

MULTI-SPECIES MODELS OF TIME-VARYING  
CATCHABILITY IN THE U.S. GULF OF MEXICO

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# MULTI-SPECIES MODELS OF TIME-VARYING CATCHABILITY IN THE U.S. GULF OF MEXICO

James T. Thorson

## (ABSTRACT)

The catchability coefficient is used in most marine stock assessment models, and is usually assumed to be stationary and density-independent. However, recent research has shown that these assumptions are violated in most fisheries. Violation of these assumptions will cause underestimation of stock declines or recoveries, leading to inappropriate management policies. This project assesses the soundness of stationarity and density independence assumptions using multi-species data for seven stocks and four gears in the U.S. Gulf of Mexico. This study also develops a multi-species methodology to compensate for failures of either assumption.

To evaluate catchability assumptions, abundance-at-age was reconstructed and compared with catch-per-unit-effort data in the Gulf. Mixed-effects, Monte Carlo, and bootstrap analyses were applied to estimate time-varying catchability parameters. Gulf data showed large and significant density dependence (0.71, s.e. 0.07,  $p < 0.001$ ) and increasing trends in catchability (2.0% annually compounding, s.e. 0.6%,  $p < 0.001$ ).

Simulation modeling was also used to evaluate the accuracy and precision of seven different single-species and multi-species estimation procedures. Imputing estimates from similar species provided accurate estimates of catchability parameters. Multi-species estimates also improved catchability estimation when compared with the current assumptions of density independence and stationarity.

This study shows that multi-species data in the Gulf of Mexico have sufficient quantity and quality to accurately estimate catchability model parameters. This study also emphasizes the importance of estimating density-dependent and density-independent factors simultaneously. Finally, this study shows that multi-species imputation of catchability estimates decreases errors compared with current assumptions, when applied to single-species stock assessment data.

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## CHAPTER 1 – INTRODUCTION AND LITERATURE REVIEW

### 1.1 Stock assessment and catchability

Fishery stock assessments are designed to aid management decisions by providing quantitative analysis of probable fishery responses given alternative management options (Hilborn and Walters 1992). They generally estimate historical abundance, as well as the biological parameters that are necessary to estimate optimal yield. Stock assessments often incorporate many types of data including aggregate catch, fishery catch-per-unit-effort (CPUE), independent survey indices, and age composition data obtained from subsampling fishery landings. These data are combined with plausible biological assumptions to evaluate the consequences of different management options, both to ensure compliance with legal requirements (MSFMA 2007) and to facilitate communication with stakeholder groups.

Stock assessments often use fishery-dependent CPUE data to detect changes in fish abundance. A linear relationship (Eq. 1.1) is generally used to fit a population dynamics model to CPUE-derived indices.

$$\hat{I}_{CPUE} = qN + \varepsilon \quad (1.1)$$

Where:

$\hat{I}$  is an estimate of abundance, from CPUE or scientific surveys

$q$  is catchability

$N$  is abundance

Stock assessment model parameters are then estimated by minimizing the statistical error ( $\varepsilon$ ) between observed indices ( $\hat{I}_{CPUE}$ ) and model predictions of available abundance ( $qN$ ). During this estimation process, model predictions of abundance ( $N$ ) must be scaled to CPUE-derived indices using a constant called the catchability coefficient ( $q$ ).

Stock assessments often include the assumption that the catchability coefficient is constant over time or random around a stationary average. Often, this assumption is only modified when management changes (e.g. size limits, area closures) have significantly impacted fishing practices and, thus, catch-per-unit-effort. In the case of significant management changes, the catchability coefficient is generally assumed to be different before and after a management change but constant within each period. Fishery catch-per-unit-effort data are often assumed to be proportional to stock abundance because, assuming a random distribution of fish and fishers and a constant stock area, a doubling in stock abundance will double the frequency of an encounter between fish and fisher (Walters and Martell 2004).

The standard equation relating CPUE and abundance (Eq. 1.1) implies two important assumptions:

1. Density-independence – CPUE data are assumed to be density-independent, and thus to scale linearly with abundance. If this assumption is violated, the CPUE index may be either hyperstable or hypersensitive (Walters and Martell 2004). A hyperstable index will show a damped response to abundance changes (e.g. a 10% decrease in CPUE during a 50% decrease in abundance), while a hypersensitive index will change more strongly than stock abundance (for example, an 80% CPUE decline during a 50% abundance decrease). Hyperstability has been shown to contribute to catchability-lead stock collapse in pelagic stocks (Pitcher 1995).
2. Stationarity – The catchability coefficient is assumed to be constant when abundance is constant, such that fishery catch rate indices will not change except due to abundance changes. If this assumption is violated, changes in CPUE-derived indices may reflect changes in fishing practices instead of stock abundance.

Many processes may drive changes in catchability over time. By violating the density-independence or stationarity assumptions, these processes may decrease the usefulness of CPUE-derived data as an index of abundance. Processes causing time-varying catchability (e.g. either density dependence or nonstationarity) may be classified

as anthropogenic, environmental, biological, or caused by management. Examples include but are not limited to:

1. Anthropogenic: technological improvements (Robins et al. 1996), fish aggregation devices (Arreguín-Sánchez 1996), changes in fisher targeting effort levels (Salthaug and Aanes 2003).
2. Environmental and biological: oceanographic changes (Gudmundsson 1994), changes in fish range (Hutchings and Myers 1994), fish behavioral changes (Smoker et al. 1998), or interspecific competition for the hook (Rothschild 1967).
3. Management: area closures (Field et al. 2006), changes in size, bag, or trip limits (Oliviera et al. 2009), and hook or gear regulations (Prince et al. 2002).

Such factors are usually either (1) assumed not to be of great importance, (2) assumed not to cause unidirectional changes, (3) dealt with during index standardization, or (4) considered too complex to be estimated from the available data.

Stock assessments compensate for time-varying catchability using a number of different methods. Methods range from discarding or standardizing CPUE-derived indices to explicitly modeling catchability within state-space models (Wilberg et al. in press). State-space models can be constructed to estimate catchability as an unobserved variable, simultaneously with historical abundance and other variables or parameters of interest. Other models can be constructed to estimate density-dependent and density-independent factors using single-species or multi-species data. Although state-space methods have been shown to be effective at estimating historical catchability in simulation studies (Wilburg and Bence 2006), estimates of density-dependent and density-independent factors could provide a more parsimonious method to compensate for time-varying catchability. Estimates of time-varying factors could also be developed without diverting information from variables of direct interest to fisheries managers (i.e. historical abundance, optimal yield), and will provide a basis for forecasts of catchability. Methods will differ in performance given different underlying population or data-collection characteristics, and performance can be evaluated both (1) in terms of statistical accuracy in detecting historical trends and (2) optimizing management objectives over plausible biological and management scenarios.

It is possible for studies to estimate the density-dependent and -independent processes causing time-varying catchability. In this case, it is appropriate to model time-varying catchability as a power function of available abundance, and as a compounding function of time (Eq. 1.2).

$$q_t = q_0 e^{t\beta} \left( \sum_a S_a \bar{N}_{a,t} \right)^{-\alpha} \quad (1.2)$$

Where:

$\alpha$  is density dependence

$\beta$  is a residual, compounding trend in catchability

$t$  is time (in years)

$\sum_a S_a \bar{N}_{a,t}$  is available abundance (the sum of abundance-at-age and selectivity-at-age)

In this model, catchability satisfies stationarity and density independence assumptions when  $\alpha = 0$  and  $\beta = 0$ , respectively. When  $\alpha > 0$ , catchability increases during stock declines. In an extreme case,  $\alpha = 1$  implies that catchability is inversely proportional to abundance, and CPUE will be constant for all abundances, causing CPUE-derived indices to have no value for predicting abundance. By contrast,  $\alpha < 0$  causes catchability to decrease during stock declines (Pitcher 1995).

It is possible for CPUE to decrease slower than abundance during stock declines (i.e.  $\alpha > 0$ ) for a variety of reasons. Reasons include the spatial aggregation of fish within a diversity of habitat qualities, and the ability of fishers to find and target fish aggregations even during stock changes. In such a case, abundance declines are marked not by decreases in fish density, but by contractions in total stock range or even local extirpations. Spatial aggregation of fish within optimal habitats may be expected for demersal, social species with high site fidelity such as Atlantic cod (*Gadus morhua*, Winters and Wheeler 1985, MacCall 1990, Walters and Martell 2004).

Assuming stationarity and density independence when these assumptions are violated will cause an assessment to be either hyperstable (underestimating extreme decreases in abundance) or hypersensitive (erroneously identifying extreme changes in

abundance). Of these two, hyperstability is more problematic because it can lead to overly optimistic management policy and increase the risk of overfishing. Assuming  $\beta = 0$  leads to hyperstability when increasing fishing power masks significant decreases in abundance (i.e. when  $\beta > 0$ ). Assuming  $\alpha = 0$  leads to hyperstability when CPUE drops more slowly than abundance during population declines (i.e. when  $\alpha > 0$ ).

## 1.2 Catchability

Ricker (1975) defined catchability as “the fraction of a fish stock which [sic] is caught by a defined unit of fishing effort” (Eq. 1.3), while Gulland (1977) defined catchability as the density-independent constant between nominal effort (e.g. hooks-hours) and fishing mortality (Eq. 1.4).

$$\text{Ricker: } \frac{C}{N} = qE \quad (1.3)$$

$$\text{Gulland: } F = qE \quad (1.4)$$

Where:

E = effort,

C = catch,

F = instantaneous fishing mortality, and

$$F \propto \frac{C}{N}$$

Such definitions have a long history, and may be traced as far back as Baranov in 1916 (Radovich 1973). They can easily be re-arranged to demonstrate the formulation for catchability used in VPA models (Eq. 1.1).

The relationship between catch-per-unit-effort and abundance can also be derived from the Schaefer (1957) catch equation (Eq. 1.5), instead of from the previous Ricker/Gulland equations.

$$C = qNE \tag{1.5}$$

Importantly, the Schaefer catch equation can be generalized using a modified Cobbs-Douglas catch equation (Hannesson 1983; Eq. 1.6).

$$C = qN^\alpha E^\omega \tag{1.6}$$

Where:

$\omega$  is a nonlinear scaling of CPUE to nominal effort (“effort dependence”)

In the Cobbs-Douglas equation,  $\omega$  captures cooperative or competitive effects between fishermen searching for or locally depleting a fish stock. If  $\omega = 0$  in the Cobbs-Douglas catch equation, it reduces to the Paloheimo (a.k.a. Csirke-MacCall) equation (Paloheimo 1964, Pitcher 1995).

The relationship between catch rates and abundance may also be derived upon a generalized yield function (Jin et al. 2002, Hannesson 2008; Eq. 1.7).

$$C = qA(t)F(X_1, X_2, \dots, X_n)N^\alpha \tag{1.7}$$

Where:

$A(t)$  represents a cumulative shift in the production function over time

$F(X_1, X_2, \dots, X_n)$  represents the effect of production inputs  $X(1)$  through  $X(n)$

$(X_1, X_2, \dots, X_n)$  represents production inputs such as labor and capital

In this equation,  $A(t)$  is known as total factor productivity (TFP) and may be estimated using a number of econometric methods (see Squires 1992). The definition of TFP (Eq. 1.7) shows that it is exactly analogous to the catchability coefficient. The similarity between TFP and the catchability coefficient implies that econometric methods will be applicable to the estimation of time-varying catchability.

### 1.3 Evidence for Time-Varying Catchability

Recent assessment reports for the Gulf of Mexico have included analyses of the impact of density-independent increases in catchability (i.e.  $\beta \neq 0$ ). A density-independent increase in catchability in the Gulf of Mexico could plausibly be caused by technological improvements, gear improvements, or captain experience. Hypotheses regarding increasing catchability are supported by logbook studies of vessels that use global position system (GPS) technology. These studies have found a 12% increase in catchability within 3 years of adopting GPS technology (Robins et al. 1996). Density-independent increases in catchability were also found in studies of the Atlantic cod (*Gadus morhua*) fishery near Lofoten, which showed 2-7% annual increase in catchability, depending on gear (Hannesson 1983). Lacking direct evidence, Walters and Maguire (1996) suggested assuming an increase in fishing power over time on the order of 3% per year, and a similar proposal has recently been investigated in assessment models for reef fish in the Gulf (SEDAR-12a 2006, SEDAR-12b 2006).

Past studies have also demonstrated density-dependent catchability for a variety of gears and target species. The collapse of the Atlantic cod fishery near Newfoundland is partly attributed to a damped decrease in CPUE as abundance fell as would be caused by density dependence (Hutchings and Myers 1994, Walters and Maguire 1996). Using 130 years of data, Hannesson (2008) estimated  $\alpha = 0.60$  for an Atlantic cod fishery near Norway, while Hutchings and Myers (1984) estimated  $\alpha = 0.48-0.52$  for an Atlantic cod fishery in Newfoundland, and MacCall (1976) estimated  $\alpha = 0.61$  for a Pacific sardine (*Sardinops sagax*) fishery in California. Other studies have estimated  $\alpha = 0.576$  (Skjold et al. 1996),  $\alpha = 0.132-0.99$  (Hannesson 1983), or  $\alpha = 0.25-0.36$  (Harley et al. 2001) depending on gear, species, and targeted age-class. Although reef-fish habitat selection studies are sparse, Lindberg et al. (2006) demonstrate density-dependent habitat selection in controlled experiments for Gulf of Mexico gag grouper (*Mycteroperca microlepis*). Density-dependent habitat selection may drive year-to-year stability in catch rates in quality habitat, despite decreases in stock-wide abundance.

### 1.4 Mechanisms for Changes in Catchability

A variety of biological and management processes might cause time-varying catchability, whether causing increases, decreases, continuous trends, or short-term anomalies. These processes include, but are not limited to:

#### Anthropogenic

1. Technological changes: It is likely that improvements in fishing technology will cause improvements in the ability of fishers to catch fish (i.e. catchability). Fisher experience levels are also likely to cause changes in catchability as fishers enter or leave a fishery. Technological and gear improvements include bigger motors and boats, which allow new fish aggregations to be exploited, as well as sonar and GPS plotters, which allow fishers to accurately target and return to productive habitats and aggregations (Hannesson 1983, Robins et al. 1996, Skjold et al. 1996).
2. Fish aggregation devices: Increased deployment of fish aggregation devices, as well as changes in bottom habitat, can cause changes in distribution and fish densities with accompanying changes in catchability (Arreguín-Sánchez 1996).
3. Changes in fisher targeting: Fishers will probably change their targeting preferences to maximize profits as market prices, fishing costs, and CPUE levels change (Hutchings and Myers 1994, Salthaug and Aanes 2003). These economic changes might also cause changes in the dynamics of the exploited fish population (Hannesson 1983, Hilborn et al. 2003).

#### Environmental and Biological

4. Changes in fish abundance: Decreases in abundance will often cause a less-than-proportional change in CPUE-derived indices (MacCall 1990). Mechanisms for this response ( $\alpha > 0$ ) include fisher search behavior, which allows targeting of undiminished aggregations (for pelagic fish) or unreduced fishing grounds (for demersal fish) despite stock-wide decreases. Density-dependent catchability might also be caused by fish behaviors, where fish (such as gag grouper in Lindberg 2006) select preferentially for optimal habitat, causing a between-year replenishment of optimal fishing grounds despite stock-wide decreases.
5. Changes in fish range: Range expansions and contractions will affect fish

- densities. Given that catch rates are related to local densities, range changes will change the CPUE of fishermen (Hutchings and Myers 1994, Arreguín-Sánchez 1996, Walters and Maguire 1996).
6. Oceanographic changes: Oceanographic changes or cycles may cause concentration or dispersal of fish, as in the Peruvian anchoveta (*Engraulis ringens*) fishery (Hilborn and Walters 1992, Gudmundsson 1994). Oceanographic changes might force fishers to change their customary fishing behaviors or locations, and may also cause changes in fish densities within their preferred habitats.
  7. Fish behavioral changes: Changes in fish behavior often will occur seasonally or across years due to a variety of changing hormonal and environmental cues. Fish behavioral can also be affected by long-term genetic changes, caused by either natural or artificial selection. When hormonal, environmental, or genetic changes affect feeding habits or fish densities, they will cause either seasonal or continuous changes in catchability (Smoker et al. 1998, Soldmundsson et al. 2003, Cooke et al. 2007)
  8. Competition for gear: Species will often compete for limited gear (i.e. limited bait, hooks, or space) in fisheries where gear simultaneously catches multiple species. This “competition for the hook” will cause underestimation of abundance primarily for less-abundant species (Rothschild 1967).

