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Enhancing single-species stock assessments with diverse ecosystem perspectives: a case study for Gulf of Mexico red grouper (*Epinephelus morio*) and red tides

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Abstract: Impacts of *Karenia brevis* red tide blooms have been an increasing cause of concern for fisheries management in the Gulf of Mexico (Gulf). The 2019 Gulf red grouper (*Epinephelus morio*) stock assessment was confronted with the challenges of quantifying and parameterizing red tides during both historical and projection time periods. Red tide mortality was estimated for each age class in the model solely in 2005 and 2014 during severe events. Given the considerable uncertainty surrounding the 2018 red tide and its substantial implications on the status of the population, several projection scenarios were evaluated. Under the assumption of no 2018 red tide mortality, near-term catches were projected to nearly double, a predicted outcome that appeared to be in contrast with recent record low catches and fishing industry perceptions of major stock depletion. In the event that the 2018 red tide caused mortality, but was not accounted for in projections, the recommended catch levels would lead to high probabilities of overfishing and potentially stock collapse. Collectively, these results highlight how consideration of uncertainty in projections can help avoid unintended consequences.

Résumé : Les impacts de marées rouges associées aux proliférations de *Karenia brevis* sont source d'inquiétudes croissantes pour les gestionnaires des pêches dans le golfe du Mexique. L'évaluation de 2019 du stock de mérous rouges (*Epinephelus morio*) dans le golfe s'est butée aux défis que constituent la quantification et la paramétrisation des marées rouges pour les périodes tant passées que futures projetées. La mortalité associée aux marées rouges a été estimée pour chaque classe d'âge dans le modèle uniquement pour 2005 et 2014 durant des épisodes de grande intensité. Étant donné l'incertitude considérable entourant la marée rouge de 2018 et ses répercussions importantes en ce qui concerne l'état de la population, plusieurs scénarios de projection ont été évalués. Dans l'hypothèse qu'il n'y aurait eu aucune mortalité associée à la marée rouge de 2018, il est projeté que les prises à court terme doubleraient presque, une prévision que semblent contredire des prises à leur plus bas enregistrées récemment et les perceptions, au sein de l'industrie de la pêche, d'un important appauvrissement du stock. Dans l'éventualité que la marée rouge de 2018 ait entraîné une mortalité, mais qu'elle n'ait pas été prise en considération dans les projections, les niveaux de prises recommandés se traduiraient en de fortes probabilités de surpêche et, potentiellement, l'effondrement du stock. Collectivement, ces résultats soulignent le fait que la considération de l'incertitude dans les projections peut aider à éviter des conséquences inattendues. [Traduit par la Rédaction]

Introduction

It is widely recognized that the environment influences fish populations — especially as overfishing is reduced — and calls to incorporate the environment as part of an ecosystem approach to fisheries management have increased over the last few decades (Pikitch et al. 2004; Link et al. 2020). Identifying environmental influences on population dynamics is not novel; fisheries oceanography has elucidated the spatial distribution of marine resources in relation to the biotic and abiotic environments for over a century (Hjort 1914; Hare 2014). What has generally hindered ecological considerations in fisheries stock assessments is a combination of appropriate modeling tools, data availability (i.e., long time series), and known mechanisms impacted by the environmental driver.

Stock assessment models are mathematical formulae that recreate historical population dynamics with the goal of projecting tactical scientific advice on stock status and providing fisheries managers with appropriate near-term catch levels. Integrated assessment models allow the incorporation of different factors and relationships within a traditional single-species stock assessment framework. For example, and contingent upon data availability, life history processes such as growth and natural mortality can be linked to external stressors (Maunder and Watters 2003; Methot et al. 2018). Some stock assessments may indirectly incorporate environmental or ecosystem stressors, for example through the consideration of habitat variables when standardizing abundance indices (Forrestal et al. 2019). As data collection improves and research elucidates the mechanisms being driven by environmental factors (e.g., Gulf of Maine northern shrimp (*Pandalus borealis*); Richards and Jacobson 2016), next-generation stock assessment models are expected to explicitly incorporate ecosystem, environmental, and socioeconomic drivers when developing tactical catch advice (Lynch et al. 2018). Routine incorporation of these drivers will lead to increased model complexity and may not necessarily improve assessment model fit, particularly since assessment models indirectly account for "environmental" influences through process uncertainty (Lynch et al. 2018).

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While progress has been made in terms of including ecosystem information within the stock assessment process (see review of over 200 US stock assessments in Marshall et al. (2019)), the majority of environmental or ecological interactions identified were not directly or quantitatively incorporated into the assessment. In reality, ecosystem drivers are infrequently implemented in tactical advice (Skern-Mauritzen et al. 2016) because (*i*) the use of environmental data can increase scientific uncertainty (King et al. 2015); (*ii*) of a lack of understanding regarding the actual mechanism driving the changes (Lynch et al. 2018); or (*iii*) hypothesized relationships can break down over time (e.g., wind stress and recruitment of Atlantic cod (*Gadus morhua*); Hare et al. 2015). Ideally, the benefit of including environmental factors must be weighed against the risk of incorrectly specifying the mechanism, potentially leading to inaccurate catch advice compared with the status quo of not including these factors. Yet, if highly influential factors are unaccounted for by an assessment model, biased derived outputs could misrepresent stock dynamics (Wilberg and Bence 2006; Deriso et al. 2008; Cao et al. 2017). Omissions of key processes, such as episodic mortality rates that act on the same scale as fishing mortality, could have unintended consequences on projections of future stock conditions and derived landings streams (Lynch et al. 2018). Sudden changes in the fishery or the environment that occur in the last years of the assessment or during the projection period may also cause management advice to fail.

As one of the most difficult ecological processes to characterize in stock assessments, natural mortality is frequently assumed constant over time (Deroba and Schueller 2013; Johnson et al. 2015). This parameter is often indirectly estimated using life history information such as maximum age or growth parameters (e.g., Then et al. 2015). In reality, natural mortality likely varies over time and age as a result of predation pressure (Fu and Quinn 2000; Gårdmark et al. 2012; Richards and Jacobson 2016) or environmental change (Jiao et al. 2012). Pulses in episodic natural mortality can arise from substantial alterations to ecosystem dynamics such as unfavorable environmental conditions (e.g., cold snaps; Matich and Heithaus 2012) or harmful biota (e.g., bacterial infections; Walter et al. 2007).

Episodic mortality events can also be attributed to harmful algal blooms, which occur worldwide and affect organisms ranging from primary producers to apex predators (Glibert et al. 2005). Red tide harmful algal blooms caused by the dinoflagellate *Karenia brevis* frequently occur throughout the Gulf of Mexico (hereinafter Gulf; Magaña et al. 2003), with particular intensity in the east on the West Florida Shelf (Vargo 2009). Brevetoxin, a neurotoxin produced and released by *K. brevis*, can cause extensive fish kills (Flaherty and Landsberg 2011) and near-extirpation of shallow-water (<40 m) reef biota (Smith 1975). Red tide events are hypothesized to be ichthyotoxic through absorption of brevetoxin across gill membranes (Abbott et al. 1975; Baden 1988), ingestion of toxic biota (Landsberg 2002), or, upon cell death and decomposition, creation of hypoxic or anoxic zones (Walter et al. 2013). Even after *K. brevis* cells drop below detection levels, brevetoxins can remain a source of toxicity and introduce a lag in natural mortality of affected fauna (Landsberg et al. 2009).

Understanding of mortality due to red tides primarily originates from reported beach sightings in the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute (FWRI)'s Fish Kill Database (Gray DiLeone and Ainsworth 2019). While blooms can impact offshore species, mortality events may go unnoticed or underestimated if dead fish sink to the bottom (Steidinger and Ingle 1972). Shallow-water groupers, including Atlantic goliath grouper (*Epinephelus itajara*), red grouper (*Epinephelus morio*), gag grouper (*Mycteroperca microlepis*), and scamp (*Mycteroperca phenax*), were documented within fish kills in 1971 in the eastern Gulf (Smith 1975). Red grouper were observed within fish kills during National Marine Fisheries Service's (NMFS) surveys in 2005 (Walter et al. 2013) and 2014 (Walter et al. 2015; Driggers et al. 2016). More recently, dead groupers during the 2018 red tide dominated social media posts and news programs.

Originally motivated by stakeholder concerns over the impacts of red tides on reef fishes, red tide mortality in 2005 has been included in stock assessments for Gulf gag and red grouper since the late 2000s (SEDAR 2009*a*, 2009*b*). The most recent Gulf red grouper assessment was faced with new challenges of parameterizing multiple red tide events, in both the historical (1986–2017) and projection periods (2018+), as well as addressing growing concerns due to recent record-low landings and unmet quotas (Fig. 1). We first investigate the benefits of incorporating red tide mortality into the historical period modeled and briefly review data streams used to identify years with severe red tide events. We discuss how stakeholder insights contributed to the development of potential red tide scenarios for 2018, the first projection year, in light of the considerable uncertainty surrounding the 2018 red tide event ongoing at the time of the assessment. Owing to the lack of quantitative data on the severity of the 2018 red tide event, results from the projection scenarios were presented as a decision table (Punt 2017) to illustrate how uncertainty surrounding the 2018 red tide event and its impact on the Gulf red grouper stock could affect projected catch advice. The projection scenarios revealed a clear trade-off between projected catch and population size that must be considered by fisheries managers. These results emphasize the benefits of including ecological considerations in the management process and highlight a situation where status quo management (i.e., implementing catch advice without considering environmental stressors) could have led to stock depletion.

