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PAST, ONGOING AND FUTURE RESEARCH ON CLIMATE CHANGE IMPACTS ON TUNA AND BILLFISHES IN THE WESTERN ATLANTIC

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SUMMARY

Climate change is likely to impact migration, spawning and recruitment of Atlantic tunas and billfishes, however potential responses and mechanisms remain largely unknown. A multi-disciplinary, multi-agency research group has been using a combination of historical environmental and biological data, ecological experiments and climate modeling work to begin to address this knowledge gap. A summary of research activities over the past ~4 years is presented here. Results to date suggest that responses of highly migratory tunas and billfishes are likely to be species-specific. Temperate species such as Atlantic bluefin tuna are potentially most vulnerable. In order to estimate future trends in recruitment, an understanding of the basic ecology of early life history stages is vital, but has frequently been neglected in previous research. Collaborations across disciplines between ecologists, modelers and other researchers have allowed us to link smaller-scale laboratory studies with regional-scale models of environmental change, and to move towards development of species-specific impact models.

RÉSUMÉ

Le changement climatique a vraisemblablement une incidence sur la migration, la reproduction et le recrutement des thons et des istiophoridés de l'Atlantique, néanmoins les mécanismes et les réponses potentielles demeurent inconnus en grande mesure. Un groupe de recherche multidisciplinaire et regroupant plusieurs agences a utilisé une combinaison de données biologiques et environnementales historiques, des expériences écologiques et un travail de modélisation climatique pour commencer à combler cette lacune dans les connaissances. Un résumé des activités de recherche menées ces quatre dernières années est présenté dans ce document. Les résultats jusqu'à présent donnent à penser que les réponses des istiophoridés et des thonidés hautement migratoires sont probablement spécifiques aux espèces. Les espèces tempérées, telles que le thon rouge de l'Atlantique, sont vraisemblablement les plus vulnérables. Afin d'estimer les tendances futures du recrutement, il est crucial de comprendre les fondements de l'écologie des premières étapes du cycle de vie, ce qui a fréquemment été négligé dans les recherches antérieures. Des collaborations interdisciplinaires entre des écologistes, des modélisateurs et d'autres chercheurs nous ont permis de faire le lien entre des études en laboratoire à plus petite échelle avec des modèles à échelle régionale de changement climatique et de faire progresser le développement de modèles d'impact spécifiques aux espèces.

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RESUMEN

Es probable que el cambio climático influya en la migración, la reproducción y el reclutamiento de los túnidos e istiofóridos atlánticos, sin embargo siguen sin conocerse posibles respuestas y mecanismos. Se ha establecido un grupo interdisciplinar y de varias agencias utilizando una combinación de datos medioambientales y biológicos históricos, experimentos ecológicos y trabajos de modelación climática para empezar a abordar esta laguna en nuestros conocimientos. Aquí se presenta un resumen de las actividades de investigación de aproximadamente los últimos cuatro años. Los resultados hasta la fecha sugieren que es probable que las respuestas de los túnidos e istiofóridos altamente migratorios sean específicas de cada especie. Es probable que las especies templadas como el atún rojo sean potencialmente las más vulnerables. Con el fin de estimar tendencias futuras en el reclutamiento, es fundamentar entender la ecología básica de las primeras etapas del ciclo vital, pero este aspecto ha sido frecuentemente desatendido en investigaciones anteriores. La colaboración de varias disciplinas como ecologistas, especialistas en modelación y otros investigadores nos ha permitido vincular los estudios de laboratorio a pequeña escala con modelos de cambio medioambiental a escala regional y avanzar en el desarrollo de modelos de impacto específicos de cada especie.

KEYWORDS

Bluefin tuna, Skipjack tuna, Habitat, Long-term changes, Climatic data, Fish larvae, Environmental Conditions, Fishery oceanography

1. Background

The Intra-America Sea (IAS) comprises the semi-enclosed Caribbean Sea (CBN) and Gulf of Mexico (GOM) in the western Atlantic Ocean, and contains essential habitat for a number of highly migratory tunas and billfishes. Water temperature is of high physiological importance to these animals, as it impacts their cardiac function (Blank *et al*. 2004), swimming abilities (Dizon *et al*. 1977), spawning activity (Medina *et al*. 2002), egg hatching (Miyashita *et al*. 2000; Wexler *et al*, 2011) and larval growth (Wexler *et al*. 2011; Garcia *et al*. 2013). However, tolerances among species vary widely. Tropical species such as skipjack tuna (SKJ: *Katsuwonus pelamis*) and yellowfin tuna (YFT: *Thunnus albacares*) are found in waters of up to 30-32°C, and prefer ambient temperatures >16°C (Boyce *et al*. 2008). Conversely, the temperate Atlantic bluefin tuna (BFT: *Thunnus thynnus*) feed extensively in waters <10°C, and may be physiologically stressed by temperatures >28-29°C (Block *et al*. 2005; Blank *et al*. 2004).

