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Potential medium-term impacts of climate change on tuna and billfish in the Gulf of Mexico: A qualitative framework for management and conservation

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ABSTRACT

A systematic review of scientific papers on the potential impacts of climate-driven environmental changes on tuna and billfish in the Gulf of Mexico (GOM) was conducted to identify the climate-driven pressures and their associated potential impacts on the reproductive success and survival of tuna and billfish, and which of those impacts may have more relevance for their management and conservation in the GOM by 2050. An Impact Screening Analysis (ISA) was developed to evaluate the potential climate impacts discovered in the literature synthesis by assessing each impact against four criteria, and assigning it a ranking based on likelihood of occurrence (High, Medium, or Low). Results show three types of climate-driven pressures within the High ranking: increased water temperature; changes in ocean circulation and eddy kinetic energy; and changes in storm and wind patterns. Our findings provide valuable information to advance our understanding of key climate-driven physico-chemical processes that can impact the biology of tuna and billfish in the GOM, and enhance conservation and management of these species.

1. Introduction

In coastal and marine ecosystems, rising levels of atmospheric carbon dioxide (CO_2) over the last century have resulted in associated climate alterations in physico-chemical characteristics of the oceanic water column, including increased sea surface temperature (SST), increased rates of sea level rise (SLR), and ocean acidification (OA). Concurrently, increases in global air temperature and SST have led to changes in precipitation patterns, ocean circulation, and storm and wind occurrence (Gosling et al., 2011; Doney et al., 2012; Moser et al., 2014). Fig. 1 summarizes the most relevant interconnections between these climate-dependent changes (i.e., climate drivers) that alter physico-chemical characteristics and processes of both the atmosphere and the oceans, thus representing key potential climate-driven pressures for important biological, ecological, and environmental processes. The terms of climate drivers and pressures used here are based on the driver-pressure-state-impact-response (DPSIR) approach (see Oesterwind et al., 2016 for a detailed definition of climate drivers and pressures within the DPSIR framework approach).

Climate is a key factor driving environmental conditions that regulate the abundance, distribution, physical condition, and habitat use of fish populations, with implications for their exploitation and conservation (Brander, 2010; Jennings and Brander, 2010; Koehn et al., 2011; Fuller et al., 2015; Muñoz-Expósito et al., 2017). Therefore, climate-related alterations may have numerous biological and ecological effects on marine fish and their habitats, including changes in survival, phenology, and shifts in species distribution (Chen et al., 2011; Pinsky et al., 2013). Hence, in addition to issues such as overfishing, pollution, and marine ecosystem degradation, marine scientists and fishery managers need to also consider the potential impacts of climate change on fish survival, distribution, and fisheries productivity (Ottersen et al., 2004; Martinez Arroyo et al., 2011).

As for many other global coastal marine ecosystems, the Gulf of Mexico (GOM) region is characterized by complex interactions among ecosystem drivers and stressors that are likely to be impacted by climate-driven alterations, with important implications for higher-level ecosystem dynamics and the management of natural resources (Biasutti et al., 2012; Moser et al., 2014; Karnauskas et al., 2015). Understanding

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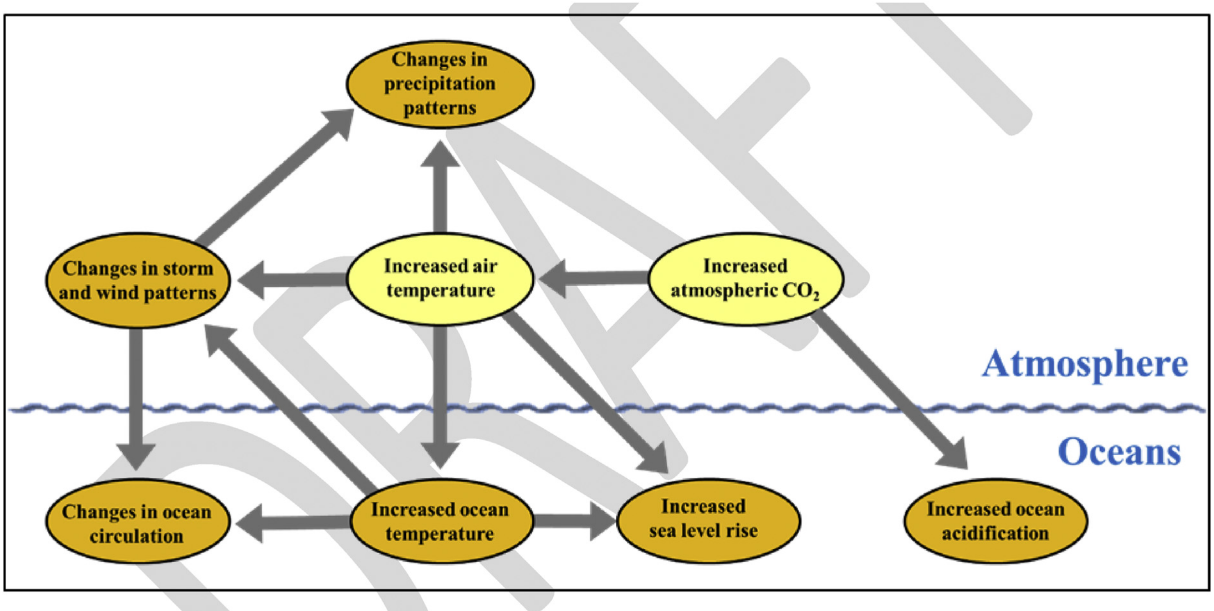

Fig. 1. Schematic diagram of potential climate-driven pressures (light brown ovals) to environmental characteristics of the atmosphere and oceans related to the primary climate-dependent drivers of rising atmospheric carbon dioxide (CO_2) and associated increase in air temperature (yellow ovals) in the Gulf of Mexico. Arrows indicate existing links between climate pressures (e.g., "increased ocean temperature" have impacts on "changes in storm and wind patterns"). This diagram and its framework and terminology are based on the driver-pressure-state-impact-response (DPSIR) approach (see Oesterwind et al., 2016). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the likely impacts of global climate change on the resources and habitats in the GOM is particularly important given the large investment in restoration that will be made over the next several decades as a result of the settlement for the 2010 *Deepwater Horizon* (DWH) oil spill. Specifically, $8.8 billion has been allocated for natural resource restoration in the GOM through the Natural Resource Damage Assessment (NRDA) portion of the DWH global settlement agreement, of which, approximately $380 million has been allocated for the restoration of fish and water column invertebrates.