### Management

9. Changes in fishing effort: Changes in the level of nominal fishing effort (i.e. hook-hours) will often cause changes in fishing practice. These changes in fishing practice will allow competitive or cooperative fisher behaviors to affect fishing success and catch rates (Ricker 1975, Hutchings and Myers 1994).
10. Size limit changes: Changes in size and bag limits can cause sudden decreases in catchability by redefining acceptable catch, forcing fishers to discard – and hence not record – a portion of previous catch (SEDAR-10 2006-a).
11. Area closures: Spatial regulations will affect CPUE and catchability by causing a spatial redistribution of fishing effort. Effort may be distributed away from optimal fishing grounds or towards spatial boundaries where fish densities are

- increased. Area closures will also change fish densities through ecosystem effects or biological interactions (Field et al. 2006, McGilliard and Hilborn 2008).
12. Hook and gear regulations: Fisheries managers often regulate or promote changes in the fishing gears used by commercial or recreational fishers. Examples include the mandated shift from J-hooks (standard hooks that are shaped like a “J”) to circle-hooks in the Gulf of Mexico. This shift has increased CPUE for pelagic and Gulf of Mexico longlines (Prince et al. 2002, Falterman and Graves 2002, Hoey 1996).

### **1.5 The Importance of Trends in Catchability**

Catchability increase may have a large impact on status benchmark determination, causing large and important bias in estimates of stock abundance for recent years. The impact of time-varying catchability is shown for Gulf of Mexico gag grouper (Fig. 1, SEDAR 10 2006-a). In this example, the 2004 Gulf of Mexico gag grouper assessment included analyses assuming both stationary and 2% non-compounding annual increases in catchability. Constant catchability analyses estimated  $F/F_{msy} = 2.9$ , while analyses assuming an increase in catchability estimated  $F/F_{msy} = 3.3$ . Thus, assuming an increase in catchability implied an additional 10% reduction in fishing mortality (SEDAR 10 2006-a). Increasing catchability also results in a greater difference between current and mandated biomass, implying that a longer time will be required to return the gag grouper in the Gulf of Mexico to federally mandated abundance.

Model runs assuming a 2% non-compounding annual increase in catchability provided a statistically superior fit to data in the Gulf of Mexico SEDAR assessment for gag grouper compared with a scenario assuming stationary catchability (SEDAR 10, 2006-a). Based on the Akaike information criterion, the increasing catchability scenario is deemed 5000 times more plausible than assuming constant catchability in the Gulf for gag grouper (Burnham and Anderson 2002).

No study has compared stock assessments results when including catchability trends and hyperstability with the results arising from the standard assumptions (density independent and stationarity). However, standard models fail badly when applied to data

that are simulated assuming density-dependent catchability (NRC 1998). The impact of simultaneously assuming changing catchability and CPUE hyperstability upon the status of biological benchmarks in the Gulf of Mexico is unknown.

## **1.6 Current approaches to catchability**

Current single-species assessments can address time-varying catchability in a number of different manners. Methods could include: (1) standardizing CPUE-derived index data, (2) discarding or down-weighting suspect data, (3) state-space models, and (4) models that estimate the effect of plausible causal processes. Multiple methods are often used within a given stock assessment, although few studies have reviewed the impact of these different methods on either (1) statistical accuracy of historical abundance estimates, or (2) long-term management performance (as analyzed using management strategy evaluation).

Index standardization uses vessel-specific logbook data to minimize the impact of those processes that are suspected to affect catchability. These logbook data generally record the location, date, catch, and effort of vessels individually and may be used in a number of different analyses (reviewed in Maunder and Punt 2004). The most common analysis is the delta-lognormal model, which combine both presence-absence and catch-rate data into a single CPUE time-series (Lo 1992). This model is then used to estimate a year effect as an explanatory variable for catch rates. This year effect is interpreted as the impact of year-specific abundance on catch rates. Standardization generally requires defining a subset of years and blocks for which data are most reliable (Stephans and MacCall 2004). Stepwise model selection can be used to identify a parsimonious set of covariate factors that increase model precision. Covariate factors often retained in stepwise model building include year, spatial area, trip length, and fisherman license type, ensuring that the latter terms are eliminated as conflating factors in CPUE-index data (Hilborn and Walters 1992). However, standardization often fails to compensate for technological changes, as may be caused by GPS trackers or sonar, and rarely controls for boat length (Salthaug 2001, Brown 2005, Cass-Calay 2005, Ortiz 2005, McCarthy 2006).

Stock assessment scientists often down-weight or discard suspect data (NRC 1998). Suspect data often include outliers at the beginning of fishery development (Fonteneau and Richard 2003), or around an important change in management. However, these methods may limit the usefulness of stock assessment methods by decreasing the amount of data that is available for analysis.

Assessment scientists may choose to use state-space models to simultaneously estimate time-varying catchability, historical abundance, and other management parameters (Porch 1999, Wilberg and Bence 2006). These methods treat catchability as an unobserved (i.e. latent) variable that is estimated using data augmentation methods (Tanner and Wong 1987). Catchability is estimable in these models by comparing information derived from age-composition, fishery-independent, and CPUE-derived index data. Plausible constraints are placed on between-year changes in catchability, and catchability can be modeled to follow an autoregressive structure or environmental covariates.

State-space approaches to catchability (i.e. simultaneous estimation of catchability and historical abundance) will be problematic for several reasons. By estimating many additional parameters for time-varying catchability, these models may or may not be parsimonious. Model parsimony is theorized to increase the precision of parameter estimates and shrink confidence intervals for those parameters (Burnham and Anderson 2002). For this reason, assessment scientists typically seek to identify a minimal number of parameters that can effectively synthesize existing data (Richards and Schnute 1998).

Assessment scientists may choose to control for changes in catchability that can be attributed to a specific cause (e.g. density dependence, effort dependence). When catchability is suspected to be time-varying, scientists can use results from other studies, regions, or stocks (as a point value or Bayesian prior) to control for likely changes. Using results from other regions to inform the selection of time-varying catchability parameters was recently done in the SEDAR assessment for red grouper (SEDAR-10 2006-b), and was discussed for gag grouper (SEDAR-10 2006-a), to compensate for a suspected 2% annual increase in catchability due to technology improvements.

### **1.7 Can catchability be multi-species?**

As single-species assessment models, virtual population analysis and statistical catch-at-age methods only use information from a single species under study. By contrast, multi-species models use information from several species to account for biological and/or economic interactions between populations or fishing fleets. Multi-species models often estimate changes in parameters such as natural mortality or recruitment that are estimated as a stationary average in many single-species models (Magnusson 1995, Hallowed 2000). However, all stock assessments in the Gulf of Mexico have so far exclusively applied single-species methods.

Information regarding time-varying catchability can be obtained without using limited data for a given species of interest. Many U.S. fisheries management regions (including the Gulf of Mexico) have multiple fisheries that target similar species with similar gears. I hypothesize that these similar fisheries and will be affected by many of the same processes for time-varying catchability. Similar processes include: similar gears and technological changes; similar oceanographic or environmental changes; and similar management changes. Although other processes are not similar among species within a single complex, scientists may attempt to control for these processes by including economic data. For example, relative price could be investigated to account for changes in relative effort and fisher targeting, while estimates of catchability density-dependence can control for range expansions and contractions as well as changes in distribution.

Given the similarities in environmental and biological effects, technological changes, and management changes that simultaneously affect many species in a shared area, changes in catchability will probably be similar for multiple species within a complex. In cases where this is true, multi-species estimation of time-varying catchability models will probably improve the precision of single-species stock assessments. This is because multi-species models can compensate for time-varying catchability without using the limited information for a single species of interest. This prevents limited information from being “used up” in the estimation of quantities that are not directly relevant for fisheries managers.

Studies have attempted to estimate catchability by applying virtual population or statistical catch-at-age analyses to catch-at-age data (Porch 1999, Wilburg and Bence

2006). However, Stokes and Pope (1987) suggested that catchability isn't detectable using catch-at-age and commercial data based upon simulated data for three fleets and five years. By contrast, Hannesson (2008) found compelling evidence for exponential trends in catchability in 130 years of data for the Atlantic cod fishery near Lofoten. No known study has investigated the estimation of catchability trends from multi-decade simulated or real-world catch-at-age data, or approached catchability within multi-species modeling.

## **1.8 Outline of Research**

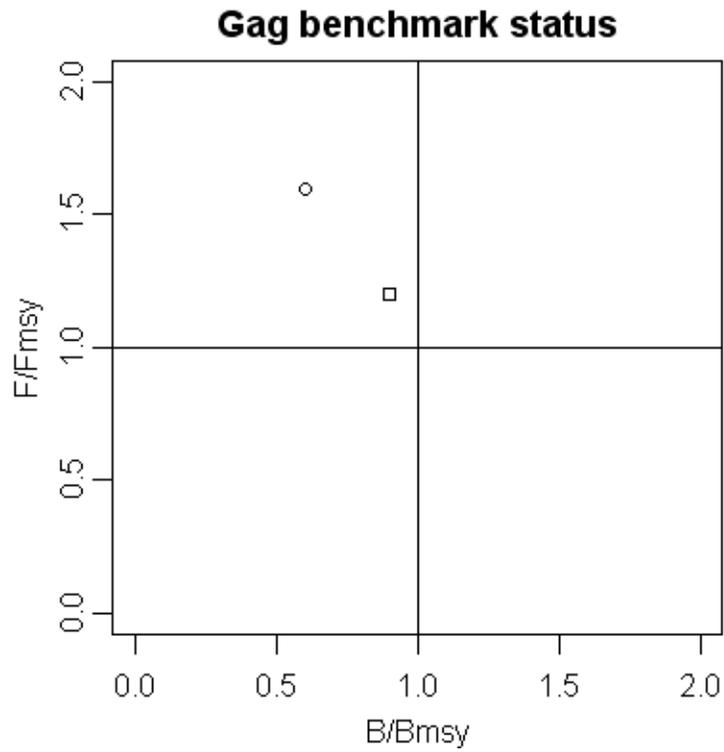
Time-varying catchability remains a central concern in the U.S. Gulf of Mexico and other U.S. fisheries management regions, and will cause important bias in stock assessment results when present. These biases will be especially pronounced during stock decline and recovery. To compensate, scientists can construct models to estimate the processes that are suspected to affect catchability (i.e. density dependence, technology improvements). These estimates can then be included in subsequent stock assessments, thereby allowing these assessments to accurately estimate historical abundance and evaluate proposed management actions. It is also possible to estimate multi-species models for time-varying catchability, allowing compensation for changing processes without diverting information from the estimation of important management benchmarks.

This study estimates two processes that are hypothesized to cause time-varying catchability in the U.S. Gulf of Mexico. This study also develops a methodology to compensate for time-varying catchability by using multi-species data to estimate catchability parameters that may then be used within single-species stock assessments. Chapter 2 estimates catchability parameters in a multi-species catchability model (i.e. time trends and density dependence) using catch-at-age, fishery-independent, and CPUE-derived data for seven stocks in the Gulf of Mexico. Mixed-effects and Monte Carlo methods are used to assess the sensitivity of results to data uncertainties and variability among stocks. Chapter 3 uses simulation modeling to evaluate the relative performance of six single-species and multi-species procedures for estimating time trends, density dependence, and annual catchability. Data are simulated with quantity and quality

similar to that which is available in the Gulf of Mexico. Procedures using similar species to estimate catchability parameters are evaluated in comparison with the standard assumptions (density independence and stationarity). Chapter 4 develops five hierarchical models for time-varying catchability, and uses the deviance information criterion to select an optimal model. This model then is used to develop seven Bayesian priors for density dependence and trends for use in future single-species stock assessments.

Taken together, this study will examine whether time-varying catchability is an important factor in Gulf of Mexico stock assessments. It will also evaluate whether estimation procedures using multi-species data can accurately estimate and compensate for processes causing time-varying catchability. Finally, this study examines whether it is possible to use currently existing data to develop Bayesian priors for catchability parameters, and whether these methods will improve model performance when compared with the current catchability assumptions. I hypothesize that time-varying catchability will be important in the Gulf of Mexico. I also hypothesize that multi-species procedures will improve model performance when compared with the standard assumptions, and that multi-species data can be used to compensate for time-varying catchability through the development of Bayesian priors.

Figure 1.1 – Gag grouper benchmark status, assuming constant (square) and 2% non-compounding increases in catchability (circle), as plotted against  $F/F_{msy}$  (a fishing benchmark, y-axis), and  $B/B_{msy}$  (a biomass benchmark, x-axis).



## CHAPTER 2: CATCHABILITY TRENDS AND DENSITY DEPENDENCE FOR A GULF OF MEXICO MULTI-SPECIES FISHERY

### 2.1 Introduction

The catchability coefficient is a parameter used in many stock assessment models to scale fishery-dependent indices derived from catch-per-unit-effort (CPUE) data to total stock abundance (Eq. 2.1).

$$\hat{I} = q \sum_a S_{a,t} \bar{N}_{a,t} + \varepsilon \quad (2.1)$$

where:

$\hat{I}$  is an index of abundance (such as standardized CPUE)

$q$  is the catchability coefficient

$S_{a,t}$  is selectivity-at-age

$\bar{N}_{a,t}$  is abundance-at-age, averaged over a time period

$\varepsilon$  is measurement or process errors

Application of this equation implies two basic two assumptions:

3. Density independence – Standardized CPUE data are assumed to be proportional to abundance. This assumption is violated when catchability is density-dependent, causing the CPUE-derived index to be either hyperstable or hypersensitive (Walters and Martell 2004).
4. Stationarity – Catchability is assumed to be constant when abundance is constant, such that fishery catch rate indices will not change except due to abundance changes. If this assumption is violated, increases in CPUE-derived indices may reflect improvements in fishing practices instead of stock abundance increases.

Stock assessment scientists may relax these assumptions by defining a generalized model for catchability (Eq. 2.2), where it is a power function of available abundance (calculated

as the sum of year-averaged abundance-at-age and gear-specific selectivity-at-age) and undergoes a compounding trend over time.

$$q_t = q_0 e^{t\beta} \left( \sum_a S_{a,t} \bar{N}_{a,t} \right)^{-\alpha} \quad (2.2)$$

Where:

$\alpha$  is density dependence

$\beta$  is a compounding trend in catchability

$t$  is time, measured in years

This estimation model satisfies density independence and stationarity assumptions when  $\alpha = 0$  and  $\beta = 0$ , respectively.

Anthropogenic, environmental, biological, and management processes may drive changes in catchability over time (Skjold et al. 1996, Robins et al. 1996, Hannesson 1983, Rothschild 1967, Field et al. 2006, Gudmundsson 1994), causing  $\beta$  to be non-zero. Such factors are usually either considered unimportant, random over the length of the time-series, dealt with during index standardization, or else too complex to be estimated from the available data. However, it seems unlikely that such factors as technical improvements in fishing and catching fish are random over time. Such factors will cause biased estimates in stock assessment models (NRC 1998, Wilberg and Bence 2006).

Recent assessment reports for the Gulf of Mexico and South Atlantic fisheries management regions have questioned the soundness of the stationarity assumption. In particular, Gulf gag grouper assessments have debated incorporating a 2% non-compounding annual increase in catchability. Such assessments indicate that approximately 40% less fishing mortality is needed to attain maximum sustainable yield (SEDAR-10 2006-c). Technological improvements such as GPS plotters and other gear changes are postulated to drive this 35% increase in catchability since the 1980's.

Studies from other fisheries have also examined the soundness of the density-independence assumption (Harley et al. 2001, Walters and Maguire 1996, Hutchings and Myers 1994, Pitcher 1995). In Equation 2,  $\alpha > 0$  causes catchability to increase during stock declines, thus contributing to CPUE hyperstability. In an extreme case, catchability

is inversely proportional to abundance when  $\alpha = 1$ , and CPUE will be constant for all abundances causing CPUE-derived indices to have no value for predicting abundance. By contrast,  $\alpha < 0$  causes catchability to decrease during stock declines, contributing to CPUE hypersensitivity. Thus, a hyperstable CPUE-derived index ( $\alpha > 0$ ) damps the effect of changes in abundance on CPUE-derived indices while a hypersensitive CPUE-derived index ( $\alpha < 0$ ) magnifies changes in abundance (Fig. 1, Fig. 2).

Using 130 years of data, Hannesson et al. (2008) estimated the equivalent of  $\alpha = 0.70$  for the Atlantic cod (*Gadus morhua*) fishery near Lofoten, while Hutchings and Myers (1994) estimated a density dependence of  $\alpha = 0.48$  to  $\alpha = 0.52$  for Atlantic cod fisheries and MacCall (1976) estimated a density dependence of  $\alpha = 0.67$  in pelagic fisheries for Pacific sardine (*Sardinops sagax*) near California. CPUE-derived indices may decrease slower than abundance during stock declines for a variety of reasons, including density-dependent habitat selection in a heterogenous habitat (MacCall 1990, Walters and Maguire 1996). In this case, abundance declines are marked not by decreases in fish density in areas of targeted fishing, but by contractions in total stock range or even local extirpations, as may be expected for demersal, social species with high site fidelity such as cod. Conversely, abundance increases may be marked by range expansions or by colonizing new habitat, again causing hyperstability. Other studies have estimated a density dependence of  $\alpha = 0.58$  (Skjold et al. 1996) for the ICES Atlantic cod (*Gadus morhua*) trawl fishery or ranging from  $\alpha = 0.132$  to  $\alpha = 0.99$  (Hannesson 1983), depending on gear, species, and targeted age-class. While modeling studies have modeled hypersensitive CPUE (i.e.  $\alpha < 0$ ) for species assemblages or in the presence of spatial management (McGilliard and Hilborn 2008, Kleibler and Maunder 2008), I assume that density dependence will range between  $\alpha = 0$  and  $\alpha = 1$  in this study, making it a cause of CPUE hyperstability.