Despite these differences, spawning activity for all Atlantic tunas (Ueyanagi, 1971; Richards *et al*. 1993; Espinosa-Fuentes & Flores-Coto, 2004; Muhling *et al*. 2010; Lindo-Atichati *et al*. 2012), swordfish (Govoni *et al*. 2003) and other billfish (Ueyanagi, 1971; Vasquez-Yeomans, 2000; Prince *et al*. 2005) has been reported within at least some portion of the IAS. While some species such as SKJ spawn over large areas throughout much of the year (Nishikawa, 1978), others show much more spatiotemporally restricted spawning. BFT is the most extreme example, spawning only in the GOM and immediate surrounds from April to June (Muhling *et al*. 2013; Knapp *et al*. 2014). Increasing water temperatures therefore have high potential to impact migration, spawning, larval survival and recruitment of tuna populations in the IAS, but responses are likely to be species-specific.

Collaborative research activities conducted since 2010 between the NOAA Early Life History (ELH) lab and the NOAA Atlantic Oceanographic and Meteorological Laboratory (AOML), the University of Miami, the University of South Florida, Roffer's Ocean Fishing Forecasting Service (ROFFS), the University of South Carolina and other academic and government partners have focused on the potential impacts of climate change on Atlantic tunas and billfishes. This work has was initiated using NOAA funding, and been supported by NASA's Earth Science and Biodiversity and Ecological Forecasting programs since 2011. Lines of investigation have examined both larval and adult life stages, across temperate, sub-tropical and tropical ocean environments. The aim of this document is to summarize our results to date, our current activities, and potential areas for future research and collaboration.

2. Research Approaches

2.1 Bluefin tuna spawning grounds in the Gulf of Mexico

Atlantic BFT has the most spatially and temporally restricted spawning grounds of all the Atlantic tunas. Despite an extensive adult range, spawning activity in the western Atlantic has been recorded primarily from the northern Gulf of Mexico (GOM) and immediate surrounds (Richards *et al*. 1993; Muhling *et al*. 2011a). Spawning appears to be strongly temperature-dependent, commencing when waters warm to ~24°C in spring, and tailing off once surface temperatures reach 28-29°C in early summer (Muhling *et al*. 2010).

To investigate the potential impacts of climate change induced warming on BFT spawning in the GOM, we combined a weighted ensemble of global IPCC-CMIP3 (Coupled Model Intercomparison Project) climate models with predictive habitat models for larval BFT occurrence (Muhling *et al*. 2011b). Habitat models were parameterized using larval collections from the National Marine Fisheries Service Southeast Area Monitoring and Assessment (SEAMAP) Program, and environmental data from *in situ* CTD casts. Relationships between larval distributions and water temperatures were defined using classification tree models, which were then applied to projections of environmental conditions in the GOM under CO_2 emission scenario A1B through to 2100.

Results showed a strong decrease in habitat suitability. At present, spawning primarily occurs during April – June. Under climate change, there was a decrease in suitability during the current spawning window, with a weak increase in suitability in March. Areas in the GOM with high probabilities of larval occurrence decreased in late spring by 39 to 61% by 2050, and 93 to 96% by the end of the 21st century (**Figure 1**). This preliminary study suggested that BFT are potentially highly vulnerable to climate change, based on their low tolerance of warm waters, and their use of spatially restricted sub-tropical spawning grounds (Muhling *et al*. 2011b).

2.2 Regional downscaled climate models for the Gulf of Mexico and Caribbean Sea

Global climate models predict an increase in upper ocean temperatures in the North Atlantic of around 2°C by the end of the 21^{st} century, and a slowing of the Atlantic Meridional Overturning Circulation (AMOC) of up to 25% (Schmittner, 2005). These changes are potentially significant to ecosystems and species throughout the region. However, global climate models have a typical spatial resolution of about 1°, which is too coarse to properly resolve the strength, position and eddy-shedding characteristics of regional current systems such as the Loop Current. Projections of future conditions from global models thus cannot account for changes in these systems, despite their importance to upper ocean thermal characteristics.

To address this issue, we used the Miami Isopycnic Coordinate Ocean Model (MICOM) to dynamically downscale global climate models to a regional scale (Liu *et al*. 2012). The MICOM model was coupled to an atmospheric mixed layer model (AML) to account for interactions at the air-sea interface. The spatial resolution of the coupled model was 0.1° in the GOM, decreasing linearly to 0.25° for the rest of the North Atlantic Ocean.

The downscaled model projected a reduction in the volume transport of the Loop Current by 20 – 25% during the remainder of the 21^{st} century. This may result in a slowing of the rate of warming in the northern GOM when compared to projections from global models. The downscaled model has since been updated to use the new CMIP5 climate model outputs as boundary conditions and the Modular Ocean Model (MOM) as the downscaling model. Biogeochemical fields will soon be incorporated, in addition to physical parameters such as temperature. Downscaled model outputs have been provided to a diverse range of research groups and agencies, and continue to be available to interested collaborators.

2.3 Climate change impacts on bluefin and skipjack tuna in the Intra-America Sea

BFT is the largest of the Atlantic tunas, and perhaps the best understood biologically. However, in contrast to the temperate BFT, most other commercially important Atlantic tuna species are more closely affiliated with tropical regions and habitats. YFT, SKJ and bigeye tuna (BET) support extensive fisheries throughout much of the Atlantic, however comparatively little is known of their susceptibility to climate change.