Therefore, understanding the most likely effects of climate change on species targeted for restoration will help restoration managers incorporate changing conditions into long-term restoration planning for these resources in the GOM. Additionally, this information will advance our understanding of the effect of changing environmental conditions on the biology and ecology of migratory species that utilize GOM habitats during critical stages of their life history.

Climate-driven changes represent a potential threat that can impact the survival and reproductive success of offshore species, although these potential impacts have been less studied compared to impacts on coastal species and habitats (IUCN, 2016). This is particularly true for potential impacts to offshore species in the GOM (Justic et al., 1996; Scavia et al., 2002; Mendoza-Alfaro and Alvarex-Torres, 2012). Atlantic highly migratory species (HMS) are among the pelagic species that may be impacted by climate-driven environmental changes in the GOM marine ecosystem. Atlantic HMS discussed in this analysis include tunas (Atlantic bluefin, *Thunnus thynnus*; skipjack, *Katsuwonus pelamis*; and yellowfin, *Thunnus albacares*) and billfish (blue marlin, *Makaira nigricans*; swordfish, *Xiphias gladius*). These species represent an important component of pelagic resources in the GOM, and support economically important commercial and recreational fisheries. Despite considerable effort exerted by the U.S. government for the management and conservation of tuna and billfish, including fishery regulation and recently planned and implemented restoration projects (i.e., the Oceanic Fish Restoration Project implemented through the Phase IV NRDA Early Restoration Plan for the DWH oil spill), there remains a lack of comprehensive understanding of the multiple impacts of climate change on the biology, survival, and reproductive success of these species and how these impacts could affect the outcomes of restoration actions targeting these species.

In the case of tuna and billfish, most work has been largely based on longer-term projections of climate change impacts by the end of the 21st century, both in the GOM (Muhling et al., 2015) and other oceanic regions (Lehodey et al., 2013, 2015; Dueri et al., 2014; Gilman et al., 2016). For example, the Atlantic Bluefin Tuna Status Review Team considered potential climate impacts on tuna in their most recent status review report for the species (Atlantic Bluefin Tuna Status Review Team, 2011) and the NOAA Fisheries' Final Essential Fish Habitat 5-Year Review for Atlantic Highly Migratory Species provides a broad overview of the potential impacts of climate change to HMS (NOAA Fisheries, 2015). The Climate Action Plan for the GOM, released under the NOAA Fisheries Climate Science Strategy, identifies major climate drivers for the GOM and makes recommendations to help meet climate science needs for the region, including vulnerability assessments for marine species in the GOM and identification of research gaps related to identified climate impacts (Lovett et al., 2016).

While these previous efforts have considered climate impacts in the GOM generally or climate impacts on HMS across regions, this paper aims to more specifically examine climate impacts on HMS targeted for restoration in the GOM region over timeframes relevant for restoration decision-making.

To address this critical gap, we conducted a thorough literature review on climate change impacts on tuna and HMS inside and outside the GOM. To provide a standardized terminology and framework for our analysis and enhance its replicability and accountability, we adopted the driver-pressure-state-impact-response (DPSIR) approach that has been used for integrated environmental assessments of terrestrial and aquatic ecosystems (Levin et al., 2008; Oesterwind et al., 2016). For the specific terminology and definitions of climate-related drivers, pressures, states, impacts, and responses, refer to Oesterwind et al., 2016.

The compiled body of literature and scientific knowledge was used to identify potential climate-driven pressures that can cause changes in environmental (i.e., biophysical, chemical, and ecological) state and associated impacts to the reproductive success and survival of tuna and billfish, and to determine which of those climate-driven pressures may have more relevance for the management and conservation of these species in the GOM over the next 30–40 years. We were interested in this medium-term horizon due to the current planned effort for management and conservation of these species in the GOM and interest among various federal, state, and local agencies and their partners to restore tuna and billfish species injured by the DWH oil spill. The information generated by this analysis is critical for adding to understanding of how multiple climate-driven pressures and changes in environmental states can potentially affect the desired outcomes of restoration projects aimed at enhancing tuna and billfish survival and reproductive success. This information will also enhance understanding on key marine environmental processes for these species and facilitate efforts to enhance their resiliency to future climate impacts in the GOM.

2. Methods

2.1. Literature synthesis

Peer-reviewed, published studies on the potential climate-driven changes in environmental states and associated impacts for tuna and HMS species inhabiting the GOM, at all life stages, were gathered through a thorough search of the peer-reviewed scientific literature available through June 2017 on Google Scholar and ResearchGate. Search terms included those terms related to climate change effects in the GOM (e.g., "climate impacts", "climate threats", "climate change", "Gulf of Mexico", "Caribbean Sea") combined with terms related to tuna and HMS species (e.g., "tuna", "tuna larvae", "billfish", "swordfish", "sharks", "highly migratory species"). Here, impacts are considered as those resulting from climate-driven changes in environmental states that may have an influence on the species biology, ecology, survival, reproductive success, and habitat use. Impacts can result from environmental changes in water condition that can lead to associated physiological or metabolic stress to the species.

Additionally, all publications collected were cross-referenced to identify references that were not included in the original search results. After screening the resulting papers for relevance to climate impacts on tuna and billfish in the GOM, selected papers were reviewed in detail for the following information: *i*) potential climate-related impacts to individual species, life stages (as identified in each paper as eggs, larvae, juveniles, or adults), or groups of species or life stages; *ii*) the potential for each impact to be realized in the GOM by 2050; *iii*) level of evidence for the impact (i.e., modeled = the impact was identified through quantitative modeling and forecasting; observed = the impact was identified based on experimental hypothesis testing, laboratory experiments, and/or scientific measurements and observations; theorized = the impact was identified based on untested hypotheses or theoretical reasoning; professional judgement = the impact was identified by professional experts on tuna and billfish in the Gulf of Mexico). This first step in the review process was necessary to assess whether a paper had relevant and appropriate information for the next step in the analysis.

For the purpose of the study, given the limited information available on the effect of OA on tuna and billfish, we included information on sharks. Papers focused on sharks provided the best available information, given the similarities in biology, life history, niche, and feeding behavior between these species and tuna and billfish species, although we acknowledge the existence of lower fecundity in sharks compared to tuna and billfish.

2.2. Impact screening analysis

For the purpose of our analysis we adopted a qualitative framework approach, given that the volume of and level of evidence in the scientific literature related to the potential impacts of climate change on tuna and billfish in the GOM vary by species. We developed an Impact Screening Analysis (ISA) to evaluate and identify potential climate-related changes in environmental states and associated impacts to tuna and billfish most likely to occur over the medium-term (30–40 years) in the GOM. The ISA assessed whether the impact met each of four criteria: 1) evidence of a detectable change by 2050; 2) evidence of the potential impact from a minimum of two independent studies; 3) the climate research or modeling was conducted in the GOM; and 4) the climate research or modeling was conducted on the specific species or habitat of interest.

