Potential impact of climate change on the Intra-Americas Sea: Part 2. Implications for Atlantic bluefin tuna and skipjack tuna adult and larval habitats

Barbara A. Muhling [a,b,*], Yanyun Liu [a,c], Sang-Ki Lee [a,c], John T. Lamkin [b], Mitchell A. Roffer [d], Frank Muller-Karger [e], John F. Walter III [b]

[a] Cooperative Institute for Marine and Atmospheric Studies, University of Miami, Miami, FL, USA
[b] Southeast Fisheries Science Center, NOAA, Miami, FL, USA
[c] Atlantic Oceanographic and Meteorological Laboratory, NOAA, Miami, FL, USA
[d] Roffers Ocean Fishing Forecasting Service, Melbourne, FL, USA
[e] College of Marine Science, University of South Florida, St Petersburg, FL, USA

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ABSTRACT

Increasing water temperatures due to climate change will likely have significant impacts on distributions and life histories of Atlantic tunas. In this study, we combined predictive habitat models with a downscaled climate model to examine potential impacts on adults and larvae of Atlantic bluefin tuna (*Thunnus thynnus*) and skipjack tuna (*Katsuwonus pelamis*) in the Intra-Americas Sea (IAS). An additional downscaled model covering the 20th century was used to compare habitat fluctuations from natural variability to predicted future changes under two climate change scenarios: Representative Concentration Pathway (RCP) 4.5 (medium–low) and RCP 8.5 (high). Results showed marked temperature-induced habitat losses for both adult and larval bluefin tuna on their northern Gulf of Mexico spawning grounds. In contrast, habitat suitability for skipjack tuna increased as temperatures warmed. Model error was highest for the two skipjack tuna models, particularly at higher temperatures. This work suggests that influences of climate change on highly migratory Atlantic tuna species are likely to be substantial, but strongly species-specific. While impacts on fish populations remain uncertain, these changes in habitat suitability will likely alter the spatial and temporal availability of species to fishing fleets, and challenge equilibrium assumptions of environmental stability, upon which fisheries management benchmarks are based.

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1 . Introduction

Average upper ocean temperatures have increased markedly in many regions of the world in recent decades (Hansen et al., 2006; Rhein et al., 2013), and evidence of associated shifts in the distributions of marine populations continues to accumulate (Last et al., 2011; Nye et al., 2009; Pinsky and Fogarty, 2012). Temperature-sensitive organisms may respond by moving poleward, to deeper waters, or they may become locally extinct from key habitats altogether in response to warming conditions (Dulvy et al., 2008; Fodrie et al., 2010; Perry et al., 2005). The life history requirements, migratory behavior and motility of each species will affect its ability to adapt to a changing environment, or to relocate to more favorable habitats (Koehn et al., 2011; Sharp, 1978). While organisms with broad physical tolerances may be able to withstand warming temperatures with a minimum of adaptive behavior, those already existing close to their physical limits are more likely to be significantly affected (Dulvy et al., 2008; Rijnsdrop et al., 2009).

In addition to changes in spatial distributions, climate change may influence marine species through loss or degradation of habitat, altered rates of larval survival and recruitment potential, and subsequent impacts on stock resilience, as a result of physiological and behavioral responses to environmental gradients (Ciannelli et al., 2005; Perry et al., 2005; Scavia et al., 2002). Where species are exploited and/or managed, climate change will introduce additional complexities. Although the potential role of environmental variability in stock dynamics is being increasingly recognized, and capacity to incorporate climatic changes is improving (Daskalov, 1999; Jacobson and MacCall, 1995; Punt and Hilborn, 1997; Wayte, 2013), most fisheries are still largely managed and assessed under the assumption that ocean climate characteristics are stationary. Robust fisheries management in a changing climate that may alter abundance, distribution or productivity of fish stocks will require incorporating predicted climatic impacts (Hobday et al., 2013).

* Corresponding author at: NOAA/SEFSC, 75 Virginia Beach Drive, Miami, FL 33149, USA. Tel.: +1 305 361 4289.
E-mail address: Barbara.Muhling@noaa.gov (B.A. Muhling).

The Intra-Americas Sea (IAS) comprises the semi-enclosed Caribbean Sea (CBN) and Gulf of Mexico (GoM) in the western Atlantic Ocean. In recent years (2005–2010), climatological summer surface temperatures in the region, particularly the GoM, have been among the warmest recorded globally. Continued warming in this geographical area may therefore test thermal tolerances of resident species beyond currently observed limits worldwide. In addition, the position of the northern GoM coast limits poleward expansion, and may restrict the ability of species to avoid unfavorably warm water temperatures through northern displacement.

The IAS is essential habitat for a number of highly migratory fish species, particularly tunas and billfishes (Schaefer, 2001). 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 (Gordoa & Carreras, 2014; Miyashita et al., 2000; Wexler et al, 2011) and larval growth (Garcia et al., 2013; Wexler et al., 2011). Indirectly, water temperature may also drive migration patterns (Fromentin et al., 2014), and dynamics of prey species (Trenkel et al., 2014). However, temperature tolerances among species vary widely. Tropical forms 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 of >16 °C (Boyce et al., 2008). Conversely, the temperate Atlantic bluefin tuna (BFT: *Thunnus thynnus*) feed extensively in waters of <10 °C, and are likely to be physiologically stressed by temperatures > 28–29 °C (Blank et al., 2004; Block et al., 2005; Boyce et al., 2008).

Despite these differences, spawning activity has been reported for all Atlantic tunas within at least some portion of the IAS (Espinosa-Fuentes & Flores-Coto, 2004; Lindo-Atichati et al., 2012; Muhling et al., 2010; Richards et al., 1993; Ueyanagi, 1971). 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, with the western population spawning only in the GoM and immediate surrounds from April to June (Knapp et al., 2014; Muhling et al., 2013).

Increasing water temperatures are therefore highly likely to impact migration, spawning, larval survival and recruitment of tuna populations in the IAS. Different species may show different responses and vulnerabilities, depending on their physiology and life history. When a simple habitat model for occurrence of larval BFT was previously applied to an IPCC-AR4 climate model projection, results suggested almost complete loss of spring spawning habitat in the late 21st century (Muhling et al., 2011a). However, a subsequent study in which downscaled global climate models to a regional scale indicated that temperature projections for the northern GoM may be over-estimated by global models (Liu et al., 2012). This was due to the inability of these low resolution models to resolve the characteristics of the Loop Current. Liu et al. (2012) instead predicted that the major circulation features of the GoM will weaken substantially by the late 21st century, slowing the rate of warming in the northern GoM. These results imply a need to consider the dynamics of regional current systems when predicting the biological and ecological impacts of climate change.

Here, we aimed to extend current knowledge of climate change impacts on tunas in several ways. First, we obtained projections of future conditions using a high-resolution ocean model. This model was constrained with new versions of surface forcing fields, and initial and boundary conditions obtained from the Coupled Model Intercomparison Project phase-5 (CMIP5) model simulations, under 20th century, Representative Concentration Pathway 4.5 (RCP 4.5) and 8.5 (RCP 8.5) scenarios (Liu et al., this issue). In addition, to explore the usually-neglected impact of natural climate variability on the region, we used outputs from a high-resolution dynamically downscaled ocean model, for the period 1871–2008 (Liu et al., this issue). These experiments provided simulations of ocean temperature conditions for more than a century before the present day, and projections for nearly one century into

the future. We applied temperature fields from these models 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. Variability in adult and larval habitats, and potential losses and gains into the future were then quantified.