To evaluate the soundness of density independence and stationarity assumptions requires an estimate or index of abundance that does not assume density independence or stationarity. This was accomplished using tuned virtual population analysis (VPA), which uses catch-at-age data and fishery-independence calibration indices. Although relative abundance may also be estimated directly from fishery-independent indices without using VPA recursion (e.g. Harley et al. 2001), VPA allows interpolation between

and extrapolation beyond available fishery-independent data, as well as allowing inclusion of age-structure and age-based selectivity.

Joint estimation of catchability trend and density dependence parameters has previously been accomplished only using vessel-specific data (e.g. Skjold 1996), very long time-series data (e.g. Hannesson et al. 2008), or without great precision (e.g. Hannesson 1983). However, the authors are unaware of any studies that have previously attempted joint estimation of the two parameters using multi-species, multi-fishery data within a common region. This multi-species approach may prove useful for many fish complexes in the United States and elsewhere, given the lengths of time series that are generally available. Both parameters are vitally important to stock assessments, given that catchability trends from technology may cause considerable upward bias in abundance estimates, while density dependence and the hyperstability it causes may drive or mask evidence of important abundance declines, or even cause density-dependent stock collapse (Pitcher 1995).

This study attempts to jointly estimate a catchability trend  $\beta$  and density dependence parameter  $\alpha$  for all Gulf of Mexico fisheries that have sufficient data. These parameter estimates may both (1) justify inclusion of catchability trends and density dependence in Gulf of Mexico stock assessments and (2) provide a point-estimate or Bayesian prior of these parameters for future stock assessments in the region or elsewhere.

## **2.2. Methods**

### 2.2.1 Data availability

Gulf of Mexico stock assessments are routinely conducted through the Southeast Data, Assessment, and Review (SEDAR) process. All Gulf of Mexico SEDAR assessments were reviewed in July of 2008 to determine which stocks had sufficient data for the present analysis. Species were selected that had catch-at-age data spanning at least 15 years and at least one fishery-independent and one CPUE-derived index of abundance. The catch-at-age and fishery-independent data were necessary to obtain an

estimate of abundance-at-age without assuming density independence or stationarity of CPUE-derived indices; the fishery-dependent CPUE data were necessary in the calculation of catchability.

Of 16 SEDAR assessments that were publicly available, the following six had the necessary data: gag grouper (*Mycteroperca microlepis*; SEDAR-10 2006-a), red grouper (*Epinephelus morio*; SEDAR-10 2006-b), red snapper (*Lutjanus campechanus*; SEDAR-7 2005), mutton snapper (*Lutjanus analis*; SEDAR-15 2008), king mackerel (*Scomberomorus cavalla*; SEDAR-16 2008), and greater amberjack (*Seriola dumerili*; SEDAR-9 2006). Red snapper assessments have identified differences in populations east and west of the Mississippi river, so red snapper is treated as two separate stocks following recommended SEDAR procedure (SEDAR-7 2005). Data availability is summarized for all stocks in Table 2., while species-specific data sources and standardization methods for CPUE-derived indices as conducted in SEDAR assessments are available at the corresponding author's website ([www.filebox.vt.edu/users/thorson/Supplementary Info.doc](http://www.filebox.vt.edu/users/thorson/Supplementary%20Info.doc)).

For all seven stocks, catch-at-age data started between 1981 and 1987 and ended between 2003 and 2006, covering 18-26 years and between 6 and 30 separate age-classes. Such catch-at-age data were generally estimated from the Gulf of Mexico trip interview program, collected as a boat-side intercept survey and started in 1984 (SEDAR-7 2005).

Fishery-dependent, CPUE-derived abundance indices existed for all seven stocks, and were categorized as marine recreational fisheries statistical survey (MRFSS), headboat, handline, or longline fisheries. Data included 405 years of data from 30 separate CPUE time-series. Fishery-dependent indices were often split in SEDAR assessments at years of important management changes (such as size limits or bag limits) that may otherwise have caused problems in comparison of CPUE. Only splits that were recommended within SEDAR assessment documentation were considered. "Continuous CPUE" sensitivity analyses were also performed in which no CPUE indices were split to evaluate model sensitivity to different index standardization procedures.

The availability of fishery-independent data varied greatly among stocks. Greater amberjack only had one such index. Red grouper, king mackerel, and red snapper had two each. Gag grouper had three indices, while mutton snapper had six available indices.

With the exception of king mackerel, fishery-independent indices included a SeaMAP video trap index for all stocks (Gledhill et al. 2007).

Both fishery-dependent and -independent indices were used exactly as produced for SEDAR assessments, and no additional standardization was performed for this analysis. The SEDAR standardization process generally involves a two-stage process: (1) trip subsetting, often using species co-occurrence (Stephens and MacCall 2004), and (2) delta-lognormal modeling as proposed by Lo (1992) to combine occurrence and CPUE data into a single time-series. Both steps may control for spatial, temporal, technological, or fisher targeting changes, and ideally ensure that the resulting CPUE-derived index satisfies stationarity and density independence assumptions (MacCall 1976).

Index standardization also provides an estimate of coefficient of variation (C.V.) for each index in each year, and C.V. estimates were compiled from SEDAR documents (see corresponding author's website). These yearly C.V. estimates are derived from both (1) sample size for each index year and (2) estimated variance in random effects within the delta-lognormal standardization. However, both fishery-dependent and -independent indices may exhibit additional errors, caused by multiple processes including differences between sampling range and unit stock range. For this reason, C.V. estimates should not be considered as precise or unbiased (Porch personal communication 2008)

Estimates of selectivity-at-age were necessary for the calculation of available abundance, and were generally provided by assessment authors (gag grouper: Dr. Mauricio Ortiz, mutton snapper: Dr. Joe O'Hop), provided in SEDAR documents, or estimated from the selectivity of related gear, as documented at the corresponding author's website. Fishery-independent surveys were often assumed by assessment documents to have selectivity-at-age of either 0 or 1, based on the spatial distribution of ages for a given stock in relation to the sampling areas. Fishery-dependent selectivity was often estimated internally to SEDAR assessment models.

Available data had a variety of region-, species- and gear-specific issues. These include: unknown bycatch and discard mortality rates in the estimation of kill-at-age (Burns et al. 2004, McCarthy personal communication 2008), management changes that obscure the effect of abundance on CPUE, in particular for King Mackerel (McCarthy

2006), and index standardization methods specific to the Gulf. However, data issues should not prevent inference to other Gulf of Mexico stocks that use similar data sources and index standardization methods.

### 2.2.2 Abundance estimation

Catchability trend and density dependence were estimated by first estimating abundance-at-age without using CPUE-derived index data. All calculations and estimation were performed within the *R* statistical environment (R Development Core Team 2006), unless otherwise noted. To estimate abundance-at-age, calibrated virtual population analyses (VPAs) were run for each species to estimate abundance-at-age, using only fishery-independent indices for calibration. These fishery-independent indices were themselves assumed to satisfy stationarity and density independence assumptions. Justifications for this assumption include: (1) that consistent sampling gear prevents catchability trends in survey indices due to technology improvements; (2) that randomized sampling design excludes the search behavior that may underlie density-dependent catchability; and (3) that sampling across a representative set of the unit stock range accurately captures the effects of density-dependent habitat selection.

VPAs recursions were run using Pope's approximation (Hilborn and Walters 1992, Equation 10.3.9) in an algorithm equivalent to that used in Restrepo and Legault (1994), while assuming that selectivity was equal for the two oldest age groups. This algorithm employs a plus-group and requires only one exogenous parameter to begin recursive estimation of all complete cohorts. Estimation of incomplete cohorts was started by using average selectivity from years with complete population reconstruction to estimate fishing mortality-at-age in the final year (Hilborn and Walters 1992). Other incomplete cohorts procedures were explored but yielded little difference in estimated abundance-at-age.

Fishery-independent indices were then used to calibrate the one free parameter required for recursive estimation of both complete and incomplete cohorts. This was accomplished by iteratively calculating index weightings, and minimizing the index-weighted residual sum of squares difference between log-scaled index data and log-

scaled available abundance. Available abundance was defined as the product of abundance-at-age and index-specific selectivity-at-age for each index. Fishery-independent indices were weighted as the square root of a bias-compensated estimate of index error, calculated from the difference between each index and VPA estimates of available abundance. This procedure implicitly assumes that fishery-independent indices have independent and log-normal observation errors that are homoskedastic within each index. Fitted F-terminal values and 95% confidence regions from a Monte Carlo simulation of fishery-independent data based on C.V. estimates were used to diagnose the convergence of VPA abundance estimates to fishery-independent indices. Other weighting methods were also explored for VPA calibration and produced less plausible F-terminal estimates.

### 2.2.3 Data Analysis

Estimates of abundance-at-age were then combined with selectivity-at-age to calculate gear-specific available abundance. This was used to estimate density dependence and trend parameters (Eq. 2.3) as the log-scaled combination of catch rate (Eq. 2.1) and generalized catchability (Eq. 2.2) models.

$$\log(\hat{I}_{t,S,G}) = \gamma_1 D_1 + \gamma_2 D_2 + \dots + \gamma_n D_n + \beta t + (1 - \alpha) \log(S_{a,S,G} \hat{N}_{a,S}) + \Phi \quad (2.3)$$

Where:

$D_1 \dots D_n$  are dummy variables for all combinations of species and gear

$\gamma_1 \dots \gamma_n$  are coefficients for species-gear dummy variables

$(S_{a,S,G} \hat{N}_{a,S})$  is the VPA estimate available abundance for a given stock and gear

$\Phi$  is a normal error distribution

Parameters and confidence intervals in Eq. 2.3 were estimated using ordinary least squares, generalized least squares, feasible weighted least squares, mixed-effects modeling, nonparametric bootstrap, Monte Carlo simulation, and Bayesian inference.

The catchability trend coefficient  $\beta$  from Equation 3 was transformed to represent an annual compounding trend by exponentiating  $\beta$  and subtracting one. A log-linear model was used for two reasons: (1) it normalizes the lognormal errors in catchability-by-year estimates, arising from the lognormal error in delta-lognormal standardized CPUE-derived indices, and (2) it ensures that yearly slope coefficients are expressed as a relative percent change, allowing all CPUE series to have a comparable metric despite different absolute magnitudes in catchability and catchability change.

#### 2.2.4 Parameter estimation

I used ordinary least squares (OLS) to fit Equation 3 in the absence of density dependence to estimate a trend in catchability when assuming density independence (i.e.  $\alpha = 0$ ). This was done for all stocks pooled or using the stock as a fixed-effect. OLS was also used to jointly estimate  $\alpha$  and  $\beta$ , and F-tests were performed to test for stationarity and proportionality assumptions ( $\alpha \neq 0$  and  $\beta \neq 0$ ). Joint estimates were conducted for all stocks pooled, or treating each stock as a fixed effect. Although  $\alpha > 1$  (i.e. hyperaggregation) was considered to be implausible, fixed-effect estimates were not bounded to provide a diagnostic for imprecise estimation. Use of OLS to estimate catchability trends and density dependence has been done previously in Hannesson (1983). Mixed-effects (ME) modeling was also implemented using the “lme4” package in *R* (Bates et al. 2008). This procedure combines results from pooled and fixed-effects estimation to account for commonalities in trend and density dependence between different stocks (Davidson and MacKinnon 2004). All procedures assume that measurement errors arising from estimation of available abundance (i.e. VPA estimation) will be considerably smaller than measurement errors in CPUE (Draper 1998).

I applied generalized least squares (GLS) as a sensitivity analysis to account for different levels of observational error in CPUE-derived index data, using standard deviation calculated from C.V. estimates as weights. This procedure was not expected to perform well, both because (1) C.V. estimates may have biases for reasons explained previously and (2) C.V. estimates appeared extremely inaccurate to the authors when compared between different species and gear. A version of feasible weighted least

squares (FWLS) was also used in a 2-step process, estimating data weights from the regression of OLS residuals on the interaction of gear and species factors (Davidson and MacKinnon 2004). This FWLS model was designed to account for index-specific differences in precision, and other FWLS models were also explored. Although Chen and Poloheimo (1998) demonstrate that GLS performs well in simulation experiments, the authors do not know of any previous study that has applied this method or FWLS to catchability estimation.

I applied other sensitivity runs to explore uncertainties in model structure (Prager and MacCall 1988), both from VPA reconstruction of abundance and for uncertainties in index data and selectivity. Sensitivities included (1) assuming uniform gear selectivity to assess the importance of selectivity-at-age data, and (2) using CPUE time-series data that are not split to assess the importance of index standardization methods that compensate for management changes (often in the form of effort controls) by splitting time-series indices.

#### 2.2.5 Nonparametric bootstrap and Monte Carlo simulation

I used nonparametric bootstrap (Efron and Gong 1983) to analyze the sensitivity of modeled results to the specific stocks included in the study. This was performed by re-sampling with replacement from the set of fish stocks (i.e. east and west red snapper, gag grouper, red grouper, king mackerel, greater amberjack, and mutton snapper) used in OLS parameter estimation.

I used Monte Carlo simulation to assess the sensitivity of modeled results to data uncertainties (Restrepo et al. 1992), both in (1) yearly abundance-at-age, due to imprecise tuning indices, and (2) yearly CPUE time-series data, used to calculate catchability. Fishery-independent and CPUE-derived data were used in conjunction with C.V. estimates and an assumed log-normal observational error to simulate new fishery-independent and CPUE-derived data. These simulated data sets were then used to repeat VPA abundance-at-age estimation and with OLS to estimate annual compounding trend and density dependence

## 2.2.6 Bayesian inference

I performed a Bayesian analysis using OpenBUGS software called within *R* using the “BRugs” package (Thomas 1994, Thomas et al. 2006). Priors included extremely wide, normal priors for catchability trend and density dependence and a wide exponential prior for data variance. Starting parameters were generated randomly, and 1000 adaptive-samples with target acceptance rate of 0.45 were used as burn-in before 10,000 samples with trimming of 50. Trimmed results were displayed with a 95% probability ellipsoid, calculated from the MCMC covariance matrix (Fox 2008). Convergence was assessed by calculating the Gelman-Rubin statistic  $\hat{R}$ , calculated from three sampling chains (Gelman and Hill 2007) for each parameter. Results were checked against a Bayesian analysis conducted in *R*, sampling across trend and density dependence while concentrating across data variance and using a Metropolis within Gibbs sampling algorithm (Albert 2007). Similar to regression methods, Bayesian inference implied the assumption that measurement errors in available abundance were much less than errors in CPUE-derived index data.

## 2.3 Results

### 2.3.1 Abundance Estimation

Stock abundance is increasing for king mackerel, gag, red grouper, and greater amberjack, and is stable or fluctuating for eastern red snapper, western red snapper, and mutton snapper. Importantly, VPA estimates contain contrasts between periods of increasing and decreasing abundance, both when comparing between and within each stock. These contrasts were necessary in the estimation of density dependence. Estimated abundance also showed larger changes for mutton snapper and greater amberjack than did CPUE-derived indices, and appeared to conflict with CPUE-derived index trends for red grouper. Fig. 3 displays the fit of VPA abundance estimates to fishery-independent data for each of seven stocks individually, while Fig. 4 displays the fit to CPUE-derived fishery-dependent indices.

F-terminal estimates and 95% confidence intervals were plausible for all seven stocks. Western red snapper and mutton snapper had the lowest terminal fishing mortality rates, while eastern red snapper and red grouper had highest fishing mortality rates. Given only one fishery-independent calibration index, greater amberjack had the widest 95% confidence interval for terminal fishing mortality. Table 2 lists fitted values for F-terminal and 95% confidence regions in final year for each species.

### 2.3.2 Parameter estimation

Estimates of catchability trend  $\beta$  by OLS when assuming no density dependence ( $\alpha = 0$ ) are displayed in Table 3 both for all species pooled and using species as a fixed effect. Estimates were negative except for the two red snapper stocks. The pooled estimate was -2.23% compounding annually, while single-stock estimates ranged from -13% (greater amberjack) to 3% (eastern red snapper).

Joint estimates of catchability trend and density dependence are listed Table 3. F-tests for the inclusion of density dependence and time trend effects (i.e.  $\alpha \neq 0$  and  $\beta \neq 0$ ) were highly significant (alpha:  $F=106$ ,  $p<0.0001$ ; beta:  $F=12$ ,  $p=0.0006$ ). Pooled estimates of density dependence and annual compounding trend are 0.71 (s.e. 0.07) and 2.0% (s.e. 0.6%), respectively. Density dependence estimates using species as a fixed effect range from 0 (eastern red snapper) to 1.4 (red grouper), while trend estimates range from -8% (greater amberjack) to 6% (gag grouper). As expected, estimates using species as a random effect show similar patterns but are generally pulled towards the OLS pooled estimates. Mixed effects estimates ranged between 0.22 (eastern red snapper) and 1.11 (red grouper) for density dependence and -7% (greater amberjack) and 5% (gag grouper) for compounding annual trend.