Potential climate change impacts were then assigned rankings based on the following rules: "High" - all four criteria were met; "Medium" – three of the four criteria were met; "Low" – two or fewer of the four criteria were met.

3. Results

3.1. Climate drivers and pressures impacting the Gulf of Mexico

Future projections based on global climate models indicated that ocean temperatures in the North Atlantic will experience an increase of ~2 °C by the end of the 21st century, with a simultaneous 25% reduction in the strength of the Atlantic Meridional Overturning Circulation (AMOC) (Liu et al., 2012). The AMOC is the primary ocean circulation system in the Atlantic Ocean, contributing to the flow of warm, higher salinity water in the upper layers of the water column and associated heat transport from the South Atlantic and tropical North Atlantic to the subpolar and polar North Atlantic (Schmittner et al., 2005). More recently, several researchers questioned the large coarse resolution of these global climate models (typically of 1° longitude x 1° latitude), which are incapable of integrating the dynamic characteristics of mesoscale eddies and regional current systems that are key drivers of thermal features of the upper ocean in the GOM (Liu et al., 2012). Consequently, recent downscaled climate models provide more robust forecasts of the regional climate changes in the GOM to address weaknesses in previous models (Liu et al., 2015; Muhling et al., 2015).

Regional climate models for the GOM suggest that the average intensity of precipitation will increase over the southeastern states and in the Midwest/Mississippi River basin, with larger increases in precipitation closer to the coast in the GOM region (Biasutti et al., 2012). Additionally, larger dry anomalies have been predicted east of the Mississippi River, and recent climate projections by the Intergovernmental Panel on Climate Change (IPCC) showed that more than 75% of the models (A1B scenario, 2075–2099 minus 20th century, 1975–1999) projected dry anomalies over Louisiana and Mississippi in summer and positive anomalies across the entire northern GOM in the fall (Biasutti et al., 2012). Rapid climate-driven changes in land cover and use have been projected to occur across the Mississippi River basin (Foley et al., 2013). Collectively, the results of these climate model predictions suggest that, by the end of this century, precipitation events will be more frequent during the fall across the northern coast of the GOM region, but less frequent during the summer east of the Mississippi River, in coastal areas of Louisiana and Mississippi.

As for climate observations on water temperature, the mean offshore (> 200-m depth) SST in the GOM has been increasing over the last 30 years (Karnauskas et al., 2013), and SST is projected to rise by 2–3 °C in the GOM by the latter half of the 21st century (Biasutti et al., 2012). Climate-related changes in oceanic circulation in the GOM are predicted to affect physico-chemical characteristics of offshore waters (Liu et al., 2015). In this regard, the Loop Current (LC) is the prevailing feature of the oceanic circulation in the eastern GOM and contributes to the formation of the Florida and Gulf Stream Currents. In the present climate, the effect of the LC is to warm the GOM, including the northwestern basin, due to episodic formation of warm-core anticyclonic (clockwise) eddies that pinch-off the LC and move westward at frequencies of approximately every three to 17 months (Dietrich and Lin, 1994; Mendoza-Alfaro and Alvarex-Torres, 2012). These mesoscale eddies extend to depths of several hundred meters and remain offshore of the continental shelf. As they spin against the continental slope, they can force exchanges of water masses across the continental shelf break (Morey et al., 2003; Mendoza-Alfaro and Alvarex-Torres, 2012). An important component of the AMOC, the LC transport is projected to slow down by about 25% during the 21st century (Schmittner et al., 2005; Drijfhout and Hazeleger, 2006) with significant reduction expected by 2050 (Liu et al., 2012).

Climate-related changes are also projected to alter the dynamic of tropical storms and hurricanes across the GOM region. According to the most recent climate models, global average tropical cyclones intensity is expected to increase by 2–11% while frequency is expected to decrease by 6–34% (Knutson et al., 2010). This means that the frequency of more intense and damaging tropical storms and hurricanes is projected to increase globally, including in the GOM (Biasutti et al., 2012).

More limited information is available for the current state of knowledge and future predictions of OA, considered as the change in the water inorganic carbon chemistry due to the increased input of CO_2 from the atmosphere (Wanninkhof et al., 2015), in the GOM. OA leads to a decrease in pH in coastal regions that can also result from higher nutrient loading associated with increased freshwater runoff. This scenario is conducive to eutrophication, with increased microbial respiration and remineralization of organic matter contributing to higher CO2 production and thus lower seawater pH (Cai et al., 2011; Wallace et al., 2014). In this regard, modelling results from the GOM suggest that eutrophication from the Mississippi River will most likely increase the occurrence of OA (Cai et al., 2011).

3.2. Climate-driven pressures and impacts to tuna and billfish in the Gulf of Mexico

Of the 6 climate-driven pressures represented in Figs. 1 and 5 were found to be linked to several changes in environmental states and associated impacts to tuna and billfish: increased water temperature; changes in precipitation patterns; changes in ocean circulation; ocean acidification; and changes in storm and wind patterns. These specific pressures, and their consequential environmental state changes, can affect recruitment and adult survival that, overall, can potentially lead to reduced reproductive success in tuna and billfish (Fig. 2). Overall, our analysis did not find evidence for SLR as a key climate-driven pressure for tuna and billfish. The analysis included a total of 44 studies, which were published between 1967 and 2017.

3.2.1. Increased water temperature

Changes in water temperature have various potential impacts on the survival of tuna and billfish species, as well as on the survival and development of their eggs and larvae (Table 1), which can lead to changes in habitat utilization and distribution of the species, as well as to negative physiological effects on different life stages.

Results of recent climate modelling indicate an increase in temperature-induced habitat losses for Atlantic bluefin tuna (hereafter referred as bluefin tuna) larvae in the northern GOM by 2090 (Muhling et al., 2015), with a decrease of 39–61% in high probabilities of bluefin tuna larval occurrence in late spring (May–June) and higher increase of suitable habitats in March (62%) by 2050 (Muhling et al., 2011) (high ranking; Table 1). Climate models also suggest that increased SST will likely result in the northward shift of suitable habitat for bluefin tuna larvae in the GOM by 2050 (Muhling et al., 2011), and may also lead to earlier bluefin tuna spawning in the spring (Muhling et al., 2011; Domingues et al., 2016) (high ranking; Table 1). These results are in accordance with an observed larval temperature preference threshold of 30 °C for tuna species, generally (Reglero et al., 2014), and an observed larval temperature preference threshold of about 28–30 °C for bluefin and yellowfin tuna (Muhling et al., 2010, 2011; Wexler et al., 2011; Domingues et al., 2016). Therefore, water temperature > 28–30 °C may potentially impact (high ranking; Table 1) egg survival and larval stage development in bluefin and yellowfin tuna, and their distribution.

