Evaluating the risks of red tide mortality misspecification when modeling stock dynamics

Skyler R. Sagarese[a*] and William J. Harford[b,c]

[a] NOAA Southeast Fisheries Science Center, 75 Virginia Beach Drive, Sustainable Fisheries Division Miami, FL 33149 skyler.sagarese@noaa.gov

[b] Cooperative Institute for Marine and Atmospheric Studies, University of Miami, Miami, FL,
[c] Present address: Nature Analytics, 551 Lakeshore Rd E, Suite 105, Mississauga, Ontario, L5G 0A8, Canada; bill@natureanalytics.ca

Abstract

Extensions of single-species stock assessments to include ecosystem considerations are one step towards achieving an ecosystem approach to fisheries management. While red tide mortality has been estimated within base assessment models for both gag grouper and red grouper in the Gulf of Mexico since the late 2000s, considerable uncertainty remains regarding how best to incorporate this source of mortality in stock assessment and the potential risks of misspecifying its timing and its effect across age-classes. We conduct simulation testing of an approach to estimating red tide mortality, which treats red tide as a bycatch fleet where all encountered fish are discarded dead. Accounting for episodic natural mortality events by correctly specifying the years in which these events occurred was the most unbiased and precise approach for estimating population quantities, although the estimated red tide mortalities were highly variable in magnitude. While not estimating red tide mortality provided reasonably unbiased estimates of terminal biomass and fishing mortality rate, which are used to determine stock status, caution must be exercised when red tide events occur in the terminal year(s), as ignoring episodic mortality can lead to these events being misinterpreted in model fitting and inflating estimates of fishing mortality (and potentially overfishing status). Our simulations highlight the importance of continued data collection on how red tides affect marine resources, and continued community and stakeholder engagements to gain an understanding of the historical timing and impact of red tide events.

*Corresponding author contact: 305-361-4272; skyler.sagarese@noaa.gov

Key Words
Stock assessment, episodic mortality, simulation analysis, precision, bias

Highlights:

- Simulation tests estimation of red tide mortality in stock assessment
- Current approach produces unbiased but imprecise estimates of red tide mortality
- Ignoring episodic mortality may inflate fishing mortality estimates and stock status

1. Introduction

Progress towards ecosystem-based fisheries management continues to be made as part of U.S. marine resource policy (Marshall et al., 2018). In the U.S., advances towards ecosystem-based management are increasingly carried out through the scientific process of Integrated Ecosystem Assessment (Levin et al., 2009; Dell'Apa et al., 2015; Reum et al., 2021). An Integrated Ecosystem Assessment comprises a spectrum of approaches from fishery-focused models that incorporate environmental and ecological interactions to holistically focused assessments of cumulative coastal pressures on ecosystem services (Cook et al., 2014; Grüss et al., 2015). Single-species stock assessments remain the principal approach for providing management advice for U.S. fisheries and those that incorporate environmental and ecological interactions can be thought of as occupying one end of the Integrated Ecosystem Assessment spectrum. As an example, population processes such as natural mortality are often assumed to be constant over the time period modeled within stock assessments (Lee et al., 2011; Piner et al., 2011; Deroba and Schueller, 2013; Johnson et al., 2015). However, natural mortality can vary over age, space or time due to predation pressure (Fu and Quinn II, 2000; Gårdmark et al., 2012), environmental change (Jiao et al., 2012), or episodic events such as cold snaps (Matich and Heithaus, 2012) or red tide events (Sagarese et al., 2021).

Within the Gulf of Mexico (Gulf), Integrated Ecosystem Assessment-focused research has formed a foundation for incorporating environmentally-linked fish die-offs into stock assessment as well as the development of management strategies aimed at responding to these events (Harford et al., 2018; DiLeone and Ainsworth, 2019; Reum et al., 2021). Red tide blooms in the Gulf have been reported for hundreds of years and are linked to the dinoflagellate *Karenia brevis* (Steidinger, 2009). These blooms may cause fish mortality through acute exposure or bioaccumulation of the neurotoxin brevetoxin but also through asphyxiation from hypoxic water (Landsberg et al., 2009). Since blooms generally start offshore at depth (Steidinger and Vargo, 1988), and are transported inshore by winds and tidal currents (Steidinger and Haddad, 1981), these events can go unnoticed if dead fish remain on the bottom (Steidinger and Ingle, 1972). Mass mortalities of marine vertebrates and fishes were detected during red tide events in 2005 (Landsberg et al., 2009; Flaherty and Landsberg, 2011), 2014 (Driggers et al., 2016), and more recently in 2018 and 2021. The Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute harmful algal bloom database identifies species vulnerable to red tides, with observations largely derived from beach sightings of coastal species (Sagarese et al., 2017; DiLeone and Ainsworth, 2019). Growing anecdotal evidence suggests that shallow-water groupers (family: Serranidae) are notably affected by red tide events (Smith, 1975, Walter et al., 2013, Driggers et al., 2016, Karnauskas et al., 2019), possibly due to high site fidelity (Kiel, 2004; Lindberg et al., 2006; Saul et al., 2013), which may limit their movements away from affected areas. However, quantifying the effects of red tide events on marine species has proven particularly challenging due to complications with field collections and rapid decomposition of affected individuals (Driggers et al., 2016).

The potential impact of the 2005 red tide on groupers was first questioned by stakeholders in 2006 during stock assessments for gag grouper *Mycteroperca microlepis* (SEDAR, 2006a) and red grouper *Epinephelus morio* (SEDAR, 2006b). In response, updates of these two assessments in 2009 were the first to explicitly estimate extra mortality attributed to the 2005 red tide (SEDAR, 2009a, 2009b). In 2014 and 2015, assessments for both species transitioned to the integrated Stock Synthesis modeling platform (Methot and Wetzel, 2013), which increased flexibility for modeling red tide mortality (SEDAR, 2014, 2015). Time series serving as proxies of red tide mortality were developed using statistical models that estimated the probability of red tide severity between 1998 and 2010 (Walter et al., 2013). Sagarese et al. (2015) tested a suite of stock assessment methodologies that enabled red tide mortality rates to be estimated, with these methodologies varying in their treatment of time-varying mortality. For example, natural mortality rates can be linked to empirically derived indices of bloom severity (Walter et al., 2013), or natural mortality can be represented using a bycatch fleet approach to represent dead fish (discards) attributable to red tide blooms or other episodic mortality events (Methot et al., 2020; Sagarese et al., 2021). Ultimately, both assessments employed a binary index of red tide severity to identify years where red tides were depicted as severe (i.e., above a statistically defined threshold value). This approach was preferred because baseline levels of red tide mortality are likely included in estimates of natural mortality derived from empirical data (Walter et al., 2013). Die-off rates occurring from severe red tide events may well exceed the magnitudes of natural mortality rates reported for gag grouper (0.159 year^{-1}; SEDAR, 2021) and red grouper (0.144 year^{-1}; SEDAR, 2019).

The most recent stock assessments for both species employed the bycatch fleet approach to estimate the magnitude of mortality from the red tide event of 2005 (SEDAR, 2014, 2015). This approach treats red tide as a "fishing fleet" with 100% of its "catch" discarded as dead (i.e., 100% discard mortality) in select years coinciding with severe red tide events. While this approach does not require input data (i.e., estimated removals), it does require the specification of the length- or age-based selectivity of a red tide bloom. By modeling red tide as a bycatch fleet, the assessment model estimates the rate of the red tide mortality in the pre-defined years (i.e., severe red tides) based on contrast in the other data streams. The bycatch fleet approach was preferred because of concerns with imposing correlative relationships between observed indices of bloom severity (and inherent data concerns) and age-specific mortality rates within the stock assessment. While the bycatch fleet approach does not eliminate the need to understand susceptibility of age classes to red tides (also required for other approaches linking age-specific mortality to indices), different selectivity patterns can be tested in sensitivity runs. Further, selectivity patterns can be adjusted as additional data are collected, such as length- or age-compositions of fish killed by red tides (Walter et al., 2015) or age-specific estimates of red tide mortality (Vilas et al., 2021).

Not surprisingly, the details associated with accounting for red tide mortality rates within stock assessment has led to the recommendation of subjecting these approaches to simulation testing (SEDAR, 2014, 2015, 2019, 2021). Here, we foster a more nuanced understanding of the ability of the bycatch fleet approach in Stock Synthesis to estimate episodic mortality through simulation testing. First, we examine the influence of the bycatch fleet approach and related selectivity assumptions on estimation of population parameters (e.g., spawning stock biomass and fleet-specific fishing mortality rates), stock status, and red tide mortality rates. Second, we consider the issue of stock assessment over-parameterization and evaluate whether allowing the stock assessment to identify the years in which episodic mortality events are thought to occur leads to substantial errors in mortality estimates in some years. Third, we evaluate the extent to which estimation of these quantities are affected by ignoring the presence of extreme red tide mortality events altogether within stock assessment. Evaluating the accuracy and precision of the bycatch fleet approach to estimating episodic mortality is timely given calls for ecosystem considerations in stock assessments because of its potential utility for other forms of episodic mortality (e.g., mortality due to cold events or disease).

2. Materials and Methods

2.1 Operating model structure

The Gulf red grouper base-model (SEDAR, 2019) was first used to explore the sensitivity of parameter estimates and management quantities to the selectivity of the red tide bycatch fleet. The stock assessment was conducted using Stock Synthesis version 3.30.13 (Methot and Wetzel, 2013; Methot et al., 2020), and the model configuration is summarized in Table 1 and Fig. 1. Since fishery removals occurred prior to 1986 (but were too uncertain for inclusion), initial fleet-specific fishing mortality rates for three commercial fleets (vertical line, longline, and trap) and one recreational fleet were estimated from initial equilibrium catches (i.e., pre-model equilibrium) assumed to be normally distributed with a log-scale standard error (SE) of 0.05. Data inputs concerning removals for each fleet included landings and discards, both of which were assumed to have lognormal error structures and relatively large SE estimates (0.15 – 0.3; Fig. 2). Each fishing fleet had a unique selectivity pattern as well as time-varying retention to account for changes in management regulations that affected retention (e.g., bag limits or quota) or minimum harvest size (Table 1; Fig. 1). Indices of catch-per-unit-effort (reported in units corresponding to catch histories) were derived using landed fish only for the commercial vertical line and longline fleets and for the recreational headboat fleet, and for all catch (landings and discards) for the recreational charter and private modes combined.

Fishery-independent indices of relative abundance and survey length-compositions were included from four representative surveys: (1) the Southeast Area Monitoring and Assessment Program Summer Groundfish Survey (representing juvenile and younger adult red grouper); (2) the National Marine Fisheries Service's Bottom Longline Survey (covers entire depth range of adults throughout shelf); (3) the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute Hook and Line Repetitive Time Drop Survey (covers core habitat off Florida); and (4) the Combined Video Survey (longest time series across habitats and sizes). All indices of relative abundance had a lognormal error structure and were scaled to an average SE of 0.3 across the entire time series. However, the relative annual variation in the scaling derived from the standardization approach was maintained within each index. Composition data including age compositions of landed fish, discard length-compositions for the fishing fleets, and survey length-compositions were assumed to follow a multinomial error structure, where the variance was determined by the input effective sample size which was the square root of the number of length or age observations. An ageing error matrix linked to observed age compositions was input as a vector of mean ages (with standard deviations) and enabled generation of imperfect observation of ages (e.g., age with possible bias and imprecision) from true ages (Fig. 1).

Red tide mortality was estimated in the Gulf red grouper base-model via the bycatch fleet approach. Both 2005 and 2014 were recognized as being severe enough for inclusion by a combination of quantitative and qualitative input from stakeholders (SEDAR, 2019; Sagarese et al., 2021). Quantitative support for 2005 was obtained from the index of red tide severity discussed above (Walter et al., 2013). However, calibration issues between satellite data sources cautioned the use of the index updated through 2017, which revealed 2014 just below the threshold value (Sagarese et al., 2018). Ultimately, 2014 was deemed severe based on stakeholder insights that the 2014 red tide event devastated red grouper and degraded critical habitat (Karnauskas et al., 2019; SEDAR, 2019; Sagarese et al., 2021). All age-classes were assumed vulnerable to red tide mortality, following anecdotal evidence regarding age-specific red tide mortality across age classes based on spatial overlap of fish distributions with red tides-affected areas, particularly during 2005 (Chagaris and Sinnickson, 2018).