To improve the current knowledge of climate change effects on tuna species with different tolerances and life history characteristics, we extended and updated the 2011 study in several important ways. Liu *et al*. (2012) showed the importance of considering climate change at regional scales, and so we first obtained projections of future conditions using a high-resolution ocean model constrained with surface forcing fields, and initial and boundary conditions obtained from the newer CMIP5 model simulations. Projections were calculated for three scenarios: historical (a 20th century simulation), RCP 4.5 (a medium-low future emission scenario) and RCP 8.5 (a high future emission scenario). These experiments provided high resolution (0.1 x 0.1°) simulations of ocean temperature conditions for more than a century before the present day, and projections for nearly one century into the future. Temperature fields from these models were applied to habitat suitability models constructed for two life stages (adults and larvae) of two tuna species within the broader IAS region: one tropical (SKJ) and one temperate (BFT). Habitat models were parameterized using present day data, and then applied to both past and future projections of ocean conditions. Larval data were obtained from the SEAMAP program, while adult data were sourced from the ICCAT Task II database. To avoid issues associated with varying sampling and fishing efficiencies, and changes in stock sizes, biological data were considered at presence/absence level only.

Results showed marked temperature-induced habitat losses for both adult and larval BFT on their northern Gulf of Mexico spawning grounds, supporting results obtained from the 2011 study (**Figure 2**). However, in the new simulations, habitat degradation was somewhat mitigated by a predicted slowing of the Caribbean Current – Loop Current system. This was only evident in the high-resolution downscaled climate model. This result highlighted the importance of using regionally-downscaled climate models for studies of this type. In contrast to BFT, habitat suitability for both life stages of SKJ tended to increase as temperatures warmed. However, habitat model misclassification error for the two SKJ models increased at higher temperatures, resulting in considerable uncertainty around future projections. The importance of considering habitat in three dimensions (ie including diving behaviors) was also evident, as was the potentially confounding factor of fish body size in determining thermal limits. Despite these multiple sources of error and uncertainty, the contrasting effects of climate change on fish species with different physiologies and traits was clearly evident.

2.4 Temperature limits and body sizes of adult fishes

Estimates of climate change impacts on highly migratory fish species is complicated by variations in habitat use during different life stages. The ability of tunas and billfishes to tolerate warm waters often decreases with age and size, while their ability to tolerate cold waters may increase, depending on physiological characteristics (e.g. Barkley *et al*. 1978).

To investigate this phenomenon further, we extracted lengths and sexes of all recorded tunas and billfishes (swordfish, marlin, sailfish) from the NOAA Pelagic Observer Program (POP) database, covering the western Atlantic between 1992 – 2011. Satellite surface temperatures were extracted for each recorded set date and location (mean of start and end of set and haul) using the Marine Geospatial Ecology Toolbox (Roberts *et al*. 2010). Eight-day mean surface temperatures were obtained from the NOAA 4km AVHRR Pathfinder v5.1 dataset (1992 – 2009), and the MODIS Aqua 4km dataset (2003-2011). Relationships with surface chlorophyll, sea surface height and water depth were also considered (not shown here).

Example results are shown for swordfish (**Figure 3**). Catches in the Sargasso Sea and in cooler waters north of the Gulf Stream front were characterized by larger fish, while smaller fish were caught in the Gulf of Mexico, and along the US east coast. A strong separation of swordfish by size was observed across the climatological position of the Gulf Stream Front to the east of Newfoundland. Consequently, temperature associations of swordfish were strongly dependent on size. Smaller fish were proportionally more common in warmer waters, while larger fish (mostly females) were associated with cooler waters. These results show that discerning temperature effects on highly migratory species is likely to be complicated by the size- and sex-dependent responses of fish to their environment. Future continuation of this work will investigate the potential for building size-dependent models of temperature habitat for swordfish, and other Atlantic tunas and billfishes.

2.5 20th century variability

Phenomena such as the El Nino Southern Oscillation (ENSO) and the Atlantic Multidecadal Oscillation contribute to considerable decadal-scale environmental variability in the Atlantic Ocean. These have the potential to influence foraging, spawning and nursery grounds of multiple marine species (e.g. Condron *et al*. 2005; Garcia-Soto & Pingree, 2012). Examination of biological responses to past environmental conditions and extreme events can therefore assist in determining potential climate change impacts.

In order to further investigate broad-scale patterns of environmental variability for the second half of the 20th century, a high resolution biogeochemical model was constructed for the entire Atlantic Ocean. Five fields of interest were then extracted: temperature at the surface and at 200m depth, current velocity at the surface, oxygen at 200m depth, and chlorophyll at the surface. A hierarchical cluster analysis was used to group points in time and space, and to define biogeographical provinces characterized by similar conditions. Spatiotemporal changes in environmental conditions were determined by calculating the Pearson correlation co-efficient between each variable of interest at each latitude-longitude point, and the year, and then plotting this statistic in space.

Results are preliminary at this stage, but show a general warming of much of the tropical and sub-tropical Atlantic since 1950 (**Figure 4**). These regions include spawning grounds for many highly migratory Atlantic fish species, including SKJ, which is shown as an example. The cluster analysis of biogeographic provinces showed a separation of habitats initially based on surface temperature (latitude). However, considerable structure was evident in the tropical and sub-tropical regions. The GOM was separated from the Sargasso Sea by cooler temperatures at depth, and from the Equatorial Atlantic by high oxygen concentrations. The Gulf Stream extended the sub-tropical habitat northwards along the US east coast, while habitats along the western African coast were largely unique to the region. Ongoing work will define the nature of variability and changes in these habitat types through the past six decades, and investigate the use of these provinces by tunas and billfishes at different life stages.