Sensitivity analysis estimates are listed in Table 4. Estimates range closely around pooled OLS results. GLS estimates differed more from OLS estimates than did FWLS, probably due to inconsistencies in prior C.V. estimates. Other FWLS estimation methods yielded similar results. OLS estimation using unsplit time series data showed a smaller increasing trend in catchability than did split time series data, as expected for data

that do not compensate for management effort controls (which would be expected to decrease catchability).

### 2.3.3 Nonparametric bootstrap and Monte Carlo simulation

Bootstrap and Monte Carlo simulation results are displayed in Figure 5. The top panel shows density dependence and annual compounding trend estimates using a non-parametric bootstrap of the set of stocks to demonstrate the sensitivity of results to the stocks included in the analysis. The scatter plot of nonparametric bootstrap results has a tightly bounded, roughly ellipsoid distribution with little correlation between parameters. The 95% confidence region does not overlap with zero density dependence, although it does slightly overlap zero in catchability trend. The bottom panel displays results from a Monte Carlo simulation of the data using C.V. estimates and assuming a lognormal error to resample both fishery-dependent and -independent data. Results show a strong positive correlation between trend and density dependence parameters, and again exhibit a stronger deviation from zero for density dependence than for catchability trend. As expected, both analyses are centered at OLS estimates.

### 2.3.4 Bayesian inference

MCMC sampling yielded a Gelman-Rubin statistic of less than 1.1 for each parameter, showing no evidence for non-convergence in the MCMC sampling algorithm. The trimmed MCMC chain for density dependence and trend parameters is plotted in Figure 6, along with a 95% credibility ellipsoid as estimated using the MCMC sample covariance matrix (Fox 2008). The 95% ellipsoid shows a positive correlation between parameters and ranges between 1% and 3% annual catchability trend and 0.55 and 0.90 for density dependence. By this standard, both parameters are significantly different from standard assumptions of density independence and stationarity. Results were similar for the Bayesian analysis programmed in *R*, and show a smaller confidence region than did nonparametric bootstrap or Monte Carlo simulation.

## 2.4 Discussion

### 2.4.1 Management and stock assessment implications

A 2% compounding annual increase in catchability was observed in this study after accounting for the conflating effect of abundance trends and density-dependent catchability. However, estimated trends were negative without compensating for density dependence. The difference in trend estimates with and without density dependence implies that trend estimates are highly sensitive to the treatment of other time-varying catchability processes (particular density-dependent catchability), and that care should be used when compared trend estimates among studies that use different treatments for these processes.

Both trend and density dependence parameters were statistically significant based on OLS, Bayesian, and bootstrap analyses, although Monte Carlo simulation did not show a statistically significant trend parameter. This study's estimate of density dependence contradicts the standard assumption that CPUE scales proportionally to abundance (i.e. that  $\alpha = 0$ ). Non-zero density dependence in catchability has many important implications for fisheries management. Observed density dependence implies that fishery-dependent indices are less sensitive to abundance changes than fishery-independent indices. Thus, management advice based primarily on CPUE-derived indices (such as for historical reconstruction of carrying capacity) may underestimate the magnitude of abundance changes, and fishery-dependent data will tend to underestimate the magnitude of stock recovery for rebuilding stocks as well as the magnitude of stock declines during stock collapse. The latter may contribute to catchability-led stock collapse (Pitcher 1995), and is especially important given that stock recovery is highly dependent on quickly identifying stock collapse (Hutchings and Reynolds 2004). For Gulf of Mexico stocks, observed density dependence may also lead to underestimates of stock recovery, causing overly restrictive harvest regulations.

This study's estimate of increasing trends in catchability (after compensating for density dependence) has important implications for stock assessment, both in the Gulf of Mexico and elsewhere. Over twenty years, such a trend will cause significant

overestimation of abundance, implying that CPUE-derived indices may be highly biased. Furthermore, many Gulf and southeast region assessments use historical CPUE-derived index data to reconstruct virgin biomass estimates, and bias in these estimates will have important implications in the estimation of management benchmarks. Tight agreement of my catchability trend estimate (after compensating for density dependence) with other studies regarding catchability trend suggests that increasing trends should be routinely investigated for stocks that utilize fishery-dependent CPUE data.

My results suggest that the sign or magnitude of catchability trends may be difficult to predict *a priori* when density dependence is present but not modeled, and that estimates of catchability trend in these cases may not be easily interpretable. Given the abundance trends for stocks in this study, assuming density independence ( $\alpha = 0$ ) led to negative estimates of catchability trend ( $\beta < 0$ ) over time. This negative trend is at odds with the technological improvements in Gulf fishing practices since the 1980's. Assuming a catchability trend in stock assessment models without also compensating for density dependence is not recommended for stocks with rapidly changing abundance, as density dependence may cause catchability to vary greatly from *a priori* assumptions and will greatly decrease model predictive capabilities.

My results also suggest that single-species estimates of trend and density dependence in catchability will be highly imprecise. Wide variability and implausible results (i.e.  $\alpha > 1$ , where CPUE would be inversely related to abundance) for single-species OLS estimates suggest that future stock assessment models should not freely estimate a density dependence parameter based only on single-species assessment data. Free estimation of density-dependent catchability will decrease the importance assigned to the magnitude of overall abundance change in CPUE-derived indices. Down-weighting the magnitude of CPUE-derived index changes may be a bad use of available information. By contrast, mixed-effects estimation combined single and multi-species information to yield catchability parameter estimates that were more plausible. I recommend that that future stock assessments use mixed effects or hierarchical estimation, in a Bayesian prior or penalized likelihood function, to constrain the free estimation of density dependence and catchability trend parameters. Such methods would use limited assessment data more efficiently, and may provide stronger inference

regarding the scale of abundance changes. It remains unclear how multi-species estimates of density-dependent catchability would affect relative management benchmarks (i.e.  $F/F_{msy}$  and  $B/B_{msy}$ ).

#### 2.4.2 Comparison with previous studies

Density dependence estimates in this study ( $\alpha = 0.7$ ) are higher than the meta-analysis results of Harley et al. (2001,  $0.25 < \alpha < 0.36$ ), and similar to the 130 year time-series results of Hannesson et al. (2008;  $\alpha = 0.7$ ). Differences are probably caused by differences in the treatment of error-in-variables, which will lead to over-estimation of  $\alpha$  in studies (such as Hannesson et al. 2008 and the present study) that do not compensate for this effect.

The demersal species used in this study have not previously been documented to exhibit density-dependent catchability. This high density dependence estimate may be explained in at least three ways. First, density dependence may be caused by tight communication and cooperation between fishers (Radovich 1973), such as may increasingly occur in the Gulf. Second, density dependence may be exacerbated by step one of the CPUE index standardization process used in the Gulf. This step, developed by Stephens and MacCall (2004), involves the subsetting of logbook data to exclude non-target trips, identified using species occurrence and multi-species catch data. By excluding zero-catch trips, this procedure may obscure information that is used in step two of the index standardization process, regarding the spatial contraction of effort accompanying spatial and abundance changes. Third, theory suggests that species with high mobility and density-dependent habitat selection may exhibit density-dependent catchability (MacCall 1990), and Lindberg et al. (2006) found high density-dependent site selection in gag grouper in the Gulf. This habitat selection, along with between-year dispersal, may explain unexpectedly high density dependence in catchability.

Annually compounding trend estimates from this study ( $\sim 2.0\%$ ) are extremely close to estimates from studies that also compensated for density-dependent catchability. Examples include Hannesson et al. (2008), who found a 2.3% continuously compounding increase in catchability, and Skjold et al. (1996), who found a 2.1% continuously

compounding increase. Although previous SEDAR assessments for red grouper in the Gulf of Mexico and South Atlantic had already included an assumed 2% annual increase in catchability, this assumption lacked compensation for density-dependent catchability and could still probably be improved. In particular, this 2% annual increase in catchability probably overestimates effective changes in catchability because it lacks compensation for decreases in catchability caused by density dependence and increases in stock abundance.

My results imply that economic analyses of fishing productivity should incorporate a nonlinear return to increases in stock abundance as a factor of production. Some economic studies already incorporate such nonlinearity and interpret catchability change as evidence for changing fishing efficiency over time (Squires 1992, Hannesson et al. 2008) while others do not appear to do so (Tingley et al. 2005). When compared with increases in labor efficiency, these estimates may give insight into fleet capitalization as well as the competitiveness of a fishery against other national industries (as explained in Hannesson et al. 2008). Economic studies may benefit from using informative priors for density dependence, as estimated from similar species or stocks.

#### 2.4.3 Areas for future research

Future studies could explore different specifications for either (1) density dependence, such as using the generalized catch equation of Richards and Schnute (1986) to compensate for gear saturation (Radovich 1973) and spatial refuges (Walters and Martell 2004), or (2) for catchability trend, such as a random-walk process in conjunction with density dependence. This second proposal was explored in Wilberg and Bence (2006), who found that density dependence was badly estimated when also estimating a random-walk catchability. This difficulty may possibly be overcome by using an informative prior for hyperstability, based upon similar species. Studies may also explore additional, life history-based hierarchical models of catchability trend and density dependence. Hierarchical or correlation studies may identify the life-history characteristics that underlie hyperstability and, in doing so, provide guidance in the interpretation of limited CPUE data for data-poor species.

Past studies have highlighted the need to develop and compare different procedures for time-varying catchability (NRC 1998). My study has shown that density-dependent catchability is strongly present in a major fisheries complex in U.S. waters, and that multi-species methods allow estimation of both density-dependent and -independent factors on catchability using data of the quantity and quality that is current available for many fisheries management regions. I suggest that future stock assessment models incorporate density-dependent catchability using hierarchical, multi-species estimation of Bayesian priors. Density-dependent catchability is especially important during stock recovery and decline and thus is centrally important to fisheries management given that rapid detection of population declines is vital for all fisheries management objectives.

Table 2.1 – Data availability by stock. Multiple lines for fishery-dependent data (ex: Headboat & Gag Grouper) signify times when CPUE data were split by the SEDAR-approved standardization process.

Species	Catch-at-Age	Fishery-Dependent	Fishery-Independent
Gag Grouper	1984-2004 Ages: 0-12	MRFSS: 1981-2004 Headboat: 1986-1990 1991-2000 2001-2004 Handline: 1990-2000 2000-2004 Longline: 1990-2000 2000-2004	1. SeaMAP Video: 1993-1997, 2002, 2004 2. Copper Belly: 1993-1997, 2002, 2004 3. Otter Trawl: 1996-2004
Red Grouper	1981-2005 Ages: 1-30	MRFSS: 1986-2005 Headboat: 1986-1990 1991-2005 Handline: 1990-2005 Longline: 1990-2005	1. SeaMAP Video: 1993-1997, 2002, 2004, 2005 2. SEFSC Longline: 2000-2005
Greater Amberjack	1987-2004 Ages: 0-5	MRFSS: 1981-2004 Headboat: 1986-1997 1998-2003 Handline: 1993-2004 Longline: 1993-2004	1. SeaMAP Video: 1992-1997, 2001, 2002, 2004
King Mackerel	1981-2006 Ages: 0-11	MRFSS: 1981-2006 Headboat: 1986-2006 Handline: 1993-2006	1. SeaMAP Fall Plankton: 1986-1997, 1999-2004, 2006 2. Small Pelagic Trawl Survey: 1989-1996, 2004, 2006

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Mutton Snapper	1981-2006	MRFSS: 1981-2006	1. FL Keys visual Surrey (exploited): 1999-2004, 2006
	Ages: 1-24	Headboat: 1981-1991, 1995-2006	2. FL Keys visual survey (pre-exploited): 1999-2004, 2006
		Handline: 1990-2006	3. Haul seine survey: 1999-2006
		Longline: 1990-2006	4. NMFS-UM Reef visual census: 1994-2005
			5. Riley's Hump, FL visual Surrey: 2001-06
			6. SeaMAP video (near Dry Tortugas, FL): 1992-97; 2002, 2004-06
Red Snapper (East)	1984-2003	MRFSS: 1984-2003	1. SeaMAP Video: 1992-1997, 2002
	Ages: 0-15	Handline: 1996-2003	2. Plankton: 1986-1997, 1999-2002
			3. Age-0 trawl: 1984-2003
			4. Age-1+ crawl: 1984-2003
Red Snapper (West)	1984-2003	MRFSS: 1984-2003	1. SeaMAP Video: 1992-1997, 2002
	Ages: 0-15	Handline: 1996-2003	2. Plankton: 1986-1997, 1999-2002
			3. Age-0 trawl: 1984-2003
			4. Age-1+ crawl: 1984-2003

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Table 2.2 – F-terminal for the oldest age class in the final year, as estimated by calibrated VPA, along with 95% confidence interval derived from Monte Carlo simulation of fishery-independent calibration data using C.V. estimates

	GG	RG	GA	KM	MS	RS-East	RS-West
2.5% quantile	0.0185	0.0700	0.0349	0.0305	0.0022	0.0944	0.0039
F-terminal estimates	0.0251	0.0933	0.0723	0.0432	0.0028	0.1788	0.0093
97.5% quantile	0.0350	0.1165	0.1718	0.0585	0.0033	0.2186	0.1233

Table 2.3 – Estimates of annual compounding catchability trend when assuming density independence ( $\alpha = 0$ ) and when jointly estimating density dependence and trend, either using data pooled across all stocks and ordinary least squares (“Pooled OLS”) or estimating for each species separately using fixed effects (SS FE) or mixed effects (SS ME) methods.

	Trend (with density independence)		Density dependence (joint estimate)			Trend (joint estimate)		
	Pooled OLS	SS FE	Pooled OLS	SS FE	SS ME	Pooled OLS	SS FE	SS ME
Pooled	-2.23%	-	0.7134	-	-	2.00%	-	-
GG	-	-1.23%	-	0.8575	0.7993	-	5.91%	5.10%
RG	-	-0.09%	-	1.4322	1.1122	-	5.04%	3.72%
GA	-	-13.18%	-	0.5626	0.6049	-	-7.74%	-6.83%
KM	-	-0.95%	-	0.5424	0.6710	-	1.49%	2.03%
MS	-	-3.76%	-	0.3086	0.4918	-	-1.37%	0.07%
RS-East	-	2.90%	-	0.0017	0.2225	-	2.94%	3.93%
RS-West	-	1.76%	-	0.4432	0.7947	-	1.74%	1.58%

Table 2.4 – Joint density dependence and annual compounding trend estimates for all species pooled using various sensitivity analyses.

	Density dependence	Catchability trend (transformed)
GLS	0.8260	0.23%
FWLS	0.6892	2.04%
OLS Unbroken time-series	0.7202	1.25%
OLS Uniform gear selectivity	0.6381	2.80%

Figure 2.1 – The scaling of CPUE-derived indices to abundance, given different degrees catchability density dependence (solid:  $\alpha = 0$ ; dotted:  $\alpha = 0.5$ ; short dash:  $\alpha = -0.5$ ; long dash:  $\alpha = 1.5$ ).

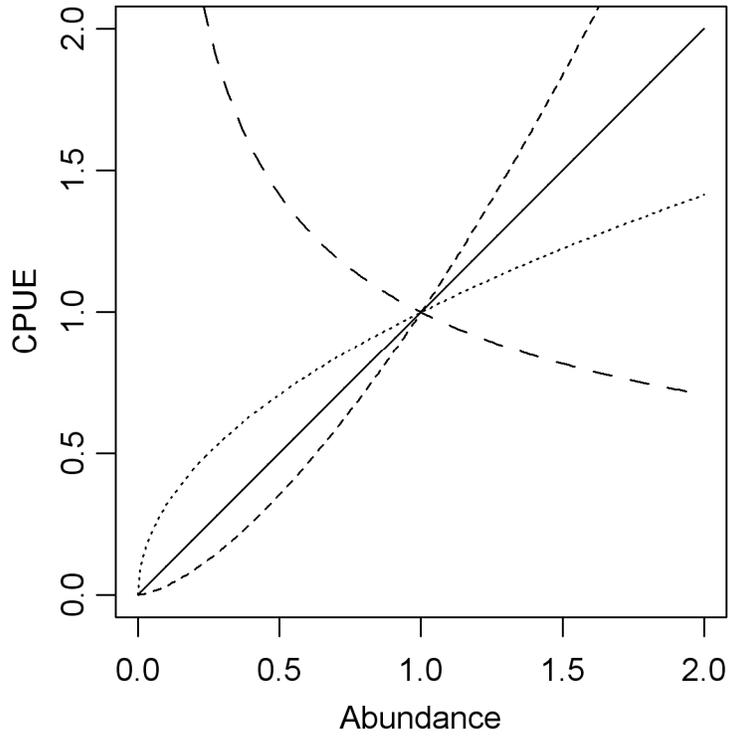


Figure 2.2 – The effect of hyperstability ( $\alpha > 0$ ; dashed line) and hypersensitivity ( $\alpha < 0$ ; dotted line) upon CPUE-derived indices, given an underlying change in abundance (solid line). Hyperstability dampens the effect of abundance changes on CPUE-derived indices, while hypersensitivity causes extreme changes in CPUE-derived indices.