For the second operating model, which was fitted to actual data, the age-based selectivity pattern of the red tide bycatch fleet was modified to affect adult red grouper only to evaluate the impact on management quantities and status determination in the event that red tide events did not affect age-0 and younger red grouper. Age 5 was based on field collections of 16 red grouper (aged 5 – 9 years) during the 2014 red tide event (Walter et al., 2015). Although no red grouper older than 9 years were observed, this analysis assumed that all red grouper older than 9 years could be vulnerable to red tides given the spatial overlap between this red tide and their habitat (Driggers et al., 2016). A projection achieving a spawning potential ratio target of 30% at equilibrium (i.e., 100 years) was conducted and stock status was determined by dividing the estimated spawning biomass in the final year of the model (2017) by the spawning biomass at equilibrium (SEDAR, 2019; Sagarese et al., 2021). Projections assumed that forecasted recruitment would continue at recent average levels (2010 – 2017), recent fishery dynamics (selectivity, retention, and discard mortality) would persist, forecasted landings would maintain an allocation ratio of 76% commercial to 24% recreational by weight, and that the 2018 red tide (in the first year of the projections) was similar in magnitude to the 2005 red tide event.

2.2 Simulation Approach

Simulation testing was carried out by using two operating models (OMs) that were created based on the assumed population dynamics from the actual stock assessment (SEDAR, 2019). Simulated data sets for each fishing fleet and for each fishery-independent survey (Fig. 2) were generated from: (1) the Gulf red grouper base-model (i.e., OM1); and (2) the sensitivity run where red grouper aged 5+ were vulnerable to red tides (i.e., OM2). Data sets were generated using the parametric bootstrap routine in Stock Synthesis (Methot et al., 2020). Each new data set was generated based on the variance properties specified for the original data, with new observations obtained from corresponding sampling distributional assumptions that are made in specifying the likelihood function that is used in assessment model fitting (Methot and Wetzel, 2013). One thousand new data sets were generated and retained for simulation testing. Data concerning the magnitude of red tides were not simulated by either OM since input catches are not required for the bycatch fleet approach to estimating episodic mortality. Instead, years in which red tide mortality was to be estimated by a given AM were specified *a priori* (Table 2). Focusing solely on observation error in this analysis allowed an evaluation of how red tide mortality estimated using the bycatch fleet approach would vary with changing data inputs given their uncertainty. Additional sources of error were not incorporated to ensure results were not confounded by competing processes.

2.3 Assessment model configurations

Four Stock Synthesis assessment models (AMs) were specified, in some instances matching the structure of the OMs and in some instances representing a mismatch between AM and OM structure in terms of the red tide bycatch fleet (Table 2). Three of the four AMs implemented the bycatch fleet approach to estimating episodic mortality (years for estimation specified in Table 2). Other parameters estimated by each AM included four initial and 119 annual fleet-specific fishing mortality rates, two growth parameters (remaining life history parameters were fixed), two recruitment parameters (steepness remained fixed), 25 annual recruitment deviations, 20 selectivity parameters and four time-varying retention parameters (Table 1). The first assessment model, AM1, is the same as OM1, in which estimation of red tide mortality events in 2005 and

2014 is specified to occur via a bycatch fleet and all age-classes are correspondingly affected (i.e., 0 – 20+). The second assessment model, AM2, has the same configuration as OM2 in that red tide mortality events in 2005 and 2014 affect ages 5+ and are estimated via a bycatch fleet. In the third assessment model, AM3, no red tide mortality is estimated (i.e., no bycatch fleet). The fourth assessment model, AM4, allows for non-zero values of red tide mortality to be estimated in each year of the time series, 1986 to 2017, via a bycatch fleet under the assumption that all age classes are vulnerable to red tide mortality. A factorial approach was applied to evaluate the robustness of each AM in estimating population dynamics parameter values from each OM (Table 2). Since the magnitude of red tide mortality was not simulated by the OM, all AMs except AM3 estimated the magnitude of red tide mortality in pre-specified years (Table 2) from the contrast in the bootstrapped values for the other data streams.

2.4 Simulation testing and performance metrics

Precision and bias in estimation of population parameters and derived management quantities are presented herein, whereas additional performance metrics are provided in Supplementary Appendices A and B. Relative bias (R_q) of a given estimator, θ, is calculated:

$$R_q = \frac{\hat{\theta}_{q,} \qquad \theta}{\theta} \tag{1}$$

where $\hat{\theta}_{q,AM}$ is the estimated quantity from a given AM using the q-th simulated dataset, and θ_{OM} is the quantity from the OM used to generate the dataset. In summary tables, median relative bias (median of R_q across Q total simulated replicates) is reported as a coarse performance metric of estimator bias. Estimator precision is reported as the standard deviation of estimator replicates divided by the estimator mean, $\bar{\theta}$; otherwise, known as the coefficient of variation (CV):

$$CV = \frac{\sqrt{\frac{1}{Q-1}\sum_q^Q \left(\hat{\theta}_q \quad \bar{\theta}\right)^2}}{\bar{\theta}} \tag{2}$$

Performance metrics are calculated for the following estimators of population parameters and derived management quantities: recruitment variability, fishing mortality, unfished equilibrium recruitment (R_0), and terminal year estimates of spawning stock biomass (SSB), recruitment, the SSB ratio (ratio of SSB to unfished SSB), fishing mortality and fleet-specific fishing mortality. Comparisons of estimated time series to 'true simulated' values are made in the Supplementary Appendices for SSB, the SSB ratio, total fishing mortality and age-0 recruits. In addition, the relative bias and precision associated with estimates of red tide mortality in years 2005 and 2014 were calculated for AMs that included estimation of these quantities. For these comparisons, θ_{OM} was specified as the red tide mortality rates obtained from each OM. Red tide mortality is reported in terms of apical rates and the proportion of biomass killed by red tides, with the latter metric considered a more appropriate metric for comparison given that apical values will have different population impacts (due to different ages ranges associated with the rate). Temporal trends in relative bias of red tide mortality estimates are also examined for AM4.

3. Results

3.1 Operating model structure

In producing OM2, the base-model was re-fit to actual data sets under the constraint that red tide mortality events in 2005 and 2014 affected only ages 5 and older. No major discrepancies in model performance were noted between OMs, although OM2 had a slightly lower negative log-likelihood (by 2.028 units), a slightly larger gradient and a few additional recruitment deviations with CVs exceeding one (Table 3). Key parameter estimates were generally similar between fitting the OMs to the actual data sets, with the exception of recruitment variability, which was higher in OM2 (0.860 vs 0.815), and apical red tide mortality rates, which were higher but less uncertain in OM2 (Table 3). Both OMs revealed similar trends in total biomass, spawning stock biomass (SSB) and the SSB ratio, with large declines evident in 2005 and 2014 due to additional mortality attributed to red tide events (Fig. 3A-C). OM2 predicted a larger recruitment estimate for 2001, but smaller recruitment estimates for other above-average recruitment events, and terminal recruitment estimates were nearly identical (Fig. 3D). Fishing mortality trends were nearly identical between OMs, and the proportions of biomass killed by red tides were similar among OMs for both the 2005 (29.5 to 32.3%) and 2014 (21.3 to 27.3%) events (Table 3; Fig. 3E). When red tide mortality affected all age classes, the 'true' simulated red tide mortality was 0.34 year^{-1} (CV = 0.31) for 2005 and 0.26 year^{-1} (CV = 0.43) for 2014 in OM1 (Table 3), where each value represents the apical mortality rate. Following re-fitting to generate OM2, where red tide mortality affected ages 5+, red tide mortality for OM2 was 0.47 year^{-1} (CV = 0.26) for 2005 and 0.37 year^{-1} (CV = 0.35) for 2014 (Table 3). While small differences in current F and SSB were observed between models, the F reference point was identical and the SSB reference point was very similar, leading to no change in stock status determination (Table 3).

3.2 How well does the bycatch fleet approach estimate time-varying natural mortality?

When AMs were specified such that years in which a red tide event occurred were known (i.e., AM1 and AM2), current spawning biomass and current fishing mortality rates were well estimated (CV range: 0.095 to 0.137) and had low bias (bias range: -0.091 to 0.047; Fig. 4; Table 4). In the cases of AM1 and AM2, virgin recruitment also showed minimal bias (-0.001; Fig. 5; Table 4). Across all four AMs, the SSB ratio in 1986 was positively biased (bias range: 0.084 to 0.129), although this bias was largest for the case where red tide mortality was not estimated in model fitting (i.e., AM3; Table 4). This result occurred both when OM and AM were configured identically and when AM3 and AM4 were applied, thus it appears that this bias in initial population characteristics could be a complication in model specification that is unrelated to estimation of red tide mortality events.

Estimation of red tide mortality (apical rates) was imprecise across simulations (CV range for 2005: 0.281 to 0.799; CV range for 2014: 0.334 to 0.841), and in some circumstances, there was evidence of systematic underestimation of red tide severity (Fig. 6; Table 4). Considerable underestimation of red tide mortality in 2005 and 2014, both in terms of apical rates and the proportion of biomass killed by red tides, occurred for AMs that assumed that all age classes were vulnerable to red tide (i.e., AM1 & AM4), regardless of OM. A strong negative bias in the proportion of biomass removed by red tides was evident for AM1 (bias range: -0.115 to -2.122) and AM4 (bias range: -0.371 to -2.689), with greater bias identified for the 2005 red tide event. Conversely, constraining estimation of red tide mortality to ages 5+ produced reasonably unbiased estimates of red tide mortality for 2014 (bias range: -0.034 to -0.043), again, regardless of whether OM1 or OM2 was used to generate simulated data sets. In contrast, AM2 also underestimated the proportion of biomass removed during 2005 (bias range: -1.309 to -1.882).

In examining AM4, it became apparent that AM configurations that allow for red tide mortality estimation freely in each year have a propensity for highly variable and strongly biased outcomes in estimates of red tide mortality (Fig. 6; Table 4). A substantial proportion of simulations produced a relative bias of -1 (or 100% underestimation; however, no issues with model convergence were evident) of apical red tide mortality rates in 2005 and 2014, suggesting that allowing the AM to determine when episodic natural mortality events occur can overlook years in which large mortality events actually occurred. For AM4 simulations, annual estimates of red tide mortality in terms of both apical rates and the proportion of biomass killed by red tides for both OMs were frequently estimated in non-red tide years, although median values remained near zero for many years (Fig. 7). While imprecision in estimation of quantities using AM4 also occurred for terminal spawning biomass (CV range: 0.118 to 0.127), the terminal fishing mortality was extremely imprecise (CV range: 0.557 to 0.581; Table 4; Fig. 4). Thus, given the frequency of red tide events that we simulated, it appears that allowing the AM to freely estimate red tide mortality in each year can result in highly biased and highly variable estimates of key quantities.

3.3 What happens when stock assessment ignores red tide events?

For AM3, bias and precision in estimation of terminal spawning stock biomass was not demonstrably different from AM1 and AM2 (Fig. 4). The recruitment variability parameter had a positive relative bias, on average, of 0.044 to 0.148, for OM2 and OM1, respectively (Fig. 5). This positive bias did not, however, lead to temporal trends in age-0 recruitment, especially in relation to years in which red tide events occurred (Fig. 8). Thus, we did not observe evidence to suggest that recruitment deviations were inadvertently accounting for red tide-induced changes to abundance. However, mortality rates for the fishing fleets were positively biased under AM3 (Fig. 8). Positive trends in relative bias of fishing mortality were evident in years surrounding those where red tide events occurred, suggesting that fishing mortality can be inadvertently inflated when time-varying natural mortality is not correctly accounted for in the fitting routine.

4. Discussion

In conducting simulation testing of the bias and precision of the bycatch fleet approach for estimating episodic mortality, our results support three conclusions about accounting for time-varying natural mortality events within stock assessment. First, accounting for episodic mortality events by correctly specifying the years in which these events occurred was the most unbiased and precise approach to estimation of those population quantities that typically support fishery management, among the approaches we examined using simulated data. Our results suggest that there is considerable informational value in being able to correctly identify years in which episodic mortality events occurred (i.e., AM1 and AM2), rather than reliance on event estimation freely across all years (i.e., AM4). Second, the bycatch fleet approach for estimating episodic mortality produced (time-varying) red tide mortality estimates that were variable across simulations, and thus, these estimates should be considered highly uncertain. Thus, while accounting for episodic mortality events in stock assessment may help to improve reliability of certain quantities of interest (e.g., fishing mortality rates), it is not advisable to rely on estimates of event magnitudes, for example, in deriving correlations with ecological metrics, or as a sole driver of decision-making reactivity. Third, assessment model configurations that do not account for such events (i.e., AM3) can provide reasonably unbiased estimates of terminal biomass and fishing mortality rate; quantities which are important to decision-making and are used in conjunction with reference points obtained from projections to determine stock status.

