	0.3	+ve hit	hit.p	2011
COWCODSCAL	94.4	CR	0.1	+ve hit	+ve hit	2007

CROCKPCOAST	77.2	EN	0.6	+ve hit	false	2009
DEEPCHAKESA	23	not threatened	0.8	miss	-ve hit	2008
DEEPFLATHEADSE	48.2	not threatened	1.4	-ve hit	-ve hit	2007
DSOLEPCOAST	20.9	not threatened	1.5	-ve hit	-ve hit	2005
DUSROCKGA	(200.1)	not threatened	1.5	-ve hit	-ve hit	2007
ESOLEPCOAST	(170.1)	not threatened	6.4	-ve hit	-ve hit	2007
FLSOLEBSAI	(1097.6)	not threatened	1.9	-ve hit	-ve hit	2008
FLSOLEGA	(61.5)	not threatened	2.6	-ve hit	-ve hit	2010
GAGGM	(16.3)	not threatened	1.0	miss	-ve hit	2004
GAGSATLC	16.5	not threatened	0.9	miss	-ve hit	2005
GEMFISHNZ	70.9	EN	1.6	false	false	2006
GEMFISHSE	69.7	VU	0.2	+ve hit	+ve hit	2007
GHALBSAI	86.9	EN	1.5	false	false	2009
GOPHERSPCOAST	(69.8)	not threatened	2.5	-ve hit	-ve hit	2005
GRAMBERSATLC	(0.6)	not threatened	1.3	-ve hit	-ve hit	2006
HAD5Y	(308.7)	not threatened	1.1	-ve hit	-ve hit	2007
HADFAPL	46.6	not threatened	0.7	miss	hit.n	2011
HADGB	(1085.4)	not threatened	1.5	-ve hit	-ve hit	2007
HADICE	(66.6)	not threatened	1.6	-ve hit	hit.n	2011
HADNEAR	(311.7)	not threatened	3.4	-ve hit	hit.n	2010
HADNS-IIIa	(147.1)	not threatened	1.5	-ve hit	hit.n	2011
HADV1a	21.1	not threatened	0.8	miss	hit.n	2011
HERR30	(49.3)	not threatened	1.2	-ve hit	hit.n	2011
HERRIsum	3.9	not threatened	1.3	-ve hit	hit.n	2011
HERRNIRS	(11.2)	not threatened	1.2	-ve hit	hit.n	2010
HERRNS	(55.1)	not threatened	1.1	-ve hit	hit.n	2011
HERRNWATLC	(782.9)	not threatened	1.6	-ve hit	-ve hit	2005
HERRV1a	45.9	not threatened	0.9	miss	hit.n	2010
HERRV1aVIIbc	87.7	EN	0.2	+ve hit	hit.p	2010
KELPGREENLINGORECOAST	22.8	not threatened	1.4	-ve hit	-ve hit	2005
KINGKLIPSA	27.7	not threatened	1.2	-ve hit	-ve hit	2008
LNOSEKAPCOAST	24.7	not threatened	1.8	-ve hit	-ve hit	2007
LSTHORNHPCOAST	28.5	not threatened	2.7	-ve hit	-ve hit	2005
MACKGOMCHATT	(82.4)	not threatened	3.6	-ve hit	-ve hit	2004
MORWONGSE	86.1	EN	0.3	+ve hit	+ve hit	2007
MUTSNAPSATLCGM	(25)	not threatened	1.0	-ve hit	-ve hit	2006
NPOUTNS	(56)	not threatened	1.3	-ve hit	hit.n	2011
NROCKBSAI	(108.8)	not threatened	1.4	-ve hit	-ve hit	2009
NROCKGA	59.9	VU	1.6	false	false	2008
NRSOLEEBSAI	(1154)	not threatened	3.1	-ve hit	-ve hit	2007
NZLINGESE	67.8	VU	0.7	+ve hit	false	2007
NZLINGLIN3-4	38.1	not threatened	3.0	-ve hit	-ve hit	2007
NZLINGLIN5-6	25.6	not threatened	4.0	-ve hit	-ve hit	2007
NZLINGLIN6b	43.6	not threatened	2.3	-ve hit	-ve hit	2006