Additionally, increased water temperature can directly (through higher oxygen demand for the biotic compartment within the water column) or indirectly (through the associated water column stratification) favor the transition to less oxygenated or hypoxic water conditions, which are also known to affect the survival and growth rate of yellowfin tuna larvae (Wexler et al., 2011) (low ranking; Table 1). Concurrently, rising SST in the GOM can potentially increase habitat suitability for larvae of the more tropical skipjack tuna compared to larvae of more temperate species, such as bluefin tuna, and other similar tropical and subtropical species, such as yellowfin tuna, with a predicted expansion of both adult and larval habitat of skipjack tuna by 2090 (Muhling et al., 2015) (low ranking; Table 1). This result is likely due to adult bluefin and yellowfin tuna avoiding warmer waters (> 30 °C), which can limit their cardiac capacity (Blank et al., 2002), favor overheating (Sharp and Vlymen, 1978) and metabolic stress (Block and Stevens, 2001; Teo et al., 2007b), although yellowfin were found to be less sensitive to SST changes compared to bluefin tuna (Teo and Block, 2010) (medium ranking; Table 1). In turn, the increase in metabolic stress in bluefin tuna was drawn as a potential condition that can enhance post-release mortality from fishery interactions (Block et al., 2005; Teo et al., 2007b) (medium ranking; Table 1), which we argue will be even higher in waters with lower dissolved oxygen concentrations ($[O_2]$) or hypoxic conditions ($[O_2] < 2\,mg\,L^{-1}$). Hence, waters warmer than 30 °C may affect survival of tuna after release from fishing gear (e.g., longline) due to potential increase in metabolic stress, as proposed in adult bluefin tuna (Medina et al., 2002).

Moreover, rising water temperatures are also expected to occur outside the GOM in areas that serve as important feeding grounds for bluefin tuna, such as the northwestern Atlantic and the Gulf of St. Lawrence, Canada (Wilson et al., 2015). Dufour et al. (2010) theorized that climate-driven alterations in the productive north Atlantic area and its trophic dynamics may influence changes in the feeding migration and spatial distribution of bluefin tuna, which may have potential repercussions for bluefin tuna reproductive success during breeding and spawning in the GOM (Domingues et al., 2016) (low ranking; Table 1).

Increased water temperature in the GOM will likely affect reproductive migration phenology in adult bluefin tuna. Tagged adult bluefin tuna in the GOM during spring were found to be associated with waters between 24 and 27 °C (Block et al., 2005; Teo et al., 2007a). Therefore, water temperature > 30 °C are likely to reduce the extent of breeding areas (Teo et al., 2007a, 2007b; Muhling et al., 2015; Domingues et al., 2016). In the GOM, this is likely to result in reduced reproductive success and survival in this species by 2050 (Muhling et al., 2011) (medium ranking; Table 1).

Within the context of climate-driven changes in water temperature, results from recent high-resolution ocean climate models suggest that the future warming of the GOM may be lower than previously thought. Reduction (20–25%) of the LC warming effect will have a cooling impact in the GOM, mainly in the northwestern deep basin (Liu et al., 2012, 2015). This area overlaps with the spawning ground for bluefin tuna between March and June (Schaefer, 2001; Muhling et al., 2010; Teo and Block, 2010). Hence, the projected reduction in LC strength resulting in a cooling effect may at least partially reduce the potential negative impact of increased SST on bluefin tuna spawning that may occur by 2050 (low ranking; Table 1).

Rising SST may also potentially lead to a change in the spatial distribution of blue marlin habitat in the GOM. The species may move into deeper waters, following vertical migration of their prey (e.g., squid), as warmer water masses extend deeper in the water column. Light penetration and $[O_2]$ in these deeper waters may be a key limiting factor for this species and other billfish (Prince and Goodyear, 2006; Kraus and Rooker, 2007) (medium ranking; Table 1).

Fig. 2. Summary of potential climate-dependent drivers, pressures, environmental state changes, impacts to adult and eggs and larvae of tuna and billfish in the Gulf of Mexico by 2050, and implications (i.e., responses) for management and conservation. (CO_2 = Carbon dioxide, $[O_2]$ = Dissolved oxygen concentration, BUM = Blue marlin, BFT = Atlantic bluefin tuna, HMS = Highly migratory species). This diagram and its framework and terminology are based on the driver-pressure-state-impact-response (DPSIR) approach (see Oesterwind et al., 2016) modified for our analysis purpose. Note that the linkages between climate-dependent drivers, pressures, environmental state changes, and impacts depicted in this figure are those that are most relevant to tuna and billfish in the Gulf of Mexico by 2050, as indicated by our literature review and analysis. Additional linkages and causal relationships may exist that are not depicted here. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.2.2. Changes in precipitation patterns

Similar to the effects of increased water temperatures described above, changes in precipitation patterns may affect species distribution and habitat use, and lead to negative effects to species biology and physiology.

Changes in precipitation runoff may have a substantial influence on water quality, given that coastal water masses in the northern GOM are largely influenced by freshwater runoff from the Mississippi River. Increases in average precipitation intensity over the continent will likely increase freshwater input to the considerably large Mississippi River watershed, which will likely increase carbon fluxes and nutrient inputs in the GOM (Ren et al., 2015). This increased nutrient delivery, which occurs seasonally, will enhance primary production and sediment transport to estuarine and coastal waters and favor $[O_2]$ depletion and development of hypoxic conditions in the water column (also due to increased water column stratification), increasing the hypoxic zone

Table 1
Summary of potential climate pressures and associated changes in environmental (i.e., biophysical, chemical, or ecological) state and impacts on tuna and billfish, with the identified potential for the impact to be realized (High, Medium, and Low; see the main text for the definition of the criteria) over the next 30–-40 years in the Gulf of Mexico, and how the impact was identified (Modeled = quantitative modeling and forecasting, Observed = based on experimental hypothesis testing and/or laboratory experiment, and/or scientific measurements and observations, Theorized = based on untested hypothesis or theoretical rationale, Professional judgement = based on the professional judgment of experts on tuna and billfish in the study area). GOM = Gulf of Mexico, LC = the Loop Current, T = Temperature, $[O_2]$ Dissolved oxygen concentration, BFT = Atlantic bluefin tuna, YFT = Yellowfin tuna, SKJ = Skipjack tuna, BIL = Billfish, BUM = Blue marlin, SWO = Swordfish, SHK = Sharks.