Our results demonstrate that *a priori* selection of the correct years for estimating these mortality rates can improve accuracy of quantities such as terminal SSB and fishing mortality rate, which are used in conjunction with reference points to establish population status. Some cautions are needed however, with respect to the way equilibrium reference points are defined against the presence of time-varying natural mortality. In producing OMs that differed in selectivity of the red tide bycatch fleet (i.e., by fitting or re-fitting against the actual data), we obtained consistent biological reference points, principally because productivity parameters of the OM were fixed and not estimated. However, the presence of red tide events could modify the context for defining reference points, especially if red tide events become more frequent and severe. For instance, the natural mortality rate derived from life history may differ from the average lifetime natural mortality rate experienced by long-lived cohorts that encounter multiple episodic natural mortality events during their lifetime. Legault and Palmer (2016) found that an increase in natural mortality during the assessment period often led to decreased MSY reference points. Additional simulation work (see O'Leary et al. (2021) for a noteworthy example) is needed to determine how the frequency and magnitude of future red tide events may impact the estimation of and context for defining fishery management reference points.

When considering the effects of observation error on AM bias and precision, our results suggest that the bycatch fleet approach is not capable of estimating red tide mortality when estimated freely across all years. There was a tendency for consecutive years to have non-trivial estimates of red tide mortality, as the model appeared incapable of precisely distinguishing event timing, perhaps due to the assumed constant selectivity-at-age and smearing of cohorts across years. Previous simulation work aimed at accounting for underreported landings found increased uncertainty in management quantities for noisy survey data (Bousquet et al., 2010). The complexity of incorporating ecosystem considerations warrants additional simulation testing, particularly using more complex OMs incorporating process and structural uncertainties. While Harford et al. (2018) simulated complex biological mechanisms (including red-tide mortality) with an assessment model that attempted to capture these complexities, their management strategy evaluation highlighted the multi-faceted nature of the challenges associated with assessment under time-varying natural mortality. There is a need to determine the most robust approach for estimating red tide mortality in the historical time period of stock assessments given increases in available data (e.g., time- and age-specific indices of red tide mortality; Vilas et al., 2021). Further, we have shown that ignoring episodic mortality altogether can sometimes lead to these events being misinterpreted in model fitting and resulting in inflated estimates of fishing mortality where uncertainty in catch estimates is relatively high (i.e., SE > 0.05), potentially leading to an overfishing status (Sagarese et al., 2021). This is particularly true in the Southeast US where base stock assessments in the Gulf of Mexico often include highly uncertain time series of both landings and discards, particularly for recreational fisheries that can dominate total removals. Although acknowledging greater uncertainty in removals within the base-model can appear more realistic to managers, this additional flexibility can have unintended consequences on model performance and stability, and should be evaluated through simulation.

While failing to account for episodic mortality events can still provide reasonably unbiased estimates of terminal biomass and fishing mortality rates in the circumstances we evaluated, there was also cause to avoid this short-coming where episodic events are prevalent. Stakeholders have adamantly expressed concerns over the impacts of red tides on grouper populations, and accounting for red tide mortality directly in the assessment model notably improved the fits to multiple indices of relative abundance for Gulf red grouper (Sagarese et al., 2021). In cases where episodic natural mortality events are severe enough for population level impacts, fleet mortality rates can inadvertently become inflated when time-varying natural mortality is ignored. Accordingly, where an episodic mortality event is thought to have occurred towards the terminal assessment year, but is not explicitly accounted for in stock assessment, caution should be taken in interpreting fishing mortality estimates relative to overfishing benchmarks. The model which did not estimate red tide mortality (i.e., AM3) performed fairly well in terms of bias and precision in management quantities relative to AM1 and AM2. However, this result was largely due to the timing of the red tide events (i.e., not in the terminal years).

In situations where it is challenging to identify specific years in which episodic mortality events have occurred, scientific partnerships with industry and with coastal communities can directly contribute to the information available for stock assessment. For example, the 2019 Gulf red grouper stock assessment relied heavily on input from stakeholders to determine years where red tides were deemed severe (SEDAR, 2019). Observations were obtained from an online data collection tool hosted by the Gulf of Mexico Fishery Management Council. In addition, two stakeholder driven engagements were hosted by the Southeast Fisheries Science Center (SEFSC) in response to the 2018 red tide event that occurred on the West Florida Shelf: (1) participatory stakeholder workshops focused on elucidating the impacts of red tides on local resources and reliant communities; and (2) oral history interviews to obtain insights from fishermen on the water, allowing the development of a timeline of historical red tide events and their impacts (Karnauskas et al., 2019). Ongoing efforts by SEFSC to reconstruct historical timelines of red tide events from oral histories and reviews of available literature will be invaluable in helping pinpoint severe years, particularly for the time period prior to the availability of satellite data.

While simulation testing was disappointing with respect to the precision of red tide mortality estimates, improvements upon the statistical basis for time-varying aspects of stock assessment could ultimately provide defensible indices of red tide severity or mortality along with estimates of observation error. For instance, natural mortality can be directly linked to an environmental index (aka the model method, Schirripa et al., 2013) or annual blocks can be specified for each age class, with the environmental index value treated as a prior estimate (e.g., of extra mortality added to baseline levels) with an associated standard deviation (aka the modified data method, Schirripa et al., 2013). A recent capability added to Stock Synthesis can be used in specifying episodic mortality as a “predator” where extra mortality (M2) is estimated as an addition to the base natural mortality instead of estimating it as a pseudo fishing fleet (Methot et al., 2021). Although this approach does not remove the need to specify selectivity, treating red tide or other sources of episodic mortality as a predator is more intuitive and reduces confusion with treating it as a type of fishing mortality. Further, the bycatch fleet approach to estimating episodic mortality as applied in this study may be too flexible. Modeling red tide mortality as a “predator”, where red tide indices allow, would directly incorporate observation error inherent in the environmental index and bound the red tide mortality estimates between plausible values based on available estimates (e.g., index of red tide mortality as in Vilas et al. (2021)). However, episodic events may still warrant consideration of a binary approach to inclusion (i.e., only considered when above a statistical threshold), since baseline levels of episodic mortality could already be captured in base natural mortality estimates based on longevity estimates.

A potential limitation of the present study is the reliance on bootstrapped datasets to adequately capture the full breadth of variation that can arise in data streams, as simulated data can be more constrained in this manner than observed data. For example, while comparisons across all OM and AM combinations illustrated imprecision in estimation of derived quantities such as the SSB ratio and fishing mortality rates for each fishery, the process of generating bootstrap samples could constrain the resulting level of imprecision of those key quantities. Estimation of initial conditions such as fishing mortality is largely dependent on the bootstrapped age composition data, and it is possible that the bootstrapped dataset is not representing the full range of uncertainty in initial conditions (e.g., bootstrapped data may not be as poor quality as observed data). Unfortunately, an inability to begin modeling from an unfished state is common for grouper assessments in the Gulf because of incomplete and highly uncertain removals due to species identification issues and other data limitations (SEDAR, 2014, 2015).

Growing evidence of negative impacts of red tides on groupers (Driggers et al., 2016; DiLeone and Ainsworth, 2019; Karnauskas et al., 2019) has led to one of the most transparent fish-environment relationships for inclusion into a stock assessment. It is clear that severe red tides lead to death - whether through absorption (Abbott et al., 1975; Baden, 1988), ingestion of toxic biota (Landsberg, 2002), or, from resulting hypoxic or anoxic zones (Walter et al., 2013) - and some positive relationship exists between density of the dinoflagellate *Karenia brevis* and the resulting mortality rates on fishes. While incorporating this mechanism into a stock assessment would appear relatively straightforward, the red tide-grouper story in the Gulf has demonstrated challenges associated with taking an ecosystem approach to fisheries management. The first complication is data availability, in this case the lack of a continuous and consistent time series of red tide severity (or red tide mortality) coupled with large observation errors and difficulties associated with classifying event severity. The second hurdle is the specification of (or allowing the model to specify) the exact relationship between environmental covariates and grouper population dynamics – is it only episodic natural mortality? Could these events lead to changes in catchability or recruitment events? Or could it be all of the above? Recent research suggests that severe years of red tide are associated with hypoxic conditions (Turley et al., 2021), and further reports from fishermen indicate that grouper aggregate outside these hypoxic zones, making them increasingly vulnerable to intense fishing. In addition, the areas hard hit can remain vacant of groupers and any marine life for many years (SEDAR, 2019). Additional field studies (e.g., tagging studies) and advancements in stock assessment techniques or simulation studies are needed to help disentangle the various mechanisms behind mortality, catchability, and recruitment -- all of which are highly variable across space – and their impacts within the stock assessment (e.g., what is the risk of misspecification of the mechanism?).

Recent events highlighting the unpredictable nature of both the environment and economy (e.g., COVID-19), combined with the lack of or lags associated with data collection, highlight the importance of building relationships and obtaining insights from fishermen "on the water" who could help identify unfavorable situations (e.g., concerning drops in abundance) or when important factors are at play. Such information could then allow for quick turn-around, e.g., forecast potential risks with projections. Alternatively, interim assessment approaches could be developed to quickly determine whether the projected population dynamics deviate from expectation, potentially due to environmental factors, without having to directly incorporate and understand the exact mechanistic causes of abundance fluctuations (SEFSC, 2019; Huynh et al., 2020). For example, the 2020 interim analysis conducted for Gulf red grouper employed an index-based harvest control rule that compared the forecasted relative abundance with the observed relative abundance derived from the NMFS bottom longline survey (SEFSC, 2019). This analysis confirmed that the 2018 red tide event had a notable impact on the population, and that the assumption of high red tide mortality in 2018 (i.e., approximating the 2005 red tide) made during the projections used to determine catch advice was appropriate. Such interim approaches are valuable "health checks" and will allow more adaptive management in the face of a changing climate.

Focusing solely on incorporating the environment into a single-species stock assessment ultimately may not be the best use of resources. Rather than, or in addition to, direct incorporation into the stock assessment model, environmental considerations can also support the assessment process through other means, such as rationale for setting of precautionary catch buffers that acknowledge the potential for re-occurrence of fish die-offs (Harford et al., 2018). In addition, decision tables can be used to communicate alternative states of nature, such as those presented during the 2019 Gulf red grouper assessment which projected stock conditions across a range of potential 2018 red tide severity scenarios for consideration by managers when setting catch advice (SEDAR, 2019; Sagarese et al., 2021). In reality, and particularly where resources are limited, moving beyond traditional single-species stock assessment will likely require an "outside-the-box" multi-disciplinary approach. While grouper assessments that include red tide considerations in the Gulf represent a noteworthy step towards implementing ecosystem-based fisheries management, continued data collection on how red tides affect marine resources and continued community and stakeholder engagements are needed to gain an understanding of the historical timing and impact of red tide events.

Author credit statement

Both authors contributed via conceptualization, methodology, and writing - review and editing. WH conducted the analyses.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank all the researchers and stakeholders for their contributions to the Gulf red grouper stock assessments, as well as Richard Methot Jr. for his guidance throughout the process. This work would not have been possible without the efforts of NOAA/National Marine Fisheries Service staff, GMFMC staff, state partners, and academic partners. Additional thanks are extended to M. Karnauskas, L. Ailloud, K. Siegfried, and the reviewers for their input. This work was supported by the National Oceanic and Atmospheric Administration Marine Fisheries Initiative Program. This research was carried out [in part] under the auspices of the Cooperative Institute for Marine and Atmospheric Studies (CIMAS), a Cooperative Institute of the University of Miami and the National Oceanic and Atmospheric Administration, cooperative agreement #NA10OAR4320143. The scientific results and conclusions, as well as any views and opinions expressed herein, are those of the authors and do not necessarily reflect those of any government agency.

References

Abbott, B., Siger, A., Spiegelstein, M., 1975. Toxins from the blooms of *Gymnodinium breve*, in: LoCicero, V.R. (Ed.), Proceedings of the First International Conference on Toxic Dinoflagellate Blooms. Massachusetts Science and Technology Foundation, Wakefield, MA, pp. 355–365.

Baden, D., 1988. Public health problems of red tides, in: Tu, A.T. (Ed.), Handbook of Natural Toxins. Marcel Dekker, New York, NY, pp. 259–277.