NZLINGLIN72	42.8	not threatened	2.6	-ve hit	-ve hit	2007
NZLINGLIN7WC	30.6	not threatened	2.0	-ve hit	-ve hit	2008
NZLINGWSE	41.3	not threatened	1.2	-ve hit	-ve hit	2007
NZSNAPNZ8	82	EN	0.4	+ve hit	+ve hit	2005
OROUGHYNZMEC	75.9	EN	1.1	false	false	2004
OROUGHYSE	90.4	CR	0.5	+ve hit	+ve hit	2007
PATGRENADIERSARG	10.5	not threatened	1.7	-ve hit	-ve hit	2006
PCODBSAI	49.3	not threatened	1.1	-ve hit	-ve hit	2008
PCODGA	29.1	not threatened	0.9	miss	-ve hit	2008
PERCHEBSAI	(434.1)	not threatened	1.3	-ve hit	-ve hit	2009
PHAKEPCOAST	67.4	VU	1.7	false	false	2008
PLAICECHW	32.5	not threatened	0.8	miss	hit.n	2010
POLLFAPL	(14.7)	not threatened	1.9	-ve hit	hit.n	2011
POLLNEAR	(113.9)	not threatened	1.8	-ve hit	hit.n	2011
POLLNS-VI-IIIa	(6.2)	not threatened	1.2	-ve hit	hit.n	2010
POPERCHGA	(332.7)	not threatened	1.4	-ve hit	-ve hit	2010
POPERCHPCOAST	70.2	EN	0.6	+ve hit	false	2007
PSOLENPCOAST	29.4	not threatened	1.7	-ve hit	-ve hit	2005
PSOLESPCOAST	(19.5)	not threatened	0.8	miss	-ve hit	2005
PTOOTHFISHMI	46.6	not threatened	2.3	-ve hit	-ve hit	2010
PTOOTHFISHPEI	61.3	VU	1.9	false	false	2008
REXSOLEGA	(36.3)	not threatened	2.5	-ve hit	-ve hit	2007
REYEROCKBSAI	(8.4)	not threatened	1.1	-ve hit	-ve hit	2009
REYEROCKGA	18	not threatened	1.6	-ve hit	-ve hit	2007
RPORGYSATLC	23.8	not threatened	0.5	miss	-ve hit	2004
RSNAPEGM	91.4	CR	0.2	+ve hit	+ve hit	2003
RSNAPSATLC	97.5	CR	0.0	+ve hit	+ve hit	2006
RSNAPWGM	57.2	VU	0.3	+ve hit	+ve hit	2003
SABLEFEBSAIGA	31.4	not threatened	1.0	-ve hit	-ve hit	2008
SABLEFPCAN	44.3	not threatened	0.5	miss	-ve hit	2004
SBT	94.2	CR	0.2	+ve hit	+ve hit	2009
SBWHITACIR	(4.4)	not threatened	1.3	-ve hit	-ve hit	2006
SFLOUNMATLC	(58.2)	not threatened	0.7	miss	-ve hit	2007
SILVERFISHSE	46.3	not threatened	1.1	-ve hit	-ve hit	2006
SKJCWPAC	(9.7)	not threatened	4.0	-ve hit	-ve hit	2006
SMOOTHOREOCR	41.4	not threatened	2.3	-ve hit	-ve hit	2006
SMOOTHOREOWECCR	68.2	VU	1.2	false	false	2004
SNOWGROUPSATLC	90.5	CR	0.2	+ve hit	+ve hit	2002
SOLECS	(28.4)	not threatened	1.8	-ve hit	hit.n	2011
SOLEIS	81.9	EN	0.4	+ve hit	hit.p	2011
SOLEVIII	18.4	not threatened	0.9	miss	hit.n	2011
SOUTHHAKECR	55.9	VU	2.1	false	false	2006
SOUTHHAKESA	34.7	not threatened	3.0	-ve hit	-ve hit	2007
SPANMACKSATLC	(20.2)	not threatened	0.3	miss	miss	2007