2 . Methods

2.1 . Adult data

Catch rate data for adult BFT and SKJ were obtained from the International Commission for the Conservation of Atlantic Tunas (ICCAT) Task II database, downloaded from www.iccat.es. All gear types were
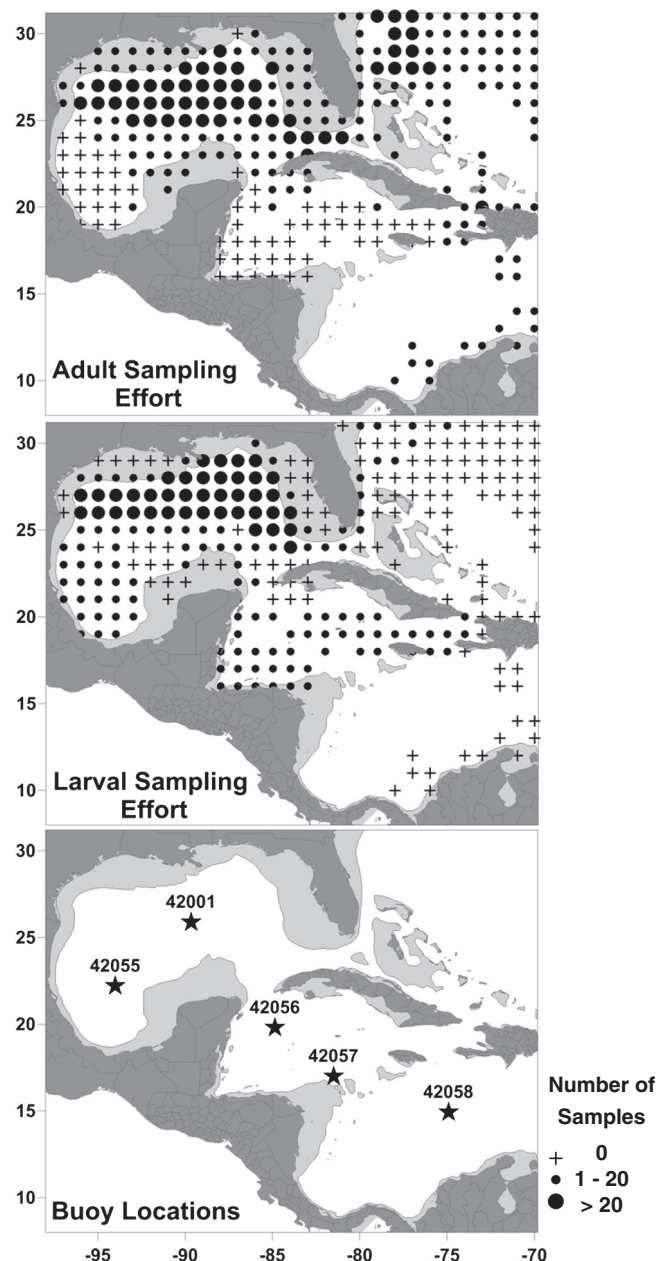

Fig. 1. Total number of data points available for adult (top), and larval catch locations (middle). Locations of five buoys used to calculate surface temperature trend by month are also shown, with NOAA identification numbers (bottom). The shaded region in each map represents the 200 m depth contour.

considered, however 98.2% of records for the GOM/CBN region were from pelagic longlines. To reduce biases from temporal changes in stock sizes, reporting rates, and fishing methods, only presence/absence data from 2000–2009 were used for habitat model development. Monthly data gridded at 1 × 1 degree resolution (the highest resolution available) were included in analyses (Fig. 1). To visually assess habitat model predictions, data from 1990–2009 were overlaid on probabilities of occurrence for the present day. Data from these two decades were used for this purpose as they included greater coverage of the CBN region than data from the 2000s only. However, data coverage for both adults and larvae was much greater in the GoM than the CBN (Fig. 1).

2.2. Larval data

Larval data were obtained from the South-East Monitoring and Assessment Program (SEAMAP) database (Lyczkowski-Shultz and Hanisko, 2007). Sampling effort has typically covered the shelf and off-shore areas of the northern GoM in spring, and inshore and shelf areas in summer and fall, and has been ongoing since 1982. More recent cruises since 2009 have completed some limited sampling in the south-western GoM and CBN (Fig. 1). The most complete time series available were from bongo and neuston net sampling. The bongo net is a 61 cm diameter round net with 333 μm mesh, towed obliquely to 200 m depth, or within 2–5 m of the bottom (Richards et al. 1993). The neuston net is 1 × 2 m with 950 μm mesh, and is towed at the air–sea interface. Samples were sorted, and larval fish were identified to the lowest possible taxa, at the Sea Fisheries Institute Plankton Sorting and Identification Center, Gdynia and Szczecin, Poland. In order to account for sampling inefficiencies among net types (Muhling et al., 2012), larval fish data were used at the presence/absence level. If either or both nets at a sampling station recorded a species of interest, the station was considered to be positive.
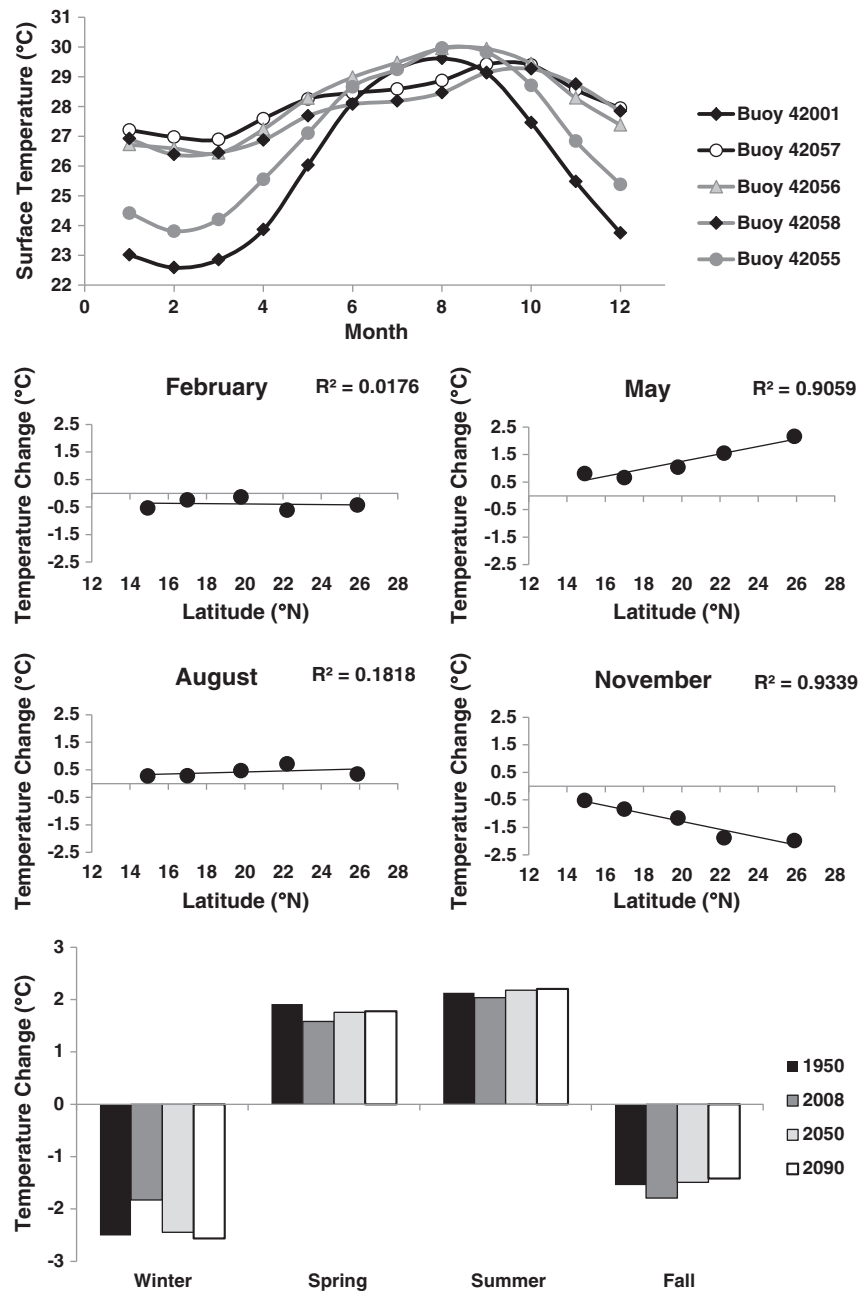

Fig. 2. Mean monthly surface temperatures at five buoys in the IAS region (top). Linear correlations between mean month-to-month surface temperature change and latitude for all five buoys in February, May, August and November (middle). Mean season-to-season surface temperature change from downscaled model outputs, for 1950, 2008, 2050 and 2090 (bottom).

Table 1
Details of habitat suitability models for adult and larval skipjack and bluefin tuna, using boosted regression trees. Sensitivity, specificity and the Area under the Receive Operating Characteristic curve (AUC) are shown for the training and validation portions of the data. SST refers to sea surface temperature and T200 is temperature at 200 m. Variable importance is scored out of 100.

	Adult BFT	Adult SKJ	Larval BFT	Larval SKJ
Misclassification cost	4	5	5	3
Sensitivity: training (%)	81.8	83.5	80.8	83.6
Specificity: training (%)	84.1	69.2	71.4	49.5
AUC: training	0.91	0.85	0.84	0.73
Sensitivity: validation (%)	71.0	76.6	63.9	72.9
Specificity: validation (%)	83.3	68.0	72.9	53.4
AUC: validation	0.85	0.78	0.77	0.68
Variable importance: SST	81.1	36.4	66.3	100
Variable importance: T200	34.2	37.6	54.9	18.2
Variable importance: depth	100	100	20.1	29.4
Variable importance: Monthly SST trend	75.7	31.7	100	38.3

2.3 . Environmental data

Reliable environmental data were not recorded along with adult catch data, and so relevant environmental measurements were obtained from remotely sensed satellite data. Surface temperature values were extracted from the NOAA 4 km AVHRR Pathfinder v5.1 dataset, at monthly resolution, using the Marine Geospatial Ecology Toolbox (Roberts et al., 2010). Temperatures at 200 m depth were extracted from the 0.25 × 0.25° "Estimating the Circulation and Climate of the Ocean, Phase II" (ECCO II) project (www.ecco2.org), also at monthly resolution. Water depths were extracted from NOAA's 1 minute GEODAS bathymetry database.