Climate pressure	Potential impact to the resource due to changes in environmental state	Potential for realization of impact over the next 30–40 years in GOM	How the impact was identified - Reference, Year
Increased water temperature	Suitable areas for BFT larvae may shift up north by 2050, and occurrence of BFT larvae in GOM may decrease in late spring by 39–61% by 2050, with higher decrease in May–June and higher increase in March–April.	High	Modeled - Muhling et al., 2011, 2015 Observed - Teo et al., 2007a; 2007b
	Water T > 28–30 °C may affect BFT and YFT eggs and larvae survival and development	High	Modeled - Muhling et al., 2010, 2011; Reglero et al., 2014; Domingues et al., 2016 Observed – Wexler et al., 2011 Theorized and Professional judgement – Karnauskas et al., 2013
	Water T > 30 °C reduces BFT and YFT cardiac functionality making spawning adults more vulnerable to overheating and hypoxia	Medium	Theorized - Sharp and Vlymen, 1978 Observed – Block and Stevens, 2001; Blank et al., 2002; Teo et al., 2007b Theorized and Professional judgement – Karnauskas et al., 2013
	Water T increase leads to higher metabolic stress in BFT, which may cause enhanced post-release mortality from fishery (e.g., longline)	Medium	Theorized and Professional judgement - Block et al., 2005; Teo et al., 2007a; 2007b; Karnauskas et al., 2013
	Water T increase may lead to change in vertical distribution (i.e., increased utilization of deeper water) in BUM, although light and $[O_2]$ might be key limiting factors	Medium	Theorized and Professional judgement - Kraus and Rooker, 2007; Karnauskas et al., 2013 Observed – Prince and Goodyear, 2006
	Water T increase will lead to higher negative impacts for breeding BFT than for YFT and SKJ	Medium	Modeled - Muhling et al., 2015 Observed – Teo and Block, 2010 Theorized and Professional judgement – Karnauskas et al., 2013
	Water T increase may favor larval stages of SKJ compared to other tuna	Low	Modeled - Muhling et al., 2015 Theorized and Professional judgement – Karnauskas et al., 2013
	Water T increase facilitates hypoxia, which can affect YFT eggs and larvae survival and growth rate	Low	Observed - Wexler et al., 2011 Theorized and Professional judgement – Karnauskas et al., 2013
	Water T increase in the north Atlantic (feeding ground of BFT) may alter prey quality and adult BFT growth rate	Low	Theorized and Professional judgment - Dufour et al., 2010; Karnauskas et al., 2013; Wilson et al., 2015; Domingues et al., 2016
	The potential warming of western GOM waters might not be so dramatic, due to a reduction in the LC influence that will slow the rate of warming in the northern GOM, thus reducing the impact of water T increase in tuna and BIL in the northwestern GOM	Low	Modeled - Liu et al., 2012
Changes in precipitation	Increased freshwater run-off will lead to higher primary productivity in coastal areas, which may lead to higher predation rate on tuna and BIL eggs and larvae	Medium	Theorized and Professional judgement - Grimes and Kingsford, 1996; Rabalais and Turner, 2001; Teo et al., 2007b
	Increased freshwater run-off will lead to decreased BIL and SWO larval survival in water mixed with coastally derived water masses with lower salinity and higher T	Medium	Modeled - Rooker et al., 2012 Observed and Professional judgement – Lamadrid-Rose and Boehlert., 1988; Idrisi et al., 2003
	Hypoxia can affect tuna eggs and larvae survival and development. Decreased $[O_2]$ can delay hatching in BFT and YFT eggs.	Low	Observed, Theorized and Professional judgement - Miyashita et al., 1999; Wexler et al., 2011
	Hypoxia can enhance metabolic stress in BFT and BIL, which may cause enhanced vulnerability and post-release mortality from fishery (e.g., longline)	Low	Theorized - Teo et al., 2007a; 2007b; Prince et al., 2010
	Spreading (horizontally and vertically) of hypoxia may reduce acceptable habitat (habitat compression) for BUM and BIL. Habitat compression may enhance foraging opportunities for BUM due to similar habitat constrain in their prey in near surface waters	Low	Theorized and Professional judgement - Green, 1967; Barkely et al., 1978; Prince and Goodyear, 2006
	Changes in $[O_2]$ may limit the depth of acceptable habitat for BIL and tuna (hypoxic threshold for tuna and BIL considered as $< 3.5\,mL\,L^{-1} = 4.7\,mg\,L^{-1}$ and YFT found to rarely move in waters with $[O_2] < 5.7\,mg\,L^{-1}$), particularly in the breeding phase (March to June) for BFT	Low	Theorized and Professional judgement - Prince and Goodyear, 2006; Teo et al., 2007a Observed – Ingham et al., 1977; Gooding et al., 1981; Bushnell and Brill, 1991; Cayré and Marsac, 1993; Brill, 1994, 1996; Idrisi et al., 2003
	Hypoxia can affect cruising speed in SKJ, and HMS, and affect their feeding rate (hypoxic threshold for tuna and BIL considered as $< 3.5\,mL\,L^{-1} = 4.7\,mg\,L^{-1}$ and YFT found to rarely move in waters with $[O_2]$ concentration $< 5.7\,mg\,L^{-1}$)	Low	Theorized and Professional judgement - Prince and Goodyear, 2006 Observed – Ingham et al., 1977; Gooding et al., 1981; Bushnell and Brill, 1991; Cayré and Marsac, 1993; Brill, 1994, 1996; Idrisi et al., 2003

(*continued on next page*)

Table 1 (*continued*)

Climate pressure	Potential impact to the resource due to changes in environmental state	Potential for realization of impact over the next 30–40 years in GOM	How the impact was identified - Reference, Year
Changes in ocean circulation	Potential reduction in the LC influence to form warm, anticyclonic eddies may reduce survival of eggs and larvae in BFT and BIL in the northwestern GOM by 2050	High	Modeled and Professional judgement – Teo et al., 2007b; Tidwell et al., 2007; Lindo-Atichati et al., 2012; Liu et al., 2012; Rooker et al., 2012
	Changes in eddy kinetic energy by 2050 will likely affect the breeding behavior of BFT	High	Modeled – Teo et al., 2007b; Liu et al., 2012
Increased ocean acidification	More acidic waters (decreased pH) alter olfactory functions in SHK and fish	Low	Observed – Munday et al., 2009; Dixson et al., 2010, 2015
	Increased ocean acidification will impact YFT eggs hatching time and larvae survival and growth	Low	Observed and Professional judgement – Bromhead et al., 2015; Dixson et al., 2015
Changes in storm and wind patterns	Changes in microturbulence might affect BFT and YFT larval feeding rate and growth	High	Modeled - Teo et al., 2007b Observed – Kimura et al., 2004; Kato and Kimura, 2005
	Increased frequency of more intense storms between June and September will likely affect survival of YFT and BIL larvae, and will likely be less impacting for BFT larvae (spawning occurs between March and June)	High	Modeled – Teo et al., 2007b Observed – Kimura et al., 2004, Kato and Kimura, 2005 Theorized and Professional judgement – Biasutti et al., 2012
	Hurricanes can amplify negative effects of increased precipitation (e.g., hypoxia, higher productivity and predation on larvae) and cool-down water temperature too fast, which will likely affect survival of tuna and BIL eggs and larvae	Medium	Theorized and Professional judgement – Rabalais et al., 2009; Biasutti et al., 2012 Observed – Wexler et al., 2011

that already occurs in the GOM each summer (Rabalais and Turner, 2001).

