

EVALUATING THE IMPACT OF STOCK STRUCTURE UNCERTAINTY IN  
STOCK ASSESSMENTS OF SAILFISH IN THE ATLANTIC OCEAN

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by

Catarina Wor Lima


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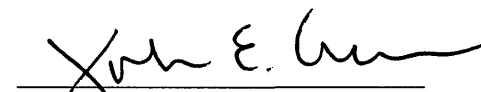
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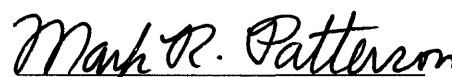
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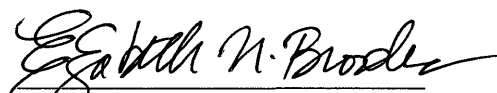
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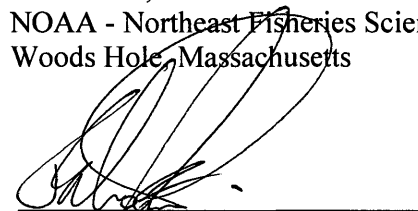
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## DEDICATION

I dedicate this thesis to my parents for their enduring support and encouragement throughout my educational journey.

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EVALUATING THE IMPACT OF STOCK STRUCTURE UNCERTAINTY IN  
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## CHAPTER 1: INTRODUCTION

## PROJECT OVERVIEW

Delineating the stock structure of a harvested species is a major prerequisite for understanding its population dynamics, conducting reliable stock assessments, and providing effective management. Nonetheless, stock structure uncertainty is pervasive in fisheries science. This problem is partly due to the intrinsically multifaceted concept of a stock and also because the definition of a stock can vary according to the objective of scientific inquiry (Cadrin et al. 2005, Hammer and Zimmermann 2005). For example, evolutionary studies usually focus on identifying genetically distinct groups (Waples and Gaggiotti 2006, Lowe and Allendorf 2010) while fisheries-oriented research tends to focus on delineating ecologically distinct units (Waldman 2005). From a fisheries management perspective, these ecological units should be treated separately and are to be maintained at levels in which yield is maximized and sustainable use of the resource is promoted (Cope and Punt 2009). Although evolutionary stock units might be homogeneous from the genetic perspective, they can exhibit heterogeneity in life history characteristics (Pawson and Jennings 1996, Cushman et al. 2009, Hobday and Punt 2009, Svedäng et al. 2010). Consequently, relying uniquely on genetic methods for the identification of manageable units might lead to a failure in attaining management objectives and sustainability of the resource.

Knowledge of ecological stock structure of a species is considered essential for effective management. The reason for such importance is related to the fact that most commonly used stock assessment methods rely on the assumption that stocks

are discrete and self-recruiting units with homogeneous life history parameters (Begg et al. 1999a, Begg and Waldman 1999). However, these assumptions are frequently violated either because of insufficient information to delineate discrete stock units or because of the existence of greater stock complexity (e.g. occurrence of mixing between stocks or presence of different subunits within a single stock; Secor 1999, Kerr et al. 2010, Ying et al. 2011). The assumption of an incorrect stock structure together with the use of stock assessment techniques that do not account for mixing or stock structure uncertainty can lead to severe bias in the estimation of stock assessment parameters and consequently, in the derived management benchmarks (Arrizabalaga et al. 2007, Brooks and Apostolaki 2007, Apostolaki et al. 2003).

Stock assessment uncertainty can originate from two different types of error when defining a stock (Punt 2003). The first type occurs when multiple stocks are assessed as a single unit. In this scenario, differences in life history parameters and susceptibility to fisheries might lead to a decrease in biocomplexity (Hilborn 2003); local depletion; or, in the extreme, the loss of genetic diversity (Stephenson 1999). The second type of error occurs when only a portion of a stock is assessed as a closed unit. Although this error is less commonly addressed in the literature, it can also lead to severe bias in stock assessment estimates (Butterworth and Geromont 2001, Field et al. 2006). The movement of individuals across the borders of the area assigned for the stock leads to the instability of stock size and productivity parameter estimates, thereby decreasing the reliability of the overall assessment results and derived management benchmarks (Fabrizio 2005). Both scenarios are prone to producing misleading results, increasing risks of incorrect stock status

determination, or even leading to ineffective management strategies (Begg et al. 1999b).

Even though it is known that stock structure uncertainty can elevate the risks associated with estimation of management benchmarks, the number of species for which formal stock structure delineation methods have been implemented is relatively small. Population structure studies require comprehensive and interdisciplinary analyses, which frequently imply the need for the collaboration of scientists with various research expertise (Fabrizio 2005, Cadrin et al. 2010). These analyses are usually time-consuming and in many cases require sampling protocols that are cost prohibitive. These difficulties are particularly true for large migratory species, such as tunas and billfishes, for which genetic differentiation is usually low and sample availability is limited (Ward et al. 1994, Ward 2000). However, although it might be very hard to eradicate this uncertainty, its impacts can be evaluated and quantified by the use of operating models. Operating models consist of computer-simulated data used to mimic population dynamics under known assumptions. For these models, “reality” is known so the output of any analysis can be compared to the true parameters that underlie the data.

In this thesis, simulation analyses are used to quantify the effects of stock structure uncertainty on species with limited available information, using the Atlantic sailfish (*Istiophorus platypterus*) as a case-study. An operating model was developed and employed to generate data from “known” stock structures. Stock assessments were then conducted under various stock structure assumptions to evaluate the effects of stock structure uncertainty on assessment results and derived management benchmarks.

## Sailfish

Sailfish, *Istiophorus platypterus*, are widely distributed throughout the world's oceans, occurring primarily in tropical and subtropical waters (Nakamura 1985). Like other billfishes of the family Istiophoridae, sailfish are oceanic and epipelagic, typically associated with shallow warm waters above the thermocline (Hoolihan et al. 2009). Sailfish differ from other pelagic istiophorids in that they are often closely associated with islands and coastal waters (Nakamura 1985, Orbesen 2008). Although less frequently, sailfish are also found in oceanic waters throughout the Atlantic, especially in Equatorial areas (Die 2010, Wor et al. 2010).

The sailfish is an important species for recreational and artisanal fisheries worldwide. It is also commonly caught as bycatch by pelagic longline fisheries targeting various tuna species and swordfish (Arocha and Ortiz 2006). Despite the relevant social and economic values associated with sailfish fisheries, information about life history characteristics is still limited. Age and growth parameters were estimated for sailfish from the southwestern Atlantic Ocean using combined sexes (Freire 1998), but subsequent studies on age and growth done in the Pacific Ocean (Chiang et al. 2004, Ramírez-Perez et al. 2011) and Persian Gulf (Hoolihan 2006) indicated that the species exhibits sexually dimorphic growth. Maturity ogives were estimated for Atlantic sailfish by Arocha and Marcano (2008) and by Mourato et al. (2009); however, both studies limited their samples to the western Atlantic and only the latter used histology for the determination of maturity stages. Within the eastern Atlantic, Diouf (1994) and N'da and Soro (2009) presented evidence of

spawning activity off Senegal and Ivory Coast, respectively, but no maturity ogives were estimated.

In the Atlantic Ocean, sailfish are managed by member nations of the International Commission for the Conservation of Atlantic Tunas (ICCAT). For assessment purposes ICCAT assumes the existence of separate stocks in the eastern and western Atlantic. This stock structure was first defined during the second ICCAT Billfish Workshop in Miami, FL, in 1992, and was based on the reported coastal nature of sailfish, the lack of trans-Atlantic movements observed from the recoveries of conventional tags, and differences in average size of sailfish landed in the western and eastern Atlantic (Anonymous 1994). However, during the 2009 Sailfish Stock Assessment, the validity of the two stock model was questioned. It was noted that there is a lack of genetic heterogeneity among sailfish collected throughout the Atlantic Ocean (Graves and McDowell 2003) and that commercial catch composition data indicate a continuous distribution of sailfish catches across the equatorial Atlantic (Anonymous 2010). It was recommended that an exploratory analysis considering alternative stock scenarios be conducted at the assessment meeting, but this was not undertaken due to time limitations. The impacts of alternative stock structure assumptions thus remain unevaluated and, consequently, the risks of assessing the stock without accurate knowledge of the underlying stock structure remain unknown.

To address this problem, this thesis employs an operating model to generate Atlantic sailfish populations of known stock structures. The data obtained from these simulated populations were assessed under various stock structure assumptions so that the effects of erroneous assumptions could be evaluated.

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CHAPTER 2: IMPACTS OF STOCK STRUCTURE UNCERTAINTY IN STOCK  
ASSESSMENT DERIVED MANAGEMENT BENCHMARKS

## ABSTRACT

The ability to accurately delineate stock structure is a major pre-requisite of stock assessments. Despite its importance, there is usually some level of uncertainty associated with the stock structure assumption. The magnitude of this uncertainty and its effect on the stock assessment results has not been thoroughly investigated in many exploited species. In this study, simulation analyses were used to quantify the effects of stock structure uncertainty on species with limited available information, using the Atlantic sailfish (*Istiophorus platypterus*) as a case-study. An age-structured operating model was developed to simulate abundance, catch and effort data, assuming three possible stock structure scenarios, two levels of mixing and two fishing histories. Changes in management benchmarks estimates ( $B/B_{msy}$  and  $F/F_{msy}$ ) were evaluated. Stock structure uncertainty and mixing were found to cause substantial bias in the management benchmarks. However, the magnitude and direction of the bias were found to be highly dependent on the exploitation history of the stock.

## INTRODUCTION

Fisheries stock assessment methods have improved greatly over the last several decades. Advancement of stock assessment theory and statistical techniques accompanied by increases in computer power have aided development of sophisticated fisheries population dynamics models and parameter estimation methods (Hilborn 2012, Schnute et al. 2007). Application of stock assessment methods routinely involves integrating fisheries data from multiple sources and characterizing scientific uncertainty of model outputs (Quinn 2003). However, despite notable theoretical and analytical progress, a general lack of informative fisheries data and knowledge regarding life history characteristics of exploited species remains a challenge in assessing many exploited populations (Methot 2009).

One fundamental component of stock assessments that is frequently overlooked is stock structure delineation (Cadrin and Secor 2009). In many assessments, stock structure is assumed based on jurisdictional management boundaries that may not necessarily match the spatial distribution and structure of the exploited population (Smedbol and Stephenson 2001, Hammer and Zimmermann 2005). This apparent lack of concern regarding biological stock structure is likely associated with the formidable effort required to identify distinct stock units. Research on stock structure delineation usually requires comprehensive and multidisciplinary analyses, involving investigation of spatial patterns in abundance, levels of genetic and demographic connectivity, life history parameters and differentiation of

morphometric and meristic characteristics among stocks (Begg and Waldman 1999, Cadrin et al. 2010). Such a research effort is difficult to undertake and, in many cases, cost prohibitive (Begg and Waldman 1999). Even when strong evidence of spatial population structure is present, stock structure can be neglected due to lack of data to support the implementation of spatial heterogeneity in stock assessments (Berger et al. 2012).