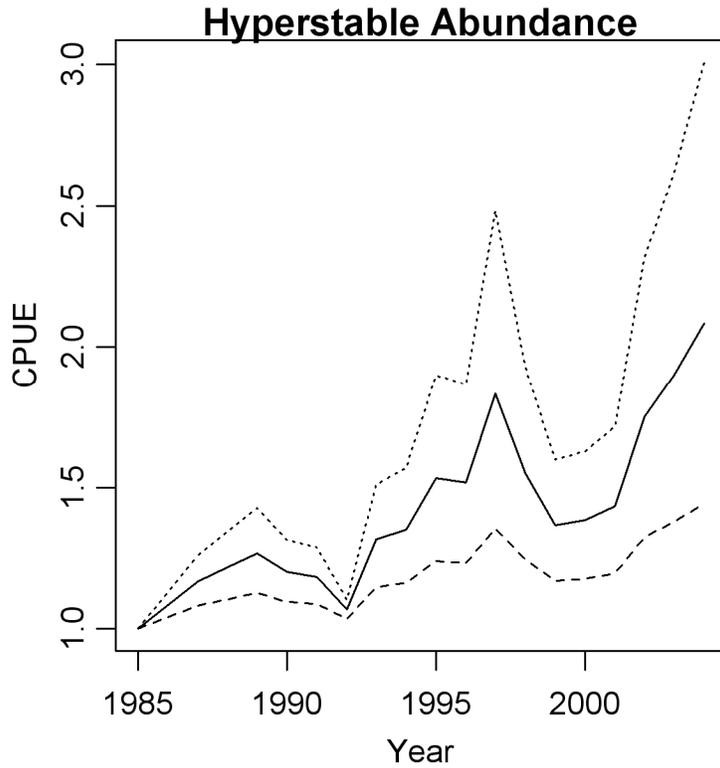


Figure 2.3 – Total abundance estimated from calibrated VPA, compared with the calibrating fishery-independent indices. Symbols represent different fishery-independent indices (Table 1, column 3: Black square – 1; White diamond – 2; Black triangle – 3; White square – 4; Black diamond – 5; White triangle – 6).

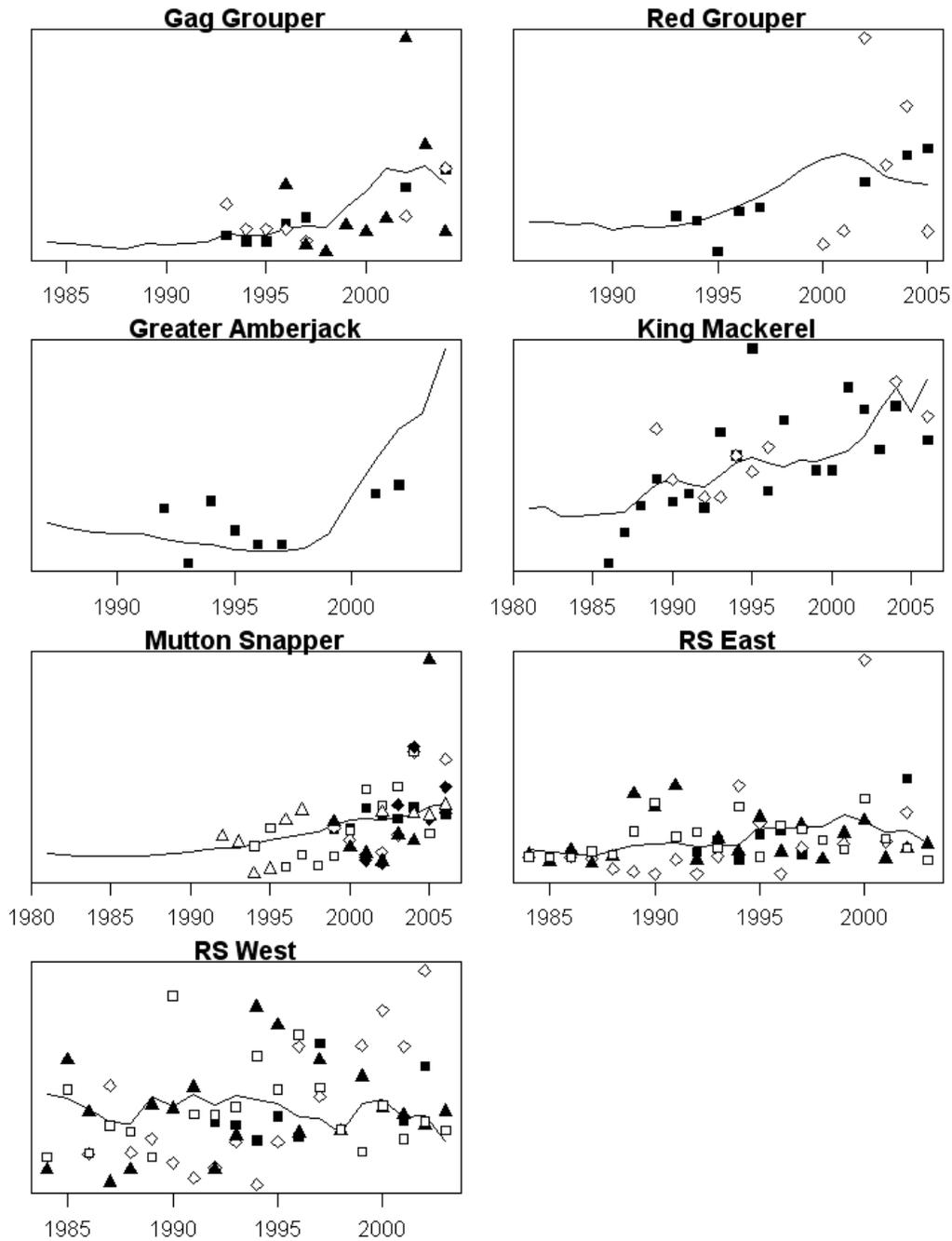


Figure 2.4 –Total abundance estimated from calibrated VPA, compared with CPUE-derived fishery-dependent indices for each species. Each symbol refers to a type of fishing gear (Black square – MRFSS; White diamond – Headboat; Black triangle – Handline; White square – Longline).

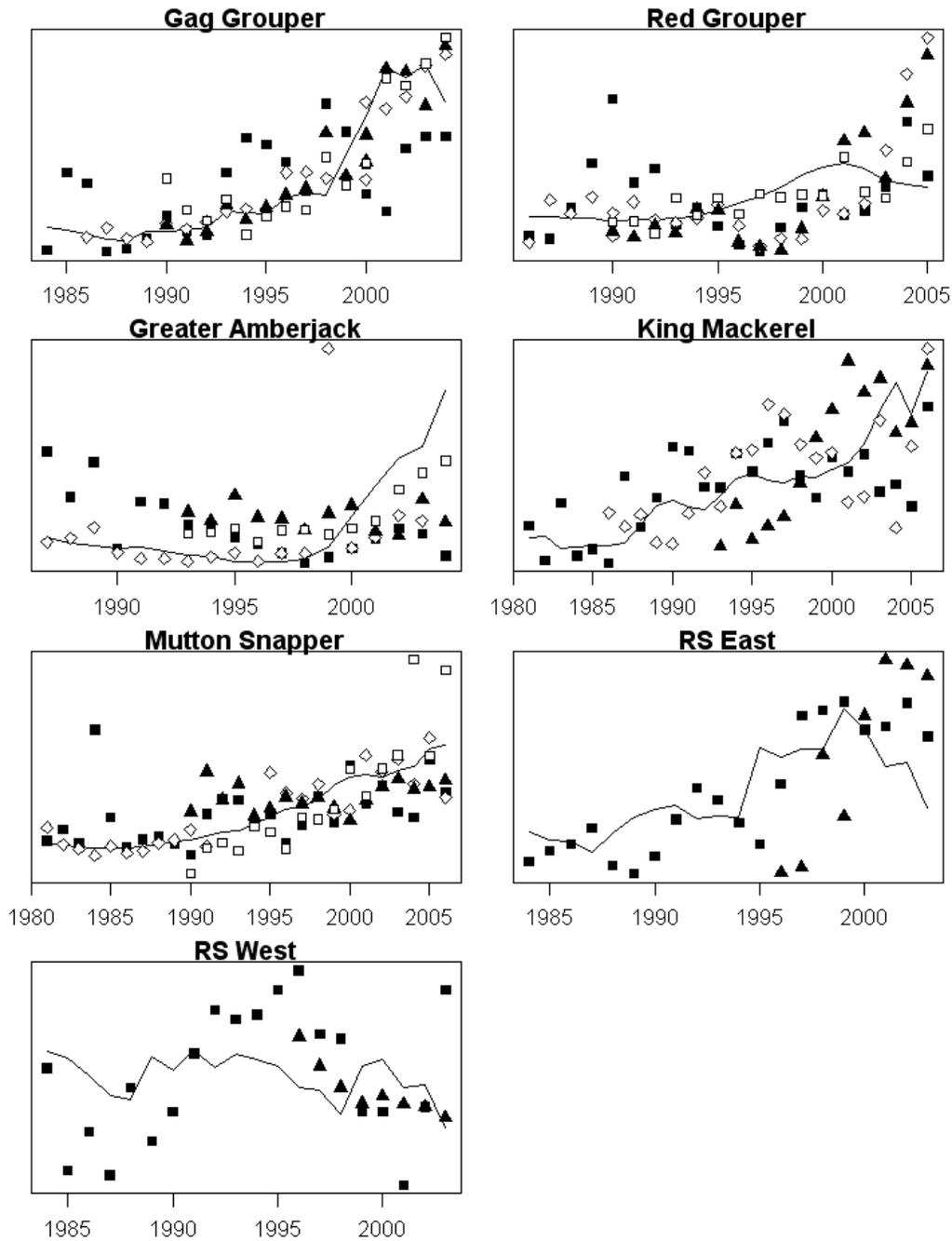


Figure 2.5 – Panel graph showing density dependence and compounding annual trend estimates from a nonparametric bootstrap of stocks (top) or a Monte Carlo simulation of fishery-dependent and -independent data based on prior estimates of coefficient of variation (bottom). Ninety-five percent confidence ellipsoids are included to demonstrate joint confidence regions as well as covariance structure.

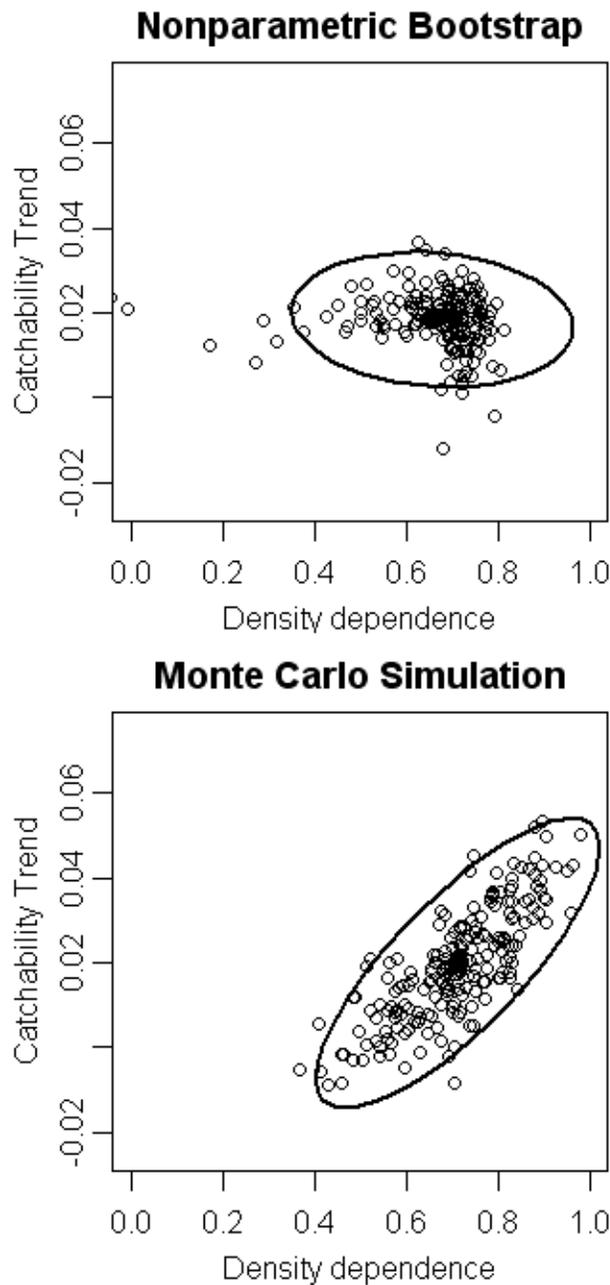
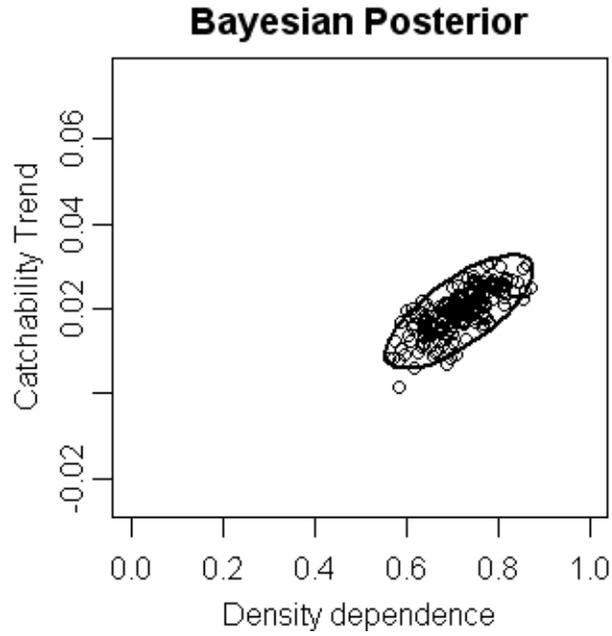


Figure 2.6 – Bayesian posterior of density dependence and compounding annual trend parameters as sampled using WinBUGS. A 95% probability ellipsoid is included to demonstrate the joint confidence region, as well as covariance structure.



## CHAPTER 3: A SIMULATION EVALUATION OF SINGLE-SPECIES AND MULTI-SPECIES ESTIMATES OF TIME-VARYING CATCHABILITY

### 3.1 Introduction

Many stock assessment models use the catchability coefficient to scale abundance indices such as fishery-independence surveys or catch-per-unit-effort (CPUE) data to stock abundance. Although catchability is usually assumed to be constant, previous studies have observed that it frequently varies over time. Violation of this assumption will introduce significant bias into stock assessment results (NRC 1998), although catchability changes that are non-directional or random over index length will be less important for stock assessment. Studies have demonstrated the prevalence of density-dependent catchability (Harley et al. 2001), where catchability changes as a function of abundance. In stocks with rapidly changing abundance, even a small degree of density dependence will drive large changes in catchability overall. Other factors may also interact to produce a residual trend in catchability, the direction of which may be difficult to predict *a priori*. Many fishery-dependent indices will likely exhibit increasing catchability trends due to technical improvements such as global positioning system navigational aids (Robins et al. 1996, Hannesson 2008).

Stock assessment scientists can compensate for time-varying catchability using a variety of catchability models and state-space methods (Wilberg et al. in review). Compensating for time-varying catchability could significantly improve management performance by avoiding overfishing caused by misinterpretation of hyperstable CPUE indices, and will also mitigate the risks of catchability-led stock collapse (Pitcher 1995). Time-varying catchability can be modeled using density dependence and trends parameters (Eq. 3.1), where catchability is a power function of abundance and undergoes a compounding trend (Chapter 2).

$$q_t = q_0 e^{t\beta} \bar{N}^{-\alpha} \quad (3.1)$$

Where:

$\alpha$  is catchability density dependence  
 $\beta$  is a residual compounding trend in catchability  
 $t$  is time, measured in years  
 $q_0$  is the catchability coefficient  
 $q_t$  is a time-varying catchability coefficient  
 $\bar{N}$  is average abundance

This model (Eq. 3.1) reduces to the standard assumption of constant catchability when  $\alpha = 0$  and  $\beta = 0$  (i.e. when assuming catchability is density-independent and stationary, respectively). Catchability increases during stock declines when  $\alpha > 0$ , causing CPUE-derived indices to exhibit a damped response to abundance. Catchability decreases during stock declines when  $\alpha < 0$ , causing CPUE to be hyperdepleting by magnifying the effect of changes in abundance on indices (Pitcher 1995).