Larval collections were accompanied by various depth-resolved environmental observations. Conductivity–Temperature–Depth (CTD) casts were conducted at most SEAMAP stations, providing *in situ* temperatures at the surface and 200 m depth. Where cast data were missing or unavailable, temperatures at the surface and at 200 m depth were obtained from the Gulf of Mexico HYCOM + NCODA 1/25° Analysis (2008 − present, daily resolution). The linear correlation coefficient

between *in situ* and modeled surface temperatures (where both were available) was 0.90 with a slope of 0.93 at the surface, and 0.91, with a slope of 0.95 at 200 m. This suggested that the modeled data provided satisfactory estimates of *in situ* conditions, with minimal bias. Water depths were obtained in the same manner as for adult data.

One additional important variable was the seasonal trend of the surface temperature. Spawning may be triggered by both the presence of suitable temperatures, and by the rate of change of temperature (*e.g.* Medina et al., 2002). To estimate the seasonal trend in surface temperature by year, we used data from five buoys spread across the study region (Fig. 1). Data were downloaded from www.ndbc.noaa.gov. Buoys located at more northern latitudes showed a more pronounced seasonal signal, with lower surface temperatures in winter and fall. Mid-winter (February) and mid-summer (August) temperature rates of change were weak, and not strongly related to latitude. In contrast, mid-spring (May) and mid-Fall (November) rates of change were more pronounced, and were strongly related to latitude (Fig. 2). Buoy 42001 in the northern GoM has been recording almost continuously since 1984, and so mean monthly surface temperature trends from this buoy were applied to all larval and adult records from the GoM, specific to the year of capture. Monthly climatologies were used for larval stations sampled in 1982–83. The other four buoys have only been recording since 2005, and so climatological monthly means for surface temperature trends were averaged for the three CBN buoys, and applied to all samples collected in the CBN. On a seasonal basis, temperature rates of change between the mid-20th century, and the early, mid and late 21st century, from modeling outputs (below, and Liu et al., this issue) were similar, and so present day values for this parameter were applied to both past and future projections of habitat suitability.

2.4 . Habitat modeling

Four habitat models were built for this study: one each for larval and adult SKJ, and larval and adult BFT. Models were developed in DTREG software (Sherrod, 2003), using boosted classification trees. These models are non-parametric, flexible, can model highly non-linear relationships and interactions, and can cope well with zero-inflated data (Elith et al., 2008). For the presence/absence models, misclassification
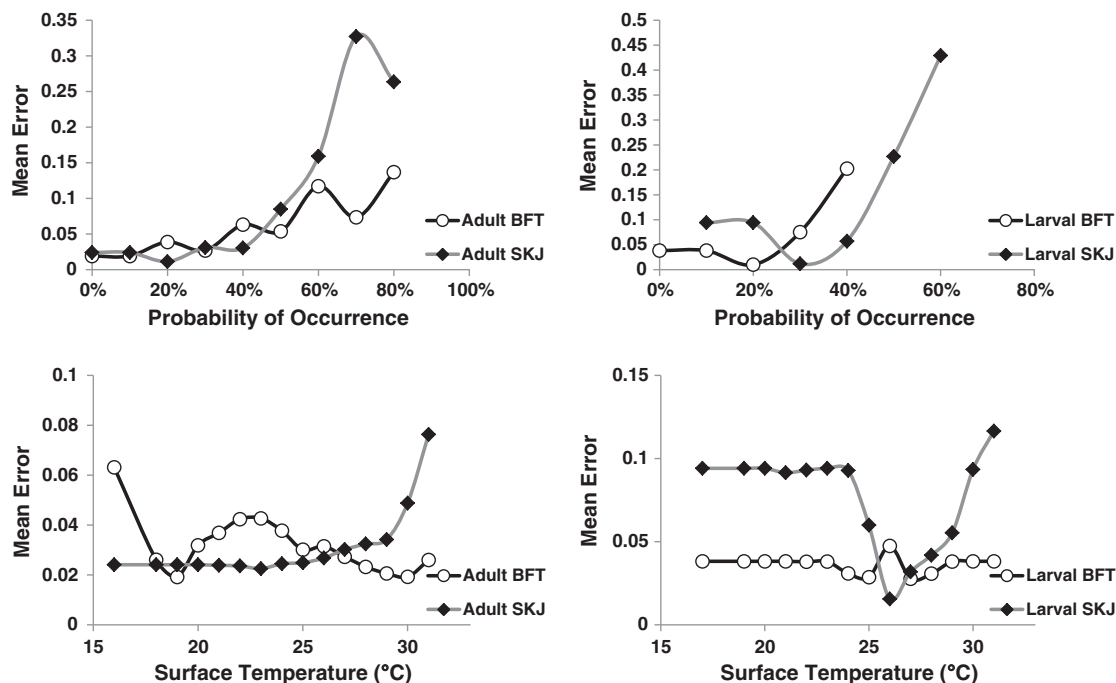

Fig. 3. Boosted classification tree model errors, plotted against probability of occurrence (top) and sea surface temperature (bottom). Only results from data used to train models are shown.

costs can be adjusted to give greater weight to placing positive occurrences in good habitat, which is useful for organisms which may be under-reported, or with sub-optimal catch efficiencies (*e.g.* Muhling et al., 2012). Models were validated using v-fold cross validation (Sherrod, 2003). The final model for each run was selected automatically by maximizing the Area under the Receive Operating Characteristic curve (AUC). The closer the AUC is to 1.0, the better the model is considered to be (Sherrod, 2003). The misclassification cost was then adjusted iteratively over several model runs, until >80% of positive catches were placed in predicted favorable habitat. The importance of each predictor variable to the final model was calculated by its importance in splitting data within trees, and was ranked out of a maximum possible score of 100.

The error of each model was quantified using probability calibration (Sherrod, 2003). The predicted probability of occurrence for each model was binned in 10% increments (*i.e.* 0–10% probability of occurrence, 10–20% *etc.*), and the predicted and observed proportions of positive samples were compared. For example, if the mean predicted probability of

occurrence within the 10–20% bin was 0.15, but the observed proportion of positive stations was 0.17, the error for that bin would be 0.02. This error was then applied to all predictions from that particular habitat model falling between 10 and 20% probability of occurrence.