Materials and methods

Modeling approach

A forward-projecting statistical catch-at-age model was used to model the population dynamics of Gulf red grouper using Stock Synthesis (Methot and Wetzel 2013; Methot et al. 2018). Within Stock Synthesis, projections are implemented starting from the year after the final year of data of the assessment utilizing the same population dynamics equations and modeling assumptions while holding constant the fishery dynamics (e.g., allocation of catch among fleets, selectivity, and retention) from the most recent years. Derived quantities are produced including full time series of recruitment, abundance, biomass, spawning stock biomass (SSB), and fishing mortality rates, with uncertainty estimated from the model fit to observed data (Methot and Wetzel 2013). Observed data for three commercial (longline, vertical line, and trap) and one recreational fishing fleet included landings (with age compositions), discards (with length compositions if available), and catch-per-unit-effort indices of relative abundance. Relative abundance and size data from four fishery-independent surveys were also included. Specific details on data inputs and model configuration of the Gulf red grouper stock assessment are discussed in the online Supplementary Material[1] and in the full stock assessment report (SEDAR 2019).

Estimating red tide mortality

Within Stock Synthesis, episodic natural mortality due to red tide impacts is treated most precisely by modeling the red tide as a "fishing fleet" with catch that results in 100% discard mortality (i.e., the "catch" does not contribute to the landings, and all "captured" fish die; Table 1). A more straightforward way to treat red tide mortality would seemingly be to link the impacts directly to natural mortality; however, this approach is disadvantageous as

[1]Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2020-0257.

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Fig. 1. Commercial and recreational landings (dashed lines) and quotas (solid lines) for Gulf red grouper. Vertical red bars in top panels identify years where severe red tide events occurred. Gray bars in lower panels represent the percentage of quota landed, with the horizontal red line indicative of quota closures. Commercial data from 2010 through 2019 were obtained from the individual fishery quota database accessed 4 December 2019 (https://portal.southeast.fisheries.noaa.gov/reports/cs/CommercialQuotasCatchAllowanceTable.pdf); remaining years were obtained from the Gulf of Mexico Historical Commercial Landings and Annual Catch Limit Monitoring (https://www.fisheries.noaa.gov/southeast/gulf-mexico-historical-commercial-landings-and-annual-catch-limit-monitoring; updated 7 November 2018). Recreational data from 2010 through 2017 were obtained from recreational historical landings (https://www.fisheries.noaa.gov/southeast/recreational-fishing-data/gulf-mexico-historical-recreational-landings-and-annual-catch; updated 9 March 2019), and data from 2018 and 2019 (through June) were obtained 4 December 2019 from https://www.fisheries.noaa.gov/southeast/2018-and-2019-gulf-mexico-recreational-landings-and-annual-catch-limits-acls-and-annual. [Colour online.]

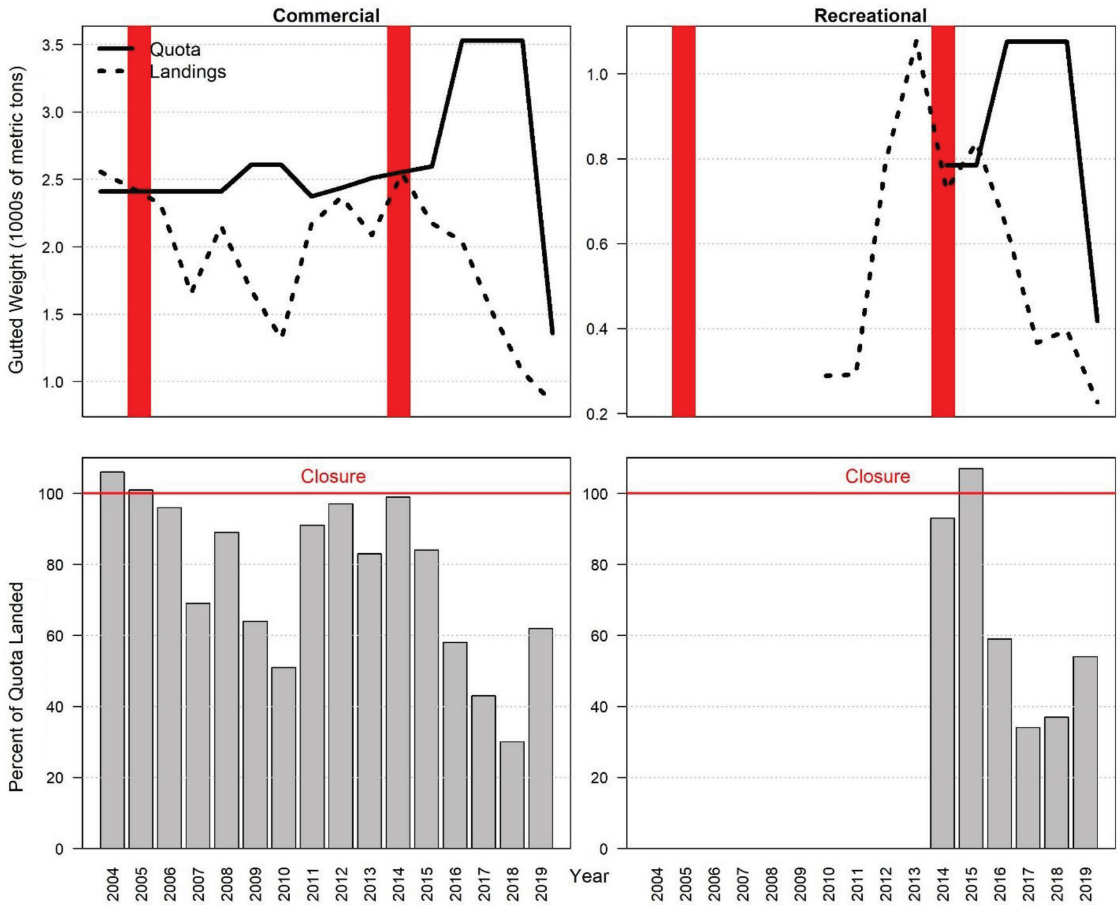


Table 1. Equations within Stock Synthesis for estimating mortalities due to fishing and red tide.

Derived quantity	Equation
Directed fishing mortality ($\mathbf{F}_{\mathrm{Dir}}$) by fishing fleet	$\mathbf{F}^{\mathrm{Fleet}}_{\mathrm{Dir,Age,Year}} = \boldsymbol{S}^{\mathrm{Fleet}}_{\mathrm{Dir,Age}} \boldsymbol{F}^{\mathrm{Fleet}}_{\mathrm{Dir\_Mult,Year}} \mathbf{Ret}^{\mathrm{Fleet}}_{\mathrm{Dir,Age,Year}}$
Directed discard fishing mortality $\mathbf{F}_{\mathrm{Disc}}$) by fishing fleet	$\mathbf{F}^{\mathrm{Fleet}}_{\mathrm{Disc,Age,Year}} = \boldsymbol{F}^{\mathrm{Fleet}}_{\mathrm{Dir\_Mult,Year}} \left(1 - \mathbf{Ret}^{\mathrm{Fleet}}_{\mathrm{Dir,Age,Year}}\right) \mathrm{DM}^{\mathrm{Fleet}}_{\mathrm{Dir}}$
Total directed fishing mortality ($\mathbf{F}_{\mathrm{Tot\_Dir}}$) by fishing fleet	$\mathbf{F}^{\mathrm{Fleet}}_{\mathrm{Tot\_Dir,Age,Year}} = \mathbf{F}^{\mathrm{Fleet}}_{\mathrm{Dir,Age,Year}} + \mathbf{F}^{\mathrm{Fleet}}_{\mathrm{Disc,Age,Year}}$
Red tide mortality ($\mathbf{F}_{\mathrm{RT}}$)	$\mathbf{F}_{\mathrm{RT,Age,Year}} = \boldsymbol{S}_{\mathrm{RT,Age}} \boldsymbol{F}_{\mathrm{RT\_Mult,Year}}$
Total fishing and red tide mortality ($\mathbf{F}_{\mathrm{Tot}}$)	$\mathbf{F}_{\mathrm{Tot,Age,Year}} = \sum_{\mathrm{Fleet}} \mathbf{F}^{\mathrm{Fleet}}_{\mathrm{Tot\_Dir,Age,Year}} + \mathbf{F}_{\mathrm{RT,Age,Year}}$

Note: S = selectivity, Ret = retention, DM = discard mortality, Mult = multiplier. All other equations for Stock Synthesis provided in Methot and Wetzel (2013).

it requires definition of a continuous time series of red tide mortality (i.e., an independent statistical estimate of the natural mortality due to red tide each year). Treating red tide mortality as a 100% discard fishing fleet is a more statistically robust way of estimating the environmental effect, given the available information, as it requires only specification of the years where the stock is thought to be substantially impacted by red tide mortality. The integrated assessment model is then allowed to estimate the actual rate of the mortality from the red tide based on data sources already in the model (e.g., indices of abundance, changes in annual age compositions). The selection of this method for incorporating red tide mortality, and determination that there was sufficient contrast in the data to allow independent estimation of the red tide mortality rate, was based on substantial research tied to prior stock assessments (e.g., SEDAR 2015). Owing to the lack of data on age-specific (or size-specific) red tide mortality, the impact of red tide was assumed equal across age (and size) classes. Years where red tide mortality was allowed to be estimated within the stock assessment model were identified from a combination of quantitative and qualitative data sources discussed below. To illustrate the differences in model outcomes solely due to the inclusion of red tide mortality in the base assessment model, we conducted a sensitivity run that excluded red tide mortality.

Quantitative data sources for parameterizing red tide mortality

Red tide blooms are monitored by FWRI, but sampling is done opportunistically and largely in response to existing blooms; thus, the data cannot be used alone to quantify red tide severity (Christman and Young 2006). The 2015 Gulf red grouper assessment included red tide mortality in 2005 based on an index of red tide severity derived from sea-viewing wide field-of-view sensor (SeaWiFS) satellite data and FWRI cell count data from 1998 through 2010 (Walter et al. 2013; SEDAR 2015). Attempts to extend this index for the current evaluation (i.e., through 2017) were complicated by two factors: (*i*) difficulty in calibrating between SeaWiFS and moderate resolution imaging spectroradiometer (MODIS) satellite data (Sagarese et al. 2018) and (*ii*) uncertainty surrounding whether total grouper mortality is linearly related to red tide cell densities. Another quantitative index of red tide mortality suggested that the 2005 red tide bloom severely affected grouper populations while also suggesting that more recent blooms (e.g., 2014) had a lesser impact (Chagaris and Sinnickson 2018). Ultimately, caveats and uncertainties associated with these quantitative measures of red tide severity precluded the incorporation of these continuous indices within the assessment model (SEDAR 2019), and necessitated an alternative approach.