An increase in primary production in coastal waters, coupled with the projected temperature-driven northern shift in more suitable habitat for bluefin tuna larvae in the GOM by 2050 (Muhling et al., 2011), may reduce bluefin tuna egg and larval survival due to increased predation (Teo et al., 2007b). An increase in predation associated with increased primary productivity has commonly been reported for pelagic fish larvae in the northern GOM and the Mississippi River plume mixed with the Gulf waters (Grimes and Kingsford, 1996; Rooker et al., 2012) (medium ranking; Table 1). Perhaps, because of higher predator concentrations, breeding bluefin tuna have shown a significant preference for oligotrophic waters with lower chlorophyll concentrations in the northwestern GOM instead of mesotrophic or eutrophic waters (Teo et al., 2007b).

Higher primary productivity in coastal waters associated with increased nutrient inputs from freshwater runoff will likely favor hypoxia. Hypoxia has several impacts on tuna across various life stages. Reduced $[O_2]$ and hypoxia can affect bluefin tuna eggs and larval survival and development (Miyashita et al., 1999), and has been observed to delay hatching time in bluefin and yellowfin tuna eggs (Wexler et al., 2011) (low ranking; Table 1). Hypoxia can also enhance metabolic stress in adult bluefin tuna (Teo et al., 2007a), which may be a cause of mortality (e.g., post-release mortality). In skipjack tuna, the threshold of hypoxia observed to negatively impact habitat use is $[O_2] < 3.5\,mg\,L^{-1}$ (Gooding et al., 1981), while yellowfin tuna were found to rarely move into waters with $[O_2] < 5.7\,mg\,L^{-1}$ (Cayré and Marsac, 1993). If $[O_2]$ falls below these thresholds, the cruising speed of tuna and billfish may change, with unknown consequences for their survival and reproductive success (Gooding et al., 1981; Brill, 1996) (low ranking; Table 1).

Similar to tuna, the abundance of billfish larvae is predicted to decrease in GOM waters mixed with coastally-derived, lower salinity, warmer water masses originating from freshwater runoff associated with changes in precipitation patterns over land (Lamadrid-Rose and Boehlert, 1988; Idrisi et al., 2003; Rooker et al., 2012). Decreases in billfish larval abundance may be directly related to changes in salinity and temperature or higher predation rates (medium ranking; Table 1).

Hypoxia can enhance metabolic stress in billfish (Prince et al., 2010), which can result in reduced survival and reproductive success. Additionally, the expansion of hypoxic waters, both horizontally and vertically throughout the water column, may reduce suitable habitat, a process known as habitat compression, for blue marlin and billfish (Prince and Goodyear, 2006) and has also been hypothesized to occur with tuna species (Green, 1967; Barkely et al., 1978) (low ranking; Table 1). However, Prince and Goodyear (2006) theorized that habitat compression may actually enhance foraging opportunities for blue marlin due to concurrent habitat constrains for their prey, which can increase predator-prey interactions in surface waters.

Changes in $[O_2]$ may limit the depth of suitable habitat for billfish (Prince and Goodyear, 2006; Teo et al., 2007a), with the threshold considered as $[O_2] < 3.5\,mL\,L^{-1}$, or $< 4.7\,mg\,L^{-1}$ (Ingham et al., 1977; Gooding et al., 1981; Bushnell and Brill, 1991; Brill, 1994; Idrisi et al., 2003; Prince and Goodyear, 2006).

3.2.3. Changes in ocean circulation

Larvae of bluefin tuna are mainly found along the continental slope in the northwestern GOM (Nishida et al., 1998; Teo et al., 2007b), but, along with billfish larvae, are also common in the LC frontal zone in the central GOM (Richards et al., 1989; Teo et al., 2007b; Rooker et al., 2012; Domingues et al., 2016), and within the boundaries of anticyclonic eddies in the western GOM (Lindo-Atichati et al., 2012). Breeding bluefin tuna are most commonly found in deeper waters of the continental shelf in the western and central GOM, mainly in March and April, which are areas characterized by a higher occurrence of cyclonic (i.e., cold-core) and anticyclonic (i.e., warm-core) eddies (see Bakun (2013) for a description of the physical/biological linkages between mesoscale eddies dynamics and bluefin tuna larvae abundance). By contrast, yellowfin tuna are found throughout the GOM, and are more commonly found in shallower coastal waters than bluefin tuna (Weng et al., 2009; Teo and Block, 2010).

Reduction in warm water transport from the LC toward the western GOM through eddy formation and propagation may affect bluefin tuna breeding behavior by 2050, as it has been demonstrated that adult bluefin tuna breeding in the GOM between March and June prefer areas of moderate eddy kinetic energy associated with mesoscale eddies and meanders, features that are found primarily in the western GOM (Teo et al., 2007b; Teo and Block, 2010) (high ranking; Table 1). Additionally, decreased transport of warming waters by mesoscale anticyclonic eddies pinching-off the LC (Liu et al., 2012) may reduce egg and larvae survival for bluefin tuna and billfish due to less optimal temperature (Tidwell et al., 2007; Teo et al., 2007b; Lindo-Atichati et al., 2012; Rooker et al., 2012) (high ranking; Table 1).

3.2.4. Increased ocean acidification

Less information is available related to the potential impact of OA on tuna and billfish. Overall, OA is considered to have more negative impacts on the survival and development of eggs and larval stages compared to adult life stages for fish and marine organisms (Harvey et al., 2013). The potential impacts of OA specifically for adult stages of tuna and billfish has not been investigated, although recent studies document how OA may alter olfactory performance in juvenile and adult sharks and other fish species (Munday et al., 2009; Dixson et al., 2010, 2015), which may reduce their predatory skills and survival (low ranking; Table 1). To our knowledge, Bromhead et al. (2015) was the first attempt to study the impacts of increased OA on yellowfin tuna eggs and larvae survival and growth rate by employing experimental increases in the partial pressure of CO_2 (pCO_2) in laboratory-reared eggs and larvae. Results from this study suggest that OA is likely to delay hatching time in yellowfin tuna eggs and growth rates in yellowfin tuna larvae (Bromhead et al., 2015) (low ranking; Table 1).