In the absence of data to properly represent spatial structure, many stock assessments are based on the assumption that stocks are closed populations with homogeneous life history characteristics. Violation of this assumption can lead to bias in parameter estimates and, consequently, in the estimation of management benchmarks (Montenegro et al. 2009, Cope and Punt 2011). Stock structure can be erroneously specified in two different ways: 1) when multiple populations are treated as a single stock unit, and 2) when one population is incorrectly assessed as multiple units (Punt 2003). In the first case, differences in productivity and resilience among the populations can increase the potential for localized depletion of the most susceptible groups (Montenegro et al. 2009, Ying et al. 2011), while in the second case the assumption that each population is a closed unit is violated leading to bias and increased uncertainty in the estimated management benchmarks (Butterworth and Geromond 2001).

Stock structure delineation is especially problematic for large migratory species such as tunas and billfishes (Graves and McDowell 2003). In such species genetic differentiation is usually low (Ward et al. 1994), biological samples are limited, and tagging studies are often not conclusive in evaluating the degree of mixing between stocks. Tagging programs for highly migratory species usually rely on voluntary tagging and reporting by recreational and commercial fishers (Orbensen

et al. 2008) or on pop-up satellite archival tags, which can be of limited use due to the high costs associated with tag acquisition and deployment (Kerstetter and Graves 2008). Consequently, stock structure uncertainty is not an uncommon characteristic in assessments of large migratory species. Nevertheless, the impacts of such uncertainty on the estimated parameters and management benchmarks can be evaluated and quantified by the use of simulation studies (e.g., Atlantic bluefin tuna *Thunnus thynnus* [Butterworth and Geromond 2001, Apostolaki et al. 2003] and swordfish *Xiphias gladius* [Brooks and Apostolaki 2007]).

In this study, we describe a simulation study designed to investigate the impacts of stock structure uncertainty on the stock assessment results and derived management benchmarks of Atlantic sailfish *Istiophorus platypterus*. An operating model was developed to generate populations under various stock structure assumptions. Mixing was also considered for some scenarios and it was defined to occur every year after the spawning event with fish exhibiting natal homing. The goal of this paper is to address two main questions: i) how does an incorrect stock structure specification affect estimated management benchmarks and conclusions regarding stock status? and ii) to what extent does mixing in combination with an incorrectly specified stock structure also affect those same estimated quantities and stock status conclusions?

## METHODS

This study consists of a simulation framework parameterized according to the biological and fisheries information available for Atlantic sailfish. An age-structured operating model was used to generate data under seven alternative scenarios which were based on the most plausible stock structure layouts for the species in the Atlantic Ocean.

### Atlantic sailfish fisheries

Sailfish is an important species for recreational and artisanal fisheries worldwide. In the western Atlantic Ocean, artisanal fisheries targeting sailfish are concentrated in the tropical areas of the Atlantic, such as around Caribbean Islands and off the coast of Venezuela and Brazil. In the eastern Atlantic, similar fisheries operate from the coast of Senegal southward to the Gulf of Guinea. These artisanal fisheries mainly employ surface longline in the western Atlantic and surface drift gillnets in the eastern Atlantic (Arocha and Ortiz 2006). Recreational fisheries also occur on both sides of the Atlantic Ocean, with an economically important rod-and-reel fishery occurring in the western Atlantic (Kerstetter and Graves 2008) and hand-line fisheries occurring in the eastern Atlantic, mainly off Senegal and Ivory Coast (Diouf 1994). Sailfish are also frequently caught as by-catch in the pelagic longline and purse-seine fisheries targeting swordfish and various tuna species throughout the Atlantic (Arocha and Ortiz 2006).

### Atlantic sailfish stock structure

Atlantic sailfish are managed by member nations of the International Commission for the Conservation of Atlantic Tunas (ICCAT). For assessment purposes ICCAT assumes the existence of separate stocks in the eastern and western Atlantic. This stock structure was first defined in 1992 during the second ICCAT Billfish Workshop in Miami, FL and was based on the reported coastal nature of sailfish, the lack of trans-Atlantic movements observed from the recoveries of conventional tags, and differences in average size of sailfish landed in the western and eastern Atlantic (Anonymous 1994). However, during the 2009 ICCAT sailfish stock assessment, the validity of the two stock concept was questioned because of a noted a lack of genetic heterogeneity among sailfish collected throughout the Atlantic Ocean (Graves and McDowell 2003) and because commercial catch composition data indicated a relatively continuous distribution of sailfish catches across the equatorial Atlantic (Die 2010, Wor et al. 2010). Accordingly, the stock structure scenarios considered in this simulation study were based on the alternative stock structure hypothesis proposed during the 2009 Atlantic sailfish stock assessment (Anonymous 2010).

### Population dynamics

Age- and stock-structured population dynamics models for Atlantic sailfish with region- and gear- specific catches were used to generate data under seven alternative scenarios, representing three different stock structures: single, west/east (W/E) and northwest/southwest+east (NW/SWE) stocks (Figure 1). Additionally, sub-scenarios reflecting two levels of mixing among the populations were considered: 10% and 30% maximum mixing rates (Table 1). It was assumed that

mixing would occur every year, immediately after spawning, and that fish would return to their natal habitat for the spawning event (Figure 2). Also, mixing rates were assumed to be a function of age in an effort to account for ontogenetic migration patterns such that older fish may be more likely to migrate than younger individuals.

In the population dynamics models presented here, the term “region” is used to specify four different geographic areas in the Atlantic ocean: the northeast, southeast, southwest and northwest (NE, SE, SW and NW, respectively). The term “stock” is used to define the fish population with homogeneous life history characteristics that uses the same spawning area. For the different scenarios each stock might inhabit one or more regions and if mixing is considered, the fish from a given stock might be allowed to move to regions primarily inhabited by other stocks.

In each scenario, the number of individuals-at-age at the beginning of each time step and from each stock ( $N_{a,t,s}$ ) were considered to be equally divided among the regions inhabited by a stock immediately after a spawning event:

$$N_{a+1,r,t+1,s} = \frac{N_{a,t,s}}{n_{r \in s}} \cdot e^{-(M + \sum_{g \in r} F_{g,r,t} \cdot sel_{a,g,t})} \quad (1)$$

$$N_{a+1,t+1,s} = \sum_{r \in s} N_{a+1,r,t+1,s} \quad (2)$$

where:

$N_{a,r,t,s}$  is the number of fish at age  $a$ , within region  $r$ , at time  $t$  and from stock  $s$

$n_{r \in s}$  is the number of regions  $r$  inhabited by stock  $s$

$M$  is the natural mortality, assumed to be constant over region, time, ages and stocks

$F_{g,r,t}$  is the fishing mortality for gear  $g$ , in region  $r$ , at time  $t$

$sel_{a,g,r}$  is the selectivity at age  $a$ , gear  $g$ , in region  $r$

$r \in s$  denotes the region  $r$  inhabited by stock  $s$

$g \in r$  denotes the gear  $g$  deployed in region  $r$

For the scenarios in which mixing between stocks was allowed (i.e. those numbered 3, 4, 6 and 7), ontogenetic movement of fish was described by a logistic function:

$$P_{s:s',a} = \frac{\lambda_s}{1 + e^{-\rho \cdot (a - a_{mig})}} \quad (3)$$

where:

$P_{s:s',a}$  is the proportion of fish at age  $a$  from stock  $s$  that move into the area occupied by stock  $s'$

$\lambda_s$  is the maximum fraction of migrants from stock  $s$

$\rho$  is the rate at which  $\lambda_s$  is reached

$a_{mig}$  is the age at which 50% of the maximum fraction of migrants are allowed to move, which was taken to be equal to the age at which 50% of the individuals are mature.

In these scenarios the number of fish in each region after mixing is given by:

$$N_{a+1,r,t+1,s+s'} = N_{a+1,r,t+1,s} \cdot (1 - P_{a,s:s'}) + N_{a+1,r,t+1,s'} \cdot P_{a,s':s} \quad (4)$$

Spawning biomass for each stock (females only) was given by:

$$B_{t,s} = \sum_{a=1}^{a_{\max}} N_{a,t,s} \cdot f \cdot PM_a \cdot W_{a,s} \quad (5)$$

where:

$f$  is the proportion of females in the population, assumed to be constant over all ages and stocks.

$PM_a$  is the proportion of mature females at age  $a$

$W_{a,s}$  is the weight of individuals at age  $a$  for stock  $s$

Recruitment to each stock was assumed to occur at age 1 and be density dependent following the relationship proposed by Beverton and Holt (1957). A parameterization of this model in terms of steepness (defined by Mace and Doonan 1988) was used:

$$N_{1,t+1,s} = \left( \frac{0.8 \cdot R_{0,s} \cdot h \cdot B_{t,s}}{0.2 \cdot B_{0,s} \cdot (1-h) + (h-0.2) \cdot B_{t,s}} \right) \cdot \frac{1}{f} \quad (6)$$

where:

$R_{0,s}$  is the unfished recruitment for stock  $s$

$B_{t,s}$  is the spawning stock biomass at time  $t$  and for stock  $s$

$B_{0,s}$  is the unfished spawning biomass for stock  $s$

$h$  is steepness, defined as the proportion of unfished recruitment  $R_{0,s}$  produced by

20% of unfished spawning biomass  $B_{0,s}$ .

The input data used in the stock assessment models were catch at the end of the year (or yield in biomass,  $Y$ ) and catch per unit effort (CPUE):

$$Y_{a,r,g,t,s} = \frac{F_{r,g,t} \cdot sel_{a,r,g}}{M + \sum_{r \in S} \sum_{g \in F} F_{r,g,t} \cdot sel_{a,r,g}} \cdot N_{a,r,t,s} \cdot (1 - e^{-(M + \sum_{r \in S} \sum_{g \in F} F_{r,g,t} \cdot sel_{a,r,g})}) \cdot W_{a,s} \quad (7)$$

$$Y_{r,g,t,s} = \sum_{a=1}^{a_{\max}} Y_{a,r,g,t,s} \quad (8)$$

$$CPUE_{r,g,t,s} = q_{r,g} \cdot \frac{Y_{r,g,t,s}}{F_{r,g,t}} \quad (9)$$

where:

$q_{r,g}$  is the area- gear- specific catchability coefficient, which was assumed constant over time

The catchability coefficients were considered to be higher for those gears operating in the eastern Atlantic ocean in order to account for potential higher vulnerability of sailfish to the gears operating in the east (Table 2) (Prince et al. 2010). Selectivity at age followed gear- region-specific logistic curves and were different when the stocks being fished followed distinct growth curves (Table 2).