Scientists may choose to estimate  $\alpha$ ,  $\beta$ , or  $q_t$  for various reasons. Estimates of  $\alpha$  and  $\beta$  will be useful to stock assessment scientists for comparison between different regions and stocks. Estimation of density dependence ( $\alpha$ ) may also be a parsimonious method for dealing with time-varying catchability for some stocks, and will be important for the projection of fishery responses to stock rebuilding (Wilberg et al. in review). Density dependence ( $\alpha$ ) could also be useful as a proxy for habitat-selective behavior (Shephard and Litvak 2004) while trend ( $\beta$ ) could be useful as a proxy for technical improvements (“technology creep”). However, stock assessments will ultimately use annual catchability ( $q_t$ ) in the calibration of statistical models to CPUE-derived index data, so this parameter will be most useful within stock assessment models. Studies with limited data may estimate trend ( $\beta$ ) without density dependence ( $\alpha$ ) for the sake of parsimony, whereas studies with abundant data may jointly estimate both parameters.

This study used simulation modeling to analyze the effect of density dependence, time-varying catchability, between-species variability in density dependence, and data quality and quantity upon catchability estimation. An operating model was structured as follows. First, different plausible models for catchability were identified. Second, annual catchability ( $q_t$ ) was simulated given year-specific abundance, and stock- and gear-

specific density dependence. Third, CPUE-derived indices were simulated using the simulated catchability data and abundance data after incorporating measurement error.

Six single and multi-species methods for estimating catchability model parameters were then applied to these simulated data, and were evaluated in comparison with standard catchability assumptions. Procedures included (1) single-species catchability estimates, (2) multi-species catchability estimates derived from pooling data across all species in a region, and (3) “imputed” catchability estimates that estimate density dependence and trend for a species of interest by using data from similar species. Single-species, multi-species, and imputed methods were used to estimate either (I) catchability trends or (II) trends and density dependence simultaneously. The precision and accuracy of density dependence ( $\alpha$ ), trend ( $\beta$ ), and year-specific catchability ( $q_t$ ) from all six procedures were compared with errors arising from the standard assumptions of density dependence and trend.

I hypothesize that single-species, multi-species and imputed estimation of catchability parameters will improve estimation of time-varying catchability when compared with standard catchability assumptions (i.e. no trend and density independence). If this hypothesis is correct, these methods would improve performance for both input-control and output-control fisheries management tactics without “using up” limited single-species information (Walters and Martell 2004). Multi-species estimation methods could also be used to develop region-specific Bayesian priors for time-varying catchability parameters. Procedures were evaluated both (1) to identify optimal methods for estimating density dependence ( $\alpha$ ) and trend ( $\beta$ ) for a multi-species fishery complex, and (2) to determine whether multi-species models of catchability will have less error in annual catchability ( $q_t$ ) than the errors arising from the standard assumptions.

### **3.2 Materials and Methods**

An operating model was developed to closely parallel the data quality and quantity that is currently available for the U.S. Gulf of Mexico (Chapter 2). This data includes catch-at-age data, fishery-independent indices, and CPUE-derived indices for gag grouper (*Mycteroperca microlepis*; SEDAR-10 2006-a), red grouper (*Epinephelus*

*morio*; SEDAR-10 2006-b), mutton snapper (*Lutjanus analis*; SEDAR-15 2008), king mackerel (*Scomberomorus cavalla*; SEDAR-16 2008), greater amberjack (*Seriola dumerili*; SEDAR-9 2006), and eastern and western stocks of red snapper (*Lutjanus campechanus*; SEDAR-7 2005). All stocks exhibited similar density dependence and trend parameters when estimated using hierarchical methods (Chapter 2). Subsequent calculations were performed using the R statistical platform (R Development Core Team 2008).

### 3.2.1 Generating simulated data

I simulated data using an operating model that was designed to represent plausible hypotheses regarding time-varying catchability in the Gulf of Mexico. Parameter values were set to a “base” scenario that represents likely values for the Gulf of Mexico, but were also varied among “sensitivity” values that were selected to span the range that was considered to be plausible. Operating model parameters are listed in Table 2, and are referred to as “base” and “sensitivity” values throughout the study.

A multi-species fishery complex was simulated as having a fixed number of stocks ( $n_{\text{stocks}}$ ). Each stock was assumed to provide a fixed number of CPUE-derived indices of abundance ( $n_{\text{CPUE}}$ ) as well as some estimate of abundance developed without using fishery-dependent data. The complex was either assumed to have large data availability (Base:  $n_{\text{stocks}} = 7$ ,  $n_{\text{CPUE}} = 4$ ) or limited data availability (Sensitivity:  $n_{\text{stocks}} = 3$ ,  $n_{\text{CPUE}} = 2$ ).

The following catchability models were deemed to be plausible and were included in the operating model:

Base: a 2% annual, non-compounding catchability trend as caused by gradual

improvements in fishing efficiency (Model 1). A similar trend has been observed previously by Hannesson (2008), and has been incorporated into previous stock assessments in the U.S. southeast region (SEDAR 10 2006-a, SEDAR 10 2006-b);

Sensitivities: stationary catchability (i.e.  $\beta = 0$ ; Model 2); knife-edge increases as caused by sudden technical changes (Model 3); and technological shocks, where technical

improvements gradually increase catchability over 3-4 years (Model 4; Robins et al. 1998).

Catchability models were designed to cover a plausible range of underlying hypotheses regarding technical changes in catchability. Models are listed in Table 1 and are depicted in Figure 1.

Simulated (“true”) abundance in the operating model for all stocks was derived from abundance estimates of seven stocks in the Gulf, derived from calibrated VPA without using fishery-dependent data (Chapter 2). These “true” abundance trends were based on real-world data and had variable time-series length, as depicted in Figure 2 (gag grouper – 21 years; red grouper – 20 years, greater amberjack 18 years; king mackerel – 26 years; mutton snapper – 26 years; eastern red snapper – 20 years; western red snapper – 20 years). The “true” abundance time series included periods with both increasing and decreasing abundance, and these contrasts were necessary to distinguish density-dependent and independent processes causing time-varying catchability.

I assigned each CPUE-derived index an index-specific density dependence that was calculated as a two-stage random-effect. This procedure implies that all stocks deviate from a region-wide, underlying density dependence, and is plausible given that most stocks have similar life-history strategies and share a common multi-species fishing industry (with common fishing gears and practices). First, each stock was assigned a density dependence calculated from a complex-wide density dependence (Base:  $\alpha_{\text{complex}} = 0.50$ ; Sensitivity:  $\alpha_{\text{complex}} = 0.0$ ) and a normal error (Eq. 3.2).

$$\alpha_{\text{stock}} \sim N(\mu = \alpha_{\text{complex}}, sd = p_{\alpha} sd_{\text{complex}}) \quad (3.2)$$

Second, density dependence for each index was calculated from stock-specific density dependence and a normal error (Eq. 3.3).

$$\alpha \sim N(\mu = \alpha_{\text{stock}}, sd = p_{\alpha} sd_{\text{stock}}) \quad (3.3)$$

Random-effect errors had a standard deviation that were calculated as a proportion (Base:  $p_\alpha = 100\%$ ; Sensitivities:  $p_\alpha = 0\%, 200\%$ ) of between-stock variability and within-stock variability in density dependence ( $sd_{\text{complex}} = 0.28$ ,  $sd_{\text{stock}} = 0.05$ ) as estimated in the Gulf of Mexico using hierarchical methods (Thorson unpublished data, Bates et al. 2008). Proportions of observed variability were chosen to show the effects of no variability (0%) or extreme variability (200%) in density dependence between indices. The latter value (200%) was considered the greatest that was plausible given that, at this level, more than one-fifth of all index-specific density dependence values were greater than one (when assuming a normal distribution for random effects), causing these CPUE-derived indices to be inversely related to abundance.

”True” annual catchability was calculated from an underlying catchability model, “true” abundance, and index-specific density dependence (Eq. 3.4).

$$q_t = q_{\text{underlying}} N^{-\alpha} \quad (3.4)$$

Fishery-dependent index data were calculated from “true” annual catchability, “true” abundance (Eq. 3.5), and a measurement error (Eq. 3.6).

$$CPUE = q_t N * \exp[\varepsilon_t] \quad (3.5)$$

$$\varepsilon_t \sim \varphi_{AR} \varepsilon_{t-1} + (1 - \varphi_{AR}) N(\mu = 0, \sigma = sd_{CPUE}) \quad (3.6)$$

The measurement error ( $sd_{CPUE} = 0.25$ ) had a magnitude similar to estimates in the Gulf of Mexico (Chapter 2) and first-order autocorrelation ( $\varphi_{CPUE} = 0.50$ ).

I modeled catchability estimation procedures as having imperfect information about “true” abundance. Abundance information was assumed to originate from either (a) basic stock assessment methods such as calibrated VPA without using fishery-dependent data (e.g. Chapter 2), or (b) fishery-independent index data (e.g. Harley et al. 2001). Different abundance information sources were compared to evaluate which information source was optimal for estimating catchability model parameters. Errors

between “true” and known abundance were modeled as a lognormal measurement error (Eq. 3.7).

$$\hat{N} = N * \exp[\zeta_t] \quad (3.7)$$

This measurement error was modeled as having variable magnitude, and to include first-order autocorrelation (Eq. 3.8).

$$\zeta_t = \varphi_N \zeta_{t-1} + (1 - \varphi_N) N(\mu = 0, \sigma = sd_N) \quad (3.8)$$

Abundance information arising from assessment models without using CPUE-derived data was assumed to have small but highly autocorrelated errors (Base:  $sd_N = 0.1$ ,  $\varphi_N = 0.75$ ). By contrast, abundance information arising from fishery-independent surveys was assumed to exhibit independent (i.e. low autocorrelation) errors of greater magnitude (Sensitivity:  $sd_N = 0.5$ ,  $\varphi_N = 0.1$ ).

### 3.2.2 Estimating catchability parameters from simulated data

Given data simulated using different model inputs as described above, I simulated seven different catchability estimation procedures. Procedures are summarized in Table 3, and differed in terms of (1) what assumptions they made and (2) what data they used. Each procedure estimated three parameters: density dependence ( $\alpha$ ), catchability trends ( $\beta$ ), and annual catchability ( $q_t$ ). Density dependence ( $\alpha$ ) and trends ( $\beta$ ) were estimated by fitting catchability model equations to simulated data using ordinary least squares (OLS) while annual catchability ( $q_t$ ) was estimated by applying  $\alpha$  and  $\beta$  estimates to a simple catchability model (Eq. 1).

Procedure 1 used single-species data and assumed that density dependence and trend were not present ( $\alpha = 0$  and  $\beta = 0$ ; Eq. 3.9).

$$\log\left(\frac{I_t}{N}\right) = \beta_1 D_1 + \beta_2 D_2 + \dots + \beta_n D_n \quad (3.9)$$

Where:

$D_1 \dots D_n$  are dummy variables for all combinations of species and gear

$\gamma_1 \dots \gamma_n$  are coefficients for species-gear dummy variables

Procedures 2-4 assumed density independence while estimating a catchability trend ( $\alpha = 0$ , estimate  $\beta$ ; Eq. 3.10).

$$\log\left(\frac{I_t}{N}\right) = \beta_1 D_1 + \beta_2 D_2 + \dots + \beta_n D_n + \beta_t t \quad (3.10)$$

This trend was assumed to be the same for all stocks. Procedure 2 used single-species data. Procedure 3 “imputed” catchability parameters by estimated trend (Eq. 10) using all available species except one and applying results to the remaining species. Procedure 4 used all available species to estimate trend (Eq. 3.10).

Procedures 5-7 jointly estimated density dependence and trend (estimate  $\alpha$  and  $\beta$ ; Eq. 3.11).

$$\log(I_t) = \gamma_1 D_1 + \gamma_2 D_2 + \dots + \gamma_n D_n + \beta t + (1 - \alpha) \log(N) \quad (3.11)$$

This trend and density dependence was assumed to be the same for all stocks. Procedure 5 used single species data, while Procedure 6 imputed catchability and Procedure 7 used multi-species data.

I hypothesized that the procedures that “imputed” catchability parameters (Procedures 3 and 6) would be plausible methods to compensate for time-varying catchability in single-species stock assessments. These procedures use data from species that are similar to a species that is being assessed to estimate a catchability model. These

catchability parameters would then be used to compensate for time-varying catchability in the assessment without using limited data from the assessment species. Procedures using this “imputation” method were hypothesized to yield more precise and accurate estimates of annual catchability than the errors arising from standard assumptions (e.g. Procedure 1).

### 3.2.3 Evaluating catchability parameter estimates

To evaluate the precision and accuracy of catchability model parameters, I compared trend estimates with optimal values. Optimal trend values were considered to be the estimates that would arise from OLS in the absence of any measurement errors, process errors, or variability in density dependence, and were calculated by regressing the underlying catchability model (Table 1) on density-independent catchability (Eq. 3.10). Procedure 1 (i.e. assuming that  $\alpha = 0$  and  $\beta = 0$ ) was excluded from comparison with optimal trend estimates because it assumed the absence of trend. No attempt was made to compensate estimates for bias due to inaccurate abundance information (i.e. measurement error bias) prior to the comparison of estimated and optimal results. Consequently, treatments also show the impact of variable degrees of measurement error on estimation accuracy. Catchability trend estimates for Procedures 2-7 were displayed as boxplots, while the optimal value was shown as a horizontal line. Procedures were evaluated in terms of accuracy (that boxplot median values were centered on the horizontal line showing the optimal value) and precision (that boxplots have tight interquartile ranges, tight whiskers, and few outliers).

First, I evaluated trend estimates given different underlying models for catchability while holding other model factors at base levels. Second, trend estimates were evaluated given different values of density dependence and different sources of abundance information while holding other model factors at base levels. Third, trend estimates were evaluated for different degrees of variability in density dependence and different quantities of data while holding other model factors at base levels.

### 3.2.4 Evaluating annual catchability estimates

I estimated error in estimates of annual catchability ( $q_t$ ) and compared this error among Procedures 1, 3, and 6. These procedures were included because I considered Procedures 3 and 6 to be parsimonious methods of estimating annual catchability, and might provide less error in annual catchability estimates than the standard assumptions (Procedure 1). Results were displayed as density plots of the average error ( $Error_q$ ) arising from Procedures 1, 3, and 6. In these density plots, precise estimation of annual catchability was shown by density distributions with most of their mass close to 0 ( $Error_q = 0$ , towards the left)

I calculated average error in annual catchability estimates ( $Error_q$ ) by comparing estimated annual catchability with “true” annual catchability from the operating model (Eq. 3.12).

$$Error_q = \frac{1}{n} \sum_t \frac{\hat{q}_{t,centered} - q_{t,centered}}{q_{t,centered}} \quad (3.12)$$

Where:

$n$  is the number of years in a time-series

$\hat{q}_{t,centered}$  is estimated catchability, scaled to have a mean of 1

$q_{t,centered}$  is “true” catchability, scaled to have a mean of 1

In this comparison, both true and estimated catchability time-series data are scaled to have a mean of one, because only the relative difference in overall trends is important. The error was expressed as an average across the entire catchability time series.

Particular operating model parameters were varied within plausible ranges, while other parameters were left at base values. First, errors in estimated annual catchability ( $Error_q$ ) were compared for different underlying models for catchability (Table 3.1) and different sources for abundance information (assessment models vs. independent surveys), while holding other model factors at base values. Next, errors in estimated annual catchability ( $Error_q$ ) were compared for different density dependence and different between-index variability in density dependence given a stationary model for catchability

(Model 1) while holding other model factors at base values. One panel in the latter comparison satisfies the standard assumptions ( $\alpha = 0$  and  $\beta = 0$ ) and was interpreted as a control, to evaluate the errors caused by estimating trend (Procedure 3) or jointly estimating trend and density dependence (Procedure 6) when the assumptions of Procedure 1 are perfectly met.

### 3.3 Results

#### 3.3.1 Optimal methods for estimating catchability trend

A comparison of procedures (Fig. 3.3) given different models for density-independent catchability (from top to bottom: stationary catchability; 2% non-compounding annual increase; 30% knife-edge increase; 2 technology shocks) shows that joint estimation procedures (Procedures 5-7) yield unbiased estimates of trend regardless of the underlying catchability model that is hypothesized. Procedures that assume density independence ( $\alpha = 0$ , Procedures 2-4) are highly biased in their estimates of trend. Multi-species procedures (Procedures 3, 4, 6, 7) show greater precision (i.e. have smaller interquartile ranges) than single-species procedures (Procedures 2, 5), and imputed procedures (Procedures 3, 6) show little decrease in precision when compared with pooled procedures (Procedures 4, 7).

A comparison of procedures (Fig. 3.4) given different degrees of density dependence (Left:  $\alpha_{\text{complex}} = 0$ ; Right:  $\alpha_{\text{complex}} = 0.50$ ) and different sources of abundance information (Top: From a model,  $\text{sd}_N = 0.1$ ,  $\varphi_N = 0.75$ ; Bottom: From fishery-independent survey,  $\text{sd}_N = 0.5$ ,  $\varphi_N = 0.1$ ) shows that trend estimates are highly biased when density dependence is present but not estimated (Fig. 4b, Procedure 2-4). The precision of trend estimates is also not greatly diminished if estimating density dependence when density dependence is absent (Fig. 4a, Procedure 5-7). Estimates using abundance derived from fishery-independent data (Fig. 3.4c, 3.4d) show a large bias in trend estimates when compared with estimates using modeled abundance. This bias is caused by measurement error (Draper 1998), which is assumed to be small for modeled abundance ( $\sigma = 0.1$ ) and large for fishery-independent data ( $\sigma = 0.5$ ).