3.2.5. Changes in storm and wind patterns

Changes in storm and wind patterns may impact species distribution and affect eggs and larval survival. Surface wind speed, which increases with tropical cyclones and hurricanes, was predicted to significantly affect the habitat use of breeding adult bluefin tuna, which show a preference for moderate wind speeds (Teo et al., 2007b). Microturbulence, for which wind speed is a key determinant, affects the survival of fish larvae (Dower et al., 1997; MacKenzie and Kiorboe, 2000). As reported by Teo et al. (2007b), although greater microturbulence can increase the feeding rate of larvae due to increased frequency of physical contact between larvae and their prey (Rothschild and Osborn, 1988), it can also reduce the capacity of larvae to capture and handle prey (MacKenzie and Leggett, 1993). Similarly, moderate levels of microturbulence can improve the feeding rate and growth of yellowfin tuna (Kimura et al., 2004) and Pacific bluefin tuna (Kato and Kimura, 2005) larvae, with optimal wind speed between 7.5 and 12.5 $m\,s^{-1}$ (Kato and Kimura, 2005) (high ranking; Table 1).

Hurricanes and storms can also contribute to abrupt sea surface cooling, which may have direct implications for the development and survival of tuna eggs and larvae, since the growth rate for yellowfin tuna eggs and larvae has been shown to decrease as temperature decreases (Wexler et al., 2011). Additionally, the increase in freshwater discharge to coastal waters following the passage of storms and hurricanes will increase primary production, water stratification, and the occurrence of hypoxic conditions (Rabalais et al., 2009). This was observed in the Lower Atchafalaya River basin of Louisiana following Hurricane Andrew in 1992, Hurricane Rita in 2005, and Hurricanes Gustav and Ike in 2008 (Rabalais et al., 2009).

Considering the timing of hurricane season for the GOM (from June to November), and the spawning seasons for bluefin tuna (from March to June), yellowfin tuna (from May to November) and billfish (from May to September), an increase in the frequency of more intense hurricanes in the GOM is likely to have a greater impact on yellowfin tuna and billfish eggs and larvae than on bluefin tuna eggs and larvae (high ranking; Table 1).

4. Discussion

This study provides the first comprehensive review of the state of knowledge in peer-reviewed scientific journals of the potential impacts of climate change on the biology, ecology, and reproductive success of tuna and billfish species in the GOM, focused specifically on providing a summary of relevant impacts likely to occur over a medium-term period relevant for near-term restoration and management decision-making.

Using the ISA approach, we assessed the potential for each of the identified climate-driven impacts to occur in the GOM by ~2050. Our results suggest that the climate impacts with the highest potential for realization (High categories) are primarily associated with three climate-driven pressures: increased water temperature; changes in ocean circulation and eddy kinetic energy; and changes in storm and wind patterns.

In the GOM, increases in SST higher than unfavorable threshold conditions (i.e., > 30 °C) may lead to geographic and temporal changes in breeding locations in Atlantic tunas by 2050. This scenario is considered to be particularly likely for bluefin tuna, due to this species inhabiting more temperate waters and being less adapted to warmer water temperatures than tropical tunas (e.g., yellowfin tuna) and billfish species inhabiting the GOM. Bluefin tuna are most commonly found in the GOM during their spawning season, between April and June, while they spend the rest of their adult life stage in the Atlantic, which is characterized by more temperate SST conditions (Teo and Block, 2010). However, a recent study reported the occurrence of occasional spawning grounds of likely smaller bluefin tuna in the northwest Atlantic, although based on a limited number of larvae collected in the study area (Richardson et al., 2016). Hence, the increase in SST in the GOM may result in a spatial-temporal change in the species breeding areas, with a northern shift and an earlier outset of spawning events compared to the current spawning season. This spatial-temporal change may not occur for other tropical tuna and billfish species. In fact, SST is considered as the most important parameter influencing the timing and location of breeding and spawning for bluefin tuna (Masuma et al., 2006; Teo et al., 2007a, 2007b), but not for yellowfin tuna (Teo and Block, 2010).

Moreover, the change in SST will lead to environmental conditions that may favor the development of larvae of skipjack tuna compared to other tuna and billfish species. This may lead to a niche expansion of skipjack tuna in the GOM by 2050 compared to bluefin and yellowfin tuna (Muhling et al., 2015). This scenario will likely affect bluefin tuna more than yellowfin tuna, given that bluefin tuna have a relatively shorter spawning period (1–2 months) compared to yellowfin tuna (Collette et al., 2001).

Similarly, increased SST can lead to changes in the vertical distribution of billfish, such as blue marlin. However, it is unclear whether light penetration in the water column and levels of $[O_2]$ may be important limiting factors preventing the species from effectively deepening their vertical niche compared to current conditions. More studies are needed to further investigate these aspects of billfish behavior and habitat use.

Warmer waters have important negative implications for the survival and reproductive success of tuna and billfish, due to increased potential for metabolic stress associated with overheating and decreased water $[O_2]$, which would be expected to augment fishery and post-release mortality. However, it is worth noting that the forecasted reduction in the LC warming of the northwestern GOM shelf area, which overlaps with the bluefin tuna spawning grounds, may offset the negative effects of increased SST on bluefin tuna described above (Liu et al., 2012). Additional studies are needed to clarify the role of medium-term changes in LC oceanographic dynamics and the potential cooling effect these changes could have on the northwestern GOM and on habitat suitability for spawning bluefin tuna and their larvae.

The climate-driven changes in ocean circulation that will have the highest potential to impact the reproductive success of tuna and billfish in the GOM by 2050 are changes in the propagation of warmer, anticyclonic eddies. Specifically, the potential reduction in the role that these eddies have in transporting water masses, and the highly concentrated patches of larvae contained within their boundaries, throughout the northwestern GOM (Bakun, 2013, Lindo-Atichati et al., 2012, as described further above) may be an important impediment to successful recruitment in tuna species, particularly for bluefin tuna. Therefore, alterations in eddy formation, propagation, and kinetic energy may have relevant consequences for the survival of eggs and larvae and the overall reproductive success of tuna and billfish in the GOM.