For the stock assessments in which mixing was taken into account, separate CPUE and yield series were generated for the proportion that remained in the area of origin and the proportion that migrated into another stock area. Yield and CPUE for the proportion that stayed in the area of origin is given by:

$$Y_{a,r,g,t,s} = \frac{F_{r,g,t} \cdot sel_{a,r,g}}{M + \sum_{r \in S} \sum_{g \in R} F_{r,g,t} \cdot sel_{a,r,g}} \cdot N_{a,r,t,s} \cdot (1 - P_{a,t,s:s'}) \cdot (1 - e^{-(M + \sum_{r \in S} \sum_{g \in R} F_{r,g,t} \cdot sel_{a,r,g})}) \cdot W_{a,s} \quad (10)$$

$$CPUE_{r,g,t,s} = \left( q_{r,g} \cdot \frac{Y_{r,g,t,s}}{F_{r,g,t}} \right) / (1 - P_{t,s:s'}) \quad (11)$$

while yield and CPUE for the proportion that migrated out of the area of origin is given by:

$$Y_{a,r,g,t,s:s'} = \frac{F_{r,g,t} \cdot sel_{a,r,g}}{M + \sum_{r \in S} \sum_{g \in R} F_{r,g,t} \cdot sel_{a,r,g}} \cdot N_{a,r,t,s} \cdot P_{a,t,s:s'} \cdot (1 - e^{-(M + \sum_{r \in S} \sum_{g \in R} F_{r,g,t} \cdot sel_{a,r,g})}) \cdot W_{a,s} \quad (12)$$

$$CPUE_{r,g,t,s:s'} = \left( q_{r,g} \cdot \frac{Y_{r,g,t,s}}{F_{r,g,t}} \right) / P_{t,s:s'} \quad (13)$$

Observational error was implemented by assuming multiplicative error structure around the estimates of CPUE. Standard deviation was set to 10% of each area- gear-specific CPUE overall mean and one thousand series were recorded:

$$CPUE_{r,g,t} = q_{r,g} \cdot \frac{Y_{r,g,t}}{F_{r,g,t}} \cdot e^{\varphi_{r,g} \cdot \frac{\sigma^2}{2}} \quad \varphi_{r,g} \sim N(0, \sigma^2) \quad (14)$$

Parameter values and constants required for the operating model were based on available literature and fisheries information (Table 2). Size at maturity information were obtained from Mourato et al. (2009) and length-weight relationships from Prager et al. (1994). The von Bertalanffy equation provided by Freire et al. (1998) for sailfish in the southwest Atlantic was used for length-at-age and the lengths obtained from that model were subsequently transformed from eye to keel to lower-jaw-to fork-length according to Prager et al. (1994). The model

provided by Freire et al. (1998) was modified for the W/E and NW/SWE scenarios. For these scenarios, the E and SWE stocks followed the growth curve in Freire et al. (1998) but its  $L_{\infty}$  was increased by 10 cm in order to account for the larger average size of sailfish on the eastern Atlantic (Arocha and Ortiz 2006, Prince et al. 2010). This difference in  $L_{\infty}$  caused sailfish not only to reach larger sizes but also to grow faster, for example a fish with 190 cm from lower jaw to fork would be 17 years old if it is from the western Atlantic and 14 years old if it is from the eastern Atlantic.

Two time series of fishing mortality (F) were considered as sub-scenarios: (i) a contrast sub-scenario in which the population was fished down the early years of the series, followed by a period of recovery and subsequent decline and (ii) a one-way-trip sub-scenario in which the population was fished down throughout the years of the simulation.

Stocks were assumed to be at virgin state in 1956 and abundances were projected for 52 years. Catch data were generated for eight region- and gear-specific fisheries starting in different years, as indicated in the ICCAT data series, and operated until the last year considered in the simulations (2008). Selectivity vectors were approximated by a logistic curve fitted to the average catch-at-age for each of the region- and gear-specific series. Although the operating models developed in this study were based on Atlantic sailfish biological parameters and fisheries data, they should not be considered exact descriptions of natural Atlantic sailfish populations given that the values of several parameters were assumed. The simulated stocks should, nevertheless, be sufficient for the purposes of this study.

### Stock assessments

Stock assessments were performed using the software ASPIC: A Stock-Production Model Incorporating Covariates (ver.5) and Auxiliary Programs (Prager, 2011). This program uses a continuous-time version of the surplus production model (Prager 1994) and is commonly applied in ICCAT stock assessments, including the most recent sailfish assessment (Anonymous 2010). Assessment models were fitted using the Schaefer surplus production model with catch-CPUE series as input and the minimization routine was conditioned on yield.

Initial guesses for the stock assessment parameters were based on quantities derived from the operating model. The maximum population size, or carrying capacity ( $K$ ), was set to the total exploitable biomass based on average selectivity of the population in 1956, one year before the beginning of the fisheries in the operating model. Initial guesses for the catchability parameters ( $q_{r,g}$ ) were identical to those used to generate CPUE data. Finally, the productivity parameter ( $r$ ) was determined by fitting the assessment model (Prager 1994) to data obtained from the operating model but assuming that  $K$  was known and equal to the initial guess. The value obtained for  $r$  was used to generate an initial guess for maximum sustainable yield ( $MSY$ ), as required by ASPIC, by solving:

$$MSY = \frac{r \cdot K}{4} \quad (15)$$

The assessments were performed under the correct and incorrect stock structure assumptions for all scenarios. Assessments were performed under the correct stock structure assumption in order to determine the “true” management benchmarks. Those “true” management benchmarks were subsequently compared

to the management benchmarks obtained from assessments under the incorrect stock structure assumption.

### Performance statistics

The ratios between biomass and fishing mortality in each year of the time-series and at maximum sustainable yield ( $B/B_{MSY}$  and  $F/F_{MSY}$ ) were used to assess the deviations from the control scenarios. These quantities were chosen because they are unitless and do not depend on the population size, thus allowing for comparisons of benchmarks across distinct stock structures. Deviations were expressed by percent difference which is given by:

$$\%D = \left( \frac{\hat{\theta} - \theta}{\theta} \right) \cdot 100 \quad (16)$$

where:

$\hat{\theta}$  is the estimated benchmarks when an incorrect stock structure is assumed.

$\theta$  is the benchmark obtained under the correct stock structure assumption.

The impacts of misspecification of stock structure on the stock status determination were also evaluated. The stocks were considered to be overfished when  $B/B_{MSY} < 1$  and occurrence of overfishing was determined by  $F/F_{MSY} > 1$ . We compared the stock status between the “true” stock structure assumptions and the alternative incorrect assumptions in each scenario for all years and simulations. The overall percentage of the simulations in which stock status was erroneously determined was calculated for each year, along with the maximum and minimum percent of incorrect stock status determination across the time series.

## RESULTS

The “true stock status” for each scenario was obtained by performing the stock assessment under the correct stock structure assumption, assuming that the true value of  $K$  was known and using the deterministic CPUE series (no error added). Trends in the  $B/B_{MSY}$  and  $F/F_{MSY}$  estimates differed for the contrast and the one-way-trip sub-scenarios (Figure 3) but were similar across all stock structure scenarios considered. For the contrast sub-scenarios,  $B/B_{MSY}$  continuously declined until the mid 1980s followed by an increase and recovery from the overfished state ( $B/B_{MSY} > 1$ ). This recovery was reversed by a subsequent decline in  $B/B_{MSY}$  and return to the overfished state ( $B/B_{MSY} < 1$ ).  $F/F_{MSY}$  followed an inverse pattern in the contrast sub-scenarios. It increased in the earlier years and overfishing ( $F/F_{MSY} > 1$ ) occurred from the mid 1960s until the mid 1980s. A drop in  $F/F_{MSY}$  occurred in the mid 1980s followed by an increasing trend of  $F/F_{MSY}$  until the end of the time-series. For the one-way-trip sub-scenarios,  $B/B_{MSY}$  decreased and  $F/F_{MSY}$  increased over time. The overfished state was only reached by the mid 1990s although overfishing started to occur much earlier in the series (Figure 3). The results from 1,000 assessments were stored for each sub-scenario and assessment results were only considered viable when convergence was reached and estimates of  $r$  were reasonable for the species ( $0.1 < r < 1.0$ ), similarly to methods used in the most recent sailfish stock assessment (Anonymous 2010).

### No-mixing scenarios

Differences between the “true biomass” trend and the assessment results (estimated  $K$ ,  $MSY$  and  $q_{r,gS}$ ) were observed even when the stock structure was correctly specified. As expected, these differences were generally more pronounced for the one-way trip sub-scenarios (Figure 4). In these scenarios, the CPUE series do not include a rebuilding period and therefore are less likely to contain adequate information to support the estimation of  $r$ .

Percent differences were calculated for all scenarios considering assessments under true stock structure and alternative incorrect assumptions. For most assumed stock structures, percent difference estimates were more variable for the contrast sub-scenarios and during the later years of the simulations (Figures 5-7). Also, trends in the percent difference estimates over time were usually less well defined for  $F/F_{MSY}$  than for  $B/B_{MSY}$  (Figures 5-7).

Regarding changes in stock status, the percentage of times in which stock status was incorrectly specified was quite variable over the years, regardless of the stock structure or sub-scenario considered. However, it appears that the intervals for percent of stock status misspecification were broader for  $F/F_{MSY}$  than for  $B/B_{MSY}$  (Table 3). The maximum and minimum percent values of stock status misspecification for the different scenarios ranged from 93% overestimation-90% underestimation to 34% overestimation-75% underestimation for  $B/B_{MSY}$  and 100% overestimation-100% underestimation to 0% overestimation-14% underestimation for  $F/F_{MSY}$  (Table 3). In relation to the estimates in the last year of the simulation, the percentage of times in which stock status was incorrectly determined was generally higher for the contrast sub-scenarios with  $B/B_{MSY}$  being overestimated and  $F/F_{MSY}$  being underestimated (Table 3).

### Single stock structure

When a single stock was taken to be the correct underlying structure, stock assessments were performed under W/E and NW/SWE assumptions. Benchmarks from these assessments were directly compared to the true management benchmarks for the single stock. In this scenario, performance of assessments for smaller areas lead to biased estimates of management benchmarks with median percent difference values for  $B/B_{MSY}$  as high as 40% or as low as -40% with even more extreme values for  $F/F_{MSY}$  in some years (Figure 5). Also, for the W/E alternative assumption, median percent differences indicate that deviations from single true estimates were higher for the E than for the W (Figure 5a<sub>1-4</sub> and 5b<sub>1-4</sub>). In contrast, there was no evident difference between median percent difference values for the two stocks in the NW/SWE alternative structure (Figure 5c<sub>1-4</sub> and 5d<sub>1-4</sub>). In general, for all alternative assessments considered, the observed direction of the bias for  $B/B_{MSY}$  was reversed for  $F/F_{MSY}$ . However, the direction of the bias changed when comparing the percent difference trends between the two sub-scenarios for almost all alternative assessments (Figure 5). This suggests that the error is highly dependent on the exploitation history of the population.

### W/E stock structure

When separate W/E stocks were taken to represent the true underlying stock structure, assessments were performed assuming a single stock and the derived benchmarks were compared to the true E and W benchmarks. In this scenario, median percent difference values were as high as 40% but were frequently even higher when the single stock assessment results were compared to the E stock true estimates in both sub-scenarios (Figure 6). The general pattern observed for the

$B/B_{MSY}$  percent difference estimates were again roughly reversed for  $F/F_{MSY}$  (Figure 6).

Regarding the direction of the bias, the single stock assessment mostly underestimated  $B/B_{MSY}$  when compared to both W and E true estimates for both sub-scenarios (Figure 6a<sub>1-2</sub> and 6b<sub>1-2</sub>). However, median percent differences indicated overestimation in the later years when compared to the W stock true estimates in both sub-scenarios (Figure 6a<sub>1</sub> and 6b<sub>1</sub>).

When single stock estimates of  $F/F_{MSY}$  were compared to the W stock in the contrast sub-scenario, percent differences showed a declining trend with overestimation occurring earlier in the series and underestimation in the later years (Figure 6a<sub>3</sub>). Still for the contrast sub-scenario, when comparing to the E true trajectory, single stock  $F/F_{MSY}$  was underestimated in the early and later years but was highly overestimated in the intermediate years of the series (Figure 6a<sub>4</sub>). For the one-way-trip sub-scenario,  $F/F_{MSY}$  was mainly underestimated when the single stock assessment results were compared to the W stock assessment and overestimated when compared to the E stock assessment (Figure 6b<sub>3-4</sub>).