Bousquet, N., Cadigan, N., Duchesne, T., Rivest, L.P., 2010. Detecting and correcting underreported catches in fish stock assessment: trial of a new method. Can. J. Fish. Aquat. Sci. 67(8), 1247–1261. https://doi.org/10.1139/F10-051.

Chagaris, D., Sinnickson, D., 2018. An index of red tide mortality on red grouper in the Eastern Gulf of Mexico. SEDAR61-WP06. SEDAR, North Charleston, SC, 16 pp. https://sedarweb.org/docs/wpapers/S61_WP_06_red_tide_mortality_index.pdf.

Cook, G.S., Fletcher, P.J., Kelble, C.R., 2014. Towards marine ecosystem based management in South Florida: investigating the connections among ecosystem pressures, states, and services in a complex coastal system. Ecol. Indic. 44, 26–39. https://doi.org/10.1016/j.ecolind.2013.10.026.

Dell'Apa, A., Fullerton, A., Schwing, F., Brady, M.M., 2015. The status of marine and coastal ecosystem-based management among the network of U.S. federal programs. Mar. Policy 60, 249–258. https://doi.org/10.1016/j.marpol.2015.07.011.

Deroba, J.J., Schueller, A.M., 2013. Performance of stock assessments with misspecified age-and time-varying natural mortality. Fish. Res. 146, 27–40. https://doi.org/10.1016/j.fishres.2013.03.015.

DiLeone, A.G., Ainsworth, C., 2019. Effects of *Karenia brevis* harmful algal blooms on fish community structure on the West Florida Shelf. Ecol. Mod. 392, 250–267. https://doi.org/10.1016/j.ecolmodel.2018.11.022.

Driggers, W.B., Campbell, M.D., Debose, A.J., Hannan, K.M., Hendon, M.D., Martin, T.L., Nichols, C.C., 2016. Environmental conditions and catch rates of predatory fishes associated with a mass mortality on the West Florida Shelf. Est. Coast. Shelf Sci. 168, 40–49. https://doi.org/10.1016/j.ecss.2015.11.009.

Flaherty, K.E., Landsberg, J.H., 2011. Effects of a persistent red tide (*Karenia brevis*) bloom on community structure and species-specific relative abundance of nekton in a Gulf of Mexico estuary. Estuar. Coast. 34(2), 417–439. https://doi.org/10.1007/s12237-010-9350-x.

Fu, C., Quinn II, T.J., 2000. Estimability of natural mortality and other population parameters in a length-based model: *Pandalus borealis* in Kachemak Bay, Alaska. Can. J. Fish. Aquat. Sci. 57(12), 2420–2432. https://doi.org/10.1139/f00-220.

Gårdmark, A., Östman, Ö., Nielsen, A., Lundström, K., Karlsson, O., Pönni, J., Aho, T., 2012. Does predation by grey seals (*Halichoerus grypus*) affect Bothnian Sea herring stock estimates? ICES J. Mar. Sci. 69(8), 1448–1456. https://doi.org/10.1093/icesjms/fss099.

Grüss, A., Schirripa, M.J., Chagaris, D., Drexler, M., Simons, J., Verley, P., Shin, Y.-J., Karnauskas, M., Oliveros-Ramos, R., Ainsworth, C.H., 2015. Evaluation of the trophic structure of the West Florida Shelf in the 2000s using the ecosystem model OSMOSE. J. Mar. Syst. 144, 30–47. https://doi.org/10.1016/j.jmarsys.2014.11.004.

Harford, W.J., Grüss, A., Schirripa, M.J., Sagarese, S.R., Bryan, M., Karnauskas, M., 2018. Handle with care: establishing catch limits for fish stocks experiencing episodic natural mortality events. Fisheries 43, 463–471. https://doi.org/10.1002/fsh.10131.

Hoenig, J.M., 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. 82, 898–903.

Huynh, Q.C., Hordyk, A.R., Forrest, R.E., Porch, C.E., Anderson, S.C., Carruthers, T.R., 2020. The interim management procedure approach for assessed stocks: responsive management advice and lower assessment frequency. Fish. Fish. 21(3), 663–679. https://doi.org/10.1111/faf.12453.

Jiao, Y., Smith, E.P., O'Reilly, R., Orth, D.J., 2012. Modelling non-stationary natural mortality in catch-at-age models. ICES J. Mar. Sci. 69(1), 105–118. https://doi.org/10.1093/icesjms/fsr184.

Johnson, K.F., Monnahan, C.C., McGilliard, C.R., Vert-Pre, K.A., Anderson, S.C., Cunningham, C.J., Hurtado-Ferro, F., Licandeo, R.R., Muradian, M.L., Ono, K., Szuwalski, C.S., 2015. Time-varying natural mortality in fisheries stock assessment models: identifying a default approach. ICES J. Mar. Sci. 72(1), 137–150. https://doi.org/10.1093/icesjms/fsu055.

Karnauskas, M., McPherson, M., Sagarese, S., Rios, A., Jepson, M., Stoltz, A., Blake, S., 2019. Timeline of severe red tide events on the West Florida Shelf: insights from oral histories. SEDAR61-WP20. SEDAR, North Charleston, SC, 16 pp. https://sedarweb.org/docs/wpapers/S61_WP_20_Karnauskasetal_red_tide.pdf.

Kiel, B.L., 2004. Homing and spatial use of gag grouper, *Mycteroperca microlepis*. MS thesis, University of Florida, Gainesville, FL.

Landsberg, J.H., 2002. The effects of harmful algal blooms on aquatic organisms. Rev. Fish. Sci. 10(2), 113–390. https://doi.org/10.1080/20026491051695.

Landsberg, J.H., Flewelling, L.J., Naar, J., 2009. *Karenia brevis* red tides, brevetoxins in the food web, and impacts on natural resources: decadal advancements. Harmful Algae 8, 598–607. https://doi.org/10.1016/j.hal.2008.11.010.

Lee, H.H., Maunder, M.N., Piner, K.R., Methot, R.D., 2011. Estimating natural mortality within a fisheries stock assessment model: an evaluation using simulation analysis based on twelve stock assessments. Fish. Res. 109(1), 89–94. https://doi.org/10.1016/j.fishres.2011.01.021.

Legault, C.M., Palmer, M.C., 2016. In what direction should the fishing mortality target change when natural mortality increases within an assessment? Can. J. Fish. Aquat. Sci. 73(3), 349–357. https://doi.org/10.1139/cjfas-2015-0232.

Levin, P.S., Fogarty, M.J., Murawski, S.A., Fluharty, D., 2009. Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean. PLoS Biol. 7, e1000014. https://doi.org/10.1371/journal.pbio.1000014.

Lindberg, W.J., Frazer, T.K., Portier, K.M., Vose, F., Loftin, F., Murie, D.J., Mason, D.M., Nagy, B., Hart, M.K., 2006. Density-dependent habitat selection and performance by a large mobile reef fish. Ecol. Appl. 16(2), 731–746. https://doi.org/10.1890/1051-0761(2006)016[0731:DHSAPB]2.0.CO;2.

Lorenzen, K., 2005. Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis. Philos. Trans. R. Soc. Lond., B, Biol. Sci. 360, 171–189. https://doi.org/10.1098/rstb.2004.1570.

Marshall, K.N., Levin, P.S., Essington, T.E., Koehn, L.E., Anderson, L.G., Bundy, A., Carothers, C., Coleman, F., Gerber, L.R., Grabowski, J.H., Houde, E., 2018. Ecosystem-based fisheries management for social–ecological systems: renewing the focus in the United States with next generation fishery ecosystem plans. Conserv. Lett. 11(1), e12367. https://doi.org/10.1111/conl.12367.

Matich, P., Heithaus, M.R., 2012. Effects of an extreme temperature event on the behavior and age structure of an estuarine top predator, *Carcharhinus leucas*. Mar. Ecol. Prog. Ser. 447, 165–178. https://doi.org/10.3354/meps09497.

Methot, R.D., Wetzel, C.R., 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. Fish. Res. 142, 86–99. https://doi.org/10.1016/j.fishres.2012.10.012.

Methot, R.D., Wetzel, C.R., Taylor, I.G., Doering, K., 2020. Stock Synthesis User Manual Version 3.30.15. U.S. Department of Commerce, NOAA Processed Report NMFS-NWFSC-PR-2020-05. https://doi.org/10.25923/5wpn-qt71.

Methot, R.D., Wetzel, C.R., Taylor, I.G., Doering, K., Johnson, K.F., 2021. Stock Synthesis User Manual Version 3.30.18. U.S. Department of Commerce. Available for download at https://github.com/nmfs-stock-synthesis/doc/releases (accessed 31 January 2022).

O'Leary, C.A., Thorson, J.T., Miller, T.J., Nye, J.A., 2020. Comparison of multiple approaches to calculate time-varying biological reference points in climate-linked population-dynamics models. ICES J. Mar. Sci. 77(3), 930–941. https://doi.org/10.1093/icesjms/fsz215.

Piner, K.R., Lee, H.-H., Maunder, M.N., Methot, R.D., 2011. A simulation-based method to determine model misspecification: examples using natural mortality and population dynamics models. Mar. Coast. Fish. 3, 336–343. https://doi.org/10.1080/19425120.2011.611005.

Reum, J.C., Townsend, H., Gaichas, S., Sagarese, S., Kaplan, I.C., Grüss, A., 2021. It's not the destination, it's the journey: multispecies model ensembles for ecosystem approaches to fisheries management. Front. Mar. Sci. 8, 75. https://doi.org/10.3389/fmars.2021.631839.

Sagarese, S.R., Bryan, M.D., Walter, J.F., Schirripa, M.J., Grüss, A., Karnauskas, M., 2015. Incorporating ecosystem considerations within the Stock Synthesis integrated assessment model for Gulf of Mexico Red Grouper (*Epinephelus morio*). SEDAR42-RW01. SEDAR, North Charleston, SC, 27 pp. https://sedarweb.org/docs/wpapers/S42_RW_01_red_tide.pdf.

Sagarese, S.R., Lauretta, M.V., Walter III, J.F., 2017. Progress towards a next-generation fisheries ecosystem model for the northern Gulf of Mexico. Ecol. Mod. 345, 75–98. https://doi.org/10.1016/j.ecolmodel.2016.11.001.

Sagarese, S.R., Walter III, J.F., Harford, W.J., Grüss, A., Stumpf, R.P., Christman, M.C., 2018. Updating indices of red tide severity for incorporation into stock assessments for the shallow-water grouper complex in the Gulf of Mexico. SEDAR61-WP07. SEDAR, North Charleston, SC, 12 pp. http://sedarweb.org/docs/wpapers/S61_WP_07_Red Tide Severity_SWG.pdf.

Sagarese, S.R., Vaughan, N.R., Walter III, J.F., Karnauskas, M., 2021. Enhancing single-species stock assessments with diverse ecosystem perspectives: a case study for Gulf of Mexico Red Grouper (*Epinephelus morio*) and red tides. Can. J. Fish. Aquat. Sci. 78, 1168–1180. https://doi.org/10.1139/cjfas-2020-0257.

Saul, S., Walter III, J., Die, D., Naar, D., Donahue, B., 2013. Modeling the spatial distribution of commercially important reef fishes on the West Florida Shelf. Fish. Res. 143, 12–20. https://doi.org/10.1016/j.fishres.2013.01.002.

Schirripa, M.J., Methot, R.D., et al., 2013. Incorporating various Gulf of Mexico Integrated Ecosystem Assessment products into the Stock Synthesis Integrated Assessment Model framework. SEDAR33-DW10. SEDAR, North Charleston, SC, 17 pp. https://sedarweb.org/docs/wpapers/SEDAR33-DW10- Schirripa%2C Methot%2C et al. 2013 Incorporation of IEA Products for SEDAR 33.pdf.

SEDAR (Southeast Data, Assessment, and Review), 2006a. SEDAR 10 Gulf of Mexico Gag Grouper Stock Assessment Report. SEDAR, North Charleston, SC, 250 pp. https://sedarweb.org/docs/sar/S10SAR2 GOM Gag Assessment Report.pdf.

SEDAR (Southeast Data, Assessment, and Review), 2006b. SEDAR 12 Gulf of Mexico Red Grouper Stock Assessment Report. SEDAR, North Charleston, SC, 358 pp. https://sedarweb.org/docs/sar/S12SAR1 Gulf Red Grouper Completev2.pdf.