2.5 . Past and future conditions

Outputs from two sets of downscaled ocean model experiments were applied to habitat models constructed from present day data: one projected conditions from 2006–2098, and the other reconstructed conditions from 1871–2005 (EXP_4.5, EXP_8.5, EXP_20CR, Liu et al., this volume). The Modular Ocean Model version 4.1 (MOM4) (Gnanadesikan et al., 2006; Griffies et al., 2004) was used as the downscaling model. The regional MOM4 model domain covered the Atlantic Ocean between 100°W and 20°E bounded north and south by 65°N and 20°S, respectively, with a horizontal resolution of 0.1° over the
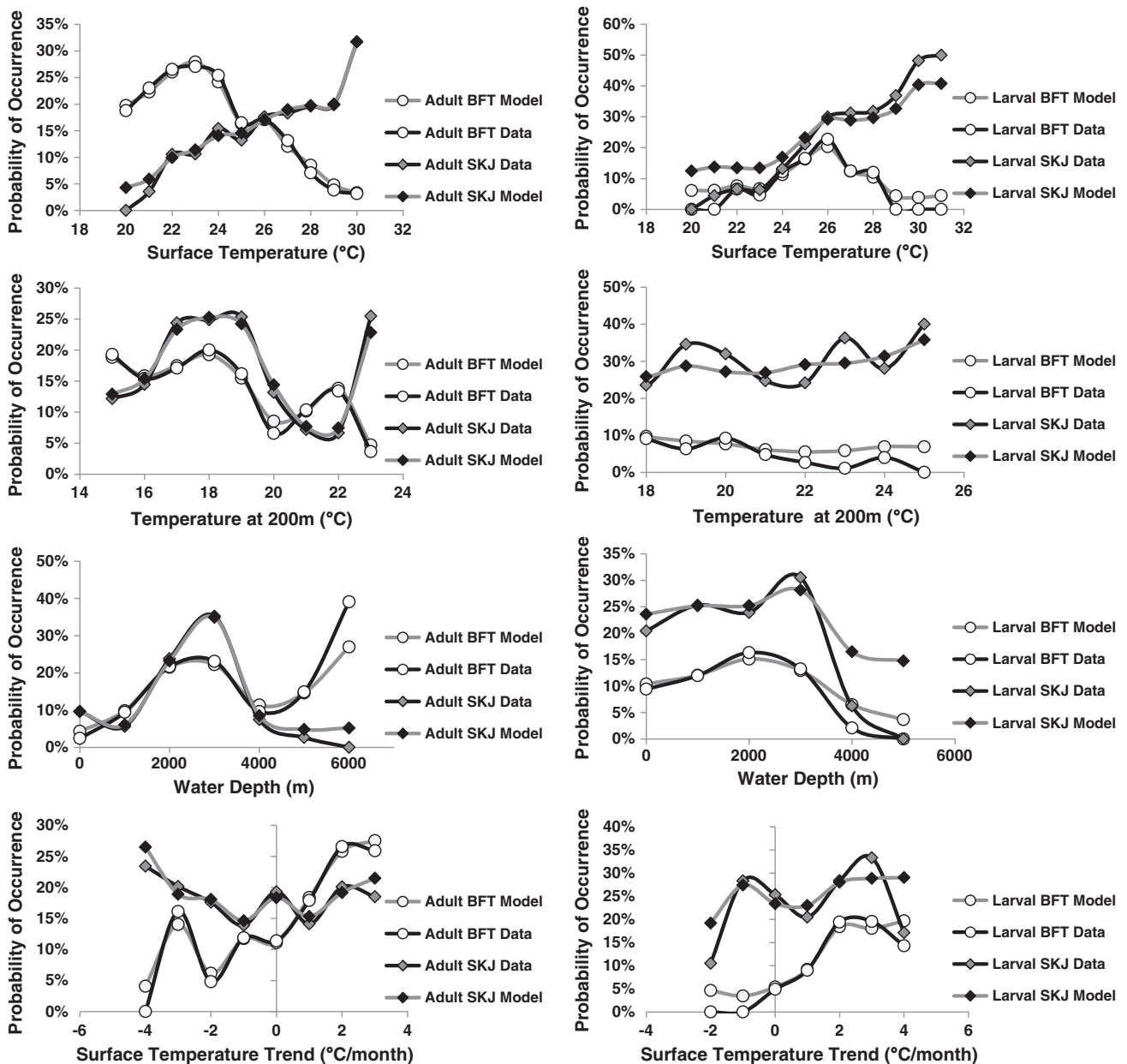

Fig. 4. Comparison of modeled *vs.* observed probabilities of occurrence for adult and larval skipjack and bluefin tuna. Relationships with binned surface temperature, temperature at 200 m depth, water depth and monthly surface temperature trend are shown.

GoM and CBN region from 10°N to 30°N, and from 100°W to 70°W decreasing linearly to 0.25° in the rest of the model domain.

The downscaled model of future conditions was driven by surface forcing fields from a set of CMIP5 climate models, for three different scenarios: 20th century, RCP 4.5 (medium–low future emission scenario) and RCP 8.5 (high future emission scenario). A total of 18 CMIP5 models were selected, and each was ranked and weighted based on their ability to replicate observed temperature at 0, 100 and 200 m, and Atlantic Meridional Overturning Circulation (AMOC) for the last 30 years of the 20th century (Liu et al., this issue). Biases in surface forcing fields were minimized by computing the difference between late 20th century conditions predicted by the CMIP5 models *versus* an observed climatology.

The downscaled model of past conditions was driven by surface forcing fields from the 20th Century Reanalysis version 2 (20CR) dataset (Compo et al., 2011). The initial and boundary conditions were derived from the Simple Ocean Data Assimilation version 2.2.6 (SODA 2.2.6) product (Giese and Ray, 2011), and all input fields were bias-corrected following the same methodology used for the model of future conditions. The first 30 years of model outputs were discarded to exclude any potentially spurious spin-up effects. Mean temperatures at the surface and at 200 m depth were then summarized by season, year and 0.25 × 0.25° latitude–longitude points, and run through the habitat models built using present day data. This resulted in probabilities of occurrence in space and time for larvae and adults of the two species of interest, from 1900 through to 2090. Probabilities were kriged and mapped in Surfer 9 (Golden Software), to aid interpretation.

To assess the effect of using a downscaled model on predictions of habitat suitability, habitat model predictions were compared between models run on temperature outputs from the downscaled model, and coarse resolution temperature projections from global climate models (Liu et al., this issue). Global climate model outputs were interpolated onto a 1 × 1° grid, and results were compared between the years 2050 and 2090, for RCP scenarios 4.5 and 8.5. The habitat model for larval bluefin tuna during spring was used as an example.

3. Results

3.1. Habitat models and environmental variables

Boosted regression tree models were successfully parameterized for both life stages of both species of interest (Table 1). The model for adult BFT showed the highest ability to distinguish between favorable and unfavorable habitat, with both sensitivity and specificity > 80%, while the model for larval SKJ had the lowest (sensitivity of 83.6% was only achieved if specificity was 49.5%). The larval BFT model lost the most precision between training and validation, suggesting the greatest tendency towards over-fitting.

Surface temperature was of the greatest importance to the adult BFT and larval SKJ models (score of 81.1 and 100, respectively). Temperature at 200 m was of moderate importance to the larval BFT model (score of 54.9), and of lesser importance to the other models. Water depth was the most influential variable for both adult models. SKJ showed a parabolic response, with peak probabilities of occurrence between ~2000 and 4000 m. Adult BFT were also most abundant within this depth range, and also in very deep waters > 5000 m, reflecting their occurrence north of the Bahamas. The surface temperature trend was of greater importance to the BFT models than to the SKJ models.

Model errors for all four models tended to increase at higher probabilities of occurrence (Fig. 3). Both adult and larval SKJ models showed markedly higher errors at warmer (>29 °C) temperatures, while BFT models did not. Model errors were generally higher for larval models than those for adults.

Scatter plots of both modeled and observed probabilities of occurrence against the four predictor variables highlighted strong differences among species and life stages (Fig. 4). While adult SKJ showed a positive response to increasing surface temperature, adult BFT showed a generally negative response if temperatures exceeded 24 °C. Similarly to adult SKJ, larval SKJ were more likely to be encountered in warmer waters. In contrast, larval BFT peaked in abundance between 24 and 28 °C, and were rare in waters warmer than 29 °C. Model predictions generally
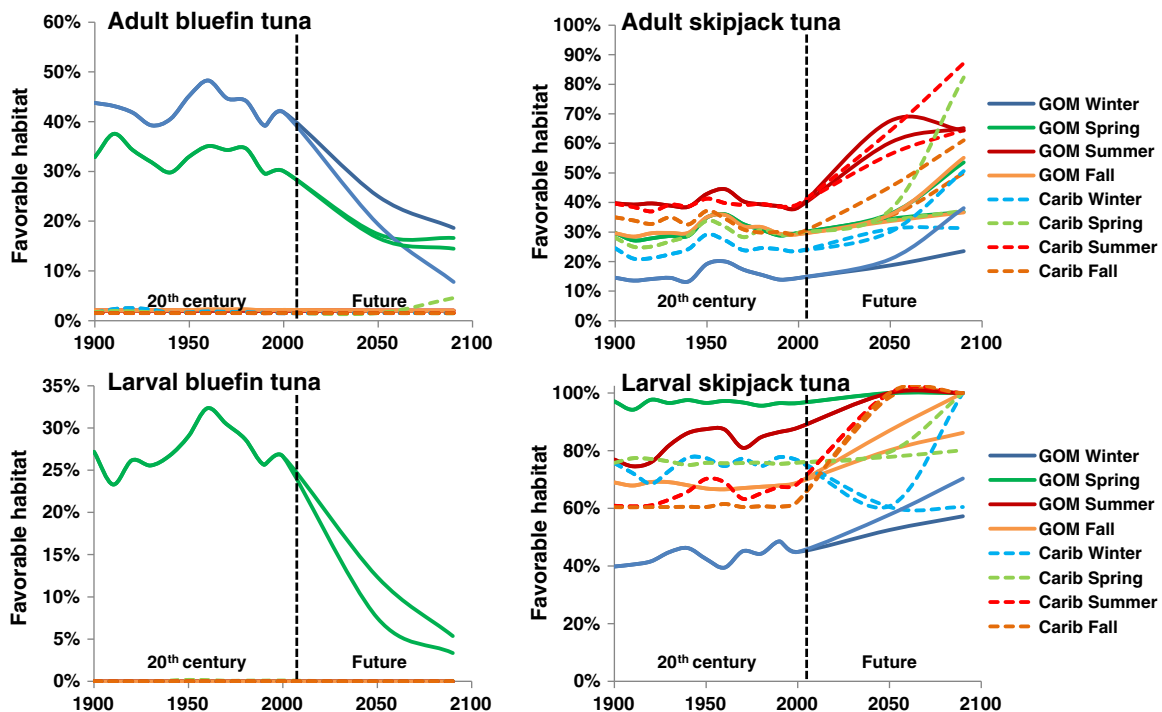

Fig. 5. Decadal time series of favorable habitat (spatial grid points with >20% predicted probability of occurrence) for adult and larval skipjack and bluefin tuna, 1900 to 2090. Series are shown by season for the Gulf of Mexico and Caribbean Sea. Diverging lines of the same color and style represent the two RCP scenarios: 4.5 and 8.5. For adult and larval BFT, the RCP 8.5 scenario is always the series with the less favorable habitat predicted for 2050 and 2090. For adult and larval SKJ, the RCP 8.5 scenario is always the series with the higher probability of occurrence in 2050 and 2090.

matched well with observations, although both SKJ models over-estimated probabilities of occurrence at cooler temperatures.