Qualitative data sources for parameterizing red tide mortality

Stakeholder insights and observations from the fishing grounds collected via two independent efforts played a key role in (*i*) supporting estimation of mortality of groupers due to red tides in 2005 and 2014 and (*ii*) assisting with parameterizing the potential impacts of recent red tide events on the red grouper stock. A voluntary online data collection tool hosted by the Gulf of Mexico Fishery Management Council provided general information on whether respondents had observed groupers in suspected red tide fish kills (no specific questions were asked; Fig. 2). In response to concerns about the 2018 red tide event raised by stakeholders, an initiative was put into place by the Southeast Fisheries Science Center to systematically explore fisher perspectives regarding red tides using an oral history interview process detailed in Karnauskas et al. (2019). In brief, key informants with extensive fishing experience in the eastern Gulf were asked to recall major red tide events that they had encountered in their careers and were directed to describe biological, social, and economic impacts of these events. Oral history interviews were recorded and qualitative or quantitative information was extracted from each described event (when available) regarding the red tide severity, temporal extent of the event, ecosystem recovery time, and species killed (Karnauskas et al. 2019). The independent descriptions of each red tide event were then compiled into a database, such that the most recent 2018 event could be compared with past events in terms of its relative severity, spatial and temporal extent, and the species impacted. Because we had a semiquantitative basis for comparison (e.g., the percentage of fishers rating a red tide event as "extreme" versus "major"), we could then use the oral history data to develop projection scenarios, which are described below.

Projecting catch advice in the face of uncertain red tide events

Since no quantitative data on the severity of the 2018 red tide event was available during assessment development, five potential levels of suspected red tide mortality in 2018 were developed using a combination of observations from stakeholders to gauge severity and historical estimates of red tide mortality in 2005 and 2014 derived from the assessment model (Table 2). For added insight into how the frequency and occurrence of red tide events could impact projected dynamics in the near term (i.e., 5 years), additional projections were run that looked at (*i*) two consecutive red tides occurring in 2018 and 2019 that were similar in magnitude to 2005; (*ii*) background levels of 0.05 and 0.1 red tide mortality for each year between 2018 and 2022; and (*iii*) a 2005 red tide event occurring in 4 years (i.e., 2018 and 2022). The potential impact of these scenarios on sustainable catch levels and stock status was explored using two approaches: (1) calculating the impact of red tide on optimal overfishing limits in the case that the true magnitude of the mortality event was known and (2) quantifying the consequences of fishing at different fixed catch levels assuming the magnitude of the mortality event was unknown.

The first approach was to calculate the annual catches that represented a constant fishing mortality rate in each year that achieved a spawning potential ratio (SPR) target of 30% at equilibrium. Since steepness was fixed at essentially 1.0, the projections assumed that forecasted recruitment would continue at recent average levels (2010–2017, 17.4 million fish). Recent fishery dynamics were carried forward throughout the projection period, including the following: (*i*) allocations, where 76% and 24% of the landings quota are assigned to the commercial and recreational fisheries, respectively, and (*ii*) constant selectivity and retention equal to 2017. Commercial and recreational landings in 2018 and 2019 were based on final landings estimates and assumptions (e.g., removing allowable catch), respectively. Red tide mortality was input as fixed values in the appropriate years based on the scenarios described above. This represents the best practices approach that would be implemented in the case that red tide was known and acts as a baseline. The second approach evaluated the consequences of not accounting for the red tide event for two fixed catch scenarios: (1) implementing fixed catches at a static level equal to the catch achieved in 2017, which was one of the lowest on record and defined the 2019 annual catch limit (GMFMC 2019) or (2) implementing fixed catches at the levels estimated to achieve a 30% SPR target under an assumption of no red tide mortality in 2018.

The results of each of the scenarios described above are quantified through three metrics: (*i*) the average probability of overfishing during the first 5 years of the projection (2020–2024); (*ii*) the average probability of being overfished during the same 5 years; and (*iii*) the probability of stock collapse by 2024. The probability of overfishing in each year was determined by calculating the projected catch probability densities if fished at $F_{SPR30\%}$ in a given year, accounting for uncertainty in population size and scenario specific target catch in previous years, and then summing up the area under each curve that was less than the scenario-specific target catch for that year. The probability of being overfished was determined by summing up the area under the probability density function of SSB for each red tide scenario that fell below the minimum stock size threshold (50% of the SSB when achieving 30% SPR in equilibrium). The probability of collapse by 2024, defined as dropping below 5% of unfished SSB, was determined by summing up the area under each probability density function of the SSB ratio (SSB divided by unfished SSB) for each red tide scenario.

Results

Exclusion versus inclusion of red tide mortality

In the absence of red tide mortality as an explanation for sudden decreases in abundance, the assessment model estimated

Fig. 2. Summary of findings from the Gulf of Mexico Fishery Management Council's voluntary online data collection tool "Something's Fishy with Red Grouper". The number of respondents are given (A) by sector; (B) by location (NMFS Shrimp Statistical Zones); (C) that observed red grouper in suspected red tide fish kills by location; and (D) by the type of response, where negative refers to concerns over reduced abundance and positive refers to optimism (e.g., seeing lots of sublegal red grouper). Note that results characterize broad conclusions and not a specific year. [Colour online.]

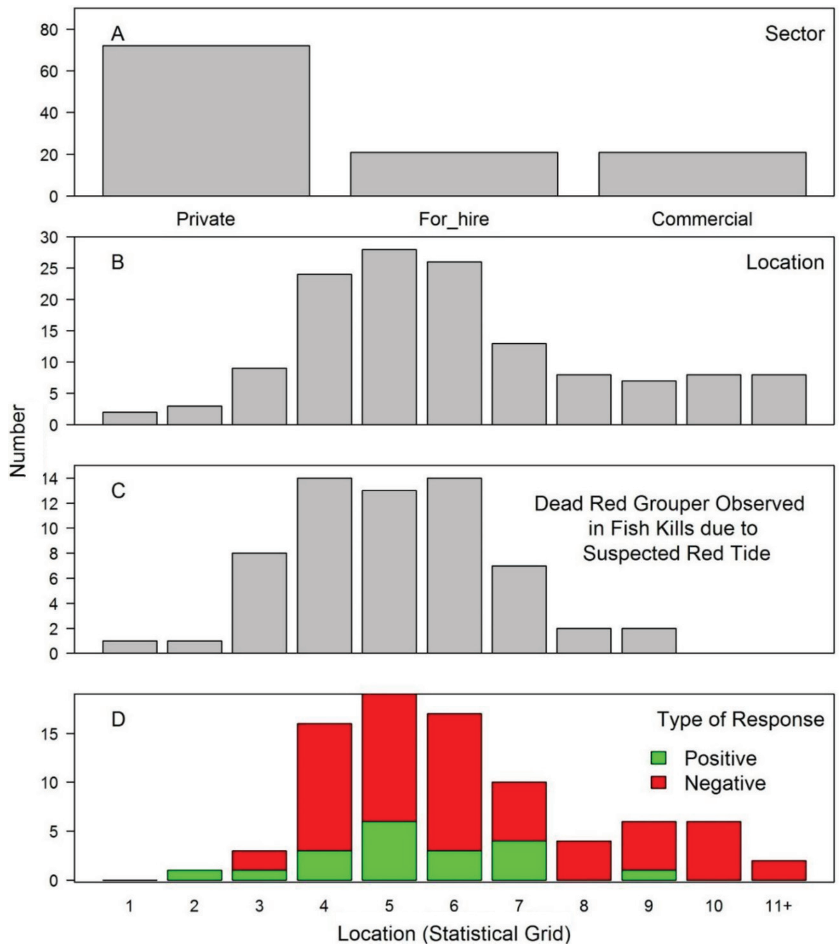
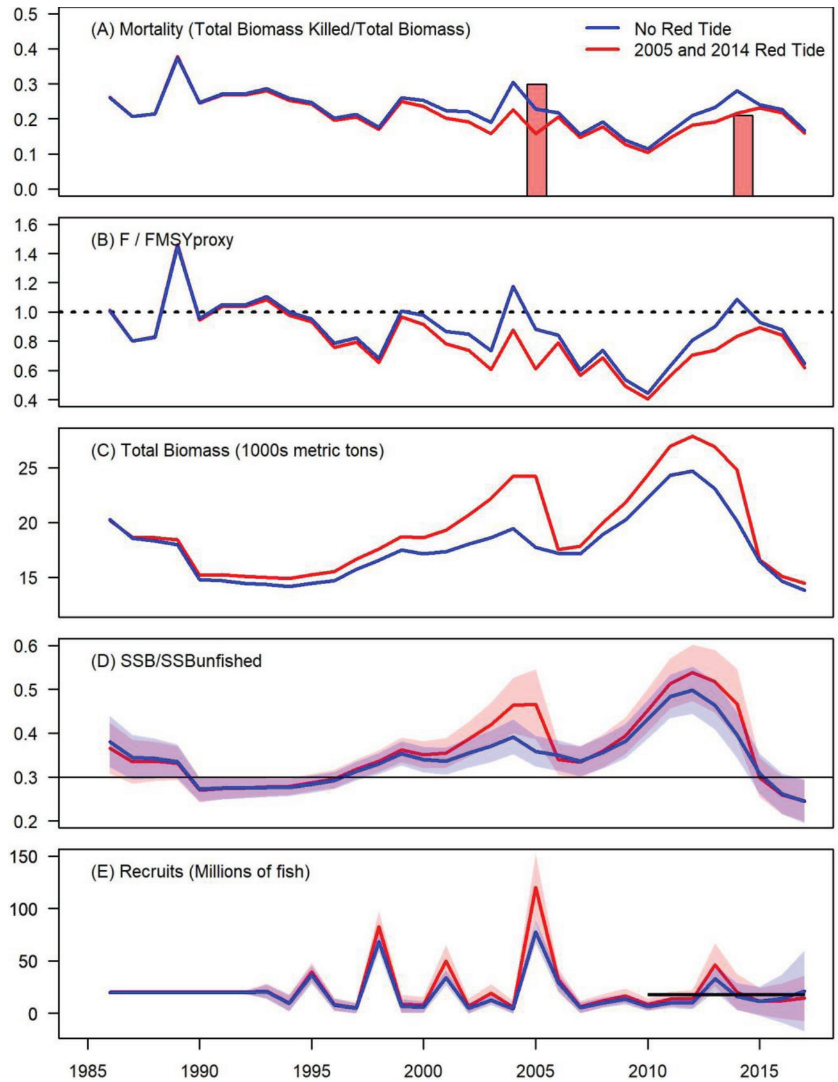


Table 2. Development of red tide severity scenarios assumed in the projection period for Gulf red grouper.