SEDAR (Southeast Data, Assessment, and Review), 2009a. SEDAR 10 Update Gulf of Mexico Gag Grouper Stock Assessment Report. SEDAR, North Charleston, SC, 171 pp. https://sedarweb.org/docs/suar/Gag_2009_Assessment_Update_Report.pdf.

SEDAR (Southeast Data, Assessment, and Review), 2009b. SEDAR 12 Update Gulf of Mexico Red Grouper Stock Assessment Report. SEDAR, North Charleston, SC, 143 pp. https://sedarweb.org/docs/suar/Red_Grouper_2009_Assessment_Update_Report.pdf.

SEDAR (Southeast Data, Assessment, and Review), 2014. SEDAR 33 Gulf of Mexico Gag Stock Assessment Report. SEDAR, North Charleston, SC, 609 pp. https://sedarweb.org/docs/sar/SEDAR 33 SAR- Gag Stock Assessment Report FINAL_sizereduced.pdf.

SEDAR (Southeast Data, Assessment, and Review), 2015. SEDAR 42 Gulf of Mexico Red Grouper Stock Assessment Report. SEDAR, North Charleston, SC, 612 pp. https://sedarweb.org/docs/sar/S42_SAR_0.pdf.

SEDAR (Southeast Data, Assessment, and Review), 2019. SEDAR 61 Gulf of Mexico Red Grouper Stock Assessment Report. SEDAR, North Charleston, SC, 285 pp. https://sedarweb.org/docs/sar/S61_Final_SAR.pdf.

SEDAR (Southeast Data, Assessment, and Review), 2021. SEDAR 72 Gulf of Mexico Gag Grouper Stock Assessment Report. SEDAR, North Charleston, SC, 318 pp. https://sedarweb.org/docs/sar/S72_SAR_FINAL.pdf.

SEFSC (Southeast Fisheries Science Center), 2019. Interim analysis for Gulf of Mexico Red Grouper. Technical Report prepared for the January 2020 Gulf of Mexico Fishery Management Council Scientific and Statistical Committee Meeting. SEFSC, Miami, FL, 9 pp. https://gulfcouncil.org/scientific-and-statistical-meetings/archive/ (item 08a downloaded via meeting materials).

Smith, G.B., 1975. The 1971 red tide and its impact on certain reef communities in the mid-eastern Gulf of Mexico. Environ. Lett. 9(2), 141–152. https://doi.org/10.1080/00139307509435843.

Steidinger, K.A., 2009. Historical perspective on *Karenia brevis* red tide research in the Gulf of Mexico. Harmful Algae 8, 549–561. https://doi.org/10.1016/j.hal.2008.11.009.

Steidinger, K.A., Haddad, K., 1981. Biologic and hydrographic aspects of red tides. Bioscience 1981, 814–819. https://doi.org/10.2307/1308678.

Steidinger, K.A., Ingle, R.M., 1972. Observations on the 1971 summer red tide in Tampa Bay, Florida. Environ. Lett. 3(4), 271–278. https://doi.org/10.1080/00139307209435473.

Steidinger, K.A., Vargo, G.A., 1988. Marine dinoflagellate blooms: dynamics and impacts, in: Lembi, C., Waaland, J.R. (Eds.), Algae and Human Affairs. Cambridge University Press, Cambridge, UK, pp. 373–401.

Turley, B., Kelble, C., Karnauskas, M., 2021. Association between hypoxia and red tide between 2003-2019 on the West Florida Shelf. SEDAR72-DW10. SEDAR, North Charleston, SC, 14 pp. https://sedarweb.org/docs/wpapers/S72_WP_10_gag_hypoxia.pdf.

Vilas, D., Chagaris, D., Buczkowski, J., 2020. Red tide mortality on gag grouper from 2002-2018 generated by an Ecospace model of the West Florida Shelf. SEDAR72-WP01. SEDAR, North Charleston, SC, 17 pp. https://sedarweb.org/docs/wpapers/S72_WP_01_red_tide_Mortality_Ecospace_v3.pdf.

Walter, J.F., Christman, M.C., Landsberg, J.H., Linton, B., Steidinger, K., Stumpf, R., Tustison, J., 2013. Satellite derived indices of red tide severity for input for Gulf of Mexico Gag grouper stock assessment. SEDAR33-DW08. SEDAR, North Charleston, SC, 43 pp.

https://sedarweb.org/docs/wpapers/SEDAR33-DW08- Walter et al. 2013 red tide indices for Gag.pdf.
Walter III, J.F., Sagarese, S.R., Harford, W.J., Grüss, A., Stumpf, R.P., Christman, M.C., 2015. Assessing the impact of the 2014 red tide event on red grouper (*Epinephelus morio*) in the Northeastern Gulf of Mexico. SEDAR42-RW02. SEDAR, North Charleston, SC, 27 pp. https://sedarweb.org/docs/wpapers/S42_RW_02_Red Tide event_2014_Final_v2.pdf.

Figure Captions

Fig. 1. Summary of life history and fishery dynamics for Gulf red grouper.

Fig. 2. Data sources included in the Gulf red grouper assessment model. Values in parentheses are the SE for each data input assumed in the model where necessary, whereas values in the boxes are input sample sizes set to the square root of the number of observations for composition data. Distributions are described in the text.

Fig. 3. Derived quantities for Gulf red grouper model runs where red tide mortality affects ages-0+ (red) and ages-5+ (blue). Metrics include (A) total biomass, (B) SSB, (C) SSB ratio, (D) recruitment, and (E) mortality including fishing mortality (lines, landings + dead discards) and red tide mortality in years where estimated (vertical bars).

Fig. 4. Histograms of relative bias in terminal year (2017) spawning stock biomass (SSB) and fishing mortality rate (F) for simulations from two operating models (OMs; columns) and with fitting according to four assessment model configurations (AMs; rows). Note that *x*- and *y*-axes differ between panels, the thin dashed lines represent the 25th and 75th percentiles, and the thick dashed line represents the median.

Fig. 5. Histograms of relative bias in virgin recruitment (R_0) and inter-annual recruitment variability (σ_R) for simulations from two operating models (OMs; columns) and with fitting according to four assessment model configurations (AMs; rows). Note that *x*- and *y*-axes differ between panels, the thin dashed lines represent the 25th and 75th percentiles, and the thick dashed line represents the median.

Fig. 6. Histograms of relative bias in red tide mortality (fraction of biomass killed by red tide) in 2005 and 2014 for simulations from two operating models and with fitting according to assessment model configurations that included estimation of these quantities. Note that *x*- and *y*-axes differ between panels, the thin dashed lines represent the 25th and 75th percentiles, and the thick dashed line represents the median.

Fig. 7. Annual red tide mortality estimates (apical rates and proportion of biomass killed) obtained from AM4 for simulations from two operating models (OMs). Box plots show distribution of estimates across simulations according to median estimates (thick lines), inter-quartile range (boxes), 1.5 time the inter-quartile range (whiskers) and outliers (open circles). Vertical bars indicate years with red tide mortality specified in each operating model. Note that *y*-axes differ between panels.

Fig. 8. Annual relative bias of age-0 recruitment and estimated fishing mortality (landings + dead discards) for AM3 for simulations from two operating models (OMs). Box plots show distribution of bias across simulations according to median bias (thick lines), inter-quartile range (boxes), 1.5 time the inter-quartile range (whiskers) and outliers (open circles). Vertical bars indicate years with red tide mortality specified in each operating model.

Table 1. Summary of model structure for the Gulf red grouper base model. Additional details are provided in SEDAR (2019).

Process	**Details**
No. of areas and seasons	1
Modeled time period	1986-2017
Life history	
Age classes	0 to 20+ (plus group)
Length to weight	Fixed
Age to length	Von Bertalanffy growth with fixed asymptotic length ($L\infty$ = 79.99 cm Fork Length) and variability (CVyoung = 0.142; CVold = 0.164); estimated growth rate (*K*) and length at minimum age (1-year)
Natural mortality	Age-specific vector estimated externally and fixed; based on Lorenzen (2005) with Base M = 0.144 year^{-1} (Hoenig 1983) and vulnerable to the fishery at 5 years
Maturity	Logistic function of age fixed; 50% at 2.8 years and 29.2 cm Fork Length
Sexual transition	Logistic function of age; 50% at 11.2 years and 70.7 cm Fork Length
Batch fecundity	Function of length and converted to age using the growth curve
Fecundity-at-age	Product of maturity-at-age, transition-at-age, and batch fecundity-at-age; fixed
Recruitment	
Stock-recruit relationship	Beverton-Holt
Steepness	Fixed at 0.99 (for convenience of projections; not biologically realistic)
Natural logarithm of virgin recruitment (Ln(R_0))	Estimated
Recruitment variability (σ_R)	Estimated
Recruitment deviations	Estimated from 1993-2017 (age composition data start in 1991); no early estimates
Commercial	
Vertical line and longline	
Length-based selectivity	Dome-shaped; estimated peak and width of plateau parameters; fixed ascending and descending width parameters; set initial and final selectivity parameters to decay
Retention: 1986-1989	Fixed at full retention for all sizes
Retention: 1990-2008	Fixed inflection at federal size limit and at full retention; fixed knife-edge for vertical line but estimated width parameter for longline
Retention: 2009-2017	Fixed inflection at federal size limit and at full retention; estimated width parameter
Trap	
Length-based selectivity	Dome-shaped; estimated peak and width of plateau parameters; fixed ascending and descending width parameters; set initial and final selectivity parameters to decay
Retention: 1986-1989	Fixed at full retention for all sizes
Retention: 1990-2006	Fixed inflection at federal size limit, knife-edge, and at full retention
Recreational	
Length-based selectivity	Dome-shaped; estimated peak, width of plateau, ascending and descending width parameters; set initial and final selectivity parameters to decay
Retention: 1986-1989	Fixed at full retention above Florida state size limit
Retention: 1990-2017	Fixed inflection at federal size limit and knife-edge; estimated asymptote due to bag limits

Fishery-independent survey	
Combined video	Logistic; estimated size at inflection and width for 95% selection parameters
Summer groundfish	Dome-shaped; estimated peak, width of plateau, ascending and descending width parameters; set initial and final selectivity parameters to decay
Bottom longline	Logistic; estimated size at inflection and width for 95% selection parameters
Repetitive time drop	Logistic; estimated size at inflection and width for 95% selection parameters

Table 2. Differences in red tide configurations between operating models (OMs) and assessment models (AMs) and scenarios (X) testing the performance of the bycatch fleet approach to estimating red tide mortality.

Red tide specifications	**AM1 / OM1**	**AM2 / OM2**	**AM3**	**AM4**
Red tide mortality estimated	2005 and 2014	2005 and 2014	-	1986-2017
Constant selectivity	Ages 0+	Ages 5+	-	Ages 0+

Model	**AM1**	**AM2**	**AM3**	**AM4**
OM1	X (Self-test)	X	X	X
OM2	X	X (Self-test)	X	X

Table 3. Comparison of model performance and key parameter estimates (with coefficients of variation) for base model (OM1) and the sensitivity run with red tides affecting ages 5+.

Metric	OM1	OM2
Model Performance		
Negative log-likelihood	537.486	535.458
Gradient	0.000105	0.000156
Number of estimated parameters (bounded)	178 (0)	178 (0)
Correlations exceeding 0.7 (0.95)	6 (0)	5 (0)
Parameters with CVs exceeding 1	8 (recruitment deviations)	11 (recruitment deviations)
Parameter Estimates		
Initial fishing mortality rate (year^{-1})		
Commercial vertical line	0.129 (0.187)	0.128 (0.187)
Commercial longline	0.090 (0.200)	0.089 (0.200)
Commercial trap	0.019 (0.219)	0.019 (0.219)
Recreational	0.245 (0.204)	0.245 (0.204)
Recruitment variability (σ_R)	0.815 (0.137)	0.860 (0.136)
Natural log of virgin recruitment (Ln(R_0))	9.925 (0.004)	9.931 (0.004)
Unfished SSB (relative eggs)	2,494,130 (0.035)	2,509,200 (0.036)
2017 SSB (relative eggs)	613,517 (0.103)	661,791 (0.106)
2017 SSB/unfished SSB	0.246 (0.099)	0.264 (0.100)
2017 Fishing mortality	0.160 (0.140)	0.148 (0.143)
Virgin recruitment (1000s of fish)	20,443 (0.035)	20,567 (0.036)
2005 red tide mortality rate (year^{-1})	0.339 (0.309)	0.469 (0.255)
2005 percent of biomass killed by red tide	29.5%	32.3%
2014 red tide mortality rate (year^{-1})	0.257 (0.429)	0.369 (0.346)
2014 percent of biomass killed by red tide	21.3%	27.3%
Stock Status		
F reference point ($F_{MSYproxy}$)	0.259	0.259
Current F (2015-2017 mean)	0.203	0.192
Overfishing occurring (Current F/ $F_{MSYproxy}$)	No (0.77)	No (0.74)
SSB reference point ($0.5SSB_{MSYproxy}$)	374,120	376,402
Overfished (2017 SSB/$0.5SSB_{MSYproxy}$)	No (1.64)	No (1.76)

Table 4. Performance of derived quantities for simulations from two operating models (OMs) and with fitting according to four assessment model configurations (AMs).