Both adult and larval BFT showed a weak, negative relationship with temperature at 200 m depth, while larval SKJ showed a slight positive response (Fig. 4). Adult SKJ were most commonly recorded where water depths were between 2000 and 3000 m, while adult BFT were most common at deeper depths (up to 6000 m). Larval occurrences of both BFT and SKJ decreased where water depths were >3000 m, however both larval models over-predicted probabilities at deeper water depths. The surface temperature trend was more important for BFT than SKJ, with both adult and larval stages more commonly encountered where trends were positive (i.e. during spring).

3.2. Temporal changes in habitat suitability

Predicted changes in future temperature conditions from the down-scaled climate model resulted in marked effects on predicted habitat suitability for both life stages of BFT and SKJ (Fig. 5). Habitat extent from 1900–2000, as measured by the proportion of spatial grid points where probabilities of occurrence for adult BFT were >0.2, was highest in the GoM during winter and spring. Spring habitat extent peaked during the early 20th century, while winter habitat was highest during the 1960s–1970s, due to cooler surface temperatures during these time periods. After 2010, habitat extent in both winter and spring decreased strongly, with steeper declines apparent under RCP 8.5.

Impacts of climate change on adult SKJ appeared to be more positive (Fig. 5). Habitat extent in both the GoM and CBN increased throughout the 21st century, particularly under RCP 8.5. Increases were predicted to be strongest in the CBN in spring, summer and fall. All trends were fairly linear between 2000 and 2100, with the exception of the GoM in summer, which showed little change between probabilities of occurrence between 2050 and 2090.

Similarly to adult BFT, larval BFT were predicted to be negatively affected by future warming (Fig. 5). Habitat extent was highest in the GoM during spring throughout the 20th century, particularly in the 1960s. After 2000, however, habitat suitability decreased, particularly under RCP 8.5. In contrast, habitat extent for larval SKJ increased after 2000, particularly during summer and fall.

3.3. Spatial changes in habitat suitability

Habitat models generally predicted distributions of target species with reasonable accuracy for the early 21st century (present day) (Figs. 6, 7). Adult BFT were most common in the GoM and north of the Bahamas in winter and spring, and rare elsewhere except the farthest east portion of the study area in summer and fall. Larval BFT were only collected in spring, throughout the northern GoM, and also occasionally in the southwest GoM and far western CBN (Fig. 6). By 2090, under RCP 8.5, winter and spring habitat for adult BFT in the GoM was strongly reduced, including during the spring spawning season. However, suitable habitat remained east of the Bahamas in summer and fall.
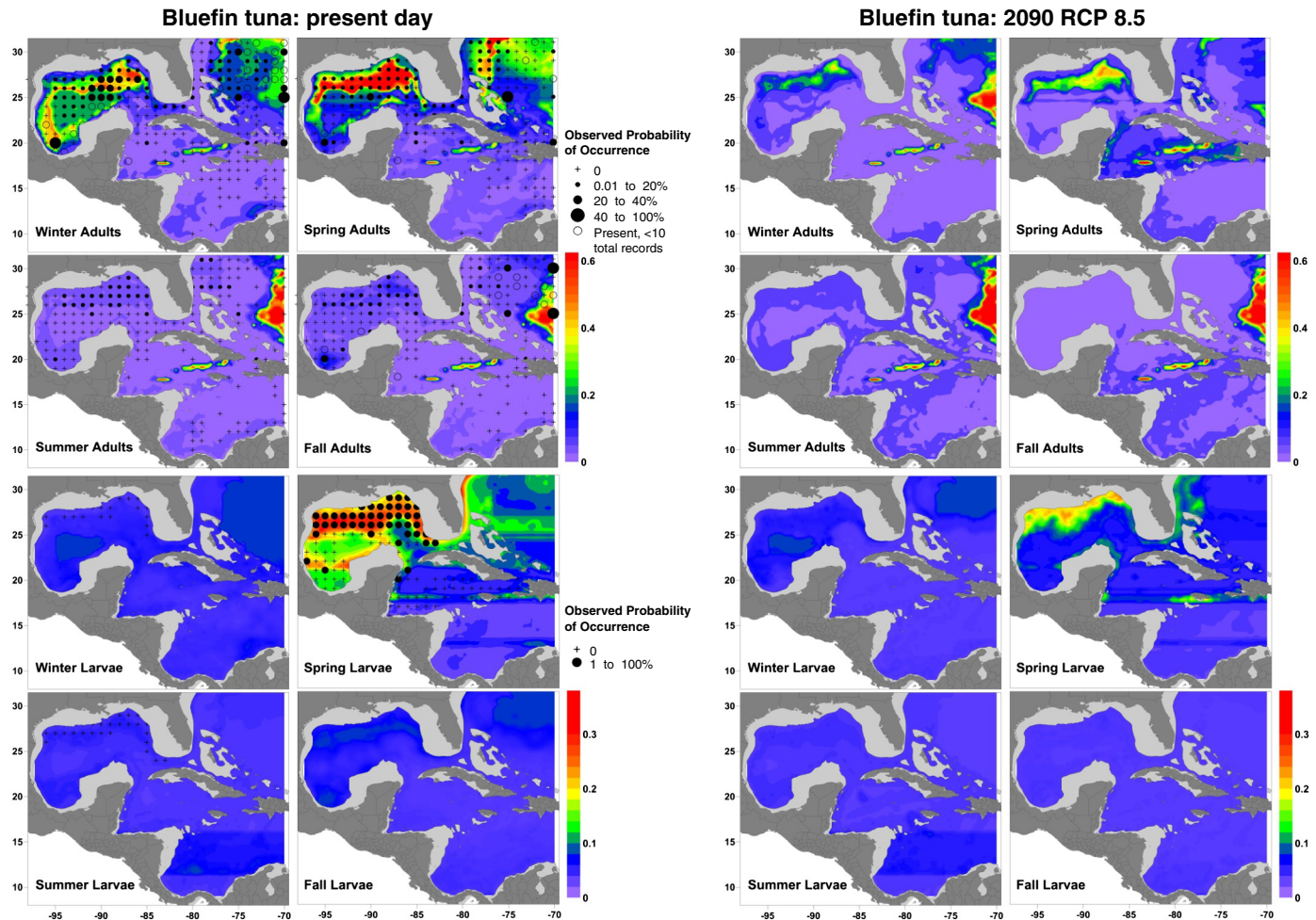