2018 red tide mortality scenario	Red tide severity	Justification	Assumed impact on population
None	None	• Status quo approach lacking ecosystem considerations	Not affected
Half 2014	Low	• Minor impact • Some stakeholders reported fewer groupers in fish kills during 2018 when compared with 2005 and 2014	Half the 2014 estimate of red tide mortality
2014	Medium	• Moderate impact • Some stakeholders reported moderate impact on groupers similar to 2014	Equivalent to 2014 estimate of red tide mortality
2005	High	• Major impact • Many stakeholders reported major impacts on groupers similar to 2005	Equivalent to 2005 estimate of red tide mortality
Double 2005	Extreme	• Severe impact • Many stakeholders identified 2018 as devastating, worse than 2005, and lasting longer than previous events	Double the 2005 estimate of red tide mortality

Note: Assumed red tide mortalities for use in projections were based on historical red tide mortality estimates derived from the assessment model (see Table 3). Stakeholder details provided in Karnauskas et al. (2019).

Fig. 3. Comparison of (A) mortality (lines encompass landings plus dead discards from all fisheries; bars reflect red tide mortality estimates (biomass killed by red tides/total biomass)); (B) ratio of F to $F_{SPR30\%}$ (FMSY proxy), where points above the horizontal dashed line indicate overfishing; (C) total biomass; (D) spawning stock biomass (SSB) ratio (horizontal line reflects target of 30%); and (E) recruitment (horizontal line between 2010 and 2017 highlights recent mean recruitment used in projections). [Colour online.]



higher fishing mortality rates (i.e., biomass killed divided by the total biomass) during those years with severe red tides and adjacent years (Fig. 3A). In particular, excluding red tide mortality led to an overfishing status in 2004 and 2014 (Fig. 3B). Prominent declines in total biomass, SSB, and the SSB ratio occurred when red tide mortality was estimated in 2005 and 2014 (Figs. 3C and 3D). Estimated red tide mortalities corresponded to dead biomass totaling 29.5% and 21.3% of the population in 2005 and 2014, respectively (Table 3; Fig. 3A). For context, the biomass killed by red tide compared with all the fisheries combined (landings and dead discards) was roughly 65% and 50% for 2005 and 2014, respectively. Excluding red tide mortality in the assessment model generally led to lower peak recruitment estimates and less uncertainty, except for the most recent years where greater uncertainty in recruitment was evident (Fig. 3E).

Overall, model performance was relatively similar between model runs including and excluding red tide mortality, although the no red tide model exhibited more parameter correlations exceeding 0.7 and a few additional recruitment deviations with coefficients of variation (CVs) exceeding 1 (Table 3). Parameters estimated in the no red tide model were generally within 5% of the base model estimates (Table 3). Additional years (e.g., 2015) and combinations of years where red tide mortality was estimated were explored as sensitivity runs during the assessment, with higher uncertainty (CV > 1) evident in red tide mortality estimates when estimating red tide mortality in consecutive years (i.e., 2014 and 2015; SEDAR 2019).

The most notable benefit of including red tide mortality in the historical period of the stock assessment was lower root mean squared error (RMSE) values, implying better fits for most indices (Fig. 4). Relative abundance trends within most indices increased until 2005, after which substantial single-year declines in observed indices, commensurate with a mortality event, were exhibited. Similar declines in observed abundance occurred following 2014, although abundance has remained low. The estimation of red tide mortality in 2005 and 2014 allowed the model to explain the large drops in relative abundance, with lower RMSE values for all indices except the Marine Recreational Information Program Charter-Private index (Fig. 4). While improved fits to indices of adult red grouper (notably commercial vertical line, commercial longline, combined video index, and bottom longline survey) were revealed, stock size and fishing mortality in the last year of the assessment

Table 3. Comparison of model performance and key parameter estimates for Gulf red grouper assessment models estimating red tide mortality (Base) and not estimating red tide mortality.

Metric	Base	No red tide
Model performance		
Negative log-likelihood	537.486	544.366
Gradient	1.05E-04	3.92E-05
No. of estimated parameters (bounded)	178 (0)	176 (0)
Correlations exceeding 0.7 (0.95)	6 (0)	8 (0)
Parameters with CVs exceeding 1	8 (recruitment deviations)	10 (recruitment deviations)
Parameter estimates (with CV)		
Recruitment variability (sigmaR)	0.815 (0.137)	1.017 (0.112)
Virgin recruitment, or equilibrium recruitment in the absence of fishing (ln(R0))	9.925 (0.004)	9.882 (0.003)
Unfished SSB (relative eggs)	2 494 130 (0.035)	2 388 350 (0.033)
2017 SSB (relative eggs)	613 517 (0.103)	583 381 (0.106)
2017 SSB ratio	0.246 (0.099)	0.244 (0.104)
2017 fishing mortality	0.160 (0.140)	0.167 (0.142)
Virgin recruitment (1000s of fish)	20 443 (0.035)	19 576 (0.033)
2005 red tide mortality	0.339 (0.309)	—
2005 percentage of biomass killed by red tide	29.5%	—
2014 red tide mortality	0.257 (0.429)	—
2014 percentage of biomass killed by red tide	21.3%	—

remained similar (Fig. 3), suggesting little impact of these historical red tides on projected catch advice because they did not occur towards the end of the time series.

Projecting catch advice in the face of uncertain red tide events

Severity of 2018 red tide

When assuming no red tide mortality in 2018, projected landings were expected to peak in 2020 around 4000 metric tons (t) before declining and leveling off after 2035, with the SSB ratio projected to exceed the target of 0.3 in 2020 but decline thereafter (Fig. 5A). This spike in projected landings and SSB ratio was a combination of the relatively strong recruitment event that occurred in 2013 and the projection specification of fishing at the rate that achieves an SPR of 30% in equilibrium (0.258), which was much larger than recent fishing mortality rates for each fleet. The assumed level of red tide mortality in 2018 had a large impact on projected landings, with increased severity of red tide mortality resulting in lower near-term projected landings (Fig. 5A). For the worst-case scenario, which assumed the 2018 red tide event was twice as severe as the 2005 event, the SSB ratio was predicted to drop below the minimum stock size threshold (50% of the SSB when achieving 30% SPR in equilibrium) between 2020 and 2024, triggering an overfished status (Fig. 5A). The remaining scenarios of 2018 red tide severity did not reveal the same concerning drops, although the SSB ratios remain below the target level of 0.3 until after 2035. Similar changes were noted across the different red tide scenarios when maintaining 2017 catch levels, as the most severe red tide scenario (double 2005) was projected to drive the stock into an overfished state (Fig. 5B).

Frequency and occurrence of red tide events

Results for the two consecutive severe red tide events occurring in 2018 and 2019 were similar to the results above assuming double 2005 red tide mortality in 2018. Projected equilibrium landings were much reduced in the near term, averaging just under 1800 t, as the stock was depleted into an overfished state (Fig. 5A). Even maintaining current catch at 2017 levels would lead to an overfished state (Fig. 5B). Assuming low background levels of red tide mortality in the first 5 years of the projections, which could remove the need to quantify the severity of the 2018 red tide, resulted in reductions in projected landings and SSB ratio estimates for the equilibrium projection (Fig. 5A). Assuming annual red tide mortality of 0.1 between 2018 and 2022 led to the SSB ratio approaching the minimum stock size threshold in 2023 (Fig. 5A). When maintaining landings at the 2017 catch level in the projections, the stock remained just below the target of 0.3 under background levels of 0.05 red tide mortality between 2018 and 2022, whereas a background level of 0.1 led to reduced SSB ratios (Fig. 5B). In the event of severe red tides similar to 2005 occurring in 2018 and in 2022, the stock was projected to drop into an overfished state in 2024 and 2025 (Fig. 5A) but remain just above this threshold when maintaining landings at 2017 catch levels (Fig. 5B).