Model	Precision of estimator (CV)				Median relative bias of estimator			
	AM1	**AM2**	**AM3**	**AM4**	**AM1**	**AM2**	**AM3**	**AM4**
Terminal (2017) Spawning Stock Biomass								
OM1	0.104	0.106	0.110	0.127	-0.008	0.047	-0.032	0.075
OM2	0.096	0.095	0.102	0.118	-0.049	0.026	-0.070	0.056
Terminal (2017) Fishing Mortality								
OM1	0.135	0.137	0.141	0.557	-0.046	-0.091	-0.025	0.005
OM2	0.130	0.129	0.135	0.581	0.000	-0.070	0.018	0.016
Virgin Recruitment (Ln(R_0))								
OM1	0.003	0.003	0.003	0.010	-0.001	-0.001	-0.005	0.016
OM2	0.003	0.003	0.003	0.010	-0.001	0.000	-0.005	0.019
Recruitment Variability (σ_R)								
OM1	0.085	0.096	0.087	0.083	-0.056	0.008	0.148	-0.056
OM2	0.073	0.084	0.086	0.072	-0.150	-0.116	0.044	-0.141
Unfished Spawning Stock Biomass (SSB_0)								
OM1	0.033	0.034	0.031	0.103	-0.012	-0.009	-0.045	0.172
OM2	0.033	0.034	0.030	0.103	-0.011	-0.002	-0.053	0.211
1986 Spawning Stock Biomass Ratio (SSB / SSB_0)								
OM1	0.070	0.069	0.067	0.095	0.091	0.095	0.126	0.110
OM2	0.071	0.071	0.067	0.100	0.085	0.084	0.129	0.107
2005 Red Tide Mortality (apical estimate)								
OM1	0.426	0.390	-	0.799	-0.365	-0.126	-	-0.536
OM2	0.343	0.281	-	0.658	-0.427	-0.134	-	-0.499
2014 Red Tide Mortality (apical estimate)								
OM1	0.424	0.439	-	0.841	-0.131	0.045	-	-0.411
OM2	0.399	0.334	-	0.716	-0.354	-0.053	-	-0.458
Biomass Removed by 2005 Red Tide								
OM1	-	-	-	-	-2.122	-1.882	-	-2.689
OM2	-	-	-	-	-1.784	-1.309	-	-2.034
Biomass Removed by 2014 Red Tide								
OM1	-	-	-	-	-0.115	-0.034	-	-0.377
OM2	-	-	-	-	-0.269	-0.043	-	-0.371

Fig. 1.

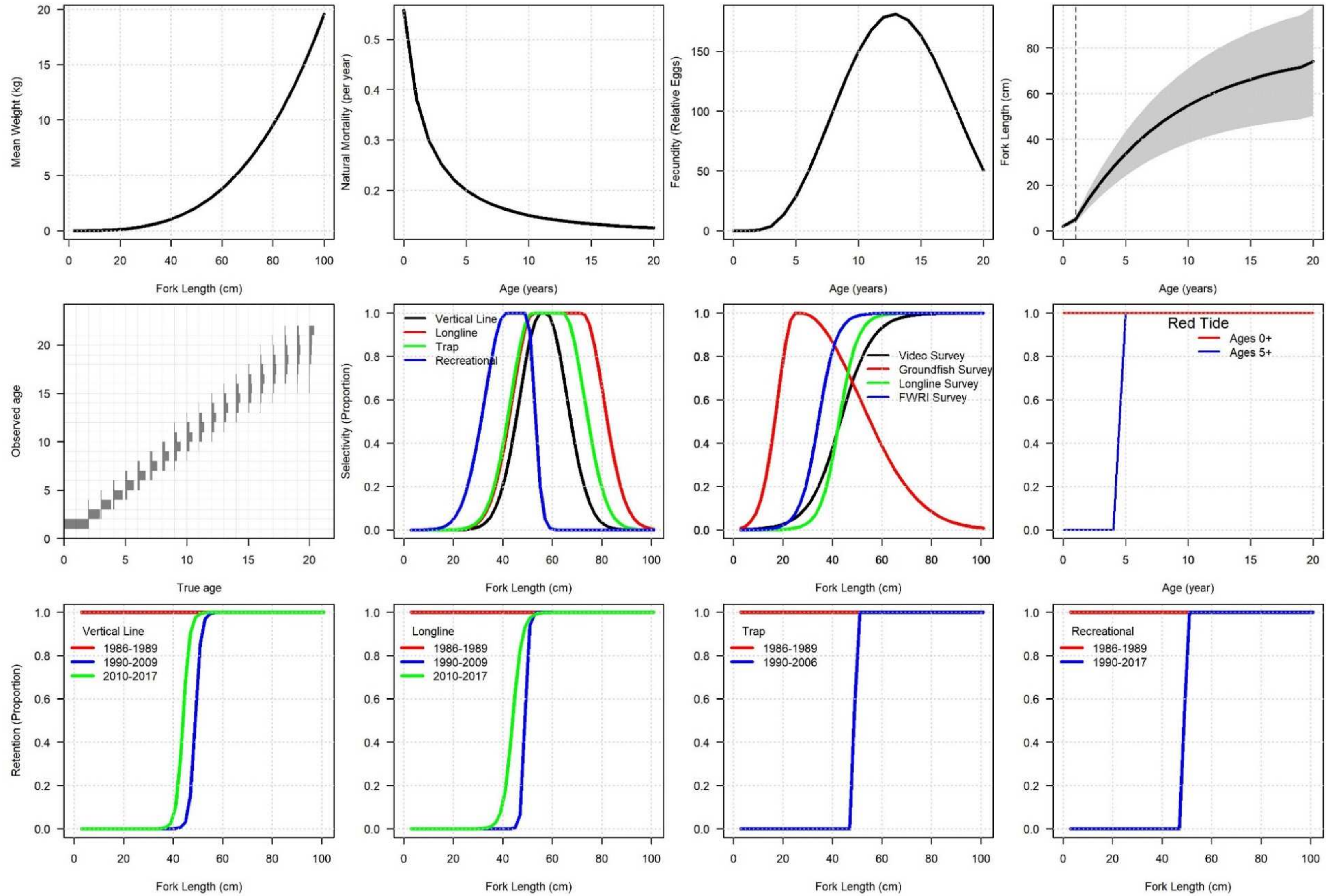
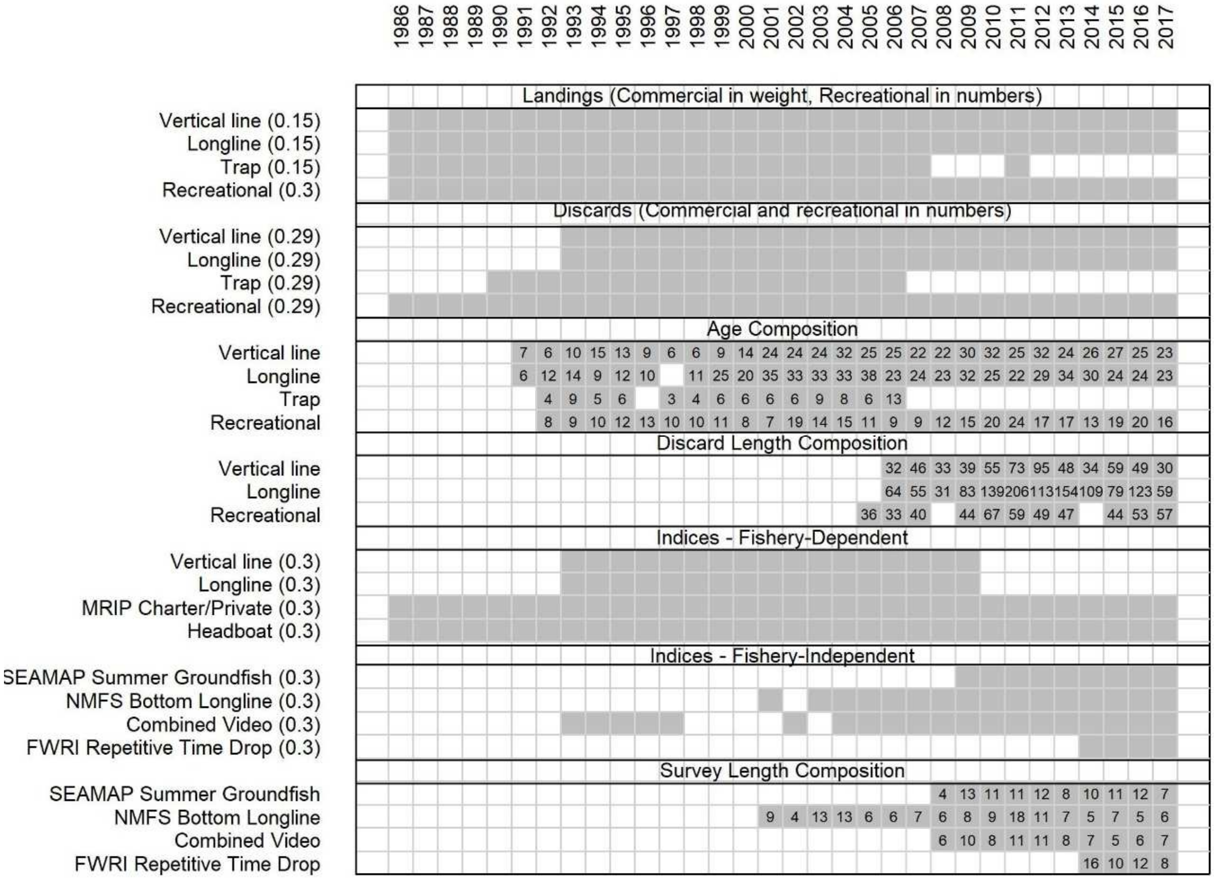

Mean Weight (kg)
Fork Length (cm)
Natural Mortality (per year)
Age (years)
Fecundity (Relative Eggs)
Age (years)
Fork Length (cm)
Age (years)
Observed age
True age
Selectivity (Proportion)
Vertical Line
Longline
Trap
Recreational
Fork Length (cm)
Video Survey
Groundfish Survey
Longline Survey
FWRI Survey
Fork Length (cm)
Red Tide
Ages 0+
Ages 5+
Age (year)
Retention (Proportion)
Vertical Line
1986-1989
1990-2009
2010-2017
Fork Length (cm)
Longline
1986-1989
1990-2009
2010-2017
Fork Length (cm)
Trap
1986-1989
1990-2006
Fork Length (cm)
Recreational
1986-1989
1990-2017
Fork Length (cm)

Fig. 2.



Landings (Commercial in weight, Recreational in numbers)
Vertical line (0.15)
Longline (0.15)
Trap (0.15)
Recreational (0.3)
Discards (Commercial and recreational in numbers)
Vertical line (0.29)
Longline (0.29)
Trap (0.29)
Recreational (0.29)
Age Composition
Vertical line
Longline
Trap
Recreational
Discard Length Composition
Vertical line
Longline
Recreational
Indices - Fishery-Dependent
Vertical line (0.3)
Longline (0.3)
MRIP Charter/Private (0.3)
Headboat (0.3)
Indices - Fishery-Independent
SEAMAP Summer Groundfish (0.3)
NMFS Bottom Longline (0.3)
Combined Video (0.3)
FWRI Repetitive Time Drop (0.3)
Survey Length Composition
SEAMAP Summer Groundfish
NMFS Bottom Longline
Combined Video
FWRI Repetitive Time Drop

Fig. 3.