2.6 Larval ecology studies

To understand the likely impacts of climate change on marine species, the direct and indirect effects of the biophysical environment on species of interest must first be defined. Temperature affects multiple physiological processes in fish, from eggs to larvae, juveniles and adults. However, the nature of these relationships remains poorly known in most species. This is particularly true for early life stages, even though year class strength in many stocks may be determined by mortality in the larval or early juvenile phases.

As a result, a portion of our research activities on climate change and large pelagic fishes has been devoted to studies on larval ecology. Research areas include larval aging using otoliths (Malca *et al*., this volume), examination of feeding success, diets and prey selectivity using gut contents analysis (Llopiz *et al*., this volume), and genetic analyses of tuna larvae and eggs (Quattro *et al*., unpub. data). Results from these studies are initially being applied to improve the current larval BFT index (Ingram *et al*., 2010), and development of predictors for recruitment. However, in the near future, models will be developed linking environmental conditions to larval distribution, growth and feeding success. This will improve our understanding of mechanistic connections between the biophysical environment, larval success and recruitment under both present day and future conditions. While larval ecology studies have initially focused on BFT, we have also begun to examine larval swordfish and billfish from the GOM and CBN. These larvae will be aged, and genetically identified to species where necessary. This latter activity will also contribute significantly to the improved delineation of spawning grounds for Atlantic billfishes.

Since 2009, we have participated in spring research cruises in the GOM and CBN which add to or complement the annual NOAA northern GOM bluefin tuna larval survey (**Figure 5**). These cruises have completed additional sampling in the southwestern GOM, western Caribbean, and north of the Bahamas, and have been designed to permit more detailed ecological studies of larvae collected. Larvae have been processed for genetic identification, aging, gut contents analysis, and tissue stable isotope research, in collaboration with other research groups from both within the US, and internationally. These additional sampling activities have been instrumental in improving our understanding of the ecology of tuna and billfish larvae in the region, and will be continued on an annual basis in future years if funding allows.

2.7 Larval modeling studies

Temperature, prey fields, predation mortality and oceanographic structure all influence the proportion of eggs, larvae and juveniles that encounter conditions favorable for survival. Relationships are rarely univariate or linear, and so some form of life history model is an appropriate way to predict ultimate survival rates for early life history stages. These methods have been investigated for larval BFT using two different methods to date: a one-dimensional delay-differential equations model (1DM), and an Individual Based Model (IBM).

The 1DM assumed that adult BFT spawning was triggered by temperature, and that eggs released were proportional to adult biomass. Adult biomass decreased once temperature reached known physiological stress points (e.g. Blank *et al*. 2004). Egg hatching times were shorter under higher temperatures, while larval growth rates were faster (based on current literature). Daily mortality rates were high for eggs (predation) and larvae (predation and starvation), and lower for juveniles. These rates are able to be tuned by temperature; however at present the nature of these relationships is not well known. One weakness of the 1DM is that it cannot consider two-way interactions with prey and predator fields. This was addressed by building a larval IBM in Java, using the MASON multi-agent simulation toolkit (Luke *et al*., 2005), which allowed “spawned” larvae to move and interact with prey and predators in time and space. Spatial interactions between individuals were parameterized to result in a prey, predator, piscivory, or neutral event. The model structure allowed larvae to starve if they did not encounter food within a set timeframe, to be eaten by planktonic predators, and to become piscivorous after a certain age (**Figure 6**).

Results of the 1DM showed that simple increases in temperature resulted in earlier onset and cessation of spawning, and higher concentrations of larvae earlier in the year (**Figure 7**). Assuming that larvae were not food limited, warmer temperatures could result in higher eventual recruitment of juveniles. The initial IBM experiments suggest that piscivory among larvae is a potentially important regulator of recruitment. Future work in this area will use results from ecological studies to more accurately parameterize larval models for multiple species, and to elucidate potential current and future drivers of recruitment.

3. Future Research Directions

Our research activities will continue to link studies of larval tuna and billfish ecology to models describing larval behaviors, planktonic ecosystems, and regional environmental variability and change. We will continue to collate historical data sources, particularly from plankton and larval fish surveys, and from various satellites that provide observations on multiple oceanographic parameters. We will also continue to collect new data on annual cruises in the GOM and CBN. Results from ecological studies will be used to parameterize detailed individual-based models, and determine the potential effects of climate change on larval survival and recruitment. In addition, our regional climate modeling work is incorporating biophysical components into downscaled climate models, which will allow us to examine multiple climate drivers on biological populations.

We also aim to continue collaborative activities with other institutions working on tuna and billfish spawning grounds in other parts of the Atlantic, particularly in the western Mediterranean. For example, Muhling *et al*. (2013) compared environmental conditions on BFT spawning grounds in the GOM vs. waters around the Balearic Islands. This work found that temperature was of significant importance in determining spawning activity. We hope to extend this collaboration to consider climate change impacts on tuna larvae on both sides of the Atlantic.