A comparison of procedures (Fig. 3.5) given different between-index variability in density dependence (Left:  $sd_{\text{complex}} = 0.28$  and  $sd_{\text{stock}} = 0.05$ ; Right:  $sd_{\text{complex}} = 0.56$  and  $sd_{\text{stock}} = 0.10$ ) and different quantities of data (Top:  $n_{\text{species}} = 7$ ,  $n_{\text{CPUE}} = 4$ ; Bottom:  $n_{\text{species}} = 3$ ,  $n_{\text{CPUE}} = 2$ ) shows that neither within-complex variability nor data limitations have a strong impact on the accuracy of trend estimates. However, the precision of trend estimates is reduced by both variability in density dependence and a decrease in available data, with the latter causing a greater reduction in precision. Multi-species joint estimation (Procedure 7) continues to perform well even given high variability and limited data (Fig. 3.5d).

### 3.3.2 Comparing multi-species catchability models and standard assumptions

A comparison of annual catchability estimation errors ( $\text{Error}_q$ ) between Procedures 1, 3, and 6 (Fig. 3.6) given different catchability models and abundance information sources (Top: Abundance from a model,  $sd_N = 0.1$ ,  $\varphi_N = 0.75$ ; Bottom: Abundance from fishery-independent index,  $sd_N = 0.5$ ,  $\varphi_N = 0.1$ ) showed that joint imputation (Procedure 6) was most accurate for a variety of underlying catchability models given abundance information arising from assessment models. However, when using abundance information arising from fishery-independent surveys, Procedures 1 and 3 showed higher accuracy than Procedure 6 (Fig 3.6b, 3.6d, 3.6f, 3.6h). Experimentation showed the autocorrelated error in abundance information ( $\varphi_N$ ) had little effect on the annual catchability estimation errors, and that increased error in abundance information caused error in annual catchability estimates by causing an upward bias in estimates of density dependence ( $\alpha$ ). This bias had magnitude and direction as expected for error-in-variables models (Draper 1998), which will cause upward bias in estimates of density dependence. Although Procedure 3 improved accuracy slightly compared with the standard assumptions (Procedure 1), joint estimation of density dependence and trend (Procedure 6) was better able to compensate for the impact of changing abundance on annual catchability when accurate abundance information was available (Fig. 3.6a, 3.6c, 3.6e, 3.6g).

A comparison of annual catchability estimation errors ( $\text{Error}_q$ ) between Procedures 1, 3, and 6 (Fig. 3.7) given different density dependence (Left:  $\alpha_{\text{complex}} = 0$ ; Right:  $\alpha_{\text{complex}} = 0.5$ ) and between-index variability in density dependence (Top:  $\text{sd}_{\text{complex}} = 0.01$  and  $\text{sd}_{\text{stock}} = 0.01$ ; Bottom:  $\text{sd}_{\text{complex}} = 0.28$  and  $\text{sd}_{\text{stock}} = 0.05$ ) showed that joint estimation of density dependence and trend (Procedure 6) did not dramatically increase errors even when standard assumptions (i.e.  $\alpha = 0$  and  $\beta = 0$ ) were perfectly met (Fig. 3.7a). This was also true when variability in density dependence was included (Fig. 3.7c). Moreover, any degree of density dependence again causes joint estimation (Procedure 6) to outperform other procedures (Fig. 3.7b, 3.7d).

### 3.4 Discussion

#### 3.4.1 Stock assessment implications

My results demonstrate that multi-species estimation of a simple catchability model provided precise and unbiased estimates of catchability trend and density dependence parameters across a wide range of fishery complex characteristics. This was true even in circumstances of extreme between-stock variability in density dependence, such as may occur for stocks with different life-history strategies within a common management region, or for different fishery gears and practices. Results were only impacted significantly when abundance information (derived without using CPUE data) was of low quality (i.e. had errors of large magnitude). However, recent studies (Chapter 2) have used VPA abundance estimates, calibrated using with fishery-independent data, as an input for catchability parameter estimation. Simulation analysis (Thorson, unpublished data) has suggested that these VPA estimates of abundance may have relatively small errors (coefficient of variations  $< 0.15$ ). In this instance, multi-species imputation appears adequate for unbiased and precise estimation of catchability parameters.

Multi-species joint estimation of density dependence and catchability trend greatly improved the precision and accuracy of annual catchability estimates compared with (1) the errors implied by the standard catchability assumptions or (2) when only

estimating catchability trend. This was true even without using data from the particular species of interest (e.g. using Procedures 3 and 6), and implies that future stock assessments may use information from similar species to yield parsimonious estimates of catchability parameters. Using data from similar species is conceptually simple and may be immediately applied to stock assessments in the Gulf of Mexico where a multi-species catchability model has already been estimated (Chapter 2). Importantly, multi-species and imputation procedures did not dramatically increase errors even when standard assumptions were met (e.g. when underlying catchability was Model 1 and  $\alpha_{\text{complex}} = 0$ ).

Estimates of underlying catchability that assumed density independence ( $\alpha = 0$ ) when density dependence was present led to considerable bias in catchability trend estimates. Thus, *a priori* estimates of underlying catchability may diverge considerably from “true” annual catchability when abundance is changing and density dependence is present (even in small values). This divergence may lead to unsound assumptions about annual catchability when models do not account for density dependence. By contrast, joint estimates of catchability and density dependence were unbiased across a wide range of operating model parameters, and multi-species joint estimation generally had high precision when compared with single-species methods.

### 3.4.2 Comparison with other studies

Numerous studies have highlighted the importance of time-varying catchability to fisheries management (NRC 1998, SEDAR in review). Time trends and density dependence may (1) cause overfishing (and concomitant reductions in yield) by overestimating current stock biomass, (2) require continuous modifications or monitoring of effort-control management tactics, or (3) contribute to catchability-led stock collapse (Walters and Martell 2004, Hutchings and Myers 1994, Pitcher 1995). Although index standardization and state-space modeling methods may compensate for some of these problems (Maunder and Punt 2004, Wilberg and Bence 2006, Wilberg et al. in review), these methods also may divert limited single-species data away from parameters of management importance (i.e. management benchmarks, stock-recruit parameters). By contrast, my results show that data from similar species within a region is an additional

source of useful information regarding catchability parameters (i.e. trend trends, density dependence, and effort dependence). This agrees with results from Zhou et al. (2008), which used hierarchical Bayesian modeling to estimate a catchability model for banana prawns (*Penaeus merguensis*) in northern Australia.

Using similar species within a region to estimate catchability parameters (i.e. trend and density dependence) is conceptually similar to other meta-analysis results. In particular, Harley et al. (2001) used mixed effects modeling and multiple stocks to estimate a Bayesian prior for CPUE density dependence. However, region-specific factors (i.e. index standardization methods, fishery targeting practices, etc.) may have a greater impact on CPUE density dependence or trend than can be faithfully estimated using a meta-analysis of world-wide fisheries. In this case, localized studies (such as this) may provide stronger inference to region-specific concerns or factors. Region-specific studies may also prove easier to explain to local stakeholders, who can ensure that data from their region is being used to drive management.

### 3.4.3 Future studies

Ultimately, I propose using data from similar species within a region to develop a Bayesian prior for region-specific stock assessments. However, evaluating the accuracy of a Bayesian prior was deemed to be too computationally intensive to implement within a simulation modeling exercise. I assume that the comparative errors (standard assumptions vs. single-species, multi-species, and imputed estimation procedures) arising from OLS estimation in this study will be similar to errors arising from Bayesian or other statistical methods. Future studies could attempt to verify this assumption by simulating estimation procedures that are more computationally intensive (i.e. frequentist hierarchical estimation) within a more-limited range of operating model parameters or assumptions.

Future simulation models could also compare long-term management performance (e.g. expected future yield, risk of stock collapse, etc.; Walters and Martell 2004) among (1) standard catchability assumptions, (2) state-space or random-walk methods (Wilberg and Bence 2006), and (3) when imputing catchability parameters from

similar species within a region. Management performance may have more importance for fisheries managers than the estimation accuracy evaluated in this study, and is frequently evaluated using management strategy evaluation methods (Smith et al. 1999). However, long-term management evaluation requires identification of management priorities and will be more meaningfully done on a stock-by-stock basis. Future studies might also explore the ability of specific stock assessment models (including virtual population analysis, statistical catch-at-age, and stock synthesis models) to estimate density dependence and time trends internally while performing single-species stock assessments. Results from these methods may again be linked in region-specific catchability models.

#### 3.4.4 Stock assessment recommendations

Previously, many assessment scientists have not considered the estimation of catchability parameters to be feasible given to the limited data that is available for any single-species stock assessment (Stokes and Pope 1987). However, recent studies such as Robins et al. (1996), Hannesson (2008), and Thorson (Chapter 2) have used long time-series data, vessel-specific longbook data, or multi-species data to estimate statistically-significant deviation from standard catchability assumptions. The multi-species approaches proposed in this study should be widely applicable given the types, quantity, and quality of data that is generally available in the United States, and may prove a useful avenue for both (1) validating the increasing trends in catchability that have been estimated elsewhere (e.g. Hannesson 2008), and (2) justifying inclusion of catchability density dependence into future stock assessment methods.

I propose that the multi-species methods used in this study are a novel way to evaluate the soundness of the standard catchability assumptions (i.e.  $\alpha = 0$  and  $\beta = 0$ ). These assumptions are often difficult to evaluate or relax, and imputed estimation (Procedures 3 and 6) can both evaluate and relax these assumptions without “using up” the limited data that is available for any single-species stock assessment. In cases where these assumptions are deemed inadequate, estimation of a Bayesian prior for region-wide catchability hyperparameters could be a statistically-robust method to incorporate multi-

species catchability data into single-species assessment models. Results suggest that data from similar species within a region are an under-utilized resource for evaluating common catchability assumptions and provide a parsimonious method to compensate for time-varying catchability.

Table 3.1 – Models for underlying changes in catchability due to technology

Model	Catchability
1	$q_{\text{underlying}} = 1 + 0.02t$
2	$q_{\text{underlying}} = 1$
3	$\begin{cases} q_{\text{underlying}} = 1 & 1 \leq t \leq 10 \\ q_{\text{underlying}} = 1.30 & 11 \leq t \leq t_{\text{max}} \end{cases}$
4	$\begin{cases} q_{\text{underlying}} = 1 & 1 \leq t \leq 6 \\ q_{\text{underlying}} = 1.05 & t = 7 \\ q_{\text{underlying}} = 1.08 & t = 8 \\ q_{\text{underlying}} = 1.11 & 9 \leq t \leq 12 \\ q_{\text{underlying}} = 1.16 & t = 13 \\ q_{\text{underlying}} = 1.19 & t = 14 \\ q_{\text{underlying}} = 1.22 & t \geq 15 \end{cases}$

Table 3.2 – Operating model parameters with base and sensitivity values

Parameter	Base value	Sensitivity value(s)
Quantity of available data	Full data ( $n_{\text{stocks}} = 7, n_{\text{CPUE}} = 4$ )	Limited data ( $n_{\text{stock}} = 3, n_{\text{CPUE}} = 2$ )
Complex-wide density dependence	$\alpha_{\text{complex}} = 0.5$	$\alpha_{\text{complex}} = 0$
Catchability model	Model 1	Model 2, 3, 4
Proportion of observed between-stock and within-stock variability in density dependence	$p_{\alpha} = 100\%$	$p_{\alpha} = 0\%, 200\%$
Abundance information source	Assessment model ( $\text{sd}_N = 0.1, \varphi_N = 0.75$ )	Fishery-independent survey ( $\text{sd}_N = 0.5, \varphi_N = 0.1$ )

Table 3.3 – Seven different estimation procedures differ in the assumptions they make regarding density dependence and trend (assumed equal to 0 or estimated) and the data they use (single species, imputed, or pooled).

Procedure	Assumptions		Data usage		
	Density dependence ( $\alpha$ )	Trend ( $\beta$ )	Single-species	Imputed	Pooled
Standard assumptions					
1	0	0	X		
Proportional					
2	0	Est.	X		
3	0	Est.		X	
4	0	Est.			X
Joint Estimation					
5	Est.	Est.	X		
6	Est.	Est.		X	
7	Est.	Est.			X

Figure 3.1 – Four different catchability models are shown. Included are: a constant catchability; a 2% non-compounding annual increase; a 30% knife-edge increase; and a two-step technological shock.

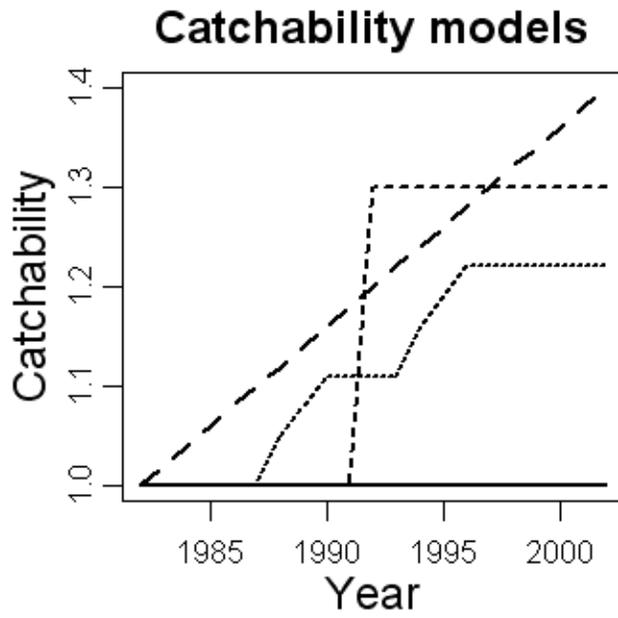


Figure 3.2 – Relative abundance estimated from calibrated VPA, used as “true” abundance for seven simulated stocks.

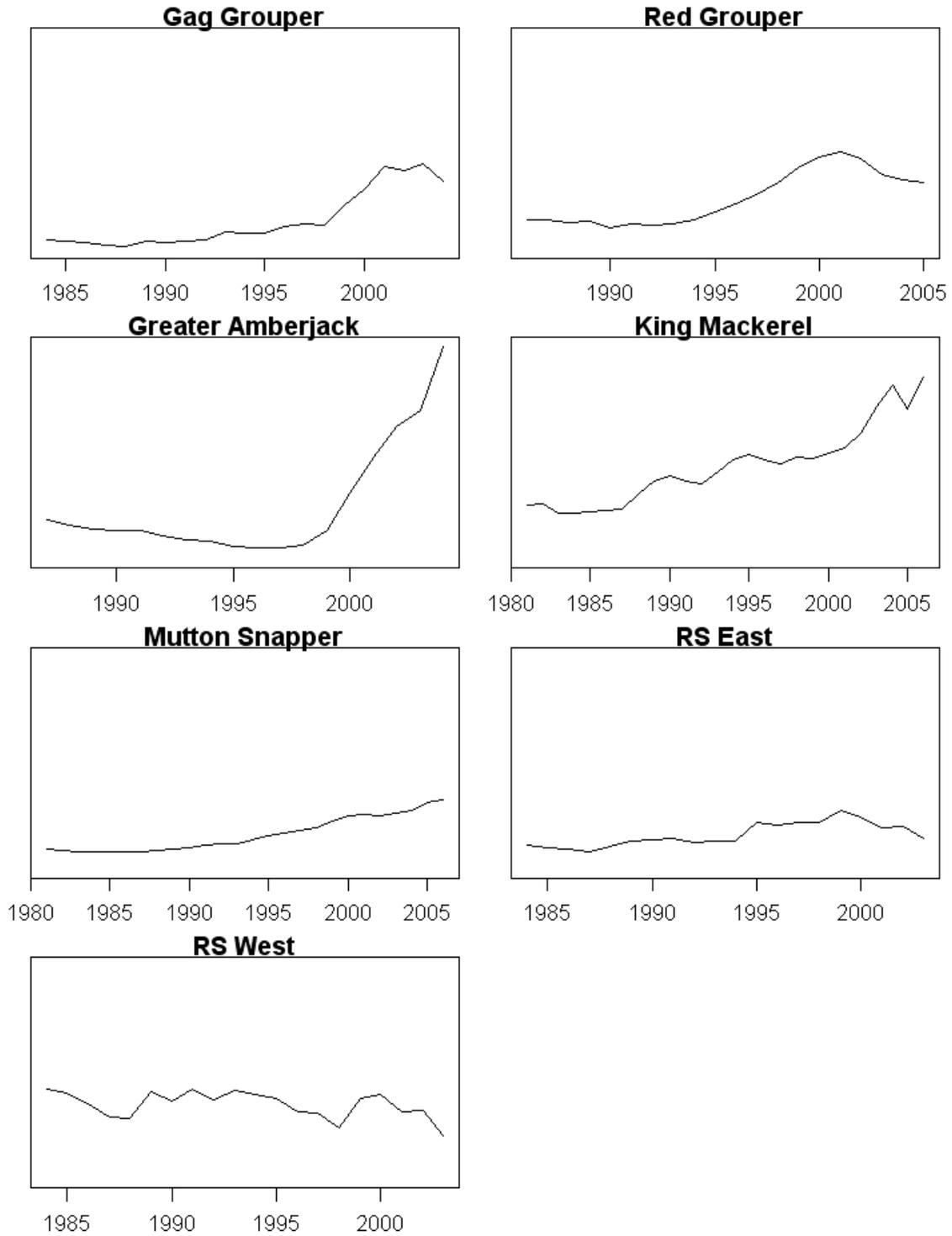


Figure 3.3 – Boxplots of trend estimates for Procedures 2-7 given different underlying models for catchability (vertical panel axis). Other model factors are set to base values and the horizontal line is an optimal estimate for compounding trend.