Fig. 6. Kriged predicted probabilities of occurrence for adult (1990 – 2009) and larval (2000 – 2013) bluefin tuna by season (contours). Results are shown for the 2000s, and for 2090, under RCP 8.5. Observed data from the ICCAT Task II database (adults) and SEAMAP plankton surveys (larvae) are also shown for the same time period (post maps). Locations where adults were recorded, but effort was low, are shown as open circles.
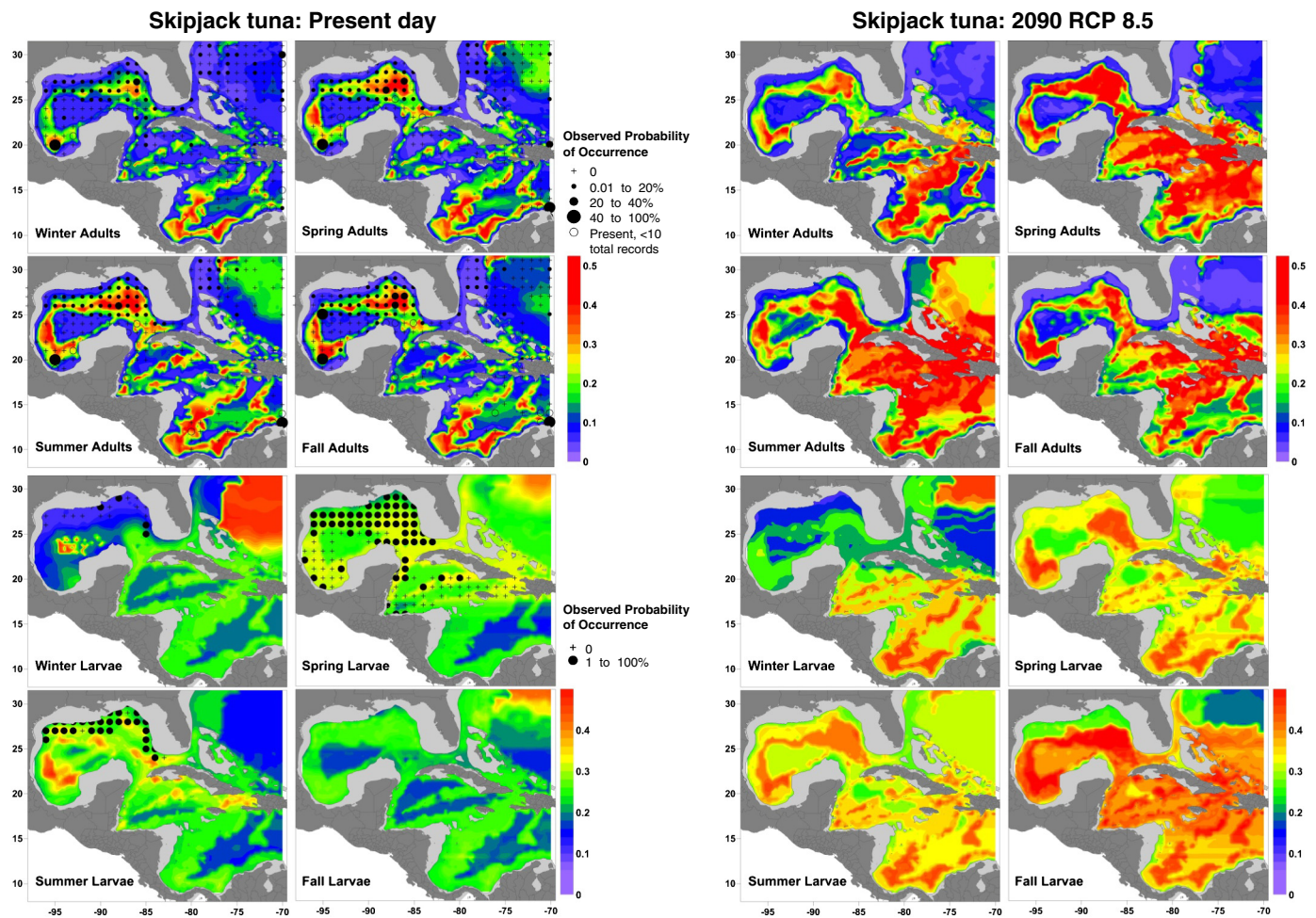
Fig. 7. Kriged predicted probabilities of occurrence for adult (1990–2009) and larval (2000–2013) skipjack tuna by season (contours). Results are shown for the 2000s, and for 2090, under RCP 8.5. Observed data from the ICCAT Task II database (adults) and SEAMAP plankton surveys (larvae) are also shown for the same time period (post maps). Locations where adults were recorded, but effort was low, are shown as open circles.

Probabilities of occurrence for larval BFT in the northern GoM during spring were also much lower by 2090 (Fig. 6).

Under present-day environmental conditions, adult SKJ were common throughout the GoM, with the exception of very deep waters in the central-western GoM, and shallower waters on the continental shelf (Fig. 7). Effort in the CBN was low, but some catches were recorded in this region in all seasons. SKJ larvae were rare in winter, but found at most sampled locations in the GoM in spring and summer. Limited collections in the CBN during spring also recorded SKJ larvae, suggesting that spawning is spatiotemporally widespread (Fig. 7). Ocean warming by 2090, under RCP 8.5, resulted in a general expansion of adult SKJ habitat in all seasons, particularly in the CBN. Predicted probabilities of larval SKJ occurrence also increased throughout the region (Fig. 7).

Model errors for adult BFT were generally low, reaching around 5% in regions of higher occurrence during the present day (Fig. 8). Under RCP 8.5, model errors decreased in the GoM, due to higher levels of certainty regarding responses to warm waters, but increased east of the Bahamas. Slightly higher probabilities of occurrence south of Cuba (Fig. 6) were also associated with higher errors. Model errors for larval BFT were fairly low in general (5–6%), and constant across the study area, except in the northern GoM during present day spring. In general, reductions in both larval and adult BFT on the northern GoM spawning grounds were associated with low model errors (<5%).

Errors for SKJ models were generally higher than for BFT (Fig. 9). The predicted increase in adult habitat in the CBN by 2090 was associated with error rates of >10%. The larval SKJ model showed the highest

rates of uncertainty, particularly in regions where habitat suitability was predicted to increase. In contrast, present-day favorable habitat in the GoM during spring was associated with lower model errors.

3.4. Habitat model comparison using downscaled vs. low resolution climate models

Predicted probabilities of occurrence for larval bluefin tuna in spring were slightly more favorable when temperatures were obtained from the downscaled climate model (0.25 × 0.25° resolution), as opposed to from the low resolution global climate models (1.0 × 1.0° resolution) (Fig. 10). The greatest difference was observed for RCP 8.5 in 2090, where the proportion of grid points in the northern GoM (north of 25°N) with predicted probability of occurrence >20% was 4.5% for the global model, and 11.0% for the downscaled model. The downscaled model under RCP 4.5 provided the most favorable habitats, and the low resolution model under RCP 8.5 the least favorable (Fig. 10).

4. Discussion

Results from this study suggest that larval and adult occurrences of BFT and SKJ can be fairly well predicted in the GoM and CBN using a combination of water temperature and depth. Adult BFT were rarely encountered during warmer months, except east of the Bahamas in cooler waters, while adult SKJ became more abundant from spring through to fall. Occurrences of both BFT and SKJ larvae increased as temperatures
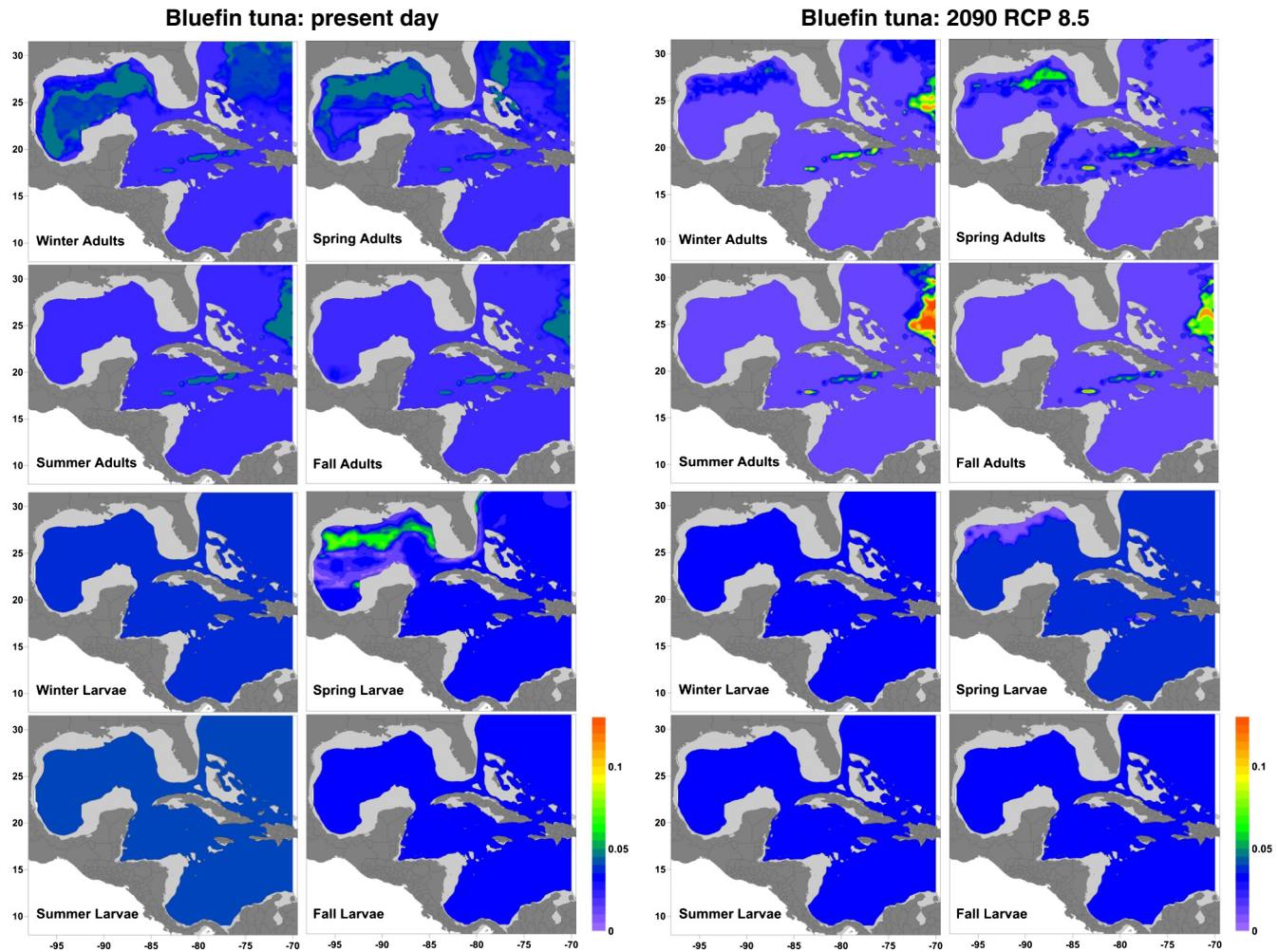
Fig. 8. Kriged model errors for adult and larval bluefin tuna by season. Results are shown for the 2000s, and for 2090, under RCP 8.5. Errors were determined from the predictive success of the boosted classification tree models at different habitat suitability levels.