#### NW/SWE stock structure

Similar to the W/E scenario, assessments were performed under the assumption of a single stock and the derived management benchmarks were compared to the NW/SWE true benchmarks. The single stock assessment showed high percent difference estimates when the single assessment results were compared to the SWE contrast scenario (Figure 7a<sub>2 and 4</sub>). Also, estimates were, in general, more precise for the one-way-trip scenario than for the contrast sub-scenario (Figure 7). The direction of the bias was variable across sub-scenarios for

the early and intermediate years of the series. However,  $B/B_{MSY}$  was consistently overestimated in the later years of the series when compared to both NW and SWE stocks for both sub-scenarios (Figure 7a<sub>1-2</sub> and 7b<sub>1-2</sub>). On the other hand,  $F/F_{MSY}$  was underestimated when compared to both stocks considered and for both sub-scenarios (Figure 7a<sub>3-4</sub> and 7b<sub>3-4</sub>).

### Mixing scenarios

For the scenarios in which mixing was considered, stock assessments were performed using deterministic data (no error added) under two different conditions. First, in order to determine the true benchmarks, assessments were performed taking mixing into account. This was done by using catch and CPUE series from all the areas where fish were caught, as described in equations 10-13. In those assessments catch and CPUE series for fish captured inside their natal habitat and captured outside those regions were used. Second, stock assessments were performed with the deterministic data but ignoring mixing, that is, all the catches for a given region were attributed to the stock that naturally inhabits that region. Results for the 10% and 30% levels of maximum mixing were quite similar, hence only the results for the 10% maximum mixing scenarios are presented. Biomass trend results for the true biomass trends and assessments with and without mixing reveal no difference between the true biomass trends and the assessments in which mixing was considered. However, substantial divergence from the true series was observed in all scenarios when mixing was ignored (Figure 8).

In relation to stock status determination, the percentage of times in which stock status was erroneously determined varied broadly over the years, as indicated by the maximum and minimum percent values across all years. For  $B/B_{MSY}$  the

ranges varied from 67% overestimation and 98% underestimation to 13% overestimation to -2% underestimation, whereas for  $F/F_{MSY}$  the ranges varied from 95% overestimation and 99% underestimation to 0% overestimation and 17% underestimation (Table 4). When considering only the last year in the series,  $B/B_{MSY}$  was overestimated and  $F/F_{MSY}$  was underestimated for all scenarios and the percent of stock status misspecification tended to be higher for the contrast sub-scenarios (Table 4).

*W/E with 10% maximum mixing stock structure*

As seen in other scenarios, the percent difference trend shown for  $F/F_{MSY}$  was generally the inverse of the one presented for  $B/B_{MSY}$ , regardless of the alternative structure being considered (Figure 9). When assessments were performed without taking mixing into account, median percent differences were relatively low (<10% in both directions) for the W stock in the contrast sub-scenario (Figure 9a<sub>1 and 3</sub>). For all other assessments under the correct structure but ignoring mixing, the median percent difference values were considerably higher (Figure 9a<sub>2 and 4</sub> and 9b<sub>1-4</sub>). The direction of the bias was, once again, dependent on the exploitation history. The trends in percent differences estimates changed for different sub-scenarios (Figure 9a<sub>1-4</sub> and 9<sub>1-4</sub>).

When the single stock structure was assumed, the comparisons against the W and E stocks considering mixing was very similar to those obtained from scenario 2 (W/E, no mixing). The trends were similar in both direction and magnitude of the median percent differences (Figure 9c<sub>1-4</sub> and 9d<sub>1-4</sub>), with precision of the estimates tending to be higher for the single stock assumption (Figure 9).

NW/SWE with 10% maximum mixing stock structure

In this scenario, the tendency of  $B/B_{MSY}$  and  $F/F_{MSY}$  to show inverse percent difference trends was also evident (Figure 10). Another general pattern for this scenario was that percent difference estimates were more precise for the one-way-trip sub-scenario than for the contrast sub-scenario (Figure 10).

When assessments were performed under the NW/SWE structure but without taking mixing into account, the magnitude of the median percent difference were relatively lower than that observed in other scenarios with most values being lower than 20% in both directions (Figure 10a<sub>1-4</sub> and 10b<sub>1-4</sub>). In relation to the direction of the bias,  $B/B_{MSY}$  tended to be underestimated for both NW and SWE stocks for both contrast and one-way-trip scenarios, except for the later years of the NW stock in the one-way-trip sub-scenarios (Figure 10a<sub>1-2</sub> and 10b<sub>1-2</sub>).  $F/F_{MSY}$  was also underestimated in the early and later years for both stocks and both sub-scenarios, but showed an overestimation tendency for middle years (Figure 10a<sub>3-4</sub> and b<sub>3-4</sub>).

When assessments were performed under the single stock structure assumption, the magnitude of median percent difference values was higher than that observed for the NW/SWE no-mix assumption. Differently from what was shown in scenario 3 (W/E 10% mixing), the direction of the bias under the single stock assumption did not resemble the results obtained in scenario 5 (NW/SWE), implying that mixing might have a greater impact if the NW/SWE stock structure is true. The direction of the bias when the single stock was assumed was not constant across sub-scenarios (Figure 10c<sub>1-4</sub> and 10d<sub>1-4</sub>), indicating that the fishing history is important to the impact of stock structure misspecification. Similarly to scenario 3

(W/E 10% mixing), the precision of the estimates appear to be higher for the single stock assumption (Figure 10).

## DISCUSSION

Accurate delineation of stock structure remains a challenge to the management of many exploited species. These difficulties are usually associated with the extensive amount of work and data required to define of a species' stock structure or to the existence of greater complexity within populations, such as the presence of contingents within a management unit or the presence of migration and mixing among stocks (Cadrin and Secor, 2009). In this study, I used a simulation framework composed of multiple scenarios considering three stock structures, two levels of mixing, and two fishing histories to evaluate how stock structure uncertainty and mixing affect the estimation of management benchmarks. My overall conclusion is that stock structure uncertainty leads to an increased error in the estimates of management benchmarks, but the direction of the error seems to be highly dependent on exploitation history.

For the scenarios in which mixing between stocks did not occur, results showed that both magnitude of the bias and level of precision can be considerably impacted by stock structure misspecification. When a single stock was erroneously assessed as multiple units (scenario 1), the management benchmarks obtained for each area did not accurately reflect the true stock results, regardless of the alternative structure being considered. Similarly misleading results were obtained in a simulation study by Butterworth and Geromond (2001) when assessments were performed under the assumption of two stocks when the truth was better described by a single stock unit.

An analogous situation to assessing only a portion of a stock as a closed unit occurs when marine protected areas are implemented and assessments are performed based solely on the area that remains open to the fisheries. Kraak et al. (2009) formed similar conclusions by simulating a single stock for which a closed area was implemented and only information from the area open to the fisheries was used in the assessments. They found that the stock assessment results were biased as assessments were based on data from only a portion of the stock. Field et al. (2006) also pointed out that, in the absence of data from closed areas, the performance of stock assessments could severely compromise the ability to estimate the status of stocks. In this study we found that when stock assessments were performed using only a portion of the data for one stock, poor estimation of management benchmarks was achieved.

In the scenarios in which mixing did not occur and multiple stocks were incorrectly combined as a single unit (scenarios 2 and 5), the estimates of management benchmarks were also strongly biased. The risks associated with erroneously combining multiple stocks for assessment and management purposes have been recently examined. Some studies indicated that strong bias can arise if there are relevant differences in biological parameters (Berger et al. 2012, Punt and Donovan 2007, Hall and Donovan 2002) or in fishing history (Hobday and Punt 2009, Montenegro et al. 2009). In contrast, other studies have emphasized that despite the lost ability to detect detailed local population trends, combining stocks increases the amount of data available for the assessments and may allow for a better performance of parameter estimation procedures (Cope and Punt 2011). We found that combining multiple stocks in a single assessment (scenarios 2 and 5) did not improve the estimates of management benchmarks and resulted in magnitudes

of bias similar to those obtained when a single stock was erroneously subdivided in multiple units. These results highlight the importance of stock structure delineation studies as the most reliable way to avoid bias in the management benchmarks due to stock structure uncertainty.

Mixing between stocks was also considered in this study (scenarios 3, 4, 6 and 7) and results indicated that mixing can cause a considerable amount of bias in the estimation of management benchmarks, even when the correct stock structure is assumed and low levels of mixing are considered. Surprisingly, the median percent difference values indicated that the bias associated with ignoring mixing was in general as high as the bias for grouping both stocks as a single unit. Estimates were also found to be more precise when a single stock was assumed, which is likely a result of more available data for the assessments and due to the similar fishing histories of the two stocks (i.e. similar trends in the abundance indices). Other studies have reported similar results when investigating the impacts of mixing among populations on stock assessments results. For example, Hart and Cadrin (2004) found that assessment results for yellowtail flounder *Limanda ferruginea* can be highly sensitive even to low levels of mixing. Ying et al. (2011) simulated a metapopulation of small yellow croaker *Larimichthys polyactis* in eastern China and concluded that ignoring the spatial structure and connectivity among subpopulations, even at low movement rates, could lead to bias in the estimates of population parameters and stock status. In a simulation study containing two stocks of Atlantic swordfish *Xiphias gladius*, Brooks and Apostolaki (2007) concluded that mixing among stocks can influence the management recommendations for the species, stressing the importance of characterizing movements between stocks with greater detail.

When considering the impacts of mixing for the two stock structures simulated in this study, mixing had a greater impact when the NW/SWE structure was assumed. This result is likely associated with the larger differences in stock size among the stocks considered in those scenarios. Since the SWE stock is much larger than the NW, the migration from the SWE to the NW is much more likely to affect the stock assessment results. A similar case was observed by Hart and Cadrin (2004) when investigating the impacts of connectivity among three U.S stocks of yellowtail flounder in the northwestern Atlantic. In their simulation, one of the stocks was much smaller than the other two units and the impacts of dispersal on that stock were greater (Hart and Cadrin 2004). This effect is also believed to happen for the bluefin tuna populations in the Atlantic. There are two stock units for that species in the Atlantic and the eastern unit is much larger than western stock. For this reason, the documented mixing among populations is thought to have a greater impact on the western unit, leading assessments results to portray a larger and more productive stock when mixing is not taken into account (Apostolaki et al. 2003, Taylor et al. 2011).

This study contains some limitations and although these are not believed to significantly affect the results obtained, it is important to take them into account when considering the applications of this study. The operating model used to simulate the populations consisted of an age-structured model while ASPIC, the stock assessment model employed, consists of a surplus production framework. Differences in the two models did occur, and were probably the cause for the differences in the assessments when  $K$  was assumed to known and when all parameters were estimated. These differences are likely caused by the fact that ASPIC does not account for age-specific processes affecting the size of the

population, such as age-specific selectivity and maturity (Prager 1994). A more complex age-structured assessment model could have been used to overcome these differences. However, such an assessment procedure would probably be unrealistic for sailfish in the Atlantic due to the difficulties associated with collecting age-structured data. The operating model used in this study also considers many parameters to be constant over time, such as the catchability coefficient, natural mortality and selectivity. Although this assumption might be considered somewhat unrealistic, it was made so that results would be easier to interpret and the impacts of stock structure misspecification could be readily identified. Finally, another limitation is related to the number of scenarios considered. This study considers a limited number of possible stock structures and only mixing with complete natal fidelity. It is possible that Atlantic sailfish are structured differently from the scenarios considered here and might be subject to a higher level of connectivity among populations, which could be easily evaluated by extending the model presented here. The stock structure and mixing hypotheses analyzed in this study are, however, considered to be the most plausible based on current knowledge of Atlantic sailfish distribution (Anonymous 2010).