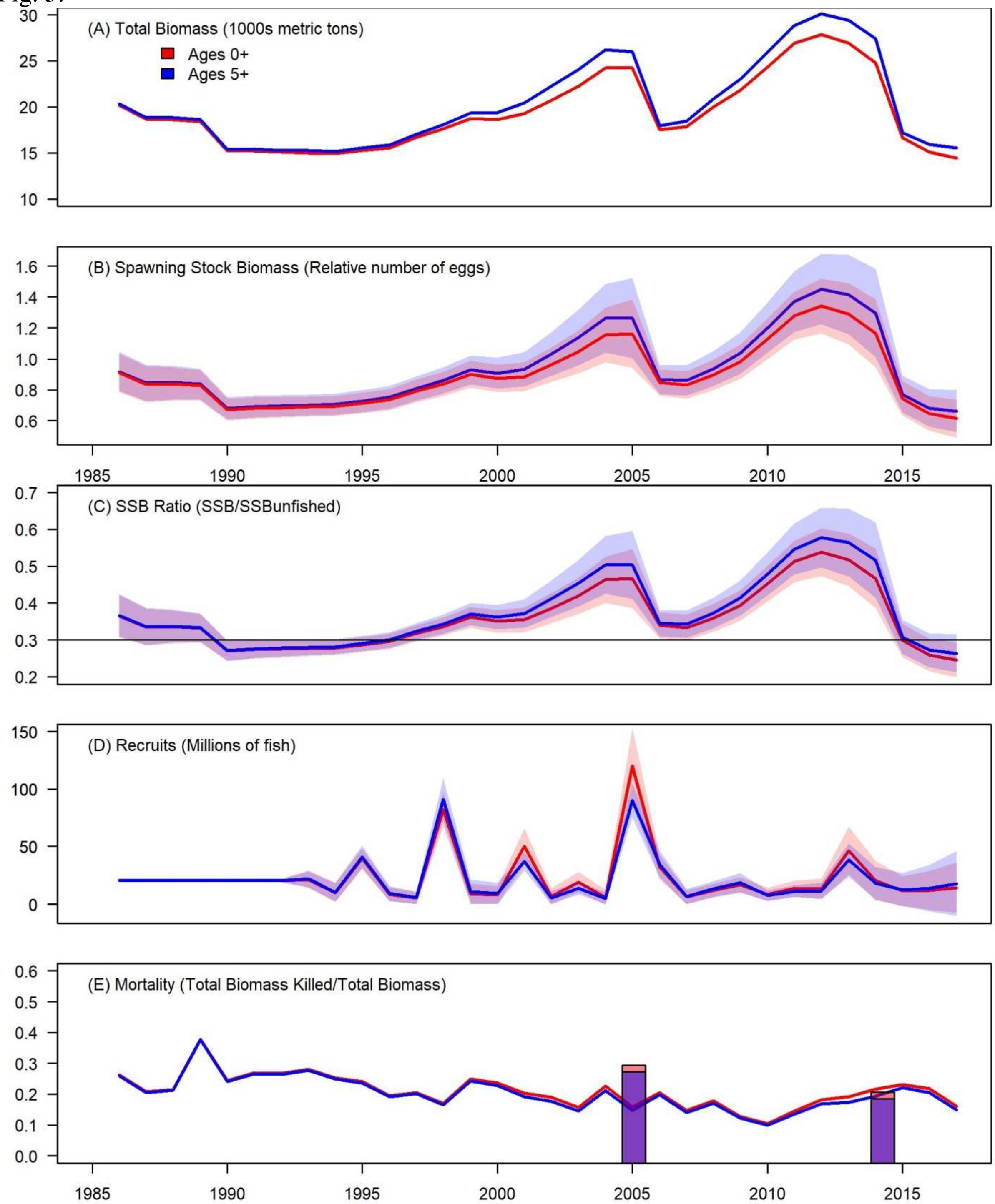

(A) Total Biomass (1000s metric tons)
Ages 0+
Ages 5+
(B) Spawning Stock Biomass (Relative number of eggs)
(C) SSB Ratio (SSB/SSBunfished)
(D) Recruits (Millions of fish)
(E) Mortality (Total Biomass Killed/Total Biomass)
1985
1990
1995
2000
2005
2010
2015

Fig. 4.

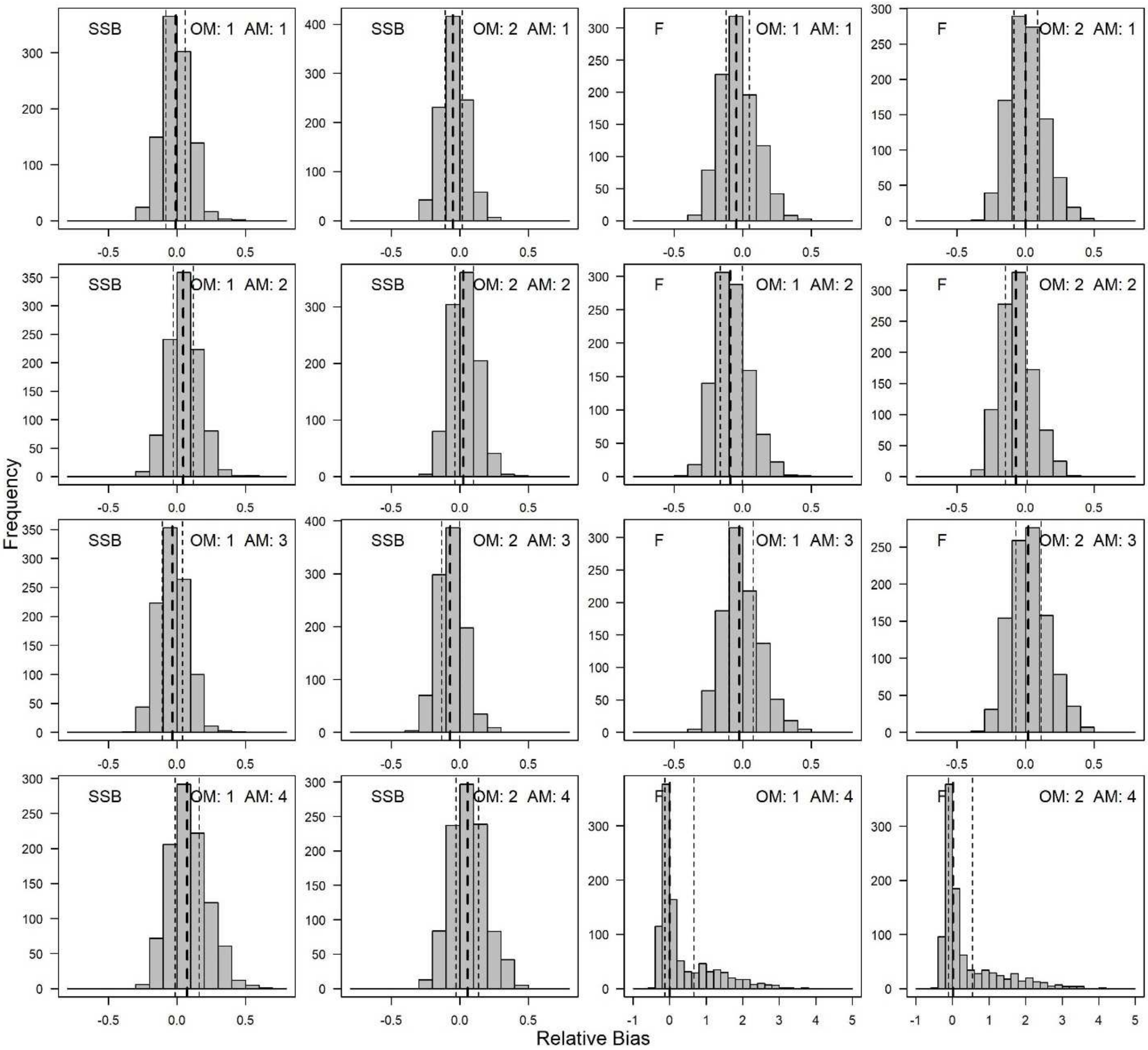
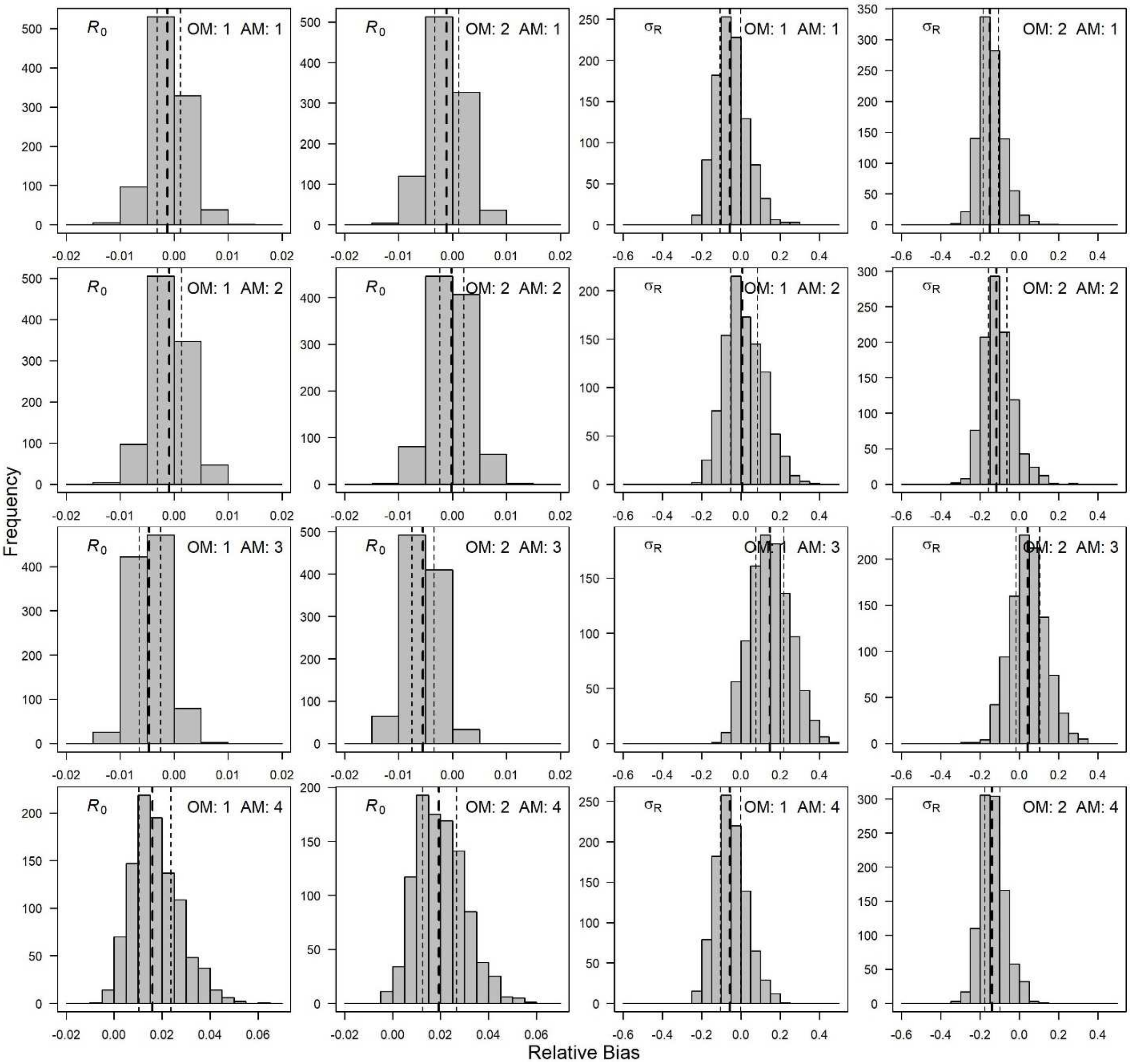

SSB OM: 1 AM: 1
SSB OM: 2 AM: 1
F OM: 1 AM: 1
F OM: 2 AM: 1
SSB OM: 1 AM: 2
SSB OM: 2 AM: 2
F OM: 1 AM: 2
F OM: 2 AM: 2
SSB OM: 1 AM: 3
SSB OM: 2 AM: 3
F OM: 1 AM: 3
F OM: 2 AM: 3
SSB OM: 1 AM: 4
SSB OM: 2 AM: 4
F OM: 1 AM: 4
F OM: 2 AM: 4
Frequency
Relative Bias

Fig. 5.



R_0 OM: 1 AM: 1
R_0 OM: 2 AM: 1
σ_R OM: 1 AM: 1
σ_R OM: 2 AM: 1
R_0 OM: 1 AM: 2
R_0 OM: 2 AM: 2
σ_R OM: 1 AM: 2
σ_R OM: 2 AM: 2
R_0 OM: 1 AM: 3
R_0 OM: 2 AM: 3
σ_R OM: 1 AM: 3
σ_R OM: 2 AM: 3
R_0 OM: 1 AM: 4
R_0 OM: 2 AM: 4
σ_R OM: 1 AM: 4
σ_R OM: 2 AM: 4
Frequency
Relative Bias

Fig. 6.