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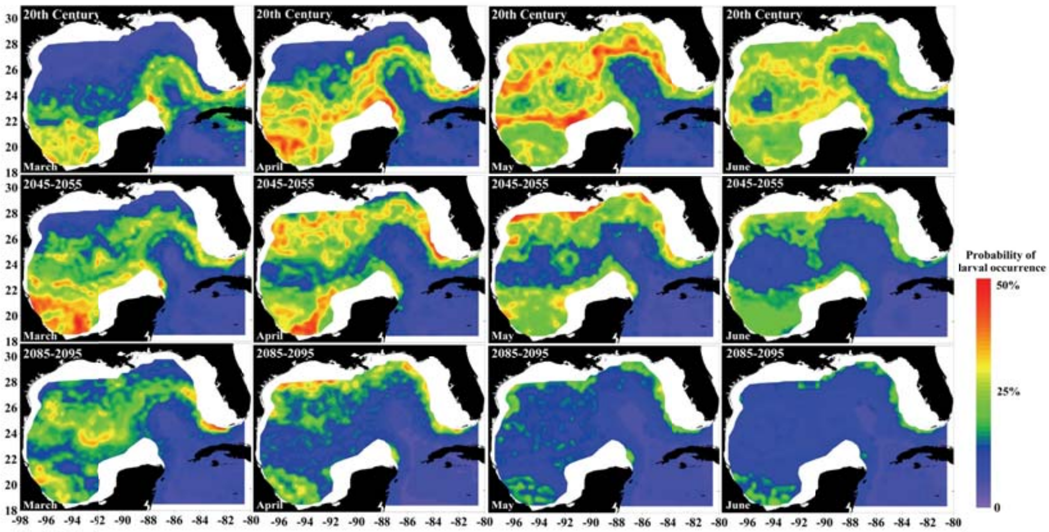

Figure 1. Prediction of the extent of habitat suitable for the occurrence of larval bluefin tuna in the Gulf of Mexico under late 20th century conditions (1971 to 1999), and projected conditions in 2045 to 2055, and 2085 to 2095, for the months of March, April, May and June. The probability of occurrence (%) is shown, based on output from the boosted classification tree model using weighted mean temperature values (Muhling *et al.* 2011b).

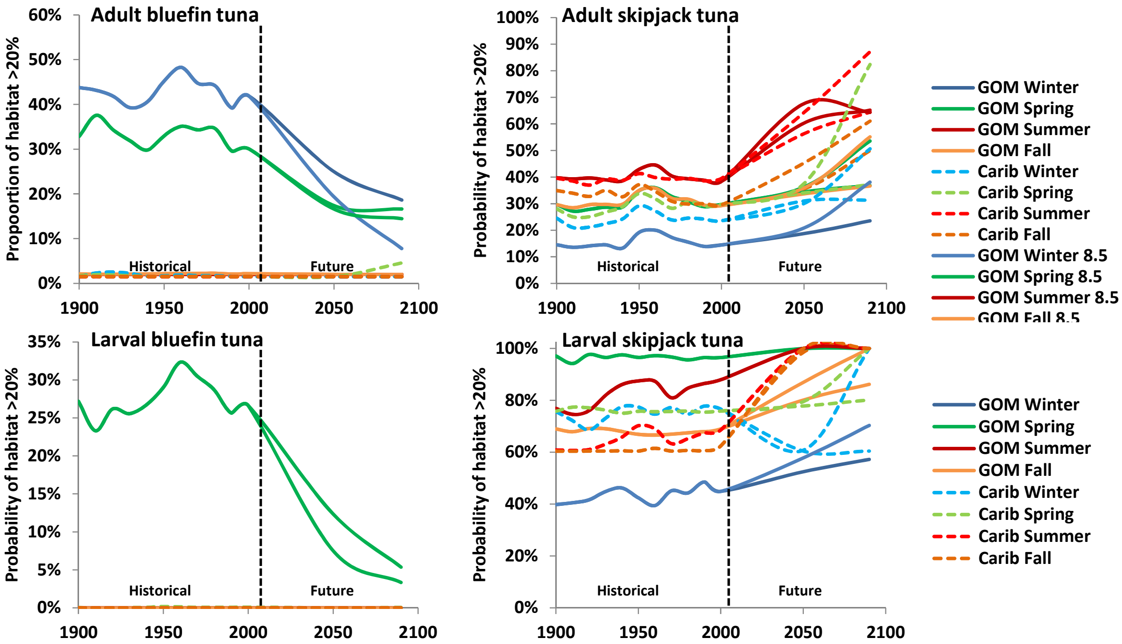

Figure 2. Decadal time series of favorable habitat (spatial grid points with >20% predicted probability of occurrence) for adult and larval skipjack and bluefin tuna from a 20th century (1900-2008), and future (2000-2090) downscaled model. Probabilities of occurrence are sourced from boosted regression tree models, and are shown by season for the Gulf of Mexico and Caribbean Sea.