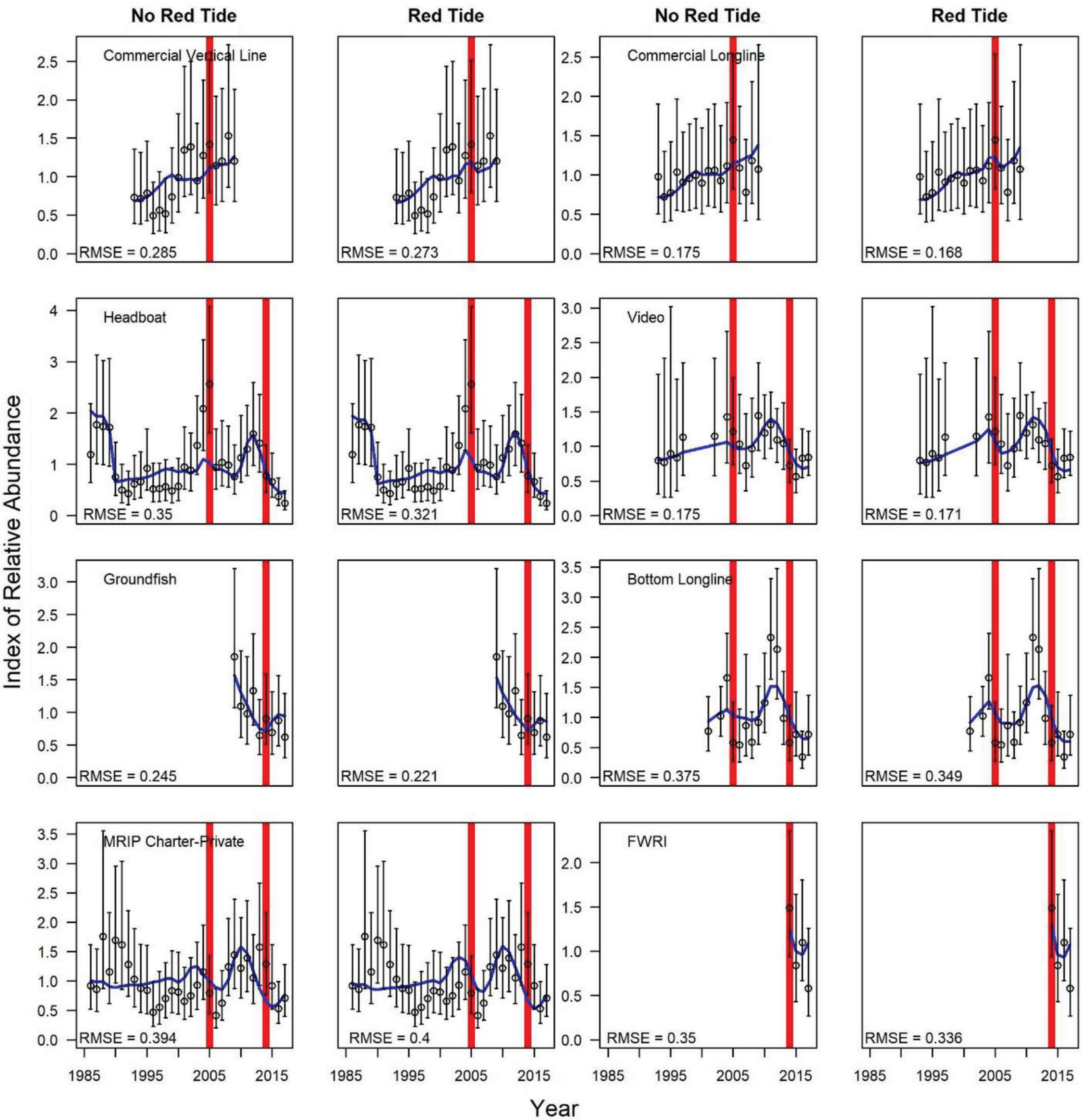
Guidance for developing catch advice for management

In the event of a minor to a very severe red tide occurring in 2018, the probability of overfishing was predicted to greatly exceed 50% if the overfishing limit was set assuming no red tide mortality in 2018 (Table 4). In other words, if management was based on an incorrect assumption of zero red tide mortality in 2018, the resulting catch advice averaging 3500 t between 2020 and 2024 would result in overfishing if in fact a major red tide event did occur in 2018. If the landings projected by the no 2018 red tide scenario were implemented for management advice starting in 2020, by 2024 there would be at least a 20% probability of collapse if the 2018 red tide was similar to 2005 or more severe (Table 4). Further, the SSB ratio would approach zero (i.e., population collapse) within 15 years for all scenarios if a moderate to severe red tide event occurred (Fig. 5C). A minor to very severe red tide occurring in 2018 would also result in relatively higher probabilities of overfishing (85%–100%) and of being overfished (7%–100%; Table 4). With the exception of the worst-case scenario (double 2005), the probabilities of overfishing and of being overfished were predicted to remain well below 50% if the 2017 catch levels were maintained in the short term (Table 4). This finding supports the 2019 change in the red grouper annual catch limit (GMFMC 2019).

Discussion

This case study demonstrated the importance of considering ecological processes when recreating historical trends in population dynamics as well as when projecting future conditions for the determination of tactical catch advice. Given that baseline levels of red tide mortality are likely already accounted for in natural mortality estimates derived from maximum age and input

Fig. 4. Model fits to indices of abundance both without and with red tide mortality estimated in 2005 and 2014 (years identified by vertical red bars). Blue line reflects the expected index, dots reflect observed index values, and vertical lines reflect lower and upper bounds for each annual index observation. Note that *y* axes differ among panels. MRIP, Marine Recreational Information Program; FWRI, Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute. [Colour online.]



into the assessment model, red tide mortality was incorporated solely in years warranting extra episodic mortality due to severe red tides. In this instance, if projected landings did not account for any red tide mortality in 2018, the implementation of the Gulf of Mexico Fishery Management Council's Acceptable Biological Catch Control Rule (GMFMC 2011) would have recommended an increase in allowable catch from about 1800 t (GMFMC 2019) up to ∼3500 t for each year between 2020 and 2024. This increase would have been highly controversial given the record low landings in the last few years (Fig. 1) and perception of low stock abundance by stakeholders (Fig. 2). The potential for severe red tide events occurring in the future, as well as the proposed increase in both frequency and intensity (Moore et al. 2008), introduces considerable uncertainty when projecting population trajectories in the short term. For this reason, a decision table of potential risks associated with catch levels across red tide severity scenarios accompanied the stock assessment and ultimately enabled fishery managers to consider the uncertainty associated

Fig. 5. Projected landings (left panels) and resulting SSB ratios (right panels) across red tide projection scenarios: (A) achieving 30% spawning potential ratio (SPR) in equilibrium, (B) maintaining 2017 catch levels, and (C) removing the projected catches from achieving 30% SPR in equilibrium while assuming no effect of the 2018 red tide event (red line in panel A). [Colour online.]

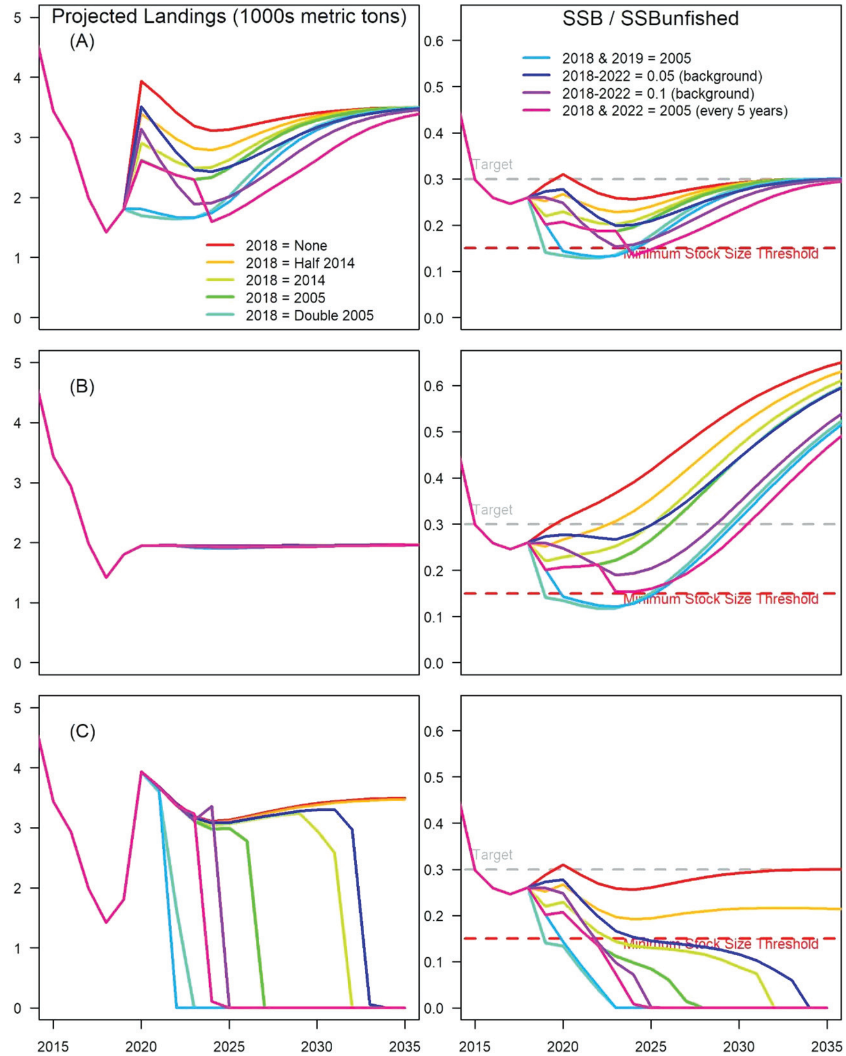


Table 4. Estimated probabilities of overfishing, of being overfished, and of stock collapse for Gulf red grouper under projection scenarios.

	Assumption about 2018 red tide mortality				
Scenario	None	Half 2014	2014	2005	Double 2005
Probability of overfishing					
Equilibrium	0.50	0.50	0.50	0.50	0.50
Maintain 2017 landings	0.00	0.01	0.05	0.11	0.83
Remove equilibrium landings assuming no effect of 2018 red tide	0.50	0.85	0.99	1.00	1.00
Probability of being overfished					
Equilibrium	0	0	0.02	0.05	0.78
Maintain 2017 landings	0	0.001	0.01	0.04	0.83
Remove equilibrium landings assuming no effect of 2018 red tide	0.01	0.07	0.30	0.56	1.00
Probability of being collapsed by 2024					
Equilibrium	0	0	0	0	0
Maintain 2017 landings	0	0	0	0	0.01
Remove equilibrium landings assuming no effect of 2018 red tide	0	0.01	0.05	0.20	1.00

Note: Equilibrium is defined as achieving an SPR of 30%.

with the 2018 red tide event when setting catch levels by evaluating the probability of overfishing across scenarios. As highlighted by this analysis, if a severe 2018 red tide event occurred but was not considered when setting management advice, this decision could have led to the collapse of the stock.