warmed seasonally during spring, but while BFT larvae collections decreased at surface temperatures above 26 °C, SKJ larvae were most abundant in waters warmer than 29 °C. Spawning patterns for BFT were more typical of a temperate species, with a spatiotemporally restricted spawning window focused on the northern GoM during spring. In contrast, SKJ spawned across much of the year, and larvae were collected throughout the study region.

Adults of both species were associated with water depths of 2000–4000 m, with BFT also abundant in deep (>5000 m) waters north of the Bahamas. BFT have previously been associated with continental slope waters in the GoM, and may thermoregulate and feed by diving to ~200 m in this region (Teo et al., 2007). Larvae of both BFT and SKJ were most abundant where water depths were <4000 m.

Predicted effects of climate change into the 21st century were also distinct among the two species considered. Warming waters resulted in strongly decreased habitat extent for adult and larval BFT, with the major spawning ground in the GoM predicted to become highly unsuitable for either life stage by 2090, under RCP 8.5 (the most extreme scenario). Under RCP 4.5, declines in suitable habitat were slower; however the overall trend remained negative. A shift in spawning to earlier months of the year (i.e. winter) as temperatures warmed was not predicted. Muhling et al. (2011a) showed a similar result, whereby a slight gain in spawning habitat during March and April in the earlier 21st century was lost by the end of the century.

Conversely, effects of warming waters on SKJ were generally positive, with a predicted expansion of both adult and larval habitat through

to 2090. This increase in habitat was observed in both the GoM and CBN. However, habitat model errors for both adult and larval SKJ were greatest at warmer temperatures, suggesting a high degree of uncertainty with the magnitude of these predictions.

The lack of knowledge on relationships among environmental conditions, physiology and behavior in highly migratory fish species compounds this uncertainty. The general avoidance of warm water masses by adult BFT is fairly well documented (e.g. Teo et al., 2007), and is presumed to be related to temperature limits on cardiac capacity, resulting from their unique physiology (Blank et al., 2004). In contrast, much less is known about upper thermal tolerances of tropical tunas. Dizon et al., 1977 examined captive SKJ, and suggested an upper temperature limit of 33 °C. However, results such as these are difficult to apply to wild fish. Many published temperature "limits" inferred from observed distributions of tuna species use primarily or exclusively surface temperatures, largely because of its accessibility (e.g., Boyce et al., 2008; Collette and Nauen, 1983). This overlooks the ability of these species to utilize pelagic habitats in three dimensions. SKJ in the Pacific have been shown to dive to several hundred meters depth during the day (Schaefer & Fuller, 2007), and larger tunas such as BFT and yellowfin tuna dive even deeper (Block et al., 2005; Dagorn et al., 2006). The actual temperatures experienced by fish in any geographic location may therefore differ substantially from temperature at the surface. In addition, oxygen concentrations are strongly influential in determining temperature tolerances (Barkley et al., 1978; Blank et al., 2004), leading to altered diving behaviors and thermo-regulatory capacities in regions
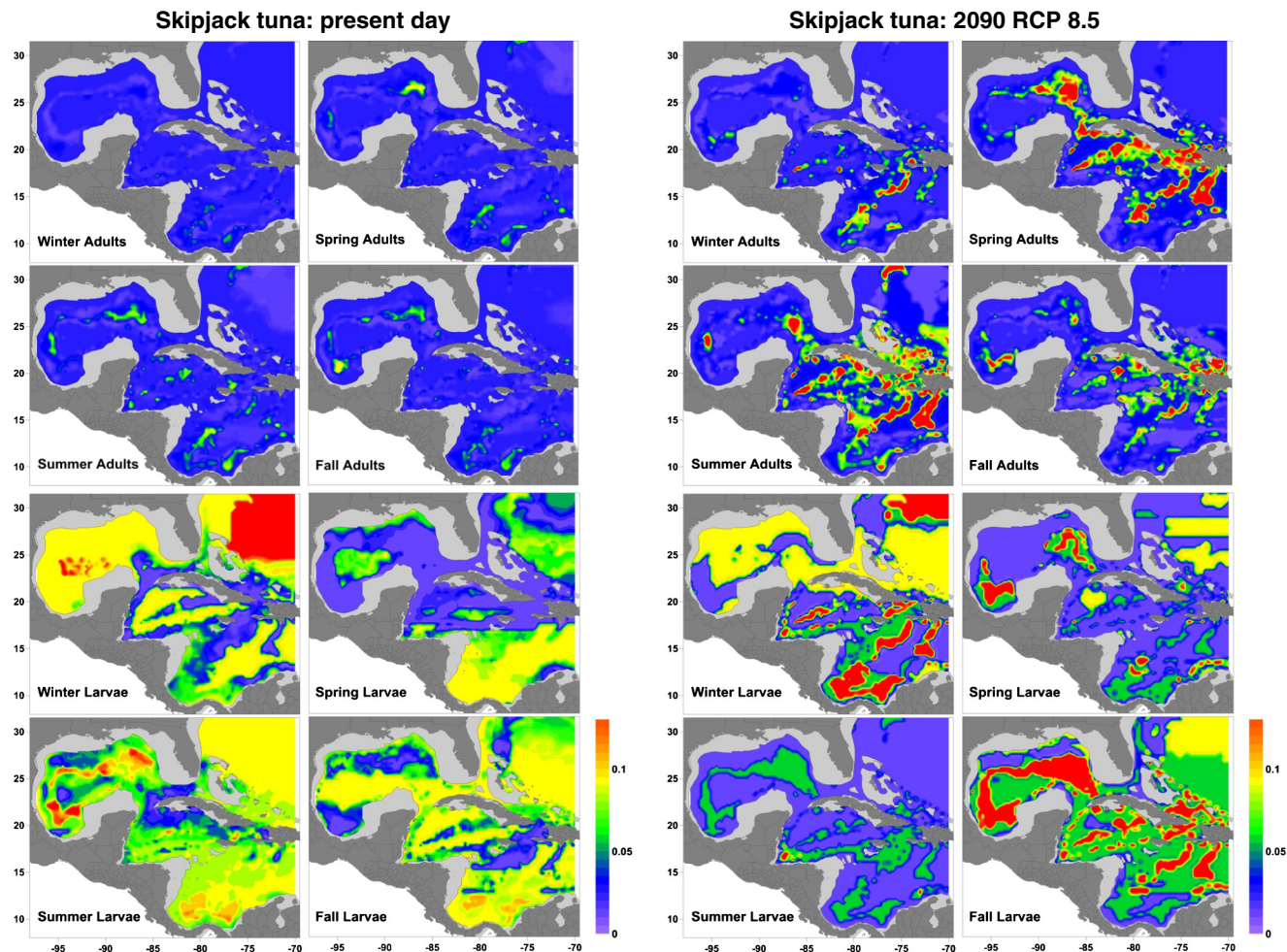
Fig. 9. Kriged model errors for adult and larval skipjack tuna by season. Results are shown for the 2000s, and for 2090, under RCP 8.5. Errors were determined from the predictive success of the boosted classification tree models at different habitat suitability levels.

with shallow anoxic layers (Prince and Goodyear, 2006). Lastly, the body size of many tunas and billfishes determines their thermal tolerances, with smaller fish generally more tolerant of warm waters, and less tolerant of cold (Barkley et al., 1978; Boyce et al., 2008; Brill, 1994). These factors, combined with complex heat-conserving mechanisms in tunas, make it difficult to ascertain exactly how stressful locations with particular temperature characteristics will be (Carey and Teal, 1969; Jusup et al., 2011).