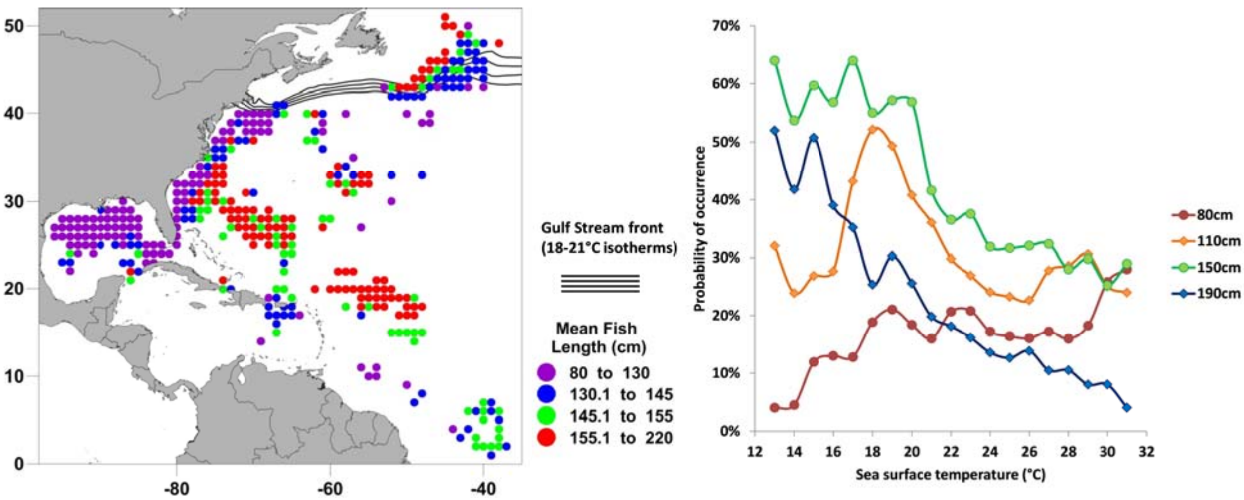

Figure 3. Left: Mean swordfish body lengths from the NOAA Pelagic Observer Program database, 1992-2011. The climatological position of the Gulf Stream from the NOAA Pathfinder 4km AVHRR dataset is also shown. Right: Surface temperature associations for swordfish of different sizes.

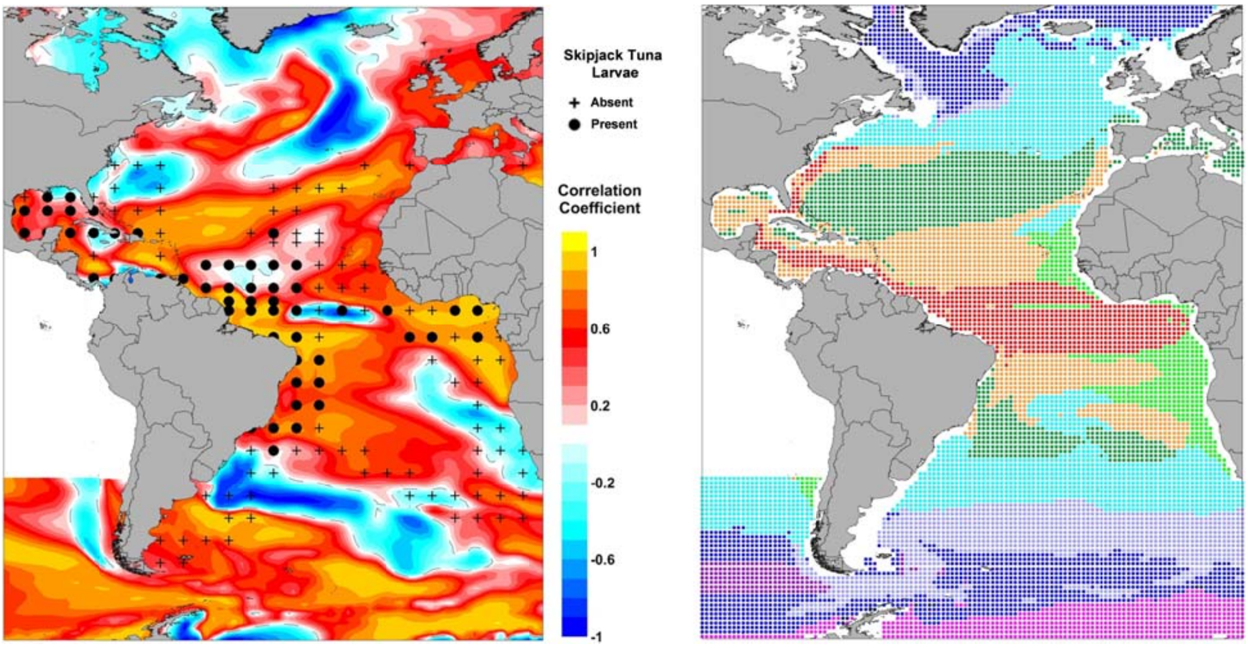

Figure 4. Left: decadal-scale spatial trends of summer sea surface temperature, 1950s – 2000s. Distributions of larval skipjack tuna, compiled from historical surveys, are also shown. Right: Biogeographic provinces from a cluster analysis of temperature (0 & 200m), current velocity, (0m) oxygen (200m) and chlorophyll (0m), sourced from a biogeochemical model for the Atlantic Ocean (Liu *et al*. unpublished data).