The results presented here confirm that the existing stock structure uncertainty regarding sailfish populations in the Atlantic could lead to severe bias in the estimation of management benchmarks. This bias could, in turn, lead to the formulation of suboptimal management recommendations. To avoid this risk, it is necessary to expand the current knowledge of the spatial structure of Atlantic sailfish as well as mixing and migration rates among existing stocks. Conventional methods such as comparison of life history characteristics and natural tags between individuals from different areas and tagging studies to determine the degree of

demographic connectivity among populations are highly recommended (Begg and Waldman 1999, Rooker et al. 2008, Goethel et al. 2011). But the use of new methods to investigate such questions, such as the analysis of catch and effort data (Cope and Punt 2009) and use of chemical markers (Dickhut et al. 2009) should also be considered.

In conclusion, the results show that stock structure uncertainty can cause considerable bias in the estimates of management benchmarks. However, the effects of stock structure misspecification are tightly related to exploitation history and hence it becomes very difficult to predict the impacts stock structure misspecification might cause. Mixing also showed a significant impact on the estimates of management benchmarks, even when the correct stock structure was being assumed. I suggest that an increase effort should be driven toward stock structure delineation research as well as in the development of alternative methods to help elucidate issues associated with stocks connectivity and stock structure uncertainty.

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**Table 1.** Operating model scenarios and assessment assumptions considered to evaluate stock structure uncertainty for sailfish in the Atlantic Ocean.

Operating model		Stock assessment
1	Single	1a single* 1b east/west 1c northwest/southwest+east
2	east/west	2a single 2b east/west*
3	east/west (10% maximum mixing)	3a single 3b east/west
4	east/west (30% maximum mixing)	4a single 4b east/west
5	northwest/southwest+east	5a single 5b northwest/southwest+east*
6	northwest/southwest+east (10% maximum mixing)	6a single 6b northwest/southwest+east
7	northwest/southwest+east (30% maximum mixing)	7a single 7b northwest/southwest+east

\* indicates control stock assessment.

**Table 2.** List of parameter values and fisheries used in the operating model.

Parameter	Notation	Values
recruitment at virgin levels – single stock	$R_0$	2,000,000 fish at age 1
recruitment at virgin levels – W and E stocks	$R_0$	1,000,000 fish at age 1 (each)
recruitment at virgin levels – SWE stock	$R_0$	1,500,000 fish at age 1
recruitment at virgin levels – NW stock	$R_0$	500,000 fish at age 1
steepness of the recruitment function	$H$	0.7
natural mortality	$M$	0.2
maximum age	$a_{\max}$	18
female proportion	$F$	0.5
catchability coefficient (W)	$q$	$1 \cdot 10^{-6}$
catchability coefficient (E)	$q$	$2 \cdot 10^{-6}$
Life history models		
Parameter values		
Age and growth (Freire et al. 1998)		$L_{\infty}=179.6$ , $k=0.1466$ and $t_0=-1.246$
Conversion from eye-keel to lower-jaw-fork-length (Prager et al. 1994)		$a$ (intercept) = 11.240 and $b$ (slope) = 1.076
Size at maturity (Mourato et al. 2009)		$a=0.119$ and $L_{50}=154.935$
Length-weight (Prager et al. 1994)		$a=1.28 \cdot 10^{-6}$ and $b=3.2439$
Fishery	Acronym	Starting year
hand line - northeast Atlantic	HLNE	1967
longline - northeast Atlantic	LLNE	1957
gillnet - southeast Atlantic	GNSE	1973
longline - southeast Atlantic	LLSE	1957
longline - southwest Atlantic	LLSW	1957
gillnet - northwest Atlantic	GNNW	1991
longline - northwest Atlantic	LLNW	1957
sport fisheries - northwest Atlantic	SPNW	1960
	Selectivity parameters	Selectivity parameters - $L_{\infty}+10$
	$a=2.00$ $a_{50}=9.92$	$a=4.24$ $a_{50}=8.15$
	$a=0.84$ $a_{50}=9.04$	$a=1.07$ $a_{50}=7.84$
	$a=1.51$ $a_{50}=9.25$	$a=1.67$ $a_{50}=7.90$
	$a=0.83$ $a_{50}=7.66$	$a=1.45$ $a_{50}=5.56$
	$a=1.45$ $a_{50}=6.22$	$a=4.77$ $a_{50}=5.14$
	$a=3.68$ $a_{50}=8.10$	-
	$a=1.68$ $a_{50}=6.31$	-
	$a=2.37$ $a_{50}=6.97$	-

**Table 3.** Percentage of times when stock status was incorrectly specified for the no-mixing scenarios (1, 2 and 5). Positive numbers indicate overestimation and negative numbers indicate underestimation of parameters.

"true" stock structure	"alternative" stock structure	sub-scenario	B/Bmsy				F/Fmsy			
			last year	maximum	minimum	last year	maximum	minimum		
scenario 1										
single	W		22%	23%	-98%	-11%	88%	-100%		
	E		91%	93%	-90%	-90%	99%	-100%		
	NW	contrast	57%	63%	-91%	-41%	100%	-100%		
	SWE		55%	56%	-100%	-50%	100%	-53%		
	W		1%	99%	-5%	-1%	100%	-100%		
	E	one-way-trip	1%	2%	-98%	-1%	100%	-100%		
	NW		5%	89%	-31%	-4%	100%	-100%		
	SWE		0%	34%	-75%	0%	100%	-100%		
scenario 2										
W/E	W-single		34%	51%	-100%	-20%	92%	-26%		
	E-single	contrast	34%	44%	-94%	-20%	100%	-100%		
	W-single	one-way-trip	1%	4%	-96%	-5%	0%	-14%		
	E-single		1%	1%	-100%	-5%	100%	-5%		
scenario 5										
NW/SWE	NW-single		68%	69%	-100%	-64%	100%	-71%		
	SWE-single	contrast	68%	70%	-35%	-64%	100%	-100%		
	NW-single	one-way-trip	20%	31%	-61%	-38%	0%	-100%		
	SWE-single		20%	20%	-98%	-38%	100%	-100%		

**Table 4.** Percentage of times when stock status was incorrectly specified for the 10 % maximum mixing scenarios (3 and 6). Positive numbers indicate overestimation and negative numbers indicate underestimation of parameters.

"true" stock structure	"alternative" stock structure	sub-scenario	B/Bmsy			F/Fmsy		
			last year	maximum	minimum	last year	maximum	minimum
scenario 3								
W (10% max mixing)	W		1%	13%	-2%	-1%	69%	-86%
E (10% max mixing)	single	contrast	24%	52%	-100%	-5%	92%	-73%
	E		60%	67%	-98%	-50%	96%	-68%
	single		1%	35%	-89%	-5%	100%	-97%
W (10% max mixing)	W		0%	61%	-30%	0%	7%	-100%
E (10% max mixing)	single	one-way-trip	1%	4%	-95%	-5%	0%	-17%
	E		14%	15%	-84%	-16%	80%	-35%
	single		1%	1%	-100%	-5%	100%	-5%
scenario 6								
NW (10% max mixing)	NW		48%	49%	-57%	-44%	46%	-45%
SWE (10% max mixing)	single	contrast	41%	41%	-99%	-38%	99%	-39%
	SWE		29%	37%	-96%	-29%	93%	-43%
	single		41%	59%	-45%	-38%	99%	-99%
NW (10% max mixing)	NW		9%	13%	-72%	-32%	0%	-97%
SWE (10% max mixing)	single	one-way-trip	3%	5%	-95%	-14%	0%	-88%
	SWE		5%	16%	-83%	-15%	72%	-37%
	single		3%	5%	-96%	-14%	100%	-14%

Figure 1. Stock delineation for the three stock structures considered in this study.

Figure 2. Time line for succession of events in the population dynamics model.

Figure 3. True  $B/B_{MSY}$  and  $F/F_{MSY}$  estimates over time for contrast (left) and one-way-trip (right) sub scenarios. Estimates refer to the single stock scenario but other scenarios presented very similar trends.

Figure 4. Biomass trends for the three no-mixing scenarios considered. Solid lines represent estimates assuming  $K$  is known. Dashed lines represent assessment under correct stock structure but with all parameters being estimated.

Figure 5. Boxplots of percent differences for  $B/B_{MSY}$  and  $F/F_{MSY}$  series between true single stock and alternative assessments structures (scenario 1). Center lines inside boxplots indicate median percent difference, hinges represent 25% and 75% quantiles. Gray horizontal line assigns zero and red dashed line indicates -40% and 40% percent difference.

Figure 6. Boxplots of percent differences for  $B/B_{MSY}$  and  $F/F_{MSY}$  series between true east and west stocks and alternative single assessments structure (scenario 2). Center lines inside boxplots indicate median percent difference, hinges represent 25% and 75% quantiles. Gray horizontal line assigns zero and red dashed line indicates -40% and 40% percent difference.

Figure 7 – Boxplots of percent differences for  $B/B_{MSY}$  and  $F/F_{MSY}$  series between true northwest and southwest+east stocks and alternative single assessments structure (scenario 5). Center lines inside boxplots indicate median percent difference, hinges represent 25% and 75% quantiles. Gray horizontal line assigns zero and red dashed line indicates -40% and 40% percent difference.

Figure 8 – Biomass trends for the 10% maximum mixing scenarios. Solid lines represent estimates assuming  $K$  is known. Dotted lines represent assessment considering mixing, under correct stock structure but with all parameters being estimated. Dashed lines represent assessment when mixing is ignored.

Figure 9 – Boxplots of percent differences for  $B/B_{MSY}$  and  $F/F_{MSY}$  series between true east and west stocks with 10% maximum mixing (scenario 3) and alternative no mix (top two rows) and single (bottom two rows) assessments structures. Center lines inside boxplots indicate median percent difference, hinges represent 25% and 75% quantiles. Gray horizontal line assigns zero and red dashed line indicates -40% and 40% percent difference.

Figure 10 – Boxplots of percent differences for  $B/B_{MSY}$  and  $F/F_{MSY}$  series between true southwest+east and northwest stocks with 10% maximum mixing (scenario 7) and alternative no mix (top two rows) and single (bottom two rows) assessments structures. Center lines inside boxplots indicate

median percent difference, hinges represent 25% and 75% quantiles.

Gray horizontal line assigns zero and red dashed line indicates -40%

and 40% percent difference.