As a result, predictions of thermal tolerances and climate change impacts tend to vary widely across different studies, even where the same species is considered. For example, Dueri et al. (2014) predicted an expansion of unsuitable habitat for SKJ in the equatorial Pacific under climate change, with surface temperatures of >31 °C considered unsuitable. Robinson et al. (2014) assumed a thermal maximum for SKJ of 30 °C, and also showed poleward shifts in habitat suitability off southeastern Australia. In contrast, results from this study suggest a general expansion of habitat for SKJ in the GoM and CBN. These differences are partially due to the different rates of projected warming among regions, partially due to the use of downscaled vs. global climate models, and partially due to the different values assumed for upper tolerance limits.

Assessment of the true upper thermal tolerance for SKJ and other tropical tunas is currently difficult, as they are captured in some of the warmest offshore waters currently found on earth. Data from this study show high observed probabilities of occurrence at surface temperatures from 29–31 °C. Higher resolution data from the United States pelagic longline fishery show catches of SKJ at surface temperatures of up to 31.7 °C, as determined from 8 day composites from the

Pathfinder 5.1 satellite dataset (NOAA NMFS, unpublished data). Downscaled model outputs show that mean July–September surface temperatures in the GoM may reach up to ~32.5 °C under RCP 8.5 by the end of the century. Realistic projection of future biological impacts depends strongly on definition of upper tolerance limits, and these are clearly not known with sufficient certainty for many species. Additional laboratory research combined with increased availability and use of tagging studies would help to reduce this uncertainty.

An additional source of error with predicting climate impacts on marine species is with the spatial resolution of global climate models (Stock et al., 2011). These models are generally too coarse to represent regional current systems, including the Caribbean Current and Loop Current in the IAS (Liu et al., this issue). A high-resolution downscaled model for the IAS suggests a general weakening of this regional current system, which is likely to slow future warming in the northern GoM, due to heat transport effects. This spatial heterogeneity is of direct relevance to the use of the GoM by temperature-sensitive fish species, such as tunas, and highlights the usefulness of developing regional climate models. Muhling et al. (2011a) examined habitat loss for larval BFT in the GoM using coarse resolution IPCC CMIP3 models, and predicted very low habitat suitability in spring by 2090. While results from this study also showed a significant decline in larval BFT habitat through to 2090, the decrease was somewhat less severe for the downscaled model vs. the global climate model ensemble, due to the slower rate of warming predicted by the downscaled model.

Another advantage to the use of regional models in this study was the availability of the 20th century experiments. These allowed us to
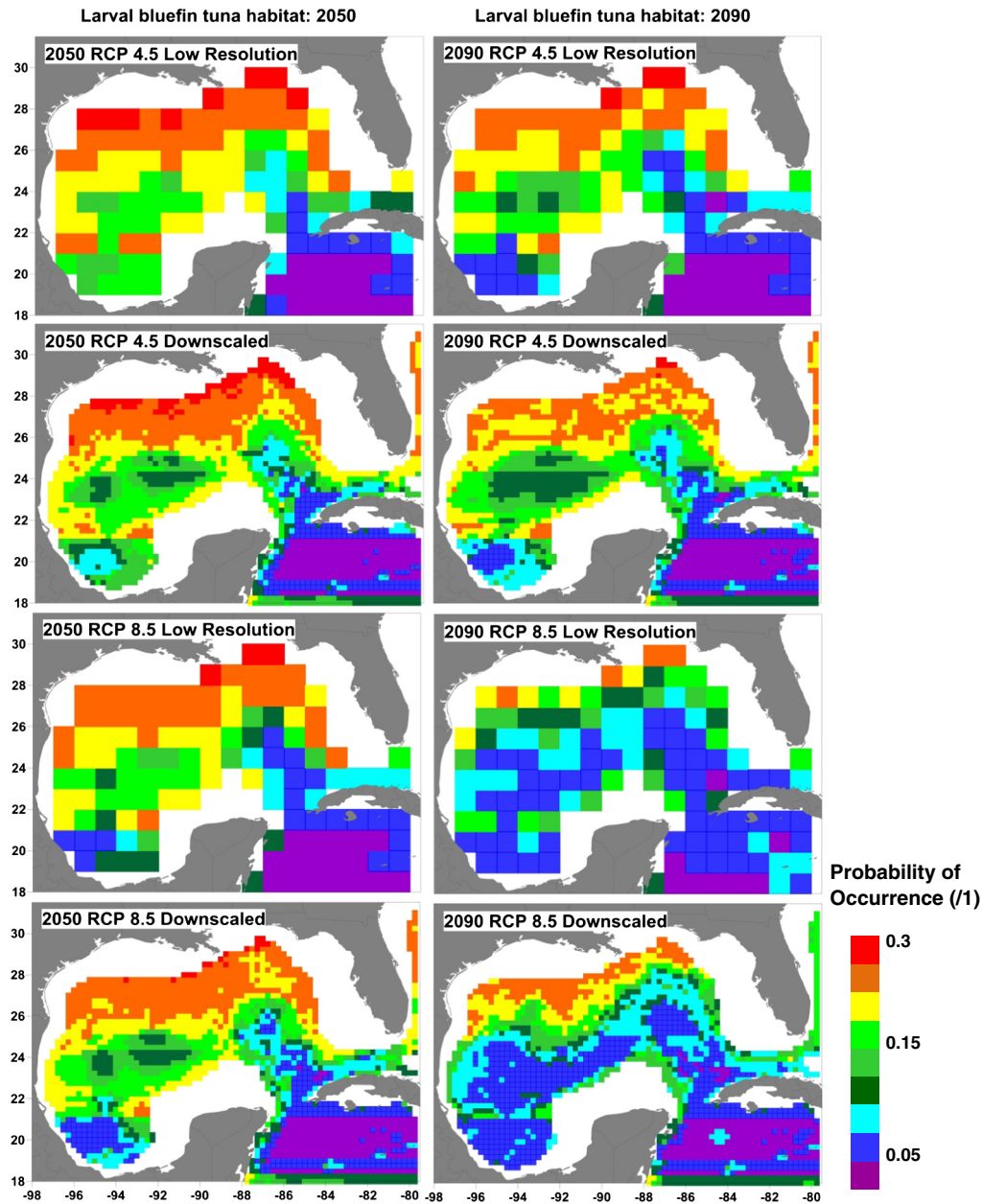
Fig. 10. Mean spring (April–June) probabilities of larval bluefin tuna occurrence compared between habitat models run on downscaled temperature data, and low resolution data from global climate models, interpolated onto a 1 × 1° grid (Liu et al., this issue).

place predicted future habitat changes into the context of past natural variability, and to consider the potential effects of natural variability on habitat fluctuations with climate change. As most extant scombrids evolved to their present forms between 3.8–1.8 million years ago during the Middle to Late Pliocene (Santini et al., 2013), these species have persisted through very different climatic regimes, likely with very different levels of productivity and abundance. However results from this study indicated that future changes in environmental conditions will quickly surpass those experienced within the 20th century, and lead to more rapid changes in habitat suitability for both BFT and SKJ than in the last 100 years, and likely throughout geological history.

Given that this rapid time limits the potential for genetic adaptation, the population-level impacts largely will depend upon the capacity to respond to habitat changes afforded by the phenotypic plasticity of the species (Reed et al., 2010). The loss of spawning habitat for BFT in the GoM may lead to utilization of alternative spawning grounds in the future, or increased use of currently marginal areas. Low numbers

of larval BFT have been collected north of the Bahamas and in the Yucatan Channel, suggesting some current use of other spawning areas (Muhling et al., 2011b; NOAA NMFS unpublished data). However, the near exclusive use of the GoM in spring for spawning by the western stock and the much more restricted spawning locations for the species complex worldwide (Reglero et al., 2014) suggest limited phenotypic plasticity for alternative spawning locations. In contrast, SKJ have much broader spawning distribution and may have greater capacity to respond. A key factor contributing to phenotypic plasticity is the presence of contingents (Secor, 1999) where some groups follow different behavioral or migratory patterns than the population as a whole. This may confer population resiliency by spreading life history strategies over the physiologically acceptable range of conditions. Identifying and protecting such contingents may be a key factor in allowing populations to respond to climate change.

In conclusion, results from this study suggested that climate change impacts on BFT and SKJ in the IAS will be significant but distinct.

Substantial habitat loss for both adult and larval BFT was predicted for the main spawning ground in the northern GoM as temperatures warm, while SKJ showed increasing habitat suitability throughout much of the study area. Despite multiple uncertainties in the modeling process, resulting from model inputs, fish physiology and life history traits, this field of study continues to be of substantial importance to understanding how species may respond to climate change and the resulting impacts on fisheries. While the exact impacts upon fisheries remain uncertain, such dramatic changes in habitat suitability are likely to challenge the equilibrium assumptions upon which management benchmarks such as maximum sustainable yield are based, and may alter the spatial or temporal availability of fish to fishing nations. The global importance of both BFT and SKJ motivate continued cross-disciplinary research to improve our understanding of how climate change will impact each species.

Acknowledgments

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