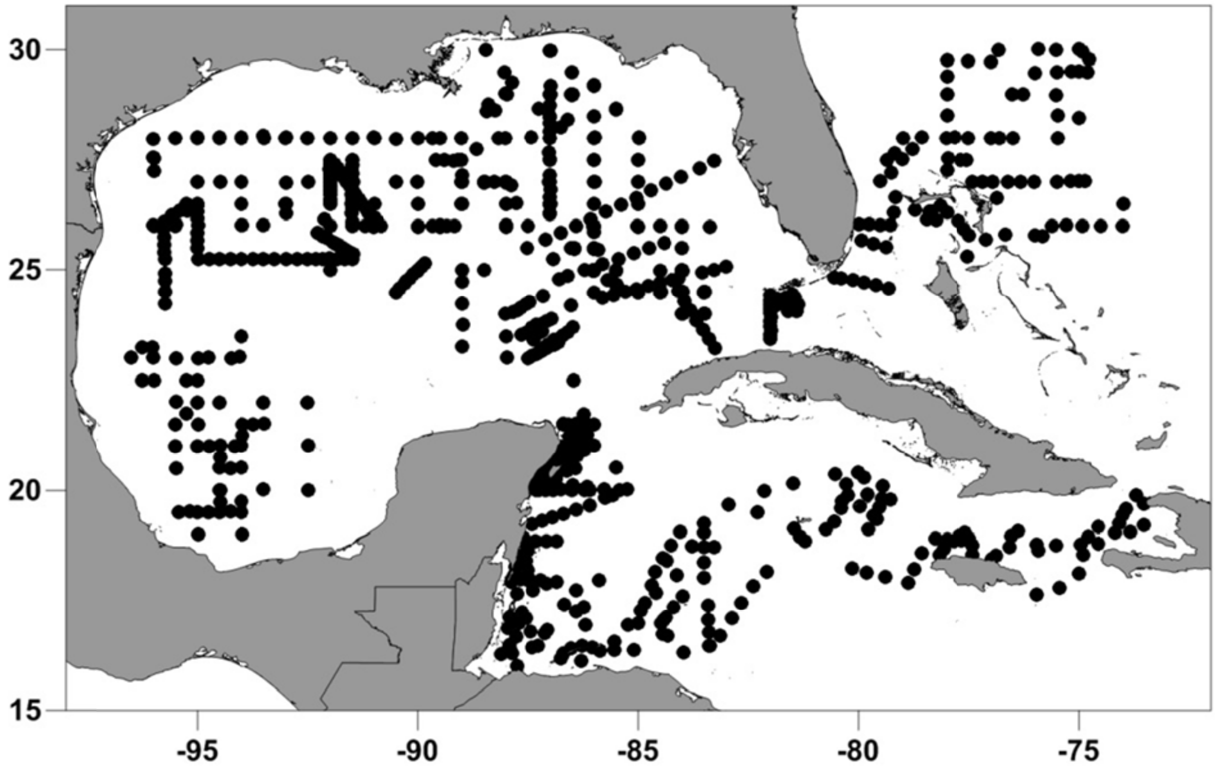

Figure 5. Stations sampled during larval ecology cruises, 2009 – 2013.