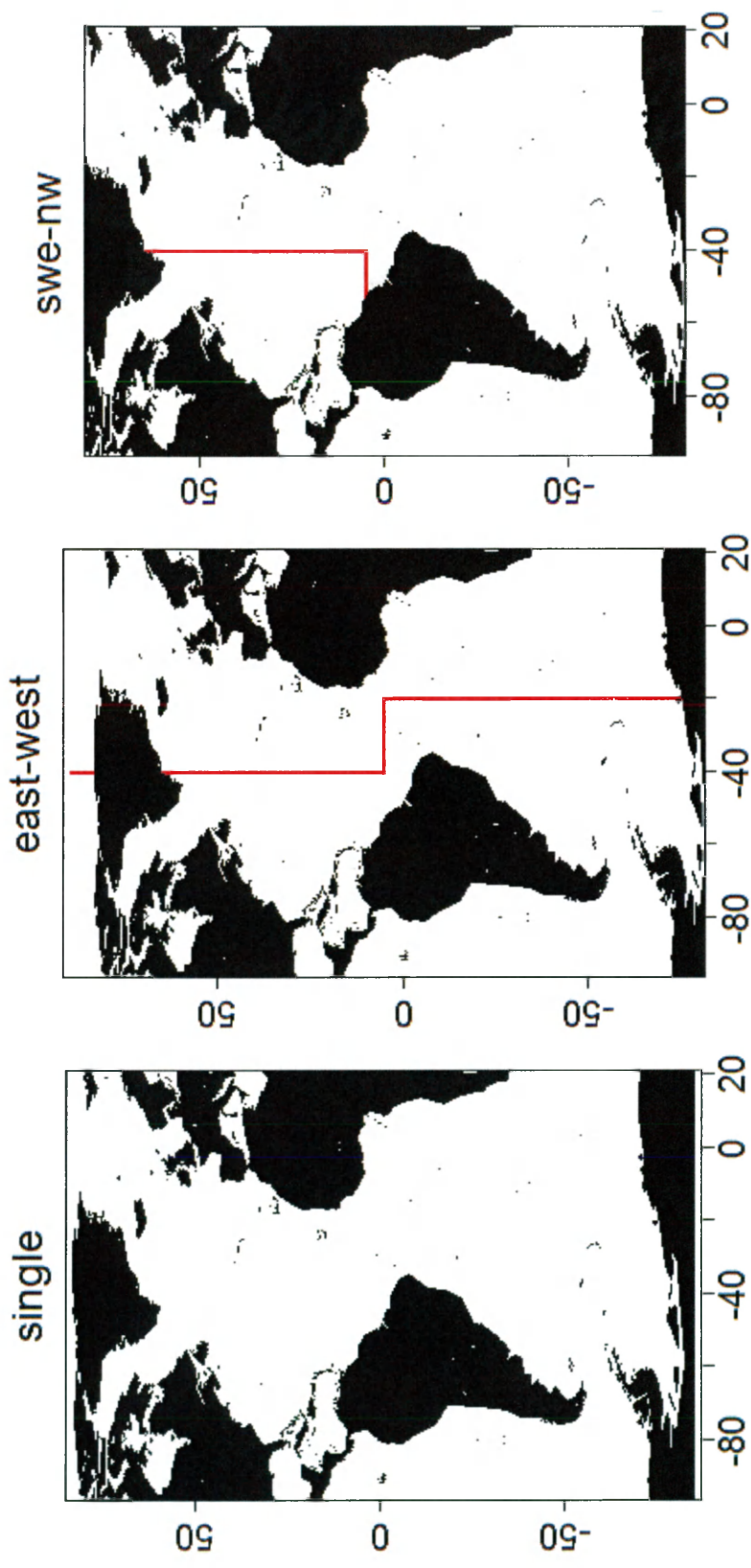


Figure 1.

Figure 2.

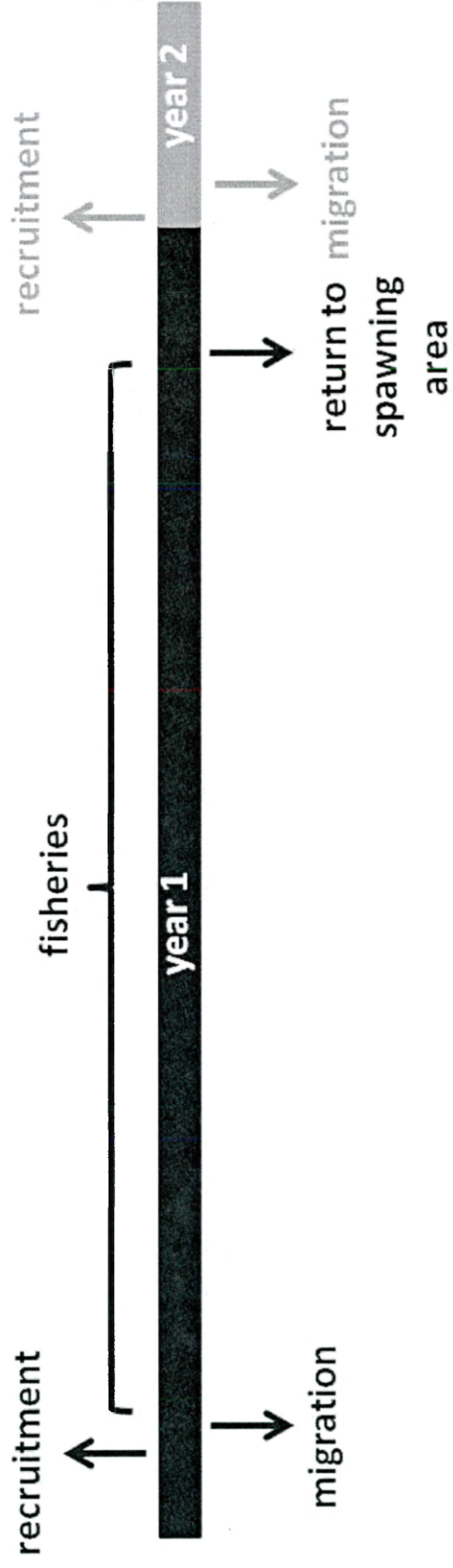
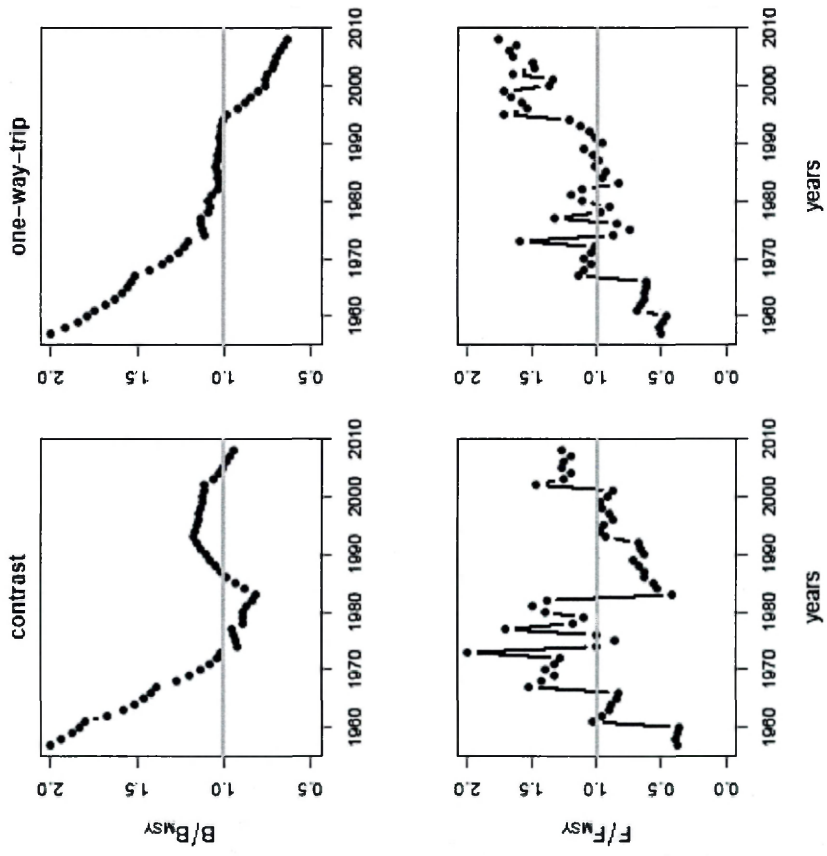


Figure 3.



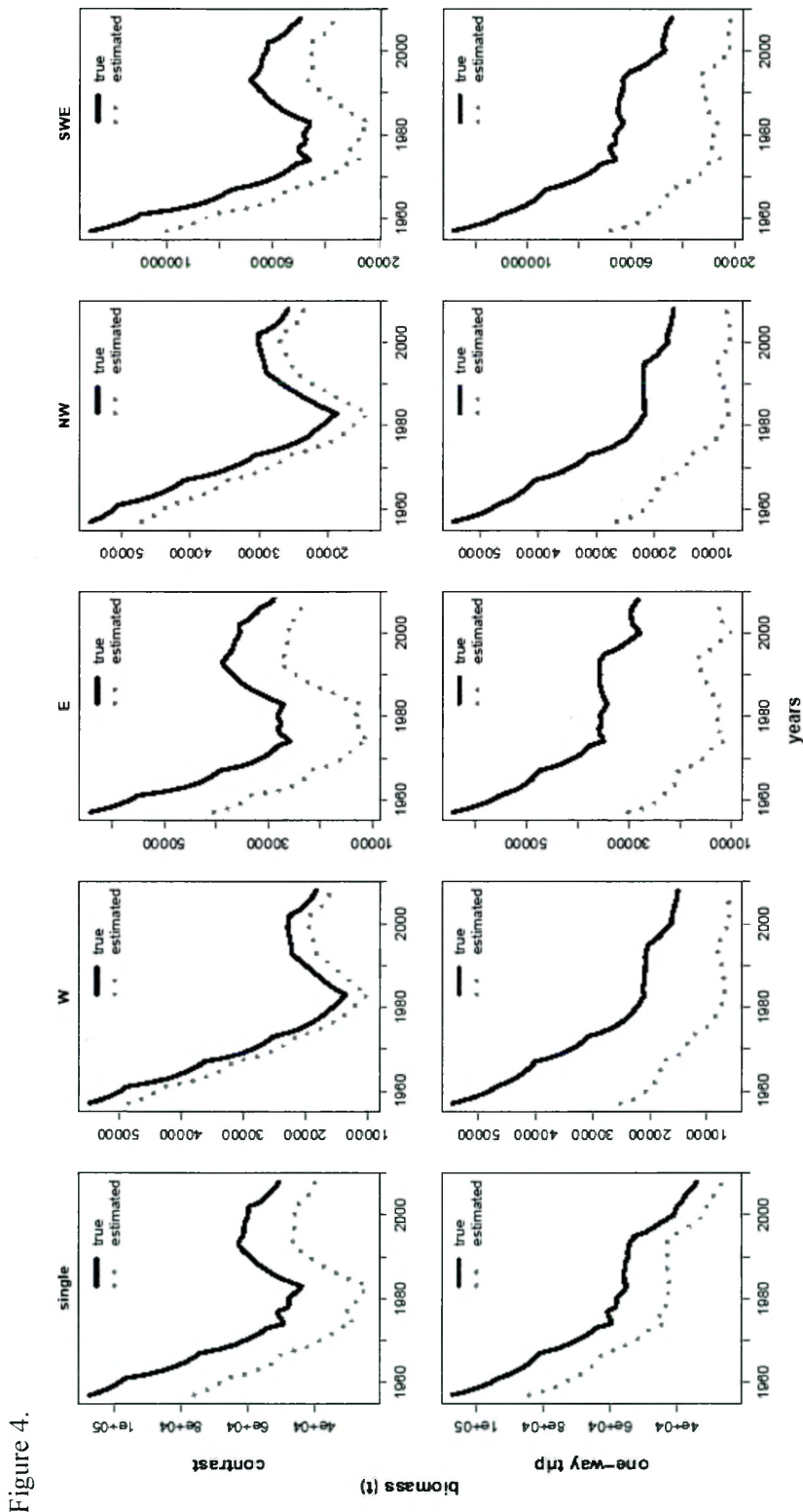


Figure 4.