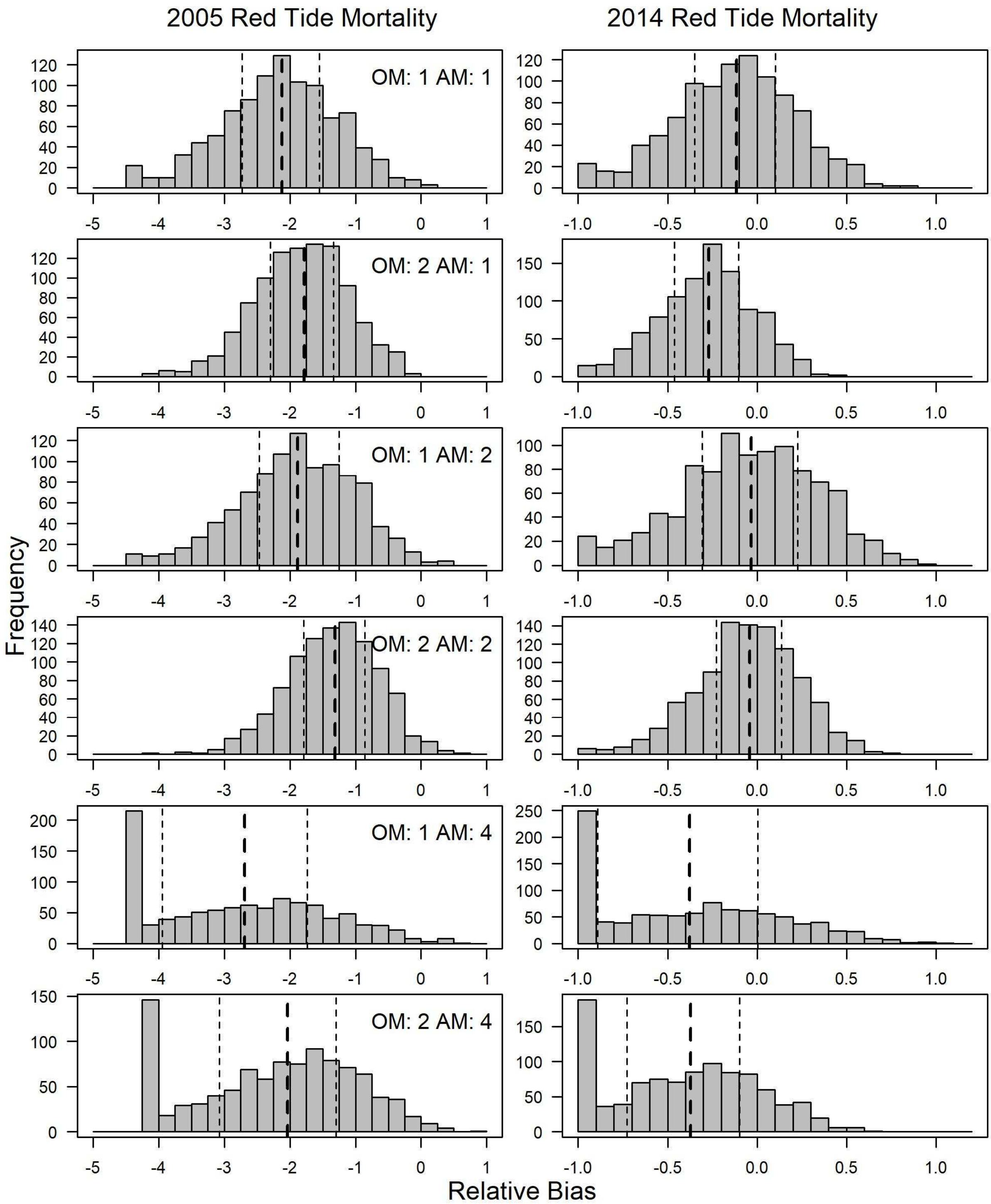

2005 Red Tide Mortality
2014 Red Tide Mortality
OM: 1 AM: 1
OM: 2 AM: 1
OM: 1 AM: 2
OM: 2 AM: 2
OM: 1 AM: 4
OM: 2 AM: 4
Frequency
Relative Bias

Fig. 7.

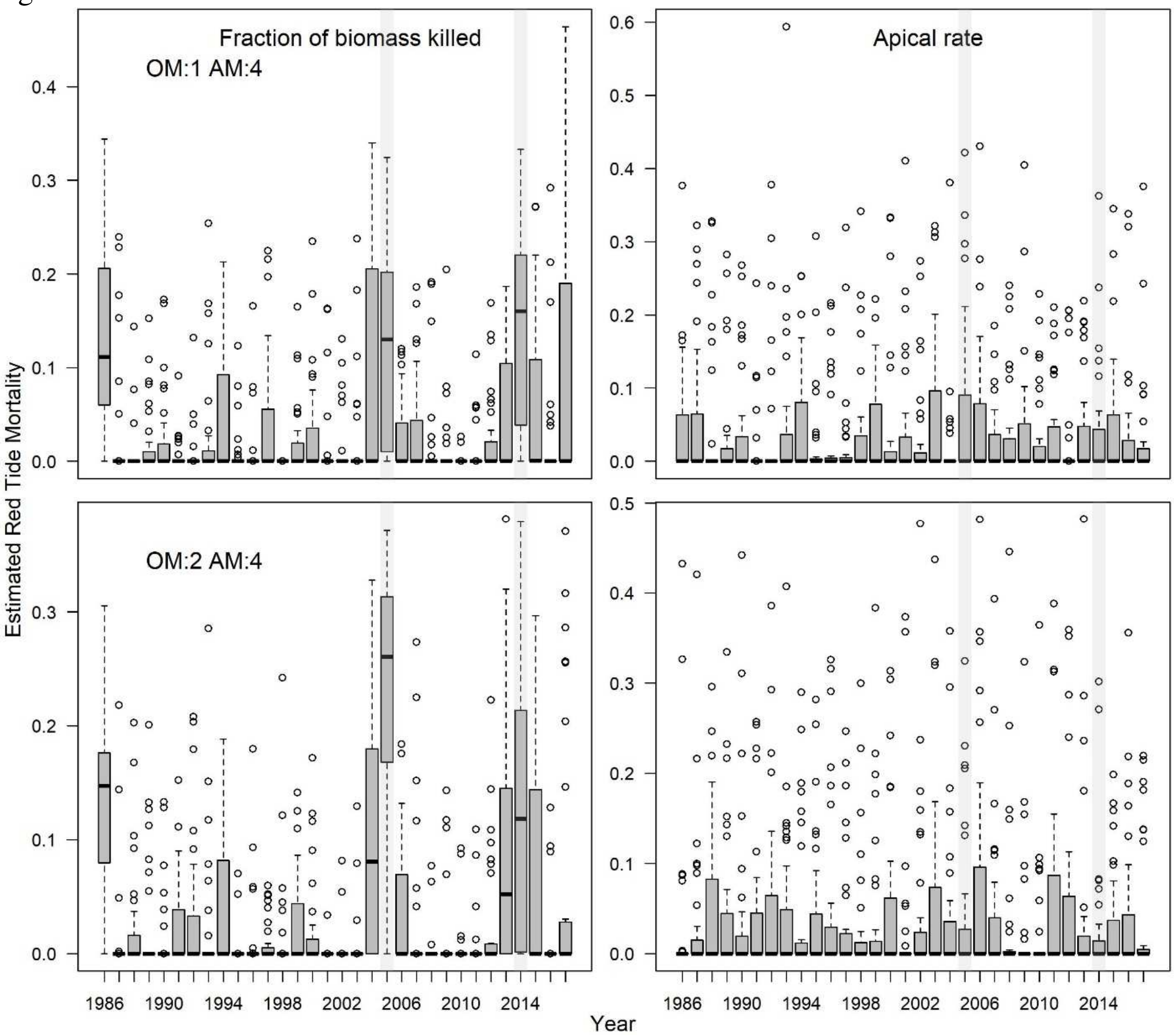
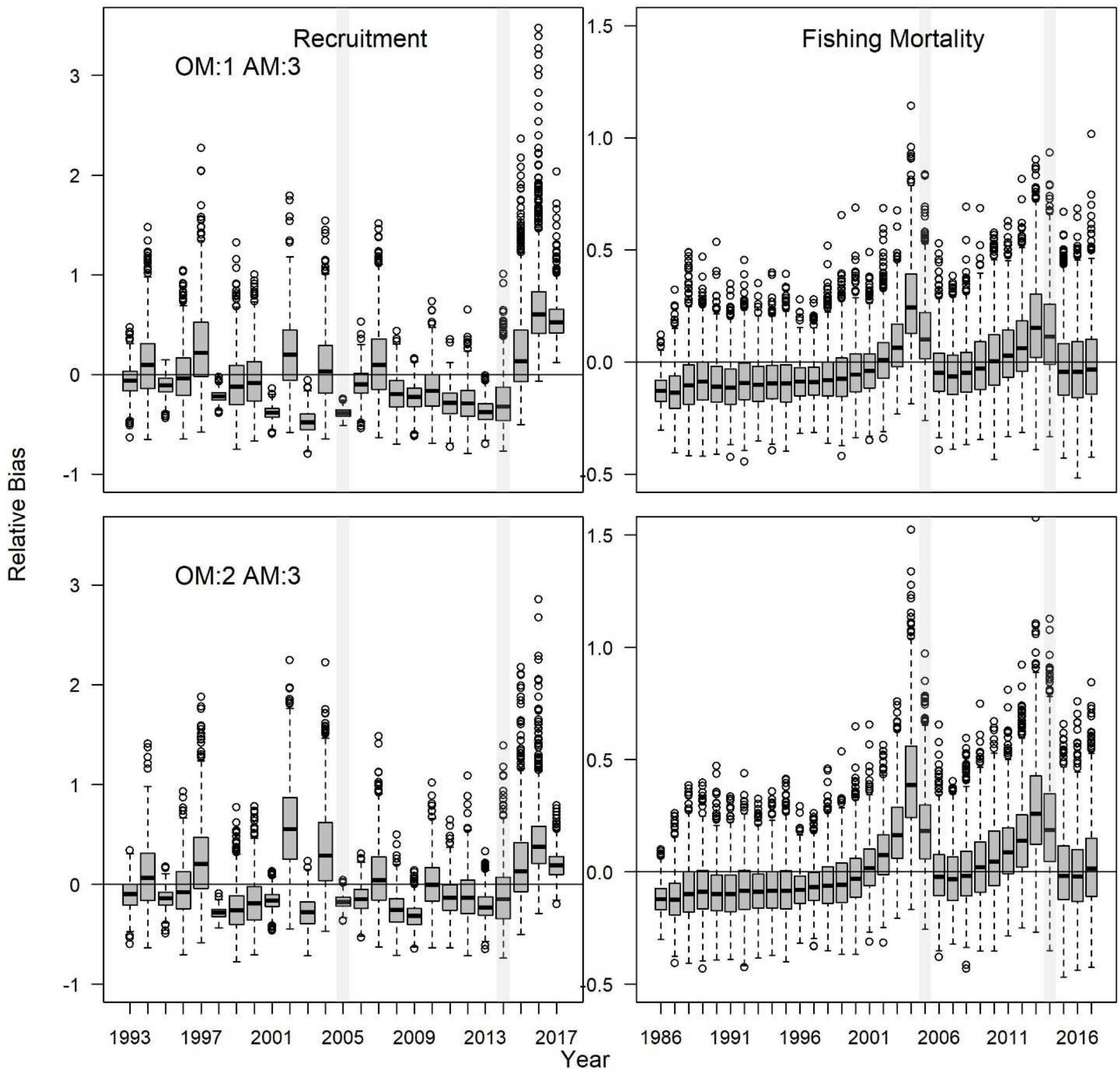

Fraction of biomass killed
OM:1 AM:4
Apical rate
OM:2 AM:4
Estimated Red Tide Mortality
Year
1986
1990
1994
1998
2002
2006
2010
2014

Fig. 8.



Recruitment
OM:1 AM:3
Fishing Mortality
OM:2 AM:3
Relative Bias
Year
1993
1997
2001
2005
2009
2013
2017
1986
1991
1996
2001
2006
2011
2016