SSTHORNHPCOAST	37.1	not threatened	1.6	-ve hit	-ve hit	2005
STFLOUNNPCOAST	(118.9)	not threatened	1.3	-ve hit	-ve hit	2005
STFLOUNSPCOAST	(283.3)	not threatened	1.6	-ve hit	-ve hit	2005
STMARLINSWPO	25.8	not threatened	0.6	miss	-ve hit	2003
SWHITSE	41	not threatened	0.7	miss	-ve hit	2007
TIGERFLATSE	(132.5)	not threatened	2.1	-ve hit	-ve hit	2006
TILESATLC	66.2	VU	1.0	+ve hit	false	2002
TREVALLYTRE7	58.8	VU	1.5	false	false	2005
WAREHOUSE	93.5	CR	0.5	+ve hit	+ve hit	2006
WAREHOUWSE	74.2	EN	0.5	+ve hit	+ve hit	2006
WEAKFISHATLC	75.9	EN	0.2	+ve hit	+ve hit	2008
WHAKEGBGOM	59.5	VU	0.3	+ve hit	+ve hit	2007
WHITNS-VIIId-IIIa	35.9	not threatened	0.6	miss	miss	2010
WHITVIIek	35.5	not threatened	1.5	-ve hit	hit.n	2010
WINFLOUN5Z	6.2	not threatened	0.3	miss	miss	2006
WINFLOUNSNEMATL	33.8	not threatened	0.1	miss	miss	2007
WITFLOUN5Y	72.1	EN	0.3	+ve hit	+ve hit	2007
WPOLLAI	80.3	EN	0.9	+ve hit	false	2008
WPOLLEBS	37.1	not threatened	0.9	miss	-ve hit	2008
WPOLLGA	69.9	VU	0.8	+ve hit	false	2008
YELLCCODGOM	(8.5)	not threatened	0.2	miss	miss	2007
YELLGB	(86.1)	not threatened	0.1	miss	miss	2007
YELLSNEMATL	(159.3)	not threatened	0.1	miss	miss	2007
YEYEROCKPCOAST	84.9	EN	0.4	+ve hit	+ve hit	2006
YFINATL	31.6	not threatened	1.1	-ve hit	-ve hit	2006
YFINCWPAC	43.3	not threatened	1.3	-ve hit	-ve hit	2005
YSOLEBSAI	(460)	not threatened	2.0	-ve hit	-ve hit	2008
YTROCKNPCOAST	38.6	not threatened	1.4	-ve hit	-ve hit	2005
ANCHOBAYB	(1.9)	not threatened	1.8	-ve hit	hit.n	2011
CODVIIek	56.1	VU	0.9	+ve hit	false	2011
HADROCK	17.1	not threatened	1.7	-ve hit	hit.n	2011
HERRSIRS	(79.1)	not threatened	2.3	-ve hit	hit.n	2010
PLAICNS	(1.5)	not threatened	1.7	-ve hit	hit.n	2010
POLLIEG	34	not threatened	1.5	-ve hit	hit.n	2011
SEELNSSA1	(130.5)	not threatened	1.6	-ve hit	hit.n	2011
SEELNSSA2	(111.2)	not threatened	1.4	-ve hit	hit.n	2011
SEELNSSA3	(108.2)	not threatened	0.9	miss	hit.n	2011
SOLENS	(3.2)	not threatened	1.0	-ve hit	hit.n	2010
SOLEVIIId	(25.2)	not threatened	1.5	-ve hit	hit.n	2011
WHITVIIa	84.9	EN	0.2	+ve hit	hit.p	2011

Table C.2:

Table C3. The proportion (%) of populations meeting each of four possible alignment outcomes (positive hit, negative hit, miss or false alarm) under four different scenarios using IUCN Criterion A4. The A4 criterion a population as being threatened if a 30% decline is observed over the longer of 10 years or three generations. A) Current estimated Red List status or B) Estimated Red List status following the population’s greatest decline, each compared to upper (more conservative; B_{msy} or B_{pa}) or lower (riskier; $0.5B_{msy}$ or B_{lim}) reference points.

	Ref. point	Hit(+ve)	Hit (-ve)	Miss	False Alarm	# of populations
A) Current Status	Upper	28.3	39.2	12.0	20.5	166
	Lower	17.5	47.6	3.6	31.3	166
B) Greatest Decline	Upper	51.8	16.9	1.8	29.5	166
	Lower	33.7	18.1	0.6	47.6	166

Table C.3:

Table C4. Alignment of populations over a 15 year decline period. The proportion (%) of populations meeting each of four possible outcomes (positive hit, negative hit, miss or false alarm) over a decline period of 15 years for all populations when A) their current estimated Red List status or B) their estimated Red List status following their greatest decline is compared to either their upper (more conservative; B_{msy} or B_{pa}) or lower (riskier; $0.5B_{msy}$ or B_{lim}) reference points.

	Ref. point	Hit(+ve)	Hit (-ve)	Miss	False Alarm	# of populations
A) Current Status	Upper	10.8	54.8	29.5	4.8	166
	Lower	9.4	71.7	12.7	7.2	166
B) Greatest Decline	Upper	46.4	29.5	9.0	15.1	166
	Lower	30.1	35.5	3.0	31.3	166

Table C.4:

Figure C.1: Time series of adult biomass for the 166 assessed marine fish populations. Population codes and associated descriptions are listed in Tables S1 and S2. Colored dotted lines correspond to fisheries reference points: B_{msy} or B_{pa} (green), $0.5B_{\text{msy}}$ (yellow), $0.2B_{\text{msy}}$ or B_{lim} (red). Colored circles and thick dashed lines show the three-generation period considered for the Red List evaluation; colors correspond to the estimated Red List category: CR (red), EN (orange), VU (yellow), or not threatened (black), under Criterion A1. Thick dashed lines are illustrative only and do not indicate regression lines.