Changes in storm and wind patterns will favor increased occurrence of low [O_2] or hypoxic conditions in coastal waters resulting from increased freshwater runoff, with multiple negative impacts on tuna and billfish (i.e., reduced recruitment success, increased predation on eggs and larvae, and suboptimal temperature and [O_2] conditions for egg and larvae development and adult post-release survival). Overall, these impacts will likely increase the level of metabolic stress on adults and juveniles, and will also affect the reproductive success in tuna and billfish due to reduced survival of eggs and larvae.

We recognize that the negative effects of the various climate-driven pressures and associated impacts described above on tuna and billfish will not act in isolation, but will manifest in more complex synergistic and antagonistic ways at various spatial-temporal scales, although their predicted outcomes on tunas and billfish are not well understood yet (Hobday et al., 2015). For example, increased SST could cause a northern shift of bluefin tuna spawning areas to potentially less saline, more productive waters, with higher predation on eggs and larvae and lower [O_2]. In this scenario, increased SST favors water column stratification, which contributes to the development and maintenance of hypoxic conditions. Therefore, the synergistic effect of increased water temperature and reduced [O_2] should be considered when evaluating the magnitude of the negative implications of climate-driven impacts on the potential future reproductive success of bluefin tuna. Similarly, an example of an antagonistic effect between climate impacts is the potential reduction of the warming effect of the LC for the spawning ground of bluefin tuna in the northwestern GOM (Liu et al., 2012). This change may contribute to cooling of these areas and ameliorate or reduce the forecasted warming of water masses that is predicted based on increased SST alone. Hence, the potential decrease in the warming effect of the LC in the northwestern GOM may slow down the overall SST warming of this area.

Additionally, it is worth nothing that some of the results of our review and analysis originate from information gathered from various scientific peer-reviewed studies, each of them with different uncertainties in climate scenarios due to the specific climate models considered. Similarly, there are various climate-driven pressures (e.g., increased SST, OA) that include a high level of uncertainty, both at a general level and locally in the GOM region.

The multiple single, and synergistic and antagonistic effects, of the climate-driven pressures and their associated changes in environmental states and impacts on tuna and billfish in the GOM described above have several implications (i.e., responses in the DPSIR framework, Oesterwind et al., 2016) for the management and conservation of these species, with different implications for adults compared to eggs and larval life stages. However, we recognize the need for further studies to fill current gaps in scientific knowledge related to the various impacts of climate change on HMS, with larger gaps existing for some species. For example, the impact of OA on tuna and billfish has not been clearly addressed, although preliminary results are available for sharks (Dixson et al., 2015).

In general, an adaptive management framework can be used to help maximize success of restoration actions in a dynamic and changing environment (Walters, 1986). Adaptive management includes monitoring and scientific support to address critical information gaps, evaluate the outcomes of restoration and management actions, and utilize this new information to inform future decisions. This approach is consistent with the adoption of the precautionary principle (Article 6.5) and the use of best scientific evidence available (Article 6.4) when managing fishery resources, as stated in the Code of Conduct for Responsible Fisheries of the Food and Agriculture Organization of the United Nation of 1995 (http://www.fao.org/docrep/005/v9878e/v9878e00.htm), which was further implemented by NOAA Fisheries in 2012 (http://www.nmfs.noaa.gov/ia/resources/publications/ccrf/nmfs_imp_plan.pdf) and reflected in the National Standard 2 of the Magnuson-Stevens Fisheries Conservation and Management Act (https://www.st.nmfs.noaa.gov/science-quality-assurance/national-standards/ns2_revisions), which is the main law governing U.S. marine fisheries.

For example, the Programmatic Damage Assessment Restoration Plan/Programmatic Environmental Impact Statement (PDARP/PEIS) for the DWH oil spill includes restoration techniques to, among other things, enhance the post-release survival of tuna and billfish captured in pelagic longline fisheries, minimize interactions and reduce bycatch, and promote use of alternative fishing gears (i.e., green stick and buoy gears) as a strategy to reduce mortality within HMS populations injured by the spill (see Section D.3.2. in the PDARP/PEIS, http://www.gulfspillrestoration.noaa.gov/sites/default/files/wp-content/uploads/Chapter-5_Restoring-Natural-Resources_508.pdf). Given the synergistic impacts of increased SST and reduced [O_2] in the water column, future restoration projects that identify, test, and deploy modifications in fishing gear or adjustments in fishing behaviors should consider monitoring (e.g., environmental conditions, post-release survival) and adaptive management strategies to adjust to spatial-temporal changes in habitat use by breeding adults during the spawning season (e.g., bluefin tuna between March and April). Such projects, along with those projects focusing on improving post-release survival, may need to account for increased stress due to changes in abiotic conditions (e.g., decreased [O_2]) in tuna and billfish (Fig. 2). Furthermore, restoration projects, as part of the larger management framework for HMS, should account for spatial-temporal changes in bluefin tuna breeding grounds in the northwestern GOM and accommodate a more dynamic management approach to restoration implementation (See Maxwell et al., 2015; Wilson et al., 2015 for examples of dynamic fisheries management approaches that could be applied to restoration implementation). Finally, efforts to assess the effectiveness of restoration and management actions should account, when possible, for changes in baseline populations due to the impacts of climate change on species survival and reproductive success. Additional targeted research and supplementation of existing monitoring programs for tuna and billfish should be considered to improve understanding of shifts in spawning habitat use and identify locations to target for bycatch reduction efforts (Fig. 2).

5. Conclusions

Numerous climate-driven changes in environmental state are likely to impact the biology, ecology, survival, and reproductive success of tuna and billfish in the GOM over the next 30–40 years. Based on the research that has been conducted to date and published in scientific peer-reviewed journals, we were able to identify three climate-driven environmental pressures that are most likely to significantly impact tuna and billfish biology and habitats in the GOM by 2050: increased water temperature; changes in ocean circulation and eddy kinetic energy; and changes in storm and wind patterns. However, it should be recognized that research has only begun to address and attempt to quantify the multiple synergistic and antagonistic impacts that various climate-dependent changes can have on these species and their habitats. Results of our analysis suggest that more effort is needed to more thoroughly understand these impacts for tuna and billfish, and that more studies are needed to fill gaps at the species level (e.g., effects of increased SST, OA, and reduced [O_2] on species post-release mortality from pelagic longline fisheries). Within this context, our results may have multiple implications for the management and conservation of these species in the GOM, including ongoing efforts by federal, state, and local governments to perform restoration for these and other resources injured by the DWH oil spill. The current state of knowledge supports the need for additional monitoring and an adaptive management approach to the restoration, management, and conservation of tuna and billfish in the GOM within the context of a changing environment. In turn, this information will enhance our knowledge and understanding of the key marine environmental processes that are paramount for the biology of these species in the GOM.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.marenvres.2018.07.017.

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