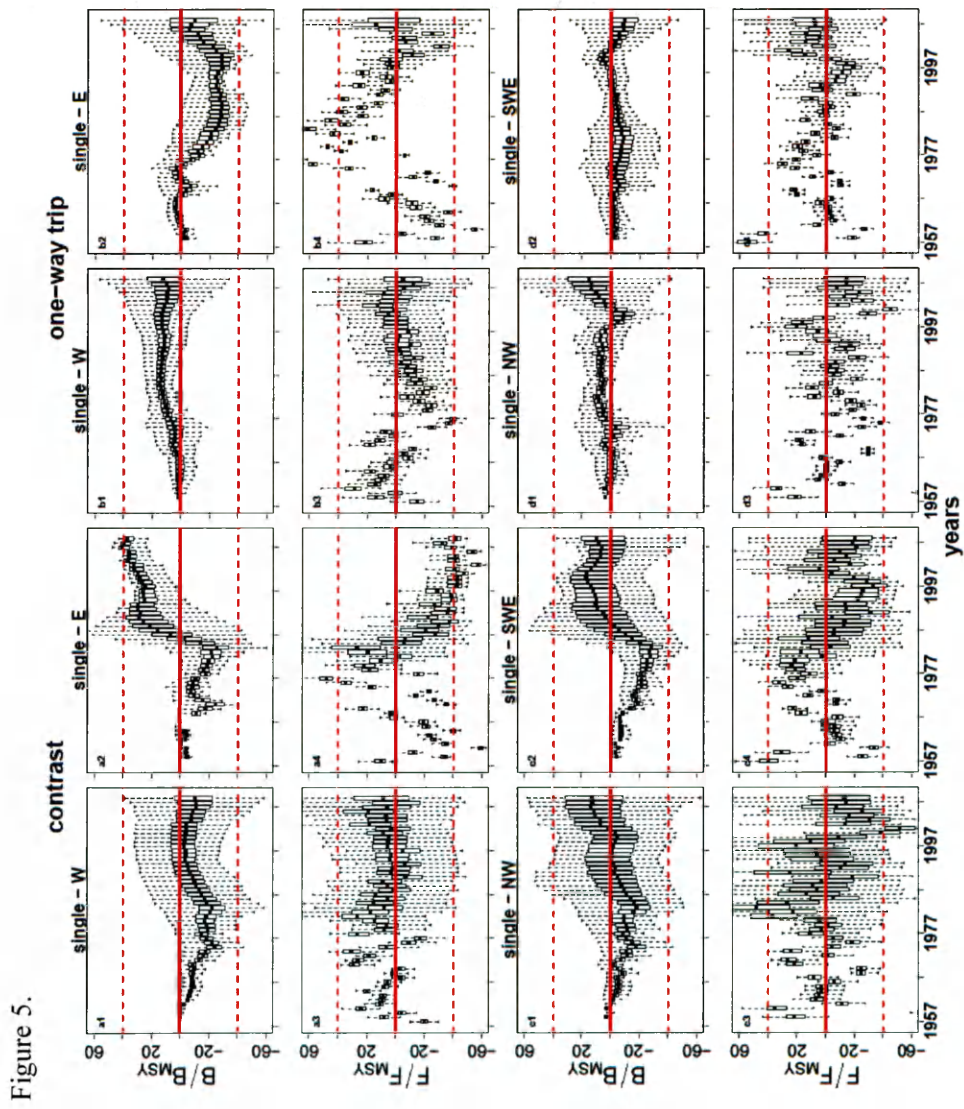


Figure 5.

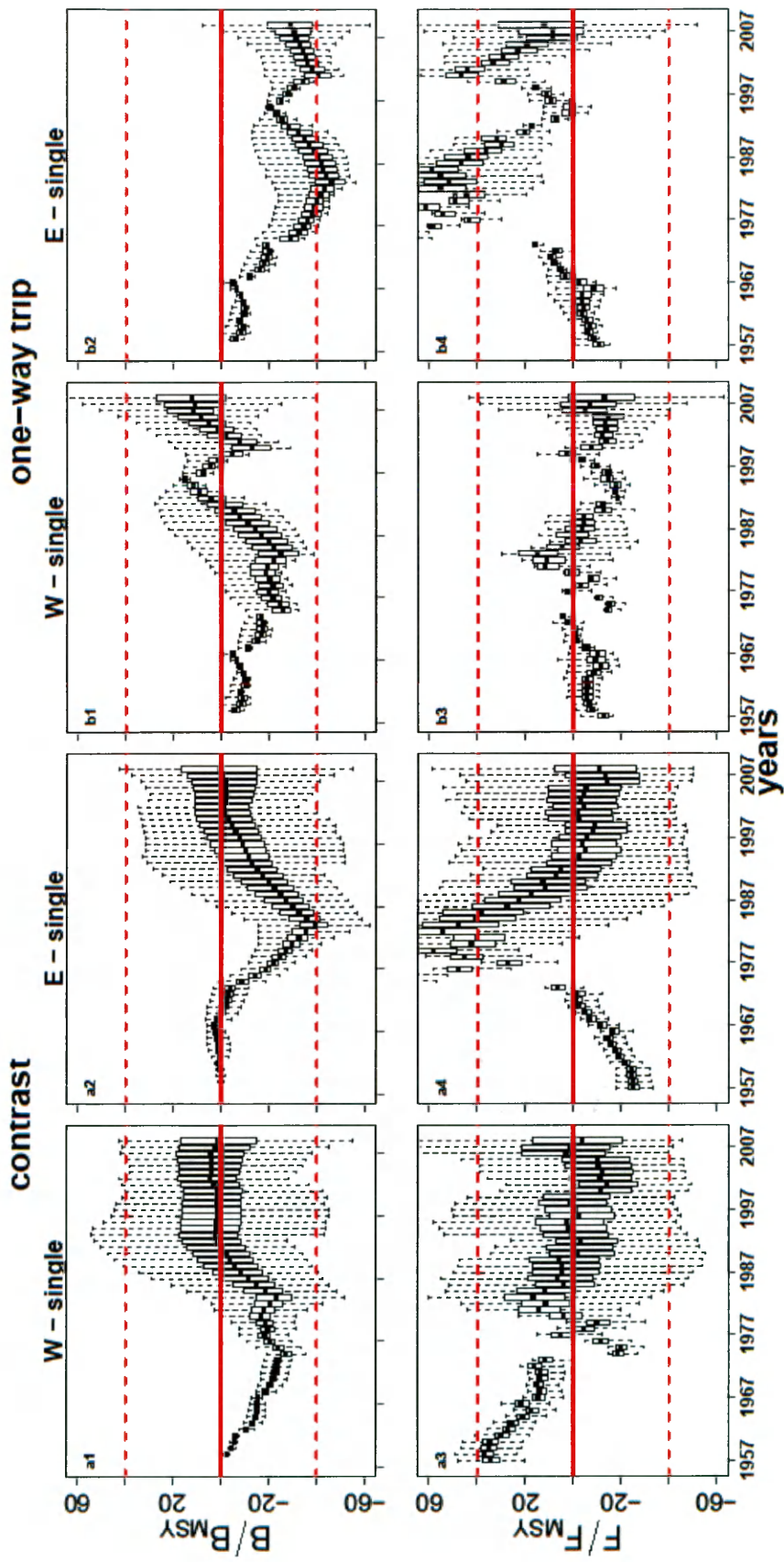


Figure 6.

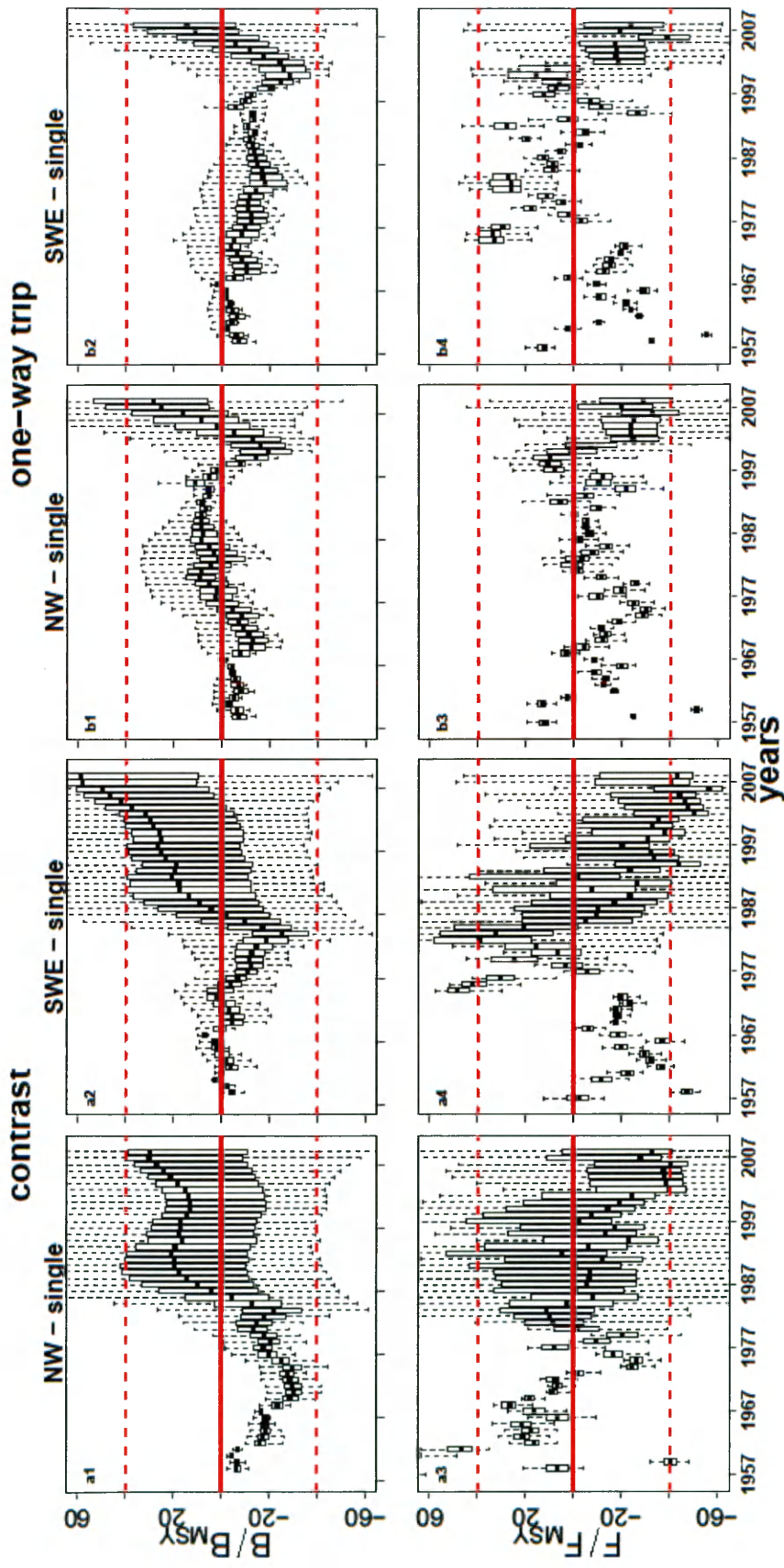


Figure 7.