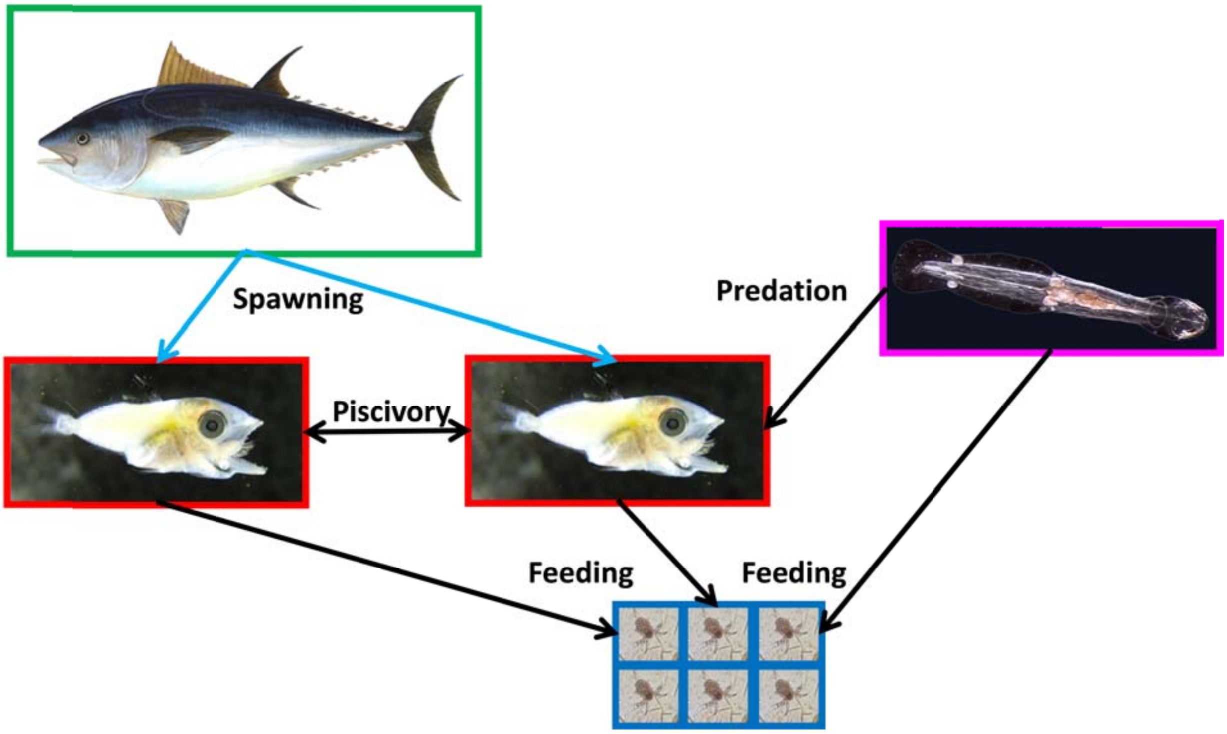

Figure 6. Basic structure of an Individual Based Model for larval bluefin tuna, showing relationships among adult fish, larvae, zooplankton (prey) and planktonic predators (chaetognath shown as an example) (Images: NOAA).

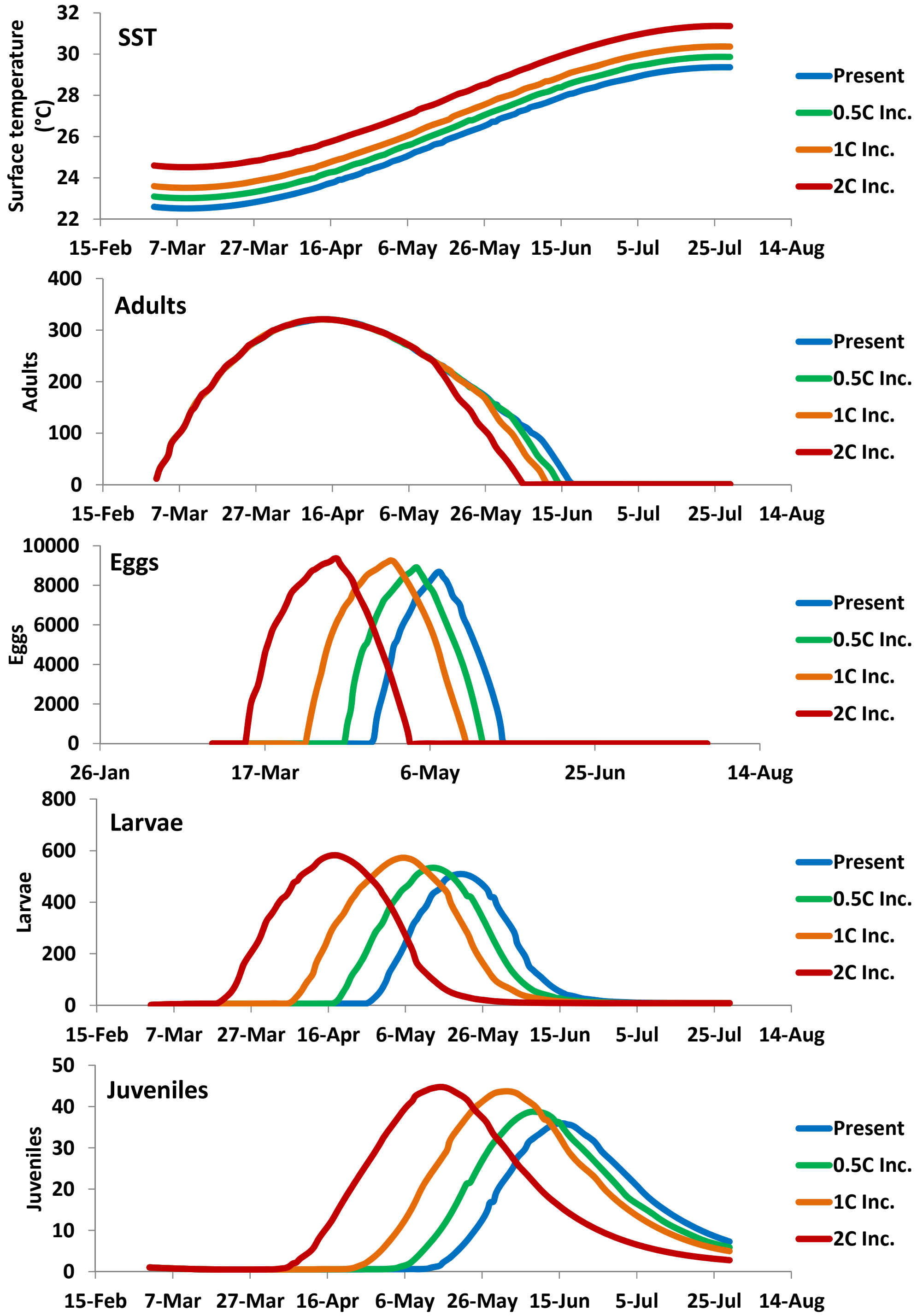

Figure 7. Preliminary results of a one-dimensional delay differential equation model, showing relative abundances of adults, eggs, larvae and juveniles of bluefin tuna on their spawning grounds, under four temperature scenarios.