While growing evidence suggests that red tides are a key environmental stressor for red grouper and other West Florida Shelf reef fish (Driggers et al. 2016; Gray DiLeone and Ainsworth 2019), major sources of uncertainty remain. Presently, red tide mortality is assumed to impact all age classes equally, including age-0 red grouper. High mortality for age-0 red grouper in 2005 was supported by spatial overlap between the distributions of age-0 red grouper and red tide presence described in Chagaris and Sinnickson (2018), although age-0 red grouper are infrequently encountered by fishery-independent surveys (SEDAR 2015). Collection of specimens during red tide events would allow for the species composition and size and age selectivity of mortality to be determined and possibly (although unlikely) allow for some minimum estimates of total mortality. Following the 2014 red tide in the Big Bend region, the NMFS Panama City laboratory collected 16 red grouper between 5 and 9 years old from fish kills (Walter et al. 2015). However, obtaining samples from fish kills is extremely difficult due to rapid decomposition of specimens and human health hazards (Driggers et al. 2016). Understanding how red tides affect offshore fishes is highly complex, owing to a lack of understanding of how red tide is distributed throughout the water column (i.e., at depth) and how offshore species may respond. The majority of studies on red tides focus on surface areas due to data availability (i.e., satellite data; e.g., Stumpf et al. 2003). The fact that blooms can start at depth (Steidinger and Vargo 1988), combined with the sinking or consumption by predators of affected fish (Steidinger and Ingle 1972), highlights the need for further research to track these events at depth and determine potential impacts on offshore species, benthic habitats, and ecosystem trophic structure. It is possible that fish may vacate affected regions and return after the bloom subsides (Dupont et al. 2010), a hypothesis that could be addressed by acoustic tracking studies or visual censuses of affected and surrounding reefs via remotely operated vehicles. After noting a lack of regular inhabitants at reefs (e.g., groupers) following the 1971 red tide, recreational divers off Florida documented return of fishes a month later (Steidinger and Ingle 1972), supporting the hypothesis that some fish redistribute spatially in response to red tides. Increased stakeholder participation, for example, through cooperative research collections made by fishers (e.g., the Florida Commercial Watermen's Conservation; www.floridawatermen.org), will greatly improve our ability to track the evolution and spatial distribution of these events and provide further observations of impacted offshore species of economic and ecological importance.

Operationalizing ecosystem considerations within the stock assessment process can greatly increase the amount of time and resources needed to evaluate and maintain required data inputs. While quantitative indices of red tide severity were considered during the assessment (Sagarese et al. 2018; Chagaris and Sinnickson 2018), additional research was recommended to further refine each approach. Research is currently ongoing, first, to process MODIS data for use in developing the red tide index, and, second, to refine the methodology used to develop the index. Even with an updated spatiotemporally explicit index of red tide severity, however, it is not clear whether FWRI cell counts of *Karenia brevis* correlate with bloom toxicity and how red tides cause mortality of groupers. Other stressors associated with red tide, such as hypoxia, may also cause mortality; for example, a recent laboratory study of stone crabs (*Menippe mercenaria*) found that several days of exposure to hypoxia caused just as much mortality as exposure to hypoxia and brevetoxin combined (Gravinese et al. 2020). Furthermore, red tide impacts many different components of the ecosystem, and because of trophic interactions there may be indirect effects on the survival of red grouper. Insights from the oral history interviews point to other ways that red tide may affect the population, which potentially confound the estimation of red tide mortality within the stock assessment. For example, some interviewees observed that fish move out of areas most heavily impacted by red tide, congregating along the edges of these zones and making them easier to target by spearfishing for a period of time. Another widely reported perspective was that severe red tide events cause mortality to benthic organisms, degrading the habitat on which grouper depend and delaying their return to some areas. Although these processes are likely limited to small spatial scales and may not be applicable to or detectable at the population level, there remains the potential for confounding effects from changes in catchability, recruitment, and mortality as they relate to red tide events.

Additional research refining the spatial distributions of red tides for ecosystem models could allow an ecosystem-level evaluation of how red tides affect the movement and population dynamics of red grouper, their prey base, and other species (e.g., Gray DiLeone and Ainsworth 2019). Recent advancements in spatial modeling have enhanced understanding of the ontogenetic spatial distribution of both Gulf gag and red grouper (Grüss et al. 2017). Efforts are currently underway to modify how species respond to red tide events over space within the Ecopath with Ecosim and Ecospace modeling platform (Pauly et al. 2000) to advance ecosystem modeling in the Gulf (Chagaris and Sinnickson 2018). In addition, an exploration of vessel monitoring system data could address whether fishing effort is shifting to unaffected regions during red tide events and also be used to understand whether increased catchability just outside red tide areas is a frequent and widespread phenomenon. Increased understanding of the suite of impacts of red tide on various aspects of the fish population biology decreases the chance of incorrectly specifying or accounting for the environmental factor within the assessment model.

Even in the case of red tide blooms, where the environmental stressor can clearly be tied to the cause of episodic mortality (e.g., through direct observation of extensive fish kills), it is noteworthy that a large number of assumptions must be made when factoring the effect into the assessment. For example, assumptions are made regarding the age classes affected, the time span at which effects operate, and the specific parameters affected (e.g., mortality versus catchability). The complexity inherent in including environmental drivers quantitatively into stock assessment models — even in cases where there is solid justification for inclusion — highlights the trade-offs associated with intensive mechanistic research to improve understanding of the environment–fish stock relationship versus efforts to simply manage the stock under the uncertainty of potential episodic events of unknown impacts with the appropriate level of caution. Along the lines of the latter option, another possible approach for incorporating ecosystem dynamics into the management process would be to develop a harvest control rule that is robust to ecosystem changes (Lynch et al. 2018). A recent evaluation of the predictive performance of complex stock assessment and ecosystem models in the California Current Ecosystem found that model outputs tend to smooth out the variability in stock dynamics and overestimate stability (Storch et al. 2017). Their results suggest that complex models may not necessarily accurately capture complex ecosystems and recommend that simpler harvest control rules may result in more robust management (Storch et al. 2017). Harford et al. (2018) explored two types of harvest control rules in the face of uncertain episodic natural mortality events for Gulf red grouper: one based on dynamic decision-making in response to severe red tide events and another based on static decision-making intervals coupled with precautionary catch reductions. Simulation results showed that the current approach (conduct an assessment every

5 years with no annual catch limit reduction due to red tides) led to the highest probabilities of overfishing (36%) and of the stock becoming overfished (20%) and suggested that precautionary catch limits (buffering annual catch limits to account for uncertainty associated with red tides) or reactive decision-making (e.g., severe red tide initiates a stock assessment) could lead to more robust management via achieving fishery objectives.

There is also a need to increase the ability of management to respond to major changes in the ecosystem or the fishery with greater lead time. Allowing management to become more "proactive" and less "reactive" would allow more efficient use of marine resources, as industry would be able to take advantage of positive influences on the stock and prepare in advance for negative influences. In the present case study, assumptions surrounding the effect of the 2018 red tide on the red grouper population were highly influential on the catch advice due to the timing of the assessment and environmental effect; the bloom was ongoing at the time of the assessment and impacted the first year of projections. Environmental stressors occurring in the initial forecast years of an assessment are highly likely to be influential, yet in practice assessment forecasts are based on recent averages and very rarely reflect real-time events (Goethel et al. 2018). In a climate where environmental extremes are becoming increasingly frequent, it then becomes important to increase the information flow among fishers, scientists, and managers (Fulton et al. 2013; Hare 2020; Wilson et al. 2018), so that current changes in the environment have the opportunity to be integrated into projections. In the absence of such communication, major shocks or stressors to the system may not become apparent to the science and management communities until their effect has been observed in the data, at which point management can only be adjusted in response. Information from stakeholders can be incorporated quantitatively in the stock assessment, as shown here, but changes to the ecosystem can also be incorporated qualitatively or quantitatively outside the stock assessment cycle (Zador et al. 2017). For example, interim analyses using indicator-based harvest control rules for years between stock assessments could help to more rapidly (and with fewer resources) track changes in relative abundance in response to episodic events (Huynh et al. 2020).

Management strategy evaluations (MSE) are a critical next step to help determine the impact of including or excluding environmental considerations, in this case red tide mortality, on tactical advice derived from stock assessments. However, this was outside the scope of the present study. MSEs are a powerful approach that simulates the entire management system from data collection and monitoring to stock assessment and environmental considerations (Hertz and Thomas 1983; Sainsbury et al. 2000; Butterworth et al. 2010; Punt et al. 2016). Within a simulation framework designed around Gulf red grouper, one could test (1) whether environmental considerations are necessary to be included during assessment model development; (2) how best to accommodate episodic mortality events when modeling stock dynamics if warranted; (3) the cost of including an environmental covariate in an assessment model when no such relationship exists in reality (or of configuring the wrong mechanism); (4) the risk of competing processes, such as underreported landings versus natural mortality (Cadigan 2015); (5) the cost of omitting an environmental process from an assessment model when it does exist (i.e., robustness of single-species models to ecosystem dynamics); and (6) how including future episodic events could impact equilibrium reference points. Recent MSEs have suggested that inclusion of environmental considerations can result in greater uncertainty and have a negligible impact on achievement of management goals (Punt et al. 2014; King et al. 2015). However, MSE work in southeastern Australia concluded that the consequences of ignoring a shift in recruitment resulting from climate change were greater than assuming a shift had occurred (Wayte 2013).