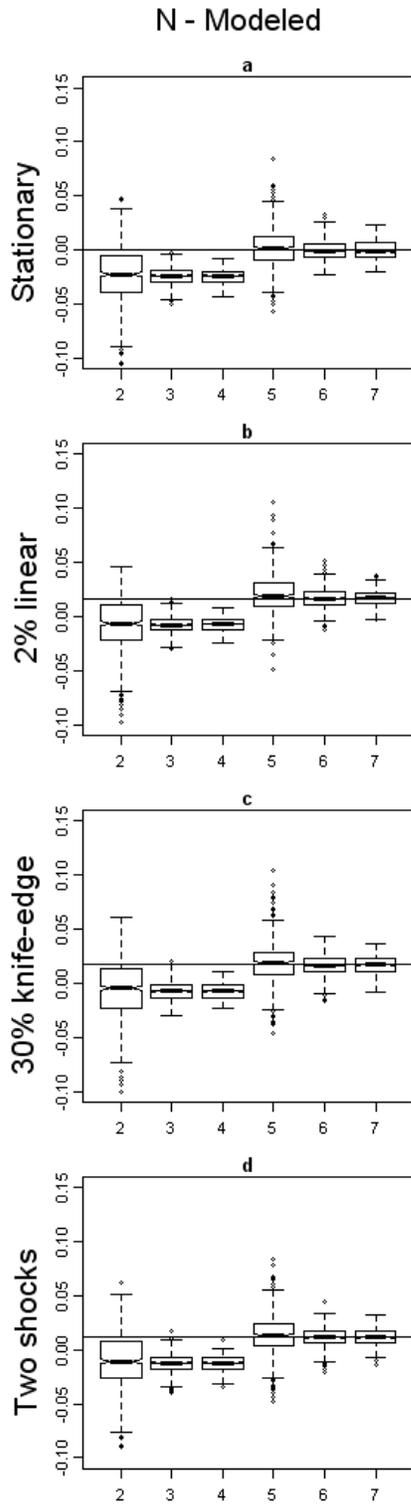


Figure 3.4 – Boxplots of trend estimates for Procedures 2-7 given different degrees of underlying density dependence (horizontal panel axis) and abundance information arising from stock assessment models (top panel row) or fishery-independent indices (bottom panel row). Other model factors are set to base values and the horizontal line is an optimal estimate for compounding trend.

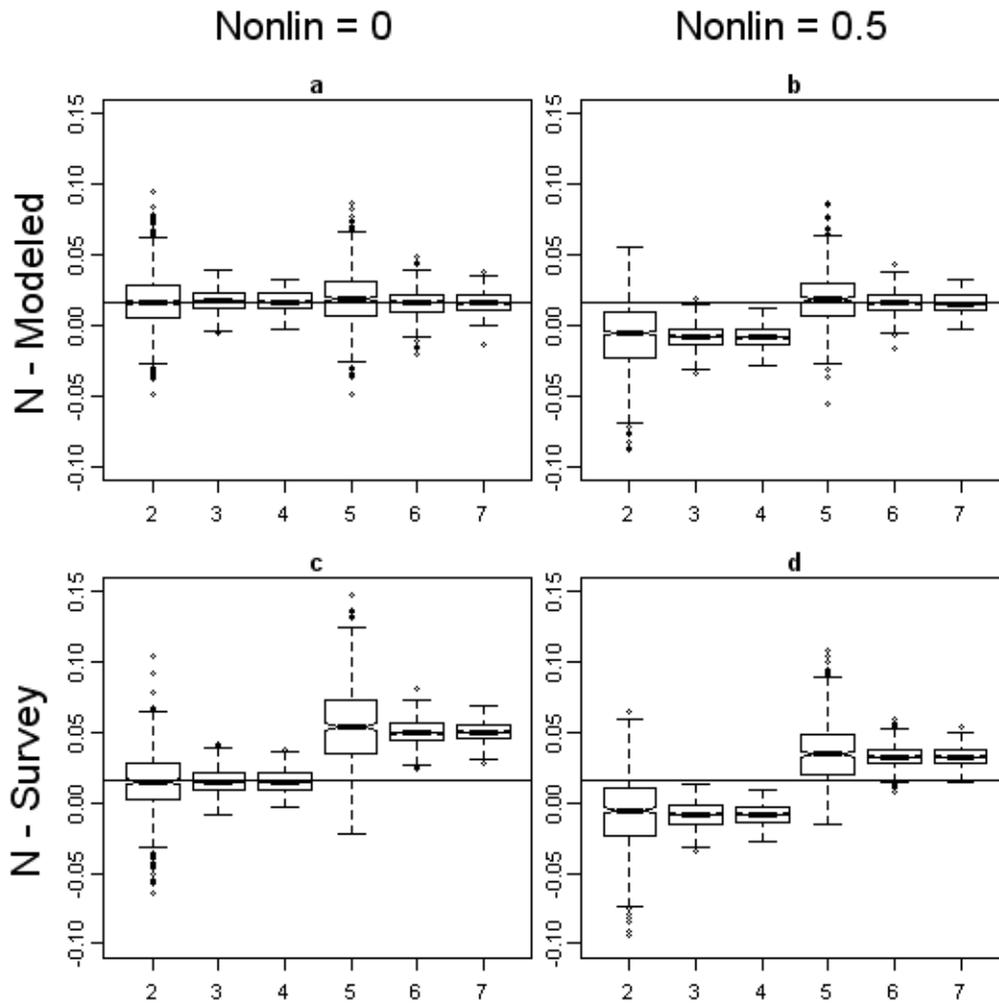


Figure 3.5 – Boxplots of trend estimates for Procedures 2-7 given different proportions of the density dependence variability observed in Gulf of Mexico stocks (horizontal panel axis), either when using large amounts of data (Top row: 7 species, 4 CPUE per species) or limited amounts of data (Bottom row: 3 species, 2 CPUE per species). Other model factors are set to base values and the horizontal line is an optimal estimate for compounding trend.

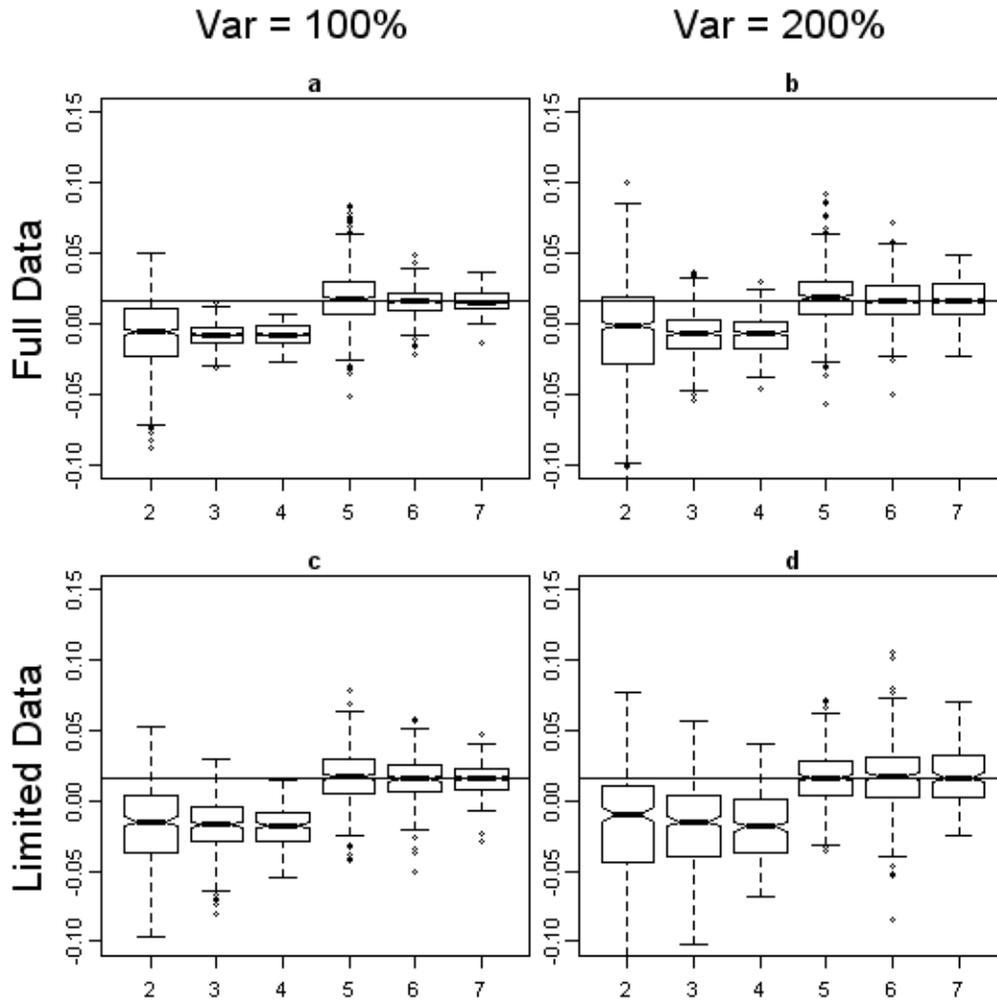


Figure 3.6 – Empirical distribution of error in estimates of annual catchability ( $Error_{qt}$ ) is shown on the x-axis for three estimation procedures (solid line = Procedure 1; dotted line = Procedure 3; dashed line = Procedure 6) given different hypothesized scenarios for underlying catchability (vertical panel axis), either when using abundance information from stock assessment models (left column) or fishery-independent indices (right column). Other model factors are set to base values.

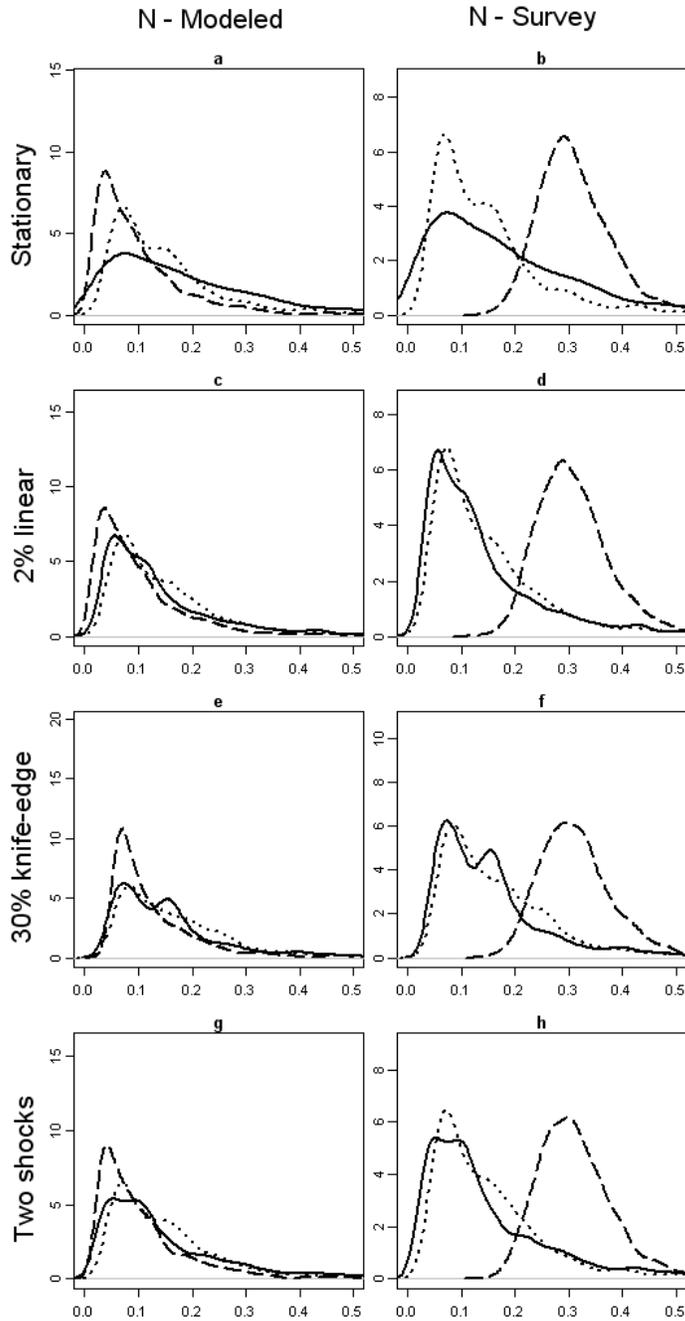
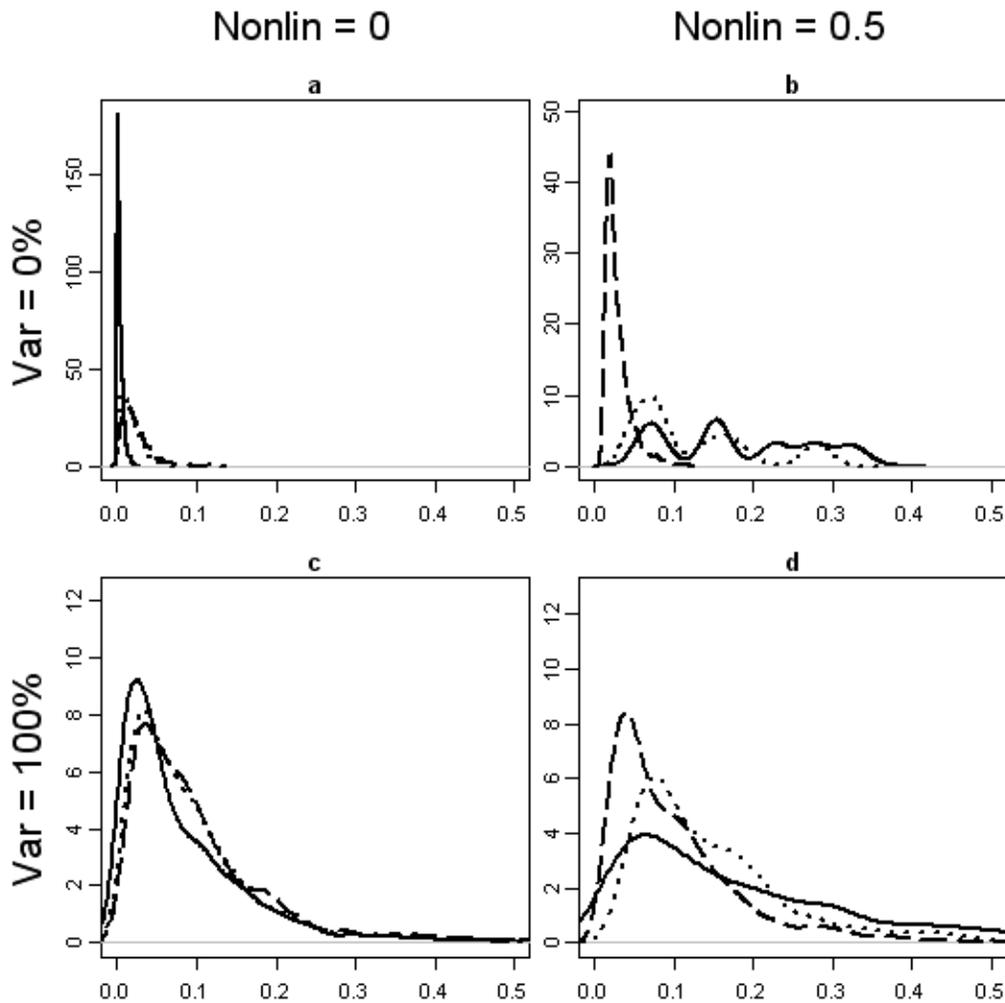


Figure 3.7 – Empirical distribution of error in estimates of annual catchability ( $\text{Error}_q$ ), is shown on the x-axis for three estimation procedures (solid line = Procedure 1; dotted line = Procedure 3; dashed line = Procedure 6) given different magnitudes of density dependence (Horizontal panel axis) and different proportions of the density dependence variability observed in the Gulf of Mexico (vertical panel axis). Other model factors are set to base values except the underlying catchability ( $q_{\text{underlying}}$ ), which is set to Model 2 (“stationary”). The upper-left panel satisfies the standard assumptions ( $\alpha = 0$  and  $\beta = 0$ ).



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