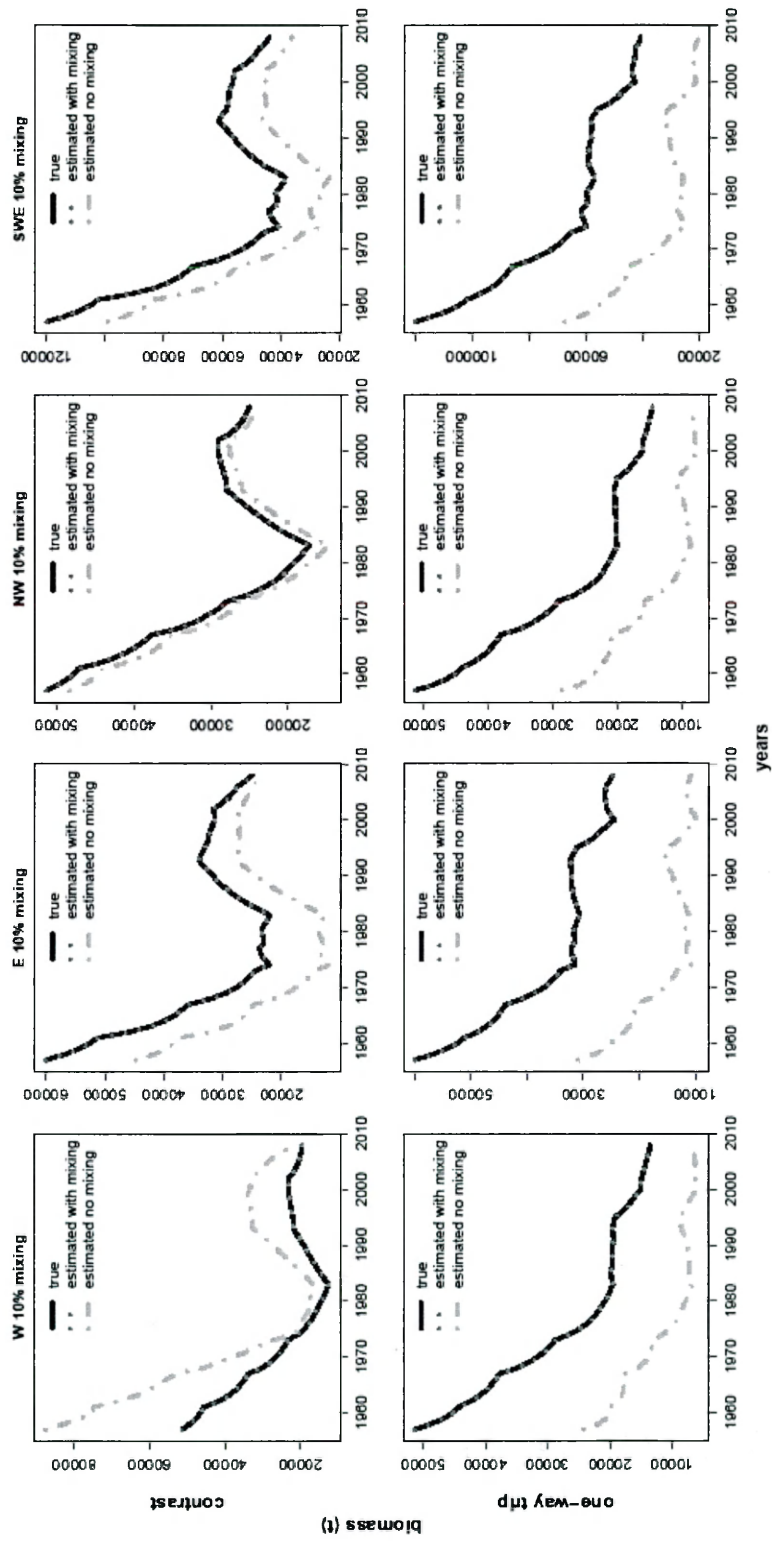
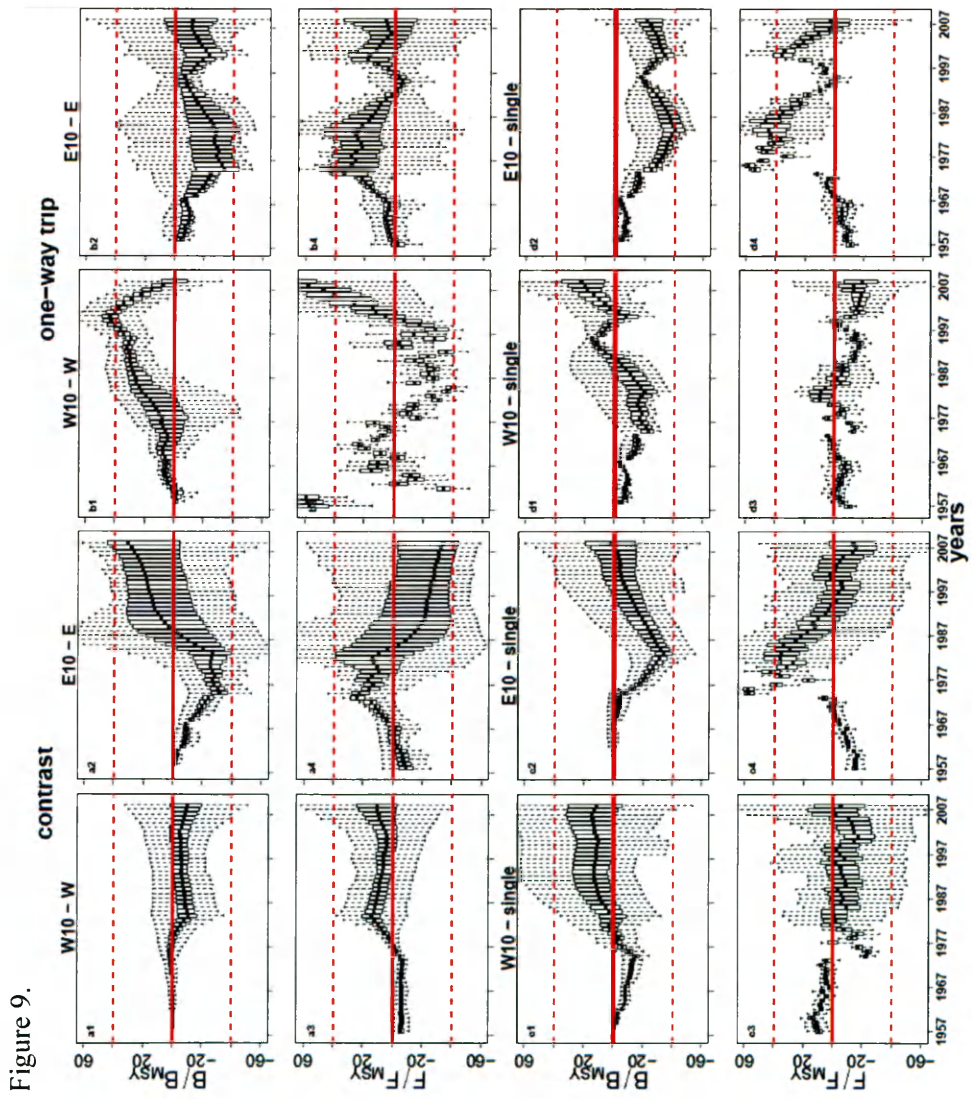


Figure 8.



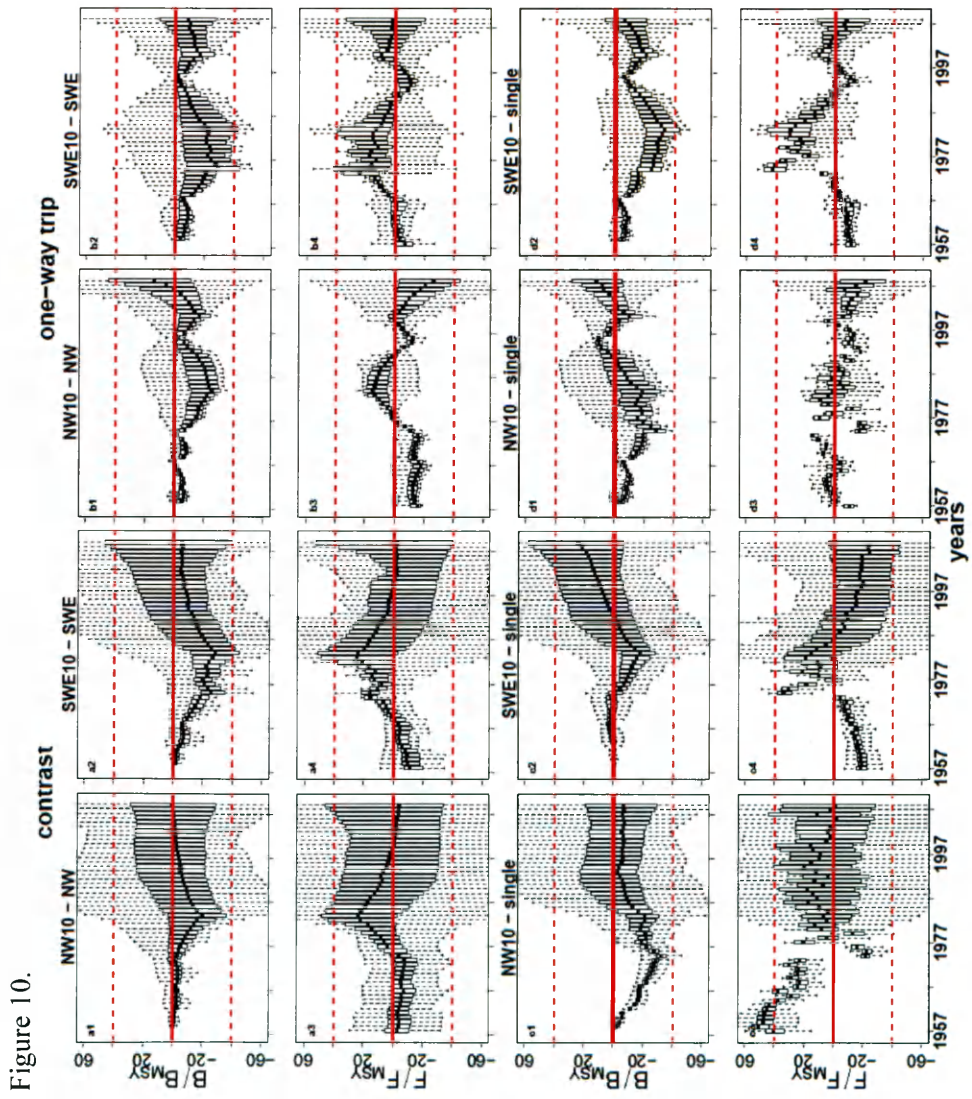


Figure 10.

## VITA

### **Catarina Wor Lima**

Born in Recife, Pernambuco, Brazil, 12 December 1985. Graduated from Escola Recanto High School in 2003. Earned a Bachelor of Science in Fisheries Engineering from the Universidade Federal Rural de Pernambuco in 2008. Entered the masters program in College of William and Mary, School of Marine Science in 2009.