The expectation of climate change has created substantial interest in how marine species will respond to changing environmental conditions and fishing pressures. Increased collection of data using satellites, buoys, and biological surveys will enable ecosystem considerations linking the environment to population dynamics to be included in future fisheries management, both through single-species stock assessments and more holistic strategic ecosystem-based modeling approaches. With temperature changes expected to influence tropical organisms, particularly corals (Hoegh-Guldberg 1999; Donner et al. 2005), harmful algal blooms are likely to increase in frequency, intensity, and duration within tropical regions (Moore et al. 2008). Dinoflagellates are expected to out-compete other photosynthetic organisms due to their swimming ability, which allows them to exit the upper stratified surface waters and access nutrients in the deeper layers (Falkowski et al. 2004; Moore et al. 2008). Therefore, the influence of episodic algal blooms on marine species, including economically important groupers, could impact ecosystem dynamics and associated services such as commercial and recreational fisheries and local economies, as observed during 2018 on the West Florida Shelf. A comprehensive assessment of species-specific distributions in relation to red tide could identify vulnerable and less-vulnerable species, leaving fishery managers with insight into alternative harvest scenarios based on environmental conditions and expected changes in fisheries production.

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References

Abbott, B., Siger, A., and Spiegelstein, M. 1975. Toxins from the blooms of *Gymnodinium* breve. *In* Proceedings of the 1st International Conference on Toxic Dinoflagellate Blooms. *Edited by* V.R. LoCicero. Massachusetts Science and Technology Foundation, Wakefield, Mass. pp. 355–365.

Baden, D. 1988. Public health problems of red tides. *In* Handbook of Natural Toxins. *Edited by* A.T. Tu. Marcel Dekker, New York. pp. 259–277.

Butterworth, D.S., Bentley, N., De Oliveira, J.A., Donovan, G.P., Kell, L.T., Parma, A.M., et al. 2010. Purported flaws in management strategy evaluation: basic problems or misinterpretations? ICES J. Mar. Sci. **67**: 567–574. doi:10.1093/icesjms/fsq009.

Cadigan, N.G. 2015. A state-space stock assessment model for northern cod, including under-reported catches and variable natural mortality rates. Can. J. Fish. Aquat. Sci. **73**(2): 296–308. doi:10.1139/cjfas-2015-0047.

Cao, J., Thorson, J.T., Richards, R.A., and Chen, Y. 2017. Spatiotemporal index standardization improves the stock assessment of northern shrimp in the Gulf of Maine. Can. J. Fish. Aquat. Sci. **74**(11): 1781–1793. doi:10.1139/cjfas-2016-0137.

Chagaris, D., and Sinnickson, D. 2018. An index of red tide mortality on red grouper in the Eastern Gulf of Mexico. SEDAR61-WP-06. SEDAR, North Charleston, S.C.

Christman, M., and Young, L. 2006. Executive summary. Available from https://myfwc.com/research/redtide/monitoring/database/.
Deriso, R.B., Maunder, M.N., and Pearson, W.H. 2008. Incorporating covariates into fisheries stock assessment models with application to Pacific herring. Ecol. Appl. **18**(5): 1270–1286. doi:10.1890/07-0708.1. PMID:18686586.
Deroba, J.J., and Schueller, A.M. 2013. Performance of stock assessments with misspecified age-and time-varying natural mortality. Fish. Res. **146**: 27–40. doi:10.1016/j.fishres.2013.03.015.
Donner, S.D., Skirving, W.J., Little, C.M., Oppenheimer, M., and Hoegh-Guldberg, O. 2005. Global assessment of coral bleaching and required rates of adaptation under climate change. Global Change Biol. **11**(12): 2251–2265. doi:10.1111/j.1365-2486.2005.01073.x.
Driggers, W.B., Campbell, M.D., Debose, A.J., Hannan, K.M., Hendon, M.D., Martin, T.L., and 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. doi:10.1016/j.ecss.2015.11.009.
Dupont, J.M., Hallock, P., and Jaap, W.C. 2010. Ecological impacts of the 2005 red tide on artificial reef epibenthic macroinvertebrate and fish communities in the eastern Gulf of Mexico. Mar. Ecol. Prog. Ser. **415**: 189–200. doi:10.3354/meps08739.
Falkowski, P.G., Katz, M.E., Knoll, A.H., Quigg, A., Raven, J.A., Schofield, O., and Taylor, F. 2004. The evolution of modern eukaryotic phytoplankton. Science, **305**(5682): 354–360. doi:10.1126/science.1095964. PMID:15256663.
Flaherty, K.E., and 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. doi:10.1007/s12237-010-9350-x.
Forrestal, F.C., Schirripa, M., Goodyear, C.P., Arrizabalaga, H., Babcock, E.A., Coelho, R., et al. 2019. Testing robustness of CPUE standardization and inclusion of environmental variables with simulated longline catch datasets. Fish. Res. **210**: 1–13. doi:10.1016/j.fishres.2018.09.025.
Fu, C., and Quinn, T.J., II. 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. doi:10.1139/f00-220.
Fulton, E., Jones, T., Boschetti, F., Chapman, K., Little, R., Syme, G., et al. 2013. Assessing the impact of stakeholder engagement in management strategy evaluation. Int. J. Econ. Manage. Eng. **3**(3): 82–98.
Gårdmark, A., Östman, Ö., Nielsen, A., Lundström, K., Karlsson, O., Pönni, J., and Aho, T. 2012. Does predation by grey seals (*Halichoerus grypus*) affect Bothnian Sea herring stock estimates? ICES J. Mar. Sci. **69**(8): 1448–1456. doi:10.1093/icesjms/fss099.
Glibert, P.M., Anderson, D.M., Gentien, P., Graneli, E., and Sellner, K.G. 2005. The global, complex phenomena of harmful algal blooms. Oceanography, **18**(2): 136–147. doi:10.5670/oceanog.2005.49.
GMFMC. 2011. Final generic annual catch limits/accountability measures amendment for the Gulf of Mexico Fishery Management Council's red drum, reef fish, shrimp, coral and coral reefs, fishery management plans (including environmental impact statement, regulatory impact review, regulatory flexibility analysis, fishery impact statement. Gulf of Mexico Fishery Management Council (GMFMC), Tampa, Fla. p. 378.
GMFMC. 2019. Modification of Gulf of Mexico red grouper annual catch limits and annual catch targets framework action to the fishery management plan for reef fish resources of the Gulf of Mexico including environmental assessment, regulatory impact review, and regulatory flexibility act analysis. Gulf of Mexico Fishery Management Council (GMFMC), Tampa, Fla. p. 87.
Goethel, D.R., Smith, M.W., Cass-Calay, S.L., and Porch, C.E. 2018. Establishing stock status determination criteria for fisheries with high discards and uncertain recruitment. North Am. J. Fish. Manage. **38**(1): 120–139. doi:10.1002/nafm.10007.
Gravinese, P.M., Munley, M.K., Kahmann, G., Cole, C., Lovko, V., Blum, P., and Pierce, R. 2020. The effects of prolonged exposure to hypoxia and Florida red tide (*Karenia brevis*) on the survival and activity of stone crabs. Harmful Algae, **98**: 101897. doi:10.1016/j.hal.2020.101897. PMID:33129455.
Gray DiLeone, A., and Ainsworth, C.H. 2019. Effects of *Karenia brevis* harmful algal blooms on fish community structure on the West Florida Shelf. Ecol. Model. **392**: 250–267. doi:10.1016/j.ecolmodel.2018.11.022.
Grüss, A., Thorson, J.T., Sagarese, S.R., Babcock, E.A., Karnauskas, M., Walter, J.F., III, and Drexler, M. 2017. Ontogenetic spatial distributions of red grouper (*Epinephelus morio*) and gag grouper (*Mycteroperca microlepis*) in the US Gulf of Mexico. Fish. Res. **193**: 129–142. doi:10.1016/j.fishres.2017.04.006.
Hare, J.A. 2014. The future of fisheries oceanography lies in the pursuit of multiple hypotheses. ICES J. Mar. Sci. **71**(8): 2343–2356. doi:10.1093/icesjms/fsu018.
Hare, J.A. 2020. Ten lessons from the frontlines of science in support of fisheries management. ICES J. Mar. Sci. **77**(3): 870–877. doi:10.1093/icesjms/fsaa025.
Hare, J.A., Brooks, E.N., Palmer, M.C., and Churchill, J.H. 2015. Re-evaluating the effect of wind on recruitment in Gulf of Maine Atlantic Cod (*Gadus morhua*) using an environmentally-explicit stock recruitment model. Fish. Oceanogr. **24**(1): 90–105. doi:10.1111/fog.12095.
Harford, W.J., Grüss, A., Schirripa, M.J., Sagarese, S.R., Bryan, M., and Karnauskas, M. 2018. Handle with care: establishing catch limits for fish stocks experiencing episodic natural mortality events. Fisheries, **43**(10): 463–471. doi:10.1002/fsh.10131.
Hertz, D., and Thomas, H. 1983. Risk analysis and its applications. John Wiley & Sons Ltd., New York.
Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe reviewed in the light of biological research. Rapports et procès-verbaux des réunions, Vol. 20. Andr. Fred. Høst & Fils, Copenhagen, Denmark.
Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Mar. Freshwat. Res. **50**(8): 839–866. doi:10.1071/MF99078.
Huynh, Q.C., Hordyk, A.R., Forrest, R.E., Porch, C.E., Anderson, S.C., and 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. doi:10.1111/faf.12453.
Jiao, Y., Smith, E.P., O'Reilly, R., and Orth, D.J. 2012. Modelling non-stationary natural mortality in catch-at-age models. ICES J. Mar. Sci. **69**(1): 105–118. doi:10.1093/icesjms/fsr184.
Johnson, K.F., Monnahan, C.C., McGilliard, C.R., Vert-Pre, K.A., Anderson, S.C., Cunningham, C.J., et al. 2015. Time-varying natural mortality in fisheries stock assessment models: identifying a default approach. ICES J. Mar. Sci. **72**(1): 137–150. doi:10.1093/icesjms/fsu055.
King, J.R., McFarlane, G.A., and Punt, A.E. 2015. Shifts in fisheries management: adapting to regime shifts. Philos. Trans. R Soc. B Biol. Sci. **370**(1659): 20130277. doi:10.1098/rstb.2013.0277.
Karnauskas, M., McPherson, M., Sagarese, S., Rios, A., Jepson, M., Stoltz, A., and Blake, S. 2019. Timeline of severe red tide events on the West Florida Shelf: insights from oral histories. SEDAR61-WP-20. SEDAR, North Charleston, S.C. p. 16.
Landsberg, J.H. 2002. The effects of harmful algal blooms on aquatic organisms. Rev. Fish. Sci. **10**(2): 113–390. doi:10.1080/20026491051695.
Landsberg, J.H., Flewelling, L.J., and Naar, J. 2009. *Karenia brevis* red tides, brevetoxins in the food web, and impacts on natural resources: decadal advancements. Harmful Algae, **8**: 598–607. doi:10.1016/j.hal.2008.11.010.
Link, J.S., Huse, G., Gaichas, S., and Marshak, A.R. 2020. Changing how we approach fisheries: a first attempt at an operational framework for ecosystem approaches to fisheries management. Fish Fish. **21**(2): 393–434. doi:10.1111/faf.12438.
Lynch, P.D., Methot, R.D., and Link, J.S. (Editors). 2018. Implementing a next generation stock assessment enterprise. An update to the NOAA Fisheries stock assessment improvement plan. NOAA Technical Memorandum NMFS-F/SPO-183. Office of Science and Technology, National Marine Fisheries Service, NOAA, Silver Spring, Md. doi:10.7755/TMSPO.183.
Magaña, H.A., Contreras, C., and Villareal, T.A. 2003. A historical assessment of *Karenia brevis* in the western Gulf of Mexico. Harmful Algae, **2**(3): 163–171. doi:10.1016/S1568-9883(03)00026-X.
Marshall, K.N., Koehn, L.E., Levin, P.S., Essington, T.E., and Jensen, O.P. 2019. Inclusion of ecosystem information in US fish stock assessments suggests progress toward ecosystem-based fisheries management. ICES J. Mar. Sci. **76**(1): 1–9. doi:10.1093/icesjms/fsy152.
Matich, P., and 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. doi:10.3354/meps09497.
Maunder, M.N., and Watters, G.M. 2003. A general framework for integrating environmental time series into stock assessment models: model description, simulation testing, and example. Fish. Bull. **101**: 89–99.
Methot, R.D., and Wetzel, C.R. 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. Fish. Res. **142**: 86–99. doi:10.1016/j.fishres.2012.10.012.
Methot, R.D., Jr., Wetzel, C.R., and Taylor, I.G. 2018. Stock Synthesis User Manual Version 3.30.12. NOAA Fisheries, Seattle, Wash.
Moore, S.K., Trainer, V.L., Mantua, N.J., Parker, M.S., Laws, E.A., Backer, L.C., and Fleming, L.E. 2008. Impacts of climate variability and future climate change on harmful algal blooms and human health. Environ. Health, **7**(2): S4. doi:10.1186/1476-069X-7-S2-S4. PMID:19025675.
Pauly, D., Christensen, V., and Walters, C. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J. Mar. Sci. **57**(3): 697–706. doi:10.1006/jmsc.2000.0726.
Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., et al. 2004. Ecosystem-based fishery management. Science, **305**(5682): 346–347. doi:10.1126/science.1098222. PMID:15256658.
Punt, A.E. 2017. Strategic management decision-making in a complex world: quantifying, understanding, and using trade-offs. ICES J. Mar. Sci. **74**(2): 499–510. doi:10.1093/icesjms/fsv193.
Punt, A.E., A'mar, T., Bond, N.A., Butterworth, D.S., de Moor, C.L., De Oliveira, J.A., et al. 2014. Fisheries management under climate and environmental uncertainty: control rules and performance simulation. ICES J. Mar. Sci. **71**(8): 2208–2220. doi:10.1093/icesjms/fst057.
Punt, A.E., Butterworth, D.S., Moor, C.L., De Oliveira, J.A., and Haddon, M. 2016. Management strategy evaluation: best practices. Fish Fish. **17**(2): 303–334. doi:10.1111/faf.12104.
Richards, R.A., and Jacobson, L.D. 2016. A simple predation pressure index for modeling changes in natural mortality: application to Gulf of Maine northern shrimp stock assessment. Fish. Res. **179**: 224–236. doi:10.1016/j.fishres.2016.03.003.
Sagarese, S.R., Walter, J.F., III, Harford, W.A., Grüss, A., Stumpf, R.P., and 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-WP-07. SEDAR, North Charleston, S.C.

Sainsbury, K.J., Punt, A.E., and Smith, A.D. 2000. Design of operational management strategies for achieving fishery ecosystem objectives. ICES J. Mar. Sci. **57**(3): 731–741. doi:10.1006/jmsc.2000.0737.

SEDAR. 2009*a*. SEDAR10 Update: Gulf of Mexico Gag Grouper Stock Assessment Report. Southeast Data Assessment and Review (SEDAR), North Charleston, S.C. Available from http://sedarweb.org/docs/suar/Gag_2009_Assessment_Update_Report.pdf.

SEDAR. 2009*b*. SEDAR12 Update: Gulf of Mexico Red Grouper Stock Assessment Report. Southeast Data Assessment and Review (SEDAR), North Charleston, S.C. Available from http://sedarweb.org/docs/suar/Red_Grouper_2009_Assessment_Update_Report.pdf.

SEDAR. 2015. SEDAR42: Gulf of Mexico Red Grouper Stock Assessment Report. Southeast Data Assessment and Review (SEDAR), North Charleston, S.C. p. 612. Available from http://sedarweb.org/docs/sar/S42_SAR_0.pdf.

SEDAR. 2019. SEDAR61: Gulf of Mexico Red Grouper Stock Assessment Report. Southeast Data Assessment and Review (SEDAR), North Charleston, S.C. p. 285. Available from http://sedarweb.org/docs/sar/S61_Final_SAR.pdf.

Skern-Mauritzen, M., Ottersen, G., Handegard, N.O., Huse, G., Dingsør, G.E., Stenseth, N.C., and Kjesbu, O.S. 2016. Ecosystem processes are rarely included in tactical fisheries management. Fish Fish. **17**(1): 165–175. doi:10.1111/faf.12111.

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. doi:10.1080/00139307509435843. PMID:1239373.

Steidinger, K.A., and Ingle, R.M. 1972. Observations on the 1971 summer red tide in Tampa Bay, Florida. Environ. Lett. **3**(4): 271–278. doi:10.1080/00139307209435473. PMID:4627989.

Steidinger, K.A., and Vargo, G.A. 1988. Marine dinoflagellate blooms: dynamics and impacts. *In* Algae and Human Affairs. *Edited by* C. Lembi and J.R. Waaland. Cambridge University Press. pp. 373–401.

Storch, L.S., Glaser, S.M., Ye, H., and Rosenberg, A.A. 2017. Stock assessment and end-to-end ecosystem models alter dynamics of fisheries data. PLoS ONE, **12**(2): e0171644. doi:10.1371/journal.pone.0171644. PMID:28199344.

Stumpf, R., Culver, M., Tester, P., Tomlinson, M., Kirkpatrick, G., Pederson, B., et al. 2003. Monitoring *Karenia brevis* blooms in the Gulf of Mexico using satellite ocean color imagery and other data. Harmful Algae, **2**(2): 147–160. doi:10.1016/S1568-9883(02)00083-5.

Then, A.Y., Hoenig, J.M., Hall, N.G., and Hewitt, D.A. 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. ICES J. Mar. Sci. **72**(1): 82–92. doi:10.1093/icesjms/fsu136.

Vargo, G.A. 2009. A brief summary of the physiology and ecology of *Karenia brevis* Davis (G. Hansen and Moestrup comb. nov.) red tides on the West Florida Shelf and of hypotheses posed for their initiation, growth, maintenance, and termination. Harmful Algae, **8**(4): 573–584. doi:10.1016/j.hal.2008.11.002.

Walter, J.F., Hoenig, J.M., Wood, R.J., and Marti, K. 2007. An estimator of episodic mortality in bivalves with an application to sea scallops (*Placopecten magellanicus*). Fish. Res. **86**(2): 85–91. doi:10.1016/j.fishres.2007.05.001.

Walter, J., Christman, M.C., Landsberg, J.H., Linton, B., Steidinger, K., Stumpf, R., and 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, S.C.

Walter, J.F., Sagarese, S.R., Harford, W.J., Grüss, A., Stumpf, R.P., and 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-RW-02. SEDAR, North Charleston, S.C.

Wayte, S.E. 2013. Management implications of including a climate-induced recruitment shift in the stock assessment for jackass morwong (*Nemadactylus macropterus*) in south-eastern Australia. Fish. Res. **142**: 47–55. doi:10.1016/j.fishres.2012.07.009.

Wilberg, M.J., and Bence, J.R. 2006. Performance of time-varying catchability estimators in statistical catch-at-age analysis. Can. J. Fish. Aquat. Sci. **63**(10): 2275–2285. doi:10.1139/f06-111.

Wilson, J.R., Lomonico, S., Bradley, D., Sievanen, L., Dempsey, T., Bell, M., et al. 2018. Adaptive comanagement to achieve climate-ready fisheries. Conserv. Lett. **11**(6): e12452. doi:10.1111/conl.12452.

Zador, S.G., Holsman, K.K., Aydin, K.Y., and Gaichas, S.K. 2017. Ecosystem considerations in Alaska: the value of qualitative assessments. ICES J. Mar. Sci. **74**(1): 421–430. doi:10.1093/icesjms/fsw144.